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Todd K. Shackelford
Viviana A. Weekes-Shackelford
Editors

Encyclopedia of Evolutionary Psychological Science

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With 277 Figures and 93 Tables

 Springer

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About the Editors



Todd K. Shackelford received his Ph.D. in evolutionary psychology in 1997 from the University of Texas at Austin. Since 2010, he is Professor and Chair of the Department of Psychology at Oakland University (<http://www.oakland.edu/psychology>) in Rochester, Michigan, where he is Co-Director of the Evolutionary Psychology Lab (www.ToddKShackelford.com). In 2016, he was appointed Distinguished Professor by the Oakland University Board of Trustees. He led the founding of new Ph.D. and M.S. programs (<http://www.oakland.edu/psychology/grad/>), which launched in 2012. Shackelford has published around 300 journal articles and his work has been cited over 22,000 times. Much of Shackelford's research addresses sexual conflict between men and women, with a special focus on men's physical, emotional, and sexual violence against their intimate partners. Since 2006, Shackelford has served as Editor of the journal *Evolutionary Psychology* (www.epjournal.net) and in 2014 founded the journal *Evolutionary Psychological Science* (<http://www.springer.com/psychology/personality+%26+social+psychology/journal/40806>) as Editor-in-Chief.



Viviana A. Weekes-Shackelford received her Ph.D. in evolutionary developmental psychology in 2011 from Florida Atlantic University. She currently teaches at Oakland University and is Co-Director of the Evolutionary Psychology Lab, along with her colleague and spouse Todd K. Shackelford. Her research over the years has been evolutionarily inspired and has had the broader goal of gaining a more comprehensive understanding of violence and conflict in families and romantic relationships. Her research interests and publishing record cut across the psychological domains of forensics, development, social, personality, clinical, and criminology. She teaches courses such as psychology of gender, evolutionary psychology, research methods, and statistics. Her most recent endeavor includes creating a podcast/YouTube channel (Darwinian Diva) that aims to reach beyond the walls of academia to share her passion for scientific exploration, to reinvigorate those already on the scientific exploration train, whether it's academics, grad students, undergrad students, other curious minds, and to lure in newbies that are looking for a new way of thinking about topics ranging from romantic relationships to parent/child relationships, from birth control to sexual control, and from the foods that satiate us to the thoughts that stimulate us.

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A

2D:4D

- ▶ [Digit Ratio](#)
- ▶ [John Manning](#)

A Man of Stature

- ▶ [Big Man](#)

Abhorrence

- ▶ [Disgust](#)

Ability and Willingness of Victim to Retaliate

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Synonyms

[Avenge](#); [Penalize](#); [Punish](#); [Revenge](#); [Strike back](#)

Definition

Action taken in return for an injury or offense.

Introduction

The concept of retaliation has historically been defined from both a behavioral and functional aspect. At its core, retaliation is based upon the premise of inciting organisms to increase benefit while reducing cost to oneself (McCullough et al. 2013). If a target organism can emit the potential ideal for retaliation toward an aggressor organism (typically in the form of retaliation itself), the target organism may increase its chances of lifetime productivity and may continue to evolve due to this willingness to retaliate. In other words, by making the potential costs of harm too high for an aggressor (imminent retaliation), the target organism is more likely to survive by avoiding harm against oneself.

Definitions that have previously influenced academics in the conceptualization of retaliation have typically been defined from a functional perspective. The *Oxford English Dictionary* defines revenge as both an act and a desire. To be more specific, Govier (2002) wrote “When we seek revenge, we seek satisfaction by

attempting to harm the other [persons] as a retaliatory measure” (p. 2). Additionally, Uniacke (2000) also noted that “revenge is personal and non-instrumental: with revenge we seek to make people suffer because they have made us suffer, not because their actions or values require us to bring them down” (p. 62). Finally, scholars within the social sciences have further defined retaliation as “the intention to see the transgressor suffer” (Schumann and Ross 2010, p. 1193) along with a plethora of definitions focused upon retaliation being offered as a response to a violation and/or infliction of harm upon a person or one’s property (Govier 2002). However, for this entry, the use of McCullough et al. (2013) definition will be used. They purport retaliation to be a “deterrence system designed to change other’s incentive regarding the self.” In other words, in order to survive, *Homo sapiens* have developed cognitive adaptations specifically designed to utilize the benefits of retaliatory behavior.

Evolutionary Benefit of Retaliation

Many scholars believe retaliation evolved for three adaptive purposes. First, the possibility of retaliations’ ability to directly deter would-be aggressors. Secondly, if an aggressor chooses to harm another individual, retaliation may be a source of penalization for the transgressor’s wrongdoing. Lastly, retaliation encourages societal cooperation by discouraging aggressors from taking advantage of other individuals within their societal unit.

Benefit of Direct Deterrence

As previously noted, the first benefit of retaliatory action developed within many species is the ability for an organism to alter an aggressor’s behavior and ultimately prevent initial and/or future incidents of harm. In other words, if the costs of harming another organism become too high (greater than the benefits), then an aggressor may reconsider his/her actions and desist his/her aggressive behavior (Govier 2002).

Specifically, some scholars purport the evolution and adaptation of retaliatory behavior as

a direct means to provide additional costs for individuals who may seek to engage in harmful behavior, therefore, directly deterring a would-be transgressor from targeting persons who are willing to provide retaliatory impositions. In other words, a victim who is willing to retaliate (i.e., economically, socially, legally) against his/her aggressor is less likely to experience initial or future harm due to the high cost victimization would require from the aggressor. Therefore, the adaptive retaliate systems provide the benefit of increasing lifetime productiveness for would-be victims (Govier 2002). Through direct deterrence, academics believe that when an aggressor has made the decision to inflict harm, an individual who has a history of retaliation or is believed to be willing to retaliate is less likely to be chosen as a potential victim (Schumann and Ross 2010). In other words, a potential victim’s willingness to retaliate may change an aggressor’s incentive to inflict harm.

Empirical evidence in concert with the concept of direct deterrence lies within economic games (i.e., sequential and iterated prisoner’s games) (Axelrod 1984). For example, in sequential games, only a single round of interaction is played with options of cooperation or defection being allowed. However, the second player in the round makes his/her move only after viewing the first player’s initial selection. Research indicates that the second player is more likely to make a defective choice if the initial player begins by choosing the same. Alternatively, if the first player makes the decision to cooperate as his/her first choice, the second player is also more likely to choose the choice of cooperation (Hayashi et al. 1999). In addition, iterated prisoner’s games involving multiple rounds of play either with the same partner or with different partners also found that inmates almost always counter defection with defection (Bixenstine and Wilson 1963).

Additional experiments within social psychology have also discovered the ability for retaliatory action to directly deter a potential aggressor. In a study conducted with undergraduate males, Diamond (1977) found that participants who believed they could harm their instigator without retaliation were more likely to provide stronger punishments

(shocks) to the individual whom they believed had wronged them. However, participants who believed their actions could be avenged after inflicting harm upon the confederate were not as quick to retaliate.

Further evidence in support of the potential for direct deterrence indicates that retaliatory behavior may also be incited by others known to the victim. For instance, a domestic violence study conducted in Madrid, Spain, concluded that women with more male relatives (especially located within close proximity) were less likely to be victims of domestic violence (Figueredo 1995). These findings are believed to result from a protective and retaliatory effect against harm. In other words, even if a victim is not willing to provide retaliatory behavior by his/her own hands, knowing individuals who may be willing to retaliate against an aggressor on behalf of a potential victim still increases the costs of exploitation/harm beyond any potential benefit allotted to the transgressor.

Benefit of Penalization for Wrongdoing

Secondly, retaliation as a source of penalization for wrongdoing has also been found to be psychologically beneficial for *Homo sapiens* victims. For instance, Adams (1965) found that participants reported feelings of distress when they felt treated unfairly or wronged by another individual. Therefore, the act of retaliation may result in a reduction in an individual's distress level if the individual believes equality to the situation can be restored. In addition to retaliation among *Homo sapiens*, retaliatory action has also been found to be a form of punishment among nonhuman organisms as well (Clutton-Brock and Parker 1995). In support of this ideal, Clutton-Brock and Parker (2005) believed that victim retaliation would produce productiveness gains for the avenging organism by reducing the likelihood that the aggressor would repeat the harmful actions to the organism in the future, thus, increasing a victim's odds for survival.

Benefit of Deterring Third-Party Aggressors

In addition to the potential benefits of direct deterrence and correcting wrongful action, retaliatory

behavior may also be beneficial in the deterrence of third-party aggressors. Scholars believe the expression of aggression by an individual which signals an avenger's potential for retaliation could potentially deter potential third-party aggressors. Historically, *Homo sapiens* have lived in small bonded units without the protection of larger governing bodies; thus, a reputation for a willingness to retaliate against interpersonal harms may have been a vital component to the protection of the unit (Govier 2002). Moreover, violence in the name of honor and the use of violent retaliation has historically been well documented by researchers (McCullough 2008; McCullough et al. 2013). Therefore, the reputation of retaliatory action appears to have been evolutionarily vital to the survival of the primitive family unit.

In concert with the premise of retaliation as an adaptive feature for the promotion of reputational concerns, cognitive studies have found the mechanisms associated with retaliation to be responsive in the presence of third parties. For instance, laboratory studies have found that victims retaliate more vehemently when third parties are present, communicate with the victim that he/she is aware of the injustice, and tell the victim he/she looks powerless as a result of the aggressor's actions (Kim et al. 1998).

Conclusion

Alternative to these three potential benefits associated with retaliation is the potential costs (for both aggressor and avenger) associated with avenging behavior. While retaliation may result from the intention to encourage cooperation, instances of counter-revenge and feuding have also been noted (Kim and Smith 1993). For instance, while an avenger may view retaliation as an equalization of intent, the initial transgressor may consider the action excessive and, thus, feel the need to retaliate against the avenger (Govier 2002). This form of revenge and counter-revenge may result in a perpetuating cycle of aggressive and/or violent behavior. Since retaliatory action may result in additional costs to an organism, individuals who feel they have been wronged

may seriously weigh both the potential costs and benefits before asserting retaliatory action. Due to the potential for further harm by an aggressor who feels the need for counter-revenge, the initial avenger may choose to reject personal retaliation and pursue additional legal channels to attain justice.

Cross-References

- [Altruism](#)
- [Altruistic Punishment](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)

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Ability to Recognize Individuals

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Synonyms

[Individual recognition](#), [Individual discrimination](#),
[Face recognition](#)

Definition

The ability to recognize individuals is a highly advantageous skill for social living species. Although not always clear, an important distinction in the literature is that between individual discrimination and individual recognition. Individual discrimination is the ability to differentiate one individual from all the rest, whereas individual recognition is the ability to differentiate each individual from every other individual and is the most precise form of recognition (Beecher 1989). This entry discusses the evidence for the recognition of conspecific individuals in nonhuman animals, specifically through the auditory and visual systems.

Introduction

Studying nonhumans provides important insight into the evolution of human sociocognitive skills,

such as individual recognition. As in human societies, most social species live in groups that are structured by kinship, dominance, and reproductive status (Smuts et al. 1987), making the ability to recognize others critical to navigating their social world. Animals may use olfactory, auditory, behavioral, or visual cues to recognize others. As much of the research has been conducted in the auditory domain, research on vocal recognition is first discussed briefly. Then, because most social living animals, particularly mammals (including humans), are highly reliant on vision, the majority of the text will focus on recognition within the visual domain.

Of course, there are many different types of recognition, including the recognition of one's own species, kin recognition (see entries on ► [“Kin Recognition”](#) and [“Kin Classification Systems Support Kin Recognition”](#) for more information), the recognition of familiar versus unfamiliar individuals, individual recognition, the recognition of sex, age, and so on. Individual recognition is the most precise form of recognition. Therefore, the discussion will center on individual recognition within one's own species or the ability to discriminate one particular individual from every other conspecific individual. Individual recognition underlies many sociocognitive processes, facilitates group cohesion, and is prerequisite for more complex behaviors such as reconciliation (see ► [“Reconciliation”](#)). This implies that there was strong evolutionary pressure in group-living species to individually recognize others and remember those with whom they have interacted.

This entry will focus on the nonhuman primate (NHP) literature because we ourselves are primates and, thus, the majority of research on individual recognition in animals has focused on NHPs (although see section [“Face Recognition in Non-primates”](#) for evidence in other species). Moreover, some researchers have posited that social problems may have been the most cognitively complex problems that humans may have faced in our recent evolutionary history, and this may help explain our large brain to body ratios compared to the rest of the animal kingdom (e.g., Byrne and Whiten 1988). Thus, NHPs provide us with the opportunity to study the evolutionary

function of human sociocognitive skills and visual perception within a comparative framework. Studying other NHPs allows us to determine whether a particular trait is shared with humans due to common evolutionary history (i.e., homology) or due to shared evolutionary pressures (i.e., convergence).

Auditory Recognition

A large portion of the research examining the ability to recognize individuals has been conducted in the auditory domain, primarily through playback experiments in which researchers record naturally occurring vocalizations and then play the prerecorded stimuli back to subjects in order to gauge the subjects' responses to novel situations or in order to reproduce events that may occur naturally. Playback experiments designed to help elucidate the ways in which NHPs classify each other have found evidence that NHPs recognize their infants, more distant kin, and their neighbors (e.g., Cheney and Seyfarth 1990; Rendall et al. 1996).

For instance, a study conducted on wild vervet monkeys (*Cercopithecus aeithiops*) played the scream of a 2-year old juvenile in the presence of its mother and two other adult females (who had offspring of their own) while they were separated from their offspring. The mother of the juvenile responded more quickly than control mothers, looking and approaching the speaker from which the call originated, indicating that vervet monkeys recognize their infant as distinct from other infants. Furthermore, it was noted that the control females responded by looking at the infant's mother, often before the mother made any movement. The anticipatory behavior of the control females suggests that they recognized the relationship between the screaming juvenile and its mother (i.e., third party relationship; Cheney and Seyfarth 1990).

Other evidence in the auditory domain indicates that the ability to recognize individuals may go beyond immediate kin. Rendall and colleagues (1996) first found that adult female rhesus macaques (*Macaca mulatta*) responded faster and

looked longer towards the origin of matrilineal kin calls compared to non-kin, suggesting that they were able to discriminate the calls of matrilineal kin from non-kin. Following this, they implemented a habituation-dishabituation paradigm to test for individual recognition. In this paradigm, subjects typically experience a series of habituation trials during which an exemplar of the stimulus class is repeatedly presented, in this case, various calls of one matrilineal relative. Following habituation, the test stimulus of either the same or different class is presented, such as the call of a second matrilineal relative. A significant difference in response (dishabituation), such as a longer looking time, is taken as evidence that the subject judged the two types of stimuli as different. Following habituation in this study, females responded significantly more to the call from the second matrilineal relative, suggesting vocal recognition at the individual level.

There is also evidence that vocal recognition may extend beyond the boundaries of the group. For example, vervet monkeys reacted more strongly to the calls of individuals from a neighboring group when the calls originated from an inappropriate territory compared to when the calls originated from within the groups' typical territory. This implies that the monkeys had expectations about where those individuals should be (Cheney and Seyfarth 1990).

Many of the studies described above have been taken as evidence for individual vocal recognition. However, for individual recognition to take place, subjects must not only recognize a call as familiar but also perceive that it belongs to a specific individual (Beer 1970). Although it is certainly possible that individual recognition occurred in the aforementioned studies, subjects may have categorized the vocalizations at a more general level rather than identifying each of these individuals specifically. For instance, mother-offspring recognition may simply involve discrimination between one's own offspring from all others. This should be considered discrimination, rather than individual recognition. Moreover, the discrimination of one's own offspring or kin from all others may occur through signature cues such as family specific acoustic cues.

Likewise, the recognition of group mates may simply involve the discrimination of familiar versus unfamiliar vocalizations. In the case of the vervet monkeys, vocal recognition of neighbors may reflect an association between a familiar neighbor's sound and its familiar location.

Thus, while these studies present behaviors that seem to indicate individual recognition, controlled laboratory studies that manipulate the exposure to stimuli allows researchers to better evaluate the importance of particular features and how such information is organized in the brain. To date, however, the majorities of laboratory studies have focused on how animals perceive, process, and organize nonsocial information. The few experimental studies that have employed social stimuli to examine how animals acquire complex social knowledge have primarily been conducted in the visual domain (although intermodal studies are notable exceptions, e.g., Adachi and Hampton 2011).

Visual Face Recognition in Nonhuman Primates

Much of the research on visual recognition has employed two-dimensional photographs as experimental stimuli in place of real-life objects to assess human and nonhuman sociocognitive processes. The use of photographic stimuli is more reliable than presenting real objects or individuals because it allows researchers to manipulate subjects' exposure to social information, helping rule out alternative hypotheses. Moreover, the use of photographs provides controlled investigation of image qualities such as brightness, contrast, viewpoint, and so forth. A number of studies have used indirect measures, such as looking time duration or habituation-dishabituation procedures, to examine individual recognition in the visual domain; however, some have used more objective measures, requiring subjects to make a direct response in the task. Although studies that require an objective response from subjects tend to require more extensive training, these studies provide conclusive results for individual recognition, particularly the perception and recognition of faces. Faces are

a highly salient class of visual stimuli as they provide primates, both human and nonhuman, and perhaps other species as well (discussed below) with valuable social information such as the age, sex, individual identity, and the emotional state of others (for reviews see Bruce and Young 1998; Leopold and Rhodes 2010; Parr 2011). Thus, the ability to individually discriminate faces and use the information present in faces likely played an important role in primate evolution.

Neurological Evidence

Within the primate order, the majority of neurological, developmental, and behavioral research suggests a common evolutionary route for the visual recognition of faces. First, growing evidence indicates that at least some species of non-human primates possess a face processing system that shares similar neural underpinnings with humans. From a large body of behavioral and neurological data, we know that humans possess a specialized mechanism for face processing (see Tsao and Livingstone 2008, for a review). Functional magnetic resonance imaging (fMRI) studies in humans have revealed a system of face-selective areas in the inferotemporal (IT) cortex that are involved in face recognition, including (but not necessarily limited to) the fusiform face area (FFA), the occipital face area (OFA), and an area of the superior temporal sulcus (STS-FA). These areas may be specialized for different functions. For example, the FFA is thought to be involved in processing identity, whereas the OFA is involved in processing face parts and the STS-FA appears to respond selectively to emotional expression and eye gaze and therefore is thought to be involved in the processing of changeable aspects of the face (Tsao and Livingstone 2008).

Electrophysiological studies in rhesus macaques have found regions in the rhesus macaque brain similar in number and relative size to those in humans. Neurons in the STS of the temporal cortex respond to a variety of human and monkey faces, changes in facial expressions, eye gaze, and facial orientation (Tsao and Livingstone 2008). These findings suggest certain

homologies between cortical areas in the human and monkey brain suggesting a common neural mechanism for face recognition in primates. Although this may be true for at least some primate species, it is unclear whether a common face-processing system exists for all primates. That is, a basic structure from which species specializations may have evolved.

Behavioral Evidence

The behavioral evidence for a common face recognition system among primates has been mixed. For instance, it is unclear to what degree NHPs rely on second-order configuration, which refers to the relative spatial arrangement of facial features unique to each individual that are thought to provide the information necessary for individual face recognition in humans. Humans incorporate both the basic configuration of the components of a face (i.e., the eyes, which are above the nose, which are above the mouth), or first-order configuration cues, and second-order configuration cues (e.g., the relative spacing and positioning of facial features) into a single perceptual whole through a fast-acting process referred to as holistic processing. This is exemplified by the inversion effect, in which humans are slower and less accurate in recognizing faces (but not objects) when they are presented in an upside-down orientation compared to an upright orientation, due to the disruption of holistic processing (Valentine 1988). Holistic processing (and the inversion effect) is often taken as evidence that face processing is different from nonface object processing in that faces are represented as a whole rather than as a combination of component parts (eyes, nose, mouth) and the relations between them.

Yet, behavioral evidence of the inversion effect in NHPs is mixed. In chimpanzees (*Pan troglodytes*), the inversion effect seems to be dependent upon expertise, such that chimpanzees demonstrate the inversion effect for human and chimpanzee faces but not capuchin faces or cars (Parr 2011; see also Tomonaga et al. 1993). However, this does not seem to be the case for monkeys (Parr 2011). Thus, it is possible that the inversion effect may reflect one facet of face processing (i.e., holistic processing) that is an adaptive

specialization of the face recognition system of apes and humans, yet further work is needed to rule out the possibility that differences in methodology contributed to inconsistent results. Comparative research on the inversion effect outside the primate order would also be helpful in elucidating the role of holistic processing in face recognition abilities.

On a more general level, behavioral research on NHPs' ability to individuate conspecific faces have provided relatively consistent results. One of the most direct ways to evaluate NHPs' ability to individuate faces is to present them with a task in which they must match the same individual across different viewpoints. This task helps rule out the possibility that subjects are relying on irrelevant perceptual features specific to each photograph, such as symmetry or lighting, to discriminate the stimuli and thus provides additional evidence that face recognition is distinct from basic visual processing. Accordingly, positive results obtained from studies employing paradigms that require direct responses from subjects are generally accepted as evidence for individual recognition (see Parr 2011, for a review). Using this type of methodology, all of the species tested thus far, including chimpanzees, orangutans (*Pongo* spp.), rhesus macaques, crested macaques (*Macaca nigra*), and capuchin monkeys (*Cebus apella*), have demonstrated the ability to discriminate conspecific faces (Micheletta et al. 2015; Parr 2011; Talbot et al. 2015, *in press*).

Previous studies typically examined this ability using unfamiliar faces; however, many of the more recent studies have included familiar facial stimuli as well. The majority of these studies have found differences in performance based on familiarity, suggesting that experience with, exposure to, and the familiarity of faces may play a critical role in influencing face recognition. In humans, changes in lighting, facial expression, or viewpoint of the facial stimuli impair the ability to recognize unfamiliar, but not familiar, faces (Bruce and Young 1998). Likewise, chimpanzees, orangutans, and capuchin monkeys all performed better when individuating familiar conspecific faces across viewpoints compared to unfamiliar

conspecific faces (Parr 2011; Talbot et al. 2015, *in press*). However, one Old World monkey, the crested macaque, discriminated familiar and unfamiliar faces equally well (Micheletta et al. 2015).

The fact that this effect has been observed in New World monkeys, but not Old World monkeys, which are more closely related to Hominoids (apes), suggests one of three possibilities. First, it may have been present in the common ancestor of Hominoids and New World primates but was subsequently selected against in Old World primates. However, this seems improbable given the presumed benefits of recognizing familiar individuals and because traits tend to be preserved in all of the descendants of a common ancestor unless there were strong selective forces working against the trait. To date, we have been unable to identify such a pressure in Old World monkeys.

A second possibility is that the familiarity effect is a convergent trait of the face-processing system, affected by selective social pressures, with species that live in larger, more complex social groups exhibiting greater nuances in face perception. However, this seems unlikely for several reasons. First, crested macaques live in large multi-male, multi-female groups of up to 100 individuals, whereas tufted capuchins groups are significantly smaller, ranging in the teens to low twenties in size. Second, orangutans, a species that only recently became a primarily solitary species, also exhibit the familiarity effect (Talbot et al. 2015), suggesting that once the effect is established, there does not seem to be sufficient selective pressure for losing it. It may be that the face recognition system evolved in the primates and is maintained despite the diversity in social group size and organization, indicating that current group size or organization is not the key feature.

A third possibility is that differences in methodology may have impacted results. The classic methodology for experiments requiring training calls for the use of novel test stimuli to be presented a limited number of times. In tests of individual recognition, therefore, each individual should only be presented once or twice in order

to evaluate any potential differences in spontaneous discriminations as a function of familiarity with those individuals, not the test stimuli themselves (Talbot et al. [in press](#); Thompson 1995). However, in the NHP face recognition literature, there is a trend to adapt a loose definition of “novel,” in part due to the scarcity of high-quality photos that met criterion for testing. For example, new photos of the same individuals observed in training are often used during testing, and/or subjects are repeatedly presented with the same stimuli. Although this is a difficult standard to achieve, the novelty of both the photos and the novelty of the individuals represented in those photos is imperative for a true transfer test. Otherwise, it is impossible to rule out nonconceptual factors, such as memorization of the training stimuli, to explain subjects’ performance. Overall, current evidence indicates that despite apparent differences among species, the familiarity effect is nonetheless a widespread phenomenon observed in many species that exhibit individual recognition.

Developmental Evidence

Much evidence shows that faces are highly salient social stimuli for humans and NHPs from a very early age. Infants orient more towards face-like patterns compared to nonface-like patterns (Pascalis and Kelly 2009). These “face-like patterns” can be as simple as three dots arranged in a triangular fashion, reflecting the basic arrangement of the eyes above the nose, which is above the mouth, which is referred to as first-order configuration. First-order configural cues are important for identifying faces at the categorical level, that is, discriminating faces from nonfaces. Both human and NHP infants demonstrate a preference for faces even when they have never seen a face. In a particularly telling study, infant Japanese macaques (*Macaca fuscata*) raised in an enriched, but face-deprived, environment for 6–24 months demonstrated a preference for both human and monkey faces over other complex visual stimuli, indicating an innate preference for first-order configural cues (Sugita 2008).

Still, other developmental evidence corroborates the importance of familiarity and the role of

exposure on individual face recognition. In particular, evidence suggests that early exposure to faces during a critical developmental period may fine-tune cortical networks to become specialized for the prototypical face to which an individual is exposed. Following a face-deprivation period, infant Japanese macaques preferred to look at and selectively discriminated the species that it was first exposed to (either human or conspecific faces). Likewise, 6-month old human babies discriminated both human and monkey faces, but at 9 months of age, they only discriminated human faces. These results elucidate the role of experience in the development of the “species-specific effect,” which has been likened to the “other race effect” in which it is easier to recognize members of one’s own ethnic group or species, or, perhaps more accurately, to the prototypical face to which one is frequently exposed (see Pascalis and Kelly 2009, for a review).

There is evidence in humans and NHPs that the species-specific effect and the other-race effect can be reversed with appropriate experience. For example, a classic study found that rhesus macaques exhibited a species-specific effect in which they discriminated conspecifics, but not domestic animals, yet after several months of exposure to the domestic animals, the macaques could discriminate them as well (Humphrey 1974). Korean children reared exclusively with Koreans and later adopted by Caucasian families between the ages of three and nine demonstrated the same own-race effect as Caucasians exhibit as adults, suggesting that this effect may be reversible with experience (Sangrigoli et al. 2005). Moreover, children as young as 3 months old demonstrated the other-race effect, yet, short-term exposure to other-race stimuli was sufficient to cancel this effect (Sangrigoli and Schonen 2004). Taken together, these studies suggest that experience with and exposure to faces greatly influences face processing both within and across species. In addition, there may be a critical period during early developmental during which the face processing system undergoes perceptual narrowing, but with appropriate exposure this is reversible to a certain extent.

Face Recognition in Non-Primates

Face recognition is by no means limited to the Primate order, but compared to human and NHPs, less is known about whether other animals discriminate and process faces and the underlying cognitive and neural processes by which they may do so. Although the literature on individual recognition in non-primate species is still relatively nascent, growing evidence across the animal kingdom suggests that individual recognition and face recognition, in particular, may not be as rare as once thought.

Similar to humans, sheep (*Ovis aries*) prefer conspecific faces to heterospecific faces, and familiar faces to unfamiliar faces. Using facial cues alone, sheep discriminated between different species, and, within their own species, the breed and sex of conspecifics. Sheep can learn to discriminate individual faces of adult sheep and can remember up to 50 familiar faces over a period of 2 years. However, individual discrimination is poorer on young lambs and unfamiliar individuals. Moreover, sheep rely on configural cues for the recognition of familiar faces, like humans and most NHPs. Neurological evidence suggests that primates and sheep may share similar neural pathways. The temporal cortex of the sheep brain contains cells that respond selectively to faces compared to other visual stimuli. The responsiveness of particular categories of these cells varies based on dominance (the size of horns), familiarity, breed, and potential level of threat (see Tate et al. 2006, for a review). Collectively, these studies provide strong evidence for a similar face processing system in sheep and primates, with the notable exception that particular groups of face-selective cells have specialized functions that are of social and ecological relevance to each species.

In birds, much of the evidence for visual individual recognition is tangential. For instance, rooks (*Corvus frugilegus*) are social corvids that live in large colonies and form long-term social bonds, suggesting that they have a strong possibility of recognizing group members individually (Emery et al. 2007). Yet, evidence of individual

recognition in this species is lacking. Bird and Emery (2008) presented rooks with a strongly affiliated conspecific and an unfamiliar conspecific through multiple modalities (including live, video, and static images) and found that rooks preferred to look at their affiliated conspecific over an unfamiliar conspecific when videos and live stimuli were used. From this evidence, the authors concluded that rooks recognize the individuals in the video. However, this should not be taken as evidence of individual recognition as the rooks may simply be discriminating familiar from unfamiliar individuals, a considerably less precise form of recognition. Perhaps the most convincing evidence of individual recognition in birds comes from budgerigars (*Melopsittacus undulates*). Budgerigars discriminated conspecific faces from heterospecific faces and discriminated between conspecific faces, suggesting individual discrimination (Brown and Dooling 1992, 1993). While evidence demonstrating that multiple views of the same individual were perceived by budgerigars as the same individual would provide more conclusive for individual recognition, like the other species discussed, conspecific face recognition in budgerigars appears to be reliant on configural processing, as subjects processed faces in their normal configuration more efficiently than inverted faces or faces with scrambled features.

Most fish live in stable social groups or shoals throughout their lives and demonstrate behaviors that are indicative of social intelligence (see Bshary 2011 for a review). For instance, stickleback fish will not cooperate with individuals who have previously cheated in dangerous predator inspections, suggesting individual recognition and memory of conspecifics. Yet the means by which recognition occurs is poorly understood. Olfactory and chemical cues are likely modes of communication in an aquatic environment as water typically aids the dispersal of such cues; however, recent work suggests the importance of visual cues, particularly facial cues, in more precise forms of recognition in fishes. A recent study found that African cichlid fish (*Neolamprologus pulcher*) discriminated familiar individuals from

unfamiliar individuals using facial features (i.e., color patterns) alone (Kohda et al. 2015). Moreover, two species of damselfish (*Pomacentrus amboinensis* and *P. moluccensis*) use ultraviolet facial patterns for species discrimination and potentially for individual recognition as well (Siebeck et al. 2010). However, more research needs to be done in order to confirm that fishes individually discriminate conspecifics using these distinctive facial cues.

Some species of paper wasps, like the Northern paper wasp (*Polistes fuscatus*), exhibit highly variable facial and abdominal color patterns, which are used to individually recognize their nest-mates. Sheehan and Tibbetts (2011) compared the face learning abilities of *P. fuscatus* and *P. metricus*, a closely related species that does not possess elevated phenotypic variation like *P. fuscatus* and has not been shown to individually recognize conspecifics. *P. fuscatus* more accurately and quickly discriminated pairs of normal conspecific and heterospecific faces compared to manipulated face images (composed of the same colors and patterns of normal faces) and nonface images, whereas *P. metricus* did not. This suggests that the specialization for face learning in paper wasps is not based on general pattern or shape discrimination and it is not due to species-specific variability in faces. Furthermore, morphological measurements demonstrate that *P. metricus* has more acute vision than *P. fuscatus* ruling out the possibility that differences in visual acuity may explain the results. Thus, specialized face learning in paper wasps appears to be a cognitive adaptation that likely evolved in response to social pressures as *P. fuscatus* colonies are founded by multiple queens and exhibit a linear dominance hierarchy, whereas *P. metricus* typically nest alone (Sheehan and Tibbetts 2011).

Conclusion

Many animals possess the ability to visually discriminate conspecifics. Collectively, these studies strongly suggest that a face-processing system is

not human, or even primate, specific. Current evidence suggests that individual recognition may be a cognitive adaptation that evolved convergently in response to ecological and social pressures. Some species (e.g., sheep and NHPs), currently appear to have more complex forms of recognition, which indicates that recognition may have evolved in a stepwise fashion with more general forms of recognition (e.g., species discrimination) emerging before more precise forms (e.g., individual recognition). It seems likely that certain aspects of face perception, such as the preference towards orienting towards simple face-like patterns or even particular features of the face such as the eyes as this was imperative for predator detection, may share a deeper evolutionary history, whereas, other, more specialized facets of face perception, such as the use of second-order configural cues, may have evolved more recently during primate evolution, explaining its presence in humans and apes but not consistently observed in monkeys. Further work in a variety of species that vary in terms of sociality, ecology, and evolutionary history will clarify which facets of face perception result from homologous or convergent processes.

Cross-References

- [Face and Object Recognition](#)
- [Individual Discrimination](#)
- [Kin Recognition](#)
- [Prosopagnosia \(Face Recognition\)](#)
- [Reconciliation](#)

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Abnormal Fears

► Phobias

Aborticide

► Abortion

Abortion

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Synonyms

Aborticide; Foetal death; Loss of conceptus

Definition

Early pregnancy loss can be described comprehensively as “a disturbance in pregnancy occurring before the period of fetal viability resulting in expulsion or retention of pregnancy” (Daftary and Chakrvarti 2007). The expulsion or extraction of the fetus or embryo weighing less than 500 g (20 weeks of gestation) from the uterus, spontaneous or induced, is called abortion (FIGO 1976).

Introduction

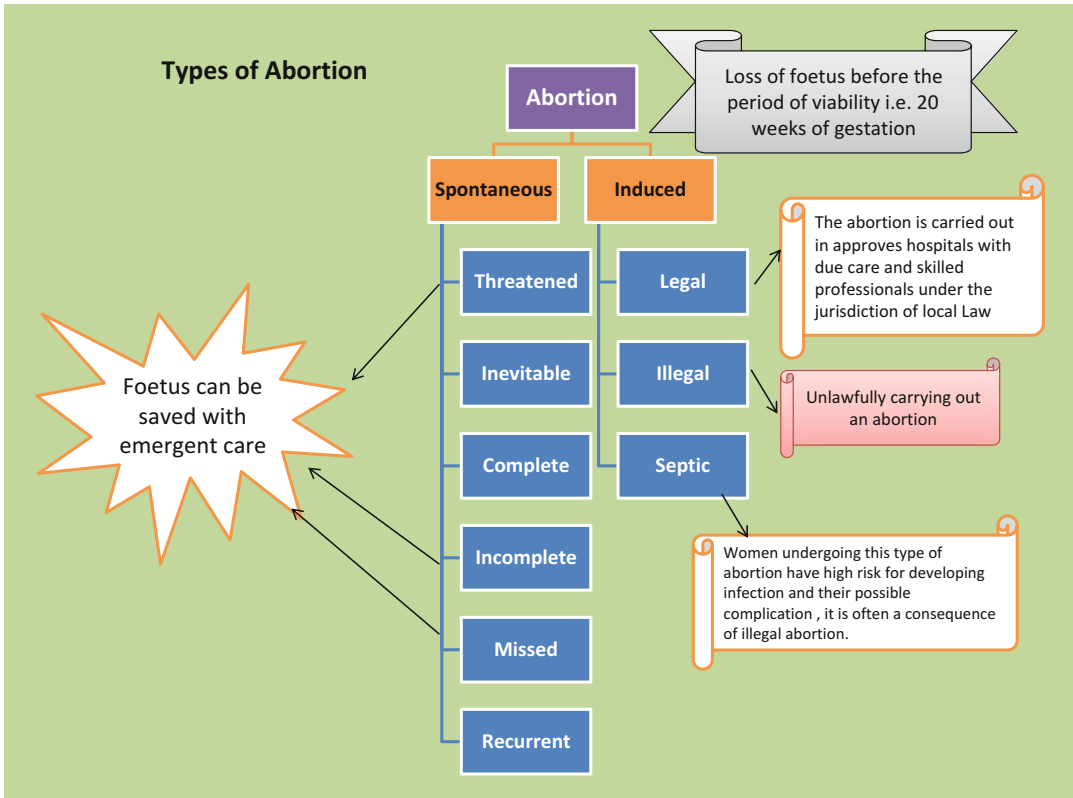
Motherhood is arguably one of the best feelings in the world. A joy for women to bring new life into the world, but pregnancy comes with its share of challenges. Abortion is one of the most dreaded outcomes of “pregnancy.” The primary manifestation of abortion is vaginal bleeding; it occurs in up to 25% of pregnancies prior to 20 weeks (Myles et al. 1993). It is a major cause of anxiety for all women, especially those who have experienced previous pregnancy loss and may be the presenting symptom of life-threatening conditions, such as ectopic pregnancy. Bleeding should always be considered as abnormal in pregnancy and investigated appropriately (Myles et al. 1993).

Incidence

There has been a significant decline in the rate of abortions compared to the 1990s in the developed

countries, but the developing countries still present with great number of abortions. The reported number of abortions are significantly less in number than the ones that occur (Sedgh et al. 2016). A recent multicentric study reported that there has been a significant decline in the number of abortions from the past millennia to the present times. Concern about the condition and quality of the services related to abortion pose a great concern throughout the world (Bearak et al. 2019). The worldwide incidence reported was 35 abortions per 1,000 (90% uncertainty interval 33–42) women within 1 year of reproductive age. Within the time period of 1990–2010, it was observed that the developing countries showed no significant decline in the number of abortions (only 2 points from 1990 to 2014 [39 (37 to 47) to 37 (34 to 46)] calculated with an uncertainty interval of 90%). It was also found that 73% of the abortions were sought out by married women, and 27% was obtained by unmarried women. In this same study, it was also reported that globally 27% of pregnancies ended up in abortions (Sedgh et al. 2016).

As of 2010–2014, an estimated 36 abortions occur each year per 1,000 women aged 15–44 in developing regions, compared with 27 in developed regions. The abortion rate declined significantly in developed regions since 1990–1994; however, no significant change occurred in developing regions (Sedgh et al. 2016). By far, the steepest decline in abortion rates occurred in Eastern Europe, where use of effective contraceptives increased dramatically; the abortion rate also declined significantly in the developing subregion of Central Asia. Both subregions are made up of former Soviet Bloc states where the availability of modern contraceptives increased sharply after political independence – exemplifying how abortion goes down when use of effective contraceptives goes up (Bearak et al. 2019). Abortions occur as frequently in the two most-restrictive categories of countries (banned outright or allowed only to save the woman's life) as in the least-restrictive category (allowed without restriction as to reason) – 37 and 34 per 1,000 women, respectively (Sedgh et al. 2014). In much of the world, 20–24-year-old women tend to have the highest



Abortion, Fig. 1 Types of abortion

abortion rate of any age-group, and the bulk of abortions are accounted for by women in their 20s (Sedgh et al. 2016).

The World Health Organization (WHO) estimated that worldwide 210 million women become pregnant each year and that about a third of them or approximately 80 million end in miscarriage, stillbirth, or induced abortion. More than 40% of women will have miscarriage some time in their reproductive life. Approximately 20% of all pregnancies end up in miscarriages (spontaneous abortion), and about 80% of these occur in the first trimester, within 2–3 months of gestation (WHO 2018).

Types of Abortion

Threatened Abortion

A clinical entity where the choriodecidual hemorrhage (the process of abortion) has begun, but

not progressed to the stage of irreversibility. The cervix is not open, and the products of conception are not expelled (Fig. 1).

Clinical Features

The woman will present with the history of amenorrhea (no monthly bleeding) for more than 6 weeks. Currently bleeding which is fresh and scanty. Mild uterine cramps and backache (sometimes painless bleeding). Signs of early pregnancy like morning sickness, vascularization of the vagina, etc. will be present. On vaginal examination, cervix will feel soft with the os closed.

Investigations

A hemoglobin estimation of the blood to determine severity of bleeding needs to be done. A per abdominal or transvaginal ultrasonography to determine the gestational sack. A urine pregnancy test to confirm the hCG positivity. Blood test for

serum hCG may be serially done to determine any abnormality in the doubling time, which could indicate the possibilities of survival.

Treatment

The only aim in the treatment is to extend maximum support to the pregnancy in order to increase chances of survival of the pregnancy. Hospitalization and complete bed rest until bleeding stops. Hormonal supportive therapy, hematinics, laxatives, and sedatives if required. The patient is advised to continue treatment, restrict activity, and avoid lifting any heavy weight. Sexual intercourse is best avoided as long as the risk for fetal loss remains (Dutta 2004).

Inevitable Abortion

In this type of abortion, the process of abortion has begun and progressed to such an extent that expulsion of the products of conception seems inevitable.

Clinical Features

The woman will present with the history of a variable period of amenorrhea along with vaginal bleeding with passage of fresh blood and clots and pain due to uterine contractions and cervical dilation.

Signs

A clinician will observe pallor, cold, clammy extremities, tachycardia, hypotension, and on per vaginal examination it will reveal; cervix will feel soft to firm and bulky, corresponding to the period of gestation.

Investigation

A blood group and cross matching test along with several blood tests are needed to determine the condition of the woman. Ultrasonography may be needed to confirm the expulsion or residue for the products of conception.

Management

As pregnancy is unavailable, it is terminated. The method of evacuation of the uterus depends on the duration of pregnancy. General treatment includes resuscitation with intravenous fluids and

cross matched blood if required. If pregnancy is less than 12 weeks, suction and evacuation is performed. The duration of the pregnancy is more than 12 weeks, intravenous oxytocin or (uterotonic) PGF_{2α} is administered, and spontaneous expulsion is awaited (Jacob 2012).

Prophylactic immunization of tetanus toxoid, antibiotics, and intramuscular 50 µg anti-D, if the mother has an Rh-negative blood group, has to be given to prevent complications after this abortion. Ultimately the examination and histopathology of the products to ascertain any recognizable pathology.

Complete Abortion

Complete abortion can be described as a condition in which products of conception are expelled out completely from the uterus, and the uterine cavity is empty.

Clinical Features

The woman presents with the history of variable period of amenorrhea followed by lower abdominal pain, vaginal bleeding with passage of products, and followed by a decrease in the bleeding and pain. A vaginal discharge that usually subsides in a week.

The clinician may observe substantial vaginal bleeding during the course of abortion; the patient may be in a state of circulatory collapse.

Investigations

Per abdominal ultrasonography confirms that the abortion is complete, and the cavity is empty.

Management

Medical management is usually conservative. Sedatives, hematinics, tetanus toxoid, anti-D (in Rh-negative mothers), and methergine are given (Dutta 2004). Rarely, curettage may be necessary if the bleeding continues or the USG reveals products in the uterine cavity. The family and friends are asked to support the woman in recovery of physical and psychological nature.

Incomplete Abortion

In the incomplete variety, the abortion has occurred but the process is incomplete. The

cervical os is open and the products of conception are partly expelled.

Incomplete abortion can be presented by a history of amenorrhea, vaginal bleeding, continuous or recurrent passage of fleshy mass per vagina, and severe lower abdominal pain of colicky nature. Clinician may observe pallor, signs of shock, products of conception may be felt in the cervical canal or vagina an open internal Os, uterus feeling soft on examination.

Management

The patient is resuscitated if in shock with intravenous fluids and blood if required. Dilatation and curettage to empty the uterus using blunt curette under general anesthesia.

Missed Abortion

In missed abortion the fetus is dead and retained inside the uterus for a variable period of time. Woman shall present with the history of amenorrhea, with lower abdominal pain accompanied with vaginal bleeding or brownish discharge and spotting, and with subsidence of the pregnancy symptoms.

The sign and symptoms reported clinically presented by, uterine size felt smaller than the period of amenorrhea. On examination per-vaginum the cervix is felt soft with internal closed internal os open, and retrogression of breast changes.

Investigation

Urine test for pregnancy becomes negative. Ultrasonography per abdomen shows loss of gestational sack, and Doppler examination reveals absence of fetal heart sound.

Management

Patients suffering from incomplete abortion can be managed by a gynecologist by a procedure called dilatation and curettage to prevent infection. The expelled products are examined to ensure completeness. The women can also be advised to take injections of tetanus toxoid and Anti D Antibodies, in such cases (Daftary and Chakrvarti 2007).

Recurrent Abortion

Spontaneous and recurrent abortion occurring consecutively on three or more occasions is called

habitual abortion. It may be primary or secondary, if it occurs after the birth of viable babies.

Etiology

The etiological factor for recurrent abortions can be divided into two main categories; *maternal* and fetal. Maternal cause include systematic disorders such as syphilis, diabetes mellitus, chronic nephritis, essential hypertension, and Rh incompatibility. Hormonal problems like progesterone deficiency, polycystic ovarian disease (PCOD), and thyroid dysfunction can also be contributing factors. Structurally cervical incompetence has been a very common cause of abortions. Developmental abnormalities of uterus such as bicornuate uterus and septate uterus and for some idiopathic causes (Daftary and Chakrvarti 2007) contribute to recurrent abortions. *Fetal* causes are mainly chromosomal defects.

Investigations

The causes for recurrent abortions need to be investigated very thoroughly (Jacob 2012), and pregnancy should be planned and monitored under specialist supervision.

Management

Management of such case require a lot of interventions at various levels. Counselling of the couple to alleviate anxiety is a very essential and effective strategy. Surgical correction of uterine abnormality if possible and genetic counselling as indicated should be carried out. women who suffer from hormone deficiencies are also advised to take hormonal therapies to prevent abortion.

Induced Abortion

Induced abortion refers to the deliberate termination of pregnancy prior to fetal viability. In India, induced abortion was legalized as health welfare measure under the Medical Termination Of Pregnancy Act (MTP Act). This law permits the termination of pregnancy for selected indications.

The specified indications for induced abortion are as follows.

Criminal Abortion

Criminal abortion refers to abortions performed by quacks (untrained and unauthorized persons) often in insanitary and unhygienic conditions leading to increase morbidity and mortality as a result of complications such as traumatic injuries, infection, incomplete evacuation, and hemorrhage. In India, women used to resort to quacks to procure abortions of unwanted pregnancies resulting in loss of young lives. This prompted the government of India to adopt the MTP Law as a health welfare measure to prevent the practice of criminal abortions (Dutta 2004).

Septic Abortion

A type of abortion associated with sepsis of the products of conception. There is increased association of sepsis in illegal induced abortion because of (1) improper antiseptic measures, (2) incomplete abortion, and (3) inadvertent injury to the genital organs and adjacent organs (Payne et al. 2018).

A septic abortion can have associated bacterial infections of the following types:

Aerobic: *Escherichia coli*, *Pseudomonas*, β -hemolytic streptococci, and *Enterococcus faecalis*.

Anaerobic: *Bacteroides*, *Clostridium*, *Neisseria gonorrhoeae*, and *Chlamydia trachomatis* are also possible pathogens.

Septic abortion is usually a dangerous condition if ignored and may lead to life-threatening complications and lead to maternal mortality.

Diagnosis

Septic abortion can be identified by the following manifestations:

History of recent termination of pregnancy (by unauthorized person).

Variable period of amenorrhea along with high fever, chills and rigors, vomiting, diarrhea and diffuse abdominal pain.

Foul smelling vaginal discharge, which is often purulent, accompanied by vaginal bleeding and history of passage of products of conception per vagina.

The woman shall present with the signs of pallor and sweating, pyrexia, tachycardia and decreased blood pressure, features of toxemia, general abdominal rigidity, guarding and/or tenderness, abdominal distension, and ileus (Jacob 2012).

Investigations

Detailed investigations case specific of blood and associated viscera must be performed.

Management

It is important to notify the police whenever a criminal abortion is suspected. Patient is admitted to the hospital. Shock is to be treated aggressively. Antibiotics and evacuation of uterus under anesthesia are usually employed. In severe cases (Udoh et al. 2016), oxygen 6–8 L/min IV crystalloids and plasma expanders are used to manage the condition conservatively.

Challenges and Issues Regarding Abortion

Abortion is often not regarded medically as “serious” and is usually not investigated further when it occurs for the first time. As a result many women do not receive an explanation of their loss (Bearak et al. 2019). There is no evidence to associate abortion with an overall increased risk of psychiatric morbidity. However, feelings of anger, grief, and guilt are common, and almost half of all women are considerably distressed at 6 weeks following abortion (Melese et al. 2017).

Women who lose pregnancies in the second trimester face the same risk of postpartum “mood disorder” as women in the normal puerperium. Grief reactions are usually more severe and may persist for up to 6 months following the loss of their pregnancy (Melese et al. 2017).

These reactions often create vulnerability toward developing psychological maladaptation

leading to predisposition of the women going through the phenomenon.

Global Efforts and Legislature About Abortion

Abortion being one of the most important areas and also a condition affecting the health status of any country, there have been global efforts to understand the extent of the issue and the legal aspects of this phenomenon (Johnson et al. 2018). A global database for abortion policies has been established. Their latest findings reported that only 32% of the countries allow abortion on the request of the women without the need for justification. About 82% of the countries allow abortion to save the life of a woman, 64% of countries have been allowing abortion on the grounds of physical and psychological health, and 51% allow abortion on the grounds of fetal condition, and 46% allow women to undergo abortion if the pregnancy is a result of rape (Johnson et al. 2018). This gives us a picture of the phenomenon globally; India has a legislation regarding the MTP Act (Medical Termination of Pregnancy), which allows women to access safe abortion services in government and private facilities since 1971 which had also been amended on various occasions resulting in increased access and low cost safe abortion services in India (Singh et al. 2018).

Conclusion

Abortion is a traumatic event in a woman's life, but it is also a nature's mechanism of preventing major genetic and other abnormalities from occurring in the offspring if it occurs naturally or an indication of other serious issues in the health of the mother and the unborn child. This chapter deals with abortion in brief; there are a lot of causes that can be related to the mother and the fetus which contribute to abortion. The effects of abortion are very varied, effecting all spheres of life of the woman as well as her family. Abortion is associated with hormonal and physiological and psychological changes. It also depletes the mother's health reserves and can also contribute

to difficulties and other aspects of her life. Abortion also has a profound social effect, which in some cultures enhances the woman's difficulties in multiple folds. There have been attempts by the governments to provide women with perks of additional medical leaves up to 6 weeks post abortion to help them build up their lost strength. This is a progressive step towards gender sensitivity. Still there are nations making abortions illegal, which is a great threat to a woman's choice of having a child. There is necessity to build up consensus worldwide to provide access to women for medical care of abortion, safe abortion services, and effective contraception post abortion to build the health and economy of women.

Cross-References

- [Maternal Abandonment and Maternal-Fetal Conflict](#)
- [Miscarriage](#)

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Absence of Events to Distinguish True Friends

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Synonyms

Events; Friends; Friendships; Reciprocal altruism

Definition

The evolutionary perspective argues that we have evolved to monitor events that would help identify true friends. These events are usually harsh or unfavorable, which are absent in our safer and more stable modern environments.

Introduction

Friendship confers many adaptive benefits that aid survival and reproduction (Buss 1989; Lewis et al. 2011; Tooby and DeVore 1987), especially when one successfully distinguishes true friends from fair-weather ones. However, with modern environments and tools, it is challenging to discern the different types of friends. This current entry reviews the benefits of friendship and outlines how modern context influences our evolved psychology in identifying true friends.

Benefits of Friendships

Ancestrally, friendships provided humans with benefits that aided survival (Cosmides and Tooby 1992; Lewis et al. 2011; Tooby and DeVore 1987). Being in groups allowed hunters to work together when hunting large animals (Baumeister and Leary 1995). Hunting together as a team yielded nutritious food with lower rates of deaths and injuries (Buss 2016; Tooby and DeVore 1987). They were also able to share food resources (Buss 2016; Hill and Kaplan 1988; Lewis et al. 2011), and this was especially important as food was a scarce resource in the ancestral past (Buss 2016). Having friends also provided the opportunity to form alliances, which was critical in times of conflict as their loyalty and support were vital in emerging victorious (DeScioli and Kurzban 2009). Moreover, since conflicts in hunter-gatherer societies predominantly revolved around fighting over resources, having a group of friends would not only have allowed one to win but also served to prevent conflicts (Bukowski et al. 1994; DeScioli and Kurzban 2009; Tooby and DeVore 1987). Recent

studies have also shown that having friends decreases mortality risk (Giles et al. 2005; Holt-Lunstad et al. 2010).

Apart from facilitating survival, friendships also provided mating opportunities for both men and women (Lewis et al. 2011). Opposite-sex friendships can potentially develop into romantic relationships, especially since people seek the same attributes in opposite-sex friends as they would in a mate (Buss and Schmitt 1993; Lewis et al. 2011). Developing friendships with individuals of the same sex also conferred mating benefits. Men tend to befriend other men who are more resourceful as this desirable trait of resourcefulness – that women have evolved to prefer in men – would be “transferred” to themselves, thus boosting their success in mating (Lewis et al. 2011; Vigil 2007). Likewise, with the evolved preference of men for physical attractiveness, women gravitate toward befriending other physically attractive women in order to reap the benefits of being around higher-quality men (Buss 1989).

From an evolutionary perspective, human psychology and behavior are products of evolved psychological mechanisms – adaptations that have developed over time as a result of successfully solving recurrent survival and reproduction problems. With the survival and reproductive benefits humans have enjoyed by having friends, natural selection would have favored mechanisms that motivated us to seek and develop friendships.

Events and the Identification of True Friends

According to the theory of reciprocal altruism, altruistic tendencies toward friends develop when benefits are reciprocated (Cosmides and Tooby 1992; Trivers 1971). However, not all friends provide benefits or reciprocate in times of need. As a hunter-gatherer, if one mistakes a fair-weather friend for a true friend, they would face costly outcomes that would threaten their survival (less so in reproduction) (Tooby and Cosmides 1996). For instance, when a hunter-gatherer is cornered by predators or enemies,

fair-weather friends were not likely to offer their aid in order to ensure their own survival. This would have resulted in a lower chance of survival for that attacked individual. Hence, we have developed mechanisms that allowed us to deal with the adaptive problem of friendship mimicry, specifically to monitor clarifying events that would allow us to distinguish our true friends from fair-weather ones (Tooby and Cosmides 1996).

Unfavorable events provide humans with the opportunity to assess the extent of a friend’s engagement in an individual’s physical and social welfare, in other words, allowing one to gauge the genuineness of the friendship (Tooby and Cosmides 1996). Help rendered during harsh times, particularly when a cost may be incurred, was especially meaningful as such help is likely to be critical for survival and reproduction.

In ancestral times, hunting was conducted in large groups as success rates were low and was too risky to do be done alone (Tooby and DeVore 1987). This allowed men to come together to share hunting-related skills (Lewis et al. 2011) and build alliances (DeScioli and Kurzban 2009), which were opportunities to foster friendship. More importantly, it allowed men to identify those who would offer help when it became dangerous.

Women spent a significant amount of time on childcare and gathering plant food (Lewis et al. 2011; Silverman et al. 2007). These activities provided an opportunity for helping and tending to offspring, and, consequently, friendships develop over the emotional closeness that grew during these activities (Ackerman et al. 2007; Lewis et al. 2011). Such deep engagements, as coined by Tooby and Cosmides (1996), promoted genuine friendships.

The Absence of Events in the Modern Environment

Modern environments, which are safer and more stable than those from ancestral times, lack such clarifying events that allowed humans to assess the genuineness of friendships. The absence of

those opportunities that allowed humans to foster deep mutual dependence leaves people with low confidence of their social bonds, consequently leading to more people to feeling lonely despite having social contacts (Tooby and Cosmides 1996). Moreover, advances in technology are transforming the way friendships are formed, especially with social media.

Social Media

With social media, one makes friends easily – it can be as straightforward as sending a friend request (Mahmood and Desmedt 2012). Mahmood and Desmedt (2012) created a fake Facebook account, and across 285 days, 62% of their friend requests were accepted by strangers, and the account received 6.67 times more requests from strangers in latter 185 days. People can also be “unfriended” on social media and not be notified of it (Sibona and Walczak 2011). In the event of unhappiness, usually expressed via a social media post, “help” from “friends” on these platforms is usually sent in the form of virtual hugs or likes. Hence, as much as social media facilitates connection with like-minded people, there is a significant lack of cues we have evolved to monitor in this platform to assess the genuineness of friendship. The presence of novel cues in social media, such as virtual hugs, only serves to hijack our assessment of true friends as our brains and mechanisms have not evolved to process such novelties (Li et al. 2018).

Cosmopolitan Societies

Friendship is similar to kinship (Ackerman et al. 2007). Hence, apart from clarifying events, friendship can develop when kinship indicators, such as familiarity and similarity, manifest through behaviors, such as mutual grooming and dressing, are present (Park and Ackerman 2011). However, in modern cosmopolitan societies, it is common for multiethnic individuals to live together (Kanazawa and Li 2015). This, again, is a novel phenomenon as humans lived in ethnically homogenous groups in ancestral times (Oppenheimer 2004). As kinship indicators allowed one to identify friends (Christakis and Fowler 2014), the differences that exist among

multiethnic individuals in a cosmopolitan society would mean that one will have a harder time doing so. Moreover, any individual who looked, spoke, and behaved differently would not have been from one’s group ancestrally. Our brains process people of different ethnicity to be potential threats – similar to ancestral environments (Kanazawa and Li 2015). Therefore, friendship forged within the context of the modern cosmopolitan society may not be as strong as the ones that were forged among humans in the ancestral times.

Conclusion

Friendship is a significant aspect in the lives of humans over the course of evolutionary history. Having facilitated the chances of survival and reproduction, we have evolved several mechanisms that allowed us to seek and develop friendship. However, not all friends are engaged in ensuring our physical and social welfare; fair-weather friends behave similarly to true friends when circumstances are good but are less likely to extend their help in times of need, leaving us vulnerable to threats. Therefore, we have evolved to monitor behaviors in clarifying events to deal with the adaptive problem of discriminating true friends from fair-weather friends. Ancestrally, these events are harsh in nature, and having friends who helped, especially when it could involve some cost to the individual, was especially meaningful.

However, our modern environment lacks the events that once provided humans with the opportunities to foster deep engagements and social bonds. Additionally, with the recent advancement in technology and globalization, it is becoming increasingly difficult to identify true friends despite the expanded opportunities to meet like-minded others through social media or the multiethnic cosmopolitan society we live in. Further research using the evolutionary approach of the *mismatch theory* (Li et al. 2018) and the *savanna-IQ* hypothesis (Kanazawa 2009) should be done to investigate novel cues in the modern context that would allow us to tease apart true friends from fair-weather ones.

Cross-References

- Fair-Weather Friends Versus True Friends
- Friendship and Modern Life
- Opposite-Sex Friend
- Same-Sex Friend

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Absence Prior to Puberty

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Synonyms

Age of menarche; Father absence; Reproductive maturation

Definition

How absentee parents during early life shape developmental trajectories (i.e., reproductive timing)

Introduction

A large body of research has shown associations between features of childhood family environment and aspects of well-being in adolescence and adulthood (Belsky et al. 1991; Brumbach et al. 2009; Chang and Lu 2018; Mendle et al. 2009; Rickard et al. 2014; Simpson et al. 2012). One such widely replicated finding is that girls who grow up in father-absent households reach reproductive maturity (usually indexed as age at menarche) at younger ages than girls who reside with their fathers (Belsky et al. 1991; Ellis and Essex 2007; Gaydosh et al. 2018; Mendle et al. 2009; Tither and Ellis 2008). Earlier female reproductive maturation, in turn, has been implicated in a number of downstream health consequences such as higher risk for developing cardiovascular disease (Prentice and Viner 2013), reproductive cancers (Gong et al. 2013), and negative psychosocial outcomes (e.g., sexual delinquency, anxious, and depressive symptomology) (Belsky et al. 1991; Mendle et al. 2019). Thus, the causes of variation in the pacing of female reproductive maturation are noteworthy from a public health perspective. Evolutionary social scientists have tested hypotheses, deduced from an

adaptationist approach, accounting for observed patterns in this variation. Recently, the very existence of a consistent causal link between father absence and early menarche has become controversial in light of concerns about methods, analytical procedures, and the range of human populations sampled in this research (see Sear et al. 2019; Sohn 2017). In this article, we review the history of research on effects of parental absence (usually, but not exclusively, father absence) on reproductive development. We also describe critiques of this work and avenues for future research.

Life History Theory

Life history theory (LHT; MacArthur and Wilson 2001; Pianka 1970) concerns trade-offs faced by organisms with respect to energy allocation. The three most general trade-offs are somatic effort (growth plus maintenance) versus reproductive effort, mating versus parenting effort (the two subtypes of reproductive effort), and quality versus quantity of offspring (Stearns 1989, 1992). A slower LH strategy prioritizes somatic effort over reproductive effort, parenting effort over mating effort, and offspring quality over offspring quantity. A faster LH strategy prioritizes the opposite energy allocations. Rates of extrinsic mortality are thought to be the principal driver of LH variation, with higher rates selecting for a faster LH. As a framework for studying human individual differences, LHT generates hypotheses about the covariation of developmental, physiological, psychological, and social traits, as well as hypotheses about their causal antecedents (Del Giudice et al. 2015). For example, increased impulsivity and decreased prosocial motivation are expected to co-vary as psychological components of a faster LH strategy. Early age at menarche (a form of prioritizing reproductive effort over somatic effort) has long been hypothesized as fast LH indicator (Rushton 1985). However, given the multi-decade duration of the human female reproductive lifespan, interindividual differences of a few years in age at menarche contribute only modestly to overall LH trajectory (Del Giudice 2018).

Psychosocial Acceleration Theory

Independently of research programs applying LHT to human individual differences, Draper and Harpending (1982) developed a model of the facultative calibration of reproductive strategies by the environmental cue provided by father presence or absence. They argued that father absence reliably signals to a child that in his or her social setting, short-term mating relationships, entailing little paternal investment, are both normative and adaptive. Belsky, Steinberg, and Draper (1991) built on this work by situating father absence as just one component of a broader construct, early childhood affective experience within the family, that was hypothesized to channel psychosocial development and reproductive strategies (e.g., preference for short-term vs. long-term mating relationships) in adaptive directions. *Psychosocial acceleration theory* was the name given to the causal link between harsh early environment and earlier maturation. Chisholm et al. (1993) explicitly integrated LHT with psychosocial acceleration theory, arguing that affective features of early environments serve as reliable cues of local death rates. Thus, father absence and other contributors to harsh early affective environments (e.g., rejecting, insensitive parenting) set children toward a faster LH trajectory. The foregoing brief intellectual history highlights the independent origins of psychosocial acceleration theory and the LHT-informed study of human individual differences and their eventual integration (Belsky 2012; Belsky et al. 2015; Black et al. 2017; Chang and Lu 2018; Chisholm et al. 1993; Del Giudice and Belsky 2011; Ellis et al. 2009, 2012; Ellis and Essex 2007; Richardson et al. 2018; Rickard et al. 2014).

Reviewing and synthesizing available behavioral and endocrinological evidence, Ellis (2004) concluded that father absence accelerates girls' pubertal development, whereas greater parent-child warmth and parental marital quality delay it. Contrary to the competing energetics theory of pubertal timing, earlier menarche is not associated with greater lifetime reproductive success. Since 2015, researchers have debated the roles of *biometric* and *psychometric* LH indicators in

hypothesis building and testing (Baldini 2015; Copping et al. 2017; Del Giudice 2019; Figueredo et al. 2015; Nettle and Frankenhuys 2020; Sear 2020; Zietsch and Sidari 2019). A subset of these debates concerns the uncertain associations between age at menarche (a purely biometric LH indicator) and age at sexual debut (which is partly a function of psychological traits). For example, Richardson et al. (2018) found evidence to suggest that temporary father departure in an otherwise intact family predicted earlier age of menarche, and earlier age at menarche predicted earlier sexual debut, but there was no direct causal path between temporary father departure and age at sexual debut.

Criticisms and Debates in Literatures

In recent years, the universality of the relationship between father absence and onset of reproductive maturation has been questioned. Here we highlight three sources of controversy: demonstrating causality from cross-sectional data, representativeness of the human populations sampled, and possible genetic confounds (Barbaro et al. 2017; McLanahan et al. 2013; Sear et al. 2019; Sohn 2017).

Cross-Sectional Data and Causality

A major weakness of the use of cross-sectional correlational data to test the effects of father absence on reproductive maturation is that it cannot establish casual relationships (McLanahan et al. 2013). Across households, father absence likely has multiple causes and multiple effects, making it very difficult to estimate its direct effect on early menarche. Longitudinal studies, incorporating controls for potential confounds, have confirmed hypothesized effects on reproductive maturation of father absence and in one case mother absence (see below) (Chang and Lu 2018; Gaydosh et al. 2018; Mendle et al. 2009, 2019). These types of studies allow stronger causal inferences and can track long-term persistent effects of parental absence during early

childhood. Longitudinal data also provide some flexibility with regard to various types of statistical techniques for making causal inferences, for example, lagged-dependent variable models, growth curve models, and multilevel modeling (see review McLanahan et al. 2013).

Notably, Chang and Lu (2018) used a longitudinal study design to investigate the effects of parental absence on rural Chinese “left-behind” children (defined as those who experienced the absence of both parents for more than 6 months repeatedly for 3 or more years). Structural equation modeling revealed two dimensions of environmental harshness, extrinsic risk (on which parental absence loaded), and resource scarcity. Among a number of effects of these predictors on developmental, cognitive, and behavioral outcomes was the association between parental absence with accelerated sexual maturation and psychometric indicators of faster LH strategy. A key point is that parental absence was not stratified by parents’ sex. The effects of mother absence on daughters’ reproductive timing remain unclear, possibly due to small sample size (Sear et al. 2019).

It is important to note that while efforts have been made to increase the ability to determine causality with the use of longitudinal data and advanced statistical techniques, these methods are not without limitations. Researchers should carefully consider their use in designing studies, in light of the specific research questions and the available resources (see McLanahan et al. 2013).

Populations

Most early research into the associations between father absence and age of menarche was conducted in populations characterized, to use Henrich, Heine, and Norenzayan’s (2010) coinage, as WEIRD (Western, educated, industrialized, rich, and democratic). In small-scale societies with little market integration, findings often failed to reveal associations between father absence and age of menarche (Sear et al. 2019; Sohn 2017). Thus, the psychosocial acceleration hypothesis might apply only to a limited range of

human populations, and indeed it may be least applicable to societies most similar to those in which most of the natural selection shaping human developmental programs occurred. In general, girls growing up in WEIRD societies experience greater food security and access to medical care and fewer demands for physical labor, than girls growing up in non-WEIRD societies (Henrich et al. 2010; Sear et al. 2019). Furthermore, family and social structures generally differ between WEIRD and non-WEIRD societies. In the former, the prevalence of nuclear families and low fertility means that fathers provide a large proportion of the investment received by each child, so a father’s departure typically represents a substantial reduction in parental investment received. In the extended families commonly found in non-WEIRD societies, other adult kin, and sometimes older siblings, can provide compensatory investment following a father’s departure (Ellis 2004; Sear et al. 2019). Rather than father absence per se hastening female pubertal development, it seems that father absence, in some sociocultural contexts, serves as a cue of local mortality risk (Chang and Lu 2018; Ellis 2004). Additional cross-cultural research, and statistical techniques like growth curve models, multilevel modeling, and natural experiments, for systematically comparing predictive models of reproductive maturation across populations, will paint a more nuanced picture of the effects of father absence and other cues on the development of LH trajectories (McLanahan et al. 2013; Sear et al. 2019; Sohn 2017).

Genetic Confounds

Statistical associations between father absence and earlier menarche do not necessarily demonstrate that the former causes the latter. An alternative explanatory model posits that both traits are heritable and are genetically correlated. *Genetic correlation* occurs when the genetic variation that affects one trait correlates with the genetic variation that affects a second trait (Plomin et al. 2013). To the extent that LH strategy comprises a functionally integrated, partly heritable, cluster of

physiological and behavioral traits (Figueredo et al. 2004), men who are more likely to leave their mates and children will also be more likely to transmit to their daughters, genes that predispose them toward earlier menarche. Even small genetic correlations could confound the phenotypic correlation between the two traits (Barbaro et al. 2017). Several empirical study design types afford the opportunity to disentangle the effects of genes from the effects of early life stress on reproductive maturation (Barbaro et al. 2017; Barnes et al. 2014; Ellis 2004; Gaydosh et al. 2018; Mendle et al. 2019; Tither and Ellis 2008).

Classic twin studies partition phenotypic variation into the proportions due to (1) genetic variation, (2) effects of the non-shared or idiosyncratic environment (which includes measurement error), and (3) effects of the environment shared by the twins (Plomin et al. 2013; Tither and Ellis 2008). Effects of harsh early environments on reproductive timing are expected to manifest as shared environmental effects on age at menarche, but these are not found (Barbaro et al. 2017). However, Tither and Ellis (2008) controlled for genetic effects by comparing non-twin sister pairs whose genetic father left the household when the older sister was about 12, while the younger sister was about 5. As would be expected from psychosocial acceleration theory, the younger sisters experienced earlier menarche than the older sisters, and they also experienced earlier menarche than younger sisters in a control sample of families in which the father did not leave the household.

Finally, genome-wide association studies (GWAS) allow researchers to identify potential candidate genes that might be tied to father absence and earlier age of menarche. For instance, the *LIN28B* gene, which plays a central role in female development, and its SNP variants were identified as potentially impacting female reproductive timing (see Perry et al. 2009; Zhu et al. 2011). Other findings support a gene $\times$ environment interaction between *LIN28B* and father absence on female sexual maturation age, although finer-grain methodologies for accounting for genetic variation is needed (see Schlomer and Cho 2017). The importance

of gene $\times$ environment interactions stems from the aforementioned concerns related to genetic contributions resulting in spurious relationships. Gene $\times$ environment interactions essentially demonstrate individual variation as a function of differing genotypes responding to differing environments. For instance, environmental risk factors for certain diseases are passed down from parents to offspring which may play a larger role than heritability of the actual disease. The result is variation in how the disease phenotype manifests. Interestingly, a recent study used polygenic scores, derived from GWAS data to test for genetic confounds. No evidence of genetic confounds in the associations between women's polygenic score for accelerated menarche and father absence were found. Women's polygenic scores for earlier age at first birth were, however, associated with father absence, providing preliminary support for potential genetic contributions for that relationship (Gaydosh et al. 2018).

Conclusion

In WEIRD societies, the association between father absence and early menarche is among the most robust findings in the social sciences (Ellis et al. 2009; Mendle et al. 2009; Richardson et al. 2018; Tither and Ellis 2008). These findings represent a test of the application of LHT to human individual differences. However, a number of important questions remain unresolved. Father absence and early menarche are not consistently associated in the small-scale societies that more closely resemble ancestral human environments (Sear et al. 2019; Sohn 2017). Additional research is needed to specify how sociocultural contexts influence the environmental cues by which the timing of reproductive maturation is calibrated. For example, mother absence, which for obvious reasons is much rarer than father absence, might also affect the timing of reproductive maturation (Chang and Lu 2018). Finally, the relative effects of harsh early environments and genetic predispositions on reproductive maturation remain an open question (Barbaro et al. 2017; Gaydosh et al. 2018; Schlomer and Cho 2017).

Cross-References

- [Bruce J. Ellis](#)
- [Cultural Universals](#)
- [Development](#)
- [Early Childhood and Adolescence](#)
- [Environmental Unpredictability](#)
- [Father Absence](#)
- [Harsh Environments](#)
- [Jay Belsky](#)
- [Life History Theory](#)
- [Parental Investment and Parenting](#)
- [Paternal Care](#)
- [Paternal Investment](#)
- [Predictors of Sexual Debut](#)
- [Puberty in Girls](#)
- [Reproductive Timing](#)

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Absolutism

► Objectivity

Absorption

► Assimilation

Abstinence

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Synonyms

Pregnancy prevention; Sobriety

Definition

The practice of restraining from a particular behavior.

Introduction

Abstinence is a broad term that can cover many different behaviors that one may wish to avoid indulging. Although this term can be used in several contexts, abstinence in regards to sexual intercourse will be the focus. Largely used as a personal strategy to avoid pregnancy and sexually transmitted diseases (STDs), it is often associated with the avoidance of vaginal intercourse but can also include the avoidance of *all* sexual activity. Individuals will often have varying definitions of what is considered to be abstinence, but they ultimately have the same goal in mind.

Abstinence in Sex Education

The topics discussed in sex education is a controversial issue. Assuming that the sex education provided in schools is a driving force behind sexual lifestyles, the information that is taught within these courses should be scrutinized. Guidelines for this information are not universally distributed throughout the United States. Depending on where an individual lives in the country, the course may have an abstinence-only focus which stresses the effectiveness of abstinence either by comparing it to other birth control methods or by exclusively discussing abstinence as a birth control strategy.

According to the Centers for Disease Control and Prevention (CDC 2016), the USA has one of the highest rates of teen pregnancy among developed countries. Due to this high rate, many studies have been conducted in order to evaluate how effective the different strategies are for teaching sex education, specifically abstinence-only education. Carr and Packham (2016) recently evaluated the different outcomes of teen pregnancy and STD presence in states in which sex education courses stress abstinence. It was found that there were no differences in teen pregnancy rates or STD rates regardless of what was taught in the courses (Carr and Packham 2016). This recent study replicated what has been found in earlier studies. Abstinence-only education does not reduce the prevalence of teen pregnancy or STDs compared

to a more comprehensive course that discusses various different forms of birth control including abortion. In fact, it has been shown that individuals who participate in comprehensive sex education courses have a lower likelihood of teen pregnancy (Kohler et al. 2008).

The evidence of previous research concludes that abstinence-only education is ineffective in decreasing teen pregnancy rates and STD rates, but the causes are not quite as clear. One of the main arguments for why sex education should be more comprehensive is because of the instinctual nature of sexual intercourse. Especially during adolescence, the presence of the sexual drive will lead many to participate in sexual activities, regardless of what sexual education they have been exposed to. In order for adolescents to be better equipped to make informed decisions concerning their sexual behaviors, a comprehensive education that covers various birth control methods will provide more of a benefit than an education focused on abstinence.

Conclusion

Abstinence is a personal lifestyle choice that gives the individual a strategy that will not lead to pregnancy. Despite it being the most effective birth control method, when it is taught as the sole form of birth control in sex education, it may actually lead to riskier sexual behaviors as compared to having a more comprehensive course.

Cross-References

- [Contraception](#)
- [Sex Education in Schools](#)
- [Sexual Intercourse](#)

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Abstract Concept Formation

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Synonyms

[Abstraction](#); [Conceptual representation](#)

Definition

Concepts are formed when an organism is capable of representing a mental construct that subsumes multiple related exemplars. Exemplars may be related by virtue of shared physical features, functions, traits, capacities, relationships, or other unifying characteristics. Abstract concepts are representations of conceptual categories containing exemplars that are not strictly tied to observable features of the stimuli and that typically subsume several more concrete categories. Forming such concepts requires inference or generalization from observed features to the construct that ties exemplars together.

Introduction

The idea of abstraction is somewhat nebulous, and evidence for such in nonhuman minds is somewhat elusive. It has been suggested that most animals are not capable of abstraction by both historic (Locke 1690/1975) and more recent figures (Mackintosh 2000), and even those that believe some animals capable of some degree of abstraction have placed limits on their capacities, stipulating that they may not be capable of

reasoning about certain types of relations (Penn et al. 2008) or unobservables (Vonk and Povinelli 2006). Part of the difficulty in providing evidence for abstraction in nonhumans stems from the challenge in defining what it means to be abstract in the first place; conventional definitions focus on the idea that abstract concepts require generalization beyond strictly observable features to include constructs for unobservables such as traits, functions, and causal forces.

As such, an abstract concept can encompass qualities that are associated by virtue of underlying causal forces, thematic representations, or relations between items. Vonk and Povinelli (2006) focused on the notion of unobservables to represent a class of objects that are strictly hypothetical and cannot take on physical form: constructs such as thoughts, memories, ideas, beliefs and physical forces, such as gravity. The numerical concept of zero, or the absence of something, can also be considered abstract, as can the idea of sameness or difference, which pertains to the relationship between objects. Abstraction is required when the relationship between exemplars within an overarching category must be *inferred* based on observable qualities rather than derived directly from them. That is, having a concept of sameness goes beyond matching something orange to something else orange based on perceived perceptual similarity to abstracting the general relation “same” that could potentially be generalized to two green items or two items of the same shape or material.

Experimental Methods to Study Abstraction

The human capacity for language allows for representational content to be communicated. Humans have words for constructs that cannot be visualized, such as thoughts, physical forces, and language itself. Nonhumans do not have the luxury of communicating their thoughts in symbolic form, and therefore the content of their minds must be inferred through categorization tasks, such as matching-to-sample (MTS) and two alternative forced choice tests (2AFC),

where they are required to match a comparison stimulus to a sample based on a perceived relation (similarity as in traditional identity MTS or conceptual MTS tasks, or difference, as in oddity MTS tasks), or to choose members among pairs of items that belong to the same conceptualized category (2AFC tasks). Nonhumans are quite skilled at perceiving perceptual similarity and categorizing items that share qualities such as shape or color (Vonk 2003), but there is less evidence for their ability to categorize on the basis of more abstract qualities, such as social relationships (Vonk 2002; Vonk and Johnson–Ulrich 2014). One area in which many nonhumans excel is numerosity, which has been suggested to comprise a lower level of abstraction that might serve as a foundation for higher level symbolic thinking, which in turn may give rise to language and analogizing (Coolidge and Overmann 2012).

Researchers have presented stimuli at various levels of abstraction with categories ranging from concrete to more abstract. Concrete categories include exemplars that may look very much alike, such as bears versus humans, whereas abstract categories are broad and contain many diverse exemplars, such as “animal,” which contains insects, reptiles, fish, birds, and various mammals. Both great apes and American black bears have been shown to form categories at each level of abstraction tested, when presented with natural categories, but it has proven difficult to determine which features these animals use to perform the tasks successfully (Vonk and Galvan 2014). The possibility remains that animals are relying on perceptual features, such as particular color, luminosity, and contrast patterns to control responding in these tasks, rather than generating an overarching category such as “animal.”

Perhaps the most abstract concept assessed in nonhumans is the capacity to represent mental states, in particular the mental states of others. This capacity is known as theory of mind (ToM) and has been widely studied in both human children and nonhuman species. Although evidence for ToM in nonhumans has been hotly contested (Penn and Povinelli 2007), researchers have begun to converge on the idea that at least some species, such as great apes, may have an

understanding of some mental states, such as seeing and intentions. Evidence for understanding of knowledge states and beliefs is more equivocal. It has yet to be demonstrated that any nonhuman species represents the range and breadth of abstract concepts that can be communicated by humans through the use of symbolic systems, most notably language.

Conclusion

The extent to which nonhumans represent concepts for things that are abstractions of real objects remains uncertain as researchers struggle to make progress with experimental paradigms that will allow for a careful dissection of processes linked to observable features and those that depend upon an internal representation of an overarching conceptual category subsuming such features (Vonk and Povinelli 2006).

Cross-References

- [Concept Formation](#)
- [Concept Formation](#)
- [Learning](#)
- [Non-Human Primates](#)
- [Same-Different Categorization](#)
- [Theory of Mind](#)
- [Unobservability Hypothesis, The \(Vonk and Povinelli, 2006\)](#)

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Abstraction

- [Abstract Concept Formation](#)

Abuse

- [Physical Aggression](#)

Abusers: Husbands, Boyfriends, and Former Sexual Partners

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Synonyms

[Intimate partner violence](#); [Men’s aggression against women](#).

Definition

Abusers are those individuals who use strategies of intimidation, threat, isolation, and physical and sexual aggression against a victim. There are different forms of abuse, which can be broadly categorized into physical, sexual, and emotional abuse. When the victims are women, the abuser is often someone close to the victim, especially male partners and male ex-partners.

Introduction

Aggression in the context of a relationship, also called intimate partner violence (IPV), has been documented across several cultures (see Archer 2006), having detrimental impacts on the victims' health, such as physical injuries, poorer cognitive functioning, and psychological problems (Lawrence et al. 2012) and on the relationship, predicting relationship dissatisfaction (Hammett et al. 2017). While Archer (2000) found in a meta-analysis that among young American couples, women are slightly more likely to use physical aggression than men, men are more likely to cause an injury in their partners, such that women represent 62% of injured partners. In the United States (US), 33% of female murder victims are killed by their partners against 3% of male murder (Fox and Zawitz 2007b). In fact, data collected worldwide demonstrated that 30% of women reported to have experienced intimate partner violence at some point in their lives, while 38.6% of female murders are committed by intimate partners (Devries et al. 2013). Such statistics demonstrate that women's current or former partners are often their abusers, and despite much research looking for potential explanations from different perspectives, predicting and preventing intimate partner violence remains a challenge.

Ultimate explanations of male aggression against women have traditionally highlighted social and cultural aspects as the driving factors behind this phenomenon. For example, a feminist perspective emphasizes the role of a patriarchal

system, marked by male dominance, in male abuse against women (Johnson 2011). More comprehensive approaches have considered a combination of several factors such as individual, interpersonal, and family factors; neighborhood and community; and policy, systems, and society (Beyer et al. 2015). In this entry, however, I will consider an evolutionary perspective, exploring the idea that male intimate partner aggression has evolved because it served survival goals, therefore reflecting male reproductive striving. Before discussing why men are particularly aggressive toward their partner or former partners, I will first discuss why men have a tendency to be more physically aggressive than women. For the purposes of this entry, the terms partner aggression and partner abuse will be used to describe any episode of physical, sexual, or emotional abuse practiced by a current or former partner.

Human Aggression: Why Are Men More Physically Aggressive than Women?

In our evolutionary past, when resources that were necessary for survival, such as food, shelter, and mates, were in short supply in the environment, to secure such resources, individuals needed to engage in competition with others, which usually required physical aggression. Whilst the winner of the contest would take home the prize, the loser would end up seriously wounded or dead (Campbell 2015). Although both men and women need resources, and therefore both would benefit from competition, the costs associated with engaging in competition vary across sexes. Overall, while men are more prone to engage in contests, women are generally more cautious and avoid physically aggressive competition.

To understand the nature of these differences, we need to take a closer look at the roles of men and women in reproduction. While men's direct contribution to reproduction is limited to copulation, women carry a disproportionate reproductive burden (Fathalla 2015). Women are responsible for the intrauterine care of fetuses and embryos

during a 9-month pregnancy, which is among primates the longest duration of gestation. On top of this, women are also responsible for post-natal parental care, particularly breastfeeding that may last several years. Whilst men increase their reproductive success by dominating other male competitors to secure access to females for copulation and other resources, women do best by avoiding direct conflict and staying alive to protect their offspring (Campbell 2015). This helps to explain why, overall, men are usually more aggressive and more willing to take risks than women are. This also offers an idea of how women became more vulnerable to partner aggression, but it is not the whole picture. Furthermore, this does not explain why men can be particularly aggressive toward their own partners.

How Did Women Become More Vulnerable to Partner Aggression?

One of the main assumptions of Trivers' (1972) parental investment theory is that the sex that invests more heavily in reproduction will be more selective in choosing a partner. This means that men would benefit from mating with basically any fertile woman, whereas women would be more selective and pick a mate with the best possible genes, or a mate that is willing to provide women with resources such as protection and parental care (Puts 2016; Trivers 1972). As such, women become a valuable limiting resource for men because men's opportunities to reproduce are constrained by women's willingness to mate with them (Daly and Wilson 1988). This creates a clear conflict of interest and if there were no consequences, the use of physical force would allow men to secure access to as many partners as possible and as a result, give them higher chances to reproduce and pass on their genes, as it happens among other primates (Baniel, Cowlshaw, and Huchard 2017). Although sexual coercion among humans is not rare (Jeffrey and Barata 2017), explaining men's aggression against their female partners is not that straightforward and other factors also need to be considered.

From an evolutionary perspective, Smuts (1992) argues that male aggression against women may have become relevant in the context of exclusive mating relationships, reflecting men's reproductive striving. Long-term committed relationships are the preferred human mating strategy that evolved to ensure people's reproductive success (Maner and Miller 2010) by solving adaptive problems such as investment in offspring, acquiring resources, and maintaining female fecundity (Conroy-Beam et al. 2015). Sex-specific benefits for women would include greater access to resources and gaining protection, whereas for men the main benefits would be increasing probability of paternity and access to better mates (Buss 2003). Smuts (1992) hypothesizes that, in our evolutionary past, women became more vulnerable to aggression from their own partners because other men would be less likely to interfere and risk jeopardizing male-male alliances. Although this explanation is only speculative, it helps to understand how women may have become more vulnerable to intimate partner aggression; however, it does not explain what motivates men to hurt their own partners.

Why Do Men Hurt Women They "Love"?

Although exclusive romantic relationships have provided several benefits for both sexes and solved adaptive problems, such arrangements also have created extra adaptive problems. Once a high-fitness partner has been secured, individuals face potential threats, such as the threat of mate poachers, to the relationship that may lead to infidelity or to relationship dissolution, which would imply the loss of all the benefits brought about by an exclusive relationship (Conroy-Beam et al. 2015). Infidelity represents a great threat to relationships, representing one of the main reasons for divorce (Fincham and May 2017). Whilst it may be disturbing for both sexes, men find it particularly costly, because infidelity may result in investment of men's resources in other men's offspring, and damage to their reputation (Shackelford et al. 2015). In fact, men's jealousy over women's infidelity is one of the main driving

forces behind lethal and nonlethal male aggression against their partners (Stieglitz, Gurven, Kaplan and Winking 2012). This is consistent with the hypothesis that romantic jealousy is an evolved adaptation designed to preserve a relationship, avoid infidelity by the partner, and therefore, retain access to the partner's relevant resources (Daly et al. 1982). Cues of a partner's infidelity activate jealousy emotions that, in turn, will put in motion strategies to deal with such a threat (Bendixen et al. 2015).

Strategies designed to solve the adaptive problem of partner potential infidelity and prevent relationship dissolution are regarded as mate retention strategies (Buss 1988). Buss (1988) identified several mate retention tactics directed either to the partner (intersexual tactics), which is our focus in this chapter, or to a potential rival (intrasexual tactics). Tactics directed to the partner can be both positive, which means that they operate by providing benefits to the partners such as love and care, and negative, in which case they operate by inflicting costs on the mate. The cost-inflicting tactics within the set of intersexual strategies are: (1) *direct guarding*, involving vigilance, concealment of mate, and monopolization of mate's time; (2) *negative inducements*, which describe behaviors such as infidelity threat, punishment of mate threat to commit infidelity, and emotional manipulation; and (3) *public signs of possession* that reflect verbal and physical possession signals. Such behaviors reflect one's attempts to restrict and regulate partner's sexual autonomy and are hypothesized to be an adaptive solution for the problem of intrasexual competition for mates because ancestral men who used such strategies were more reproductively successful since they were better at avoiding threats from rivals and at preventing partner's infidelity.

Such categories describe different forms of controlling women's sexuality by using force or its threat to increase the chances that a female will mate with the aggressor or to decrease the chances that a female will mate with a rival. Therefore, male abuse against their female partners is an attempt at deterring the partner from engaging in infidelity, which could result in paternity uncertainty and mistakenly allocating resources to a

rival's offspring. In fact, Shackelford et al. (2015) across several studies demonstrated that male mate retention tactics, particularly direct guarding and negative inducements, predict male aggression and abuse in general, providing further evidence for the hypothesis that male aggression toward their female partners reflects a male reproductive strategy.

In some extreme cases, abuse may take the form of rape. Evolutionary psychologists have hypothesized that men sexually violate their partners in circumstances of increased risk of sperm competition, which is the competition of a different male's sperm to fertilize a female's egg (McKibbin et al. 2013). This would happen particularly when a man suspects or finds out that his partner has been sexually unfaithful, in which case she risks being impregnated by a rival. In such cases, men may force themselves on their partners to engage in sperm competition and avoid investing in offspring that is not their own. A study testing this hypothesis directly demonstrated that men who suspected of a partner's infidelity were more likely to perform sexually coercive behaviors, such as rape (Goetz and Shackelford 2006). This supports the hypothesis that men have evolved psychological mechanisms that will motivate them to commit partner rape in the prospect of sperm competition as a response to partner infidelity.

Despite, or as a consequence of, a male's efforts to retain a mate, the partner may end the relationship, which may also motivate male aggression against women. Partner defection causes not only the loss of their resources but can also negatively affect the formation of new relationships. For example, it has been documented that the discovery that someone was rejected by their former partner negatively affects people's desire for dating them (Stanik et al. 2010). As such, because relationship dissolution results both in the loss of the former partner's resources and problems to have access to a new partner, the rejected man may make use of a series of strategies either to prevent the partner from dating again or to regain access to the partner or both. Over the course of our evolutionary history, women have suffered male abuse because of

sexual rejection. Strategies may include threats, stalking, and violence, which may reflect a desperate tactic and last attempt to reacquire the partner, reflecting a mate retention strategy (Buss and Duntley 2014).

Is There a Typical Abuser Profile?

Male aggression against women in general functions as a controlling tool over women's behaviors because of the high costs to women of physical injury inflicted by men. However, most men do not abuse their partners or make use of extreme measures of coercion such as physical aggression. This suggests that, on a proximal level, there are variables that influence the usage and/or intensity of male partner abuse, such as the own attributes of the abuser. Studies have focused particularly in identifying any common characteristics in abusers to elaborate a male abuse profile. However, despite some typologies available in the literature (e.g., Holtzworth-Munroe and Stuart 1994), studies have failed to provide systematic evidence regarding the psychological characteristics of abusers (Dobash et al. 2009). Recent research profiling male abusers comparing generally extra-family violent men and generalist batterers showed that these two groups do not significantly differ in their individual, family, and community characteristics, suggesting that aggression toward a partner shares a common ethology with general aggression (Juarros-Basterretxea et al. 2018). Gondolf (2002) compared intimate partner abusers to men from the general population, but did not find substantial differences regarding psychological problems, although a small proportion of men in the first group are described as having serious psychological problems. As pointed out by Dobash et al. (Dobash et al. 2009), such mixed evidence suggests that male abusers are not actually mentally disturbed, but that they are just ordinary men, which makes it harder to predict and prevent such problems.

However, despite the apparent absence of an abuser's typical profile, men's attributes seem to influence the usage and intensity of aggression toward their partners as studies have shown

differences between abusers and non-abusers. Such differences appear to confirm the evolutionary view of male aggression as an instrument of male domination over women. For example, partner male abusers, in comparison to non-abusers, report lower self-esteem, which is associated with jealousy, greater justification of male dominance, and use of aggression for conflict resolution (Díaz-Aguado and Martínez 2015). Men's possessiveness, jealousy, and sense of entitlement are also characteristics that contribute to partner abuse, particularly to extreme cases that end in murder (Daly and Wilson 1988). Analyzing those men who make use of extreme forms of violence, neuropsychological studies analyzing male batterers have demonstrated that this group presents low performance of tests on executive functioning, verbal skills, and vocabulary (Bueso-Izquierdo, Hart, Hidalgo-Ruzzante, Kropp, & Pérez-García 2015), suggesting that these men may use violence as their form of communication in the relationship. On top of that, male batterers also have thinner brain areas related to emotion processing such as prefrontal and limbic brain areas, in comparison to other criminals, suggesting that they have poorer emotion regulation (Verdejo-Román et al. 2018). Such characteristics seem to describe a dominant and possessive male profile that find violence as a way of solving conflicts, particularly in the context of a relationship. This is consistent with the evolutionary hypotheses describing men's abusive behaviors as a way of retaining a partner and ultimately enhancing their reproductive success.

Conclusion

The evolutionary theory can tell us a lot about why men are usually more physically aggressive than women, and why they quite often direct their aggressive behavior toward their partner. In this entry, I have reviewed some evidence supporting the evolutionary view that male aggression toward their partners may be a reproductive strategy. Essentially, physical, psychological, or sexual abuse performed by men in the context of a romantic relationship are extreme, and sometimes

desperate, strategies to prevent their partners from engaging in infidelity or ending the relationship. I demonstrated this by reviewing current literature on male mate retention strategy and jealousy, demonstrating that abusive men are more jealous and possessive. In turn, jealousy predicts the usage of mate retention tactics that reflect men's efforts to retain a valuable partner and consequently ensure access to the partner's resources. Such strategies may include different types of abuse, going as far as physical aggression. Therefore, the different forms of abuse perpetrated by men against their partners are part of male reproductive strategies, reflecting men's attempt at dominating women. I discussed how male partner abusers tend to be more jealous, justify male dominance, and have poorer emotion regulation, which contributes to the usage of more extreme forms of abuse, such as physical aggression.

It is important to consider here, however, as argued by Smuts (1992) that adopting an evolutionary view of spouse abuse is not an attempt to justify intimate partner aggression or to explain the relations between the sexes using deterministic assumptions. The aim of this entry was simply to discuss the idea that male partner abuse happens because men found aggression to be a powerful tool to dominate women and enhance their reproductive success. This does not mean, however, that men are inherently aggressive, and women are inherently submissive. Male partner abuse is not inevitable, and as discussed earlier in this chapter, most men do not use measures of control over their partners, but that there are certain male attributes and circumstances that may trigger such behaviors. Additionally, despite the temporary "advantages" that the use of aggression apparently brings for men, there are a number of costs that – not rarely – outweigh its benefits.

Cross-References

- ▶ [Aggression for Sexual Access](#)
- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Violence to Control Women's Sexuality](#)

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Access to Alloparents

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Synonyms

Allocare; Allomother; Babysitting; Childcare;
Cooperative breeders

Definition

An alloparent is any individual who is not the biological parent, who helps to raise the child by providing direct or indirect investments. Alloparents may include kin members such as

grandparents, siblings, aunts and uncles, as well as nonkin such as friends, neighbors, and professional caregivers.

Introduction

Several prominent scientists studying human behavior from an evolutionary perspective have proposed that humans are cooperative breeders. Cooperative breeding is loosely defined as a breeding system where mothers require help from other individuals for successful childrearing (Hrdy 2005).

This proposal stems from the observation that human neonates are incredibly helpless compared to other primates, only able to carry out basic functions. Human prematurity at birth is coupled with a slow development and maturation period throughout childhood and adolescence. Consequently, children require high levels of care over a prolonged period of time to successfully reach adulthood. Such intensive caregiving is a near-impossible task for mothers to complete on their own – especially given the fact that, at least in natural fertility populations, mothers tend to have multiple dependent offspring.

It has been argued that these factors have led to the coevolution of facultative parental investment (i.e., fathering) as well as “alloparenting” (i.e., nonparental childrearing support) (Hrdy 2005). Indeed, alloparenting is arguably a cross-cultural universal, though who helps and how they help varies within and between populations.

Alloparenting can be conceptualized in different ways depending on the type of investments and its effects on parenting. Further, the general relationships between alloparental investments and parental investments may vary from population to population. Evolutionary theory predicts that the relationship between alloparental and parental investments will influence pair-bond stability.

Cross-Cultural Examples of Alloparenting

Starting with forager populations, hunter-gatherers generally have a wide network of

allomothers who provide care and share food with infants and children. For example, in both the Hadza of Tanzania and the !Kung of Botswana, weaned toddlers who are too heavy to be carried are left in camp while their parents go on foraging and hunting trips. These toddlers stay in camp with other children, teenagers, and a few adults who provide informal care (Hewlett and Lamb 2005). In the Efe of the Democratic Republic of Congo, infants were found to have an average of 15 caregivers at 4 months old (Hewlett and Lamb 2005), and in the Aka of the Central African Republic, infants were found to have an average of 21 caregivers (Meehan 2009). While mothers are generally the main caregivers across all these populations, childrearing among foragers is largely a collective venture whereby children have access to numerous alloparents.

With agriculture, the childrearing system tends to focus more strongly on maternal care. Nonetheless, the necessity of “help for mothers” is often acknowledged as women face trade-offs between agricultural labor and childcare. For example, in some sub-Saharan agriculturalists such as the Giryama of Kenya and Fulani of Bukina Faso, women who are responsible for food cultivation and childrearing collaborate with each other to share food-processing tasks and child care. In the Gussi of Western Kenya, the job of assisting mothers with childcare is often given to older daughters (LeVine et al. 1996).

In developed populations with stronger nuclear family norms, childcare is generally treated as the responsibility of the mother. Nonetheless, kin and nonkin allomothers universally contribute to childrearing. In addition to fathers, grandmothers have been found to be particularly important alloparents who provide childcare and influence parenting behaviour. When alloparenting by kin is less common, state provision of formal childcare takes prominence, such as the “collectivist” approaches to childcare seen in Nordic countries (Emmott 2015).

Categories of Alloparental Investment

Alloparents who provide help with childrearing, in essence, are providing investments into child

quality (i.e., improving their fitness and future reproductive success). Across 37 high-fertility, high mortality populations, the presence of alloparental kin has been associated with greater child survival, though who matters for children seems to vary between populations.

Alloparental investments can be categorized and differentiated as: (1) direct versus indirect investments, (2) caregiving versus provisioning, and (3) substitutive versus additive investments.

First, direct alloparental investments are *any investments made by the alloparent straight to the child*, for example, by providing direct childcare, playing, or teaching. Indirect alloparental investments are *investments made by the alloparent to the child via a mediator*, for example, when an allomother provides monetary support to the mother who uses that money to feed the child. Second, these alloparental investments may also be described as caregiving and provisioning. By default, caregiving is a direct investment made straight to the child. Provisioning, on the other hand, involves a transfer of resources either directly to the child or indirectly via a mediator. Finally, allomaternal investments may either be substitutive or additive, depending on the impact it has on parental investments. As the terms suggest, substitutive investments *replace parental investments*, allowing parents to direct their freed-up energy, time, and resources into other domains of behavior. In contrast, additive investments are additional investments children receive *without impacting parental investment levels*.

Studies suggest that alloparental investments through direct care and provisioning often substitute maternal investments in high-fertility populations, encouraging mothers to divert their time to and effort into other activities. In the Karo Batak farmers of Indonesia, help from matrilineal alloparents was associated with greater childcare and lower levels of farm work by the mother, while help from patrilineal alloparents was associated with lower levels of childcare and greater levels of farm work by the mother (Kushnick 2012). Similarly, in the Aka foragers, direct caregiving by allomothers was associated with lower levels of maternal care and higher levels of foraging (Meehan 2009).

Across developed populations, direct grandparental caregiving has been associated with reduced maternal childcare and greater labor force participation, suggesting a substitutive relationship between direct alloparental care and maternal investments. However, this is not a universal relationship found across countries (Assave et al. 2012). Further, indirect alloparental investments through financial help have been found not to correlate with maternal investment activities (Emmott 2015), suggesting provisioning for children in developed populations may be an additive rather than a substitutive investment.

Alloparents and Pair-Bond Stability

Assuming that pair-bonds function as a reproductive contract, evolutionary theory predicts that pair-bond stability is influenced by the trade-off in the “loss” of other mating partners (i.e., future reproduction/mating effort), against inclusive fitness benefits of a cooperative pair-bond (i.e., current reproduction/parenting effort). Given the facultative nature of paternal investments, a key determinant of this trade-off is the impact of fathers on child quality. If successful childrearing is dependent on paternal investments, this should serve as an incentive to maintain cooperative pair-bonds. In contrast, if mothers can successfully rear children without help from fathers, the costs of maintaining a relationship may outweigh the benefits. Indeed, studies have suggested that divorce across developed populations is more likely when women are financially independent.

Alloparent availability may impact pair-bond stability by influencing the necessity of paternal investments for successful childrearing. If alloparental investments can effectively substitute paternal investments, the costs of pair-bond dissolution on child fitness are reduced. This may lower the incentive for mothers and fathers to maintain their pair-bonds, as well as increase the incentive for parents to seek alternative mates. While research in this area is sparse, studies have found evidence of increased alloparental investments followed by father absence (Bentley and Mace 2009). An examination of the Standard

Cross-Cultural Sample has found that populations with higher rates of allomaternal childcare are associated with higher rates of divorce (Quinlan and Quinlan 2007).

Conclusion

Alloparenting is a fundamental aspect of the human childrearing system, with examples of alloparenting seen across societies. Childrearing support from a range of helpers can directly and indirectly influence child quality, which in turn may influence parental behavior. It is important to remember that the trade-offs mentioned above exist among a myriad of other costs and benefits surrounding parental/alloparental investments and pair-bonding. One must also not forget the importance of cultural norms and rules which may encourage or restrict behavior. Nonetheless, if alloparental investments are effectively able to substitute paternal investments, evolutionary theory predicts that it would facilitate pair-bond dissolution.

Cross-References

- [Kin Selection](#)
- [Life History Theory](#)
- [Women's Long-Term Strategies](#)
- [Parental Investment Theory](#)
- [Women's Long-Term Strategies](#)

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Access to Resources

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Synonyms

[Resource availability](#)

Definition

Opportunity to acquire food, shelter, mates, and other necessities for survival and reproductive success.

Introduction

Natural selection is a straightforward process: Variation exists among individuals, and some of

Denise D. Cummins is retired.

this variation is heritable. Some heritable attributes allow individuals to better cope with survival pressures such as predation or climatic changes and to enjoy greater success when competing for resources or mates. These individuals will leave more copies of their genes in the gene pool than individuals with less successful traits. The genetic contribution of an individual to the next generation's gene pool (relative to the average for that population) is referred to as fitness.

From an evolutionary standpoint, therefore, the fundamental problem that an organism must solve is maximizing reproductive success which in turn reduces to maximizing access to fertile mates and resources.

An individual's access to mates and resources depends on several factors. The spatial arrangement of resources in habitats influences the distribution of individuals within the habitat and their ability to acquire resources. The space between individuals is generally greater in habitats in which resources are uniformly or randomly distributed. Many environments are characterized by "patchy" resources; the density of resources (such as forage plants and water) varies spatially (clumped resources) or temporally (e.g., abundant during the rainy season and sparse during the dry season). When resources are distributed this way, individuals tend to "clump" together around them. These "clumps" typically are more than simple aggregates. Instead, they frequently constitute social groups that are characterized by kinship and rank relationships that greatly influence access to available resources.

Sociality refers to the degree to which individuals in an animal population tend to associate and interact with each other in social groups. Social living yields a reduction in predator pressure by improved detection or repulsion of enemies, improved foraging and hunting efficiency, improved defense of limited resources against intruders, improved access to potential mates, and improved care of offspring through communal feeding and protection. But there are also costs associated with sociality, including increased competition within the group for fertile mates and resources.

Kinship and Access to Resources

A key characteristic of social species is an inclination to behave more altruistically toward kin than toward unrelated individuals. Individuals are more likely to share resources with genetic kin, alloparent their offspring, and come to their defense during agonistic encounters. This is referred to as kin selection.

Status and Access to Resources

In most species, particular individuals have priority of access to resources in competitive situations. These individuals are referred to as high status, those who have lower priority of access are called low status, and the social structure of the groups is called a status (or dominance) hierarchy. Because of this differential access to resources, higher-status individuals are less likely to die of predation or starvation and more likely to leave living offspring (Clutton-Brock 1988). Among species in which status is unstable, the level of reproductive success achieved by any individual is directly related to the length of time during which that individual is high ranking (Altmann et al. 1996). Accordingly, there is a direct relationship between status and *inclusive fitness*, (reproductive success of individuals and their closely related kin).

Among humans, status hierarchies are apparent in the social groups of children as young as 3 years of age (Smith 1988). Human societies frequently take the form of status hierarchies, such as caste systems, feudalism, and modern socioeconomic stratification. Socioeconomic status has been reliably and repeatedly linked to several health indices, and these correlations cannot be explained simply in terms of differential access to health care, smoking, or other objective factors (Adler et al. 1993). Put simply, status is directly tied to an individual's ability to survive, to reproduce, and to take care of oneself, one's offspring, and one's kin.

Investigations of social interactions in a variety of species (including humans) suggest that status hierarchies are supported by a collection of

specific *cognitive* skills and that those who achieve high status are those who are particularly adept at them. These skills include (a) being adept at learning the implicit rules that constrain behavior in one's social group and monitoring compliance with them, (b) forecasting and influencing the behavior of others, and (c) forming powerful alliances based on reciprocal obligations (reciprocal altruism) (Cummins 2005). High-ranking individuals monitor the behavior of subordinates in order to protect their privileged access to resources. Subordinates engage in deceptive behavior that improves their access to resources. For example, they conceal objects or behaviors from others by hiding them from view, acting quietly so as not to attract attention, avoiding looking at a desirable object themselves, or distracting attention away from the desired object or forbidden behaviors. Subordinates also garner a larger share of resources by forming alliances with forbidden individuals through surreptitious food sharing or grooming, alliances that can be called upon during contests of rank.

Sex Differences in Access to Resources

There is a significant initial difference between potential reproductive success of males and female mammals. The ceiling for reproduction is much higher for males than females because sperm are plentiful and continually replenish, while eggs decline in number during a female's lifetime. Females also necessarily invest more energy in reproduction than do males (e.g., pregnancy and lactation) and are typically more involved in the care of very young offspring.

Female reproduction, therefore, is limited primarily by access to resources. Once a pregnancy has occurred, females cannot increase their reproductive success by engaging in further matings. Because of the greater cost to females in producing young, they increase their lifelong reproductive success by investing in their offspring to ensure their survival.

In contrast, males can increase their reproductive success by maximizing the number of fertile

females with whom they mate. If the number of males in a population is approximately equal to that of females, then there exists enormous pressure for competition among males for access to fertile females, and there will exist greater variability in male reproductive success: For every male who gains reproductive access to a disproportionate share of females, other males lose opportunities to reproduce. For this reason, male reproduction is limited primarily by access to fertile mates.

These differential reproductive pressures manifest as different mating strategies (or implicit biases) for men and women (Schmitt et al. 2003). Men seek mating opportunities with as many fertile females as possible, while females are choosy, preferring fertile mates with ample resources. Men tend to seek and acquire resources as markers of success, which in turn provides access to a wider pool of potential mates. In contrast, women primarily seek resources to support and maintain themselves and their children (World Bank Development Report 2012). Income considerations are secondary to family issues, and women will delay childbearing in order to acquire resources.

These sex differences are not obligate human traits but are instead facultative traits – they are deployed or modified to suit current environmental exigencies. For example, in polygynous societies that restrict the avenues women may pursue to obtain resources, women typically prefer to be one of many co-wives of a prosperous man than the only wife of a poor one (Betzig 1986). But when men do not constitute reliable avenues to greater resources relative to what women themselves can acquire directly, female mating strategies shift. Kasser and Sharma (1999) analyzed mate preference data across 37 cultures and found that females strongly prefer resource-acquisition characteristics in mates when their cultures limit their reproductive freedom and their educational opportunities. Zentner and Mítura (2012) examined the desirability of mate attributes among nearly 12,000 individuals across 31 nations and found that sex differences in mate preferences declined proportionally to increases in nations' gender parity.

Conclusion

An individual's access to resources depends not simply on the availability of resources in the environment but also upon the individual's place within the social group. Individuals are more likely to share resources with kin than non-kin. They are also more likely to share resources with non-related individuals if those individuals have shared resources with them in the past (reciprocal altruism). In competitive situations, some individuals achieve priority of access to resources, and are referred to as high-status or high-ranking individuals. Lower-ranking individuals improve access to resources by forming alliances with high-ranking individuals. In some species, lower-ranking individuals also increase their access to resources by engaging in deception.

Cross-References

- [Competition for Resources Desired by Females](#)
- [Cooperative Alliances](#)
- [Dominance and Health](#)
- [Dominance in Humans](#)
- [Female Mate Choice](#)
- [Higher Status in Group](#)
- [In Nonhuman Primates](#)
- [Kin Selection](#)
- [Mate Selection Strategy](#)
- [Mate Value](#)
- [Nonhuman Primates](#)
- [Primate Dominance Hierarchies](#)
- [Reciprocal Altruism](#)
- [Reproductive Strategy](#)
- [Resource Competition](#)
- [Resource Defense](#)
- [Sex Differences](#)
- [Sexual Contact and Sexual Disgust](#)
- [Sexual Strategies Theory](#)
- [Social Status and Economic Resources](#)
- [Social Dominance and Sexual Access](#)
- [Status and Dominance Hierarchies](#)
- [Status and Redistribution of Resources](#)
- [Status and Reproductive Success](#)

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Accuracy of Self-Knowledge

- [Accuracy of Self-View](#)

Accuracy of Self-Perception

- [Accuracy of Self-View](#)

Accuracy of Self-View

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Synonyms

Accuracy of self-knowledge; Accuracy of self-perception; Self-awareness; Self-insight

Definition

Accuracy of self-view refers to having accurate (or realistic) perceptions and making accurate evaluations about oneself (e.g., one's traits, abilities, attitudes, and so on); it is usually operationalized as the extent to which the individual's estimates of themselves agree with independent estimates obtained from knowledgeable others, observations of behavior, and implicit assessment.

Introduction

The notion that accurate self-view is important has a long history dating back to the Greek dictum to "know thyself," originally engraved on the Temple of Apollo at Delphi. In theory, accurate self-knowledge enables one to establish realistic expectations of oneself and is essential for self-regulation and self-development. Indeed, accurate perception of self and reality is considered to be a prerequisite of mental health and psychosocial adjustment (e.g., American Psychiatric Association 2013). Yet, many findings highlight obstacles to accurate self-perception and suggest that most people are rather poor at self-assessment (e.g., Brown and Dutton 1995).

Perspectives on Accuracy of Self-View in the Psychological Literature

Over 100 years ago, Freud noted that the conscious mind is simply the tip of the iceberg. Thoughts, memories, and desires that are unacceptable to the rational and conscious self are held below the surface of conscious awareness, although they continue to exert a great influence on behavior. Their full expression is prevented by the unconscious deployment of defense mechanisms, some of which are more primitive (e.g., reaction formation) and other more mature (e.g., sublimation; Freud 1936). Although the defense processes in themselves are not pathological phenomena, they often turn out to be detrimental. Simply put, the cost of self-deception is psychopathology. And so, the aim of psychoanalysis is making the unconscious conscious, which requires subjecting an automatic and unconscious regulation to conscious thinking (Freud 1904). Insight and the attainment of accurate self-knowledge are seen as primary curative factors also in humanistic psychotherapy (Rogers 1951).

Many theorists share Freud's skepticism about how well people can know themselves. In fact, the contention that information is processed unconsciously is now a basic assumption of cognitive science. The so-called cognitive unconscious is not the consequence of defenses against self-threatening perceptions, but reflects the architecture of the mind. Numerous dual-process theories posit the existence of two interactive modes of information processing and, hence, two ways of knowing oneself, one conscious (rational, analytic, controlled, explicit), and the other unconscious (experiential, intuitive, automatic, implicit; Wilson 2009). As postulated by Epstein's (2003) cognitive-experiential self-theory, people's self-views are best understood in terms of their implicit self-theories. These automatically constructed theories address the four basic needs: to maximize pleasure and minimize pain, to maintain relatedness with others, to maintain the stability and coherence of one's

conceptual system (i.e., self-verification), and to enhance self-esteem (i.e., self-enhancement). People's implicit self-schemas cannot be accessed directly and may or may not be accurately reflected in their explicit self-evaluations. Previous studies on the relationship between implicit and explicit attitudes and self-esteem have shown that they are weakly to moderately correlated (e.g., Greenwald and Farnham 2000). Also, there is neurological evidence of divided consciousness, with the left and right hemispheres processing information differently and encoding different kinds of knowledge (Krebs et al. 1988).

The idea that people pursue accurate self-knowledge is a key assumption of social comparison theory (Festinger 1954) and self-assessment theory (Trope 1979). Other social-cognitive approaches posit that there are various motives affecting the way people expect, process, and react to the self-relevant information. According to Sedikides and Skowronski (2000), these are valuation motives (i.e., self-enhancement and self-protection), learning motives (i.e., self-assessment and self-improvement), and homeostatic motives (i.e., self-verification). Of these motives, only self-assessment prompts people to seek out accurate and objective self-relevant information, and it may operate independently, coincide, or conflict with other motives. Which of these self-motives governs one's reaction to feedback depends on individual differences and situational influence (e.g., task or attribute ambiguity). Nonetheless, several studies have found defensive motives (i.e., esteem- and consistency-related) to be more powerful determinants of the self-evaluation process than accuracy concerns (e.g., Sedikides 1993). The self-serving attributional bias and the illusion of control are examples of the phenomena that reflect self-enhancement biases in self-perception (e.g., Krebs et al. 1988).

In order to integrate the various models of self-perception, and to capture the role of basic motivational, cognitive, and affective processes in the self-perception process, Robins and John (1997) offered four metaphors of the self-perceiver. In some ways people are scientists, motivated by self-assessment and dispassionately searching for truth. In some respects they act like consistency seekers, driven by self-verification, and in some

they behave like egoists, motivated toward self-enhancement, and like politicians, concerned with popularity. These metaphors are not personality types, but serve as lenses through which self-perception accuracy and deviations from accuracy can be analyzed and interpreted.

As noted by Funder (2003), the avoidance of judgment error and the achievement of accuracy should not be treated as the same things. His realistic accuracy model suggests that accuracy is a function of the relevance, availability, detection, and utilization of behavioral cues. In other words, the accurate judgment of personality is possible provided that one emits relevant behavior, notices, and interprets it correctly. The model implicates that to know oneself better, one should first and foremost seek out contexts that encourage one's self-expression (Funder 2003).

Evolutionary Account of Accuracy of Self-View

The evolutionary adaptive utility of an accurate self-view appears to include enhancing functioning of the individual within the group as well as facilitating functioning of the group as a whole. For example, accurate self-knowledge allows individuals to engage in environments that match their skills and abilities – if an individual discovers that they are good at child-watching, exercising this skill to its fullest extent would likely benefit them and the group. Also, accurate self-knowledge enables individuals to find their positions in the social hierarchy, hence reducing conflict with conspecifics (Sedikides and Skowronski 2000). If an accurate self-view is adaptive, why would an inaccurate one be tolerated by the selection process?

Some theorists suggest that self-deception make individuals better able to deceive others (e.g., von Hippel and Trivers 2011). Because humans inadvertently reveal their deceptive intent through verbal and nonverbal clues, those who are taken in by their own lies make their deception harder to detect. Also, self-deception benefits deceivers by reducing the cognitive load associated with deceiving and by reducing retribution if their lies are exposed. It should be noted that,

by helping to better deceive others, self-deceptive beliefs serve both short-term strategies of cheating and long-term strategies that depend on maintaining reciprocity relationships (Nesse 1990).

Others argue for a pragmatist view of knowledge and suggest that biases in self-conception function as pragmatic shortcuts for self-understanding that, all in all, give rise to functional conclusions and behaviors that enhance an individual's fitness (e.g., Krebs et al. 1988). Beliefs that make one feel good, secure, and in control are adaptive, regardless of whether or not they are accurate in an ultimate sense, because they enhance one's health, chances for success, and social attractiveness and, thereby, also the likelihood of survival. Moreover, false beliefs tend to validate themselves – a phenomenon known as the self-fulfilling or behavioral confirmation effect (e.g., Snyder 1984). There is, however, a limit to self-deception. Since, from an evolutionary perspective, the benefits of group living exceed the costs, the adaptive value of false self-beliefs will depend upon the support they receive from others.

Measurement of Accuracy of Self-View

Because of a lack of absolute measures of a person's attitudes, traits, abilities, and so on, there is no way to know the person's true personality, and so it is difficult to evaluate whether one's self-view is accurate. The most commonly used methods for the assessment of accurate self-knowledge rely on comparison of self-reports of personality with: (1) ratings of personality provided by knowledgeable others, (2) observed behavior in relevant situations, and (3) implicit personality measures. None of these sources provides objective criteria against which self-perceptions can be compared, but rather reflects different definitions of accuracy. Thus, the so-called criterion problem remains.

Robins and John (1997) proposed a framework that identifies six conceptually based categories of accuracy criteria: operational/reality (i.e., whether individuals' self-perceptions correspond to direct operational criteria), social consensus (i.e., whether individuals' self-perceptions match

up with how others see them), functional/pragmatic (i.e., whether individuals' self-perceptions serve adaptation), normative models (i.e., whether individuals' self-perceptions align with the prescriptions of the normative model), information processing (i.e., whether individuals' self-perceptions result from the use of valid cues), and internal consistency (i.e., whether individuals' self-perceptions are consistent with their other self-beliefs or across social roles). As recommended by these authors, accuracy researchers should use multiple criteria to examine accuracy and should always state explicitly which ones they have chosen and why (Robins and John 1997).

Conclusion

Accuracy of self-view is an area of some debate within the psychology literature, and the question of whether people's self-views reflect what they are truly like will likely remain open to further discussion. Despite this, there seems to be a consensus among authors that parts of self-related knowledge are difficult to access consciously (e.g., information that is self-threatening and/or was acquired in early childhood). It is also recognized that both accurate and biased self-perceptions have an adaptive value, although the distorted ones are more likely to prove costly in the long run.

Cross-References

- [Self-Concept](#)
- [Self-Deception](#)
- [Self-Reports](#)

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Acheulean

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Synonyms

[Hand axe](#); [Cleaver](#); [Core tool](#)

Definition

A term used to classify a class of stone tools that all share a distinct oval/pear shape.

Introduction

The Acheulean class of stone tools is believed to have evolved from the Oldowan stone tools as far back as 1.76 million years ago. It has many qualities that make it different from the previous generation of stone tools, which include shape, and potential use. Furthermore, it is important to note that the Acheulean class of tools “were the dominant technology for the vast majority of human history” (Tattersall 2012).

The Acheulean Class of Tools and Their Importance

Approximately 1.76 million years ago, early humans ceased to use the Oldowan class of stone tools and adapted the Acheulean class of tools. This set of tools all share a similar shape, that of an oval or pear. An important difference between this class of tools and the older Oldowan tools is the supplementation of using some form of hammer made of bone, or wood to better refine the forefront of the tool. Another difference is that these tools are often symmetrical, and they have a sharp edge on both sides. There are many types of tools associated with the class of Acheulean including cordate, pointed, ovate, ficron, and several others. It is important to note that not all Acheulean class tools were

constructed from the same materials. The materials that were used to construct these tools were sourced from the type of local stones. Therefore, there is a large variability in materials used for the construction of Acheulean tools. For example, “in Western Europe, the most common type of stone used for constructing Acheulean tools is flint. In Africa, rocks such as basalt and mudstone were common” (Paddayya 1976). Furthermore, “In all cases the toolmakers worked their hand-axes close to the source of their raw materials, suggesting that the Acheulean was a set of skills passed between individual groups” (Gamble 1999). The actual manufacturing process of these tools often began with roughing out the teardrop shape of the tool with a harder rock. Afterwards, the edges of the tool would be sharpened by removing flakes of stone. This process would continue until the tool was considered satisfactory by the toolmaker. The Acheulean class of tools appear to be multipurpose in nature, and their uses would include hacking branches from trees, cutting apart hunted prey, or even removing hides from prey. Acheulean toolmakers may have held some form of social power, as knowing these skills would certainly give someone a large amount of respect and admiration within early social circles.

Conclusion

The Acheulean class of tools was an incredibly important piece of human development. Being the most used set of tools in human history, it is possible to further examine them to gain insight into not only early life, but perhaps early society as well.

Cross-References

- [Human Tool Making](#)
- [Stone Hammers](#)

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Acoustic Competition

- [Vocal Competition](#)

Acquaintance Rape

- [Rape and Dating](#)

Acquisition

- [Encoding and Sleep](#)

Act Nomination Method

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Synonyms

[Acts](#); [Behavioral manifestations of adaptations](#); [Behaviors](#)

Definition

The act nomination method is a means by which evolutionary scientists can identify the behavioral manifestations of psychological adaptations.

Introduction

All adaptations, decision rules, cognitive procedures, personality traits, and mating strategies must be manifested in actual behavior, broadly conceived. The act nomination procedure is simply one method for identifying those behavioral manifestations (Buss and Craik 1983).

Early research using this method identified manifestations of personality traits such dominance, submissiveness, aggression, and cooperation. During the first phase of a study, participants would be asked: "Think of the most dominant individual you know or have observed. In the spaces below, list 10 acts this person has performed that reflect or exemplify their dominance." The instructions typically had participants nominate dominant acts that a man might perform and separately nominate dominant acts that a woman might perform.

This procedure would typically yield 100 or more distinct acts, presumably covering the sample space of dominant actions. Examples include:

He controlled the outcome of a committee meeting without the others being aware of it;
She demanded a backrub;
He insisted that others do menial chores rather than doing them himself;
She settled a dispute among members of the group.

A key benefit of the act nomination method is sampling from the entire domain of act manifestations. This method can be viewed as a "bottom-up" method of identifying important behavioral phenomena that can supplement the "top-down" or theoretically driven identification of relevant actions.

A second step in the research program involves identifying which acts are most central to the category of dominance or most prototypical of the concept of dominance. The third step involves assessing people on reported performance of the relevant acts. Performance can be identified through self-reports, observer reports such as intimate partners, or videotapes of interactions that are subsequently coded for the relevant acts.

This set of act frequency methods sometimes yields findings unanticipated by extant theoretical frameworks. In the case of dominance, for example, studies found that dominant men were more likely to perform "egoistic" or self-serving dominant acts, such as getting others to perform menial chores, sitting at the head of the table, or insisting that the group go to the dominant person's favorite restaurant (Buss 1981). Dominant women, in contrast, were more likely to perform "communal" dominant acts, such as settling disputes within the group or taking charge of the committee meeting, although dominant members of both sexes tended to perform both sorts of dominant acts.

The field of personality psychology has largely ignored the behavioral side of traits and motives. It has sometimes linked personality traits to important life outcomes, such as predicting scholastic achievement and future income (conscientiousness), divorce probability (impulsivity), and conflict within romantic relationships (emotional instability). The field has largely failed, however, to identify the behavioral manifestations of the traits that bring about these important life outcomes.

Identifying the Behavioral Output of Psychological Adaptations

Since the early explorations of act manifestations of personality traits, the act nomination methods have been more vigorously applied to phenomena closely linked with evolutionary psychology. These include acts of mate attraction (Buss 1988a), acts of mate retention (Buss 1988b), acts of mate poaching (Schmitt and Buss 2001), intersexual and intrasexual deception (Tooke and Camire 1991), status hierarchy negotiation (Kyle-Heku and Buss 1996; Lund et al. 2007), and many others. These explorations furnished research instruments that can be used by empirical scientists. And they have yielded important empirical discoveries previously undiscovered in evolutionary science. Examples include identifying different acts and tactics used by women and men to attract short-term versus long-term mates (Schmitt and Buss 1996), sex differences in

predictors of the effort allocated to mate retention, with men devoting more effort to guarding young attractive mates and women more effort to guarding mates higher in status and financial resources (Buss and Shackelford 1997).

Looking to the future, the act nomination method can be applied to domains that have yet been examined, but that must have behavioral manifestations. As one example, Cosmides and Tooby (1992) have identified a “cheater detection” adaptation in social exchange; people are selectively attentive to people who take benefits without reciprocating by paying costs. A key next question is: What do people do when they discover a cheater in social exchange? Do they walk away, ostracize, physically abuse, or inflict reputational damage? A more comprehensive understanding of cheater detection and other social exchange adaptations will require the identification and study of their behavioral manifestations of these adaptations – an agenda that can be facilitated by act nomination and act frequency methods.

Beyond cheater detection and social exchange, the agenda for identifying behavioral manifestations should be a core part of the exploration of all psychological adaptations. These include adaptations for kin detection, kin altruism, sibling rivalry, and kin favoritism; mate ejection; coalitional formation and maintenance adaptations; the behavioral immune system; evolved emotions such as envy, pride, and disgust; and many others.

Conclusion

In sum, the act nomination and act frequency methods have several forms of utility for evolutionary scientists. First, they can identify a range of behavioral manifestations in a “bottom-up” manner that provide an important complement to “top-down” or theoretically driven procedures. Second, they furnish research methods that can be used to make novel empirical discoveries, such as gender differences in the ways in which seemingly similar adaptations are instantiated in everyday actions. Third, they help with an indispensable agenda for adaptationist

researchers – identifying the actual behavioral output of psychological adaptations that has rendered them visible to natural and sexual selection.

Cross-References

- [Adaptation](#)
- [Personality](#)
- [Mating](#)

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Action

- [Selectionist Models: Implications for Behavior](#)

Action Regret

- [Sexual Regret](#)
-

Active Bait Fishing

- [Bait Fishing](#)
-

Activist

- [Peter Kropotkin](#)
-

Acts

- [Act Nomination Method](#)
-

Act-Utilitarianism

- [Utilitarianism](#)
-

Ad Exposure

- [People's Responses to Personal Ads](#)
-

Ad Hominem

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Synonyms

[Tu Quoque](#), [argumentum ad hominem](#), [character attack](#)

Definition

Ad hominem is an informal fallacy whereby an interlocutor, often on the losing side of a debate or argument, resorts to character-based attacks directed at their opponent without any reference to the content or substance of her argument.

Introduction

Making arguments and convincing others of a proposal is an essential part of human social and political life. Without engaging in arguments and the proposing of solutions, human beings would either be constantly warring with one another (why worry about convincing others when force works just as well) or forced to develop a wide range of skills. Both of these tasks, arguably, are considerably more time consuming than convincing others through well-developed and well-articulated arguments. But arguments are not always perfect, nor are we always in a position to adequately assess them. In such circumstances, arguers and assessors often employ extra-argumentative tactics to appear convincing. One such tactic is the ad hominem attack.

Traditionally, ad hominem attacks or the ad hominem fallacy take two forms: (1) Abusive and (2) Circumstantial (Johnson 2009; Putnam 2010). The circumstantial ad hominem, or tu quoque, is often employed when the principles a person advocates in her argument are inconsistent with her past actions. In colloquial terms, this is the classic “practice what you preach” objection (Johnson 2009; Putnam 2010). Abusive ad hominem attacks, on the other hand, involve a “direct attack on the arguer’s character” (Johnson 2009; Putnam 2010). That is, instead of appealing to inconsistency between principles promoted and actions taken, abusive ad hominem attacks are less sophisticated by going after a person’s character traits without appeal to logical or behavioral consistency. For example, someone might charge the arguer with having poor aesthetic taste simply based on their political or otherwise irrelevant character trait.

Are Ad Hominem Attacks Ever Reasonable?

Given the description above, it is difficult to see the argumentative worth of employing any sort of ad hominem attack. To do so, one risks being labeled an unreasonable and irrational interlocutor. Recently, however, much work has been spent challenging the traditional position that ad hominem attacks are irrelevant in evaluating an argument. In *Reconsidering the Ad Hominem*, Christopher Johnson argues that abusive ad hominem attacks, in certain limited circumstances, can be quite useful and acceptable. There are three such instances. First, and in light of our epistemic and cognitive limitations, ad hominem attacks can be reasonable when we are not positive of the arguers premises. In this instance the evaluator is telling the arguer: “While I am not sure of your premises, you have the reputation of being a swindler and cheat. Thus, one can give very little weight to the belief you are now telling the truth.” The second scenario involves challenging an arguer’s interests or background so as to cast doubt on her ability to assess certainty. Depending on the arguer’s background or motives, their interpretation of facts and her demand for certainty may be said to be too low or too high (2009). Third, and in some ways similar to the second scenario, one might appeal to ideological differences and background for drawing concerns of the arguer’s claims. Here, we might think of the classic scenario where a progressive politician critiques the policy recommendations of a conservative politician based purely on their ideological differences (as opposed to whether the policy recommendations fail to improve lives or solve a developing problem) (Johnson 2009).

Ad Hominem Attacks and Decision-Making

Contrary to traditional economic theory, behavioral economics posits that *homo economicus* fails both descriptively and pragmatically (Jolls et al. 1998). Setting aside some of the controversial insights of the behavioral economic program, one thing that is

of interest to us here is the insight that human beings often employ heuristics when information costs are high. In other words, human beings have what is called bounded rationality. According to Gigerenzer and Gaissmaier (2011), a heuristic is “a strategy that ignores part of the information, with the goal of making decisions more quickly, frugally, and/or accurately than more complex methods.” Arguably, the employment of the ad hominem meets some, if not all, of these elements. In fact, the first scenario described above applies to Jolls et al.’s notion of bounded rationality. Decision-makers such as policymakers are under austere time constraints and may find it difficult to read and digest policy options proposed by their opponents. Thus, it appears reasonable, under the conditions, that they resort to abusive ad hominem attacks quite often.

Given these insights, it might be further argued that employing ad hominem attacks during an argument might contribute to our cognitive efficiency. As rational decision-makers, we are not always equipped with the most up to date and relevant information for all situations where a decision or judgment is required. As such, it is not only more convenient, but also necessary to employ heuristics or cognitive shortcuts that might allow us to make the best decision possible given these cognitive and intellectual restraints. Here, ad hominem attacks can be quite useful. Assessing, let alone winning, an argument does not always come easy. The average arguer will find it difficult to remember or recall all the relevant facts necessary to properly assess or produce an argument. As such, employing ad hominem attacks can be quite useful (Van Eemeren et al. 2000; Yap 2013).

Conclusion

In light of these insights, it would appear that ad hominem attacks are not to be dismissed as intellectually lazy and suspect. To the contrary, they can often prove to be significant resources in light of our cognitive and epistemic limitations. Further, one might also argue that employment of such tactics is not always methodologically or morally dubious. This is not say that there is no

instance in which an ad hominem attack can be deemed unreasonable. But it is important for communities to determine under which conditions such attacks are excusable and/or reasonable and when they are merely cheap rhetorical tactics.

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Ádám Miklósi

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Synonyms

[Professor](#); [Researcher](#)

Definition

Ádám Miklósi (Ph.D., D.Sc.) is a professor and researcher at Eötvös Loránd University (Hungary) where he is the Director of the Family Dog Project and the Head of the Department of Ethology.

Introduction

Dr. Ádám Miklósi has been studying dog-human relationship from an ethological perspective for

nearly two decades and, along with his colleagues, has have revealed a number of interesting findings and insights when investigating parallels between the behavior of people and dogs (“Ádám Miklósi” [n.d.-a](#)). His most recent research focuses on communication and social learning, but he is also interested in canine emotional expression and in the genetic underpinnings of dog behavior (“Ádám Miklósi” [n.d.-a](#)). Moreover, because dog behavior provides the opportunity to theorize and design social robots that are inspired partly by the behavior of the family dog, Miklósi has worked on formulating the direction of a new research area: “etho-robotics” (“Ádám Miklósi” [n.d.-a](#)). He has authored more than 270 publications on dogs, animal cognition, animal science, animal behavior, behavioral biology, ethology, human-robot interaction, behavioral science, behavioral ecology, and primatology (“Ádám Miklósi” [n.d.-b](#)).

Projects and Research

Miklósi was born September 25, 1962, in Budapest. He received his Ph.D. in 1995 in biology and his Doctor of Science in 2005 (“Ádám Miklósi” [n.d.-a](#)). He has also received multiple awards for his work, including the Frank A. Beach Comparative Psychology Award (The best paper of the year in the *Journal of Comparative Psychology*) in 2003, the Distinguished Scholar Award in 2010 from the International Association of Human-Animal Interaction Organisation, the ELTE Faculty of Natural Sciences prize for coaching science students in 2011, and the Pál Juhász-Nagy prize for Talent Management in 2011 (“Ádám Miklósi” [n.d.-a](#)).

The Family Dog Project

The Family Dog Project is the largest canine research group in the world. It was founded in 1994 and is comprised of researchers from three different European institutions: Eötvös Loránd University, Department of Ethology and the Hungarian Academy of Sciences, Comparative Behavioral Research Group and the Comparative Ethology Research Group. The Family Dog

Project was founded in 1994 to study the dog-human relationship, and it has since published over 100 papers in peer-reviewed journals on behavioral and cognitive aspects of dog-human relationships. Along with publications, they also engage in public outreach through free online seminars and video abstracts describing various research and conclusions drawn by researchers with the Family Dog Project.

Researchers with the Family Dog Project hypothesize that dogs evolved to survive alongside humans, and they aim to understand the contributions of both humans and dogs to the dog-human relationship. This means they study not only the mental abilities of dogs but also any human or dog behavior that is related to the dog-human bond. Thus, the Family Dog Project has not only revealed important insights in dogs but also in us, people (“Family Dog” n.d.).

The Family Dog Project hosts a comprehensive website (<https://familydogproject.elte.hu/>) where dog owners can sign up to participate in research with their dogs. Citizens living near Budapest, Hungary, are welcomed to join in live participation at the universities, while dog owners from farther away are invited to fill out online surveys.

Book Publication

Dr. Miklósi is the author of *Dog Behaviour, Evolution and Cognition*. The second, fully updated edition was published by Oxford University Press in 2014. The book advertises itself

This is the first book to collate and synthesize the recent burgeoning primary research literature on dog behaviour, evolution, and cognition. The author presents a new ecological approach to the understanding of dog behaviour, demonstrating how dogs can be the subject of rigorous and productive scientific study without the need to confine them to a laboratory environment. *Dog Behaviour, Evolution, and Cognition* starts with an overview of the conceptual and methodological issues associated with the study of the dog, followed by a brief description of their role in human society—almost a third of human families share their daily life with the dog! An evolutionary perspective is then introduced with a summary of current research into the process of domestication. The central part of the book is devoted to issues

relating to the cognitive aspects of behaviour which have received particular attention in recent years from both psychologists and ethologists. The book’s final chapters introduce the reader to many novel approaches to dog behaviour, set in the context of behavioural development and genetics. Directions for future research are highlighted throughout the text which also incorporates links to human and primate research by drawing on homologies and analogies in both evolution and behaviour. The book will therefore be of relevance and use to anyone with an interest in behavioural ecology including graduate students of animal behaviour and cognition, as well as a more general audience of dog enthusiasts, biologists, psychologists and sociologists. (Miklósi 2014)

Summary of Research

Dr. Miklósi’s main research focus is on dog behavior and cognition, but his interests are much broader. For dogs, he has been involved in numerous studies on dog-human interactions. One of his most cited papers is the article “Comparative social cognition: what can dogs teach us?”. In this article, Dr. Miklósi and his coauthors takes the position that dogs, via domestication, are adapted for living with humans and have marked changes in their social interactions with humans based on this evolution (Miklósi et al. 2004). In addition, Dr. Miklósi is interested in the evolution of dogs; thus, he has conducted significant research comparing dogs and wolves in their abilities to understand human communication cues. One of his most cited articles demonstrates a large difference between dogs and wolves in their communication with humans: dogs look at human faces and wolves don’t (Miklósi et al. 2003). This may reflect how dogs have evolved to live alongside humans. One communication cue of particular interest to many researchers right now is the ability to understand human pointing gestures. Dr. Miklósi has studied the ability of many other species (aside from dogs and wolves) to follow humans points. He wrote a review article about the pointing abilities in many species, specifically discussing the influence of domestication and ape competitive sociality (Miklósi and Soproni 2006). Dr. Miklósi has more recently branched out of the comparative fields and into robotics. Dr. Miklósi has

started studying how humans interact with robots and electronic devices, for example, in human interactions with robot-dog behavior (Miklósi and Gácsi 2012).

Conclusion

Dr. Miklósi is a leader in the field of comparative cognition and ethology, specializing in dog-human social interactions. He is particularly interested in the role of domestication in the evolution of dog behavior and the dog-human relationship. Dr. Miklósi performs many roles in this field: he is a prolific author of scientific research and is leader of the largest dog research group in the world, but he has also engaged in significant public outreach about dog cognition with the publication of his book, *Dog Behaviour, Evolution and Cognition*, as well as the free online seminars available via the Family Dog Project's website.

Cross-References

► [Canines](#)

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Adaptation

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Synonyms

[Adaptationism](#)

Definition

An adaptation (in the evolutionary sense) is a feature/trait that serves a particular function in an organism's environment and improves that organism's ability to survive (i.e., its fitness).

Introduction

Although the word adaptation is used in a number of different ways and its definition debated, most biological researchers agree that adaptations offer organisms higher fitness in their environments, thus enabling the organism to survive and reproduce (Kitano 2002). Adaptations arise as a result of evolutionary changes in the genetic constitution of a population of organisms (Zeigler 2014). Thus, an evolutionary adaptation may be considered as both a "process" impacting and organisms' morphology, as well as a "feature" of the organism itself (Bock 1980).

Individual adaptations also referred to as adaptive traits/features are thus particular traits of the organism which enable species survival (O'Brien and Holland 1992). These adaptive traits are inherited by offspring from their parents and arise through processes such as genetic mutations, interactions between these genetic components

and the environment, or copying or *recombination* errors in the genetic material (Boyd and Silk 2009). For an adaptation to persist in a given population, it must increase the reproductive success of the population. However, changes in the population or environment may also result in adaptations becoming *vestigial* (i.e., *useless*) (Zeigler 2014). Adaptations may be observed at multiple levels of biological organization, all the way from the individual or organism to that of the population or species (Krimbas 2004).

Factors Important in Considering Adaptations

While the concept of an adaptation is intimately linked to that of the environment (i.e., how well suited is the feature to the demands of the environment), it is important to note that identifying the force of selection responsible for the adaptation is also an essential consideration (Bock 1980). To demonstrate that an adaptation has occurred, one would ideally need evidence indicating that natural selection is responsible in driving any underlying genetic changes associated with the feature. Given the difficulties with measuring natural selection (e.g., Morrissey and Hadfield 2012), the approach in comparative studies has been to infer that adaptive evolution has occurred based on our investigations of mean phenotypic change and the assumption that natural selection exerts a powerful influence on all organisms (Endler 1986). At a population level, adaptive traits tend to increase in frequency due to the reproductive advantage conferred on members carrying these traits (Tooby and DeVore 1987). This makes an adaptation a reliable and identifiable characteristic of a species (Krasnow and Truwx 2017). A further important feature of an adaptation is that an adaptation is not considered the optimum solution (i.e., the best or most favorable solution) to a given environment (Brock 1980) but is in fact a response to an ancestral problem, manifested in decedents of the species (Boyd and Silk 2009). This has led to debate on the role of adaptation in the evolutionary process.

While an organism might possess an adaptation, it will also possess several other features which arose as byproducts of the evolutionary process and were not the targets of selection

(Gould and Lewontin 1979). Adaptations may also be constrained by other features as is seen with developmental constraints which prevent the occurrence of mutations that have a deleterious effect on the organism. An example of a developmental constraint is the near universal occurrence of seven cervical vertebrae in all mammals due to pleiotropic effects linked to increased cancer risk (Galis 2002). Many attributes of organisms arose as evolutionary byproducts and are thus not amenable to an adaptive explanation (Gould and Lewontin 1979).

Examples of Adaptations

Adaptations can be grouped into a number of different categories depending on the level of comparison. For instance, comparative anatomists might be interested in structural adaptations which are physical changes to the structure of an organism. An example of a structural adaptation is the development of wings for flight or evolutionary changes in the pelvis to support bipedal locomotion. Other scientists might be interested in evolutionary changes to the behavior of an organism known as behavioral adaptations. An example of a behavioral adaptation includes the emergence of sociality in a species (e.g., pack hunting behavior or communication).

While adaptations are often considered solutions, which emerged in the more distant evolutionary past, some adaptations are more recent. For example, there is evidence of selection resulting in changes to human diet and providing pastoral communities with the ability to digest lactose (Tishkoff et al. 2007). Similarly, there is strong evidence of selection resulting in structural changes to human blood, and thus conferring carriers of this trait with resistance to the malaria parasite (Allison 1954).

Conclusion

While adaptations are difficult to identify and test, the concept of an adaptation remains central to understanding the evolutionary process and in helping us to reconstruct the evolutionary history of all species, including our own.

Cross-References

- [Adapted Mind, The](#)
- [Adaptationist Program, The](#)
- [Adoption Preferences](#)
- [Biological Function](#)
- [Boredom as an Adaptation](#)
- [Evolution](#)
- [Evolutionary Medicine](#)
- [Evolution of Intelligence](#)
- [Evolution of Teaching](#)
- [Evolution of the Brain, The](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Human Enculturation](#)
- [Natural Selection](#)

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Adaptation and Natural Selection

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Definition

In his book, *Adaptation and Natural Selection*, George Williams (1966) discusses what is meant by the term “adaptation” and what can be done to further the study of that phenomenon. Throughout the course of the book, he provides an overview of past research on the subject and challenges misconceptions, such as group selection, which he believes to be misguided attempts at understanding adaptation.

Introduction

George Williams’ 1966 book, *Adaptation and Natural Selection*, seeks to define what is meant by researchers discussing the adaptation of species and clarify differences in understanding of the term and the process it describes. The main purpose of adaptation, as Williams understands it, is to promote the survival of the individual and that individual’s ability to reproduce in order to preserve their genes. Through the process of evolution, adaptations that are useful for the survival of the individual are retained and passed on to future generations. Contrary to the beliefs of some other scientists at the time, however, Williams asserts that such adaptations do not necessarily make for a more complex organism with more complex DNA; rather, adaptations are substituted in, not added to, an ever-increasing cumulative DNA.

Adaptation, he argues, does not necessarily progress the species to a more complex one, but a more fit one.

Another key concept outlined by Williams is the difference between the passing on of genotypes and phenotypes. This distinction proves important in his discussion of the presence or lack thereof of group selection. He argues that while an individual's environment can affect the phenotypic expression of their genes, that environment is not necessarily influencing which genotypes will be passed to the next generation. This is because while the environment can cause variation in the expression of phenotypes, that expression is not what is passed on. Though several organisms might express a genotype differently, they all possess the same genotype, and in the end, it is that genotype that is passed to the next generation. The fact that it is the genotype, and not the phenotype, that is passed through generations provides a foundation for Williams' criticism of the idea of group selection.

To distinguish between individual and group level selection, Williams refers to organic and biotic adaptation, respectively. An adaptation that produces modifications to the individual that aids in its survival and reproduction is referred to as organic adaptation, which leads to the evolution of the species. In contrast, a biotic adaptation is an adaptation that promotes group survival and cannot be explained by organic evolution. He argues that while biotic adaptation might occur, it is difficult to find an instance where what appears to be biotic, or group, evolution is actually the cumulative result of individual adaptations. Whereas it might seem like a group has adapted together, the truth in most situations is that the group is composed of adapted individuals, and this individual adaptation is what contributed to the survival of the group.

Conclusion

Williams concludes that in order to be truly useful to the study of organisms and their evolution, the term "adaptation" needs to be clearly defined and the field of study related to the adaptive traits of

organisms similarly narrowed down. Previous researchers, he argues, have applied the term too liberally, labeling traits that do not have a true directed purpose as adaptations when they are not. Rather, a true adaptive trait should be defined as one that serves a tangible function produced through natural selection and could not have happened by chance, citing the development of the eye as one such adaptation; it is obvious that the eyes of organisms have an expressed purpose, which has been honed over time through selection processes and is not a chance development that happens to benefit the organism. Once this more narrow view of what an adaptation is accepted, then a new field of study – which he tentatively refers to as teleonomy – will be able to emerge and dive deeper into what constitutes an adaptation and how they function.

Cross-References

- [George Williams](#)
- [George Williams on Group Selection](#)

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Adaptation Failure

- [Maladaptations](#)

Adaptation for Single Births

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Synonyms

[Gestation](#); [One offspring](#); [Pregnancy](#)

Definition

The propensity for primates, including humans, to have only one fetus at a time.

Introduction

Mammalian infants are born at either of two stages: altricial or precocial. Altricial infants are those that are born immature and helpless, e.g., rodents. Precocial infants are born able to move about soon after birth, e.g., deer. Animals that are born precocial, like primates, are K-selected, meaning that they give birth to a smaller number of offspring at a time (MacArthur and Wilson 1967; Martin 1983; Pianka 1970). Humans are part of a group of primates known as “higher primates” which typically give birth to single offspring at a time (Martin 2007). Having fewer offspring at a time allows the fetus to have a larger body size at birth and be more developed at birth in order to increase the chance of survival (Martin 2013). The adaptation for having a single fetus at a time may be a result of the ancestral morphology, or shape, of the uterus.

Uterine Morphology

During pregnancy, a fetus develops and grows in the uterus. Placental mammals have a uterus which has two chambers, or spaces, allowing for multiple fetuses to gestate, or grow, at a time (Martin 2013). Women are one of the few mammalian exceptions that have a uterine morphology where the uterus only has a single chamber (Martin 2013). The single-chambered uterus develops early in-utero from the fusion of reproductive tracts (Martin 2013). Today, a low percentage of women (0.033%) are born with a two-chambered uterus (Martin 2013). Although these women can still have viable pregnancies, their babies are typically born premature and via medical interventions, such as cesarean section (Martin 2013).

The adaptation for humans to have single births may be a result of the overall space

provided in the uterus to support developing fetuses. Primates are born at a more developed, or precocial, stage and thus are typically born at a relatively larger body size compared to altricial mammals. A fetus that is larger therefore affords less space in the uterus to support multiple fetuses to develop (Hamlett and Wislocki 1934). With fewer fetuses in the uterus at a time, a fetus can have a longer gestation, or pregnancy, period. A lengthened gestation period provides extra time for the fetus to grow in body size. Gestation length in precocial species is almost three times longer than that of altricial species (Martin 2007). This trend extends within precocial species, such as the primates. Relative to maternal body size, apes have longer gestation lengths than monkeys. Humans, as apes, have a gestation period of, on average, 40 weeks, whereas some monkeys have gestation periods of less than half that amount of time.

Another way to view how the gestation period influences the number of offspring is to consider the amount of energy it takes to gestate and grow a fetus. Increased gestation lengths in humans and the other apes increase the energetic burden placed upon the mother through the prolonged nutrient supply to the fetus. The timing of birth is now thought to be due to when the maternal metabolic limit is reached, and the mother can no longer support the fetus's caloric needs (Dunsworth et al. 2012). In single birth, this metabolic limit is reached at 40 weeks and then birth occurs (Dunsworth et al. 2012). In multiple births, however, the mother's metabolism must support more than one fetus, increasing her metabolic demands throughout the gestation. This decreases the length of gestation, as the Mother's metabolic limit will be exceeded sooner rather than when the Mother is only providing for one fetus. Women who have twins have an average gestation length of 37 weeks, three weeks earlier than what is seen in an average singleton birth (Martin 2013). An infant born this early also affects the birth weight, coinciding with the standard threshold for premature infants (Martin 2013).

Decreased time in utero decreases the birth weight of the infant. The average birth weight of a single human infant is 7.5 pounds whereas in twins, the average birth weight decreases to, on

average, 5.25 pounds (Martin 2013). Premature births and lower birth weights are associated with greater health risks such as coronary heart disease and hypertension (Trevathan 2010). Additionally, premature infants require more direct care from the Mother in order to survive than those infants born fully developed. In premedicinal times and throughout our evolutionary history, this would have caused excess strain and burden on the Mother and may have resulted in a higher infant mortality.

Evolutionarily, primates are adapted to giving birth to one infant at a time because it is beneficial for their reproductive success. The metabolic limit for fetal growth is determined by the mother (Dunsworth et al. 2012), and having a single offspring allows for a longer gestation period and a healthier infant. A single fetus can grow larger and more developed in utero without conceding space to multiple fetuses.

Conclusion

Humans typically give birth to one offspring at a time due to the morphology of the human uterus only supporting one embryo at a time. The single-chambered uterus evolved early in primate evolution and allows the fetus to be born more developed, as well as larger in body size. These adaptations ensured a better chance at survival in the evolutionary environment in which we, as primates, evolved, as well as in today's modern world.

Cross-References

- [Fertility](#)
- [Narrowing Birth Canal](#)
- [Reproductive Strategy](#)

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Adaptationism

- [Adaptation](#)
- [Adaptationist Program, The](#)

Adaptationist Framework

- [Adaptationist Program, The](#)

Adaptationist Perspective

- [Evolutionary Social Psychology](#)

Adaptationist Program, The

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Synonyms

[Adaptationism](#); [Adaptationist framework](#)

Definition

An approach to testing theories about species-typical traits that focusses on the fit between an organism's traits and relevant features of that species' ancestral ecology.

Introduction

How do birds know when to fly south? How do they find their way? How do people learn to speak and read? When are they generous? When are they cruel?

When studying these and other questions about the nature of naturally selected organisms, one can gain a distinct advantage by considering the ecology in which the organism's ancestors evolved and what problems they faced. The adaptationist program offers a framework and approach for testing theories about naturally selected organisms.

The Adaptationist Framework

An adaptationist does not assume or purport that all (or even most) features of organisms are *adaptations*. An organism, or the "nature" of a species (e.g., "human nature"), can be dissected into an infinite number of features (e.g., having two arms, possessing a right hand, having an odd number of fingers on that hand, the relative gravity between those fingers, the configuration of those fingers that enables grasping, and so on). Not all features have specific adaptive value. The basic commitment of the adaptationist theoretical orientation is that – out of this impossibly large set – it is useful to think of a particular feature as being one of three kinds of things: adaptations, by-products, or noise (Tooby and Cosmides 1992).

Adaptations are those features that are themselves a solution to an ancestral adaptive problem. These features have an inheritable basis that increased in frequency in the population over evolutionary time *because* the individuals exhibiting these features had a reliable reproductive advantage over others (Tooby and DeVore 1987). Because of this causal relationship, the design of adaptations can be understood in part

by the fit between the form of the adaptation and the function of solving its adaptive problem. Adaptations, therefore, are reliable characteristics of a species: they tend to be common or universal in the species – reliably developing at some point in the life span – given the necessary environmental input.

While adaptations are those features that solved an adaptive problem over evolutionary history, the phenotype created by this ancestral selection will have many features that did not themselves solve any adaptive problem. Rather, they are by-products of the adaptation. By-products are reliable characteristics of a species, like adaptations, but by-products were not the target of selection that drove their own existence and instead were merely carried along with the feature under selection (the adaptation).

For example, the blood of humans and most vertebrates has the features "can bind and transport oxygen" and "appears red when oxygenated." The former feature is an adaptation, as binding and transporting oxygen through the body solves a crucial adaptive problem. The latter is probably not an adaptation, as turning red when oxygenated solved no known adaptive problem. Instead, we can best explain the reliable presence of the "appears red when oxygenated" feature as a by-product of the fact that blood cells evolved to use the iron in hemoglobin to solve the "bind and transport oxygen" adaptive problem and the physical properties of the way iron and oxygen bond.

Features that are neither adaptations nor by-products are noise. Noise refers to features that are not reliable characteristics of a species. In the blood example, a noise feature would be whether you have an odd or even number of blood cells; you might have one or have the other, but it is random and not a reliable feature of our species.

The Adaptationist Approach

The adaptationist program provides an approach for testing theories about species-typical traits. Because of the fit between features of an adaptation and relevant features of the ancestral ecology (like the fit between features of a lock and a key), a theory that a trait is an adaptation for

solving a particular adaptive problem necessarily entails predictions about the features the trait should and should not have (Williams 1966). In contrast, a theory that a trait is a by-product of another adaptation makes different kinds of predictions about the features the trait should have (e.g., they should not be particularly well designed for solving the by-product function). That is, a primary form of evidence for testing adaptationist theories is *design evidence*: evidence that features of the trait are specialized and coordinated in such a way to solve a particular adaptive problem efficiently and economically over the range of ancestral conditions. The justification for this appeal to design evidence is that – in the absence of natural selection for features that solve a particular adaptive problem – it is exceedingly unlikely that a collection of random mutations will fixate in the genome together by neutral drift. This is a probabilistic inference similar to the inference made in hypothesis testing that the data are exceedingly unlikely if a null hypothesis is correct. Here, the implicit null model is that there was no specific selection for solving the adaptive problem in question. Following up on the blood example, consider a theory that blood involves an adaptation for appearing red when oxygenating as a signal of vitality to others. This theory predicts there should be design features enabling broadcast of the signal (perhaps arteries close to the body surface, transparent skin, obscured veins, etc.). This theory's predictions fail, especially in contrast to the competing theory that blood evolved for oxygen transport (predicting features like a vascular system to distribute oxygenated blood, architected interaction with the respiratory system for gas exchange, etc.), and that redness is a by-product. Plausible theories about particular adaptations or by-products must make specific predictions that can be tested in this way.

Critiques of the Adaptationist Program

The adaptationist program has been widely influential and is the foundation of work in evolutionary biology and evolutionary psychology. It has also been criticized within the academic

community and the popular press, often on the basis of what has been termed “Panglossianism” and “just so storytelling” (Gould and Lewontin 1979). The Panglossian critique (named for the endlessly optimistic Dr. Pangloss) argues that work in the adaptationist program assumes that all traits are adaptations, seeing function where none meaningfully exists. By this definition, adaptationism fails if any features of any organism are not adaptations. However, as illustrated above, the adaptationist program explicitly opposes the view that all traits are adaptations; in fact, many if not most of the features of organisms are properly construed as by-products on the adaptationist account.

The “just so storytelling” critique argues that adaptationist theories make no testable predictions and are merely an exercise in telling stories that things are “just so.” However, as illustrated above, adaptationist theories – that is, theories that a trait is an adaptation for solving a particular adaptive problem, or a by-product of a trait that is an adaptation for solving a particular adaptive problem – are explicitly testable theories because they make predictions about the designs the trait should possess. In fact, the foundational premise of the adaptationist toolkit is that adaptationist theories are uniquely generative of predictions about the features of organisms; no other class of theory can predict in advance previously unknown features of organisms.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adapted Mind, The](#)
- [Founders of Evolutionary Psychology](#)
- [George Williams](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

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Adaptations

► [Evolution of Adaptations](#)

Adaptations for Navigating Social Hierarchies

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Synonyms

[Behavioral and mental traits for navigating social hierarchies](#); [Strategies for navigating social rank hierarchies](#)

Definition

Adaptations for navigating social hierarchies are the evolved behavioral traits, cognitive and social skills, and emotions (reflected in human brain structure) that facilitate social hierarchies. They are manifested in hierarchical social categorization, dominance, prestige, or leadership motive systems for attaining and maintaining high social rank and verbal and nonverbal symbols signaling status.

Introduction

A hierarchical organization of social relations is ubiquitous in the animal kingdom (including

among humans). This is a starting point for considering the issue of adaptations for navigating social hierarchies in human society. Based on that, the representatives of the humanities and social science analyze the common evolutionary mechanisms of the origin of such adaptations, namely, evolved behavioral and mental traits (strong associates with brain system), that have contributed to the survival of our ancestors. These continue to determine the psychology and social behavior of contemporary humans.

The entry considers the most elaborated now evolved adaptations for navigating social hierarchies, such as an ability in humans to categorize and recognize others' roles in social hierarchies, motive systems (dominance, prestige, leadership) that stimulate the attainment and maintenance of high social rank, and verbal and nonverbal symbols signaling social status.

Hierarchical Social Categorization

Social categorization implies classification of people (as well as objects) according to different criteria that result in classifying them as different social groups (e.g., gender, race). One of the basic criteria for such differentiation is their position on the hierarchical ladder (according to perceived power, amount of different resources, skills, and so on). From an evolutionary perspective, hierarchical social categorization – an ability to recognize people as part of a certain social group associated with high or low social rank – is an evolved adaptation that facilitates the navigation of social hierarchies and thereby increases the chances of survival and reproductive prospects, at least in our ancestors.

It is now proposed that the ease, fluency, and desirability with which we perceive the social rank of others and identify our own status in the process of social comparison point to human preference in hierarchical social relations, although people may claim the opposite (Zitek and Tiedens 2012). Perhaps this is because the hierarchical principle for social group organization is an efficient way to maximize group cohesion and productivity (Koski et al. 2015). As Qu

and colleagues emphasize: “Not only are there benefits to obtaining a dominant position within the hierarchy, but the accurate representation of dominance relationships can help individuals form effective social alliances” (Qu et al. 2017, p. 893).

However, in contemporary society hierarchical social categorization may cause prejudice, biased perceptions, and stereotyped attitudes. This is so because we have often based our social classifications on signals and cues that do not match modern contexts. For example, we can ascribe leadership to those who are tall and physically strong. Such traits were important for leaders of our ancestors in savanna environments but are not very important for managers of modern organizations (the mismatch hypothesis, see, e.g., Li et al. 2017, Van Vugt et al. 2008).

Motive Systems for Navigating Social Hierarchies

Motive systems that stimulated humans to obtain and maintain high social rank can be different (more about this below), but all of them have a common evolutionary foundation. High status was a guarantee of reproductive success in ancestral communities. The recent studies demonstrate that even in modern society, men (but not women) with high social rank (measured by personal income) have more offspring than those with low incomes (Hopcroft 2015).

Dominance (force or the threat of force) and prestige (freely conferred deference) are considered dually evolved strategies for navigating social hierarchies (Henrich and Gil-White 2001).

The dominance strategy is historic first and is held in common with nonhuman primates, while prestige appeared later and is unique (or less developed in other animals) to human society. The dominance pathway “arose in evolutionary history in response to agonistic conflicts over material resources (e.g., food, mates), which were common among nonhuman species, but also persist in contemporary human societies in the form of psychological conflicts.” (Cheng and Tracy 2014, p. 5).

The prestige strategy emerged when our ancestors lived in relatively small hunter-gatherer communities (Maner and Case 2016, p. 7). Henrich and Gil-White consider prestige status a product of the changes in selective environments when cultural transmission was manifested in “abilities to identify and preferentially to copy models wh[ich] are likely to possess better-than-average information” (Henrich and Gil-White 2001, p. 167), which became important for our ancestors’ survival. Those whom others copy as skilled/knowledgeable models (the variant of paying deference) achieve their status through knowledge, expertise, performative skills, and the like. Such preferred models have prestige (Henrich and Gil-White, p. 167). Thus, prestige is a consequence of the evolution of direct social learning capacities (*infocopying* ability imitation) that differ from the analogous capacities in other species (Henrich and Gil-White, p. 173, with reference to others).

Besides the differences in phylogenetic history, dual strategies for navigating social rank hierarchies differ according to the source of deference, mechanisms of influence, nature of group hierarchies, role of social bonds, and personality correlates (Maner and Case 2016).

Deference to the dominant person is based on force or threat of force, whereas it is freely conferred by others to prestige status persons (e.g., Maner and Case 2016; Henrich and Gil-White 2001).

Henrich and Gil-White emphasize that prestigious people are never feared. The domain of words associated with prestige includes terms such as influence (not authority, or dominance, or power), honor, reputation, homage, reference, deference, and the like (Henrich and Gil-White, p. 168). The mechanisms of influence for prestige are admiration, respect, liking, and social modeling and for a dominance strategy are coercion, intimidation, aggression, and manipulation of reward and punishment (Maner 2017; Maner and Case 2016; Cheng and Tracy 2014; Henrich and Gil-White 2001).

Dominance and prestige adaptations for navigating social hierarchies are observed in different social environments. The maintenance of dominant social rank suggests steep

hierarchical relations with large and rather fixed distances between the top and lower positions. The prestige strategy is associated with relatively flat social relations and a domain-specific hierarchy (Maner and Case 2016).

The core of a dominance strategy comprises the social skills to form temporary coalitions to achieve certain goals for improving and maintaining high status. Navigating prestige in hierarchical relations involves the proposed abilities to form and maintain trusting social bonds for a long time (Maner and Case 2016).

The differences in personality correlates are also fixed. Thus, according to Maner, being “high in narcissism, hubristic pride, aggressiveness, disagreeableness, Machiavellianism, and psychopathy” is associated with a dominant status person, while being “high in agreeableness, self-esteem, need for affiliation, social monitoring, fear of negative evaluation, and conscientiousness” are the traits of a prestige-based high status person (Maner 2017, p. 2). Moreover, researchers (e.g., Van Vugt 2006) point to a substantial genetic component in such personality traits as extraversion, intelligence, empathy, and ambition that are associated with leadership. At the same time, nowadays it is emphasized that no clear evidence exists concerning genes that exclusively promote social dominance or subordination (van der Kooij and Sandi 2015).

Suessenbach and colleagues add leadership to dominance and prestige motives for obtaining high status. Although leadership itself can be achieved through dominance or prestige strategies, the authors state that the desire to be leader, i.e., “a desire to take initiative and responsibility in one’s group to direct it to a common group goal” (Suessenbach et al. 2019, p. 9), can be a functionally autonomous motive promoting hierarchical organization in social groups. Add to that the idea of Van Vugt, who developed an evolutionary theory of leadership. Using empirical data he has proved that under selection pressure – the necessity to solve problems in a coordinated way – the behavioral role strategies were formed in leader and followers (e.g., Van Vugt 2006). Thus, such basic role distinction also contributes to promoting social rank hierarchies in human society.

Van Vugt (2006) and others (e.g., Bastardo and Van Vugt 2019) also propose that leadership (following implies voluntarily deference) and dominance (following does not freely confer influence) are different evolutionary pathways to attaining high status. The main adaptive function of leadership is achieving coordination and collective action by a group of individuals (King et al. 2009). The contemplated followership strategy for navigating social hierarchies is less studied. However, in research already conducted (Bastardo and Van Vugt 2019), following the right leader is considered as an usefully evolved adaptation in the ability to reap benefits from coordinated action.

Communicating Systems Signaling Social Rank

Emotions, verbal and nonverbal communication signals, cues, etc. are also considered as evolved adaptations to hierarchical social relations and a result of solving certain adaptive problems.

In Steckler and Tracy’s (2014) research, the facilitated role of emotions in individuals’ navigation of the social hierarchy is examined. First, experiences of a certain emotion motivate individuals to attain, improve, or maintain social rank. Second, displaying status-relevant information to others through status signals and cues suggests that “emotion expressions may help individuals avoid costly disputes that can arise when rank levels of the various parties are unknown” and “may allow both parties to quickly know how the social interaction should proceed” (Steckler and Tracy 2014, p. 202). Third, recognizing others’ emotions promotes adaptive behavior, for example, deferring to high-level status (Steckler and Tracy 2014, pp. 201–203).

Henrich and Gil-White emphasize that prestigious people do not initiate grudges in subordinates but love, respect, awe, and deference (Henrich and Gil-White 2001). Those who have a dominant status experience “hubristic” pride (marked by arrogance and conceit, correlated with aggression and even antisocial behavior), whereas with prestige, “authentic” pride is manifested in accomplishment, confidence, and

successful social relationships (Cheng et al. 2010; Tracy et al. 2009).

Pride is considered as part of the affective-motivational suite underlying different avenues of rank attainment (Cheng et al. 2010). Among other factors relevant to attaining, maintaining, and communicating social rank emotions (e.g., shame, envy, contempt, admiration, disgust, anxiety, fear, happiness, sadness), pride is considered as an evolved adaptation that plays a central role in the orchestration of hierarchical social relations (Tracy et al. 2010).

Although the majority of research does not differentiate between communication systems of dominance and prestige, the adaptive pathways for obtaining rank seem to have differences. Thus, Witkower and colleagues have recently demonstrated that people with dominance and prestige strategies communicate their status through different nonverbal displays. Generally, dominance strategies are associated with expansive behavioral displays (including expressions of pride) that feature “arms extended out from the body, with hands either on hips or raised above the head with clenched fists, chest expanded, head tilted slightly upward, and a small smile” (Witkower et al. 2019, p. 5), whereas prestige entails “expansiveness, smiling, and an upwards head tilt” (Witkower et al. 2019, p. 62).

Finally, language skills are also considered as instruments for obtaining high social positions via both coercive and prosocial strategies. For instance, Massey-Abernathy and Haseltine (2019) revealed that the more vocal an individual was, the more dominant he/she was rated by others. Cheng et al. (2016) demonstrated that in face-to-face group interactions, raising and deepening vocal pitch were associated with low and high rank accordingly.

Conclusion

From an evolutionary perspective, the human mind comprises many functional psychological adaptations specifically designed to solve the particular adaptive problems of ancestral group life (e.g., Van Vugt et al. 2008). Among such problems is the challenge of collectively coordinating

action in achieving certain goals that facilitated the survival of the human species. Adaptations for navigating social hierarchies were one of those evolved decisions.

It is proposed that evolved behavioral patterns, cognitions, emotions, and underlying motive systems comprise dual strategies for navigating social hierarchies: dominance (based on fear and force) and prestige (stems from expertise and skills). The biological predisposition to form hierarchical social relations based on leadership and followership is also considered among such basic evolved adaptations.

Social categorization according to hierarchical criteria is one of the elements of social cognition needed for maintaining social rank relations. Communicating signals and cues allow the correct categorization of others according to their social rank. They also allow a display of own status. Finally, emotions (as an element of communication systems) motivate attainment, improvement, or status maintenance.

Cross-References

- [Biosociology of Dominance and Deference](#)
- [Dominance Hierarchy](#)
- [Dominance in Humans](#)
- [Male Dominance Hierarchies](#)
- [Navigating Social Relationships](#)
- [Nonverbal Indicators of Dominance](#)
- [Primate Dominance Hierarchies](#)
- [Social Hierarchies](#)
- [Status Hierarchies](#)

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Adaptations for Reciprocal Altruism

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Synonyms

Reciprocal cooperation; Reciprocity; Social exchange

Definition

According to Hamilton (1964), altruism entails suffering a cost to confer a benefit. Trivers (1971) defines reciprocal altruism as an exchange of altruistic behaviors between individuals so as to produce a net benefit to both individuals. Traits that enhance reciprocal altruism, including punishment of nonreciprocators, have been defined as reciprocal altruism adaptations.

Introduction

There is a long-standing misconception that evolution is based on a fierce competition and

therefore rewards only selfish behavior. On the contrary, cooperation can be observed across life, including among genes, cells, individual organisms, and groups of organisms, including diverse human societies ranging from hunter-gatherer tribes to nation states.

In his seminal work *Inclusive Fitness*, Hamilton (1964) describes the evolution of altruism among genetically related individuals. Trivers (1971) suggests that reciprocal cooperation can be favored between unrelated individuals, calling the circumstance wherein individuals help one another in turn and preferential aid those who helped them in the past, reciprocal altruism. He proposed three prerequisite conditions for the evolution of reciprocal altruism. First, the fitness benefits to the recipient of help must outweigh the costs to the benefactor. Second, the probability of repeated interactions among the same individuals must be very high. Third, there must be a symmetry of donor role-recipient role exchanges, with a sufficiently frequent reversal to yield roughly equal experiences at both roles.

Nowak (2006) suggests that the aforementioned reciprocal altruism is a type of direct reciprocity, wherein the probability of another encounter between the individuals exceeds the cost-to-benefit ratio of the altruistic act. Additionally, there can be indirect reciprocity and network reciprocity. Indirect reciprocity is thought to promote cooperation only when the probability of one's reputation being known exceeds the cost-to-benefit ratio of the altruistic act. Meanwhile, network reciprocity is thought to be favored when the benefit-to-cost ratio exceeds one's average number of neighbors. Some scholars argue that reciprocal altruism is a mutual behavior that should be distinguished from altruism because it can initiate a causal chain of events that lead to a net benefit for both actors and recipients. For this reason, several authors suggest that it would be more appropriate to adopt the term reciprocity or reciprocal cooperation in place of reciprocal altruism (West et al. 2011).

Reciprocal altruism raises intriguing questions about human nature, such as why people help each other and how cooperation can evolve in a competitive world, in which selfish behavior is supposed to ensure survival. These questions

have attracted the attention of researchers from various disciplines, including game theorists, psychologists, and biologists. A useful model of two-party reciprocity is the prisoner's dilemma (PD) game. In PD games, an always cooperate strategy (unconditional cooperation) in which one cooperates at every opportunity regardless of partner reciprocation is beaten by an always defect strategy, and thus individuals engaging in unconditional cooperation and always defect eventually disappear from the population. Conversely, a tit-for-tat strategy (conditional cooperation) can be maintained by natural selection and is evolutionarily stable as long as there is sufficient probability of future interactions among participants (Axelrod and Hamilton 1981).

The existence of conditional cooperation as an adaptive human behavior would presuppose that the human brain has specialized mechanisms mediating conditional cooperation that would have been selected for in human ancestors living in social groups and engaging in social interactions for millions, and probably tens of millions, of years (Cosmides and Tooby 1992). Such mechanisms, which may constitute adaptations favoring reciprocal altruism, would appear to have had a profound influence on human behavioral tendencies. Adaptations favoring reciprocal altruism are presented below.

Conditional Reasoning

The concept of conditional reasoning entails an "if P then Q" construct that posits Q to be true if P is true. People have been found to perform poorly on Wason's four-card selection task, a standard paradigm for investigating conditional reasoning, with only 5–30% of normal subjects responding with the logically correct answer under most conditional rule experiments, even when the rule describes familiar content drawn from everyday life (Cosmides and Tooby 2007). However, when the conditional rule involves reciprocal altruism and detection of a violation corresponds to looking for cheaters, 65–80% of subjects detect violations accurately in the Wason selection task (Cosmides and Tooby 1992, 2013). Cosmides and

Tooby (1992, 2013) suggest that this propensity may be due to innate social contract algorithms that are adaptative for detecting cheaters. For example, there is no logical inference by which “If P then Q” implies “If Q then P.” However, if P and Q refer to benefits and requirements, it is natural to infer that “If you accept benefit B from me, then you must satisfy my requirement R” also implies “If you satisfy my requirement R then you are entitled to receive benefit B from me.” Thus, one that chooses the “benefit accepted” card with the “requirement not satisfied” card can be readily classified as a cheater, regardless of whether the selection pair is logically correct in a particular Wason selection task.

Recent brain imaging studies (Fiddick et al. 2005) have shown that brain damage can impair one’s ability to detect social-contract cheaters selectively, while leaving intact the ability to detect violations of precautionary rules. Such observations confirm that the brain engages in conditional reasoning processes that are specialized for detecting cheaters in the reciprocal altruism.

Trust and Trustworthiness

Trust and trustworthiness are crucial components of human cooperation behaviors in reciprocal altruism. Trust can be studied with sequential PD games, involving serial trust-reciprocity-feedback stages (Krueger and Meyer-Lindenberg 2019). In behavioral economics, trust has been defined as making oneself vulnerable to exploitation with the expectation that their trust will lead to a return benefit. According to a traditional economic analysis, no participant should ever trust an anonymous participant in a one-off game (Dunning et al. 2012). However, people do exhibit trust in economic games and the people who are trusted frequently honor that trust by returning money, thereby demonstrating trustworthiness.

Trust and trustworthiness can lead people to form spontaneous relationships with new partners and therefore to develop general trust (Yamagishi 2011). Specifically, Yamagishi (2011) suggests that a high opportunity cost in an environment of

social uncertainty favors investment of cognitive resources into the development of social intelligence. People who have acquired social intelligence can be more attentive to detecting information about others’ trustworthiness, enabling them to have a high level of general trust. Accordingly, general trust can be treated as a by-product of acquiring social intelligence and has been shown to be adaptive (Yamagishi 2011). Meanwhile, not taking opportunities to exploit others in circumstances of high social uncertainty can lead to rewards for trustworthiness by way of the social capital of a good reputation. In this sense, reputation, which can be rewarding or punishing, can moderate a person’s actions, fostering continued reciprocal cooperation. Thus, trust and trustworthiness may serve to enable reciprocal altruism by facilitating the formation of spontaneous relationships with new partners. Accordingly, potential cooperative partners may be identified, either by labeling or by reputation, based on their trustworthiness increasing the likelihood of future cooperation. Note that these impacts of trust and trustworthiness are represented in the direct and indirect modes of reciprocal altruism, respectively: labels allow for direct reciprocity, whereas reputation allows for indirect reciprocity.

Fairness and Fairness-Based Morality

A basic principle of fairness in cooperation is that those who have contributed more should receive more. Indeed, a sense of fairness can lead individuals to give resources to individuals whose welfare is not beneficial to their own (Baumard et al. 2013). Such behavior occurs in environments beyond the scope of mutualistic social behaviors, wherein the giving behavior may have no direct or indirect benefit for the actor. Some authors suggest that fairness-based choices may reflect an adaptation of reciprocal cooperation that has evolved into the development of a pillar of morality in the form of a sense of fairness (Baumard et al. 2013).

According to the mutualistic model of cooperation (Baumard et al. 2013), individuals will maximize mutual benefits in reciprocal cooperation by

choosing partners who provide a fair distribution of benefits. There are two major types of mutualistic models of cooperation: partner control and partner choice. Partner control models encompass a tit-for-tat strategy, wherein participants can penalize partners who fail to cooperate in subsequent trials of an iterated PD game (Axelrod and Hamilton 1981). In partner choice models, individuals are only able to promote cooperation by choosing and being chosen by a cooperative partner. Consistent with partner choice models, humans do have the psychological dispositions necessary for effective partner choice (Pradel et al. 2009). Moreover, people can distinguish good cooperators from bad cooperators (Tooby et al. 2006), and people do exchange information about the cooperativeness of partners in hunter-gatherer societies (Wiessner 2005). Thus, the evolution of fairness-based morality would be expected to have occurred in two stages (Baumard et al. 2013). First, individuals favoring partners who share the costs and benefits of cooperative interactions evenly would be motivated by selfish reasons and a Machiavellian psychological calculus. Subsequently, competition among cooperative partners can lead to the selection of an intrinsically motivated psychological concern for fairness.

In this evolution process, partner choice leads to fairness-based behavior, and the distribution of benefits in mutualistic cooperation is constrained by the pool of potential partners. That is, individuals would not establish cooperative relationships in which the benefits they receive are inferior to the average benefits they see others receiving in the same pool of potential partners. This principle of a market of potential partners leads to the selection of a sense of fairness, a psychological adaptation of reciprocal cooperation (Baumard et al. 2013).

In summary, the mutualistic theory of morality claims that reciprocal cooperation is sustained on the evolutionary level by mutualistic morality on a psychological level. Furthermore, according to the mutualistic theory of morality, this biologically evolved moral sense enables the cultural evolution of morality via the aforementioned mechanism of partner choice.

One-Shot Generosity, a Bedrock Feature of Human Nature

A well-known prediction of a one-shot cooperative interaction is that the equilibrium strategy would be to always defect (Delton et al. 2011). However, predictions of traditional economic models of rationality are often contradicted by empirical observations. That is, individuals often exhibit generosity, violating the expectations of fitness maximization that predict selfishness (Fehr and Henrich 2003). Agent-based computer simulations indicate that generosity in one-shot interactions is a predictable byproduct of the selection for cooperation in the brain's decision-making systems.

Indeed, repeated social interactions are quite different from a one-shot interaction owing to the potential for the production of net benefit to both partners in future series of cooperation (Axelrod and Hamilton 1981). Under the circumstances of repeated interaction, individuals may tend to be generous because the potential for benefit in future cooperation exceeds the benefit of an immediate defection (Axelrod and Hamilton 1981). Therefore, individuals are faced with the problem of distinguishing one-shot interactions from repeated interactions, a problem that has been systematized in the standard Neyman-Pearsonian decision problem. In this paradigm, a false-positive error occurs when one mistakes a one-shot interaction for a repeat interaction, and a miss occurs when one mistakes a repeated interaction for a one-shot interaction (Delton et al. 2011). The outcomes of these two types of errors are asymmetric because the cost of a miss (losing all benefits of future cooperation) is far greater than the cost of a false positive (risking a single incident of being exploited). As a result, individuals will cooperate "irrationally" even when it is exceedingly probable that they are having a one-shot interaction (Delton et al. 2011). In summary, the conditions of potential repeat interactions and there being a great potential benefit of cooperation, which promote the evolution of reciprocity, will also tend to promote one-shot generosity secondarily.

Revenge and Forgiveness

Revenge and forgiveness result from psychological adaptations that became species-typical because of their efficacy in enabling human ancestors to solve recurrent social problems during the course of evolution (Williams 1966). McCullough et al. (2013) defined revenge on a functional basis as:

a targeted imposition of costs or withholding of benefits, in response to a cost-inflicting (or benefit withholding) event, that results from a cognitive system designed (i.e., selected) for deterring other organisms from imposing costs (or inducing other organisms to confer benefits) upon oneself or other individuals in whom one has fitness interests. (p. 4)

To the extent that such a cognitive system can boost lifetime reproductive fitness, the ability to change others' incentives toward the self may evolve (Tooby and Cosmides 1996). In this context, four types of deterrence have been described: (1) direct deterrence of cost imposition; (2) indirect deterrence of cost imposition; (3) direct deterrence of benefit withholding; and (4) indirect deterrence of benefit withholding (McCullough et al. 2013).

Revenge carries costs that can potentially offset its deterrence benefits. In most cases, a critical cost of revenge lies in others' also having revenge systems. In the sequential PD paradigm, defecting when players are using a tit-for-tat strategy yields a cycle of mutual defection, known as the echo effect (Axelrod 1984), which reduces payoffs drastically for both participants.

Forgiving strategies, such as "generous tit-for-tat", can reduce the chance of getting trapped in defect-defect spirals. Forgiveness has been defined as a set of motivational changes whereby an individual becomes less motivated to retaliate against and maintain estrangement from an aggressor, while becoming more motivated by good will for the aggressor (McCullough et al. 2013). Thus, revenge and forgiveness have complementary biological functions, wherein mechanisms for revenge can deter harm, while forgiveness mechanisms can lead to problem-solving related to the preservation of valuable relationships despite prior harm. Both sets of mechanisms help to consolidate reciprocal altruism.

Gratitude

Gratitude refers to an emotional appreciation typically evoked by the perception that one has benefited from the generosity of another (McCullough et al. 2008). Assumed to be an important facilitator of reciprocal altruism (Trivers 1971), gratitude appears to mediate at least three functions in reciprocal altruism. First, gratitude can signal the transmission of a benefit. The intensity of the gratitude would be particularly high when the beneficiary recognizes that (1) the benefactor acted intentionally, (2) the altruistic action was costly to the benefactor and/or highly valuable to the beneficiary, and (3) the action was not driven by kinship obligations (McCullough et al. 2008). Second, gratitude may trigger reciprocal behavior. That is, the greater the intensity of gratitude evokes, the higher the possibility the beneficiary will want to provide the benefactor something in return. Hence, gratitude can introduce psychological states that support generosity and cooperation (McCullough et al. 2008). Moreover, the expression of gratitude from beneficiaries may reinforce prosocial behavior in benefactors. Thankfulness expressed by recipients conveys a signal to the benefactor that his or her support is acknowledged and thus likely to be reciprocated in the future. In this way, gratitude in beneficiaries can make them appear to be safe targets for future investments of the benefactor (McCullough et al. 2008).

Anger

Actual or intentional exploitation or harm from others triggers anger (Izard 1977). If a transaction is judged to be unfair, anger could motivate one to perform retaliatory actions, inflicting costs on the transgressor. Such sequelae may force the target of anger to augment their view of the angered individual's welfare and reduce the possibility of such a transgression in future (Sell et al. 2009; Trivers 1971).

The aggression caused by anger can have ramifications that exceed the cost of the offenses committed (Trivers 1971) and sometimes even

destroy a cooperative relationship. Such over-reaction is logical if one considers that a too-low punishment for the current offense may encourage an offender to cheat in the future. The natural selection for a strong exhibition of aggression in response to exploitation may thus deter cheating (Trivers 1971). Individuals in a position to enact greater benefits or harms on others may be more prone to expressing anger when dealing with reciprocal fairness grievances than those in less influential positions. Such influence could become an important bargaining chip, and individuals with these powers may expect the beneficiary to attach heightened importance to their benefits in accordance with their contribution (Sell et al. 2009).

Guilt

The sense of guilt is a negative emotional state that occurs when one realizes that s/he has violated a moral or social standard (Tangney et al. 2011). Typically, guilt is elicited when one realizes s/he has inflicted harm on another, either intentionally or unintentionally (Keltner and Buswell 1996). In the context of reciprocal altruism, a beneficiary may feel guilt after cheating a feedback expectation, an act that induces punishment when it is discovered to have been perpetrated intentionally (Trivers 1971). Functionally, guilt directs the transgressor's attention toward the harm imposed on another, introducing emotional discomfort and motivating one to compensate and behave reciprocally in the future to prevent disrupting a reciprocal relationship. Moreover, the anticipation of guilt prevents social transgressions, leading one to focus on the self-harm that would come from the potential degradation of a cooperative relationship (Fessler and Haley 2003).

Empathy and Sympathy

Empathy encompasses multiple related capacities: the capacity to share in the emotional state of another; the capacity to use reason to

understand the cause of another's state; and the capacity to understand and adopt another's perspective to be in line with that person. Empathy may have arisen from intensive parental care and then been applied to a wider network of social relationships. Consistent with reciprocal altruism theory, individuals tend to show empathy to cooperators, but empathy may be suppressed, or even replaced with *schadenfreude*, for defectors (de Waal 2007).

In psychology, three levels of empathy are recognized (de Waal 2007). The lowest level is emotional contagion, which refers to being affected by another's emotional or arousal state. For example, one may experience aversive vicarious arousal when seeing others in pain, which may motivate him or her to engage in altruistic behavior to reduce such feelings. The second level of empathy is sympathy or sympathetic concern, which refers to feelings of sorrow or concern for the distress or need of others. Finding and helping those in need of help underlies the building up of reciprocal relationships. Individuals in distress now might offer reciprocal support in the future. The greater the potential benefit to the recipient, the greater the sympathy and the more likely one is to engage in an altruistic gesture. Trivers (1971) suggests that sympathy can facilitate detection of people in need and motivate altruistic behavior based on the needs of beneficiaries. The third level of empathy is empathic perspective-taking, which refers to the capacity to understand another's specific situation and needs, combined with vicarious emotional arousal. The main manifestation of empathic perspective-taking is targeted helping of others according to their specific situations and goals.

In conclusion, human mind contains specialized mechanisms (adaptations) designed for reciprocal altruism.

Cross-References

- ▶ [Ability and Willingness of Victim to Retaliate](#)
- ▶ [Altruism Norms](#)
- ▶ [Anger Proneness](#)
- ▶ [Be Forgiving](#)

- Benefit to Another at Cost to Self
- Cheater Detection
- Cheater Detection Adaptations
- Cooperation Varies with Genetic Relatedness
- Costly Signaling and Altruism
- Evolution of Cooperation
- Evolution of Morality
- Evolution of Reciprocal Altruism
- Evolved Moral Foundations
- Fairness in Primates
- Food Sharing and Nonhuman Reciprocal Altruism
- Frans de Waal
- Game Theory
- Game Theory as a Foundation of Evolutionary Psychology
- Gratitude, Sympathy, and Empathy
- Hamilton's Rule and Theoretical Implications
- Helping and Genetic Relatedness
- Helping and Inclusive Fitness Benefits to Helper
- High-Cost Altruistic Helping
- Ingredients of Reciprocal Altruism
- Iterated Prisoner's Dilemma Model
- Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)
- Moral Emotions
- Morality Is Cooperation
- Prisoner's Dilemma and Cooperation
- Problem of Altruism
- Problem of Cheating
- Psychology of Reciprocal Altruism
- Puzzle of Altruism, The
- Puzzle of Altruism, The
- Recalibration Theory of Anger
- Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- Reciprocal Altruism and Cooperation for Mutual Benefit
- Reciprocal Altruism and Cooperation for Mutual Benefit
- Reciprocal Altruism and Group Living
- Reconciliation
- Repeated or Iterated Prisoner's Dilemma
- Reputation and Altruism
- Rescuing Friends and Relatives
- Rescuing Strangers

- Robert Axelrod's (1984) *The Evolution of Cooperation*
- Robert Trivers
- Science and Morality

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Adaptations to Avoid Ostracism

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Synonyms

Shunning; Social exclusion

Definition

Humans evolved strategies to avoid being ignored, left out, or ostracized. By avoiding ostracism, our evolutionary ancestors were better suited to their environment. Such adaptations helped ensure our survival and reproduction.

Introduction

The need to belong is a basic feature of human psychology and characterizes us as a species (MacDonald and Leary 2005). Ostracism threatens this need. To help our ancestors achieve their survival and reproductive goals, people evolved adaptations to prevent ostracism. Below, examples of adaptations to avoid ostracism are listed.

Social Pain

Physical pain evolved to alert us to environmental threats and to serve as a preventative force against physical injuries (Bolles and Fanselow 1980). *Social pain*, the aversive experience associated with ostracism, arose from an evolutionary push to co-opt the physical pain system to respond to social injuries (e.g., ostracism; Chester et al. 2012). Much like physical pain, individuals with a blunted sense of social pain exhibit greater ostracism in their daily lives (Chester et al. 2015). The prospect of ostracism's sting prevents people from doing things that could cause them to experience ostracism.

Conformity, Obedience, and Norm Adherence

Group members who disobey group norms often experience ostracism (Kurzban and Leary 2001). This tendency is even observed among our close Chimpanzee relatives (Goodall 1986). Thus, it behooves people, especially those at the lower rung of the social ladder, to act in ways that conform to group standards. Our powerful tendency to conform to group norms and obey authority figures likely reflects the need to prevent ostracism across our species' history (Latané 1981).

Reciprocity and Free-Loading

For society to flourish, people must cooperate and pool resources. Distressing times often propel people to help rather than hurt others. But people also seek to maximize their personal outcomes. Rather than giving their fair share, people rely on others' generosity. To prevent people from enjoying the benefits of group membership without contributing, humans have evolved cheater detection mechanisms that serve to identify and ostracize free-riders (Price et al. 2002). To prevent ostracism, group members must reciprocate assistance from others and contribute equally to collective tasks.

Self-Control

We'll never know if people were born to be bad or good. What we do know is that selfish, antisocial actions can cause ostracism. To restrain egocentric tendencies, individuals must use self-control, the ability to place higher-order goals above immediate desires (Baumeister et al. 2007). Self-control processes arise from the prefrontal cortex, a brain structure that is disproportionately large in humans (Dunbar 2002). The prefrontal cortex likely evolved to prevent selfish impulses from translating into ostracism from the group.

Conclusion

Early humans evolved in small groups, relying heavily on each other for their well-being. In that context, ostracism was a death sentence. As a result, humans evolved adaptations to avoid ostracism. Through social pain, adherence to group norms, contributing equally to group goals, and using self-control to restrain our selfish impulses, we can avoid being ostracized.

Cross-References

- [Avoiding Stigmatization](#)
- [Stigmatization and Ostracism](#)

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Adaptations to Human Sperm Competition

► History of Sperm Competition in Humans

Adaptations to Sperm Competition

► Sperm Competition Tactics

Adaptations: Product of Evolution

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Definition

Structure or behavior of an individual that is the long-term outcome of the process of natural selection.

Introduction

The word adaptation has a vernacular and two technical senses. In a vernacular sense, an

individual's adaptation is simply the adjustment of this individual to new conditions. For instance, when the temperature at the place you are located increases sufficiently, you start sweating. Your temperature adjusts or adapts to this new temperature. This is an adaptation in the vernacular sense, which is different from what evolutionary biologists and psychologists are referring to when they use the word “adaptation,” although a link between the vernacular and the technical senses exists. An adaptation, for an evolutionary scientist, is both a structure (for instance, an organ) or a behavior which is the outcome of the process of natural selection, and the evolutionary process by which such a structure was produced. Thus, one technical meaning of the term “adaptation” in evolutionary sciences refers to the product of natural selection, while the other refers to the process by which such a product is obtained.

The Process of Adaptation

One of the greatest achievements of Darwin's (1859) theory is that it can explain how complex structures to which we attribute functions are the products of an unguided process. William Paley, a famous theologian, is well known for having formulated a version of the “watchmaker analogy” in his influential book *Natural Theology* written in 1802, one version of which is the following. If you stumble upon a rock on the beach, it is unlikely you will ask who designed the rock and whether the rock has a purpose. But if you now stumble upon a watch, you will want to know who produced the watch, as well as the purpose of this complex object. Design calls for a designer, in this case a watchmaker, according to Paley. Natural selection can explain complex “watch-like” structures, ones which appear to bear the hallmarks of intentional design, without recourse to any sort of intentional designer. This type of reasoning led Richard Dawkins (1986, p. 21) to claim that: “[n]atural selection is the blind watchmaker, blind because it does not see ahead, does not plan consequences, has no purpose in view. Yet the living results of natural selection overwhelmingly impress us with the appearance of design as

if by a master watchmaker, impress us with the illusion of design and planning.”

How can natural selection achieve this result without invoking a designer? Suppose you have a population of individuals that all differ in their characteristics. For instance, some individuals are able to detect light, while others are not. Suppose also that being able to detect light produces an advantage in terms of survival or reproduction, so that on average light-sensitive individuals have a larger number of offspring than light-insensitive individuals. The reason for this advantage could be because seeing light permits an individual to detect some movements and consequently escape predators more often than light-insensitive individuals. Finally, suppose that individuals transmit their ability to detect light to their offspring with some fidelity. On average, light-sensitive individuals produce light-sensitive offspring more often than light-insensitive individuals do. At the next generation, we expect the population to have a higher proportion of light sensitive individuals than it had in the previous generation. This recipe for evolution by natural selection, which at its cores invokes variation, difference in fitness (reproductive output), and heredity has been proposed a number of times ever since Darwin presented his own version in the *Origin* (for a review of them see Godfrey-Smith 2009; for a famous version see Lewontin 1970). It embodies the principles by which a population can adapt to its environment. Yet, all one gets after one generation is a population in which individuals are slightly better able to escape predators than they were in the previous generation, nothing like complex structures such as an eye.

But suppose now you repeat this process over and over again for thousands of generations, with some individuals exhibiting new variation (acquired by random or blind mutations) at each generation. For instance, one mutation could increase or decrease the number of cells able to detect the light, change their position, etc. With such a process of blind variation (i.e., random from the point of view of the individual bearing this difference in terms of the advantage or disadvantage it will produce), the population will start

exhibiting increasingly complex structures. And, in fact, this is precisely what Nilsson and Pelger (1994) demonstrated. Using a computer simulation, they showed that by random mutations increasing or decreasing in different ways the optical quality of a patch of light-sensitive cells, a structure similar to that of the mammalian eye or eye of an octopus can evolve in less than 2000 steps (1829 to be precise), where each step can modify one element of the structure of the patch by one percent. Given the fidelity with which traits are typically transmitted from generation to the other, they estimated that it would take less than 400,000 generations to evolve an eye. This is, according to them, a pessimistic estimate since natural selection would typically work on several elements of the structure of the eye at once, while their simulation only tweaked one element at a time.

Nilsson and Pelger’s simulations represent a proof of concept: With a simple process producing blind or random variation, differential success, and transmission of characteristics over time, complex structures or behaviors can emerge. These structures are adaptations.

Adaptive, Maladaptive, and Adaptation

How many steps does it require for a structure to become an adaptation? In the case of the eye presented above, this is equivalent to asking for the threshold point at which the structure is sufficiently different from the patch of light-sensitive cells so that we can call it an adaptation to detect and escape from predators (assuming the bearer of the structure is prey). There is no definitive answer to this question. But recognizing that it has no definitive answer leads to some interesting distinctions, especially in the context of human cognition in its modern environment. An adaptation, as we characterized it, is the product of natural selection. Yet, we also saw that after one generation natural selection already produces a difference: the proportion of the most successful variants will increase (of course this assumes that genetic drift can be neglected). Should we call the difference an adaptation?

Strictly speaking one might want to do so and accordingly call this a *simple* adaptation (or one-step adaptation). In some contexts, this is exactly what is done. For instance, being a heterozygote with the sickle-cell variant of hemoglobin, which results from a single mutation from normal hemoglobin, is regarded as a classical adaptation against malaria (Kwiatkowski 2005). Unfortunately, being a homozygote with the sickle-cell variant leads to a disease known as “sickle-cell anemia.” That said, when the structure or function is more complex, such as an eye, a small difference improving the success of individuals when compared to others is called “adaptive” rather than an adaptation. This distinguishes cases in which a structure has been selected for millions of years in an ancestral environment and yet has a negative effect on fitness in the modern environment – think about the adaptive role of liking sugar in an ancestral environment and its current role on obesity and cardiovascular diseases – from cases in which the adaptation still has an advantageous role in the modern environment. In the latter case the adaptation is also adaptive, while in the former it is not; the adaptation is now maladaptive.

Furthermore, the adaptive/adaptation distinction permits us to account for structures that had no previous function (something known as an evolutionary by-product) and suddenly become advantageous. In such a case, the structure is adaptive without being an adaptation. For instance, some scholars have argued that the beliefs in supernatural agents encountered in many religions started originally as a by-product of an adaptation to detect agency in the environment (Boyer 2001). Since it is costlier not to detect an agent when there is one than to detect an agent when there is none (think about the consequence of not detecting a predator or opponents when there is one), the thesis that beliefs in supernatural agency are a by-product of our evolved cognition is a plausible hypothesis. From this by-product, some people have argued that specific beliefs about supernatural agents, for instance that they are interested in human morality, have an adaptive value without necessarily being an adaptation: it might currently increase the fitness of people more prone to have such

beliefs without having been selected for in the past (for a review of these different hypotheses see Bourrat 2015). If an adaptive process goes on for many generations, an adaptive structure will become an adaptation.

Conclusion

Adaptation is a fundamental concept of Darwinian apparatus. Without this concept, it would be extremely difficult to make sense of the biological complexity around us. In particular, it plays an important role in evolutionary psychology since many complex behaviors, despite their lack adaptiveness in the current environment (or even their deleterious effects, a phenomenon known as evolutionary mismatch), are often regarded as adaptations for an ancestral human environment, known as the environment of evolutionary adaptedness (EAA). Despite the perils of having an adaptationist story for every trait (known as “just so stories”), as forcefully argued by Gould and Lewontin (1979), by and large, the success of evolutionary sciences rests upon generating such stories and then rigorously assessing whether they withstand diverse empirical tests.

Cross-References

- [Adaptationist Program, The](#)
- [By-Products of Adaptations](#)
- [Maladaptations](#)
- [Mismatch Between Evolved Morality and Modern World](#)

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Adapted Mind, The

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Synonyms

[Adaptation](#); [Conceptual integration](#); [Evolutionary psychology](#)

Definition

One of the seminal books in the establishment and development of evolutionary psychology as a distinct method of inquiry in the behavioral sciences.

Introduction

The Adapted Mind (Barkow et al. 1992) outlined two major goals: the introduction of evolutionary psychology and the connection between evolutionary psychology and fields such as biology, anthropology, sociology, economics, and history. One of the overarching themes present in the work is the push for collaboration, or conceptual integration, amongst the social sciences. As the physical sciences, such as chemistry and physics, have compatible theories for the workings of the world, the social sciences should adopt a similar system

for compatibility and common language between them. Doing so would allow for converging lines of evidence for scientific discoveries and help alleviate the present problem with reproducibility in the social sciences (see Brase 2014 for an explanation of one such framework).

Barkow et al. (1992) explains the basic mechanisms of evolution by natural selection, wherein heritable variations in individuals that provide an advantage for the propagation of genes to future generations is the driving force. Importantly, adaptations take many (e.g., thousands of) generations to spread throughout a population. More simply, evolution is a very slow process, and it does not respond to rapid environmental changes. Instead, adaptations are built to solve very specific and persistent problems; they are domain specific (Tooby and Cosmides 1992). A common misconception, as addressed in the chapter by Symons (1992), is that a trait which is an evolved adaptation does not imply that that trait is presently adaptive. An adaptation was designed to solve a specific problem that existed across many generations in the past, and present technologies may have rendered such an adaptation neutral or even maladaptive. For example, sugar tastes sweet and the taste of sweetness is an indicator of fruits at their most nutritious. Presently, with the abundance of refined sugar, our propensity to seek sugar-rich foods may be maladaptive. However, if industrialized people were to be faced with conditions that required foraging for food in order to survive, the attraction to sugar would, once again, become adaptive to satisfy caloric needs.

The remainder, and vast majority, of the adapted mind is dedicated to providing examples of how evolutionary psychology can be integrated into specific research areas within the behavioral sciences. These include chapters on nonhuman primate origins of social interaction and cooperation (by McGrew & Feistner), on mating and sexual behaviors (by Buss, by Ellis, and by Wilson & Daly), on caring for offspring (by Boulton & Smith, by Fernald, by Mann, and by Profet), on language and perception (by Pinker & Bloom, by Shepard, and by Silverman & Eals), on environmental preferences (by Kaplan and by Orians & Heerwagen), on intrapsychic processes (by Nesse

& Lloyd), and on new approaches to studying culture (by Barkow). Each topic incorporates the need to collaborate across disciplines and the same push to approach investigation from an adaptive, domain-specific stance.

Conclusion

After more than two decades, the main arguments from this work: pushing for collaboration and a domain-specific approach to research, are still relevant. The Standard Social Science Model (a term introduced by Tooby and Cosmides 1992) still exists in contemporary texts purchased by undergraduate students, and Barkow et al. argued that this model isolated the behavioral sciences from other fields. By implementing a more collaborative approach, fields like psychology stand better equipped to earn credibility from other sciences and from the layperson.

Cross-References

- [Adaptationist Program, The](#)
- [Founders of Evolutionary Psychology](#)
- [Jerome H. Barkow](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

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Adaption

- [Assimilation](#)

Adaptive Benefits of Matriliney and “Walking Marriages” in Mosuo Culture

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Synonyms

[Culture](#); [Kin](#); [Mating](#); [Matriliney](#); [Paternity uncertainty](#); [Resources](#)

Definition

Arguably the last known surviving matrilineal tribe in China, the Mosuo offers interesting insights into familial and mating arrangements to support reproduction.

Introduction

Due to its unconventional relationship norms and family structure, the Mosuo tribe is typically seen as a sociocultural puzzle. The evolutionary perspective, however, assumes that social structures that can exist or have existed are likely to be functional and supported by adaptations that enable their sustained functioning. Therefore, the Mosuo pose an interesting case study of alternative reproductive arrangements and elucidate the evolutionary motives facilitated by such arrangements. More specifically, Mosuo practices can work because they enable the Mosuo to overcome a variety of adaptive problems typically faced by individuals in more conventional pair-bonded

relationships. In this entry, we describe the features of the Mosuo, discuss some hypothesized adaptive benefits of Mosuo mating and familial practices, review the available evidence for those hypothesized adaptive benefits, and suggest areas for further research.

General Characteristics of the Mosuo

Although rare, matrilineal societies can be found in various places around the world, including Africa (e.g., the Akans), India (e.g., the Nair), and Australasia (e.g., the Vanatinai). Matrilineal society, also called matriliney, refers to a socially ordered community that adheres to a kinship system in which ancestral descent is traced through maternal instead of paternal lines (the latter being termed patrilineage or patriliney). The Mosuo represent the last matrilineal society in China and are among the few left in the world that are still somewhat thriving and gaining considerable public attention in recent decades. They consist of a population of approximately 40,000 minority Chinese living on the border of Sichuan and Yunnan provinces in the Himalayan Mountains (Walsh 2005). How long they have practiced their way of life is disputed, with experts believing the culture to be somewhere between a few hundred to over 2,000 years old (Dawson 2018; Wen et al. 2004). While the Mosuo have both matrilineal and patrilineal subpopulations due to intermingling with other cultures and the influence of modernization, the current entry will focus on the matrilineal Mosuo residing near Yongning and Lugu Lake, both of which are situated in Yunnan Province (Mattison 2011).

Until recently, the majority of Mosuo were subsistence agriculturalists, raising crops such as buckwheat, corn, wheat, potatoes, and garden vegetables mainly for their own consumption and engaging in animal husbandry of livestock as a significant sideline (Shih 2010). Starting in the 1980s and increasingly through the 1990s, a subset of the Mosuo inhabiting the stretch along Lugu Lake have carved out a living from profits driven by tourism (Mattison 2011; Walsh 2005).

Although family-owned hotels and shops have also resulted in substantial income variation among households, most families residing in areas away from the lake retain agricultural traditions as their major source of subsistence (Mattison 2011).

Among traditional Mosuo, family property and resources are controlled by female heads of households and are normally handed down to their daughters and their daughters' children (Holden et al. 2003). Mosuo men do act as temporary co-stewards of resources, but whatever rights they have to resources, nominal or real, will be transferred to their sisters' children. Mosuo men are expected to prioritize and dedicate labor to their natal households rather than their romantic partners' households (Cai 2001). As we will see later, Mosuo men and women romantically consort in the woman's home, after which the men return to their own residences to continue investing in their natal households, providing caregiving in particular to their sisters' children. As lineage affiliation among the Mosuo is matrilineal, children of both sexes fall under their mother's lineage and typically reside with her throughout their lives. The most important inherited resource shared by a household until recently was land, but money and other durable goods have increasingly become more important, especially in areas where tourism is prevalent (Mattison 2011).

Reproductive Practices of the Mosuo

The Mosuo practice a system of romantic pairing known as "walking marriage" or *sese* (Cai 2001; Mattison 2011; Shih 2010). When females come of age at approximately 13 years old, they can start to take lovers from men within the tribe, having as many or as few as they desire over their lifetime. Male companions spend their days helping in their own homes or carrying out jobs such as fishing, farming, or construction and visit the women's homes at night, often secretly (Shaitlyn 2010). Thus, throughout the course of their unions, men visit their lovers mostly at night while retaining separate residences.

According to ethnographers of the Mosuo, walking marriages involve no contract between lovers, paternity is not assured but is also unimportant, and multiple concurrent unions are possible and do not incite jealousy (e.g., Cai 2001; Shih 2010). Moreover, not only do men engaging in *sese* have no obligation to participate in their partners’ lineages, but they are also expected to refrain from doing so due to potential tensions that may arise between their own families and their partners’ relatives (Cai 2001; Mattison 2011). For instance, a man who spends too much time at a partner’s household risks being judged as neglecting his own family or as interfering in the partner’s household. As such, the children that result from walking marriages are seldom raised by their biological fathers; instead, the brothers of the mother (i.e., the maternal uncles) take on paternal responsibilities and serve as father figures. It can also be said that paternal investments are irrelevant in the Mosuo context. As the typical duties of a conventional father, such as the provision of resources and nurturance of offspring, are provided by the mother’s kin in her natal household, investments from biological fathers are rendered unnecessary. Correspondingly, there is also no stigma attached to not knowing who a child’s father is (Shaitlyn 2010).

Challenges to Relationship Orthodoxy

From an evolutionary perspective, adaptations are features and characteristics that exist to promote the reproductive success of organisms (Williams 1966). These adaptations also include psychological traits such as mate preferences and mating strategies, which guide individuals toward acquiring mates who are most likely to bring them the highest chance of reproductive success (Buss and Barnes 1986).

For instance, reproduction hinges critically on women’s valuable reproductive resources, such as their limited eggs and heavy investment in offspring (e.g., internal gestation and lactation). Yet, the processes of reproduction (e.g., pregnancy, childbirth, childrearing) can be very costly to

women and render them highly vulnerable (Trivers 1972). Thus, while men may have evolved a preference for cues to fertility and reproductive potential in prospective mates (e.g., youth, health, physical attractiveness), women evolved a preference for partners who can offer resources and protection (Symons 1979). In addition, as females are the more heavily investing sex, women tend to be on average more cautious than men when selecting potential mates. In contrast, men are much less biologically constrained, and they can also directly increase their overall reproductive success by increasing the number of partners that they inseminate – a generally undesirable strategy for women who, especially during ancestral times where birth control did not exist, must incur pregnancies and are potentially bound to several years of maternal investment for any given sexual encounter (Li and Yong 2018). Therefore, whereas men stand to benefit by pursuing multiple mates, women benefit more from being choosy about the quality of their partners and are less interested than men in having multiple partners. Lastly, across various human societies, fatherhood is the norm as the support afforded by fathers in addition to mothers increases the survival and reproductive viability of offspring (Geary 2005). As such, women tend to prefer men with fatherhood qualities, such as the ability to protect them and their offspring, provide resources, and nurture young (Buss and Barnes 1986). The benefits of having both parents raise children increases the desire for long-term pair-bonding in humans. Reflecting these preferences, monogamous heterosexual marriages prevail across the world (Herlihy 1995).

The mating preferences and approaches of the Mosuo differ substantially from those widely adopted or practiced in other cultures. Specifically, the concept of fatherhood does not exist among the traditional Mosuo or exists instead in the form of care from maternal uncles. Mosuo women also may not be as concerned about a potential mate’s resources and social status as would be predicted by evolutionary theories of human mating. Moreover, Mosuo women do not expect their romantic partners to commit to the relationship and are themselves open to having

multiple partners. These unconventional practices of the Mosuo pose a significant challenge to our beliefs about family structure, in particular the common practice of nuclear families comprising children and pair-bonded parents, as well as what we know about the dynamics of human mating and attraction.

Mosuo Practices as Solutions to Adaptive Problems

By doing away with fatherhood and keeping the lineage within the maternal side, Mosuo familial and relationship arrangements may help to solve a range of adaptive problems otherwise faced by people in more conventional marriage arrangements. The following is a list of hypothesized adaptive solutions afforded by traditional Mosuo practices.

Solution to Women's Problems of Assessing the Commitment and Quality of Mates

Evolutionary theories of mating suggest that women are confronted with the adaptive challenge of assessing prospective partners' willingness to commit and ability to provide protection and resources, primarily because the survival prospects of a woman and her offspring hinge critically on the male partner's commitment and provisioning (Symons 1979). In Mosuo contexts, however, women who are childbearing or childrearing have their needs met through the resources, protection, and nurturance provided by their natal households (Cai 2001; Shih 2010). With her and her offsprings' welfare taken care of through the help of kin, a Mosuo woman is unlikely to incur the typical costs associated with partner desertion or the selection of an inept mate. Consequently, she can afford to exert less effort in mating assessments, which also carry the burdensome secondary challenge of determining whether potential mates are being deceptive about their mate quality (Tooke and Camire 1991). Moreover, Mosuo women are relatively freer to make relationship choices based on other factors such as physical attraction or personality compatibility.

Solution to Men's Problems of Demonstrating Mate Quality and Intrasexual Competition

Conversely, given that Mosuo women's requirements in mate selection are less stringent than those of women seeking conventional relationships, Mosuo men do not have to incur the costs associated with protracted courtships and displays of worth and formidability in order to attract mates (Grammer 1989). The intensity of intrasexual competition between men will also likely be reduced, at least on the basis of outdoing each other through the accumulation and display of resources and status (Buss 1988).

Male intrasexual competition can be harmful not only to the men themselves but also to the society wherein these men compete. Among males vying for female attention, the motive to compete produces a preoccupation with gaining resources, status, and dominance, which can translate into a variety of outcomes ranging from injuring or killing mating rivals (Wilson and Daly 1985) to increased risk-taking (Ronay and von Hippel 2010) to an acute obsession with work and income (Yong et al. 2019), all of which can put men's health at risk. At a societal level, the male desire to accrue resources in order to compete intrasexually may exacerbate status disparities between men who have resources (and are thus capable of accruing even more resources) and those who do not, leading to a host of societal problems related to social and economic inequality (Wilkinson and Pickett 2009). The inherently aggressive nature of male intrasexual competition has also been argued to be an underlying cause of societal instability, such as gang violence (Wilson and Daly 1985) and even terrorism (Kanazawa 2007). Thus, Mosuo practices that diminish men's need to compete for mates may reduce men's exposure to harm as well as promote societal stability and peace.

Solution to Men's Problem of Increasing Sexual Access to Multiple Mates

As men stand to directly improve their reproductive success by increasing the number of females they can inseminate, men may have evolved a preference for sexual variety and to desire multiple partners in short-term sexual relationships

(Li and Kenrick 2006). The orthodox female preference for relationship exclusivity and long-term commitment, however, often constrains men’s ability to enact a quantity- and variety-driven reproductive strategy. As men in Mosuo contexts are not expected to commit to their romantic partners, they are free to fulfill their desire for sexual quantity and variety – an approach that negates the problems otherwise confronted by men who try to seek extra-pair matings while in conventional relationships. Given the potentially severe consequences of being caught having a sexual affair, such as physical retaliation from the cheated partner’s family or the legal repercussions of infidelity, men are typically careful to seek additional partners only surreptitiously. In contrast, Mosuo men are permitted to do so without fear of those repercussions as the preferences of the opposite sex are not violated.

Solution to the Problem of Paternity Uncertainty

As human reproductive biology entails internal female fertilization, men face the problem of being cuckolded, that is, investing care and resources in children who are actually sired by other men – an adaptive problem not faced by women. The uncertainty over whether offspring are theirs increases to some extent the incentive for men to focus more on mating than on parenting (Geary 2005). Given the freedom and acceptability for Mosuo women to mate with as many men as they wish, Mosuo men’s confidence in paternity over children produced through walking marriages is relatively low. However, because Mosuo men are not required to raise their own putative offspring, paternity no longer becomes a concern (Cai 2001). Indeed, although Mosuo men may sometimes opt to care for their own offspring (whom they cannot be certainly sure are theirs), they primarily channel their caregiving efforts to their sisters’ children instead. As women are almost certainly sure that the offspring they produce are theirs, the brothers of Mosuo women have a reliable degree of certainty over the relatedness of the nephews and nieces they help raise, thereby eliminating the possibility of investing in unrelated children.

Doing away with the need for relationship commitment therefore allows both men and women in the Mosuo tribe to sidestep the problems that emerge from potential as well as actual infidelity in conventional relationships. For instance, it is unlikely that Mosuo individuals feel the need to expend substantial effort in mate guarding, nor would they be as prone to the troublesome experience of romantic jealousy as would couples in conventional relationships who fear the loss of investment from their valued partners (Shaitlyn 2010; Yong and Li 2018). On the flipside, being subjected to intense mate guarding can also be extremely harrowing. As men have a strong desire to avoid being cuckolded and raising unrelated children, they may take extreme actions to deter or punish mates for sexual infidelity which can sometimes lead to serious physical injuries or even death (Goetz et al. 2008). These are all effectively avoided by the Mosuo.

Matriliney as daughter-biased investment may also function as an adaptive solution by parents to optimize allocation of resources in terms of inclusive fitness (Holden et al. 2003; Hamilton 1964). Many societies pass on wealth and property through the male line because men’s but not women’s mate value is intricately tied to status and resources. As such, bequeathing wealth and property to sons promises higher reproductive returns as sons can be made more desirable and thus stand to benefit more than daughters from being endowed with such resources (Trivers and Willard 1973). However, because paternity uncertainty tends to be high for the Mosuo, transmission of wealth and property through males may lead to loss of resources to nonkin. Therefore, paternity uncertainty may have served as a historical antecedent for early Mosuo parents to adopt matrilineal practices and bias investment of wealth and property toward daughters rather than sons so that these resources will be channeled toward actual progeny.

Solution to the Problem of Familial Instability

In most formalized long-term relationship contexts, people officially marry into families, and this often involves the female marrying into the male household. This practice creates obstacles to

cooperation and avenues for rifts due to genetic unrelatedness between the household and incoming individuals. For instance, given that the female is nonkin, her affines may minimize cooperation with her or even exploit her. When the couple have children, the female may also be more inclined to view herself and her children as a genetically related unit distinct from her partner's household and then value the interests of her unit over those of the household. These misalignments in genetic self-interest can lead to familial instabilities as evidenced by the numerous instances of infighting in imperial families throughout recorded history (Soulliere 1988). The Mosuo avoid such rifts by not having contractual marriages and emphasizing involvement and commitment primarily to one's natal household (Cai 2001); as such, Mosuo households minimize "contamination" from the intrusion of nonkin with divergent genetic interests, so to speak. Indeed, Mosuo individuals have expressed that they prefer not entangling daily life and responsibilities with love affairs, with one woman saying "who wants a mother-in-law?" (Dawson 2018). Hence, the consistently high degree of genetic relatedness in Mosuo households due to the relative absence of lowly related individuals and high certainty of relatedness through the maternal line strongly facilitates familial solidarity and cooperation.

Solution to the Problem of Conflict over Whom to Invest in

People in conventional relationship and familial contexts may also face the dilemma of having to choose between one's natal family and their romantic partner (which may include affines) in situations of conflict. This is often difficult to resolve because both parties are typically important in conventional contexts – the natal family is genetically related; therefore helping them is directly beneficial for inclusive fitness (Hamilton 1964); at the same time, the romantic partner is a reproductive mate and co-parent; therefore helping them is directly beneficial for reproductive success and indirectly beneficial for inclusive fitness (Pillsworth and Haselton 2005). This conflict

may manifest as, for example, the dilemma over who to give one's limited resources to or the dilemma of deciding who to save in a life-threatening situation. Failure to finesse this quandary can result in anger and distrust from the side that feels shortchanged (Sell 2011). Among the Mosuo, the norm of returning to and investing in the natal family makes clear that one's kin should be prioritized, thus eliminating the burden of having to make such choices and reducing the potential for conflicts and undermined relationships.

Empirical Evidence for the Adaptive Benefits of Mosuo Practices

Despite growing awareness and media coverage of the Mosuo in recent decades, surprisingly little research has been conducted that allows us to confirm the hypothesized benefits of Mosuo practices as an alternative to conventional relationships structured around formal marriage. To our knowledge, only two studies have been conducted that directly validate the benefits we proposed. First, a study by Thomas et al. (2018) found that costly cooperation among the Mosuo, such as traveling over long distances to provide help, varied most strongly and positively as a function of kinship or genetic relatedness over other factors such as need, affinal relations, or proximity, thus confirming that inclusive fitness indeed underlies Mosuo helping and cooperative behaviors.

Second, Mattison (2011) examined matriliney as a possible group-level adaptation and proposed that daughter-biased transmission of wealth may serve as a solution to the problem of resource loss due to paternity uncertainty. She predicted that, all things being equal (e.g., males and females would equally benefit from inheriting wealth), complete certainty over paternity in sons' offspring would be needed in order for resources to be transmitted equally to sons and daughters. As paternity certainty is likely to be low among men engaging in walking marriages, her framework predicts daughter-biased investment of resources, which is indeed generally the case for the traditional

Mosuo. Hence, daughter-biased resource transmission through matriliney appears to be an adaptive solution to the problem of potential resource losses under conditions of high paternity uncertainty. When viewed from another perspective, a shift toward daughter-biased investment may have been a key factor that enabled the Mosuo to do away with fatherhood and unlock the benefits associated with not having to depend on the commitment of romantic partners.

Future Research

Albeit scarce, the available evidence so far suggests that our predictions of the advantages of Mosuo practices are in the right direction. More empirical research is certainly needed to examine our numerous speculations and, in all likelihood, uncover further adaptive benefits brought about by such unorthodox practices. This will not only enlarge our perspective on the possibilities for human relational arrangements – including their various pros and cons – but also contribute further to our understanding of mating psychology and behavior.

The Mosuo and other cultures with atypical mating rituals and practices also allow us to identify potential shifts in mate preferences and selection criteria and thus promise interesting and novel insights. For instance, given that Mosuo men do not need to attract women using status and resources, Mosuo women are likely to select men based on other traits such as physical attractiveness. Correspondingly, we may also predict high levels of physical attractiveness in Mosuo men due to the selection pressure exerted by women on this trait.

Although it is commonly assumed that matriliney shifts the balance of power in favor of females and thus offers more benefits to females, the current analysis also suggests that males can benefit tremendously from matrilineal practices. Some of these insights can be borrowed to engender further investigations into how conventional or modern familial and relationship structures can be modified to benefit both sexes.

Conclusion

The current entry demonstrates the utility of the Mosuo tribe as a case study of alternative reproductive arrangements. Through this analysis, we elucidated a range of benefits afforded by Mosuo practices, thereby showing that conventional long-term relationships structured around monogamous marriages may not necessarily be the most ideal despite their ubiquity across the globe. Although this analysis does not suggest that we do away with conventional marriages, it brings to light many of the costs we may incur in conventional marriages and expands our understanding of the effects as well as pros and cons of alternative mating arrangements.

Cross-References

- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Benefits of Commitment and Marriage](#)
- ▶ [Benefits to Kin](#)
- ▶ [Children without Paternal Investment](#)
- ▶ [Cultural Differences](#)
- ▶ [Cultural Evolution](#)
- ▶ [Cultural Variation](#)
- ▶ [Female Mate Choice](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
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- ▶ [Parental Effort Versus Mating Effort](#)
- ▶ [Parental Investment](#)
- ▶ [Paternal Care](#)
- ▶ [Paternal Investment](#)
- ▶ [Paternal Investment Relative to Maternal Investment](#)
- ▶ [Paternal Role](#)

- Paternity Certainty
- Paternity Uncertainty
- Paternity Uncertainty and Investment in Sons and Daughters
- Seeking Extra-Pair Partners
- Sexual Conflict and Sex Differences in Parental Investment
- Trivers-Willard Hypothesis

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Adaptive Hypotheses of Infanticide

► [Infanticide in Nonhumans](#)

Adaptive Lag

► [Mismatch Between Evolved Morality and Modern World](#)

Adaptive Learning

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Synonyms

[Adaptive plasticity](#); [Associative learning](#); [Cultural learning](#); [Cultural transmission](#); [Optimal imitation](#); [Optimal learning](#)

Definition

A category of learning strategies which promotes an individual's assimilation of successful behaviors, traits, and skills, increasing an individual's level of fitness in a given environment

Introduction

A construct of interest to both the fields of developmental and evolutionary psychology is *Adaptive Learning*, sometimes referred to as adaptive plasticity, which some researchers have labeled as an overarching category of learning strategies that contribute to an individual's level of fitness in a given environment (Kameda and Nakanishi 2002). Currently, adaptive learning has been reviewed within the context of its relationship to

the Baldwin effect, which states that the utilization of *Adaptive Learning* increases the rate at which a species undergoes evolutionary changes to the phenotype (Sznajder et al. 2012). However, this entry seeks to provide a broader overview of the area of research investigating *Adaptive Learning* and the strategies that it comprises. These learning strategies include prestige-biased learning (Atkisson et al. 2012; Chudek et al. 2012; Henrich and Broesch 2011), majority-biased copying (Evans et al. 2018), conformity (Haun et al. 2014; Kameda and Nakanishi 2002; Morgan et al. 2015; Muthukrishna et al. 2015), and play (Lew-Levy and Boyette 2018). These strategies explain the adaptive nature of learning and subsequent evolutionary benefits. This entry seeks to provide an analysis of these *Adaptive Learning* strategies, primarily focusing on the broader categories of *Conformity and Imitation* and *Prestige Bias*.

Conformity and Imitation

To be successful in an environment, it is often necessary to conform to the demands of the majority in order to receive acceptance into the community. Additionally, individuals that do not have the resources to devote to individual learning may opt to selectively copy the majority if the behavior displayed is shown to improve culturally significant skills. One example of imitation was shown in a study conducted by Lew-Levy and Boyette (2018) in which the authors observed learning through imitation in Aka and Ngandu village children in the form of work-themed play. They found that children spent less time engaging in work-themed play as they got older, because they begin to engage in these real work tasks more as they mature. Lew-Levy and Boyette also found that a child's ethnicity and gender were associated with the types of roles they practiced; they adopted the roles that were most representative of their own identity, despite having access to models of different gender and ethnicity. For example, the researchers found that children were only practicing activities that were relevant to life in their village and did not incorporate play based on skills of foreigners or those from other villages.

Lew-Levy and Boyette inferred that play has an adaptive learning function as it helps children develop necessary skills consistent with life in their immediate environment.

An earlier work conducted by Kameda and Nakanishi (2002) investigated the cost of social learning in unstable environments. The researchers used a game called “where is the rabbit” where participants were asked to judge the location of the rabbit for 60 rounds. They found that as the cost of individual learning increased, participants became less likely to conform. Kameda and Nakanishi state that the increase in the cost of individual learning creates an imbalance where fewer people become information generators, and therefore if the environment is changing over time and fewer people are generating new information about the environment, it is not beneficial to conform to potentially outdated information. This shows the adaptive nature of this strategy, as the individual evaluates the sources of information within the evolving context of the immediate environment.

Additionally, Haun et al. (2014) investigated differences in conformity likelihood across human, orangutan, and chimpanzee children. They found that human children were more likely to conform to the actions performed by a majority of demonstrators, even if this action was just as effective as an action previously used by the child. The other great ape children did not adjust their actions to conform to the demonstrators. In addition, children were more likely to conform when they were in the presence of the demonstrator and less likely in their absence. Children also conformed to a new action just as frequently when there were one or three demonstrators. This shows an individual’s drive to model effective behaviors as well as to conform to the cultural expectations of their environment.

In a similar study, Morgan et al. (2015) investigated how children conform in uncertain environments. They found that children in the 3- to 4-year age range had a strong drive to conform to an action performed by a total majority of demonstrators, but not the actions of a less than total majority. Six-year-olds conformed in an equal proportion to the number of demonstrators, and

7-year-olds showed a similar drive to conform to total majorities, as well as an increased drive to conform to less than total majorities. These results led Morgan and colleagues to infer that as children age, they begin to develop the ability to utilize and interpret different social and asocial information when making their own decisions, much like the decision-making competencies of an adult.

A study by Muthukrishna et al. (2015) investigated conformist social learning biases in an experiment requiring participants to indicate the longest line presented in an array of varying size and number (similar in design to Asch’s 1951 experiment). They found across their two studies that very few participants in each respective study showed no signs of conformity. Muthukrishna et al. propose that these findings may reflect an underlying adaptive benefit to conformity in that it may be beneficial to the survival of a group to improve cooperation. Also, through observation (i.e., social learning), an individual can learn potentially costly information by witnessing another perform a dangerous task (e.g., watching someone eat an unknown berry that could be poisonous).

Finally, Evans et al. (2018) investigated selective copying and the utilization of “optimal” imitation in children. In their study, children watched demonstrators perform varying levels of relevant actions in order to retrieve a capsule from a “sweeper box” device. They found that when children witnessed a single method being performed by every demonstrator, the children were more likely to copy the relevant actions. In addition, children were also shown to copy less than total majorities, but not as often as total majorities and primarily when performed unanimously. However, when an irrelevant action was demonstrated unanimously, children were shown to only copy the irrelevant action in the next immediate trial. Additionally, 6-year-old children were less likely than 4-year-old children to copy irrelevant actions when performed by a less than total majority. Evans and colleagues interpret these findings as evidence of children becoming “optimal” imitators, meaning that children will examine the usefulness of a copied behavior in practice and then determine if the behavior is worth adopting.

Collectively, the findings presented in this section show the processes used by both children and adults to develop the skills necessary for the survival of themselves and their community. This is done through selective copying of observed behaviors and evaluating their usefulness through practice to determine their real benefit. Additionally, children and adults show a reliance on the consensus of the community to help determine what skills are desirable and beneficial.

Prestige Bias

Individuals may selectively choose to learn from sources of information deemed to be the most prestigious source available. A prestigious individual is deemed to have expertise in multiple domains even if they are only adept at a single skill or trade. Henrich and Broesch (2011) investigated the role of cultural transmission networks present in Fijian villages through a series of individual interviews. They found that when a potential model excelled in fishing, they were more likely to be chosen as a model for growing yams, but not a model for learning about medicinal plants. Additionally, those who excelled at growing yams were more likely to be sought after as a source of information on fishing as well as medicinal plants. However, the authors noted that individuals with more formal education were deemed to be a poor source of information for all three domains assessed. This is perhaps due to a belief that the skills being taught in schools do not translate well to success in the village community.

In another study investigating the impact of prestige, Chudek et al. (2012) found that across two experiments, children were more likely to model their behavior after a demonstrator that received at least 10 seconds of preferential attention from “bystanders” while modeling the behavior over a demonstrator that did not receive the same amount of attention. This pattern was particularly strong when modeling the use of an object, with a slightly weaker effect for food preferences and no effect for language learning. Findings from a second experiment led Chudek et al. to conclude that prestige may be derived

from attentional biases, as children are shown to preferentially attend to the demonstrator that received more attention from other “bystanders.” The researchers believe these findings are potentially important for survival purposes, as the implications of choosing a poor model for food preferences could have life-threatening consequences.

In a study that focused on the prestige bias present in adults, Atkisson et al. (2012) investigated social learning with adults participating in a hunting simulation with temporally-varying environments. They found that as individuals transition into novel environments, they improve in their ability to determine when it is the most beneficial to learn from someone else. Additionally, the authors found that participants were more likely to engage in social learning when performing poorly. As participants begin to become accustomed to the novel environment, they also begin to more accurately differentiate between successful and unsuccessful behaviors for the environment, choosing to persist in the performance of successful behaviors. However, Atkisson and colleagues note that they did not find any supporting evidence for an increase of reliance on prestige bias in novel environments over stable environments. The authors believe that incorporating a stronger transition from a stable to a novel environment in their experiment might increase a participant’s reliance on prestige-biased transmission in novel environments. Furthermore, this lack of reliance on prestige information may be due to a changing environment; if the new environment requires different adaptations, information from prestigious sources could be of lesser value. Atkisson et al. also note that the amount of attention a specific model receives impacts the participant’s decision to adopt the behavior exhibited by that model. The authors infer that the presence of prestige information in real-world settings can be a useful indicator of whom to trust and imitate.

Prestige bias can be a valuable *Adaptive Learning* strategy as an individual will be able to learn a set of skills that have been demonstrated to be successful in the current environment relatively quickly and at a low cost to the learner. The benefit

of selecting a prestigious source of information can help develop an individual's proficiency at hunting, gathering and growing food, and recognizing potential threats in the environment. However, prestige-biased transmission may become less viable as the environment changes, as some of these skills may no longer be effective in the new environmental conditions. In such a case, the individual should be capable of determining the prestigious source's information and then selectively attend to a new source as better information becomes available.

Related Findings and Conclusions

These studies indicate some modern and evolutionary advantages of acquiring successful and environment-specific skills. Either through conformity and imitation or through prestige-biased transmission, the benefits generated from utilizing these adaptive strategies can have a significant impact on an individual's level of fitness. Researchers have also studied the potential role of adaptive learning strategies in other aspects of daily life, including the acquisition of religion (Beck and Forstmeier 2007; Gervais and Najle 2015). These studies investigate the cultural role of developing religion as a species, as well as the potential adaptive advantages to be gained through the sometimes costly obligations of following a religion that may hinder an individual's level of fitness (i.e., celibacy). Adaptive learning strategies show clear real-world implications as they can help in a variety of environments. In an evolutionary context, it is beneficial to conform to the will of the group to receive their support and learn from them. This is also true for imitation, as it is critical to survival that an individual copy the most successful designs available for tools, such as arrows (see Atkisson et al. 2012), as choosing a poor model can be costly and potentially life-threatening. To conclude, whether an individual seeks to improve their work performance or provide for their family with improved hunting skills, seeking out the best source of information will help refine and develop their skills.

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Cultural Evolution](#)
- ▶ [Cultural Inheritance](#)
- ▶ [Cultural Transmission](#)
- ▶ [Development of Adaptations](#)
- ▶ [Evolution of Adaptations](#)
- ▶ [Imitation](#)
- ▶ [Imitation and Mimicry](#)
- ▶ [Increasing Longevity](#)
- ▶ [Learning](#)
- ▶ [Learning Versus Imitation](#)
- ▶ [Play and Social Learning](#)
- ▶ [Play and Tool Use](#)
- ▶ [Religion](#)
- ▶ [Religious Beliefs](#)
- ▶ [Social Learning](#)

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Adaptive Memory

- [Evolution of Memory, The](#)

(Adaptive) Phenotypic Plasticity

- [Adaptive Plasticity](#)

Adaptive Plasticity

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Synonyms

(Adaptive) Phenotypic plasticity; Developmental plasticity; Flexibility; Malleability

Definition

Property of a given genotype to produce different phenotypes depending on different environmental conditions, thereby enhancing organisms' fitness.

Introduction

The relationship between organism and environment is highly dynamical and can be thought of as a trade-off between the demands imposed by the environment and the organism's adjustments to those demands. On the one hand, the environments change; on the other hand, organisms fit the requirements posed by the new conditions "in the struggle for life." Phenotypic plasticity, the capacity of a genotype to give rise to different phenotypes in response to different environmental conditions, is crucial if organisms are to adapt to new environments. Adaptive plasticity is simply the phenotypic plasticity that enhances the organisms' fitness.

Although plasticity has been known for over a century, until recently it was taken to be uninteresting or even irrelevant. Currently, however, it arouses great interest; proof of this is the fact that while <10 papers were published per year before 1983, about 1300 papers were published in 2013 (Forsman 2015: 282). This exponential growth was promoted by the recent questioning of the traditional evolutionary framework (see below).

This entry will show why adaptive phenotypic plasticity is currently of such importance and will introduce its main characteristics. In addition, it will illustrate this property with the most paradigmatic instance of plastic phenotype, i.e., learning, the evolutionary consequences of which are emphasized by the so-called Baldwin Effect.

What Is Adaptive Plasticity?

Phenotypic plasticity, which comprises very different phenomena (Bateson and Gluckman 2011; Pigliucci 2001), is the property of a specific genotype to give rise to different phenotypes in the face of different environmental circumstances. This property is one of the two main adaptive mechanisms possessed by organisms, the other being population-level allele frequency change. However, as pointed out by Sultan (2017: 4), the emergence of favorable new genetic variants is rare and random, whereas plasticity has the great

advantage that it provides the organism with immediate adaptive variation and in many individuals at the same time.

The key tool for the analysis of phenotypic plasticity is the notion of norm of reaction, defined as “the set of phenotypes produced by a given genotype in a specified range of developmental circumstances” (Sultan 2015: 21). However, it should be noted that the two notions are not equivalent: the norm of reaction is a function describing the genotype-specific relationship between environments and phenotypes, whereas plasticity is an attribute of the norm (Pigliucci 2001: 7).

Plastic responses to environmentally induced factors presuppose cue-response systems (see Sultan 2015), in which an organism perceives some aspects of the environment as information and is able to respond to the cue through specific phenotypic effects. The cues, which cover a huge typology, may be anticipatory (an environmental change is predictable through reliable cues) or immediate (direct environmental influences) (Sultan 2015).

As regards the kinds of plasticity, a distinction is widely acknowledged (see Sultan 2015 and references) between adaptive and inevitable plasticity. The former encompasses phenotypic responses to the environment that are functionally adaptive, whereas the latter characterizes the factors that limit physiological or developmental processes (for instance, organisms developing in environments with scant nutrients experience only limited growth). Another distinction worth considering (partially related to the former) is that which exists between active (anticipatory phenotypic changes in response to environmental cues) and passive plasticity (direct influence exerted by the environment on chemical or physiological processes) (for discussion, see Forsman 2015).

Unfortunately, the exact relationship between phenotypic plasticity and adaptive evolution remains unclear. Obviously, any instance of phenotypic plasticity that increases fitness in response to new environments or new environmental conditions is beneficial for the organism, in relation to nonplastic beings. However, this situation cannot be automatically conflated with an adaptation. Furthermore, it should be remembered that the notion of adaptation is poorly understood

(Pigliucci 2001: 160). It is, therefore, extremely difficult to draw the line between adaptive and nonadaptive plasticity.

Plasticity provides organisms with an obvious advantage to successfully cope with new environments or environmental conditions, thus reducing the threat of extinction; consequently, it allows “a better phenotype-environment match across multiple environments than would be possible by producing a single phenotype in all environments” (DeWitt et al. 1998: 77–78). In contrast, if the environments remain constant over time, the aforementioned benefit does not apply.

However, it is also obvious that plastic organisms cannot adapt to any environmental conditions, and consequently no organism exhibits a perfect or infinite plasticity (DeWitt et al. 1998: 78). The lack of such a “Darwinian monster” (Pigliucci 2001: 174), i.e., an organism that copes perfectly with any environment, shows that (the evolution of) plasticity depends on the existence of associated costs. In this sense, DeWitt et al. (1998: 78) establish the distinction between costs and limits: “A cost of plasticity is indicated in a focal environment when a plastic organism exhibits lower fitness while producing the same mean trait value as a fixed organism. In contrast, a limit of plasticity is evident when facultative development cannot produce a trait mean as near the optimum as can fixed development.” These scholars make reference to five costs (maintenance costs, production costs, information acquisition costs, developmental instability, and genetic costs) and four limits (information reliability limit, lag time limit, developmental range limit, and the epiphenotype problem; for discussion, see DeWitt et al. 1998). While acknowledging the theoretical value of those costs and limits, Pigliucci (2001: 175ss.) argues, however, that those constraints on plasticity can hardly be distinguished from an empirical perspective.

Finally, a further point in question is the deep implications of phenotypic plasticity for evolutionary theory, as emphasized by West-Eberhard (2003). This scholar argues that phenotypic plasticity strongly influences adaptive evolution through phenotypic accommodation, which integrates developmental and evolutionary change without the need for genetic change to take

place. According to West-Eberhard's (2003) framework, the evolution of a new adaptive trait through natural selection begins with a genotypically or environmentally induced phenotypic change. The initial viability of the change is increased through adaptive plasticity (phenotypic accommodation), this step being followed by genetic accommodation through natural selection. Accordingly, "Genes are followers, not necessarily leaders, in phenotypic evolution" (West-Eberhard 2003: 158). In other words, genetic changes follow (i.e., do not necessarily precede) phenotypic change, in such a way that genetic novelties are not required in order for phenotypic novelty to evolve. Therefore, according to West-Eberhard (2003), phenotypic plasticity has a prominent role in facilitating and accelerating three main evolutionary processes: the origin of novelty, speciation, and macroevolution.

The following section illustrates the property of phenotypic plasticity with its most powerful instance, i.e., learning, by showing how learning capacity can give rise to new directions of evolutionary change. This aspect is known as the Baldwin Effect.

A Brief Overview of the Baldwin Effect

The Baldwin Effect (Baldwin 1896) is a (controversial) mechanism which speeds up natural selection (for discussion, see Weber and Depew 2003; Longa 2005). It can be broken down into two steps. The first one has to do with phenotypic plasticity, which enables an organism to develop new behaviors when exposed to new environmental conditions, or to adapt itself, through learning, to behaviors observed in the environment (for instance, by mimicking the phenotypic result of a mutation arising in another individual). Phenotypic plasticity thus provides the organism with fitness, which in turn enables it to stave off extinction. Therefore, the starting point of the process is a phenotypic change arising as a consequence of an ontogenetic adaptation made possible by the organism's plasticity. However, for the Baldwin Effect to apply, a second and crucial step is required, namely the genetic assimilation of the phenotypic trait previously learned as a response to a given stimulus. In

this step, the plastic learning mechanism for the phenotypic trait is replaced by a rigid mechanism based on heredity. It is in this sense that learning can guide evolution.

If the learning of a given phenotypic trait varies within a population, some individuals will be capable of learning the trait better than others. Natural selection will favor those who acquired the ability more easily (for example, on the basis of limited exposure to the stimulus), because those individuals will increase their fitness. Further down the evolutionary line, mutations will occur (in a non-Lamarckian sense) which will produce the same type of trait without the need for learning, the outcome being the reduction (or the deletion) of phenotypic plasticity for the trait. In other words, natural selection will tend to act on plasticity, by confirming and accelerating the evolutionary change which originally began via learning. It is for this reason that the Baldwin Effect speeds up evolution.

For a full understanding of the Baldwin Effect, it is also crucial to bear in mind that learning presupposes a trade-off between the costs and benefits associated with such a capacity. Although learning has undeniable advantages, it also has clear disadvantages. For example, it requires time, attention, and effort, and the learned behavior is exposed to dangerous contingent factors that might well be deleterious. Yet the disadvantages disappear if the learned behavior becomes inherited. The Baldwin Effect, therefore, reduces the costs of learning.

To sum up, the Baldwin Effect is another instance that shows, in agreement with West-Eberhard's framework, that genes are followers, not leaders, in evolution.

Conclusion

The traditional evolutionary framework completely ignored phenotypic plasticity because this property did not fit in with the evolutionary assumptions of the Evolutionary Synthesis and the resulting Neo-Darwinist thought. The reason is clear: because evolution was taken to be a mere change in allelic frequencies, environmental conditions and phenotypic plasticity were put aside, for neither aspect was genetic and they were,

therefore, considered to be irrelevant from an evolutionary point of view.

However, such traditional Neo-Darwinian assumptions are now being strongly challenged. In fact, there exists a wide range of extragenetic factors that do become inherited, many of them passing environmental information to the offspring (Sultan 2015) and producing nongenetic although inherited adaptations. This means that the genotype cannot dictate the adaptation to the environment (i.e., there cannot be a single predetermined developmental outcome); rather, the phenotype becomes actively generated through the developmental process (Sultan 2017). Accordingly, the environmentally induced phenotypic variation has a crucial role in creating the conditions that produce an adaptive genetic response (let us remember genes as followers, not as leaders). To sum up, the status of the environment greatly surpasses the role of a mere selective filter (Sultan 2015: 41). It is for this reason that phenotypic plasticity will presumably gain an increasingly important role in evolutionary biology in the years to come.

Cross-References

- Adaptation
- Adaptation and Natural Selection
- Adaptive Learning
- Development
- Development of Adaptations
- Differential Reproductive Success
- Ecological Factors and Rape
- Environmental Unpredictability
- Learning
- Ontogenetic Adaptations

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Adaptive Play Behavior

- Evolution of Play

Adaptive Polymorphisms

- Alternative Adaptive Peaks

Adaptive Problem of Detecting Kinship

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Synonyms

Altruistic behavior; Coresidence; Genetic relatedness; Incestuous behavior; Kin detection system; Maternal perinatal association; Nepotism;

Definition

Evolution of cues used by humans to detect kin in order to avoid incest and promote altruistic behavior toward genetic relatives.

Introduction

As a highly social species, humans interact and cooperate with many individuals; however cooperation among relatives tends to be greater than among unrelated individuals (Hamilton 1964). Throughout history, humans of all known cultures have always tended to feel and behave differently toward family members than to individuals to whom they were not genetically related. This behavior, which is not exclusive to humans, is distinguished by two important traits: on the one hand, the display of a highly altruistic behavior in which their own welfare could be sacrificed to help family members and, on the other hand, an innate aversion to any sexual contact with genetic relatives. From the evolutionary point of view, natural selection has favored this behavior because it conferred a selective advantage to the individuals displaying it. These desirable features increased in frequency to the point that nowadays they have become a universal feature of the species.

Species' typical traits have been favored by evolution because they solved an adaptive problem for the organism that displayed it. Therefore, it is correct to infer that the behaviors displayed by humans toward family members have been selected because they solved an adaptive problem, at least in the environment of evolutionary adaptiveness. However, it is important to note that thousands of species display social behaviors that are influenced by genetic relatedness. Altruistic behavior or nepotism correlates with the amount of shared genes that are identical by descent. Therefore, organisms display this behavior in response to cues of genetic relatedness. In humans, genetic relatedness correlates with the willingness to help in a hypothetical situation and the amount of imbalance tolerated in a reciprocal relationship (Burnstein et al. 1994).

Avoiding Interbreeding

Social groups and closeness to relatives lead to two entirely different adaptive problems, avoidance of inbreeding and willingness to support kin. Breeding with relatives increases the probability of conceiving individuals with two copies of recessive deleterious genes. These genes tend to produce either an *in utero* early death or the birth of offspring with congenital abnormalities. Therefore, genes that coded for behaviors that led to incestuous behavior have eventually caused their own disappearance by being present in always fewer handicapped bodies. On the other hand, genes that promoted behavior that avoided sex with genetic relatives have been favored by natural selection. This has led to their increased presence in offspring that would have been healthier and reproductively more successful than the ones produced by incestuous sex. As a result, the successful genes have spread in the population to a point of ubiquity in human populations.

Development of Altruism

The second adaptive problem associated to genetic relatedness involves the ability to identify kin in order to support them. Altruistic behavior toward kin is a consequence of genes aiming to spread themselves; thus natural selection has favored the permanence of motivational systems that, in an all else equal situation, increase the willingness to help close genetic relatives as opposed to unrelated ones. A genetic makeup that encourages helping relatives so that they reproduce more effectively would increase the probability of spreading new copies of those genes in the population. This means that genetic designs that promote altruistic behaviors will always be favored as long as the cost to the individual's own reproduction is offset by the benefit to the reproduction of its kin member. The degree of relatedness between relatives has a great impact on the expression of this behavior since the more closely related two individuals are the higher the probability that they share the same genetic makeup.

Kin Detection Systems

In order to effectively solve the above adaptive problems, organisms would have developed the ability to identify who is and who is not a genetic relative and estimate the closeness of this relatedness. Detecting genetic similarity is therefore an important adaptive problem, and not an easy one to solve. Organisms cannot “see and compare” DNAs. It appears that the problem has been somehow solved by the development of a *kin detection system*. By analyzing and outweighing several unrelated cues, this system seems to generate an internal index of relatedness. Based on the results, the system then feeds two different motivational systems, one that promotes sexual attraction/aversion and the other family-directed altruism. It is important to note that familiar relationships do not seem to be identified in the same way, for instance, the system uses different cues to determine relatedness between parents and offspring when compared to siblings.

One of the main cues used to establish relatedness to offspring is similarity. People tend to rate strangers that look similar to them as more trustworthy and less sexually attractive. Mammalian mothers have almost 100 % confidence in their maternity. Therefore they regard any infant who is present after birth as their own child even if they do not resemble her. Fathers on the other hand must use other cues such as phenotypic similarity. A study by Apicella and Marlowe (2004) found that fathers favor children who look more like them (Apicella and Marlowe 2004). This not only refers to physical similarity (ancestral males would have had very little exposure to their own image) but nonvisual cues of self, such as personality, behavioral traits, and smell. In addition, since his mother and sibling share a proportion of his genes, a male could also use their faces as templates.

To gauge relatedness to siblings, the system has evolved to detect mainly two cues: maternal perinatal association (MPA) and duration of coresidence during the period of parental investment. MPA is established when an individual sees their mother caring and nursing a newborn; this means with a high probability that the newborn is

his sibling and will be tagged as such. As a consequence, the motivational systems will be promoting high levels of altruistic behavior and high levels of sexual aversion. It is obvious that MPA only works for older siblings. Thus, in order to detect genetic relatedness to older siblings, the brain uses a different cue which takes into account the coresidence period with other children when growing up (approximately between ages 0 and 18). In hunter-gatherer societies, the duration of childhood coresidence is highly correlated with the degree of kinship (Lieberman et al. 2007). There are several studies that have shown that early coresidence causes sexual disinterest between siblings and even unrelated individuals raised together from childhood (Westermarck effect) (Wolf 1995). Interestingly time of coresidence is proportional to the degree of aversion to incest; thus, the longer a youth coresides with an older sibling, the more disgust elicited by the thought of incestuous sex. This extends to moral judgments of third parties where the length of coresidence predicts how morally wrong youngsters find third-party incest.

The MPA cue is overly predominant over coresidence; in other words they are not additive. MPA is enough to generate high levels of altruism and sexual disinterest which do not seem to be modified by time of coresidence. In order to obtain similar levels of altruism and sexual aversion in younger siblings, 14–16 years of coresidence are needed. Thus, coresidence only has an effect if the MPA cue is absent. Since both cues are not additive, they must somehow be associated; it has been suggested this is done by a “kinship estimator.” The kinship estimator combines the cues in a non-compensatory way, following a decision tree pattern. In addition the kinship index seems to be generated in an unconscious way and therefore not affected by conscious beliefs. This is evidenced by cases of step or adoptive siblings. In this case coresidence generates altruistic behavior and sexual aversion despite the fact that the individuals know they are not genetically related. This shows that the criteria used by the kinship estimator prevail over conscious beliefs. Although the two cues mentioned above seem to be the strongest ones,

in their absence other cues such as physical resemblance and olfactory signals indicating similarity of the major histocompatibility complex are also taken into account by the system. This is especially relevant in case of distinguishing for instance, maternal half-siblings from full-siblings (DeBruine et al. 2008).

Conclusion

It is important to note that the mechanisms described above are prevalent across species. Nowadays modern humans possess other more sophisticated means of assessing kinship which have been added, not replaced, to existing ones (Geary 2005). These processes seem to be controlled by the neocortex and tend to be complemented and overridden by aforementioned more primitive ones (Park et al. 2008).

As discussed above, animals are not born with knowledge of which individuals are kin. Kin-recognition mechanisms are dependent on learning, enabling individuals to acquire the association between specific members of the group and kin-relevant responses. As a consequence, kin recognition is susceptible to mistakes. A minority of individuals are still inclined to engage in incest. This could arise from the lack of exposure to cues of kinship during upbringing. For instance, opposite-sex siblings that had been separated for considerable time during childhood are more likely to engage in incestuous activity (Bevc and Silverman 2000). In this case these behaviors can occur with intact brain mechanisms. Another explanation for this behavior could be a malfunction of the kin detection system in which due to damage, the motivational system that causes sexual attraction is not turned off by cues of kinship.

Although the presence of a kinship estimator seems to agree with an evolutionary premises, some issues are worthy of consideration. The evolutionary approach bases its assumptions on contemporary hunter and gatherer societies. All these societies express on one way or another incest taboos, but there is evidence that not all ancestral groups conformed to the structural organization of

the groups alive today. Modern hunter and gatherer lifestyle is quite restricted to few areas that share similar landscapes and limited immigration/emigration. Our ancestors, on the other hand, occupied a wealth of different habitats ranging from the African savannah to arctic regions. As a consequence of this, it is very likely that social structures were quite diverse among those groups.

It is reasonable to deduct that the kinship model of incest avoidance is more adaptive in societies that do not involve significant immigration/emigration. Here kin detection is important in order to favor altruistic behavior and an increase in the number of kin.

In many animal species that live in social groups, this excess of kin members is usually solved by emigrating before mating season. Usually as soon as males reach reproductive age, they move away from the familiar unit reducing the risk of inbreeding. In these cases there is no evolutionary pressure to develop an incest avoidance mechanism. In the case of humans, it is not well known if this was the case during ancestral times. Although there is some evidence that at least in some early *H. sapiens* groups, males moved away, it is not known whether this happened in the majority of groups. It has been argued that without this information the adaptive benefit of evolving a kinship detector is not well supported (Richardson 2015).

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Benefits to Kin](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Facial Resemblance and Kinship Detection by Strangers](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
- ▶ [Incest Avoidance](#)
- ▶ [Kin Detection by Odor](#)
- ▶ [Kin Recognition](#)

- [Kin Recognition and Classification in Humans](#)
- [Kin Selection](#)
- [Parental Investment](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)
- [Presence of Siblings](#)
- [Resemblance](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Westermarck Effect](#)

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Adaptive Problems

- [Sex Differences, Initiating Gossip](#)

Adaptive Solutions to Socialization

- [Robert Kurzban on Group Processes](#)

Adaptive Specialisations

- [Carruthers on Massive Modularity](#)

Adaptive Variation

- [Alternative Adaptive Peaks](#)

Adiposity

- [Obesity](#)

Adjunct Mother

- [Aunt Care](#)

Adjustment

- [Assimilation](#)

Adjustment of Copulatory/Ejaculatory Investment

- [Male Prudence and Sperm Limits](#)

Adolescence

- [Genetic Influences of Puberty](#)
- [Puberty in Girls](#)

Adolescent Issues

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Synonyms

Issues related to adolescent development; Teen-age issues

Definition

Adolescence is the developmental period between childhood and adulthood. It is a unique time characterized by dramatic social transformations (e.g., friendships become more intimate) that occur alongside significant physical, cognitive, and psychological changes.

Introduction

Adolescence (broadly spanning 10–22 years old) is a unique period in development characterized by rapid and dramatic biological, cognitive, and social changes. For instance, most adolescents go through puberty, which involves hormonal shifts that trigger the development of primary and secondary sex characteristics and physical growth, in addition to changes in emotionality and behavior (e.g., Connolly et al. 1996). The adolescent brain also undergoes important structural and functional changes, including increased synaptic pruning (which contributes to growth in cognitive abilities) and further development of the prefrontal cortex (a brain region implicated in processes such as decision-making and personality expression, e.g., Casey et al. 2008; Steinberg 2010). Both resulting from and amidst these changes, adolescents' social worlds begin to evolve. For instance, beginning in early adolescence (10–14 years old), youth spend the majority of their waking time with their *peers* (rather than

their families, e.g., Collins and Laursen 2004; Montemayor 1982).

Over the years, adolescents' peer experiences have garnered significant theoretical and research attention. Often, the focus is on the ways in which peers can cause *harm* (e.g., vis-à-vis peer pressure and victimization). However, many adolescents form positive and supportive relationships with their peers that foster *healthy* development and well-being. This entry will explore the unique features of adolescents' peer experiences, distinguishing between those at the dyadic- (i.e., experiences between two adolescents, such as friendships) and group-level (i.e., experiences involving the larger peer group, such as popularity and peer victimization) of social complexity. Different perspectives on the significance of peers in the lives of adolescents will be offered, including an evolutionary perspective that emphasizes the positive and negative trade-offs (Buss 1995; Hawley 2011).

Friendships

Beginning with the peer experience of *friendship* (i.e., voluntary relationships between two same-age peers that are characterized by mutual affection or liking), it is well established that the large majority of adolescents, at any given time point, have at least one *mutual* friendship as determined by reciprocated friendship nominations (i.e., Zoe nominates Sophia as a friend *and* Sophia nominates Zoe as a friend; Parker and Asher 1993; Rubin et al. 2015). Most of these adolescent friendships, especially those considered by both adolescents to be a *best* friendship, are with same-sex peers. In fact, a robust finding in the developmental sciences literatures is that the majority of friendships across the lifespan tend to be with same-sex peers (Hartup and Stevens 1997). This is perhaps best explained by the *homophily hypothesis*, such that individuals are most attracted to, and subsequently form friendships with, those who are similar in observable characteristics, such as sex, race, and behavior (Kandel 1978). That said, there is a significant increase in the frequency of *other*-sex friendships throughout

the adolescent developmental period (Poulin and Pedersen 2007). In fact, a gradual *coming together* of boys and girls occurs during adolescence whereby adolescents first develop crushes on and begin to interact with other-sex peers and then later form other-sex friendships and mixed-sex peer groups. This coming together of the sexes, in turn, helps facilitate the formation of adolescents' first heterosexual *romantic* relationships, thus beginning the evolutionarily important process of mating.

The features or qualities of friendships also begin to change during the adolescent period. For instance, relative to friendships during childhood, adolescent friendships become more intimate (Buhrmester and Furman 1987). This developmental change is particularly pronounced for girls and is mostly due to adolescents' engaging in increased levels of *intimate disclosure* to their friends (i.e., telling each other secrets; Rose and Rudolph 2006). Although friendships become increasingly intimate during adolescence, they also become increasingly characterized by jealousy and other negative relationship processes (i.e., *co-rumination* or repeated discussion of negative feelings and problems by both relationship partners; Rose 2002), which may explain, in part, why adolescent friendships become particularly vulnerable to conflict and break-up (Benenson and Christakos 2003; Bowker 2011). Indeed, a recent study found that approximately 50% of adolescent friendships dissolve across a single school year (Meter and Card 2016). Thus, many friendships during adolescence would not be considered *reliable* alliances. And, many adolescents report stress and sadness when their friendships end, likely because many adolescents experience friendship dissolution as a significant *interpersonal loss* (Bowker 2011). Another rarely discussed reason, however, for the fragility of adolescents' friendships is that adolescents have greater choice over their peer relationships than they did when they were children, and thus, many may *choose* to end friendships that are not satisfying, fulfilling, or promoting of resources. In this regard, the *self-initiated* termination of certain adolescent friendships may be advantageous for individual growth and development, but very little

research has evaluated this more positive aspect of friendship dissolution.

Moving beyond the prevalence and characteristics of adolescents' friendship experiences, friendship is a central construct of study in the adolescent literature because of its influence on adjustment outcomes. In other words, there is a large, ever-growing body of research showing that friendships impact adolescents in numerous and significant ways. For example, adolescents with mutual friends report higher levels of self-esteem and psychological well-being relative to those without mutual friends (for recent review, see Rubin et al. 2015). Importantly, the effects of adolescent friendships on psychological well-being appear to be both immediate *and* lasting. Bagwell et al. (1998), for instance, found that having a friend in early adolescence predicted positive psychological well-being in young adulthood. These effects were found after controlling for peer acceptance (at the group-level of social complexity, as explained in more detail below), findings consistent with those from many other studies showing that the effects of friendship on psychological and other types of adjustment during adolescence are *unique* (e.g., Erath et al. 2008). Of course, there is significant variability in the ways in which adolescents' friendships impact individual adjustment. For example, the *characteristics of the friends* matter such that adolescents whose *friends* are suffering psychologically or are delinquent are likely to be *negatively* influenced by their friends over time through *socialization* processes (e.g., Poulin et al. 1999; Zalk et al. 2010). From an evolutionary perspective, forming successful friendships (especially with prosocial peers) likely fulfills needs to belong and promotes access to resources (i.e., sources of help and support), above and beyond those available to an individual acting alone, while forming friendships with those in distress interferes with the benefits of friendships (Buss 1995). Finally, it should be acknowledged that individuals of all ages vary in their abilities to form and maintain friendships, and some individuals, including adolescents, find themselves in less desirable and maladaptive friendships because they are rejected, excluded, and

victimized by their peers (peer difficulties at the group-level of social complexity, which are described in the following section), and thereby left without any other options.

The Peer Group

Friendships during adolescence are oftentimes embedded in larger peer groups, such as *crowds* (i.e., large, reputation-based groups such as “populards,” “jocks,” and “brains”; Prinstein and La Greca 2002) and *cliques* (e.g., smaller groups composed of multiple friendships; Urberg et al. 1995). Crowds and cliques are important to study, as research shows that adolescents are not only influenced by their close friends but also these larger peer group experiences. For instance, Hussong (2002) found that adolescents (aged 16–19 years old) were more likely to use drugs and alcohol if their best friends did, and *also* if the cliques and crowds with which they affiliated were frequent substance users. In addition, affiliation with highly regarded/valued crowds, such as the “populards” or “jocks,” has been found to promote positive psychological well-being (i.e., high self-esteem, low levels of loneliness) whereas low-status crowd (e.g., “burnouts”) affiliation appears to have the opposite effect (La Greca and Harrison 2005; Prinstein and La Greca 2002). From an evolutionary science perspective such findings are not too surprising, as being a part of a larger group has its advantages (i.e., in terms of resources, protection, etc.), especially a larger group with power (e.g., Buss 1995). Nevertheless, the aforementioned findings nicely illustrate that it is not only friendships that matter during adolescence but larger peer groups do as well.

In addition to cliques and crowds, researchers oftentimes study adolescents’ levels of popularity, rejection, and victimization, all of which reflect how adolescents *fare* with the larger peer group. Adolescents are uniquely aware of their peers and the social dynamics in their schools, and thus, researchers often ask them to report on who is highly popular, rejected, and victimized in their grade and school. Such procedures (also

known as *sociometric* and *peer nomination* procedures; see Cillessen 2009) allow researchers to determine who receives the most nominations for these group-level experiences, and from there to understand how variability in such experiences is associated with outcomes such as psychological well-being. For instance, adolescent *popularity* has garnered considerable theoretical and empirical interest, in part because it peaks in terms of importance during early-to-middle adolescence (LaFontana and Cillessen 2010). Adolescents who are perceived by peers as popular tend to be well-adjusted in a number of ways (e.g., socially skilled, attractive, athletic, Cillessen et al. 2011) and are well-known and highly visible in the larger peer group. As a result, they are oftentimes powerful and influential among peers (Cillessen et al. 2011). Obtaining high levels of popularity is considered *adaptive*, from an evolutionary perspective, as it increases individual access to or control over tangible, social, and sexual resources. Popular youth, however, often use a combination of aggressive and prosocial (e.g., kind and helpful) strategies to achieve their popularity (Archer and Coyne 2005; also see *Resource Control Theory*, Hawley 1999); this tendency toward aggression causes them to not always be highly *accepted*, or well-liked, by peers (Parkhurst and Hopmeyer 1998). Popular youth also commonly achieve high status by engaging in other “norm-violating” behaviors (i.e., substance use, rule-breaking) that can be harmful to their individual development and to their peers but, at the same time, are viewed as cool and mature during adolescence (Cillessen et al. 2011; also see *Maturity Gap Hypothesis*, Moffitt 1993). As such, there appear to be trade-offs associated with achieving high status among peers during adolescence.

Of course, not all adolescents fare well with their peers, and instead, some adolescents are *rejected* (i.e., disliked) and *victimized* by their peers. Adolescents may be rejected if they display traits or behaviors that are not highly valued by the peer group, including shy or withdrawn behavior or aggressive behavior (Parkhurst and Asher 1992); the same adolescents might also be highly victimized by their peers. Other

adolescents, however, might be victimized because they are perceived as weak or vulnerable in some way (and therefore, an “easy” target for bullies). For example, adolescents without friends, who appear psychologically distressed, are obese, or have a developmental or learning disability, experience high levels of peer victimization (Hong and Espelage 2012). Victimization takes many forms, including physical (e.g., kicking, hitting, pushing), verbal (e.g., threatening, insulting, name-calling), and relational (e.g., excluding, ignoring, spreading rumors/gossip; Archer and Coyne 2005; Dodge et al. 2006) and can occur in person or online (Salmivalli and Peets 2018). Although bullying and peer victimization are common during childhood, they increase during early adolescence for a number of reasons, including less adult supervision and new links between rule-defying behavior and social status (Cillessen and Mayeux 2004; Moffitt 1993). Not surprisingly, both rejected and victimized youth tend to suffer psychologically (e.g., elevated levels of loneliness, depressive symptoms, anxiety), although some of these negative outcomes may be mollified by protective factors such as having a close friendship (Parker and Asher 1993). Beyond mental health outcomes, peer victimization and rejection have also been found to negatively impact physical health (e.g., dysregulated cortisol responses) and to interfere with academic functioning (e.g., Erath et al. 2008; McDougall and Vaillancourt 2015). As such, over the past few decades there has been widespread interest in prevention and intervention efforts targeting peer rejection and victimization, many of which are school-based and call on peers to assist and intervene (e.g., Yeager et al. 2015). However, such programs, especially those focused on peer victimization and those in the United States, have been limited in effectiveness, in part because many adolescents are reticent to protect their peers out of fears for becoming targets themselves (Salmivalli and Peets 2018). Thus, negative group-level peer experiences continue to be a serious concern during adolescence.

Conclusion

Despite seemingly obvious applications of evolutionary science to understanding adolescent issues, developmental psychologists have been slow to adopt this framework. Just a few years ago, one prominent psychologist observed: “. . . at the time of this writing, Google Scholar located only four articles with the word ‘evolution’ or ‘evolutionary’ in the title from all the English language journals on adolescence. This gap is extraordinary in light of the reproductive maturity of the average 15-year-old and evolutionists’ interest in reproduction” (Hawley 2011, p. 307). For the most part, developmental research on adolescent issues has taken a risk-based approach focused on elucidating when and why problems occur (e.g., how behaviors such as aggression contribute to peer and psychological problems). Evolutionary scientists, however, have cautioned against the tendency to strictly pathologize adolescent “problem” behaviors (e.g., aggression/bullying, substance use, sexual activity) and instead have suggested a more balanced perspective that allows for the possibility of both positive and negative trade-offs for any behavior. In addition, it has been suggested that many “problem” behaviors during adolescence occur because they are high risk/high reward. For example, substance use can be considered risky as it could lead to detrimental or even fatal outcomes, but, it can also be viewed as potentially adaptive/rewarding by fostering improved group standing and belongingness (Ellis et al. 2012). As such, drawing upon an evolutionary science perspective could enrich the study and understanding of adolescent development by focusing on such trade-offs.

Beyond striving for better integration of evolutionary and developmental sciences, there is still much to be learned about the varied issues pertaining to adolescent development, only a small subset of which were discussed in this entry. For instance, many issues related to adolescence are changing with the proliferation of technology, and researchers have been slow to catch up. In the future, there will be a great need to better

understand the ways that social media has impacted adolescents' social worlds, including problems with peers (e.g., cyberbullying, peer exposure and influence; Hawley 2011), and also potential benefits (e.g., reduced loneliness, the facilitation of intimacy between friends). Furthermore, given our increasingly connected world, cross-cultural variations and similarities in adolescent development and peer experiences are imperative to better understand and could lead to an deeper knowledge of which aspects of adolescent development are universal (and thus biologically or evolutionarily based) versus context-bound. In addition to cultural differences, it is also important to consider that many individual-level differences (e.g., in personality and other traits) may impact or alter the types of friendships and group-level experiences adolescents have. For example, there is a growing literature revealing variability in the reasons that some adolescents choose to *withdraw* or keep away from their peers (e.g., shyness versus preferences for solitude), and how these differences impact how they are perceived by peers and their psychological well-being (see Rubin et al. 2009). Finally, more multidisciplinary research that cuts across disciplines is needed to fully understand the complex ways that adolescents' social, biological, and cognitive functioning interact to predict short- and long-term outcomes.

Cross-References

- [Altruism Defined by Benefits Conferred](#)
- [Fair-Weather Friends Versus True Friends](#)
- [Bullying](#)
- [Cognitive Changes in Adolescence](#)
- [Friendship](#)
- [Peer Competition and Cooperation](#)
- [Peer Feedback and Norms](#)
- [Peer Groups](#)
- [Peer Pressure](#)
- [Peer Rejection](#)
- [Peer Rejection, Sex Differences in Initiation of](#)
- [Peer Socialization](#)

- [Same-Sex Friendships](#)
- [Sex Differences in Same-Sex Aggression](#)

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Adolescent Parenthood

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Synonyms

Parental investment; Teenage pregnancy

Definition

Producing and caring for an offspring by a parent who is under the age of 20 years-old.

Introduction

Adolescent parenthood has been associated with many negative outcomes, such as decreased physical and mental health of the offspring (Pinzon and Jones 2012). Although there have been fluctuations in the rate of teenage pregnancies in the United States, there has been a relatively steady decline in the number of children born to adolescents through the 1990s and 2000s (Pinzon and Jones 2012). This entry will discuss some of the negative outcomes associated with adolescent parenting as well as some of the evolutionary psychological theories behind human mating and parenting. A large portion of evolutionary research on parenting focuses on the paternity uncertainty hypothesis, the mating opportunity cost hypothesis, and parent-offspring conflict theory.

Paternity Uncertainty Hypothesis

Because males can never be certain about whether they are the biological father of their putative offspring, they may engage in behaviors to decrease their uncertainty and/or conserve their resources by decreasing their resource expenditure on their offspring (Trivers 1974). Human female fertilization is internal, indicating

that maternity is 100% certain, but paternity is oftentimes in doubt. Facial resemblance and odor recognition are two cues men use to familiarize themselves with the child (Alvergne et al. 2009). Fathers of children whose faces resemble their own reported greater levels of emotional closeness with them than those lacking facial resemblance (Daly and Wilson 1988). Fathers also showed more affection and attachment to children whose smell they can easily recognize. Men invest more resources, time, and affection in children who are genetic offspring than those who are genetically unrelated offspring (i.e., stepchildren). In addition, fathers who have a romantic relationship with the mother and/or cohabitate with the mother are far more likely to invest in parenting than fathers who are not currently romantically involved, or cohabitating, with the mother of their offspring (Daly and Wilson 1988). A number of factors play a role in this dynamic, including the type of romantic involvement the couple had during the pregnancy and after birth, paternal ability to provide and support kin, as well as the father's level of education, socioeconomic status, relationship with his family of origin, ethnic background, cultural values, moral values, and spirituality (Jones and Pinzon 2012).

Mating Opportunity Cost Hypothesis

The mating opportunity cost hypothesis indicates that males are less likely to take on parental care because, in doing so, they risk missing additional mating opportunities. Although females can acquire many mates, they are not able to reproduce as frequently as males because of the 40-week gestation period of pregnancy (Buss 2012). During these 40 weeks, the pregnant female is not able to reproduce again, but males could seek extra mates to increase their reproductive opportunities. The reproductive success of males is limited to the available number of fertile females that can successfully conceive. Adolescent males are typically not ready to settle with just one female and are very aware of the possibility of potential mates.

Parent-Offspring Conflict Theory

Parent-offspring conflict occurs when parents' perceived needs of their offspring differ from the offspring's perceived needs and desires (Trivers 1974). Because of adolescents' lack of experience and resources, they are less likely to raise a child effectively and correctly. Infants are completely dependent upon their parents for survival, which calls for the parents to consistently be available and prepared. The theory of parent-offspring conflict predicts that each child will generally desire a larger portion of the parent's resources than the parents want to give (Daly and Wilson 1988). With both the parents and the offspring being young, one would expect conflict between the two to be more frequent than if the parent was of an adult age and mindset. This could lead to negative outcomes for the offspring. For example, a young parent may not have the patience to raise a young child or be willing to sacrifice certain activities or resources – such as developing relations with friends via social gatherings, or spending money on desired but unnecessary items (e.g., jewelry and other convenience items) – that may be necessary to forego when raising a child. Parent-offspring conflict may also arise if a parent decides to secure a new mate. Acquiring a new mate may lead to a decrease in available resources, which could lead to greater competition for these dwindling resources and, therefore, greater conflict. Parent-offspring conflict over the parent's mating decisions remains a topic that is not often explored empirically (Buss 2012).

Decreased Life Expectancy

Adolescent parents' offspring often suffer from decreased life expectancy. There are many cases of child neglect and infanticide brought on by the pressures of life that adolescents do not effectively handle in their best judgement. The proportion of births leading to infanticide are highest among women between ages 15 and 19 years-old (Bugos and McCarthy 1984). Teenage mothers show the highest rates of infanticide, more than three times higher than any other age group (Daly and Wilson 1988). Infants of adolescent mothers also have an increased risk of adverse health outcomes including higher incidences of perinatal

mortality, low birth weight, preterm birth, developmental disabilities, and poorer developmental outcomes (Jones and Pinzon 2012).

Paternal desertion is also cause for concern regarding the offspring's health and life expectancy. Child mortality rates significantly increase when the father is not present (Hurtado and Hill 1992). When abandoned by the father, adolescent mothers are left with few choices, including abandoning or giving up the child for adoption, killing the child and investing available resources toward mating, or simply living with it and raising the child alone. Younger and/or unwed mothers are more likely to commit infanticide, devoting their efforts more toward other adaptive problems, such as surviving or attracting men who are willing to invest resources in them (Buss 2012).

Many cases of inadequate care of infants born to adolescent parents can be explained by drug usage, domestic violence, psychological disorders, and potential socioeconomic problems. Research conducted in Sweden illustrated the long-term socioeconomic effects of adolescent parenthood (Vinnerljung et al. 2007). Specifically, adolescent parents possess an increased likelihood of low educational attainment, single living arrangements, and welfare dependency – supporting the view that childbearing during adolescence is a risk factor for poverty in later life.

Violence during pregnancy is most recognized between the ages of 12 and 24 years old. Approximately 61% of the subjects in their study have experienced IPV, with 37.5% reported having experienced it during pregnancy (Mylant and Mann 2008). Studies conducted in urban areas revealed that homicide is the leading cause of death of reproductive aged women (Daly and Wilson 1988).

Infants of adolescent mothers have an increased risk of adverse health outcomes, including higher incidences of perinatal mortality, low birth weight, and developmental disabilities (Jones and Pinzon 2012). In fact, infant mortality rates are significantly greater for infants of adolescent mothers under the age of 15 (Phipps et al. 2002).

Having multiple children during adolescences has also been associated with several

negative outcomes. Repeat births have been linked to decreased educational achievement, increased dependence on governmental support, increased infant mortality, and low birth weight (Jones and Pinzon 2012). Research has revealed that a repeat or second pregnancy occurs in 19% of adolescent mothers within 1 year of the first birth. That probability increases to 38% within 2 years of the first birth, with higher rates for those with low socioeconomic status (Partington et al. 2009).

There are also many factors that contribute to improved outcomes of adolescent mothers that are recognizable. Studies have shown that having completed school before becoming pregnant, actively participating in a program for pregnant adolescents, having a sense of control over one's life, experiencing little social isolation, and limiting the number of children one produces are all factors associated with improved outcomes of adolescent mothers (Jones and Pinzon 2012). Another study showed that although these factors improve an adolescent mother's success outcome, it did show negative effects concerning the offspring. More than two-thirds of women in that study had completed high school, had regular employment, and were not dependent on the government for income. However, even with these positive effects for the mother, there may still be negative outcomes for the offspring. That same study found the offspring of those adolescent mothers displayed greater rates of difficulties at school and behavioral problems at home than did offspring of adult mothers (Jones and Pinzon 2012).

Conclusion

Ultimately, adolescent parenting can produce many risks for offspring. However, this is not to say that negative outcomes afflict all adolescent parents. Adolescents are still developing, which may impede their progress as a parent. Although there are many negative outcomes for infants of adolescent parents, there are many family factors associated with improved outcomes for both adolescent mothers and their children. These include early childcare for the infant provided by the

infant's family of origin, social and familial support that also allows the adolescent parent to finish school, playful interaction between the infant and father, and stability of marital status for the adolescent mothers (Jones and Pinzon 2012).

Cross-References

- ▶ [Abstinence](#)
- ▶ [Adolescent Issues](#)
- ▶ [Oral Sex and Sexual Debut](#)
- ▶ [Prevalence of STDs](#)
- ▶ [Sex Education in Schools](#)
- ▶ [Sexual and Reproductive Development](#)
- ▶ [Sexual Coercion and Dating](#)
- ▶ [Sexual Debut](#)
- ▶ [Sexual Intercourse](#)
- ▶ [Sexual Socialization](#)
- ▶ [Sexual Stigmatization](#)

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numerous factors that influence an adoption, including cultural norms, parent's traits and resources, and the social and legal parameters surrounding adoption. One important potential influence on parents' decision to adopt is information about the children themselves. In particular, cues of resemblance/kinship, age, and child attributes can all influence the desire to adopt a child. From an evolutionary perspective, each of these traits can influence the costs and potential outcomes of an adoption, making them highly relevant to adoption decisions.

Adolescents

► Goals

Adoption

- Evolutionary Paradox: Adoption
- Paternity Uncertainty and Investment in Sons and Daughters
- Resemblance

Adoption Preferences

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Synonyms

Adaptation; Alloparenting; Facial cues; Family

Definition

What child traits influence parents' desire to adopt?

Introduction

Adoption is a complex behavior that can take many forms and offer many functions. There are

Resemblance/Kinship

Evolutionary theory suggests that parents should invest in related children so long as the cost to themselves (i.e., their own genes) is offset by the benefit to the shared genes in the related children (Trivers 1972). This means that for many parents, cues of resemblance or kinship will be high on the list of preferred traits in an adoption (Volk and Quinsey 2002). The most likely circumstances for this form of adoption are when one or both of the parents die (Halbmayer 2004), a not uncommon event in the evolutionary past (Volk and Atkinson 2008), or when they are incapable of caring for a child (a more recent likelihood; Scelza and Silk 2014; Stolley 1993; Testa 2004). Under these circumstances, the related adopting parent functions enable the survival of the related child (a large benefit) for a relatively modest cost (a smaller cost than birthing and raising one's own child – particularly if the child is older). This is likely a relatively ancient pattern of behavior as chimpanzees have been observed to adopt younger siblings if they are maternally related (Hobaiter et al. 2014). In these circumstances, resemblance is likely to exist to some degree due to shared genetics. In North America, just under half of all adoptions are by kin who are supporting children with a living parent (Stolley 1993), while 31 % of fostered children are raised by kin (Testa 2004). These numbers might well be higher as many families rely on informal systems of adoption and fosterage to support ill-equipped

biological parents. Thus kinship appears to be an important motivating factor in adoption.

But clearly, known kinship is not the only motivation behind adoption given that at least half of adoptions in North America occur with parents adopting unrelated children. Under these circumstances, cues that suggest resemblance and kinship may still matter. Many adoption practices are well aware of most parents' desire to adopt children who resemble them physically and/or behaviorally and often attempt to simulate or generate that resemblance (Hamilton et al. 2007; Howell 2006). A North American social worker was quoted by Weegar (2000, pg. 367) as saying "We also try to match physical appearance. I had one family that I was able to match a child, a little girl, with a family that the mother looked remarkably like a biological parent. I mean, if you look at the pictures you would think that they were related. . . It was a fantastic match. . .because the child looks like she belongs to the family. . .we make an effort to match people in terms of physical appearance, in terms of values. . .religious beliefs, those sorts of things."

Both men and women express a greater desire to hypothetically adopt a child that resembles them (Volk and Quinsey 2002, 2007). Families invest more in offspring who are genetically related than in unrelated children (Gibson 2009). Facial cues have received the most attention, in part because they are at least moderate predictors of actual genetic relatedness (Alvergne et al. 2007).

Interestingly, numerous studies have documented that men value cues of resemblance more than women do in a hypothetical adoption paradigm (Volk 2009; Volk and Quinsey 2002, 2007). From an evolutionary perspective, this may be due to the fact that men face paternity certainty risks, while no such risks occur for birth mothers, making men in general more sensitive toward cues of paternity (Alvergne et al. 2009). Anecdotally, during the 1990s when Western adoption of Chinese infants was highly pervasive, it is widely believed that the Chinese government deliberately matched children with adoptive families based on the resemblance of the child to the adopting father (Volk 2011).

Age

Another crucial cue for adoption is age. From an evolutionary perspective, older children are much more likely to survive than younger children (Volk and Atkinson 2013). Thus, it is something of a paradox that adopting parents strongly prefer to adopt younger children (Howell 2006; Stolley 1993; Volk 2011). Adults also show a preference toward hypothetically adopting children with younger-looking faces (Luo et al. 2011; Volk et al. 2005). Among older children, adults prefer cues of immature behavior (Blasi et al. 2015). Older adopted children are more likely to be raised by kin than non-kin (Volk 2011), presumably to offset the costs of adopting an older child with the benefits of adopting one who is genetically related.

Thus, child age presents an apparent paradox – why would adults prefer to adopt younger children who are less likely to survive? One proposed answer is that younger children allow parents more flexibility in shaping a child's behavior and identity to fit their own (Hamilton et al. 2007; Howell 2006). This may be less important for kin, explaining part of the reason why they would be willing to adopt older children (Talle 2004). An alternative answer is that infants have evolved facial cues that are more effective in soliciting parental care than older children because of their greater need for parental care (Volk et al. 2007). Lorenz (1943) termed these cues as "kinderschema" and noted that they are present in nonhuman species as well. In all likelihood, the influence of age likely represents a combination of these factors, as adults prefer the malleability of younger children while simultaneously being more affected by more effective solicitation of care by younger facial cues.

Health

Health is another important cue for parents as it is a signal that relates to both the potential costs (investment) and benefits (survival) of parental care (Volk and Quinsey 2002). Given the very levels of infant and child mortality in the

environment of evolutionary adaptedness (~26 % and 47 %, respectively; Volk and Atkinson 2013), it is not surprising that cues of good health are positively associated with a desire to adopt while cues of poor health are not (Volk et al. 2005; Waller et al. 2004). Most national (vs. international) adoptions in Western countries tend to involve children who are at a higher risk of having physical and/or mental issues (Stolley 1993). In contrast, international adoptions are often used as a means of reducing or even eliminating the higher health risks associated with national adoption (Howell 2006; Miller 2005). Among hunter-gatherers and pre-modern societies, cues of low health were potentially lethal signals that could result in infanticide or abandonment of infants (Cunningham 2005; Silk 1990). Nevertheless, it is worth noting that in comparison to cues of youthfulness, that are themselves associated with lower health, health is a weaker predictor of adoption preferences (Volk et al. 2007).

Cuteness

Yet another important cue for parents in adoption scenarios is cuteness or attractiveness. Anecdotally, cuter children are more likely to be adopted than less attractive children in actual adoptions (Volk 2011). This is backed up by research showing a cross-cultural preference for cute children (Volk 2009; Volk and Quinsey 2002). In contrast to resemblance, the appeal of cuteness appears to be stronger for women than for men (Volk and Quinsey 2002). The appeal of cuteness may relate to the display of good genes that signal a valuable investment (Volk and Quinsey 2002). It is therefore not surprising that cues of cuteness are strongly correlated to both younger age and positive health (Volk et al. 2007).

Conclusion

To summarize, adoption is a complex behavior that can have multiple forms and functions. It appears to be influenced by a range of infant and

child characteristics including relatedness, age, cuteness, and health. Generally speaking, adults appear to be motivated both by cues that signal the benefits of adoption (e.g., genetic relatedness), the costs of adoption (e.g., poor health), and the mitigating factors on those costs and benefits (e.g., cuteness as an indication of good genes and young age as an indicator of familial malleability). These preferences are undoubtedly only part of a complex decision process that involves other parental, social, and economic factors. Nevertheless, it does appear that there are consistent patterns of adoption preferences that hold across cultures and history and that these preferences are generally aligned with adaptive evolutionary outcomes.

Cross-References

- [Consolidating Familial Power](#)
- [Evolutionary Paradox: Adoption](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Resemblance](#)

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Adrenaline

► Epinephrine

Adrenogenital Syndrome

► Congenital Adrenal Hyperplasia (CAH)

Adult Attachment

- Attachment in Adulthood
- Pair-Bonding in Other Mammals
- Romantic Attachment

Adult Sex Ratio

► Sex Ratio and Men's Long-Term Mating

Adultery

- Frequency of Infidelity
- Infidelity Risk
- Seeking Extra-Pair Partners

Advanced Age

► Senescence

Advanced Tool Use

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Synonyms

Utilization of complex instruments

Definition

The ability to develop and utilize objects, such as long blades and primitive sickles in order to better hunt, process prey, and survive.

Introduction

It is believed that the first *Homo sapiens* tools were originally developed approximately 250,000 years ago. Tools developed within this timeframe lacked the characteristics that would classify them as advanced. Advanced tools, and their use, is believed to have begun roughly 100,000 years ago. Examples of these tools include spears with spearheads, longer blades, and sickles. These are considered to be improvements and demonstrate a higher process of thought among *Homo sapiens*.

The Importance of Advanced Tool Use and Its Practicality

Advanced tool use is a very important milestone in evolution. The departure from primitive tools, i.e., clubs, primitive spears, is an important distinction with regard to *Homo sapiens*. Prior to the development of advanced tools, tools were quite simple. These included simple oval stones

fashioned into “hand axes,” among other primitive tools. When comparing these two different kinds of tools, this shows an increased cognitive ability, as well as demonstrates an increased physiological ability to use them. The utilization of advanced tools came with many benefits. For example, processing hunted prey, which can involve removing edible food, furs, bones, or anything else that could serve a use, and the cleaning process for food itself became easier. Another benefit of advanced tools is the ability to hunt game of all sizes. Prior to this development, only small- and medium-sized game was effectively hunted for food. Obviously, this change had a huge impact on the diet of the *Homo sapiens*. For example, “Toolmaking would have facilitated access to a wider range of foods and the ability to process those foods more intensively or efficiently, likely making them more palatable and yielding more calories” (Pobiner 2016). With the increased ability provided via the advanced tools, the means to hunt larger game and even aquatic game arose. It is important to note that not all advanced tools were used solely for hunting purposes. Tools that had sharp, flat edges would most likely be not as useful as a sharp, pointed edge for hunting, but perhaps useful in helping to remove hide from hunted animals, which would provide a benefit of its own.

Conclusion

In conclusion, the development of advanced tools ultimately allowed *Homo sapiens* to better adapt to their environment. The ability to not only gather more food but also a greater variety of food provided a significant advantage to the *Homo sapiens*. Furthermore, the ability to better process hides and other materials certainly helped to improve the quality of life for *Homo sapiens* as well.

Cross-References

- [Advanced Tools of Neanderthals](#)
- [Evolution of Tool Use](#)

- [Human Tool Making](#)
- [Stone Hammers](#)

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Advanced Tools of Neanderthals

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Synonyms

[Device](#); [Implement](#); [Instrument](#); [Utensil](#)

Definition

An instrument of manual operation; an implement, usually held in one's hand, for performing or facilitating.

Introduction

Tool use in hominins is considered a leap in our evolutionary history. It indicated both an understanding of symbolic learning and how to use the environment to one's advantage. For Neanderthals, tools were usually simple, made of either bone or stone, and frequently specialized for one or another use, typically using the same set of techniques to create them. There is well-documented evidence that tool use did exist at Neanderthal sites; however, there is still debate over whether or not Neanderthals invented their own tools, or if they learned them from the encroaching Anatomically Modern Human populations migrating from Africa (Soressi et al. 2013; Tyron and Faith 2013).

The time period when Neanderthals were living in Europe and making these tools is known as the Middle-Paleolithic (Simek 1998; Villa et al. 2008). This era is compared with the Upper-Paleolithic, which is usually more associated with human migration in to Europe from Africa.

Toolmaking

Typically, tools in Europe were made of flint, whereas in Africa tools tended to be made of flint, quartz, and sandstone (Lazuen 2012). Two main tool-making practices were utilized by Neanderthals. For stone, the levallois technique was used, which involved flaking pieces of stone off of the core to create a sharp edge or point (Lazuen 2012; Tyron and Faith 2013). A different form called the Lissoir Style, *lissoir* being French for "to make smooth," describes the specific method by which the Neanderthals would have prepared bone (as opposed to stone) tools for use, usually preparing animal skins to be worn (Soressi et al. 2013).

While most Neanderthal tools appear to have been made for scraping and toughening animal hides (Vos 2015), research done by Bodea et al. (1999) suggests that they may have also been used for hunting. Remains from a wild ass, found in Syria, included the point of a levallois tool embedded in the vertebra. The angle and depth at which the tip was buried suggests that it is unlikely that the tool was used for cutting or preparing the animal for meat or wear. The authors discussed whether or not the tool was attached to a handle (hafted), or if it had been the tip of a projectile. Overall, this tool is suggestive of some of the other uses that levallois tools may have served for Neanderthals (Villa et al. 2008; Bodea et al. 1999).

One valuable discovery made at some middle Paleolithic sites includes bitumen, that was likely fired and used as glue for hafting purposes. The birch used to make this material would likely have been sourced from several kilometers away from the site at which this evidence was found, which provides remarkable clues about Neanderthal creativity and ingenuity (Villa and Soriano 2010).

The hafting process would have consisted of creating a stone tip that was pointed on both the upper and lower sides of the long edge, with a flat back. The flat back was mounted on to a wooden shaft, which would have been shaved to an angle at the edge. The stone was then secured using the bitumen glue and/or muscle sinew from previously hunted fauna (Villa and Soriano 2010).

Examples

It appears as though Neanderthals were likely good hunters, contrary to what was believed several years ago, especially considering the evidence above featuring the wild ass. As such they had a variety of stone tools at their disposal for everything from killing, butchering, and preparing animal hides (Villa and Soriano 2010; Villa et al. 2008). Several stone tools found have been examined for various technical elements as well as for a better understanding as to what they were used for and how. It was clear based on the evidence that the tools had been created using the levallois technique. Notches on some of the tools indicated that they may have been hafted, or mounted onto a handle, for more efficient use. Overall, two different hunting tools were found. One larger, and one smaller, assumedly used differently (Tyron and Faith 2013).

Soressi et al. (2013) discussed four different tool fragments found at known Neanderthal sites, suggesting that these are some of the first and oldest tools to be associated with these hominins. They appear to show little wear from carnivore or other potential sources of modification other than the Neanderthals who shaped them. The bones likely come from the ribs of large hoofed animals, and all included striations that suggest a consistent method, the *lissage*, for polishing and grinding the bones into the desired shape. The authors suggest that the likely use for these bones would have been to prepare animal skins (Soressi et al. 2013; Barras 2013).

The researchers made a point to compare these bone tools with others to ensure that environmental wear, which can sometimes produce similar objects, was not the source of the shaping of the

bones. It was found that these bones were very likely shaped intentionally, and would have served the very specific purpose of toughening animal hides to be worn and preserved, making these tools highly specialized. This adds to the debate about whether or not Neanderthals invented these tools independently, or if they were learned from modern humans migrating from Africa (Soressi et al. 2013; Barras 2013).

Smaller stone tools have been discovered in Europe in increasingly larger numbers. It appears as though they were intentionally manicured to be smaller in size. They date to the approximate period when Neanderthals would have inhabited this area, between 400 and 40 kya. Central Europe revealed large numbers of these unique tools, which researchers have called *Taubachian*, to distinguish them from other tools of the era (Borel et al. 2016).

Borel et al. (2016) conducted research on these smaller tools in order to ascertain what they may have been used for. Comparing features of the environment from geography, to flora and fauna, the researchers sought to get a full understanding of the context under which these tools were made. Dating approximated the era of these tools to be roughly between 116 and 70 kya. It appeared that the size and shape of the tools was clearly intentional, and the edge that was used for a specific task was consistent, meaning that the opposite side of the tool was likely the part that was gripped by the user. However, shapes between tools were not consistent, and there was no way to effectively categorize the tools for use, based on this feature. It appears as though most of the tools were used for scraping; however, there is no way to be certain that that was the only use tools at a given site may have had. It is relatively clear that the makers and users of these tools were Neanderthals. Some tools may have been attached to various other materials, such as handles, to make the tool more effective (Borel et al. 2016).

Another feature that is yet unclear is whether or not, in more forested areas, use of stone tools coincided with the use of wooden tools as well. Four wooden spears were found in the mud of the banks of a lake in what is now Germany, along with the skeletal remains of a family of horses

(Villa et al. 2008). Cuts on the bones of the horses match the spears as well as tools that are similar. The wooden spears were all made of spruce, and one of pine; however, the consistency with which they were made suggests an understanding of the raw materials of the area. Other impact scars on the tips of certain tools indicate use as projectiles, either attached to thrusting or throwing spears (Villa and Soriano 2010). Naturally this lends more support, as well, to the idea that wooden tools may have been part of the Neanderthal toolbox (Borel et al. 2016; Villa et al. 2008).

The expertise with which these tools were made suggests that they were made by craftspeople who understood well their purpose and materials, as well as knowledge of the raw materials in the area (Borel et al. 2016; Villa et al. 2008). The fossilized tools we see today suggest a consistency through which they were made and used, suggesting that the hominins who made them understood the various textures of bones and stones, well enough to create this successful method for creating these tools (Soressi et al. 2013; Barras 2013). This idea is supported by the other tools found at the site, made from stone, include hand-axes, and knives, showing that Neanderthals likely had several kinds of tools in their repertoire.

Controversy

It is still a topic of debate whether or not Neanderthals began producing tools before or after the arrival of *Homo sapiens* into Africa. Fossil records from the Arcy-sur-Cure site in France date one of the youngest Neanderthal sites known, at 34,000 years ago. The authors assert that the hominins that lived here were, in fact, Neanderthals, based on a series of features related to skeletal remains. This helps indicate that Neanderthals lived up until relatively recently in our evolutionary history, which implies that coexistence or at least contact between Anatomically Modern Humans and Neanderthals, was likely given the temporal and geographic overlap between them in Western

Europe (Hublin et al. 1996). Rossano (2010) claims Neanderthals were expert “toolmakers,” meaning that it is possible that they made tools independent of human influence. Additionally, the age of most of these tool remains suggests that they were made by Neanderthals before humans arrived (Tyron and Faith 2013).

Modern human tools were much more advanced and could be categorized by many different functions, more so than the Neanderthal tools could. Additionally, (Klarreich 2004; Klein 2003) suggests that Neanderthals may have been able to copy the toolmaking of modern humans, but they did not seem to do much to pass them further. If it was the case that Neanderthals learned tool use from modern humans, why wouldn't they have learned to master all of the complex tools that the humans made, instead of just a simple few, especially when the evidence suggests that Neanderthals did have the mental capacity to master craftsmanship (Villa et al. 2008).

However, lack of evidence, in some cases, makes it difficult for bone remains to be identified as being a true tool, or simply bones that have been modified by other parts of the environment (Soressi et al. 2013). What does appear to be clear is that there are tools of many kinds all over Europe, suggesting that tool production and use in Neanderthals was not limited to one particular geographic climate or one particular group of hominins, which could easily suggest their inventiveness independent of modern humans (Borel et al. 2016).

Conclusion

Part of the important implications of toolmaking in Neanderthals and other hominins is the fact that they represent symbolic thinking and social learning. Tool use was likely passed on from one person to another via observational learning by the student (Barras 2013). The cognitive demands of symbolic thinking likely helped the development of working memory in Neanderthals, and could have potentially helped with other forms of communication, such as language (Gibson 1991; Rossano 2010).

There are other cultural practices that do not seem to have a clear origin, such as the burying of the dead, which marks a significant milestone in hominin cognition as it establishes differentiation between life and death (Barras 2013). Villa et al. (2008)) argue that more research on hunting tools in Europe during the middle-paleolithic period is necessary for having a better understanding of the behavior of Neanderthals at the time.

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Advantageous Side Effects

► Beneficial Side Effects

Advantages of Having Close Blood and Affinal Relationships

► Benefits of Profound Kinship Connectedness (and Problems from a Lack Thereof) Through an Evolutionary Mismatch Lens

Adverse Effects of Alcohol in Utero

► Teratogenic Effects of Alcohol Exposure on the Fetus

Advertisements

► Advertising

Advertising

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Synonyms

Advertisements; Research methods; Data

Definition

Advertisements, which are widely available, can provide insights into the evolved preferences of target audiences and serve as a useful supplement to other methods in evolutionary psychology research.

Introduction

Advertisements present an important source of data for evolutionary psychologists. Advertising is ubiquitous in our fast-paced, modern world, and people living in urban places are exposed to hundreds, if not thousands, of advertisements daily. Yet, little research exists that describes how advertisements can be prudently utilized. This chapter discusses how advertisers create content that strategically exploits consumers' values and preferences and how advertising content can provide insights into various aspects of our evolved psychology.

Advertising: More Than Meets the Eye

Advertising refers to a paid, mediated form of communication from an identifiable source, designed to persuade the receiver to take action, either now or in the future. The selection of advertising content by advertisers and marketers is far from arbitrary, as marketers seem to know that advertising that appeals to people's intrinsic preferences or beliefs, such as their values, attitudes, and tastes, is more attention grabbing, influential, and persuasive (Yong et al. 2016).

As advertising tends to appeal to individuals' intrinsic preferences and values, the content of advertisements and commercials offers researchers an important source of empirical data. Advertisements exploit the intuitions or insights that marketers have about their target audiences, which allow researchers to infer particular psychological features of these target audiences.

Advertisements Reflect Evolved Psychology

At a fundamental level, advertisements reflect evolved psychological preferences and present a window into human nature. The following sections describe some important inferences that can be made of our evolved psychology from advertisements.

Mate value traits. Men and women prefer traits in a mate that can improve their own reproductive success. Because women's fertility declines as a function of age, men's reproduction is constrained by their access to reproductively valuable or fertile mates (Trivers 1972). In response to this adaptive challenge, men evolved to prefer physical features that signal youth, health, and fertility in sexually mature women, including firm skin, breasts, and buttocks, and a low waist-to-hip ratio (Buss and Schmitt 1993). In contrast to women, men face a slower decline in fertility across the life span, so identifying fertile partners is less crucial for women. Instead, because ancestral men varied in their ability to provide resources that aid the survival of women and their offspring, women, more than men, evolved to value a partner's social status, which is closely related to his ability to provide resources and protection (Buss and Schmitt 1993).

The content of advertisements provides a unique avenue to examine the validity of these mate preferences. More specifically, the theory of evolved mate preferences predicts that advertisements will tend to portray men and women according to their relevant mate value traits in advertisements, specifically senior and high-status men and young and physically attractive women. Indeed, a variety of studies analyzing a wide range of magazine advertisements, television commercials, and other forms of mass media have found that exemplary women are typically shown as being young and physically attractive and exemplary men as having high status (Saad 2004). Female characters in advertisements are more likely to be distinguished by their looks, such as being physically attractive and dressing provocatively, while male characters tend to be portrayed as demonstrating skill or having important occupational roles (Yong et al. 2016). The display of

older age also appears to be more acceptable for men than women, as women are less likely to be shown on prime-time television with gray hair compared to men.

Another source of evidence for mate value traits can be found in personal advertisements, where individuals attempt to entice the interest of potential mates. One study analyzed over 300 personal advertisements in a respectable Californian singles digest and found that women advertised their appearance-related traits much more than men did, whereas men emphasized their status-related traits more than women did. A more recent study examined online personal advertisements and found that little had changed; men are more likely than women to exaggerate their income and social status, while women are more likely than men to misrepresent their physical appearance and underreport their age (sometimes both at the same time by using photos taken 10-plus years ago).

Relationship duration preference. Compared to women, who are required to invest heavily in the production of offspring because of internal gestation and postpartum suckling, men are physiologically required to make a relatively smaller contribution of only a few sex cells during sexual intercourse. Therefore, children carry much higher costs to women than men, especially in ancestral times when access to food and health care was scarce, if they result from sex with a partner who is unwilling or unable to provide resources and protection (Trivers 1972).

These differences in the costs of short-term, uncommitted sexual relationships meant that men, more so than women, could maximize their reproductive success by acquiring more mates. Therefore, men, more than women, evolved to have a range of psychological mechanisms that facilitate a short-term mating strategy and increase their access to a wider pool of sexual partners, such as proclivity for sexual variety and heightened sensitivity to cues of sexual receptivity (Buss and Schmitt 1993).

Advertisers indeed exploit this preference for short-term mating by depicting women, but not men, as attractive sex objects (Saad 2004). The

presentation of sexually attractive and receptive females can make an advertisement more attention grabbing and influential. For instance, one study utilized a visual cueing task in which participants had to focus on a particular stimulus and then shift their attention to a different point on the computer screen. Men had greater difficulty disengaging their attention to the new point on the screen when the initial stimulus was an attractive woman, while women did not experience this effect when the initial stimulus was an attractive man (Maner et al. 2007).

Presenting images of sexually attractive and receptive females in advertisements also increases men's cognitive disinhibitions and impulsivity (Yong et al. 2016). One study found that male participants increased their likelihood of discounting the future—regarded as a disinhibited, impulsive preference for immediate gratification—when exposed to pictures of attractive members of the opposite sex, while this effect was not found for female participants or participants who were exposed to pictures of unattractive opposite sex members (Wilson and Daly 2004). Disinhibition has consequences for reduced self-control and deficiency of deliberative decision-making and also has been shown to increase the likelihood of spending or acquiescing to persuasive messages. Indeed, in a study of loan advertisements conducted on a South African sample, advertisements that included a photograph of an attractive woman led to increased demand for the loan, and this effect was driven by male consumers. Thus, when attractive, skimpily clad women are recruited as models by organizers of car showroom events, advertisers are exploiting men's short-term mating psychology to make their messages more effective. These differences in the portrayal of the sexes have been found to span generations and time periods as well as across cultures, suggesting a consistent trend (Yong et al. 2016).

Advertisers have also historically taken advantage of women's preferences for committed, long-term relationships. For instance, it has been argued that appealing to the family ideal and the importance of love in advertisements can create

the belief that shopping provides a solution and relief to these unfulfilled needs. Further research can be conducted to see if appeals to long-term relationships still persist in advertisements aimed at women today.

Gains and losses. Kahneman and Tversky's (1979) seminal prospect theory provides an important model for understanding human decision-making behavior under risk. Prospect theory stresses that gains and losses are evaluated relative to the status quo as a reference point. As our ancestors likely operated close to subsistence level as their status quo, resource losses often entailed a high chance of starvation and death. Thus, for most humans, resource losses generally loom larger than gains. By manipulating the "reference points" that enter decision rules or preferences, consumer choices can be influenced, and invoking potential losses is a particularly powerful stimulus for demand if it triggers loss aversion (Kahneman and Tversky 1979).

Various studies have found that loss-framed appeals in advertisements and persuasion messages tend to be more effective than gain-framed appeals when loss aversion was triggered. In a direct marketing field experiment to persuade people to use a particular credit card in Israel, people were approached and told that there are either "many disadvantages in using cash instead of ZionCard" (loss frame) or "many advantages in using ZionCard instead of cash" (gain frame). Indeed, loss-framed messages induced higher credit card usage than gain-framed messages (Ganzach and Karsahi 1995). Similarly, advertisers influence female consumers by exploiting loss aversion in intrasexual competition contexts (Yong et al. 2016). Advertisers often deliberately highlight women's physical shortcomings and insinuate that if women do not purchase their products and services, they will bear the consequences of retaining their physical flaws. Indeed, as early as the 1920s, advertisements for products such as mouthwash and soap have unabashedly stated that women who do not care about their looks (e.g., maintain good oral or skin hygiene) will fail to attract and retain a mate. The wildly successful cosmetic industry is a testament to the

effectiveness of such advertising messages that play on female physical attractiveness and mate value, as women spend more than men on goods and services that enhance appearance (Saad 2004). During economic crises, while most industries suffer losses, beauty and cosmetic industries (where females are the primary consumers) either are unscathed or may even experience a boom, as the number of financially stable men drops and intrasexual competition for such men intensifies (Hill et al. 2012).

Status signaling. Just as advertising can inform theories and hypotheses about evolved psychology, an evolutionary perspective may provide insight into how advertising has played a major role in shaping the materialistic values around which modern societies and economies function. In particular, advertisements may exploit a fundamental need for men and women to signal high social status to others. Having a high relative position in the local social hierarchy is evolutionarily important as it was linked to resource access and likely conferred survival and reproductive advantages in the ancestral past (Buss and Schmitt 1993). Social status is dependent not only on one's own skills and accomplishments but is ultimately something that is conferred by others. That is, others must see and acknowledge a person's standing in order for him or her to have a level of status. Given the evolutionary importance of status and the role that others' perceptions play, people may have evolved to display markers of their social status to others when possible.

In modern economies, advertising and product marketing have helped create a plethora of consumer avenues through which individuals can signal their social status—for example, widely recognized brand names in handbags, automobiles, watches, clothing, phones, schools, and holiday destinations are among the thousands of material products and services through which status can be signaled. Indeed, material luxuries are a highly viable means of status signaling underlying conspicuous consumption. Importantly, the status that individuals signal with each material purchase is only fleeting, as more and more people also acquire the same items, and product life

cycles become increasingly shorter (Li et al. 2015). Studies have indeed demonstrated that advertising across television and print media has increasingly depicted and appealed to a materialistic lifestyle among consumers in cultures as diverse as the United States and Japan.

Conclusion

In summary, advertisements present an abundant and convenient source of empirical data for evolutionary psychologists. By examining psychological traits in advertising content, researchers can make inferences about human nature and use advertisements to gauge the validity of evolutionary theories on human psychology. At the same time, an evolutionary psychological perspective can shed light on why advertising works and how it has contributed to the materialism that pervades modern society.

Cross-References

- [Conspicuous Consumption](#)
- [Intrasexual Competition](#)
- [Long-Term Mating](#)
- [Men's Mate Preferences](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Sex Differences](#)
- [Sexual Strategies Theory](#)
- [Short-Term Mating](#)
- [Social Status](#)
- [Social Status and Economic Resources](#)
- [Women's Mate Preferences](#)

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Advertising Effects

- [People's Responses to Personal Ads](#)

Aesthetic Display

- [Art Production, Appreciation, and Fitness](#)

Affair

- [Sex Differences for Pursuing](#)

Affective Bond

- [John Bowlby and Attachment Theory](#)

Affiliation

- ▶ [Tend and Befriend Adaptations](#)

Affiliation and Sexual Behavior

- ▶ [Sex as Bonding Mechanisms](#)

Affiliation and Sexuality

- ▶ [Sex as Bonding Mechanisms](#)

Affiliative Bonds

- ▶ [Cost of Same-Sex Friendships](#)
- ▶ [Same-Sex Friend](#)

After Life

- ▶ [Spiritualism](#)

Age

- ▶ [Risk Variation with Parent Age](#)
- ▶ [Youth and Fertility](#)

Age Categories

- ▶ [Categorization by Age](#)

Age Categorization

- ▶ [Categorization by Age](#)

Age Differences in Marriage Partners

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Definition

Age differences between spouses have been observed across different cultures, such that men are usually older than their marriage partners. Such arrangements are more prevalent than both same-age and women-older marriages.

Introduction

The age gap between partners has been a popular topic of debate, filling tabloids with articles on celebrity couples with “huge age differences,” speculating whether they are truly happy and whether it is really love that bonds them together. Not surprisingly, age difference is one of the main aspects that individuals consider when selecting a romantic partner. In heterosexual relationships, men are on average older than their partners, a pattern observed across cultures, such that the age gap between partners is 2–3 years in developed countries (Kolk 2015). Such a pattern is observed even in gender egalitarian societies, such as Norway. These marriage arrangements are more common than same-age marriages and women-older marriages. For older men, marrying a younger woman can mean having a beautiful, adventurous, and dynamic partner. In contrast, older men are often perceived as more successful and confident, given that they have had more time to acquire resources and experience, a characteristic that is often attractive to women. In this entry, I will discuss consequences of dissimilarities between spouses and why men consistently prefer younger women than themselves, whereas women do the opposite.

Consequences of Age Disparity Between Spouses

The age differences between spouses may have consequences in different domains. For example, the age gap between parents has an inverted U-shaped association with number of children in a Polish sample (Kuna et al. 2018). Having a younger partner is positively associated with symptoms of depression in elderly people (Pradeep and Sutin 2015). Australian men and women reported to be more satisfied with a younger partner than with an older partner, suggesting that age-different couples are less resilient to problems in the relationship in comparison to same-age couples (Lee and McKinnish 2018). Age dissimilarity between spouses also affects other aspects such as commitment to the relationship (Lehmiller and Agnew 2008), infidelity, and risk of contracting sexually transmitted diseases (Maughan-Brown, Kenyon, and Lurie, 2014). Why then are such relationships prevalent across cultures, if there are so many apparent disadvantages associated with engaging in age-dissimilar relationships?

Theoretical Explanations of Age Differences Between Spouses

Sociocultural approaches argue that the preferences for men-older relationships are a result of social norms and gender roles (Klinger-Vartabedian and Wispe 1989). On the other hand, Bergstrom and Bagnoli (1993) further claim that the relative desirability of women as marriage partners becomes more apparent at an earlier age than do men, proposing an equilibrium model to explain the preferences for men-older marriages. In this model, educationally and professionally ambitious men choose to wait until they have achieved educational and economic success to get married. On the other hand, those men who do not believe they can enhance their educational and professional opportunities will offer to marry at a younger age. *In equilibrium*, women are expected to marry at a younger age than men; however, more desirable women will be more likely to marry older men in comparison with less desirable women.

An evolutionary perspective, a common explanatory model, predicts that individuals will generally pursue partners with attributes that can increase their reproductive success. As such, because women invest more heavily in reproduction (Trivers 1972), they will favor partners who are able to invest in them and in their offspring, can physically protect them, and are likely to be good parents (Puts 2016). Consistent with this view, Buss (2007) reviewed different studies showing women across several cultures tend to value attributes such as good financial prospects more than do men and attributes that are related to higher earning potential such as ambition, social status, and older age. Men, on the other hand, tend to value physical appearance, a cue of women's fertility and reproductive value, which are attributes associated with younger age and vitality. Such patterns help to explain the age gap between spouses and the sex differences on preferences for partner age. While women will prefer older partners, since they are more likely to have finished their education and built up a good career, men will prefer younger women because attractiveness and fertility are more apparent at an early age.

Conclusion

Men and women have different reasons for engaging in men-older marriages as a result of sex-specific partner preferences related to the reproductive value of women and the earning ability of men. While men prefer younger women because at a younger age the reproductive value of women is more apparent, women prefer older men because they are more likely to have acquired economic and other resources to provide for their partners and for the offspring.

Cross-References

- ▶ [Long-term Mating](#)
- ▶ [Mate Preferences](#)
- ▶ [Sex Differences in Long-term Mating Preferences](#)

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Age Disparity

- Older Men

Age Groups

- Categorization by Age

Age of Child

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Synonyms

Baby schema; Infant; Kinderschema; Parental investment

Definition

The developmental age of child that is associated with the highest parental investment.

Introduction

The age of a child is shown to have important effects on parental investment decisions. This is likely because the age of the child may be associated with the child's ability to survive (Volk et al. 2005; Hrdy 1999). For example, newborns are less likely to survive without parental care compared to older children due to lower levels of health-related development at that stage (e.g., less developed immune systems; Voora et al. 1982) and higher dependency on parental care compared to older children (Hrdy 1999; Volk and Atkinson 2008). Therefore, the offspring that shows the highest chance of survival, which is generally the older child, should typically receive the most parental investment as this child will more likely produce offspring and help propagate parents' genes (Trivers 1972). However, this would suggest that parent may be predisposed to make parental investment decisions more strongly based on parents' own interests of propagating their genes rather than the child's interest. On the other hand, younger infants are certainly more in need of parental care for survival compared to older children (Hrdy 1999; Volk and Atkinson 2008). Therefore, it could also be hypothesized that parents may be predisposed to make parental investment decisions based on what is best for the

child. If this is the case, then parents' investment decisions could be perceived to be more strongly dependent on children's interests rather than parents' immediate (evolutionary) interests. So who do parents actually invest in: younger or older children?

A close look at the data on parental investment based on age of the child suggests that parental investment decisions may be more complex than any of the above two theories would independently suggest. Franklin and Volk (2017) helped shed some light on this when they proposed an inverted "U" curve associated with child age and parenting decisions. This is based on evidence which suggests that adults may have the strongest caregiving predispositions toward children between 3 and 6 months old, which represents the peak of the inverted "U" curve (Franklin and Volk 2017; Franklin et al. 2018). The bottom left of the curve represents adults' least positive perceptions and caregiving behaviors toward newborns. This is presumably in part because the newborn stage is associated with the highest mortality rates across childhood and therefore may be the riskiest age for parental investment (Volk and Atkinson 2008). Finally, the bottom right of the curve suggests that adults' perceptions and caregiving behaviors tend to slightly reduce after 6 month stage (Franklin and Volk 2017).

The reason for adults' apparent peak in caregiving perceptions and behaviors at 3–6 months is likely because this is the stage at which there may be an optimal balance between children's robust health and need/dependency on parental care (Franklin and Volk 2017; Franklin et al. 2018). For example, compared to newborns, 3 and 6 month olds are more likely to survive illnesses and infections without serious medical intervention (Voora et al. 1982). Additionally, older children can more independently survive without parental care. Therefore parents may not ultimately evolutionarily benefit from investing in older infants at the expense of younger infants (Franklin et al. 2018). Therefore, investment in infants between 3- and 6-month-olds appears to be the safest investment that still allows parents to ensure infant survival without depleting too much of parents resources.

Conclusion

The underlying factors that are suggested to influence the peak in parental investment toward children between 3- and 6-month-old infant strengthen the idea that in cases of conflict between parents' and children's interests, evolutionary pressures may have favored parents' interests over those of children (Trivers 1974). More specific to parental investment based on child's age, it appears that parents may be predisposed to invest in offspring at an age at which the offspring will optimize parental parents' resources. Therefore, the age of the child may be an important factor to consider when trying to understand the complexity associated with caregiving decisions.

Cross-References

- [Parental Investment](#)
- [Parental Investment Theory](#)
- [Parent-Offspring Conflict](#)

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Age of Menarche

- [Absence Prior to Puberty](#)

Age of Mother at Birth of Her Child

- [Maternal Age](#)

Age of Parent

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Synonyms

[Developmental psychology](#); [Fertility](#)

Definitions

Parental age. Although it might seem obvious what “parental age” refers to, it should be noted that age at first menarche, age at first sexual encounter, and age of first birth may not, indeed typically do not, coincide. Biosocial factors, such as status, must also be included. Also worthy of note is that humans are unusual mammals in that females can live for 25 or more years after maternal viability stops (at around age 50). Menopause may well be an adaptation to grand-parental investment beyond child-bearing years (Buss and Schmitt 1993).

Life History Theory. A mid-level biological account of the differential allocation of resources to growth or repair. In general animals can fall into fast (relatively high risk, low investment) or slow (low risk, high investment) patterns of child-bearing (Stearns 1976).

Introduction

Humans are obligate – indeed intensive – investors in their offspring, with the minimum potential parental investor being the male (Trivers 1972). Long gestation, and lengthy infantile dependence (including lactation – which is shortened compared to other primates) combined with a huge amount of social learning, with both status and resource inheritance, means that life history mechanisms can play out along a number of key areas. A key one of these is parental age. Theory needs to explain how these features cluster together, either as a complete package or as a mosaic of features (Bogin and Smith 1996).

Evolution and Parental Age

When Robinson Crusoe discovered that he was not alone, his economy changed from simple resource management to the need to understand a complex interplay of intentional forces (von Neumann et al. 2007). Humans are all similarly born into worlds which are highly complex in social terms. Their own species constitute some of their key rivals, and potential allies – both kin and nonkin. Although other primates are social, the need to adjust to a complex social world seems to be a key difference for our species that probably helps to explain a complex mosaic of effects. For example, while chimpanzees and gorillas have to put a lot of thought and resources into preventing infanticide, this is unlikely to have been a major selective factor in recent human evolution (Geary and Flinn 2001).

Instead, human males often, but not always, invest in offspring, and this investment can take the form of status, resources, skill acquisition, and so on. In this respect, older males tend to have more mate value than younger ones, all things being equal. However, younger male reproduction will be selected for in the standard life-history cases where males are less likely to invest and fit the general patterns of risk taking, and low parental investment (Stearns 1976).

When it comes to women, age is much more critical to offspring fitness, with females having to

trade off fertility (which usually peaks at around the age of 20, although this varies with respect to accelerated life histories) and reproductive value (which includes social resources, and the crucial ability to generate and sustain networks of alloparenting) (Walker et al. 2006). In general, earlier menarche, age at first sex, age at first pregnancy, and shorter inter-birth intervals tend to cluster together, along with indicators of fast life history strategy such as lower birth weights, absent fathers, and increased birth complication risks (Nettle et al. 2011).

Conclusion

Although life history models do effectively predict and describe human parental age decisions, the picture is complicated by a set of interlocking factors surrounding the unique human capacity for social competition through coalition formation (Geary and Flinn 2001). Future research needs to be aware of the way these factors inter-related and are tackled in the unique niches that humans occupy.

Cross-References

- [Cooperative Breeding](#)
- [Fertility](#)
- [Life History Theory](#)
- [Parental Investment](#)
- [Reproductive Value](#)
- [Social Development](#)

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Age of Weaning in Human Evolutionary History

- [Duration of Breast Feeding in Ancestral Environments](#)

Age Perception

- [Social Categorization by Age of Faces](#)

Agency-Detection

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Synonyms

[Attribution of intentionality](#); [Identification of animated actors](#); [Mind perception](#)

Definition

The ability to identify intentional actors in the environment.

Introduction

Agency detection is an evolutionarily based psychological capacity to see an event to be motivated by an action tendency. This perception is universal among humans, and it may be widely shared among nonhuman animals. In the case of humans, however, to the source of this tendency, the agent, various mental states, including beliefs, feelings, and intentions, are readily assigned. These mental states may include dispositions of the agent, such as his or her attitudes and personality traits although cultures may differ widely in the degree to which these dispositions are prioritized. Here, we review evidence for these possibilities and argue that agency detection may be instrumental in promoting norm-abiding behaviors, including prosocial behaviors to ingroup members, and thereby in the formation of both modern religions and increasingly large societies based on them.

Agency Detection Is Adaptive

Personal agency implies an intention to act in some way toward objects, both real and imagined. Agency involves a behavioral tendency based on beliefs about the objects as well as feelings toward them. The experience of agency is fundamental to psychological functioning and well-being. Agency detection is the attribution of similar qualities of action to others. Being able to understand that what happens to us is in part the consequence of other agents' thoughts and feelings, as well as their action tendencies based on such thoughts and feelings, is a prerequisite for all meaningful responses to them and hence the basis of social interaction in general. These other agents do not necessarily have to be other humans. They could also be non-animals or even inanimate objects. Many researchers argued that humans are hypersensitive agency detectors, meaning that they are biased to overattribute intentional action as the cause of a current and ambiguous event. This hypersensitive agency detection tendency has sometimes been explained in terms of higher costs of failing to notice potentially dangerous

agents, relative to false alarms, during the ancestral past. Attributing intentions to others involves two mutually reinforcing steps. In the first step, the hypersensitive agency detection tendency recognizes an action tendency. The second step consists of attributing mental states such as beliefs, desires, and intentions to the source of the action tendency, the agent. This second step involves the capacity for mentalization (i.e., theory of mind). Both steps are thought to have evolutionary origins.

Agency Detection as an Early Step of Social Inferences

Many animals may be assumed to possess at least some rudimentary agency detection device for the abovementioned reason: They would be helpless victims of others without. For instance, escaping away from an attacking predator requires a perception of its action tendency. Such flight reactions may be brought about by automatic perception-behavior links and involve mainly subcortical structures. It may be safe to hypothesize that most animals detect action tendencies. These tendencies detected, in turn, inform subsequent coping actions.

However, in the case of higher primates, especially humans, the second step of mental state ascription may play prominent roles. This second step of agency detection serves more flexible regulation of social behaviors. Humans infer others' subjective mental states, such as their beliefs, intentions, and emotions to accommodate their actions to those of others. The capacity of inferring such mental states, called theory of mind, is crucial for both social coordination and cooperation.

This capacity comes into play even when seeing movement of geometrical figures. In their classic study, Heider and Simmel (1944) asked their participants to describe the movements of three geometrical figures (a square, a triangle, and a circle) in a video clip. The participants described the figures as though they were humans acting intentionally (e.g., "The big triangle is chasing the small one"). Thus, it is evident that

humans are highly primed not only to detect action tendencies in non-animate figures but also to ascribe mental states to them. This study is one of the first to demonstrate that once an intentionally behaving agent has been detected, people move beyond the initial detection of agency and ascribe mental states to the agent (although it is clear to everybody that squares or triangles do not have any mental experience at all).

The second step of agency detection (ascription of mental states to an agent or simply mentalization) is most prominent in humans and possibly unique to them. Indeed, there is reason to hypothesize that the human brain evolved to support this mental capacity. The neocortex ratio, i.e., the volume of the neocortex (the gray matter) to the volume of the entire brain, is much larger for humans than for any other known species. This big brain is remarkably costly: It makes up for only about 2% of the body weight yet consumes roughly 20% of the energy intake. So, there must be benefits of this costly big brain; otherwise, it would not have evolved. According to the “social brain hypothesis,” one of the central payoffs of that big brain comes from the fact that humans evolved *to be* social beings. Generally speaking the human brain evolved in order to increase the chances that the body that it inhabits will survive and produce offspring. For both purposes (surviving and breeding offspring), forming relatively large groups of individuals is conducive. Living in larger groups of people who share and exchange information and functional practices and pass them on from one generation to the next is such an evolutionary advantage. It provides protection against predators and allows the execution of larger joint tasks. Hence, from this perspective we may hypothesize that humans evolved to be social and cultural beings. Yet, the complexity of life in larger groups of individuals requires much more social coordination and cooperation, and accordingly, the mental devices that make this regulation possible may have evolved to be highly elaborated and efficient.

Consistent with this line of argumentation, Dunbar (1992) showed that across primate species the neocortex ratio correlates with the typical group size that these animals live in. The larger

the groups they form, the more mental capacity for social regulation is required which is reflected in the accordingly larger neocortex ratio. Mentalization plays an important role in this concern. Of course, the capacity of mentalization is only one of multiple mental tools that enable this social regulation and facilitates coordination in larger groups.

Universal vs. Culture-Specific Aspects of Social Inferences

It is important to note that the mental states that are ascribed to the agency detected may or may not be dispositional. Cultures vary in the tacit beliefs about the nature of “person” or the self (Markus and Kitayama 1991). In Western cultures, including North American cultures and West-European cultures, there is a belief in the independence of the self. The self is thought to be defined by a set of internal attributes, such as personality traits and attitudes. With this cognitive schema in mind, people may explain another person’s behavior by focusing on the most salient aspect of him or her, namely, the person’s traits and attitudes. In contrast, in many cultures outside of the West, there is a pervasive belief of the self as interdependent. The self is thought to be embedded in significant social relations, and as a consequence, it is defined by relational features, such as social expectations, roles, duties, and obligations. With this alternate cognitive schema in mind, people in non-Western cultures may explain the seemingly identical behavior of another person, not by his or her internal attributes, but instead by situational forces that imping on him or her, such as social roles and expectations.

The cultural analysis above implies that, although people in all cultures infer mental states when having detected agency, the precise nature of the mental states that are inferred may show cultural variation. In Western societies, these mental states are likely to be dispositional. Hence, it may be quite common that people refer to another person’s personality traits and attitudes. However, the mental states that are inferred do not have to be dispositional. They can be cognitions,

perceptions, and beliefs regarding the surrounding, as seen from the agent's point of view. Indeed, in non-Western cultures, the mental states inferred during agency detection may be related more to the agent's perception of his or her surroundings. The agent may therefore be seen to have perceived social expectations, or norms, or to have been obligated or pressured to act the way he does.

To investigate the degree of dispositional inference, we may start by simply asking participants to explain another person's behavior. An early study finds that European Americans explain the other's behavior by referring to his or her traits and attitudes. But Indians refer primarily to social roles, duties, and obligations in doing so. Subsequent studies have used a similar paradigm and found that the weight of dispositional (vs. situational) causes is higher for Westerners than for people in non-Western cultures, including East Asians, South Asians, and Arabs.

Another way to investigate dispositional inference is to have participants observe another person's behavior and infer attitudes of this person. The question is whether the attitudes inferred would correspond to the behavior. If observers have an independent schema of the person or the self, then they may perceive the other person's behavior to have been caused by a trait or attitude that corresponds to the behavior. However, if they have an interdependent schema, they may be more attuned to situational forces, especially when such forces are salient. Under such conditions, the tendency to infer the corresponding attitude or traits may be attenuated.

In a classic series of experiments, American participants were provided with a brief essay expressing either a pro or con attitude on a political issue of the time. The participants then inferred what the author's real attitude on the issue would be. Not surprisingly, individuals who read a pro essay attributed a more favorable attitude to the author than those who read a con article. What is surprising is the tenaciousness of this effect. The inferences of the attitude that corresponded to the essay content occurred even when participants were explicitly told that the essay writer was requested to express the particular position expressed in it. It therefore appears

that participants were insufficiently attentive or cognizant of the social pressure that supposedly existed. Hence, the effect observed was considered a psychological bias. The claim was that people are primed strongly to infer dispositions of another person even in the presence of social pressures on him or her.

However, within this original experimental scenario, it is evident that the essay writer chose to comply with the request. Hence, it would seem reasonable to infer a degree of willingness the writer had to write the essay. This consideration might be especially relevant since the essays used in the original series of studies did include some arguments, which may have augmented the impression that the writer was willing to write the essays. Thus, the original series of studies did show robust correspondent inferences, but it is not all that clear whether these inferences would constitute any psychological bias. To mitigate this possibility, in some subsequent studies, participants were shown a video of another person who was merely reading an essay written by someone else. Even under these conditions, the correspondent inferences persisted.

Furthermore, within the original series of studies on the topic, the social pressure was described in a brief paragraph embedded in the experimental instructions. Hence, the social pressure may not have been psychologically salient enough. To address this possibility, researchers asked their participants to pose a social constraint on another person and then to judge the attitude of this other person. Specifically, the participants were to directly ask another person to state one position or another on certain topics and then to infer the real attitude the person would have on the topics. The researchers found a persistent tendency to infer the attitude corresponding to the attitude expressed. In short, at least in Western cultural contexts, the inference of another person's attitude that corresponds to his or her action seems quite strong to the point in which it is excessive. That is, this tendency may represent a genuine psychological bias.

Will this bias, called the correspondence bias, generalize to cultures outside of the West? If people in non-Western cultures believe the person or

the self to be interdependent with the surroundings, they may be sensitized to situational constraints as a determinant of behavior. If so, the correspondence bias may not be as robust as it demonstrably is in Western cultural contexts. Initial effort testing this possibility used the original attitude inference paradigm and did not provide support to this expectation. Remember, however, in the original attitude inference paradigm, it must have been very easy to dismiss the situational constraint (a request by someone) since, after all, the target person had agreed to comply with the request. Moreover, the situational constraint was embedded in experimental instructions and thus supposedly lacking in cognitive salience. Further, the essay contained substantive arguments, again suggesting that the target person willingly wrote the essay. What if dismissing the situational constraint were made more difficult?

One study examined this possibility by having participants actually experience the situational constraint (i.e., being asked to write an essay in support of a given political position). Without this experience, both Americans and East Asians inferred the same degree of corresponding attitudes. Even with the added procedure designed to make the situational constraint salient, Americans continued to make correspondent inferences. For Koreans, however, this effect was substantially attenuated under this condition. In another study, participants were asked to request a target person to read a pre-prepared essay written by someone else. Afterward, they inferred the real attitude of the target while watching the person reading the essay. As may be expected from prior work in the USA, Americans continued to show a reliable correspondence bias. Under this condition, however, Japanese showed no correspondence bias. In yet another experiment, Miyamoto and Kitayama (2002) prepared two kinds of essays. One was a standard essay that was typically used in this literature. As noted above, the essay was composed of several arguments that were reasonable. Another was a much-abbreviated version of the essay that was both short and devoid of any substantive argument. Consistent with prior American findings, American participants in the Miyamoto and

Kitayama (2002) studies continued to show a reliable correspondence bias even in the abbreviated essay condition. In contrast, but consistent with the prior cross-cultural evidence reviewed here, Japanese participants showed no correspondence bias in the abbreviated essay condition.

One theory of the correspondence bias holds that when observing another person's behavior, people infer an attitude corresponding to the behavior *automatically* (Gilbert and Malone 1995). This spontaneously inferred attitude becomes an initial anchor for subsequent reasoning. Thus, only later do they attend to situational factors and take them into account. The prominent correspondence bias evident among Americans can be explained by assuming that the situational adjustment is often secondary, more deliberate or optional, and thus insufficient. Thus, the initial anchor is not sufficiently adjusted by the situational constraint. Applying this anchoring-and-adjustment theory to the cross-cultural evidence reviewed above, one can argue that regardless of cultures, people automatically infer the agent's attitude that corresponds to the observed behavior. However, Asians may know that situations have powerful influences very well and thus mindful of making due adjustment of the effect of situational forces as long as these forces are salient enough.

One crucial basis for the anchoring and adjustment theory of the correspondence bias comes from the phenomenon of spontaneous trait inferences. It has been repeatedly shown at least in European American samples that when behaviors are presented within a memory paradigm (so that there is no explicit demand to infer any attitudes from the behaviors), people automatically infer attitudes corresponding to the observed behaviors. If the anchoring-and-adjustment theory of the correspondence bias should apply to East Asians, the phenomenon of spontaneous trait inference ought to be as strong among East Asians as among European Americans.

Na and Kitayama (2011) tested this prediction. They ran a memory task first, in which participants were to memorize many pairs of both a face and a behavior. Later, under the guise of an intervening task before the memory test, participants were asked to perform a lexical judgment

task. In this task, a number of words and non-words were shown one at a time. The participants judged whether each sequence of letters was an English word or not. The words used in the lexical traits were either the traits corresponding to the behaviors included in the memory test or their antonyms. Importantly, as a fixation, one of the faces used in the memory test was used. Thus, on some trials, one of the faces was shown, followed by a trait that corresponded to the behavior that had been paired to the face during the memory test. On some other trials, the face was followed by an antonym of the corresponding trait. On yet other trials, the face was followed by nonwords.

Imagine that during the memory test, people automatically infer a trait from a behavior shown and associate the trait to the face that is paired with the behavior. Then, during the lexical judgment task, the face should activate this trait, which may facilitate the speed of the lexical judgment. This is exactly what Na and Kitayama found for European Americans. This demonstrates that the spontaneous trait inference is quite robust. Moreover, the trait that is spontaneously inferred is also spontaneously bound to the face of the person who performed the behavior. The facilitation of lexical judgment by paired faces, however, was negligible for East Asians, indicating that spontaneous trait inference is very fragile at best among them. This study shows that the assumption that trait inference is automatic and obligatory regardless of culture is likely to be invalid. The cultural variation in the correspondence bias seems to go more deeply than the anchoring-and-adjustment theory would suggest. It may be the case that initial inferences of attitudes or traits that correspond to observed behaviors are automatic among those engaging in European American cultures, but they are not among those engaging in East Asian cultures.

We should hasten to add that East Asians will, and surely can, infer attitudes when they intend to. Moreover, they may adjust their inferred attitudes more fully by attending to situational constraints than European Americans do. However, the assumption that the initial inference of corresponding attitudes or traits is automatic and obligatory is likely to be incorrect, contrary to the

anchoring-and-adjustment theory of correspondence bias. Moreover, it is important to underscore another important point. That is, the correspondence bias is often weak or negligible, especially when situational constraints are made salient for East Asians. This conclusion, however, does not mean that East Asians are not thinking about anything. On the contrary, East Asians are likely to infer situational constraints as experienced by the target, thereby drawing inferences about their beliefs and perceptions about the impinging social situation from the target's point of view. It is these inferences about the target person's mental state that make it hard for them to draw dispositional inferences that correspond directly to the observed behaviors.

Agency Detection Is a Crucial Factor for the Emergence of Religious Intuitions

The great majority of people worldwide believe in some kind of supernatural being or god, despite the lack of any objective evidence for it. Many cognitive theorists (e.g., Norenzayan et al. 2016) have argued that the belief in supernatural beings arose as a nonadaptive by-product of ordinary and adaptive cognitive functions, including mentalization (in concert with teleological thinking and mind-body dualism). Mentalization (as the second step involved in agency detection) does not only allow individuals to infer the minds of others, but it also supplies the cognitive foundation for assuming the existence of supernatural agents, such as gods or spirits. Believers tend to treat gods as humanlike others and ascribe certain traits to them (e.g., "God is a good father"), or mental states such as intentions (e.g., "God wants us to treat each other as brothers and sisters"), or feelings (e.g., "God is angry if we do not follow his rules"), etc. They may also believe that they actually interact with God who is thought to respond to their prayers. In fact, consistent with the account of religious intuitions as by-product, studies with Christian participants have shown that during prayers the same brain regions are active that are also associated with theory of mind. In addition, reduced mentalization capacity

has been shown to coincide with reduced belief in God. In sum, there is strong supportive evidence for the proposition that religious intuitions arose as a by-product of adaptive mental capacities which partly relate to agency detection.

The tendency to see intentional beings may also provide a default explanation for many otherwise inexplicable natural incidents. For instance, it is easy to see thunderstorms to have been caused by a furious god. All cultures seem to have developed similar ideas independently of each other and given different names to the god they invented. It is called Thor in Germanic mythology, for example. It has been suggested that, by inventing an intentional explanation for otherwise random, and uncontrollable, natural events, people take solace in an illusory sense of being able to control the events by, for example, begging their god for his mercy. Accordingly, this tendency should be particularly strong when natural explanations are lacking and when the motivation to explain unfolding events is strong.

There is evidence for this proposition. First, the belief in God may be more strongly held by people who are deprived of control. Evidence is consistent. When the sense of personal control is lowered experimentally, there is a boost in the belief of religious deities. Second, the emotion of awe is based on a recognition of something overwhelmingly bigger than life. It therefore makes one feel much smaller, lacking in personal control, in the presence of the awe-inducing events. This induced sense of uncertainty in personal control may be linked to increases in religiosity. Building on this reasoning, Vandesolo and Graham (2014) tested whether the feeling of awe induced by overwhelming natural sceneries may increase religiosity. The researchers presented their participants with either (i) awe-inducing video clips taken from BBC's *Planet Earth* to their experimental participants or (ii) positive or neutral videos that were not awe inducing. In comparison to those in the control condition, participants in the awe condition reported increased intolerance of uncertainty, as well as increased belief that the universe is controlled by supernatural agency and increased religiosity.

Furthermore, the impact of awe on the belief in supernatural agency was statistically mediated by uncertainty tolerance.

The mechanisms that we reported so far may also explain the emergence of religious intuitions. Norenzayan et al. (2016), however, moved beyond the religion as cognitive by-product account, arguing that religion (in particular the belief in a punitive, monitoring God) played an important role in the cultural evolution of modern large-scale societies. Once supernatural beings are perceived, they may have an additional function of inducing an uncanny sense of "being watched," which in turn may increase norm-congruous behaviors, including prosocial behaviors to ingroup members. Evidence is strong that incidental exposure to eyes of others or even stimulus configuration that can be interpreted as such (e.g., three dots arranged in a reversed triangular shape) is sufficient to increase prosocial behavior. Evidence for the link between the sense of being watched by a supernatural agent and norm compliance can be found very early in socialization. Piazza et al. (2011) had young children between the age of 5 and 9 perform a challenging task: They had to throw a ball several times at a target from some distance, with their nondominant hand, while looking away from the target. The task was difficult. But it was possible to cheat. For example, they may come closer to the target, they may look back and see the target, or they may even use their dominant hand. Moreover, the children were tempted for cheating since they anticipated a little gift when one of the balls stuck at the target. Unbeknownst to the children, however, they were videotaped. Within this setting, the researchers introduced an invisible person named "Princess Alice," who was alleged to be sitting on a chair in the room watching the children perform the throwing task. Half of the children received this instruction and the remaining half did not. As may be expected, the children in the Princess Alice condition cheated less than those in the control condition. Furthermore, children's expressed belief in the existence of Princess Alice significantly predicted the reduction in their cheating behavior.

Conclusion

Agency detection refers to the inference that observed events in the environment are being caused by intentionally acting others. First, an action tendency is recognized, and then second, mental states such as beliefs, feelings, and intentions are ascribed to the agent that is detected. These mental processes are supposedly adaptive in an evolutionary sense, and moreover, especially in the case of humans, they provided a basis for the perception of supernatural agency in natural, supposedly completely random events. Evidence shows that this perception is motivated in part by a desire to find control over natural, otherwise, random events. Of importance, the perception of supernatural agency, and religion, may have been instrumental in promoting norm-abiding behaviors, including prosocial behaviors to ingroup members, thereby contributing to increased efficiency in social coordination and cooperation. The putative evolutionary force operating to make the inference possible over the course of primate evolution is consistent with the social brain hypothesis, which holds that primate brains evolved in order to facilitate social life in larger groups.

While the process of agency detection is likely universal, it does take culturally variable forms. For a long time, it is commonly assumed in the case of humans that agency detection necessarily entails the perception of dispositions such as personality traits and attitudes when another person's behavior is observed. At the first glance, this psychological bias, variously called the fundamental attribution error and the correspondence bias, may appear a direct consequence of agency detection. Indeed, this bias is both pervasive and robust among Westerners. However, it is elusive among non-Westerners. Evidence suggests that people in Asia, Arab regions, and Latin regions tend to see mental states of another person from the person's perspective. Thus, the mental states that are inferred relate to the person's perception of social expectations and norms, rather than his or her intentions, goals, or attitudes. Thus, the fundamental attribution error appears to be a

culture-specific manifestation of the universal tendency of agency detection.

Altogether, agency detection is an evolutionarily prepared psychological capacity that likely increased the chances of survival and reproduction in the ancestral past. This capacity is engrained, with its manifestations heavily dependent on cultures. Over the last 10,000 years of human evolution, it likely provided a crucial basis for religion and religious movements, which in turn played key roles in promoting increasingly large modern societies. As a feature of the social brain, agency detection is an important piece of completing a full understanding of human evolution, culture, and socio-cultural and biological adaptation.

Cross-References

► [Social Brain Hypothesis](#)

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Age-Related Reproductive Potential

► [Children Have Greater Reproductive Value than Sibs](#)

Aggregation

► [Grouping and Predation](#)

Aggression

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Synonyms

[Assault](#); [Attack](#); [Hostility](#); [Violence](#); [War](#)

Definition

Aggression generally refers to the intended harming or targeted injury of one organism by another.

Introduction

Among humans and other animals, there exists a variety of behaviors by which individuals try to impose costs on other individuals. Male walruses fight for dominance, lions hunt for prey, a man smashes a mosquito, a woman poisons her abusive husband, etc. Given this variety of aggressive behaviors, aggression is sometimes defined in broad, abstract terms (e.g., the targeted infliction of disorder on one organism by another; Tooby and Cosmides 2010). Sometimes aggression is defined in more specific terms to demarcate a subset of aggressive behaviors (e.g., using the

term indirect aggression for inflicting harm via the manipulation of other people or gossip). Researchers in biology, psychology, anthropology, sociology, public health, psychiatry, and political science have worked to document and understand aggressive behavior. Below is an overview of some of this research with a focus on human aggression. The overview follows Tinbergen's four questions and thus discusses why aggression might have evolved, how aggression might have evolved in humans, how aggression develops over the human life course, and how the psychological mechanisms that regulate aggression work.

Why Has Aggression Evolved?

The short answer to why aggressive behaviors have evolved is that aggression sometimes pays off; sometimes the benefits of violence are greater than the costs. Survival machines that would be more likely to aggress in those circumstances, in which it is likely to yield resources relevant for survival and reproduction, would reproduce more than those that would not aggress in those situations. Over successive generations, such aggressive survival machines would become more numerous because of natural selection (Dawkins 2006). Of course, there are different resources that allow organisms to reproduce, such as food, safe places to sleep, safety of offspring, high social status, or mating opportunities. In general, organisms might use aggression for two distinct goals: organisms can use aggression to remove obstacles to their fitness (e.g., humans might remove snakes from their homes), and they can use aggression as bargaining power (e.g., a stronger man might bargain with a weaker man for a larger than equal share of some resource; Tooby and Cosmides 2010). The costs and benefits of aggressive behavior depend on the resource at stake and the features of the organisms involved. The aggressive hunting behavior of lions (in which a lion and its prey are in a contest over the use of the prey's meat) has probably evolved for slightly different reasons than the aggressive intrasexual competition among male walruses (in which two male

walruses are in a contest over opportunities to mate with certain female walruses).

Some of the adaptive problems relevant to human aggression have been illuminated by theorizing about rational agents. The logic of the costs and benefits of violence is rather complex when aggression occurs between rational agents (Pinker 2002, 2011). In the seventeenth century, Thomas Hobbes described three incentives for violence: competition, diffidence (fear or distrust), and glory (honor or credibility). When there is competition over some resource, the agents will invade (aggress) for gain. When there is distrust among the agents, they will invade for safety. Because of the incentive for credibility, the agents will invade for reputation. Hobbes noted that these three incentives explained why humans might fight over resources like wives and cattle, why they might fight to defend these resources, and why they might fight over insults and other signs of undervalue.

To understand why agents might aggress for reputation, consider how the three incentives are connected: survival machines that obtain more reproductively relevant resources outcompete others. Therefore, survival machines have reason to suspect that others will want to take their resources (e.g., by theft or murder). This sets off a vicious circle. Because each agent has reasons to distrust the other, they both have a reason to attack first, to strike preemptively. This vicious circle is called the Hobbesian trap of the security dilemma. There is a solution to this security dilemma: deterrence or having a credible policy of retaliation. Such a policy can consist of (1) refraining from preemptive attacks, (2) being strong enough to survive an attack by the other, and (3) being strong enough to retaliate in kind. Because this policy involves retaliation, it imposes costs on the attacker and so removes the incentive for the other (the attacker) to invade for gain. Furthermore, because this policy involves being strong enough to survive an attack and retaliate, it removes the incentive for the other to invade because of distrust (because the other no longer has to fear being the target of a preemptive attack). Note that deterrence only works when the policy of retaliation is credible.

If one agent doubts that the other is able to retaliate, the agent has reason to suspect a preemptive attack, which sets off the vicious circle. To remove any doubt that one is able to retaliate, the agent could strive to respond to each sign of undervalue – however slight – with retaliation. Hobbes also described another solution to the security dilemma: the Leviathan, a bystander that punishes any use of aggression. Because the agent can expect to be punished when using aggression, there is no longer an incentive to invade for gain. This removes the incentive to invade for safety, which in turn removes the incentive to invade for reputation.

This theorizing about rational agents suggests that humans might have evolved aggressive traits to manage distinct adaptive problems (gaining resources, defense, and reputation). Possible additional adaptive problems for which humans might have evolved aggressive traits are inflicting costs on intrasexual rivals, negotiating dominance hierarchies, deterring mates from sexual infidelity, reducing resource expenditure on unrelated children, and gaining otherwise inaccessible mating opportunities (Buss and Shackelford 1997). Furthermore, recent research has argued that certain aggressive traits may have evolved by sexual selection, meaning that certain aggressive behaviors might have evolved specifically because individuals of the opposite sex perceive these behaviors as attractive (Archer 2009a).

How Has Human Aggression Evolved?

Aggression is ubiquitous among animals, but it also comes in many varieties. This precludes a simple account of the phylogeny of aggression in humans or how aggression has evolved in humans. Many aggressive behaviors (predation, intrasexual competition) are present in many mammal species and might be traced to aggressive behaviors in common ancestors of these species. Other aggressive behaviors that are prevalent among humans, such as war (aggression between two or more multi-individual coalitions), are not common among mammals (Tooby and Cosmides 1988).

A key question regarding the phylogeny of aggression in humans is whether a particular aggressive trait is a homologue of a similar trait in another species (the traits in the two species evolved from a single trait in a common ancestor) or is an analogue of a similar trait in another species (the traits in the two species evolved independently). There have been multiple studies with animals showing that aggressive behaviors (e.g., hunting, defense of territory) are based on some cost-benefit analysis. In species that are phylogenetically distant, such resemblances in the aggressive traits are likely analogous structures (Archer 2009b).

Some violent traits in humans might be homologues of traits observed in other primate species. For example, a particular aggressive trait observed in both humans and chimpanzees might have evolved from a trait present in the common ancestor of both species. However, there is considerable debate about what kind of aggressive behaviors were the characteristic for the common ancestor of humans, chimps, and bonobos (e.g., Boehm 2012).

Although it might appear that humans have evolved few specifically aggressive features – in contrast to deer with antlers and lions with sharp canines, the human body has few features that appear to be exclusively for harming others – this does not mean that ancestral humans were peaceful. A gruesome form of aggression – cannibalism – seems to have been practiced by ancestral humans (Fernández-Jalvo et al. 1999). Substantial research in archeology and anthropology has explored to what extent warfare has occurred over human evolution. Given that uncertainties are greater when interpreting older archeological findings and when extrapolating from current hunter-gatherer tribes to increasingly ancient times, exactly how much warfare there was among ancestral humans remains a topic of debate.

How Does Human Aggression Develop Over the Life Course?

As humans appear to have evolved few or no conspicuous aggressive organs such as antlers,

the development of aggression in humans is not linked to the growth of particular organs. However, humans do seem to reliably develop motivations for aggression.

Recent research suggests the following developmental trajectory of physical aggression in humans: infants develop physically aggressive behaviors such as hitting and biting before the age of two. The frequency of such aggression increases till about the age of three. After that, the frequency of physical aggression decreases (Alink et al. 2006). In addition, it seems that men and women develop to be violent in different ways. Various forms of physical aggression (e.g., fist fights) are more common among men than among women, whereas indirect forms of aggression (gossip, social exclusion) seem more common among women than among men (Archer 2004). Notwithstanding the general pattern that humans of both sexes seem to become less violent as they get older, there is evidence that certain forms of high-risk violence such as homicide are most prevalent among young adult men (e.g., Wilson and Daly 1985).

As alluded to in the discussion of why aggression evolved, it is unlikely that natural selection has evolved indiscriminate aggressive behaviors. That is, over the course of human evolution, there has likely been a selection for being aggressive in those situations where it yields benefits. This implies that humans likely have evolved to develop contingent aggressive behaviors and to regulate their aggression based on some cost-benefit analysis. (Even very aggressive individuals are not aggressive all the time toward all others.) Hence, the development of aggressive behaviors might be influenced by factors that affect the development of psychological mechanisms involved in the cost-benefit analysis or in behavioral inhibition. This reasoning might help explain why certain individual difference variables (e.g., psychopathy, self-control) or environmental variables (e.g., having a mother who smoked during pregnancy) are associated with increased aggression.

Clearly, aggression varies across human societies. So it seems that in some cultures, people grow up to be more aggressive (or differently

aggressive) than in other cultures. Evolutionary-minded researchers have studied cross-cultural variation in aggression. Some research suggest that variables related to mating strategies influence the development of aggression. For example, data from foraging societies in the standard cross-cultural sample shows that warfare within societies correlates positively with the proportion of polygyny (Marlowe 2003). Another finding is that homicide rates across the states of the USA correlate positively with teenage birth rates, a variable indicative of a fast reproductive strategy (Hackman and Hruschka 2013).

Of course, various forms of learning are involved in the development of aggressive behaviors. But it makes little sense to talk about human aggression in general being either innate or learned (Pinker 2002). Humans evolved capacities to learn certain things more quickly than others, and some forms of aggression (e.g., smashing a mosquito biting your arm) require less or different learning than other forms of aggression (e.g., bullying, armed combat).

How Do the Psychological Mechanisms That Regulate Aggression Work?

Several commonsense explanations or folk-psychological theories of “how aggression works” have intuitive appeal. It might feel as if a series of insults creates some kind of aggressive pressure that will reduce when you retaliate. This implies a hydraulic or pneumatic model of aggression (i.e., describing aggression regulation mechanisms as resembling pumps, communicating vessels, or other devices involving a liquid or gas-like substance under pressure). A prediction of such a hydraulic model is that expressing aggression (catharsis, “letting the anger out”) should reduce aggression. However, there is not much evidence that catharsis reduces aggression (Bushman 2002). Another commonsense notion is that perceiving violence makes people violent. Although learning certainly influences aggression, researchers have argued that it is time to discard general learning models that assume that aggression is an automatic and maladaptive

response to perceiving violence (Ferguson and Dyck 2012).

There are different ways to describe how aggression regulation mechanisms work. An information-processing perspective suggests that aggression regulation mechanisms work like other cognitive systems, using fast and frugal “if-then” heuristics (e.g., Todd and Gigerenzer 2007). As humans can engage in aggression for various reasons (e.g., predation, dominance, revenge, jealousy, sadism), there are probably multiple information-processing mechanisms involved in regulating aggressive behavior, each involving specific heuristics and each implemented in particular neurological pathways. Thus, in terms of information processing, each of the aggression regulation mechanisms consists of if-then rules that convert specific inputs into outputs. As alluded to above, the inputs might consist of specific cues about the costs and benefits of aggression.

Other ways to describe aggression regulation mechanisms involve identifying the common physiological or psychological antecedents, for example, the hormones, neural activity, emotions, or beliefs that are associated with aggression. For example, aggression has been associated with low serotonin (Duke et al. 2013), high testosterone (Dabbs and Morris 1990), and consumption of certain psychoactive substances (e.g., alcohol, cocaine; Boles and Miotto 2003). However, aggression is not produced by a single hormone or neurotransmitter. Research in neuroscience has yielded diverse descriptions of the brain systems underlying aggressive behaviors. Such research typically distinguishes two or more complex neural systems, e.g., systems for affective aggression, predatory aggression, and defensive aggression (Adams 2006; Blair 2004).

Several emotions have been related to aggressive behaviors: anger (Sell et al. 2009), hate (Sell 2013), revenge (McCullough et al. 2013), and jealousy (Harris 2003). Although research of non-human animals suggests that fear (or fear-like affective states) is involved in defensive aggression, there has been little research of fear-motivated aggression in humans. The recalibrational theory of anger proposed by Sell

et al. illustrates that current research aims to explain aggressive behaviors as being the product of regulatory mechanisms. In short, this theory proposes that anger is a negotiation tactic to bargain for better treatment. For anger to be successful as a negotiation tactic, it should correlate with having a better bargaining position. The research by Sell et al. suggests that some of the mechanisms that regulate aggression are influenced by cues of having a good bargaining position: their data showed that among men, physical strength was a predictor of anger and aggression, whereas among women physical attractiveness was a predictor of anger and aggression.

Aggression has also been related to the phenomena of dehumanization and anthropomorphizing. Humans seem to be able to decrease and increase their attributions of humanlike traits such as intentions and suffering to animals (including humans) and nonanimals (Brandt and Reyna 2011). In general, humans might be less prone to aggress toward entities that are perceived as relatively humanlike (e.g., your pet cat or dog) and more prone to aggress toward entities that are perceived as less humanlike (e.g., a fish, a human who committed a heinous crime; Bastian et al. 2013).

Conclusion

Aggression is part of human life: conflict, rape, violence, and weapons are human universals. As all behaviors, aggressive behaviors are amenable to the four kinds of explanations outlined by Tinbergen (ultimate function, phylogeny, development, proximate mechanism). Human aggression has been studied in various disciplines, with each discipline focusing on particular kinds of aggression. There is no unified or general psychological model of human aggression. One way to organize various forms of human aggression is to distinguish aggressive behaviors based on the identities of the victim and the perpetrator (e.g., parent–child, male–female; Campbell 2005). The challenge for evolutionary psychologists is to continue to use insights of related disciplines to build better explanations of the various forms of human aggression.

Cross-References

- ▶ [Attractiveness and Anger-Proneness](#)
- ▶ [Boys Physical Bullying](#)
- ▶ [Bullying](#)
- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Culture of Honor](#)
- ▶ [Culture of Honor and Individual Differences](#)
- ▶ [Decline of Violence](#)
- ▶ [Derogation of Promiscuity](#)
- ▶ [Dominant Acts Expressed \(Buss 1981\)](#)
- ▶ [Employment Status](#)
- ▶ [Girls Psychological Bullying](#)
- ▶ [Humans: Within-Group Conflicts](#)
- ▶ [Individuals that Impose Costs](#)
- ▶ [Living in Groups](#)
- ▶ [Marital Status](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)
- ▶ [Procedures for Dealing with Bullies](#)
- ▶ [Same-Sex School Bullying](#)
- ▶ [Self-Assessment of Fighting Ability](#)
- ▶ [Sex Differences in Anger Proneness](#)
- ▶ [Sex Differences in Death by Homicide](#)
- ▶ [Sexual Coercion and Violence](#)
- ▶ [Sexual Jealousy](#)
- ▶ [Strength and Anger-Proneness](#)
- ▶ [Verbal Derogation](#)

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Aggression for Sexual Access

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Synonyms

[Sexual aggression](#); [Sexual coercion](#); [Rape](#)

Definition

Aggression that is used to gain access to sexual activity to which one of the participants does not consent.

Introduction

This article describes evolutionary psychological (EP) perspectives on aggression that is used to gain access to sexual activity to which one of the participants does not consent. Rape is one of the extreme forms of sexual aggression, and it will be focused on primarily in the discussion here.

EP perspectives seek to identify ultimate causes of behavior, complementing the focus on proximate causes characteristic of other psychological theorizing. In addressing ultimate causation, evolutionary psychologists have often asked whether the ability to inflict sexual aggression, and/or to avoid being a victim of it, contributed to reproductive success in our species' ancestral history, possibly giving rise to dedicated psychological mechanisms pertaining to coercive sex. Although addressing such questions is standard in EP theorizing, some critics have raised concerns that this might imply that sexual aggression is "natural" in the sense of inevitable or morally neutral, an implication the authors clearly wish to avoid (i.e., the naturalistic fallacy).

Sexual Aggression in Other Species

Relevant to EP theories of aggression for sexual access is evidence of sexual aggression in other species. In fact, physical force, harassment, and other intimidation to obtain sex have been reported in many species. Based on a review of the literature on forced copulation among non-humans, Lalumière et al. (2005) identified specific characteristics in those species that exhibit sexual coercion. Across all nonhuman species in which forced copulation has been observed, it is always perpetrated by males on females. Despite the tendency of females in some species to be assertive in the mating process, these authors could not find one instance of a female forcing sex on a male. Further, males are more likely to target fertile than infertile females for forced copulation. Relatedly, forced copulation does occasionally result in insemination, fertilization, and offspring. Also, males of most species tend not to engage solely in coercive sexual behaviors. In fact, most males who engage in forced copulation sometimes, at other times, court females. Finally, Lalumière et al. (2005) recognized the role of individual differences in sexual aggression. Certain males are more likely than others to engage in forced copulation. Some males are more successful at sexual aggression than others. Lalumière et al. conclude that sexual aggression (particularly in

the form of forced copulation) "...is a tactic used by some males under some conditions to increase reproduction" (p. 59).

A particularly interesting species is the orangutan, one of the few nonhuman primates for which sexual coercion is common. There is evidence for two distinct classes of orangutan males: large males and small males. Small males are relatively unsuccessful in obtaining sex with females via courtship. Although both types resort to forced copulations, they are more often perpetrated by small males, who force more than 80% of their total copulations at some orangutan sites, although only about half or fewer of their copulations are forced at other sites, suggesting the role of environmental contingencies such as population density and sex ratio (Knott 2009).

The evidence from orangutans can be contrasted with other similar species in which forced copulation has not been reported, such as bonobos and common chimpanzees. This suggests the importance of factors such as the isolated social system unique to orangutans among the apes (see Smuts 1995, for analyses emphasizing the importance of female coalitions as a deterrent for male sexual aggression across various primate species and potential implications for humans). Chimpanzee males have been found to harass and intimidate females, however, which can increase future sexual access to the target. For example, long-term data from a study of wild chimpanzees showed that a female's willingness to initiate copulation with a male is positively correlated with how frequently the male has been aggressive toward her, suggesting that female mate preferences are constrained by sexual coercion (Muller et al. 2011). A related study (Muller et al. 2007) found that male chimpanzees achieved more matings with females toward whom they were more aggressive and directed more aggression toward more fecund females.

Frequency of Sexual Aggression in Humans

Another issue relevant to an evolutionary-based model of aggression for sexual access is its

frequency in human history, because regularly occurring events are more likely to have a “...logic embedded in the dynamics of natural selection for reproductive success” (Wrangham and Peterson 1996, p. 138). Sexual coercion does appear to have occurred throughout human history (e.g., Chagnon 1994), and as discussed below, as with other species it is the case that among humans, males are much more likely than females to use aggression for sexual access. Cross-cultural surveys reveal that male sexual aggression occurs in most societies today. Moreover, even relatively rape-free societies described in such surveys (e.g., Sanday 1981) have social rules intended to counter male sexual aggression, suggesting that there is universal risk for such behavior.

Data suggest that particularly when fear of punishment is reduced, signaling conditions in which the costs of sexual coercion are low or the perpetrator has anonymity, many men do rape, such as in times of war. At least one-third of men admit some likelihood of sexual coercion if they could be assured that they would not suffer negative consequences (e.g., Malamuth 1989). In addition, sexually coercive fantasies are common among men. In one study 54% of college men “fantasized about forcing a woman to have sex” (Greendlinger and Byrne 1987). Similarly, 33% of a community sample of men sometimes or frequently fantasized a scene “where you rape a woman” (Crèpault and Couture 1980). Imagined sexual aggression is a key predictor of actual sexual aggression (e.g., Knight and Sims-Knight 2003). Imagined aggression may reveal important information about evolved mental mechanisms.

Sex Differences

The EP paradigm considers clues to motivational differences between men and women that may have a bearing on the potential occurrence of aggression for sexual access. Differences in minimal parental investment contribute to a greater likelihood that a man will be motivated to have sex with certain women than vice versa and that, for men, sex may be more easily separated from

emotions associated with long-term mating. Such differences create conflicts that can result in some men using coercion to overcome female reluctance and resistance. Consistent with the predictions derived from parental investment theory, as well as with the evidence from non-human species, is the finding that across various societies and recorded human history there are large sex differences in the use of sexual coercion. Males are typically the perpetrators, and females are disproportionately the victims. For example, an estimated 19.3% of American women have been raped during their lifetime versus an estimated 1.7% of men (Breiding et al. 2014). For female rape victims, an estimated 99% had only male perpetrators; 79% of male victims also had only male perpetrators. If one examines criminal statistics, the sex differences are huge. The US Bureau of Justice Statistics has reported that 99% of those imprisoned for rape were men (Greenfeld 1997). Although there are cultural differences in the frequency of sexual aggression, large sex differences are found even in the most egalitarian and low general violence nations (e.g., Kråhe et al. 2014).

Overview of EP Models

Symons (1979) first discussed extensively whether rape is produced by adaptations or by-products of adaptations. Adaptations are naturally selected (i.e., they resulted in increased ancestral reproductive success). Criteria for establishing adaptation within evolutionary science include attributes of economy, efficiency, complexity, precision, reliability of development, and functionality in solving a specific problem. By-products are incidental characteristics that did not evolve because they solved adaptive problems. For example, male nipples, which have no design functionality, are by-products of the adaptive value of nipples in women (Symons 1979).

Symons (1979) concluded that the available data are insufficient to presume that rape is a facultative adaptation in humans. Rather, rape may be a by-product of male adaptations that produce sexual arousal and adaptations that

motivate coercion to secure desired goods. This model, in that it places the propensity to sexually aggress within a larger framework of aggressive tendencies that describes a propensity for antisocial behavior in general, is an example of what has been somewhat similarly referred to in the criminology literature as a “generalist model” (see amplification below). Later EP models of rape have extended Symons’s proposal to include rape as a by-product of both sexual desire and a generalized possessiveness or desire to control others or as a manifestation of an alternative strategy, for example, psychopathy, whereby rape is a by-product of the use of coercion in other areas (Mealey 1995). All of these essentially argue that those individuals who are relatively prone to use aggressive tactics in many circumstances will also use them to gain sexual access but that there are not specialized mechanisms that evolved for using coercive tactics to gain sexual access.

The contrasting model is one that suggests that there are specialized evolved mechanisms pertaining to rape. This type of model corresponds to some degree to the “specialist model” in the criminological literature. In EP theorizing, Thornhill and Palmer (2000) have advanced this model in proposing that there may be various specialized adaptive mechanisms designed to address fundamental problems of sexual access, including decision rules designed to (a) evaluate female vulnerability to rape, essentially by identifying scenarios in which potential reproductive benefits of aggression for sexual access would have exceeded potential costs (e.g., injury or social ostracism); (b) identify cues associated with fertility (e.g., age, ovulation status), so that the most fertile women could be preferentially targeted; (c) optimize sperm counts produced during rape; (d) motivate rape under conditions of sperm competition; (e) motivate rape in men who lack sexual access to females (the “mate deprivation” hypothesis); and (f) produce sexual arousal specific to opportunities of rape. These theories of adaptation as they relate to sexual aggression have been further elaborated and expanded upon elsewhere (e.g., Camilleri and Stiver 2014). This article will evaluate theory and data specially pertaining to sexual arousal specific to forced

sex, explaining how such an adaptive decision rule might be selectively constituted.

The adaptation hypothesis suggests that, in ancestral environments, being sexually coercive under some circumstances (and, particularly for women, having the capacity to avoid being sexual coerced) contributed to reproductive success sufficiently frequently to have resulted in some change in the evolved psychological architecture that would not have occurred without the recurring fitness consequences of sexual coercion. Therefore, this hypothesis posits specific psychological mechanisms pertaining to sexual aggression. Such specialized mechanisms might include reactions such as emotions or arousal patterns that, in the proximate environment, mediate between relevant environmental cues and behaviors.

Although the topic of this article is aggression for sexual access, it is important to note that it is actually more likely that specialized mechanisms for avoiding sexual aggression evolved in women than that specialized mechanisms for engaging in aggression for sexual access evolved in men. Underlying this assertion is the idea that the reproductive costs to ancestral women of losing the ability to choose among mating partners due to sexual aggression would have been greater than the reproductive increase to men of, at times, using coercive sex. In the past few years, this topic of female counter-adaptation to the risk of male sexual aggression has been an area of emphasis of EP rape research. The authors have explored this research in more detail elsewhere (Huppin and Malamuth 2016).

Data Pertaining to the Generalist Versus Specialist Models

As outlined above, two schools of thought have developed: “generalist” and “specialist” theories of sexual offending. Generalist models suggest that the propensity of offenders to sexually aggress can be explained by a broad-spectrum tendency toward unwarranted aggression. Research on convicted rapists has to some degree been supportive of this perspective. Most

convicted rapists are generalists vis-à-vis antisocial behavior. They have a history of nonsexual offenses, their criminal records often resemble those of other offenders, and on most measures of antisocial traits and behaviors, convicted rapists are comparable to other types of violent criminals (Lalumière et al. 2005). These men engage in various antisocial acts because they differ from other men not necessarily on some specific mechanism for sexual aggression but on mechanisms underlying general antisocial behaviors. They may be more likely to steal or to use coercion for obtaining any desired goal.

Although similarities between sexual and nonsexual offenders are substantial (e.g., Fanniff et al. 2016; juvenile sexual and nonsexual offenders show equivalent general recidivism rates over a 7-year follow-up), generalist explanations of male sexual aggression still paint an incomplete picture. A meta-analysis of 59 studies comparing male adolescent sex and non-sex offenders, for instance, did not support the notion that adolescent sexual offending can be parsimoniously explained by generalist theories of sexual aggression (Seto et al. 2012; see also Fanniff et al. 2016; juvenile sex offenders show higher sexual recidivism rates than other offenders, although this rate was low). Findings such as this suggest the need to consider “specialist” models of sexual aggression or at least to supplement contributors to general delinquency (e.g., lack of inhibitory self-control, high impulsivity, low empathy, and/or callousness) with risk factors specific to sexual aggression (e.g., sexual arousal to violence, hostile masculinity, impersonal sexual attitudes) in a combined model (Lussier and Cale 2016). From an EP “specialized mechanism” perspective, the question is not whether sexual coercion is a better strategy for males than engaging in consensual sex but whether for some ancestral males, under some circumstances, it may have been reproductively effective to use aggression for sexual access as compared to not using it. In other words, did recurrent ancestral conditions exist under which for some men, some of the time, an overall fitness increase resulted from sexual aggression? Although the hypothesis that sexual aggression contributed to reproductive success has been

criticized on grounds that rape rarely leads to conception, Gottschall and Gottschall (2003) estimated pregnancy rates resulting from penile-vaginal rape among women of reproductive age to be twice that of consensual per-incident rates (6.4% to 3.1%). Controlling for age, rape pregnancy rates per incident remained 2% higher than consensual rates (see also Holmes et al. 1996, indicating a rape-related pregnancy rate of 5.0% per rape or 6.0% per victim in a national sample of reproductive age women; for indirect corroboration, see Beirne et al. 2011, in a sample of 105 normally ovulating sexual assault victims, identifying “a trend and a distinct rise in the number of assaults when the victims were in the middle of their cycle” [p. 315], that is to say at peak fertility).

Another factor to think about when considering the potential fitness outcomes of sexual coercion is the fact that a substantial minority of women continue to have sex with the men who sexually assault them (Koss 1988). This is particularly true of completed sexual assault, pointing to the use of sexual coercion as a tactic to secure subsequent copulations. Illustratively, Ellis et al. (2009) identified more than two thousand North American undergraduate women who reported having been sexually assaulted, dividing victims into two groups: assault blocked (59.4%) and assault completed (40.6%; i.e., sexual intercourse occurred). A sizable number of women in both groups indicated future intercourse at least one time with the assaulter, with more women in the assault-completed group (27.2%) than in the assault-blocked group (19.4%) reporting this outcome. Overall, these results indicate that “at least a minority of men may have evolved tendencies to use assaultive tactics to secure mating opportunities beyond those obtained by men who only employ ‘voluntary’ tactics” (p. 461) (see also Wilson and Durrenberger 1982; 39% of rape victims had another date with their assaulters, compared to 12% of victims of attempted rape).

Relatedly, in Holmes et al.’s (1996) study, 41.2% of rape-related pregnancy cases involved repeated assaults, one of which was assumed to have resulted in the pregnancy. Although the data are unclear about what percentage of these women

endured multiple assaults from a single perpetrator (indicating only that for these victims, rape-related pregnancy occurred in a context of ongoing abuse), it does point to the possibility that sexual coercion may have increased the likelihood of future copulations with the victim.

Sexual Arousal to Force

One hypothesized candidate for a specialized psychological mechanism motivating aggression for sexual access that has received focused attention is sexual arousal specific to forced sex, referred to here as *sexual arousal to force* (SAF). Such arousal may be a manifestation of a broader category of sexual arousal generated by controlling or dominating women, which can be accomplished by the use of force.

Using an adaptation model, R. Thornhill and Thornhill (1992) discussed SAF and argued that higher sexual arousal to coercive sex among men should be associated with greater success with coercive sexual tactics, thereby contributing to ancestral reproductive fitness under some circumstances. They noted that given the costs of forced mating in ancestral environments, including possible loss of status or life, men might be expected *not* to have evolved preferences for forced sex and, therefore, *not* to evidence SAF. If, however, under some recurrent ancestral environments, the reproductive benefits of forced mating outweighed the costs, psychological mechanisms enabling sexual arousal despite a woman's lack of consent may have evolved. Harris, Rice, Hilton, Lalumière, and Quinsey's (2007) selectionist hypothesis of psychopathy provides an example of a model suggesting that SAF could reflect a design feature of a rape adaptation. This hypothesis asks: "Do psychopaths respond more to sexual stimuli depicting violence, coercion, and rape simply because they are indifferent to the suffering of others, or does psychopathy entail a mechanism promoting coercive sex?" (p. 20). Harris et al. (2007) suggest that sexual aggression could be a fundamental feature of psychopathy.

Hagen (2004) argues that specialized mechanisms pertaining to rape would not be expected

unless the problems involved in "successfully" committing such an act in ancestral environments were not the same problems as with the use of aggression in other contexts. The occurrence of sexual arousal in the context of coercive acts may be an important distinguishing characteristic. For most aggressive acts, sexual arousal would be irrelevant or even detrimental. Because the preferred sexual strategy for most men in most circumstances is to pursue consensual sex, the most common calibration of sexual arousal mechanisms should be to become sexually inhibited by indications of lack of sexual receptivity by women. However, if an individual were to effectively sexually aggress in ancestral environments, such behavior may have required reversing of the default arousal pattern. This may be hypothesized as a unique adaptive problem associated with sexual coercion as contrasted with the use of coercion in nonsexual contexts.

In evaluating empirical data, the next section relies on studies that measure SAF (often by direct genital measures), and it suggests that studies using related measures, such as reported dominance as a motive for sex and rape fantasies, assess closely related constructs that are also relevant to the present analysis.

Proposed Evolved Function of Sexual Arousal to Force

Within some ancestral circumstances, the inhibition or activation of sexual arousal in response to cues associated with using force might have affected the likelihood of successfully dominating and exerting sexual control over an unwilling woman. Some emotions motivate avoidance of particular stimuli, whereas others motivate approaching or pursuing particular stimuli. Just as fear of spiders motivates avoidance of specific threats, sexual arousal cued to the use of force may motivate sexual aggression. This hypothesis is supported by the meta-analysis of Allen et al. (2000), which documented that sexual arousal is associated with positive psychological affect, a precursor of approach or pursuit.

This hypothesis that sexual arousal cued to the use of force may serve as an approach emotion designed to increase the likelihood of engaging in sexually coercive behavior may be contrasted with non-evolutionary hypotheses of SAF. For example, Marshall and Fernandez (2000) hypothesized that SAF is not designed to facilitate sexual coercion but instead that the causal connection is in the opposite direction. Marshall and Fernandez argue that SAF and other forms of “deviant” sexual arousal are the result of repeated sexual offending. This model suggests that, because the offender lacks the requisite social skills and confidence to engage in consensual sex, he uses coercive tactics repeatedly, eventually resulting in the conditioning of SAF. Other hypotheses have also conceptualized such arousal as an abnormality that is likely to be evidenced by a small percentage of men.

An evolutionary-based model uniquely suggests that, due to calibrating mechanisms grounded in the consequences in ancestral environments, a substantial percentage of “normal” men evidence the sexual arousal pattern that facilitates sexual coercion. How might such calibration occur? In keeping with the proposition that humans share a common evolved psychology that enables relevant developmental experiences to “set” mechanisms at different levels, the model we outline here (labeled the *evolutionary functional* [EF] model) emphasizes some relevant perceived negative experiences with women that may set the sexual arousal versus sexual inhibition to force mechanism more in one direction or the other. Although full testing of such a process would require a longitudinal study that would be difficult to conduct, it may be possible to prime similar processes to create a *state condition* related to the *trait condition*. Yates et al. (1984) found that college men who were insulted by a woman were more sexually aroused by rape portrayals as compared to portrayals of consensual sex. Creating general arousal by physiological exercise instead of an insult by a woman did not result in a similar increase.

Other relevant findings pertain to the trait rather than the state of anger and hostility toward women. These studies indicate that men who are

hostile to women, typically on measures that include items referring to perceived rejection from women, show relatively high SAF as contrasted with men who are relatively low on such measures of hostility toward women. For example, many studies focusing on the *confluence model of sexual aggression* (Malamuth and Hald 2017) have found a strong connection between measures of individual differences in men’s hostility toward women and their SAF or similar constructs such as dominance as a motive for sex and men’s rape fantasies. Other studies examining differences between behaviorally sexually non-aggressive men and sexual aggressors (some of whom are likely to have the relevant calibration of increased SAF) have found similar results (e.g., Murnen et al. 2002). Several priming studies have revealed that sexually aggressive men may be more prone to automatically associate women with hostility, sex, and power (e.g., Leibold and McConnell 2004). Barbaree (1990) reported a study with a rapist who was asked to imagine raping women for whom he held different emotional feelings. He found that the greater the hostility to the woman, the greater the sexual arousal to rape cues. Forbes et al. (2004) found that the key component linking various measures of male dominance ideology (e.g., attitudes supporting aggression or sexism) to aggression against women is hostility toward women. Baumeister et al. (2002) have summarized many studies indicating that experiencing rejection by women, particularly by men who are relatively narcissistic, contributes to sexually aggressive behavior. Taken together, these findings provide some support for the hypothesis that perceived blocked access to desired women and associated hostility toward women may affect the calibration of men’s sexual arousal patterns in ways that could affect the likelihood of committing sexually coercive acts.

How might a mechanism of SAF operate to affect the likelihood of committing sexually coercive acts? Consider a simple distinction between two types of men: one for whom the best prospects involve mating only with a consenting partner and the other a man whose prospects could be augmented by using sexual aggression.

(A more dimensional conceptualization would be preferable here but a simple dichotomy is used to facilitate explication.) If one were to design a psychological mechanism that provided the best decision rule (for total ancestral fitness) for each of these men, what might be its properties? For the first man, there would be sensitivity to cues when a sexually desired female indicated disinterest, disgust, or other negative responses. This would be an effective mechanism for inhibiting approach tendencies where persisting in sex with an unwilling female would have high costs compared to pursuing consensual sex with alternative mating prospects. However, for the second type of individual, it could have been ancestrally adaptive to have this inhibiting mechanism disengaged. Potentially, for this latter type, there may even have been fitness benefits to increased SAF relative to consenting sex because engaging in coercion may require relatively greater persistence and energy to overcome the resistance of an unwilling partner. Consistent with this hypothesis, Bernat et al. (1999) found that the penile tumescence of self-identified sexually aggressive men who also held callous sexual beliefs increased when force was introduced into a sexual scenario (see also Lawing et al. 2010; finding that adolescent sexual offenders high in callous/unemotional traits showed more sexualized aggression and had a greater number of victims than other adolescents with a sex offense).

This analysis suggests that type 1 men should show inhibited SAF, whereas type 2 men should show at least equal sexual arousal to consensual and coercive sex (i.e., the shutting off of the inhibiting mechanism) or even greater arousal to some types of coercive sex (the activation of a mechanism creating greater sexual arousal). The distinction between two types of men bears some similarity to the distinction between large and small orangutans insofar as that distinction may serve as a useful illustration of how differently situated individuals may respond based on their unique developmental and current circumstances. In summary, if there were ancestral conditions in which, for some men, some of the time, there was an overall fitness increase resulting from sexual coercion, then for these men it may

have been important not to be inhibited by cues of a woman's unwillingness and to potentially be sexually aroused by dominating and controlling the victim.

Specialization and Coercive Potential

How might one select two groups of men for comparison purposes to correspond to the hypothesized two types? Previous researchers have compared convicted rapists to other men. Because most convicted rapists seem to be relatively more generalists, this is not the ideal comparison, however. The data indicate that it is among non-criminals, particularly those drawn from college populations, that specialization may be most evident. In such general community samples, men who self-identify as having committed sexual coercion show more evidence for "specialization" rather than relatively generalized antisocial characteristics. Ronis et al. (2010) found that self-identified sexually coercive community men exceeded incarcerated rapists on diverse measures of sexual and paraphilic fantasies, including sadism, sexual preoccupation, and bondage. Self-identified sexual coercers among criminals who had not been convicted of sexual crimes also showed higher scores on such sexual and paraphilic fantasy than convicted rapists, suggesting that, even among criminals, self-identification might be a better way to identify specialists for sexual aggression than only considering the crime for which the person was convicted. Overall, these data support the conclusion that most of those currently identified by the judicial system and convicted of acts of sexual aggression display less evidence of specialized psychological mechanisms than other self-identified sexually coercive men. However, caution is necessary in interpreting the data provided by convicted rapists, who might seek to portray a positive image because of the belief that this will increase their likelihood of being paroled.

Researchers focusing on noncriminal samples have seldom addressed whether sexually aggressive men engage in other forms of antisocial behavior. The authors conducted analyses

focusing on this issue in our longitudinal database of close to 150 men (for a discussion see Huppín and Malamuth 2016). Several measures were administered to the same men at about 20 years old (Time 1) and then again 10 years later (Time 2). Measures assessing SAF and other characteristics and behaviors showed a pattern supporting specialization. Other findings provide corroboration for such a specialized mechanism (for a discussion see Huppín and Malamuth 2016). Malamuth and Impett (1999) conducted a series of mediational analyses to directly test the hypothesis that high SAF is a specific mediator of forced sex. They found evidence supporting SAF as a specific mediator of coercive sexual behavior.

Malamuth and Hald (2017) recently reviewed a large number of studies, primarily with non-criminal samples pertaining to the “Confluence Mediational Model” (CMM) of sexual aggression. This model incorporates both “generalist” mechanisms and “specialized” mechanisms. The research provided a great deal of support for this model.

Conclusion

EP theory and research seek to better understand the ultimate causes and the design of evolved psychological mechanisms underlying manifest behavior. In addressing aggression for sexual access, there has been considerable focus on whether there may have been, on average, fitness consequences in recurring ancestral environments of the ability to successfully inflict sexual aggression.

The discussion in this article focusing primarily on perpetrators suggests three competing models:

1. There were no recurring fitness consequences of using sexual aggression; therefore, the mind does not include mechanisms relevant to aggression for sexual access.
2. Fitness consequences were a function of the ability to selectively use aggression in various arenas, with sexual conflict being one of many, but no specific adaptive problems existed

unique to using coercion in the sexual arena. The mind, therefore, includes mechanisms designed specifically to motivate coercion in various arenas, including but not limited to sexual aggression.

3. Because there were unique adaptive problems associated with the use of coercion in the sexual context (e.g., how to maintain an erection and subdue a victim who is fighting back), specialized mechanisms evolved that enabled the effective use of aggression for sexual access. Such specialized modules evolved because there were fitness benefits in ancestral environments specific to the selective use of sexual aggression that differed from the use of coercion in nonsexual contexts.

In seeking to identify potential candidates for specialized mechanisms, it is useful to reiterate that sexual aggression may be produced by differing motivations and antecedents. The data support the conclusions that rapists identified by the legal system are frequently generalists who commit various types of antisocial behavior and often may not reveal the activation of specialized mechanisms motivating sexual aggression. However, among convicted rapists there has also been considerable evidence of sexual arousal to force that differs from that of non-rapists. In contrast, in the general population, sexual aggressors as compared to non-aggressors, have both higher levels of general antisocial mechanisms as well as specialized mechanisms particularly relevant to gaining sexual access via aggression.

Cross-References

- [Evolution of Female Resistance](#)
- [Forced Copulation](#)
- [Rape and Dating](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion as a Mechanism of Sexual Selection](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Conflict Theory](#)

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Aggressive Behavior

- [Costs of Aggression](#)
- [Development of Aggression](#)

Aggressive Behaviors

- [Men Riskier, More Aggressive](#)

Aggressive Fantasies

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Synonyms

[Fantasy aggression](#); [Fantasy violence](#); [Violent fantasy](#)

Definition

The imagination of actions which have the goal of causing injury to another organism

Introduction

Aggressive fantasy refers to the imagination of an act which has the goal of injuring another organism. Functionally, aggressive fantasy may serve to increase the availability of aggressive actions in response to real-world situations and to normalize such aggressive behaviors (Guerra et al. 2003;

Huesmann and Eron 1984). Furthermore, in extreme circumstances, aggressive fantasies could also serve as precursors to homicide, through homicidal ideation. If acted upon, homicide has the potential to lead to benefits such as preventing premature death, removing rivals, and gaining resources, among others (Duntley and Buss 2011).

Research on the relationship between aggressive fantasy and real-world aggression dates back more than 60 years. Initially, such research aimed to determine whether aggressive fantasy functioned as a cathartic influence, allowing an individual to displace real-world aggression, and harmlessly release any hostile impulses they may have (Mussen and Rutherford 1961). However, most subsequent research has examined aggressive fantasy as a negative influence, suggesting that fantasizing about aggression stimulates hostile impulses and increases aggressive behaviors. This shift occurred as data increasingly demonstrated that aggressive fantasy had a positive correlation with aggressive behavior. As a result, aggressive fantasy is generally conceptualized as a form of social information processing, where additional factors, such as sex, empathy, psychopathy, violence exposure, and fantasy absorption, may influence the relationship between aggressive fantasy and aggressive behavior (Dean and Malamuth 1997; Smith et al. 2009; Williams et al. 2009).

The Catharsis Hypothesis

The catharsis hypothesis states that engaging in aggressive fantasy allows an individual to harmlessly release their aggressive impulses, and effectively displace their aggression, leading to a reduction of overt aggression (Dollard et al. 1939). Some early research supported this hypothesis; a study by Feshbach (1955) found that participants displayed less aggression toward an experimenter who was rude to them if they were given the opportunity for fantasy than if they were given no opportunity for fantasy. Additionally, research also showed that, in boys who were aged 9–10, aggressive movements decreased

aggressive fantasy relative to nonaggressive movements, which suggested that enacting an aggressive goal response results in a cathartic effect, reducing future aggression and aggressive fantasy (Murray and Feshbach 1978).

Evidence Contrary to the Catharsis Hypothesis

In spite of the limited amount of support for the catharsis hypothesis, however, a preponderance of evidence suggests that aggressive fantasy does not have a cathartic effect and even leads to increases in aggression rather than a decrease. For instance, one study showed that lower-class boys were more likely to display overtly aggressive behaviors when they described an aggressive story than when they described a nonaggressive story (Mussen and Naylor 1954). Additionally, children who were assigned to watch an aggressive cartoon subsequently expressed more aggression than those who either observed a nonaggressive cartoon or did not observe a cartoon at all (Mussen and Rutherford 1961). In another experiment, frustration was induced in groups of kindergarten students, and then spontaneous fantasy behavior was either elicited or suppressed. Results showed that children who engaged in fantasy behavior behaved in a significantly more aggressive manner than kindergarteners who did not engage in fantasy play (Lockwood and Roll 1980). Finally, in another study, subjects who hit a punching bag while ruminating about someone who made them angry behaved more aggressively in a subsequent task than subjects who hit a punching bag while thinking about exercise (Bushman 2002). Thus, although the catharsis hypothesis had some limited support among early studies, the majority of research on the subject suggests that such fantasies increase, rather than decrease, real-world aggression.

Aggressive Fantasy as Social Cognition

Current research tends to conceptualize aggressive fantasy as social cognition, which functions

to normalize violent and aggressive actions, as well as further aggressive fantasies (Guerra et al. 2003). Simultaneously, aggressive fantasies are cognitively rehearsed, and over time, the availability of aggressive actions is increased in response to real-world situations (Huesmann and Eron 1984). Research supports this hypothesis; a study by Guerra and colleagues examined longitudinal data in children from first to sixth grade and found that increased exposure to violence predicted increased aggressive fantasies, normative beliefs about aggression, and aggressive behaviors. Furthermore, the strength of these relationships increased over time, suggesting that exposure to violence leads to the development of aggressive social cognitions and the imitation of violence as children get older (Guerra et al. 2003). Similarly, a study examining preschool children found that those who tended to engage in higher rates of aggressive fantasies were more likely to display antisocial and aggressive behavior, less likely to help a friend and less likely to display empathic moral sensibilities than children who did not typically engage in aggressive fantasies (Dunn and Hughes 2001). Finally, research on media exposure, including television shows, movies, and video games, shows that exposure to violent media causes increases in aggressive cognitions, aggressive behaviors, and violence (Carnagey and Anderson 2004; Huesmann and Taylor 2006).

Other Factors Affecting Aggressive Fantasy

Research has also examined potential third variables, which may influence the relationship between aggressive fantasy and aggressive behaviors. For instance, research has shown that, among young boys, having a mother who is supportive of aggression leads to a positive correlation between aggressive fantasy and aggressive behavior, while boys whose mothers disapproved of aggressive behavior had a negative correlation between aggressive fantasy and aggressive behavior (Lesser 1957). Additionally, children who are highly prone to fantasy display reduced

aggression after they watch a fantasy film, but children who are not fantasy prone display increased aggressive behavior after watching the same fantasy film. While this finding may seem counterintuitive, it is likely due to the fact that children who fantasize more often are more accustomed to fantasy than the others are, resulting in a reduced effect of the fantasy on their subsequent behaviors relative to children who do not fantasize frequently (Biblow 1973). Also, research examining deviant and aggressive sexual fantasies has found that psychopathy moderates this relationship, such that in those with high psychopathy, such fantasies are strongly associated with behaviors enacting these fantasies, but in those with low psychopathy, there is no such correlation between the fantasies and the behaviors enacting them (Williams et al. 2009). Finally, aggressive fantasy and aggressive behavior may be moderated by violence exposure, such that these variables have a strong, positive correlation at high levels of violence exposure, but no relation at low levels of violence exposure (Smith et al. 2009).

Conclusion

Research on aggressive fantasy suggests that such fantasies do not have a cathartic effect on aggression. On the contrary, current research suggests that such fantasies function as social cognitions, which serves to normalize aggressive or violent behavior, and increase aggressive cognitions and behaviors over time. However, research also suggests that several additional variables may be involved in this relationship, including parental approval, proneness to fantasy, psychopathy, media exposure, and violence exposure. Future research should continue to examine the influence of other variables on the relationship between aggressive fantasies and aggressive behaviors.

Cross-References

- [Homicide](#)
- [Imitative Aggression](#)
- [Physical Aggression](#)

- [Sexual Aggression](#)
- [Social Cognition](#)

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Aggressive Imitation

- [Imitative Aggression](#)

Aggressiveness

- [Facial Width to Height Ratio and Dominance](#)

Aging

- [Life Expectancy and Reproduction](#)
- [Senescence](#)
- [Theory of Senescence](#)

Agonistic Interactions

- [Primate Dominance Hierarchies](#)

Agonistic Support

- [Feelings of Excitement and Brotherhood](#)

Agreeableness

- [Five-Factor Model](#)

Agropastoral Cultures of Violence

- [Culture of Honor and Nepotism](#)

Agropastoral Honor Cultures

- [Culture of Honor and Nepotism](#)

Aid

- [Charity](#)

Alarm Call

- [Predator Confusion Hypothesis](#)

Alarm Call Confuses Predator

- [Predator Confusion Hypothesis](#)

Alarm Call Creates Confusion

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Synonyms

[Confusion effect](#)

Definitions

Alarm calls may signal the presence of a predator, creating confusion and reducing the threat of predation.

Introduction

Group living increases the likelihood that predators will be detected through cooperative vigilance. This social structure is particularly beneficial if individuals can alert others to potential threats as soon as these are detected. Hence, alarm calls are evident in a numerous group living species across a range of taxa including fish, birds, and mammals (e.g., Bessey and Heithaus 2013). These alarm calls may convey a range of important information such as predator type or location through varying the number or rate of calls, amending the intensity or volume of call, or generating calls that are qualitatively different (Zuberbuhler 2000). It has been suggested that those signaling the presence of a predator may be at increased risk of detection by predators. The present entry outlines the manner in which alarm calling may impact on group behavior, create confusion, and hence reduce the likelihood of predation.

Alarm Calling

A range of theories have been proposed to explain the tendency to produce alarm calls which may draw attention to the caller, delay escape, and increase the personal risk of detection and capture for the caller. In particular, these calls may deter predators, startle predators leading to the release of captured prey, encourage others to seek cover, or attract individuals to the vicinity in order to defend vulnerable group members (Goedert et al. 2014). It has been suggested that producing an alarm call may not increase the individual risk of predation. For example, calls providing an honest signal of caller quality may reduce the likelihood that the individual is targeted by predators or alarm calls may signal to the predator that it has

been detected, encouraging the predator to abandon the attack (Bergstrom and Lachmann 2001; Laiolo et al. 2007). Similarly, alarm calls may contain a range of features which reduce the conspicuousness of the signaler. Hence, calls may be difficult for predators to localize or ventriloquial (Wood et al. 2000).

Confusion

Alarm calls may also create a confusion effect which reduces the likelihood of successful attack (Cresswell 1994). This confusion may result from the number of individuals seeking cover and vocalizing or from the presence of additional predators and heterospecifics attracted by the alarm calls and increased activity (Chu 2001). Solitary prey may be quickly captured though many unsuccessful attempts are often required for predators to capture a member of a group living species. Hence, the confusion effect makes it difficult for predators to identify, track, and attack single members of a group and leads to a greater number of attacks required per kill (Curio 1976). It is of course important to consider the form and function of alarm calls separately for each prey and predator type.

For example, Belding's ground squirrels (*Spermophilus beldingi*) produce distinct alarm calls in the presence of mammalian terrestrial (multiple note trills) and avian aerial (single note whistles) predators. Squirrels producing trills are more vulnerable to terrestrial predation, and mammalian predators appear attracted to those producing these calls. Therefore, alarm calls (trills) produced in response to mammalian predators appear to be a form of kin focused protection. In contrast, aerial predators (raptors) rarely capture squirrels after an alarm call has been produced, and alarm callers are less likely than noncallers to be killed (Sherman 1985). Those most likely to produce the calls were close to the predator and further from cover. Hence, the production of single note whistles in response to aerial predators appears to reduce the likelihood of personal risk of predation.

Conclusions

In some circumstances, the increased activity among group members which follows alarm calling may confuse predators, leading to a *reduced* rather than increased threat of predation for alarm callers.

Cross-References

► Predator Confusion Hypothesis

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Alarm Callers Are Females with Greatest Genetic Representation

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Synonyms

Cooperation; Dispersal; Nepotism; Partial migration; Philopatry; Primate

Definition

Philopatry is the retention of individuals in the natal group or territory (Ekman et al. 2001). *Kin selection* is a selective interaction between relatives that increases the fitness of the recipient at the expense of the fitness of the actor. Such behavior will be selected if the cost to the actor (c) is less than the benefit to the recipient (b) multiplied by the coefficient of relatedness (r). This can be summarized with Hamilton's law: $br > c$ (reviewed in Silk 2002). *Nepotism* is behavior between relatives through which the actor provides a benefit to the recipient regardless of any increase or decrease in the fitness of the actor (Silk 2002).

Introduction

Philopatry to and dispersal from a natal group is a critical element of any animal's life history and is driven by three primary selection pressures: kin selection, resource competition, and inbreeding avoidance (Moore 1992; Lawson Handley and Perrin 2007). Because these forces are frequently sex specific, philopatry often also follows a sex bias. In female philopatric species, females will be best represented genetically because maternal lineages continue across generations, unaffected by migration patterns.

While a combination of these selection pressures promotes a species-specific dispersal strategy, kin selection is the strongest predictor of dispersal given that relatives can only interact if neither has dispersed from a group (Moore 1992). Nepotistic behavior promotes kin selection and has been observed in a variety of mammal and bird species (reviewed in Lawson Handley and Perrin 2007). For example, in birds, offspring are offered exclusive access to food and defended from competitors by parents (Ekman et al. 2001).

This entry reviews the role of alarm vocalizations as nepotistic behavior in female philopatric species.

Kinship as a Determinant of Alarm Calling

Alarm calling is a prevalent antipredator behavior among many species. Males are typically better suited to defending a group against predators given their larger size and more capable adaptations (e.g., larger canines – Gould et al. 1997). Where the vocal repertoire in a species differs between male and females, males are therefore often assumed to provide the majority of protection from predators; however, the nepotistic nature of any such behavior, including selective alarm calling, has only been tested empirically in a small number of bird and mammal species (Ekman et al. 2001).

In return, immigrant males in female philopatric groups that benefit females with antipredator behavior are expected to be accepted and tolerated within the group. This was found not to be the case in vervet monkeys (*Chlorocebus pygerythrus*), where no sex differences in alarm calling rate were found (Baldellou and Peter Henzi 1992). Similarly, Bolt et al. (2015) found no significant difference in vocalization rates between dominant alpha males and subordinate immigrants in female philopatric ring-tailed lemurs (*Lemur catta*). Instead, male vocalization rates correlated with increased predation risk and temporal vocalization rates of other group

members, subsequently interpreted as attempts to confuse predators. This is consistent with Gould's previous study of *L. catta* at the same site in which no difference in vigilance behavior was found between sexes, nor was any relationship found between vigilance behavior and male ranking (reviewed in Gould et al. 1997).

Instead, in other female philopatric primate species, females exhibit higher rates of anti-predator behavior than males. For example, Verreaux's sifaka (*Propithecus verreauxi*) females emit alarm vocalizations in response to predators at a higher rate than males (Lewis 2005). In ring-tailed lemurs (*Lemur catta*), alpha females are the most vigilant member of the group, which is consistent with female dominance over typically immigrant males (Gould et al. 1997). Siberian jay (*Perisoreus infaustus* – Griesser and Ekman 2004) alpha females produce alarm calls at a significantly higher rate when in proximity to offspring compared to immigrant males. This behavior not only confers a nepotistic benefit but also suggests that the presence of immigrants is more costly to alpha females than alpha males, possibly because of increased competition.

Intrasexual differences also influence nepotistic alarm calling. In three female philopatric species (vervet monkeys; capuchin monkeys, *Cebus apella nigritus*; ground squirrels, *Spermophilus* spp.), females with more offspring issue alarm calls in response to predator encounters at greater rates than those with fewer offspring (reviewed in Wheeler 2008). This pattern has been attributed to variation in parental care, as females with more offspring stand to gain greater evolutionary benefit with increased offspring survival.

Conclusion

Where antipredator behavior is nepotistic, it can be considered a behavioral mechanism of kin selection and will select for a sex-biased strategy of dispersal. For example, nepotistic antipredator behavior only benefits the recipient as long as they remain in the natal group or until the actor and the recipient disperse together (parallel dispersal – Lawson Handley and Perrin 2007). Such a benefit

would be expected to delay dispersal for recipients of both sexes; however, in species with strong matrilineal hierarchies (e.g., vervet monkeys; baboons, *Papio* spp.; macaques, *Macaca* spp. – reviewed in Silk 2002), this will lead to female philopatry. For example, even where both male and female parents exhibit nepotistic behavior, only female offspring remain in the natal group. Numerous other selection pressures will drive male dispersal in addition to any altruistic trade-offs – for example, low social integration is the primary cause of male dispersal in blue monkeys (*C. mitis*). Similarly, in other taxa, certain costs will apply that lead to sex differences within parental nepotism.

While antipredator behavior is often both observable and empirically testable, nepotistic behavior is not restricted to protection from predation. Among others, selective infant care by parents (e.g., vervet monkeys) and nepotistic coalition formation to invade mixed-sex groups (e.g., gray langurs, *Presbytis entellus*) have all been identified as altruistic mechanisms of kin selection (Moore 1992). Advances in substantiating primate recognition highlight the role of reciprocal altruism outside of kin. Future behavioral research complemented by work at the genetic level will provide confirmation of the forces driving cooperative behavior and the evolution of female philopatry (Silk 2002).

Cross-References

- Alarm Calling Predicted by Inclusive Fitness
- Females Remain with Natal Group

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Alarm Calling

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Synonyms

Alert calling; Antipredator calling; Distress calling; Mobbing calling

Definition

Vocal behavior emitted in response to a threatening situation

Introduction

The term alarm calling is used to refer to an acoustically diverse group of animal vocalizations, emitted in response to some threatening event, usually a predator. Alarm calling is widespread among social animals, although most data are from primates, rodents, and birds.

Evolutionary Function

This behaviour is puzzling from an evolutionary perspective. The term is used to refer to an acoustically diverse group of animal vocalizations, emitted in response to some threatening event, usually a predator. Alarm calling is widespread among social animals, although most data are from primates, rodents, and birds. Why should an individual vocalize in the presence of a predator and hereby reveal its location and attract attention? How can such seemingly maladaptive behavior evolve?

Different non-exclusive hypotheses have been proposed to explain the evolution of this seemingly paradoxical behavior (Stephan and Zuberbühler 2016). They differ both in terms of the presumed beneficiary (selfish vs. altruistic alarm calling) and in terms of the targeted recipient (predator vs. conspecifics).

Selfish Alarm Calling

One group of hypotheses presumes that alarm calling is directly beneficial to the caller, either because it impacts on the predator or because it induces behavior in other prey that is beneficial to the caller. First, alarm calls can signal detection to a predator, the **perception advertisement hypothesis**. This strategy is particularly effective with predators that hunt by surprise and abandon hunting after detection. The hypothesis can also explain alarm calling by lone individuals and nonsocial species. Related to this is the **pursuit-deterrence hypothesis**, put forward to explain stotting behavior in ungulates, a visual alarm signal that showcases a prey's superior locomotor capacities and the futility of pursuit.

However, selfish alarm calling is not always aimed at the predator. Under the **prey manipulation hypothesis**, alarm calling functions to trigger escape behavior in other prey, which creates general pandemonium that distracts the predator and, as a consequence, increases the caller's own survival changes. Under the **cooperative defense hypothesis**, alarm calling is also aimed at other prey, but to trigger predator approaching and chasing ("mobbing"), which increases the likelihood of the caller's own survival.

Altruistic Alarm Calling

A second group of hypotheses presumes that alarm calling evolved to benefit the caller indirectly by favoring genetic relatives and other valuable group members. Under the **kin selection hypothesis**, alarm calling provides genetic advantages to a caller, which is the case if the caller is surrounded by own offspring or other closely related individuals. Following Hamilton's rule, alarm calling can evolve even if it is costly to the signaller, provided it sufficiently benefits genetic relatives. In some species, there is evidence that callers maximize their indirect fitness benefits by taking the audience into account, for instance, by alarm calling more in the presence of young and vulnerable offspring than other audiences (e.g., yellow-bellied marmots, Blumstein 2007).

Finally, costly alarm calling may also evolve if it favors a caller's reproductive success by preserving mating opportunities, the **sexual selection hypothesis**. This argument has been made for adult males in polygynous species. For example, in Diana monkeys males produce acoustically highly conspicuous alarm call that carry over long distances, much beyond what is predicted for communication to the predator or other group members, suggesting that male alarm calls operate in male-male competition and female choice. However, this is most likely a secondary evolutionary process, by which already existing alarm calls are subject to the forces of sexual selection to take on an additional function in reproduction.

Information Content

Call Production

What kind of information is encoded in animal alarm calls? Communication involves at least two partners, a signaller and a recipient, which may experience different processes. First, the **acoustic structure** of alarm calls is determined by the shape of the signaller's vocal tract, which provides recipients with reliable information about the caller's body size, age, sex, and identity (Bowling et al. 2017). In addition, psychologically relevant events often have physiological effects, such as changes in heart rate, skin temperature, or hormone levels, which create further variation in a signaller's vocal tract shape and, consequently, the acoustic quality of alarm calls, Morton's motivational-structural rules (Morton 1977). Since this process is determined by a caller's prior experience with an event, call production is also under cognitive control.

Call Comprehension

Recipients, on the other hand, may either be directly affected by the acoustic structure of alarm calls (Owren and Rendall 2001), or they have learned about the referential relations between alarm call types and events (Schlenker et al. 2016). One ongoing debate is about the nature of the mental representations, or memories, that mediate between alarm calls and events (Seyfarth et al. 2010). If an alarm call is only given to a narrow set of situations, listeners can directly infer the eliciting event, even in the absence of further cues, to the effect that the call obtains something akin to **lexical meaning**. However, most studies are unable to pin down more specifically what type of information is conveyed, such as the type, behavior, or distance of the predator, and many alarm calls are given to a range of situations that do not share clear similarities – at least from a human perspective (Dezecache and Berthet 2018). Here, listeners appear to rely on **pragmatics** to identify the event that has caused the call. A number of playback studies have tested this idea and produced

evidence that referentially broad alarm calls can obtain relatively specific meaning during a process by which listeners can associate the call to a range of possible events and then choose among the most probable one. Also, some species use social knowledge to react to others' alarm calls. For example, vervet monkeys react less strongly to alarm calls given by juveniles, possibly because they give alarm calls to wider range of disturbances than adult monkeys that only call in cases of real danger.

Call Sequences: Temporal and Morphological Structure

Alarm calls are often emitted in sequences, raising the possibility that information could be conveyed by resulting **structural** differences, such as due to variation in temporal structure. This is the case for titi monkeys that emit alarm calls more regularly in predator-related than non-predator-related sequences. In black-capped chickadees, call rate differences also exist, but here they have been linked to size differences of predators. Another relevant example is alarm call sequences in black-and-white colobus and guereza monkeys, which produce sequences of few roars when encountering leopards and many roars when encountering crowned eagles, a difference discriminated by listeners.

Second, alarm call sequences sometimes consist of different call types, which result in sequences that qualify as ordered **permutations** or unordered **combinations** (Zuberbühler *in press*). An example of call combinations is titi monkeys combining A and B alarm calls into sequences, whereby the proportion of B-call combinations reliably encodes predator type and location.

An example of a permutation is male Campbell's monkeys combining "krak" alarms (typically given to leopards) and "hok" alarms (typically given to eagles) with an acoustically invariable vocal unit ("oo") in cases of non-imminent danger. Recipients discriminate krak from krak-oo alarms, suggesting that -oo performs a semantic operation. The system thus resembles a common operation in human

language, **affixation**, whereby an utterance with lexical meaning is combined with a meaningless affix, to generate a derived meaning.

Another example of a permutation is male Campbell's monkey "boom" calls, produced prior to subsequent krak-oo, whenever the disturbance is non-predatory (e.g., falling tree). In playback experiments, Diana monkeys discriminated alarm sequences with and without preceding booms, suggesting that the booms altered the meaning of the sequence.

Permutations have also been found in putty-nosed monkeys. Here, males produce series of pyows to terrestrial disturbances and series of hacks to crowned eagles. In addition, males sometimes add brief combinations of several pyows, followed by several hacks. The pyow-hack transition appears to carry its own meaning, unrelated to the meaning of the constituent parts, by announcing forthcoming group movement. The pyow-hack transition hence resembles an **idiomatic** expression, i.e., the meaning of the call combination cannot be derived from the meaning of its parts, similar to English expressions such as "raining cats and dogs," i.e., raining heavily.

Compositionality

An important discussion is whether any animal call sequence qualifies as truly **compositional** (Townsend et al. 2018). Compositionality is a defining feature of human language whereby the meaning of an expression is determined by the meaning of its parts and the rule that combines them. Some of the best current examples of animal compositionality come from studies on bird alarm calls. For instance, Japanese tits possess "alert" calls that warn conspecifics about the presence of predators and "recruitment" calls that attract conspecifics in non-dangerous situations, for example, to food. When mobbing a predator, however, tits combine the two calls to "alert-recruitment" sequences, which engage nearby conspecifics into cooperative antipredator behavior. Interestingly, reversed sequences do not elicit mobbing behavior, suggesting that the system is both permutational and compositional (Zuberbühler *in press*).

Ontogeny and Learning

Comprehension

How do animals acquire their alarm calls? Most ontogenetic studies of alarm calls have focused on recipients, i.e., how animals learn to comprehend the meaning of alarm calls. In many species, infants appear to be born with partly innate knowledge of alarm calls. For example, newborn ground squirrels react to conspecific alarm calls by freezing or increasing vigilance. Similarly, cross-fostered dunnocks cease to beg for food when hearing conspecific, but not foster parent alarm calls. Nevertheless, their response is weaker compared to normally raised chicks, suggesting that learning plays a moderating role (Hollen and Radford 2009). In many species, however, alarm call comprehension is subject to social learning. Social learning is highly adaptive, especially in acquiring antipredator behavior, as it protects infants from committing fatal errors. For example, infant meerkats that have stayed close to adults are more likely to respond appropriately to alarm calls than other infants.

Production

Research on the ontogeny of alarm call production is more limited. Generally, learning appears to have only minor effects on the acoustic structure of alarm calls. For example, in species such as yellow-bellied marmots, great gerbils, and meerkats, juvenile and adult alarm calls are nearly identical. Partly, this may be because the acoustic structure of animal alarm calls itself has been under strong selection pressure. For example, bird raptor alarms are often difficult to localize (presumably to prevent detection), whereas monkey leopard alarms are highly conspicuous (presumably to promote dissuasion). A notable exception is the **fork-tailed drongo** that, in addition to its own species-specific alarm calls, is able to mimic other species' alarm calls, although this ability functions in deceptive foraging.

Usage

Call use, finally, appears to be more plastic, but again relatively little work has been carried out. As a basic principle, infants must learn to recognize the dangerous species, which can happen through a process of either elimination or addition. For example, young vervet monkeys begin by giving alarm calls to a broad range of stimuli, including non-predatory species (e.g., flying pigeons), albeit in a nonrandom manner: eagle alarms are produced to flying animals, leopard alarms to terrestrial species, and snake alarms to snake-like objects. This has also been demonstrated in monkeys experimentally exposed to unfamiliar threat. For example, green monkeys exposed to a drone will produce alarm calls that resemble vervet monkey eagle alarms. The inverse process has been described in infant chimpanzees that do not appear to have any pre-existing knowledge of alarm call use but learn by observing others interacting with unfamiliar threats.

Conclusion

Alarm calling is of importance to various scientific disciplines, including evolutionary theory, behavioral ecology, animal cognition, comparative linguistics, and philosophy of mind. They are relatively uncomplicated to work with and easily recognizable, due to their context specificity and unique acoustic structure. They have been essential in addressing a range of basic questions, such as the evolution of altruism, the behavioral ecology of predator-prey relations, and the evolution of animal cognition. Detailed behavioral analyses, based on naturalistic observations and experiments across a wide range of species, have produced much progress and provided a window into the animal mind and some of the basic forces that drive evolution.

Cross-References

- [Alarm Call Creates Confusion](#)
- [Alarm Callers Are Females with Greatest Genetic Representation](#)

- Alarm Calling and Kinship
- Alarm Calling Predicted by Inclusive Fitness
- Alarm Calling upon Predator Detection
- Alarm Calls
- Predator Confusion Hypothesis

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Alarm Calling and Kinship

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Synonyms

Alert call; Altruistic behavior; Kin selection; Warning call

Definition

Vocal behavior of prey animals to defend themselves and others from predation.

Introduction

Alarm calling is a widespread phenomenon in the animal kingdom, usually produced by individuals during predation attempts, a context with large fitness consequences, suggesting that the behavior has been under strong selection pressure. But there is something paradoxical about animal alarm calls. Why should an individual, faced with a potentially lethal predator, behave in conspicuous ways to warn others, rather than trying to escape or hide from the danger? This seemingly altruistic behavior has posed a major challenge for evolutionary theory and become the topic of countless studies. Two major research themes have been addressed with studies on animal alarm calls: the cognitive processes involved in call production and perception and the evolutionary forces that have shaped the behavior. The following sections review some of the current research trends in both areas.

The Cognition of Animal Alarm Calls

In many species, alarm calls seem to “stand for” something in the external world, which has raised questions about potential parallels to human language and the idea that alarm calls are useful to investigate cognitive processes underlying vocal communication. However, this line of research has remained controversial, mainly because of difficulties in describing the nature of the internal processes triggered by external events. Discussions often revolve around how “cognitive” these internal processes and psychological states are, for example, whether predatory events merely trigger specific emotions (e.g., fear) to which alarm calls are hardwired. Empirical support for this position comes from studies showing that animals sometimes give alarm calls to non-predatory situations, such as putty-nosed monkeys (*Cercopithecus nictitans*) and other primates producing “eagle” alarms to falling trees or baboon fights, as well as “terrestrial predator” alarms to a wide range of disturbing events, which include encounters with non-predators.

Also relevant is that, in many species, alarm calls show only limited acoustic flexibility. In birds, alarm call structure is often highly conserved across species, especially to aerial predators (Marler 1955). One hypothesis is that these aerial alarms have evolved to conceal the location of the signaler by limiting sound propagation and directional cues (for review, also see Marler 2004). For example, the “seet” alarms of many bird species appear to be a hardwired response to the limited auditory range of raptors, which limits the amount of information a signaler can encode in this call type.

Some other studies, however, have found more flexibility in alarm calling behavior with sometimes tight relationships between external events and corresponding signals, including event-specific differences in acoustic structure, call rates, or sequential organization of calls. For example, in several species it has been shown that not only predator type but also predator size, predator distance, and predator behavior can trigger distinct alarm call behavior, suggesting that some animals can represent external events in

complex ways and have means to communicate them to their nearby audiences. Here, a particularly interesting line of research has been to look at sequences of alarm calls. Although many primate and non-primate species have restricted vocal repertoires with rigid call structures, some species appear to have overcome this limitation by producing call sequences of different composition that are sometimes linked to specific external events. Differences in perceived urgency can also lead to different call combinations, with information about external events sometimes additionally included.

A second controversy concerning the internal states associated with animal alarm calling revolves around the question of whether animals give alarm calls with the intention to inform others. Human language appears to be built on this principle, insofar as speakers convey mental content that is directed at particular partners and largely for their benefit, after relevant judgments that can be rather complex (Sperber 1986). The alternative extreme position to this view is that callers do not understand what they communicate, but that selection has equipped them to produce specific signals in specific situations, with callers remaining oblivious to the social consequences of their behavior.

One way to address this second controversy is to study the impact of the audience on an individual’s alarm calling behavior. Although not fully clarified, results so far suggest that, in chimpanzees (*Pan troglodytes*), alarm vocalizations are not mere automatically triggered utterances but indeed represent a means to communicate the nature of a danger to others. However, there is also important negative evidence, such as female vervet monkeys (*Cercopithecus aethiops*) failing to use alarm calls to change the knowledge state of their offspring in dangerous situations. For the time being, the underpinning cognitive processes of animal alarm calling, especially its intentional nature, remain nebulous for many species, with no clear phylogenetic trends.

A third research theme centers on considerations about the other end of a communicative interaction, the cognition involved in processing alarm calls. One basic question here is whether

receivers react directly to the physical features of calls (e.g., Rendall et al. 2009) or whether this is mediated by a mental representation of the call-eliciting event, i.e., whether calls carry specific information for the recipient (Seyfarth et al. 2010). Although more research needs to be done, there is some evidence that predator alarm calls in primates elicit responses due to their referential links to external events, not because of their physical features. In primates, predator alarm calls can trigger specific anticipations in recipients, suggesting that they do more than just spreading a motivation within a group, but possibly activate a relatively specific mental representation of the predator normally associated with the alarm call.

If receivers are able to extract and encode information when hearing a call, then another question is whether they infer the same information that the signaler originally responded to and whether they take the identity of the caller into account. Here, more progress has been made, largely due to the relative ease with which receivers can be tested with field experiments. An emerging pattern is that animals typically take the identity of the caller into account, as well as the pragmatic circumstances of a call-eliciting event.

In sum, current evidence is in line with the more general hypothesis that signalers and receivers are driven by different internal states and that there is a cognitive disparity between them. Thus, unlike in human language, producing and comprehending alarm calls might be linked to different cognitive underpinnings that probably followed different evolutionary pathways but are, nonetheless, often taking place in the same individual. However, more research is needed here to address this problem more directly.

The Evolution of Animal Alarm Calling

The second major research topic with animal alarm calls concerns the question of why it is adaptive for an individual to produce conspicuous vocalizations that reveal its presence and location to a dangerous predator and, as a result, increase

predation risk. The prediction here is that alarm calling must have some beneficial effects for the caller that outweigh the obvious costs incurred; otherwise, selection would have acted against it.

Three levels of selection have been identified to explain the evolution of alarm calling, i.e., alarm calling to enhance the caller's own survival (individual selection), the survival of its relatives (kin selection), or its reproductive success (sexual selection). If a caller can accrue benefits due to one or several of these forces, then the costs of alarm calling might be outweighed, and selection will favor the behavior, according to "Hamilton's rule" (Hamilton 1963). It is important to consider that the three levels of selection are by no means mutually exclusive but represent three possible ways by which an individual can maximize its genetic contribution to future generations, as follows.

Individual Selection: Alarm Calling to Enhance Signaler Survival

Although alarm calls generally reveal a caller's location, they can have a number of secondary beneficial effects, namely, by impacting on the behavior of other animals, in ways that increase the probability to survive for the signaler. Two main mechanisms have been identified, a direct one by influencing the predator's hunting behavior ("perception advertisement" or "pursuit deterrent" hypotheses; Frankenberg 1981) and an indirect one by influencing other prey's anti-predator behavior ("prey manipulation" hypotheses; Charnov and Krebs 1975).

Perception Advertisement

Some predators rely on stealth and experience, and experience significantly reduced hunting success if prey animals are aware of their presence. Signaling perception to a predator can therefore be adaptive if the predator is likely to abandon a hunting attempt and move on to target other individuals. If alarm calls have a predator-deterrent function, then the prediction is that a predator's hunting behavior must change in response to alarm calls. In one study, forest leopards, "*Panthera pardus*" were radio-tracked, and the resulting ranging data revealed that forest

leopards hunted by approaching monkey groups to hide in nearby vegetation, apparently to wait for unaware individuals to descend. Data also showed that leopards abandoned their hiding positions soon after detection by alarm calling monkeys, often additionally accompanied by approaching the predator directly.

However, most animals are hunted by a range of predator species that differ considerably in their hunting strategies, to the effect that alarm calls only work as a perception advertisement signals for some but not other predators.

The perception advertisement hypothesis therefore presupposes some relevant cognitive capacities on behalf of the prey, insofar as callers not only have to discriminate predator classes but also need knowledge about their respective hunting strategies, in order to adjust their alarm calling behavior accordingly. African forest monkeys, for example, readily produce loud alarm calls to two of their predators, leopards and crowned eagles, but remain silent to two other major predators, chimpanzees and humans, and there is evidence that the different antipredator strategies are learned. In a study on Diana monkeys, "*Cercopithecus diana*" in Taï National Park, Ivory Coast, it was shown that groups in the center of a chimpanzee territory behaved differently to the simulated presence of chimpanzees compared to groups living at the periphery of a territory (Zuberbühler 2000). Chimpanzees spend the majority of time in the core area of their territories and only occasionally venture into the peripheral parts. As a result, monkey groups in the center of a chimpanzee territory will have more experience with chimpanzee behavior than monkey groups living in the periphery. Chimpanzees also face predation pressure by leopards and, when encountering a leopard, respond with specific calls ("SOS" screams). In one experiment, chimpanzee SOS screams to leopards were broadcasted to different groups of Diana monkeys. As predicted, groups in the center of chimp territories responded more often with their own leopard alarms than groups in the periphery, who mostly responded cryptically with no signs that they could discriminate the chimpanzee SOS screams from screams given during fights with other group members.

The most likely interpretation is that peripheral Diana monkeys had fewer opportunities to observe chimpanzees responding to leopards compared to central groups and were thus mostly prevented from learning the meaning of the different chimpanzee calls.

Many animals are hunted by aerial predators and have evolved acoustically distinct alarm calls to defend themselves. For example, crowned eagles (*Stephanoaetus coronatus*) are specialized primate predators. Although they can sometimes be deterred by alarm calling monkeys, often in combination with physical attacks by adult males (KZ and CS, unpublished data), they remain extremely dangerous for monkeys, with attacks sometimes happening several times per day. Crowned eagles typically hunt by sitting and waiting in the upper forest canopy for an approaching group of monkeys. Their attacks are sudden and at short range by launching upon an individual from their perch. If unsuccessful they can engage in prolonged hunting efforts on a group of monkeys, sometimes by hunting in pairs, suggesting that callers must gain benefits other than perception advertisement when alarm calling to aerial predators.

In sum, although alarm calls can have dissuasive effects on some predators or in some situations, perception advertisement and predator deterrence cannot fully account for the evolution of animal alarm calls.

Prey "Manipulation"

A caller's probability to survive a predation attempt can also increase if alarm calls trigger behavior in other prey animals that benefits the caller or that leads to more efficient antipredator responses. For example, if alarm calls trigger flight in others, a predator may find it more difficult to focus on the caller, who can benefit from "safety in numbers" (Bednekoff and Lima 1998) or "confusion" effects (Milinski and Heller 1978). While safety in numbers simply decreases the probability of being caught due to stochastic processes (a dilution effect), the confusion effect relates to increased capture time for a predator (and thus an increased probability to escape for prey), possibly due to a sensory overload of

chaotic movements during flights. If alarm calls trigger such movements, the caller will benefit not only from dilution but also from confusion effects.

However, alarm calls may also induce collective antipredator behavior, such as predator mobbing. This can occur if calling attracts others for a communal antipredator response, in line with the etymological origin of alarm as “all’arme” (= to arms). Alarm call-induced cooperative defense can be observed in many species (Curio 1978), but it can also occur in hetero-specific associations, for instance, between males of different guenon species living in polyspecific groups. Predators are often repelled by mobbing groups of prey animals, most likely because they are prevented from carrying out their preferred hunting strategy.

A third direct benefit of alarm calling arises if callers can provide essential learning opportunities for less experienced individuals during predator encounters, which will increase the number of reliable sentinels for future predatory events, a mechanism that has been proposed for meerkats. In one classic experiment, Curio et al. (1978) conditioned naïve blackbirds to alarm call to a harmless object by social cues alone. The main manipulation consisted of presenting a demonstrator bird with a raptor model (to elicit alarm calls) in the presence of a second naïve bird. The observer bird did not see the call-eliciting raptor but was allowed to see a novel, but harmless, model during the conspecific’s alarm response. When retested, observers responded with alarm calling to the harmless object, suggesting that blackbirds learn antipredator behavior from conspecifics by observational learning, without a need for direct predator experience.

To conclude, individuals can gain direct fitness benefits from producing alarm calls to predators in two major ways, either by directly interfering with the predator or by causing a change in the audience, which lowers the predator’s hunting success, and effects may occur simultaneously during natural hunting events.

Alarm Calling to Favor Kin

Another main explanation for the evolution of alarm calls is to interpret them as a form of

extended parental care, i.e., reproductive individuals alarm call to prevent predation on their offspring (Blumstein et al. 1997). A more general version of the same idea is that alarm calling is adaptive if this benefits other individuals with whom the caller shares a substantial proportion of its genome (Smith 1965). The kin selection hypothesis of alarm calls makes several testable predictions. Most importantly, the alarm calling behavior of an individual should be a function of the costliness of alarm calling, the benefits for listeners, and the (cumulative) relatedness between the caller and the nearby listeners, according to Hamilton’s rule. Moreover, solitary individuals should not vocalize (unless calls carry over long distances and benefit distant relatives).

Empirical support for these assumptions is surprisingly inconsistent. Female Siberian jays (*Perisoreus infaustus*) utter more alarm calls when with their own offspring compared to other conspecifics, but males give alarm calls regardless of their relatedness to other group members (Griesser and Ekman 2004). Alarm calls as form of parental care is sometimes also seen in males. For example, in blue monkeys (*Cercopithecus mitis*), the single males produced higher rates of alarm calls if their group members (including own offspring) were closer to a simulated danger than further away, regardless of the male’s own distance to the predator (Papworth et al. 2008). However, the effect was only observed for eagle not leopard-related dangers.

Evidence for an effect of non-descendant kin is generally rare. Exceptions are female Gunnison’s prairie dogs (*Cynomys gunnisoni*), calling more to terrestrial predators in the presence of non-descendent kin than other individuals, and similar effects have been reported for Belding’s ground squirrels (*Spermophilus beldingi*; Sherman 1985) in which anti-predation behavior toward terrestrial predators increased with the presence of non-descent kin, but no such effects were found to aerial predators. In contrast, Columbian ground squirrels (*Spermophilus columbianus*) showed increased anti-predation behavior in the presence of non-descent kin toward aerial predators and no effect of kinship toward terrestrial predators (Macwhirter 1992).

Inconsistent patterns for the impact of kinship on alarm calling were also found in vervet monkeys. While captive females alarm called more in the presence of kin, it was also found that higher-ranking females called more than lower-ranking females, with no correlation between rank and the presence of kin (Cheney and Seyfarth 1985).

Finally, male Thomas langurs (*Presbytis thomasi*) and yellow mongooses (*Cynictis penicillata*) do not alarm call when alone (Wich and Sterck 2003; Le Roux et al. 2008), but solitary Campbell's monkey, "*Cercopithecus campbelli*" males living in a polyspecific association with Diana monkeys have been observed to alarm call to predators (KZ, unpublished data).

However, kin selection may have favored other aspects of animal alarm calling, notably the evolution of individually distinct acoustic cues. In Belding's ground squirrels, alarm calls not only encode identity, but the acoustic similarity between alarms is a function of genetic similarity (McCowan and Hooper 2002). Acoustic cues of kinship may provide receivers with important information to decide whether a caller should be helped during a predation attempt.

In conclusion, genetic relatedness appears to have influenced the evolution of alarm calling, but the link between the kinship and alarm calling is often unclear, most likely due to additional factors having impacted on the evolution of alarm calling (see previous section).

Alarm Call Evolution in Relation to Sex

A third way for an individual to increase its inclusive fitness during costly alarm calling is if the behavior enhances future access to mating partners and opportunities to sire offspring. Several studies suggest that alarm calling may function in this way, but along different pathways. First, alarm calling may function in intersexual selection, such as mates (usually males) advertising their quality to choosy partners. Second, alarm calling may function in intra-sexual selection as a way to compete for access to sexual partners. Interestingly, in forest guenons, it is mainly the single adult males that engage in conspicuous alarm calling, which can be heard far beyond the group boundaries, suggesting an additional

function in male–male competition. If males differ in their ability to engage in predation defense, then females may choose group males accordingly, while their alarm calling behavior might serve as a cue for their genetic quality or physical condition. In primates, indirect evidence comes from gray-cheeked mangabeys (*Lophocebus albigena*) in which the highest-ranking males engage most actively in predator-mobbing behavior (Arlet and Isbell 2009), suggesting a link between antipredator behavior and reproductive success.

In various mammal taxa, vocal structures, such as call duration, fundamental frequency, or formant frequencies, are linked to body size and competitive strength, suggesting that female receivers should attend to these cues. For instance, female red deer hinds and female koalas attend to acoustic cues of vocalizations to infer and compare the males' physical characteristics and momentary condition (Reby et al. 2010; Charlton et al. 2012). Other evidence comes from birds (e.g., Beecher and Brenowitz 2005) and anurans (e.g., Ryan and Rand 1990). Here, differences in the variability of notes, call rate, call intensity, or call duration in calling males appear to form the basis for female mate choice.

Whether or not sexual selection has been equally at work in alarm call evolution, however, is less clear. Many species produce alarm calls in sexually dimorphic ways, both at the level of call structure and call use. For instance, male vervet monkeys and male domestic chicken are more likely to alarm call in the presence of (unrelated) adult females than other individuals, which is predicted neither by kin nor individual selection. In red jungle fowls (*Gallus gallus*), male alarm call rates and mating frequencies are correlated, although this may be the result of differences in previous mating success rather than a way to increase a male's attractiveness.

Some other relevant evidence in support of sexual selection comes from Diana monkeys, in which both sexes emit predator-specific alarms to leopards and eagles. Recent evidence has shown that males alarm call, not just to provide predator information to nearby group members and the presence to distant rivals but also to advertise to

their own females their willingness to defend the group. When confronted with contradicting predatory information (e.g., perceiving a leopard followed by own females' eagle alarm calls), males prioritize the information provided by the females and respond with eagle alarm calls, contrary to their own experience (Stephan and Zuberbühler 2016). In contrast, if females are presented with contradicting information, they ignore the male's alarm calls and only respond to the predator they have witnessed themselves. Another effect was that, as soon as a male produced alarm calls that referentially matched the females', the females stopped giving their own alarm calls. One interpretation of these findings is that, by referentially matching his alarm calls to the females', the male signaled his readiness to engage with the predator identified by the females. In this view, the females used the male's compliant behavior as kind of a "stopping rule" for own risky antipredator behavior. In sum, the study demonstrates an advanced coordination between the two sexes during predatory events, which goes beyond advertising mere physical condition and includes others' assessments of external events and signaling readiness to engage with them. One likely evolutionary scenario is that males have been under sexual selection pressure to act this way. What remains to be tested is whether this type of coordinated alarm call behavior in males indeed leads to more surviving offspring. One prediction is that compliant males are more preferred as group males, have longer tenure, and sire more offspring than males that produce alarm calls in response to their own assessment.

Overall, differences in alarm calling between females and males are a widespread and well-known phenomenon, and vocal signals have been shown to provide direct means to access mating partner quality. The Diana monkey study mentioned before suggests another way by which sexual selection could have acted on male callers, beyond providing cues linked to physical condition, in that males use alarm calls to advertise their antipredator commitment. But how exactly females choose males based on variation in their antipredator commitments is subject to further investigation. One possibility is that their tenure

as single group males is constantly at stake and that males who show decreased commitment over time will eventually be expelled and replaced by another male. Generally, polygynous systems are supposed to be especially susceptible to be targeted by sexual selection, and a sexual dimorphism in call structure and usage might give first hints on functional differences between male and female calls.

Conclusion

There is solid evidence that selection has acted in different ways on the evolution of alarm calls, contributing in various ways to the increase of an individual's inclusive fitness. What is more difficult to show is how exactly costly alarm calling enhances a caller's own survival, the survival of its kin, and its future reproducing success in different animal species. In all likelihood, selection has shaped alarm calling behavior in different ways and in a cumulative manner (Zuberbühler 2002). Predator deterrence benefits may have originally triggered the evolution of alarm calling behavior, but kin and sexual selection may have contributed additionally, in parallel with a species' social evolution. Also important is that, even within species, selection may have acted differently on different age/sex classes causing differences in alarm calling behavior, as illustrated by, e.g., sex-specific patterns of alarm calling in Diana monkeys.

In sum, studies on alarm calling behavior need to take into account how a species' ecology and social organization constrain individuals in how they can maximize their inclusive fitness. Predation is one of the most important evolutionary forces and continues to exert selection pressure on animal behavior. Across species, future studies should consider the relative potential contribution of individual, kin, and sexual selection on the evolution of alarm calling behavior.

Finally, alarm calling has long been thought as cognitively simple, the result of basic stimulus (predatory event)–response (alarm call) arithmetic. But new evidence across a range of species shows that behavioral decisions during

predation can be cognitively complex, with signalers taking contextual information into account and producing alarm calling flexibly to maximize their benefits. In primates, receivers can infer complex information from calls by integrating pragmatic cues and social variables, suggesting that alarm calling reflects a species' cognitive capacities as well as any other type of social behavior.

Cross-References

- ▶ Alarm Call Creates Confusion
- ▶ Alarm Callers Are Females with Greatest Genetic Representation
- ▶ Alarm Calling
- ▶ Alarm Calling Predicted By Inclusive Fitness
- ▶ Alarm Calling Upon Predator Detection
- ▶ Alarm Calls
- ▶ Hamilton's Rule
- ▶ Hamilton's Rule and Kin Investment
- ▶ Hamilton's Rule and Genetic Relatedness
- ▶ Hamilton's Rule and Theoretical Implications

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understood for decades. Calling individuals suffer direct costs (e.g., predation), and so the ultimate function was initially described as a residual behavior thought to have evolved as a signal from parents to offspring (Maynard-Smith 1965). Subsequent theories described the behavior as individually selective. Trivers (1971) suggested that alarm calls reduce the caller's vulnerability, while calls may also reveal the predator's location (Dawkins 1976) or else promote antipredatory behavior in socially living primates. Finally, Hamilton (1971) hypothesized that announcing a predator's presence may promote aggregation by potential prey and reduce the likelihood that any one individual is killed (reviewed in Cheney and Seyfarth 1981).

Alarm Calling Predicted by Inclusive Fitness

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Synonyms

Altruistic nepotism; Antipredatory behavior; Kin selection; Vocalization

Definition

Alarm calling: vocalizations that alert other animals to immediate danger (Sherman 1977).

Inclusive fitness: a theory to explain cases when an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own (Hamilton 1963, p. 354).

Introduction

Alarm calling is an inherently dangerous behavior, and its adaptive function was poorly

Alarm Calling and Kinship

Across taxa, alarm call production is correlated with the probability that kin are within acoustic range (Sherman 1977); alarm callers derive inclusive fitness benefits by warning kin of danger (Bergstrom and Lachmann 2001). In female-philopatric species (where males disperse), adult females produce more calls than adult males, suggesting proximity to relatives drives alarm calling. But that may not be the most parsimonious explanation.

Subsequent investigation into Sherman's (1977) data on Belding's ground squirrels (*Urocitellus beldingi*) found that females with offspring produce more calls than males do, suggesting that rather than inclusive fitness, it was direct fitness benefits that drive the behavior.

Blumstein and colleagues (1997) later supported the idea of direct benefits as well, demonstrating that in yellow-bellied marmots (*Marmota flaviventris*), a primary predictor of female alarm calling was whether her pups had emerged from underground dens that year. The two hypotheses are not mutually exclusive. That is, as Cheney and Seyfarth (1981) noted, for a female to protect her offspring, she must also stay alive, and so alarm calling may target a broad audience to ensure the survival of multiple individuals. They found support for both

hypotheses in vervet monkeys (*Chlorocebus pygerythrus*), whereby adult females' alarm called more than adult males, but there was no relationship between calling and number of offspring or the proximity to offspring as might be expected.

A few studies have attempted to test the various hypotheses of alarm calling in primates, with similar findings. Forest guenon alarm call behavior in Tai Forest, Ivory Coast, for example, varies with predator-type (leopard vs. chimpanzee) and is thought to be evolved to deter (especially cryptic) predators that depend on surprise attacks. When the above hypotheses were tested against each other in the same species, new world tufted capuchins (*Cebus apella nigrinus*) showed similar patterns. Like the guenons, the capuchins exhibited predator-specific responses as well. Thus, there is growing evidence that alarm calling to felid predators has evolved as a self-preservation behavior, while calling to predators that can be more readily mobbed (e.g., snakes) may be better explained as a kin-selected behavior.

Conclusion

Shelley and Blumstein (2005) conducted a phylogenetic analysis to investigate whether alarm calling had evolved initially as a selfish or else nepotistic (promoting inclusive fitness) behavior. Their results supported the idea that it initially evolved to communicate to predators, not to nearby kin, and thus while benefits to relatives likely contributed to the persistence of the trait in a population, it was less important than the benefits incurred by the callers themselves. In summary, results from investigations into the function of alarm calling in social animals converge on indirect benefit to group members, often kin, but also on direct benefit to the caller and their offspring.

Cross-References

- Alarm Callers Are Females with Greatest Genetic Representation
- Females Remain with Natal Group

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Alarm Calling upon Predator Detection

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Synonyms

Alarm calls warn relatives; Anti-predator vocalization; Co-efficient of genetic relatedness (r); Predator attraction; Predator deterrence hypothesis; Proximate behavior; Shared genetic material; Squirrel family *Sciuridae*; Ultimate behavior

Definition

When a predator is seen, animals from various taxa produce alarm vocalizations. In some cases,

alarm calling when a predator is nearby drives the predator away, but in other cases, the caller is pursued by the predator. Calling therefore often leads to greater risk to the vocalizer. Some rodents make anti-predator vocalizations despite this greater threat to themselves because doing so may warn their close relatives of a nearby predator. By warning relatives, they are preserving additional copies of their own genes.

Introduction

Animal species ranging from birds to mammals are well known to produce alarm calls in response to perceived threats, ranging from unknown and potentially harmful stimuli to known predators. Alarm calls vary in urgency, and some low-arousal calls are produced in response to potential dangers (e.g., an unfamiliar object or animal flying overhead), while others are produced in response to more direct dangers (e.g., a predatory bird swooping from the sky to catch prey species, then perching on a nearby branch) (Bradbury and Vehrencamp 1998). When a prey species produces an alarm call, it can be part of a mobbing response, which involves multiple conspecifics banding together to intimidate a predator and drive it away. Alarm calls can also be produced as part of an escape response, where callers vocalize while fleeing from predators (Zuberbühler et al. 1997). For both types of alarm calling situation, various hypotheses have been proposed to explain why vocalizing is an adaptive response for prey species and for individual callers within groups of prey species. Calling may drive the predator away, leading to direct benefits to the alarm caller. However, calling may also lead to the alarm caller being targeted by the predator, meaning that other explanations are useful for understanding why this behavior would persist over evolutionary time in prey species (Maynard 1965).

Alarm Caller Targeted by Predator

Animals ranging from birds to mammals make alarm calls when a predator is seen. Such alarm

calls are thought to put the vocalizer at risk by attracting the attention of predators. According to theoretical predictions (Hamilton 1964; Dawkins 1976), predators are alerted to a prey individual's presence and location by their alarm calls, which are often loud and recurrent. In the case of group-living prey animals, predators would more likely pursue a noisy individual over a silent one (Maynard 1965). Animals who vocalize in response to a threat are therefore more likely to be pursued by that predator, according to theoretical biologists (Hamilton 1964; Maynard 1965; Dawkins 1976). Although results are mixed (e.g., Cresswell 1994; Zuberbühler et al. 1997), evidence from several mammal and bird species supports the idea of callers being targeted by predators. For example, in the American pika (*Ochotona princeps*), predatory weasels were seen actively pursuing alarm callers immediately following their vocalizations (Ivins and Smith 1983). In Belding's ground squirrel (*Urocitellus beldingi*), predators including coyotes and weasels were seen chasing callers following their alarm vocalizations (Sherman 1977). For Gunnison's prairie dog (*Cynomys gunnisoni*), individuals did not alarm call if they were in very close proximity to a predator, suggesting increased risk from alarm calling (Hoogland 1996). For bell miner (*Manorina melanophrys*) bird nestlings, vocalizations of any kind increased risk of consumption by avian or rodent predators (McDonald et al. 2009). In each of these cases, vocalizing is thought to have put the prey individual at greater risk (Sherman 1977). Alarm calling is therefore not an adaptive behavior at proximate level for individuals of these species, meaning it does not enhance their personal survival. Evolutionary explanations are necessary to account for the development and persistence of anti-predator vocalizations in these animals.

Alarm calling is more obviously adaptive for species where vocalizing by an individual directly discourages predatory pursuit (Maynard 1965). Alarm calling in response to a predator's presence is advantageous if calling drives the predator away, thus decreasing the level of threat to and directly benefiting the individual who calls (Hamilton 1964). The pursuit deterrence

hypothesis (Sherman 1977) suggests that alarm calling is adaptive for the caller because it discourages predatory targeting and leads to increased survival for the caller. Vocalizations are therefore directed towards predators rather than nearby conspecifics (Wheeler 2008). Anti-predator vocalizations are the acoustic dimensions to multifaceted mobbing behaviors, which communicate to stealth predators that prey are aware of their presence (Sherman 1977; Bradbury and Vehrencamp 1998). Evidence that acoustic signaling deters an ambush predator from approaching or pursuing prey has been found in a number of taxa, ranging from birds to mammals such as ungulates and primates. For the Eurasian skylark (*Alauda arvensis*), individuals who sang when chased by predatory falcons were less likely to be caught than animals who remained silent (Cresswell 1994). For the klipspringer antelope (*Oreotragus oreotragus*), alarm calling was thought to signal predator awareness and to discourage pursuit (Tilson and Norton 1981). For primate species including Campbell's guenon (*Cercopithecus campbelli*), the sooty mangabey (*Cercocebus atys*), the Diana monkey (*Cercopithecus diana*), the lesser white-nosed monkey (*Cercopithecus petaurista*), the western black and white colobus (*Colobus polykomos*), and the western red colobus monkey (*Colobus badius*), stealth predators such as leopards stopped pursuing monkey groups that made alarm calls at high rates (Zuberbühler et al. 1997). In each of these cases, animals made alarm vocalizations in response to perceived threat, and these calls reduced their own risk of predation by driving predators away at increased rates.

Anti-predator vocalizations are highly variable in their utility to individuals (Bradbury and Vehrencamp 1998). For some species, alarm calls encourage predator pursuit and increase vulnerability to predation (e.g., Ivins and Smith 1983), while for other species, alarm calls drive predators away (e.g., Cresswell 1994). Anti-predator vocalizations are adaptive at proximate level if they directly discourage a predator from pursuing an individual but are not advantageous to the individual if calling encourages predatory pursuit (Maynard 1965; Sherman 1977). Other

hypotheses for the evolution of alarm calling should therefore be considered. If alarm calling does not lead to increased survival for the caller, evolutionary explanations involving inclusive fitness, altruism, group selection, and genetic representation in the animal's social group should also be investigated.

Alarm Callers and Genetic Representation

Prey animals from a broad range of taxa produce alarm calls in response to threats. While in some cases alarm calling has been found to discourage pursuit by stealth predators (e.g., Zuberbühler et al. 1997), for other species, alarm calling puts the individual who calls at greater risk of pursuit (Maynard 1965; Dawkins 1976; Sherman 1977). For prey species where the latter applies, theoretical models predict that alarm calling would be adaptive for individuals if calling improved the chances of survival for their relatives (Hamilton 1964; Dawkins 1976). How related an alarm caller is to a relative can be determined by the co-efficient of genetic relatedness (r), which quantifies the level of genetic relationship between any two individuals of the same species (Wright 1922; Hamilton 1964). The co-efficient reflects the probability that at any given genetic locus, genes passed down will be identical due to shared ancestry between individuals. Clones or identical twins would have a relatedness co-efficient of $r = 1$, while unrelated individuals would have a co-efficient close to $r = 0$. Clones or identical twins would therefore share 100 % of the genes found at specific loci due to inheritance from common ancestors, while unrelated individuals would share no genes found at specific loci due to shared inheritance. Amongst non-clone relatives, individuals are most closely related to their offspring, full siblings, and parents (all $r = 0.5$) and less closely related to grandparents, aunts/uncles, cousins, and half-siblings ($r = 0.25$ or less) (Wright 1922).

According to theoretical predictions by Hamilton (1964) and Maynard Smith (1965), individuals are more likely to alarm call, thus putting

themselves at greater risk of predation, in situations where doing so benefits their close relatives (i.e., offspring, siblings, and parents) by warning them of a nearby threat. Therefore, individuals would make alarm calls in dangerous situations and put themselves at increased risk because their signaling would lead to increased survival for kin, thus saving copies of the caller's own genes from predation (Dawkins 1976; Sherman 1977). Evidence supporting this idea has been found for numerous rodent species from the squirrel family (*Sciuridae*). For example, female Belding's ground squirrels (*Urocitellus beldingi*) who had relatives in their group made alarm calls at higher rates than other group members (Sherman 1977, 1981). Similarly, individual Richardson's ground squirrels (*Urocitellus richardsonii*) were most likely to alarm call when they had offspring or siblings nearby (Davis 1984). For the Eastern chipmunk (*Tamias striatus*), adult females called at higher rates when close to relatives, who were likely to live in neighboring burrows (da Silva et al. 2002). In the Alpine marmot (*Marmota marmota*), adult males who were related to most group members alarm called at higher rates than other individuals (Barash 1976). In the black-tailed prairie dog (*Cynomys ludovicianus*), individuals alarm called at higher rates when offspring, siblings, or parents lived nearby (Hoogland 1995), while in the Gunnison's prairie dog (*Cynomys gunnisoni*) females with nearby kin or offspring made anti-predator calls at the highest rates (Hoogland 1996). Despite these many examples of rodents from the squirrel family, strong evidence for the increased genetic relatedness of vocalizers to nearby conspecifics is lacking for species in other taxa, although other social mammals, such as the tufted capuchin (*Cebus apella*), have been tested (Wheeler 2008). There is clearly wide variation in how anti-predator alarm calls are functional and adaptive for each animal species. Consideration of the life history of many *Sciuridae* rodents, where close kin such as parents, offspring, and siblings (all $r = 0.5$) typically live or are located in close proximity to alarm callers, may help explain why genetic representation significantly affects alarm calling behavior in many species of this taxonomic group. For other

animal species, theoretical explanations other than genetic relatedness should be considered in addressing how alarm calling behavior is adaptive.

Conclusions

Although anti-predator vocalizations are used by prey animals across taxonomic groups, there is wide variation in how these vocalizations are employed. Alarm calls attract predator attention and put the vocalizer at increased risk in species including ground squirrels and birds but drive the predator away in prey species including antelope and monkeys (Sherman 1977; Tilson and Norton 1981; Zuberbühler et al. 1997; McDonald et al. 2009). Different explanations exist addressing why alarm calls are adaptive for each animal species. Alarm calls may function in predator deterrence or may lead to an alarm caller being targeted by a predator (Wheeler 2008). In situations where alarm calling brings additional risk, individuals may call if close kin such as offspring, siblings, or parents are nearby. By warning relatives, alarm callers from the squirrel family are thought to promote the survival of their genes as represented in their kin (Sherman 1977, 1981). However, for other animal taxa, other adaptive explanations should be considered for the persistence of risky alarm calls.

Cross-References

- ▶ [Alarm Call Creates Confusion](#)
- ▶ [Alarm Callers Are Females with Greatest Genetic Representation](#)
- ▶ [Alarm Calling](#)
- ▶ [Alarm Calling and Kinship](#)
- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)
- ▶ [Alarm Calls](#)
- ▶ [Deceptive Alarm Calls](#)
- ▶ [Evolutionary Arms Race](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Prey Availability](#)

- [Prey Choice](#)
- [R = Coefficient of Relatedness](#)
- [Vigilance, Sentinels, and Alarms](#)

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Alarm Calls

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Synonyms

[Alerting calls](#)

Definition

Communication is ubiquitous in animals and involves one individual influencing the behavior of another individual through the use of signals or cues (see the ► [“Communication, Cues, and Signals”](#) entry for more information). Animals often communicate when they detect a potential predator by producing alarm signals. Although such signals can be produced via different modalities, many species rely on vocal signals – alarm calls (Bradbury and Vehrencamp 2011). Alarm calls function to alert others of the potential danger related to a perceived predator. In order for such communication to be adaptive, the benefits associated with alarm calling in the presence of a predator must be greater than the costs.

Introduction

Both the physical structures of alarm calls and the motivations behind their production are important to understanding signal function (Bradbury and Vehrencamp 2011). In birds and mammals, and possibly other groups, vocal signals that are

low-frequency and harsh are often produced by individuals behaving aggressively. Low-frequency sounds are easier to locate; animals often use calls with this structure to mob or indicate distress. Signals that are higher in frequency and that possess relatively little frequency modulation are often produced by fearful signalers. These signals are more difficult to localize and likely function as alarm calls meant primarily for receivers of the same species as the signaler. Receivers often freeze or flee when high-frequency alarm calls are produced.

When considering the adaptive functions of alarm calls, the costs and benefits of producing an alarm signal must be determined. For alarm calling to be adaptive, the benefits of signaling must outweigh the costs over time. There are several hypotheses to explain the adaptive benefits of alarm signaling (Caro 2005; Wheeler 2008). Under the *kin selection hypothesis*, an alarm signaler will risk making an alarm call and attracting the attention of the predator because the signal may increase the sender's indirect fitness by alerting and potentially saving related family members. Similarly, the *parental care hypothesis* proposes that the signaler will risk alarm calling because the signal may increase their direct fitness by alerting their own offspring. Under the *selfish herd hypothesis*, a sender produces an alarm call to attract other individuals, thus increasing the number of individuals present and thereby reducing the probability of predation for the signaler. Similarly, the *mobbing recruitment hypothesis* predicts that a signaler risks making an alarm call because it will attract others to the area to harass the predator and increase the chances that the predator leaves. The *predator confusion hypothesis* states that the signaler risks making an alarm call because it may cause a sudden burst of movement from others as they flee, which confuses the predator and reduces the threat. Lastly, with the *pursuit deterrence hypothesis*, a signaler risks sending an alarm call because the call may cause the predator to give up the hunt after it has been spotted by its prey. These hypotheses are not mutually exclusive; for example, when testing the adaptive function of alarm

calling in wild capuchins, *Cebus apella nigrinus*, Wheeler (2008) found that in the presence of a predatory viper, the kin selection, parental care, and mobbing recruitment hypotheses were all supported. Capuchins, therefore, alarm call to recruit others to mob the predator but also to communicate to their offspring and related family members. The functions of alarm calls may thus differ depending on the composition of the group and the predator threat level.

Semantic Alarm Calling

Some individuals can encode specific information in their alarm calls about the type of predator, the predator threat level, or both (Gill and Bierema 2013). Semantic, or referential, alarm calls are signals that refer to specific predator types or predator behavior patterns (Seyfarth et al. 1980). In a seminal experiment, Seyfarth et al. (1980) used a playback method to test different alarm calls produced by vervet monkeys, *Cercopithecus aethiops*, in response to three different predators: leopards, eagles, and snakes. These varying alarm calls were considered referential because they were each produced by signalers in specific contexts (i.e., each was produced in relation to the specific predator detected), and the behavior of the receivers differed depending on the type of predator that elicited the alarm calls. For example, when vervet monkeys heard playbacks of leopard alarm calls, the monkeys more often ran high up into a tree, which is the adaptive behavioral response to this type of predator. Vervets produced different behavioral responses to playbacks of the eagle and snake alarm calls, revealing specificity in receiver response.

Other species may encode information into their alarm calls that indicates the threat level of the potential predator, rather than the predator type. For example, Siberian jays (*Perisoreus infaustus*) produce alarm calls when predatory hawks are detected, but the specific structure of the calls is related to whether the predator is perched (lower-risk) or attacking (high-risk; Griesser 2008). Chickadee, tit, and

titmouse species also vary the number of specific note types in their “chick-a-dee” calls in relation to the level of risk associated with different sizes of predators they have detected.

Deceptive Alarm Calling

Whereas it is typically adaptive for signalers to produce alarm calls when a predator has been detected, and for receivers to react to alarm calls appropriately, some individuals use alarm calls in non-predator contexts in deceptive ways. These false alarm calls are seen in several species. For example, great tits, *Parus major*, alarm call to deceive competitors of the same species as the signaler for food, even when there is no predator threat (Møller 1988). These deceptive calls cause surrounding individuals to be temporarily distracted and/or flee, thus allowing the deceptive signaler better access to limited food resources.

Deceptive alarm calling can occur between members of different species. For example, the fork-tailed drongo, *Dicrurus adsimilis*, is able to mimic the alarm calls of meerkats, *Suricata suricatta*, and can deceive meerkats by producing the meerkats’ own species-specific alarm call (Flower 2010). Meerkats eavesdrop on the alarm calls of drongos and thus benefit from their species-specific alarm calls. Meerkats that react to a drongo’s mimicked meerkat alarm incur the cost of abandoning found food. However, because drongos also regularly produce honest alarm calls, the meerkats benefit from using a “better safe than sorry” strategy when drongos alarm call (Flower 2010). A general view of deceptive alarm calling is that such calling persists in many systems because the costs of responding to false alarm calls (when a predator is not present) in a food context are much smaller than the costs of failing to respond appropriately to true alarm calls (when a predator is present).

Conclusion

Alarm calls are one class of vocal signaling related to anti-predator behavior (Caro 2005). Other

classes of signal used in anti-predator contexts include predator deterrence, mobbing, and distress signals. Predator deterrence signals function minimally to communicate to the predator that it has been detected, and may also provide information regarding the signaler’s condition or evasion ability. Mobbing calls function to attract members of the same and different species as the signaler to gather, harass, and deter the predator to drive it from the area. Individuals may also produce distress calls when they are physically captured or constrained by a predator, potentially to cause the predator to release the distressed individual.

Alarm calls represent an important class of animal signals in that they are strongly related to individual fitness and also because many of them seem to involve complicated cognitive processing on the part of signalers or receivers or both. For example, alarm calls falsely produced in contexts of contested resources (like food or mates) often represent cases of tactical deception and suggest signaler awareness of perceptions or knowledge of receivers. In some species, signalers vary production of alarm calls in sophisticated ways to communicate about not just predator presence but also predator behavior. Additionally, some of the most structurally complex signals in animal communication function in anti-predator behavior. One example is the already mentioned “chick-a-dee” call of black-capped chickadees and related species. Another example involves the syntax-like combination of different vocalizations in putty-nosed monkeys (*Cercopithecus nictitans*) to signal increased predator threat (Arnold and Zuberbühler 2004).

Taken together, alarm calls are an important type of vocal communication that signal about potential predator threats. While these vocalizations may draw the attention of a predator, species that utilize alarm calls do so in an adaptive way, with benefits generally outweighing the costs of signaling. There are several hypothesized functions of alarm calls, including to alert others, to recruit others, and to confuse or deter the predator. Further research can highlight the adaptive value of more nuanced aspects of alarm signaling, such

as distinctive alarm calls made by parents for their offspring compared to other adults in the immediate environment (e.g., Suzuki 2011).

Cross-References

- [Communication, Cues, and Signals](#)
- [Costly Signaling](#)
- [Deceptive Alarm Calls](#)
- [Manipulation and Dishonest Signals](#)
- [Predator Confusion Hypothesis](#)
- [Signal Reliability](#)
- [Vocal Communication](#)

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Alarm Calls Warn Relatives

- [Alarm Calling upon Predator Detection](#)

Alcohol

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Synonyms

[Ethanol](#)

Definition

Alcohol is a by-product of fermentation of sugar.

Introduction

When alcohol is discussed in the context of health, often it refers to consumable forms of alcohols. In this regard, ethanol is often taken up for discussion or debate. Less often methanol is also discussed in the context of health due to its toxic effects. Worldwide, ethanol is used as alcoholic beverages in social gatherings (World Health Organization 2018). When alcohol is used in harmful pattern, it results in significant health hazards. Harmful use of alcohol increases the vulnerability for many noncommunicable as well as infectious diseases. Alcohol has negative impact on maternal and child health. Alcohol attributes to many psychiatric disorders and accidents. Hence, it stands as an obstacle before the Sustainable Development Goals (World Health Organization 2018). This entry aims at giving a brief over view of alcohol with special emphasis on health and sociocultural aspects of ethanol.

Chemistry of Alcohol

Alcohol is a hydrocarbon formed by the process of hydroxylation. The first alcohol in the alcohol series is methanol (methyl alcohol), which contains single carbon atom and is denoted by the chemical formula “CH₃OH” (Henze and Blair

1931). Ethanol or ethyl alcohol (C_2H_5OH) is next in the series. Different names have been denoted to alcohols (propanol, butanol, pentanol, etc.) with different numbers of carbon atoms. Alcohol is a volatile, inflammable, and colorless liquid. It is a good organic solvent.

As per their structure, alcohol has been classified into primary, secondary, and tertiary alcohol (Henze and Blair 1931). There are various names used for different concentrations and mixtures of ethyl alcohol. Absolute alcohol is a concentrated form of alcohol that contains less than 1% of water and more than 99% of ethyl alcohol. A concentrated form of alcohol is prepared by the process of repeated fractional distillation, which is commonly known as “rectified spirit.” “Denatured spirit” is referred to the ethyl alcohol that is made undrinkable by adding methyl alcohol. Methanol is used in the preparation of wood paints. It is also used as fuel. There are many uses of ethanol, other than its use as alcoholic beverages; however, from the point of view of medicine, alcohol is used for preparation various medications and disinfectants. It is also used in the treatment of methanol poisoning.

Among different alcohols, ethanol is the form of alcohol that is consumable. Ethanol is commonly prepared by the process of fermentation of sugar (fructose or starch). The raw materials for production of alcohol are fruits, rice, wheat, rye, barley, and potato. The concentration of alcohol is regulated by certain chemical processes (distillation). Certain alcoholic preparations (e.g., beer) contain lower concentration of alcohol, whereas certain other preparations (e.g., rum, whisky) contain higher concentrations of alcohol.

Alcohol: Developmental Significance

From the developmental point, certain arguments were put forward by the researchers. The convincing ones are – alcohol as a component of diet (as source of calories) or alcohol as a substitute to water (Vallee 1994). Evidences support that alcohol use might be a maladaptive ancestral

strategy to meet the nutritional needs (Dudley 2000). However, certain vulnerability factors and the chemical and clinical properties of alcohol resulted in development of alcoholism as a pathological entity (Dudley 2000).

Across the life span, the onset of alcohol commonly occurs during the second to third decade of life. This period mostly refers to the phase of adolescence. Common psychological characteristic features of adolescence are novelty seeking, risk taking, and experimenting. These behaviors have attribution to initiation of alcohol use (Ellis et al. 2012). Exposure to alcohol during different developmental stages produces different anatomical and physiological changes in the brain (Klintsova et al. 2013).

History of Alcohol Use in the World

Alcoholic beverages are used worldwide. The pattern of use of alcohol across the globe depends upon several factors like availability, accessibility, affordability, and sociocultural-moral values. Use of alcohol in world history can be traced back to the ancient times irrespective of the country and culture. History of alcohol use is depicted in ancient mythological stories. The most ancient literature of the world, the *Vedas*, gives vivid description of use of alcohol and its impact on the individual vividly (Sharma et al. 2010). Description of alcohol is also mentioned in ancient civilizations India, China, Egypt, Babylon, Africa, Europe, Aztecs, and North America. Ancient literature mentions about use of alcohols during festivals, celebrations, social gatherings, as well as certain cultural rituals. In the ancient times, there was increased alcohol use in certain castes and among people of higher status. Similarly it was prohibited among certain cultures and caste (Keller 1979; Sharma et al. 2010; Unnithan 1985). In the recent times, modernization, globalization, and migration resulted in acculturation and deculturation. Also, there is easy access to alcohol. All these factors attribute to prevalence of alcohol use among socioeconomic strata and sociocultural groups.

Alcohol: Pharmacokinetics and Pharmacodynamics

Alcohol is commonly absorbed from the stomach and proximal part of small intestine. Absorption of alcohol is better in empty stomach, and peak concentration of alcohol in blood is often reached approximately after an hour of alcohol consumption. Various factors determine the rate of absorption and time taken to reach peak blood concentration. Alcohol is commonly metabolized in the liver, and a fraction of it is also metabolized in the lungs and kidney. The enzymes that metabolize alcohol are alcohol dehydrogenase and aldehyde dehydrogenase. The effect of alcohol in the central nervous system is exerted through GABA_A, serotonin, as well as cholinergic receptors (Sadock and Ruiz 2015). Alcohol in human body can be quantified by analyzing blood, breath, and urine. Estimating the blood alcohol concentration is of clinical as well as forensic significance (Jones 1996).

Alcohol: Effects on Physical Health

The alcohol use contributes to significant health hazards worldwide. Alcohol has been identified as an important cause of morbidity and mortality (Griswold et al. 2018). As per the global burden of diseases report, 3.8% of females and 12.2% of males of 15–49 years of age die due to alcohol-related health problems (Griswold et al. 2018). Evidences support the association of alcohol with more than 60 different medical disorders (Room et al. 2005). Alcohol affects all the organs of the body. Alcohol consumption in pathological pattern results in hepatic (fatty liver, alcoholic hepatitis, cirrhosis of liver, hepatic failure), pancreatic (pancreatitis), and renal damage (renal failure, hepatorenal syndrome). Alcohol has toxic effects on erythropoiesis (anemia, pancytopenia) and body immune system. Alcohol is a gastric irritant, which produces damage to gastric mucosa resulting in gastritis, nausea, vomiting, as well as acid peptic disease. Alcohol users are more likely to develop esophageal varices, portal hypertension, ascites, cerebellar degeneration,

myopathy, neuropathy, metabolic disturbances (hypoglycemia, electrolyte imbalance), testicular atrophy leading to sexual dysfunction, gynecomastia, as well as menstrual irregularities (in females using alcohol) (Association 2013; Sadock and Ruiz 2015). Alcohol can increase the risk of malignancies (hepatocellular, pancreatic, as well as gastrointestinal).

Alcohol can adversely affect the development of brain, when exposed in early life and produces neurodegeneration (Dalal and Kar 2014). Long-term exposure to alcohol results in neuroinflammation, activation of microglial system, and oxidative damage of neuronal cells (Dalal and Kar 2014). Alcohol is a central nervous system depressant. It acts through the GABAergic neurotransmitter system. During intoxication with alcohol, various neurocognitive side effects (slurring of speech, motor incoordination, ataxia, stupor, coma) are reported, which are often related to the blood alcohol concentration. Alcohol has significant cardiovascular effects. Alcohol can cause hypertension, cardiomyopathy, and cardiac failure. Alcohol produces nutritional deficiencies.

Alcohol is having fetotoxic effect. Mothers using alcohol during pregnancy expose the fetus to alcohol. Chronic fetal alcohol exposure results in fetal alcohol syndrome, which is characterized by intellectual disability, facial dysmorphism, retardation of growth, and behavioral abnormalities (Denny et al. 2017).

Ingestion of methyl alcohol (methanol) is having severe harmful effects. Methanol poisoning results in metabolic acidosis and impairment of cellular homeostasis (Kraut and Kurtz 2008). Methanol poisoning produces neurological damage and renal failure as well.

Alcohol: Effects on Mental Health

Chronic and unrestrained use of alcohol often results in development of alcohol use disorder. The term “alcohol use disorder” incorporates harmful use, abuse, and dependent pattern of alcohol use. Alcohol use disorder often results in physical as well as social dysfunction, other than psychological impairments (emotional, cognitive,

and behavioral). Genetic factors do play some role in development of alcohol use disorders (Tawa et al. 2016). Male gender, certain personality-related vulnerabilities, pre-existing psychiatric illness, family history of alcohol use disorder, and stress are common risk factors for development of alcohol use disorder (Gowin et al. 2017). The *Diagnostic and Statistical Manual*, fifth edition (DSM 5), mentions alcohol-related disorders as an umbrella term to incorporate alcohol use disorder, alcohol intoxication, withdrawal syndrome of alcohol, other alcohol-induced disorders, and unspecified alcohol-related disorder (Association 2013). Individuals using alcohol for a long time develop craving (an intense urge to consume alcohol), tolerance (over time increasing the amount of alcohol consumption to get same amount of pleasure), preoccupation with the thoughts of alcohol, significant interference in the familial and socio-occupational activities, and withdrawal symptoms (disturbed sleep, tremor, palpitation, anxiety, sweating) (Association 2013). Sometimes the individuals with chronic and heavy alcohol use develop more severe and life-threatening withdrawal symptoms like seizure and delirium (delirium tremens). The withdrawal symptoms often develop between 12 and 72 h of reduction in amount or stoppage of alcohol consumption.

Individuals, who are dependent on alcohol, often continue taking alcohol despite physical, socioeconomic, as well as legal complications. During alcohol intoxicated state, there occurs disinhibited behavior, slurring of speech, unsteadiness of gait, mood swings, and increased reaction time. The clinical manifestations depend upon the blood alcohol concentration and chronicity of alcohol use. At higher blood alcohol concentration, the individual may go to coma, and death may happen. Many individuals often consume large quantity of alcohol in a single occasion, which is often known as binge drinking. Alcohol use disorder often follows a relapsing remitting course. Presence of psychiatric comorbidities like schizophrenia, bipolar affective disorder, depression, attention deficit hyperactivity disorder, and antisocial personality disorder increases the risk of alcohol use disorder (Association 2013; Sadock and Ruiz 2015). Alcohol use increases the risk of dementia. Chronic use of alcohol causes

personality changes. Alcohol increases the risk of suicide. Alcohol use is associated with development of amnestic syndrome (Wernicke-Korsakoff syndrome). Chronic alcohol use may result in development of auditory hallucinations (alcoholic hallucinosis) and morbid jealousy (paranoid delusions).

Conclusion

Alcohol (ethanol) has enormous impact on health. Wide use of alcohol across the globe resulted in significant burden of care, disability, and socio-occupational impairment. Despite country-specific legislations to regulate its marketing, transportation, and use, it still stands as a major obstacle in attaining the Sustainable Developmental Goals.

Cross-References

- Alcohol-Related Violence
- Ethanol
- Frugivory By-Product Hypothesis

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Alcohol and Balance

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Synonyms

Effects of alcohol on balance

Definition

Alcohol intoxication has deleterious effects on balance. It is referred to as an ototoxic drug.

Introduction

Alcohol intoxication has negative effects on one's balance in many ways. The vestibular system is greatly affected even if ingested in small amounts. It is concluded that alcohol intoxication causes a series of multifaceted deterioration of body movement.

Effects of Alcohol on Balance

The effects of alcohol intoxication can be devastating to one's health in a number of ways. More specifically, ethanol intoxication causes impairment in postural sway (Woollacott 1983). Its effects are well investigated on other structures of the brain and body, i.e., the oculomotor system, but there have not been many reports on the acute effects of alcohol on the vestibular system (Nieschalk et al. 1999). Nieschalk et al. have demonstrated in their study that alcohol intoxication affects mainly the vestibulocerebellum, a finding that disputed previous findings of Diener et al. (1983) who supported the fact that intoxication by alcohol affects mainly the spinocerebellum. Nieschalk et al. is consistent with Ikeda et al.'s (1980) research who indicated that small doses of ethanol interfere more with the synaptic transmission in the lateral vestibular nucleus (LVN) monosynaptic and polysynaptic II neurons than synaptic transmission in the spinal trigeminal nucleus (STN) relay neurons and interneurons.

Modig et al. (2012b) have comprehensively investigated alcohol-related impairments on postural control at specific blood alcohol concentration (BAC). They have found that alcohol has deteriorating effects on postural control based on certain doses, time of alcohol ingestion, and the direction of movement. Specifically, the researchers have noted that between 0.06% and 0.10% BAC, any increase in alcohol

intoxication would result in a decrease in postural control. They further noted that ethanol consumption causes more destabilization in lateral motion than in anteroposterior motion and that intoxication decreases the adaptation mechanism, particularly for stability control in a lateral motion.

Further evidence on the relationship of alcohol and balance is supported by a research done by Tianwu et al. (1995) who concluded that a moderate quantity of alcohol affects both the oculomotor system as well as the vestibular system. They suggested that one of the reasons that postural instability takes places after alcohol consumption is reduced vestibular function. Consistent with this view, Bellé et al. (2007) suggested that alcohol interferes with hearing and balance, causing deleterious effects on the organisms referring alcohol as an ototoxic drug.

How Alcohol Affects Balance

When alcohol is digested in high amounts, the cupula in the semicircular canals becomes lighter than the endolymph, making it sensitive to gravity, a process referred to as the buoyancy hypothesis (Fetter et al. 1999). Consequently, this process lead to positional alcohol nystagmus (PAN) and rotatory vertigo. Fetter et al. (1999) concluded that alcohol intoxication causes a vertical velocity offset, which may represent a toxic effect on the central vestibular pathways, producing a tone imbalance of the vertical vestibulo-ocular reflex.

Furthermore, when under alcohol intoxication, there is an inability to use gravitational cues when there is an attempt to determine distance. Therefore, the person relies in visual information instead (Hafstrom et al. 2007). Hafstrom et al. further concluded that alcohol intoxication in high levels initiates a decompensation of small subclinical vestibular asymmetries and a dysfunction of the otolithic organs. In essence, alcohol intoxication causes a series of complex and multifaceted deterioration of body movement (Modig et al. 2012a).

Conclusion

The devastating and deleterious effects of alcohol intoxication on balance were briefly reviewed. When the vestibular system is affected, the person is lead to rely on other cues to determine distance—such as vision; a process that has potentially dangerous effects in one's health.

Cross-References

► Vestibular System

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Alcohol and Rape on College Campuses

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Definition

The association, on and about college campuses, between ethyl alcohol consumption and the use of force or threat of force to achieve penetration of an individual without their consent.

Introduction

Incidence of aggression, risky sexual behavior, and rape peaks during adolescence and young adulthood. On college campuses, rape has been occasioned by heightened alcohol use, including binge drinking. Consequently, alcohol abuse has been advanced as a possible cause of rape and also a possible instrument with which males are able to more successfully rape females. This brief entry presents an evolutionary perspective on the possible role of alcohol in rape on and about college campuses, attending to potential interactions between the psychoactive effects of alcohol and hypothesized rape and rape avoidance adaptations. Throughout, tentative language is used to describe the nature of the association between alcohol use and rape because no causal effect of the former on the latter has been established (Lovett and Horvath 2009).

Alcohol Consumption on College Campuses

Most college students (appx. 60%) report recent alcohol use, and they are more likely to report binge and heavy alcohol use than their noncollege peers (Center for Behavioral Health Statistics and

Quality [CBHSQ] 2015). It is well recognized that alcohol impairs activity in the prefrontal areas of the brain that support executive functions including planning, working memory, and inhibition (George and Koob 2010; George and Stoner 2000). This impairment engenders decreases in capacity for integration of information stored in memory, contextual cues, and future goals, resulting in greater discounting of the future and impulsiveness or more present-oriented and risk-prone behavioral responding. The effects of alcohol on behavior are not only due to its impairment of prefrontal activity but also to its direct influence on dopamine transmission and thereby incentive salience (i.e., experienced utility). Through its effects on brain function, alcohol decreases attention to potential future consequences and also amplifies the experienced value of cues to immediate reward in the local environment. Consonantly, alcohol consumption has been linked to risky sexual behavior, delinquency, accidents and injuries, and also legal consequences among college students.

Rape on College Campuses

Surveys of college students suggest that among the types of sexual assault, unwanted sexual contact and coercion are most common, followed by incapacitated rape (i.e., completed rape while the victim was intoxicated), and then forcible rape (Fedina et al. 2016). Estimates of the prevalence of sexual assault, including rape, vary widely. According to Fedina, Holmes, and Backes (2016), this is partly due to measurement and definitional differences. For incapacitated rape, prevalence estimates have ranged from 1.8 to 14.2% for females and been observed at 1.9% for males, while forcible rape estimates have ranged from 0.5 to 8.4% for females and from 0.6 to 0.7% for males (Fedina et al. 2016). Notably, these estimates rest largely on samples of White, heterosexual, female students in traditional colleges. The prevalence of sexual assault among minority females may be higher, and rape incidence is likely underestimated generally due to underreporting.

Evolution, Alcohol, and Rape

Rape has been observed across all human cultures, and males in many nonhuman species have evolved strategies to sexually coerce and rape females (McKibbin and Shackelford 2011). As in nonhuman species, human perpetrators of sexual assault are nearly always male, and victims are most often female (Testa and Livingston 2009). The data have not rejected either of the possible evolutionary explanations for human male rape of females: (a) rape reflects a specialized psychological adaptation in males or (b) rape is a spandrel (i.e., a characteristic that is a by-product of the evolution of some other trait) reflecting adaptations that solve other, perhaps more general, problems (e.g., adaptations for acquiring resources that cannot be obtained except by force; McKibbin and Shackelford 2011).

Strikingly, at least half of all sexual assaults are occasioned by alcohol consumption (Testa and Livingston 2009). One possible explanation of the linkage between alcohol consumption and rape perpetration is that, through its modulation of brain activity, alcohol amplifies cues to the execution of adaptations contributing to rape via effects on the perceived biological value of potential victims, diminished ability to shift attention away from perceived sexual opportunities, reduced capacity for inhibiting sexual arousal, and reduced awareness of costs that could stem from rape. Indeed, male college students report that alcohol increases their sexual desire and disinhibition, risk taking, and aggression (Abbey et al. 2014; Cooper 2002). Alcohol also decreases control of penile reactions and has disinhibiting effects, among males, on responses to sexually aggressive depictions (George and Stoner 2000). The possibility that sexually aggressive males experience the effects of alcohol in unique ways has received little attention, though some evidence suggests convicted rapists may not display the typical alcohol-induced genital suppression effects shown by non-rapists (Wormith et al. 1988). Finally, it is important to note that studies have shown that alcohol beliefs or

expectancies interact with consumption to influence sexual experience. For instance, research indicates that alcohol amplifies *pre-drinking* intention to have sex and increases sexual arousal primarily among males who expect this effect (George and Stoner 2000).

Another possibility is that males identify females who are vulnerable or exploitable by attending to their alcohol consumption. Rape exacts a severe toll on females in terms of injury or death, circumvention of mate choice, disruption of parental care, and partner abandonment and has occurred throughout recorded history (Thornhill and Palmer 2000). Thus, some researchers have theorized that females may have evolved tactics to avoid rape and the associated harms. Stemming from this, research suggests that women execute a suite of rape avoidance behaviors (McKibbin and Shackelford 2011). These behaviors include avoiding strange men, avoiding appearing sexually receptive, avoiding being alone, and awareness of surrounding/defensive preparedness. From an evolutionary perspective, then, alcohol consumption might be seen as facilitating male rape of females through interference with female rape avoidance adaptations.

Consistent with the above, research suggests that alcohol increases vulnerability to sexual assault by making victims less likely to attend to cues to danger and less able to resist forcible rape (Lovett and Horvath 2009). Indeed, the victim was too intoxicated to resist in the majority of rapes of female college students (Testa and Livingston 2009), and drinking within risky contexts has been identified as *the* risk factor for sexual victimization (Testa and Livingston 2009). Alcohol may also make victims less able to remember the details of an assault, which could facilitate serial offending by making them less likely to report their victimization and by decreasing the likelihood that the offender is convicted. In general, then, alcohol consumption might make some females ideal targets for would-be male rapists.

Research indicates that in the majority of reported sexual assaults involving psychoactive substances, male perpetrators targeted females

self-intoxicated through alcohol consumption and exploited their alcohol-induced vulnerability (Lovett and Horvath 2009). Male perpetrators were often older than their victims, met them in the hours before the assault, and offended in bars and clubs, homes, or vehicles. In some contexts, they were also less likely to have also consumed alcohol themselves (e.g., when assaults occurred in vehicles). In contrast with rape and sexual assault generally, alcohol was more commonly involved when parties did not know each other well and in the context of bars and parties. Thus, males generally did not use alcohol as a “date rape” drug but rather selected victims they recently met on the basis of their alcohol consumption. Taken together, these findings suggest that alcohol consumption makes some females less (a) likely to avoid strange men, (b) avoidant of being alone, (c) aware of their surroundings, and (d) able to resist forcible rape. Alcohol consumption in females also appears to serve as a cue to sexual exploitability for male rapists. This targeting behavior on the part of perpetrators appears to be under-recognized and should be considered as a part of rape prevention efforts (Lovett and Horvath 2009).

Finally, it is important to attend to how perceptions of responsibility for rape are affected by alcohol involvement. People attribute more blame to victims and less to perpetrators when alcohol is involved (George and Stoner 2000; Lovett and Horvath 2009). Rapists may also attach less responsibility to perpetration when alcohol is involved, consistent with evidence that when listening to a date rape analogue, male college students took longer to stop a rapist from further advances when they consumed or expected alcohol (George and Stoner 2000). Similarly, sexually aggressive males who did not consume or expect alcohol themselves took longer to stop a date rape when the perpetrator and victim were depicted as drinking (Bernat et al. 1998). This pattern in attribution of responsibility suggests that alcohol may serve to minimize the blame and legal consequences rapists experience, and perhaps expect to experience, as a result of perpetration.

Conclusion

Rape on college campuses has been linked to alcohol consumption. This brief entry presented an evolutionary perspective on the possible role of alcohol in rape on and about college campuses, reviewing evidence suggesting that alcohol may contribute to rape through its effects on the brains of would-be male rapists, as well as by interfering with the functioning of rape avoidance adaptations employed by potential female victims.

Cross-References

- ▶ [Drugs and Rape on College Campuses](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Rape](#)
- ▶ [Rape Avoidance](#)
- ▶ [Rape and Dating](#)
- ▶ [Rape in Warfare](#)
- ▶ [Sexual Coercion and Rape](#)
- ▶ [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- ▶ [Victims of Violence](#)

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Alcohol Violence

► Alcohol-Related Violence

Alcohol-Related Violence

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Synonyms

Alcohol violence

Definition

Alcohol-related violence is defined as “violence associated with use of alcohol.”

Introduction

Alcohol use disorder is the most common form of substance use disorder worldwide (Degenhardt et al. 2018). In 2010, alcohol use disorder alone accounted for 9.6% of the disability-associated life years (DALYs) caused by mental and substance use disorders, worldwide (Whiteford et al. 2013), whereas in 2016, it became 4.2% (Degenhardt et al. 2018). Violence associated with alcohol use includes both intentional and unintentional injuries. Evidences support that the risk of both of these increases with alcohol use (Degenhardt et al. 2018). Evidences support that in nearly one third of firearm violence, the person who used firearm was found to be in a state of acute alcohol intoxication. Worldwide, nearly 50% of the violent crimes are associated with alcohol use (Gutwinski et al. 2018). One in every four perpetrators, who committed sexual crimes, was found to be under the influence of alcohol, as reported by the victims of the sexual crime (Gutwinski et al. 2018).

Alcohol also attributes to violent behavior directed toward self (suicidal behavior) by use of serious means like firearms (Branas et al. 2016). The aggressive and violent behavior associated with alcohol is highest among all substances (Miczek et al. 2004). Alcohol use increases the risk of domestic violence including intimate partner violence (Wilson et al. 2017). Many violent crimes are committed under the influence of alcohol (Murdoch and Ross 1990). The risk of violence after consumption of alcohol is five times the risk of violence in a sober state (Gutwinski et al. 2018). Alcohol disrupts social inhibition; hence individuals under influence of alcohol behave in a disinhibited manner, due to which alcohol is also commonly known as “liquid courage” (Gutwinski et al. 2018).

Attributes of Violence Associated with Alcohol Use

Violent behavior is often associated with alcohol use. Violence associated with alcohol use is attributable to several biological, psychological, as well

as sociocultural (environmental) factors. The biological factors explain how specific effects of alcohol on brain result in aggression, whereas the psychological factors explain the relevance of personality characteristics responsible for aggression associated with alcohol use. Sociocultural factors explain the importance of environmental influence on alcohol-related violence.

There are evidences of definite neurobiological association with alcohol-related violence. Alcohol-related violence is modulated through neurotransmitters like serotonin, glutamate, and gamma-aminobutyric acid (GABA) in the metabotropic and ionotropic receptors of dorsal raphe nucleus (Miczek et al. 2015). The aggressive behavior associated with alcohol use is aggravated through the complex interaction of neuropeptide Y, vasopressin, endogenous opioids, and corticotrophin-releasing factor with the above neurotransmitters (Miczek et al. 2015). Some evidences support that the gene coding for different subunits of GABA-A receptor predicts the occurrence of aggressive behavior after consumption of alcohol (Miczek et al. 2004). Alcohol produces neurodegeneration and structural alteration in the brain. These changes are more evident in the frontal cortex, limbic system, and hippocampus. The neurodegenerative process is more intense if alcohol had been consumed during the adolescence (Crews and Vetreno 2014). As limbic system is involved in regulation of emotions and prefrontal cortex is involved in cognitive appraisal of events/contexts, decision-making, and impulse control, their dysfunction due to alcohol may result in the aggressive and violent behavior (Crews and Vetreno 2014). Long-term repetitive use of alcohol and binge drinking causes alteration in the neurobiology and may contribute to violent behavior. During acute intoxication with alcohol, there occurs an impairment in the impulse control ability of the prefrontal cortex leading to impulsive and disruptive behavior (Potenza and de Wit 2010).

Heavy drinking often leads to violence. The individual under influence of alcohol often initiates the altercation, which leads to verbal argument, physical fights, and assault (Murdoch and Ross 1990). Alcohol-aggression expectancy also

predicts alcohol-related violence. Aggression expectancy after consumption of alcohol is more among males than females. In accordance with this, among the genders, alcohol-related violence is more common in males (Tedor et al. 2018).

Deficits in executive control and social learning also attribute to alcohol-related violence. People who display violent behavior, under influence of alcohol, often have history of learning such behavior through multiple similar social contexts (Gutwinski et al. 2018).

The social cognitive model explains the relevance of social cognition in alcohol-related violence. As per this model, alcohol use increases the expectation of aggressive behavior in the individual consuming alcohol. Alcohol activates various networks of alcohol-related memory (Gutwinski et al. 2018). The alcohol myopia hypothesis explains that alcohol narrows down the attention in perceptual field resulting in missing certain cues in different social contexts, which often lead to misinterpretation of events and information. This misinterpretation may result in conflict and violence (Gutwinski et al. 2018).

Alcohol-related violence also depends on the amount of alcohol consumed in a single setting. Those who are non-dependent users and are prone to heavy drinking are more likely to experience sedative effect acutely, whereas those with moderate level of drinking are likely to display disinhibited behavior and aggression (Gutwinski et al. 2018).

Evidence supports the persistence and increase in antisocial behavior with increased alcohol use in adolescence and early adulthood (Hammerton et al. 2017). People with antisocial personality often show violent behavior and have increased propensity for alcohol abuse. Hence, among persons with antisocial personality, alcohol-related violence is common.

Chronic and dependent users of alcohol are more likely to display aggressive behavior. Various mechanisms are responsible for the aggressive and violent behavior associated with acute and chronic use of alcohol. Alcohol impairs the executive control, which is responsible for increased amount of alcohol intake and violent behavior (Heinz et al. 2011).

Availability and accessibility to alcohol may increase the risk of alcohol consumption and alcohol-related violence (Speer et al. 1998). Peer pressure may also result in consumption of alcohol and bingeing, which may attribute to alcohol-related violence. Many other environmental factors like permissive environment, crowding, and availability of alcohol at an affordable price can be a determining factor of alcohol-related harm (Hughes et al. 2011). In night parties, many people often binge on alcohol. Usually, violence is expected, when people binge on alcohol (Pedersen et al. 2016). Alcohol induces violent behavior by means of developing personal affronts and jealousy as well as by sharpening the emotions. Binge drinkers often attribute alcohol to violent behavior, and they also expect conflict and violence to occur when they consume alcohol (Pedersen et al. 2016).

Prevention of Alcohol-Related Violence

Alcohol-related violence is preventable. Alcohol-related violence can be reduced or prevented by reducing the intake of alcohol, predicting the possibility of violence (by analyzing the context, mood state, and past experiences), responding cautiously to people who are under the influence of alcohol, and taking appropriate safety measures (by keeping vulnerable population like children and self away from the individual, who is in an intoxicated state) (Wilson et al. 2017).

For effective prevention of alcohol-related violence, the following factors need to be addressed (Pernanen 1998):

1. Personal or individual factors (personality, mood state, psychiatric illness)
2. Alcohol-related/specific factors (availability, accessibility, affordability, type of alcoholic preparation)
3. Contextual or situational factors (peer pressure, context of alcohol use, setting of alcohol use)
4. Cultural factors (permissiveness)

Systematic addressing of the above factors may facilitate effective prevention of alcohol-related violence.

Strategies that work on supply reduction by restricting the selling of alcohol are also found to be successful in effectively reducing alcohol-related violence (Duailibi et al. 2007). Some early evidences support that having a national policy on alcohol control and its effective implementation may be beneficial in preventing alcohol-related violence (Kearns et al. 2015). Many developing countries don't have a robust policy; and if at all it exists, either it is not fully followed or not properly monitored, which might be responsible for higher alcohol-related violence.

Conclusion

Violence associated with alcohol use is a biopsychosocial phenomenon. Alcohol-related violence ranges from intimate partner violence to heinous violent crimes. Alcohol-related violence is preventable to a larger extent. Understanding the predictors of alcohol-related violence and effectively treating individuals, who behave violently under the influence of alcohol, may be an effective prevention strategy of violence associated with alcohol use.

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- ## Alert Call
- Alarm Calling and Kinship
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- ## Alert Calling
- Alarm Calling
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- ## Alerting Calls
- Alarm Calls
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- ## Alfred Russel Wallace (1858)
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- ## Synonyms
- Charles Darwin; Darwinism; Evolution of psychological faculties; Human evolution; Natural selection; Sexual selection

Definition

Alfred Russel Wallace (January 8, 1823–November 7, 1913) was a British naturalist, geographer, and theoretician in biology. Mostly known as the co-author of the *Theory of Evolution by Natural Selection* along with Charles Darwin, Wallace was also the founder of biogeography.

Introduction

Human evolution, particularly the evolution of high psychological faculties, was a controversial topic on the rising of evolutionary theory in the mid-nineteenth century. A comprehensive reading of *The Origin of Species* (Darwin 1859) reveals the discomfort generated by the inclusion of human beings in the evolutionary process. Sooner or later, Darwin would be pressured to solve this matter. An important part of this pressure came from the coauthor of the theory of evolution by natural selection, Alfred Russel Wallace, who had his own arguments to solve the matter of how human beings are part of the evolutionary process.

This entry focuses on the development of Alfred Wallace as a naturalist, as well as the context in which he developed his version of the theory of evolution by natural selection. The debate between Darwin and Wallace about the role of human psychological faculties in the evolutionary process is introduced, and the contributions of Wallace as a naturalist, collector, theoretician in biology, and social thinker are presented.

The Birth of a Naturalist

The story of Alfred Russel Wallace is frequently shadowed by Charles Darwin's. Wallace's role in history has often been limited to the episode of the co-discovery of natural selection as the mechanism for the evolution of species, suggested as a non-relevant contribution to Darwin's theory, or used to call into question Darwin's originality and ethical behavior during the process of publication of the theory.

Although Wallace's contributions to science are mostly associated to the co-discovery of natural selection, his story is that of a passionate naturalist and collector, an independent theoretician, a scientist with wide interests, sometimes controversial, and a thinker concerned with contributing to social progress.

Alfred Russel Wallace was born on January 8, 1823, near Usk, England, in the context of a socially disadvantaged family, due to his father's unfortunate decisions and the characteristic difficulties of the Victorian era. These difficulties lead to frequent housing changes, between London and Hertford, that promoted in him a sense of uncertainty as well as a capacity to adapt to new contexts, which would be of great value during his life (Raby 2001).

Despite financial shortcomings, the Wallace family had a good appreciation for education, so great efforts were made to send the male children to school. At home, Alfred found a good library, where he learned to read and write at an early age and acquired a taste for books and intellectual joys.

Alfred's religious formation was conventional, associated with the "Church of England." According to Wallace himself, he only experienced a moment of intense religious interest during his childhood, but this interest ceased when he questioned the nature of God and evil, not finding a satisfactory answer (Wallace 1905). Despite his skepticism, Wallace would keep a certain predisposition to believe in supernatural phenomena, which was the source of some discredit between his scientific colleagues, later in his career.

After his 14th birthday, Wallace travelled to London, where he lived with his brother John, and later, he started to work with his brother William as an assistant topographer. During the long journeys at this job, and despite the hard work involved in land surveying, Alfred developed an interest in the collection of specimens and a great interest for taxonomy (Wallace 1905).

In 1843, year in which his father died, Alfred published an article titled "The South-Wales Farmer," an anthropological work and the first of many papers published in scientific and non-scientific sources. Shortly after, when he became

an adult, Alfred obtained a job as a teacher in a private school in Leicester; this post was an opportunity to read some books that made an influence in his future work as a naturalist: *The History of the Conquest of Mexico* and *A History of the Conquest of Peru* by William Prescott; *The History of America* by William Robertson; and *Personal Narrative of a Journey to the Equinoctial Regions of the New Continent* by Alexander von Humboldt; they all made an impression on him and motivated his interest to visit the tropics. He also read *An Essay on the Principle of Population* by Thomas Malthus (Raby 2001). Some of these books were also documented by Darwin as an important motivation and background on the development of his own way of thinking about nature (Darwin 1887).

Amazon Basin

In Leicester, Wallace met Henry Walter Bates, with whom he shared a short but meaningful time in the Amazon and who became a good friend for life. Both Wallace and Bates started an academic interchange, mainly focused on the problem of the origin of man, either as creation or as the result of an evolutionary process. In this intellectual context, Wallace read, again and again, some crucial books for the development of his own thought. Among them are *Vestiges of the Natural History of Creation* by Robert Chambers, *The Voyage of the Beagle* by Charles Darwin, *Principles of Geology* by Charles Lyell, the work of Jean-Baptiste Lamarck, and *A Voyage up the River Amazon* by William Edwards.

The readings, the relationship with Bates, and his love for species collection altogether convinced him to follow a professional career as a collector. Wallace and Bates planned a voyage to the northern Brazilian state of Pará. On April 26, 1848, they departed from Liverpool onboard the *Mischief*. A month later, they arrived in Salinas, on the Brazilian coast, and then, after two additional days along the river Tocantins, they arrived in Pará (Wallace 1905).

During the following months, they travelled along the rivers Tocantins and Amazon, and a

series of channels that connect them, while collecting animal and plant species and developing their skills as professional collectors. The next year, Herbert Wallace came to the Amazon to join his older brother, and they visited several towns along the Amazon river. Wallace and Bates distanced themselves, but periodically met each other in the region, planned expeditions together, and remained as mutually esteemed colleagues for the rest of their lives. Herbert came to the Amazon along with Richard Spruce, a naturalist specialized in Botany. Like Wallace, Spruce had a humble origin, an irreducible interest in nature, and a strong sense of will and resigned his career as a professor to dedicate himself to specimen collection (Von Hagen 1945).

During the journey along the Amazon, Wallace visited Monte Alegre, Santarem, Obydos, Vila Nova, and the mouth of the Negro river (Guainia). From there, Wallace decided to go to Barra (now Manaus). The following months were dedicated to excursions along the Negro river, looking for specimens, especially the umbrella bird, an exotic species that Wallace captured and sent to England. Nevertheless, being disappointed with the limited success achieved in the region, Wallace went up the river, leaving his brother in Barra, not knowing that this was the last time he was to see him. When he was ready to return to England, Herbert fell ill with yellow fever and died. Alfred only knew that his brother had died months after, which caused him great emotional pain.

During his stay in the Amazon region, Wallace turned from collector to observer. His first manuscript was a series of observations of the umbrella bird (Raby 2001, p. 300, note 46). His observations encouraged him to ask questions about the distribution of species, a crucial matter for his later scientific contributions. At the same time, the way of life of the inhabitants on those places fed his social and political ideas, which were aligned with a socialist, egalitarian ideal of human society (Raby 2001).

On July 12, 1852, Wallace sailed back to England aboard the *Helen* with a vast collection of insects and invertebrates; a living collection of animals, especially birds and mammals; and his

personal drawing collection. After 3 weeks, the *Helen* caught fire, and all Wallace's collection was lost. It was a tragedy for him, not only from a scientific viewpoint but from a financial one. After travelling 500 miles on boats, Wallace and the rest of the *Helen's* passengers were picked up and taken to England by the *Jordeson* (Wallace 1905). The return trip had taken 80 days; Wallace had returned to England, empty-handed.

The Malay Archipelago

During the next year, Alfred received invitations to scientific societies, collaborated with museums, and met other naturalists. Nevertheless, Wallace felt out of place. His relationships with other scientists did not go beyond occasional meetings, and the abovementioned activities led to little or no economic retribution (Browne 2002). Wallace started to think in another expedition, and after many considerations, he set off on a journey to Singapore in March 1854, starting an 8-year expedition in the Malay Archipelago, which was determinant for his career and later contributions to knowledge.

The exuberance of the archipelago was very similar to that of the Amazon and a dream for a collector. Hundreds of new species, mainly insects, constituted the basis of Wallace's work. During his stay in Borneo, he had the opportunity to observe, capture, and prepare specimens of many species, including orangutans (Wallace 1890).

Early in 1855, Wallace worked in a manuscript titled "On the Law Which Has Regulated the Introduction of New Species," published in the *Annals and Magazine of Natural History*. In this, later called the *Sarawak Law paper*, he stated: "Every species has come into existence coincident both in time and space with a pre-existing closely allied species." Since then, Wallace suggested that evolution occurs in a gradual way and that his law explained the organization of species, their geographical and geological distribution, and some of their anatomical features (Wallace 1855). Wallace's arguments pointed out some principles that fitted both his observations and

Darwin's similar ideas presented in *The Voyage of the Beagle* (1845), but Wallace's ideas did not suggest yet a mechanism that explained those principles.

Although the theoretical exercise had been pleasant for Wallace, this did not produce any income. On the other side of the world, his agent and clients did not find his theoretical task to be productive. Some of them openly indicated that his best options to contribute to science were found in his great capability for collecting; consequently, he should not be distracted by other activities which did not correspond to a man like Wallace (Raby 2001). Additionally, the Sarawak manuscript apparently did not produce any reaction among naturalists. Wallace sent the manuscript to Darwin (October 10, 1856), with whom he had corresponded in relation to requests by Darwin for information and specimens (Browne 2002). Initially, Darwin considered the manuscript unoriginal and dismissed it – perhaps due to a poorly detailed reading – based on the use of certain terms that differed from his own or the accepted scientific language. However, other academics saw something in it. Edward Blyth and Charles Lyell read the manuscript with a very different look and adverted Darwin that Wallace had a clue about the matter he was interested the most (Raby 2001).

During the 8 years he remained in the Malay Archipelago, Wallace systematically visited the main isles, Borneo, Sumatra, Bangka, Java, Bali, Lombok, Flores, Celebes (now Sulawesi), Timor, Maluku Islands, and New Guinea, as well as other smaller islands. Along with species collection, Wallace developed the ideas of the *Sarawak Law paper* about the distribution of the species and made observations about the inhabitants of the Malay islands who, as well as the species, exhibited important differences in their appearance and behavior. His anthropological and political interests were not to be open until his arriving in England; this would be one of his favorite discussion topics during his maturity and old age (Raby 2001).

Wallace found that the distribution of species suggested a divisor biological line between the regions of Asia and Australia, which he initially

(1863–1880) located at the east of Borneo, but it was later modified (1910) to put it at the east of Celebes. The line was built on the basis of the distribution of populations and species, according to Wallace's postulates showed with detail in *Island Life* (Wallace 1881/1998). The outline corresponded to important differences in fauna which can be noticed despite the relative closeness between the isles. The distribution of the original and modified lines responded to the particularities of the Celebes isle which was remarked by Wallace as peculiar, and he called Celebes an “ancient continental” island, the same category in which he put the Greater Antilles (Cuba, Haiti, Jamaica, and Puerto Rico) and Iceland.

During the time Wallace was developing his collection, his reflections about the influence of humans over nature were manifested in some of his writings. There is no doubt that Wallace was capable to overtake the utilitarian vision of his time and foresee the destiny of nature in the hands of human beings. His experience as a naturalist had an effect on his perception about nature and the human inhabitants of those regions, getting rid of the common prejudices from both his time and culture.

The Ternate Essay

Darwin's response to the Sarawak manuscript was initially unfavorable, but when Lyell and Blyth drew attention about the real value of the paper, Darwin read it more carefully. In his response letter (May 1857), Darwin expressed his agreement with some of Wallace's ideas, also expressing very clearly that he had been working on a very related problem for the past 20 years; finally, he encouraged Wallace to collect more data (Darwin 1887). Once again, it seemed that few people regarded Wallace as a theoretician; instead, he was expected to collect and send evidence to be used by other “thinkers.” Nevertheless, Wallace interpreted Darwin's letter as an encouragement. He had already received Bates' opinion whom, in a letter dated November 19, 1856, reminded Alfred that the origins of the

ideas put on the Sarawak manuscript could be traced to conversations they had in South America (circa 1845) about the geographical distribution of species. Bates praised Wallace's simplicity, maturity, and originality. Although Wallace was not giving credit to Bates in the manuscript, it was clear that the ideas presented in it had been originated from conversations with him and Spruce, during the long isolation periods in the Amazon (Von Hagen 1945).

Early in 1858, Wallace stopped at the island of Ternate. From there, he started several expeditions to the neighboring isles. In one of these, Gilolo (now Halmahera), Wallace fell sick, as many other times in the past, due to tropical fevers. During the feverish moments of his illness, Wallace came up with key ideas for a new theory. In the *Sarawak Law paper*, he had established that species transform in sequence, but some of them change more rapidly than others. But the hard question behind it was *how*. The answer came to Wallace in a very similar way as Darwin's: from Malthus' essay. When Wallace was recovering from a fever, he remembered Malthus' book which he read 11 years before; he was particularly interested in Malthus' idea that in every population, some individuals survive and some die, due to disease, accidents, famine, or wars. But why? What is the reason some individuals can survive those events and others cannot? The answer, Wallace said (1905), came in an unexpected way. Those who survive can do it because they are better prepared to cope with environmental challenges. The healthiest can survive to disease; the strongest, fastest, or smartest can survive to its enemies; the best hunter can survive to scarcity. Then, Wallace concluded that this process, repeated again and again, would lead to an improvement of the race, to changes of the species. A change, derived from a “special requirement from the environment,” could act over a particular feature, producing the characteristic isolation of the species over time. Unlike Darwin, Wallace stated his arguments highlighting the relationship between the individual and his environment, ignoring the competition between individuals of the same species. This difference in views was perhaps due to Darwin's interest on artificial

selection and its use as an analogy for natural selection, which suggested him a competition between individuals. In contrast, Wallace's interest on the geographical distribution of populations seemed to reveal a more relevant and fixed relation between individual and environment, in which the latter imposes an adaptive standard for each population (Bowler 1983). In any case, the idea emerged, twice!

During the following days, Wallace sketched the main elements of the theory and sent a paper to Darwin. Wallace had dated the letter on February 1858, and, although it was not conceived entirely on Ternate, he reported that island as the place where the idea originated because that was his place of residence. The document is widely known as the *Ternate Essay*.

Co-Discovery of Natural Selection

The events related to the presentation of Darwin and Wallace manuscripts to the Linnean Society have been extensively documented and interpreted in multiple ways, to reiterate the value of Darwin as discoverer of the mechanism of natural selection in some cases, to highlight Wallace's co-discovery and his role as a catalyst for the publication of *The Origin of Species*, or even to question the ethics on the resolution of the problem about the precedence of ideas between Darwin and Wallace (e.g., Browne 2002; Darwin 1887; Raby 2001; Wallace 1905). This is one of the most commented and well-documented episodes in the history of science.

Darwin was in the midst of a personal tragedy because of the serious illness, and subsequent death, of his little son, Charles. In the middle of this situation, and visibly affected by the impact of receiving the same solution that he gave to the most important problem of his work, Darwin left the moral dilemma he was facing to his closest friends, Charles Lyell and Joseph Hooker. They decided to present the *Ternate Essay*, along with some fragments of the draft of *The Origin of Species*, and a copy of the letter to Asa Gray – dated a year before and containing descriptive elements of the theory – at a meeting of the

Linnean Society. The great effort of Darwin's friends to give a satisfactory solution to the dilemma was made to preserve Darwin's precedence in the presentation of the theory. It seems, however, that there was also some solidarity with someone who represented a social class and an academic lodge, trying to deal with the untimely and disruptive arrival of someone from "other means" (Browne 2002).

Darwin and his circle accepted that the unexpected letter from Wallace had been the stimulus that forced the presentation of the theory in a short version. Wallace served as a catalyst for Darwin's work and served as a social catalyst to facilitate its acceptance, at least among a circle of colleagues who, while listening to Darwin with interest, were not yet ready to accept his theory; in fact, Lyell and Hooker only became enthusiastic Darwinists since this episode in which their participation was so crucial.

The way in which Wallace handled and interpreted this episode is, however, everything but a claim of precedence or reproach to the actions of Darwin or his colleagues. It is not possible to interpret with certainty if this was the result of Wallace's modest personality, or certainty about the sequence and nature of events, or both.

Once Darwin's manuscript was sent, it seems that Wallace only received a message about what happened in Down and London in late September or early October, when he received letters from Hooker and Darwin himself, dated at mid-July (Darwin 1887), in which they explained what occurred in the Linnean Society. Wallace had vital occupations to think about it. At that time, he was busy searching for birds-of-paradise, exotic, and beautiful specimens that would be highly appreciated by collectors and produce important profits. But, once he received the information, he considered that the solution was not just acceptable, but made honor to his work (Wallace 1905). In a letter sent to his mother on October 6, he mentioned the episode and manifested his joy with the outcome as well as with the chance to have an interaction with Darwin, Hooker, and Lyell upon his return to England (Raby 2001).

On the other hand, despite some difficulties, things started to go well. The collections Wallace sent to his agent in England sold well, and he had discovered a number of new species, including several species of birds-of-paradise and many species of butterflies, and even received recognition from taxonomists, who named new species with his name.

The following year, he received an advance of *The Origin of Species*, and there he found the mature work of a first-class researcher who, according to Wallace's own story, thwarted the development of his own book about the theory. Wallace expressed admiration for Darwin's work to Henry Bates, highlighting the extensive evidence presented, the clarity of Darwin's arguments, and the scope of his ideas (Wallace 1905).

Back to England

On February 1862, after 8 years out of his homeland, Wallace returned with alive animals (2 birds-of-paradise for the zoo), with a collection of stuffed animals (about 3000 pieces corresponding to a thousand species of birds, 20,000 specimens of beetles and butterflies of around 7000 species, including those sent by mail to his representative), with a name as a naturalist, and with a network of important naturalists whom he could now call "colleagues."

Finally, he began to receive some recognition. As a member of the Zoological Society and the British Ornithologists' Union, he frequented the meetings and was often invited to the Linnean Society (to which he was only accepted as a full member in 1871) and to the Ethnological Society of London. As foreseen, he was introduced by Darwin to the group of scientists who supported the theory of natural selection, which at that time did not exceed ten people. Wallace answered the call writing several articles in support of the theory and adding new data. He also published several articles on butterflies, parrots, and other species, in journals of prestigious societies.

However, all these achievements did not materialize in a stable job. It is not clear if his social status, his scientific ideas, or his personal style

were the reason why he was rejected from various positions in museums and scientific societies. Those difficulties were alleviated in part by his relation and subsequent marriage with Annie Mitten in 1866.

Around 1865, Wallace began to frequent spiritualism sessions. Contrary to his solid attitude as a scientist to deal with nature problems, he was willing to accept with little skepticism the tricks that all kinds of charlatans used to fool the naïve population who sought a connection with the "other world." Wallace had a weak point because of the emotional effect of his brother's death in Pará, and he was not only willing to believe, but he became an advocate of these practices.

In the following years, Alfred Wallace published two of his most important works, *The Malay Archipelago*, which he dedicated to Charles Darwin (1890), and *Contributions to the Theory of Natural Selection* (1870). Darwin read the first one with pleasure, but when he read the *Contributions*, he was surprised that his vision about the evolution of man differed in important ways to that of Wallace. At the end of the book, Wallace presented an idea about a supposed state of perfection, a final goal, to which the superior races (humans) were destined. Certainly, this idea was not shared by Darwin.

Mental Processes: Evolutionary Continuity or a Superior Force?

The development of Darwin and Wallace's evolutionary theory was stimulated by their desire to understand the origin of human beings. Although Darwin refused to talk about it in *The Origin of Species* (Darwin 1859), the extension of his ideas to humans was of great interest for him. In *The Descent of Man* (1889), Darwin developed the basis of his vision of evolution by natural and sexual selection and how they applied to the emergence of high psychological functions. From the second chapter of *The Descent of Man*, Darwin explicitly pointed out that the "mental qualities" are transmitted between species and within the human species. Thus, he suggested that there is an evolutionary continuity between man and

other animal species, which is evident by the transmission and preservation of certain psychological faculties that, although more complex in humans, are governed by similar mechanisms.

Darwin sustained the idea of evolutionary continuity of mental faculties by means of the comparison of anatomical characteristics between humans and primates – like the relative size of the skull regarding body size, related with some complex behaviors that suggest the presence of high psychological faculties, thus showing the affinity between humans and higher primates. The continuity that humans have with respect to other closely related primate species – which is evident at the moment of pointing out the similarities between them at anatomical, functional, and, especially, psychological level – led Darwin to conclude that the evolutionary principles also apply to the human species in all aspects, including the development of high cognitive faculties. These faculties, therefore, emerged by natural selection (Darwin 1889).

It is well known that the statements made by Darwin in *The Origin of Species* and in *The Descent of Man* provoked the most diverse reactions, for and against Darwinian ideas. Some of those objections about the emergency and development of psychological processes and mechanisms came from Alfred Wallace, who, despite being coauthor of the theory of evolution by natural selection, also had profound differences in terms of the applicability of the theory to the psychological abilities of humans.

Wallace made a series of observations to show the plausibility of evolutionary theory. In *Darwinism* (1889), he showed the main arguments of the theory of natural selection, including some contributions coming from several critics during the 30 years after the publication of *The Origin*. His ideas remained almost unchanged, supported by the law of multiplication of organisms, the law of limited population, the law of heredity, the law of variation, the law of unceasing change of physical conditions upon the surface of the Earth, and the law of equilibrium of nature (Wallace 1867). Nevertheless, Wallace himself clarified from the beginning that his

understanding of Darwinian theory offered very personal views about some specific topics.

On the emergence of high psychological functions, Wallace proposed very different ideas from Darwin's. In chap. XV of *Darwinism* – dedicated to the application of evolutionary theory to humans, Wallace supported the relevance of natural selection when talking about the morphological modifications suffered by humans, thanks to the similarities with some primate species. However, Wallace put more emphasis in some notorious anatomical differences: the erect posture of humans, absent in the other primate species; differences in the size of the skull which are evident between human and the other primates, but minimal or absent between the “civilized man” and the “savage man”; the presence of large canine teeth in primates, in contrast to humans whose canines are as large as the other teeth; and the absence of body hair in humans, among other differences. Based on these differences, Wallace concluded that the human speciation process began a long time before the speciation of the other primates, and then he started to show his particular reasoning about the emergence of the defining characteristics of human species, that is, psychological faculties. Before showing his own ideas, Wallace highlighted the inadmissibility of Darwin's argument about the applicability of natural selection to the emergence of high psychological faculties (Wallace 1889).

To illustrate his particular viewpoint, Wallace alluded to some intellectual manifestations only seen in humans – mathematics, music, arts, and philosophy – which also are manifested in an exceptional way in a reduced group of persons from the entire population. Wallace added that these complex manifestations cannot be the result of the mere process of natural selection because they are not useful nor necessary behavior for the survival of the species (it should be noted that, for both, Wallace and Darwin, the mechanism of natural selection is intimately attached to the idea of “struggle for existence” or “survival of the fittest”). This justifies the fact that those complex manifestations are not uniformly distributed across the whole population, but just observed in a

reduced number of persons. Thus, Wallace pointed out the incapacity of natural selection theory to explain the emergence of high-intellect manifestations:

The point to which I wish specially to call attention is, that to prove continuity and the progressive development of the intellectual and moral faculties from animals to man, is not the same as proving that these faculties have been developed by natural selection; and this last is what Mr. Darwin has hardly attempted, although to support his theory it was absolutely essential to prove it. Because man's physical structure has been developed from an animal form by natural selection, it does not necessarily follow that his mental nature, even though developed *pari passu* with it, has been developed by the same causes only. (Wallace 1889, p. 463)

From that point, he concluded that the psychological faculties owned by the human species emerged as a consequence of the action of a certain superior force: a force argued to be present in nature, but remained far beyond the scientific knowledge of his time.

The fact that Wallace presented such a daring hypothesis is something shocking, mostly after showing a well-developed scientific thinking along his life. Wallace himself knew beforehand that the addition of a spiritualist argument in his discourse would be taken as scientific heresy among his colleagues.

Before the publication of *Darwinism*, Wallace had already made manifest his spiritualist argument in some manuscripts and meetings. What began as simple, naïve comments about the difficulties of the theory of natural selection to give account of human faculties became a structured discourse, attached to his way of thinking. In a review of the tenth edition of *Principles of Geology* and the sixth edition of *Elements of Geology* by Sir Charles Lyell, published in the *Quarterly Review*, Wallace (1869) mentioned the “Overruling Intelligences” for the first time, showed as entities that supposedly molded the development of the human intellect. According to Wallace, some morphological traits of humans cannot be explained by natural selection, like the brain, the speech organs, the hand, and the external shape of the human body. Wallace concluded that it was necessary to admit that the human mind

must be the product of a supreme mind which controls the action of evolution laws, in order to make such a perfect organization of the moral and mental capabilities of the human being.

The following year, 1870, Wallace wrote a first essay dedicated completely to question the evolutionary theory applied to man. In fact, the title of his essay was clear enough: *The Limits of Natural Selection as Applied to Man*. In this essay, Wallace extensively argued about the impossibility of natural selection theory to explain the emergence and development of the intellectual and moral capabilities of humans, proposing as alternative the action of Supreme or Overruling Intelligences, arguing that these intelligences are ruled by the same physical laws that rule the universe and, therefore, can be scientifically studied.

As it was expected, Darwin's response was quick, and then a very interesting discussion about the role of the human psychological faculties in the evolutionary process ensued. In a letter sent in March 1869 (Marchant 1916), Darwin anticipated the “heresy” Wallace was about to commit with his review of Lyell's books:

I shall be intensely curious to read the *Quarterly*: I hope you have not murdered too completely your own and my child [the theory of natural selection]. (Marchant 1916, p. 241)

Then, after having read the review, Darwin manifested his disagreement with Wallace with another letter dated on April of the same year:

As you expected, I differ grievously from you, and I am very sorry for it. I can see no necessity for calling in an additional and proximate cause in regard to Man. But the subject is too long for a letter. I have been particularly glad to read your discussion, because I am now writing and thinking much about Man. (p. 243)

Nevertheless, in a letter dated January 1870, Darwin showed his rejection about the inclusion of additional causes to explain the emergence of human faculties (Marchant 1916). In fact, his tone reveals his altered mood when reading Wallace's essay about the *Limits* of natural selection:

[...] But I groan over Man—you write like a metamorphosed (in retrograde direction) naturalist, and you the author of the best paper that ever appeared in the *Anthropological Review*! Eheu! Eheu! Eheu! Your miserable friend, C. Darwin (p. 251)

Darwin's Response

Darwin's answer about Wallace's spiritualist argument has its basis on a briefly developed idea on *The Origin of Species*: Sexual selection. A detailed reading of Darwin's work shows that in *The Origin of Species*, the argument about sexual selection is referred only in some fragments of chap. IV. But in *The Descent of Man*, this topic is the basis for the whole book (Darwin 1889). There is a question about why Darwin made such a broad discussion about sexual selection. And the answer is very simple: because this is the full explanation of the response Darwin did to Wallace in relation to the evolution of human psychological faculties (Ruse 2009).

Darwin partially agreed with Wallace on the fact that natural selection cannot fully explain some characteristics of humans such as the intellectual and moral ones, but Darwin also thought that it is completely unnecessary to invoke spiritual forces to answer the question. The simplest answer could arise by adjusting to the laws that had already been established with respect to the evolution of the species. So, Darwin thought that sexual selection could be the answer: the effects of the struggle with conspecifics can lead to great differences on reproduction and breeding (Ruse 2009). Some individuals with certain characteristics like an enhanced intelligence to make good decisions (e.g., mate choice) would have a better chance to reproduce. The idea behind sexual selection as the determinant mechanism on the emergence of high psychological faculties is that intraspecific struggle (whether by ritualized male combat or by female mate choice) allows the selection of the most appropriate characteristics to make possible the reproduction of offspring tending toward variability. As it was already stated in Darwinian arguments, variation is required to ensure adaptive adjustment to changing environmental conditions. Likewise, constant variation is necessary to ensure that the *species* do not fully *specialize* (Cartwright 2008). All of it, along with an accelerated process of development of the brain, made possible the selection of certain traits which, if not determinant in the struggle for existence, eventually

constituted very attractive elements for mate selection. Therefore, high intellectual qualities emerge because of their great value for reproduction. Darwin made it clear on *The Descent of Man*:

He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverance, strength and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain. (Darwin 1889, p. 617)

Immediately after the publication of *The Descent of Man*, Wallace returned the favor, and, in a letter dated January 20, 1871 (Marchant 1916), he manifested his disagreement supported on his spiritualist argument, even though he agreed with the application of the laws of natural selection on human evolution from some related species:

Your chapters on Man are of intense interest, but as touching my special heresy not as yet altogether convincing, though of course I fully agree with every word and every argument, which goes to prove the "evolution" or "development" of man out of a lower form. My only difficulties are as to whether you have accounted for *every* step of the development by ascertained laws. (Marchant 1916, p. 256)

From that moment, the positions of both authors regarding the evolution of the human psychological faculties remained practically unchanged; their arguments were refined and evidenced their deep differences in understanding human nature. The discussion between Darwin and Wallace continued over the years, even after their deaths; the relationship between evolutionary theory and cognitive faculties continued to be a subject of discussion for the behavioral sciences during the following century and continues to be central to the explanation in psychological theory.

Conclusion

The interest of Alfred Wallace in humanity led him to try to understand not only his origin but his future. His idealism, manifested in a spiritual vision of the origin of human nature, was also expressed in his way of seeing the social organization of our species. Influenced by his social origin, his early experiences as a surveyor, his encounter with native populations from two very distant places of the world, and his experience with the colonialist systems in America and Asia led him toward a socialist vision of the distribution of the land. For Wallace, it was not enough to believe in an idea; there was an obligation to become a promoter of such idea. In 1881, he was elected as the president of the *Land Nationalisation Society* and published several books about land distribution, one of them published just weeks before he passed away.

In his mature years, Wallace was frequently invited to present his ideas in societies, events, and public meetings. One of his most important tours was in North America, where he was able to return to his most beloved and habitual activity, that of a naturalist. He visited multiple cities and natural parks, enjoying the immense natural wealth of that continent.

Alfred and Annie had three children: Herbert – who died at the age of 7, Violet, and William. It is well known that one of the most frequent preoccupations of Alfred and his family was their economic situation. Due to the fact that he was not able to obtain a permanent job position, he had to write paid articles for several publishers. In 1881, a year before his death, Darwin assumed a defense of Wallace and successfully managed a request to the English Government for a pension for his outstanding civil services to the Crown. This episode was an indicator of Darwin's character, who, despite his differences with Wallace in the development of the evolutionary theory, highly appreciated the value of a man dedicated to exploring and understanding nature, always trying to discover their secrets in an honest manner and, above all, a man whose ideas catalyzed his greatest achievements as a scientist.

Alfred Russel Wallace died on November 7, 1913, at the age of 90. His wishes for a modest fate were respected, and he was buried in Broadstone, Dorset. Two years later, a medallion in his honor was installed near the grave of Charles Darwin in Westminster Abbey. This represents the seal of destiny of two men who discovered the essential mechanism of the origin of species and the way we understand the nature of life. For Wallace, the thread of his life was the desire to understand the role of human beings in the universe, their origin, their relationship with nature and with their own kind, and his commitment with the more sublime ideals of justice and equality.

Cross-References

- [Charles Darwin: Theory of Natural Selection](#)
- [Controversies in Evolutionary Psychology](#)
- [Early Perspectives on Evolutionary Change](#)
- [Evolution of Intelligence, The](#)

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Alfred Russel Wallace and Charles Darwin

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Definition

Alfred Russel Wallace (8 January 1823–7 November 1913) and Charles Darwin

(12 February 1809–19 April 1882) are jointly credited with contributing the doctrine of natural selection to the scientific literature. There can be no doubt that they independently conceived of the same theory; the priority question was settled amicably by a joint publication in 1858.

Introduction

Darwin has become, with considerable justification, the flag-bearer of evolution, but many of his (near-)contemporaries poured over the same questions. The obverse side of hero worship is indignation over those who were overlooked: the perniciousness of Darwinists allegedly shown by the manner in which Wallace, a formidable biogeographical scientist in his own right, was robbed of the priority credit. However, history and human relationships can be, and thankfully often are, more subtle than squabbles over priority. In reality, Darwin's response was admirably honorable, and the real interest resides in appreciating both men's contributions against the backdrop of contemporary views on varieties in nature.

Affinity and mutability: the origins of an idea

Evolution, as *phenomenon*, is the corpus of observations attesting to the fact that life on earth has not always been the same. Over the course of mega-anni, ecosystems and the species that inhabit them have changed, often and dramatically. Evolution, as *theory*, is any account seeking to explain these facts, including contrarian accounts that attempt to explain the facts *away*, that is, to repudiate the measurement of the deep time scale, or the sweeping nature of the changes, or both. Or, spurred by an urge to reconcile respect for scientific observation with religious piety, one might countenance a theory of intelligent redesign, in which the creator continually revises and recreates.

The philosophical landscape was quite different in the time of Darwin and Wallace. The nature

and media of the changes observed took center stage. Mendelian genetics was being developed at the time, but would not be widely recognized until the turn of the century (Fisher 1936) – and molecular genetics lay even further in the future. Even if such gaps in contemporary knowledge seem all but fatal handicaps to us, we should examine without prejudice the development of evolutionary thought against the intellectual backdrop of the time.

The similarity or “affinity” that exists between parent and child, raven and crow, perhaps even shark and tiger, or octopus and jellyfish, must always have been evident to naturalists. But what were they to make of this affinity, and how could it allow one life form to pass into the other?

The idea of inheritance of acquired characteristics, previously widely accepted, had begun to fall by the wayside. This doctrine, traditionally associated with Jean-Baptiste Lamarck (1744–1829), who certainly gave it a crisp wording (Lamarck 1809), presupposes that the next generation may somehow be imprinted with the striving of the parents. We observe adaptive changes through the course of an individual’s lifetime, e.g., hypertrophy of muscles under strain, or learning – and we also observe adaptive changes over the course of generations. It is natural to suppose that similar mechanisms are at work and that, consequently, adaptive changes can be passed on through gamete or spore. In Lamarck’s thought this was wedded to the concept of an inherent force striving toward greater complexity; whereas Darwin imagined a neat mechanism for the inheritance of acquired characteristics, whereby each organ or tissue brings forth a microscopic representative “avatar” that contributes to the gamete (stretching this idea perhaps beyond its limit, we may here vaguely discern the outlines of modern epigenetics), Wallace roundly considered the experiments refuting Lamarckism to have settled the question, which, in any case, he felt was rendered moot by the operation of natural selection.

The ineffable affinity that ties living beings together finds a striking expression in Genesis 1:26: “God said, Let us make man in our image,

after our likeness: and let them have dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing.” If man is made in God’s likeness, then the stuff that life is made of (muscles, sinews, blood, etc.) must be present in the human body in perfect proportion and harmony. Moreover, such perfection must be lacking in all other live forms, in increasing degree as we descend a hierarchy known as the *great chain of being*. One could view all nonhuman beings as lacking in reason, for instance, or regard the Mollusca as being out of proportion, relative to the divine formula of man, in being mostly composed of muscle. Thus we account for both the affinity and diversity of life and even have a rudimentary form of genetics in which species are defined by a divinely ordained “formula of (dis)harmony/(dis)proportion.”

This point of view severely constrains the definition and malleability of species and forbids *transmutation*, the ability of species to evolve into one another. We concur with Darwin that it is “absurd to talk of one animal being higher than another,” but if we momentarily allow that life is ordered hierarchically, we should applaud Lamarck for his boldness in proposing that life strives to move *up* this ladder. Going against such radical ideas, *prima facie* evidence for an immutable, ingrained (and Divinely ordained) “formula” was seen in the tendency for domestic animals, when released into the wild, to “revert to type,” that is, while breeding in captivity may have stretched the makeup of the beasts away from the divine formula, when left to its own devices, the species springs back, or regresses, to its true inborn form. Varieties may temporarily depart from the original type, but not forever, nor without bound.

It is precisely this doctrine that Wallace seeks to refute in his essay “On the Tendency of Varieties to Depart Indefinitely From the Original Type” where he argues that the apparent “regression” of domesticated animals gone feral can be explained precisely because the harsh conditions of the natural environment that produced “the original type” must again give rise to something quite like it. But as these challenges

change, so will the way the species respond to them, free to wander away arbitrarily far in morphogenetic space.

It seems uncanny to modern eyes that Wallace is talking so eloquently about natural selection without ever using these words; but that is just the terminology that was introduced with Darwin. Wallace's thinking is clearly along the familiar lines of linking the lifetime reproductive success of an individual to its ability to, first, survive through to these reproductive events and, second, amass the resources that are to be invested in offspring. He cites the stock examples of characteristics such as camouflage, strong thigh muscles, and sharp claws as the sort of traits that aid the organism in achieving this success. He observes that, were nature to provide for every zygote to grow into an adult, the biomass of every species would grow exponentially – a manifest absurdity on a finite planet, which explains why selective pressure is huge.

One may well imagine Darwin's consternation when Wallace sent him his essay in March of 1858: "If Wallace had my MS. sketch written out in 1842, he could not have made a better short abstract." Darwin offered to help Wallace publishing his views. Moreover, Darwin had previously communicated writings on his ideas, which would allow him to "prove that I take nothing from Wallace. I should be extremely glad now to publish a sketch of my general views in about a dozen pages or so. But I cannot persuade myself that I can do so honourably. . . I would far rather burn my whole book than that he or any man should think that I had behaved in a paltry spirit" (Darwin 1958).

A compromise was found, and Wallace's essay was published along with an extract from Darwin's essay of 1844 (Darwin and Wallace 1858). Darwin's "Origin of Species," on which he had been working since the mid-1850s, was published a year later (Darwin 1858). Darwin's ideas on evolution had first crystallized during his voyage on the *Beagle* in the 1830s and had been maturing ever since (Darwin 1958).

The wealth of case studies, the breadth of knowledge of natural history and biogeography,

as well as its thoughtful style of argumentation made "Origin" the standard-bearer for evolution. The primary obstacle it overcame during its day was the doctrine of immutability, which was abandoned in favor of ongoing speciation and common descent.

Conclusion

Against a background of pre-Mendelian genetics, rejection of the transmutation of species for traditionalist-religious reasons, and expeditions yielding a wealth of biogeographical data, Wallace formulated the mechanism of natural selection independently of Darwin, who recognized Wallace's insights as essentially identical to his own and shared the credit, in what effectively amounted to a preview publication of his "Origin of Species."

Cross-References

- [Adaptation and Natural Selection](#)
- [Charles Darwin: Theory of Sexual Selection](#)
- [Evolution of Adaptations](#)
- [Genetic Determinism](#)

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Alienation

► [Loneliness in Modern Life](#)

All Psychology Is Evolutionary Psychology

► [Evolutionary Perspective, The](#)

Allergic Reactions

► [Allergies](#)

Allergies

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Synonyms

[Allergic reactions](#)

Definition

An excessive pathological reaction of the immune system towards environmental substances, such as foods and pollens, that are tolerated by the immune system of nonallergic individuals.

Introduction

Allergies have become increasingly prevalent over recent decades, particularly in the West. As a consequence, interest has grown regarding why such a phenomenon exists in the first place, especially given the risk of experiencing a potentially fatal allergic reaction called anaphylaxis (Gross 2015). Early explanations typically viewed

allergies as merely immunological errors. However, the evolutionary persistence of allergic capability suggests that it has an adaptive value for the host, of which exerted a strong enough positive selection pressure to outweigh the physiological costs and risk of fatality. Margie Profet became a notable theorist for why allergies evolved with her controversial hypothesis regarding what this benefit of allergies may have been.

The Toxin Hypothesis

In her paper published in 1991, Profet proposed the “toxin hypothesis” which argues that allergies evolved as a defense mechanism against toxins. Toxins are unfortunately ubiquitous in the natural world and cause acute bodily damage to a host. Many are also secondarily mutagenic or carcinogenic, resulting in cumulative damage by inducing mutations or cancer, respectively. While the body has other defenses against toxins, Profet suggested that allergies provide an adaptive last line of defense against those which have previously proven able to bypass the host’s primary antitoxin defense mechanisms. Given the high prevalence and danger of toxins, if allergic capability does indeed provide protection then the phenomenon may have conferred a net advantage across mammalian history, thus explaining its evolutionary retention.

To support her hypothesis, Profet described how substances which tend to trigger allergic reactions (allergens) are commonly toxic, despite this characteristic being previously overlooked and underappreciated. It appeared to her that it was no coincidence that allergenic potential is often in line with toxicity, whether in terms of acute toxicity, mutagenicity, or carcinogenicity. As she pointed out, the four most strongly allergenic metals from the natural environment (arsenic, beryllium, chromium, and nickel) are known to be unambiguously carcinogenic. She also acknowledged that some allergens do not actually appear toxic themselves but noted that in these cases they commonly act as carrier proteins for low-molecular-weight toxins, thus ultimately aiding in toxin-induced damage.

Profet argued that the manifestation of allergies shows adaptive design for protecting the body from toxins before they, and any contained or adhering mutagens, can cause damage. She reasoned that symptoms like sneezing, coughing, vomiting, and diarrhea are consistent with serving a purpose of aiding the physical expulsion of toxic allergens from the nasal passages, lungs, stomach, and intestines, respectively. Meanwhile, she suggested that other symptoms like bronchial constriction, swollen sinuses, and a drop in blood pressure are suited to help block or slow the dissemination of toxins around the body. Interestingly, the benefit of these allergy symptoms may be twofold in that they might facilitate the conditioning of avoidance behavior which reduces future toxin exposure.

Profet also described how less salient features of allergies show good design for the toxin hypothesis but contrastingly poor design for an alternative idea known as the helminth hypothesis. This hypothesis purports that allergies evolved to protect against helminths (parasitic worms) rather than toxins and consequently views allergies towards the diverse range of non-helminth allergens as a by-product of pathogen defense. One example feature suggested by Profet as consistent with the toxin, but not helminth, hypothesis is the urgent and risky nature of allergies. Allergic reactions operate with a rapidity and severity that seems to imply design for countering threats that are able to cause serious harm within minutes or hours. Unlike toxins though, helminths do not impose serious harm in such a short time frame upon parasitizing a host. Profet reasoned that, in addition to other features, it would appear dysfunctional for allergies to have evolved this way if serving a purpose of protecting against helminths.

The toxin hypothesis received great interest from media and the general public with its novel and relatively radical view on the evolution of allergies. However, the hypothesis faced skepticism from the scientific community. Some criticism focused on Profet's educational background, but the predominant concern was the limited evidence demonstrating that allergic capability actually helps to protect against toxins. As interest in

allergies has grown within the last decade, an increasing amount of evidence for the hypothesis has emerged. Support largely comes from two major sources, including research on the association between allergies and risk of cancer and research on the protective effect of allergic capability towards venom.

Allergies and Cancer

One line of evidence commonly used for the toxin hypothesis is the observation that individuals with a history of allergies tend to have a lower risk of developing cancer. Since the early research described by Profet (1991), various meta-analyses and literature reviews have suggested that evidence for this inverse allergy-cancer correlation is substantial, most notably for the risk of glioma (e.g., Amirian et al. 2016). It is reasoned that the lower risk of cancer in allergic individuals reflects the fact that allergies protect the body from toxins, of which many are carcinogenic. However, many researchers consider that this relationship may have arisen rather fortuitously. The immunosurveillance hypothesis, for example, suggests that it occurs simply because allergies are a side effect of a hyperactive immune system that is more efficient at identifying and attacking both foreign allergens and domestic precancerous cells (Il'yasova et al. 2009). Unlike the toxin hypothesis, this suggests that it is not allergies that are reducing the risk of cancer, but the hypervigilant immune system instead. As a result, it is uncertain whether the inverse allergy-cancer correlation is appropriate to use as evidence for the toxin hypothesis.

Nevertheless, the literature on allergies and cancer can be argued as more consistent with the toxin hypothesis. For example, the toxin hypothesis predicts that the inverse allergy-cancer association should occur specifically for cancers of tissues and organ systems that are directly exposed to carcinogens from the external environment and from which the toxic substances can be expelled by allergy symptoms. Conversely, the immunosurveillance hypothesis predicts that the inverse association should be present for cancers

of *all* tissues and organ systems. A comprehensive review of the literature conducted by Sherman et al. (2008) indicated that research findings are more often consistent with the former prediction, suggesting that the allergy-cancer association may in fact provide suitable, albeit merely correlational, evidence for Profet's toxin hypothesis.

Allergies and Protection Against Venom

Within recent years, a line of experimental evidence has emerged that demonstrates a protective value of allergic capability. These experiments have particularly utilized venoms as they consist of highly toxic components that can cause severe and life-threatening tissue damage and, perhaps unsurprisingly, also have a high allergenic propensity. For example, Marichal et al. (2013) conducted a study in which they injected a group of mice with small doses of honeybee venom (simulating one or two stings), triggering production of venom-specific immunoglobulin E (IgE) antibodies. IgE antibodies are a critical component of the allergic response as they precipitate the release of chemicals, such as histamine, that cause the typical allergy symptoms. The research found that the mice had significantly better outcomes when challenged three weeks later with near-lethal doses of the venom compared to a naïve control group of mice. Specifically, they were three times more likely to survive, had less severe sublethal reactions, and experienced a lower risk of anaphylactic shock. Further, mice who were genetically lacking IgE or the IgE receptor, FcεRI, did not experience this acquired protective immunity against venom. The authors concluded that key elements of allergic reactivity (IgE-related responses) are critical for enhancing host resistance to harmful venoms, thus supporting the toxin hypothesis.

Conclusion

Profet's hypothesis that allergies are an adaptation to protect against toxins provided a rather provocative explanation for why they exist. The idea may

have initially generated criticism, but it has been increasingly advocated by the scientific community, as encouraged by the growing amount of supporting evidence. The hypothesis certainly requires more testing though and it may be worthwhile for researchers to investigate the potential benefit of allergies for a wider range of toxins, in line with the diversity of allergens. Regardless of the outcome, the hypothesis has provided a refreshing viewpoint on allergies and has stimulated novel questions for allergy research. Ultimately, it is hoped that improving the functional understanding of allergies will pave the way for some concrete developments in the prevention, diagnosis, and treatment of this growing phenomenon.

Cross-References

► [Darwinian Medicine and Survival Problems](#)

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Alliance

► Cooperation Among Fishes

Alliance Formation

► Coalitional Relationships

Alliance Formation Theory

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Synonyms

[Evolution of human male homosexuality](#), [Evolutionary theory of homosexuality](#)

Definition

A theory holding that homosexual behavior in human males derives from selection for behavior that reinforces male alliances.

Introduction

The incidence of exclusive same-sex sexual preference (exclusive homosexuality) in humans is greater in men than in women and varies across cultures and historical periods (LeVay 2011). The incidence in contemporary Western cultures is estimated to range between 2 % and 6 % (Barthes et al. 2013). Exclusive homosexuality is an evolutionary paradox, because it does not contribute to reproduction; consequently, it is unclear how genes that may contribute to it are inherited and maintained in the population. The trend in theory and research has been to identify a single explanation. However, recently, some authors have made compelling arguments for more

complex and multicomponent explanations that involve both ultimate (evolutionary) and proximate (environmental, developmental) factors (e.g., LeVay 2011; Poiani 2010).

The alliance theory of male-male sexual behavior in humans posits the development of one of the components that may contribute to the existence of exclusive homosexuality in humans: the evolutionary component. It takes into account theory of human evolution and unique species-specific aspects of human evolution. Nonexclusive homosexual behavior occurs in many animals (Bagemihl 1999), and its causes and functions may be similar in some species and quite different in others (Poiani 2010). Consequently, human homosexual behavior should be studied in the context of the evolution of humans and closely related species. The expression of homosexual behavior among primates varies across species and tends to be confined to Old World monkeys, apes, and humans. This suggests both shared phylogenetic origins and current adaptive value (Poiani 2010).

The Alliance Theory

The alliance theory holds that homosexual behavior reinforced alliances between hominin (human ancestor) males that contributed to their ability to survive and ultimately to find female mates and reproduce (Kirkpatrick 2000; Muscarella 2000, 2006). This may have been particularly adaptive in the case of juvenile males who are likely to have been peripheralized or pushed to the outer edge of the group for some period of time as is seen with juveniles in other species. The juveniles remain peripheralized until they are able to work their way up the male dominance hierarchy. At this time they are vulnerable to predation, intra-species aggression, and lack of resources. The use of homosexual behavior as sociosexual behavior that reinforces alliances is seen in other primates. Dyadic relationships increase the status of both individuals, and their alliance allows both to more effectively defend against aggressors and prevent the taking of resources such as food. The expression of homosexual behavior in human males across history and across cultures can often be

interpreted as supporting alliances between the individuals (Kirkpatrick 2000). There may have been even greater selection pressure for the expression of homosexual behavior as a mechanism of alliance formation in humans because of a factor unique to human evolution.

The Role of Dominance Hierarchies

As described in the alliance theory, one of the most important aspects of human evolution was the development of complex social organization and the characteristics that allowed for this including the abilities to cooperate, form alliances, and live in a dominance hierarchy. Dominance hierarchies would have been in flux for hominins, and one's positions of subordination and dominance would have changed across the lifespan due to developmental changes and changes in the membership of the hierarchy itself as a function of births, deaths, illness, and injury. Human males in particular appear to have evolved numerous behavioral characteristics that facilitate the development and maintenance of within-coalition dominance hierarchies (Geary et al. 2003). In many social animals homosexual behavior serves a sociosexual role for the expression and maintenance of positions of dominance or subordination in a hierarchy and for the establishment of pair-bonds that lead to alliance formations (Poiani 2010). This is particularly evident in humans' closest primate relatives, chimpanzees and bonobos (Muscarella 2000). Homosexual behavior in humans is speculated to be an exaptation, that is, it may have evolved originally as a sociosexual behavior related to the expression of dominance and subordination and selection acted upon it further, because it also contributed to the development and reinforcement of alliances that contributed directly to survival and indirectly to reproduction (Muscarella 2006).

Conclusion

The alliance theory actually describes selection for bisexual behavior, that is, nonexclusive

homosexual behavior under certain circumstances and heterosexual behavior, which is the sine qua non of reproduction and the passing on of genes that may be related to homosexual behavior. The theory does not account for exclusive homosexual behavior which is posited to be due to an interaction between the species-specific and genetically influenced expression of homosexual behavior characteristic of humans and developmental, ecological, cultural, and psychological factors (Kirkpatrick 2000; LeVay 2011; Muscarella 2006; Poiani 2010). The alliance theory does not address female homosexual behavior although it may also be related to alliance formation (Muscarella 2000; Poiani 2010). However, the evolutionary nature of human female dominance hierarchies and coalitional strategies is very different from that of human males (Geary et al. 2003), which may affect the expression of homosexual behavior in human females (Muscarella 2015). The alliance theory has heuristic value, but to date, there is no empirical evidence that supports it.

Cross-References

- Cultural Differences in Sexual Socialization
- Evolution of Cooperation
- Evolution of the Brain, The
- Living in Groups
- Same-Sex Relationships
- Sex as Bonding Mechanisms
- Why Humans Are Unique

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Alliances

- ▶ [In-Group Versus Out-Group](#)
- ▶ [Prisoner's Dilemma Outcomes](#)
- ▶ [Science and Morality](#)

Allocare

- ▶ [Access to Alloparents](#)

Allocation of Attention

- ▶ [Selective Attunement to Adaptive Problems](#)

Allogrooming

- ▶ [Cooperative Grooming](#)

Allomother

- ▶ [Access to Alloparents](#)

Allomothering

- ▶ [Aunt Care](#)
- ▶ [Mothers and Maternal Grandmothers and Childhood Survival](#)

Alloparenting

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Synonyms

[Babysitting](#); [Caregiving](#); [Communal breeding](#); [Cooperative breeding](#); [Cooperative childrearing](#)

Definition

Caregiving by nonparental caregivers, who provide direct and/or indirect investments to a child

Introduction

Who helped you develop into the person you are today? Most of us may think about a parent or parents, but many of us would also recognize the important role of other people. Perhaps it's a teacher, a grandparent, or a neighborhood friend. The fact that we are supported by many people in our childhood is, in fact, very unusual: In non-human mammals, support – or investments – for juveniles are typically and solely provided by the biological mother. Only 9–10% of mammals display parental care, where biological fathers are additionally involved in raising offspring, without the support of other helpers (Kleiman and Malcolm 1981). In humans, we see a notably different system of facultative fathering, where

biological fathers may or may not provide investments into their children, combined with a range of additional caregivers beyond the biological parents. These additional caregivers, or alloparents, can include siblings, grandparents, and extended kin, as well as nonrelatives such as step-parents, friends, and neighbors.

Support from alloparents, meaning “other parents,” is arguably an obligate human characteristic. This is because, compared to other primates, humans have an extended childhood and adolescence: while the conceptualization and timing of adulthood does somewhat vary between cultures, broadly speaking, humans do not become “mature” and self-sustaining until their mid-teens to early 20s. During childhood and adolescence, we experience a prolonged period of physical growth and skills development, making us dependent on sustained support from parents and alloparents to survive, develop, and successfully reach adulthood. Nonparental caregivers are therefore *necessary* for successful reproduction and childrearing in humans – although who supports parents and how varies cross-culturally.

But how did alloparenting evolve? Why do alloparents help in childrearing, and how do they influence parental fitness? This chapter provides an overview of alloparenting in humans, outlining different types of alloparenting, broadly addressing the evolution of alloparenting and providing a brief review of key alloparents in humans across cultures.

Defining Alloparenting

In its essence, alloparenting is a transfer of time, energy, and/or resources to non-offspring, with opportunity costs against any other behavior. This can be conceptualized as *alloparental investments* into a non-offspring which, all things being equal, is expected to increase non-offspring biological fitness (with fitness meaning the ability to survive and reproduce). Humans join the 3% of mammalian species where alloparenting is the norm, where successful reproduction and offspring survival is dependent on the help from

nonparental caregivers (Lukas and Clutton-Brock 2012).

To date, research on alloparenting in humans is often referred to as the “cooperative breeding literature.” However, there has been some debate among researchers on whether humans should be classified as cooperative breeders at all. Partly, this may be the outcome of some confusion and variation around what cooperative and communal breeding means between disciplines. These terms are often used ambiguously, and sometimes interchangeably, likely exacerbated by the fact that “communal breeding” and “cooperative breeding” are often unaccompanied by clear definitions.

Is Alloparenting the Same as Cooperative Breeding?

In the nonhuman animal literature, cooperative breeding is defined as a system where a dominant female monopolizes breeding, aided by subordinate and nonbreeding alloparents who forgo their own reproduction. In contrast, communal breeding refers to a system where multiple females reproduce, often pooling their resources and young (Lukas and Clutton-Brock 2012). Confusingly, humans have been argued to be both cooperative and communal breeders. The long pre- and post-reproductive life stages in humans have been interpreted as evolved characteristics of reproductive suppression, which is a defining characteristic of cooperative breeding (Lukas and Clutton-Brock 2012): Older, reproductively mature children may temporarily “forgo reproduction” and help care for their younger siblings, while grandmothers have been argued to have a long post-reproductive lifespan to help care for their grandchildren. At the same time, mothers rarely, if ever, monopolize reproduction in human groups. As a species, we typically live in groups of multiple parents with children, where parents and alloparents share resource and care. This pattern seems to be similar in feature to communal breeders.

Clearly, humans do not fit neatly into either category of communal or cooperative breeding as strictly defined. Instead, humans cooperate broadly and flexibly around reproduction and childrearing, with alloparenting being a norm.

With this context, in this chapter we purposely avoid labelling humans as cooperative breeders. Instead, we stick to the terms *alloparenting* and introduce the term *cooperative childrearing*. The word “cooperative” is maintained, as there is no denying that alloparenting is a cooperative act (reviewed in more detail below). However, by directing attention to “childrearing,” which is uniquely attributable to humans and children, it clarifies that the human system varies from cooperative breeders in the strictest sense. In humans, alloparenting does not necessarily mean individuals forgo reproduction, while recognizing that some alloparents do.

How is Alloparenting Conceptualized?

Alloparenting is an inherent part of cooperative childrearing. However, like cooperative and communal breeding, alloparenting as a term has been defined, conceptualized, and categorized in different ways within and between disciplines. This is perhaps reflective of the fact that alloparents can invest in different ways, with different pathways of investment transfer. To fully capture the diversity in alloparental investments, alloparenting in humans can be conceptualized in three distinct ways: (1) provisioning vs caregiving, addressing the types of alloparental investments, (2) direct vs indirect, addressing the pathways of alloparental investments, and (3) additive vs substitutive, addressing alloparenting systems.

Types of Alloparental Investments: Provisioning Versus Caregiving

Alloparental investment behaviors can be broadly categorized into *provisioning*, which is a transfer of resources to parents and/or children, and *caregiving*, which is a transfer of time and energy to care for the child. Alloparental investments via provisioning can involve any form of resource, including food, wealth, and other materials, and the generation of resources (i.e., production) is often an important aspect of provisioning. For example, hunting behavior by men in forager populations are often conceptualized as provisioning activities. Similarly, in developed populations, grandparents providing financial transfers to parents and grandchildren can be

conceptualized as provisioning. Alloparental investments via caregiving include physical care and feeding children, as well as teaching and play. For example, across societies, older children or adults often carry infants and young children, which is a type of caregiving activity.

It is important to note that production activities are often incompatible with caregiving. This means alloparents, like parents, are generally unable to do both things at the same time (Emmott 2015). In the Hadza hunter-gatherers of Tanzania, for example, mothers are reportedly not able to carry toddlers while they go out and forage for food, and so must leave these relatively young children in camp (Blurton Jones et al. 2005). Similarly, in developed populations, the conflict between employment and providing childcare is widely recognized (e.g., see Allen 2003), as unsurprisingly not many workplaces allow people to bring children on a regular basis. Because of these difficulties in combining provisioning and childcare, alloparents may specialize in providing a particular type of investment.

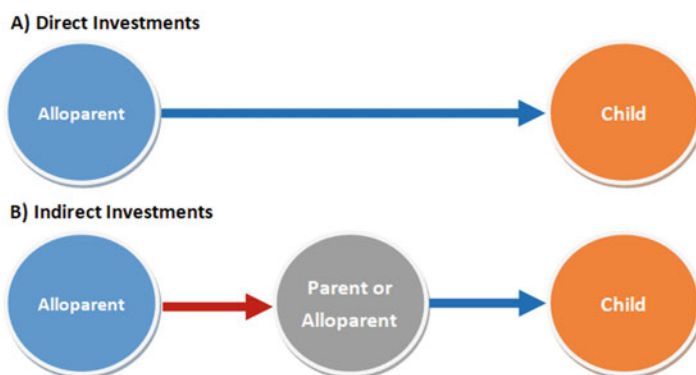
Pathways of Alloparental Investments: Direct Versus Indirect

Because alloparenting in humans exists within a social network, alloparenting behaviors can be described in terms of the pathway it takes for the time/energy/resources to be transferred to the child, or how alloparental investments into children “arrive.” Broadly, there are two types of alloparental investment pathways: direct investments and indirect investments.

Direct investments are defined as any form of alloparental time/energy/resource which is transferred directly to the child (Fig. 1). For example, in the Gussi of Western Kenya, mothers reportedly assign “sibling alloparents” to their toddlers who become partly responsible for carrying, feeding, and generally looking after the younger sibling (LeVine et al. 1996). In the UK, stepfathers have been found to provide care to their unrelated young children, including playing with children, reading to them, and feeding them (Emmott and Mace 2014). In Japan, a traditional custom called “otoshidama” exists where kin and non-kin adults gift money directly to children over the New Year

Alloparenting,

Fig. 1 Representation of (a) direct investments and (b) indirect investments by alloparents. Children always receive direct investments. Indirect investments can be transferred to another investor (parent or alloparent) who utilizes it to provide direct investments



period. Under this custom, children generally have the autonomy in how they spend their otoshidama money, and parents are not involved in the “financial transfer” apart from perhaps providing some advice to their children on the ways to spend the money (personal observation by author, EHE). In all these examples, alloparents invest in children *directly* without going through other caregivers and parents.

Note, direct investments do not necessarily require direct contact between the alloparent and child. In the Agta foragers from the Philippines, for example, the majority of observed childcare could be defined as passive, proximity-based care without direct engagement. Here, children stay in camp and play together while adults forage, but one or two older adolescents or older adults would stay behind to “keep an eye” on the children (personal observation by author, AEP). Some may question whether such a minimal investment activity is, in fact, meaningful direct alloparenting. However, regardless of the level of effort involved in passive childcare, alloparents are still likely to be experiencing opportunity costs as they could be doing other activities. While passive childcare is often viewed as an “inferior” type of direct investments in Western cultures, passive childcare can be crucial because, regardless what the caregiver is doing for the majority of the time, alloparents are able to react and help the child when required (Meehan et al. 2013).

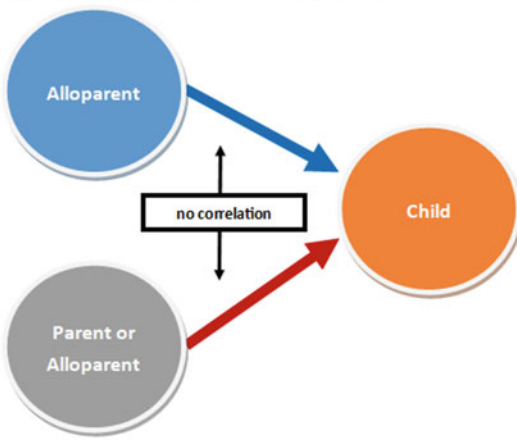
Indirect investments are defined as any form of alloparental time/energy/resource transfer made to an individual, who then *converts* the gained

time/energy/resource into direct investments to the child (Fig. 1). To put it differently, the transfer from an alloparent to the child is fully mediated by an “intermediate” person. Indirect investments can, for example, be directed towards the parent who then uses this extra support to provide care to the child. In rural Ethiopia, maternal grandmothers were found to frequently contribute to heavy domestic tasks, while paternal grandmothers contributed to agricultural labor, which were both associated with greater child survival (Gibson and Mace 2005). Here, while grandmothers were not directly engaging with the children, their indirect contributions to household production and labor were likely “transferred” into child quality. Such activities by alloparents can be classified as indirect investments, as the alloparent raises resources or frees some time for the parent, who is then able to direct investments towards the focal child.

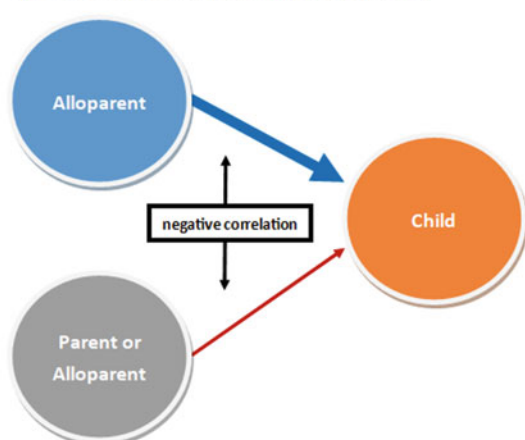
Alloparenting Systems: Substitutive Versus Additive

Within the cooperative childrearing system, direct and indirect alloparental investments do not happen in isolation but exists within a dynamic network of caregivers around the child and parents. All things being equal, alloparental investments are expected to have a beneficial effect on child quality. However, whether or not alloparenting has a “net benefit” for child quality depends on if and how other caregivers react to that alloparenting. Broadly, alloparenting can be *additive*, where it does not influence the level of maternal or paternal investments, or it can be *substitutive*,

A) Additive Alloparental Investments



B) Substitutive Alloparental Investments



Alloparenting, Fig. 2 Representation of (a) additive alloparental investments and (b) substitutive alloparental investments by alloparents. In additive alloparental invest, the amount of alloparental investments do not influence parental investments. In substitutive alloparental

investments, there is a negative correlation in the investments between the alloparent and parent (or another alloparent), where an increase in alloparental investments are associated with a decrease in parental investments

where mothers and/or fathers reduce their investments which is “topped-up” by alloparents. While alloparenting under both systems are expected to benefit parental fitness, substitutive alloparenting is not expected to lead to higher child quality. Depending on the quality of alloparental investments, substitutive alloparenting may even have a detrimental effect on child fitness.

Additive alloparental investments are transfers of time/energy/resources into the child, which does not influence the investment behavior of mothers and/or fathers (Fig. 2). This has sometimes been discussed as “constant breeder input,” where parental investments are insensitive to the behavior of alloparents (Kushnick 2012). Whether alloparenting is additive – as in, whether parental investments are insensitive to the help from others – may depend on whether the parental investment behaviors are replaceable. For example, breastfeeding is (usually) dependent on the mother, and alloparents may have less scope to influence breastfeeding compared to other types of parental investment behaviors (Kushnick 2012), particularly in contexts where formula milk is not readily available.

In an additive alloparenting system, children always experience a “net gain.” Additive

investments are therefore expected to lead to higher child quality, and it may be more likely to be found in contexts where parents optimize child quality over quantity (and therefore parents do not “reduce” investments when others provide help). For example, in a UK sample, contact with maternal and paternal grandparents were not associated with differential levels of maternal or paternal caregiving (Emmott 2015), suggesting grandparental direct investments in this population may be additive. In contemporary China, living near maternal grandparents and availability of them as alloparents was not associated with differential levels of maternal caregiving (Chen et al. 2000).

Substitutive alloparental investments are transfers of time/energy/resources into the child, which then “releases” parents from having to make those investments (Fig. 2). Parents then redirect their energy into other activities, helping them achieve higher fitness. This is sometimes referred to as “load lightening,” where the more help parents receive from alloparents, the less investments they provide to their children (Kushnick 2012). For example, in the Maya and Pume, for every 10% increase in direct alloparental care was associated with a 25% decrease in the probability of maternal caregiving, estimated to be a potential

saving of 165 kcals per day (Kramer and Veile 2018). This suggests that alloparents in these populations were allowing mothers to withdraw from childcare, giving them extra time and energy to carry out other activities. Similarly, in the Aka foragers of the Central African Republic, grandmother caregiving was associated with a reduction in maternal childcare and an increase in maternal foraging activities (Meehan et al. 2013), suggesting grandmothers were substituting maternal caregiving which allowed mothers to divert her time and energy into production.

With substitutive investments, alloparenting does not necessarily lead to a “net gain” for children due to the reduced investments from mothers and/or fathers. For example, in the Maya and Pume example previously mentioned, direct alloparental care was not associated with increased physical child quality, measured by child weight (Kramer and Veile 2018). In fact, if the alloparenting quality is inferior, receiving substitutive investments from alloparents could lead to *reduced* child fitness. For instance, in the UK, availability of grandmothers as alloparents has been associated with lower levels of breastfeeding (Emmott and Mace 2015), presumably as grandmothers are able to “substitute” infant feeding via formula, thereby increasing the incentives for mothers to stop breastfeeding. Given the benefits of breast milk for infant development, such substitutive alloparenting may not be beneficial for children. Similarly, in the Agta foragers, maternal and paternal grandmothers have been observed to become the main caregiver of an infant while the mother temporarily left camp to look for work. However, because this led to breastfeeding cessation, and grandmothers did not have access to formula and/or clean water, it was not uncommon for these infants to become very malnourished, parasitized, suffer from severe gastrointestinal disease, and sometimes die as a result (personal observation by author, AEP). In such cases, alloparenting, despite all the best intentions, does not lead to benefits for the child.

While substitutive investments do not necessarily lead to higher child quality, they may nonetheless increase parental fitness via increased

fertility. Such substitutive investment systems may be more prevalent in populations where it is adaptive for parents to optimize child quantity over quality. For instance, in contemporary Thailand, residence with paternal kin after marriage was associated with higher fertility for parents, but it did not influence child outcomes (Snopkowski and Sear 2013). The consequence of increased fertility may also be increased sibling competition, with potentially negative consequences for child outcomes (Lawson et al. 2012).

Whether alloparenting is substitutive or additive may vary between maternal and paternal kin: From an evolutionary perspective, there is an unequal cost to reproduction between the sexes, where males can reproduce “cheaply” by providing relatively unlimited sperm, while females pay a higher cost due to their larger, limited eggs. In mammals, this is followed by a long gestation and lactation period for females, which is energetically expensive. Because of this asymmetry in the costs in reproduction, we hypothesize a sexual conflict between the sexes where the optimal number of offspring is expected to be higher for males than females. Given this mismatch, there may be greater incentives for paternal kin (i.e., father’s family) to help parents achieve higher fertility by providing substitutive alloparental investments, while maternal kin (i.e., mother’s family) may be better inclined to help parents achieve higher child quality. For instance, in the China example mentioned above, living near or with paternal grandparents was associated with reduced maternal caregiving (Chen et al. 2000), which could be because paternal grandparents “released” mothers from providing childcare so she could reinvest this energy into activities which lead to higher fertility. Similarly, in the Karo Batak subsistence agriculturalists of Indonesia, receiving help from paternal kin was associated with mothers increasing farmwork, while receiving help from maternal kin was associated with mothers spending more time carrying children (Kushnick 2012). This could be because paternal kin facilitated higher levels of maternal production which can be transferred into higher fertility (because female reproduction is limited by resources). In contrast, maternal kin may have

facilitated higher levels of investments into existing children, thereby increasing child quality.

The Evolution of Alloparenting in Humans

When considering the evolution of alloparenting in humans, it is important to note that alloparenting behavior in itself has been observed across many species. In nonhuman primates, allo-mothering (which includes alloparenting and fathering) is common, having been described in 74% of the 154 species where data is available (Tecot and Baden 2015). However, in most species, this behavior is not a defining feature of their breeding system, and may even be “misfired” alloparenting whereby caregiving behaviors are misdirected to non-offspring.

In contrast, alloparenting in humans is arguably a defining feature of human childrearing and is observed across human populations: In the Aka foragers, infants have been found to have, on average, 21 different caregivers which include kin and non-kin (Meehan et al. 2013). In the Hausa of Nigeria (sub-Saharan agriculturalists), children had 4.8 different caregivers on average (LeVine et al. 1996). In contemporary developed populations, parents rely on relatives such as grandparents, aunts, and uncles for childcare, as well as more formal arrangements such as day-care centers and crèches (Allen 2003; Langer and Ribarich 2007).

How did alloparenting evolve to become a diverse yet obligate human characteristic? Researchers have argued that alloparenting is both a cause and consequence of our unusual life-history, which involves a “premature” birth of infants, essentially helpless for a substantial postnatal period, followed by an extended childhood and adolescence. The combination of prematurity and slow growth means that human offspring are particularly dependent on alloparental investments for survival and optimal development into adulthood. It has been hypothesized that the level of alloparenting required is so high in humans that mothers were unable to successfully raise children without alloparents in our

evolutionary history (Hrady 2009). It has also been hypothesized that alloparenting coevolved with other species-typical characteristics such as short interbirth intervals leading to multiple dependent children, and a long, post-reproductive lifespan (Hrady 2009).

Underpinning the species-level evolution of alloparenting and cooperative childrearing are individual-level selection pressures. For the recipient, the fitness benefits of alloparental support seems intuitive, where children and parents who receive time, energy, and/or resources have improved survival and reproduction (Sear and Coall 2011). But why do alloparents help, given that it is associated with some form of cost? As with any form of cooperation, the evolution of such helping behaviors is puzzling due to a “free rider” problem: Those who receive help but do not help in return gain the largest fitness benefit, meaning the “free rider” phenotype would rapidly spread through the population, resulting in the population no longer being cooperative. Therefore, assuming selection pressures act on individual traits, alloparenting would only evolve if there are some kind of fitness benefits from helping. Outlined below are the hypothesized individual fitness benefits for alloparenting which may explain the evolution of cooperative childrearing, focusing on indirect fitness benefits (what alloparents gain via improving the survival/reproduction of their relatives) and direct fitness benefits (what fitness benefits alloparents gain by improving their own survival/reproduction).

Indirect Fitness Benefits

An individual’s inclusive fitness is the sum of their own fitness (i.e., direct fitness) and the fitness of kin (i.e., indirect fitness). Therefore, alloparents may gain indirect benefits by improving the fitness of their relatives. This means alloparenting can evolve via kin selection, where a costly behavior can be selected for if the fitness benefits gained by the receiver (B), weighted by the coefficient of relatedness between the helper and the receiver (r), is larger than the fitness costs incurred by the helper ($rB > C$). In case of additive alloparental investments, investing in related children

is expected to increase the alloparent's inclusive fitness if this resulted in increased survival and future reproductive success of that child. In case of substitutive alloparental investments, alloparenting may increase inclusive fitness by facilitating parents who are relatives to decrease parental investments into a specific child, allowing them to invest more in fertility (i.e., having more children) and/or increasing investments in other children.

If kin selection is an important aspect of alloparenting, we would expect alloparents to preferentially help relatives. Evidence strongly supports the role of relatedness as a driver of alloparenting in humans: For example, across traditional societies, maternal grandmother presence has been found to be more likely to be associated with higher child survival compared to paternal grandmother presence, supposedly due to higher relatedness certainty amongst maternal kin (Sear and Mace 2008). Similarly, in contemporary societies, maternal grandparents have been found to invest more in their grandchildren than paternal grandparents (Pollet et al. 2009).

However, regardless of relatedness, when benefits of cooperation are low, the motivation to allomother can diminish and alloparenting may consequently be withheld. In humans and other animals, evidence suggests that alloparenting is sensitive by broader “pay-offs,” which can be influenced by factors such as reproductive value, resources/wealth and local competition (Sear and Mace 2008). While kin selection and indirect fitness benefits are a pervasive explanation for cooperative behavior, it is important to note that it is not the *sole* explanation for alloparenting. In humans, parents and children frequently live amongst and cooperate with friends and other nonrelatives. Even if parents, children and alloparents are related, alloparents may help for different reasons – gaining both direct *and* indirect fitness benefits. Just because two individuals are related does not mean their cooperation is *only* motivated by indirect fitness benefits. To fully understand why alloparents provide help, it is essential to consider what individuals gain beyond indirect fitness benefits.

Direct Fitness Benefits

Kin selection is unlikely to explain all cases of alloparenting, as cross-cultural evidence suggests humans frequently help raise unrelated children. Instead, alloparents may be motivated to help raise children because they gain a “direct benefit” leading to higher fitness. For instance, individuals may gain valuable parenting experience which improves their parenting skill, leading to higher reproductive success in the future. Alloparenting may also serve as a costly signal which helps alloparents access reproductive opportunities, or it can be part of a reciprocal relationship in the broader cooperative social system. All these pathways may increase the individual's fitness, promoting the maintenance of cooperative childrearing.

Learning-to-Mother/Parenting Experience

The learning-to-mother hypothesis, first proposed by Jane Lancaster, posits that young, non-reproductively active females may alloparent to learn and develop their mothering skills, since more experienced mothers tend to have better infant outcomes. This has been broadened to parenting more generally, where male and female helpers could gain direct benefits via caregiving skills development (Kramer and Veile 2018). Such “parenting practice” could be adaptive for alloparents if offspring are highly vulnerable and dependent on high quality care for survival.

To date, this hypothesis has been mainly discussed in the context of female alloparenting found amongst nonhuman primates. For example, in female vervet monkeys, alloparenting experience before their first birth was associated with higher survival of their firstborn infants (Fairbanks 1990). However, for this hypothesis to be convincing, there are some questions which need to be addressed: First, if infants are so vulnerable, why would mothers allow inexperienced, unskilled individuals to provide childcare? This is likely to *cost* mothers and infants rather than help, and in fact this has been proposed as one of the reasons why alloparenting is not more widely observed among primates (Hrdy 2009). Second, does alloparenting actually lead to parenting skills development and higher

reproductive success in adulthood? The evidence is currently sparse. For example, an analysis of Mayan data found that girls who spent more time in allocare did not have more surviving children as adults (Kramer and Veile 2018). Importantly, the parenting experience hypothesis only applies to direct alloparental investments, involving direct care, and does not explain any form of indirect investments commonly observed among humans. Nonetheless, future studies could investigate the parenting experience hypothesis in humans, for example by explicitly testing whether caregiving by pre-reproductive individuals lead to higher parenting skills in later life.

Costly Signaling and Mating Effort

The Bateman's principle states that male reproductive success is limited by access to females, while female reproductive success is limited by access to resources. This means females across species are generally the choosier sex in terms of reproduction, and males need to compete and advertise their quality. Men may therefore opt to incur the cost of alloparenting as a way to signal his quality, known as "costly signaling." Costly signaling via provisioning for mothers and children may be a particularly important factor for male alloparenting in humans: While nonhuman primate males rarely share food with others, hunting followed by extensive food-sharing is observed widely across forager populations. Some have argued that hunting and food-sharing by men function as a costly signal, where men "show off" their health and skill, becoming more attractive to potential reproductive partners. For example, in the Mermain islanders of Australia, men cooperatively hunt turtles which are shared with the group, meaning turtle-hunters provision parents (indirect alloparental investments) as well as children (direct alloparental investments). In this population, turtle hunting has been argued to be a form of costly signaling as hunting turtles successfully require high levels of skill, which is socially recognized (Smith et al. 2003). Compared to other men, turtle-hunters have more reproductive partners (Smith et al. 2003), suggesting this provisioning activity in this

particular population may be directly benefiting male reproductive success.

Given female reproduction is limited by resources, men could also provide allocare in exchange for mating opportunities, similar in concept to a reciprocal exchange (see "Reciprocity" section below). Alloparenting by stepfathers is one such example, where it has been hypothesized that stepfathers provide care to stepchildren in order to form and maintain a reproductive pair with mothers (Anderson 2000). In the USA, stepfathers were on average less educated and had lower levels of income than fathers (Anderson 2000). Partnering with mothers (rather than women with no children) and helping raise their children may be a way to overcome their "lower provisioning potential," allowing them to successfully partner with a woman and eventually have their own children (Anderson 2000).

Of course, alloparenting as costly signaling and mating effort is primarily applicable to men, or at least for individuals seeking reproductive opportunities – and does not explain alloparenting by other individuals such as women, children, and post-reproductive adults. It is also important to note that whether male provisioning and caregiving functions as a costly signal may depend on population context: In the Tsimane forager-horticulturalists from Boliva, for example, patterns of caregiving by men suggested that men were unlikely to be providing alloparental childcare as a costly signal. This is because men tended to provide care when a child's mother was absent rather than when the child's mother was present (Winking et al. 2009). This suggests that men provided childcare based on the need of alloparenting, rather than the opportunity to "show-off" their potential parenting skills to women. Overall, the costly signaling hypothesis is limited by its ability to alloparenting more generally and is likely to be only applicable to a small proportion of male alloparents.

Reciprocity

Alloparenting may exist as part of a reciprocal cooperative interaction, understood as "I'll scratch your back if you scratch mine." Such cooperation can evolve if the cost of helping

someone in the present is outweighed by the benefits the helper receives in return at some point in the future, lessened by the probability that this benefit may or may not occur. In humans, the probability of not of receiving the later benefit (i.e., not getting your back scratched) may often be small as we have repeated interactions with the same individuals across large sections of our life. Individuals can also be picky about who they interact with, and may preferentially assort with individuals who cooperated with them previously (an in turn, excluding those who do not cooperate).

Researchers have found significant support for reciprocity driving cooperation across different domains of human behavior, although few have explicitly explored the role of reciprocity in childrearing. An exception is work by Jaeggi et al. (2016) who demonstrate the importance of reciprocity in explaining alloparental caregiving in the Tsimane forager-horticulturalists from Boliva. In developed populations, reciprocal interactions around alloparenting often involve financial payment, such as professional nannies and childminders (e.g., see Allen 2003), but studies have also described alloparenting between neighbors and friends as part of a reciprocal arrangement. Interestingly, work in other species suggests that the fitness payoffs of cooperating are higher when the environment is marginal and unpredictable (Jaeggi et al. 2016), and living in larger groups, cooperating and pooling resources can be an adaptive strategy to buffer against environmental fluctuations. In humans, cooperative childrearing may therefore have evolved to mitigate risks that come with less secure, more variable environments. In this system of reciprocal helping, individuals ultimately end up benefitting as they provide help when they can afford to do so, in exchange for help later on when they are in need.

To summarize, alloparenting can be conceptualized as a cooperative behavior involving immediate costs to the helper and benefits to the recipient. Ultimately, alloparenting is hypothesized to only evolve if there is some form of fitness benefit to the helper. In humans, alloparents likely gain benefits in different ways

depending on the context, where alloparenting for close kin brings indirect and direct fitness benefits, while alloparenting for nonrelatives, friends, and strangers is expected to be associated with direct fitness benefits. This multifaceted cooperation likely facilitated and coevolved with the unique human life history, ultimately leading to cooperative childrearing from such a broad range of alloparents becoming an obligate human characteristic.

Key Alloparents Across Cultures

Who helps with childrearing and how they help varies across societies. This is not surprising given the many different selection pressures which encourages (or discourages) alloparenting, meaning the costs and benefits for alloparenting is likely to be context dependent. Nonetheless, there are particular alloparents in humans who have been frequently identified as important for parents and children.

Grandparents

The “Grandmothering hypothesis” states that the unusual postmenopausal lifespan in humans evolved due to the importance of grandmother support for successful reproduction and childrearing (Hrady 2009). It posits that reproductive cessation through menopause facilitates alloparenting, in that grandmothers can care and provide for their grandchildren without experiencing reproductive conflict with the mother. Studies have shown that grandmothers are more willing to provide alloparental investments (Gibson and Mace 2005). Alloparental investments from grandmothers may be particularly important during the “costly” period of infancy and young childhood, when children are particularly dependent on others for support.

Grandparents, particularly maternal grandmothers, may be important alloparents in humans. Assuming paternity certainty, grandmothers are 25% related to their grand-offspring, and therefore gain significant indirect fitness benefits due to this cooperation. A review of kin presence and its associations with child survivorship found that

maternal grandmother presence was positively correlated with child survival in 69% of studies on traditional, natural fertility populations ($n = 46$, Sear and Mace 2008). Paternal grandmothers were positively associated with child survival in 53% of studies ($n = 17$, Sear and Mace 2008). Literature on grandmothers in developed populations also highlight they are important providers of childcare and financial support and may be particularly important for children's psychological and socio-emotional development (Sear and Coall 2011).

However, the importance of grandmothers as alloparents may be context dependent. In developed populations, grandparents may be particularly important caregivers when families are under stress and/or in need of support (Sear and Coall 2011), meaning if families are "doing well," grandmothers may not be particularly important for children and parents. In the Aka foragers, grandmother absence (thereby lack of grandmother alloparenting) was only associated with a negative effect on child developmental outcomes in patrilocal camps, where mothers lived with the father's relatives (Meehan et al. 2014). The authors suggest the association between grandmother absence and poorer child outcomes was not observed in matrilineal camps, because the availability of other maternal kin as alloparents in these camps buffered the "loss" of a grandmother. This highlights that, while grandmothers are important alloparents in a range of cross-cultural populations, wider alloparental networks can also be important for parents and children. Whether or not grandmothers are key alloparents may therefore depend on who else is around to help beyond grandmothers.

Siblings and Other Children

In higher-fertility populations, children often have multiple siblings who can be important caregivers, who frequently provide a lot of the direct alloparenting a child receives (Kramer and Veile 2018). Importantly, in the Pume and Maya, childcare from siblings was not associated with significant decreases in economic activities or education, suggesting children were not suffering from opportunity costs due to their helping

(Kramer and Veile 2018). This suggests that children, and siblings in particular, may be very willing alloparents as they do not suffer enduring fitness costs from being alloparents. Indeed, studies have shown the "benefits" siblings may bring to children: in the Gambia, older sisters were associated with increased survival of younger siblings (Sear and Mace 2008).

However, children can also be competitors for parental investments and household resources. As such, having a large number of siblings, and high levels of sibling competition, may lead to poorer fitness outcomes for children (Lawson et al. 2012). While studies to date investigating the number of siblings and child outcomes in different populations have returned mixed results (Lawson et al. 2012), a large-scale study using data from 27 countries across sub-Saharan Africa found that higher fertility (and therefore more siblings) was associated with higher child mortality, highlighting the possible detrimental effect sibling competition (Lawson et al. 2012). Again, this highlights the importance of local context. In situations where resources or investments are plentiful, siblings may serve as very helpful alloparents. However, in situations where siblings need to compete with each other for resources or investments, siblings may hinder rather than help.

Beyond siblings, other unrelated children can certainly be alloparents. This may be particularly important in societies where children spend time together as a group, such as in the Hadza foragers where children and young adolescents stay in camp and play while adults hunt and forage (Blurton Jones et al. 2005), as well as in developed and developing populations where children spend an extended period of time with each other at school. Among the Aka foragers, where a range of alloparents care for children, unrelated children are described as an important part of the wider caregiving network (Meehan et al. 2013). While children caring for children is not a well-recognized form of caregiving in Western contexts, and in fact sometimes conceptualized as harmful, it is a widely observed behavior which is likely to impact child quality – and studies show children make meaningful contributions as alloparents (Meehan et al. 2013).

Peers of Parents and Other Households

In communal breeding species, other mothers and parents – who may or may not be related – are important sources of support as they pool resources to raise offspring. In humans, parents may form a collaborative network with other households because they live nearby, where parents and alloparents to collaborate to raise children. Often, other households in the collaborative network are relatives: For instance, among the Pimbwe, the number of maternal aunts and uncles who were likely of reproductive age (i.e., mother's adult siblings) was associated with higher child weight, particularly for families with low socioeconomic status where parents and children “in need” benefitted by receiving help from aunts and uncles (Hadley 2004). The benefits of aunts and uncles have also been reported in developed populations, where they are often important caregivers and sources of support for children (Langer and Ribarich 2007). It is important to note, however, that aunts and uncles are not necessarily expected to be beneficial alloparents, and it is likely to be dependent on local context. In situations where parents experience local resource competition with their adult siblings, the presence of aunts and uncles may even be detrimental.

Given that humans live in complex groups and display high levels of cooperation with unrelated individuals, there is potential that non-kin peers and households are also important alloparents. However, at present, the literature on alloparenting by unrelated peers is generally limited, while there is work on the importance of diverse and unrelated social networks. In the Agta (Philippines) and BaYaka (Republic of Congo) foragers, nonrelatives were essential components of mothers' social networks. In these populations, mothers who were directly connected (in terms of proximity) to many individuals in their social network, be them kin or non-kin, had higher fertility. This suggests that having access to a large number of different types of helpers may be important for parents to successfully reproduce (Page et al. 2017). Having a diverse and

flexible social network may be more adapted to tackle variable and unpredictable environments experienced by many hunter-gatherers. In contrast, relying on a limited number of co-resident relatives, who have their own childcare and subsistence demands, may not be an optimal strategy to ensuring childcare demands are met. Overall, this suggests that both individuals beyond your household *and* your relatives are likely to be important alloparents – at least in forager populations – but this requires further exploration. We can also hypothesize that such unrelated peers and households may be of particular importance in low-fertility populations with neolocal norms, as family members may simply be unavailable for alloparental support.

Institutional Alloparents

In many developed settings, the demographic transition and smaller family sizes have meant parents have fewer relatives to rely on as alloparents. This has also coincided with strong nuclear family norms where parents are perceived as primary caregivers of children (Emmott 2015). Arguably, the cooperative childrearing system in developed populations now rely less on informal social networks, but more so on institutional alloparenting where the state and other institutions provide or organize support to help raise children. This includes professional workers whose role is to support families and children, such as social workers and teachers, as well as financial provisioning and subsidies via welfare payments and tax breaks. In Nordic countries, for example, childcare is perceived to be a joint responsibility between the parents and the state, and consequently the state guarantees subsidized or free formal childcare for parents (Emmott 2015). Studies show institutional alloparenting across developed populations may be beneficial for children, with formal childcare associated with better child development (Melhuish 2004). However, the quality of caregiving by institutional alloparents are known to vary, and poor-quality care may have detrimental effects on children's outcomes (Melhuish 2004).

Conclusion

Alloparenting is a diverse yet cross-culturally observed behavior which exists as part of the cooperative childrearing system in humans, hypothesized to have coevolved with our unusual life history. Important alloparents include grandparents, children and siblings, and other households – and in developed populations, institutional alloparenting is provided where the state provides financial transfers for families and/or organizes “professional alloparents.” However, who provides alloparenting and how they help varies within and between populations.

The motivation for alloparents to help raise children depends on the indirect and direct fitness benefits they gain from cooperating. Therefore, in trying to understand the ultimate reasons behind alloparenting (or why alloparenting exists), it is important to consider a multitude of factors such as what individuals gain from helping kin, if they learn new skills, if they achieve social standing, or whether helping now ensures that they receive help in the future. Nonetheless, in particularly harsh environments, co-operators may become competitors for resources. In this sense, an evolutionary approach to alloparenting predicts variations in the structure and nature of cooperative childrearing systems depending on the local population context. In some populations, particular types of kin may be important – such as grandparents and siblings. In other populations, it may be fellow parents and other households who mainly contribute and support childrearing. Whatever the form of cooperative childrearing systems, however, what is clear is that humans require additional support from alloparents for successful childrearing and reproduction.

Cross-References

- ▶ [Adoption Preferences](#)
- ▶ [Childcare](#)
- ▶ [Child Care](#)
- ▶ [Consolidating Familial Power](#)
- ▶ [Cooperation](#)

- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Forms of Adoption](#)
- ▶ [Function of Adoption](#)
- ▶ [Grandfather Investment Versus Grandmother Investment](#)
- ▶ [Grandparenting](#)
- ▶ [Helping](#)
- ▶ [Kin Selection](#)
- ▶ [Maternal Grandmother Invests Most](#)
- ▶ [Mothers and Maternal Grandmothers and Childhood Survival](#)
- ▶ [Nonhuman Reciprocal Altruism](#)

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Alloparenting and Female Same-Sex Behavior

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Synonyms

Bisexuality; Helpers at the nest; Same-sex behavior

Definition

The alloparenting hypothesis posits that female sexual fluidity – “situation-dependent flexibility in women’s sexual responsiveness. . .that makes it possible for some women to experience desires for either men or women under certain circumstances, regardless of their overall sexual orientation” (Diamond 2008, p. 3) – was selected because it facilitated the acquisition of and bonding to an alloparent (a non-biological caregiver for one’s offspring).

Introduction

As Darwin outlined in *The Descent of Man* (1871), reproduction is the engine of evolution. Sexual selection favors traits that increase an organism’s ability to reproduce; therefore, seemingly counterproductive behaviors such as same-sex sexual activity and romantic relationships

pose an evolutionary puzzle. Although there have been several hypotheses put forward to attempt to explain same-sex sexual behavior in men [cite relevant Encyclopedia entries here], relatively little has been posed to explain such behavior in women. One exception is Kuhle and Radtke's (2013; see also Kuhle 2013) alloparenting hypothesis positing that sexual fluidity in women evolved as an adaptation that increased ancestral women's abilities to form pair-bonds with females who could help them rear children to reproductive age.

Alloparenting

Alloparenting has been observed in an array of species and is particularly common in our primate cousins (Hrdy 1999). Among squirrel monkeys, relatives and non-kin engage in reciprocal alloparenting of infants (Roulin 2002; Williams et al. 1994). Among Japanese macaques, mothers allow other females to hold, watch, and protect infants (Bardi et al. 2001; Redmond 2008). Bonobo females form strong pair-bonds that last the duration of their lives (Furuichi 2011; Kano 1992). When a female reproduces, other females are significantly involved in the life of the young bonobo (De Lathouwers and Van Elsacker 2004; Furuichi 2011; Kano 1992). To cement pair-bonds within the troop, female bonobos engage in various forms of sex with troop members, especially with females who may serve as allomothers.

In humans, Kuhle and Radtke (2013) argue that alloparenting may have been a way for ancestral women to acquire a second form of parental investment for their children in the face of paternal desertion, death, or divestment of resources. Hrdy (1999, 2007, 2008) surmises that without cooperation from both kin and non-kin alloparents, humans may have been unable to flourish as a species because human infants are so altricial. Close kin are not always the dominant allo-caregiver; unrelated women often contribute substantial allomothing across cultures (Bentley and Mace 2009; Hrdy 1999; Meehan 2009).

Sexual Fluidity

Relative to men, women are more likely to report bisexual attractions than exclusive same-sex attractions (Baumeister 2000; Diamond 2006, 2007, 2008; Peplau 2001; Peplau and Garnets 2000). Additionally, US women aged 18–44 years are more than twice as likely as men to report being attracted to and having had sexual contact with members of the same sex (Chandra et al. 2011). Women's fluid sexuality is also evidenced physiologically (Chivers 2005, 2010). As opposed to men, women do not experience a significantly greater genital arousal from stimuli of their preferred versus non-preferred sex (Chivers and Bailey 2005; Chivers et al. 2004).

For the present purposes, a fluid sexuality is one that is potentially sexually responsive to both sexes (but not necessarily at the same point in time). It avoids a focus on changes in one's sexual identity or sexual orientation.

Sexual Fluidity as a Conditional Female Mating Strategy

According to the alloparenting hypothesis, sexual fluidity increased ancestral women's reproductive success by diminishing the costs of four adaptive problems that resulted in a deficiency of paternal investment and by promoting the acquisition of allomothing investment from unrelated women: (1) an absence of paternal investment due to rape, (2) reduced paternal investment due to paternal defection, (3) reduced paternal investment due to paternal death, (4) and reduced paternal investment due to a dilution of resources (Kuhle and Radtke 2013). Under this view, most heterosexual women are born with the capacity to form romantic bonds with both sexes. Female sexual fluidity is a conditional reproductive strategy where the pursuit of men is the default strategy, and same-sex sexual responsiveness is triggered when inadequate paternal investment occurs or when women with alloparenting capabilities are encountered. Sexual selection is hypothesized to have designed sexual responsiveness mechanisms in women that are sensitive to the situations and

experiences that were recurrently associated with the availability of paternal and allomothing investment over evolutionary history. The alloparenting hypothesis makes 14 testable predictions. Although there are several studies relevant to the first three predictions (see original article), no empirical evidence yet exists that bares upon predictions 4–14.

1. Relative to women who have never been abused by their male mates, women who have experienced abuse by male mates will be more likely to have subsequently engaged in same-sex sexual behavior.
2. Relative to women who have never been raped by men, women who have been raped by men are more likely to have subsequently engaged in same-sex sexual behavior.
3. Relative to women who were never abused as children, women who experienced physical or sexual abuse by men during childhood or adolescence will be more likely to have subsequently engaged in same-sex sexual behavior.
4. Women whose husbands divested in them for the sake of other women are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands' investment did not diminish from being diluted among other women.
5. Women whose husbands deserted them are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands remain mated to them.
6. Women whose husbands have died are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands are alive and investing in them.
7. In the absence of paternal defection, desertion, and death, wives of husbands whose investment has diminished are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands' investment is sufficient.
8. A woman's mate value (MV) will be an important moderating variable on her likelihood of engaging in same-sex sexual behavior. All things being equal, lower MV women will be more likely than higher MV women to engage in same-sex sexual behavior in the face of male abuse, rape, divestment, desertion, and death because they are less able to acquire sufficient paternal investment from other men.
9. Women who have formed deeper, emotional friendships with women who exhibit alloparenting potential are more likely to have engaged in same-sex sexual behavior than women with fewer such friendships.
10. Women who experience extreme stress associated with childrearing are more likely to report having engaged in same-sex sexual behavior than women without such stress.
11. Women with an unrestricted sociosexuality (Jackson and Kirkpatrick, 2007; Simpson and Gangestad, 1991) will be more likely to engage in same-sex sexual behavior than women with a restricted sociosexuality. The more willing and comfortable a woman is in engaging in casual sex without love, commitment, or closeness, the more likely she is to experience a dearth of paternal investment postpartum and hence need allomothing investment.
12. Women with few kin available to alloparent will be more likely to engage in same-sex sexual behavior than women with abundant alloparenting help from kin.
13. Women will be more likely to engage in same-sex sexual behavior during non-fertile versus fertile phases of their menstrual cycles. In the context of a plural marriage, same-sex sexual behavior during ovulation comes with opportunity costs that detract from reproduction. However, such behavior during non-fertile phases could promote the forming and grooming of alloparenting relationships among women.
14. If sexual fluidity serves to promote female-female bonds, heterosexual women who evidence high levels of fluidity (e.g., the most nonspecific patterns of genital arousal) should have a larger number of close female friends compared to heterosexual women with lower levels of fluidity.

But Why the Sex?

Sex is an effective means of forming, increasing, and sustaining pair-bonds between people (Brigman and Knox 1992; Hazan and Diamond 2000; Leigh 1989; Meston and Buss 2009). Sexual behavior with male mates promotes women's feelings of commitment to these partners (Meston and Buss 2009). A similar process of sexual behavior-induced commitment is likely to occur between female partners. As female same-sex behavior in bonobos appears to increase both the survival of the mother and her offspring (Furuichi 1989; Hohmann and Fruth 2000; Parish 1994, 1996), it is likely that future research will reveal that sexual relations between female bonobos increase pair-bonding and help ensure that a mother's offspring are cared for by alloparents (Radtko 2012). The alloparenting hypothesis suggests that psychological mechanisms underlying a similar process of same-sex sexual behavior in the service of alloparenting evolved in human females and is particularly likely to be triggered among women who encounter an absence of paternal investment, or the availability of allo-mothering investment.

Conclusions

The alloparenting hypothesis entwines several diverse phenomena including (a) female sexual fluidity in human and nonhuman primates; (b) heterosexual women's potent genital arousal to both sexes; (c) the rates of rape, physical abuse; and sexual abuse as a function of sexual orientation; and (d) the ubiquity of alloparenting among human and nonhuman primates. The alloparenting hypothesis also outlines 14 testable predictions, 12 of which specify variables that will shunt some women into forming same-sex romantic bonds that facilitate alloparenting. No other hypothesis for sexual fluidity is as wide ranging or as falsifiable.

Since the engine of evolution is reproduction, same-sex sexual behavior appears to be an enigma. However, it is resolved if, instead of hindering reproduction, the trait actually

facilitates it. In light of the alloparenting hypothesis, a trait that formerly appeared maladaptive – sexual behavior between women – is recast as an adaptive outcome. This hypothesized contingent adaptation may have increased ancestral women's ability to form pair-bonds with women who helped them rear children to reproductive age in the face of male rape, death, desertion, and divestment of resources, as well as during stressful childrearing times, or simply when a suitable allo-mother presented herself. Being born with the ability to go both ways may have been beneficial to ancestral women.

Cross-References

- ▶ [Alloparenting](#)
- ▶ [Alloparenting and Grandparenting](#)
- ▶ [Sexual Identity](#)

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Alloparenting and Grandparenting

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Definition

A system of parenting where people other than the parents act in a parental role and help raise children that are not necessarily their own.

Introduction

As the social animals we are, we have evolved in ways that promote cooperation because

individuals who help each other are more likely to survive in threatening environments than those who do not cooperate. Additionally, because the end goal of evolution is not necessarily to survive but to reproduce and pass one's genes on to future generations, we have evolved mechanisms that will increase the chances of survival of our offspring. One such mechanism involves having other members of the group aid in the rearing of a child, a term that is known as alloparenting. The following section describes how alloparenting works, and why people may willingly help raise a child that is not theirs.

Alloparenting

According to Bentley and Mace (2009), alloparenting is when children are cared after by individuals who are not their biological parents. This includes uncles, aunts, grandparents, siblings, or even other members of the community that are not necessarily immediately genetically related to the children. Because females in general tend to have higher parental investment, it should not come off as a surprise that other females of the group are more likely to help a mother with her child than are men. Additionally, because offspring are the future of one's genes, an individual female engaging in alloparenting would have to make sure her child will not incur any harm while in the care of other members. As a result, individuals whom the mothers believe will give the child back without injury are more likely to be trusted by the mother (Hrdy 2009). Non kin members may engage in alloparenting behaviors, but it is typically individuals who are blood-related to the child who are more likely to do so, which supports kin selection theory. An aunt helping raise her nieces and nephews shares more genetic makeup with them than a random member of the community, and thus getting them into the future allows some of her genes to survive as well. Meanwhile, non kin members may also provide help, but the reasons and mechanisms for it may differ from those of family members. While kin selection theory

explains why uncles, sibling, and grandparents engage in alloparenting, reciprocal altruism theory may shed light on why non kin will also help rear a child. A female may agree to care after a child that is not hers because she knows that the child's mother may be more likely to return the favor and care after her own offspring if the need ever arises.

Grandparenting

A very common form of alloparenting is grandparenting. Grandparents have an influence over the development of their grandchildren (Szinovacz 1998) and can affect a grandchild's behavior in both direct and indirect ways, such as directly interacting with them and offering advice. It is not uncommon for the older members of a society to help care after the young. Additionally, when it comes to grandparents, it is the mother's parents who typically invest more in grandchildren than the father's parents. This may be due to differences in paternal certainty; the mother's mother can be absolutely sure that her grandchildren are hers, and although the mother's father has a chance that his daughter is not his, which would mean the grandchildren share no genetic makeup with him, he can at least know the children are the mother's. Grandparents from the father's side, however, have no way of knowing if his son has been cuckolded and if any grandchildren are theirs. As a result, the maternal grandmother tends to invest more than the paternal grandmother, and the same goes for the grandfathers.

A prevailing question in evolutionary psychology is why women stop being fertile at a given age. After all, if the end goal is the further reproduction of one's gene, shouldn't natural selection favor longer reproductive periods? Hrdy's (2009) grandmother hypothesis offers a possible explanation of why women experience menopause. This hypothesis suggests that women become infertile at a certain point in their life to stop focusing on having children and to start focusing on taking care of the children and grandchildren

they already have. Infertile women in hunter-gatherer societies still collect as much food and work as much as they did during their reproductive years. This means they can provide for any kin they may have, and because grandchildren share a portion of their genes with their grandmothers, investing in the survival of the young would have benefits for the grandmothers' genes. By staying active in caring for her children and grandchildren, an elderly female can help her daughter eat and stay healthy so that the daughter can focus on bearing more children and provide extra resources to ensure the children's survival. To support this idea, women with a strong relationship with their mothers are more likely to have more children themselves and to start having them at a younger age than women who do not have close relationships with their mothers. Additionally, grandchildren of grandmothers who did not live long enough to help their daughter reproduce are less likely to survive past infancy.

Conclusion

Alloparenting is an effective strategy to increase the likelihood that one's offspring survive. Members who are not genetically related to a child may still help raise him or her, but perhaps because of an unspoken expectation that the favor be returned (reciprocal altruism), whereas other kin members such as uncles, aunts, siblings, and grandparents may aid in the rearing of a child because the child is still a vehicle of some of the kin member's genes. Additionally, grandparents, particularly grandmothers, seem particularly prone to invest time in their grandchildren.

Cross-References

- ▶ [Differential Parental Investment](#)
- ▶ [Maternal Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)

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Alloparents

- ▶ [Grandparenting](#)
- ▶ [Higher Survival with Older Siblings](#)
- ▶ [Kinship and Emotional Closeness](#)
- ▶ [Presence of Siblings](#)

Allopreening

- ▶ [Cooperative Grooming](#)

Alms

- ▶ [Charity](#)

Alpha, Beta, and Gamma Males

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Synonyms

[Male status](#); [Rank order](#); [Social hierarchy](#)

Definition

The ranked order of males within a group.

Introduction

The terms alpha, beta, and gamma male are typically used to describe an individual's position within a social hierarchy. In linear hierarchies, alpha males are the highest-ranking males within a group, followed by beta, and then gamma males. While this section is focused on male social status, it should be noted that females can also form strong social hierarchies. Dominance hierarchies can commonly be found in taxa exhibiting group living, where frequent conflict among individuals can occur. Individual rank can be used to predict the outcome of agonistic interactions between males and thus be used to deter some of these aggressive encounters. This section will discuss some examples of how these terms are used across a variety of taxa.

Nonhuman Primates

Much of the research on dominance hierarchies comes from studies on nonhuman primates. In these groups, a male's rank is based on a combination of age, health, competitive ability, and even maternal status. As such, males achieving alpha status are usually in their prime. While these hierarchies can be relatively stable, a male's ranking is not permanent. One's status can change as other males enter or leave groups or through rank changes within a group (Hamilton and Bulger 1990). Since challenges to alpha males can result in severe injury, males will often remain in their natal group until they reach their physical peak. The tenure of any alpha male can vary greatly among species but can be very short-lived, in some cases shorter than 6 months (Hamilton and Bulger 1990).

The position of an alpha male can incur significant costs to the individual. Higher-ranking males participate more in activities related to policing group conflicts and are often under threat

of takeover by other males. However, one primary advantage of maintaining alpha status is obtaining higher reproductive fitness compared to other males in the group. Alpha males have priority access to ovulating females and fertilize a significantly higher proportion of offspring during their tenure compared to males in subordinate positions (Jack and Fedigan 2006). In multi-male groups, the reproductive skew between alphas and other males can be striking, but there is large variation among primates (Hagar 2003). Some of this variation in reproductive skew is likely driven by social interactions between alphas and other males. Males of varying status will form alliances, which can either reinforce current male rankings or overthrow an established alpha. In return for their help in these endeavors, alphas may "exchange" breeding opportunities with these subordinates (Snyder-Mackler et al. 2012), leading to higher reproductive success of beta or gamma males.

Canines

The term alpha male is often used in association with canines to designate the highest-ranking male within a pack. Much of the early work on social hierarchies in canines came from studies of captive wolf populations. In these populations, multi-male and female groups can consist of non-related individuals, which form structured social hierarchies in both sexes (Rabb et al. 1967). The alpha male and female are the main breeding pair and can behaviorally restrict the courtship of other adults in the pack (Rabb et al. 1967). While relatively stable, changes in social status can occur if an alpha is removed or becomes injured. Also, alphas can form alliances with other males to protect and shield one another during attacks (Rabb et al. 1967). However, it is possible that if the status of the alpha male declines, so does the status of his associated males.

The packs of wild populations are very different than those of captive populations. In the wild, packs tend to consist of familial groups that include parents and their offspring (Mech 1999). Although multifamily packs can exist, this is rare.

The alpha male and female are the primary breeders of the pack. Once offspring reach a certain age, they will leave the natal pack to form their own in a different territory (Mech 1999). Alpha males are also responsible for scent marking their specific territories (Peterson and Page 1988), which can be maintained over multiple years. When conflicts arise between packs, it is the alpha individuals that primarily participate in these aggressive interactions (Peterson and Page 1988).

Like wild wolves, African wild dogs (*Lycaon pictus*) form familial packs consisting of an alpha breeding pair, their offspring, and sometimes the siblings of one of the alphas. The siblings are subdominant to the alpha pair but will cooperatively participate in hunting and protecting the offspring (Malcolm and Marten 1982). While there are some instances of subdominants mating with one of the alpha pair, the proportion of offspring subdominant males successfully fertilize is currently unclear.

Birds

Dominance hierarchies are often associated with group living; however, alpha/beta relationships can occur in non-group-living species. In the lance-tailed manakin (*Chiroxiphia lanceolata*), males form long-term cooperative breeding groups, with one male being dominant to one or more unrelated males. This species has a lekking mating system where males and females congregate and compete for mates during the breeding period. Alpha and beta males cooperate in performing elaborate mating displays to attract females. The energetic investment that beta males make in the partnership can be costly. They can engage in excess of three million duet calls and spend more than 1000 h performing displays during their time with an alpha male (McDonald and Potts 1994). However, alpha males obtain the majority of the reproductive success from these parings, and beta males rarely mate. Beta males do eventually benefit by the fact that they are more likely to become an alpha male if they have participated in these cooperative

groups (McDonald and Potts 1994). Succession in this group is hierarchical with beta males moving into the alpha position once it is vacant.

Marine Isopods

While the terms alpha, beta, and gamma are usually related to male rank within social hierarchies, it should be noted that this is not always the case. In the marine isopod (*Paracerceis sculpta*), these terms are used to describe three different male reproductive morphs (Shuster and Wade 1991). The morphs are genetically determined by a single autosomal locus and represent alternative mating strategies. Alpha males are the largest morph and defend females within the central cavity of intertidal sponges (spongocoels). Beta males are intermediate in size and resemble females. These males mimic female behavior to enter spongocoels occupied by alpha males and females. Gamma males are much smaller than the other two morphs and effectively sneak into occupied spongocoels. The reproductive success of each morph is dependent upon the relative density of males and females within the spongocoel. When only one female is present, the alpha male fertilizes the majority of the offspring (Shuster and Wade 1991). As the number of females increases, the reproductive success of beta and gamma males increases and can surpass the alpha male. Across natural populations, the average reproductive fitness of each morph is relatively equal (Shuster and Wade 1991).

Conclusion

Social hierarchies can dictate how individuals interact with one another within a group. In group-living species, male ranking is typically correlated with male reproductive success, with alpha males receiving most of the mating opportunities. Beta and gamma males will contribute to the group and may form alliances with an alpha, sometimes in exchange for mating opportunities. Beta males may also cooperate to increase their likelihood of obtaining the alpha position once it

becomes vacant. While these ranked terms often indicate male social status, it should be noted that they can also be used to describe different male alternative reproductive tactics in many taxa.

Cross-References

- [Making the Best of a Bad Job](#)
- [Mating Strategy Equilibria](#)
- [Sneak Copulation as an Alternative Mating Strategy](#)

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Alteration

- [Genetic Predispositions](#)

Alternating Attention

- [Selective Attending](#)

Alternative Adaptive Peaks

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Synonyms

[Alternative Strategies](#); [Adaptive Polymorphisms](#); [Adaptive Variation](#)

Definition

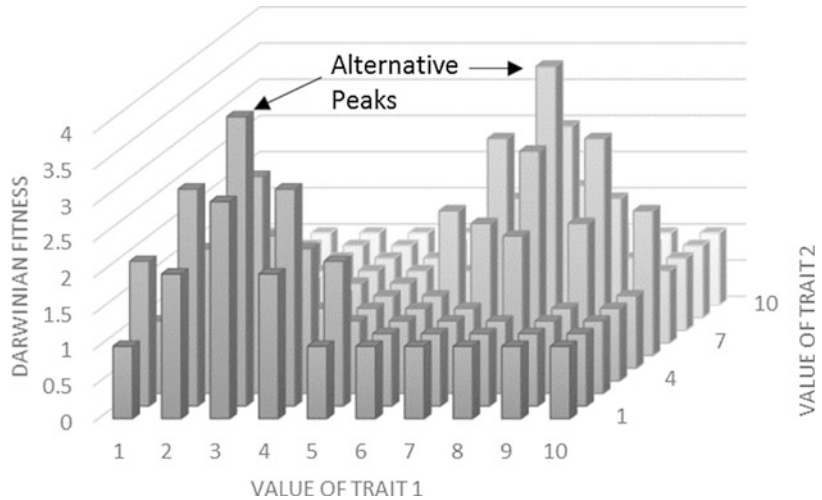
A set of two or more phenotypic states that result in higher fitness than other states. This is in contrast to situations in which there is a single optimal phenotype, with all variation surrounding that optimum being maladaptive.

Introduction

Sewall Wright introduced the concept of the fitness landscape to visualize the relationship between an organism's genotype or phenotype and its Darwinian fitness (Wright 1932). In most such visualizations, fitness is represented on a vertical Z-axis, such that the highest points on the landscape produce “adaptive peaks” centered over phenotypic combinations (on the X and Y axes) that have the highest fitness (Fig. 1). Adaptive processes, specifically natural selection or learning, are expected to move the phenotypes of populations or individuals from lower points on the landscape towards the

Alternative Adaptive Peaks, Fig. 1

A 3-axis fitness landscape with alternative adaptive peaks. The horizontal axes represent the phenotypic state of two traits (1 and 2), while the vertical axis represents the Darwinian fitness of individuals with particular combinations of traits. In this landscape, there are two alternative adaptive peaks: Trait 1 = 3, Trait 2 = 2, and Trait 1 = 8, and Trait 2 = 6



adaptive peaks. In some cases, there will be more than one peak on an adaptive landscape, alternative adaptive peaks (Fig. 1).

The fitness landscape is likely to be dynamic, such that the height and position of peaks are shifting when any aspect of the environment (including the social environment) changes (Lewontin 1978). When populations find themselves in valleys, adaptive processes should drive their phenotypes to the nearest peak. In some cases, populations can climb toward local peaks (local optima) that are shorter than the highest peak (global optimum), thus expressing phenotypes that are less optimal than other possible phenotypes. Traditional gradualist models of evolution predict that it will be difficult for populations on a local optimum to shift to a higher optimum as the population must first pass through an adaptive valley, in which phenotypes are less fit than they were at the local optimum. Sewall Wright argued that some combination of large mutations and genetic drift would allow small subpopulations to form phenotypes distant enough from local maxima that they reach the valleys (or saddles) of landscapes where selection will allow them to climb higher alternative peaks.

Alternative Adaptive Peaks

The fitness landscape metaphor has been used to help explain the persistence of adaptive genetic

and phenotypic variation in populations, for example, the existence of personalities in humans (Nettle 2011). Populations with two or more behavioral strategies with equal fitness payoffs can be visualized as a landscape with two or more “alternative adaptive peaks” of equal height. There are two general situations in which such alternative peaks are expected to arise; where there is negative frequency or density dependent selection and where individuals within populations live in environments that vary across space and time.

Negative frequency-dependent selection occurs when the fitness advantage of a behavioral or phenotypic strategy decreases as it is more commonly used. Biological sex ratios represent an example of this type of selection, as whichever sex is more common tends to have lower fitness, thus maintaining a 50:50 sex ratio in most animal species (Maynard Smith 1978). Frequency-dependent selection can be visualized on a dynamic adaptive landscape as the lowering of peaks as they become occupied, and the concurrent rising of less occupied peaks (Arnold et al. 2001). The frequency of each strategy is expected to reach a stable equilibrium when the fitness of individuals using each strategy is equal, when peaks are of equal height.

A classic model of behavioral strategies maintained by negative frequency selection is the producer-scrouter polymorphism of foraging animals (Barnard and Sibly 1981). Producers

invest energy to find or prepare food before consuming it, while scroungers rely on food found and prepared by scroungers. The first individual to scrounge will typically achieve higher fitness than producers, because it has potential access to the food produced by the rest of the population. However, as the frequency of scroungers increases (and the frequency of producers decrease), the fitness payoff for scroungers gets progressively lower, until it matches that of the producers. At this point, the height of adaptive peaks is equal and the frequency of each strategy is at a stable equilibrium.

It has been hypothesized that psychopathy (a cluster of traits including egocentrism and a lack of empathy) is maintained in human populations via negative frequency-dependent selection (Mealey 1995). As with the scrounger strategy, this hypothesis argues that the selfish/cheating behavior only thrives when a larger portion of the population is cooperative and susceptible to exploitation by psychopaths.

A related concept, “competitive disruptive selection,” describes situations in which what would be a single adaptive peak under low competition conditions becomes a stable local minimum when that peak becomes occupied at higher population densities. This would favor the diversification of phenotypes around that minimum. For example, in high population density conditions, where competition for prey is intense, stickleback fish with morphology that differs from the mean are at an advantage in specialized foraging (Svanback and Bolnick 2007).

Alternative peaks may also arise and maintain consistent variation when individuals within populations live in different environments. In this case, one horizontal axis might represent the habitat in which an individual found, while the other represents a trait that its utility depends on habitat. For example, the fitness payoffs for life history strategies, such as early investment in reproduction, depend on features of the habitat in which organisms are living. In a now-classic example of life history variation, Austad (1993) demonstrated that opossums living on islands where there was little risk of predation invested less in early reproduction and more in later

reproduction compared to mainland opossums, where predation greatly reduces the probability of surviving long enough to reproduce later in life.

Adaptive Peaks and Personality

Applying adaptive hypotheses to explain human behavioral variation (e.g., personalities) is a relatively new endeavor, and thus, few studies have been published to date. Gangstad (2011) points out that low amount interculture variation in personality, compared to the consistently large intrapopulation variation, indicates that heterogeneous environments probably do not account for persistence of personality. This pattern instead favors the hypothesis that within environment, processes, like negative frequency dependence, maintain this variation. For example, Sulloway (2011) suggests that birth order effects may be driven by processes akin to competitive disruptive selection, as competition over roles and/or resources within human families favors to development of differences among siblings.

Conclusion

Adaptive peaks and the fitness landscapes on which they reside are useful metaphors for understanding adaptive evolution and development. However, as with most metaphors, the fitness landscape is limited in several ways. In particular, the fitness of individuals surely relies on more than two interacting traits, but our ability to visualize multidimensional landscapes that result when three or more traits influence fitness is limited. Moreover, the instability of the landscape – the degree to which its shape may change from moment to moment makes it difficult to use the landscape to predict where population phenotypes will be moving at evolutionarily relevant timescales (Kaplan 2008).

Cross-References

- [Adaptation and Natural Selection](#)
- [Adaptationist Program, The](#)

- ▶ [Cultural Variation](#)
- ▶ [Daniel Nettle](#)
- ▶ [David Buss](#)
- ▶ [Evolutionary Personality Psychology](#)
- ▶ [Frank Sulloway \(1996\) on Birth Order](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Game Theory](#)
- ▶ [Individual Differences](#)
- ▶ [Life History Strategies](#)
- ▶ [Personality](#)
- ▶ [Sex Ratio](#)

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Alternative Mating Tactic

- ▶ [Sneak Copulation as an Alternative Mating Strategy](#)

Alternative Reproductive Tactics

- ▶ [Making the Best of a Bad Job](#)

Alternative Strategies

- ▶ [Alternative Adaptive Peaks](#)

Altriciality Life Span Hypothesis

- ▶ [Grandmother Hypothesis, The](#)

Altriciality Lifespan Hypothesis

- ▶ [Grandmother Hypothesis of Menopause](#)

Altruism

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Synonyms

[Cooperation](#); [Game theory](#); [Prisoner's dilemma](#)

Definition

when an organism behaves in ways that produce benefits for others with a cost for himself.

Introduction

Evolution is based in adaptive value traits that prevail (reproduce) in a limited-resource environment. Thus, fierce competition should be inevitable. Paradoxically, altruistic acts are widespread in nature and an organizing principle in human societies (Nowak 2006). Hamilton (1963) described the evolution of altruistic behavior as a stable strategy in kinship relations, pointing that such acts are costly to the individual but beneficial to his genes, therefore being a fitness-enhancing strategy. However, cooperative acts are also observed among non-kin, in one-shot interactions (Boyd et al. 2003; Fehr and Gächter 2002; Gächter et al. 2008), and in highly diverse societies (Henrich et al. 2006). When fitness is measured in terms of genetic combined to cultural reproduction, new beneficial forms of altruistic acts can emerge (Nowak 2006). From the enormous amount of data on the subject of altruism, it is possible to describe five scenarios that may favor the occurrence of cooperation as a stable fitness-enhancing strategy: kin selection, direct reciprocity, indirect reciprocity, group selection, and spatial cooperation (Nowak 2006).

Kinship Altruism or Inclusive Fitness

Kinship altruism was first proposed by Hamilton (1963) as a mathematical model to quantify probabilities for altruistic behavior. It states that an altruistic behavior could be a stable strategy when it helps the agent to increase the frequency of his genes in the gene pool. Therefore, it should be directed toward relatives, in the proportion of the relatedness, and only when gains are greater than the losses imposed to the agent (Hamilton 1963, 1964). This description is known as Hamilton's law for kinship altruism.

This model gained solid support from research on brotherly care in female eusocial hymenoptera. These haplodiploid insects show varying degrees

of relatedness with sisters fathered by the same male presenting 0.75 of genetic similarity, mother and brood presenting 0.5, and brothers and sisters presenting only 0.25. Research shows, as predicted by Hamilton's law, that brotherly care in these species varies in a direct relation with the relatedness coefficient (Hare and Trivers 1973; Mueller 1991; Sündstrom et al. 1996).

Direct Reciprocity

Proposed by Trivers (1971) as a model to describe conditions in which natural selection favors altruistic behaviors toward non-kin and even between individuals of different species. As predicted by Hamilton (1963, 1964), in direct reciprocity interactions, the altruistic act may be maintained when the costs for the agent are low and the benefits to the recipient are great (Trivers 1971). Alongside the costs of the act, another critical variable for the occurrence of direct reciprocity altruism is the number of interactions.

The scenario of the prisoner's dilemma (Gale et al. 1951) has been the main model for predictions about direct reciprocity. In the dilemma, two criminals have been apprehended suspected of commit a serious offense. There is no evidence linking the men to this crime. To produce some evidence, the prosecutor proposes a plea bargain to both men in separate: if one of them confesses and implicates the other, the confessor will be set free for compliance, and the other will be imprisoned for 10 years. If both confess, both will remain in jail for 5 years. If none of them confess, both can be convicted of a minor crime and stay in jail for 1 year.

In one-shot interactions between two encounters, the most stable strategy is to defect, that is, to implicate the other (Axelrod 1984; Nowak 2006; Nowak and Highfield 2011; Trivers 1971). By defecting, the encounter is paying no costs and earning benefits. In fixed-number repeated interactions, the most profitable strategy may be the tit for tat (Axelrod 1984), to cooperate in the first interaction (do not confess), and repeat the previous action of the encounter in subsequent interactions, but always to defect in the last interaction. This is so because when the probability of future interactions is high, to cooperate may be an

individually selected strategy once it can be reciprocated. The recipient will also be compelled to reciprocate the cooperation, because, if he defects, the first cooperator may curtail any new cooperative actions toward him. Considering that cooperate is to pay low costs to produce great benefits, he may be losing more fitness by not to reciprocate. But, as it is a fixed-number interaction, the last interaction is identical to a one-shot interaction; thus, defection is again the more beneficial choice (Axelrod 1984). Cooperation, as the best strategy, may only emerge when the two encounters meet repeatedly in an unknown number of interactions and both are able to produce similar amounts of benefits at similar amounts of effort (Trivers 1971).

Additional evidence suggest that a *win-stay, lose-shift* strategy may be more profitable in direct reciprocity interactions than was *tit-for-tat* (Nowak 2006; Nowak and Highfield 2011). The rule in its strategy is to cooperate at the first interaction and then to repeat your own previous choice after winnings and change it otherwise.

Indirect Reciprocity

Altruism is also observed in ephemeral interactions, with no possibility for direct reciprocation. In such scenarios, there is also a benefit for cooperate, in the form of reputation building (Nowak 2006; Nowak and Highfield 2011; Wedekind and Milinski 2000). A person may help a stranger in need because this stranger is a known cooperator. Reputation is here understood as an image score, the person's status within the group, which is assessed by the members of the group and taken into account in social interactions (Wedekind and Milinski 2000).

In a model designed to show the evolution of cooperation through reputation, Nowak (Nowak and Highfield 2011) created a simulation in which each agent meets another only once and is given a choice to provide help or not. For every aid, one unit is added to a personal public score. Nonetheless, for every defection, one unit is removed. It is not possible to know how many times a specific agent cooperated or not, and the "helping score" or image score is only known by a fraction of the population; thus, different agents

have differing levels of information about the same individual. Results showed that when cost-to-benefit ratio is sufficiently low and the amount of information about the encounter's reputations is sufficiently high, cooperation favors a good reputation. Similar results have been found in experiments with humans (Wedekind and Milinski 2000) and nonhuman animals (Bshary and Grutter 2006).

Transmission of reputation depends on third parties' participation and mechanisms for reputation spread like simple observation, gossip, and eavesdropping (Bshary and Grutter 2006; Nowak and Sigmund 2005; Tomasello 2016). Because of the need for information transmission, indirect reciprocity is more probable in small groups or in subgroups of bigger populations (Leimar and Hammerstein 2001; Nowak and Sigmund 1998).

Group Selection

One of the most controversial issues in the puzzly field of altruism is if selection can act on groups as units. The concept of group selection was proposed by Darwin to account for scenarios where intense between-group competition favors costly behavior that improve performance at group level. These costs would be reverted in individual benefits because in frequently cooperative groups, individuals may fare better (Nowak and Highfield 2011).

Defenders of this position present evidence from theoretical (Wilson 1975; Wilson and Sober 1994), simulation models (Boyd et al. 2003; Nowak and Highfield 2011), and laboratory experiments (Fehr and Gächter 2002; Gächter et al. 2008; Gülerk et al. 2006) showing that groups where cooperators abound are richer and less prone to extinction.

In simulation models (Nowak 2006; Nowak and Highfield 2011), similar groups with varying levels of cooperation and defection (pure cooperator, pure defector or mixed group) were created. Members only cooperate or defect within its group, and individuals may reproduce in proportion to individual payoffs. But groups also reproduce. At a certain group size, the group splits in two and the poorest group is extincted. Results showed that group selection favors

pure cooperator groups. However, within mixed groups, defectors reproduced faster than cooperators. That is, in within selection, defectors do better, but in between groups, more cooperators correlate with faster reproduction. Boyd, Gintis, Bowles, and Richerson (2003) also observed the positive effect of a higher number of cooperators on maintenance of stable cooperation, but with better results in groups where altruistic punishment (a costly act to punish defection) was present.

Other important aspect in group selection is migration. In Nowak's model (Nowak and Highfield 2011), migration had a detrimental effect, undermining cooperation. He concluded that for the evolution of group selection, migration must be maintained at low rates. Adversely, in Boyd, Gintis, Bowles, and Richerson (2003) model, immigrants were able to imitate patterns of cooperation and altruistic punishment, maintaining cooperation at high stable levels.

Critics of the idea of group as units of selection are based on the argument that the outcomes of a highly cooperative group act on within-group selection, having between-group selection as a second-order product (Dawkins 1994; Wilson 1973). The basic argument is that for group selection to be a pressure in evolution, group extinction rates must be high enough to compete with individual selection, which is highly improbable in nature (Wilson 1973). That is, group selection may be possible, but does not account for the evolution of cooperation in real-life situations.

Spatial Cooperation

In well-mixed populations where every member has equal chances to interact to one another, defectors tend to be more successful than cooperators (Nowak and Highfield 2011). But it is a common feature in real-life social organizations that some organisms interact more often than others (Nowak 2006; Nowak and Highfield 2011). Some theoretical works have taken into account how the geographic disposition of the agents may influence the occurrence of

cooperation (Killingback and Doebeli 1996; Maynard Smith 1982; Nowak and May 1992).

In simulation models (Nowak 2006; Nowak and Highfield 2011; Nowak and May 1992), members of a group are distributed in a chessboard-like field. Each member interacts only with its eight neighbors in a prisoner's dilemma. After each interaction, the winner earns the loser's spot. Those members were programmed to act as pure (unconditional) cooperators or pure defectors (for variations in strategy, see Killingback and Doebeli 1996). Variation across simulations occurred in the amount of each type of member and its position on the chessboard. Results from interactions were displayed by color pattern; at each trial, blue cells represented cooperators and red for defectors, green showed cells previously occupied by a defector and taken by a cooperator, and yellow showed ex-cooperative cells. General results showed the coexistence of cooperation and defection across different starting frequencies of cooperators versus defectors, with either static or shifting configurations. Average frequency of cooperative interactions ranged around 31.78%, independently of the scenario. Authors concluded that cooperation is a stable strategy, even in the absence of variables as kinship, reciprocity, and altruistic punishment.

Real-life studies in spatial ecology have shown the presence of stable strategies of cooperation in neighbor's interactions (MacLean and Gudelj 2006; Momeni et al. 2013; Nadell et al. 2016). For opposing results, see Hauert and Doebeli (2004). However, the generality of such conclusions is still to be known, once literature, especially from *public goods games* (PGG), suggests that organisms are primarily conditional cooperators (Chaudhuri 2010; Gächter and Thöni 2007; Rabin 1993).

Conclusion

Although costly, altruism is a widespread pattern of behavior present in various species. It may be so because altruistic acts are more probable when

costs to the altruist are low compared to benefits to the recipient and the altruist may be directly benefited by inclusive fitness, in kinship altruism, or in future interactions by reciprocity and other proximal mechanisms.

Proximal mechanisms as reputation, reciprocity, and altruistic punishment may require complex cognitive functions as remembering, language, mind theory, and so on (Nowak 2006; Nowak and Highfield 2011; Tomasello 2016). Thus, altruism may reach its full complexity only in human interactions.

Cross-References

- ▶ Altruism in Kin Selection
- ▶ Cooperation Among Fishes
- ▶ Cooperation Among Nonchimpanzee, Non-human Primates
- ▶ Cooperation in Social Carnivores
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Emotional Closeness Predicted by Relatedness
- ▶ Evolutionary Paradox: Adoption
- ▶ Group Selection
- ▶ Hamilton's Rule and Genetic Relatedness
- ▶ Hamilton's Rule and Kin Investment
- ▶ Hamilton's Rule and Theoretical Implications
- ▶ Helping and Genetic Relatedness
- ▶ Helping and Inclusive Fitness Benefits to Helper
- ▶ Helping and Reproductive Value of the Recipient
- ▶ Helping More Likely with Close Kin than More Distant Kin
- ▶ Moral Language Regulation
- ▶ Moral Tribes
- ▶ Observation of Altruism
- ▶ Primate Cooperation
- ▶ Prisoner's Dilemma and Cooperation
- ▶ Prosocial Behavior
- ▶ Reciprocal Altruism
- ▶ Reputation and Altruism
- ▶ Rescuing Strangers
- ▶ Selection for Cooperative Relationships
- ▶ Significance of Helping

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Altruism Advertises Cooperativeness

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Synonyms

Prosocial behavior

Definition

Altruism refers to benefit provisioning behavior, and cooperation is defined as exchange between two or more individuals which is mutually beneficial.

Introduction

Altruism is defined as a behavior that is beneficial to a receiver but costly to the altruist (Trivers 1971). Altruism is a phenomenon which causes evolutionary theorists trouble when tying it into the overall play of evolution. Why be altruistic to someone you do not know?

The reason why altruism is a puzzling phenomenon is because it is costly in nature. Being altruistic has also been argued to be costly to an individual's fitness, beneficial to the receiver's fitness but at a cost to the altruist. Because of the fitness deficit between altruist

and recipient, Sanchez and Cuesta (2005) argue that altruism should therefore cease to exist over time if it provides us with no direct evolutionary advantage(s). However, we observe altruism in everyday life; giving up one's seat for an elderly person on public transport, helping someone by carrying their shopping, or stopping to help someone in an accident.

Evolutionary theorists have spent decades exploring the psychological mechanisms that drive altruism towards those we are not related to (see Kurzban et al. 2015 for a recent review). According to the principles of natural selection, altruism must have evolved in order to convey benefits to others and to increase one's fitness, otherwise, due to its costly nature, it should not have evolved.

There are several explanations to explain the signaling purpose of altruistic behavior. Explanations derive from individual selection where the altruist expects reward from his or her action (this suggests that altruism is selfish as opposed to selfless – see Ruse 2012). Further explanations derive from indirect and direct reciprocity (Roberts 1998), where altruistic behavior evolves through engaging cooperatively with others. Reputation building has also been proposed (Nowak and Sigmund 1998), where altruism increases one's reputation through continued cooperation with others, thus suggesting a good reputation can be sought from displays of altruism, which signal cooperative intent towards others. Multilevel selection has been used to explain the evolution of altruistic behavior, arguing that natural selection, when operated on a group level, increases the survival of a group. For example, if a group contains more altruists compared to other groups, it increases the likelihood that the group which contains altruistic people will outperform and have increased longevity compared to the group of non-altruists. In relation to cooperativeness, although altruism (at face value) is a costly endeavor, multilevel selection diminishes the personal cost of altruistic behavior, as altruism may advertise cooperativeness through multilevel selection by increasing the survival of a group (Wilson 2015).

Altruism is crucial, on a societal and individual basis, as we need to be both on the receiving end of altruism and be engaging in altruistic displays to survive, particularly through being chosen as partners in cooperative ventures (Ruse 2012). Throughout our evolutionary history, cooperation has been crucial in increasing survival. Even today, cooperation is just as important to governments maintaining relationships with one another, personal and social ventures, with kin or non-kin alike. The decisions we make in everyday life, whether they involve family, friends, acquaintances, enemies, or strangers with whom you are walking along the street, are influenced by conflict and cooperation. Day to day decisions such as deciding whether to confront a colleague about taking advantage of your good nature or deciding whether to deal with the free rider in a group task are both influenced by cooperation or conflict.

For altruism to evolve, the benefits associated with these traits should provide benefits through reciprocating altruistic behavior, leading to cooperation (Kurzban et al. 2015). If the benefits of cooperation are greater than the cost of cooperation, benefits can be accrued by continuously cooperating with those who cooperate with us.

Cooperative tendencies refer to a variety of behaviors and traits. For example, cooperation can encompass altruism, furthering the notion that altruistic behavior signals or advertises cooperative intent (Baumard et al. 2013). Reciprocal altruism (Trivers 1971) suggests that people are altruistic towards others when there is a mutual benefit in being so. This theory suggests that altruism is rewarded through reciprocation, suggesting the benefits of altruism somewhat match, or exceed, the costs of engaging in the altruistic act (Trivers 1971), implying the interaction is repeated, and the recipient will reciprocate in the future, thus leading to cooperative behavior. One of the conditions set by reciprocal altruism is that the altruistic cost should provide a larger benefit to the receiver than the altruist. Manktelow (2012, p. 80) states "If you take a benefit, then you pay a cost." Evidence suggests that humans

are not simply altruistic in order to gain immediate benefits, but altruistic behavior may lead to immediate and/or future gains through cooperative ventures (Stevens and Hauser 2004).

Being cooperative may not always benefit an individual in the short-term and may in fact be costly in the short-term, but actors may “recoup their losses in the future” (Stevens and Hauser 2004; p. 60). Reciprocal altruism has been extensively studied in a range of economic contexts, and due to the societal importance of cooperation, humans have developed cognitive functions to ensure cooperation is embedded into our society, which may also be a reason why cheater detection and free riders are (generally) punished in society. After all, in order to monitor social exchange fairly and prevent others from reaping benefits without paying a cost, we must detect and punish cheaters (Manktelow 2012).

Conclusion

In summary, altruistic behavior can often signal cooperative intent when communicating with others. This can be through direct observation, through reputation building, indirect, and direct reciprocity.

Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Prosocial Behavior](#)

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Altruism Advertises Generosity

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Synonyms

[Cooperation](#); [Public goods](#); [Reciprocity](#)

Definition

Public altruistic actions advertise about personal qualities such as generosity, which can be a signal of abilities, resources, and good social opportunities.

Introduction

Altruism is the intention to benefit others at a cost to oneself (Van Vugt and Van Lange 2013). Altruistic behavior and generosity are in the micro-foundations of social order (Simpson and Willer

2015). Some theories were developed to explain animal and human prosocial outcomes as generosity and cooperation in the evolutionary context: the kinship altruism and the reciprocal altruism theories (Hamilton 1964; Komter 2010), which indicate that altruistic behavior could contribute to increase survival chances among genetically related and non-related individuals. More recently, the competitive altruism theory (Van Vugt et al. 2007) proposed that altruism is the process through which individuals attempt to outcompete each other in terms of generosity, because altruism enhances the status and reputation of the giver (Hardy and Van Vugt 2006).

Altruistic behavior advertises some desirable underlying quality that is costly to obtain and therefore hard to fake, such as resource control, genetic endowment, health, or vigor (Barclay 2010). Generous behavior is one of the many forms of advertising some qualities as potential exchange partners (Van Vugt et al. 2007). Human generosity includes volunteering, donating to charities, and informal helping that contributes to the society's common good. Although generosity is not restricted to human beings, it is a critical part in our evolution as cooperative beings and plays an important role for the maintenance and further evolution of the species (Komter 2010, Glanville et al. 2016).

Along this entry, we discuss how altruism advertises generosity and what is the role that this public generosity plays in the evolutionary fitness of human societies by showing some contributions of altruistic behavior to the survival chances.

Public Generosity as a Status Signal

The reason that organisms cooperate with genetically related individuals can be easily understood by Hamilton's inclusive fitness theory, the kin selection theory. Helping members of your kinship increases your chance to survive because natural selection would favor behaviors that benefit either the organisms themselves or those who share their genes (closely related kin) (Hamilton 1964; Van Vugt et al. 2007). On the other hand,

reciprocal altruism theory (Trivers 1971) offers an explanation about being altruistic toward unrelated organisms. This behavior could be selected if the receiving party is reciprocal to the giver at some point in the future. Thus, providing benefits to other individual leads to reciprocation, which serves the survival chances of all parties involved (Komter 2010).

The reciprocal altruism can be a problem once altruists may be exploited by individuals who fail to reciprocate (Hardy and Van Vugt 2006). So how the cooperation is maintained if the reward of generous acts toward genetic strangers is not certain? Reputation and visibility may be important forces accounting for human generosity and cooperation (Komter 2010). Hardy and Van Vugt (2006) indicate that altruistic actions are in fact a signal about the altruist personal qualities. When altruism is socially displayed, a reputation can be built: the altruistic acts can signal abilities, resources, and good social opportunities, representing more attractive partner because of the signal to provide future benefits (Barclay 2010). Also, altruistic benefits increase social status and thus the likelihood to be chosen as a mate or ally (Hardy and Van Vugt 2006).

Indirect reciprocity theory (Alexander 1987) proposes that altruistics sometimes receive community rewards and support as a compensation because of the public good that these individuals bring to the community (Hardy and Van Vugt 2006). As reward, the group may foster reputation, status, and prestige of the altruistic individual before the group for being generous (Komter 2010). On the other hand, by contributing and building a good reputation of generosity, this individual becomes more attractive to future exchange partners, and its public generosity acts as a signal of evolutionary fitness (Hardy and Van Vugt 2006; Komter 2010).

Although the reciprocity system promotes altruism and cooperation, when reputations are at stake, this is likely to induce a process of competitive altruism because the individuals attempt to outcompete in terms of generosity to have status and reputation as altruistic act consequence (Hardy and Van Vugt 2006). Thus, who behave in generous or cooperative ways receive reputational

rewards as a powerful force that shape prosocial action (Simpson and Willer 2015). According to Hardy and Van Vugt (2006), competitive altruism emerges if the behavior is costly for the actor to display; the behavior is easily observable to others; the signal is a reliable indicator of some underlying trait or characteristic of the signaler; the behavior benefits the actor who displays it in the long run.

Under these circumstances, altruistic and cooperative individuals become more central in the network because of their reputational benefits of prosociality (Komter 2010). The visibility of altruistic actions advertises qualities of generosity and leads to more prosocial behaviors in the community, which create social ties grounded on the selective advantages of altruism (Komter 2010; Simpson and Willer 2015).

Conclusion

Concluding, the public nature of altruistic actions provides a good opportunity to advertise one's generosity. When acts of altruism toward genetic-related or non-related ones are public, they advertise about desirable traits and qualities that cannot be easily observed, such as generosity, which advertises good exchange partners. A practical implication is that altruism in society can be fostered by encouraging people to publicly display their generosity (Hardy and Van Vugt 2006) and that groups can flourish if their constituent members move beyond narrow self-interest (Simpson and Willer 2015).

Cross-References

- [Altruism](#)
- [Evolution of Reciprocal Altruism](#)
- [Indirect Benefits of Altruism](#)

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Altruism Among Nonkin

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Synonyms

[Nonhuman reciprocal altruism](#)

Definition

Nonkin altruism is helping nonrelatives at a cost to one's lifetime reproductive success. By this definition, a strategy of nonkin altruism cannot evolve and persist. If an "altruistic" trait is adaptive, then "altruists" that pay a cost in the short-term to help a nonrelative must gain a net reproductive benefit in the long-term, in which case

the behavior is not altruistic but rather mutually beneficial.

Introduction

The concept of altruism is of great interest to both psychologists and evolutionary biologists, but it has different meanings in each context, which creates a semantic problem for the field of evolutionary psychology and other social sciences concerned with the evolution of human cooperation (West et al. 2011). In psychology, altruism often refers to *intentions and motivations* to help others without regard to one's own self-interest. In evolutionary biology, however, altruism refers to a behavior that increases the recipient's direct fitness (lifetime reproductive success), while decreasing the actor's fitness (Hamilton 1964; West et al. 2007).

Evolutionary Altruism

According to the standard inclusive fitness definition of altruism (Hamilton 1964; West et al. 2007, 2011), altruism between nonkin cannot be evolutionarily stable. Altruism can only be explained by *kin selection*. To understand why, remember that altruists, under this definition, will have on average fewer surviving offspring over a lifetime relative to nonaltruists, resulting in the eventual loss of the altruistic trait in the population. The only way genes underlying the altruistic trait could remain in the population is if genetic relatives, carrying those genes, gain increases in reproduction that counter the loss in reproduction of the altruist (indirect fitness). For this reason, altruism towards nonkin is not common and it is nonadaptive when it does occur.

So why is the term "altruism" heard so frequently? Some authors define altruism as a helping behavior that is costly to the actor in the **short term**. Under this definition, altruism among nonkin is *cooperation* that is initially costly, where *cooperation* is defined as a behavior that benefits another individual (see ► "Reciprocal Altruism and Cooperation for Mutual Benefit"). However,

for any cooperative behavior to evolve, ultimately the benefits must outweigh the initial costs. For example, *reciprocal altruism* is one mechanism of recuperating costs. By giving you my food when you are hungry, I decrease my current fitness by putting my life slightly at risk (a short-term cost). But later if you feed me when I am hungry, then I gain a net benefit from my earlier investment (higher fitness). In this and many cases where the term "altruism" is used, the behavior is not truly altruistic because there is no net cost to lifetime reproductive success. Because of this problem, the term *reciprocal altruism* is often replaced by the term *reciprocity* or *reciprocal cooperation* with the understanding that reciprocal altruism is not truly altruistic (Carter 2014). For information on other forms of cooperation please see ► "Reciprocal Altruism and Cooperation for Mutual Benefit".

Group Selection

Rather than measuring fitness changes relative to the entire population, some authors measure these changes relative to the social group. This definition is used by the *group selection* or *multilevel selection* framework for modeling social evolution, which uses an alternative set of definitions than the traditional definition given above, which are used by *inclusive fitness theory*. Although they can sound quite distinct in words, these two modeling approaches are mathematically equivalent (Lehmann et al. 2007; Marshall 2011; West et al. 2007).

Let us examine how these differences play out using a very simple scenario. Imagine that two warring tribes, the Reds and the Blues, are fighting over resources. The Reds are highly cooperative and vicious fighters. The Blues are not so cooperative, but there are many more of them. Let us assume that all the individuals in both tribes are on average genetically unrelated. Within the Reds is a class of individuals known as Fighters. These warriors have a genetic predisposition to fight and if necessary give up their lives for the good of their tribe. The Blues do not have any individuals willing to do this. Due to the Fighters in the Red Tribe,

the smaller tribe of Reds is beginning to outbreed and outcompete the larger tribe of Blues over a few generations. Let us say that the average fitness of Blue individual is therefore only 0.1. The average fitness of Red individual is let us say 2. But because the Red Fighters were more likely to die during combat and gained no reproductive advantage over other Reds, let us say their average fitness is 1. The question is now, "Is the Fighter trait altruistic?"

Without doing any math at all, it can be seen how inclusive fitness theorists and multilevel selection theorists might answer this question differently. If the Fighters are compared to the whole population, then they are not altruists because the Fighter trait gives them a direct reproductive advantage over the Blues (and hence a benefit relative to the average individual in the population). So, from an inclusive fitness perspective, the Fighter trait would be considered cooperative because it benefits other Reds, but not altruistic, because by helping their tribe succeed, they also help increase their own reproductive success relative to the whole population. In contrast, a multilevel selection approach might view a Fighter as an altruist, because they gained less of an advantage over the Blues, compared to the other Red individuals who were not Fighters. From this perspective, they are altruists *within* the Red tribe. It is important to keep in mind that, if the Fighter trait is adaptive, it must increase the actor's net *inclusive fitness*, regardless of whether it is considered altruistic or not.

Psychological Altruism

Returning to the concept of altruism from a psychological perspective (motivation), how does it relate to the evolutionary definition? First, it is important to note that evolutionary altruism is not necessary to explain psychological altruism. If people who truly cared about the wellbeing of others (i.e., showed psychological altruism) were also on average more likely to survive or reproduce, then this motivational tendency is not evolutionarily altruistic but rather cooperative. Psychological altruism can be explained by many nonaltruistic forms of cooperation enforced by punishment, reciprocity, or indirect reciprocity that lead to

psychological tendencies to care about others under certain contexts or with certain cues. Alternatively, cases of psychological altruism might not be due to any evolutionary process. Evolution explains heritable variation in traits, not specific actions or behaviors and certainly not specific thoughts and motivations. Psychological altruism is a mixture of inherited traits and acquired social norms.

Conclusion

Psychological altruism between nonkin is common and widespread and does not pose an evolutionary puzzle. Evolutionary altruism poses a puzzle whose solution depends on how you define altruism. If altruism is defined as a behavior that on average decreases the actor's lifetime fitness, then altruism is not expected to ever evolve among nonkin. However, under other definitions that measure costs on smaller time intervals or relative to group members, nonkin altruism can be evolutionarily stable.

Cross-References

- ▶ [Altruistic Punishment Enhances Reputation](#)
- ▶ [Nonhuman Reciprocal Altruism](#)
- ▶ [Reciprocal Altruism and Cooperation for Mutual Benefit](#)

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Altruism and Costs to Altruist

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Synonyms

Benefit and cost asymmetries; Benefit to another at cost to self; Cost-benefit analysis; Costs of cooperate; Reproductive benefits must outweigh costs

Definition

The act of producing a benefit to a recipient generates a cost to the behavior.

Introduction

Natural selection may only favor behaviors that benefit the organism performing them. However, altruistic acts, where an individual pay a cost to produce a benefit to another, are widespread in nature. Seen in isolation, altruistic acts may seem counterproductive, and selection should pressure against them. But when analyzed in a wider perspective, including variables such as kinship, reciprocity, reputation, altruistic punishment, and so on, altruistic behavior turns to be a case of reciprocal interaction with benefits to both sides. One of the key features in this wider analysis is the cost-to-benefit analysis.

Cost and Benefit Toward Kin and Nonkin

It is possible to define costs and benefits as states or resources that an organism may pursue or avoid, respectively (Woodford 2019). They are effects of particular behaviors that affect locally the individuals involved in the interaction but also affect the gene pool of the population (Hamilton 1963; Woodford 2019). In evolution, the ultimate goal of any organism is to maximize fitness by reducing costs and increasing gains (Buss 1988). That is the same idea in the rule of cost-benefit analysis: the individual may choose the alternative with higher benefits at lower costs. In the evolution of altruism, the same rationale must be applied: the amount of help perceived (benefit) must be greater than the amount of effort (cost) expended, both measured in terms of reproductive success (Hamilton 1963, 1964; Trivers 1971).

Hamilton (1963, 1964) was the first to propose a description of the controlling variables for altruistic acts to emerge. In his prediction, based on kinship altruism, one important aspect was “if the advantage conferred is large enough compared to the personal disadvantage” (Hamilton 1963, p. 355). The coefficient of relatedness is a critical parameter to predict how an altruistic act is more or less advantageous in terms of natural selection. But even in order to increase inclusive fitness by helping kinship, cost has limits. Costs may be compensated in a direct proportion of genetic relatedness. In Hamilton’s example, in altruistic acts toward siblings, advantage must be at least twice the cost; for half-brothers, profit must be four times the cost; and so on.

Trivers (1971) proposed the description for a stable altruistic interchange between nonkin also based on cost-to-benefit ratio analysis. For reciprocal altruism to thrive, two unrelated individuals must alternate the roles of behavior and recipient with the behavior paying a low cost for a great benefit (he suggested a proportion of 1/20 cost for 1/2 gain), and each individual must be able to pay similar amounts of the cost for similar amounts of gain in future (an undetermined number of) interactions. Individuals may be compelled to altruism in direct reciprocity scenarios because of the certainty of future gains. They are paying

low costs to earn greater benefits in future interactions. Defection in this case means the curtailing of possibilities of substantial help at low costs.

Empirical supporting evidence presents the probability of an altruistic act as aligned to cost-to-benefit analysis in kin and nonkin reciprocal interactions. In Stewart-Williams (2007) study, 295 participants completed a questionnaire about probabilities of offering differing levels of help (low-cost, medium-cost, or high-cost help) to siblings, cousins, acquaintances, or friends. Results showed that for low-cost help, participants were akin to help friends more often, followed closely by siblings, cousins, and then acquaintances. For medium-cost help, siblings and friends were preferred and chosen equally. In high-cost help, siblings would receive more help than any other with cousins and friends in second place with similar results. When reciprocity was at stake, help was more probable to acquaintances, showing a pattern of conditional cooperation expected in nonkin interactions. Such results confirms the predictions about cost-to-benefit ratio analysis: (1) unconditional (nonreciprocal) altruism is preferentially directed to kinship in proportion to the relatedness; (2) the bigger the costs, the fewer and more related the recipients; and (3) reciprocity as a conditional altruistic act is directed to nonkin (for similar results, see Webster (2003)). These predictions are also observed in anthropological data (Essock-Vitale and McGuire 1980) and simulation models (Boyd and Richerson 1992).

In social discounting analysis, it is possible to measure the value of producing a gain to another person with a cost to oneself, at a given social distance (Jin et al. 2017; Jones and Rachlin 2009). Therefore, social discounting may be a measure for the probability of an altruistic act given a certain degree of nearness. Jones and Rachlin (2009) had 103 participants completing questionnaires about three dimensions of discount. On the social discount questionnaire, participants were asked to make an imaginary list of the 100 closest persons to him. The dearest person should be the number one in the list. The last person should be a mere acquaintance. Based on this order, the participants were exposed to a series of hypothetical

choices between keeping some money to themselves and forgoing it in order to give some money to a person from the list. The amounts of money were manipulated at each trial in a way that the amount for the participant suffered a constant decrease while the amount for the other person was fixed. Values started from \$85 for the participant or \$75 for one person of the list until \$0 for the participant or \$75 for someone from the list.

Results showed a direct relation between social proximity and giving up the money for himself in the benefit of a relative or close friend. Many participants changed from money to himself to money to a close person when the decrease in his amount reached \$70, that is, as soon as the benefit for himself was below the benefit to another.

Second-Order Costs: Altruistic Punishment

Cost-to-benefit analysis predicts the occurrence of altruism even concerning second-order costly acts as altruistic punishment. This pattern of behavior may occur in public good scenarios, where each member of a group can benefit from a limited common resource. The maintenance of the good is a shared responsibility. Each member may pay a cost $c > 0$ to produce a benefit b to the common good being $b > c$ (Gintis 2000). Increases in the marginal value of the public good have a double effect: enhancement of the benefits from contribution and reduction of the net costs for contributions (Goeree et al. 2002). Decreases in its value tend to lead to a collapse of the good, the tragedy of the commons (Hardin 1968). Three patterns of behavior can be observed in public goods scenarios: to free ride, benefit from the good without paying any costs; to cooperate only, by paying costs only for the maintenance of the good; and to punish free riding, by paying costs either to the maintenance of the good and to punish free riders.

Altruistic punishment may be worth the cost, only when the cost-to-benefit ratio to the punisher is low, that is, small costs impose great losses, and the frequency of punishing acts declines over time (Boyd et al. 2003). But although the extra costs, altruistic punishment pays back. Evidence shows

that altruistic punishers are preferred partners in interactions (Güerker et al. 2006; Henrich 2006; Nelissen 2008) and they receive more help in future interactions (dos Santos et al. 2010). Besides, groups composed by altruistic punishers are richer, with members cooperating more often and in higher amounts, compared to groups without punishers (Fehr and Gächter 2002; Gächter et al. 2008; Güerker et al. 2006). Compared to the total amount earned by cooperators only, the losses in the average amount earned by punishers are under 2% (Güerker et al. 2006). Additionally, cooperation typically collapsed in the absence of punishment with increasing in free riding frequencies over time (Fehr and Gächter 2002; Boyd et al. 2003; Güerker et al. 2006).

Reputation and Costly Signaling

Altruism is worth the cost even in one-shot interaction with no possibility for reciprocation or punishment for free riding. Such scenario should lead to complete noncooperation, but this collapse can be prevented as long as it contributes to a good image score or reputation (Nowak 2006; Nowak and Highfield 2011; Wedekind and Milinski 2000). Reputation may function as a costly signaling. Costly signaling theory states that altruistic acts return to the behavior as social influence (Gintis et al. 2001). When individuals honestly incur in costs to provide others, they build a reputation as more capable physically and economically. Those traits increase the attractiveness of helpers enhancing their chances to be chosen as sexual partner, ally, or friend, therefore enhancing reproductive success (Barclay 2011; Griskevicius et al. 2007). In costly signaling, the cost-to-benefit ratio is subverted: the more costly the act, the bigger the benefits to the behavior (Jordan et al. 2016).

When reputation is at stake in an economic game (contributions to the group were public), participants contributed with higher amounts (Fox and Guyer 1978; Hardy and Van Vugt 2006; Milinski et al. 2002). Reputation as high contributor paid back as good cooperators were preferred partners in future interactions (Hardy

and Van Vugt 2006); it boosts cooperation in a population, even when such behavior is initially rare (Gintis et al. 2001); and it may prevent the collapse of a public good (Milinski et al. 2002).

It is possible that to cooperate in one scenario may signalize the probabilities of to cooperate in another. Jones and Rachlin (2009) found a parallel between social discounting and cooperation in public good scenarios. Participants who chose to forgo more money to benefit a dear person contributed more with the public good.

The common link among such different scenarios favoring altruism is that part of the benefit returns to the behavior (Brown and Vincent 2008; Nowak 2006). Brown and Vincent (2008) demonstrated that when there is no direct benefit for cooperation, the only stable evolutionary strategy is complete noncooperation.

Conclusion

Theoretical models and the supporting empirical evidence place the cost-to-benefit analysis at the center of the altruism issue. Cost-to-benefit ratio analysis provides accurate previsions about the probability of occurrence of an altruistic act in a myriad of interactions. Thus, an altruistic act can be understood as an individual, selfish strategy that has the helping of others as a mean to an end (Brown and Vincent 2008; Dawkins 1989; Woodford 2019). Brown and Vincent (2008) consider an altruistic act as *enlightened self-interest* behavior and opposed to *tragedy of commons* behavior, to free ride. That is, even in self-interest, to help others is qualitatively different from free ride, and evidence presented here suggest that altruism may be a more profitable selfish strategy.

Cross-References

- ▶ [Benefit and Cost Asymmetries](#)
- ▶ [Benefit to Another at Cost to Self](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Costly Signaling and Altruism](#)
- ▶ [Costs of Punishing](#)
- ▶ [Reproductive Benefits Must Outweigh Costs](#)

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Altruism and Watching Eyes

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Synonyms

Cues of being watched; Eyespots; Observation cues; Prosocial; Social cues; Surveillance cues

Definition

Altruism is a highly prosocial behavior whereby an individual will promote the welfare of others at a cost or risk to themselves. People tend to participate in more altruistic behaviors when they feel like they are being watched by others. The “watching eyes” effect is the phenomenon whereby an image of a pair of eyes can positively influence a person’s altruistic behavior.

Introduction

Altruism is an act that promotes the welfare of others at the cost to the self. It has been the subject of much interest within behavioral sciences (see chapters ► “[Kin Selection Hypothesis](#)” and ► “[Reciprocal Altruism](#)” for further details). Humans however are unusually ubiquitous in displays of altruism toward unrelated strangers and will often engage in competitive altruism (Roberts 1998). *Being seen* to be altruistic by group members could have a number of fitness

benefits. These may include access to mates, resources, and future reciprocal help. For a full background, see topics on costly signalling, competitive altruism, and indirect altruism. It may also promote in-group favor and reduce social ostracism. Such is the strength of the reputation of *being seen* to be altruistic, that even subtle cues of being watched, such as by a pair of eyes, can be enough to promote prosocial behavior. In a seminal paper, Haley and Fessler (2005) demonstrated that prosocial behavior could be manipulated by the presence of visual eyespots. Since 2005, there have been a plethora of laboratory, online, and real-world studies which have supported the “watching eyes” effect. However, in their recent meta-analysis, Northover et al. (2017) suggested the strength of the watching eyes effect is mixed and highlight at least 18 studies in the last 9 years which have obtained nonsignificant results. Significant effects of the watching eyes effect may be therefore conditional on features of the environment, quality of the surveillance cue, participant traits, or methods of data analysis (Northover et al. 2017).

Reputational Fitness Benefits of *Being Seen to Be Altruistic*

Much of human behavior has evolved as a consequence of living in large social groups. For example, when observed, we change our behavior to fit in line with what is socially desirable. As the saying goes, “No man is an island.” Displays of altruism, in particular, has been shown to increase when observed by other group members. For example, in a public goods game study, Hardy and van Vugt (2006) found that donations to group funds significantly increased when donations were made public rather than private. This suggests there are reputational fitness benefits for showing off altruism. These may be twofold: One, it reduces the chance of violating social norms and being ostracized from the group. Two, it heightens chances of future reciprocal help (indirect altruism) and access to resources and mates (costly signalling). From an evolutionary perspective, it pays for someone to behave altruistically when being observed. Those ancestors that increased altruism when watched by others would be at a

fitness advantage over those who did not. But how strong is this evolutionary drive to be *seen to be* an altruist – do we actually need to be watched or do we just need to feel as though we are being watched by others?

Altruism and the Watching Eyes Effect

Research has shown that even subtle cues of being watched can have a significant influence on individuals' altruistic behavior, with some studies showing that this effect can be invoked by simply displaying a pair of eyes on a computer screen or on a poster. In their seminal study, Haley and Fessler (2005) conducted a series of dictator games (psychological scenarios which are used to explore unselfish behavior) and found that a stylized image of a pair of eyes on a computer screen substantially increased generosity among participants (Fig. 1).

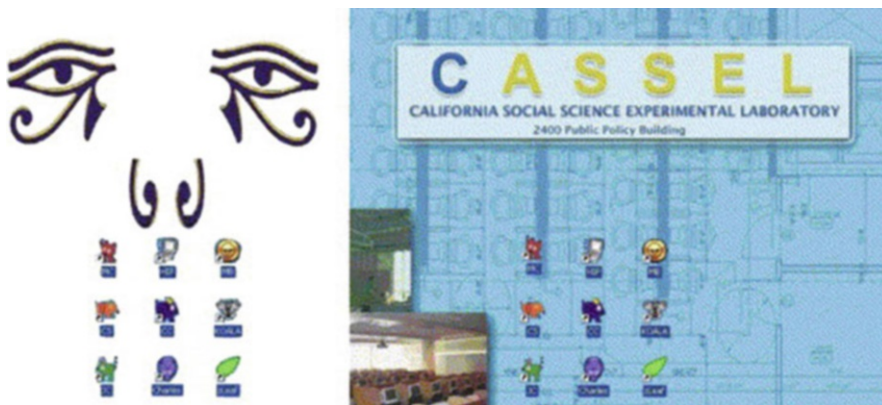
Burnham and Hare (2007) further supported this and showed that feeling of being watched are so intrinsic that even being observed by a robot could increase cooperation. They compared donations to six rounds of a public goods game and found that individuals “watched” by images of a robot; “Kismet,” presented on their computer screen, contributed 29% more than the subjects without Kismet. However, since Haley and Fessler’s (2005) paper was published, there have been both successful replications and null findings reported in the literature. In a 2013 replication,

Nettle et al. (2013) found that while the watching eyes effect did not significantly increase the mean amount of money donated, it did significantly increase the probability of donating something rather than nothing (combined odds ratio 1.39). This suggests that while the watching eyes effect may not increase the donations of the already generous, it could elicit donations from those who may not have originally done so.

Bateson et al. (2006) went further to examined the effect of an image of eyes on contributions to an honesty box and found that when people were exposed to an image of eyes on a nearby noticeboard, they gave three times more money than when they were exposed to an image of flowers. This suggests the watching eyes effect may help at reducing free riders (those who take more from the group than giving back) and encourage group norms (Fig. 2).

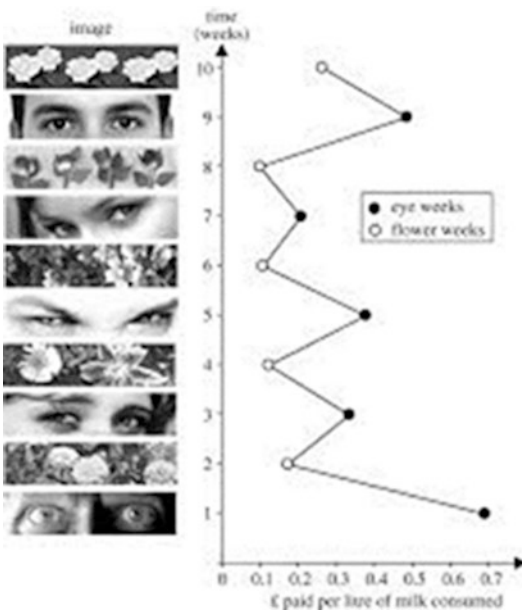
Studies which followed found that prosocial behaviors such as generosity (e.g., charity donations), morality (e.g., a drop in bicycle theft and increased voter turnout), and green behaviors (e.g., a reduction in littering) were substantially enhanced under conditions of “being watched” by images of eyes (for an overview, see Northover et al. 2017).

However, the strength of the watching eyes effect depends on how the eyes themselves are presented. For example, across three studies, with a total of 612 participants, Manesi et al. (2016) found that the gaze of the eyes made a difference; compared to averted eyes or closed eyes, only



Altruism and Watching Eyes, Fig. 1 Eyespots (left) and control (right) desktop displays. (Image of eyes taken from Haley and Fessler’s 2005 paper)

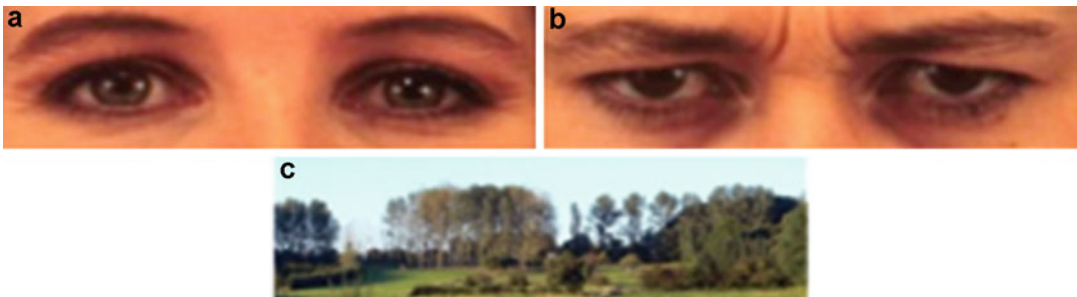
direct eye gaze elicited the desire to help others. Furthermore, the emotion of the eyes can be important. When unkind eyes were compared to kind eyes or a control (images of trees), Pauwels et al. (2017) found that only unkind eyes increased the first mover's motivations to cooperate in a prisoner's dilemma game. In other words, unkind eyes boosted initial cooperation. The authors suggest unkind eyes urge the first mover to live up to the expectation of the interaction partner and conform to social norms (Fig. 3).



Altruism and Watching Eyes, Fig. 2 Image of eyes taken from the Bateson et al. 2006 paper

If a simple image of a pair of eyes on a computer screen or poster is enough to positively influence prosocial behavior, then these results point to a potentially low-cost and simple way of encouraging prosocial behavior in a much wider range of contexts such as reducing food waste, reducing energy consumption, and reducing littering. In fact, the “watching eyes” effect has been used in advertising campaigns by the HMRC aimed at tax evaders and by Keep Britain Tidy in reducing dog fouling.

Other potential avenue of the “watching eyes” effect is in online charity giving. Online charitable donations have been decreasing despite that charities can reach many more potential donors via the Internet than they can via more traditional fundraising methodologies (e.g., door to door canvassing). However, previous studies of the “watching eyes” effect in online environments have failed to find significant results (e.g., Saunders et al. 2016). It has been suggested that this could be because as the online environment is a truly anonymous setting, the eye cues are not effective in making people *feel* like they are being observed, and it is the belief of being watched by another person which is critical in generating the “watching eyes” effect. There is a growing literature which has started to cast doubt on the effect of watching eyes with recent, comprehensive meta-analyses finding no support for the “watching eyes” effect (e.g., Northover et al. 2017). At best, the results have found the “watching eyes” effect to be inconsistent or have found the effect to be heavily conditional on a range of factors. These include the



Altruism and Watching Eyes, Fig. 3 The two types of eye cues, kind eyes (a) and unkind eyes (b), and the control cue (c). (Image of eyes taken from the Pauwels et al. 2017 paper)

environment (e.g., whether the behavior was public vs. anonymous), the type of eye cue (e.g., photo vs. stylized eyes, perceived valence of the eyes image, gender of the eyes image, etc.), participant traits (e.g., gender), or the method of data analysis to name a few factors (see Northover et al. 2017 for a comprehensive list). In short, the finding of more recent research suggests the “watching eyes” effect may not be effective in *all* environmental context.

Since Haley and Fessler’s (2005) influential study, there has been an exponential growth in the use of the Internet with the introduction of companies such as Google and Facebook (to name just a couple). In a time where we are constantly exposed to images of people via the Internet or television and are used to feelings of being watched (e.g., CCTV), perhaps we have become habitualized to these cues and images of eyes are no longer effective in evoking feelings of being observed. The mixed results suggest that any effect of monitoring cues is to some extent dependent on the characteristics of the environment and the specific watching stimuli used. If researchers can pinpoint the characteristics of the environment and the stimuli which can evoke the watching eyes effect, this would provide an inexpensive method of encouraging prosocial behavior which can be utilized in a range of applications from online charitable donations to reducing energy waste.

Conclusion

The “watching eyes” effect posits that altruistic behaviors could be encouraged by making people feel that they are being observed. Despite promising early studies, recent results have become mixed, and there is now doubt to whether the “watching eyes” effect exists in all environmental contexts. However, the “watching eyes” effect is still a potentially fruitful research avenue. By exploring more rigorously the conditions under which subtle cues of being watched could enhance prosocial behaviors, the findings could lend itself as an inexpensive way to encourage a broad range of prosocial actions.

Cross-References

- [Charity](#)
- [Costly Signaling and Altruism](#)
- [Eyespots](#)
- [Game Theory](#)
- [Indirect Benefits of Altruism](#)
- [Kin Selection Hypothesis](#)
- [Prisoner’s Dilemma and Cooperation](#)
- [Prosocial](#)
- [Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reputation and Altruism](#)

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Roberts, G. (1998). Competitive altruism: From reciprocity to the handicap principle. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1394), 427–431. <https://doi.org/10.1098/rspb.1998.0312>.

Saunders, T. J., Taylor, A. H., & Atkinson, Q. D. (2016). No evidence that a range of artificial monitoring cues influence online donations to charity in an MTurk sample. *Royal Society Open Science*, 3, 150710. <https://doi.org/10.1098/rsos.150710>.

equally important in the natural world are behaviors such as grooming, food-sharing, and charity, where an individual organism actually incurs a cost to help benefit another. This contribution will therefore explore why such altruistic behaviors, whereby an individual incurs a cost in order for another to benefit, can be adaptive if they are costly, by looking at the benefits conferred by these acts to others.

Altruism Between Relatives

► C < Rb

Altruism Defined by Benefits Conferred

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Synonyms

Cooperation; Kin selection; Prosocial; Reciprocal altruism

Definition

An act of altruism involves not just a cost to the altruist but also means that another individual will benefit in different ways from the act.

Introduction

The traditional view of evolution by natural selection emphasizes how individual organisms have adaptive traits that aid their *own* survival and reproductive success, so that they pass their own genes onto future generations. When people therefore think of natural selection, they think of traits that benefit an individual directly and often at the expense of others, such as aggression, competition, and dominance, come to mind. However,

The Puzzle of Altruism

Charles Darwin himself recognized that altruism was a challenge to his theory of evolution by natural selection. He knew that it was a common and ubiquitous behavior observed in different species, and that for his theory not to be shown to be false, altruism needed to be shown to be adaptive. Darwin articulated this challenge clearly in *The Descent of Man* (Darwin 1871) when he wrote:

It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those who were the most faithful to their comrades, would be reared in greater numbers than the children of selfish and treacherous parents belonging to the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature. The bravest men, who were always willing to come to the front in war, and who freely risked their lives for others, would on an average perish in larger numbers than other men.

Benefits to the Group

An early attempt to answer how altruism could be adaptive suggested that it is the group, rather than the individual, that is being selected for. Group selection (Wynne-Edwards 1962) suggested that individuals incur costs to be altruistic to others so that their group is more likely to survive. A typical example of this would be a group with a limited amount of food, where each individual group member incurs the cost of low food intake. By doing so, they ensure that all other group members can get enough to eat and therefore the group is maintained and can be successful. Although originally a popular view, theoretically group selection could not work, as a selfish

individual who invaded that group would take all the benefit of available food left by other altruistic group members, leaving the group depleted. In other words, an individual can always exploit any benefit of altruism conferred to a group.

However, in the previous two decades, the notion of selection of groups has made somewhat of a comeback, albeit under a different name. Multi-level selection states that, under certain circumstances, groups of organisms behaving in a certain way (e.g., altruistically) can be selected for in the same way that individual organisms can (Wilson and Sober 1994). As a result, the different levels or “nested hierarchy” of units (e.g., groups, individuals) can all be acted on by natural selection, meaning that all need to be considered when understanding how altruism has evolved.

Benefits to Genetic Relatives

According to William Hamilton (1964), we can look to our kin as the beneficiaries of our altruistic behaviors. This is because these individuals share a number of our genes, and by helping their own survival and reproduction, we in turn are increasing the likelihood that these genes of ours will be present in future generations (albeit in another’s body). This is the principle behind Hamilton’s theory of inclusive fitness and relates to kin selection. Furthermore, the amount of help given to relatives is positively correlated to the amount of relatedness we share with them (in other words, how many genes on average we share with them). Therefore, closer relatives such as siblings of offspring are more likely to benefit from our altruistic acts as we share a large number of genes with them (50%) than would our cousins with whom we share only 12.5% of our genes.

To fully understand how and when relatives can benefit from our altruism, we can use Hamilton’s rule, see Fig. 1.

Therefore the larger the value of relatedness, the greater the difference between the cost to the altruist and the benefit conferred on the recipient can be. An example could be that you are more likely to rescue your sister from a burning building (where there is both high benefit due to high

$$rB > C$$

r is the relatedness between the individuals
B is the benefit to the recipient of the act
C is the cost the actor incurs for performing the act

Altruism Defined by Benefits Conferred, Fig. 1 A summary of Hamilton’s rule

relatedness with your sister and also high costs of the act) than you are your second cousin (where benefit is greatly reduced due to lower relatedness, whereas the costs of entering the burning building are still high).

There is plenty of evidence of the benefits conferred by kin selection in humans. For example, In the USA, individuals are more likely to inherit the wealth of close genetic relatives (Smith et al. 1987). Elsewhere, members of South American tribes are more likely to receive free labor from relatives (Hames 1988) and on the Pacific atoll of Ifaluk, individuals received more shared food from relatives (Betzig and Turke 1986).

Benefits to those Who Helped Previously

Hamilton’s theory of kin selection soon became an established means of explaining how altruism can confer benefits, but it still did not fully explain the many examples we see of altruistic acts, particularly those where the beneficiary is unrelated. In response to this, Robert Trivers developed the theory of Reciprocal Altruism (Trivers 1971). According to this theory, individuals will help another unrelated individual in the expectation that that individual will return the favor in the future. In order for this to occur, Trivers proposed a number of conditions that must exist; first the cost of performing the altruistic act must be less than the benefit that is conferred on the recipient; secondly, reciprocal altruism will only occur in species that are highly social, which ensures that there are regular interactions between individuals for such acts to occur (and be reciprocated); finally, reciprocal altruism will also only occur in species with the necessary cognitive capacities, such as long-term memory, reasoning and perception.

Because of these three conditions, reciprocal altruism has mostly been observed in primate species, such as male baboons who work together at times to usurp higher-ranking males for access to fertile females (Packer 1977) or chimpanzees who use reciprocal altruism for cooperative grooming (Brosnan and de Waal 2002). It can also readily be observed in our everyday lives and exists cross-culturally such as with food-sharing among Hiwi and Ache families (Gurven 2004). It has also been observed in less suspected species such as vampire bats, who share blood meals with others in a group in a reciprocal altruistic way (Wilkinson 1984).

Conclusion

Despite the initial view that altruism was contradictory to Darwin's theory of evolution by natural selection, neo-Darwinian thinkers identified that such selfless behavior can be adaptive for the altruist when the benefits that the receiver gains are examined more. The two traditional explanations for altruism, that of kin selection and reciprocal altruism, changed how psychologists and biologists thought about this behavior and showed that, via increased inclusive fitness or greater returns in the future, it is the altruist themselves who benefits. As such, it raises the question of whether these acts are true altruism or not, as the actual initial costs to an individual of such an act are eventually outweighed by the direct benefits they receive in the long term.

Cross-References

- [Altruism](#)
- [Indirect Benefits of Altruism](#)
- [Kin Selection](#)
- [Reciprocal Altruism](#)

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Altruism Displays Cooperative Potential

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Synonyms

[Conspicuous prosociality](#); [Costly signaling](#); [Impression management](#)

Definition

A conspicuous demonstration of outward prosociality in order to signal one's capacities and inclinations for helping and working with others.

Instances of cooperative activity among individuals that are not kin-related are generally rare

throughout much of the animal kingdom but are a prevalent and enduring feature of human societies; steeped as they are in massive social and cultural complexity. The ability and capacity to forge alliances and engage in cooperative endeavors with conspecifics has created the foundational conditions for humans to build social and normative institutions, develop commerce and legal codes, engage in warfare, and create public infrastructural works for common benefit (Fehr and Fischbacher 2003). Social norms, which establish benchmarks for situational social behavior, and the looming threat of punishment and sanction for those who transgress such norms, serve as the macro-level regulatory mechanism governing large-scale cooperation among humans. At the micro level, cooperation is undergirded by a suite of faculties within the human emotional repertoire, including prosociality, compassion, shame, guilt, and a sense of fairness and othermindedness (Gintis et al. 2003; Lehmann and Keller 2006).

Convergences in common evolutionary history have produced commonalities between humans and non-human primates in terms of the behaviors and preference structures which facilitate cooperation. Activities such as coalition building and support, mobilization of territorial defense systems, engagement in guardianship of children by extended family, and social grooming are all seen across the different primate species. Humans, however, differ markedly in terms of the scale, scope and manifest variety of their cooperative behavior. Cooperative interaction among humans regularly extends beyond the boundaries of the immediate group, and the resulting social ties often endure long after the individuals comprising them have moved beyond occupying the same physical space. Furthermore, humans, unlike our closest primate relatives, exhibit strong generalized preferences for performance outcomes which benefit *others* (Burkart et al. 2009).

A major source of insight from the hominid branching of the evolutionary history of primates has been the advent of cooperative breeding during the Pleistocene era. In this context, early humans, having been presented with novel environmental challenges due to changes in

geographic dispersal, needed to develop new foraging and subsistence strategies in order to acquire sufficient caloric resources in their new habitats (Johnson and Earle 2000). A key part of this overall stratagem was reliance by mothers on other guardians to assume some share of the burden of child-rearing – a phenomenon known as *alloparenting*. Under these conditions, it is thought that humans evolved an increasingly complex array of cognitive faculties purposed toward a kind of proactive prosociality, whereby individuals became more inclined to provide benefits to others in spite of their relatively distal genetic relatedness to them. While other primates engage in some degree of allopaternal care, the degree of kin relatedness in these primate societies is very high when compared to humans. This suggests that the selection pressures that have created the conditions for cooperative behavior among humans differ from those found among other primates (Kramer 2010; Van Schaik and Burkart 2010).

Perhaps the greatest differences in this respect are the dual evolution of cultural and physiological adaptations among humans, and the emergence of massive interdependence within our species. The centrality of information transmitted through culture to the human condition has no analogue in other primates, or indeed any other animal. Relative to other primates, ancestral humans occupied a greater diversity of physical environments and relied on a substantially greater breadth of resources, and therefore had to develop the requisite psychophysiological capacities to navigate these added complexities. Consistent with the cooperative breeding hypothesis, the complications inherent in these vast environmental parameters would have made single guardian child-rearing all the more difficult, and in turn created the conditions through which guardianship from other adults became an adaptive evolutionary imperative. Moreover, as universal participation in all affairs of group life – child-rearing included – became a necessity as humans learned to operate within environmental novelty, an effective and efficient means of transferring knowledge from one individual to another would have demanded additional adaptive solutions. Culture and language represent evolution's

answers to these adaptive puzzles (Smaldino 2014; Tomasello et al. 2012).

Taken together, the increasing interdependence found among ancestral humans, and the vehicle of culture for the efficient interpersonal transmission of survival-contingent information, meant that an effective signaling mechanism for cooperation was required within the human ecological niche. Ancestral humans had to be sure that a potential cooperator was both sufficiently interdependent within the group and a reliable source of accurate, culturally transmitted information. The uniquely human strain of altruism evolved precisely to fulfill such a need for an effective signaling mechanism. Consistent with costly signaling theory – whereby the performance of a costly altruistic act serves as a reliable signal of the altruist's trustworthiness and dependability – altruism functions as an outwardly observable display trait which attests to the cooperative potential of the altruist in question (Fehr and Fischbacher 2003; McAndrew 2002).

Furthermore, the unique complexity of human social structures provides an explanatory basis for the long-term, enduring, and dispersed nature of altruism in our species. Whereas other primates lack the sophisticated capacities for culture that we do, and as such their reputations for altruism are heavily constrained by the immediacy of the group in which they are embedded and the fleetingness of the acts performed and subsequent benefits accrued, the reputational benefits of a single act of altruism could potentially be realized by an individual human throughout the course of a lifetime. The singular performance of some suitably personally costly act might temporarily disadvantage an individual in a highly temporally constricted sense (a consideration which itself might preclude other primates from performing similar acts), but the same individual might amass a greater preponderance of social recognition benefits in the long run. In this sense, an emphasis on the “potential” component of cooperative potential is warranted. Other primates might recognize individual instances of costly altruistic behavior and make assessments of conspecifics accordingly, but there is little to suggest that non-human primates recognize such acts as being meaningfully reflective of the inclination of

altruists to perform other acts of altruism at some unspecified time in the future. Among humans, altruism serves just this end – showcasing itself as a hallmark for cooperative potential generally.

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Altruism in Kin Selection

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Synonyms

[Altruism](#); [Parental care](#); [Inclusive fitness](#)

Definition

When an organism behaves to produce benefits for his kinship with a cost for himself.

$$k > \frac{1}{r}$$

where k stands for the relative gain produced and r represents the coefficient of relatedness or the probability of sharing a gene. That is, altruistic acts will be more probable when the coefficient of relatedness exceeds the cost-to-benefit ratio.

Introduction

The classical natural selection theory cannot account for scenarios where an animal behaves to promote benefits to others by paying its costs (Hamilton 1963, 1964). One possibility to explain such scenarios may be that the recipient of the altruistic act shares some genes with the behavior. The altruistic act, in this way, may reduce the behavior's fitness although enhancing his genes fitness, what is known as inclusive fitness. Therefore, altruistic acts toward relatives may be a fitness-enhancing strategy.

The coefficient of relatedness is the key aspect of kin selection. It is classically expressed in Haldane's words that he would risk his life to save two brothers or eight cousins, but not less (Hamilton 1963; Nowak and Highfield 2011). Such calculation emphasizes the altruistic act as a selfish strategy (Dawkins 1976), based solely in the increasing of gene's fitness.

Evidence for nepotistic behavior abounds (Burnstein 2005). The classical model to draw predictions about kinship altruism come from the studies about brotherly care in female eusocial hymenoptera.

Hamilton's Law of Kinship Altruism

W. D. Hamilton construed his model for the selection of Altruistic acts on a criticism against the idea that an individual behaves in cooperative ways in the benefit of the species. Findings in population genetics at that time already pointed that general adaptive advantages on a group does not affect within group selection (Wright 1948). Besides, he was interested in a mathematical model that could account for predictions about the probability of occurrence of an altruistic act. The first step of Hamilton's law is the broadening of the concept of fitness. While fitness is a measure of an individual's ability to reproduce (Nowak and Highfield 2011), Hamilton (1964) proposed the concept of inclusive fitness as a measure for gene replication not dependent on individuals alone but encompassing also the relatives. That is, an organism may pass on his genes by reproducing and by helping kin to reproduce.

A costly act may favor the inclusive fitness, therefore being selected (1) when behavior and recipient share some genes, (2) in a direct proportion of the amount of genes shared, and (3) when cost-to-benefit ratio is high with small costs producing great benefits. This description was elaborated in the equation:

Studies on Brotherly Care in Female Eusocial Hymenoptera

Because of its haplodiploid reproduction, with males being haploid and females being diploids, the kinship coefficient in eusocial hymenoptera relatives takes a special course. Between sisters fathered by the same male, it reaches 0.75, bigger than the common kinship coefficient of 0.5 between mother and offspring and far superior than the kinship among hymenoptera sisters and brothers (0.25 on average). Such genetic configuration indicates that female hymenoptera produce more fitness by caring their sisters than by breeding or caring their brothers. Thus, studies about sexual behavior and brotherly care in female non-queen hymenoptera can shed light on predictions about inclusive fitness altruism.

Hare and Trivers (1973) showed that although the amount of males and females in haplodiploid colonies is similar, females weighed three times more than their brothers, meaning that their sisters, the workers, fed them more than their brothers.

Mueller (1991) observed possible bias in investment toward brothers or sisters in colonies

of *Augochlorella striata* bees where the foundress queen was either maintained or removed, being replaced by a worker. When a worker becomes the new queen, the other workers will no longer take care of siblings but of nephews and nieces. Results showed that in colonies with replaced queens, males weighed more than females and significantly more than the males from foundresses queen's colonies, suggesting that when kinship among workers and brothers and sisters is the same, there is a bias in investment toward brothers. Sündstrom et al. (1996) observed similar biases in colonies of *Formica exsecta* with monogamic or polyandric queens. In polyandric queen's colonies, the kinship between worker and offspring is equal for males and females, on average. Results showed that in colonies with singly mated queens, the elimination of male eggs is observed, a pattern absent in multiply mated queen colonies. Such evidence points to an inclusive fitness pattern of behavior from hymenoptera workers.

Proximal Mechanisms in Kinship Altruism

One of the major critiques about altruism in kin selection is based on the assumption that altruistic acts toward kin may not require gene sharing, but instead, behavioral characteristics that are preferred in social partners and maintained by proximal mechanisms, as reciprocity (Allen-Arare et al. 2008). That is, altruistic acts are better predicted by a history of reciprocal exchange interactions, regardless of the coefficient of relatedness (Allen-Arare et al. 2008; Chapais 2001; Moore 1992). Support for kin selection as a special type of interaction, apart from reciprocity, should demonstrate that higher frequencies of unreciprocated help happens among kin; the larger the cost, the more related must be agent and recipient; and reciprocal interactions are a necessary feature in nonkin help exchanges (Essock-Vitale and McGuire 1980).

Some anthropological data do support kinship altruism as a special kind of interaction that do not work as the same way as reciprocity. Essock-Vitale and McGuire (1980) resumed qualitative

anthropological descriptions in highly diverse human societies showing that the occurrence of unreciprocated help is more common (above chance level) among closer kin, with distant kin and nonkin reciprocating gifts. While unreciprocated gifts or aid among kin is usually ignored, when it happens among nonkin, consequences are gossiping, the rupture of social ties and the interruption of future gifts.

Morgan (1979) accompanied whale-hunting groups of Yupik Eskimo in Gambell Village, Alaska. Whale hunting is the major economic activity within this group and is a very risky activity with high rates of accidents and life threatens. For each crew, Morgan verified the coefficient of relatedness and its frequency in hunting. He observed that the most active groups had crews mostly composed by close relatives (all males) being either father and sons or brothers and their sons (coefficient of relatedness ranging from 0.33 to 0.55). Large families usually had more than one crew, so they could easily find backup members, and when one crew faced an accident, related crews usually came into aid. Crews composed by nonrelatives had unstable compositions and more difficult to find backup members, and when they faced accidents during hunt, they received less help. If kinship altruism could be reduced to a reciprocity exchanges, there should be no difference among family or nonfamily crews.

On the other hand, there are also evidences showing that reciprocity alone may account for some helping behavior among kin. Gurven et al. (2001) showed that in the indigenous reservation-living Ache people (forager-horticulturists), there is a widespread practice of food distribution between households with clear preference for a household recipient that contains at least one close relative, but the amount of food donated is contingent to previous food exchanges.

Jaeggi and Gurven (2013) showed in a meta-analysis on 32 independent studies on food-sharing behavior in human foragers and non-human primates that when controlling for reciprocity and kinship (only 10 studies), there was no difference in the frequencies of helping behavior, suggesting similar patterns toward kin and nonkin regulated by proximal variables.

Conclusion

Altruistic acts toward kin may be a fitness-enhancing strategy once it provides inclusive fitness and increases the frequency of a gene in the gene pool deemed to the reproduction's success of an organism and its relatives. As predicted by the Hamilton's law, such acts are more probable the more related are the two individuals, with costs being lower than the benefits promoted. Such predictions find strong support in evidence among eusocial hymenoptera. Additional evidence, especially from primatology, suggest, however, that inclusive fitness may be less important for the maintenance of altruism among kin with proximal mechanisms like direct reciprocity and mutualism playing a major role (Allen-Arare et al. 2008; Chapais 2001; Moore 1992).

Cross-References

- [Altruism](#)
- [Cooperation Varies with Genetic Relatedness](#)
- [Genetic Relatedness](#)
- [Hamilton's Rule and Genetic Relatedness](#)
- [R = Coefficient of Relatedness](#)

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Altruism Norms

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Synonyms

[Patterns of helping behavior](#); [Prosocial norms](#)

Definition

Altruism refers to any helping behavior whose intended goal is to improve another's welfare,

typically at some cost to the helper. Altruism norms are defined as the typical patterns of behavior seen surrounding these selfless acts. This chapter will summarize prototypical norms of altruism that are commonly seen in families and societies.

Introduction

Altruism norms have evolved and changed throughout the course of human history and can include things such as self-sacrifice, philanthropy, or just doing a good deed. It has been suggested that altruism is influenced in part by genetic factors but more so by the types of societies to which individuals are exposed (Bell et al. 2009). Altruism can be seen as an evolved mechanism that is molded to fit within the norms of different cultures, yet it operates automatically when loved ones, family members, or even strangers require help.

Kin Selection and Pro-family Norms

Engaging in altruistic behavior can be costly for an individual, but in certain scenarios it could be beneficial (evolutionarily) to better others rather than the self. For instance, if an individual were in a scenario where food needed to be rationed and food supplies were low, it might be more beneficial for this individual to allocate resources to those who would make better use of them (i.e., an elderly individual giving up food supplies to younger individuals). From an evolutionary perspective, this effect would be expected in familial environments as it is more important that the genes survive rather than the individual as copies of one's genes lead to greater genetic fitness than if one were to survive without reproducing. Research has shown that when placed into situations in which various individuals needed help, participants were more likely to help those who were more closely related to them as opposed to those more distantly related (Burnstein et al. 1994). In fact, when asked how likely they would be to donate an organ to someone who desperately needed an organ transplant, most

people preferred to donate their organs to those who were related to them rather than strangers (Borgida et al. 1992). While this could be the result of an individual learning that family takes care of family throughout their upbringing, children are also more willing to help their siblings rather than their friends (Tisak and Tisak 1996). While humans are excellent at recognizing when family members are in need, there are times where family members are forsaken in favor of non-family members.

Altruism Norms and Expectations of Altruism in Society

Although in most cases family would take priority, individuals often act altruistically toward other members of their society. Trivers (1971) believed that this behavior represents reciprocal altruism, or the idea that helping someone now may increase the likelihood of them helping us in the future. Reciprocal altruism affords both the helper and the recipient the possibility for reward, but this requires the helper to have a certain level of trust that the beneficiary will reciprocate at some point. Even though trusting another to reciprocate may be risky at times, engaging in altruism could increase one's genetic fitness. In fact, research has shown that people publicly punish selfish individuals to signal their lack of selfishness, and when individuals engage in costly helping (i.e., altruism), they are seen as more trustworthy by others (Jordan et al. 2016). While being seen as more trustworthy could certainly increase genetic fitness, research has found that people prefer to help attractive target figures. This could suggest that the goal is to increase their own genetic fitness through potentially reproducing with the attractive target figure (Farrelly et al. 2007). While the previous points are on ways in which altruistic behavior can be promoted, studies have shown ways to diminish the likelihood of altruistic behavior. Participants were asked to prepare a talk on the biblical Good Samaritan or a job talk, with the idea being that when they were asked to think about an altruistic figure (e.g., the Good Samaritan), they would, in turn, behave more

altruistically; the results did not support this, with neither being a significant predictor for altruistic behavior. These participants were randomly assigned to be told that they would be late, on time, or early to the following appointment prior to leaving. The researchers found that those participants who were told they were late for their next appointment were significantly less likely to help a stranger in need compared to the other conditions (Darley and Batson 1973). This implies that when helping others is detrimental (e.g., making us late to an important appointment), we are less willing to help them in their times of need.

While being on time can allow individuals to engage in altruistic behavior, recent research on gender roles in altruism has revealed another predictor of altruistic behavior. Rand et al. (2016) found that women are more likely to be expected to engage in altruism rather than men. Not only are women expected to be more altruistic, they experience greater punishment when failing to behave altruistically as compared to men. When participants were asked to use their intuition (rather than deliberation) when deciding to reciprocate an act of altruism, only women showed increased levels of altruism. Furthermore, when women described themselves with more masculine attributes (e.g., dominance), they were less likely to engage in altruism following a deliberation period. While women may be expected to be more altruistic, research has also found that when participants were asked to play games with others, they behaved in a more cooperative manner when they were told their decisions would be made public, rather than private (Hardy and Van Vugt 2006). Those participants who made public, cooperative choices were seen as having a higher social status than those who answered privately. While those are specific examples of individual groups, most societies tend to promote reciprocity norms through the golden rule. This idea seems to work well in societies as people prefer to help those who have helped them at some point in the past (Whatley et al. 1999), suggesting that helping another will result in the recipient of the help being more willing to provide their help at a later date to the helper.

Conclusion

The goal of this chapter was to cover altruism norms, specifically those in families and societies. Individuals tend to prefer to help family members rather than nonfamily members, but this is not always the case. Individuals may choose nonfamily members if the goal is not to necessarily pass on genetic fitness through bettering a family member but rather to secure a mate who displays some desired attribute (e.g., attractiveness). While most societies promote reciprocal altruism through use of the golden rule, individuals may choose to ignore a stranger in need if the cost is perceived to be too great. Additionally, certain traits or physical aspects of a person, such as trustworthiness or gender, may result in them being perceived to behave more altruistically in social situations, but, in general, people prefer to engage in altruistic behavior with those who have helped them in the past.

Cross-References

- [Altruism](#)
- [Kin Altruism](#)
- [Reciprocal Altruism](#)

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Altruistic Behavior

- [Adaptive Problem of Detecting Kinship](#)
- [Alarm Calling and Kinship](#)
- [Kin Recognition](#)

Altruistic Nepotism

- [Alarm Calling Predicted by Inclusive Fitness](#)

Altruistic Punishment

Tünde Paál
Pécs, Hungary

Synonyms

[Costly punishment](#); [Moralistic punishment](#); [Strong negative reciprocity](#)

Definition

A willingness to impose sanctions on norm violators at the punisher's own cost, in the absence of (immediate) material return

Introduction

Altruistic punishment is one of the central mechanisms and manifestations of *strong reciprocity*, the theory of which is regarded today as one of the most influential attempts at explaining the evolution of human cooperation (Bowles and Gintis 2011; Fehr and Fischbacher 2003, 2004; Fehr et al. 2002; Fehr and Gächter 2002; Fehr and Gintis 2007; Fehr and Henrich 2002; Fehr and Rockenbach 2004; Fowler 2005; Gintis et al. 2003, 2008; McElreath et al. 2003). It denotes a predisposition to cooperate with others and a willingness to punish at personal cost those who violate cooperative norms. This altruistic form of punishment has been well documented both in real life and in laboratory experiments. It is altruistic in the sense that it occurs even in situations where no future benefits for the punishing individual or the individual's genes are possible: in one-shot scenarios among strangers under conditions of strict anonymity (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003).

Experimental Evidence

In the laboratory, altruistic punishment has been observed most commonly in experimental games developed within the framework of game theory. In the *ultimatum game*, two players decide over the division of a fixed sum of money. Player A can make one proposal to player B, who can accept or reject it. If B accepts the proposal, the money is shared accordingly; if B rejects, both players receive nothing. Since the game is one-shot and anonymous, the self-interested outcome would be for player A to offer the lowest possible amount and for B to never reject. However, this outcome is almost never achieved: player Bs typically

reject offers lower than 30%, regarding them as unfair, and, anticipating this, player As typically offer around 50% (Fehr and Fischbacher 2005; Gintis et al. 2003).

In the ultimatum game, player Bs are directly affected by player As' proposal. There is evidence, however, that a number of people are willing to employ altruistic punishment against those who behave uncooperatively toward a third person (Fehr and Fischbacher 2004). In the *third-party punishment game*, players A and B take part in a *dictator game*. It has the same structure as the ultimatum game, except that here player B has no option of rejecting A's proposal; she/he has to accept whatever is offered. The game is anonymously observed by player C, who is not affected by player A's decisions. However, C is endowed by a fixed sum of money and has the opportunity to impose a fee upon A after witnessing A's offer. The fee is costly, for one-third of the decided amount is deducted from C's initial endowment. Nevertheless, in the experiment (Fehr and Fischbacher 2004), 55% of Cs punished A for offers below 50%, and the amount of punishment increased with the perceived unfairness of the offer. This tendency of disinterested third parties to use altruistic punishment is in line with the supposed role of strong negative reciprocity as a norm enforcement device in real-life situations, e.g., in the upholding of food sharing norms in hunter-gatherer societies (Bowles and Gintis 2011; Fehr and Fischbacher 2005).

Altruistic punishment has been well documented in multilateral experimental situations, as well. These typically resemble *social dilemmas*: n-person situations in which everyone would gain by cooperation but each individual has an incentive to gain at the expense of the others. The behavior that would be beneficial for all is less profitable for the individual than the selfish alternative, yet it would severely harm the interests of the community if everyone followed self-regarding strategies (Gintis 2009; Van Lange et al. 2007; Van Lange and Joireman 2008; Van Vugt and Van Lange 2006). The *public goods game* is one of the most widely applicable models for such dilemmas (Bowles and Gintis 2011; Camerer and Fehr 2004; Fehr and Gächter 2002; Gintis et al.

2003). This game typically consists of more than one rounds, in groups of $2 + n$ players. In each round, the players are provided with a certain amount of money, and they have to decide how much of it (if any) to contribute to a common account (i.e., the public good) and how much to keep in their own private account. The individual contributions are summed up and multiplied by a factor of usually 3. The resulting sum is then equally divided and added to the players' private accounts, independently of their individual contributions. In public goods games without costly punishment opportunity, the amount contributed to the public good gradually declines over time, which can be explained by the fact that those players who are inclined toward strong reciprocity do not cooperate at any cost – their cooperation is conditioned by the other group members' behavior. In the absence of other options, they signal their dislike of the free riders' strategy by lowering their own contributions. If, however, the players are given the option to use targeted, costly punishment against each other, the game unfolds differently. Sanctioning behavior follows the principles of strong negative reciprocity; the players who impose punishment even at their own expense are those who have an initially cooperative approach to the situation; sanctions are used against those participants who contribute nothing or only substandard amounts to the public good; and, the existence of punishment opportunities results in a stable and high level of contributions, thus re-establishing cooperation. Thus, by acting to raise the level of contributions to the public good, altruistic punishment itself serves as the so-called second-order public good (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Fehr and Gächter 2002).

There is some controversy surrounding the external validity of the experimental findings. In particular, Guala (2012) has argued on the basis of anthropological evidence that the results do not translate from the laboratory to the field. While his critique has sparked intense debate, it seems true that in real-life circumstances people may strive to find other solutions beside costly punishment; alternatively, under the right circumstances, the mere threat of sanctions or purely symbolic

forms (gossip) can serve as incentives for cooperation (Van Lange et al. 2014).

Proximate Mechanisms

It has been suggested that in the experimental scenarios described above, the sole motivation for sanctioning behavior is strategic: the punishers' desire to maximize their payoffs relative to the punished individuals (Price et al. 2002). However, there is evidence indicating that this is not the case. In a prisoner's dilemma experiment by Falk et al. (2005), the cost of punishment was the same for the punisher and the punished player, so it was not possible to influence and affect the difference in payoffs via sanctioning. However, almost 60% of players who cooperated in the game imposed substantial amounts of punishment on defectors. It seems that costly punishment is to a large extent motivated by the negative emotions strong reciprocators feel when observing unfair decisions and the positive emotions induced by their own sanctioning behavior (Bowles and Gintis 2011; Declerck et al. 2013; Fehr et al. 2002; Fehr and Camerer 2007; Rilling et al. 2002). Studies combining neuroimaging methods with economic games have shown that both first-person and third-person punishment behavior activate reward-related brain regions (De Quervain et al. 2004; Strobel et al. 2011). Thus, it seems that humans are endowed with proximate mechanisms that render altruistic punishment pleasurable even when it yields no financial gains.

The punishment mechanism seems to be especially sensitive to structural modifications to the experimental situation. It is highly relevant whether the punishment is costly or cost-free, whether it comes from other members of the group or from an external observer, whether the group composition is stable or changes from round to round, and whether the participants are able to keep track of the earnings of each other during the game; group size and even the nationalities of the players are important modifying features as well (Balliet et al. 2011; Falk et al. 2005; Fehr et al. 2008; Hermann et al. 2008; Nikiforakis

2010). The effectiveness of costly punishment seems to be more pronounced in cultures with higher levels of interpersonal trust (Balliet and Van Lange 2013). At the same time, punishment can serve roles other than the sanctioning of unfair behavior. In some public goods game-type experiments, it has been found that a small but hardly insignificant proportion of the punishment was imposed on those cooperators who earned above average during the earlier rounds of the game (Bochet et al. 2006; Falk et al. 2005). Placing sanctions on cooperators may also serve as revenge; in the case of the so-called antisocial punishment, the defectors retaliate for the punishment they received before from the cooperators themselves (Hermann et al. 2008).

Evolutionary Origins

Costly punishment might yield pleasurable feelings, yet the finding that it is not the most economically beneficial strategy in public goods games (high contributors, who neither receive nor give out punishments, are the most successful) raises the question of the possible evolutionary origins of such an altruistic strategy. The answer may be found in the theories of multilevel selection and gene-culture coevolution. According to the literature (Bowles and Gintis 2011; Gintis et al. 2003), in the relevant evolutionary period of the Pleistocene, intergroup competition constituted a formidable force in the dynamics of human evolution. Human groups often had to face dispersal or extinction threats due to wars, famines, environmental disasters, etc. Groups with a relatively high proportion of strong reciprocators enforcing cooperation norms were much more likely to survive such events. Moreover, humans have unique cognitive and emotional capabilities enabling us to create and communicate social norms, among which are norms of altruism, cooperation, and the suppression of within-group competition. In such circumstances, within-group selection forces acting against strong reciprocators weaken to the extent that eventually they invade a population of self-regarding types (Bowles and Gintis 2011; Fehr and Fischbacher

2005; Gintis et al. 2003; Richerson and Boyd 2004). The use of moralistic punishment as a norm enforcement device may spread among the members of an entire population through the mechanism of conformist transmission, the behavioral norm of imitating the most successful members in a community (Bowles and Gintis 2011; Richerson and Boyd 2004).

Conclusions

We have seen the experimental evidence for altruistic punishment, the central behavioral expression of strong reciprocity, and there is every reason to suppose it is prevalent in real-life situations, as well. The main motivation behind this tendency lies in proximate mechanisms shaped by evolutionary forces and conditions that rendered this behavior, in spite of its costs, invaluable in the upholding of social norms.

Cross-References

- ▶ Altruistic Punishment and Strong Reciprocity
- ▶ Cross-Cultural Punishment
- ▶ Costs of Punishing
- ▶ Evolution of Cooperation
- ▶ Free Riding
- ▶ Game Theory
- ▶ Gene-Culture Coevolution
- ▶ Multilevel Selection Theory
- ▶ Strong Reciprocity

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Altruistic Punishment and Strong Reciprocity

Tünde Paál
Pécs, Hungary

Synonyms

Costly punishment; Moralistic punishment; Strong negative reciprocity

Definition

A willingness to impose sanctions on norm violators at the punisher's own cost.

Introduction

The theory of *strong reciprocity* is regarded today as one of the most influential attempts at explaining the evolution of human cooperation (Bowles and Gintis 2011; Fehr and Fischbacher 2004, 2005; Fehr et al. 2002; Gintis et al. 2003). It denotes a predisposition to cooperate with others and a willingness to punish at personal cost those who violate cooperative norms. This altruistic form of punishment has been well documented both in real life and in laboratory experiments. It is altruistic in the sense that it occurs even in situations where no future benefits for the punishing individual or the individual's genes are possible: in one-shot scenarios among strangers under conditions of strict anonymity (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003).

Experimental Evidence

In the laboratory, altruistic punishment has been observed most commonly in experimental games developed within the framework of game theory. In the *ultimatum game*, two players decide over the division of a fixed sum of money. Player A can make one proposal to player B, who can accept or

reject it. If B accepts the proposal, the money is shared accordingly; if B rejects, both players receive nothing. Since the game is one shot and anonymous, the self-interested outcome would be for player A to offer the lowest possible amount and for B never to reject. However, this outcome is almost never achieved: player Bs typically reject offers lower than 30%, regarding them as unfair, and, anticipating this, player As typically offer around 50% (Fehr and Fischbacher 2005; Gintis et al. 2003).

In the ultimatum game, player Bs are directly affected by player A's proposal. There is evidence, however, that a number of people are willing to employ altruistic punishment against those who behave uncooperatively toward a third person (Fehr and Fischbacher 2004). In the *third-party punishment game*, players A and B take part in a *dictator game*. It has the same structure as the ultimatum game, except that here player B has no option of rejecting A's proposal; he/she has to accept whatever is offered. The game is anonymously observed by player C, who is not affected by player A's decisions. However, C is endowed by a fixed sum of money and has the opportunity to impose a fee upon A after witnessing A's offer. The fee is costly, for one-third of the decided amount is deducted from C's initial endowment. Nevertheless, in the experiment of Fehr and Fischbacher (2004), 55% of Cs punished A for offers below 50%, and the amount of punishment increased with the perceived unfairness of the offer. This tendency of disinterested third parties to use altruistic punishment is in line with the supposed role of strong negative reciprocity as a norm enforcement device in real-life situations, e.g., in the upholding of food-sharing norms in hunter-gatherer societies (Bowles and Gintis 2011; Fehr and Fischbacher 2005).

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than one rounds, in groups of $2 + n$ players. In each round, the players are provided with a certain amount of money, and they have to decide how much of it (if any) to contribute to a common account (i.e., the public good) and how much to keep in their own private account. The individual contributions are summed up and multiplied by a factor of usually three. The resulting sum is then equally divided and added to the players' private accounts, independently of their individual contributions. In public goods games without costly punishment opportunity, the amount contributed to the public good gradually declines over time, which can be explained by the fact that those players who are inclined toward strong reciprocity do not cooperate at any cost – their cooperation is conditioned by the other group members' behavior. In the absence of other options, they signal their dislike of the free-riders' strategy by lowering their own contributions. If, however, the players are given the option to use targeted, costly punishment against each other, the game unfolds differently. Sanctioning behavior follows the principles of strong negative reciprocity; the players who impose punishment even at their own expense are those who have an initially cooperative approach to the situation; sanctions are used against those participants who contribute nothing or only substandard amounts to the public good; and the existence of punishment opportunities results in a stable and high level of contributions, thus reestablishing cooperation. Thus, by acting to raise the level of contributions to the public good, altruistic punishment itself serves as a so-called second-order public good (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Fehr and Gächter 2002).

Proximate Mechanisms and Evolutionary Origins

It has been suggested that in the experimental scenarios described above, the sole motivation for sanctioning behavior is the punishers' desire to maximize their payoffs relative to the punished individuals. However, there is evidence indicating that this is not the case. In a prisoner's dilemma experiment by Falk et al. (2005), the cost of

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Conclusion

We have seen the experimental evidence for altruistic punishment, the central behavioral expression of strong reciprocity, and there is every reason to suppose it is prevalent in real-life situations, as well. The main motivation behind this tendency lies in proximate mechanisms shaped by evolutionary forces and conditions that rendered this behavior, in spite of its costs, invaluable in the upholding of social norms.

Cross-References

- Altruistic Punishment
- Costs of Punishing
- Evolution of Cooperation
- Game Theory
- Strong Reciprocity

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Altruistic Punishment Enhances Reputation

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Synonyms

Altruism among nonkin; Group selection; Public goods game

Definition

The costly act of produce a loss to a noncooperative behavior enhances the reputation of a group as cooperative one.

Introduction

During the evolutionary history of the human species, some survival increasing activities were group ones, consisting in a public good (Fehr and Gächter 2002). Hunting, warfare, and protection of common resources are some good examples. In public good situations, each member of the group benefits from the good, and its maintenance is a shared responsibility. Some members of the group will pay costs for the maintenance of the public good, the cooperators, while others will benefit from the good without paying any costs, the free riders. Increases in the number of the free riders will lead to a collapse and consequent extinction of the public good, harming the whole group (Hardin 1968). One measure to prevent such increases is to punish free riders, in order to curb such behavior. Thus, altruistic punishment may be an evolutionary selected strategy to maintain high levels of cooperation in large groups of unrelated individuals.

However, the punishment of free riders means additional individually costly acts, creating a second-order public goods problem (Fehr and Gächter 2002; Gülerk et al. 2006). Paradoxically, altruistic punishment is widespread, present in

highly diverse human societies (Henrich et al. 2006).

In models concerning group selection, the punishment strategy may be sustainable because the reduction of free riding produced by the altruistic punishment may overcome the costs of punishment by producing a more cooperative group composition (Fowler 2005; Gächter et al. 2008; Henrich and Boyd 2001). Once cooperation is established, the costs of punishment would tend to decrease and be compensated by the increased frequency of cooperative interactions, and so, weakening individual selection operating against altruistic punishers (Boyd et al. 2003; Gächter et al. 2008). Those groups may also create a reputation as rich ones, attracting more immigrants (Boyd et al. 2003). Experimental procedures and simulation models have been proposed to demonstrate the evolution of altruistic punishment and its impact within and between group selection.

The Public Goods Game

The main experimental scenario for the study of altruistic punishment and group benefits is the *public goods game (PGG)*. In such game, each player starts with a personal fund, and, in one or multiple trials, each member of the group can contribute or not to a common fund. The amount donated to the common fund is then enhanced and equally divided by all group members. This game encompasses all the main features of a public good in real-life situations: the shared responsibility to the public good maintenance and the individual benefits from the public good regardless the amount of expenditures of each group member. In the study of altruistic punishment, one more feature is added. After the division of the common fund, any member of the group can give a part of his individual fund to produce a loss in the individual fund of another member. This act will be named altruistic punishment when the loss is imposed to an individual who free rides. Generally, the loss produced is bigger than the amount gave by the punisher and leaves the free rider with less resources he could've accumulate if he had cooperated.

Experimental data have produced mixed results regarding the theoretical model for selection of altruistic punishment. Such variation is deemed to several parameters that may influence the experimental observation of the phenomenon. Once altruistic punishment is more probable under a reciprocity situation, a scenario that favors its occurrence may have a long number of interactions (Gächter, Renner & Sefton (2008) suggest a number of 50 trials), a stable configuration where members won't be replaced (Gächter et al. 2008), the costs are relatively low to produce high losses on the punished (Boyd et al. 2003; Egas and Riedl 2008), or some information about the participant's cooperative behavior in previous trials (Barclay 2006). Contrarily, scenarios that may discourage altruistic punishment are characterized by single or few interactions, instability in the composition of groups, and no information about member's reputations (Fehr and Gächter 2002; Fehr and Rockenbach 2003). The effect of altruistic punishment on reputation may be correlated to some outcomes like average group earnings, the impact of punishment on punisher earnings, the presence of aversion inequity motivations, and immigration rate.

Benefits in Group Average Earnings

One of the arguments against the selection of altruistic punishment as a stable strategy is that the costs of punishment are both decreasing punisher's fitness and producing very small increments to group mean payoffs, that is, not compensating the losses (Boyd et al. 2003). Hermann et al. (2008) showed that in some circumstances, even altruistic punishers (also high contributors) may be punished by average contributors, suggesting that altruistic punishment strategy may also need strong social norms of cooperation in order to be reinforced.

However, some experimental data suggests that highly punitive groups are richer than no punitive ones. Gächter et al. (2008) exposed 207 participants in groups of 3 to 1 of 4 conditions: punishment available and 50 trials (P50), punishment available and 10 trials (P10), no punishment available and 50 trials (N50), and no punishment in 10 trials (N10). The authors found that the greater average profit in cooperation occurred in

P50 groups. Fehr and Gächter (2002) exposed 240 students in groups of 4, to 6 periods of a PGG in 1 of 2 conditions, punishment and no punishment. Results showed that average investments were higher in punishment conditions with cooperation increasing over time while having a sharply decrease reaching no cooperation at all in more than half of the groups in non-punishment conditions. Such results demonstrate that punishment available groups produce more cooperation and bigger net earnings, compensating the costs of punishment by increasing the amount donated by cooperators.

Number of Interactions and Reputation

On the role of the number of interactions, as suggested by theoretical models, repeated interactions raise cooperation probabilities. In Gächter, Renner, and Sefton (2008) study, the presence of a punishment option increased the average earnings in longer interactions (50 trials) and had the opposite effect on brief interactions (10 trials). In a complementary way, the presence of punishment in a scenario of single interactions produced less cooperation than in conditions where no punishment option was available (Barclay 2006 – study 2; Fehr and Rockenbach 2003). Such data highlights the major role of the number of interactions, instead of personal reputation, as critical for the emergence of beneficial outcomes of altruistic punishment.

However, altruistic punishment is also consistently observed in one-shot anonymous interactions where participants will play each trial with a different, unknown person (Fehr and Gächter 2002; Gülerk et al. 2006). Even in such scenarios, reputation can play a critical role. Two kinds of reputation may be considered: the individual reputation as a punisher, which may be a controlling variable when dealing with known persons, and the group's reputation as a cooperative one, operating in anonymous interactions.

Some data demonstrated that participants prefer to interact with altruistic punishers, when given the choice (Gülerk et al. 2006; Henrich 2006; Nelissen 2008), and help altruistic punishers in future interactions (Santos et al. 2010). In Gülerk, Irlenbusch, and Rockenbach (2006) study, the whole evolution of between-group

cooperation could be observed. They had 84 participants playing multiple (30) anonymous one-shot interactions. At each trial, the participant had to (1) choose to be in a punishing or punishing-free interaction; (2) choose to endow some or no contribution to a common fund; and, in punishing groups, (3) choose to recompensate (by giving one token of his own) or punish (by giving one token to produce a loss of three tokens) other participants.

Results showed that, at initial trials, most participants choose to be in a punishing-free interaction and donate smaller amounts in this condition, with almost half of participants acting as free riders. Still at initial trials, punishment was frequent in the punishing interaction with free riders obtaining heavier losses than in the punishing-free interaction. At the sixth interaction, there is a shift with most of the participants choosing to be at the punishing interaction. This proportion increases along trials with more than 90% of participants choosing this condition at final trials. In punishing interactions it is also observed increases in the amount endowed over time. It produced progressive increments in payoffs, compensating the losses from punishment acts. At the end of the trials, reduction in payoffs of punishers compared to non-punishers was less than 2%.

This data illustrates a probable scenario in real-life group configurations concerning cooperation: frequently cooperative populations may do better as a group in between-group selection, creating a reputation that attracts immigrants, who intend to benefit from it. If those immigrants imitate native's behavior by cooperating and punishing free riders, cooperation is sustained in a stable level.

In PGG procedures, some behavior patterns can be drawn. Most of the participants are conditional cooperators (Chaudhuri 2010), persons who measure their contributions on average contributions of others. Punishers are usually *strong reciprocators* (Fehr and Gächter 2002; Gülerk et al. 2006), persons with a predisposition to make above-average contributions and punish low contributors. These punishers may be willing to sanction free riders, even when they are third parties, not being affected in a specific episode (Fehr and Fischbacher 2004). They are preferred partners and are seen as more trustworthy, group

focused, and reputable than non-punishers (Barclay 2006). Punishers tend to shift strategy by raising their future contributions, even when interactions are anonymous and/or one-shot, that is, the future interaction may not be with the punisher (Fehr and Gächter 2002; Gülerk et al. 2006; Raihani and McAuliffe 2012). Thus, the punishment provides increases in cooperation rates in future interactions, benefiting population as a whole.

Equity Motivations

Some evidence have pointed that inequity aversion may be a trait linked to the maintenance of cooperation (Brosnan and de Waal 2014; Brosnan and Bshary 2016; Hughes et al. 2018; Raihani and McAuliffe 2012). Rabin (1993) describes that conditional cooperation, that is, to cooperate (help) in cooperative groups and hurt the noncooperative ones by free riding, produces, respectively, mutual-max outcomes, with increase in other's payoffs, and mutual-min outcomes, when participants minimize each other's payoffs.

Fowler, Johnson, and Smirnov (2004) consider that two types of inequity are at stake in PGG: the individual amount of contribution compared to the average contribution and the net profit after the division of the public good resources. In the first situation, a free rider might be a person whose contribution fell below the average amount. In the second situation, a free rider might be the person who earned above-average net payoffs. Fehr and Gächter (2002) proposed that, in their procedure, altruistic punishment was driven by deviations from the average group endowments toward the public good. The more distant the participant's contribution from the average, the more this person was punished. Punishers were usually the strong reciprocators. Fowler, Johnson, and Smirnov (2004) offered a different interpretation for the same data. They assert that, in the referred procedure, payoff deviance is equal to contribution deviance. However, when a model drew from regression analysis considering the absolute values instead of deviance from the mean, results suggested that payoff was the critical controlling variable. This model showed that contribution had less effect on punishment probability when payoff is high and has no effect on punishment when

payoff is at its lowest. This analysis suggests that punishment is correlated to high net earnings instead of low contributions and the altruistic punishment may work for the reduction of inequality.

Raihani and McAuliffe (2012) and Dawes et al. (2007) found similar results, showing that probability of punishment acts is correlated to free riding that produced inequality, but not by free riding alone. Besides, participants who reject inequality are most prone to punish free riding (Johnson et al. 2009).

The literature about inequity aversion suggests that the refuse of inequality may be a strategy to avoid free riders. In this way, the display of inequity aversion behavior patterns may increase the probabilities of having a cooperative interaction, thus, putting such trait as a reputation enhancer.

Simulation Models

Until here, discussions about the evolution of altruistic punishment are based in theoretical models and experimental data. With simulation models, Boyd et al. (2003) propose that between-group selection, measured on the basis of immigration rate, would be the selection pressure for altruistic punishment strategies. The model starts with the assumption that cooperative groups, those with high numbers of altruistic punishers, are less prone to extinction. In such groups, the frequency of punishers and cooperative behavior may be positively correlated, and individual selection against punishers must be weak, because it is a common behavior, so costs are shared. In simulations, authors manipulated population size in four levels 4 (usual limit for experiments), 16, 64, or 256 members and the presence or absence of altruistic punishment. The altruistic punishment was also manipulated in light punishment (cost of being punished as twice the cost of cooperate) and high punishment (cost of being punished as four times the cost of cooperate). Several other parameters were manipulated to address common group transformation characteristics.

Main results showed that frequency of cooperation tends to decrease as a function of population size, but this fall is sharply slower in groups with punishers. Besides, in light punishment situations, it does not sufficiently reduce the average payoff

of free riders, creating the ideal scenario for raisings in free riding frequencies. Other important result is that increases in cooperation are sustainable only when the costs of being a punisher decline over time. If such costs are fixed over time, cooperation declines.

One important measure of the success of the group was the immigration rate. Groups that did better in terms of average payoffs created a reputation of being rich ones, attracting more immigrants. These simulation findings add information that are too laborious to be included in experimental models like the impact of group size on cooperation, immigration rate, and the reduction of punishment costs as crucial to the increase in cooperation.

Conclusion

Theoretical models have trouble to explain how cooperation can emerge and be selected among unrelated individuals dealing with public goods. The altruistic punishment strategy offers an answer to this puzzle but also suffers from the problem of being, at first, an individual costly strategy. Experimental data and simulation models have shown that cooperation typically collapses in the absence of punishment (Fehr and Gächter 2002; Boyd et al. 2003). The possibility of punishment not only stabilizes human cooperation but also maintains it at high levels, with low costs for punishers and bigger profits compared to non-punishing collectivities (Fehr and Gächter 2002; Gülerk et al. 2006). That is, altruistic punishment may be critical for the maintenance of cooperation. Groups that present high levels of altruistic punishment are richer and less prone to extinction and have better reputation, attracting more immigrants.

Cross-References

- [Altruism](#)
- [Altruism Among Nonkin](#)
- [Altruism and Costs to Altruist](#)
- [Cooperation](#)

- **Ingredients of Reciprocal Altruism**
- **Reciprocal Altruism and Group Living**
- **Reputation and Altruism**

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Altruistic Rewarding and Punishment

- **Strong Reciprocity**

Altruistic Suicide

- **Kin Selective Suicide**

Amalgamated Families

► Stepfamilies

American Left

► Political Left, The

Amotz Zahavi

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Synonyms

[The handicap principle](#)

Definition

Exploring costly traits as signals.

Introduction

Amotz Zahavi was a pioneer in evolutionary theory, who proposed the famous *handicap principle*. In 2016, Zahavi was awarded a lifetime achievement award by Tel Aviv University for his work and contribution to the department of Zoology. Prior to this, he was awarded the Society for the Protection of Nature in Israel prize by the Israeli Ministry of Education for his contribution to the environment. He was also awarded the Fryssen Foundation's International Prize for his work on social communication (Amotz Zahavi [n.d.](#)).

Prior to work conducted by Amotz Zahavi, costly behaviors (those which appear to be fitness reducing and costly to perform) appeared to be counterintuitive to Darwinian selection. Zahavi, by proposing the handicap principle, sought to further explain the adaptive benefits of costly behaviors and why they are central to both natural and sexual selection. Zahavi revolutionized the way we view behavior, arguing “handicaps” are usually present to signal our fitness (Zahavi 1975). These handicaps can take physical form such as possessing the famous peacock's large and “expensive” tail, or behavioral acts such as expensive purchases, often carried out to communicate or signal one's superior fitness to others. Zahavi's work has been applied to a wide range of disciplines including psychology, biology, and physiology, with strong applications to a wide range of species and behavior. His work has contributed to our understanding of animal, human behavior, communication, coloring, social hierarchy, and the development of physical qualities which serve a strong survival purpose.

The Handicap Principle

Amotz Zahavi observed and provided a theoretical framework for understanding human and non-human signalling behavior. From mating displays, language, elaborative displays among a variety of species, Zahavi was fascinated as to why we use elaborate displays, which are often observed as “costly” in nature. The term costly here refers to the idea that the trait/behavior is expensive to perform (or a physical feature is expensive to possess), often leading to “waste.” To perform such an act, one must be able to afford such wastage, as it does not come “cheaply.” These traits/features can be elaborate, yet costly in nature, often performed to advertise one's fitness.

Zahavi applied the handicap principle to a range of behaviors, including altruism. As an example, Zahavi argued that although traits such as altruism can often be viewed as behavior which is costly, it relays a signal of honesty, as those who can afford to bear the cost of being altruistic must be in some way superior compared to those who

are unable to bear the costs from engaging in an altruistic cost (Zahavi 1995, 2003). Furthermore, costly signalling theory has been used to explain costly displays of “expensive” traits such as prosociality, as it signals one’s ability to confer the benefits associated with altruistic behavior (Zahavi and Zahavi 1997).

One key facet of Zahavi’s work is that although sexual selection suggests that traits evolve to increase reproductive success, these traits can often be “copied” by rival mates. As a result, “true” handicaps are those that rivals are unable to imitate, thus relaying the fact that possessing a “true” handicap means the bearer is able to bear the costs of possessing the trait. For example, although Gazelles often perform “stotting” when escaping from predators, which can be seen as behavior which is costly (or Springbok’s leaping into the air when seeing a predator), it signals to the predator (and those around them) that the Gazelle can afford to expend their energy on this expensive act, thus signalling strength, deterring the predator. However, it is important to note that Zahavi argued that these traits had to be reliable and honest. It is not worth it for a Springbok to jump in the air if he or she is unable to run fast. Similarly, without an abundant supply of wealth, one is unable to waste it.

Costly Signalling Under Mate Choice

Stemming from costly signalling theory and the handicap principle, Zahavi was aware that certain expensive traits can be beneficial in mate choice. For example, from Zahavi’s work, theorists argue that several traits have evolved through sexual selection as handicaps in order to act as mating signals (Miller 2007), such as prosociality (see Bhogal et al. 2016, *in press*; Farrelly et al. 2007) and conspicuous spending (Miller 2009).

Conclusion

Amotz Zahavi’s contribution to evolutionary science has proved invaluable to our understanding of why we often handicap ourselves in social

interactions. The handicap principle has provided scholars from a wide range of disciplines with understanding of why we perform costly behaviors, and what these displays signal to others, often benefiting us in a variety of contexts, thus acting as adaptive behavior. The simplicity and complexity of the handicap principle extends to human and nonhuman species, explaining a plethora of traits and behaviors which were initially a puzzle to evolutionary theory.

Cross-References

► [Mating](#)

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Amphimixis

► [Sexual Reproduction](#)

Amputated Limbs

- [Phantom Limbs](#)

AN

- [Anorexia Nervosa](#)

An Abstract of an Essay on the Origin of Species and Varieties Through Natural Selection

- [On the Origin of Species](#)

An Essay on the Principle of Population

- [Malthus on Population](#)

Analogical Reasoning

- [Concept Formation](#)

Anatomical Adaptations for Fighting

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Synonyms

[Combat](#); [Physical Characteristics](#)

Definition

Anatomical adaptations for fighting include muscularity, body size, the structure of the fist, the protective skeletal buttressing of the face and skull, and the distribution of pain receptors. These features evolved as adaptations for success during males' long history of fighting with other males over status, access to resources, and reproductive opportunities. Because males fight more often than females the causes of selection on these traits would have been stronger on males. Accordingly, males exhibit greater expression of these physical traits than do females.

Introduction

We are a very violent species and although recorded human history shows high rates of violence, evidence from contemporary foragers indicates that we were even more violent as hunter gatherers. Violence, particularly between males, is part of our primate heritage.

As in other primates, humans exhibit important sex differences in the propensity for violence (Wrangham and Peterson 1996). Males are much more likely than females to fight each other to achieve status, access to resources, and reproductive opportunities. Males are more aggressive, on average, in many situations than are females (Archer 2004). Conflicts between men are more violent than those between women. In every culture for which there is information, male–male homicide rates are higher than male–female or female–female rates (Daly and Wilson 1988). Moreover, males are more likely than females to be involved in nonlethal fights (Collins 2008).

Before the invention of weapons, hominin fighting consisted of hand-to-hand combat involving the punching, slapping, kicking, and grappling commonly observed in modern chimpanzees, gorillas, and untrained humans (Wrangham and Peterson 1996). If the reproductive success of ancestral males was correlated with their success in fights, then the causes of selection on the physical traits that increased their chances of winning a fight would have been stronger on

males than on females leading to the prediction that males will exhibit greater expression of the traits that increase their chances of winning fights. Selection on the traits associated with fighting ability was likely intense because the potential loss of fitness consequences that can result from losing a fight (e.g., the loss of status, injury, or death) are severe.

Muscles

Victory in a fight comes from being able to punch, kick, grapple, or use hand-held weapons to dominate an opponent to the point of surrender, severe injury, or death. Prior to the use of firearms, human muscle power was used to propel primitive projectile weapons (e.g., boomerangs, darts, knives, spears, sticks, stones). Anatomical adaptations needed for the high speed, overhand throwing of projectile weapons first appear together in early *Homo* (Roach et al. 2013). Hand-to-hand combat and the use of primitive weapons favor bigger over smaller and stronger over weaker combatants. This is clearly demonstrated by the observation that in societies with combat sports, weight classes are used in competitions because discrepancies between competitors in body size influence the outcomes of fights. Therefore, if fighting was a more important cause of selection on males than females, then males should be bigger and stronger, on average, than females. Moreover, males should have greater upper-body strength than females because mainly chest, shoulder, and arm muscles are used during fighting and to propel primitive projectile weapons.

Sex differences in muscular size strength are well established. Males have more muscle mass in both absolute terms and relative to body mass than do females. Female muscle strength, even when controlling for differences in fat free body mass, limb or body size, ranges from 40 % to 75 % of male strength. The sex difference is even greater for upper-body than lower-body muscle strength indicating stronger selection on males than females for upper-body strength. Moreover, male muscle fibers are shorter and have greater angles

of pennation (i.e., the angle of the muscle fibers to the force-generating axis of the muscle) which contributes to sex differences in muscular strength (Chow et al. 2000).

The faster a fighter subdues his opponent the better and, indeed, most fights between males are very short, usually involving a few punches or kicks before they are over (Collins 2008). Even organized combat sports which frequently have rules that prolong fighting (e.g., gloves that reduce the risk of injuries to puncher's hands and the prohibition of tactics like biting and eye gouging) place a premium on competitors quickly defeating their opponents. In fighting competitions, episodes of fighting are typically short (e.g., Olympic Greco-Roman wrestling, 3 rounds of 3 min each, Ultimate Fighting Championship, championship professional mixed martial arts, 3 rounds of 5 min each). Except for professional boxing, in which championship bouts have the potential to last up to 36 min (12 rounds x 3 min/round), total fighting time, excluding the rest periods of 1 min between rounds, typically lasts no more than 15 min. The premium on quickly defeating an opponent during a fight favors the intense, rapid actions (e.g., punches, jabs, kicks) associated with the rapid, strong contractions characteristic of type II (fast-twitch) muscle fibers. Males have a greater proportion of type II fibers, on average, than do females, suggesting that the need to produce rapid, strong contractions required during fighting was a stronger cause of selection on males than females. In addition, male muscles are better able than female muscles to produce the anaerobic power necessary for the rapid, intense actions needed during fighting. For example, patterns of male muscle activation monitored during physical actions like those used during foraging, hunting, and fighting showed that jumping and punching accounted for 73 % of the incidences of maximum muscle activation and the size of the muscles of the back and leg were related more to the demands of the explosive power needed during fighting rather than either sprinting or long distance running (Carrier et al. 2015). The high heritability of the traits of muscles such as their size, static and

explosive strength, and trainability suggests a long history of positive selection on them, especially in males.

Human Fists

The hand is an important anatomical weapon. It is used to threaten, injure, and sometimes kill rivals. When clenched into a fist, it permits punching and striking with great force while simultaneously reducing the risks of hand injuries. The fist provides buttressing that increases the stiffness of the second metacarpo-phalangeal joint thereby transferring force through the thenar eminence, the fleshy pad proximal to the thumb, and compared to an open hand doubles the ability of the proximal phalanges of digits 2 and 3 to transmit punching force (Morgan and Carrier 2013). The structure of the human hand is consistent with the hypothesis that fighting was an important cause of selection on hand anatomy. Moreover, males, because they are larger, have bigger fists than females. The causes of selection associated with the use of fists during fighting likely contributed to this sexual size dimorphism because a larger fist delivers more force.

The Head and Face

Frequent fighting during human history would have been an important cause of selection shaping the anatomy of the human face. This is shown by the fact that the head and face are the most frequent targets during fights and getting punched in the face is responsible for most facial fractures in modern societies. Not surprisingly, males suffer more facial injuries than do females (Carrier and Morgan 2014). These patterns suggest that if fighting was an important cause of selection in hominins, then human faces should possess adaptations that reduce the risk of injury from being struck by fists. Traits that help protect the face from damage from fists include its flatness, robust bone structure, and enlarged jaw muscles (Carrier and Morgan 2014). In addition, blows to the head have less damaging effects on males than females

as shown by the fact that female athletes suffer a greater frequency of concussions than do males playing the same sports. This sex difference may result from males having stronger neck and jaw muscles, on average, because there are no sex differences in cranial thickness (Lynnerup 2001). The more robust faces and larger and stronger jaw and neck muscles of males suggest that their heads evolved to avoid damage during fighting. Consistent with this hypothesis is the observation that a male's strength and fighting ability can be accurately assessed from observing his face alone.

Pain Tolerance

Fighting involves both powerfully striking opponents and absorbing blows from them. Therefore, the ability to "take a punch" and continue fighting is advantageous to combatants. Individuals with low pain tolerance would be more likely to give up and surrender quickly during a fight. Therefore, if fighting was a more important cause of selection in males than females, then males should be more tolerant of pain than are females. Contrary to folk wisdom that females have a higher pain threshold than males, experiments show that males perceive a stimulus of given intensity as being less painful, are less likely to perceive a stimulus of given intensity as painful, and are more tolerant of pain than are females. Moreover, males have fewer pain receptors in their faces than do females (Mowlavi et al. 2005).

Conclusion

Several traits indicate that fighting was an important cause of selection on human anatomy, especially for males. The larger bodies of males and their greater upper body muscle mass, strength, and muscle characteristics are all adaptive for the intense, rapid, and forceful actions required for success during fighting. The structure of fists is adaptive for causing maximum damage to rivals without incurring injury. Faces, especially those of males, evolved in ways that minimize damage from being struck by the fists of rival combatants.

Finally, males have fewer pain receptors in their faces and are more tolerant of pain than are females, allowing them to better deliver and receive blows and continue fighting.

Cross-References

- [Aggression](#)
- [Combat Sport](#)
- [Team Sport](#)
- [Male Adaptations That Facilitate Success in War](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Male Warrior Hypothesis](#)
- [Male-Male Competition](#)
- [Men But Not Women Will Have Adaptations for War](#)
- [Physical Aggression](#)
- [Play Fighting in Boys](#)
- [Self-Assessment of Fighting Ability](#)
- [Sex Differences](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Sex Differences in Aggression](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Sexual Dimorphism](#)
- [Sexual Size Dimorphism](#)
- [Team Sport](#)
- [War](#)

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Ancestor Worship

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Synonyms

[Animism](#); [Indigenous religion](#); [Shamanism](#);
[Totemism](#); [Tribal religion](#)

Definition

The communicated acceptance of the supernatural claim that dead ancestors influence, and/or are influenced by, their living descendants and, more loosely, the rituals associated with such claims.

Introduction

Anthropologists studying traditional kinship-based cultures have frequently, and perhaps universally (Steadman et al. 1996), encountered the claim that dead ancestors (i.e., deceased progenitors) can still influence, and/or be influenced by, their living descendants. In such cultures,

generation after generation of descendants not only communicates their acceptance of such claims, but they participate in traditional forms of sacrifice and other rituals to demonstrate their veneration of their dead ancestors and their willingness to accept the influence of those ancestors by following the traditional patterns of behavior they proscribed. This activity is typically labeled ancestor worship, and it is described as religious because the claims made about the actions of dead ancestors are supernatural in the sense of being beyond verification by the senses. Ancestor worship is potentially of extreme importance to evolutionary explanations of religion because its apparent ubiquity, including its presence among human foragers, suggests it might be a very early, if not original, form of religion.

Evolutionary explanations of ancestor worship, like essentially all explanations of all forms of religion, start with the assumption that the belief in the supernatural claims causes the religious behavior. In the case of ancestor worship, the typically unquestioned assumption is that ancestor worship is caused by the belief that dead ancestors really can influence, and/or be influenced by, their living descendants. This leads to attempts to explain why people hold this belief in the absence of empirical evidence. There is empirical evidence that *living* progenitors influence, and are influenced by, their living descendants, but there is no empirical evidence that this is also true of *dead* ancestors. Given that dead ancestors are kin to their living descendants (i.e., individuals related through birth links) and kin selection appears to have great explanatory power concerning behavior involving closely related kin, evolutionary explanations of ancestor worship have often considered the possibility that kin selection may have been involved in the evolution of ancestor worship.

Main Text

Evolutionary explanations of religion can be conceptually divided into those postulating that beliefs in the supernatural are adaptations favored by individual-level selection (Sosis and Alcorta

2003), adaptations favored by group-level selection (Wilson 2002), or are merely by-products of other adaptations (Boyer 2001). All of these hypotheses follow the orthodoxy of assuming belief and therefore ask why natural selection may have either favored the behavior caused by those beliefs (i.e., see religious behavior as an adaptation) or how such beliefs could be a side-effect of selection for other mental adaptations (i.e., see religious behavior as a by-product).

Perhaps the most obvious way kin selection could be involved in the evolution of ancestor worship is through the similarity of the venerated/worshipped ancestor and the respected living parent, a similarity so strong that Freud proposed it as the basis for all religion (Freud 1913). Further, just as parents are expected to have evolved to encourage altruism among their offspring (Trivers 1974), in ancestor worship, dead ancestors are claimed to greatly desire their descendants to exhibit altruism toward each other, producing what anthropologists refer to as the axiom of kinship amity (Fortes 1969). The psychological mechanisms producing these similarities could be either adaptations increasing the inclusive fitness of individuals engaging in religious behavior, or perhaps the survival of religious groups, or by-products of other adaptations.

There are, however, a number of challenges to the use of kin selection to explain ancestor worship. First, there is the difficulty, if not impossibility, inherent in attempts to explain any form of religion and of identifying if it is actually the religious belief that causes the behavior, or even who, and if anyone actually holds such a belief (Rappaport 1999; Steadman and Palmer 2008). This can be avoided by focusing on identifiable behavior and its identifiable effects. This means restricting explanations of ancestor worship to what the living descendants of dead ancestors *say* about those ancestors and the effects of this *talk* on the behavior of the other living co-descendants of those ancestors.

There are also challenges specific to explaining ancestor worship with kin selection. First, although some rituals focus on only the recently deceased ancestors, rituals also include a focus on ancestors deceased for many generations. This is

crucial because the individuals participating in, and most influenced by, these rituals are typically the descendants of the dead ancestor being named, venerated, or worshipped in the ritual. When that ancestor is a parent or grandparent, these descendants are limited to the very close kin (siblings, aunts, uncles, nieces, nephews, first cousins) whose interactions may have been subject to kin selection. However, in the typical forms of ancestor worship centered on an ancestor deceased for many generations, the ritual involves and influences the behavior of many descendants who are so distantly related that kin selection would have no influence on the evolutionary consequences of their interactions. This is particularly important because so much of the interaction occurring among these distantly related co-descendants involves sacrifice and other forms of altruism.

To explain the altruism exhibited toward these distantly related co-descendants, it is first necessary to account for how such distantly related co-descendants (e.g., members of the same clan) could come to be identified as kin. When, *and only when*, the transmission of a traditional clan name, or other marker of kinship, persists over many generations, do “large lineages or clans . . . grow up over time as the descendants of the original ancestor/ancestress accumulated” (Fox 1967, p.122). van den Berghe and Barash (1977) provide examples of huge numbers of individuals who share the same descent name, whose existence implies the traditional transmission of a descent name over many hundreds of generations: “large unilineal kin groups such as clans and lineages with memberships running into hundreds or thousands, or indeed in a few cases, millions” (p. 821). The same process of copying behavior from ancestor to descendant for many generations that allows the identification of huge numbers of co-descendants from one generation to the next is also responsible for transmitting the axiom of kinship amity to each subsequent generation.

Conclusion

The time and effort put into faithfully transmitting names from ancestor to descendant over many

generations may help decide whether religion is an adaptation or by-product. This is because the high cost of transmitting the tradition of ancestor worship suggests that there must have been some evolutionary advantage to such transmission that offset this cost. An explanation of how traditions causing altruism toward very distant kin could have evolved requires a concept of evolutionary success (i.e., fitness) that takes into consideration a multigenerational time scale compatible with the many generations required for large clans to form (Dawkins 1982). The concept of measuring evolutionary success by the number of descendants alive after many generations has been referred to as “descendant-leaving success” (Steadman and Palmer 2008), in contrast to the conventional use of “reproductive success” when measuring evolutionary success in the next generation, or at the most, counting grandchildren. At the very least, explanations ignoring traditions, and only focusing on evolved psychological mechanisms, cannot account for the talk about long-deceased common ancestors encouraging altruism toward distantly related co-descendants. Thus, evolutionary explanations ignoring traditions are unable to account for ancestor worship, nor religion in general.

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Cultural Inheritance](#)
- ▶ [Cultural Universals](#)
- ▶ [Increased Grandchild Survival](#)
- ▶ [Kin Recognition](#)
- ▶ [Kinship](#)
- ▶ [Religion](#)
- ▶ [Selectionist Models: Implications for Behavior](#)

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Ancestral Birth Spacing

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Synonyms

[Interbirth interval \(IBI\)](#)

Definition

Time elapsed between a birth and the previous birth.

Introduction

Variation in birth spacing can have substantial effects on lifetime reproductive success: spacing births too close together leads to maternal depletion and lowered infant survival, whereas spacing births too far apart results in the production of fewer offspring over the life-course than is optimal for maximizing reproductive success. In this entry, ancestral primate birth spacing

patterns are discussed, and how humans compare with nonhuman primates. This is followed by discussion of some of the evidence that birth spacing patterns have been shaped by evolution and addresses whether women in modern industrialized nations should adhere to ancestral birth spacing patterns.

Nonhuman Primate Birth Spacing

Our closest living genetic relatives, the great apes, have longer average birth intervals than humans. Birth spacing patterns in apes and humans are summarized in Table 1. There are a number of explanations for birth spacing differences between primate species; some evolutionary lineages contain species with similar birth intervals simply through lineage effects. Small body size and short lifespans are also associated with shorter birth spacing when comparing species (Mitani and Watts 1997). One social factor in primates which appears to be important is shared infant care between mothers and others in the social group (allocare or allomaternal care). Species which have allomaternal care have shorter birth intervals than species in which the mother alone provides all of the care for her offspring (Mitani and Watts 1997).

What Do We Know About Birth Spacing In Our Human Ancestors?

Our best insights into typical birth spacing in our ancestors come from studies of living hunter-gatherers or foragers. Forager birth intervals are typically between two and three years (see Table 1). These short intervals when compared with apes may be part of a broader life-history pattern in which humans, like many other primates with short average birth intervals, use allo-maternal helpers (especially grandmothers) to achieve short birth intervals and as a consequence higher fertility (Hawkes et al. 1998).

In both nonhuman primates and in human forager societies, birth intervals are shorter after an infant dies (e.g., Blurton Jones 2016). Much of this

Ancestral Birth Spacing, Table 1 Mean closed birth intervals, where a birth follows a previous birth in the period of time in which the study was carried out, in apes and humans

Group or species	Mean closed birth interval in years	Source
Ache foragers living on reservation (S. America)	2.6	Hill and Hurtado 1996, p. 257
Hadza foragers (Africa)	2.8	Blurton Jones 2016, p. 335
Yanomamo foragers (S. America)	2.9	Melancon 1982
Ache foragers (S. America)	3.1	Hill and Hurtado 1996, p. 254
United Kingdom (1970 British Birth Cohort)	3.4	Waynforth 2015
Aka foragers (Africa)	3.5	Hewlett 1993
!Kung foragers (Africa)	3.7	Bentley 1985
Gorilla	3.9	Watts 1991
Chimpanzee	6.0	Nishida et al. 1990
Sumatran orangutans	9.3	Wich et al. 2004

effect is likely to be due to a more rapid return to ovulation with the cessation of breastfeeding and the other energetic demands of motherhood that suppress normal menstrual cycling and fertility in mothers of infants (Wood 1994).

Evolutionary Optimality Models of Birth Spacing

Birth spacing patterns have evolutionary selection pressure on them due to a trade-off between the number of offspring that can be produced in a reproductive lifespan and the survival of the offspring. This trade-off contains other potential compromises, such as between number of offspring produced and maternal survival. There have been several tests of whether observed birth spacing fits with the birth spacing pattern that would be evolutionarily optimal in forager societies. To carry out a test of optimality, it is necessary to know what effects different birth intervals have on child survival in the conditions that the society lives. This can be achieved by measuring survival both of the newborn child and their older sibling(s) who have been supplanted as the youngest child. With this information, it is then possible to calculate the average number of surviving children a woman will have over her reproductive career given different birth intervals. In Hadza foragers of Tanzania, there is evidence for a trade-off between timing and number of children produced; close birth intervals (less than 2 years) are associated with an increased risk of mortality

in both the supplanted older child and the younger child (Blurton Jones 2016). For the Hadza, optimality modelling of birth intervals suggested that intervals of between 2 and 3 years lead to the greatest number of surviving children. When applying this model back to observed birth intervals over a Hadza woman's reproductive life, Blurton Jones found that the overall pattern of birth intervals approximately fit what was predicted by the optimality model, except that there were more short intervals than predicted (Blurton Jones 2016). Hill and Hurtado (1996) used a similar optimality modelling approach to test whether birth spacing was optimal in Aché foragers living on an indigenous reservation in Paraguay. In contrast to the optimality model calculated for the Hadza data, for the Aché no intermediate optimum birth interval was found: women's reproductive success was maximized by having the shortest observed birth intervals and the most children possible.

The Hadza and Aché forager data were used to formulate mathematical optimality models of whether observed birth intervals were consistent with infant mortality levels as a function of birth intervals. This is because the amount of parental care provided influences a child's chances of survival. However, not all mortality can be influenced by giving more parental care or giving it exclusively to a child for longer. This type of mortality which is insensitive to energetic allocation to immune function or tissue repair is termed extrinsic mortality. Two situations in which there is increased extrinsic mortality are

famine and warfare. When these and other extrinsic causes of mortality are considered, the evolutionarily optimal birth interval is shorter under conditions of high extrinsic mortality (Quinlan 2007). This may be one reason why observed birth intervals are shorter than expected in studies of forager intervals.

In sum, if we assume that throughout recent human evolution resources were reasonably scarce and child mortality was common, intermediate birth spacing of between 2 and 3 years is likely to be the norm for our species and has been selected for by natural selection.

Proximate Mechanisms Underlying Birth Spacing

Although birth spacing decisions can be made consciously by parents, much of the variation in birth spacing is likely to result from the high energetic cost of reproduction. Lactation and caring for an infant are very energetically costly. The ovulatory cycle of well-fed breastfeeding mothers does not resume for around 10 months after the birth of a child on average due the metabolic burden of breastfeeding (Valeggia and Ellison 2009). This is likely to be longer in nutritionally stressed populations but would still not alone account for birth spacings of 2–3 years typically observed. Women can extend postpartum infertility by sucking their child more frequently and for longer durations (Vitzthum 2009). Culturally based factors also play roles; in the Hadza, men report that sexual access to women with young children is more difficult to achieve (Blurton Jones 2016, p. 346). In the absence of modern contraceptive methods, cultural practices and taboos which restrict male access to mothers of toddlers is a common way that mothers can achieve their desired birth spacing.

Differences Between Women and Between Births

Alloparental care, particularly from grandmothers, which is hypothesized to explain short

human birth intervals compared with other higher primates, also explains some of the differences between individual women in birth intervals. For example, in a noncontraceptive using population in India, the presence of a grandmother in the household was associated with shorter birth intervals (Nath et al. 2000). This is most likely because the grandmother is able to relieve the mother of some of the energetic burdens associated with having an infant.

If evolution has shaped birth spacing decisions, it is also expected that infant viability itself will predict birth spacing. Parents would be expected to parentally invest less in unviable offspring and to subsequently have a short birth interval. This was found to be the case in a British sample, where the birth of an infant with chronic health problems was associated with shorter following birth intervals (Waynforth 2015). However, this pattern should only hold when parents are not able to substantially improve their infant's viability by increasing parental care.

An existing offspring would be expected to benefit from a longer birth interval than may be in the mother's reproductive interests, thus parent-offspring conflict is relevant to the evolution of birth spacing patterns (Trivers 1974). Extended nursing would serve to tax the maternal energy budget and extend the postpartum return of ovulation. Haig (2014) has proposed additional mechanisms which function due to the presence of cells from an embryo remaining in the mother's body long after birth (microchimerism). These cells may lengthen the next birth interval by affecting conception and implantation of subsequent potential sibling competitors for maternal resources.

Predictions Which Have Not Consistently Been Upheld in the Research Evidence

Male infants require more parental investment: boys are born larger than girls after a slightly longer gestation length and require more maternal resources as infants. The expectation would therefore be that birth intervals are likely to be longer after the birth of a son. The evidence in support of this in forager and other populations

living in nonindustrialized conditions is mixed; Mace and Sear (1997) found evidence for longer intervals after the birth of a boy, but Blurton Jones (2016) did not, and these mixed results are also reflected in the literature from other societies. Similarly, mothers in good physical condition or who live in good conditions would be expected to have shorter birth intervals. This is not the case in the Hadza (Blurton Jones 2016), but when Aché foragers moved to living an easier life on reservations, birth intervals became shorter (Hill and Hurtado 1996).

Do Ancestral Birth Spacing Patterns Remain in Modern Industrialized Societies?

As can be seen in Table 1, modern British birth intervals have a similar mean to forager intervals and do not appear to deviate from what optimality models predict for the Hadza, which is 2–3 years. Longer birth intervals are selected for by natural selection when infant and child mortality are raised by having to care for two young children simultaneously. Given very low infant and maternal mortality rates when compared with forager societies, reproductive success would likely be maximized by very short birth intervals in modern industrialized societies, and thus modern average birth intervals do not reflect or have not tracked the current optimum.

Some of the details of variation in birth intervals in modern industrialized societies differ from the Hadza and other forager societies. In Britain families with large completed family, sizes tend to be characterized by longer birth intervals, and birth intervals are significantly shorter at higher parity in Europe and the United States (for fourth and later born babies) (Waynforth 2015; Andersson 1999; Weinberg and McCarthy 1989). In Sweden and the United States, birth interval length has been declining in recent decades. In the United States, this decline has been the greatest in women with higher education levels (Weinberg and McCarthy 1989). This suggests that decreasing birth intervals in recent

decades are driven by women closely spacing births to minimize career disruption and maximize lifetime financial income.

Conclusion: Should Women in Modern Industrialized Societies Space Births More Than 2 Years Apart?

With the rise in application of evolutionary approaches to health-related behaviors in recent decades, many consider ancestral patterns of behavior to be the healthiest approach to apply to living in modern industrialized conditions; it is best to do what we were evolved to do. Nowhere is this type of view more common than in diet and exercise, for example, for followers of the paleo-diet. The World Health Organization and other public health bodies recommend spacing births more than 2 years apart. This is due to the weight of evidence that close birth spacing results in increasing infant morbidity and mortality. However, the most modern statistical approaches to studying birth intervals such as multilevel modelling suggest that public health organizations have overestimated the risks to children of close birth spacing in modern industrialized societies (Ball et al. 2014). In addition, the health risks of infant morbidity and mortality due to short birth spacing would need to be balanced against the health benefits associated with increased maternal income from minimizing career disruption; in modern industrialized societies, income remains positively associated with many child health outcomes. Thus although the World Health Organization urges families to space births at least 2 years apart, it is not clear that well-fed women living in societies with good access to healthcare should worry about close birth spacing.

Cross-References

- ▶ [Alloparenting and Grandparenting](#)
- ▶ [Birth Spacing and Birth Order](#)
- ▶ [Conflict Between Parents and Offspring](#)
- ▶ [Cooperative Breeding](#)

- [Extrinsic Mortality](#)
- [Genetic Conflict](#)
- [Helpers at the Nest](#)
- [Infant Survival](#)
- [Life History Theory](#)
- [Optimal Clutch Size](#)
- [Parental Investment](#)
- [Quantity Versus Quality of Offspring](#)

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Ancestral Environment

- [Climate and Habitat Diversity](#)

Ancestral Threats Versus Modern Threats

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Introduction

Survival threats posed by the environment have continuously tormented and challenged human

beings. From an evolutionary perspective, the brain mechanisms associated with fear were designed by natural selection to contend with these threats. The list of hazards likely faced by our ancestors included snakes, spiders, heights, darkness, and strangers. Our ancestors' concerns about dangerous stimuli such as these have been carried over to modern humans. In addition to evolutionary threats (e.g., predators and diseases), modern humans encounter a staggering array of novel threats (e.g., ionizing radiation, automobile accidents, and chain saws) that did not exist until very recently on an evolutionary time scale.

Ancestral Threats

Throughout human evolution, the ability to identify threatening situations has been a critical feature of our psychological structure. A failure to recognize and thwart a threat could have been fatal for our ancestors. The concept of biological preparedness – a theory about the psychology of fear and our reactions to threats – argues that the successful identification of environmental threats leads to a reproductive and survival advantage for the individual (Seligman 1971). In this view, children learn to fear some threats more quickly than others and, consequently, seem biologically prepared to avoid poisonous animals but less prepared to detect the difference between the sidewalk and street traffic.

The environment of evolutionary adaptedness (EEA) is the ancestral environment to which a species is adapted or the set of selection pressures that shaped an adaptation. A central premise of evolutionary science is that forces in our distant past helped make us who we are today. The EEA refers to a group of selection pressures occurring during an adaptation's period of evolution responsible for producing the adaptation (Tooby and Cosmides 1992). A selection pressure can be any factor in a population that impacts reproductive success. Physical, social, and intrapersonal pressures from our ancestral past help to shape our current human design because all animals have heritable variations that are selectively favored or disfavored in accordance with reproductive success (Buss 1995). Each adaptation has its own

EEA, or set of adaptive problems, that shaped it over evolutionary time.

Researchers have found that some of the threats present in the EEA (e.g., snakes and spiders) can induce stress responses to modern humans even at the very young age of 6 months (Hoehl et al. 2017). It is not even necessary for humans today to have had negative experiences with the creatures to fear them. They are likely embedded in us thanks to our ancestors' coexistence with them for 40 to 60 million years. More modern threats include knives, airplanes, and syringes, but they have not been around long enough to establish a threat response from birth.

Modern Threats

A modern threat is anything that poses a problem today that was not prevalent throughout human history. While snakes, spiders, and other predators are referred to as ancestral threats, today we must also be cautious of fast-moving automobile traffic, firearms, and razor blades. A brief list of deadly modern threats would include automatic weapons, electricity, weaponized nanotechnology, pollution, fried foods, alcohol, drug overdoses, decompression, power drills, and helicopters.

An adaptationist approach to studying behavior involves examining the environment in which the brain evolved; at the same time, the modern industrialized world of today differs in many important respects from the EEA. This mismatch serves as a useful starting point for understanding the function and design of current psychological mechanisms. The primary threats to most people today, especially in modern urban settings, are different than the environmental threats dominant up until a few centuries ago. We now increasingly face threats that are substantively different, more technical, and in some ways less tangible.

The list of novelties offered by our modern world but not present in the EEA includes agriculture, electricity, refrigeration, large-scale weapons, medicines, mass communication, effective contraceptive devices, and virtually unlimited access to all types of proteins and carbohydrates. We are navigating our current social and physical world with psychological mechanisms designed

to solve problems associated with survival and reproduction in an ancestral environment much different than the one we live in now.

Because adaptations evolved over many generations, they are said to be “in tune” with reliable features of the environment. It is possible for an adaptation to fail to perform properly (i.e., fall “out of tune”) if the environment changes. A behavior that is maladaptive in one environment may not be maladaptive in other environments. Returning to an earlier example, one could make the case that salt, fat, and sugar negatively impact health when consumed in large quantities over long periods of time. However, this is not an evidence of maladaptivity in the EEA. Moreover, the “lack of fit” to the current environment does not change the intense desire for those substances formed in the EEA.

Natural selection molded mechanisms into our ancestors’ brains that were specialized for focusing cognitive energy on humans and other animals. These adaptive traits were then passed on to us. According to some research, humans today are biased to pay attention to other people and animals much more so than nonliving things, even if inanimate objects are the primary hazards for modern, urbanized populations (New et al. 2007).

Globally, the top causes of death in 2016 according to the World Health Organization (WHO) were heart disease, stroke, pulmonary disease, respiratory disease, and Alzheimer’s and other dementias. Combined, these five issues are implicated in approximately 23 million deaths (World Health Organization 2016). If the danger detectors in our brains were perfectly in tune with our current industrialized world, we would focus our attention on threats that have a greater chance of bringing us down. Statistically speaking, you are much more likely to die from heart disease in our modern world than jet engine failure or a lion attack. Yet we seem to be overly anxious about airplane crashes and the odd death-by-tiger story and less panicked by cardiac health and lung infections.

Conclusion

Throughout human evolution, the ability to identify threatening situations has been a

critical feature of our psychological structure. A failure to recognize and thwart a threat could have been fatal for our ancestors. In contrast, the primary threats to most people today, especially in modern urban settings, are different than the environmental threats dominant up until a few centuries ago. We now increasingly face threats that are substantively different, more technical, and in some ways less tangible.

Cross-References

- [Gordon Orians](#)
- [Landscape Preferences: Climate and Weather](#)
- [Natural Versus Artificial Environments](#)
- [Savanna Hypothesis and Landscape Preferences, The](#)

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Ancestry

- [Birthrights and Bloodlines](#)

Ancient Homosexuality

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Synonyms

[Sexual expression](#); [Sexual orientation](#)

Definition

Same-sex attraction in early recorded history.

Introduction

Despite recent attention to the issues surrounding gender identity and sexual orientation, human same-sex attraction is not a novel phenomenon. Historical, anthropological, cross-cultural, and archaeological evidence points to frequent same-sex attraction and sexual behavior in early recorded human history. The consistent instantiation of same-sex behavior throughout time and across disparate civilizations suggests the possibility that evolutionary processes have helped to shape human same-sex attraction (Bailey et al. 2016). This entry presents some interpretations of the evidence for same-sex attraction in early history, focusing on manifestations of same-sex attraction in antiquity.

The Multitude of Same-Sex Attractions

The earliest evidence for the existence of same-sex attraction dates back to pre-civilization. Archaeological records describe Mesolithic rock art depicting same-sex male sexual activity (Nash 2001) and tombs containing male skeletons accompanied by female-typical artifacts (Hollimon 1997). Scholars have interpreted this evidence as suggesting both same-sex attraction and the conceptualization of same-sex attraction via stereotypical gender roles, similar to views of

same-sex attraction common today (Kite and Deaux 1987; Tskhay and Rule 2015).

Additional written evidence of same-sex attraction exists within the New Kingdom period of ancient Egypt (1292–1069 BCE). These records describe sexual relations between pharaoh Neferkare and his general Sisene (Meskell 2001). Similar conclusions have been made from the ancient Greek writings of Sappho, who described romantic relations between women (Campbell 1982) and homosocial lifestyles (i.e., close bonds) between men (e.g., nude athletics; Scanlon 2005). Perhaps the best-known examples of same-sex attraction in antiquity come from Spartan Greece, where records suggest that mature Spartan men engaged in sexual relations with their younger trainees (Bertosa 2009). The variety of evidence thus suggests some degree of acceptance and understanding of same-sex relations in these societies.

Indeed, ancient writers, medical practitioners, and philosophers have developed multiple typologies of same-sex attraction that resemble contemporary understanding of the expression of sexual orientation and gender identity (Boswell 1982/1983). Furthermore, in Plato's *Symposium*, Aristophanes developed a theory of same-sex attraction proposing that all people seeking romantic relationships with other humans have a need to reunite with their primordial twin, regardless of whether this twin is male or female. Thus, similar to modern time, same-sex attraction in the ancient past was a subject of discussion and research, requiring theoretical interpretation.

Conclusion

In sum, evidence from early Western history highlights a pattern of same-sex attraction in multiple cultures and prehistory. Same-sex attraction and its multiple forms of expression therefore seem to have been recognized and studied in antiquity. Early definitions of same-sex attraction appear to have conceptualized it in terms of more common heterosexual gender roles that resemble those still active today.

Cross-References

- [Personality, Gender, and Culture](#)
- [Sexual Identity](#)
- [Sexual Orientation and Human Sexuality](#)

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Ancient Music

- [Music and Hormones](#)

Androgen

- [Testosterone](#)

Androgenic Hormone

- [Testosterone](#)

Anger Proneness

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Synonyms

[Angry personality](#); [Probability of anger](#); [Trait anger](#)

Definition

Anger proneness refers to individual differences in the frequency, intensity, and duration of anger across time and situations.

Introduction

Anger is conceptualized as a common emotional response to loss, goal thwarting, and frustration (Berkowitz 1989). Anger is observed cross culturally, and the behavioral referents of anger – threatening, aggressive, and dominant behaviors – are also observed across species. Although anger is often deemed a “negative” emotion, the ubiquity of anger across contexts coupled with observations of anger-related behaviors across species suggests that the emotion has resulted in some adaptive advantages over the course of human evolution.

Anger has been operationalized in many ways, and most definitions include a combination of cognitive, behavioral, and affective responses made in response to threat (Ronan et al. 2014).

Cognitive processes of anger include selective attention toward threatening stimuli, hostile attributions, rumination, and aggressive fantasies. At the behavioral level, anger may be accompanied by muscular tension, cardiovascular reactivity, verbal aggression, and physical violence. The affective and physiological change characteristics of anger were likely selected because they facilitate aggressive behaviors observed in freeze-flight-fight responding. The conditions that provoke anger also tend to alter the motivational functions of various stimuli, particularly those associated with threat and injury. For instance, under conditions of pain and frustration, the sights, sounds, and other sensations that arise from harm to others may be temporarily more motivating and reinforcing. The verbal and non-verbal expression of anger functions to signal to adversaries that the individual is more likely to aggress or retaliate.

Like other negative emotions including sadness and fear, anger itself may be experienced as an aversive state of being that individuals themselves prefer to avoid or escape. However, the motivational function of anger is distinct from other negative emotions because it tends to increase the likelihood that the individual will approach rather than flee the triggering stimulus. Within the framework of freeze-flight-fight responding, such attempts to approach the source of threat could be adaptive when the threat cannot be avoided, risk of harm from fighting is minimal, or if attacking the adversary may deter future attacks.

Contemporary models distinguish state or episodic anger triggered by momentary aversive conditions from anger proneness – the overall propensity for an individual to become angry (Alcazar and Deffenbecher 2013). Within the Five Factor Model (FFM) of personality traits (a dimensional model of openness, extraversion, agreeableness, conscientiousness, and neuroticism), anger-prone individuals are conceptualized as those with high levels of neuroticism coupled with low levels of agreeableness, presenting as more neurotic, emotionally labile, and less trusting of others. Individuals may adopt several strategies to regulate their anger.

Individuals may adopt styles where anger is directly expressed through verbal and physical aggression, inhibited and suppressed, or expressed assertively to others. Depending on the situation and other traits of the individual, anger-prone individuals may be quietly hostile, verbally aggressive, or physically violent. Angry behaviors may be reinforced and maintained to the extent that they yield instrumental gains, dominance, status, and power over others. Those prone toward suppressing anger may experience paradoxical increases in anger as these individuals must self-monitor whether they are engaging in angry thought processes. As a result, an ironic process occurs in which angry thoughts and emotions are kept longer in conscious awareness (Burns et al. 2012).

Evolutionary Models of Anger

Whereas episodic angry behaviors may serve important protective and communicative functions, relatively stable individual differences in anger proneness present interesting problems for evolutionary psychology because of the negative consequence of chronic anger. Evolutionary psychology assumes behaviors are more likely to be selected and persist if they increase the reproductive fitness of the individual. A high propensity toward anger could undermine reproductive fitness when anger-prone individuals indiscriminately generalize aggressive behaviors across many contexts and fail to attend to the long-term consequences. For instance, many current social contexts actively prohibit and punish aggressive behaviors, anger is linked to a number of health risks including pain (Burns et al. 2012) and cardiovascular disease (Iyer et al. 2010), and aggressive behaviors may increase exposure to injury and death. Whereas intermittent anger may signal others to attend to the needs and boundaries of an individual, chronic expression of anger may be viewed as off-putting by others and ultimately push others away particularly in family, work, and other social settings where cooperation is valued. Considerable loss of resources can also occur

through incarceration, job loss, and other social sanctions of angry and aggressive behaviors.

Several hypotheses have been proposed to explain the plausible evolutionary function of stable individual differences in anger and aggression. The polygynous human mating system coupled with relatively lengthy social and reproductive careers leads to a risk proneness in young males, such that competition for mates, resources, and even social status can lead to male-male confrontation as competition emerges (Fessler 2010). This risk-prone behavior can be generalized to physical risk taking and violence, including homicide, in male-male confrontation and competitions. In competition for mates, a single transgression by another male adversary could reduce one's reproductive fitness. Risks to reproductive fitness could also accumulate over time to the extent that other potential adversaries come to view the individual as weak or vulnerable. Individuals more prone to experiencing anger and expressing it through aggression, violence, and other risky behaviors could in some settings be more likely to deter competitors. Fessler and colleagues found that men who voluntarily participate in nonviolent/nonphysical risk-taking behavior are conceptualized as being larger and stronger by potential mates, enemies, and allies, despite actual physical characteristics. In addition to deterring adversaries, achieving such social status could also attract allies and potential mates. However, in some contexts physical risk-taking behavior (e.g., violence) leads men to be conceptualized as more violent which can cause others to view them as a threat and thus not someone with whom they wish to associate or mate.

Mechanisms of Selection

Aggressive and emotional behaviors have been observed throughout the animal kingdom, albeit humans appear unique in their abilities of self-awareness of their own behavior. Animal models of aggression are well-established paradigms of research. This suggests that variation and selection of angry or aggressive behaviors has existed throughout much of phylogenetic history.

Individual differences in irritable infant temperament – before substantial socialization has occurred – may be predictive of future aggressive behavior. Several areas of research suggest that the propensity toward anger may be selected at multiple levels including the genotype.

Emerging evidence suggests that anger has multiple genetic determinants, specifically in the realm of gene-environment interactions. The monoamine oxidase (MAOA) genotype moderates the effects of childhood maltreatment on male antisocial behaviors (Byrd and Manuck 2014). There is also a three-way interaction in which the serotonin transporter (5-HTT) gene, the MAOA gene, and childhood sexual abuse interact to predict aggressive behavior (Zhang et al. 2017). In each case, genetic components appear to moderate how individuals respond to trauma and adversity.

Based on the abovementioned work on gene-environment interactions that predict aggression, it is plausible that phylogenetic contingencies also have selected neurological structures that enabled animals including humans to adapt to unique characteristics of their environment. Given the physical tolls of chronic anger, a highly heritable and rigid anger-prone phenotype could undermine reproductive fitness if the biological and interpersonal costs outweigh the benefits of deterring adversaries. For instance, the anger-prone phenotype would be expected to be less adaptive in social environments marked by high levels of parental investment and low levels of competition from adversaries. Thus, it may be the case that genetic variation allows for some individuals to be more sensitive to threat and develop anger proneness through operant, respondent, and higher-order learning processes. The importance of individual development in the development of anger and aggression is well recognized in the practice of clinical and forensic psychology. For instance, in the clinical evaluation of aggression, a number of developmental events such as prior history of traumatization, exposure to aggressive models, and the individual's age at the time of their first significant episode of aggression are assessed in order to make classifications about future risk of aggression (Ronan et al. 2014).

Selection of angry and aggressive behaviors might also occur at the level of culture if such behaviors help groups overcome the problems that they face. As with selection of angry behaviors at the individual level, contexts may have existed and continue to exist in which aggression and anger proneness may facilitate the defense and preservation of resources such as food and shelter. In contexts where resources are scarce and competition and deceit is common, a greater sensitivity to threat and higher degree of anger proneness may deter potential adversaries from attacking the individual, their kin, or affiliates. Emerging evidence on the distribution of personality traits in the United States suggests that personality traits of neuroticism and agreeableness cluster in systematic ways, and this clustering may contribute to regional differences in culture (Rentfrow 2010; Rentfrow et al. 2013). Northeastern states tend to have higher aggregate levels of neuroticism and lower levels of agreeableness implying that this region may be more irritable and temperamental compared to other regions in the United States. One possible explanation is that people with similar interests tend to cluster together or land in the same region for similar reasons. Rentfrow uses the example that those high in agreeableness tend to stay in their hometown, while those high in extroversion and openness tend to move away, often clustering in areas that value diversity. Another theory is that people are influenced by those around them via socialization and reinforcement and thus become more similar. Finally, personality traits, including anger proneness, could be impacted by ecological influence.

Conclusion

Anger is often considered a momentary reaction to frustration or other sources of stress. Anger proneness refers to stable differences in how often and how strongly people experience anger across situations. Anger-prone individuals may be

at greater risk of injury and chronic health problems. However, anger may serve important functions for individuals and groups especially when it motivates individuals to persevere and defend themselves, their kin, their resources, and status.

Cross-References

- [Attractiveness and Anger-Proneness](#)
- [Sex Differences in Anger Proneness](#)
- [Strength and Anger-Proneness](#)

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Angry Personality

► [Anger Proneness](#)

Animal Behavior

► [Field of Comparative Psychology, The](#)

Animal Communication

► [Animal Signalling](#)

Animal Emotions

► [Marc Bekoff](#)

Animal Intelligence

► [Nonhuman Intelligence](#)

Animal Signaling

► [Vocal Communication](#)

Animal Signalling

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Synonyms

[Animal communication](#); [Signals](#)

Definition

Signals are an important aspect of social behavior in the biological world, as they allow information and/or influence to be transmitted between organisms via intermediary signalling and response behaviors. This is often interpreted through an evolutionary lens, whereby the relevant behaviors are assumed to have co-evolved; however, alternative definitions and formalizations exist in the literature.

Introduction

The evolutionary science of animal signalling began with Charles Darwin's *The Expressions of the Emotions in Man and Animals*, published in 1872, and signalling has been central to the study of animal behavior (ethology) since then. In 1973, the Nobel Prize in Medicine was jointly awarded to three ethologists whose work was pioneering in this regard: Karl von Frisch, Konrad Lorenz, and Niko Tinbergen. This included work on the phenomena of imprinting by hatchling birds, and von Frisch's description of the complex, information-rich "waggle dance" of worker bees, by which the details of distant food sources are encoded and communicated to others in the hive. Since then, animal signalling has been the subject of laboratory and field studies on animals ranging from

microbial life to large vertebrates including primates and cetaceans. Several bodies of theoretical literature have also been spawned, with cross-over applications to the human sciences.

Forms of Animal Signalling

Animal signalling occurs in a wide variety of forms and contexts. Striking cases occur across species boundaries and in highly asymmetric relationships, for example, between prey animals and their predators as in the case of the leaping (stotting) behavior of Thompson's Gazelles during pursuit by predators, and vivid coloration of some amphibian or insect species to advertise their toxicity. However, most animal signalling takes place between conspecifics and functions to regulate social behavior. Most signals are also biologically fixed and involuntary, in the sense of either being expressed developmentally (such as coloration) or reactively, e.g., via visual or audible cues of aggression, fear, and sexual arousal, and nonvisual signals such as pheromones and physical contact. Such traits and behaviors are typically innate and robust across a species, though there are known cases, such as whale song, where signal variants propagate by cultural transmission and social learning.

Many vertebrates also engage in behaviorally complex signalling systems, such as the alarm calls of several monkey species and the gestural systems of great apes. Vervet monkeys emit alarm calls that discriminate between different types of predator (e.g., snake, eagle, leopard, baboon) which in turn elicit "best response" avoidance behaviors from alerted conspecifics (e.g., climb a tree, hide under a bush, etc.) (Seyfarth et al. 1980). Communicative behaviors of chimpanzees and other great apes have been extensively studied and include both reflexive signals (such as baring teeth to communicate aggression) and dozens of vocalizations and gestures (such as clapping and beckoning) which facilitate social interaction. These appear to be intentional in performance but are also innate and robust with respect to usage, with many gestural signals being common across the great ape clade, including human children (Byrne et al. 2017). However, there is

ongoing debate about the intentionality, ontogeny, and origins of these gestural systems, including the degree to which learning and ritualization plays a role, as well as the implications that can be drawn regarding the evolution and acquisition of human language (Tomasello and Call 2019).

Evolutionary Explanations

Several theoretical and formal approaches have been developed to explain the evolution of animal signalling. Amotz Zahavi famously proposed the "handicap principle," whereby costly or risky traits or behaviors can be interpreted as strategic signals of underlying qualities, for example, the spectacular tail of the peacock as a costly investment in advertising the male's quality as a mate. Though initially focused on sexual selection, Zahavi and others have argued that the handicap principle is broadly applicable to signalling throughout the biological world, and it has been formalized using evolutionary game theory as a signalling game by which "high-quality" senders can advertise themselves as such by sending a signal that is too costly for low-quality individuals (Grafen 1990; Zahavi and Zahavi 1997). The stotting behavior of Thompson's Gazelles during pursuit by predators is one putative illustration of this model: the high leaps are less risky if the animal already has a good chance of getting away, and can therefore serve as an honest signal for the predator to switch targets, to the benefit of both animals. If fitness benefits for receivers and high-quality senders align in this way, then conditional signals and responses can co-evolve.

However, there is disagreement about the degree to which the handicap principle and costly/strategic signalling underpins signalling ontogeny. An alternative proposal, especially in cases of sexual selection, is the "truth in advertising" principle (Kodric-Brown and Brown 1984), which states that some animal signalling takes place costlessly via traits which also serve the purpose they advertise. For example, an impressive set of antlers on a stag can both help their bearer compete for mating privileges but also deter weaker opponents from competing. In a seminal text on animal signalling, Maynard

Smith and Harper also draw the distinction between handicap signals and “index signals,” which are honest because of an intimate relationship between their method of generation and the trait being signalled for, such that they are difficult or impossible to fake. Their example is the roar of a stag, which is a costless-yet-honest signal of the stag’s size and strength, because these qualities are what determine the tone and volume of the roar (Maynard Smith and Harper 2003). Other theoreticians have emphasized game-theoretic models and interpretations which are more general and nuanced than the classic handicap formulation, including signalling games where senders and receivers have more common interest, and there is scope for richer communication (Skyrms 2010). Importantly, these different signalling models have different implications with respect to costs and benefits, and resulting evolutionary trajectories. Alternative frameworks have also been developed by theoretical biologists which are more closely linked to the specifics of ecological context (e.g., Hebets et al. 2016).

Information, Influence, and Evolution

Given the diversity of signalling forms and explanatory approaches, the scientific study of animal signals is spread across many disciplines. It can involve observational studies of animals (in the wild and in captivity) and experimental studies, but there is also a considerable body of theoretical and formal work on biological signalling, e.g., carried out via evolutionary game theory and other modelling approaches.

This means that working definitions of signalling do not always agree. One common criterion for a signal is that it encodes and transmits information, so any observable trait of an organism that is correlated with an unobservable trait could be a “signal” of it to some other organism. More commonly, however, as outlined by Maynard Smith and Harper (2003), signalling is seen by evolutionary biologists as an evolved *mutualistic* relationship, where the sharing of information improves the fitness of both senders and receivers. This definition is narrower and more precise: “any act or structure which alters the behaviour of other

organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith and Harper 2003, p. 3). For example, bleeding did not evolve to attract sharks, so blood in the water, while informative, is not a signal in this co-evolutionary sense and is instead a *cue*.

Cues are one way of breaking the co-evolutionary condition: receivers adapt to take advantage of information that the sender reveals in a way that was not itself selected for. Conversely, senders might adapt to take advantage of preexisting receiver responses in order to *manipulate* them. One cross-kingdom example is the *Ophrys speculum* orchid, which attracts male *Campsocilia ciliata* wasps by mimicking the chemical signals of a sexually receptive female wasp so effectively that males preferentially copulate with the flower rather than with actual females (Ayasse et al. 2003). Cues and dishonest manipulation are both one-sided phenomena where an exploitative adaptation in either the sender or the receiver was not responded to by counter-adaptation in the other. Given there is no selection for the cue or manipulable trait, its persistence therefore requires additional explanation particular to the case; e.g., for the wasp species, remaining vulnerable to the orchid’s manipulation is probably less costly than altering the relevant parts of its mating strategy.

However, the co-evolutionary definition is not universally accepted. In an early dissent, Dawkins and Krebs (1978) described it as the “classical ethological” approach to signalling and proposed their own definition of signalling as *influence*. On this view, what is essential to signalling is that the sender intervenes on the receiver’s behavior by triggering conditional responses. This bundles together as signals both co-evolved signals and dishonest manipulation, as in the orchid-wasp case. Notably, this fits with how the term is used by at least some biologists; for example, throughout the Ayasse et al. paper describing the orchid-wasp case, the authors describe the deceptive pheromones manufactured by the *Ophrys speculum* orchid as “chemical signals.”

Three distinct uses of “signal” can therefore be found in the literature: (i) a narrow sense where signals are both informative and influential,

contrasted against cues and manipulations, (ii) the signals-as-information sense which includes cues but not manipulation, and (iii) the signals-as-influence sense which includes manipulations but not cues. In many contexts, the differences are merely semantic, but in others, the three uses would imply different evolutionary narratives regarding which behaviors (sender and/or receiver) have been selected for and why.

Animal Signalling and Human Behavior

Other than language, many attempts have been made to explain distinctively human traits via applications of animal signalling theory. These are often speculative and controversial. Some early theorists and popularizers of sociobiology ascribed evolved, innate, non-intentional signalling functions to exaggerated morphological features such as turned-out lips and enlarged ear lobes, breasts, and penises. A range of signalling explanations have also been proposed for intentional behaviors as diverse as conspicuous consumption, generosity, suicide bombing, grief, regret, and religion. Many proposals state that the costliness of such behaviors can be explained via the handicap principle or other signalling mechanisms but few attempts to interpret and quantify the relevant costs and benefits in a way that plausibly fits the relevant game-theoretic models (Grose 2011). Evidence for testable predictions (where these exist) has also been mixed or difficult to obtain, compounded by the additional modes of selection and transmission which human enculturation enables.

Conclusions

Animal signals are a common object of study in the biological sciences, where there is a large body of both case studies and theoretical literature. However, there are disparate approaches to describing and explaining animal signalling, with ongoing debates at both the conceptual and empirical level. Evidence of evolutionary causation also becomes problematic outside of

cases where (i) innate sender and receiver behavior means there is a one-to-one mapping between stimulus and response and (ii) fitness differences are readily discernible. Signalling theory, as developed in the study of animal signals, is therefore an intriguing and potentially powerful tool for crafting evolutionary explanations, but moving beyond simple verbal models of signalling requires a challenging degree of engagement with the complexities of both the signalling explanations and their application.

Cross-References

- [Communication, Cues, and Signals](#)
- [Costly Signaling](#)
- [Costly Signaling and Altruism](#)
- [Costly Signaling Theory](#)
- [Evolution of Communication](#)
- [Manipulation and Dishonest Signals](#)
- [Sexual Signaling During Ovulation](#)
- [The Handicap Principle](#)

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Animism

- [Ancestor Worship](#)

Anisogamy

- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)

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Synonyms/Keywords

[Female gangs](#); [Indirect aggression](#); [Intrasexual aggression](#); [Maternal investment](#); [Urban gangs](#)

Definition

Anne Campbell was a prominent evolutionary psychologist most noted for her work examining sex differences in aggression and her ethnographic studies of female gang members.

Introduction

Anne Campbell received her Doctorate in Experimental Psychology at Oxford in 1977. Two years later, Campbell began researching female gang members by living in New York City and talking with members of three gangs. She published her findings in her book *Girls in the Gang*. In February of 2017, Anne Campbell passed away, but her research on sex differences in aggression and on the intrasexual aggression of women continues to inspire others (Cross 2017).

Anne Campbell's work in the field of evolutionary psychology primarily focused on intrasexual aggression among women and female gang members. Campbell was one of the first evolutionary psychologists to articulate that women engage in less direct aggression than men, not only because there are fewer incentives for this behavior among women relative to men, but also because of women's vital role as a caregiver and the threat posed to that role by their involvement in direct aggression (Campbell 1999). This theoretical insight generated many empirical studies examining sex differences in aggression, competition, violence, and mating strategies. Campbell is also well known for her ethnographic work that she conducted while observing three different female gangs in New York. This work shed light on the motivations for women's involvement in gangs, which had previously been largely ignored by researchers whose primary focus was on male gang members (Campbell 1984). This entry provides an overview of the research accomplishments of Anne Campbell throughout her career.

Sex Differences in Aggression

A large literature in social and evolutionary psychology has documented marked sex differences

in aggression (e.g., Archer 2009; Campbell 1999). For example, research has shown that across cultures, males use more direct aggression than females from the age of two, onward. Early theorizing in evolutionary psychology explained these sex differences as the result of distinct mating strategies among males and females that incentivize aggressive and violent competition for access to mating opportunities among men, but not women (Archer 2009; Daly and Wilson 1988). A primary contribution made by Campbell was the theoretical argument that women's relatively lower levels of aggressive behavior could be attributed not only to reduced incentives relative to men, but additionally to an increased cost of aggressive behavior owing to women's primary and essential role as a caregiver.

Campbell used parental investment theory (Trivers 1972) as a foundation to explain why females are less likely to participate in direct aggression. She argued that women not only invest in their offspring more than men, but also that this investment is absolutely essential to the survival of her offspring. Studies have indicated that the death of the mother can increase the likelihood of her infant's death by a factor of five, whereas the death of the infant's father increases the offspring's mortality likelihood by a factor of three. Other studies report a child mortality of 100% following the death of the mother (Campbell 1999). Because females are vital to the survival of their offspring they must protect themselves in order to ensure that their offspring survive. As a result, engagement in physical aggression is often too risky for females, as their offspring's life depends on the mother's survival. Additionally, although intrasexual competition and aggression among women could allow women to compete for higher *quality* mates, the advantages of acquiring a greater *quantity* of mates is much reduced owing to women's large investment in each offspring and the reduced reproductive capacity that this investment constrains. However, for males, the benefits of intrasexual aggression typically outweigh the costs. This is owing to the fact that the costs of aggression are less steep (the survival of their young does not depend on their own survival)

and the benefits are greater because men's intrasexual aggression, if successful, can yield both a higher quality and quantity of mating opportunities. Additionally, a man's decision to opt out of aggressive competition with other men for mating opportunities could result in his complete exclusion from the mating market.

Campbell therefore argued that although there are benefits to be had for women engaging in intrasexual competition (e.g., increased quality of mates, stronger mate retention), competition involving direct aggression that would put women at risk of injury or death, would be avoided as a means of protecting oneself and one's offspring. Campbell supported this argument with evidence of sex differences in aggressive acts. For example, she noted that as the type of aggressive act increases in terms of direct violence, the gap in sex differences also increases, as women do not tend to participate in the riskier aggressive acts (Campbell 1999). Campbell also noted that women think more carefully about the potential consequences of impulsive actions (including aggressive acts), which may discourage them from participating in these actions. Women are less impulsive due to the necessity of their survival in order to take care of their young. Indeed, females must not only consider their own survival, but also the survival of their offspring (Cross et al. 2011).

These sex differences in aggression are not explained by sex differences in experienced anger. Indeed, research by Campbell (2006) illustrates that men and women experience similar levels of anger in response to physical danger. Rather, what appears to down-regulate women's aggressive behavior is their experience of fear. Campbell argues that fear may act as an emotional inhibitor of direct aggression by women, thereby reducing their risk of incurring serious injury. For example, females report more fear of physical harm than males. Women may be more fearful of physical harm due to their role in the survival of their young. These findings support Campbell's maternal investment theory (Campbell 1999, 2006). However, there are occurrences when the risks of nonaggression outweigh the benefits of nonaggressive actions.

For example, research suggests that oxytocin has a role in the reduction of fear in mothers during an attack on their young. In this instance, the overriding of the fear response is necessary, as the mother must put her life at risk by retaliating if she is to ensure the survival of her offspring. Oxytocin can also promote affiliative behavior in women. Instead of demonstrating a “fight or flight” response, females will often request help and protection from other females. By bonding with other females, mothers are able to protect themselves and, therefore, their offspring (Campbell 2008).

Although men tend to participate in more direct aggression than females, women and men have a similar age-assault curve, wherein violence is more prevalent during their teenage years (Campbell 1995). This research suggests that the motivation for aggression in both males and females is the same: the elimination of romantic rivals. During the teenage years, both males and females are entering their reproductive prime and are primarily motivated by the desire to secure potential mates. However, due to the maternal investment instinct that women possess, they are disinclined to use aggressive and violent behaviors to compete for those mating opportunities which may result in bodily harm, relative to men. Women, instead, are more likely to use indirect aggression, such as the verbal derogation of competitors in order to appear superior to their romantic rivals. This aggressive behavior is typically expressed indirectly, such as through gossip, rather than verbal derogation directed directly toward a romantic rival. This behavior is used in order to shield the aggressor’s identity, which will protect the aggressor from retaliation. This tactic is useful to women, who wish to protect themselves in order to care for their offspring. However, indirect aggression is less advantageous for men, as they must appeal to potential mates by demonstrating their dominance over other men in a more direct and public fashion (Campbell 1995, 1999, 2004). Campbell’s emphasis on the important role of maternal investment added much more depth and predictive power to the traditional evolutionary framework for explaining sex differences in intrasexual aggression. These insights

continue to play an important role in the work of many evolutionary psychologists.

Female Gang Members

Although there has been a fair amount of research on gangs and their members, very few researchers have systematically examined the role that women play in their involvement in gangs. When researchers did examine female gang members, it was often to explain the way in which male gang members viewed them. This research sorted female members into different categories, such as “Sex Objects” and “Tomboys,” but did not reduce male gang members to such labels. Campbell was one of the first researchers to directly examine the experiences and motivations of female gang members. In order to do so, Campbell spent 6 months in New York engaged in intensive observations of, and interviews with, three different gangs: The Sandman Ladies, The Sex Girls, and The Five Percent Nation.

Campbell applied the same evolutionary background when researching female gang members as she did when studying aggression in other females. She noted that most of the aggressive actions demonstrated by female gang members were performed in order to appeal to or guard mates. Additionally, although female gang members are more likely to use violence than other women, the pattern of aggression still fits that which was described above. That is, female gang members tend to use indirect aggression rather than direct aggression in order to shield their identity and protect themselves and their young. Seeking mates is especially important for female gang members, as most join gangs in order to escape poverty by finding a mate who will provide financial security and protection for the woman and any offspring she may have. Because these women depend so heavily on their partners, they engage in intense competition with other women in order to guard their mate from rivals. Female members enact these mate-guarding behaviors by using indirect aggression in order to derogate rivals. Indeed, most of the aggressive behaviors demonstrated by female members are directed

against romantic rivals. When direct aggression is used by females, the fights are less likely to include firearms than male gang fights, demonstrating the less violent nature of female intrasexual fights. One especially common reason for fighting is due to the female gang member's need to protect her reputation or integrity. These fights may also occur due to the member's desire to defend the honor of her child or her partner (Campbell 1984, 1991).

Conclusion

Anne Campbell made many contributions to the literature on gangs and to the field of evolutionary psychology, especially regarding sex differences in intrasexual aggression. In particular, Campbell's research gave voice to the female psychology of aggression—a topic that had been taken for granted as simply the inverse of men's psychology. This research was achieved through her ground-breaking theoretical advancements as well as her rigorous empirical and observational research. The research that she conducted continues to inspire researchers and provides fertile ground for the generation of new research ideas.

Cross-References

- [Intrasexual Rivalry Among Women](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Urban Gangs](#)
- [Verbal Derogation Among Women](#)

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Anonymity

- [Deindividuation](#)

Anonymity of Cyberbullying

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Synonyms

[Cyber/Internet/online harassment](#); [Cyberstalking](#); [E-bullying](#); [Electronic aggression](#); [Electronic bullying](#)

Definition

Although cyberbullying shares certain categorical features synonymous with traditional types of bullying, cyberbullying itself is a unique

phenomenon that occurs through the use of technology (e.g., social media, email, chat rooms, instant messaging, text messaging, or websites) rather than through traditional face-to-face (e.g., physical fights, destruction of property, verbal insults) or in-person (e.g., gossiping, ostracism) modalities. Anonymity is often an essential component of cyberbullying and is used to refer to anonymous posts and interactions in which a person's identity cannot be determined through the computer IP address, usernames, or handles. Further, anonymity can also be used as a description when the actual name/identity of a person's offline presence is more difficult to determine even in the obvious existence of an online one (e.g., impersonating another individual, computer IP address, usernames, or handles).

Introduction

With rising technology use, more social interactions occur through the internet (e.g., social media, websites, chat rooms) or other electronic means (e.g., texting, messaging systems). An important facet of this online social communication is an applied or assumed anonymity within interactions (e.g., posting anonymous comments). In fact, people are often recognized online by their username or handle in which they establish an online persona as opposed to their actual one (e.g., GoTheDistance2016 vs. Joe Smith). However, in many cases people are not as anonymous as they perceive themselves to be as a result of computer IP addresses that are typically attached to online activity. Many electronic devices (e.g., cell phones) also track data and activity and link the information with specific users. The perceived anonymity of online and electronic social interactions is considered by many (though not all) researchers to be an important feature of cyberbullying. Researchers who do not consider anonymity to be an important distinguishing feature of cyberbullying note that other forms of bullying can also be characterized by anonymity (e.g., not knowing who started a rumor or who defaced someone's possessions). Cyberbullying can be perpetrated by a single person or a group of people

and is characterized as repetitive aggressive acts or messages that occur online or electronically with an intention to inflict suffering, harm, embarrassment, or discomfort to another person. Approximately 50% of youth have been estimated to have experienced and been involved in cyberbullying.

Recent research has been conducted to determine whether people who are involved in bullying at school (i.e., traditional forms of bullying including overt/physical, indirect/relational) as bullies, victims, or bully-victims are also involved in cyberbullying. The evidence to date is mixed with some researchers finding that over 80% of youth who bully others through cyber or electronic means also bully others at school through traditional forms of bullying; similarly, over 80% of victims of cyberbullying are also victimized at school (e.g., Raskauskas and Stoltz 2007; Juvonen and Gross 2008). In contrast, other researchers have found substantially less overlap; for example, approximately 70% of school bullies and victims and 50% of bully-victims were not involved in cyberbullying (Kowalski and Limber 2013). Regardless of the percentage of overlap, researchers do agree that certain environmental factors like being male, having friends involved in delinquent activities, and having non-trustworthy nonsupportive friends are predictive of being involved in cyberbullying. Additionally, engagement in cyberbullying is also predicted by frequent internet use and high levels of computer/internet abilities (e.g., Ybarra and Mitchell 2004). Given that a substantial amount of youth are involved in cyberbullying, it is important to consider whether the anonymity associated with cyberbullying leads to more negative outcomes than traditional forms of bullying.

Role of Anonymity

Although traditional forms of bullying can occur anonymously (e.g., uncertainty about who started a rumor or defaced possessions), the role of anonymity is considered a crucial predictor of the *severity* of cyberbullying (Barlett et al. 2016; Vanderbosch and Van Cleemput 2008). Perceived

anonymous online activity predicts crueler online behavior (i.e., the online disinhibition effect; Suler 2004) compared to nonanonymous online activity. The association between perceived anonymity and being a perpetrator of cyberbullying is mediated by positive attitudes toward cyberbullying. The online disinhibition effect (i.e., crueler online behavior compared to face-to-face behavior) has also been explained by perceived anonymity in online activity leading to reduced self-awareness and, in turn, increased deindividuation. There is also evidence that having anonymous interaction partners reduces the level of intimacy during online disclosures and feelings of closeness. Overall, anonymity appears to reduce anxiety levels for the perpetrator, perhaps because there's a perception of fewer negative consequences.

Negative Outcomes Associated with Cyberbullying

Cyberbullying is associated with a host of negative outcomes (e.g., Tokunaga 2010). Specifically, being the target of cyberbullying is robustly associated with increased internalizing problems such as anxiety, depression, loneliness, suicidal ideation, and suicide attempts/self-harm and externalizing problems such as increased substance use, alcohol use, rule-breaking behavior, and aggression. In addition, cyberbullying experienced during adolescence is associated with negative developmental outcomes including poor school performance and increased avoidance of school. There is also an association between low self-esteem and teens who seek out opportunities to interact online with strangers (Valkenburg and Peter 2011).

An important feature distinguishing cyberbullying from more traditional forms of bullying is that specific aggression acts are not isolated to a single area such as a school or park but rather can rapidly spread to multiple domains such as multiple social media sites, chat rooms, and text/picture messages. Moreover, many online interactions are asynchronous in nature. The negative outcomes associated with being bullied has been

hypothesized to be exacerbated in cyberbullying due to the wider group of people who see, and often respond to, the aggressive acts as well as the longevity and permanency of the aggressive acts. There is also evidence that youth with low levels of self-control are more likely to engage in cyberbullying than their peers with high self-control suggesting that youth engaging in cyberbullying are not carefully considering the ramifications of their online aggressive behavior; this lack of using self-control may be partially due to the perceived anonymity of their behaviors.

Conclusion

Although cyberbullying shares characteristics similar to traditional forms of bullying, the motives and desire to engage in cyberbullying over more traditional forms may differ. One component that sets cyberbullying apart is the presence of real or perceived anonymity in an online space. A child who is smaller in stature or lower on the social hierarchy may not have the "power" to induce fear in a traditional bully-victim interaction. However, size becomes irrelevant in the case of cyberbullying, and the power gained in the bully-victim relationship is now done so by anonymity. By virtue, certain characteristics that precluded an individual from being a traditional bully is not a concerning factor in becoming a cyber one. As a result, the anonymity of cyberbullying has been proposed by some researchers to increase the severity and negative outcomes associated with being the target of aggressive online and electronic acts compared with experiencing other forms of bullying. Other researchers, however, have noted that anonymity is not limited to cyberbullying and can also be a component in more traditional forms of bullying. Regardless, it does appear that anonymity in cyberbullying is more prominent and apparent to targets and bystanders and that the feeling of anonymity, perceived or in actuality, predicts more severe levels of cyberbullying.

More recently, the legal and ethical responsibilities of how to protect those experiencing cyberbullying in conjunction with the

safeguarding of an individual's constitutional rights has become heavily debated. The perceived anonymity of a perpetrator, coupled with a known constitutional protection, may actually further encourage the use of cyberbullying compared to a more traditional form. Clearly, the anonymity that can be achieved within cyberbullying does indeed make it a unique phenomenon worthy of continued study. With the rising use of technology for the foreseeable future, the greatest task we may be faced with is how to encourage positive uses of social interaction while simultaneously mitigating negative attributes like cyberbullying.

Cross-References

- [Child Abuse and Bullying](#)
- [Procedures for Dealing with Bullies](#)
- [Sex Differences in Cyber Bullying](#)

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Anorectic

- [Anorexia Nervosa](#)

Anorexia

- [Anorexia Nervosa](#)

Anorexia Nervosa

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Synonyms

[AN](#); [Anorectic](#); [Anorexia](#); [Eating disorders \(EDs\)](#); [Fear of weight gain](#); [Food restriction](#); [Low weight](#)

Definition

According to APA.org (“Eating Disorders”, 2018), anorexia nervosa is defined as an eating disorder characterized by individuals (most commonly adolescent girls) who restrict their eating to the point of starvation due to the false belief that they are overweight or carrying too much weight (i.e., an obsessive drive for thinness).

Introduction

Eating disorders (EDs) are abnormal eating patterns and behaviors that can be detrimental to one's overall health (i.e., physical and psychological) and, in extreme cases, can result in death. EDs are most frequent in industrialized societies, and 95% affected are women. Symptoms of eating disorders are present in at least 10% of school-aged girls co-occurring with medical, dietary, and psychological issues. Anorexia nervosa is defined as an eating disorder characterized by individuals (most commonly adolescent girls) who restrict their eating to the point of starvation due to the false belief that they are overweight or carrying too much weight (i.e., an obsessive drive for thinness). On a similar note, bulimia is an eating disorder characterized by individuals who eat an excessive amount of food followed by purging through vomiting, laxatives, and/or excessive exercise ("Eating Disorders", APA.org, 2018).

Both anorexia and bulimia share three major characteristics: disturbed body image, an obsessive strive for thinness, and an almost identical geographical distribution.

Because of these similarities, many evolutionary theories conceptualize both anorexia and bulimia as having the same underlying etiology and thus are thought to both derive from the same general mechanism(s). According to a review by Kardum, Gracanin, and Hudek-Knezevic (2008), current evolutionary theories on the development of eating disorders (anorexia specifically) are adapted-to-flee-famine hypothesis (Guisinger 2003), kin selection theory (Hamilton 1964), the model of parental manipulation (Trivers 1974), reproductive suppression hypothesis (Wasser and Barash 1983), sexual competition hypothesis (Abed 1998), and social attention-holding power (Gatward 2007).

Adapted-to-Flee-Famine Hypothesis

The present theory posits that ED symptomologies (i.e., restricting food, denial of starvation, hyperactivity) are a result of an evolutionary adaptation to cope with times of famine. In ancestral

times, food was not readily available and migration was necessary to find food sources.

In support of this theory, it has been found that many species refuse food intake during times of migrating and breeding. Additionally, increased activity is elevated during times of limited food resources assumedly to increase chances of finding food resources. Anorexic-like syndromes are found in several low body weight species, and anorexia has been found to be highly heritable, suggesting that such symptoms were evolved to be advantageous in the ancestral environment.

The adapted-to-flee-famine hypothesis does not explain why those who suffer from anorexia refuse to eat when food is plentiful and why hyperactivity is not always a marker for anorexia.

Kin Selection Theory

The kin selection theory contends that anorexia is adaptive for favoring intra-familial prosocial behavior (i.e., caring, helping, self-sacrificing) over reproductive success. Common attributes of those who suffer from anorexia are overprotective attitudes regarding family members and incessant worrying about their well-being. Reproductive suppression elevates a female's inclusive fitness by assuring the reproductive success of her family members. In other words, a female becomes anorexic as a way to completely devote herself to taking care of her family members so that they are more likely to survive and have children of their own. By not bearing children, the female is not using up vital resources that her family may need to adequately function and thrive.

The Model of Parental Manipulation

The model of parental manipulation has three underlying hypotheses (note: these are all unconscious drives): (1) parents influence (e.g., dominant and overprotective mothers) the onset and maintenance of EDs by preventing the daughter from finding a partner and/or preventing detachment from the parent(s) to find a partner; (2) eating disorders elevate parental reproductive fitness by

allocating resources to children of higher reproductive value; and (3) EDs reduce fitness of those who suffer from them by evoking reproductive suppression. That is, parental fitness increases because reproductive suppression weakens or diminishes the reproductive value of the sufferer, which in turn preserves familial resources by not having to provide for possible additional offspring. Overall, the female experiences a switch from genetically based selfish behavior (i.e., reproducing) to selfless behavior (i.e., not reproducing) for the sake of preserving and optimally utilizing resources for her family.

Reproductive Suppression Hypothesis

The present theory suggests that females suppress their reproduction when the current conditions are not in favor of reproductive success or offspring survival. That is, the female believes that the benefits of suppressing reproduction (i.e., depleting fat stores to the extent of stopping the ovulatory cycle; amenorrhea) outweigh the costs and that resources will be more plentiful and readily available in the future to assure reproductive success. This reproductive suppression is done through extreme dietary behaviors, and preferring a thinner body ideal can be a way to manipulate the timing of reproduction.

A variant of this hypothesis was proposed by Surbey (1987). Females can become anorexic as a way to stunt development. If a female is predisposed to mature earlier in a modern day society that favors late maturers, anorexia is a way to change a female's natural developmental trajectory to one of a late maturer. Again, this is done by reducing fat through strict dietary behaviors. The benefit of late maturers in modern society is that it takes reproduction (i.e., reduces libido, attracts fewer males, induces amenorrhea) out of the equation when academic and professional success are more valued in the female's family.

The reproduction suppression hypothesis fails to address the symptoms of hyperactivity and distorted body image prevalent in those who suffer from anorexia and does not explain why an alternate and less costly method to suppressing

reproduction in women was not evolved, why anorexia exists in postmenopausal women, and why anorexia is most common in those who are white and wealthy.

Sexual Competition Hypothesis

The present hypothesis proposes that eating disorders are the product of "runaway" (spiraled out of control) intra-sexual competition in Westernized societies. As a result of decreased long-term mating strategies and increased female social and economic independence in the modern Westernized environment, intra-sexual competition among females for long-term mates has increased. Thinness has been related to youthfulness and the ideal "nubile shape" that was once a signal of fertility in ancestral times. The present hypothesis posits that eating disorders are an unconscious attempt for females to better match the nubile body shape that signals a longer period of fertility when competing with other females for a long-term mate in Westernized societies.

The sexual competition hypothesis does not account for proximate causal factors of eating disorders and does not provide an explanation for eating disorders among males.

Social Attention-Holding Power

The social attention-holding power hypothesis incorporates response to threat to evolutionary ideas to understand the onset of EDs.

The present hypothesis explains that ED symptoms are a result of social attention-holding power (i.e., the ability to gain and maintain attention and investment from members of a group) and the need to belong in a social context. This concept also ties into the degree a person feels in control in a social context: a dominant (i.e., high status or position) person feels more in control, and a submissive (i.e., lower status or position) person feels less in control. It is assumed that the need to belong has ancestral roots due to the idea that in the ancestral environment, it was likely that exploitation led to death. In other words, being

excluded meant less access to vital resources to assure survival.

Unlike ancestral times where being heavier meant having greater access to resources, modern day society favors thin individuals, as being thin is representative of status and control (i.e., the ability to afford healthy foods and gym memberships). In summation, this new drive for thinness can set off the threat of famine response, eliciting the onset of an eating disorder.

Conclusion

Eating disorders (EDs) are abnormal eating patterns and behaviors that can be detrimental to one's overall health and, in extreme cases, can result in death. EDs are most common in adolescent women in industrialized societies. There are several current evolutionary theories behind the onset of eating disorders that have yet to be extensively investigated.

Cross-Reference

► [Eating Disorders](#)

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Anorgasmia

► [Orgasmic Disorders](#)

Antagonizing

► [Child Abuse and Bullying](#)

Anterior Cerebral Cortex

► [Frontal Cortex](#)

Anthropological Universals

► [Cultural Universals](#)

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 ► [Michael Tomasello](#)

Anthropology

► [Towards Methodological Pluralism in Psychological Sciences](#)

Anthropomorphism

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Synonyms

[Attribution of human traits](#); [Imposing humanlike characteristics](#)

Definition

The attribution of human traits, motivations, and persona-like qualities to nonhuman animals and/or inanimate objects.

Introduction

The perception that nonhuman animals and inanimate objects possess human characteristics, motivations, and personalities is described as anthropomorphism. Application of anthropomorphic interpretations may reflect both the conceptual nature of anthropomorphism and its use as a critical means of understanding phenomena and patterns of behavior. Anthropomorphic thinking may, at times, be imprecise in relation to real world phenomena, whereby human traits are projected in an exaggerated manner onto a nonhuman animal or object in order to predict or depict their internal states, desires, thoughts, and motivations. This kind of anthropomorphism is most often found in children's books, cartoons, films about animals, and even some nature documentaries. In contrast, another form of anthropomorphism involves applying psychological principles in very systematic and biologically accurate ways, providing unique insights into an animal's or species' life history.

In understanding the origins of anthropomorphism, we can ask why humans feel the need to

impose human-like qualities on other animate beings and inanimate objects? Are there psychological and evolutionary functions (adaptations) derived by anthropomorphizing that assist in problem solving in social and environmental milieus, in a cause-and-effect manner? Are humans the only species that anthropomorphize? Do domestic dogs, for example, anthropomorphize human behavior in relation to their own canine frame of reference? Given that so many behaviors are shared between closely related species (possibly stemming from common ancestors and similarities in nervous systems, physiology, and anatomy), are other species also prone to anthropomorphic tendencies?

Anthropomorphism and Perspective-Taking

Taking another species' perspective (or that of an inanimate object) is crucial to the process of anthropomorphism. The famous question posed by the philosopher, Nagel (1974), of "What does it feel like to be a bat?", is indicative that humans do process other species' experiences by attempting to take their perspectives, although it is not clear how effective we are at this task. It may be very difficult to project oneself within the mindset of an octopus whose body is so different from that of a human, or to truly imagine seeing with the compound eyes of a dragonfly (Dennett 1991). However, the process of anthropomorphizing may be a reflection of the capacity to empathize to some degree (Mitchell et al. 1996). Empathic processes might include thoughts projected onto others, such as, "If I were that dog, what would I feel in that situation?", and, "If I were that orangutan, what would I say if I could talk?"

It is noteworthy that humans tend to anthropomorphize animals that more closely resemble themselves and have a high "cuteness" factor (e.g., are reminiscent of babies in features and actions) as more human-like in their motivations and responses. For example, nonhuman primates are more likely to be anthropomorphized as child-

like or as surrogate humans, while an animal as distinct from humans as a cockroach, or an inanimate object such as a rock, may not be described as possessing the same extent of internal states and emotions. The foundation of these differences may lie in humans' ability to more easily empathize with creatures that are biologically more like them and are closer taxonomically.

Anthropomorphism of Nonhuman Animals

When humans infer that nonhuman animals are psychologically, cognitively, consciously, emotionally, and even spiritually like humans, they can be said to be imposing an anthropomorphic interpretation on the behaviors they observe and inferring human-like internal states (Mitchell et al. 1996). Fundamentally, the tendency towards anthropomorphism diverges into either a "subjective" and/or an "objective" interpretation of nonhuman animal behavior. Under some circumstances, the term "anthropomorphism" is applied pejoratively, referring to a highly subjective, inaccurate, and anthropocentric (human-centered) nature of referencing behaviors as human-like for explanation, but without regard to a realistic assessment of the animal's internal state(s).

Occurrences of inaccurate anthropomorphic inferences are often used for effect in children's books to create a sense of empathy with an animal character, particularly in illustrating a moral code (e.g., greed, kindness, sympathy, etc.). For example, Winnie-the-Pooh, as a children's book character, is highly personified and depicted entirely in anthropomorphic terms. He speaks and is friends with humans and other species with whom he interacts, not at all reflecting a wild bear's behavior or ecological requirements. Inaccurate anthropomorphic inferences may also occur in some nature documentaries: voice-overs provide a running commentary of the internal thoughts and motivations, feelings, and desires of animals, presenting a blurred, subjective version of the facts to explain events as they unfold visually. By personifying the animals in such a

subjective manner, the documentary becomes more story-like and possibly enhances its entertainment. Even so, the audiences may develop greater empathy and recall additional information about that species than if the documentary was presented in a drier, more objective style (Dolins et al. 2010).

Under some circumstances, however, it may be both accurate and acceptable to interpret other species' behaviors using a human-like frame of reference. This is because what we understand about human behavior, the psychological principles, may also be true for other species, particularly those closely related to humans, such as nonhuman primates and other large-brained, long-lived, highly social species, such as dolphins, elephants, parrots, etc. With these animals, an anthropomorphic interpretation may provide a biologically insightful explanation in an objective framework.

Anthropomorphism as a Critical Tool

In science in general, and in the scientific study of animal behavior, Ethology, it has long been a tradition to avoid the use of anthropomorphic interpretations of animal's internal states and motivations. The tendency is to explain behavior in the most objective, reductionist manner, so to avoid subjectivity, consistent with a Behaviorist framework. This is in contrast to a framework that posits higher order thinking and emotions in nonhuman animals, yet is still objective. In more recent years, it has become clear that the strength of evidence in support of the biological continuum (in cognition, emotions, and other internal states) between humans and other species should influence our interpretations of nonhuman animal behavior, and not surprisingly, our interpretations of human behavior as well (Darwin 1859; 2006). Much of this evidence is based on parallels among closely related species and even more distantly related species in anatomical features and consequent function and behaviors, as well as similarities in the neural connectivity (pathways) of the central nervous system and brain (e.g., Spocter et al. 2010).

An excellent example is Barbara Smuts' (1985) detailed study of wild olive baboons in Kenya and Tanzania over two years, which provided her with insights into the social relationships between males and females. Her observations lead to a significant understanding of baboons' patterns of sociality that were based on objective behavioral assessments using ethograms and operational definitions as proscribed by ethological methods. Smuts referred to these tightly bonded social relationships as "friendships" between baboons (1985), which from a reductionist viewpoint, could be viewed as consistent with an anthropomorphic explanation. However, applying the term, anthropomorphism in the positive sense, Smuts' framework summarized and described behavior patterns that parallel those occurring in human societies and between human males and females who develop close bonds lasting over many years. These "friendships" as we would define it for humans were between pairs of baboons and persisted over long periods of time. Smuts' close observations of these baboon friendships were based on empirical observations of the number and frequency of grooming bouts between individuals; proximity during feeding, resting, and travel; and for some friendships, the number and frequency of copulations between male and female friends, although some friendships remained platonic. Smuts' research further revealed that the choice of whom to copulate with in a baboon troop was not random. The patterns suggested that females more often chose to mate with males who were her friends. These male friends were individuals with whom she selectively spent significant amounts of time in close proximity without fear, groomed more often compared to others, and allowed them to play with her offspring (Smuts 1985).

Through Smuts' insight into another primate species' patterns of sociality, her detailed and empirical observations from within a theoretical framework of behavioral analysis, and anthropomorphic application of human psychological principles, her research substantially shifted the perception of nonhuman primate social behavior within the fields of primatology, animal behavior, and animal cognition.

Anthropomorphism and Anecdotes

Where do we draw the line between objective and subjective observations and interpretations of behavior? Is one observation sufficient (i.e., an anecdote) or is that deemed too subjective? If an observation of a behavior is made just once, is it a data point or an anecdote? Should it always be the requirement to have repeated observations of a behavior under controlled experimental conditions that are purely objective and empirical, and open to being tested statistically against the random probability of its occurrence? Ethological methods for studying animal behavior uses repeated observations of the same set or sets of behaviors to accumulate data for statistical analyses. It takes time to become an experienced observer who accurately assesses the frequency of each behavioral occurrence. However, there are types of behaviors that are rarely and/or only very briefly displayed, as occurs in highly effective types of problem solving and innovation. The existence and significance of these rare behaviors may be diluted, and/or lost, in pursuit of an empirically driven, repeated measures framework.

In his book, *Animal Intelligence* (1888), George Romanes used descriptive anecdotes that he deemed valid, received from individuals whom he considered to be experienced, reliable observers. From these anecdotes, he deduced patterns of insightful problem-solving abilities in animals. Later, Wolfgang Köhler (1925) in addition to assessing captive chimpanzees' cognitive abilities in controlled experiments, also used one-time observations of these apes' insightful problem-solving behaviors. Indeed, incredibly valuable insights have been derived from anecdotal evidence, often in the form of narratives, where an individual animal or animals demonstrate an isolated occurrence of an unusual behavior that can only or most easily be explained by attributing human-like cognition and/or motives. For example, Köhler's most referenced study of chimpanzee tool use in problem-solving involved providing the chimpanzees with sticks that if combined in the right order could create a longer stick to reach bunches of bananas that had been hung high up. Boxes for stacking were also

provided, to help reach the bananas with the elongated stick. One of the chimpanzees, Sultan, after repeated efforts to attach two shorter sticks together, eventually fitted them together into a longer stick. He also placed boxes on top of one another, and so was able to retrieve the bananas. This solution demonstrates insight into the problem and shows innovation by combining the elongated stick with the stacked boxes to achieve the height necessary to obtain the food. Not only are anecdotes such as this one useful for understanding behavior in a particular context, it also provides an avenue for theoretical investigations of broader behavioral patterns and for examining intelligence across species as an adaptation.

In their two book series, *Machiavellian Intelligence* (1989, 1997), Byrne and Whiten accrued anecdotes of accurately observed single instances of primates' innovative problem solving and/or cases of deception. It would be very difficult to create controlled experiments to collect these kinds of empirical data on a repeated basis. When combined, these large numbers of accurately observed events by reliable observers (primatologists) formed a significant database and paralleled that of repeated measures and observations. Through this method and the insights derived, Byrne and Whiten were able to generate new hypotheses and questions about the evolution of primate intelligence, to postulate differences in social intelligence across phylogeny, and to identify potential selective pressures on intentional manipulation of social partners (e.g., as occurs in deception).

Another example is the comprehensive avian IQ index that was created by Louis Lefebvre (Lefebvre et al. 2004) based on "the reported frequency of behavioral innovation as an operational measure of cognition" (p. 233). Lefebvre stated that he and his team look for patterns in reported anecdotes that help explain and validate innovative and intelligent behavior in birds that otherwise appear as individual occurrences. When assembled into a cohesive set of independent and individual observations, it becomes clear that the patterns of intelligent behaviors occur would not have been predicted from

previous theoretical positions on avian behavior and innovative problem solving. Moreover, the behavioral flexibility displayed by some individual birds and species was found to be an essential adaptation for survival compared to others who did not demonstrate this adaptive capacity. Based on the combined anecdotal evidence, Lefebvre et al. (2004) writes that, "In birds, innovation rate is associated with the ability of species to deal with seasonal changes in the environment and to establish themselves in new regions, and it also appears to be related to the rate at which lineages diversify. Innovation rate provides a useful tool to quantify inter-taxon differences in cognition and to test classic hypotheses regarding the evolution of the brain." (p. 233). Thus, summarized anecdotes and the process of anthropomorphic identifiers of intelligent behaviors in birds (and other species) provide opportunities to expand theoretical boundaries of our understanding of the evolution of problem-solving functions correlated with changes and/or differences in the brain, across species.

Anthropomorphism of Animal-Human Chimeras

Human-made artifacts in the archeological record were often wrought to resemble extraordinary nonhuman animals or chimeric creatures composed of a nonhuman animal morphed with a human. It is likely that the cultures that were responsible for these artifacts placed a value on animals as other than just as a means of survival (e.g., as food). Animals may have served as stand-in humans or human surrogates with special powers that superseded nature, potentially in a religious or spiritual context (Passariello 1999). Shamanistic powers, for example, are thought to derive partially from animal spirits that confer some of the animal characteristics and the special powers emanating from that animal to the human. This mixing of human and animal, as exemplified in the Lion Man Figurine (Smithsonian, <http://humanorigins.si.edu/evidence/3d-collection/>

artifact/lion-man-figurine), may have conferred the animal's powers in a kind of symbolic projection into the human psyche and social-religious-spiritual sphere (Passariello 1999).

Conclusion

Accuracy in understanding and predicting the behaviors of others, including nonhuman animals, requires both observational data and a conceptual framework in which to interpret those data. The conceptual framework most often involves the consideration of human intentions, thoughts, desires, emotions, and motivations. When these attributes are imposed, in exaggerated form, on nonhuman animals or even inanimate objects, it is labeled "anthropomorphic" in the pejorative sense. However, when we apply our understanding of psychological principles to nonhuman animals (e.g., in research), it can also be described as "anthropomorphism" in a positive sense, and may lead to important insights and assist in generating novel theoretical frameworks and hypotheses to better understand other species' behaviors. Thus, anthropomorphism can take two main forms, one that inaccurately applies exaggerated human characteristics to nonhuman animals and inanimate objects, and another where it is used as a critical tool to investigate and construct a framework in which to explain/understand the behavior of other humans and non-human animal species. The division between subjectivity and objectivity largely parallels the division of an inaccurate application of anthropocentric qualities compared to an insightful projection into understanding behavior.

In summary, we are left with more questions than answers about the function of human's ability and desire to use anthropomorphism to explain their world: Is it possible to form truly objective representations of another species' behavior without using insight that we would apply in understanding another human or human society; insight that when applied to another species is referred to as anthropomorphism? And, is the anthropomorphic process necessary for survival, acting as a

filter through which individuals perceive and navigate their social and physical world?

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Anti-cuckoldry

► Prevention of Infidelity

Anti-cuckoldry Adaptations

- [Psychological Evidence for Human Sperm Competition](#)

Anti-cuckoldry Tactics

- [Solution to Paternity Uncertainty](#)
- [Sperm Competition Tactics](#)

Antigay Bullying

- [Homophobic Bullying](#)

Antimicrobial Hypothesis

- [Antimicrobial Hypothesis, The](#)

Antimicrobial Hypothesis, The

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Synonyms

[Antimicrobial hypothesis](#); [Cultural transmission](#);
[Pathogens](#); [Taste preferences](#)

Definition

Drawing from the insights that bacterial growth is promoted by higher temperatures and spices

can inhibit or kill bacteria, the antimicrobial hypothesis of spices argues that cultures in warmer regions of the world are more likely to include spices in their recipes (and benefit from the antimicrobial properties of spices) relative to cultures in cooler regions.

Introduction

Pathogenic microbes, such as disease-causing bacteria and viruses, have posed a threat to the health and reproduction of many organisms for as long as microbes have existed, thereby constituting a significant recurring adaptive problem (Thomas et al. 2012). In turn, the selection pressure imposed by pathogenic microbes gives rise to various physiological and behavioral adaptations that facilitate the prevention of microbial infections, such as the immune system, feelings of disgust, and avoidance instincts (e.g., Curtis and Biran 2001; Tybur et al. 2016). The cultural transmission of practices that may help to ward off pathogenic microbes (as well as a corresponding favorability toward those practices) also constitutes another important line of defense. The current entry discusses one such cultural practice – the use of and taste for spices (Billing and Sherman 1998) – as an important accompaniment to humans' array of antimicrobial defenses.

Spice Use Through the Ages and Across Regions

Spices refer to dried and aromatic plant substances whose primary food function is for seasoning and flavor rather than nutrition. These include seeds (e.g., cardamom), fruits (e.g., chilli pepper), leaves (e.g., cilantro), and roots (e.g., garlic). Spices derive their distinctive flavors from chemicals that are produced in order to fend against pathogens and parasites. Food spicing may have originated from early hunter-gatherers who unwittingly improved the flavor of their game by encasing the meat in certain types of leaves. Over time, early

civilizations began realizing the useful properties of spice plants (Rosengarten 1981; Tapsell et al. 2006). For example, the Ancient Indians (approximately second to fourth century BC) documented their discoveries of the antiseptic and digestion-aiding properties of spices such as sesame and cloves, while the Ancient Egyptians (~1500 BC) initiated a classification that grouped spices such as garlic, onion, and thyme as health boosters. The antimicrobial prowess of spices was also well recognized as can be seen from their extensive use in the embalming and preservation of bodies. Spices progressively became high in demand. When the Goths besieged Rome in 408 AD, they demanded a ransom of 5,000 pounds of gold and 3,000 pounds of pepper. Marco Polo, Christopher Columbus, and Hernando Cortes count among the famous explorers who changed history while seeking faster routes to the spice-rich Indies.

Although spices have been used in food preparation throughout the world for centuries, patterns of spice use differ considerably across regions. More specifically, spice use varies as a function of regional temperature such that countries with higher average temperatures tend to incorporate more spices into their recipes (Billing and Sherman 1998). This pattern paints a puzzling picture. First, it is not clear why spices would be popular only in some cuisines despite their health benefits and usefulness as a preservative (Tapsell et al. 2006). Second, given that spices can make people feel hot and perspire, it seems counterintuitive that cultures in warmer regions would exhibit a stronger preference for spices. Third, although the use of spices is most often attributed to their role as a flavor enhancer, this does not address the ultimate, evolutionary question of why people would find foods tastier when flavored with spices. In light of these puzzles, and drawing from the insight that higher ambient temperatures are more conducive to bacterial growth (Genigeorgis 1981), Billing and Sherman (1998) hypothesized that the use of spices arose as protection from food-borne bacteria that are more likely to thrive in warmer climates.

Antimicrobial Hypothesis of Spices

Recipes containing meat products that have been kept for some time at room temperature in hotter, tropical climates exhibit a substantial hike in bacterial concentration (Genigeorgis 1981). Noting both the tendency for bacteria to proliferate at higher temperatures and the antimicrobial properties of spices, Billing and Sherman (1998) argued that spices are popular in warmer regions because they help to kill or inhibit food-spoiling bacteria, thereby contributing to the health and reproductive success of people who find their flavors enjoyable. To test the hypothesis, they examined 4,578 traditional meat recipes from a sample of 36 countries for the number of spices used out of 43 spices. Meat recipes were selected for analysis over nonmeat recipes (e.g., vegetable recipes) because of their greater likelihood of breeding bacteria and carrying food-borne illnesses. The number of spices used in the recipes was then compared between countries with varying average temperatures.

The results supported the prediction that countries with higher average temperatures add more spices to their recipes relative to countries with lower average temperatures. The researchers found that in ten of the hot-climate countries, namely, Ethiopia, Kenya, Greece, India, Indonesia, Iran, Malaysia, Morocco, Nigeria, and Thailand, every meat-based recipe included at least one spice. By contrast, in cold countries such as Finland and Norway, respectively, 19 of 62 and 25 of 77 meat-based recipes did not use any spices. The results also showed that higher average temperatures (such that food-borne pathogens would be most prolific) were associated with the use of spices with stronger antimicrobial effects. A follow-up study found that, on average, vegetable-only recipes called for significantly fewer spices than meat-based recipes (Sherman and Hash 2001), thus lending further support to the argument that spice use is aimed specifically at treating food that is more prone to spoilage.

Billing and Sherman (1998) examined the alternative hypothesis that inhabitants of warmer tropical regions eat more spices simply because

more spice plants are grown there. They analyzed the distribution of spice plant growth within countries and found no correlation between average temperature and the number of spices grown in a country. This suggests that some warmer regions appear to favor the use of spices even though the inhabitants of those areas do not necessarily have a larger proportion of local spice plants to select from.

The antimicrobial hypothesis can be extended beyond temperature and spice use to other factors that influence the risk of food-borne illnesses, such as raw or undercooked recipes, and the use of other types of seasoning with similar antimicrobial effects, such as olive oil and vinegar (Medina et al. 2007). For example, a study by Ohtsubo (2009) showed that recipes containing uncooked products, such as Japanese dishes consisting of raw fish or meat (e.g., sashimi), are more likely to incorporate the use of vinegar than recipes containing cooked or heated food. Likewise, meat dishes made from raw ground meat, such as the European steak tartare dish, also tend to include more seasoning in their preparation.

Another important contribution of the antimicrobial hypothesis is its ability to account for why humans would have a taste for spices in the first place. Chilli peppers, for example, produce chemicals that create a painful burning sensation when exposed to bodily tissue and are typically avoided by herbivorous animals. Despite the aversive effects of contact with chilli peppers, people can enjoy eating them. From an evolutionary perspective, humans may have adapted a taste for such flavors to motivate the consumption of spices and reap the associated health benefits. That said, considerable variation exists in people's liking of spicy food. For example, Indian dishes feature strong flavors contributed by the wide variety of spices used, whereas Scandinavian cuisine tends to be bland. Correspondingly, Scandinavians may be less tolerant of spices while Indians enjoy them. This facultative proclivity for spices therefore reflects our ability to adaptively calibrate preferences in response to environmental conditions.

Conclusion

Humans have, for centuries and arguably longer, exploited the chemicals designed to safeguard plants to season food and prevent food-borne illnesses. The antimicrobial hypothesis of spices provides an important evolutionary account for the peculiar correlation between spice usage and regional temperature. Examples of other antimicrobial food preparation practices that extend beyond the use of spices in hot climates, such as the treatment of raw recipes with vinegar, attest to the general validity of the hypothesis. These examples show that under the veneer of cultural differences in taste preferences, which are undoubtedly an important proximate reason for the different varieties of cuisines on offer, lies key survival and reproductive concerns at a fundamental level.

Cross-References

- ▶ [Cultural Differences](#)
- ▶ [Cultural Transmission](#)
- ▶ [Cultural Variation](#)
- ▶ [Ecological Influences](#)
- ▶ [Ecology](#)
- ▶ [Pathogen Protection](#)
- ▶ [Pathogen Resistance](#)
- ▶ [Pathogen Risk](#)

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essay *On the Suffering of the World*, Schopenhauer said that the general rule of life is misfortune and suffering (1851). Because people are aware of the impending threat of death, they must struggle against both pressure from time and, in other moments, boredom or despair. As a result, Schopenhauer considered humans to not just be sentenced to death but also to life. He considered the state of nonexistence to be a blessed calm of nothingness, a stark contrast to the disturbance of life. In fact, Schopenhauer questioned whether the human race would still exist if the decision whether or not to have children was completely free of sexual impulses. He thought that if people were thinking rationally, they would choose to forgo having children in order to spare new people from being burdened with life (Schopenhauer 1851).

Antinatalism

- ▶ [Debating Procreation \(With David Benatar\)](#)
- ▶ [Permissibility of Reproduction](#)

Anti-natalism

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Definition

Anti-natalism is the ethical view that it is immoral for people to have children. This principle has been supported and defined in various ways, and this entry summarizes what the construct is, some reasons for why anti-natalism may not be a popular idea, and why some people might choose to postpone or forgo procreation.

Introduction

While the origins of the term anti-natalism are unsure, much of the ideas found in anti-natalism were expressed historically by the nineteenth-century philosopher Arthur Schopenhauer. In his

The Philosophy of Anti-natalism

In the twenty-first century, anti-natalism has been popularized by South African philosopher David Benatar. According to Benatar (2006), people should not reproduce because being brought into existence is always a grave harm; in his view, existence affords more cost than benefits. While life contains some good, much of life is bad, and everyone that comes into existence suffers in some way. Many people live in poverty or with disability; most people will experience a slow decline and various diseases later in their life, and everyone will eventually die. Benatar (2017) compared everyday life to a hamster on a wheel; much of people's time is spent doing mundane tasks in order to keep them alive and comfortable, such as sleeping, going to work, and eating.

The only way for someone to not experience suffering is to not be born at all (Benatar 2006). Those who do not exist cannot suffer from any loss of the good because they cannot experience its absence; furthermore, it is good that they miss out on the suffering that they would have experienced if they had been born. Any amount of suffering is a net bad, because that suffering could have been avoided by never existing (Benatar 2006). Even if there were much less suffering than there currently is, procreation

would still be wrong as all people would still be guaranteed to suffer some, which they would have avoided if they were never brought into existence. So why do individuals continue to reproduce and pass on their genes, continuing this cycle of human misery?

The Human Bias Toward Optimism

According to Benatar (2006), people are not reliable at assessing the quality of their own lives, and this is because humans have a bias toward optimism about the human condition. The optimism bias is a common phenomenon where people overestimate how likely they are to experience positive events and underestimate how likely they are to experience negative events (Sharot 2011). A moderate level of optimism can be beneficial in motivating people to adapt their behaviors in order to reach a future goal, and optimism has been shown to promote physical and mental health. A bias toward optimism has been shown to motivate people to persevere toward goals that, though they are unlikely to be achieved, would be beneficial to the person if they were achieved (Sharot et al. 2007). Haselton and Nettle (2006) argued that it is better to be optimistic so long as the cost of the false alarm for a positive event is relatively low compared to the cost of missing out on an opportunity that would enhance the individual's fitness.

Humans Choosing to Delay and Forgo Reproduction

For the most part, research has not been conducted on what influences people's opinions on whether or not others have a moral responsibility not to reproduce, though some factors cause individuals to accelerate or delay (and sometimes forgo) their own reproduction. For example, reminders of personal mortality cause people from a higher SES (socioeconomic status) background to report a desire to postpone reproduction until later in life and, conversely, cause people from a lower SES background to report a desire to accelerate reproduction (Griskevicius et al. 2011). People that

desired to postpone reproduction, likely having fewer children in the process, reported wanting to achieve a better position to care for any children they may eventually have by attaining more education and work experience (Griskevicius et al. 2011). Women with higher levels of education desired to delay reproduction longer than women with lower levels of education (Tavares 2016). Additionally, that research found that women who were higher in openness to experience desired to delay reproduction longer.

Certain personal factors are also linked to people choosing to forgo reproduction entirely. Early in life both more intelligent young adult men and women, as measured by childhood intelligence, were more likely to desire to remain childless (Kanazawa 2014). Though, later in life, only more intelligent women were more likely to have remained childless, more intelligent men were not more likely to remain childless for life (Kanazawa 2014). This sex difference in desire for children has been shown elsewhere. Fritsche et al. (2007) found that reminders of death led men to report desiring to have more children than they desired to have when not being reminded of death, but reminders of death did not cause a difference in the number of children women desired having.

Conclusion

This entry has covered the philosophical thought of anti-natalism and some factors that can cause people to delay or forgo reproduction. Anti-natalism was covered using the work of philosophers Arthur Schopenhauer and David Benatar. People's proclivity to see their lives as being better than they really are was described using research conducted on people's bias toward optimism, which can work to increase their fitness. The desire of some people to delay having children was described using research conducted on childhood SES level and amount of education. And sex differences in people's desire to have less children and forgo reproduction entirely were explored using research conducted on intelligence level and reminders of mortality. Though

research has been conducted on why people might choose to delay or forgo reproduction, thus defying an evolutionary drive to reproduce, more investigation needs to be done to examine why people might hold anti-natalist beliefs.

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Antinatalism Key Text

- [Better Never to Have Been](#)

Antinatalist Philosophy of David Benatar

- [Better Never to Have Been](#)

Anting

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Synonyms

[Einemsen \(German\)](#)

Definition

The deliberate application of ants and ant secretions (or other pungent substances) by birds to their plumage and skin.

Introduction

Anting (or *Einemsen*) is a term originally used by ornithologists in the 1930s to describe the application of ants by birds to their plumage (Whitaker 1957; Chisholm 1959). Birds perform anting behavior presumably to apply to their feathers or skin some substance produced by the ants (formic acid or other secretions). With the passage of time, the term has been used more broadly to include application to the plumage of objects or substances other than ants (e.g., citrus fruits, mothballs, burning cigarettes), because the postures and movements performed by actively anting birds are similar regardless of the object used. This prompted Simmons (1966) to distinguish “true anting” (the use of ants during the activity) and “anting with substitutes.” Regardless, anting is a more or less stereotypical form of anointing behavior. It is often categorized with other forms of avian maintenance behavior, such as sunning, bathing, and dusting (Simmons 1966), although not all researchers consider anting’s primary function to be for plumage maintenance.

Forms of Anting and Its Global Prevalence

Anting by birds occurs in two forms (Simmons 1957, 1966; Whitaker 1957). During *active*

anting, birds pick up ants (or other organic and inorganic objects) with their bill, often crushing the ants in the process, and dab or sweep them through the plumage of the wings and tail, particularly the undersurfaces; some species also sweep ants through other parts of the body plumage (breast, rump). During *passive anting*, birds stand, settle, or wallow on an aggregation of ants (an ant mound or other locations where ants are concentrated) with their wings and tails partly spread, sometimes provoking the ants to attack by poking at them with the bill or making stirring motions with the wings, and allow the ants to crawl through the plumage. The two forms of anting have also been termed, respectively, “ant-application behavior” and “ant-exposure behavior” (Simmons 1966). During active anting, birds may blink and use the nictitating membrane, shake and scratch the head, rub the eye on the shoulder, stamp the feet, lose balance, and tumble over. Passive anting birds may stand several times and resetttle in new locations. Anting birds are often easier to approach than when engaged in other activities, suggesting that anting serves some kind of adaptive function that favors the behavior despite the increased risk to predation.

More than 210 bird species worldwide have been reported to ant (Simmons 1957; Whitaker 1957; Chisholm 1959; Craig 1999). It is particularly widespread among the Passeriformes (perching birds), perhaps not surprisingly as most extant bird species are members of this order. It has also been reported for a few species of at least nine other avian orders, although Simmons (1966) questioned whether reports for non-passerines represent true anting. Active anting is the form most often reported for the majority of passerines, although passive anting appears prevalent in some families comprised of larger species, such as Turdidae (thrushes) and Corvidae (jays, crows, and ravens). Most birds appear to practice only one form of anting, but both forms have been reported for a small number of genera and species (Simmons 1957, 1966), a pattern that may result from the difficulty of studying anting in wild birds and the unpredictability of the behavior.

Anting behavior probably evolved in relation to ants rather than any of the reported ant substitutes (Simmons 1966), such as citrus fruits. Ants favored by birds for use in anting typically are worker castes of species that do not sting but exude or spray chemicals for attack and defense (Groskin 1950; Whitaker 1957; Simmons 1966) and often involve ant genera in two subfamilies with global distributions: Formicinae (e.g., *Camponotus*, *Formica*, *Lasius*) and Dolichoderinae (e.g., *Iridomyrmex*, *Dorymyrmex*, *Tapinoma*).

Hypotheses for the Function of Anting

At least three broad hypotheses have been proposed as explanations for why birds ant:

1. *Food Preparation*: anting serves to remove distasteful chemicals from ants (specifically formic acid) before they are eaten. This hypothesis was favored by several early investigators (see Chisholm 1959). Recently, Eisner and Aneshansley (2008) showed that captive blue jays (*Cyanocitta cristata*) performed anting at a much higher rate prior to ingesting ants when presented with ants whose acid sacs were intact. Anting caused the ants to discharge their formic acid spray and empty the acid sac before they were eaten. When the same jays were presented with ants whose acid sacs were surgically removed, the birds almost invariably ate them without anting first. This research, when combined with prior studies cited in their paper, led Eisner and Aneshansley to conclude that anting is essentially a food preparation activity. However, this conclusion does not account for many other observations and controlled studies where birds failed to eat the ants after actively anting (Simmons 1957; Whitaker 1957; Chisholm 1959), nor does it address passive anting, where ants are allowed to discharge their chemical defenses and rarely get eaten.
2. *Feather Care*: anting serves some sort of feather maintenance function, such as
 - (a) suppression of arthropod ectoparasites

(feather lice, ticks, and mites), (b) suppression of feather-degrading bacteria and fungi, (c) removal of stale lipids from skin and feathers, or (d) decreasing skin irritation associated with feather molt. Formic acid is known to kill bird arthropod ectoparasites and suppress feather microbial growth under controlled conditions (Simmons 1966; Craig 1999; Revis and Waller 2004), but does not appear to be effective against either when applied in concentrations released by ants as a component of their secretions. Nor does the seasonal peak in anting by wild birds correspond to peaks in ectoparasite loads (Potter 1970). Thus anting to control ectoparasite and microbial infestations is not clearly supported by available evidence. Simmons (1966) proposed that anting may increase the flow of saliva for use in preening and that it would help in removing stale preen oil and other lipids. This possibility awaits experimental investigation, but anting often occurs during new feather growth, presumably a time when feathers are relatively free of stale preen oils and other lipids. Finally, there is evidence that peaks in anting by wild birds in some regions correspond to timing of molt (Potter 1970; Potter and Hauser 1974). Wild birds tend to ant while replacing feathers of the wings, tail, and belly, all of which are accessible to the bill, and they tend to sunbathe (sun) while replacing feathers of the head, neck, and back, which are less accessible to the bill. Wild birds also tend to ant during periods of high summer humidity shortly after heavy precipitation, which can induce simultaneous loss and replacement of feathers. Anting and sunning are thus considered by Potter and Hauser to be complementary comfort-motivated behaviors for applying heat (the thermogenic effect of formic acid or other ant substances, solar radiation) to soothe irritated skin. This remains a viable explanation for the function of anting, but a challenging one to test under natural conditions. Also, it is not clear how effective anting always is (particularly active anting) for exposing irritated skin to ant secretions, as birds sometimes apply ants to areas other than the base of

feathers (Whitaker 1957; Simmons 1966), where skin irritation should be located.

3. *Self-Stimulation*: anting serves to provide a purely pleasurable sensation. This hypothesis is the least favored by most investigators. Whitaker (1957) suggested that anting birds appeared to derive sensual pleasure during anting, possibly even sexual stimulation, as a result of the thermogenic effect of the ants. She noted that her captive oriole preferentially directed anting to the underparts of the tail and possibly the cloaca, and these body regions are also mentioned in other reports of anting (Simmons 1957; Potter 1970; Potter and Hauser 1974). The idea of a skin-stimulus function was also promoted by Chisholm (1959). Simmons (1966) argued against this hypothesis on evolutionary grounds, observing that selection would act against birds performing just for pleasure a stereotyped behavior in a place and manner which makes them much more vulnerable to predator attack. While it may be questioned whether or not birds derive (in a purely aesthetic sense) sensual or even sexual pleasure from anting, the central thesis of this argument is similar to that promoted by Potter and Hauser (1974) that anting serves to soothe irritated skin and thereby provides a pleasurable sensation to the anting individual.

Conclusion

The function of anting remains unclear. Studies under natural conditions are hampered by the (as yet) unpredictability of the behavior, so most close observational and experimental studies have been undertaken with captive or tame birds. Examination of accumulated opportunistic observations made under natural conditions reveals some patterns in anting activity, such as the relationship with feather replacement (Potter and Hauser 1974), but rarely are details available which might help clarify all circumstances promoting the behavior, and the suite of environmental variables associated with anting in the wild remains poorly documented.

Nevertheless, it seems from the accumulated observational and experimental data that anting probably serves more than one function, perhaps dependent on each individual bird and a proper combination of psychological and environmental conditions.

Cross-References

- [Adaptation](#)
- [Bird Tool Use](#)
- [Corvids](#)
- [Nonhuman Tool Use](#)
- [What Makes a Tool](#)

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Antipathy

- [Prejudice](#)

Antipredator Behavior

- [Vigilance, Sentinels, and Alarms](#)

Antipredator Calling

- [Alarm Calling](#)

Antipredator Vocalization

- [Predator Confusion Hypothesis](#)

Anti-predator Vocalization

- [Alarm Calling upon Predator Detection](#)

Antipredatory Behavior

- [Alarm Calling Predicted by Inclusive Fitness](#)

Antisocial

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Synonyms

[Delinquent](#); [Deviant](#); [Dyssocial](#)

Definition

Violation of societal standards, social norms, and/or established rules of behavior and action.

Introduction

The term antisocial describes actions that violate laws, social norms, and established standards of appropriate behavior, including destructive, violent, and aggressive behavior toward others. Personality characteristics of individuals who engage in antisocial behavior include impulsivity, a lack of empathy, and a lack of morality. The development of antisocial behaviors has been shown to be due to a complex interaction of genetic heritability, environmental, and contextual factors.

Antisocial

The term antisocial is generally used to describe actions that violate societal standards and laws or activities that do not adhere to established social norms. Saddock and Saddock (2007) describe antisocial behavior as actions that are “illegal, immoral, or both” (p. 891), adding that the presentation of antisocial behaviors vary in frequency and severity. Tuvblad and Beaver (2013) describe antisocial behavior as encompassing various possibilities of destructive behavior including behavior that causes harm to others, involves property damage or destruction, violates the rights of others, as well as violent and aggressive actions toward others. Historically, the term antisocial has been used to replace broad labels such as psychopathic and sociopathic (Silverstein 2007).

Specific personality characteristics have been identified in individuals who engage in antisocial behavior. Rasmussen (2005) outlined a number of characteristics that comprise the antisocial personality style, including a limited response to punishment; impulsive decision-making that does not involve a consideration of possible negative consequences; high activity level in the pursuit of a desired goal with a great deal of attention focused on personal gain; an inclination to act aggressively and unethically as a means to get their way; a disregard for the effect their actions have on others; and a willingness to

manipulate and lie to avoid negative consequences or obligations. Silverstein (2007) identified the key characteristics of the antisocial personality style as an “absence of guilt, lack of remorse, incapacity to form intimate or lasting relationships, an engaging or charming manner, shallow or insincere affective experience, and lack of concern about or empathy for other people” (p. 158). The core aspect of the diagnosis of antisocial personality disorder is represented by “a pervasive pattern of disregard for, and violation of, the rights of others” (American Psychiatric Association 2013, p. 659). This pattern may include a variety of features including a lack of conformity to social norms of lawful behavior, dishonesty, impulsivity, aggression and irritability, disregard for the safety of self or others, irresponsibility, and a lack of remorse (American Psychiatric Association 2013).

A variety of etiologies and risk factors have been proposed to explain antisocial behavior. These suggested causes and risk factors fall into individual, environmental, and social categories. The prevailing belief is that these factors interact to influence the expression of antisocial behaviors and personality characteristics. Although numerous studies have demonstrated a significant genetic influence on antisocial behavior, a more complete explanation highlights the interaction between genetic predisposition and environmental factors (Niv and Baker 2013). A dysfunctional family environment, which has also been identified as a prominent risk factor, “may also reflect common heritable vulnerabilities in both parents and children” (Paris 2015, p. 69). Contextual factors including living in violent and economically disadvantaged communities have also been found to contribute to the development of antisocial behavior (Chamberlain 2003).

Conclusion

The term antisocial has been utilized to label actions that violate the rights of others, involve damage or destruction of property, or represent

a deviation from established laws and societal norms. Empirical research has identified characteristics that comprise an antisocial personality style including a lack of response to punishment, cognitive and behavioral impulsivity, and a lack of empathy. Numerous risk factors have been identified as contributing to the development of antisocial behavior, with significant research supporting an interaction of genetic, environmental, and social factors.

Cross-References

- ▶ [Antisocial Personality Disorder](#)
- ▶ [Criminal Behavior](#)

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Antisocial Behavior

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Synonyms

[Dysfunctional](#); [Maladaptive](#); [Undesirable](#)

Definition

Antisocial behavior is a description for all behaviors, attitudes, and personality traits that people engage in that appear to be dysfunctional, in that they often have negative interpersonal and societal outcomes.

Introduction

Antisocial personality traits like psychopathy, narcissism, and Machiavellianism are correlated with sexual coercion (Figueredo et al. 2015), criminality (Hare 1985), and deception (Azizli et al. 2016). Antisocial behavior can be presented alone or in the context of antisocial personality disorder (see Hashmani 2018a). Unsurprisingly, traits, like these, and the behaviors that may manifest from them have led professionals to strive to reduce these traits and their behaviors to relatively little avail. It may be that attempts to reduce antisocial behaviors and traits have generally failed because efforts to do so are based on a faulty premise. This premise is the often implicit, but dominant, cultural and academic epistemology known as the standard social science model. This model is built on philosophical “insights” from Rousseau who considered people to be “noble savages” corrupted by society and can be seen in modern clinical and social psychology in the form of “environmental determinism.” Environmental determinism is a philosophical position that

places contextual, cultural, and circumstantial factors as the primary and immediate cause of behaviors and values (including antisocial ones) and attempts to dismiss or downplay the role of genetics, biology, or physiology in accounting for human (but generally not nonhuman animal) behavior. Much of this work in psychology and the social sciences has been fueled by explicit and implicit blank slate thinking, which has been portrayed as flawed (Pinker 2003). In essence, when people who adopt this framework are asked why there is “evil” in the world, they reply: because of conditioning, bad childhood experiences, or modeling “bad” behavior.

Over the last 30 years, a challenge has been brought to this type of thinking in the form of evolutionary psychology (Confer et al. 2010), referred to as an interactionist paradigm (Crawford and Anderson 1989). That is, evolved and genetically rooted psychological adaptations interact with contextual factors to drive behaviors (i.e., solutions) that over evolutionary time have resulted in positive fitness benefits on average (populations evolve, not individuals, and in each generation variation is born. Therefore, the presence of individual differences in antisocial behavior does not challenge this model in a serious way.). These solutions may not fit modern concepts of “good” or “evil” as they can come at the cost of the group, which is implicitly treated as more important than the individual (Jonason et al. 2012). From this perspective, “bad” behavior or “evil” (There is an implicit rejection of religious notions of the origins of evil.) – antisocial behavior – might be considered pseudopathologies (Crawford and Anderson 1989) whereby they benefit the individual at the cost of the group. For example, deception, a common antisocial trait, often involves an individual engaging in a selfish act, without the concern of another’s well-being (Gneezy 2005). Although socially frowned upon, agentic pursuits and their motivations are of utmost importance to evolutionary researchers. In essence, this model makes one question what is meant by “evil” and suggests defining evil as anything that does not fit our group’s interest, even when such actions might serve the individual’s adaptive or social goals.

Evolutionary Models of Antisocial Behavior

This entry aims to detail modern thinking on evolutionary models of antisocial behavior. The authors will review how life history theory redresses the (relative) theoretical vacuum in classic and most modern research on antisocial behavior and traits. We will also attempt to review research on antisocial behavior (broadly construed) and highlight that while such behaviors might have undesirable consequences, they also have potentially “positive” outcomes as well.

A characteristic limitation of work on antisocial behavior has been its rather atheoretical, descriptive nature. Only recently have authors made attempts to understand antisocial traits and behaviors using a strong theoretical framework in the shape of life history theory (see Del Giudice 2014). This theory – taken from evolutionary biology – holds that organisms make trade-offs between efforts dedicated to mating and survival. The idea is that life is a zero-sum game whereby any energetic resources dedicated toward one task (e.g., mate searching) cannot be reallocated to other tasks (e.g., finding food). Researchers using a life history paradigm to understand antisocial traits and behaviors suggest that what is really reflected in these traits is trade-offs for short-term, mating (i.e., *r*-selected) decisions at the cost of long-term, survival (i.e., *K*-selected). This can explain some of the apparent illogical behaviors associated with antisociality. For instance, when presented with a smaller sum of money today or a larger sum of money in 1 year, those high on antisocial traits choose the former over the latter (Jonason et al. 2010). From a life history perspective, it is possible that people high on these traits have cognitive biases that nudge them to take smaller, immediate outcomes, because they are trading off “mating” needs against “survival” needs.

Informed by life history theory, there are a number of potential reasons for the emergence of apparently antisocial traits and behaviors. For instance, life history theorists (Frankenhuis and Del Giudice 2012) have identified three key dimensions to modulate how organisms allocate

their resources: *resource availability*, *extrinsic mortality-morbidity*, and *unpredictability*. Higher mortality-morbidity and unpredictability shift organisms toward *fast* life history strategies (e.g., a focus on reproduction, reduced investment in long-term bonding, and increased investment in short-term mating), which thereby promote risk taking, aggression, and other forms of antisocial behavior. Additionally, from an evolutionary perspective, natural selection favors mechanisms that produce risk taking when the fitness benefits outweigh the costs, even if these may be deemed socially unacceptable. Though these behavioral strategies may have unfavorable consequences to a subset of individuals, natural selection will still favor the traits if they increase fitness adaptability on average. Additionally, developmental mismatch contributes to the development of antisocial behaviors. An evolutionary developmental mismatch approach (rather than a developmental psychopathology model) suggests that children's negative stressors increase the adaptive fit between organisms and their environment. This perspective suggests that environmental mismatch in either direction (i.e., moving from a supportive to harsh environment and vice versa) evokes fitness costs (Cameron et al. 2005). More specifically, individuals who develop in harsh environments may on average achieve lower fitness than individuals in flourishing environments; nonetheless the former group should be better adapted to environmental harshness than the latter group (Frankenhuis and Del Giudice 2012). These aforementioned reasons are based on the premise that heritable tendencies interact with environmental contingencies in an adaptive heuristic framework to produce some output or response that attempts to maximize one's fitness given contextual limitations (Crawford and Anderson 1989).

Take, for instance, the commonly used distinction of "externalizing" and "internalizing" disorders (Del Giudice 2014). Externalizing disorders (e.g., oppositional defiant disorder, conduct disorder, and antisocial disorder) may represent *fast* life history trade-offs that result in impulsiveness, aggressiveness, and antisocial behaviors (Krueger et al. 2002). Moreover, these fast life strategies are correlated with numerous

pathological antisocial traits, such as negative affectivity, detachment, antagonism, and psychoticism (Jonason et al. 2017). Such traits may stem from harsh and unpredictable environments in childhood (Clark 2005). Conversely, slow life history strategies entail restricted sociosexuality, planning, responsibility, and altruism, with a tendency toward long-term romantic relationships. Rather than the externalizing spectrum, slow spectrum disorders often consist of obsessive-compulsive pathological traits (i.e., dysfunctional protective responses and hypersensitivity; Del Giudice 2014), anorexia nervosa, and depression (e.g., chronic guilt and hyperactive altruistic concerns; O'Connor et al. 2002).

The life history model also provides a priori reasons for sex differences in these types of behaviors. Ancestral men and women faced asymmetrical costs and benefits for how they solved adaptive problems. The benefits (e.g., more offspring) are greater for men who engage in exploitive social/sexual behavior (Jonason et al. 2009), whereas women who engaged in such behavior pay for reproductive costs (Jonason and Lavertu 2017). Unsurprisingly, men (compared to women) are more competitive, tend to seek dominance over others, and use physical aggression (Archer 2009), whereas women tend to be better characterized by antisocial behavior that acts to upregulate women's protective defensives (McGuire and Troisi 1998), as seen in obsessive-compulsive disorders, eating disorders, and depression (Del Giudice 2014).

The most fundamental implication of this model for antisocial traits is that even the most abhorrent behaviors can have adaptive benefits and adaptive costs (see Table 1). For instance, interpersonal aggression (e.g., Jones and Neria 2015) may have costs to both the victim (e.g., potential physical harm) and the perpetrator (e.g., punishment and possible jail time) but can result in increased reproductive fitness by protecting one's fitness interdependence partners and improving survival with the accrual of resources (Archer 2009). On the other hand, coalitionary aggression in chimpanzees can lead to numerous benefits to one's fitness including increased social bond strength, health, and

Antisocial Behavior, Table 1 A summary of ten common antisocial behaviors and their hypothetical adaptive costs and benefits

	Costs	Benefits
1. Aggression	Possibility of death from injury. Possibility of incarceration leads to being relinquished from society and, thus, reproductive opportunities	Increases attention from the opposite sex – seen as “competent.” Means of gaining power and having increased access to resources and potential mates
2. Bullying	Lack of mutual relationships formed – loss of protection/support if in danger or need of resources	Rising to the top of social hierarchies by gaining popularity. Reduces competition from others for desired resources. Develops physical self-protection from one’s “tough” appearance
3. Casual/exploitive sex	Increased risk of disease. Passing on poor/unwanted genes	Increased reproductive outlets. More offspring
4. Deception	If discovered as a liar, one may be socially shunned and ostracized by society	Self-deception: we deceive ourselves to protect against attacks to our happiness and well-being. Deceiving others is a means to achieving one’s goals, at the expense of others’ success
5. Domestic violence	Possible repercussions or attacks by other members of society. Possible physical injury from victim	Means of keeping one’s reproductive partner, rather than spending resources looking for another mate
6. Future discounting/impulsivity	Long-term needs and desires possibly ignored. May have chosen a smaller reward, rather than waiting for a larger reward (i.e., less gain if ignoring future discounting)	Short-term/immediate gains. If limited quantities of resources (e.g., scarce food), the impulsive individual will obtain the reward, while others fail
7. Psychopathy	Lacks ability to create close connections with others – can be viewed as an outcast by society. Can scare off potential mates	Lack of “normal” emotions (guilt and shame) can assist in selfish advantage. For example, these emotions can be disabling and mentally exhausting. Lack of empathy depersonalizes the victim and facilitates crime
8. Prejudice/racism	Limits reproductive outlets to one’s own race/social group. Limited options lead to less success and less possibilities to spread genes	In social living, one must respond functionally to the affordances of others. In order to obtain cooperative groups, one must recognize outsiders with potential threats
9. Substance use	Increased risk of death by substance abuse. Can lead to addiction, and, thus, one must allocate financial resources for more substances	Substances lower one’s inhibitions and fears. Can lower and mask physical or emotional pain
10. Theft	Possible risk of attack by victim. Risk of incarceration	Increased accumulation of resources and assets

number of offspring (Gilby et al. 2013). Moreover, psychopathy (see Table 1) can bring about numerous benefits, such as a reduction of *primary emotions* (e.g., guilt, shame, remorse), which may be emotionally exhausting and disabling, while also facilitating crime through depersonalizing the victim (Hashmani 2018b).

While it is easy to fixate on the costs, a more balanced model of antisocial traits and behaviors must include the benefits as well. Such a full understanding – while often unpalatable – has implications for theory and treatment. Understanding the function of the behavior and its

correlated traits should give better insight to “fixing” or reducing such tendencies in societies/individuals. For instance, although antisocial behavior can lead to negative consequences such as social rejection and criminality, there are also adaptive qualities that provide clarity on why these behaviors still persist in today’s society. For example, engaging in physical fights carries the potential to cause harm and the possibility of death; however, men who do not participate in fights increase the likelihood of being shunned from reproduction and, therefore, decrease reproductive success (Del Giudice 2014).

Alternatively, by exploiting and deceiving others in order to obtain a high social status, one can increase their own reproductive success, thereby providing evidence for these adaptive yet socially unwanted traits. These traits, in the eyes of society and clinicians, are deemed as dysfunctional and abnormal, yet from an evolutionary standpoint, they provide a way of maximizing reproductive success (Brüne 2014).

Conclusion

This entry approached the topic of antisocial behavior from an evolutionary perspective in order to accentuate the adaptiveness of these socially undesirable traits. We briefly discussed life history theory, where organisms must allocate their time to either mating or survival, and how these actions correlate with fast and slow life strategies. While highlighting numerous insights provided by an evolutionary approach (e.g., pseudopathology, externalizing disorders, and heritability), we discussed the adaptive costs and benefits of antisocial traits. The hope of this entry is to facilitate awareness to evolutionary psychologists in exploring the adaptive benefits of antisocial traits while also facilitating a framework for clinicians to understand the ancestral sex differences when treating men and women.

Cross-References

- [Personality Disorders](#)
- [Psychopathy \(Mealey\)](#)
- [Strength and Anger-Proneness](#)

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Antisocial Personalities

► [Psychopathy \(Mealey\)](#)

Antisocial Personality

► [Psychopathy](#)

Antisocial Personality Disorder

► [Psychopathy \(Mealey\)](#)

Antisocial Personality Disorder (ASPD)

► [Psychopathy](#)

Anxiety

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Synonyms

[Apprehension](#); [Nervousness](#); [Worry](#)

Definition

Distress or uneasiness of mind caused by fear of danger or misfortune

Introduction

Anxiety is a normal human emotion that is experienced by all in different situations and in different measures. Anxiety is often confused with fear, but the two are not synonyms. Fear is an alarm response to present or imminent danger, whereas anxiety is a future-oriented mood state associated with preparation for possible, upcoming negative events (Barlow 2002). Anxiety evokes fight-or-flight response and energizes a human being both psychologically and physiologically to deal with a situation or challenge. However, excessive or continued anxiety, which is disproportionate to the threat, presents in absence of any threat, or persists even when the threat has waned, is unhealthy and can become a troublesome problem for many. Such anxiety states could be acute as well as chronic and could lead to impairment in social, occupational, and other important areas of functioning.

Anxiety Disorders

Among psychiatric disorders, anxiety disorders are most prevalent (Kessler et al. 2010). As per estimates made in the year 2013, it is believed that

one in nine people all over the world has suffered from an anxiety disorder during previous year (Baxter et al. 2013). Common symptoms of anxiety disorders are:

- Psychological: worry, excessive thinking, feeling of being at the edge
- Physiological: headache, tremors, dry mouth, nausea, diarrhea, shortness of breath, palpitations, sweating (especially in palms), frequent urination

The symptoms could vary in frequency, intensity, and chronicity from person to person and also among different anxiety disorders. Detailed discussion about anxiety disorders is beyond the scope of this chapter; however, a brief description is provided in Table 1.

Diagnosis of anxiety disorder is reached after taking a detailed history that covers important aspects of onset and chronology of symptoms, triggers (if any), childhood and developmental history, and personality and coping mechanisms. Several self-report questionnaires are also available that can help in screening for anxiety disorders. Symptoms of anxiety could also be present along with other psychiatric disorders like depression, bipolar disorder, alcohol and other substance use disorders, etc. Also, many a times, such symptoms could indicate toward physical illnesses like thyroid diseases (more common in hyperthyroidism), heart diseases, respiratory diseases, seizures, and tumors of the endocrine system. Therefore, a complete assessment including check-up for physical illnesses is a must before declaring an

anxiety problem as a psychiatric disorder (Craske and Stein 2016).

Treatment of Anxiety Disorders

Anxiety disorders could be treated with drugs as well as through psychotherapy. Many a times, combined approach needs to be used to help a patient. Among drugs, antidepressants belonging to the class of selective serotonin reuptake inhibitors and serotonin-noradrenaline reuptake inhibitors are first line of treatment. Benzodiazepines though carrying some risk of abuse and dependence have robust efficacy for treating anxiety and work wonderfully when used under proper clinical advice and guidance (Craske and Stein 2016). Psychotherapy is carried out by trained psychiatrists, psychologists, psychiatric social workers, and psychiatric nurses. Commonly employed psychotherapies used to treat anxiety disorders include (Bandelow et al. 2015):

- Mindfulness-based therapy: This therapy uses a blend of Eastern Buddhist philosophy-based education and meditation to help the subject focus on the present instead of worrying about either the past or future.
- Behavior therapy: This involves gradual exposure of person to cause of anxiety and, thus, getting used to the same without getting anxious.
- Cognitive behavioral therapy (CBT): In CBT, patient is taught to recognize pathological

Anxiety, Table 1 Common anxiety disorders (American Psychiatric Association 2013)

Panic disorder	Characterized by recurrent, unexpected episodes of intense anxiety, palpitations, and fear of imminent death
Generalized anxiety disorder	Characterized by anxiety and worries in almost all situations (home, work, school, etc.)
Social anxiety disorder	Characterized by anxiety and/or avoidance of social interactions/situations and fear of negative judgment and embarrassment in social situations
Agoraphobia	Characterized by anxiety and/or avoidance of open spaces, closed spaces, crowds, or being alone outside home
Specific phobia	Characterized by anxiety attached with specific objects (which are otherwise not dangerous) like certain animals/insects, blood/medical procedures, height, etc.
Separation anxiety disorder	Characterized by anxiety about separation from attachment figures that is inappropriate to age

feelings, thoughts, and behaviors and to replace those with positive and helpful thinking.

- Family therapy: This treatment helps family members to communicate and deal with conflict in healthy ways.
- Biofeedback: This is done with help of biofeedback machine which provides feedback of body functions and helps the patient to achieve control over the same.

Along with specific therapeutic measures, many general activities can also help in managing anxiety disorders. These include deep breathing exercises; muscle relaxation exercises; balanced healthy diet; life changes to reduce stress; avoiding overuse of alcohol, caffeine, and nicotine; and participating in support groups.

Conclusion

Anxiety is a normal emotion and, when excessive, could develop in pathological states, i.e., anxiety disorders. Anxiety disorders could be disabling and dysfunctional for many but are treatable. Treatment includes drugs and psychotherapy.

Cross-References

- Anxiety Disorders
- Correlates of Fear
- Fears and Phobias
- Social Anxiety
- Stranger Anxiety
- Stress Reduction and Mental Health

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Anxiety (Randolph Nesse)

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Synonyms

Anxiety disorders; Evolutionary psychiatry;
Threat detection systems

Definition

From an evolutionary perspective, anxiety can be considered as a psychological hazard-detection system. In uncertain environments, the costs of responding to false cues of danger are often miniscule as compared to those resulting from undetected threats. Therefore, the anxiety response has evolved a bias toward false alarms under conditions of uncertainty. We discuss general and specific types of anxiety responses, underlining how the nature of these are often determined by the particular types of threats in the environment.

Introduction

Anxiety disorders are among the most common psychiatric disorders, with the global point prevalence estimated at 7.3% and lifetime prevalence reported as high as 33% in some countries (Baxter et al. 2013; Bandelow and Michaelis 2015). They refer to a series of DSM (*Diagnostic and Statistical Manual of Mental Disorders*) recognized mental disorders such as generalized anxiety, social anxiety, phobias, and obsessive-compulsive disorders. In clinical cases, anxiety tends to be unnecessary, excessively frequent, and severe; nevertheless, in certain circumstances, an anxiety response is expected and non-pathological. To fully understand pathological anxiety, it is essential to first consider the evolutionary function of the normal anxiety response, from which the vulnerability to mental illness stems. While the field of psychiatry has considerably advanced in deciphering the physiological mechanisms underpinning anxiety, ultimate explanations remain relatively unexplored in modern medicine.

Nesse rightly notes, “One hundred and fifty years after publication of *The Origin of Species*, new advances demonstrate the utility of evolutionary biology in medicine, but few physicians and medical researchers have taken a course on evolutionary biology, and no medical school teaches evolutionary biology as a basic science for medicine. It is as if engineering students never learned physics” (Nesse et al. 2010). He has developed an evolutionary checklist of the reasons for our susceptibility to illness, with three overarching explanations: selection is

too slow, there are trade-offs and constraints on selection, and apparent defects are in fact useful (see Table 1, Nesse 2004).

The principal evolutionary explanation for anxiety rests on the last point, which stresses that anxiety is a useful defense; and under conditions of uncertainty, excessive anxiety is usually less costly to fitness than insufficient anxiety. This entry introduces error management theory to explain how certain cognitive biases can be favored by natural selection. This is then applied to the domain of hazard-detection anxiety response, illustrated by Nesse’s smoke detector principle. Finally, the other two aspects of the checklist – time lags and constraints on selection – are briefly considered to illustrate the potential for dysregulation and misfiring of the anxiety response.

Anxiety as a Useful Defense

Error Management Theory and Cognitive Biases

Though the set of heuristic procedures constituting our cognitive function have been fine-tuned over millions of years, conditions of uncertainty make errors unavoidable. Signal detection theory (Green and Swets 1966) notes that in our perception of a situation, we can form four kinds of beliefs: two being accurate representations of the situation, a signal being present in reality and the organism detecting it (hit), there being no signal (just noise) and the organism detecting none (correct rejection); and two being errors in our judgment, a signal being present but the

Anxiety (Randolph Nesse), Table 1 Nesse’s six reasons framework for why our bodies aren’t better designed against anxiety disorders. (Adapted and modified from Nesse 2004)

Selection is too slow
The body is poorly adapted to modern environments
Older threats might not exist, but defenses against them do
Selection cannot do everything
Trade-offs between better-equipped defenses and aversive mental states
Constraints on cognitive design
What appears to be a defect is actually useful
Defenses are useful even if aversive
Defensive traits can increase reproduction, even if not health

organism not detecting it (miss), there being no signal present but the organism detecting one (false alarm; Table 2).

Cognitive biases refer to systematic errors in our judgment that are domain-specific. These biases, as understood by the error management theory, have evolved to promote behavioral responses that will, on an average, maximize fitness under conditions of uncertainty (Haselton and Nettle 2006). More specifically, in scenarios where the costs of false-positive and false-negative errors have been asymmetric over evolutionary history, natural selection has favored those biases which lead to making the least costly error. Nesse has applied this framework to the domain of hazard-detection and the anxiety response (Nesse 2005).

Biases in Anxiety and Hazard-Detection

In the case of hazard-detection systems, misses (false negatives) are often much more costly than false alarms (false positives). Hence these systems, whether designed by human engineering (e.g., smoke detectors) or natural selection (e.g., cough, immune responses, anxiety), tend to systematically overestimate the presence of a hazard, as illustrated by Nesse’s *smoke detector principle* (Nesse 2005). Owners of a “paranoid” smoke detector pay the cost of having to respond to false alarms, but with the benefit that they are unlikely to incur the financial and health costs associated with not responding to a real fire. In the case of an “optimistic” smoke detector, these costs and benefits are reversed. The cost-benefit ratio in this case is far more favorable in the first situation ($B_{\text{paranoid}} : C_{\text{paranoid}} > B_{\text{optimistic}} : C_{\text{optimistic}}$), explaining

why it is useful to design smoke detectors as “paranoid,” i.e., overcautious. The optimal sensitivity is achieved at the point where the marginal protective benefit is equal to the marginal cost of responding to more false alarms.

Emotions are psychological adaptations that function to motivate fitness-maximizing behavior in a flexible context-specific manner. In the context of hazard-detection, anxiety is the relevant emotion, which can be expressed in different forms. Each subtype of anxiety can be protective against a specific type of threat, for example, escape/avoidance in response to predators in the environment or submission/appeasement in cases of social anxiety where an individual fears ostracism (Nesse 1994). In much the same way that a smoke detector is a human-engineered device designed to encourage a defensive behavioral response to a fire (leaving the building), anxiety can be thought of as a biological hazard-detector stimulating defenses (such as vigilance and physiological arousal) in response to potential threats in the environment. Therefore, it too has been selected to systematically make false positive rather than false negative errors, making us susceptible to disorders where anxiety at the mere hint of danger is common (Nesse 2004).

Given the emphasis of psychiatry on mental well-being, there is a tendency to focus on the benefits of positive affect and costs of negative affect. However, given that the currency of natural selection is genetic fitness, some traits which harm our well-being can still evolve if they enhance our reproductive success (Nesse 2015). So even though the cost of protective responses can be high in individual instances and even entail associated suffering, the mechanisms serve us in

Anxiety (Randolph Nesse), Table 2 Signal detection theory – four types of belief

Signal Detection	Situation	Signal Present (Signal + Noise)	Signal Absent (Noise Only)
YES		True positive (Hit)	False Positive (False Alarm)
NO		False Negative (Miss)	True Negative (Correct Rejection)

survival. It is, thus, important to consider the overlooked (fitness) benefits of negative affect and costs of positive affect (see Nesse 2004 on diagonal psychology). The smoke detector principle illustrates the survival value of false alarms, explaining why some occurrence of unnecessary anxiety, although unpleasant, is to be expected from an adaptationist stance. Indeed, epidemiologic evidence suggests that long-term survival in people with low anxiety proneness is lower than those with medium levels (Bateson et al. 2011). From this perspective anxiety can begin to be regarded as a design *feature* rather than design *flaw* (Haselton and Nettle 2006).

Selection Is Slow and Subject to Constraints

Natural selection is unguided and slow, and there is usually a time lag between environmental change and biological adaptation. Given the stark differences between modern environments and those encountered by our ancestors for the majority of our evolutionary history, the anxiety response is prone to misfiring. This can result in extreme anxiety responses to stimuli that now carry little risk or are rarely encountered, as well as acceptance of some evolutionarily recent dangers with too much equanimity. The objects of phobias clearly demonstrate this – we have too much fear of spiders and snakes but too little fear of driving fast, saturated fat, and cigarettes (Nesse 1994).

Even plastic features of our psychology are subject to cognitive constraints, and exposure to environmental threats during critical periods in development can have long-lasting psychological effects, even if the threat is absent in later life. Though this early life environmental calibration is energetically more economical than lifelong plasticity, it can also provoke unnecessary and excessive anxiety if individual circumstances change substantially. It is well established that psychosocial stressors such as violence and neglect in childhood are strong predictors of anxiety disorders in adulthood, irrespective of later life improvements in social environment (Heim and Nemeroff 2001).

Conclusion

Anxiety helps in preparing an organism for dealing with threats at the physiological, cognitive, and behavioral levels, and from an adaptationist stance, false alarms are to be expected. If a drug were created that abolished all anxiety, it could be as harmful as a drug that induced anxiety of crippling degree (Nesse 1994). An evolutionary approach considers the functional benefit of psychological processes, acknowledging that they have evolved to maximize fitness rather than well-being and are subject to the constraints and time lags of natural selection. Thus, the utilization of evolutionary psychology and cognitive-affective theories can positively further the field of psychiatry in understanding threat detection, precautionary responses, and “why diseases exist” (Stein and Nesse 2011). Though classical psychiatry generally tags intense or prolonged negative affect to be abnormal, irrespective of the situation, deficits in negative affect and excesses of positive affect are rarely recognized as disorders. An evolutionary perspective provides a more balanced view (Nesse 1994).

Cross-References

- [Anxiety Disorders](#)
- [Evolutionary Psychiatry](#)
- [Social Anxiety](#)

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Anxiety Disorders

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Synonyms

Anxiety; Defense regulation; Fear; Threat detection

Definition

Anxiety disorders are a class of mental health conditions that include persistent and excessive feelings of anxiety or fear as a core feature (American Psychiatric Association [APA], 2013). Anxiety is typically associated with feelings of unease, restlessness, or concern about a future threat (APA 2013). Fear is typically associated

with a state of arousal in response to an immediate threat, either real or perceived (APA 2013).

Introduction

Anxiety is typically associated with unease, restlessness, or concern about the possibility of a future threat (APA 2013). In some instances the threat may be vague, unknown, or unidentifiable (Ranchman 2009). Fear is a response to an immediate object or situation that is threatening, or that an individual perceives to be threatening (APA 2013). Although the two are connected, fear is roused in response to an imminent threat and wanes once the threat is removed, whereas anxiety can be diffuse and may persist in the absence of any identifiable threat (Ranchman 2009). These emotional states are usually felt as something negative and unwanted. While most people experience appropriate levels of anxiety, some people experience very little anxiety while others experience debilitating anxiety.

If someone presents with anxiety or fear that is so severe or persistent that it causes considerable distress or functional impairments, then he or she may meet the clinical criteria for a diagnosis of an anxiety disorder (APA 2013). Evolutionary psychology contributes to the study of anxiety disorders by suggesting that their core features, anxiety and fear, are expressed because they provide an adaptive function when elicited in contexts in which an individual's fitness, or success contributing genes to the subsequent generations, is at risk (e.g., Marks and Nesse 1994). Additionally, evolutionary theory has provided a basis for models that describe optimal anxiety regulation and that explain why humans are prone to experiencing excessive anxiety.

The Anxiety Disorders

Anxiety disorders are characterized by distress or functional impairments caused by anxiety or fear that is immoderate or unwarranted given the circumstance or that persist beyond an appropriate period of time (APA 2013). Several disorders are

subsumed under the class of anxiety disorders, including separation anxiety disorder, selective mutism, specific phobias, social anxiety disorder, panic disorder, agoraphobia, generalized anxiety disorder, and substance- or medication-induced anxiety disorder (APA 2013). The 12-month prevalence of anxiety disorders in the United States is estimated to be 18.1% (Kessler et al. 2005). The majority of cases are classified as being relatively mild, but a considerable portion of the US population experiences moderate or serious symptoms (Kessler et al. 2005).

Treatments for anxiety include pharmacological and therapeutic interventions. Drugs commonly used to treat anxiety target neurotransmitters that mediate the expression of anxiety symptoms (Shah and Han 2015). Cognitive-behavioral therapy is the recommended nonpharmacological treatment method (Shah and Han 2015). Cognitive-behavioral therapy is more effective than current alternative therapies and has been widely adopted by clinicians (Ranchman 2009). Clinicians may recommend that both treatments be administered concurrently to help alleviate symptoms. In other instances, however, clinicians may decide that only one course of treatment is necessary. While evolutionary theory has provided a framework for understanding the function of anxiety and fear and has contributed to models that help account for humans' proneness to excessive anxiety, it has, at present, done little by way of advancing treatments for anxiety disorders.

Anxiety and Fear

Anxiety and fear, both negative emotions, are component parts of a cognitive and behavioral repertoire that motivates organisms to avoid incurring fitness costs (e.g., loss of life, injury, loss of social networks, loss of reproductive partners) and to mitigate fitness costs in circumstances when danger is unavoidable (Nesse and Ellsworth 2009). Although the two are often taken to be synonymous, they are distinguished by the presence or absence of a threat. Anxiety is a state of anticipation of danger that is yet to be encountered and is potentially unknown, whereas fear is an

emotional arousal response to a threatening being, object, or situation (APA 2013; Ranchman 2009). The behavioral patterns associated with fear and with anxiety are distinguishable. While fear readies an individual to cope with an imminent threat (e.g., fight or flee), anxiety prepares an individual to circumvent danger (e.g., remain vigilant, cautious, or avoidant) (APA 2013). Additionally, the neural activation associated with each emotional state is somewhat distinct (Öhman 2008). Anxiety can be seen as taking the principal role in anxiety disorders because, whereas fear responses are generally more time and location specific, much of the distress or functional impairment involved in these disorders is caused by a preoccupation with avoiding the feared being, object, or situation.

During periods of anxiety, people tend to exhibit heightened vigilance, they may be irritable, pace, experience difficulty sleeping, and be highly attentive to, or avoidant of, things that they believe to be related to their anxiety. Anxious individuals may ruminate on thoughts that something is wrong and may experience difficulty concentrating. Further, when faced with ambiguous indicators of threat (i.e., something that could be perceived either as threatening or nonthreatening), individuals who are in a state of heightened anxiety are biased towards perceiving a threat compared to nonanxious controls (Eysenck et al. 1991; Richards et al. 2002). Physical symptoms associated with anxiety can include changes in heart rate and in breathing, perspiration, muscle tension, and feelings of nausea.

Some researchers and clinicians emphasize a difference between trait anxiety and state anxiety (Spielberger 1966). Trait anxiety refers to the level of anxiety that an individual generally feels. State anxiety refers to the level of anxiety that an individual experiences at a particular moment and is potentially aligned with fear.

Fear is typically experienced only when a threat is perceived to be imminent. During periods of fear, people tend to experience intense arousal, tension, and feelings of dread. This arousal and muscular tension facilitates the escape from, or the defense against, danger; this is known as the fight or flight response (Cannon 1929). Fear is

usually localized to a time and place at which danger is present. Fear typically subsides once the danger is no longer present. However, anxiety may take the place of fear once the perceived danger is removed.

The Function of Anxiety and Fear

Evolutionary theorists have proposed that emotions are cognitive and behavioral patterns that have been shaped by selective forces because they increase fitness when elicited in appropriate contexts (Marks 1987). Emotional responses, such as anxiety and fear, have been described using the metaphor of computer programs (Nesse 1990). In the same way that computer programs are designed to achieve specific tasks, emotions adjust behaviors and cognitions to achieve specific goals. Anxiety and fear adjust one's behavior and cognition to prevent or reduce incurring fitness costs (Marks and Nesse 1994).

Anxiety and fear responses are advantageous in situations that threaten physical harm, death, social exclusion, damage to one's reputation or status, the loss of a sexual or romantic partner, or the loss of anything else connected to one's fitness (Marks and Nesse 1994). Specifically, anxiety affords the opportunity to avoid threatening situations. Fear provides the arousal necessary to escape or defend against danger and, in doing so, avoid or lessen associated fitness costs. It has been noted that, at times, fear causes immobility, which can reduce damage when an injury has occurred (Bracha 2004) and can prevent harm when faced with heights or predation (Marks and Nesse 1994). Fears and anxieties tend to be more pronounced when individuals sense that they are vulnerable to danger, or if humans have been vulnerable to a specific threat throughout evolutionary history (e.g., snakes, heights, separation from a social group) (Boyer and Bergstrom 2011; Neuberg et al. 2011).

When dealing with a potential threat, not all responses will yield equally desirable outcomes. Fortunately, humans are flexible, basing their responses on the nature of the perceived threat (Marks and Nesse 1994; Neuberg et al. 2011).

For example, an individual who is alone in an unknown area will vigilantly monitor the area for general signs of danger and may prepare to flee or fight if a threat is detected. A fight or flight reaction would be completely inappropriate, however, in a situation in which a socially subordinate person must continue to work closely with a socially dominant person. Instead, it is likely that the subordinate person will continually monitor the dominant's facial expression for signs of disapproval and may prepare to engage in submissive or appeasing behaviors to protect against negative social or professional ramifications (Trower and Gilbert 1989). Individuals who are keenly attuned to threats, and respond appropriately, will outcompete individuals who are less vigilant or respond inappropriately to threats.

Anxiety-Like Responses in Non-Human Species

Non-human animals commonly display defensive behaviors that are similar to those displayed by anxious humans. Non-human animals display signs of heightened vigilance when they perceive cues of danger (e.g., they will cease feeding, scan their environment, and remain still), they attend to threat cues, avoid perceived threats, and they will either attack or attempt to flee when faced with danger. Additionally, non-human animals that are in this anxiety-like state are more likely to respond to ambiguous threat signals as though they are threatening (Burman et al. 2009). Furthermore, drugs that effectively reduce symptoms of anxiety in humans similarly attenuate defensive behaviors in non-human species (Blanchard et al. 2011). Thus, the commonality between anxiety and defensive behaviors suggests that the two are related and are evoked to accomplish similar fitness goals.

Anxiety and Defense Response to Individual Threat Cues

It has been proposed that defenses are regulated via a response system that inclines animals to

assess and respond to threat cues in the environment, the so-called security motivation system (Szechtman and Woody 2004; Woody and Szechtman 2011). The authors proposed that animals continuously assess their environment and are sensitive to cues that, even subtly or indirectly, indicate danger. Once a threat cue is detected the security motivational system is activated. When the system is activated, animals will experience apprehension. This apprehension will evoke precautionary surveying of the area to acquire information about the potential threat. The security motivational system will deactivate only when animals engage in threat reduction behaviors, such as leaving the area, checking that no threat is present, or washing to remove a suspected contaminant. When a threat cannot be mitigated through behavioral means, humans may engage in ritual behavior (e.g., prayer, performance of superstitious practices) to regain feelings of control over their situation (Eilam et al. 2011).

Consistent with this model, individuals who believed that they were exposed to a contaminant reported elevated anxiety and demonstrated a change in heart rate, both of which persisted until they were able to engage in appropriate threat reduction behaviors (Hinds et al. 2010). It has been suggested that symptoms of obsessive-compulsive disorder (which was previously considered an anxiety disorder) are caused by an inability to feel satisfied that one's threat reduction behaviors have sufficiently removed the risk of danger (Szechtman and Woody 2006).

Optimal Threshold of Response to Cues of Threat

If someone were to respond to every cue that could possibly signal danger, he or she would have time and energy for little else. However, if someone fails to respond to real danger he or she may incur severe fitness costs. Consequently, threat response systems are under the influence of opposing selection pressures. If threat detection could operate perfectly, all stimuli would be accurately identified as either threatening or non-threatening, and no unnecessary costs would be

incurred. Such perfection cannot be achieved, however, because cues of the presence and severity of threats are often ambiguous. Signal detection theory has been used to describe how threat detection should be designed to optimally respond to threat (Nesse 2001). Signal detection theory is a mathematical technique designed to differentiate between a true signal and random background information in the face of uncertainty (e.g., Green and Swets 1966).

The general logic for signal detection theory, as it applies to threat detection, follows from the understanding that individuals are continuously receiving information (i.e., sensory stimuli) from their environments but much of this information is nonessential "noise." Individuals must make judgments about what information is important and requires a response and what information is unimportant. Making such judgments proves challenging because signals of threat are often ambiguous. Consequently, individuals must establish a threshold at which a signal will elicit a defense response. Below this threshold, stimuli will be considered noise and will be ignored.

If the cost of failing to respond to a threat and the energetic cost of responding to a threat were equal, signals that could indicate threat should elicit a defense response at approximately chance level (in the same way that one would guess the outcome of a coin flip). However, although individuals waste resources when they unnecessarily engage in defensive behavior, the cost of failing to engage in necessary defense behavior, even once, could result in fitness losses (e.g., injury, loss of life, loss of social networks, loss of reproductive partners). Nesse (2001) mathematically demonstrated that, if the cost of failing to respond to a threat cue were greater than the energetic cost of defense, selection would favor a system that errs on the side of excessive responding.

Nesse (2001) suggested that this principle could be understood using the metaphor of a smoke detector and has, thus, been called the smoke detector principle. If a smoke detector sounds whenever someone is cooking, a lot of time will be wasted attending to these false alarms. Yet, it is essential that a smoke detector sounds each time there is a real fire. An optimal

smoke detector should reliably catch every fire and will, thus, permit false alarms in the interest of achieving this level of sensitivity. Similarly, it is essential that an individual detects real threats, but, to achieve this sensitivity, false or unnecessary responses will occur. As a consequence, an optimally working defense regulation system permits vulnerability to excessive expressions of anxiety.

Exactly where this threshold needs to be set to optimally detect threats will vary based on an individual's circumstance. Individuals in dangerous environments, and individuals who are particularly vulnerable to certain threats, should have relatively low response thresholds and, therefore, will respond to a greater number of false alarms (Bateson et al. 2011). As such, these individuals are expected to frequently experience excessive or unwarranted anxiety. This reasoning may help account for some of the seemingly unrelated correlations between anxiety disorders and individual or demographic characteristics (e.g., correlations between anxiety symptoms and status as a discriminated minority member, an individual who has been victim to domestic violence, or a citizen of a war-torn region) (Bateson et al. 2011).

Optimal Levels of Trait Anxiety

Across the lifetime it is generally preferable to experience low to modest levels of anxiety. Research examining the association between trait anxiety and death by non-natural causes (i.e., death that was not caused by illness, physical condition, or age; e.g., accidental death or death by suicide) suggests that both low and high levels of trait anxiety are associated with higher mortality. High anxiety is associated with a greater risk of non-natural, non-accidental death, such as death by suicide, following the age of 25 (Lee et al. 2006). People with low levels of anxiety do not frequently seek professional care because they do not experience distress due to their lack of anxiety. However, individuals with low anxiety are at greater risk of accidental death, (Lee et al. 2006; Neeleman et al. 1998) particularly before the age of 25 (Lee et al. 2006). When

considering the relationship between anxiety and general mortality the association appears to be U-shaped – higher mortality rates are found among individuals with low anxiety and individuals with high anxiety compared to individuals with mid-range levels (Mykletun et al. 2009). As such, individuals who fall on both extremes of the anxiety continuum may be said to suffer impairments caused by excessive or insufficient anxiety, respectively.

Conclusion

Anxiety and fear responses are advantageous in situations that threaten one's fitness. Nevertheless, anxiety is often experienced superfluously, resulting in energetic cost with no benefit. This cost is outweighed by the exorbitant cost that could ensue if someone is unprepared for a situation that could result in loss of life, social ties, resource holdings, or reproductive partners. It is not always clear what signs may indicate threats to fitness. As such, it is advantageous to over respond to ambiguous signs of threat so that dangerous events can be avoided. Yet, for some people, anxiety may present in a manner that causes considerable distress and may be sufficient for a clinical diagnosis of an anxiety disorder. Evolutionary theory affords important insights into anxiety's function and regulation, but this thought has not generally been incorporated into clinical treatment.

Cross-References

- [Anxiety](#)
- [Anxiety \(Randolph Nesse\)](#)
- [Correlates of Fear](#)
- [Darwinian Medicine and Survival Problems](#)
- [Defending Against Attack](#)
- [Defending Against Predator](#)
- [Emotions](#)
- [Evolutionary Clinical Psychology](#)
- [Fears](#)
- [Fears and Phobias](#)
- [Phobias](#)

- [Social Anxiety](#)
- [Stress Reduction and Mental Health](#)

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Anxiety of Strangers

► Stranger Anxiety

Aplysia

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Synonyms

Mollusk; Sea slug; Snail

Definition

Aplysia is a species of sea snail, commonly referred to as sea hares because of their posterior tentacles that protrude like ears do in hares.

Introduction

Aplysia became known to the scientific world through the published work of Eric Kandel, a well-known neuroscientist for his research on memory and learning for which he shared the

Nobel Prize in Physiology or Medicine in 2000. Kandel's breakthrough came through his pioneering work with *Aplysia*, which provided a wealth of information regarding non-associative learning and its forms (habituation and sensitization).

Habituation and Sensitization in *Aplysia*

Among low-level organisms, *Aplysia* has become a fitting model for studies of how neurons and neural circuits regulate behaviors. What attracts scientists into studying them is their simplicity and the huge size of their neurons, which are easy to manipulate and work with. Also, *Aplysia* exhibits abilities on learning establishing thus its appropriateness for applying cell biological approaches to the investigation of learning and memory mechanisms Moroz (2011). Of particular interest to Kandel and colleagues was the gill and siphon withdrawal defensive reflex of *Aplysia*. *Aplysia* has a mantle cavity on its dorsal surface that protects the gill. The gill lies beneath the mantle shelf, which terminates at the back of the cavity in a fleshy, funnel-shaped spout, the siphon, which contracts to eject water from the gill. A two-component reflex is triggered when stimulation is applied to the siphon (mantle shelf) causing both the siphon and the gill to be retracted, protecting the organism from potential threat. These two components consist of two involuntary reflexes, the so-called siphon withdrawal reflex (SWR) and the gill withdrawal reflex (GWR). The gill- and siphon withdrawal reflex (GSR) is mediated by distinct neuronal pathways, enabling scientists to record activities on the synaptic and neuronal level and to directly link synaptic plasticity to behavioral plasticity. The neural circuits of these reflexes are comprised of monosynaptic connections from sensory neurons to motor neurons, as well as polysynaptic connections containing excitatory and inhibitory interneurons. Kandel's and associates' work on this invertebrate animal regarding the cellular mechanisms underlying habituation and sensitization observed that while light siphon stimulation would naturally cause retraction, repetitive siphon

stimulation produced short-term habituation lasting for a few hours. On the other hand, long-term habituation was demonstrated by repeating multiple training sessions across several days. A single habituation training session consisting of regular trials separated with a time interval of 30 s produced typical reductions in response of the siphon withdrawal reflex. The replication of these training sessions once per day for 4 days produced a progressive buildup of habituation within each session. Habituation preservation was tested the next day and weeks 1 and 3 after training, and when compared to group, the experimental group exhibited greater habituation. The gill withdrawal component of the reflex was also tested for long-term habituation with the same procedures showing that siphon training produces long-term habituation in both components of the reflex Castellucci et al. (1970). Furthermore, in another series of experiments, noxious shocks at the rear produced an increase in the siphon withdrawal reflex and in the gill withdrawal reflex. A single shock increased the reflex for 15 min to an hour. After repeated shocks sensitization seemed to last up to several weeks. Four brief noxious electrical shocks were applied daily for 4 consecutive days. Sensitization retaining was measured again at day 1 and weeks 1 and 3. Also greater sensitization was observed with the addition of more shocks and by spacing the training sessions (two daily shocks within 10 days) Pinsker et al. (1973).

Generally it was indicated that short-term and long-term habituation results from homosynaptic depression of excitatory neurotransmission, while heterosynaptic facilitation of the sensorimotor connection caused sensitization. Habituation was not brought up by changes in the activity of sensory or motor neurons. Specifically sensory neurons release less neurotransmitter because of changes in calcium channels regulating neurotransmitter release, leading to the functional inactivation of the synapse in the long term. Nevertheless habituation still occurs after direct electrical stimulation of the motor nerve, avoiding that way the sensory receptors. This is essential as it reveals that the reduction in response is not due

to sensory adaptation. Furthermore, motor fatigue is also eliminated by showing that direct stimulation of the motor neurons can still provoke a normal reaction after habituation has occurred. Carew (1984) provides more detailed description of the work with *Aplysia*.

Conclusion

The physiological modification of the neural circuits that underlie behavioral plasticity in *Aplysia* has yielded fundamental information that can be extended to all animals providing valuable information on non-associative learning processes.

Cross-References

- [Habituation](#)
- [Non-associative Learning](#)
- [Sensitization](#)

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Apoptosis

- [Cell Death as an Adaptation Against Cancer](#)
- [Early Stage of Brain Development at Birth](#)

Aposematism

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Synonyms

Warning coloration; Warning display; Warning
signal

Definition

Anti-predator strategy in which prey exhibit warn-
ing signals coupled with some form of secondary
defense.

Introduction

Among the many strategies that animals have evolved to deter predators, aposematism is one of the most intriguing. Already in 1877, Sir Alfred Russell Wallace provided thoughts about how distasteful butterflies would benefit from displaying “showy” colors that made them stand out among other butterflies. This, Wallace suggested, helped them being easily seen and recognized, and, consequently, avoided by their enemies (Wallace 1877). The term aposematism, first used by Sir Edward Poulton in 1890, is composed of two words of Greek origin, *apo* (away) and *sema* (sign) and refers to an anti-predator strategy that consists of the display of warning signals by prey in order to inform predators about their unprofitability (Poulton 1890). The warning signal, often a conspicuous color or pattern, a characteristic odor, or a distinctive sound, functions as a primary defense. This means that it operates *before* the predator attacks the prey. Prey

unprofitability is in turn conveyed by any physical, chemical, or morphological attribute that deters the predator *after* the attack. These attributes are considered a secondary defense. Once the predator attacks the prey, it goes through an unpleasant experience that will evoke an aversive reaction to that particular kind of prey in future encounters. Thus, the predator learns the association between the warning signal and the secondary defense, which leads to aversion (Ruxton et al. 2004). Although aposematic organisms are frequently conspicuous, not all conspicuous animals are aposematic and, indeed, not all aposematic species are obviously conspicuous (Endler and Mappes 2004).

What Makes Warning Signals Efficient?

Warning signals are often distinctive and conspicuous, because they must be easy to recognize, learn, and remember for predators (Ruxton et al. 2004). For example, it has been suggested that red, yellow, and black are efficient warning signals because they endow a high contrast against most vegetation, but also because their appearance is relatively constant regardless the light environment (Stevens and Ruxton 2012). Furthermore, red and yellow are simply colors that undefended prey do not often bear, as they clearly increase prey detectability. A few studies have shown there is an innate bias toward these colors, but there is still evidence that, in most cases, this aversion is learnt. Colors such as red, yellow, and black (Fig. 1) combined with odors such as pyrazine are thus common features among aposematic prey.

Theoretical Expectations and Cognitive Aspects

Previous studies have shown that there can be some extent of innate aversion to certain colors and color patterns. However, there is also a wide consensus supporting the idea that learning is an important process involved in the eventual



Aposematism, Fig. 1. Examples of aposematism in nature. (a) *Arctia plantaginis*, the wood tiger moth; (b) Amazonian caterpillar (c) *Dendrobates tinctorius*, the

dyeing poison frog; (d) a butterfly of the genus *Heliconius*. Note the prevalence of yellow and red in combination with black

avoidance of aposematic prey by their predators. In that respect, a basic assumption of aposematism theory is that predators find easier to learn one signal to be avoided rather than several (Mappes et al. 2005). Therefore, natural selection is expected to exert a powerful pressure against warning signal variation. Despite this expectation, there are several aposematic organisms displaying variable warning signals even within the same population (polymorphism), spanning from insects and arachnids to amphibians and reptiles (Rojas et al. 2015). One among several non-mutually exclusive explanations for the maintenance of this variation is related to another cognitive process, *generalization*, which occurs when a predator transfers its learned avoidance from an aposematic prey to another one bearing a similar

appearance. Aposematism, however, is not an all-or-none strategy (Mappes et al. 2005). Some aposematic prey are not overtly noxious but only have an unpleasant taste that does not represent a major risk for the predator. This illustrates how secondary defense is about relative profitability, as high toxicity is not required. Accordingly, predators in search of food are capable to assess the toxin content of some prey and decide whether or not to eat it depending on their hunger level and their previous toxic load.

Secondary Defenses Can Vary Too

In the same way that primary defenses are expected not to vary in order to enhance predator

learning, secondary defenses are predicted to exhibit little or no variation within a population of individuals bearing the same warning signal. This variation is, however, more common than previously assumed (Speed et al. 2012). In fact, its implications are far from trivial for the dynamics of aposematism because individuals with weaker than average defenses may delay or obstruct predator learning, with negative consequences for the prey population. In several cases the production or sequestration of secondary defenses can be costly, as can be the production of the primary defense, and thus their effectiveness might depend on the availability of resources in the animal's environment. The variation in secondary defenses can be linked to a corresponding variation in the primary defense, such that stronger warning signals are coupled to more efficient secondary defenses. In these cases the warning signal might be considered an *honest* indicator of the quality of the secondary defense (Summers et al. 2015).

Variation in Secondary Defenses Can Lead to Cheating

Once a predator has learned to avoid prey bearing a particular warning signal, other prey sharing their appearance can gain protection too (Ruxton et al. 2004). This has given rise to the imitation of the warning signal by individuals of a different species who lack the secondary defenses. Thus, the non-defended species gets protection from predators without having to incur the expenses that the secondary defenses entail. This phenomenon is known as *Batesian mimicry*, and it works only if the number of “cheaters” (i.e., the non-defended individuals) is kept under a threshold where predators have still enough encounters with defended prey to maintain the aversion. Textbook examples of Batesian mimicry include the coral snakes, which serve as models to species of brightly colored, non-defended, or mildly defended colubrid snakes, and the swallowtail butterflies in the genus *Papilio*, whose coloration mimics that of several different species of unpalatable butterflies. But Batesian mimicry can also occur between animals of completely different groups,

such as the nestling of the Cinereous Mourner bird whose coloration and behavior resemble an aposematic caterpillar. It can also be the case that two or more defended species share a common warning signal, in a phenomenon known as *Müllerian mimicry*. This results in a benefit for all species involved because they share the costs of predator education, decreasing the per capita risk. Among Müllerian mimics, probably the best well-known cases are the *Heliconius* butterflies and the frogs in the *Ranitomeya imitator complex*, both of which occur in the Neotropics.

How Does Aposematism Originate and Evolve?

One central question in evolutionary biology is how the first aposematic individuals appeared and, most importantly, managed to multiply and spread (Mappes et al. 2005). This is puzzling because presumably the first individuals showing, for instance, conspicuous coloration would have been easy to detect for predators (Alatalo and Mappes 1996). Thus, those prey would have been injured or killed without being able to reproduce and reach the numbers required in order to elicit avoidance learning in predators. Likewise, the first defended prey that did not display a memorable signal, such as conspicuous coloration, would have been eaten without offering learning possibilities to the predator, who would have found more difficult to associate dull-colored prey with their unprofitability. This paradox has been under active debate and is still partly unresolved. However, some explanations have been proposed. For example, it has been suggested that both the primary and secondary defenses may have increased gradually or that both defenses may have first been associated with a selective pressure other than predation. In addition to these, there is some empirical evidence that predators such as birds are often reluctant to attack unfamiliar prey items for either short (neophobia) or prolonged periods of time (dietary conservatism). In this context, especially if familiar prey are available and abundant, these biases may favor the rise and

spread of novel color morphs and would have thus allowed for the spread of the first aposematic individuals. Other studies suggest that aposematism might have first appeared, and been favored, in aggregations of defended prey (Alatalo and Mappes 1996). This is because processes of learning and memorization of a signal will work better the more common the signal is. In other words, a predator is more likely to learn about the unprofitability of certain prey, if it encounters it frequently (Endler and Mappes 2004). Thus, the success of aposematism relies on “strength in numbers.”

Aposematism and Multimodality

Aposematic organisms can have warning displays that stimulate two or more sensory channels in the receiver, the predator, in this case. For instance, they can stimulate their visual system when detected and then their taste receptors when attacked. For this reason, warning displays are thought to be multimodal (Rowe and Guilford 1999). Multimodal warning displays are assumed to improve associative learning, the type of learning that predators go through, because they supply more information than displays consisting of just one sensory modality. Consequently, the interaction between two types of signals (say visual (color) and chemical (taste)) is predicted to be more effective than each signal separately. Relatively recently researchers have started to redirect their attention to the role of multimodality in the dynamics of aposematism.

Conclusion

Aposematism is a strategy by which prey deter predators combining an easy-to-recognize and memorable warning signal with some type of secondary defense. As a result of coevolution between predators and prey, aposematic species are often conspicuous. Yet, not all conspicuous

organisms are aposematic, just like not all aposematic individuals are conspicuous. For this reason, aposematism should be deemed as a continuum of warning signal conspicuousness and secondary defense efficiency rather than as an all-or-none anti-predator strategy. There is still much that warrants in depth investigation about the underpinnings of aposematism. For instance, it is essential to investigate in depth the role(s) of variation in predator community composition, as well as of interindividual differences in cognitive abilities among predators, in the evolution of warning signals, and the rise and maintenance of warning signal variation. Likewise, more attention should be given to the existing variation in secondary defenses and its function(s) in the interactions between predators and prey. Also, more studies are needed to gain a better understanding of the costs of both primary and secondary defenses and whether the resources for their production or sequestration are antagonist or synergistic. Finally, it is necessary to increase current knowledge on the link(s) between warning signals and secondary defenses, and life-history, behavioral, and ecological traits.

Cross-References

► [Müllerian Mimicry](#)

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Apparel

- [Clothing](#)
- [To Afford Protection Against Climate and Weather](#)

Appeal to Nature Fallacy

- [Naturalistic Fallacy, The](#)

Appearance

- [Appearance/Beauty in Girls](#)

Appearance Enhancement Effort

- [Desire to Be Included Among Desirable Women](#)

Appearance/Beauty in Girls

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Synonyms

[Appearance](#); [Attractiveness](#); [Dominance](#); [Youth](#)

Definition

Physical attractiveness in prepubescent females.

Introduction

Attractiveness is more important to females, as males weigh female attractiveness much more than females weigh male attractiveness, and beauty plays a role in social evaluations from infancy in girls. Physical appearance might represent a female's youth and reproductive value, leading to intrasexual (same-sex) competition among girls with attractiveness as a primary target.

Cultural Differences in Beauty

In all human societies, physical characteristics are an important factor in determining whom one finds attractive. Individuals across all cultures appear to have the same basic range of internal states, emotions, and external signals, but humans demonstrate plasticity of emotional response regarding what is physically attractive. Characteristics considered to be attractive vary considerably across cultures, and there is a fair degree of malleability in responses to external stimuli (Hyde and DeLamater 2008). In some cultures, for example, scars, tattoos, or piercings can be considered to be very attractive, while in others, they

are seen as ugly disfigurements (Workman and Reader 2014). Additionally, what a given culture finds attractive may change over time, and generations and may even differ between subsections of a society, such as emotional response to tattoos for younger members of society. The details of physical beauty can be diverse; however, there are cross-cultural agreements in what is judged to be beautiful. For example, bad complexion is considered to be unattractive in just about every human society (Hyde and DeLamater 2008). Additionally, many diverse cultures have a consensus regarding which individual faces are deemed attractive (Buss 2015).

Attractiveness

Psychological factors that affect attraction include similarity, familiarity, proximity, reinforcement (attraction associated with rewards or positive feelings), self-evaluation maintenance (individuals strive to maintain or improve their self-esteem through desirable or popular others), and attachment (attraction based on relationships early in development) (Clark and Pataki 1995). However, people are most attracted to good-looking others. Infants as young as 3 months old will gaze longer at attractive faces, compared to less attractive ones, indicating a very early-emerging bias (Buss 2015). Additionally, the more attractive an individual is rated, the more positive personality traits and life outcomes are ascribed to that individual (Eagly et al. 1991).

Individuals tend to focus on two major domains of attractiveness: facial and physical. For facial features, averageness is one characteristic; the more average a face is to a general population, the more attractive its rating. For example, if different individual faces are blended together, blended faces are rated as more attractive than individual faces, and the more blended or average they become, the higher they are rated on attractiveness (Buss 2015). Another major factor that affects both facial and physical attractiveness is symmetry. The more symmetrical a face or body is, the more attractive it is rated. The appeal of symmetry is found even in infants who prefer to

look longer at symmetrical patterns than asymmetrical ones (Etcoff 1999).

Physical Attractiveness in Females

Even though there are many cross-cultural differences in the details of what is attractive, one consistent universal finding is that males overall place greater importance on physical attributes when selecting a potential mate (Buss 2015). Attractiveness is significantly more important to males evaluating females than vice versa. Males are still evaluated based on physical appearance, with the ideal in many cultures, being tall, trim, narrow hips, broad shoulders, and square jaw (Hyde and DeLamater 2008). However, physical appearance in males only appears to be of increased importance for females in short-term mating contexts. For long-term relationships, the actions and achievements of men are primary considerations for women when considering a stable romantic partner. Males are valued predominantly for ambition, stability, maturity, economic resources, financial prospects, and high social status for long-term relationships (Buss 2015; Langlois et al. 2000). For females, it is the appearance that males primarily consider when evaluating a potential romantic partner, not just in short-term relationships but in long-term contexts as well. For heterosexual men, brain reward centers (particularly the *nucleus accumbens*) are activated simply by viewing attractive female faces (Buss 2015). Highly attractive women are significantly more likely than less attractive women to marry a wealthy man, while men who have the highest education and occupational status actually tend to be rated on lower ends of attractiveness scales (Udry and Eckland 1984).

Regarding physical features of females, there are a few general measurements that have emerged as strongly influential on attractiveness and beauty ratings. Physical attractiveness in women is based primarily on secondary sexual characteristics, such as breast size, hip size, and fatty deposits on buttocks. For example, waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist (at the narrowest

point around the torso, under the iliac crest) by the circumference of the hips (at the greatest protrusion of the buttocks); body mass index (BMI), which is calculated by dividing body weight by height squared; and curvaceousness, which refers to the degree of the “hourglass shape,” such as the bust-to-waist ratio, have all been identified as important physical attractiveness factors (Buss 2015). Secondary sexual characteristics important to physical attractiveness measurements in females all appear after sexual maturation; however, attractiveness does not just begin to have an effect at puberty. Attractiveness plays a role in social evaluations from infancy.

Beauty Before Puberty

One of the defining aspects of physical immaturity is cuteness. Cuteness in babies is generally dependent on protruding cheeks, a large forehead, and large eyes below the horizontal midline of the skull (Ectoff 1999). Neonatal features of cuteness are thought to trigger parental care. For example, babies with higher ratings of attractiveness are more likely to have mothers who spend a greater amount of time holding them close, making eye contact, and making more vocalizations (Ectoff 2011). During childhood, attractive children (compared to unattractive children) are judged more positively and treated more positively and exhibit more positive behaviors and traits (Langlois et al. 2000). Similar to adults, appearance cues appear to be more important for females than males, with girls providing more appearance stereotypes than boys and both sexes providing more appearance stereotypes when describing girls than when describing boys (Miller et al. 2009).

Culturally, the importance of attractiveness has increased dramatically in the United States in the twentieth century, and this is reflected particularly in young girls. Prior to WWI, girls rarely mentioned their bodies in terms of strategies for self-improvement or struggles for personal identity, but in contemporary societies, girls are concerned with the shape and appearance of their bodies as a primary expression of their individual identity

(Brumberg 2010). Part of the shift from “good works” to “good looks” can be attributed to modern cultural acceptance and promotion of sexualization in young girls. For example, the modern child beauty pageant emerged in the early 1960s and currently includes approximately 250,000 pageants for girls in the United States with age categories as early as 0–11 months. Toy and clothing manufacturers regularly market items to young girls that feature sexualized content. The increase in sexualization of young girls has become so pervasive that the American Psychological Association, in 2008, assembled a task force to address public concern. While sexualization of young girls continues to be an issue, beauty does factor into social relationships, particularly dominance in intersex hierarchies, among girls in childhood.

Beauty and Dominance in Girls

Beauty does not just have advantages for females in direct mating contexts; attractiveness has many intersexual (same-sex) advantages in childhood. A strong relationship between attractiveness and popularity is found in girls, beginning in childhood as young as 3 years of age (Hyde and DeLamater 2008). Meta-analyses have demonstrated that children rated as attractive, compared to unattractive, were more popular, were better adjusted, and even had higher intelligence and performance competence, with no other moderating variables found (Langlois et al. 2000). Beauty is an especially strong contributor to young girls’ popularity in school, along with social skills and family socioeconomic status, which girls also use in intrasexual competition (Buss 2015).

Beauty is thought to be a path to social dominance for girls, leading to a higher status that is then maintained by derogating other girls about their physical appearance in particular, along with their sexual fidelity (Buss 2015). For example, girls (particularly more-attractive girls) commonly use words like “ugly” and “slutty” to insult other female peers, calling into question for boys (potential future mates) their attractiveness and sexual purity. Further, hearing an appearance-

related derogation about a specific woman, such as “fat and ugly,” can actually influence men’s ratings of attractiveness of that woman (Buss 2015).

Girls generally employ indirect (relational) aggression to establish dominance over same-sex peers, compared to boys who use direct (physical) aggression (Buss 2015). Relational aggression includes gossiping, shunning another person, spreading vicious rumors, breaking contact with the person as revenge, or befriending someone else as revenge. Bullying in girls typically includes derogation specifically related to another girl’s physical experience or sexual fidelity, theoretically to inflict costs in intrasexual rivals as intrasexual competition increases from childhood to middle adolescence. Moreover, female aggression often originates in motives such as jealous rivalries, competition over boys, and the desire to be included among the “desirable” group of other women (Buss 2015).

Evolutionary Benefits of Beauty in Females

There are many social advantages to being attractive. People are more likely to offer help to an attractive person (even if they do not like them) and to let an attractive person win an argument (Ectoff 1999). Compared to unattractive individuals, attractive individuals tend to be more confident and at ease socially, less likely to fear negative opinions, and more likely to demonstrate more entitlement (Ectoff 1999). Considering how cross-culturally ubiquitous the effects of attractiveness are and how early in development it begins to shape behavior, beauty seems to have played a major role in evolutionary history.

A dominant evolutionary theory as to why females are disproportionately evaluated on physical attributes is youth. Females’ reproductive capacity declines as she ages, dropping to essentially zero around age 50 (Buss 2015). Women have a relatively narrow window of opportunity to successfully reproduce during their entire lifespans. Males eager to reproduce

would have to selectively target those females that would be most likely to produce healthy, viable offspring. Any physical signals that would indicate a female’s reproductive value would have been desirable to males throughout human’s phylogenetic history. The physical cues to health, such as symmetry and averageness which would indicate a lack of infections, parasites, or disease, are still preferred by contemporary males. Faces that show a high degree of asymmetry have been linked to negative health indicators and may reflect psychological, emotional, and physiological distress (Buss 2015).

Younger females have higher reproductive value, because their future reproduction is expected to be higher, so features that indicate youth are expected to be particularly desirable in males. Research has indicated that males do prefer females that are younger than themselves, with the difference in age preference increasing as males get older (Buss 2015). Signs of youth, such as smooth and clear skin, would indicate reproductive value and therefore be desirable traits for males. Males demonstrate a strong predisposition for youth overall, as homosexual men are just as interested in youth and beauty in their partners as heterosexual males (Ectoff 1999). Females also demonstrate a predisposition to use their physical features to facilitate attractiveness. For example, flirtation is similar across many cultures, with women smiling, lifting eyebrows, display eyes, and looking away, which suggests a biological predisposition for a sexual behavior pattern (Hyde and DeLamater 2008).

Conclusion

What constitutes attractiveness varies considerably among cultures, but there are several universal factors that influence whether or not an individual is deemed attractive. Characteristics include good complexion, facial averageness, facial and physical symmetry, WHR ratio, BMI, and curvaceousness, which have all been theorized as displaying reproductive value. While

attractiveness in males is important in short-term mating contexts, attractiveness in females is much more important overall, as males primarily select mates based on physical appearance and beauty. Preferences for attractive faces begin in infancy, and young girls associate attractiveness with popularity and social dominance, from as young as 3 years old to middle adolescence. Early developmental emergence and cross-cultural universality of importance, along with the many social benefits, demonstrate the adaptive functions of beauty in girls.

Cross-References

- [Opposite-Sex Relationships](#)
- [Sex Differences in Cognitive Development](#)
- [Sex Differences in Sexual Socialization](#)
- [Sex Differences in Social Development](#)

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Appearance-Reality Task

- [Smarties Task, The](#)

Appeasement

- [Reconciliation](#)

Applications of Evolutionary Psychology

- [How Evolutionary Psychology Can Still Explain Behavior](#)

Applied Behavior Analysis

- [Methods and Enduring Impact of Behaviorism](#)

Appraisals: Construals

- [Changes in Self-Esteem Motivate Behavioral Changes](#)

Appraised Helplessness and Self-Slaughter

- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)

Apprehension

- [Anxiety](#)

Apprenticeship

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Synonyms

Training

Definition

A system of training a new generation of practitioners of a trade or profession with on-the-job training and often accompanying study.

As discussed elsewhere in this work (Peedicayil 2018), cultural inheritance involves the storage and transmission of information by communication, imitation, teaching, and learning. In this context, there is evidence that complex social behaviors like human altruism and mate choice (Rushton et al. 1986), social attitudes (Martin et al. 1986), personality (Eaves et al. 1999), and the human sex ratio (Lipatov et al. 2008) are culturally transmitted. The cultural transmission of such behaviors, for obvious reasons, will occur effectively only in an animal species that is social, i.e., where the members live in groups and interact freely with one another. Human beings are the archetype of that type of animal species and the groups they live in are termed societies (Wilson 2000). Indeed, the famous Greek philosopher Aristotle had stated “Man is by nature a social animal” (Aristotle 2015). All of man’s unique social behavior is pivoted around the use of language (Wilson 2000).

Regarding apprenticeship, it is found in humans because of the advanced level of cultural inheritance found in humans when compared to other animals. Apprenticeship refers to a system of training a new generation of practitioners of a trade or profession with on-the-job training, and often accompanying study (Wikipedia 2018). Apprenticeship also allows the practitioners to gain a license to practice in a regulated profession. Most of the training of those being trained is done while working for an employer who helps

the apprentices learn their trade or profession in exchange for their continued labor for an agreed period during which the apprentices achieve adequate capabilities. The system of apprenticeship is thought to have first developed in the late middle ages (the period of European history lasting from about 1250–1550 AD) and to have been supervised by craft guilds and town governments (Wikipedia 2018). Apprentices usually began at 10–15 years of age and would live in their teacher’s house. The modern concept of internship is similar to apprenticeship but not as rigorous. Also similar to apprenticeships are the professional development arrangements for new graduates in the accountancy, engineering, management consultancy, and law professions (Wikipedia 2018).

Cross-References

► Cultural Inheritance

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Approximate Number System

- [Quantity Estimation](#)

Aptation

- [By-Products of Adaptations](#)
- [Evolutionary By-Products](#)

Aquatic

- [Fish, Amphibian, and Reptile Tool Use](#)

Arbitrary

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Synonyms

[Conventional form-meaning mapping](#); [Noniconic form-meaning mapping](#); [Symbolic signs](#)

Definition

Arbitrary signs are signs where the relation between signifier and signified is solely a matter of convention and there is no natural connection between them. Words are considered arbitrary in the sense that the sound pattern of the word does not resemble its meaning and there is no intrinsic relation between the two. Thus, meaning cannot be inferred from a word's sound, and the same meaning can be expressed through different sound patterns.

Introduction

The nature of the relation between words and referents has long been a topic of discussion. Plato's *Cratylus* is an early testimony of the debate between a conventionalist stance that views this relation as purely a matter of convention and a naturalist stance that views this relation as stemming from a natural, nonarbitrary, connection. In the past century, ever since de Saussure (1916), the arbitrariness of the linguistic sign has become a central tenet of linguistic theories. Words are considered symbols, conventionally related to their referents; the form of the word does not resemble its meaning. For example, the word *big* is smaller than the word *small*. This is in contrast to motivated signs such as icons, whose form corresponds to their meaning (e.g., children crossing sign), or indices, causally related to their referents (e.g., footprints in the sand) (Peirce 1932).

Arbitrariness in Language

The arbitrary relation between form and meaning has even been designated a design feature of language by Hockett (1960), thus defining it as a necessary requirement distinguishing language from other communication systems. For example, posture can convey information, but its form is not arbitrary with respect to its meaning or function. Similarly in honeybees, the speed of the dance and its direction are not arbitrary with respect to the distance and location of the food. However, some animal communication systems, for example vervet monkeys alarm calls, are considered arbitrary. Although these alarm calls contain acoustic features that are not arbitrary with respect to their function (e.g., high amplitude, abrupt onset), the acoustic distinction between the alarm calls for different predators appears arbitrary (see Seyfarth and Cheney 2003). This design feature has also been used to distinguish spoken language from spontaneous gestures that typically accompany speech. While both speech and gesture convey meaning, they do so in fundamentally different ways. Whereas in speech meaning is

represented by discrete arbitrary symbolic units, gesture represents meaning through a nonarbitrary mapping of meaning onto continuously varied form (McNeill 1992). The arbitrary nature of the sign alleviates the need to rely on a circumscribed rigid set of form-meaning mappings, thereby enhancing the power of language to convey a richer more complex array of meanings.

The arbitrariness of the sign seems evident when one considers the range of expressions used to refer to the same object across different languages. To take a familiar example, the same animal is called *dog* in English, *kalb* in Arabic, and *perro* in Spanish. Not only do these words differ from each other, there is no way of knowing a word's meaning save for knowing language-specific linguistic conventions. In the absence of an intrinsic relation between word and referent, there is no way of inferring the meaning of the word from the sound alone. Although there are onomatopoeic words that phonetically imitate the sound they represent (e.g., buzz), these typically constitute a very limited class. Furthermore, even onomatopoeic words are not universal and vary cross-linguistically; for example a dog bark sound is *woof* in English, *guau* in Spanish, and *wan* in Japanese, suggesting they are conventionalized to some degree.

Iconicity in Language

Onomatopoeias represent one example of sound symbolic words exhibiting a nonarbitrary iconic relation between form and meaning, and there are several other instances of sound symbolism in language. One example comes from ideophones (also termed mimetics or expressives) which are words that depict sensory imagery (Dingemanse 2012) but are not confined to the auditory modality. That is, they can represent sound impressions, but they may also represent sensory impressions of color, shape, or even movement; for example *gorogoro* in Japanese for a large object rolling. Though relatively uncommon in Indo-European languages, ideophones are ubiquitous in many African, East Asian, and indigenous South American languages (see Dingemanse 2012). Even

speakers of languages in which ideophones are scarce show sensitivity to sound symbolic mappings between phonemes and specific meanings, as evidenced by laboratory experiments using invented or foreign vocabulary. Sapir (1929) was the first to document sound symbolic mapping between phonemes and object size. For example, high front vowels (e.g., /i/) are associated with smallness, whereas low back vowels (e.g., /a/) are associated with largeness. As high front vowels have higher frequency, Ohala, Hinton, and Nichols (1997) claim this mapping reflects a cross-linguistic cross-species “frequency code” associating high frequency sounds with smallness and low frequency sounds with largeness. This code is grounded in the biological inverse relation between vocalizer size and frequency of the vocalization. According to Ohala et al., the frequency code is also apparent in the use of rising intonation to express politeness or uncertainty and in non human agonistic vocalizations.

In addition to vowel sounds being related to size, there is also evidence for sound symbolism in the iconic mapping between phonemes and object shape. This relationship was first described by Köhler (1929), who found that the pseudo-word *maluma* was associated with a rounded shape and *takete* with an angular shape (subsequently termed the kiki-bubba effect by Ramachandran and Hubbard 2001). Phonological sound symbolism has since been found for various additional meanings (e.g., brightness, speed, taste). It has also been found cross-linguistically and in prelinguistic infants (see Perniss et al. 2010 for a review), further supporting the idea that it is not based on arbitrary linguistic conventions. Findings of such cross-modal associations in language have led Ramachandran and Hubbard (2001) to suggest that cross-modal correspondences between visual object properties and sounds provided the underpinnings for the development of a proto-language and played a key role in language evolution. Despite this line of research showing sound symbolic biases in interpretation of pseudo-words, the small inventory of actual sound symbolic words in Indo-European languages contributed to the relegation of phonological iconicity to a marginal role in language.

Yet the role of cross-modal correspondences in language is not limited to sound symbolic words. Moving from segmental units like phonemes to suprasegmental prosodic properties of speech reveals another source of information that does not act in accordance with the principle of arbitrariness. Although most research has focused on the role of prosody in conveying emotion, recent research has shown that prosody can also convey semantic-referential information. Language users can capitalize on existing cross-modal correspondences and convey information about object properties by modulating their pitch, loudness, and speech rate; for example, the modulation of pitch can convey information regarding object vertical location, motion, and size (see Perniss et al. 2010, for a review). This nonarbitrary gradual mapping between form and meaning in prosody can be seen as a form of spoken gesture (Shintel et al. 2006).

Conclusion

Taken together, these findings suggest a role of iconicity at different levels of language, from the level of the phoneme to suprasegmental prosodic structures. Other findings have also documented the role of iconicity in syntax (see Perniss et al. 2010). Thus, while not denying the fundamental role of arbitrariness in language, the assumption that the relationship between words and meaning is essentially arbitrary (e.g., Hockett 1960) needs some reconsideration. Iconic non-arbitrary form-meaning mappings may play a larger role in language than previously realized, and future research should clarify the extent to which they affects language comprehension and production.

Cross-References

- [Alarm Calls](#)
- [Language](#)
- [Linguistic Evolution](#)
- [Sign Language](#)

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Archaeological Records

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Definition

Archaeology is the study of the material remains of human activity, and an archaeological record is the evidence that informs such studies.

Introduction

The components of the archaeological record can include artifacts, which are objects that have been

moved or altered through human activity (i.e., stone tools, plant remains, or bones from a butchered animal), or features, which are immobile alterations to a site (i.e., burial pits or fireplaces). Archaeological records are often ancient but may also include objects or activities that are quite recent. Prehistoric archaeology is the study of human societies that are typically pre-urban, without surviving written records. Historical archaeology is the study of sites where either oral or written records or accounts can be accessed to inform the interpretations of those sites. It should be noted that these written or oral accounts may either correspond with or conflict with the evidence obtained from the site through archaeological investigations.

Archaeological Records

Archaeological records are typically revealed through the excavation of a site, which is a place that contains evidence of human activity. While evidence may be found on the surface, such surface finds can be difficult to interpret because they lack temporal context within the site. Temporal context or control of a site's contents is typically gained through the understanding of stratigraphy at a site. Stratigraphy is the layering of sediments within the ground. The interpretation of stratigraphy is dictated by the law of superposition, which states that in an unaltered sequence of sediments the oldest layers will be at the bottom and younger layers toward the top. Artifacts or features found within these layers can be placed within the timeframe of the formation of that site, with objects found in the deeper layers likely to be older than those found closer to the surface. A precise understanding of the spatial patterning of artifacts and features, both horizontally and vertically, within the context of a site's stratigraphy is crucial to the interpretation of the site. Artifacts that are believed to be in an original, undisturbed context within the site are referred to as *in situ*. Because archaeological excavations remove sediments, which permanently alters the site and may destroy contextual evidence, accurate

record keeping is very important for the preservation of information contained in the site's contents.

Stratigraphy within a site provides only very broad temporal context to these artifacts. Stratigraphic position can only tell which artifacts or features are likely to be older than other objects found at that site, a type of context known as relative dating. Relative dating is unlikely to be able to provide numerical ages for artifacts because of this fairly imprecise and site-specific level of interpretation. Numerical ages, known as absolute dates, can be obtained when there are materials deposited within the stratigraphy of the site that are suitable for a variety of dating techniques, such as radiocarbon or potassium-argon dating, that can measure the length of time that those materials have been buried at the site. Sometimes, these absolute dates can be obtained directly from artifacts of interest, such as bones, teeth, or charcoal, while other times these dates can be useful for providing ages for layers within the stratigraphic profile of a site. These dates provide crucial context for the artifacts found within the site, which enables broader interpretations of the site's functions.

Taphonomy is the study of the processes that result in fossilization of organisms, and a knowledge of these processes and the biasing outcomes they may introduce are useful for understanding and interpreting the archaeological record. Archaeological sites are imperfect for a variety of reasons, which must be acknowledged in any analysis or interpretation of a site's significance. A number of different phenomena can affect which materials are present in a site and how those materials may have been preserved. One such biasing effect can be the soils within the site itself. Highly acidic soils will damage or destroy many organic materials, which can significantly impact interpretations of a site and its contents. Burrowing animals or insects may also disturb a site's contents over time, a process known as bioturbation. Erosion by wind and water could have disturbed or even removed small artifacts and degraded details of features. Fast-moving water, such as rivers or floods, may even remove and

redeposit artifacts in different locations. Archaeologists must be aware of these processes and consider their potential effects in rendering conservative interpretations of a site.

Materials recovered from an archaeological investigation are typically described and classified during the process of analysis. This process often involves the artifacts or features from a site being separated into various “kinds” or “types” and placed into various typologies. Typologies are based upon the various physical characteristics of artifacts or features and are used to place various sites or artifacts within the broader context of cultural or behavioral change. Stone tools provide several examples of these typologies in recognized complexes such as the Oldowan or Acheulian. Typologies can be useful for facilitating conversation and study of the complexities of the archaeological record but are often the subject of discussion and debate within the archaeological literature.

A variety of theoretical perspectives within archaeology have had a profound impact on the interpretations of sites (see Praetzelis 2015 for further discussion). These perspectives question that idea that anything can be known with certainty and acknowledge that human beings are inherently biased by our individual experiences. These theoretical approaches to data analysis provide means to mitigate these biases. It should be noted that there is no single dominant theory of archaeology but instead a variety of theories used by archaeologists to provide the framework through which they interpret artifacts and sites. These different theoretical approaches allow archaeologists to treat evidence from sites in different ways and may lead them to come to different conclusions about that evidence. For example, Marxist theory examines archaeological residues through the lens of class hierarchies within economic systems. Alternatively, Structuralism proposes that underlying, sometimes unconscious structures inherent to human thought shape various cultural constructions. Feminist theory emphasizes the interpretation of gender roles as evidenced in archaeological residues as a means of understanding past cultures.

Conclusion

Ultimately, the goal of the archaeologist is to use the evidence from a site to reconstruct details of land use, behavior, culture, economy, and subsistence of local human groups and place those activities within a temporal context. This collection of evidence comprises the archaeological record.

Cross-References

- [Burials](#)
- [Olduvai Gorge, The](#)
- [Paleoanthropology](#)
- [Tool Use](#)

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Archaic Adaptive Introgression

- [Neanderthals and Humans](#)

Archeology

- [Evolution of Tool Use](#)

Architectural Acoustics

- [Cathedral Acoustics](#)

Archival Research

- [Census Data](#)

Ardipithecus Group

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Synonyms

Ardipiths; *Orrorin*; *Sahelanthropus*

Definition

One or more genera of fossil hominoids, including some probable hominids, dating from the late Miocene to the middle Pliocene (~ 7.0–3.4 Ma, millions of years ago) of East and Central Africa; the name *Ardipithecus* is derived from the Afar for “ground” or “floor” (*ardi*) and the Latinized Greek for “monkey” or “ape” (*pithecus*, Greek *pithekos*).

Introduction

The *Ardipithecus* group consists of, to date, three proposed genera and four proposed species of fossil hominoids (the group that includes apes and humans) and further unclassified materials varyingly considered as representing the earliest members of the human lineage (hominids or hominins; hereafter, hominids) after the split with the chimpanzee and bonobo lineage approximately 8 Ma. *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus kadabba* are known from a relatively small number of fossils; *Ardipithecus ramidus*, the most recent form, is represented by a partial skeleton (“Ardi”) and considerable associated materials. The distinction between members of the *Ardipithecus* group, and their relationships to fossil and living apes, as well as later hominids such as *Australopithecus* and *Homo*, are matters of considerable discussion.

Discoveries and Initial Arguments

The *Ardipithecus* group, quite appropriately, began its history with an air of mystery – an air that, in truth, has never fully dissipated. In 1994 the new species *Australopithecus ramidus* was named to house some craniodental and arm elements from the Middle Awash, Ethiopia, dated to a then-ancient (for a hominid) 4.4 Ma (White et al. 1994). Great apes, especially male ones, are characterized by large canines that project beyond those of other teeth, with long upper eyeteeth that sharpen (hone) against the premolars beneath them. That *Australopithecus ramidus* lacked this canine/P₃ complex, as in *Homo*, was at the time the predominate evidence to classify it a hominid. Little could be said about whether it was bipedal, another flagship hominid characteristic. The following year, a pithy correction elevated the find to the novel genus *Ardipithecus* (White et al. 1995). Meanwhile, word spread that the Aramis group had discovered a partial skeleton of *Ardipithecus ramidus*, one which could potentially answer the critical question of how it moved about in life. Thus began what popularly became known as the “Manhattan project of paleoanthropology,” as others waited while the Middle Awash group meticulously, and quietly, analyzed the find.

The wait would be occupied by even more ancient fossils. The first, dubbed the “Millenium Ancestor,” involves a small collection of craniodental and postcranial elements from the Lukeino formation of Kenya, dated to around 6 Ma, and which were assigned to a novel genus and species *Orrorin tugenensis* (Senut et al. 2001). Arguments for the hominid status of *Orrorin* include its rather diminutive upper canine but center especially on several femur fragments argued to have bipedality-related features. These included an elongated femoral neck, contrasting with great apes, and an obturator externus groove – found on the back of the femoral neck, it has long been associated with frequent extension of the hip in erect, human-like posture and movement (Pickford et al. 2002). Associated fauna and other evidence suggests a general environment of woodland with varying degrees of open space, and lake margin.

This was immediately followed by the announcement of more ancient (5.2–5.8 Ma) *Ardipithecus* specimens from the Middle Awash, which after several years were placed in a new species *Ardipithecus kadabba* (Haile-Selassie 2001; Haile-Selassie et al. 2004). The key hominid features are an incipiently incisor-like canine, and a proximal foot phalanx with a “dorsally canted” joint surface, similar to later hominids and thought to be indicative of marked dorsiflexion of the toes during the “push-off” phase of bipedal locomotion (Latimer and Lovejoy 1990). The paleoenvironment of *Ardipithecus kadabba* has been characterized in detail and described as ranging from heavily closed to grassy woodland; any habitat preferences for *kadabba* within such a menagerie are at present difficult to determine (Su et al. 2009).

Perhaps the most enigmatic of the early proposed hominids is *Sahelanthropus tchadensis*, described from a very old (6–7 Ma) cranium, along with a partial mandible and some isolated teeth, from Chad (Brunet et al. 2002). Small canine teeth with tips worn flat (rather than pointed) and a relatively anterior foramen magnum placement, both suggested to its discoverers hominid, rather than ape, affinities. The estimated cranial capacity is within the range of adult chimpanzees and bonobos (320–380 cm³); the face, on the other hand, is far less projecting than in living apes or australopithecines. At the same time, the cranium exhibits unusually large brow ridges – a feature present in living apes but absent or only moderately developed in later hominids until Asian *Homo erectus* some five million years later. Paleoenvironmental work suggests a range of potential habitats from lake-edge forest to grassland. Along with an australopithecine mandible found in the same region and dating to roughly 3.5 Ma, *Sahelanthropus*, whatever it might represent, evidences that central Africa, in addition to the traditional early hominid-bearing locales of southern and eastern Africa, is vital to interpreting earliest human evolution.

The year 2009 brought the description of the *Ardipithecus ramidus* partial skeleton (ARA-VP-6/500, nicknamed “Ardi”) and other specimens from this form, along with a detailed examination

of its habitat. As outlined below, much of what is known on the *Ardipithecus* group comes from this work – which does much to clarify their taxonomy and, further, challenges several widespread assumptions about human origins.

Classification and Hominid Status

The various taxonomic names given to members of the *Ardipithecus* group might be considered, at present, more akin to convenient or confusing (depending on perspective) metaphors than actual species which lived in the ancient natural world. Their placement into three genera, by extension, is especially nonconservative. While they are found from differing times and places, there is too little overlapping fossil evidence to clearly differentiate them, and generalist forms (such as most or all hominids, see below) by nature inhabit broad geographic regions, often over extended periods. The ecologically pliable Virginia opossum (*Didelphis virginiana*), for example, is widely distributed from Central to North America with a range that is seemingly ever-increasing. With expected variation, it probably existed in relatively modern form over half a million years ago, and its genus dates back at least to the Late Miocene (6.8–9 Ma) of South America (Cozzuol et al. 2006). Such ecological considerations offer abundant cause for constraint in paleoanthropological classification.

Whether the various members of the *Ardipithecus* group represent hominids is perhaps the most important matter of controversy. In general, the older the fossils, the greater the disagreement. Historically, one sticking point was that some specimens dated from earlier than certain biomolecular estimates for the time of the *Pan-Homo* divergence. With improved methods, however, it is now thought likely that this event occurred earlier than 7 Ma (Langergraber et al. 2012); in other words, before any of the fossils under consideration were deposited. With this concern removed, the known morphology of the earliest potential hominids is the predominate evidence that can be brought to bear on the issue.

Sahelanthropus, for example, has been suggested to represent a non-hominid ape on several grounds, including that the canine measurements, and foramen magnum position, are potentially less differentiated from living African apes than originally suggested. Responses have focused on the seemingly derived characters of the skull – closer to later *Australopithecus* and *Homo* than living African apes – especially of the cranial base (Guy et al. 2005). The bipedality-related features of *Orrorin* and *Ardipithecus kadabba* have similarly been questioned, although current consensus, concerning taxonomic placement at least, trends towards those of the original describers (e.g., Richmond and Jungers 2008). Given the totality of the evidence, these forms can at present be considered probable hominids, with their more specific affinities to be determined by future fossil evidence.

The materials from *Ardipithecus ramidus* are more copious and conclusive. Over 100 specimens, from a minimum of 36 individuals including the female “Ardi,” have been described (White et al. 2009). This comparatively large sample confirms that both *Ardipithecus ramidus* males and females possessed small canine teeth lacking the aforementioned honing complex, with very little canine size differentiation (dimorphism) between sexes (Suwa et al. 2009). This is a very humanlike characteristic. Other aspects of the dentition, as well as limb proportions and features of the pelvis, hand, and foot are also derived in the direction of *Australopithecus* and *Homo* (Lovejoy et al. 2009a, b, c). While some initial reactions to *Ardipithecus ramidus* were critical, a holistic consideration of the materials available, including a detailed consideration of the cranial base, strongly tie *Ardipithecus ramidus* to later hominids (Kimbel et al. 2014; Sayers et al. 2012). Whether *Ardipithecus* or another member of its group was directly ancestral to *Australopithecus* is an open question, although at present there are no other viable alternative candidates.

Locomotion

Locomotor behavior plays an important role in how a vertebrate explores its world. That humans

and our immediate forerunners walk (or walked) obligately on two legs is particularly intriguing, given not only that it is unique among primates, but that it makes us slower, more injury-prone, and much less capable of climbing than our non-human primate relatives.

The remains of *Ardipithecus ramidus*, with respect to movement, are an interesting mix of the primitive, perhaps very primitive, and the derived. The foot retains the divergent, grasping big toe of other primates, and indeed has been argued to be, in some respects, more similar to an Old World monkey than that of an ape. At the same time, it shows the dorsal cant of the proximal foot phalanges common to all later hominids (Lovejoy et al. 2009a). The pelvis in outline is short top-to-bottom and wide side-to-side – although this is more apparent in the humanlike upper pelvis than the ape-like lower – and its rotated ilium indicates a reorientation of the gluteal muscles that would have helped prevent “pelvic-tilt” during two-footed, upright movement (Lovejoy et al. 2009d). The legs were likely somewhat longer than the arms, trending in the later hominid direction; the hands evince no evidence of the knuckle-walking seen in extant African apes (Lovejoy et al. 2009b, c). A partial foot skeleton from 3.4 Ma, from the central Afar of Ethiopia, indicates an animal with an *Ardipithecus*-like foot living *contemporaneously* with australopithecines that possessed a more human-like lower appendage (Haile-Selassie et al. 2012).

Taken together, *Ardipithecus ramidus* has been characterized as a “careful climber” in the trees and a “facultative biped” on the ground. Unlike living apes and monkeys, which can and often do walk bipedally for at least short distances, *Ardipithecus ramidus* appears to exhibit skeletal adaptations for this strange mode of progression. The most likely interpretation is that of a transitional biped with only a subset of the distinctive locomotion-related characteristics found in *Australopithecus* and *Homo*. The limited sample from earlier suspected hominids is consistent with a similar diagnosis, although a fuller appreciation of their locomotor repertoire can only come with further fossil discoveries.

Ecology and Behavior

Finding food, avoiding predators, and producing offspring have long been recognized as the primary concerns of animals. The generalized dentition of *Ardipithecus ramidus* – with small incisors, relatively thick enamel, and lack of shearing surface – suggests a more varied, omnivorous diet than the mainly fruit-and-leaf fare of extant great apes. *Sahelanthropus*, *Orrorin*, and *Ardipithecus kadabba* varyingly share elements of this structure (Suwa et al. 2009). At the same time, locomotor limitations, ape-sized brains (300–370 cm³ based on a sample of two), and an apparent lack of modified stone tools associated with members of the *Ardipithecus* group suggest comparative limitations in abilities for the hunting of mobile game, as seen occasionally in living chimpanzees and bonobos (or with tool-assistance in *Homo*). The evidence suggests the beginnings of a marked dietary and ecological generalism that only increased with later hominids, and which the demographic success of this group was likely dependent upon (Sayers and Lovejoy 2014).

The locomotor traits of *Ardipithecus ramidus* suggest a relatively helpless animal little enabled to escape potential predators via speed and agility when compared to living great apes. Associated carnivores include hyaenas, large cats, and bears; indeed, carnivore tooth marks are common on *Ardipithecus* remains, although the degree to which this represents predation versus scavenging has not been determined (WoldeGabriel et al. 1994). Also unknown is the degree to which members of the *Ardipithecus* group used their wits to avoid predators; later australopithecines, which also have modest brain sizes, do show endocast evidence of neural reorganization that might have been marshalled to meet such challenges. Evidence for comparison in the *Ardipithecus* group is limited, but preliminary work suggests that such changes might date to as early as *Sahelanthropus tchadensis* at 6–7 Ma (Bienvenu et al. 2013).

Then there is the matter of sex. The unimposing canines in members of the *Ardipithecus* group, and confirmed lack of canine dimorphism and lack of a functional honing

canine/P₃ complex in *Ardipithecus ramidus*, suggest a social system with less overt physical male-male competition than in extant great apes (Lovejoy 2009). In other words, gorilla-like polygyny is unlikely. Currently available evidence also suggests limited skeletal body size dimorphism, which would reinforce this conclusion (White et al. 2009).

Repercussions for the Savanna Hypothesis of Human Origins

In his *Philosophie Zoologique*, Jean-Baptiste Lamarck (1809/1984, p. 170) suggested that chimpanzee-like protohumans might have given up the habit of climbing trees “by force of circumstances.” At the same time, he reasoned, early human progenitors may have habitually stood upright to be able to see over long distances, resulting in an erect disposition and a foot that could no longer be used like a hand. The implications were that human origins might have occurred in a relatively open area. Such were the roots of the savanna hypothesis – the idea that humans initially evolved on relatively dry plains, while apes stayed in the forests – which would hold sway in paleoanthropology over the next two centuries (Bender et al. 2012). Reconstructed *Australopithecus* and early *Homo* habitats, while no means limited to savanna-like locales, included enough open country elements that the hypothesis was considered mainstream, if not accepted wisdom.

Findings associated with the *Ardipithecus* group present a definite challenge to this scenario. The fossil forms considered here lived in environments with varying amounts of canopy cover. The most detailed and damning reconstructions have been attempted for *Ardipithecus ramidus*. While the general environment where they lived consisted of a mosaic of ecotypes, the *Ardipithecus* remains themselves are strongly associated with woodland fauna. The woodland diagnosis is also compatible with isotopic evidence indicating an *Ardipithecus* diet heavy in C₃ plants and/or the animals which fed on them – most woody plants use a “C₃”

photosynthetic pathway, while four-carbon pathways are characteristic of those from dry or seasonal locations (Louchart et al. 2009; Suwa et al. 2009). If the postcranial features of *Ardipithecus* are indeed accepted as representing incipient adaptations for bipedality, then it is increasingly unlikely that this crucial shift occurred in an open habitat.

Repercussions for the Chimpanzee Model of Human Origins

Many workers have utilized living apes, especially the common chimpanzee, as anatomical or behavioral models of the last common ancestor of *Pan* and *Homo*, or of various early hominids. The influence this has had on a crucial part of the scientific process – how questions are framed – is probably incalculable. How do you get a human pelvis from a chimpanzee pelvis, while connecting the dots with fossils such as those from *Australopithecus*? How do you get a human social system from that of a chimpanzee?

Evidence from the *Ardipithecus* group – at present the fossils closest to the *Pan-Homo* last common ancestor – suggests that the wrong questions have been asked. None of these fossils bear an especially close resemblance to chimpanzees in major characteristics other than brain size. The postcranial elements suggest a contrasting style of locomotion, which by extension suggests differing strategies of finding food and evading predators. The dentitions and associated evidence also suggest differing foraging behavior from that of chimpanzees. And the meager, almost pathetic, canines suggest contrasting modes of association with fellow group members.

This does not lessen the importance of chimpanzees or any other animals in considerations of human origins. It merely indicates that, like all creatures, humans and their progenitors were and are unique. A holistic consideration of all evidence – from fossils, the archaeological record, many extant species, and evolutionary ecology – will be vital in ascertaining how they lived, and how the human form originated (Sayers and Lovejoy 2008; Sayers et al. 2012).

Conclusion

The *Ardipithecus* group includes those creatures most relevant to reconstructions of the *Pan-Homo* last common ancestor and earliest hominid evolution – and their fossilized remains have challenged several longstanding assumptions concerning hominid origins. Although their precise affinities to fossil and living primates are still being determined, future evidence from members of this group will undoubtedly shed further light on the human evolutionary journey.

Cross-References

- ▶ [Australopithecus Group](#)
- ▶ [Bipedal Locomotion](#)
- ▶ [Great Apes](#)
- ▶ [Orrorin tugenensis](#)
- ▶ [Paleoanthropology](#)
- ▶ [Primates](#)
- ▶ [Savanna Hypothesis, The](#)
- ▶ [Sexual Size Dimorphism](#)

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Ardipiths

► [Ardipithecus Group](#)

Arena Display

► [Lekking](#)

Argument from Nature

► [Naturalistic Fallacy, The](#)

Arguments

► Controversies

Arithmetic Mimicry

► Müllerian Mimicry

Arizona Life History Battery (ALHB)

► K-Factor (Figueredo)

Arousability

► Stress Reactivity

Arranged Marriages

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Synonyms

Parental choice; Parental mate choice

Definition

An arranged marriage occurs when the decision about whom to marry is made, entirely or in part, by people other than the spouses themselves. Generally, marriages are arranged by parents and/or other close kin (older siblings, aunts and uncles, grandparents), though marriage arrangements

may also be the purview of lineage heads, tribal elders, clan chiefs, or bureaucratic representatives of state authority.

Introduction

Arranged marriages come in a variety of forms, from those in which the spouses have no part in the decision to marry to those in which the spouses exercise full control; for the sake of clarity, this continuum can be broken into four types:

1. In the strongest form of arranged marriage, marriage decisions are controlled entirely by others, typically parents and/or other senior kin, and spouses have no say in the matter – their consent is neither requested nor needed for the legality or cultural legitimacy of the marriage.

2. More commonly, marital decisions are left to others, but the spouses themselves may have some influence over the process, through persuasion or veto power, and may be expected to state their consent as part of a marriage ritual or by signing a marriage registry.

3. The least strict form of arranged marriage occurs when marriage decisions involve a collaboration between parents (or other senior kin) and the spouses themselves; in such cases the bride or groom is simply one among several decision-makers; an alternate form is when spouses choose their own partners but their choice is subject to approval by parents or others.

4. Finally, in the absence of arranged marriage, marital decisions may be made by the spouses themselves, autonomously, without the legal or social need for reference to others – though even in societies where autonomous marriage decisions are normative, parents and friends may still have some informal influence over decisions (Buunk et al. 2008; Goode 1959). Marriages in which spouses choose each other are also referred to as “courtship marriages.” There is a correlation between courtship marriage and the privileging of love or attraction as a basis for marriage – a practice typically known as “love marriage” (Coontz 2006).

Two common misunderstandings should be dispelled here: First, *a marriage which is arranged for one partner may not always be arranged for the other partner*. For example, marriages may be arranged between the wife's parents and the husband; this is an arranged marriage from the perspective of the wife, but not from the perspective of the husband, though the use of the term "arranged marriage" will still generally be applied to the marriage as a whole. Second, *arranged marriage is not synonymous with forced marriage*, as a large fraction of arranged marriages are made with either the explicit or implicit consent of the spouses and do not involve coercion. That being said, societies that prefer arranged marriage may tolerate the coercion of spouses in some cases, especially when parents and elders view a marriage to be in the best interests of the family, lineage, or spouse. In such societies, the ability of junior family members to resist marriage decisions may be limited, yet the anthropological literature describes a number of ways in which prospective brides and grooms, even those who are young and relatively powerless, resist arranged marriages to which they are opposed. If repeated refusal will not work, they can engage in verbal arguments, refuse to participate in marriage rituals, refuse to speak or eat, run away, or even threaten to commit suicide (Apostolou 2015).

In arranging marriages, parents or elders may focus on the characteristics of the prospective spouse and/or the characteristics of their parents or families. In societies where arranged marriages are common for dynastic reasons such as family status or inheritance, family characteristics (wealth, social connections, rank, caste, title) are often more important than the personal characteristics of the spouse. In contrast, societies that allow spouses more input or autonomy in marriage decisions often give more weight to the characteristics of the spouse. In general, parents have been shown to have more interest in economic or socially important characteristics of spouses, such as family background, status, and wealth (e.g., Apostolou 2012; Buunk et al. 2008), while children have been shown to have more interest in personal and physical characteristics

of prospective spouses, such as their youth, physical attractiveness, or personality traits (e.g., Apostolou 2012; Buunk et al. 2008). From an evolutionary perspective, another way of putting this is that parents may favor spouses with high potential for investment and cooperative behavior with family members, while children may prefer traits signaling heritable fitness (Buunk et al. 2008).

The study of arranged marriage has been of interest to anthropologists and some sociologists for decades but has more recently become a focus of study in evolutionary social science. While different in emphasis, these approaches draw our attention to several key empirical and theoretical points that should be considered when contemplating the evolution and function of arranged marriage.

Arranged Marriage Is Normative in Most Preindustrial Societies

A close study of the ethnographic record makes it clear that arranged marriage is in one form or another normative in a large majority of traditional human societies (Apostolou 2007, 2010; Walker et al. 2011), meaning that *systems of arranged marriage have been far more common historically and cross-culturally than have autonomous or "love" marriages*. This is true even in most small-scale societies, including hunter-gatherers; in fact, there is good reason to believe that arranged marriage has a deep history that is central to the evolution of human social organization (see discussion below; Chapais 2008; Walker et al. 2011). The fact that autonomous marriage decisions are the exception rather than the rule suggests that there are two important questions in the study of arranged marriage. We not only need to explain (1) why human marriages are so commonly arranged, when this practice evolved, and how this fits into the evolution of human social organization and mate choice but also (2) why marriage decisions in a minority of societies are autonomous and how this relates to patterns of arranged marriage in human evolutionary history.

Arranged Marriage Is Linked to Alliance Formation and the Retention of Rank and Resources

In most societies, marriage links the kin groups of a couple economically and socially, with important consequences for the living members of both families as well as future generations. Yet in many societies, spouses, and especially women, often marry at young ages; thus, the decision about whom to marry is thought to be too important to be left to a young couple who may not have the knowledge, experience, or judgment to make the best decision about how to forge such a critical alliance. In some cases, autonomous marriage may even be seen as threatening the social order (Goode 1959). Under such circumstances, marriages are often arranged based on considerations of family compatibility with respect to the strategic resource, status, or reproductive interests of the parents or family, emphasizing such characteristics as social rank, wealth, religion, political faction, potential alliances, spousal age, perceived fecundity, or perceived likelihood of investment from one or both spouses (Apostolou 2012; Flinn and Low 1986; Trivers 1974). Compatibility of the couple may also be considered but may not be a high priority.

Arranged marriage is more common – and more strictly observed – in societies where marriage is tied to important social obligations or property transfers (Apostolou 2010, 2012; Lévi-Strauss 1949/1969; Flinn and Low 1986). In such societies, marriage is viewed partially or primarily as a contractual or practical arrangement rather than or in addition to a personal relationship; thus, personal and social expectations about marriage are often very different than in societies where marriage is organized around personal choice and/or romantic attachment. Specifically, in cultures practicing arranged marriage, marriage entails formal obligations to multiple groups of people, including one's spouse, in-laws, parents, children, lineage members, and possibly others. It is commonly claimed that personal fulfillment will come through family life, including children, supportive kin, and a respectable social position. Romantic love for one's spouse is thought of as either something that will develop after marriage

or as too unstable and risky an emotion to be the basis for the crucial social and economic decision of marriage (Coontz 2006).

Arranged Marriage Is a Mechanism of Norm Enforcement

Arranged marriage is also a primary mechanism by which marriage rules and customs are developed, perpetuated, and enforced (Apostolou 2013; Chapais 2013, 2014; Flinn and Low 1986); these include rules of exogamy (marriage outside of a socially defined group), endogamy (marriage within a socially defined group), preferential marriage norms (e.g., cross-cousin marriage), hypergyny (women marry into a higher social rank), and isogamy (women and men of equal rank marry). Rules of exogamy, for example, are generally thought to function to expand social connections to other families, lineages, or clans (Chapais 2013, 2014; Flinn and Low 1986; Lévi-Strauss 1949/1969); exogamy may also reduce competition within social groups and promote cohesion in larger social units. Endogamy, by contrast, maintains group boundaries, including those of social classes or castes; allows the retention of wealth, rights, and privileges within families or social groups; and maintains social compatibility among spouses (Flinn and Low 1986; Lévi-Strauss 1949/1969). Autonomous choice by spouses, particularly those marrying at young ages, may discount such customs in favor of personal attraction, while parents, kin, and elders may have a greater stake in the perpetuation of such norms which they perceive as serving the strategic interests of themselves and their extended family or kin group, many of whom may be affected economically or socially by marriage decisions (Coontz 2006).

Arranged Marriage Is an Evolved Practice with a Deep Evolutionary History

Humans resemble many other animals in that we form pair bonds. However, human mate choice is

not just about mating. Most human reproduction occurs within marriage and human marriages virtually always entail a complex series of cultural customs, rituals, norms, rules, restrictions, and sanctions that are culturally evolved and which serve to define the material/economic and social functions of marriage for a couple as members of kin groups and society at large. There are no clear equivalents of either marriage itself or the practice of marital arrangements among nonhuman animals (Chapais 2013, 2014; Flinn and Low 1986) making marriage both a human universal (or at least a near-universal) and also part of the argument for human uniqueness (Chapais 2008; Walker et al. 2011).

Classic evolutionary characterizations of mate choice among most species of animals – especially mammals – often emphasize the concepts of male competition and female choice, in which relatively low-investing males are seen as competing over the chance to mate with high-investing females (Trivers 1972). Though following the mammalian pattern of higher obligate investment by females (due to lengthy internal gestation and long periods of lactation), human mate choice frequently does not follow this pattern. In fact, as Apostolou (2007, 2010, 2012) and others (Buunk et al. 2008) have argued, in human societies, marriage is far more often controlled by parents or senior kin, or by husbands, and relatively infrequently by women themselves, making “female choice” – though a common assumption of evolutionary psychology models – a questionable assumption about or descriptor of human marriage behavior. In fact, “parental choice” has likely been just as important, if not more important, than female choice in human evolutionary history. Relatively unrestricted mate choice may be common in modern Western societies, but free choice of sexual or marriage partners has not been normative either historically or cross-culturally.

Arranged marriage is not just normative in preindustrial societies in general but also among modern foragers living in disparate parts of the world, suggesting that parental choice is likely to be ancient and may characterize the evolution of humans as a species (Apostolou 2007; Chapais 2008, 2013; Walker et al. 2011). In fact, a

phylogenetic analysis of marriage practices among foragers by Walker et al. (2011) suggests that arranged marriage is likely to be at least 50,000 years old. Moreover, many scholars (e.g., Chapais 2008, 2013, 2014; Coontz 2006; Lévi-Strauss 1949/1969) have made the argument that marriage evolved – or at least has as one of its primary functions – to create and/or cement alliances between families or lineages. This suggests that the practice of arranged marriage may have coevolved as a key aspect of the practice of marriage itself.

Two Evolutionary Models of Arranged Marriage

Evolutionary theorists generally view arranged marriage as a functional custom that arises as a result of past fitness benefits to parents/kin and the children for whom marriages are arranged – though the practice may be retained either because it continues to be functional or because of cultural evolutionary forces that make it difficult to change. There are two primary evolutionary perspectives on arranged marriage:

1. That parents and children have greatly overlapping fitness interests such that parental involvement in marriage decisions can be viewed as a form of parental investment beneficial for the child and the parent alike
2. That arranged marriage is a form of parental manipulation by which parents “win” a parent-offspring conflict over mate choice

As discussed above, since arranged marriages lie on a continuum from more to less coercive, these perspectives are not necessarily in opposition. Forms of arranged marriage in which children have some degree of choice or veto power, as well as situations in which children approve of and/or cooperate with parental decisions even if they were uninvolved in the process of decision-making, are more likely to represent mutually beneficial situations and/or milder forms of parental manipulation, whereas forms of arranged marriage in which parents have full power, or in which

offspring objections are ignored or overruled, are more likely to reflect parent-offspring conflict and stronger forms of parental manipulation.

Arranged Marriage as Parental Investment.

The social and genetic interests of parents and offspring overlap substantially given that they share 50% of their genes, that children represent parental fitness prospects, and that children are dependent upon parental investment for their own fitness prospects. For these reasons, both parents and children may benefit from shared decision-making about marriage, and, in fact, children may benefit more because of parents' greater social status, resource access, experience, and bargaining power. In fact, in many societies, a lack of parental participation in offspring marriage decisions may negatively affect the ability of children to obtain high-quality spouses or negotiate marriages.

Indeed, to the degree that parental interests overlap with those of their offspring, parental involvement in marriage decisions can be viewed as a form of parental investment in which parents (or other relatives) use their wealth, social rank, or alliances to improve the marital and thus reproductive prospects of children (Trivers 1972), particularly if children marry at young ages, when their own resource holdings, social rank, or negotiating powers are limited. Arranging a good marriage can directly improve reproductive prospects by enhancing the resource access and social status of the child, grandchildren, and future generations. In fact, marriage costs can be seen as a means of purchasing or securing the parental investment power of the spouse and his or her family for the benefit of grandchildren. Moreover, using one's influence or resources to arrange a good marriage for one child/relative also aids other children in the family by improving their social connections and access to wealth – indirectly improving their marriage prospects – and thus their potential long-term status, resource access, and fitness.

There is ample evidence that parental resources in the form of land, animals, household goods, houses, cash, education, and specialized skills – either transmitted through inheritance or marriage payments, or embodied in the characteristics of

the spouse – allow children to marry higher-status or wealthier partners, to marry at younger ages, or to have greater earning potential than would be the case without such investment (Boone 1986; Flinn and Low 1986; Kaplan 1996; Voland 1998). Moreover, the death of a parent before a child's marriage may have a negative effect on the status of the spouse obtained (Voland 1998). We could also predict that in societies with arranged marriage, parents will be more effective than children at obtaining high-status spouses on the marriage market and that people in arranged marriages will have higher quality spouses on average than those in love marriages, though these predictions have not been tested. Additionally, if polygyny results from mutualistic arranged marriage decisions, women in monogamous and polygynous unions should have similar levels of reproductive success, as is the case among the Kipsigis (Borgerhoff-Mulder 1990).

Arranged Marriage as Parental Manipulation of Offspring Mate Choice. Arranged marriage may also be seen as a classic example of parental manipulation of offspring mate choice in the contest of parent-offspring conflict. Though all else being equal, parents are expected to invest evenly in all of their offspring, offspring are twice as related to themselves as to their parents, siblings, or offspring, creating an inherent motivation for parent-offspring conflict and sibling rivalry over the direction and degree of parental investment (Alexander 1974; Trivers 1974). Natural selection favors both sides of this conflict – children who are able to obtain more resources from parents and parents who are able to resist such attempts at manipulation – leading to an arms race whereby neither parents nor children have a consistent evolutionary advantage (Alexander 1974; Trivers 1974). Yet in humans, more so than in other animals, parents often control resources needed by offspring to effectively survive, reproduce, and compete for mates and resources – meaning that human parents may be more consistently favored in some types of parent-offspring conflict (Alexander 1974; Apostolou 2007; Buunk et al. 2008).

Where parents have more power than children, by virtue of their age and physical size (especially

when compared to young children), their higher status in the group, or their control of wealth and privileges (Alexander 1974), parents are expected to use their influence to arrange marriages for their children to assure the strategic interests of the parents in terms of both proximate goals, such as wealth or social status, and ultimate goals, such as long-term fitness. However, in societies where children have greater economic independence or physical autonomy, they may be more effective at subverting attempts at parental control of marriage decisions and instead be able to make decisions focused on their own social and reproductive interests (Apostolou 2011). The fact that marital arrangements operate on a continuum cross-culturally from full parental control to virtually no parental control and that significant flexibility also exists within cultures by social class and gender suggests that this is an area of active strategy and negotiation strongly affected by individual and family characteristics as well as local socioecology.

Since human parents or other senior kin generally control important resources (Boone 1986; Flinn and Low 1986; Voland 1998), to the degree that reproductive decisions are related to resource access, parents are likely to use these resources to exert control, or at least influence, over the marital decisions of their children of both sexes (Apostolou 2007). Likewise, for children in many human societies, access to resources and status are highly dependent on parental resources or status, meaning that the most effective reproductive strategy may be to allow one's parents to control one's mating and marriage decisions in order to ensure continued access to or inheritance of parental resources (Apostolou 2010; Voland 1998). In contrast, securing one's own resources may allow more control over mate choice, including marriage decisions, but the benefits of such actions may not outweigh the costs.

Key Factors Affecting Who Controls Marriage Decisions

There are several cross-cultural patterns with respect to whether, how often, or for whom

marriages are arranged. These patterns are causally interrelated but separated here to highlight trends useful for predicting the likelihood or form of arranged marriage, either across societies or between individuals in different socioecological positions within societies.

Age of Marriage

Arranged marriage is more common in cultures with younger ages at marriage. A common emic rationale for this is that given their lack of life experience, young people are unable to make good choices about marriage partners, and thus parents or other senior kin need to make these decisions for them. An alternative explanation (e.g., Apostolou 2007, 2010, 2012), is that when children are married at younger ages, parents will be more effective at implementing or enforcing their own choice of spouse, since children will be economically dependent and less able, either physically or socially, to resist parental decisions.

Gender

Cross-culturally women are more likely than men to have their marriages arranged for them and are also less likely to have influence over jointly made marriage decisions (Apostolou 2007, 2010). For example, the standard cross-cultural sample suggests that courtship (autonomous) marriages are the dominant marriage form of first marriages for women in only 8.3% of forager societies but the dominant form of first marriages for men in 40% of forager societies (Apostolou 2010). This pattern strongly covaries with age at marriage (as women often marry younger than men) and the economic autonomy of the spouses (cross-culturally men are more likely than women to be economically autonomous at the time of marriage).

Evolutionary social scientists have linked this pattern to the relative reproductive value of women on the marriage market. Given the larger obligate parental investments made by women (larger gametes, gestation, lactation), female parental investment is a limiting resource among humans, such that, in most ecologies, males are expected to compete over it (Trivers 1972). Parents of daughters will thus tend to have greater

leverage in the marriage market and are expected to use this leverage to exert greater control over the reproductive choices (including the marital decisions) of daughters as compared to sons (Apostolou 2007, 2010, 2012; Perilloux et al. 2008). With much to lose should a daughter receive less than her value on the marriage market, if only by way of lost opportunities, parents are expected to attempt to preserve her value by engaging in forms of “daughter guarding” (Perilloux et al. 2008). Yet parents are still expected to control or influence the marriage decisions of sons when possible, especially in high-status families or in circumstances of high paternal investment (Apostolou 2010, 2012).

Mothers are also less likely than fathers to be involved in marriage decision-making and may have less influence than fathers when they are involved (Apostolou 2007, 2010), though this pattern is more pronounced in agricultural and/or pastoralist societies in which marriage decisions are based on property and where property is often controlled by men.

Material Wealth

Marriages are more likely to be arranged in societies or subcultures where material wealth, heritable property, or physical capital are transferred at marriage or inherited only by the heirs of legal or socially recognized marriages (Apostolou 2010; Boone 1986; Flinn and Low 1986). The wealth being transferred is typically under parental control, giving parents influence over spousal decisions. Parents have strategic interests in seeing their wealth go to their children or their children’s families; thus, they are often interested in marrying their children to high-quality spouses with good connections and use their control of the purse strings to influence or enforce marriage decisions (Apostolou 2007, 2010, 2012; Buunk et al. 2008), even in modern industrial societies where parental influence on marriage is more limited (Apostolou 2011). In general, if there are larger marriage payments (bridewealth, dowry, indirect dowry) given at the time of marriage, or larger amounts of property to be transferred by parents to heirs, we should expect greater parental control of marriage decisions.

Titles, Rights, Statuses, and Offices

Marriages are more likely to be arranged in societies or subcultures where titles, rights, statuses, or offices are transferred at marriage or inherited by spouses or children through marriage. Examples are numerous cross-culturally, including the hereditary titles of the European aristocracy which were typically inherited patrilineally but only through church-sanctioned marriages and the inheritance of Jewish ethnicity through the mother among many Orthodox and Conservative Jews.

Family Alliances

Marriages are more likely to be arranged in societies or subcultures where alliances between families are of greater economic and/or political importance. Such alliances can be either made or strengthened through marriage, and the choice of spouse will affect not just the status and opportunities of the individual getting married but also the status and opportunities of the parents, siblings, and other more distant kin (Chapais 2013, 2014; Coontz 2006; Flinn and Low 1986; Lévi-Strauss 1949/1969). A good marriage can build family wealth and connections, while a bad marriage presents a significant loss in terms of opportunity costs. The more important such alliances are to family fortunes, the more control parents are likely to exert over the marriage decisions of their children.

Economic Independence

Marriages are more likely to be arranged in societies or subcultures where children are economically dependent on their parents. Economic dependence is common among children and adolescents in most cultures and among adult children in societies where subsistence relies on access to heritable resources such as land or animals. Increasing economic independence of children, due in large part to education-based job markets and late marriage, is one reason that the transition from agrarian to market economies is often associated with reduced parental control over marriage and increased marital choice by children (Apostolou 2011). This is also one reason why marriage decisions of daughters are more likely to be controlled than those of sons, since cross-

culturally, daughters are more likely to be economically dependent as adults and are married at younger ages when most children are still economically dependent (Apostolou 2007, 2010, 2011). The colonization of new territories may also have allowed for more spousal choice because of the existence of a frontier where young people without property could obtain land and resources without parental help (Volland 1998).

Laws and Institutions

A cultural evolutionary perspective draws our attention to the presence of institutions that may impact marital decision-making. Such institutions are the result of cultural evolutionary processes in which social norms, customs, or laws evolve as a means of adaptation to the physical environment, subsistence practices, and the social environment and may subsequently serve to constrain individual decisions in line with cultural niche construction (e.g., Odling-Smee et al. 2003). In a separate line of reasoning, Chapais (2014) has argued that arranged marriage is an example of an “evoked universal” in which the unique human kinship configuration interacts with aspects of the social, technological, and physical environments to produce cultural practices such as arranged marriage under predictable circumstances.

Institutional systems may affect whether marriages are arranged as well as who has the authority to arrange marriages. In societies where kinship provides a primary means of social organization, family or lineage heads might be responsible for arranging marriages, but chiefs or maximal lineage heads might play this role instead – or at least have to approve of marriages arranged by families or lineages (e.g., Harrell 1997). Alternatively, in preindustrial state societies, the power to arrange marriages might rest with the family head but might also be held by local government officials (Gose 2000; Harrell 1997) unrelated to the individuals whose marriages they are arranging. In fact, in some preindustrial societies, the ability to arrange marriages for lineage members, coalition members, or subjects may even be seen as an attribute of good leadership (Chagnon 1967).

In contrast, traditional systems of marital arrangement may be challenged either by changes in subsistence practices which increase child autonomy and age at marriage, putting pressure on such systems from within, or increasingly by the application of international norms imported from industrialized countries, either as part of colonialism over the last several centuries or globalization in the present and recent past. Such new norms or laws may impact age at marriage, marriage payments, the transfer of marital or family property, or the form that consent to a marriage must take (Harrell 1997).

Missionaries, boarding schools, and colonial legal systems have especially eroded the authority of families to arrange marriages by:

- (a) Enforcing norms or laws allowing or prescribing that all individuals, but especially women, formally consent to marriage (e.g., Hanks and Hanks 1950; Mason 1967)
- (b) Directly undermining the rights of families to arrange marriages sometimes by substituting the authority of priests or mission schools (e.g., Hanks and Hanks 1950) but also by removing or reducing the traditional requirement for family approval
- (c) Making and enforcing norms or laws that prevent the marriage of children or adolescents (Apostolou 2013; Mason 1967), thus raising the age at marriage and putting individuals in a better position to influence their own marriage decisions.

Such changes were often made in the context of other attempts to alter indigenous marriage systems, including attempts to eradicate polygyny, polyandry, the levirate, or child marriage.

While legal changes may technically put decision power in the hands of children over parents, unless children also achieve economic or social independence of their parents, we should expect poor enforcement or uptake of such laws in places where children are more economically dependent, or where traditional dynastic considerations with respect to marriage (property, offices, alliances) still obtain.

Arranged Marriage Is Patterned by Subsistence and Social Organization

While human social behavior is highly diverse and thus any attempt at predicting practices of arranged marriage (or any other custom) cross-culturally is inherently tricky, there are broad patterns that are useful in understanding the custom of arranged marriage in evolutionary perspective as well as trends in arranged marriage in the modern world.

Arranged marriage is common among hunter-gatherers, particularly for first marriages and for women (Apostolou 2007; Harrell 1997). Apostolou (2007) reports that of 190 extant foraging groups for which sufficient ethnographic data exists, 69.9% had marriage that was primarily arranged by parents, 17.7% had marriages primarily arranged by the kin group, 8.1% had marriages arranged through courtship subject to parental approval, and only 4.3% of societies had courtship as the primary form of marital arrangement – though it should be noted that these numbers best classify the situation for women's marriages and first marriages, as men's marriages and second marriages are less likely to be arranged. Additionally, Walker et al. (2011) report 85% prevalence of arranged marriage among hunter-gatherer groups. Similar patterns also obtain in horticulturalist groups (Chagnon 1967), suggesting that these patterns may be linked to (relative) egalitarianism rather than to subsistence per se.

Arranged marriage among foragers is not related to environmental variables such as temperature or latitude (Walker et al. 2011) but does covary with several social variables. Differences in levels of gender hierarchy and/or female autonomy may help explain differences among groups (Begler 1978; Friedl 1975), with groups that are more gender egalitarian allowing for more autonomy of choice, particularly for women, as compared to groups that are more patriarchal. Societies where a greater role is played by bride service or bridewealth are also likely to have a greater degree of parental control (Walker et al. 2011). While first marriages are commonly arranged, divorce (or at least informal marital dissolution) is relatively common in small-scale

groups, and second marriages are often not arranged (Harrell 1997). Arranged marriage is also associated with a higher prevalence of polygyny (Walker et al. 2011), though this relationship is often primarily driven by the arrangement of marriages for women (Marlowe 2003).

Arranged marriage becomes more common and control by parents or elders over spousal choice stricter, in agricultural and pastoralist societies where heritable wealth in land or animals become the most important resources and are often strongly associated with marriage decisions. For example, Apostolou (2010) finds that only 7% and 0% of first marriages for women and 23.2% and 16.7% of first marriages for men are *not* arranged in agricultural and pastoralist societies, respectively. Apostolou (2010) also identifies two important trends in marriage decisions when comparing foragers to agriculturalists and pastoralists. First is increasing control of marriage decisions by men (primarily but not limited to fathers), likely due to increasing male control of the means of subsistence (land or animals). Second is the increasing control that parents have over the marriages of their sons; as parents increasingly control property use and inheritance, sons are increasingly motivated to comply with their parents' and especially their father's wishes in terms of marriage partners. In contrast, among hunter-gatherers, where there is little heritable property, a man's personal characteristics, including his foraging abilities, are a key factor in marital decisions, giving him comparatively more power over his own marriage.

Agricultural and pastoralist societies are also often stricter with respect to marriage in other ways, for example, by making divorce impossible or difficult, as was common in many large state societies in Europe and Asia in the medieval and early modern periods under Christian, Hindu, Buddhist, and Confucian leadership (as well as in their colonies in South America and elsewhere). In such societies, property transfers at marriage, such as bridewealth or dowries, generally paid by parents, also become more common and expensive, increasing both the ability of parents to control marriage decisions and their motivation to do so (Apostolou 2012; Boone 1986; Flinn and Low 1986).

Arranged marriage practices have commonly broken down as societies have undergone colonialism, industrialization, market transition, and/or other aspects of economic development (Apostolou 2011; Coontz 2006). As discussed above, this pattern has been linked to both (a) the growing economic independence of children from parents, as is true in modern industrial societies where children earn money through wage-labor jobs based on skills training and/or formal education, and (b) subsequent or concurrent changes in laws that restrict the power of parents to control the marriage decisions of children, either by reducing their power to disinherit children (as with the introduction of the Napoleonic Code), by enforcing rules of spousal consent, or by introducing laws establishing a legal age of marriage (a practice common in both the colonial period and more recently).

Cross-References

- [Bridal Cost](#)
- [Ecology of Pair-Bond Stability](#)
- [Parental Investment Theory](#)

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human body or the horns of mammals – treated as an artist's canvas (Carmen et al. 2012).

Although both of these two definitions focus on very similar *Homo sapiens* cognitive capacities, how these cognitive capacities have been created and how they then function through the production of art are conceived of in different ways across the two definitions. In the non-Darwinian account, *Homo* cognitive capacity for art is seen as being primarily of learnt origins, while in the Darwinian account, cognitive capacity for art is seen as primarily of evolutionary origins.

Art

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Definition

Art is conventionally defined as the corpus of human activities devoted to creating visual, aural, language-based, and/or performance-related artifacts and processes that express an individual's (or a group's) imaginative ideas, concepts, and/or skills and techniques, these artifacts having been designed to be consumed by an audience and enjoyed for their aesthetic beauty, emotional engagement, and/or intellectual stimulation.

A Darwinian definition of art would be a little different from this type of conventional definition of the scope of art. Art can better be defined in evolutionary terms as those artifacts that are produced by means of activities and thoughts that employ the corpus of evolved psychological mechanisms that are adaptations which have been designed to engage and fulfill a set of evolved emotional and intellectual capacities for aesthetic pleasure, technical ability, creative construction, critical engagement, expressing individual identities, and relational human experiences. These artifacts can even be specific results of biological evolution – such as the skin of the

Introduction

This entry will examine the origins and adaptive function(s) of art (including literature) conceived in its broadest terms. It will first discuss theories of the general role of art in human culture, and it will then consider four interconnected types of art as individual case-studies of how evolutionary themes are found at the center of all artistic *genres* and practices. The four interconnected *genres*/styles are: prehistoric art, erotic/pornographic art, horror narratives, and the Gothic imagination.

These particular *genres*/styles have been selected in part because the main issues related to them – sex/reproduction and the avoidance of death-by-predators – are some of the most important issues facing animal life as it has evolved on planet earth, and in part because Charles Darwin explicitly placed both erotica (“making rude pictures”) and horror (“evolved symptoms of terror”) within his evolutionary framework for understanding the origin of instincts (Darwin 1874 [1871], 577, 1999 [1872], 309).

This entry will also develop and present (in outline) a novel sexual-fantasy theory of the evolutionary origins of art. As has previously (and rightly) been explained: “in our species, love and art are, I suggest, inherently related” (Dissanayake 2010, 144). The importance of the connection between reproduction strategies and artistic expression has previously been partially acknowledged in the literature, but its significance within

the Darwinian framework has not been fully understood. Through a sexual-fantasy theory of the origin of art, the connection between art and animal reproduction will be placed at center-stage of *Homo-hominid* evolution.

The Adaptive Function(s) of Art

It is common in the literature on the link between art and evolution to debate the various possible adaptive functions of art in relation to its evolutionary origins, such as the by-product theory, the exaptation theory, Darwin's own sexual selection or display theory, the social cohesion theory, and the cognitive development theory.

In the by-product theory, art is not itself seen as an adaptation but as a by-product of the evolution of other cognitive adaptations such as language. Related to this is the exaptation theory in which art evolved initially for one reason, say in conformity with the sexual selection theory, but then evolved to fulfill other adaptive functions over time.

In Darwin's sexual selection or display theory, artistic practices have developed as adaptations that assisted individuals in creating display ornamentation that facilitated success in reproduction (Darwin 1874 [1871], 573–577). In the social cohesion theory, art has developed in order to help facilitate shared attention and thereby strengthen the coordination of social activities among the group. In the cognitive development theory, art functions as a means by which individuals can develop and rehearse social interactions that in turn aid cognitive development (Boyd 2005). The specific adaptive functions of both pornographic art and horror narratives that will later be advanced in this entry fit partly within the cognitive development theory.

Also, it is important to stress that art is not just the physical objects conventionally understood to be art products alone, it is also the practices and behaviors associated with making, viewing, using, and interacting with these art objects in their totality (Boyd 2005, 162). Thus, both art objects themselves and artistic practices and behaviors have been subject to significant long-term evolutionary pressures.

Prehistoric/Erotic Art

It is currently the conventional wisdom that art as a general *Homo-hominid* activity originated sometime between 60,000 and 30,000 years ago (Mithen 1996, 176–178). Although one or two items possibly older than this have been discovered (Levinson 2002, 72), there is a clear clustering of a range of art objects that have been found at this later date-range.

The discovery of various ancient human-made artifacts with graphic sexual content has raised the question of whether they can accurately be described as prehistoric erotica or pornographic art. For example, a 28,000-year-old dildo, 28,000-year-old erotic Aboriginal rock art, the 25,000 year-old Venus of Willendorf, ancient Greek and Roman pottery decorated with nude figures engaged in sex acts, and the Turin erotic papyrus dated from 1150 BC, all clearly either relate to or depict various forms of sexual activity, and some commentators have consequently described these artifacts as the earliest known forms of pornographic art (Anon 2013; Taylor 1996, 120–123). Without further evidence showing precisely how they were used, it is not possible to decide whether they were meant to be used as pornography or not, although the possibility that they were remains (Miller 2010, 160).

Collating these examples of prehistoric erotica with the previously given date-range for the origins of art, this means that pornographic art could have originated alongside the earliest forms of *Homo-hominid* art. Further circumstantial evidence for this is that in contemporary foraging cultures, “young men make charcoal drawings of breasts and vulvas on rock overhangs, carve them on tree trunks, and scratch them in the sand” (Pinker 1999, 472).

It is certainly true that sex, fertility, and reproduction were very common themes of much of ancient art (Levinson 2002, 72). As has been explained:

Prehistoric art, much of which has explicit sexual content, obviously depicts the things that people thought about, but it may not fairly reflect what they actually did. A Stone Age rock engraving made in eastern Siberia . . . depicts a man on skis, attempting to sexually penetrate an elk. (Taylor 1996, 12)

Again, due to the lack of evidence about how it was designed to be used, it is unknown whether this image was meant literally or symbolically. It could have been designed to celebrate the pleasures of having sex with animals (literally), or it could equally have been meant to show how all animal species are one whole within nature (symbolically).

It is more certain that Chinese pillow books (starting around 200 BC) had functions analogous to that of some contemporary pornography, these being pragmatic manuals on how to have sex in a variety of different ways (Hart 2001, 40). However, the term “pornography” did not come into use in English until 1857, being derived from Greek terms relating to the description of the activities of prostitutes. In between the birth of *Homo*-hominid art in prehistoric times and the mid-nineteenth century, it seems reasonable to assume that both written descriptions and images of sexual activity designed for use as pornography were created and have existed for some considerable period of time. This means in turn that pornography is not a modern invention and has evolved over a significant period of time.

A Sexual-Fantasy Theory of the Evolutionary Origins of Art

Even if the sexual imagery created by hominids 30,000 years ago was not initially designed as erotica or pornographic art, pornography certainly evolved from this type of imagery and hence it is an evolution from the naturalistic portraits of human figures that had begun in ancient art. This is not evolution in the Darwinian sense but the function that pornography could fulfill might conceivably be (or become) adaptive.

This issue of whether pornographic art could be adaptive in the Darwinian sense is further complicated by the fact that sexual behavior has evolved over a long period of time. For example, it has been suggested that the birth of language was linked to the evolution of the imagination. Out of the imagination then evolved poetry and the sharing of fantasies, which in turn affected sexual behavior by facilitating mutual empathy

and contemplation in relation to heightening the pleasures of sex (Taylor 1996, 50–51).

The creation of imaginary universes is, it has been claimed, unique to human beings (Carroll 2007, 640). Darwin was aware of this suggestion and posited that the faculty of the imagination had been “of inestimable service to man for his progressive advancement” and linked it to wonder, curiosity, and “an undefined sense of beauty” (Darwin 1874 [1871], 93). He described it as follows: “The *Imagination* is one of the highest prerogatives of man. By this faculty he unites former images and ideas . . . and thus creates brilliant and novel results” (Ibid. 74). In Darwin’s theory, the aesthetic senses of both animals and human beings had evolved partly through processes of sexual selection, as the ability to evaluate the display ornaments of the opposite sex (inter-sexual selection: usually but not always female choice) was crucial to reproductive success.

A novel sexual-fantasy theory of the evolutionary origins of art could be constructed along lines that are extrapolated from this set of ideas. Dating the origins of the evolution of language is controversial, but as the latest date suggested in the literature is around 50,000 years ago, it seems likely that some form of language had evolved by the time that the ancient erotic art objects considered here were created (Buss 2004, 383). It has correspondingly been suggested that:

... [the development of] language was responsible for the considerable cultural differentiation observed in Africa in the period 100,000 to 50,000 years ago. The development of art to incredible levels of sophistication is typical of behaviorally modern humans in the last 40,000 years. (Cavalli-Sforza 2002, E47)

The evolution of language, therefore, predated the evolution of sophisticated art and it is a plausible hypothesis to suggest that the former may have been linked to the evolution of the latter.

A sexual-fantasy theory of the origins of art could be developed in relation to the evolution of language and then art as a result of sexual selection processes as follows. As has been outlined, a number of changes in the sexual behavior of the *Homo* lineage developed as co-adaptations related

to an increased tendency to form long-term bonds between mates:

To aid in bond maintenance sexual activity is enhanced through sexual selection. Improved bonds provide security for children and hence a greater contribution to later generations from the effective bond formers. Women cease to show estrus and are sexually responsive more or less continuously. Coition becomes very frequent and highly rewarding. (Crook 1972, 249)

Together with these behavioral changes, physical changes in *Homo*-hominids occurred that enabled this more rewarding sex, such as a reduction in body hair and the evolution of a relatively large penis compared to other primates, these being similarly enhanced through sexual selection pressures.

In parallel with these changes in *Homo* behavior and physical form, after language had first evolved and in line with the evolution of the brain that facilitated this development, the cognitive ability of humans to imagine, fantasize, and communicate about sexual activity greatly increased at this time. With the evolution of artistic expression that followed on from this, involving the bringing together of pre-existing modules of mental cognition to create a more general form of imaginative intelligence, both sexual and non-sexual themes were then explored as art in various visual media such as wood/stone carvings and cave paintings, and in various forms of narrative such as songs and poems.

The evolution of the human capacity for imagination and fantasy was also linked to the ability of humans to use art objects in various different functional capacities, including (potentially) as pornographic art. As has been explained, human beings exhibit a “huge repertoire of mental imagery and sensual feeling” for use in their erotic experiences (Dutton 2009, 100). Darwin allocated a special courtship function to song and he implied that poetry and thereby art had initially developed from this type of courtship display (Darwin 1874 [1871], 567, 570–572). The sexual-fantasy theory of the origins of art is consistent with the archeological record, as much prehistoric art has sexual themes, but it is not conclusively proved by it. It also fits with a previously articulated suggestion that the human

orgasm is a vividly aesthetic experience (Comfort 1961, 105, 111–112).

Moreover, prehistoric art with sexual themes is not exclusively male-orientated, as ancient phallic batons have been found that look very similar to modern dildos (Taylor 1996, 128). Female sexuality was, therefore, expressed in erotic art from its very beginnings. As has been explained about the wider significance of female eroticism:

We must not believe that sexuality and the erotic for primitives were limited solely to the experiences of intercourse and orgasm. In practice sexuality, and especially female sexuality, is functionally expressed in pregnancy, birth and suckling no less than in intercourse . . . the female sees sexuality and the erotic as embracing a far wider functional spectrum. (Rawson 1973, 5–6)

It is also significant that the loss of body hair as early hominids evolved into modern human beings acted to facilitate the decorative adornment of the body (Taylor 1996, 98), the latter being a key part of the sexual selection theory of the origins of art.

It would be possible to combine the sexual-fantasy and the sexual selection theories of the origin of art into a single approach, which would hypothesize that both sexual fantasies and sexual enhancements partly found expression in the evolution of the decorative adornment that is central to the sexual selection theory of evolution.

The Adaptive Function(s) of Narrative Art

Another key evolutionary development for *Homo sapiens* art was the development of behavioral adaptations to assist in predator avoidance. In the Pleistocene environment of evolutionary adaptedness (EEA), violent threats to human life came from two main sources: attacks by animal predators (e.g., lions, tigers, bears) and by other human competitors (either in-group or out-group). Consequently, predator avoidance was a key skill that was required for survival (Tooby and Cosmides 2001, 15; Barnett 2018a).

It has consequently been hypothesized that a specific mental module or dedicated neural

network evolved to deal with predator avoidance issues that today can be detected in children as young as 3 years old (Buss 2004, 94). This anti-predator defense system has cognitive, auditory, olfactory, and visual components designed to detect specific aspects of predator behavior. The visual component is especially important, as detecting predator movements was a key defensive ability (Barrett 2005, 205), that was linked to the attention-summoning component of the emotions of horror and terror (Tooby and Cosmides 2001, 18). The emotions of terror and horror have, therefore, evolved in direct response to the threats to human life that were represented by animal predators and human competitors.

Horror narratives/art – or the predator-prey interaction *genre* – has an enduring popularity because its evolutionary equivalents rehearsed scenarios of extreme threat and danger from predators that were much more prevalent among our evolutionary ancestors than they are today. The fact that horror narratives operate most effectively using visualized modes of storytelling is not, therefore, a coincidence (Barnett 2014).

However, if individuals waited until they were actually under attack before they thought about how to escape such predator threats, then their chances of survival were less than if they had previously rehearsed such scenarios in a safe environment, and understood strategies that could be used to escape from such encounters alive. Becoming familiar with the strong emotions evoked by murderous assault in a relatively safe environment is another function of predator narratives, so that such emotions do not become overwhelming when they are experienced in real-life situations, as is the further development of relevant brain circuitry (Tooby and Cosmides 2001, 16).

The oral re-telling of “campfire” tales of predator attacks or deadly inter-human conflict was one effective means by which knowledge of previous incidents could be transmitted from individual to individual and also across the generations (Sugiyama 2006, 328–329). Early forms of visual art such as cave paintings and ivory, bone and stone carvings may have served a similar function

(Bahn 1992, 361), enabling the visual recording of information about animal movements and behavior both figuratively and symbolically (Mithen 1996, 196). Also, related story narratives such as forager oral traditions contained information about hunting, gathering, and their associated localized dangers.

The more detail about past predator attacks that was conveyed in such narratives – how exactly did the lion attack and what where the nature of the injuries that it inflicted? – then the better this would be for understanding how such attacks could be avoided in the future. As a basic tenet of predator-prey interaction is that the strategies of both sides continually evolve in mutual antagonistic interaction, new narratives providing updated information on the latest developments in strategy and tactics are always required.

However, although the basic reality of predator danger was an evolutionary constant that was experienced by all humans in the EEA, the specific predators that early humans faced varied considerably in relation to their geographical location. Therefore, the folk-fiction of each region provided stories of the animals that were common to that area, and sometimes embellished the animal behavior with supernatural traits:

In tropic[al] countries we have stories of supernatural snakes, who appear in various forms, as were-snakes ... We also see in the tropics elephants, lions, tigers, baboons, gorillas, and so forth ... while in colder climes we have the fox, the wolf, the bear, and their confreres. In island countries we find a large element of the supernatural associated with fishes and sea-animals ... (Scarborough 1967 [1917], 233–234)

Consequently there is a direct correspondence between the dangerous animals found in local literatures and those found in local environments (Sugiyama 2006, 328).

The Evolution of Gothic Art

It has been suggested that the origins of eighteenth-century Gothic literature involved the rediscovery of old folktales and oral traditions that had survived through nonliterary forms of

propagation (Scarborough 1967 [1917], 6–7). The interpretation presented here requires that these folktales, for example, about the dangers of predators and the animal side of human nature, were subconsciously transformed as needed by those in the eighteenth century involved in fashioning the Gothic movement.

Gothic fiction was thus in part a re-imagining of much earlier – what were described by its creators as “medieval” – folk-representations of predator and other natural dangers. This link to the EEA was explicitly recognized by early writers on Gothic fiction: “When well conducted, a grateful astonishment, a welcome sensation of fear, will alike creep through the bosom of the Sage and the Savage” (Drake 1800, 141). Predator dangers were also recognized: “There are many animals . . . considered as objects of terror. As serpents and poisonous animals of almost all kinds” (Burke 1792 [1757], 120).

The Gothic imagination can thus be identified with certain key themes: an interest in nature, both real and imaginary; a concern for the medieval/EEA past environment; a preoccupation with the consequences of marriage; the unleashing of dangerous animal passions; and an interest in the supernatural generation of terror. Most of these themes have direct Darwinian translations.

As well as providing the physical environment for much of the drama portrayed in the Gothic novel, the commonly employed imposing architectural edifice of the castle provided a key metaphor employed in Gothic literature. The castle became a symbol of a noble family lineage and its contemporary problems, either personal, familial, or in wider social terms, e.g., as in *The Castle of Otranto* (1764) and *The Castles of Athlin and Dunbayne* (1789). The architectural edifice of the castle was therefore a metaphor for ancient family heritage and the history of a family clan. It is also no accident that the Gothic novel is sometimes labeled the Gothic romance: if the setting is often a castle, then the narrative often relates to matters of mating/sex.

Another early writer on this topic linked the Gothic imagination to the natural environment/EEA of what she called “the Celtic nations”:

Climate, temper, modes of life, and institutions of government, seem all to have conspired to make the superstitions of the Celtic nations melancholy and terrible . . . the genius of the mountain, the spirit of the floods, the oak endured with sacred prophecy, made men walk abroad with a fearful apprehension . . . On the mountains, and in the woods, stalked the angry spectre . . . (Montagu 2000 [1769], 36)

In the Gothic tradition, the natural environment/EEA was a key source of potential danger, with nature sometimes being seen as animated by powerful supernatural forces, this being a central feature of ancient and medieval superstitions.

This emphasis on environmental dangers links the Gothic imagination directly to the evolutionary function of horror narratives as was considered in the previous section. In the Gothic novel, “there is a decided and definite attempt to use the terrible forces of nature to reflect the dark passions of man” (Scarborough 1967 [1917], 13), indicating that predators can be human as well as nonhuman.

Moreover, the psychological origins of Gothic romance have been laid firmly in a long-previous period in which supernatural beliefs were much more prevalent than they are today, when people were more given to the telling of “all the folk-tales of terror than at the present time,” even though “the idea of the inter-relations of the passions of man and nature is not original with the Gothicism” (Ibid.). The birth of eighteenth-century Gothic literature was thus dependent on much older forms of storytelling and the link between the evolution of human nature and the natural world of the EEA, a conception which produced Dorothy Scarborough’s definition of Gothic literature as the eighteenth-century novel of terror that deals with medieval materials.

The poet Samuel Taylor Coleridge wrote two lectures in 1818 on “The Gothic Mind,” in which he connected the aesthetic concerns of the Gothic imagination with the geographical origins of the Goths as a people, declaring that:

. . . Gothic art is sublime. On entering a cathedral, I am filled with devotion and awe . . . The Goths . . . Gazing on their rugged mountains, surrounded by impassable forests, accustomed to gloomy seasons, they lived in the bosom of nature . . . the dark wild imagery of nature, which surrounded him, and the freedom of his life, give his mind a tendency to the infinite . . . (Coleridge 2000 [1818], 96–97)

Here is described a type of interaction with the EEA that is suggested by Darwin's theory of evolution by means of natural selection applied to mental architecture, i.e., contemporary evolutionary psychology.

Conclusion

This entry has attempted to locate sex/reproduction and the avoidance of death-by-predators as two of the most important issues of human life that have driven the evolution of those psychological mechanisms that are focused on artistic expression, and the related artistic activities that are generated by the relevant cognitive architecture of *Homo sapiens*. A novel sexual-fantasy theory of the evolutionary origins of art was also presented in outline, although this sexual-fantasy theory is speculative to a degree and cannot be proved beyond any doubt in a short encyclopedia entry on the wide-ranging topic of art in general. Three other short case-studies of prehistoric art, horror narratives, and the Gothic imagination were also presented as a means of linking the two key art-focused themes of sex and death-by-predators together.

It is certainly the case that erotica/pornography and horror are the two most controversial *genres* out of the very wide range of *Homo sapiens* art and literature. This is probably because they are – arguably – two of the most important, socially valuable, culturally influential, and aesthetically stimulating *genres* (Barnett 2017, 2018b). In fact, a case could be made that, actually, all artistic content produced by *Homo sapiens* falls broadly within these two *genres* widely conceived, with the inclusion of some significant content focused either on sex/reproduction (erotica/pornography) or death-by-[animal/human]-predators (horror) in all art. However, this broad categorization of all art content might prove a little controversial for a few commentators.

Pornography is conventionally defined as a work specifically designed to evoke a sexual response in the viewer, but it seems implausible to suggest that so-called nonpornographic imagery depicting clothed women and men is not similarly sexually stimulating: evolution has designed the human physique (and certain forms

of human interaction) to be arousing in any and all of their various presentations. So-called non-pornographic imagery of two clothed individuals who are interacting in sexual activity can be just as deliberately arousing as so-called pornographic (or nude) imagery of the same subject-matter, so the “deliberately sexualized imagery” definition of porn is not particularly precise.

The fact that erotica/pornography and horror currently constitute the least worthy and respected *genres* among most art and literary critics and are also regarded by these same critics – with a few notable exceptions, e.g., Comfort 1961 (on erotica) and Clasen 2012 (on horror) – as the least artistically significant *genres*, illustrates how lacking in understanding these critics are of Darwin's work and its direct consequences for understanding the evolution of all human behavior, including all artistic behavior.

Cross-References

- Art Production, Appreciation, and Fitness
- Cultural Evolution
- Fiction
- Human Visual Neurobiology
- Music
- Music and Hormones
- Play
- Pornography and Women's Short-Term Mating
- Sexual Selection

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Art Production, Appreciation, and Fitness

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Synonyms

[Aesthetic display](#); [Art](#); [Creative expression](#); [Cultural display](#); [Symbolic behavior](#)

Definition

“Line, color, pattern, and/or form used by humans to modify an object/body solely to attract attention to that object/body” (Coe 2003, p. 173).

Introduction

Although there are hints of earlier art activity (Malotki and Dissanayake 2018), the oldest, uncontentious evidence of art behavior

consists of shell beads and engraved ochre dated to roughly 75 ka (Henshilwood et al. 2002). This tells us that art behaviors emerged in a hunting-and-gathering context and thus are not an outgrowth of conditions associated with “civilization” – agriculture, permanent settlements, high population densities, social stratification, personal wealth, and economic specialization. Their presence in forager societies makes these species-typical behaviors (Brown 1991) particularly puzzling, because they impose considerable time and energy costs yet appear to yield no fitness benefits. Consequently, opinion is divided over whether these activities are adaptations or by-products: one camp explores their possible adaptive functions (e.g., Miller 1999; Coe 2003; Hagen and Bryant 2003; Malotki and Dissanayake 2018) and another explains their emergence in terms of the preexisting cognitive capacities they co-opt (e.g., Pinker 1997; Verpooten and Nelissen 2010). Resolution of this debate requires precise ethological parsing of the phenomena in question. Although often referred to collectively as “the arts,” different art forms recruit different cognitive and motor capacities. For example, the capacities involved in painting (e.g., using the hands to apply pigment to a surface in the form of patterned marks and shapes) are very different from those involved in dance (e.g., making repetitive, rhythmic movements with various parts of the body). This suggests that “the arts” are not a unitary phenomenon and may not share the same evolutionary trajectory. Moreover, modern societies tend to assign these behaviors to different categories (e.g., visual arts, plastic arts, temporal arts), which appear to be based on the chief sensory mode through which they are affected: vision (painting/drawing), touch (sculpture), hearing (music), and kinesthesia (dance). Because each of these behaviors prioritizes a different sensory mode, it is unlikely that all are generated by the same set of procedural rules. Yet the fact that these behaviors are aimed at the senses, perceived as belonging to the same ethological category, and often deployed ensemble suggests underlying similarities in structure or usage.

Identifying these congruencies is critical to resolving the question of adaptation.

Ethology, Ecology, and Adaptation

Cross-culturally, art behaviors and/or their outputs (i.e., objects, performances) share several characteristics. The most obvious is that they arouse attention and emotion, and are the product of agency. Although rudimentary, this observation enables us to rule out phenomena that are aesthetically arousing but not produced by agents, such as sunsets and rainbows. It also points to the manipulative nature of these behaviors: they consist of actions performed to provoke aesthetic emotional arousal (e.g., pleasure, excitement, joy, awe, curiosity). This distinction is readily apparent in modern market economies, in which millions of individuals regularly consume products (e.g., music, fashion, décor) engineered to elicit aesthetic responses, and other individuals specialize in the design, manufacture, and/or delivery of these products (Pinker 1997). Thus, art behavior can be characterized as aesthetic behavior, and parsed into (a) the aesthetic responses elicited and (b) the actions that elicit these responses. The former includes art appreciation, and the latter includes art production/performance.

Aesthetic behavior is not unique to humans: many species engage in aesthetic displays, typically in the context of courtship or territory defense. As in humans, these displays can be multimedia events, involving movement, sound, and/or visuals (e.g., male cichlids vibrate their body when displaying their egg spots to females), and some species (e.g., bower birds, puffer fish) even produce aesthetic artifacts. These behaviors appear to be aimed at eliciting aesthetic responses via one or more sensory channels. In some species, aesthetic displays are generated primarily by males, but in others both sexes participate. For example, courting pairs of red-crowned cranes (*Grus japonensis*) engage in coordinated interactive displays that resemble pair dancing in humans, and courting/mated pairs in many bird and several gibbon species engage in duetting

(Fitch 2006). These characteristics suggest that human art behaviors are analogous to signals, animal traits designed to influence the behavior of other agents via their sense organs (Krebs and Dawkins 1984). For example, Verpooten and Nelissen (2010) argue that two- and three-dimensional iconic representations are analogous to mimics, signals that exploit existing sensory biases by simulating cues to which the bias is sensitive. Just as egg spots in male cichlid fish simulate female eggs, they argue, figurative art simulates real-world entities such as animals and landscapes.

Many human art behaviors appear to operate in a similar manner, simulating environmental stimuli that recurrently impacted human fitness and to which humans have evolved sensory (a.k.a. perceptual) biases (Eibl-Eibesfeldt 1988). These biases serve to direct attention and motivate fitness-promoting responses to potentially beneficial or hazardous entities in the environment (e.g., water, predators, mates), the effect of which is to make some stimuli in our environment more attention-getting and emotionally arousing than others. Perceptual biases also help us make sense of the chaos of sights, sounds, textures, and scents in the world around us. For example, humans find it easier to detect a dark figure against a light background than vice versa. This bias reflects a regular feature of the environment, where figures are often silhouetted against the brightness of the sky. Another bias is contrast, used to detect the edges of objects and topographical features, which is critical to identifying objects by shape and navigating the landscape. The human visual system is also biased toward pattern; since many animals have spotted or striped bodies, this bias is useful for detecting both predators and prey. Another important bias is the *peak shift effect*, whereby an exaggerated form of a preferred stimulus is found more attention-getting and arousing than its normal form (Ramachandran and Hirstein 1999). This effect is likely at play in the bright, saturated colors used in fashion and marketing, the amplified movements and postures used in dance, and the intensified acoustics (e.g., timbre, volume, rhythm) used in music.

Our visual system also attends preferentially to symmetry, which is an important cue of agency (Zoeller et al. 2018) and mate quality (Sugiyama 2016). This may account, in part, for the popularity of the human form in visual art, and its foregrounding in dance. Other stimuli mimicked by dance are self-propelled movement (another important cue of agency) and speed and direction of movement (critical to predator–prey discrimination; Barrett 2005). Eyes, too, are an important cue of agency, and eye direction (like motion) is an important source of information about intentional state, especially in the context of predator evasion (Barrett 2005). Across species, a direct gaze is widely interpreted as a threat, which may explain the cross-cultural prevalence of bulging, staring eyes in representations aimed at warding off evil (Eibl-Eibesfeldt 1988).

Humans also exhibit landscape preferences, which are hypothesized to aid in habitat selection and navigation (Orians and Heerwagen 1992). By directing attention to cues of habitat quality (e.g., routes, resources, hazards) and triggering aesthetic responses, these biases are believed to help guide decisions about when to move, where to settle, and what activities to pursue in a given locale. For example, research indicates that humans prefer environments that have water, large trees, a focal point, changes in elevation, semi-open space, even ground cover, distant views to the horizon, and repeated patterns. Many of these features facilitate scanning, interpretation, and navigation of the landscape; others are cues to the presence of plants, game, and predators. These cues and biases can be exploited in painting, photography, film, architecture, and interior design to attract attention and trigger affective responses. This may explain why landscapes are such a popular subject in many Western and Asian art traditions. Although this genre is absent in forager populations, weather, seasonal, and navigational cues (e.g., stars, moon, rainbow, lightning) are frequently depicted in their art and myth cross-culturally. For example, abstract representations of topographical features and routes (painted on bodies, artifacts, and rock faces) feature prominently in Aboriginal ritual (Mountford and Tonkinson 1969), and tales that

describe landmarks, topographical features, and travel routes are common across forager oral tradition (Scalise Sugiyama 2017). This emphasis on cues rather than holistic representations of the landscape may reflect forager information-gathering techniques; for example, Ju/wa men view their environment “not as scenery ... but as a series of small, very distinct messages—a freshly broken twig, flattened grass without dew where an animal was resting, the footprints of a certain kind of beetle” (Thomas 2006, p. 179).

Acoustic biases related to language processing (e.g., rhythm, intonation) may also figure in art behavior (Eibl-Eibesfeldt 1988). These biases are exploited in verbal art (poetry, oral storytelling; Scalise Sugiyama 2017) and are likely to play in music and dance (Eibl-Eibesfeldt 1988). All of these art forms are characterized by rhythm which, depending on the tempo, can accelerate or decelerate breathing, and tends to synchronize behavior and coordinate action in groups. Melody, too, affects breathing. Lullabies, for example, slow listeners’ heart rate and make breathing more flat and regular; inhalation coincides with the rise of the melody and expiration coincides with the descent. Not surprisingly, jazz has opposite emotional and physiological effects.

In short, although perceptual biases did not evolve for art production or appreciation, they play an important role in these behaviors because they influence what we find attention-getting and emotionally arousing. Given that there is no evidence of a neural network dedicated to aesthetic sensation, emotion, or meaning (Chatterjee 2014, p. 28), perceptual biases are the most likely source of the emotional responses evoked by aesthetic artifacts and performances. Consciously or unconsciously, artists can use these biases to grab our attention and engage our emotions. On this view, art behaviors stem from the ability “to manipulate the mechanisms which underlie our perceptual bias to trigger aesthetic experiences” (Eibl-Eibesfeldt 1988, p. 33). Even though (unlike female cichlids) humans can distinguish between the real thing and a representation of that thing, the representation nevertheless engages us because it mimics

features that our perceptual systems are designed to notice and respond to. In terms of their emotional effects, then, animal signaling and art behavior appear to be analogous.

This leaves the question of whether, like animal signals, art behaviors are evolved traits. In nonhuman animals, signaling behaviors typically evolve from already existing movements that originally had no signaling function. For example, many signaling behaviors in birds can be traced back to preening, feather-settling, and temperature-regulating movements or movements that prepare for flight (Krebs and Dawkins 1984). Through this process, known as *ritualization*, the structure or behavior pattern acquires a new, signaling function. Signals can also evolve from existing signals that originally evolved for a different communicative function. For example, the crouching movement used in courtship by females of several songbird species appears to derive from the food-begging crouch of juveniles. In the course of ritualization, a trait may become modified in ways that increase its effectiveness as a signal – for example, it may become highly repetitive, exaggerated in amplitude, or stereotyped in pattern. This process may be driven, in part, by the peak shift effect, with more exaggerated forms of the signal outcompeting less pronounced forms.

Several researchers have noted that art behaviors exhibit ritualization—that “what the artist tries to do (either consciously or unconsciously) is to not only capture the essence of something but also to amplify it in order to more powerfully activate the same neural mechanisms that would be activated by the original object” (Ramachandran and Hirstein 1999, p. 17). Some see this tendency as evidence of adaptation. Dissanayake, for example, argues that the temporal arts (e.g., music, song, poetry, and storytelling) evolved from infant-directed speech, which is characterized by higher pitch, exaggerated pitch excursions, broader pitch and amplitude variation, slower speed, longer pauses, and increased repetition (Malotki and Dissanayake 2018). Certain aspects of infant-directed demonstration – e.g., greater interactiveness and range of motion, repetitiveness, and exaggerated facial

expressions and body movements (Brand and Shallcross 2008) – also appear to be at play in art behavior (Eibl-Eibesfeldt 1988; Scalise Sugiyama 2017). Miller, in contrast, sees these properties as evidence that art and other cultural behaviors evolved as courtship displays, on the logic that “comparison between courtship displays is easier if the displays share many elements in common so deviations indicating inferior production ability can be easily noticed” (1999, p. 78).

These claims are complicated by the fact that teaching also exhibits these properties. Csibra and Gergely (2009) show that the transmission of generalizable knowledge is characterized by the use of ostensive-communicative behaviors, or *natural pedagogy*. These behaviors are hypothesized to be signals that communicate (a) intent to transmit generalizable knowledge and (b) the intended recipient of that knowledge. Significantly, ostensive communication is highly ritualized, exhibiting marked use of repetition, pattern-with-variation, exaggeration, and interactiveness. This behavior is present in other species as well. For example, humpback whale song features “consistent repetition of certain units at the beginning or end of phrases [that] might represent a form of ‘rhyme’ that enables easier recall, paralleling a function of rhyme in traditional human oral traditions” (Fitch 2006, p. 192). This research is consistent with the hypothesis that art behaviors are signaling behaviors and leaves open the possibility that they are adaptations, but does not shed light on what (if any) their adaptive functions are. The use of exaggeration and repetition appears to be characteristic of signaling in general; it is not limited to art behavior, infant-directed speech/demonstration, teaching, or even to humans.

Csibra and Gergely’s research suggests the intriguing possibility that art behaviors are subsets of teaching behavior. This is consistent with evidence that art behaviors transmit generalizable knowledge (Marshack 1972; Mithen and Mithen 1990; Scalise Sugiyama 2017). Nor does it preclude the possibility of their being co-opted for other purposes, such as advertising mate or

coalition quality (Miller 1999; Hagen and Bryant 2003), promoting intragroup or intergroup cooperation (Jochim 1983; communicating ethnic identity (Pardoe 1995), Coe 2003; Malotki and Dissanayake 2018), or demarcating/defending territory (Parkman 1986; Hagen and Hammerstein 2009). Whatever their evolutionary trajectory, the forager ethnographic record shows that art behaviors are used for diverse purposes and that none appears to be dedicated to a single function. For example, body decoration (e.g., hair style, tattoos, jewelry) is used to establish cooperative relationships (Marshall 1976), initiate warriors (Mendoza 2007), celebrate victory in battle (Owsley et al. 2007), ward off evil or bring good luck (Bogoras 1904–1909; Mendoza 2007), mark social status (Ray 1938), enhance attractiveness (Bogoras 1904–1909; Chagnon 1997), and advertise hunting or fighting prowess (Bogoras 1904–1909). Similarly, music and/or dance are used in a range of contexts, including healing (Lee 1984), shamanism (Chagnon 1997), alliance formation (Chagnon 1997; Hagen and Bryant 2003), warfare (Mendoza 2007), hunting (Turnbull 1983), conflict resolution (Rasmussen 1929; Marshall 1976), and status competition (Rasmussen 1929). Parietal and portable art (e.g., painting, petroglyphs, cupules, decorated artifacts) are used in the performance of rituals (Mountford and Tonkinson 1969; Parkman 1986), to mark resource locations and territorial boundaries (Parkman 1986), and to assert patrimony and associated rights (Barbeau 1929).

The use of art behaviors for so many different purposes challenges the claim that any or all of them are adaptations, and makes it difficult to determine which application came first. However, it also points to a characteristic that distinguishes human aesthetic display from that of other animals: nonhuman species do not appear to invent novel aesthetic performances or products. Most are limited to one stereotyped form of aesthetic output. For example, bower birds decorate their nests, but individuals within a given species decorate their nests in essentially the same way (e.g., with blue objects). Animals in the wild produce neither the range nor the volume of aesthetic artifacts that humans do. The variety of

human aesthetic output begs the question of how a single mechanism or module could generate such a wide range of behaviors, and suggests that they are most parsimoniously explained as inventions, not adaptations.

This explanation accords with one of the most distinctive characteristics of our species: the ability to innovate. Lacking the keen senses and anatomical advantages that other animals possess, humans depend for their survival on *improvisational intelligence*, a highly developed capacity for inventing new ways of doing things (Barrett et al. 2007). This ability enables humans to invent solutions to problems as they arise, as well as solutions for storing and sharing this knowledge. It also enables them to devise means of deploying information tactically, in order to manipulate the mental states and behavior of conspecifics. The latter ability casts the social nature of aesthetic display in a Machiavellian light: the visual, plastic, and temporal arts may be cultural inventions arising from a motivation to influence conspecifics in ways that advance the fitness interests of the producer/performer. In short, whereas the aesthetic repertoire of non-human species is limited to evolved display behaviors, humans can invent new types of aesthetic display and new applications for them. In the course of experimenting with line, color, sound, movement, etc., our ancestors would have discovered the attentional and emotional effects produced through exaggeration, repetition, and figurative representation; discovery of the social applications of these effects would have followed shortly.

Their Machiavellian applications can explain not only the diversity of forms and contexts in which art behaviors occur, but the demographic patterns they exhibit. With the exception of infants, humans of all age and sex categories engage in these behaviors, which is what we would expect from a species that depends on invention, cooperation, and manipulation of conspecifics to meet the problems posed by its environment. At virtually all points in the lifespan, humans can increase their fitness by devising new ways of influencing the behavior of others. Under

such conditions, selection will favor motivational mechanisms that encourage and reward curiosity, exploration, and experimentation across the lifespan. On this view, art behaviors can be seen as a form of play (Malotki and Dissanayake 2018). The emotional rewards of play encourage organisms to explore and experiment in ways that advance development of capacities needed later in the lifespan (Tooby and Cosmides 2001). An example is subsong, which occurs during the juvenile period in birds with vocal learning. Characterized by “random, muted warblings of greater duration than ordinary song” (Ficken 1977, p. 579), in some species this behavior is essential to accurate song learning, and may be analogous to the role that babbling plays in language development (Fitch 2006, p. 190). Similarly, drawing, painting, and carving may develop motor skills involved in tool making; singing may develop capacities involved in language production; and dance may develop capacities involved in locomotion and (in group dancing) coordinated action. Recreational engagement in these activities may also provide opportunities to observe their effects on others and discover new contexts for their deployment.

The use of art behaviors to influence conspecifics points to their symbolic aspect. Although art behaviors can be used solely to attract attention and arouse emotion (e.g., fashion, décor, landscape design), they are typically suffused with meaning by their producers, audiences, or both. Thus, although not all symbolic behavior (e.g., drum telegraphy, notation, Morse code) is art behavior, all figurative art is iconic, and much “abstract” art is indexical or symbolic. Instructive here are the comparative mark-making abilities of children and captive chimpanzees. Both begin by scribbling and experimenting with the types of marks they can make on a surface; however, in the fourth year of life, children begin to make marks that are representative, whereas chimpanzees never advance beyond making scribbles and crude circles (Morris 2013). Moreover, children’s mark-making has a distinct developmental trajectory: in a study of nearly one million children’s drawings

from thirty different countries, Kellogg (1969) identified twenty basic scribbles that all children make, and five stages of drawing development that all children go through. At each stage, children generate marks of increasing complexity until, in the last stage, they produce marks that are referential. The crudeness of chimpanzee mark-making and its apparent lack of content are most parsimoniously explained in terms of *Pan's* comparatively limited capacities for invention, tool manufacture/use, social manipulation, and symbolic behavior. Conversely, because these capacities are highly elaborated in *Homo*, it is likely that their developmental trajectory structures the ontogeny of mark-making in children, and that mark-making and other signs (acoustic, gestural, tactile) are cultural inventions, not adaptations.

Conclusion

Although certain art behaviors are species-typical in humans, there is disagreement over whether they are by-products or adaptations and, in the latter case, over their evolved function. The ethnographic record indicates that, across forager societies, art behaviors are used for a wide range of purposes, and thus does not clearly support one hypothesized function over another. The strong congruencies between animal signals and art behaviors suggest that the latter are most parsimoniously explained as the result of complex interactions between evolved perceptual biases and adaptations for innovation, communication, symbolic behavior, and manipulation of the physical and social environment.

Cross-References

- [Language](#)
- [Machiavellian Intelligence](#)
- [Music](#)
- [Ostensive Communication](#)
- [Play](#)
- [Signaling](#)
- [Storytelling](#)
- [Symbolic Behavior](#)

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Articulation

► Differentiation

Articulatory Loop

► Phonological Loop and Rehearsal

Artificial Insemination

► Medically Assisted Reproduction

Artificial Selection

- Breeding Systems
- Eugenics
- Silver Fox Domestication Experiment

Artificial Stimulus

- [Supernormal Stimulus](#)

Artificially Exaggerated Stimulus

- [Supernormal Stimuli \(Konrad Lorenz\)](#)

Artistic Expression

- [Music and Hormones](#)

As a Precursor to Partner Violence

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Synonyms

[Mate guarding](#); [Proprietariness](#); [Proprietary mate retention tactics](#)

Definition

Some mate retention tactics, especially costly tactics aimed at keeping an intimate partner faithful, may be precursors to violence in romantic relationships.

Introduction

Cost-inflicting mate retention tactics are a form of mate retention in which one partner uses mate

retention strategies that are costly to the other partner. Cost-inflicting mate retention tactics may take a variety of forms and can include derogating a partner, threatening a partner or a rival, and checking the whereabouts of a partner (online or in person). Costs that occur may include reduced ability to seek an extra pair partner (i.e., a partner outside of the pair bond), feeling scared or intimidated, reduced ability to work or forage, and lowered self-esteem. Cost-inflicting tactics are typically thought of as being caused by sexual jealousy and are aimed primarily at keeping a romantic partner faithful, especially when there may be an increased risk of infidelity (Cousins and Gangestad 2007; Shackelford et al. 2005). It has been well documented that sexual jealousy often precipitates violence, including homicide (e.g., Wilson and Daly 1995). There are a variety of cost-inflicting mate retention tactics as described in the literature including vigilance, emotional manipulation, proprietariness, controlling behaviors, and mate guarding.

Types of Costly Mate Retention Tactics That Predict Intimate Partner Violence

Generally, mate retention tactics are employed to preserve romantic relationships, but not all mate retention tactics predict intimate partner violence. In a series of studies assessing the relationship between intimate partner violence and mate retention, researchers found that men's emotional manipulation, one type of costly mate retention tactic that involved men stating they would "die" if their partner left them, was linked with violence, as was men's vigilance regarding their partner's activities and monopolization of their partner's time (Shackelford et al. 2005).

In other research that assessed both partners in dating couples, men's use of the costly mate retention tactic proprietariness predicted physical aggression, while attentiveness, a benefit-provisioning mate retention tactic, did not predict violence. Proprietary mate retention tactics included time monopolization and vigilance about a partner's activities, as well as bad mouthing their partners to other men and telling

their partners they would not find a better mate (Cousins and Gangestad 2007).

Sex Differences in Cost-Inflicting Mate Retention Tactics

Although both men and women may inflict costs on romantic partners, much of the evolutionary literature has focused on men's use of costly mate retention tactics (e.g., Wilson and Daly 1995). Two reasons for the focus on men's costly mate retention tactics are that, firstly, men risk being cuckolded while women do not and, secondly, during the course of evolution, the costs and benefits of using various mate retention tactics may have been different for men and women. Women faced higher costs from any tactic that could put them in physical danger because women's offspring are dependent on them (Campbell 2001). The fitness payoffs for physical aggression are much lower for women than for men, and for this reason, there is a large sex difference in the use of physical aggression; men are much more likely to use physical aggression than women. This is not to say that women are never aggressive, but they tend to use verbal or other indirect forms of aggression (Bettencourt and Hernahan 1997).

When assessing the link between cost-inflicting mate retention tactics and intimate partner violence, the sex difference in physical aggression remains. Both men and women who believed their partner was sexually interested in someone else increased their use of proprietary mate retention tactics (Cousins and Gangestad 2007). However, proprietary men, but not proprietary women, were more likely to be physically aggressive toward a partner. This indicates that both men and women may benefit from use of costly mate retention tactics, but men and women assess which tactics will result in the largest benefit. Women may benefit from being proprietary, but proprietariness does not lead to physical aggression in women. While women receive fitness payoffs for proprietariness but not physical aggression, men receive fitness payoffs for use of both proprietariness and physical aggression.

Other research has not shown a sex difference in the link between costly mate retention tactics and physical aggression. For instance, Graham-Kevan and Archer (2009) did not find a difference in men's and women's use of controlling behaviors. They also found that controlling behaviors were correlated with physical aggression in both men and women, contrary to other evolutionary research.

Men's Use of Cost-Inflicting Mate Retention Tactics and Women's Fertility

Evolutionary theorists have predicted that men are more likely to use cost-inflicting mate retention tactics on women that are (a) young and (b) in the fertile phase of the menstrual cycle. Since women are not always fertile, men should seek cues of fertility in mates. One gross measure of fertility is age. Women that are postmenopausal are no longer fertile. Even younger women are only fertile for a small portion of the menstrual cycle, during the late follicular phase when there is a mature egg. In one study, researchers found that women's fecundity was related to men's use of control, but not to violence (Graham-Kevan and Archer 2009). In this case, women were considered fecund if they had no children and were under 40 or if they had a child over age 1 but under age 4. In a study assessing women's fertility status and their partner's use of mate retention tactics, researchers found that men were more proprietary when women were in high fertility, especially when women showed an interest in other men (Gangestad et al. 2002).

Fertile women may also use some forms of costly mate retention tactics more than non-fertile women. For instance, studies indicate that younger or fecund women, compared to older women, may isolate partners more (Graham-Kevan and Archer 2009), use more emotional manipulation (Buss and Shackelford 1997; Graham-Kevan and Archer 2009), conceal mates more, and cause more injuries toward their partner (Graham-Kevan and Archer 2009). Other studies show a different effect. For instance, in a classic

study on mate guarding, Flinn (1988) did not find evidence for higher levels of mate guarding among fecund women. Differences across studies may be due to how costly mate retention tactics are measured or which specific tactics are assessed.

Conclusion

Some forms of costly mate retention tactics have been linked with physical aggression. For instance, proprietariness has been linked with physical aggression in men, but not women (Cousins and Gangestad 2007), while controlling behaviors have been linked with physical aggression for both men and women (Graham-Kevan and Archer 2009). Infidelity risk appears to increase the use of costly mate retention tactics, but does not increase the use of benefit-provisioning mate retention tactics (Cousins and Gangestad 2007).

Cross-References

► [Prevention of Infidelity](#)

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ASD

► [Special Case: Autism](#)

Asexual Reproduction

► [Reproduction](#)

Asocial

► [Monoamine Oxidase and Antisocial Behavior](#)

Assault

- [Aggression](#)
- [Sex Differences in Aggression](#)
- [Violence](#)

Assessing Faithfulness

► [Perceptions of Infidelity Cues](#)

Assessing Genetic Similarity

► Helping and Genetic Relatedness

Assessment of Fighting Ability

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Synonyms

Formidability assessment

Definition

The process by which cognitive programs predict the winner of a physical conflict in order to make adaptive decisions about whether to engage in or withdraw from conflict.

Introduction

Although humans and other social species faced many different recurrent problems over evolutionary history, accurately gauging the fighting ability of same species competitors was undoubtedly a pressing concern. Organisms that could accurately identify competitors' fighting ability would have been better at assessing the likelihood of succeeding in a physical conflict, which in turn would have facilitated decisions to escalate or withdraw. In the long run, making strategic decisions based on accurate assessment of fighting ability would have led to a longer lifespan with more opportunities for mating, increasing an organism's reproductive success. Thus, it seems likely that natural selection would have favored the evolution of a cognitive program that could accurately assess fighting ability.

What Would a Cognitive Program that Assesses Fighting Ability Look Like?

To work well, a program that assesses fighting ability would have to be sensitive to cues that accurately track fighting ability. Such cues, including size, weight, and weaponry, are well documented amongst nonhuman animals (Arnott and Elwood 2009). In addition, there is a long history of evidence that nonhuman animals can accurately assess the fighting ability of other same species competitors. For example, betta fish (*Betta splendens*) use lateral displays of body size to determine whether to engage in conflict (Simpson 1968). Red deer (*Cervus elaphus*) employ roaring contests before escalating against other deer (Clutton-Brock and Albon 1979). These examples and others like them demonstrate three important points. First, there are cues that provide reliable information to the organism about the likelihood of success in conflict. Second, organisms adjust their behavior based on this information. Third, the program must be sensitive to cues from multiple sensory modalities.

Recently, evolutionary psychologists have proposed that humans are also likely to have cognitive programs that track fighting ability. Humans, like other nonhuman mammals, have a long history of intrasexual (same-sex) male physical aggression (Daly and Wilson 1988). Thus, it would greatly benefit men to be able to accurately assess when aggression is likely to result in a beneficial or detrimental outcome. Although women are far less likely to participate in these aggressive encounters, being able to accurately predict the outcomes of male-male conflicts would have still been important when choosing a mate. Evidence supports this idea that women's mate preferences favor men with greater fighting ability (Fink et al. 2007). Given these pressures, it seems likely that both men and women would have evolved cognitive programs that can accurately assess this critical variable.

Although many traits contribute to fighting ability, by and large the most reliable cue to fighting ability in humans is upper body strength. This is because for the vast majority of human evolutionary history, the most effective means of

fighting was by using the upper body to strike, choke, or otherwise injure a competitor. Even after combat tools such as rocks, clubs, and spears became common, upper body strength was still necessary to wield these tools. In sum, upper body strength is an *honest signal* (i.e., one that cannot be faked) of fighting ability as it reliably indicates capability to use physical force. Thus, any easily identifiable cue that accurately tracks upper body strength (e.g., muscle mass) would be a likely cue for the cognitive program to track.

Insofar as upper body strength is a reliable cue to fighting ability, selection would have favored cognitive programs that could accurately assess strength while minimizing risk to the assessor. These programs would be most effective if they could quickly pick up subtle strength cues from competitors and remain reliable when these cues are obscured (e.g., when clothing is worn). Similarly, they should rely minimally on direct interaction with the competitor, so as to minimize the risk of physical harm. The visual system is a likely candidate to meet these design requirements. Minimizing risk, humans can assess others from a distance without any physical interaction, and the visual system is acute enough to ascertain small differences in body size.

In addition to the visual system, another system that is a likely candidate to detect cues of fighting ability is the auditory system. Although vision is very useful for directly assessing the size of a competitor's upper body, it is not uncommon for vision to be impaired by darkness or obstructed by intervening obstacles. Given this recurrent problem, supplementary programs that could assess formidability in different ways are likely to have been selected, and these programs may convey different information about fighting ability than visual assessment. Like the visual system, the auditory system can make assessments of strength from a distance, minimizing the risk of physical harm to the assessor. However, it is unclear what auditory cues humans use to detect fighting ability. One potential cue is vocal pitch. Although men rate lower pitched voices as dominant (Puts et al. 2006), pitch does not track physical strength (Sell et al. 2010). Despite this disconnect, it is possible that pitch might provide incremental

information about fighting ability independent of physical strength or that there are other unknown acoustic cues aside from pitch per se that track fighting ability.

Evidence for a Cognitive Program that Assesses Fighting Ability

The aforementioned design requirements for a cognitive program that assesses fighting ability can be grouped into three hypotheses. First, humans must be able to assess cues to upper body strength. Systems that would be likely to track these cues include the visual and auditory systems. Second, upper body strength should strongly track judgments of fighting ability. This is necessary if upper body strength is actually relevant to assessing fighting ability. Finally, upper body strength should predict the likelihood of engaging and succeeding in physical conflict.

In support of this first hypothesis, Sell and colleagues (2009a, 2010) demonstrated that judgments of men's upper body strength from photographs correlated strongly ($r = 0.71$) with strength as measured by weight-lifting equipment. Similarly, judgments of men's upper body strength from voice recordings also correlated moderately ($r = 0.45$) with weight-lifting strength. Both of these relationships were stable at the level of the participant when analyzed with multi-level modeling, demonstrating that accuracy is an individual level phenomenon and not just an artifact of averaging across multiple raters. Finally, humans were still able to accurately assess strength from facial photos alone, which obscure the most salient cue to upper body strength, the musculature of the upper body.

The second hypothesis posits that observed upper body strength should also strongly track judgments of fighting ability. Support for this hypothesis has been found as well. Judgments of perceived strength and the likelihood of winning a physical fight are almost perfectly correlated, suggesting production by the same cognitive program. This same pattern emerges regardless of whether those ratings are based on photos or recordings of the voice (Sell et al. 2009a, 2010).

Moreover, these judgments are strongly predicted to the same degree by strength as measured with weight-lifting equipment. Not only do individuals agree that fighting ability and upper body strength are related but both judgments accurately track observed physical strength.

The final and most important hypothesis posits that upper body strength should predict willingness to engage and succeed in physical conflict. For men, upper body strength moderately predicts actual history of fighting (e.g., fights in the past 4 years) as well as reported success in conflict (Sell et al. 2009b). However, this work has relied extensively on retrospective self-report, rather than directly testing whether strength predicts success in actual dyadic interactions. One reason this indirect approach may be common is because of ethics; regardless of how enlightening it would be to have raters assess the formidability of male targets and then test their accuracy by having those men fight, it would be highly unethical to do so.

However, in an ingenious design, Little et al. (2015) were able to test this exact question. They showed untrained individuals several headshots of mixed martial arts (MMA) fighters who had recently fought against each other. In a forced choice task, these untrained individuals were able to predict the winner of such fights at rates greater than chance (55%). Furthermore, these judgments of who would win the fight were highly correlated with judgments of strength ($r = 0.82$).

What is most impressive about this result is that MMA fighters are a highly physically homogenous group: they are all extremely physically fit and further matched in classes by their weight. In addition, raters were untrained and could only rely on facial features. The fact that raters were able to perform above chance at all is impressive. In more naturalistic settings where raters have more sources of information and the fighters are less homogenous, it is quite likely that human assessment is much more accurate.

In sum, humans do seem to be able to accurately assess upper body strength. Upper body strength not only tracks ratings of fighting ability but also actually predicts a greater likelihood of

success in physical conflict. These results have been verified with highly controlled lab studies where strength is measured using weight-lifting machines as well as in more realistic designs where individuals must predict the results of actual bouts between professional fighters.

Sex Differences in Fighting Ability and Its Assessment

One of the largest sex differences in humans is in muscle mass and, as a result, muscular strength. In particular, human men have approximately 90% more upper body strength than women, with 99% of women being less strong than the average man (Lassek and Gaulin 2009). Additionally, variability in men's strength is also considerably higher than for women. This huge degree of sexual dimorphism is likely the result of intrasexual (same-sex) competition between men for mates. As fighting ability is largely due to upper body strength, stronger men would have been more likely to succeed in these aggressive competitions. This would in turn have given them more access to desirable mates and increased their reproductive success.

This sexual dimorphism means that human men are better equipped to use aggressive strategies than women and in fact have historically been the perpetrators of physical violence (Archer 2004). This raises the possibility that the cognitive program that measures fighting ability might be especially tuned to assess upper body strength in men. There is some evidence in support of this hypothesis; Sell and colleagues demonstrated (2009) that strength ratings of men (from facial photographs) correlate more strongly with actual upper body strength ($r = 0.39$) than strength ratings for women ($r = 0.21$). However, it is possible that this attenuated relationship for women may simply be due to the restricted range of female strength relative to male strength. The cognitive program that assesses fighting ability has less variability to rely on when making assessments of female strength, which may artifactually constrain estimates of accuracy.

Another possibility is that men and women might have different abilities in assessing strength. One plausible reason might be that men, who are exposed to more aggressive conflicts, might be better able to ascertain the strength and fighting ability of other competitors. However, it is also possible that there are no sex differences in assessment of these variables. Predicting the likely outcome of a physical confrontation is relevant for both men and women, even if women do not typically participate in the conflict. Additionally, as fighting ability is an honest cue to male mate quality, it is likely that women would have need for the same cognitive program to make judgments about who to mate with. Existing data suggests that any differences in strength assessment are small and inconsistent.

Although sex differences in muscular strength are one of the largest in humans (Cohen's $d = 3$), they are dwarfed by differences in vocal pitch. Male pitch is only half as high as female pitch (Cohen's $d = 4.5$), and these differences develop during puberty (Puts et al. 2006). This immense sex difference in pitch is unique to humans and suggests that sexual selection may be responsible for the emergence of lower pitched voices in men. Several lines of research support this hypothesis. Men rate lower pitched voices as more dominant (Puts et al. 2006). Women prefer men with deeper voices, and these differences are exaggerated at times close to ovulation (Puts 2005). As mentioned previously, however, there is currently no direct evidence that pitch accurately tracks physical strength (Sell et al. 2010).

Sexual dimorphism in vocal pitch occurs during puberty and is primarily due to physical changes in men's vocal cords that result from elevated testosterone levels. Testosterone also increases muscle growth (Bhasin et al. 1996), providing a potential explanation for why pitch might accurately track fighting ability. These changes are exclusive to men and raise the possibility that the cognitive program that measures fighting ability through vocal cues might be especially tuned to assess men. Consistent with this idea, Sell and colleagues found (2010) that strength ratings of men (judged from voice recordings) correlate more strongly with actual upper body

strength ($r = 0.51$) than strength ratings for women ($r = 0.26$). While this may point to a cognitive adaptation that is better designed to operate on men's voices, it is still possible that this smaller relationship may be due to a restriction of range on female strength.

The existing evidence strongly supports the idea that men and women are equally skilled at assessing fighting ability from both visual and auditory cues, even though men are much more likely to engage in and be victims of aggression. Similarly, there is some evidence that humans are better equipped to assess male fighting ability than female fighting ability. However, a key issue with this conclusion is that there is considerably more variability in male strength (and thus fighting ability) than there is for female strength. This restricted range makes prediction more difficult, as the cognitive program must make judgments about smaller fluctuations in strength.

Evidence that Assessment of Fighting Ability Is Species Typical

If a cognitive program did evolve through natural selection to assess competitors' fighting ability, this program should operate effectively regardless of whether the individuals assessed are from similar or foreign cultures. In contrast, if the assessment of fighting ability is transmitted through culture specific cues, it should be worse when judging foreign individuals. In support of species-typical assessment, American raters were able to accurately judge strength from facial photographs and recordings of voice for American men, Tsimane men from Boliva, and Andean men from Argentina (Sell et al. 2009a, 2010). These strength estimates tracked perceptions of fighting ability as well as actual history of fighting, suggesting that a species-typical cognitive program is likely.

Conclusion

There is considerable evidence that aggression between humans has long been a part of our

species' history. Nonetheless, there are considerable costs of escalating conflict when one is unlikely to win. It seems likely that humans would have evolved cognitive programs that could accurately assess fighting ability by tracking reliable cues like upper body strength. Experimental evidence supports this prediction; both men and women can assess upper body strength from visual and auditory cues, and upper body strength in turn predicts willingness to engage in and succeed in physical confrontations. In addition, these adaptations appear to be species typical. There is some evidence that such programs are better equipped to assess male fighting ability, but this evidence might just be a statistical artifact of the restricted range of female strength.

Cross-References

- [Aggression](#)
- [Evolution of Fighting Assessment Abilities](#)
- [Fighting Assessment](#)
- [Intrasexual Competition](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Male-Male Competition](#)
- [Mate Preferences](#)
- [Physical Aggression](#)
- [Psychological Mechanisms](#)
- [Resource Competition](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Signals of Body Size](#)
- [Size and Dominance](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- [Upper Body Strength](#)
- [Upper Body Strength and Fighting Ability](#)
- [Upper Body Strength from Photo](#)
- [Vocal Indicators of Dominance](#)

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Assessment of Unfaithfulness

- [Perceptions of Infidelity](#)

Assimilation

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Synonyms

Absorption; Adaption; Adjustment

Definition

The act of absorbing or adjusting experiences, information, etc. into an existing system.

Introduction

The term assimilation describes the process of absorbing or adjusting experiences or information into an existing system. It is derived from the Latin word *assimilatio*, meaning “likeness” or “similarity.” Assimilation hence refers to making something more similar. In psychology, the term is used in various theoretical circumstances with differing connotations. We will focus on three highly influential theoretical models in which the concept of assimilation plays a central role: (a) Jean Piaget’s genetic theory of learning, (b) the inclusion-exclusion model of social judgment formation by Schwarz and Bless, and (c) John Berry’s theory of acculturation strategies.

Jean Piaget’s Genetic Theory of Learning

Developmental psychologist Jean Piaget (1936) described his work as genetic epistemology, i.e., the scientific study of the origins of human rationality and thinking. Piaget studied children’s ability to count, to talk, or to reason, but did not seek to assess their performance. His primary questions were, in a sense, deeper, seeking to understand how children acquire the fundamental concept of

numbers, how they learn to differentiate between a word and the concept it identifies, or how they process causality. Before Piaget’s work, children were primarily seen as less competent thinkers than adults. Piaget became intrigued by children’s thinking errors and the reasons they gave for them. To him, these reasons revealed that the errors are due to systematic and necessary steps in the development of concepts that children have to take in order to ultimately generate appropriate mental models of the world.

According to Piaget, children are born with a genetically inherited and evolved mental structure on which all subsequent learning and knowledge are based. This mental structure is of course very basic and needs refining. Piaget saw mental schemata as sets of linked mental representations of the world that humans use both to understand and to respond to situations. He defined schemata as “cohesive, repeatable action sequence possessing component actions that are tightly interconnected and governed by a core meaning” (1957, p. 7). Put more simply, Piaget’s schemata are the basic modules which allow humans to organize knowledge since their infancy. Obviously, the first schemata that children possess are extremely simple. They are the reason why children are equipped with innate, i.e., genetically programmed, reflexes. For instance, newborn babies have a sucking reflex that is triggered once something touches their lips, be it nipples, a person’s finger, or a comforter. In Piaget’s terms babies have a sucking schema. Intellectual growth is viewed as adaptation or adjustment of mental schemata to the world. According to Piaget this adaptation can take place through two distinct processes: assimilation and accommodation. Assimilation means that an existing schema is used to deal with a newly encountered object or situation, even if the schema does not fully fit. If the existing schema does not work at all and needs to be changed to deal with a new object or situation, the process is called accommodation. Assume, e.g., that the only four-legged animal that a child has ever seen is a dog. The process of assimilation would imply that the child calls all other

four-legged animals of similar size (e.g., cats) a dog, simply because cats are similar enough to dogs. This generalization, albeit incorrect, is a necessary and adaptive step in dealing with the new encounter. If the child acquires more knowledge about the differences between cats and dogs, it builds new and more fine-graded mental schemata that are yet derived from the initial simple ones. This latter process of changing an existing schema and adapting it to newly acquired knowledge about the world is called accommodation. In sum, Piaget described cognitive development as the interplay of assimilating and accommodating mental schemata.

Social Judgment Formation

How do we generally judge or evaluate other people or objects in a given context? How does contextual information shape our judgments? Norbert Schwarz and Herbert Bless (Schwarz and Bless 1992) have argued that if individuals are asked to form a judgment about some target stimulus, they first need to retrieve some cognitive representation of it from their memory. Additionally, they need to determine some standard of comparison to evaluate the stimulus. Both the representation of the target and standard of comparison are, in part, context-dependent. One critical source of contextual information is preceding judgmental tasks a person has been confronted with. Information that has been used for answering those preceding questions is most likely to come to mind again when later being asked related questions. This can happen in two different ways: assimilation and contrast. Assimilation effects occur if later judgments reflect the information that has been rendered accessible in the respondent's mind by previous questions, as well as the implications of that knowledge. This is to say that a later judgment is more similar to the preceding one than it would have been had no prior question been asked. Contrast effects describe the opposite direction of influence.

Whether assimilation or contrast effects occur is a function of how the information that comes to mind due to the preceding questions is

mentally categorized. In order to form a judgment about a certain target, people construe a temporary representation of it. If this mental representation includes the information rendered accessible by preceding questions, assimilation effects are likely to be found. However, the same piece of information may also result in a contrast effect. This is expected to be the case when the information is excluded from the cognitive representation of the target. To illustrate, in one classic empirical test of this model, Schwarz and Bless (1992) assessed how evaluations of the German conservative party, the Christian Democratic Union (CDU), would be biased by reminding respondents of one of its most highly esteemed members, Richard von Weizsäcker. In one experimental condition, respondents were reminded of von Weizsäcker in such a way that they were likely to include him into their temporary representation of the CDU. To this end, the participants were asked to recall the party of which "Richard von Weizsäcker has been a member for more than 20 years." Relative to a control condition without this preceding question, the participants evaluated the CDU more positively, thus exhibiting an assimilation effect. In another condition, however, people were reminded of von Weizsäcker in such a way that they were unlikely to include him in their mental representation of the CDU. This was achieved by asking them "which office Richard von Weizsäcker holds, that sets him aside from party politics?". At the time the study was conducted, von Weizsäcker served as Federal President of Germany, an office that required him to take a neutral stand on party issues. When later being asked to evaluate the CDU, these participants provided less positive judgments than those of a control group without preceding question. As compared to the highly esteemed Richard von Weizsäcker, the overall representation of the CDU appeared to be less positive. In sum, whether information that is rendered accessible in the respondents' mind yields assimilation or contrast effects in later judgments depends on whether it is included in the mental representation of the judgment target or not.

Intercultural Relations and Acculturation Strategies

The term assimilation is also used in the context of intercultural relations. In this context, assimilation refers to the process whereby persons acquire the culture of another group in which they come to live, by adopting its attitudes and values and its patterns of thinking and behaving – in short, its way of life. Assimilation is one of four acculturation strategies identified by John Berry (1997). Acculturation is the sum of those phenomena taking place when individuals of different cultural backgrounds come into continuous first-hand contact with each other, yielding subsequent changes in the original cultural patterns of either or both groups. It is mainly used to refer to the patterns that describe how migrants adapt to a new host society. According to Berry, acculturating individuals have to actively manage a central conflict inherent in such contexts: cultural maintenance versus contact and participation. Cultural maintenance refers to the consideration of whether it is valuable to maintain one's original identity and characteristics ("yes" or "no"). Contact and participation refer to the consideration of whether it is of value to maintain relationships with the larger/host society ("yes" or "no"). Depending on these answers, four different acculturation strategies can be identified (those being, separation, marginalization, integration, and assimilation). The assimilation strategy is characterized by the unwillingness to maintain one's own original cultural identity while instead seeking daily interactions with members of the host culture only. The opposite strategy, placing very high value on holding on to one's original culture while avoiding contact with the new one, is called separation. Integration, as the third strategy, is followed, if people seek to find a balance between participating as an integral part of the new culture while at the same time maintaining some degree of cultural integrity. The fourth strategy is called marginalization which means that there is no or little interest to get into contact with the new culture while also not trying to maintain one's culture of heritage.

While assimilation has previously been seen as the integral part of any individual's journey into acceptance by the host culture, more recent

studies have shed doubt on the assumption that assimilation is invariably positive. This is best reflected in its effect on mental health and well-being. For example, assimilation is reported to be related to more risky sexual behavior, higher risks of delinquency and substance abuse in adolescents, as well as lower educational outcomes. However, it has been found to boost migrants' self-esteem and increase positive attitudes toward the host culture. Based on these findings, Berry argues that host societies will likewise be most successful in dealing with immigration, if they endorse multiculturalism, i.e., valuing and fostering diversity, rather than seeking assimilation of the immigrants.

Conclusion

The term assimilation means making something similar and describes the process of absorbing or adjusting experiences or information into an existing system. We have described three different circumstances in which the term plays a central role in psychological theorizing. Jean Piaget's genetic theory of learning is one of the first attempts to systematically study cognitive development. According to Piaget, children are born with genetically inherited mental schemata which are used and modified during the course of learning and development. Piaget described cognitive development as the interplay of assimilating and accommodating these mental schemata. Assimilation means that an existing schema is applied to a newly encountered situation or object. Changing an existing schema if it is not sufficient to deal with the new information is referred to as accommodation. The second theoretical context where the term assimilation is used is related to models of social judgment formation which are concerned with how contextual information shapes human judgments. In this context, assimilation effects are identified by judgments and contextual information being positively correlated. If, however, contextual information biases judgment into the opposite direction, this is called contrast. The inclusion-exclusion model by Schwarz and Bless specifies conditions under which either

assimilation or contrast can be expected. Finally, assimilation is one of four different acculturation strategies identified by John Berry. It is characterized by individuals giving up their own cultural identity while becoming absorbed into the host society. Assimilation has less beneficial psychological consequences than the strategy of integration, meaning that the individual maintains his or her cultural heritage while at the same time becoming an active participant in the host culture.

Cross-References

► [Differentiation](#)

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Assisted Reproduction

► [Medically Assisted Reproduction](#)

Assisted Suicide

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Synonyms

[Death](#); [Euthanasia](#); [Physician-assisted death](#); [Self-inflicted suicide](#); [Suicide](#)

Definition

Suicide with the help of a third party, usually by terminally ill patients with the help of a physician.

Introduction

The terms physician-assisted suicide, physician-assisted death, and euthanasia are often used interchangeably, though there are notable differences. The difference between assisted suicide and assisted death is mainly semantic. Both are defined as a physician aiding the patient in initiating his or her own death with prescriptions, medications, or other means. Alternatively, voluntary active euthanasia, by definition, has a physician actively employing the means to initiate death (Quill and Batlin 2017). For the purpose of this focus, the term assisted suicide (AS) will suffice for all types of suicide aided by physicians and exclude euthanasia.

Although the Hippocratic Oath forbade the practice of assisted suicide, there are reports that physicians of antiquity were known to give suffering patients poison to accelerate their death. However, the advent of Christianity took the Hippocratic Oath a step further by linking suicide with eternal damnation, thereby ending physician participation with suicide in Western culture for nearly 2000 years. The American debate on AS was stoked by an article (eventually found to be a fabrication), published in 1988 in the *Journal of the American Medical Association* entitled, “It’s over Debbie.” The article described a resident physician giving a lethal dose of morphine to a terminally ill and suffering 20-year-old woman, with her mother giving tacit approval at her bedside (Anonymous 1988). The discussion of AS in the United States exploded with the notoriety of Dr. Jack Kevorkian, a Michigan pathologist, who eventually facilitated the death of at least 130 people. He was eventually sentenced to prison although not for the AS that he had practiced with his first 129 patients but rather for participating in euthanasia with his last patient. In addition, he had the audacity of having the taped event nationally televised on CBS’ “Sixty Minutes” (Lessenberry 1994).

Current legal and moral conflicts remain. Though a clear majority of the American public favors AS (as high as 70%), the majority of physicians oppose it (see Van Norman 2014). Assisted suicide became legal in Oregon in 1994, followed by Washington, Vermont, Montana, California, the District of Columbia, and most recently Colorado. Other nations that allow for suicide (and in some countries, euthanasia) include the Netherlands, Switzerland, Belgium, Luxemburg, Columbia (Van Norman 2014), and as of 2015, Canada.

The moral divide has strong voices on both sides. The most commonly cited argument affirming AS is the issue of autonomy: Individuals have the right to determine the fate of their own lives, including the right to die on one's own terms. A second point of affirmation includes the idea of beneficence, that the relief of suffering is for the greater good. Third, the termination of life-sustaining treatment is thought by some to have no moral difference than AS, thereby neutralizing it to a moral equivalent. And on a practical level, 60% of Medicare payments in the United States are expended in the last 6 months of life (Lessenberry 1994), which brings into focus the discussion of where health-related financial resources are best spent. The question arises as to whether or not AS would become a benefit to society as a whole by containing costs or represent what others fear may become akin to "death panels" and lead toward a slippery slope.

The arguments in opposition of AS are frequently the affirming opinions turned on their head: that the power of autonomy ends before suicide, because suicide precludes further autonomy. As for beneficence, the premature ending of life denies any further possibility of the good that comes with life itself. Commonly, the slippery slope argument is offered up that AS is the first of several steps leading toward a Nazi-like political utility used for self-serving needs. Further, complications with AS have occurred creating a potential for increased suffering as well: difficulties with infusions from IVs, potential for additional pain, and the possibility of failure in the process of dying, stoking dread in patients and families (Quill and Batlin 2017). The arguments

fearful of the slippery slope are tenuous; clusters of data from both the Netherlands, and the state of Oregon demonstrate the use of AS to be numerically stable over nearly two decades (Steck et al. 2013).

Often, and mistakenly, the perception of the primary use of AS is to relieve intractable pain. In the United States, less than 25% of AS involves a primary concern related to pain, the most frequent usage (over 60%) in the United States of AS stems from the diagnosis of cancer (Steck et al. 2013). By a large majority, the most frequent subjective request for AS was due to loss of autonomy, followed by loss of enjoyable activities, then loss of dignity (Yang 2016). The most likely people to change their minds in pursuing AS are depressed patients. The issues of consent, and the potential need for further psychiatric treatment in the depressed individual, creates persistent controversy. The depressed patient brings into question the significance of existential suffering and, further, whether a physician is best suited to judge the quality and significance of that quality of pain. The non-depressed, fully informed patient that has agreed to follow through with AS is often referred to as "the rational suicide." The demented patient, whose family may request AS, presents further controversy in that the patient is unlikely to be able to demonstrate capacity and has no true autonomy in the matter.

Conclusion

The greater need for palliative care, psychiatric intervention, family involvement, and community support is evident as AS becomes a greater part of the fabric of our culture. These situations emphasize and reinforce the need for appropriate screening and second opinions. Controls and legal safeguards preventing abuse of AS consist of admixtures of waiting periods, witnesses, diagnostic criteria, capacity, written requests, and the option to opt out by the patient as well as the physician.

The debate regarding AS remains active and emotional, with religious, academic, political, and ethical considerations.

Cross-References

- [Death](#)
- [Factors Associated with Suicide](#)
- [Jack Kevorkian](#)
- [Kin Selective Suicide](#)
- [Suicide](#)

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Associationism

- [Associative Learning](#)

Associations

- [Cost of Same-Sex Friendships](#)
- [Same-Sex Friend](#)

Associative Learning

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Synonyms

[Associationism](#); [Conditioned associations](#); [Instrumental associations](#); [Learning through associations](#)

Definition

Associative learning is a type of learning that involves the acquisition of new associations between environmental conditions and/or interoceptive states that govern and regulate the learning outcome.

Introduction

Associative learning constitutes a fundamental notion in numerous theoretical and operational models of learning (McSweeney and Murphy 2014). The basic theoretical models related to associative learning indicate either in an explicit and/or implicit way the acquisition of new associations that govern the learning outcome (Shanks 1995). Specifically, associative learning constitutes the capacity of living creatures to detect reliable and consistent associative relationships that are formed between environmental conditions and/or interoceptive experiences (Delamater and Lattal 2014). This type of learning enhances the capacity of living creatures for adaption and survival as it renders organisms able to expect upcoming events and maintain resources (Baum 2017).

Historical Background of Associative Learning

The idea that organisms possess the capacity to achieve learning through the acquisition of new associations has its historical origins back to the Ancient Greeks and associationism (McSweeney and Murphy 2014). Aristotle, a Greek philosopher described associative memory principles, an approach that became widely known as associationism. Specifically, Aristotle suggested that the retrieval of thoughts or images evokes the retrieval of other thoughts or images that have formal similarities with the initial thought or image. In other words, Aristotle proposed that learning is achieved through the association of environmental conditions that constantly occur together (Baum 2017).

Even though early philosophers in the associationist movement and early researchers in the fields of both human associative memory and behaviorism had studied associative mechanisms that today would be considered to be similar to the ones that Ivan Petrovich Pavlov described, I. P. Pavlov was the first who officially and methodologically designated and described an associative learning process at a theoretical as well as at an operational level in the scientific community through the publication of conditioned reflexes in 1927 (Shanks 1995). Pavlovian and/or classical conditioning is a type of associative learning that involves the formation of new behavioral responses through the acquisition of new associations. Specifically, during the course of classical conditioning, an organism adjusts in response to the detection of sequential relationships between stimulus of environmental and/or proprioceptive nature (Spence 1978).

This type of associative learning is named “conditioning” since its inventor, I. P. Pavlov, used the term conditioned reflex to label and designate the learning outcome (Schachtman 2011). I. P. Pavlov assumed that new reflexive responses can be developed through the acquisition of classically conditioned associations between neutral stimuli, that is, stimuli which originally do not induce any particular response, and unconditioned stimuli, that is, biologically relevant stimuli which reflexively evoke an unconditioned response (Spence 1978). Through the acquisition of a classically conditioned association between a neutral stimulus and an unconditioned stimulus, the first turns into a conditioned stimulus and acquires the capacity to induce a conditioned response that is qualitatively similar to the unconditioned response. I. P. Pavlov examined various reflexes, yet his most widely known experiments revolved around responses to food (Schachtman 2011).

The Study of Gastrointestinal System and Its Role in Classical Conditioning

I. P. Pavlov discovered the associative mechanism of classical conditioning accidentally while examining the physiological processes of the

gastrointestinal system. Specifically, I. P. Pavlov was examining the alternations of dogs’ saliva and digestive fluid secretion through their mouth and stomach while feeding. At some point, during the experimental procedures that I. P. Pavlov set in order to observe the alternations of dogs’ saliva and digestive fluid secretion in response to feeding, he observed that the subjects’ (i.e., dogs) saliva and digestive fluid were also secreted every time he and his associates arrived in the laboratory. Consequently, I. P. Pavlov decided to experimentally examine the mechanisms and functional structures that let the dogs secrete saliva and digestive fluid in his presence as well, rather than exclusively to the presence of food in response to which the dogs reflexively and automatically secrete saliva and digestive fluid (Spence 1978).

I. P. Pavlov and his associates systematically and methodologically administered for several times a neutral stimulus (i.e. sound of a bell) to the dogs just before they were presented to their usual food, that is, a meat powder. When this trial was conducted numerous times I. P. Pavlov and his associates observed that the dogs were also secreting saliva and digestive fluid when the stimulus of the sound of the bell was administered alone, that is, in the absence of food (Shanks 1995). Ultimately, I. P. Pavlov came to the conclusion that the constant pairings of the sound of the bell and the food resulted in the formation of an association between the sound of the bell and the food. Specifically, the sound of the bell which at the beginning was neutral stimulus, a stimulus that does not elicit a response, acquired the capacity to elicit a response, which is qualitatively similar to the one that the food naturally and automatically elicits. The dogs’ response became classically conditioned and respectively the sound of the bell turned into a conditioned stimulus. Consequently, the new response that was learned as a reaction to the sound of the bell is termed a conditioned response (Schachtman 2011).

The Evolution of Classical Conditioning

The theory of Classical conditioning has considerably evolved after the work of I. P. Pavlov

in conditioned reflexes. The initial model of classical conditioning was operationally and theoretically elaborated by the work of several learning theorists in the USA. Specifically, theorists in the field of learning in the USA formed different techniques for assessing the functional qualities of associations between conditioned stimuli and unconditioned stimuli (Allen and Madden 1985). In addition, they also found new conditioning processes and reinterpreted the fundamental processes of the conditioning that became known through the procedures that I. P. Pavlov proposed (Wills 2012).

A considerable factor that led to substantial modifications of the initial theory of classical conditioning is the integration of cognitive functions in it. Specifically, even though, the work of I. P. Pavlov on conditioned reflexes was widely spread in the USA, it received a considerable amount of criticism in 1950. Most of the criticisms on his ideas were expressed in 1950 by the well-known Polish neurophysiologists named Jerzy Konorski and Stefan Miller. Jerzy Konorski and Stefan Miller initiated the primary cognitive conceptualization of respondent conditioning. Their work constitutes the precursor of the well-known and highly influential Rescorla–Wagner model of classical conditioning (McSweeney and Murphy 2014). In addition, at the same period, the psychiatrist Joseph Wolpe as well as the psychologists John Watson developed treatment plans that were based on the principles of classical conditioning so that to change dysfunctional behaviors into functional ones. This attempt to apply learning principles in the development of clinical interventions became known as behavioral modification and significantly increased the use of such interventions by psychiatrists and psychologists (Staddon 2014).

The theoretical conceptualization of classical conditioning has significantly changed with the introduction of the Rescorla–Wagner model in classical conditioning in 1972 (McSweeney and Murphy 2014). The Rescorla–Wagner model proposes that while living beings interact with their environment, develop causal expectations that enable them to estimate the relationships between environmental conditions. According to

this model, learning involves acquiring knowledge related to the way that the environment is causally organized. Specifically, an organism becomes able to achieve learning by developing solid associations between environmental components (Rescorla 2008). Yet even if the environmental components become contiguous and in turn organisms form associations between them, the environmental components need to also allow the acquisition of knowledge related to causal relationships. In other words, the fundamental idea is the concept of contingency and how an organism perceives it (McSweeney and Murphy 2014). This model by integrating cognitive elements within the formation of associations indicated the acceptance of both cognitive functions and associative processes in the brain, something that quickly earned the favor of experimental psychologists (Klein and Mowrer 1989).

Even though living beings sometimes form conditioned associations based only on a conditioned stimulus–unconditioned stimulus contiguity, there are numerous cases in which learning appears to enable living beings to anticipate the presentation of the unconditioned stimulus due to the presentation of the conditioned stimulus (Pearce and Hall 1980). In such cases, learning takes place through a contingency relationship that is probabilistically manifested (McSweeney and Murphy 2014). For instance, when the likelihood of the unconditioned stimulus being presented is equal to the likelihood of the conditioned stimulus being and not being presented the conditioned association cannot be achieved. In contrast, when the likelihood of the unconditioned stimulus being accompanied by the conditioned stimulus is higher than the likelihood of the unconditioned stimulus being presented in the absence of the conditioned stimulus, a conditioned association could be achieved. For that reason, respondent conditioning is considered to reflect the ability of living beings to identify and learn possible associations between signals and important environmental conditions (Staddon 2014).

Nowadays, respondent conditioning is viewed as a multifaceted associative mechanism that involves many types of responses, rather than involving only glandular and visceral reactions,

as it was initially considered. Respondent conditioning among other factors also relies on how relevant is the conditioned and the unconditioned stimulus, the appearance of other stimuli while conditioning takes place, and the degree of surprise that the unconditioned stimulus evokes (McSweeney and Murphy 2014). In addition, the evolution of the connectionist framework that models human cognition revived the attention in respondent conditioning as a productive technique for the study of associative learning. Therefore, nowadays, classical conditioning is most accurately defined and designated by its procedural method, which encompasses the preservation of firm control over the presentation of stimuli (Shanks 1995). In addition, it is highly important to take into consideration that the principles that accurately differentiate classical conditioning between other forms of associative learning, such as operant conditioning and associative memory, are limited. Specifically, classical conditioning is most accurately differentiated by the extent to which the form of the conditioned response is determined by the choice of the unconditioned stimulus (Allen and Madden 1985). Furthermore, a classically conditioned response is usually unaffected by instrumental contingencies. For example, pigeons cannot be easily prevented from pecking (conditioned response) at a separate key light (conditioned stimulus) which was paired with food (unconditioned stimulus) even if pecking stops the distribution of food (Wills 2012).

Further Conditioning: Second-Order Conditioning, Generalization, and Discrimination

Second-Order Conditioning

Stimuli that have acquired conditioned associations can set the ground for further conditioned associations. For example, when a kid experiences fear in the presence of darkness resulting to the darkness being a conditioned stimulus that induce a response of fear, an additional stimulus that exists in the setting of darkness such as specific noises can acquire too qualitatively similar

operations with the conditioned stimulus and induce a fear response despite the fact that these noises did not accompany the stimulus that initially induced the fear response in the dark setting (Ramnero and Torneke 2011). This phenomenon is usually termed second-order conditioning. Once more, the stimulus of darkness is likewise one that is not so neutral, as humans are biologically predisposed to more easily associate it with fear than other stimuli (McSweeney and Murphy 2014).

Generalization

An additional and very significant functional process of classical conditioning is the propensity to react in a qualitatively comparable manner to similar stimuli, a process that is termed stimulus generalization (Staddon 2014). The term stimulus generalization when it comes to classical conditioning defines the process through which a specific response would spread in such a manner that other stimuli that have qualitatively similar traits with the initial classically conditioned stimulus would acquire the ability to also induce the classically conditioned response (McSweeney and Murphy 2014). For instance, a kid that has been scratched and wounded by a dog would not only respond with fear whenever sees that specific dog. Specifically, this kid is very well likely to respond with fear to the presence of dogs which are similar enough. However, if the kid was scratched by a large dog and the height of the dog is a dominant feature of the conditioned stimulus, it is likely that a very small dog would not induce a conditioned response of fear. Yet if the dog's barking is a dominant feature of the conditioned stimulus, then a very small dog's barking could operate as a conditioned stimulus and induce a conditioned response of fear. In other words, in order for an organism to respond in a qualitatively similar way to different stimuli, the stimuli must be similar enough (Ramnero and Torneke 2011).

Stimulus Discrimination

The opposite conditioning operation to generalization is a process termed stimulus discrimination. Stimulus discrimination is the capacity of an organism to detect and respond to differences

between stimuli, that is, the capacity to detect similarities among stimuli. For example, I. P. Pavlov's dogs at the beginning exhibited stimulus generalization since they were secreting saliva and digestive fluid in response to a variety of sounds that were different than the sound that was initially classically conditioned (Ramnero and Torneke 2011). However, if the dogs had consistently received only a specific sound before they were fed, their capacity to differentiate, that is, to discriminate, among similar stimulus would be enhanced and in turn, they would secrete saliva and digestive fluid only in response to the specific sound that precedes feeding (Shanks 1995).

The processes of generalization, discrimination, as well as the equilibrium among them, are of vital importance for living beings in order to learn to adapt and survive (Baum 2017). Specifically, in some situations is of vital importance to exhibit stimulus discrimination and just respond to specific stimuli. For instance, a living being that must assess an area which is full of ice where a discrepancy in the white-color shows the degree to which is safe or dangerous to pass through the ice must have the capacity for stimulus discrimination. However, in other situations, stimulus generalization has higher adaptive and survival significance, such as the case of an organism which is chased by a variety of predators. In such a scenario, this living organism must respond to everything that presents in front of it.

Classical Conditioning and Emotional Functioning

Classical conditioning could be used to gain an insight into the way that a person's emotive experience of the world is developed during childhood (McSweeney and Bierley 1984). For instance, despite the fact that only certain stimulus could induce fear responses early on in an individual's life, as the person grows up would acquire further associations which will obtain qualitatively similar operations with the ones that an unconditioned stimulus possesses, that would from then on induce fear responses (McSweeney and Murphy 2014). Therefore,

through classical conditioning, phenomena acquire new associations with external stimuli such as behaviors of other people, certain environmental conditions as well as internal stimuli, such as other emotions and interoceptive experiences. For example, a young boy who experiences sadness and is recurrently challenged by a father who is behaving in a manner which induces fear in the boy, via the process of classical conditioning, the father's behaviors could lead the young boy to develop an association between the affects of sadness and fear, and thus every time he feels sadness (conditioned stimulus) a response of fear is induced. In other words, this boy has learned through classical conditioning to experience fear every time he is sad (Thines 1987).

Classical conditioning shapes individuals' responses from early on in their lives and continues to influence the way in which a person relates to the world during the course of all of his/her life (Ramnero and Torneke 2011). The recognition that affective responses could also be induced by classically conditioned associations has its roots early in the development of behaviorism (Thines 1987). Specifically, John Watson, who is considered the father of "behaviorism," embraced I. P. Pavlov's work on conditioned reflexes and decided to implement its principles to investigate the way that the affective response of fear emerges in people. In addition, classically conditioned responses are fundamental to gain an insight in the way that individuals who experience trauma respond to a specific stimulus such as loud noises, fire, dark, or a preparator's perfume (Shanks 1995).

Classical conditioning enables environmental components and/or conditions to acquire a physiological capacity that did not have before. In other words, an environmental component and/or a condition that possessed other functions or none now acquires a new function, an acquisition that has adaptive significance for any species. Specifically, classical conditioning provides to a living being the chance to alter its behavior and thus increasing its capacity to adapt and survive (Ramnero and Torneke 2011). For example, a kid might jump on a road full of cars, lacking the association between such situations and threat.

However, the kid possesses a physiological system that responds to specific unconditioned stimuli such as abrupt cries, screams, and violent acts with an unconditioned response of fear. In a plausible scenario where his/her mother or his/her father responds with a loud scream or exhibits a violent act when the kid tries to jump on the road, the road and/or other relevant stimuli would acquire qualitatively similar functions with the unconditioned stimulus of a loud scream, enabling the road and other relevant stimuli from then on (conditioned stimulus) to induce a conditioned response of fear. The acquisition of this new association would enable the kid to alter his/her behavior when it comes to a crowded road. A further example that depicts the way that classical conditioning could enhance the capacity for adaption and survival is a woman who is attacked in a remote parking place. One month later she goes to the same parking place and she begins to feel dizzy, chest pains, numbness in the hands, and a sense of terror and as a result, she immediately leaves the place. In this scenario, the woman became classically conditioned to a previously neutral stimulus (remote parking) which has now induced a physiological response of fear due to its association with the unconditioned stimulus of assault leading the woman to leave immediately from the remote parking and avoid a possible future attack (McSweeney and Murphy 2014).

The Contributions of Edward Thorndike in the Study of Associative Learning

The experimental studies of Edward Thorndike with cats in puzzle boxes widened the theoretical notion of associative learning by integrating the concept of consequences to the associative processes of learning (McSweeney and Murphy 2014). Thorndike through his work depicted that the theoretical notion of associative learning is applied not only in reflexive responses and sensory substitution but also to the acquisition of new behavioral responses. Specifically, Thorndike restrained cats in a puzzle box, and then he prompted the cat to escape so that to be able to obtain

food (i.e., fish) that was left outside of the puzzle box (Ramnero and Torneke 2011). Consequently, the cat tested various ways in order to get outside of the puzzle box and obtain the food. Ultimately, and through experimentation, the cats learned that when they pressed the lever they were obtaining the food and thus they experienced positive consequences. As a result, the frequency with which the cats were pressing the lever significantly increased (Shanks 1995).

The cats' behavioral responses of trying to press the lever were not reflexive in nature as the unconditioned responses in Pavlov's experimental studies (Staddon 2014). Specifically, the cats' behavioral responses were governed by the consequences that followed them. In other words, when the cats pressed the lever the door was opening, a sequence that enabled the cats to acquire the association between the lever pressing and the opened door. This type of learning that enables living beings to operate in their environmental context became widely known as operant conditioning. In contrast to Pavlov's process of learning through which organism passively acquire new associations, operant conditioning constitutes a general as well as an active theoretical model of learning (Shanks 1995).

Thorndike's experimental studies related to the associative mechanisms that govern animal behavioral responses let him develop the law of effect which constitutes the primary official law of associative learning that is psychological in nature (Wills 2012). Thorndike's law of effect assumes that a behavioral response that is followed by positive consequences is more likely to become associated with the environmental conditions where it was initially exhibited and thus increase in frequency. In contrast, the behavioral response that is followed by negative consequences is less likely to appear when a living being faces equivalent environmental conditions in a future time and thus the behavioral response reduces in frequency until it is eliminated (Shanks 1995). In addition to the law of effect, Thorndike proposed the law of exercise which assumes that the intensity of an association between a behavioral response and environmental conditions is highly influenced by the rate of occurrence of

previous pairings between that environmental conditions and the specific behavioral response (Ramnero and Torneke 2011).

The Contributions of Skinner in the Study of Associative Learning

The work of Thorndike related to the mechanisms that underlie associative learning was spread and expanded by B.F. Skinner (McSweeney and Murphy 2014). Specifically, Skinner, in addition to the notion of consequences, integrated the concept of reinforcement as a functional means through which associations are acquired, regulated, and maintained (McSweeney and Murphy 2014). Specifically, Skinner claimed that the extent to which a behavioral response becomes associated with environmental conditions relies on the proportion and the rate of intensity of reinforcement that occurs as consequences of the behavioral response that is exhibited by an organism. In other words, in operant conditioning, a living creature responds intentionally on associations that are formed between environmental conditions so that to acquire and/or maintain reinforcement that follows the response (Wills 2012). Therefore, in operant conditioning reinforcement constitutes the crucial factor that influences the acquisition and preservation of the learning outcome (McSweeney and Murphy 2014).

Skinner (1938) examined operant conditioning through experimental studies with animals that were placed in a box called the “Skinner box” which was analogous to Thorndike’s puzzle box (Shanks 1995). Through his experimental studies related to the functional processes of operant conditioning, Skinner observed three kinds of responses that have the potential to occur after the performance of behavioral responses (Klein and Mowrer 1989). Those include the neutral responses, that is, responses that do not affect the frequency of an action. The reinforcers that constitute responses that can be positive (i.e., adding a response) or negative (i.e., removing a response) that increase the frequency of the behavioral response that precedes the reinforcer. Finally, Skinner observed responses that

possess punishing qualities (i.e., punishers), which could also operate either positively or negatively, yet contrary to reinforcers, punishers decrease the frequency of a behavioral response (Schachtman 2011).

Types of Reinforcement

As already mentioned, positive reinforcement increases the probability that a behavioral response will be exhibited in the future by offering a consequence that the organism perceives as rewarding, that is, offers a favorable outcome. For instance, if a mother cooks to her son his favorite food every time he is cleaning his room, he will be more likely to repeat this behavioral response in the future, thus strengthening the behavioral response of cleaning his room (Schachtman 2011). In negative reinforcement, a behavioral response is strengthened by ending, eliminating, or avoiding an aversive consequence such as a distressful stimulus and/or condition (Shanks 1995). For instance, a person that has a headache and takes an aspirin which stops the headache she/he would be more likely to take an aspirin when she/he reexperience a headache in the future to eliminate the headache, thus strengthening the behavioral response of taking an aspirin when a headache is experienced by that person (Ramnero and Torneke 2011).

Reinforcement of peoples’ behavioral responses could be achieved by a variety of stimuli, that is, from a favorite food or a nice compliment. Yet reinforcers are categorized between primary reinforcers and secondary reinforcers (Ramnero and Torneke 2011). The reinforcers that are biologically important are called primary reinforcers. They are also referred to as unconditional reinforcers. A primary reinforcer arises naturally and does not necessitate any effort or type of learning. For instance, nutrition, sleep, oxygen, and sexual activity are only a few examples of primary reinforcers that occur naturally, that is, they operate without the need for previous learning. The majority of primary reinforcers are evolutionarily significant (Shanks 1995). That is, they have been taking place since the beginning of time and enhanced organisms’ capacity to adapt and survive. Furthermore, primary reinforcers are more

efficient in comparison to secondary, that is, conditioned reinforcers, regarding the learning outcomes (Baum 2017). For instance, a young boy that is hungry is more likely to clean his room if his mother tells him that when he finishes he could have his favorite food, rather than cleaning his room for 5 euros. Primary reinforcers could be used to positively as well as negatively reinforce a behavior. Secondary reinforcers and/or conditioned reinforcers obtain their reinforcing capacities through the acquisition of an association with a primary reinforcer and/or other secondary reinforcers (Schachtman 2011). For instance, money could positively and/or negatively reinforce a behavior due to their association with the acquisition of numerous primary reinforcers such as nutrition, water, clothes, and accommodation just to name a few. In addition, attention and approval are reinforcers of interpersonal nature that are referred to as social reinforcers, and they also have the capacity to positively as well as negatively reinforce a behavior (Ramnero and Torneke 2011).

Furthermore, it is highly important to distinguish reinforcers that exert their effect through feedback, a central element of cognitive learning (Wills 2012). Specifically, in cognitive learning feedback is considered to be a reinforcer that exerts its effect through associative learning (Shanks 1995). Specifically, feedback, that is, information related to the environmental influences, that a behavioral response exerts significantly influences the learning outcome (Schachtman 2011). Shanks (1995) adds that the adaptive qualities that the feedback possesses provide a theoretical framework to explain the reasons why a lot of human learning is achieved despite the nonappearance of apparent reinforcers such as nutrition, clothing, and shelter.

Responses with Punishing Qualities

Punishment constitutes an important notion in the theory of operant conditioning. The main functional quality of punishers is to decrease the frequency of an undesired behavioral response. Specifically, in positive punishment, an aversive stimulus is added when an organism displays an undesired behavioral response (Ramnero and

Torneke 2011). Consequently, the organism learns that whenever that specific behavioral response is exhibited, he/she receives negative consequences and thus the possibility of repeating that behavioral response decreases. For instance, an individual who receives a fine because she/he was driving above the speed limit (McSweeney and Murphy 2014). The punishment in response to her/his behavior would discourage her/him from driving above the speed limit in the future. In negative punishment, a needed object is removed in response to the performance of a certain undesirable behavior by an organism. Consequently, the organism learns that whenever that behavior is exhibited the needed object is removed; thus, the organism would be less likely to exhibit that behavior in the future so that to avoid the removal of the needed object (Shanks 1995). For example, every time a young boy speaks impolitely to his mother, the last take away his mobile phone for a week away, a consequence that is discouraging him from repeating that behavior again in a future time.

As mentioned above, Thorndike claimed that learning is composed of the development of associations between stimuli and reactions and that these associations are developed every time a reaction is rewarded (McSweeney and Murphy 2014). The work of Thorndike on learning theory set the ground for the development of a number of theoretical models of associative learning that postulate that learning is governed by the formation of stimuli-responses associations (Ramnero and Torneke 2011). Despite that stimuli-responses associations are still considered to be involved in learning, theoretical models of associative learning since 1970 directed more their attention on stimuli-stimuli rather than stimuli-responses associations (Shanks 1995). This shift was done for a number of reasons. Firstly, this shift is considered by many researchers to be entirely practical. Specifically, Thorndike supported his theoretical inferences on experimental research of operant conditioning during which an animal (i.e., usually a cat) exhibited a behavioral reaction (i.e., press a lever) which was followed by the acquisition of a reward (i.e., food). The issue with this experimental design is that the cat, not the researcher,

determined when the response will be rewarded; thus, it is hard to determine the exact occurrence of each episode of learning (Wills 2012). Therefore, theorists and experimenters directed their focus on classical conditioning where a neutral stimulus signifies the occurrence of a biologically relevant stimulus and thus induces a classically conditioned response. Despite that each trial is completely controlled by the person that conducts the experiment, the indications of learning in this experimental procedure task are detected when the neutral stimulus acquires qualitatively similar qualities with the ones that the unconditioned stimulus has and in turn induces a classically conditioned response that is also qualitatively similar with the unconditioned response (Schachtman 2011).

Associationism as a Theory of Mental Structure

The notion of associative learning has been adopted by a variety of related theoretical perspectives which understand learning as the acquisition of associations between stimulus-response contingencies (i.e., instrumental conditioning) or the acquisition of associations between stimulus-stimulus contingencies (i.e., Pavlovian conditioning) or the acquisition of associations between stimulus-valence contingencies (i.e., evaluative conditioning) (McSweeney and Murphy 2014). Associative learning theorists have consistently proposed that the acquisition of associations between environmental contingencies is encoded in the form of an associative structure (Hall 2002). The operational concept of associative structure depicts the nature of the relationship that associates two separate mental states. An example of an associative structure is an association between honey and mustard. Specifically, in this scenario honey and mustard develop an associative structure which functions operationally (Delamater and Lattal 2014). That is, when the mental state of honey becomes activated, triggers also the activation of the mental state of mustard and the other way around.

The operational and theoretical conceptualization of associative structures indicates that

associations maintain symmetric cause-effect relations. That is, if an individual has formed an association between honey and mustard, the honey should trigger the activation of mustard and the mustard should trigger the activation of honey. However, Thorndike and Skinner claimed that the order through which organisms learn affects the causal order of recall. In other words, if an individual hears only honey and mustard, then honey would be more likely to acquire the capacity to trigger the activation of mustard rather than the other way around. Therefore, a central operational principle in the examination of associative structures indicates that organism must learn the associative elements in a randomized sequence (Hall 2002).

In addition, it has been cited that the philosophical movement of British Empiricism wanted to designate a systematic and well-defined theoretical perspective based on associationism that would enable them to decrease the extent to which they had to rely on intrinsic functions (Staddon 2014). Similarly, the behavioral movement wanted also to develop a systematic and well-defined theory based on associationism. Theorists that advocate about the development of a theoretical perspective of thinking entirely have consistently proposed that the formation and maintenance of an association between two elements is regulated, by the rate of recurrence of former associations between the associated elements (Shanks 1995). This perspective hypothesized that associative structures encrypt, at least covertly, the rate of recurrence of former associations between elements that become associated. Additionally, the intensity of this associated connection is regulated through the past experience of these two elements by an organism. That is, the past experience of learned associations by an organism regulates the present operational outline of the analogous associative structures (Hall 2002).

Contemporary Study of Associative Learning

Throughout the twentieth century, a substantial amount of time was devoted for the extensive study to the fundamental mechanisms that

underlie both classical conditioning and operant conditioning (Wills 2012). Yet the study of classical and operant conditioning was conducted for different purposes. On the one hand, there were theorists and researchers who advocate that the experimental study of behavior merits a distinct and experimentally solid type of analysis (Staddon 2014). Theorists and researchers that were advocates of this view proposed that the study of the operational associations between environmental conditions and behavioral dynamics was adequate for understanding, predicting, and controlling behavior (Shanks 1995). On the other hand, there were theorists and researchers that advocated that the experimental analysis of learning in behavioral terms was just a means through which one can study the fundamental processes of the mind. For instance, Pavlov claimed that the operational procedures related to the study of classical conditioning phenomena could have utility exclusively to the degree that the role of the relevant brain processes is considered (McSweeney and Murphy 2014).

Furthermore, due to the operational procedures of classical conditioning in which two stimuli are presented at the same time, it is considered that learning related to this associative connection relies on the dynamic characteristics of stimuli-stimuli associations. Additionally, research related to this hypothesis indicated that the conditioned stimulus acquires the capacity to trigger a representation of the unconditioned stimulus that has been associated with it (Shanks 1995). As mentioned above theorists and experimenters directed their focus on classical conditioning for various reasons. Firstly, classically conditioned associations acquire the capacity to fundamentally influence organism's behavioral responses. Specifically, classically conditioned associations constitute a mechanism which enables an organism to adapt to impending biologically important conditions (Schachtman 2011). Moreover, the operational principles of classical conditioning enabled mental health professionals to develop and implement effective treatment interventions for affective abnormalities and substance abuse. Last but not least, Pavlovian conditioning equipped

learning theorists and researchers with an efficacious experimental design that enables for a significantly accurate analysis of the way that organisms form associations between environmental and interoceptive stimuli (McSweeney and Murphy 2014).

The Rescorla–Wagner Model of Classical Conditioning

A highly influential model of classical conditioning was developed and presented by Robert A. Rescorla and Allan R. Wagner (McSweeney and Murphy 2014). Despite that over than 40 years have passed from its publication, there are no indications of a decrease in its influence in the field of learning in general and in the subfield of associative learning specifically (Schachtman 2011). The Rescorla–Wagner model proposed that while living beings interact with their environment, develop causal expectations that enable them to estimate relationships between environmental conditions (Wills 2012). According to this model, learning involves acquiring knowledge related to the way that the environment is causally organized (Rescorla 2008). An organism becomes able to achieve learning by developing solid associations between environmental components (Shanks 1995). Yet even if the environmental components become contiguous and in turn the organism forms associations between them, the environmental components need to also allow the acquisition of knowledge related to causal relationships (Wills 2012). Actually, the fundamental idea is the concept of contingency and how an organism perceives it. This model by integrating cognitive capacities within the formation of associations indicated the acceptance of both cognitive functions and associative processes in the brain, something that quickly earned the favor of experimental psychologists (Shanks 1995). However, despite its great influence, the theoretical model presented by Robert A. Rescorla and Allan R. Wagner did not go without challenge. Specifically, it has been cited that various research data within the learning literature could not easily be explained through this

model, and some of these data led to the development of other theoretical models related to associative learning (McSweeney and Murphy 2014).

The Role of Prediction Error in the Study of Associative Learning

Contemporary research related to the environmental conditions that are necessary to assist and enhance learning has consistently suggested that learning progresses as an operation of the difference between the predicted and the acquired result (McSweeney and Murphy 2014). That is, the level of learning that is achieved by an organism in a given moment is reflected in the degree of this prediction error. For instance, high level of prediction error results in high degree of learning, whereas the small level of prediction error results in a smaller degree of learning (Delamater and Lattal 2014). Moreover, the concept of the prediction error is significantly important as it enhanced understanding of conditioned responses of fear and modified the lens through which the operations of specific neurobiological mechanism are understood (Wills 2012).

In addition, the process of the prediction error is not only involved in the acquisition of new associations but is also involved in the inhibition of that learning. That is, in trials where the predicted result is higher than the one that it is acquired, that is, the prediction error is negative, the associative intensity is considered to be loosened (McSweeney and Murphy 2014). The associative phenomenon of the negative prediction error is usually examined through the process of extinction (Rescorla 1993). That is, the process where a contained stimulus consistently occurs without the anticipated unconditioned stimulus, something that ultimately leads the conditioned response to weaken and finally extinguished (Schachtman 2011).

Most of the current theoretical perspectives related to learning propose that extinction is governed by the error correction process, a conceptualization that became widely known through the classical conditioning model of Rescorla–Wagner (McSweeney and Murphy

2014). This model claims that learning takes place when an important incident that constitutes an unconditioned stimulus is surprising (Rescorla 1968). In addition, this model proposes that when the process of extinction begins, the absence of the unconditioned stimulus when the conditioned stimulus is received is surprising too (Wills 2012). In order for the prediction error to be fixed, the association with the unconditioned stimulus is loosened till the conditioned stimulus precisely foresees the no unconditioned stimulus result (Rescorla 1993). Given an adequate quantity of extinction, this model presumes that the force of an association could be fully extinguished (Schachtman 2011).

Theoretical perspectives related to error correction are also congruous with neurobiological research related to the mechanism of associative learning. Specifically, it has been consistently cited that the brain encrypts error signals throughout the course of extinction (McSweeney and Murphy 2014). For instance, in appetitive conditioning, the firing of midbrain dopaminergic neurons is considered to hold a variety of significant roles, such as detecting reward prediction errors (Rescorla 1993). Furthermore, it has been consistently proposed that the extinction mechanisms are based on the process of prediction error correction. Specifically, learning initiates a reinforcer with surprising qualities when signals and/or actions foresee one (Wills 2012). In addition, the process of extinction is defined as an additional type of learning and not a process that erases learning. Therefore, it is assumed that prediction error develops a new form of learning which is challenging or interfering with the initial learning (Shanks 1995).

Conclusion

Pavlov's and Thorndike's operational procedures related to the study of the formation of conditioned behavioral responses are now considered conventional illustrations of simple types of associative learning that enabled researchers to experimentally examine the significance of generating intelligent action (McSweeney and

Murphy 2014). In addition, due to its examination with regard to recently developed associative bonds between elements derived from the environment and actions, the commitment of forming a fully mechanistic conceptualization of behavior is almost within grasp. Moreover, understanding in depth the mechanistic abilities as well as their operational importance across species enabled theorists in the field of experimental psychology to conduct efficacious comparative examinations of behavioral responses (Wills 2012). Theoretical models of associative learning are interested in the underlying mechanisms that regulate the associative connection that is developed when two stimuli accompany each other. During the twentieth century, the theoretical notion of associative learning has to a great extent been influenced through theoretical perspectives in the fields of behavioral psychology, cognitive psychology, social psychology, developmental psychology, and evolutionary psychology (McSweeney and Murphy 2014). In the late twentieth century, some of the underlying mechanisms of both classical and operant conditioning have been significantly elaborated in a theoretical as well as in an operational level. Specifically, the work of Robert A. Rescorla in classical conditioning, the work of Allan R. Wagner on associative learning, and the work of Nicholas Mackintosh in conditioning and associative learning had a great influence on the contemporary theoretical as well as operational advances that have been achieved in the fields of classical and operant conditioning and our understanding of behavioral dynamics.

In addition, the contemporary study of associative learning has been mainly focused on three central domains: firstly, to the environmental conditions that are necessary to assist and enhance associative learning (Wills 2012), secondly, to the contextual as well as the structural characteristics of associative learning, and thirdly, to the theoretical as well as the operational processes required in interpreting associative learning into overt behavioral functioning. Conceptualizing the central difficulties related to associative learning in such a manner proceeds a long way in the direction of designating standards for a

sophisticated analysis of associative learning mechanisms. In addition, provides a solid basis for the organization of research findings that can add to the preexisting knowledge related to associative learning (Schachtman 2011).

Cross-References

- Adaptive Learning
- Classical Conditioning

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Associative Tool Behavior

► Sequential Tool Use

Assortative Mating

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Synonyms

Assortment; Endogamy/exogamy; Homogamy/heterogamy

Definition

Assortative mating is the nonrandom coupling of individuals based on resemblance on one or more characteristics (Buss 1984).

Introduction

“Tell me what company thou keepest and I’ll tell thee who thou art” (Miguel de Cervantes, Don Quixote, Chap. XXIII).

Assortative mating (AM) is one of the major departures from random mating. It occurs in two forms, positive AM or homogamy, when phenotypes of mated partners are more similar than would be expected under random mating, and negative AM or heterogamy (disassortative mating), when the mated partners are more dissimilar than they would be under random mating. Assortment is usually measured as a correlation between the values of the same phenotypic or genotypic characteristics across mating partners. The primary effect of AM is a change in the expected genotypic frequencies from those expected under the Hardy-Weinberg law. Positive AM has much the same effect as inbreeding. It increases the relative frequency of homozygotes, while negative AM has the opposite effect, i.e., it increases the relative frequency of heterozygotes. Until now, AM has been explored on a vast range of variables including sociodemographic, physical characteristics, health behaviors, psychopathology, intelligence and other cognitive abilities, values, attitudes, as well as a wide range of personality traits. For almost all of them, positive assortment has been found to a greater or lesser degree, while negative AM has rarely been found. One example is spousal dissimilarity at human leukocyte antigen alleles within the major histocompatibility complex region, although the evidence has been equivocal (Havlicek and Roberts 2009). Regarding psychological variables, Buss (1984) obtained negative AM for dominance and submissiveness dimensions on spouse reports and interviewers’ ratings. Similarity between partners is usually considered as a trait-specific assortment, but sometimes also as a cross-trait assortment. Trait-specific assortment is similarity in a particular characteristic such as height, intelligence, or extraversion, while cross-trait assortment is a coupling that is based on congruency on different, but similarly valued traits, such as a tendency for extraverted women to mate with conscientious men (Buss and Barnes 1986).

Theoretical Considerations and Possible Functions of AM

Several theoretical explanations of AM are proposed. The theory of complementary needs is based on the modified version of Murray’s needs scheme (Winch et al. 1954). The authors proposed

that during mate selection, individuals choose a person who shows the highest potential to satisfy one's needs. The rule for needs satisfaction is complementarity rather than similarity. It comes in two forms: (1) a need of a person A is qualitatively different than that of a person B (e.g., one person has high need for dominance, and the other for deference), and (2) the intensity of a need is opposite in a person A compared to the same need in a person B (e.g., one person has high, and the other low need for achievement). Although the authors reported some supporting evidence, later studies were unable to replicate them. A social psychological explanation of AM is based on the concept of consensual validation. It is assumed that people choose similar partners simply because finding commonalities with other people is inherently rewarding (Byrne 1971). Therefore, if there is a correlation between similarity and validation of one's worldview, learning through conditioning will eventually lead to the preference for similarity. In a theoretical explanation of AM, Buss (1984) suggested that people create extensive and enduring environments through the selection of a mate. By choosing a similar mate, a partner is also selecting a social environment that corresponds to his/her existing characteristics. Therefore, AM may be considered as an important mechanism for creating genotype-environment correlations that may consequently affect adult personality development. For example, if two extraverts mate, they are likely to reinforce each other's initial personality predispositions by selecting specific environments (e.g., attending big parties) and avoiding others (e.g., going to the cinema). Another process through which AM may affect adult personality development includes the concept of a pacer, i.e., a person who is moderately discrepant in a certain trait from the target individual, and is therefore an optimal model for the development of the target person (Buss 1984).

The genetic similarity theory proposed by Rushton et al. (1984) is a more general version of Hamilton's inclusive fitness theory. They suggested that organisms behave in a way to increase the fitness not only of their blood relatives, but also of all genetically similar organisms regardless of their kinship status. The authors

applied this assumption to many aspects of human behavior, including AM. Specifically, they hypothesized that phenotypical matching of mates is only a proximal mechanism whose function is to increase the probability of mating with a genetically similar organism. The theory predicts many advantages of mating with optimally genetically similar individuals such as increased altruism, relationship stability, increased genetic similarity with progeny, all of which result in a higher parental investment as well as fecundity. Some of the supporting evidence for this theory are positive associations of assortative mating and marital quality, stronger assortment on more genetically based characteristics, and genetic similarity of couples in genes coding for blood types (Rushton 1989). However, the theory as well as the evidence was strongly criticized by many authors (see Open Peer Commentary of Rushton 1989). The objections were mostly related to the irrelevance of genetic similarity for the prediction of altruism for nonkin because it does not predict similarity in other genetic loci, methodological and statistical issues in correlating heritability and assortative mating index, as well as potentially biased results of blood antigen analyses in the sample of disputed paternity cases. An alternative evolutionary explanation of AM involves an imprinting-like process. According to this explanation, an opposite-sex parent's image is imprinted early in the child's development. During this sensitive period, only closely related persons, usually parents, are likely to be present. After reaching maturity, a person will try to find a partner similar to the opposite-sex parent resulting in the similarity between the person and his/her partner. It seems that individuals have been selected to reach an optimum balance between inbreeding and outbreeding, because both types of mating have reproductive cost and benefits (Bereczkei et al. 2002).

Figueredo and Wolf (2009) explain AM in the context of Life History Theory (LHT). As it is well known, LHT describes the strategic allocation of resources between major components of fitness such as survival and reproduction. LHT assumes that species living in harsh (high-risk of mortality), unpredictable, and uncontrollable environments evolve fast LH traits, while species

living in predictable, stable, and relatively safe and controllable environmental conditions evolve slow LH traits. Conditions favoring faster LH strategies have a selective advantage from the higher rates of genetic recombination and hence exogamy that leads to lower parental effort and a greater number of offspring, thus increasing the probability that at least some proportion of them will survive under unpredictable conditions. On the other hand, in order to preserve well-adapted genomes, conditions favoring slower LH strategies lead to endogamy, higher parental effort, and lower rates of genetic recombination. Therefore, AM coefficients for heritable characteristics will be higher for slower than for faster LH strategies (Figueredo and Wolf 2009).

Mechanisms Underlying AM

Relevant question regarding AM is whether it is due to initial assortment, i.e., partners are already similar in some phenotypic characteristics at the beginning of their relationship, or convergence, i.e., partners become more similar in these characteristics over time as a function of increased familiarity, interactions, and synchronized routines (Luo 2017). Furthermore, similarity correlations may reflect active assortment or a preference for mating with a partner who is similar on a particular characteristic, or social homogamy, which refers to the mating with a partner who lives in a shared social environment and has similar social background (e.g., similarity in age, education, socioeconomic status). In contrast to active assortment, social homogamy refers to passive, indirect influences on partners' similarity, because people similar in social background may also share other characteristics such as attitudes, values and interests (Luo 2017). For most examined characteristics, evidence provides stronger support for initial assortment rather than convergence, and active assortment rather than social homogamy (Watson et al. 2004). Along with the processes mentioned above, mating market operation may also contribute to the similarity between partners. Based on the principle of social exchange theory, mating market operation affects the selection of a mate in a way that partners with highly desirable characteristics have more

opportunity to mate with similarly desirable partners, leaving the less desirable to mate with each other (Luo 2017). Similarity between partners in a long-term relationship may be also due to the process of attrition. Namely, partners with lower levels of similarity may end their relationship earlier, which may lead to the increased similarity in partners who remained in a relationship (Luo 2017).

Assortative Mating for Various Characteristics

Compared to other characteristics, socio-demographic variables show the strongest assortment across human populations, with the highest AM for age (from 0.70 to 0.95) (Watson et al. 2004), and education (from 0.50 to 0.65) (Hur 2003; Rosenfeld 2008). An increase in educational homogamy has been found in USA, but the results vary across the education distribution and are sensitive to the measures of couples' similarity (Schwartz 2013). A strong assortment for race and religion has been found, but at least in USA it has declined over the twentieth century (Rosenfeld 2008).

AM is widespread for a number of physical characteristics including height, weight, and BMI, the degree of these assortments being low to modest (from 0 to 0.30) (Hur 2003). A meta-analysis has shown that AM for height is relatively constant over time and that it is slightly, although not significantly stronger in Western than in Non-Western populations (Stulp et al. 2017). Regarding weight, research has shown that partners do not become more similar in this characteristic with increased length of their relationship. Furthermore, research of facial similarity showed that partners are perceived to be more facially similar to one another than it was expected by chance, but the association between relationship length and facial similarity remains unclear. A meta-analysis has obtained mean correlation of 0.49 between partners for physical attractiveness (Feingold 1988).

Generally, AM for social and personal values and attitudes tends to be moderately positive, ranging from 0.20 to 0.50 (Luo and Klothnen 2005). However, political and religious attitudes consistently show higher AM correlations (from

0.42 to 0.74) (Watson et al. 2004). It appears that partners' similarity in political attitudes depends partly on shared genetic factors (genotypic AM) and also on similarities in social and cultural background (social homogamy) as well as partner-specific shared environmental effects such as common habits and friends (Kandler et al. 2012). However, evidence concerning convergence has been somewhat inconsistent, with some studies showing convergence in values and attitudes, while others show that partners' similarity in social and political attitudes was present at the beginning of the relationship and increased very little over time (Luo and Klohnen 2005).

The majority of studies report a positive assortment between married partners for cognitive ability measures ranging between 0.20 and 0.45 (Watson et al. 2004). Some studies have found that AM is particularly strong for verbal abilities (around 0.50) compared to nonverbal, such as spatial ability, perceptual speed, and visual memory (around 0.30), that may be due to the easier assessment of someone's verbal than nonverbal ability. AM for *g* factor has also been found to be substantial, with average correlations between the partners of about 0.40 (Plomin et al. 2013). Higher positive assortment has been found for those abilities that are more saturated by *g* factor, i.e., those showing higher heritability (Nagoshi and Johnson 1986). It seems that the mechanisms underlying AM for intelligence are initial assortment rather than convergence, and active assortment rather than social homogamy (van Leeuwen et al. 2008).

Low to moderate degree of positive AM has been found for numerous personality traits, with correlations rarely exceeding 0.30. However, one of the exceptions seems to be sensation seeking, for which the strongest AM has been repeatedly found (McCrae et al. 2008). The majority of evidence has been obtained on Five Factor model, which is assumed to provide a comprehensive account of personality (McCrae et al. 2008; Watson et al. 2004). The studies usually show the most consistent evidence of positive AM for openness, followed by agreeableness, conscientiousness, and neuroticism, while extraversion shows inconsistent results varying from low negative to moderate

positive assortment (McCrae et al. 2008; Watson et al. 2004). For example, in a sample of newlywed couples, Watson et al. (2004) have found significant negative assortment for extraversion on both self- (−0.17) and spouse-ratings (−0.14). However, some studies have found little or no AM for five factor personality traits (e.g., Luo and Klohnen 2005). On the level of five factor personality traits facets, differences in assortment have been especially pronounced for openness domain, showing moderate positive assortment for aesthetics and values, and no assortment at all for fantasy and feelings (McCrae et al. 2008).

AM for socially undesirable personality traits has been rarely explored. Moderate positive assortment has been obtained for all Dark Triad traits, a cluster of three antisocial personality traits, psychopathy, Machiavellianism, and narcissism (Kardum et al. 2016). Machiavellianism has shown the highest degree of assortment probably because this trait is a more attitude-like concept, and attitudes, as already mentioned, show a higher degree of positive assortment. Positive assortment has also been found for numerous other personality traits, with low to moderate correlations between partners (McCrae et al. 2008; Watson et al. 2004).

For most personality traits, evidence supports initial assortment more strongly than convergence because similar effects have been found in both younger and older couples (McCrae et al. 2008), as well as when relationship length has been controlled for (Watson et al. 2004). Additionally, few existing longitudinal studies have found some convergence, but limited only to several traits (see Rammstedt and Schupp 2008). Research has also shown that AM in personality traits is due to active assortment rather than socio-demographic background variables such as age and education (McCrae et al. 2008; Watson et al. 2004).

Other factors influencing AM for personality traits have been rarely and nonsystematically examined. Although there are theoretical reasons for assuming that AM may be universal because mating patterns have been strongly influenced by evolutionary pressures, there is some evidence of cross-cultural differences in assortment for

personality traits. Examining AM for five-factor personality traits on married couples in four Western cultures, McCrae et al. (2008) have found some subtle cultural differences. However, the results obtained on newlywed couples from mainland China showed stronger similarity on personality traits (from 0.33 to 0.66) than those usually obtained on Western cultures, while the degree of AM in demographic variables and attitudes was mostly similar to Western cultures (Chen et al. 2009). This suggests that cultural differences may promote assortment in personality. The level of a trait can also affect the degree of AM. Namely, assortment may be differentially expressed across trait levels. For example, a higher degree of positive assortment has been found for slow rather than fast LH strategy (Figueredo and Wolf 2009). Furthermore, Lee et al. (2009) showed that a degree to which certain traits serve as indicators of individuals' values could be an additional factor that modifies the degree of AM. They found higher positive assortment for honesty-humility and openness to experience than for other HEXACO personality traits. Furthermore, these two traits serve as dispositional bases for individuals' value system, thus exerting important effects on one's identity. Additionally, some features of personality traits such as visibility, malleability, and social desirability (Luo 2017), as well as different data sources may also affect the degree of AM. For example, McCrae et al. (2008) have found the largest differences in the degree of AM between self-self and partner-partner reports for extraversion and the smallest for agreeableness. The abovementioned factors influencing the degree of AM in personality traits are often atheoretical, and their effects relatively weak.

Positive AM has also been obtained for numerous adverse behaviors including alcoholism, smoking, aggression and violence (Agrawal et al. 2006), as well as disorders including anxiety, depression, schizophrenia, bipolar disorders, and autism (Nordsletten et al. 2016). Studies have found low to moderate positive correlations (from 0.07 to 0.45) between partners for drinking behavior (Grant et al. 2007), as well as for ever-smoking (0.18) and current smoking status (0.43) (e.g., Boomsma et al. 1994). It seems that partners'

similarity for cigarette smoking, nicotine addiction, regular alcohol consumption, and alcohol dependence is mainly due to initial assortment (Agrawal et al. 2006), although some studies support both initial assortment and convergence hypotheses of partner similarity for substance use (Fleming et al. 2010).

Positive AM between romantic partners has been found for various antisocial behaviors. For example, moderate to strong assortment for violent offending has been found (about 0.40), and it may be attributed to both phenotypic assortment and social homogamy (Frisell et al. 2012). It seems that convergence could also be a mechanism underlying AM for antisocial behaviors. The convergence for these behaviors has usually been explained by behavioral contagion, implying that behavior of a partner "infects" the behavior of other partner, thus increasing the similarity between them over time (Moffitt et al. 2001).

Examining the patterns of AM within and across 11 major psychiatric disorders on population-based cohort, Nordsletten et al. (2016) have found widespread positive assortment both within and across this spectrum of disorders. The highest AM has been found for autism (0.47), and the lowest for bipolar disorder (0.15). Within-disorder correlations were marginally higher (from 0.11 to 0.48) than cross-disorder correlations (from 0.01 to 0.42). However, the correlations were either not obtained or were weaker among the selected cases of non-psychiatric conditions (e.g., Crohn's disease, multiple sclerosis), but of similar incidence and age at the onset of the relationship (from -0.03 to 0.10). Several mechanisms underlying AM for psychiatric disorders have been recognized including initial assortment, secondary assortment (i.e., mate selection based on characteristics that correlate with psychiatric morbidity such as personality traits, age and education), social homogamy, marital interactions, and exposure to common negative stressful environment. However, the evidence concerning these mechanisms is weak and inconsistent, especially in the context of specific psychiatric disorders.

There is also meta-analytic evidence of modest positive AM for both traditional and emerging risk factors of ischemic cardiovascular disease (e.g., blood pressure, smoking, factors linked to

bodyweight, metabolic syndrome). Furthermore, a concordance for dichotomous outcomes such as hypertension, smoking, diabetes, and obesity has also been obtained. Initial assortment seems to be responsible for similarity between partners in most traditional cardiovascular risk factors, while shared marital environment influenced mainly lipid metabolism (Di Castelnuovo et al. 2009).

Consequences of AM

AM has several important evolutionary, genetic, psychological, and social consequences. Two major evolutionary benefits from positive assortment have been suggested. Positive assortment for similar genes adds to the parents' inclusive fitness by increasing gene representation in their offspring and genetic potential for altruistic behaviors between parents and between parents and their offspring (Thiessen et al. 1997). Regarding genetic consequences, AM increases the contribution of additive genetic variance so that the offspring differ more from the average than they would if partners mate randomly. Even if similarity between partners is modest, it may increase genetic variability in the population because its effects accumulate over relatively few generations (Plomin et al. 2013). For example, the increase in heritability due to AM may explain why some psychiatric disorders (e.g., schizophrenia, ADHD) have such high heritability notwithstanding reduced fecundity (Plomin et al. 2016). Furthermore, positive assortment may influence the estimates of heritability because it increases correlations for first-degree relatives, and if it was not taken into consideration, it could decrease heritability estimates and its effect would be attributed to shared environment (Plomin et al. 2013).

There are several complex interactions between genetic and social consequences of AM. As already mentioned, AM creates genotype-environment correlations that can have numerous important implications. For example, homogeneity of the rearing environments created by similar partners may have important consequences for their children's development. Positive AM increases, while negative decreases the variability of a certain characteristic in future generations, which may have important psychological and social consequences. For

example, characteristics that are more variable also become more salient and thus represent the bases for differentiation among individuals as well as for their social evaluation (Buss 1983). Greater variability in certain characteristics may increase the number of individuals at the tails of the distribution with either positive (e.g., exceptionally creative individuals) or negative consequences (e.g., autism as the genetic result of assortative mating of two high systemizers; Baron-Cohen 2006).

Positive AM for numerous characteristics such as intelligence, attitudes, interests, and personality traits predicts various relationship outcomes such as higher satisfaction and quality of relationship and lower relationship dissolution (Luo and Klohnen 2005). There are several partly overlapping psychological explanations for similarity-satisfaction effect. The first suggests that similarity fosters partners' self-verification, improves understanding, and increases closeness (Luo 2017). Other explanations encompass mere exposure effect or a preference towards familial stimuli and implicit egotism or a preference towards whatever reminds us of ourselves (Pelham et al. 2002). Because AM for socioeconomic variables (education, occupation, income, class background, race/ethnicity, and religion) is an important factor that determines the characteristics of families and their reproduction, it may have relevant social consequences such as inequality within and between generations, as well as long-run population change (see more in Schwartz 2013).

Conclusions

On a vast range of variables, positive rather than negative AM has been found. The highest degree of similarity has been obtained for socio-demographic variables and attitudes, followed by moderate similarity for cognitive abilities, psychiatric disorders, antisocial and adverse behaviors, and the lowest for physical characteristics and personality traits. Initial and active assortments have most frequently been suggested as mechanisms underlying AM, with the evidence for convergence and social homogamy being scarce.

Advances in theory and empirical research are highly needed because AM has important evolutionary, genetic, psychological, and social consequences.

Cross-References

- [Dating](#)
- [Marriage](#)
- [Mate Choice Effects](#)
- [Mate Preferences](#)
- [Opposite-Sex Relationships](#)
- [Pair-Bonding](#)
- [Relationship Choices and Sexuality](#)
- [Resemblance](#)
- [Sex Differences Versus Gender Symmetry](#)

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Assortment

- Assortative Mating
- Cooperation Varies with Genetic Relatedness

Athletic Competition

- Team Sport

Atrophy

- Use It or Lose It

Attachment

- Parent Influences

Attachment in Adulthood

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Synonyms

[Adult attachment](#)

Definition

Attachment in adulthood addresses the role of the attachment system in adult relationship functioning and dynamics. In the normative course of development, individuals transfer attachment functions from the child-caregiver relationship to peer relationships, principally to romantic relationships. Within these, individual differences regarding romantic attachment have been found to exert significant influence over important aspects of relationship functioning, including the stance toward intimacy, communicative strategies, and emotion regulation.

Introduction

Originating in British psychoanalyst and child psychiatrist John Bowlby's formulations about the nature of human bonds (see "John Bowlby: Pioneer of Attachment Theory"; "Evolutionary Foundations of the Attachment System and Its Functions"), attachment theory has stimulated an enormous corpus of research, particularly on attachment during infancy and childhood. Bowlby himself was however convinced that attachment is an integral part of human life not just in childhood, but "from the cradle to the grave" (Bowlby 1969, p. 208). This statement remained a hypothesis until the end of Bowlby's active career but has spurred a growing body of

theory and research during the past three decades. The results and current status of this research are the main focus of the current entry.

Since a major part of the research concerning attachment in adulthood has explored the role of attachment in pair bonds, the following depiction mainly revolves around this specific type of relationship. Theory and research pertaining to the status of pair bonds as the normative attachment relationships of adult life are described and discussed, and methodological issues as well as research regarding individual differences in romantic attachment are reviewed. Finally, the entry also addresses an important controversy regarding the status of the attachment system in romantic relationships.

Pair Bonds as Attachment Relationships

The Defining Features of Attachment Bonds

Attachment in childhood denotes the affectional bond that children form to their primary caregiver (s), and that is typically established within the first 8 months of life (Bowlby 1969). The bond is complementary (i.e., the child forms the bond to the caregiver – not the other way around) and has four defining features: (1) *proximity maintenance*, referring to the maintenance of proximity to the caregiver and the monitoring of the caregiver's availability; (2) *separation distress*, referring to the child's distress and protest in response to separations; (3) *safe haven functioning*, referring to the child's turning to the caregiver for comfort and support when distressed; and (4) *secure base functioning*, referring to the child's use of the caregiver as a reference point for exploration of the environment. In addition, and as implicated by these features, the attachment construct presupposes that the attached individual perceives the attachment figure as stronger and wiser than the self, particularly in challenging situations.

In conceptualizing adult relationships as attachments, theorists have argued that these features of the child-caregiver relationship eventually become transferred to the close relationships of adult life. However, important changes are also expected to occur in the development from

infancy to adulthood (Hazan and Shaver 1994). First, adults come to develop a significantly higher capacity for emotion regulation and mental representation of others, leading to important differences between child and adult attachment dynamics, not least regarding the capacity to tolerate separations. Second, whereas the child's relationship with the caregiver predominantly involves the attachment system and the caregiver's relationship with the child predominantly involves the caregiving system, in adult relationships, these systems typically become integrated together with the sexual mating system, with sexual attraction usually being the precipitating force that brings adult partners into intimate contact. Third, and related to the integration of these behavioral systems, the complementary or asymmetrical nature of child attachment relationships becomes substituted for more reciprocal or symmetrical relationships, with adult partners mutually seeking and providing security (Hazan and Shaver 1994; Mikulincer and Shaver 2016).

From Parents to Peers: The Gradual Transfer of Attachment Functions

Cindy Hazan and colleagues (Fraley and Davis 1997; Hazan and Zeifman 1994) have suggested that children gradually transfer attachment functions from the caregiver(s) to other relationships, which may eventually come to display the defining features of attachment bonds. Based on their studies exploring children's and adolescents' preferences for specific people in attachment-relevant situations, they argue that children, from approximately 6 years of age, generally prefer to spend time with peers than with their parents, indicating that the proximity-seeking function of the attachment system has been transferred to peer relationships. They further note that by adolescence, peers generally seem to be preferred over parents even as sources of emotional support, at least in mildly distressing situations, with the confiding and comfort-seeking aspects of teen relationships paralleling the safe haven behaviors previously directed primarily toward caregivers. However, at this stage of development, most adolescents still seem to regard their caregivers as bases for security and sources of separation distress. Full-

blown attachments to peers (i.e., bonds involving the four defining features of attachment relationships, including the secure base function) seem not to be established until late adolescence or early adulthood. Among the individuals who, by that time, have transferred their principal attachment from a caregiver to a peer, 80% refers to a romantic partner, indicating that pair bonds be the prototypical or normative instantiation of attachment in adulthood (Fraley and Davis 1997; Hazan and Zeifman 1994).

The establishment of adult attachment seems to follow a chronological sequence that corresponds with the child's establishment of attachment to a caregiver, with proximity-seeking and safe haven behaviors arising early in the relationship, while separation distress and the secure base function take longer to develop (see "Offspring-Parent Attachment"). Importantly, the occurrence of separation distress and secure base functioning in adult relationships seems to depend on relationship status (Hazan and Zeifman 1994). Whereas most romantic partners in relationships of at least 2 years regard their partner's presence as the primary source of security and their absence as the most distressing, the majority of romantic partners in shorter relationships still locate these components of attachment in the relationship with parents, indicating that romantic relationships require approximately 2 years to develop into attachment relationships (Hazan and Zeifman 1994). It is worth noting, though, that a more recent study has indicated that merely 6 months may suffice (Heffernan et al. 2012).

Similarities Between Pair Bonds and the Child's Bond to Its Caregiver

Beyond the findings described above, pair-bond and infant-caregiver relationships also display a number of unique similarities, which are thought to indicate the presence of attachment dynamics in pair-bond functioning and hence adding to the plausibility of conceptualizing pair bonds as attachment relationships (Zeifman and Hazan 2016).

Phenomenological similarities. In the seminal work first conceptualizing pair bonds as attachments, a number of phenomenological

similarities were noted between infant-caregiver and romantic relationships (Hazan and Shaver 1987; Shaver et al. 1988). One such similarity concerns the nonverbal behavior in infant-caregiver and pair-bond relationships, with behaviors such as holding, touching, cuddling, kissing, caressing, smiling, and clinging, as well as sustained eye contact and body investigation, being characteristic of both types of relationship. Although, admittedly, some of these behaviors can appear in isolated form even in other relationships (e.g., friendly kisses, caressing as a part of “casual sex”), the occurrence of these intimate behaviors together is largely unique for relationships between romantic partners and between children and caregivers (Hazan and Shaver 1987; Shaver et al. 1988).

Unique similarities are also evident in the verbal domain. For instance, verbal communication between infants and caregivers typically involves “cooing,” “singing,” and “babbling” on the infant’s part and high-pitch, slow-tempo verbalizations with a “singing” pattern of intonation on the caregiver’s part (i.e., “infant-directed speech”). Most adult relationships are void of this type of communication, but similar phenomena are visible in pair bonds, where partners tend to communicate with a “singing” pattern of intonation and speak with a higher and wider pitch, rendering their voices a more caring tone.

Yet another similarity concerns reunion behaviors, where infants typically display active signaling behaviors (smiling/crying, vocalizing) and proximity seeking (e.g., requests for being lifted) following short separations. Similar behaviors also occur between romantic partners – albeit after more prolonged separations – with positive vocalizations, feelings of euphoria, and requests for physical proximity being typical behaviors upon reunion.

A fourth similarity concerns the idealization occurring in both infant-caregiver and pair-bond relationships. The infant’s appreciation of the caregiver as stronger and wiser – a crucial aspect of the attachment bond – regularly implies a tendency to attribute to the caregiver an unrealistic degree of strength and knowledge. A similar pattern of idealization normally occurs in the initial

stages of romance, where the partner’s negative qualities are usually downplayed and the other is given a certain air of perfection.

Reactions to separation and loss. Bowlby (1969) demonstrated what appears to be a universal pattern of reactions in children, in response to prolonged separations from caregivers. This pattern, which he termed the “protest-despair-detachment” sequence, involves initial reactions of protest, in the form of hyperactivity, agitation, extreme anxiety, and resistance to comfort from others, generally followed by a period of depressive reactions, including inactivity, apathy, and disrupted sleeping and eating. Ultimately, if the caregiver remains absent, the child typically detaches emotionally and gradually regains normal functioning.

Adults’ reactions to inexplicable and involuntary separations from, or the death of, a romantic partner generally follow the very same sequence, further indicating that the attachment system is operative in pair bonds (Zeifman and Hazan 2016). For instance, adults initially tend to react with intense anxiety and denial in response to unexpected loss of a partner, and disorganized behaviors are common (e.g., looking for the deceased one or talking about him/her as if he/she were still alive). This phase is later replaced by a prolonged period of mourning, usually characterized by painful yearning and depressive reactions, such as withdrawal and food or sleep disturbances. With time, most adults regain their organization regarding the loss of the partner; the loss becomes accepted, and a certain degree of emotional detachment takes place, facilitating the resumption of normal functioning and enabling the remaining partner to “open up” to new pair-bond relationships.

Apart from infant/child-caregiver relationships, the protest-despair-detachment sequence is observed almost exclusively in pair bonds. Although the loss of dear relatives and friends can cause profound emotional pain, these losses typically don’t evoke the intense anxiety or panic associated with the loss of a partner, and they are generally less challenging for the individual’s mental organization. The stronger reactions specifically associated with the loss of a partner are

easily understandable from an attachment perspective – they make adaptive sense, if the lost partner served as a primary source of emotional security. Their normative occurrence in adults facing loss of their long-term partners also further strengthens the notion of pair bonds as attachments in adulthood (Zeifman and Hazan 2016).

Physical and psychological health effects.

Child-caregiver and pair-bond relationships also seem to have a similar and uniquely powerful impact on physical and psychological well-being. Paralleling the importance of attachment for the child's physical and psychological development (see "Effects of Attachment Quality and Organization"), there is also ample evidence for the health benefits of close adult relationships, especially pair bonds, as well as for the health decrements of not establishing or losing such bonds. Loss of romantic partners has been associated with increased susceptibility to a number of physical and psychological ills, including impaired immune system functioning and various forms of psychopathology (Ehrlich 2019; Keyes et al. 2014). Indeed, except for the death of a child, divorce or death of a partner are generally perceived as the most distressing events in adult life. Moreover, this distress appears to be qualitatively different from the distress following from the loss of friendships and seems not to be sufficiently compensated by the social provisions of other adult relationships, indicating that certain emotion-regulating functions of the pair bond are not fully available in other adult relationships (Zeifman and Hazan 2016). Neither is this distress evoked in the early stages of relationships that only later develop into attachment relationships. For children, the loss of a primary caregiver is associated with long-term developmental consequences only if it occurs after an attachment bond has been established. Correspondingly, the protest-despair-detachment sequence of reactions following a partner's decease is generally only observable in romantic relationships of at least 2 years' duration (i.e., relationships of the duration typically associated with the formation of full-blown adult attachments; see above). In sum, the severe distress following the loss of a deeply loved other – the very hallmark of

attachment bonds – is mainly present within child-caregiver relationships and long-term pair bonds (Zeifman and Hazan 2016).

Neurobiological Evidence of the Pair Bond as an Attachment Relationship in Adulthood

The advent of neuroimaging techniques and advances in hormonal assays have allowed researchers to examine possible neural and endocrine underpinnings of adult attachment. This research has further strengthened a number of the findings and theoretical proposals described above. For example, Bartels and Zeki (2000) have found that, compared to photographs of friends, photographs of long-term romantic partners evoke a different pattern of neural activity in individuals, implicating regions involved in attachment, a finding that seems to support the idea of pair bonds as the normative instantiation of attachment in adulthood. Subsequent research has also demonstrated different patterns of neural activation at different stages of romantic relationships. Whereas partners in early stages of romance display increased release of dopamine and norepinephrine in response to photographs of their partners (Xu et al. 2011), partners in the more advanced stages of romantic relationships show increased release of serotonin and endogenous opioids (Acevedo et al. 2012). While the former is associated with reward, the latter is associated with stress regulation and implied in infant-mother bonding, further supporting the claim that attachment-related processes are involved primarily in later stages of romantic relationships. Moreover, they also point to the centrality of emotion and stress regulation in both infant-caregiver and pair-bond attachments. In infancy, the hypothalamic-pituitary-adrenal (HPA) axis (a neuroendocrine system essential for regulation of stress) is responsive to caregiver interventions, reflecting the infant's use of the caregiver as a safe haven for comfort and stress regulation (Gunnar and Donzella 2002). Corresponding findings from studies on adult romantic relationships have shown physical contact with the partner to reduce cortisol levels (the end product of the HPA axis stress response) in long-term partners (Ditzen et al. 2007). Furthermore, just as in infant-

caregiver relationships, the cortisol stress response tends to be coordinated within long-term romantic relationships, but not within friendships (Feldman 2017), with the specific nature of coordination varying with relationship quality (Saxbe and Repetti 2006). Adult romantic relationships and infant-caregiver relationships also display a unique endocrine synchrony, not the least with regard to oxytocin (a neuropeptide associated with feelings of calm and well-being; Feldman 2017).

Individual Variations in Romantic Attachment

Based on the large body of evidence described above, it has become generally accepted that long-term pair bonds typically develop into definitional attachment relationships. However, having focused on the normative development in romantic relationships, the previous discussion has left unanswered the question of how to view individual variations in romantic attachment. Bowlby argued that early experiences with the primary caregiver(s) gradually become internalized, forming internal working models of self and others (IWMs; cognitive-affective representations; see “Effects of Attachment Quality and Organization”). The IWMs were thought to display a relatively high degree of stability throughout development and to become generalized to other close relationships later in the individual’s life (i.e., general continuity). Due to new experiences in the attachment relationship (e.g., depression in the caregiver or a caregiver becoming increasingly available after recovering from substance abuse), they were however also thought to be open for revision to some extent (i.e., lawful discontinuity).

Early accounts of adult attachment (Hazan and Shaver 1987; Shaver et al. 1988) drew on this idea, in hypothesizing that the continuity and generalization of IWMs would typically result in distinct adult romantic attachment styles, largely analogous with the major attachment categories in infancy (i.e., secure, avoidant, and anxious-ambivalent; the disorganized category in

childhood was introduced later; for a further description, see “Individual Variations in Attachment”), and exerting influence over different aspects of adult relationship dynamics. The existing research pertaining to this hypothesis is the main focus of the current section. However, before proceeding, some remarks on methodology are made.

The Measurement of Individual Variations in Adult Attachment

In reviewing research on individual variations in adult attachment, it should be noted that existing research has emerged from two different research traditions: one stemming from the field of social-personality psychology and one from developmental-clinical psychology. While the former has largely explored attachment-related dynamics in adult relationships, mainly through the use of different self-report instruments, the latter has focused on adults’ representations of *childhood* attachment relationships in relation to different developmental aspects of life (e.g., the intergenerational transmission of attachment). The developmental-clinical tradition has also employed more in-depth methods of measurement, principally the Adult Attachment Interview (AAI; for a description, see Hesse 2016), a well-validated interview instrument, measuring the adult individual’s current state of mind with regard to parent-related attachment. However, although a large number of important findings have been obtained within the developmental-clinical tradition, not least regarding correspondence between parents’ own attachment representations and their children’s attachment classifications (Hesse 2016), these findings fall outside the scope of the present entry.

Second, while assessments of child-caregiver attachment regard the quality of the relationship, assessments of romantic attachment concern the individual’s stance regarding attachment-related aspects of pair bonds. Theoretically, the latter is motivated by the assumed continuity and generalization of IWMs that imply a relative stability in individuals’ ways of relating, even between different and somewhat varying relationships. There has however been a considerable debate within

the social-personality tradition, regarding how to capture this stance most accurately. Early self-report measures of romantic attachment (e.g., Hazan and Shaver 1987) were based on the assumed analogy with childhood attachment and therefore assigned individuals to one of the major attachment categories. However, these measures were soon criticized for rendering unstable results, for disregarding evidence of overlap between the categories, and for neglecting important within-category variations. Consequently, the categorical approach came to be largely abandoned, in favor of a view on adult attachment variations as dimensional, and possible to capture by scaling individuals with respect to attachment-relevant dimensions – predominantly dimensions of avoidance and anxiety.

The most widely used instrument based on this view is the Experiences in Close Relationships Scale (ECR; Brennan et al. 1998), a 36-item scale based on extensive factor analysis of previous measures, which yields scores on two orthogonal, continuous dimensions, “avoidance” of closeness, intimacy, and dependence and “anxiety” about abandonment and of being insufficiently loved. The first dimension represents a disposition for attachment system deactivation, while the second represents a disposition for attachment system hyperactivation, and the two factors can also be used (via factor rotation) to obtain measurements of negative versus positive models of self and others (Mikulincer and Shaver 2016).

Psychometric evaluations clearly support the dimensional conception of romantic attachment (Mikulincer and Shaver 2016). Mainly for didactical reasons, the categorical or typological terminology has however partly been kept within the social-personality tradition. Individuals scoring low on both dimensions on the ECR, or displaying a positive model of self *and* others at the representational level, are then said to have a secure “attachment style.” An avoidant attachment style is represented by two different types: dismissing avoidant and fearful avoidant attachment. Whereas the first type is characterized by high avoidance but low anxiety, or a (defensively) positive model of self but a negative model of others,

the latter is characterized by high avoidance *and* high anxiety, or a negative model of *both* self and others. Finally, the preoccupied (cf. resistant/ambivalent) attachment category is characterized by high anxiety but low avoidance, or a negative model of self but a positive (though inconsistently so) model of others (Mikulincer and Shaver 2016).

While the use of such terminology could give the impression of discrete types, it should be borne in mind in the discussion below that the categorical terms sometimes used usually refer to regions in a two-dimensional space, in which people are continuously distributed.

The Developmental Continuity of Individual Differences in Attachment

Bowlby’s idea about general continuity and lawful discontinuity of attachment representations has gained support from empirical studies. Some (but by no means all) longitudinal studies investigating the link between infant behavior in the strange situation procedure (SSP; the predominant instrument for assessment of infant attachment; see “Individual Variations in Attachment”) and later classifications on the AAI have shown a correspondence between the two, especially with regard to the broader secure-insecure dimension (i.e., secure versus insecure SSP-behavior in infancy has been predictive of secure versus insecure response patterns on AAI in adulthood). Changes in attachment representations, particularly from secure to insecure, have also been linked to major distressing events within attachment relationships (i.e., divorce, parental psychopathology), supporting the notion of lawful discontinuity (Waters et al. 2000). A relatively high degree of correspondence has also been found in research examining the stability of romantic attachment over time, as assessed with repeated self-reports as well as with interview measures (Feeney 2016). However, as regards to one of the main assumptions of romantic attachment theory – that the continuity and generalization of IWMs from childhood partly explain variations in romantic attachment – existing evidence is limited. Although longitudinal data suggest associations between various aspects of

caregiving in childhood and subsequent romantic attachment, these associations seem not to be strong and consistent enough to offer a reliable set of predictors for romantic attachment (Fraley and Roisman 2019). Other efforts to evade this problem have also been limited in their success; for example, studies investigating the link between representations of childhood attachment, as measured by the AAI, and self-reported romantic attachment have at best established weak correlations (e.g., Haydon et al. 2011).

Admittedly, attachment theory assumes no full correspondence between childhood and romantic attachments. According to most theorists (e.g., Overall et al. 2003), individuals develop a hierarchy of IWMs, with generalized models of self and others at the top, models for classes of relationships (e.g., parents, romantic partners) at an intermediate level, and models for specific relationships (e.g., mother, present partner) at the bottom. While the generalized models are thought to inform perceptions of self and others on the lower levels in a top-down manner, new relationship experiences with a specific partner could also, in a bottom-up manner, affect the models for the class of romantic partners, without altering the models for parents. However, since the models emerging from the parental relationships are thought to form the basis for subsequent models on other levels, some degree of correspondence is still expected.

Although the weak evidence of such developmental correspondence poses an issue for romantic attachment researchers, caution should be raised against interpreting from weak or inconsistent evidence for correspondence that no correspondence exists. One explanation for the lack of consistent evidence is that the self-report measures predominantly used when assessing romantic attachment mostly capture limited, conscious parts of an individual's IWMs, while in reality IWMs are to a large extent unconscious (e.g., due to defensive exclusion; see "Psychodynamic Foundations to Attachment Theory"). This might cause trouble for researchers employing self-reports – especially when studying insecure forms of attachment – because insecurity is characterized by incoherent IWMs, as manifest, for

example, in conscious self-perceptions that might well be incompatible with the individual's actual (unconsciously motivated) organization of behavior in attachment-relevant situations. Supporting this line of thought, a tendency has been found in individuals classified as dismissing/avoidant on the AAI to report themselves as secure on self-report measures (DeHaas et al. 1994). Other studies (e.g., Roisman et al. 2005) have found a stronger link between childhood and romantic attachment, when controlling for idealizing tendencies (associated with the dismissing/avoidant category on the AAI). Hence, weak or inconsistent developmental correspondence may partly be due to measurement issues, rather than to profound theoretical problems. It should also be accentuated that the issue at hand only pertains to the explanatory value of childhood attachment in explaining variations in self-reported romantic attachment, and not to the presence of attachment dynamics in romantic relationships, which is well established (as seen above). Neither ought it be thought to cast too dark a shadow over the extensive and rich research that has been conducted based on self-report measures. Even if the degree of congruency with *childhood* attachment remains unclear, decades of research have indicated that the most widely used instruments are reasonably valid with regard to *romantic* attachment at the group level (see Mikulincer and Shaver 2016), yielding an abundance of important and theoretically coherent results. Some of these results are briefly depicted below.

Adult Attachment and Relationship Quality

Individual variations in romantic attachment have been robustly linked to multiple aspects of relationship quality. In early studies (e.g., Hazan and Shaver 1987), self-designated secure individuals tended to be accepting, supportive, and trusting toward their partner and could depend on the partner without losing autonomy. Avoidant individuals were found to display fear of closeness, a pragmatic view on romance, and difficulties in trusting the partner, while anxious-ambivalent individuals, in contrast, tended to fall in love often and easily and to demand a high degree of closeness and reciprocity from their partner.

Although these initial studies, as noted by their authors, suffered from methodological limitations, results from subsequent and more methodologically advanced research has broadly been in line with these findings. Secure romantic attachment tends to be predictive of higher relationship satisfaction and higher levels of trust and commitment, while insecurity generally predicts sub-optimal relationship functioning, with high avoidance being specifically associated with low levels of intimacy and support and high anxiety with demanding behavior and conflict. Increasingly, researchers have also investigated variables mediating the effect between romantic attachment style and relationship quality. The results indicate that many of the positive effects of secure attachment are, at least partially, mediated by the more constructive communicative strategies and higher levels of emotional openness associated with this attachment style (for an overview, see Feeney 2016).

Adult Attachment and Emotion Regulation

A vast number of studies have linked the insecure forms of adult attachment to various deficiencies in emotion recognition and regulation (see Mikulincer and Shaver 2016). Generally, highly avoidant individuals facing distressing situations attempt to inhibit any emotional state that interferes with the deactivation of attachment-related needs, through defensive strategies such as cognitive distancing or suppression of emotions. The vulnerability of this strategy has been highlighted by studies investigating individuals' reactions to prolonged stress, where these defensive strategies have been found prone to collapse under the pressure of chronic demanding conditions, resulting in high levels of distress in avoidant individuals (e.g., Reizer et al. 2010). In line with these findings, avoidant individuals' ability to suppress distressing thoughts and emotions has been found to diminish with increased cognitive load (Mikulincer and Shaver 2016). Interestingly, while being inclined to suppress distressing emotions and thoughts, a *heightened* perceptual vigilance for emotional stimuli at an early stage of information processing has also been observed in avoidant individuals (Chun et al. 2015). Contrary

to common belief, these results suggest that avoidant individuals are in fact highly attentive to emotional stimuli – albeit in order to keep them from being processed further.

Anxious individuals, in contrast, often display a heightened focus on, or even exaggeration of, negative emotions and potentially threatening stimuli, leaving them vulnerable to rumination and self-amplifying cycles of distress. Numerous studies also indicate a hyperactivation of attachment-related painful emotions and thoughts in anxious adults and a weak ability to control separation-related thoughts, resulting in an exacerbation of the distress related to separations (Mikulincer and Shaver 2016).

Romantic Attachment or Reproductive Strategies?

Attachment theory regards the developmentally immature infants' tendency to form attachment bonds as rooted in evolutionary benefits of securing protection and care from stronger and wiser others, with individual variations in childhood attachment ultimately reflecting different strategies for maintaining this protection (i.e., survival strategies; see “Evolutionary Foundations of the Attachment System and Its Functions”). However, while the infant's survival until reproductive age can arguably be viewed as the primary biological function of the child's bond to its caregiver, reproduction could reasonably be held as the primary function of romantic relationships. Indeed, evolutionary psychologists within the attachment field (e.g., Kirkpatrick 1998) have argued that the sexual mating system, rather than the attachment system, should be regarded as the primary behavioral system in romantic relationships and that romantic “attachment” styles ought to be viewed as variations in mating strategies (i.e., reproduction), not as organizers of protection (i.e., survival). Other theorists (e.g., Zeifman and Hazan 2016) have responded by pointing out that evolution could well “make new use” of systems originally developed with a different function and that the evolutionary function of romantic attachment could be to promote enduring pair bonds so

mates could provide better mutual support (see “Pair Bonding” for a further discussion of evolutionary aspects of pair bonds). Variation with regard to mating behavior is also far too widespread within the different attachment styles for them to be reduced to mating strategies. Leaving this dispute unsettled, it nevertheless highlights an important gap in existing research on adult attachment. As noted by Mikulincer and Shaver (2016), although the importance of the attachment system for adult relationship dynamics is well established, little empirical work has investigated the mutual influence of attachment, caregiving, and sexual mating systems on pair-bond dynamics, and the available evidence does little to verify the presumed superior influence of the attachment system.

Conclusion

In line with Bowlby’s assertion about the lifelong importance of attachment, research has demonstrated the crucial role of attachment in adulthood. Close adult relationships, most notably long-term romantic relationships, typically develop into attachment bonds, displaying all the characteristic components of attachment relationships. Moreover, individual variations in adult attachment have been shown to be of great significance with regard to a multitude of important aspects of relationship functioning. Nonetheless, important research questions, not least regarding the link between childhood and romantic attachment and the interrelations between the attachment, caregiving, and sexual mating systems in adult relationships, still largely remain to answer.

Cross-References

- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Individual Variations in Attachment](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Offspring–Parent Attachment](#)

- [Pair Bonding](#)
- [Romantic Attachment and the Prototype Hypothesis](#)

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Attachment Opportunity

► Effect on Attachment

Attachment Parenting

► Co-sleeping

Attachment Security

► Effect on Attachment

Attachment Theory

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Definition

Bowlby's theory of attachment includes several important foundational constructs. First and foremost, attachment relationships are clearly presented as a biological predisposition evolved to ensure survival. Individuals are proposed to

develop attachment relationships with caregivers and seek and maintain proximity to these caregivers when stressed, ill, or afraid. Differences in sensitivity of care were proposed to be associated with individual differences in attachment. Although Bowlby was particularly interested in the parent-child relationship, he was clear that attachment representations would be important for relationship functioning from “cradle to grave.” Infants tend to develop a primary attachment with their predominant caregiver; however, infants can develop multiple attachment relationships, and, throughout childhood and adulthood, we organize these attachment relationships into a hierarchy. And finally, Bowlby proposed that once formed, attachment representations would be stable – in particular in adulthood – although attachment representations could change in response to changes in caregiving during childhood or traumatic or salient events during adulthood.

Early Years

The roots of attachment theory were first established in the 1930s and 1940s when a number of clinicians observed the negative effects of maternal separations early in life. John Bowlby was one of many who observed this effect; for example, in 1944 he outlined how poor parenting influenced the behavior of a group of juvenile thieves. It was not until 1950, when he was offered a short-term contract to work at the World Health Organization (WHO), that he had the opportunity to organize his and others' work in the area. The resulting report from his WHO contract, published in 1951, summarized what was known to date about the negative effect of poor caregiving and maternal separation on infants' health and well-being. Bowlby later reported that several reviewers pointed out that an overarching theory to explain these observations was missing. In Bowlby's quest to develop such a theory, he was greatly influenced by both psychoanalytic theory and ethology. Perhaps, it would be more accurate to state that his development of attachment theory, rooted in his psychoanalytic training, was further strengthened as he acquired knowledge about evolutionary theory and ethological principals, in particular work of

Robert Hinde, Konrad Lorenz, Harry Harlow, and Charles Darwin. It was not until the late 1950s that Bowlby presented his theory of attachment to the British Psychoanalytic Society in London, and the initial reactions were quite negative. In Bowlby's words “many psychoanalysts... remained unconvinced and sometimes very critical.” Despite this criticism, Bowlby's research group at Tavistock continued to amass support for the theory of attachment which culminated in his trilogy – attachment and loss (volume 1, Attachment; volume 2, Separation: Anxiety and Anger; volume 3, Loss: Sadness and Depression).

Bowlby consulted and collaborated with several notable scientists while developing his theory of attachment including Harry Harlow, Konrad Lorenz, and Robert Hinde, but it was, however, his collaborations with Mary Ainsworth that helped to put attachment research on the psychological map. In 1950, Mary Ainsworth traveled to London and, by chance, applied for a research position advertised in the London Times and joined Bowlby's research team at Tavistock. With Bowlby, she began studying the effects of maternal separation on child development; however, she was well prepared to contribute to his work. Previous to this move, Ainsworth had completed her PhD at the University of Toronto, and there had begun exploring the concept of security with William Blatz in her dissertation work – it was Ainsworth who defined the concept of the “secure base” building upon her research initiated in Canada. Ainsworth worked at Tavistock until 1954 when she traveled to Uganda, but she, of course, continued both her work in attachment and her lifelong collaboration with Bowlby. Following her time in Uganda, she moved to Baltimore, and finally in 1958 she was given a permanent position at Johns Hopkins all the while continuing her collaborations with Bowlby and her operationalization of attachment.

Use of Attachment Behaviors

Attachment relationships, and the use of attachment behaviors, are clearly presented as a biological predisposition evolved to ensure survival.

Bowlby (1969/1991) spent considerable time describing the nature and function of behaviors that lead to attachment. Infants use several behaviors to seek proximity to their attachment figures (e.g., crying, vocalizing, following) and also use behaviors to maintain proximity (e.g., smiling, clinging). Once infants are mobile and confident in the care of their attachment figure, they tend to use the attachment figure as a “secure base from which to explore,” returning to the caregiver’s safe haven (i.e., proximity to the attachment figure) for comfort and reassurance when needed. He proposed that infants are biologically predisposed to seek and gain proximity to caregivers and in these relationships develop a sense of whether they are worthy of love and support and a sense of whether their caregivers can be trusted and relied upon to provide care and support. Over the course of infancy and childhood, these views of the self and the other develop into sophisticated internal working models of what to expect from close others, and these internal working models guide behavior over the lifespan.

His observations and work with John Robertson on the destructive impact of early parent-infant separations lead him to conclude that children learn to tolerate longer parental separations; however, both children and adults find separations from attachment figures to be distressing and will go through a predictable sequence of behaviors – distress, despair, and detachment (see below). In fact, even predominately secure individuals report distress when separated for prolonged periods of time with little or no contact (Bowlby 1973/1991). This focus on separations is not surprising given his tendency toward ethology and the importance of parental protection on survival.

When separated from caregivers, infants were observed to react with a predictable sequence of behaviors which Bowlby suggested would have ensured their survival. First, when initially separated, infants will protest to attract the attention of caregivers and, if possible, attempt to search for caregivers. Sensitive and responsive caregivers respond to these initial vocalizations by returning and comforting infants; infants with less sensitive or unresponsive caregivers (in our evolutionary past and the present) develop representations that

care will not be given or inconsistently received. Over time, the individuals’ experience supports the development of internal working models of attachment – individuals’ belief that the self is worthy of care (or not) and that the care needed when they express distress will be forthcoming (or not).

From Bowlby’s observations of children who experienced prolonged separations from their primary caregivers, he proposed that the next phase of separation – if protests and searching are not successful – would be a period of despair. In this phase, infants stop their protests as well as their search; this reaction is proposed to have developed to protect infants from predators when their initial vocalizations to seek proximity to caregivers were not successful.

Finally, Bowlby observed that infants who experienced prolonged separations – and following a period of distress and despair were not reunited with their caregivers – moved to a phase he described as detachment. He believed that these infants were proposed to experience detachment from their separated caregiver, thereby allowing the opportunity to develop attachment relationships with new caregivers who may be better suited to provide the necessary care and support needed to ensure survival.

Separations and Reunions

Ideally, children should feel secure in the presence of caregivers, and when threatened they should seek proximity to caregivers for protection. Children, who are separated from insensitive or rejecting parents, may have developed insecure representations of their relationship with these parents, and therefore they may struggle when coping with the stress of the separation and the associated effects on the family. Furthermore, regardless of degree of security, both children and adults find separations from attachment figures to be distressing – even predominately secure children and adults go through the phases of distress, despair, and detachment when separated for prolonged periods of time with little or no contact (Bowlby 1973/1991).

Ainsworth continued to provide support for Bowlby's theory and expanded upon the idea that although the goal of attachment (i.e., seeking a secure base) is similar for all children, their mechanisms for seeking proximity differ depending on caregiving experiences, in particular the sensitivity and responsiveness of the caregiver (Ainsworth et al. 1978). It was Ainsworth and colleagues who first suggested that the reunion, as well as the separation, is informative in understanding attachment. In a series of articles in the late 1960s and early 1970s, Ainsworth and colleagues introduced the *Strange Situation* (SS). For example, Ainsworth and Bell (1970) presented one of the first studies to describe their methodology. Interestingly, although perhaps deliberate on their part but clearly overshadowed by subsequent work, their initial focus was on the attachment behaviors during the separations and reunions and not attachment categories: Their article clearly summarized the SS procedure and behind-the-scenes observation techniques. In particular, they highlighted the importance of infants' signaling of the parent, actively approaching the parent, and the aversive behaviors of the infants that illustrated distress. They outlined that the experimenters were trained to record observations of infants' locomotion and crying as well as manipulation and visual exploration of available toys. Furthermore, the importance of coding infants' behaviors such as proximity and contact seeking, contact maintenance, interaction avoiding, and interaction resisting as well as search behaviors during the separation episodes was highlighted. Their findings hint at individual differences and, perhaps more importantly, provide empirical support for Bowlby's earlier assertions that infants separated from their caregivers will go through a predictable sequence of distress.

Sensitivity of Care

Attachment theory provides an interesting framework work to explore the effects of parenting and caregiving for several reasons. First, Bowlby (1973/1991, 1980/1991) proposed that our attachment representations developed from sensitivity

of care received from our primary caregiver. Bowlby proposed that attachment security resulted from responsive, appropriate caregiving and that as a result of this care, individuals developed a sense of the self as worthy of care and a belief that others would be responsive and sensitive when caring (Bowlby 1980/1991) – it was Bowlby's assertion that personality development was influenced consciously by these experiences that caused criticism from his psychoanalytic colleagues. He proposed, and considerable research has supported, that children should feel secure and contented when safely in the presence of caregivers (secure base), and when threatened they should seek proximity to caregivers as a safe haven.

Measurement of Individual Differences in Infant Attachment

Ainsworth's most prolific contribution to attachment theory and research is without a doubt the operationalization of infant attachment categories (Ainsworth et al. 1978): secure (B), avoidant (A), and resistant (C) – as well as Main's fourth category disorganized (D). Ainsworth's work not only provided the theoretical and empirical foundation for decades of research in infant attachment; her earlier operationalization of infant attachment also provided the foundation for research in adult attachment. Based on their responses to the SS, infants are classified into one of the following four categories:

1. Children who are categorized as secure (B) have developed a trust in their caregivers' availability and responsiveness and react to the stress of the SS in ways that highlight their positive expectations. In particular, secure infants seek proximity when reunited with caregivers and can return to play when comforted.
2. Children who are categorized as avoidant (A) have developed a belief that they cannot turn to their caregivers for comfort, and during the SS, avoidant infants typically avoid the caregiver upon reunion and control – but do not regulate – their negative emotions.

3. Children who are categorized as resistant (C) have learned that care will be unpredictable, and during the *SS* they seek comfort inconsistently often switching from clingy and sobbing to withdrawing and angry. They cannot be comforted upon reunion and do not return to play with the available toys.
4. The disorganized category was added by Main and colleagues who expanded the examination of parent-child attachment to high-risk samples. Children who are categorized as disorganized (D) are often in the care of parents who are abusive (physically, emotionally, and/or sexually), and in response to the extreme stress of their home life, these children do not present a coherent attachment strategy during the *SS* (e.g., freezing rather than proximity seeking).

The *SS* procedure provided the impetus for considerable research (well over 7,000 citations for Ainsworth et al. 1978), and over the past 50 years, it has been well established that one of the negative consequences of poor parenting is the development of insecure attachment. Insecurely attached individuals, by definition, tend to have childhood experiences that are characterized by lack of care and high control. Insecure children develop a sense of the world as inconsistent (resistant) or rejecting (avoidant), and it is well established that insecure attachment negatively influences child development. Considerable work has explored attachment beyond infancy into childhood. For example, research has demonstrated that insecure children are less socially competent, are more likely to have emotional and behavioral problems, are more likely to have medical problems, and score lower on tests of achievement than secure children. Secure children report pleasurable interactions with their parents; avoidant children, although often non-confrontational, will minimize interactions with parents; anxious-ambivalent children describe difficult relationships mixed with hostility, sadness, and immature proximity-seeking attempts; and disorganized children display negative, punitive behaviors, rejection and/or embarrassment of the parent, and sometimes overly bright, although inappropriate, affect.

Measurement and Development of Adult Attachment

From the beginning, Bowlby asserted that attachment representations were important “from the cradle to the grave” (1969/1991, p. 208) and noted that in adolescence and adulthood, there would be a “change of the figures towards whom the [attachment] behavior is directed” (1969/1991, p. 179). Although several scholars wrote about the importance of attachment across the lifespan, it was not until the mid- to late 1980s that two groups of researchers independently began to explore the measurement of adult attachment. Their work focused on somewhat different approaches to assessing adult attachment, and the two areas of adult attachment research remain, somewhat, at odds with each other. Main and colleagues developed an interview-based assessment of adults’ attachment of their family of origin which focused on the coherence of their representations (Main et al. 1985), whereas Hazan and Shaver (1987) introduced a simple three-paragraph forced-choice self-report questionnaire that focused on adult romantic relationships. Not surprisingly, since they both modeled their assessment from Ainsworth’s work, both originally proposed three categories and, it is well known that both measures of attachment have proved to be powerful predictors of adult behavior.

Main et al.’s (1985) adult attachment interview (AAI) continues to be the primary method of assessing adult attachment in developmental and clinical fields despite the time-consuming training and coding of attachment interviews (see Hesse 2016 for a summary). The interview coding protocol which assesses individuals’ coherence of their current state of mind with respect to their families of origin (past-focused) results in one of four attachment categories: autonomous (secure), dismissing, preoccupied, and unresolved/disorganized. Bakersman-Kranenburg and van IJzendoorn (2009) summarized the data from over 10,000 AAIs addressing issues of baseline proportions in clinical and nonclinical samples, gender distributions, as well as differences in distributions for adolescents and individuals from

low SES samples, ethnic minorities, and non-Western countries. Using the four-category classification of a sample of nonclinical mothers ($n = 700$) as their baseline, their findings indicated that nonclinical fathers, adolescents and students, individuals from at-risk samples, and individuals from clinical samples were more likely to be classified as dismissing than mothers from nonclinical samples. Individuals from at-risk samples were also more likely to be classified as unresolved, and individuals from clinical samples were also more likely to be classified as unresolved or preoccupied.

Hazan and Shaver introduced a simple three-paragraph forced-choice self-report measure of adult attachment modeled from Ainsworth's three infant categories focusing on adult romantic relationships. Their three categories – secure, avoidant, and anxious-ambivalent – proved to be quite productive, but the categorical measurement was met with some concern by personal relationship researchers. Although the three-category measure did not stand the test of time, this seminal article provided the impetus for the next few decades of work on adult attachment.

Although the self-report methodology assessing attachment of close peer relationships is controversial – some would say that peer relationships are not attachment relationships (see below for discussion and van IJzendoorn and Bakermans-Kranenburg 2010 for a recent example) – research exploring the importance of adult peer attachment relationships continues to be prolific, and the effects of adult peer relationships on adult social behavior are well documented.

In 1990, Bartholomew published a paper which merged the work of Main et al. (1985) and Hazan and Shaver (1987) as well as Bowlby's original descriptions of the self- and other-models. Specifically, Bowlby had proposed that throughout childhood, individuals develop a sense of whether they are worthy of love and support (or not) and a sense of whether others can be trusted and relied upon to provide care and support (or not). By adulthood, these views of the self and the other are well established and have developed into sophisticated internal working models of what to expect from close others,

and these internal working models guide behavior over the lifespan. Bartholomew suggested that the intersection Bowlby's proposed dimensions of the self-model and other-model resulted in a four-category model of attachment. Secure individuals were defined to have developed a positive model of both the self and others, and considerable research has supported that secure individuals have high self-esteem and self-confidence as well as high trust and support with others. Preoccupied individuals were defined to have developed a negative model of the self and a positive model of others; similarly, considerable research has supported that preoccupied individuals tend to have conflicting views of the self and others which tends to negatively impact their relationships. Bartholomew noted that her definitions of secure and preoccupied prototypes were consistent with both Main et al. and Hazan and Shaver. Although the previous researchers had each proposed one type of avoidance, Bartholomew expanded this definition of avoidance by proposing that avoidance could be either fearful (similar to Hazan and Shaver's description of avoidance) or dismissing (similar to Main et al.'s description of avoidance). Fearful individuals were defined to have developed a negative model of both the self and others and tend to consistently report higher levels of depression, neuroticism, marital conflict, and interpersonal sensitivity. Dismissing individuals were defined to have developed a positive model of the self and a negative model of others and reported high levels of self-esteem and self-confidence but low levels of trust and warmth in their relationships. Researchers have indicated that both types of insecure-avoidant adults deny symptoms of distress (dismissing) or are afraid to ask for help (fearful) as they believe that others will reject their attempts at proximity seeking or challenge their feelings of distress.

In her early work, Bartholomew presented both interview and survey measures to assess the four-category model (see Bartholomew and Horowitz 1991; Griffin and Bartholomew 1994). Although the interview proved to be the most reliable method, researchers tended to gravitate toward the less time-consuming, albeit less reliable, self-report surveys. The four-paragraph measure (RQ,

Relationship Questionnaire) was modeled from Hazan and Shaver's three-category measure with an additional paragraph describing the dismissing category (see below). Participants were typically asked to rate each of the four categories on a Likert scale from "not at all like me" to "very much like me" and then choose the one category from the four that was "most like them." The Relationship Scale Questionnaire (RSQ) was simply a list of the 17 statements from the RQ, and participants were asked to rate each of the items on a Likert scale from "not at all like me" to "very much like me." The four scales were computed by averaging the items. The paragraphs from the RQ categories (Griffin and Bartholomew 1994) are as follows:

Secure: It is easy for me to become emotionally close to others. I am comfortable depending on others and having others depend on me. I don't worry about being alone or having others not accept me.

Fearful: I am somewhat uncomfortable getting close to others. I want emotionally close relationships, but I find it difficult to trust others completely or to depend on them. I sometimes worry that I will be hurt if I allow myself to become too close to others.

Preoccupied: I want to be completely emotionally intimate with others, but I often find that others are reluctant to get as close as I would like. I am uncomfortable being without close relationships, but I sometimes worry that others don't value me as much as I value them.

Dismissing: I am comfortable without close emotional relationships. It is very important to me to feel independent and self-sufficient, and I prefer not to depend on others or have others depend on me.

Personal relationship researchers were concerned with the reliability of early measures, but they were also drawn to the concept of adult attachment, and the early 1990s saw a wave of studies proposing new measures of attachment. Brennan et al. (1998) collated the items from these attachment measures (323 items which assessed 60 attachment constructs from

14 different scales) and proposed a new measure the Experiences of Close Relationship scale (ECR). The ECR has two orthogonal dimensions (attachment anxiety and attachment avoidance) and improved reliability over the RSQ. The ECR-R (Fraley et al. 2000) attempted to correct some of the limitations of the ECR; however, both the ECR and the ECR-R proved to be inadequate measures of security and imprecise assessments of Bartholomew's four-category model (see Mikulincer and Shaver 2007) – both scales are imperfect due to the limitations of the existing item pool. Although these measures – Bartholomew's RSQ, the ECR and ECR-R – continue to be well used in the literature, researchers continue to work on improving questionnaire measures of adult attachment (see Scharfe 2016).

Are Adult Close Relationship Attachment Relationships?

Despite the fact that Bowlby asserted that attachment representations were important across the lifespan and that a change of attachment figures would be observed in adolescence and adulthood, there is some controversy about who serves as attachment figures in adulthood. Personal relationship researchers have insisted that adult romantic partners and friends as well as family members may serve as attachment figures. Considerable work has provided empirical support that lovers, friends, and family members serve as attachment figures for adults. This line of research began with a listing of reasons why adult love relationships may be attachment relationships in Hazan and Shaver's (1987) seminal article. Since that time, personal relationship researchers have demonstrated that one can observe attachment behaviors in adult relationships (i.e., proximity seeking, proximity maintenance, safe haven, secure base), similar to infants and children there are consistent, measureable individual differences in adult attachment; that adults express anxiety if their attachment figure is not accessible; and that adults experience distress if separations from their attachment figures are prolonged.

Attachment Internal Working Models and Hierarchies

Bowlby (1969/1991) highlighted specific developmental changes in attachment relationships over the lifespan, and the various measures of adult attachment have allowed researchers to begin to explore this feature of his theory more fully. For example, Bowlby proposed that attachment representations started from one primary attachment relationship in infancy, but he acknowledged that early on, often soon after attachment to the primary caregiver was evident, infants would begin to establish the development of attachment relationships to other caregivers. Specifically, infants were proposed to develop a primary attachment with the caregiver who satisfied their basic needs – this primary attachment relationship was the most intense regardless of the number of secondary attachment relationships. Infants and children, however, do receive care from other caregivers, within and outside of their family of origin, and they may also develop secondary attachment bonds to these individuals. Considerable work has provided support that infants and children will develop attachment relationships with adults who are not their primary caregiver.

During these early years, attachment relationships are typically unidirectional – the caregiver fulfills the attachment needs of the child. By the time we reach adolescence and adulthood, most individuals have multiple attachment relationships which are organized into a “state of mind” or internal working model, and these relationships can be reciprocal (i.e., both individuals fulfill and provide attachment needs). Furthermore, Bowlby proposed that in adulthood, there would be a “change of the figures towards whom the [attachment] behavior is directed” (1969/1991, p. 179) and that adolescents and adults tend to organize their attachment relationships into a hierarchy.

Bowlby (1969/1991) proposed that during adolescence, the child’s attachment to their parents would change due to the importance of other adults in the child’s life as well as the sexual attraction to their peers. There has been considerable research exploring the change of attachment from parents to

peers initiated by Hazan and Zeifman (1994). They reported that, between the ages of 8 and 14 years, adolescents reported that they approached peers for proximity and safe haven functions and parents for secure base functions (see also Nickerson and Nagle 2005). They also noted that during late adolescence (15–17 years), those individuals who had formed peer romantic relationships were less likely to approach their parents for attachment functions (see also Mayseless 2004; Nickerson and Nagle 2005), although research findings have not been consistent on this point. Consistent with Bowlby’s suggestion that, for most individuals, the bond with parents would continue throughout life, researchers have found that one’s mother, in particular, continues to be an important attachment figure throughout the lifespan (Pitman and Scharfe 2010).

Bowlby (1969/1997) also proposed that individuals, regardless of age, would organize their attachment relationships into a hierarchy and would demonstrate a preference for a primary attachment figure. Over the past two decades, several researchers have found support that individuals do tend to organize their attachment relationships into hierarchies, and these findings have been found across the lifespan in several diverse samples (e.g., Doherty and Feeney 2004; Pitman and Scharfe 2010; Trinke and Bartholomew 1997). Interestingly, mothers tend to be listed at or near the top of the attachment hierarchy across the lifespan.

Attachment Stability

Paradoxically, Bowlby (1980/1991) proposed that once formed, attachment representations would remain stable but could also change over the lifespan. Specifically, he proposed that once formed, internal working models of attachment would remain relatively stable in adulthood; however, he highlighted that changes may occur during development (see Del Giudice 2009; Del Giudice and Belsky 2010 for an evolutionary explanation for these changes) but may also change in adulthood in reaction to particularly traumatic events (see Scharfe 2003 for a summary of the lifespan research). Researchers have demonstrated that parent-infant attachment shows

moderate-to-high stability (e.g., Waters 1978) and that change is likely when infants' caregiving environments change (e.g., Thompson et al. 1982; Vaughn et al. 1979). In particular, there is some evidence that it is important to determine how sensitively changes were managed (e.g., NICHD Early Child Care Research Network 2001). Similar findings have been reported exploring stability of attachment throughout childhood (e.g., Howes and Hamilton 1992).

Bowlby (1973/1991) proposed that by adulthood, attachment representations would be well developed and more "constrained" and less adaptive to change. Over the past few decades, researchers have reported moderate-to-high stability of adult attachment representations regardless of the method of assessment (e.g., Scharfe and Bartholomew 1994). To date, several studies have examined the stability of attachment from infancy to adulthood and have found moderate stability when social environments remain relatively stable (e.g., Waters et al. 2000).

Conclusion

Bowlby's theory of attachment includes several important foundational constructs including the proposal that attachment behavior was instinctual and important across the lifespan. He also described characteristic attachment behaviors and individual differences in attachment as well as both adaptive and maladaptive care environments. Finally, he outlined the development of multiple attachments and hierarchies of attachment as well as the development of internal working models of attachment and proposed conditions to expect both stability and change of attachment. Considerable research over the past 40 years has provided empirical evidence for these foundational constructs.

Cross-References

- ▶ [Attachment in Adulthood](#)
- ▶ [Early Attachment Experiences and Romantic Attachment](#)

- ▶ [John Bowlby](#)
- ▶ [John Bowlby: Pioneer of Attachment Theory](#)
- ▶ [Measurement: Categorical Versus Continuous](#)
- ▶ [Sex Differences in Attachment](#)

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Attack

► Aggression

Attention

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Synonyms

Awareness; Concentration; Consciousness;
Focus; Mindfulness

Definition

The cognitive and behavioral process during which one becomes actively, and consciously, aware of one or several stimuli, while cognitively suppressing irrelevant stimuli. Attention is an executive function.

Introduction

George is 8 years old and he is attending the third grade of elementary school. During his first year

of elementary school, when he was 6 years old, he was diagnosed with Attention Deficit Hyperactivity Disorder (ADHD, predominantly inattentive presentation) as he was meeting the diagnostic criteria of the fifth edition of the Diagnostic and Statistical Manual (DSM-5; American Psychiatric Association 2013). Specifically, George met six of the seven DSM-5 criteria for inattention, namely:

- (a) He was failing to pay good attention and made careless mistakes
- (b) He could not focus for long periods of time
- (c) He was often failing to listen when others were speaking to him
- (d) He would not pay good attention to directions or instructions
- (e) He would easily be distracted by trivial stimuli in his environment (e.g., in the classroom or during homework)
- (f) He would fail to organize his belongings and actions or plan ahead for activities

As it is evident by the criteria that George was meeting for ADHD, his difficulties are interfering with his everyday activities, functioning, and cognitive processes. His difficulties are mostly evident in the classroom when he has to pay attention to the teacher, concentrating in writing and reading or solving mathematics, and follow instructions or directions that he receives verbally or in writing, such as in tests. At home, George cannot sit for long periods of time to complete his homework as his attention cannot be maintained longer than 20 min. His parents complain that he often appears to be daydreaming instead of following conversations that they would like to have with him. Finally, teachers and parents were immensely concerned about George's inability to inhibit trivial stimuli out in order to concentrate to an action that he is supposed to complete. For example, he tends to play with his pencils or erasers instead of completing a written assignment that only needs his full attention for 30 min. In other words, he finds it difficult to suppress irrelevant stimuli (i.e., things on the desk) and focus on the most important stimulus (i.e., his assignment).

Attentional Process: Selective Attention, Divided Attention, Sustained Attention, and Alternating Attention

Selective Attention

Neuroscientists, psychophysicologists, and cognitive psychologists' experiments revealed that we solve our problems of sensory overload (the abundance of large numbers of stimuli at a given point) by choosing the most important/relevant sensations or stimuli that are important at any given time, while suppressing irrelevant sensations or stimuli that are simultaneously present in our environment (Zhong-Lin 2008). This could be a good definition for attention, especially selective attention (focusing on the most relevant stimulus). This of course has evolutionary value, as humans (and other animals) need to be selective in an environment of numerous stimuli and attend to the stimulus that is most likely to have the highest survival value. For example, paying attention to a dangerous animal in your immediate surroundings, while ignoring a beautiful butterfly on a flower next to you that you would normally enjoy watching.

Cognitive scientists found that our selective attention enhances the subjective (individual perception) physical qualities of stimuli that we concentrate on, while it could do the opposite to stimuli that remain outside our immediate focus. For example, a red flower appears brighter (stimulus enhancement) when we select to pay attention to it and all other nature around it becomes duller (noise reduction) or stays completely out of our perception (noise exclusion). Our selective attention applies to all of our senses (auditory, tactile, gustatory, visual, and smell) and very pertinent to our memory (e.g., attending to a specific piece of information that you learned) and other cognitive processes.

Divided Attention

Divided attention is also an attentional process. During this process, we pay attention to more than one stimulus or action (e.g., multitasking). For example, in dichotic listening (Ingram 2007), we could be able to pay attention to a person we are having a conversation with, while at the same time

paying attention to the train announcements in the arrival hall.

Sustained Attention

Sustained attention is the ability to focus on a stimulus (or stimuli) or action for a period of time without being distracted by other stimuli or actions (Oken et al. 2006). Neuropsychologists using norm referenced tests assess a person's sustained attention in order to extract conclusions about a person's ability to remain focused on an action or stimulus, at least as long as the average of the population. In our introductory case study, George most probably faces difficulties in maintaining his concentration on tasks that take a long time to be completed (e.g., writing a 2000 word essay on a topic).

Alternating Attention

Our ability to alternate our focus (attention) between stimuli or actions is another aspect of our attention that is crucial to our survival and is often measured in neuropsychological assessments (Sohlberg and Mateer 2001). For example (using the example with the person paying attention to a dangerous animal), a huntergatherer could be very vigilant and pay attention to a dangerous animal in his surroundings, but at the same time he could be switching his attention at times to collecting mushrooms for dinner. Good alternating attention exhibits cognitive flexibility that allows you to go back and forth on different activities or switch from one important stimulus to another. Cognitive flexibility is highly positively correlated with intelligence measures. The ability to shift our attention (mental shift) as needed, and not persevere on certain stimuli, is learned early in life and is part of our educational systems.

Attention Disorders

Deficits or impairments in attention are not only evident in ADHD, but also in frontal lobe (or other brain areas) damage, schizophrenia, memory disorders, anxiety, depression, or as a side effect due to substance use or medical treatments (Gitelman 2003). Attention disorders could be rehabilitated

with medication, behavioral and cognitive therapy, relaxation techniques, and/or combination of these and other treatments.

Conclusion

Attentional resources could be voluntarily allocated to stimuli or actions (Pinto et al. 2013); this is also called a top-down process, where the brain decides what calls for our attention (e.g., deciding that it is time to pay attention to my teacher in the classroom and forget about a discussion I had before class). Alternatively, Pinto et al. (2013) state that our senses could direct us to a stimulus or action in a bottom-up process where a sense alters the brain to allocate its attention to a particular stimulus or action (e.g., a sudden noise turns our head towards the source of sound).

Attention, whether bottom-up or top-down, is a process that is crucial to our everyday functioning and ultimate our survival. Therefore, scientists are constantly improving the assessment methods and rehabilitation techniques for attentional deficits, while certainly the improvement of attention and its aforementioned components is pertinent in individuals without attentional disorders, as well. This is evident by the invention of medications or substances and development of methods for attention and concentration improvement.

Cross-References

- [Interference](#)
- [Personal Memory](#)
- [Self-Observation](#)
- [Working Memory](#)

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Attention and Memory

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Synonyms

Awareness; Cognition; Consciousness; Inquisitiveness; Recall; Recollection; Reminiscence; Selection

Definition

Attention and memory are a set of linked, cognitive processes. Attention refers to a number of processes – some deliberate, others unconscious – where a discrete aspect of information is selected over other, ignored information. Memory involves reproducing or recalling what had previously received attention and priority. These are related processes, as information maintained and attended to then becomes a more durable memory.

Introduction

In both humans and the animal kingdom, attention and memory have functional relevance. Both groups rely on these cognitive processes, in similar ways. Attention describes the “who” and “what” of our conscious experience, as it helps keep something “alive” longer. This is the case for all animals, as they must encode and understand their dynamic environment, with the complexities associated with locating food and water, protecting their young, and so on. These aspects of their environment are then prioritized in memory, as well. Todd et al. (2005) had previously suggested that several topics from traditional cognitive psychology are at odds with evolutionary theory. However, recent research from both the attention and memory literatures would largely disagree with this suggestion. The current review discusses recent findings from these literatures, with an emphasis on humans’ natural tendencies to attend to and remember (1) dangerous and fear-relevant stimuli, (2) attractive and other positive aspects in their environment, and (3) self-relevant information. Each of these emphasizes the role of evolutionary priorities driving cognitive processes.

Dangers and Fear-Relevant Stimuli

Fear exists to inform and respond to someone or something perceived as dangerous or a potential threat. However, it is also a very normal reaction to danger, and researchers can agree that fear is an adaptive emotion (i.e., a fight or flight response) which in turn is self-protecting (Slobounov 2008). Fear can be expressed through physical reactions and/or behavioral expressions (e.g., sweating, rapid heartbeat, shortness of breath). Individuals that are faced with fear generally tend to either avoid the danger or use defense mechanisms against it. Along with fears, phobias can provoke exaggerated responses that are also in line with avoidance behaviors, the key component in the disorder. Isbell’s (2006) theory suggests that evolutionary fear-relevant stimuli, when compared against neutral stimuli, should activate threat responses, particularly those related to attention;

however, this effect should not be dependent solely upon the stimuli and task materials, such as the often used snake- and spider-detection task using neutral backgrounds (though predators are often prioritized in both attention and memory systems; Kazanas and Altarriba 2017, 2018).

In one such example, LoBue and Rakison (2013) showed that compared against other objects and animals, snakes are detected more automatically. When compared against spiders, studies have found that the fear and threat of snakes are higher (Shibasaki and Kawai 2011), though spiders can be recognized faster (Öhman et al. 2012). Quick detection displayed by non-human primates is limited to snakes, so it is unclear as to whether spiders hold a significant status in human perception (Shibasaki and Kawai 2009).

Research on emotion and retrieval have shown that, while negative information drives attention and memory, this often comes at the expense of missing positive and neutral information. For example, Kensinger et al. (2007) have shown that younger adults tend to remember the details for negative stimuli more so than for neutral stimuli, but there is also the thought that young adults may not be as able to correctly identify the visual aspects of positive objects. Multiple studies have shown that negative items tend to benefit from enhanced vividness (Dewhurst and Parry 2000; Kensinger and Corkin 2003; Kensinger and Schacter 2006; Ochsner 2000). Because of this, individuals tend to claim that they *recognize* a positive stimulus when it was first introduced, but do not *commemorate* the details of its presentation (Dewhurst and Parry 2000; Ochsner 2000). Storbeck and Clore (2005) also noted that positive information can be incorrectly retrieved when compared alongside negative information (Kensinger and Schacter 2006; Levine and Bluck 2004). Kensinger et al. (2007) note that negative stimuli are prioritized in memory, suggesting that emotion effects may depend on both the valence and arousal of the stimuli.

Negative experiences – and their resulting memories – can have their consequences, including post-traumatic stress disorder (PTSD), where

fear is known as the most important emotion in this disorder. PTSD is a pathological response to trauma that may develop after exposure to an event or ordeal in which death, severe physical harm, or violence occurred or was threatened. Traumatic events that could potentially trigger PTSD include but are not limited to violent personal assaults, natural or unnatural disasters, accidents, or military combat. A large amount of the PTSD literature is based on conspecific research (e.g., war veterans), and the results may not be representative of other PTSD populations. Cantor (2009) asked whether predator-induced PTSD differs from conspecific-induced PTSD. He found that one way to examine this could be to use shark attack file data sources. Cantor (2009) also asked whether shark attack victims display less generalized avoidance, particularly less fear of conspecifics, along with a more specific thalassophobia (i.e., a fear of the ocean). PTSD studies to date have not examined the predator question, though the rates of conspecific-induced PTSD (the result of assaults) tend to be higher than rates of environmental PTSD. Generally, the literature relevant to PTSD and evolutionary psychology helps us to understand that what is adaptive for one environment might not be for other environments. Cantor (2009) concluded by stating that:

Fear motivates the defensive behaviors, the chief of which in mammals are deployed according to distance from the source of threat and other contextual variables. Those defensive behaviors are avoidance, attentive immobility, withdrawal, aggressive defense, appeasement, and tonic immobility, operating in conjunction with vigilance and risk assessment. The origin of PTSD may have involved an enduring heightened defensive reorientation that has become adaptive. This evolutionary perspective brings together psychological, social systems, and neuro-scientific research findings. (p. 1046)

Quite often, negative information carries a higher value than positive information, which then attracts more attention and other cognitive processing. This higher value is noted by various physiological responses, automatic detection and recognition, increased memorability, and, in extreme circumstances, psychopathology.

Attraction and Other Positive Aspects in the Environment

On the other hand, positive qualities and characteristics can also drive attention and memory processes. The attraction literature provides many relevant examples. Individuals observe various things about each other upon their first encounter, but the most common is generally the physical appearance of the other's face. Faces are typically categorized into what is attractive and what is considered less attractive. Attractiveness can be measured using scales (i.e., 1 = low attraction and 7 = high attraction) or simply making a choice (i.e., *A is more attractive than B and C*), etc. These seemingly automatic decisions translate into a number of interesting outcomes. For example, the attraction literature finds more attractive males reporting a larger number of short-term sexual partners and more attractive females reporting a larger number of long-term sexual partners (Rhodes et al. 2005).

Why are attractive individuals more likely to grab our attention? From an evolutionary perspective, perhaps, symmetry can signal one's overall health; preference for such symmetry is in line with by-products of the way brains process that information. Averageness and sexual dimorphism (femininity in female faces, masculinity in male faces) also factor into sexual behaviors within and outside of relationships (Rhodes et al. 2005). Researchers have hypothesized that if attractiveness is such an important feature for mate selection, then attractive people should have a higher success rate with their partners than that of their peers. Rhodes et al. (2005) found that a male's facial attractiveness correlates with their number of short-term sexual partners and the opposite is true for a female's facial attractiveness, which correlates with their number of long-term sexual partners. They also tested the impact of body attractiveness, finding that male body attractiveness correlated with the number of short-term sexual partners. Importantly, this was not the case for female participants, as there was no correlation between their body attractiveness and sexual behaviors.

In another line of investigation, researchers have explored memory with emotional distractors and manipulated focused and distributed attention. For example, Srinivasan and Gupta (2010) found that happy faces were acknowledged more so than sad faces when the conditions were lower and attention was more distributed. They also noted that identification of either sad or happy faces was contingent upon how the attention was distributed. Furthermore, recognition of happy faces when they were preceded by neutral stimuli was greater than recognition of happy faces preceded by sad faces. This conclusion suggests that happy faces rely on distributed attention or fewer attentional resources when differentiated from sad faces. In a similar study, Srivastava and Srinivasan (2010) found that happy faces were also recognized better, even under a limited attention manipulation, when compared against sad faces. They went on to discuss that better recognition of happy faces could be related to the commonality of happy faces. Their results are also consistent with other arguments that assume individuals have more previous experience with happy faces in photographs (Gupta and Srinivasan 2009; Jackson and Raymond 2006). Srivastava and Srinivasan (2010) further discussed that because humans are skilled at recognizing faces with emotion, they are not certain why there would be a tendency to more correctly identify happy versus sad expressions in faces. With that, familiarity may not be responsible for differences in the time course of attention across happy and sad faces.

Research suggests that as individuals age, how they commemorate emotionally important information changes, too. For example, Mather and Carstensen (2005) suggest that older adults might have a memory bias toward positive and self-relevant information because they typically remember stimuli that are connected to positive emotions rather than negative emotions. Eppinger et al. (2010) have found results consistent with these predictions, as older adults showed better memory performance for positive stimuli than for negative stimuli. One explanation for these results is that older adults tend to have a more difficult time differentiating between the information that is being presented (Eppinger and Kray 2011).

Together, these findings show the attention biases and memorability of positively-valenced information, such as the finding that happy faces can be more easily recognized than sad ones. Positive qualities can also result in interesting behavioral outcomes, as is the case with attractive individuals having a greater number of sexual partners.

Self-Relevant Information

Humans, like animals, are particularly sensitive to events that can have an impact on their value and even social standing (Weisbuch et al. 2009). They tend to examine their environment for indications that are relevant to their said relational value, even on a pre-attentive level. The “cocktail party effect,” for example, is when an individual focuses their attention toward a particular voice in the commotion of a party or environment, often when their name or other salient information can be heard among that commotion. Individuals tend to think a great deal about what other people evaluate and perceive of them and also try to gain insight into how, in future endeavors, others will respond to them (Leary and Guadagno 2011). However, some of these evaluations are idle imaginings, while others stimulate deep distress when they suggest that one’s past, present, or future relational value is lower than desired. This additional focus, or prioritization, underlies the self-reference effect.

The self-reference effect – a mnemonic benefit for information processed for its self-relevance – has been most often observed with noun stimuli (see Klein 2014 for a review of this literature). In a relevant vein of the self-reference literature, researchers have also found a mnemonic benefit for information processed for its survival value. In this paradigm, participants rate a list of words according to the following prompt:

In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you’ll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words

may be relevant and others may not – it’s up to you to decide. (Naime et al. 2007, p. 264)

Researchers from a number of independent laboratories have replicated a “survival advantage”: a mnemonic benefit for words, pictures, and locations encoded this way (Kazanas and Altarriba 2015). Klein’s (2012, 2014) work has suggested self-reference as a potential mechanism underlying this effect, as participants consider their very survival as they encode the to-be-remembered information. Or, self-reference and survival processing may benefit from similar, elaborative encoding mechanisms (Kroneisen and Erdfelder 2011), as self-preservation is a highly salient adaptation.

Conclusions

The adaptive value of attention and memory cannot be overstated. Researchers have noted the attention-grabbing nature of a number of self-relevant stimuli: dangers in the environment, attractive individuals, and, most commonly, an individual’s name or other interests. Research supports the enhanced memorability of these objects and individuals, as well. Findings supporting these attention and memory enhancements are numerous, with researchers using both physiological and behavioral measurements. Each of these findings contributes to our understanding of the cognitive underpinnings of evolutionary psychology.

Cross-References

- [Different Functions of Memory](#)
- [Evolved Physiological Reactions](#)
- [Facial Attractiveness](#)
- [Fears](#)
- [Fears and Phobias](#)
- [Mate Choice Effects](#)
- [Mate Preferences](#)
- [Predators as Attention-Grabbing](#)
- [Selective Attending](#)
- [Universal Human Fears](#)

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Attention and Perception

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Synonyms

Observation; Selective focus; Sensitivity; Understanding

Definition

Before information can be used in a meaningful way, it must first be attended to within the perceiver's environment. Once information is attended to, how it is interpreted by the individual based on current goals, drives, and motives determines how it is perceived. Humans have an automatic tendency to focus their cognitive resources on stimuli that convey messages of potential danger (threat to survival) or mate prosperity (reproductive success). However, how these stimuli are perceived must be examined in the context of its evolutionary function in order to understand their adaptive relevance to the human cognitive system.

Introduction

The ability to efficiently attend to information within one's environment is a vital cognitive skill that allows an organism to appropriately interact with the world. However, not all information (particularly fitness-enhancing information)

is processed equivalently nor do all varieties of stimuli garnish the same attentional response (see Öhman et al. 2012 for a review). Attention can be understood as the prioritizing of a select set of information within one's environment, as deemed pertinent by the individual based on one's goals, deemed importance, salience, and past practices (Jiang and Sisk 2019). It allows an individual to focus their cognitive resources on a subset of all available information. From an evolutionary perspective, the types of details that become automatically and most readily directed by this attentional focus are thought to be those most relevant to the survival and success of the individual's genetic longevity.

Furthermore, information in the environment can be interpreted from a variety of standpoints based on the context of interaction. This susceptibility of stimuli to be perceived in different fashions can be understood as a crucial adaptation of human cognition. The research discussed in this entry will highlight the various ways in which human attention and perception influence each other and demonstrate an attunement toward evolutionarily relevant problems within the modern era.

Capture by Predatory Threat

Threats to the physical health of primates have existed in a variety of capacities causing them to develop methods of protection. For example, a quick and accurate detection of potential predators and harmful objects would facilitate one's ability to procure a safe escape or position of self-defense. In modern society, the occurrence of human predation (e.g., attacks from tigers and pythons) in many cases is not as eminent as it was for our Paleolithic ancestors. However, the residual adaptations of our cognitive system to respond to such potential threats remain present and are activated through heightened attention toward dangerous stimuli allowing for an assessment of the level of imminent threat. To test this assertion, Yorzinski et al. (2014) recorded the eye movements of individuals as they viewed evolutionarily dangerous (snakes, lions) and benign

(lizards, impalas) animals. Photo arrays were created so that there was one dangerous animal intermixed with seven non-dangerous animals, as well as the reverse. Participants viewed the arrays, one at a time, with the task of locating the unique photo (i.e., target) as quickly as possible. Regardless whether the photos were presented in vibrant, full color or in reduced quality, black-and-white format, the visual scan paths (eye movements) illustrated a clear pattern of attentional capture by the dangerous animal photos. When a dangerous animal was the target, participants were faster at locating the image than when a non-dangerous animal was the target. Conversely, when dangerous animals were the to-be-ignored photos, participants demonstrated difficulty in disengaging from these images. The authors concluded that the presence of evolutionarily threatening predators both grabs and maintains human attention due to the innate features of these animals, even when task-irrelevant (see Calvillo and Hawkins 2016 [on animacy effects] and Shabbir et al. 2012 [on pattern repetition] for additional factors in attentional superiority toward predators).

This attentional priority for evolutionarily dangerous creatures has also been found to extend into unconscious perception. Because humans are not naturally equipped with physiological resistance to counteract dangers such as venom and suffocation, having the ability to quickly detect animals that have the possibility of being a threat is a lifesaving adaptation of human visual cognition. Using an inattention blindness paradigm that allows for the examination of the types of information that are given attentional superiority, New and German (2015) tested participants' ability to detect threatening images presented unexpectedly. While completing a computer task requiring participants to focus on the center of the screen, an image appeared in the corner of the screen that resembled either an evolutionarily threatening (spider) or a non-threatening shape (housefly, hypodermic needle). When probed to identify the surprise image, participants were most accurate in detecting and indicating the location of the image when it resembled a spider, as compared to an evolutionarily non-threatening

shape. Similar results indicating early, automatic, and sustained attentional capture by fear-inducing images have also been shown using event-related potential (brain wave recordings) techniques (Leutgeb et al. 2015).

The results from New and German (2015) suggest attention is not equally allocated to all types of threatening information, but rather natural and evolutionarily based dangers produce a bias for immediate processing. The authors concluded that the human visual system is designed with a preparedness toward detecting information that has been deemed evolutionarily important, regardless of explicit awareness. However, other researchers have suggested that all threat cues, both modern and historically relevant, are efficient at automatically capturing attention. Spatial attention (i.e., focus in a visual scene) is facilitated by the presence of threatening images, particularly when the threat is directed toward the self (e.g., a gun pointed toward the observer; Carlson et al. 2009). Notably, this eliciting can occur even when conscious perception of the threat is diminished. Objects and creatures that can pose a threat to one's survival are processed with a particular advantage to allow for rapid detection, even in the absence of observer perceptual awareness. It appears that humans have an automatic drive to detect and gather information about potential dangers within their visual field.

Attunement Toward Fearful Messages from Others

Besides the viewing of natural predators, threat can be detected through observing the facial and emotional expressions of others. Emotion-evoking stimuli have been shown to be effective at capturing attention by instilling a particular value, such as a fearful face indicating a threat alert. This value can, in return, convey a message of urgency toward action to increase survival likelihood when it is of a threatening nature (see Öhman et al. 2012). A threatening message that can be quickly conveyed with urgency allows for a greater chance that the receiver can distance themselves from danger.

While assessing the role emotional faces play in facilitating risk avoidance, Becker et al. (2014) demonstrated that memory is prioritized toward remembering and detecting threatening faces. Participants were tasked with memorizing photos of male and female faces, with half of each gender making a slightly angry facial expression. When presented with a series of faces that included all of the studied faces as well as additional unstudied faces, participants were more efficient at identifying the faces that had been a part of the original study set if they were *males* displaying an angry facial expression, regardless of participant gender (Experiment 1) and outgroup status (race; Experiment 2). In line with evolutionary accounts of men holding more aggressive social roles than women, male participants displayed faster response times to the threatening male faces than female participants indicating men have a particularly heightened vigilance for identifying signs of physical threats in other men.

The authors interpreted this pattern of results to indicate robust support for automatic sensitivity toward angry faces, particularly for men with social goals relevant to identifying the motive of potential mate stealing and physically threatening individuals (also see Sulikowski and Burke 2014 for heightened attention to objects related to social roles). This capturing of attention by valenced faces has also been found in young children, indicating that the significance of an emotional message is understood early on and has a genetic component in allocating spatial attention (Elam et al. 2010). Once a threatening face has been detected, it remains in a position of privilege in memory. This readiness to encode fear-inducing messages helps to facilitate identification of information that can be used to garner the safety level of a face when it is encountered at a later point. Thus, the heightened awareness of potentially dangerous stimuli not only enhances the immediate survival of the organism but also its future success.

Besides visual cues, auditory indications of distress and danger are effective at automatically directing attention. Vocalization patterns can be used to convey messages to others about one's internal state. For example, whines, particularly when used by infants toward caregivers, tend to indicate a sense of helplessness through an

increased pitch, slowed speech production, and amplified loudness (Chang and Thompson 2010). These special acoustic characteristics have been shown to capture diverted attention in adults and increase attentiveness toward the source of the whines. Ultimately, this attention-grabbing vocalization has the possibility to naturally elicit the help the individual needs from others.

As in the case of fear-filled messages, throughout the literature emotion has repeatedly been shown to play a key role in directing attention, influencing memory, and, consequently, manipulating conscious perception (Pessoa 2005). However, results from these studies must be interpreted within their individual contexts. Emotion-inducing information is generally processed in a rapid manner that overrides attention to simultaneously ongoing processes so that the message conveyed by the stimuli is prioritized (e.g., Elam et al. 2010). Under these circumstances, attention is diverted from its intended focus thereby adding to the pressures of attentional load capacity. When unattended information of an emotional nature demands attention, an emotion processing advantage is demonstrated. Therefore, individuals with varying sizes of attentional reservoirs may not display the same degree of responding to emotional information. In addition, individual differences in sensitivity to label a stimulus as fearful or threatening (Pessoa 2005), past experiences (Jiang and Sisk 2019), and contextual framing of a situation (Wang 1996) could influence how attention is directed. For example, if an angry face is perceived as a neutral expression, a threat response may not be activated for that individual and no enhanced attempts at self-preservation will occur. In other words, visual and verbal messages intending to convey a sense of urgency by directing attention toward a threat identified by one individual may not be perceived in the same fear-induced fashion by the receiver.

Relationship Maintenance and Procurement

An understanding of the world is not based solely on the direct information that is picked up by one's sensory organs. Rather, the types of information that make it into one's attentional focus

and how that information is interpreted can lead to various outcomes of perception (Carrasco and Barbot 2019). The evolutionarily relevant goals of finding viable mates and proper survival resources have been shown to be supremely influential in dictating the type of stimuli one will notice in a scene and how those stimuli will be evaluated.

One such example of how the object of an individual's attention can influence their perceptual experience of the world is found in the misattribution of ambiguous noises and sights to an illogical source that aligns with the object of one's attention. White and Fessler (2013) looked at this phenomenon in bereaved pet owners. Long-term pet owners who recently (within the past 2 years) lost a cat or a dog were surveyed for their frequency of falsely attributing sounds (e.g., another dog barking), visualizations (e.g., mistaking another pet as one's own), and compulsions (e.g., urge to look for or feed the pet) to the presence of their late pet. Grieving individuals who most frequently viewed the deceased pet's photos (taken while alive) were more likely to commit instances of false pet recognition, and this occurrence decreased as the time elapsed since the loss increased. Forming an emotional relationship requires a significant amount of time and effort that, if successful, can have a benefit to fitness or, if unsuccessful, be resource depleting. Following the death of a person or pet, the surviving party may feel reluctant to abandon the expensive investment and continue to search for cues that the lost agent remains a viable relationship partner. The authors suggest that misattributing ambiguous sensory information during the grieving process may serve to direct the bereaved's attention toward definitive evidence as to the possibility of rectifying the lost relationship bond. Namely, when attention is focused on a lost pet via frequently viewing photographs, the cognitive systems are readied to perceive ambiguous stimuli in a way that aligns with the desire to maintain the connection.

Due to the intense benefits associated with creating bonds, the desire to do so encompasses a large portion of the evolutionary literature. From an evolutionary perspective, there is an innate drive in humans to identify and secure viable mates so as to prolong and pass on one's genes

to the next generation. For men, this revolves around the desire to find healthy, fertile females who can successfully carry offspring. For females, the search for a strong, resourceful protector and provider to assist in child-rearing is at the forefront. When individuals' motivations related to the likelihood of mating success are manipulated, visual attention is also influenced (Chang and Lu 2012). Specifically, while viewing images of the opposite sex, men tend to focus their attention on a female's waist/hip area (indicative of fertility status) when motivated by a short-term relationship potential but focus on the face area (provides age and nurturing capacity information) when faced with long-term relationship motives. However, when information pertaining to the social status and resource acquiring success is present, both males and females tend to demonstrate early attentional persuasion toward attractive men (DeWall and Maner 2008). This attention toward males with a perception of a high social status aligns with females' adaptive preparedness to identifying resource-rich mates and males attending to threats of potential mates. The shift in visual attention based on one's reproductive goals supports the notion that perceptual attention has evolved in a sex-specific manner.

Attention to Nutritional Resources

How information pertaining to nutritional needs of an individual is perceived can also be influenced by where attention is directed. Repeated exposure to high-calorie food options has been linked with increases in observer desire to obtain and consume unhealthy nutrient options and poor body health (Alblas et al. 2018). In particular, individuals who do not have practiced self-regulation skills and also maintain a mentality of food restriction (i.e., chronic dieting) are easily primed to acknowledge the presence of food-related information. Having food-related thoughts readily in mind leads to an increased ease of perception for relevant environmental cues. This preparedness to orient toward satiating, high-calorie food has also been demonstrated by individuals in a state of hunger (Sänger 2019) as well as those experiencing stress (a response to

perceived threat; Klatzkin et al. 2019). While rapid detection and ingestion of food can be a valuable asset for individuals with a deficit of nutrition availability, such as our hunting-gathering ancestors, it can also be dangerous to the physical health of those living in a resource-enriched modern environment. Yet, an enhanced attentional and perceptual sensitivity to this necessary resource remains a crux of our cognitive processing system. The ability to quickly detect food sources as they become available in the environment allows for the option to encode and obtain or leave the food item, depending on one's most relevant goals and the amount of additional cognitive resources available (e.g., working memory capacity, self-regulation, attentional focus).

Food selection quality has also been shown to be influenced by a diner's mating goals. When dining in a public setting, individuals may manage their personal appearance through the nutritional quality of meal selection. In a recent study, Baker et al. (2019) asked a large sample of individuals to imagine themselves on a dinner outing accompanied by a new classmate who was either attractive or unattractive. When asked to make hypothetical food selections to eat in front of their assigned partner, heterosexual males and females dining with the opposite sex tended to order options with fewer calories the more attractive they perceived the dining partner. However, only individuals *not* currently in a romantic relationship demonstrated this indication of a personal desire to improve or maintain one's health via nutrition conscious choices. In other words, individuals with the potential to secure a mate attempted to display signs of fitness and increase personal mating likeability. Social context and personal mating motives, both food-irrelevant aspects, can be used to portray a positive image to viable mates through behavioral choices.

Conclusion

The literature reviewed briefly demonstrated a natural, innate attunement of human cognitive processing toward obtaining evolutionarily

significant goals. Attention is captured and maintained by information relating to the detection and avoidance of danger, procurement of viable mates, and obtaining nutritional resources. How this information is interpreted and dealt with by the individual can be influenced by the observer's motivations, goals, and evolutionary drives. While attention and perception often coincide in allowing an individual to explore and understand the environment, it is paramount to consider how the mechanisms driving these processes have adapted and evolved to shape their priorities.

Cross-References

- Adaptations: Product of Evolution
- Associative Learning
- Attention and Memory
- By-Products of Adaptations
- Communication, Cues, and Signals
- Emotions
- Evolution of Mammalian Vision, the
- Evolutionary Cognitive Psychology
- Evolutionary Hierarchy of Needs
- Face and Object Recognition
- Fundamental Motives
- Identifying Adaptive Functions
- Predators as Attention-Grabbing
- Problem Solving
- Response Bias
- Selective Attending
- Selective Attunement to Adaptive Problems
- Sex Differences in Same-Sex Aggression

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Attentional Capture

- [Predators as Attention-Grabbing](#)

Attire

- [To Afford Protection Against Climate and Weather](#)

Attitude

- [Prejudice](#)

Attraction

- [Evolution of Desire, The](#)
- [Facial Disfigurement](#)

Attraction During High Fertility

- [Attraction During Ovulation](#)

Attraction During Ovulation

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Synonyms

[Attraction during high fertility](#); [Ovulatory shifts in attraction](#)

Definition

Shifts in attraction, in both men and women, during ovulation.

Introduction

Although women typically benefit most from engaging in long-term mating strategies (i.e., attaining and maintaining long-term, committed romantic partners), women can benefit from engaging in short-term mating strategies during ovulation – the short window of time in which the likelihood of conception is most probable. Recent research has suggested that in order to simultaneously reap the benefits associated with both short- and long-term mating, women have evolved dual-mating strategies. Consistent with this idea of dual mating, women's attraction to short-term mates who may offer genetic benefits to potential offspring increases during ovulation. Notably, these ovulatory shifts manifest through (a) changes in women's mate preferences such that women more strongly prefer traits associated with high genetic quality, (b) changes in behaviors such that women more frequently engage in behaviors aimed at attracting high-quality, short-term mates, and (c) changes in men's attraction to women that coincide with women's ovulation. In this chapter, we review each of these ovulatory shifts in turn.

Ovulatory Shifts in Women's Mate Preferences

Heterosexual women are attracted to men's physical and psychological traits that are associated with the willingness and ability to invest in future offspring (e.g., intelligence, access to resources, dependability, trustworthiness, willingness to provide paternal care). Indeed, they demonstrate consistent preferences for these traits across their ovulatory cycles (for a review, see Gildersleeve et al. 2014). In addition to these investment-signaling traits, heterosexual women are attracted to men's physical and psychological traits that are associated with high genetic quality (e.g., masculinity, muscularity, social dominance, intrasexual competitiveness). Men that possess such traits, however, often pursue short-term mating strategies, which are associated with higher rates of infidelity, less warmth and agreeableness, and lower levels of commitment (see Cantú et al. 2014). Accordingly, such men are often risky long-term mates. Evolutionary perspectives suggest that in order to minimize these risks while also maximizing the genetic benefits (for potential offspring) that such men have to offer, women evolved an ovulatory shift in mate preferences such that they more strongly value traits associated with high genetic quality in potential short-term mates during ovulation. That is, women temporarily adopt short-term mating strategies such that they are more attracted to cues of genetic quality in potential short-term mates (because a short-term sex partner's genetic quality could directly influence the genetic quality of any potential offspring) during peak fertility compared to less fertile phases of their ovulatory cycles.

Consistent with this notion, a growing body of research has demonstrated an ovulatory shift in women's attraction to physical cues indicative of high genetic quality. Indeed, women demonstrate a greater preference for indicators of masculinity such as facial masculinity (for review of this work and other similar work, see Gangestad et al. 2005), body masculinity and muscularity (specifically when evaluating potential short-

term mates; Gildersleeve et al. 2014), and vocal masculinity (for review of this work and other similar work, see Gangestad et al. 2005) near ovulation compared to less fertile phases of their ovulatory cycles. Likewise, high (compared to low) fertility women report stronger attraction to the scent of men who possess higher levels of testosterone, presumably because testosterone leads to facial masculinity and increased musculature (Thornhill et al. 2013).

Research has also demonstrated ovulatory shifts in women's attraction to men's nonphysical cues indicative of high genetic quality (e.g., social dominance, competition, riskiness, genetic diversity). One study, for example, demonstrated that women are more attracted to aggressive, arrogant, and socially respected (i.e., intrasexually competitive) men as short-term partners near ovulation compared to less fertile phases of their ovulatory cycles (for review of this work and other similar work, see Gangestad et al. 2005). Likewise, high (compared to low) fertility women are more attracted to men who appear less faithful (for review of this work and other similar work, see Gangestad et al. 2005), which is likely due, at least in part, to the notion that such men are pursuing short-term mating strategies – strategies that only high genetic-quality men can successfully pursue. Moreover, women report increased attraction to outgroup men near peak fertility compared to less fertile phases of their ovulatory cycles (Salvatore et al. 2017), which is likely due, at least in part, to the genetic diversity that such men can offer any potential offspring. Finally, women are more attracted to men who display multiple indicators of genetic quality (i.e., charisma, confidence, and social dominance) as potential short-term mates when they are near peak fertility compared to less fertile phases of their ovulatory cycles (Cantú et al. 2014). Notably, supporting the robustness of this growing literature, a recent meta-analysis examining women's preferences for multiple cues of genetic quality demonstrated that high (compared to low) fertility women had an overall stronger attraction to cues of genetic quality when evaluating potential short-term mates, but not

when evaluating potential long-term mates (Gildersleeve et al. 2014; cf. Wood et al. 2014).

It is worth noting that these ovulatory shifts in mate preferences are not unique to single women. Even partnered women who are actively engaged in long-term, committed relationships experience increased attraction to cues of high genetic quality during ovulation. Interestingly, however, the implications of such increased attraction differ depending on the genetic quality of women's current long-term partners. Specifically, ovulatory shifts in attraction to cues of genetic quality can have negative implications for women whose long-term partners exhibit low genetic quality but positive implications for women whose long-term partners exhibit high genetic quality. For instance, ovulating women with less (versus more) symmetrical long-term partners, an indicator of genetic quality, are less sexually attracted to their current partners and more sexually attracted to alternative partners outside of their current relationships (i.e., extra-pair partners; for review of this work and other similar work, see Gangestad et al. 2005). In contrast, ovulating women with more (versus less) symmetrical long-term partners report increased sexual attraction to those partners (for review of this and similar work, see Gangestad et al. 2005). It is likely that there are numerous implications of accumulated drops and spikes in sexual attraction over the course of long-term relationships. We are not aware, however, of any research that has explored such long-term implications. Future research may benefit from doing so.

Ovulatory Shifts in Women's Behavior

Women's behaviors also shift during ovulation, which likely function to increase their ability to attract high genetic-quality partners. For instance, women's clothing choices fluctuate across their ovulatory cycles. Indeed, women dress in more attractive and sexy attire (for review of this work and other similar work, see Haselton and Gildersleeve 2011) and are more likely to wear

red clothing, which men find particularly attractive, during the fertile phases of their ovulatory cycles compared to the luteal phases (Eisenbruch et al. 2015). Likewise, in an effort to enhance their appearance and thus attract high genetic-quality mates, women are more likely to restrict their caloric intake (Meltzer et al. 2015) during the fertile phases of their ovulatory cycles compared to the luteal phases. Finally, evidence demonstrates that women's flirtatious behaviors fluctuate across their ovulatory cycles. One study, for example, demonstrated that heterosexual women displayed more flirting behaviors when interacting with men who exhibit cues of high genetic quality near peak fertility compared to less fertile phases of their ovulatory cycles (Cantú et al. 2014). Notably, women were no more or less likely to display increased flirting behaviors when interacting with men who lacked such high genetic-quality cues. Moreover, high (compared to low) fertility women report greater interest in attending social gatherings where they are likely to meet available men, and are more likely to agree to dance with men when at a nightclub (for review of this work and other similar work, see Haselton and Gildersleeve 2011).

Ovulatory Shifts in Men's Attraction to Women

Such ovulatory shifts do not appear to be unique to women – men have demonstrated similar shifts in attraction that coincide with women's ovulation. That is, some research has demonstrated that men are more attracted to women who are in the fertile phases of their cycles compared to their luteal phases, which is seemingly adaptive given that ovulation represents women's brief window of reproductive opportunity. For instance, men report increased attraction to high (compared to low) fertility women's voices and scents (for review of this work and other similar work, see Haselton and Gildersleeve 2011; also see Gangestad et al. 2005). Notably, such ovulatory shifts in attraction also emerge among partnered men. One study, for instance, demonstrated that heterosexual men are more attracted to their current long-term female partners when they are near peak fertility

compared to less fertile phases of their ovulatory cycles (Cobey et al. 2013).

Why do such shifts occur in men? Although research has not yet uncovered a clear explanation, it is possible that women experience physical changes during ovulation that men perceive either at an automatic or explicit level. Another possible explanation may be that women emit pheromones that men receive via olfactory communication. Future research would benefit from further examining these and other potential explanations for shifts in men's attraction that coincide with women's ovulation.

Conclusion

Compared to most primates, women's ovulation is relatively concealed. Nevertheless, there are notable shifts in (a) women's mate preferences, (b) women's behaviors aimed at attracting high genetic-quality partners, and (c) men's attraction to women that coincide with women's ovulation. Among women, such ovulatory shifts in mate preferences and behaviors appear to be aimed at procuring a high genetic-quality mate, which would in turn increase the genetic quality of any potential offspring. Among men, such ovulatory shifts in their attraction to women appear to be aimed at procuring women with high likelihoods of conception, which would in turn increase their likelihood of successfully reproducing. Taken together, these ovulatory shifts carry important implications for both women and men, regardless of whether they are seeking new partners or maintaining current relationships.

Cross-References

- [Ovulation](#)
- [Reproductive Strategy](#)
- [Women's Preferences During Ovulation](#)

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Attractive

- [Hollywood Actors](#)

Attractiveness

- [Appearance/Beauty in Girls](#)
- [Male Counter Strategies to Cyclic Shifts](#)
- [Male Qualities and Likelihood of Orgasm](#)
- [Sex Differences](#)
- [Sex Differences in Attractiveness of Humor](#)
- [Sexual Signaling During Ovulation](#)

Attractiveness and Anger-Proneness

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Synonyms

[Aggression](#); [Strength](#); [Weight](#)

Definition

Perceived positive physical characteristics influence aggression.

Introduction

Evolution asserts that physical markers and superior traits will endure generations of breeding to absolve undesirable traits from remaining. In this process, it is argued that attractiveness remains a desirable trait among the population. Examination into evolutionary psychology and its influence on attractiveness has established how physical and psychological traits influence human behavior. The development of research into attractiveness and human behavior claims that individuals who are considered attractive have a higher predisposition to anger. In this new area of research into attractiveness and anger, it explores how certain physical characteristics of an individual are perceived as attractive, but also how having these characteristics influence behavior, such as anger.

Attractiveness

Attractiveness can be considered subjective to individuals who are observing individual's physical characteristics and it's considered to be a disadvantage to be unattractive (Griffin and Langlois 2006). For different sexes, attractiveness can be measured using several physique markers on the human body. One notable physical marker of attractiveness remains body structure. It is

believed that individuals who are considered attractive place a higher regard to weight as a measure of their attractiveness (Horvath 1981). Females who have larger curvature compared to females with less curvature in their body types were seen as more attractive by both males and females (Horvath 1981). Therefore, females who are considered “full-figured” or fat have a higher likelihood to be viewed as an unattractive individual. With this view as a prominent indicator of the perception of attractiveness for individuals, females are inclined to believe that they are overweight when they remain within the healthy weight range, but also neglect to perceive themselves as underweight when they were (Connor-Greene 1988). Females are more likely to be within a healthy weight range, but still perceive themselves as overweight (McCreary and Sadava 2001). The perceptions of body physique for females continue to influence human behavior by having females diet in unhealthy ways, such as using laxatives and vomiting as an effective weight-loss strategy, to manipulate others’ perceptions for a positive response to their attractiveness. (Connor-Greene 1988). Females who were underweight for a healthy body structure continued to perceive themselves as more attractive (McCreary and Sadava 2001). Weight as the measure for body structure impacts the perceptions of attractiveness for females which can influence their behavior to obtain a higher level of perceived attractiveness.

Females are usually the focus of research regarding body structure and attractiveness. However, males have similar perceptions from their body structure to influence their behaviors. Contradictory to females, males tend to rather gain weight rather than lose weight when they felt dissatisfied with their bodies (Connor-Greene 1988). Gaining weight for males shows that males have muscle and strength as their body structure and is perceived as a valuable trait among women. Men who were considered overweight still perceived themselves lighter than they were, but still considered themselves more attractive and healthier than overweight females (McCreary and Sadava 2001). Body structure can also be perceived using smaller facial characteristics that help others perceive their body as attractive. In face structure, women

associate a man’s face shape, specifically prominent jaws, with their perceived masculinity and strength perceiving them as attractive individuals (Windhager et al. 2011). Thus, if a male has certain facial characteristics that manipulate females to believe that their body structure is muscular, then they will be considered attractive. One reason why women may perceive certain masculine features of males as attractive is because they consider these features to be a sign that these males are healthy (Fink et al. 2006). If females are more likely to believe that males are healthy individuals, then there is a possibility for a desirable relationship between the pair that creates the potential for future offspring. Perceived attractiveness between sexes shows that there remain significant differences between what is considered attractive for females and for what is considered attractive for males. Thus, females are perceived as attractive when they have a lower weight, while males are perceived as attractive when they have more weight.

Attractiveness and Anger

Anger is a fundamental part to human behavior that appears in infancy and remains throughout the life course across cultures and individuals (Sell et al. 2009). Since anger appears early on in one’s life, examining aggression in children has shown that attractiveness and anger remain correlated with one another. Teachers of preschoolers report that aggressive children are perceived as some of the most physically attractive individuals (Hawley et al. 2007). Using others to measure the perceived attractiveness of children show that other’s perception of attractiveness does not influence the internal feelings that can lead to anger. Rather, physically attractive children are more anger-prone than unattractive students. Examining the overall physical attractiveness of children and adolescents shows that more physical attractiveness leads to a higher likelihood of anger-proneness.

Anger is asserted and expressed differently between the two sexes, similar to how the perceptions of attractiveness vary significantly between the two sexes. Females’ perceptions of their own attractiveness are correlated with their proneness

toward anger, even when controlling for the strength of the female (Sell et al. 2009). Thus, controlling for a physical indicator of attractiveness that is seen in males (i.e., strength), females who are considered attractive using the standards set by other females act aggressive when they are being measured using their stereotypes. Being physically attractive is a fundamental predictor in popularity and superiority for females and in order to maintain the social position females engage in covert aggression against others (McBride 2011). Therefore, females who are considered more physically attractive are more likely to engage in anger and aggression.

Females that are perceived to be physically attractive are prone toward anger. However, unlike the differences in measuring physical attractiveness between sexes, males are also more prone to anger when they are perceived as physically attractive (Sell et al. 2009). Since musculature is an important predictor of physical attractiveness in males, as an indicator to his strength often determined by body weight, both strength and attractiveness are highly correlated with one another (Sell et al. 2009). Hypermasculine males, or macho men, are more likely to respond with anger when they are faced with threats to their sense of perceived attractiveness by a woman (Downs and Gold 1997). Similar to females, males who are perceived as physically attractive are more prone to anger.

Conclusion

Attractiveness is considered a subjective trait and is “in the eye of the beholder.” However, individuals who are perceived as being physically attractive are more likely to respond with anger to stimuli. Attractiveness is a perceived quality of human life that varies between the sexes. While females want to be skinnier as an indicator of attractiveness, males tend to want to gain more weight as an indicator of strength which influences perceived attractiveness. Females who are perceived as being more physically attractive are more prone to the emotion of anger compared to females who are unattractive. Similarly, males who

are considered physically attractive are also more prone to anger compared to males who are not considered attractive. Overall, attractiveness leads to anger-proneness among individuals throughout the life course and across cultures.

Cross-References

- [Hollywood Actors](#)
- [Sex Differences in Aggression](#)
- [Strength and Anger-Proneness](#)

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Attractiveness Effort

- [Desire to Be Included Among Desirable Women](#)

Attribution of Human Traits

- [Anthropomorphism](#)

Attribution of Intentionality

- [Agency-Detection](#)

Audition

- [Hearing](#)

Auditory Cerebral Cortex

- [Primary and Secondary Auditory Cortex](#)

Auditory Cortex

- [Auditory Neurobiology](#)

Auditory Nervous System

- [Auditory Neurobiology](#)

Auditory Neurobiology

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Synonyms

[Auditory cortex](#); [Auditory nervous system](#)

Definition

The physiology of the auditory system of the brain

Introduction

It is noteworthy to state that the physiology of the auditory nervous system has been studied mostly in experiments with animals rather than with humans (Moller 2013). Next, the physiology of the nervous system is briefly discussed, along with frequency selectivity being the main property of the auditory nervous system. As parts of the auditory system, the primary and secondary auditory systems are involved in a higher processing and analysis of sound information. Finally, the mechanosensors are briefly discussed, as they contribute to a process known as mechanotransduction – a physiological process which living cells sense and respond to mechanical stimuli by transducing them into electrochemical signals which, in turn, elicit cellular responses (Bavi et al. 2017).

Structure of the Auditory System

Anatomically, the auditory nervous system consists of ascending and descending systems that create a link between the ear and the auditory cerebral cortex. The axons from the ear connect to neurons in the cochlear nucleus, which in turn connect to other nucleus in higher locations in order to reach the cerebral cortex. The neurons from these systems descend from the

central structures to the nuclei located in a surrounding distance, including the area of the ear (Moller 2013).

There are two separate pathways called classical ascending pathways, also known as the tonotopic system, and nonclassical, or adjunct systems, which are known as the extralemniscal, diffuse, or polysensory systems. There are specific nuclei (Demanez and Demanez 2003) between the auditory nerve and the primary auditory cerebral cortex, which are located in the classical ascending pathway. These nuclei are the cochlear nucleus (CN), where the auditory nerve fibers are divided into dorsal, anteroventral, and posteroventral fibers; the central nucleus of the contralateral inferior colliculus (ICC); the lateral portion of the ventral division of the contralateral medial geniculate body (MGB); and the superior olivary complex which are made by three main nuclei: the superior lateral, medial, and trapezoid body nuclei. These nuclei handle the acoustic information based on the synaptic transmissions and their position in the brain (Moller 2013; Velluti 2008). The neurons in the ventral MGB connect to the primary auditory cerebral cortex (AI) and other auditory cortical areas (Moller 2013).

The auditory nerve (AN) in humans has around 30,000 fibers and it is part of the eighth cranial nerve (CN VIII). It also includes the superior and inferior vestibular nerve (Moller 2013). The majority of the fibers in the auditory nerve help to innervate inner hair cells (Pickles 2012). In order for the auditory nerve to achieve action potential, certain events must take place. Firstly, the sound waves create sound vibrations that reach the tympanic membrane, which in turn trigger the movement of the middle ear's ossicles. As a result, the sound vibrations travel from the ossicles to the oval window membrane, which elicits movement of the cochlear fluids and the basilar membrane. The motion of these structures bend the hair cells' cilia which determine the excitation of the hair cells and finally action potential is generated (Velluti 2008).

There is the so-called frequency selectivity as the main property of the auditory nervous system.

The frequency selectivity of the basilar membrane is responsible for the frequency tuning of the auditory nerve cells and cells in the classical ascending auditory pathways. Nerve fibers of the auditory nerve, cells of the auditory nuclei, and those of the auditory cerebral cortex are anatomically arranged on the basis of their characteristic frequency. This structure is known as the tonotopic organization (Moller 2013; see Polley et al. 2014 for a review on topography and tonography).

Primary and Secondary Auditory Cortex

The auditory cortex involves a complex organization of connections that lead to the processing of auditory information (Moller 2013). The auditory cortex is responsible for the perception of sound and aids with the understanding and production of sounds (Hackett 2015). The complete anatomy of the human auditory cortex is not completely known, nor completely understood, as there is yet an exact consensus between the scientists concerning the exact anatomic positions of the auditory components of the auditory brain (Moller 2013).

Specifically, the primary auditory cortex occupies the cortex of the supratemporal plane and is surrounded by auditory association areas in circular sulcus and the superior temporal gyrus (Pandya 1995). Based on information taken with the use of MRI, the location of the primary auditory cortex seems to be located on a region on the medial two thirds of Heschl's gyrus, linked to Brodmann's area 41 (Pickles 2012; Wasserthal et al. 2014; Moller 2013). There have been efforts to create a tonotopic mapping of the auditory cortex, but this has been a challenging process. The small size of the auditory cortical fields and the lack of a common consensus in regards to the specific locations of the auditory cortex made the process of the tonotopic mapping difficult (Saenz and Langers 2014). However, efforts to topotopically map frequency has proven to be successful (Isaa et al. 2017; Wolak et al. 2017). Equally mapped is the modulation rate (Lithari and Weisz 2017), sensory tuning bandwidth

(Saenz and Langers 2014; Wang and Eliades 2017), and sound intensity (Bilecen et al. 2002).

The Secondary Auditory Cortex

Some neurons from the secondary auditory cortex respond to other stimuli, besides sound. These stimuli are somatosensory, such as touch and vision (Moller 2013). Based on recent research, there is a structural connectivity between the visual and the auditory cortex (Chen et al. 2013) and a multimodal sensory interaction between the sensory cortices (Hosokawa et al. 2017). Both primary and secondary auditory cortices occupy only a small fraction of the neocortex, which is composed of association cortices (see Moller 2013, p.103).

Mechanosensor

These are molecules that interact with other molecules and are affected by mechanical forces. In certain cases, these molecules engage in biological reactions (Shen et al. 2017).

In the cell, these molecules are responsible for a process known as mechanotransduction. This is a physiological process which living cells sense and respond to mechanical stimuli by transducing them into electrochemical signals which, in turn, elicit cellular responses (Bavi et al. 2017).

Furthermore, mechanosensors work as molecular reporters inside the cells that connect external mechanical stimuli at the surface of the cell to intra cellular signaling events and downstream effectors through mechanosensory proteins (Bavi et al. 2017).

In eukaryotic cells, there are three main mechanosensors: (1) the caveole, microvilli, and cilia; (2) intra- or extracellular elements such as the actin cytoskeleton, a cadherin rich cell to cell junction, glycocalyx; and (3) mechanosensitive ion channels. There is a possibility that a combination of these mechanosensors contribute to the mechanotransduction (Bavi et al. 2017).

Certain studies have attempted to study the exact role and structure of the mechanosensors

using sophisticated techniques such as magnetic nanoparticles and magnetic fields (Shen et al. 2017; see Kita et al. 2013, for the birth of a mechanosensor).

Fritzsche, Beisel, Pauley, and Soukup (2007) suggest that the evolution of the mechanosensors is interpreted as different mechanosensory organs which were developed in different phyla. Structural designs of ion channels were also found, suggesting that the evolution of mechanosensors took place independently (Delmas and Coste 2013).

Moreover, Kung (2005) in his study described a unifying principle for mechanosensation based on the use of mechanosensitive ion channels. He suggested that channel proteins sense forces from the lipid bilayer involved in opening and closing the mechanosensitive ion channels.

Conclusion

The anatomy and complexity of the auditory nervous system was briefly discussed, which is involved in the processing of acoustic information. The auditory system is divided in the primary auditory system and the secondary auditory system. The mechanosensors contain living cells which are sensitive to mechanical stimulation, leading to biological responses - a process called mechanotransduction.

Cross-References

- [Mechanosensor](#)
- [Primary and Secondary Auditory Cortex](#)

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Auditory Perception

► Hearing

Auditory Properties of Rooms

► Cathedral Acoustics

Auditory System

► Hearing

Auditory System, The

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Synonyms

Inner ear; Middle ear; Outer (external) ear; Peripheral auditory system

Definition

The structures of the outer (external) ear, middle ear, and inner ear.

Introduction

The auditory system is responsible for hearing and is consisted of the peripheral and central auditory system. The peripheral auditory system includes the structure of the outer ear, middle ear, and the inner ear (Romand and Ehret 1997; Velluti 2008). The cochlea and otoliths are also involved into the inner ear structure, and are briefly discussed as well.

The Outer Ear

The outer ear consists of the pinna, the ear canal, and the ear drum (Pickles 2012; Munir and Clarke 2013). The function of the pinna is to receive sound in order to transmit it to the cochlea – where all acoustic information is processed – through the ear canal (Seikel et al. 2010; Moller 2013). The sound then travels to the middle ear through the ear canal, otherwise called the external auditory meatus. The ear canal secretes cerumen (wax) which has a minor antibacterial function and protects the ear from minor injuries. The skin of the ear canal is covered with various nerves responsible for the heart rate, blood circulation, and fainting (Moller 2013).

The Middle Ear

The middle ear is an air-filled space and is located behind the tympanic membrane which contains the bones of hearing (ossicles) called malleus, incus, and stapes (Munir and Clarke 2013). These ossicles constitute the ossicular chain which help with the transmission of sound to the tympanic membrane and then to the inner ear (Seikel et al. 2010). Another part of the middle ear is the Eustachian tube which occupies the air space between the nose and the throat (Balkany and Brown 2017).

In the middle ear there are two tympanic muscles that are connected to the ossicles. These are called the stapedius and the tensor tympani. The function of the stapedius is to rotate posteriorly the footplate of the stapes stiffening the ossicular chain. The function of the tensor tympani is to pull the malleus anteromedially, thus reducing

the movement of the tympanic membrane. These two muscles stiffen the transmission system of the middle ear, monitoring the acoustic signal in the lower frequencies, thus protecting the ear from high intensity sounds (Seikel et al. 2010).

An additional part of the middle ear is the Eustachian tube, which forms a link between the nasopharynx and the middle ear. The cranial nerve VII passes runs through this pathway (Munir and Clarke 2013). The function of the eustachian tube is to allow mucous flow away and oxygen run through and out of the tube. It, also, works as a way to equalize the pressure levels in situations where pressure is changed such as under the water or in high altitudes (Balkany and Brown 2017).

Reichert's (1837) hypothesis on comparative morphology has contributed to the evolutionary understanding of the middle ear's ossicles, the malleus, and incus. According to his study, these ossicles were derived from the cartilages of the upper and lower jaw elements of the articular and quadrate amniotes. Further evidence was found to support this hypothesis based on fossil records in South Africa and Russia (Takechi and Shigeru 2010).

Furthermore, Manley (2010) has noted that the tympanic middle ears were developed independently and that their origin is unique. He further explained that evolution takes place independently in similar groups, and that the results developed from the same structures could be similar. He also mentioned of the possibility of a random evolution and that the developments of the middle and inner ear were essential for hearing in high frequencies. With the enlargement of the brain, the tympanic middle ear in therian mammals was developed, subsequently creating a secondary palate that helped with the development of a pressure system in the middle ear (Manley 2010).

The Inner Ear

The inner ear is sectioned into the cochlea and the balance system (the vestibular system). The first representation of the human and mammalian cochlea was discovered in 1561 (von Bekesy 1948) and the phenomenon of resonance was

proposed by Duverney in 1683 (Mudry 2000) who based his observation on the resonance of two piano strings in tune with each other. The careful drawings of Magnus Gustaf Retzius (Jelliffe 1920) who depicted the cytoarchitecture of the organ of Corti has given an elaborate description of the membranous labyrinth, cross sections of the cochlea, and the surface of the organ of Corti based on different stages of development (Johnsson and Hawkins 1967).

The balance system, otherwise called vestibular system, is made up of a vestibule, located between the cochlea and the semicircular canals. A structure called the osseous labyrinth (or bony labyrinth) is consisted of the cochlea, the vestibule, and the semicircular canals. The membranous labyrinth lies in the osseous labyrinth; it can be described as a sac filled with fluid (Boulpaep and Boron 2005). Both the bony and the membranous labyrinth are complex balance organs of the inner ear (Hain and Helminsky 2007).

Cochlea

The cochlea has a snail shape and has compartments filled with fluid. These compartments are in a form of a spiral and contain the organ of Corti, which is the receptor for acoustic information (Chang and Khana 2013). The organ of Corti and the vestibular organ are enclosed in the temporal bone (Moller 2013). There are more than 15000 hair cells in each cochlea which yield electrical signals based on the vibrations of the inner ear fluid; consequently, these electrical signals are perceived by the brain as hearing (Balkany and Brown 2017).

The cochlea distinguishes the sounds based on their frequency in order different sounds activate different auditory nerve fibers. This takes place in the inner hair cells. The outer hair cells help to reduce the friction on the basilar membrane and increase its vibration breadth. They also increase frequency selectivity, according to the intensity of sound, and frequency selectivity is decreased when the intensity of sound is increased, which causes the cochlea to function in a nonlinear way in order to compress the sound before the innervation of the auditory nerve. This process helps to

distinguish the sounds in the auditory nerve based on their intensities (Moller 2013).

The organ of Corti, as a part of the cochlea, is composed of a specialized structure consisted of hair cells, and is located on the basilar membrane. In essence, this structure organizes the auditory transduction (Pickles 2012, pp. 28–33). It is covered with a gelatinous and fibrous fold called the tectorial membrane, consisted of molecules and collagens known as tectorins, which play a significant role for the hearing process (Pickles 2012, pp. 28–33; Richardson et al. 2011). The organ of Corti generates sharply tuned traveling waves by the process called mechanotransduction based on electrochemical reactions in the cochlear scalae (Pickles 2012).

Otolith

Otoliths are describes as tiny carbonate particles that compose the otolithic membrane. The otolithic membrane accommodates the utricle and the saccule inside the vestibule (Chang and Khana 2013; Seikel et al. 2010). It, also, covers the utricular macula which is a sensory organ consisted of hair cells and cilia. The saccule is located near the scala vestibuli in the vestibule and is consisted with macula and the otolithic membrane. The linear motion or the tilting of the head creates a movement force between the otolithic membrane and the macular surface, which result in the bending of the hair cells (Oghalai and Brownell 2012).

Conclusion

The main structures of the peripheral auditory system were discussed, namely, the outer ear, middle ear, and inner ear, along with the structures of the cochlea and the otoliths.

Cross-References

- Cochlea
- Inner Ear

- ▶ Middle Ear
- ▶ Organ of Corti
- ▶ Otolith
- ▶ Vestibular System

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Aunt Care

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Synonyms

[Adjunct mother](#); [Allomothering](#)

Definitions

Aunts, paternity Uncertainty, Kin caregiving, Matrilateral, Patrilateral, Asymmetric kin investment

Introduction

Despite being forgotten in research, maternal and paternal aunts are highly invested and play an essential role of an “adjunct mother,” thereby providing childcare, guidance, support, and affection to their nieces and nephews (Milardo 2009, p. xvi). The aunt-child relationship can be consanguineous or formed through marriage and therefore includes the sisters of a father (paternal aunts) or mother (maternal aunts) or the wives of father’s brothers (paternal aunts) or mother’s brothers (maternal aunts).

One of the most decisive factors in the degree of investment in nieces and nephews is a sense of solidarity or the relationship between parents and their siblings’ family, which can be further

influenced by contextual factors listed here. For instance, higher “associational (frequency of contact between parents), consensual (the similarity of attitudes and emotions between parents), functional (perception of support), normative (sense of obligation) and a structural (residential proximity) solidarity” (Milardo 2009; p. 12) can remarkably moderate ideas of kin-keeping and investment in nieces and nephews.

Laterality and Gender Effects

Notably, the scholarly examination of above listed contextual factors brings into light the concept of asymmetric kin investment or the laterality effect. Studies in favor of laterality effect suggest the occurrence of higher investment in nieces and nephews by a maternal aunt than a paternal aunt. To elaborate, in matrilineal societies, blood-related maternal aunts perceive a stronger sense of genetic relatedness and emotional closeness in comparison to paternal aunts. These perceptions are further influenced by paternity uncertainty, opportunities for frequent contact, stronger relationships between sisters, and young female’s (in this case maternal aunt’s) interest in learning maternal behaviors (Salmon 1999; Parent et al. 2013). Additionally, Tanskanen (2015), in the Finnish sample, showed that childless aunts are more likely to invest in their nieces and nephews, perhaps because they have more time and resources.

On the contrary, studies from patrilineal societies conclude otherwise. Patrilineal societies mandate higher associational, structural, and normative solidarity to the husband’s family to ensure higher perceptions of genetic relatedness and a lower uncertainty of paternity. Consequently, patrilineal societies have more significant investment by paternal aunts than maternal aunts (Pashos 2000; Milardo 2009; Euler and Weitzel 1996).

Despite cultural variations on the laterality effect, aunts being females and therefore normed kin-keepers undoubtedly provide more intense and frequent caregiving to their nieces and nephews than uncles. To further

investigate, Gaulin et al. (1997) compared their US sample with Euler and Weitzel (1996). The authors reported that in the US sample, aunts invested more regardless of whether they are paternal or maternal. Therefore, unlike Euler and Weitzel (1996) study of German families, laterality played a smaller role than gender in the US sample.

Impact of Aunt Care on Development in Minority Families

After grandparents, aunts contribute the most in all domains of development. Aunts can be a role model, teacher, friend, or an allomother and provide meaningful family connections that can have a lasting and valuable effect on the development trajectory during adversity (Ellingson and Sotirin 2006) to strengthen families (Davis-Sowers 2012).

As noted, these positive effects are particularly relevant and distinct in minority families. Parent et al. (2013) found that among African American families in the USA, the warm relationship between maternal aunt and their nieces and nephews was negatively associated with internalizing and externalizing behaviors. Cross-cultural comparison studies in the USA and Finland reproduced similar results. Erola et al. (2018) found that resources at an extended family level, particularly of uncles and aunts, are positively associated with socioeconomic attainment among nieces and nephews. Likewise, Allen et al. (2008) concluded that among Latino families, extended family members such as aunts are untapped resources that bridge the intergenerational gap between parents and adolescents.

Aunt Care and Aunts

Davis-Sowers (2012) examined the determinants of the aunts’ decision to care for their nieces and nephews in Black families. He found that aunts have little to no authority in denying/accepting care. The participants reported that decisions to parent are deeply rooted in gendered norms,

sense of obligation to the family, an occurrence of crisis-like situation, and religious values that promote kin-keeping. Despite the lack of agency, aunts were inclined to caregiving as it offers opportunities to build a personal identity, a higher sense of self-efficacy, and satisfaction of making a difference in the lives of their family.

The above article Davis-Sowers (2012) alludes to feminist criticisms of gendered caregiving. Strong-Boag (2009) agrees that after grandparents, aunts are first in line to provide care. Nevertheless, this reliance at the time crisis contributes to unpaid emotional and physical labor for women and undue pressure of being responsible for children's future.

Conclusion

Currently, we have a handful of research that solely pertains to the impact of aunt care on lifespan development. In extended family care literature, aunts are lumped together with grandparents and uncles, and therefore examining their role is challenging. The research supports the positive and vital role of aunts on individual development. Since many aunts are expending time, energy, and effort in maintaining or supporting relationships with their nieces and nephews, scholarly examination of their role is warranted.

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Aural Perception

► Hearing

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Definition

Aurelio José Figueredo is an evolutionary personality psychologist who has made significant contributions to research on sexual violence, environmental harshness and unpredictability, and on psychometric approaches toward measuring human life history.

Aurelio José Figueredo is an Evolutionary Personality Psychologist from the University of

Arizona in Tucson, who serves in the Departments of Psychology and Family Studies and Human Development. In addition to his full professor appointments, Professor Figueredo directs the Ethology and Evolutionary Psychology (EEP) graduate program. His most notable contribution to the field of evolutionary psychology was to more fully develop the *psychometric approach* to the assessment of human life history strategy by discovering the *K-Factor*, a latent higher-order construct of psychological, behavioral, and cognitive traits that are theorized to comprise a cohesive and comprehensive life history strategy. Since its inception in the early 2000s, the psychometric approach has generated much derivative research as well as controversy (see Copping et al. 2014). The sections below briefly discuss Professor Figueredo's private life, education, and a selection of his contributions to the field of evolutionary psychology.

Private Life

Aurelio José ("AJ") Figueredo was born in Victoria de las Tunas, Oriente, Cuba, on 27 December 1955 to Yolanda Fulgencia Rodríguez and Alfredo Odón Figueredo. He had two older siblings at the time, Alfredo Ezequiel Figueredo and Yolanda Inocencia Figueredo. Most notably, AJ's older brother became an Anthropologist who eventually achieved the status of world expert in Caribbean Archaeology and Territorial Archeologist for the US Virgin Islands. When he was only 3 years old, AJ's parents had to flee their native country under threat of execution by the newly established communist dictatorship of Fidel Castro; 9 months later, AJ and his two older siblings emigrated to the USA to join their parents, escorted by their grandmother María del Pilar Lalana de Figueredo. His younger sister, Ana María Figueredo, was later born in Brooklyn, New York, and is the only original immediate family member besides AJ remaining alive at the time of writing. AJ has been married since 1983 to Maureen Jacobs Figueredo, and she gave birth to one daughter, Alyssa Mia Figueredo, in 1987.

Academic Education

Having spent most of his childhood on the east coast, AJ moved west and earned a bachelor's degree in Psychology at California State University, Los Angeles, in 1983. AJ was then accepted into the University of California, Riverside, earning his master's degree in 1985 and receiving his doctorate degree in 1987, specializing in comparative psychology, physiological psychology, and quantitative psychology. His graduate advisor was Lewis Petrinovich, a comparative psychologist who worked extensively on song learning in the white-crowned sparrow and, later in life, wrote several books on the evolution of human moral intuitions.

The breadth of AJ's early training involved ethological and comparative research mainly focusing on biologically prepared behavioral development in insects, specifically focusing on conditioned host selection in the parasitoid jewel wasp, as a function of changing ecological conditions during development (Figueredo 1987, 1989). He additionally extended his comparative work to include the conditioned response to sex pheromones in the oriental fruit moth (Figueredo and Baker 1992), the quantitative ethology of song learning in the zebra finch (Figueredo et al. 1992), and the latent structure of personality dimensions in both stump-tailed macaque and the zebra finch (Figueredo et al. 1995) as well as in the common chimpanzee (King and Figueredo 1997).

Major Contributions to Evolutionary Psychology

The Evolutionary Psychology of Sexual Violence. Professor Figueredo's early work focused on the cross-cultural examination of aggressive behavior, especially sex offending, intimate partner abuse, and family violence as well as sexually motivated interpersonal aggression in general. This body of cross-cultural research asserted that issues that precipitated intimate partner violence were primarily fueled by sexual conflict between men and women. Men in these situations sought to control and retain sexual access to women by

coercive and aggressive means (Figueredo and McCloskey 1993). Further, the men often engaging in these coercive strategies were found to be low in mate value (*Competitively Disadvantaged Male Theory*; Figueredo and McCloskey 1993) and to have fast life history strategies (Figueredo et al. 2012; Gladden et al. 2008). Another finding from this body of research is that aggressive individuals are abusive and conflictual across different social domains (Figueredo et al. 2012), including the abuse of women and children (Figueredo and McCloskey 1993; Gladden et al. 2013; McCloskey et al. 1995).

The Hierarchical Latent Structure of Human Life History Strategy (the K-Factor). Briefly, life history theory posits that organisms are given a finite amount of bioenergetic resources that they must allocate across varying facets of development. These trade-off decisions are influenced by the local conditions of the environment in which the organism resides, with resource allocation occurring in developmental domains that best maximizes resources for survival and reproduction (see Life history theory or Fundamental Strategies, encyclopedia entries). Life history strategies reside on a continuum, whereby fast life history strategies are oriented toward short-term mating and low parental care, while slow life history strategies are oriented toward long-term mating and high parental care. While Professor Figueredo has contributed to many aspects of human life history theory, one of his most notable contributions to the study of human life history was to put forth and test the hierarchical latent structure of the *K-Factor*, a psychometric extension of Rushton's (1985) psychosocial life history model (see Figueredo et al. 2013 for a summary). Both models posit that life history strategies encompass a coordinated suite of traits and characteristics that range from reproductive history (e.g., age of puberty, number of births, etc.) to behavioral, cognitive, and personality traits. One of the most comprehensive measures of life history strategies (*K*) was developed by Professor Figueredo and his colleagues called the *Arizona Life History Battery* (ALHB; Figueredo 2007) and the short-form version called the *Mini-K* (Figueredo et al. 2006). Most recently, they have introduced a psychometrically superior short form

called the *K-SF-42* (Figueredo et al. 2016a), having developed a novel method for creating cross-culturally valid and generalizable short forms. Empirical work using these and equivalent measures of life history strategies have found evidence that *K* is both a heritable (Figueredo and Rushton 2009) and temporally stable individual trait (Brumbach et al. 2009; Figueredo et al. 2014a); a recent meta-analysis has also shown that *K* influences a wide array of psychosocial traits (Figueredo et al. 2014b). According to Figueredo et al. (2013, p. 3), *K* has been empirically demonstrated to:

- (1) positively and significantly predict Executive Functions, Trait Emotional Intelligence, Mate Value Inventory, Mate Value Scale, Rosenberg Self Esteem Scale, Self-Adjective Checklist, Social Economic Exchange Scale, Collective Self Esteem Scale, Positive Assortative Mating, Female Physical Height, Long-Term Mating Sociosexual Orientation, Moral Intuitions, In-Group Loyalty, as well as Secure Attachment, Supportive Communication, and Long-Term Satisfaction in Romantic Relationships, both cross-sectionally and longitudinally; and (2) negatively and significantly predict the Mating Effort Scale, Short-Term Mating Sociosexual Orientation, Escalated Mate Retention Tactics, Affective and Punitive Responses to Sexual or Emotional Infidelity, Intimate Partner Violence, Interpersonal Aggression, Female Intrasexual Competitiveness, Disordered Eating Behavior, Negative Ethnocentrism, Negative Androcentrism, Levenson's Primary Psychopathy Scale, Levenson's Secondary Psychopathy Scale, Machiavellianism Scale, Buss-Perry Aggression Questionnaire, Proactive-Reactive Aggression Questionnaire, and General Social Deviance.

Controversies Surrounding the K-Factor The *K-Factor* has generated empirical interest across many substantive domains such as interest in babies (Zilioli et al. 2016) and across international contexts (reviewed in Figueredo et al. 2015). However, the *K-Factor* has also generated controversy from developmental life history researchers (Copping et al. 2014). Critics of the psychometric approach to life history are mainly concerned with statistical aggregation across measures, such as how ALHB is constructed (Copping et al. 2014), and are also concerned that these measures have not been adequately validated with biodemographic indicators of life history

(Copping et al. 2014). Critics have also asserted that statistical aggregation of higher-order life history factors may obfuscate developmental psychological sequences, obscuring possible inquiry into pathways that may shape the behavioral development of life history strategies across the life course (Copping et al. 2016). Professor Figueredo and his colleagues have defended the use of aggregated measures in cross-sectional samples as a “snapshot” of experiences and developmental milestones from that point in an individual’s life (Figueredo et al. 2015, p. 312). Accordingly, advocates of each position agree that both points of view indeed represent valid and complementary perspectives and have conceded to continue improving the measurement and development of measures that best accurately capture human life history strategies (Copping et al. 2016; Figueredo et al. 2015).

Environmental Harshness and Unpredictability Evolutionary models – particularly life history models – emphasize the important role the environment plays on intraindividual variation on different suites of traits (Stearns 1992). Extrinsic sources of illness, disability, and death in adulthood that are not accounted for by age or health status are purported to be major drivers in the evolution and development of life history strategies such that increases of extrinsic morbidity-mortality may accelerate life history strategies (Charnov 1991; Ellis et al. 2009). Professor Figueredo, along with Bruce Ellis and other colleagues (Ellis et al. 2009), examined the impact of adult extrinsic morbidity-mortality by proposing two distinct ecological constructs: environmental harshness and unpredictability. The American Psychological Association conferred the George A Miller Award for an Outstanding Recent Article on General Psychology upon this paper in 2010. According to this model, environmental harshness and unpredictability are independent drivers of life history evolution and development. Harshness at the population level is defined by increases in adult extrinsic morbidity-mortality and is usually often operationalized in modern human populations at the individual level by measures of low socioeconomic status (e.g., Simpson

et al. 2012) or exposure to violence (Brumbach et al. 2009). Unpredictability is defined at the population level as the amount of fluctuation in adult extrinsic morbidity-mortality and is operationalized in modern human populations at the individual level through measures of unpredictability such as the number of household or school relocations or family transitions (e.g., Simpson et al. 2012).

Current Research Activities Professor Figueredo and international team of collaborators are currently working on integrative models of social biogeography that follow the social *sequelae* of human life history at the population level in the achievement of higher levels of social harmony, macroeconomic complexity, aggregate productivity, and advanced cognitive development (Figueredo et al. 2016b). In addition, Professor Figueredo and colleagues have been developing a statistical model designed to disentangle the intrinsic gene-environment correlations in commonly used developmental data (such as parental, neighborhood, and economic sources of harshness and unpredictability) from truly extrinsic environmental influences.

Cross-References

- ▶ [Bruce J. Ellis](#)
- ▶ [Environmental Harshness](#)
- ▶ [Environmental Unpredictability](#)
- ▶ [K-Factor \(Figueredo\)](#)

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Australopithecus africanus

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Definition

First African hominin discovered; The species has several historically important specimens

Introduction

Australopithecus africanus is an early fossil hominin known from several localities in South Africa, most notably Swartkrans Cave. It is one of the most well-represented hominin fossil species, with large numbers of associated cranial and postcranial elements. Dating has proven difficult, due to the complex cave geology and lack of volcanic sediments in the known localities, but current estimates for this species range from 3.0 to 2.0 Ma (e.g., Herries and Shaw 2011).

History

This species includes several historically important fossils, most notably the juvenile specimen known as the “Taung child.” As described by Raymond Dart in 1925, this specimen represented the first known early African hominin and was confirmation of Darwin’s hypothesis that the earliest humans would be found in Africa. However, cultural and scientific prejudice, notably the wide acceptance of the fraudulent Piltdown specimen, prevented its acceptance as a human ancestor in the wider scientific community for almost 20 years. Various fragmentary specimens were discovered over the next several decades (e.g., Broom 1936), but it was not until the discovery of more complete adult specimens such as Sts 5 (aka Mrs. Ples, see Figure 1) at Sterkfontein (discovered 1947) that *Australopithecus*

Australopithecus aethiopicus

► *Paranthropus aethiopicus*



***Australopithecus africanus*, Fig. 1**

africanus was widely acknowledged as human (e.g. Clark 1950).

Anatomy

A. africanus is broadly similar to other known species of *Australopithecus*, in that it possesses several primitive apelike anatomical retentions, including, cranially, a projecting subnasal region, a notable canine root, a relatively flat cranial base, and a cranial capacity between 400 and 500 cc. There appear to be several anatomical specializations related to dietary adaptation in the face (the buttressing of the “anterior pillar” alongside the nasal aperture, Rak 1983) and teeth (overall large postcanine dentition, Broom and Robinson 1947), and a diet of relatively tough foods is therefore inferred. Postcranially, this species is also similar to other early hominins in the genus, with a body size ranging from 1.1 m (for inferred females) to 1.4 m (for inferred males), relatively long arms, a well-developed thumb, and clear evidence of bipedalism in the pelvis and lower limb. There is a sufficiently large sample to assign individual skulls to sex, and the range of known adult specimens (e.g., Sts 5 and Stw 505) indicates a relatively high degree of sexual dimorphism, consistent with other well-represented early hominins (e.g., *Paranthropus*, *A. afarensis*), and a gorilla-like social structure is therefore inferred.

Evolutionary Relationships

The phylogenetic position of *A. africanus* has changed over the last 50 years, as the fossil record, particularly from East Africa, has expanded dramatically. Until the 1970s, this species was seen as the best candidate for direct ancestry to all later human species, including both the genus *Homo* and the robust genus *Paranthropus* (e.g., Tobias 1978). However, currently, *A. afarensis* and *A. aethiopicus*, both from East Africa, are seen as the likeliest ancestors for those two genera, and *A. africanus* is typically relegated to a terminal side-branch of human evolution (Strait and Grine 2004). More recently, an analysis of dental morphology has proposed that *A. africanus* may be ancestral to the later South African species *A. sediba* (Irish et al. 2013).

Conclusion

Australopithecus africanus played a critical role in the acceptance of Africa as the location of the origin of human evolution. Anatomically, it is similar to other species in the genus, with many apelike retentions. The current consensus is that it represents a phylogenetic dead-end in the human tree, but the continued production of specimens at Sterkfontein and other sites means that this species represents a wealth of critical information on anatomical adaptations in early fossil humans.

Cross-References

- [Australopithecus Group](#)
- [Human Evolution](#)

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Australopithecus boisei

► *Paranthropus boisei*

Australopithecus garhi

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Definition

Early human ancestor from 2.5 million years before present.

Introduction

Australopithecus garhi is an extinct fossil hominin species identified from remains discovered between 1990 and 1998 at the Bouri locality, in the Middle Awash region of the Afar Regional State, Ethiopia. The remains of this species, which date to roughly 2.5 Ma based on argon-argon dating techniques, are composed of unassociated cranial and postcranial elements discovered over

some 9 sq. km. Hypotheses for conspecificity for some of these elements are based on proximity at the time of collection; the more distant remains are associated primarily based on discovery in the same or temporally similar geological horizons.

Anatomy

The cranium (as known from holotype specimen BOU-VP-12/130) is characterized by extremely large postcranial dentition, well within the range of the robust group, *Paranthropus*, and it possesses a notable sagittal crest. However, this species lacks several anatomical traits uniquely seen in *P. robustus* and *P. boisei*, including molarization of the premolars, reduced anterior dentition, and a concave to flat midface; in fact the anterior dentition is notably large in this species. Other than the dental dimensions, *A. garhi* shows primitive anatomy typical *Australopithecus*: a ~ 450 cc cranial capacity, an apelike protruding subnasal region, and prominent canine roots. Postcranially, known elements (which were not discovered in direct association with cranial elements) demonstrate the characteristic *Australopithecus* pattern of relatively long arms; bipedalism is inferred, although there are no articular ends (which would allow more direct inference of locomotor pattern) preserved on the published femur.

Evolutionary Relationships

Phylogenetically, the position of *A. garhi* is unresolved. The initial publication (Asfaw et al. 1999) suggested the possibility of ancestry to the genus *Homo*, noting the lack of alternatives in the fossil record between 2 and 3 Ma. However, formal phylogenetic analysis has generally failed to support this hypothesis (e.g., Strait and Grine 2004), and subsequent discoveries have identified more likely alternatives for the ancestry of *Homo*.

Contemporaneous with Cutmarked Bone

Cutmarked bone, from several localities across several square kilometers, was found in general

stratigraphic association with the holotype cranium, and stone tools are known from the 2.6 Ma horizon at the Gona location, some 100 km distant (de Heinzelin et al. 1999). However, whether *A. garhi*, or another contemporaneous hominin, is responsible for this material, is not currently possible to demonstrate.

Conclusion

Australopithecus garhi is a hominin discovered in Ethiopia and dates to 2.5 million years before present. It is characterized by anatomy generally similar to other species of *Australopithecus*, but with notably large postcanine teeth.

Cross-References

- [Australopithecus Group](#)
- [Human Evolution](#)

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Australopithecus Group

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Synonyms

[Australopiths](#); [Kenyanthropus](#); [Paranthropus](#);
[Praeanthropus](#)

Definition

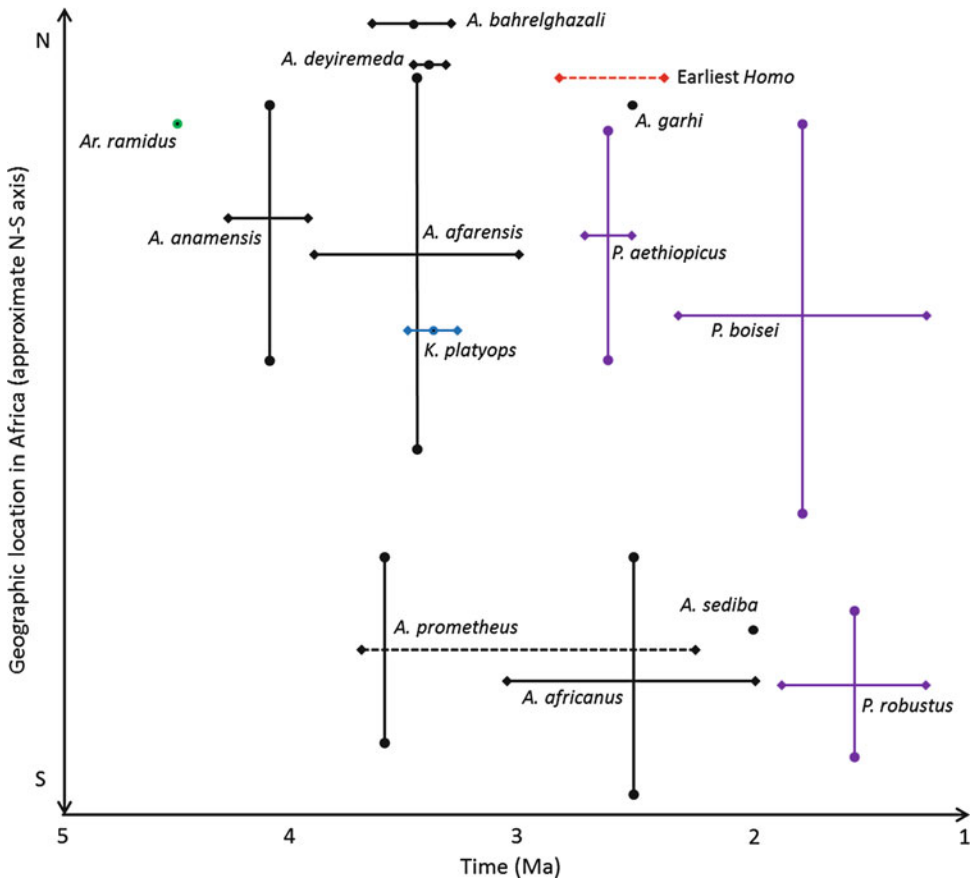
A genus (or group of multiple genera) of fossil hominins ranging in geological age from the Pliocene through the early Pleistocene (~4.2–1.2 Ma = Mega-annum, or millions of years) of Africa, the name *Australopithecus* comes from Greek for “ape” (pithekos) and Latin “of the south” (australis), for the geographical location of the first material discovered, in South Africa.

Introduction

The *Australopithecus* group (“australopiths”) consists of up to twelve species of Plio-Pleistocene hominins (members of the human lineage following the phylogenetic divergence from chimpanzees and bonobos) mostly included in the genus *Australopithecus* (but several species are commonly included in a distinct genus, *Paranthropus*, and one species is named in a distinct genus, *Kenyanthropus*). Additionally, some researchers suggest that the earliest members of the genus *Homo* should actually be transferred to *Australopithecus*, leaving just *Homo erectus* and its descendants in *Homo*. The genus *Australopithecus* is almost certainly paraphyletic, meaning that it does not form a natural group; instead, one or more lineages are more closely related to members of other genera (e.g., *Paranthropus* or *Homo*). Australopiths were ape-like hominins that retained relatively small brains and probably some adaptations to the arboreal environment (i.e., long arms for tree climbing), yet were clearly upright bipeds (adapted to walking on two legs), some of which were primitive tool users. Determining which australopith lineage gave rise to later hominins (i.e., *Homo*) is a major area of focus and controversy in paleoanthropology (Fig. 1).

History

The genus *Australopithecus* was not the first hominin genus other than *Homo* to be named, but it is the oldest one that is still used (*Pithecanthropus*, for example, has been



Australopithecus Group, Fig. 1 Australopiths in time and space. Species are arranged according to their documented presence in the fossil record (x-axis; Ma = Mega annum: millions of years before present) and approximate geographic locality (y-axis; arranged from south to north). Species known from more than one locality or date, or when a range of dates is published, are shown with vertical and horizontal bars, respectively. Single points indicate that a species is known from one site and date; a dashed line indicates that the date is controversial

(as is the case with *A. prometheus*) or links material not currently assigned to a species to affiliated material (as is the case with the Ledi-Geraru mandible and the A.L. 666-1 palate, the earliest *Homo* material). *Homo* material <2 Ma is not shown but is represented in both East and South Africa and elsewhere outside Africa. Color codes indicate different genera: green *Ardipithecus*, black *Australopithecus*, blue *Kenyanthropus*, purple *Paranthropus*, red *Homo*

subsumed within *Homo* as *H. erectus*). Named in 1925 by Raymond Dart, *Australopithecus africanus* was immediately challenged by Dart's senior colleagues in England, largely due to the influence of the later-discredited Piltdown material and the early developmental age of the *A. africanus* type specimen, a juvenile skull from Taungs. Throughout the 1930s and 1940s, Robert Broom amassed a number of adult specimens that he initially attributed to a new species, *A. transvaalensis* (then later a new genus, *Plesianthropus* – “near man”), the most famous

of which is the Sts 5 cranium, nicknamed “Mrs. Ples.” Broom and his assistant John Robinson, who carried on work at Sterktontein after Broom's death in 1951, also discovered Sts 14, the first partial skeleton of an early hominin that preserved numerous associated postcranial (below the skull) bones and therefore provided information on the way in which *A. africanus* walked. Robinson (1972) and later Owen Lovejoy and others (e.g., Lovejoy et al. 1973) studied this material to understand the anatomy and biomechanics of bipedalism in an early hominin. The new, adult material

attributed to *A. africanus* mostly put to rest the idea that Dart's "African ape of the south" (or "southern ape of Africa") was anything but a bipedal, early member of the human lineage.

Additionally, Broom discovered what he considered two species of a new genus that he named *Paranthropus*, meaning "alongside man" (*P. robustus* and *P. crassidens*; although a minority of researchers today still recognize material from Kromdraai and Swartkrans, respectively, as separate species, the latter material is generally subsumed within the former species). These craniodentally (concerning the skull, including teeth) "robust" hominins were distinct from the more "gracile" *A. africanus*, which later led to the introduction and common use of "gracile and robust australopithecines" to refer to the two groups, the former later subsuming within it a new species called *Australopithecus afarensis* (see below). Today, the terms are outdated, both because neither *A. africanus* nor *A. afarensis* was particularly gracile in craniodental morphology and because "australopithecine" invokes a taxonomic statement (subfamily designation) that is considered by many to be too broad and therefore inaccurate (i.e., "hominin" refers to a tribe, Hominini, whereas Homininae, a subfamily, includes all African great apes – hominins and members of the chimpanzee/bonobos and gorilla lineages). Therefore, the term "gracile" has been largely abandoned and "robust australopith" is preferred in colloquial reference to members of the genus *Paranthropus*. In the 1950s, Louis and Mary Leakey discovered Olduvai Hominid 5 (OH5), a cranium belonging to what they called *Zinjanthropus boisei* ("Boise's eastern African man"), a hyper-robust species clearly adapted to heavy/tough/repetitive chewing, and hence nicknamed "Nutcracker Man."

In 1962, Sherwood Washburn organized a Wenner-Gren Foundation-funded meeting of prominent paleoanthropologists, primate anatomists, molecular anthropologists, primate behavioral ecologists, and the three primary leaders of the modern synthesis of evolutionary biology, George Simpson, Theodosius Dobzhansky, and Ernst Mayr, to discuss the current state of taxonomy in the human fossil record. While all of the

entries in what would become an edited volume (Washburn 1963) are now considered classic contributions, Mayr's paper on the taxonomy of fossil hominids had a particularly strong influence on what Washburn called the "new physical anthropology." Recognizing the surfeit of genera in the hominin fossil record, Mayr recommended that just two be recognized, *Australopithecus* (including *Plesianthropus*, *Paranthropus*, *Zinjanthropus*, and other genus names proposed for early hominins) and *Homo* (including archaic – e.g., Neandertals – and modern humans and a plethora of other genus and other species names now referred to as *Homo erectus*). Many paleoanthropologists followed suit, including Robinson, who sunk *A. africanus* into *Homo* but retained *Paranthropus*, thus adopting a distinct, two-genus system to that proposed by Mayr (Robinson 1972).

In the 1970s, discoveries in East Africa, specifically from Laetoli in Tanzania and Hadar in Ethiopia, led to the naming of a new species of *Australopithecus*, *A. afarensis* (although for taxonomic reasons some researchers prefer the genus *Praeanthropus* – "pre-man"). The material it was based on included the type specimen, a mandible from Laetoli (Laetoli Hominid 4; LH 4) discovered by Mary Leakey and her team, and a partial skeleton from Afar Locality 288 (A.L. 288-1) colloquially known as "Lucy," along with other craniodental and postcranial material from nearby localities (e.g., A.L. 129), discovered by Donald Johanson and Maurice Taieb. Since the naming of *A. afarensis*, much more material has been discovered, including the A.L. 333 "First Family," a collection of craniodental and postcranial fossils attributable to a group of individuals killed around the same time, A.L. 444-2, a large partial skull (Kimbel and Deleze 2009), and DIK-1-1, the skull and partial skeleton of a young individual similar in developmental age to the Taung child, from Dikika, Ethiopia (Alemseged et al. 2006). *A. afarensis* is both geologically older (3.9–3 Ma) and morphology more primitive in some ways than *A. africanus* (3.0–2.1 Ma); thus, it was interpreted by Johanson and Tim White to be ancestral to an *A. africanus*-*Paranthropus* lineage on one hand, and the genus *Homo* on the other (Johanson and White 1979).

The discovery of the KNM-WT 17000 (“the Black Skull”) cranium from West Lake Turkana in Kenya can be interpreted as a challenge to Johanson and White’s phylogenetic hypothesis (Strait and Grine 1997). Initially named *Australopithecus boisei* (Walker et al. 1986), it was later subsumed into the species *Paranthropus aethiopicus* based on a unique combination of features that were in some ways primitive (*A. afarensis*-like: e.g., very small braincase and a prognathic, or jutting face, as opposed to the flat, “dished” face of *P. robustus* and *P. boisei*) and in others derived (*P. boisei*-like: “robust” features of the skull, including a wide face and a sagittal crest, a protrusion of bone along the midline of the skull). If *A. afarensis* was ancestral to *P. aethiopicus*, which was in turn ancestral to *P. boisei*, then *A. africanus* was freed from its phylogenetic position between *A. afarensis* and *Paranthropus*. An analysis of nasoalveolar (nasal and upper jaw) morphology also supports the monophyly (ancestral-descendant relationship) of all *Paranthropus* species to the exclusion of *A. africanus* (Villmoare and Kimbel 2011).

Multiple new species have been discovered and named throughout the 1990s and 2000s, falling geologically and phylogenetically on both sides of *A. afarensis*. White and colleagues discovered new craniodental and postcranial material at Aramis in Ethiopia and named a new species, *Australopithecus ramidus*, which was later transferred to a new genus, *Ardipithecus*, based on its distinct and more primitive traits. *Ardipithecus ramidus* is now known from a partial skeleton and a plethora of other specimens (White et al. 2009). Another new species, *Australopithecus anamensis*, is additionally thought to be more primitive and potentially ancestral to *A. afarensis*. Specimens later attributed to *A. anamensis* were initially discovered in the 1960s at Kanapoi in Kenya. New material discovered in the 1980s and 1990s, including both craniodental and postcranial fossils, led Meave Leakey and her team to name the species in 1995 (Leakey et al. 1995). White and his team working at Aramis and Asa Issie in Ethiopia discovered new material that they attributed to *A. anamensis*, including jaws and a femur

(White et al. 2006). *Ar. ramidus* and *A. anamensis* date to 4.4 and 4.2–3.9 Ma, respectively, and form what White and colleagues describe as an ancestor-descendant relationship (White et al. 2006). In South Africa, a nearly complete skeleton from Sterkfontein nicknamed “Little Foot” (StW 573) was recently re-dated to ~3.7 Ma (Granger et al. 2015); if correct, it represents the oldest material in South Africa and is contemporaneous with *A. afarensis*. Its discoverer, Ron Clarke, has resurrected Dart’s species name for *Australopithecus* material from the South African site of Makapansgat, *A. prometheus*.

Other new species, either contemporary with or post-dating *A. afarensis*, include *A. barelghazali* (Brunet et al. 1995) in Central Africa (Chad, 3.6 Ma), *A. garhi* (Asfaw et al. 1999) and *A. deyiremeda* (Haile-Selassie et al. 2015) in Ethiopia (2.5 and 3.4 Ma, respectively), and *A. sediba* (Berger et al. 2010) in South Africa. The latter species is the best known, represented by two partial skeletons from Malapa (Malapa Hominin 1, or MH1, and MH2, 2.0 Ma), along with additional material from multiple other individuals. Both *A. garhi* and *A. sediba* have been argued to be the sister taxon (most closely related and sharing an exclusive relationship) to the genus *Homo* but neither is universally supported. A third new taxon, *Kenyanthropus platyops* (“flat-faced man from Kenya”), was named by Meave Leakey and colleagues in 2001 and also proposed as a candidate for that phylogenetic position (Leakey et al. 2001). Represented by a nearly complete but damaged cranium from West Turkana (KNM-WT 40000), the cranium is argued to share derived traits with members of the genus *Homo*, including a flat face with a non-jutting jaw.

One major problem stems from the relative ambiguity of the genus designation and how to decide what defines a particular genus. Bernard Wood and Mark Collard (1999) suggested that the earliest members of the genus *Homo* (*H. habilis* and *H. rudolfensis*) should be transferred to the genus *Australopithecus* based on an adaptive zone model, where factors like body size, diet, and locomotion separate species into *Australopithecus*

and *Homo*. This requires both craniodental and postcranial fossils to assess, however, and adequate material is not available for most species. *A. sediba*, which is adequately preserved and argued to share derived traits of the skull, teeth, and postcranium with members of the genus *Homo*, retains relatively small body size and adaptations to climbing, so would be classified in *Australopithecus* under this system, whereas it might be subsumed in the genus *Homo* or placed in a new genus under a strict, cladistic (i.e., character and parsimony-based) analysis (Berger et al. 2010; Dembo et al. 2015).

Locomotion

One thing that is clear is that members of the *Australopithecus* group demonstrate unequivocal evidence for bipedal locomotion, unlike earlier potential members of the hominin lineage (e.g., *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus kadabba*). *A. anamensis*, *A. afarensis*, and *A. africanus* show derived features of the foot, knee, ankle, pelvis, spine, and cranial base consistent with adaptation to habitual bipedalism (Robinson 1972; Lovejoy 2005). These features include a non-grasping foot with an adducted hallux (in-line big toe) and a large calcaneus (heel bone), a flat ankle joint, a large plateau at the knee joint, valgus (inward) angle of the femora, short and curved blades of the pelvis, sigmoidal curvature of the vertebral column with both thoracic kyphosis (posterior curvature) and lumbar lordosis (anterior curvature), and an anteriorly positioned, horizontally angled foramen magnum (“big hole” at the base of the skull) through which the spinal cord passes. Additionally, the Laetoli footprints preserve trace fossil evidence of bipedalism in the probable hominin that made them, *A. afarensis* (Masao et al. 2016).

Much discussion has been devoted to the retention of primitive features in the postcranial skeleton of *A. afarensis* and its implications for climbing vs. terrestrial bipedalism in this species (see Ward 2002 for a review). Disagreement centers on the interpretation of these features as primitive, nonfunctional traits in a committed

terrestrial biped vs. retained adaptations to climbing. Suffice to say, it seems likely that *A. afarensis* was a committed terrestrial biped that could forage and take shelter in the trees (Ruff et al. 2016). Unexpectedly, *A. africanus* seems to be better adapted to climbing than *A. afarensis* (Berger 2002). This suggests that either *A. africanus* has become secondarily more arboreal or that it retains the primitive condition and *A. afarensis* is more derived toward terrestrial bipedalism, perhaps in convergence with later members of the genus *Homo*; recent work on early hominin calcaneal robusticity has been interpreted in support of the latter hypothesis (Prang 2015).

Brain Size, Body Size, and Sexual Dimorphism

The late Miocene putative hominin, *Sahelanthropus tchadensis*, and early Pliocene *Ar. ramidus* both have chimpanzee-sized brains, with cranial capacities ranging from 360 to 370 cc (cm³) and 300 to 350 cc, respectively (Zollikofer et al. 2005; White et al. 2009) (chimpanzees average ~366 cc; Grabowski et al. 2016). Members of the *Australopithecus* group are characterized by an average cranial capacity of ~450 cc, ranging from ~400 to 500 cc (Falk et al. 2000). For comparison, early members of the genus *Homo* have slightly larger brains (624 cc in *H. habilis*, but as low as 509 cc; ~750 cc for early *H. erectus*, but as low as 546 cc) (Grabowski 2016); however, *H. floresiensis* and the recently discovered species *H. naledi* overlap with the australopiths (426 cc and 465–560 cc, respectively) (Berger et al. 2015; Grabowski et al. 2016).

Early hominins also vary in body size, again with overlap between australopiths and some members of the genus *Homo* (e.g., *Australopithecus* average ~ 32 kg; *H. habilis* average ~ 33 kg) (Grabowski et al. 2016). Relative brain size is probably more relevant than raw brain size because brain size and body size are evolutionarily correlated and therefore have coevolved (Grabowski 2016). When body size is taken into account and an encephalization quotient (EQ) is

calculated by comparing observed brain size relative to predicted brain size given regression estimates on body weight, the difference between chimpanzees (EQ = 2.4) and australopiths (e.g., *A. afarensis*, EQ = 3.2; *A. africanus* = 3.8; *A. sediba* = 3.9) becomes more pronounced, and members of the genus *Homo* (except *H. floresiensis*, EQ = 3.8) become more distinct from *Australopithecus* (e.g., *H. habilis*, EQ = 5.0; early *H. erectus* = 4.6; later *H. erectus* = 6.0; modern *H. sapiens* = 7.6 (Grabowski et al. 2016).

Sexual dimorphism, differences in morphology (size and shape) between sexes of a single species, can only be estimated for reasonably well-documented extinct species. *A. afarensis* meets this criterion, but researchers do not agree on the degree of sexual dimorphism in this taxon (see Reno and Lovejoy 2015 for a recent review and perspective on new material), although it is almost certainly greater than that observed in modern humans. Given this non-consensus and lack of a clear relationship between sexual dimorphism (in body size or canine size) and sociosexual system amongst primates, little can be said about australopith social groups at this time.

Tool Use

Darwin proposed that bipedalism evolved in the context of freeing of the hands for tool and weapon use; however, until recently, the oldest tools in the archaeological record (the Oldowan) were 2.6 Ma, greatly postdating the emergence of the hominin lineage and thought to be associated with either early *Homo* or *Paranthropus*. Newly discovered, more primitive stone tools from West Turkana, Kenya (Lomekwi 3), dated to 3.3 Ma (Harmand et al. 2015) suggest that earlier species of *Australopithecus*, or perhaps *K. platyops*, which was discovered nearby, were tool users. It is notable that bone tools may have been used by *P. robustus* for activities like digging (e.g., termite mounds; Backwell and d'Errico 2001); similarly, other non-stone materials such as wood and bamboo may have been used by early hominins but would be unlikely to preserve in the fossil record.

Conclusion

Australopiths are a group of Plio-Pleistocene hominins with a large temporal and geographic distribution, ranging over 3 million years (>4–1 Ma) throughout East and South Africa and into Central Africa. In addition to *Australopithecus*, other genera are often included in the group or even subsumed within *Australopithecus*, including *Paranthropus*, *Kenyanthropus*, and arguably *Ardipithecus*. The group is clearly paraphyletic, that is, it is not a natural group because at least some lineages are more closely related to the genus *Homo* (e.g., *K. platyops* or *A. sediba*). Future fossil and archaeological discoveries will undoubtedly both clarify and complicate our understanding of relationships amongst the *Australopithecus* group of hominins.

Cross-References

- ▶ [Ardipithecus Group](#)
- ▶ [Australopithecus africanus](#)
- ▶ [Australopithecus garhi](#)
- ▶ [Bipedal locomotion](#)
- ▶ [Homo floresiensis](#)
- ▶ [Homo habilis](#)
- ▶ [Homo heidelbergensis](#)
- ▶ [Homo neanderthalensis](#)
- ▶ [Homo rudolfensis](#)
- ▶ [Orrorin tugenensis](#)
- ▶ [Paranthropus aethiopicus](#)
- ▶ [Paranthropus boisei](#)
- ▶ [Paranthropus robustus](#)
- ▶ [Sexual Size Dimorphism](#)

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Australopithecus robustus

- [Paranthropus robustus](#)

Australopiths

- [Australopithecus Group](#)

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Autism

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Synonyms

[Autism spectrum disorder \(ASD\)](#)

Definition

Autism is classified as a neurodevelopmental disorder with three common characteristics: impairments in social functioning, impairments in communication, and restrictions in behavioral repertoire or repetitive behaviors. The definition of autism has changed over time and is still controversial. Currently, the DSM V calls for a diagnosis of “Autism Spectrum Disorder” (or ASD) for people who previously would have fallen into any of three categories in the DSM IV. Those categories included (a) autism, (b) Asperger’s Syndrome, and (c) Pervasive Developmental Disorder-Not Otherwise Specified.

Introduction

When the movie “Rain Man” came out in 1988, there was a scene in which a medical professional was so unfamiliar with the term that he assumed that Tom Cruise’s character Charlie Babbit had said “artistic.” Clearly, autism had not yet really penetrated the cultural consciousness. Since then, autism has been a topic of increasing interest to people in the areas of clinical psychology, behavioral therapy, governmental policy, behavioral genetics, and medicine. There has been a large push to understand the disorder and to improve the quality of life of people with autism spectrum disorders. To the cognitive and evolutionary psychologists, the study of autism has been an illuminating endeavor which is helping us to

understand the social functions of the typical and atypical brain. This entry briefly covers how autism is identified, how it has increased in prevalence, how it can help evolutionary and cognitive psychologists understand neural organization via theoretical models, and some current issues affecting the autism community today.

Identifying Autism

There is no single symptom that can be used to identify a person with autism, and the impairments are usually recognized as a somewhat idiosyncratic pattern within a person. No particular deficit associated with autism, be it social, communicative, or behavioral, is guaranteed to be clearly present in a given person with autism. Generally, the characteristics that are seen as typical in autism are not clearly or sharply demarcated from the behavior of neurotypical people, which often makes it difficult to identify whether a person is properly identified as having autism, or has more mild, autism-like social or communicative impairments.

Increasing Prevalence of Autism

In 1943, Leo Kanner was the first to describe autism as a distinct syndrome. It was referred to as “childhood schizophrenia” before being called “infantile autism” and then just “autism” before being replaced by “autism spectrum disorder.” Incidences of autism were quite rare for decades, and even by 1975 it was estimated that only 1 in 5000 individuals were diagnosed with autism. A great deal of attention has been paid to a so-called autism “epidemic,” since the number of diagnosed cases of autism have risen dramatically in the past few decades and rates currently stand at about 1 in 68 (Weintraub 2011). However, it is unclear that this indicates a difference over time in the actual rate of autism in the population. More individuals are being diagnosed thanks to looser diagnostic criteria, increased awareness and acceptance, and the presence of programs designed to help autistic individuals (Fombonne

2009; Wing and Potter 2002). While heredity certainly accounts for a great deal of the reason some people have autism while others don’t, the leftover environmental variance is largely unexplained. However, it is always important to note that vaccination, in any format or vaccination schedule, has failed to be linked in any way with autism (DeStefano et al. 2013).

Interest to Evolutionary Psychologists

Autism is of special interest to evolutionary psychologists because it highlights the modular nature of social cognition and its dissociation from other functions (including general intelligence). Asperger’s Syndrome, specifically, is a category of ASD in which development in communication is not delayed and general intelligence is often unimpaired. Nevertheless, the person with Asperger’s syndrome may report being confused and bewildered by the social world. While everyone else seems to know what to do based on subtle social cues contained in tone of voice, body language, or subtext, the person with autism is often oblivious to nonliteral messages and is unable to act in a way that someone might if they were intuitively responsive to those signals. Simon Baron-Cohen has termed this phenomenon “Mindblindness.”

Therefore, a person with autism who is intelligent and communicative can allow for a very revealing comparison to neurotypical populations. By comparing the tasks on which a person with autism is (and is not) impaired, psychologists can learn more about the modular structure of the neurotypical brain.

In general, people with autism show a deficit on traditional “false belief” tasks, where a participant is asked to predict what a person will do when that person is acting based on an untrue (or out-of-date) belief or assumption. Interestingly, this impairment seems to be specifically about the minds of others and not out-of-date information *per se*. In one task, Leslie and Thaiss (1992) demonstrated that children with autism performed on par with their neurotypical peers when predicting behavior based on an out-of-

date photograph. This led the researchers to the conclusion that there was something about the ability to appreciate representations *in the head* of other people that was specifically impaired in autism. The brain module responsible for such functions was later termed the “Theory of Mind Module” or ToMM.

If such a module exists, it is important to know what is included in the proper domain of that module. More recent evidence has indicated that people with autism do not necessarily struggle with interpreting eye gaze or appreciating the basic desires and intentions of others. However, more complex or “higher order” social calculations like interpreting more cryptic desires or reading an emotion from facial cues are likely to elude a person with autism.

Alternative Cognitive Models for Autism

In addition to theories that focus on the dysfunction of a module specifically for Theory of Mind, other researchers have proposed that at least some of the deficits observed in autism are the result of impaired executive function (Kenworthy et al. 2008), or perhaps a lack of ability to integrate sensory information into a cohesive view of the world (Happé and Frith 2006).

Current Issues

The search continues for environmental factors which contribute to cases of autism. Within the autism community, there is some disagreement regarding whether this search for a cause and cure is really the best use of resources, or whether the focus ought to be in helping those with autism lead the most productive and satisfying lives possible.

Conclusion

Autism (also known as “autism spectrum disorder”) is a diagnosis involving communication,

social, and behavioral deficits. Its origins are not well understood, nor are its causes. Autism awareness has grown immensely over the last few decades, as have rates of diagnosis, but it is as yet unclear whether this is because more people actually have the symptoms of autism, or whether awareness, acceptance, and changing diagnostic criteria are the reason why so many people meet the criteria for autism spectrum disorder.

Cross-References

- ▶ Evolutionary Psychiatry
- ▶ Executive Functioning
- ▶ False-Belief Test, The
- ▶ Mindblindness
- ▶ Simon Baron-Cohen (Darwinian Psychiatry)
- ▶ Theory of Mind

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Autism Spectrum Disorder

- ▶ [Social Disabilities](#)
- ▶ [Special Case: Autism](#)

Autism Spectrum Disorder (ASD)

- ▶ [Autism](#)

Autistic Disorder

- ▶ [Special Case: Autism](#)

Autobiographical Memory

- ▶ [Episodic Memory](#)

Automatic Functioning

- ▶ [Procedural Knowledge](#)

Autonomic Nervous System

- ▶ [Polyvagal Theory](#)

Avenge

- ▶ [Ability and Willingness of Victim to Retaliate](#)

Aversion

- ▶ [Universal Human Fears](#)

Avian Clutch Size

- ▶ [Bird Clutch Size](#)

Avian Sperm Competition

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Synonyms

[Post-copulatory sexual selection](#); [Sperm competition in birds](#)

Definition

Sperm competition arises when a single female mates with more than one male. In such cases, post-copulatory processes involving sperm-sperm competition may represent an important component of sexual selection.

Introduction

Social monogamy is the prevailing mating system among birds, with males sometimes providing a substantial proportion of parental care. Until quite recently, therefore, polyandry was believed to be rare or absent in birds. Over time, however, there were growing indications that genetic polyandry does indeed occur in birds. Evidence came from a range of sources, including behavior (female

pursuit for extra-pair copulations, direct observation of extra-pair copulations in the field, males guarding females during the fertile period) and/or sex-biased heritability of morphological traits or plumage coloration (Griffith et al. 2002). The advent of molecular tools for determining paternity has revolutionized our understanding of genetic mating systems in birds. It is now apparent that genetic polyandry is relatively common in this group.

Extra-pair Paternity in Birds

The first DNA-based molecular study on multiple paternity in a free-living organism focused on house sparrows (Wetton et al. 1987). Since the late 1980s, more than 30,000 offspring of around 200 avian species have been screened for paternity status. It soon became obvious that the risk of sperm competition (often measured as the level of extra-pair paternity; EPP) varies considerably among bird species. Despite being common in many populations, EPP is completely absent in at least 10% of avian species (Griffith et al. 2002). In a typical socially monogamous avian species, about 11% of offspring result from extra-pair behavior. It is worth noting that, although molecular determination of paternity helps assess the risk of sperm competition, this value may actually underestimate both the frequency of extra-pair copulation and the risk of sperm competition in avian populations as not all extra-pair copulations result in extra-pair fertilizations. Attempts to explain interspecific variation in EPP levels have identified phylogeny as an important factor determining the occurrence of EPP in birds. As an example, EPP appears to be comparatively common in passerines, a phylogenetic branch comprising more than half of all avian species, with the proportion of extra-pair offspring approaching 80% in some species (Griffith et al. 2002). Several other ecological (e.g., population density, migration status, latitude) or life-history correlates of EPP (often associated with phylogeny) have now been identified in birds.

Across species, the varying risk of sperm competition due to polyandrous mating by females is

associated with a number of morphological and behavioral adaptations. Although males generally lack external genitalia, in some groups (e.g., ducks and ratites) the phallus has evolved to transfer semen directly into the female reproductive tract. In songbirds, the cloacal protuberance (or promontory) appearing around male cloaca during the breeding season may provide a similar function. As in other groups, the size of the testes (measured during the breeding season) increases with increased levels of sperm competition across avian species, as does the proportion of sperm-producing seminal glomera within the testes (Birkhead 1998). These adaptations may provide an advantage over other males in terms of larger and more competitive ejaculates (particularly useful when sperm competition occurs). In general, ejaculates in highly promiscuous species (such as the polygynous Galliformes) are selected to be of high quality, whereas ejaculates in genetically monogamous species with relaxed or absent sperm competition (such as owls, falcons, or penguins) often contain a large proportion of abnormal or immature sperm. Mate guarding and frequent within-pair copulations are also typical of promiscuous avian species.

The morphology of the sperm itself is exposed to strong selection pressure after copulation. In birds, as in other internally fertilizing vertebrates, selection on sperm can occur through female choice ("cryptic female choice") or through male-male (sperm-sperm) competition. While the former remains little studied in birds due to obvious methodological issues, the latter has received much attention recently. There have been a number of studies on the evolutionary context of spermatozoa morphology and function in passerines, with results showing a positive association between extra-pair paternity, sperm speed, and sperm length across species (e.g., Kleven et al. 2009).

Female birds typically store sperm for some time (the duration often determined by the typical clutch size of the species) in sperm storage tubules (SSTs), located at the uterovaginal joint. For a given species, SSTs are typically three times longer than the sperm cell, indicating intimate coevolution between sperm length and SSTs (Birkhead

1998). As sperm must fit into the SSTs, balancing selection on sperm size should be stronger in species with a high risk of sperm competition. As a result, variation in sperm length around the species-specific sperm size optimum should be reduced. Indeed, there is a strong negative correlation between variation in sperm length across males of the species and typical EPP rate (risk of sperm competition) for the species, suggesting that this estimate can be used as a reasonable surrogate for sperm competition risk across passerine species (Albrecht et al. 2013).

Unfortunately, intraspecific studies are less convincing in identifying sperm traits associated with superior male fertilization success, although careful experimental studies have identified sperm length and velocity as traits affecting sperm fertilization performance in at least some species (Bennison et al. 2015). As mentioned above, female control over fertilization (cryptic female choice) remains a “black box” in studies of promiscuous mating systems in birds. A clear example of female control over fertilization has been demonstrated in waterfowl, however, where “cryptic anatomical mechanisms of choice” (dead-end sacs or fake vaginas) in females have evolved to control for the outcome of frequent forced copulations with unwilling males (Brennan et al. 2007).

One might ask how sexual promiscuity (sperm competition) evolved and how is it maintained in avian populations? The consensus is that EPP is adaptive for males in that, through promiscuous behavior, males may increase the number of sexual partners and their own fitness. The benefits of EPP to females are less obvious as an increase in the number of sexual partners typically has no effect on female fitness. Females may gain indirect benefits, however, in terms of high-quality offspring, which leaves open the possibility that EPP evolved to compensate for hasty or inaccurate choice of social mate. The potential indirect benefits of sperm competition in birds have been intensively studied over the past two decades, with mixed results and generally inconclusive evidence (e.g., Arnqvist and Kirkpatrick 2005).

On the other hand, promiscuous behavior also carries potential costs to one or both sexes. As an example, males may be able to reduce parental care in response to female infidelity, which could constitute strong selection pressure against female promiscuity (Arnqvist and Kirkpatrick 2005). Indeed, EPP is almost absent in avian clades where males are largely responsible for food delivery to incubating females and growing offspring (e.g., in birds of prey or owls). Numerous other potential costs have been associated with promiscuous behavior, and these are reviewed in Forstmeier et al. (2014). This has led some to consider female promiscuity in birds to be a nonadaptive behavior evolving as a by-product of strong selection on promiscuous behavior in males (intersexual antagonistic pleiotropy or the “genetic constraint” hypothesis). Though a controversial idea, it has recently received solid experimental support (Forstmeier et al. 2011). Nevertheless, it remains difficult to explain why females in some species pursue extra-pair matings, despite the low strength of selection on male extra-pair paternity (contribution of EPP to overall male fitness) in these species. Despite intense research into this enigmatic behavior over the last three decades, there is still no general agreement as to whether promiscuity evolved as a male or female strategy in birds.

Conclusion

The risk of sperm competition varies substantially across avian species, making this group an ideal subject for studies on the evolution of behavioral, physiological, and morphological adaptations, as well as for assessing the potential benefits to female of genetic polyandry. Social monogamy is the prevailing mating system in birds and, from a sociobiological point of view, studies on the factors affecting postcopulatory processes in avian promiscuous systems could increase our understanding of human reproductive systems and behavior, particularly as most human cultures also promote social monogamy.

Cross-References

- [Sperm Competition: Evidence in Nonhumans](#)
- [Insect Sperm Competition](#)
- [Non-Primate Mammal Sperm Competition](#)
- [Primate Sperm Competition](#)
- [Sperm Competition Theory](#)

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Avoidance

- [Facial Disfigurement](#)

Avoiding Stigmatization

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Synonyms

[Ostracism](#); [Rejection](#); [Stereotypes](#)

Definition

Humans have evolved strategies that helped them remove group members who hampered group efficiency. By labeling characteristics and behaviors, also known as stigmatizing, groups could identify and remove inefficient and undesirable group members. To avoid social rejection, our ancestors developed ways to avoid stigmatization.

Introduction

We all know him. The guy who wears unusual clothing, or maybe talks a little too loud. He gives innocent people dirty looks, leading others to reject him. Nobody wants to be “that guy.” No matter who it is, he has some characteristic that leads people to avoid or ignore him. People learn to identify this stigmatizing feature and, if they also have it, how to conceal it. Avoiding stigmatization helps people avoid numerous negative consequences, such as social rejection.

Stigmatization

In our evolutionary history, forming groups and lasting relationships gave our ancestors an upper

hand. By forming groups, our ancestors were able to rely on others for protection, resources, and reproductive needs (Kurzban and Leary 2001). Small groups provide tremendous advantages. However, as group numbers increase, so do the risks. Referring to living in groups, Alexander (1974) stated, "There are automatic and universal detriments, namely, increased intensity of competition for resources, including mates, and increased likelihood of disease and parasite transmission" (p. 328). To combat these threats, people need to identify inefficient and undesirable members in order to reduce the group to a manageable size.

The most desirable group is one in which group members equally contribute to shared goals. Those who do not contribute hurt the group and are viewed as a weak link (Turner 1982). To determine the weak links, a set of specific traits or characteristics are defined in order to segregate and remove those individuals. Anyone with that trait would be considered more of a cost than a benefit. This classification of individuals based on a characteristic is stigmatization (Kurzban and Leary 2001). Stigmatized characteristics can be based on whether an individual identifies with an outside group, such as racial, ethnic, or religious groups (Kurzban and Leary 2001).

The possession of a stigma informs group members that you lack the abilities required to perform the tasks necessary for group survival. Once marked, groups turn to denigration in order to look superior and force the lesser out (Turner 1982). In turn, the stigmatized individual will become rejected by the group. To avoid the stress and discrimination, stigmatized individuals will isolate themselves before rejection, only interacting with those in which they feel normal (Becker 1981). However, a stigmatization does not always mean instant rejection.

The amount of control a person has over a stigmatizing factor is correlated with negative attitudes and behaviors towards that individual (Mehta and Farina 1997). The more perceived control over the characteristic, the more the individual is discriminated against. For example, people often view obesity as something that people can control through diet and exercise. The

possibility of controlling one's weight adds to the ridicule and discrimination endured by obese individuals. Cancer patients, though stigmatized, do not face a similar fate due to the lack of control over developing the condition. Lack of control is not always a saving grace. The mentally ill and physically disabled are exceptions to that correlation (Mehta and Farina 1997).

Hiding Stigmas

Being linked to a stigma results in prejudice and discrimination (Kurzban and Leary 2001). To avoid ridicule and rejection, people try to hide the stigma. Some stigmas, like obesity, are difficult to hide. These individuals are forced to isolate themselves or attempt to cover their stigma to minimize the effects (Becker 1981). Once stigmatized, individuals will attempt to avoid further stigmatization. For example, because African Americans feel stigmatized, they show greater reluctance to seek medical attention for a stigmatizing medical condition (Anglin et al. 2006).

Some stigmas, however, are considered invisible. For example, some stigmas leave a psychological, rather than physical, mark on people, such as having a history of child abuse. An invisible stigma only becomes visible when people reveal it.

To try to keep stigmas invisible, there are three common tactics: counterfeiting, avoidance, and integration (Woods 1994). Counterfeiting involves pretending not to have the undesirable stigma. To make the cover story believable, individuals go to great lengths. For example, a diabetic child may eat and drink things that harm them in order to appear normal.

Counterfeiting involves creating a new identity. It also allows individuals to socialize with peers. On the other hand, avoidance entails telling half-truths, avoiding relevant topics, and censoring (Woods 1994). Though it is not an entirely new identity, individuals keep their distance from others, hiding their personal lives.

Both counterfeiting and avoidance shield people from being not being stigmatized, but they also come with consequences. Concealing a stigma

can lead to psychological strain, emotional stress, and stress-related illnesses (Smart and Wegner 2000). Fear and anxiety can increase these negative reactions (Smart and Wegner 2000).

The last tactic – integration – involves disclosing the stigma to peers. Disclosure can entail verbally informing everyone of the stigma, or even visually showing people the characteristic. For example, gay employees may tell their friends about their partner or bring their partner to work events. Though integration can provide relief, it also provides the risk associated with stigmatized people. That is, the reduction of stress through disclosure may lead to rejection. Because of these risks, individuals with invisible stigmas use varying strategies with different peers.

Controlling Stigmas

To avoid further stigmatization and rejection, people adapted the ability to control one's impulses, self-control (Baumeister et al. 2007). In a social interaction, controlling what one's says in order to hide their stigma requires a great deal of mental control. The stress and uncertainty of never knowing if your stigma will be discovered along with attempts to suppress negative stereotypes can be draining. For example, when African American students were primed with stigmatized thoughts, they showed lower self-control (Inzlicht et al. 2006). People placed in a stigmatizing situation for too long may become depleted, leading to poor self-control. Their poor self-control can lead to the discovery of their hidden stigma.

Conclusion

Nobody wants to be stigmatized. Being stigmatized can lead us to become socially rejected. Because we have a powerful need to belong, people evolved strategies to avoid stigmatization. Avoiding stigmatization is easier for some people than others. Visible stigmas often lead people to isolate themselves from the group, joining with others who make them

feel normal (Becker 1981). Stigmatized individuals will also do what it takes in order to avoid further stigmatization, even if it means avoiding doctor's visits (Anglin et al. 2006).

Other characteristics, such as AIDS or cancer, are easier to conceal. Though concealable, individuals are often left in a tough position. They risk rejection by disclosing it, but they also suffer from concealing their stigma. People avoid being stigmatized because they do not want to be rejected. Thus, we evolved the desire to avoid stigmatization.

Cross-References

- ▶ Adaptations to Avoid Ostracism
- ▶ Stigmatization and Ostracism

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Awareness

- ▶ Attention
- ▶ Attention and Memory
- ▶ Consciousness

Axons

- ▶ Early Stage of Brain Development at Birth

B

B. F. Skinner and Behaviorism

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Synonyms

[Burrhus Frederic Skinner](#); [Radical behaviorism](#)

Definition

B. F. Skinner (1904–1990) was an American psychologist who pioneered the field of behavior analysis and developed the philosophy of radical behaviorism. Skinner is widely known for his experimental work with rats and pigeons, the technologies that he developed (e.g., the operant conditioning chamber or *Skinner box*, schedules of reinforcement), and the philosophy of radical behaviorism, which underlies and unifies the basic and applied work of behavior analysts. He expanded the scope of his science and philosophy to issues of human culture and survival, spawning the application of his behavioral science to improve the human condition.

Introduction

At the heart of Skinner's contribution is *operant conditioning*, which focuses on the influence of consequences on behavior. As a tool to understand behavior, Skinner developed the concept of the *three-term contingency*, consisting of the antecedent, the behavior, and the consequence. The antecedent is the environmental condition prior to the occurrence of a particular behavior. When an organism behaves, it interacts with its environment, producing a stimulus change or consequence. When behavior is followed by certain consequences, the strength or probability of that response occurring in the future increases; this is the process of reinforcement. If the probability of behavior decreases following a consequence, the process of punishment is in effect. The three-term contingency occurs within the context of an individual's current state, with particular establishing operations (e.g., satiation, deprivation) influencing the consequences that will be reinforcing or punishing at a particular moment. See the ► [“Conditioning and Association”](#) entry for an additional discussion of operant conditioning.

For Skinner and the behavior analysts who follow in his tradition, the function of the behavior (i.e., the particular consequence that the behavior produces) is more important than the structure (i.e., topography) of the behavior. Indeed, *operant*

classes are sets of behaviors that have the same function. A great variety of topographically distinct responses can produce the same outcome, even with simple behaviors. Take, for example, a hungry rat in an operant conditioning chamber. In the chamber (the environmental setting), the rat can press a lever (behavior), which produces food (consequence). Although the rat can press the lever in a variety of distinct ways (e.g., with its paws, its nose, its flank), the act of depressing the lever and closing the attached microswitch is the same. Thus, the operant in this case is the lever press; any response that closes the microswitch can be reinforced by the contingent delivery of food to a previously food-deprived rat.

Sometimes, the behavior that increases in strength is not directly related to the production of the reinforcer. Skinner (1948) described this phenomenon as superstition, where a behavior is adventitiously reinforced, and the learner acts as if the behavior that they engaged in was causally related to the outcome. In his classic demonstration, Skinner provided access to food to a hungry pigeon on a time-based schedule, independent of the bird's behavior. The response that the pigeon happened to be engaging in at the time of food delivery (e.g., stepping, turning) was strengthened, especially with short inter-food intervals. Even though there was not a causal relation between the bird's behavior and the delivery of the food, the responses were still strengthened, similar to superstition in humans and other animals.

The principles of behavior analysis, including reinforcement and punishment, have cross-species generality. Following in the tradition of Watson (1913), behavior analysts embrace the idea of continuity of species, wherein the laws that govern the behavior of human and nonhuman animals are the same. Skinner (1984) suggested that the operant conditioning process supplements natural selection. Organisms that are able to learn based on the consequences of their behavior are more likely to survive than organisms that are not sensitive to such environmental changes, and the importance of learning may vary across organisms. Furthermore, the stimuli that organisms are likely to be sensitive to are biologically prepared.

For example, monkeys may be easily conditioned to show a fear of snakes, but not of flowers (Cook and Mineka 1989). Thus, the phylogenetic history of the species influences the stimuli that influences an individual's behavior.

The Darwinian model of natural selection suggests that the environment applies pressure on species. Given particular environmental conditions, certain organisms are more likely to survive (i.e., have a selective advantage) than others. With differential reproduction, the traits that were advantageous in that environment become more common in the population. Similarly, the Skinnerian behavioral tradition applies selectionist logic to behavior. Instead of focusing on the population of an organism, the radical behaviorist is interested in the population of behavior as the level of analysis. As particular responses are strengthened in a behavioral repertoire (i.e., become more common), other responses necessarily decrease in frequency. This process is exemplified in the process of shaping (e.g., Skinner 1951), wherein successive approximations of a response are differentially reinforced to produce an end goal.

Verbal Behavior

When at a dinner party in 1934, Skinner was faced with a challenge to use behavioral terms to explain why one of his dining companions uttered a particular sentence: *No black scorpion is falling on the table* (Claus et al. 2007; Skinner 1957; Palmer 2006). As a reply to this challenge, he published *Verbal Behavior* (1957), a book that describes the application of behavior analysis to language. Unlike other forms of behavior, verbal behavior is reinforced by the response of a listener, rather than by the direct action on the environment. Whereas the word serves as a common unit of analysis for linguists, the functional relations between the verbal responses are more important in verbal behavior. In this conceptual structure, verbal behavior can be organized by its type (e.g., mand, tact, interverbal), and the conditions under which these responses occur can be established scientifically.

Skinner's work was famously criticized by psycholinguist Noam Chomsky (1959). This book review has been described as overthrowing the behavior-analytic approach to language; Palmer (2006) suggested that some cognitive psychologists "embraced it as a kind of Emancipation Proclamation, a justification for rejecting the methodological constraints of behaviorism" (p. 256), and he described the review as an oft-cited initiating event for the "cognitive revolution" in psychology. As a reply, behavior analysts contend that Chomsky failed to understand Skinner's book and, therefore, drew erroneous conclusions (cf. MacCorquodale 1970) and that the "cognitive revolution" does not meet the standards of a scientific revolution (O'Donohue et al. 2003).

Despite the concerns that Chomsky raised about the ability for behavior analysts to adequately describe language, the approach Skinner developed has been highly influential in the field of behavior analysis. It has also been highly successful in teaching language skills to individuals with developmental disabilities, including autism. Skinner's approach to the functional units of verbal behavior (e.g., tacts, mands) allows for these components of behavior to be targeted for separate intervention, building increasingly complex verbal repertoires (Sundberg and Michael 2001). Fortunately for behavior analysts (and the individuals who have benefited from their approach to verbal behavior), their field was strong enough to survive an inflammatory book review (cf. Schlinger 2008).

The Philosophy of Behaviorism

In addition to the empirical work through which Skinner established the principles of operant conditioning and verbal behavior, he also developed the philosophy of radical behaviorism. Chiesa (1994) suggested that radical behaviorism produced "probably the most coherent philosophy of science in psychology today" (p. 7), underlying the science of behavior analysis, including the subdisciplines of the *experimental analysis of behavior* and *applied behavior analysis*. This conceptual systematization allows for clear

delineation of what behavior analysts study and the methods that they use.

The term *behaviorism* was first used by John Watson in 1913 to describe his new type of psychological science. The phrase *radical behaviorism* was used to contrast Watson's work as an extreme (i.e., radical) departure from other versions of psychology at the time (Schneider and Morris 1987). B. F. Skinner later used the term *radical behaviorism* to differentiate between the *methodological behaviorism* of John Watson. Since the mid-1960s, this was the most common label for Skinner's approach (Schneider and Morris 1987), and his 1974 popular press book, *About Behaviorism*, was devoted to making this philosophy more broadly understood. Whereas methodological behaviorism ruled out the influence of events that were not directly observable (cf. Watson 1913), radical behaviorism allowed such events to be considered, but instead considered them as behavior (e.g., Skinner 1945, 1974).

The philosophy of behaviorism allows a coherent science of behavior analysis to exist. This science emphasizes the importance of studying behavior as a primary topic of interest rather than as a proxy for some other events or structure (e.g., Chiesa 1994). The goals of behavioral science are to describe, predict, and influence or control behavior. To achieve these goals, certain philosophical assumptions must be met, including determinism, or the notion that given the same initial circumstances, only the same outcomes could occur. Whereas deterministic thinking is a given in sciences like physics or chemistry, it becomes more contentious when applied to the behavior of humans. A primary point of contention is the rejection of free will. In the behavioral perspective, the denial of free will means that behavior of all organisms (human and nonhuman) is caused by the individual's past experience and the contemporary environment. There is no room in a scientific analysis for causal factors beyond these two. If it was possible for the individual to respond based on free will (i.e., independently of their learning history), there would be no way to predict or control the behavior of those organisms, since any unexplained variability could be attributed to the will of the organism.

Beyond the reliance on determinism, or perhaps because of it, behavior analysts are pragmatic in their work. Following the philosophic tradition of William James, the *useful working* of procedures and philosophies is of great import to behavior analysts (Lattal and Laipple 2003). The pragmatic approach has defined the research agenda of behavior analysts and shaped their methodology. Interestingly, evolutionary psychologists also cite William James as an intellectual founder (e.g., Suplizio 2007), but the components of his work emphasized by each field differ. Whereas behavior analysts focus on environment-behavior relations, evolutionary psychologists seek psychological mechanisms related to survival (cf. Tooby and Cosmides 1989).

The focus on behavior defines the subject of enquiry in behavior analysis. With this approach, there is an emphasis on behavior of the individual, relying on single-subject or within-subject experimental designs (cf. ► [“Methods and Enduring Impact of Behaviorism”](#) entry). For any given organism, behavior analysts believe that behavior is a result of three primary factors: the evolutionary history of the species (phylogeny), the learning history of the individual (ontogeny), and cultural factors. Phylogenic factors influence the stimuli to which an organism might be sensitive and limit the responses that are possible. As much as a human might want to, they will never be able to fly on their own or see ultraviolet light without assistive technology. A parakeet, however, has a distinct advantage in both of these domains. The ontogenic history of the organism encompasses every experience that the organism has, including reinforcement and punishment. Based on their past experiences and the contemporary environment, an individual will act in predictable ways. Skinner suggested that he was not an originator of his behavior (or the science that he developed) but instead that he was a locus for contingencies and evolutionary history to come together to produce the outcome.

The third level of selection that Skinner (1984) described was the cultural practices of the group. This level applies uniquely to human behavior, which is highly sensitive to the behavior of others.

Cultural selection allows for the transmission of traits and behaviors across groups of unrelated individuals. Such transmission allows the development of educational practices, religion, scientific behavior, and other mechanisms that support human survival.

Social Applications of Behaviorism

With the ability to predict and influence behavior, Skinner saw the power of his behavioral technology to improve the human condition. He published several influential mass-market books to describe his ideas, including *About Behaviorism*, *Beyond Freedom and Dignity*, and *Walden II*. In these works, Skinner was able to reach a broad audience. A central theme of this work was the notion that society was failing in important ways and that the application of the science of behavior analysis could improve the world. The problems that Skinner described included issues of education, population growth, and the distribution of scarce resources. All of these problems reduced, to Skinner, to problems of human behavior. Without changing the way our species behaved, Skinner foresaw the dramatic escalation of these problems to the point where human survival would be threatened. He wrote, “The choice is clear: either we do nothing and allow a miserable and probably catastrophic future to overtake us, or we use our knowledge about human behavior to create a social environment in which we all shall live productive and creative lives and do so without jeopardizing the chances that those who follow us will be able to do the same” (1978a, p. 66).

In *Walden II*, Skinner described the application of behavioral technologies to create a society in which leisure is abundant, work is divided evenly, and resources are made available to everyone, i.e., *the good life* is achieved via careful planning and experimentation. Skinner (1978a) noted that the society that he describes involves minimal ownership of property and, therefore, had a lessened environmental impact than contemporary society. The goals in the society he described were to produce pleasant personal interactions via the

technology of behavioral science. Practices which this group uses, from education to government, are effective; if a practice does not work, it is abandoned, in an experiment of social design (Skinner 1978b). Although it was a work of fiction, the novel spawned several intentional communities, including Twin Oaks in Louisa, Virginia, and Los Horcones in Sonora Mexico. These communities put into practice Skinner's ideas presented in his novel (cf. Kincaid 1973), and they continue to exist today.

Following the initial work of Skinner, the application of behavioral technology to a wide array of important problems has expanded exponentially. Crime prevention, education, environmental sustainability, etc. all have benefited from the efforts of applied behavioral science (cf. Biglan 2015). His impact has been far-reaching, and his work has directly improved the lives of individuals around the world.

Conclusions

Skinner's contributions to psychological science, especially operant conditioning and the philosophy of radical behaviorism, provide a selectionist framework to understand behavior. This framework provides analogues between the Darwinian model of natural selection and the behavioral changes that occur within the life span of an organism. Skinner's analysis of verbal behavior greatly expanded the application of his science, despite the criticism it faced. His contributions provided the foundations for the science of behavior analysis, including the experimental analysis of behavior and applied behavior analysis. The ultimate goal of Skinner's science of behavior was to make the world a better place for its contemporary inhabitants and future generations via environmental interventions.

Cross-References

- [Conditioning and Association](#)
- [Methods and Enduring Impact of Behaviorism](#)

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BA

► Brodmann Areas

Bab-El-Mandeb Strait

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Synonyms

[Mandeb Strait](#)

Definition

Refers to a strait of water located between modern-day Yemen on the Arabian Peninsula and the African countries of Djibouti and Eritrea.

Introduction

The Bab-el-Mandeb Strait is primarily used with regard to modern times as a means to transport large amount of oil via its connection to the Red Sea and the Suez Canal. According to the African origin of modern human's hypothesis, the Bab-el-Mandeb holds a significant role of importance in the dispersal from Africa.

The Bab-El-Mandeb Strait and its Evolutionary Importance

In order to understand the importance of the Bab-el-Mandeb Strait, it is imperative to have a basic understanding of the African origin of modern humans. The African origins theory, also referred to as the “Out of Africa Theory,” states that the early migration of modern humans, otherwise known as *Homo sapiens*, evolved and eventually the African continent. According to So and so, “Currently available genetic and archaeological evidence is generally interpreted as supportive of a recent single origin of modern humans in East Africa. However, this is where the near consensus on human settlement history ends, and considerable uncertainty clouds any more detailed aspect of human colonization history” (Liu et al. 2006). There are three primary variations of this theory, including the “Strong Garden of Eden,” or the “African Eve,” model which posits that after modern humans first emerged in Africa between 200–150 kya, they dispersed to other parts of the world after 100 kya and replaced all archaic hominins without any genetic admixture (Beyin 2011). The second potential variation is the “Weak Garden of Eden” which asserts that anatomically modern humans evolved in a restricted area of Africa sometime after 200 kya and dispersed to separate regions around 100 kya replacing all archaic forms. According to the latter model, each human population is thought to have passed through a bottleneck in their respective destinations and then recovered after favorable conditions returned. (Beyin 2011). The third and final variation of this theory “argues for multiple dispersals of early modern humans out of Africa. Originally posited by Lahr and Foley, this hypothesis recognizes three dispersal events in the Upper Pleistocene, and perhaps a fourth one recently proposed by Armitage” (Beyin 2011).

Regardless of which variation actually occurred, the first wave of dispersal took place around 130,000–150,000 years ago, while the second wave took place around 70,000 years ago. The second wave of migrants crossed the Red Sea via the Bab-el-Mandeb Straits. Although at the present time the Strait is approximately

20 km (12 miles) wide, 50,000 years ago the sea levels were significantly lower, thus making the Strait much narrower. If this theory was able to be proven, the Bab-el-Mandeb Straits would have seen the first major migration of modern humans. Furthermore, via its connection to the rest of the world, it would have allowed modern humans to spread to essential anywhere.

Conclusion

In conclusion, the Bab-el-Mandeb Strait should be considered a place of high evolutionary importance. If the previously mentioned theories are able to be proven true, then the Strait will have been the gateway for the spread of modern humanity.

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Baby Brain

- [Mother's Brain Size Decrease During Pregnancy](#)

Baby Schema

- [Age of Child](#)

Baby Talk (BT)

- [Motherese](#)

Babysitting

- [Access to Alloparents](#)
- [Alloparenting](#)

Back-Burner Relationships

- [Sexual Access and Friendship](#)

Badge

- [Color Red](#)

Badges of Status

- [Male Oramentation](#)

Bait Fishing

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Synonyms

[Active bait fishing](#); [Baiting](#)

Definition

The active placement or manipulation of edible or inedible items, to attract or distract potential prey, facilitating prey capture.

Introduction

Bait fishing is a rare form of tool use that has been observed primarily among herons (family

Ardeidae), as well as a small number of other water birds (Ruxton and Hansell 2011). It involves the placement of a buoyant object on the surface of a body of water, which serves to attract or distract fish, and potentially increases the chance of capturing prey when fishing. The objects used as bait are often food items – such as insects or bread – that are highly attractive to fish, but small inedible items, including sticks or feathers, can also be used. In clear instances of bait fishing, birds will bring items to the water that they found elsewhere (Lovell 1958), or they will keep the floating item within striking distance by actively repositioning the item before it drifts out of reach.

To date, although bait fishing has been observed in a number of different species, it remains an uncommon behavior. No individuals have been observed to rely solely on bait fishing to obtain food, and this behavior has only been observed in a proportion of individuals within a population. Analogous behaviors have been observed among a few other species of animal, where bait has been used to attract different types of prey (discussed in more detail below). These behaviors are most commonly described using the term “baiting” rather than bait fishing.

Bait Fishing by Water Birds

Bait fishing was first anecdotally observed and reported in the 1950s (Lovell 1958). Lovell, throwing bread to birds at a lake in Florida, observed a green-backed heron (*Butorides striatus*) fishing from a small wall. When Lovell threw bread toward the heron, the bird took the bread to the water’s edge, and then, rather than eating it, the heron placed the bread in the water. When the bread began to drift away the heron repositioned it closer to the wall. After a few moments Lovell observed a fish begin to nibble on the bread, and, suddenly, the heron successfully speared the fish. Lovell remained at the lake and observed the heron performing this behavior repeatedly over a number of days.

To date, bait fishing has been observed in the wild or in captivity among at least seven different

heron species, as well as two species of gull and one species each of kite, sun bittern, and kingfisher (reviewed in Ruxton and Hansell (2011) and Shumaker et al. (2011)), and reports of this behavior in additional species continue to amass. Bait fishing has been studied most extensively among the green-backed herons – in which the behavior was first identified – which have been observed to fish with bait in multiple locations around the world, including southern America, Japan, and parts of western Africa (Higuchi 1988). Note that green-backed herons are sometimes classified into two species (the green heron, *B. virescens* and the striated heron, *B. striatus*) but are now most commonly considered to be a single species.

The items that are used as bait appear to vary across locations. At sites studied in Japan, green-backed herons have been observed to use almost any nearby items as bait, including bread, popcorn, flies, insects, sticks, leaves, feathers, and berries (Higuchi 1986), while in other areas the items observed to be selected as bait have been more restricted. On a few occasions, herons have been observed to break a large stick into a smaller piece and then use this as bait, which can be considered a form of tool manufacture (Higuchi 1986; Shumaker et al. 2011). Given the differences that might exist in attracting fish, some researchers draw a distinction between bait fishing using edible and inedible items, referring to the latter as “lures” (Ruxton and Hansell 2011).

This bait-fishing behavior can be viewed as an extension of a more conventional fishing technique – the stand-and-wait method – where a predator remains stationary until prey comes within reach then delivers a rapid strike to capture their prey. In this context, provisioning bait is expected to increase the bird’s success, by enticing fish to swim within the bird’s striking distance more often than would occur without bait. However, although there are some indications that bait fishing can be an efficient technique, the prediction that bait fishing is more effective than alternative fishing tactics, not involving bait, has yet to be explicitly tested. In one of the most systematic observational studies, Higuchi recorded the success rate of adult and juvenile green-backed

herons engaging in bait fishing using a range of different baits and lures. Adult herons were highly successful when using flies as bait, catching a fish on 86% of observed attempts and on 56% of attempts when using other insects. In contrast they obtained a fish on only 29% of attempts using sticks and 25% when using berries, both items that were commonly placed onto the water by the birds. Juveniles were substantially less successful than adults, typically only placing inedible objects on to the water's surface (Higuchi 1986). These results demonstrate that fishing with edible bait was more profitable than using inedible lures, but it remains unclear how bait fishing compares to other fishing tactics. A detailed observational study of three herons indicated that considerable individual differences could be found in both the propensity to engage in bait fishing and the chances of success, which may have been linked to features of the birds' territories (Higuchi 1988). Thus, one possible explanation for the rarity of this behavior is that bait fishing may rarely be more effective than other fishing techniques (Ruxton and Hansell 2011).

Origins of Bait Fishing

Relatively little is known about the origins of bait-fishing behavior. It is plausible that passive bait fishing – where birds wait near bait or lures already present on the water's surface – could have acted as a precursor either behaviorally or evolutionarily to active bait fishing (Gavin and Solomon 2009; Lovell 1958). Other researchers have suggested that “dunking” behaviors, where food is dipped into water before it is eaten, could have preceded the placement of bait, by enabling a bird to form an association between placing items in water and the presence of fish (Ruxton and Hansell 2011). Given that bait fishing is rare, but has been observed in a number of different locations, it has likely arisen a number of times independently. Thus, this behavior may have a variety of different origins. Although some researchers have speculated that bait fishing requires special cognitive abilities (reviewed in Ruxton and

Hansell (2011)), much like other instances of tool use, there is currently no reason to believe that bait fishing depends on advanced cognition (Shumaker et al. 2011).

Baiting Behaviors in Other Species

In addition to the behavior of water birds, using bait to catch fish has also been observed among one group of brown capuchin monkeys, a species known for its wide range of tool-use behaviors (Mendes et al. 2000). Here, capuchin were observed to catch fish with their hands, and on several occasions an individual threw food items into the water, or held the food under the surface with one hand, potentially to attract fish. Analogous baiting behaviors have also been noted in a small number of other species (see Shumaker et al. (2011) for a comprehensive list). As one example, assassin bugs have been reported to use the carcasses of termites as bait to entice other termites out of their nests (McMahan 1982). Of particular note, burrowing owls have been observed to place mammalian dung close to their burrows, which appears to function as bait for dung beetles, a major component of these birds' diet (Levey et al. 2004). By experimentally manipulating the presence or absence of dung in front of a number of owls' burrows, Levey and colleagues demonstrated that the owls consumed far greater quantities of dung beetles when the dung was present, indicating that the dung does attract dung beetles. Burrowing owls regularly replace dung when it is removed, demonstrating that they engage in active baiting.

Recently, it has been suggested that crocodiles and alligators also perform a form of baiting. Dinets and colleagues report anecdotal evidence that crocodilians – residing in areas with large populations of egrets and other wading birds – often lie in shallow water with sticks positioned across their snouts (Dinets et al. 2015). On one occasion a crocodile was observed to catch an egret as it approached one of the sticks, suggesting that this behavior potentially functioned to attract birds seeking scarce nest material. In a systematic study, crocodiles were observed with sticks on

their snouts a number of times ($n = 11$ observations); however, the researchers did not observe birds attempting to take the sticks, nor did they observe successful predation of birds. Thus, whether this behavior is an example of baiting is not yet known.

Conclusion

In conclusion, bait fishing is a rare form of tool use, where buoyant items are actively placed by an animal on the surface of the water to attract or distract potential prey. This behavior has been most frequently observed among herons (*Ardeidae*), as well as in a small number other water birds. It can involve the placement of a range of different items to attract prey, with flies being one of the most successful types of bait. Analogous behaviors – often referred to as baiting – have been observed among other species, predominantly to catch invertebrate prey.

Cross-References

- [Bird Tool Use](#)
- [Crocodilian Bait Hunting](#)
- [Fish, Amphibian, and Reptile Tool Use](#)
- [Food Dunking](#)
- [Innate and Learned Tool Use](#)
- [Nonhuman Tool Use](#)
- [Role of Experience in Tool Use](#)
- [What Makes a Tool](#)

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Baiting

- [Bait Fishing](#)

Balance

- [Physical Health](#)
- [Regulation of Body Temperature](#)

Balance and Motion

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Synonyms

[Vestibular system](#)

Definition

The vestibular system of the inner ear contains various structures responsible to keep the person's balance and posture

Introduction

The balance system, otherwise called vestibular system, is a complex system with many structures. These are the bony labyrinth, the membranous labyrinth of the inner ear, the cerebellum, the eyes, the brain cortex, and the muscles and joints which connect to the brainstem known as the vestibular nuclei (Munir and Clarke 2013; Chang and Khana 2013).

The Vestibular System

The vestibular system contains two structures known as the macula and crista ampullaris; these are sensory neuroepithelium (Chang and Khana 2013). They consist of sensory mechanoreceptors called hair cells contained in a neuroepithelium membrane. Russel and Sellick (1978) are credited with being the first to study the mammalian inner cells. The job of these cells is to distribute the movements of the cochlea partition to the central nervous system for processing (Pickles 2012, p. 57; Chang and Khana 2013).

The basic structure of the hair cell is a single large kinocilium and about 100 stereocilia on its end (Chang and Khana 2013; see Pickles 2012, pp. 57–66). The structure of the kinocilium is that of a motile cilium with nine peripheral doublet microtubules and two central microtubules (Cuschieri 2009). The stereocilia are long microvilli organized in rows behind the kinocilium in a descending order. The polarity of the receptors is established by the kinocilium, and the stereocilia holds the sensory transduction. Deflections of the stereocilia in the direction of kinocilium opens ion channels that causes an influx of potassium and calcium ions and an efflux of sodium ions, causing depolarization of the receptor membrane. When the stereocilia are deflected in the opposite way away from the kinocilium, this action closes the channels and the receptor cells is hyperpolarized (Cuschieri 2009).

The Bony and Membranous Labyrinth

The bony and the membranous labyrinth is a part of the peripheral vestibular system. This complex balance organ of the inner ear contains the cochlea and the semicircular canals. It is filled with perilymph (Hain and Helminsky 2007), a substance that resembles the cerebral fluid, and it is used by the perilymphatic duct into the subarachnoid space (Chang and Khana 2013). The perilymph is contained in the space between the bony labyrinth and the membranous labyrinth (Pickles 2012). The membranous labyrinth contains sensory epithelium and surrounds the perilymph inside the bony labyrinth. There is a fluid called endolymph which is contained in the membranous labyrinth. This fluid is similar in composition to the intracellular fluid, and it is produced by the capillaries in the stria vascularis in the wall of the cochlear duct and is immersed by the endolymphatic sac (Chang and Khana 2013).

The membranous labyrinth also consists of the utricle, the saccule, and the lateral, superior, and posterior semicircular ducts. Each structure contains a sensory neuroepithelium called the macula. The macula's physiological property is adaptation. Therefore, when the head performs minor movements, the bent hair cells and the depolarized membrane potentials return to normal. The function of the utricle is to sense horizontal movement and the function of the macula of the saccule is to sense vertical movement. Both the utricle and saccule respond to linear acceleration, forces of gravity, and the minor movements of the head (Chang and Khana 2013).

Semicircular Canals

The semicircular canals partially embody the bony labyrinth (Munir and Clarke 2013). The structure of each semicircular canal is perpendicular to the other canals on the ipsilateral side and coplanar with the contralateral canals (Chandrasekhar 2013). The neurosensory elements of each canal are called the crista and the cupula and lie perpendicular to the plane of the canal (Chandrasekhar 2013).

The function of these three semicircular canals is to sense the turning motion of the head (Munir and Clarke 2013). The otolithic organs contained in the canals respond to the pull of gravity and provide mass to the hair cells of the balance system.

Vestibular Ganglion

Another structure called the vestibular ganglion, also known as Scarpa's Ganglion, is located in the lateral portion of the internal auditory meatus, and it is composed of approximately 20,000 bipolar cell bodies receiving afferent impulses from the hair cells of the crista ampullaris and the maculae (Chang and Khana 2013). According to Lorente de No (1926, 1931, as cited in Ballantyne and Engström 1969), the vestibular ganglion is consisted of five parts differentiated from each other on the size of their cells. These parts are called pars magnocellularis anterior; pars parvicellularis anterior; pars magnocellularis posterior; pars magnocellularis posterior; and pars parvicellularis posterior. The vestibular ganglion appears to be divided into a superior and inferior part united by an isthmus (Tascioglu 2005). The peripheral processes from the superior ganglion innervate the ampullary crests of the superior and lateral semicircular ducts and macula of the utricle, and the peripheral fibers from the inferior ganglion innervate the macula of the saccule (Tascioglu 2005). Also, the axons from the superior and inferior parts of the vestibular ganglion come together to form the vestibular nerve. In combination with the cochlear nerve, it becomes the vestibulocochlear nerve (Chang and Khana 2013).

Vestibular Nuclear Complex

Vestibular input is processed by the vestibular nuclear complex, which consists of four nuclei: medial, superior, lateral, and inferior (see Tascioglu 2005). This is the primary processor of any vestibular input.

It is noteworthy that the vestibular nuclei have four main connections: (1) connections with the ocular muscles; (2) connections with the Postural Back muscles; (3) cerebellar connections and; (4) connections with higher centers. These four connections constitute the Central Vestibular System (see Cuschieri 2009, for more info about these connections).

The Cerebellum

Moreover, the cerebellum is vital for the control of finer movement (Munir and Clarke 2013). The role of the cerebellum in the vestibular system is to function as an adaptive processor monitoring vestibular performance and to readjust vestibular input through inhibitory input as necessary (Chang and Khana 2013). The "vestibulocerebellum" (Chang and Khana 2013) is consisted of the flocculonodular lobe and the vermian cortex. Efferent information is received from the bilateral vestibular nuclei from the ipsilateral cerebellum. The projection fibers included in the cerebellum go directly to the ipsilateral vestibular nuclei and to the ipsilateral fastigial nucleus (Chang and Khana 2013). The axons from the fastigial nucleus project to the contralateral vestibular nucleus through the juxtarestiform body, an area that is significant in terms of postural reflexes and orientation (Chang and Khana 2013). The vestibulocerebellum controls body balance and posture and is linked to the ocular motor neurons (Cuschieri 2009).

The Cortex

The cortex is the part of the brain that is responsible for conscious awareness and the manipulation of space (Munir and Clarke 2013). However, specific information regarding complex cortical vestibular connections is not yet thoroughly explained nor is there a consensus of the location of a vestibular cortex (Chang and Khana 2013). Studies on humans have suggested that the main cortical processing region is most likely in or near the parietal or insular cortex (Chang and Khana

2013). Based on a conjunction analyses (see Lopez et al. 2012), it was found that the regions showing convergence between two stimulation methods were located in the median and posterior insula, parietal operculum, and retroinsular cortex. The right hemispheric parietal opercular area OP 2 was demonstrated to be the most consistent area of activation, based on a study from Zu Eulenburg et al. (2012). The authors further suggest that the cytoarchitectonic area OP 2 in the parietal operculum may represent the human homology to the vestibular area PIVC as proposed by Guldin and Grüsser (1998) in non-human primates.

Furthermore, signals from the cortex to the muscles and vice versa via the motor nerves are needed to maintain posture and balance. Additional visual stimuli from the eyes constantly inform the nervous system regarding motion in the environment (Munir and Clarke 2013). Specifically, the vestibulo-ocular reflex is at play, which helps to coordinate eye movement in order to stabilize retinal images while the head rotates (Chang and Khana 2013). The ocular muscles cause eye movement responding to stimuli from the brainstem (vestibular nuclei) as well as from the cortex in order to maintain focus while the head exercises movement. Information from all these structures is sent to the brainstem for processing regarding balance (Munir and Clarke 2013).

Alcohol and Balance

Alcohol intoxication has devastating results on the brain and the body. Postural sway is directly affected as well as the oculomotor system. Studies has shown that indeed alcohol interfere more with the synaptic transmission in the lateral vestibular nucleus (LVN) monosynaptic and polysynaptic II neurons (Nieschalk et al. 1999; Ikeda et al. 1980).

The deleterious effects of alcohol are further supported based on a research of Modig et al. (2012). In their study, they have found that, based on the dosage, postural control is affected, specifically latera motion rather than anteroposterior. They added that alcohol intoxication

decreases the adaptation mechanisms used for stability in lateral movement.

Specifically, the cupula in the semicircular canals becomes lighter than the endolymph leading to the process called the buoyancy hypothesis (Fetter et al. 1999). Fetter et al. added that alcohol intoxication causes a vertical velocity offset, which may be toxic to the central vestibular pathways, producing a tone imbalance of the vertical vestibulo-ocular reflex. There is also more reliance in visual information when alcohol is digested in high levels, as well as a decompensation of small subclinical vestibular asymmetries and a dysfunction of the otoliths (Hafstrom et al. 2007).

Conclusion

The main structures of the balance system (vestibular system) were explained. These contain the bony and membranous labyrinth which contains the cochlea and the semicircular canals. There is also the vestibular ganglion, also known as Scarpa's Ganglion, with its bipolar cells that contribute to keep the person's equilibrium. The cerebellum and the cortex are responsible to the control of finer movement and the perception and awareness of space. The intoxicating results of alcohol on balance have also been briefly reviewed.

Cross-References

- [Cerebellum, The](#)
- [Frontal Cortex](#)
- [Effects of Alcohol on Balance](#)
- [Semicircular Canals](#)

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Balance System

► Inner Ear, The

Band Societies

► Hunter-Gatherer Societies

Barbara Smuts and Robert Smuts

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Introduction

Robert Smuts (1920–2003) and Barbara Smuts (1950–) are father and daughter scholars recognized for their interdisciplinary work in evolutionary psychology. Barbara Smuts has conducted research on social relationships and social cognition in primates and other species. Robert Smuts conducted historical research on women's labor participation and later contributed to theoretical discussions on sex roles within evolutionary psychology. The two scholars worked together at the University of Michigan and collaborated to produce a seminal paper on the evolution of sexual coercion.

Barbara Smuts

Barbara Boardman Smuts is a biologist and anthropologist whose research has addressed the evolutionary significance and proximate maintenance of social relationships in primates, canines, and cetaceans. She received her B.A. in anthropology from Harvard University in 1972 and her PhD in neuro- and biobehavioral sciences in 1982 from the Stanford University Medical School and continued at Stanford as a fellow at the Center for Advanced Study in the Behavioral Sciences. She served on the anthropology and psychology faculty at the University of Michigan between 1984 and retirement in 2013. After retirement, she continues to conduct research on social behavior in domestic dogs.

Smuts established her early career as a primate behavioral ecologist. After receiving undergraduate training from evolutionary anthropologist Irvén Devore and evolutionary biologist Robert Trivers, she conducted a doctoral research study of male-female social relationships in a troop of wild olive baboons (*Papio cynocephalus*) in Gilgil, Kenya. This 2-year study culminated in the publication in 1985 of the book *Sex and Friendship in Baboons* (Smuts 1985). This was among a handful of texts that formed the foundation of modern primatology by applying rigorous data collection and analysis methods while maintaining important elements of an ethnographic approach. Smuts documented the special social relationships, or “friendships,” that formed between female baboons and one or more males in their groups. Males protected female friends and their offspring from attacks by other individuals and, in turn, received preferential mating access to the females. These findings emphasized a role for female choice and alternative male mating strategies in a system typified by male-male competition, stimulating broader interest in the complexities of primate social relationships. These findings, and later research on other primates, have spurred continuing research and debate into whether males form friendships with females and their young as parenting investment, in order to protect offspring that they may have sired; as mating investment, in order to increase their chances of mating with the female in the future; or both. Smuts and David Gubernick produced an important comparative analysis on this issue, outlining predictions for both paternal effort and mating effort hypotheses and arguing that paternity certainty alone is an inadequate predictor of male interactions with infants across species (Smuts and Gubernick 1992). Smuts published additional articles on her field studies with baboons, including analyses of gestural communication (Smuts and Watanabe 1990) and reproductive rates (Smuts and Nicolson 1989). She collaborated with co-editors Dorothy Cheney, Robert Seyfarth, and Richard Wrangham on the comprehensive text *Primate Societies* (Smuts et al. 1987), a taxonomically based review of social behavior in primates which is widely

implemented as a text in undergraduate anthropology and psychology courses. Linking her interests in primatology and human behavior, Smuts also coauthored a transformative paper on *The Human Community as a Primate Society* (Rodseth et al. 1991), which identified key evolutionarily derived features of human social organization by positioning humans within the context of primate socioecological diversity.

In evolutionary psychology, Smuts is perhaps best known for a series of influential papers advancing an evolutionary perspective on male aggression against females. A 1992 paper used comparative evidence from primates to propose an evolutionary perspective on male violence against women (Smuts 1992a). Smuts argued that many forms of intersexual aggression function to facilitate male reproductive strategies via the control of female sexuality. By viewing sexual violence as an evolutionary phenomenon rather than merely as a social problem, Smuts was able to generate a number of testable predictions about the prevalence of coercive behavior across human societies, suggesting potential countermeasures. A 1993 paper, coauthored with her father Robert W. Smuts, provided a comprehensive evaluation of the potential sexually selected functions of male aggression against females, along with female counter-strategies, in a wide range of mammals (Smuts and Smuts 1993). This paper provided an operational definition of sexual coercion and argued for the recognition of sexual coercion as a third form of sexual selection. In 1995, Barbara Smuts extended this framework to argue that male incentives to control female sexuality underlie the origins of patriarchy (Smuts 1995). This work placed Smuts with Sarah Blaffer Hrdy, Jane Lancaster, and others as a key figure in “Darwinian feminism,” a paradigm shift in biology that increased the attention to females as active players in the evolution of human and animal societies.

Smuts’ research has covered a wide range of topics relevant to the development, maintenance, and function of long-term social relationships. This has included studies of chimpanzee social relationships (Baker and Smuts 1994; Wrangham and Smuts 1980), infant development and mother-

infant interactions in wild bottlenose dolphins (Mann and Smuts 1998, 1999; Smolker et al. 1993), social play and friendships in dogs (Bauer and Smuts 2007; Smuts 2014; Trisko et al. 2016; Ward et al. 2008), and the evolution of cooperation (Pepper and Smuts 2000). Smuts has also authored more personal work on her experiences with animals as individuals (Smuts 2001, 2006) and has provided commentaries for *Scientific American*, *Discover Magazine*, *Natural History* magazine, *American Scientist*, *The New York Times*, and National Public Radio. She won several prestigious awards, including the Presidential Young Investigator Award from the National Science Foundation, the Distinguished Scientific Award for an Early Career Contribution from the American Psychological Association, and the John Burroughs Association prize for Best Nature Essay of 2001.

Robert Smuts

Robert W. Smuts received his Bachelor of Arts degree in history from Queens College in 1941. He attended Harvard Business School, but his education was interrupted by service in Patton's Third Army in World War II. After the war, Smuts spent 8 years at Columbia University as a lead investigator for the Conservation of Human Resources Project and the National Manpower Council. His influential book, *Women and Work in America*, provided a historical analysis of the changing role of women in the workforce between 1890 and the early 1950s (Smuts 1959). This report documented the factors that led increasing numbers of women to seek work outside the home, the obstacles they met there, and the shifts in societal attitudes about women's role in the economy. In a related paper, Smuts used the historical context of this research to question the government's labor force statistics, which, owing to changes in how women's labor was documented, painted a rosier picture of increases in female workforce participation than was warranted (Smuts 1960). These works were notable because, in providing objective documentation of changing women's economic roles, they

also highlighted the large disparities still present in opportunities, conditions, and compensation. In a similar vein, Smuts wrote about the underutilization of African Americans in the workforce, arguing that segregation and discrimination remained significant obstacles for educational and employment opportunities (Smuts 1957).

Smuts left Columbia University to work in public relations at Ford Motor Company, where he wrote speeches for Henry Ford II and other top executives. After retirement, Smuts took graduate courses and engaged in seminars in evolution and behavior led by a cadre of eminent evolutionary biologists, including G.C. Williams, W.D. Hamilton, Peter Grant, and Richard Alexander. These experiences cemented an early interest, shared with his daughter, in the role of biological factors in human behavior and historical cultural change. From this perspective, he wrote on cultural shifts in body image for women, noting that while fatness was once a valued indicator of health, fertility, and resource access, modern Western societies value thinness (Smuts 1992b). Drawing on his earlier work, Smuts attributes this change to increased women's economic participation, arguing that, in an environment where starvation is no longer a significant threat, women use thinness as a signal of status and a means to compete with each other and with men. This paper elaborates a theme of Smuts' writing in evolutionary psychology, that behavior is highly responsive to context, such that evolutionarily novel conditions may drive new and unexpected strategies. His argument has been interpreted as a critique of the adaptationist program in evolutionary psychology (Tooby and Cosmides 1990), which has emphasized the importance of past environments for shaping current psychological adaptation. The conceptual debate is exemplified in Smuts' engagement with David Buss' work on commonalities in mate preferences across cultures (Buss 1989; Smuts 1989, 1991a, b).

Conclusion

Barbara and Robert Smuts, together and independently, have produced foundational,

multidisciplinary works on the evolution of social interactions and the processes of cultural change that comprise essential knowledge for scholars in evolutionary psychology and anthropology.

Cross-References

- [Sexual Coercion as a Mechanism of Sexual Selection](#)

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Bargaining Model of Suicidal Behavior

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Synonyms

Costly apology model of suicidal behavior; Costly signaling model of suicidal behavior

Definition

The bargaining model of suicidal behavior frames such acts as costly signals of need. The following conditions are necessary for the model to operate: (1) the victim encounters of a fitness threat in the environment prior to suicidal behavior; (2) there is a conflict of interest between the victim and invested social partners such that the social partners are not otherwise willing to provide support based on less costly signals alone (e.g., verbal communication); (3) the victim is otherwise powerless to remove the fitness threat on her own; (4) more often than not the victim survives the attempt; (5) the nonlethal suicide attempt communicates to social partners that she is truly in need; (6) the social partners assist the victim in removing the fitness threat.

Introduction

Suicide is a universal human tragedy. According to the World Health Organization, suicide is the sources of more deaths than all wars and homicides combined (Lozano et al. 2013). In light of evolution, we know that all behaviors are either the functional output of psychological mechanisms, by-products of mechanisms that evolved for other reasons, or the product of dysfunctioning mechanisms, and suicidal behaviors (SB) are no exception. Mental health professionals and investigators tend to reasonably assume that SB is a

consequence of one or more dysfunctions. However, theoretically and empirically, evolutionary scientists know that increasing fitness can come at the expense of survival such exhibited in the cases of semelparity or intrasexual combat. Considering the universality of suicidal behavior, some evolutionary researchers have investigated suicidal behavior in an evolutionary light. One popular model called the inclusive fitness model proposes that suicide death could have evolved to benefit genetic kin when the victim (1) has low reproductive potential and (2) is a burden on genetic relatives (e.g., de Catanzaro 1984). The inclusive fitness model concerns suicide death. However, humans have evolved physiological and psychological traits to prevent harm such as pain receptors and conditioned avoidance that are difficult to overcome. In fact, in the USA, most suicidal behavior is nonlethal (Syme et al. 2016). The bargaining model of suicidal behavior (BRM) concerns the evolved function of nonlethal suicide completions.

The BRM, formally developed by biological anthropologist Edward Hagen and tested by Syme et al. 2016, frames self-inflicted harm with intent to die as a costly signal of need. The following conditions are necessary for the model to operate: (1) the victim encounters of a fitness threat in the environment prior to suicidal behavior; (2) there is a conflict of interest between the victim and invested social partners such that the social partners are not otherwise willing to provide support based on less costly signals alone (e.g., verbal communication); (3) the victim is otherwise powerless to remove the fitness threat on her own; (4) more often than not the victim survives the attempt; (5) the nonlethal suicide attempt communicates to social partners that she is truly in need; (6) the social partners assist the victim in removing the fitness threat.

Conflicts of Interest, Costly Signaling, and Suicidal Behavior

Zahavi observed that human speech is a cheap form of communication that is unreliable when there is a conflict of interest between two parties

and therefore an incentive for one to deceive (Zahavi 1993). Taking this view, the BRM suggests that we should predict suicidal behavior to place when there are high stakes conflicts of interest where parties cannot believe each other based on verbal communication alone.

Powerlessness, Fitness Threats, and Suicidal Behavior

According to the BRM, suicide attempts should outnumber suicide completions, and suicide attempts should be more common among those with high reproductive potential whose fitness is constrained but who are otherwise healthy. According to data from the Center for Disease Control, the rate of suicide attempts in young adults exceeds the rate of completions by factors of 10–100 or more, and this ratio diminishes with age (Syme et al. 2016).

In this framework, suicidal behavior is a last resort of the powerless. Farberow and Shneidman (1961) described suicide as a “cry for help.” Psychiatrist Erwin Stengel reported that suicide attempts often occurred in response to an intolerable social or emotional situation and were often nonlethal. Suicidal behavior is thus a plea entailing a gamble with death (e.g., Stengel 1956). The BRM pinpoints severe, fitness threats, such as physical or sexual abuse, as precursors that make this gamble with death worthwhile from the standpoint of natural selection. According to a WHO study, trauma exposure predicts subsequent suicidal ideation and attempts in a dose-dependent sequence (Stein et al. 2010).

Cross-Cultural Research on Suicidal Behavior

Ethnographic data from a range of unique cultures unambiguously demonstrates that SB can effectively communicate dissent and serve as a check on abuse and exploitation, and the BRM frames these protest themes of suicidality in game theoretic terms. For instance, Firth characterized acts

of SB among the Tikopia as a form of protest, particularly for sons in conflict with domineering fathers (Firth 1936). In the Middle East, SB among women is often regarded as recourse against oppressive kin or restrictive social structures (e.g., Billaud 2012), and the anthropological literature abounds with comparable models (see Syme et al. 2016 for review).

Syme et al. (2016) tested the BRM and the inclusive fitness model against 53 distinct cultures from the probability sample of the Human Relations Area Files. In support of the BRM, most victims of SB were powerless (e.g., had little social influence), were in conflict with powerful social partners who were otherwise invested in them (e.g., parents, community leaders), had experienced some type of fitness threat (e.g., rape, physical abuse), and, if they survived, social partners often helped to remove the fitness threat (e.g., put a stop to an arranged marriage). There was comparatively weaker evidence for the inclusive fitness model, which possibly characterized a small fraction of cases in northern latitudes where the environment is harsh, and where the support of noncontributing community members can present a burden. However, these suicides often required the assistance of another, which presents a problem to the theory that suicide for the sake of inclusive fitness is an evolved mechanism.

Conclusion

The BRM conceptualizes SB as a means of communication. In the model’s framework, the functional goal of at least some SB is to credibly signal a desperate need for social support, while death is a by-product of the signal’s high cost. There are several lines of evidence that support this hypothesis. If the BRM is operating, then the function of SB is to obtain protection, and unrelenting abuse would trigger future SB. The cost of the signal, which in this case manifests in self-harm, guarantees to observers that the signal is honest, i.e., the victim of SB is experiencing a severe social threat for which she needs social aid.

Cross-References

- [Edward Hagen](#)
- [Suicide as Kin-Directed Altruism](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)

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Baringa's (1996) Crayfish

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Synonyms

[Dominance](#); [Hierarchies](#); [Sociality](#)

Definition

Social status and social behavior can alter the function of the nervous system within crayfish. This research details the experiments that show that dominant and subordinate crayfish can express different serotonin receptors in the nervous system as well as modulate the sensitivity of those receptors expressed.

Introduction

Neuroethology is the study of the neural basis of behavior, and one of the assumptions of the field includes a concept that behavior arises from the underlying neural architecture of the organism's central nervous system. Several studies have supported the concept that changes in the nervous system, either during development or via changes in neurotransmitter function, as a result of experiences, alters the types of behaviors demonstrated by the organism. For many years, this concept was considered a one-way process whereby the neurobiology influenced behavior. However, the classic studies by Don Edwards and his lab showed that behavior can alter not only the neural architecture but also the neural functioning. Specifically, the social system, including the suite of behaviors and the neurobiology of those behaviors, of the crayfish served as evidence that demonstrated that the social status of an individual (dominant or subordinate) can subsequently alter the modulation of behavior by the neurotransmitter serotonin. In addition, the release and modulation of serotonin can then alter nervous system structure, which influences the types of behavior being exhibited by crayfish with either a dominant or subordinate status. This work opened a new approach to neuroethology in that both the behavior and the nervous system of an animal are now considered plastic and flexibly adaptable to social and environmental influences.

Background on Social Behavior

Sociality carries with it several ambiguous ideas, and the degree to which an organism displays

sociality is different across the animal kingdom. Social systems vary from highly organized and (potentially) genetically related organisms that exhibit cooperation (i.e., the social systems in eusocial insects, some species of birds, and primate communities) to the other end of the scale where organisms exhibit aggressive interactions during brief periods of the year, such as mating periods. Crayfish are a model system for studying social dynamics in general and, specifically, the neuroethology of social behavior. Crayfish exhibit agonistic behavior in the laboratory and in the field (Moore 2007). Within laboratory settings, social dominance and hierarchy formation are quite common (Goessmann et al. 2000; Gherardi and Daniels 2003). Thus, crayfish are organisms that display social behavior and can serve as a neural and behavioral model for the development of social hierarchies (Herberholz et al. 2003).

The first observations of social behavior and agonism in crayfish were based off of the obvious visual displays and the use of the large weaponry (claws) (Bovbjerg 1953). Since Bovbjerg's initial observations, the agonistic behavior of crayfish under different conditions has been well established (see below). This large body of work has shown that the interaction of two crayfish leads to agonistic contests that progressively escalate until one of the opponents withdraws (Bovbjerg 1956). Through these interactions, a dominance relationship is formed. For crayfish, a dominance relationship is one in which subsequent social interactions between these pairs is highly predictable (Daws et al. 2002).

The formation of a dominant and subordinate relationship has consequences for time and energy budgets as well as the acquisition of resources. Indeed, the alterations in behaviors exhibited by dominant and subordinate animals formed the basis for the neurological studies of the Edwards lab (more on this later). Subordinate animals rarely seek to engage a dominant opponent and often retreat when approached by a dominant individual (Daws et al. 2002). Dominant animals can actively seek out subordinate crayfish to reinforce their status through short, low-intensity interactions. Although, it must be noted that most of these descriptions of behaviors are from

laboratory studies often in confined aquaria. The social behavior demonstrated by crayfish in the field tends to be of shorter duration and lower intensity than those behaviors found in the lab (Bergman and Moore 2003). The continued reinforcement of status can not only have long-term effects on subsequent behavior but also on sculpting the nervous system of both the dominant and subordinate animals. To understand the role of neuromodulators, like serotonin, and how alterations in nervous system function can produce differing behaviors, the basic dynamics of crayfish agonistic interactions needs to be explained.

Crayfish agonistic interactions are highly ritualized meaning that a set of displays, sensory signals, and behaviors are consistently seen across different species of crayfish and different environmental conditions (Moore 2007). As with many decapods, when two crayfish are placed within a confined area, they will eventually engage in an agonistic interaction. The interaction begins with an approach behavior where the crayfish extend their chelae (claws) in a lateral fashion. Sometimes, the crayfish will modulate the height of their body, which is thought to be a threatening display. These two behaviors usually occur when the crayfish are separated by one to two body lengths of space. The next stage in a contest occurs when the crayfish open their chelae and actively push the opponent around the tank. What is interesting about this stage of the fight is that neither animal closes the chelae to use as a weapon. This has been termed "boxing" because the crayfish appear to be trying to move the opponent around the fighting arena rather than inflict serious harm. If neither crayfish retreats, the level of aggression usually increases such that the chelae are used to grab the opponent in an attempt to flip them over. The final stage escalates when the crayfish appear to try to injure their opponent by grasping with the chelae and ripping at different body parts. While infrequent, some interactions may result in injuries, lost limbs, or even death.

Agonistic interactions are terminated and a dominant or subordinate relationship is formed when one of the crayfish retreats from the fight. Retreating can take one of two different forms. First, the losing crayfish simply backs away and

fails to engage in further fights. The second method, known as a tailflip, is far more rapid. During a tailflip, the losing crayfish rapidly contracts the muscles on the lower part of the abdomen which causes the telson to curl under the crayfish quickly. This motion launches the crayfish backwards and off of the substrate in a rapid retreat fashion. [As a side note, there are actually multiple styles of tailflips each with their own different underlying neural mechanisms (Herberholz et al. 2001)]. The decision to retreat, either by tailflip or a slow retreat, determines the winner and loser of the fight and establishes the roles of dominant and subordinate crayfish. Thus, the neural mechanisms that influence the control of this retreat were the basis of the series of studies performed in the Edwards lab. Before those experiments are described, the different behavioral and environmental influences on social status will be outlined.

The Behavioral and Environmental Influences on Social Status

Dominance and levels of aggression in crayfish are influenced by several different factors that can be categorized as either extrinsic (environmental and sensory influences) or intrinsic (physical or physiological) to the crayfish (Moore 2007). Extrinsic factors include the presence of resources (shelters and food) and sensory signals (visual, chemical, and mechanical signals). Crayfish that have "ownership" over a resource like a territory, shelter, or food source are more likely to defeat and become dominant over intruding crayfish (Graham and Herberholz 2009). Unfortunately, the direct role of different sensory signals on dominant and subordinate status is still unknown, but chemical signals seem to be an important aspect of crayfish social interactions.

The role of intrinsic factors has received the bulk of the social status work in crayfish. The most obvious intrinsic factor that influences dominance is size of the animal or size of the chelae. Larger animals with larger weaponry are dominant over smaller animals (Pavey and Fielder 1996). The sex of the crayfish also influences dominance status as size-matched males tend to be dominant over females (Wofford et al. 2015).

Reproductive status can also serve as a varying intrinsic quality that dictates dominance. Within many crayfish species, both the male and female cycle between a reproductive and non-reproductive state. Reproductive crayfish are dominant over nonreproductive crayfish (Figler et al. 1995). Previous social history and neurochemistry are critical factors in the dominant status of crayfish. As in many species, crayfish exhibit what is known as winner or loser effects (Daws et al. 2002). Crayfish with a previous social history of winning are more likely to remain dominant and win their next set of agonistic encounters. In an opposite fashion, crayfish that have recently lost encounters are more likely to continue to lose subsequent contests and become or remain subordinate. The winner and loser effects within crayfish are reversible signaling that any underlying neural changes that are associated with dominant and subordinate behavior must also be plastic. Since the retreat, by tailflip, determines the outcome of agonistic interactions, the Edwards group (Shih-Rung Yeh and Don Edwards with others) focused their neurological work on the flexibility and modulation of the tailflip circuitry in the crayfish. The ability to artificially manipulate dominant status through winner and loser effects gave them the experimental model which would directly connect social status and neurobiology.

The Underlying Neurobiology of Social Status

With the advent of modern techniques in neurobiology, several groups began working on the neural circuitry of dominant and subordinate behavior, with particular attention being paid to the neurons involved in a retreat response (tailflip) and the role of serotonin in dominant and subordinate animals (Edwards and Kravitz 1997). The tailflip circuitry of the crayfish has been a favored neurobiological prep since the pioneering work of Wiersma (1947). Since that initial work, the neurons involved in the tailflip response as well as the neuromodulation of that response have become fairly well known. Crayfish can exhibit three different types of tailflips, classified by the neural control necessary to perform the behavior (Krasne et al. 2014). The details of these three responses

and their role in the ecology of the crayfish are beyond the scope of this entry, but the critical feature of these tailflips is the identified neurons that control each of their activations. Each of the tailflips are controlled by two giant command neurons: the medial giants and the lateral giants. The command neurons are found in bilateral pairs along the dorsal position of the ventral nerve cord of the crayfish. Within invertebrate systems, the diameter of the neuron determines conduction velocity. Thus, both giant neurons (up to 80 μm in diameter) have a high speed of conduction which evokes rapid tailflips. Both neurons activate structures called motor giants and fast flexor motor neurons which further explain the rapid response of the crayfish tailflip. Finally, these neurons are termed command neurons because they control the entire sequence of activation of the tailflip from neuron to behavioral output. Modulation of the sensitivity of these neurons can also modulate the speed and sensitivity of activation of the tailflip (Krasne 1969; Krasne and Edwards 2002). This modulation introduces the possibility that social behavior and dominance (as determined by which animal does not retreat) may be explained by the sensitivity of the neurons controlling the tailflip response. This hypothesis, coupled with the presence of winner and loser effects, is what the experimental work by the Edwards lab tested with their classic study (Yeh et al. 1996, 1997).

The details of their experiments are elegantly simple (Yeh et al. 1996, 1997). They first placed two socially naïve crayfish in an aquarium and waited until a dominant and subordinate relationship had firmly been established. After this relationship was established, both crayfish were dissected and the lateral giant neurons were tested for their sensitivity to serotonin. Using electrophysiological techniques, the researchers applied different concentrations of serotonin to the bath surrounding the dissected neurons from subordinate, dominant, and control (i.e., socially naïve) animals. During application, they measured the excitatory postsynaptic potential of the lateral giants to test their excitability to different concentrations of serotonin. The results showed that serotonin had the ability to modulate the

excitability of the lateral giant neurons, meaning that serotonin sets the gain of the neurons. The exact effect of serotonin on modulating this response depended upon the social status of the crayfish. In dominant animals, serotonin increased the sensitivity of the lateral giants which increased the probability of firing and the opposite effect was seen with the subordinate animals. Thus, a first set of conclusions that can be drawn from this work is that the modulation of social neural networks by serotonin is dependent upon the social history of the crayfish.

However, this initial result was counterintuitive. If dominant animals are more sensitive to serotonin and their lateral giants are more likely to fire, why does this lead to dominance? The researchers used a set of different compounds on the dissected neurons in an attempt to understand the exact physiological mechanism of change that is occurring at the neural level. They found that different classes of serotonin receptors were being expressed in the dominant and subordinate animals. One class of serotonin receptors increases the excitability of the lateral giant neurons and a second class of receptors reduces the excitability of the lateral giants. Dominant crayfish expressed more of the first class of receptors (excitability) and the subordinate animals expressed more the second class of receptors (less excitable). Work in another lab (Ed Kravitz from Harvard) has shown that the lateral giant neuron is also involved in activating other neurons that release serotonin in other areas of the crayfish nervous system (Kravitz 2000). These other areas are involved in modulating levels of aggression in crayfish. Thus, an increase in excitability of the lateral giant, which is mediated by the expression of certain receptors, also increase the level of aggression in crayfish by activating a global release of serotonin. Thus, a second conclusion from this work is that changes in social status can change which serotonin receptors are expressed within crayfish, which in turn affects sensitivity to circulating serotonin.

These changes in sensitivity to serotonin are not permanent and are reversible. In a continuation of their experimental design, the Edwards group placed two subordinate crayfish within a

tank and waited for one of the previously subordinate animals to become dominant. Again, the lateral giant neurons were dissected from the animal and placed in a petri dish to measure their responsiveness to serotonin. The responses of the lateral giant were reversed and instead of the activation being suppressed by serotonin, the responses were enhanced. The neurons now responded as if they came from a dominant crayfish. This change in firing sensitivity took around 2 weeks to occur. In a final test of their findings, the researchers paired two dominant crayfish in a tank to test whether dominant crayfish altered their neurophysiology in a similar fashion to the subordinate animals. Surprisingly, the dominant crayfish exhibited much higher levels of aggression and their fights ended in death at a far higher rate than other fight conditions. After one of the crayfish eventually exhibited subordinate behaviors, Yeh and Edwards tested their lateral giants for serotonin sensitivity. Unlike the change in physiology found in the paired subordinate fights, the “losing” dominant crayfish still exhibited the enhanced sensitivity to serotonin. Yeh and Edwards demonstrated that dominant animals may exhibit subordinate behavior, but their nervous system still exhibited the dominant physiology for long periods after losing their dominant status. Although social status can change a nervous system's sensitivity to serotonin, both the initial change and any subsequent change in physiology is dependent upon the social status of the crayfish. Subordinate crayfish exhibit loser effects due to a decreased sensitivity to serotonin, but this change in neural sensitivity is reversible on a short time scale. Conversely, dominant crayfish exhibit enhanced sensitivity to serotonin and this change in enhanced sensitivity is a long-lasting change, exhibiting the possibility that winner effects are more potent than loser effects in crayfish.

Conclusion

The results from this study demonstrated three essential points for the plasticity of the nervous system. First, behavior, in general, and social

status, specifically, alters the functional properties of the nervous system of the crayfish. From a neuroethological point of view, behavioral experiences alter nervous system function. Second, this change in nervous system function can vary depending upon the prior experience. Serotonin functionality in crayfish enhanced excitation of escape neurons in dominant animals and suppression excitation in subordinate animals. Third, the temporal properties of this change are also dependent upon the behavioral experience. Changes in serotonin sensitivity were longer lasting in dominant animals than subordinate animals. Taken together, these results have clearly demonstrated a more plastic or flexible nature of the nervous system that is highly dependent on the type and intensity of behavioral experiences.

Cross-References

- [Dominance Hierarchies](#)
- [Dominance Hierarchy](#)
- [Male Dominance Hierarchies](#)
- [Serotonin and Dominance](#)
- [Shifting Dominance](#)
- [Status and Dominance Hierarchies](#)

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Bateman's Principle

► Reproductive Variance

Bateman's Principle: Sex Differences in Reproductive Success Variance

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Synonyms

Minimal obligatory parental investment; Sex difference in reproductive success variance

Definition

Bateman's Principle states that there is greater variance in the reproductive success of males compared to females, which has implications for mating and relationship psychology in humans.

Introduction/History

In the late 1940s, English geneticist and botanist Angus John Bateman published a seminal work

detailing what would later be called Bateman's Principle: the notion that compared to females, males in most species exhibit greater reproductive success variance. That is, males tend to differ more in reproductive success than females do (Bateman 1948). Bateman's intention was to corroborate and refine Darwin's sexual selection theory despite his unrelated botanic research interests. Previous evidence had suggested that, in virtually all species studied, males were willing and eager to pair and copulate with any female, while females were more discriminatory when selecting male mates. This asymmetry was thought to be responsible for the greater intra-sexual competition observed among males compared to females (Tan 1946). Darwin (1871) had previously argued that the mating system of a particular species was the primary cause of these sex differences in discrimination and competition, and that intramale selection (i.e., competition among males to be the mate choice of one or more females) was most prominent because it was engendered by the most common mating systems, monogamy with more males than females and polygyny. However, according to Bateman this reasoning was flawed, and Darwin had it backward. If the mating system determined sex differences in discrimination and competition, why would monogamy with more males than females and polygyny be exponentially more common than other mating systems? The overwhelming prevalence of these mating systems instead led Bateman to believe that intramale selection *caused* the emergence of particular mating systems. As Bateman succinctly put it, "It is thus desirable to search for a fundamental cause of intra-masculine selection, independent of mating system and probably inherent in the mechanics of sexual reproduction" (1948, p. 352).

Accordingly, Bateman set out to illuminate the mechanics of sexual reproduction he thought might be responsible for intramale selection. Studying fruit flies (*Drosophila melanogaster*), he found evidence that male fruit flies' reproductive success was dependent on the number of partners they were exposed to and copulated with, while female fruit flies' reproductive success was not dependent on this factor. Bateman

reasoned that these findings were ultimately caused by differences in fertility limitations between males and females. Males, on the one hand, produce an overabundance of sperm that theoretically could beget an extremely high number of offspring, far more than most males have ever or will ever produce. This led him to conclude that males' reproductive success is not limited by their gamete production. Females' reproductive success, on the other hand, is limited by their gamete production as females produce only a limited number of eggs in their lifetimes. Moreover, females exert substantially more energy nurturing their eggs than males do nurturing their sperm, suggesting that females act as the "limiting factor" in reproduction.

Overall, Bateman found solid evidence for his theory that mechanical reproductive differences between males and females give rise to intramale selection. Because males are not limited by their gamete production, while women are, males are more eager to mate with any and multiple females, while females are more selective when choosing a mate. It derives that high-quality males are able to mate with a large number of females while low-quality males are not. Females, on the other hand, should have relatively fewer problems finding a mate. In a nutshell, the reproductive success of males is more variable than the reproductive success of females.

Evidence in Humans

As theorized by Bateman (1948) and later expanded upon by Trivers (1972), evidence for sex differences in reproductive success variance (Bateman's Principle) in humans is overwhelming. While comparing data across vastly different societies, Betzig (2012) found strong evidence that males exhibited greater variability in reproductive success (in this case, number of children conceived) compared to females. Further, she found that this effect was moderated by the subsistence of the society in question: the variance of reproductive success was similar for both men and women in hunter-gatherer societies (low subsistence), while the variance of reproductive success

was substantially higher for men than for women in full-time agriculturalist societies (high subsistence). The author reasoned that this moderation effect occurs because as subsistence intensifies, the size and available resources of societies increase, which causes more pronounced hierarchical societal structures.

Indirect evidence for Bateman's Principle also emerged from evolutionary psychology research. For example, evidence strongly suggests that men evolved to be more aggressive, violent, and competitive than women in order to successfully partake in intense intrasex competitions for females (Daly and Wilson 1994). In their study, Buss and Dedden (1990) reported that men, compared to women, were much more likely to physically assault other men when competing for women, while women, compared to men, were much more likely to use non-violent means (e.g., verbal aggression) when competing for men. Evidence also suggests that women are choosier when selecting mates compared to men. For instance, Clark and Hatfield (1989) found that women, compared to men, had a much higher threshold for accepting an invitation to go on a date or have sex with an attractive stranger of the opposite sex. When men were invited to engage in sex by a female stranger, three-quarters of them accepted, but when women were invited to engage in sex by a male stranger, none of them accepted. Lastly, evidence clearly suggests that men are more promiscuous and interested in short-term relationships than women (Simpson and Gangestad 1991). Lippa (2009) compared data on sociosexuality (i.e., one's endorsement of and willingness to engage in noncommitted sex) in 53 nations ($N > 200,000$) and found that in every single nation, men reported higher sociosexuality than women (average $d = 0.74$).

Other Factors

Despite the overwhelming evidence in favor of Bateman's Principle in humans, other factors influence reproductive success and mating psychology in humans. For example, sex-ratios (i.e., the ratio of males to females in a society) affect the

reproductive success and strategies of the average individual in a given society (Moss and Maner 2015). Men in societies where women outnumber men have greater marriage and reproductive success compared to societies where men outnumber women (Pollet and Nettle 2007). Societal rules, laws, and customs, which can prohibit or discourage polygamy, also have an effect on the average individual's reproductive success.

Conclusion

To summarize, Bateman's Principle is the phenomenon by which males have a greater variance in their reproductive success than females. While this phenomenon had been identified in many species before Bateman's theorization, Bateman was the first to propose that the proximate cause of this difference laid in the sexual reproduction mechanics that distinguish males and females. Females act as the "limiting factor" in reproduction due to the limited number of gametes they produce compared to males, who produce gametes in abundance. This sex difference in reproductive success, which applies to many species including humans, has a number of implications: males engage, on average, in more intense and physical competitions for females than females do for males, and males, on average, are less selective when choosing a sexual partner than females.

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Battering

- [History of Abuse](#)

Battle

- [War](#)

Bawling

- [Crying](#)

Bayes Net Theory

- [Causal Reasoning in Rats \(Blaisdell et al. 2006\)](#)

Bayes Theorem

- [Psychological Determinism](#)

Be Forgiving

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Synonyms

[Forgiveness](#); [Reconciliation](#)

Definition

Forgiveness mechanisms are designed to solve problems connected to preserving valued relationships in spite of previous damages. To be forgiving is to be able to change the motivation and emotional states towards someone who has harmed us, leaving behind a disposition for revenge with negative states of mind, for overcoming of animosities with positive states of mind.

Introduction

Forgiveness is an inbuilt human nature resource and a standard human social instinct (McCullough 2008). Forgiveness is defined as a prosocial change in relation to a transgressor in spite of his harmful attitudes (McCullough et al. 2000). In general, being forgiving is associated with relational, emotional, and physical well-being (McCullough 2008).

The literature indicates several elements as related to forgiveness, among which are the personality of the individual, specific elements of the individual who has done something wrong, the relationship between the offender and the victim, as well as other socio-cognitive aspects (Billingsley and Losin 2017; McCullough 2008). These combined elements influence the individual to experience forgiveness as a set of motivational changes that has a positive effect. As a result of forgiveness, individuals feel less motivated to take revenge on the aggressor, as well as less

motivated to be displeased with them; these motivational changes are increased by the goodwill of the aggressor (Karremans and Van Lange 2004).

Thus, forgiveness is considered to be an internal process of overcoming animosities and negative emotions, replacing them with positive states, which enable the reparation of the relationship with the aggressor (McCullough 2008). In this context, reconciliation may be understood as one of the more basic consequences of forgiveness, seen as it aids in the maintenance of the social structure (Billingsley and Losin 2017; Strang 2002). By preserving relationships, the benefits of group life are maintained, ensuring survival and development.

Thus, it is necessary to understand how evolution selected forgiveness from its adaptive mechanisms. The evolutionary functions of forgiveness aid in comprehending the context in which this action was selected, how and why. In addition, there are ways to perceive different types of forgiveness in each culture. This way, to identify forgiving individuals it is also necessary to understand the factors that enable human beings to forgive.

Evolutionary Functions of Forgiveness

According to McCullough (2008), in his book “Beyond Revenge: The Evolution of the Forgiveness Instinct,” there are two functions over which the ability to forgive was naturally selected. The first refers to the ability to help ancestral humans to live well with their genetic relatives; the second refers to the ability to help ancestral humans establish and maintain cooperative relationships with nonrelatives. However, it is important to point out that the human ability to forgive only exists under specific circumstances.

Initially, it is understood that severe retaliations and revenges against genetic relatives, such as killing brothers, sisters, and children, decreased inclusive fitness. So, the function of forgiveness to promote good coexistence with relatives was probably selected as a solution to some problems, such as avoiding that genes be decimated by reducing the relatives’ aptitude. Thus, forgiveness

allowed that alliances between groups were developed and maintained.

The second function of forgiveness may have evolved from the need of cooperation between nonrelatives. In the Prisoner’s dilemma (Axelrod 1997), one of the more efficient strategies is Tit-for-tat, a primordially cooperative strategy, but that retaliates and forgives. Being forgiving in this situation may be beneficial because, if, after deserting, your partner starts cooperating again, you instantly cooperate with him, showing you are willing to be in an alliance again. Cooperation results in higher payoffs than desertion. The studies about strategies that followed found that a few unexpected situations happened in cooperation and other strategies became more adaptive; however, detailing them is not important at the moment. In any case, the common ground is that organisms that survived the selective process had forgiveness as an adaptive skill.

Thus, forgiveness was selected with the function of developing and maintaining alliances between relatives and nonrelatives, motivating them to return to cooperation by restoring the relationship that may have been broken by some desertion or conflict. Forgiveness may have evolved to help organisms in promoting and adapting their genetic relatives and in cooperating with nonrelatives. Therefore, the main adaptive function of forgiveness seems to be to help individuals preserve their valuable relationships (McCullough et al. 1997). However, even though humans have developed mechanisms to forgive, being forgiving is more likely to happen among cooperative partners, that is, to members of the small groups of people closest to them. In fact, forgiveness helps preserve the relationships that are most valuable, from family, partners, and close friends where there is the key element of trust (Kurzban 2003, McCullough 2008).

Be Forgiving

Nonhuman animals, such as chimpanzees, often engage in friendly behavior such as kissing, touching, and hugging after aggressive conflicts (de Waal and van Roosmalen 1979). Although reconciliation and forgiveness are not exactly the

same thing, the greatest goal of forgiveness and its greatest effect is reconciliation (Karremans and Van Lange 2004). However, forgiveness is a conditional adaptation; despite having the capacity, forgiveness will only happen under certain circumstances (McCullough 2008). Thus, there are three main conditions that activate forgiveness, which will be briefly exposed below.

The first is careworthiness: to be forgiving of transgressors who are seen as appropriate targets for kindness and compassion. Getting involved with others demands physical and psychological energy, so the targets of greater care and forgiveness will be genetic relatives. Forgiveness is based on the same mechanisms that generate care (McCullough et al. 1997, 1998). With regard to forgiveness directed toward individuals not close to us, empathy plays a fundamental role in promoting forgiveness (Batson and Ahmad 2001; Giancola 2003).

The second condition is the expected value of a relationship, where forgiveness is more likely when the victim realizes that the relationship with the offender is valued. In relationships where there is a high expected value before transgression, being forgiving is more likely because the threat of losing a valued relationship motivates finding ways to restore that bond. The prediction of future positive and valuable interactions with the transgressor also influences the willingness to forgive (McCullough 2008).

The third condition to be forgiving is perceived security, that is, people are more inclined to forgive those who are not willing or able to harm again in the future. People are more likely to forgive someone who behaved unintentionally or unconsciously than willful and malicious transgressions (Strang 2002). Therefore, under such circumstances, it is possible to activate the mechanisms of forgiveness, socially identified with some signs such as apologies, gestures, and self-abasing displays and compensative behaviors.

Conclusion

As stated earlier, forgiveness can be defined as a prosocial change of attitude towards someone

who has committed some kind of emotional or physical harm (McCullough 2008). Among the functions attributed to forgiveness is the aid in developing relationships with peers, with or without blood ties, in a cooperative way (de Waal and van Roosmalen 1979). At more complex levels of analysis, forgiveness has allowed the development and maintenance of alliances, especially in situations where one party violates explicit or implicit social norms (Billingsley and Losin 2017).

Thus, forgiving individuals are those who perceive offenders as worthy of care under certain circumstances, for being valuable to the victim. In this way, individuals who seek forgiveness try to awaken these psychological conditions in people, by apologizing, engaging in self-abasing displays, in addition to trying to compensate the victim (McCullough 2008).

Cross-References

- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Women's Prosocial Dominant Acts](#)

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Behavioral Economics

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Definition

Behavioral economics is conventionally defined as economic theory that incorporates insights

from contemporary psychology, cognitive science, cultural theory, human physiology/emotional states, and neuroscience. However, the term “behavioral economics” can be seen as potentially subversive because it can be taken to suggest that the remainder of economics is non-behavioral and – by implication – excessively abstract and therefore partially inaccurate.

Introduction

This entry will first provide an account of the nature and scope of behavioral economics as it was outlined by one of its founding fathers, George Katona. This entry will then go on to discuss the work of four very important more recent behavioral economists – Daniel Kahneman, Amos Tversky, Richard Thaler, and Vernon Smith – in more detail. Following this, in the latter part of the entry, it will consider the consequences of some ideas developed by evolutionary psychologists and biologists for the nature of behavioral understanding in economics more widely conceived. It will accomplish this task by means of case-studies of how two individual concepts from economics, the invisible hand metaphor and the maximization conception of economic rationality, fit (or do not fit) within the framework of analysis provided by evolutionary psychology. Finally, a relatively new subfield of behavioral economics – neuroeconomics – will briefly be considered in relation to its significance for evolutionary psychology.

George Katona

George Katona (1901–1981) was a pioneer in the field of behavioral economics with an early background in Gestalt psychology who was born in Budapest, but who later emigrated to the USA and worked at the Cowles Commission and then the University of Michigan (Katona 1960). He was the author of *Psychological Analysis of Economic Behavior* (Katona 1951) and the inventor in the mid-1940s of the US Index of Consumer

Sentiment (ICS), an innovative empirical measure of consumer expectations.

Katona defined behavioral economics as containing three fields of analysis: empirical studies of the behavior of businesspeople/consumers; analysis of decision-making processes in relation to behaviors like spending, saving, and investing; and the study of economic motives, attitudes, and expectations at a deeper level. He also identified subfields of behavioral economics as follows: the study of consumer/savings/business behavior; how income is spent and augmented; the nature of different market systems and associated behaviors; politico-economic attitudes (e.g., attitudes to taxation, government spending and so on); and workplace behavior/broader organizational behavior (Katona 1980, 3–6).

To examine one topic in more detail, the mainstream economist’s conception of rational behavior, on this topic Katona explained that:

In contrast to the emphasis of [mainstream] economic theory on rationality, defined as weighing available alternatives and choosing the alternative that maximizes utility or profits, behavioral economists found a common occurrence of habitual behavior – doing what has been done in the past, following established routines and following leaders – occasionally interrupted by genuine decision making. Only in those relatively few instances when the decision really matters do strong motivational forces arise that lead businessmen and consumers to proceed in a circumspect manner. Even then the alternatives considered are usually restricted according to their attitudes and expectations, and a satisfying course of action is chosen rather than one that will optimize the outcome. (Katona 1980, 13–14)

This account articulates the significant difference between what were classified by Katona as the unrealistic assumptions of much of mainstream economics, and the more realistic assumptions of his own brand of behavioral economics. Elsewhere, he presented a more detailed account of how he believed human actions and decision-making processes operated, highlighting five ways in which real-world behavior differed significantly from that proposed by utility-maximization-based economics.

Real human behavior reflected the influence of multiple and sometimes competing motives, for

instance with respect to evaluating the sometimes-opposing multiple qualities of goods; real behavior involved a significant degree of group decision-making in addition to individual decision-making, for example, family-based or firm-based decision-making; real behavior involved the prevalence of uncertainty about the future, for example, in relation to spending capacity; real behavior involved ignorance of at least some of the relevant facts, for example, in relation to the scope of a given product's market availability; and finally, real behavior involved a degree of confusion/uncertainty about how decision-making processes should best be undertaken, even if all the relevant facts were available (Katona 1980, 27).

Following on directly from J.M. Keynes's work in the 1930s on the importance of psychological propensities for an understanding of economic behavior (Katona 1942, 17; Barnett 2017), Katona and his brand of behavioral economics was virtually the sole efforts of a lone wolf in the first two decades after World War Two. However, by the end of the twentieth-century, behavioral economics had developed significantly and blossomed into a very important subfield of economics in its own right, partly through the very influential efforts of two key individuals, Daniel Kahneman and Amos Tversky.

Daniel Kahneman and Amos Tversky

Daniel Kahneman (1934–) is well-known for his work on heuristics and biases, loss aversion, prospect theory, framing effects, and choice under uncertainty. He is the co-author of *Judgment under Uncertainty: Heuristics and Biases* (Kahneman and Tversky 1982) and was awarded the Nobel Prize in Economics in 2002 for his work on prospect theory. Amos Tversky (1937–1996) was Kahneman's co-author of the work on prospect theory, and his important contribution to this theory was acknowledged posthumously in the Nobel Prize citation about Kahneman from 2002. Some of Tversky's work on heuristic choice mechanisms has been usefully employed by contemporary evolutionary psychologists (Todd and Gigerenzer 2007, 206).

In their work on heuristics and biases, Kahneman and Tversky argued that individual decisions are often made using a limited number of heuristic principles that simplify the decision-making process, but which can lead to either moderate or severe errors in certain situations. They have also identified various specific biases that people can be subject to, such as the representativeness heuristic, the conjunction effect, base-rate neglect, and the law of small numbers. In the latter case, Kahneman and Tversky's research suggested that individuals tended to exaggerate how often a small sample accurately resembled the wider population from which it was drawn.

In their work on prospect theory, Kahneman and Tversky maintained that the real carriers of value to human individuals were relative changes in wealth and welfare, rather than final or absolute states. For example, the same degree of wealth could connote extreme poverty for one person and great wealth for another, depending on the particular context of their lives. The billionaire whose total wealth was suddenly reduced to only \$10,000 would feel like they had been greatly impoverished, whereas if a rich benefactor gave a homeless individual with no possessions at all \$10,000 as a gift, then they would feel almost like a millionaire.

Following on from this, Kahneman and Tversky maintained that people are generally loss-averse, i.e., they value an equivalent loss higher than an equivalent gain. People also exhibit diminishing sensitivity to ongoing gains made of the same extent as they accumulate and are subject to the framing effect or to precisely how a particular issue is formulated. Differently framed formulations of the same question can sometimes result in very different answers. For example, patients can respond differently when it is recommended that they have surgery with a 70% survival rate, compared to the same surgery when it is recommended with a 30% chance of death.

Kahneman and Tversky not only frequently collaborated with themselves in their behavioral economics innovations but sometimes with other individuals as well. One very significant such individual was Richard Thaler with respect to collaborative work on the endowment effect

(Kahneman et al. 1991). The endowment effect is the hypothesis that people ascribe greater value to an item merely because they currently own it, as compared to what their valuation of the same item would be if they did not own it or if someone else owned it.

Richard Thaler

Richard Thaler (1945–) is well-known for his work on the consequences of the limitations of rationality, the nature of social preferences, and a lack of self-control for how economic decisions are made, and how they affect market outcomes. He is the co-author of *Nudge: Improving Decisions about Health, Wealth, and Happiness* (Thaler and Sunstein 2008) and the author of *Quasi Rational Economics* (Thaler 1994). He was awarded the Nobel Prize in Economics in 2017 for his work on bridging the gap between the economic and the psychological analyses of decision-making.

Thaler's co-authored book *Nudge* analyses how groups and organizations can assist individuals in making superior choices in their daily lives from a perspective of libertarian paternalism. Thaler and Sunstein divided human thinking/thought processes into two types: automatic/instinctive versus reflective/self-conscious. According to Thaler and Sunstein, in part because of differences/conflicts between the two types of thinking, individuals can be subject to various biases, fallacies, and heuristic frameworks, which may in certain situations lead to them making bad decisions and/or mistaken judgments.

The various heuristic frameworks and/or biases outlined by Thaler and Sunstein include: anchoring, or relying too much on one trait or one piece of information when making judgments, rather than using a wide range of information; availability, or using an example very easily brought to mind rather than a more relevant example that is more difficult to locate; status quo bias, or blindly continuing an existing behavior without further contemplation; and the herd mentality, or being too influenced by other people and/or existing trends.

From the perspective of evolutionary psychology, it could reasonably be hypothesized that some of these biases and heuristic frameworks are psychological mechanisms/instincts that have evolved by natural selection to provide human beings with a “fast and frugal” means of making decisions in situations in which speed of decision-making is a crucial factor at play (Todd and Gigerenzer 2007, 197). However in other situations, when speed is not so crucial, using these same instincts/biases, without additional reflective/self-conscious thought, might result in mistaken judgments and decisions being made.

Vernon Smith

Vernon Smith (1927–) is an experimental economist who was awarded the Nobel Prize in Economics in 2002, and who is known also for his work on understanding the nature of behavioral rationality. As Smith himself explained, “experimental market economics and behavioral economics are complementary” (Smith 2008a, 155).

Rationality is usually defined by mainstream economists as some type of maximization behavior in pursuit of self-interest. Methodological individualism underlies this approach, where each human being is regarded as a separate, self-contained unit of decision-making and action. However, a fundamental principle of evolutionary biology – inclusive fitness – challenges this approach, as genetic relatedness means that individuals are embedded in kinship groups (Barnett 2015, 653). In fact from a gene's-eye perspective, there are no such things as individuals, as genetic code is shared among family members.

Smith's definition of constructivist rationality widens the framework of operation of maximization-type rationality by applying it to individuals and to organizations. Its function is explicitly limited to the *conscious* analysis of superior alternative feasible pathways and it refers to optimal design in the incentive structure (Smith 2008b, 138). However, Smith is aware that this constructivist rationality is not comprehensive and requires augmentation by a different type of

rationality that takes account of the non-conscious aspects of behavior.

He defined his own version of ecological rationality in expansive terms as follows. An ecologically rational order was:

an undesigned ecological system that emerges out of cultural and biological evolutionary processes: homegrown principles of action, norms, traditions and “morality.” Ecological rationality uses reason – rational reconstruction – to examine the behavior of individuals based on their experience and folk knowledge, who are “naïve” in their ability to apply constructivist tools to the decisions they make; to understand the emergent order in human cultures; to discover the possible intelligence embodied in the rules, norms, and institutions of our cultural and biological heritage that are created from human interactions but not by deliberate human design. People follow rules without being able to articulate them, but they can be discovered. (Smith 2003, 469–70)

Smith was careful to explain the relation between his two types of rationality. Constructivist rationality accepted current economic structures (e.g., particular market auction systems) as given and attempted to formally model these structures using explicit rules of behavior and operation. Ecological rationality in contrast asked: how did these structures come into being (Smith 2003, 471)?

For evolutionary psychologists, however, ecological rationality has facilitated adaptive problem-solving in relation to the contexts that the human mind encountered during its long-period of evolution. As has been explained about environmentally specific statistical regularities:

... heuristics that use just a little of the patterned [environmental] information and process it in simple ways can make decisions that are fast, accurate, and adaptive ... Adaptive behavior emerges just when the mechanisms of the mind are properly matched to the (information) structure of the environment – producing what we call *ecological rationality*. (Todd and Gigerenzer 2007, 199)

As all ecologically rational cognitive processes relate to specific, concrete problems, they are context-dependent/path-dependent rather than general in nature (Egidi and Rizzello 2006, 675).

While Smith was confident that both of his types of rationality had relevance to understanding how

markets operated, evolutionary psychologists see their conception of ecological rationality as being in conflict with the standard account of rationality provided by most economists. Thus, it has been suggested by some evolutionary psychologists that “we should expect humans and other animals to show ‘ecological rationality’, rather than the economists’ perfect rationality” (Dunbar and Barrett 2007, 128). Contrast this with how economists usually interpret Smith’s work in experimental economics: “People are *more* rational than the agents in our models” (Eckel 2008, 570: emphasis added).

Smith concluded one article with a list of “working hypotheses” that originated from his work on experimental economics. Listed as number five was the idea that rules governing markets as institutions emerge as spontaneous order, through evolutionary processes that have adapted them to requirements:

What emerges is a form of “social mind” that solves complex organizational problems without conscious cognition. This “social mind” is born of the interactions among all individuals through the rules of institutions that have to date survived cultural selection processes. (Smith 2003, 500)

In the final section of this entry, it will be suggested that the idea of the emergence of a “social mind” is potentially equivalent to the hidden hand metaphor common in economics, and also to a well-known and long-standing fallacy in evolutionary biology.

The Invisible Hand

The invisible hand is perhaps the most famous metaphor found in all of economics: individuals pursuing their own self-interested behavior invariably end up serving the good of society as a whole. As a metaphor, it is used primarily to lend support to a *laissez faire* approach to economic policy or providing an instinctive argument as to why less governmental or state control and intervention is generally better than more.

The idea of the invisible hand also has what can be called a technical meaning, i.e., if it were possible to calculate the effects of an aggregate of all individuals pursuing unbridled self-interest,

versus this aggregate with additional controls on self-interest that were designed “for the social good,” then the result would necessarily and always be superior in the former case than the latter. It will be demonstrated here that this technical meaning of the invisible hand is false, as it is the equivalent of an argument that was previously made in support of the idea of group selection in evolutionary biology, an argument which is now accepted as erroneous.

This basic parallel has recently been made by Robert Trivers, a leading evolutionary biologist. Trivers wrote that mainstream economists:

... argue that individuals acting for personal utility will tend to benefit the group; they are (thus) often blind to situations where unrestrained pursuit of personal utility leads to disastrous effects on group benefits ... This is a well-known fallacy in biology, with hundreds of examples. Nowhere do we assume in advance that the two kinds of utility are positively aligned ... the result is the equivalent of the group selection fallacy – yes, selection acts on individual utility but magically enough, general utility is thereby generated? (Trivers 2013, 311–312)

As economists are not always well-versed in evolutionary biology, this entry will outline the consequences of Trivers’ parallel between the invisible hand and group selection in more detail, in order to illustrate how behavioral economics needs to take account of the principles of evolutionary biology.

One argument previously advanced in support of group selection is now acknowledged as mistaken, what will be called the “higher good” argument. The “higher good” argument is that evolution by natural selection can sometimes act for the good of the group or the species as a whole, when in fact evolution only ever acts to promote the interests of individual genetic lines. The consequences of natural selection acting on genes for higher-level units such as families, tribes, nations, species, and ecosystems cannot be known a priori, instead the particular circumstance have to be examined before the effects of evolution on higher-level units are known. The meaning of this mistake will be elaborated in what follows.

Consider a group of birds that are divided into two types of foragers, prudent and imprudent foragers, each subgroup initially being of equal size.

The former birds restrain their feeding and reproduction in order to manage their environment for the long-term, while the latter birds eat and reproduce as much as is physically possible (Wilson 2007, 50). If the invisible hand were to operate on this hypothetical group, then it would balance the behaviors of the two subgroups to produce a long-run equilibrium that maintained the environment in a healthy state for both types of foragers to enjoy, by selecting to some degree against the imprudent foragers who naturally reproduce more quickly, so as to maintain the initial position of ecological balance.

However what would happen in the real world would be that, because the imprudent foragers have the higher relative fitness and reproduce more, they would increase their percentage frequency in the group over time. The fact that this would eventually produce a population collapse after the growing number of imprudent birds exhausted their food source is in no way precluded by natural selection, as it never acts “for the good of the group” or the good of the ecosystem.

Another example was provided by Trivers himself. In some types of monkeys, male infanticide of dependent offspring of current mates, who were fathered by other males, was in the past interpreted by biologists as a population-control mechanism designed to serve the good of the group, by ensuring that the total population level was kept in line with the local ecology (Trivers 1985, 74). In fact, this murder simply serves the individual interest of the current male partner by bringing the female into reproductive readiness more quickly and preventing her attention being taken by offspring from previous mates (Trivers 2013, 308). Since a “horrific” example of monkey behavior was being considered (the murder of infants), there was a human desire to believe that a “higher good” would be the outcome (population management), but in fact, nature has no such desire to guarantee the good of the group.

The fact that the “higher good” argument for group selection is erroneous has a twofold parallel with the invisible hand in economics, what can be translated into the rightwing invisible hand fallacy

and the leftwing anti-invisible hand fallacy. If the rightwing invisible hand fallacy is that the “good” invisible hand magically guarantees that individuals pursuing their self-interest will always result in the social good being enhanced, then the leftwing anti-invisible hand fallacy is the opposite that the absence of the invisible hand (or a wicked invisible hand) guarantees that individuals pursuing their self-interest will never result in the social good being enhanced.

The scientific position based on the analogy with natural selection is that sometimes individuals pursuing their self-interest will translate into the social good being enhanced and sometimes it will not do so, it all depends on the specific details of the particular example that is being considered. Although producing a “higher good” above the individual level is never an aim of natural selection, it is sometimes an accidental byproduct. The examples considered above of natural selection acting to produce negative results for the group, need, therefore, to be supplemented by other examples in which group benefits do result, but only by accident. In order for behavioral economics to fully recognize the implications of evolutionary biology for understanding behavior, it has to incorporate this type of scientific reasoning into its foundations.

Neuroeconomics

One relatively new subfield of behavioral economics is, therefore, particularly promising from an evolutionary perspective: neuroeconomics. Neuroeconomics combines analysis from neuroscience with aspects of behavioral and experimental economics and also cognitive psychology. It uses some of the methods developed by neuroscientists to study brain activity in order to investigate the relationship between economic behavior and the neural matter, the neural mechanisms, and the neural structures of the brain (Lohrenz and Montague 2008). By discovering the brain regions linked to particular thought/feeling processes, the neurological foundations of economic decision-making can potentially be better understood.

For example, in relation to neural representation of temporal discounting, or whether an individual prefers \$X today or \$X + 1 in 1 week, it has been discovered that there are two specific neural systems involved in deciding the final outcome: a more impulsive system located in the limbic system, and a more rational system located in the prefrontal cortex (McClure et al. 2004). Another study has highlighted the neurological foundations of asset investment decisions, suggesting that insula activation was linked to higher degrees of investment risk with respect to particular stock/bond choices, and that striatum activity was linked to more aggressive investment choices (Kuhnen and Knutson 2005). It has been suggested in consequence that the function of the insula is to model the hypothesized outcomes of particular risk-taking behaviors.

From the perspective of evolutionary psychology, neuroeconomics provides one potential avenue for the possibility of locating individual psychological mechanisms in specific regions of the brain, and thus the possibility of beginning to identify the concrete neurological bases of these mechanisms. Or, in other words, of creating models of the evolved computational architecture of the mind “that can be cashed out genetically” (Tooby and Cosmides 2005, 63), in order to contribute towards mapping an evolutionary psychological equivalent of *Grey’s Anatomy* (Goetz and Shakelford 2007, 15).

Conclusion

This entry, like another related entry on economists and evolutionary psychology (Barnett 2018), has attempted to present both a basic account of some of the main contributions of some well-known behavioral economists and to evaluate these contributions to some extent using concepts imported from evolutionary psychology and evolutionary biology. It has also evaluated a few basic principles of mainstream economics, like the invisible hand, in similar fashion.

From the perspective of evolutionary psychology, behavioral economics has certainly made a

sincere effort to counter some of the unrealistic assumptions and principles of neoclassical economics by presenting numerous examples of sub-optimal, irrational, biased, distorted, mistaken, and incomplete behaviors, and by providing some more realistic assumptions and principles to replace the unrealistic abstractions of much of mainstream economics. Some of these more realistic assumptions and principles overlap to a degree with those of evolutionary psychology, for example, Smith's use of the ecological rationality concept.

However, in some other areas, costly signaling theory and the handicap principle, for example, behavioral economics, has yet to fully recognize the importance of modern evolutionary concepts (Miller 2009, 91; Spence 1973), even though institutionalist economists have been analyzing conspicuous consumption since the end of the nineteenth century (Veblen (1925) [1899]). This neglect is epitomized by the work of George Akerlof and Robert Shiller, both of whom have fully acknowledged the importance of psychology for economics (Akerlof and Shiller 2009): unfortunately, this acknowledgment is only of the importance of psychology [sic], not of evolutionary psychology.

Many evolutionary psychologists would argue that what is really required in order to make behavioral economics fully realistic is for economists to embrace wholeheartedly an evolutionary approach to their subject, and place all of their theories on more solid Darwinian footings. One potentially positive breach in this regard has recently been provided by neuroeconomics. However if all of economics as a subject embraced evolutionary psychology as its underlying foundations, then it would become entirely behavioral, truly realistic, and take its rightful place as a new branch of the natural sciences (Cosmides and Tooby 2005, 585).

Cross-References

- [Economists and Evolutionary Psychology](#)
- [Evolution and the Theory of Games](#)

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Behavioral Engagement

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Behavioral Evolution

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Behavioral Flexibility

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Behavioral Game Theory

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Behavioral Inheritance

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Beneficial Side Effects

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Synonyms

[Advantageous side effects](#)

Definition

The unintended or undesired outcomes that are beneficial.

Introduction

Side effects are often considered as undesirable. Side effects are often unintended. Side effects can be considered as by-products. When an intervention is done, it often aims at achieving a specific goal. The specific goal is often achieved through a specific mechanism at a specific site. However, the impact of an intervention may go beyond the desired or intended effect, which is often referred as side effect. In simpler terms, it can be said that the outcome of an intervention consists of desired effect and side effect (i.e., outcome = desired effect + side effect). The Merriam-Webster dictionary defines *side effect* as “a secondary and usually adverse effect (as of a drug)” and also refers to it as side

reaction (Merriam-Webster Dictionary 2006). Side effects are also commonly known as adverse effects. Side effects are often discussed in the context of different medications or interventions.

The side effect may be hazardous as well as beneficial. For example, tricyclic antidepressants like amitriptyline are often used in the treatment of depression; sedation is a common side effect of amitriptyline. Many patients report excessive sedation with amitriptyline, which is a hazardous side effect, whereas several patients with depression report insomnia too and report improvement in their sleep after treatment with amitriptyline, which can be considered as a beneficial side effect.

Beneficial Side Effects: Relevance

Understanding the biological, psychological, as well as sociocultural factors in the context of health also requires thorough understanding about beneficial side effects. An individual's basic needs (food, shelter, and sex) also have certain beneficial side effects too. Nature has designed sexual behavior in living organisms, which is meant for procreation (reproduction); some developmentally higher organisms (human) derive pleasure from sex (recreation). Here, recreation is the beneficial side effect of sex. Similarly, food and shelter are required for the survival and protection of the individual; however, pleasure is a secondary effect and biologically not intended in most of the living organisms; hence, it can be considered as beneficial side effect.

Illness (disease or disorder) causes significant impairment of functioning of the individual and compromises the productivity. However, it been seen that individuals, who are ill are often exempted from many socio-occupational roles and responsibilities. Individuals with illness also get certain disability benefits and extra care. These benefits can be considered as beneficial side effects of illness. Many patients demonstrate abnormal illness behavior or play the role of sick, being reinforced by the rewarding illness benefits (Kar and Kumar 2015).

Beneficial Side Effects: Clinical Implications

Beneficial side effects may have relevance in management of medical as well as psychiatric disorders. The effects of medications and other therapeutic interventions are judged in the patients. The effects of medications or interventions that are often acknowledged as undesired may be beneficial in certain category of clients. The beneficial side effects have been reported in various clinical research. Cleophas et al. (2002) in their study found a beneficial role of commonly used antihypertensive agents (beta blockers). They found that elderly population, who are often at risk of postural hypotension due to reduced baroreceptor sensitivity, may benefit from the use of beta blockers (Cleophas et al. 2002). Similarly, temozolomide is used as a chemotherapeutic agent for treatment of low-grade glioma; it is found to be effective in reduction of seizure frequency (Koekkoek et al. 2015). Selective serotonin reuptake inhibitors (e.g., fluoxetine) are commonly used for the treatment of depression and anxiety disorders. Fluoxetine and other selective serotonin reuptake inhibitors have the side effect of delayed ejaculation, which is found to be useful in males with premature ejaculation and erectile dysfunction (Power-Smith 1994). Hypnotic therapies are used for producing relaxation and subjective well-being. In a study on patients with chronic pain, it was found to produce certain other additional effects like decreases pain and better perceived control on pain, which are beneficial side effects of the intervention (Jensen et al. 2006). Tobacco use is one of the common substance use disorder worldwide. Nicotine is the active principle of tobacco, which is having addictive properties. Nicotine is associated with various health hazards; however, nicotine is found to be beneficial in weight regulation, ulcerative colitis, Alzheimer's disease, Tourette syndrome, as well as reducing neuroinflammation (Jarvik 1991; Noda and Kobayashi 2017). Similarly, evidences support the beneficial role of cannabidiol-enriched cannabis in the management of treatment refractory pediatric epilepsy (Dravet syndrome, Lennox-Gastaut

syndrome, idiopathic epilepsy) (Porter and Jacobson 2013).

Patients with depression, anxiety disorder, and obsessive-compulsive disorder often experience ruminations. Ruminations can be disastrous, but sometimes it becomes beneficial. Individuals, who frequently ruminate have difficulty (commit more errors) in tasks that require executive control like goal shifting. However, when they involve in tasks that do not require goal shifting and rather require goal maintenance, their performance remains better. It is a beneficial side effect of rumination (Altamirano et al. 2010). Even some evidences support that individuals who learn or listen to music show certain improvements in nonmusical domains (e.g., spatial abilities), which can be referred as a beneficial side effect of music (Schellenberg 2003).

Many a times, clinicians choose to use the side effects of a medication for a therapeutic purpose. Here, due to beneficial effect, the particular side effect becomes desirable, hence intended.

Conclusion

Beneficial role of side effect of an intervention or a pathophysiological process makes it acceptable and desirable many a times. Understanding beneficial side effects of an intervention will help the clinician in redirecting the side effects for the betterment of health.

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Benefit and Cost Asymmetries

► Altruism and Costs to Altruist

Benefit Group Relative to Other Groups

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Synonyms

Ingroup favoritism; Parochial altruism

Definition

Behavior and decisions in favor of a group with which an individual affiliates

Introduction

Living in groups implies that people develop attitudes and behaviors based on group membership. Identifying different groups is associated with asymmetrical reactions toward their members. Such asymmetries exist in various types of reactions: cognitive (biases), affective and attitudinal (prejudice), and behavioral (discrimination). Sometimes, researchers consider them as parts of the same process or use these terms as synonyms. However, most contemporary researchers agree that it is important to differentiate between prejudicial attitude and discriminatory behavior. At the behavioral level, people tend to allocate resources and make other decisions benefiting their group and prefer cooperation with the members of their group. Intergroup discrimination is thought to underlie variety of important social problems ranging from discrimination in labor or education to wars and genocide.

Ingroup Favoritism in Animals

Evolutionary origin of ingroup-benefiting behavior is supported by many facts of similar reactions in various species. Ingroup behavioral preference is common not only for primates but also for other animals such as dolphins, elephants, meerkats, lizards, birds, ants, etc., and some researchers even use similar terminology to describe behavior of microbes (Strassmann et al. 2011). In animal studies, ingroup favoritism is typically understood as a form of cooperative behavior. Typical examples of cooperation include territory defense or acquiring, joint struggle for food or mates, and communal nesting, although some researchers also include more specific forms of behavior such as grooming or interactions during water search (Masuda and Fu 2015). Importantly, animal studies show that

such cooperation is not necessarily based on kinship but can be based on more complex affiliations and social structures.

Ingroup Favoritism in Humans

Within human societies, benefiting one's own group is much more diverse and complicated, often moderated by various factors such as social status, normative beliefs, or multiple identities. One of the first experimental studies demonstrating ingroup-favoring behavior was conducted in the 1950s by a group of psychologists headed by M. Sherif. They used a field experiment in a summer camp, by arbitrary dividing boys into two groups and fostering competition between them (Sherif et al. 1961). The group membership manipulation was successful, and the members of each group easily formed both positive attitude toward ingroup and negative attitude toward outgroup, with corresponding behavioral outcomes. Later, J. Tajfel et al. (1971), using laboratory experiments, confirmed that differential reactions can be the result of absolutely arbitrary, temporary, and contextual group memberships imposed by an experimenter – what is currently known as a “minimal group.” In these experiments, participants were divided into two groups on the basis of irrelevant criteria (e.g., perceived accuracy of simple task performing or preference for Klee or Kandinsky paintings) and had to allocate resources between the members of the two groups. The study showed that participants not only tended to benefit their own group but also that they strived to maximize the *difference* in rewards between groups rather than maximizing ingroup profit. The experiments using “minimal-group paradigm” allowed to suppose that the tendency to make decisions in favor of one's own group is a direct consequence of self-categorization, i.e., identifying oneself with a particular social group or category. This means that the tendency to benefit ingroup is present even when group members don't know each other and don't interact and don't have personal benefits from the discriminating behavior.

Later, numerous psychological studies demonstrate intergroup discrimination using various methods and situations. The most common laboratory experiments use two-player games:

- Allocation matrixes: participants allocate rewards and/or penalties between ingroup and outgroup members.
- Dictator games: participants play a role of a “dictator” freely distributing rewards between him-/herself and a different player who can be ingroup or outgroup member.
- Trust games: Participants play a role of an “investor” receiving endowment which can be partially or in a whole transferred to a trustee (ingroup or outgroup), who can return any sum from the reward multiplied by an experimenter.
- Social dilemmas such as prisoner’s dilemma, when two participants simultaneously decide what share of their endowment to give to each other (Balliet et al. 2014).

In addition to laboratory experiments, psychologists conduct field studies of discriminating behavior using such methods as observation of helping behavior, hiring and housing audits, studies of policy profiling, and opinion surveys (Greenwald and Pettigrew 2014).

Most of the studies supported the view that ingroup favoritism is a common strategy underlying intergroup relation. Comparing many experimental studies using various tasks and conditions, psychologists from the Netherlands concluded that discriminating in favor of one’s group is the most frequent strategy although some studies show preference for outgroup members. Psychological studies of ingroup favoritism cover both artificial, experimentally created and natural groups based on race, ethnicity, nationality, political and organizational affiliation, support for a sport team, and others. In general, discriminatory behavior is typical for any types of group membership (Balliet et al. 2014). At the same time, other factors can affect nuances of group-based discrimination. For example, expectation of future interaction makes discriminating behavior favoring ingroup member more probable, although mere categorization is often sufficient for ingroup

favoritism. The existence of common knowledge about group membership also fosters ingroup favoritism showing that individuals care about their reputation necessary for living in a group. Social status considerations and normative beliefs can also affect the tendency to favor one’s group.

Importantly, discriminating behavior can result from two distinct types of prejudice: positive attitudes toward ingroup members and negative attitude or hostility toward outgroup members. Although they may seem to be two sides of the same process, the contemporary social psychology sees them as distinct and stresses that discrimination can result from favoring ingroup without hostility to outgroup (Greenwald and Pettigrew 2014). Moreover, identifying oneself with particular group is sufficient for discriminatory behavior and doesn’t need a clearly defined outgroup (Balliet et al. 2014).

Explanations of Ingroup Favoritism

In explaining the origins and mechanisms of ingroup favoritism, a number of theories have been proposed, mostly within social psychology and evolutionary approaches. In social psychology, ingroup favoritism is explained by social identity and self-categorization theories, balance identity theory, system justification theory, social dominance theory, uncertainty reduction theory, bounded generalized reciprocity theory, and others (Greenwald and Pettigrew 2014; Everett et al. 2015). Evolutionary approaches are generally based on mathematical models, applied to animal populations, and include direct reciprocity, indirect reciprocity, tag-based cooperation, group selection, spatial structure, and other models (Masuda and Fu 2015). Less recognized in social psychology are theories deriving discrimination from the society’s structural and normative organization (Greenwald and Pettigrew 2014).

Despite important nuances between the theories, the key discussion in contemporary psychological science is between theories deriving ingroup-favoring behavior from social identity and those focusing on actual and future interactions (Balliet et al. 2014; Everett et al. 2015). Identity-based

approaches derive ingroup favoritism from the self-categorization process and the universal motivation for positive self-esteem. If a clear distinction between ingroup and outgroup is present, whatever is the rationale for such a distinction, individuals tend to perceive themselves and others in terms of their group membership (depersonalization). When individuals perceive themselves this way, they may consider ingroup members as part of themselves, and their motivation for self-esteem or positive evaluation can project onto ingroup members. Favoring ingroup increases its power and/or superiority over outgroup, thus increasing individual's self-regard. Interaction-based approaches, on the contrary, consider ingroup favoritism as a more rational, belief-based behavior. Benefiting people having something in common with an individual can be a rational strategy when the future interactions with them are more probable than with outgroup members. Expectation of future interactions and direct or indirect reciprocity can lead to ingroup-favoring behavior.

At present, it is difficult to conclude which of the existing theories and approaches better explain complex and multifaceted discriminatory behaviors in modern societies. Most methods and studies have important limitations associated with measurement procedures, boundary conditions, representativeness of samples, lack of cross-cultural comparisons, etc. A large-scale comparison of psychological studies conducted by the Netherland psychologists led them to the conclusion that evolutionary explanations are generally more appropriate than the self-categorization theory, because they correctly predict that favoring ingroup doesn't need the clearly defined opposition between ingroup and outgroup (Balliet et al. 2014). However, such a comparison also has methodological limitations and doesn't cover studies not based on laboratory experiments.

Last decade, the development of social and cognitive neuroscience allowed a better understanding of neural mechanisms underlying ingroup favoritism. Some studies showed that even the "minimal-group" membership leads to different neural reactions to ingroup and outgroup members in a way more consistent with identity-based rather than interaction-based approaches.

For example, costly helping to ingroup members involves greater activation in anterior insula, a brain region associated with empathy (Hein et al. 2010). Another study showed that ingroup-benefiting allocation of rewards was associated with activity in the medial prefrontal cortex and anterior cingulate cortex, regions associated with self-processing and thus probably indicating that in these cases participants perceived ingroup members as part of themselves (Volz et al. 2009). However, these findings don't mean that the ingroup-favoring decisions should be necessarily determined by the only neural mechanism. Indeed, a recent study showed that reward-related neural processes can support trust and cooperation with ingroup members, whereas trust and cooperation with outgroup members involve neural systems responsible for control functions (Hughes et al. 2017).

Conclusion

Ingroup favoritism and discrimination against other group are by no means a fundamental aspect of human social behavior underlying many important social phenomena, both positive (e.g., teamwork) and negative (e.g., wars and xenophobia). The complexity of social interactions, beliefs, and identities may partially explain why so many theories of discrimination based on group membership exist and why no one of them seems to be sufficient. Studies show the diversity of human reactions toward the social groups indicating that probably the search of a single mechanism underlying them is a wrong strategy. Instead, a more integrative approaches, focusing on both identity construction and expectations of reciprocity, taking into account such factors as cultural norms or social status, is supposed to be the main direction of future research (Everett et al. 2015).

Cross-References

- [Cooperation](#)
- [In-Group–Out-Group Bias](#)
- [In-Group Versus Out-Group](#)

- [Prejudice](#)
- [Reciprocal Altruism and Group Living](#)
- [Social Neuroscience of Self-categorization](#)

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Benefit Provisioning

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Synonyms

[Benefit-provisioning behaviors](#); [Benefit provisioning domain](#); [Benefit-provisioning mate retention behaviors](#)

Definition

Benefit-provisioning behaviors are mate retention behaviors that are intended to increase the incentives of staying mated to the current partner and, in turn, deter defection from the relationship. These behaviors can include things such as buying gifts for the partner, altering one's appearance, and different sexual behaviors.

Introduction

After attracting a mate, humans are faced with the adaptive problem of retaining the mate. Successful mate retention prevents other problems associated with reproduction such as cuckoldry and defection of resources (Buss 1988). Therefore, it is likely that a series of adaptations would have evolved to aide individuals in their mate retention. Indeed, an entire taxonomy of these mate retention behaviors have been identified, and these mate retention behaviors range in nature from acts that inflict costs on the partner (i.e., cost-inflicting behaviors) to behaviors that bestow benefits on the partner (i.e., benefit-provisioning behaviors; Buss 1988). Despite their difference in tactics, each of these mate retention behaviors is intended to deter the partner from defecting from the relationship.

Mate Retention Domains, Categories, and Tactics

As mentioned above, simply attracting a mate is not enough to ensure successful reproduction and the survival of offspring. Humans must also make efforts to prevent their partner from defecting from their relationship (i.e., losing a reproductive resource). It has been demonstrated that both sexes engage in extra-pair mating (Greiling and Buss 2000), as well as mate poaching behaviors (Schmitt and Buss 2001). Thus, the risk of defection is present both within and outside of the relationship. Therefore, a series of behaviors should be present to help counter these risks and should also be focused on the partner, as well as

sexual rivals. Indeed, we see that a variety of behaviors have been identified, which target the partner and/or sexual rivals.

In some of his early work, David Buss (1988) sought to develop a complete taxonomy of human mate retention behaviors. Through an act nomination procedure, 104 different acts were determined, which can be classified into two broader domains, five distinct categories, and 19 tactics of mate retention. The domains of mate retention behavior reflect whether benefits are being provided to the partner, or whether costs are being inflicted to the partner, and thus are given the names benefit-provisioning and cost-inflicting behaviors, respectively. Put another way, benefit-provisioning behaviors operate to incentivize the partner to stay in the relationship (e.g., by buying an expensive gift for the partner), whereas cost-inflicting behaviors operate to make the partner's defection from the relationship costly (e.g., by limiting their access to members of the opposite sex). Therefore, both domains operate to solve the adaptive problem of mate retention by ensuring that the partner remains invested in the current relationship while reducing the likelihood of their defection from the relationship.

Subsumed under these two domains are five distinct categories of mate retention behaviors; each of which distinguish whether these behaviors are ultimately targeted toward the partner or the rival. Under the domain of cost-inflicting behaviors are the categories of direct guarding (e.g., watching over the partner, controlling their free time), intersexual negative inducements (e.g., derogating competitors in front of the partner, manipulating the partner), and intrasexual negative inducements (e.g., derogating the partner in front of competitors, acting violent toward rivals). Under the domain of benefit-provisioning behaviors are the categories of positive inducements (e.g., buying gifts for the partner, showing love and affection for the partner) and public signals of possession (e.g., publicly commenting about the partner, using physical reminders that the partner is mated). In turn, the categories of direct guarding, intersexual negative inducements, and positive inducements can be seen as targeted toward the partner, whereas the categories of

intrasexual negative inducements and public signals of possession can be seen as targeted toward rivals. Benefit-provisioning behaviors as a whole, and the categories under benefit-provisioning behaviors, will be discussed in detail below.

Benefit-Provisioning Behaviors

Broadly speaking, benefit-provisioning behaviors involve doing things that incentivize the partner to stay in the relationship and to broadcast the nature of the relationship to rivals. Put another way, the individual is attempting to change their partner's assessment of the relationship to be more favorable and is signaling to others that their partner is taken. In turn, these actions can increase the partner's relationship satisfaction, and make defection from the relationship less likely. The various benefit-provisioning behaviors are classified into the separate categories of positive inducements and public signals of possession, as well as in the tactics that make up these categories.

Positive Inducements

The category of positive inducements includes behaviors that are intended to convey to the partner that remaining in the relationship is beneficial. For example, positive inducements include showing affection toward the partner, buying gifts, and performing different sexual behaviors for the partner. Additionally, there are a variety of positive inducement behaviors that an individual can employ to make their partner's assessment of the relationship more favorable.

Moving to the tactic level, the details of the positive inducement behaviors can fully be seen. The first tactic under positive inducements is resource display. Here, individuals are attempting to convey to their partners that they have the ability to acquire resources and provide these resources to their partner. Thus, they may do things such as buying an expensive gift for their partner or taking their partner out for a meal at an expensive restaurant. In both actions, the

individual is making an attempt to convince their partner of their ability to provide for them and any potential offspring.

The second tactic under positive inducements is love and care. Using this tactic, individuals are displaying to their partner that they are emotionally invested in the relationship. Thus, they may do things such as professing their love to their partner, acting kind or nice to their partner, or complimenting their partner on their appearance. Across these behaviors, the individual is displaying their investment in the relationship and, in turn, their willingness to invest in potential offspring.

Outside of displaying affection and resources, individuals may also make efforts to enhance their appearance. Therefore, in the third tactic of positive inducements, appearance enhancement, individuals may be doing things such as wearing fashionable clothing or using makeup or other means to make themselves more attractive. Each of these behaviors attempts to signal high mate value to the partner, which should in turn increase their commitment to their partner and decrease the appeal of attractive rivals.

Individuals may also engage in mate retention behaviors that involve particular sexual behaviors. More specifically, when employing the tactic of sexual inducements, individuals may perform sexual favors for their partner or engage in sexual activity to please their partner. Therefore, this tactic is intended to keep the partner sexually satisfied and, in turn, decrease the likelihood that they seek out mating opportunities outside of the relationship.

The final tactic under the category of positive inducements is submission and debasement. This tactic is unlike the others, as it is more of an attempt to appease the partner, as opposed to directly bestowing benefits on the partner. Using this tactic, individuals may drastically change their behavior in order to fit the desires of their partner. For example, they may be willing to forego their own desires in order to let their partner have their way. Therefore, this tactic makes the relationship more favorable by conferring the benefit of having the partner's desires met without sacrifice.

Public Signals of Possession

The second category of benefit-provisioning behaviors is public signals of possession. Here, individuals may engage in some behaviors that involve giving gifts to the partner. However, the main focus across these behaviors is to signal to others that the partner is currently taken (mated). In turn, the individual is signaling their investment to their partner. This signal of increased investment is what incentivizes the partner to remain in the relationship (i.e., this is how the benefit is being bestowed on the partner). As was the case with positive inducements, there are a series of tactics under the larger category of public signals of possession.

The first of these tactics is verbal possession signals. Here, individuals may make remarks that refer to their partner in conversation with others, particularly same-sex rivals, in an attempt to thwart any attempts to disrupt the relationship. In a similar manner, individuals may brag about their partner to same-sex rivals or describe how much they and their partner are in love to dissuade these rivals. The second tactic under public signals of possession, physical possession signals, is identical in intent. However, instead of describing the nature of the relationship to others, individuals may engage in behaviors such as kissing their partner in front of others or placing their arm around their partner as a physical sign of their commitment.

The third tactic, possessive ornamentation, takes on a slightly different approach to convey the same message to same-sex rivals. Using this tactic, individuals may engage in behaviors such as having their partner wear a ring to signify that they are taken, along with wearing other forms of jewelry and clothing to signal the status of the relationship. Therefore, this tactic involves doing things to convey to others the status of the relationship without the individual being present. In turn, although these behaviors involve giving something to the partner, their intention is focused on same-sex rivals (i.e., they are intrasexual in nature).

The tactics described above include a variety of individual acts that are included in single items of

the Mate Retention Inventory (MRI; Buss 1988; Buss and Shackelford 1997; Buss et al. 2008). Additionally, these tactics describe behaviors that a variety of individuals have reported engaging in. Therefore, it is likely that the use of mate retention behaviors varies across individuals and across different points in the relationship. Indeed, previous work has demonstrated that individual differences such as mate value, self-esteem, and personality influence the use of mate retention behaviors.

Mate Value and Benefit-Provisioning Behaviors

Broadly defined, mate value reflects the degree to which an individual possesses traits associated with reproductive success (e.g., health, youth, and beauty). That is, individuals who have a number of these traits are considered to be high in mate value. Therefore, selecting for, and retaining mates that are high in mate value would be reproductively advantageous. However, having a partner who is high in mate value may influence the degree to which individuals have to engage in mate retention behaviors. Additionally, individuals who are high in mate value may be able to engage in mate retention behaviors that their low mate value counterparts cannot.

As mentioned above, individuals mated to partners higher in mate value face the problem of retaining these partners and maintaining their access to these valuable reproductive resources. Individuals who are high in mate value are more likely to be the subject of mate poaching attempts (i.e., attempting to secure others' mates as your own) and, in turn, are more likely to defect from the relationship. Therefore, their partners should be more motivated to engage in mate retention behaviors and may be particularly motivated to engage in specific mate retention behaviors.

Indeed, it has been demonstrated that individuals mated to partners higher in mate value engage in more benefit-provisioning behaviors and less cost-inflicting behaviors (Miner et al. 2009; Starratt and Shackelford 2012). These effects

have been most extensively studied in men and suggest that men who are mated to women of higher mate value engage in more benefit-provisioning behaviors (Starratt and Shackelford 2012). Additionally women who report their partners to be high in mate value also report that their partners engage in more benefit-provisioning behaviors (Miner et al. 2009). However, one's own mate value does not appear to influence self-reported benefit-provisioning behaviors (Starratt and Shackelford 2012). That is, men who rate themselves as higher in mate value do not report engaging in more benefit-provisioning behaviors themselves. Therefore, it appears that the partner's mate value has the most direct influence on mate retention behaviors.

Self-esteem and esteem for the partner have also been used as measures of mate value (Holden et al. 2014a). More specifically, it was proposed that those high in mate value should also score higher on measures of self-esteem. Additionally, those who are high in mate value should in turn be held in a higher regard by their partner (i.e., more esteemed by their partner). Using these measures of mate value, results similar to previous studies are observed. That is, women who hold their partner in a higher regard also report that their partner engages in more benefit-provisioning behaviors and less cost-inflicting behaviors (Holden et al. 2014a). Therefore, these effects of partner's mate value on benefit-provisioning behaviors appear to be robust and stable findings.

Personality and Benefit-Provisioning Behaviors

A number of personality traits have been found to be associated with benefit-provisioning behaviors. These personality traits span multiple models of personality and include both normal and pathological forms of personality. The earliest work on personality and benefit-provisioning behaviors investigated connections between the five-factor model of personality and specific tactics of mate retention.

The five-factor model of personality (FFM; Costa and McCrae 1992) is one of the most widely

studied and influential models of personality. This model characterizes personality across the five factors of extraversion, agreeableness, conscientiousness, neuroticism, and openness. Each of these five factors has been shown to be associated with mate retention tactics under the benefit-provisioning domain. However, neuroticism, extraversion, and agreeableness all appear to be particularly associated with benefit-provisioning behaviors. More specifically, neuroticism and extraversion have both been found to be positively associated with the benefit-provisioning tactics of verbal possession, physical possession signals, and possessive ornamentation (de Miguel and Buss 2011). This suggests that those who are more sociable, but also more socially vigilant and emotionally unstable, may engage in the most of these types of benefit-provisioning behaviors. Interestingly, agreeableness was found to be negatively associated with each of these tactics that signal possession (de Miguel and Buss 2011). Therefore, it may be that individuals who score high in agreeableness refrain from using these tactics to avoid upsetting their partner. Alternatively, it may be that individuals who score high in agreeableness also see these tactics as disingenuous in nature. For the tactics of sexual inducements, appearance enhancement, and submission and debasement, an identical pattern of associations emerges. That is, neuroticism and extraversion are both positively associated with these tactics, whereas agreeableness was negatively associated with these tactics. Taken together, these findings suggest that personality influences mate retention behavior and that certain individuals may be more willing to bestow benefits on their partner.

Personality traits under the HEXACO model of personality (Lee and Ashton 2012) have also been considered in relation to benefit-provisioning behaviors. The HEXACO model of personality provides an extension of the FFM by adding a sixth factor of personality. This sixth factor of personality is referred to as honesty-humility and assesses the degree to which an individual is concerned with acting in a fair, modest, and sincere manner. Therefore, individuals who score high on honesty-humility of

personality may avoid doing things that could be considered disingenuous or false.

This aspect of personality seems to influence the mate retention behaviors that individuals use, as it has been found that honest-humility is negatively associated with the benefit-provisioning category of positive inducements (Holden et al. 2014b). This suggests that individuals who score high on this personality trait would avoid engaging in behaviors such as buying gifts for their partner, displaying their love, and enhancing their appearance to please their partner. However, it may be that these individuals avoid engaging in these behaviors in contexts where they feel as though these actions could be considered false. That is, individuals high in honesty-humility may not consider it fair or sincere to give a gift, for example, without a reason to do so. Therefore, individuals high in honesty-humility may not completely avoid these benefit-provisioning behaviors and may be concerned with how these behaviors are perceived.

An alternative explanation of this negative relationship would suggest that those who score low in honesty-humility use positive inducements as a means to manipulate or deceive their partners. Indeed, honesty-humility has been found to be negatively associated with a number of cost-inflicting behaviors, some of which involve similar forms of manipulation (Holden et al. 2014b). More importantly, low scores on honesty-humility have been found to be associated with each of the Dark Triad traits (i.e., narcissism, Machiavellianism, and psychopathy), which are characterized by having an inflated sense of self-worth, along with acting in a cold, callous, and manipulative manner (Paulhus and Williams 2002). Interestingly, the Dark Triad traits have been found to be associated with increased use of a number of cost-inflicting behaviors (Jonason et al. 2010), which would further support the idea that individuals low in honesty-humility may be using positive inducements in a manipulative manner. Furthermore, these findings suggest that various aspects of personality influence the decisions that individuals make about their mate retention behaviors and that it is worthwhile to investigate how other individual differences influence mate

retention. For example, the associations that different attachment styles have with mate retention behaviors are currently being investigated (Barbaro et al. in press).

Conclusion

Although mate retention is a universal human concern, there are a variety of behaviors that individuals may employ to retain their mates. Some of these behaviors function to increase the costs associated with defection from the relationship (i.e., cost-inflicting behaviors), whereas others function to increase the benefits associated with remaining in the relationship (i.e., benefit-provisioning behaviors). The focus of this entry has been on these benefit-provisioning behaviors, which involve doing things such as displaying love and affection for the partner, buying gifts for the partner, and engaging in various sexual inducements. Additionally, the associations between a number of individual differences and benefit-provisioning behaviors were discussed. Individuals who are higher in mate value tend to engage in more benefit-provisioning behaviors, as do individuals who are high in extraversion and neuroticism, whereas individuals who are low in honesty-humility and low in agreeableness engage in more benefit-provisioning behaviors. Therefore, despite being a universal concern, it appears as though different individuals may attempt to solve the problems surrounding mate retention in a variety of ways. However, regardless of which specific act individuals employ, all benefit-provisioning behaviors function to incentivize the partner's continued investment in the relationship.

Cross-References

- [Act Nomination Method](#)
- [Coalitional Mate Retention](#)
- [Cost Inflicting](#)
- [Individual Differences](#)
- [Long-Term Mating](#)
- [Mate Retention](#)

- [Mate Retention After Children](#)
- [Mate Retention and Romantic Attachment](#)
- [Mate Retention Strategies](#)
- [Mate Retention Tactic](#)
- [Mate Value](#)
- [Use of Mate Retention Strategies](#)

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Benefit Provisioning Domain

► Benefit Provisioning

Benefit to Another at Cost to Self

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Synonyms

Benevolence; Niceness; Prosocial behavior; Selflessness

Definition

Altruism is defined as a voluntary costly act that benefits another organism, usually a conspecific (see Table 1).

Introduction

The study of altruism dates back at least to Darwin, who wrote, “Can we consider the sting of the wasp or of the bee as perfect which . . . inevitably causes the death of the insect”? (Darwin 1859) (Chapter 6). Darwin wondered how suicidal bee stings could persist – shouldn’t the stinging bees lose the evolutionary competition to other bees

Benefit to Another at Cost to Self, Table 1 Altruism in a framework of effects on self and other(s)

	Cost to another	Benefit to another
Cost to actor	Spite	Altruism
Benefit to actor	Selfishness	Mutualism

that do not commit suicide? There are currently five accepted theories that explain altruism and one open debate.

All of the accepted theories share the same underlying logic. The genes that create the apparently altruistic behavior benefit from the behavior. What appears to be altruistic is, in fact, selfish, when viewed from the perspective of the genes.

Accepted Theory #1: Kin Selection

Kin selection (Hamilton 1964) explains costly acts as benefiting genes in relatives. A bee may die when it stings an invader. This is bad for the individual bee, but good for the genes in the bee that are also likely to be shared by the other bees in the same hive. Altruistic behaviors that benefit genetic relatives help the underlying genes increase in the population.

Accepted Theory #2: Reciprocal Altruism

Reciprocal altruism (Trivers 1971) examines costly acts in the context of relationships. A person might sacrifice for a friend today and be repaid in the future. One act, examined in isolation, appears to be altruistic; when summed over the individuals’ lifetimes, however, the relationship benefits all parties.

Accepted Theory #3: Indirect Reciprocity

Indirect reciprocity (Alexander 1979; Nowak and Sigmund 1998) sees future repayment as the explanation for costly acts. Indirect reciprocity is similar to reciprocal altruism in counting costs and benefits over an organism’s lifetime. The apparent altruism is repaid in the context of

the relationship. One difference, however, is that reciprocal relationship sees the repayment coming from the individual who was helped, while indirect reciprocity allows repayment by third parties.

Accepted Theory #4: Costly Signaling

Costly signaling (Zahavi 1975) explains altruistic acts as part of a longer-term reputation management strategy. The costly act may alter the reputation of the “altruist.” The ability to help out someone in need may demonstrate, for example, health and vigor of the altruists. This perception of health and vigor might change the behavior of other organisms in a way that more than compensates for the altruist act.

Accepted Theory #5: Group Selection

Group selection (Wilson and Sober 1994) occurs when altruistic acts benefit the group in a way that also helps the genes of the altruist. If groups break up and reform with sufficient regularity, then even though the altruist does sacrifice for the benefit of the group, the genes of the altruist can increase as a percent of the overall population.

Open Debate: Strong Reciprocity

Strong reciprocity (Fehr et al. 2002) is purported as the sixth explanation for altruistic acts. For example, people in anonymous laboratory experiments in large cities will give money to strangers under some circumstances (Kahneman et al. 1986). These altruistic acts cannot be repaid through any of the five accepted theories. The participants are not kin, ruling out kin selection. The acts are anonymous so cannot be repaid through direct or indirect reciprocity. Similarly, no signals can be sent in an anonymous setting, so costly signaling is not possible. Finally, the participants are not in evolutionary relevant groups, thus ruling out group selection (Burnham and Johnson 2005). Strong reciprocity

faces continued debate about its existence and relevance.

Conclusion

The field of altruism has undergone tremendous change in the last few centuries and decades. There are five widely accepted explanations for altruistic behavior.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruism Advertises Cooperativeness](#)
- ▶ [Altruism Advertises Generosity](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism and Costs to Altruist](#)
- ▶ [Altruism and Watching Eyes](#)
- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Altruism Displays Cooperative Potential](#)
- ▶ [Altruism in Kin Selection](#)
- ▶ [Altruism Norms](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Altruistic Punishment Enhances Reputation](#)
- ▶ [Antisocial](#)
- ▶ [Antisocial Behavior](#)
- ▶ [C < Rb](#)
- ▶ [Cheater Detection](#)
- ▶ [Cheater Detection Adaptations](#)
- ▶ [Genuine Altruism](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Reputation](#)
- ▶ [Reputation and Altruism](#)
- ▶ [Reputation as a Context for Men's Aggression Against Men](#)

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Benefit-Provisioning Behaviors

► Benefit Provisioning

Benefit-Provisioning Mate Retention Behaviors

► Benefit Provisioning

Benefits

► Living in Groups

Benefits of Commitment and Marriage

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Synonyms

Conjugality; Fidelity; Loyalty; Mating; Pair-bonding

Definition

Commitment and marriage are human behaviors that occur in the context of family formation, sexual fidelity and cohabitation.

Introduction

There are a number of benefits of pair-bonding and sexual commitment, which may have favored the evolution of monogamous and polygynous marriage systems: (1) marriage enables mate guarding, which, for men, helps to ensure paternity of the children that they commit to rearing and for women secures the resources, protection, and labor of a man; (2) pair-bonding enables reciprocal division of labor in the rearing of children, thereby optimizing the investment of parental care by each sex; (3) sexual intercourse is a powerful route for transmission of disease, which has selected against promiscuity and favored having one or a few sexual partners; (4) pair-bonding enables a reciprocal care relationship, which promotes good health and longevity.

Why Marriage?

There is much flexibility in the human mating system, with examples of monogamous, polygynous, polyandrous, heterosexual, and homosexual relationships in different cultures throughout history. However, in most cultures, we find some formal rules around the union of men and women, which we may describe as marriage. In many societies, particularly in Africa, the Middle-East, and Muslim parts of Asia, polygynous marriage is allowed, whereas in much of the rest of the world, polygyny is discouraged or illegal and marriage is a monogamous commitment. In recent years, it has been allowed for individuals of the same sex to become married in some countries, but historically, marriage has meant a commitment between a man and a woman, in which obligations of sexual, emotional, and financial loyalty are entered into.

It is often said that marriage is an institution, in reference to its central role in the structure and organization of societies. It is typical for children to be raised in a household which is headed by a married couple and often for those children to leave the household when they themselves enter into a marriage. It is also seen that factors linked to social status, such as wealth and employment, affect the desirability of individuals in the marriage market (Goldman 1993; South 1991). However, biological factors, such as health, age, and height, may be much more important to the choice of a marriage partner (Kiernan 1988; Lipowicz 2014). It is likely that much of the decision-making about a potential marriage partner occurs at a subconscious level, for example, individuals may evaluate the level of genetic similarity or dissimilarity in a potential partner through their body odor (Kromer et al. 2016; Roberts et al. 2008).

Taking an evolutionary perspective, we may assume that the organizational structure of society is to a large extent evolved, which is not to say that the institution of marriage has been hard coded into our genetic makeup via natural selection. It is to say that the social structures that currently exist have succeeded through the trials of many generations, with cultural institutions contributing to that evolution, but not necessarily dictating it. The evolutionary hypotheses that have been put forward in relation to marriage are here dealt with in turn:

Marriage Is a Form of Mate Guarding

In polygynous and monogamous marriage, other males are excluded from sexual encounters with the wife, thereby ensuring the paternity of the children that the husband commits to rearing. It is possible to view marriage as an institutionalized form of mate guarding, which has evolved because the most dominant males are the most successful when it comes to getting married, and it is in their interests to defend in law what might be viewed as the ultimate form of paternalism. But while there is evidence that healthier and more successful males are more likely to marry (e.g., Lipowicz 2014; Goldman 1993), it may be too simplistic to argue that males are the only ones

who are mate guarding within marriages. It has also been argued that women practice mate guarding to secure the resources of their husband, as these are often vital for the rearing of children (Buss 2002).

In comparative studies, we find that monogamous species consistently show less dimorphism than polygynous ones, including in primates (e.g., Clutton-Brock 1985), most likely because males are not engaged in violent combat for access to mates in monogamously pairing species, as compared to polygynous ones. It has been argued, based on the fossil record, that sexual dimorphism declined over the course of human evolution, suggesting that a transition from polygyny to monogamy may have begun prior to the evolution of *Homo sapiens* (Lovejoy 1981). A difficulty with this argument is that polygyny does occur in many human societies, although it may not necessarily be the dominant form of marriage, with many monogamous marriages also occurring within such societies (White et al. 1988).

An issue to consider with mate guarding is that it can imply that one partner is exerting control over the behavior of the other to enforce their loyalty. In these circumstances, it may be in the interests of the guarded partner to circumvent the enforcement and seek extramarital partners. The question of how human behavior is evolved to deal with these issues is an active area of research in evolutionary psychology (e.g., Buss and Shackelford 1997; Shackelford et al. 2006).

Marriage Facilitates Reciprocal Division of Labor in the Raising of Children

The raising of children requires investment of time, energy, and resources – the same time, energy, and resources that are required for one's own survival and well-being. In economic theory, it has been argued that there is a quality-quantity trade-off in the raising of children, whereby parents face a choice of having more children or investing more in fewer children (Becker 1960; Becker and Lewis 1973). The principle that humans must raise socially competitive offspring means that parents must balance family size against offspring success (Lawson and Mace 2011). If we also take into account sexual

selection – whereby individuals of the highest perceived quality are those who gain the greatest reproductive success – we see the importance of investing in the development of children. For parents, the question is how to provision children with an optimal level of investment while still producing enough children that the risks of not leaving any genetic heirs are too high.

It has been argued that humans would never have evolved without the combined effort of males and females to raise children, given the very long phase of infancy and the demand that this places on parents (Hrdy 2011). This is also the argument put forward by Fortunato and Archetti (2010) based on inclusive fitness theory—that monogamous marriage is an evolutionarily stable strategy for the allocation of resources to the next generation, promoting the survival of offspring by not fragmenting inherited resources. The importance of female choice and faithfulness in the development of monogamous pair-bonding systems (as compared to promiscuous mating systems) is emphasized by Gavrilets (2012), because providing for a female and her offspring becomes a viable strategy for low-ranked males to increase their reproductive success.

Marriage Reduces Transmission of Diseases Through Sexual Intercourse

The close proximity and exchange of bodily fluids involved in sexual intercourse is a powerful means by which human diseases are transmitted. There are numerous examples of bacterial (e.g., gonorrhea and syphilis) and viral sexually transmitted diseases (STDs) (e.g., genital herpes, hepatitis, and HIV). The impact of STDs ranges from irritation to premature death, with many causing chronic debilitation, infertility, and even damage to unborn children. It is for this reason that natural selection may favor monogamous over promiscuous behavior, simply because those with a tendency for promiscuity suffer higher mortality and morbidity through disease (Bauch and McElreath 2016).

In smaller groups, with a small degree of mixing with other groups, disease transmission would have been less of a problem, as may promiscuity, but as the human ancestor transitioned to

a bipedal ape, able to cover long distances and make contact with far flung groups, the potential for the transmission of disease would have increased, and we can hypothesize that less promiscuous behavior would have been favored by selection. In the modern world, STDs are abundant, and there is little doubt that promiscuity, including unprotected extramarital sex, increases the human disease burden (e.g., Reniers and Watkins 2010).

Marriage Is a Reciprocal Care Relationship

A number of studies have identified that married persons tend to live longer than singles (e.g., Hu and Goldman 1990; Lillard and Waite 1995), though the exact reasons for this are not clear. There are broadly two theories to explain the phenomenon. The first is that marriage itself has a protective effect on survival, through the support network and socioeconomic advantages that it brings. The second theory is that there is selection into marriage of individuals who are likely, even prior to marriage, to live longer, because of a high-quality genetic or physical profile, which also makes them attractive to the opposite sex.

It has proved very difficult to disentangle the protective effect of marriage from selection into marriage, because individuals move in and out of the married category, while the impact of becoming widowed or divorced may be more harmful to health and longevity than remaining as a lifetime single (Ben-Shlomo et al. 1993; Tucker et al. 1996). It appears, however, that marriage is more beneficial for men, in terms of its effect on longevity, particularly when men are married to younger women (Drefahl 2010; Foster et al. 1984; Gellatly and Störmer 2017).

Indications are that women exhibit a stronger preference for an older man in their first marriage than men do for a younger woman (Bozon 1991), which possibly relates to the desire for a “provider.” However, it may be the case that women are choosing men who, having lived longer, have demonstrated their survival and their ability to acquire skills or wealth. It might similarly be in men’s interest to select among older women, who have had longer to demonstrate their survival abilities, except that there is a shorter reproductive

window for women, which causes men to select more heavily on traits associated with fertility.

Conclusion

The importance of family formation and raising of children is no doubt fundamental to the existence of marriage, but we must also consider that reduction of disease transmission, mate guarding, and reciprocal care are important contributory factors to the existence and benefit of marriage.

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Benefits of Distractibility

- [Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches](#)

Benefits of Gossip

- [Social Consequences of Initiating Gossip](#)

Benefits of Profound Kinship Connectedness (and Problems from a Lack Thereof) Through an Evolutionary Mismatch Lens

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Synonyms

[Advantages of having close blood and affinal relationships](#); [Disparity between the prehistoric environment and the current one](#); [Issues associated with not having intimate bonds with one's relatives](#)

Definition

Being physically and emotionally close to one's kin was instrumental for ensuring well-being and

survival in the brutal ancestral context. Although the contemporary world is generally a much more secure and socially progressive place to live in, the lack of adequate support from one's kin (which are relatively more evident in the present day as people become more independent from their kin due to greater perceived safety and opportunities) might nonetheless still lead to adverse consequences for the affected individual (as relatives are still principally more likely to aid him/her across a variety of life domains than non-kin).

Introduction

Throughout the course of evolutionary history, *Homo sapiens* have generally lived in small closely knitted groups comprising predominantly of biological and affinal relatives (Hill et al. 2011). Within these groups, both biological and affinal relatives have a vested interest evolutionarily in the survival and reproductive success of the individual (the latter category of relatives being indirectly concerned as a result of a shared interest in the well-being of one's descendant/s with whom they are genetically affiliated) (Hughes 1988). Maintaining a strong emotional connection with these kin and living one's life in close proximity to them were predictably helpful in reducing the risk of injuries/death and in enhancing the chances that one would subsist long enough to propagate his/her genes into the future generations in the typically harsh, unpredictable prehistoric world (where food was infrequently available and threats from predators/rival tribes were prevalent); vice versa.

However, due to the tremendous transformations in terms of the physical and societal conditions in the recent era (e.g., the virtual elimination of all natural predators in numerous parts of the world and the perceived availability of a massive array of attainable resources in the globalized information age), many humans are now venturing away and residing independently from their kin (while not always maintaining a close connection to them) (e.g., Hank 2007). Such a relative lack of physical and emotional

bonds with one's kin are expected to result in a range of negative repercussions primarily because *Homo sapiens* are not yet evolutionarily prepared (in terms of cognitive and social capacities which will require countless generations to evolve) to function just as competently in a context that is largely devoid of kin (O 2018a).

Effects of (a Lack of) Close Connections with Kin in the Modern Environment

Despite massive changes in the social and physical spheres of the world since prehistory, humans in the present context are still believed to be more likely to help and support their kin across a vast range of life domains than non-kin as the welfare of the former is pivotal in the direct/indirect dissemination of one's genes into succeeding progenies (Hughes 1988). Indeed, a variety of studies conducted on modern-day humans has corroborated such a premise. For instance, kin were reported to be more inclined to provide an individual with considerable amount of useful resources (e.g., lending him/her a massive sum of money) in times of need as compared to non-kin (including friends) in contemporary societies (e.g., Fitzgerald and Colarelli 2009). In addition, modern-day humans have revealed that they were generally more prepared to assist relatives, rather than those who were not related to them, in their search for a stable partner (Jonason et al. 2007); and research work has appeared to suggest that they were also more committed and nurturing when looking after their kin's offspring as compared to those from non-kin (e.g., Sallnäs et al. 2004). Likewise, contemporary humans have also indicated a greater desire to save their kin (instead of non-kin) from a serious life-threatening situation (e.g., saving him/her from a building that was on fire) (Burnstein et al. 1994).

In light of such a diverse array of highly-valuable assistance that could potentially be rendered by one's kin, it is imaginable that the absence of intimate physical and emotional

bonds with them in the present day would lead to a host of negative outcomes for the individual. Because many individuals presently have kin who are located relatively far away, and that many may also not have a strong emotional connection to their relatives due to a lack of regular interactions over the years (e.g., Hank 2007) – which was a factor that has been empirically shown to be positively related to one's propensity to help (Rachlin and Jones 2008), these individuals are expected to be more at risk of experiencing unresolved issues regarding insufficient resources (e.g., they might have encountered some forms of financial difficulties and are struggling to raise enough money to clear their large debts within a strict time frame) than their counterparts who are residing near to (and have maintained close links with) their kin. Analogously, these individuals are believed to be more likely to struggle to find a suitable long-term partner (and could hence remain single and childless as a result) or could conceivably find it harder to cope with balancing work and parenting duties if they have children, in the absence of the valuable assistance from their kin. Furthermore, these individuals are likewise postulated to be more likely to die without their kin around them if they are unfortunate enough to be involved in a life-threatening situation (e.g., being trapped in rising waters after a flood). In fact, it was predicted that these individuals are also more susceptible to be successful suiciders (if they are actually contemplating to kill themselves as a result of some severe emotional distress) due to their faraway kin not being nearby to intervene adequately in a swift manner (O 2018b).

Conclusion

On the grounds that kin were generally more inclined to be concerned about one's welfare (as compared to non-kin) across human prehistory (even in the modern day), the evolutionarily novel relative absence of close physical and emotional contact with these individuals are believed to significantly affect one's functioning (and

possibly survival) and reproductive success in the current context.

Cross-References

- ▶ [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
- ▶ [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)
- ▶ [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)
- ▶ [Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches](#)

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Benefits of Short-Term Mating

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Synonyms

Intersexual selection; Mate preferences; Sex differences

Definition

Direct and indirect benefits of engaging in short-term mating relationships.

Introduction

According to sexual strategies theory (SST), men and women evolved to adopt mating strategies that were aimed to solve recurring adaptive problems faced ancestrally (Buss and Schmitt 1993). Since men and women differ in their reproductive biology, sex differences are a fundamental component of SST, and therefore, the biological differences between the sexes influences the temporal dimension of mating strategies. For women, the heavy investment of pregnancy and child rearing means that reproduction is a costly process, whereas men only invest in sperm production, and paternal investment is not always certain. These sex differences in reproduction factor into the mating strategy utilized by men and women, as maximizing reproductive success may be favored by the least investing sex and maximizing parental investment may be favored by the more investing sex. Although humans engage in both short-term (i.e., casual sex, extra-pair infidelities) and long-term (i.e., pair bonding, long-term commitment) mating strategies, what benefits can be obtained from utilizing a short-term mating strategy in both sexes? What

characteristics in a potential mate do individuals rely on when assessing short-term mating relationships? And lastly, what evidence exists on utilizing a short-term mating strategy in both sexes?

Men's Short-Term Mating Benefits

Biologically, men are the least investing sex, which according to parental investment theory should influence their differential reproductive success in being less discriminate in mate choice (Trivers 1972). Being less discriminative in mate choice does present challenges. One adaptive problem men have faced in mating has been in identifying which women were fertile, considering the role of cryptic or concealed ovulation. Women do not display overt cues indicating fertility as other nonhuman primates do, therefore recognizing cues that indicate fertility would have been an advantage for men's reproductive success. Additionally, being able to identify which women are accessible while decreasing commitment and risks associated with mating have been key restraints. Given these key restraints, mating strategies should be influential in maximizing reproductive success, such as pursuing a short-term mating strategy that aims to pursue quick sexual encounters with minimal commitment. For instance, men's mating psychology that express desire for an increased number of partners, interest in sex after a short period of time of knowing women, and relaxing their mate preferences for short-term mating have been supported by research using sexual strategies theory (Buss and Schmitt 2019).

What are some of the benefits associated with pursuing a short-term mating strategy in men? For men, maximizing differential reproductive success through indirect benefits (i.e., genetics) is an advantage in short-term mating. Men can increase their reproductive success by 50% if involved in a short-term mateship, which is of course dependent upon the survival of the child from conception considering the rough environmental conditions that would have been present during ancestral times (Buss and Schmitt 1993). Nevertheless, an

immense amount of research, both descriptive and experiential, have found strong support for men's desire to engage in short-term mating and to allocate importance to characteristics associated with genetic benefits (e.g., physical attractiveness). This suggests that the heritability of physical characteristics is an important consideration for men when pursuing short-term mating strategies. Physical characteristics, such as full lips, clear skin, symmetry, and low waist-to-hip ratios, are informative traits men rely on to solve the adaptive problem of concealed ovulation, and they are often the standards of attractiveness that are placed on women (Buss and Schmitt 1993).

Empirical evidence has shown men's prioritization of physical characteristics for short-term mating. Sexual dimorphic features in women, such as feminine facial characteristics, are often preferred over masculine facial features during a short-term mating context (Grammer and Thornhill 1994; Little et al. 2011). Feminine facial features advertise reproductive cues, and therefore, preferences to these features would directly be associated with men's reliance on physical traits in short-term mating for maximizing reproductive fitness. However, there are differences in the importance of physical characteristics when asked to prioritize facial features in comparison to bodily features. Although feminine facial features are often preferred, given the role of estrogens in facial femininity, they may convey reproductive value, as opposed to current reproductive fertility. Experimental studies have shown that men prioritize bodily over facial cues when asked to consider a potential mate for a short-term over a long-term mating context (Confer et al. 2010; Jonason et al. 2012; Perilloux and Cloud 2019). Studies incorporating behavioral ratings, such as eye tracking procedures, have also shown men's interest to specific features associated with fertility where visual attention is centered on ideal waist-to-hip ratios (Dixson et al. 2011). Research using fMRI has highlighted important areas of the brains associated with reward processing, most notably the nucleus accumbens, when viewing women who advertise physical features associated with fertility (Platek and Singh 2010).

Although certain physical features may connote fertility in women, men's preferences for these features is influenced by life history factors, such as ecological conditions. The ecology of one's environment provides cues of the availability of resources, and individuals may trade-off choosing a partner with good genes over one who is willing to invest. Under a harsh ecological condition, choosing a partner who is willing to invest may be a better strategy, since sharing resource pools may provide offspring with better survival, whereas in a safe ecological condition, conditions are conducive to better survival and choosing a partner with good genes may be a better mating strategy (Geary et al. 2004), favoring short-term mating. In contrast, in harsh ecological conditions, short-term mating may be an optimal strategy, as the risk of mortality is high and cues in the ecology may prompt individuals to adopt a strategy favoring early reproduction (Belsky et al. 1991). For short-term mating, men have shown a preference to feminine women during harsh ecological conditions, suggesting that ecological cues prompt a faster reproductive strategy in difficult environments. Safer environments prompt men to choose women who display masculine facial characteristics, where men choose low-quality but high-investing mates (Little et al. 2007).

For men, pursuing a short-term mating strategy increases the likelihood of reproductive success because multiple matings are more likely to lead to more offspring as opposed to a long-term investment with one partner (Trivers 1972). Although men have an evolved preference for short-term mating given the different adaptive problems faced between the sexes, mating behaviors reflect these preferences. For instance, men are more willing to agree to a sexual proposition when asked by women; however, when women are given the same proposition by men, the response is not mutual (Clark and Hatfield 1989). Men are more likely than women to seek out prostitution services, and their preferences for physical characteristics in prostitutes are reflected in short-term mating research. For instance, prostitutes that display ideal physical features, such as low BMI, medium breast size, and youthfulness

are more valued, as indicated by the prices of services (Prokop et al. 2018; Sohn 2016). Altogether, men's prioritization on physical characteristics indicate that benefits associated with short-term mating are geared to maximize reproductive success as evidenced by preferences to features associated with fertility and reported behaviors for casual sex.

Women's Short-Term Mating Benefits

Since women are the most investing sex biologically, they gain more from being discriminatory in choosing the best fit mate. By being choosy in mate choice, they can choose a partner that displays high quality or a partner that displays parental investment. When pursuing a short-term mating strategy, women have faced mate selection problems, such as finding a mate who can provide immediate resources, good genetics, and mates who may serve as backups from current relationships (Buss and Schmitt 1993). According to strategic pluralism theory, short-term mating carries the trade-off of choosing a mate who displays good genetics over parental investment. Since women's reproductive success is dependent on ovulatory status, mating strategies may be calibrated to maximize reproduction during peak fertility. Several studies have shown that women's mating strategies influences their preferences for types of men that display features of good genetics and men who are can provide immediate resource acquisition, and short-term mating strategies may be preferred when fertility is optimal.

What are some of the benefits associated with pursuing a short-term mating strategy in women? One benefit of short-term mating is the heritability of good genetics from choosing a mate who displays high quality features. Good genes, such as masculinity, muscularity, and symmetry, are features women find ideal when pursuing a short-term mating strategy, known as the good genes hypothesis (Buss and Schmitt 2019). Sexual dimorphic features, such as pronounced brow ridges and jaw line, are phenotypic markers of increased testosterone, and given testosterone's immunosuppressant effects, women use these

cues in men as honest signals of immunocompetence (Folstad and Karter 1992). That is, men who display these masculine features can afford the immunosuppressant effects of testosterone. Preferences to these physical characteristics have been largely supported by research, both descriptive and experimental. When asked to choose between men who display masculine versus feminine facial features, women choose masculine facial features when pursuing short-term mating (Jones et al. 2018). Other features associated with good genes, like physical attractiveness, has also been preferred by women when considering men for a one-night stand compared to a long-term relationship (Kenrick et al. 1993). Since short-term mating is likely to lead to immediate sexual access, women's mate choice has shown to maximize physical characteristics that signal genetic heritability if reproduction were to occur.

However, preferences for masculinity in men may reflect women's short-term mating strategy in solving the adaptive problem of immediate resource acquisition. Men who display formidable features such as muscularity are considered stronger, and strength is an important contributor in resource acquisition (Puts 2010) and men's attractiveness (Sell et al. 2017). Men with muscular (i.e., mesomorphic) body types are preferred and are rated as more attractive by women with short-term mating strategies (Provost et al. 2006, 2008). Women's preferences to muscularity have also been reflected in their viewing behavior when assessing men as potential mates. Using eye tracking to assess attentional biases to men's physical characteristics, women focus most of their viewing time to the chest region of men's bodies, a region associated with formidability (Durkee et al. 2017; Pazhoohi et al. 2019). Additionally, women who pursue short-term mating strategies have shown to attend to the chest region longer (Garza and Byrd-Craven 2019), suggesting that short-term mating strategies not only influences mating preferences but actual behavior.

Short-term mating preferences in women have been shown to be affected by the reproductive cycle. In humans, reproduction can only occur when fertility is high, and mating effort has been shown to shift during times of peak

fertility, known as the ovulatory shift hypothesis (Thornhill and Gangestad 1999). This hypothesis suggests that during peak fertility, women should prefer men with characteristics associated with good genetics, such as physical attractiveness and muscularity (Gangestad et al. 2007). Research has shown that women assess men with ideal physical characteristics as more attractive for short-term mates near ovulation (Gangestad et al. 2007). A large-scale meta-analysis study has also supported fertility shifts in short-term mating to high-quality men. When assessing a partner as a short-term mate, preferences for physical characteristics indicative of genetic quality were strongest during peak fertility, more specifically for body masculinity and men who display social dominance (Gildersleeve et al. 2014).

Other research has pointed to the role of life-history strategies and women's calibration of mating strategies for men with ideal physical traits. For instance, when considering ecological conditions, it may be beneficial to pursue a short-term mating strategy when there are limited resources. Experimental research has demonstrated that women prefer masculine facial features for short-term relationships in safe compared to harsh ecological contexts (Little et al. 2007; Marcinkowska et al. 2018), suggesting that safer environments provide women with increased offspring survival, therefore channeling their investments to high-quality men. This trade-off for good genes over parental investment suggests that women do not have more to gain from an investing partner if resources are readily available. This finding has also been found in cross-population research when considering measures of safe environments, such as high health and economic indices. Women in more favorable environments prefer men with more masculine facial features (Marcinkowska et al. 2018), and dispositional short-term mating seems to influence these preferences. Since favorable environments are associated with greater sexual openness, women with short-term mating motivations are more likely to express preferences for more masculine partners (Marcinkowska et al. 2018). In contrast, women from harsh ecological conditions have shown to prefer short-term mating when closer to ovulation (Kim et al. 2018), in

line with the perspective that harsher environments decrease offspring survival and pursuing a mate who can invest may not be the most optimal strategy over maximizing reproduction (Belsky et al. 1991). In harsh environments, mortality risk is high, and therefore, choosing a partner who displays good genetics may increase the viability of offspring survival in a difficult environment (Belsky et al. 1991). Furthermore, preferences for masculine men for short-term mating may be a product of securing direct benefits (i.e., resource acquisition, protection) from a partner in a difficult environment.

A function and benefit of short-term mating in women is the possibility of mate switching. The mate switching hypothesis proposes that women engage in short-term mating when currently involved in a relationship to secure a backup mate in case a relationship ends, make it easier to leave the current relationship, trading up in mate value, or to assess one's own mate value in the current mating market (Buss 2016; Buss and Schmitt 2019). There are many reasons as to why women would engage in mate switching behaviors, but one key predictor is relationship satisfaction. Relationship satisfaction predicts women's infidelity and desire for other men regardless of fertility status (Gangestad et al. 2005), suggesting that switching mates for good genes may not explain short-term mating behaviors in women currently in relationships. Other research has shown that interest in other men when currently in a relationship is influenced by sex with current partners, as lack of sex with current partner increases desire for other men (Pillsworth et al. 2004). Moreover, women who reported their partners low in sexual attractiveness were more likely to report extra-pair desires; however, this was not likely to occur if they reported their partners to be high on investment attractiveness (Pillsworth and Haselton 2006). Women involved in mate switching may be interested in characteristics associated with long-term investment that are not currently provided by their current partner. Being involved with a partner who is not economically successful and meeting a potential mate who is more successful than their current partner are all inclinations associated

with infidelity (Greiling and Buss 2000). Women have also reported their ideal traits in an affair partner, and they include characteristics indicative of investment, such as being honest, stable, and dependable (Greiling and Buss 2000; Kenrick et al. 1990).

Conclusion

Short-term mating strategies provide different benefits to each sex. For men, maximizing reproductive success is a benefit, as shown by their preferences to key physical features that indicate fertility and their willingness to maximize mating opportunities. For women, acquiring indirect (i.e., good genes) and direct (i.e., resource acquisition, protection) benefits seem to be influential reasons to engage in short-term mating. However, human mating is incredibly nuanced, as contexts, culture, and individual differences drive preferences for engaging in short-term mating strategies. Nonetheless, sexual strategies theory (SST) provides a framework for why humans engage in different mating strategies, as well as identifying the benefits obtained from choosing one strategy over another.

Cross-References

► [Sexual Strategies Theory](#)

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demonstrates how traits that harm individual organisms can be maintained by natural selection; thus, an organism can, therefore, increase genetic representation in future generations even if that organism fails to reproduce (Liddle et al. 2011). There is evidence to suggest that suicide terrorism can function to benefit the fitness close kin.

Benefits to Kin

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Synonyms

[Inclusive fitness](#); [Kin selection](#); [Terminal altruism](#)

Definition

One evolutionary theory of suicide terrorism proposes that the act is committed in order to benefit the close kin of the attacker.

Introduction

Suicide terrorism is a politically motivated aggressive act wherein the perpetrator willingly sacrifices his or her life with the goal of inflicting harm on typically civilian casualties. One evolutionary theory of suicide terrorism proposes that terrorist organizations manipulate followers into embarking on suicide missions in order to benefit genetic kin. This theory of suicide terrorism is rooted in kin selection (Smith 1964), a form of altruism based on Hamilton's rule ($rb > c$) where r is the degree of genetic relatedness, b is the reproductive benefits to related kin, and c is the cost to the agent (Hamilton 1963). According to this theory, an organism should act altruistically when the reproductive benefits to its kin are greater than the costs of the act to the organism. Kin selection

Theoretical Overview: Suicide and Benefits to Kin

Though there is scant data on suicide in non-human animals, self-sacrifice through death is evidenced in a variety of species such as sterile castes of the order Hymenoptera for the purpose of colony defense (Preti 2007). Likewise, in *E. coli* self-sacrifice might function to limit the transmission of a bacteriophage to related organisms (Refardt et al. 2013).

In regards to humans, psychologist Denys deCatanzaro proposed that one with low reproductive potential who is imposing net fitness costs on biological kin would improve his or her inclusive fitness by committing suicide (de Catanzaro 1981; 1984; 1991). Though theorists have not directly applied deCatanzaro's inclusive fitness model to suicide terrorism, aspects of the model are relevant. Moreover, the end goals are identical: to increase fitness by increasing the reproductive success of close genetic kin at a cost to the self. A suicide terrorist should have relatively low reproductive potential (e.g., poor prospects for mating opportunities) such that the reproductive benefits to kin should outweigh the costs to the suicide attacker. There are two means through which attackers might benefit their kin that when combined are unique to the context of suicide terrorism: monetary compensation and heightened familial reputation.

Terror organizations such as Hamas and Hezbollah promise to provide financial compensation to the families of prospective suicide attackers. As of 2002, Hamas, for instance, paid the families of suicide attackers between \$10,000 and \$25,000 and often in addition offered medical services. In cultures such as those in the Middle East, this money can contribute to bride's wealth

wherein the groom provides payment to the bride's family in the form of money, goods, or other services. Thus, financial gains to one's siblings can promote their reproductive success, which might factor into the decision of one to opt into suicide terrorism or for a parent to encourage offspring to execute such missions. Blackwell (2006) modeled the inclusive fitness benefits of suicide terrorism, finding that theoretically suicide terrorism can incur inclusive fitness benefits, particularly in large, middle class families with many males. In fact, suicide attackers and their families tend to be wealthier on average than their social counterparts (Krueger and Malečková 2003).

Heightened social reputation is another asset that is bestowed upon the families of suicide attackers that might benefit their fitness. Motivations such as these could be fostered through cultural values such as collectivism and honor-based codes of conduct, which are endemic to regions where suicide terrorism is found. In fact, honor cultures strongly encourage retaliation against external threats and aggressors for the sake of both the individual and their social group, and evidence suggests that such strategies could be evolutionarily stable in certain contexts (Nowak et al. 2016). Suicide terrorism is a form of political retaliation typically employed to combat more powerful opponents (Pape 2005; Hafez 2006). In these communities, members celebrate suicide attackers as religious "martyrs" and heroes of their homeland, and they might devote shrines and websites to honor their sacrifice (Hafez 2006). The reputational benefits often extend to the kin of the suicide attackers, which could confer reproductive benefits such as additional income and access to mates. At present, however, data is lacking to sufficiently demonstrate that the reputational benefits of suicide attack translate into inclusive fitness benefits.

Conclusion

Empirical evidence indicates that suicide terrorists might be motivated to benefit their kin through the attack, thus increasing their inclusive fitness. However, more research is necessary to confirm these models.

Cross-References

- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Benevolence

► Benefit to Another at Cost to Self

Bereavement Following a Child's Death

► Death of Healthy (vs. Sick) Child Followed by More Grief

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Synonyms

[Mate Choice](#); [Symmetry](#)

Definition

Physical signals of attractiveness in humans

Introduction

The work of Bernhard Fink and his collaborators has a clear focus on the sexual signals that are revealed via our physical bodies. Based on the assumption that what is deemed physically attractive is by and large universal, Fink's research attempts to uncover what adaptive information these attractive physical traits are signaling to potential mates.

Facial Attractiveness, and 2D:4D Ratio

One such physical trait is our faces, and what they may signal in mate choice. In a review,

Fink and Penton-Voak (2002) examined previous research in an attempt to identify what features of faces make them attractive. They conclude that the key features include symmetry, indicators of hormone levels (such as testosterone), and "averageness". Evolutionary psychology suggests that such features act as reliable cues of an individual's health, an important trait in mate choice, thus making them attractive (Fink and Penton-Voak 2002).

Drawing on one of the above facial features, symmetry, Fink et al. (2004) examined what this may signal about an individual's developmental stability, which could account for its role in mate choice. Using 2D:4D ratio as a proxy indicator of fetal hormonal environments, they found that this was significantly related to facial asymmetry, but in opposite directions for men and women. Fink et al. (2005) further investigated how 2D:4D ratio interacts with facial features differently between men and women. By comparing key facial characteristics with 2D:4D ratio in a sample of men and women, Fink et al. (2005) found that prenatal hormone levels affect men and women's faces differently. Also, although 2D:4D ratio affected men and women's face shapes in a similar manner, this effect was three times stronger for men. From these findings, it can be concluded that facial (a)symmetry and shape acts as an important and honest signal of quality due to its links to the early developmental environment of individuals (in terms of fetal testosterone/estrogen levels), thus accounting for their importance in attractiveness judgments.

Furthermore, Fink et al. (2001) examined if skin texture of faces affects their perceived attractiveness. It was found that men's judgments of the attractiveness of women's faces varied in response to differing skin texture, which, Fink et al. (2001) conclude, shows that skin texture acts as an honest cue of good health and fertility. Likewise, Fink et al. (2006a, b) showed that facial skin coloration also influenced attractiveness ratings. They found that skin color distribution influenced perceptions of women's age (thus acting as a signal of youth) and also judgments of their attractiveness and health.

Body Morphology and Movement

However, what do facial features related to attractiveness reveal about the rest of the body, and how may the rest of the body influence physical attractiveness? To answer the former question, Fink et al. (2006b) sought to find out how facial indicators of psychological traits of attractiveness, masculinity, and dominance may relate to the actual physical trait of strength. They found that men's hand-grip strength did indeed positively relate to women's ratings of their perceived levels of all three psychological traits. Therefore it seems that there exists clear links between signals from faces and from bodies that can play a key role in mate choice. This is further supported by Fink et al. (2010) who found that ratings of attractiveness, masculinity, and dominance in men's faces were positively correlated with the same ratings in the bodies. Therefore Fink et al. (2010) conclude from this that it is the same mechanisms that cause the development of such cues in both men's faces and bodies, thus contributing to them both being important sources of sexual signals of attractiveness in mate choice.

In terms of how the body may physically signal attractive traits for mate choice, Fink et al. (2014) found a positive relationship between men's body symmetry and their physical hand-grip strength. As physical strength will be a desirable trait in sexual selection (for both inter- and intrasexual selection) and be an honest indicator of quality, it will develop together with other indicators (such as body symmetry) to play a role in attractiveness in men. More recently, Fink has explored how perceptions of physical signals of quality in bodies are influenced by the signaler's body movements. In an early investigation, Fink et al. (2012) took measurements of men's personality traits and also recorded them dancing to a simple rhythm. After anonymizing the recordings, these were then shown to a sample of women to rate for the quality of the dancing. Fink et al. (2012) found that women's assessments of the quality of dancing correlated with a number of these traits, suggesting that such body movements may be able to act as an honest signal of other underlying

characteristics. Subsequent research shows that dance quality can also signal traits that positively relate to men's attractiveness, such as physical strength (Weege et al. 2015). This suggests that future research into sexual signaling of physical traits in men should incorporate moving as well as static cues, as humans of course do in the real world.

Conclusion

The work of Bernhard Fink and various colleagues have been pivotal in making the connections between physical signals in our bodies, what these signals relate to, and how and when these are viewed as attractive in mate choice. This is central to the view of evolutionary psychology that what is attractive is universal and has an adaptive value in sexual selection. Furthermore, recent investigation into movement via dancing quality offers a novel approach to research into attraction, and through utilizing modern technological advances, Fink and colleagues offer a clear sense of how humans realistically view potential partners in mate choice.

Cross-References

- [Body Attractiveness](#)
- [Facial Attractiveness](#)
- [Fluctuating Asymmetry](#)
- [Physical Attractiveness](#)

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Betrayal

- ▶ [Human Deception](#)
- ▶ [Prisoner's Dilemma Outcomes](#)

Better Genetic Material

- ▶ [Good Genes](#)

Better Never to Have Been

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Synonyms

[Antinatalism key text](#); [Antinatalist philosophy of David Benatar](#)

Definition

A book by the philosopher David Benatar, published in 2006, advocating the antinatalist claim.

Introduction

According to David Benatar, it is “better never to have been” and it would be morally better if the human race was extinct. That is, coming into existence always causes serious harm to the individual, and therefore, procreating is always morally wrong (the antinatalist claim). In this way, it would be best if the human race became extinct as then there would be no one to suffer this harm. This is not to say that the antinatalist claim is one that promotes human death (mass suicide, genocide or speciocide, devastating natural disasters, etc.). In some cases, the antinatalist would support the death of an individual but typically only when the individual is experiencing immense suffering and would prefer to die sooner rather than later. This is not a particularly radical view and many, if not most, people would concur in at least some possible cases. Instead, the antinatalist is against the creation of new lives and not (necessarily) the premature end to existing lives. The word “premature” is particularly significant as, again, it is important to keep in mind that every single person that is born will die at some point. Therefore, if the antinatalist ideal was realized, this would actually reduce death as there would be no more people to die. In this way, the view that death is typically a bad thing is proposed to be supportive of the antinatalist claim as procreators effectively create a death every time they create a life: As anyone who is born will eventually die, extinction would technically minimize death overall as once extinction is achieved, there will be no more death.

Antinatalism

Although death is – more often than not – an extremely unpleasant and painful experience, it is not the only suffering an individual will

experience by coming into existence, and it is suffering that is particularly central to the antinatalist claim. If you consider an existing person first, when they experience pain, it is clearly bad and when they experience pleasure, it is good. Likewise, when they are deprived of experiencing pleasure, it is bad and when they are “deprived” of experiencing pain, it is good. These axiological values could theoretically be weighed and summed to produce an overall axiological value of a particular life relative to an alternate life. That is, it is easy to evaluate a person’s life as better if they experience more pleasure and/or less pain than an alternative life. However, this logic relies on comparing one possible life to another possible life and has the underlying assumption that there *has* to be some sort of life: It is this aspect that the antinatalist claim refutes. Instead, the antinatalist claim considers the axiological value (the abstract value and “goodness” of all varieties) of *any* possible life to *no* life at all. When there is no person, there is nobody who can be directly benefitted or harmed. Therefore, the point of reference for a comparison is drawn solely from the scenario when a person would have existed. Essentially the claim is comparing two possible worlds rather than two possibilities within one world: one world in which a person exists and one in which that same person does not exist. We then evaluate which world is better with reference to the interests of this individual (Benatar 2013, p. 125). As the individual only exists in one of these two possible worlds, that world is our point of reference for comparison.

As it is possible to assign an axiological value to one possible life compared to another possible life, the antinatalist reasoning can be illustrated by comparing two such cases and then comparing these to a world where the individual did not come into existence at all. Firstly, when a world where the individual experiences a great deal of pain (a lot of bad) and experiences very little pleasure (very little good) to a world where they never came into existence at all, it is reasonable to conclude that the latter is better. More so, the lack of the pain that *could* have been in this world (had the individual been born) is argued to be a good thing, even though there is

nobody who directly benefits from not experiencing this pain. That is, the absence of pain is considered a good thing even if there is nobody to experience the pain.

Second, when a world where the individual experiences a little bit of pain (a little bit of bad) and experiences a great deal of pleasure (a lot of good) is compared to a world in which this person never came into existence, it may, at first glance, seem reasonable to conclude that the former is better. However, according to the antinatalist claim, this logic does not follow: Benatar asserts that for this world to be better, we would be stating that the *lack of the pleasure* that could have been in this world is clearly a bad thing, even though there is nobody who is deprived of experiencing this pleasure. However, if there is nobody who is deprived of experiencing this pleasure, then the lack of pleasure in the later world is not, according to the antinatalist claim, axiologically bad. Conversely, it is proposed that the lack of the small amount of pain that the individual would have experienced is still a good thing even though there is nobody who is benefitted by not experiencing this pain (as with the first world considered but to a smaller scale). Therefore, even in this case where there would only be a little pain, it is still proposed by the antinatalist that it is actually also better if this person had never existed: That is, it is not bad that they do not experience the pleasure they would have if they had existed (no matter how much pleasure there would have been), but it is still good that they avoid the pain they would have experienced if they had existed (no matter how small the amount of pain would have been). Although it is clearly not *as much of a good thing* that this person did not exist in the second world than it is that they did not exist in the first world, in both cases not existing, it is still deemed better than existing. Essentially, this logic forms the basic asymmetry in axiological value between possible worlds that justifies the antinatalist claim: Coming into existence always causes harm to the individual because the absence of pleasure is only bad when there is someone who is being deprived of that pleasure, but the absence of pain is good even if there is

Scenario A (X exists)		Scenario B (X never exists)
(5) Absence of Pain (Good)	(1) Presence of Pain (Bad)	(3) Absence of Pain (Good)
(6) Absence of Pleasure (Bad)	(2) Presence of Pleasure (Good)	(4) Absence of Pleasure (Not bad)

Better Never to Have Been, Fig. 1 Replication of “The basic asymmetry amplified” (Benatar 2013; pg. 136)

nobody around to benefit from its absence, so it is not possible for the axiological value of existing to outweigh not existing (see Fig. 1; the asymmetry manifests between cell #4 and cell #3 and #6). Benatar’s antinatalist claim has been challenged by other philosophers. For example, Bradley (2010) points out that when considering “betterness,” the laws of logic (citing the Albert Brogan and G. H. von Wright view) dictate that the presence of pleasure in existing people is *better* than the absence of pleasure in nonexistent people, even if the absence of pleasure in non-existing people is considered neutral (see also Harman 2009).

Conclusion

“Better Never to Have Been” is a book by the philosopher David Benatar advocating the anti-natalist claim that it would be better for the human race to stop reproducing and become extinct. The argument is based on a logical asymmetry when comparing two theoretical worlds: one where a person exists and the other where they do not exist. Although the presence of pleasure in the first world is a good thing and the absence of pain is a good thing in both worlds, the absence of pleasure is only a bad thing (as deprivation) in the world where the person exists and the absence of pain is greater (i.e., no pain at all) in the world where they do not exist. The text is highly controversial and its logic challenged.

Cross-References

- [Anti-natalism](#)
- [Child Abuse](#)
- [Child Homicide](#)
- [David Benatar](#)
- [Responsibility for Child Suffering](#)

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Between-Community Raiding

- [Chimpanzee Raiding](#)

Between-Group Competition

- [Competition Between Groups](#)

Between-Group Hierarchy

- [Social Dominance Orientation \(SDO\)](#)

Between-Group Killing

- [Humans: Between-Group Conflicts](#)

Bias

- [Prejudice](#)

Biased Grandparental Investment

- [Grandfather Investment Versus Grandmother Investment](#)

Biases

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A cognitive bias refers to any systematic deviation from accuracy or “rationality” in judgment and decision-making. Some commonly examined biases include the following: *confirmation bias* (the tendency to interpret new evidence as confirming one’s existing beliefs); *hindsight bias* (the tendency to overestimate one’s ability to have forecasted known outcomes); *base rate neglect* (the tendency to ignore general frequency information and instead focus on specific information); and *sexual over-perception* – the tendency for men to over-perceive sexual interest in others.

Simon (1955) first proposed that people use simple mental shortcuts (*heuristics*) for judgment and decision-making, leading to what appears to be biased decision-making. The “heuristics-and-biases program” achieved greater prominence as a result of the publication of Tversky and Kahneman’s (1974) seminal *Science* paper. Tversky and Kahneman’s work has largely focused on understanding heuristics and biases as *errors* in judgment and decision-making. That is, heuristics and biases were seen as violations of the standard utility-maximizing “rational” economic model of decision-making. However, this approach of understanding heuristics and biases as “errors” rather than products of adaptive decision-making processes has been widely criticized, especially by evolution-minded researchers.

A more contemporary, evolution-informed understanding suggests that cognitive biases may arise for three possible reasons. First, the use of mental shortcuts (*heuristics*, which reflect bounded rationality) may have systematic breakdowns, which lead to errors. Second, some errors in decision-making may have had (historical) asymmetries in their fitness cost, with the consequence that organisms evolved to favor errors that had the lowest net cost (manifesting in *error management biases*). Third, people may appear to make systematic errors because the laboratory tasks or evaluation standards used to measure such “errors” were unnatural and incompatible with the design of the human mind (manifesting in *artifacts*; reviewed in Haselton et al. 2009). In the following, we review each source of cognitive bias briefly.

Biases as a Product of Bounded Rationality

Traditional economic utility-maximizing models of decision-making assume that actors have accurate and complete information, enough time to assess all decision alternatives, and enough cognitive capacity to go through a complete deductive process. The *bounded rationality* approach suggests that most decisions are products of simple

heuristics that are cognitively efficient and robust to diverse environments (Gigerenzer and Selten 2002). Moreover, research has demonstrated that heuristics often have high ecological validity. Some evidence suggests that heuristics operating on limited information are superior to decisions made with complete information (e.g., Gigerenzer and Goldstein 1996; reviewed in Todd and Gigerenzer 2007). However, while effective in a wide variety of circumstances, heuristics are prone to breakdown in systematic ways, leading to biases in judgments and decision-making (Tversky and Kahneman 1974).

The hindsight bias, for example, has been demonstrated to be at least partly a product of bounded rationality. This bias has been hypothesized to be a product of a memory-updating heuristic when decision-makers do not have access to memory cues. Supporting this hypothesis, the hindsight bias is reduced when participants are given relevant memory cues (reviewed in Blank and Nestler 2007). Some theorists argue that biases resulting from heuristics are due to the methodological neglect of decision environments. They argue that cognitive abilities were designed for specific environments and problems, and that these abilities cannot be properly understood or assessed when studied out of context (e.g., Gigerenzer et al. 1999). Expanding on the importance of ecological rationality, evolutionary theorists posit that ancestral environments should also be considered when investigating biases.

Error Management Biases

Error management theory (Haselton and Nettle 2006) suggests that some biases reflect adapted preferences for errors with lower fitness costs. When inferring the presence or absence of a target in a stimulus, judgments can be falsely positive or falsely negative. However, false positives and false negatives cannot be simultaneously eliminated. Traditional signal detection theory (Tanner and Swets 1954) posits that instruments should instead be biased toward the least costly error. Error management theory thus integrates evolutionary logic and signal detection theory.

Error management theory posits that biases are shaped by historical fitness costs. For example, the sexual over-perception bias can be explained by the potential costs of searching for a receptive mating partner (Haselton and Buss 2000). Falsely perceiving sexual interest (false positive) costs an individual courtship effort, whereas failing to perceive sexual interest (false negative) costs a reproductive opportunity. Since men do not have to make the metabolic investment in gestation and lactation, a missed reproductive opportunity carries a far larger cost than a wasted courtship attempt (Haselton and Buss 2000). Error management theory posits that certain biases exist because of environments and challenges that are proxies of fitness. However, biases can also arise when humans reason in environments that are unfamiliar to the evolved mind.

Biases as Artifacts

Some evolutionary theorists argue that many documented instances of biases are actually artifacts of unnatural research designs. These theorists argue that humans are functionally rational when reasoning about evolutionarily relevant information (e.g., Cosmides and Tooby 1996). However, biases can occur when either the problem format or the problem content is incompatible with a mind shaped by natural selection.

Human bias is often inferred from inaccuracy when estimating probabilities or likelihoods (Tversky and Kahneman 1974, 1983). Biases stemming from innumeracy, for example, might only occur because humans are not suited to reasoning with percentages and probabilities. Humans should be more proficient at estimating likelihoods when they are framed as discrete, naturally occurring events (Gigerenzer 1997; Cosmides and Tooby 1996). For instance, organisms must understand their probability of success when deciding whether to hunt a specific animal. However, organisms did not experience rates of success as percentage values or odds ratios. Instead, successes and failures were likely historically recalled as individual events. For example, consider someone projecting the success of a

hunting attempt. It is likely that inference of the probability of success should be a product of the frequency of recent attempts (e.g., three of the last ten hunting attempts were successful), rather than a product of a percentage probability (e.g., 30% of hunting trips end in success). Consistent with this hypothesis, people are more accurate at making predictions when questions are framed as natural frequencies, rather than probabilities (reviewed in Gigerenzer and Hoffrage 2007). The extant research suggests that many instances of bias might not necessarily be errors. Rather, such biases may be better understood as the consequence of the incompatibility between stimuli and mind.

The heuristics and biases program has demonstrated that human reasoning often deviates from utility-maximization and norms of rationality. Biases can impact outcomes in judicial, economic, and medical settings (e.g., Harley 2007). It is thus important to understand the functional, evolutionary reasons for bias in order to develop effective interventions. Theories that only assume that biases are the result of flaws in the human mind are limited in their explanatory power. By contrast, ecological and evolutionary theories have produced many testable (and empirically supported) predictions about the nature of bias. In particular, cognitive mechanisms that manifest in biases reflect the importance of the historical (and contemporary) structure of decision environments, as well as the importance of problem formats and contents.

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Biculturalism

► Cross-Cultural Similarities

Bidirectional Violence

► Defense Against Attack

Big Brain Evolution

► Brain Size Growth in Humans and Nonhuman Primates

Big Five

► Personality

Big Man

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Synonyms

A man of stature; Standing tall

Definition

“Big Man” is used to signify both an important individual as well as one large in size.

Introduction

The phrase “Big Man” is used to signify both an important individual as well as one large in size, both historically and cross-culturally (Ellis 1992; Murray and Schmitz 2011; Sahllins 1963). Contemporary English language is also riddled with phrases that highlight an association between size and status (or the lack of it) – “a man of stature,” “standing tall,” “he was belittled” – and the phrase “high status” itself incorporates a vertical dimension. This conflation of size and status across many different language groups and cultures has a rather straightforward explanation: On average, those in position of power or high in status tend to be taller and bigger than those who are not. Positive associations between size and status have been observed in all kinds of cultural groupings, from hunter-gatherer groups to agricultural populations to industrialized societies (Ellis 1992; Murray and Schmitz 2011; Sahllins 1963; Stulp and Barrett 2016).

Why Are “Big Men” Big Men?

There are several reasons why bigger or taller individuals tend to reach higher status than those who are smaller and shorter (see discussions in Stulp and Barrett 2016; Stulp et al. 2012, 2015). First, bigger individuals may have some physical superiority over others, allowing them greater access to resources (which typically is taken to signify some form of “status”). This is often corroborated with cross-species evidence: In many species, larger males may display a substantial advantage in fights with other males over access to resources and females (Ellis 1994). A second reason is that size, or at least height, is positively associated with health (Stulp and Barrett 2016). Such an association can arise when favorable childhood growth conditions (plenty of nutritional resources during development) lead to a both a healthier and larger physique. Good childhood conditions may also favor the development of better cognitive skills, leading to a positive association between height and measures of intelligence, thus offering a third reason why taller men may occupy positions of higher status (Silventoinen et al. 2006). In societies with heritable material wealth (e.g., land, money), the association between size and status can also arise because of a fourth process, whereby an individual inherits both favorable growth conditions and social status. All of these reasons, either alone or in combination, may account for positive cross-cultural patterns between size and status, and why individuals of high status are often described as “big men.”

In contemporary industrialized populations, where physical force is prohibited by law, physical superiority is likely to play a marginal role in achieving higher status (Stulp et al. 2015). Nevertheless, consistent positive associations are observed between male and female height and various proxies of social status. An additional factor that might contribute to these positive associations is biased perceptions relating to height and overall body size: Taller individuals, particularly men, are perceived to be more attractive, intelligent, competent, dominant, and better leaders (Blaker and Van Vugt 2014). The increased social status accorded to taller individuals (on average) may thus arise due to

preferential treatment in response to such perceptions. Indeed, studies suggest that tall individuals experience positive discrimination in the labor force and also that people seem to favor tall (er) individuals as their political leader (Stulp et al. 2013; Murray and Schmitz 2011). Thus, the positive association between height and status in contemporary populations may be at least partly due to perceptions and biases that do not necessarily correspond to an individual's ability. Indeed, although consistent positive associations are observed between height and several measures of social status (most readily explained by favorable childhood circumstances), the strength of these associations is typically very low in magnitude. The perceptual links between size and status may therefore be somewhat out of proportion to the actual link between the two. Ironically then, the use of phrases like “Big Man” and “belittled” may actually contribute to the persistence of an association between size and status, because such phrases undoubtedly feed into perceptions associated with size.

Conclusion

“Big Man” clearly is not a gender-neutral term, which reflects the fact that men historically have been more likely to hold political power and leadership positions, not least because men are physically much stronger than women (on average), which seems to be one of the requirements for leadership in earlier times. The times, though, are changing: Women in industrialized populations often achieve high status and positions of leadership, and on some measures of status (such as education) women outrank men in several populations. Moreover, in more equal societies, the gap in height between those of low and high status is closing. If this trend continues, phrases like “Big Man,” “a man of stature,” and “standing tall” will continue to be less relevant.

Cross-References

- Height and Dominance
- Size and Dominance

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Bigamy

- Polyandry

Bilingualism

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Synonyms

Multilingualism

Definition

Speaking two language, with varying degrees of proficiency.

Introduction

Language is the means by which a message is communicated. Language can be spoken, heard, written, and/or read. Language consists of phonology (rules governing how sounds are formed in words), morphology (units of meaning), semantics (vocabulary and rules governing word combinations), syntax (formation of sentences), and pragmatics (how language is used in interaction and the intent or meaning of messages). This entry will address issues of monolingualism and bilingualism with regard to the evolution of language. The foremost difference is that a monolingual has fluency in one language, while bilinguals speak two languages, with varying degrees of proficiency, i.e., perfect ability is not required. Bilinguals speak their languages at the levels that are needed, not always with proficiency.

According to Chomsky (1965), most individuals are born with the capacity for learning and speaking their “native” language, or the predominant language used within their community. The nativist perspective stated that the ability to learn grammar and language is “hardwired” into everyone’s brain. Language develops without being formally taught; all human beings share a common set of cognitive abilities such that cultural

variabilities are negligible. Pinker and Bloom (1990) suggest that language is attributable to human biology, rather than culture: “like echolocation in bats or stereopsis in monkeys, not like writing or the wheel.” However, individuals who are raised in feral conditions or severe neglect with little to no exposure to language early in life demonstrate very limited language acquisition (Fromkin et al. 1974); therefore, it seems that language is a combination of nativist and exposure factors.

Darwin’s theory of natural selection explains how an organism’s possession of heritable traits allows them the ability to adapt, more readily survive, and reproduce. Language is adaptive because it allows for communication among the group, cooperation, and social currency (Hagen 2008). However, Whorf (1956) believed that differences in language, grammars, and how the languages are used in different cultures affect the manner and way in which the speaker perceives the world and their environment. The products of the mind are a function of the social communities where individuals interact with each other. Thus, it is important to consider sociocultural influences on how the brain functions.

This entry will identify (a) historical influences on the acquisition of language, such as evolution of physiological improvements that promoted language, (b) cultural pressures that promote monolingualism and bilingualism among different social groups, and (c) the adaptive function of bilingualism while promoting the view that speaking more than one language produces differences in how the brain is functionally organized.

Physiological Adaptations Promoting the Evolution of Language

Numerous hominid fossils allow us to draw inferences as to how speech and language originated. The examination of prehistoric fossils demonstrates that the human species has undergone extreme and detailed physical mutations in the brain, cranium, pharynx, laryngeal, and supralaryngeal vocal tract physiology (SVT; Hagen 2008). The discovery of findings such as the

bipedal female adult hominid from 3.2 million BCE, *Australopithecus afarensis*, and even older (4.0–4.2 million BCE) hominid species, *Australopithecus anamensis* and *A. ramidus* (4.4 billion BCE), has allowed researchers to examine vocal change physiology across time. Hagen (2008) found that *A. ramidus* displayed a mixture of hominid and ape features, and, even though australopithecines walked upright like humans, they had chimp-like skull shapes and characteristics, which would suggest that they may have not been any more cognitive and linguistically developed than other nonhuman primates. For instance, the chimpanzee (our closest genetic relative) is not capable of speech and vocal capabilities as humans are. They are physically unable to form vowels or consonants due to variances in their vocal tracts (Hagen 2008). If ancient hominid ancestors were nonlinguistic, yet biologically similar to modern humans, what happened between the hominid species and current *Homo sapiens* that allowed the genetic makeup to foster speech and language? As cited in Hagen (2008), Lieberman (2006) posits that this transition seems to be related to cranial capacity. There was a hefty increase in size of the cranium for early australopithecines, from 400 cc (3 million BCE) to 800 cc (2 million BCE) for *Homo habilis* and 1000 cc for *Homo erectus* (1.5 million BCE) and then finally 1400 cc for modern *Homo sapiens* (as cited by Hagen 2008). Another physiological change noted would be the development in the flexion (bending) of the base of the skull. This is thought to not only permit a longer pharynx (i.e., the throat) but also constitutes a lower positioning of the larynx (below the epiglottis, responsible for phonation, articulation, and speech) in the throat (Hagen 2008). Skull fossils including the larynx from those of the *Homo ergaster* (1.8 million BCE; same species as *Homo erectus*) were found to have limited elastic capacity compared to more recent species such as found by Tattersall (1995) *Homo heidelbergensis* (1 million BCE; as cited by Hagen (2008). The resulting lower position of the larynx assisted in the production and evolution of speech and, consequently, spoken language; however, this adaptation also came

with difficulties. Lieberman (1998) pointed out this lower location of our larynx makes it much more likely that humans will choke on food; humans are the only mammals that cannot breathe and swallow at the same time (as cited by Hagen 2008). Dean et al. (2001) found this alteration in turn led the human supralaryngeal vocal tract to require a smaller jaw, lowering our potential for nutrient processing and resulting in less efficient mastication as our nonlinguistic predecessors, who used their jaws primarily for food crushing (as cited by Hagen 2008). However, the evolutionary adoption of one trait for a purpose other than what natural selection had intended results in transforming our vocal tract from one of an eating to a resonating and sound-producing chamber capable of speech. It is still unknown whether prehistoric hominid beings possessed language capabilities. Bickerton (1990) suggested that the *Homo erectus* was in fact capable of a simpler form of language: deemed protolanguage or essentially language without syntax. The *Homo habilis* skull suggests hemispheric specializations, suggesting some language abilities were present in the *Homo erectus* (as cited by Hagen 2008). In the following section, we will consider how some communities developed predominantly monolingual or bilingual language usage.

Geographical Pressures Leading to Either Monolingualism or Bilingualism

Homo sapiens began migrating to Eurasia from Africa around 120,000 BCE and most likely possessed full linguistic capabilities. The population of humans at this time was much fewer in number, estimated at no more than one tenth of one percent of our current population (Gamble 1993). However, when these social groups started increasing in number, maintaining administrative infrastructure became problematic, and consequently the groups began to splinter and disperse. This likely led to geographical separation among the groups, ultimately resulting in loss of contact. Their languages drifted, and groups formed their

own dialects and eventually their own languages. The social structure of nomadic hunter-gatherers would have facilitated an engagement with other groups, and mastering languages from other groups is a critical evolutionary adaptation. This multiple language adaptability would have promoted the maintenance of social bonds among various cultures and prevention of conflicts. As Hagen (2008) specified, the primary language is used to resolve intra-cultural conflicts (or conflicts within the same social community), and second languages are utilized to resolve intercultural conflicts (or conflicts across social communities). The diversity of languages that emerged was in an effort to found and preserve cultural differences that would provide an improvement of survival. Not only would the acquisition of another language demonstrate a magnitude of social respect, but it would also help maintain intercultural affairs (such as bonds, trade, etc.) as well as a way to avoid hostility (Hagen 2008).

From a historical perspective, bilingualism has gone through many recurrent trends and extinction. A potential reason for early ancestors not learning more than one language might have resulted from population “bottlenecks” that the world was experiencing. For example, the massive eruption of a volcano in Sumatra around 75,000 BCE (Lake Toba eruption) resulted in a population drop so detrimental that only a few thousand humans were spared. Having such a small population, and paired with a nomadic lifestyle, more than one language would not have been a necessary skill to acquire (Hagen 2008).

The standard for most children to become fully fluent in a language usually requires about 2–3 years of exposure and use for conversation. Since these nomadic individuals could not contribute to this type of (linguistic and geographic) consistency, the need to learn multiple languages did not seem to be of benefit. The ebb and flow of monolingualism and bilingualism over time may have resulted from dispersion of hunter-gatherers (i.e., promoting monolingualism) and consequently at later times the forming of communities and cities (promoting bilingualism).

Sociocultural Pressures Leading to Either Monolingualism or Bilingualism

The cooperative disposition of the egalitarian communities would facilitate the need for communication. As Jacques-Rousseau alluded to in *The Social Contract*, the egalitarian sense of equal freedom is something we are born with, and people only deviate from this for the sake of utility (Rousseau and Gourevitch 1997). Learning another language would promote mutual respect in addition to fostering fellowship, trade, and resolution of intergroup conflicts (Hagen 2008). Contrary to this idea of cooperation, the English philosopher, Hobbes, believed that individuals are inherently violent, and morality does not exist. In Shermer’s (2004) book *The Science of Good and Evil*, he touched on Jane Goodall’s evidence of this primitive and aggressive behavior when observing our distant ancestors, the *Pan troglodytes* (chimpanzee), in Tanzania (as cited by Hagen 2008). Even though both Rousseau and Hobbes describe common behavior in response to varying predicaments, survival of the species favors the Rousseau dynamic. The species is much more likely to survive and flourish when there is cooperation and concern for others present.

Alternatively, bilingualism has been extinguished through cultural perceptions not tied to geographical limitations. Foreign languages have never been extinguished in any other country as quickly as in the United States. The concept of speaking one language is much more prevalent in the West, whereas most of the world’s population is bilingual. From the colonial days to the mid-twentieth century, the essence of “one nation, one language” was the thought process, even suggesting that this mentality would facilitate a sort of linguistic perfection. Americans during this time believed that immigrants coming to the United States should speak only English; the dedication to monolingualism was seen to be representative of faithfulness, harmony, and democracy among the country. Nebraska, for example, has had laws (from 1919) banning teaching of any foreign languages below ninth

grade. The state of Nebraska organized a campaign in its honor known as “Good English” and even had students quote language loyalty oaths. Some individuals posit that the mentality behind this type of action was related to the common misconception that bilingualism created mental confusion and damaged immigrant children’s ability to adapt to their new surroundings.

This perspective continued on as recently as the early twentieth century. The prevalent belief was that bilingualism does not benefit individuals, but instead hinders cognitive abilities of dual-language persons, especially in children. A common misconception is that genetic differences between races prohibited immigrants to learn English, which in turn was perceived as a lower intelligence level. The other explanation was that since the child spoke in their foreign language at home, and English at school, perhaps the dual vocabulary and lexicon impeded each other. Peal and Lambert (1962) shed light on this issue and found that, when controlling for social class, bilingualism actually produced higher results on a number of intelligence tests. They not only found that two vocabularies actually improved comprehension for bilingual individuals but also enhanced multiple higher cognitive abilities including concept formation (Liedtke and Nelson 1968), metalinguistic awareness (Cummins 1978), and code-switching, which demonstrates intellectual advantages (Hughes et al. 2006). The next section explores neuroanatomical differences and cognitive benefits of bilingualism as a positive adaptation and a mechanism to improve brain function and plasticity.

Hemispheric Lateralization and Specialization in Language Processing

The first identification of the brain being acknowledged as the center of language was indicated in the *Edwin Smith papyrus*, in approximately 3500 BC (Ahlsén 2006). The specific neuroanatomical location was later discovered by Broca upon autopsy of two of his patients; both had suffered severe language-speaking deficits, yet

retained relatively good comprehension abilities with impaired speaking abilities. Both had injuries to the inferolateral frontal cortex (Broca 1861). He surmised that linguistic symptoms were caused by these left hemisphere lesions, and therefore language was located, and lateralized, in the left hemisphere. Later, Carl Wernicke (1874) identified the temporal-parietal regions as the processing center of language comprehension, an area separate from spoken language. He also proposed the idea of language functions localized in the gyri (brain convolutions). Other evidence has supported this belief of language-related initiation, specifically in areas such as the gyri (lingual and fusiform), middle prefrontal areas (such as the dorsolateral prefrontal cortex), the insula, and even middle and inferior temporal gyri and temporal pole (Obler and Gjerlow 1999). Processing language, as well as the language acquisition center, is predominantly associated with the language centers located in the left hemisphere of the primary and secondary auditory cortices, more specifically the perisylvian region of the left hemisphere (Hagen 2008). The right hemisphere has been labeled the nondominant hemisphere as noted by studies indicating that significant speech, language, and reading disabilities occur when lesions are located in the left hemisphere (Ardila and Ostrosky-Solis 1984). Abutalebi et al. (2001) suggested that activation of the right hemisphere occurs in mirror regions during language tasks. Although evidence for right hemisphere function of certain linguistic abilities has been found, 97% of nondisabled right-handed people and 70% of nondisabled left-handed people have left hemisphere lateralization (Obler and Gjerlow 1999). This presumption of left hemisphere lateralization was identified in Lenneberg’s 1964 study of language loss in young children with left hemisphere brain injuries. Lenneberg et al. (1967) later proposed evidence to support a critical period hypothesis (CPH), a theory in which language acquisition and linguistic ability are tied to biological age, cutoffs, and language fossilization (i.e., language growth stopping at a certain age). This hypothesis is explored in the context of early versus late second language acquisition. Lenneberg

et al. (1967) postulated the critical period consisted of 2 years to about 14 years of age. Patkowski (1980) examined the concept of a sensitive period, which references a preferred age for second language acquisition and windows of opportunity for best acquiring language. He investigated the idea of native-like acquisition of syntax in a nonnative language and hypothesized that it would be more difficult to achieve native-like fluency unless the individual began to acquire the second language before the age of 15. He surmised that this native proficiency is not necessarily dependent on the age of puberty, but rather the utilization of sociolinguistic conditions prior to puberty, such as exposure, practice time, etc. Consequently, it is possible to acquire a second language after this "critical period"; however, it is somewhat harder to reach native-like fluency in the second acquired language after the sensitive period (Patkowski 1980).

Neural plasticity may be an underlying mechanism promoting greater fluency with earlier second language (L2) acquisition. Plasticity also mediates recovery of language functioning such that when second language acquisition occurs before 7 years of age, language is more resilient to disease and injury compared to those who learn after this sensitive period (Fabbro 2001). Hagen (2008) states that almost all childhood aphasia studies have shown 75–100% recovery rates. In addition, Paradis (1977) found that after a stroke there were different degrees of rehabilitation in each language for bilinguals. Hernandez et al. (2000) stated that there have been no clear rules in relation to recovery patterns; however, they found that factors such as first language learned, language use before aphasia, and language dominance all played into varying degrees of language recovery. While these studies demonstrate the influence of age of acquisition and plasticity on first language (L1), and L2, language localization is also an important element to consider.

Brain organization and language localization for monolingual and bilingual individuals is not a straightforward proposition. The left hemisphere has been known for most expressive and receptive language functions. However, brain

localization for bilingual individuals may differ for their L1 and L2. For example, Gomez-Tortosa et al. (1996) presented a case study of a bilingual patient with selective impairment in L1 (but not L2) after surgery to remove a lesion in her left perisylvian area of the brain. Alternatively, L2 could be localized in the right hemisphere. Dehaene et al. (1997) identified, using fMRI, that although L1 seems to be mediated by a similar brain network in individuals they assessed, the L2 produced activation in left and right temporal and frontal areas, occasionally restricted only to the right hemisphere (namely, the right superior temporal gyrus and superior temporal sulcus). Perani et al. (1996) used positron emission tomography (PET scans) and revealed that when late second language learners listened to L1 (i.e., their native languages), it activated brain areas that are not apparent in L2 (i.e., the second language) for late second language acquisition learners. These brain areas included both left and right temporal lobes, left inferior parietal lobe, and left inferior frontal gyrus. These findings demonstrate variation in patterns of localization and lateralization of function. A meta-analysis of 66 studies suggests that age of acquisition was a strong predictor of lateralization (Hull and Vaid 2007). When L2 learning occurred before the age of 6, bilateral organization was common, whereas after the age of 6, both languages were predominantly left lateralized. Hull and Vaid (2007) suggest that when infants are learning two languages simultaneously, pragmatic cues are needed to differentiate between the two languages, which underlies the right hemisphere involvement. Alternatively, they suggest that the extensive requirement for learning two languages promoted involvement of both hemispheres and produced automaticity in these areas. The age of 6 is a specific time in brain development during which neural wiring and pruning take place (Huttenlocher and Dabholkar 1997, as cited by Hull and Vaid 2007). Right hemisphere involvement in language acquisition after this point may be less efficient and involves less automaticity than left hemisphere involvement. For example, recent research utilizing a timed picture-naming

task provided evidence that early second language learners exhibited faster response times and speed accuracy compared to those who learned their second language later (Kohnert et al. 1998).

Conclusion

Both physiological adaptations and sociocultural processes favor and promote bilingual speaking in communities. Evolutionary forces across time have warranted the opportunity for our brains to evolve and be ready for the learning of language such that our vocal tracts are not only necessary for eating but evolved for speech. Although the downsides include not being able to breathe and swallow at the same time, increased likelihood of choking on food, and decreased nutrient processing (Hagen 2008), the benefit of developing such complex vocalizations as symbolic language far outweighs these costs. Brown et al. (1985) postulated that the use of symbolic language allowed for complex thought and heightened the cognitive capacity of the human brain as evidenced in the increasing size of the cranium (as cited by Hagen 2008) and volume of prefrontal brain matter (Schoenemann et al. 2005). With these physiological adaptations in place, humans were poised to begin a new phase of adaptation involving complex oral linguistic communication within and across social communities. As humans began migrating to other areas and splintering due to instabilities in large community sizes, languages diverged and evolved as well. However, some communities had the opportunity to utilize second language acquisition through sociocultural interaction, whereas others were constrained by geographical isolation or cultural mores to speak only one language. For those who had geographical access to communities speaking another language, learning a second language was adaptive because it promoted development of intercultural bonds and access to resources.

Not only would speaking two languages be adaptive socioculturally but also cognitively and physiologically. A pattern emerges in the research on the areas of the brain associated with speech

and language. The left hemisphere is specialized for language processing, but bilingual brain organization is dependent on factors such as age of acquisition, exposure, and practice; consequently, learning a second language is recommended before the age of six (Hull and Vaid 2007) or before one reaches puberty (Patkowski 1980) due to greater brain plasticity. Indeed, the acquisition of a second language has profound effects on the brain, leading to improvements in executive function (Bialystok 2015), task switching (Prior and MacWhinney 2010), conflict resolution (Bialystok et al. 2012), and metalinguistic awareness (Galambos and Hakuta 1988), as well as and serving as a protective factor against age-related dementia and Alzheimer's disease (Bialystok et al. 2012). The neurological benefits of bilingualism have been found to increase gray matter volume in bilinguals, compared to monolinguals (Olulade et al. 2016).

In a world that is becoming more globalized, the benefits of bilingualism cannot be ignored. While geographic limitations may inhibit direct communication with others, communities can be easily accessed through the Internet. Exposing children to other languages early in life and fostering communication digitally as well as in person could lead to lasting positive changes in the brain and cognition, as well as promote cultural competence. Bilingualism can be adaptive since it allows individuals to have exposure to other cultures through different languages, in addition to establishing a sense of interconnectedness.

Cross-References

- ▶ [Critical Period of Acquisition](#)
- ▶ [Immigrant Parents](#)
- ▶ [Language Acquisition](#)
- ▶ [Language Acquisition in Infants and Toddlers](#)
- ▶ [Language Development](#)
- ▶ [Language Dysfunction](#)
- ▶ [Language and Handedness](#)
- ▶ [Language Modularity](#)
- ▶ [Language Instinct](#)
- ▶ [Steven Pinker](#)

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Biliousness

- [Nausea](#)

Binet-Simon Tests

- [Intelligence Testing](#)

Binge Eating Disorder

- [Eating Disorders](#)

Binocular Disparity

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Synonyms

[Binocular parallax](#)

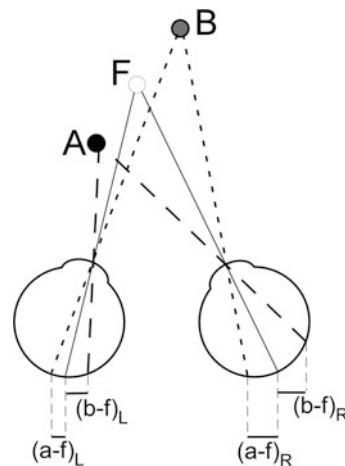
Definition

Binocular disparity is a binocular depth cue produced by a difference in retinal projection of the

same object onto left eye and right eye retinas as a result of a horizontal separation of the eyes.

Introduction

Stereopsis, or the perception of the “true” location of the objects in depth obtained on the basis of binocular information, requires the two eyes to be located at different lateral positions so that they receive slightly different projections onto their retinas when focused on the same point in space (Fig. 1). In addition, stereopsis requires coordinated eye movements; disorders that interfere with this coordination such as amblyopia and strabismus lead patients to report perceiving two images of a single object (diplopia or double vision; Otero-Millan et al. 2014). Although the importance of binocular disparity in achieving depth perception in primate vision is well established, its role in vision of other animals is less clear, particularly for animals with laterally located eyes.

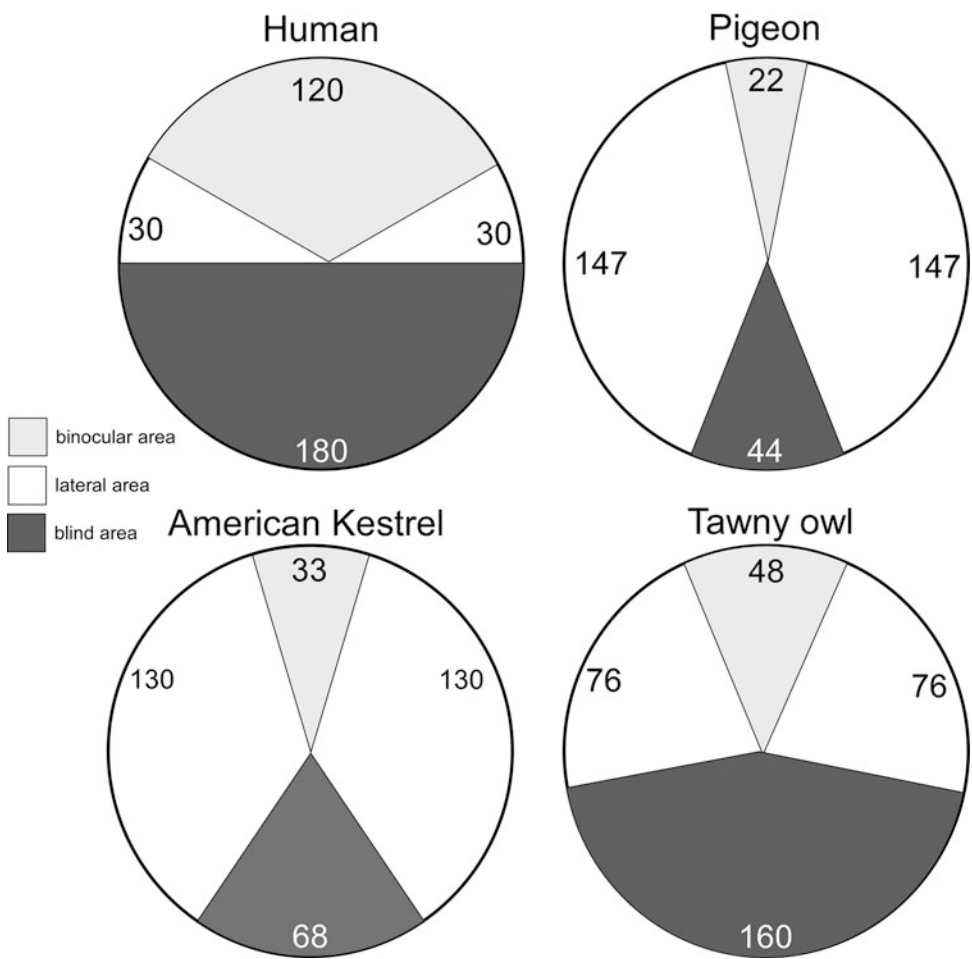


Binocular Disparity, Fig. 1 Geometry of binocular disparity and stereopsis. As both eyes simultaneously fixate on a point *F*, it falls on their foveae. The point *A* lies closer to the observer (i.e., before the point of fixation) than the point *B*; therefore, the projections of these points fall on different locations in the *left* and the *right* eyes. Consequently, the distance from the fixation to the projection of each point (denoted as *a-f* or *b-f*) will be different for the *left* and the *right* eyes; this difference is termed binocular disparity and can be used for recovering depth information

Use of Binocular Disparity for Depth Perception in Humans and Nonhuman Animals

When a person looks at a certain point, their eyes fixate on that point, and its projection falls directly onto a fovea of each eye (Fig. 1). Because of the lateral separation of the eyes, the objects in front of the fixation point and behind it will project to a slightly different points on the retina; for example, the retinal distance between points A and F in Fig. 1 is smaller for the left eye than for the right eye (Ponce and Born 2008). This binocular disparity serves as a basis for stereopsis.

Although binocular disparity has been most actively studied in context of depth perception, it also has other benefits. For example, stereoscopic use of binocular disparity improves detection of camouflaged animals against a background that is similar in color and in texture (Wardle et al. 2010). Binocular comparisons also aid in recognition of occluded objects by assisting in discriminating true object borders from the borders created by occlusion (Nakayama et al. 1989). All vertebrate animals have two eyes, and some degree of binocular overlap is present even in animals with laterally located eyes (Fig. 2). However, the function of this binocular overlap



Binocular Disparity, Fig. 2 Diagrams of visual fields of humans and three bird species with the eyes at rest (with the bill or the nose facing forward). Pigeon and American

kestrel have laterally located eyes, whereas tawny owl has frontally located eyes (The avian visual fields are adapted from Martin (1994))

and its involvement in depth perception remains a subject of a lively debate, particularly in birds. Although some authors assert that avian binocular field produces stereoscopic depth perception, just as it does in primates (e.g., Nieder 2003), others argue that binocular disparity in avian vision is used primarily for in control of a beak placement and during visual inspection of items held in the beak (Martin 2009). Instead, depth perception in birds is proposed to rely on motion parallax produced by repetitive head movements (Kral 2003). The relatively large binocular field of owls (Fig. 2) is argued to be a byproduct of enlarged eyes and elaborate outer ears that prevent lateral placement of the eyes, an argument supported by a much smaller binocular field found in other birds of prey (Martin 2009). Unfortunately, global stereopsis (a process involving processing and comparison over a large portion of retina) has been convincingly demonstrated in only one bird species, barn owl (van der Willigen 2011), leaving the argument unresolved. In contrast, motion parallax has been shown to produce reliable depth perception in both humans and nonhuman animals (Kral 2003).

Although many insects have two or more eyes, their eyes are immobile and have a fixed focus; thus, most insects are unlikely to be able to use binocular disparity for depth perception and must rely on other cues such as motion parallax (Kral 2003). Relatedly, a few insects with a clearly established stereopsis appear to use it in a much more limited fashion than humans (e.g., for estimating distance to prey but not its size; Nityananda et al. 2016).

Conclusion

Binocular disparity in humans is an undoubtedly important cue aiding depth perception; anecdotal reports from the patients who underwent a successful vision recovery emphasize a dramatic improvement in their ability to perceive depth and to detect object boundaries (Ponce and Born 2008). In contrast, the evidence for extensive use of binocular disparity in depth perception in nonhuman animals is limited, with some authors

suggesting that monocular depth cues such as motion parallax may play a more important role, even in species with a considerable binocular overlap (Kral 2003; Martin 2009).

Cross-References

► Depth Perception

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Binocular Parallax

► Binocular Disparity

Bioacoustics

- [Vocal Indicators of Dominance](#)

Bioethics

- [Moral Concerns](#)
- [Neuroethics](#)

Biofield Therapies

- [Therapeutic Touch](#)

Biofunction

- [Biological Function](#)

Biography of Charles Darwin

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Biolinguistics

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Biological Determinism

- [Genetic Determinism](#)
- [Steven Pinker on Genetic Determinism](#)

Biological Ecology

- [Life History Theory](#)

Biological Exuberance

- [Evolution of Homosexuality](#)

Biological Function

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Synonyms

[Adaptation](#); [Biofunction](#); [Causal role](#); [Fitness effect](#); [Purpose](#); [Selected effect](#)

Definition

In biology, functions are attributed to the traits, behaviors, and parts of living things. A thing's function can refer to its purpose, a benefit it confers on an organism, or the causal role it contributes to a more complex system capacity.

Introduction

Biologists attribute functions to a diversity of natural phenomena, from chemical and cellular processes to the organs, traits, and behavior of organisms. It is common for them to say, for example, that the koala's pouch has the function of protecting its young, that the function of the bee dance is to direct other bees to pollen, or that chlorophyll in plants functions to absorb light and convert it into energy. Yet the term "function" is ambiguous, carrying importantly different meanings and occupying distinct explanatory projects in the biological sciences. This entry will introduce two characteristic features of biological functions, then overview three dominant analyses, each of which targets a distinct sense in which functions are conceptualized in the biosciences.

Functions, Teleology, and Normativity

What do biologists mean by “function”? In its most basic sense, “function” can simply refer to an effect something produces (Hardcastle 2002). For example, when geneticists say that amino acids function to catalyze RNA transcription, they just mean that RNA transcription is an effect brought about by amino acids. In some cases, however, when biologists assign functions, they seem to be saying something more.

Functions are commonly associated with two qualities. The first is purposiveness or “teleology”: functional ascriptions seem to tell us why something exists (Neander 1991). A koala’s pouch is for protecting its young, and chlorophyll’s purpose in plants is to transform light into energy. The second is *normativity*: a thing’s function often determines the standards by which it operates. Often biologists wish to say that, even when something fails to do something, it nonetheless *should* have. A single plant that does not produce chlorophyll *fails* to fulfill its function, and so is in a state of *dysfunction*.

The teleological feature functions has, in particular, provoked controversy and consternation (Neander 1991). It is easily accommodated in the case of artifacts, where we can articulate what something it is supposed to do by referencing human goals. The function of a microwave, for example, is to heat food because its inventor designed it for this use. In biology, however, the goal is to define function naturalistically, without presupposing the existence of a human, or supernatural, designer.

This has led some sceptics to suggest that functions do not belong in science (Davies 2003). This stance, however, sits uneasily with the ubiquitous and explanatorily powerful use of functional explanation in biology (Garson 2016). Analyses of biological function thus tend to either provide a naturalistic interpretation of teleology or else define function in a way that carries no commitment to it.

Causal Role Functions

The Causal Role analysis defines biological function in non-teleological terms. The motivation

behind this approach is not merely the perceived impossibility of naturalizing teleology, but a need to accommodate a widespread and non-purposive sense of function in biology (Cummins 1975; Hardcastle 2002). In many contexts, biologists are less concerned with explaining why an entity or trait exists than they are in analyzing the causal role it plays in a biological system (Cummins 1975; Amundson and Lauder 1994).

Briefly put, a causal role (CR) function is the output a system’s component produces that contributes to a system-level capacity (Cummins 1975). Take, for example, the function of the heart. The heart is a subcomponent of the cardiovascular system, which circulates oxygen, nutrients and hormones throughout the body. Within this complex system, the heart contributes to circulation by pumping blood. The CR analysis thus says that the function of hearts is to pump blood.

However, referring to *the* function of hearts is slightly misleading. A component’s CR function is always assigned relative to a system capacity that biologists are interested in (Hardcastle 2002). As complex systems possess a multitude of capacities, a component can be subject to more than one kind of functional analysis. Biologists can provide a functional analysis of a heart’s blood pumping, or they might instead be interested in analyzing the beating noise it makes, its size, or its weight. A system component can be assigned several functions, depending on the interests of researchers.

The CR account is pragmatic in spirit and places few limitations on what natural phenomena biologists can subject to functional analysis. However, it faces two key criticisms.

First, its neglect of teleology means it cannot distinguish between a function and a “fortuitous effect” (Neander 1991). In the realm of artifacts, we think that a vase can be used as a paperweight or a pen-holder, but its *proper* function is to hold flowers. Similarly, goes the intuition, a heart produces a range of effects which are not its proper function. The heart’s beating noise, for example, helps doctors diagnose cardiac pathology, but the heart’s function is not to make noises.

Second, the CR account struggles to accommodate the normativity of functions (Neander 1991). The kind of functional analysis that the

CR account generates describes what a system's component does is, as opposed to what is ought to do. A consequence of this is that biologists cannot say that a heart in cardiac arrest is malfunctioning; rather, it merely lacks the function of pumping blood, in much the same way that it lacks the function of photosynthesizing light or deterring nocturnal predators.

Selected Effect Functions

The Selected Effect (SE) theory aims to naturalize teleology (Millikan 1984; Neander 1991). Recall that functions are teleological when they tell us what something is for: hearts are for pumping blood; chlorophyll is for photosynthesis; etc. According to the SE theory, a thing's function *qua* purpose is determined by facts about its causal history. While in the case of artifacts, the relevant causal history concerns the decisions of a designer; in the case of biological entities, the designer is supplanted by Darwinian processes of natural selection.

SE functions are borne by traits that are *adaptations* – traits that organisms possess because they have given their ancestors a survival advantage. A trait's SE function is whichever of its effects is responsible for this advantage. For example, zebra stripes are thought to deter disease-carrying flies. Some biologists hypothesize that fly-deterrence is what led the striped phenotype to be reproduced over time: historically, zebras with stripes survived to leave more offspring than those without. If this hypothesis is correct, zebra stripes are an adaptation, and their function is to deter flies.

The historical constraint allows the SE analysis to distinguish between functions and accidental benefits (Griffiths 1993). Let's say that as well as their fly-deterrence effect, stripes also camouflage zebras from predators. On the CR account, both effects could be considered a function of the stripes. The SE analysis, in contrast, says that insofar as stripes were only selected because they deter flies, the fly-deterrent effect is their function, and camouflage is merely a "fortuitous effect."

This constraint also enables the SE analysis to deal with normativity (Griffiths 1993). A traits'

SE function is not simply one of its current causal capacities, but the one that has produced fitness benefits for members of its ancestral lineage (Garson 2016). This means that an organismic trait can have a function even in cases where it fails to perform it. Thus, we can say that a heart in cardiac arrest malfunctions because it fails to pump blood because pumping blood is the effect for which ancestral hearts were selected.

However, the SE analysis has a more limited scope than the CR account. Exactly how limited depends on how common adaptations are, and there is disagreement over this (Godfrey-Smith 2001). Nevertheless, there are other kinds of traits that biologists wish to subject to functional analysis, including vestiges (traits that are no longer an adaptation), spandrels (traits that were never an adaptation), and non-heritable traits of sterile animals (Hardcastle 2002). Finally, determining a trait's selection history, or whether it was selected at all, can also be very difficult, and for this reason, the SE analysis has been considered over-demanding (Garson 2016).

Fitness-Contribution Functions

The practical problems of studying selection history aside, biologists are often interested in the current fitness of a trait, or the likelihood it will be selected, rather than the selective regime that caused it to be reproduced (Bigelow and Pargetter 1987). While the fitness-contribution (FC) theory defines biological function using the conceptual resources of evolutionary theory, it is forward-looking: the function of a trait is the effect it contributes – or is disposed to contribute – to organismic fitness, regardless of the trait's causal origin (Bigelow and Pargetter 1987).

According to the simplest version of the theory, a trait has a FC function if it is *adaptive*: that is, when it raises the average fitness of organisms who possess it, when compared with those that do not. Take, for example, Darwin's dark peppered moth, which proliferated in polluted urban environments. The moth prevailed because its color, in this context, was adaptive: it enabled it to hide from predators. The FC function of the darker phenotype trait is thus to camouflage

moths, because camouflage increases the likelihood that it will survive and reproduce more than moths with a lighter-colored phenotype.

What this example illustrates, however, is that a trait's fitness is environment-dependent. A single trait can have a high average fitness value under one set of environmental conditions, and a low average fitness value under another. While a dark-colored phenotype aided the survival of peppered moths in polluted cities, it was a likely target for predators in the countryside, where lighter moths proliferated. Environment-dependence makes function-attributions unstable, with traits having different functions depending on time and place (Garson 2016).

The Propensity Theory is a version of the FC theory that tries to deal with this by specifying that a trait's function is whatever fitness advantage it is *disposed* to confer on an organism in its "natural habitat" (Bigelow and Pargetter 1987). This means that a trait can in principle have a stable function across environments that are hostile or unfavorable. The task of defining a "natural habitat," however, is unclear and unsettled. Indeed, if the natural habitat is simply the environment in which the trait evolved, then biologists can no longer bracket the trait's history, a key reason for preferring it over the SE account (Garson 2016).

Conclusion

The foregoing analyses can agree, in principle, on what function something has. Hearts can have the function of pumping blood because this effect contributes to circulation (CR), is the product of natural selection processes (SE), or increases the fitness of organisms who possess them (FC).

Even in cases where they agree, however, the three senses of function perform an importantly different explanatory purpose (Godfrey-Smith 1993). The SE function explains why a trait is there, the CR sense of function explains how a component part contributes to a systemic capacity, and the FC explains how a trait contributes to an organism's fitness in a contemporary environment.

The fact that these three senses of biological function are associated with distinct and fecund explanatory projects makes function pluralism,

the position that there is more than one legitimate concept of function within biology, a plausible stance (Godfrey-Smith 1993).

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Evolutionary Mismatch](#)
- [Functional Fixity](#)
- [Function Versus Capability](#)
- [Identifying Adaptive Functions](#)
- [Just So Stories](#)
- [Physiological Mechanisms](#)

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Biological Markets

- [Cooperation Among Nonchimpanzee, Non-human Primates](#)

Biological Sex of Friend

► [Gender of Friend](#)

Biologically Significant Stimulus

► [Unconditioned Stimulus](#)

Biologist

► [E. O. Wilson](#)

Biology of Homosexuality

► [Genetic and Prenatal Components of Homosexuality](#)

Biology of Human Gender, The

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Synonyms

[Digit ratio](#); [Femininity](#); [Gender development](#); [Masculinity](#); [Prenatal androgens](#); [Sex differences](#)

Definitions

The development of human gender identity may be influenced by organizational effects of prenatal hormones. This includes physical and neural development. Digit ratio (or 2D:4D) is a proxy of fetal hormones that correlates negatively with prenatal testosterone and positively with prenatal estrogen. Studies investigating associations between 2D:4D and sex-dependent traits suggest that in addition to genetics, prenatal hormones contribute to the determination of gender.

Introduction

At birth, humans are typically assigned to their biological sex (male or female) on the basis of their genitalia. But there is evidence from fetal studies that the sexual differentiation of the body occurs before the sexual differentiation of the brain (Swaab 2007; Bao and Swaab 2011). This gives the opportunity for considerable plasticity with regard to the social roles that are considered appropriate for males and females. These roles vary across societies such that it is appropriate to refer to the sexes as “male” and “female,” but to their culturally influenced gender roles as “masculine” and “feminine.” Here, we address the problem of the biological core of gender roles. Does it exist, and if so how important is it in influencing behaviors that we consider to be “masculine” and “feminine”? These questions are important in both a Darwinian and a social-cultural context. Our direct fitness is measured in number of offspring. It is in part dependent on the function of our gonads. However, if there is a mismatch between gonadal development and the sexual differentiation of the brain, then the result may be a reduction in fitness. Such transgendered individuals may be fairly common. In a large ($n > 255,000$) online study (The BBC internet study; Reimers 2007), 47.3% of participants gave their gender as female and 52.7% as male. In answer to the question “*Regardless of your biological sex, what sex do you feel?*”, a total of 4.0% of “males” selected “female” and 4.3% of “females” selected “male.” Clearly, there may be

both sociocultural and biological factors at work here. We briefly consider the former before discussing the latter in more detail.

Gender and Social Influences

One influential model regarding the social etiology of gender is the *gender schema theory* (Bem 1981). This envisages gender-associated information is transmitted by schemata or networks of information. Bem maintained that there are individual differences in the degree to which people hold these gender schemata. These differences can be seen by the degree to which individuals are sex-typed.

Another important theory which considers social factors in the determination of gender is that of *social role theory* (Eagly 1997). This suggests that the labor division between men and women is a major determinant of gender differences. Thus, men and women are expected to fulfill different roles in the work force and then assumed to exemplify the characteristics of those roles. Work force roles are strongly related to interest in things (stronger in men) and in people (stronger in women) and these preferences are remarkably robust across cultures (Lippa 1998). Such patterns could be construed to support both a social and a biological influence on gender.

The concepts of masculinity and femininity and their marked plasticity can also be applied to societies (Hofstede 1991). Thus, a society can be called masculine when emotional gender roles are distinct. Men are assumed to be tough and preoccupied by material success and women are supposed to be tender and concerned with the quality of life. In contrast, a feminine society is one in which the emotional roles overlap such that both men and women are tender and concerned with the quality of life. The *Masculinity Index* (MAS) is a society-measure of preference for achievement, heroism, assertiveness, and material rewards for success – independent of economic development. Countries such as Slovakia (MAS = 110), Japan (MAS = 95), and Hungary (MAS = 88) have high masculinity scores, while Sweden (MAS = 8), Norway (MAS = 8), and the

Netherlands (MAS = 14) lie at the opposite end of the masculinity spectrum (Hofstede 1991). It is to be emphasized that MAS scores are independent of economic indices such as gross domestic product. Clearly, there are factors other than national wealth at work here.

Gender and Biology

The plasticity of gender patterns is remarkable. However, this does not preclude a substantial biological effect on gender. Swaab and colleagues (Bao and Swaab 2011; Swaab 2004, 2007; Swaab and Garcia-Falgueras 2009) have discussed the interdependent biological processes involved in the formation of the reproductive system and in the subsequent sexual differentiation of the brain. In boys, the penis, prostate, and scrotum are formed during fetal weeks 6–12. This begins under the influence of the Y-linked SRY gene (Berta et al. 1990) and continues with the production of testosterone and dihydrotestosterone. In girls, the development of the sexual organs primarily depends on an absence of large amounts of androgen. The masculinization/feminization of the nervous system and behavior occurs later in gestation and results predominantly from the permanent “organizing” effects of testosterone in the second trimester of development. Brain areas that show sex differences that relate to gender include the bed nucleus of the stria terminalis, the third interstitial nucleus of the anterior hypothalamus, and the shape of the corpus callosum (Saraswat et al. 2015). At puberty, the brain circuits that have been organized prenatally are activated by sex steroids (hence the term activational effects). In addition to this large effect of prenatal androgen, there are also genetic and epigenetic influences on the sexual differentiation of the brain during the second trimester (McCarthy et al. 2009). Associated with the sexual differentiation of the brain are medical conditions that are more common in females (e.g., anorexia nervosa, bulimia, and Alzheimer’s disease) or in males (autism, attention-deficit hyperactivity disorder [ADHD], and stuttering).

Prenatal androgens, such as testosterone, have also been implicated in the etiology of transgender

identity. Transgender individuals have a gender identity that differs from their assigned sex, and in this regard, there is a preponderance of males over females (Bao and Swaab 2011). Some transgender individuals seek medical intervention to transition from one sex to another and are referred to as transsexuals. As with transgender individuals, male-to-female transsexuals (MTF) are more common than female-to-male (FTM) transsexuals (Bao and Swaab 2011). Transgender identity is not related in any substantial way to sexual orientation, suggesting different etiological pathways (Pauly 1998). Twin studies have provided evidence of a strong genetic influence on transgender identity (e.g., Heylens et al. 2012), and there are a number of studies indicating MTF individuals show atypical cerebral networks in both gray and white matter structures (reviewed by Saraswat et al. 2015). Overall, the characteristics of transgender individuals suggest a behavioral trait that is fixed early in development and is not substantially influenced by social factors.

The more nuanced effects of prenatal androgens on gender may be seen in studies using morphological proxies of fetal hormones and in assays of fetal hormones. With regard to morphological proxies, digit ratio (2D:4D) – the relative lengths of the second and fourth digits – is the most commonly used trait. The 2D:4D ratio is influenced by a balance of fetal testosterone to estrogen such that 4D length is increased relative to 2D length when prenatal testosterone concentration is high relative to prenatal estrogen. Therefore males, with their high levels of prenatal testosterone, have longer fourth digits relative to second than do females (male 2D:4D < female 2D:4D; Manning et al. 2004). Much of the sex-dependent variation in 2D:4D appears to be determined in a rather narrow window of development towards the end of the first trimester (Manning 2002; Szwed et al. 2017). With regard to fetal sex steroids, data have been obtained from hormonal assays of routine amniocentesis tests performed during the second trimester of development (Baron-Cohen et al. 2004).

Digit ratio studies have reported many associations between 2D:4D and sex-dependent traits. They include links between low 2D:4D (high

prenatal testosterone relative to estrogen) in autism (Manning et al. 2001) and ADHD (Martel et al. 2008), and high 2D:4D (low prenatal testosterone relative to estrogen) in schizophrenia (Qian et al. 2016). Studies of 2D:4D in transsexuals has yielded mixed results. In some reports MTF individuals have higher (more feminized) 2D:4D than normative male controls but no effect in FTM individuals (e.g., Schneider et al. 2006). In contrast, FTM transsexuals have been reported to have lower 2D:4D than controls, but no effect in MTF individuals (e.g., Wallien et al. 2008). These discrepancies may, at least in part, result from differences in measuring finger lengths (see Leinung and Wu 2017 for discussion).

With regard to social role theory, 2D:4D and other testosterone-dependent traits have been linked to the labor division between men and women. Manning et al. (2010) have reported data from the BBC Internet study, showing that the proportion of women (PW) across occupations is moderated by two morphological correlates of testosterone (2D:4D and height) and a systemizing–empathizing score [SQ–EQ] – a putative behavioral correlate of prenatal testosterone. Systemizing is the drive to analyze systems or construct systems while empathizing measures a person’s ability to understand thoughts and feelings of others (Baron-Cohen et al. 2004). PW varied per occupation from 17% in engineering and research & development to 94% for homemakers. Tall women with low 2D:4D and high SQ–EQ scores tended to be found in low PW (male-dominated) occupations. Focusing on individual occupational preferences in the BBC study, Manning et al. (2017) found that low (masculinized) 2D:4D was related to preferences in heterosexual men and women for “male-type” occupations such as car mechanic, builder, and carpenter. Thus, we can see that a proxy for high prenatal testosterone (relative to estrogen) may interact with the pressures postulated by social role theory. The result may be that prenatally masculinized women are attracted to “male-type” occupations.

Mean 2D:4D and the magnitude of sex differences in 2D:4D vary across nations. Such variation may correlate with between-nation variation in gender-related traits. For example, high

national 2D:4D has been shown to correlate with high national scores for uncertainty avoidance and neuroticism (Manning and Fink 2011). Interestingly, countries that show the smallest sex differences in national 2D:4D also have low scores for gender inequality (Manning et al. 2014). This finding may map on to the national Masculinity Index (MAS). Further work is necessary to clarify this relationship.

Studies of 2D:4D and gender-related traits may overlap with reports concerning prenatal sex hormones and behaviors such as autistic traits and “tomboy” play patterns. With regard to the former, children with autism tend to avoid eye contact. A tendency for high levels of eye contact is associated with low concentrations of fetal testosterone (Lutchmaya et al. 2002) and high 2D:4D (Saenz and Alexander 2013). With regard to the latter, high levels of “male-typical” play in boys and girls are related to high concentrations of fetal testosterone (Auyeung et al. 2009). “Tomboyism,” a tendency for girls to play with boys and boy’s toys, is also associated with low (masculinized) 2D:4D.

Conclusion

Gender is highly variable across individuals and across societies. These patterns speak to the notion that factors such as occupational roles are the major determinants of gender. However, there is much evidence that prenatal influences of both genes and sex steroid hormones contribute to the determination of gender. Such biological influences provide the substrate upon which social factors are built upon. In that sense they may provide the key to what we perceive as gender.

Cross-References

Digit Ratio

- [Hormone Effects on Human Fetal Development](#)
- [Sex Differences](#)
- [Sexual and Reproductive Development](#)
- [Sexual Orientation and Human Sexuality](#)

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Biology of Language

► Neurobiology of Language

Biology Versus Environment

► Nature Versus Nurture

Biometrical Modelling

► Twin Studies

Biomusicology

► Evolutionary Musicology

Biosemiotics

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Definition

The term *biosemiotics* derives from the Greek root *bios* (“life”) *semeion* (“sign”) and suffix *-ika* (“study of”). Biosemiotics is thus the study of sign processing both within and between living systems.

History and Overview

The contemporary interdisciplinary research agenda of Biosemiotics has its roots in the pioneering work done by the linguist Thomas A. Sebeok (1920–2001) in bringing biologists and semioticians together to develop more fine-grained understandings about animal communication practices – and, in particular, about how those practices might underlie the evolution of human language use (Sebeok 1990, 2001).

Sebeok initially christened his interdisciplinary research project *zoösemiotics* – “a discipline within which the science of signs intersects with ethology, devoted to the scientific study of signaling behaviour in and across animal species” (Sebeok 1969).

However, as the number of researchers from various fields of study (including zoology, neuroscience, comparative psychology, and even molecular biology) began to grow, the focus of this interdisciplinary enterprise likewise expanded to include the study of signaling processes within organisms, as well as between them. Accordingly, by the 1990s, researchers in this still-developing area of study were using the term *biosemiotics* to denote the shared research agenda of exploring how signaling processes both internal to, and exchanged between, organisms could be understood as the products of evolutionary adaptation and change (Hoffmeyer 2009).

Much of the early work done in this project sought to build upon the insights of experimental physiologist Jakob von Uexküll (1864–1944) as well as the logician Charles Sanders Peirce (1839–1914) in the analysis of animal communication systems and display behavior (Favareau 2006). From von Uexküll, whom Nobel Prize winners Konrad Lorenz and Nikolaas Tinbergen called “the father of animal behavior study,” Sebeok and his colleagues incorporated the notions of species-specific sensory worlds and the imprinting of meaning upon stimuli via sensation-action feedback cycles (von Uexküll’s *umwelt* and *functional circle* ideas, respectively), while many of von Uexküll’s other pioneering ideas were simultaneously being

developed in the sciences of cybernetic feedback control and neural networking (von Uexküll 2010; Kull 2003).

Developing a “scientific logic of sign relations” was the lifework of mathematician, logician, and philosopher Charles Sanders Peirce, and many biosemioticians employ Peirce’s nested hierarchy of *iconic*, *indexical*, and *symbolic* relations (Peirce 2010) in their analyses of, respectively, primary sensory experience, object-action association patterns, and higher-level lawful behavior arising from the species-specific ways in which such association patterns are systematically organized. Most notably, Peirce’s sign logic is used by neuroscientist and biological anthropologist Terrence Deacon in his 1997 book *The Symbolic Species: The Co-Evolution of Language and the Brain*, to argue for a view of human language evolution which has its roots in earlier forms of animal sign processes, but which becomes distinctive with the uniquely human ability to create signs that signify not just real-world events and objects, but also signs that signify other signs (Deacon 1997).

With the death of Thomas Sebeok in 2001, the center of gravity for the biosemiotics project shifted to the University of Copenhagen under the auspices of biochemist and molecular biologist Jesper Hoffmeyer and the philosopher of science Claus Emmeche who, along with cybnetician Søren Brier, and the Estonian botanist and theoretical biologist Kalevi Kull, established the Biosemiotics Group at the University of Copenhagen in the early 1990s and who together hosted the first international Biosemiotics conference in 2001. That conference has been held annually, in various cities in Europe and in North America, every year since then, and the field, while still early in its development, now has its own international society, peer-reviewed journal, and book series.

Conclusion

With evolutionary psychology, biosemiotics seeks to productively bring together researchers in the life sciences, the social sciences, and the

humanities in order to develop a naturalistic understanding of the use, structure, biology, and evolution of sign processing in living systems (Kull et al. 2009).

Cross-References

- [Animal Communication](#)
- [Evolution of Language](#)
- [Information Theory](#)
- [Semiotic Constraints](#)

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Biosocial

- [Individual Differences](#)

Biosocial Approach to Sociology

- [Biosociology](#)

Biosocial Model of Social Status

- [Biosociology of Dominance and Deference](#)

Biosocial Research

- [Biosociology](#)

Biosociology

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Synonyms

[Biosocial approach to sociology](#); [Biosocial research](#)

Definition

Biosociology is an umbrella term for the contributing research areas (including but not limited to neurosociology, evolutionary sociology, and social science genomics) that studies the role of evolved biological factors (genetic, neural, hormonal, etc.) in different dimensions of social behavior, as well as being concerned with the biosocial mechanisms of social phenomena and processes at both micro and macro levels.

Introduction

Biosociology began to develop during the 1990s, growing out of findings from initiatives such as the Decade of the Brain and the Human Genome Project. Its development was significantly influenced by other disciplines (e.g., social and cultural neurosciences, evolutionary psychology, behavioral genetics, and other related science subjects), whose findings – intentionally or not – fell within the domain of traditional sociology. Partly as a response to that, social scientists have tried to incorporate biological variables into sociological conceptions combining data generated in the aforementioned research areas with those generated in sociology, while maintaining disciplinary boundaries.

Evolutionary Sociology: Applying Evolutionary Theory to Sociology

Some sociologists consider observed behavioral and other human traits as evolutionarily acquired adaptations with historic utility, but which may be of lesser value in a modern social context. Typical aspects of interest to evolutionary sociology are social phenomena and processes at the macro level, where they considered as institutionalized forms of certain behavioral adaptations. Thus, patrilineal inheritance of property as a norm in certain countries, restrictions on female social mobility, gender differences in earning potential, and other aspects of patriarchal regimes are treated as social mechanisms that facilitate maintenance of male social dominance and, from an evolutionary perspective, that allow males control over the behavior of reproductive-age females to maximize confidence in paternity (Hopcroft 2015). Among other themes, sociologists are also interested in the development of human emotionality (including its contribution to formation and maintenance of the strong social ties that allowed human ancestors to cooperate for protection against predators (Turner 2014)), systems of representation of high or low status within social groups (essentially a recapitulation of those observed in nonhuman primate society), and

underlying neurohormonal mechanisms (Mazur 2015). The major recent findings of evolutionary sociology are reflected in *The Oxford Handbook of Evolution, Biology, and Society* (Hopcroft 2018) and in *The New Evolutionary Sociology: Recent and Revitalized Theoretical and Methodological Approaches* (Turner and Machalek 2018).

In Search of Neurobiological Mechanisms of Sociality

Neurosociology centers on the association between human brain activity and micro and macro level social phenomena and processes, its role in their formation, and a reciprocal effect. The main subject of interest to neurosociology is the neurobiological mechanisms underlying social behavior in members of different social groups, taking into account variation in their position within the social structure, cultural values, political ideologies, etc. Sociologists working in this area attempt to incorporate experimental findings from neuroscience into traditional sociological concepts, as well as (albeit much less frequently) conducting their own research using neuroscientific methods and meta-analysis. Among others, current research interests focus on issues of social identity and interactions, instrumental rationality, social solidarity, mechanisms of social learning, and the neural correlates of persistent inequality. Publications such as the *Handbook on Neurosociology* (Franks and Turner 2013) and *Neurosociology: The Nexus between Neuroscience and Social Psychology* (Franks 2010) have significantly supported formal acceptance of this research area.

Genetic Factors in Social Behavior and Development of Social Science Genomics

In accordance with recent scientific findings, some social scientists estimate the weight of genetic factors – along with the social conditions under which their influence is manifested – in

contributing to sexual behavior, gender and racial differences, academic success, cognitive abilities, socioeconomic status, levels of well-being and happiness, deviant behavior, sex, and gender role behavior, etc. Such studies commonly use genetic information available in selected preexisting databases, including those maintained by the National Longitudinal Study of Adolescent Health, the National Survey of Midlife Development in the USA, and the Middle-Aged Danish Twin Survey. Polygenetic score analysis is now considered a promising methodology facilitating estimation of genetic predisposition to human traits of interest to sociologists. Thus, attempts to take into account genetic factors in the consideration of social behavior contribute to the development of social science genomics potentially within sociology (Freese 2018).

Fluid and Nascent Emerging Boundaries Between Biosociological Approaches

Boundaries between different biosociological approaches are not fixed. Thus, sociologists working within evolutionary sociology and neurosociology may investigate overlapping subject areas. For example, they may study features of neural activity associated with or affecting social behavior (primarily a focus of neurosociology) as a result of adaptive behavioral processes arising from evolutionary development (primarily a focus of evolutionary sociology). In such a case, some sociologists employ the term “evolutionary neurosociology” (e.g., when studying the role of emotions in the formation and representation of social rank differences (TenHouten 2017)).

There are also biosociological works which did not fit into any of those research areas. For example, some sociologists emphasize neurophysiological measures of social inequality (stress, health, etc.), while others emphasize the concept of transformation of social identity under the influence of the information obtained via DNA testing. However, all sociologists aim to construct more balanced (i.e., incorporating more equal weighting of biological and social factors) and up-to-date sociological concepts and theories.

Formally, social scientists, whose researches falling under the rubrics of biosociology, are consolidated into Evolution, Biology, and Society Section of the American Sociological Association (section was founded in 2007). Since 2016, the specialized Frontiers journal *Evolutionary Sociology and Biosociology* has also been published.

Conclusion

Results deriving from biosociology research demonstrate that the social behavior of modern humans is at least partly determined by stable forms of behavioral adaptations (evolutionary sociology), explained by human brain structure (neurosociology), and probabilistically determined by genetic factors (social science genomics). Despite this progress, however, the development of biosociology remains in its infancy. Perspective depends on social scientists’ level of knowledge regarding biological sciences, as well as on the willingness to adapt current sociological methodology and theory. Many sociologists attempting to develop current biosociological approaches have faced prejudice from colleagues who fear that sociology will be reduced to other disciplines, or that new approaches may encourage racism, sexism, or other forms of social discrimination. Such biophobia is partially rooted in the history of sociology, connected with E. Durkheim’s concept regarding the sufficiency of social factors to explain social phenomena, as well as with false ideological connotations accompanying the development of Social Darwinism. Given current knowledge regarding the determinants of human nature, equating the sociological with the non-biological is a significant obstacle to development of sociology as a reputable scientific discipline.

Cross-References

► [Biosociology of Dominance and Deference](#)

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Biosociology of Dominance and Deference

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Synonyms

Biosocial model of social status; Biosociology of social dominance hierarchy; Biosociology of social status hierarchy

Definition

The Biosociology of Dominance and Deference is a biology-inspired sociological approach analyzing evolutionarily evolved neurobiological mechanisms of different dimensions of human social ranking in terms of power, influence, prestige, and access to different resources which contribute to the development of traditional sociological conceptions on social stratification and social inequality.

Introduction

Dominance hierarchy is currently widely recognized as universal in the animal kingdom. It is not coincidental that this problem came to the attention of researchers from different disciplines, including neuroscience, social and cultural neuroscience, and evolutionary psychology. As a result, in the last decades many findings concerning the biological nature of hierarchical relations among animals (including humans) were obtained that are potentially helpful for the sociological understanding of human interactions based on social rankings.

Evolved Adaptations to Hierarchical Social Relations

In the perspective of evolutionary sociology, stable forms of behavioral and other traits associated with producing and maintaining hierarchical social relations are considered as evolved adaptations that promote our ancestors' survival. Adaptations to hierarchical social relations have become part of human biological nature (including structure of the brain). Individuals, who possessed ability to navigate in socially differentiated society, correctly identified rank signals, and behaved in accordance with their own position in the social hierarchy, survived more frequently in comparison with those who lacked such abilities.

Emotions (Ten Houten 2017), communication signs (Mazur 2005, 2015), and sexual behavior

strategies (Hopcroft 2016) as such adaptations have recently been studied from the perspective of sociology. Thus, it has been demonstrated that secondary emotions of “pride” (formed from angry and joy) and “shame” (which comprises fear and sadness) appear as adaptive reactions to high and low status in social dominance hierarchy. Pride allows a person to achieve and demonstrate his/her dominant position, while shame provides subdominants a means to express a deferent low-status position and avoid punishment, negative evaluation, or the help to receive necessary resources. As a result, an ability to transmit, express, and recognize emotions as a signal about dominant or subordinate status is useful for everyone, regardless of place in the social hierarchy (Ten Houten 2017).

Mazur (2005, 2015) divides all status signals according to constant and controllable signs. The first are almost unchangeable (e.g., sex, ethnic markers, age, reputation), while the last can change for representation of domination or submission in accord with the actual situation and human purposes (e.g., gestures, tone of voice, semantic content, items of dress, and accessories).

The differences in male and female behavioral strategies reflect the differences in the adaptive problems that they solved – to increase the probability of more offspring, invest only in own offspring, and get support from men during the period of childbearing and raising children (Hopcroft 2016). Such biological predispositions are expressed in the deference of young females to males (but not other young females), and the absence of the reverse (only deference of males to other males is observed), which are supposed to help females guarantee their support, material and otherwise, from males. On the other hand, such inherently discriminatory attitudes of men at puberty toward young women in many cultures increases men’s social status, which is favorable for finding mates; in accord with that is the finding in recent studies (e.g., Hopcroft 2015) of the association between the socioeconomic status of males, but not females, and the number of offspring. This also explains the status parity between adult men and women of

nonreproductive age or even higher status (Hopcroft 2009). A greater biological determinacy of female behavior toward children (childbearing, lactation, nursing), as well as existing hormonal differences between the sexes make women more attuned to children’s upbringing; this is one of the reasons why the majority of positions of power, privilege, and influence in society belong to men (Huber 2007).

Biosocial Mechanisms of Social Dominance

In biosociological studies of dominance, findings concerning the homogeneity of the basic biological mechanisms among all social primates are taken as a starting point. Thus, the neurohormonal mechanisms of the human system of reporting about high or low status are considered the same as for nonhuman primates, as are the basic signals themselves (apart from language).

As a neurohormonal mechanism, the influence of testosterone on the dominant orientated behavior as well as the reciprocal effect are tested in the context of differently mediated social factors, including anticipation of a contest, the perceived importance of the outcome, the outcome of the contest, and some others (Mazur 2005, 2015). Along with the testosterone factor relevant to the biosocial model of dominance and deference, the associations between the neurophysiology of stress and high/low human status are discussed, in particular, the biosocial mechanisms whereby high ranking persons experience stress less frequently and can intentionally impose stress on those below them on the hierarchy to maintain their dominant position (Mazur 2015). Stress, together with other neurophysiological differences reflected in human health, is now studied as a new dimension of social stratification (Groosby et al. 2018). Finally, the first attempts have been made to incorporate genetic factors in considering traditional sociological issues; these concern the intergenerational transmission of socioeconomic status in terms of educational attainment (Liu 2018).

Conclusion

Striving for high status and material well-being is rooted in human biology although it is culturally elaborated. However, no matter how sophisticated this refinement is, the biological nature of people formed in the process of long evolution has not disappeared. Understanding it allows (bio)sociologists to analyze the underlying causes of social behavior associated with the social dominance hierarchy that were formed as a result of the interaction between biological factors and the environment. Such research complements current sociological conceptions on social status and social inequality by biological factors and, potentially, makes them more complete and exact.

Cross-References

- [Adaptations for Navigating Social Hierarchies](#)
- [Biosociology](#)
- [Serotonin and Dominance](#)

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Biosociology of Social Dominance Hierarchy

- [Biosociology of Dominance and Deference](#)

Biosociology of Social Status Hierarchy

- [Biosociology of Dominance and Deference](#)

Biparental Care

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Synonyms

[Mutual parental investment](#)

Definition

Biparental care is the situation whereby male and female parents share responsibility for raising their mutual offspring.

Introduction

Across the animal kingdom, patterns of parental care vary from no care through uniparental female

or male care to biparental care where both parents invest in the offspring. Among the vertebrates, biparental care is highest in avian species where it is estimated to be the case for 81% of species (Cockburn 2006) and lowest in mammals where estimates are below 10% (Kleiman 1977). This observed variation raises the question as to what are the evolutionary driving forces for the emergence of biparental care.

The Biparental Care Hypothesis and the Evolution of Monogamy

According to the biparental care hypothesis, this pattern of exclusive cooperation in care of mutual offspring evolves when each parent achieves higher reproductive success than either can through polygamy (Wittenberger and Tilson 1980). Hence biparental care is seen as a driving force for monogamy. Support for this hypothesis has come from a number of studies involving parental removal in species of birds, fish, and amphibians (see, e.g., Møller 2000; Tumulty et al. 2014). In such studies the male of the pair is generally removed leading to a reduction in offspring survival. This has been taken as evidence that, if one parent were to perish, the remaining widowed parent would not be able to provide sufficient care for the offspring alone. The unusually high incidence of biparental care in birds is generally regarded to be a result of the extensive resource requirements for the development of flight-capable fledglings. Clearly outside of bats, this is not an issue for mammalian species.

This mammalian pattern of little or no male parental care is also the case for the majority of primate species. While some species of lesser apes such as the agile gibbon do engage in biparental care, among the great apes, male care of offspring is virtually nonexistent. In contrast, although human mating patterns vary across cultures, monogamy with biparental care is commonly observed (even in cultures where polygyny is accepted). Hence humans are, as a species, high in what Robert Trivers has described as “male parental investment” (MPI, Trivers 1972). This raises two important

questions: why is biparental care so common in our species, and what effect has high MPI had on human evolution?

Bipedalism and Biparental Care in Human Evolution

Over the last four million years, human ancestors have exhibited a rapid increase in brain volume accompanied by a narrowing of the pelvic girdle to enhance bipedal locomotion. These two, arguably conflicting, changes led to an increasingly large brain having to fit through an increasingly narrow pelvis. The solution to this problem was to give birth to a developmentally younger fetus. This, in turn, led to hominin babies being born at increasingly immature and dependent stages of development. Moreover, it also led to an increase in the length of infancy. According to the provisioning hypothesis, due to the dependency of human neonates, it paid human males to shift from polygynous mating patterns to pair-bonded ones which thereby boosted reproductive success for both parties (Lovejoy 1981). It also increased selection pressures for improved bipedal locomotion since this freeing up of the hands allowed hominins to gather and bring back a wide range of foods. Note that in this model of human evolution, bipedal locomotion and pair bonding are inextricably linked. Although the provisioning hypothesis has been criticized for being male centered, features of it are widely accepted as an explanation for the evolution of biparental care in our species. In particular, with the division of labor that human biparental care allows for (broadly speaking men hunt and women forage), the range of nutritional items increased for all in the proto-family unit. It may also be that the increase in meat in our ancestral diet allowed for the expansion of the human brain (the brain demands 20 times as much energy as muscle tissue and consists largely of protein). To some, the formation of biparental care and the resultant increase in protein and energy-rich foods available to the growing child were a watershed moment in human evolution (Wrangham 2009).

Biparental Care and Human Psychological Dispositions

Evolutionary psychologists consider that biparental care has helped to shape human psychological dispositions. Following the evolution of biparental care, the introduction of meat into the ancestral diet may be seen as a necessary precursor to an increase in brain size, but it was not sufficient. In addition to an appropriate change in diet, an increase in brain size (and the resultant increase in intelligence) can only arise if there are selective pressures for this development. An increase in MPI is known to have a number of effects on both male and female reproductive behaviors. Due to their increased effort in offspring production, males become more choosy about whom they will mate with, and females become more competitive over potential male partners (Stewart-Williams and Thomas 2013; Stewart-Williams 2017). This means that, once biparental care is established in a population, both sexes then demonstrate a degree of choosiness, and both exhibit a degree of same-sex competitiveness (it should be noted, however, that females are likely to remain the choosier sex due to maintaining a higher level of parental investment than males). Same-sex competitiveness and opposite-sex choosiness are the main components of sexual selection (i.e., the opposite sex does the “selecting” rather than the environment as in natural selection).

In 2000 American psychologist Geoffrey Miller began to champion the notion that, once biparental care had evolved, the main driving force for increasing brain size and intelligence became sexual rather than natural selection. Drawing on Darwin’s (1871) work on the relationship between sexual selection and the evolution of human abilities, he called this the mating mind hypothesis. Miller proposed that, with an increasingly dependent offspring being born into a challenging savannah environment, it paid both sexes to recombine their genes with caring and intelligent individuals (Miller 2000). Given that sexual selection can act more rapidly than natural selection, it can be argued that the emergence of biparental care was a major factor in driving both human intellectual and emotional abilities

toward the advanced levels we see today (Workman and Reader 2014).

Conclusion

Where biparental care is observed in the animal kingdom, it is seen as a driving force for monogamy. This also appears to be the case for our own species. For our hominin ancestors, the evolution of biparental care is likely to have had a profound effect on our behavior including increases both in choosiness in males and in levels of female/female competition. It may also have provided a driving force, through sexual selection, for expansion of human intelligence and cooperative behavior.

Cross-References

- ▶ [Paternal Investment Relative to Maternal Investment](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Reproductive Success](#)
- ▶ [Sex Differences in Parenting and Parental Investment](#)

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Bipedal Gait

► Bipedal Locomotion

Bipedal Locomotion

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Synonyms

Bipedal Gait; Bipedal Motion

Definition

The phenomenon of walking upright on two hind limbs, as opposed to using both forelimbs and hind limbs for running, climbing, etc.

Introduction

Bipedal motion is one of the features of modern humans that most drastically separates us from other primates and great apes. Several different theories as to how we developed bipedal motion relating to diet, terrain, and morphology have

developed and changed over the years as physical evidence has increased and refined the ways we think about hominin bipedalism. With the understanding that some theories have been discarded or severely changed since their debuts, presented here is a full analysis of each of the predominant theories of bipedal motion in humans, including those that have not been reconsidered in several years due to compromising evidence. Additionally, there are certain biological and physiological explanations for bipedal locomotion and how that anatomy compares to that of our ancestors and modern nonhuman primates.

One major assumption made by researchers is that adopting a bipedal form of locomotion was adaptive in such a way that it aided survival and carried on into modern human anatomy. The Miocene era, which was a time of dramatic climactic change around 4.4 million years ago, is the approximate time during which bipedalism is thought to have evolved (Hunt 1994). Each of the following theories cites the hypothesized environment during the Miocene era and why bipedal locomotion would have been adaptive for that environment at that time.

Geological as well as fossil evidence has indicated that the climate and environment in Africa were wetter and more lush than they are today. It is supposed that animals could have been living in an area that was relatively well covered by trees, being similar to a forest or woodland (Hunt 1994; Thorpe et al. 2007).

Since the Miocene era was a time of such change, some theorize that hominins would have begun moving from a more forested habitat, to a more open one. As they did so, they would need to develop a bipedal stance to see further, without the assistance of trees (Ravey 1976). A bipedal stance would have also assisted the animal in cooling itself when out in direct sunlight, especially since there would be less skin area coming into view of the sun while standing (Ruxton and Wilkinson 2011). It is also thought that these early hominins would have transported themselves bipedally in the trees before climbing down and continuing to be bipedal (O'Higgins and Elton 2007; Thorpe et al. 2007). Another theme in the theories of bipedalism is that

developing a bipedal gait would have freed up the arms for carrying things like tools or food (Brace 1962; Watson et al. 2007). Each of these ideas is examined in greater detail below.

Potential Origins for Bipedal Locomotion

The Miocene period was characterized by a particular group of hominin ancestors, the Australopithecines, and *Ardipithecus ramidus*. Both of these ancestors to the hominin lineage have left behind important evidence as to how they traveled, and both display lower-limb anatomy that would have likely supported bipedal motion (DeSilva 2009; Lovejoy and McCollum 2010).

Predator Avoidance

As hominins migrated towards open spaces, many may have become bipedal to cope with the wide surroundings and changes in feeding habits, especially for the smaller of these hominoids. Additionally, it has been suggested that as these animals are foraging through tall grasses and may be unable to see over them while in a quadrupedal position, the development of a bipedal stance would have aided in their ability to see threats. While this line of reasoning may not have produced bipedalism quickly, even short moments of bipedal posture may have been the difference between life and death for some of these smaller hominins (Ravey 1976).

Similar to this argument, Brace (1962) points out that Australopithecids, defending themselves from large carnivores, would have needed to use hand-held weapons and tools, since they lacked the large canines seen on other primates. Without the use of weapons, these early hominins would have been completely defenseless. Since it is clear that they survived, they must have done so by using weapons to defend themselves and developed an upright stance as a response to this (Brace 1962).

While increased viewing distance would have potentially been an immediate difference between life and death, observations of modern nonhuman primates show that they rarely engage in bipedal

forms of social display to resolve conflicts or to assist in vigilance over the social group. It has not been truly tested whether or not there would have been a significant increase in viewing distance for the australopithecines, by standing upright, and this would likely not have occurred often enough to substantiate evolving an entirely new method of locomotion (Hunt 1994).

Thermoregulation

When people walk, they use more energy and produce more heat. This heat can accumulate greatly especially on a fur-covered animal in direct sunlight (Queiroz do Amaral, Quieroz do Amaral 1996). An examination on energy usage by upright-walking hominins can provide evidence for later hair loss in hominins as we became bipedal. Ruxton and Wilkinson (2011) created a model to predict the average amount of energy humans use while walking outside in direct sunlight at different times of day. They compared results of the model between fur-covered and hairless hominins. Results indicated that fur-covered hominins would likely have been unable to walk long distances in direct sunlight, in habitats that would have looked the way Africa did. This assumes that the greatest source of heat comes from internal production from an animal using energy (Ruxton and Wilkinson 2011).

The main conclusion that these authors came to base on their analysis stated that it is unlikely that hominins developed bipedal motion *because* it would have been more energy efficient. The evidence for this is presented in the fact that walking on 2 ft produces more internal heat than merely standing, and would have made walking long distances incredibly difficult for fur-covered animals. This implies that hominins would have needed to evolve bipedal motion through other circumstances and then lose some of their hair coverage as a result (Ruxton and Wilkinson 2011). It is also hypothesized that there would have likely been a large amount of tree coverage around this time, in Africa, meaning that the thermoregulatory reasons for bipedalism likely would not have been relevant, based on the environment.

This would then cause selection for reduced hair coverage as a way to promote heat loss.

Evidence from human body parasites from around 3mya suggests that this may have been around the period when hominins were losing body hair. This is likely already one million years after hominins came definitively bipedal; however, this is a loose hypothesis (Ruxton and Wilkinson 2011). However, Queiroz do Amaral asks whether or not being hairless would have been more adaptive for regulating heat loss as hominins became bipedal, not after (1996). She suggests that loss of body hair would have occurred before or in conjunction with the evolution of bipedalism, not after bipedalism had already evolved. This is because the reduction in body hair could have compensated for the higher energy required to move bipedally, even in a potentially forested environment (Queiroz do Amaral, Quieroz do Amaral 1996).

While it may seem convincing that increased sunlight would have been an important motivator for bipedalism to occur, early Miocene habitats would have been much more covered than the environment in Africa is today. This means that while walking upright would have decreased the amount of sunlight and heat reaching an animal, there would not have been an intense need to do so because the amount of sunlight reaching the ground would already have been compromised by tree coverage. Essentially, the amount of heat reduced by standing upright in these conditions would have likely been so insignificant that adapting an entirely new form of transportation would have been unlikely and inefficient (Hunt 1994; Ruxton and Wilkinson 2011).

Arboreal Locomotion

Observations on the locomotor patterns of non-human apes indicate that the posture and gait of orangutans when walking across tree branches is different than that of other apes. Interestingly enough, orangutans appear to move through the trees in ways similar to that of modern humans moving across the ground (O'Higgins and Elton 2007; Thorpe et al. 2007). Orangutans could have developed this form of walking through branches since it appears to be safer, as they have the ability to grasp upper branches for balance. Thorpe et al. (2007) use this to later assert that one particular

early hominin, *Australopithecus afarensis*, could have been a biped at short distances.

Again, as the arboreal climate in Africa became less dense, primates had few options. It is hypothesized that arboreal bipedalism would have transferred effectively into terrestrial bipedalism, while other great apes, who were built for vertical motion in trees, would have more likely moved towards the knuckle-walking we see today in Gorillas and Chimps. This can be substantiated by certain physiological evidence found in the skeleton of modern humans. Evidence for cranial morphology that allow for the skull to sit right at the top of the spinal column in a vertical fashion suggests an upright posture, since humans have the ability to balance themselves above a central point. Lumbar and spine anatomy in modern non-human apes, they are unable to naturally balance themselves this way and therefore would struggle to walk bipedally. To adjust for this, they are forced to bend their knees and hips to achieve this balance. These features were likely not part of the anatomy of the last common ancestor that humans shared with these apes (Lovejoy and McCollum 2010). Therefore, the authors assert that the knuckle-walking we see in modern non-human primates was never a precursor to modern human bipedalism because of this necessary skeletal realignment (Thorpe et al. 2007). Other evidence provided by the skeletal remains of *Ardipithecus ramidus*, discussed in detail later, also helped to remove the presumption that humans walked with a bent-hip-bent-knee locomotor pattern (Lovejoy and McCollum 2010).

Lovejoy and McCollum (2010) hypothesize what the locomotor patterns of the last common ancestor between humans and chimps may have been like. They suggest that the LCA would have likely moved around the lower arboreal setting, as opposed to leaping across canopies at the top. This may have also put them closer to the ground, where they may have moved in small bursts as well. It is possible that this form of terrestrial transport may have occurred on four limbs instead of two, based on metacarpal evidence found in *Ardipithecus ramidus* (Lovejoy and McCollum 2010).

However, the evidence provided by *Ardipithecus ramidus* potentially provides an

important shift in these origins by making it unlikely that hominins were arboreal bipeds after a certain point in our evolution. The upright hanging anatomy seen in chimps and other apes were constructed for suspension, and modern humans have no similar anatomy that would suggest that we would have spent large amounts of time putting our arms up or putting weight on our shoulders (Lovejoy and McCollum 2010). Additionally, the anatomy of the lower limbs from remains from early hominins does not suggest they would have had the flexible ankle joint necessary for climbing or moving around in an arboreal setting (DeSilva 2009).

Because there has been substantial evidence that upright climbing in trees tends to lead to the development of a stiff lumbar spine, which would be unideal for bipedal motion, early hominins were likely not bipedal in an arboreal setting before being bipedal in a terrestrial setting. The authors mention that it would have been the differences in lumbar anatomy that fueled bipedal motion more so than pelvic anatomy, as was previously assumed (Lovejoy and McCollum 2010). Adjustments to the pelvis likely would have come after these adaptations to the spine.

Gathering and Carrying Food

Likely the most popular theory behind bipedal motion in humans is the Food-Carrying theory, which dictates essentially that hominins would have started to collect small amounts of food from trees and then would have needed to walk short distances to deposit it, or to collect more food from different trees. Studies and observational research have been done to examine how nonhuman primates cope with situations that may have been similar to those in the EEA. Research on Japanese Macaques helps provide support for bipedal locomotion as an adaptation for changes in food sources or collection (Hewes 1964).

It has already been suggested that as the environment in Africa moved from being forested to more open, early hominins would have needed to walk longer distances between food sources or may have even begun scavenging (Hewes 1964). Observations on macaques demonstrated that if one finds a food source that is too large to eat

quickly, the macaque will bipedally carry it back to a safer place. Other macaques who observed this process repeated it themselves (Hewes 1964). It appears as though the longest distance for this sprint of bipedal running or walking is usually around 30 m.

Studies on modern macaques have provided all sorts of evidence that help support this theory. A change in diet changed the behavior of the Macaques as they began to walk short distances bipedally, to access or collect more food. It is possible that they learned this in part from seeing the human observers walking on 2 ft (O'Higgins and Elton 2007).

An observational study on chimpanzees was done to test and observe the kinds of bipedal carrying behaviors they exhibited. The researchers changed the availability of certain kinds of nuts to see whether or not behaviors differed between moments of low-competition and high-competition for resources (Carvalho et al. 2012). During periods of high competition, instances of bipedal carrying quadrupled, and the number of resources carried at a time while walking bipedally was double that when the chimps were walking on three limbs. In additional studies, chimpanzees carried significantly larger amounts off food while walking bipedally in other scenarios. They were also able to transport all of their resources further, to private areas where they could be consumed without the risk of sharing. Environmental uncertainty and change may have created situations that favored those who could carry as many resources as possible (Carvalho et al. 2012).

These findings are in tangent with evidence presented by Hunt (1994). Chimpanzees prefer to gather food from smaller trees when possible and would usually be positioned on the ground while doing so. This meant that they did not have to do as much vertical climbing to get to the food they needed. If the chimpanzees of today are similar to our large-bodied primate ancestors, it is possible that these ancestors participated in similar terrestrial bipedal food gathering at smaller trees. He also noted that chimpanzees were able to collect more food while moving bipedally (Hunt 1994).

Feeding and gathering habits that combined terrestrial motion and arboreal climbing could be a potential explanation for this odd combination in Australopithecine anatomy. The evidence suggests that short bursts of bipedal walking combined with small amounts of arboreal climbing could have been the main protocol for getting food. The evidence suggests that australopithecines would have both gathered fruits by suspending themselves from branches, as potentially transported other foods across short distances on the ground (Hunt 1994).

Hypotheses concerning the carrying of tools have also been proposed; however, modern chimpanzees have been observed using and carrying tools quadrupedally, or holding a stick or rock with one limb and walking on the other three. This indicates that bipedalism is certainly not necessary to use tools, especially because there is no reason that tools need to be used while standing up. Other nonhuman primates show signs of using tools while sitting or kneeling (Hunt 1994). This implies that there would have to be other selective pressures causing bipedalism in tangent with tool use, for this to be a viable hypothesis. Infant carrying may have also influenced the evolution of bipedal motion, as the early australopithecines no longer had the flexible, grasping foot seen in other primates. Since they would have been unable to cling to their parents for long periods of time, parents would have needed to carry them (Watson et al. 2007).

Biology of Bipedalism

There is still a certain amount of disagreement between scholars on whether or not early hominins were tree-climbers, before adapting for terrestrial bipedalism. Fossil evidence indicates that bipedal locomotion likely emerged around four million years ago, again, during the Miocene period. There may have been an important split in lineage between what are now modern humans and chimpanzees, as it is hypothesized that our last common ancestor existed between four and eight million years ago, (DeSilva 2009). Many believe this ancestor would have been more closely related to modern chimpanzees than

modern humans. A comparison between the knee and ankle anatomy of modern chimpanzees and early hominins suggests that while these early humans may have been adept climbers, they were nowhere near as anatomically suited for it as modern chimpanzees are (DeSilva 2009). The joint angle of the tibia in chimpanzees is naturally bent, while that of humans is much more vertical, it would have likely been unsafe for early hominins to attempt to climb the way other primates did.

Bipedal motion in humans came with significant changes to skeletal structure. One specific change would be the fact that humans are upright, meaning the hands and arms can be used for carrying or gathering food (Lloyd du Brul 1962). Here (Lloyd du Brul 1962) insinuates that the origin of a bipedal posture came from this need to carry food, as was mentioned earlier. Additional skeletal changes include the reconstruction of the foot to be arched and elongated, the pelvis is flared, and knees are bent. Knees have also been reconstructed to maintain the weight of the human body while standing, without too much fatigue (Lloyd du Brul 1962). Additionally it is noted that flexibility in the hip and shoulder for humans is part of what defined human ability to walk on 2 ft without the added need of a tail for balance (Marks 1987).

The australopithecines appeared to have certain anatomical features that were almost transitional between earlier apes and modern humans, similar to what is seen in the later discovered *Ardipithecus ramidus* (Shipman 2010). Pelvic shape, for example, is much wider than that of modern chimpanzees, but is not nearly as bowl-shaped and circular as modern humans (Hunt 1994).

In summary of the pattern that we find in *Australopithecus afarensis*, the upper body features anatomy that appears to be ideal for arm-hanging, whereas the lower body appears to be more adept for bipedal walking. The curved finger bones and short lumbar indicate that this animal would have been a capable climber, likely hanging from tree branches to gather food (Hunt 1994; Tuttle 1981). However, the anatomy of the lower body of *Australopithecus afarensis* suggests that it would be sufficient for bipedal motion, although

this likely would have been less efficient and more stressful to the skeletal system, compared to bipedalism in modern humans. They likely wouldn't have been as habitually bipedal as modern humans are today (Hunt 1994).

Overall the comparison of morphology between modern humans, modern chimpanzees and *Australopithecus afarensis* suggests flaws in previous assumptions for the origins of bipedality. The presence of both arboreal upper anatomy and bipedal lower anatomy in *A. afarensis* indicates that their method for gathering food would have likely not been purely due to either terrestrial feeding or arboreal feeding (Hunt 1994).

Homo erectus demonstrates the first real indication of changes in post-cranial anatomy, compared to *Australopithecus afarensis*. Arboreal adaptations appear to stay all throughout the anatomy of the *Australopithecines* until the next species in the hominin lineage evolved. This is a sign that the arboreal upper body of the *australopithecines* must have been adaptive for one reason or another, of course, until it wasn't (Hunt 1994).

Ardipithecus Ramidus

In 2009, analysis was published on recent anthropological evidence that had been discovered in Ethiopia. The findings were that of 36 individuals from around 4.4 million years ago. The most complete skeleton was from a female, nicknamed "Ardi." Hers is currently the oldest hominin skeleton to date, and combined with the remains of the 35 others, provides compelling evidence that they likely walked bipedally. The full name for this group has been termed *Ardipithecus ramidus* (Shipman 2010).

It was originally believed that our large human brains evolved long before other human features such as bipedalism, or our dental anatomy, however these remains indicated that this was not the case. *Ardipithecus Ramidus* showed both indications of being bipedal, as well as having dentition that had human-like features. Much of her anatomy appears to be transitional between humans and chimps. She shares many features with both modern nonhuman apes, and modern hominins, however she appears to be evolving further away from our last common ancestor (Shipman 2010).

For many years, the remains of several different kinds of australopiths have been unearthed, all of whom are very different, but the one trait that they all shared, was that they were bipedal. While *Ardipithecus* was likely bipedal, they likely had the ability to maneuver around trees like most apes. Comparatively, their arboreal motion was likely similar to that of another early ape, the *Proconsul*, which was likely not as easy as earlier ancestors.

While *Ardipithecus* was likely not the last common ancestor between humans and chimpanzees, analyzing "Ardi's" remains can provide insight as to what that ancestor may have looked like or how it may have moved. Contrary to what may have been previously thought, *Ardipithecus ramidus* is not a transitional biped, she is a fully-established biped (Shipman 2010). As an additional hominin, she presents movement from potentially awkward bipedalism to more efficient bipedalism.

Conclusion

The evidence above provides several different and enticing arguments for the origins of bipedal locomotion. From changes in evolutionary environment suggesting the need for increased visibility, to adaptations that came from being bipedal in the previous arboreal setting. However, it appears that as more evidence on the Miocene hominins is discovered, the more complicated it becomes to explain their anatomy and potential behavior.

Modern non-human primates have demonstrated that there are ways of coping with certain environmental issues without needing to walk upright, indicating that the selective pressures that caused modern humans to evolve bipedal locomotion would have had to be intense and prolonged to justify a complete transformation in skeletal structure. To date it appears that the best evidence we have for studying hominin bipedalism comes from the recently discovered remains of *Ardipithecus ramidus*. Her anatomy still features arboreal adaptations in the upper body, but this could have been carryover from an earlier ancestor.

It is important to remember the amount of time it takes certain adaptations like this to evolve. When comparing the skeletons of modern humans with modern nonhuman apes it is clear that there was a complete structural reorganization. Even if this process started around 4.4 million years ago, it would have likely been hundreds of thousands of years before there were indications of truly bipedal skeletons, devoid of any arboreal upper body. Patience is required when sifting through the evidence, to deal with the fact that we, as modern humans, exist much further down the evolutionary line, and have much to thank our ancestors for.

Cross-References

► Bipedalism

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Bipedal Motion

► Bipedal Locomotion

Bipedalism

► Size Dimorphism and Locomotion

Bird Clutch Size

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Synonyms

Avian clutch size

Definition

The number of eggs laid in a single brood (or nest) by one or more female birds.

Introduction

Variation in the number of eggs laid in a single brood has fascinated researchers, especially ornithologists, since at least the 1940s. The number of eggs laid by a female varies enormously among taxonomic groups. Generally, it is constant and small, as in albatrosses and King Emperor penguins that lay one egg. In other species, clutch size is variable, and sometimes large, as in the partridge, which can lay between 14 and 20 eggs. The factors that are associated with the evolution of clutch size are, perhaps, one of the oldest topics in life history theory. To this end, several processes have been proposed that may influence selection on bird clutch size. Attempts to understand causes of avian clutch size variation range from intra- and interspecific studies, work on intrinsic (e.g., body mass, migratory behavior, nest type, diet) and extrinsic (e.g., latitude, temperature, precipitation, seasonality) potential drivers of such variation, to investigations of phylogenetic effects that may constrain clutch size variation. This entry provides a review of the information on bird clutch size, specifically from a perspective of the conflict of interest between parents and offspring over optimum clutch size.

David Lack and Clutch Size

The ornithologist David Lack was the first researcher to study the evolution of bird clutch size, in the 1940s (Lack 1947, 1948). Lack's work was seminal, as it attempted to explain variation in clutch size in terms of individual selection, while many researchers at the time considered that clutch size evolved to allow a population or species to persist. Lack reasoned that a bird would lay the number of eggs that maximized the number of young that successfully left the nest (i.e., fledged). In altricial birds – those whose newly hatched young are immobile and require extensive nourishment – Lack argued that the ability of the parents to feed their offspring was the main factor influencing the number of fledged young.

Lack's pioneering theory, however, assumed a harmonious setting within bird families. The theory assumed, at least for a single parent, that selection acts on clutch size to maximize the number of fledglings per clutch. However, what is optimal for a single parent need not be so for both parents, nor for the young involved.

Parent-Offspring Conflict

Conflicts of interest over the allocation of resources are a natural consequence of selection acting upon individuals that are not genetically identical. For instance, sexual reproduction leads to a situation in which parents and the offspring they produce are not genetically identical. Thus, natural selection could act in somewhat different ways on parents and their young. Robert Trivers, in the 1970s, explored the consequences and implications of this conflict in what is now known as the classical theory of parent-offspring conflict (Trivers 1974). Trivers' notable work was based upon Hamilton's rule (Hamilton 1964a, b) – another remarkable contribution that revolutionized our understanding of social evolution – to articulate a theory in which parental interests are challenged by offspring demanding more parental investment than is optimal from the parental point of view.

Briefly, Trivers' theory of parent-offspring conflict can be understood with the following simple situation (which can be extended to include other sources of conflict). The scenario involves a single parent that raises one offspring per breeding season. This parent will face a trade-off between continuing to invest in the current young and keeping the resources to improve its own survival or to invest in future offspring. The trade-off could manifest itself as several potential combinations of these mentioned life-history components. For instance, resources should be invested in the current offspring if the benefits in terms of its fitness are greater than the costs to future offspring, measured as their fitness.

Suppose that offspring, somehow, can influence parental resource allocation. The offspring

also faces a trade-off. This time, the trade-off is between resource being allocated to itself or to its future siblings. There is no doubt that the offspring benefits from receiving those resources. However, the costs, in terms of lost fitness to siblings, are substantial, because they all carry copies of the same genes. It is worth noting that the cost must be devalued by the relatedness between siblings. Therefore, the offspring will favor the diversion of resources towards itself when $benefit > relatedness * cost$, which is different from the criterion used by the parent ($benefit > cost$).

The “battleground” within which parent-offspring conflict takes place can take many forms. For instance, conflict can occur over the distribution of resources between current and future, unborn offspring, which is termed interbrood conflict. Another form of the conflict is that between members of the same brood, that is, intrabrood conflict. It is the latter that will be treated in more detail in the following section.

Clutch Size and Conflict

Most of what follows has been extensively discussed by Godfray and Parker (1991), thus readers should refer to that work for a more detailed discussion of the theory involving clutch size and conflict. For a more recent review of the topic, see Kilner and Hinde (2012). As the number of young in a clutch increases, the average fitness of the individual offspring is reduced. The main proposed mechanism underlying this decline in fitness is the competition between clutch members for limiting resources. Assuming this mechanism, clutch size is thus determined by the trade-off between the number and fitness of offspring in a clutch. What follows from this logic is that parents will be selected to produce a clutch size that maximizes the fitness returns of that clutch. The basic scenario, when all young have the same fitness, leads to the issue of augmenting the product of the number of young and average fitness. This result is known as the “Lack clutch size.”

From a parental perspective, it would be optimal if all offspring obtained their necessary share of resources, and not more, while not engaging in any type of intrabrood competition that could lead to a reduction in their fitness. Below, it is outlined how offspring competition within a brood generates conflict with the parent’s optimal “decision.” Then, an examination is presented on how competition between siblings, potentially, leads to selection on parents to reduce their clutch size. Chick hierarchies are discussed as a potential adaptation to reduce the negative effects of sibling competition. Finally, siblicide, possibly the most severe form of sibling conflict – when one sibling deliberately kills another – is discussed.

Intrabrood Sibling Conflict and Clutch Fitness

Bird sibling conflict and its evolution have most often been studied in the context of intrabrood competition between young and the evolution of begging. An assumption of how begging mediates the conflict between siblings is that increased begging translates into increased resources. In some bird species, it seems that parents allow the young to decide feeding priorities. Young frequently jostle among themselves to be closer to the parent when it arrives with food. However, in other species, parents seem to completely ignore begging, and feed, instead, the largest chick first and more frequently.

While increasing begging will, generally, lead to more individual benefits to the offspring producing the solicitation, begging can also incur costs. These costs can be experienced solely by the individual, when the costs are mainly metabolic, or they might be shared with brood mates, as with the attraction of predators that could be lured by the average levels of begging from the brood (Skutch 1949). Theoretical models predict that as clutch size increases, the reduction in parental fitness will also increase, both when costs are experienced individually or shared among brood mates. The extent of the reduction in fitness is dependent on clutch size and also on how the costs are spread among the brood. But, the main message is that competition among offspring will lead to a reduction in the fitness of the clutch.

Sibling Competition and Selection on Clutch Size

Sibling competition, as discussed above, potentially leads to a reduction in offspring fitness. Therefore, sibling conflict may act as a selective pressure that will lead to a reduction in clutch size. The underlying mechanism is that in reduced clutches, there is more resource available *per capita*. Theoretical models predict that forms of sibling conflict (namely the shared or individual costs) will usually reduce clutch size in the order of 20–30 %, which is substantial, when compared to a scenario of no sibling competition.

Offspring Hierarchies

Offspring do not all have the same competitive abilities. Several bird species begin to incubate their eggs before clutch completion, leading to an asynchrony in hatching, which leads to a hierarchy in chick size. The resulting differences in chick size are likely to be associated with different competitive abilities. Sibling hierarchies can thus influence resource distribution and competitive solicitation. The study of sibling hierarchies has been of much interest to evolutionary biologists, with as much as eight different hypotheses proposed as explanations for the evolution of the asymmetry between young. One proposition is that the hierarchy is an adaptation by the parent to reduce sibling competition. The underlying reasoning is that the hierarchy leads to a preemptive division of resources, which minimizes fitness costs raised by competition.

Siblicide

Offspring killing one another in a brood is a well-known process that influences brood size in birds (Mock 2004). Siblicide is common among raptors and also in cranes, gannets and boobies, herons, pelicans, penguins, and skuas. When siblicide occurs in a species, it may be either facultative or obligate. The former may occur when, for instance, environmental conditions are unfavorable, and parents cannot provide enough resources to fledge successfully more than one young. In species with obligate siblicide, on the

other hand, parents may lay a second or third egg as an insurance against the failure of the first egg.

Conclusion

This chapter has discussed that clutch size is often a product of several intrinsic and extrinsic factors that shape selective pressures on the number of eggs laid by female birds. Individual parents and offspring have different fitness optima, due to their nonidentical genetic constitution. This difference may lead to a conflict between each individual's interests, and the consequences of the conflict can be detrimental to both parts involved. While offspring have little – or no – influence on the determination of the number of eggs that will be laid, competition between members of the same brood has important evolutionary implications for clutch size.

Cross-References

- [Conflict Between Parents and Offspring](#)
- [Optimal Clutch Size](#)
- [Sibling Conflict](#)

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Bird Tool Use

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Synonyms

Causal reasoning; Object manipulation; Physical cognition

Definition

Birds using an unattached object as a means of (better) attaining a goal when their beak or talon is not sufficient.

Introduction

The ability to use and make tools has played a significant role in our notion of human cognitive evolution ever since Darwin proposed that our minds evolved like our bodies. Tool use was seen as one of our defining features, until Jane Goodall discovered that chimpanzees also made and used a variety of different tools. Although Goodall's observations eventually opened the door to the comparative study of tool use in other primates, otters, rodents, cetaceans, birds, reptiles, fish, amphibians, and even some invertebrates, the idea that nonhuman animals can use and even make tools has been a bitter pill for some to swallow. Tool use has become so entrenched in our idea of what it means to be human, that its very notion is intimately tied to that of human intelligence; tool use has to be a special and highly cognitive behavior. Studies in birds have been at the forefront of unraveling the tangled relationship between tool use and intelligence and revealing some intriguing findings along the way.

Some Clarifications

Once Goodall's studies had been made public, the idea that chimpanzees habitually used and made

tools was rapidly accepted, especially with the publication of photographs in *National Geographic* and ultimately film of the apes in action. Chimpanzees possess hands like ours, they have a similar visual system (and subsequent hand-eye coordination), and they have large brains. Such acceptance was not going to be so easy for birds, which do not have the same obvious manipulative limbs, comparatively small brains and supposedly reduced mental capacities. However, Gavin Hunt published an important paper reporting that New Caledonian crows (NCC) made and used two types of tools: specially shaped leaf tools differing in the number of design steps required to produce them and hooked stick tools (Hunt 1996). Other cases of avian tool use have become apparent: woodpecker finches on the Galapagos Islands removed spines from cactus to use as tools to probe into cavities and into bark to retrieve grubs, green heron used "bait" to lure fish to the surface to be more easily taken as food (Higuichi 1988), and Egyptian vultures dropped rocks onto ostrich eggs in order to gain access to the contents inside (Thouless et al. 1989). The most recent definitive survey of animal tool use by Shumaker et al. (2011) reported 35 different categories of avian tool use, including dropping, throwing, baiting, hammering, digging, reaching, inserting, and absorbing, using a variety of natural and manmade objects, across a diverse range of bird groups, but with the highest frequency found in the corvids (crows, jays, magpies, and ravens).

Despite this diversity of tool use in birds, many cases are ambiguous and not from strictly scientific sources. One issue is whether a case of object manipulation should be interpreted as tool use at all. To some degree, this depends on whether the behavior can be attributed as intentional or goal-directed. For example, black eagles and ravens have both been described dropping sticks and stones onto humans from above. This act has been interpreted both from a low-level perspective, as part of a mobbing response towards an intruder, and from a high-level perspective, as an expression of frustration. However, for both interpretations, the mechanics of the act are the same. When comparing dropping a nut onto a rock versus dropping a rock onto a nut, both actions may

be performed by the same individual as part of its behavioral repertoire; however, only the latter can be interpreted as tool use (by known criteria). Please note that deriving this interpretation does not assume that one action is more cognitively complex than the other (see later). Dropping a nut when flying may require certain skills in assessing the correct height from which to drop certain sizes of nuts, the cost: benefit ratio of height to number of conspecifics present (so that the contents of nut may be reached before competitors), the speed required to produce an adequate drop to initiate a substantial break in the shell, the appropriate surface on which to launch the nut onto, etc. (Zach 1979). By comparison, dropping a rock onto a nut may only require the application of a simpler rule – “choose the largest rock you can carry, and drop it onto the nut until it breaks”.

Another potential problem with many of the records of avian tool use is the fact that many are anecdotes, reporting only rare or single occurrences, rather than cases that have been the focus of systematic study and experimentation. This does not mean these records have no value, rather they reinforce the view that tool use in birds is rare and except in a few cases, nonhabitual. Of these cases, found only in captivity and which have been studied using empirical methods, not all subjects perform the behaviors, and the actions are only used in a specific context – the procurement of food out of beak reach.

What Is Tool Use?

Despite sophisticated tool use in a limited number of avian species in captivity (and even fewer examples in the wild), the frequency of tool use is much greater in the apes, both in terms of the diversity of tool types (and functions) and their flexibility. However, the cognition underlying tool use in birds does not appear to be less sophisticated than in apes (and there is good evidence that the physical cognition of crows in some tool-related problems is more sophisticated than demonstrated by apes). Shumaker and colleagues' (2011) survey of animal tool use documents

dozens of examples of tool use in birds, but there are some issues of ambiguity about what may be classified as **true** or **borderline tool use**. A classic illustrative example is the difference between a song thrush repeatedly bashing a snail onto a path or a large stone in order to break the shell and eat the contents. Some might argue that the thrush is using the hard rock surface as a tool (as it cannot open the shell without this external object). However, this is presented typically as borderline tool use as the bird has not detached the rock to be used as a tool that can be carried and manipulated independent of its location. By comparison, Egyptian vultures pick up rocks and drop them onto ostrich eggs in order to break open the shells and eat the contents. In this very similar case, this has been classified as true tool use, as the tool is a detached object (rock) used to procure something (food) ordinarily incapable of being accessed without a tool. Similarly, crows dropping hard-shelled nuts onto roads in Japan or California in order to crack them open on a hard surface (and increase this possibility by dropping them onto roads for cars to drive over) is not an example of tool use, albeit an impressive display of problem-solving (Cristol et al. 1997). This is also a case of borderline tool use, as even using a car to crack open the nuts is not tool use as defined.

The difference between what is viewed as tool use and what is not can be subtle, but it is important when trying to determine whether there are taxa unique tool capabilities and whether these capabilities are dependent on cognition. Perhaps most interestingly, there appear to be brain size differences between avian species that are true tool users and species that only use borderline tools (Lebeuvre et al. 2002), with the true tool users having larger (relative) brains and a larger nidopallium. Although the nidopallium has been implicated in complex cognition in birds, whether having a larger nidopallium reflects a cognitive advantage is currently not known.

Anatomy of a Tool User

Can any bird become a tool user? Are there conditions (morphological, physiological, motivational,

ecological) that make tool use more or less likely? The fact that tool use (especially habitual tool use) is rare suggests that a number of preconditions need to be in place in order for tool use to have evolved in one species but not another. This is especially clear when assessing tool use capacities in closely related species. For example, despite there being 45 *Corvus* species, only one, NCCs, habitually make and use tools. A number of other *Corvus*, such as rooks, readily use tools in captivity (Bird and Emery 2009a), but there has never been any reported case of tool use in this species in the wild. Fundamentally, why should a species evolve using a tool over evolving a physical specialization adapted for procuring the same food as acquired through tool use, such as a specialized beak? The beaks of finches on the Galapagos Islands are a classic case of morphological adaptations for foraging. Seed-eating finches have beaks adapted for eating seeds, whereas fruit-eating finches have beaks adapted for eating fruit, etc. Woodpecker finches did not evolve beaks suited to any particular diet but which are suited for manipulating tools. One problem with morphological adaptations is their rigidity. They have evolved for one purpose, which makes them difficult to apply to different problems: a seed-eating beak cannot easily be used for eating fruit and vice versa. It is not clear why woodpecker finches (or indeed NCC) did not evolve specialized beaks, but this fact may have sped up the journey to tool use in these two species. Both species have short, straight beaks that help them hold tools with greater grip strength but also with an increased control of subtle movements. A failure to specialize may have driven these species to generalize their diets (omnivory), which in turn increased opportunities for foraging on a wide variety of plant and animal species, some of which were only accessible with a tool.

These species also possess other morphological adaptations. NCCs, for example, have the widest binocular visual overlap of any bird so far tested (Troschianko et al. 2012). As such, the contralateral eye can see the working end of a stick tool held in the beak on the opposite side. However, Martinho et al. (2014) suggest that because crows prefer to hold the tool in such a way that

the tip is on the same side as their preferred eye, they control the tool using monocular vision. It is not clear what advantage either system would provide.

Tool Use in the Wild: Four Case Studies

Despite a plethora of tool use reports in wild birds, there is not the space to describe them all here. Yet, a brief discussion of some cases of natural and habitual tool use is worthwhile in order to demonstrate the diversity of different uses of objects as tools, and the range of species that use external objects for actions which their bodies alone are incapable. The cases reported here were chosen because they have been the best studied and provide unambiguous evidence for true tool use.

Egyptian Vultures (*Neophron percnopterus*)

Egyptian vultures have been observed carrying stones in their talons, carrying them aloft and then either throwing them onto ostrich eggs or picking up rocks in their beaks and carefully dropping them onto eggs. This is an example of drop tool use (Shumaker et al. 2011). An experimental study of this behavior found no evidence that this behavior was learned socially, and vultures tended to prefer rounded or egg-shaped stones rather than jagged rocks as missiles (Thouless et al. 1989). It is not clear whether these preferences relate to the stones' efficiency or the subject's previous experience. Studies have yet to be performed concerning the vultures' understanding of properties of the rock (size, shape, weight, height from which the rock needed to be dropped, etc.) or the egg (shell strength, breakage point, etc.).

Green-Backed Herons (*Ardeola striata*)

Herons across different continents have been observed using lures, such as insects, bread, twigs, and feathers held in the tip of the bill, as bait for fish, which take the bait, and then subsequently are caught by the heron holding the bait (Ruxton and Hansell 2011). This is an example of bait tool use (Shumaker et al. 2011). Seven out of

12 species of herons catch fish this way, displaying either active or passive bait-fishing. Active bait-fishing uses a lure either dropped and left or held in the bill; as such it is a supposed demonstration of goal-directed behavior. Passive bait-fishing are cases when a heron benefits from a fisherman dropping a lure or one naturally floating in the water, and then taking the fish attracted to that lure. It is not clear how active bait-fishing developed, perhaps after forming a causal link between observing a fish take a bait and intentionally using a bait to catch a fish. Although individual differences in this behavior have been studied, subsequently finding that not all individuals perform this behavior or they differ in the level of their skill (and subsequently success), little is known about the underlying cognitive abilities involved (Higuchi 1988).

Woodpecker Finches (*Cactospiza pallida*)

Woodpecker finches are found exclusively on the Galapagos Islands, primarily Santa Cruz. They use twigs or cactus spines (either found or naturally detached) which they hold in their beaks to poke into bark to dislodge their prey, wood-boring beetle larvae. This is an example of probing tool use (Shumaker et al. 2011). In many cases, the finches modify these tools, shortening them so they are easier to handle. This form of tool use seems to be innate, as juvenile finches do not need to observe an adult before they use their first tool (Tebbich et al. 2001). However, whether finches use a tool depends on where they are located on Santa Cruz and the season. Tool use only occurs in the arid zone and only in the dry season. In the wet season, the grubs move to the surface and so can easily be accessed without tools, whereas in the dry season, the grubs bury themselves deep under tree bark (Tebbich et al. 2002). Finches acquire approximately 50 % of their total food from prey captured using tools in the dry season in the arid zone.

New Caledonian Crows (*Corvus moneduloides*)

Like woodpecker finches, NCCs appear to fill in the ecological niche usually occupied by woodpeckers on the mainland. Huge grubs are found under tree bark or buried within leaf litter that are

unreachable without a tool to prize them out. NCCs use three types of tools: probing tools of different shapes made from the tough, barbed leaflets of *Pandanus* plants and sticks either with or without hooked ends (Hunt 1996). Both tools are created using a multistep process (see “Tool Manufacture”). Both types of tool utilize a hook, either natural barbs located on one side of the leaf or a hook that is created and then fashioned by removing the stick from the original tree. These hooks function in levering a grub from out of its otherwise inaccessible hiding place. There are four main types of leaf tools: wide, narrow, single step, and multi-step, with the narrow and multi-step the more complex to make. These different types are not found distributed equally across New Caledonia, suggesting that the different tool types are either environmentally constrained in some way (e.g., by the amount or quality of the raw material), which is unlikely as they are made from the same plant, or individuals have adapted an original design into innovative new designs that have been copied and taken elsewhere, which has been proposed as a case of cumulative cultural evolution (a trait that has been suggested to be uniquely human). This process could have been the result of crows learning a new design from watching other crows or possibly extrapolating from the leaf counterparts left after a tool is made, then moving to a different population (perhaps after leaving the family) and the new design spreading through the new population.

Tool Use in Captivity: Three Case Studies

Despite the limited number of birds that regularly use tools in the wild, there are other birds that are capable of using objects as tools in captivity. Why? Most birds are beautifully adapted to gaining and processing food with bodily adornments evolved through millions of years, namely beaks (and feet; parrots). Although tool use may provide a cognitive constraint on whether tool use evolves in one species, but not another, we think this is unlikely in closely related species, especially those for which we find evidence for

similar cognitive abilities in tasks not dependent on using tools (Teschke et al. 2011). It is more likely that ecological and/or morphological constraints have driven one species to use a tool and not another. Indeed, there is accumulating evidence that tool users do not outperform closely related species on tool-related or other cognitive tasks (see below).

Goffin's Cockatoos (*Cacatua goffini*)

Goffin's cockatoos are typically found in Indonesia but are a popular pet. They have not been reported to use tools in the wild, although little field work has been performed on this species, due to difficulties in tracking them in the dense forests where they live (a pattern seen for many Psittaciformes). However, a single individual, Figaro, housed in a large captive group in Vienna, Austria, was discovered to have taken long elongated splinters from his wooden aviary to rake in an out of reach cashew nut (Auersperg et al. 2012). Figaro made the tool shorter, presumably so that it was easier to handle. Parrots are relatively rare tool users, probably because the types of foods they naturally encounter and subsequently incorporate into their diet – despite being tough skinned or possessing shells – can be processed using a combination of very tough beaks that shear and smash and gripping feet that hold such items steady when being manipulated with the beak. In this current example, such anatomical adaptations would have been useless for the simpler act of retrieving an out of reach object.

Kea (*Nestor notabilis*)

Kea are alpine parrots living in the mountains of the Southern Island of New Zealand. Like many island birds, they have quickly taken over niches typically occupied by other animals, in the case of kea, carrion birds (although like other carrion feeders, they are omnivorous). Compared to the beak of a cockatoo, which is ideal for crushing and peeling off the tough shells of nuts and the skin of hard fruit, keas beaks are curved and adapted to tearing flesh. This they do, even on live sheep, to the consternation of farmers. As with cockatoos, there may be little reason for kea to use tools in the

wild, but in captivity they can use sticks as tools (Auersperg et al. 2011). Numerous cognitive tests have revealed that kea solve novel problems, especially when learning from others (Huber and Gajdon 2006).

Rooks (*Corvus frugilegus*)

Rooks are corvids that have a wide distribution across Europe and Asia as well as an introduced population in New Zealand. Their behavior has been studied quite extensively, especially their breeding biology and social interactions, yet there are no reports of them using tools. This might be because they have rather long beaks compared to other crows, which are used for digging deep into soil for earthworms as well as creating elaborate cache sites. Such an anatomical adaptation leaves little requirement for a tool. It is a different story for captive rooks who have demonstrated the flexible use and understanding of tools, such as stones and sticks in multiple problem-solving contexts (Seed et al. 2006; Bird and Emery 2009a, 2009b). For example, when presented with a puzzle-box in which a collapsible platform held up by a magnet can be triggered to release the treat it is holding up, it took only five trials for a number of rooks to learn the affordances of this task (where stones could be accidentally knocked into the puzzle-box, and therefore demonstrate how it works). The birds rapidly applied this knowledge to using the best tool for a specific function, such as dropping a large stone into a wide tube or a small or thin stone into a narrow tube. In a different task, in which a small bucket containing food was located at the bottom of a tube, rooks were provided with wooden V-shaped hooks, either functional (the V was turned upright) or nonfunctional (the V pointed downwards). Rooks spontaneously chose the functional hook to retrieve the bucket and get the reward (Bird and Emery 2009a).

Is Nest-Building an Example of Tool Use?

Another consideration that is almost unique to birds is the question of whether nest-building is

a specialized form of tool use. Until recently, this would not have been seen as an important question, as the act of nest-building was seen as a purely instinctual behavior, under genetic and hormonal control, and little within the realms of comparative cognitive science (Hansell 2000). However, recently the psychological processes underlying nest-building have become the focus of intense scrutiny (Breen et al. 2016), revealing hitherto unheard of roles for learning and physical cognition that lend themselves to a more complex interpretation of this ubiquitous behavior. If we apply the definition of tool use to nest-building, mechanistically they are very similar. Indeed, in some respects, nest-building is a more complex mechanical process than all known forms of avian tool use (Breen et al. 2016). However, the fact that a behavior appears complex does not mean that it is complex. So it is with tool use, so it (probably) is with nest-building. However, the very same actions that are essential for selecting an appropriate tool and using it correctly within a specific context are basically the same processes for both tool use and nest-building. This area is in need of further research.

Tool Use and the Avian Brain

Tool use is dependent on a wide suite of abilities, such as motor skill learning, beak(hand)–eye coordination, and causal reasoning. This is amplified when considering a taxon which does not have hands, and has to both hold and manipulate an object using the beak (and very occasionally the feet), that is located close to their eyes. As such, tool use should also be dependent on a highly evolved brain. Although there are no studies of the neural basis of tool use in birds, a number of correlates between the propensity to use and make tools and some measure of the brain (absolute and relative size of the whole brain, pallium or subdivisions of the pallium, size of the cerebellum or its subdivisions, or even specialized neurons) have been reported. For example, there is a clear relationship between brain (and nidopallium) size and the frequency of reported cases of true tool use (Lefebvre

et al. 2002), which is more prevalent in corvids and parrots (which tend to have larger brains anyway). Within corvids, NCCs have larger association areas, such as the nidopallium and mesopallium than other corvids (Melhorn et al. 2010), but it is not clear what this size increase actually means with regard to cognition.

Even if we accept that cognition plays some role in tool use (however, see below), we are less likely to argue that it is not a complex manual skill. As such, we might expect that the area of the brain most closely associated with manual dexterity and motor learning, the cerebellum, should be different in tool users compared to nontool users. Indeed, tool-using birds have a more significantly folded cerebellum (i.e., increased foliation) than nontool using birds (Iwaniuk et al. 2009). Again, how this relates to the production of a complex skill is unknown.

Is Tool Use Intelligent?

Despite the ubiquity of tool use across the animal kingdom, to the public, the ability to use a tool is synonymous with intelligence: humans can use tools, so any creature that can also use a tool must be intelligent. Is there any experimental evidence to support this claim? Comparative psychologists have designed a number of clever tasks in an attempt to reveal what an animal may understand about the property of an object that allows it to be a functional tool in one context but not in another. Tasks have also been designed to establish whether animals understand the concept of causality; that their actions in using a tool have specific consequences (effects). Perhaps surprisingly, animals that are highly proficient tool users in the wild are no better at using tools appropriately in a problem-solving context in captivity. For example, a classic test of causal reasoning is the trap tube task. A subject is presented with a transparent tube, with food located at its center. On the underside of the tube is a trap into which the food will fall if moved into it. To remove the food from the tube, the subject has to insert a tool and use it to maneuver the food out of the tube while avoiding the trap. Chimpanzees,

capuchins, and woodpecker finches eventually learn after dozens of trials to produce the correct behavior (insert a stick into the correct side) and remove the treat (Emery and Clayton 2009). However, when the tube is inverted, so the trap no longer presents an obstacle to removing the treat, subjects persevere on poking the tool into the side in which they had previously been successful. Some commentators have stated that this suggests these subjects do not understand the task, despite the fact that the rational choice is to continue what has been previously been successful. An adaptation of this task, with the addition of a nonfunctional trap in which food can either fall through or pass over a solid base (two-trap-tube task), was also adapted for use by non-tool-using species, such as rooks, by presenting a tool already inserted into the tube, so all the subject had to do was pull from the correct side to avoid the functional trap. Rooks were capable of solving both adaptations more rapidly than chimpanzees could solve the original task, transferring to the alternate version, and one bird also solved a version in which possible learning cues were removed, suggesting causal reasoning (Seed et al. 2006). NCCs tested on a similar version performed like rooks and also transferred to a novel trap table task (Taylor et al. 2009), whereas there was little evidence that woodpecker finches could solve this task, with the exception of one bird (Teschke and Tebbich 2011).

In order to determine whether tool users possess an advantage over nontool users in terms of cognition, one needs to design a task that tests for physical reasoning but which is not dependent on the animal performing the task being a tool user. The two-trap tube task asks the subject nothing more than the ability to pull a stick; the cognitive requirements are dependent on the ability to discriminate between different courses of action and their consequences. A different task designed for tool users and nontool users alike is the collapsible platform task (Bird and Emery 2009a). A perspex box with a vertical tube on top contains a platform inside held upright with a magnet. Dropping an object of sufficient weight/size/shape into the tube dislodges the platform and releases a reward to the

subject. By adjusting the width of the tube and the strength of the magnet, a subject can be tested for their understanding of what constitutes a functional tool. For example, a large stone can be placed into a wide tube but not a narrow tube or a small stone may be too light to displace a stronger magnet or a long stone may fit inside a narrow tube, but only if oriented lengthways. Bird and Emery (2009a) tested rooks on a series of these problems after initially training them to place stones into the tube on top of the test box (using shaping and rapid learned). The rooks performed successfully on the first or second trial of every problem they were presented, including transferring to sticks of different sizes and shapes, as well as presenting cases where on a previous trial they had been successful (i.e., the tool was functional), whereas on the next trial the context changed, and the same tool was no longer functional. The rooks were also successful on sequential tool use tasks, in which they had to choose one tool in order to gain access to a second tool that could be used to access food.

A different task in which subjects were required to drop stones into a tube was designed around an Aesop's Fable called "The Crow and the Pitcher" in which a thirsty crow spies a pitcher of water, but the level of the water is too low for the crow to drink. The crow hits upon the idea to add stones to the pitcher, so raising the water to a high enough level to drink. Bird and Emery (2009b) designed a comparable task with a tasty treat floating on the surface of the water. Rooks (with experience of the collapsible platform task) started adding stones into the water-filled tube until they could reach the worm on the surface. They tended to choose the largest stones and rapidly learned to avoid placing stones into a sand-filled tube when presented alongside a water-filled tube. Additional studies using the Aesop's Fable task have been performed on other non-tool-using birds such as Eurasian jays (Cheke et al. 2011) as well as tool-using New Caledonian crows (Taylor et al. 2011; Logan et al. Taylor 2014) with a number of very clever variants designed to determine whether the birds' performance was due to instrumental conditioning, causal reasoning, or even insight.

Importantly, there does not appear to be any difference between the performance of tool-using crows and other non-tool-using corvids.

Conclusion

Birds as a group are as proficient tool users as primates, but their interest in tools tends to be restricted to the acquisition of food. By comparison, primate tool use is more diversified across different technical and social functions. It is not yet clear what role tool use may have played in the evolution of avian cognition, as so few species regularly use tools in the wild, and the performance of tool-using and non-tool-using species on tests of physical cognition does not appear to differ. It is suggested that tool use in birds may have evolved as the consequence of morphological adaptations and environmental factors, rather than some increase in brain power leading to cognitive specializations.

Cross-References

- [Brain Size and Intelligence](#)
- [Causal Reasoning](#)
- [Cephalopod Tool Use](#)
- [Confounding Use of Tools on Physical Tasks](#)
- [Convergent Evolution of Intelligence](#)
- [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- [Corvids](#)
- [Evolution of Tool Use](#)
- [Fish, Amphibian, and Reptile Tool Use](#)
- [Innate and Learned Tool Use](#)
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- [Meta-Tool](#)
- [Nonhuman Tool Use](#)
- [Primate Tool Use](#)
- [Proto-Tool](#)
- [Role of Experience in Tool Use](#)
- [Sequential Tool Use](#)
- [Stick Tools for Foraging](#)
- [Tool Use](#)
- [What Makes a Tool](#)

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Birds

- [Corvids](#)
- [Fairness in Corvids](#)

Birth Attendants

- [Birthing Complications](#)

Birth Control

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Synonyms

[Combined oral contraceptives](#); [Hormonal contraceptives](#); [Hormone-based contraception](#); [Oral contraceptives](#); [Ovulation suppression](#)

Definition

Any method that prevents the conception of offspring in sexually active women.

Introduction

Birth control became popular in the 1960s when it was introduced to the public as a means of preventing unwanted pregnancy, which has played a major role in the movement of sexual liberation for women (Cobey et al. 2011). Birth control is unique to humans because it grants women the decision to choose who they want to conceive offspring with while giving them the liberty to engage in copulation with those they do not want to bare children with. Of course, sexual intercourse without the implication of pregnancy only works if the method of birth control is used correctly. Hormonal contraceptives work by mimicking pregnancy in the female body through the implementation of synthetic hormones like estrogen and progesterin, disrupting the natural hormonal cycle. It does this by preventing ovarian hormone production. Also, since such a method is evolutionarily unnatural, there are several physiological, psychological, and behavioral implications for taking birth control. Additionally, recent studies on birth control have revealed partially concealed ovulation across humans, since it has been shown that naturally ovulating women emit more signals to the opposite sex during peak

ovulation with men detecting such signals for successful mating as compared to unnaturally cycling women.

The Evolutionary Roots of Birth Control

In present day, there are several different types of hormonal contraceptives on the market ranging from oral contraceptives (i.e., birth control pills) to the use of a patch that absorbs hormones through the skin and into the bloodstream. Oral contraceptives are the most popular form of birth control, making up 82% of all birth control users (Wellington et al. 2012). Other methods of hormonal birth control with varying effectiveness include vaginal rings, injectables, and implants. Methods of birth control that do not emit hormones in order to interfere with the natural ovulatory cycle include IUDs (i.e., intrauterine devices that are inserted in the uterus and into the fallopian tubes, blocking the sperm from fertilizing eggs located in the ovaries of women), condoms (both female and male), and sterilization. Lastly, women can track their ovulatory cycles to predict whether or not they are experiencing peak ovulation and only choose to have sexual intercourse on the days they are least likely to get pregnant. Of course, this type of birth control is the least effective when it comes to both contracting sexually transmitted infections (STIs) and preventing pregnancy. That is, the human body is designed to get pregnant, and each body has its own unique biology, so it's better to be safe and use other methods of birth control alongside the natural method.

As aforementioned, women are more likely to conceive a child during peak ovulation. According to the typical female ovulatory cycle, there are 5 to 6 days during a complete cycle when women can conceive (Carmen et al. 2013). The ovulatory cycle lasts about 28 days with the conception period occurring at the beginning of each cycle. There are three total phases in the ovulatory cycle: menses, follicular, and luteal. During the luteal phase, the risk of pregnancy is at its lowest, and progesterone levels are at its highest point. Ovulation occurs

during the menses cycle and for only 1 day out of the 28-day cycle. On this day, the vagina produces a substance chemistry that allows sperm to survive in the female reproductive system. That is, during this time period, the sperm is capable of fertilizing an ova over the course of about 5 days, as long as it is encapsulated in the right fluid chemistry at room temperature. On the days where the window of peak ovulation is not open, the female vagina actually produces a fluid chemistry that has a spermicidal effect, making it much harder to conceive a child on those days. Such a complex cycle explains why humans did not conceive an insurmountable amount of offspring during ancestral times and why the use of natural birth control (i.e., having intercourse in accordance to one's ovulatory cycle in order to increase or decrease the likelihood of pregnancy) is more effective (75–98%) than many might think. On top of that, women were usually pregnant or breastfeeding during ancestral times, which prevented them from ovulating frequently.

During peak ovulation, it has been observed that women behave differently as compared to times when they are not ovulating, assumedly to attract more desirable mates for reproductive success (Carmen et al. 2013). According to Gangestad and Thornhill's (1998) ovulatory-shift hypothesis, women are more likely to engage in behaviors to attract mates during periods of high fertility. Such behaviors include sexual opportunism (i.e., making sexual advances when available) and more positive attitudes, sexual interest, infidelity, and willingness to engage in sexual activity with unfamiliar men (Geher 2014).

These behavioral changes during the ovulatory cycle are related to mating intelligence (MI). Mating intelligence is considered to be the reproductive system of the mind. In other words, MI is the degree of cognitive ability to successfully engage in proper mating strategies that will increase the chance of choosing the most fit partner to assure the reproduction of vital offspring. Cognitive abilities that comprise of MI include mate choice, acquiring the targeted mate, mate retention, and mate decisions regarding the dissolution of

courtship. Additionally, predictors of high MI consist of greater and more frequent acts of both giving and receiving oral sex (i.e., indicators of courtship and determining mating value) and reproductive success (RS). Sensibly, it has been observed that MI significantly increases during peak fertility as preferences to access “good genes” increase. Because birth control interferes with the natural ovulatory cycle, the absence of peak ovulation in women on hormonal contraceptives makes it less likely for them to experience a spike in MI during times when they would usually be ovulating (Carmen et al. 2013).

As mentioned, hormonal birth control works by mimicking pregnancy in the female body through the implementation of synthetic hormones like estrogen and progesterin, disrupting the natural hormonal cycle. Because the female body believes it is pregnant, it cannot go through its natural process of fluctuating hormones suitable for reproductive success. In other words, the female body already thinks it succeeded in conceiving a child, so it does not need to go through the process of ovulation for the duration of the pseudopregnancy or the length of time the female is using birth control.

During a natural ovulatory cycle, estradiol levels are highest at peak ovulation. These high levels of estradiol are believed to be the cause of behavioral changes observed across women, elevating mating intelligence. Additionally, men are more receptive to such behavioral signals indicating a rise of MI. For example, a study performed on female strippers reported that men are far more likely to tip female strippers when they are ovulating as compared to female strippers who are not ovulating or who are on birth control. Such estradiol-linked MI behaviors that could account for this phenomenon include elevated female initiations for sex, a greater masculine preference, more risk-taking behaviors, an elevated tendency to wear skimpy clothing, higher instances of erotic movement and dancing, and more symmetrical body parts (Geher 2014). In addition to bigger tips, males reported feeling more attracted to the voices and scents of ovulating women. Men also found photos of ovulating women to be more attractive. In

accordance, these findings are linked to a concept known as concealed ovulation.

Concealed ovulation is when female organisms and their suitors are unaware of when females are ovulating. Due to findings that support a change in female behaviors and male receptiveness during female peak ovulation, it turns out humans experience a more low-key form of overt ovulation. That is, if female humans really had concealed ovulation, their mating patterns would stay the same regardless of whether or not they were ovulating or on birth control. Because of this, it is more suitable to say that human females experience partially concealed ovulation, since most of their elevated mating behaviors during peak ovulation are somewhat below awareness or the threshold of consciousness.

Since hormonal birth control is not a natural mechanism in the human species, it understandably does not go without its physiological, psychological, and behavioral implications or side effects. In a sense, birth control goes directly against the environment of evolutionary adaptiveness (EEA). According to the evolutionary theory, all organisms are meant to survive and pass on their genes through reproductive success. Birth control halts that natural process. That is, with the freedom for women to control their own fertility, there are inevitable consequences.

On a physiological level, birth control has been shown to elevate the risk of myocardial infarction (heart attack), ischemic stroke, and blood clots. On the other hand, birth control has also been shown to decrease the prevalence of ovarian and endometrial cancer (Welling et al. 2012). Psychologically, birth control has been reported to elevate intense affective responses toward infidelity and sexual jealousy, which is thought to be a consequence of synthetic estradiol in birth control, but not due to synthetic progesterin (i.e., another substance that is usually in birth control). Other psychological effects include higher rates of depression and a decreased interest in sex.

Juxtaposed with the increased MI behaviors experienced by naturally cycling women during peak ovulation, women on birth control experience a whole host of different “synthetic-hormone-induced” reactionary behaviors. Such

reported behaviors include greater mate retention tactics (e.g., emotional manipulation, physical violence, intrasexual competition) from increased levels of emotional jealousy, greater engagement in short-term mating as compared to long-term mating throughout the entire ovulatory cycle, more sexual partners, and reduced sexual functioning (Welling et al. 2012). Overall, the absence of natural hormones throws typical mating strategies out of whack and decreases cyclical and perhaps more beneficial mating intelligence tactics across women. The trade-off, of course, is preventing pregnancy, which is a result of our Western cultural landscape at a time where personal success has the tendency to trump building a family at a young age.

Aside from the negative implications of birth control, there are objective differences between women who use birth control as compared to women who do not. One difference is affect variability. Naturally cycling women experience greater affect variability during their cycle than women on birth control. That is, many women experience greater mood stability while taking birth control because there are no longer mood swings associated with the varying influx of hormones during the natural ovulatory cycle. In addition, this stabilizing effect is especially true for women who experience intense premenstrual emotional symptoms associated with low progesterone to estrogen ratios (Oinonen and Mazmanian 2002). The greatest difference in affect variability occurs during menstruation (i.e., withdrawal bleeding) when naturally cycling women have a tendency to experience elevated negative mood states as compared to unnaturally cycling women.

Interestingly, Natale and Albertazzi's (2006) study on mood swings across the menstrual cycle found that there were only significant mood differences between naturally cycling women and those who were on birth control when the women who were on birth control had premenstrual syndrome. Despite this, the ovulatory cycle (natural or unnatural) generally does impact mood and mood patterns across all women, especially when it comes to depression-dejection symptoms. For all women, it is typical for mood to

worsen before menstruation and for mood to lighten post-menstruation. Overall, birth control pills help to better stabilize mood in women suffering from premenstrual syndrome, but do not significantly (albeit slightly) stabilize or improve mood across healthy individuals. These findings suggest that more research needs to be done in order to determine how much birth control really does affect cyclical mood states during the ovulatory cycle but suggests differences do exist, especially for those who suffer premenstrual symptoms out of the range of normalcy. The takeaway here is that the differences are more subtle than one might think.

Another studied change in behavior between naturally and unnaturally cycling women is sexual interest and response (Graham et al. 2007). Birth control decreases the level of testosterone in a woman's body, which is responsible for a healthy libido. Because of this, it has been reported that women who have been on birth control for at least 3 months show a decrease in sexual interest and response. Also, according to Graham et al. (2007), there is a relationship between decreased libido and a lower frequency of sexual thoughts across birth control participants. However, despite these findings, many birth control participants did not experience a lowered sex drive or lowered sexual satisfaction with their partner. Such findings suggest, again, that more research needs to be done on how much the testosterone-lowering effects of birth control actually change sexual behavior. Because birth control is used so prominently across Western cultures, such apparently negligible differences don't appear to be enough for women to stop using contraceptive birth control.

One more difference between birth control users and nonusers is the aforementioned difference in affective jealousy. Women who are on birth control have reported experiencing higher overall levels of jealousy as compared to non-birth control users. Such a finding suggests that state jealousy must be hormone sensitive, and it has been deduced that estrogen levels are the culprit (Cobey et al. 2012). In other words, naturally cycling women experience more jealousy in their most fertile state, when estrogen levels are

high, while women on birth control experience a more steady yet consistently higher level of state jealousy throughout the entire cycle as compared to naturally cycling women in their non-fertile state. In addition, women, taking oral contraceptives who are paired, experience more jealousy than women taking oral contraceptives who are single. Overall, such an interesting finding posits that birth control alters mating intelligence and thus mating strategies in bizarre ways and perhaps plays a role in negatively impacting romantic partnerships.

An additional study conducted by Cobey et al. (2011) supported his previous findings on the relationship between estradiol levels and self-reported jealousy across women, by showing that elevated levels of ethinyl estradiol affect all types of operationalized jealousy. These jealousy types include reactive, possessive, and anxious jealousy. On top of that, the results remained significant even after controlling for relationships status, age, and mood. Lastly, this study found that there is no correlation between self-reported jealousy and progestin dosages, which further supports that estrogen and its synthetic counterparts are the jealousy-inducing culprits.

In the previous discussion, we have viewed birth control through the lens of hormonal contraceptives. Since birth control can be conceptualized as any method that prevents the conception of offspring in sexually active women, it's interesting to note how birth control might have been implemented in the ancestral landscape, before the rise of medicine. A fascinating theory to examine is the reproductive suppression hypothesis for explaining eating disorders (Wasser and Barash 1983). The reproductive suppression hypothesis posits that females suppress their reproduction when the current conditions are not in favor of reproductive success or offspring survival. That is, the female believes that the benefits of suppressing reproduction (i.e., depleting fat stores to the extent of stopping the ovulatory cycle, amenorrhea) outweigh the costs and that resources will be more plentiful and readily available in the future to assure reproductive success. This reproductive suppression is done through extreme dietary behaviors, and

preferring a thinner body ideal can be a way to manipulate the timing of reproduction.

In addition, a variant of this hypothesis was proposed by Surbey (1987). Surbey theorized that females can become anorexic as a way to stunt development. If a female is predisposed to mature earlier in a modern-day society that favors late maturers, anorexia is a way to change a female's natural developmental trajectory to one of a late maturer. Again, this is done by reducing fat through strict dietary behaviors. The benefit of late maturers in modern society is that it takes reproduction (i.e., reduces libido, attracts fewer males, induces amenorrhea) out of the equation when academic and professional success is more valued in the female's family. Overall, anorexia nervosa may explain an extreme method of birth control in ancestral times that has span of control in the modern landscape.

Conclusion

Birth control is a means of preventing unwanted pregnancy and is unique across modern human females. Birth control within itself goes against EEA causing a whole host of negative implications while defying the main objective for all living organisms to survive and successfully reproduce. Overall, much more research needs to be done on both the negative and positive implications of birth control.

Cross-References

► Contraception

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Birth Gaps

- [Birth Spacing and Birth Order](#)

Birth Interval

- [Birth Spacing and Birth Order](#)

Birth Level

- [Birth Spacing and Birth Order](#)

Birth Order

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Synonyms

[Family constellation](#); [Family order](#); [Sibling order](#)

Definition

The idea that the order in which a child is born within their family has influence over their development and personality.

Introduction

Birth order theory is the idea that the order in which a child is born within their family has influence over their development and personality. The theory was originally introduced by psychotherapist Alfred Adler in the 1920s (Eckstein and Kaufman 2012). Since Adler's initial research, others have attempted to make contributions to the theory. However, research has resulted in inconsistent findings attributed to confounding factors that arise from the multifactorial context of family environment, thus, leaving birth order's influence on development and personality a debated scientific topic.

Cognitive Development

Some studies suggest that cognitive development, such as intelligence, personality, and sexuality, can be affected by the order of an individual's birth within their family. Several of these previous studies have concluded that first-born children have slightly higher IQ's than later-born children (Belmont and Marolla 1974;

Rohrer et al. 2015; Silles 2010). Furthermore, IQ was found to decrease roughly 1.5 points per birth order position, and, overall, a randomly selected first born child is 52% more likely to have a higher IQ than a randomly selected second born child. This effect was found to be even greater when compared within the same family (Rohrer et al. 2015). Robert Zajonc attributed these effects to a model he first introduced, called the confluence model, which examines the development of individual differences in a social and environmental context. His research suggests that the lack of other siblings allows a first-born child to begin their development in an environment surrounded by adults and adult level intellect (Zajonc and Sulloway 2007). However, this model does not apply to only children and found that first-born children further benefit from the “tutor effect” in which older siblings help and teach their younger siblings, furthering their own proficiencies while doing so. Additionally, the model predicts “functional first-borns,” which are children who have a sibling at least 5 years older, that then benefits from the same or similar intellectual increases and may outscore the older sibling on intellectual testing (Zajonc and Sulloway 2007). The confluence model considers confounding and interrelated variables that influence an individual’s intellectual development in regard to birth order, taking into account factors such as the spacing between children and family size that influence the context of a child’s opportunities and resources for development within the family.

Researchers have found that similar social and environmental constructs surrounding birth order affect personality development. More current research regarding birth order and personality focuses on Frank Sulloway’s Big Five personality traits, which include extroversion, neuroticism, agreeableness, conscientiousness, and openness (1996). Sulloway took an evolutionary approach and suggested that personality was an adaptation to family dynamics (such as disparities in age, size, and power), which translate into personality differences between siblings that depend on birth order (Sulloway 1996). Rather than birth order itself being the

independent cause of personality, it is acclimatization to the surrounding environmental and social needs (that results from the order of birth) that shapes the individual. For example, since first-born children often take a parental or guiding role towards younger siblings, they tend to develop strong leadership qualities – making first-borns more controlling and dominating (Eckstein and Kaufman 2012). Because of their dominance, first-borns tend to be less agreeable, whereas later-born children tend to become more extraverted as they work to assert themselves. Being parental surrogates causes first born children to score higher on conscientiousness. First-borns and later-born children experience different kinds of openness to experience with first-borns scoring higher in objective intelligence and later-born children tending to be more imaginative due having to explore how they fit in a pre-existing family environment. Within the emotional stability category, first-born children are predicted to be more anxious and neurotic, whereas later-born children are predicted to be more depressed, self-conscious, and impulsive (Rohrer et al. 2015). Although there are various studies that explore the relationship between birth order and personality, many are confounded by the difficulty to control the variables studied that are statistically related to birth order (such as family size and social and economic demographics). Because of this, there are conflicted findings, especially in regard to personality and the Big Five, in which limited hypothesis have been proven true.

Beyond intelligence and personality, birth order has an effect on one’s sexual orientation as well, most notably with men via the fraternal birth order effect. This theory states that men have a greater probability of homosexuality the more older brothers they have, by an increase of 33% per each older brother. The same cannot be said for women, males with multiple younger siblings, or males with multiple older sisters. (Blanchard 2001; Bogaert 2003). Researchers believe this may be a byproduct of past human behavior that would inevitably reduce the probability of sons to compete among each other or with first or earlier born sons (Bogaert 2003).

Ultimately, this aspect of personality is influenced by birth order, but only under certain circumstances.

Physical Development

In some circumstances, birth order has effect on the physical development of humans. Similar to sexual orientation, having older brothers can affect the height of a man. This influence, again, may be a byproduct that shifts competition away from the oldest son (Bogaert 2003). Bogaert found that, when controlling for biological mechanisms, older siblings tend to be bigger than younger siblings (2003). Although, in regard to overall physical performance, later-born children tend to perform higher than first-born and only children. This higher performance is likely due to later-born children attempting to reach and surpass their older siblings' abilities and parents being more protective over first-born and only children (Krombholz 2006).

Pitfalls of Birth Order Theory

Despite the large number of studies surrounding birth order theory, birth order likely has less influence than suggested by pop psychology. Birth order can have some impact on an individual basis, but factors that are determined by birth order (such as family density), as well as other variables such as social and economic status influence an individual's development and personality more consistently. Additionally, patterns shown in many studies tend to not be replicable or consistent from study to study, making results inconsistent and unreliable.

Conclusion

The order in which an individual is born into their family and the influence that order has on one's development and personality has long been studied and debated. Researchers have found birth order to predict both cognitive and physical

development. However, these findings are limited and often inconsistent, oftentimes only strengthened by popular belief. More current research regarding birth order is taking into account confounding variables and focusing on how family environment and dynamics play a role in shaping an individual.

Cross-References

- [Birth Order and Parental Investment](#)
- [Birth Order and Sibling Relationships](#)
- [Birth Spacing and Birth Order](#)
- [Fraternal Birth Order, The](#)
- [Frank Sulloway \(1996\) on Birth Order](#)

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Birth Order and Parental Investment

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Synonyms

Family order effects; Sibling position effects

Definition

Parents may differentially invest limited resources in offspring who have a higher likelihood of survival, which is often older children; and equal division of parental investment across multiple children tends to have differing effects across firstborns, middleborns, and lastborns.

Introduction

During his visit to the Galápagos Islands in 1835, Charles Darwin was puzzled by the extensive diversity he observed among 13 species of Galápagos finches. These birds, he later realized, were actually members of a single, closely related avian group that had evolved its remarkable diversity through competition over time. Human siblings are a lot like Darwin's finches, as they also tend to diversify in various ways – for example in intellectual performance, personality, and social attitudes (Sulloway 2010). Some of this diversity among siblings is genetic. On average, full siblings share only half of their genes unless they are identical twins. Furthermore, even though siblings are brought up within the same family, they do not fully share the same family environment. And their differing family experiences are systematically related to birth order and parental investment.

From the perspective of evolutionary biology, Trivers (1972) defined parental investment as any

investment in individual offspring by a parent that increases the offspring's chances of survival and reproduction at the cost of the parent's ability to invest in other offspring. Parental investment can take various forms, including material resources such as food and other basic necessities; financial support for education and professional training; cognitive stimulation (for example, time spent reading to children or helping them with their homework); and interpersonal investment, such as attention, affection, and general encouragement (Hertwig et al. 2002). Intentionally or unintentionally, parents often invest unevenly in their offspring according to birth order. Such differences in parental investment are one of the mechanisms that drive offspring to compete with one another.

Sibling competition is particularly well documented among birds and mammals. When competing over valued resources, older offspring typically exhibit aggression toward younger ones, which, in extreme cases, can end in siblicide (Fig. 1). In an effort to diminish such fierce and generally costly competition, siblings tend to obey Charles Darwin's (1859) "principle of divergence." According to this principle, which has been widely validated through studies of other animal species, divergence is generally adaptive because it reduces direct competition for scarce resources.



Birth Order and Parental Investment, Fig. 1 A Verreaux's eagle chick has created a large wound in its one-day-old sibling. Sibling aggression in this species almost always leads to the death of the younger sibling (Photograph courtesy of Peter Steyn)

How Parental Investment Is Related to Birth Order

Before the beginning of the nineteenth century, nearly half of all children died before the age of 5, and even today infant mortality rates are still very high in some developing countries. When resources are limited, parents may invest more heavily in offspring who have a higher likelihood of survival and hence of passing their genes onto future generations. Older children are in a more favorable position as they have already survived some of the lethal diseases of childhood and therefore possess a greater prospect of future survival than do their younger siblings (Sulloway 1996). In addition, firstborns are often granted a greater role in perpetuating the family line, wealth, and traditions, especially in preindustrial societies. A good example is the custom of primogeniture, leaving inheritance to the oldest son, a practice that prevailed during much of the premodern period (Hrdy and Judge 1992). Apart from being favored by a greater share of family inheritance, firstborns – regardless of sex – are often given privileges through other social customs, including birth ceremonies, leadership roles, teknonymy (renaming a parent after a child), and having authority over their siblings in adulthood (Rosenblatt and Skoogberg 1974).

In modern society, as resources become more plentiful, parents tend to become increasingly egalitarian and to invest more or less equally in their offspring. Even when this is the case, however, the cumulative pattern of parental investment still tends to differ among siblings, and often produces inequality that is related to birth order (Hertwig et al. 2002). Because firstborns and lastborns both experience a period of exclusive parental investment when other siblings are not yet born or have grown up and left the home, they generally receive a greater share of resources compared with middleborns. Thus, the relationship between parental investment and birth order tends to be quadratic or U-shaped. Nevertheless, for those aspects of parental investment that are particularly important for human development during infancy or early childhood – for example, vaccinations and cognitive stimulation – lastborns

never obtain an advantage over middleborns. In such cases, an egalitarian motive among parents results in linear relationships between parental investment and birth order because each additional child dilutes the available family resources.

Theories about how birth order influences parental investment are well supported by empirical studies. Horton (1988), for instance, examined the relationship between birth order and nutritional status in 1,903 households in the Bicol region of the Philippines. He found that older children were more nutritionally advantaged over their younger siblings. Numerous other studies have shown that firstborns are more likely to receive vaccinations than are laterborns (Hertwig et al. 2002). A study of 14,192 children born between 1915 and 1929 in Sweden found that laterborn children had a considerably higher mortality risk compared with their firstborn counterparts (Modin 2002). Price (2008) reported that firstborns in two-child families received, each day, about 25 more minutes of quality time engaging with their parents compared with laterborns. In an investigation of 11,420 children of respondents from the National Longitudinal Survey of Youth 1979, Lehmann et al. (2014) found that mothers were more likely to breastfeed and to provide cognitive stimulation for their firstborn children. These empirical findings exemplify the linear relationship that is expected between birth order and some forms of parental investment. We need to bear in mind, however, that other forms of parental investment that are confined to adolescence and early adulthood have not been adequately investigated and, in some cases, are likely to manifest U-shaped relationships between birth order and parental investment.

Intelligence and Education

Birth order differences in parental investment can have profound influences on siblings in various ways. Abundant empirical evidence has shown that laterborn children tend to have lower IQs than their firstborn counterparts. For example, studies using large Norwegian administrative datasets ($N > 241,000$) have found that,

compared with secondborns, firstborns have IQ scores that were around 0.2 standard deviations, or 3 points, higher (Black et al. 2011; Kristensen and Bjerkedal 2007). In the same studies, these findings were confirmed by within-family comparisons, which cannot be confounded by socioeconomic or other differences in family background. Of particular interest in the Norwegian data is the fact that when birth rank changed as a result of the early death of an older sibling, the IQ scores of younger siblings increased, showing that IQ corresponds with functional rather than biological birth rank. Another large within-family study using Swedish administrative data ($N = 222,034$) also found that intelligence declined with increasing birth order (Barclay 2015). However, the overall evidence for the relationship of birth order to intelligence is mixed, as some studies have found no significant relationship. Most of these exceptional instances involve small sample sizes that often lacking adequate statistical power, or studies carried out with young children, for whom the influence of birth order is not yet fully manifested (Sulloway 2007; Zajonc and Sulloway 2007). Still, well-designed studies have also shown that lower-IQ parents tend to have larger families, and lower-IQ offspring, compared with higher-IQ parents (Rodgers et al. 2000; Wichman et al. 2006). This relationship has been ascribed to genetics and its influence on social status, which in turn correlates with family size. This confound has not always been adequately addressed in studies of birth order and intelligence, although it is not a relevant factor in within-family studies, such as the large Norwegian study conducted by Kristensen and Bjerkedal (2007).

Despite debate about birth order and intelligence, there is consistent evidence indicating that firstborns have an advantage over their laterborn siblings in educational performance and attainment. The following are just a few examples. In a study using sibling data from the UK, Bu (2016) found that firstborns not only had higher educational aspirations but also were more likely to gain post-sixteen qualifications allowing access to higher-level courses within the UK educational system. Using data that included the

entire Norwegian population, Black et al. (2005) also found a negative relationship between birth order and educational attainment. They reported that the difference in educational levels between the first and the fifth child in a five-child family was comparable to the black-white racial difference. Apart from the indirect influence on educational attainment through IQ, some birth order differences in education may also be explained by disparities in parental investment arising from differences in available financial resources as family size increases.

Personality and Social Attitudes

Birth order differences in parental investment, as well as closeness to parents, influence personality, self-esteem, parental identification, and the overall parent-child relationship. In one study, siblings who were favored by their parents, or who reported low levels of parent-offspring conflict, were more conscientious, agreeable, and extraverted; whereas those not favored by parents, or who reported high levels of parent-offspring conflict, were more open to experience and tended to identify less strongly with parental values and to question parental authority (Sulloway 1996, 2001). In a study asking participants to compare themselves with their siblings on various personality measures, Paulhus et al. (1999) found that firstborns were more conscientious and achieving; laterborns, by contrast, tended to be more agreeable, liberal, and rebellious. Such within-family studies are particularly instructive because there cannot be any confounds caused by uncontrolled socioeconomic disparities between different families. Sulloway (2001, 2010) performed a meta-analysis of 10 different within-family studies ($N = 7,218$), including that by Paulhus et al. (1999). These meta-analytic results showed that firstborns scored higher than laterborns on measures of conscientiousness, one aspect of extraversion (being assertive), and one aspect of neuroticism (anxiety). By contrast, laterborns scored higher on traits relating to agreeableness, most other aspects of extraversion, one aspect of neuroticism (self-consciousness), and several

indicators of openness to experience that are associated with unconventionality and open-mindedness. In another meta-analysis involving 8,340 participants in 24 different studies of athletic participation, Sulloway and Zweigenhaft (2010) showed that laterborns were more likely to engage in dangerous sports and to take more risks in professional athletics. For example, among 700 brothers who played Major League baseball in the United States, younger brothers were 1.7 times more likely to attempt to steal bases than their older brothers, and they were 1.4 times more likely to successfully complete a stolen base attempt.

Middleborns, who generally receive the least amount of parental investment, are reported to have lower self-esteem and to be more self-conscious compared with firstborns and lastborns (Kidwell 1982; Sulloway 2001). Studies have also shown that middleborns are not as close to their parents as are their siblings. For example, middleborns are less likely to turn to parents for emotional support in response to traumatic events (Rohde et al. 2003; Salmon and Daly 1998). This finding is a good example of the U-shaped relationship that is expected between birth order and some cognitive and behavioral outcomes.

Although within-family studies are nearly always supportive of birth-order differences in personality and social behavior, some very large between-family studies have found only small effects (Damian and Roberts 2015; Rohrer et al. 2015). Recent research involving more than 500,000 participants in an Internet personality survey using the Big Five Inventory has shown that reasonably impressive birth order effects exist in between-family samples when a variety of methodological precautions are observed, such as taking into account interactions between birth order and other demographic variables, including age, gender, sibship size, social class, race, and nationality (Sulloway et al. 2016). In addition, analyses need to be performed at the trait level, rather than at the broader dimension level to prevent differences in some aspects of personality from canceling themselves out (for example, assertiveness – a firstborn attribute, and being fun-loving – a laterborn attribute, would both be

scored under the dimension of extraversion). Some birth order effects are also relationship specific, in that the personality differences obtained when study participants rated only themselves were different from the results obtained when participants rated themselves and another person, which in turn differed depending on the specific identity of the other person being rated (for example, a sibling, a friend, or a romantic partner). One should also keep in mind that birth order is only an imperfect proxy, or mediator, of the real causes of sibling differences in personality. Three examples of important influences that are mediated by birth order are differences in parental investment, involvement in surrogate parenting, and physical size. Because researchers rarely examine these other causal variables, investigations typically overlook influences on personality that are revealed by more carefully designed approaches to the study of “family niches” (Sulloway 2001; Sulloway et al. 2016).

The influence of parental investment on parental identification and the parent–child relationship extends to social attitudes. More specifically, higher levels of parent–offspring conflict are associated with more liberal social attitudes among offspring (Sulloway 1996). In a study of 569 Chinese Tokok families in Indonesia, older siblings were more obedient to their parents’ wishes and more conservative, socially and politically, compared with their younger siblings (Skinner 1992). Among Japanese-American immigrant families, Manaster et al. (1998) found that firstborns were more likely than laterborns to carry on family traditions, including speaking the Japanese language, and were also more likely to be political and religious conservatives. In a meta-analysis of 20 previous studies, Sulloway (2001) reported that laterborns were 20 % more likely than firstborns to endorse a liberal political viewpoint, which was roughly equivalent to the gender gap in voting behavior in the United States. These results are consistent with another series of studies based on historical data, which found that laterborns were twice as likely as firstborns to support radical revolutions in science and various social and political domains (Sulloway 1996).

Conclusion

In sum, considerable theoretical and empirical research has shown that parents invest unevenly in their offspring in relation to birth order. As a result, siblings with differing birth orders tend to compete for parental favor and to diversify in various ways, including in their intelligence, education, personality, parental identification, and social attitudes. Under most circumstances, birth order effects are relatively modest, but it is likely that these effects will be greater in magnitude whenever they have been elicited by an appropriate stimulus that taps patterns of behavior learned in childhood. Parental investment is just one among several potential mechanisms that generate and explain these observed birth order differences. Much still remains to be learned about other psychological mechanisms that underlie sibling differences. One conclusion, however, is now well established, namely, that the family is not a uniform environment for offspring, and differences in within-family experiences cause siblings to diverge in a multiplicity of ways.

Cross-References

- [Differential Parental Investment](#)
- [Maternal and Offspring Condition](#)
- [Parental Investment Theory](#)

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Birth Order and Sibling Relationships

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Synonyms

[Family relationships](#); [Family size](#); [Sibling configuration](#); [Sibling constellation](#)

Definition

In medieval English, the word “sibling” was used to refer to all relatives or “kin,” but in the

early twentieth century, anthropologists defined siblings as individuals who share one or both biological parents. However, the rise in new and complex family forms has broadened this definition to include children who grow up in the same family (e.g., stepsiblings, foster siblings, adopted siblings) and who are biologically related but live in different families, as in the case of “donor siblings” conceived using the same gamete donor. Adding to this complexity, definitions of siblings are even broader in non-Western cultures and can include all children living in a community.

Introduction

Children develop social and cognitive skills through repeated, meaningful interactions with those with whom they share intimate close relationships. As the most enduring of all close relationships, sibling relationships have unique potential not only to influence children's development but also to contribute to well-being across the life-span. Alongside this longevity, three other unique features underpin the importance of sibling relationships. First, unlike friendships, sibling relationships are involuntary. Thus, while young children quickly learn to refrain from showing negative behaviors toward friends who might otherwise simply walk away from the friendship, they can be unrestrained in their expressions of negative emotions toward siblings. As a result, sibling interactions often have a love-hate “no-holds barred” quality. Although sibling conflicts can be exhausting for parents, they also provide fertile contexts for learning about differences in points of view and for developing effective means of repairing interactions after a disagreement. A further consequence of the involuntary nature of sibling relationships is that, for mixed gender sibling dyads, intimacy can cross the gender barrier that segregates peer interactions in the playground. For many children then, siblings provide unique opportunities to become familiar with the opposite sex.

A second distinguishing characteristic of sibling relationships is that they are “diagonal” in

nature. That is, within the sibling relationship, the companionship, fun shared pretend play, and reciprocity that characterize close relationships between children are combined with vertical elements of parent-child relationships (e.g., caregiving, pedagogy). Reflecting this diagonal structure, siblings often fulfill many roles, for example, as playmates, caregivers, rivals, and role models. While effects of sibling role models have largely been studied in relation to risk-taking behavior (e.g., early sexual activity, drinking, substance use – for a review, see McHale et al. 2012), they are also evident in relation to prosocial behavior (e.g., Pike and Oliver 2016). Note also that while the age gap that underpins the diagonal nature of early sibling relationships becomes less significant as children grow up, the diagonal quality of sibling relationships may persist as older siblings continue to forge a path for younger siblings, in negotiating their rights and responsibilities as adolescents and in coping with external stressors such as exams, leaving home, and becoming independent.

The third feature of sibling relationships that deserves note is their interplay with other close relationships. For example, sibling conflict is linked to parent-child and marital conflict and is also exacerbated by parents' differential treatment of siblings (e.g., Brody 1998). Indeed, accounts of sibling rivalry date all the way back to biblical times (e.g., Joseph and the coat of many colors given to him by his father, which almost drove his brothers to fratricide). Thus sibling influences can be indirect as well as direct, with children closely monitoring parents' interactions with siblings for signs of favoritism and unequal treatment or unhelpful parental comparisons of siblings leading to poor adjustment (Buist et al. 2013). Sibling relationships also intersect with children's friendships. Echoing the importance of sibling relationships as a forum for children's learning to form and maintain harmonious interactions, longitudinal evidence shows that children exposed to persistently high levels of sibling conflict (from ages 3 to 6) were, at age 6, especially likely to display bullying behavior toward unfamiliar peers (Ensor et al. 2010). Studies of adolescent siblings also indicate that older siblings can act as gatekeepers

to deviant peer groups (e.g., Ardelet and Day 2002). Thus, through interactions with both parents and friends, siblings can exert indirect influences on well-being and adjustment.

As noted below, evolutionary perspectives hinge on the premise that studies of nonhuman species can yield insights into the origins of human behaviors, such as sibling cooperation. In this regard, while studies of birds have informed accounts of sibling competition (as exemplified by the behavior of the baby cuckoo), studies of mammals have also been more informative with regard to the evolutionary advantages of sibling cooperation. In particular, mammalian offspring spend much longer in close contact with the mother, and hence siblings can influence development postnatally as well as in utero. Thus, alongside the obvious competition between siblings for resources, among mammalian species, the presence of a sibling may be advantageous prenatally (e.g., by jointly producing sufficiently strong hormonal signals to maintain a pregnancy), postnatally (e.g., by increasing the efficiency of thermoregulation), and in adult life (e.g., by forming coalitions for hunting or defense) (for a review, see Hudson and Trillmich 2008). While few studies of sibling relationships in nonhuman primates have adopted longitudinal designs, a 10-year study of male chimpanzees showed that, compared with unrelated males, maternal brothers showed more equitable levels of grooming and more stable bonds (Mitani 2009), indicating that sibling relationships contribute to group cohesion. Thus, from earwigs to chimpanzees, animal studies confirm the potential benefits as well as costs of growing up with siblings.

Evolutionary Theories of Family Relationships

Evolutionary theory suggests that psychological processes have evolved due to natural selection, as a means of increasing reproductive fitness. Several evolutionary theories may help make sense of sibling dynamics (for a more in-depth review, see Pollet and Hoben 2011). Hamilton's

(1964) theory of the evolution of altruistic behavior suggests that individuals will engage in behaviors that do not improve their own reproductive fitness if these behaviors increase the reproductive fitness of a genetically related individual and thus confer an indirect fitness benefit to the donor. This theory is often expressed as an equation $Br > C$, where B is the benefit of the behavior to the recipient, r is the degree of genetic relatedness between the donor and the recipient, and C is the fitness cost to the donor. According to this equation, altruism will occur if the benefit times the relatedness is greater than the cost to the donor. Importantly, this theory suggests that individuals are more likely to engage in prosocial behavior toward siblings than toward unrelated individuals and that prosociality toward siblings should depend on the level of genetic relatedness. For example, prosociality among full siblings should be greater than among half-siblings, which should in turn be greater than among stepsiblings.

Another relevant evolutionary perspective is parent-offspring conflict theory (Trivers 1974). According to this theory parents are expected to invest the maximum resources available in their offspring even if this is detrimental to themselves or to future offspring. At the same time, offspring may try to obtain more resources than the parent is able to give to maximize their reproductive potential, leading to a conflict between parent and offspring. An implication of this theory is that sibling competition for parental resources may be beneficial for offspring to maximize their individual reproductive fitness, even if this is to the disadvantage of their parents and siblings. In the next sections, sibling conflict and competition are explored in relation to these evolutionary accounts.

Sibling Conflict

Conflict is a hallmark of sibling relationships and as discussed above is prominent in literary and biblical accounts of sibling relationships. Data from naturalistic observations suggest that in interactions between young siblings, conflict is frequent, occurring on average 3.5 times an hour (Kramer et al. 1999). Sibling conflict is often

thought of as a “horribly normal” part of childhood in Western cultures, but in non-Western cultures, sibling conflict may be less prominent (e.g., White and Hughes 2017). While sibling conflict may be troublesome for parents, theorists have suggested that it may provide an important context for learning about others’ thoughts and feelings and may therefore contribute to the early advantage in social understanding observed for siblings compared with only children (Devine and Hughes 2018). However, extreme levels of sibling conflict, particularly physical violence, may provide a training ground for aggressive behavior in other contexts. Although this chapter will focus on human siblings, sibling conflict is prevalent among animals. For example, sibling fighting over access to food is common in many species of birds and may even lead to siblicide (for a detailed exploration of family conflict among animals, see Mock 2004).

As noted above Trivers’ (1974) theory suggests that sibling conflict arises because siblings are direct rivals for parental resources, a view that is shared with many psychoanalytic perspectives of sibling conflict. Michalski and Euler (2007) suggest that children may actively seek to obtain more parental resources by manipulating their parents’ perceptions of their needs. For example, they argue that reports of firstborn children showing developmental “regressions” (e.g., waking up in the night having previously slept through) following the birth of a new sibling may reflect a strategy to gain a larger share of parental resources now that these resources are being divided with another child. Children are likely to become less reliant on parental resources as they grow older and particularly when they leave the parental home and start their own families. One might expect, therefore, that sibling conflict should reduce as children age. Empirical studies of sibling relationship quality over childhood provide some evidence for a decrease in sibling conflict in adolescence, but the lack of long-term longitudinal studies of sibling relationships, particularly those spanning the transition to adulthood, means it is unclear how levels of sibling conflict change from childhood to adulthood (White and Hughes 2017).

What factors influence sibling conflict? According to Trivers' (1974) theory, sibling conflict will depend on the degree to which there is competition for parental resources. Therefore, higher levels of sibling conflict might be expected in larger families (in which there are more siblings competing for a given amount of parental resources) and in families with lower socioeconomic status (in which parental resources are more limited). The few studies that have examined links between sibling relationship quality and family size or socioeconomic status have generated mixed results (see White and Hughes 2017), perhaps reflecting the effect of other influences on sibling conflict or differences in methods of measuring sibling interactions.

Sibling conflict should also be related to the degree of genetic relatedness between siblings, because siblings who share two biological parents are competing more directly for parental resources than half-siblings or stepsiblings. Support for this proposal comes from a study by Michalski and Euler (2007) in which university students reported more current and prior conflict with full siblings than with half- or stepsiblings. Furthermore, students reported an age-related decline with full siblings and half-siblings (but not stepsiblings). These findings suggest that genetic relatedness plays a role in competition for parental resources and also highlights the importance of examining trajectories of sibling conflict over time separately for different types of siblings.

Sibling Cooperation

Comparative, developmental, fossil, and neurobiological evidence has led theorists to argue that late human evolution was dominated by selection for intragroup prosociality over aggression – that is, the “survival of the friendliest” (Hare 2017). Most individuals encounter their first opportunities for cooperation in the context of sibling interactions; understanding sibling cooperation therefore holds the promise of identifying processes that make us uniquely human.

Sibling cooperation takes many forms, of which perhaps the most obvious is turn-taking.

Learning to take turns with a prized object (e.g., a new toy) is doubly rewarding, in that it not only minimizes the distress associated with disputes but also increases enjoyment by maximizing the time children spend actually playing. Parents are therefore highly motivated to teach children to share their possessions with their siblings. However, turn-taking is an important form of cooperation even when there are no prized objects at stake. For example, games of shared fantasy hinge on all actors playing their part and so require the coordination of different points of view (e.g., on whether a broomstick will fly to the moon or another destination). Cooperating with a sibling therefore provides valuable opportunities to practice mentalizing skills and so provides a likely explanation of why the presence of siblings is associated with accelerated development of “theory of mind” skills (Devine and Hughes 2018). Direct support for this view comes from the finding that differences in older siblings' cognitive sensitivity (i.e., the ability to provide information in a helpful and accessible manner) help to explain variation in the extent to which young children's theory of mind development benefits from the presence of a sibling (Prime et al. 2016).

Helping is another obvious example of sibling cooperation. As detailed below, the asymmetrical nature of sibling relationships means that it is more usual for an older sibling to help a younger sibling (e.g., in acquiring a new skill, or solving a problem). However, even very young toddlers take delight in finding ways to be helpful, and so helpful behaviors can be reciprocal within the sibling relationship. Recently, the power of a developmentally sensitive within-family design has been used to investigate birth order effects on preschool children's cooperative abilities. Specifically, in a study involving a socio-demographically diverse sample of 144 Canadian families, Prime et al. (2017) found that youngest children displayed the highest levels of cooperation while middle children were also advantaged but only if their siblings were prosocial. Here it is worth noting that findings from a study of 524 pairs of 3- to 8-year-old twins show that individual differences in spontaneous instigation of cooperation with a sibling reflected

environmental rather than genetic factors (Lemery and Goldsmith 2003). Understanding how structural factors (e.g., birth order) and social factors (e.g., relationship quality) interact to enculturate children into adopting cooperative attitudes is an important direction for future research.

As for turn-taking, helping does not require a physical task or problem but can also be manifest at a mental level, through the formation of alliances in polyadic conflict (Persram et al. 2017). Importantly, such alliances are most likely when a sibling faces an external threat. Despite their differences, siblings can usually be counted upon to look after each other. Empirical evidence to support this view comes from studies that portray siblings as supportive fellow travelers through stressful times, such as family change (e.g., Kempton et al. 1991). Literary examples of sibling cooperation also abound. For example, in Jane Austen's *Pride and Prejudice*, Elizabeth and Jane have a very low opinion of their flighty younger sister, Lydia, and yet step in to the parental role by striving to protect her reputation when she elopes with the perfidious Wickham. Returning to the self-domestication hypothesis (i.e., that late human evolution can be described as a "survival of the friendliest"), sibling alliances may therefore provide the building blocks of societal norms that underpin civilization.

Findings from animal research lend weight to the argument that sibling cooperation is an ancestral behavior that can be retained to compensate for insufficient levels of parental investment. For example, studies of earwigs indicate increased sibling cooperation (as assessed by food transfer) in the context of low maternal food provision (Kramer et al. 2015). While a parallel between the novels of Jane Austen and the results of research on earwigs might seem far-fetched, the importance of this context of "insufficient parental investment" deserves note: if their parents had been more effective as figures of support, would the Bennett sisters have shown such high levels of sibling cooperation? Highlighting the potential importance of siblings as figures of compensatory support, elevated levels of caregiving between siblings are often reported in studies of sibling relationships in traditional non-Western cultures,

in which parents are required to work long hours away from home during the day (e.g., Cicirelli 1994). Against this view, however, is the positive relationship between maternal warmth and children's prosocial behavior, widely reported in studies involving within-population comparisons (e.g., Dunn 1998). In other words, studies of individual differences suggest direct "spillover" effects between parent-child and sibling relationships. Support for this alternative view also comes from the finding that fathers' active involvement in childcare increases the likelihood of preschoolers' displays of affection and concern toward infant siblings (Song and Volling 2015). Clearly then, more work is needed to understand the variety of ways in which family processes influence sibling cooperation.

Asymmetry in Sibling Relationships: Origins of Birth Order Effects

A key area of study within the sibling literature has been the effect of birth order, that is, the ordinal position an individual sibling holds within the family. In the next sections, the effects of birth order on parenting, academic achievement, and personality are discussed, but first the origins of sibling differences are explored. An important feature of sibling relationships (with the exception of twin relationships) is the age gap between siblings. In childhood this age gap is associated with a disparity in social, emotional, and cognitive abilities that promotes an asymmetry in roles within sibling interactions. In childhood, older siblings typically take the lead in sibling interactions as initiators of both positive and antagonistic behavior and also spontaneously engage in teaching and caring for their younger sibling. Younger siblings are keen imitators of their older sibling and are active learners in teaching situations.

Recent research suggests that the asymmetry in sibling roles within interactions may have implications for children's adjustment. Using data from the Avon Longitudinal Study of Parents and Children, Pike and Oliver (2016) examined the associations between children's prosocial behavior and behavior problems and the quality

of their sibling relationship over a 3-year period beginning when the younger sibling was 4 years old. Their findings showed that older siblings' behavior was a stronger predictor of younger siblings' behavior across time than the reverse, and this was true for both prosocial behavior and behavior problems. Moreover, older siblings' prosocial behavior was more strongly associated with positivity in the sibling relationship than younger siblings' prosocial behavior, both cross-sectionally and across time, although a similar pattern of findings was not found for behavior problems and sibling negativity. These findings suggest that, reflecting their dominance within sibling interactions, older siblings have a dominant influence on individual behavior and sibling relationship quality across time.

The age gap between siblings also contributes to children's differential experiences of the same family. For example, siblings experience key family events at different times and receive differential treatment by parents and other family members because of their birth order, as well as other factors (e.g., gender, temperament). These non-shared environmental influences account for findings that siblings within the same family are often very different from one another (Plomin et al. 2001). Non-shared environmental influences may also occur because children seek to differentiate themselves from their sibling by developing distinct interests and personal qualities and seeking out different "niches" within the family. This process of sibling "de-identification" was first described by Adler who proposed that sibling rivalry for parental attention and family resources arose as a means for siblings to overcome feelings of inferiority. According to Adler, de-identifying with a sibling provided a way to overcome feelings of inferiority and thus reduce sibling conflict. However, empirical support for a link between de-identification and reduced sibling conflict has been mixed (Whiteman et al. 2007).

Birth Order and Cognitive Performance

The study of birth order and cognitive performance began with Francis Galton's investigation

of the characteristics of fellows of the Royal Society, in which he observed that firstborns were overrepresented among these "men of science". Nearly 150 years later, interest in birth order as a predictor of achievement or cognitive performance remains prominent in the fields of psychology and sociology. Three main theories have been proposed to account for effects of birth order on academic achievement. These theories also explain effects of family size, which is frequently conflated with birth order, but in the interest of brevity, only birth order effects will be discussed here. The resource dilution hypothesis (Blake 1981) suggests that children's achievement relies on investment of time and money from parents. These resources are finite such that the addition of each new child in the family results in a reduction of resources available to any one particular child. This theory suggests that within a given family size, firstborn children will outperform later-born children because they have spent more time as the sole recipient of parental resources. Moreover, youngest children are likely to outperform middle children as they have a period of time alone with their parents after the other children have left home. A further corollary of this theory is that birth order effects are likely to be most marked in poorer families where parental resources are more limited.

In contrast, the "confluence" model (Zajonc and Markus 1975) suggests that two competing processes contribute to children's academic achievement: the "intellectual environment" within a family, which is based on a weighted average of the intellectual abilities of all members, and the learning opportunities provided by teaching a younger sibling. According to this account, birth order effects are not static but vary over the course of a child's lifetime and depend on the structure of the family. For example, in a two-child family, when comparing children's academic achievement at the same age, the firstborn will have an advantage at a very young age (i.e., before the second child is born) and then again in adolescence when the child has gained from opportunities to teach their sibling. Finally the admixture hypothesis suggests that genetic or environmental differences between

families, rather than within-family processes, give rise to birth order effects on academic achievement (e.g., Rodgers et al. 2000). For example, birth order effects may arise because of differences in family size based on parental intelligence or socioeconomic status.

Empirical studies examining these three accounts of birth order effects on achievement have been mixed. For example, using a national representative cohort study, Kanazawa (2012) showed that birth order was not linked to children's performance on cognitive tests once family size was controlled statistically, supporting an admixture hypothesis. In contrast, in a similar-sized study, Iacovou (2008) showed that middle- and youngest-born children had lower academic achievement than firstborn children, and the size of these effects varied with family size. The author interpreted these findings as support for the confluence hypothesis whereby for youngest children the benefits of having time with just their parents at home and the lack of opportunity to teach younger siblings cancel each other out so that youngest children's achievement is similar to that of middle-born children. However, this hypothesis is difficult to test empirically, highlighting the methodological challenges in understanding the effects of birth order on academic achievement.

Birth Order and Personality

The notion of birth order effects on personality stems from psychoanalytic perspectives on the sibling relationship and has long held traction in popular culture. Sulloway (1996) developed an evolutionary niche-picking model to explain birth order effects on personality, suggesting that traditional patterns of parental investment, in which parents typically invest more in first-born sons (the heir) than in later-born sons (the "spare"), give rise to different strategies to increase parental investment. Specifically, Sulloway (1996) argues that firstborns, who are traditionally their parents' main heir, display personality characteristics and hold beliefs and attitudes that mirror those of the parents, while

later-born children are more likely to hold beliefs, attitudes, and personality characteristics that differ both from their parents and from their older sibling. Using historical data about scientist brothers and their willingness to subscribe to new scientific theories, Sulloway (1996) suggests that firstborn siblings are more likely to conform and accept the status quo, whereas later-born siblings are more likely to rebel and show creativity. Sulloway (1996) also suggests that older siblings are more likely to use physical power to assert themselves, leading to lower agreeableness, but may attempt to please their parents by caring for younger siblings, leading to higher levels of conscientiousness. In contrast, later-born siblings may rely on social support to assert themselves and thus become more extraverted and may be more open to experiences because they have had to find innovative ways to find a family niche and differentiate themselves from their siblings.

This niche-picking hypothesis has attracted considerable research attention, but several large-scale well-controlled studies have failed to replicate Sulloway's findings. In a representative US sample of 377,000 high school students, Damian and Roberts (2015) found that, after controlling for effects of age, sex, sibship size, socioeconomic status, and family structure, the average association between personality characteristics and birth order was so small as to be negligible. Rohrer et al. (2015, 2017) confirmed these findings in two further studies that used both within- and between-family approaches to analyze birth order effects conducted and found no meaningful effects of birth order on either broad personality characteristics or narrower personality traits. Rohrer et al. (2015) suggest that these findings may indicate that birth order effects may be observed in behavior within the family but may not influence behavior outside of this context or that birth order may influence aspects of personality into which most people have little self-insight.

Birth Order and Parenting

As discussed above, the resource dilution model also predicts that parents' psychological resources will be diluted with each new child, such that

parental warmth and sensitivity may be reduced for later-born children. However, this hypothesis has been challenged in several ways by empirical evidence from longitudinal studies. For example, using growth curve models to analyze four waves of data on parenting practices gathered biennially between 1994 and 2000 from a nationally representative sample of over 2000 Canadian mothers of 2- to 5-year-olds living in continuously intact, two-biological-parent households, Strohschein et al. (2008) concluded that increased family size led to the reallocation, rather than the dilution, of parenting resources. Likewise, in a 5-year longitudinal study of 201 sibling pairs, Shanahan et al. (2007) reported that age-related drops (from ages 7 to 19 years) in experience of parental warmth were sharper for firstborn children than for later children, suggesting a “learning from experience” effect, rather than a “resource dilution” effect.

Research on earlier stages of parenting provide mixed support for this “learning from experience” hypothesis. In a study of 364 Dutch families with two children seen at home around the younger child’s first, second, and third birthday, Hallers-Haalboom et al. (2017) found no association between changes over time in parental sensitivity to each child and concluded that rather than being affected by experiences with the firstborn, sensitivity toward the second-born is driven by children’s unique characteristics and developmental stages. In contrast, Bernier et al. (2018) have argued that effects of birth order and sibship size on maternal sensitivity are likely to vary for specific components of sensitivity and depend on mothers’ own attachment relationships. Specifically, while maternal attunement and cooperation did not differ by birth order, mothers who had an insecure relationship with their own caregiver appeared less available and positive toward their later-born children than toward their firstborn child, perhaps because the competing needs of different children had a stronger impact on their cognitive flexibility and well-being.

Together, the four sets of findings outlined above highlight the dangers of oversimplifying accounts of how birth order might affect parent-child interactions. Parents expecting a second child are often amazed to discover that, despite

their all-consuming love for their first child, they can also tumble headlong in love with a second child. By analogy, the resource dilution hypothesis is based on the false premise that psychological resources are finite: when faced with competing demands for attention, many parents are able to deploy creative strategies to ensure that they can meet the needs of all their children. However, as demonstrated by the moderation effect reported by Bernier et al. (2018), this ability to respond calmly and flexibly is likely to hinge on parents’ own well-being and security of attachment.

Conclusion

In this short chapter, we have tried to do justice to the rich learning opportunities that result from the enduring and familiar nature of sibling relationships, as well as from the multiple intersections between interactions with siblings and within other close relationships. Three aspects of evolutionary theory were noted: (i) the salience of genetic relatedness as a context for prosocial and conflict behavior (giving sibling relationships their well-recognized “love-hate” quality); (ii) parent-offspring conflict, which can lead to alliances between siblings and cooperation in the context of low parental investment; and (iii) the importance of intragroup cooperation within late human evolution, leading to a “survival of the friendliest” in which, once again, sibling interactions provide a fertile ground for developing key skills for adult success. Having described the different forms of sibling conflict and cooperation, we finished this chapter by considering birth order effects on cognitive achievement, personality and parenting. Key mechanisms underpinning potential birth order effects include not only negative consequences of resource dilution but also positive consequences of parents learning from experience or older siblings gaining skills by taking on caregiving or teaching responsibilities. Adding to this complexity, birth order effects are temporally dynamic and may also covary with other contrasts associated with family size (e.g., education, affluence). As a result, birth order effects are typically small in magnitude,

restricted to within-family contexts, or moderated by structural or interpersonal factors (e.g., the age gap between siblings or parents' own emotional security) that affect parents' ability to be flexible in sharing their attention between children. Such effects are therefore likely to be eclipsed by the powerful nature of siblings' direct influences upon each other, be that as sparring partners and rivals, or as sources of companionship, affection, and support.

Cross-References

- [Antisocial Behavior](#)
- [Cooperation](#)
- [Full Siblings Versus Half Siblings](#)
- [Play](#)
- [Theory of Mind](#)

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Birth Position

► Birth Spacing and Birth Order

Birth Spacing and Birth Order

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Synonyms

Birth gaps; Birth interval; Birth level; Birth position; Child spacing

Definition

The amount of months or years in between consecutive siblings within a family; the biological or functional position in which an individual resides in a group of siblings with a family.

Introduction

Since the biblical times of Cain and Abel, there have been noted differences between individuals from both within and outside of a family unit due to their birth position. Professionals have likened differences between siblings to Darwin's theory evolution because they believe that individuals will try to differentiate themselves from siblings to obtain the most parental resources for survival (Sulloway 1996).

Differences had been noted between siblings in a family depending on birth order as early as 1874 with Sir Francis Galton; however, the majority of birth order research did not begin until after 1928 – the year when Alfred Adler hypothesized about personality differences between birth order cohorts. More recent birth order research has not only focused on personality but it has also focused on individual factors such as: intelligence, parental involvement, sexuality, etc. Since 1928, there have been many disagreements within the academic community about the validity of research results claiming differences in personality or other individual factors between birth orders. Many of these opposing arguments have focused on the varying amounts of children and spacing of children between families not being accounted for in prior research (Ernst and Angst 1983). Recent studies that control for various social factors, however, have been used to combat some of these complaints – showing potential validity of birth order effects.

Although research has been conducted on the effects of birth order on various individual factors, an individual must first understand the effects of birth spacing before inferences on birth order effects can be made. This is because the spacing between the birth of siblings can be used to

increase or decrease competition – ultimately effecting the development of social behaviors.

Birth Spacing, Birth Order, and its Influence On Child Personality, Intelligence, Sexuality, and Health

In 1874, Sir Francis Galton stated his observation that fellow members of his academic community were more likely to be the eldest born child in their family than any other nominal birth order position. There are five nominal birth order positions commonly recognized by researchers: first-born, second-born, middle-born, last-born, and only-born.

Though the positions of the first-born, last-born, and only-born are generally salient and agreed upon, there are many discrepancies between whether an individual should be placed within the nominal position of second-born or middle-born based on where they lie in their sibling cohort – also known as a sibship. For some researchers, being labeled as a “second-born” can indicate the younger sibling in a two-sibling dyad (Price 2007) or can be used interchangeably with “middle-child” for sibships of three where they are neither the youngest nor the eldest (Saroglou and Fiasse 2003). In conversation, second-born can also be used to describe the second-born child in a sibship of four or more children. And, lastly, any child that is in a sibship that is not the first-born often falls under the umbrella term “later-born” – meaning that they were not the first child born in the family.

Also, an individual's birth order can be used to describe both their biological and functional birth order within their family. According to Sulloway (1996), an individual's biological birth order is a static descriptive determined by the order in which they were born – independent of the death of another sibling or other changes in family structure. Oppositely, functional birth order is an unfixed descriptive used to describe where an individual lies within a sibship depending on the amount of living individuals in the sibship. Due to advances in modern medicine in industrialized

societies, an individual's functional birth order is less likely to change due to death of a sibling (McLanahan 2004). Rather, modern changes in functional birth order occur due to changes in family structure such as the adoption of a non-biological sibling or a parent remarrying an individual with children from a prior marriage or union (Sulloway 1996; McLanahan 2004).

Because of the varying dynamic between biological and functional birth order effects, there have been many branches of research conducted on how birth order effects individual factors such as personality, intelligence, sexuality, and mate preference and how they can be exacerbated by the spacing between births of siblings. However, for the purposes of this entry, birth order will be discussed as if it pertains to both a child's biological and functional birth order as observations have shown that individual will most likely adapt to their functional birth order if there is a change early in life (Sulloway 1996).

Birth Spacing, Fertility, and Child Outcome

In developed nations, there has been a dramatic decrease in the amount of children produced by mothers over the past 50 years. Partially explained by the increasing availability and social acceptability of oral contraceptive pills, women today are having two to three less children than their 1970 counterparts with the average mother today having an average of 2.5 children in comparison to the 5.1 children of years past (Feldman et al. 2009). Some researchers, such as Kanazawa (2012), report the conscious decrease in the number of children born by each mother "evolutionarily novel" because it contradicts the notion made by many Darwinian evolutionary theorists that an organism must produce as many offspring to be seen as "fit" (p. 1161). If a woman was to maximize her reproductive potential, she could become pregnant within 8 weeks of giving birth – depending on maternal health or nursing practices (Bereczkei 2001).

However, as briefly indicated above and discussed further in depth in future sections, human reproduction rates have not always contradicted the Darwinian "survival of the fittest" theories. In previous centuries, due to high

child mortality rates perpetuated by unadvanced medical practices, families would have large amounts of children in them to ensure that at least one child would reach reproductive maturity to propagate their families genes (Sulloway 1996). Today, the practice of bearing multiple children has become outdated due to advances in medicine which have drastically reduced child mortality rates. Now, parents are actively limiting the number of children they have to ensure that they have the enough resources (such as money, attention, and time) to care for each child they bring forth (Sulloway 1996; McLanahan 2004). By having enough resources, parents are able to ensure that their children not only reach reproductive maturity but they are also able to become productive members of society (McLanahan 2004).

Though there are dramatic differences in the amount of children born per family when comparing the families of today with the families that lived centuries prior, there are actually few differences in the spacing of children. According to the World Health Organization, women should not actively try to become pregnant within 24 months of giving birth (Hambimana-Kabana et al. 2016). If a mother is to become pregnant prior to 24 months after giving birth, there is a larger risk that she will have a miscarriage or stillbirth if she is in a developing country because she will not have the necessary medical services available (Ahmed et al. 2015; Hambimana-Kabana et al. 2016). By increasing the time between births, mothers will be able to decrease competition to recover and restore their health after enduring childbirth (Lee 1980; Bereczkei 2001). However, in a review conducted by Conde-Agudelo et al. (2012) it has been indicated that while increasing the time between births might buffer the competition between siblings, very brief spacing as well as extremely long spacing between children could also have aversive influences on the health of both the mother and offspring.

Mother's with shorter intervals in between consecutive births might have decreased health as the demands of caring for a newborn (i.e., nursing) might cause nutrient deficiencies which can lessen the overall health of the mother.

These negative effects are exacerbated when the mother conceives a subsequent child before she is done nursing as she will now have a fetus and an infant vying for her nutrients (Conde-Agudelo et al. 2012). Further, maternal vitamin deficiencies which can occur after the birth of an offspring, if not restored, can cause considerable negative detriments to subsequent offspring (Conde-Agudelo et al. 2012; Fotso et al. 2013). In regard to the effect short intervals between births can have on child health and survival, in a research conducted on children born in Africa by Fotso et al. (2013) found that children who had an older sibling born less than 18 months before them but they themselves are not the last-born were more likely to die in infancy. Similar to children of mothers born with folate vitamin depletion, research provided in the review conducted by Conde-Agudelo et al. (2012) indicates that extended gaps between children (i.e., more than 5 years) is attributed to negative offspring outcomes (birth weight, preterm birth, etc.) and maternal outcomes (preeclampsia, labor dystocia).

In traditional hunter-gatherer societies, women might increase the spacing between births to not only decrease the competition between siblings for resources but to decrease the amount of energy they expend while caring for the child. For !Kung women, longer birth intervals are encouraged to reduce the workload as !Kung women would physically carry their children while gathering food (Lee 1980; Jones 1986). Because !Kung women traditionally carried their children until they reached 4 years of age, having multiple children under the age of four would increase the energy expenditure of the mother – ultimately decreasing the total amount of resources available to the children (Lee 1980). Lee (1980) continues to state that, in a society that is no longer solely dependent on hunting and gathering for survival, spacing might no longer be necessary to survival; however, spacing might still be necessary to ensure that each child reaches their developmental potential.

The statements made by Lee (1980) might be best explained by Trivers' (1974) *Parent-Offspring Conflict*. With *Parent-Offspring*

Conflict, it is thought that for all mammals – not just humans – parental investment is higher at the beginning of the offspring's life than when the offspring is more independent. This is posited to be because the pressure and demands of the offspring in its early life does not surpass what the mother is able to provide or impact her future reproductive status but the demands of an older offspring might. Mother's will then begin to wean her child by no longer actively providing milk to her child and might reject the advances made by her offspring to nurse. This timeline provided by the *Parent-Offspring Conflict* (Trivers 1974) can further support the research supporting longer birth intervals between subsequent births as it ensures that parents will not have conflicts with multiple offspring at one time.

Research has indicated that, when comparing subsequent births following the birth of a first-born female or male child, there are larger spaces following the birth of male children than female children (Blanchard and Bogaert 1997). Blanchard and Bogaert (1997) continue to create three explanations for the findings. The first explanation, similar to statements made by Sulloway (1996), is that there has historically been a higher social value placed on male children when compared with female children – making a parent who gives birth to a female child more likely to have smaller birth intervals as they try to bear a son. Oppositely, the second explanation created by Blanchard and Bogaert (1997) might discredit their previous explanation by stating that space between male births might be more explainable by the potential negative reaction of the mother's immune system in reaction to the antigens produced by the male fetus which could cause a male fetus to spontaneously abort. Or, as their last explanation entails, caring for a male child might be more time consuming than caring for a female child – reducing the chance that the parents could engage in a successful copulation for subsequent pregnancies (Blanchard and Bogaert 1997). It is hard to determine, however, if the negative results of shorter spaces between births are because of the spaces themselves or because of extraneous factors such as breast feeding, income, and amount of caregivers.

There have been many recorded benefits the inclusion of breast milk for the first year of life on infant development (Berezkei 2001; Victoria et al. 2016). Breast feeding has also been used as a natural method to regulate the spacing between pregnancies with studies indicating that mothers who breastfeed are half as likely as mothers who do not breast feed to become pregnant after the birth of a child (Victoria et al. 2016). While breast feeding, however, has been found to regulate births, it has also been found that, with increasing births, mothers are less likely to breastfeed their children (Buckles and Kolka 2014). Therefore, not only will the reduction of breast feeding decrease the amount of time between spacing of future children, it can also impair the development of later-born children as they will not receive the necessary nutrients during critical development periods (Berezkei 2001).

For low-income mothers, confounds can be explained by the fact that, on average, low-income mothers have more children than mothers with higher incomes, and there are typically shorter intervals for families with large numbers of children (Feldman et al. 2009). Therefore, some children might have negative outcomes because their families are not able to provide the medical treatment or other services necessary to reduce the negative effects of competition for maternal resources between siblings in early developmental stages. Studies have also found that low-income mothers are more likely than other mothers to be single parents; however, not all mothers rely solely on the father of their child for parenting support – causing differences in birth spacing (Cancian and Reed (2009). Rotering and Bras (2015) found that, for mothers that rely on other family members for child support, spacing between births is increased if the family member is the male grandfather of the child but decreased if the family member is the uncle of the child.

Because of these above mentioned confounds, it is apparent that there are many factors that are responsible for the spacing between births. Regardless, many studies have indicated that small spaces between births can cause increased competition between siblings which, therefore, encourage them to develop different strategies to

obtain the most parental resources which will be discussed in following sections.

Birth Order, Personality, and Parental Investment

Although Sir Francis Galton was the first to hypothesize that first-born's might be more equipped to become scientists because he found that the majority of his peers were first-borns, birth order effects on personality were not truly examined until 1928 with Alfred Adler – the creator of individual psychology. Adler's birth order hypotheses has been found to correspond with the Five Factor Model – also known as the "Big Five" model – of personality which include traits such as: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism.

Adler broadly states that first-borns tend to be more assertive, quick to please, risk averse, and academically gifted while their younger counterparts are often found to be more agreeable, outgoing, sensation-seeking, and altruistic (Sulloway 1996; Krause et al. 2014). Adler also hypothesized that first-born children typically score higher in neuroticism because their lives are fundamentally changed when a new child is introduced into their family because they are no longer the sole recipient of their parent's affection (Marini and Kurtz 2011).

The results of these initial hypotheses, as well as similar birth order studies conducted by other researchers, are supported by the statements made by Sulloway (1996) who posited that personality differences between siblings might be an evolutionary adaptation – similar to the adaptations of Darwin's finches – used to gain more resources by appealing to their parents in a way that their other sibling or siblings do not. These remarks are founded on the historical basis that, prior to medical advances, parents would have to produce large number of offspring to increase the chances of having a child survive into adulthood to continue their line of genes through reproduction – regardless of their social class (McLanahan 2004). Because the likelihood of surviving to adulthood was not as high as it is in present day, the child's chance of survival was determined almost solely by the amount of resources they were able to procure from their parent (Sulloway 1996).

Sulloway (1996) continues to mention, that although in these families there were numerous children within a family from whom the parents could choose to invest their resources into, parents were most likely to place the most investment into their first-born – especially if they were a male (Healy and Ellis 2007). This emphasis on male heirs, which is still present in many areas of the non-Western world, can be explained by the custom that the eldest males are responsible for “continuing their family name” and were to be responsible for assuming the position of the leader of the family upon the death of their father or other male relative (Sulloway 1996). By having a potential of increased status – and the potential for ownership – eldest males were more likely to find a mate and have higher quality of life than their younger male siblings (Sulloway 1996). Regardless of the sex of the sibling, however, having two or more siblings within a family encourages differentiation of personality, as Sulloway (1996) states, to appeal to one, if not both, parents to receive the resources necessary for survival.

Presently, in Western society, due to the advances in medicine and affordability of healthcare, the odds of losing a child before they reach adulthood have drastically decreased. And, similarly, due to social changes, there is not as much emphasis placed on the offspring needing to be male – unless you are a part of the Royal Family and in search for an heir (McLanahan 2004; Augustine et al. 2015). However, children still remain dependent on their parents for resources which will increase their social, cognitive, and reproductive potential – encouraging siblings to continue developing diverging personalities (Sulloway 1996; Price 2007).

As mentioned above, a first-born’s life is completely changed when a new sibling is introduced into the family because they are no longer the sole recipient of their parent’s resources. Rather, they now must share them with a sibling and will soon find that their parent’s resources are not continuous – encouraging them to develop the particular personalities initially hypothesized by Adler. Sulloway (1996) advances that first-borns are more likely than their later-born siblings to

score higher on measures of conscientiousness and lower on measures of openness to experience (Beck et al. 2006; Krause et al. 2014). These first-born personality traits can be used to encourage a parent to provide resources as scoring high in conscientiousness means that they are more likely to follow parent’s commands – something that many parents yearn to have happen. Similarly, low scores on openness to experience can be seen as a positive adaptive trait as first-borns are more likely to earn their parents favor by being less likely to participate in risky behavior or rebel in teenage and young-adult years.

Conversely, although scoring low in conscientiousness and high in openness to experience could be interpreted as being counterintuitive personality traits that would decrease the amount of parental resources received by later-borns, in some cases, the opposite is true. By being less responsive to parent commands or being more inclined to engage in behavior that could lead to injury or other negative consequence, a later-born child might ultimately receive more parental attention than their rule-following first-born counterparts (Sulloway 1996).

While some sibling personalities might be developed to appease to their parents, some divergent personalities can develop as siblings interact with one another – a key example being that first-borns are arguably more assertive and dominant in comparison to their later-born siblings (Minnett et al. 1983; Sulloway 1996). The development of more assertive or dominant personalities has been attributed to first-borns as they attempt to salvage any control that they had in their lives due to being “dethroned” by the arrival of a younger sibling (Marini and Kurtz 2011). Not only are first-borns more likely to be considered dominant or more assertive when compared to their younger siblings, but due to their age, they are more likely to attempt to “teach” their younger siblings and impose rules (Minnett et al. 1983; Price 2007). Later-born siblings, therefore, have been found to develop personalities that make them traditionally more easy-going, agreeable, and altruistic to deal with the dominating personalities of their first-born siblings. Part of this last statement, however, has been found to be true only for the last-born

child in three child sibships because, in a study conducted by Saroglou and Fiasse (2003), when controlling the study population for nominal birth order, it was determined that last-borns were more likely to display acts of altruism than their first- and middle-born siblings.

While in sibships of two or more siblings are encouraged to develop diverging personalities to gain resources from their parents and to accommodate for the personalities with their siblings, the same cannot be said for only-children who grow up without siblings. Researchers and lay people often believe – and therefore propagate the stereotype – that only children are spoiled because they do not have to compete for parental resources like individuals from sibships (Mottus et al. 2008). Going through childhood without a sibling has also been thought to have negative effects on social or intellectual development – as only-children do not have siblings to help them learn how to navigate the “real world” (see section “[Birth Order, Birth Spacing, Intelligence, and the Only Child Dilemma](#)”; Zajonc and Markus 1975; Price 2007; Mottus et al. 2008).

Though there might be some truth to these beliefs about only children, Mottus and colleagues (2008) believed that these beliefs might be perpetuated stereotypes and might not fully reflect the personalities of only-children. Therefore, they created a study in which they asked young adults to describe the personality of other individuals and themselves based on the Five Factor Model and how many siblings they had (Mottus et al. 2008). Results of this study found that individuals were more likely to view only-children as having negative personality traits (i.e., being more unstable, lonely, etc.) while individuals who came from sibships were rated more positively (i.e., happy, altruistic, etc.) – indicating that individuals do believe stereotypes about only-children (Mottus et al. 2008). However, when discussing the results of the self-descriptive section of the study, Mottus and colleagues (2008) found no significant differences between groups to indicate validity of the stereotypes surrounding only-children. Mottus and colleagues (2008) continue to state that they believe that the negative stereotypes surrounding

only-children orientated in earlier times in which parents were pressed to have multiple children to ensure that there would be at-least one successor that would reach adulthood and successfully reproduce (Mottus et al. 2008).

As hinted at in the paragraphs above, although there have been found to be differences in personality due to birth order, it should be noted that Adler’s research, as well as much of the research conducted after his, on birth order effects on personality only had two categories used to describe individuals – “first-born” and “later-born” (Saroglou and Fiasse 2003; Marini and Kurtz 2011). Because there were only two groups included in these studies, an individual who was labeled as a later-born could be either a second-born, middle-born, or last-born. By not discriminating individuals of higher birth orders into their respective nominal categories, it is difficult to determine if the results reported by Adler are representative of all of the higher-order population or that there was possibly a nominal birth order that was overrepresented among the population – potentially skewing the results. This problem is highlighted by the results of Saroglou and Fiasse (2003) who found that certain personality dimensions, such as rebelliousness, were more descriptive of middle-born children in three children sibships.

Lack of multiple birth-order categories is not the only complaint made by researchers, since Adler’s founding statements, many criticisms have been made about the research design and the potential confounds created by a majority of birth order studies. While there have been many opponents of birth order research which has ascertained connections between birth order and the Five Factor Model, Ernst and Angst (1983) arguably has the most extensive argument as they dissect the results of birth order studies going back 40 years prior (Healey and Ellis 2007). In their review, Ernst and Angst (1983) state that many of the studies conducted after Adler’s 1928 birth order-personality hypotheses did not control for important confounds created by study design, family size, annual family income, and extraneous family factors such as religion (Healey and Ellis 2007).

The first problem with many birth order studies listed by Ernst and Angst (1983) is that, not only do they not differentiate the specific birth orders of later-borns, they also make their assumptions on personality using a between-families method rather than a within-family method. Therefore, results of studies assessing birth order effects on personality are comparing all later-borns against all first-borns as a group, rather than comparing first-borns against later-borns within a family.

Another potential confound in birth order research is that, by not distinguishing the specific birth order position of later-borns, a majority of prior research neglects the overall size of the sibship that an individual comes from. Because of medical advances and the introduction of birth control, many parents are no longer focusing on the quantity of children they produce because, as mentioned previously, the chance of their child dying prior to reaching adulthood has drastically reduced. Now, parents in the middle- and upper-class with higher levels of education are now focusing on the quality of the children they produce. By doing this, these parents are ensuring that all of the children that they give birth to – not just the eldest born male – have the potential to lead productive lives that lead to social, economic, and reproductive success (McLanahan 2004). However, while some parents are reducing the number of children that they produce, lower-class individuals are still producing large numbers of children due to lack of education or availability of various birth control methods (Ernst and Angst 1983; McLanahan 2004). Therefore, a significant difference in personality for higher birth-order children might not be due to their birth order, rather it might be due to the variance in their social-economic status (Ernst and Angst 1983; Beck et al. 2006).

Similarly, critics such as Ernst and Angst (1983) elaborate that children of larger families might also come religious backgrounds, such as Catholicism or Mormonism, that encourage large families – regardless of social-economic status. Not only can religious affiliation have an effect the amount of children in a sibship, it can also effect the development of personality as some religions also place an emphasis on certain

personality traits which they view favorable. These statements are supported by the results Saroglou and Fiasse (2003), which found that individuals who considered themselves to be religious were more likely than their nonreligious counterparts – regardless of birth order – to have higher scores on the conscientiousness and agreeable factors of the Five Factor Model. Analyzing family structure further, Saroglou and Fiasse (2003) went on to find that, in terms of religion, the middle-born is the least inclined to describe themselves as religious and are more likely to have more dynamic personalities because they do not have as many constraints on their personality as first- and last-born children. However, by indicating that there are differences when controlling for nominal birth order, it is clear that birth order has some effect on personality – even if it is hard to discriminate at some points.

Birth Order, Birth Spacing, Intelligence, and the Only-Child Dilemma

As with personality, there are many widely held beliefs on how an individual's birth order affects their intelligence and academic achievement. First-borns have traditionally been believed to be the most likely to succeed academically and have higher intelligence compared to their later-born siblings. Recent theories and models of intelligence, such as the confluence model (Zajonc and Markus 1975) or the resource dilution model, attribute the intellectual success of first-borns to the access of parental resources and the dynamic interaction between other siblings (Downey 2001). However, in regards with only-children, many of these models and theories conflict with resent research that indicate that growing up without siblings can have a detrimental effect on an individual's development of intellectual ability and academic achievement (Price 2007).

The confluence model created by Zajonc and Markus (1975) was designed to explain how the intellectual environment in which a child is raised has a large effect on the future intelligence and later academic achievement. Equations labeled parents as holding the highest intellectual ability by giving them values of "100." Newborn infants were given scores of "0" to indicate that they had

yet to develop any sense of intellectual prowess; however, this score was designed to increase as the child grows older. These scores would be averaged to indicate the level of intelligence of the environment the child is born in by averaging the scores of parents and any child currently present in the family. Therefore, first-borns were born into environments with the highest amount of intellectual potential as each additional sibling would be born into an intellectually inferior environment when compared to the siblings born before them. Zajonc and Markus (1975) also detail that these results are only true when utilizing within-family measures because individual differences between families in regard to family environment reduces the significance in intelligence differences between first-borns and later borns.

Birth order effects on intelligence might be more pronounced in within-family study designs because, when using a between-family study design, birth order effects might be influenced by various social factors such as parental intelligence. Therefore, a later-born from a family with high-intelligence parents might have the same – if not higher – intelligence than a first-born child with parents of low intelligence (Zajonc and Markus 1975). However, being born to lower-intelligence parents might not be the only factor that influences the development of child intelligence because studies have shown that intelligence can be correlated with the availability of parental resources such as attention and money (Zajonc and Markus 1975; Ernst and Angst 1983; Downey 2001).

The resource dilution model is similar to the above-mentioned confluence model because it posits that first-born children will have the highest potential for intellectual ability and that results should only be interpreted within the family because individuals from smaller sibships will obtain more resources than individuals from larger sibships (Downey 2001). This increased intellectual ability for first-borns is believed to occur because, since they will have a time in which they do not have to compete with siblings, they will obtain the most resources over time (Downey 2001).

Aspects of the resource dilution model are supported through the findings of Price (2007) who found that, when comparing the amount of time a parent of two children spends with each child at any particular longitudinal developmental time (i.e., if the children are 2 years apart, measurements would be taken once both children reach 5 years of age, not when one is five and the other is three), both mothers and fathers spend upwards of 25 more minutes with their first-born than their last-born child. Overtime, this difference in parent resource distribution at different developmental stages translates to at least 2000 hours more attention given to the first-born than the second-born. Price (2007) continues on to state that most parents do not know that they are doing this because, by trying to give equal attention to their two kids, they do not realize that they spend more time with one child over another at a certain developmental point. Researchers attempting to find an evolutionary basis for this differential treatment might connect these results with the statements made by Sullo way (1996) that state that even though the families that were alive a century ago had multiple children – parents were more likely to place a greater emphasis on having their first-born survive into adulthood, often neglecting the later-born children. Therefore, first-borns will receive more attention than any later-born child during early developmental stages.

Increased attention can therefore affect intelligence because, when an older child receives more attention than a younger child at early developmental stage, they might receive more assistance than their younger siblings when learning to master specific subjects (Price 2007). Results of Price (2007) are consistent with the resource dilution model because it was found that this effect was likely to perpetuate with the increasing amount of births with the last-born child receiving the least amount of attention during critical developmental times.

Though later-born children might not receive the same amount of parental attention as a first-born child during critical developmental periods, many first-borns or other lower birth order siblings show their mastery of certain subjects by

teaching their younger siblings – potentially making up for the lack of parental attention a later-born child might experience in early childhood (Minnett et al. 1983; Price 2007). This introduction of teaching behaviors in which older siblings are inclined to assist younger siblings might be broadly explained by the evolutionary theory of kin selection because older siblings – especially if they are female – are more likely than their younger siblings to reconstruct concepts that are mastered to their two siblings to whom which the same material is foreign (Pollet and Nettle 2007). And, although teaching behaviors might be a way in which older siblings way of assist or invest their younger siblings, teaching has been found to be more beneficial to the child giving the lesson (Price 2007). This could be because, as mentioned, to teach materials to their younger siblings, older children must find novel ways of explaining material to their younger siblings to help them better understand a concept that they are unfamiliar with – ultimately increasing the older child's mastery of the subject.

The positive effects of teaching behaviors have also been noted by Zajonc and Markus (1975) who state that, while teaching behaviors might increase the intelligence of the a first-born or lower birth order child, these effects are greatly dependent on the birth spacing between siblings. This is because, for the current last-born child in a sibship not having someone with whom they can reinterpret their newly mastered concepts decreases their potential for increased intellectualism; however, if the gap is too large between siblings, the same can be said for children of lower birth order positions (Zajonc and Markus 1975). Zajonc and Markus (1975) continue to state that these negative effects are most prominent in families with multiple children where the spacing between each subsequent child is large. This is because, as mentioned, not having someone with whom a last-born can share their newly learned information with during early developmental stages decreases potential for intellectualism. Therefore, children with larger age gaps in-between them and their youngest sibling will have a lower intelligence because they will

not have someone to share information with during formative, early developmental stages, and, conversely, larger age gaps have been shown to have more benefit the last-born child than short gaps because having older, more mature siblings increases the intellectuality of the family they are born into (Zajonc and Markus 1975). It should be noted, however, that the confluence model is the only model that reviews smaller age gaps as being beneficial. Reviewing the resource dilution model, smaller age gaps have been seen to increase competition between siblings whereas larger age gaps would decrease the amount of differentiation each child needs to gain parental resources to increase their intelligence (Downey 2001).

Regardless of the amount of time elapsed between births, research reports that individuals who do not have younger siblings, such as last-borns and only-born children, are more likely to have deficits in intelligence because they are not given the same experience to teach as children with younger siblings (Zajonc and Markus 1975; Price 2007). However, the notion that an only-child has a decreased amount of intelligence because of their lack of siblings conflicts with both the resource dilution model and confluence model – introducing an issue which could be seen as an only-child dilemma.

This dilemma surrounding only-born children occurs because, after controlling for social confounds, such as income or single parenthood, only-children should have similar outcomes as first-borns when using the resource dilution model or the confluence model because they will be born into a family environment of higher intelligence and will not have to compete for as many parental resources (Zajonc and Markus 1975; Downey 2001). Being an only-born child should also intercede with statements made by both models saying that smaller sibships should have higher levels of intelligence than larger sibships because the only-born is the only child in the family. Because of these potential conflicting results for only-born intelligence, more research should be conducted before any definitive statements are made regarding the effect of being an only-born child on intelligence.

Birth Order and Sexuality

With the increased prevalence of individuals who openly identify as homosexual in Western society, research has been conducted to determine how family factors, such as birth order, might influence the development of homosexuality among males and females. Of the present research conducted on the influence of birth order on sexuality, the maternal immune hypotheses – sometimes known as the fraternal birth order effect – has been argued to be the most probable explanations for the prevalence of homosexuality among males and MF (male-to-female) transsexuals (Gomez-Gil et al. 2011).

The maternal immune hypothesis posits that the likelihood of a male child being homosexual increases with the growing number of older brothers born before him (Blanchard 2001; Gomez-Gil et al. 2011). This would mean, for an example, in a family of all male sons, there is a higher chance that the last-born son will be homosexual than the first-born son – even in two-sibling dyads (Blanchard and Bogaert 1996). Prevalence of male homosexuality occurring in later-borns is believed to be caused in utero as the mothers immune system combats antigens – specifically H-Y antigens – produced by male fetus (Blanchard 2001). This immune reaction increases in intensity with each subsequent male pregnancy because, similar to when your body develops an illness that it had previously recovered from, Blanchard (2001) states that mothers immune systems build in memories in which they are able to detect when a new fetus is male. Blanchard and Bogaert (1997) claim that these immune reactions might therefore cause subsequent male children to have lower levels of various sex hormones than the male children in their biological family born before them. Decreases in these hormones might ultimately be used to explain why, with each sequential male child, the likelihood of them being homosexual increases to where they are 33% more likely to be homosexual than their older brothers born before them (Blanchard and Bogaert 1996; Blanchard 2001). Because homosexuality prevalence has been found to increase with each

additional male birth, homosexual males are more likely to come from large, predominantly male, sibships (Blanchard 2001; Gomez-Gil et al. 2011). However, if a male is from a large sibship, but the majority of his siblings are female, he will not have the same likelihood as being homosexual as the male described in the prior sentence

Similar results were found in a study of MF transsexuals that found that homosexual MF transsexuals (individuals who were born male who transitioned to be female, but are still sexually attracted to men) are more likely than heterosexual MF transsexuals to be a higher birth order child in a family with multiple male children (Gomez-Gil et al. 2011; Hambimana-Kabana et al. 2016). And, in both transsexual and nontranssexual studies, the amount of time between births of males did not influence the prevalence of homosexuality among later-born males (Gomez-Gil et al. 2011; Hambimana-Kabana et al. 2016).

As mentioned previously, however, the maternal immune hypothesis cannot be used to explain the prevalence of homosexuality among women. This is because, according to Blanchard (2001), female fetuses do not produce an H-Y antigen and therefore are not affected by maternal immune response during development.

Birth Order and Mate Selection

As mentioned in the earlier section entitled “[Birth Order, Personality, and Parental Investment](#),” it was discussed that, historically, first-born males have had an advantage when they have reached sexual maturity and are in search of a mate. Sulloway (1996) states that this is because, as the proclaimed benefactor of their parents inheritance and land, first-borns were able to gain the attention of more unmarried women because they were more likely to be able to provide for their future wife and children better than their younger brothers who do not receive an inheritance. By having more potential marriage prospects than their younger siblings, eldest males were not only able to choose a woman who would provide multiple children,

but he could also marry a woman who would make him happy – like many of the men and women in present day.

To explain how birth order might influence the selection of a mate, especially when emotions or personalities are involved, Walter Toman created the duplication hypothesis. According to the duplication hypothesis, an individual is most likely to choose a spouse with whom they can best recreate the birth order in which they resided as a child (Toman 1971). Therefore, if an individual was a first-born in their sibship, they will be more likely to be in a relationship someone who was a later-born in their sibship. However, researchers such as Hartshorne et al. (2009) have found conflicting results indicating that individuals might actually be more likely to choose a mate that shares their birth order.

In his study, Hartshorne and colleagues (2009) found that college students are more likely to form relationships, both romantic and platonic, with people that share their birth order rather than individuals of other birth positions. Hartshorne and colleagues (2009) continue to say that these increased prevalence of same-birth order dyads in relationships might be due to the similar personalities between members of shared birth position – decreasing the validity of the old saying “opposites attract.”

Choosing a mate of the same birth position might ultimately be of evolutionary value because similarities in personality might assist with the successful co-parenting of future children – ensuring they produce socially and cognitively competent children, perpetuating evolutionary value.

Conclusion

Since the founding remarks of Sir Francis Galton in 1874, there have been many hypotheses used to infer information on how birth order effects have evolved over time to effect personality, intelligence, sexuality, and mate selection. Many of these initial hypotheses indicate that within a family, the first-born is traditionally at an advantage in comparison to his siblings.

Today, this is believed to be because he is able to attain more resources and is born into an environment of higher intellectuality, while in years past, it was because he would be the beneficiary of the family inheritance and therefore was provided more resources to survive into adulthood.

Other hypotheses created indicate that, for males, birth order might play a large role in determining their sexual preferences with later-born males being more likely to be homosexual if in a multiple-male child sibship. While some of these recent studies have focused on sexuality, other studies have reviewed the effect of birth order on mate preference – leading to two conflicting hypotheses either agreeing or disagreeing with the age old saying “opposites attract.”

By living in an ever-changing society, family dynamics are also changing. While these hypotheses can be used to partially explain differences between birth orders, because of changing dynamics, more research should be conducted before definitive statements are made.

Cross-References

- ▶ [Adaptation for Single Births](#)
- ▶ [Birth Order and Parental Investment](#)
- ▶ [Birth Order and Sibling Relationships](#)
- ▶ [Competition for Parental Investment](#)
- ▶ [Competition for Resources Desired by Females](#)
- ▶ [Competitive Altruism](#)
- ▶ [Duration of Breast Feeding in Ancestral Environments](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Parental Investment](#)
- ▶ [Personality](#)
- ▶ [Presence of Siblings](#)
- ▶ [Resource Competition](#)

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Birthing Complications

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Synonyms

[Birth attendants](#); [Cesarean section](#); [Obstructed labor](#)

Definition

Childbirth is a complicated process for humans that is often accompanied by anxiety and discomfort, which can be relieved with emotional support.

Introduction

Giving birth seems to be more complicated and challenging for women than it is for females of most other mammalian species. A number of explanations for birthing complications have been offered including the large size of the human neonate, the anatomical limitations of the bipedal pelvis, unwarranted medical interventions in what is usually a straightforward process, and complex psychological and emotional reactions to labor and delivery.

Human Birth

Most human births occur vaginally with the infant in the vertex (head down) position and without problems, but complications occasionally arise, some of which benefit from consideration within the context of human evolutionary history and, especially, evolutionary psychology. Example birthing complications that can be considered in an evolutionary context include prolonged labor, abnormal or unusual presentation of the fetus (e.g., breech), cephalopelvic disproportion, and

both medical and elective cesarean section. Additionally, many unproblematic deliveries may be designated as complicated based on highly subjective definitions and varying hospital practices (Cunningham et al. 2014).

Anatomical Factors and Birthing Complications

As a result of our evolutionary history, humans have large babies and complex birth canals, leading to challenging births. Humans are not unique in having difficult births, however – monkey infants are also large relative to their mothers' bodies, and births in captive primates sometimes present difficulties that can result in infant death without assistance from veterinary staff. Complications that have been reported for monkeys include breech deliveries, dystocia, and cephalopelvic disproportion but at far lower rates than reported for humans (Schlabritz-Loutsevitch, et al. 2018). What is unusual about human birth is the series of rotations the infant undergoes as it navigates through the tight dimensions of a pelvis that has evolved for bipedal walking rather than for easy birth. Furthermore, human births typically occur with some form of social support and assistance, a phenomenon that has been reported for other primates but is far from routine and expected (Trevathan 2015).

Unlike the quadrupedal pelvises of monkeys and apes in which the birth canal is a relatively straight passageway from inlet to outlet, the human adaptation to bipedalism has resulted in a birth canal that is twisted in the middle. Additionally, the way in which the infant begins its emergence from the birth canal is different for humans and nonhuman primates. Most monkeys are born with the head extended in a face presentation (Trevathan 2015; Schlabritz-Loutsevitch et al. 2018), a type of delivery that would be considered an obstetric complication in humans. The monkey infant typically continues to emerge facing the same direction as the mother ("occiput posterior"), whereas the typical human presentation is "occiput anterior" with the back of the infant's head against the front of the mother's pelvis so that it emerges facing away from the mother. This emergence pattern has been suggested to account for the selective

value of having assistance at birth for guiding the infant from the birth canal (Rosenberg and Trevathan 2018). Giving birth in the presence of another person who can wipe the fluids from the newborn infant's face, unwrap the umbilical cord from around the neck if it is too tight, and guide the infant toward the mother's breast may avoid complications that are often associated with childbirth. Helping the infant make contact with the breast may play a role in inhibiting postpartum hemorrhage, one of the most common causes of maternal death related to childbirth (<http://www.who.int/mediacentre/factsheets/fs348/en/>). Human mothers can do this alone, but maternal and infant mortality and morbidity have probably been reduced throughout history when assistance is provided.

What Role Do Psychological and Emotional Factors Play in Making Birth Complicated for Humans?

The ultimate explanation for assistance may be lowered mortality (and greater reproductive success for those who have assistance), but the proximate explanation is more likely that the laboring female seeks emotional support at a time when she feels vulnerable and anxious. Humans are notably socially gregarious mammals, and seeking companionship during times of heightened emotions is normal and expected. Giving birth is probably one of the most emotionally and physically challenging life events that a woman experiences (Simkin 1996). Women who report feeling anxious and fearful about the pain of childbirth are often advised to be treated with pharmaceutical and other medical interventions up to and including elective cesarean section. Randolph Nesse (1991) has argued that a number of psychological problems can better be understood as *defenses* that have been naturally selected because of their benefits to survival and reproductive success. Examples are phobias that may lead a person to avoid potential dangers such as snakes, rocky ledges, and jumping out of airplanes. Sadness in response to a failed love relationship, flunking a test, or being fired can provide time to reflect on causes and to develop strategies for improving outcomes in subsequent ventures. Following this logic, anxiety during

labor and delivery can lead the typically gregarious human female to seek companionship and social support when she is preparing to give birth. Anxiety can also help a woman to focus cognitively, emotionally, and physically on the task of delivering an infant. In all of these examples, the phobia, sadness, or anxiety can become extreme, leading to a variety of undesirable outcomes that have negative fitness consequences, at which point they become, in Nesse's words, "defects" that may require medical or psychological interventions.

What Role Do Modern Medical Interventions Play in Making Birth Complicated for Humans?

Although it is clear that there are complications associated with childbirth that cannot be resolved without medical intervention, many would argue that there are perhaps more cases in which intervention *causes* complications. At the very least, there is increasing evidence that obstetric interventions add to the financial costs of childbirth and reduce maternal satisfaction with their birth experiences without adding any benefits for women at low risk for complications (Tracy and Tracy 2003; Tracy et al. 2007). Furthermore, interventions at one birth often lead to intervention in subsequent deliveries.

The ultimate intervention when birthing complications become life threatening is surgical delivery of the fetus, or cesarean section. The most common medical reasons for cesarean section in the United States are labor arrest (34%), problems with fetal heart rate (23%), fetal malposition (17%), multiple gestation (7%), and suspected fetal macrosomia (4%) (Barber et al. 2011). Many of these "causes" relate to expectations that are culturally constructed and that may not be considered as legitimate reasons for cesarean section in some contexts (Rosenberg and Trevathan 2018). For example, labor arrest is based on highly variable definitions of what length of time in labor becomes excessive, leading to surgical delivery (Zhang et al. 2010). In other words, although long labors often lead to healthy neonatal outcomes, if attendants perceive labor length as excessive, they often offer

cesarean section. Without support for alternative options, an exhausted mother in labor may quickly accept this suggestion and deliver her infant surgically.

Conclusion

In conclusion, birthing complications may require technological interventions up to and including cesarean section, but increasing awareness of the range of healthy variability in physical and emotional aspects of birth will likely improve outcomes for women and infants all over the world. Understanding the evolutionary context of the physical challenges of giving birth and the powerful emotions surrounding this event will likely lead to improved environments of birth, reductions in the well-known high rates of cesarean section, and improved emotional health following what is likely one of the most significant experiences of a woman's life.

Cross-References

- [Anxiety \(Randolph Nesse\)](#)
- [Bipedal Locomotion](#)
- [Brain at Birth](#)
- [Cooperative Breeding](#)
- [Early Stage of Brain Development at Birth](#)
- [Evolutionary Medicine](#)
- [Narrowing Birth Canal](#)

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Birthrights and Bloodlines

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Synonyms

Ancestry; Castes; Clan; Ethnicity; Heraldry; Heritage; Inheritance; Inherited status; Lineage; Parental investment; Pedigree; Primogeniture; Royal lineages; Ruling class

Definition

The way ancestry influences social behaviors and interactions.

Introduction

Humans receive three crucial things from their ancestors: their genes, their kin, and their

traditions (Lyle Steadman, 1981, personal communication). Like all forms of life, humans are tremendously influenced by the genes they inherit from their ancestors. Starting at conception, these genes interact with countless aspects of the environment, in complex ways that are just beginning to be understood, to form the physiological and behavioral phenotype of the individual. Like many species, a key aspect of the environmental factors influencing a human's development is the closely related kin, both living ancestors (e.g., parents and grandparents) and co-descendants of those ancestors (e.g., aunts, uncles, nieces, nephews, and first cousins), that the developing individual interacts with throughout their lifetime. However, although many species copy the behavior of parents (Avital and Jablonka 2000), humans are unique in the extent to which their development and evolutionary success are influenced by traditions: the behaviors that have been passed down from one generation of their ancestors to the next, sometimes for hundreds of generations, before being copied by the developing human. Some of the traditions passed down through specific sequences of ancestors and descendants (i.e., bloodlines) drawing the most attention from evolutionary psychologists have been those leading to the intergenerational transmission (i.e., inheritance) of various forms of wealth and status (i.e., birthrights).

The Generational Depth of Bloodlines and the Breadth of Co-descendants

The evolutionary study of birthrights and bloodlines can be conceptually organized on the basis of the generational depth of the bloodlines in question, which in turn determines the breadth of currently living co-descendants being studied. Studies on differences in how parents treat offspring (Borgerhoff Mulder 2000), including the differential transmission of wealth and status to those offspring, involve differences between siblings. This research often uses the evolutionary concept of parental investment theory to study differences based on the sex of the offspring, and the concept of parent-offspring conflict to study

other differences such as birth order (Draper and Hames 2000). Such studies have been performed on populations at various levels of social complexity, and tend to focus on how sex and birth order influence the inheritance of wealth, property, and status, and how these differences in inheritance influence, in turn, the inclusive fitness of the individual siblings. Perhaps the most well-known influence of birth order is primogeniture, where the first born son inherits most of all of the wealth, property (e.g., land, house), and/or status (Low 1990).

Sometimes studies on intrafamily differences in parental treatment of offspring focus on the relative status of the family within the larger social environment. One type of this category of studies examines how the sex of the offspring influences their inheritance and treatment by parents in relation to the family's relative socioeconomic status. These studies often examine the hypothesis that sons will receive better parental treatment and inherit more in higher socioeconomic classes (Dickemann 1979), while the same will be true of daughters in lower socioeconomic classes (Cronk 1989). This hypothesis is based on the fact that whenever formal or de facto polygyny occurs, the highest quality males will have greater reproductive success than the highest quality females, but the lowest quality females will have greater reproductive success than the lowest quality males. Primogeniture within a family can also be studied within the larger context of interfamilial differences in wealth, power, and status (e.g., European monarchies).

Studies focusing primarily or exclusively on differences between families focus on the consequences of differences in behaviors, wealth, and status transmitted through longer lasting multi-generational bloodlines to form lineages, clans, and ethnic categories. These studies sometimes focus on the inheritance of certain positions of status such as headman and shaman among foragers and other highly traditional cultures. However, most of this research focuses on inequalities which have become more extreme as social complexity and social stratification has increased. These range from royal lineages to the development of caste systems but have in common a

focus on the long-term inheritance of wealth, power, and status in certain lineages (Shenk et al. 2010).

Conclusion

While these studies of bloodlines and birthrights have been very productive, perhaps the most fundamental and important influences of traditions have been largely overlooked by evolutionary researchers. This is the influence of traditions on behavior toward co-descendants of a common ancestor. This influence not only includes identifying these individuals as kin but influencing these individuals to behave in certain altruistic ways toward these individuals (Palmer et al. 2016), a form of behavior characterized as the axiom of kinship amity (Fortes 1969). This is a puzzle to orthodox evolutionary theory because this amity extends far beyond the range of kin selection and produces altruism failing to conform to predictions generated by reciprocal altruism and multilevel (i.e., group) selection. The consequences of such traditions include the ubiquitous segmentary nature of bloodlines, which tends to characterize human social organization (Coe et al. 2010). Thus, incorporating traditions into evolutionary explanations of human behavior is a major challenge.

Cross-References

- [Birth Order and Parental Investment](#)
- [Differential Parental Investment](#)
- [Grandparental Investment and Genetic Relatedness](#)
- [Kin Recognition and Classification in Humans](#)

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Bisexual Behavior

- [Same-Sex Sexual Behavior](#)

Bisexuality

- [Alloparenting and Female Same-Sex Behavior](#)
- [Sexual Orientation and Human Sexuality](#)

Bistability

- [Environmental Unpredictability and Bet-Hedging](#)

Bitter

► Taste

Blank Slate

► Standard Social Science Model

Blank Slate, The

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Keywords

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Romanticism

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human nature; Utopian vision

Definitions

Taken to its literal extreme, a *blank slate* view of human nature is “the idea that the human mind has no inherent structure and can be inscribed at will by society or ourselves” (Pinker 2002, p. 2); “The belief that humans are very malleable and that most group and sex differences are caused by variation in the environment, not by differences in genes” (Winegard 2018).

An *implicit* or *quasi-Blank Slate* (i.e., *Blank-slate-like*) theory of human nature involves believing that biology is important, in some way, for

explaining human minds and behavior, but often maintaining the idea that nature and nurture are disjoined and/or opposing causes (rather than integrated), with environments (particularly socially constructed knowledge) being considered the predominant causes of many/most aspects of human personality, cognition, and social behavior, independent of consideration of evolutionary/genetic/biological causes.

Introduction

In *The Blank Slate: The Modern Denial of Human Nature* (2002/2016), Steven Pinker describes how and why many modern academics and intellectuals reject (sometimes vehemently) a biologically based conception of human nature in favor of an epistemological view (known as a *Tabula rasa* or Blank Slate view) that all human knowledge comes from perceptual and experiential learning. Modern academics and intellectuals appear to accept and defend the latter view based, at least partially, on fear of four perceived implications of a biopsychological conception of human nature: (1) fear of inequality, (2) fear of imperfectability, (3) fear of determinism, and (4) and fear of nihilism. He argues the feared perceived implications from acknowledging an evolved human nature are nonsequiturs. In addition, Pinker (2002/2016) argues blank slate views are often associated with (1) a belief in the “noble savage” myth that people are inherently morally pure and corrupted only by “bad” societal influences and (2) a belief in the “ghost in the machine”; the assumption that human choices are free from biology. These auxiliary beliefs support and protect the Blank Slate view by “explaining” bad behavior independently of biology or any evolved human nature. Pinker’s book documents the great lengths that intellectuals have gone to deny influences of human nature and to promote a Blank Slate-like view within academia and the larger culture. He defends the idea of an evolved (and sex-differentiated) human nature with empirical evidence and responds to common moral and political criticisms of an integrated-evolutionary view of human nature.

This entry describes why a *literal* blank slate view is intellectually incoherent and implicit or quasi-blank slate views are also scientifically indefensible, but common. It describes ways blank slate perspectives conflict with biologically unified perspectives on how, mechanistically, “nature” (i.e., evolved organization through genetic/epigenetic influence) interacts with experiential learning. It contrasts blank-slate-like interpretations of recent findings of environmentally induced epigenetic changes with an evolutionary-selectionist interpretation of such findings and argues that recent epigenetic research is more naturally supportive of selectionist accounts of development which suggest evolution has shaped epigenetic mechanisms that include both genes and the “built-in” developmentally relevant “environments.” Finally, it argues that blank slate beliefs are deeply entwined with, and partly motivated by, ideologically based concerns driving a rejection of the notion of evolved psychological and sociological characteristics (Horowitz et al. 2014; Von Hippel and Buss 2017; Winegard 2018; Van den Berghe 1990), leading to an untenable, intellectually bankrupt view of human psychology and societies (Van den Berghe 1990).

Human Nature and the Role of the Environment: Instruction Versus Selection?

Taken to its literal extreme, the Blank Slate (BS) view is the (scientifically incoherent) “belief that humans do not have a “nature” and are entirely molded by environmental/cultural forces” (Winegard 2018). This view implies that, prior to experiential learning, there is no substantial evolved organization to (or biological constraints on) human psychology, experiential learning mechanisms, or behavior. It also implies there are no “innately” structured psychological differences between the sexes.

BS views also assume that pure *instruction* (e.g., by meaningful “information”) from the environment and culture dominate brain, mind, and behavioral development (Gazzaniga 1992). In other words, BS views assume the role of

experience in the development and functioning of higher brain functions is to freely *instruct* or “teach” neuro-cognitive internal machinery about how to do, operate, organize, construct, or assemble something new; it assumes few built-in governing and enabling constraints on how social and cultural environments infuse novel “content” (e.g., new associations) into the human brain’s machinery, reshaping human psychology as if brain’s were “silly putty” (Pinker 2002) being shaped by a culture, supposedly separate from evolutionary-genetic influence. Because a *literal* (incoherent) blank slate has *no* innate “if-then rules” for how to respond adaptively to ecological contexts in particular ways (i.e., epigenetic rules, describable by reaction norms), an organism could not respond in *any* predictable way (or at all) to environmental stimuli presented by its particular socio-ecological context, let alone with species-specific adaptive behavior. Thus, a *literal* blank slate, is scientifically incoherent and untenable (Tooby and Cosmides 1992).

Possibly because a *literal* blank slate is obviously nonsensical, many social scientists and others adopt *implicit* or *quasi*-blank slate (blank-slate-like) assumptions about the power of socialization (e.g., influences of parenting, media, the presentation of “information,” raising awareness through education, gender roles, “rape culture,” patriarchy, toxic masculinity, etc.) and use those assumptions to ground the belief that properly structured experience can completely “overcome” any biological influences of human nature and effectively re-engineer the human mind and human society, at will, according to current cultural, political, or moral preferences.

To make any sense, however, a quasi-blank slate set of assumptions requires that many “if-then rules” guiding how to respond to a given ecological situation are, themselves, created through experience, “without any reference to biologically adaptive outcomes” (Wilson 2007) or that there are only a few, relatively general, such innate rules that govern how experiential learning “forms” human psychology/knowledge. Using information-processing terminology to describe such “If-then rules,” Tooby and Cosmides (2016, p. 34) write,

Even if a program that causes a particular kind of learning was itself learned, there had to be a prior program that caused the learning to occur, and so on. Logic forces us to conclude that there had to be, at some point in the developmental causal chain, a program that caused learning but that was itself unlearned.

In other words, ultimately, the “rules” that we create to describe how individuals are affected, developmentally, by environmental stimuli and how individuals learn from environmental experience must be innate. Therefore, coherent “environmentalists” and “nativists” must agree there are innate “rules” or regularities for how experience changes psychology and behavior, but disagree about the form, content, specificity, and number of those “rules” (or “programs”) (Tooby and Cosmides 2016).

An extreme implicit BS thinker might confidently claim pure environmental causation by stating that “Society *dictates* that boys/men should act one (“toxic”) way to be masculine and girls/women should act another to be feminine” and predict that changing such “societal messages” about gender-related behavior and preferences will solve a number a societal problems/behaviors. Such claims are, however, made without considering at least three biologically viable possibilities: (1) innate differences between biological males and females that contribute to average differences in their psychological/behavioral characteristics, (2) biological differences that contribute to the sex-differentiated characteristics of the society itself (because “societies” aren’t mysteriously uncaused or disconnected from individual brains), and (3) biological differences that contribute to cross-culture/society (and cross-species) consistency seen in the same pattern of sex difference characteristics. In other words, these claims are “just-so stories” about pure socio-cultural causation and they are contradicted by substantial evidence of consistent biological sex differences across species (e.g., Janicke et al. 2016) and across human cultures.

In contrast to BS-like thinking, evolutionary and biopsychological perspectives in the behavioral sciences suggest there is a biologically prepared human nature that has been substantially shaped by various forms of selection and that this evolutionarily shaped

organization is itself what, adaptively, both *enables and constrains* different social and ecological conditions to elicit the many varieties of human behaviors that occur (Lumsden and Wilson 1980, 1981; Tooby and Cosmides 1992). Some evolutionary perspectives suggest that, during proximate-developmental time, specific environmental features *select* from (or “trigger”) the evolutionarily prepared “contents” of human nature. The most extreme form of a (proximate-level) *selectionist* theory “is that an organism comes delivered to this world with all the world’s complexity already built-in” and “the environment selects from the built-in options” rather than modifying them (Gazzaniga 1992; see also Edelman 1987).

Evolutionary perspectives invite us to ask *why* a particular kind of experience has the particular effect it does, rather than *whether or how much* of something is due to environmental experience (Gaulin and McBurney 2004). In other words, in many respects, a satisfactory explanation of why experience (including aspects of cultural experience) affects individuals in particular ways *requires* an evolutionary perspective. These ultimate-level “why” questions also guide us toward asking better proximate-developmental and mechanistic questions. Thus, both BS theorists and evolutionary perspectives propose the environment is developmentally (and theoretically) crucial, but many evolutionary thinkers argue BS-like theorists (often) misunderstand a sensible way to conceptualize the *role* of the environment and *how* experience interacts with biological machinery (note: there is also variety in how evolutionary theorists conceptualize the role of the environment; see Gladden & Jacobs, ► [“Information Processing and the Interdisciplinary Perspective”](#) entry, this volume).

Experiences do not capriciously change our psychology or behavior. As Gaulin and McBurney 2004, p. 10) put it, in information-processing talk, “Evolution has preprogrammed an interaction between genes and environment.” Since evolutionary selection is fundamentally about organisms being shaped by the consequences of environmental change, only by the oddest of assumptions could anyone expect an evolutionary perspective to deny the capacity for

change in response to environmental features (Wilson 2007). It should be an obvious prediction of evolutionary theory that selection crafts proximate mechanisms *enabling (and constraining)* organisms to respond adaptively to, recurrently, important environmental stimuli (e.g., unlearned reinforces and punishers). But BS-like assumptions and an *unconstrained* vision of human nature can promote misunderstanding about *how* experience has its effects and *how* experience/context interacts with biological machinery to guide behavior.

Fear of Genetic Determinism, the False Nature-Nurture Dichotomy, and (Intraindividual) Gene-Environment Interactions

Most Psychologists seemingly agree that many, most, or even all behavioral traits are “due to both nature and nurture.” And most will repeat that behavioral traits result from an “interaction” between genes and environment. So, superficially, BS-thinking doesn’t appear to be a widespread problem in Psychology. But when asked to explain, *mechanistically*, how experience shapes a *single individual’s* traits and *how* genes and environment “interact,” disagreement becomes obvious. For example, many persist in talking about genes and environment as entirely separate influences on individuals that each *independently* affect a trait. These separate influences, the thinking goes, have *additive* effects on the individual’s trait, with some traits seen as more “inherited” or “innate” and others as more due to the environment. This (misguided) way of thinking allows for implicit BS thinking to flourish because, if we can control the “environmental” portion of the trait, a person with such dichotomous nature versus nurture thinking believes it “overrides” the nature portion. This way of thinking is *mechanistically* incoherent because it incorrectly assumes that nature and nurture are opposed forces, inexplicably working *competitively* against each other. Similarly, it’s inconsistent with a true *mechanistic interaction* where the activity of particular genes (and other inherited factors) depend on (i.e., are

“switched on or off” by) particular evolutionarily important social and ecological conditions, and the effects of particular environments depend on particular genes. It’s important to point out that the term “interaction” is more commonly used as a *statistical* term to account for behavioral *differences* across individuals in a sample rather than a *mechanistic* one (as used above) to describe actual causes at the *intraindividual* gene-experience interactions. These two levels of understanding cannot be carelessly conflated.

A second misguided, B.S.-like way of thinking about how experience and genes “interact” is to think that individuals inherit a broad “range” (or “potential”) for traits and experience/environments determine where, within that range, an individual ends up. But while this might be a useful way to describe, for novice undergraduates, how to think about how genes and environment “work together,” genes don’t literally prescribe or transmit any “range” per se. More importantly, Gaulin and McBurney 2004, p. 9) point out that this way of thinking doesn’t go far enough to describing *how* (mechanistically) experience shapes traits:

Many social scientists make the following kind of argument: Nature (or the genes) sets the limits, but experience shapes the trait within these boundaries. This is the familiar claim that our genes have us on a long leash, and it is a second naïve meaning of the claim that x is due to both nature and nurture. It is just as erroneous as the percentage approach. The problem with this way of thinking is that it fails to address the very large problem of exactly how experience shapes the trait. How can it shape the trait except by rules of gene-environment interaction that are coded in the genes? Could UV_B exposure raise IQ? Yes, if there were genes encoding such mechanisms, and no if there were not. To say that experience shapes the trait with broad boundaries amounts to sweeping most of the interesting questions under the rug. . .

The “nature as setting a broad potential” idea might be descriptively true (as far as it goes), in a (superficial) sense. But this way of thinking enables/encourages dichotomous, non-mechanistic, and noninteractive (i.e., implicit B.S.) beliefs to proliferate. These ways of thinking about nature and nurture allow many people to believe in a mind/brain with blank slate-like properties without believing they believe in a blank

slate because they are able to acknowledge that genetic effects are important for *something* (determining a nebulous broad “range” or “limit” or “potential”), but still end up treating nurture as the *predominant* determining force to shape us like “silly putty” within an extremely broad range or limits (without clearly defining what those are). The “nature as setting a broad potential” view is blank slate-like because it doesn’t go far enough in explaining *how* (mechanistically) experience shapes the trait.

These ways of thinking are inconsistent with much evolutionary thought about what genes evolved to do. Genes respond to particular features of the environment in a particular way that is *organized by innate* “if-then rules,” shaped by evolution. Pitting them against each other or treating them as entirely different types of opposing forces isn’t mechanistically sensible. And, as Pinker (1997/2009, p. 33) points out, “having a lot of built-in machinery should make a system respond *more* intelligently and flexibly to its inputs, not less.” So, while an innate organization does, of course, place guiding constraints and structure on the kinds of effects environments will have (i.e., it won’t work anything like silly putty), an understanding of the evolved structure of the mind is not just consistent with, but often *necessary* to effectively identify factors that could minimize social problems. Studying human nature with an evolutionary perspective encourages attempts to understand the particular evolved “if-then rules” or regularities by which environments have their effects.

Tooby and Cosmides (1992) pointed out well that the (developmentally relevant) *environment evolves*. Many genes evolve to be triggered by particular events experienced by the organism and, thus, in some nonliteral “if-then rule” sense, the “environment” is “innate”:

The assumption that only the genes evolved reflects a widespread misconception about the way natural selection acts. Genes are the so-called units of selection, which are inherited, selected, or eliminated, and so they are indeed something that evolves. But every time one gene is selected over another, one design for a developmental program is selected over another as well; by virtue of its structure, this developmental program interacts with some aspects of the environment rather than others, rendering certain

environmental features causally relevant to development. So, step by step, as natural selection constructs the species’ gene set (chosen from the available mutations), it constructs in tandem the species’ developmentally relevant environment (selected from the set of all properties of the world). Thus, both the genes and the developmentally relevant environment are the product of evolution

From their perspective, human nature (the evolved structure of the human brain/mind) *is* a set of reliably-developing, complicated, computer-like *programs* (complex sets of instructions/algorithms) that determine how environments affect behavior. Natural selection, they say, sculpts these “programs” by operating on a “systematically caused *relationship* between information and behavior” (Tooby and Cosmides 2016; but see Gladden and Jacobs 2019, this volume). In other words, these Darwinian “programs” are what Lumsden and Wilson (1980, 1981) termed *epigenetic rules*. With respect to gene-culture coevolution theory, Wilson (1998) described how innate epigenetic rules select/guide how features of the local culture affect psychological development:

Genes prescribe epigenetic rules, which are the neural pathways and regularities in cognitive development by which the individual mind assembles itself. The mind grows from birth to death by absorbing parts of the existing culture available to it, with selections guided through epigenetic rules inherited by the individual brain. (p. 138).

Natural selection operates on variation in epigenetic rules, not genes acting alone or independently of environmental interactants. This means that understanding why environments have particular developmental effects often can’t be understood without understanding evolved epigenetic rules (i.e., biological human nature).

BS Assumptions and Confirmation Bias Mislead Interpretation of Epigenetic Studies of Experience-Induced Gene Regulation Changes

In a recent variant of BS-like thinking, many social scientists with implicit-BS assumptions believe results from epigenetic studies of experience-

induced, gene expression changes confirm their belief that “environments” rather than “genes” control the associated behavioral changes by *instructing*, *directing*, or causally *leading* the genes to make changes involved in behavioral outcomes. Or such findings about DNA methylation are believed (by implicit BS theorists) to (1) “give us license to...embrace a holistic interactionism” without careful/proper causal analysis of its component interacting parts (Pinker 2016, p. 434) and/or to (2) radically alter our understanding of genes and development (e.g., González-Pardo and Álvarez 2013). But a *concept* of epigenetic changes during development, activated by the environment and interacting with genotypes is older (e.g., Waddington 1942) than Watson and Crick’s (1953) publication of the physical structure of DNA. So, these new discoveries about the actual physical mechanisms of genetic *activity* are exciting and enlightening, but not *conceptually* new or revolutionary. Indeed, epigenetic rules of human social behavior were the central feature of Lumsden and Wilson’s (1981) theory of gene-culture coevolution, which suggests a strong nativist/selectionist view of cultural learning that “genes hold culture on a leash” because genes prescribe innate epigenetic rules of culture (though the “leash” is flexible). Thus, new mechanistic discoveries supporting the concept of experience-induced epigenetic changes does not imply that environments are suddenly more important than previously thought or “taking the lead” over DNA in controlling phenotypes. Such epigenetic discoveries were, apparently, expected/predicted by sociobiologists decades before most social scientists had ever heard of epigenetics. Further, it is an error to think that “genetic” and “epigenetic” effects or developmental processes are inherently different things because DNA doesn’t work by magic or somehow autonomously, disconnected from any external regulation. Thus, “genetic” effects are always “epigenetic” (in a developmental process rather than inheritance sense) because a gene is, presumably always, regulated by something other than its own *volition*. These basic epigenetic findings don’t suggest anything about the

“relative importance” of environments versus genes in controlling/leading the development of phenotypes or anything specific about the degree of canalization of the trait. Since evolutionary selection is obviously expected to craft innate mechanisms enabling organisms to respond adaptively to (recurrently) important environmental stimuli (as described above), only by the oddest of assumptions should anyone expect experience to be unable to change gene expression in an *adaptively constrained* way (Pinker 2016). But this doesn’t free the environment to alter human nature (or epigenetic rules).

A proximate-level selectionist interpretation (as described above) of studies examining experience-induced epigenetic changes in gene expression proposes that evolution organizes a diverse neural, psychological, and behavioral repertoire *in advance* and that environmental features “select from” or trigger these evolutionarily prepared sets of neural and phenotypic options. Thus, organisms come to produce behavior that solves environmental adaptive problems effectively, not because the environment *instructs* the genes how to do something new, but because evolution has shaped epigenetic mechanisms that behave *as if* they include both genes *and* the “built-in,” developmentally relevant “environmental cues” or triggers. From this view, the environmental features associated with specific classes of adaptive problems developmentally trigger innately organized and environmentally contingent “options” and such environmentally activated epigenetic effects are themselves under the constrained control of DNA, along with inherited transcription factors (e.g., gene “switches”). Furthermore, Chernyavskaya et al. (2017) point to evidence that “DNA methylation does not serve as a universal mechanism of repressing gene expression” and “although DNA methylation contributes to the regulation of some genes, many studies have led to the conclusion that this function is the exception rather than the rule.” In other words, DNA methylation changes are not always, themselves, causal of gene expression changes. Further, Hannon et al. (2018) found that variation in DNA methylation at sites associated with environmental variables is also partly heritable, possibly suggesting control

by genes as to whether and how much particular environmental factors affect DNA methylation.

Unconstrained Visions of Human Nature and Leftist Political Homogeneity among Social Scientists

Pinker (2002), citing Thomas Sowell's *A Conflict of Visions*, argues that blank slate-like beliefs, including a belief in human perfectibility are based in an *unconstrained* (or *utopian*) vision of human nature and are, generally, (though not always) associated with leftist political beliefs. In contrast, evolutionary psychological perspectives suggest a *constrained* (or *tragic*) vision by acknowledging enduring characteristics of human nature and acknowledging individual biological variation. Arnhart (2005) notes:

those with the realist" (constrained) "vision of life believe that since the moral and intellectual limits of human beings are rooted in an unchanging human nature, a good social order must make the best of these natural limitations rather than trying to change them. But those with a utopian vision of life believe that since the moral and intellectual limits of human beings are rooted in social customs and institutions that are changeable, the best social order would arise from rationally planned reforms in these customs and institutions that would perfect human nature. (p. 6)

In the *Utopian/unconstrained* vision, human nature changes with social circumstances and by tinkering with those social circumstances we will re-fashion human nature. In the *Tragic/constrained* vision, social circumstances/traditions are "...spontaneously evolved rather than rationally designed" (Arnhart 2005, p. 7) and "let us work around the shortcomings of human nature" (Pinker 2002, p. 288). Pinker (2002) agrees that "the new sciences of human nature really do vindicate some version of the Tragic Vision and undermine the Utopian outlook" (p. 293) and advocates for thinkers on both the political right and left to modify their political alignments as we learn more about human nature.

Consistent with the idea that deeply entrenched ideological convictions drive beliefs in an unconstrained human nature and an implicit blank-slate, Buss and Von Hippel (2018) (see

also Von Hippel and Buss 2017) reported the results of a survey of 335 Social Psychologists, finding that, although Social Psychologists overwhelmingly report they believe in evolutionary theory and that it generally applies to humans, they are much more split about whether evolution has shaped many social attitudes and preferences (with a significant minority evidently rejecting the idea) and divided about whether some specific findings/conclusions that contradict blank slate-like beliefs are likely to be true. They found some preliminary evidence that far left political ideology correlates slightly with at least some blank slate-like beliefs (e.g., rejection of the possibility that "sex-differentiated hormones such as testosterone and estrogen have a major influence on our attitudes and behavior"). One limitation of these findings is that there are almost no politically conservative social psychologists, so the sample is overwhelmingly politically homogeneous like the field has become since the 1990s.

Duarte et al. (2015) advocated for increased political diversity in social psychological science to reduce ideological and confirmation biases, particularly because the field deals with ideologically controversial topics that human reasoners are hopelessly biased about. When there are too few conservative perspectives on ideologically charged topics (i.e., lack of viewpoint diversity), there is insufficient collective scientific correction. As Haidt (2013) notes, just as the political right is full of young-earth evolution deniers and climate change deniers, the political left is full of IQ-deniers, heritability deniers, biological sex difference deniers, evolutionary psychological science deniers, and stereotype accuracy deniers. Each of the latter "science-denial groups" involves blank slate-like thinking. Thus, if BS-like thinking on "hot-button" topic becomes sufficiently orthodox, it can slow or even halt scientific progress in those areas.

The situation for human nature denial in Sociology is even worse. In a sample of 155 Sociological theorists, Horowitz et al. (2014) found:

Just over half the theorists in our sample deny the role of natural selection in shaping a range of human tendencies. Many more are unwilling to acknowledge the plausibility of evolutionary arguments applied to sex differences.

Much Sociological theory treats “culture” or “society” as an uncaused (autonomous) cause, separate from individual biological brains, and not connected to psychological explanations involving evolution or genes (Van den Berghe 1990). A common charge is that evolutionary or “genetic” explanations of societal phenomena are “reductionist.” Dawkins (1996) defends hierarchical (intertheoretic) “reductionism” as a fundamental scientific tenet for trying to make sense of things:

“To call oneself a reductionist will sound, in some circles, a bit like admitting to eating babies. But, just as nobody actually eats babies, so nobody is really a reductionist in any sense worth being against. The nonexistent reductionist – the sort that everybody is against, but who exists only in their imaginations – tries to explain complicated things directly in terms of the smallest parts, even, in some extreme versions of the myth, as the sum of the parts! The hierarchical reductionist, on the other hand, explains a complex entity at any particular level in the hierarchy of organization, in terms of entities only one level down the hierarchy; entities which, themselves, are likely to be complex enough to need further reducing to their own component parts; and so on. It goes without saying though the mystical, baby-eating reductionist is reputed to deny this – that the kinds of explanations, which are suitable at high levels in the hierarchy are quite different from the kinds of explanations which are suitable at lower levels. This was the point of explaining cars in terms of carburettors rather than quirks. But the hierarchical reductionist believes that carburettors are explained in terms of smaller units. . . , which are explained in terms of smaller units. . . , which are ultimately explained in terms of the smallest fundamental particles. Reductionism, in this sense, is just another name for an honest desire to understand how things work.” (Richard Dawkins 1996, p. 13)

Conclusion

Many behavioral scientists with blank slate-like beliefs hold misconceptions about evolutionary psychological perspectives (e.g., Von Hippel and Buss 2017), including believing that evolutionary psychology advocates “genetic determinism” rather than an integrated interactionist perspective. Implicit blank slate views are entangled with unconstrained visions of human nature, the naturalistic fallacy, and sacred liberal values

concerning fairness/equality and social justice. When, due to a lack of political viewpoint diversity, sacred beliefs/values are overwhelmingly agreed upon (and “socially enforced”) within social science fields when truth and sacredness do inevitably come into conflict, there is a lack of sufficient scientific correction or truth-seeking against the conventional view. Evolutionary psychological perspectives on development, behavior, and culture run against the orthodoxy within social sciences because they are perceived to challenge deeply held assumptions/convictions about human nature, perfectibility, freedom, and equality.

Cross-References

- ▶ [Information Processing and the Interdisciplinary Perspective](#)
- ▶ [Selectionist Models: Implications for Behavior](#)
- ▶ [Standard Social Science Model](#)

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Blast Injury

- [Specific Brain Damage](#)

Blended Family

- [Stepfamilies](#)

Blending

- [Metaphor and Analogy](#)

Bleuler's Syndrome (Obsolete)

- [Schizophrenia](#)

Blindsight

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Synonyms

[Cortical blindness](#); [Riddoch-Syndrome](#)

Definition

The term Blindsight has been coined to describe a seemingly paradoxical clinical phenomenon that arises following injury to primary visual cortex (V1): While patients with Blindsight appear to lack any conscious visual experience, they are sometimes still able to detect visual stimuli when carefully tested (Weiskrantz et al. 1974).

Introduction

Selective lesions of V1 that spare the rest of the brain are rather uncommon in the clinic. Yet several intriguing cases have been described that typically arose from selective traumatic injuries or strokes. Standard clinical tests commonly reveal spatially restricted blindness, also called scotoma, in the part of the visual field affected by the lesion. If the scotoma spans the visual hemifield opposite the affected cortical hemisphere, this type of blindness is often diagnosed as hemianopia. The terms Blindsight or Riddoch-Syndrome were developed in academic contexts (Weiskrantz et al. 1974; Zeki and Ffytche 1998), following careful testing of these patients under rigorous laboratory conditions when these individuals showed residual, V1-independent visual function, yet with no or severely distorted conscious visual experience.

Phenomenology of Blindsight

Blindsight patients typically deny that they have any visual experience inside their scotoma. However, when given certain visual tasks and asked to guess (forced response), these subjects are still able to perform. For example, when a small spot of light is displayed to a visual region that is covered by their scotoma, these patients generally fail to report the presence of any stimulus. However, when encouraged to guess the location of the small light spot, their performance is well above chance and often accurate. In some sense, these patients appear to possess an (unconscious) sense of sight (Weiskrantz et al. 1974; Poppel et al. 1973). In order to understand the nature of this V1-independent visual function, scientists have tested Blindsight patients on a battery of tasks. The broad picture that has emerged from these studies is that Blindsight patients generally perform well on forced response tasks involving salient stimuli that are either very bright or contain motion (summarized in Schmid and Maier 2015; Cowey 2004). Moreover, some patients retain basic visual spatial navigation skills and are able

to walk through a corridor of obstacles. These patients are also able to perform certain eye-hand coordination tasks, such as shaping their hand appropriately for grasping an object inside their scotoma. Some patients are even able to detect certain facial expressions when faces are shown to their scotoma. Blindsight patients are also able to use visual information presented outside their scotoma to solve perceptual completion tasks inside their scotoma. However, residual vision during Blindsight is generally limited to the detection of visual stimuli. When subjects are asked to discriminate between competing object attributes, they usually fail. Even for the case of visual motion, Blindsight patients can successfully detect the presence of a stimulus, but are nonetheless unable to discriminate between different motion directions. Color vision and the perception of shapes seem to be entirely lost following V1 lesions. Animal studies showed that in many mammalian species, such as rats, mice, and cats vision seems virtually unaffected even if the entire primary visual cortex is removed or inactivated. However, this is not true for our closest relatives, as monkeys seem to undergo Blindsight in a similar fashion as human patients.

Blindsight and the Brain Mechanisms of Conscious Perception

Whether Blindsight offers the potential to study (un-)conscious brain function is a matter of intense debate (Zeki and Ffytche 1998; Cowey 2004). Initial concerns that Blindsight merely reflects an experimental artifact arising either from nonspecific light scatter resulting in excitation of lesion surrounding neurons or from incomplete cortical lesions with surviving gray matter islands were dismissed on the basis of tightly controlled experiments. For example, research in macaque monkeys with artificially created lesions demonstrated Blindsight in the absence of any surviving cortical tissue. A second concern with Blindsight has centered on whether subjects are completely unconscious of visual stimuli presented to their scotoma. For example, one

Blindsight patient tested in Zeki's laboratory for residual motion vision reported the sensation of "a moving shadow." Because a similar observation was reported earlier by the neurologist Riddoch, Zeki suggested the term Riddoch-Syndrome as a substitute to Blindsight (Zeki and Ffytche 1998). This and related observations have given rise to a recent trend to differentiate between different Blindsight subtypes (I and II) that differ in their degree of (somewhat) conscious versus (fully) unconscious visual processing.

Neurobiology of Blindsight

Neuroimaging of Blindsight patients has revealed that many visual cortical areas retain some responsiveness to visual stimulation in the absence of input from primary visual cortex (reviewed in Schmid and Maier 2015; Cowey 2004). This kind of V1-independent activity has been shown for area MT, an area that is particularly sensitive to visual motion, as well as for other parts of visual cortex, including object and face-sensitive regions of the brain. These results are only partially consistent with the findings of animal studies. Studies in which V1 was cooled down to temporarily eliminate neuronal activity, repeatedly demonstrated a lack of visual responses in cortical areas outside V1, with the exception of area MT. However, studies in which V1's cortical gray matter was permanently destroyed and animals were tested over longer periods of time, akin to the human injury conditions, have found residual visual responses in a number of visual cortical areas. It thus is likely that neuronal plasticity is an important factor in mediating visual recovery. Indeed, neurons in cortical area V4 that were found to be silent during V1 cooling, regained responses, in particular sensitivity to visual motion, following prolonged recovery after chronic V1 injury. Given these findings of V1-independent activation of higher cortical areas, the question remains how visual information from the retina bypasses (removed) V1 to reach these parts of the brain. Early work in monkeys suggests that the superior colliculus (SC), a small structure in the midbrain that receives direct

retinal input, is critical for V1-independent vision. Inactivation of SC abolished Blindsight in V1 lesioned monkeys and resulted in the elimination of visual responses in area MT. However, there are also direct connections from the retina-recipient visual thalamus (► [Lateral Geniculate Nucleus](#), or LGN and the pulvinar nucleus) to visual cortical areas other than V1. While silencing LGN has been shown to abolish Blindsight behavior and activation of adult visual cortex, pulvinar appears to be of particular importance during development. As SC shares connectivity with both LGN as well as pulvinar, exactly which of these subcortical routes underlie Blindsight remains unclear.

Conclusion

Blindsight is an important phenomenon for understanding visual perception. In particular, Blindsight research has revealed profound insights into the circuitry of the visual system and its ability to reorganize and recover following injury and extensive training.

Cross-References

► [Lateral Geniculate Nucleus](#)

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Blood Feuds

► Culture of Honor and Nepotism

Blood Injection Injury Phobia

► Fears and Phobias

Blood Sharing by Vampire Bats

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Synonyms

Food sharing in vampire bats; Vampire bat food sharing

Definition

Vampire bats regurgitate food to others in their social group.

Introduction

In many birds and mammals, mothers will regurgitate food to feed their dependent young, but regurgitated food donations among adults have only been reported for the three species of vampire bat (Wilkinson et al. 2016). In the common vampire bat, where this behavior has been most studied, mothers regurgitate food to their pups but will also feed familiar related and unrelated adults (Carter and Wilkinson 2013a, b; Wilkinson 1984). Since it was first reported in 1984, vampire bat food sharing has been a classic example of “reciprocal altruism” or reciprocity — the hypothesis

that helping is adaptive because it promotes reciprocal help.

Vampire bats feed on nothing but blood, typically from large animals such as cows and horses. They feed only once per night, licking about 15 ml from a bite they make with their sharp incisors. Adult bats miss a meal once every 11 nights on average, while young bats miss a meal on almost one third of their nights (Wilkinson 1984). Due to a limited ability to store energy as fat, a vampire bat is likely to starve to death if it fails to feed on more than two consecutive nights (Wilkinson 1984). Regurgitated food donations can therefore save an unfed bat’s life.

Why do Vampire Bats Share Food?

Regurgitated blood sharing likely evolved originally from extended maternal care. Mothers that feed their young this way gain an obvious direct fitness benefit by promoting their offspring’s survival. But females can also gain indirect fitness benefits by feeding other maternal relatives such as their own mothers, granddaughters, or half-siblings. This *kin selection* is possible because females often remain in their natal population. Moreover, successful foragers can obtain a large blood meal, so the costs of sharing are low for the donor and the benefits of receiving are high for the recipient. Since kinship is symmetrical, a simple rule of kin-biased sharing would lead to a symmetrical pattern of helping. For instance, mothers and daughters are likely to each feed the other on different nights whenever one has failed and the other has not. Once this symmetrical helping has been established through kin selection, the direct fitness benefits of receiving reciprocal help contribute more to a donor bat’s inclusive fitness compared to the indirect fitness benefits of aiding the survival of close relatives (Wilkinson 1988). This symmetry will become enforced as *reciprocity* if the bats prefer to invest in food-sharing relationships that yield better reciprocal returns. This scenario predicts that donors share food for two reasons: it aids the survival of close relatives and it helps maintain social bonds that will lead to reciprocal helping when the donor is in need.

This hypothesis is supported by the relative importance of social factors that affect the decisions of vampire bats to share food. Bats target their donations to kin and nonkin that are likely to reciprocate. Despite frequent roost switching, female vampire bats form stable associations with both kin and nonkin, and regurgitations between adults are predicted independently by both kinship and co-roosting association. In the wild, donations among adults occurred primarily between close relatives and only between bats that roosted together at least 60 % of the time. When kin were removed from a group and the unrelated bats were experimentally fasted, they were disproportionately fed by groupmates that they had fed previously (Wilkinson 1984). These results suggest that both kinship and reciprocal help are predictors of food sharing. But what is the relative importance of each?

Long-term captive studies show that reciprocal help is about eight times more important than kinship for explaining the variation in donation rates among familiar individuals (Carter and Wilkinson 2013a, b). Nonkin food sharing was common for long-term associates that first encountered each other as adults, so bats were not “tricked” into thinking all their cagemates were related. Each female bat forms her own fairly consistent network of donors. When one of her primary donors is removed, she receives less food overall compared to when a nondonor is removed; this shows that food-sharing partners in the social group are not interchangeable (Carter and Wilkinson 2015b).

One of the likely benefits of extending sharing to nonkin is that donors can create and maintain more potential sharing partners. Experimental evidence suggests helping nonkin expands the network of possible donors beyond what would be possible if sharing was limited to close kin (Carter and Wilkinson 2015b). When primary donors, mostly maternal kin, were prevented from sharing, females that previously shared food with more nonkin were fed by more individuals and therefore received more food. When kin donors are unavailable, nonkin can therefore act as a safety net.

Evidence suggests that vampire bat food sharing requires enduring social bonds that are also maintained through other cooperative services, such as allogrooming. These stable cooperative bonds are in many ways similar to those found in primates. Compared with other bats, vampires have enlarged brains, especially the neocortex (Baron 1996), a brain region which is linked to social complexity in primates (e.g., Dunbar and Schultz 2007). Vampires are also the only bats known to engage in high levels of social grooming (Carter and Leffer 2015). Social grooming and food sharing are highly correlated in vampire bats (Carter and Wilkinson 2013) and are regulated by at least some shared hormonal mechanisms, including oxytocin (Carter and Wilkinson 2015a). Unlike food sharing, social grooming can occur at any time making it a less costly and more flexible way to invest in a social relationship, and most food-sharing bouts begin with social grooming.

Conclusion

Food sharing in vampire bats illustrates why processes like kin selection and reciprocity should not be considered as alternative adaptive explanations for helping behavior. Instead, these processes are likely to co-occur and interact in groups with relatives, including humans. Reciprocity can occur among close relatives, and indeed it may often require kin-selected symmetrical helping to become evolutionarily stable. Social cooperation is often stabilized by an interactive combination of direct and indirect fitness benefits. A good way to disentangle the evolutionary benefits is to ask: For predicting helping behavior, what is the relative importance of cues to kinship, sex, social rank, past or future cooperation, and the availability of alternative partners?

Cross-References

► [Nonhuman Reciprocal Altruism](#)

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Blow Job

- [Fellatio](#)

Blubbering

- [Crying](#)

BMI

- [Body Fat Percent and Distribution](#)

Boar Effect

- [Father-Absence and Stepfather Presence](#)

Body and Hand Gestures

- [Ta-ta](#)

Body Attractiveness

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Definition

“Body attractiveness” refers to judgments of the human physical form that excludes facial cues. It could refer to judgments of any human bodily characteristic, either in isolation or as a whole.

Introduction

Evolutionary psychological theories have been used to explain judgments of attractiveness of a range of human morphological traits, typically in isolation of other traits. The aim of this section is not to provide a comprehensive account of all such application of evolutionary psychological theories but rather to provide several key examples, beginning with what is perhaps the most widely cited of such theories: the waist-to-hip ratio hypothesis of women’s body attractiveness.

The Waist-to-Hip Ratio Hypothesis

According to some evolutionary psychologists, a key problem faced by ancestral human populations was the identification of mate value. To overcome this problem, “perceptual mechanisms” are argued to have evolved in ancestral populations to detect and use information conveyed by phenotypic traits in determining an individual’s quality as a potential mate.

Singh (1993) believed that the waist-to-hip ratio – a sexually dimorphic trait – was one such phenotypic trait. Singh also argued that, in contemporary human populations, low female waist-to-hip ratios are reliably associated with improved health and fertility outcomes, and so over evolutionary time men will have evolved to use the waist-to-hip ratio as a direct, universal, and “first-pass” assessment of women’s underlying fitness. To test this idea, Singh developed line drawings of the female form that systematically varied with respect to overall body weight and the waist-to-hip ratio. In a series of experiments using these stimuli, he reported that figures with low waist-to-hip ratios were judged as the most attractive and that ratings decreased with increasing waist-to-hip ratio.

Although the waist-to-hip ratio hypothesis is perhaps the most popular application of evolutionary psychological thinking to body attractiveness, it is also one of the most widely critiqued. For one thing, line drawings have been criticized for lacking ecological validity. In other words, they do not capture the range of body variation that can be perceived in real-life figures and may simplify the way in which real-life judgments of attractiveness are made. When more realistic stimulus sets (including photographs, three-dimensional images, and video clips of real women) have been rated by Western European and North American men, women’s body weight has been found to account for the majority of variance in ratings, whereas waist-to-hip ratio typically explains less than 2 % of variance (Tovée and Cornelissen 2001). These studies suggest that, if men are indeed using women’s waist-to-hip ratios in judgments of attractiveness, it plays a much less important role than overall body size.

A second problem with Singh’s (1993) hypothesis is highlighted by studies that have demonstrated cross-cultural variability in men’s waist-to-hip ratio preferences. Specifically, men from hunter-gatherer and rural sites show a preference for high, rather than low, waist-to-hip ratios, even after controlling for body size (Swami and Tovée 2005a). Other studies have found that men from some subcultures in Western societies, such as

“fat admirers,” also show a preference for high, rather than low, female waist-to-hip ratios. In short, there appears to be a good deal of inter- and intra-cultural variance in waist-to-hip ratio preferences. In view of these problems, some scholars have argued that the female waist-to-hip ratio does not in fact play a direct role in men’s judgments of women’s attractiveness. Instead, the waist-to-hip ratio may be used in judgments of a person’s biological sex when that information is unknown in advance (Johnson and Tassinari 2007). That is, because the waist-to-hip ratio is sexually dimorphic, it may make sense for humans to have evolved to use this phenotypic trait when trying to ascertain the sex of a person. Once this process of social categorization is complete, attractiveness judgments are formed on the basis of additional bodily cues that reflect socio-cultural ideals.

Body Size

As noted above, women’s body size (or body mass index) is one of the strongest predictors of their body attractiveness and explains the majority of the variance in men’s ratings of their attractiveness. While many scholars have relied on socio-cultural theories to explain men’s body size preferences, particularly the idealization of thinness in Western, industrialized societies, this does not discount evolutionary psychological explanations. For example, body size provides a reliable and honest cue of both health and fertility, and humans may have evolved perceptual mechanisms that make use of body size when making judgments of attractiveness. Of course, what is considered an “optimal” body size will vary between populations, and any such perceptual mechanisms may recalibrate as local distributions of body sizes change. As such, instead of expecting uniform cross-cultural preferences for a particular body size, we should anticipate that mate choice vis-à-vis body size will vary depending on local contextual factors. Indeed, the available evidence consistently points to cross-cultural variation in what is considered the ideal body size, with individuals in contexts of

low socioeconomic status consistently showing a preference for heavier body sizes than those from high socioeconomic contexts (Swami 2015).

One specific explanation for this variation, derived from evolutionary psychological theorizing, is that body size provides an honest cue of resource security. This proposition highlights the fact that a primary function of adipose tissue is the storage of calories, which in turn suggests that body fat is a reliable predictor of food availability. In situations marked by resource uncertainty, therefore, individuals should come to idealize heavier individuals, as larger body size would be associated with access to resources. Conversely, thinness in such contexts may be associated with increased incidence of ill health and, in women, lower fertility. Aside from the cross-cultural evidence of an inverse relationship between socioeconomic status (a covariate of resource security) and ideal body size in both women and men, several additional lines of evidence support this reasoning. First, experimental studies have shown that hunger and stress have an effect on men's body size preferences, such that hungry and stressed men prefer a significantly heavier body size than satiated or unstressed men (Swami and Tovée 2012). These findings mirror reports that hunger intensifies selection for a larger body size in some nonhuman species. Second, archival data suggests that heavier body sizes are idealized in American actors and actresses during periods of socioeconomic hardship.

Breast Size

Eye-tracking studies suggest that, when judging the attractiveness of a woman, respondents spend more time looking at the breasts and upper body than any other bodily region. Despite such evidence, the significance of prominent female breasts has proved difficult to explain from an evolutionary perspective, particularly as the human female is the only primate that has permanent, full-form breasts when not pregnant. A number of theories that have been discounted on the basis of lack of evidence include the suggestion that the breast served functional roles such

as milk storage for breast-feeding babies, comfort for nursing infants, and heat stress avoidance. On the other hand, it is possible that biomechanical constraints as a result of sexually dimorphic fat deposition placed unique demands on human female morphology, which resulted in the selection of breasts. Once enlarged, sexual selection may have enhanced the expression of permanently enlarged breasts, with breasts variously argued to act as a sign of age, sexual maturity, or fertility (Barber 1995).

An alternative suggestion is that one function of breasts is to act as an honest signal of fat reserves in non-lactating women, which in turn indicates access to food or resources. This perspective is consistent with the fact that the human breast is partly composed of adipose tissue. Although the amount of adipose tissue varies relative to glandular tissue, human females are unique compared to other species in that the adipose tissue of the mammary gland is situated mainly in subcutaneous and abdominal regions. By contrast, breast size in human female appears to be more strongly correlated with the amount of adipose tissue rather than mammary tissue. In addition, the genetic contribution to human breast size is largely unique to this phenotype and not shared with body mass index. Combined with their prominent display, it is possible that the female breast functions, partly at least, as an indicator of adipose tissue storage. Supporting evidence for this hypothesis comes from studies indicating that hungry men have a stronger preference for larger breasts than satiated men, as well as cross-sectional data showing that men in environments experiencing relative resource insecurity show a stronger preference for larger breasts than their counterparts in contexts of relative resource security (Swami and Tovée 2013).

Men's Body Shape

In terms of men's body attractiveness, it is generally reported that men with low waist-to-chest ratios (or whose torsos have an "inverted triangle" shape) are rated as more attractive than men with

more tubular body shapes (Swami and Tovée 2005b). It has been suggested that low waist-to-chest ratios are indicative of greater mesomorphy or muscularity, which is consistent with the idea that male muscularity enhances ratings of attractiveness. A good genes hypothesis of men's body attractiveness might suggest that men with low waist-to-chest ratios are considered attractive because they are also optimally healthy. However, the evidence does not appear to support this argument. Studies that have included measures of mesomorphy in examining health outcomes suggest that increased mesomorphy is actually a risk factor for ill health. Men's increased body size from muscularity may be associated with higher attractiveness, but it is also associated with poorer health outcomes.

However, there may be advantages of greater mesomorphy which offset complications associated with health and well-being. For example, increased muscularity may intimidate rival men (detering them from making cuckoldry attempts) or provide enhanced defensive abilities. In such a scenario, the health costs of developing increased muscularity may be outweighed by their benefits, which may also be passed on to offspring. In a similar vein, Barber (1995) has suggested that women may have evolved to find men with a certain physique attractive because this body shape was beneficial to men in past evolutionary history. For example, it is possible that a low waist-to-chest ratio, which is associated with physical strength and upper-body muscle development, was an adaptation for intrasexual competition among men in evolutionary history, either via direct fighting or through intimidation.

Conclusion

While the focus of this section has been on waist-to-hip ratios, breast size, waist-to-chest ratios, and body size, it should be noted that evolutionary psychological theories have also been applied to a number of other morphological traits. For example, evolutionary psychologists have also proposed theories to account for the attractiveness of leg-to-body ratios, body hair, height, skin

tone, body symmetry, and foot size, among other characteristics (Swami and Furnham 2008). What is clear from this research is that there are a multitude of factors that shape attractiveness judgments, and an important direction for future research is the development of meta-theoretical perspectives that are able to combine distal, evolutionary factors with more proximate sociocultural factors. In addition, it will be important for scholars to consider morphological traits as a whole rather than in isolation.

Cross-References

- [Facial Attractiveness](#)
- [Physical Attractiveness](#)
- [Vocal Attractiveness](#)

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Body Disposal

- [Death in Christianity](#)
- [Death in Islam](#)

Body Fat Percent and Distribution

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Synonyms

[BMI](#); [Body mass](#); [Waist-to-hip ratio](#); [WHR](#)

Definition

The role of body fat and its distribution in sexual selection

Introduction

White fat is the body's main energy store and is deposited in two main reservoirs: as visceral fat in the abdomen and as subcutaneous fat on the thighs and buttocks. The visceral component of abdominal fat is more detrimental to long-term health than subcutaneous fat. This may be for partly mechanical reasons; the deposition of fat around the organs in the abdominal cavity may interfere with their normal function. Additionally, the development of insulin resistance (which contributes to diabetes and vascular disease) is attributed to an adipokine called retinol-binding protein 4 (RBP4), which is generated by fat cells. Visceral fat generates greater amounts of RBP4 than subcutaneous fat, and so visceral fat potentially has a disproportionate impact on health.

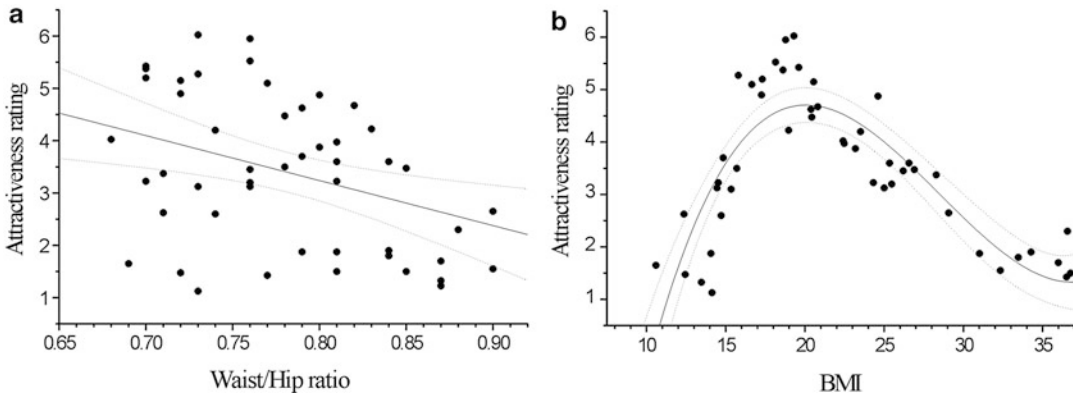
The distribution of fat on the body differs between the genders. Men and women produce both testosterone and estrogen. It is the relative balance of the two which determines fat distribution. In women, the higher level of estrogen mediates the distribution of fat primarily onto the thighs and buttocks as subcutaneous fat deposits. In men, the higher level of testosterone promotes fat deposition in the abdomen as visceral fat. Thus, it is possible that lower body shape (reflecting this pattern of fat deposition) could be a cue to relative hormone levels. This is usually indexed by the circumference of the waist divided by the circumference of the hips (the waist-to-hip ratio or WHR). A lower WHR (i.e., a more curvy lower body) could potentially signal higher estrogen levels, and a lower WHR (around 0.7) has been linked to a more successful outcome in artificial insemination procedures. It is also potentially a cue to health due to the link between visceral fat and type 2 diabetes and hypertension.

The most commonly used measure of overall body fat is the body mass index (BMI). This is a measure of weight scaled for size, or more precisely it is the subject's weight (Kg) divided by the square of their height (m²). Although BMI is generally a good measure of body fat in population studies, it does have some limitations on an individual level. The measure assumes that individuals have the average proportion of muscle to fat. Thus, it overestimates the fat level of someone who has an above average muscle content for their weight (such as an athlete) and underestimates the fat level of someone who has an above average fat content (such as someone with a more sedentary lifestyle). Despite these shortcomings, BMI is still the most widely used measure of body fat due to its ease of use and its noninvasive nature (Table 1).

People can be separated on the basis of BMI into several categories. The BMI range of 18.5 to 24.9 is the healthiest range and is often also called the "normal" BMI range although this is a misnomer. In many Western industrial societies, such as the United States, the normal or average BMI is actually in the overweight BMI range, as the increased consumption of cheap high calorie food and reduced manual labor have led to a

Body Fat Percent and Distribution, Table 1 The World Health Organization (WHO) classifications of BMI categories

<16.00	16.00–16.99	17.00–18.49	18.50–24.99	25.00–29.99	30.00–34.99	35.00–39.99	≥40.00
Severe thinness	Moderate thinness	Mild thinness	Normal range	Pre-obese	Obese class I	Obese class II	Obese class III



Body Fat Percent and Distribution, Fig. 1 Plots of attractiveness as a function of (a) WHR and (b) BMI, respectively, for 50 photographs of women. Each point represents the average of the 40 attractiveness judgments

made by 40 male subjects on each image. Regression lines (*solid line*) and their 99 % confidence limits (*dotted lines*) are superimposed (Redrawn from Tovee et al. 1999)

general increase in body weight across the population. Additionally, there are ethnic differences. For example, the upper limit of the healthy BMI range is 22.9 for people of Chinese and South Asian origin. This is because for a given BMI, Chinese and South Asian people have a significantly higher proportion of their mass made up from body fat, and most importantly, a significantly higher proportion of it is stored as visceral adipose tissue in the intra-abdominal cavity.

The BMI categories are very broad divisions, although the central BMI category is referred to as the healthiest category. This does not mean all the values within this category are equally healthy. Longitudinal epidemiological studies suggest that a BMI value of around 20 to 21 is the optimal value in Western Caucasian populations for health and long-term survival.

The Role of Body Fat in Mate Selection

Singh (1993) hypothesized that because WHR potentially provides information about

reproductive status and long-term health risks, there are good evolutionary reasons to expect WHR to be used in attractiveness judgments and mate choice. The role of WHR in attractiveness was supported by studies that asked observers to rate sets of either line-drawn figures of women's bodies (e.g., Singh 1993) or altered photographic images (e.g., Streeter and McBurney 2003). In these studies WHR is manipulated by altering the width of the waist of the figures. The results from such studies have led to the conclusion that a WHR of approximately 0.7 is most attractive with higher (i.e., less curvaceous) WHRs being rated less attractive by Western observers. However, altering the width of the waist not only changes WHR but also apparent BMI. As WHR rises, so does apparent BMI, making it impossible to say in these image sets whether changes in attractiveness are due to WHR, BMI, or both (Tovee and Cornelissen, 1999). An additional problem with these studies is that some of the manipulations may result in images outside the natural range of variation and as a result lack ecological validity (Fig. 1).

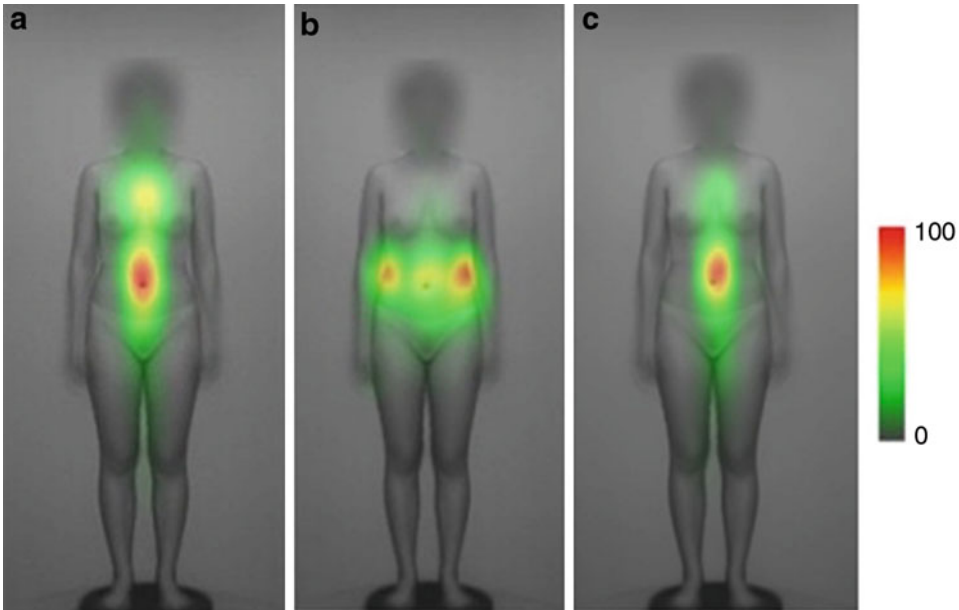
To overcome these shortcomings, a number of studies have been carried out using digital photographs, 3D scans, or videos of women's bodies which show a degree of independence in their BMI and WHR variation, and these studies suggest that BMI is the primary predictor of attractiveness judgments (e.g., Tovee et al. 1999; Fan et al. 2004; Rilling et al. 2009). However, under normal circumstances, BMI and WHR covary in Caucasian populations. For example, the Health Survey for England, which includes directly obtained measurements from 1808 Caucasian women of reproductive age (16–45) ranging in BMI from around 15–45, shows a correlation between BMI and WHR of 0.45. For studies of attractiveness, the correlation between features such as BMI and WHR raises the problem of collinearity among explanatory variables and raises the question of whether WHR or BMI is the primary cue used in attractiveness judgments.

In an attempt to address this problem, Singh and Randall (2007) asked observers to rate the attractiveness of pre- and postoperative photos of women who had plastic surgery to redistribute fat from around the waist to the hip and buttock regions. It is suggested that this reduces WHR without significantly changing BMI. Postoperative photographs were judged as more attractive than preoperative photographs. Singh and Randall concluded that WHR is a key predictor of female attractiveness, independent of any effect of BMI. However, the view of the women in the images was restricted to a back or oblique view of their lower torso and upper thighs only. So, given that the relative size of the waist and hips was the only information available to observers, it is perhaps not surprising that their preferences were affected by WHR. The question remains as to how these women would have been rated if the whole body had been visible to observers. Moreover, both behavioral and eye movement studies suggest that the degree of stomach depth (i.e., the degree to which the stomach protrudes) is used as the primary cue to judge BMI. This surgical intervention, which artificially alters this part of the body, may lead observers to perceive a difference in BMI in the

before and after condition. This is important because the observers have only the visual image to go on, and if the image appears to vary in BMI (even if there is no significant change in the BMI of participants in the photographs), then the observers will react to the images as though they do alter in BMI. Thus, the apparent BMI and WHR of the pictures may covary, and it is not clear whether the reported changes in attractiveness ratings were due to changes in WHR, apparent BMI, or some mixture of the two.

An obvious solution to this problem is to simultaneously record observers' eye movements while they make perceptual judgments. Although human eyes can attend to a visual field of around 200°, detailed information can only be received from a central region of around 2°, corresponding to the fovea. As a result, the information in a picture can only be sampled in discrete “bite-sized” chunks corresponding to the observer's current fixation position. Thus by tracking an observer's fixation position, it is possible to gain a direct measure of which regions of an image are being sampled at any one time and therefore which regions are likely to be contributing information to the perceptual judgments.

Therefore, Cornelissen et al. (2009) recorded the eye movements of three groups of male and female observers when they rated a set of 46 photographs of female bodies. The first group of observers rated the images for attractiveness, the second group rated for body fat, and the third group rated for WHR. If either WHR and/or body fat is used to judge attractiveness, then observers rating attractiveness should look at those areas of the body which allow assessment of these features, and they should look in the same areas when they are directly asked to estimate WHR and body fat. So it is possible to compare the fixation patterns for the explicit judgments with those for attractiveness judgments and infer which features were used for judgments of attractiveness. As can be seen in Fig. 2, observers' fixations for attractiveness and body fat clustered in the central and upper abdomen and chest, but not the pelvic or hip areas, consistent with the hypothesis that WHR had little influence over attractiveness judgments. The pattern of fixations



Body Fat Percent and Distribution, Fig. 2 Contour plots of the fixation distributions for observers making (a) attractiveness, (b) body fat, or (c) WHR estimations overlaid onto the image of the reference body. In order to facilitate inspection of the data across all judgments,

fixation density in the left and central columns has been converted to a percentage score, indicated by color bars (0–100), with red indicating the highest density (Redrawn from Cornelissen et al. 2009)

for attractiveness ratings was very similar to the fixation patterns for body fat judgments, but the fixations for WHR ratings were significantly different from those for attractiveness and body fat suggesting WHR was not being used in attractiveness judgments.

In an alternative, Crossley et al. (2012) used a 3D interactive software system which allows participants to produce a photorealistic, virtual female body with their ideal size and shape. Both male and female participants created a slim body with a low BMI value of 18.5 (at the lower end of the “normal” BMI range). As part of the shape charges, both male and female participants also narrowed the waist which also altered the WHR. To test whether the shape change was purely an effect of creating a low BMI body or represented a choice for a more curvy body as well, Crossley et al. modeled the expected way that shape should change as BMI decreased, and they found a significant deviation in shape from this expectation. This suggests that WHR does

play a small but significant role in attractiveness preferences which is independent of BMI.

Cross-Cultural Judgments

If overall body mass honestly signals an individual’s health and reproductive potential and a specific value of this feature signals optimal health and fertility, it follows that in environments where the optimal values for these features differ due to differences in environmental pressures, the attractiveness preferences should also be different. Moreover, as observers moved from one environment to another, it would be adaptive for them to alter their attractiveness preferences to those that accurately reflected optimal health and fertility in their new environment. This seems to be the case for people of the same ethnic group, living in different socioeconomic conditions; people of lower socioeconomic status (SES) preferred bodies of a higher BMI than those of a higher SES

(Swami and Tovee 2005). Additionally, Zulu migrants moving from a low SES environment (rural South Africa) to Britain (relatively high SES environment) modify their preferences toward those of people in Britain (Tovee et al. 2006). This suggests that these preferences are part of a flexible behavioral repertoire, acquired through social learning, which allows humans to adapt and respond to changing conditions within an environment or when moving between environments. In this case, the change in preferences is likely to be mediated both by social interactions and the media environment. The Western media emphasize a preference for a slim and shapely body as the female ideal, and the ubiquitous nature of this ideal in television, magazines, and advertisements is likely to accelerate the putative changes to body size preferences (Boothroyd et al. 2016)

Conclusion

Both the amount and distribution of body fat are important predictors of health and fitness, and both body features have been linked to attractiveness judgments. Overall fat content (usually indexed by BMI) seems to be used as the primary cue to physical attractiveness judgments, and this may be because the covariation of overall fat and its distribution means that choosing a particular body mass will also tend to be choosing a particular body shape. However, body shape (as indexed by WHR) is also a significant independent predictor of attractiveness independent of body mass and may be used in fine-tuning judgments between bodies of a similar BMI.

Cross-References

- [Evolutionary Standards of Female Attractiveness](#)
- [Men's Mate Preferences](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)
- [Sexual Signalling](#)
- [Waist-to-Hip Ratio](#)
- [Women's Mate Value](#)

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Body Language

► Body Posture

Body Mass

► Body Fat Percent and Distribution

Body Mass Index

► Obesity

Body Modification

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Synonyms

Body ornamentation; Mods; Piercings; Tattoos

Definition

The deliberate or purposeful alteration to the human body/anatomy.

Introduction

Body modification is a more permanent form of human ornamentation. Forms of body modification include corseting, piercing, tattooing, subdermal implants, and ear gauging. Perhaps most common in Western culture is piercing – particularly the ears. Other, commonly pierced

areas include the nose, tongue, lip, eyebrow, and even the genitals. Tattooing is a form of *permanently* ornamenting the body with artistic pieces via ink inserted into the skin with a needle. The Maori and other Western Pacific cultures have a rich history of ornamenting their bodies via tattooing. Today, tattoos are widely accepted multi-cultural phenomena across the world. This is a very interesting human universal.

Another type of body modification that has gained popularity is ear gauging in which an individual slowly stretches a hole in their ear (typically in the ear lobe) over time. Larger jewelry is gradually placed in the hole, occupying the space and allowing the ear to heal around the jewelry. The size of gauge (hole) can vary from the size of a needle to the size of a small fist.

Within certain populations and during specific historical time periods corseting was a widely practiced custom in which a female would squeeze her waist into a metal-ribbed bodice that remained tightened throughout the majority of the day. The figure that was implied through the artificial tightening of the corset is thought to mimic that of a 0.7 waist to hip ratio, which is thought to signal reproductive fitness. The use of this method was typically very painful to the individual and often resulted in organs being forced into different parts of the torso. Within the last year “waist training” has re-gained popularity, interestingly, with the Kardashian family at the helm of the movement. Though modern waist training is not as archaic as past methods, it still presents a similar evolutionary cost vs. benefit ratio in which an individual is essentially risking their health to appear attractive (by certain standards).

Extreme Modification

Extreme body modification takes this cost versus benefit ratio a step further. Subdermal implants (insertion of material under the skin) are one of the more common forms of extreme body modification. The areas that individuals get enhanced vary widely, but a common area is the forehead where horn shapes can be suggested through modification. Some individuals use this

form of modification for sexual enhancement. Males can get a procedure referred to as “pearling” in which bio material is inserted under the skin of the penis systematically to make it have a permanent “ribbed” sensation.

Another form of extreme modification is tongue splitting, where the tongue is split down the middle (by either cutting or binding over time), resulting in two useable half portions of the tongue – if the procedure is a success and infection is avoided. In fact, this procedure is highly risky, and if not done correctly, individuals can lose their sense of taste or even their ability to use the muscles in their tongue. Other extreme forms of modification include ear pointing (where the tips of the ears are pointed to mimic elves from fantasy novels), eyeball tattooing (tattooing the whites of the eyes), and even *extraocular* jewelry (where a small piece of jewelry is inserted under the sclera and over the white of the eye).

One of the most novel forms of body modification is in the form of *biohacking*, where a magnet placed under the skin allows the individual various benefits based on the type of procedure. Some magnets allow individuals to become sensitive to magnetic fields in their environment; others alert individuals to when they are facing north by moving slightly, or RFID chips allow individuals to open doors, computers, or even safes.

Evolutionary Implications

From an evolutionary perspective, body modification is particularly fascinating because it would seem that the potential costs of infection/nerve damage/scarring outweigh the benefit of appearing attractive to potential mates. Essentially, body modification – including extreme body modification – is a complex form of costly signaling.

Cross-References

- Advertising
- Ancestor Worship
- Appearance/Beauty in Girls

- Art
- Beneficial Side Effects
- Burials
- Camouflage
- Carving
- Competition Between Groups
- Costly Signaling
- Culture of Honor and Individual Differences
- Emotions
- Facial Attractiveness
- Facial Disfigurement
- Good Genes
- Greater Risk-Taking and Status
- Health Cues
- Human Ornamentation
- Individual Differences
- Male Ornamentation
- Manipulation and Dishonest Signals
- Peer Groups
- Peers
- Scarification

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Body Ornamentation

- Body Modification

Body Parts Awareness

- Proprioception

Body Position

- Body Posture

Body Posture

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Synonyms

Body language; Body position; Kinesics

Definition

Body posture refers to the way that the body is positioned, including whether one is standing or sitting, the relative positions of body parts, and how much space the body occupies. Body posture is a form of nonverbal communication.

Introduction

Body posture can be used to communicate information, intentions, and emotions without the need to produce speech. Body posture is informative about emotional states (Niedenthal 2007), and it has been shown that people are better at identifying facial displays of emotion when these are paired with congruent body postures (Mondloch et al. 2013). Furthermore, posture can modulate one's own emotional experiences. For example, Stepper and Stack (1993) found that participants who received good news while adopting a slumped posture felt less proud and had lower mood than participants who received the same news while their head and shoulders were held high and straight.

This section explores ways in which dominance is expressed through body posture, the evolutionary purpose of postural cues of dominance and their physiological underpinnings, and finally how these cues influence behaviors such as mate selection. Dominance here is defined as the actual or perceived power of individual(s) over others. Postural indicators of

dominance include adopting open and erect stances (Darwin 1872/2009) and actions such as placing the hands on the hips and jutting out the chest. Postures that increase the amount of space an individual occupies also signal dominance. In contrast, closed, contractive body postures signal submissiveness and powerlessness.

Dominance, Posture and Behavior

The Evolutionary Benefits of Dominance and Dominant Behaviors

In the introduction, dominance was defined broadly as the actual or perceived power of individual(s) over others. Why is power desirable? Powerful individuals tend to have a greater sense of control over their mind and body, as well as greater access to resources in society. At first it may appear that exhibiting dominant cues is only beneficial to the dominant individual. However, individuals within social groups often rely on one another to achieve goals and maintain social stability, and power relations are key to this process. In our evolutionary past, it is likely that violence and aggression were used to establish dominance. Nonverbal communications of dominance may therefore have evolved to signal to non-dominant individuals that challenging the dominant individual's authority could have negative consequences and may even lead to violence. This would deter others from challenging the dominant member of the group and lessen the likelihood of violence or social unrest. Thus postural indicators of dominance not only benefit the dominant individual but may also serve the purpose of defining and maintaining power relations which minimize conflict within social groups. For an example from the animal kingdom, consider that in over 500 h of observation, Hall (1964) did not report one violent encounter between male Patas monkeys (*Erythrocebus patas*) in a social group despite noting a number of aggressive threats and bodily cues signaling dominance. In humans, Schaal et al. (1996) reported that young boys who were perceived as dominant were able to impose their will on others

while maintaining social attractiveness, whereas physically aggressive or violent young men were not socially dominant. Thus nonverbal dominant cues likely evolved, at least in part, to maintain social stability and minimize violence within social groups.

Hormones: The Physiological Basis of Dominance

Are there any physiological markers of dominance? The hormone testosterone has been associated with feelings of dominance and power. For example, engaging in dominant behaviors increases testosterone levels. Mazur and Booth (1998) reported that testosterone levels tend to increase in anticipation of competition (whether aggressive or nonaggressive). Furthermore, testosterone levels tend to rise in winners and fall in losers after a competition (Mazur and Booth 1998). Thus testosterone both drives and responds to competitive and dominant behaviors. In addition, Schaal et al. (1996) found that higher levels of testosterone in young men were associated with perceived social dominance.

The hormone cortisol, which has been associated with feelings of stress and submissiveness, may compliment testosterone. Supporting this, Carney et al. (2010) found that the relative levels of testosterone and cortisol are modulated by body posture. In one study, they reported that participants who adopted high-power poses (open, expansive postures which signal dominance) for 2 min (two poses were held for 1 min each) showed an increase in testosterone levels and a decrease in cortisol levels. In stark contrast, participants who adopted low-power poses (small, contracted postures which signal submissiveness) for 2 min showed a decrease in testosterone levels and an increase in cortisol levels. Thus dominant postural cues may serve the purpose of maintaining social stability and minimizing violence by communicating caution to others, and this appears to be facilitated at the physiological level through immediate and direct effects of posture on the hormonal state of both dominant and non-dominant individuals.

Behavioral Consequences of Dominant Cues: Mate Preferences and Selection

Postural cues of dominance can influence mate selection. It has been suggested that masculine and dominant men are more sexually attractive to women (Sadalla et al. 1987), and thus displaying dominant postural cues may improve mating success for men. For example, Ahmetoglu and Swami (2012) reported that both introverted and extroverted women rated men with open body posture and gesticulation as more attractive than men with closed body posture.

It has been further suggested that fertile women prefer dominant men. In a recent meta-analysis, Gildersleeve et al. (2014) assessed the evidence for the ovulatory shift hypothesis (Gangestad et al. 2005), which suggests that women are more attracted to men who they perceive to have characteristics which reflect higher genetic quality – including dominance – on high-fertility days during their menstrual cycle than low-fertility days.

Given this natural fluctuation in how attracted women are to dominant men across the menstrual cycle, behaviors which alter this cycle may have consequences for mate choice. One such behavior is the use of the contraceptive pill. For example, Penton-Voak et al. (1999) found that women who were taking the pill showed weak or no preference for vocal or facial masculinity. Alvergne and Lummaa (2010) reviewed evidence which showed that using the pill can affect a woman's attraction to men and interfere with her ability to select a preferred partner. For example, they highlighted that without the natural fluctuation in attraction to masculine and dominant cues, women who take the pill may choose partners who are less genetically different from themselves. This means that the children of pill users may be less heterozygous which could lead to poorer immune function and diminished perceived health or attractiveness (Alvergne and Lummaa 2010; Roberts et al. 2005). However, the specific implications of behaviors such as pill use and major life events such as childbirth on attraction to dominant cues and mate choice are not yet fully understood.

Conclusion

In summary, body posture broadly refers to the spatial relations between body parts, the positioning of the body, and how much space the body occupies. Posture can communicate emotions to others and also modulate our own emotional experiences and behaviors. Hormones play a role in facilitating the relationship between body posture, emotions, and behavior. Specifically, changes in posture have been shown to be accompanied by changes in the relative levels of testosterone and cortisol (Carney et al. 2010), two hormones which are associated with dominant and submissive behaviors, respectively. Men who are perceived as dominant but do not engage in violent behavior are capable of exerting power over others in their social group while still being seen as socially attractive (Schaal et al. 1996). Thus dominant postural cues may serve the evolutionary function of preserving social stability by maintaining power relations which deter violent or dissenting behaviors from nondominant individuals. Dominant postural cues also have consequences for mate choice since, according to the ovulatory shift hypothesis (Gangestad et al. 2005), women are more attracted to dominant men during times of high fertility. By altering hormonal levels and eliminating this natural fluctuation in attraction to different men, behaviors such as taking the contraceptive pill may have consequences for mate choice and the health outcomes of future children (Alverge and Lummaa 2010; Roberts et al. 2005), but research in this area is still ongoing. To conclude, dominant body posture can be used to communicate emotions and has important consequences for the short-term experience of one's own emotions and experiences. Dominant body posture can also influence longer-term choices including selecting a mate.

Cross-References

- [Body Attractiveness](#)
- [Physiological Mechanisms](#)
- [Signals of Body Size](#)

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Body Reserves and Food Storage

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Synonyms

Energy balance; Fat; Feeding; Obesity; Overweight

Definition

The decision controlling consumption of food and storage of nutrients in the body.

Introduction

Humans, just like other animals, are adapted to store nutrients in their body. Body reserves consist of fat, glycogen, and other nutrients, but the storage of fat is most usually considered, not least as part of the effort to understand and so treat obesity. The health issues caused by obesity make understanding the evolutionary reasons that people become overweight urgent. Researchers have advanced several hypotheses for people becoming overweight, and there remains controversy about the important selective pressures that must be incorporated in models of energy storage.

Theories of Appetite and Obesity

The mammalian body stores energy in the form of lipids and glycogen. There are no significant stores of protein, although muscles and organs can be broken down for energy during starvation. Minerals and vitamins are stored in small amounts. When the energy contained in the digestive system is exhausted, glycogen stored in the liver and muscle is used. Only after that is fat used (McCue 2010). However, fat is an highly energy

dense substance and constitutes the vast majority of the calories stored in the body of most animals (Wells 2010).

Fat has many roles in animals (Pond 1998). Known advantages of stored fat include as a source of energy when food is not available or cannot be eaten (migration, breeding, hibernation, winter). There are fat stores close to lymph nodes to provide immediate fuel for the immune system. Fat stores in human females, or at least their location, are under sexual selection because it exaggerates body shapes associated with fertility, or the ability to supply lactation for infants. For some animals, especially cetaceans (dolphins and whales), fat is an insulating material; however, at human levels the heat conservation effect of fat is negligible. Researchers have predominantly focused on the role of fat as an insurance against the inability to find food, such as in famines. Therefore, there has been a focus on the incidence of famine, and mortality associated with famine, during human history (Speakman 2006; Prentice et al. 2008).

The prevailing viewpoint is that body reserves are controlled by a system shaped by natural selection so that the evolved behavior is adaptive – that is, enhances the ability to survive and reproduce. It is therefore surprising that eating behavior often results in obesity in humans and associated animals. Much research effort in to body reserves has had the main objective of explaining human susceptibility to obesity. There are many proposed hypotheses for obesity, many invoking physiological mechanisms that are maladaptive in modern environments with evolutionarily novel food stuffs (Speakman 2013).

Following *Tinbergen's Four Questions* (Tinbergen 1963) proposed hypotheses can be categorized as proximate or ultimate. The former focus on physiological or psychological mechanisms that cause fat storage or over-eating. The latter propose how an eating and fat storage system may have been designed by natural selection such that it drives obesity in a modern environment. While they are often considered to be competing hypotheses, mechanistic hypotheses can explain *how* an ultimate explanation is

implemented. For example, an urge to consume sugary and fatty foods during winter festivals – such as Christmas – is a mechanism that implements the storage of extra fat in case of food shortage that would happen in winter in evolutionary history. This entry focuses on those hypotheses that take evolutionary and/or psychological approach, either by discussing psychological mechanisms or by predicting how an energy balance system would be designed by natural selection.

Avoiding Starvation

The thrifty genotype hypothesis proposed that humans, having evolved in unpredictable environments, are genetically predisposed to eat excess food in times of plenty, so that they have sufficient stores for times of need (Neel 1962). Eating whenever food is available in the modern Western environment of “continuous feast” can lead to obesity. There is evidence that body fatness or the drivers of it are heritable; one study showing that around two-thirds of the variation in BMI can be attributed to variation in genes (Allison et al. 1995).

It is clear that individuals do not gain weight indefinitely, but tend to defend a defined level of energy reserves: however heavy people are, their weight tends to be fairly constant over time. This observation underpins the set-point model of the control of adiposity, which supposes that the body has a target level of fat (Kennedy 1953). This idea was supported by the discovery of the role of the hormone leptin, which is produced by lipid-storage tissues and inhibits appetite (Zhang et al. 1994). The set-point model compares intake control to a system like a thermostat: if energy reserves are below a given threshold, the animal eats; if above that threshold, the animal does not eat. Since the change in body mass can be determined by the energy-balance equation of energy intake minus energy expenditure, it is possible to lose fat either by decreasing intake or increasing expenditure.

A challenge to the thrifty genotype hypothesis has always been the great variability within human populations in fat storage, with most individuals able to resist the supposed urges from their

genes with variable success in obesogenic societies (Speakman 2014). An idea that attempted to address this challenge is the thrifty phenotype hypothesis, which suggest a thrifty phenotype is not genetically determined but may be induced by experiences early in life (Barker 1997). For instance, there is some evidence that obesity in pregnancy leads to larger birth weight via greater levels of glucose in the mother’s blood (Tyrrell et al. 2016). Adverse effects may be “interpreted” by the baby’s systems as a challenging environment leading to the greater storage of fat (Wells 2007). However, maternal effects are insufficiently strong to alone explain the incidence of obesity.

The doubts about these various assumptions required for the thrifty genotype hypothesis lead to consideration of how the genome may underlie obesity via other mechanisms. The thrifty-epigenotype model (Stöger 2008) proposes that selection has led to metabolic thrift being highly conserved due its importance. This would explain why while there are many genes indicated in determining body weight, they are all of small effect. Epigenetic effects – such as DNA methylation – caused by food shortage in the distant past have been preserved in modern people. In other words, this is a merging of the thrifty genotype and phenotype hypotheses.

The food insecurity hypothesis (Nettle et al. 2017) is an extension of the thrifty models that explains the greater incidence of obesity among lower socio-economic groups by suggesting that uncertainty in one’s environment in terms of money (resources for acquiring food) triggers an increased investment in insurance. Consideration of the thrifty epigenotype model may explain the deviation from predictions: if an individual’s socio-economic status differs from that of their parents then they may not have the expected level of obesity.

More recently (Speakman 2018), Speakman has proposed that the selective pressure to store fat is not from starvation risk but from the risk of dying from disease if body reserves are low. This occurs because pathogens induce under-eating leading to weight loss during illness. Pathogen-induced anorexia by being an enforced restriction

on food intake, from the viewpoint of evolutionary models of energy balance, is identical to famine. However, this viewpoint does not suffer from the objection that famines, or deaths during famines, are insufficiently common to exert sufficient selective pressure to maintain thrifty genes. It also means that it is possible for an animal to starve to death while external food supplies are still abundant.

Mechanistic Models

Effect of environmental factors on the target fat level suggests a different perspective that focuses on individual mechanisms. These mechanisms combine to result in a certain level of fat, an idea known as the settling point model (Wells 2010). This proposes that the body reserves level is not under active control, but is a consequence of the balance between energy expenditure and energy use. A heavier body has greater costs so weight gain can be somewhat self-limiting, but the weight settled on depends on extrinsic factors such as food quality and opportunities to exercise.

There will be evolved mechanisms that affect food intake and energy expenditure, and selection acts on the outcomes of their interactions. From this viewpoint, the settling point model is focused on mechanisms that could combine to achieve a set point, without any need for the set point itself to be stored in the system. Thus, these proposals are not mutually exclusive, but are at different types of answer *sensu* Tinbergen's Four Questions.

Some specific mechanisms have been proposed. In modern environments people consume more highly processed, carbohydrate-rich food that quickly increase glucose levels in the blood. The carbohydrate insulin model predicts that the consumption of carbohydrate leads to insulin spikes which prompts more eating and lower activity to preserve fat, and that this is excessive so overall weight is gained (Ludwig and Ebbeling 2018). However, mice do not show increased food consumption in response to insulin nor reduce their activity (Ludwig and Ebbeling 2018).

The hedonic over-ride hypothesis posits that sugars and fats are so strongly rewarding that the energy consumption control systems are

overwhelmed, leading to weight gain (Berridge et al. 2010). By comparison to the effect of simulant drugs, it has been suggested that the reinforcement may even lead to food addiction (Gearhardt et al. 2011). Evolutionarily such strongly rewarding responses make sense because rich foods would be relatively scarce, and so there is little selective pressure to avoid becoming addicted.

The protein leverage hypothesis focuses on the other side of the consequence of an increase in carbohydrate-rich foods: the reduction in the relative amount of protein. Because a smaller proportion of food, especially meat, is protein, people have to eat more to get their protein requirement. Protein is not stored by the body but may still play an important role in determining body reserves of energy. The protein leverage hypothesis states that obesity results from a simple rule to eat the correct amount of protein, applied when the ratio of protein to carbohydrate + fat of food is reduced as in the modern Western diet (Simpson and Raubenheimer 2005). There have been many tests of this hypothesis by constraining the macronutrient content of animals in the laboratory, with strong support for the idea that a protein target when protein supplies are constrained leads to over-eating (Raubenheimer and Simpson 2019). However, others have found that if the protein to fat ratio and the availability of lipid are both altered then the amount of lipid may be driving previous results (Hu et al. 2018), although studies on other species do not necessarily undermine the hypothesis that protein leverage may drive obesity in humans (Raubenheimer and Simpson 2019).

Optimality Models

While ideas of set points have long been considered, the selective pressure that acts to push down the set point has been neglected. The probability of starvation decreases as the storage of fat increases. So in the absence of all other pressures, it would be best to store as much fat as possible. That humans and other animals do not suggests that there are costs associated with fat storage. By understanding why animals are not always as fat as possible, we might be able to predict the variation within populations.

Progress in understanding fat storage has frequently followed from research on the adaptive use of energy reserves by animals. Such models are common in behavioral ecology in which energetic reserves mediate the trade-off between various fitness-enhancing activities, such as feeding, courting mates, and being vigilant. These models successfully predict the behavior of animals by assuming that their behavior is optimal for any given level of reserves, such as when and which foods animals should consume (Houston and McNamara 1999). Such models typically use optimization, predicated on the conception that natural selection is an optimizing algorithm that should result in animals making appropriate responses to conditions (Stephens and Krebs 1986).

This research has shown that the amount of fat stored by animals is not a direct consequence of availability and expenditure but is strategically regulated (Macleod et al. 2005; Macleod and Gosler 2006; Bonter et al. 2013). This research is mostly based on small birds. One might expect that animals would be fattest when food was easiest to find. Actually, birds are fattest in winter when food is scarce and/or the ambient temperature low and so metabolic expenditure is high (Rogers 1987; Grubb and Pravosudov 1994). This predicts that individuals killed by predators (or disease) are the leaner ones, as they forage more, or take more risks, in order to gain weight.

One type of cost is intrinsic: carrying fat has energetic consequences, locomotion takes more energy when a body is heavier. The other type of cost is extrinsic: locomotion may be slower when a body size heavier, which may reduce the ability of predators to catch their prey and for prey to avoid being caught by their predators. If the risk of predation when foraging is greater than the risk when not foraging, or if there are energetic costs of carrying fat then there will be some limit on fat storage. This limit will be lower if foraging is more energetically costly than not foraging, such as due to locomotive costs (Houston and McNamara 1999). The need to conserve fat by reducing demands has been suggested to be the reason that during starvation protein catabolism starts well before fat reserves are exhausted:

reducing muscle mass reduces energy consumption and so prolongs survival (Higginson et al. 2014).

Neutral Selection

In attempting to explain the variation in body weight, Speakman has proposed the ‘drifty genotype’ hypothesis (Speakman 2008), based on the idea that it has been the removal of predation risk that leaves humans vulnerable to obesity. This hypothesis is based on a model of body reserves (amount of fat and other energy stores) control that imagines there is not one but two critical reserves levels, labeled “thresholds.” The lower threshold causes the animal to increase reserves so it is not in danger of starving. The upper threshold causes the animal to decrease reserves to avoid predation due to reduced maneuverability. If reserves are between the thresholds, there is no intervention and reserve levels vary according to environmental drivers, such as food supply. In this way, the dual-intervention point model combines the ideas of (genetic) set-points responding to evolutionary pressures and settling points – controlled by environmental triggers – that act between the intervention thresholds. It is proposed that the virtual elimination of the risk of predation on ancestral humans meant there is no selective pressure on the upper threshold. Genetic drift in the genes that control the upper threshold has resulted in the wide range of body sizes we observed today, because different genotypes have moved random amounts.

This genetic drift means that there would have been no recent selection on genes that control adiposity, in contrast to the thrifty genotype hypothesis, which assumes that the risk of starving in a famine selects for high BMI. Recent analysis of selection on the genes that have been associated with BMI has failed to find such evidence of strong selection (Wang and Speakman 2016), as assumed by the drifty genotype hypothesis.

When originally proposed the dual intervention point model did not include an explanation for why the animal is indifferent to the level of reserves if they are between the thresholds. If intervention is costly (i.e. searching for food),

then it would be better to be further from the threshold than near the threshold. The animal can only be indifferent to the level of reserves if the long-term survival is constant between the thresholds, which can only occur if both predation risk is constant if reserves are below the upper threshold and the risk of starvation is constant above the lower threshold, or if between the thresholds the increase in one is exactly cancelled out by the decrease in the other.

One implementation of a dual intervention point model (Higginson et al. 2016) was an attempt to understand how it could be adaptive to have two thresholds. Assuming a cost to switching between weight gain activity that incur predation risk and a weight losing activity at lower risk, the optimal strategy is to have two thresholds. However, the location of these two thresholds depends on both the starvation risk and the predation risk, so both would move.

In answer to this criticism Speakman (2018) presented an explicitly mathematical description of the dual intervention-point model, based on the role of uncertainty in the body “knowing” how much energy is currently stored. This model was based on the standard behavioral ecology models of an increasing rate of predation and a decreasing rate of starvation (due to pathogen-induced anorexia during illness) as body fatness increases. If both functions are convex, then the total mortality is a U-shape. Under the assumption that the system is fairly insensitive to small changes in fat level, the system would not intervene provided reserves were around the bottom of the “U”. The intervention points are set by natural selection to be around the point that the mortality increases steeply.

For this system to result in widespread fat levels (from lean to morbidly obese), the thresholds have to be controlled by independent genes, allowing the upper threshold to drift while the lower threshold remains constant. Genes do not code for outcomes but for mechanisms that cause outcomes and further developments to this hypothesis will need to focus on the mechanistic explanation *sensu* Tinbergen’s 4 Whys: That is, to establish *how* the system implements the loss of body reserves when the upper threshold is

exceeded in a way that does not affect behavior and outcomes at lower levels of reserves. For instance, to stop gaining weight at the upper threshold the hedonic response to food must be switched off and the response to high lipid stores be strong. At the lower threshold, the opposite is true. Developments to the theory need to address how the mechanisms that control feeding behavior, including hormonal feedbacks from lipid stores and hedonic responses to food, would be independently determined by different genes.

Exploiting Gluts

The focus of research on evolutionary explanations for obesity has assumed that the positive selection pressure for storing fat is the insurance against food shortage, particularly famines. There has long been debate over whether famines are sufficiently common (Speakman 2006; Prentice et al. 2008). But storing energy allows animals to avoid looking for food when it is risky or less profitable. For instance, passerine birds avoid foraging after dusk and many mammals hibernate over winter. Energy stores are built up during times of food abundance when it is easy to acquire calories. In the natural world and in human history, gluts of food are common. In temperate environments, food is plentiful in autumn, when hibernating animals quickly gain weight. Many tropical environments have highly seasonal rainfall which results in overabundance of food at some times and severe shortage in others.

Models based on the idea of a target level of reserves have been developed that incorporate the role of occasional gluts of food, rather than just the risk of food shortage (McNamara et al. 2015). If energy reserves can be built up cheaply when food is abundant, humans may have evolved two set-points: one for normal conditions and one in glut conditions. The latter is much higher despite some health costs because it is not expected to last and the other costs are avoided while reserves are high. In modern constant glut conditions, people are always at the upper set-point. This model predicts that the mortality rate from obesity in constant glut conditions should be roughly equal to the mortality from predation (or disease) in our ancestors.

Another model incorporates information in that the long-term food availability is not known perfectly and is learnt from experiences (Higginson and McNamara 2016). The target level is therefore dependent on what is learnt, and if the system expects food shortages to be common then more fat should be stored. This model led to the suggestion that severe diets may “teach” the system that food shortages are common, leading to yo-yo dieting and long-term weight gain as often observed (Dankel et al. 2014).

How optimal fat storage might be predicted to respond to increase in the availability of food depends on the costs of gathering extra calories (Houston and McNamara 1989). If the availability of food increases then whether this leads to an increase in body reserves depends on the statistical characteristics of the food supply the animal is adapted to. If the food supply is not clumped over time and space then increasing food availability decreases fat levels due to the reduced need for insurance against a run of bad luck.

In contrast, if the food supply is clumped such that the risk of starvation is negligible most of the time (e.g., occasional famines), and between famines the animal has time to replenish fat stores, increasing food availability increases fat storage. This is because the gain rate only affects the probability of predation because the animal is highly likely to reach any target before the next famine so only has to ensure it gets there while minimizing the costs of reaching exposure to predators. Increased food availability means it is “cheaper” to gain weight and so it is optimal to gain more weight.

Experiments involving supplementing food supplies usually result in animals gaining weight (Boutin 1990), suggesting that animals perceive supplementary food as cheap to acquire rather than indicating reduced likelihood of food shortage in the future. If humans perceive the widespread availability of food in the modern world as cheap to consume but not reassuring in terms of the future, then we would expect widespread obesity. Understanding the control of body reserves sufficiently to prevent obesity may require incorporating the insights from all the current models.

Conclusion

Evolutionary models of body reserves have the ability to identify the mechanisms that control eating and energy expenditure, and therefore identify how they might have gone awry in obese people.

Cross-References

- [Calculating Starvation Risk](#)
- [Tinbergen’s Four Questions](#)

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Body Shape

► Waist-to-Hip Ratio

Body Temperature Regulation

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Synonyms

Thermoregulation

Definition

Thermoregulation is the process through which the central nervous system employs information

from temperature and other sensors to adjust the activity of tissues that are specifically responsible for heat production and those that regulate heat loss from the body.

Introduction

In mammals, the temperature of the body core (T_{core}) is a critical physiological variable that is tightly regulated to optimize cellular function, in particular enzyme kinetics and membrane ion flows. T_{core} represents the heat content of the body, which is the balance point between the heat produced by the metabolic processes of the body and the heat lost from the body to the ambient environment. The primary basis for heat production is the breakdown of ATP, the energy molecule which most cells employ to accomplish their basic and tissue-specific functions. The conversion of ATP to ADP to perform work is an inefficient process in which approximately 50% of the triphosphate bond energy in ATP is lost as heat. Thus, basal heat production (i.e., basal metabolic rate) arises from all the fundamental, ATPase-facilitated cellular processes from molecular transport and the maintenance of ion gradients across membranes, to protein synthesis and cell division. Added to basal metabolic heat production is the intermittent generation of heat from the wide variety of tissue-specific functions, most significantly the postural and locomotor activity of skeletal muscles and the acquisition of fuel and elimination of waste in the gastrointestinal organs and the liver. Heat is lost by conduction and radiation from the body surface (i.e., the skin, a.k.a. the body shell) to the molecules of the ambient environment (e.g., air or water) whenever the temperature of the immediate environment is lower than that of the body surface, and conversely, the body will gain heat (negative heat loss) when exposed to an environment that is warmer than the body surface, or to a source of radiant energy (e.g., infrared heat lamp) that is absorbed by the body. The amount of heat available to be lost is strongly dependent on the level of blood flow in skin blood vessels.

Fundamental Thermoregulatory Circuits

In mammals, T_{core} is regulated by the central nervous system through its neural control of a variety of behaviors and physiological processes that influence the amount of heat lost to the environment or that produce heat (Morrison and Nakamura 2019; Romanovsky 2014; Tan and Knight 2018). The primary goal of the dedicated thermoregulatory circuits in the brain is to maintain a stable T_{core} that is optimal for the function of the cells in the brain and the body tissues. These circuits are also responsible for adjusting T_{core} to new levels to optimize organismal performance in response to various challenges or during behavioral states. For example, T_{core} is increased to improve immune responses to fight infection, and T_{core} is reduced to lower cellular metabolism when food intake is eliminated during sleep or fasting. The basic neural circuits for thermoregulation contain (1) sensory or afferent components consisting of thermoreceptors; (2) neural integration networks in which thermal signals are integrated with a wide variety of inputs related to metabolic and osmotic status and behavioral state; and (3) efferent or motor components which are neural pathways that respond to the outputs of the integration network to control thermoregulatory behaviors and to determine the levels of activity on the nerves controlling the tissues (thermoeffectors) responsible for heat loss and heat production.

Effector Mechanisms for Body Temperature Regulation

The repertoire of thermoregulatory behaviors is extensive, from simple curling up or limb extension body positions to complex clothing and home heating and air conditioning systems. In general, the goal of thermoregulatory behaviors is an adjustment in the level of heat loss to reduce the “thermal discomfort” of being in an ambient temperature environment that is outside the thermoneutral zone. Additionally, thermoregulatory behaviors such as warm-seeking and cold-seeking

behaviors can make a significant contribution to state-dependent changes in T_{core} . For instance, in immune system responses, movement to a warm environment contributes to the increased T_{core} during fever, and the preference for a cold environment helps reduce T_{core} during septic shock.

The principal tissues for thermoregulatory heat production (thermogenesis) are brown adipose tissue (BAT) (Cannon and Nedergaard 2004) and skeletal muscle, through shivering (Nakamura and Morrison 2011). In BAT, an uncoupling protein in the mitochondrial membrane shunts the proton gradient energy from ATP production into heat, which is carried away from the BAT depots via the circulation. Thermogenesis in BAT is controlled by the sympathetic nerves that innervate this adipose tissue. The increased tension and short, rapid contractions of skeletal muscle during shivering consume significant amounts of ATP and thus result in increased heat production. Shivering thermogenesis is driven by the same alpha motoneuron innervation of skeletal muscle that controls normal postural and locomotor activity.

The principal mechanism for influencing the loss of metabolic heat from the body is the regulation of cutaneous blood flow: increasing skin blood flow by dilating the skin blood vessels increases heat loss (if the ambient temperature is less than T_{core}), while constricting cutaneous blood vessels reduces skin blood flow and conserves metabolic heat in the body core. Heat transfer to the environment occurs from the skin in humans, from the ears of rabbits and elephants, and from the tails of rats and mice. Skin blood flow is controlled by the cutaneous vasoconstrictor sympathetic nerves that innervate the smooth muscle of blood vessels (McAllen and McKinley 2018). There is an additional sympathetic vasodilator innervation of skin blood vessels in humans. Heat loss can be augmented by evaporating water from body surfaces, such as sweating in humans, panting in dogs, and saliva spreading in rodents. This is the only effective mechanism for heat loss in an environment that is warmer than T_{core} . Heat loss can be reduced by piloerection, in which the erect hairs on the body surface retain a thin layer of warm air that provides an insulating barrier

between the skin and the colder ambient air. Sweat glands and hair follicles receive sympathetic innervations that are activated in heat defense and cold defense responses, respectively.

Thermosensory Pathways Influence the Nerve Activity Controlling Thermoeffectors

Thermoreceptors in the skin provide the brain with “advanced warning” of an environmental temperature challenge to T_{core} . Cutaneous thermoreceptors are specialized sensory nerve endings in the skin whose cell membranes contain ion channels that respond to non-noxious levels of cooling or warming of the skin. Thus, cold thermoreceptors become active when exposed to cool ambient temperatures, causing increased activity on cold sensory nerves that synapse in the dorsal horn of the spinal cord. Warm thermoreceptors are activated when the skin is exposed to warm environment and lead to increased activity on warm sensory nerves that also enter the spinal cord. Cold and warm sensory nerves from the head synapse in the trigeminal nucleus in the brain stem. The temperature within the body core is sensed by cold and warm thermoreceptors in many tissues within the body and also by uniquely temperature-sensitive neurons in localized regions of the brain.

Thermosensory signals are transmitted from the spinal cord to an intermediate brain stem site in the parabrachial nucleus and then to the thermoregulatory integration center in the preoptic area of the hypothalamus (Nakamura and Morrison 2008). The outputs of the preoptic area influence the motor or efferent pathways controlling the activity of the thermoeffector tissues described above. Spinal and trigeminal thermal information is also conveyed to the thalamus and then to the cerebral cortex for the conscious perception and localization of thermal stimuli. The neurons in the preoptic area provide a basis for the integration of thermal afferent signals with those related to behavioral states (e.g., sleep, during which there is a fall in T_{core}), metabolic status (e.g., fasting or hypoglycemia, which results in a fall in T_{core} to lower the metabolic demand for fuel), immune responses (e.g., fever, in which T_{core} is elevated to improve host defense

responses), and cardiovascular status (e.g., hemorrhage, which elicits a fall in T_{core} to reduce metabolism in the face of a reduced tissue delivery of energy substrates).

The integrated outputs of the preoptic area provide excitatory, primarily glutamatergic, and inhibitory, primarily GABAergic, influences on hypothalamic (e.g., dorsomedial hypothalamus) and brain stem (e.g., raphe pallidus) neurons whose activity is critical for activating the sympathetic and somatomotor nerves that determine the level of thermoeffector activity. In particular, the raphe pallidus contains both sympathetic and somatomotor premotor neurons that project to the spinal cord to provide a critical excitatory input to the sympathetic preganglionic neurons and alpha motoneurons, respectively. To complete the thermoregulatory reflex circuits, various populations of sympathetic preganglionic neurons drive the different sympathetic nerves to BAT, cutaneous blood vessels, sweat glands, and hair follicles, while various populations of alpha motoneurons drive shivering in different groups of skeletal muscles.

During cold defense (or fever), heat conservation behaviors are engaged, heat loss is reduced by increasing cutaneous vasoconstriction and piloerection and inhibiting sweating, and BAT and shivering thermogenesis are increased. During heat defense, heat loss behaviors are initiated, sympathetic cutaneous vasoconstriction and piloerection are inhibited and sweating is activated to increase heat loss, and BAT and shivering are inhibited to reduce thermogenesis. Increases in brain temperature lead to fatigue as a mechanism to reduce metabolic heat production from exercising muscle. The significant water and electrolyte loss during heat defense in a warm environment presents increased cardiovascular and osmotic challenges, stimulating thirst and requiring substantial fluid consumption to prevent cardiovascular collapse and death. In combination with certain tissue adaptations, the thermoregulatory circuits in the brains of hibernating and torpid mammals enable them to markedly lower their T_{core} to reduce cellular metabolism during extended periods of reduced food availability.

Areas for Future Research

Although many aspects of the functional organization of the dedicated thermoregulatory circuits in the central nervous system have been discovered, considerable additional research is needed to provide a more detailed understanding of these circuits and how their pharmacology might be harnessed to combat disease. What are the neural mechanisms responsible for the changes in Tcore that accompany different behavioral states such as sleep (Chung et al. 2017; Kroeger et al. 2018) or hibernation (Tupone et al. 2017)? How do nonthermal inputs impinge on the basic thermoregulatory network to influence Tcore (Madden and Morrison 2016)? How does traumatic brain injury affect the thermoregulatory network to produce neurogenic fever? How can our understanding of these alterations in the central thermoregulatory circuits be recruited to discover new therapies, such as deep hypothermia, or new pharmacological approaches to alter Tcore and metabolism to combat disease and improve recovery from injury?

Conclusion

The principal thermoregulatory effectors are the cutaneous blood vessels for control of heat loss, the BAT, and skeletal muscle for thermogenesis and sweating for evaporative heat loss. The activation of these effectors is regulated by parallel but distinct, effector-specific, core efferent pathways within the central nervous system that are strongly influenced by shared cutaneous thermal afferent signals. Thermal sensory information is integrated with a variety of other metabolic and behavioral signals in the preoptic hypothalamus to generate a constellation of output signals that optimize the use of available energy and fuel supplies to maintain or adjust body temperature to cope with environmental challenges or the requirements of various behaviors.

Cross-References

► [Regulation of Body Temperature](#)

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BOLD-MRI

► [fMRI](#)

Bond

► [History of Attachment Theory](#)

Bonding

- ▶ [Emotional Closeness Predicted by Relatedness](#)
 - ▶ [Eye Contact with Adults Versus Babies](#)
-

Bone Lissoir

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Synonyms

[Smoother](#); [Similar tools are also called Slickers and Burnishers in modern leather-work](#)

Definition

A leather-working tool constructed out of an animal bone.

Introduction

The bone lissoir was a tool that was speculated to be used by Neanderthals. The primary function of this tool was increasing the pliability and water resistance of hides or skins.

The Bone Lissoir and Its Importance

The bone lissoir was first discovered in France and is considered to be one of the first specialized tools used by Neanderthals. It is a simple tool consisting of a curved bone, such as a rib, that has one end shaped to a rounded, curved end. The choice of a bone for this tool was ideal, primarily due to the fact that bones are somewhat flexible and would not break as easily as other materials. The use of wood would most likely be less than ideal, as chances are it would snap easier than bone. Furthermore, the use of stone tools such as handaxes would certainly rip or damage the hide, thus

rendering it useless. However, bone blends the strength of stone with some of the flexibility of wood, providing the correct amount of pressure needed to work the pelt. “Neanderthals sometimes made scrapers, notched tools and even handaxes from bone. They also used bone as hammers to resharpen their stone tools, but here we have an example of Neanderthals taking advantage of the pliability and flexibility of bone to shape it in new ways to do things stone could not do” (McPherron 2013). The deliberate shaping of the smooth, curved end provides evidence for intentional specialization of the tool, as the ribs of deer or reindeer do not have a smoothed end naturally. Furthermore, abrasions along the sides of the smoothed end further support the idea that this tool was modified in some way. It is believed that the tool was used to apply pressure with the curved edge on animal hides and pelts in an upward fashion. Doing so stretches the hide as well as increasing its luster, water resistance, and durability. Modern leatherworkers use a similar tool today in order to make hard leather be shaped into various clothing items and accessories. Discovered bone lissoirs have been dated to approximately 50,000 years ago, which, according to current theoretical models, do not line up with Neanderthals and modern humans in Europe in general. According to Shannon McPherron, senior archaeologist in the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology in Leipzig, “The dates make the bone tool finds the earliest known of their type associated with Neanderthals. Usually, such tools have been identified with modern humans who came upon the scene at a later time, but the dating and their location within a context of MTA stone tools, which are usually associated with Neanderthals, suggest that they were created by Neanderthals, not modern humans” (McPherron 2013).

Conclusion

The bone lissoir was perhaps the first specialized tool used by Neanderthals. Even though it may have been constructed over 50,000 years ago, its design has transcended time, and similar methods

are used today in order to work various leathers and other materials. Its importance with regard to evolutionary studies is also quite profound. Its dating has suggested that Neanderthals were the ones that first invented the bone lissoir, not modern humans. Although this certainly does not prove anything, it does offer the opportunity for further research.

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Bonobo Sexuality

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Bonobos (*Pan paniscus*) stand out among primates for the frequency and flexibility with which they engage in sexual behavior. To a far greater degree than chimpanzees, their congeners, bonobos mediate their social relationships using sex, frequently substituting sociosexual behaviors for aggression. The relative prevalence of sex and rarity of both intra- and inter-group aggression is the defining feature of bonobo sexuality.

Bonobos are highly social and cognitively complex animals, and as such, their sexuality can only be understood from a social perspective. Bonobos live in large, permanent social groups, though the entire group is rarely together due to the fission-fusion structure of their communities: subgroups for traveling and foraging form and split on a daily basis (White 1988). Bonobos are male philopatric and females leave their natal community shortly after attaining sexual maturity (Furuichi 1989). Therefore, resident adult females tend to be unrelated. Bonobos are unusual among anthropoid primates in that they are female dominant. The absence of kin typically limits the

formation of bonds between members of the dispersing sex, but female bonobos maintain their dominance over males, in spite of their smaller body size, through the use of strategic alliances cultivated through female-female affiliation (White and Wood 2007). Bonobo males remain strongly bonded to their mothers throughout their lives, and these pairs frequently travel together (Furuichi 1989; Surbeck et al. 2011). Mothers support their sons in aggressive encounters, and, as a result, sons of high-ranking mothers tend to become the highest-ranking males. Higher-ranking males, in turn, tend to produce more offspring (Surbeck et al. 2011).

Like other primates, bonobos engage in sexual behavior for conceptive purposes, and female bonobos give birth every 4–6 years (Kano 1992; de Waal 1997). Mating is promiscuous, paternity certainty is low, and there is no evidence of direct paternal care or male infanticide. However, much of the sexual behavior in bonobos is sociosexual in nature and is used to reduce tension, indicate social status, and maintain relationships both within and between social groups (de Waal 1997). Sociosexual behavior is most simply defined as sexual behavior that does not have a conceptive benefit for either partner (Wrangham 1993). Bonobos use various copulatory positions, including ventro-ventral (Kuroda 1980), which is used in almost one out of every three copulations in the wild (Kano 1992). This position is rarely, if ever, employed by chimpanzees. Female bonobos seem to prefer the ventro-ventral position to the more common primate position of dorso-ventral (Kano 1992). The vulva and the clitoris have a frontal orientation in bonobos, and the clitoris is more prominent than in the chimpanzee (Savage-Rumbaugh and Wilkerson 1978), suggesting that the female genitalia are adapted for ventro-ventral contact. Non-conceptive sex is practiced among partners of all ages and both sexes, and infants begin participating at a young age (Kano 1992). Genito-genital (G-G) rubbing commonly occurs between females in the ventro-ventral position. Fellatio, mouth-to-mouth kissing, and hand-to-genital contact also sometimes occur (de Waal 1987). Sociosexual behavior is observed at relatively high frequencies in captive populations

where food provisioning and small enclosures elevate group tension (Savage-Rumbaugh and Wilkerson 1978; de Waal 1987) but is also common in wild populations (e.g., Kuroda 1984). Sociosexual encounters are most frequent in feeding contexts, such as arrival at a large fruiting tree, or in other situations where individuals may need to diffuse tension, such as following an aggressive encounter.

A key tenet of the hypersexuality seen in bonobos is extended female sexual receptivity. Female chimpanzees are only sexually receptive during the tumescent phase of their ovarian cycle which typically lasts for 12–13 days in a 35-day cycle. After conception, females may experience a small number of sexual swellings, though some may continue to cycle long into gestation. After birth, females experience a period of lactational amenorrhea that lasts an average of 3.5 years. Once cycling resumes following lactational amenorrhea, a female may only experience a handful of cycles before conceiving again (Tutin 1979; Wallis 1997; Deschner et al. 2003; Thompson 2013). A female chimpanzee, therefore, may only be sexually receptive for <4% of her life. In contrast, bonobo females may be sexually receptive for up to 48% of their lives (Wrangham 1993). Sexual cycles in bonobos last approximately 42 days and with a tumescent period of an average of 10–14 days, though this is highly variable and can exceed 30 days (Douglas et al. 2016). After the onset of sexual cycles at around 7 years (~2 years earlier than in chimpanzees), females are maximally swollen nearly continuously until shortly before their first birth (Kano 1989). Bonobos experience sexual swellings later into pregnancy than do chimpanzees and, after birth, resume cycling much earlier, sometimes in under a year (Kano 1989). Despite their increased receptivity, bonobos mate at a lower rate than chimpanzees (Furuichi 1987); each encounter lasts on average only ~13 s. Bonobo females tend to concentrate their matings when their swelling is at a maximum firmness, rather than maximal size, a period that better corresponds to the duration of maximal swelling in chimpanzees (Furuichi 1987). Bonobos also have increased opportunity to mate as a

result of their grouping patterns. Females spend close to 100% of their time in proximity to at least one male (White 1988; Kano 1992), while chimpanzee females range alone up to 40% of the time (Wrangham and Smuts 1979; Murray et al. 2007).

Intrasexual competition limits the mating success of both males and females, while intersexual competition is rare in bonobos (Hohmann and Fruth 2003; Surbeck et al. 2011). Indeed, male aggression against females is near its lowest when females are maximally tumescent. Sexual coercion may be ineffective in bonobos because males fear retaliation from both females and males. This suggests that the benefits of affiliative relationships between males and females may outweigh any reproductive advantage males receive through being aggressive to females (Hohmann and Fruth 2003). Moreover, because swellings are extremely unreliable as an indicator of ovulation (ovulation can even occur outside the maximally swollen period) (Reichert et al. 2002; Douglas et al. 2016), bonobo males may need to maintain relationships with females over the entire cycle, making mate guarding an inefficient and likely ineffective strategy (Hohmann and Fruth 2003).

The stark differences between chimpanzee and bonobo sexuality are hypothesized to originate from differences in feeding ecology that affect sociality (Wrangham 1993; Hare et al. 2012). Evolutionarily, bonobos are thought to have had increased access to large patches of high-quality, terrestrial foods that can be consumed during travel, which may have limited within-group feeding competition (Wrangham 1993). Reduced competition allows females to associate for longer periods and more frequently in mixed-sex parties outside of her ovulatory period and increases opportunity for female-female coalitions (Hare and Wrangham 2012). For males, continual access to females and the weak connection between ovulation and swelling reduced the effectiveness of sexual coercion as a reproductive strategy (Hohmann and Fruth 2003). Support for ecological differences in the current chimpanzee and bonobo ranges is mixed (Hohmann et al. 2010), leaving this question open to debate. However, ongoing research into cognitive differences between the two species supports the hypothesis that chimpanzees and bonobos

evolved under divergent environmental conditions that have favored higher levels of cooperation, sharing, and even empathy in bonobos (Hare et al. 2012).

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Bonus Family

► Stepfamilies

Book

- No Two Alike
- Nurture Assumption, The
- Risk of a Lifetime, The

- [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)
- [Would You Kill the Fat Man?](#)

Booty Call

- [Friends with Benefits](#)

Booty Calls

- [Casual Sex](#)

Booty-Calls

- [Costs of Short-Term Mating for Women](#)

Border Patrols

- [Chimpanzee Raiding](#)

Borderline Tool

- [Proto-tool](#)

Boredom as an Adaptation

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Synonyms

[Adaptation](#); [Creativity](#); [Evolutionary mismatch](#);
[Innovation](#); [Learning](#); [Play](#)

Definition

Boredom is an affective state, typically unpleasant and characterized by scarce stimulation and concentration in the current situation or activity that may have evolved to motivate bored individuals to pursue more desirable states of being.

Introduction

Boredom is an affective state that involves low arousal, disinterest in the present setting, and feelings of dissatisfaction. Bored individuals may also feel that time passes more slowly (Fisher 1993). Physical signs of boredom in an individual typically include leaning the head back, yawning, and decreased motor activity (Park et al. 2019). Most people typically perceive the experience of boredom as displeasurable and would prefer to avoid it if possible. For instance, Wilson et al. (2014) found through 11 studies that many people preferred receiving electric shocks rather than being left alone with nothing to do. Yet, the ubiquity of boredom in the human experience suggests that boredom may be a well-designed psychological mechanism that conferred an evolutionary advantage in host organisms – that is, our evolutionary ancestors who were prone to boredom were better off than those who were not. An evolutionary approach to boredom suggests that more attention should be paid toward understanding the role of this important emotional state in the lives of human beings.

Reasons for Boredom

Research has identified several causes of boredom. From an individual difference perspective, some people may be more prone to boredom than others. For example, individuals who score high on extraversion require more stimulation to remain aroused and engaged in tasks and are more likely than introverts to be bored when presented with monotonous tasks (Fisher 1993). Researchers have also sought to establish boredom proneness as a stable trait using assessments such as the Boredom Proneness Scale or the Boredom Susceptibility Subscale (Vodanovich 2003).

Boredom may also be caused by situational factors, such as when one has nothing to do and is inadequately stimulated (Fisher 1993). Importantly, the opposite of boredom is not necessarily a state of busyness. The perception of surfeit, which arises when an activity is deemed to be in excess to the point that it is no longer desirable, can also prompt feelings of boredom, especially when combined with task monotony, predictability, and feelings of confinement (Toohey 2011). In such cases, boredom can be triggered when the task environment lacks novelty and variety in stimulation. Similarly, the availability and quality of social interaction in the task environment may also contribute to feelings of boredom. For example, a social environment comprising slow or unemotional exchanges between coworkers may prompt the onset of boredom (Fisher 1993).

Behavioral constraints in the task context may also produce boredom (Fisher 1993). Rules and task regimentation limit the variety of stimulation available in the work environment and also infringe on people's need for autonomy by restricting their choices in work activities and behaviors. Such restrictions inadvertently induce some level of psychological reactance, which may manifest as a need to reassert control over choice freedom and a greater liking for prohibited activities simply because they are forbidden (Fisher 1993). In this manner, present activities decline in attractiveness and become boring by comparison.

Boredom as an Evolutionary Adaptation

While the experience of boredom is usually accompanied by a lack of motivation and resentment in the *present* activity setting, it might also adaptively predispose a person to pursue *future*, more viable alternative activities and goals. Bored individuals often report restlessness and a desire to be engaged in something else instead (Bench and Lench 2013). The drive induced by boredom, which motivates individuals to seek alternative activities and more desirable circumstances, might have been adaptive for early humans adjusting and living in ancient environments. In particular, the capacity to feel bored and to respond in ways aimed at reducing boredom

may have helped ancestral humans avoid stagnation, learn new skills, and devise creative solutions to overcome survival and reproductive challenges in ancient environments. The proclivity to feel dissatisfied with the current situation and improve upon it through innovation, such as the development of new technology or new ways to exploit the environment, may have also given ancestral humans an edge over conspecific rivals in competition for scarce resources. Consistent with this view, researchers have found that boredom triggers thought processes and behaviors that are conducive to creativity, in particular by motivating individuals to engage in divergent thinking and exploratory behaviors (Park et al. 2019).

Boredom may also play a signaling role in the regulation of mastery and play, thus keeping individuals engaged so long as learning and play activities return stimulating, interesting, or rewarding outcomes. The boredom experienced by an individual during an activity may reflect the activity's diminishing utility and, hence, declining satisfaction for the individual (Eastwood et al. 2012). As such, boredom can be adaptive for learning because it reduces interest in the current, unsatisfying activity and motivates the search for new activities or surroundings that promise greater stimulation (Bench and Lench 2013). Hence, boredom facilitates a reduction in effort investment in unstimulating activities and drives the pursuit of alternative goals, thereby enabling humans to engage in social, cognitive, and emotional experiences that would have otherwise been missed (Bench and Lench 2013).

The experience of boredom may also be adaptive in mating contexts. Some preliminary evidence supporting this idea comes from studies that have examined sex differences in susceptibility to boredom and found that males are more prone to boredom than females (Sundberg et al. 1991). In mating situations where males are required to invest significant effort in self-presentation and intrasexual competition for the attention of and access to potential mates, the experience of boredom may help curb overexpenditure of mating effort, especially when sexual attention is either unreciprocated or already acquired. Thus, boredom may help males

optimize their investments in mating effort and prompt them to move on to the next candidate when it is more reproductively viable to do so. In so doing, males can avoid fixation on mates who are either unresponsive or who have already been potentially fertilized and continue to attract as many mates as possible.

Evolutionary Mismatch Between Modern Environments and Innate Capacities for Boredom

A state of boredom readies the individual for the pursuit of alternative experiences that could be beneficial to learning and development (Bench and Lench 2013). However, modern technologies, in particular handheld mobile devices, afford people a quick and addictive solution to deal with “dead time,” or small pockets of time where people are unfocused on any specific activity (Røpke and Christensen 2012), by providing near-reflexive levels of access to social media as well as stimulation via mobile gaming applications (Lord et al. 2015).

This scenario illustrates an evolutionary mismatch between humans’ innate capacity to experience boredom and features of the modern environment that are rife with stimulation designed to eliminate or dull the experience of boredom (Li et al. 2018). From a mismatch perspective, such novel forms of stimulation hijack our capacity for boredom, which should otherwise usefully impel humans to engage in creative thinking processes, seek new forms of stimulation, and change the status quo, thus causing people to miss out on the adaptive benefits of feeling bored. These periods of dead time, which are commonly experienced during daily commutes or service waiting times, are antecedents of boredom that may have functioned to motivate the drive for creativity and innovation. Thus, an evolutionary perspective suggests caution when choosing to occupy dead time with filler activities afforded by modern mobile technologies: while this might stave off the aversive feeling of boredom in the short run, it can also starve individuals of the impetus needed to become more creative and explore activities beneficial to survival and development.

Conclusion

Boredom might seem like an inconsequential or troublesome phenomenon at first glance. However, an evolutionary perspective suggests that boredom may serve important adaptive functions, in particular the search for more desirable or rewarding activities and circumstances (Bench and Lench 2013; Fisher 1993). Thus, the antecedents and consequences of boredom as well as how boredom unfolds over time deserve further research attention. If the mechanisms underlying boredom are better understood, individuals and organizations can go beyond seeking how to eliminate boredom and instead design activities and environments that can harness the benefits of boredom and optimize human functioning.

Cross-References

- [Adaptation](#)
- [Evolutionary Mismatch](#)
- [Learning](#)
- [Multiple Matings](#)
- [Play](#)

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Bottle Feeding

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Synonyms

Dry nurse; Formula feeding

Definition

Feeding a baby with milk (or formula) from a bottle instead of from the mother's breast.

Bottle Feeding Is an Evolutionary Mismatch

Introduction

Until recently in human evolutionary history, there were no alternatives to vaginal deliveries or breastfeeding, and nursing used to last 3–4 years (Tönz 2002). Nowadays fewer than 40% of infants worldwide are breastfed for the first 6 months of life, and among high-income families, it drops to a meager 18% (see Gallup et al. 2016 for details). Bottle feeding is an evolutionary

mismatch because it puts the mother and baby out of phase with the defining feature of mammalian evolutionary history.

Formula Is a Poor Substitute for Breastmilk, and Bottle Feeding also Puts Mothers at Risk

Because of nutritional deficiencies in formula (e.g., the absence of long chain polyunsaturated fatty acids necessary for healthy brain growth and development, colostrum which contains antibodies from the mother, and bacteria on the mother's breasts that cultivates and jump starts the baby's intestinal flora and immune system), bottle-fed children can be cognitively challenged, immunocompromised, and prone to suffer from asthma. To make matters worse, mothers who bottle feed are more likely to become overweight (Chapman 2009); more prone to develop breast cancer (Stuebe et al. 2009a), ovarian cancer (Su et al. 2013), rheumatoid arthritis (Jacobsson et al. 2003), type 2 diabetes (Steube et al. 2005), myocardial infarct (Steube et al. 2009b); and have an elevated risk of experiencing postpartum depression (Gallup et al. 2010).

Bottle Feeding Simulates Child Loss

Until recently, the decision not to breast feed would have been tantamount to committing infanticide. More often, it was the case that the failure to breast feed was occasioned by stillbirth or other forms of neonatal fatality, and therefore at the level of the mother's basic biology bottle feeding simulates child loss (Gallup et al. 2010). The death of a child is a powerful trigger for depression, and bottle feeding increases the risk of postpartum depression by as much as 50%. Consistent with this analysis, depressive episodes can accompany weaning as well because it also simulates child loss. To complicate matters further, nowadays some women with postpartum depression are treated with antidepressants and are advised to stop breastfeeding because of problems posed by the medication getting into their breastmilk. Mothers who bottle feed their babies also report wanting to hold their babies more, which may be reminiscent of nonhuman primates where mothers often persist in clinging to and carrying their dead babies for prolonged periods of time. Hospital

practices of separating babies from their mothers for the first few days of life and keeping them in nurseries also unwittingly simulate child loss and may increase the risk of postpartum depression.

Bottle Feeding Increases the Likelihood of Autism in Your Next Child

Most people also don't realize that bottle feeding puts the evolved birth spacing mechanisms on hold. Pregnancy and breastfeeding are nutritionally very expensive, and reimpregnation shortly after birth could adversely affect the quality of milk for the baby while also compromising the nutritional status of the prenatal environment for the fetus. As an evolved solution to this problem, breastfeeding triggers hormonal changes that postpone the resumption of the menstrual cycle (lactational amenorrhea) and inhibit the release of eggs (lactational anovulation). As a result, mothers who opt to bottle feed are more likely to get pregnant again sooner after the birth of a child (Gallup und Hobbs 2011). Research shows that the risk of autism is three times higher among children who are conceived within a year of their next oldest sibling (Cheslack-Postava et al. 2011), and this may be due to incomplete recovery of the prenatal environment. The high degree of concordance in autism, not only among identical twins, but among fraternal twins as well, is consistent with this prenatal environment hypothesis (Ronald et al. 2006). Closely spaced pregnancies also put babies at an elevated risk of sibling rivalry, being born prematurely, and dying prior to 5 years of age (Rutstein 2008).

Bottle Feeding and Caesarean Sections

Just like bottle feeding, caesarean sections were not an option during our evolutionary history. Indeed, C-sections are also an obstacle to breast feeding because they often lead to delayed contact between the baby and the mother, side effects of drugs used during C-section deliveries that leave babies groggy and less responsive, and diminished postpartum levels of oxytocin and prolactin that would otherwise promote maternal bonding (for a review see Gallup et al. 2016). Being overweight is an artifact of modern agriculture, and it is another impediment to breast feeding because

of difficulties overweight mothers experience when attempting to hold the infant and embarrassment about breast feeding in public. To complicate matters further, obese women are also more likely to have C-sections (Sebrie et al. 2001).

In terms of evolutionary mismatches, it is also important to note that babies born by C-section are immunocompromised because they do not ingest some of the bacteria in the mother's vagina as would usually occur during a normal vaginal delivery. As a consequence C-section babies are at an elevated risk of developing asthma.

Putting Evolved Mechanisms Back on Track

Breastfeed if you can, but if you can't, use condoms after your baby is born in order to prevent an untimely pregnancy. If you have to work, try expressing breastmilk and have a caretaker bottle feed the breastmilk to your baby. To overcome problems with expressing milk try recreating the context in which breastfeeding occurs, such as looking at a picture of the baby when you express milk. An even better strategy would be to position a camera over your shoulder to make a video clip of your baby breastfeeding that includes sounds the baby makes while suckling to capture what you experience when you breastfeed. Then express milk while watching the video and smelling the baby's clothes. Indeed, it would be interesting to compare both the quantity and the quality of milk expressed by women under these enhanced conditions, relative to an environment not augmented with personal reminders of the infant.

Conclusion

Bottle-feeding presents serious consequences for both infant and mother. Suggestions to overcome some of these are made.

Cross-References

- ▶ [Breast Feeding](#)
- ▶ [Breast Feeding and Mother-Infant Attachment](#)
- ▶ [Breastfeeding in Modern Environments](#)
- ▶ [Breast Milk Composition](#)

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Bounded Rationality

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Synonyms

Ecological rationality

Definition

Theory of imperfectly rational decision-making processes under cognitive resource limitations.

Introduction

The theory of bounded rationality, proposed by Herbert A. Simon (1957), is a progenitor of the behavioral turn in modern economics. It provided a viable and realistic alternative to the idea of *homo economicus* and the optimality criterion of utility maximization. Simon called his alternative criterion *satisficing*, the decision-making process whereby a course of action is chosen if it yields at least as much value as an ecologically adaptive *aspiration level* (Simon 1955). As distinct from theories that assume perfect rationality and optimal behavior, the theory of bounded rationality takes into account human cognitive limitations, decision processes, and environmental adaptations. Summarizing bounded rationality, Simon wrote that “Human rational behavior [...] is shaped by a scissors

whose two blades are the structure of task environments and the computational capabilities of the actor” (Simon 1990).

The Theory of Bounded Rationality

Simon criticized the assumption of perfect rationality in economics by emphasizing natural biological limits of human cognitive processes (Simon 1955). While standard economic theory of decision-making considers environmental resource constraints (e.g., income and market prices), the theory of bounded rationality additionally takes into account cognitive constraints and adaptations. Cognitive constraints include the limited capacity of our minds in processing information about the outside environment, for example, in forming limited representations of the decision problems due to short-term memory constraints (Simon 1990). Cognitive adaptations include decision-making strategies such as rules of thumb or heuristics that allow problem simplification (Simon 1979).

Satisficing is the decision criterion Simon proposed in his theory of bounded rationality as replacement for the criterion of utility maximization (Simon 1986). For a boundedly rational agent, decision-making processes involve exploration of uncertain environments for attaining goals (e.g., finding food for survival) using adaptive cognitive algorithms (e.g., heuristics). The search process comes to a halt, or at least it is momentarily paused, when a “good enough” solution is found. Simon shows how satisficing can allow survival in uncertain (e.g., basic animal behavior foraging) and complex worlds (e.g., a chess game) without utility maximization (Simon 1956).

Another important theoretical component of Simon’s theory of bounded rationality is the idea of *aspiration level*, which determines the threshold of value for determining whether a solution is satisfactory or not (Simon 1955). Simon suggests that boundedly rational decisions are adapted to the environment in at least two ways. First, the aspiration level depends on the environment: “A vague principle would be that as the

individual, in his exploration of alternatives, finds it *easy* to discover satisfactory alternatives, his aspiration level rises” (Simon 1955, p. 111). Second, boundedly rational decision-making processes benefit from shortcuts such as heuristics – mental shortcuts that work well in certain environments and that save cognitive effort (Simon 1990).

Influence

The theory of bounded rationality has been very influential in behavioral sciences, and it has paved the way to new research fields such as behavioral economics. However, different interpretations of the theory – in particular, whether heuristics tend to be beneficial or not – resulted in two distinct but intimately related behavioral research agendas. On the one hand, Daniel Kahneman and Amos Tversky’s “biases and heuristics” approach focused on uncovering cognitive biases that result in poor decisions (Kahneman 2003). On the other hand, Gerd Gigerenzer’s “fast and frugal heuristics” approach emphasized how – despite cognitive limitations – simple rules are often reliably beneficial because they are ecologically rational (Gigerenzer and Goldstein 1996). Even though Simon’s own views were perhaps better aligned with the latter interpretation of heuristics, the “biases and heuristics” interpretation became prevalent in behavioral economics and resulted in an emphasis on nudges or external tools for improving decision-making (Thaler and Sunstein 2008). These different traditions for interpreting the role of heuristics and biases continue to shape behavioral research, such as dual-process perspectives on social and moral decisions (Isler and Yilmaz 2019).

Conclusion

The theory of bounded rationality initiated a foundational reconsideration of economic theories of decision-making from the perspective of

evolution and psychology. The effects of Simon's theory on behavioral research are still ongoing.

Cross-References

- [Rational Actors](#)
- [Resource Scarcity](#)

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Bow-Wow

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Synonyms

[Imitation of sound](#); [Onomatopoeia](#); [Origin of language](#)

Definition

The bow-wow theory supports that language emerged through “onomatopoeia” or the imitation of the sounds in the natural world.

Introduction

The early bow-wow theory of language was first introduced by Max Müller, a philologist who was at a later stage criticized about his point of view (Sprinker 1980). Bow-wow theory postulates that the origin of language arose through “onomatopoeia,” which, in simple words, is the imitation of sounds in nature (Moran and Gode 1986). Specifically, the sounds from animals were the most imitated from the environment. On the one hand, Thorndike (1943) was doubtful about the credibility of this theory as the beginning of language. On the other hand, recent studies support that being able to mimic sounds in the natural environment was of paramount importance in the evolution of language (Malle 2002).

A major drawback of this theory is the fact that people use different words to describe the sounds of animals according to their country and more specifically due to their language. For instance, the sound of a pig can be translated differently across the countries. In English a pig makes the sound “oink-oink”; in Russian it makes the sound “hyru-hyru,” while in Chinese it makes the sound “oh-ee-oh-ee.” Therefore, the sound and pronunciation of the words are not similar among the different languages. The hypothesis that language is determined by how a person interprets a sound was rejected, since there are many languages, and nobody can suggest that human vocabulary arose from these sounds (Thorndike 1943).

Conclusion

The overall idea of the bow-wow theory is that the beginning of language can be linked to the era when the progenitors begun to mimic the sounds in their natural environment. The natural world was of paramount importance in the origination of

language since the sounds of animals played a significant role in the invention of the vocabulary used in verbal communication.

However, the theory holds several limitations that many theorists criticized and questioned its credibility. One, the sound and pronunciation of the words are not similar among the different languages. For example, the sound of a specific animal can be translated differently among the people of different countries, yet animals from the same species make the same sound across the world. The other challenge is that there are few onomatopoeic words in the languages worldwide. In case the theory was credible, then it should have plenty of words out from the basic rule of onomatopoeia.

Cross-References

- [Ding-Dong](#)
- [Origin of language](#)
- [Pooh-Pooh](#)
- [Ta-Ta](#)

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Boy and Girl Social Learning

- [Sex Differences in Social Development](#)

Boys

- [Play Fighting in Boys](#)

Boys Bully More Than Girls

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Synonyms

[Female-female competition](#); [Intrasexual competition](#); [Male-male competition](#)

Definition

Bullying is a form of aggression where a more powerful individual causes significant harm to a less powerful individual to obtain goals including access to sexual opportunities (e.g., dating and mating partners; Volk et al. 2014). Intrasexual competition for access to dating and mating opportunities is known as sexual selection (Geary 1998). As a form of sexual selection, parental investment is the resources (e.g., time, energy) allocated by parents toward offspring (Trivers 1972). Sex differences in the level of parental investment may help to explain why boys bully more than girls.

Introduction

Bullying significantly impacts the lives of many children and adolescents worldwide. Traditionally, bullying has been viewed as a maladaptive behavior; however, there is evidence to suggest that bullying may be part of an evolutionary adaptation designed to obtain at least three benefits: reputation, resources, and reproduction, all of which are likely to aid in maximizing

biological fitness (see Volk et al. 2012). Sex differences in bullying perpetration consistently find that boys are more likely to engage in bullying than girls, particularly as it relates to physical bullying (e.g., hitting, pushing, kicking). This sex difference in bullying may be tied to evolutionary explanations that provide support for a similar sex difference found in the aggression literature (see Archer 2009).

Sex Differences in Bullying

In contemporary society, most violent crimes (e.g., homicide) and virtually all wars have been perpetrated and fought by males (Georgiev et al. 2013). In addition, the propensity for males to be more aggressive than females may have served an adaptive function in the ancestral environment to improve male reproductive success (Georgiev et al. 2013). From an evolutionary perspective, sex differences in aggression have been argued to be a product of sexual selection (Archer 2009). As a subtype of aggression, bullying behavior may have also evolved as a strategy to obtain goals related to mating and reproduction that were adaptive in the ancestral past and are still adaptive today (Volk et al. 2012). Therefore, similar to aggression, sex differences in bullying may also stem from sexual selection as it relates to intrasexual competition.

Considering that males are usually competing for mates and females are selecting mates (Trivers 1972), bullying may be an adaptive, sex-specific strategy particularly for males. The tendency for males to be the more competitive sex might be related to their lower parental investment in offspring (Trivers 1972). Since males spend less time, energy, and resources producing and raising offspring, they are able to get back into the mating pool sooner to compete again for access to the higher investing females (Puts 2010). Furthermore, males have more variability in reproductive success than females (i.e., males have a greater likelihood of producing a large number of offspring or none at all) heightening the level of competition between

males (Ellis et al. 2012). Lower parental investment in offspring combined with a higher variability in reproduction may explain why males are evolutionarily more tolerant toward risk (Volk et al. 2012). As a result, males are more likely to engage in physical bullying than females because their costs are lower (i.e., they are less important for infant survival; Campbell 1999) and their benefits are higher (i.e., the greater variance in reproductive success rewards taking risks to obtain high benefits, whereas playing it safe can result in zero success; Ellis et al. 2012).

While Trivers' (1972) parental investment theory may explain why males are typically the more competitive sex, it may also explain why females tend to avoid engaging in physical bullying. Compared to males, females have higher parental investment making it especially important to survive and stay away from damaging confrontations in order to care for offspring (Campbell 1999). Furthermore, females have less reproductive variability than males due to internal gestation and breastfeeding, which does not allow them to re-enter the mating pool as quickly (Geary 1998) and uses up a significant amount of energy that is necessary to be successful in physical confrontations (Georgiev et al. 2013). Higher parental investment in offspring combined with a lower variability in reproduction may explain why females are evolutionarily less tolerant toward risk (Volk et al. 2012). As a result, females are less likely to engage in physical bullying than males because their costs are higher (i.e., they are more important for infant survival) and their benefits are lower (i.e., less variance in reproductive success as females are limited by periods of gestation; Campbell 1999). Based on these evolutionary costs and benefits, males may have been selected with a disposition to engage in direct conflict, thus more likely to use riskier, physical bullying, while females may have been selected with a disposition to avoid physical danger, thus more likely to use covert, relational bullying (e.g., gossiping, rumor spreading; Archer 2009). However, while males and females may engage in both physical and relational forms of bullying, the tendency for males to perpetrate more physical

bullying than females may also be reflected in their morphology.

Before the use of objects as weapons, humans relied on their bodies to inflict physical damage on rivals (Georgiev et al. 2013). In general, males are taller, heavier, stronger, and more muscular compared to females (Archer 2009). Males also possess specific physical and cognitive characteristics that may signal their dominance and ability to exclude rivals from the mating pool by force (e.g., beards, eyebrow hair, deep voices, superior targeting abilities for weapon use; see Puts 2010). Moreover, males allocate a large amount of energy toward muscular development granting them the strength and speed required to win damaging confrontations, whereas females direct more energy to meet the demands of internal gestation and breastfeeding at the cost of muscular development (Georgiev et al. 2013). These data suggest that males' anatomy may have been selected to engage in physical bullying in order to compete successfully for access to mates.

In summary, differences in parental investment as a function of contrasting reproductive strategies and physical characteristics may provide an answer as to why males are more likely than females to engage in bullying, particularly physical bullying. Using an evolutionary approach to understand sex differences in bullying may also be useful for informing anti-bullying programs and improving intervention outcomes to reduce bullying within schools.

Intervention and Implications

Current anti-bullying interventions have often focused on increasing the costs of bullying (e.g., punishing bullies to change their behavior), while failing to recognize the motives or goals that underlie much of bullying (Ellis et al. 2015). School disciplinary policies using this approach may not reduce bullying, and in some cases may actually increase the frequency of the behavior (see Ellis et al. 2012). However, adopting an evolutionary perspective of bullying highlights both

the salient costs and benefits of bullying, which tailors the intervention to the specific goal-directed nature of bullies (Ellis et al. 2015). Ellis and colleagues (2015) have proposed a new, evolutionary-inspired bullying intervention, Meaningful Roles, which takes into account the cost-benefit model of bullying and consists of two components. First, bullies are provided with meaningful roles and responsibilities such as giving them "jobs" within the school (e.g., being a door-greeter). Next, students receive positive peer feedback for exhibiting prosocial behaviors. Considering that bullies may not be willing to give up a behavior that results in favorable outcomes (Volk et al. 2012), Meaningful Roles is focused on creating a positive school climate by reducing bullying through prosocial options that still allow bullies to achieve their goals without needing to resort to antisocial behaviors (Ellis et al. 2015). Most importantly for this topic, the roles chosen to be used can be tailored to sex-specific goals that can better accommodate the goals and desires of male bullies.

Conclusion

An evolutionary approach that emphasizes the adaptive function of aggression, particularly for males' reproductive fitness, may serve to help better understand why males bully more than females. Sexual selection may provide the most complete understanding for sex difference in aggression (Archer 2009), which may also inform sex differences in bullying. Diverging levels of parental investment and reproductive variability between males and females (Geary 1998) may underlie much of the sex differences in bullying – the heightened propensity for males to engage in more physical bullying than females. In addition, males may also have physical adaptations that prepare them for direct conflict over access to mates (Georgiev et al. 2013). Therefore, bullying may have evolved as a sexual strategy for males, more than females, to compete with rivals for sexual opportunities. As such, anti-bullying interventions need to be cognizant of the evolutionary

function of bullying to obtain goals and focusing on redirecting bullies toward more gender-appropriate prosocial alternatives to obtain similar goals (Ellis et al. 2015), particularly as it relates to sexual selection involving male and female intrasexual competition.

Cross-References

- [Boys Physical Bullying](#)
- [Girls Psychological Bullying](#)
- [Same-Sex School Bullying](#)

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Boys Physical Bullying

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Synonyms

[Aggression](#); [Peer victimization](#)

Definition

Physical bullying is a direct form of bullying that involves overt acts of physical aggression, such as hitting, kicking, and shoving. Physical bullying is goal-directed, can cause significant harm, and occurs within the context of a power imbalance (Volk et al. 2014).

Introduction

Being involved in bullying, (especially as a victim) can lead to negative mental health outcomes, such as anxiety and depression (Volk et al. 2012). Until recently, bullying was considered to be a product of a maladaptive development (Volk et al. 2012). However, a maladaptive development cannot easily account for the prevalence of bullying across cultures and history (Volk et al. 2012). This has encouraged researchers to suggest that bullying has evolved as an adaptive strategy that uses aggression to obtain gains in three major evolutionary goals: reproduction, reputation, and resources (Volk et al. 2012, 2014). Research has demonstrated that, typically, boys engage in more physical bullying while boys and girls engage in roughly equal levels of relational bullying (Volk et al. 2006). In order to understand why boys engage in more physical bullying, it is essential to examine the evolutionary function behind physical bullying for males.

Why Do Males Engage in More Physical Bullying?

Men and women encounter different adaptive challenges regarding their ability to successfully produce offspring. The most significant challenge to men's reproductive success is the limited number of fertile women. Fertile women are less available because of the higher levels of maternal versus paternal investment in offspring (e.g., gestation and breastfeeding; Gangestad and Simpson 2000). On the other hand, the major challenge to women's reproductive success is to find a mate with the motivation and ability to provide and invest resources in them and their offspring (Buss and Schmitt 1993; Gangestad and Simpson 2000).

In order to adapt to these challenges, men and women have developed different sexual strategies for "selecting, attracting, and maintaining a mate" (Ellis et al. 2012, p. 601). Overcoming these challenges is essential for reproductive success. Therefore, men and women have evolved to prefer specific traits in the opposite sex as a resolution to these constraints (Geary 2010). Due to females' higher parental investment, females have evolved as the more selective sex and thus more emphasis is placed on female mate preferences. Women have developed two major mate preferences in order to adapt to the challenges they face in regards to reproductive success. The first preference is a mate who is capable of providing resources. This preference can be displayed in qualities such as ambition, income, education, and social status (Geary 2010). The second preference is genetic fitness, so that their offspring can inherit good genes. Indicators of genetic fitness include a tall and muscular frame, physical strength, and attractiveness (e.g., facial symmetry) (Geary 2010). This means that women are more focused on attracting a mate versus depriving other women of their mates (i.e., polyandry).

On the other hand, men can greatly benefit from depriving other men of their mates (polygyny) as their reproductive success is constrained by the limited availability of fertile women. This means there is greater variance in male's reproductive success as they are more

likely to be on the end of two extremes: either having no children or having many children (Volk et al. 2012). As a result, males compete for access to fertile females and must then engage in risky forms of competition to ensure reproductive success (Geary 2010). Males expend much of their reproductive effort into competing against other males for mates (Geary 2010). Men can also afford to engage in riskier forms of competition as they are not obligated to invest in their offspring to the same degree as females (Volk et al. 2012). For example, if a father dies during a fight, their death has fewer consequences on the survival of their offspring as the mother is the main caregiver. In contrast, maternal death strongly influences child mortality, in which infants are more likely to die as a direct result of their mother's death (Sear and Mace 2008).

In this way, physical bullying has many evolutionary functions for males. Physical bullying provides males with the opportunity to show off the preferred traits to potential mates (Volk et al. 2012). Physical bullying requires the bully to use physical strength to exert power over the victim. By using physical strength to bully, males are demonstrating an indicator of genetic fitness (Gangestad, and Simpson 2000). Physical bullying in particular can be a means to directly obtain resources and thus demonstrate their ability to provide for their mate and offspring. In addition, by obtaining more somatic resources, bullies have the necessities to grow larger in size, which is also an indicator of genetic fitness (Volk et al. 2012).

A male's social status can also be a means of demonstrating their ability to provide resources and to increase their access to more potential mates (Geary 2010). By using physical bullying, males can employ dominance in the social hierarchy and gain popularity. Being at the top of the social hierarchy can lead to many benefits; for example, having more control over resources and more access to potential mates (Volk et al. 2012). Furthermore, males engage in physical bullying as a way to enhance their social status. Bullies attempt to create a reputation that signals to other competitors that they are "tough" in order to deter retaliation (Ellis et al. 2012).

Physical bullying has also evolved as an effective strategy to compete with other males for access to potential mates (Volk et al. 2012). Adolescence in particular is marked by an increase in male to male competition, as adolescents become capable of reproduction and begin to date (Geary 2010). As a result, physical bullying is most prevalent during this age period (Volk et al. 2012). Physical bullying is considered to be a higher risk strategy as it is directly observable and requires physical contact, which can easily lead to detection or to serious injury and even death (Volk et al. 2012). Males will use physical bullying as a way to strengthen bonds between in-group members. When in-group members assist in bullying, they demonstrate their allegiance to the group (Volk et al. 2014). Males will also use physical bullying to target out-group members. With a dedicated group of allies, males demonstrate their ability to protect their mates and offspring.

Conclusion

In order for bullying interventions to be effective, they must first acknowledge that bullying is used as an adaptive strategy to obtain somatic, social, and sexual benefits and work towards increasing the cost of bullying, while still providing alternative prosocial strategies that will lead to these same benefits (Ellis et al. 2015). Therefore, to reduce the rates of physical bullying among males, it is pertinent to consider the evolutionary functions behind this behavior and to provide alternative methods to accomplish the previously mentioned goals of physical bullying.

One of the main characteristics of physical bullying that should be addressed in interventions is that it is an overt form of aggression that can be easily detected. To avoid detection, adolescent males tend to engage in physical bullying in places that have low adult supervision; for example, the playgrounds, hallways, and bathrooms in schools. In addition, teachers or other school staff who do witness physical bullying may not identify it as bullying but instead attribute the behavior to the “boys will be boys” ideal. Without adult

intervention, this ideal reinforces physical bullying as accepted behavior. For example, in hunter-gatherer societies, physical bullying is not a common occurrence due to frequent adult intervention and because it is not considered as a social norm (Volk et al. 2012). Therefore, the first step to reduce physical bullying is to increase adult supervision. This can include increasing the school staff during recess, having hall monitors or installing video surveillance, and educating parents and teachers on how to identify physical bullying. When weighing the costs versus benefits to engage in physical bullying, an increase in the possibility of being detected will be an additional consequence the perpetrator must consider.

Adolescents have learned to use physical bullying as an effective strategy to obtain benefits in resources, reputation, and reproduction. To date, bullying interventions have failed to make a significant impact in reducing bullying because they demand adolescents to give up bullying without providing any alternative strategies. An intervention entitled “The Meaningful Roles Intervention” is designed to implement alternative prosocial strategies for achieving adaptive goals (Ellis et al. 2015). This intervention incorporates two major components: a job program, in which students are provided with meaningful responsibilities, and a praise note system, in which students publically praise students for engaging in prosocial behavior (Ellis et al. 2015). These two components provide students with the opportunity to use prosocial strategies to obtain social status by publically contributing to the group in a prosocial manner and by creating a positive reputation for engaging in prosocial behavior (Ellis et al. 2015).

The second evolutionary function of physical bullying is to demonstrate genetic fitness (Geary 2010). As previously stated, physical bullying is used as a strategy to publically display physical strength (Gangestad and Simpson 2000). An alternative method for demonstrating physical strength that has a lower cost but still accomplishes the same goal is participation in competitive sports, as they publically demonstrate physical strength and skill (Volk et al. 2012). Bystanders can also be encouraged to use their

physical strength to defend victims, as this is also a display of genetic fitness through prosocial behavior (Volk et al. 2012).

The third evolutionary function that was discussed was using physical bullying to compete for potential mates by strengthening allies and targeting competitors (Volk et al. 2012). An intervention that has been relatively effective in increasing the cost of bullying is called the KiVa program (Ellis et al. 2012). This program focuses on devaluing bullying in the peer group by teaching adolescents how they can be indirectly supporting peers who bully by rewarding their aggressive behavior. This program also focuses on increasing the cost of bullying by encouraging bystanders to intervene more frequently (Ellis et al. 2012). In summary, in order to reduce physical bullying among males, interventions must work with the goals of bullying by replacing the aggressive strategies with prosocial strategies that are just as effective in obtaining gains in resources, reputation, and reproduction (Ellis et al. 2015).

Cross-References

- [Boys Bully More Than Girls](#)
- [Girls Psychological Bullying](#)
- [Life History Theory](#)
- [Mate Selection Strategy](#)
- [Parental Investment and Sexual Selection](#)
- [Paternity Uncertainty](#)
- [Reproductive Strategy](#)
- [Same-sex School Bullying](#)
- [Sex Differences in Cyber Bullying](#)
- [Sex Differences in Jealousy](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Strategies Theory](#)

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Boys' Rough-and-Tumble Play

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Introduction to Rough-and-Tumble Play

Rough-and-tumble play (R&T) refers to physically vigorous behaviors such as wrestling, chasing, pushing, and so on, that are primarily playful, not aggressive. R&T is observed in most mammals and accounts for about 10% of their time and energy resources (Bjorklund and Pelligrini 2002). In humans, it emerges around 3 years of age and has been documented in every culture in which it has been studied (Byrd-Craven and Geary 2007). The development of R&T play follows an inverted U-shaped pattern, with R&T frequency peaking at roughly 8–10 years of age (Pelligrini

and Smith 1998), and then declining in frequency at puberty. It has generally been assumed to have a function, and several functional hypotheses have been proposed to explain R&T. Broadly, functional hypotheses may be distinguished by whether they hold that the functional (survival or reproductive) benefits of R&T are immediate or delayed.

Sex Differences in Play

Robust sex differences are found in R&T, with males engaging in it more frequently than females in many mammalian species and nearly all human cultures (Bjorklund and Pelligrini 2002). Androgens, such as testosterone, have been implicated in producing these sex differences, and higher testosterone is associated with higher levels of R&T in males (Graham and Burghardt 2010). Rough-and-tumble play generally occurs more often in polygynous and/or gregarious species than monogamous or solitary species, and in the sex that competes for mates and resolves social conflict through physical aggression or contests in adulthood (Byrd-Craven and Geary 2007). Indeed, the sex difference in frequency of R&T in children strongly favors boys, and it has thus been proposed that sex differences in R&T play reflect sex differences in intrasexual competition during human evolution and serve to provide the practice needed to develop competitive or fighting skills.

Rough-and-Tumble Play as Training for Fighting Skills

On this view, R&T can serve as practice for species-specific behaviors that facilitate survival or successful reproduction in adulthood, especially when direct practice of that behavior, such as fighting, might be dangerous or costly. R&T play during the juvenile period might then serve as motor training or practice for fighting. If the purpose of R&T is training for fighting skills, sex or individual differences in frequency of R&T ought to be reflected in later developmental outcomes (Smith 2007).

There is little direct evidence linking R&T in youngsters to serious fighting ability in adulthood, however. While play may enhance physical fitness, many effects of exercise are not long lasting, which suggests that adults should also engage in R&T. It has been suggested that play might facilitate the development of appropriate muscle fiber types, however this view has received little experimental support (Graham and Burghardt 2010). Furthermore, critics of this view contend that play fighting is not effective or valuable practice for serious fighting. A critical aspect of fighting in squirrel monkeys, for instance, is the inflicting of bites (Biben 1998); however, real or inhibited biting is absent from play fighting in this species, making it perhaps an imperfect model for learning how to fight effectively. In rats, too, play fighting does not resemble aspects of real fighting in important ways. During serious fighting, rats compete for access to the rump and lower flanks of their opponent's body, which are bitten on contact (Pellis and Pellis 2007). During play fighting, rats compete for access to the nape of their play partner's neck, which is nuzzled on contact. Some motor patterns useful for combat are present in play; however, it has been argued that some of the characteristics that make R&T playful rather than aggressive are in fact counterproductive to learning how to fight effectively, including the inhibition of wounding, self-handicapping, and role-reversals that characterize R&T in many species. As motor skills are practiced effectively only through faithful reproduction of that motor pattern, it seems unlikely that play serves as a means for practicing specific skills, such as fighting.

Rough-and-Tumble Play for the Development of Cognitive Skills and Social Competence

While the evidence for R&T as motor skills training or practice for combat in adulthood is lacking, evidence suggests that R&T might be necessary for the development of social competence, especially the kinds of competencies that might be useful for later agonistic encounters. During R&T, dominant or older players often self-handicap so that their partners can assume a

superordinate position (i.e., the player who pins the other) and they can gain experience in a subordinate one (Bjorklund and Pelligrini 2002; Biben 1998). For example, it has been suggested that opportunities to gain experience in both a subordinate and superordinate role are important for juvenile squirrel monkeys, with animals not receiving enough experience in either role growing up to be bullies or thin-skinned, respectively. Therefore, gaining experience in both of these roles may relate to developing social competence.

Studies that have attempted to deprive young animals of play may lend support for the view that R&T helps facilitate the development of social competence. Play deprivation studies often suffer from the complication that successfully eliminating play may depress other social behaviour as well. However, experiments aimed at disentangling the effects of play deprivation from general social deprivation suggest that experience in R&T play is critical for the development of cognitive, emotional, and social competency in rats. When juvenile rats are deprived of opportunities to engage in R&T play, they exhibit social and cognitive deficits, most notably hyperdefensiveness to the approach of another animal and difficulty coordinating movement during sexual or competitive encounters with a social partner, along with impairments in solving various cognitive tasks (Pellis and Pellis 2007). R&T play-deprived rats appear to be overly stressed by novel encounters and socially inept at responding to them. Rats reared in pairs with mesh partitions between them preventing them from engaging in R&T still had cognitive and social deficits in adulthood. The same was true for juvenile rats reared in the same cage as an adult or a drugged juvenile littermate incapable of R&T, an arrangement that provides the opportunity for social contact but not for R&T play. However, when juvenile rats reared in isolation were given access to an age-matched partner for one hour a day, the rats engaged in play fighting for most of that hour and did not show cognitive deficits as adults. Rats reared with littermate siblings engage in R&T play for roughly an hour a day, and so it is perhaps unsurprising that an hour of daily access to R&T play is sufficient to prevent the cognitive

deficits associated with play deprivation. It has been suggested that experience with the juvenile-typical pattern of R&T play may provide feedback to the brain structures responsible for generating such play, which then promotes the development of those structures (Pellis and Pellis 2007). Two such areas are the orbitofrontal cortex (OFC) and the medial prefrontal cortex (mPFC), which are involved in modifying behaviors to different partners, and coordinating movements with a social partner, respectively (Pellis et al. 2010). Juvenile play fighting is thought to induce the release of growth factors in this area, and rats with damage to these structures exhibit the same social deficits that play-deprived rats do (Pellis and Pellis 2006). Thus, it seems that experience in juvenile R&T is a critical component of normal social development, possibly through its influence on the development of relevant areas of the brain.

Given the similarities between R&T in humans and nonhuman animals, it is possible that R&T experience in childhood promotes the development of social competence in adulthood in humans, too. Indeed, evidence from primate studies suggests that the effects of play deprivation in monkeys are similar to those seen in rats. Harlow's social deprivation studies with rhesus monkeys, wherein infant monkeys were reared with only a terry cloth mother, led to animals with severe sexual and social deficits (Pellis and Pellis 2006). However, when these animals were given 30 minutes of contact with peers, monkeys with terry cloth surrogates did not show such social deficits in adulthood. While these studies do not directly address the relative contributions of play versus general social deprivation, social isolation in monkeys reveals a similar pattern of social deficits to those seen in rats: hyperdefensiveness to social stimuli the isolated monkeys perceive as threatening, and difficulty coordinating movements and behavioral sequences effectively with a social or sexual partner.

In humans, there is a relationship between R&T and social competence. During childhood, R&T play in boys is positively associated with measures of popularity and friendship. Chasing and fighting, two aspects of R&T play, are positively related to peer acceptance for boys but not girls. Boys who

engage in more play fighting are more popular, better at solving social problems, and are more flexible on the playground (Pelligrini and Smith 1998). It has been argued that certain features of R&T, such as self-handicapping and role-reversals, facilitate the acquisition of flexibility in behavior in children, which is useful for social problem solving. It is plausible, then, that the relationship between R&T and social competence is causal. Moreover, longitudinal studies have revealed that R&T play predicts children's later emotional expressiveness and emotion regulation (Lindsey and Colwell 2013).

Conclusion

Thus, a large body of evidence from rodents and primates links peer-to-peer R&T as juveniles to later social competence and emotional regulation skills. Humans are social animals, and so developing the social competencies necessary to adapt to the complexities and challenges of group living seems important from an evolutionary perspective. However, despite its obvious benefits, more direct tests of whether R&T play improves survival or reproduction in humans are needed. Moreover, even if R&T has no current adaptive benefit, this does not mean that such play was not subject to selection in the past. Different aspects of play might have current or past adaptive benefits. In addition, more research is needed to determine which aspects of R&T play are necessary to produce improvements in these skills. Despite this, the evidence largely supports the development of emotional and social competency as a likely function of R&T play.

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Brachiation

- [Nonhuman Primates: Species Typical Movement](#)

Brain at Birth

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Synonyms

[Neonatal brain size](#); [Neonatal brain/body allometry](#)

Definition

The absolute size, relative size (brain/body ratio), and stage of neurodevelopment in a species' brain at the time of birth.

Introduction

The size and developmental stage of the newborn brain is highly variable across different mammalian species. For decades, the state of mammalian brains at birth has been the focus of great interest by researchers in developmental and reproductive biology, biological anthropology, and the evolution of life history. Although methods for comparing species' brains at birth have varied widely, two major approaches have generally been used to examine birth timing and mammalian brains at birth. First, thanks to several large datasets (e.g., Sacher and Staffeldt 1974; Harvey and Clutton-Brock 1985), neonatal brain size, body size, gestation length, and similar variables have been analyzed by researchers in anthropology, life history, and evolutionary biology. A second approach uses more detailed analyses in a smaller numbers of species – particularly model species in developmental biology, where more detailed data are available – to focus on brain growth and development during fetal and early postnatal stages of ontogeny. These complementary approaches have increased our understanding of when species are born during neurodevelopment, and how this affects the early postnatal development of their offspring.

Caution is warranted in any discussion of “neonatal brain size” for one simple reason: birth does not align different species at similar time points in either neurodevelopment (i.e., the highly conserved order of neurogenesis, axon extension, myelination, etc.) or in the growth of the brain (e.g., changes in brain size over time, or brain/body proportions over time). Instead, birth captures a single cross section in the dynamic process of neurodevelopment, and that snapshot is taken from different moments depending on which species is under consideration. This has led numerous commentators to critique the use

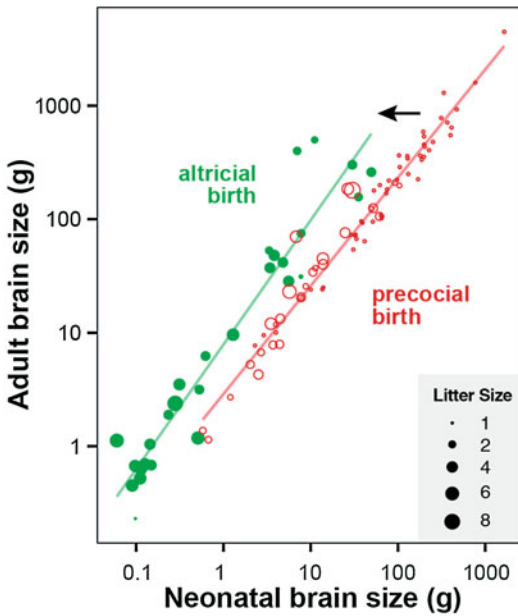
of birth as an anchor point to compare different species' neurodevelopment (Newell-Morris and Fahrenbruch 1985; Finlay and Workman 2013; Halley 2017).

If species' brains are so different at birth, what can we reasonably learn from studying brains at this seemingly arbitrary time point? In fact, a central variable in evolutionary life history relies almost entirely on birth timing: whether a given species is altricial or precocial at birth. Briefly, altricial species are born in a relative stage of somatic and neurological immaturity, and undergo a larger portion of brain development after birth. Precocial species complete a greater portion of neurodevelopment prenatally and are born in more mature states. Examining how birth timing differs between altricial and precocial species can help to explain one of the most important evolutionary features of human brain development: our species' unusual degree of altriciality among primates.

How Large Are Mammalian Brains at Birth, and Why?

The smallest neonatal mammalian brains are less than 1/10th of a gram, and are found in small marsupials (which give birth to extremely immature embryos) and rodents. By contrast, an African elephant (*Loxodonta africana*) newborn brain is more than 1600 g, on the larger end of the range of adult human brains (Sacher and Staffeldt 1974). As we might expect, these differences in neonatal brain size reflect differences in the adult brains they will become – there is a roughly linear relationship between neonatal and adult brain size when these variables are shown in log-log form (Martin 1982; DeSilva and Lesnik 2008). Nevertheless, some species have smaller neonatal brain sizes than we should expect for mammals of their adult brain size (Fig. 1). Where does this variation come from?

First, it is important to understand how evolution alters neurodevelopment to produce brains of differing size. Larger brains are generally produced by stretching out the process of neurodevelopment over time – that is, by delaying



Brain at Birth, Fig. 1 Neonatal brain size vs. adult brain size in a sample of 103 placental mammals. Neonatal brain size and adult brain size are highly correlated, with larger brained species giving birth to larger brained newborns. However, species that give birth to larger litters tend to be born earlier in neurodevelopment (i.e., altriciality, solid green circles) when compared to species born later in neurodevelopment (i.e., precociality, open red circles). Because birth is pushed forward relative to neurodevelopment in altricial species with large litters (black arrow), they have smaller neonatal brain sizes even when adult brain sizes are similar. For example, altricial species' neonatal brains are a lower percentage of adult brain size (~16%) compared to precocial species (~43%). OLS regression models are shown through precocial ($n = 75$) and altricial species ($n = 28$). Dataset from Halley 2016 (original sources listed in that paper)

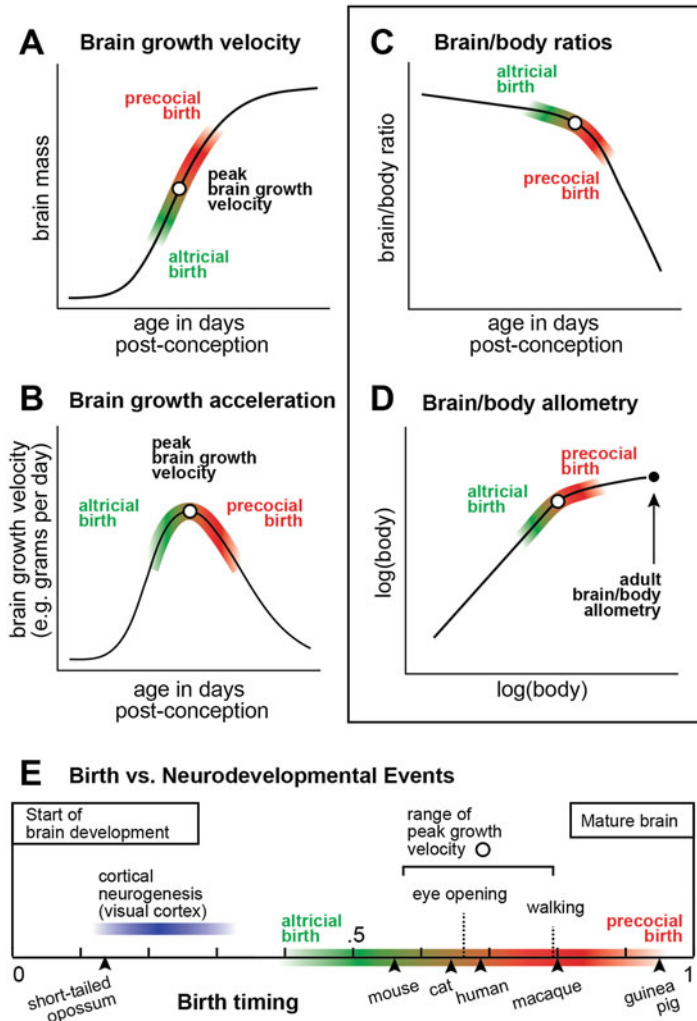
the onset of neurogenesis from progenitor cell populations, the processes of axon extension and pruning, and the myelination of axons fibers and the tracts they compose (Workman et al. 2013). This means that generally speaking, at any given fetal or neonatal brain size, a large-brained species will be at earlier neurodevelopmental stages than a smaller-brained species. A two gram rat brain belongs to a mature animal, while a two gram human brain (~115 days gestation) is still undergoing primary cortical neurogenesis (estimated from data in Halley 2017).

Mammalian brain growth exhibits a characteristic sigmoid (s-shaped) pattern over time since conception, consisting of (1) an early, largely fetal period of exponential growth; (2) an inflection point of peak growth velocity, when brains are growing at their fastest in mass per day; and (3) a deceleration phase of slower brain growth resulting in a mature adult brain (Halley 2017; Fig. 2a, b). Just as the schedule of neurodevelopment is stretched out to build a larger brain, this characteristic pattern of brain growth is also extended. Birth is highly variable across species relative to this general growth pattern. Dobbing and Sands (1979) originally described variation in birth timing around peak growth velocity, which they called the “brain growth spurt.”

Generally, altricial species are born before peak velocity, and precocial species are born after it; this is because peak growth occurs at a similar time to eye opening (Halley 2017; Fig. 2e), a crude but useful method for distinguishing species born earlier or later in neurodevelopment.

The most altricial mammalian species are marsupials, which are born in an embryonic state and undergo most of neurodevelopment postnatally during a period of lactation and weaning (Ashwell et al. 1996; Renfree et al. 1982). For example, the short-tailed opossum *Monodelphis domestica* is born after only 14 days of gestation, and due to their unusually slow rate of brain development, they are only beginning to undergo cortical neurogenesis by the time they are born (Puzzolo and Mallamaci 2010). By contrast, the most mature (precocial) species at birth tend to be placental mammals with a single offspring per gestation period. Examples include many ungulates (e.g. horses), which can locomote shortly after birth. Precocial species are born during later stages of neurodevelopment with more mature sensory and motor systems, generally after neurogenesis is largely complete – a period characterized by myelination of existing connections and the pruning of synaptic connections between brain areas (Sherwood and Gomez-Robles 2017).

Whereas larger brains are the consequence of stretching out both growth and developmental



Brain at Birth, Fig. 2 Simplified diagrams of birth timing vs. brain growth, brain/body growth, and neurodevelopmental events. (a) Brain growth in mass over age since conception (i.e., growth velocity) exhibits a sigmoid pattern of growth, consisting of exponential growth, peak velocity, and deceleration phases. Altricial species are born earlier along this trajectory, and precocial species are born later. (b) Growth velocity in mass per day changes over development, reaching its highest point at peak velocity. This is the derivative of the function shown in a. (c) Brain/body ratios generally decrease over development, though some species with exceptionally slow body growth (e.g., primates) have retained higher proportions for longer periods of time. After peak velocity of brain growth, brain/body ratios decrease. As we saw with brain velocity, species differ in the timing of birth relative to brain/body

allometry over development. (d) The same relationship shown in c, now in log-log coordinates that are commonly used to analyze developmental allometry. (e) Birth timing of several mammalian species, plotted against a highly conserved pattern of neurodevelopment. The x-axis represents a standardized 0–1 score of neurodevelopmental events (from Workman et al. 2013), with zero representing the start of brain development and one representing a fully mature brain. Marsupials are born in an extremely immature, altricial state, around the onset of neurogenesis in the neocortex. All eutherians are born later in neurodevelopment, with more altricial neonates born earlier (prior to eye opening) and all precocial neonates born later (after eye opening). Humans are more altricial than other primate species (see main text)

patterns over longer periods of time, most eutherian species seem to grow their brains at similar rates (i.e., growth acceleration) over the early exponential period of development when most of neurogenesis is underway (Passingham 1985; Deacon 1990; Halley 2017). Notably, species with larger adult brains or with larger neocortices (like primates [Barton and Harvey 2000]) do not appear to exhibit faster brain growth during this period than smaller-brained mammals. Similarly, species with larger brain/body ratios than other mammals of similar body size (i.e., “encephalization”), either at birth or as adults, do not have faster brain growth *in utero* (Halley 2017). Only a few groups of mammals seem to exhibit unusually slow brain growth (e.g., marsupials [Renfree et al. 1982; Halley 2017] and bats [Martínez-Cerdeño et al. 2017]), for reasons that remain poorly understood.

Because more altricial species are born earlier relative to neurodevelopment (Fig. 2e) and brain growth (Fig. 2a), they are born with brains that compose a smaller fraction of the adult brains they will become. Figure 1 shows neonatal brain size compared against adult brain in a sample of altricial ($n = 26$) and precocial ($n = 75$) species, with larger data points indicating litter size. We can clearly see that altricial species are born in larger litters, and both variables are associated with having a smaller neonatal brain relative to adult brain size. The same effect can be seen in comparing neonatal brain size vs. adult body size – altricial species exhibit smaller neonatal brains than we should expect (Pagel and Harvey 1990). If we assume that similarly-sized adult brains are produced from similar brain growth patterns (Halley 2017), these findings are the consequences of earlier birth in altricial, large-litter species (black arrow) causing them to be born at a smaller proportion of adult brain size – and at earlier stages of neurodevelopment.

A number of studies have examined early postnatal brain growth patterns across anatomically modern humans and our phylogenetic relatives (e.g., Neanderthals [Ponce de Leon et al. 2008],

chimpanzees [Sakai et al. 2013], and other extant primates [Leigh 2004]) in order to determine how human brain growth patterns evolved. While we should expect larger brains to exhibit extended brain growth and development patterns, analyses of postnatal growth alone can be misleading. Humans do exhibit faster postnatal brain growth than other primates (Leigh 2004; Ponce de Leon et al. 2008), but this is not unexpected – larger brains always achieve higher growth velocities, since the period of exponential growth is longer, and peak velocity is reached at a larger brain size (Halley 2017). The larger problem with analyzing postnatal patterns in isolation (an unavoidable problem when fetal data are unavailable, either in extant or fossil species) is that birth does not align similar parts of different species’ sigmoid brain growth trajectories (Fig. 1). It therefore becomes unclear whether postnatal growth patterns are sampling similar or different parts of a given brain growth pattern (e.g., acceleration or deceleration phases). For example, Sakai and colleagues found that humans exhibit larger increases in white matter proportions than chimpanzees or macaques during early postnatal life (Sakai et al. 2013) – but these changes do not result from a unique human growth phase, but instead as an artefact of using birth as a temporal anchor (Finlay and Workman 2013).

How Large Are Mammalian Brain/Body Ratios at Birth, and Why?

Human brains are exceptionally large within the primate lineage, but humans do not have the largest mammalian brains – whales and elephants have brains that dwarf the human brain in absolute mass (Crile and Quiring 1940). Humans also do not have the largest brain/body ratios within the mammalian radiation – these belong to the smallest mammals, given that brain/body ratios are smaller in larger animals (i.e. Haller’s rule). Primates generally and humans specifically are

only unique among mammals in exhibiting unusually high brain/body proportions once body size has been taken to account (i.e., “encephalization”). This has led many researchers to ask whether neonatal brain/body proportions – rather than absolute brain size – might be unique within primates.

Whereas the growth of the brain or body against linear time since conception follows a regular sigmoid (s-shaped) growth pattern (Fig. 2a), brain/body proportions over ontogeny generally decrease over fetal and postnatal development (Fig. 2c). When we plot an individual species’ brain/body proportions over development using log-log coordinates (as is customary; cf. Count 1947; Halley 2016), what emerges is a characteristic two-stage growth pattern that is common to all mammalian species that have been studied (Fig. 2d). During early prenatal development, both brain and body growth are exponential, and brain/body ratios tend to either stay fairly constant (isometric growth) or decrease slightly (negatively allometric growth) (Fig. 2d). This variation has been directly linked to differences in species’ body growth (Halley 2017). Briefly, species that decrease in brain/body proportions more over development tend to have faster body growth, rather than slower brain growth (Halley 2016). In all species, this early period of brain/body growth comes to an end as brain growth reaches “peak velocity,” or the fastest period of brain growth in grams per day (Fig. 2a). Once peak velocity has passed, brain/body ratios fall dramatically, continuing to do so until the organism is fully mature (Fig. 2c).

Primates are unique among mammals in exhibiting unusually high brain/body proportions across all of prenatal development, a developmental feature that is also true at birth (Count 1947; Holt et al. 1981; Martin 1982; Deacon 1990; Halley 2016). Primate prenatal “encephalization” is apparently unrelated to either adult brain/body proportions or the relative size of the neocortex within different primate species (Halley 2016). Analyses of fetal growth patterns in primates suggest that high fetal and neonatal brain/body proportions are a consequence of primates’ exceptionally slow *body* growth, rather than

exceptionally rapid *brain* growth (Halley 2017). Slow body growth has also been observed in primate postnatal development (Leigh 2004), and appears to be linked to their exceptionally slow life histories (Harvey and Clutton-Brock 1985).

Similar to brain growth over time, altricial species are born earlier along brain/body growth plots when compared to precocial species (Halley 2016). Roughly speaking, brain/body proportions tend to decrease over development, and so altricial species tend to exhibit higher brain/body ratios at birth. The major exception to this pattern is seen in primates, which are precocial and exhibit high brain/body proportions at birth linked to slow body growth (see above). The large degree of variation in both birth timing and body growth rates between mammalian species make neonatal brain/body proportions a complicated measure to interpret, and they should not be taken as proxies for fetal brain growth patterns or neurodevelopmental stage in comparative studies (Halley 2017).

Human Neonatal Brain Size and Secondary Altriciality

One of the central questions in human evolution concerns our species’ relative altriciality among primates: human neonates are born at earlier stages of neurodevelopment than other primates are. While primates are generally considered to be precocial at birth in comparison with other mammalian radiations – meaning we have relatively long gestation, small litter size, and are born more mature than other mammals are – humans are nevertheless at the altricial end of the primate spectrum. Humans are born at earlier stages of neurodevelopment than other primates (Sherwood and Gomez-Robles 2017), and have grown a smaller proportion of their adult brain size by the time of birth (Harvey and Clutton-Brock 1985; Martin 1982). This phenomenon has been called “secondary altriciality” and is thought to contribute substantially to our species’ exceptional degree of neuroplasticity in early postnatal life (Sherwood and Gomez-Robles

2017). The most straightforward explanation of human altriciality is that evolutionary increases in human brain size since the last common ancestor with chimpanzees (Kaas and Preuss 2013) required longer periods of neurodevelopment, and that human gestation did not lengthen proportionate to this change in the duration of brain development.

A central theory for human altriciality is that in the course of human evolution, shortening of the pelvis to accommodate the biomechanical demands of bipedal locomotion led to difficulty in fitting the neonatal head through the birth canal. According to the “obstetric dilemma” theory, these complications led to evolutionary pressure to shorten gestation in the human lineage, causing human neonates to be born “early” and causing our exceptional degree of altriciality at birth (e.g., Washburn 1960; Rosenberg and Trevathan 1995). A number of critiques of this widely cited theory have been raised in recent years. First, human gestation is not unusually short for a primate of our maternal body size (Dunsworth et al. 2012), only relative to neurodevelopment. It is unclear why brain development should be the benchmark by which to measure “proper” gestation length or deviations from it, given how variable birth timing is across mammals relative to brain growth (Halley 2017) and neurodevelopment (Workman et al. 2013). Second, human encephalization has been the evolutionary product of increases to brain size. Given that larger brains are grown by extending the *duration*, rather than the *rate* of brain fetal brain growth (Halley 2017), it is not surprising that evolutionary increases in brain size necessitate longer neurodevelopmental periods. This should make human brains smaller at birth, as a percentage of adult brain weight, even if gestation length has been held perfectly constant. A critical review and alternative hypothesis to the “obstetric dilemma,” focusing on metabolic demands of pregnancy rather than pelvic constraints, was recently proposed by Dunsworth and colleagues (Dunsworth et al. 2012).

Regardless of whether human altriciality is a consequence of birth constraints or simply lengthening our period of brain growth and development, humans’ relative degree of altriciality has

important consequences for early cognitive development, and even for certain features of human culture. One example is the prevalence across human cultures of “alloparenting,” or cooperative breeding (Hrdy 2011), including traditions associated with assistance during parturition (birth assistance, midwifery) and in cooperative child rearing (e.g., Trevathan 1987). While some nonhuman primates may seek the company of conspecifics during birth, both the degree and the prevalence of birth assistance in humans seem sufficient to consider it a behavior unique to our species. Finally, the exposure of human infants to the external environment during relatively plastic stages of brain development (e.g., synapse formation and pruning) likely plays a central role in our species’ unique degree of behavioral flexibility (Sherwood and Gomez-Robles 2017).

Conclusion

Mammals differ widely in the timing of birth relative to both brain growth and brain development. Generally speaking, smaller mammals with larger litters are born earlier along brain growth patterns, earlier in neurodevelopment, and earlier along brain/body allometric trajectories. Larger-brained placental mammals, or more encephalized species as adults or at birth, do not grow their brains faster during gestation, but do exhibit a slower pace in the timing of neurodevelopmental events. Species born earlier during neurodevelopment are generally altricial, with relatively immature young. While primates are more precocial compared to other mammals, humans exhibit an exceptional degree of altriciality relative to other primate species. This is likely a consequence of the extended neurodevelopmental schedule required to build the largest extant primate brain, rather than a shortening of gestation length in human evolutionary history. Human altriciality exposes the newborn brain to environmental stimuli during earlier stages of brain development, contributing to an exceptional degree of plasticity in our species that can be linked to unique features of human reproduction and perinatal care.

Cross-References

- [Narrowing Birth Canal](#)
- [Brain Development](#)
- [Brain Size Growth in Humans and Nonhuman Primates](#)
- [Costs and Benefits of a Large Brain](#)
- [Early Stage of Brain Development at Birth](#)
- [Narrowing Birth Canal](#)

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Introduction

The human brain is arguably the ultimate result of natural selection. It is the most complex organ in the human body with approximately 100 billion neurons and over 100 trillion synaptic connections. This basic description does not include the billions of supporting cells or the complex genetic, hormonal, chemical, and electrochemical interactions that are constantly occurring. The brain gives rise to our sensations and perceptions, houses our memories, and more generally directs our behavior. Therefore, understanding how the human brain develops is of great interest and importance to many fields of psychology. Generations of scientists have examined brain development in humans and other animals by utilizing our understanding of evolution and shared phylogenetic properties. This entry provides an overview of brain development from conception to late adolescence and provides examples of the various environmental and genetic factors known to impact the developmental process.

Brain Community Structure

► [Evidence of Brain Modularity](#)

Brain Death

► [Medical Definitions of Death](#)

Brain Development

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Synonyms

[Brain growth](#); [Neural development](#); [Neurogenesis](#)

Definition

Brain development, which occurs rapidly early in life but continues throughout life, involves the interplay of genetic expression and environmental impacts on the growth and maturation of neurons and the connected networks they form.

Stages of Neuron Development

We now have a good understanding of the basic stages and mechanisms of mammalian brain development (Stiles and Jernigan 2010). Studies describing the neurobiology of brain development range from the neural organization of the entire brain to the cellular level of neurons, and on to the molecular level of various genetic and chemical factors. Together, this research finds that brain development results from the dynamic interplay of factors that are constrained by genetics but affected by a constantly changing experiential and environmental context. In order to discuss the influence of genetic, environmental, and other factors on brain development, it is important to first understand the basic progression of neurons from stem cells to maturity. Although neurons are not the only important cells in the brain, they are the fundamental functional unit of nervous tissue that transmit and receive nerve impulses (Pinel and Barnes 2018).

Following conception, the zygote is comprised of a mass of undifferentiated cells. Through genetic and chemical factors, this mass of totipotent cells begins to differentiate into the cells that will form different tissues in the body. Cells destined for the brain progress to a more specific class of pluripotent cells and then finally a multipotent form that can divide readily into different types of neurons (Kohwi and Doe 2013). The first recognizable structure of the early brain is known as the neural plate. This plate can be further divided into an outer ectoderm layer, a middle mesoderm, and an inner endoderm component. Chemical signals, which are critical to many aspects of neural organization during development, are released from early cells in the mesoderm layer (Kiecker and Lumsden 2012).

The stem cells of the neural plate proliferate rapidly in the first trimester in humans. This rapid growth initiates a folding of the neural plate into the neural tube. Interestingly, this early folding into a tube shape forms the fluid filled inner space which will develop into the ventricles and also begins to symmetrical hemispheric organization of the mature brain (Pinel and Barnes 2018). The immature neurons continue to divide rapidly during this phase in the layer directly adjacent to the early ventricle. This so-called ventricular zone forms the foundation for the neural layers and structures that will form above.

Once the ventricular layer/zone is formed, the neurons begin to migrate away in two different directions. Radial migration involves the immature cells moving directly up from the ventricular zone. In this way, subsequent layers of the neuron form on top of each other with newer arrivals settling in the outer most layer of the neural tube. Chemical guidance is critical during this phase so toxins or a lack of natural chemical signals can drastically disrupt the normal migration of neurons (see below). The other form of migration, known as tangential, involves neurons move along the neural tube as opposed to up to the outer layers (see Greig et al. 2013). Glial cells, essential support cells in the brain, are also known to contribute to normal migration by providing scaffolding and path setting for moving neurons (see Ohshima 2015). Although genetic

programming appears to determine the timing and types of chemical signals released, the eventual location and connections of each neuron does not seem to be predetermined.

Once the neurons migrate to various locations, chemical signaling between the cells allows them to aggregate into organized structures. In this way, the early forebrain, midbrain, and hindbrain begin to take shape. Cell adhesion molecules (CAM's) on the surface of the neurons are thought to support the process of aggregation (Mori et al. 2014). These molecules recognize chemical signals on neighboring cells and adhere to them. The brains of genetically modified mice, where these CAMs had been disrupted, showed devastating errors in aggregation and subsequent growth (Lien et al. 2006).

Another important and usually temporary characteristic of neurons during aggregation is the large number of gap junctions that form between cells. As their name implies, these connections are formed from sets of narrow tubes called connexins that directly link the cells and allow cytoplasm to be exchanged (Lien et al. 2006). Hypothetically, this direct exchange allows each cell to confirm chemically that it has ended its migration in a favorable location.

Although the majority of neurons end up in the correct locations, some do not. When this occurs, the aberrant neurons are eliminated via programmed cell death known as apoptosis (Miguel-Aliaga and Thor 2009). This is preferable to the disorganized process of necrosis that results in harmful inflammatory release of cytoplasm into the extracellular fluid. In this way, neurons are initially overproduced with the expectation that not all migration and aggregation will occur successfully. The excess nonfunctional cells are effectively pruned from the brain via apoptosis in a similar fashion to what is observed with synapses (see below).

To this point, the cells have remained immature and lack the connections and electrochemical activity that characterize mature neurons. This begins to occur with the growth of axons (typically sending signals) and dendrites (typically receiving signals). Different types of neurons express different forms of axons and

dendrites but the stages of growth are fairly consistent (see Kerstein et al. 2015). Axons typically begin to grow from the neuron cell body with a fingered structure called the growth cone. These fingers or filopodia are very chemosensitive and essentially smell their way through the growing brain. Pioneering growth cones often form first and lay down a chemical track for subsequent axon growth from neighboring neurons. In this way, tracts or multiple axon bundles form between brain structures in genetically predetermined ways. For example, neurons from the retina follow a chemical pathway created by early axons to connect the eye to the lateral geniculate nucleus of the thalamus and then on to the occipital lobe of the brain which processes vision (see Dudanova and Klein 2013).

While axons are forming, dendrites begin to grow to receive incoming contacts and form synapses. Synapses are the gaps where the nervous impulse passes from one cell to another. This often occurs chemically via the presynaptic release of neurotransmitters and the subsequent activation of postsynaptic receptors. Initially, synapses are thought to form somewhat indiscriminately based on chemical signals shared between the axons and dendrites (see Ou and Shen 2010). This process of synaptogenesis is also facilitated by the presence of glial cells such as astrocytes (Tsai et al. 2012). Astrocytes were initially thought to supply the high levels of cholesterol needed during synapse formation but current theories have been expanded to include astrocytes processing, transferring, and storing chemical information from neurons (see Clarke and Barres 2013). Like neurons, synapses are overproduced in earlier phases of development and are then pruned over time. Synapses appear to undergo a Darwinian-like process where those connections that function and are active based on external and internal stimulation survive while less active or misplaced connections are eliminated (Hebb 1949).

Once the axons and dendrites have been connected through thousands of synapses per neuron and the pruning process is well underway, the final major developmental process of myelination begins to occur. Myelination

involves the wrapping of new axons in a fatty coating that is part of supporting glial cells. This wrapping speeds up the transmission of action potentials (neural signals) by allowing them to jump passively, and essentially instantaneously, between unmyelinated nodes along the axon. Axons can then send action potential quickly across relatively long distances within the body (from the spinal cord to the toes, for example). Importantly, when myelination occurs, neurons lose some of their flexibility or plasticity. There is a trade-off then between plasticity and efficiency of communication as the brain develops (see Purger et al. 2016). This helps explain the existence of critical and sensitive periods of development since myelination ends the highest levels of plasticity as different brain structures develop. Oligodendrocytes, which are the main glial cells responsible for myelination in the central nervous system, actually suppress subsequent axon growth after a brain structure matures.

In summary, neurons form from multipotent stem cells shortly after conception, proliferate near the early ventricles, migrate and then aggregate to their final locations in the brain. Axons and dendrites develop to allow for action potentials and synaptic communication. Excess neurons and synapses are pruned in a Darwinian fashion and the maturing networks are made more efficient but less plastic by the process of myelination. In the sections that follow, the influence of genetics, experience, diet, and toxins on these stages of brain development are explored. Although a comprehensive review of each of these areas is beyond the scope of this entry, examples are provided of the research that has occurred in each field.

Influence of Genetics, Epigenetics, and Genetic Disorders on Brain Development

It is appropriate to begin any discussion of factors that influence brain development with a section on genetics. Mutations or inherited genetic disorders clearly have a profound impact on the growing brain; yet the more common processes involve the influence of the external environment and

chemicals on gene expression (del Blanco and Barco 2018). The relatively new field of neural epigenetics examines changes in the brain caused by modification in gene expression rather than mutation of the genetic code itself (see Sweatt 2013). Through these processes, evolution, genes, experience, anatomy, and behavior all interact in complex feedforward and feedback directions. Brain development is the result of genetic inheritance that comes through reproductive fitness of the parents. In utero and later environmental exposures and experience influence the expression of the genes to create the anatomy and functioning of the brain at all stages of development. The person then brings this anatomical and functional state to all daily situations that are encountered which results in the behavior expressed. Behavior then feeds back ultimately to reproductive fitness and the cycle continues (Pinel and Barnes 2018).

Genes, the material substance that is passed from parent to offspring, are nucleotide sequences of DNA housed in the nucleus of every cell. Essentially, the expression of a gene results in the production of a protein molecule. These proteins are then incorporated in the membranes and organelles of developing cells. Genes provide a template and the resulting proteins are the active agents in biological development. Thus, genes cannot participate directly in biological processes and do not directly result in different eye color or varied temperaments in a developing child. It is the epigenetic processes associated with expression through protein production that directly alters the makeup and activity of brain cells.

Epigenetic processes result in either increases or decreases in protein production. Two well-known epigenetic mechanisms are histone remodeling and DNA methylation. In histone remodeling, the DNA that makes up the individual genes wrap around a histone protein. When these proteins change shape due to signals related to cell activity or external chemical cues, the DNA that is wrapped around it are also modified (see Bintu et al. 2016). DNA methylation occurs when a methyl group attaches to the gene, usually at a cytosine site, and alters the transcription rate of

the gene (see Schubeler 2012). Regardless of the specific epigenetic mechanism, the key idea is that protein synthesis, and the resultant form and function of brain cells, can be influenced by external factors.

One early and particularly relevant animal example examined the influence of maternal care and early life stress on the neurons of young rats (Weaver et al. 2004). This study found that increased pup licking, grooming, and nursing behavior by rat mothers altered the offspring epigenome (gene expression) at a glucocorticoid receptor (GR) gene promoter in the hippocampus. Pups of mothers with high levels of care were found to have differences in DNA methylation, as compared to offspring of lower care mothers. These differences emerged over the first week of life, were reversed with later exposure to a more caring mother, and persisted into adulthood. Importantly, these changes altered the hypothalamic-pituitary-adrenal (HPA) responses to stress, suggesting a causal relation between epigenomic state, GR expression, and the maternal influence on stress responses in the offspring. Essentially, early stress related to poor maternal care lead to brain changes and a more reactive stress response in adulthood. While human experiments of this type are obviously not possible, these results strongly suggest that brain development can be altered by changes in gene expression based on external factors.

Epigenetic changes influence brain development; yet some of the most devastating effects occur when the genetic code itself is mutated or an abnormal gene is inherited. Usually, the genetic alterations that lead to altered brain development are polygenomic (result of many genes). In these cases, such as most Autism Spectrum Disorders (ASD; see Bourgeron 2015), it is very difficult to discover the direct connections between genetic and brain differences. For ASD, several dozen genes have been implicated with less than 5% of cases being explained by a single gene mutation (Mullins et al. 2016). Although ASD has been associated with developmental changes in the cerebellum, amygdala, frontal cortex, and the fusiform face area, there is little agreement on the

nature of the differences and the specific role of certain genes (Amaral et al. 2008).

There are cases where genetic influences on brain development are better understood. The disorder phenylketonuria (PKU) results from a single gene defect where sufferers lack an important enzyme called phenylalanine hydroxylase. This enzyme, that normally converts phenylalanine into tyrosine, is needed to synthesize the neurotransmitter dopamine. PKU also results in a toxic buildup of phenylalanine in the brain. Children born with PKU quickly develop intellectual delays and suffer from seizures, vomiting, hyperactivity, and brain damage (Strisciuglio and Concolino 2014). The combined effects of a toxic increase in phenylalanine and low dopamine levels leads to increase apoptosis, changes in brain activity, and likely abnormal protein synthesis through epigenetic mechanisms. Thankfully, PKU can now be detected at birth or through methods like amniocentesis so babies can be placed on a diet devoid of phenylalanine (see Casey 2013). This does not eliminate all cognitive effects but does limit the worst symptoms and brain changes. As discussed in the next section, the timing of the dietary changes is important because the brain develops through sensitive periods after which damage can be mostly irreversible (Pinel and Barnes 2018).

Another example of a clear genetic impact on brain development is Down syndrome (see Dekker et al. 2015). In what amounts to a genetic accident, Down syndrome occurs when an extra chromosome 21 is created in the egg during ovulation. When fertilized, the resulting zygote has what is known as a trisomy or three chromosome 21 segments. The result is an overproduction and/or abnormal production of proteins associated with that chromosome. This results in bodily disfigurement, intellectual impairment, and medical complications. At the electron microscopic level, the neurons of individuals with Down syndrome appear to be immature. The dendritic spines in the hippocampus that are normally slender and elongated are seen to be short and stubby (Sylvester 1983). This may partially explain the difficulties these individuals show with learning and memory since the hippocampus is critical

for these processes. It is clear that genetic factors influence brain development but it is also clear that epigenetic changes result from what the child experiences in their everyday lives.

Influence of Experience on Brain Development

In utero, the different phases of neurodevelopment discussed in the first section proceed, for the most part, without the influence of the outside world. During this period, the core components of the nervous system from the spinal cord to the cortical structures of the telencephalon are established. These early events provide the initial arrangement of connections within the brain, and this patterning is both underspecified and plastic at birth. The genetic program of brain development is also staggered so that brain stem structures, those that support basic bodily functions such as breathing, become functional first and certainly before full term birth. Conversely, the neocortex, which processes higher functions like learning and our senses, is still immature and plastic when a child is born (Pinel and Barnes 2018).

Light, sound, specific physical contact, food, and many other sensations begin to be experienced by a newborn. Neurons begin to respond to this sensory input via sensory organs. Those neurons that are active in this new sensory environment tend to add synapses, form networks, and survive while underactive or misplaced neurons are eliminated. As discussed in the last section, this activity also changes the gene expression and leads to altered levels of protein synthesis and growth. Despite rapid growth during the first several years of life (Li et al. 2015), the human brain matures very slowly compared to other animals. As a result, experience has a longer time to impact neural development.

Although clever marketing schemes attempt to convince parents to purchase certain toys or books to properly enrich their newborns, research consistently shows that simply being allowed to interact with other people and the environment is sufficient for normal brain development (Pinel

and Barnes 2018). It is only when extraordinary cases of sensory deprivation and abuse are considered that the impact of experience on brain development can be fully appreciated. One such case involved a young girl known as Genie (Curtiss 1977). She was admitted to hospital at age 13 and was extremely underweight for her age. She could not stand up straight, chew solid food, or control her bladder. Psychologically, she was extremely afraid, could not speak, and made almost no sounds. Genie was the product of unspeakable neglect and abuse from the age of about 20 months until her discovery. She spent her days alone, in the dark and often restrained to a potty chair (see Rymer 1993).

Upon her discovery, great efforts were made to counteract the developmental deprivation she experienced. Initially, rapid improvements were observed. Genie began to walk more normally, make sounds, and say words. Unfortunately, despite this early success, her behavior never became typical. Her speech did not follow grammatical norms and she continued to exhibit silent tantrums among other emotionally dysregulated behaviors. Genie's case is relevant to the important concepts of permissive and instructive experience along with critical and sensitive periods of development (see Assali et al. 2014). Permissive experiences allow genetic programs to be expressed whereas instructive experiences shape the information in the genetic programs and influence the trajectory of neural development. In Genie's case, her genetic complement was ostensibly intact at birth and the normal programs of development were initiated through permissive interactions with the environment. After the 20 months, the amount of external stimuli required for normal development was drastically reduced which had permanent detrimental effects.

The types of experiences needed for normal development are time dependent (Makinodan et al. 2012). Genie passed through several critical periods of brain development without sufficient external stimuli. These critical periods are essential windows of opportunity for stimuli, such as spoken language, to influence the developing brain. Since Genie was not spoken to, read to, or

shown printed words, she was never able to fully acquire these abilities. Sensitive periods occur when it may be optimal but not essential to receive relevant sensory experience. For example, learning a second language may be easier when you are younger (sensitive period) but can be accomplished at any age. Although the term critical period is frequently used, most effects of experience have been shown to occur during sensitive periods (Morishita and Hensch 2008). This finding is important since it suggests that learning and enrichment later in life may be able to counteract earlier missed opportunities.

Environmental enrichment is another important concept related to the influence of experience on brain development. Enrichment can be thought of as the opposite of the deprivation described above. Animal studies have shown that rearing young rats in complex environments leads to larger and more complex brain structures (Greenough 1975). Specifically, studies have found that environmental enrichment in the form of larger cages, toys, and running mazes leads to a thicker neocortex and more synapses per neuron in several brain structures related to learning and memory. Direct observation of these types of microscopic brain changes is obviously not possible in humans but many brain imaging studies have found similar increases in activity following specific forms of enrichment (May 2011). Although it is not possible to directly connect these brain changes to specific enhancements of behavioral ability, it is widely accepted that increased complexity in neuronal circuits suggest increased capacity for learning, sensory sensitivity, and resistance to acquired brain damage in adulthood.

Experience can also influence brain development in more specific ways. Ocular dominance columns form in the developing visual cortex where certain cells respond preferentially to one eye or the other (Hata and Stryker 1994). When the sensory input is altered by blindfolding one eye for a few days early in development, the ocular dominance pattern is altered leading to lifelong detriments in the blindfolded eye. Importantly, this does not occur if both eyes are blindfolded. This confirms that sensory

experience can create a competitive process between inputs to neurons in that functional (active) inputs will take over dysfunctional (non-active) inputs and alter the developmental structure of the brain (Hubel et al. 1977).

Another classic set of experiments in this field investigated the topography of sensory cortical maps. Here, experience in the form of a repeated motor behavior was found to reorganize the activity of the neurons in the motor cortex. When monkeys repeated a novel task, that was similar to a child learning to use a spoon, approximately 700 times, the neural representation of the fingers involved in the task grew in size relative to the unused fingers (Merzenich et al. 1987). This finding, and many other similar results, confirmed that sensory experience can alter the functional neural networks of the brain in lasting ways.

Although the mechanisms that underlie these changes in networks are not fully understood, the basic process has been described. During early development, brain areas are linked to each other through many diverse synaptic connections. Over time, some of these tracts become dominant with larger numbers of synapses but smaller side branches remain. When the behavior of the organism changes or the brain is altered by damage that reduces or eliminates the activity of the dominant connections, the lesser used pathways are strengthened through synaptic plasticity based on increased activity (Borodinsky et al. 2012). At the cellular level, this type of plasticity has been classically described by Donald Hebb (1949). Hebb proposed that when one neuron was involved in activating another neuron through synaptic contact and the second neuron fired an action potential as a result, the connection between the two cells would be strengthened. This is colloquially known as, “neurons that fired together, wire together.” Although this concept is most often used to explaining adult neural plasticity underlying learning and memory, it is obviously also relevant to the development of the brain. Experience is the external driving force that changes neural activity through the sensory systems but other factors such as nutrition and environmental toxins also play a key role in brain development.

Influence of Diet and Environmental Toxins on Brain Development

Optimal brain development involves proper nutrition and low levels of environmental toxins both prenatally by the mother and postnatally by the child (del Blanco and Barco 2018). The developing human body and brain are, however, amazingly resilient to mild alterations in diet and low level of environmental exposure (Garret and Hough 2018). One of the central issues for in utero development is the role of the placental barrier. This semipermeable structure exists between the blood of the mother and the fetus. This structure blocks many large molecules from crossing and therefore protects the developing infant (Blundell et al. 2016). Critical smaller elements and molecules including oxygen and sugars are obviously transported readily across the barrier but this also allows for potentially harmful small molecules such as alcohol and some viruses to directly affect the fetus.

In a comprehensive review, Bolton and Bilbo (2014) examined the brain development of the fetus that resulted from the diet and obesity of the mother. They concluded that maternal obesity and a high-fat diet during gestation/lactation likely “programs” offspring long-term for increased obesity in themselves, along with increased vulnerability to mood disorders. This programming is thought to occur by the perinatal diet propagating inflammation in the brain of the fetus/infant, since obesity and high-fat diets are both associated with exaggerated systemic levels of inflammatory mediators. These immune molecules (e.g., interleukin [IL]-6, IL-1b) are known to play a role in both placental function and brain development. Previous research has shown that any disruption of growth factors or neurotransmitters (e.g., serotonin) by inflammation early in life can permanently alter the trajectory of fetal brain development.

An example with both a dietary and potentially toxic component is the consumption of alcohol by a pregnant mother. Fetal alcohol syndrome (FAS) is a condition that results from sustained level of alcohol consumption at

moderate to high levels during pregnancy (Caputo et al. 2016). This consumption results in a wide range of physical, developmental, and cognitive alterations and deficits in the infant. The brain is the organ most affected in children with FAS. MRI studies show smaller brain volumes in both gray and white matter and alterations in the corpus callosum which is the main communication pathway between the left and right hemispheres of the cortex (Roussotte et al. 2012). Once alcohol crosses the placental barrier, it negatively impacts the development of blood vessels which limits blood flow and the delivery of oxygen to the developing brain (Carmeliet et al. 1996). It also interferes with the migration and aggregation processes outlined above. This leads to increased apoptosis and an underdeveloped brain at birth (Smith et al. 2014).

Environmental toxins are also known to impact brain development. Heavy metals such as mercury and lead can interfere with neuronal activity at the cellular and synaptic level. In their review of this area, Karri et al. (2016) concluded that concurrent exposure of heavy metals, such as lead (Pb), cadmium (Cd), arsenic (As), and methylmercury (MeHg) are particularly harmful due to their long-lasting effects on the brain. These metals all have a binding affinity with NMDA receptors (a receptor for glutamate which is the main excitatory neurotransmitter in the brain), the sodium-potassium pump (which is critical for maintaining the resting potential and resulting action potentials of all neurons), and other cellular processes critical to neuronal function. The presence of these metals interferes with the migration, aggregation, and later functioning of neurons throughout development. Brain abnormalities and varied cognitive deficits related to learning and memory have been consistently observed following heavy metal exposure (Karri et al. 2016). These findings have resulted in the removal of lead from paint and gasoline among other changes.

Psychoactive drugs provide a final example of environmental exposure that is known to alter brain development (Repo et al. 2016). Unlike the earlier examples in this section, this exposure

typically occurs later in development. An example is the use of cannabis by adolescents. Cannabis and its main psychoactive ingredient tetrahydrocannabinol (THC) activate the endogenous endocannabinoid (eCB) system. The eCB system includes two inhibitory presynaptic G-protein coupled receptors, cannabinoid1 (CB1) and cannabinoid2 (CB2). CB1 receptors, which are activated by THC, are expressed throughout the brain in many neuronal populations (Newton et al. 2009). The eCB system regulates the release of neurotransmitters and contributes to long- and short-term synaptic plasticity (see review, Mechoulam and Parker 2012).

Neural structures rich in CB1 receptors such as the amygdala, hippocampus, and the prefrontal cortex in particular are not fully developed in adolescence. The lack of frontal lobe maturity, a structure important for behavioral inhibition and decision-making, is particularly well documented (Pinel and Barnes 2018). Since all of these brain areas are also related to the HPA axis, they are critically involved in the stress response which can be altered by eCB manipulation (Romeo and McEwen 2006). In order to model the scenario where adolescents turn to cannabis to help them cope with stress, Weeks et al. (2015) conducted an animal experiment that placed rats in a stress condition before THC was administered. Once the rats reached adulthood, behavioral testing for fear/anxiety was conducted and brain tissue was processed for synaptic analysis using confocal microscopy. Behavioral results indicated that chronic adolescent THC administration following stress caused adult rats to be more impulsive but not more fearful. Synaptic results indicated significantly fewer synaptic proteins in the lateral amygdala in the stress/THC rats relative to controls. Taken together, these results suggest that preexisting stress followed by THC administration leads to a unique profile of behavioral and synaptic changes. This experiment provides an important example of the continued impact of environmental exposure on brain development into the adolescent phase of development.

Conclusion

The preceding sections described the main phases of brain development and explored examples of factors that are known to influence these processes. The impact of the external environment occurs via epigenetic mechanisms both in utero and after birth. While the discussion focused on earlier phases of development, it is important to acknowledge that the brain continues to develop and change throughout the lifespan. One current controversy related to later development is the topic of adult neurogenesis. Traditionally, the brain was thought to grow rapidly in utero and then more slowly as the child aged. No new neurons were thought to form after late adolescents. That changed when animal studies using birds first identified adult neurogenesis (Goldman and Nottebohm 1983). Since then, evidence has mounted that new neurons form in many species, particularly in more plastic structures such as the hippocampus. This process hypothetically allows these structures to contribute more readily to processes like the formation of new memories that requires higher levels of flexibility. More recent studies have questioned whether this process occurs in humans. One group has found that human hippocampal neurogenesis drops sharply in children to undetectable levels in adults (Sorrells et al. 2018).

Later in the lifespan, brain development is typically defined by a slow rate of neuron loss and typically involves mild cognitive decline (Pinel and Barnes 2018). Researchers looking at this last phase of brain development frequently examine the differences between normal neural decline and more dramatic changes that occur due to disorders like Alzheimer's disease (Rosenberg and Kosslyn 2014). Whereas disease typically creates dementia which is characterized by pronounced memory loss and confusion, normal aging typically involves a decline in fluid intelligence, executive function, and the ability to form new memories (Salthouse 2005). As people live longer and more of the population enters this phase of life, further research in this area will be critical.

The study of brain development continues to present both challenges and opportunities to psychologists seeking to understand the fundamental processes that underlie cognitive development and the neural systems that mediate them. While many fundamental processes have been well defined, the emerging field of neural epigenetics will continue to help us understand the influence of the environment and a person's behavior on the ever changing expression of their individual genome. It is through these complex interactions and feedback loops that we will continue to enhance our understanding of brain development and the factors that influence this critical process.

Cross-References

- [Early Stage of Brain Development at Birth](#)

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Brain Development in Infancy

- [Brain Growth in the First Year](#)

Brain Energy Absorption

- [Energy Consumption](#)

Brain Evolution

- [Costs and Benefits of a Large Brain](#)
- [Evolution of the Brain, The](#)

Brain Evolution Resulting from Cooking

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Synonyms

[Encephalization](#); [Thermal processing of food](#)

Definition

Cooking as a potential explanation for the evolution of the disproportionately large human brain.

Introduction

The disproportionately big human brain is a conundrum – it is larger than would be expected for a primate of our size, and it is a very energetically expensive organ. Since human basal metabolic rate (BMR) is not elevated to match such a big brain, the extra energy needed to sustain it suggests a dietary explanation. Feeding the large brain would likely require a shift to a high-quality diet: one comprised of energy-rich, easily digestible foods. This hypothesis is supported by a number of anatomical features: smaller teeth, jaws, stomachs, and a shorter large intestine. Two key elements of human subsistence –

cooking and meat eating – have been proposed as a possible means of achieving this high-quality diet.

Encephalization and Trade-Off Theories

The human line has experienced a remarkable increase in brain size during the last couple of million years: the first major expansion occurred around 2 million years ago (MYA) with the second one following around 800,000 years ago (YA), when the brain increased to its modern level. A modern human's average brain is 4.6 times larger than expected for our body mass and takes up to 20 % of our body's resting metabolic rate (RMR) in comparison to only 9 % for other primates (RMR is conceptually related to the basal metabolic rate, though BMR is more accurately measured). This substantial energetic cost to the body, however, is not accompanied by a corresponding increase in BMR to supply the extra energy, as a mature human's BMR is quite typical of primates. How, then, do humans feed the expanded energy needs of the large brain when the basal metabolic rate remains fixed?

Various theories have been proposed to explain how the expansion of such a costly brain occurred in the human lineage. Aiello and Wheeler's expensive-tissue hypothesis (Aiello and Wheeler 1995) suggests that a size reduction in the gastrointestinal tract (only 60 % of what is expected for a primate our size) energetically balances increases in brain size. The metabolically expensive tissue of the brain is thus offset by a smaller gut – another metabolically costly organ. Such decreased gastrointestinal tract points to diet as a major determinant, with less bulk and higher digestibility of energy-packed foods (e.g., low-fiber plants, fruits, meats) requiring relatively smaller guts. In humans, the colon is only 20 % of the total volume of the digestive tract, compared to 50 % in apes. Since big colons permit fermentation of fibrous low-quality plant foods, humans are relatively poor at utilizing uncooked plant fiber. Aiello and Wheeler propose that cooking – a way to externalize part of the digestive process – might have been an important factor in attaining such a

high-quality diet. The authors' hypothesis of the gut-brain trade-off, however, is challenged by Navarrete et al. (2011), who failed to find the negative correlation between relative brain size and digestive tract for 100 mammal species.

Another theory has been proposed by Fonseca-Azevedo and Herculano-Houzel (2012), who suggest a trade-off between brain size and body size, with larger primates having smaller brains due to caloric restraints that cannot fuel both the brain and body to be large. These caloric restraints are a result of the limited number of hours available for feeding per day and the low caloric yield of raw foods. Their calculations show that, with a raw food diet similar to that of extant nonhuman primates (e.g., great apes), the *Homo* species would have to feed for more than 9 h a day to afford their total body mass and brain size (Cornélio et al. (2016) challenges these calculations, concluding that only 5–6 h of daily foraging would have provided enough energy to sustain a large brain). With this theory of the brain versus body growth trade-off, Fonseca-Azevedo and Herculano-Houzel also point to a high-quality diet as early humans' strategy to circumvent the caloric restraint, with cooking specifically as a way to provide more calories in less feeding time.

Cooking: The Human Universal

The significance of cooking for our biological evolution was not widely discussed until the twentieth century. Because fire was considered to be first controlled by *Homo sapiens*, the origins of cooking were placed only recently – less than 200,000 YA. The shift to a high-quality diet was thus popularly attributed to eating more animal foods. Later archeological evidence gave rise to other approaches, placing cooking as early as 1.8 MYA (around the emergence of *H. erectus*) and increasing academic interest in its role in human evolution. Wrangham's book, *Catching Fire: How Cooking Made Us Human* (2009), supports the earlier adoption of cooking (1.8 MYA) with plenty of time to allow for a larger brain.

Cooking is both a unique and universal human feature: every human culture cooks, while no

other species does. The hypothesis that *Homo erectus* already cooked food by 1.8 MYA is mainly supported by the fact that specific features of *H. erectus* (small mouth, small blunt molars, and smaller gut) are difficult to explain unless a diet of soft easily digested foods was available year-round. In terms of archeological record, there is sparse evidence of fire use as far back as 1 MYA, but it is reasonable to accept its use specifically for cooking after about 800,000 YA. With these timelines we can expect cooking to produce genetic change, considering that other examples of dietary modifications causing genetic adaptations occurred in much less time – such as with dairying and lactase enzyme persistence into adulthood. Indeed, there appears to be genetic evidence for our adaptation to cooked foods (Carmody et al. 2016).

Cooked Starches, Large Brain

Cooking can increase energy gained from food by improving nutrient digestibility, reducing body's costs of digestion, and decreasing the energy spent on immune defenses (by eliminating foodborne pathogens). For humans, the most consistent evidence for cooking's ability to increase net energy gain of food is for starchy vegetables, though there is evidence for meat and nuts as well (► [“Increased Energy/Reduced Digestion”](#)).

Starchy foods in particular could have been important in the evolution of a large brain and particularly in cooked form. The brain tissue is characterized by high glucose demands (the human brain uses up to 60 % of the body's glucose in a resting state), and a consistent diet of cooked starchy plants – the richest form of dietary glucose – can meet such demands quite well. Cooking starches gelatinizes them, allowing the digestive enzyme in our saliva (salivary amylase or AMY1) to begin digesting it. Humans are in fact unusual in the high number of AMY1 genes (six copies, in comparison to only two in other primates), which makes starch digestion more efficient. Hardy et al. (2015) propose that the rapid increase in brain size from the Middle Pleistocene (about 800,000 YA) was energetically affordable due to

the coevolution of cooking and increases in expression of AMY1, as raw starches are poorly digested by this enzyme. While nonthermal methods of food processing, like grinding and blending, can also improve starch digestibility, they cannot achieve the same effectiveness as gelatinization through heat.

Coevolution of cooking and salivary amylase AMY1 would have resulted in higher availability of glucose necessary for the enlarging brain. This is important, because even when the brain uses ketones (by-products of high levels of fat oxidation) during long periods of fasting, its normal functioning still absolutely requires 30–50 g of dietary glycemic carbohydrate per day. One would have to generate large stores of glycogen during periods of sustained fasting, requiring a diet that provides a caloric surplus consistently. The energy expenditure necessary to obtain starchy tubers and roots would have been far lower than that to obtain animal foods for a reliable food source (Carmody et al. 2011).

A Case for Cooking: The Modern Raw Foodist

Some unexpected evidence for the importance of cooking comes from studies with raw food communities. “Raw foodists” are groups living in industrialized societies that avoid cooked foods for perceived health benefits. Studies consistently show insufficient energy on such diets for maintaining body weight (Carmody and Wrangham 2009; Koebnick et al. 1999). In Koebnick et al. (1999), this energy deficiency resulted in 50 % of the female respondents experiencing amenorrhea or the absence of menstruation. These outcomes are surprising, considering that modern raw foodists enjoy access to a rich variety of high-energy foods free of seasonality constraints. In addition, they process their diets quite extensively through dehydration, blending, sprouting, and pickling, which can increase the food's caloric value. Adding cold smoked meats to the raw plant diet did not improve the odds of becoming underweight, so the lack of meat does not appear to hinder

reproductive function or one's energy status. The energy deficiency seen with long-term modern raw foodists, even with the addition of meat, suggests that the diet to which humans are adapted evolutionarily has to include cooked foods.

Nonthermal Processing: An Alternative Hypothesis

Cornelio and colleagues (2016) challenge the hypothesis that cooking is a prerequisite to our brain expansion: they propose that it is the use of tools that helped early hominins increase their daily energetic intake, as well as the inclusion of new food sources – meat and seeds. The author's work with mice indicated no weight gain on a cooked meat diet, suggesting that cooking was not necessary for increasing caloric intake of foods. Not including cooked starches limits the study's conclusions, however, since cooking would be applied to both meat and plants. Carmody et al. (2011) include both foods in their cooked versus raw design and find that mice on cooked meat and plants retain weight, while mice on the raw versions lose it, contrasting Cornelio and colleagues' results. Carmody et al. (2011) also challenge the tool use hypothesis by testing the effect of both cooking and non-thermal food processing methods, such as pounding. They demonstrate that with starches, mice lose weight on the raw diet whether the starchy food is whole or pounded, yet retain weight on the cooked version. With meat, mice lose weight from all versions of the diet but they lose less of it with the cooked meats, again showing higher caloric gain with thermal processing. Therefore, processing methods involving tool use do not appear to match cooking in their ability to increase the net energy value of foods.

Conclusion

According to the archeological record available so far, cooking does not appear to predate the first rapid brain expansion around 1.8 MYA. However, for the second main period of hominin brain

expansion (around 800,000 YA), cooking could have been the crucial element for brain size acceleration by enhancing energy gain from raw foods.

Thermal processing would increase the energy gained from foods, providing the extra calories for an expanding brain. In addition, cooking starchy foods and evolving the extra copies of salivary amylase to efficiently digest them would supply the brain with glucose – its main source of fuel. Nonthermal food processing, such as tool use, could alternatively allow this shift to a high-quality diet. Studies with raw foodists are one challenge to this approach, as even the addition of meat and various processing methods does not improve odds of becoming underweight on an uncooked diet. Another challenge are mice studies that show higher net energy gain from cooked versions of meats and starches than those processed non-thermally. Cooking, thus, is not paralleled by other processing methods and remains an important factor in theories of encephalization.

Cross-References

► [Increased Energy/Reduced Digestion](#)

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Brain Fitness

- [Resources for Brain Development](#)

Brain Growth

- [Brain Development](#)
- [Resources for Brain Development](#)

Brain Growth in the First Year

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Synonyms

[Brain development in infancy](#); [Early brain development in a child](#)

Definitions

Brain development in the first year refers to normal development of a child's brain in order to achieve developmental milestones.

Introduction

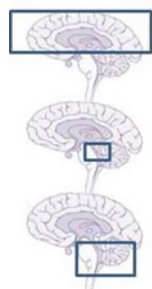
Brain development in a child is a continuous process. It encompasses the neurological and psychological development beginning from fertilization and continues throughout life. Surrounding environment has an impact in overall development of the child. The child's brain develops rapidly in the first year of life, and the child rapidly acquires new skills. The rate of brain growth in the first year is the highest of all succeeding years. The child's brain volume doubles and reaches approximately three-quarters of adult brain volume by the end of the first year. Developmental milestones are also attained expeditiously in the first 12 months. At birth, the human child has very little cortical function, and a child only feeds and sleeps. But at her first birthday, she may walk independently and can typically speak few words.

Embryology of Brain Development

The nervous system develops with formation of a neural tube from the ectoderm. Both ends of the neural tube close by 28 days after fertilization. Once the neural tube is complete, three primary vesicles develop at the cranial end of neural tube to form the brain: *the forebrain vesicle*, *the midbrain vesicle*, and *the hindbrain vesicle* (Snell 2010).

Forebrain (*prosencephalon*) develops from the forebrain vesicle to form cerebral hemispheres (telencephalon) and diencephalon (Fig. 1). Midbrain vesicle forms the midbrain (*mesencephalon*). Hindbrain (rhombencephalon) develops from the hindbrain vesicle to form metencephalon (pons, cerebellum), and myelencephalon (medulla oblongata).

Proliferation of cells in the neural tube around the central canal continues adding to the size and bulk of neural tissue. Progenitor cells in the neural tube differentiate into neurons and neuroglial cells. Each cerebral hemisphere arises by lateral expansion of the forebrain vesicle at the beginning of the fifth week of development. As each cerebral hemisphere rapidly expands, the convolutions form gyri separated by sulci which become



Primary division	Subdivision	Mature structures
Prosencephalon (forebrain)	Telencephalon	Cerebral hemisphere, basal ganglia, hippocampus
	Diencephalon	Thalamus, hypothalamus, pineal body,
Mesencephalon (midbrain)	Mesencephalon (midbrain)	Tectum, tegmentum, crus cerebri
Rhombencephalon (hindbrain)	Metencephalon	Pons, Cerebellum
	Myelencephalon	Medulla oblongata

Brain Growth in the First Year, Fig. 1 Divisions of the developing brain from three primary vesicles. The boxes in the left over the brain corresponds approximate portions of forebrain, midbrain, and hindbrain



Brain Growth in the First Year, Fig. 2 Sequential development of cerebral hemispheres. Brain surface is relatively smooth at 3 months. With rapid increase in cortical surface different lobes with sulci and gyri become prominent gradually

evident on its surface. Up to 3 months of age, the surface of the brain is relatively smooth. Rapid growth of cortical surface through multiple infolding occurs, thereby vastly increasing the surface area of the cortex. Appearance of major fissures occurs in the fifth month. The major fissures include the Sylvian fissure, the central sulcus, the parieto-occipital sulcus, and the calcarine sulcus. The major fissures divide the brain into different lobes. The secondary sulci and the tertiary sulci appear in the seventh to ninth months of gestation, and by birth a child’s brain resembles an adult brain (Fig. 2).

Normal Developmental Process in the First Year

Brain development during the first year of life not only involves an increase in number of brain cells but also forms more connections. Brain

development is a very dynamic process with proliferation of dendritic branches, myelination, pruning of brain cells, and connections that are not being used. The way a child develops from birth to 1 year can be assessed clinically by examining various parameters like head circumference, brain volume, and systematic assessment of developmental milestones (Swaiman 2012). Some of these entities are explained in greater detail below.

Head Circumference

The average head circumference at birth is 33–35 cm. Head circumference is clinically a rough estimate of brain volume and mass. Presence of a microcephaly (small head) or macrocephaly (large head) is abnormal. During the first 3 months of life, head circumference increases approximately at a rate of 2 cm per month. During the period of 3 to 6 months of age, head circumference increases at a rate of 1 cm per month. During the second half of the first year of life, head

circumference increases at a rate of 0.5 cm per month. Together, during the first year, head circumference increases by approximately 11–12 cm.

Brain Volume

The average brain volume at birth is 341 cm³. It is 558 cm³ at 90 days (Knickmeyer et al. 2008). Total brain volume at 2–4 weeks of age is approximately 36% of its adult size. By 1 year, total brain volume reaches 72% of adult brain volume. Increase in brain growth in the first year is 101% from its value at birth. In other words, a baby's *brain doubles* in size over the *first year*. The majority of this growth is in gray matter, with minimal contribution from white matter. Gray matter increases by 149%, while white matter increases by 11%. The cerebellum increases by 240% in the first year which is out of proportion to rest of the brain growth (Knickmeyer et al. 2008).

Biology of Brain Development in the First Year

Neuronal organization, increase in brain volume, differential myelination, dendritic proliferation, newer synaptic contacts, synaptic pruning, and maturation of neuronal transmission continue well after birth and contribute to brain maturation.

Myelination

The process by which axons are covered by an extra layer of fat called myelin begins in the third trimester. In the intrauterine life, brain myelination is restricted to the fibers of the basal ganglia. The brain at birth is largely unmyelinated, and the process of myelination becomes rapid after birth. Myelination insulates certain portions of neurons and makes the neuronal circuit more functionally mature. Myelination of the brain and spinal cord is accomplished by *oligodendrocytes* (a type of glial cell), whereas in peripheral nerves, myelination is carried out by *Schwann cells*. These cells wrap around the axons in multiple layers so that their cell membranes provide sequential layering of lipid around the axon. Myelination of the child's brain progresses rapidly to approach adult pattern by the end of the

second year, though myelination continues at a slower pace far into adulthood.

At birth, human children have little cerebral function. Myelination of different nerve pathways (*tracts*) like corticobulbar, corticospinal, tectospinal, and spinothalamic tracts proceeds in a systematic pattern. The corticospinal fibers complete myelination by the end of the second year.

Dendritic Proliferation

During brain development, nerve cells sprout branches that form new connections from one cell to many others. In the newborn there are fewer axons, and their organization is very much simple with relatively few connections. As the child ages, the axons and dendrites profusely branch (*arborization*) to form multiple connections (Kolb and Fantie 1989). Dendritic proliferation and new synaptic contacts followed by differential myelination make the electrical circuits of the brain more efficient.

Pruning

During the process of brain development, cellular proliferation occurs, creating excess neurons and glial cells. A large number of these cells are programmed to die. Pruning refers to the process of dying off of brain cells and elimination of connections that are not used or are harmful. Pruning increase the efficiency of neuronal transmission.

Glial Development

Gradual proliferation, maturation, and organization of glial cells are important for efficient and effective neuronal function and metabolism. The glial cells in the central nervous system are *oligodendrocytes*, *astrocytes*, *ependymocytes*, and *microglia*. Oligodendrocytes myelinate the nerve fibers in the central nervous system. Due to multiple processes, a single oligodendrocyte can form as many as 60 internodal segments in axons of multiple neurons. Astrocytes provide supporting framework, limit spread of neurotransmitters, store glycogen, and produce trophic substances and growth factors. Ependymal cells form a single layer of cells around the ventricles and the central canal of the spinal cord. They possess microvilli

and cilia which help in the flow of the cerebrospinal fluid. Microglia may be inactive in a normal brain, although some current research suggests they may help to fine-tune neuronal circuits and assist with synaptic and structural plasticity. They proliferate in disease and inflammatory conditions and help in phagocytosis.

Imaging Studies of Brain Development

MRI techniques provide excellent anatomical resolution to study the human brain development in infancy. Studies have shown that gray matter volume increases significantly more than white matter volume during the first year of life (Knickmeyer et al. 2008). Gray matter volume begins to decline, and white matter volume begins increasing at 6–7 years and continues through adolescence. The decline in gray matter may be associated with synaptic pruning and cortical maturation (Gogtay et al. 2004).

18-FDG positron-emission tomography (PET) studies have shown that in infants below 5 weeks of age, utilization of glucose is maximized in the sensory and motor cortex. This is in concordance with the fact that these areas are clinically and physiologically the most mature areas at birth. Brain metabolism in other areas increases gradually. By 8–9 months, there is evidence of active metabolism of glucose throughout the cortex (Chugani and Phelps 1986).

Primitive Reflexes and Disappearing Signs

A newborn is born with a unique set of reflexes (Kliegman et al. 2016) that are present either at birth or in the following few months. They gradually disappear around 1 year of age (Amiel-Tison and Grenier 1986). Their persistence beyond certain ages is of pathologic significance and indicates impaired brain development. As cerebral function matures, the primitive reflexes gradually disappear due to suppression by the matured brain. In some of the central nervous system diseases, these reflexes reappear in adulthood due to

loss of cortical function. Reappearance of primitive reflexes in adulthood is pathological signs of lobar dysfunction (lobar release signs):

1. Moro reflex

When a baby is held suspended in supine position with the examiners hands supporting her back and head, and when the head is dropped back a few centimeters, there is rapid abduction of the arms, hip flexion, and leg extension. This sign is present in all full-term newborns. This is usually lost at 4–5 months of age. The center for this reflex is thought to be present in the lower pons and medulla.

2. Tonic neck reflex/fencing posture

In supine position, when the baby's head is turned to one side, the arm and leg to which side the head is turned are extended, while the opposite arm and leg are flexed. This reflex is present at 1 month of age and disappears by 6 months. Persistence of obligate tonic neck reflex is indicative of asymmetric CNS development and predicts choreoathetoid cerebral palsy.

3. Crossed adductor reflex

This reflex consists of contraction of bilateral hip adductors when either knee jerk is elicited. It is present at birth and disappears by 7–8 months of age. Its persistence beyond this period is suggestive of early corticospinal tract lesion.

4. Other pyramidal signs

While eliciting plantar reflex, the baby's knee is flexed, and the thigh is externally rotated. In this position, the outer aspect of the sole is firmly scratched with a blunt point such as a key. The direction of scratching then turns inward toward the middle of metatarsophalangeal joint. A normal response in adults consists of flexion of the metacarpophalangeal joint of the great toe and flexion of the other toes. An abnormal response in adults involves great toe extension and fanning of the other toes, suggesting pyramidal tract lesion and is known as positive Babinski sign. A positive Babinski sign is considered normal in children up to the age of 1 year.

5. Grasp reflex

This reflex is elicited by stroking the palm of the child with a finger, to which the baby usually grasps the finger. This is present in all term newborns and disappears by 4 to 5 months of age.

6. Parachute reflex

When a baby is held in horizontal position with face downward and is then thrust downward, she extends her arms to break the fall. This is well developed by 6 to 7 months of age.

7. Rooting reflex

By lightly touching the corner of the lip of the baby, there is sucking movement of lips with deviation of mouth in the direction of the stimuli. This reflex disappears by 3 to 4 months of age. This reflex helps the baby find the breast to begin feeding.

8. Sucking reflex

By lightly touching the center of the lip, sucking movement of lips occurs. This reflex develops in the 32nd week of pregnancy and is fully developed at term. Premature babies may have a weak sucking reflex and difficulty in feeding.

using the limbs and trunk like neck holding, rolling over, sitting, and standing.

Language Development

Language is one of the most critical parts of child development. It helps the child to communicate and helps in developing relationships. There are two main areas of language: *receptive language* and *expressive language*. Receptive language refers to understanding and comprehension of language. Expressive language is the use of language through speech to communicate needs, thoughts, and ideas. Development of language is dependent on both *perceptual abilities*, such as ability to hear and understand sound and on *motor control* of larynx, lips, palate, tongue, and muscles of facial expression.

Social and Cognitive Development

Social and cognitive development plays an important role in emotional development of the child and prepares the child to act and respond to different social situations. Children become aware of their surrounding and understand their needs, desires, and feelings. These skills help them to judge others' behavior and to engage with others in a meaningful way (Table 1).

Postnatal Developmental Milestones During the First Year

Developmental milestones are a set of physical or behavioral signs of development and age-specific tasks that most children can do at a certain age. There are different domains of child development such as motor development, language development, and social and cognitive development.

Motor Development

Motor skills are the movement that occurs when the nervous system and muscles work together which are intended for various purposeful activities. Motor skills generally fall within two types: *gross motor* and *fine motor*. Fine motor skills refers to small movements of fingers, toes, and wrists to fulfil tasks like picking up a small object with the hand, holding a rattle, or lifting a spoon from the floor. Gross motor skills are larger movement

Conclusion

The rate of brain growth in the first year is the highest of all succeeding years. The child's brain volume doubles and reaches approximately three fourth of adult brain volume by the end of the first year. Gray matter volume increases significantly more than white matter volume during the first year of a child. At birth, human child has very little cortical function and motor functionalities such as sucking and swallowing which are essentially reflex in nature. Many primitive reflexes appear during infancy and gradually disappear as the brain matures. Increase in brain volume, myelination of nerve fibers, dendritic proliferation, synaptic pruning, neuroglial organization, and maturation of neuronal transmission continues after birth and contributes to brain maturation and efficient brain function. A child must achieve certain

Brain Growth in the First Year, Table 1 Key developmental milestones in the first year (Kliegman et al. 2016; Swaiman 2012; Kolb and Fantie 1989; Amiel-Tison and Gosselin 2001; Illingworth 1987)

Age in months	Gross motor	Fine motor	Language	Social and cognitive
1	Turns head when supine Chin up when prone	Infantile grasping	Makes sounds other than crying Startles to loud noise	Gazes at bright objects Regards mother's face Comforted by sound of human voice
2	Extends and turns neck in prone position Tries to steady head briefly when held	Hands unfisted 50% Retains rattle if placed in hand	Coos Social smile	Follows large objects with contrast Recognizes mother Responds to adult voice and smiles
3	Keeps head above horizontal for longer periods Rolls to side	Inspects fingers Bats at objects	Chuckles Babbling Vocalizes when talked to	Reaches for parent's face
4	Sits with trunk support Pulls to sit with no head lag Rolls front to back	Clutches objects and clothes Plays with rattle	Laughs aloud Vocalizes when alone Localizes to sounds Varies pitch of vocalizations	Selective attention to parents faces
5	Sits with pelvic support Moves back to front	Grasps cube using whole hand (palmar grasp) Transfers object: hand-mouth-hand	Expresses anger with sounds other than crying	Recognizes caregiver Forms attachment to caregiver
6	Sits momentarily Pivots in prone on belly Exerts weight on forearms in prone position	Transfers hand-hand Grasp objects with both hands	Listens and vocalizes Smiles and vocalizes at mirror	Removes cloth on face Bangs and shakes toys
7	Sits without support (steady)	Grasps using side of hand (radial-palmar grasp)	Increasing variety of syllables	Explores different aspects of a toy
8	Gets into sitting Pulls to sitting/kneeling	Grasps with all four fingers and side of thumb (scissor grasp) Takes cube out of cup	Says "Mama" (non-specific) Imitates sounds	Let parents know her mood Seeks object after it falls to the ground
9	Begins creeping Crawls	Thumb-forefinger grasp Bangs two cubes together	Orients to name well	Uses sounds to seek attention Separation anxiety Social gestures
10	Creeps well Stands with one hand held Walks with support of two hands held	Isolates index finger and pokes	Says "Dada" (specific) Waves "bye-bye"	Uncovers toy under cloth Learns fear Gives attention when name is called
11	Walks with support of one hand held Pivots in sitting Stands few seconds	Throws objects Stirs with spoon	Says first word Vocalizes to songs	Looks at pictures in book

(continued)

Brain Growth in the First Year, Table 1 (continued)

Age in months	Gross motor	Fine motor	Language	Social and cognitive
12	Stands well with arms high and legs splayed Independent steps	Fine pincer grasp of small objects Can hold a pencil Towers two cubes	Uses several gestures with vocalizing Vocabulary of 5–10 words	Opens lid of a box to find objects Kiss on request

B

developmental milestones in different domains such as motor development, language development, and social and cognitive development in order to qualify for peer competition.

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Cross-References

- Brain Development
- Brain Imaging

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Brain Imaging

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Synonyms

Neuroimaging; Neuroradiology

Definitions

Brain imaging is the use of modern technology to study structural anatomy, physiology, and metabolism of brain.

Introduction

The evolution of modern brain imaging is synchronous with medical imaging with the discovery of X-ray in 1895 by German physicist Wilhelm Roentgen. It started with plain radiography of skull in different views and progressed with discovery of contrast agents and modification of X-ray technique for image acquisition. Radiographs taken after in vivo introduction of various contrast agents lead to development of pneumoencephalography, ventriculography, and

angiography. Modification of X-ray technique with continuous stream of X-rays collected on an input screen after passing target organ allowed real time visualization of moving anatomical structures like a video called *fluoroscopy*.

The introduction of *Ultrasound*, *Computed Tomography*, and *Magnetic Resonance Imaging* revolutionized medical imaging in terms of resolution, spatial, and three dimensional imaging. With digital revolution, images can be obtained quickly and downloaded onto a computer and multiple modification, subtraction, and 3D reconstruction can be carried out. Ultrasonography and Magnetic Resonance Imaging are unique in the sense that they do not expose patient to ionizing radiation like X-ray.

In addition to structural imaging of cranial cavity and brain, functional imaging of brain and study of cerebral metabolism is now possible with advancement of MRI techniques and Nuclear Medicine Imaging. Nuclear Medicine Imaging expose patients to radiation but unlike X-ray the source of radiation in these modalities are radioactive substances (radioisotopes/radionuclides).

History of Brain Imaging

Wilhelm Roentgen in 1895 used the X-rays to produce the first ever plain radiographic image of his wife's hand. Since then radiograph of every body part was taken including that of skull and cranial cavity. In brain imaging air was the first contrast media introduced in vivo. *Ventriculography* and *Pneumoencephalography* are the first contrast radiographic techniques using air discovered by American neurosurgeon Walter Dandy (1886–1946) in 1918. He introduced ventriculography by injecting air to the lateral ventricle of brain via a surgically created burr hole and then took radiographs of head. In Pneumoencephalography he introduced air into subarachnoid space around the brain via a lumbar drain placed invasively in the midline of lower back. Ventriculography and Pneumoencephalography are highly invasive diagnostic procedures and with availability of newer and safer imaging modalities these are no more used and are the things of past (Kornienko and Pronin 2009).

A more useful contrast radiography that revolutionized the diagnosis and therapeutic intervention of vascular brain diseases is *Cerebral Angiography* introduced by Portuguese neurologist Egas Moniz (1874–1955) in 1927. He used intra-arterial radiopaque dyes as contrast media to highlight brain vasculature in radiographs.

The invention of *Computed tomography (CT)* in 1970s was a milestone in medical imaging and provided instant detailed anatomic images of brain in multiple sections noninvasively and revolutionized not only emergency management of head injury and neurologic emergencies but also neuroscience research. Allan McLeod Cormack and Godfrey Newbold Hounsfield shared Nobel Prize for Physiology or Medicine in 1979 for the invention of Computed tomography.

Nuclear magnetic resonance imaging was used in 1940s to determine the structure of complex molecules. Its application in medical imaging was developed gradually with contributions by many researchers. Peter Mansfield and Paul Lauterbur received the Nobel Prize for Physiology or Medicine in 2003 for their contribution to MR imaging. Over the last 30 years MRI techniques have undergone tremendous refinements providing excellent internal architecture of brain and have dominated the field of functional imaging (Raichle 2009).

Concurrently with development of CT and MRI in the early 1980s, the development of safer bio-compatible radio-isotopes and gamma cameras leads to introduction of nuclear medicine imaging and allowed positron emission tomography (PET) and single photon emission computed tomography (SPECT) for functional imaging of the brain.

Conventional and Contrast Radiography

X-rays are a form of electromagnetic radiation and are generated from a cathode ray tube. As the X-rays pass through the body, they are differentially absorbed and attenuated by tissues depending on its density. After passing through the body it interacts with the photographic film. Simply said, X-rays blackens the photographic film.

In the body, air attenuates X-rays a little. So the body part containing air allows the X-rays to pass with little absorption and blackens the photo film maximally. The order of attenuation power in body tissues is as follows: **Bone** > **water** > **fat** > **Air**. Bone attenuates X-rays the most and after passing bony tissue, little X-ray is available to interact with photographic film. Hence, bone appears white in X-ray film (Armstrong and Wastie 2001).

As a result of revolution in digital technology, images can be loaded onto computer screens quickly and print outs can be taken (if needed) without need for darkroom procedure to develop photographic film.

Modifications to this X-ray technique and availability of intravascular contrast agents allow a continuous stream of X-rays to be digitally collected on a computer to allow real-time visualization of moving anatomical structures in fluoroscopy and angiography.

During angiography it is often difficult to visualize the contrast agent passing in the blood vessels with the overlying bony structures. That problem is circumvented with the advent of computers and softwares that digitally silence the signals from bony structures making excellent visualization of blood vessels as in digital subtraction angiography of cerebral vessels.

Ultrasonography

Ultrasound is a high frequency sound wave produced by piezoelectric materials. The sound waves travel through the body and bounce back from the internal organs. The piezoelectric material also receives the sound waves and the signals are interpreted by a computer to generate a real-time image on the display (Armstrong and Wastie 2001).

Though ultrasonography is the second most commonly performed imaging modality in medicine, its use in brain imaging is limited. It is used for brain imaging of infants to avoid radiation exposure and due to presence of fontanelles in infants it provide good acoustic windows for brain imaging. Another use of ultrasound techniques is Doppler ultrasound that enables

determination of blood flow, direction, and velocity within a vessel. So transcranial Doppler is frequently used in clinical practice and in research to study flow dynamics in major cerebral blood vessels.

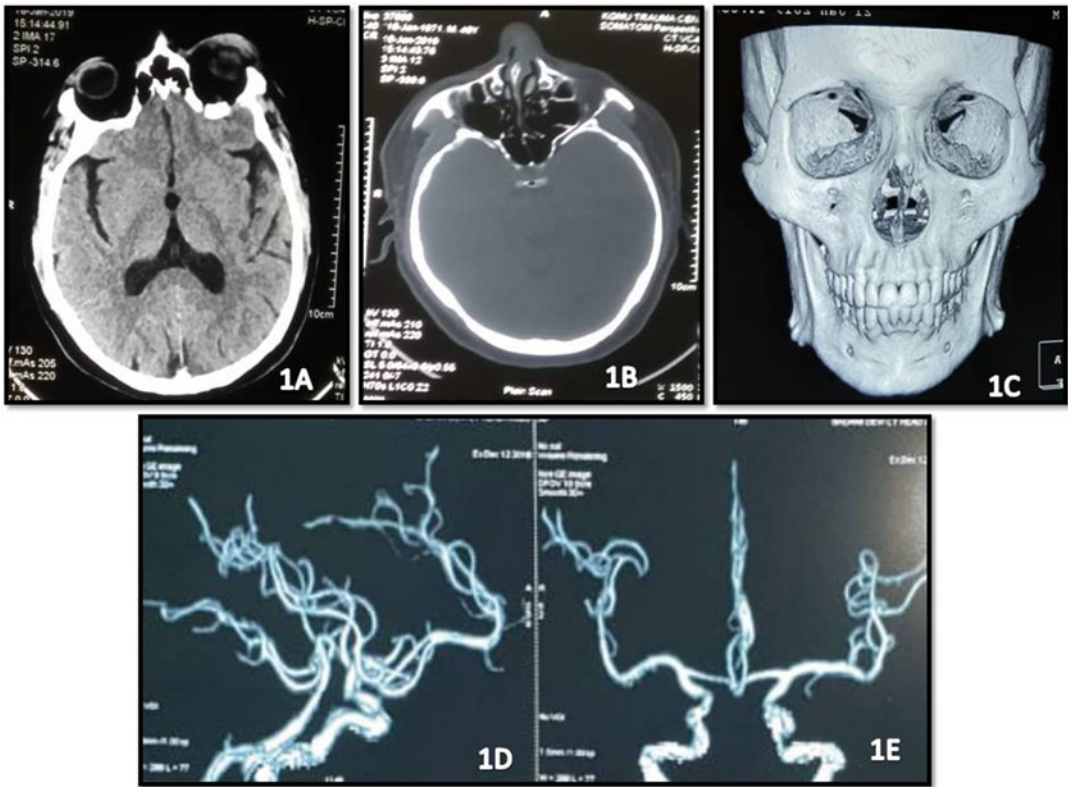
Computed Tomography (CT Scan)

CT scanner obtains a series of images of the body in the axial plane with a rotating gantry containing the X-ray tube and detectors, which revolve around the patient. The signals are digitally processed to construct a two-dimensional grey-scale cross sectional image of a body slice. As CT is based on attenuation principle of X-rays, the image follows the same order of attenuation power in body tissues. However, CT has a far higher contrast resolution allowing the assessment of tissues with minor differences in attenuation characteristics.

Modern multidetector CT machines allow movement of the patient's table along with patients body during the gantry revolution, thus speeding up the image acquisition process greatly reducing the scan time to seconds for a typical brain scan. It is also possible to reformat the image in different planes with help of computers. With thinner collimation, better spatial resolution, and improved computer technology, it is possible to reconstruct three-dimensional images of specific tissues like bone windows or 3D reconstruction of skullbase and facial skeleton. CT angiography of cerebral vessels and 3D rendering of vessels is also possible (Fig. 1).

Magnetic Resonance Imaging (MRI)

Magnetic resonance imaging is based on the spin properties of proton in the presence of a strong magnetic field. Water is present in all biological tissues and the protons within the hydrogen nuclei of water are regarded as magnetic dipoles randomly oriented in space. In the presence of a magnetic field as within a MRI scanner, the magnetic dipoles are aligned with the magnetic field. On applying a brief pulse of radio waves, the



Brain Imaging, Fig. 1 CT Scan of head and brain with different reconstructions. (a) shows axial scan of brain parenchyma. (b) is a axial bone window with brain parenchyma

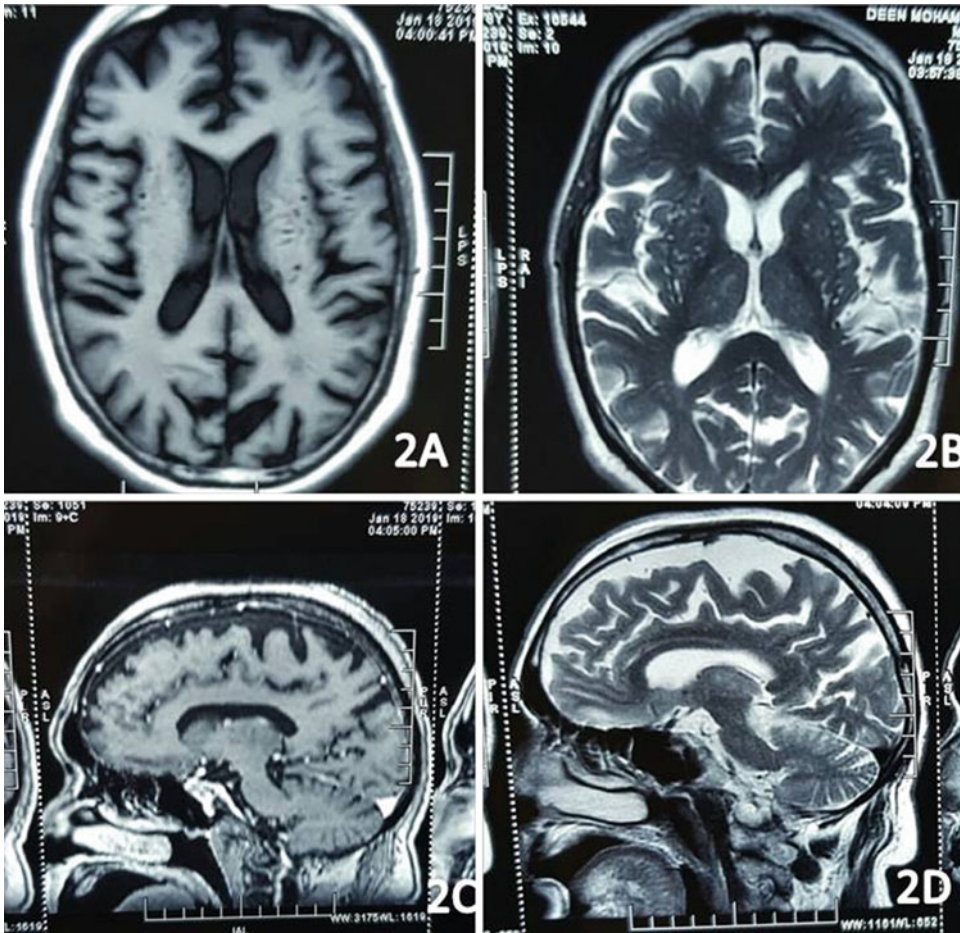
silenced. (c) represents a 3D reconstruction of facial skeleton. (d) and (e) are CT angiogram of cerebral blood vessels in lateral and antero-posterior views, respectively

dipoles absorb energy and deflected. When the radiofrequency pulse is removed, the dipoles emit small radio pulse signals and re-align themselves (relax). These signals are digitally processed and spatially encoded in a powerful computer to construct an image. The signals produced depend upon the properties of different tissues and the manner and rate of relaxation of the hydrogen nuclei. By altering the scanning parameters like the time between radiofrequency pulses (*Time to Repetition*) and the time between radiofrequency pulse and signal reception (*Time to Echo*), two types of relaxation can be measured: the T1 and T2 relaxation times. Accordingly T1-weighted images and T2-weighted images can be obtained (Adam et al. 2014).

The T1-weighted images of brain show fluid such as cerebrospinal fluid (CSF) as black (dark) and fat as white (bright). T2-weighted images of

brain show a bright signal from cerebrospinal fluid and a darker signal from fat. Gadolinium forms the basis of intravenous MRI contrast agent which reduces the T1 and T2 relaxation times resulting in a high signal on T1-weighted images. MRI also takes into account the physiologic and dynamic processes in the brain at molecular level such as Brownian movement of molecules and flow related diffusion effects to produce image contrast (Fig. 2).

The advantages of MR imaging include excellent spatial and contrast resolution of soft tissues, multiplanar imaging, and absence of ionizing radiation. Advanced MRI sequences can also be used to assess flow within vessels to produce angiograms of cerebral blood vessels. MRI imaging is advancing rapidly with availability of newer sequences so that each sequence can highlight a specific anatomic or functional area within brain



B

Brain Imaging, Fig. 2 T1 and T2 MRI sequences of brain. (a) and (b) represents T1 and T2 axial images of brain, respectively. (c) and (d) represents T1 and T2 sagittal images of brain, respectively

like nerve fiber tracts, CSF spaces, early ischemic changes, brain edema, and functional imaging associated with neural activity (Armstrong and Wastie 2001).

The main safety issues in MRI are presence of powerful magnetic field, possibility of contrast reaction, and long time taken for scanning. Strong magnetic field can make metallic objects to become dangerous projectiles and can dislodge MRI incompatible implants, devices, or foreign bodies. So MRI is contraindicated in persons with ocular metallic foreign bodies, cardiac pacemakers, cochlear implants, aneurysm clips, etc. MRI takes long time for image acquisition and patients require to be co-operative and still within the scanner. So

scanning is difficult for persons with pain or irritability or anxiety and for babies who may need general anesthesia. The advantages and disadvantages of MR imaging are summarized in Table 1.

Functional magnetic resonance imaging (fMRI) uses the different magnetic properties of oxygenated and deoxygenated hemoglobin to look for blood flow patterns in different areas of the brain in relation to performance of different thought, perception, or physical activity. With a specific action related to thinking, perception, speech, or motor activity, the area in the brain responsible for that function gets activated and blood flow to that area increases. The changes in flow patterns are detected in fMRI to reveal specific

Brain Imaging, Table 1 Pros and cons of commonly used modalities in brain imaging

	Conventional radiography	Ultrasound	CT Scan	MRI	Nuclear medicine
Pros	Easy to obtain	No radiation exposure	High spatial and tissue resolution	No radiation exposure	Functional imaging and study of cerebral metabolism possible
	Very low cost	Portable to bedside	Contrast resolution enhanced by intravenous contrast agents	Extremely good soft-tissue resolution	Imaging of the whole body possible
	Real time imaging possible with fluoroscopy	Very low cost	Very fast image acquisition	Contrast resolution enhanced by intravenous contrast agents	PET scanning is valuable in diagnosis of metastatic Brain tumors and study of metabolic disorders
		Good soft-tissue resolution	3-dimensional and multiplanar reconstruction possible: 3D image of skull and cranial cavity, CT angiography	Imaging technique of choice for brain pathologies like tumors, stroke, epilepsy.	
		Good for assessment of ventricle size in infants due to presence of fontanelles	Imaging of choice for head injury and neurologic emergencies	Functional imaging possible	
		Doppler studies allow study of cerebral blood flow dynamics		Safe in pregnancy	
Cons	Radiation exposure	Limited use in brain imaging	Very high radiation exposure	Contraindicated for ocular metallic foreign bodies, Pacemakers, Cochlear implants, aneurysm clips	High radiation exposure and needs handling of radio-isotopes
	No cross sectional/spatial image	High inter observer variability	Poor brain resolution compared to MRI	Claustrophobia	Poor contrast and spatial resolution
	Poor soft tissue resolution	Images cannot be reliably reviewed once imaging is over	Relatively contraindicated in pregnancy due to risk of radiation	Long time taken for image acquisition so patients requires to be still, making it difficult in children who may need anesthesia	Often nonspecific and confounding
				Expensive and availability is limited	

brain areas. The subjects are presented with visual, auditory, and sensory stimuli or asked to perform some simple motor tasks while within the MRI scanner. fMRI can reveal brain areas activated

with these processes. The major applications of fMRI other than research are localization of motor strips, localization of speech areas, and identification of memory laterality in the temporal lobe

for neurosurgical planning (Logothetis 2008). Due to absence of radiation, high spatial resolution, and moderately high temporal resolution, fMRI is replacing PET for functional brain imaging (Detre and Floyd 2001).

Nuclear Medicine Imaging

Nuclear medicine imaging provides not only anatomical image of the brain but also functional and metabolic information. For this the patient is given intravenously a special radiopharmaceutical containing a radioisotope that emits gamma rays. Depending on the absorption, distribution, and extent metabolism of the radiopharmaceutical in the body, differential amount of gamma rays are emitted by different body parts. Gamma rays are detected using a gamma camera and images are obtained. The most commonly used radiopharmaceutical contains technetium 99 m as Gamma rays emitter. It scans the whole body and used in detection of occult metastasis anywhere including skull and brain as metabolic hotspots because cancer tissues increasingly take up the radiopharmaceutical and emit maximum Gamma rays (Elgazzar 2011).

Two extensions of Nuclear medicine imaging which are more relevant for both anatomic and functional imaging of brain are *positron emission tomography* (PET) and *single-photon emission computed tomography* (SPECT).

Positron emission tomography (PET) is an imaging technique which detects positron emitted from radionuclides. A positron is an antielectron, which is positively charged. The most commonly used PET radionuclide is 18-fluorodeoxyglucose (FDG) with fluorine 18 as positron emitter. Tissues that are actively metabolizing glucose take up this compound and show up as a hot spot. PET is extremely useful for functional brain imaging. On performance of different thought, perception or physical activity specific brain areas are metabolically activated and utilize more glucose so that the areas can be identified. Instead of glucose 18-fluorine can be tagged to other ligands to map different aspects of neurotransmitter activity and to study different metabolic diseases of brain. For

example, 18-fluoro-6-L-dopa when injected to body, distribution of dopaminergic neurons in brain can be studied. PET is useful to identify primary cancer site when patient presents with a brain metastasis with unknown primary. It is also used for the assessment of response to treatment and recurrence of tumor.

SPECT uses gamma ray emitting radionuclides which is rapidly taken up by the brain. This involves cerebral blood flow imaging using a “SPECT agent” (e.g., Technetium-99 m hexamethylpropyleneamine oxime) which is rapidly uptaken by brain without redistribution. A common use of SPECT is to localize the site of seizure onset when anatomic imaging is nondiagnostic. During seizure SPECT will identify focal hyperperfusion and in the interval between seizures it will identify focal hypoperfusion in the area of brain responsible for seizure onset.

Magnetoencephalogram

Magnetoencephalogram (MEG) measures magnetic fields of brain. Magnetic field is produced when electrical current flows inside neurons of cortical gray matter of brain. Magnetic field is perpendicular to the direction of intracellular currents in neurons. Whereas electroencephalogram (EEG) measures the electrical current via scalp electrodes, magnetoencephalogram (MEG) measures magnetic fields of brain by extremely sensitive devices. For Magnetoencephalogram, subjects are not placed inside a magnetic field as in MRI. Rather magnetic field detectors are placed around patients head to measure the magnetic fields produced by the brain. Magnetoencephalography is used for identifying the origin of cortical seizure (epileptogenic focus) and in presurgical mapping of eloquent cortex. MEG directly measures the electrophysiological changes in brain. So it has higher temporal resolution compared to fMRI. fMRI detects changes in regional blood flow and oxygen use by hemoglobin to assess functional activity of brain which is slower than electromagnetic activity detected by MEG.

Advantages and Disadvantages of Different Brain Imaging Modalities

The CT scan and MRI constitutes the bulk of brain imaging ordered in hospitals now a days. The advantages and disadvantages of commonly used modalities in brain imaging are summarized in Table 1.

Conclusion

Both structural and functional imaging of brain is now possible with an array of imaging modalities. Though CT and MR imaging constitute the major bulk of brain imaging modalities presently performed in a clinical setup, other techniques have their due share in medicine and research. Conventional radiography, CT scan, and nuclear medicine imaging expose patients to ionizing radiation in varying proportions and must be performed appropriately. The risk of such examinations has to be weighed against the benefit to the patient in terms of increased diagnostic yield and techniques that do not use ionizing radiation, such as ultrasound and MRI, should be carefully considered as alternatives, particularly in children and pregnant women (Royal College of Radiologists 2017).

Cross-References

► [fMRI](#)

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Brain Lesion

► [Specific Brain Damage](#)

Brain Lesion Studies

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Synonyms

[Brain mapping studies](#); [Brain structure-function mapping](#)

Definition

Studies of brain anatomical-physiological relationships that focus on investigating the physical or cognitive effects of clearly delineated lesions, i.e., damage to tissue from disease, injury, or malformation.

Introduction

Some of the earliest brain lesion studies were done in subjects with a specific impairment, usually of language, and were mapped to the relevant region of damage via postmortem studies. Modern brain lesion studies, which investigate a range of functional impairments, including language, motor, and cognition, usually rely on in vivo

neuroimaging to detect, quantify, and map brain lesions to their associated impairments.

Historical Brain Lesion Studies

One of the first examples of a brain lesion study was in the famous patient nicknamed “Tan,” as this was the only word this patient was able to say. This patient, Louis Victor Leborgne, suffered from epilepsy and, as it was discovered after his death via an autopsy performed by Paul Broca in 1861, a lesion in the posterior inferior frontal gyrus. This area roughly corresponds to Brodmann’s areas 44 and 45 and is also known as Broca’s area. This is one of the first examples of mapping a highly circumscribed lesion location in the brain to a very specific function, i.e., language production. Others were to follow. In 1874, Karl Wernicke identified regions at the temporal and parietal lobe boundary that, when lesioned, would result in the patient having fluent but disordered speech. One other famous example of lesion studies is the famous case of Henry Molaison, who suffered from epilepsy and had surgical resection of the anterior two thirds of his hippocampi, parahippocampal cortices, entorhinal cortices, puriform cortices, and amygdala (Scoville and Milner 1957). His case played an important role in the understanding of brain anatomy and the formation of memories, and his brain anatomy was made publicly available after his death in 2008 (Annese et al. 2014).

Modern Brain Lesion Studies

Modern brain lesion studies focus on relating quantitative neuroimaging metrics to related impairments. One main analysis method is that of voxel-lesion symptom mapping (VLSM) that relates brain anatomical lesions to specific physical or cognitive impairment on a voxel-wise basis (Bates et al. 2003). Recent advances in functional MRI and diffusion MRI, which allow quantification of the anatomical and physiological connections in the brain, have been used to

investigate the network effects of lesions. Some recent examples are those that quantified the functional (Boes et al. 2015; Sutterer et al. 2016) and structural connections (Kuceyeski et al. 2015, 2016) that were disrupted due to a particular lesion, which then allowed for further insight into the integrated, network effects of a primary lesion area.

Simulated Brain Lesions

Noninvasive brain stimulation techniques, e.g., transcranial magnetic stimulation (TMS), allow for modulation of neuronal activation in highly circumscribed areas of the cortex that is transient in nature. Recent studies using repetitive TMS investigate the use of so-called transient “virtual” lesions in the brains of healthy controls to map particular area(s) and networks in the brain to cognitive or physical impairments or enhancements (Pascual-Leone 1999). For example, one recent study showed enhanced visual-spatial attention resulting from a virtual lesion in the parietal cortex (Hilgetag et al. 2001), while another showed deficits in complex motor sequence processing after virtual lesions of Brodmann’s area 45 (Clerget et al. 2013).

Conclusion

Brain lesion studies have historically and in modern times allowed for a clearer understanding of the relationship between anatomical regions of the brain and associated functions. Modern neuroimaging and simulated lesion studies are being used to not only understand the effect of the primary area of the lesion but also the effect of the lesion on the functional and structural network connections in the brain.

Cross-References

- [Brain Imaging](#)
- [Specific Brain Damage](#)
- [Split-Brain Patients](#)

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Brain Mapping Studies

► Brain Lesion Studies

Brain Metabolic Costs

► Energy Consumption

Brain Size

► Brain Size and Intelligence

► Cognitive Buffer Hypothesis, The

Brain Size and Intelligence

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Synonyms

Behavioral flexibility; Brain size; Complexity; Intelligence

Definition

The intelligence of an animal is related to the external and intrinsic properties of the brain which determine its functions.

Introduction

To the common observer, it would seem obvious that animals differ in their intelligence and that human intelligence, at least from our own biased perspective, is far superior to that of other animals. But what exactly is animal intelligence and how is it linked to the parameters of the brain?

Knowledge on animal intelligence is not only of interest to comparative ecologists, evolutionary psychologists, and neuroscientists, but it is also important to the general public as this helps shape public perception regarding welfare, care, and use of animals.

What Is Animal Intelligence?

One of the major obstacles in comparing intelligence across species remains the acceptance of a universally accepted definition of intelligence and how to measure it. In humans, intelligence is usually defined as: “... *a general capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It is not merely book learning, a narrow academic skill, or test taking smarts. Rather, it reflects a broader and deeper capability for comprehending our surroundings- ‘catching on’, ‘making sense’ of things, or ‘figuring out’ what to do*” (Gottfredson 1997). In other words, human intelligence is the sum effect of our mental capacities which includes our abilities to communicate, think abstractly, and reason. Human intelligence is thus readily assessed using established intelligence tests (Intelligence Quotients, IQ tests) which, although challenged on the basis of their application across cultures, have proven to be fairly robust instruments for assessing verbal, numerical, or visual-spatial reasoning in humans. However, this same definition of intelligence cannot be directly applied to the study of nonhuman animals and thus a broader definition of animal intelligence is defined as the ability of an animal to be able to solve problems occurring in their natural environments (i.e., the degree of behavioral flexibility) (Roth and Dicke 2005). Examples of this include naturally occurring challengers such as locating food sources, intraspecific communication and social interactions with conspecifics, as well as spatial orientation (Dicke and Roth 2016). Using behavioral flexibility as the central measure for comparison, cross-species investigations have revealed that the evolution of intelligence is not unique to

humans but has evolved independently in several groups of animals, including certain insect, mollusk, bird, and mammalian species (Butler and Hodos 2005).

Absolute and Relative Brain Size

When comparing brains across species it is tempting to think of large brained animals as being more intelligent than smaller brained species and that intelligence is simply a result of absolute differences in brain size. Not surprisingly, when one compares absolute brain size across mammals, the human brain is far surpassed by that of large bodied terrestrial and aquatic mammals like the elephant and the blue whale. For example, the human brain weighs approximately 1350 grams while the elephant brain weighs more than 5 kg (Maseko et al. 2011) and that of the blue whale (the largest aquatic mammal) weighs in excess of 7 kg. At face value, this would lead one to believe that elephants and whales are far superior to humans in intelligence, but this conclusion is unlikely given that whales have fairly simple neocortices (Striedter 2005), and that there exists no behavioral data to support this argument. Similarly, larger bodied artiodactyls (e.g., ox, giraffe, camel) outstrip many nonhuman primates in terms of absolute brain size, even though monkeys and apes in particular are well known for their complex behavioral repertoire, cognition, and flexibility (Jolly 1966). These observations point to the fact that simple comparisons of absolute brain size across species are rather misleading and that absolute brain size does not align with our observations of animal intelligence across species.

Another approach which has been used to compare brains across species has been to evaluate relative brain size (i.e., relative to body size) using either brain:body mass ratios or allometric plots of brain size against body size. When comparing brain:body mass ratios, the human brain is calculated as occupying 2% of total body mass, whereas the fraction of body mass dedicated to brain mass in the blue whale is only 0.01% of its total body mass (Striedter 2005). While

these observations align with our expectations of greater intelligence in humans relative to whales, comparisons of small bodied species such as the shrew (van Dongen 1998) and harvest mouse (van Shaik 2006) suggest otherwise as these species have brain:body mass ratios larger than humans (between 4% and 10% of their total body mass). To address this problem, comparative biologists have also compared species brain:body mass data using allometry to evaluate proportional changes in brain size across species. This approach allows one to remove the influence of body size in species comparisons and identify species which have brains that are larger (or smaller) than expected for their body size. When brain mass is plotted against body mass for all the major vertebrate groups (i.e., mammals, birds, reptiles, amphibians, and fish), the distribution of data points aligns relatively well with the behavioral complexity observed across species. Mammals tend to have larger relative brain sizes than birds, while reptiles and amphibians have larger brain sizes than most fish but smaller brain sizes than birds (Jerison 1973). Humans also have relative brain sizes which far exceed that of other animals (Manger et al. 2012).

Brain Complexity and Intelligence

While the use of allometry has seemingly reaffirmed our expectations of how differences in brain size align with comparisons of animal intelligence it is important to keep in mind that brain size and brain complexity are not one in the same thing and may change independently of one another. For instance, a species could increase its cognitive output (i.e., intelligence) relative to that of an ancestral species by changing the complexity of the brain while still maintaining (or even reducing) brain size in the descendent species. To borrow an example from the technological industry, the transition from bulky early cellular phones to that of present day smart phones was facilitated by increasing the processing power of the individual components and reducing their overall size. In a similar way, changes in brain complexity might

constitute a myriad of changes in the intrinsic properties of the brain (e.g., changes in the size of its subcomponents, changes in the number or diversity of its cellular components, changes in the degree of compartmentalization, changes in the number or diversity of synaptic or neurotransmitter components, etc.).

Some of the most striking observations of neural complexity have been found within the nervous systems of small brained invertebrates like the arthropods. For instance, while insects are endowed with a more distributed, simple nervous system, they also possess a component of the nervous system known as the mushroom bodies which underlie the cognitive and social behavior of insects (Heisenberg 2003; Perez-Orive et al. 2002; Farris 2008). Comparative studies have revealed that the mushroom bodies have undergone changes in complexity in several different insects including the Lepidoptera (butterflies), Blattoidea (cockroaches), and Hymenoptera (i.e., bees and wasps). For example, in bees the mushroom bodies are relatively enlarged (Strausfeld 2012) and are composed of calyces which differ from the smooth mushroom body surface observed in other insects and are convoluted, a pattern similar to what has happened to the increased folding of the mammalian cortical surface (Farris et al. 2004). The possession of complex mushroom bodies in insects has been shown to be associated with a high degree of behavioral flexibility, allowing insects like the honeybee to do complex navigational feats as well as elaborate social, communicative, and learning behavior (De Marco and Menzel 2005).

Further examples of changes in nervous system complexity and associated changes in intelligence are also seen within the molluscs. While most molluscs have fairly simple nervous systems, the cephalopods are an exception having developed large, complex brains and an intriguing set of complex behaviors (Moroz 2009). For example, the nervous system of the octopus is the largest among all the invertebrates and is compartmentalized into 16 lobes (Nixon and Young 2003; Roth 2015) with the vertical lobe being identified as the major control center for complex

behavior (Hochner et al. 2006). The complexity of the vertical lobe in the octopus aligns well with the range of complex behavior observed for this animal, with octopi reported to have a capacity for observational learning (Fiorito and Scotto 1992). While fish intelligence is rarely considered a point of discussion, perhaps because fish remain one of the major food sources for human consumption (Brown 2015), there are certain teleost fish which demonstrate cognitive abilities which cause us to question our a priori assertions of fish intelligence. For instance, cichlids are known to use both visual and auditory cues in the context of caring for the brood, as well as complex appeasement behavior when interacting with individuals of a higher social rank (Bshary et al. 2002). This data seems to warrant further study of the cichlid nervous system and the underlying brain regions that might mediate this complex behavior. Comparative studies of the teleost nervous system have revealed evidence that brain region size can vary in a mosaic fashion. For instance, in comparison to other closely related fish, the cyprinids (goldfish and carp) have large vagal lobes which are used for taste and food processing while catfish have evolved a unique lobe for taking in electro-sensory information from their barbels (Striedter 2005).

While the avian brain is markedly different in structure from that of mammals (most notably the absence of the six-layered lamina arrangement and a clear white matter-grey matter distinction), the expansion of the telencephalon and pallium is also believed to underlie complex behavior within birds, much like it functions for mammals (Striedter 2005). A subregion of the avian pallium is thought to be functionally equivalent to the mammalian dorsolateral prefrontal cortex (Gunturkun 2005), which in humans is involved in executive functions such as planning, cognitive flexibility, and abstract reasoning. Observations of complex behaviors in certain birds (parrots and crows) have added credence to this idea. For example, several studies have demonstrated the remarkable abilities of crows to make and use tools (Hunt et al. 2007), while magpies are also known to recognize themselves

in mirrors (Prior et al. 2008), an observation which had previously only been observed in great apes, elephants, and dolphins (although see Manger 2013 for a criticism of this analysis). In primates, as with other mammals, intelligence has been closely linked with the expansion of the prefrontal cortex (Duncan et al. 2000). In this regard, nonhuman primates are known to possess a number of complex abilities including tool usage (Kendal et al. 2010), imitation (Call et al. 2004), mirror self-recognition (Gallup 1970), and theory of mind (Povinelli et al. 1990; Tomasello et al. 2003) all of which highlight the existence of high intelligence despite brain sizes much reduced in size in comparison to that of humans (e.g., the chimpanzee brain weighs about 350 grams, four times smaller than that of the human).

These observations highlight the cooccurrence of biological complexity and intelligence in the brains of various animals and emphasize that the evolution of intelligence is not unique to humans. The exact selection pressures which favored the coevolution of complexity and intelligence in animals remain a source of ongoing debate. Among others, the importance of sociality and social learning as a driving force for overall intelligence has at least helped to explain the cooccurrence of brain complexity and intelligence in social species like primates (Whiten and van Schaik 2007; van Schaik and Burkart 2011).

Conclusion

The study of animal intelligence in a comparative context has revealed that brain size as well as brain complexity are two important considerations when trying to understand the underlying neural correlates of intelligence and the evolutionary factors which facilitated the emergence of complex behavior.

Cross-References

► [Relative Brain Size, Encephalization Quotient](#)

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Brain Size Growth in Humans and Nonhuman Primates

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Synonyms

Big brain evolution; Human brain size evolution; Primate brain size evolution

Definition

Increase in brain size found in humans and other primates over evolutionary time.

Introduction

Primates' brains are considerably larger than most other species. Big brains are uncommon because they require a large amount of energy. Possibly, because of this constraint, brain size is related to the diet of the species (Allman 1999). There is a large developmental period for human infants in order to accommodate brain size growth. The social nature of primates has led to the suggestion that a potential reason for this size increase is the necessity for social intelligence (Humphrey 1976).

Brain Size Differences

Brain size is highly correlated with body size. As body size increases, the brain increases exponentially at a rate of around 0.74 for non-primates and 0.75 for primates. Although this rate is about the same, primates have brains around 2.3 times the size of non-primates (Allman 1999). Brain size is commonly compared across species using the encephalization quotient (EQ), which is the ratio of actual brain weight to expected brain weight. Humans have an EQ of about 6.3 (Jerison 1973). It is possible to trace the change of brain size in

hominids over evolutionary time (Tobias 1987). The early hominids, australopithecines, had brains only slightly larger than the chimpanzee. If the EQ of ancestral hominin species is expressed as a percentage to that of *Homo sapiens*, then *Australopithecus afarensis* had an EQ of 41% of *Homo sapiens*, *Homo habilis* 53%, and *Homo erectus* 72%.

Brain Development

The growth of primate brains has led to an increase in cranial size. Because of bipedal locomotion, there is an evolutionary trade-off between a mother's hip size and birth size in human infants. It is suggested that humans have adapted to this restraint by continuing brain development after birth. It is estimated that approximately half of all synaptic connections are made after birth (Changeux 2004). At the time of birth, 40,000 connections are made per second (Bourgeois 1997). This dendritic growth, synapse formation, and myelination require a large amount of energy. Two-thirds of the resting metabolism in newborn babies is allocated for brain growth and functioning, which is half of the energy used by chimpanzees (Bogin 2000). Because of this extended period of development, human infants require much more parental care after birth than do other primates.

Brain Size and Diet

When the brain size among primates is plotted on a linear regression as a function of body size, the variation can be accounted for by diet (Allman 1999). Fruit-eating primates have been found to have larger brains than leaf-eating primates. This trend has also been found in other species such as bats and parrots. It is theorized that because there is an energy trade-off between the digestive organs and the brain, the easy digestibility of fruit enables increased energy flow to the brain. Fruits have a higher energy content than leaves but are more difficult to obtain. Spread over large areas, gathering fruit requires a larger amount of

spatial navigation than gathering leaves and a greater amount of temporal judgment because fruits are harvested at different times of the year. Limited availability may also result in an intense competition with other animals (Allman 1999). Differentiating between types of fruits and identifying ripeness require a color vision system, which has been shown to relate to larger neocortex sizes (Barton 1998).

Brain Size and Intelligence

There is a correlation between brain size and behavioral capacity, so it was first proposed that the EQ was a measure of intelligence (Lashley 1949). Measuring the relationship between brain size and intelligence led to the discovery that it is possible to predict brain density and the relative size of individual structures from overall brain size (Jerison 1973). The additive hypothesis theorizes that because the brain is shaped as a result of different selection pressures, some areas develop specialized neural systems over evolutionary time. These specific areas increase in size, rather than the entire brain increasing as a whole. This is supported by the rate of brain size increase across species (Jerison 1973). The evolution of the complex visual system characteristic of primates is suggested to be a large contributor to this size increase.

Intelligence is often defined as a creative behavior modification in response to the external world (Humphrey 1976). Primates have demonstrated great intellectual abilities in laboratory settings, but their environment rarely necessitates such abilities. The social situation found in primates allows for information transfer between individuals, and much of daily survival relies on subsistence technology rather than individual creativity. From this, it seems that primates have greater intelligence than what is needed to survive. The social intelligence hypothesis posits that the high intellect of primates is necessary for social processes (Humphrey 1976). Social interaction requires an intricate analysis of behavior. Anticipating the actions of others, determining appropriate responses, weighing rewards and

consequences of actions, and deciphering social cues are all necessary skills. Social interaction is viewed as a subjective transaction. Primates who live in larger groups have a larger neocortex size compared to the rest of the brain (Dunbar 2004). However, not all species who live in larger social groups have a larger brain compared to other species.

Conclusion

Compared to most animals, primates have an exceedingly large and costly brain. They make up for this energy requirement by diet changes, such as the consumption of fruit and meat (Allman 1999). Human birth occurs earlier development because the expansion of skull sizes can cause birth complications. This results in an increased duration of infant development and parental care. The most prominent explanation for this increase in brain size is the social intelligence hypothesis, which theorizes that social cooperation requires complex cognition (Humphrey 1976).

Cross-References

- [Brain at Birth](#)
- [Brain Development](#)
- [Brain Evolution Resulting from Cooking](#)
- [Brain Size and Intelligence](#)
- [Social Intelligence Hypothesis, The](#)

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Brain Structure-Function Mapping

► Brain Lesion Studies

Breakup

► Relationship Dissolution

Breast Feeding

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Synonyms

Lactation; Nursing

Definition

Feeding milk to offspring from mother's breast

Introduction

An important distinction of mammals from other animal groups is their ability to produce milk to feed their offspring from the mammary gland. The word mammal is derived from the Latin word “mammilla,” which translates to breast. One would have assumed that Carolus Linnaeus, the father of taxonomy who named the different classes of animals, would have chosen a name for mammals that was inclusive of both the males and females. Perhaps something to do with the other distinguishing features of mammals such as hair and sweat glands. However, Carolus Linnaeus allegedly chose the word mammal to depict the importance of offspring feeding from their own mothers' milk (Schiebinger 1993). Although other animals can also feed their offspring through body secretions (e.g., crop milk in various bird species; Eraud et al. 2008) they do not contain nearly the same rich and varied nutrients as mammalian milk produced in glands that are as specialized for feeding offspring (McClellan et al. 2008).

Evolution of Breastfeeding

Indeed, breastfeeding is arguably one of the most important developments of the mammalian species. Breastfeeding may have evolved approximately 200 million years ago (mya) even before other distinct mammalian characteristics such as hair/fur (Sanchez et al. 2013). There are about 4000 species of mammals today that inhabit a wide range of environments from the Antarctic seas to Australian deserts (McClellan et al. 2008; Pond 1984). One important reason that mammals are able to survive in diverse environments is their ability to lactate which helps feed their offspring and keep their offspring alive. This investment in offspring represents a divergent evolutionary step towards a slower life history strategy for mammals than for virtually all other animals (Hrady 1999). For example, female brown bears (*Ursus arctos*) can lactate even while estivating (similar to hibernating) for an entire season. Similarly, female baleen whales (*Balaena*

australis) can be starved for many months and still have the ability to lactate. These patterns across mammals suggest that breastfeeding likely initially evolved as mechanism for parents to feed offspring when food sources were scarce or varied (Pond 1997; Sellen 2007). Not to mention it was also a strategic way to utilize the body fat and nutrients already stored in mothers (Sellen 2007). Milk allows for infants to consume nutrients from the environment that have already been processed (i.e., obtained and safely digested) by their mothers (Boyd 1998). Thus lactation represents a very focused, yet malleable, form of parental investment that likely offered mammals a competitive advantage over other animals.

Breastmilk is made from important nutrients in the mother's bloodstream and body fat storage and consists of various nutrients including protein, fat, and sugar. These nutrients are essential for the growth and development of the infant (Rollins et al. 2016). More specifically, contents in mammalian milk help to provide the nutrients necessary for development of infants' immune system. Infants' immune systems across different mammals are significantly underdeveloped at birth and therefore require an extensive amount of metabolic energy to develop and maintain (Goldman 2012). By receiving these resources from mothers' milk the infant can direct other nutrients and energy toward the growth of important body parts, such as the heart, brain, and lungs.

What's more, lactation and the contents in breastmilk change as the infants' immune system develops. For example, human breastmilk starts off as colostrum, which is a very concentrated milk with many nutrients while still being easily digestible for infants (Ballard and Morrow 2013). Colostrum plays an important role in forming a protective layer in infants' gastrointestinal tracts and protecting infants from foreign pathogens. Colostrum then turns into more mature milk called foremilk (approximately 3–4 days after the birth of the infant) which is relatively less concentrated and contains various proteins and vitamins essential for the continued growth of the infant. Finally, foremilk turns into hindmilk during the course of feeding, increasing the caloric richness of the milk (Ballard and Morrow

2013). Such changes in breastmilk over the course of feeding and/or with the development of the infant are also found in other mammals (e.g., Hinde et al. 2009). At the more extreme end, mothers can terminate this costly investment in offspring by either refusing to nurse, or stopping production of milk (Hrdy 1999). Thus there is a great deal of flexibility in nursing that can allow mothers to tailor their parental investment according to individual and environmental circumstances.

Another adaptive factor that likely contributed to the use of breastmilk is the ability to protect the infant from pathogens. By triggering various biochemical reactions, the enzymes and hormones in breastmilk help newborns transition from a life in the uterus, which is a relatively sterile environment, to life in the outside world, which consists of various pathogens and bacteria (Colen and Ramey 2014). For example, enzymes in breastmilk, such as lysozyme, help destroy bacteria in the infant's digestive track (Ballard and Morrow 2013). Additionally, leukocytes (a type of white blood cell) in breastmilk directly help fight infections, which allows the infant to become immune to substances in the environment without developing any infections or inflammations (Ballard and Morrow 2013). Thus breastmilk may play a pivotal role in the success of mammalian immune systems, effectively giving them the capacity for the biochemical and/or epigenetic expression of immune responses from one generation to the next.

Additional to the nutritional and protective benefits of breastmilk, breastfeeding may have also helped offspring to be dependent on their mothers (Pond 1997). This was presumably essential for parents to ensure that infants receive nourishment regardless of the resources in the environment as well as the indirect benefit of ensuring the infant is close by in order to protect the infant. These factors would have been important to ensure infants' survival and consequently help to increase parents' evolutionary fitness. Lactation was also likely instrumental in spacing births of subsequent offspring, giving mothers yet another means with which to modulate their reproductive investment (Sellen 2007). Although

the actual mechanism of how this works is not yet completely understood, the frequency of infants' suckling is shown to be a key component in delaying mothers' sexual cycle (Stewart 1988). This would have been an important adaptation especially in species where infants are developmentally delayed (e.g., slow to acquire motor skills) and require high levels of parental investment, as is the case in primates, so that parents' investment is not spread thin by feeding and investing in several highly dependent offspring.

Variation of Breastfeeding in Animals

The contents of breastmilk across mammals share many similar components. For example, most mammalian milk share structural similarities and similar sequences of antibodies (Acharya et al. 1994; see above). Additionally, most mammals show compensatory milk growth in which animals can increase their milk supply when more than one infant is nursing at the same time as well as make metabolic adaptations during lactation (McClellan et al. 2008; Sellen 2007). Closely related species therefore produce similar breastmilk contents likely because they evolved in similar environments within similar time frames. For example, components of milk that contribute to the development of the immune system in human infants is most similar to a closely related primate, chimpanzees (*Pan troglodytes*; Goldman et al. 1998). Additionally, an antigen-binding component in human milk that protects against the α -galactosyl epitope is also found in apes and Old World monkeys but not in New World monkeys and other types of mammals, which are more distant relatives of humans compared to apes and Old World monkeys (Goldman et al. 1998).

However, there are specific components in the milk within each mammalian species that differ from the other species (Goldman 2012). Various factors may have influenced these species-specific differences. One such factor may be the result of differences in the duration of lactation. For example, baleen whales lactate for five to seven months (during which the mothers usually fast) and

produce milk with high energy outputs. In contrast, dolphins (*Tursiops truncatus*) lactate for one to 3 years (during which the mothers frequently feed) and produce milk with relatively less energy output (Ofstedal 1997). Baleen whales therefore have relatively less time to produce milk so it is beneficial for them to make less milk but compensate for the low quantity with high energy milk, whereas dolphins have more time to produce more milk and therefore would not need to produce milk with very high energy. This balance of the caloric content versus nursing duration appears to allow mammals to tailor their maternal investment to species, or even individual-specific, feeding and life strategies (Boyd 1998). For example, due to the threat of unstable pack ice, hooded seals (*Cystophora cristata*) nurse their infant pups for a remarkably brief duration of only 4 days (Boyd 1998)!

Another reason may be differences in the development of each species. For example, human and cow (*Bos taurus*) milk differ drastically in the number of antibodies such as immunoglobulin G (IgG; protects against bacterial and viral infections; Yolken et al. 1992). Newborn calves naturally have less IgGs levels but receive IgGs from the mother's colostrum (the first phase of breastmilk; see above) which consists of high levels of IgGs. Newborn calves therefore attain adequate amount of IgGs after the first nursing. On the other hand, human newborns also do not produce IgG but they receive it quite immediately from mothers through the placenta at birth. As a result, human milk did not require to make high levels of IgGs as seen in cow milk. Another example is that human newborns can survive without breastmilk for a few days with other supplements (although this is not recommended; World Health Organization 2009) but this is not the case for piglets (*Sus scrofa domestica*). This is likely because human infants have relatively higher levels of fat (about 10%) compared to piglets (about 2%) which allows human infants to sustain themselves for short periods of time (McClellan et al. 2008).

Finally, breastmilk content may also be influenced by the type of environment that the animal inhabits because milk may be able to

compensate for the lack of nutrients in the environment. For example, one experimental study showed that cows that were given grain supplements had lower milk fat concentration compared to cows that were only pasture fed (Reis and Combs 2000). This is likely because the former group of cows did not need to expend bodily resources to make high fat content milk.

Primate Breastfeeding

Unlike other mammals, primates do not seem to fit the earlier discussed breastfeeding patterns such as producing volume and quality of milk relative to body size or exposure to pathogens (Ofstedal 1984). Unlike other mammals in which milk content is analogous to body size, the milk composition in primates is relatively lower in nutrients (fat, protein, and energy) but high in lactose relative to their body size. This may be because primates' breastmilk have evolved with relatively lower reproductive rates and slower life history strategies (compared to their relative body size e.g., Hinde 2009). This is a parsimonious explanation because the relatively lower protein concentration in primate milk fits with the slow growth rate of primate infants (Sellen 2007). Additionally, the low fat concentration found in primate milk likely coevolved with continuous infant carrying whereas the high levels of lactose may have coevolved with faster postnatal brain growth in primate infants (Sellen 2007). Furthermore, there are individual variations in milk composition between mothers based on number of offspring they have had as well as the sex of their offspring (Hinde 2009; Hinde et al. 2009).

Another important exception to primates is that breastfeeding is not as "automatic" as it is with other mammals (Volk 2009). Despite primate infants' natural suckling reflex similar to other mammals, female primates require a period of learning in order to be able to successfully nurse their infants. Studies show that monkeys are less likely to be able to successfully nurse if they have not observed another monkey nurse or if they have not nursed before themselves (Volk 2009). Additionally, multiparous primate mothers

(mothers who have previously had other offspring) are more successful at nursing compared to primiparas mothers (first time mothers; Volk 2009). Researchers have suggested that this dependence on learning to breastfeed may be associated with primate species' level of intelligence (Volk 2009). For example, great apes are more intelligent compared to other primates and therefore require relatively more learning in order to successfully breastfeed. Hrdy (1999) has proposed that this learning may be a trade-off between the reliability of innate behaviors and the flexible power of a learning brain.

How Is Human Breastfeeding Different?

Humans are the primate species that is both least dependent on instinctive behavior patterns and least successful at automatically achieving nursing success (Volk 2009). Although infants possess an instinctive rooting reflex associated with nursing, it is clear that other behavioral aspects of breast feeding are not innate for either the mother or the infant. A review of captive great ape nursing showed technique-based failure rates of 18%, whereas human mothers in Western cultures reported failure rates of up to 33% due to technique problems (Volk 2009, 2002). Thus, this fundamental feature of mammalian life does not appear to be either automatic or instinctive for many human mother-infant pairs. Some of the difficulties in initiating and continuing breastfeed that are reported by women include: difficulties initiating and maintaining an appropriate "latch" (i.e., mouth to nipple contact), an inadequate volume of milk expressed by the breast, and/or cracked and/or bleeding nipples (Volk 2009).

This is perplexing when put into the context of how important successful breastfeeding would have been for the survival of human species. Throughout human history our very diverse palates and environmental choices likely meant that infants regularly encountered changing and limited dietary sources. Therefore, lactation and ability to breastfeed would have been crucial for helping infant humans to survive. Even as humans began industrialization and agriculture to serve as

their food supply the associated new pathogens and bacteria they would have introduced during such developments would have made the immunological benefits of human breastmilk very important for infant survival. Infants who are breastfed also appear to enjoy later advantages in health and mental acuity (Rollins et al. 2016). What's more, women appear to be adapted to breastfeed (or at least receive benefits from it). Women who breastfeed for 12 months or longer have their risk of ovarian and breast cancers, as well as Type 2 diabetes, reduced by almost a third (Chowdhury et al. 2015). Thus (as in the animal literature mentioned above), breastfeeding appears to offer human mothers and infants significant survival advantages, making it a prime candidate for strong evolutionary selective pressure.

So why are rates of breastfeeding so unsuccessful for women and how did women overcome this important challenge to infant and mother survival? Volk (2009) suggests three reasons. First, an emphasis on learned versus instinctive behavior may put humans at a relative disadvantage. A second related reason may be that due to infants' delay in motor development compared to other primates, they require mothers' help to successfully breastfeed, such as requiring assistance with inserting the breast far enough into the infants' mouth to allow for sufficient milk flow (Volk 2009). A third reason may be the shape and size of women's breast (Volk 2009). In comparison to body size, humans have the largest breast size of all primates. This likely occurred as a result of evolutionary sexual signaling (Volk 2009). This may have made it challenging for human infants to nurse because it may have required relatively more complex physical and/or oral movements on behalf of the infant to successfully breastfeed (Volk 2009).

Social Factors that Assist Women's Breastfeeding

Women's challenges with breastfeeding therefore appear to represent a significant evolutionary problem. If one-third of mothers have

difficulty feeding their infants, and infants required breastmilk for survival (prior to the invention of formula), one would have expected natural selection to strongly select for maternal and infant characteristics that improved the success of nursing. That natural selection hasn't done so suggests that learned technique may not have been a serious problem for ancestral women. But why?

One plausible answer is that women coped with the challenges of breastfeeding by living in cooperative communities with other mothers who could teach and assist new mothers in learning how to breastfeed their infants (Volk 2009). This simple solution does indeed appear to work exceptionally well. In less developed countries where formula is scarce, over 98% of women successfully breastfeed their infants (Houston 1981). This is typically done in the complete absence of government and/or health care interventions. Young girls can observe their mothers, aunts, and neighbours nurse their infants. When women give birth, they can receive assistance and advice with breastfeeding from other more experienced women. Such social bonds may have also been beneficial for maternal and infant care (Hrady 1999). The recognition of the importance of this form of learning has led to the various modern-day interventions such as hospital programs, professional midwives, the La Leche League, lactation consultants, and parenting workshops that are each dedicated to giving mothers support, encouragement, and the knowledge necessary to successfully breastfeed (Fletcher and Harris 2000).

Additionally, women's partners are shown to be an important support system that has a significant influence on breastfeeding success. Studies show that women who perceived their partner to favour breastfeeding were more likely to continue breastfeeding than women who perceived their partner to favour bottle feeding or did not show preference for breastfeeding method (Scott and Colin 2002). Women's partners who do not favour breastfeeding are most likely to discontinue breastfeeding. Other factors that contribute to women's decisions to breastfeed include women's level of education and beliefs in the value of breastfeeding (Rollins et al. 2016).

Human social communities may have also benefitted women who were completely unable to breastfeed. Historically, and also in some societies today, women who cannot breastfeed their infants for various reasons can receive the help of other women, known as wet-nurses, to breastfeed their children. These practices date back to at least to Roman culture and can even be found in ancient mythologies and biblical stories (Fildes 1988). This was common practice in upper-class families that consisted of biological mothers who were unable to or preferred not to nurse their infants (Fildes 1988). This is another potential form of parental care since wealthy mothers use their resources to “buy” nutrition for their offspring, allowing them to direct more resources towards other offspring and/or somatic maintenance. Similar practices can still be found in some developing countries and are termed “milk kinship” (Altorki 1980). This is typically when more than one woman breastfeeds a child. In addition to helping the survival of the infant, milk kinship can also create social bonds across different communities and classes. For example, children who have been nursed by the same woman are known as milk-siblings and considered to be equal to biological siblings in social standing. However, it remains unknown whether children who are exposed to different breastfeeders may develop higher levels of immunocompetence as a result of their exposure to the antibodies of more than one mother.

Benefits of Breastfeeding

Clearly humans may have derived characteristics of lactation from ancestral mammals and share many similar features of lactation with nonhuman primates. The persistence of breastfeeding through evolutionary history is put into perspective when you consider other changes across human evolution including transitioning from walking on four legs to two legs, increased brain size, and changes in dental structure. This suggests that the functions of breastfeeding (e.g., contents in the breastmilk and how infants digest the milk) have stayed consistent over the evolution of humans with great evolutionary benefits (Sellen 2007). Humans,

similar to other mammals, have also developed the ability to breastfeed regardless of any modest changes to their body conditions. However, although women may still be able to lactate despite slight shifts in their maternal condition, such as modest levels of exercise and/or moderate weight loss (Sellen 2007), there may be a lower limit in how much nutrition the body needs in order to produce quality breastmilk. For example, severe environmental challenges may indeed affect the quantity of breastmilk and the mother's health given the significant metabolic costs of producing milk (Monnier et al. 2015). Therefore, maternal health during and post-pregnancy is imperative for both mother and infant health.

Today, the World Health Organization recommends that infants should be breastfed within one hour of birth and the recommended duration of breastfeeding is for the first 2 years of the infants' life (World Health Organization 2009). Indeed, the benefits of breastfeeding are now widely recognized within the pediatric literature (Gartner et al. 2005). The death of thousands of children around the world can be prevented each year with increased breastfeeding practices (World Health Organization 2009). Human infants who do not receive breastmilk are more likely to die before they reach 1 year compared to infants that are (either partially or completely breastfed). However, complete breastfeeding appears to be optimal as the risk of dying due to diarrhea and other infections decreases when infants are completely breastfed (World Health Organization 2009).

In addition to helping infant growth and protecting infants against infections, breastfeeding is also shown to influence infants' circadian rhythm (Sanchez et al. 2013). The last stage of breast milk, mature milk, when given to the infant the same day it is expressed is shown to influence infants' sleep-wake cycle which benefits the infants' functioning and synchronizations of body systems. Breastfeeding can also result in higher IQ and health later in childhood (Rollins et al. 2016). Infants' behaviour of waking at night to breastfeed is also suggested to be an adaptation to extend mothers' lactational amenorrhea (via further increasing maternal fatigue/load and reduction in the hypothalamic-pituitary-ovarian

axis recovery, therefore serving as contraceptives) which may delay the time for mothers to be able to have the next child (Hrdy 1999). This increases the infants' chance of survival by reducing the possibility of a future sibling.

Breastfeeding also has various benefits for the mother. The hormones released during breastfeeding help to strengthen the mother-child bond by increasing levels of Oxytocin in mother (Rollins et al. 2016). Additionally, breastfeeding is associated with lower rates of breast cancer. One of the reasons for this is that breastfeeding may help temporarily drain the breasts of potential chemical carcinogens. As well, increase oxytocin from breastfeeding may inhibit cell proliferation and tumor growth. Additionally, lactation may reduce cholesterol levels in the breast. Moreover, in modern society, breastfeeding is also economically cheaper compared to buying infant formula (Rollins et al. 2016). Finally, breastfeeding is shown to reduced birth intervals. This is likely because when reducing the frequency of breastfeeding increases the return of ovarian cycling and therefore reduces maternal depletion (Sellen 2007).

Conclusion

Understanding breastfeeding across evolutionary history sheds light onto how adaptive this behavior may have been for various species of mammals. The fact that this behaviour appears unchanged across human evolution despite all the other changes humans have endured attests to how important breastfeeding is for human development. Unfortunately, aside from the physical limitations that women already have to endure to facilitate breastfeeding, there are various social factors that still continue to impede women's decisions to breastfeed. One of the most relevant of those factors today is mothers having to decide between breastfeeding and returning to work. Various women report that returning to work post-partum can hinder their milk supply and therefore choose not to breastfeed at all (Rollins et al. 2016). However, there appears to be slight rise in employers accommodating mothers who breastfeed as it benefits the employers by

increasing female employee's health, attendance, productivity, and satisfaction. More prevalent accommodations for mothers in the work place is still warranted. Global economic estimates suggest that "not breastfeeding is associated with lower intelligence and economic losses of about \$ 302 billion annually or 0.49% of world gross national income" (Rollins et al. 2016, p. 491). Thus there are significant incentives for promoting breastfeeding when it is possible and productive to do so. This is reflected in the enshrinement of breastfeeding and its advantages as part of the UN Convention of Rights of the Child.

Yet while most pediatricians surveyed report an increased awareness of the importance of breastfeeding, they also report lower success rates and less confidence in the costs/benefit ratio of breastfeeding for mothers (Feldman-Winter et al. 2017; attitudes measured in 1995 compared to 2014). Therefore, we suggest that it is imperative that women should be given the necessary information, tools, and support to help facilitate this very important behavior. As noted in our review, and by leading pediatricians (Rollins et al. 2016), breastfeeding is an issue that goes beyond mothers and infants to involve extended support networks that involve many others. At the same time, we recognize that there are cases where breastfeeding remains an elusive and/or impossible task, and in such cases concur with pediatricians that a healthy and happy mother/father/caregiver-infant relationship is quite possible via the use of formula (Feldman-Winter et al. 2017). While women should be informed and supported, they should not be bullied or belittled based on their breastfeeding performance (or lack thereof). Regardless of whether an infant is fed formula or breastmilk, the most important nourishment may very well come from a loving, caring relationship with their parental caregiver.

Cross-References

- ▶ [Breast Feeding and Mother-Infant Attachment](#)
- ▶ [Duration of Breast Feeding in Ancestral Environments](#)

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Breast Feeding and Mother-Infant Attachment

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Definition

Breast feeding is the feeding of breast milk to the infant.

Attachment is the emotional tie that develops from the infant to the parent.

Introduction

Breastfeeding has been shown to have positive effects upon health and nutrition of infants and has been associated with increased educational achievement and cognitive ability in childhood (Oddy et al. 2004). It is also believed to foster development of the maternal-child relationship. Studies of the association of breastfeeding with this relationship have used a variety of constructs that assess the interaction of the mother and child at different stages of child development (Kielbratoowska et al. 2015). However, the developing maternal-child relationship in early childhood is perhaps most frequently characterized by the concept of infant-maternal attachment (Ainsworth 1989), abnormal development of which is thought to predispose to many aspects of later psychosocial pathology.

Background

Attachment was first described by Bowlby, who theorized that infant behavior is adapted to complement caregiver behavior when the caregiver's behavior is appropriate and responsive to the infant's cues (Bowlby 1969). The term "attachment" refers to the tie from infant to parent and is a representation of "the internal organization of the individual" (Ainsworth 1989). A child whose mental representation of the parent as available and responsive is likely to be securely attached to the parent. When such a representation is lacking, insecure attachment occurs. For the securely attached infant, the parent provides a secure base from which to explore the environment.

A basic component of attachment theory is that infants gradually develop a relationship with a principal attachment figure and that the attachment figure's sensitivity to the infant's needs may be a critical factor for the establishment of a secure attachment (Bowlby 1969). Several decades of research (DeWolff and van Ijzendoorn 1997) have established that sensitivity is an important but not exclusive predictor of secure attachment. The exact definition of sensitivity has varied widely in attachment research, yet promptness, consistency, and appropriateness are thought to be main constituents of this construct (Shin et al. 2008).

Although Bowlby's theory acknowledged that feeding may facilitate maternal-infant proximity and thereby provide opportunity for sensitive interaction, his clinical observations led to predictions that neither feeding itself nor individual differences in feeding, such as breast or bottle, contribute to individual differences in attachment quality (Cassidy and Shaver 1999). Recently, however, several studies have suggested a possible link between breastfeeding and attachment, and these studies will be reviewed in this chapter.

The literature on breastfeeding and attachment has come from the fields of medicine, nursing, and psychology. Accordingly, PubMed, PsychINFO, CINAHL, and Embase were searched for 40 years for the following search terms: breastfeeding, sensitivity, attachment, infant-mother attachment, mother-infant relationship, bonding, kangaroo

mother care. The search yielded no randomized trials addressing the relationship of breastfeeding to either attachment or sensitivity; therefore, a meta-analysis was not possible. Although there were numerous studies on sensitivity and its possible relationship to breastfeeding, only five empirical studies addressed the relationship between breastfeeding and attachment. As a result, these formed the focus of the present review (Table 1).

These studies varied with respect to design and construct measurement. Perhaps most consistently measured was attachment security, which is measured after the child reaches 1 year of age most frequently using the Strange Situation Procedure, the Attachment Q-Sort, or the Toddler Attachment Sort (Cassidy and Shaver 1999), although other measures have been used (Tryphonopoulos et al. 2014). On the other hand, there is no generally accepted method of measuring maternal sensitivity and considerable variation in methods of measurement exists (Shin et al. 2008). Although arguments for standardization of the measurement of breastfeeding have been made (Labbok and Starling 2012), measurement continues to be inconsistent, with different definitions of breastfeeding intent, initiation, and duration, especially with respect to degree of supplementation or exclusivity. In addition, many factors, such as demographic characteristics and prior breastfeeding experience to name a few, influence breastfeeding choice and success (Brockway et al. 2017), and studies vary with respect to inclusion of such confounders.

Breastfeeding, sensitivity, and attachment share several characteristics. Among these are common endocrine aspects (Olza-Fernandez et al. 2014). Moreover, breastfeeding and sensitivity share common affecting factors. Both are positively impacted by a positive maternal emotional state that includes social support and high self-esteem (Britton and Britton 2008; Shin et al. 2008) and negatively impacted by postpartum depression (Dennis and McQueen 2009), anxiety (Britton 2007), and perceived stress (Mezzacappa et al. 2002). Compared to mothers who bottle feed their infants, breastfeeding mothers have been reported to provide a more enriched home

environment for the infant, together with greater variety of daily stimulation and play and less authoritarian parenting approaches (Jacobson et al. 1991). Attachment has been noted to be transmitted across generations (Behrens et al. 2016; Sette et al. 2015), and mothers who were breastfed as infants are more likely to breastfeed their own infants (Di Manno et al. 2015). However, no studies have explored attachment and breastfeeding in the same intergenerational population.

Breastfeeding and Sensitivity

Compared to bottle feeding mothers, breastfeeding mothers have been shown to demonstrate more elevated sensitive behaviors, such as touch, tactile stimulation, and gaze to infant (Lavelli and Poli 1998). They also demonstrate greater attentional engagement with infant distress signals (Pearson et al. 2011) and enhanced activation in brain regions associated with higher maternal sensitivity by MRI scan (Kim et al. 2011). Longitudinal investigations of breastfeeding and maternal sensitivity over the first decade using data from 1,272 families in the NICHD Study of Early Child Care and Youth Development (Papp 2014; Weaver et al. 2018) found that longer breastfeeding during the first 3 years predicted increased maternal sensitivity up to child age 11 years. Several smaller longitudinal studies have demonstrated an association of breastfeeding during infancy with later sensitivity (Britton et al. 2006; Edwards et al. 2015; Jonas et al. 2015; Tharner et al. 2012). One study noted that compared to breastfeeding mothers with low sensitivity, mothers with high sensitivity were more likely to breastfeed either partially or exclusively for longer periods during infancy (Britton et al. 2006).

In a recent review of 43 studies of the association of responsive feeding during infancy and breastfeeding, Ventura (2017) found that cross-sectional studies consistently showed greater maternal feeding responsiveness among breastfeeding mothers than among bottle feeding mothers. He also noted that a limited number of

Breast Feeding and Mother-Infant Attachment, Table 1 Studies addressing breastfeeding and mother-infant attachment

Authors, Year	Study design	Sample	Measured parameters			Breastfeeding (BF)	Confounders
			Attachment	Sensitivity			
Britton et al. 2006	Longitudinal cohort in USA, 1986–1988, recruited at 32 weeks gestation and followed after birth, and at 3, 6, 9 and 12 months postpartum	152 mother-infant pairs; <i>Maternal Ethnicity:</i> 72.8% Caucasian, 23.8% Hispanic <i>Age:</i> 37.5% 18–25 years, 48.7% 26–35 years <i>Mean income:</i> \$25,788 ± 1,684 USD <i>Education:</i> 68.4% > high school <i>Breastfeeding initiation:</i> 83.4%	Ainsworth strange situation in laboratory at 12 months	NCAST feeding sensitivity to cues subscale videotaped in home at 3 months		Determined by questionnaires on home visits at each follow- up interval: <i>Prenatal intent</i> at 34 weeks <i>Initiation</i> if BF through postnatal hospitalization <i>Duration</i> Continuous: Determined at 3, 6, 9, 12 months Dichotomous: Any at 12 months; exclusive (no formula) at 6 months	Maternal age, education, ethnicity, employment, smoking, socioeconomic status, parity, social support
Thamer et al. 2012	Longitudinal cohort in Netherlands, 2003–2005 followed at 2 and 6 months (postal questionnaires) and 14 months (laboratory sessions)	675 mother-infant pairs; <i>Maternal ethnicity:</i> All Dutch <i>Age:</i> 32 ± 3.7 years <i>Education:</i> 35.7% > bachelor's degree <i>Breastfeeding initiation:</i> 90%	Ainsworth strange situation in laboratory at 14 months	Ainsworth maternal sensitivity scales in laboratory at 14 months		<i>Duration</i> determined by postal questionnaires at 2 and 6 months: Continuous variable for any BF up to 6 months; Dichotomous for any BF: never initiated; 0–2 months; 2–6 months; > 6 months; Other dichotomous: exclusive BF combined BF/bottle exclusive BF at 2 months	Maternal age, parity, education, birth weight, infant gender, 5-minute APGAR, spontaneous delivery, cesarean section
Jackson 2016	Early Childhood Longitudinal Study: Birth cohort (ECLS-B), representative of 99% of US births in 2001, assessed at 9 months and 2 years	976 mother-infant same-sex twin pairs	Toddler attachment Sort-45 at 2 years; four	Not assessed		Duration in months up to 2 years assessed by maternal recall at both times	None

(continued)

Breast Feeding and Mother-Infant Attachment, Table 1 (continued)

Authors, Year	Study design	Sample	Measured parameters			
			Bowlby attachment categories			
Gibbs et al. 2018	Longitudinal, National Center for education statistics, early childhood longitudinal study of US births in 2001, assessed at 9 months and 2 years	8900 mother-infant pairs	At child age 2 years, Toddler Attachment Sort 45 completed by interviewer after home visit	At age 2 years, maternal sensitivity assessed by modification of Three Bags Task	<i>Duration</i> : "Predominant BF" assessed by maternal recall at 9 months categorized as: Predominant for 3–5 months (no formula feeding); <i>Predominant</i> for 6 months of more; not Predominant for 3 months or more; dichotomous variables for <i>solids</i> before 4 months and bottle at bedtime	Socioeconomic status (household income, parental education, occupational prestige), family structure, maternal education, daycare attendance, sibling size, biological parents in home; Maternal: Age at delivery, BML, smoking, depression (CES-D); Child: Birthweight, gestational age, multiplicity, ethnicity, gender
Weaver et al. 2018	Longitudinal, National Institute of Child Health and Human Development Study of Early Child Care and Youth Development recruited in 1991 after birth in 10 US sites; assessments at: 1,3,6,12,15,24,36,42,46,50,54 months and 5,6,7,9,11 years	1,272 mother-infant pairs; Maternal <i>Education</i> : 30% high school or less <i>Ethnicity</i> : 13% African American <i>Mean annual income</i> : \$37,000 USD	Attachment Q-Sort at 2 years	Maternal and paternal sensitivity in free play and problem-solving task assessed by videotaped sessions eight times between birth and child age 11 years	<i>Duration</i> as continuous variable assessed by maternal recall at each visit until cessation; dichotomous variables for breastfeeding at 6 weeks and at 6 months	Maternal race, ethnicity, years of education, romantic partner in home

longitudinal studies reported that greater responsiveness during early infancy predicted longer breastfeeding duration. Most also showed that breastfeeding mothers demonstrated greater increases in responsiveness across infancy than bottle feeding mothers. Two randomized trials that attempted to promote maternal responsiveness did not observe effects of the intervention on breastfeeding outcomes.

Breastfeeding and Attachment

Although a moderately large number of studies have addressed the relationship between breastfeeding and sensitive maternal behaviors, most have not included measurements of attachment security. The few studies that have explored the relationship of breastfeeding with attachment security are shown in the Table.

Britton et al. (2006) found no differences in breastfeeding practices between securely and insecurely attached infants. However, although Tharner et al. (2012) found an association between breastfeeding duration and attachment security in the Strange Situation, breastfeeding duration was not associated with differences in attachment classifications. It did, however, lower risk of the disorganized attachment classification. In a twin study using data from the Early Childhood Longitudinal Study: Birth Cohort (ECLS-B), Jackson (2016) found that breastfeeding duration predicted security of attachment among female but not male toddlers. In females, each additional month of breastfeeding increased the odds of a secure attachment classification by 15% and decreased the odds of obtaining an ambivalent classification by 15%; in males, breastfeeding duration was actually associated with a higher risk of avoidant attachment classification.

In an analysis of data on children from 9 months to 2 years from the National Center of Education Statistics, Gibbs et al. (2018) found an association of attachment security with predominant antecedent breastfeeding for 6 months or more. In a longitudinal investigation of breastfeeding and maternal sensitivity over the first

decade using data from 1,272 families in the NICHD Study of Early Child Care and Youth Development, Weaver et al. (2018) found that longer breastfeeding predicted secure attachment at 24 months.

Several studies addressed mediation effects of breastfeeding, sensitivity, and attachment. Tharner et al. (2012) found that sensitivity did not mediate the association of breastfeeding duration with attachment security. Weaver et al. (2018) observed that secure attachment at 24 weeks did not act as a mediator of the link from breastfeeding duration to sensitivity later in childhood. However, in a path analysis Britton et al. (2006) demonstrated a significant path between prenatal intent to breastfeed and attachment security mediated by early sensitivity.

Although all of these studies provide data to suggest a relationship between breastfeeding and attachment, none is conclusive and proof of a causal relationship is lacking.

Interventional Studies

A number of interventions have been implemented to foster attachment security and/or maternal sensitivity, but none has reported a concomitant improvement in breastfeeding (Wright and Edginton 2016). Programs to specifically promote breastfeeding have been described, and some have been shown to foster improved infant health at the community level (Brockway et al. 2017). However, none of these studies has reported enhanced attachment security coincident with breastfeeding improvement.

Skin-to-Skin Contact

Skin-to-skin contact between mothers and their infants immediately after birth, also called kangaroo mother care, is an increasingly common practice that has been associated with increased breastfeeding (Conde-Agudelo and Diaz-Rossello 2016). Although such contact could be considered a form of sensitivity, its relationship to the development of later attachment security has not been

adequately addressed (Conde-Agudelo and Diaz-Rossello 2016).

Maternal-Infant Bonding

Breastfeeding is believed to foster the development of a “bond” between the mother and infant in early infancy. In an early study (Klaus et al. 1995), mothers who nursed their infants during the first 3 h after birth and then spent more than 15 h with them over the next 3 days displayed greater emotional attraction to their infants 1 month later compared to mothers with minimal postpartum contact. The term “bonding” refers to the tie from parent to infant, a tie unique and specific to that relationship (Klaus et al. 1995). Although the effect of this bond is generally felt to be enduring (Klaus et al. 1995), the concept of bonding is incompletely defined (Behrens et al. 2016), and an association between early bonding and later attachment security remains to be established (Rode et al. 1981).

Conclusion

Existing data from a limited number of published empirical studies suggests a possible relationship between breastfeeding and maternal-infant attachment. However, such a relationship remains inconclusive, and there is no data to support a causal relationship between breastfeeding and attachment security.

Cross-References

- [Breast Feeding](#)
- [Maternal Bonding](#)

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Breast Milk Composition

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Synonyms

Human milk; Lactation

Definition

The biologically normal contents of human milk

Introduction

Human breast milk is a complex and adaptive fluid, comprised of a vast array of bioactive substances. The function of human milk is not only to provide essential nutrition to the breastfeeding infant, but also to enhance growth and development, modulate immunity, and encourage the establishment of a diverse microbiome (Andreas et al. 2015). The exact formulation of human milk is subject to huge variation. This is because the determination of the contents of human milk is through a complex interplay of maternal, infant, and environmental factors. Time-dependent changes further adapt the composition of human milk to align with a growing infant's needs, as milk progresses from colostrum to transitional and finally to mature milk. The culmination of these regulatory mechanisms is a biofluid that is specifically tailored and responsive to the needs of the infant. The primary biologically active components of human milk are lipids, protein,

nonprotein nitrogen (NPN), and carbohydrates (Andreas et al. 2015).

Components of Human Breast Milk

Lipids

Lipids are the primary energy component of human milk, providing approximately 50% of the total energy consumed by the breastfeeding infant (Koletzko et al. 2001). Human milk lipids have also been described to play a role in early growth and development. The entire milk fat content of human milk, present as an emulsion, changes from colostrum to mature milk and is the most variable component of human milk in terms of concentration (Michalski et al. 2005). The mean fat concentration of mature milk is thought to be approximately 3.60 g/dl, though this varies between individuals (Koletzko et al. 2001). Human milk contains a complex mixture of lipid species, predominantly triglycerides which make up over 98% of total fat content (Demmelmair and Koletzko 2018). The remaining lipids are diacylglycerides, monoacylglycerides, free fatty acids, phospholipids, and cholesterol (Koletzko et al. 2001).

A human milk fat globule is 4–5 μm in size, comprising of a triacylglycerol-rich core surrounded by a milk fat globule membrane.

The fat content of milk is present as milk fat globules (Image 1). These globules are formed in the mammary alveolar cells and are comprised of a membrane of polar lipids and a triglyceride-rich core. These globules are larger in the colostrum of women postpartum than in both mature human milk and in infant formula (Zou et al. 2012).

Importantly, the structural differences of milk fat globules between these milk types may change the nutritional value for the infant. A structural component of the fat globule membrane, sphingomyelins, are important for normal neurobehavioral development due to their involvement in myelination of the central nervous system (Lopez and Ménard 2011).

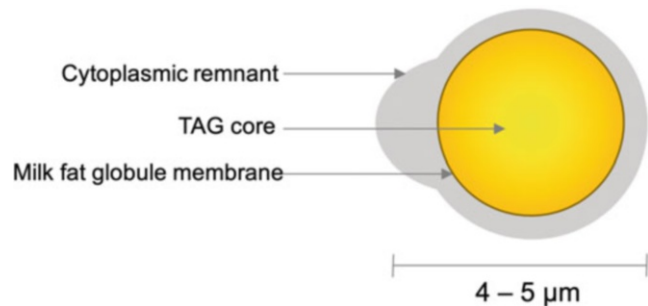
More than 200 fatty acids are present in human milk in varying concentrations. The majority of these fatty acids are present at very low concentrations, and some fatty acids (such as oleic, linoleic, and palmitic acids) dominate (Koletzko et al. 1988; Martin et al. 1993). Both short-chain fatty acids (SCFA) and long-chain fatty acids (LCFA) are present in human milk. The primary function of SCFA is to provide energy to the breastfeeding infant (Koletzko et al. 2001). SCFA are also involved in the maturation of the gastrointestinal tract. LCFA are a component of cell membranes, and their availability in breast milk has been described to play an important role in early human growth and development. LCFA have been seen to accumulate in membrane-rich tissue such as the brain during the perinatal period. It is also thought that the capacity to secrete LCFA varies between humans (Koletzko et al. 2001).

1. Protein

Over 400 different proteins have been characterized in human milk. This vast array of proteins has been shown to provide nutritional, immunological, and developmental benefits to the breastfeeding infant (Molinari et al. 2012). The cumulative majority of breast milk protein is

Breast Milk Composition,

Image 1 Human breast milk fat globule



produced by lactocytes, approximately 80–90%. The remaining protein found in milk is derived from the maternal circulation, passed into the lumen via transcytosis (Peaker 1985). As is the case for most components of breast milk, total protein content declines from early lactation (14–16 g/L) to mature milk (7–10 g/L) (Lönnerdal 2003).

Milk proteins are commonly classified into three groups; mucins, caseins, and whey proteins. Mucins are the structural proteins of the milk fat globule membrane (Lönnerdal 2003). Only a small proportion of human milk is comprised of this group. Caseins are present in higher quantities at approximately 13% of total milk protein (Lönnerdal et al. 1987). There are three casein subtypes, α -, β -, and κ -caseins, which are found together with calcium phosphate in casein micelles suspended in milk. These micelles are of an average diameter of 150–200 nm (Dalgleish and Corredig 2012).

Whey proteins are differentiated from casein proteins by their solubility, as whey proteins are not contained in micelles but are present in solution (Lönnerdal 2003). Whey proteins contain important host defense factors. For example, lactoferrin and lysozymes have synergistic bactericidal properties and have been shown to kill Gram-negative bacteria in vitro. These proteins also modulate immune function. Other whey proteins that are present in high quantities in human

milk include α -lactalbumin, IgA, and serum albumin (Lönnerdal 2016) (Image 2).

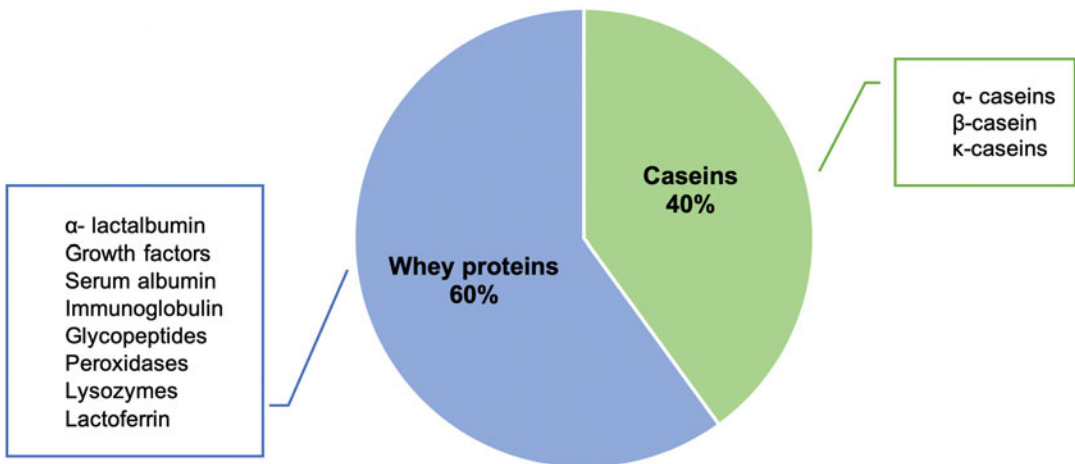
Nonprotein Nitrogen

While the nonprotein nitrogen (NPN) content of human milk is a relatively understudied area, it comprises approximately 25% of total nitrogen in milk and represents a diverse range of molecules. These include nucleotides, amino acids, peptides, urea, and creatinine (Zhang et al. 2013).

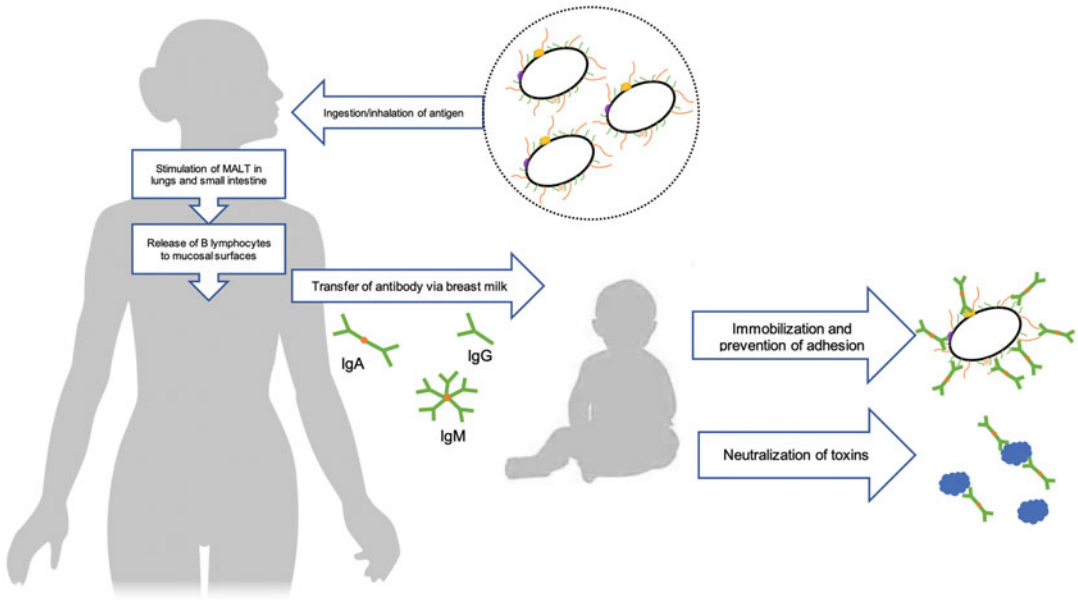
Free amino acids account for approximately 8–22% of total NPN, primarily glutamine, glutamic acid, and taurine. Glutamic acid and glutamine represent almost 50% of this fraction. These amino acids are thought to be important in early development, yet their exact role has not been defined (Zhang et al. 2013). Nucleotides are known to be essential for a variety of cellular processes such as normal metabolism. Breast milk nucleotides have also been shown to be an advantageous factor in immune function, establishment of the gut microbiome, and maturation of the gastrointestinal tract (Gutiérrez-Castrellón et al. 2007; Hess and Greenberg 2012).

Antibodies

Given the relative immaturity of the adaptive immune system in the first few months of life, infants largely rely on maternal antibodies for disease-specific immunity. These antibodies are transferred to the infant both transplacentally and



Breast Milk Composition, Image 2 Protein composition of breast milk



Breast Milk Composition, Image 3 Transfer of disease-specific passive immunity via breast milk

via breast milk (Chucuri et al. 2010). Neonatal secretions contain very low amounts of endogenous antibody; thus, the breastfeeding infant relies on breast milk antibodies for protection at the mucosal surface against invasive pathogens (Li et al. 2014). These antibodies are predominantly secretory Immunoglobulin A (sIgA), with secretory Immunoglobulin G (sIgG) and serum-derived IgG also present. Breast milk antibodies are hypothesized to be the most important protective immunological component of breast milk. SIgA likely provides this protection via direct inhibition of invasive pathogens at mucosal surfaces. This is likely achieved through neutralization of toxins and virulence factors, immobilization of the pathogens, and prevention of epithelial adhesion (Brandtzaeg 2007) (Image 3).

In response to antigens from the environment, the maternal mucosa-associated immune tissue causes the release of B lymphocytes to mucosal surfaces. This gives increased disease-specific antibody (primarily IgA) in breast milk, which provides increased disease-specific immunity through a variety of methods.

Antigenic stimulation of mucosa-associated lymphoid tissue (MALT) in both the gut and the

airways determines the antibody content of breast milk. The antibodies found in breast milk are determined in response to the infectious agents encountered by the mother throughout pregnancy. Thus, they provide protection against the pathogens the neonate is most likely to encounter in their external environment (Brandtzaeg 2003). Specific sIgA commonly found in breast milk are against pathogens which cause disease in the gut and respiratory tract. These include bacterial species such as *E. coli*, *Shigella*, *Campylobacter*, *Group B Streptococcus*, and *H. influenzae*, as well as viruses such as rotavirus (Le Doare and Kampmann 2014; Van De Perre 2003).

Vaccination of expectant mothers against common infant infections has become routine in many high-income nations and has been shown to be a highly effective prevention strategy. Antenatal vaccination works by increasing both the antibodies passed to the infant via the placenta and the antibody concentrations in breast milk against vaccine antigens. For example, the recent introduction of antenatal vaccination against *Bordetella pertussis* in the United Kingdom resulted in a sustained reduction of over 90% of both infant deaths and hospitalizations due to

pertussis infection (Amirthalingam et al. 2016). Although increased transplacental transfer of serum IgG is likely the main driving force behind the efficacy of antenatal vaccination, studies have shown that increased disease-specific breast milk IgA is also a protective factor for breastfeeding infants against a multitude of infections in the upper respiratory, lower respiratory, and gastrointestinal tracts. Antenatal vaccination, therefore, augments the protection afforded to breastfeeding infants against vaccine preventable infections via the resultant increase in breast milk antibody levels (Li et al. 2014).

Carbohydrates

There is a wide array of carbohydrates present in breast milk. The carbohydrate found at the highest concentration in human milk is lactose. Lactose is a disaccharide of glucose and galactose and is hypothesized to be at such high levels in breast milk to meet the energy demands of the human brain. Another important component of human milk carbohydrate is human milk oligosaccharides (HMO), which serve as nutritional factors for the gut microbiota (Coppa et al. 1993).

HMO are present in high concentrations in human milk. At 4 days postpartum, levels of HMO are on average 20.9 g/L and 12.9 g/L in mature milk. These oligosaccharides are built of five different monosaccharides: L-fucose, D-glucose, D-galactose, N-acetylglucosamine, and N-acetylneuraminic acid and with lactose at the reducing end (German et al. 2008). These monosaccharides are bound in varying orientations and sequences to give a vast array of HMO. Over 200 different HMO, derived from maternal lactocytes, have been identified in human milk. The specific breast milk HMO profile is predominantly determined by the mother's genotype. Four main genotypes have been described for oligosaccharide expression in breast milk. It is believed that while there are differences between these genotypes in terms of the types of oligosaccharides present, the total expression of oligosaccharide between genotypes is relatively similar (Thurl et al. 1997).

HMO influence the cells of the intestinal epithelium, inducing apoptosis and differentiation of

cell lines (Kuntz et al. 2009). HMO have also been shown to act as modulators in allergen-specific immunity by suppressing Th-2-type responses in those prone to atopy (Eiwegger et al. 2010). The immunological action of HMO is also via the support of beneficial bacteria within the gastrointestinal tract. HMO encourage the growth of these bacteria, thereby preventing colonization by disease-causing species. By this mechanism, HMO may prevent neonatal gastrointestinal or respiratory infections (Morrow et al. 2004). Gastrointestinal immunity is further enhanced via the action of HMOs as receptor decoys. HMO are similar in shape to the surface carbohydrates of intestinal epithelium, which are a binding site for many pathogenic bacteria. In mimicking the structure of these carbohydrates, HMO bind bacteria in the mucosal layer and inhibit bacterial adhesion to the intestinal epithelium thus allowing bacteria to pass through the gastrointestinal tract without causing disease (Triantis et al. 2018) (Image 4).

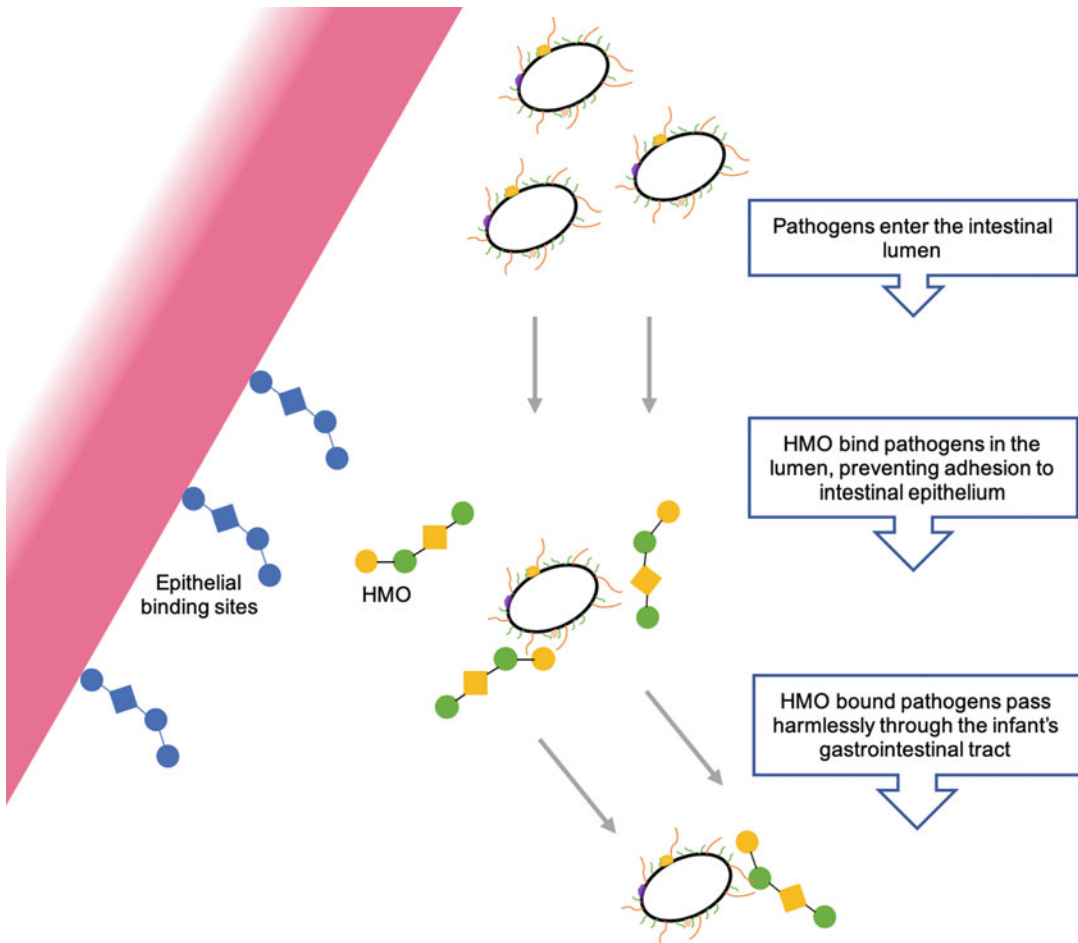
Human milk oligosaccharides are similar in shape to pathogen binding sites on the intestinal epithelium of infants. They bind invasive pathogens in the intestinal lumen, thereby preventing adhesion and invasion of pathogens, allowing pathogens to be excreted without having caused disease.

It is important to note that disease-specific protection and induction of certain cell processes is dependent on the types of HMO ingested. Given the HMO profile of an individual mother's breast milk is genetically determined, it follows that both the composition of the gut microbiota and the disease-specific protection provided to breastfeeding infants may be highly influenced by the mother's genotype.

Factors Influencing Breast Milk Composition

Time-Dependent Changes

Human breast milk begins as colostrum in the first few days postpartum before progressing to transitional milk and then mature milk at approximately 2 weeks postpartum. The transitions occurring between these categories are not distinct, instead



Breast Milk Composition, Image 4 Human milk oligosaccharides as receptor decoys

occurring as a more gradual process through progressive changes in breast milk composition. Colostrum begins with a relatively high whey protein concentration, with low casein, lipid, and lactose concentrations. Throughout the progression to mature milk, the lipid fraction increases. Included in the high whey protein levels of colostrum is a higher proportion of growth factors as well as higher total antibody, likely to supplement the immature infant immune system throughout the immediate postpartum period. Indeed, HMOs are also more concentrated in colostrum, again most likely to augment neonatal immunity (Saint et al. 1984).

Breast milk is also different in its composition depending on the timing of the most recent feed,

as well as within the period of a feed itself. There is high variability of both lipid and lactose levels throughout a feed (Hyttén 1954). Where lipid levels peak at the end of a feed, lactose levels in milk have been shown to decline as a feed progresses. Total milk fat content then declines as the time since the last feed lengthens. Lipid levels have also been shown to exhibit diurnal variation, peaking midmorning with an overnight trough (Coppa et al. 1999).

Maternal Factors

There is some evidence to show that certain maternal characteristics have the power to alter the composition of their breast milk. While maternal

age and ethnicity are unlikely to play a significant role in determination of breast milk composition, maternal diet has been shown to alter human milk (Andreas et al. 2015). The processes behind dietary regulation of milk are complex and differ between nutrients. For example, it is thought that the total lipid fraction of human milk is not influenced by dietary changes. Instead, individual species of fatty acids which are derived from maternal plasma or synthesized by the mammary gland are sensitive to a change in maternal diet (Innis 2014). Fatty acids such as monounsaturated omega-3 fatty acids have been seen to be increased in those mothers who increase their dietary intake (Novak and Innis 2011). It is important to note, however, that there is not a great deal of evidence linking maternal weight gain during pregnancy with higher milk fat content (Andreas et al. 2015).

Conclusion

Human milk provides essential nutrition to the breastfeeding infant during an intense period of growth and development. Further, human milk acts as the safety net for the relatively immature neonatal immune system, through both the transfer of passive immunity and the modulation of immune processes. The biologically active components of milk do not exist in static proportions but change in response to a myriad of factors. The precision of these regulatory mechanisms is a result of millennia of human evolution, culminating in a biofluid that is optimized to meet and respond to the needs of the growing infant.

Cross-References

- ▶ Attachment Theory
- ▶ Brain Growth in the First Year
- ▶ Breast Feeding
- ▶ Breast Feeding and Mother-Infant Attachment
- ▶ Breastfeeding Benefits
- ▶ Breastfeeding in Modern Environments

- ▶ Development
- ▶ Gut Microbiome
- ▶ Infant Survival
- ▶ Maternal Role

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Breastfeeding Benefits

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Synonyms

[Nursing advantages](#)

Definition

Advantages for the mother and child when the newborn is fed with breast milk as opposed to alternative nutritional sources such as formula.

Introduction

Breastfeeding has been highlighted as one of the most important practices for the protection of infants from pathogens during the first years of life (Morrow et al. 2005). This protection is needed to support the newborn's immature immune system after leaving the predominantly sterile womb (Niers et al. 2007). While the immune system is developed before the baby is born, it lacks experience at combating specific pathogens. As a result, maternal (IgG) antibodies are transferred to the fetus in the months leading up to the birth, supporting the immune system while it is vulnerable (Niers et al. 2007). These prenatal antibodies lose effectiveness over the first 3 months; however, breast milk has evolved to extend this assistance for the following months (Niers et al. 2007). Breast milk, though originally considered sterile, is teeming with probiotic bacteria for the digestive system of the newborn, serving to support their immune system and metabolism (Fernández et al. 2013).

Current knowledge concerning the benefits of breastfeeding almost unanimously advocate the exclusive use of breast milk for the first 6 months. There are a wide variety of substantial benefits to both mother and child, supporting the

evolutionary perspective that, as with the majority of mammalian species, humans have evolved breast milk that is tailored to maximize the likelihood of the survival of mother and child (Labbok et al. 2004).

Mortality Rate

Research concerning the risk of death within the first months of life suggest that exclusive breastfeeding has only 12 % of the mortality risk associated with not breastfeeding within low- and middle-income countries (Sankar et al. 2015). High-income countries have also been linked with lower death rates, with evidence suggesting a reduced mortality specifically concerning sudden infant death syndrome and necrotizing enterocolitis (Victora et al. 2016).

Additionally, the timing of the first feed has also been linked with a reduction of infant mortality risk. A systematic review of relevant research suggested that breastfeeding within an hour of the birth substantially decreased the risk of mortality (Khan et al. 2015). Furthermore, following this initial feeding, only partially breastfeeding the child (feeding with breast milk but also from other sources) increased the risk of mortality during the first month for the infant.

Researchers have suggested that interventions designed to optimize global breastfeeding practices could prevent 13 % of the global mortality of children less than 5 years of age (Jones et al. 2003). Supporting this, a review of studies assessing the benefits of breastfeeding to children between the ages of 6 and 23 months suggested that up to a 50 % lower risk of death was observed with continued breastfeeding (Victora et al. 2016).

Infection Risk

The bolstered immunity provided thorough breastfeeding results in a reduction in frequency and duration of infections (Fernandez et al. 2013). Research relating to this typically focuses on the protective effect on instances of diarrhea,

respiratory infections, otitis media (infection of the middle ear), and gastrointestinal infections.

Of these, diarrhea is especially costly and is estimated to be the basis of over 20 % of child deaths under the age of 5 in developing countries (Morrow et al. 2005). The glycans (complex carbohydrates) within breast milk contribute to the passive immunity gained from the mother and are linked directly with protection from diarrheal diseases (Lamberti et al. 2011). Research suggests that breast milk reduces the frequency of diarrhea, but more significantly reduces the duration of each episode (Lamberti et al. 2011). Victora et al. (2016) estimate that half of global diarrhea instances could be avoided through optimal breastfeeding practices.

Additional Benefits

A wide variety of additional benefits have been associated with breastfeeding with varying levels of empirical support. Consumption of breast milk in excess of the first 6 months has been reported as lowering childhood malignancies such as leukemia (Amitay and Keinan-Boker 2015), improved connection created between mother and child (Khan et al. 2015), better oral health (preceding 12 months of age), lower chances of obesity, and a reduction in asthma levels (Victora et al. 2016).

While these benefits for the child are relatively accepted within the scientific community, there are other proposed benefits that are more contested. While some studies have found a protective effect from allergies, the recent review by Victora et al. (2016) found little evidence to support the association. Some researchers have also proposed neurodevelopmental advantages of breastfeeding, such as increased scores on intelligence tests, though these are highly debated.

Benefits for the Mother

Breastfeeding has also been evidenced as having a variety of benefits for the mother in addition to the child. Both breast and ovarian cancer have been associated with a reduced reported frequency of

occurrence relating to the amount of lifetime breastfeeding (Victora et al. 2016). There are also reports that bone mineral density is increased through breastfeeding, though this is contested among the research.

Conclusion

Humans have evolved to produce a highly complex nutritional sustenance for newborn children that also serves to protect them from pathogens while their immune system is immature. Though imitations of this adaption have been created, there is little doubt among the scientific community relating to the superiority of breast milk, especially during the first 6–12 months of life. The proposed benefits include lower rates of infant: mortality, infection, diarrhea, malignancies (cancer), asthma, oral health, and obesity. Additionally, there are also benefits for the mother, primarily relating to lowering the risk of ovarian and breast cancers.

Cross-References

- ▶ [Bottle Feeding](#)
- ▶ [Breast Feeding](#)
- ▶ [Breast Milk Composition](#)
- ▶ [Child Mortality](#)
- ▶ [Disease Avoidance](#)
- ▶ [Infant Survival](#)

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Breastfeeding in Modern Environments

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Synonyms

Nursing in modern environments

Definition

The practice of a woman providing breast milk to her own or another woman's child in modern industrialized societies

Introduction

Breastfeeding was long the only viable way of securing infant survival. With that in mind, it is surprising that breastfeeding has evolved to be a somewhat error-prone and complicated process, especially in humans, with reported failure rates of up to 33% due to problems with breastfeeding technique (► “Breast-Feeding”). Historically, wet-nursing (► “Wet-Nursing”) became a common practice (Golden 1996) and can be traced back at least to ancient Roman and Egyptian cultures (► “Breast-Feeding” and ► “Wet-Nursing”). In contemporary Western developed countries like the USA or the UK, however, wet-nursing has become socially unacceptable (see Groskop 2007). And since the invention of artificial formula, it is also less of a necessity.

Despite known health benefits of breastfeeding for mother and infant (see below), we observe a huge variation in breastfeeding behavior in modern societies. In the following, we define breastfeeding behavior to include “*breastfeeding initiation*” (whether a mother breastfeeds her child at all), “*breastfeeding continuation*” (whether the mother continues to breastfeed her child up to a specific duration), and “*breastfeeding exclusivity*” (whether the mother exclusively provides breastmilk to her child or combines breastfeeding with bottle feeding).

Ethnographic and survey research illustrates that cost-benefit calculations play a predominant role in a mother's consideration of which infant feeding method to apply (e.g., Hannon et al. 2000; Radius and Joffe 1988). Whether to breastfeed or not to breastfeed can thus be seen, in part, as a conscious decision-making process. According to the health-belief model, however, it is not the actual costs and benefits that are most predictive for health behavior, including breastfeeding behavior, but it is the beliefs about the costs and

benefits (Emmanuel 2015). In that regard, the health-belief model is a model of bounded rational decision-making, as beliefs about the costs and benefits of breastfeeding may be biased by inaccurate information. In the following, we will therefore not only take a look at some of the actual costs and benefits that can be associated with breastfeeding but also at what sources of information may affect women's beliefs about breastfeeding. Another addition is that the cognitive system that enables people to make rational decisions coexists with a much older system in evolutionary terms that consists of a set of innate, automatic, and domain-specific mechanisms. This view, which is incorporated in dual-process theories (Evans 2003), allows bringing together the social scientific with the evolutionary literature. Whereas the former focuses predominantly on the actual costs and benefits of breastfeeding as well as the factors which affect beliefs about these costs and benefits, the latter addresses potential innate mechanisms that may lead to discriminatory maternal investment within the same families.

Health Benefits and Risks of Breastfeeding

Short of a viable alternative, in ancestral environments breastfeeding was essential for infant survival. It is only with the availability of alternatives (e.g., wet-nursing or artificial formula) that we can ask about the relative benefits and risks of breastfeeding as compared to other feeding methods. The majority of research on the health benefits of breastfeeding in modern environments compares this method to bottle feeding with artificial formula. Previous research shows that due to the immunological benefits of breastmilk, in developing countries, breastfeeding can lower the risk of morbidity and mortality of newborns driven by infectious diseases (Horta et al. 2007; WHO Collaborative Study Team on the Role of Breastfeeding on the Prevention of Infant Mortality 2000). But also in developed countries, often with some form of universal healthcare and advanced medicine, breastfeeding comes with a

number of benefits for the health and development of infants. In fact, a large number of studies exist, summarized in several systematic reviews and meta-analyses, that evidences the positive short- and long-term health impact of breastfeeding for infants (Binns et al. 2016). Breastfeeding protects strongly against many infectious diseases (ebd.), for example, extended breastfeeding in the first two years of an infant's life reduces the risk of acute otitis media (Bowatte et al. 2015). Long-term benefits of breastfeeding include higher performance in intelligence tests and better cognitive development, reduced risk of obesity in childhood and, as adults, a reduction in type-2-diabetes, and a small protective effect against high blood pressure (Binns et al. 2016). For infants born with extremely low birth weight (≤ 1500 g) or born at a very early gestational age (≤ 28 weeks), a systematic review and meta-analysis shows that breastfeeding can also decrease some forms of morbidity common in these risk groups (Miller et al. 2018).

Health benefits of breastfeeding are not limited to the infant but (continued) breastfeeding entails also some benefits for mothers. A recent review and meta-analysis of 163 empirical studies clearly points toward a reduced risk of breast and ovarian cancer, type-2-diabetes, and postpartum depression. And (continued) breastfeeding is also associated with an extended period of lactational amenorrhea. Evidence is not conclusive regarding a potential reduction of the risk of osteoporosis and postpartum weight (Chowdhury et al. 2015). One difficulty in determining the health benefits for women, however, is that certain symptoms like postpartum depression may themselves have a negative causal effect on breastfeeding initiation or continuation (cf. Figueiredo et al. 2013).

Despite the many beneficial effects of breastfeeding for both infant and maternal health, there are specific conditions under which breastfeeding may turn into a disinvestment for infants. This can be the case, for example, if a mother is affected by an infectious disease (e.g., HIV) or exposed to toxins that can be transmitted through breast milk (e.g., Dennis 2002; Bose-O'Reilly et al. 2008). Also, continued exclusive

breastfeeding can turn into an (unintended) disinvestment for infants once breast milk alone doesn't provide sufficient nutrition necessary at later stages of development (Fewtrell et al. 2007).

Other Benefits (and Costs) of Breastfeeding

If women experience discomfort, pain, or stress associated with breastfeeding, these symptoms can be considered costs of breastfeeding that a woman weighs against the known benefits of breastfeeding for herself and for her infant. Discomfort or pain could be experienced, for example, associated with postoperative pain and limited mobility after a caesarian or due to other physical or mental health conditions women may experience postpartum (Beake et al. 2017; Falceto et al. 2004). Also, work-related aspects may influence the extent to which breastfeeding is perceived as stressful or difficult. In the USA, for example, women of low status need to return to their jobs earlier than women of higher status for financial reasons and are thus disproportionately affected by the potential incompatibility of breastfeeding and work demands (Angeletti 2009). It is often higher status jobs that provide (paid) maternal leave that, with the exception of the USA, is provided by the government in many other OECD countries (Thévenon 2011). If a woman works while still breastfeeding, the specific arrangements of the workplace or the work contract may facilitate or hinder continued breastfeeding (Angeletti 2009; Galtry 1997). It is often more difficult to reconcile work and breastfeeding demands for mothers working in low-status occupations as these often provide a lower degree of flexibility (Galtry 1997).

The personal network (kin and non-kin) of a woman can be a supportive factor and thus reduce the costs associated with breastfeeding. Particularly the partner and mother of a woman are potentially influential support persons and sources of information about breastfeeding (Cisco 2017). Therefore, including these support persons in breastfeeding promotion can indirectly affect breastfeeding behavior. A recent review and

meta-analysis of intervention studies targeting the partners, that is, the children's fathers, in their promotion of breastfeeding comes to the conclusion that this type of intervention is positively associated with maternal knowledge about and favorable attitudes toward breastfeeding as well as with breastfeeding exclusivity 6 months after birth. In addition, involving fathers in the promotion of breastfeeding was negatively associated with the risk of lactational problems (Mahesh et al. 2018). Furthermore, contact to peers is positively associated with breastfeeding exclusivity, yet less so in countries where formula feeding is widespread (Sudfeld et al. 2012).

Organizations Influencing Women's Breastfeeding Decisions

International organizations, institutions of the public health sector, the formula food industry, and the media – all with their own sets of interests – target female decision making with regard to breastfeeding. For example, referring to established benefits for infant and maternal health, the WHO and UNICEF as well as government-led initiatives have followed the goal of increasing breastfeeding initiation, duration, and exclusivity (Dennis 2002; Guise et al. 2003, p. 70). Educational programs were set up to educate women about the (health) benefits of breastfeeding. Furthermore, support programs were initiated to provide women with breastfeeding instruction and support. Evaluation studies, summarized in reviews and meta-analyses, show that these do indeed have positive effects on breastfeeding initiation, duration, and exclusivity (summarized in Schnettler 2010). Another countervailing influence is the baby food industry. Not long ago, it was a common practice that it provided free commercial discharge packages along with promotional material on artificial formula via hospitals, a practice with moderate adverse effects on breastfeeding initiation, duration, and exclusivity (summarized in Schnettler 2010, pp. 85–87). Also, the media may have played a role in promoting bottle feeding for a long time. A content analysis of British newspapers and television

programming, for instance, shows that bottle feeding was shown more often than breastfeeding in the respective contents and in a way that made bottle feeding appear to be associated with higher status (Henderson et al. 2000).

Differences in Breastfeeding Between and Within Mothers

We have seen that characteristics of the immediate and wider social context affect women's breastfeeding decisions either directly by changing the cost-benefit ratio (e.g., by means of providing support or giving away free baby food) or indirectly by affecting the beliefs about breastfeeding and the information available about the benefits of breastfeeding vs. bottle-feeding. If the (perceived) costs and benefits of breastfeeding for an individual mother differ over time, the same mother may reach a different decision regarding breastfeeding initiation, duration, and exclusivity for an earlier-born than for a later-born child. For example, a young mother may not yet know about all the health benefits of breastfeeding and decide to bottle-feed her first child, whereas later on, with more information about those health benefits, she could reach a different decision for her second child. Or, as another example, a mother working for different employers over time, with varying degrees of flexibility and supportive policies for breastfeeding mothers, might have more difficulty keeping up a regular breastfeeding schedule in case of one child and less so in case of another child (Schnettler 2010).

Even though the decision to breastfeed is largely described as the outcome of a rational deliberation based on cost and benefit considerations, this decision-making process may be affected or biased by psychological mechanisms that have evolved during our ancestral past. Discriminatory breastfeeding decisions based on child characteristics would thus constitute another source of variation in breastfeeding behavior within mothers but across their different offspring. From inclusive fitness theory one may derive the hypothesis that parents discriminate their

investment toward offspring with physical or psychological characteristics (endowment) that are correlated with higher mating and reproductive success. This could involve, for example, health and physical beauty. Birth weight and gestational age are often considered proxies for endowment differences. And indeed, children born with low birth weight, despite the known benefits for this group of infants (see above), are less likely to be breastfed. However, this might have to do less with parental discrimination than health issues related to the early birth or the low birth weight that render breastfeeding difficult or not possible at all (cf. Hill et al. 1997). Under conditions of scarcity, age may be another child endowment factor affecting parental investment, as older children who have already survived more risks than younger children imply lower sunk fitness costs (cf., Salmon 2005, pp. 508–511).

A considerable amount of research has been conducted on the main effects of child gender on food allocation by parents, especially with regard to developing countries. Some studies provide evidence for preferential breastfeeding of boys in certain regions in India and China, yet a review of more than 300 studies doesn't provide a clear pattern of daughter disadvantage (Marcoux 2002). A related theory along these lines that has received a considerable academic attention is the Trivers-Willard (TW) hypothesis (► [“Trivers-Willard Hypothesis”](#)). It states that parents' reproductive fitness is increased if they alter the sex of their offspring and/or discriminate their investment based on a child's sex in a direction that is dependent on some measure of parental condition. Although it is not quite clear what parental condition measures are most appropriate and may be related to physiological condition in modern societies (► [“Maternal and Offspring Condition”](#)), empirical studies examining the TW hypothesis in modern environments often use some measure of socioeconomic status as indicator of parental condition. As earlier results were mixed with regard to the TW hypothesis (Schnettler 2010), more recent studies on the TW hypothesis in modern environments have either used large data sets from population registers to be able to detect even small differences, yet could not find a

TW-consistent pattern in their data (e.g., Kolk and Schnettler 2013, 2016), or they have used small elite samples arguing that in such groups expected effect sizes might be considerably larger than in the general population and thus detectable even in smaller samples (Schnettler 2010). A recent study on the 400 individuals estimated to be among the wealthiest US Americans (Forbes 400) reported a statistically significant difference in offspring sex ratio in accordance with the TW hypothesis, but it comes to the conclusion that the effect size is much smaller than reported in previous research. The author discussed sample selection as a potential alternative source for the apparent bias in the sex ratio (e.g., Schnettler 2013). Previous studies specifically with regard to differential breastfeeding along the lines predicted by the TW hypothesis led to mixed results (summarized in Schnettler 2010). Yet, another study that specifically compared differences in breastfeeding behavior within families, thus controlling for unobserved heterogeneity between families, found no TW-consistent pattern (Schnettler 2010).

Other Factors Associated with Breastfeeding Behavior

A common finding is that women of lower socioeconomic status, operationalized by education, occupational status, or income, show lower rates of breastfeeding initiation, duration, and exclusivity (Dennis 2002). One reason for that may be education itself: mothers with less information may know less about breastfeeding and be less able to differentiate the truth-value of various informational offerings from external actors (cf. Bergevin et al. 1983). There are other individual-level differences in breastfeeding initiation, duration, and exclusivity. For instance, there is evidence that African Americans have lower breastfeeding rates in the USA. However, a huge part of this difference may be due to socioeconomic differences (Dennis 2002). Another factor is age: young mother below the age of 20 are less likely to breastfeed their child than older mothers (Dennis 2002, p. 15).

Conclusion

To conclude, all correlates of a mother's personal situation and her breastfeeding decision affect either the cost-benefit ratio of breast versus formula feeding or the beliefs that women hold. They can thus be parsimoniously explained with reference to a rational-choice framework in which women are seen as rational decision makers who try to maximize the net benefits of breastfeeding based on their beliefs about the costs and benefits of breastfeeding. Although evolutionary theory predicts that mothers may differentially breastfeed their children, existing evidence on such differential treatment seems inconclusive. Many studies examining forms of differential breastfeeding are based on small samples and/or, with few exceptions (e.g., Schnettler 2010), rely on between-family comparisons that may be confounded by unobserved differences between mothers.

Cross-References

- ▶ [Breast Feeding](#)
- ▶ [Maternal and Offspring Condition](#)
- ▶ [Trivers-Willard Hypothesis](#)
- ▶ [Wet-Nursing](#)

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Breeding

- [Function of Reproductive Strategy \(Kurzban\)](#)
- [Life Expectancy and Reproduction](#)

Breeding Systems

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Synonyms

[Artificial selection](#); [Selective breeding](#)

Definition

Breeding systems refer to the various ways of evaluation and selection of desired genetic traits in a breed or species.

Introduction

The purpose of breeding systems is to promote and preserve genetic traits of interest in a breed or species. Specifically, the practice of breeding systems is the process by which humans breed animals or plants to selectively produce offspring with desired phenotypic traits. Breeding systems should not be confused with mating systems (see ► [“Mating Systems”](#)). Mating systems refer to the various ways in which members of a given species arrange themselves to copulate (e.g., monogamy, polygamy). In contrast, animal breeding and plant breeding involve choosing male and female individuals within a species due to their desirable genetic traits and inducing them to sexually reproduce and have offspring that will express such traits. Humans may employ breeding techniques to select traits for various purposes, including selection of aesthetically improved fur in dogs

(e.g., Clutton-Brock 1995), or satisfaction of specific market standards for financial benefits, such as the commercial beef cow herds (Hammack 2003). In the last century, the controlled exploitation of breeding systems to produce certain phenotypical traits has become a common practice in agricultural and laboratorial contexts.

The practice of breeding systems in both plants and animals has records from early prehistory (Wright 1932). Archeological records have shown that plant species, such as rice and wheat, and animal species, such as dogs, have been significantly different from their ancestors (Ahn et al. 1993). For example, there is supportive evidence showing that cashew (*Spondias purpurea*) was selectively bred in Mesoamerica (Miller and Schaal 2006). There are records of active use of breeding techniques from thousands of years ago (Lush 2008) – for example, breeding systems were practiced by the Romans, and techniques of selective breeding were found in the Persian culture (Wilczynski 1959).

In the eighteenth century, the agriculturalist Robert Bakewell contributed significantly to the development of breeding systems, playing an important role in the British Agricultural Revolution. Bakewell systematically and successfully applied selective breeding on livestock. Bakewell’s techniques led to significant advances in the genetic quality of sheep, cattle, and horses and contributed to the development of the breeding systems field (Zeuner 1963). Accordingly, Charles Darwin provided a compelling explanation on how selective breeding and domestication of various animals, such as cats and dogs, produced variation over time (see Darwin 1859).

Several innovative techniques have been developed to manipulate the genetic value of a given domestic livestock. For example, *pure-breeding*, or sometimes referred as *true breeding*, involves producing offspring by inducing genetically similar individuals to sexually reproduce (Lush 1946). The *inbreeding* technique refers to the manipulation of the occurrence of desired genetic traits by breeding genetically related individuals (Dickerson 1973). *Outbreeding* refers to a cross between individuals of a single breed

that are not closely related (Dekkers 2004). *Cross breeding* is a breeding technique in which two individuals of different breed or species produce offspring, thus combining desirable qualities of genetically unrelated individuals (e.g., Labradoodle, a crossbred dog derived from the Labrador Retriever and Poodle; Trivedi 2004). For a detailed review of the various breeding systems and techniques in plants and animals, see Richards (1986) and Clutton-Brock (1988), respectively.

Breeding Systems

Pure-Breeding

A purebred (also true bred, or pedigree) individual refers to the progeny of any two individuals in a breed that presents consistent, replicable, and predictable characteristics (Lush 1946). For example, an offspring from two purebred dogs of a single breed (say, Labrador Retriever) will exhibit the phenotypical traits of its parents (i.e., pure or pedigree Labrador Retrievers) and not the traits of the offspring's ancestral breeds (Parker et al. 2004). The purpose of purebred production is to select desired, specific phenotypical traits to serve a market niche, such as livestock industry.

Historically, humans have been using pure-breeding techniques in several animals. For example, purebred dogs are usually a modern breed of dog (Parker et al. 2004). The domestication of the horse caused the appearance of some domesticated stallions (Wade et al. 2009). Several purebred cats have been developed by humans due to their commercial benefits. In fact, cat registries identify between 40 and 70 breeds of cats (e.g., The International Cat Association 2017; Fédération Internationale Féline 2017), with new breeds being documented every year, each having unique lineage and features. Most farm animals are purebred, including pigs, goats, and sheep (for a review, see Clutton-Brock 1988).

Because the long-term use of pure-breeding techniques produces a limited gene pool, purebred animals are susceptible to an extensive variety of congenital health complications (e.g., Ackerman 2011). This is particularly

common in contexts where an emphasis on aesthetics overcomes body functionality and healthy immunological system (e.g., competitive dog breeding). Nonetheless, the costs associated with the congenital health problems may be aggravated when breeders use inbreeding techniques (e.g., Afzal 1994).

Inbreeding

The inbreeding technique results in offspring produced by genetically related individuals (Dickerson 1973). Inbreeding is often used to expose deleterious alleles. Specifically, inbreeding promotes homozygosity, thus increasing the odds of offspring to express deleterious or recessive traits (Nabulsi et al. 2003). This may lead to a reduced physiological fitness of the inbred stock (i.e., inbreeding depression; Jiménez et al. 1994). Therefore, livestock breeders may use inbreeding techniques, for example, to develop phenotypically enhanced breeds by identifying undesirable characteristics in offspring that will further be eliminated in the next stock generations. Inbreeding in plants often occurs naturally in the form of self-pollination (Richards 1986).

A breeding system was then developed to avoid the expression of deleterious alleles caused by inbreeding procedures – such a technique is referred to as outbreeding (or outcrossing; e.g., Bernstein et al. 1985). Specifically, inbreeding occurs when *genetically related* individuals produce an offspring, and outbreeding occurs when an offspring is produced by *genetically unrelated* individuals within a single breed. Inbreeding and outbreeding are often understood as opposite techniques – despite the debate about the optimal genetic relatedness for inbreeding and outbreeding systems (e.g., for a software for relatedness and inbreeding coefficients, see Wang 2011). Inbreeding techniques are often comprised by a genetic relatedness that varies from full brother and sister to cousins (e.g., Clutton-Brock 1988).

Outbreeding

Outbreeding (or outcrossing) is a breeding procedure that involves the insertion of unrelated genetic traits into a breeding line. Outbreeding

usually increases the genetic pool within a population, thus reducing the likelihood of an individual to express deleterious alleles that may cause congenital health problems (e.g., Dickerson 1973). In outbreeding, breeders may find individuals in a stock that are distantly related to a common ancestor, since all individuals within the species are susceptible to express a genetic trait if the genetic trait is carried throughout the generations (i.e., the founder effect; Ladizinsky 1985). Therefore, well-established breeds often present a large gene pool, and such a variety of genetic expression increases heterozygosity (i.e., variability and diversity of phenotypes).

Outbreeding is the most common used breeding system by commercial breeders (Dekkers 2004), since outbreeding breeders often need to increase heterozygosity to eliminate undesired genetic traits, to therefore satisfy commercial standards. As a breeder detect the desired genetic traits, he or she may strategically induce mating to eliminate associated undesired genes, thus preserving the desired ones. By doing so, breeders produce a breed that satisfies the commercial standards and that may be further used for inbreeding. Because the desired traits do not always correspond to the traits expressed by dominant genes, the outcrossing breeder may end up with breeds having several deleterious alleles – for example, many dog breeds express deleterious traits that cause congenital health problems (e.g., Parker et al. 2004). This is possible because outbreeding allows for the recessive traits to propagate throughout a population (Dekkers 2004).

Crossbreeding

The crossbreeding technique describes crosses between different breeds within a species. That is, a crossbred usually refers to an individual with purebred parents of two different breeds. The practice of crossbreeding is a well-accepted practice among commercial breeders (e.g., most lambs in the American market are crossbreds; Beermann et al. 1995). Crossbreeding allows breeders to produce a breed with a variety of desired genetic traits of two or more breeds (i.e., hybrid vigor; Crow 1948). Breeders should use crossbreeding techniques in a responsible way – some

crossbreeding in the animal industry may lack systematic procedures or may not employ techniques that optimize the benefits of crossbreeding (e.g., “mutt dogs”). For example, although crossbreeding is generally used to provide better health conditions to breeds (Beermann et al. 1995), negligent crossbreeding may promote undesired assortment of a purebred genetic pool, which may eventually lead to the extinction of a breed within a species.

A good crossbreeding technique involves the strategic selection of the genetic traits of different breed to produce a new breed (i.e., crossbred) that satisfies commercial standards (e.g., quality of meat; Touraille et al. 1989). Good use of a crossbreeding system allows breeders to produce a breed with complementary traits – that is, production can be optimized when breeding systems, such as crossbreeding, produce breeds that express the “optimal ratio” between desired and undesired genetic traits (Wright 1932). Crossbreeding may also be used to proliferate a highly desired, rare mutation without incurring the costs of an inbreeding system (e.g., propagation of deleterious alleles; Clutton-Brock 1988). In contrast, crossbreeding systems are difficult to perform with a few individuals from different breeds within a species – the genetic pool provided by the individuals from each breed may not offer enough genetic variance for the breeder to optimally propagate the desired genetic traits (Wright 1932).

Humans have been performing crossbreeding in several species. Some breeds of domestic cat that were recently recognized are crossbreds between existing, well-established breeds (e.g., Lipinski et al. 2008). In cattle, systems of crossbreeding are often used to produce breed with complementary traits. For example, crossbreeding may occur when the breeder induces mating between a purebred female and a purebred bull with desired traits, but that are adapted to different environments, resulting in individuals with desired traits of both parents (Clutton-Brock 1988). Moreover, the various breeds of sheep allow crossbreeding to be used to enhance genetic traits in lambs that may be further used for commercial purposes (e.g., Leymaster 2002).

Conclusion

Breeding systems serve to promote and preserve desired genetic traits in a breed or species. Over the past centuries, humans have developed several breeding systems (e.g., pure-breeding, inbreeding, crossbreeding). Each breeding system has unique benefits, and the use of different techniques may lead to different outcomes. For example, crossbred (vs. purebred) pigs offer substantial advantages for commercial breeders because the expression of certain complementary traits in pigs is key to satisfy the swine industry standards (Stein et al. 1990). Accordingly, most commercial swine producers use crossbred pigs rather than purebreds, especially in the carcass and meat industry (Van Wijk et al. 2005).

Breeding systems are mostly used for commercial purposes. In such a competitive market, where breeders are tempted to use different techniques to rapidly achieve commercial standards, breeding systems should be used in a responsible manner. The genetic consequences of irresponsible use of a breeding system may include a reduction in the frequencies of relevant alleles or genes, which may cause, for example, poor genetic variance or propagation of undesired, deleterious traits.

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Brett Laursen

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Synonyms

[Author](#); [Researcher](#)

Definition

Brett Laursen is a professor of developmental psychology specializing in the study of adolescent peer and parent relationships at Florida Atlantic University.

Introduction

Brett Laursen's research is predominately focused on the transmission of influence across the childhood and adolescent years. His previous scholarship includes, but isn't limited to, investigations of longitudinal influence between children and their parents, peers, siblings, friends, and romantic partners. While most of his research does not fall under the purview of evolutionary psychology, Laursen did collaborate with Lauri Jensen-Campbell to propose an evolutionarily informed developmental model of social exchange within adolescent romantic relationships. This model incorporates social exchange theory with evolutionary psychology's precepts regarding mate selection in order to propose how adolescents' romantic behaviors might be driven by different distal and proximal influences depending on their physical, social, and cognitive maturation. The foundations and a description of their model are described below.

Social Exchange Theory

According to social exchange theory, individuals keep track of the rewards and costs of each social relationship and seek to raise the former while minimizing the latter (Thibaut and Kelley 1959). Those with a higher reward/cost ratio were considered more attractive. Revisions to the theory propose that more complex patterns of exchanges are apparent in closer relationships (Kelley and Thibaut 1978). For example, in adult romantic relationships, interactions tend to fall into two patterns: (a) one where each member seeks equality of outcomes across members and (b) one where each is focused on improving both members' outcomes. A further distinction can be made between relationships where each member is focused on their own rewards (e.g., exchange relationships) from those where each member believes their partners' benefits are their own rewards (e.g., communal relationships). In general, when a romantic relationship maintains the same reward/cost ratio between both members and when each member focuses on their partner's

benefits, interdependence increases. As this occurs, romantic relationships are expected to transition from exchange to communal and from an open (voluntary) to a closed (committed or married) status.

Evolutionary Psychology

Evolutionary psychology (Buss 1995; Kenrick and Trost 1989) also provides explanations for mechanisms underlying social exchange in romantic relationships. Evolutionary psychology posits that many aspects of social relationships are adaptations which promoted the survival of human ancestors. Heterosexual romantic relationships were particularly important in this regard. Humans who utilized romantic relationships to increase personal gain and, as a result, survivability were also those who were most likely to bare and raise offspring. Consequently, in prehistory, females tended to seek mates who had greater resources to help offspring, whereas males sought mates who had physical signs of an ability to carry offspring to term (Trivers 1972; Feingold 1992). While these tendencies are apparent today, the mechanisms by which they are manifested are likely colored by the modern world.

A Developmental Model of Social Exchange in Adolescent Romantic Relationships

Building upon both social exchange theory and evolutionary psychology, Laursen and Jensen-Campbell (1999) have proposed a developmental model of social exchange in adolescent romantic relationships. This theory posits that, in the adolescent romantic domain, distal influences such as environmental constraints and evolutionary-based preferences predominate in early adolescence but typically give way to more proximal influences in late adolescence. Importantly, due to limitations in physical characteristics and cognitive abilities, young adolescents are generally limited to exchange relationships which are

focused on self-centered gains. During this time, environmental, cultural, and physical constraints hold heavy influence. For example, in many cultures today, young adolescents' dating-related freedoms are often constrained to prevent early pregnancies. Physically, many young adolescents also have not developed the secondary sexual characteristics needed to be competitive in the eyes of potential partners. Furthermore, young adolescents have not cognitively developed enough to understand that traits such as kindness and compatibility are important considerations in addition to evolutionarily informed signs of physical attractiveness. With age however, many of these limitations subside, and social exchanges grow more complex due to maturational development and changes in social norms. Older adolescents are then in a position to draw upon past experiences and are better able to recognize that beneficial relationships are those that foster individuality, are not driven solely by physical attractiveness but extend to psychological desirability, and are those that are communally focused on fulfilling the needs of both members.

Conclusion

In their developmental model of social exchange in adolescent romantic relationships, Laursen and Jensen-Campbell (1999) build upon social exchange theory to outline a guiding framework for future research on adolescent romantic relationships, an area which is often overlooked. Additional research within this framework may reveal support for the proposed proximal and distal influences of adolescent romantic behaviors, as well as identify important antecedents to the development of healthy adolescent relationships.

Cross-References

- ▶ [Adolescent Issues](#)
- ▶ [Opposite-Sex Relationships](#)
- ▶ [Social Exchange Theory](#)

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Brian Boyd

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Definition

Brian Boyd is a leading scholar of evolutionary and biocultural approaches to art, especially literature. He conceives of art as a form of cognitive play with pattern that exercises and refines our creative, cognitive, emotional, and social skills.

Introduction

Brian Boyd is a University Distinguished Professor of English at the University of Auckland. Within literary criticism, he is best known for his work on the Russian-American novelist and

lepidopterist, Vladimir Nabokov. Since the late 1990s, Boyd has also been one of the leading advocates and practitioners of evolutionary, biocultural, and cognitive approaches to the study of art, especially literature and fiction. He argues that art is a human adaptation, a form of *cognitive play with pattern* (Boyd 2009) that has coevolved with human cognition, emotion, and sociality. Boyd stresses the social and cooperative origins and effects of art. All forms of art, especially fiction, can enhance social cohesion and control (Boyd 2009, 2018).

He proposes a *multilevel model* for analyzing art and literature, comprising general evolutionary principles, the distinctly human aspect, local socio-historical variation, individual differences of authors and audiences, and details of particular works. Artists and audiences should be seen as *problem-solvers*, balancing *cost–benefit trade-offs* of the composition and reception processes, with a special focus on the problem of engaging *attention*.

Boyd's most notable works include *On the Origin of Stories: Evolution, Cognition, and Fiction* (2009), which details his account of the evolution and function of art and storytelling; and *Why Lyrics Last: Evolution, Cognition, and Shakespeare's Sonnets* (2012), an evolutionary analysis of nonnarrative verse. He also co-edited *Evolution, Literature, and Film: A Reader* (Boyd, Carroll & Gottschall 2010); and contributed to *Literary Animal: Evolution and the Nature of Narrative* (Boyd 2005), and *Darwin's Bridge: Uniting the Humanities and Social Sciences* (Boyd 2016b). He co-curated, with Steven Pinker, Geoffrey Miller, and Mark Changizi, an exhibition contrasting four different explanations of the origins of human art at the Museum of Old and New Art in Hobart (Boyd 2016a). His recent article, "The Evolution of Stories: From Mimesis to Language, from Fact to Fiction" (Boyd 2018), provides an updated account of the human capacity for and preoccupation with fiction, from mimetic to verbal communication, and from factual to invented stories. Boyd is currently working on *On the Ends of Stories*, and on a biography of Karl Popper, a founder of evolutionary epistemology.

Art as Play with Pattern

Boyd (2009) argues that art evolved from the especially strong human predilection for pattern-recognition (a way to understand the world in real time, common to most organisms) and the predilection for play as a way to hone valuable skills in nonurgent situations (common to all mammals, many vertebrates, and even some invertebrates). The amount of play in a species increases with the level of behavioral flexibility and the degree of sociality. Humans, both highly flexible and social, play even in adulthood. Like other animals, we practice our physical abilities through play. But since humans thrive mainly through the mastery of cognitive and social skills, we practice, refine, and extend them in art. As animal play-fighting, human art is, in Boyd's view, about creative exuberance and self-rewarding fun, but also about acquiring greater sense of control – both of ourselves and of our circumstances.

The Evolution of Fiction

According to Boyd (2009, 2018), in the art of fiction we play with patterns of narrative (agency, causality, context, perspective), language, and social interaction – all elements integral to human thought, communication, and sociality.

Boyd's evolutionary analysis of fiction focuses both on ontogeny and phylogeny (Boyd 2009, 2018). Ontogenetically, fiction develops out of children's pretend play, although such play is also scaffolded by the stories children are told. Phylogenetically, fictional storytelling most likely developed around 400,000 years ago when the invention of campfires allowed additional time for social interaction and information-sharing. Other precursors of fiction include dreams, confabulations, and lies.

Boyd's evolutionary account of fiction holds that the production and comprehension of fiction requires a range of cognitive capacities connected with tracking and recombining of information: event comprehension, memory, imagination, and communication (Boyd 2009, 2018). These have developed in a range of species. However,

increasing human sociality and co-dependence created the selective pressure for more information-sharing, more efficient means of communication, and a better understanding of our conspecifics. The developments of narrative, our main mode of understanding, and language, our main tool of communication, allowed our ancestors to extend their knowledge beyond what they could learn first-hand (Boyd 2018, and references therein). The more we knew about each other, the more such knowledge became crucial to our success, to effective competition and cooperation among individuals and groups. Boyd (2009, 2018) notes that fiction extends our social knowledge even further – to the hypothetical, the imagined, the exaggerated – and presents it in a condensed, evocative form so as to capture our attention and stir our emotions, which in turn amplifies and prolongs its impact.

Social Underpinnings of Art and Storytelling

Boyd (2005, 2009, 2016a) stresses the social and cooperative nature of art (in contrast to Geoffrey Miller's [2000] hypothesis that art developed as a result of the processes of sexual selection). Music, dance, storytelling, and visual arts (body painting, landscape marking, decorating of everyday objects) have been used for millennia to transfer valuable knowledge and skills, honor group traditions, pledge group allegiance, and display group's power and wealth to outsiders. Boyd points out that art depends on individual flair and skill but always in relation to social rules and traditions. Artistic endeavors can bring fame and fortune to gifted individuals but most of art, especially early in human evolution, required social approval and support. Unless the artist's activities were sanctioned by and recognized as valuable for the group, the artist would not gain any prestige or privileges. Also, in many forms of art, artists use their special talents to beautify or acknowledge the status of *others*, not themselves.

Boyd (2009, 2018) maintains that storytelling in particular is connected with our social intelligence, our capacity to understand other people's

thoughts, feelings, and intentions, and our need to monitor their behavior. Stories, both factual and fictional, help us navigate the social realm and serve as a means of social attunement.

Artistic and Biological Adaptation

Boyd (2009) argues that art is a human adaptation, not simply a by-product of human cognitive abilities (as claimed by Steven Pinker, 1997). However, Boyd points out that an evolutionary approach to art and/or literature does not depend on the idea that they are adaptations: it “simply requires that we take seriously that evolution has powerfully shaped not just our bodies but also our minds and behavior” (Boyd 2009, p. 210). More recently, Boyd has argued that “the very opposition of adaptation and byproduct reflects an overly gene- and individual-centered view of evolution” (Boyd 2018, p. 12).

In Boyd’s view, art depends largely on social learning, and the persistence of many artistic conventions may be explained via the coevolution of signals and preferences (Boyd 2016a, and references therein). Some forms of art, such as verse, may be universal, but not necessarily adaptive (Boyd 2011, 2012).

Evolutionary Theory and the Study of Art and Literature

In his approach to art and literature, Boyd (2009, 2017) highlights three aspects of evolutionary theory as particularly relevant: the idea of *continuity and variation*, the *problem-solution model*, and *cost-benefit trade-offs*. Continuity and change are at the heart of evolution and art: long-standing history is the basis for new developments and innovations, and widespread trends include local and individual variations. Evolution is about solutions to recurrent problems of survival and reproduction. The solutions that offer more benefits and/or fewer costs in a given environment are favored by natural selection and persist into future generations. Boyd suggests that art works in a similar way: both artists and

audiences are problem-solvers. They face a range of composition and comprehension problems, but the crucial problem in art is that of *attention* (Boyd 2009, 2017, 2018). Artists seek to engage the audience’s attention while reducing their own invention costs and maximizing benefits, such as prestige or financial rewards. Audience members, consciously or not, weigh up the costs of diverting their attention, time, and energy from other concerns, or from other works of art, against potential payoffs, such as pleasure, information, and intellectual and/or emotional stimulation.

The Importance of Attention

Boyd (2009, 2017, 2018) notes several reasons for the importance of attention. Firstly, attention is a limited resource and is therefore subject to intense competition, both within individual brains where numerous sensory inputs and neural processes compete for metabolically costly neural space, and within social groups where various individuals vie for positive attention as a route to status and influence. Secondly, one of the preconditions of art is the unique human disposition to *joint attention* – noticing something worth others’ attention, drawing their notice to it, and checking that they are attending to the features that caught our attention. And finally, art has to earn the audience’s attention before it can impart any meaning or fulfill any other function.

Multilevel Analysis

Evolutionary sciences seek multilevel explanations, from local ecologies to genes to large-scale societies. Similarly, Boyd (2009, 2016b) argues that the evolutionary analysis of art and literature can and should include multiple interconnected levels: (1) the **global**: evolutionary principles common to human and other species; (2) the **human**: evolutionary principles shared by different cultures and individuals; (3) the **local**: differences in culture, time, and place; (4) the

individual: characteristics of individual authors and audience members; (5) the **particular:** a specific text or work of art; and (6) the **detail:** various elements of each work as separate problems and solutions for the author and/or the audience member. How relevant each of these levels is to any given analysis will depend on the questions raised by the researcher.

Boyd demonstrates how such a model can generate new and exciting insights about the artistic and psychological dimensions of texts as diverse as Homer's epics (Boyd 2009), William Shakespeare's sonnets (Boyd 2011, 2012, 2016b), Art Spiegelman's comics (Boyd 2010, 2016b), and Dr. Seuss's children's books (Boyd 2009).

Conclusion

Brian Boyd has made a significant contribution to understanding the human capacity for and fascination with art, especially literature and fiction. He argues that art arises from and further develops adaptive human predilections for pattern-recognition, play, shared attention, and cooperation. Art boosts human creativity and gives us a sense of control over the uncertainties of our world. It enhances group cohesion while also raising the status of talented individuals. Boyd (2009, 2018) emphasizes that fiction, in particular, emerged from our adaptive predisposition for sociality, information-sharing, and play, and has had a profound impact on individual and social development, emotion, cognition, behavior, and very likely on our genes.

Cross-References

- [Adaptation](#)
- [Adaptive Learning](#)
- [Art Production, Appreciation, and Fitness](#)
- [Cooperation and Social Cognition](#)
- [Fiction](#)
- [Literature](#)
- [Play](#)
- [Problem Solving](#)

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Brian Hare

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Synonyms

[Anthropologist](#); [Author](#); [Researcher](#)

Definition

Brian Hare (Ph.D.) is an associate professor of evolutionary anthropology at Duke University in North Carolina and the founder of the Duke Canine Cognition Center. He received his Ph.D. from Harvard in 2004. He is widely published in many high-profile journals, with articles on dog and primate comparative cognition and psychology. His papers are some of the most cited on dog behavior and intelligence.

Introduction

Dr. Brian Hare is well known both inside and outside the academic community. He has received media coverage both nationally and internationally through “Daily Mail, The Telegraph, The Economist, The New York Times, The New Yorker, National Geographic, Time, The Washington Post, the Los Angeles Times, Nature, Wired, Science magazine, CNN, and ABC (Australia)” (Hare n.d.). In 2004, the Alexander von Humboldt Foundation and the German Federal Ministry of Education and Research named him a recipient of the Sofja Kovalevskaja Award, which is Germany’s most prestigious award for scientists under age 40. In 2007, Smithsonian magazine named him one of the top 37 scientists in the United States under age 36. In 2009, Dr. Hare gave keynote addresses at the annual conferences for the Assistance Dog Training Society and the Association of Pet Dog Trainers, which are among the largest dog training societies in the United States (Hare n.d.).

Professional Work

Dr. Hare is the co-founder of *Dognition* (see www.dognition.com), a service that provides dog intelligence assessments via online video tutorials. Specifically, owners can pay for the Dognition Assessment, which is composed of interactive games and putative expert analyses that are designed to give the client a unique perspective on how their dog sees the world (Dognition 2016).

Data collected through this service is intended to be analyzed and published in scientific journals, benefitting both dog owners (who learn more about their dogs) and researchers (who gain information about dog intelligence and behavior across many dogs from around the world). Dognition’s research has thus far (at least, as of 2017) resulted in the publication of one journal article (Stewart et al. 2015). This study critically examined the reliability of the data collected by dog owners via Dognition, with positive results, and also found that dogs vary independently on multiple cognitive domains based on their performances in different cognitive tasks.

Dr. Hare is also the coauthor of the book “The Genius of Dogs,” written with Vanessa Woods. This book summarizes Dr. Hare’s research on the domestication of dogs and how it influences our understanding of our family pets (Hare and Woods 2013). Furthermore, Dr. Hare has pioneered research on how domestication has affected dog cognition. His research suggests that dogs are born prepared to read human social cues, whereas wolves are not (Hare et al. 2002), and that dogs are excellent at reading human communicative cues and understanding human visual perspectives, which he argues are heritable skills that evolved during domestication via selection based on fear versus aggression toward humans (Hare and Tomasello 2005).

Theory of Mind in Chimpanzees

Although perhaps better known for his work with canines, Dr. Hare is also a major researcher in the field of nonhuman theory of mind, particularly within chimpanzees. Theory of mind is the ability to understand that other animals’ behaviors are caused by mental states. For example, the behavior of gazing at an object can be equated with the mental states of seeing the object and knowing the object is there in humans or other animals with theory of mind. Hare’s two most cited papers on this topic both detail experiments where chimpanzees are allowed to observe each other’s behavior during food (Hare et al. 2000, 2001). In both studies, the authors concluded that chimpanzees were taking into account the visual perspectives and knowledge of other chimpanzees, rather than

just responding to behavioral cues. These two studies, and the conclusions drawn by the authors, have been hotly debated (e.g., Povinelli and Vonk 2003, 2004). See the entry on Canines for more information about dog theory of mind.

Conclusion

Dr. Hare is a leading research in the field of comparative psychology, particularly with regard to dog behavior, cognition, and the process of domestication.

Cross-References

► [Canines](#)

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Bridal Cost

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Synonyms

[Dowry](#)

Definition

Marriage transactions from brides and their families to grooms and their families.

Introduction

A salient feature of marriage practices in many traditional societies is the transfer of money, goods, and services at the time of marriage. When these transfers are made from brides and their families to grooms and their families they are broadly classified as dowries. A transfer from the groom and his family to the bride and her family on the other hand is generally termed as a bride price. The custom of marriage transactions is known to have a patterned distribution worldwide (Bergstrom 1993). Out of the 1,267 societies listed in Murdock's Ethnographic Atlas, while two thirds practice bride price, only 6 % follow the custom of dowry (Murdock 1967).

Moreover, whether a given society practices dowry or bride price has also been theoretically linked to a number of socioeconomic factors such as form of inheritance system and residence of the bride after marriage, kinship organizations, dominant mode of production and the consequent economic contribution of women relative to men, social stratification, and availability of brides and grooms in the marriage market. The purpose of this key idea is to examine the body of literature on bridal cost, henceforth dowry, particularly in India, to describe the practice, both past and

present, and to explore the possible reasons for its continued prevalence despite modernization and amendments to laws.

Pre-Mortem Inheritance

A primary feature of the inheritance laws in India is the distinction between joint ancestral property, which includes land and individually acquired property usually parental wealth. Under the Hindu Succession Act before 1956, while a male was entitled to a share in ancestral property by birth and a share in parental property by survivorship, a female was excluded from succession even to her father's property (Carroll 1991). Thus, the practice of dowry can be traced back to the Hindu Succession Laws as they stood before the reforms made in 1956. Given the exclusion of daughter's rights to inherit and virilocality (system in which a daughter leaves her natal home upon marriage) the practice of dowry compensated for the legal restrictions by allowing presentation of wealth to a daughter at an appropriate time, usually her marriage in the form of movable property. Dowry is subsequently viewed as a pre-mortem inheritance of a daughter, *Stridhanam*, which prevents break-up of family property and at the same time increases her bargaining position and resources of her conjugal household (Krishnamurthy 1981; Miller 1981; Sharma 1984).

However, the historical notion of dowry as a form of pre-mortem inheritance that goes to a daughter upon marriage does not explain the variation in the practice of dowry giving. Not all Indian brides are married with dowry nor are dowry givers a purely random sample of the Indian population. Moreover, dowry and inheritance resemble one another neither in timing and value nor the manner in which they are allocated. That the dowry comes at a different time from the male inheritance, is linked to marriage, that it is worth less, and is allocated differently simply indicates that the Indian society has two ways of devolving property, one for sons and one for daughters. While the inheritance for men is guaranteed, without marriage there is no dowry

and hence no inheritance for women (Agarwal 1995). Furthermore, it is not clear, with what justification do poor families, which do not have parental property to share, spend on marriage of their daughter beyond their capacity?

To eliminate the inherent gender inequality in the Succession Laws, reforms were made in 1956 to provide *daughters* and sons an equal share in their father's property. However, a male child's right and a female child's denial to ancestral property by birth remained intact. A number of states in the southwest part of the country further amended the Hindu Succession Act to grant daughter's equal coparcenary rights by birth as enjoyed by their brothers. Specifically, the states of Andhra Pradesh, Tamil Nadu, Maharashtra, and Karnataka passed the amendments in 1986, 1989, and 1994, respectively, to make a daughter's status equal to that of sons (Agarwal 1995). These reforms were adopted nationwide in 2005 thereby making the need for any means of "indirect inheritance" for women redundant. However, while the size of bequest dowries has decreased, the reforms have not prevented the prevalence and spread of the dowry custom across India (Roy 2015).

Kinship Organizations and Mode of Production

Although the practice of dowry is largely driven by limitations on women's access to joint family property in spite of the reforms in the Succession laws, the regional dichotomy observed in the nature of marriage payments especially between North and South India is attributed to the differences in their kinship organizations. While the magnitude and frequency of dowry payments in the North is explained via its preference for marriages outside kin groups of the same or higher social standing and patrilineal inheritance system that denies women rights to family property, prevalence of equal gift giving or bride price in the Southern part of the country is credited to its recognition of women's rights to land, marriages between consanguine, and partners of equal status (Dalmia and Lawrence 2009; Trautmann 1993; Dyson and Moore 1983). It is important to note,

however, that a vast majority of studies illustrating the heterogeneity in marriage transactions between North and South India are based on ethnographies of single villages or districts that are now over 35 years old. In addition, surveys of villages and districts for the purposes of ethnographic studies are likely to describe a community's norms instead of the actual functioning of the marriage markets in the region suggesting further examination of the reasons for the variations in marriage transactions.

To this effect, Goody (1973) suggests that women's role in production, particularly their agricultural labor, is a crucial determinant of whether a bride price or a dowry will be paid at the time of marriage. Accordingly, he attributes bride price in the south to the greater value and participation of female labor in its rice-based agrarian systems and dowry in the north to its reliance on wheat production and hence plough-based cultivation where women do significantly less agricultural work compared to men. Further complicating the landscape, Gulati (1975) and Schlegel and Eloul (1987) find that even regions characterized by low rates of female labor force participation, such as Kerala, Orissa, and Assam, exhibit bride price as the predominant form of marriage payment. Furthermore, when looking at the areas of low female labor force participation stretching from North to East India, what is surprising is that the region encompasses both rice and wheat producing states, suggesting that there is more to the reasoning behind the nature and size of marriage payments observed in India (Miller 1981).

Spread and Escalation of Dowry Payments

In the 1950s a number of anthropologists noticed that communities that had traditionally paid bride prices had begun to pay dowries, while communities that were traditionally dowry paying were subject to dowries of a much greater magnitude. Consequently, a practice that was once confined to some communities among the propertied in North India soon became customary and uniform across all caste and class groups in India. Social anthropologists

often explain the universal adoption of the dowry practice as an outcome of *Sanskritization* – embracement of upper-caste patterns of behavior by members of lower caste as a means of acquiring higher social caste (Srinivas 1984). In other words, the observed shift in regime from bride price to dowry in all castes is simply a case of upwardly mobile behavior. However, this explanation is weak on two counts. First, it is unlikely that the benefit gained by lower castes in behaving like upper-caste *Brahmins* is greater than the immense destitution they often face by paying dowries. According to Anderson (2007) and Bloch and Rao (2002), while average dowry demands ranged between six to eight times the average annual income of the bride's household in the period 1960–1995, the amount of dowry payments increased 15 % between 1921 and 1984. Second, real dowry payments have increased even in castes in which historically dowries have been paid (Rao 1993).

Moreover, conditions in the marriage market also depend upon the availability of marriageable men and women. Where marriage transactions involve wealth transfer by only one gender, they signal a gender bias in the intensity of competition for marriage partners: competition is stronger among (or on behalf of) members of the gender that pays. The idea that a deficit in the population of either gender could influence marriage transactions has been around for some time (Dickemann 1979). As far back as the beginning of this century, Sir Herbert Risley (1915) used the gender imbalance argument to explain why dowry was being practiced at the top of India's hypergamous castes, while bride price prevailed at the bottom of the caste ladder. That is, the upward flow of women produced by hypergamy – practice of a woman marrying a man of superior caste or class – resulted in a surplus of women at the top and a deficit of women at the bottom. Thus, while men of higher rank received a dowry on marriage, those at the bottom paid bride price to get their wives.

Somewhat surprisingly, however, the modern-day anthropologists tend to dismiss a demographic imbalance in the marriage market as the reason for the growing popularity of dowry marriages (Bhat and Halli 1999). Although a few researchers exposed to the demographic literature

have pointed out its relevance (Rao 1993; Billig 1992; Caldwell et al. 1983), a systematic analysis of the source, size, and trend of the gender imbalance in the Indian marriage market has yet to be undertaken. While it is true that the ratio of males to females in the total population has been steadily rising in India since the beginning of this century, it is important to recognize that women marry at younger ages than men and that in a growing population with a rising annual flow of births, there could still be an excess of women at marriageable ages, because men at older ages are drawn from smaller birth cohorts. Caldwell et al. (1983) were one of the first to suspect the relevance of this phenomenon – known as the “marriage squeeze” in demographic literature – to the growing popularity of dowry marriages in India. Accordingly, marriage squeeze is viewed as the foremost reason for the contemporary marriage practices in India.

Although the imbalance in the gender ratio may explain who gets the rents from marriage, it does not, however, explain the variation in the size of these monetary payments in individual marriages. Moreover, empirical evidence in favor of rising dowries and marriage squeeze, as an explanation for the increase, is both thin and mixed. While early academic accounts by Epstein (1973) and Billig (1992) were based on small sample sizes focused on particular regions of India, the first attempt at providing statistical evidence of dowry inflation, using a sample size of 141 households, was undertaken by Rao (1993). Unfortunately, in later replications of Rao’s results, Edlund (2000) was unable to find support for the marriage squeeze argument. More recent studies, using multiple data sources, have also failed to corroborate the widespread claim that dowry payments have increased in India due to the demographic imbalance in the availability of marriageable brides and grooms (Arunachalam and Logan 2016; Dalmia and Lawrence 2010; Dalmia 2004).

Equalizing Differences

Today the popular view in India is that demographic characteristics of the bride and groom

besides age are the main drivers of the size of dowry and whether it is even paid at the time of marriage. First formalized by Becker (1991), this view is grounded in a model that sees dowry as a spot price that clears the marriage market. In other words, it proposes that dowry constitutes the price of a relevant match that is derived from the individual traits of the bride and groom and their respective households. Thus dowries compensate for bride-groom quality differences and are simply the price of a good match. This also explains the multiple price equilibria observed in the Indian marriage market where dowry varies particularly by sufficient heterogeneity in male attributes.

Rise in importance of education as a determinant of income-earning potential and hence groom attractiveness is considered to account for the increased male heterogeneity. Economic progress and modernization over time has meant that potential grooms are better educated and have more opportunities compared to their fathers (Edlund 2000). This has led to a new criterion for the selection of grooms based upon achieved status. Although women have also experienced generational progress in the realm of education, they have been unable to take advantage of the subsequent employment opportunities (Jakimow 2012). As a result, it is considered worthy to acquire as a son-in-law an educated man who maybe able to occupy a position of power and influence in the organized sector. As the number of such men is limited in relation to the number of girls in the marriageable age, the market forces come into operation and by an informal bidding process, the groom price is settled, giving the community a method of groom allocation among the bidders (Anderson 2003).

That a son’s education will have bearing on his marriage market prospects is an important factor in calculating the returns to educating that son. The expected payoff depends upon the level of investment made in human capital, and the actual outcome for each man depends on how well his family can capitalize on the investment. A related matter is that of underinvestment in daughters. Dasgupta (1993), among others, points to patrilocal marriages – custom in which a married

couple settles with the husband's family – as one source of positive externalities to human capital investment in daughters, making investments in daughters recoupable to a lesser extent than the investment in sons. With limited access to jobs and lack of rights to inherit ancestral or parental property, the bride's household looks for men who can provide security, comfort, stability, and status, which means locating the most well-educated man with the greatest economic potential that one can find (or afford), as given the constraints it seems rational to invest in a share of the grooms prospects.

Moreover, universality and early marriage are two important features of nuptiality in India. There is a strong urgency for women to be married within an acceptable age range, as an unmarried daughter can be a severe economic and social liability to her family. A supplementary reason is the belief in declining fecundity with age. The culturally prescribed necessity for women to marry varies very little with economic, social, and demographic circumstances (Caldwell et al. 1983). Such imperative is evidenced by the fact that 95 % of the Indian women are married by the age of 21 (Goyal 1988). It is said that to a suitable groom a girl should be given in marriage even if she is immature, and if she has attained womanhood her marriage should not be withheld even if the man is unworthy (Sharma 1993). Put together, in the absence of legal or socioreligious compulsions, marrying a daughter off at the cost of dowry must be considered a choice revealed preferred over the alternative of her remaining unmarried and retaining the value of dowry. This indicates that there exist "gains from marriage" for the bride's family, which are at least equal to the value of dowry given.

Furthermore, if the marriage market is competitive with no hidden information, then it may be stipulated that the "gains from marriage" for the bride's family *exceed* any "gains from marriage" for the grooms' family, and it is the net difference in gains that the latter appropriates as dowry. Consequently, in a buyer's market, created by the relative scarcity of a suitable match in combination with strong preference for early, universal and monogamous marriage the subsequent

heightened competition for eligible grooms leaves no alternative but to offer a dowry with one's daughter. Even though the demographic squeeze is resolved through an increase in the average age at marriage of women in the sense that almost all women and men find a mate, the pressures associated with the adjustments in the age difference influence the size of dowries paid (Sautmann 2011).

Empirical work by Dalmia (2004) using retrospective data on marriage transactions collected from 1,878 households in the states of Uttar Pradesh (North India) and Karnataka (South India) provides strong support in favor of the equalizing differences role of dowry payments. Exploiting the critical feature of dowry as a spot price, she regresses dowry on the characteristics of the bride, groom, and their respective households as well as implicit features of the marriage market such as the demographic availability of potential spouses, region, etc. Her results indicate that dowry is a simple economic transaction between two families, functioning to "equalize" the imbalances in the value of marriage. Measurable groom characteristics on which compensating price differentials arise in the study include groom's age at marriage, his education, and height. More recently, Arunachalam and Logan (2016) using retrospective data from the 1996 Matlab Health and Socioeconomic Survey also found strong support for the role of dowries as a price that clears the marriage market in Bangladesh.

Conclusion

Several reasons have been propounded to explain the history of dowry payments in India. These include the form of inheritance system, kinship organizations, individual and household characteristics of the bride and groom, and the demographic availability of suitable grooms in the marriage market. Although rich, academic literature examining the heterogeneity in cultural, demographic, and socioeconomic factors influencing marriage transactions has been unable to completely or sufficiently explain the

prevalence, frequency, and magnitude of dowry payments in India. While lack of availability of representative data on dowries is one reason, the shift in interest to examining the recent trend of rising dowries, referred to in the literature as dowry inflation, is another. Consequently, research on dowry is divided into two lines of exploration. While the first deals with the nature of marriage transactions, the second is focused on the rising value of real dowries that have risen well above a typical bride household's annual income despite the Dowry Prohibition Act of 1961 and its several amendments since.

In summary, while it is impossible to single out a set of factors that can explain the incidence and spread of dowry payments in India, this key idea allows us to at the least systematically examine the different theories and explanations that populate the literature on marriage transactions in the country. Further research on the two main motives suggested by researchers for the prevalence and escalation of dowries, a bequest versus a price for a good match is crucial if we are to suggest effective policy recommendations that will help curb the spread and growth in dowry payments across India.

Cross-References

- [Age Differences in Marriage Partners](#)
- [Arranged Marriages](#)
- [Cultural Differences in Mate Preferences](#)
- [Sex Ratio](#)
- [Social Status and Economic Resources](#)
- [Women "Marry Up"](#)

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Bride Price

► Nuptial Gift

Bright Male Hypothesis

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Synonyms

Intersexual selection; Mate choice

Definition

The bright male hypothesis is defined as intersexual selection (i.e., mate choice by the choosy sex, or both sexes), resulting in the evolution of extravagant secondary sexual characters that depend on which communication channel is used and that either reveal material or genetic benefits for the choosy individual.

Introduction

The bright male hypothesis suggests that specific features of male quality reliably reflect underlying benefits that individuals of one sex (usually females) may acquire from their mate choice. The underlying benefits acquired through mate choice may either be material or genetic (Andersson 1994). Material benefits may include among others a territory of superior quality, sperm of superior fertilizing ability, or a partner providing superior courtship food for the female or parental care of superior quality or quantity (Andersson 1994). Mate choice may occur among individuals of the choosy sex, usually females, but mutual sexual selection in the two sexes is also common although rarely of a similar strength in males and females. Such mate choice may occur before and/or after copulation (i.e., pre- or postmating sexual selection).

The bright male hypothesis accounts for the evolution of numerous characters that have evolved beyond the exaggeration expected under natural selection. Already Darwin (1871) provided a long list of such characters in animals, but also in humans, emphasizing the importance of direct fitness benefits, while Wallace (1889) emphasized the importance of interspecific interactions, in particular predation and parasitism, for the evolution of brightness that reflected what subsequently became known as the “good genes” hypothesis.

How can reliability of the content of sexual signals involved in signaling male brightness be enforced? The handicap principle provides a general solution to this problem by suggesting that only individuals in prime condition are able to

develop and maintain the most exaggerated secondary sexual characters because individuals in poor condition pay a disproportionately large cost for producing their secondary sexual characters (Zahavi 1975). In other words, it is the condition-dependence and the differential cost of large displays that prevent males with inferior quality. Condition in this context can be caused by resistance, amounts of essential reserves (such as antioxidants), or maternal effects transmitted to the developing egg or embryo. The handicap mechanism may work at a number of different levels. One particular mechanism is the immunocompetence handicap that arises as a result of negative effects of hormones, in particular testosterone, as a suppressor of immunity (Folstad and Karter 1992). Such immune-suppression may lead to a trade-off between efficient immunity on the one hand and high levels of sex hormones that underlie the physiological mechanisms producing secondary sexual characters or sexual behavior on the other.

Components of the Bright Male Hypothesis

The bright male hypothesis can be split into different component parts depending on the communication channel (vision, sound, smell etc.) and depending on the underlying selective agents (be they parasites or predators, for example) and the resulting sexual displays and the assessment of such displays. Ryan and Keddy-Hector (1992) have shown for secondary sexual characters that independent of communication modality individuals with the most exaggerated characters are the ones that are most preferred. This deviates strongly from contact signals such as those used for maintaining contact between individuals or for predator-prey signaling. The evolution of exaggerated secondary sexual characters can also be seen as the coevolution of signaler and receiver including the sense organs used for assessment of signals. In other words, the basis for Darwinian esthetics is sexual selection and the biology of beauty (Grammer et al. 2003).

Secondary sexual characters may be purely attractive without any other specific signaling content (Fisher 1930). This so-called sexy son mechanism implies that choosy females benefit from their mate choice through the sexual attractiveness of their sons and hence mating success in the subsequent generation and the female mate preference of their daughters. While the sexy son hypothesis is affected by mate choice, there is no specific functional benefit of mate choice except for the advantages of heritable sexual attractiveness across generations. In this way, the sexy son hypothesis differs from the other functional hypotheses by not providing material benefits or genetic benefits beyond pure attractiveness. In real life, the Fisher mechanism and the other mechanisms of mate choice are likely to represent continuous gradients rather than distinct classes of benefits.

The bright male hypothesis can also be taken literally to represent the coloration or the brightness of the skin reflecting the condition or the health status of an individual. Studies of humans have shown that the color of the skin but also its texture reliably reflects the health status of the signaling individual human (Fink et al. 2001, 2006; Grammer et al. 2003). In particular, interactions between sex hormones and microorganisms seem to determine the condition of the skin, implying that individuals with specific hormonal profiles affect the composition of the microorganisms of the skin. This interaction between humans and microorganisms of the skin is particularly prominent during puberty, when increasing levels of sex hormones affect interactions between humans and microorganisms.

The so-called microbiome is the community of microorganisms that live on and within all living organisms. The average human harbors several kg of microorganisms, mainly bacteria and fungi (Turnbaugh et al. 2007). The microbiome has been implicated in a large number of medical conditions including cancers, stomach problems, and obesity. A number of diseases that correlate with the composition of the microbiome leaves open the possibility that mate choice and the brightness of sexual displays reflect not only the condition of the individual human, but also the

interaction between humans and the underlying microorganisms that constitute the microbiome. Studies of birds have shown that secretions from the uropygial glands that constitute important antimicrobial defenses employed to the plumage and the skin also increases the brightness of the plumage as seen by conspecifics and heterospecifics (e. g., Surmacki and Nowakowski 2007).

Parasites constitute important selective agents affecting viability and reproduction of their hosts. For example, many more humans have been killed or otherwise negatively affected by parasites than by predators, and hence parasites constitute an important selective pressure affecting all living beings including humans. Even today millions of humans die due to infectious disease. Some estimates have suggested that more than half of all species are parasites. Therefore, the bright male hypothesis may rely on the important selection pressure derived from parasites. If sexual signals develop and are maintained under the influence of parasitism, then sexual signals may either reflect genetically based parasite resistance, parenting ability, or the risk of sexually transmitted disease.

Superior ability to avoid predation may constitute another basis for the evolution of extravagant secondary sexual characters (Wallace 1889). If the expression of secondary sexual characters reflects the ability to perform strenuous exercise, individuals with exaggerated secondary sexual characters should also have superior ability to escape from predators. Furthermore, predators should learn through repeated exposure to prey that prey individuals in poor condition will have the palest coloration and be the least bright. Hence, learning should reinforce the reliability of secondary sexual characters as reliable indicators of condition, and prey may start signaling their superior ability to evade escape (Cott 1947). Predation is the second-most important interspecific interaction after parasites that results in the second-largest number of deaths among free-living organisms. However, it seems unlikely that humans have suffered from high mortality caused by predators during recent evolutionary history.

Superior antioxidant status may also affect sexual displays (von Schanz et al. 1999). All metabolic processes result in the production of free

radicals that can interact with DNA and other molecules but also with surface proteins and thereby cause damage that if left on its own without repair would result in reduced performance. DNA damage if not repaired results in mutations that can reduce performance of the soma in the current generation, or if affecting gametes can result in reduced performance of offspring in the next generation due to the generally slightly deleterious effects of mutations. Free radicals can be neutralized by antioxidants such as vitamin A and E, carotenoids and intracellular antioxidants such as glutathione that generally are ingested in the diet. They are often in short supply as shown by many studies demonstrating increased performance with increased supplementation of antioxidants, but also from the preference of animals including humans for food with high antioxidant levels. Individuals may differ in their use of antioxidants, for example, because the production of immune cells such as lymphocytes results in production of free radicals, or because a high diversity of alleles of the major histocompatibility complex results in lower levels of disease and hence production of fewer lymphocytes. Finally, antioxidants and carotenoids may act as molecules stimulating the immune system and thereby reliably reflecting health status (Møller et al. 2000).

Sex differences in brain size and superior cognitive abilities have been suggested to play a role in sexual selection (Miller 1993). Indeed, larger brains in men than in women have been associated with different components of sexual behavior in humans (Miller 1993). While protean courtship behavior may account for the evolution of sexually dimorphic brains in humans, this seems unlikely to be a general explanation because sexually size dimorphic brains also have evolved in numerous other organisms that indicate an ancestral state of sexually dimorphic brains that predates humans and apes. Different species differ in their sex difference in brain size, begging the question whether such sex differences may play a role in sexual selection. Bird species in which males produce more complex songs tended to have larger sex differences in overall brain size (Garamszegi et al. 2005a). Furthermore, bird

species in which females have relatively larger brains than males have a higher degree of extra-pair paternity (Garamszegi et al. 2005b). Thus, the evolution of sperm competition may select for complex behavior and the underlying neural tissue in the sex that has superior ability to control extra-pair copulations. Preliminary intraspecific studies in birds have suggested that brain size accounts for social and sexual behavior such as arrival date, flight performance, defense of offspring, and social competition (Møller 2010).

Sperm from different males but also from different species differ in locomotory ability, morphology, and surface immunological properties, and these differences can be linked to the frequency of extra-pair copulations and competition for paternity (Birkhead and Møller 1998). Multiple paternity or extra-pair paternity are common in many different organisms including humans (mean frequency of extra-pair paternity in humans is approximately 10 % of children). Such a high level of extra-pair paternity has selected for pre- and postcopulatory paternity defenses such as mate guarding, retaliatory copulations, sperm with superior swimming ability, allocation of sperm to coincide with the timing of fertilization, and selection for sperm morphology that results in superior fertilizing ability (long flagellum and large mid-piece of the head of sperm containing more mitochondria that facilitate sperm movement). Sperm have immune receptors that allow for assessment of immunoglobulins in the seminal fluid and in the female reproductive tract, and such effects may have consequences for sperm motility and hence for fertilizing ability.

Superior genes include so-called good genes or complementary genes. The so-called good genes hypothesis is based on the assumption that males with extravagant displays reveal their underlying genetic constitution and only males with this constitution are able to produce the most extravagant secondary sexual characters. Such good genes can be passed on to the next generation through female choice of sperm and hence fertilizations. A meta-analysis of good genes sexual selection revealed a small, but statistically significant effect size among animals including humans implying that females through their mate choice can

significantly increase the viability of their offspring (Møller and Alatalo 1999). Hamilton and Zuk (1982) suggested that parasites may provide a particularly likely mechanism accounting for good genes because continuous coevolution between hosts and parasites can maintain genetic variation in resistance. In each generation, individuals with novel genotypes will be able to resist most of the parasites and hence be able to produce the costliest and most exaggerated secondary sexual characters. An alternative mechanism relies on complementarity of genes of females and their male partners so that only offspring with complementary genes due to different alleles obtained from the mother and the father will be able to produce the most exaggerated secondary sexual characters (Roberts and Little 2008). Thus, partners with different alleles will show the highest level of resistance. A potential example of such complementary alleles is the major histocompatibility complex (MHC) that is involved in production of a high level of diversity of resistance alleles in numerous organisms including humans. Studies of humans have also shown links between MHC diversity and attractiveness of potential partners (Thornhill et al. 2003; Garvar-Apgar et al. 2006).

Developmental instability may play a role in the bright male hypothesis. Developmental instability reflects the inability of an individual to produce a regular and symmetric phenotype under given environmental conditions (Møller 1990). Secondary sexual characters have higher levels of bilateral asymmetry than other morphological characters, and in many species males with the largest secondary sexual characters also produce the most symmetric secondary sexual characters (Møller et al. 1998). Because there is a small heritability of asymmetry, but a large component of additive genetic variance (Van Dongen and Gangestad 2011), females mating with males with the largest, but also the most symmetric secondary sexual characters will produce offspring with superior symmetry. Studies of humans generally show preferences for symmetric individuals, and a number of studies have linked such preferences to other preferred traits such as faces, bodies, and smells.

Male and female parental care occurs in many organisms including humans. This is the most obvious (and almost trivial) mechanism accounting for the evolution of extravagant secondary sexual characters. Since it is costly to produce and maintain such extravagant characters, only individuals in prime condition will be able to also provide significant amounts of paternal care (Hoelzer 1989). Surprisingly, the expression of secondary sexual characters is a poor predictor of the amount of paternal care in taxa as diverse as insects and birds (Møller and Jennions 2001). In fact, in bird species with a high frequency of extra-pair paternity, males provide little or no parental care, while male care is more extensive in species with little or no extra-pair paternity (Møller and Thornhill 1998). These findings are consistent with the hypothesis that male care is uncommon in species with a high level of “good genes” sexual selection, but rare in species with little or no “good genes” sexual selection. This negative relationship between frequency of extra-pair copulations and the extent of male parental care is paralleled by results from analyses of male parental care and extra-pair copulations in humans (Gangestad and Thornhill 1997).

Conclusion

The bright male hypothesis concerns the mechanisms and the function of secondary sexual characters involved in intersexual selection, i.e., mate choice. A number of different mechanisms and functions have been proposed, but their relative importance and merit in human studies largely remain unresolved.

Cross-References

- [Condition-Dependent Mating Tactic](#)
- [Costly Signaling](#)
- [Female Mate Choice](#)
- [Health Markers](#)
- [Male Ornamentation](#)
- [Paternity Uncertainty](#)

- [Sex Differences](#)
- [Sexual Selection](#)
- [Sperm Competition Tactics](#)

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Broca's and Wernicke's Aphasia

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Synonyms

Fluent aphasia; Motor aphasia; Non-fluent aphasia; Sensory aphasia

Definition

Broca's aphasia is a speech and language syndrome caused by brain injury that is characterized by an impaired ability to speak fluently but with relatively intact language comprehension. In contrast, Wernicke's aphasia is a syndrome characterized by difficulty in comprehending language, with relatively fluent speech that contains paraphasias and errors in word choice.

Introduction

Speech and language disorders arising from brain injury, known as “aphasia,” have long been recorded in human history. The terms “Broca's” and “Wernicke's” aphasia were named after two nineteenth century European neurologists, Pierre Paul Broca and Carl Wernicke, who carefully documented and characterized distinct aphasia syndromes. Broca was a French neurologist who was involved in a debate about the localization of the seat of human speech in the brain. A series of cases, including a famous patient “Tan” who could say very little other than the syllable “Tan,” led Broca to declare that speech production was associated with a specific region in the left hemisphere of the brain, the posterior inferior frontal gyrus, which came to be known as “Broca's area.” Despite their difficulty in

speaking, these patients exhibited relatively good language comprehension, and the syndrome was later termed "Broca's aphasia." Subsequent studies have shown that the areas affected in Broca's aphasia include additional gray and white matter structures in the left hemisphere beyond the inferior frontal gyrus.

A few years later, Wernicke studied and described another group of patients in which a reverse pattern of speech and language was observed, namely, extremely poor language comprehension but relatively fluent speech production (albeit with word choice and semantic errors). This pattern of language deficits was then subsequently called "Wernicke's aphasia." Based on his findings, Wernicke identified regions in the posterior part of the left hemisphere that he believed to be critical for language understanding, and this general area of left temporoparietal cortex came to be known as "Wernicke's area." As with Broca's area, subsequent research has redefined the extent of posterior cortex subserving language comprehension to include additional areas such as the left posterior middle temporal gyrus and superior temporal sulcus (Dronkers and Baldo 2009).

The question for evolutionary psychologists and biologists is to what extent and at what point in evolutionary history did these speech and language functions and their underlying brain regions evolve to subserve these specific linguistic processes. Unlike some aspects of human evolution, there is no physical trace left with respect to the evolution of language, which must instead be inferred based on other types of information, such as data from comparative studies.

Comparative Anatomy of Speech and Language

Human brains are approximately three to four times larger than what would be expected for a primate of our size. It has been suggested that the reason for this disproportionate growth is the emergence of language. In support of this supposition, human neocortex is specifically enlarged in left prefrontal and posterior temporoparietal cortices (Rilling 2014; but see Hopkins et al. 2016). It

is thought that these expanded zones in humans enabled associations to be formed across sensory modalities (e.g., to associate auditory with visual stimuli so that naming objects became possible). Whereas in "lower" mammals primary sensory cortex connects more directly with brain regions that induce an automatic motor response (e.g., fleeing from a predator), multimodal association areas in humans allowed for higher-order cognition including language.

In addition to the disproportionate expansion of language zones, another argument for the specialization of language in the human brain over the course of evolution is the fact that these brain regions are primarily lateralized to the left hemisphere. The right hemisphere homologues of Broca's and Wernicke's area do not typically result in speech and language impairments. In humans, Broca's area is both larger overall and is disproportionately larger in the left hemisphere, relative to our closest relative, the chimpanzee. Using MRI to compare Broca's area in humans and chimpanzees, Schenker et al. (2010) found similar cytoarchitecture across the two species, but, unlike in humans, Broca's area in chimpanzees did not show a leftward asymmetry. In terms of posterior language regions, the planum temporale, a portion of Wernicke's area in the superior temporal plane, is also larger in the left hemisphere in chimpanzees as it is in humans (Gannon et al. 1998); however, Wernicke's area proper appears to be, like Broca's area, disproportionately enlarged in the left hemisphere in humans (Schoenemann 2009). Interestingly, a more recently identified region critical to human language comprehension, the left middle temporal gyrus, does not exist in monkeys.

More recent comparative work has focused on the fiber pathways, or white matter, that connect critical language zones in the brain. It has been shown that the disproportionate growth in the human brain is due in part to the expansion of neural connectivity as measured by greater white matter volume (Hopkins et al. 2016; Rilling 2014). Using MRI techniques such as diffusion-weighted imaging and diffusion tractography to measure white matter, Rilling recently compared the brains of humans, chimpanzees, and rhesus

macaques and showed that a critical language pathway in the human brain known as the arcuate fasciculus has a “massive” projection beyond Wernicke’s area in the superior temporal/inferior parietal cortex and into the left middle and inferior temporal gyri (Rilling 2014). This projection was much more extensive in humans than the arcuate projection in nonhuman primates and monkeys. The targets of this brain pathway are known to be critically involved in processing word meaning and, when damaged, result in chronic Wernicke’s aphasia in humans (Dronkers and Baldo 2009).

Evolution of Motor Speech and Language Behaviors

Forms of communication, such as processing species-specific calls, have been associated with both Broca’s and Wernicke’s area homologues in monkeys (Gil-da-Costa et al. 2006). Taglialetta et al. (2008) used positron emission tomography (PET) to show that when chimpanzees signaled for food, the left inferior gyrus (part of Broca’s area) was activated, along with a few other cortical and subcortical sites. However, unlike humans, these regions are not indispensable, for example, lesions to Broca’s area homologue in monkeys do not interfere with vocalization (Kirzinger and Jürgens 1982). In a comparative fMRI study, a portion of Wernicke’s area (the superior temporal sulcus) showed specialization in humans, but not monkeys, with respect to responding to species-specific vocalizations (Joly et al. 2012).

Very specific vocalizations are present in non-human primates as well as other mammals and birds. However, much of these motor speech abilities in other species are mediated by subcortical structures that mediate automatic (i.e., instinctive) vocalizations. In terms of more voluntary motor speech acts, Broca’s area and surrounding regions appear to be critical in humans and possibly chimpanzees (Rilling 2014).

It is thought that perhaps that Broca’s area in humans evolved from an antecedent that subserved imitation. So-called “mirror neurons” in the brain have been identified in Broca’s area (homologue) in monkeys; these cells respond similarly when an

animal performs an act (e.g., reaching for an object) as when the animal *observes* another animal perform the same act (e.g., another monkey reaching for the object; see ► [Mirror Neurons](#) in this volume). Such mirror neurons have been suggested as a possible mechanism allowing for the subsequent evolution of language in humans.

Taken together, these findings suggest that more voluntary, complex language production and comprehension that characterizes human language is mediated by specialized regions in the left hemisphere and that these regions likely evolved from bilaterally mediated brain regions that subserve more basic forms of communication in other mammals.

Conclusions

There is substantial evidence from comparative studies that specialized brain regions known broadly as Broca’s and Wernicke’s area subserve complex speech and language behaviors in primates, reaching their zenith in humans. When these brain areas are damaged in humans, individuals can exhibit relative difficulty with speech production or language comprehension, disorders known as Broca’s and Wernicke’s aphasia, respectively. However, there is still considerable debate as to whether these specialized neural/cognitive structures that subserve speech and language evolved specifically for communication or whether they evolved from preexisting brain/cognitive structures that subserve other functions related to conceptual understanding. As Schoenemann (2009) states, “To the extent that a particular area known to be relevant to language appears to have also changed significantly, we are justified in inferring that this area was important for language evolution,” but he also cautions “whether [the brain area] increased specifically for language will be difficult to determine.” Moreover, Schoenemann argues that not only do we need to understand how the brain evolved to better support language in response to selective pressures related to social communication but also how cultural transmission of language adapted based on the constraints of the human brain.

Cross-References

- [Broca's and Wernicke's Areas](#)
- [Brodman Areas](#)
- [Field of Linguistics, The](#)
- [Language Dysfunction](#)
- [Laryngeal Descent](#)
- [Linguistic Evolution](#)
- [Mirror Neurons](#)
- [Neurobiology of Language](#)

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Broca's and Wernicke's Areas

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Synonyms

[Brodman areas 21, 22, 41 and 42](#); [Brodman areas 44 and 45](#); [Heschel's gyrus](#); [Inferior frontal gyrus](#)

Definition

In humans, two regions in the left cerebral hemisphere linked with the production and comprehension of speech.

Introduction

Paul Broca (1824–1880) and Karl Wernicke (1848–1905) were European physicians working in the late nineteenth century with patients with brain damage. Broca (1861a, c) described patient Leborgne (and a later, similar patient, Lelong; Broca 1861b) who was unable to produce any fluent speech, with relatively intact comprehension of what was said to him. His brain damage was largely restricted to the inferior frontal gyrus of the left hemisphere. Wernicke (1874) described a series of cases who presented with an apparently opposite pattern: poor comprehension of speech, with relatively intact abilities to produce speech sounds (although what was produced was often difficult to comprehend). These patients had lesions in more posterior regions of the superior temporal gyrus in the left hemisphere. These observations spawned many efforts to establish localization of function in the human brain, an idea that had been largely dismissed, thanks to the worst excesses of the nineteenth-century phrenology. These pioneering studies also introduced the idea of

hemispheric specialization for language. Subsequently, primatologists and comparative psychologists have worked tirelessly to try to establish the existence/extent of, and asymmetries in, homologous regions in language-lacking nonhuman primates (the great apes in particular), but some of the claims are not without controversy.

Functional Localization and Hemispheric Specialization: The Dysphasias

The work of Paul Broca, Karl Wernicke, Marc Dax, and others such as Lichtheim, spawned one of the first “growth industries” in what would, in the subsequent century, become cognitive neuroscience. Broca’s contribution was primarily to link a serious acquired language disorder (which he originally referred to as *aphemia*, “without speech,” which would later become known as *aphasia*) with a lesion of the inferior frontal gyrus (Broca 1861c). This work reinvigorated the search for functional localization in the brain. A few years later (presented in 1863, published in Broca 1865), he was to note how a series of cases with aphasia all had damage to the left hemisphere. This observation spawned innumerable experiments and theories for documenting and understanding these and related asymmetries in humans and helped to create a similar effort in nonhuman animals which continues to this day.

A decade after Broca’s work on this theme, Karl Wernicke (1874) distinguished “motor” types of aphasia (similar to the nonfluent aphasia that Broca had described) from more sensory types; localized these to anterior and posterior sectors of cortex around the Sylvian fissure, respectively; and documented that the quite fluent type of aphasia most frequently was a consequence of damage to the left superior temporal gyrus. It was Wernicke who made the most of the motor-sensory distinction between anterior and posterior types of aphasia and not Broca as some people erroneously believe. The

confused-sounding jargony speech, later referred to as a “word salad,” of patients with more sensory types of aphasia (which have since become known as Wernicke’s aphasia), could be easily misdiagnosed as some sort of confusional/demented state; Wernicke correctly understood it as a disturbance of language (Wernicke 1874).

Wernicke was heavily influenced by the ideas of Meynert and emphasized that many higher linguistic processes would not be easily associated with specific regions of the brain but emerged from the anatomical connections of a limited number of circuits between regions with specialized functional roles. These ideas reveal considerable foresight, considering the popularity of studies of human and nonhuman “connectomes,” now studied using magnetic resonance techniques such as diffusion tensor imaging.

After these sets of observations, inspired by Broca and Wernicke, work on classifying subtypes of speech and language disorder and linking them to anatomy led to an explosion in simple box and arrow diagrams of speech and language subprocesses and how they could be selectively affected by damage to different parts of the left hemisphere. “Aphasiology” was born, and for a period of about 50 years, classifications and subclassifications proliferated uncontrollably. “There are almost as many classifications of aphasia as there are aphasiologists,” (Bogen and Bogen 1976, p. 834). In spite of these excesses, an early form of cognitive neuroscience, alive and well today, was born.

This posterior comprehension, anterior production view of speech in the left hemisphere has dominated thinking in aphasia, linguistics, and behavioral neurology. More recently, in part due to the revitalizing efforts of Norman Geschwind (e.g., Geschwind 1970), it has been reenergized, albeit with a few transformations driven by a series of important caveats (Poeppel and Hickok 2004). These include, for example, rethinking of the specific deficits in so-called conduction aphasia, caused by lesions of the major nerve fiber pathway connecting Wernicke’s and Broca’s regions.

A Structural Marker for Language Areas?

In human beings, the eventual definitions of Broca's and Wernicke's areas were born out of the association of a particular type of speech or language deficit with a relatively circumscribed, specific lesion in the left hemisphere. Subsequent attempts to generate nonhuman animal models of "language"-like processing can rather stretch analogies of how vocal communication systems in nonhuman primates map onto the intricate linguistic nuances of human language (Gil-da-Costa et al. 2006; see also 'Language Preadaptations' in this Encyclopedia). Even so, such studies in nonhuman primates have, in part, contributed to the idea of a Wernicke's area in humans becoming somewhat controversial, mainly due to data from nonhuman animals and neuroimaging in humans which imply that more anterior regions of the temporal lobes are much more important than posterior regions for conspecific vocalizations and for word meaning and semantics (De Witt and Rauschecker 2013). This controversy is in stark contrast to the scientific fate of Broca's area, where most scientists tend to agree on the broad brushstrokes of its location (albeit with considerable debate about its precise functions; Grodzinsky and Amunts 2006). Broca's area in humans is quite routinely linked with putative homologues in nonhuman animals, thanks in part to the popularization of the mirror neuron doctrine which came into its own in the 1990s and early 2000s.

An additional problem for the idea of a defined, specific region for Wernicke's area is that neurologists and aphasiologists have deviated from the original claim about a region important for speech comprehension, thought to be "the superior temporal gyrus" by Wernicke (1874), into (1) a more circumscribed posterior temporal region, synonymous with the planum temporale (a triangular region in the posterior part of the superior temporal gyrus, just posterior to the "transverse gyrus of Heschl"); (2) to an even smaller region called TpT in nonhuman animals (Galaburda and Sanides 1980); or (3) to a much larger region than Wernicke suggested, also including the middle temporal gyrus, parts of the inferior temporal

sulcus, and more ventral regions of the angular and supramarginal gyri in the inferior parietal cortex (Bogen and Bogen 1976).

In spite of these discrepancies in localizing these regions in human beings, the popularization of magnetic resonance imaging for producing structural images in living human and nonhuman animals led to an explosion of comparative work on putative Wernicke's and Broca's regions. In humans, the original focus was on identifying a structural marker of underlying cerebral asymmetry for language, and thanks to Geschwind and Levitsky (1968), an attractive candidate was identified: the planum temporale, which was larger in the left hemisphere in 65 of 100 human postmortem brains. As is often the case, the original excitement about a structural marker of underlying function soon fell from favor for several reasons, including methodological arguments about how to define the planum (particularly with other structural asymmetries affecting its borders); the recognition that the leftward structural asymmetry, however defined, was not common enough to be a robust marker of leftward language dominance (over 90%, estimated by several different methods – Carey and Johnstone 2014); and poorer than hoped for inter-rater reliabilities (Dorsaint-Pierre et al. 2006; Dos Santos Sequeira et al. 2006). Having said that, these studies went some way toward identifying the degree and extent of intersubject variability and how that might inform necessary sample sizes, a question less frequently addressed in some of the cytoarchitectonic and comparative studies that followed.

The Evolution of Broca's and Wernicke's Regions: Do Nonhuman Species Have Cortical Regions That Are Homologues?

Comparative psychologists and primatologists, since the time of Darwin, have often focused on how nonhuman primates in particular compare with human beings on a number of dimensions related to what might loosely be referred to as "intelligence." It was fairly simple for these researchers to extend these explorations to brain structures in our closest cousins, in parallel with

efforts to explore the proto-linguistic capabilities of gorillas, chimpanzees, and latterly, bonobos. In fact, the anatomists anticipated these later twentieth-century trends, by using microscopic techniques in small numbers of monkeys, chimps, and humans, in efforts to establish similarities among, and differences between, primate species, particularly in terms of the structure of the cerebral cortex (see also 'Language Preadaptations' in this Encyclopedia). These approaches emphasize careful identification of borders between zones of cortex, based on the characteristics of cells (i.e., the cell architecture or "cytoarchitectonics"), seen in stained sections of postmortem brains.

One limitation of this approach, often forgotten, is that some of the earliest classic cytoarchitectonic studies, frequently cited today as evidence for cross-species homologies, were in fact designed to label subregions of the human brain using the same nomenclatures as those developed earlier in, most frequently, the brain of the Macaque or Rhesus monkey (e.g., Galaburda and Sanides 1980). The more popular version of Brodmann's map, for example, does exactly that (Zilles and Amunts 2010). Many of the later attempts at labeling cortical subregions in nonhuman animals are in fact based on one or two of the nomenclatures available from the early twentieth century, such as that devised by Brodmann (Šimić and Hof 2015), which themselves were often based on rather subjective decisions on borders and boundaries, made from observations of small numbers of human (and nonhuman) brains.

Although a few previous attempts had been made to identify Broca- or Wernicke-like regions in nonhuman animals, a mention in a seminal neurophysiological paper published in 1996 (Gallese et al. 1996) has been particularly influential to date, partially due to the elegant demonstration of single neurons that increase their firing rates when a monkey performed a specific act or observed another agent performs the same act. These cells, referred to as "mirror neurons," have led to an explosion of work on perception-action associations in human and nonhuman animals. Much of the furore that followed depended, in part, on the claim that the region in the Macaque

brain ("F5") which contains many of the mirror neurons was a "homologue" of Broca's region. Tentative comparisons in original sources have become reified in subsequent "nests" of citations that claim homology for human and monkey or great ape Broca's regions, most rather far removed from the original cytoarchitectonic and anatomical evidence on which they are ultimately based.

A further development in the comparative literature on Broca's and Wernicke's areas is the appearance of studies which claim leftward asymmetries in nonhuman animals for the target regions, clearly an analogy to the functional asymmetries described in patients by aphasiologists. Although Geschwind himself could not find good evidence for an asymmetry of the planum temporale in chimpanzees (LeMay and Geschwind 1975), Gannon et al. (1998) did so, using fixed brains for measuring the volume of the planum in a sample of 18 chimpanzees. They found leftward asymmetry in a remarkable 17 of them. That this asymmetry was considerably larger than that claimed in human samples has not gone unnoticed (e.g., Tervaniemi and Hugdahl 2003), yet this potential caveat has had little effect on the enthusiasm for this type of comparative structural work. Subsequent reports have argued for, for example, asymmetries in Wernicke's area assessed using a different method than used by Gannon and collaborators (Hopkins et al. 1998), as well as asymmetries in a premotor region claimed to be Broca's area (not entirely synonymous with the F5 of mirror neuron fame; Cantalupo and Hopkins 2001).

In spite of the caveats, many studies have moved on from these descriptions of Broca and Wernicke area homologues in nonhuman primates, to attempt to relate these structural asymmetries to behavior (e.g., Taglialetela et al. 2008). For example, Cantalupo et al. (2009) argue that asymmetries in white/gray matter ratios favor the left hemisphere on average, in a sample of 33 chimpanzee MRI scans. They also found statistically significant relationships between these measures and gesture bias (extended arm movements from the home cage begging for food), although oddly the "non-right-handed" group showed greater

leftward white to gray matter asymmetry in the frontal lobes than the right-handed group. More recently, detailed analysis of the cortical thicknesses of a sample of chimpanzees relative to humans was performed. Among a number of statistically significant findings, in spite of significantly greater gyrification in humans (particularly in Broca's region as compared to its putative chimpanzee homologue), asymmetries between left and right hemispheres were similar in the two species (Hopkins et al. 2016).

Many of the papers arguing for similarities of human and nonhuman primate brains come from one or two research groups, particularly prolific in this field and that of nonhuman primate handedness, for which they are similarly oriented. These questions can become somewhat politicized, as for some scientists arguing against human uniqueness in some evolutionary sense is an important part of their scientific agenda (Preuss 2006). Even so, biologists who are not primatologists (e.g., Vallortigara et al. 1999), as well as neuropsychologists, argue that being *unable* to contextualize human asymmetries of language (and handedness) in broad evolutionary terms would undermine the biological underpinnings of cerebral asymmetries of regions such as Broca's and Wernicke's (e.g., Corballis 2012). Of course, our last common ancestor with the great apes last walked the earth 6–10 million years ago; evolutionary changes that capture some of our species' apparent uniqueness must exist and be distinct from the other great ape species (who have also been evolving for the same period of time, in spite of a surprisingly scant archeological record of it. As intriguing as these comparisons are, a more careful appraisal of the anatomical and functional evidence claiming homologues of Broca's and Wernicke's area in nonhuman species is warranted.

Conclusion

Broca's and Wernicke's regions in the left hemisphere of humans have been identified, somewhat prematurely, with speech production and comprehension, respectively. Modifications of this model

have not changed the consensus regarding left hemispheric "dominance" of these regions, even though investigators argue about their precise extent, location, and function. Although behavioral asymmetries in other species are not uncommon, the strongest claims for regions akin to Broca's and Wernicke's area are in the nonhuman great apes, such as chimpanzees. In fact, asymmetries in these regions, however defined, have been reported for a number of different structural and morphological features, and they have been related to behavioral asymmetries in the same nonhuman animals. Nevertheless, issues of statistical power and precision remain underexplored in some of the human work on molecular architecture, which makes some of the claims of Broca's and Wernicke's homologues difficult to extensively and exhaustively evaluate.

Cross-References

- [Language and Handedness](#)
- [Mirror Neurons](#)

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Brodmann Areas

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Synonyms

BA

Definition

Brodmann has subdivided the cerebral cortex into areas, based on differences in the cellular architecture, i.e., cytoarchitecture (Brodmann 1909a). These areas were later called “Brodmann areas.”

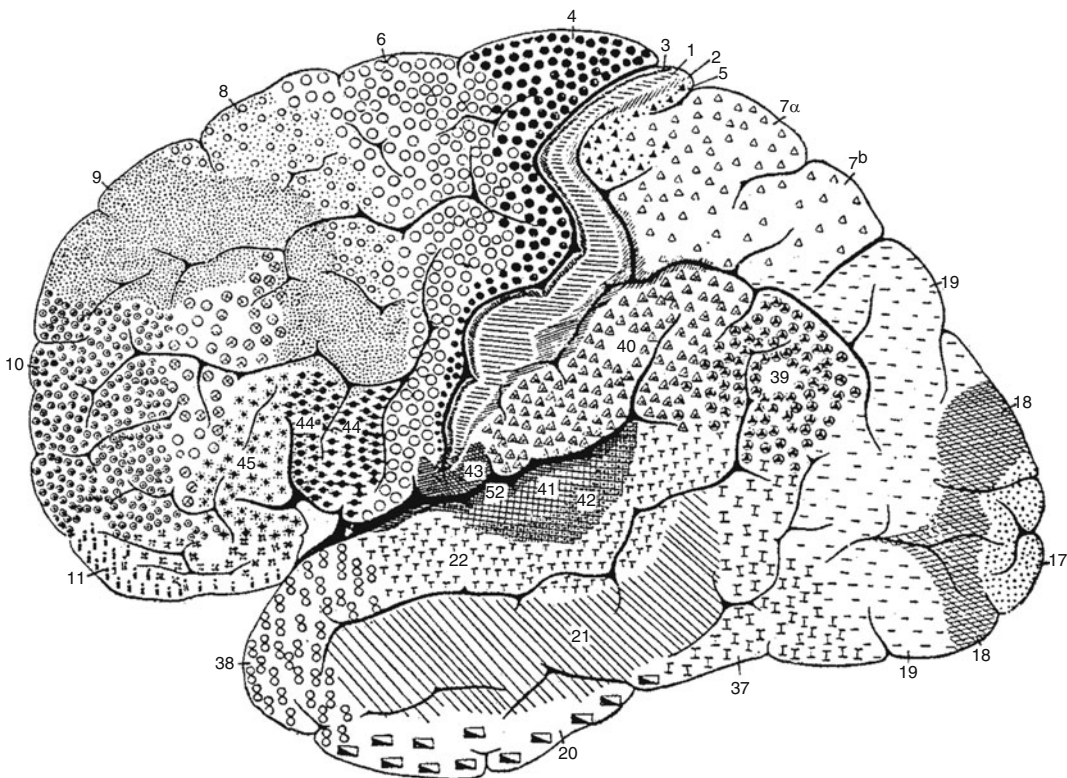
used as a reference of the brain’s microstructure for interpreting results of neuroimaging studies. However, more recent studies have shown that this map does not hold true in many brain regions, and alternative mapping strategies and new maps have been proposed (Zilles and Amunts 2010).

Introduction

Starting from the beginning of the twentieth century, the German neurologist Korbinian Brodmann (1868–1918) published several papers on the cellular architecture of the cerebral cortex in the human brain and a highly influential monograph in 1909 (Brodmann 1909a). The monograph was later translated to English (Brodmann 1909b). Brodmann showed a schematic map of the cerebral cortex including 43 cortical areas, belonging to 11 regions (Fig. 1). This map is still

Methodical and Technical Basis

Brodmann observed differences in the architecture of cells such as the presence of special cell types (e.g., Betz cells in the primary motor cortex, BA4), the type of the laminar pattern, the visibility of cellular columns, and other features in cell-body stained histological sections of a human brain hemisphere. He studied horizontal sections, and the first area that appeared in the most dorsal horizontal section was labeled as area 1; later areas got higher numbers.



Brodmann Areas, Fig. 1 Brodmann map, lateral view; areas are labeled by numbers (Brodmann 1909a)

Discussion of the Concept of Brodmann Areas

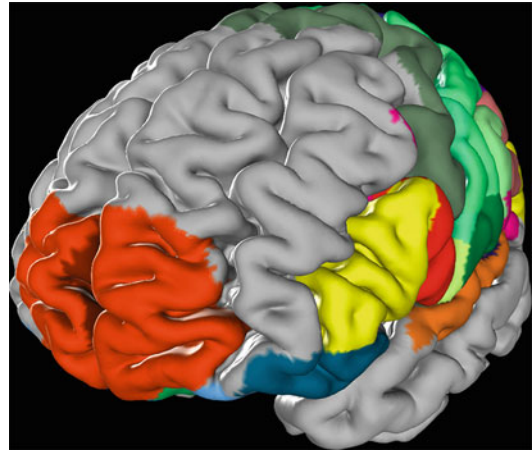
Although not proven at that time for the vast majority of areas, Brodmann was convinced that every cortical area supports a certain function. While the assumption of such relationship was straightforward, e.g., for primary motor (BA4) and primary sensory areas (e.g., BA17, primary visual cortex), it could not be proven for areas involved in higher cognitive functions at that time.

Recent studies in brains of animals, lesion and neuroimaging studies, demonstrated that Brodmann's map is incomplete or even wrong in some of the brain regions. For example, his tripartition of the visual cortex is in contrast to more recent findings indicating the presence of more than a dozen of visual areas.

A major problem of his mapping approach is the lack of information concerning intersubject variability and interhemispheric differences. It is known today that cortical areas of individual brains differ significantly in size, localization, and shape. Another point of criticism relates to the definition of borders between cortical areas based on pure visual inspection. This led to discrepancies with maps from other authors, e.g., those of von Economo and Koskinas and the map of the Russian school; for a review see, e.g., (Zilles and Amunts 2010).

Recent Mapping Strategies

Observer-independent methods have been developed to achieve a reproducible and reliable identification of borders between cortical areas (e.g., Schleicher et al. (2005)). Intersubject variability in brain structure is captured by probabilistic maps, indicating the probability of an area in standard stereotaxic space (Mazziotta et al. 2001; Roland and Zilles 1994). For example, the JuBrain Atlas (Fig. 2) contains probabilistic cytoarchitectonic maps, where borders of areas have been identified based on image analysis and statistical criteria in histological sections of ten postmortem brains; these individual maps were superimposed in standard reference space,



Brodmann Areas, Fig. 2 Maximum probability maps (MPM) of the JuBrain atlas (<https://www.jubrain.fz-juelich.de/apps/cytoviewer/cytoviewer-main.php>) and available through the collaboratory of the Human Brain Project (<https://www.humanbrainproject.eu/en/>). They are part of the SPM toolbox (Eickhoff et al. 2005) and other software packages. Mapping is based on an observer-independent method for the definition of borders in serial histological sections of ten postmortem brains (Schleicher et al. 2005). The MPM assigns each voxel of the reference space to that area, which showed the highest probability at that position (Eickhoff et al. 2005)

and probabilistic maps have been calculated (Amunts and Zilles 2015). An *in vivo* based parcellation of the cerebral cortex has been provided using multimodal magnetic resonance images from the Human Connectome Project (HCP) and an objective semiautomated neuroanatomical approach (Glasser et al. 2016). Another example of a human brain map comes from the Allen Brain Institute, integrating anatomic and genomic information (Hawrylycz et al. 2012). Multimodal and multilevel mapping approaches have been proposed to integrate the different aspects of brain organization. For a recent overview and more atlas tools see (Amunts and Zilles 2015).

Recent Understanding of Cortical Areas

It is well accepted that the cerebral cortex is composed of areas, which are characterized by a certain microarchitecture, gene expression pattern, molecular architecture connectivity, and brain function.

Various cortical maps and parcellation schemes have been forwarded, which differ in the number of areas, their ontology, and the aspect(s) of brain organization that they reflect, e.g., cytoarchitecture, connectivity, multi-modal. How the different parcellations are related to each other is an ongoing field of research. The description of human brain organization requires more than one map, which form an atlas.

Conclusion

Brodmann areas represent an important step in the history of neuroscience, but do not reflect the state of the art of cortical parcellation. The knowledge about microstructurally defined cortical areas is more than just to provide “labels” – these areas are necessary to understand brain organization and to relate brain functions to the underlying microstructure on a sound biological basis. To cover the whole network, cortical maps have to be combined with maps of subcortical nuclei. Cytoarchitecture, as introduced by Brodmann to define a cortical map, serves as a hub, to which other data modalities can be related, to link together the different aspects of brain organization in an atlas.

Cross-References

- [Brain Development](#)
- [Brain Imaging](#)
- [Brain Lesion Studies](#)
- [Broca's and Wernicke's Areas](#)
- [Environmental Unpredictability and Bet-Hedging](#)
- [Evolution of the Brain, The](#)
- [Largest Homo Brain](#)
- [Neurobiology of Language](#)
- [Neurons in the Cerebral Cortex](#)
- [Primary and Secondary Auditory Cortex](#)

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Brodmann Areas 21, 22, 41 and 42

- [Broca's and Wernicke's Areas](#)

Brodmann Areas 44 and 45

- [Broca's and Wernicke's Areas](#)

Broken Hill Man

► *Homo heidelbergensis*

Bromance

► [Male Friendship](#)

Brood Care

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Synonyms

[Parental care](#)

Definition

Any form of care that a parent devotes to their offspring at the benefit of the offspring fitness, which typically involves a cost to the parent, in terms of time and/or resource expenditure.

Introduction

Parental care includes any trait that has evolved in parents for the primary function of increasing the fitness of their offspring (Clutton-Brock 1991; Smiseth et al. 2012). Often, such traits are behavioral; parents exhibit behaviors which promote offspring survival, such as they build nests, forage to feed their young, and defend them against environmental hazards, from predators and parasites to adverse weather conditions.

For example, the female of the beewolf wasp *Philanthus triangulum* builds a subterranean nest in the sand and hunts for honeybees to feed her offspring. She flies around in places visited by foraging bees, identifies her target bee by smell and sight, and grasps and injects her target with venom. The bee will not die: she will be immotile – completely paralyzed – from now on. Then, the beewolf brings the bee to her nest – which is not a simple task, as the predator beewolf and the prey bee are approximately the same size. The nest is composed of a central tunnel and several side cells, one for each of the beewolf young. Typically, the beewolf places up to six paralyzed bee in a cell, lays an egg, and seals the cell – then she hunts for another bee, until all nest cells will contain the paralyzed bees and a beewolf egg (Strohm and Linsenmair 1999). In a few days, beewolf larvae will hatch from the eggs and they will feed on the paralyzed bees, until they will pupate and emerge as adult beewolves weeks later. In case parasite insects approach the nest (typically, parasitoids lay their eggs in beewolf nest, exploiting the preys stored by the beewolf for their own brood (Strohm et al. 2008)), the beewolf female attacks and kills them. This complex behavior – which includes building nests with a precise architecture, hunting for dangerous preys and moving them to the underground nest, defending the brood from parasites – has evolved because it favors the survival and development of the beewolf offspring.

Parental care may also comprise nonbehavioral traits, such as gestation and viviparity, where females take care of the early developmental phases of their young by keeping them into their body.

Parental care typically shows taxonomic patterns as for which sex cares (Reynolds et al. 2002) and whether it involves egg-attending, egg-caring, incubation, or provisioning the nest and/or feeding the young and protecting them from predators. Parents can care for their offspring temporarily, for short or long time periods during offspring development, or up to when offspring become adults. For example, females provide parental care in 90 % of mammalian families (and the remaining 10 % has bi-parental care), whereas most birds exhibit bi-parental care

(90 %) and only few of them have female-only care (8 %) or male-only care (2 %) (Gross 2005). In fishes, parental care is relatively rare, but, when it exists, it is more often provided by males. An important factor that contribute to set which sex cares for the young is whether egg fertilization is internal (i.e., it occurs in the female body) or external (i.e., it occurs in the external environment), which has consequences on parentage certainty (Royle et al. 2012).

Cooperative Care

In some species, other adults can cooperate with the parents in caring for the young. A typical example of cooperative care is that of meerkats, social mongooses inhabiting South African deserts. Meerkats live in groups and typically only one pair (the dominant female and male) reproduces. All other adult group members contribute to group living by taking turns in watching for predators while the other group members are foraging, and caring for the young, bringing them food, and defending them from predators, such as snakes (Clutton-Brock et al. 2001).

Parental care is also cooperative in some insects, e.g., social insects, where many (up to thousands) adults cooperate in caring for the brood of one or a few reproductives. In social insects the development of adult individuals may take from a few weeks to months during which the would-be-adults passes through different developmental phases (larvae hatch from eggs, they develop through several larval instars, then pupate, and will emerge later as adults) (Wilson 1971). During this time, brood develop in complex nests, which protect them from environmental hazards, and are fed one by one by workers who also protect them from enemies, such as parasites and predators.

Brood Parasites

Parental care is so costly that species exist that forego parental care by exploiting that of host species. The best known example is that of cuckoos,

Cuculus canorus. In this bird, females lay their eggs in the nests of another species, such as warblers, and the foster parents will incubate the cuckoo eggs and raise the cuckoo chicks, at the expenses of their own fitness. The cuckoo chicks evict the host eggs and kill the host chick, thus monopolizing all the host parents' care. Both cuckoos and their hosts have evolved special adaptations and counter-adaptations to limit parasite exploitation (on the host part) or to overcome anti-parasite defense by hosts (on the parasite counterpart). For example, cuckoos lay eggs which mimic those of the host in color and spot pattern and most hosts are able to detect (and eject) dissimilar eggs in their egg clutch (Davies et al. 1989; Kilner and Langmore 2011). Other animals have evolved similar parasitic behaviors, where the parasites do not exploit the host body, but simply one of its behavioral trait: parental care. For example, among social insects, social parasites exist who do not produce workers, as free-living social insects do, but exploit the nests and workers of host species to raise their brood, composed exclusively of reproductive males and females (Hölldobler and Wilson 1990).

Conclusion

Parentale care is a behavioural trait which offers many perspectives of conceptual and empirical analyses, in ontogenetic studies, genetics, ecology and in evolutionary biology.

Cross-References

- [Eusociality](#)
- [Gestation](#)

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Brood Defense

- [Offspring Defense](#)

Brother

- [Competition for Parental Investment](#)
- [Siblings Pose Unique Adaptive Problems](#)
- [Sibships](#)

Brothers

- [Siblings](#)

Brothers and Sisters

- [Presence of Siblings](#)

Bruce J. Ellis

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Definition

Bruce Ellis is an evolutionary developmental psychologist who has made significant contributions to research on sexual development and reproductive strategies and on biological susceptibility to environmental stressors.

Introduction

Bruce Joel Ellis is an evolutionary developmental psychologist who has held academic positions at various institutions that include senior lecturer at the University of Canterbury and the John and Doris Norton Endowed Chair in Fathers, Parenting, and Families and professor at the University of Arizona. Dr. Ellis' most recent academic appointment is professor at the University of Utah in the Departments of Psychology and Anthropology. He is also the director of the Robert Wood Johnson Foundation Research Network on Adaptations to Childhood Stress. While Professor Ellis' contributions span across diverse domains of evolutionary psychology, his notable work broadly focuses on aspects of household and ecological context and its impact on sexual development and biological responses to stress. The following entry is divided by his private life, academic education, and his contributions to evolutionary psychology.

Private Life

Bruce Ellis was born on August 28, 1961, to Lois and Thomas Ellis and grew up in Berkeley, California. He is the lastborn of five siblings. Bruce is married to Kelly Hardesty and has two children, Leah and Joel Ellis.

Academic Education

Bruce spent the early portion of his academic training in California, studying at California Polytechnic, San Luis Obispo. At Cal Poly, Bruce discovered the field of evolutionary psychology and subsequently presented its basic foundations in his Sociology of Sex Roles class, challenging the professor's traditional perspective on gender and sex differences. The presentation was said to have "caused such a stir" that the professor spent 3 h in Gestalt therapy afterward (Ellis 2011, p. 158). In 1987, he received his Bachelor of Science degree in Social Science. Following his undergraduate work, Bruce began working with Donald Symons on research examining sex differences in mating behavior. Bruce's research, even early in his career, received attention from the media and in the scientific community. His initial first-authored publication (Ellis and Symons 1990) was featured in *Playboy* magazine (Ellis 2011) and became the most cited scientific paper ever written on sexual fantasy.

Bruce moved to the University of Michigan to work with David Buss, an evolutionary psychologist who specializes in individual differences and mate selection. Bruce was also mentored by Neil Malamuth, an evolutionary psychologist who applies tenets of natural and sexual selection to aspects of sexual aggression and coercion. The breadth of his graduate work focused on mating behavior, particularly emphasizing investment and dependence in sexual and romantic relationships. Bruce earned his PhD in evolutionary personality psychology in 1995.

Following his doctorate, Dr. Ellis became an NIMH T32 postdoctoral fellow in developmental psychopathology at Vanderbilt University

(1996–1999). He was mentored by Drs. Kenneth Dodge and Judy Garber, premier developmental researchers broadly focused on examining the ecological and biological factors that impact the development of aggressive behavior and mood disorders in children. Dr. Ellis' previous work primarily focused on individual differences in mating behavior but was agnostic to developmental processes that may influence the development of sexual and reproductive strategies. Dr. Ellis' early developmental work was largely influenced by the *psychosocial acceleration theory* put forth by Belsky et al. (1991). The developmental psychopathology fellowship and the psychosocial acceleration framework provided the foundations for Bruce to shift his research to adolescent and child populations and to integrate evolutionary reasoning with developmental processes. This continues to be his primary research trajectory.

Major Contributions to Evolutionary Psychology

Professor Ellis has been credited alongside Drs. David Bjorklund and Anthony Pellegrini for formalizing the field of *evolutionary developmental psychology*. As the name implies, evolutionary developmental psychology integrates evolutionary theory with developmental psychology to create a framework whereby the influence of phylogenetic and ontogenetic forces on social, cognitive, and physical development is simultaneously and interactively examined. Professor Ellis' work broadly focuses on how environmental and household conditions shape reproductive strategies (including pubertal timing, sexual debut, sexual risk behavior, and pregnancy) and individual trajectories and susceptibility environmental stressors. The brief review of Dr. Ellis' work will highlight his research on sexual development and reproductive strategies and biological susceptibility to environmental stressors.

Sexual Development and Reproductive Strategies The psychosocial acceleration framework put forth by Jay Belsky et al. (1991)

postulates that social and reproductive strategies in adolescence and adulthood are shaped by features present in early households, including socioeconomic status, parenting style, marital functioning, and parent-child relationship dynamics (Ellis and Essex 2007; Ellis and Garber 2000). One particular outcome that Dr. Ellis has focused on is pubertal timing in girls (reviewed in Ellis 2004). In 2005, Professor Ellis was a recipient of the George A. Miller Award for an Outstanding Recent Article on General Psychology for his comprehensive review of psychosocial and biological factors that impact the timing of puberty in girls (Ellis 2004). The review was additionally notable for integrating the disparate research findings from these two domains (psychosocial and biological) within a life history framework used by evolutionary developmental psychologists.

While most of the work cannot be covered in this entry, Dr. Ellis has consistently demonstrated that household quality (measured in many different ways) impacts reproductive strategies (assessed by varying self-report and biological measures). For instance, mothers with a history of depression and mood disorders had daughters with early pubertal timing (Ellis and Garber 2000). Results further demonstrated that this association was mediated by marital dysfunction and father absence, suggesting that the maternal mood disorder influenced the dynamics of the household by either causing (or a possible product of) the child's father to leave the residence (Ellis and Garber 2000). If he was still in the household, maternal mood disorder possibly caused marital discord between the parents. Ellis, along with his colleagues, was awarded another George Miller Award for creating theoretical distinctions for environmental and household stressors (Ellis et al. 2009). Traditional models of stress typically examine the effect of cumulative stress, the summation of acute and chronic stressors, and its effect on health and development. Ellis et al. (2009) created the distinctions between environmental harshness and environmental unpredictability as distinct stressors that, separately and in combination, produce distinctive developmental and health outcomes.

Biological Susceptibility to Environmental Stressors

The examination of environmental stressors and individual response to these stressors is another notable area of inquiry for Professor Ellis. Traditional stress models such as the diathesis-stress model put forth that the combination of genetic factors (diathesis) and environmental stress put certain individuals at increased risk for psychopathology. Evolutionary models of stress response, such as those put forth by Professors Ellis and Boyce (2005), provide an alternative to traditional stress models by reframing "vulnerability" to "susceptibility." In this model, certain individuals have endophenotypic susceptibilities that, in combination with environmental feedback, heighten or dampen the development of stress response systems. The rationale is that these individuals will best adapt to the environments they reside in. This stress response calibration has implications in life history domains. This *biological sensitivity to context* may be the neurobiological mechanism whereby household and environmental stressors outlined by the psychosocial acceleration model (Belsky et al. 1991) and examined by Bruce Ellis may facilitate in the development of social and reproductive strategies (Ellis 2004; Del Giudice et al. 2011). The biological sensitivity to context model has been extended and renamed as the Adaptive Calibration Model (ACM; Del Giudice et al. 2011; Ellis and Del Giudice 2014). The ACM states that the stress response system was designed to react to physical and psychosocial stressors present in the environment and to detect and encode features about the environment and inform development in ways that enhance the survival and reproduction of the organism. The ACM has been influential in guiding research on stress-health relationships.

Cross-References

- [Aurelio José Figueredo](#)
- [David Buss](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)

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Brutality

► Victims of Violence

Bulimia Nervosa

► Eating Disorders

Bullying

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Synonyms

[Aggression](#); [Harassment](#); [Violence](#)

Definition

The Centers for Disease Control and Prevention in the USA defines bullying as “any unwanted aggressive behavior(s) by another youth or group of youths” and involves a “perceived power imbalance and is repeated multiple times or is highly likely to be repeated” (Gladden et al. 2014, p. 7). Different researchers may define bullying differently, but they generally agree on three central characteristics for bullying: (a) intentionality, (b) repetition, and (c) an imbalance of power (Olweus 1993). Intentionality refers to the intent, desire, or aim to inflict harm (injury or discomfort) upon another person. Repetitiveness involves the frequency of the behavior. In general, bullying happens again and again, or the victims become afraid that it might happen again. The third criterion of a power imbalance is also important because it distinguishes bullying from other forms of conflict: power differences between the bully perpetrator and victim occur in domains that favor the perpetrator (e.g., in terms of social status or physical strength).

Introduction

Bullying is a prevalent problem among children and adolescents, with estimates suggesting that 17.9% to 30.9% of school-age children are

victimized at school in the USA (Rivara and Le Menestrel 2016). Involvement in bullying is related to concurrent psychological, social, and academic difficulties and long-term negative outcomes, such as problems in personal relationships, employment, mental health, and criminal offending (reviewed in Rivara and Le Menestrel 2016). These results, taken together, indicate the critical and urgent need for effective prevention and intervention programs to reduce bullying.

This chapter (a) highlights key theoretical perspectives on bullying, including social information process theory, social dominance theory, the social cognitive theory of moral agency, and the social-ecological framework; (b) discusses the impact of bullying on victims, bullies, bully-victims, and bystanders; (c) discusses factors related to bullying on the individual, familial, school, and cultural levels; and (d) briefly reviews components of effective bullying interventions and discusses promising bullying prevention and intervention programs.

Theoretical Perspectives on Bullying

Social Information Processing Theory

Researchers have studied bullying perpetration and factors that contribute to bullying for over three decades. Early theoretical perspectives on bullying are based on the research on aggression, conduct disorder, and emotion dysregulation. Early research in bullying considered bullies primarily as aggressive, antisocial agents with biases and deficiencies in their social information processing. Social information processing theory suggests that social information is processed in five stages: assessing and responding to social situations via social perception, interpretation of social cues perceived, goal selection, response strategy generation, and response decisions (Crick and Dodge 1994). Bullying behavior was understood to result from misinterpreting another's hostility (hostile attribution bias), showcasing biased social perceptions, and from reactive aggression to situations perceived as anger-provoking. As such, bully perpetrators were believed to have weak social skills that

cause them to engage in aggressive acts (Crick and Dodge 1994).

However, this understanding of bullies as primarily unskilled social participants was challenged after researchers distinguished between reactive and proactive aggression. Research demonstrated that bullying can also involve a *proactive, goal-directed* form of aggression rather than solely reactive aggression (i.e., intention-cue detection deficits that spur aggression). This distinction allowed the conversation to shift from bullies as solely socially unskilled or emotionally dysregulated children to bullies as *skillful manipulators* of social situations. Recent research suggests that some bullies are adept users of emotion understanding and theory of mind (which are aspects of social cognition) and that they use these skills to manipulate and organize others and achieve their social goals (Rivara and Le Menestrel 2016). Nonetheless, the occurrence of the “stereotypical bully” or “classic bully,” who is low on social skills and possesses few assets and competencies that the peer group values, is also supported by research (Olweus 1993). This heterogeneity in bully profiles likely stems from bullying being the result of a complex array of individual and environmental interactions.

Social Dominance Theory

According to social dominance theory (Pellegrini and Bartini 2001), bullying behavior can be adaptive, and individuals may use bullying and aggression as a means to gain high social status and access to more resources. This claim is supported by research that demonstrates that children who bully others often have social power within their peer network and can be perceived by peers as popular, socially skilled, and leaders (see Rivara and Le Menestrel 2016 for a discussion). Social dominance theory has been particularly useful in explaining the observed increase in aggression during the transition into middle schools. Bullying may increase during the transition to middle school because students tend to use aggression as a way to establish dominance within a group of new peers. School transitions mark a disruption of the dominance norms in the group,

as students who were the oldest and most powerful in elementary school invert to the youngest in middle schools. As these students “renegotiate their place in a large and more diverse peer group” (Pellegrini and Bartini 2001, p. 144), they renegotiate their dominance status using aggression. This increase in aggression may also be more dramatic among young adolescent boys, as they might be more likely to view aggression as socially acceptable and as an effective way to gain dominance and resources. After dominance is established at the end of sixth grade or seventh grade (about a year after school transition), aggression tends to decrease because students are aware of their status in relation to others, and the it may be too risky (e.g., the cost is too high) for individuals with lower status to challenge the individuals with higher status using bullying (Pellegrini and Bartini 2001).

The Social Cognitive Theory of Moral Agency

The social cognitive theory of moral agency suggests that moral behaviors develop as a product of their continuous and reciprocal interactions with both the social environment and internal stimuli, or cognitions (Bandura 1986). Moral reasoning is the process of reasoning between right and wrong in difficult situations. Self-regulation processes are required in order to exercise moral agency. Immoral behaviors, such as bullying or watching someone be victimized without intervening, are less likely to occur if the individual anticipates feelings of guilt and shame. However, individuals can use moral disengagement to avoid these negative feelings. Moral disengagement allows one to disengage moral standards to achieve absolution from guilt and to permit immoral conduct by using a series of cognitive processes (e.g., cognitive justification, minimizing one’s agentic role, disregarding or distorting the negative impact of harmful behavior, and blaming or dehumanizing the victim) (Bandura 1986). Research suggests that passive bystanders and bullies tend to feel less guilt or shame compared to children who often defend victims and moral disengagement has been found to predict aggressive and immoral actions, such as bullying (e.g., Wang et al. 2017).

Social-Ecological Framework

Researchers have suggested using a more comprehensive social-ecological framework to understand the complexity of bullying (Espelage and Swearer 2011; Swearer and Hymel 2015). This social-ecological model suggests that an individual interacts with his/her environment to shape outcomes. The environment includes factors and interactions among factors within the micro-, meso-, exo-, macro-, and chronosystems. In other words, individual level factors (such as social skills, empathy, emotion regulation, gender, age), family factors (e.g., parenting, domestic violence), school factors (school climate, student-teacher relationship), broader cultural factors (e.g., community violence, media), and time-related factors, as well as their interactions all contribute to involvement in bullying (Espelage and Swearer 2011).

As an extension of the social ecological framework, recently, researchers proposed integrating diathesis-stress model and social-ecological model (Social-Ecological Diathesis–Stress Model) to understand bullying and victimization. This theory suggests that the development of externalizing problems (e.g., bullying) may occur through interaction of one’s biological and cognitive vulnerability and stressful life events (e.g., maltreatment), and the complex interconnections among different systems in a child’s life that impact their outcomes. In other words, stressful life events can be exacerbated by biological diathesis (e.g., callous-unemotional traits, narcissism, and impulsivity) and cognitive diathesis (e.g., moral disengagement), which then lead to the onset and maintenance of externalizing problems, such as bullying (Swearer and Hymel 2015).

Impact of Bullying

Incidents of bullying involve multiple parties, including bullies/perpetrators, victims, bully-victims, and bystanders. Research has shown that the involvement of bullying negatively impacts everyone involved.

Victims

A vast amount of literature highlights the link between victimization and internalizing problems (e.g., depression, anxiety), low self-esteem, academic difficulties, as well as health concerns across different age groups (see review in Rivara and Le Menestrel 2016; Swearer and Hymel 2015). Although earlier research often used cross-sectional designs, recently several longitudinal studies have been used to provide a stronger link between victimization and later internalizing symptoms, such as depressive and anxious symptoms (e.g., Ttofi et al. 2011). Related to internalizing symptoms, some research supports that students involved in bullying are more at-risk for suicidal thoughts and attempts than their uninvolved peers. Victimization is also linked to later externalizing behaviors, especially for boys (Rivara and Le Menestrel 2016).

Bullies

In contrast to victimization, the consequences of perpetration have been less studied. Some research indicates that compared to their non-aggressive peers, perpetrators report lower levels of school engagement and belonging and higher rates of delinquent behavior outside school (e.g., Nansel et al. 2001). Research also suggests children who bully are more likely to exhibit psychosomatic problems when contrasted with their uninvolved peers (reviewed in Rivara and Le Menestrel 2016). Overall, more research that looks specifically at the consequences involved in bullying perpetration is still needed. This may include longitudinal research that tracks perpetrators' physical, psychosocial, and academic consequences over the short and long term.

Bully-Victims

Bully-victims likely represent the subset of bullies who are not socially adept or do not hold high social status. These students, who have the dual role of perpetrator in some situations and victim in others, tend to have worse outcomes than youth who are solely bullies or solely victims. Specifically, bully-victims report higher rates of depression, somatic complaints, and higher rates of substance use and suicidal ideation compared

to victims or bullies (see review in Rivara and Le Menestrel 2016). Research also indicates an increased probability for referral to psychiatric assessment compared to those who are primarily perpetrators and victims (Nansel et al. 2001).

Bystanders

Witnessing bullying behavior may also affect mental health. For those who have been victimized in other settings, observing the victimization of peers can constitute a psychological re-victimization or co-victimization, which can increase mental health risk (see Rivara and Le Menestrel 2016 for discussion). Even witnesses who have never been victims themselves may have heightened anxiety around their own vulnerability of being bullied, when witnessing a bullying event (Espelage and Swearer 2011). As such, it is likely that those who observe bullying are at risk for mental health concerns.

Factors Involved in Bullying

Gender

Gender differences in bullying and other violent behaviors are well documented. Overall, boys are more likely to report bullying perpetration compared to girls when it comes to physical bullying. However, gender differences in social aggression are less clear. In a recent meta-analysis, there were only slight differences (girls slightly higher than boys) in indirect/relational aggression across gender (Card et al. 2008). Differences in the rates of different types of bullying/aggression may arise from the effect of social stereotypes and prescribed gender norms: the idea that girls are more likely to spread rumors or engage in relational/social bullying can facilitate the actual occurrence of higher relational aggression in girls compared to boys. More research is needed to delineate how gender acts as a factor in different types of bullying perpetration.

Age/Grade Level

As suggested by the social dominance theory, bullying perpetration tends to increase at the end of elementary school to middle school years

and then decrease during the high school years (Olweus 1993; Rivara and Le Menestrel 2016). The increase in bullying after the initial transition to middle school suggests that students may use bullying as a way to gain social status with new peers after school transitions (see the social dominance theory section above for a discussion). Overall, older students are more likely to be a bully, less likely to be a victim, tend to exhibit lower rates of physical bullying, and show higher rates of relational bullying (Espelage and Swearer 2011). Sympathy for victims of bullying also decreases with the onset of adolescence. As such, some research indicates that younger children tend to be more supportive of victims, in terms of peer-reported defending behaviors (Salmivalli and Voeten 2004).

Disability

The prevalence of bullying among children and youth with disabilities varies across different studies, ranging from 10.7% to 94% depending on the sample and depending on the sample, disability type, educational placement (e.g., inclusion), and how bullying was defined (Rose et al. 2011). However, the overarching consensus in the literature is that disability status is a risk factor for involvement in bullying, both as perpetrators and as victims. Specifically, in bullying perpetration, individuals with certain behavioral characteristics, such as aggressiveness, challenging behaviors, and difficulties processing social cues, are more likely to bully others (Rose et al. 2011; Espelage and Swearer 2011). Students with disabilities who are placed in a restrictive or segregated educational environment (special education class) are more likely to engage in bullying. In addition, teachers' lack of intervention skills and awareness about different types of bullying are risk factors for student involvement in bullying. Furthermore, the severity and visibility of the disability, poor social skills, a lack of friendship or support network, and higher rates of peer rejection tend to increase the likelihood of victimization. These findings highlight the importance of providing individualized behavioral support to students with disabilities, such as social skills training, and of increasing teacher and staff

professional development to help detect and effectively intervene in reducing bullying. The current literature also points to the need for creating inclusive classrooms and educational environments where all students are supported and individual student needs are met (Rose et al. 2011; Espelage and Swearer 2011).

Social Skills

Social skills are observable behaviors that form an individual's overall social competence. Examples of social skills include empathy, assertiveness, cooperation, communication, engagement, and responsibility. Some bullies tend to lack basic social skills – and as such are both disliked by peers and viewed as unpopular (Olweus 1993). Other bullies hold considerable social power, are viewed as popular by their peers, and implement a sophisticated set of social skills that allow them to manipulate others (see Rivara and Le Menestrel 2016 for a review). Unlike some bullies and defenders, victims of bullying often lack social skills and struggle with peer interaction (Cook et al. 2010). As such, victims are often marginalized or disliked by peers and have fewer friends than those not involved in bullying. On the other hand, friendship can act as a protective factor against victimization; students who develop good friendships are less likely to be bullied and have fewer emotional problems (see Rivara and Le Menestrel 2016 for a discussion).

Empathy

Being able to understand and respond appropriately to others' emotions is crucial for developing healthy social relationships. In general, students who have higher levels of empathy are less likely to engage in bullying and more likely to engage in positive bystander behavior (i.e., defending the victim, supporting the victim, getting help from an adult) (Caravita et al. 2009). Importantly, research suggests there are different types of empathy, known as cognitive and affective empathy. Cognitive empathy refers to the skills and ability to recognize others' emotions and perspectives, whereas affective empathy refers to sharing others' feelings. When research differentiates between different types of empathy, different

patterns emerge. For example, Caravita et al. (2009) separated affective and cognitive empathy in their study and found that while affective empathy predicted defending behavior among boys in mid-childhood, cognitive empathy was positively related to bullying behavior in adolescence. These results indicate that the cognitive component of empathy does not necessarily impede aggressive behavior and instead may actually be leveraged by “ringleader bullies” who use their perspective taking abilities to maintain their social dominance. In contrast, affective empathy, or feeling what someone else feels, appears to be linked to defending behavior (Caravita et al. 2009).

Positive Psychological Traits and Bullying

Covitality is the emergence of positive mental health that results from possessing a personal arsenal of positive psychological assets. Recently, it has been used to evaluate the relationship between well-being and bullying. Covitality, amongst secondary aged students, is comprised of belief-in-self, belief-in-others, emotional competence, and engaged living. Studies have shown that even negligible amounts of victimization are detrimental to belief-in-others, belief-in-self, and engaged living (Lenzi et al. 2015). This demonstrates that victimization, in any amount, is harmful to subjective well-being. Further, in general, the more assets youth have, the less likely they are to experience physical or relational victimization. Taken together, research suggests that positive psychological traits are associated with bullying victimization and perpetration across grade levels.

Emotional Regulation

Emotional regulation plays a key role in students' social relationships. Students with poor emotional regulation skills may respond to bullying in aggressive or emotionally charged ways, increasing the likelihood they will be victimized in the future (reviewed in Rivara and Le Menestrel 2016). Interventions that target crucial emotional regulation skills could help victims improve their response to bullying to lessen the likelihood of the bullying continuing and also reduce the impulsivity that may be associated with bullying

perpetration in aggressive students. In addition, teaching students problem-solving skills to negotiate peer conflict may prevent them from engaging in bullying and victimization (Cook et al. 2010).

Internalizing Symptoms

While most longitudinal studies assert that psychological problems *result* from being bullied (e.g., Ttofi et al. 2011), other studies have found a “symptom-driven pathway,” where internalizing symptoms predict greater self-reported peer victimization (e.g., Kochel et al. 2012). Youth who struggle with depression have a negative cognitive style and frequently also struggle with interpersonal relationships or display a behavioral style that is perceived poorly by the peer group (Kochel et al. 2012), increasing the risk that they will be victimized. Overall, it appears that internalizing problems can function as both antecedents and consequences of bullying.

Family Factors

Punitive/harsh parenting, a high level of family conflict, and a lack of parental warmth and involvement are risk factors for bullying involvement (see Espelage and Swearer 2011 for discussion). Authoritarian parenting – a style associated with parents who are highly demanding, punitive, and less emotionally responsive to their children – is associated with aggressive behavior and bullying. Bullies tend to describe their families as having high levels of negative affect and conflict and describe their parents as indifferent and uninvolved (Espelage and Swearer 2011). It is possible that parents may model aggression during family conflict, and youth might imitate parents' behavior and using bullying to solve peer conflict. In addition, when parents are uninvolved and do not provide necessary supervision and monitoring, adolescents are more likely to be involved with deviant peers, which contributes to problem behaviors, such as bullying.

Unlike the families of bullies and bully-victims, which exhibit low cohesion and high conflict, families of victims are frequently enmeshed, with parents who are overprotective (Lereya et al. 2013). Additionally, child maltreatment is a risk

factor for victimization; children who have been abused or neglected by parents are significantly more likely to be a bully-victim or victim (Lereya et al. 2013).

Peer and School Factors

Research has repeatedly shown that school climate plays an important role in students' involvement in bullying. When students experience a negative climate at school, their bond to the school may be broken, leading them to be less likely to follow rules, including those regarding bullying. In addition, when students perceive bullying behavior as normal and approved by peers and teachers, their belief that school can effectively supervise or control their behavior is diminished; as a result, they are more likely to engage in bullying behavior and less likely to offer assistance to the victims during bullying incidents. A few important components in school climate that are related to bullying include positive student-teacher relationships, peer support, clear expectations, and consequences (for problem behavior) at school, and respect for diversity (Wang et al. 2013).

Student beliefs and attitudes surrounding aggression are another crucial element of school climate. Attitudes and peer norms regarding bullying are significantly related to bullying behavior of children (Duffy and Nesdale 2009). Although classroom norms influence children's behavior, pro-bullying peer group norms may override anti-bullying classroom norms and lead to an increase in bullying behavior in peer groups where bullying is accepted (Duffy and Nesdale 2009). As such, the "popularity norm," or whether popular students successfully use bullying as a means to establish social status, is a better predictor of bullying behavior in late elementary school than classroom norms (Dijkstra et al. 2008). When peers accept or reinforce bullying behavior by giving the perpetrators higher social status, bullying is likely to continue. A study examining the impact of bystander behavior on bullying found that bullying was negatively associated with prosocial bystander behavior (e.g., students defending the victim) and was positively related to reinforcing bullying behavior (Salmivalli et al. 2011). This finding supports the contention

that bullying is not an isolated event between a bully and a victim, but rather is a group phenomenon (Salmivalli et al. 2011). As such, school-level factors, such as school climate and peer norms, play a crucial role in impacting bullying behaviors.

Broader Social and Cultural Factors

In addition to individual, family, and school-level protective and risk factors, there are several broader social/cultural factors that contribute to bullying. For example, cultural values such as individualism have been linked to aggressive behavior. Exposure to violence in the community (e.g., living in an unsafe neighborhood, gang affiliation) or through media (e.g., TV, video games), and poverty has also been linked to aggression/bullying (Espelage and Swearer 2011; Swearer and Hymel 2015). However, the causal relationship between bullying and those social-cultural factors remain unclear.

Intervention Programs for Bullying

Effectiveness of School-Based Prevention and Intervention Programs

During the past two decades, an increased number of prevention and intervention programs targeting bullying have been developed. However, there is mixed evidence for how effective school-based programs are in preventing bullying in the USA. Some meta-analytic studies of bullying interventions have shown limited or even negative effects for decreasing bullying at schools (see Nickerson 2017 for a review). Other meta-analyses on bullying preventions/interventions suggest more positive and robust outcomes for students, such as increasing students' positive attitudes toward their school, reducing rates of bullying, and increasing positive bystander behaviors (Farrington and Ttofi 2009; Yeager et al. 2015). Researchers have posited that bullying program effectiveness appears to differ depending on methodology and experimental design, setting, developmental level, outcomes, and by specific program components (Nickerson 2017). The rest of this section visits each of these considerations in further detail.

Methodology and Experimental Design

The mixed findings that surround the effectiveness of bullying interventions may partly stem from the use of different inclusion criteria across studies (e.g., language, type of publication, sample size, types of bullying outcome measures, and a focus on studies conducted in North America) (Bradshaw 2015). The effectiveness of intervention studies is also impacted by challenges with experimental design: studies often lack a control group to examine causal effects, they sometimes lack the long-term follow-up studies which are needed to demonstrate that the intervention has lasting effects, and they rarely use randomized controlled effectiveness trials. The benefits of effectiveness trials are that an intervention is carried out by school personnel (e.g., teachers instead of trained researchers) to test the effectiveness of the intervention in more naturalistic settings (Bradshaw 2015). Yet research frequently only involves efficacy studies that inflate intervention success, as interventions tend to be implemented by highly trained researchers in controlled settings with optimal conditions. Due to the current gap between research and practice in psychology, more research is needed to examine the effectiveness of bullying prevention programs carried out by nonresearchers in real world environments.

Setting

The setting or location of an intervention also impacts its effectiveness. A comprehensive meta-analysis by Farrington and Ttofi (2009) found that bullying and victimization outcomes were less effective in the USA and Canada when compared to European countries. These results were replicated in a systematic review of bullying research, which found that the majority of studies that observed significant effects on bullying behavior appeared to have been conducted outside of the United States and with relatively homogenous samples (Evans et al. 2014). Researchers posit that North America may be a particularly difficult setting in which to design and deliver bullying prevention programs due to the heterogeneity of the intervention population (e.g., diversity of race/ethnicity, socioeconomic status, and income

inequality). Interventions in North America may require more culturally sensitive and targeted bullying interventions (Evans et al. 2014). As such, more research is warranted to determine how characteristics of the setting of bullying interventions may impact program effectiveness.

Developmental Level and Outcomes

The effectiveness of bullying prevention programs also likely depends on the developmental level of students. While most research supports that bullying interventions have a stronger effect on decreasing bullying perpetration in middle school age and older students than on younger students (Farrington and Ttofi 2009), recent meta-analyses have suggested the opposite. Yeager et al. (2015) found some effectiveness for bullying prevention programs in grades 7 and below, nullified results in grade 8, and harmful effects of bullying prevention programs in grades 9–12. As such, more research is warranted to determine how different outcomes across different age groups are impacted by bullying prevention and intervention.

Program Components

Specific program components also impact the effectiveness of bullying prevention and intervention programs. The literature considers components for decreasing bullying and victimization to include (a) developing a caring school climate by fostering empathy and kindness among students; (b) promoting students' and staff's awareness and knowledge of bullying; (c) using consistent language to enforce school-wide rules and consequences for bullying; (d) increasing adult supervision of all students on the playground; (e) providing training to promote skills and competencies for students (e.g., conflict resolution, self-regulation, problem solving) and teachers (e.g., how to handle bullying behavior, classroom management, establishing classroom rules); (f) increasing adults' role modeling of appropriate and prosocial behavior; (g) encouraging bystanders to intervene in bullying situations; and (h) involving parents (parent trainings, meetings) (Farrington and Ttofi 2009; Bradshaw 2015).

Review of Effective Bullying Intervention and Prevention Programs

Bullying interventions can successfully integrate key components (as discussed above) into a cohesive bullying prevention/intervention by considering a multitiered approach that addresses the specific social environment and educational context of the bullying phenomena. This includes systems-wide awareness, training, and discussions involving all students and stakeholders (teachers, parents, and staff) in conjunction with more targeted interventions at the peer-group and individual level for students that need additional intervention. Research supports that this multitiered, comprehensive approach is a promising way to reduce bullying perpetration (Farrington and Ttofi 2009; Bradshaw 2015). Several multi-level interventions (or interventions that can be adapted into a tiered approach) and that demonstrate promising results for bullying prevention outcomes are briefly summarized below.

Olweus Bullying Prevention Program

The Olweus Bullying Prevention Program pioneered the whole-school approach to preventing and reducing bullying (Olweus et al. 1999). This large-scale intervention, designed for all grade levels, includes school-wide components (e.g., coordinating committees, anti-bullying school rules, events, playground supervision), classroom-targeted components (classroom meetings and activities, videotaped classroom curriculum), and bully- and victim-targeted components (e.g., talking with the perpetrator, providing consequences, supporting the victim). Additionally, partnerships between parents and the school are encouraged. Results of the Olweus Bullying Program indicate general success in decreasing bullying, victimization, and antisocial behavior and in improving school climate (Olweus et al. 1999). Furthermore, in a comprehensive review, programs based conceptually on the Olweus Program were found to be more effective than their counterparts, although these effects were more consistent in non-US countries. Importantly, the strongest effects were found in studies that had a less rigorous experimental design (namely age-cohort designs) as opposed to a more rigorous

experimental design (randomized controlled trials) (Farrington and Ttofi 2009).

KiVa

The Finnish KiVa program (an acronym for *Kiusaamista Vastaan*, “against bullying”) is a bystander-based whole-school approach that attempts to reduce the social rewards and motivation of bullies by targeting bystander reactions and behaviors toward bullying events. The program targets bystander empathy, self-efficacy, antibullying attitudes, and bullying prevention skills via classroom lessons, activities, and rules, videos, and computer games. Posters and recess supervisors in vests also serve as a visual reminder to students and school personnel about the program. Parent guides on bullying and prevention are also distributed. Cases of bullying are addressed by a small team of teachers who facilitate individual and small-group discussions with the victims and bullies. Additionally, the classroom teacher meets with two to four prosocial and high-status classmates, encouraging them to support victims. Results of this intervention suggested reductions in bullying (grades 1 to 6) and victimization (grades 4–6), increased self-efficacy for defending and bystander assistance (grades 4–6), and decreased bullying reinforcement (grades 4–6 and grades 7–9) when compared to control groups (Kärnä et al. 2013).

Bullying Prevention in Positive Behavioral and Intervention Supports

Recent researchers have suggested following the Positive Behavior Supports (PBS) framework for bullying prevention. The Bullying Prevention in Positive Behavior and Intervention Supports (BP-PBIS) is a school-wide system for facilitating positive behaviors among both staff and students. Under the BP-PBIS model, school personnel can readily integrate key factors of bullying intervention across primary (school-wide), secondary (classroom or group level), and tertiary (individual) systems of support to improve school safety and prevent bullying behavior by making bullying behaviors less effective and relevant and making prosocial behavior more rewarding (Sugai et al. 2011). Facets of BP-PBS included

creating and following school-wide rules surrounding bullying, teaching students social responsibility skills, explicit instruction to students on what constitutes gossip, inappropriate remarks, cyber bullying, supervising student behavior, and faculty follow-up. BP-PBIS studies document a decrease in school suspensions and office discipline referrals for bullying behavior (e.g., see Nickerson 2017 for a review).

Social Emotional Learning Programs

Social Emotional Learning (SEL) programs explicitly teach social skills (e.g. empathy, relationship building, coping, prosocial behaviors, decision-making) as a way to improve academic and social functioning in schools. Although SEL programs rarely target only bullying behaviors, most SEL programs that aim to promote a positive school climate and decrease violent and disruptive behaviors also successfully decrease bullying and victimization (see Bradshaw 2015 for further discussion). For example, in a large-scale randomized controlled trial, using an SEL program (The Second Step Program), middle school students with disabilities experienced reduced bullying (see Nickerson 2017 for a review). SEL programs are often Tier 1 or universal programs (social skills lessons delivered to an entire school) and few programs utilize a multitiered framework in order to provide more intensive interventions for students in need. However, research suggests intensive social skills training can also be helpful for small groups of youth at risk for becoming involved in bullying or aggression (e.g., Coping Power Program). As such, future research may investigate including more intensive social skills training and emotion regulation approaches to supplement universal SEL approaches (see Bradshaw 2015 for further discussion).

Conclusion

Bullying is a very complex phenomenon, and involvement in bullying negatively impacts everyone involved, including bullies, victims, bully-victims, and bystanders. Factors at different

levels (microsystem, mesosystem, exosystem, macrosystem, and chronosystem) and their complex interactions all contribute to the development and maintenance of bullying behavior. Although there is some evidence for the effectiveness of bullying prevention and intervention programs, more rigorous research is needed. Only when all factors contributing to bullying are taken into consideration in designing and implementing the prevention and intervention programs, will schools be free from bullying.

Cross-References

- ▶ [Anonymity of Cyberbullying](#)
- ▶ [Boys Bully More than Girls](#)
- ▶ [Boys Physical Bullying](#)
- ▶ [Child Abuse and Bullying](#)
- ▶ [Cyberbullying](#)
- ▶ [Factors that Influence Bullying](#)
- ▶ [Girls Psychological Bullying](#)
- ▶ [Homophobic Bullying](#)
- ▶ [Same-Sex School Bullying](#)
- ▶ [School Bullying](#)
- ▶ [Sex Differences in Cyber Bullying](#)

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Burial

- [Death in Christianity](#)
- [Death in Islam](#)

Burials

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Synonyms

Ceremonial interments; Committal practices;
Entombment customs; Funereal rites

Definition

Established burial rites, ceremonies, and customs performed publically and/or privately by individuals or groups in the disposition of human bodies as prescribed by religions and cultural customs.

Introduction

Human remains indicating ritual disposition have been discovered throughout Europe and Asia dating back more than 100,000 years. Human burial rituals have long been considered within the social science community as universal expressions that affect and promote in-group cohesion and serve various cultural and religious functions. Evidence of ritual burials includes the specific arrangements of human remains with primitive tools, foods, weapons, and animal bones buried on or near the bodies. There has been increasing agreement among psychologists and anthropologists that traditional rituals such as human burials are considered as early evidence of human social cohesion and are believed to help establish and maintain group identity. Burial rituals emphasize communities' commonly shared life and death experiences, indicating human contemplations of the origins of creation and the veneration of ancestors. Religious scholars and social scientists agree that burial rituals are significant features of most world religions, influencing the cohesion of the cultural groups that practice them, providing practical benefits for individuals, and informing the practitioners' beliefs about life after death (Durkheim 1912/2008).

Earliest Evidence of Ritual Burials

The first hominids believed to ritually bury their dead were Neanderthals, our closest extinct human relative. *Homo neanderthalensis* lived in Europe and southwestern to central Asia between 400,000 and 40,000 years ago (Edgar and Johanson 2006). Most anthropologists and scholars agree that at least some Neanderthals ritually treated and buried their dead (Pettitt 2002). Neanderthals, who archeologists have determined lived as contemporaries with *Homo sapiens* for hundreds of thousands of years, are believed to have ritually disposed of bodies. Evidence of their burial practices, which include placement of corpses in shallow graves along with common stone tools and animal bones, are believed to indicate an emotional connection with the deceased. Dozens of their gravesites have been discovered throughout the Middle East and Europe. The oldest confirmed burial took place at Tabun Cave in Israel, around 100,000 years ago wherein the remains of a Neanderthal woman were discovered, seemingly positioned with the woman partially placed on her left side near the edge of the cave (Drake 2015).

At another site in the hills north of Madrid, Spain, archeologists discovered what is thought to be firm evidence of Neanderthals funereal rituals wherein the jaw and six teeth of a Neanderthal toddler were found amidst the remains of a series of charred hearths. There, scientists discovered several dozen herbivore antlers and a rhino skull that appeared to have been purposefully arranged in a burial ritual between 38,000 and 42,000 years ago. The inclusion of fauna, flint tools, and other artifacts in the burial sites points to Neanderthal beliefs in the spirit world and an afterlife.

Modern Human Burials

The earliest known burial site of modern humans was discovered in 1933 in a cave in Oafzeh, Israel. It contains 100,000 year old skeletons of children and adults stained and intentionally buried with lumps of red ochre. Ocher is a natural pigment

containing iron oxide, which varies in color from red to brown to yellow. The Oafzeh site also included the mandible of a wild boar and the antlers of a red deer. The remains of as many as 15 individuals were found along with dozens of fragments of red ochre and ochre-stained stone tools assembled near the human bones, leading most scientists to concur that the ochre was used in a death and burial ritual. The presence of ochre lumps led some archeologists to believe that the individuals who conducted these burials possessed some level of developed language and mathematical abilities representing symbolic thought. Evidence of such early human ritual burial behavior is also thought to represent an awareness of the conditions of life and death. These burials included evidence of artifacts seen as representations of religious rituals indicating possible concern for the dead in the afterlife (Lieberman 1991). Corpses were often buried with remnants of stone tools and parts of animals and positioned with deliberate care in holes in the ground. They often appeared as having been specially protected from the environment and animals, with some scientists positing that the dead seemed to have been lovingly cared for, which could indicate a faith in the afterlife.

Ritual Burials and Religion

The earliest evidence in the archeological record suggesting a belief in the afterlife evidenced by ritual burials coincided with the appearance of modern humans, during the “cultural big bang” 40,000–60,000 years ago (Mithen 2004). From the perspective of most of the world’s religions, ritual disposal of human dead serves to bring closure for the surviving family and friends of the deceased and shows respect for the departed. Burial rituals are also believed to assist the departed in their transition to the next life. Early human behavior as demonstrated in ritual burials is thought to represent cognition of the differing stages of life and death. For example, human remains found in Turkey revealed evidence of funerary practices 8,000 years ago in that the

bodies were elaborately manipulated before burial (Whitehouse 2012). The placement of corpses in shallow graves along with common stone tools, food items, weapons, and animal bones indicate an emotional connection to the deceased and reveal efforts by the living to support the deceased in an afterlife. These types of ritual burials are believed to have served a number of different goals, including honoring the dead and communing with gods and spirits as well as supporting bonding in-group activities (Whitehouse 2012). Regarding the continued development of religious beliefs in mortuary practices, it is likely that funeral rituals expanded over time, becoming more delineated and increasingly complex as the various religious beliefs in the afterlife became systematized and codified.

Burial rites often appear to correspond to three essential life transitions on a continuum of life to death and post-death experiences for the dying individual, the attendant(s) providing the ceremony, and the friends, family, and in-group members who witnessed their transition (Gennup [1960] 2004). According to Gennup, the life to death transition can be considered as a three-step process beginning with the preparation of the dying person, including the giving of the last rite(s), followed by the rites of transition which include the final burial of the corpse in a designated place, ending with rites of incorporation such as a prayer service offered with the intention of praying for the salvation of the deceased person’s soul (Gennup [1960] 2004). Human birth, marriage, and death express common and critical biological and social changes, making ritualized acknowledgments increasingly vital for individuals and groups. As in the performance of other religious rituals, there seems to be a tendency during burial rites wherein the community members conducting the rituals summon or invite the god(s) and spirits to assist the living. It is as if the mystery of physical death and the yearning for the assurance of an afterlife are issues which the living cannot understand or attend to without supernatural assistance, and only when the living adherents offer obeisance to their god-figures can there be an expectation of the burial rituals succeeding.

Among competing theories regarding the importance of burial rites is the idea that ritualized burials serve to restore the belief in society's permanence which is challenged whenever individual members die (Hertz 1960). Funereal rituals provide opportunities for those surviving members of the clan or culture to find common belief, faith, and to perform accepted life to death rituals which have the intention and result of affirming a genuine solidarity of purpose and unity for the group (Hertz 1960).

Ritual Burials and the Distinction Between Neanderthals and Modern Humans

It is widely accepted that Neanderthals disappeared approximately 35,000 years ago. While it has been common practice for many researchers to differentiate Neanderthals from modern humans based on their capacity for symbolic behavior as evidenced in ritual burials, recent discoveries and studies are leading some scientists to challenge the notion that early modern humans' ritualized burials were more sophisticated than Neanderthals (Riel-Salvatore and Gravel-Miguel 2013). Burial rituals have long been thought of as expressions of abstract thinking, but archeologists and social scientists are discovering evidence of Neanderthal practices commensurate with those attributed to modern humans (Riel-Salvatore and Gravel-Miguel 2013). The complexity and variety of ritual burials appear to indicate that human behavior does not always present as having evolved from simple to complex and is subject to variant living conditions and geographical locations at the times of the burials.

Conclusion

Throughout early and modern human history, burial rituals have been used to promote in-group functionality and bonding by establishing and maintaining group identity and norms. Ritual burials appear to have served to

provide opportunities for families and group members to honor their deceased for their contributions to the group and to prepare the dead for their journeys in the afterlife. Archeological evidence of tools, weapons, and food found buried with human remains support the theories that Neanderthals and early modern humans ritualized life to death transitions. Scientists continue to study how ritual burials evolved to address the universal human experiences of life and death, and beyond.

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Burrhus Frederic Skinner

► B. F. Skinner and Behaviorism

Butterfly Mimicry

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Synonyms

[Protective resemblance](#)

Definition

Protective resemblance between a butterfly and two or more species, or between a butterfly and an inanimate object.

Introduction

Butterfly mimicry is a form of protective coloration where a given species, commonly referred to as the *mimic*, increases its chance of survival by visually resembling a harmful species, the *model*, such that the receiver of the signal, the predator (e.g., birds, reptiles, or predatory insects who attack and consume butterflies), gets confused between the two and avoids the mimic (Ruxton et al. 2004). The model can either be a different species of butterfly or an entirely different species of animal. In its broadest sense, butterfly mimicry may also involve a third category, a camouflage strategy known as *Masquerade*, in which

butterflies mimic inanimate objects such as leaves, bits of lichen, or patches of tree bark (Ruxton et al. 2004). Traditionally, however, there are two main types of mimicry, and these are typically distinguished from each other by whether the mimic's signal involves deception of the predator or not (Turner 1984). In *Müllerian mimicry*, named after the German naturalist Johannes Friedrich "Fritz" Müller, who first proposed an evolutionary explanation for the phenomenon, both the mimic and the model species are harmful to the predator, which is why the signal is considered to be honest in both species and does not involve deception of the predator. Dishonest signaling through the mimicry of a harmful species by a harmless species, on the other hand, does involve deception of the predator and is known as *Batesian mimicry*, named after the English naturalist Henry Walter Bates (Bates 1862).

Müllerian Mimicry

In Müllerian mimicry, both the mimic and the model species also have, in addition to warning signaling coloration effective secondary defenses. These defenses can be either morphological, such as spines, or chemical, such as toxins. Both species benefit, because a potential predator has more opportunities to learn the meaning of the signal, which is why the relationship between Müllerian mimic and model species is said to be *mutualistic* (beneficial to both organisms). The signal receiver (predator) also benefits from this system, as it avoids potentially harmful encounters. In 1879, Müller, who at the time studied Neotropical butterflies in Brazil, published a simple explanation for this phenomenon stating that "defended species may evolve a similar appearance so as to share the costs of predator education" (Müller 1879; Ruxton et al. 2004). Müller was also the first to mathematically describe a survival benefit of being a Müllerian mimic depending on the abundance of similar and dissimilar species in its environment. The mathematical model has recently been extended to include unequal levels of unprofitability of the species to predict the relative benefit (Mallet 2001). Two types of experimental evidence for Müller's suggested

predatory mechanism underlying Müllerian mimicry have been put forward. The first is that rare unpalatable forms tend to have lower survival rates when they are distinct in appearance compared to when they are more similar to a common unpalatable species (Benson 1972). The second is that naïve predators tend to typically take a few of each unpalatable form before they start to avoid them (Kapan 2001).

Several examples of Müllerian mimicry are found among the distasteful Neotropical butterflies of the subfamily *Heliconiinae* (“longwings”) in South America (Ruxton et al. 2004; Mallet and Gilbert 1995). Many longwings form assemblages of similarly looking mimic and model butterflies known as *mimicry rings* or mimicry complexes. At least four distinct assemblages including butterflies from the *Heliconiinae* and other species are traditionally recognized, the *tiger*, *red*, *blue*, and *orange* ring (or complex) (Mallet and Gilbert 1995). The *tiger* ring consists of about 200 Neotropical species which all share a similar pattern of orange and yellow stripes on a black ground color. The *orange* ring is comprised of a group of bright orange species (including, e.g., *Marpesia petreus*, *Dryas iulia*, and *Eueides aliphera*). Additionally, there are several species pairs, the most well known of which is the *red postman* butterfly (*Heliconius erato*) and the *common postman* (*Heliconius melpomene*). Another classic example of Müllerian mimicry is the monarch butterfly (*Danaus plexippus*), which forms a Müllerian complex together with the viceroy butterfly (*Limnitis archippus*). This example was long believed to be a case of *Batesian mimicry*, with the viceroy mimicking the monarch, but research has shown that both species are harmful to predators as they both contain toxins (arguably even more so in the viceroy than the monarch), hence they are Müllerian mimics (Ritland and Bower 1991). In addition to sharing similar coloration patterns, members of each mimicry complex also tend to display similar behaviors. For example, many butterflies of the same mimicry ring form communal roosts at night, a behavior that has been shown to deter predation by birds as it increases the strength of their warning signal (Finkbeiner et al. 2012). Butterflies of each ring

also tend to fly together at day, occur in similar habitats and at similar heights above the ground, and also get together at the same time of year (Mallet and Gilbert 1995).

Evolution of Müllerian Mimicry

The more than century-old question of how Müllerian mimicry evolves is not yet fully understood. Broadly speaking, mimicry can evolve either via *advergent* or *convergent* evolution. In *advergent* evolution, the model species would remain the same, while selection acts on the mimetic species, bringing about a resemblance to the model species. In *convergent* evolution, a common selective pressure would act on all species involved, bringing about an overall resemblance between them. *Advergent* evolution via the so-called *two-step hypothesis* is the most widely accepted model for the evolution of both Müllerian and Batesian mimicry (Ruxton et al. 2004). The *two-step hypothesis* entails that mimicry evolves in two stages, the first stage is a mutational leap of the mimic toward the model which establishes an approximate similarity. This stage is then followed by gradual evolutionary change which fine-tunes the mimic’s similarity to the model (Turner 1984). One of the most frequently asked questions related to the evolution of Müllerian mimicry is: How do we know which one is the model and which one is the mimic? If Müllerian mimicry evolves through *advergent* rather than *convergent* evolution, scientists have argued that the *models* are expected to be: (1) more unpalatable, (2) more common, (3) earlier (in seasonal species), (4) larger, (5) more conspicuous, (6) more gregarious, and should have (7) a wider geographic distribution, (8) less “fuzzy” color patterns, (9) more ancient color patterns, (10) less polymorphism, and (11) less overall divergence from an ancestral color pattern than their *mimics* (Mallet 2001).

Batesian Mimicry

In *Batesian* mimicry, the mimic itself lacks an effective secondary defense, and so it is harmless to the predator, but the mimic still gains protection from predators by resembling a harmful model. As opposed to the mutualistic relationship

between Müllerian mimics, Batesian mimicry is considered to be *parasitic* (beneficial to the mimic while harmful to the model). Predators that attack the harmless mimics would soon learn that such organisms are profitable to attack and consequently, an increased number of Batesian mimics would lead to a decrease of the efficiency of the model's warning signal and so the survival of both model and mimic is reduced. Thus, the efficiency of Batesian mimicry is highly dependent on the abundances of the models and mimics and is normally considered to be effective when the unpalatable species are more abundant than the palatable species. However, the efficiency of Batesian mimicry is also dependent on the level of harm caused by models and the abundance of alternative prey (Ruxton et al. 2004). The most fundamental empirical evidence to support Batesian mimicry is that predators that have prior experience with unpalatable model species subsequently also avoid harmless species that resemble them.

Some examples of Batesian mimicry in butterflies can be found between species of the Neotropical, palatable *mimic sulfurs* (subfamily *Dismorphiinae*) and unpalatable *Ithomiini* butterflies which belongs to the *milkweed butterflies* (subfamily *Danainae*). The palatable spicebush swallowtail (*Papilio troilus*) is considered a Batesian mimic of the unpalatable pipe-vine swallowtail (*Battus philenor*). Some hawkmoth caterpillars (family *Sphingidae*), and pupa (e.g., *Dynastor darius*) have been suggested to be Batesian mimics of snakes (Ruxton et al. 2004), although this resemblance has not been tested with nonhuman predators. In cases where caterpillars and pupa resemble snakes, the resemblance between mimics and models cannot be explained by shared ancestry; however, in some cases of resemblances between adult butterflies, it is likely that the resemblance between species can be explained by shared ancestry.

Conclusion

Many mimetic systems involve a complex interplay of species which vary in their defensive attributes and predators which vary in their abilities to

deal with them. Even in Müllerian mimicry, prey may be unequally unpalatable and edibility may not be an absolute condition (Speed 1999). Different predator species may have different degrees of tolerance and an individual predator's motivation to attack prey might vary with its nutritional state, meaning that predators may still feed on weakly unpalatable prey when hungry or when there is a lack of alternative prey. In such cases, the mimetic relations between unequally defended species could be parasitic, and this phenomenon has been referred to as quasi-Batesian mimicry. As there exists a whole range in between Müllerian and Batesian mimicry, it may not always be appropriate nor simple to divide mimetic species between these two categories.

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By-Product

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Synonyms

Epiphenomenon; Side effect; Spandrel

Definition

A characteristic that arises incidentally alongside proper adaptations, rather than having been directly selected for in its own right.

Introduction

Evolution produces three types of phenotypic features: adaptations, noise, and by-products (e.g., Gould and Lewontin 1979; Buss et al. 1998). *Adaptations* are features directly selected for because of their beneficial effects on an organism's fitness. *Noise* refers to the products of random, neutral mutations and other chaotic processes such as genetic drift. *By-products*, which do not necessarily benefit reproductive fitness, are characteristics emergent of more fundamental adaptations; thus, they are "unintended" in an evolutionary sense.

Buss et al. (1998) distinguish between functionless by-products, exaptations, and co-opted spandrels. They describe functionless by-products as features that provide no evolutionary benefit to their carriers and are simply emergent derivatives of certain adaptations. Exaptations are preestablished adaptations that come to serve new evolutionary purposes over time, perhaps in response to changing environmental needs. Finally, co-opted spandrels originally emerge as functionless by-products but later become "co-opted" for new survival or reproductive purposes.

What follows is a description of the "clues" that can indicate a feature is a by-product rather

than an adaptation, including notable examples from the literature and an overview of current debates regarding the concept's application.

Identifying By-Products

Compared to adaptations, by-products may appear rudimentary or vestigial (Puts and Dawood 2006) or fail to embody "special design" principles of evolvability, reliability, efficiency, economy, precision, functionality, and complexity (Buss et al. 1998).

According to the principle of *evolvability*, the ability to drive a car cannot be a cognitive adaptation, as cars were not a feature of the early human environment and selection is not rapid enough to have produced functional driving adaptations over the last couple of centuries. Thus, the logical conclusion is that driving simply recruits a number of adjacent mechanisms such as motion tracking, spatial thinking, and motor functioning. Similarly, humans could not have evolved specific mechanisms for understanding social nuance in text messages; instead, they must draw on "stone-aged" social architecture, often causing interpretational issues and social anxiety (Srivastava 2005) (also see "Mismatch Hypothesis").

The *complexity* criterion asserts that any highly developed, cognitively "impressive" trait is likely to be an adaptation; for instance, the ability to infer the emotional states of others (e.g., Brüne and Brüne-Cohrs 2006) necessitates complex mental representations characteristic of theory of mind (ToM) ability.

The idea of "mental math" adaptations might simultaneously violate the principles of *reliability*, *efficiency*, *economy*, *precision*, and *functionality*. There appears to be unprecedented variability in mathematical ability, and many individuals struggle to acquire mental math skills despite steady entrainment in school settings. Additionally, people draw upon numerous linguistic, heuristic, and perhaps visuospatial resources from working memory when performing mathematical computations, hindering efficiency and accuracy.

Tooby (1999) argues that the deductive scientific procedure for determining by-products

from adaptations is of the same kind used in any other investigation; consider the observed mechanistic underpinnings within the “space of possibilities” to evaluate whether they perform better than a null stochastic account would predict. This sort of analysis, argues Tooby, could be performed at the genomic level, for instance, by comparing randomly generated nucleotide sequences to actual ones and employing traditional significance-testing procedures. Tooby also suggests applying the same logic to “adaptations involving larger anatomical structures, physiological processes, enzymatic pathways, the physical distribution of proteins in tissues, the timing of events in development, the logical organization of computational circuitry, or the patterns in behavior.”

Another pertinent methodological concept is that of “double-dissociation” (e.g., Hillis and Caramazza 1991; Bechara et al. 1995). Double-dissociations are patterns of findings showing that two functions operate separately from each other. For instance, if one species possesses metacognition but *not* theory of mind (ToM) and another species possesses ToM but *not* metacognition, then metacognition cannot simply be a by-product of theory of mind because it operates in ToM’s absence. Psychological studies have reported double-dissociations between conditioning and declarative knowledge (Bechara et al. 1995); item and source memory (Glisky et al. 1995); verbal and quantitative mathematical knowledge (Dehaene and Cohen 1997); and emotional and cognitive empathy (Shamay-Tsoory et al. 2009).

Plaut (1995) criticizes double-dissociation studies on account of fallacious neurobiological assumptions. His conclusion is that double-dissociations do not always indicate adaptive modularity. Among his evidence are instances in which single brain lesions produce double-dissociations in behavior, i.e., between processing of concrete and abstract lexical items.

Ongoing uncertainty exists as to whether capacities such as religious behavior (e.g., Wiebe 2008; Powell and Clarke 2012), artistic sensibility (e.g., De Smedt and De Cruz 2012), and the female orgasm (Puts and Dawood 2006; Lloyd

2009; Wallen et al. 2012) are best thought of as by-products or adaptations. An “adaptation” approach might consider ritualized behavior in the form of religious rituals as a costly signal that promotes/facilitates social cooperation and therefore confers adaptive advantage to the religious group (Sosis and Alcorta 2003; Bulbulia and Sosis 2011). Conversely, a by-product approach might suggest them to be epiphenomena of a Hazard-Precaution (H-P) system (Boyer and Liénard 2006). In this case, the by-product approach accounts for their widespread and compelling nature by suggesting that elements of religious rituals (e.g., themes) cognitively capture the H-P motivational systems, and from a cultural selection perspective, this set of human dispositions (i.e., H-P systems) could be considered an enabler of cultural transmission of particular mental representations (religious rituals).

Puts and Dawood (2006) suggest that the hallmarks of adaptive utility are found in the female orgasm. They hypothesize multiple adaptive phenotypic features: discriminative utility in mate selection; assistance in sperm uptake; selective retention of sperm; regulation of uterine contractions during intercourse; etc. Lloyd (2009) counters that the by-product hypothesis remains more likely because of the magnitude of variability in the female orgasmic response, which stands at odds with a strong directional selection account.

Another noteworthy example is Pinker’s (1997) contention that humans’ appreciation for music is a by-product of the more generalized design of the reward system. According to his account, music simply hijacks the brain’s reinforcement mechanisms like a drug. To make his reasoning clearer, he likens the appreciation of music to appreciation of high-fat foods, such as cheesecake, that were not featured in the environment of evolutionary adaptedness; in this account, both contain “megadoses of agreeable stimuli which we concocted for the express purpose of pressing our pleasure buttons.” Thus, the propensity to take pleasure from musical compositions is likely a by-product of the human reward system’s wiring, just like enjoyment of cheesecake. It is untenable that humans evolved to seek cheesecake in the early human environment (see

EEA relevance criterion, described above), and although it is a less clear-cut example, Pinker believes that music co-opts surrounding adaptations in a similar way.

This view is not unanimously shared among evolutionary psychologists. Miller (2000) contends that music performance bears the hallmarks of a sexually selected adaptation: complexity, clear reproductive significance, and elements of repetition/consistency alongside novel/spontaneous elements.

Relative Importance Across Fields

While most subdisciplines of psychology do not directly discuss the question of adaptation versus by-product, the implicit conclusions of these frameworks speak to the relative emphasis on adaptive and by-product explanations. In particular, Skinnerian behaviorist approaches often view a multitude of human traits as by-products of domain-general learning mechanisms. Among Skinner's arguments is the contention that human language is simply a complex form of domain-general reinforcement learning (Epstein et al. 1980). Chomsky (1971) famously criticized Skinner's account, mostly on the grounds of the *complexity* criterion for identifying adaptations.

More general debates on the importance of by-products in human psychology are ongoing. Gould and Lewontin (1979) criticize the evolutionary tradition for overemphasizing adaptive explanations of behavior and ignoring the ubiquity of by-products and exaptations, while Buss et al. (1998) respond to this criticism by highlighting the field's accepted standards of rigor in distinguishing adaptations from by-products (see section "[Identifying By-Products](#)" above).

The relative extent of by-products' importance in generating human behavior, cognition, and affect likely falls somewhere between the extremes suggested by behaviorist and cognitive approaches to the matter; however, such a question can and should be addressed with parsimony and consistent standards and evaluated on a case-by-case basis.

Conclusion

While by-products are often not the principal focus of evolutionary psychologists' investigations, understanding these phenomena and how they fit into the larger evolutionary picture is of crucial importance. In the present report, the clues that are often used to distinguish by-products from adaptations have been discussed; these include evolvability, reliability, efficiency, economy, precision, functionality, and complexity (Buss et al. 1998). While these variables provide a useful rubric for the classification of psychological traits into by-product and adaptation categories, their direct application to many specific cognitive and behavioral functions is a source of ongoing debate.

Cross-References

- [Adaptation](#)
- [Exaptation](#)
- [Modularity of Mind](#)
- [Spandrel](#)

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By-Product Mutualism

- [Cooperation in Social Carnivores](#)
- [Cooperative Foraging](#)

By-Products

- [Function Versus Capability](#)

By-Products of Adaptations

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Synonyms

[Aptation](#); [Co-opted adaptation](#); [Co-opted spandrel](#); [Exaptation](#); [Non-aptation](#); [Secondary adaptation](#); [Spandrel](#)

The paths of evolution – both the constraints and the opportunities – must be largely set by the size and nature of this pool of potential exaptations. Exaptive possibilities define the “internal” contribution that organisms make to their own evolutionary future. (Gould and Vrba 1982, p. 13)

Definition

An adaptation (sensu product) is an inherited and reliably developing trait that came into existence through natural selection because it helped to solve a specific problem of survival or reproduction

better than alternative designs existing in the population during the period of their evolution (after Buss et al. 1998). More specifically, “[c]haracteristic *c* is an adaptation for doing task *t* in a population if and only if members of the population now have *c* because, ancestrally, there was selection for having *c* and *c* conferred a fitness advantage because it performed task *t*” (Sober 2000, p. 85). The primary/original usage causing an adaptation to evolve is called a “function.” Much-cited examples of physiological and behavioral adaptations in various animal taxa include hibernation, echolocation, and thanatosis, whose main functions are energy conservation, navigation/foraging, and anti-predation, respectively.

By-products of adaptations include a range of phenotypes (i.e., an individual’s morphological characteristics, physiological responses, behavioral patterns, and psychological traits) whose origins, maintenance, and transformation are structurally and necessarily coupled with the evolution of adaptations, by way of historical constraints. There are two main by-products of adaptations: spandrels, and exaptations. Neither have any functional design: they did not originate as fitness-enhancing solutions to ancestral adaptive problems *during* their period of evolution. They only came about through the correlated selection of adaptations, and not because they were, themselves, *originally* selectively advantageous – even though, in the case of exaptations, they may have acquired a fitness-enhancing role at any point *after* their period of evolution.

Spandrels, also known as fitness-neutral by-products of adaptations, are *selected* (i.e., they arise through natural selection), but not *selected-for*, by-products of *selected-for* phenotypes (Gould and Lewontin 1979). They have never been, and are still not, adaptive. The chin, male nipples, and female orgasm are generally considered textbook examples of anatomical and physiological spandrels because they are non-adaptive developmental side effects of the selection for reduced mandibles in modern humans, the strong selective pressure on females to have functional nipples, and naturally selected male orgasmic capacities, respectively.

Exaptations are initially unselected traits capable of being subsequently put to (a new) usage through a process called “co-option” or “co-optation” (i.e., functional recycling of ancestral structures). An exaptation is a trait that was not originally designed and selected for its current usage, but owes its fitness-enhancing capacity to features present for other reasons, and is therefore *aptus* (i.e., “fit” in Latin) “by reason of” or “as a consequence of” (i.e., *ex-* in Latin) its form (Gould and Vrba 1982). The prefix *ex-* indicates that the trait’s quality of being *aptus* is posterior to its origin. Therefore, an exaptation is a trait that is currently adaptive without being an adaptation. Because the current (or recent) capacity of an exaptation to enhance fitness did not contribute to the original selection of this trait, the fitness benefit the trait is “exapted to” cannot qualify as a function. The (secondary) usage causing an exaptation to evolve is called an “effect” (i.e., its later/current usage; Gould and Vrba 1982). Typical morphological exaptations are feathers and fontanels, whose respective effects are flight in modern birds and easier parturition in placental mammals. Often-cited examples of behavioral and psychological exaptations in humans and non-human animals include ritualized behavior patterns as non-signaling phenotypic adaptations co-opted into communicative signals, as well as some linguistic components and religious belief as fitness-enhancing and culturally maintained by-products of specific cognitive adaptations.

Introduction

We are all familiar with the term “adaptation.” Most evolutionary scholars believe they can confidently define it and provide a host of examples of how biological evolution produced phenotypic traits that currently enhance the survival rate and reproductive success of their bearers. However, what does careful and critical scientific inquiry tell us about this level of confidence? When faced with evolutionary puzzles, such as clearly nonadaptive unfused skull sutures in reptiles and birds, what did we really learn from Darwin’s (problematically teleological) concept of “pre-

adaptation,” later renamed “exaptation” by Gould and Vrba (1982)? While paleobiologists rely on fossilized tissues or organs to test the correspondence between structural and functional components of extant and extinct species in their respective current and reconstructed ancestral environments, how can ethologists and evolutionary psychologists determine the phylogenetic origins and historical pathways of behavioral and psychological characteristics that do not leave systematic traces in the fossil record? What were the external selective pressures (i.e., adaptive problems) and internal factors (i.e., structural constraints) that were responsible for designing phenotypic adaptations and (re-)shaping their subsequent by-products over evolutionary time?

Answering these questions is a daunting task that requires (1) a solid understanding of the variety of evolutionary processes, products, and histories, (2) a strong evolutionary epistemological framework (e.g., testing specific, falsifiable, competing, and theory-driven hypotheses, with logical arguments, critical thinking, and scientific skepticism), (3) a healthy dose of Darwinian pluralism and the will to take evolutionary by-products seriously, (4) a conceptual and methodological toolkit including a number of complementary evidence-based criteria, (5) the humility to use these tools on a case-by-case basis, as there are no general rules to test hypotheses about “adaptations” versus “evolutionary by-products” that are applicable across phenotypic traits, species, and environmental conditions, and (6) a constant fight against our pervasive psychological predisposition toward teleological stories (Andrews et al. 2002).

In this review, I will strive to eschew the oversimplistic, flawed, and even counterproductive pan-adaptationist position, which consists in perceiving natural selection as the only force of evolution, minimizing the role of historical constraints on optimal designs, and believing that adaptations are ubiquitous. I will draw on different research fields (e.g., evolutionary biology, evolutionary psychology, evolutionary linguistics) and provide a series of examples of morphological, physiological, behavioral, and psychological traits whose evolution could be construed in terms of either adaptationist or

by-product accounts. I aim to show that a focus on by-products of adaptations can truly further our understanding of Darwinian evolutionary processes and the diversity of phenotypic outcomes they produce, including those with no obvious current survival or reproductive values.

Morphological By-Products of Adaptations

One of the basic tenets of Darwinian evolution holds that selection strength and phenotypic variability are negatively correlated. Therefore, one can expect that more functionally constrained phenotypes were subjected to higher selection pressures during their evolution, which should have made them less structurally variable than their less/nonfunctionally constrained counterparts, which are presumed to have evolved under weaker selection. Thus, comparative structural analysis of adaptations and their corresponding by-products may allow evolutionists to assess their relative functionality. Theoretically, this powerful structure-function interface could be applied to any pairs of behavioral traits that are linked at the proximate levels (i.e., in their developmental trajectories and underlying mechanisms) and at the ultimate levels (i.e., in their functional consequences and phylogenetic pathways).

Penis Versus Clitoris and Female Versus Male Nipples

This evolutionary-based prediction was tested in humans by examining two pairs of sexually selected morphological traits shared by both sexes, with one being an adaptation and the other being the corresponding developmental by-product. Within each sex, researchers compared interindividual variability in the size of penises versus clitorises, and the size of female nipples versus male nipples, after controlling for other morphological and environmental factors. As expected, the variability in the size of penises across men was significantly lower than that of clitorises across women; this result (1) is consistent with the fact that the former organ is an

adaptation and the latter its functionless developmental by-product, and (2) lends some support to the by-product account of female orgasm (Wallen and Lloyd 2008). However, contrary to expectations, the size of female nipples (i.e., the anatomical adaptation naturally selected for lactation) was significantly more variable than that of male nipples (i.e., the functionless developmental by-product); this result seems to discredit the premise that greater structural variability indicates weaker selection, and lower, or lack of, functionality (Kelly et al. 2018). Nevertheless, one should expand this type of investigation beyond morphological traits and variation in size. For example, one should test this hypothesis in other phenotypic traits (e.g., behavior patterns) and other types of structural variability (e.g., temporal organization of behavioral sequences).

Human Chin

Due to historical constraints within highly integrated body plans, many other morphological structures seem to have evolved as by-products of naturally selected organs. The human chin is typically considered a structural spandrel; it is an unselected-for but inevitable side effect of the construction of adjacent adaptive features that were designed to serve the combined functions of breathing, chewing, and talking, which required a reduction of our hominid ancestors' jawbone. Even though the human chin did not originate to solve any particular fitness-related problems in our ancestral past, experimental evidence suggests that sexual selection may have subsequently acted upon this morphological trait as a potential signal of health and mate value (Thornhill and Gangestad 1996). This example illustrates the multitude of fitness-enhancing phenotypic traits that were not originally built by natural selection for their later or current usages.

Human-Like Manual Proportions

Likewise, the evolutionary transition from ape-like to human-like manual proportions (with a long thumb relative to other fingers, allowing for our unique pad-to pad precision grip capability) has first led researchers to argue that the functional design of human hands originated as a fitness-

enhancing solution to the adaptive problem of tool-assisted extractive foraging. In other words, human-like manual proportions must have initially evolved as an adaptation for stone tool-making. However, this adaptationist hypothesis was ruled out after examination of the manual fossil remains of *Australopithecus afarensis*, a taxon that already showed human-like manual proportions but did not make or use stone tools (Alba et al. 2003). An alternative explanation (possibly combined with pleiotropic constraints) is that, once the selective pressures of arboreal locomotion were relaxed, finger reduction in *Australopithecus afarensis* could have emerged as a functionless by-product of the adaptation to bipedalism, and was subsequently co-opted in more recent hominins as an exaptation for stone tool-making (Alba et al. 2003).

Physiological By-Products of Adaptations

Antibacterial Enzyme and Lactose-Production Regulatory Protein

Just as evolution tinkers with preexisting structures, it also recycles physiological systems through functional shifts over time. Gould and Vrba (1982) provided a good example of such exaptational capacities across animal taxa. The body secretions (e.g., mucus, saliva, tears) of all vertebrates contain an enzyme called lysozyme that was originally selected for its antibacterial function; more specifically, this ancient molecule appeared around 500 million years ago and probably evolved as an adaptation for the dissolution of the mucopolysaccharide structure of bacterial cell walls. Around 350 million years ago, the genes coding for lysozyme underwent minor mutational alterations that gave rise to a new gene coding alpha-lactalbumin, a protein required for the synthesis of lactose, the sugar secreted in milk. During the even more recent evolution of mammals, when the need for a milk-producing system arose, natural selection simply operated on a preexisting molecule whose structure had already been modified and was co-opted for a new fitness-enhancing usage: Alpha-lactalbumin

was recruited as a by-product of an antibacterial adaptation to serve the effect of lactation in mammals.

Female Orgasm

The evolution of female orgasm has long been used as a case study in the highly debated logic of research questions pertaining to physiological by-products of adaptations. A comprehensive review of the literature showed the existence of 21 hypotheses about how female orgasm had evolved (Lloyd 2005). On the one hand, an overwhelming majority of them (i.e., 20) hold the view that this trait is an adaptation. An often-cited adaptive explanation is grounded in the “Female Choice” hypothesis, which states that a woman mating with more than one men over a period of time, possibly across different menstrual cycles, will experience orgasm preferentially with the higher-quality males. This hypothesis also assumes that female orgasm is accompanied by a mechanism of uterine upsuck that increases the chances of the female of being impregnated by the higher-quality male. However, while the first component of this scenario (i.e., female orgasm preferentially with high-quality males) has been fairly supported by empirical evidence, the second component related to fitness enhancement (i.e., preferential insemination by higher-quality males via uterine upsuck) has been refuted (Lloyd 2005). Moreover, ten of the adaptive explanations operate on the assumption that women experience orgasm frequently during sexual intercourse, whereas replicated questionnaire-based surveys of very large samples showed low rates of female orgasm during the most common and evolutionarily relevant sexual encounters (i.e., vaginal intercourse) (Lloyd 2013).

On the other hand, the “By-Product” hypothesis is the only non-adaptationist account for the evolution of female orgasm. Just as female nipples are adaptations, whereas males get nipples “for free” (due to developmental pathways that are common to both sexes), male orgasmic capacities were selected-for (because they served the function of facilitating sperm ejaculation), whereas female orgasm evolved as a functionless by-product of the physiological adaptation

counterpart in males, by virtue of developmental homologies between the penis and clitoris (Symons 1979). Importantly, the “By-Product” account for the evolution of female orgasm is not just a “null” hypothesis, as often negatively labeled by adaptationists to signify a by-default explanation that would be merely based on null results or non-supported predictions from the selectionist camp. Instead, it is a positive alternative causal hypothesis that can have independent empirical evidence in its favor. There is actually converging data to support it, including good to excellent evidence for (1) developmental homologies between orgasmic tissues shared between men and women, (2) lower interindividual variability in penis size than in clitoris size, (3) heritability of variation in female orgasmic capacities, (4) no significant correlation between the frequency of female orgasm and fitness (measured by more or healthier babies) in the context of multiple male partners, (5) cross-culturally low rates of female orgasm during vaginal intercourse, (6) effectiveness of female masturbation in producing clitoral orgasm, and (7) physiological responses (e.g., vaginal muscular spasms, body rigidity) and behavioral changes (e.g., ambivalent facial expressions, rhythmic expiration vocalizations) characteristic of orgasm in female non-human primates engaging in heterosexual and homosexual mounts (Lloyd 2005, 2013; Wallen and Lloyd 2008).

As the aphorism goes, “absence of evidence is not evidence of absence.” However, in this particular case, there is evidence for non-selection of female orgasm and no orgasmic function (*stricto sensu*) in women. Even though some women may find the by-product explanation for female orgasm demeaning, there is no scientific reason to consider it an underrated version of an adaptation. Many behavioral adaptations turn out to be morally questionable traits (e.g., some forms of homicidal behavior), whereas many evolutionary by-products are valuable in their own rights (e.g., artistic behavior). Female orgasm is not an evolutionary “best-of-a-bad-job.” Some cultures value this trait because it is associated with positive emotions and pleasure, not because of its evolutionary origins. Still, in an attempt to

rehabilitate the “By-Product” hypothesis for the evolution of female orgasm, Lloyd (2013) proposed to rename it the “Fantastico Bonus” account. In evolutionary terms, a bonus is a non-adaptation (i.e., fitness-neutral trait) that shows utility (i.e., it is helpful during an individual’s lifetime; Linde-Medina 2017). By providing sexual pleasure to women without increasing their reproductive success, female orgasm would qualify as a bonus.

Neuroplasticity

Neuroplasticity is the capacity of neural circuitry to modify itself structurally and functionally throughout ontogeny in response to environmental changes, experience, aging, and injury/pathology. As is the case with other types of phenotypic plasticity, evolutionists agree that neuroplasticity is adaptive, and evolves – it has increased throughout hominin evolution – through natural selection; however, they disagree on whether neuroplasticity itself is an adaptation, and thus a selectable trait (i.e., a direct target of natural selection, independent of the mean value of a trait across environments), or a by-product (i.e., an indirect/emergent property) of the selection on the different phenotypic optima produced via adaptive neuroplasticity and expressed in each separate environment (Via 1993). Proponents of the former/adaptationist view argue that neuroplasticity is under its own genetic control (i.e., there must be a specific set of “genes for neuroplasticity”) and genetically heritable, whereas proponents of the latter/by-product view claim that the same genes affecting the mean phenotype in each environment also affect neuroplasticity.

According to Buller (2005), “[. . .] rather than slowly adapting specialized structures in the brain to environmental demands over the course of evolutionary time, selection has designed a brain whose adaptation is its ability to adapt to local environmental demands throughout the lifetime of an individual, and sometimes within a period of days, by forming specialized structures to deal with those demands” (p. 142). In other words, neuroplasticity would be a domain-general adaptation allowing our brain to tailor domain-specific

solutions to domain-specific environmental problems. In contrast, Skoyles (1999) considered neuroplasticity an exaptation (1) arising from pre-existing neurophysiological/psychological adaptations, (2) being recently (i.e., “in a period too short for natural selection to have operated”) co-opted for “enabling brains evolved for life in simple hunter-gatherer bands to live in agricultural and high-tech complex societies,” and (3) resulting in “early humans developing the rudiments of a material and symbolic culture” (p. 439). This by-product view of neuroplasticity may contribute to solving the puzzle of the evolution of modern human cognition, including culturally beneficial mental skills that natural selection could not have anticipated (e.g., reading, vehicle-driving, chess-playing, computer-programming), but may be explained in terms of “exapted learning mechanisms” (Andrews et al. 2002).

Behavioral By-Products of Adaptations

Here, I will treat behavior patterns as selectable phenotypic traits – even though evolutionary psychologists typically consider they are not adaptations or by-products per se, because only the behavior-control neuropsychological mechanisms that produce them can be. The literature in various behavior-based disciplines (e.g., ethology, behavioral ecology, evolutionary psychology, anthropology) contains a myriad of examples that qualify as behavioral by-products of adaptations. In humans, these include (1) artistic behavior as a by-product of our adaptive capacities to over-perceive patterns and experience feelings in our environment (i.e., psychological adaptations such as an hyperactive agency-detection device or emotional processes), (2) force-copulating as a by-product of our male hominid ancestors’ adaptive sexual desire for sexual variety without long-term investment and adaptive generalized use of coercion to achieve goals in other behavioral domains, and (3) alcoholism as a by-product of our primate ancestors’ adaptive capacities to perceive the relative ripeness of fruit and predict their caloric value based on ethanol content.

Behaviors such as creating/enjoying arts, rapping, and over-drinking alcohol probably arose by co-opting cognitive processes and satisfying desires that were originally selectively advantageous in ancestral fitness-relevant contexts. Even though they serve no *function*, they might be culturally selected-for or selected-against in our modern world, and have beneficial or costly *effects* (e.g., pleasure/relaxation or harm/punishment), which would make them (mal)exaptations.

Play

Because play behavior seems purposeless in its immediate expression, biologically costly, but adaptive in its deferred benefits, it represents an evolutionary conundrum. There are many adaptationist hypotheses (e.g., sensori-motor training, preparing for the unexpected), and non-selectionist accounts (e.g., incidental side effect of surplus energy, functionless by-product of adaptive but hyperactive reward systems) for the evolution of play. In line with the exaptational view of neuroplasticity, Pellis et al. (2015) argued that, at a rudimentary/origin-relevant stage of evolution, “primary-process play” (i.e., incipient and fitness-neutral playful behavior patterns that are voluntary, repeated, rewarding, incompletely functional in the context expressed, and initiated under relaxed environmental circumstances) arose as a by-product of fortuitous conditions, adaptive or not (e.g., high metabolic energy, motivational conflict, boredom). Once evolved, these basic playful behavioral elements, characterized by some quirkiness, arbitrariness, redundancy, flexibility, and latent potential (i.e., core features of creative and adaptive variability – which is a postulate of biological evolution), would serve as a built-in reservoir of behavioral variants subsequently co-opted for beneficial/fitness-enhancing behavioral effects (i.e., an exaptation Type 2) during further evolutionary transformation into more elaborate secondary- and tertiary-process play.

Consistent with the aforementioned structure-function interface applied to pairs of morphological traits, a comparative analysis of the temporal organization of behavioral sequences expressed in two types of activities that are presumably linked at the proximate and ultimate levels, namely

object play and tool use, showed that the former was more structurally variable than the latter (i.e., its functional behavioral counterpart; Cenni et al. 2020). This result suggests that object play (i.e., a spandrel of some adaptive developmental processes) can serve as a pool of behavioral variability, and has the exaptive potential to be later co-opted for the fitness-enhancing usage (i.e., effect) of tool use.

Non-conceptive Sex

To explain the evolution of non-conceptive sex in animals, including humans, adaptationist and by-product accounts abound (Vasey 2007). In certain populations of Japanese macaques, adult females exhibit bisexual behavior: they routinely mount both adult males and adult females. Vasey (2007) proposed that, in this primate species, female-female mounting (FFM) and female-male mounting (FMM) are non-conceptive sexual behaviors that are functionally and evolutionarily linked, with FFM being an evolutionary by-product of a purported behavioral adaptation, namely, FMM. The functional hypothesis holds that FMM is a special courtship behavior, or a super sexual solicitation, that serves the function of focusing the male’s attention, preventing him from moving away, and expediting male-female mounting (MFM), in the context of high female competition for male mates. FFM would have evolved as a fitness-neutral by-product of selection for FMM, with a potential utility/bonus: Females could obtain sexual reward during mounts.

This model received some support (1) at the proximate/mechanistic level – the temporal organization of heterosexual mating sequences with FMM (i.e., the hypothesized adaptation) showed more structural signatures of functional constraints than that of heterosexual mating sequences without FMM (Gunst et al. 2020) – and (2) at the ultimate/phylogenetic level – an inter-group comparative study showed there were groups of Japanese macaques with FMM and no FFM, but no groups with FFM and no FMM, as expected if FFM was the by-product of FMM (i.e., the purported behavioral adaptation) because the latter should be more phylogenetically primitive than the former (Leca et al. 2014).

Language

The origin of language is one of the most puzzling mysteries in human evolution. Various adaptationist accounts have been proposed (e.g., “hunting coordination,” “grooming/gossiping,” “courtship,” “motherese” hypotheses; Számadó and Szathmáry 2006), but none has provided compelling evidence to attain wide acceptance.

Alternatively, converging behavioral, psychological, and neuroanatomical/physiological evidence support the by-product “Cognitive Coupling” hypothesis, which holds that complex stone tool-making and language co-evolved in early hominins, and the emergence of some linguistic components (e.g., basic syntactic rules) was facilitated by the “cognitive exaptation/hijacking” of preexisting brain mechanisms selected for hierarchical planning and sequential motor execution in the adaptive context of stone tool production (Kolodny and Edelman 2018). Indeed, systematically chipping away at a rock and building a coherent sentence are both goal-directed hierarchically organized sequential behaviors that require us to think several steps ahead. As *Homo erectus* was learning to make increasingly sophisticated stone tools (e.g., Acheulean hand axe), evolutionary changes in its brain could have paved the way for the evolution of language.

Changes in the linguistic components of modern languages (e.g., lexical items, grammatical features) are also explained in terms of exaptation, whereby “junk” morphemes may lose their original grammatical function over time, but remain “idle” for linguistic tinkering until they can be opportunistically co-opted for new/original grammatical effects (Lass 1990).

Ritualized Behavior Patterns

Like the exaptational recycling of feathers in ancestral and modern birds, serving multiple effects (e.g., sexual display, flight, water-shaders during fish-foraging) after their original function (i.e., thermoregulation), ritualization is a process by which non-signaling behavioral adaptations (e.g., breathing patterns, locomotory movements, foraging techniques, self-grooming) are subsequently co-opted for various fitness-enhancing

signaling usages in other contexts, and become exapted communicative signals (Weible 2012). For example, the pup-to-mother mouth-licking behavior as a feeding adaptation in wild canids – that functions to stimulate a regurgitation reflex, causing the mother to vomit food for her pups – was secondarily recruited for its submissiveness-signaling effect between subordinate and alpha wolves (i.e., first exaptation) and recently reused as a sign of affection between domestic dogs and human owners (i.e., second exaptation).

Ritualized signals also arose as behavioral by-products of adaptive “displacement activities” that were structurally modified by natural selection to enhance their effects. In ancestral situations of motivational conflict (e.g., fear/arousal), displacement activities were incomplete/unstructured, inefficient, and/or context-irrelevant behavioral sequences that served the function of internal pressure releaser via motor outlet (e.g., preening, self-scratching, yawning). Through ritualization, these behavioral adaptations were further exaggerated, repeated, stereotyped, or simplified, and thus exapted to more conspicuous and less ambiguous signals in diverse animal taxa, including humans (e.g., agonistic/sexual displays, vocalizations, gestural signaling, rituals) newly expressed in various contexts of communication (e.g., contest competition, courtship, anti-predatory tactic, group-decision voting, social bond-testing, praying ceremonies). The evolution of ritualized behavior patterns (like other phenotypic by-products of adaptations) is typically studied by conducting cross-species or cross-cultural comparative studies.

Psychological By-Products of Adaptations

According to Gould and Vrba (1982), the exaptational power of the human brain is immense. The “cognitive coupling/exaptation/hijacking” hypothesis (also known in neurophysiology as the “cultural recycling of cortical maps” hypothesis) holds that our extraordinary neuroplasticity and cultural capacities allowed us to co-opt preexisting cognitive adaptations or

spandrels for (new) fitness-enhancing/reducing usages (i.e., effects) or fitness-neutral utilities/bonuses through the emergence of various psychological by-product traits that are relevant to a range of domains in our modern cultural environments (e.g., notational/value/belief systems, technology, economy, arts) or are conceived as mental disorders (e.g., ADHD, depression, schizophrenia).

Even though the religious system may be a culturally evolved adaptation designed to solve the problem of cooperation in large human groups, the dominant position in the field of Cognitive Science of Religion (aka “Standard Model”) consists in viewing (raw) religious beliefs as functionless by-products of the adaptive cognitive architecture of our mind, originally designed by natural selection to solve fitness-related problems in non-religious contexts. These domain-specific psychological adaptations (or “functionally specialized computational devices”) from which the building blocks of religious beliefs and rituals (e.g., animistic bias, credibility-enhancing displays) arose include neocortical systems associated with hyperactive agency detection (e.g., pareidolia), intuitive ontological expectations (e.g., folk physics, folk biology, folk psychology or “theory of mind”), teleological reasoning, attachment, and contamination avoidance. Simply put, humans believe in gods because they are (false) pattern-detecting, cause-inferring, purpose-seeking, and story-telling animals. In a Darwinian pluralistic view, a new exaptationist model aims to integrate selectionist and by-product hypotheses of religion (Davis 2017). In the same vein, Burghardt (2018) outlined the intertwined evolutionary pathways of three by-products of adaptations reviewed herein: playfulness, ritual(ization), and belief.

Conclusion

The quest for adaptations and the demonstration that a given trait originated to serve a specific function, and thus solve survival or reproductive problems in humans’ evolutionary past, are part of the mission statement of evolutionary

psychologists. However, as stated by anthropologist David Stump (2010): “Those who hold to the idea that adaptation is the premier outcome of the all-encompassing process of natural selection will recognize the importance of the various types of exaptation and non-aptation as the “raw material” of evolution” (p. 16). In a more colloquial, maybe provocative, but equally powerful way, historical linguist Roger Lass (1990) wrote: “Historical junk, in any case, may be one of the significant back doors through which structural change gets into systems, by the re-employment for new purposes of idle material” (p. 98). This review aimed to stress that by-products of adaptations should not be considered the ugly ducklings of evolutionary research. Adaptations and their by-products are two complementary sides of the same evolutionary coin.

Let us not forget that an individual is an integrated and structurally constrained aggregate of adaptations, along with a heterogeneous class of by-products of adaptations (e.g., spandrels, exaptations Type 1, exaptations Type 2) and residues of evolutionary noise. The question of whether a specific phenotypic trait belongs to one of these three major categories, or is the outcome of a sequential combination of these products over evolutionary time, is generally open to rough debates (e.g., adaptationist versus by-product scenarios for the evolution of menopause, senescence, phenotypic plasticity, language, play, rape, homicide, and religious belief). In Roney’s (1999) view: “Distinguishing adaptations from by-products will require evolutionary psychologists to accept the challenge of empirically demonstrating evidence for special design. [...] A more rigorous union of evolutionary psychology with cognitive science may make arguments for exaptations and by-products largely academic” (p. 436). Yet, Andrews et al. (2002) carefully reminded us about the scientific value of skepticism: “[...] in the absence of evidence one way or another, we should be agnostic as to whether a given trait is optimally designed or constrained; exapted to a particular effect or specially designed for it” (p. 500).

To test “evolutionary by-product” hypotheses in humans, a promising way forward may lie in

the complex connections between biological and cultural evolution. The intriguingly rapid evolution of modern human cognition – which appears to challenge a strict and relatively slow adaptational schema – can be partly explained by inferring our species' dependence on a two-way process of evolutionary flexibility/plasticity (Coessens 2006). First, the unique and far-reaching exaptational features of the human brain have opened up an almost infinite reservoir of behavioral and cognitive possibilities, allowing our hominid ancestors to cope with increased environmental variability and resource uncertainty characteristic of the Pleistocene epoch. Over the past two millions years, members of the genus *Homo* exhibited evolved adaptability, which resulted in a surge of cultural creativity, including technological, symbolic, and artistic innovations. Second, such a culturally scaffolded landscape has provided *Homo sapiens* with enhanced affordances (i.e., a range of opportunities for actions offered by the environment), which in turn, have contributed to selecting further evolutionary flexibility in the next generation in some kind of ratchet-like effect. This cumulative bio-cultural evolutionary process has led to incremental changes as well as behaviors, beliefs, and artifacts with cultural histories, and that no individual could have invented on its own. Ultimately, by-products of adaptations have played a key evolutionary role in the ecological and demographic success of our species.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adaptationist Program, The](#)
- [Adaptations: Product of Evolution](#)
- [By-Product](#)
- [Evolution of Adaptations](#)
- [Evolutionary By-Products](#)
- [Frugivory By-Product Hypothesis](#)
- [Identifying Adaptive Functions](#)
- [Maladaptive By-Product Hypothesis](#)
- [Richard Dawkins on Constraints on Natural Selection](#)

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C

C < Rb

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Synonyms

Altruism between relatives; Hamilton's Rule;
Kin-altruistic behaviour

Definition

The cost of an altruistic act to the donor must be less than the benefit, weighted by relatedness, to the recipient.

Introduction

How is an altruistic act favored by natural selection if it incurs a cost to the actor? As the behavior would have a detrimental impact on the actor's reproductive success, the genes that facilitate the expression of that behavior would be less likely to be passed on and should decrease in the gene pool. Hamilton (1964) recognized the importance of the

relatedness coefficient in the evolution of altruism, incorporating it in a formula to explain kin-selected (Maynard Smith 1964) altruistic behavior.

Imagine a scenario where an individual sacrifices its own life to save others. One copy of the kin-altruistic gene is lost from the gene pool when the actor dies, but if ten close relatives are saved as a result of the sacrifice, several copies of the kin-altruist gene are saved, increasing its frequency in the population. As long as the fitness benefit to the recipients, weighted by their relatedness, outweigh the fitness cost to the actor a kin-altruistic gene will proliferate. This is known as Hamilton's rule (Hamilton 1964):

$$C < R * b$$

where C stands for the cost to the actor, b represents the benefits to the recipient(s), and R is the relatedness coefficient. Thus a self-sacrificing altruistic act should be favored if it saves the lives of more than two brothers/sisters ($R = 0.5$), more than four nieces/nephews ($R = 0.25$), or more than eight first cousins ($r = 0.125$). This is, of course, an oversimplistic view of the link between a gene and a behavioral act; nonetheless, it is a useful concept to illustrate the principle behind Hamilton's rule.

The rule applies to any kind of altruistic behavior, and although it is well supported in nonhuman animals (e.g., Bourke 2014), evidence in humans is scarce (Burton-Chellaw and Dunbar 2015). One

of the difficulties lies in accurately, and ethically, calculating fitness costs and benefits for an appropriate altruistic act. The benefit, measured in terms of the increase in the relative's weighted reproductive success as a result of the altruistic act, must outweigh the cost to the actor, in terms of their decrease in reproductive success. There's no point, for example, helping a sister, if the help does not enable her to have more children while simultaneously preventing the helper from having one or more children of their own. Under these circumstances, the gene for sibling-altruism would not spread.

Conclusion

An altruistic act can evolve through kin selection, as long as the costs associated with the behavior are less than the benefits that accrue to the recipient(s), weighted by their relatedness. This is known as Hamilton's Rule (Hamilton 1964) and has been widely supported in the zoological literature. Evidence from human studies is relatively scarce, in part due to methodological difficulties and ethical considerations in designing appropriate studies.

Cross-References

- ▶ [Alarm Calling Predicted By Inclusive Fitness](#)
- ▶ [Genetic Relatedness Affects Aid To Kin](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)

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Cacogenics

- ▶ [Dysgenic Concerns](#)

"Cads and Dads"

- ▶ [Paternity Uncertainty Hypothesis](#)

Cainophobia

- ▶ [Neophobia](#)

Calculated

- ▶ [Strategic Aggression](#)

Calculating Relatedness

- ▶ [R = Coefficient of Relatedness](#)

Calculating Starvation Risk

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Synonyms

[Deaths from famine](#); [Mortality rates](#); [Thrifty genotype](#)

Definition

Inferring the probability of starving to death from historical data.

Introduction

In prehistory and in historic times, humans have been at risk of such severe food shortage that they may starve to death. Such food shortages, largely in the form of long-term famines, may be due to natural conditions causing crop failure, economic or political policies, war, or combinations of these. This risk of famine is thought to have acted as a selective pressure on human physiology and cognition in determining the storage of food in the body, mainly energy in the form of fat. Various hypotheses including the thrifty genotype hypothesis explain humans' susceptibility to becoming obese due to this selective pressure (Wells 2009). Researchers have attempted to assess whether food shortage and the consequent risk of starving to death has provided sufficiently strong selective pressure to cause the high levels of obesity (Prentice et al. 2008; Speakman 2006).

Mortality Risks and Rates

Formally, "starvation" is the process of consuming insufficient calories to maintain body weight, rather than starving to death. However, for clarity herein "starvation" is intended to convey *mortality* due to insufficient calories over a sufficiently prolonged period.

The risk of starvation can be most simply calculated as the probability of dying from starvation per person per year. More properly, this is called the *rate* of starvation, since a *risk* is something that *might* happen, whereas a *rate* is events per unit of time. The rate of starvation is used to assess the selective pressure for animals, including humans, to store fat. There has been debate about whether this pressure has been sufficiently large to cause obesity in contemporary populations (Prentice et al. 2008; Speakman 2006).

The magnitude of a selective pressure relates not to the absolute magnitude (e.g., of mortality) but the variance in magnitude within a population. The extent to which the risk can be altered by mitigating adaptations is key. The risk of starvation is the rate that would be realized if there was

no mitigation. Humans are clearly adapted to mitigate the risk of starvation: this is the main role of body fat. Logical argument shows that since there is mitigation, the starvation rate cannot be used to measure the starvation risk (McNamara and Houston 1987).

Since not all people are as obese as physically possible, there is clearly some selective pressure that causes lower fat storage. Even obese people tend to defend a certain level of fat: rarely do people just carry on getting heavier indefinitely. Ecologists consider that animals are lean because the risk of being killed by a predator exerts a pressure (Houston et al. 1993). This can happen in one of two ways: carrying too much fat causes the animals to be slower or less able make fast evasive action because of their weight, or increased weight incurs greater energetic costs leading to increased need to forage thereby increasing exposure to predators (Witter and Cuthill 1993).

In the latter case the downwards pressure may not be from predation, but any risk associated with greater food consumption, such as the risk of eating poison or getting a serious infective disease. For clarity herein the selective downward pressure on reserves will be referred to as predation risk. This is a cost that is paid all the time, whereas the starvation only occurs during famines. We are interested in the long-term risks, which are calculated over a long time period. For instance, ignoring the sequential nature of survival for clarity, if a famine occurs once every 10 years and the probability of dying during a famine is 10%, then the starvation rate is 0.01. On the other hand, if predation rate is 1% per year every year then the predation rate is also 0.01.

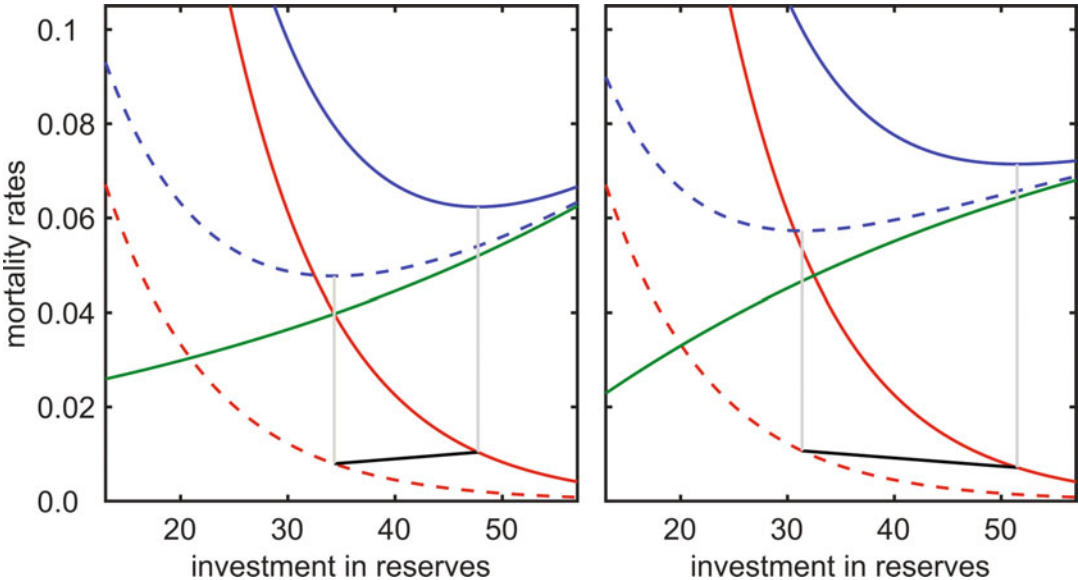
The evidence from animals suggests that the rate of predation is always higher than the rate of starvation (Collins and Kays 2011). Wild animals rarely starve to death, because they do increasingly desperate things as they get hungrier which will lead to greater predation risk. This is why animals that are killed by predators are leaner than the general population, an observation that at first sight appears to contradict the assumption of body reserves increasing predation risk (Speakman 2018). Similarly, humans in famines

eat more and more risky things (toxic or rotting food stuffs). Therefore, the total mortality during a famine could be calculated and then compared to normal conditions to calculate the increase in mortality rate due to the famine, although most deaths are not due to starvation and so do not reflect starvation risk.

Models of the trade-off between starvation risk and predation risk in determining energy storage reveal a counter-intuitive insight: that there need not be any association between starvation risk and starvation rate (McNamara and Houston 1987). These models assume that animals, including humans, are adapted to these risks and have an appropriate store of fat to minimize the total mortality rate. Starvation risk is likely to decline quickly as fat is stored and then level off. Predation rate increases with stores, but the shape of this function is challenging to measure. This is unfortunate, because it has a critical influence on the effect of the starvation risk (Fig. 1). If predation risk is concave (accelerating) as body weight increases, then an increase in starvation risk

causes an increase in starvation rate. However, this increase is not proportional because of the adjustment in the adaptive level reserves. If predation risk is convex (decelerating), the starvation rate is predicted to *decrease* if the risk increases. This occurs because the position of the minimum total mortality rate depends not on the magnitude of the two risks, but on their slopes. Specifically, the minimum total risk is where the magnitude of the two slopes are equal (and opposite sign). Furthermore, if the predation risk is constant with respect to reserves, then the starvation rate is predicted to be constant with respect to the starvation risk.

Hence, increasing uncertainty of the food supply or rate of famines may increase reserves and so increase the predation rate. It is even possible that in some circumstances the probability of starvation may increase as food availability increases. Thus, the observation that most mortality, even during famines, is not from starvation is not evidence against the role of the risk of starvation in determining fat storage strategies.



Calculating Starvation Risk, Fig. 1 Mortality rates as a function of the investment in energetic reserves in two cases, showing that starvation *rate* may increase or decrease in response to an increase in starvation *risk*. The red lines show the starvation rate, green lines the predation rate, and blue lines the total mortality rate. The grey lines indicate the optimal investment in reserves, where total

mortality is minimized. The dashed lines show rates under low starvation risk and solid lines under high starvation risk. When predation rate is accelerating (left panel), an increase in risk leads to an increase in rate. On the other hand, when predation rate is decelerating (right panel), an increase in risk leads to a *decrease* in rate. Based on the analysis of (McNamara and Houston 1987)

Even the total mortality rate does not increase in a linear manner with the starvation risk. Since there is mitigation, the historical rate of mortality from food shortage cannot be used to measure the risk of starvation. We conclude that the magnitude of the mortality during food shortages, including famines, is uninformative about selective pressures, without additional information about the other selective pressures on body reserves (Higginson et al. 2016). Therefore, further debate on this issue is unlikely to help assess explanations for obesity.

One alternative explanation for the high level of fat is that the risk of starving may be negligible whilst food shortage still impacts on evolutionary fitness, such as by reducing fecundity due to the decrease in body fat (Prentice et al. 2008), as humans are partially capital breeders (women store fat to supply pregnancy and lactation). This could be explored further, although it is not clear how it might apply in men.

Conclusion

The number of people who have starved to death in human history cannot provide a measure of the strength of selective pressure to store body fat. Any risk of starving is likely to lead to selection for fat storage, as well as various other functions of body fat.

Cross-References

► Body Reserves and Food Storage

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Calidris pugnax

► Ruff Shorebird, The

Callosotomized Patients

► Split-Brain Patients

Callosotomy Patients

► Split-Brain Patients

Callous-Unemotional Traits

► Psychopathy

Camouflage

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Synonyms

Concealment, Disguise

Definition

A phenomenon whereby organisms avoid detection or recognition by resembling the general background or specific objects therein.

Introduction

Camouflage is a phenomenon, which hides or prevents something from being noticed. As an umbrella term, it covers all strategies involved in concealment including prevention of detection and recognition (Stevens and Merilaita 2009). Camouflage exists across many biological taxa and provides among the most remarkable examples of adaptation. For example, cuttlefish (*Sepia officinalis*) can adjust their appearance in terms of color and patterning to match their respective visual habitat, but also change their shape to increase resemblance to natural objects such as coral, stones, or seaweed (Hanlon et al. 2009). Likewise grouse, ground-dwelling birds, avoid being seen by potential predators by closely resembling the background on which they nest (Thayer 1896). Despite being an ubiquitous anti-predator strategy in nature, and important in many areas of human application (e.g., military, hunting, test cars), only recently has science moved from descriptive accounts to test what camouflage

types exist, how they work, and what their adaptive value is (Nokelainen and Stevens 2016). There has been a revival in the study of camouflage among scientists spanning molecular, sensory and evolutionary biologists, visual psychologists, computer scientists, and art historians. Although camouflage can function via any sensory modality, here we outline the most extensively studied one: visual camouflage in animals.

A Short History of the Study of Camouflage

After Charles Darwin's hallmark book *On the Origin of Species by Means of Natural Selection*, much of the background in terms of what types of camouflage exist in nature was concluded prior to the 1950s. Three bodies of work were (and still are) particularly influential: *The Colours of Animals: Their Meaning and Use Especially Considered in the Case of Insects* by Edward B. Poulton (1890), *Concealing-Coloration in the Animal Kingdom: An Exposition of the Laws of Disguise Through Color and Pattern* by Gerald Thayer (1909), and *Adaptive Coloration in Animals* by Hugh Cott (1940). Since then the theory of camouflage has been refined particularly from the perspective of being an effective anti-predator strategy (Ruxton et al. 2004; Stevens and Merilaita 2011). These excellent accounts have made camouflage a textbook example of natural selection and a long-standing model system for understanding adaptation. Moreover, we know that being able to hide has been important from the very early days, as the earliest organisms bearing a coloration that suggestively served a camouflage function date back to marine animals in the Cretaceous period. However, it has proven challenging to quantify camouflage in natural settings (i.e., difficulty to quantify something that is hard to detect or recognize) and to understand how animals may appear to the appropriate receivers' perceptual systems (i.e., difficulty of seeing world through other animals' eyes).

How Different Types of Camouflage May Work

An organism that is hard to detect is cryptic. The best-known form of this is background matching, whereby both the color and pattern of the organism closely resemble visual properties of the background (Endler 1978). For example, the appearance of many nocturnal moths closely resembles the tree trunks on which they rest during daytime. Disruptive coloration, in contrast, is distinguished by high contrast elements that break up the body contour (Cuthill et al. 2005). The conspicuously striped patterns make an animal harder to detect or recognize in its respective visual environment. Detectability can also be reduced through countershading, whereby an object is darker on the surface facing higher light intensity (Rowland et al. 2007). The pale underside combined with a dark above side seen in many mammals reduces the obviousness of a shadow casted by the animal's own body (i.e., self-shadow concealment). This may also conceal the three-dimensional form of the body (i.e., obliterative shading). In aquatic environments, where there is no background to match, camouflage could be achieved through transparency, where light transmitted through the body renders the bearer virtually invisible. The silvering flanks of many species of fish may function as camouflage too (Ruxton et al. 2004). The scales construct a reflective surface that hinders detection or recognition because the vertically aligned scales operate like tiny mirrors, thus letting its bearer blend in with scattered light. Masquerading organisms (e.g., decorator crabs, stick insects) share a resemblance to inanimate objects that are typically of no interest to a predator (Skelhorn and Ruxton 2010) such as twigs, leaves, or stones (or even bird droppings). Although categorizing different types of camouflage is a useful exercise to understand how they may work, it is important to acknowledge that they are not mutually exclusive and should be considered as a continuum of a set of adaptive traits (Fig. 1).

Advantages of Camouflage in Nature

Predation is one of the strongest selective pressures in nature. Camouflage confers increased survival benefits to prey either during vulnerable life stages or during the whole life of an organism. Early work on camouflage, such as classical work on grove snails and peppered moths, underlined the importance of background resemblance. Grove snails (*Cepaea nemoralis*) carry pale shells on grasslands, whereas snails from shaded woodlands carry darker shells. These differences in shell shading are plausibly caused by divergent bird predation on different colored appearances for better background resemblance in a given light environment (Cain and Sheppard 1954). Similarly, peppered moths (*Biston betularia*) were among the earliest well-documented examples of how camouflage brings survival benefits to its carrier. Peppered moths have two color morphs: pale and dark. The appearance of the pale morph resembles more deciduous, light-colored tree trunks, whereas the dark morph matches the background best when resting on tree trunks darkened through pollution. Foraging bird predators can find mismatched moths on the tree trunks more easily, which facilitates increased matching to specific background types (Kettlewell 1955). It is important to remember that camouflage may also grant benefits to predators, particularly to those who ambush their prey, to which camouflage allows increased foraging success by getting close to their prey. For example, felid coloration often resembles that of the respective habitat's vegetation. By closely resembling the surrounds, these large carnivores are ought to be better able to approach the prey unnoticed before engaging the final pursuit to catch the prey (Caro 2005). Recent studies have quantified camouflage and its adaptive value more directly than classical accounts. It has become possible to quantify how likely an individual is to be attacked with respect to how closely the animal resembles its background as seen through the eyes of ecologically relevant receivers (Kelber et al. 2003). When detailed information of the receivers' vision, light conditions and color



Camouflage, Fig. 1 Illustrative examples of different camouflage types in nature. *Top left* is a rock ptarmigan, a grouse bird, which resembles its background, but also has disruptive markings. *Top right* lion cubs show the general resemblance to the background. *Middle left* is a common shrimp illustrating transparency, and *middle right* is a ghost

crab, which matches its background. *Bottom left* is a green shore crab, which resembles its background, but also has strong contrasting markings to break up the body shape. *Bottom right* a dolphin, which has countershading to mitigate its own body shadows (All photos by Ossi Nokelainen)

properties of the organism, and the background are obtained, the match to the background may be quantified. For example, a recent study of ground-nesting plovers demonstrated that nest survival in the wild is dependent on the degree of camouflage of the eggs (Troschianko et al. 2016). In

plovers, parents flee the nest early when a predator approaches, leaving the nest and the eggs vulnerably exposed on the ground. In contrast, in birds like nightjars that sit tight on the nest even when a predator is close, nest survival is dependent on the level of match of the adult plumage.

How Plasticity and Behavior May Facilitative Camouflage

Coloration is not a static property and some animals may change their appearance over time (Stuart-Fox and Moussalli 2009). In fact, some animals achieve background resemblance through color change. Many taxa are capable of this ranging from insects and crustaceans to reptiles and amphibians. Perhaps most impressively, cephalopods can change body coloration within seconds by using specialized pigments in their skin under neural control (Hanlon et al. 2009). However, color change is slower than this in most animals. For instance, marine crustaceans shed their carapace as they grow, and it has been shown they may adjust appearance between molts for better crypsis (Stevens et al. 2013). Also behavioral plasticity can be used to enhance the camouflage. Many animals can choose backgrounds that match their own coloration better. Quail hen chooses substrates for nesting that provide better match their own egg colors (Lovell et al. 2013). Moths adjust their body orientation and position after landing on a tree to decrease visual detection (Kang et al. 2012). Blue-footed boobies (*Sula nebouxii*) change their egg colors by rolling them in dirt, which increases the background resemblance and decreases nest predation (Mayani-Parás et al. 2015). Decorator crabs adorn themselves by attaching pieces of objects such as seaweeds on their skin that increases the resemblance to the environment (Nokelainen and Stevens 2016). The Pacific tree frog (*Pseudacris regilla*) exhibits color pattern-mediated microhabitat selection so that, in the presence of predator cues, individuals prefer a substrate that matches their own color (Wente and Phillips 2005).

How the Efficacy of Camouflage Links to Evolutionary Psychology

Beyond sensory capabilities, cognitive processes inevitably influence what makes an effective camouflage (Skelhorn and Rowe 2016). When contrasting color patterns are combined with

movement that exceeds the temporal resolution of the viewer's perceptual range, the colors appear to blend together (Stevens 2007). This physiological effect is known as flicker fusion. Movement may also create an illusion, which results in false interpretation of the direction and speed of the target, known as motion dazzle. Thus, variable stimuli have the potential to mislead animal's behavioral output. Similarly, predators have been demonstrated to be worse at finding camouflaged prey when prey populations are polymorphic (Bond 2007). This is because predators tend to focus on prey types that they have most recent experience with. The phenomenon is known as search image formation, which results in overlooking the rare morphs by predators. The followed evolutionary mechanism is known as negative frequency-dependent selection, which can maintain polymorphic prey by fluctuating morph frequencies (Gray and McKinnon 2007). Learning and cognitive processes may thus have a major effect on the value of different camouflage strategies. It is possible that predators learn some types of camouflage more quickly than others, especially the ones with high contrast markings. The value of a given type of protective coloration therefore depends not just on initial detection but also on experience and cognition.

Concluding Remarks

Despite being intuitively easy to understand, camouflage has proven difficult to study in natural settings. We still have a relatively limited understanding on the survival advantage that different types of camouflage provide to wild animals. Although categorizations are useful in order to understand how different forms of camouflage work, they may not be mutually exclusive. Recent technological advantages allow for tests of more detailed hypotheses regarding camouflage in more natural settings, taking into account animal cognitive processes and sensory stimulation across different modalities. Excitingly, we are about to understand how animals may see the world and how this may shape the preservation of the

avored forms in the struggle of existence. This will expand our understanding on camouflage and the diversity that has succeeded over the course of time on inherited characteristics under natural selection.

Cross-References

- [Countershading](#)
- [Disruptive Coloration](#)
- [Masquerade](#)
- [Predator Confusion Hypothesis](#)

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Cancer

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Synonyms

Growth; Neoplasm; Tumor

Definition

Cancer is a family of diseases unique to multicellular animals that are characterized by the uncontrolled cell growth and proliferation.

Introduction

In 1971, US president Richard Nixon declared the “war on cancer,” predicting victory within 5 years. More than 40 years later, cancer is still the leading cause of death in economically developed countries and the second leading death in developing countries. Despite major progress, the treatments developed have not lived up to expectations and cancer research is now at a crossroads, requiring a shift in the way cancer is studied and treated. More recently, scientists have increasingly entered the fray from an evolutionary perspective towards cancer. This Darwinian approach provides scientists with a novel paradigm that permits them to identify mechanisms that drive natural selection among cancerous cells within the tumor.

Cancer Evolution

Evolution is a double-edged sword for multicellular life. Acting over millions of years at the level for population of organisms, evolution animated the intricate complexities necessary for hearts, brains and living creatures including human beings. However, when evolution acts at the cellular level within an organism, it can induce tumor formations.

The problem of cancer is as old as multicellular life. During the transition from unicellular to multicellular organisms about 1 billion years ago, there was selection at the organismal level for the collaboration among single cells to foster the fitness of the newly emerged multicellular individual. This collaboration entailed that each cell had to stop maximizing its own fitness to better propagate its shared genetic material. Cancer happens when somatic cells acquire mutations that stop promoting the fitness of the multicellular organism by increasing their own cell division or survival relative to normal cells. In particular, the hallmarks of cancer (Hanahan and Weinberg 2011) represent different types of breakdowns or “cheating” of the cooperation. One hallmark of cancer is uncontrolled cell proliferation and the circumvention of programmed cell-suicide (apoptosis). Aktipis et al. (2015) have called this a form of demographic cheating. Cancer is also characterized by the stimulation of blood vessels to supply the tumor with nutrients (angiogenesis). This is an example of economic cheating. At short time-scales, these cancerous cells are successful and form neoplasms that can eventually kill the parent organism. This explains the selection of many mechanisms to suppress cancer at the individual level, including tumor suppressor genes that regulate the growth of cells and the architecture of proliferative epithelia that reduces the number of cells vulnerable to neoplastic evolution. Although cells still compete and neoplasms still develop, these mechanisms result in tumors that normally occur only later in life, when our prime reproductive years have passed.

Why do cancer suppression mechanisms not involve complete tumor elimination? The explanation for some remaining vulnerabilities to cancer may lie in evolutionary trade-offs between conflicting levels of selection. One crucial trade-off for multicellular organisms is between restraining uncontrolled cell proliferation while upholding the ability to repair tissue such as wound healing. For tissue repair processes to be successful, cells must be able to proliferate and migrate to the injured site. They must also be able to form new blood vessels to nourish the repairing

tissue. These abilities are reminiscent of some of the hallmarks of cancer (e.g., angiogenesis). It follows that species with fast and effective wound-healing mechanisms, possibly as a consequence of proneness to assault and injury, may be more vulnerable to cancer. In support for this, Archie et al. (2012) documented that baboons with more effective wound healing are subject to more aggression. Another trade-off is between cancer and embryogenesis. During embryonic development, cells often migrate to form tissues and organs. To be able to migrate, embryonic cells go through the process called epithelial-to-mesenchymal transition (EMT). Research indicates that the EMT program is reactivated in cancer cells, which may enable them to metastasize. Trade-offs between reproduction, aging, and susceptibility to cancer have also been suggested (Aktipis and Nesse 2013). Overall then, these trade-offs imply that while we could have more effective mechanisms to suppress cancer, this may entail high costs for tissue repair, embryonic development, reproduction, and longevity.

Nowell (1976) was the first to propose that the transformation of normal cells into cancerous cells represents a form of Darwinian evolution favored by natural selection, a hypothesis for which there is now ample empirical support. Heritable variation of reproductive success in a population is sufficient and necessary to cause evolution by natural selection. Natural selection occurs on a cellular level because somatic cells acquire heritable variation through somatic mutation and epigenetic events, including mutations that affect a single DNA nucleotide and the gain or loss of entire chromosomes. This variation is heritable through mitosis, and any variants that confer a selective advantage will be selected, regardless of their ultimate effects on the host's health. In fact, all of the hallmarks of cancer are phenotypes that improve the fitness of a mutant clone over competitor clones lacking the phenotype. Each variant cancer cell can then further divide to form a clonal lineage. The daughter cells, in turn, may also acquire new genetic and epigenetic abnormalities in the process of cellular reproduction. Cancer is therefore a result of

repeated clonal expansion, succeeded by clonal selection, in the adaptive tissue ecosystem. The result is a better-adapted, highly heterogeneous cancer. Although this evolutionary progression to a cancerous state is most often stopped through cancer suppression mechanisms, a tumor can develop fast and aggressively if it acquires early mutations allowing it to evade apoptosis or the immune system.

Resistance to therapy is a major problem in the treatment of most cancers. While patients often respond to the first application of therapy, they are prone to relapse. Why has it been difficult to find a cure against cancer? An evolutionary perspective sheds light onto this question: cancer – even within one person – is not a single entity. New genetic evidence from cell genomics and single cell analysis in many different types of cancer supports the existence of extensive mutational heterogeneity among cancer cells (e.g., Merlo and Maley 2010). Marusyk and Polyak (2013) have argued that this heterogeneity enables a cancer cell population to deal with selective pressures. Cancer therapies impose an artificial selective pressure, eliminating sensitive cancerous cells but leaving behind resistant cells. In other words, cancer therapies are selecting for resistant tumor cells and selecting against chemosensitive cells. As a corollary, chemotherapy that kills chemosensitive cells may simply remove clonal competition and open up space and resources. This allows the resistant lineage to expand again, with often catastrophic consequences for the patient. High genetic diversity among cancer cells is therefore arguably a key determinant of therapeutic failure. Furthermore, since each patient's cells evolve through an independent set of mutations and selective environments, the emergent tumor cell population is probably unique within each cancer patient. This, in turn, means that it is extremely difficult to find a general treatment program that is equally effective for all patients.

While an evolutionary perspective highlights the slim chances for finding a definite cure for cancer, on the bright side, it also highlights the potential effectiveness of several treatment strategies. Below are some examples:

Early Detection and Intervention

Etzioni et al. (2003) have argued that early detection poses one of the most promising approaches to prevent the growing cancer burden. A cancer that does not have enough time to produce much genetic diversity is unlikely to contain treatment-resistant cells. Early detection of neoplasm before widespread genetic heterogeneity develops already plays a key role in the control of cervical and breast cancer and is likely to become more important for the management of colorectal, prostate, and lung cancer.

Combination Therapy

Even with early diagnosis and intervention, there will remain some cancers that evolve in a covert fashion and only present late in their evolutionary development harboring chemoresistant cells, as is the case with pancreatic cancer, glioblastoma, lung cancer, and many ovarian cancers. Some researchers have suggested that combination therapy should lead to improved response rates compared to single agent therapy and reduce the likelihood of relapse. Given that cancer therapeutic resistance is a result of different mutations within the cancer population, the likelihood is relatively high that at least some cells within a large tumor cell population will carry a mutation conferring resistance to a single agent. However, the odds that a patient has cancer cells with the multiple mutations needed for resistance to several different drugs is much lower. In support for this, a meta-analysis of single-agent versus combination chemotherapy found that the latter conferred an advantage for survival, tumor response, and time to progression in women with metastasis breast cancer. However, adding more drugs also increased toxicity, indicative of a trade-off between toxicity and blocking therapeutic resistance (Carrick et al. 2009).

Individualized Cancer Therapy

Given that every patient has a unique tumor architecture, not every drug (or combination of drugs) will work similarly in every patient. Consistent with this, a large number of patients treated for cancer do not respond to therapy given to them.

Some researchers therefore emphasize the importance of a personalized medicine approach where drugs are chosen based on the underlying mutations in each patient's tumor.

Mismatch Repair

In the broader context, some researchers have focused on environmental and life-history factors that may pose a risk to cancer because they are novel in an evolutionary sense. Darwinian natural selection has “no eyes to the future.” It follows that certain gene variants that were selected in the past, because they best fit the prevailing environmental conditions now, can increase cancer rates due to changes in the physiological context in which these inherent genes now have to function. In other words, there is a mismatch between ancestral conditions and modern environments. This mismatch is the result of our rapid evolution of social behavior patterns that has outpaced our Stone Age genetics. A potent example of evolutionary mismatch is with skin cancer. There is a general agreement that exposure to the sun and ultraviolet radiation (UVR) is the main causative factor in the induction of skin cancer. Dark, or highly melanized, skin acts as a defense against UV-induced damage. However, high amounts of protective skin pigment also restraints vitamin-D biosynthesis in places that receive less sunlight. This is the leading explanation for why paler skins have evolved in higher northern latitudes where contact to UVR has tended to be low. The migration of white-skinned individuals to southerly environments creates a mismatch between skin pigment and sun exposure, which explains why white-skinned individuals are orders of magnitude more at risk for skin cancer when living in equatorial zones.

In a similar vein, the most widely accepted evolutionary hypothesis for breast cancer, the hormonal proliferation hypothesis (Eaton et al. 1994), postulates that a major contributor to the increased risk for breast cancer is a dramatic change in life-history patterns that has skyrocketed women's contact to the endogenous steroid hormones estrogen and progesterone. Hunter-gatherer women had far fewer lifetime ovulation cycles compared to women living in

developed countries. This is because the former were usually pregnant or lactating, whereas later first birth, nursing of shorter duration, earlier menarche, the use of modern birth control, and fewer children born to modern women means fewer menstrual cycles in a lifetime. During menstrual cycling, the ovarian hormones stimulate breast cell division, enhancing the risk for mutations that lead to cancer. Overall then, appreciation of environmental and life-history factors can help prevent the development of cancer via the education of lifestyle decisions, or where these are difficult to change, as might be the case for breast cancer, via focusing attention on hormonal or immunological intervention.

Conclusion

In summary, viewing cancer through an evolutionary lens may help to gain a clearer understanding of cancer. In particular, an evolutionary perspective allows us to appreciate better why cancer exists (multicellularity), how it progresses (somatic evolution), why it is not more common (selection for cancer suppression mechanisms), why cancer suppression mechanisms cannot completely eliminate cancer (trade-offs), and why it is so difficult to cure (tumor heterogeneity), as well as opening up possible avenues for cancer treatment.

Cross-References

- [Adaptive Problems](#)
- [Altruism Advertises Cooperativeness](#)
- [Cell Death as an Adaptation Against Cancer](#)
- [Competition for Resources Desired by Females](#)
- [Darwinian Medicine](#)
- [Death](#)
- [Effect of Birth Control on Women's Preferences](#)
- [Evolution of Cooperation](#)
- [Evolutionary Medicine](#)
- [Evolutionary Mismatch](#)
- [Fundamental Tradeoffs](#)
- [Mutation](#)
- [Problem of Cheating](#)

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Canines

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Synonyms

[Coyotes](#); [Dogs](#); [Foxes](#); [Jackals](#); [Wolves](#)

Definition

Family Canidae, a family within Carnivora with multiple species, including dogs, wolves, foxes, jackals, coyotes, and other dog-like mammals.

Introduction

Canines are an extremely large and varied family, including domestic dogs, but also wolves and foxes. The domestic dog is humankind's closest animal companion, having been domesticated for at least 15,000 years and possibly longer. Because of their close association with humans, whether they share our moral attributes is of high interest to researchers. Humans have the tendency to attribute many human mental states to dogs, including "secondary" emotions such as jealousy, embarrassment, guilt, shame, pride, empathy, and grief (Konok et al. 2015). Some of these are overly anthropomorphic and do not reflect the underlying psychology of dogs. For example, owners often report that their dog feels guilt over disobedience, whereas research suggests that dogs are actually displaying fear of punishment or trying to reduce punishment (Hecht et al. 2012; Horowitz 2009). However, dogs may actually feel jealousy (Harris and Prouvost 2014) and empathy (Custance and Mayer 2012). Whether dogs feel these emotions is relevant to morality, as these emotions can indicate a sense of morality.

Allchin (2009) breaks morality down into multiple levels: moral behavior, moral motivation or intent, moral systems, and moral cognition. Moral behaviors include altruistic behaviors (i.e., cooperation and helping). Moral motivations include sympathy, empathy, other innate motivations for helping, and emotions related to justice, including guilt, shame, and a sense of fairness. Moral systems are those social groups that enforce cooperation through reward or punishment. Moral cognition involves the ability to detect intentions (positive or negative) of others (theory of mind) in order to judge moral behaviors and attitudes, and the ability to keep track of the behaviors of others over time (such as reliability). This entry will discuss the moral behaviors, motivations, cognition, and systems of dogs and other canines in order to explore the evolution of morality in Canines.

Morality in Canines

Moral Behaviors

Of the moral behaviors that canines engage in, cooperation is probably the most ubiquitous.

Many species of canine engage in cooperative breeding, which occurs when individuals other than the parents help care for offspring, such as older siblings or unrelated group members (Wiley and Rabenold 1984). Cooperative breeding (regardless of the psychological modules designed to motivate it) is usually explained by kin selection (older siblings increase their fitness more easily by assisting in raising younger siblings rather than going out to find a territory and/or mate of their own), but there may also be direct benefits of staying with parents related to survival, such as for foraging or defense, and delayed benefits related to increasing chances of later acquiring a territory or mate (Wiley and Rabenold 1984). Unrelated individuals might benefit by reproductive access to the parents or breeding pair, as well as the direct benefits gained by kin (Wiley and Rabenold 1984).

Canines are unusual in that they are the only carnivore family that uses food regurgitation to provision young, with the exception of bat-eared foxes (Moehlman and Hofer 1997). Non-parents (alloparents) will provide food to both mother and pups and assist in guarding pups in dens; some actually assist by lactating as seen in red foxes and wolves (Moehlman and Hofer 1997). Others engage in communal nursing (i.e., Bengal foxes, bat-eared foxes, arctic foxes, gray zorros, red foxes, coyotes, African wild dogs, and gray wolves; Moehlman and Hofer 1997). Among smaller species, only females tend to alloparent, whereas in larger species both sexes will engage in alloparenting behavior (Moehlman and Hofer 1997). In general, the presence of alloparents in canines does seem to increase pup survival (Moehlman and Hofer 1997).

Likewise, many canines also engage in cooperative hunting, although this is limited mainly to those of larger body size (Moehlman and Hofer 1997). Black-backed jackals, golden jackals, coyotes, dholes, gray wolves, and African wild dogs engage in cooperative hunting (Moehlman and Hofer 1997). The benefits of cooperative hunting in canids are still unclear: cooperative hunting can allow the killing of larger prey, an increase in dietary breadth, and may have a higher success rate, but it is unknown whether

individual food intake increases with cooperative hunting (Moehlman and Hofer 1997). Domestic dogs can learn to cooperate with each other on a human-designed problem that mimics the reactivity of prey; food rewards were placed on the opposite side of a fence with two openings and a human experimenter controlled a sliding door that could close only one opening at a time. Although dogs cooperated, they did not monitor each other's actions in this task (Bräuer et al. 2013a).

Free-ranging dogs will cooperate in conflicts; members of one group will cooperate during aggression from or against strangers (Bonanni et al. 2010). In this case, dogs are more cooperative when they are part of smaller groups and the risk of defecting is higher (i.e., their individual contribution has a greater effect on the likelihood of winning or losing a conflict). However, there is no evidence that dogs punish those who "cheat" in this context. In addition, dogs cooperate with humans. Historically, dog domestication may have initially involved humans using dogs for assistance during hunting. In a study of modern moose hunting groups in Finland, researchers found that dogs increase hunting success in both small and large groups of hunters, especially when moose density is low (Ruusila and Pesonen 2004). Thus, dogs may have translated cooperative hunting skills from their wolf ancestors to hunting cooperatively with humans. Dogs also cooperate with humans today: dogs trained to work with blind owners as well as normal pet dogs will take turns initiating cooperative actions on an obstacle course (Naderia et al. 2001).

Recently, dogs have also been found to be cooperative to the extent of prosociality (i.e., helping others with no direct gains to the self). Dogs will help a human with a goal (e.g., pushing a button to help open a door) when humans explicitly point at a button or when they communicate verbally with the dogs (Bräuer et al. 2013b). To be clear, they perform these actions without specific training or without being given any food reward. Dogs even differentiate between generous and non-generous humans in an "eavesdropping" paradigm, using vocal cues to recognize cooperative intentions in humans (Marshall-Pescini et al.

2011). In addition, dogs behave prosocially towards other dogs that are familiar to them. When given the opportunity to manipulate a food-dispensing device, "donor" dogs will pull a bar to dispense food to another "receiver" dog, even when the donor receives no food (Quervel-Chaumette et al. 2015).

Another area where canines display moral behavior is through reconciliation. This has only been studied in dogs and wolves, but may also include other species of canines. Reconciliation falls into the category of post-conflict affiliative behaviors (i.e., friendly behaviors such as greeting, sitting/lying together, anogenital sniffing, playing, or licking), which can occur between victim and aggressor (reconciliation) or between victim and another dog (consolation or post-conflict third-party affiliation; Cools et al. 2008). These behaviors function to reduce the negative effects of aggression, such as having to leave a group (Cools et al. 2008). Dogs, like primates, show both reconciliation and consolation, especially towards familiar animals (Cools et al. 2008). These behaviors may not be new to dogs; wolves, both in captivity and in the wild, also show reconciliation and consolation, and tend to direct these behaviors towards other animals that give them coalitionary support (i.e., support during conflicts; Baan et al. 2014; Cordoni and Palagi 2008; Palagi and Cordoni 2009). In sum, canines show many behaviors that are considered to be within the sphere of morality, such as cooperation and reconciliation. However, the degree to which these behaviors are actually motivated by moral sentiments is unclear.

Moral Motivations

Domestic dogs may have *empathy*, the ability to understand and respond to other animals' emotions. Empathy can be a powerful motivator of moral behaviors in humans. Dogs are attentive to human emotional states; they gaze longer at humans when they are displaying happiness rather than sadness, even when these emotions are not directed towards the dog (Morisaki et al. 2009). In addition, other research has shown that dogs can make behavioral responses to different emotions

displayed by humans (Merola et al. 2014). When humans show either happiness or disgust after looking inside a box or around a barrier, dogs are much more likely to approach the box that was reacted to happily. However, this effect is not as strong with unfamiliar humans, suggesting that this may be a learned, rather than empathetic, response (Merola et al. 2014).

Outside of emotion reading, there is more direct behavioral evidence for empathy. Dogs are more likely to approach – and show more submissive behaviors when approaching – a crying person compared to someone who is talking or humming, and this effect holds for both familiar and unfamiliar persons (Custance and Mayer 2012). Dogs will even choose to approach and sniff, nuzzle, and lick a crying unfamiliar human instead of approaching their owner. This appears to be empathetic behavior, but the authors suggest it could be due to previous learning histories of being rewarded for approaching crying humans.

Another area of moral motivation that has been studied in canines is fairness. Domestic dogs appear to have a sense of fairness, although not in all situations. Dogs do not actually play fairly; role-switching for some behaviors do not occur during play, such as with mounts, muzzle bites, or muzzle licks, although dogs do take turns with chases and tackles (Bauer and Smuts 2007). However, dogs do have a sense of fair rewards; they display what is termed “inequity aversion” and show negative responses when rewards are distributed unevenly (Range et al. 2009). Dogs are quicker to start refusing commands when they receive no reward to a command that a partner had received a reward for, although they do not pay attention to the size of the reward or amount of work done, as primates do (discussed in Horowitz 2012). In addition, dogs prefer trainers who reward unfairly in their favor, giving more rewards to the subject than the partner, suggesting that dogs are more concerned with getting a reward than with fairness, *per se* (Horowitz 2012). Overall, dogs, and possibly other canines, do show some moral motivations, including some evidence for empathy (or at least emotion recognition) and a limited sense of fairness.

Moral Cognition

Moral behaviors may require several cognitive abilities, including good communication abilities, sensitivity to attentional states of other animals, and even theory of mind. Domestic dogs are excellent at communication with both humans and other dogs. As summarized by Kaminski and Nitzschner (2013), dogs can follow various types of human pointing (e.g., using a hand or looking in the correct direction) to retrieve food that has been hidden (usually in one of two locations, such as under cups or buckets) without evidence of learning during the experiment, suggesting that dogs come into the experiment understanding human pointing gestures. Dogs can follow points regardless of whether the human looks at the dog or the food while pointing, or even if the human walks away from the food location while pointing at it. Some dogs are able to use more subtle communicative gestures from humans to find hidden food, such as head turning, bowing and nodding, and even glancing towards food. They even seem to understand whether the gesture is intentional or not, as they ignore similar pointing gestures (such as looking at a watch to check the time) that are not accompanied by eye contact with the dog. However, they do not “eavesdrop” on informational gestures not directed towards them (i.e., when the human points at a hidden food location while looking at another human), even as puppies. Kaminski and Nitzshner (2013) suggest that dogs interpret these communicative cues as orders or instructions, rather than as informative. Indeed, dogs will even follow human points to search in locations that they already know via previous experience is not the location of the food. However, socialization is important; pet dogs and socialized wolves are better than shelter dogs at following pointing gestures (reviewed in Kaminski and Nitzshner 2013; see also Rooney et al. 2001).

Although dogs may learn to follow human communicative gestures during their lifetimes, even young puppies can follow human points, suggesting a role of domestication in selecting for dogs’ skill in reading human communicative cues. In addition, wolves that are raised by and

intensively socialized to humans can also use human communicative cues to locate hidden food, but they require more socialization and are generally outperformed by dogs when raised and tested under identical conditions. Likewise, domesticated silver foxes outperform non-domesticated silver foxes at following human points. Overall, many canid species can use human communicative cues and both domestication and socialization play a role in the development of these abilities. Along with using gestures to locate food, dogs also recognize specific play signals from humans (see Rooney et al. 2001). Moreover, dogs not only understand human communicative cues, they also communicate back with humans. As summarized by Kaminski and Nitzschner (2013), dogs will use gaze alternation (i.e., looking between humans and a desired, but inaccessible, object such as a toy) and vocalizations to communicate with humans, possibly intentionally. They persist with these behaviors until a desired behavior occurs in the human (such as retrieving the inaccessible toy for the dog). Overall, dogs are good at understanding human communications and communicating back to humans.

Canines also have good communication with other members of their own species. Most canines use body language and facial expressions to communicate emotion (e.g., fear, aggression), social status (e.g., dominance or submission), and motivations (e.g., readiness to attack, bite, flee, or play), with greater degrees and complexities of expressions found in more social species, such as wolves (Fox 1971). Most canine species also use vocal communications to communicate over longer distances, particularly in solitary species but with the exception of the wolf and coyote (Fox 1971). Domestic dogs appear to be sensitive to the attentional states of humans, particularly in understanding where their gaze is directed (see Kaminski and Nitzscher 2013, for review). Dogs are less likely to retrieve a “forbidden” treat when a human is watching them as opposed to the human having their backs turned, doing something distracting, having their eyes closed, or leaving the room. They also obey a “lie down” command faster and for longer when their

owners are facing them, rather than looking away or out of sight. In addition, they preferentially beg for food from humans who are looking at them, rather than humans who are looking away (reviewed in Kaminski and Nitzscher 2013).

Dogs also choose toys that humans are capable of seeing (as opposed to those hidden from a human, but not another dog) when given the command to retrieve a toy, suggesting that they are capable of taking into account a human’s visual perspective when making choices (Call et al. 2009). In a similar test, dogs did not distinguish between two hidden toys when the human had only watched one of the two toys being hidden, suggesting that they did not take the human’s *knowledge* into account (as described by Kaminski and Nitzschner 2013). However, dogs do appear to distinguish between humans who know where food is versus those who are just guessing where food is, even when the only difference between these two humans was where their eyes were pointing during baiting of food containers (Maginnity and Grace 2014). Overall, these results show a strong ability to understand and interpret human visual perspectives and attention, and possibly even their knowledge states. Some researchers interpret these results as showing that dogs have a theory of mind (i.e., that they understand the mental states underlying the behavioral states of attention and gaze). For example, in the forbidden treat paradigms, dogs might understand if a human *sees* you, and thus *knows* you are taking a treat. In the guesser-knower paradigm, dogs might understand that one human (whose eyes were pointed towards the containers during baiting) *knows* where the food is (Maginnity and Grace 2014). In both cases, dogs could be representing human’s knowledge states, rather than just interpreting their body or eye position. However, behavior-reading perspectives, where dogs associate certain behaviors with certain outcomes (like scolding, or being handed a treat) still cannot be fully ruled out (see Roberts and Macpherson 2011). Regardless of whether or not dogs actually have theory of mind, they appear to have sophisticated cognition related to responding to human behaviors.

Moral Systems

Canines do not appear to engage in any moral systems; there are no reports of punishment or reward of certain behaviors within groups of canines.

Conclusion

Canines overall show many behaviors that can be considered moral, such as cooperation and prosociality, as well as reconciliation. Such behaviors in canids may be motivated by empathy and possibly a sense of fairness, and may be controlled with sophisticated cognition related to communication and the attentional states of other animals. However, they do not have any moral systems enforcing such behaviors with reward or punishment, and thus they may not be moral in the sense that the canids themselves have a sense of morality.

Cross-References

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Cardiac Rate

- ▶ Heart Rate

Cardiovascular Collapse

- ▶ Medical Definitions of Death

Cardiovascular Metabolism

- ▶ Physical Health

Career Women

- ▶ Working Women

Caregiver

- ▶ Single-Mother Families

Caregiving

- ▶ Alloparenting
- ▶ Effect on Attachment
- ▶ Significance of Helping

Caregiving Sensitivity

- ▶ Maternal Sensitivity

Carnal Knowledge

- ▶ Penile-Vaginal Sex

Carnivorans

- ▶ Cooperation in Social Carnivores

Carnivore

► Predators

Carnivorous

► Evolutionary Pressure on Meat Eating

Carruthers on Massive Modularity

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Synonyms

[Adaptive specialisations](#); [Domain specificity](#)

Definition

Carruthers defines mental modules more loosely than does Fodor and provides three arguments in defense of the concept of massive modularity of mind.

Introduction

In *The Architecture of the Mind: Massive Modularity and the Flexibility of Thought*, Carruthers (2006) defends the concept of massive modularity of the human mind. He first distinguishes massive modularity (that the brain is composed entirely of modules) from Fodorian modularity (which postulated peripheral modules feeding into a domain-general central processor/s). He then provides a series of three formal arguments for the massive modularity of mind: an argument based on the architecture of complex biological systems; an argument appealing to task specificity, which is supported largely by comparative evidence; and an argument from computational tractability. The current entry summarizes Carruthers' position and notes some key challenges that his arguments have received.

The Nature of Modularity

Carruthers (2006) argues that Fodorian modules (Fodor 1983) are not consistent with a massively modular concept of mind that is "even remotely plausible" (Carruthers 2006, p. 6). Fodorian modules are conceived as domain specific (responding to information of a single class or domain, such as spatial information or visual information), have their own transducers (such as cone and rod cells serving a visual module), and are fast and automatic. Fodor (1983) conceptualized such modules as peripheral to a central processor, which he credited as responsible for reasoned thoughts, ideas, and beliefs (outputs which Fodor's modules could not achieve). Carruthers (2006), on the other hand, argues that a massively modular concept of mind stipulates that the mind is constructed *only* of hierarchically organized modules. As such, modules must be capable of any and all mental processes and outputs, including the most complex and sophisticated thoughts. Carruthers (2005) argues that mental modules are: dissociable (in that they can be changed without affecting the working of other mechanisms); functionally specific (serving a single

function, such as navigation, but using inputs from across Fodorian domains, such as both spatial and visual information); and localized within specific neural structures. In common with Fodor, though, Carruthers also requires a module's internal workings to be inaccessible to other modules, and to be mandatory, in that their processing cannot be voluntarily suppressed. Carruthers rejects Fodor's central claim that modules are encapsulated (i.e., that they cannot draw on information from elsewhere in the mind during the course of processing) in favor of a form of weak encapsulation, in which information from elsewhere in the mind is accessible but cannot be drawn upon all at once.

Wilson (2008) and Cowie (2008) charge that Carruthers' ideas, and in particular that the loss of the strong version of encapsulation, represent a weakened conception of modules. While this may be true, Carruthers (2008) argues that the goal of his book is not to extend the concept of Fodor modules to central processing functions of the mind but rather to identify the conception of modules that can most defensibly be extended to these central functions.

The Argument from Biology

The first of Carruthers' (2006) three arguments for massive modularity is the argument from biology. Quoting foundational work on the evolution of complex biological systems (for example, Simon 1962, see more recently Simon 2003) Carruthers observes that some level of modularity is a requisite for evolution by natural selection to produce incremental improvements in the functioning of a complex system. This is because random mutations must affect a reasonably small, and preferably related, collection of traits, such that when a random mutation produces an improvement to some (dissociable) component of the system (a rare enough event in itself), that improvement is not completely offset by deleterious effects on other components (the more common impact of a random mutation). He argues that the human mind is an evolved,

complex, biological system, and as such must exhibit a level of modularity.

In biological systems, this modularity is inherently hierarchical, with cells organized into tissues, tissues into organs, and organs collectively forming functional systems (such as the digestive system). Carruthers extends this feature to his description of massive modularity as well. Though he concedes that the hierarchy of mental modules could potentially be quite shallow, amounting to no more than a handful of dissociable modules, Carruthers argues that the complexity of the human mind reflects a massive proliferation of function (2005). In combination with Carruthers' assertion that modules map cognitive functions one-to-one, this implies a massively modular mind made up of a "*very great many*" modules (2005, p. 11).

This argument hinges on the proposition that modular systems provide more efficient and rapid solutions to cognitive problems than domain-general systems, which has been challenged by theorists in the past (Fodor 2000). However, Carruthers asserts that a domain-general central processor of the mind would quickly become overwhelmed and that weakly encapsulated, dissociable, and isolated modules are therefore a more efficient way of solving specific, recurring cognitive problems.

The Argument from Task Specificity

Carruthers' (2006) second argument proposes that the specificity of cognitive tasks with which a hypothetical animal must contend (using the azimuth of the sun to determine the time of day compared with the computations associated with dead-reckoning, for example) necessitates the existence of computationally specialized modules within animal minds. Carruthers invokes Gallistel's (2000) arguments to assert that no *general* learning mechanisms likely exist at all within nonhuman animals, with each distinct challenge an animal must solve, and skill it must acquire, supported by a specialized computational process. He refutes Samuels' (1998) proposition of an "informational

modularity.” This is where a nonspecialized central learning mechanism exhibits a proliferation of algorithms in response to different types of information. Carruthers argues that such a mechanism would become irretrievably overwhelmed and is in any case not consistent with the notion of parallel processing that predominates in modern theories of cognitive neuroscience. Although many of the arguments relating to task specificity are centered on comparative examples, they are tied to the human mind by an argument of common descent. It is curious that, unlike massive modularity of the human mind, Carruthers presents massive modularity of the animal mind as sufficiently uncontroversial and self-evident that it counts as *prima facie* evidence for the massive modularity of the human mind. If one accepts that massive modularity of mind, whether in humans or nonhuman animals, is a position that requires independent verification, this argument distills into a case of begging the question.

This argument also makes the assumption that the assumed modularity of animal minds has been maintained in the evolution of human minds (Wilson 2008). Carruthers accepts this point, arguing that since humans retain all of the animal mental capacities with some incremental additions, it may be assumed that these additions are also modular. However, it is possible that, even if the additions to animal minds are modular, a series of such additions could lead to the loss of modularity.

The Argument from Computational Tractability

Carruthers’ third argument is the argument from computational tractability. In this, he argues that cognitive processes are computational (i.e., the mind is the result of the computational properties of the brain). These computational processes must be sufficiently tractable that they are soluble within the human brain within a finite timescale. They must also, therefore, be frugal in the amount of information they utilize and in the complexity of algorithms they

employ. Such tractability, Carruthers argues, is only possible if the computational processes (and, by extension, the mental modules that house them) are at least weakly encapsulated (insulated from other modules), permitting them to draw only upon a predetermined set of relevant information from the rest of the mind. In making this argument, Carruthers acknowledges that the notion of a computational mind is a central premise of his version of massive modularity (and indeed a central premise of much of modern cognitive psychology). While he concedes that this is not an uncontroversial claim, Carruthers argues that computational processes offer the only feasible mode by which mental processes can be realized into physical ones – one of the few allusions he makes to the fact that theories of massive modularity of mind imply a level of mind/brain dualism that is not completely resolved.

Conclusion

In conclusion, then, Carruthers (2006) suggests a definition of modularity that is less tightly defined than that of Fodor (1983) but which allows for the central processes of the mind to be modular in addition to the more peripheral tasks proposed by Fodor (1983). Carruthers offers three arguments in defense of this conception of the mind as massively modular. Critiques of Carruthers’ position comprise claims that Carruthers modules are insufficiently tightly defined to represent a true massive modularity (Wilson 2008) and empirical disputes over the accuracy of the assumptions about animal minds and processing efficiency.

Cross-References

- ▶ [Evidence for Modularity](#)
- ▶ [Evidence of Brain Modularity](#)
- ▶ [Modularity of Mind](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)

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Carving

- [Scarification](#)

Castes

- [Birthrights and Bloodlines](#)

Castigation

- [Cross-Cultural Punishment](#)
- [Evolution of Punishment](#)

Casual Mating

- [Lowering Partner Standards in a Short-Term Mating Context](#)

Casual Sex

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Synonyms

[Booty calls](#); [Friends with benefits](#); [Fuck buddies](#); [Hookups](#); [No strings attached sex](#); [One-night stands](#); [Stranger sex](#); [Uncommitted sexual encounters](#)

Definition and Inclusion

Casual sex and hookups are largely synonymous and involve sexual behaviors that occur outside ongoing committed relationships. These brief uncommitted sexual encounters occur among individuals that are not dating or romantic partners, and they are performed without any expectations of future romantic relationships. The encounter typically occurs only once but may cover a variety of sexual or physical intimate behaviors such as kissing and petting, intimate touching, oral sex, and intercourse. With regard to types of casual sex behaviors, operational definitions are more often inclusive than exclusive (Garcia et al. 2012). Kissing, petting, and intimate touching may all be central elements in casual sex encounters – and may often precede genital manipulation and intercourse – but the only reproductive relevant behavior is vaginal intercourse.

In studying casual sex from an evolutionary psychology perspective, we strongly advise researchers to make a clear distinction between nonreproductive and reproductive sexual behaviors and to specify the casual, brief, and non-committed characteristics of the encounter. To illustrate this, reviews of studies suggest that nearly all casual sex encounters (hookups) involve kissing; nearly six out of ten engage in sexual touching above the waist, half below the waist; and one in three performed or received oral sex or engaged in sexual intercourse (Garcia et al. 2012; Monto and Carey 2014). Women and men report largely equal participation in these behaviors, but men more frequently initiate sexual intercourse than women (Baumeister et al. 2001; Grøntvedt et al. 2015). Whether the sexes differ in their initiative for nonreproductive behaviors is not known.

In this chapter, we do not consider sexual infidelity as a special case of casual sex. Neither do we consider sexual subcultures, open relationships, or same-sex encounters. We define casual sex from an evolutionary psychology perspective as *noncommitted, short-term sexual encounters involving intercourse, and thus the likelihood of becoming pregnant*. We advise alternative and specific approaches to the understanding of brief, noncommitted, nonreproductive sexual behaviors.

Introduction

Casual sex has become more common among young adults during the past two decades, and this trend has been termed “hookup culture” (Monto and Carey 2014). Popular in contemporary Western culture, people are exposed to visual images of sex and erotica, and uncommitted sexual relations are frequently portrayed, suggesting higher acceptance for sex with no strings attached. This stands in stark contrast to pre-World War II Western culture norms of courtship and mating in that was guarded and supervised by parents (Garcia et al. 2012). The 1960s initiated a period of increasing sexual liberation and availability of oral birth control, but the public opinion and

acceptance toward casual sex during the 1960s were clearly more restrictive than today (ibid.).

Apparently, cultural changes as described above may affect peoples’ acceptance of, and involvement in, casual sex. However, evolutionary psychologists have suggested that changes in attitudes toward sex in general and casual sex in particular should be considered in the light of changes in operational sex ratio, OSR (Okami and Shackelford 2001), the *ratio of marriage-aged men to women*. The reason for this is that the availability of mates affects mate preferences and mate choices. In the years following World War II, the OSR fell down to its lowest level with only 75 available men for every 100 women in America in the mid-1960s (Okami and Shackelford 2001, p. 225). With low OSR, female dyadic power waned and female-female competition for mates increased, and women needed to lower their standards for mates, putting less emphasis on status and recourses. During the 1960s, the sexual revolution began in the USA, with increased rates of pre- and extramarital sex and out-of-wedlock cohabitations. It is unlikely that this change in sexual restrictedness would have occurred in a culture with high OSR (abundance of men).

The importance of OSR for sexual restrictedness in a culture is further sustained in cross-national studies. In a 48-nation study, Schmitt (2005b) reported less sexual restrictedness in nations with higher number of marriage-aged women relative to men (low operational sex ratio). This association was strong. Further, Schmitt (2005b) sustained that women’s sexuality appears to be less fixed and more affected by harsh and demanding reproductive environments than men’s sexuality (e.g., prevalence of infant mortality, low birth-weight, teenage pregnancy, and fertility rates). Schmitt (2005b) reported that the level of demanding environment was moderately correlated with national levels of OSR. As environments become less demanding, women, but not men, become more promiscuous. In harsh environments, women move toward monogamy, while men remain relatively promiscuous. However, in each of the 48 nations, men’s sexuality was less restricted

than women's, and even in Norway, one of the most secular and gender-equal nations, men's sexuality is found to be markedly less restricted than women's (Bendixen et al. 2017; Kennair et al. 2016). Finally, there is evidence that regional variations in scarcity of female mates across US states affect the level of sexual restrictedness in men and women as predicted by evolutionary theory (Kandrik et al. 2015).

Sexual Strategies Theory

Buss and Schmitt's Sexual Strategies Theory has contributed both new theoretical and empirical insight into the variations of human sexual behavior. Rather than describing mating as either strictly monogamous or promiscuous, the theory proposes that humans have evolved a complex collection of different mating strategies, both short and long term, which are activated differently depending on context. Humans have throughout their evolutionary history encountered different adaptive problems when engaging in a short-term strategy (e.g., one-night stand or affair outside an ongoing, more stable relationship) versus a long-term strategy (i.e., marriage) (Buss 1998). In addition, women and men have encountered different adaptive problems related to mating. As such, sex differences are expected in human sexuality and mating behavior. Our mate preferences and mating decisions are thus hypothesized to be products of selection pressures during ancestral conditions. The core focus of Sexual Strategies Theory is desire and the interpersonal consequences of desire leading to emphases on conflicts and harmony between the sexes, attraction tactics, and tactics to derogate competitors with regard to sexual relationships (Buss 1998).

A long-term strategy requires an assessment of future reproductive value of potential partners, whereas a short-term strategy requires sexual motivation to engage in sex with various partners and evaluation of immediate sexual accessibility in potential partners. As predicted from Trivers' theory of parental investment, men are expected to assign a larger portion of mating efforts toward short-term mating compared to women. The direct

benefit men can achieve by applying short-term strategies is mating with a greater number of fertile partners which could lead to more offspring. Women's primary benefit of short-term mating is the increased probability of mating with a man with good genes (Gangestad and Thornhill 2008). Given that the number of offspring does not relate to the number of partners as it does for men, indirect genetic benefits are hypothesized to be the ultimate explanation for why women have short-term sexual encounters. Shifts in preferences in short-term mating settings across the menstrual cycle, particularly near ovulation, are interpreted as in favor of such a view.

Predictors of Casual Sex

Sex and Age

Men generally report more sexual desire than women (Baumeister et al. 2001), they desire more sexual variety (Schmitt and 118 Members of the International Sexuality Description Project 2003), and men are more permissive toward casual sex behavior and casual sex attitudes (Schmitt 2005b). These sex differences rank among the strongest for psychological attributes. Men are also found to be far more willing to accept an invitation to having sex with a stranger when given the opportunity (e.g., Clark and Hatfield 1989). Still, women and men report largely similar involvement in casual sex within cultures, albeit the prevalence may differ largely between cultures. (E.g., prevalence rates from studies of sexual regret (Bendixen et al. 2017; Kennair et al. 2016) suggest that two out of three Norwegian male and female students have had casual sex. Comparably, in a US sample of students, 50% of males and 44% of females reported having had casual sex.)

As noted above, men initiate sex more often than women, but there is considerable intra-sexual variation with regard to initiative. The desire component of sociosexuality (SOI) is shown to increase in initiative to sex in both sexes, and men who score high on pleasure motivations for having sex report more initiative taking (Grøntvedt et al. 2015).

Casual sex has become more common in recent decades, particularly among young adults (Monto and Carey 2014), and those who have their first intercourse at a younger age might be more likely to engage in casual sex. Age at first intercourse may again be related to a number of environmental and genetic factors.

Alcohol and Other Substances

While sex in romantic relationships rarely happens after drinking (9%) and especially not heavy drinking (5%), alcohol use is much more typical before casual sex (Walsh et al. 2014). Walsh and colleagues found that 53% of the women in their study drank before casual sex and 38% drank heavily. The same study found that 15% of the women in the study used marijuana in association with a hookup, while only 3% of women used marijuana in association with intercourse in romantic relationships. LaBrie et al. (2014) also found an increased likelihood of hookups due to drinking – approximately 30% of the participants report that they would not have hooked up or gone as far physically if they had not been drinking. Further, self-reported alcohol intoxication symptomatology (e.g., loss of inhibition) but not frequency of alcohol consumption generally is shown to be a strong predictor of hookups involving intercourse in both male and female undergraduate students (Paul et al. 2000). Interestingly, findings from a study involving survey responses as well as experimental outcomes of mating context manipulations and binge drinking among young adults suggest that heavy drinking may function as a short-term mating strategy (Vincke 2017) and that men and women intended to drink more heavily when experimentally primed for short-term relative to long-term mating situations.

Sociosexuality and Other Personality Characteristics

A number of personality characteristics may be related to young adults' participation in casual sexual behavior. Sexually unrestricted individuals (scoring high on the sociosexuality inventory) who are clearly more short-term oriented are more likely to seek out partners for casual sex

due to (1) *prior involvement* in casual sex, (2) condoning attitudes toward casual sex, and (3) increased desires for casual sex (SOI-R; Penke and Asendorpf 2008). Possibly, sociosexuality plays a role in sustained casual sex behavior, as sexually unrestricted students report less regret following casual sex encounters (Kennair et al. 2016).

Further, attachment styles appear to be related to short-term mating and casual sex. In a 56-nation cross-culture study, Schmitt (2005a) found that insecure attachment was associated with short-term mating. Others have found that being adventurous and impulsive predicts more and harm avoidance predicts less frequent hookups with sexual intercourse (Paul et al. 2000).

Self-Esteem

A person's self-esteem has been found to be related to whether one is likely to hook up. One study found that male and female undergraduates with lower self-esteem and/or self-worth hook up more often and do more often have intercourse during hookups (Paul et al. 2000). Another study found that for women in particular, low self-esteem was strongly associated with a greater number of sex partners since puberty and in the past year, as well as for casual sex (Mikach and Bailey 1999). How self-esteem feeds into casual sex behavior and whether it is an outcome, or a predictor, of casual sex are not currently known.

Ovulation and Shifts in Desire and Mate Preferences

Women's preference for short-term mates around the days of ovulation seems to shift in the direction of physically attractive men who appear confrontational, arrogant, and socially respected (Gangestad et al. 2007). The shift in mate preferences across the menstrual cycle seems to be robust and in accordance with the good gene hypothesis, particularly for cues to genetic quality such as body masculinity and behavioral dominance (Gildersleeve et al. 2014). However, it remains to be shown that changes in preferences across the menstrual cycle affect casual sex *frequency* or that these changes correspond with changes in characteristics of the casual sex

partner. Furthermore, for *facial* masculinity, which has also been presented as a cue for good genes, findings are less clear-cut, and some controversy has arisen following recent meta-analyses and reviews. Despite ovulation being concealed, women appear to leak cues that may be picked up by men. One study finds that across the menstrual cycle, female strippers are found to receive more tips around days of ovulation compared to strippers using hormonal contraception (Miller et al. 2007).

Possible Outcomes and Consequences of Casual Sex

The US Centers for Disease Control and Prevention (CDC) lists several physical consequences of risky sexual behavior, including STIs and unwanted pregnancy. It is important to note that casual sex does not need to be risky in itself, as one may have casual sex while using condoms, but frequent casual sex increases risk. CDC in the USA only mentions casual sex among foreign travelers, which seems odd. Further, official statistics addresses unmarried pregnancy, but not casual sex.

Sexually Transmitted Infections (STIs)

Sexual activity is the major risk factor of contracting an STI, due to multiple partners and these partners' likelihood of also having multiple partners. The use of condoms would reduce such risk for penetrative vaginal sex. Still, statistics or studies on the likelihood of contracting an STI particularly related to casual sex behavior are lacking.

Unwanted Pregnancy

The risk of pregnancy is basically determined by ovulation and thus varies greatly across the menstrual cycle. Among women attempting to become pregnant, the likelihood of conception with a single act of unprotected random intercourse is approximately 3%, increases markedly on the days surrounding ovulation, and peaks to nearly 9% on day 13 of the menstrual cycle (Wilcox et al. 2001). The probability of

conception also varies with frequency of intercourse and is particularly high for daily intercourse during the days near the day of ovulation. Although studies of effect of ovulation suggest there is a shift in mate preferences for coupled women at mid-cycle, the authors are not aware of published data suggesting that women actually do have more casual sex around the days of ovulation, nor if there is an increased risk of pregnancy following casual sex.

In summary, there seems to be a need for increased research within the field of physical consequences of casual sex.

With regard to *psychological* outcomes, an obvious aim of casual sex is physical pleasure, although that is probably a little too simplified, as there are many different reasons for sex (Meston and Buss 2007). While a short-term sexual orientation is associated with pleasure reasons, a short-term orientation is also associated with reasons such as experience seeking and mate guarding (Kennair et al. 2015). Therefore, one needs to consider a broad range of outcomes of casual sex. Studies of positive emotional outcomes of casual sex are, however, surprisingly rare. This may be a sign of implicit moralism or sex negativity in the research community and may result in a potentially biased depiction of the effects of casual sex.

Likelihood of Orgasm and Pleasure

Although the sex differences in reported casual sex encounters are small or nonexistent, there are massive sex differences in the likelihood of achieving orgasm when having casual sex (Kennair et al. 2016, 2018). There are also large sex differences in how highly importance of orgasm is rated and how strong physical pleasure one felt during the most recent casual sex encounter (Kennair et al. 2016, 2018). These large sex differences in physical gratification due to casual sex encounters may be relevant when considering the two sexes' motivations for casual sex behavior.

Well-Being

In a paper considering sociosexuality, Vrangalova and Ong (2014) found that

unrestricted participants who had had casual sex reported higher well-being than those who had not. In a later study, Vrangalova found that respondents who indicated low levels of autonomy as a reason for hooking up reported poorer well-being. This is partly contrasted by Townsend and Wasserman (2011) findings, suggesting that even when women deliberately engaged in casual sex, they reported increased worry with increased number of partners – with opposite findings for men. There is reason, from a gene quality perspective on mate preferences and the relevance of such indicators for short-term sex motivation, to expect associations between casual sex and various well-being outcomes (e.g., anxiety, depression, and self-esteem). From a more liberal, sex-positive perspective, one might consider that sexual activity in itself might increase well-being as is often suggested for coupled sex. We found no published evidence of this aspect of casual sex effects.

Negative Postcoital Emotions

Sexual Strategies Theory predicts that there would be sex differences in negative emotions after sex. In a cross-national study, Fernandes et al. (2016) found, in line with earlier research (Campbell 2008), that women had more negative emotions related to the need for bonding, while men had more negative emotions related to avoidance of bonding (compare to ideal relationship outcomes of hookups below).

Regret

Regret is an emotional response to counterfactual cognitive processing. Women and men differ in their regret in relation to casual sexual encounters. A robust finding is that women regret having had casual sex more than men do, while men regret passing up casual sex opportunities more than women do (Bendixen et al. 2017; Galperin et al. 2013; Kennair et al. 2016). Regretting having had casual sex is associated with worry about sexual reputation in women, while unrestricted sociosexuality and greater sexual gratification are associated with lower levels of regret in both sexes (Bendixen et al. 2017; Kennair et al. 2016, 2018). Further,

these studies suggest that taking the initiative to casual sex was associated with lower levels of regret only for women, that feelings of disgust were strongly associated with higher levels of regret, and that religious beliefs were basically unrelated to regret.

Relational Outcomes

There seem to be large sex differences in ideal outcomes of casual sex, dovetailing findings on negative postcoital emotions. Such negative emotions probably arise when one does not achieve desired relational outcome. A recent study by Weitbrecht and Whitton (2017) considered both ideal, expected, and actual relationship outcomes after a hookup. About a third of the men would ideally end up in a romantic relationship, compared to more than 60 percent of women. On the other hand, approximately 38% of men would ideally like to continue sexual relations, compared to 16% of the women. Expectations differed from ideals: women expected to continue having sex more than their ideal indicated; both groups considered the likelihood greater for continuing having sex and lower for a romantic relationship. 22% of men reported actually ending up in a romantic relationship, and 47% continued having sex. For women the actual outcome was 24% in romantic relationships, and 26% continued having sex. The authors also found that approximately 40% of participants, across a 10-week period, achieved the relational outcome they desired from a hookup – including the categories mentioned above and categories “nothing more” and “friendship.”

Sexual Harassment

Findings from several studies of adolescents and emerging adults suggest that frequency of casual sex is positively associated with being sexually harassed (Bendixen and Kennair 2017; Skoog and Özdemir 2016). Casual sex frequency (the behavior component of SOI-R) also predicts sexual harassment of peers, over and above the effect of sociosexual attitudes and desire. The above effects are largely comparable for men and women.

Conclusion

From an evolutionary perspective, casual sex is noncommitted, short-term sexual encounters involving intercourse, and thus the possibility of conception. Sexual Strategies Theory maintains that humans have evolved a complex array of strategies for short-term and long-term mating. However, due to sex differences in parental investment, men are, relative to women, expected to assign more mating efforts to short-term mating. Hence, the sexual psychology of women and men is expected to differ markedly for mating that is emotionally detached and without any commitment such as casual sex. This is especially so, due historically to the risk of pregnancy and cost for women.

As predicted by Sexual Strategies Theory, overall, men have stronger preferences for casual sex, show more positive attitudes toward uncommitted sex, and desire casual sex far more than women. Individual differences in this personality dimension affect both sexes' willingness to have casual sex, as well as how casual sex affects well-being and feelings of regret when having had casual sex. Casual sex is common among young adults and associated with the intake of alcohol. However, casual sex may have some negative outcomes in terms of increased risk of STIs, unwanted pregnancies, or sexual harassment. Following casual sex, women report more negative emotions and regret than men, and women expect romantic outcomes of casual sex more than men.

Cross-References

- Costs of Short-Term Mating for Women
- Friends with Benefits
- Hookup Culture
- Human Copulation
- Intercourse
- Impersonal Sex
- Parental Investment
- Relationship Choices and Sexuality
- Sociosexuality
- Sexual Behavior
- Sexual Strategies Theory

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Casualty

► Victims of Violence

Catastrophe

► Population Bottleneck

Catastrophes

► Climate Fluctuations in the Last 200 Ky

Categorization

► Concept Formation

Categorization by Age

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Synonyms

Age categories; Age categorization; Age groups

Definition

Age categorization is the process of categorizing others or the self as belonging to a particular age group.

Introduction

The process of age categorization serves biological, psychological, and social functions by enabling us to deal with stimuli from the world around us more effectively. For instance, categorizing the self as belonging to a particular age group can inform and provide a meaningful social

identity, which is fundamental to how we define and see ourselves (Harwood et al. 1995; Tajfel and Turner 1979; Tajfel 1981). Perceiving others' age can inform our feelings and behavior toward them, and can underpin judgments about attractiveness, which is associated with reproductive success (Jokela 2009). In this entry, we draw on social psychological, cognitive, and evolutionary theories to provide an overview of categorization by age. After defining age categories or groups and providing examples of the subjective nature of their boundaries, we provide an overview of the cognitive processes underpinning how people perceive others' age, the biological and social cues used to estimate, and categorize others by age. We consider the function of age categorization, both as a way of classifying others to simplify the world around us and classifying ourselves to help define our own identity. We then explore the social psychological and behavioral consequences or risks of age categorization and how it underpins age stereotypes, age prejudice, and aged-based discrimination.

What Are Age Categories or Groups?

Throughout the lifespan, people define themselves and others in relation to the age groups they belong to and those we do not belong to, and people mark transitions between these groups with social occasions, such as birthdays or anniversaries. The practice of remembering and celebrating birthdays ensures that as we get older, the age we have reached becomes part of our identity (Bytheway 2005). However, instead of seeing age on a continuum based on chronological age, we segment the life-course into a series of discrete age categories such as baby, toddler, child, teenager, young adult, middle-aged, older adult, and elderly. These age categories are ascribed both descriptive (e.g., character traits) and prescriptive (e.g., expected behavior) attributes, which stem from a combination of maturation and biological aging processes, social structures that segment by age and age-based stereotypes.

Signs of maturation at younger ages and biological aging are used to determine which age group

people belong to, and are correlated with the attributes people associate with age groups. However, processes of maturation and biological aging are not solely reliant on chronological age; they vary according to many factors, including genetics, gender, poverty, and birth cohort (Arber et al. 2003). In addition, biological differences between age groups are often reinforced or exaggerated by social structures and widely held age stereotypes, which can prescribe different ways of behaving for different age groups. For example, compulsory education in many countries prescribes a period of deferred responsibility and participation in educational programs (Hagestad and Uhlenberg 2005). At the other end of the age spectrum, eligibility for the state pension marks out a time at which people might stop or reduce participation in the labor market. There are also laws that prohibit certain activities for younger age groups, such as restrictions on substance use (e.g., alcohol, cigarettes), employment, and sexual activity.

In addition to social structures, age stereotypes also convey descriptive and prescriptive norms for those within different age groups. *Stereotypes* are the positive and negative characteristics and behaviors believed to be shared by most people from a particular social group (Brown 2010). Age stereotypes can increase perceived differences between age groups, but can also increase the likelihood of actual differences in interests, abilities, and personal characteristics because stereotypes can be self-fulfilling in nature (Levy 2009; Lamont et al. 2015). Age groups, therefore, reflect not only generalized developmental differences between those of different ages, but differences that have been reinforced and exaggerated through social structures and stereotypes.

Variability of Age Categorization

Age categories vary in distribution (age range), size (number of members), and in the degree to which they overlap. Moreover, the use of age group labels is not always consistent and can vary by culture, context, and over time. For instance, extended life expectancy has increased the number of people living to the age of 100, resulting in a new age group, centenarians. In UK, centenarians are the fastest growing age group, with the number of

100-year-olds almost doubling over a 14-year period (ONS 2017). Some categorizations may have multiple labels (e.g., “senior citizen,” “retired,” “pensioner”), while in other contexts, there are more relevant role-related classifications (e.g., parent, child) and in some situations, a simple “younger” verse “older” categorization is sufficient. Finally, age boundaries (the age at which people transition from one age group to another) can vary depending on the individual and the context (Abrams et al. 2011).

Although we have category labels that define age groups, the corresponding ages associated with these labels are quite variable (Bytheway 2005). For instance, research on age categorization has consistently shown that the boundaries that define “old” and “young” are fluid. The 2008/2009 European Social Survey asked respondents from 29 countries in the European region to estimate the age at which people stop being described as “young” and the age at which people start being described as “old.” On average, respondents perceived youth to end at 40 and old age to begin at 62; this may mean that people below 40 and over 62 are more vulnerable to age prejudice and discrimination due to their perceived “young” or “old” age status, respectively. However, the placement of these boundaries varies by survey respondents’ own age, gender, and country, and by their own self-categorization (Abrams et al. 2011; Ayalon et al. 2014; Basleven 2010). Both perceptions of the end of youth and the onset of old age increased with respondents’ age. Women perceived the end of youth and onset of old age to be later than did men. The “end of youth” was viewed to be as early as 34 in Norway, but as late as 52 in Greece. The “start of old age” was viewed to be as late as 65 in Greece, but as early as 55 in Turkey (Abrams et al. 2011). In addition, relative to others of the same chronological age, respondents who categorized themselves as belonging to a younger age group also perceived old age to start later (Basleven 2010). This suggests that as people age, they continually redefine others in relation to their own age group, but also that age categorizations are influenced by social contexts and social constructions of age, which could differ between countries and cultures. However,

despite a high degree of subjectivity and flexibility in the application of age categories, categorization by age and estimating others' age happens ubiquitously.

How Do We Categorize by Age?

When we first encounter others, we automatically categorize them into social groups such as age, gender, or race (Brewer 1988; Brewer et al. 1981). In fact, age is one of the first characteristics we notice about people (Fiske 1998; Kite et al. 1991). Visual perception, biological indications, and social cues all contribute to the psychological processes of age categorization. In addition to categorizing others, we also categorize ourselves by age (Giles and Reid 2005), and this is partly why there is a degree of fluidity in the application of the categories.

Visual Perception and Estimation of Age

Definitions of our own age group and the age groups of others are informed by categorization processes and are cognitively represented as prototypes. Prototypes are meaningful representations of an ingroup member in relation to a given outgroup and are a typical or representative ideal of the category. Research on face perception shows that a prototypical image is held in a physical location in the brain known as the fusiform face area (FFA) of the fusiform gyrus. The FFA recognizes and processes the location of facial features, such as the eyes, nose, and mouth, in relation to one another (Liu et al. 2010). This representation is then passed on to other regions of the brain for interpretation and assessment, such as the occipital face area (OFA) and the ventral anterior temporal lobes (vATLs) (Collins and Olson 2014). Research has shown that people have a distinct eye movement pattern, i.e., they scan faces in a particular way, when they are asked to estimate the age of unfamiliar faces (Kanan et al. 2015), and fMRI scans have shown that the FFA region of the brain is active during this process (Wiese et al. 2012). Prototypes and prototypical images held in the brain are utilized during processes of age categorization.

Although face feature changes are very gradual over time and may not seem that noticeable (to ourselves and others), humans are relatively accurate at estimating the age of others from viewing solely facial information (see Rhodes 2009). Research by Kanan et al. (2015) showed that participants were more accurate at estimating which age group a face belonged to (e.g., child, young adult, adult, and elderly) with an intraclass correlation coefficient (ICC) of 0.85, than they were at reading emotions of faces such as happy (ICC 0.75) or angry (ICC 0.65). Nkenge et al. (2008) showed 173 images of healthy Caucasian women to 48 study participants (20 men, 28 women, aged 22–64 years), who then estimated their age. On average, the participants were able to accurately estimate the age of the women just by viewing their faces, with a correlation coefficient of 0.95. However, women participants were slightly more accurate than men, who tended to perceive female faces as younger than they were. Younger participants (aged 35 and under) were more accurate than older participants (over 50 years), which could be driven by attention to different age cues. For instance, older participants' estimations were driven by lip border definition shape and eye opening size, while younger participants' estimations were driven by dark circles under eyes, smile lines (known as nasolabial folds) and the appearance of brown pigment spots on the skin (Nkenge et al. 2008). In sum, age categorization is influenced by visual processing, which can be studied via complex cognitive methods and varies depending on the age and gender of the perceiver.

Biological and Social Cues to Age

A recent review of the neuroscience of age perception revealed that the most important facial features for judging age are the size of the eyes, which become smaller with age; the size of the lips, which become thinner with age; and the evenness of skin tone, which becomes more uneven, textured, and wrinkled with age (Yarosh 2017). Skin texture and pigmentation and the greying and loss of hair are very visual clues of age, and are ones which people try to conceal and change to appear

younger, and therefore more attractive (Crary 2011). Attractiveness and perceived age are negatively correlated (Matts et al. 2007). People perceive faces with wrinkling around the eyes and mouth and uneven skin tone (e.g., presence of pigment spots) as older and less attractive, while faces of women with more even skin tone are judged to be younger and more attractive, and receive more visual attention from perceivers compared to more elderly faces (Fink et al. 2008). Perceived attractiveness is important because it underpins mate selection. Attractiveness is used to infer health and fitness of potential mates, and signals the ability to donate good genes, successfully reproduce and raise children (Halberstadt 2007; Matts et al. 2007; Perrett 2010).

For both men and women, biological and physiological changes that occur with age are mostly driven by changes in sex hormones which are highest at ages of peak fertility and then decline with age (Ferrini and Barrett-Connor 1998; Thornhill and Gangestad 2008). For instance, testosterone and estrogen build up subcutaneous bone and fat that stretches out, soften, and reduces the appearance wrinkles. Testosterone and estrogen are also responsible for thicker and darker hair for both men and women, respectively (Smith et al. 2006). Therefore, in accordance with evolutionary theory, the facial features people use to assess age are associated with sex hormones, are synonymous with perceived attractiveness, and can be used as a proxy for judging underlying reproductive potential. Indeed, physical attractiveness is significantly associated with reproductive success (Jokela 2009).

Whereas physical age cues are largely recognized consciously, for instance, people are aware of characteristics of age such as pigment spots, wrinkles, and gray hair, people also use more subtle and social cues to discern age (Perrett 2010). Social cues used to estimate age, include choice of clothes and how they fit with popular culture and fashion (Twigg 2013), tone of voice, language, and vocabulary. For example, youth culture is defined by use of certain words, invention of words or slang, and stylistic practices, such as shortening words or phrases, that are unique to teenagers (Bucholtz 2000).

The Functions of Age Categorization

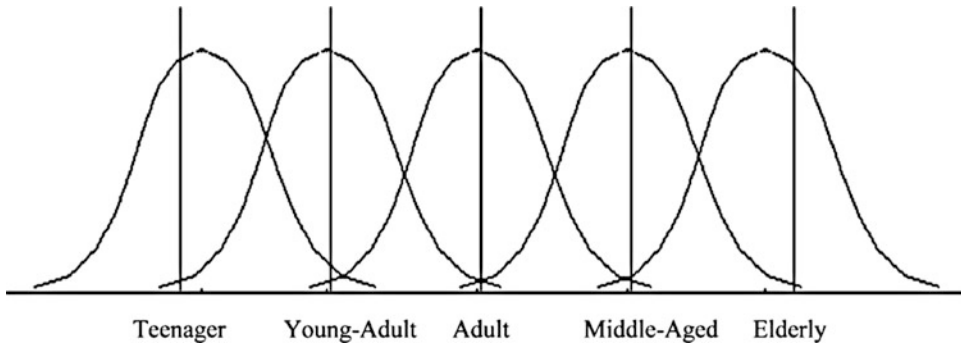
Aside from informing attractiveness and mate selection, two further functions of categorization by age is that it is cognitively efficient to categorize others, but also categorizing the self can help define our social identity.

Cognitive Efficiency: Age Categorization of Others

Categorizing others into groups, including age groups, is more cognitively efficient than evaluating each person individually for two main reasons. First, it is less cognitively demanding to place individuals in a category than to determine their individual identity, especially if that person is not previously known to oneself (Cloutier et al. 2005). Second, group categorization enables us to simplify our interactions with others and infer likely characteristics of that individual based on the strong associations and meaning attached to categories. This again makes person perception more efficient (Allport 1954; Fiske and Taylor 1991; Macrae et al. 1994). For example, in first encounters, automatic age categorization may help to determine the role and relationships between individuals (e.g., mother and son as opposed to husband and wife), or may inform appropriate topics of conversation (e.g., what school they go to as opposed to buying a house). However, automatic categorization also risks oversimplification and generalization, which can lead to ageism (discussed further in the section on the risks of age categorization).

Defining Own Identity: Age Categorization of the Self

When we are old enough to categorize ourselves as belonging to an age group, it can provide meaning through both the descriptive and prescriptive attributes afforded to different age groups. Social identity theory (e.g., Abrams and Hogg 1988; Tajfel and Turner 1979; Tajfel 1981) highlights that our age and the corresponding age group we belong to or feel we belong to can help define who we are and positively distinguish us from others, both reinforcing a positive self-concept. People tend to have a repertoire of social



Categorization by Age, Fig. 1 A self-categorization model of age categorizations. The age continuum is broken up by overlapping age categories here represented

schematically. Vertical lines represent prototypical positions within subcategories

group memberships (e.g., age, gender, nationality, political affiliation, professional group), which vary in their overall importance to the self-concept. Each social identity is represented in the mind alongside attributes that describe and prescribe typical features of the group; thus, salient group memberships can inform what we should think, feel, and how we should behave.

Giles and Reid's (2005) self-categorization model of age proposed that within each age group (from teenager onward), there are prototypical positions, denoting the most typical or prototypical representations of the age group. At the most extreme positions on the age spectrum (e.g., teenager and elderly), the prototypes will be polarized slightly away from the mean, whereas for the middle categories, the prototypes will match the mean (see Fig. 1). Prototypical positions in the group are normative positions and are influential because there is social and perceptual pressure to conform to the norm of one's ingroup (Abrams and Hogg 1990). Transitioning between age groups can elicit uncertainty because one's self-concept is moving further away from one prototypical position, before moving closer to the next. According to Giles et al. (2003), uncertainty is minimized when people adapt and accept the rules and norms of the next category and redefine themselves according to the new social identity.

The extent to which age, and belonging to an age group, forms an important part of our social identity can be captured by measuring age identification, or how much people identify with a

particular age category. Separate pieces of research suggest that both the relationship between a person's chronological age and their age identification, and the relationship between self-categorized age (i.e., the age group people feel they belong to) and age identification are curvilinear. These curvilinear relationships form a "U" shape, which show that younger and older age groups have a stronger identification (belonging) with their respective age groups (Abrams et al. 2011; Fitzgerald et al. 2011; Marques et al. 2014). This suggests either that age identification is more important for younger and older age groups or that age identity is more salient for these age groups, perhaps due to transitional changes occurring around them (e.g., becoming a young adult or moving into retirement). These transitions might be particularly difficult because of the nature of physiological and social changes, which accentuate differences between the prototypical positions in one category compared to the next (teenager – young adult, older adult – elderly). Moreover, the transition into the old-age category can be particularly difficult because the prototypical representation of the group is not particularly positive and may invoke negative stereotypes and representations of old age (Garstka et al. 2004; Kite et al. 2005).

Aside from defining the self-concept, social identities are also evaluative and allow us to positively distinguish ourselves from others. Categorization of the self, and others, is the social cognitive process through which people are

assigned to social categories, making the distinction between ingroups (groups we belong to) and outgroups (groups we do not belong to; Turner 1982; Oakes et al. 1994). Therefore, a positive self-concept is maintained when belonging to a given ingroup provides a positive evaluation of oneself in relation to the outgroup or outgroups.

The Risks of Age Categorization

Despite the cognitive and social utility of being able to perceive, understand, and categorize by age, there are also negative consequences of age categorization. Early psychological research established that once categorization has occurred (whether it relates to physical objects, people, or events), two things happen; the differences between categories are enhanced, while the differences within the categories are reduced (Tajfel 1959; Tajfel and Wilkes 1963). In other words, members of different age groups will be seen as more different, while members of the same age group will be seen as more similar than they really are. This within-category assimilation or homogenization underpins stereotypes. Self-categorization theory (Turner et al. 1987) holds that our categorization systems underpin stereotyping, prejudice, and discrimination. Therefore, a consequence of age categorization is that it might lead to and perpetuate ageism; the stereotyping of and discrimination against individuals or groups on the basis of their age (Butler 1969; Abrams 2010). Research exploring the nature of age stereotypes has largely focused on those associated with older people and how they compare with stereotypes of the young (Kite et al. 2005).

The Stereotype Content Model (SCM; Fiske et al. 2002) provides a framework for exploring old-young age stereotypes, whereby older people are stereotyped as being friendlier but less competent than younger people (e.g., Abrams et al. 2009; Cuddy et al. 2005; Fiske et al. 2002). Research shows that they are also viewed as: lacking creativity, unable to learn new skills, bad drivers (Joanisse et al. 2012; Swift et al. 2013), impaired, despondent, recluse, and vulnerable

(Hummert et al. 1994), lacking adaptability, slow, less technologically savvy (Chiu et al. 2001; Magd 2003), and also grumpy and intolerant (Hummert et al. 1994; Swift et al. 2013). Alongside these negative overarching stereotypes, evidence shows that there are also positive stereotypes in which older people are viewed as polite, able to understand others' perspectives, self-motivated, productive, reliable, and dependable (Magd 2003; Swift et al. 2013; Taylor and Walker 2003).

As well as showing domain-specificity, some of this incongruence in stereotyping arises from subtyping within age groups when combined with other characteristics such as health, socioeconomic status, or social role (Brewer et al. 1981; Hummert 1990; Schmidt and Boland 1986). For example, two contrasting subgroupings of older people have been previously labeled as "golden agers" (capable, well-informed, and independent) and the "severely impaired" (incompetent, senile, and incoherent; Hummert et al. 1994). Individuals will further vary in their use of broader and more specific stereotypes depending on their own characteristics. For example, more complex representations (shown though more specific subtypes) of the older age group have been found among those closer to that age group in age (Hummert et al. 1994).

Stereotypes of both young and old contain positive and negative content, but either valence can be problematic when erroneously applied to an individual, which can result in discrimination. Age categorization may cause people to restrict what is deemed acceptable for particular age groups based on their own or others' ageist assumptions. For example, people may be judged or they may see themselves as "too young" or "too old" to pursue particular activities or roles (North and Fiske 2013). For this reason, the very act of categorizing others into different age groups and the way people define those groups has significant implications for people's choices and actions (Swift et al. 2017).

The Risks of Ageism Model (RAM; Swift et al. 2017) summarizes three pathways that ageism can negatively impact on individuals through processes of categorizing the self and others by age.

First, via stereotype embodiment, the process through which stereotypes are internalized and become self-relevant; second, via age-based stereotype threat, the perceived risk of confirming a negative age stereotype; and lastly, via age discrimination.

According to stereotype embodiment theory (Levy 2009), age stereotypes regarding the competence, health, and capacities of older people are learnt through socialization processes and then internalized during childhood and adulthood. When people get older, these stereotypes become self-relevant. They are applied to the self through the process of self-categorization, and can become self-fulfilling, resulting in negative outcomes influencing memory, cardiovascular reactivity, and longevity (Levy 2009; O'Brien and Hummert 2006).

Stereotype threat theory (Steele 2010; Steele and Aronson 1995) posits that certain situations can put older adults at risk of confirming negative age stereotypes, potentially leading to their perpetuation. A review and meta-analysis of 22 published and 10 unpublished studies (including 82 effect sizes) revealed that older adults who were placed in a situation where they faced the threat of being “judged” negatively in terms of their age subsequently underperformed on cognitive and physical tasks (Lamont et al. 2015).

Aside from the risks of self-categorization, we may also disadvantage others by categorizing them into a given age group. Research has focused on the problem of age discrimination in health and social care (Swift et al. 2016), the workplace (Walker 1993; Abrams et al. 2016), and in the media (Martin et al. 2009; White et al. 2012) in particular. The RAM highlights the unique nature of ageism and categorization by age by outlining how we are all vulnerable to negative stereotypes and representations of age. Unlike other common forms of prejudice and discrimination (e.g., sexism, racism), ageism is not based on predominantly closed and fixed social categories, instead we move through different age groups across the lifespan. The inevitability of aging means that for most people, negative age stereotypes will eventually become self-relevant.

Conclusion

In summary, the process of categorization, or classifying people, objects, or any stimuli from the world around us into groups, is a fundamental process studied by psychologists. It underpins perception, cognition, and social interaction (Tajfel and Turner 1979). While age boundaries can be fluid, prototypical representations or images we hold in our mind about members of age groups tend to impose distinctions that we use consistently for estimating others' age (Rhodes 2009; Nkenge et al. 2008). Accurate age perception provides a selective advantage for identifying potential mates. We estimate age using visual cues such as hair color, skin texture and tone, size of the eyes, lips, and appearance of wrinkles or lines. Some of these features we try to amend to deceive others of our age. Although basic cognitive processes of perceiving and estimating others' age is relatively well understood, the subjective boundaries that define age groups are less well researched. Age group boundaries seem to vary according to setting, culture, and characteristics of the person categorizing which may vary, adding levels of complexity. Categorization by age serves a social function helping to define the self, and others in relation to the self. It can help to define the self by providing a more meaningful social identity, and help to smooth social interactions with others. However, both these functions come with risks. In accordance with the RAM, self-categorization and age discrimination from others can be particularly problematic for older adults because of negative age stereotypes associated with aging and older people. Negative age stereotypes can restrict our own decisions and behaviors to those deemed “age appropriate”. Older adults can feel under threat if they are perceived or judged negatively in relation to their age, which can impair performance. Negative age stereotypes can also be used to justify unfair or discriminatory treatment.

Cross-References

- [Salience of Category](#)
- [Social Categorization by Age of Faces](#)

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Categorization by Sex

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Synonyms

[Gender categorization](#); [Sex categorization](#)

Definition

Categorization by sex refers to the cognitive and socially informed decision processes by which observers judge whether an individual is male or female.

Introduction

Sex categorization is the act by which observers sort others into one of the most predominately used social categories. From an evolutionary perspective, the capacity to determine whether someone is a male or female underlies critical socio-evaluative and behavioral decisions including reproduction (i.e., mate selection) and survival (i.e., threat detection). This entry provides a broad

overview of the theoretical models that account for sex categorization and the sensory cues that inform our sex categorization judgments. Additionally, it describes the cognitive and evolutionarily based factors that modulate and bias sex categorization decisions, and concludes with a discussion of the broad downstream implications.

Theories of Social Categorization

Based on merely a glimpse of a person, observers rapidly and with little conscious attention make inferences about whether that person is male or female (although these two categories are not exhaustive, Westbrook and Saperstein 2015). Early theoretical models reasoned that sex categorization, and social categorization more generally, equipped observers with a beneficial cognitive shortcut that reduced the inherent complexities of the social world (Allport 1954). By judging someone as male or female, observers could rely on associated knowledge structures to make inferences about that person's potential traits and behaviors (Macrae and Bodenhausen 2000). In this way, social categorization has been argued to provide an efficient, adaptable, and highly generalizable means by which observers perceive others in terms of their potential social affordances (i.e., the functional capabilities offered to the perceiver; McArthur and Baron 1983). At the same time, these generalizations based on sex category membership also have the potential to engender more nefarious outcomes such as stereotyping, prejudice, and discrimination (Macrae and Bodenhausen 2000).

Early evidence from social psychological research largely supported the claim that social categorization by sex is ubiquitous and that it occurs relatively automatically. For instance, by studying memory, researchers showed evidence that observers spontaneously extracted and used sex categories when recalling information about speakers who were engaged in a conversation. Deemed the *Who-Said-What Paradigm*, research results consistently showed that participants made more within-category errors (e.g., misattributing a comment to someone belonging to the same social

category as the original speaker) than between-category errors (e.g., misattributing a comment to someone belonging to a different social category as the original speaker). Thus, utterances of a female speaker would be misattributed to a different woman; utterances of a male speaker would be misattributed to a different man. These consistent patterns were considered to provide strong evidence that even without the use of the social category labels (here, female/male labels), participants organized their memory in terms of sex categories (Taylor et al. 1978). Neuroscience studies further bolstered claims about the primacy of sex categorization. Specifically, in as little as 200 ms after viewing a face, electroencephalogram (EEG) signals differed for male and female faces (Ito and Urland 2003). Furthermore, developmental research suggests that sex categorization emerges early in life. Infants differentiate by sex categories and show an overall preference for female faces (Ramsey et al. 2005). In general, these studies suggest that sex categorization is a ubiquitous process operating early in our development and occurring relatively automatically.

While these examinations of person perception revealed the relative ease and pervasiveness of thinking about others in categorical terms, they also conceived of social categorization as a discreet and self-evident judgment. Based on the early visual perception of another person, the individual is categorized discretely as either male or female. This relative indifference to what compels social categorization judgments aligned with some early models of person perception, which focused specifically the consequences of social categorization such as stereotyping and person-trait inference (Brewer 1988; Fiske and Neuberg 1990). Such models were mute with respect to the process by which categorizations unfold in the first place. In the early 2000s, this particular question inspired a number of social psychologists to seek a more comprehensive understanding of how sensory information compels sex categorization judgments. Exploiting paradigms that were more common in the vision and perception sciences, these researchers isolated the specific facial and body features that inform accurate sex categorization judgments (Brown

and Perrett 1993; Cutting 1978; O'Toole et al. 1998), and these insights became integrated within the more social cognitive literature. For example, Macrae and Martin (2007) found that visual features alone can facilitate social category activation (e.g., viewing only hairstyles activated sex categories) and that under restricted viewing time (25 ms), hairstyle cues could even override the importance of actual sex category in social judgments (e.g., long haired men and short haired women activated female and male sex categories, respectively).

By taking a more integrated approach, social psychologists began unpacking the decision processes that underlie sex categorization. Specifically, by identifying both the visual cues in the target of perception that compel sex categorizations, and the cognitive and motivational factors that reside within a perceiver (e.g., stereotypes), a new field called Social Vision began to take shape (Adams Jr. et al. 2011; Balci et al. 2010; Johnson and Adams 2013). Social Vision research sought to integrate perceptual and social psychological processes to reveal not just the downstream consequences of social categorization but also the earliest determinants by which social categorization occurs.

One key insight afforded by this novel perspective was that social categorization judgments are dynamic, rather than discrete as previously thought. That is, sex categorizations arise via a dynamic process that unfolds across a brief temporal time period (Freeman and Ambady 2011; Freeman et al. 2008). This process was documented using cutting-edge methodological tools such as mouse-tracking. Participants used a computer mouse to select the appropriate category label (i.e., male/female) for a set of faces, presented individually. By tracing the trajectory of each sex category judgment, researchers discovered that not all sex categorizations were equally efficient. Categorizations of more prototypical male faces (e.g., faces morphed to be 100% male), occurred in a highly efficient and direct manner compared to categorizations of less prototypical male faces (e.g., faces morphed to be 75% male and 25% female), and a similar pattern emerged for categorizations of female

faces. These results showed that social category decisions exploit visual features and reflect their variability (often referred to as bottom-up factors that originate in the target of perception). Thus, even when the ultimate category judgments yielded the same outcome, the efficiency of the decisions, as measured by mouse trajectories, was prone to vary as a function of the visible cues in the face (Freeman et al. 2008).

In addition to the impacts of variability in the target of perception, observers themselves approach social categorization tasks with their own motivations (often referred to as top-down factors that originate within the perceiver) that can impact sex categorization judgments. For example, knowledge that men are stereotypically, and in some cases demonstrably, more violent and aggressive than women (Archer 2004) might influence social categorizations. Under conditions of uncertainty, observers might be prone to make more male categorizations, thereby adopting a “better safe than sorry” heuristic (see ► “Error Management Theory”; Haselton and Buss 2000). Indeed, sex categorization of full body images that varied in waist-to-hip ratio, showed a substantial male categorization bias – the perceived boundary between male and female was significantly skewed which led observers to categorize more body shapes as males, compared to what would be expected based on population-level distributions. Furthermore, participants, who were primed to be fearful prior to providing sex categorizations, made more male categorization judgments compared to participants who were primed with more non-threat relevant emotions such as happy or sad (Johnson et al. 2012b).

Similar top-down impacts have been documented in other contexts, as well. Results from neuroscience studies revealed that participants' sex categorizations of targets who displayed cues of gender atypical job occupations (e.g., a man as a florist or a woman as a judge) corresponded to greater activation in brain areas associated with person processing (e.g., the fusiform face area, fusiform body area, and extrastriate body area) and conceptual conflict resolution (e.g., the dorsolateral prefrontal cortex; Quadflieg et al. 2011). Together, these findings

provide evidence that top-down factors that originate in the perceiver, such as motivational concerns to safety and stereotype knowledge, can affect sex categorization judgments.

Finally, the relatively newer models of person perception provided insights about how social categorization might unfold for multiple orthogonal category dimensions simultaneously (e.g., age, sex, race/ethnicity). This research has found that the coincident perception of categories such as sex and race/ethnicity renders them interdependent. For example, the race/ethnicity categories Black and Asian often are tethered to the sex categories male and female, respectively. Thus, Black individuals are more likely to be and are more easily categorized as male; Asian individuals are more likely to be and are more easily categorized as female (Johnson et al. 2012a). The reverse is also true: cues to sex category facilitate congruent race categorizations (Carpinella et al. 2015). These findings further illuminate the way bottom-up (e.g., shared facial overlap) and top-down (e.g., shared gendered stereotypes) factors influence sex categorizations, even across different social categories.

In summary, sex categorization results from the rapid integration of bottom-up perceptual processes (e.g., features and gender typicality of faces and bodies) and top-down motivational and social cognitive processes (e.g., emotions and stereotypes) that collaborate to yield a judgment. Current models characterize these judgments as a product of a probabilistic and integrative process that occurs rapidly and readily (Freeman and Ambady 2011). Next, we specify the bottom-up cues that compel sex categorization, describe how categorizations are biased by top-down influences, and discuss the impact of sex categorization for evolutionary informed processes.

Cues to Sex Categorization

Visual Cues

While multiple sensory cues inform sex categorization judgments, a vast majority of research has focused on visual cues. These cues range from

specific features such as hairstyle to full body cues such as walk motion and the body's morphology.

Face

Early work in understanding sex categorization focused on the perception of faces, and it identified the numerous features that can reliably convey sex category information. By limiting the cues that were available to observers across a series of trials, researchers could determine the relative importance of various regions of the face for making sex categorizations. Remarkably, sex categorization accuracy was highest, and was significantly above chance, when observers viewed only the eyebrows and eyes, followed closely by the jaw, chin, and mouth. The only region that led to inaccurate categorization was the nose (Brown and Perrett 1993). This sex categorization acuity grows stronger when observers view whole faces, with sex categorization accuracy nearing 100% and taking approximately 1 s of unconstrained viewing time (O'Toole et al. 1998). Other features such as skin tone can also convey sex categories reliably, with males typically having darker and rougher skin than females (Bruce et al. 1993). Additionally, the spatial distance between specific facial features differs between men and women, including the distance between the upper eyelid and brows, thus compelling accurate sex categorizations (Campbell et al. 1999). Further still, although relatively immutable, many visual cues can be intentionally accentuated or minimized in accordance with socially constructed norms. Consequently, factors such as hairstyle (Goshen-Gottstein and Ganel 2000), facial adornments (e.g., earrings), and cosmetic use (Russell 2009) can each cue and modulate sex category judgments.

Of course, in addition to specific facial features, holistic impressions of the face also influence sex categorization. The facial-width-to-height ratio (FWHR), calculated by dividing a face's width (e.g., the distance from ear to ear) by its height (e.g., the distance from the upper lip to the upper eyelid), largely differs in men and women. A meta-analysis of 32 studies found that on average, males have higher FWHRs than females, and that greater FWHR is associated

with more masculine facial ratings (Geniole et al. 2015). Importantly, evidence suggests that high FWHRs convey threat and dominance, and that there is a small positive correlation between FWHR and male's aggressive behaviors (Haselhuhn et al. 2015). However, this work is necessarily associative, thus it is not clear whether individuals with higher FWHRs *are* more aggressive and dominant or are simply viewed and treated as such. While some researchers have advanced the hypothesis that for males, greater exposure to testosterone is associated with higher FWHRs, this remains an uncertain proposition (Bird et al. 2016; Welker et al. 2016).

Bodies

Sexual dimorphism is also observed in body cues, which in turn serve as visual cues for sex categorization. While specific visual cues from the body can lead to accurate sex categorization, such as images of hands (Gaetano et al. 2014), much work has investigated the whole body in terms of its morphology, shape, and motion. Indeed, since faces require relatively close distances to be clearly seen, being able to tell sex from further away, via body cues, likely would be evolutionarily advantageous (de Gelder 2006).

In terms of body morphology and shape, visually obvious population-level differences such as height and weight (e.g., males, on average, are taller and heavier than females) cue accurate sex categorization (Gray and Wolfe 2005). Additionally, waist size and the waist-to-hip ratio (WHR) can also reliably inform sex categorizations (Lippa 2006), with males generally having higher WHRs.

The body however is not a static figure, and a body's movement can also inform sex categorization. Using point-light displays – in which video clips of white dots, placed on the body's major joints, move through space – researchers found that observers can accurately categorize sex from a variety of movement cues such as walking, throwing, and hand waving (Barclay et al. 1978; Cutting 1978; Johnson et al. 2011; Kozlowski and Cutting 1977). When judging the sex of walk motions, shoulder movements in the frontal plane (i.e., front to back shoulder rotation;

“shoulder swagger”) and hip movements within the sagittal plane (i.e., side to side hip translation; “hip sway”) compelled male and female judgments, respectively (Johnson and Tassinari 2005). Moreover, while body shape and motion have often been investigated as orthogonal cues, research that integrated both morphology and movement cues revealed that body shape takes precedence over movement for sex categorizations. While movement did cue sex, eye-tracking data revealed that visual attention was focused more on the waist (yet only when sex was unknown), as opposed to other areas of the body, suggesting the primacy of body shape for making sex categorizations (Johnson and Tassinari 2005).

Other Sensory Cues

Accurate sex categorizations can also be informed by a variety of other sensory cues. One potent auditory cue is the voice. Based on studies identifying sex differences in vocal qualities such as fundamental frequency (perceived pitch), timbre, and formant frequency, researchers exposed listeners to vocal clips of vowel segments and found high accuracy for sex category judgments (Lass et al. 1976). Interestingly, sex categorizations based on auditory perception show similar overlaps with other observations. For example, the visible differences in the walk motions of men and women also carry a reliable acoustical signature. Merely hearing footfalls provides a sufficient amount of information for listeners to make accurate sex category judgments (Li et al. 1991).

Other sensory cues have received less empirical attention but tend to show a robust pattern implying that sex categorizations might rely on other sensory modalities, as well. For instance, male and female scents provided to observers while they made sex categorizations of point-light walker displays reliably altered their perception. Heterosexual men who smelled female pheromones judged point-light walkers as more feminine; heterosexual women who smelled male pheromones judged point-light walkers as more masculine (Zhou et al. 2014). Additionally, the emotion being conveyed in a touch depends on the dyad's sex composition (Hertenstein and Keltner 2011).

Overall, multiple perceptual cues, ranging from faces to bodies, and cutting across a range of sensory modalities, provide reliable information from which observers accurately and efficiently judge sex. These cues form the evidentiary base for our sex categorizations; however, how we interpret and evaluate these cues also influences our ultimate judgments. We now consider how sex categorization judgments might be more broadly influenced.

Modulations to Sex Categorization Processes

Observers are not merely passive recipients of bottom-up sensory inputs, but rather are active participants in the social perceptual process. Thus, in addition to the sensory information available to them, observers also harness preexisting knowledge structures and personal motivations when they render a sex category judgment. These “top-down” factors that originate in the perceiver can thus modulate our responses in ways informed by evolutionary psychology. Next, we review these processes, which span a range of social cognitive and motivational phenomenon.

Social Cognitive

One consequence of social categorization is the activation of stereotypes. While early research documented the extent of stereotype activation following exposure to images from a specific social category (Macrae and Bodenhausen 2000), recent work suggests this process is bidirectional. Knowledge of stereotypes can also influence sex categorizations. For instance, stereotypes exist regarding the expression of different emotions, with men associated more with anger and women associated more with happiness (Plant et al. 2000). Because of this, the incidental perception of emotion can bias sex categorizations. When viewing ambiguous point-light-displays of body motions, observers were more likely to judge motion displays that displayed anger (i.e., a point-light hand throwing a ball in an angry manner) as men, but body motions that

displayed sadness as women (Johnson et al. 2011). Interestingly, phenotypic characteristics of the face also overlap with these sex-based emotion stereotypes, and they influence judgments. In one study, masculinizing faces lead them to be viewed as angrier, but feminizing faces lead them to be viewed as happier (Becker et al. 2007). Similarly, facial displays of emotion also impact sex categorizations (Hess et al. 2004).

Evidence also suggests that seemingly orthogonal social categories can influence judgments about one another, such as race/ethnicity impacting sex categorizations (Stroessner 1996). Because stereotypes associated with the categories Black and Asian overlap with the categories male and female, respectively, sex categorizations differ as a function of race/ethnicity. Black faces are more efficiently categorized as men, and Asian faces are more efficiently categorized as women (Johnson et al. 2012a). The reverse is also true (Carpinella et al. 2015). Thus, as perceivers, the stereotypic knowledge we bring to the categorization process can affect sex categorization.

Additionally, some judgments show systematic biases, such as what could be regarded as a persistent male categorization bias. Across a variety of stimuli, visually sex-ambiguous features such as hands, babies faces, and body shapes (e.g., bodies that occupy the mid-point between a male and female distribution) are more frequently categorized as male than female (Gaetano et al. 2014; Johnson et al. 2012b; Nagy et al. 2000). Recently evidence from our lab suggests that this male categorization bias occurs for judgments of faces, even though they tend to be less ambiguous than other classes of stimuli. One source for this influence could stem from broader associations between a “person” or “people” and males, as we often conjure images of a man when asked to simply think of a person (Silveira 1980). In these cases, devoid of any sex-based cues, male maybe the default sex category.

Motivational and Evolutionarily Informed Influences

Beyond the effects of associative knowledge, motivational concerns also impact sex categorization. For instance, to better understand potential

mechanisms underlying the male categorization bias, researchers probed how an observer's emotion state might exacerbate/attenuate biases in judgment. They found that the tendency to categorize sex-ambiguous bodies as male was more pronounced when observers were induced to feel fearful, relative to happy or sad (Johnson et al. 2012). Why might this be the case? On average, men are more physically formidable than women, and they are stereotyped as being prone to violence (Archer 2004). Particularly under conditions of uncertainty or when experiencing threat, observers appear prone to err on the side of caution, in this case rendering more male categorizations. Importantly, this pattern is consistent with biases that have been observed in other domains of judgment (Haselton and Buss 2000). These findings highlight an important role for motivational concerns in shaping sex categorization decisions.

Although more limited in scope, some evidence indicates that individual differences in perceivers can influence sex categorization judgments through adaptive person construal mechanisms. Specifically, women who are at peak conception risk (i.e., ovulation) are faster to categorize male faces and show greater facilitation for male stereotypes than women who are at low conception risk (Macrae et al. 2002). Furthermore, among men, higher relative testosterone levels were associated with slower categorization of female faces, but no difference in the categorization of male faces. While this pattern of results was unexpected given the observations for hormonal fluctuations in women's judgments, the authors argued that perhaps men paid more attention (and had longer view times) for sexually relevant faces (Johnston et al. 2011). Overall, this work suggests that sex categorization is modulated both by the sexual relevance of the target, the sex of the perceiver, and fertility.

Evaluative and Broader Implications

From an evolutionary psychology perspective, sex categorization underlies a number of domains

including mate selection and threat evaluations. We review each of these in the final section of this entry.

Mate Selection

Attraction and mate selection often go hand-in-hand, with mate selection focused on gaining the best opportunity for healthy reproduction, and attraction serving as its primary mechanism (Little et al. 2011). One cue critical to sex categorization and attraction is masculinity and femininity. As a general pattern, feminine women are deemed more attractive than masculine women (Perrett et al. 1998). Yet, this pattern is less consistent for judgments of men, with the literature providing mixed evidence about whether masculinity enhances the attractiveness of men. Studies using a variety of methods including real and morphed faces have indicated that masculine features are judged attractive (DeBruine et al. 2006; Johnston et al. 2001), while others find that more feminine features (and less dominant ones) are judged more attractive (Little et al. 2001; Perrett et al. 1998).

One possible resolution to these discrepant findings involves the trade-offs hypothesis (Gangestad and Scheyd 2005). This hypothesis is predicated on the fact that asymmetric costs to mating shift women's preferences for masculine and feminine characteristics. For instance, since facial masculinity is associated with both positive characteristics (e.g., better health outcomes) and negative characteristics, (e.g., lower perceived warmth and greater perceived dominance; Keating 1985), women are likely to differ in the weight attributed to each consideration. Indeed, several systematic shifts in preference have been documented. For instance, women prefer more masculine faces at times when they are fertile (Johnston et al. 2001; Penton-Voak and Perrett 2000) and when making judgments about a short-term mate, rather than a long-term mate (Johnston et al. 2001; Penton-Voak and Perrett 2000).

More broadly, the compatibility between a target's perceived sex (male and female) and its gender typicality (masculine and feminine) also drives attractiveness. Specifically, once the sex of

a target is determined, the degree to which the target exhibits gender-typical versus gender-atypical actions influences judgments of attractiveness. For instance, Johnson and Tassinary (2007) found that body shape provides a potent cue to sex categorization (e.g., male or female), and body motion provides a cue to gender-typicality. To the degree that these two cues aligned, that is, a body evokes a male judgment and body motion evokes a masculine judgment (or visa versa for female body morphology and feminine gait), then targets were rated as more attractive. This finding places sex categorization as a cornerstone of attractiveness, as a target's sex provides the lens from which gender typicality and attractiveness are judged.

Threat and Trait Evaluations

As described above, men and women differ on a variety of perceived traits. One well-established pattern involves sex differences in threat and hostility. Compared to women, men are rated as, stereotyped to be, and inclined to behave in more threatening and hostile manners (Archer 2004; Keating 1985). Population-level data concurs. In fact, men comprise the bulk of homicide victims, and archeological evidence finds that mass graves from Medieval time (AD 1300–1350) include more men with injuries indicative of violence and war (Boucherie et al. 2017; Kellermann and Mercy 1992). It is perhaps unsurprising, therefore, that these actuarial accounts of sex differences are mirrored in studies that probe stereotyping: men are consistently and strongly stereotyped to be more aggressive and hostile than women (Prentice and Carranza 2002). As mentioned above, these associations between men and hostility account, in part, for a range of findings described in earlier portions of this entry. These associations also have broader implications for categorizations that occur not only for faces presented in isolation but also for groups of faces or ensembles. Indeed, observers are highly sensitive to the relative ratio of men to women in multi-person arrays, and the perceived threat posed by a group increases concomitantly as the number of men increases. Put simply, male dominated groups appear to be threatening (Alt et al. 2017).

Conclusion

Here we have characterized sex categorization as a fundamental aspect of social perception. Upon merely a glimpse, observers readily and reliably exploit cues in the face and body to categorize others as either male or female. Although largely accurate, sex categorizations are prone to external influence, as well. At times, cues within the target of perception shift categorizations to favor either a male judgment (e.g., when the target is angry or Black) or female judgment (e.g., when the target is sad or Asian). At other times, observers' own feelings and motivations steer the judgment process to favor a male categorization. As such, sex categorization appears to serve pervasive and persistent evolutionary and social needs among perceivers.

Cross-References

► [Error Management Theory](#)

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Category Salience

► Salience of Category

Cathedral Acoustics

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Synonyms

Architectural acoustics; Auditory properties of rooms; Religious building design

Definition

The designed aural qualities of large religious spaces.

Introduction

Architectural acoustic design, at its core, utilizes two fundamental properties of sound waves: reflection and absorption. The characteristics of a room that determine how sound waves are reflected and absorbed include both the materials used in construction as well as the size and shape of the room. Reverberation time is the unit of measure that identifies how sound waves respond inside a particular room. A space built with flat dense materials will generally have a long reverb time while one with rough soft materials will have a short reverb time.

Earliest Acoustic Amplifiers

There are examples of man-made structures demonstrating acoustic principles in construction of spaces used for religious services by the Mayan civilization from approximately 600 C.E. In central Mexico, there are indications that the Temples at the city of Palenque utilized different construction techniques for rooms that have different purposes. Symbols in these rooms identify different types of sound, including animal and nature sounds, the human voice, and musical instruments. One theory is that each room has been designed to amplify the type of sound the symbol identifies by utilizing different reverberation times. A modern study of these rooms shows that the voice rooms have a short reverb time that will amplify the spoken word but retain clarity, while a room with a bird symbol will have a longer reverberation time that can be used to allow a human to mimic this animal. This appears to indicate that the builders of these Temples had a basic understanding of their construction techniques' acoustical properties (Garza et al. 2008).

Renaissance Acoustics and Religious Music

Cathedrals and churches of the Renaissance period are typically large square rooms, often domed, built of marble, stone, and plaster. Vast spaces and dense materials give these rooms quite

a long reverberation time, often exceeding 10 s when the room is empty. This seems counterintuitive, though, given that the advances in musical composition of the Renaissance period were polyphonic composition (the use of multiple simultaneous melodies) and polychoral performance (the use of multiple spatially separated choirs) and that these are both impaired by long reverberation times. Advances in modern computer-assisted acoustical modeling have answered this question.

A recent survey of the Non Basilica del Santissimo Redentore in Venice, Italy identified two primary acoustical properties that worked together to reduce reverb time and improve aural clarity during musical performances. When the Redentore Basilica is empty, the room has a reverb time of approximately 7.5 s. The effect of this is that most music or spoken word in this space becomes muddy and unintelligible. However, this recent modeling of the space reproduced the Basilica as it would have appeared during the Festival of Redentore. On these festival days, the walls of the Basilica would have been covered with ornate tapestries and full of congregants, which would greatly increase the amount of sonic absorption in this space and reduced the reverberation time to 3 s. This improved the clarity of the room and would allow for a great appreciation of the ornate Renaissance musical composition.

The second acoustic property of the Basilica is that the dome of the cathedral works like a sonic reflector to focus the sound and disperse it uniformly throughout the entire space. This has a twofold effect. First, it allows each attendant at the ceremony to experience a fairly consistent musical performance regardless of their position. Second, it gives the appearance that the music is descending upon them from above with an otherworldly and encompassing quality (Boren et al. 2013).

Modern Cathedral Technology

Today, places of worship take full advantage of all the resources that developments in electronic and digital technology have provided. For example, the Lakewood Church in Houston,

Texas is a converted sports arena and can accommodate nearly 17,000 attendants. Addressing a congregation of this size would be impossible without modern amplification techniques and include problems that would have been unimaginable to the architects of previous eras.

Currently, common practice is to use the most absorptive materials and least reflective room designs to reduce the reverberation time to the smallest possible value. This will give the amplified signal the optimum amount of clarity for the spoken word. In those cases where some reverberation will enhance the quality of the music, an electronic or digital reverb device can mimic the effects of a natural reverb and can be set to the most desirable time.

Excessive reverb time is no longer the primary obstacle to audio clarity. Now, this has been replaced by feedback and phasing. Feedback is when the amplified signal from a microphone returns back into that mic and causes a loop that results in the signal increasing in volume in an out of control manner. Phasing is similar to reverberation but instead of a sound reflection off a surface it reaches two microphones at slightly different times and then both signals are amplified to a similar volume. This causes an obscuring of the original signal.

At the Lakewood Church, the pastor wears an omnidirectional lavalier microphone. This means that the microphone picks up sound from all directions and is the type of microphone that is most prone to feedback. To combat this, the location of the speakers is vital to ensure that the signal does not return to the microphone. Along with this are several Digital Signal Processors (DSP) that analyze the signal and modify it for optimum clarity and minimum feedback. To amplify the choir and their band, this church uses around 60 microphones. Forty of these are utilized for the choir themselves. In order to reduce feedback from these microphones, each member of the 200 person choir and 11 person band wears personal in-ear monitors that eliminate the need for speakers near the performers, thus significantly reducing the possibility of feedback from these sources. To reduce the instances of phasing from all of these microphones, there is an audio engineer who controls all of these sources and ensures

that only the microphones that are in use at the moment are on and that they are amplifying at an appropriate level (Emmet, 2015).

Conclusion

Throughout history, architects and engineers have sought to improve the clarity and volume of human speech. Traditionally, this pursuit has been in service of religious ceremony and creating spaces that allow for the greatest number of participants. The earliest human civilizations used simple tools to enhance the acoustic properties of natural resources and structures. As construction techniques improved in the Baroque and Renaissance eras, the acoustic properties of these cathedral spaces had a heavy influence in the compositional style and performance of religious music. Current digital and electronic technology allows for manipulation of both acoustical spaces to improve audio clarity and the audio signal to match the acoustical properties of the space.

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Catherine Salmon

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Definition

Catherine Salmon (1969–) is a leading evolutionary psychologist who is best known for her

original and engaging work on the evolutionary function of romance novels, erotic fiction, and pornography, on the evolutionary psychology of family interactions and parent-offspring conflict, on the evolutionary factors influencing body image and dieting behavior, and on the significance of birth order for understanding family relationships. She is currently Professor of Psychology in the Department of Psychology at the University of Redlands, California (USA), and has a BSc in Biology and a PhD in Psychology.

The entry will be divided into two main sections. The first main section will simply summarize the most salient content of Salmon's work as it has been presented across a range of different publications, and the second main section will engage more critically with her work and attempt to evaluate some particular aspects of it.

Erotica

In her work on the nature and function of romance novels, erotica and pornography, Salmon has convincingly argued that, because male against female human natures are profoundly different – due to sex roles in the environment of evolutionary adaptedness (EEA) being very different – the sexual psychology and consequently the sexual fantasy worlds favored by contemporary men as against contemporary women are profoundly different.

Men desire (in general) what could be termed sex-utopia (or, as has elsewhere been termed, porn-utopia), i.e., always-available, impersonal sex-on-demand from (ideally) an inexhaustible supply of beautiful, nubile women, whereas women desire what could be termed romance-utopia or relationship-utopia (Salmon 2005a, 2008), i.e., the continuous expressions of loyal commitment in a relationship with a dashing, muscular, wealthy, male hero-figure, ongoing fidelity, and frequent romantic engagements. As Salmon and Symons have explained:

We believe that genre romances are analogous to male-oriented porn in the sense that they are wish-fulfilling fantasies, well designed to pick the locks of the pleasure circuits of female brains, and largely

worthless as guides to male mating psychology or male-female relations in the real world . . . But because genre romances have been shaped in free markets by the cumulative choices of tens of hundreds of millions of women to effectively pick the locks of the pleasure circuits of women's brains, they have great power to illuminate female mating psychology. (Salmon and Symons 2010, 474)

Elsewhere, Salmon has argued that markets capitalize on preexisting (i.e., EEA evolved) preferences rather than creating new preferences by themselves, a classic example being human dietary preferences such as the evolved taste for foods that are high in sugar and fat (Salmon 2005a, 245).

Salmon's work on erotica implies more widely that the fact that men and women have evolved profoundly different sexual psychologies is a very important feature to consider when trying to understand many contemporary gender-related issues. However, because the Standard Social Science Model now employed across much of the social sciences tends to disavow such differences in sexual psychology, or at the very least to be wary of allotting them any explanatory power, the contemporary social sciences are methodologically stunted in their approach to many issues relating to sexuality and reproduction.

Family Interactions

In her novel work on family relationships and birth order, Salmon has argued that middle born children differ from first and last born children in that they generally score less on measures of family solidarity and identity, suggesting in turn that birth order influences the behavioral niche that a child will adopt from a young age (Salmon 1999). This is because first born children receive all their parents' attention for a definite period of time, as they are initially the only child in the family, and last born children often receive the same level of attention for a period, as they are usually the final child remaining in the family environment.

However, middle born children never receive all their parents' attention, as they always have competing brothers and/or sisters with whom they have to share attention and resources. Hence

Salmon argues that middle born children are more likely to be rebellious and opposed to the existing social order than first or last born children. This is due, at least in part, to the fact that they generally receive less of their parents' attention and resources than their older or younger siblings and hence are more likely to be critical of the familial social-order.

Building on the previous work of Robert Trivers, Salmon also argues that various conflicts of interest exist between parents and offspring (e.g., maternal-fetal conflict and weaning conflict), because although parents and offspring have shared genetic interests, they do not have identical genetic interests. Sibling conflict is seen by Salmon as an offshoot of parent-offspring conflict; the precise degree of sibling conflict in an individual family is affected by various intra-family factors such as birth order and birth spacing (Salmon 2005b, 522; Salmon and Shackelford 2011). Birth order and birth spacing also affect the development of individual personality traits to a degree, although very close birth spacing can reduce the impact of birth order on sibling conflict to some extent.

Body Image

On dieting, body image, and associated eating disorders such as anorexia, Salmon has argued that a concern for becoming thin by dieting may be a part of an evolved ancestral behavior that was directed to controlling the timing of human reproduction. Ancestral women who faced temporary situations that were unfavorable to childbearing could delay their reproduction by reducing their body fat in order to hinder ovulation. In the cotemporary world, the present much higher levels of female competition (and therefore higher associated stress levels) compared to the EEA could be triggering the poor reproductive environment behaviors that were part of ancestral life, such as the tendency to diet in order to lose weight (Salmon et al. 2008). Salmon is aware that this is a working hypothesis.

Elsewhere, Salmon has examined the wider role and impact of female competition for mates

and competition for status/dominance on both reproductive suppression in humans and other species, and on female behavior more generally, in order to test whether there might be behavioral mismatches between contemporary and ancestral environments in this regard. While male-male competition has been extensively studied in the existing literature, female-female competition is more subtle and elusive and therefore has proved more difficult to detect and study. In order to overcome this problem, Salmon has developed her own 20-item female-female competition stress test (FCST).

Evaluation

This final section will evaluate aspects of Salmon's work using both internal and external factors. This author is sympathetic to evolutionary psychology in general and to the aims of Salmon's work in particular but sees to a degree how individuals who might be unsympathetic to evolutionary psychology could distort aspects of Salmon's work into stereotypical forms. The terminology of "male mating psychology" against "female mating psychology" may be taken by a careless reader (either accidentally or deliberately) to mean that these two entities are entirely fixed opposites, when in reality a sliding scale operates between the "extreme female" and "extreme male" ends of a wide spectrum of nuanced sexual psychologies.

Similarly, in relation to the porn-utopia versus romance-utopia contrast (Salmon 2008; Barnett and Weedon 2014), it would be more accurate to say that there is a spectrum of human sexual fantasy universes that exist or a sliding scale that operates between the "extreme female" romance-fantasy world exemplified by Mills and Boon novels, and the "extreme male" hard-core porn-world exemplified by Pornhub's Extreme Tube. This latter point is well illustrated by the fact that today's internet porn has a large range of different styles of pornography on offer, from so-called extreme porn sex-acts such as "face fucking" and "vaginal fisting" at the very crude end of the porn spectrum, to so-called female-friendly porn,

nude-art erotica, sophisticated plot-based porn, and even comedic porn parodies at the more refined end of the spectrum.

It is evident that porn-utopia now has multiple diverse identities and also increasing female directorial participation. In fact the same is actually true of romance-utopia, which now has a very soft Mills and Boon end of the spectrum and a very racy *Fifty Shades of Grey* end of the spectrum, the latter including some sex-acts that were previously encountered only in porn-utopia.

In addition, the question of whether markets simply follow or can create taste and purchasing preferences can be seen as more complicated than Salmon appears to suggest. A more nuanced formulation would be that markets/advertising can shape consumer purchasing preferences to a degree but only within the boundaries that have been set by the preexisting cognitive architecture of the mind. For example, humans certainly do have evolved taste preferences for sugar and fat but not for the precise form in which they are presented. Therefore, markets/advertising can affect what type of chocolate bar an individual chooses to purchase (*Snickers* rather than *Mars*), but no amount of advertising could make an individual prefer the taste of dry grass to that of chocolate.

In terms of her teaching, Salmon has an overall grade of 3.6/5 at the "Rate my Professor" website – a very good score – including rankings from four students who describe her lectures very favorably (or as "awesome," with individual ratings of 4/5 or 5/5) but also including rankings from two students who describe them very negatively (or as "terrible," with ratings of 1/5). However, on further investigation into the negative comments, the 1/5 evaluations are at least partly linked to the perceived high content-level of Salmon's lectures, rather than the teaching.

Consequently, there is a consensus amongst many of the students that Salmon's lectures are at the "more difficult" end of the understanding spectrum, with a number of students reporting that her lectures are also passionately delivered and often sexuality based, which is unsurprising given the themes of her work. Extrapolating from these very different evaluations, Salmon is

(on this evidence) an inspiring teacher of bright and gifted students but perhaps a rather daunting one to some less able students.

Conclusion

Some of Salmon's research can be described as an original continuation of the themes of Donald Symons' pioneering work on sexual psychology (e.g., the romance/pornography comparison), whereas other aspects of her work (e.g., on family interactions) are creative extensions of Robert Trivers work on the evolutionary biology of family relationships. It is, therefore, not accidental that Salmon has cooperated with Symons on a number of occasions. Symons is one of the originators of contemporary evolutionary psychology and the author of *The Evolution of Human Sexuality* (Symons 1979), a pioneering account of the different psychologies of men and women. Salmon and Symons have cooperated on romance fiction (Salmon and Symons 2001, 2010) and on human sexuality more widely (Symons et al. 1996).

Perhaps one significant key to Salmon's success across such a diverse range of topics is the breadth of her understanding across the two currently separate fields of biology and psychology, providing very good evidence for the need for both depth and breadth of knowledge as a platform for conducting successful original research in evolutionary psychology and elsewhere.

Cross-References

- Pornography and Women's Short-Term Mating
- Sex Differences in Same-Sex Aggression
- Sexual Selection

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Causal Attributions

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Synonyms

Etiological attributes

Definition

The attributes that explain the association of cause with effect.

Introduction

Since time immemorial, the quest of human is to know the cause of everything. To know the “cause,” human explore, observe, experience, imagine, and believe certain things. These processes help human getting closure to the understanding about “cause.” The Cambridge English Dictionary defines *cause* as “the reason why something, especially something bad, happens” (Dictionary 2015). “Cause” is always discussed in relation to “effect.” The link that is perceived to be connecting the cause with effect is known as “attribution.” Attribution refers to “the act of saying or thinking that something is the result or work of a particular person or thing” (Dictionary 2015).

Epidemiology attempts to understand the causes associated with good health and illness (Scheutz and Poulsen 1999). There are a lot of variations (across the cultures as well as among individuals of a particular culture or geographic region) in terms of their attributions to cause(s) of good health or illness. It is always difficult to establish or find out the exact cause of an effect (health-related event), though there may be many attributions explaining the association. The

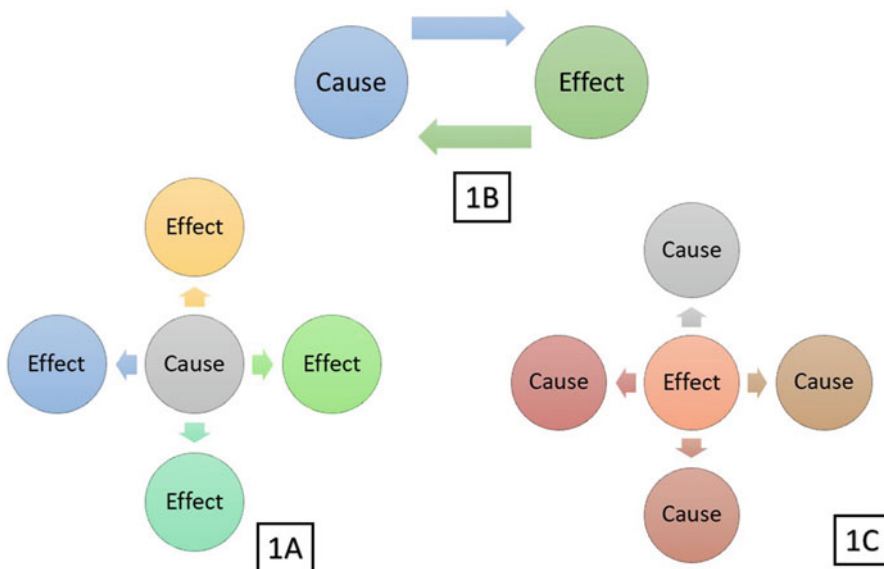
attributions are usually constructed by the experiences related to the event.

Evidences are usually build by seeing the association between causes and health-related outcomes (presence of causal factor in association with illness and elimination of the causal factor resulting in recovery or remission from illness) (Scheutz and Poulsen 1999).

Causal Attributions: Types

One cause can be attributable to multiple effects and the vice versa is equally true. For example, stress can cause multiple health-related effects like depression, anxiety disorders, substance use disorder, somatoform disorder, obesity, coronary artery disease, and diabetes; on the other way around, any of the abovementioned disorders can be attributed by multiple causes (e.g., depression can be caused by stress, genetic factors, brain damage, substance abuse, endocrinal disorders).

On the basis of above associations between cause and effect, the relationship can be one to one (Fig. 1b), one to many (Fig. 1a), as well as many to one (Fig. 1c).



Causal Attributions, Fig. 1 Possible associations between cause and effect: (a) one cause to many effects; (b) one cause to one effect; (c) many causes to one effect

The “health-related event” can have multiple causal attributes, which can be biological, psychological, social, cultural, financial, as well as spiritual. The amount of attributions to the abovementioned causal domains varies from individual to individuals. The biopsychosocial model can be attributed to the causality of various psychiatric disorders.

Attribution styles play an important role in explaining the causal attributions. The attributional styles are soft psychological constructs that describe how an event (effect) is attributed to various factors. It can be broadly external (external situation or external person) attributional bias or personal (self) attributional bias (Mehta et al. 2011).

Evolution of Causal Attributions

Kelley (1973) had proposed the “attribution theory,” which elucidates that how people synthesize explanations about a cause leading to an effect (Kelley 1973). This theory basically deals with social perception and explains causal attributes of human behavior. Temporal association of cause with an event is an important determining factor of causal attribution (Young 1995). Since ancient times, it was seen that when the cause of a particular event (e.g., illness) was not known, people tend to attribute the cause to supernatural powers. For example, for centuries together, epilepsy, cholera, leprosy, chicken pox, measles, mental illnesses, and many more health conditions were perceived to be resultant of any supernatural power; hence, the remedial measures were targeted to satisfy the God or evil spirit that were believed to cause the illness (Corrigan et al. 2001; de Boer 2010; Kazeem and Adegun 2011; Lukoff and Everest 1985). However, with time the understandings about the causes of the events have evolved. Meticulous observations and research helped people understanding about the causes of illness as a result of which the causal attributions to illness as well as wellness have changed over time.

Clinical Relevance of Causal Attributions

If the health-related events are taken into account, then the effect (outcome) can be either *illness* or *wellness*. There are various causal attributions to explain illness (what causes are responsible for development of illness?) or wellness (what causes are responsible for maintaining wellness?). Understanding the causal attributions helps in generating an explanation about illness and wellness which has significant role in providing health education. For example, poor hand hygiene attributes to development of infectious disorders like gastroenteritis; so, the health education in patients with gastroenteritis focuses about maintaining hygiene. Similarly, unprotected sexual relationship may lead to development of sexually transmitted diseases (STDs), and for successful prevention of STDs, health education focuses on safe sexual practices.

Causal attributions likely influence the pathways of care as well as help-seeking behavior. For example, patients with panic disorder often attribute their symptoms to cardiac illness and first consult cardiologists or general physicians. Although panic disorder is a psychiatric disorder, the typical phenomenology (choking sensation, palpitation, tachycardia, perspiration) often direct the attribution to physical causes. Similarly, trans (possession) episodes of dissociative disorder and auditory hallucinations of schizophrenia are often referred to supernatural power and many people seek traditional healers for its remedy. The adherence to treatment for a particular illness depends on the individual’s causal attribution for his or her illness. The individuals who attribute the symptoms of illness to a medical cause seem to be more likely to be adherent to treatment than those who attribute it to supernatural powers.

Attribution to events in normal day-to-day life usually follows a pattern. Evidences support that most people attribute the cause of success and positive events to self, whereas the causes of negative events and failures are often attributed to external factors (e.g., people, situations). This is a form of bias that operates subconsciously and often referred to as self-serving bias or attributional bias (Mezulis et al. 2004).

Cognitive distortions often lead to misattribution to cause and are often dysfunctional in nature (Bowins 2004). Cognitive distortions are commonly seen in psychiatric disorders. For example, *catastrophization* is a form of cognitive distortion commonly seen in panic disorder. The patients often misinterpret their symptoms and attribute them to a severe or devastating cause (attributing palpitation to impending myocardial infarction). The psychological interventions like cognitive behavior therapy (CBT) and cognitive therapy target the cognitive distortions as resultant erroneous causal attributions are corrected (Sadock and Ruiz 2015).

Various psychological defense mechanisms are too responsible of erroneous causal attributions. For example, defense mechanisms like rationalization and projection are commonly used by individuals with substance use disorder, where the unacceptable feelings associated with alcohol use are nullified by misdirected causal attributions (Sadock and Ruiz 2015).

After an unexpected negative event, the attribution of people to the cause of the event may become negative. Evidences support that self-blaming and blaming others for the event are associated with poor outcomes (Hall et al. 2003).

Conclusion

Causal attributions are often colored by the education, awareness, belief systems, and personal experiences of the individual. Certainty of cause can be established through evidences. Investigations many a times found to be highly useful in correcting the wrong attributions to cause(s). However, majority of the psychiatric diagnosis are made clinically and seldom on the basis of investigation(s). The changes in the body structure and function could not be always demonstrable by means of investigation; hence, the wrong attributions to causes in psychiatric illnesses could not be corrected, relying exclusively on the investigations. Therefore, there is a need to address stigma, create awareness, and properly psychoeducate people suffering from psychiatric illness to correct wrong causal attributions. In the

context of health, it is utmost important for a clinician to understand the causal attributions of the client and actively address them during the treatment for a better outcome.

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Causal Cognition

► Confounding Use of Tools on Physical Tasks

interesting, but contemporary theory is not ready for at least some of them. Thus, for the present, definition of causal reasoning remains tied to the terms of the relevant theories.

Causal Inferences

► Causal Reasoning in Rats (Blaisdell et al. 2006)

Introduction

An ability to decipher and act in accordance with the causal structure an animal encounters in a complex and varying world has clear value. A primary difficulty is that cause and effect in the world is opaque. Although animals are continuously bombarded with information about how events covary, covariation is an imperfect indicator of causation. Even with strong evidence that two events concur, there are many ways they may be related causally. That they reliably concur is evidence of a causal relation, but gives no more evidence that the one causes the other, than the converse; they may as well both be effects of a common cause or effects of effects of effects with common causes and so forth. Information about how events covary is not sufficient to decide among the possible causal relations that may exist among events, nor is it sufficient to differentiate between veridical causal relations and spurious concurrences. Human causal reasoners make causal attributions on minimal information, often on much less data than would be required of a statistician's calculations to reach similar degrees of confidence. Attribution of causality typically involves going beyond the data provided to form an interpretation of the underlying causal relations.

Three distinctions in causal cognition research are important to recognize. All three concern a conflation that has produced confusion in the past and a source of conflict when they have been cast as theoretical alternatives. Combining awareness of these distinctions with openness to what each component provides yields an opportunity to understand causal cognition from complementary research directions.

Causal learning/causal reasoning
 Descriptive/normative approaches
 Algorithmic/computational approaches

Causal Reasoning

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Definition

Causal reasoning refers to all cognition about cause and effect, except learning. "Reasoning" can refer to any post-learning cognitive processing, and the qualifier "causal" stipulates concern with cause and effect. Theories of causal reasoning may concern the structure of associations, how agents use such structures, or how that structure affects action. Although focus is most often on acquired structures, this is not a principled limitation. At least some causal reasoning research with nonhuman animals is phrased in terms of dispositions.

The topic applied to nonhuman animals is controversial. The controversy is largely due to misapprehensions about the term, but there are genuine theoretical disagreements regarding even the presence of causal reasoning as well.

"Reasoning" is a connotatively rich word, and this richness can mislead by appearing to attribute more than what a theory actually concerns. This danger can be alleviated (and some of the less productive controversies avoided) by remaining faithful to the terms of a given theory and remembering not to conflate this with the richer breadth of meaning typical of dictionary definitions. All of the connotations of "reasoning" may be

Causal Reasoning Versus Causal Learning

Causal reasoning (reasoning about cause-effect relations) is appropriately dissociated from causal learning (learning about cause-effect relations). Learning is concerned with a bottom-up analysis; reasoning, top-down. Although knowledge about how causal learning occurs bears on the study of the ultimate structure, and knowledge about this structure bears on study of the way it is acquired, and integrative research that combines analyses of causal reasoning with learning carry potential worth, their distinction should be born in mind. In particular, a theory of causal reasoning may be silent on learning, or vice versa, and so caution is warranted in drawing conclusions about one in the context of theory about the other.

Descriptive Versus Normative Approaches

Much of contemporary cognitive science employs normative theories of cognition, drawing predictions about human cognition from models of how a rational agent ought to perform analogous tasks. Such approaches are fundamentally unlike older trends in psychology, which have been predominantly descriptive. The latter includes the associative learning tradition, in particular, the “laws of learning” kind of theory, which attempts to provide functions describing the relationships between sensory input and behavioral output. Although there has been resistance to normative approaches in psychology, there has been increasing recognition that the two approaches can be complementary.

Normative approaches are prevalent in ecology and economics and so in ecological and economic approaches to cognition, such as ecological rationality, behavioral ecology, and optimal foraging theory. Natural selection provides an obvious basis for normativity in natural systems, although principled evolutionary approaches of causal cognition have yet to be developed.

Normative approaches to causal cognition are relatively new, largely an addition of the 1990s. However, theory about causality itself, a topic of importance to all the sciences, is mature, such that causal cognition researchers have inherited a fully developed body of theory to lie at the basis of their theories of causal cognition. This clarity about

how causality ought to be treated is essential for approaches that rely on it as a normative basis. Knowing how a rational agent is expected to reason about cause and effect is a potentially helpful starting point in investigating how causal cognition manifests in real animals. If cognition about cause and effect is expected to serve its possessor well, rational or optimal solutions provide a null hypothesis against which to compare natural manifestations. Normative theories make prescriptions of causal cognition which can be tested.

Normative approaches solve a major problem of descriptive causal cognition research in providing independent theoretical terms for approaching questions about cognition. This fills a gap otherwise left to reliance on anthropomorphic intuitions. It remains tempting, in practice, to encumber such theories with anthropomorphic assumptions, but a normative framing does not require it, in principle.

An early objection to normative approaches to nonhuman causal cognition notes that humans tend not to abide norms of causal reasoning and even find explicit training in such norms difficult. If even humans fail to be rational, one might argue, expectations for nonhumans to reason rationally must be low. However, human irrationality bears little on the validity of normative approaches in nonhuman animals.

Normative theories of causal reasoning make predictions about patterns of behavior that serve the animal well in the face of problems with particular structure associated with cause and effect but not about how such patterns are achieved. A normative theory makes predictions without requiring assumptions about psychological manifestation. It remains necessary to specify how the terms of the theory correspond to variables in a given experiment.

Levels of Analysis: Algorithmic Versus Computational

Like in much of psychology and cognitive science, research and theory of causal cognition exist on at least two different levels of analysis, and it is not always made explicit which level is in focus. David Marr (1982) dissociated three levels of description: implementational, algorithmic, and computational. The “implementational” level describes on the

level of physiology, the workings of neurons and muscles. The uppermost “computational” level can be thought of as a folk psychological level. It is the level dealing with goals and at which selection pressures can be identified, and so is sometimes referred to the “biological” level. The intermediate “algorithmic” or “process” level concerns how the thing operates rather than what it achieves. This is sometimes described as a “psychological” level. Normative models tend to exist on the computational level, although there is descriptive research on both algorithmic (e.g., associative) and computational (e.g., tool use research) levels.

A computational-level analysis brings insights into the goals a behavior or cognitive process is meeting, and the selection pressures it is affecting, and so the functional significance of that form. It does not specify a mechanism, cognitive or otherwise. The analysis of the animal’s behavior can therefore be rational without the animal’s cognitive apparatus abiding those same rational norms.

Associative models are most often exclusively algorithmic. Computational-level and implementational-level analyses were explicitly eschewed in behaviorist psychology. Although the resistance was justified, it was overstated. Recognition of the serious limitations of exclusively computational-level research, and that it is fundamentally unlike behaviorist approaches, were important milestones. Adding recognition that computational-level analyses also have merit, in addition to their limitations, and that the two kinds of analysis are complementary, however, is just as important. By failing to specify a corresponding computational-level analysis, an exclusively algorithmic approach attempts to describe how a cognitive process unfolds without commitment to function. Attempts to present analyses on different levels as direct competitors are misguided. By combining analyses on multiple levels, each level informs and constrains theory.

Descriptive Approaches in Causal Reasoning Research

A large part of causal cognition research in non-humans is primarily descriptive, where cues

indicating some aspect of causality are manipulated and responding is measured. One can present animals with novel problems and apparatus with identifiable causal properties. Such research has largely been presented as tests of the capacity of a focal species to reason about cause and effect. If the animal responds preferentially to causal over noncausal features, it is often taken as evidence of understanding of the relevant causes and effects. The framing of such research has typically been explicitly or implicitly anthropomorphic and otherwise largely atheoretical.

Naïve Theory Theories and Causal Power

One common approach is to phrase the question in terms of whether the animal possesses a kind of implicit belief system or theory of involved causal forces. Seeing a rooster perched on a post and then hearing its distinctive call lead to the ready judgment that the rooster caused the crow. However, there is more behind the attribution than the one event following the other: had the rooster barked, oinked, or mooed, the same attribution might not be made. Causal decisions are made not only on the basis of the qualities of the present instance but also a set of expectations about what has the power to cause what.

Michotte (1946) identified several qualities of stimuli that lead people to reliably make causal attributions to explain events that are not in fact causally related. In general, things are regarded as causally related when their movements correspond – stimuli that move in the same direction or at the same rate. For example, people very readily see the movements of balls striking each other on a billiards table as causally related. When Michotte (1946) projected animated images of one shape moving up to another and stopping, and the other then taking up the same tack, people interpreted this as the first pushing the second. If contiguity was broken, and there was a delay, the illusion of causality was disrupted. This has been taken as evidence for the suggestion that we begin with a naïve physics to help us abide the world. As the example of the mooing rooster shows, it is not just physical theories upon which attributions of causality are made but theories about the causal powers of agents as well.

Tool Use

Many animals use objects in their environment as foraging aids, for example, stones to crack nuts. A few species of passerines and primates are more sophisticated and regular in their use of tools. The woodpecker finch, for instance, uses twigs to root prey out of tree trunks (Tebbich and Bshary 2004), and Egyptian vultures have been observed dropping rocks on ostrich eggs (Hunt et al. 2006). Among the several motives for studying tool use is the manipulation of causal factors in order to study causal cognition.

A number of methods have emerged that take the approach in focus: subject animals to causal problems and measure their ability to solve them. A novel apparatus with a causally relevant, but apparent, twist is presented to the animal. Is the task solved outright? If not, does performance improve with experience? And if so, does the lesson transfer to tasks that differ on a number of variables, some relevant to the problem, some irrelevant? If the animal changes strategy to solve relevant alterations, but looks past irrelevant ones, they are deemed to have demonstrated understanding of the causality underlying the apparatus.

Trap Tube-Trap Table Contraptions

The “trap tube” is a device used to test whether, when given a causally transparent problem, animals will make use of cues that are relevant to achieving the goal. It is a transparent tube with a morsel of food (e.g., a peanut) placed in the center, just out of reach. The only way to get the food is to probe the tube with a stick, which is provided. But there is a trick: to one side of the food is a depression, into which the food will fall, and thereafter be unattainable, if pushed in the wrong direction. The “trap table” presents an analogous problem, but on a flat surface, likewise interrupted on one side by a hole. Will the animal attend such traps and pull (or push) the food out the safe way?

Members of several species have succeeded at some variant of the trap tube or trap table problem, including several primates and a few passerines: capuchin monkeys, vervet monkeys, hoolock gibbons, common chimpanzees, bonobo chimpanzees, gorillas, orangutans, human children,

human adults, woodpecker finches, rooks, New Caledonian crows, and cats. Members of each of these species came to succeed in solving the task, given practice. However performance has been mixed. Individual differences were generally large, with many individuals never succeeding and those who did usually required considerable practice. Only humans have been shown to regularly avoid the trap from the start without training (Silva et al. 2005).

The conclusions that can be drawn from success or failure at the initial trap tube, however, are limited, and much of the focus of the discussions regarding what these results mean has concerned performance on transfer tasks. Once the subject has solved the trap tube, it is tested on other apparatus that are either functionally equivalent but superficially dissimilar (e.g., transfer from trap tube to trap table) or perceptually similar but with the trap no longer functional (e.g., inverting the initial tube). Varying perceptual features of the apparatus and causally relevant features independently allow one to ascertain the kinds of cues these animals attend to when solving the problem. Rooks (Seed et al. 2006) and New Caledonian crows (Taylor et al. 2009) have readily transferred to perceptually dissimilar but functionally equivalent tasks.

The other sort of transfer task, those varying function but not form, asks whether the animal persists in avoiding the trap, even though it is no longer functional, commonly by inverting the tube. That subjects of a number of species do persist in avoiding the nonfunctional trap has been taken as evidence that such animals lack understanding of how the apparatus operates. Rather, they are assumed to have learnt by trial and error to rely on cues that are functionally irrelevant to solving the problem. Capuchin monkeys, chimpanzees, and humans all show this kind of persistence with such manipulations. There are faults with the inverted trap tube control. Notably, failure to discriminate sides is poor as a test of understanding, as the same is predicted if the animal were to treat the inverted tube as a wholly separate problem. Silva et al. (2005) subjected the trap tube and trap table tasks to humans, who were able to confirm understanding of the apparatus

and solved the task without error from the first trial. These subjects nevertheless showed the same sorts of behavioral biases on the transfer tasks seen in other species, biases that had been taken as evidence against use of sophisticated cognition, notably as evidence for a wide separation of human causal cognition from that employed by other animals. This undermines interpretations of such results as failures of understanding.

Tool Selection

Do animals select the right tool for the task? If the animal understands the causality in solving a problem that requires a tool, it should be selective about the tools it attempts to use, to select a tool appropriate to function, or perhaps modify it to suit the problem. Visalberghi et al. (1995) presented capuchin monkeys, chimpanzees, bonobos, and an orangutan with a tube with food in the middle. This was much like the trap tubes described above, but without the trap. The trick was in the tools provided. Initially they were given a single functional dowel with which they could access the food. Then they were given not a single stick, but a bundle of four, which were together too big to insert in the tube. Apes opened the bundle to use a single stick to solve the task from the start. The monkeys also came to this solution, but often first tried to use the too-big bundle as it was, ineffectively. In another condition, subjects were given an assembly of dowels in an H shape, which the monkeys persisted to attempt to insert directly, whereas the apes soon learnt to disassemble it first. The readiness with which the apes modified the tool, in contrast with the monkey's persistence, moved Visalberghi et al. (1995) to conclude that these results indicate a qualitative gap in reasoning prowess between apes and monkeys.

New Caledonian crows regularly make skewers from plant material to pull insect prey out of logs. Hunt et al. (2006) presented two such birds, in their natural habitat, with vertical holes of different depths cut in the top of a log and baited with larvae, and recorded the tools made or selected and how they were used. The crows did not initially take or make longer tools in response

to deeper holes (15 cm) and so often failed on the first attempt with these. However, the second tool collected for a deeply stashed larva was regularly longer than the first. Also, when a shallow hole required a second tool, these were shorter than the second tool collected for the deeper holes. Another tool using species, woodpecker finches subjected to an analogous laboratory study likewise did not appear to pick tools to match depth of the goal object from the first trial but tended to choose larger sticks for the second try (Tebich and Bshary 2004).

Ecology and Tool Use

Species of animals vary in use or creation of tools in the wild. While most animals show no propensity to use or make tools when left to their own devices, some do. Notably chimpanzees fashion probes from plant material to extract termites from mounds and sturdier probes to spear small primate prey hiding in tree hollows, whereas other apes show no tool use in the wild. Considering the differences among these species in use of tools in nature, it is striking that no clear species differences have been documented among great apes on performance in contrived tool use tasks. Likewise, the prolific tool user, New Caledonian crow, did not outperform rooks, another corvid but one not known for tool use (Seed et al. 2006; Taylor et al. 2009).

General Criticisms of Current Causal Cognition Research

Descriptive research on causal cognition in non-humans suffers foremost from lack of theory. This produces problems of interpretation. Focus is often on collecting evidence of cognitive sophistication in a given species, to the exclusion of any deeper understanding of that sophistication, a trend that has been rightly disparaged as "trophy hunting" (Allen 2014). Success on a task is often interpreted as evidence for the animals' understanding of the underlying causality in problem, and failures are often interpreted as failures of understanding. The problem with such terms is that it is not accompanied by cogent theory. Once the animal behaves appropriately in response to a task, or fails, this approach is out of positive

predictions. Such studies appear to be engaged in providing ammunition for popular debates rather than furthering understanding.

This is not to say that such research provides no relevant data. Transfer tests in tool use studies, for instance, do appear to provide a method for ascertaining whether the animal is using cues that are relevant to the problem, which in such cases are cues indicating function. Results indicating that corvids, at least, appear to pass such tests motivate development of theory of causal understanding. Critically, however, such results do not entail such theory.

One troubling yet widespread trend in this literature is to approach causal cognition as a dichotomy consisting of mindless association versus abstract mental modeling and present these as competing and exhaustive alternatives. Experiments are commonly phrased as tests to exclude interpretation in terms of associative learning, as a path to demonstrating causal reasoning. If results permit interpretation in terms of associative learning, it is dismissed as a failure and that is the end of the analysis. This involves simplistic, archaic interpretations of associative learning (Rescorla's 1988, lament remains current), ascribing answers to metaphysical questions that entire generations of mainstream learning researchers explicitly and adamantly eschewed. Advantages of bringing the tools of learning research into the service of analyses of how animals are solving these problems have been demonstrated (e.g., Beckers et al. 2006; Polack et al. 2013). Consistency with theories of associative learning may be regarded as a strength, rather than as a criterion for exclusion.

Another apparent source of confusion involves distortions of what successes demonstrate, encumbering them with attributions of mentality not warranted by the data. The interesting set of questions concerning intentionality or propositional representations are not addressed by such methods. The precise scope of such research remains unarticulated. Solutions to this and the above problems await developments of theory.

Particularly in studies with apes, sample sizes are often tiny, and the subjects are often very experienced, sometimes with the same paradigm, and the same individuals often feature in multiple

related studies. Furthermore, among studies that involve transfer, since many of the already few subjects never solve the basic task, quite few animals have been subjected to transfer tasks, meaning that conclusions have been drawn on very small numbers.

Graphical Models

Graphical models are representations of relevance structures. Network diagrams are used to model relevance relations (the edges) among a set of focal variables (the nodes). This includes causal relevance, and so graphical models can be used to model causal relationships. This has been extended to model *reasoning* about causal relationships as well as *learning* about causal relationships. Pearl (2000) and Danks (2014) provide good introductions.

Graphical models are described both in terms of their qualitative structure, and some quantitative measure of the strengths of the relationships depicted, often a probability distribution. The qualitative aspect of graphs permits the modeling of greater structural variety than exclusively quantitative analyses. Theories differ in the focus they place on these two aspects of graphs. Graphical model-based theories of learning have typically focused on the quantitative aspect; those of reasoning have stressed the qualitative aspect. A challenge that the field is currently rising to meet is to integrate these aspects in theory. There are theories, for instance, that concern the acquisition of qualitative structures from quantitative data (e.g., Wellen and Danks 2012; Fernbach and Sloman 2009).

Application of graphical models to analyses of causal reasoning in laboratory conditioning studies needs to make a number of assumptions. First, how the terms of the theory correspond to variables in the experiment needs to be specified. Typically, stimuli and responses are assumed to correspond to nodes in the network, and associations, to the edges. Second, assumptions need to be made about how hypothetical structures are acquired. One approach is to specify the learning process by which input data leads to the formation of specific

structures. Another is to impose constraints on the specific structures that can be acquired or are involved in learning. One may assume predispositions to acquire particular network structures. Some theories assume attentional constraints that restrict learning, for instance, to single event-outcome pairs (“local computations”) or to specific graphs (e.g., the “common effect” structure, as in Single-effect Learning Theory).

The network analogy is not unique to graphical model-based views. By a range of views, what the learner acquires can be described in terms of networks of associated events. However, whereas some theories rely centrally on network terminology, among theories that describe associations solely in quantitative terms, associations may each be represented separately and so be more appropriately described as a list of association strengths than as a network. Although the tenability of the list analogy has been challenged by demonstrations of retrospective revaluation, in which learning is affected by stimuli other than those that appear in the conditioning trial, the network analogy is not expressly motivated by typical associative theories. Evocation of the image of a network, therefore, does not necessarily imply that a view intends a coherent representational scheme in which associations are collectively accessible.

Directed, Acyclic Graphs

Graphical models come in many varieties, but analyses of causal cognition typically assume directed, acyclic graphs (DAGs). A graph is considered directed if edges are asymmetrical, indicating relevance in only one direction. This fits analysis of cause and effect, since causes determine effects, not vice versa. Acyclic means that there are no cycles in the network, no relations in which an effect produces its own cause, or some cause of its cause, etc. For instance, if fear causes running from a bear, and running from the bear causes fear, the resulting network will not be amenable to such an analysis. The assumption of directed (and acyclic) associations is a prominent feature that sets such analyses apart from typical associative learning analyses, by which associations are most often assumed to be undirected.

A network of associated events provides richer information if the associations retain information about the direction of associations.

Bayesian Networks

The Bayesian Networks formalism is a graphical model-based framework initially developed to aid the calculation of probabilities of interdependent events. It works well with cause and effect (Pearl 2000). If the edges represent causal relationships, it is a “causal Bayesian Networks,” although this stipulation does not alter how the network functions. As a good way to deal with causality, Bayesian Networks secondarily provides a normative theory of causal reasoning: how a rational agent ought to reason about cause and effect.

The theory is very spare. Bayesian Networks assume directed and acyclic graphs (i.e., DAG) and the Markov and Faithfulness conditions (described below). The relations it represents are abstract, on a computational level of description.

This normative theory is important to differentiate, both from the mathematical framework on which it is based and especially from substantive theories that make use of Bayesian Networks (e.g., Gopnik et al. 2004; Waldmann et al. 2006) and sometimes leave vague what is borrowed and what is added. Conflations of these very different kinds of theory require care and transparency. It is worth accentuating that this normative theory makes predictions without requiring assumptions about psychological manifestation.

Probabilities Versus Contingencies

Expectation and probability have clear relevance to each other, and graphical model-based approaches exploit this connection. When translating this intuition into studies with laboratory animals in conditioning procedures, it is common to speak of training contingencies in the same terms as probabilities. Although animal learning procedures present contingencies, not probabilities, the connection is not new. Similar intuitions have underlain advances in learning theory, such as inhibitory conditioning, and have featured in discussions regarding the appropriate control conditions in Pavlovian conditioning studies (Ward and Jenkins 1965; Rescorla 1967).

One danger of the tightness of this connection is that it tempts conflation of the training procedure with the learning it produces. This applies to associative models in general but is less of a concern for models that only deal with the quantitative aspect of associative strength. If a learner overestimates or underestimates a correlation, the affect on behavior might be minor. For inferring qualitative structure from statistical information, however, the assumption that learners extract probabilities from contingencies needs to be articulated as such and open to empirical challenge. For instance, Blaisdell et al. (2006) was criticized (Penn and Povinelli 2007) for presenting a negative correlation between stimuli while purporting to train a “common cause” structure, by which the two stimuli should be treated by the learner as conditionally independent. The concern is well taken, and analogous to earlier concerns with explicitly unpaired control conditions, which present a negative relation between stimuli, though the animal is intended to learn that they are independent (Rescorla 1967). However, the observation is overstated if the assumption that a training procedure that presents a statistical independence is either a necessary or sufficient condition for learning that two events are independent. Specific learning models differ on this point, and such models provide the appropriate context for discussions about how learners use statistical information. Note, furthermore, that a training schedule might carry much information (e.g., temporal relationships) that affects learning beyond just concerning the statistical relationships among stimuli that has received so much attention.

Markov Condition

The Markov Condition specifies that occurrence of any event in a network is independent of other nonadjacent events, given knowledge about adjacent events. For a directed network (and thus for Bayesian networks), the constraint is correspondingly more specific: an event is independent of all non-descendants, given its immediate antecedents. This provides a computational shortcut, because it means that the probability of an event occurring can be calculated without knowing most of the network. Consideration of the local causal

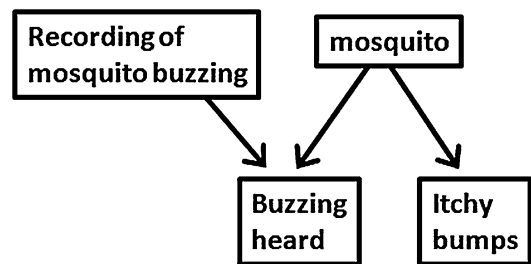
environment is enough. This renders a complex network of probabilities tractable. If to calculate the probability of an event one needed to determine the probabilities of all other events that impact it, even indirectly, predicting the occurrence of an event would quickly become forbidding as complexity increased, to be practically intractable with networks of even modest complexity. The Markov condition furthermore fits intuitions about cause and effect: for assessing the likelihood of a given outcome, knowing the status of a direct cause, *C*, one can ignore all of the causal factors behind *C*.

A complementary Faithfulness assumption is also often granted. The Faithfulness assumption is the converse of the Markov condition: if two nodes are independent (conditionally or otherwise), then they are not adjacent in the graph.

Common Effect and Common Cause Models

1. Events with a common effect are dependent given the effect.
2. Events with a common cause are dependent when the cause is unknown.

In a directed, acyclic graph that satisfies the Markov condition, there are two basic circumstances in which a valid inference can be drawn between nonadjacent events in a network, even while granting conditional independence among them. Two events with a common effect are dependent given knowledge that the effect has occurred. For example, buzzing is caused by mosquitoes, but it can also be caused by a recording of a mosquito (Figure 1). Hearing a mosquito’s buzz, the



Causal Reasoning, Fig. 1 Graphs of the two situations of the example described in the text. Arrows indicate the presence and direction of causality. The *leftmost* three nodes depict the “common effect” structure; the *rightmost* three nodes depict the “common cause” structure

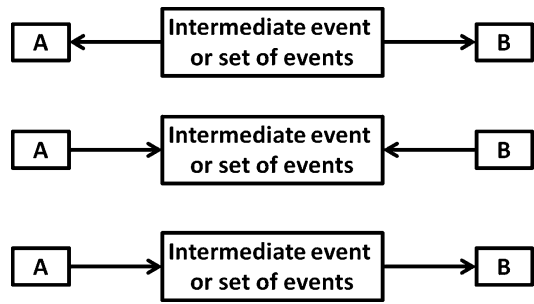
probability of finding a mosquito in the room greatly increases, as does the probability of discovering a speaker playing recorded mosquito buzzes (which is ordinarily quite rare). The buzz requires explanation and so all potential causes of the buzz become more probable. However, once we ascertain that there is indeed a recording of mosquito buzzing playing, the sound is no longer indicative of the presence of a mosquito, and the probability of finding a mosquito in the room immediately plummets back to baseline. Thus, whenever buzzing is heard (i.e., the effect is known to have occurred), the probabilities of these two causes of hearing buzzing become dependent on each other, even though they are otherwise independent. They are alternatives: confirming one reduces the probability of the other.

Two events with a common cause become dependent when the occurrence of the cause is unknown. Mosquitoes cause more than just buzzing. They also cause itchy bumps. Since mosquitoes cause both, these two events tend to go together, such that hearing a buzz in the room means that sleeveless arms are at risk. However, once the mosquito's presence or absence is known, hearing the familiar, uneven buzz gives one no additional information about the probability of acquiring a mosquito bite.

Conditionality

Graphical model-based views model mediated associations as conditional. By the Markov condition, if two nodes in a graph are not directly connected by an edge, this means that they are independent, in principle. If they are connected indirectly, via intermediate nodes, however, there is a relationship, but the relationship is conditional on those intermediate nodes.

Conditional causal associations are diverse in form (Fig. 2). These include not only effects of a common cause (Fig. 2a), and causes of a common effect (Fig. 2b), but also causes of causes of a common effect and so forth. It also includes cases where A causes some intermediate event that in turn causes B ("causal chain"; Fig. 2c). For instance, if melting ice might produce a flood, and the flood might destroy a given dock, there is a real relationship between the melting ice



Causal Reasoning, Fig. 2 Three forms of conditional causal association: common cause (*top*); common effect (*middle*); causal chain (*bottom*). In each case, the causal relationship between A and B is conditional on the status of some causally intermediate event or set of events

and the destruction of the dock. However, one's ability to predict the latter from the former is conditional on what is known about the causally intermediate event, the flood. Once we see that a flood has occurred and its ferocity, the current well-being of the dock is no longer dependent on knowledge about what ultimately caused the flood.

Conditional independence also has a statistical definition. The probability of C is conditionally independent of A, given B, just when $P(C|A, B) = P(C|B)$ [or equivalently, when $P(A, C|B) = P(A|B)P(C|B)$]. The structural and statistical definitions are important to dissociate: the former concerns the structure of learning; the latter concerns the structure of input data, which, in Pavlovian paradigms, are specified by the procedure. They are related, however. By some views, learners will acquire a conditional association just when the statistical definition of conditional independence is satisfied (e.g., Wellen and Danks 2012).

Superficially, conditional association resembles second-order learning, which has been amply demonstrated. However, dominant approaches do not conceive of second-order associations in terms of conditionality. Rather, associative strength is viewed as passing down a chain of associations, such that the associative strength of even a second-order CS is represented in the same exclusively quantitative terms as a first-order CS. Thus, conditionality is central difference between these two general perspectives.

Despite the theoretical centrality of conditionality, it has rarely been specifically asked whether nonhuman animals learn mediated associations in a way that respects conditionality. Bowers and Timberlake (2017) exploited the prediction that, if an association is conditional, given knowledge of the immediate antecedents of an outcome, information about the antecedents of such antecedents should have no impact on expectation of the ultimate outcome. Rats were presented with CS2-CS1-food training such that the CS2-CS1 and CS1-food correlations were the same in two groups, while the CS2-food correlation differed between groups. If subjects had acquired only a conditional association via CS1, responding to CS2 should depend on the strengths of the CS2-CS1 and CS1-food associations, which should be the same in both groups. Groups differed in response to CS2, with subjects appearing to track the CS2-food correlation, suggesting that the CS2-food association was not exclusively conditional on CS1. Thus, conditionality is not ubiquitous, placing pressure on contemporary theories to specify the conditions under which an indirect association is appropriately modeled as conditional, if ever.

Direct Versus Indirect Causation

Many forms of causal relation may produce correlation. An important distinction to draw is between the case in which A causes B, and those in which correlation of A and B is due to some indirect causal relation between them. For instance, multiple effects of a common cause (or multiple causes of a common effect) will often correlate; this is a causal relationship even though neither A nor B causes the other. Likewise, there are multiple ways for A to cause B. These include not only unmediated cause-effect relationships but also the causal chain structures.

These two general kinds of association warrant different behavior. One is expected to increase actions that bring about causes of desired outcomes but not mere correlates of the same outcomes. For instance, we adjust the temperature on a thermostat, but not a thermometer, and only if red leaves cause autumn should winter faeries take to painting trees. Causes are not simply (nor

necessarily) more predictive of their outcomes than are other predictors. Rather, the difference is qualitative.

Note that the line between direct causation and causal chains becomes fuzzy when reliability is very high (approaching 1). For instance, when one flips a light switch, the action can be treated as causing the light to burn, though the actual causal factors are more complex. A chain of local causes (e.g., local movement of electrons along a circuit) can thus sometimes be treated collectively as a single event. The world would otherwise be a very difficult place to learn about. Interestingly, this weird aspect is captured unintentionally by some theories of causal cognition (e.g., Wellen and Danks 2012).

Intervention

The actor is in a privileged epistemic circumstance in which the cues to cause and effect are especially clear. One's own actions can be assumed to be original causes, whereas most other causes cannot. For instance, seeing that a given light switch is always up when a light in the adjoining room is on, and down when the light is off, one might guess that the switch controls the light. However, the movement of the switch up or down in the past will have its own causes. This matters for determining the true cause of an event. Correlation is insufficient to infer causation. However, once one flips the switch, and sees that the light follows, it takes very few trials to feel certain that the light is controlled by the switch. Intervention introduces the kind of arbitrariness and control that are at the essence of experimentation. As an experimenter controls variables and observes effects to elucidate causation, producing an outcome by one's own action may aid the active learner for the same reasons. Intervention provides a reliable cue to veridical causality that is available to be exploited by an animal interacting with its environment (Bowers 2015).

Hypothesis-Based Causal Reasoning

To some observers, talk of causal reasoning implies possession of a kind of model or theory of causal relationships. Others object that such assumptions unnecessarily encumber analyses of

causal reasoning. Although this debate is largely academic, its weight is felt in the context of intervention. The capacity of intervention to elucidate causation is thought by some to rely on already having a hypothesis to test, and deciphering effects of an event involves prior beliefs about causal relations in the world. This is a viable objection to attempts to distance analysis of intervention from commitments to a more metaphysically weighty understanding of “reason.” Note, however, that even if such structure is necessary for a learner to benefit from intervention, it may not necessarily need to be representational; such structure could, in principle, be motivational (Bowers 2015). Questions of representation are separable from questions of structure.

Diagnostic Reasoning Versus Predictive Reasoning

Most causal cognition research among non-humans focuses on predictive reasoning, from causes to effects. A presented stimulus is conceptualized as the cause, and the animal is to infer its effects. In contrast, diagnostic reasoning is from effects to causes. When one sees outcomes, and attempts to decipher the causes, they are reasoning diagnostically. In terms of directed graphical models, predictive reasoning is reasoning in the direction of the arrows, and diagnostic reasoning is reasoning against the direction of the arrows. Diagnostic problems abound. Sounds of prey moving through a leafy forest floor, for instance, will often precede appearance of the cause, and this is what a predator faces. Prey animals face a similar diagnostic problem in identifying predators from their effects. Such animals may be prepared to infer causes from effects, rather than the opposite. Call (2004) provided evidence of a small preference among apes for opaque food cups that rattle when shaken, interpreted as inference of food (cause) from the rattle (effect).

Precedence

Precedence featured prominently in David Hume’s (1748) view of the perception of cause and effect. “When many uniform instances appear, and the same object is always followed by the same event; we then begin to entertain the

notion of cause and connexion” (Hume 1748, Sect. 7). Preceding events can be taken as causes of reliably following events. This works well for the billiard balls in his example, and research on Pavlovian conditioning has generally confirmed the importance of precedence in associative learning.

Furthermore, causality itself has temporal constraints that give it direction. Causes generally precede their effects. Future events do not cause past events. However, the converse is not necessarily true. Precedence is no assurance of causation, even among cases in which there is a veridical causal association. Screech of tires does not cause the car to crash, and the cricket’s chirp does not cause the cricket to appear. Not every learning situation is like Hume’s billiard table, in which the causes and effects are all apparent. If elements are hidden, an effect may be apparent before its cause. Thus, any implied appeal to natural selection for learning about precedence as a cue to causation should not be overstated.

Among attempts to study causal reasoning in conditioning paradigms, it is commonly assumed that precedence will cue perception of causation. A prior stimulus is assumed to be perceived as a direct cause of a following stimulus (e.g., Blaisdell et al. 2006). This assumption is more intuitive than principled. Predictors are often not causes of the stimuli they predict but effects of a common cause. Among contemporary theories, few articulate a stance on how order of stimuli should impact the perceived directionality of an association. Fernbach and Sloman (2009) provide an exception, echoing Hume (1748) in attributing an important role to precedence in perception of causality.

Treating Typical Conditional Stimuli as Causes and Effects

The common assumption that tones and lights and food in typical conditioning preparations will be perceived by subjects as causes and effects warrants hesitation. The conditional stimuli in such experiments do not indeed cause their consequences, of course. Such studies rely heavily on assumptions about the factors that cue attribution of causation, which exceeds current

understanding. Note that events assumed to be treated as causes by subjects in conditioning experiments are often even intuitively awkward. For instance, the burning of a light may cause shadows or squinted eyes but lacks the causal power to produce food. This qualm is anthropomorphic, but it accentuates a remaining gap in theory concerning the specific conditions under which animals are expected to draw a causal attribution about a given pair of events.

If incorrect attributions of causality can hinder the animal as much as correct causal attributions help, we should expect an animal to be discerning about what it treats as causal. If causal attribution is prone to error, and errors are costly, animals may be better served by undirected associations, as in typical associative learning models.

Blocking, Backward Blocking, and Retrospective Revaluation

Blocking (Kamin 1969) is a Pavlovian procedure and a learning phenomenon in which an animal is first trained with one cue that predicts some significant stimulus ($A+$) and is then similarly trained with a compound of two cues, including the first ($AX+$). Tested on the second cue alone (X), such a subject will show attenuated response, relative to other subjects who did not receive the initial $A+$ training with the first cue. Learning about the second cue is said to be “blocked” by conditioning with the first. This produced a crisis in learning theory, as it stumped many theories of learning, and a new class of theory rose that stressed prediction error reduction (e.g., Rescorla and Wagner 1972). Backward blocking (i.e., $AX+$, and then $A+$, leads to reduced response to X alone) is like Kamin’s (1969) blocking procedure, except that the order in which the two trial types are presented are reversed: first subjects are trained with the compound stimulus ($AX+$) and then the element ($A+$). Again, training with the element ($A+$) leads to reduced responding to the other part of the compound stimulus (X). First observed in human causal learning, it has since been demonstrated among rats, in a Pavlovian preparation comparable to Kamin’s forward blocking (Miller and Matute 1996; this study used a “surrogate” stimulus in place of the US), and the similarities

have been taken as suggestive of homologous processing.

To causal learning models, backward blocking is as much of a prediction as is forward blocking. However, backward blocking is a difficulty for most associative learning models, including those that rose in the wake of forward blocking, which generally assume that learning only occurs among stimuli present on a given trial. Unlike forward blocking, in backward blocking conditional responding to the blocked stimulus changes retrospectively, in the absence of subsequent experience with this stimulus. This makes backward blocking among the phenomena of “retrospective revaluation,” which collectively challenge learning theories to deal with more than just the stimuli present and so tend to favor views that ascribe structure to learning. Only a few such effects have been documented.

Outcome Maximality and Outcome Additivity

Outcome maximality effects and outcome additivity effects are challenging for many learning theories. Outcome maximality occurs when an effect is at its maximum quantity or intensity. If an additional potential cause of this same effect is presented, the rational causal reasoner has no evidence to judge the adequacy of this new cue to cause the effect. However, there is evidence that this new cue does not prevent the effect. Similarly, if an effect is absent, there is no evidence regarding a cue’s power to prevent it, though there is evidence regarding the same cue’s power to generate the effect. Thus, these two circumstances differ in the possibility to ascertain generative and preventive causes. Maximality and additivity effects have been observed in causal learning among human subjects. These are effects that typical associative models do not account for.

Beckers et al. (2006) showed sensitivity to outcome maximality effects among rats in the blocking paradigm. Subjects were first presented periodically with two intensities of shock. Then, they were subjected to a blocking procedure, using shock ($A+$, $AX+$). Where the shock subsequently presented during the blocking procedure was the lower of the two intensities, blocking was observed; where it was the higher intensity, there

was no sign of blocking. Thus, outcome maximality was observed.

Outcome additivity refers to a tendency for intensities or quantities of effects to add or not. For instance, though one waiter's passing produces a glass of champagne, and a second waiter's passing produces another, rarely does the appearance of both waiters simultaneously win you two glasses or a glass twice as big. Similarly, a predator coming upon signs of two crickets may rarely be able to catch both and so stand to gain no more in finding two than had there been just one. In other cases, two signs may mean double returns. Kamin (1969) had shown that blocking did not occur when the compound stimulus (AX) was trained with a much higher shock than the elemental stimulus (A), indicating that the effects of the stimuli add. Finding the second stimulus predictive of shock, they developed the conditional response to it. If returns do not add in this way, however, similar to the maximality effect, the causal power of a second potential predictor or cause that appears in the presence of the effect cannot be readily evaluated. In this case, the rational learner should remain agnostic regarding the second cue.

Beckers et al. (2006) tested this prediction by presenting rats with evidence that outcomes did not add. They did this by training them initially with two separate predictors of low intensity shock and a compound of both these predictors together with the same intensity of shock (C+, D+, CD+). Both stimuli together produced the intensity of either alone, evidence that intensities do not add. These rats were then subjected to the blocking procedure with different cues (A+, followed by AX+). Under these circumstances, blocking did not occur, indicating sensitivity of the subjects to outcome additivity.

Substantive Psychological Theories of Causal Reasoning

Whereas some graphical model-based theories limit claims to the most abstract, computational-level terms, others concern substantive, causative representations of causal associations. Substantive theories give graphical models tangible interpretation in terms of psychological entities.

A causal reasoner is thought to possess and act upon mental models approximating the form of networks of learnt relations. Among such theories are Causal Model Theory (Waldmann et al. 2006), by which "animals have a natural tendency to translate covariations into causal-model representations" (p. 310) (see also Gopnik et al. (2004)). The empirical support for Causal Model Theory remains weak.

By such views, when an animal learns a new association, it does so by augmenting a representational model of causal relations. However, the perspective otherwise provides little guidance on learning, instead focusing on the use of ultimately formed structures. Such views have been criticized for their inability to specify how given training procedures produce hypothesized structures (Penn and Povinelli 2007), but this is to exaggerate their scope. Alignment with a theory of learning can fill such gaps (Waldmann, et al. 2008). Whether one theory of learning will suffice for all cases and whether predispositions will need to be assumed are remaining challenges.

Such views invite integration with normative theories by assuming that the hypothetical, abstract structure from which a normative theory draws its predictions reflects the structure of the mental models the animal uses to reason about cause and effect. In other words, one can assume isomorphism between the computational and algorithmic levels. Causal model representations may generally manifest the qualities of Bayesian networks, for instance. The animal, by this view, is itself naïvely Bayesian, not just the scientist's analysis. These two levels of theory may complement each other, with the normative theory bringing specific predictions about form and the substantive theory giving these forms tangible interpretation in terms of psychological entities.

Mentality

Few theories of causal reasoning say anything about mentality, in favor or against. Some views speak in terms of mental models but do not make predictions about mentality itself. Normative theories concern form. Graphical models concern form. Associative learning models concern form.

Having a theory about form does not grant a theory about how it manifests. It is not obvious that structuring information in terms of directed associations requires a fundamentally different quality of mind than structuring the same information in terms of undirected associations. Thus, the apparently widespread belief that support for a theory of causal reasoning or alternative hypotheses in an animal demands a different view of that animal's mental life may be misguided, given the current state of such theories. Though rationality and mentality are easily conflated, neither requires the other: assuming abstract thought does not motivate claims of rationality nor does rationality motivate claims of abstractness.

"Causal Reasoning-like Behavior"

It is sometimes tempting to soften talk of causal reasoning by appending "-like behavior". This temptation should be resisted. Such phrasing is pragmatically ambiguous: it may be taken to imply that *x* is not *really* reasoning or that *x* is a good candidate for reasoning. If a pattern of behavior appears to be interestingly treated like causal reasoning, it is preferable to be clear about the specific similarity meant.

Learning About Cause and Effect

Although the distinction between learning and reasoning is important to recognize, they are also very relevant to each other. Analyses of causal reasoning often involve assumptions about learning and vice versa. Especially given that learning and reasoning are addressed to different extents by different theories, and by different studies, and the distinction remains fuzzy in some discourse, it is pertinent to discuss learning in the context of reasoning.

Associative Learning

Despite the presence of rhetoric explicitly contrasting causal cognition with associative learning, and the absence of a notion of "causal" in mainstream associative learning nomenclature, the mature and prolific field of research and theory concerning Pavlovian and instrumental

conditioning has clear and direct relevance to causal cognition and may be considered its strongest leg. That events have concurred in the past is a good sign that they will continue to concur, expressly because it is a good sign that they are related causally. Animals had better not learn to associate fortuitous concurrences or irrelevant details of a learning circumstance. For instance, if a fair coin comes up heads in 10 consecutive tosses, one had better not acquire the expectation that coins will always turn up heads. Hence, when we learn from witnessing events covary, we are effectively learning about cause and effect, even though mainstream associative learning views often do not use such terms.

Theory concerning associative learning has often resisted reference to cause and effect. Although this has partly to do with causality playing no essential role in many such views, the resistance has been more adamant than justified on such grounds and may often have more to do with aversion to talk of reasoning. Many thinkers, notably Anthony Dickinson and David Shanks, have stressed the relevance of associative theory to causal learning.

Superfluity of Causal Reasoning in Associationist Thought

Historically, theories of associative learning have attempted to leave no gaps for a reasoning process to fill. Associations are assumed to be used in the way they are formed, such that they require no additional processing when acted upon. This is also assumed in some theories of causal learning (e.g., Single-Effect Learning Theory). It is a virtue of a theory of learning if it does not rest too heavily on a theory of reasoning. In a history of theories impressively meeting this demand, it has been emphasized.

One expense of this emphasis has been connections drawn with theories concerning any next steps. Under pressure to capture all of the structural complexity present with association strengths, motivation is lost to connect with theories expressly concerning structure, including theories of causal reasoning. Retaining an articulated stance on reasoning, even if minimal or null, may be useful in order to clarify grounds for

comparison with views that focus on different aspects of conditional behavior or just to keep in sight what one's theory explains and leaves unexplained, to help prevent exaggeration of explanatory depth. Ostensibly reason-free views of learning may often expect some manner of post-learning processing, for instance, for combining links when responding to second-order conditional stimuli. Pretense of completeness, whether intended or attributed by casual readers, hinders integration of views that offer insight about different aspects of causal cognition.

Causal Learning

The redundant-sounding designation of "causal learning" has been left to a newer class of theories of learning that take explicit inspiration or guidance from graphical models. Thus, although such theories are overwhelmingly focused on bottom-up processes, and typically say very little about causal reasoning, they often retain a theoretical connection with theory concerning a top-down component, such as the Bayesian Networks formalism. This marks a pertinent contrast with the staunchly descriptive approach of the older associative learning tradition, which builds up to no top-down theory.

Note that structured learning itself is not a new development. Ethologists have long held that learning is structured, although such views are typically not phrased in terms of cause and effect.

That covariation is a good sign of causation is a valuable heuristic, but the information given about how events covary is ambiguous concerning the causality involved. If combining information about covariation is how we learn about causality, part of the developing animal's problem is turning information about concurring events in the environment into a scheme of causes and effects. This requires reaching beyond the evidence given to turn poorer information into richer. This is how theories of causal learning need to reach farther than the older associative learning models, which they otherwise sometimes borrow heavily from. For instance, Power PC theory is explicitly an extension of the probabilistic contrast model (Ward and Jenkins 1965), and Local Prediction-Error Learning Theory is equally explicit about

building upon the Rescorla-Wagner model (Rescorla and Wagner 1972).

Causal learning theories have slowly but steadily joined mainstream human associative learning research, thereby enriching thinking about human learning. The analogous change in research and theory based on nonhuman animals has been slower and saltatory but still present. These are not different topics, but different scientific communities (and different species), which may have insight to gain from each other. Some specific causal learning theories include Power PC (Cheng 1997), Single-Effect Learning (Waldmann et al. 2008), and Local Prediction-Error Learning (Wellen and Danks 2012), with others reviewed in Glymour (2003). See also Fernbach and Sloman (2009).

Power PC

Cheng's (1997) Power PC theory ("causal power theory of the probabilistic contrast model") of causal induction builds upon the standard contingency model (i.e., the difference between the probability of an event given a second event and given the absence of the second event: $p(B|A) - p(B|\sim A)$; Ward and Jenkins 1965). Learners begin with a propensity to develop causal attributions, and attribute causal power to a candidate cause according to the observed contingency with the purported effect, corrected for base rate probabilities in the absence of the candidate cause. This combines the "covariation" and "power" approaches to causal induction, yielding a theory about how covariation information is integrated into hypotheses about causal power.

Concluding Remarks

Owing perhaps to the newness of the field, and its spanning several scientific communities, there is a lack of communication and mutual understanding that appears to be impeding progress. The field desperately needs a conceptual overhaul. In the meantime, open minds are especially necessary, and caution about what a given theory predicts and what questions are addressed by the available data. What is the role of questions of mental

content in the study of causal cognition? What kinds of theories compete with each other as explanatory alternatives? How and to what extent do theories of different levels constrain each other? These are issues that this burgeoning field needs to work through. It seems that the field needs to reorient and embrace that it is a field made of multiple, complementary approaches that deal with separate but overlapping aspects of the problem. The scope of each approach to causal cognition research needs to be clarified, as well as what sorts of conclusions each is able to draw and how such results bear on the other approaches.

Cross-References

- ▶ Bird Tool Use
- ▶ Causal Reasoning in Rats (Blaisdell et al. 2006)
- ▶ Nonhuman Tool Use

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Causal Reasoning in Rats (Blaisdell et al. 2006)

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Synonyms

Bayes net theory; Causal inferences; Causal-model theory

Definition

The process of identifying and understanding the relationships among causes and their effects.

Introduction

As descendants of Darwin, contemporary psychologists who study animal learning try to identify continuity in species' cognitive and problem-solving abilities. As descendants of Galileo, these same psychologists prefer to study animal

learning in laboratory environments that have been standardized to reduce unwanted behaviors and automated to facilitate the presentation of stimuli and the recording of responses. It was within these traditions that Blaisdell et al. (2006) conducted three experiments to demonstrate that rats were capable of causal reasoning, a form of thinking thought possible only by humans.

The type of reasoning studied by Blaisdell et al. is often illustrated by two analogies. The first analogy illustrates reasoning about a common cause: A change in atmospheric pressure causes simultaneous changes to a barometer and to the weather. The two effects (barometric readings and weather) have a common cause (atmospheric pressure). Someone who understands these causal relationships knows that doing something that directly changes the barometric readings will not affect the weather. More abstractly, Event **A** causes Events **B** and **C**, which are independent of each other. The second analogy illustrates reasoning about a causal chain: An increase in greenhouse gases causes an increase in the temperature of the atmosphere, which causes other climatic changes. Someone who understands these causal relationships knows that doing something that increases greenhouse gases will also increase the temperature of the atmosphere, which in turn will produce other changes to the climate. In a causal chain, Event **A** causes Event **B**, which causes Event **C**.

Common-Cause Versus Causal-Chain Training

Experiment 2a is perhaps the most widely discussed experiment of Blaisdell et al.'s study. The critical features of this experiment can be summarized as follows. During a training phase, a group of hungry rats was given several presentations of a light that was followed by a tone (i.e., Light → Tone). During a second training phase, these rats were presented with pairings of a light that was followed by access to a sucrose solution (i.e., Light → Food). Because the light was a common cause of both effects (i.e., Tone and Food), the two phases together formed common-cause training.

Another group of rats was trained similarly except that their first phase consisted of Tone → Light pairings. Their second phase also consisted of Light → Food pairings. Because the two effects (Light in the first phase and Food in the second phase) each had a direct cause (Tone in the first phase and Light in the second phase, respectively), the two phases together formed causal-chain training.

To test what the rats understood about the pairings they experienced across the two training phases, Blaisdell et al. divided each group of rats into two additional groups. For one of these groups, pressing a lever produced a tone. For the other group, the tone was presented independently of a rat's behavior. Neither the light nor the sucrose was presented during the test session. The researchers recorded how often the rats nosed in the feeder aperture during the tone. Nosing in the feeder was as a measure of the rats' expectation of food.

Predictions

Common-Cause Training. According to Blaisdell et al., causal-model theory predicts that, during testing, the rats that experienced common-cause training will nose in the feeder less during the tone when it is produced by leverpressing than when it is not. The rationale for this prediction is that when a subject's behavior (e.g., pressing a lever) causes an event (e.g., Tone), the subject should fully discount the previous cause of the event (e.g., Light). In other words, even if Event **A** caused Event **B** in the past, you should not think that **A** caused **B** if you did something that caused **B**. In contrast, response-independent presentations of the tone "should lead the rats [that experienced common-cause training] to reason that the temporally prior cause **L** was probably present (but missed), and to consequently expect that **F** should also be present; therefore, they should emit many nose pokes [during the tone]" (Blaisdell et al. 2006, p. 1021). (In Blaisdell et al., **L**, **T**, and **F** refer to the light, tone, and food, respectively.)

Causal-Chain Training. For the rats that experienced causal-chain training, the amount of nosing in the feeder during the tone (during the test) should be the same regardless of whether it was or was not produced by the animal's behavior. Why? According to Blaisdell et al., if the rats integrate the pairings Tone → Light and Light → Food into a causal chain, then they should treat the tone as the cause of the light, which in turn should be treated as a cause of the food (Leising et al. 2008). Regardless of how the tone is produced, hearing it starts a causal chain that leads the rats to expect food and thus nose in the feeder.

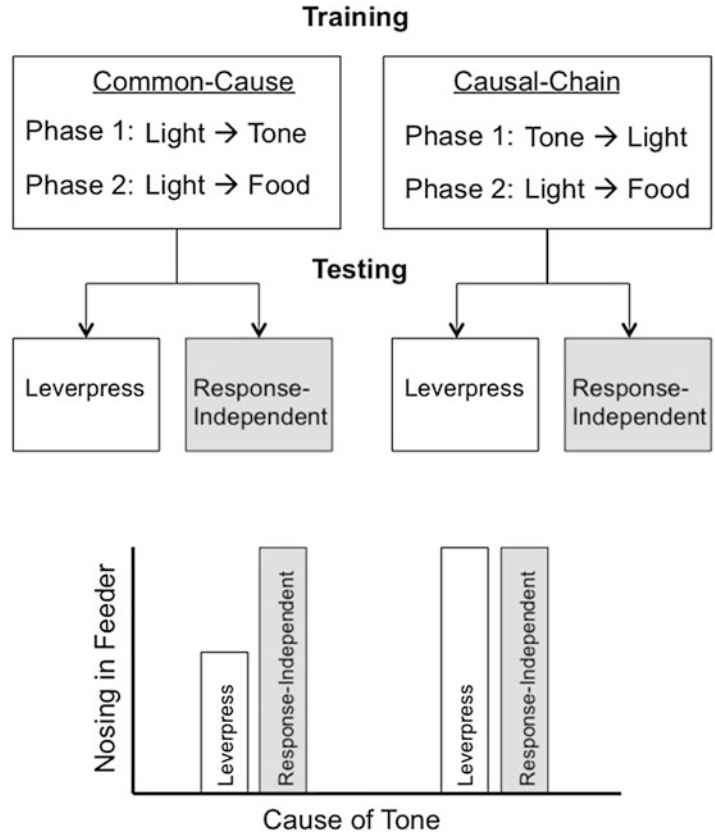
Common-Cause vs. Causal-Chain Training. The preceding analyses led Blaisdell et al. (2006) to predict that the amount of nosing in the feeder during response-independent presentations of the tone would be the same for rats that received common-cause and causal-chain training. This is also the same amount of nosing in the feeder that should occur during the tone when it is produced by a leverpress by the causal-chain rats. It is only the common-cause rats that should show a decrement in nosing in the feeder during the tone when it was produced by a leverpress. Figure 1 summarizes the procedure and the researchers' predictions.

Blaisdell et al.'s Results and Interpretation

The rats that received common-cause training nosed in the feeder less when the tone was produced by a leverpress. According to Blaisdell and his colleagues, these results were consistent with causal-model theory but not associative theories. Other researchers, though, have been less convinced (e.g., Penn and Povinelli 2007). There are two sources for this skepticism, one empirical and the other theoretical. Empirically, some researchers have been unable to replicate the most significant of Blaisdell et al.'s (2006) results – i.e., less nosing in the feeder during the tone when it was produced by a leverpress by the rats that received common-cause training. Theoretically, researchers have argued that some of

Causal Reasoning in Rats
(Blaisdell et al. 2006),

Fig. 1 A summary of Blaisdell et al.'s (2006, Experiment 2a) procedure and predictions. The bars on the *left side* of the graph pertain to the common-cause training; those on the *right side* of the graph to the causal-chain training



Blaisdell et al.'s key assumptions are questionable and vague and that their results are not inconsistent with associative theories.

Difficulties Replicating Results. Perhaps the most straightforward challenge to Blaisdell et al.'s results is that other researchers have been unable to replicate the theoretically vital interaction from the original study, whereby the presentation of the tone as a consequence of the rats' leverpressing interfered with nosing in the feeder only if the rats had received common-cause training (e.g., Burgess et al. 2012; Dwyer et al. 2009). Although failures to replicate a result can be due to many factors, one of the benefits of (higher level) causal reasoning is that it allows people and other animals to abstract the key features of a situation and then to respond appropriately. In other words, causal reasoning permits generalization. Responses that are controlled by the (lower level) perceptual and associative features of a task

are more likely to result in stimulus-bound or situation-specific responding. That Blaisdell et al.'s results are not readily generalizable casts doubt on whether these results were due to the rats' causal reasoning.

Questionable Assumptions and Methods. According to Blaisdell et al., the key prediction that common-cause rats will nose in the feeder less during the tone when it was produced by a leverpress than when it was not depends on the assumption that response-independent presentations of the tone elicit the thought that the light was presented but missed. Why? Because for the common-cause rats, response-independent presentations of the tone are not associated with food except through mediation by the light. For the tone to elicit an expectation of food, it must first elicit a memory of the light – i.e., the stimulus associated with food. Without this assumption, for the common-cause rats, the amount of nosing in

the feeder during the tone would be the same regardless of whether it was produced by a rat's behavior or not. The present-but-missed-light assumption requires close scrutiny (Penn and Povinelli 2007).

Another problem concerns the specifics of the common-cause and causal-chain training. In its simplest form, common-cause training consists of presenting one cause (*A*) followed by two simultaneous effects (*B* and *C*). In contrast, Blaisdell et al.'s (2006) common-cause training method consisted of two phases where the two effects never occurred simultaneously. Similarly, in its simplest form, causal-chain training consists of presenting one cause (*A*) followed by an effect (*B*) that is also the cause of another effect (*C*). But Blaisdell et al.'s causal-chain training consisted of training two separate direct-cause links and then supposing that the rats would connect these links into a causal chain. Blaisdell et al.'s methods deviate considerably from the simplest forms of common-cause and causal-chain training, thereby complicating interpretations of what subjects learned or how they might have reasoned about the training.

Consistent with Associative Theories. Blaisdell et al. concluded that their results were consistent with causal-model theory but not associative theories. Other researchers argue that Blaisdell et al.'s results are not inconsistent with associative theories (e.g., Burgess et al. 2012; Dwyer et al. 2009; Kutlu and Schmajuk 2012). According to these researchers, Blaisdell et al. (2006) neglected to coordinate, for example, stimulus generalization, latent inhibition, conditioned inhibition, protection from extinction, and overshadowing. Most significant is that carefully controlled studies have shown that Blaisdell et al.'s results can be explained by response competition between leverpressing and nosing in the feeder (see Burgess et al. 2012; Dwyer et al. 2009). More specifically, irrespective of the type of training the rats received, there was less nosing in the feeder during the tone when it was produced by a leverpress. Causal-model theory predicts that the effect of leverpressing will be restricted to the rats that received common-cause

training. Some theories of animal learning and behavior that can accommodate patterns of multiple responses may suggest otherwise (see Killeen 2014; Timberlake 2004).

In addition to competition between leverpressing and nosing in the feeder, some of Blaisdell et al.'s (2006) rats had a propensity for signal-directed behavior toward the light. For this reason, "the bulb on which L had been presented during training was removed from the experimental chamber. . . . A pilot experiment found it necessary to remove the light bulb on which L was presented during training to produce reliable responding to T after causal-chain training" (Blaisdell et al. 2006, pp. 5–6 of Supporting Online Material). The bulb was removed prior to testing for all rats. That Blaisdell et al. had to remove the light is evidence of the occurrence of response competition. That this competition was more apparent for the rats that received causal-chain training than common-cause training places a red flag next to any explanation for differences in these rats' behavior because of causal reasoning. Occam's razor compels scientists to use the simplest explanation that will suffice. Removing a part of the environment that interested one group of rats more than another group is a potentially simple explanation for any differences between these groups.

Conclusion

Although it was hailed as the first demonstration of causal reasoning in rats, the significance of Blaisdell et al.'s study is less clear today. There have been serious challenges to their assertion that associative theory cannot explain their results but causal-model theory can. At present, it is unclear whether rats understand that the manipulation of an effect cannot affect its cause, that exposure to sequential stimuli is the training of a causal link, that they treat absent but expected events as present but missed, or that these animals can integrate training in separate phases into a coherent causal model (Machado 2005; Penn and Povinelli 2007).

Cross-References

- ▶ Causal Reasoning
- ▶ Nonhuman Intelligence
- ▶ Why Humans Are Unique

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Causal Role

- ▶ Biological Function

Causality

- ▶ Victims Mostly Men

Causal-Model Theory

- ▶ Causal Reasoning in Rats (Blaisdell et al. 2006)

Causation

- ▶ Psychological Determinism

Cause

- ▶ Etiology

Causes of Criminal Behavior

- ▶ Criminals Are Made Not Born

Cave Art

- ▶ Prehistoric Human Art

Cave Painting

- ▶ Prehistoric Human Art

Cease-Fire

- ▶ Reconciliation

Celebrities

- ▶ Hollywood Actors

Cell Death as an Adaptation Against Cancer

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Synonyms

Apoptosis; Metabolic changes

Definition

Cellular death pathways adopted by cells to prevent cancer progression.

Introduction

Cellular adaptation is the capacity of cells to respond to different types of stimuli and adverse environmental changes. Depending upon the reproducibility attributes of cells constituting the tissues, tissues adapt differently. If cells are not able to adapt to the adverse environmental changes, cell death occurs physiologically in the form of apoptosis or, pathologically, in the form of necrosis. In cancer incidences the intrinsic elasticity acquiesce to cells to progressively evolve functions that promote cell growth, disable cell death mechanisms, and evade immune surveillance and therapy (Hanahan and Weinberg 2000). There is a delicate balance between the regulation of cell growth and cellular metabolism. In a cancer cell, these regulatory mechanisms are disturbed in multiple ways to favor active proliferation of cancer cells. This genetic as well as physiological difference between normal and tumor cells therefore acquires vital importance for development of cancer therapeutics. The oxygen regulation is one important

mechanism in cancer development, wherein it is utilized to alter the metabolism and augment formation of new blood vessels. The Noble Prize 2019 has been unraveling the mechanisms involved in sensing and adaptation of cells to oxygen. The oxygen sensing mechanisms has been an important therapeutic target for drug development. Additionally, cells possess multiple death mechanisms that differentially impact tumor progression and the response to treatment. Thus, there is growing appreciation about interdependence between cell growth, metabolism, death pathways, and cancer.

The effect of oxygen levels on cellular metabolism and physiological function has also paved the way for promising new strategies to fight anemia, cancer, and many other diseases. The awarded mechanism for oxygen sensing has fundamental importance in physiology, for example, for our metabolism, immune response, and ability to adapt to exercise. Many pathological processes are also affected. Intensive efforts are ongoing to develop new drugs that can either inhibit or activate the oxygen-regulated machinery for treatment of anemia, cancer, and other diseases. In tumors, the oxygen-regulated machinery is utilized to stimulate blood vessel formation and reshape metabolism for effective proliferation of cancer cells. Intense ongoing efforts in academic laboratories and pharmaceutical companies are now focused on developing drugs that can interfere with different disease states by either activating or blocking the oxygen-sensing machinery.

Metabolic Changes in Cancer: Implications in Cell Death

Cancer cells have multiple alternative mechanisms, not known in normal cells, which allow them to survive under highly adverse conditions. In the 1920s, Otto Warburg illustrated the use of aerobic glycolysis for energy production by the tumor cells rather than oxidative phosphorylation (OXPHOS) despite sufficient oxygen and the lesser yield of ATP. Pyruvate is one of the important metabolic intermediates present at the

intersection between lactate production and OXPHOS. In normal cells, in the presence of oxygen, the pyruvate is directed into mitochondria to be converted into acetyl CoA by the pyruvate dehydrogenase (PDH) or into alanine by transamination. Inside the mitochondria, pyruvate is completely oxidized through the TCA cycle, feeding reductive equivalents to the electron transport chain. However, in case of absence/limited supply of oxygen, pyruvate gets converted into lactic acid by lactate dehydrogenase (LDH) in a process termed anaerobic glycolysis. In contrast, cancer cells shift their metabolism toward lactate production even in the presence of oxygen mainly via genetic modifications that stabilize the transcription factor hypoxia-inducible factor (HIF) involved in the adaptation of the cells to hypoxia, under non-hypoxic conditions and generating an adaptive response to the hypoxic microenvironment (DeBerardinis et al. 2008).

In addition to glycolysis, cancer also use glutaminolysis pathway, which generates reductive equivalents such as NADPH by replenishing the TCA cycle (DeBerardinis et al. 2008). Glutamine is a conditional amino acid in the sense that, under normal conditions, it can be synthesized in most cells. Glutamine provides energy through the TCA cycle as well as nitrogen, sulfur, and carbon skeletons for proliferating cells. Tumor cells have a mitochondrial enzyme, glutamine synthase (GLS), and are therefore able to convert glutamine into glutamate, thereby generating a large pool of glutamate. In vitro and in vivo studies have shown decreased tumor cell growth in limited GLS activity (Gao et al. 2009).

Recently, it has also been shown that metabolic requirement alone does not activate metabolic reprogramming but is also regulated by oncogenes and tumor suppressors. PI3K/Akt pathway is one of the most often deregulated pathways in tumor cells. Akt is one of the essential proteins, which leads to the increased expression and membrane localization of the glucose receptor-1 (GLUT-1) and stimulates phosphofructokinase activity. It thus causes augmented glucose uptake and increased glycolytic activity. The tumor suppressor p53, on the other hand, can shift tumor cells from glycolysis to oxidative

phosphorylation (Berkers et al. 2013). Thus, the precise characterization of the metabolic pathways in different cancer cells is a growing challenge, which might lead to the discovery of drugs that specifically target proteins or enzymes altered in tumors.

Apoptosis and Its Mechanism

Apoptosis is the cell's inherent mechanism for programmed cell death, particularly essential in long-lived mammals as it plays a critical role in development as well as homeostasis (Hassan et al. 2014). There are two different pathways that lead to apoptosis: the intrinsic and extrinsic pathways that correlate with the signal type. They are also referred to as the mitochondrial and death receptor pathways, respectively. The intracellular signals include DNA damage, growth factor deprivation, and cytokine deprivation (Zaman et al. 2014), whereas the most common extracellular signals are death-inducing signals produced by cytotoxic T cells from the immune system in response to cells that are damaged or infected (Zaman et al. 2014). The pathways converge at the executioner caspases.

With the onset of apoptosis signaling, changes begin to occur within the cell. These changes include activation of caspases which cleave cellular components required for normal cellular function such cytoskeletal and nuclear proteins. As a consequence of activation of caspase, apoptotic cells starts to shrink and undergo plasma membrane changes that signal the macrophage response (Hassan et al. 2014). Apoptosis is carried out by caspases (cysteine aspartyl-specific proteases), which are a class of cysteine proteins that cleave target proteins. There are four initiator caspases (caspase-2, caspase-8, caspase-9, caspase-10) and three executioner caspases (caspase-3, caspase-6, caspase-7). The executioner caspases cleave the target protein that eventually leads to the death of the cell. The pathways are highly regulated so that apoptosis will only occur if signaled. The intrinsic pathway, in particular, is regulated by the B-cell lymphoma-2 (BCL-2) protein family, which includes

pro-apoptotic effector proteins, pro-apoptotic BH3-only proteins, and anti-apoptotic BCL-2 proteins. The anti-apoptotic BCL-2 proteins inhibit apoptosis through the inhibition of the pro-apoptotic BCL-2 proteins, BCL-2-associated X protein (BAX), and BCL-2 homologous antagonist killer (BAK). BH3-only proteins inhibit the anti-apoptotic BCL-2 proteins (Zaman et al. 2014).

Therapeutic Strategies Against Cancer Triggering Apoptosis

In cancer cells deregulated apoptosis leads to longer cell survival and more time for the accumulation of mutations causing increased invasiveness during tumor progression, angiogenesis stimulation, deregulation of cell proliferation, and interference in differentiation (Hassan et al. 2014). The most common way of treating cancer is through regulating or probably terminating the uncontrolled growth of cancer cells. Targeting the cell's own death mechanism is strikingly effective method. Moreover, targeting apoptosis is the most successful nonsurgical treatment. As the avoidance of apoptosis is the major indication of cancer and is also nonspecific to cause or type of cancer, therefore, focusing on apoptosis for developing cancer therapeutics is most efficient for all types of cancer. Several anticancer drugs are there which target various stages in both the intrinsic and extrinsic pathways (Liu and Zhu 2017). Two characteristics strategies for therapeutic targeting are stimulation of pro-apoptotic molecules and inhibition of anti-apoptotic molecules (Hassan et al. 2014). Several studies have been done on therapeutic targets, which include ligands for death receptors (Lopez and Tait 2015), inhibitors for BCL-2 (Zaman et al. 2014), XIAP inhibition (Lopez and Tait 2015), and alkyl phospholipid analogs (APL), which act as apoptotic signals (Villa-Pulgarín, et al., 2017). Any stage in the pathways can be targeted for treatment; however, there is no indication of which target is most effective. As more apoptosis-inducing anticancer drugs are designed, the most effective targets will be determined.

Conclusion

So far, extensive work has been done to attain in-depth knowledge regarding regulation of tumor metabolism. Yet for the development of drugs that specifically target tumor-related pathways, there is a need to further understand the complex networking between oncogenic signaling pathways and tumor metabolism. Metabolic reprogramming might render cancer cells highly dependent on specific enzymes or processes that could be exploited for inducing cell death. However, due to multiple options of compensatory mechanisms available to tumor cells, the search for relevant targets becomes complicated process. It is essential to understand that there is no single tumor specific metabolism, rather, several programs that differ from tumor to tumor and are adjusted to the special requirements of different tumors in different tissues. The complexity of the tumor metabolism furthermore demands in vivo models to study the effect of drugs on a whole organism. Also, still there remain some puzzling and troubling questions such as whether these treatment strategies induce resistance in tumors and whether they will cause normal cells to die in massive numbers that still remain unanswered. As a result, there is an urgent need of evidence-based long-term follow-ups on patients receiving these new cancer treatments, and the current research should focus on those strategies that can selectively induce apoptosis in malignant cells and not the normal ones.

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Census

► Surveys and Questionnaires

Census Data

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Synonyms

[Archival research](#); [Public records](#)

Definition

Data collected about an entire population, usually by national governments, to assist with state functions. When accessible by researchers, these large databases can be used to evaluate theories of human behavior internationally, over time, and inexpensively, in ways relatively uncompromised by sampling issues.

Introduction

Evolutionary psychology posits that behaviors result from complex, evolved adaptations, many of which are universal to a species (Tooby and

Cosmides 2005). As such, it must contend with hypotheses across all levels of human society, from the individual to the species. Testing theories in such a way that can confirm the influence of adaptations across populations is by no means a simple task however. While the majority of studies are carefully designed and implemented upon subsets of a population, there are many rich secondary data sources that can be used to test complex evolutionary theories on a much larger strata of the population, as well as on national and international levels. Such sources are thus promising avenues to confirm or advance contemporary theory. In this chapter, the use of census data is critically discussed, and its use in contemporary literature is illustrated with some pertinent examples.

What Is Census Data and Why Is It Advantageous to Evolutionary Psychology?

Most national governments implement some form of national census every decade. While these are designed for assisting with state functions such as taxation, they nevertheless can be used fruitfully by researchers in the field. These massive data collections are often based on in-depth surveys that catalog the basic demographic characteristics of every household within a nation, detailing everything from the number and sex of household occupants, age, number of children, employment status, and size of dwelling are among just a few of the potential fields available. This provides a snapshot of the population at a given moment in history. While the majority of the basic demographic sections of the survey remain static over time, many governments also include other measures to help supplement future public policy which can also be of use to researchers. In recent years, two societal changes have enhanced the use of such data: public disclosure of census records and online availability (normally with tools to allow users to drill down to multiple levels of municipal administration). The ease of access to such data sets makes them an attractive option for use in research.

Census data has been in use for many years in many other disciplines (particularly sociology and criminology). Generally, however, it is used less in psychology, as its focus is predominantly (but by no means exclusively) on individual level behaviors and cognitions. Evolutionary psychology of course does not ignore these factors, quite the opposite in fact. Where evolutionary psychology differs, however, is in its underlying principles based on the evolutionary science of adaptations (Tooby and Cosmides 2005). One of the core criteria of demonstrating that a behavior or cognition is an adaptation is showing that it has consequences for fitness (the ability to leave descendants). This is where census level data is incredibly useful, as it can provide a wealth of accurate, objective information on actual offspring within families and many of the factors surrounding birth and mortality rates. While this may seem limited to a traditional human behavioral ecological approach to research (often referred to critically as “counting babies” – Nettle et al. 2013) the ability to examine population-level (and levels below where it allows) reproductive output provides a crucial window into human behavior.

The second core advantage to evolutionary psychologists is the ability to use this information to carefully compare across populations internationally. An additional criteria for showing evolved adaptations includes the principle of species level universality: if it is an evolutionarily ancient trait, everyone across cultures, nations, and geography should show evidence of it. Demonstrating invariance (or its absence) provides us with powerful information regarding the origin of a behavioral or cognitive trait. As mentioned earlier, most nations conduct a form of census that allows such a comparison to be made and on such numbers to allow us a greater confidence in conclusions emerging from such data. While the impetus to establish invariance, or lack thereof, in a given trait is of course not limited to evolutionary psychology per se (as all disciplines ideally consider cross-cultural variation to be important), its theoretical significance in the study of behavioral origins makes the quest for invariance of greater importance (and is alas examined all too infrequently).

The Methodological Advantages and Disadvantages of Census Data

Two of the core advantages to the use of census data have already been discussed, in that they allow us to tackle core evolutionary questions with powerful, large-scale, national, and international data sets. There are of course added advantages. First of all, many of these data sets are freely available to researchers and can be interrogated meaningfully with relative ease. Secondly, most countries conducting a national census do so on a repetitive timetable (every decade in the UK, e.g.). This opens up opportunities to meaningfully examine stability over time within (and potentially between) nations or other geographical demarcations. While not necessarily a longitudinal study by design, the insights this approach can provide are nonetheless important (Copping and Campbell 2015). Thirdly, the data sources are often rich enough with demographic information to allow us to transform and compute other evolutionarily significant variables of interest (actual and operational sex ratios, for instance). Variables such as these that are hard to consider without an actual figure or, at the very least, an accurate estimate of local male and female populations (stratified by age) are often difficult to obtain by other means. However, the ability to calculate such variables on a population level allows us to expand the range of evolutionary questions that can be considered. Fourthly, data that allows researchers to drill down into smaller geographical units can be used to act as indicators of the local environment that can be used as measure (if only a proxy measure) of local circumstances for the purposes of modelling. This again can be informative for the purposes of testing theory, in particular, mid- or higher-level theories (such as life history theory). Finally, the use of such data allows us to partially mitigate the atomistic fallacy (where correlations on the individual level may not reflect the same relationships at higher-order group levels – Robinson 1950), something that can be hard to avoid when making conclusions and generalizations from smaller sample sizes.

There are of course limitations that one must be aware of when using such data; no method is after

all perfect. While these data are valuable for study, they can be limiting in terms of the questions that we can answer from them. Unlike a study designed to test a specific theory or research question, census data is limited to the pool of items it has collected (or that which can be meaningfully expanded from it). This often means that researchers may have to rely on variables that do not fully examine the construct of interest or that proxies have to be used instead. Despite the power of the sample, this often means we cannot always be as confident in the findings as we would like (Copping and Campbell 2015). Comparisons over time and nations also posit some difficulties if the nature of the surveys change over time and place, as national agendas change frequently with different governments. Related to this is the challenge of readily combining data sets (from other public records, e.g.) within nations so that they provide a meaningful snapshot of the conditions of interest. This can be frustrating when some fields of interest may not have been collected at the same time, forcing researchers to make additional assumptions about their data. Finally, just as examining individuals leaves us open to the prospect of the atomistic fallacy, examining higher-order levels of data can lead us to make the ecological fallacy (Robinson 1950). Just because we see something happening at the level of various social stratifications doesn't mean the same effects are necessarily generalizable to the level of the individual. Related to this is also the danger of Simpson's paradox (Simpson 1951), where meaningful differences in populations can be masked if data is aggregated on higher levels. These problems of causal inferencing however are not limited to the use of census data, and responsible researchers need to be careful in how they interpret the data so as to not make inaccurate or misleading conclusions.

How Has Census Data Been Used to Advance the Evolutionary Sciences?

There are many pertinent examples of how census data has been used over the past decades to help

answer important, evolutionarily derived questions. While these studies have some of the methodological shortcomings mentioned earlier, they are important attempts to exploit these valuable sources of data nonetheless.

One area of evolutionary psychology has benefited in particular: life history theory. Life history theory is a mid-level evolutionary theory that examines differential resource allocation across different environments and how potential trade-offs between investments can result in differential expression of various behaviors (such as aggression, early maturation, sexual precocity, etc.). Accounting for the wider environment, however, which is of course a critical stress-causing feature of daily life, is difficult to do objectively. Census data and public records however help us enormously to paint a picture of the ecological niches that modern man inhabits. An early example of how this can be achieved comes from Wilson and Daly (1997) who examined the impact of life expectancy and economic deprivation on homicide and early birthing rates. Using a combination of public health data and census data, they were able to compare 77 districts in the US city of Chicago, demonstrating that more affluent neighborhoods had higher life expectancies, which in turn had lower homicide and age-specific birth rates.

More recent work has taken these findings further. Copping et al. (2013) conducted a similar analysis using the UK census data (2001) and public records to analyze rates of criminality and teenage pregnancy across local authorities in England. They expanded the analysis to include more data that could encapsulate the environment in more detail and created a series of structural models to evaluate theories surrounding how the environment impacts upon behavior from a life history perspective. This study broadly confirmed the analysis of Daly and Wilson and also posited a model of the factors that may have differing levels of impact in increasing violence and sexual precocity. While this large-scale analysis was interesting, its findings were limited by the ecological fallacy. In an attempt to mitigate this, Copping and Campbell (2015) followed up this work by comparing the

same data from the 2001 census with the 2011 census. They found firstly that the original model was stable over the two capture points. Furthermore, they conducted a study using questionnaire data on the general public to capture similar variables to those recorded in the census. They also used postcode data from each participant to link the behavior of the individual to the local information captured in public records (in order to capture some of the wider ecological factors around each participant's home neighborhood). The findings of this study seemed to highlight a model that was very similar to the structural model created using census data only. While the two models were imperfect representations of each other, the obvious similarities between the two reinforced the conclusions of the original study and demonstrated how sources of data can be combined within research designs in novel ways to negate the ecological and atomistic fallacies.

Briefly alluded to earlier was the use of census data to calculate demographic characteristics such as sex ratios. Several theories suggest a key role for the impact of differing proportions of reproductively viable males and females, and census data provides an excellent opportunity to examine this in depth. For instance, previous research has suggested that a paucity of males can lead to elevated levels of localized violence, single-parent families, precocious sexual activity, and many other social phenomena. At the same time, a paucity of females has suggested much the same pattern. Combinations of census and public record data however seem to suggest that fewer males relative to females in the reproductive population (the operational sex ratio) is a key driver of aggression (Barber 2003; Messner and Sampson 1991) due to the instability it creates due to the lack of parental investment in offspring (as males are able to move more freely between sexual partners without having to make longer-term investments). This effect has been shown repeatedly across time periods and nations. This finding would have been difficult without readily available census data sets that accurately recorded population compositions at each point.

Future Directions and Conclusions

Evolutionary researchers need to begin exploiting these rich data sources more frequently to assist in answering pertinent research questions and to allow greater historical and cross-cultural trends to be examined. Such studies can greatly assist in answering questions regarding the universality of various behaviors. Furthermore, the use of this data can also paint pictures of various environmental settings. Cataloging local environments is a difficult task at the individual level and includes many different levels of objective and subjective perception (Nicotera 2007). Census data can at least provide some guidance on various environmental facets worthy of greater exploration. Furthermore, fruitfully combining public records with individually gathered data may also help establish the validity of many evolutionary theories while avoiding the pitfalls of the atomistic and ecological fallacies (Copping and Campbell 2015). While pertinent examples have been discussed here regarding the previous use of census data, much more can still be achieved if study designs incorporate this important source of information.

Cross-References

- Public Records
- Surveys and Questionnaires

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Cephalopod Tool Use

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Synonyms

Item manipulation

Definition

The tool must not be part of an animal itself, must be not attached to the environment, and must be manipulated by the animal to achieve some beneficial outcome (Beck 1980).

Introduction

Beck's (1980) definition of tool use can be applied to the cephalopod mollusks. It has been found in

two of the three major classes, the octopuses and cuttlefish, though not so far in the squid. Even with the limited examples that we have, tool use by this group touches on the major questions and controversies in the area. This account will evaluate the ecological and phylogenetic constraints on cephalopod tool use, where actions fit at the boundaries of the category as defined and the extent to which their use of tools is linked to cephalopods' cognitive capacity.

Why Tool Use?

Why would cephalopods use tools, given their tremendous manipulative capacity and flexibility? With their boneless muscular hydrostat movement system (Mather and Alupay 2016), eight flexible arms, and two extensible tentacles in cuttlefish and squid, the cephalopods have a tremendous ability to manipulate and move items. Their arms are lined with suckers for adhesion, and squid tentacles often have hooks to assure that fish prey is firmly held when captured. Octopuses have hundreds of suckers, and they can be folded together to make a pincer grasp that allows the animals to even untie knots in surgical silk. For instance, faced with a tightly closed bivalve shell, an octopus can perform actions that other species might use tools to assist them with. They pull the valves apart with the strong arms, drill a hole with the salivary papilla or chip the edge with a parrotlike beak, and inject a poison to weaken the adductor muscles (Anderson and Mather 2007). After pulling the valves apart, they remove flesh with a radular ribbon of teeth, having no need for tools through this sequence of actions.

One of the reasons that cephalopods might use tools even though they have such an ability to manipulate items is the medium in which they live. Mann and Patterson (2013) point out that the aquatic medium constrains and channels the use of tools by marine animals. While the oceans are immense three-dimensional ecosystems, items available as tools are likely only found on the sea bottom, in the benthic habitat. This probably accounts for the fact that squid, which generally are not near the sea bottom, have not been found

to use tools. However, there is a clear observational bias based on where researchers have been able to look. We know little about the normal behavior of a group of animals that often live hundreds of meters below the water surface and thousands of meters out into the ocean. As well, the high density of water means that actions are slowed; you cannot hammer under water. Yet this same density means that water itself can be used as a tool, and octopuses and cuttlefish, as well as fish, do so. And since sand or mud makes up much of the ocean floor, perhaps water is the best tool to move these small particles around.

Water as a Tool

Much of the known cephalopod manipulation uses water as a tool, and this is linked to the animals' anatomy. One of the basic characteristics of mollusks is the presence of a mantle cavity, somewhat analogous to mammalian lungs. Most mollusks use the mantle to secrete a rigid protective shell and then use the water-filled cavity within it for respiration, sometimes also for feeding. Coleoid cephalopods (all but nautilus) have lost the shell so the mantle expands and contracts, and in addition they have evolved a flexible funnel for exhalation. Water output can therefore be directed, and the water circulation is modified for uses other than respiration. The exhalation jet is commonly used for locomotion (Alexander 2003), especially for escape in squid, but also for other actions on the environment. Such use allows us to evaluate the specificity of Beck's (1980) definition, as well as the cognitive capacity used in tool manipulation. How does water use fit his definition?

Sepioids (cuttlefish and allies) are blimp-shaped animals that shelter in the sand or mud during the daytime. They bury by sending jets of water underneath their body and displacing the substrate and then placing more of it on top of their body. von Boletzky and von Boletzky (1970) first evaluated the actions of several species from this group and suggested that the digging procedures were a species-specific fixed action pattern. This is partly true. For instance, the cuttlefish

Sepia officinalis settles onto a sand bottom, blows jets of water out under its body, usually in a forward-back-forward-back-back patterns, and then sends a sideways shiver through its dorsal mantle to disperse the sand that has landed on it (Mather 1986). *Rossia pacifica*, a small dumpling squid, blows jets of water forward and back, pauses and then extends a pair of arms forward and laterally, cups some substrate in the distal part, and throws it back over the head and body (Anderson et al. 2004). The arm retraction sequence is fixed, continued even when the cupped arm doesn't manage to capture any sand. The similar *Euprymna scolopes* jets backward first, alternates jet directions, and then similarly sweeps sand or mud over its dorsal surface (Anderson et al. 2002).

Such use of water can be investigated for its link to cognition. Although tool use is not automatically associated with cognitive complexity, it is commonly expected to be (St Amant and Horton 2008; Hansell and Ruxton 2008). Cephalopods are known for their behavioral flexibility (Mather 1995); are these digging sequences, as Mather (1986) first thought, an exception? In fact, although sand digging has a clear sequence of acts, the sequence is internally flexible. The unit size of marine substrates varies, from tiny mud particles to visibly separate gravel pieces. Placed on gravel that cannot be dug into, *Sepia* uses its skin pattern camouflage (Hanlon and Messenger 1988) to resemble the background. If it is put on a gravel substrate, *Rossia* attempts to dig by blowing water jets, and when that does not succeed, it reaches under the body and curls the arm tips around gravel grains, pulling them out from under and throwing them forward until the animal rests in a depression and there are two gravel piles at about 45° from its anterior (Anderson et al. 2004). Then it picks up individual grains and places them on top of its dorsal surface. This behavioral flexibility allows the animal to use different actions to accomplish the same purpose, but by Beck's (1980) definition, the action had changed category from tool use (using water) to not tool use (using the arms). This also clearly illustrates how arbitrary the boundaries of defined tool use is. Hansell and Ruxton (2008) point out

that Beck (1980) was aware of how arbitrary these boundaries could be, and they argue for a clearer understanding of the continuum between tool use and similar non-tool construction behavior, especially nest making.

A similar flexibility is embedded in the sequence of actions in *Sepia* burying, as both duration of digging and number of blowing actions were affected by substrate type (Mather 1986). When sand depth was too shallow for full coverage, animals dug for longer, and transition between acts in the internal sequence of water jets was more predictable for medium and fine sand than for gravel and too-shallow sand. Clearly jet-assisted digging is a species-typical spatiotemporal pattern of movements (sensu Barlow 1968), yet it is also affected by feedback cues. *Rossia* pauses for over a minute after blowing water jets, presumably for assessment, before moving to the subsequent action of throwing sand over the dorsal surface (Anderson et al. 2004).

The better-known octopus has considerable tool use. The mantle-funnel complex is a fundamental structural unit of the octopus body (Mather and Alupay 2016) and moves water for many purposes, only some of which would qualify water as a tool. Water enters and passes along the gills for respiration. The anus and renal papilla are near the base of the funnel, so feces and urine are expelled out of it; similarly, the male “penis” passes spermatophore sperm packages to the groove in the specialized third right arm, which conveys them to the female. Ink from the ink sac passes out the funnel and is used as a visual barrier against potential predators and also a chemotactile repellent of fish (Wood et al. 2010). Since ink is an internal product, this is not tool use, even though ink is manipulated externally. But when jets of water are used to repel scavenging fish (Mather 1992), water jets join the category of tools. Fish are not the only target, as such jets may be aimed at conspecifics and even researchers attempting to evaluate home characteristics and midden heaps (Mather 1994). They may even be aimed at those in the air outside a laboratory tank that “annoy” the octopus (see Dews 1959, for a published example, but this is well known among octopus researchers). Similar water jets are used by archer

fish to knock insect prey off low-hanging branches (Schuster et al. 2004).

Octopus Tool Use for Shelter Formation

A soft-bodied animal without camouflage or repellent properties must find shelter to rest. Octopuses have a wide variety of actions to find and modify such shelter, some of which qualify as tool use. Given a choice, an octopus has clear specifications of characteristics for a shelter – somewhat larger volume than its own, small entry area, and only one entrance (Mather 1982). But in the natural environment, there are few such “perfect” homes. Thus, *Octopus vulgaris* enters a less-than-perfect space and modifies it with several actions, some of which are tool use. The octopus pushes out gravel and small rocks – not tool use. It blows out sand with water jets – tool use – and pulls off dangling algae fronds – again not tool use. Faced with an entrance that is larger than the area needed for its malleable body to pass through, an octopus brings small rocks to block the entrance, sometimes described as a wall, with a significant correlation between the area of entry and the number of small rocks gathered and placed in front of it (Mather 1994). This is also tool use, though see the problem that nest construction (Hansell and Ruxton 2008) may not be included in the category because of the “action on” specification. The variety of behaviors for the same purpose that differ in their inclusion in the tool use category reinforces the authors’ assertion that such behaviors are on a continuum of manipulation.

One clear example of octopus tool use to manipulate shelter is Finn et al.’s (2009) observation of coconut-carrying octopuses. *Amphioctopus marginatus* moving out across soft-sediment substrates often carried two halves of a discarded coconut shell with them. At some point, the octopus stops, rotates the halves of the shell back to their original orientation, and pulls them together to use as a shelter. Not only is this tool use, it suggests the foresight that must be true for all shelter “construction” (Hansell and Ruxton 2008). When the coconut shell was collected, it was not presently useful,

and it was only minutes or hours later that the octopuses choose to manipulate and reassemble into the appropriate structure. It also shows that cephalopods combine intelligence and manipulative capacity in ways that researchers can use to explore and perhaps reevaluate the boundaries of any tool use definition.

Conclusion

Tool use is present in at least two of the major classes of cephalopods, but the observed actions are the result of scattered and opportunistic evaluation of the capacity of these marine animals in the field. Given their manipulative capacity and behavioral flexibility, we can expect that many more examples will be found in cephalopods as our opportunities expand, and they will help broaden our understanding of the animal use of tools.

Cross-References

- ▶ [Meta-Tool](#)
- ▶ [Nonhuman Tool Use](#)
- ▶ [Primate Tool Use](#)
- ▶ [Sequential Tool Use](#)
- ▶ [Tool Manufacturing](#)
- ▶ [Tool Play](#)

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Cerebellum, The

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Synonyms

Cerebrum; Littlebrain; Parencephalis

Definition

The cerebellum constitutes a principal anatomical structure of the brain that is in the back part of the brainstem. The cerebellum is accountable for various operations related to the regulation of the functional qualities of motor activities including motor-coordination, motor-balance, and body posture.

Introduction

Cerebellum constitutes a principal structural section of the metencephalon that accommodates numerous ascended as well as descended major passages and a section of the reticular configuration. The cerebellum represents a big, intricate structural section of the brain stems dorsal surface and it is a significant sensorimotor structure. In human beings, the cerebellum exerts very significant operational functions related to motor control and it is also associated with various cognitional operations including attention and language and the regulation of fearful and pleasurable reactions. Yet, its functional qualities related motor control and dynamics are the most firmly recognized and generally accepted. Moreover, the cerebellum in humans is involved mostly in motor-coordination, motor-precision, and exact-timing and does not initiate movement. Furthermore, cerebellum receives information from sensorial structures of the spinal cord as well as from other structural sections of the brain and joins in this information to precisely regulate motor activities. For instance,

it has been consistently cited that impairment of the cerebellum significantly reduces the capacity to accurately coordinate motor activities and to adjust them to varying environmental circumstances.

The operational intricacy of the cerebellum is indicated by its structural design (Pinel and Barnes 2017). For instance, even though it represents just the 10% of the brain's mass, it houses more than half of the brain's neurons (Passingham and Wise 2014). Additionally, the cerebellum obtains inputs through the primary and secondary motor-cortex, inputs related to the descended motor-signals by the brain-stem motor centers, and information through the motor-activities by the somatosensory and vestibular structural mechanisms (Glickstein and Doron 2008). The cerebellum is considered to evaluate these three structural centers of information so that to coordinate constant motor-activities which had deviated from their planned reaction (Wickens 2011). Through the performance of this sequential operation, it is considered to exert a principal role in the functional process of motor-learning, mainly in the learning of the order of motor-activities in which precise coordination is a vital component in the execution of a favorable outcome (Pinel and Barnes 2017).

The consequential outcome of a diffused impairment on the cerebellum when it comes to the execution of functional and well-coordinated motor-activities is significantly overwhelming (Houk and Wise 1995). Specifically, people who experience cerebellum damage lose the capacity to coordinate in a precise way the course, strength, speed, and range of motor-activities as well as the capacity to adjust fixed designs of motor-output to varying circumstances (Mariën and Beaton 2014). Additionally, it is significantly hard to preserve stable stances, and efforts to do so often result in tremor (Allen and Courchesne 1998). There are also severe impairments in motor-equilibrium such as the way an individual move, talks, and coordinates eye-movement. Furthermore, following cerebellum damage, learning of new patterns of motor-activity is extremely hard (Pinel and Barnes 2017).

Conclusion

The last few decades, research findings based on functional brain images related to the activity in the cerebellum of clinical and nonclinical populations have consistently indicated that the functional qualities of cerebellum involve both the learning and adjustments of cognitional reactions and learning and adjustments of motor-activities in the continually changing environmental conditions so that to achieve the desired performance that facilitates adaption within a person's environment (Pinel and Barnes 2017).

Cross-References

- ▶ Phantom Limbs
- ▶ Primary and Secondary Auditory Cortex
- ▶ Proprioception

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Cerebral Cortex

- ▶ Cortical Neurons and Conducting Velocity

Cerebrum

- ▶ Cerebellum, The
- ▶ Cortical Neurons and Conducting Velocity

Ceremonial Interments

- ▶ Burials

Ceremonies

- ▶ Rituals

Cesarean Section

- ▶ Birthing Complications

Chain of Command

- ▶ Hierarchical Climbing

Change in Male Hunting Returns

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Synonyms

Production

Definition

Variation in the amount of game produced or efficiency in hunting by men.

Introduction

Research on changes in male hunting among hunter-gatherers addresses two important issues in early human evolution: the nature of the family and trade-offs in mating and parenting effort as well as the development of embodied capital. In the hunter-gatherer literature, there is a debate about the function of male hunting that has implications for understanding the role males play in the evolution of the pair bond. The traditional model argues that male hunting and other economic activities are forms of male provisioning or parenting effort designed to enhance a man's fitness through his wife's reproduction and the survivorship of their common children. Thus, it is a component of the traditional division of labor and a foundation for marriage and family. The costly signaling hypothesis (or, "show off") is an alternative to the provisioning model. It is proposed by Hawkes and colleagues who argue that men often seek large and difficult-to-acquire game animals that they widely distribute to camp members. As such, it represents mating effort by demonstrating a hunter's phenotypic quality as a potential mate and/or ally. A number of studies have been published to test the provisioning and signaling hypotheses by examining changes in male hunting returns.

Tests of Variation in Male Hunting Production

The provisioning hypothesis is relatively easy to test, but this is untrue for the costly signaling hypothesis (Hawkes et al. 1997). The provisioning model makes at least three predictions: (1) if a woman's productivity declines as a consequence of her pregnancy or lactation and the associated burden of caretaking an infant, her husband's productivity should increase to compensate for her lowered productivity; (2) the amount of time a man spends hunting or in overall food production should increase with the number of his dependent children; and (3) where males commonly share portions of their hunts, the greatest share of a hunter's catch should go to his own family.

The first prediction of the provisioning hypotheses was tested by Frank Marlowe (2003) on the hunting and gathering Hadza. He showed that men with wives who had nurslings increased their labor effort and food production in response to the lower productivity of their wives. He critically notes that these husbands switched to food resources such as honey which are not widely shared to better provide for their families. Among Ache and Hiwi hunter-gatherers (Hurtado et al. 1992) research shows daily food acquisition of a woman's spouse is negatively related to female foraging effort among the Hiwi, and it is negatively related to foraging time and daily food acquisition among the Ache. Finally, in another Hadza study (Wood and Marlowe 2013, p. 280) male productivity was shown to be associated with marital status such that "On average, single men brought food to camp on 28 % of days, married men without children at home on 31 % of days, and married men with children at home on 42 % of days." Furthermore, the total caloric value of food resources brought back to camp by these three classes of men showed the same statistically significant pattern (Wood and Marlowe 2013, p. 307) of increased production for men with children.

The second hypothesis regarding changes in men's food production was tested a bit indirectly among the Hadza. Marlowe (1999) compared the foraging efforts of men married to women who had their biological children compared to women who had the men's stepchildren. Men with biological children produced more food than men with stepchildren.

The third hypothesis on food sharing has been thoroughly investigated by Wood and Marlowe (2013) for the Hadza. Like many hunter-gatherers and other egalitarian people, food, especially game, is widely shared among coresidents. A prediction of the signaling hypothesis is that males who distribute their resources to other families disadvantage their own families. Such distributions are argued to represent mating effort through costly signaling. Detailed research by Wood and Marlowe (2013, p. 297) show this may not be the case. Their data show that successful hunters retain 42 % of all the game they take,

or 3.8 times the amount that other families receive from their kills. Similar patterns emerged when men shared small game or nongame food such as honey. While it is clear that sharing outside the family leads to increased stature for successful hunters and provides some evidence for the signaling model, alternative explanations for sharing as a form of food security through risk reduction is widely documented among foraging societies and horticultural groups where hunting is important. Finally, this is not to say that productive hunters who share widely are not more martially and reproductively successful: they clearly are (Smith 2004). However, evidence also indicates that the families of good hunters receive social and economic benefits not afforded to poor hunters for the Ache (Hill and Hurtado 1996) and in other societies where male hunting is important.

Crucial tests of the signaling hypothesis have not been forthcoming. Returning to the well-documented association between hunting ability and reproductive success among a sample of foragers (Smith 2004), it is clear that young and unmarried hunters demonstrate their abilities as good hunters by advertising their hunting successes and by sharing widely. There is evidence that such males marry early to young and fecund females. But after marriage, most of the evidence to date indicates that high hunting productivity leads to further investment in wife and offspring, is responsive to family needs, leads to the better treatment of one's family by coresidents, and it is sometimes associated with the acquisition of another wife or extra-pair copulations (Wood and Marlowe 2014).

Finally, there are also age-related changes in male hunting independent of family demand and are based on the long-term development of skills necessary to become a good hunter. For example, "...among Ache foragers of Paraguay, men's strength peaks at around 25 years of age but both meat acquired and hunting return rates (amount acquired per hour spent hunting) peak between 40 and 50 years of age" (Kaplan et al. 2010). Research by Walker et al. (2002, pp. 1–2) on seven hunting and gathering and foraging horticultural societies shows that peak hunting

efficiency is not achieved until the late 30s to early 40s in most groups and remains relatively stable for about 15 years before declining. While rates of return measure skill and potential productivity, actual productivity (daily calories produced) is more important as an effective measure of family provisioning. To this end, research by Hill and Hurtado (2009, p. 3866, Fig. 2) show that total foraging productivity (largely but not exclusively hunting) peaks between the age of 45 and 50 for the hunting and gathering Ache and Hiwi.

Conclusion

Empirical research shows increases in male hunting are most reliably associated with increased familial requirements as the number and needs of dependent children increases and the productivity of a wife decreases as a consequence of pregnancy, lactation, and childcare. Changes in male hunting are most consistently viewed as paternal effort.

Cross-References

- Costly Signaling
- Division of Labor
- Food Sharing
- Mating Effort
- Parental Investment

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Change in Ovulatory Cycle

► Cycle Variation

Changes in Adaptation Expression

► Evolution of Adaptations

Changes in Self-Esteem Motivate Behavioral Changes

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Synonyms

Appraisals; construals; Behavioral changes; overt responses; Changes in self-esteem; social pain; Interpretations; Negative affect

Definition

Fluctuations in perceived relational value may be due to ostracism, rejection, or exclusion (Leary and Guadagno 2011). These changes in self-esteem are thought to be followed by cognitive interpretations of the exclusionary situation (e.g., Smart Richman and Leary 2009; Williams 2009). Such appraisals likely influence subsequent behavioral changes, including variations in pro-social or antisocial behavior.

Introduction

Sociometer theory proposes that state, or current, self-esteem changes according to a person's perceived relational value (Leary and Guadagno 2011). Self-esteem thus typically decreases following social exclusion and increases after an episode of inclusion. Furthermore, it is widely believed that appraisals and attributions, or cognitive interpretations, of situations responsible for fluctuations in self-esteem determine subsequent behaviors (e.g., prosocial or antisocial responses; Smart Richman and Leary 2009; Williams 2009). This article reviews the observed link between self-esteem, in its function as a sociometer, and behavior.

Emotional Alarm

The decreased self-esteem posited by sociometer theory is one component of people's emotional response to exclusion, with the others being social pain and general negative affect (Smart Richman and Leary 2009; Williams 2009). However, the neuroscience literature now suggests that there is a common, unifying mechanism that underlies these experiences – the affective component of the pain response, mediated by the dorsal anterior cingulate (Eisenberger et al. 2011). Activation in this region is perhaps best described as an emotional alarm (McDonald and Leary 2005; Shilling and Brown 2016). Much as physical pain is a signal that tissue damage is occurring and that a behavioral change is necessary, social pain and

decreased self-esteem signal that one's inclusionary status is threatened and that behavioral modifications are required.

Cognitive Appraisal

Cognitive appraisals are crucial in determining exactly what that response is, however. At a basic level, neuroscientists propose that consciousness is composed of constantly changing patterns of activated neural modules, and that the activity of these systems is interpreted and spun into a narrative by the language centers of the left hemisphere (e.g., Roser and Gazzaniga 2004). These narrative creations permit individual or situational factors to shape conscious experiences. When it comes to social exclusion, even though the source of one's emotions may be obvious, people can still differ in how they explain or appraise the precipitating event, which has important consequences for their subsequent behavior (Smart Richman and Leary 2009; Williams 2009). At a conscious or nonconscious level, the individual evaluates his or her situation: *Can I connect with others after the ostracism? Can I repair my relationship following a rejection? Is the ostracism controllable?* These appraisals, in turn, determine how the individual responds to the event (Smart Richman and Leary 2009; Williams 2009).

Williams (2009) provides a good deal of evidence suggesting that a lack of perceived control is a major factor in aggressive responses to ostracism, whereas a perceived lack of belonging determines prosocial behavior. Likewise, in their review of the literature, Smart Richman and Leary (2009) emphasize expectations of relational repair as an important predictor of antisocial and prosocial behavior, among many other factors. Williams and Wesselmann (2011) recently synthesized the various appraisals as primarily involving the question of whether or not reconnection is likely in the situation. When the others around a target of social exclusion are seen as strangers, brief acquaintances, rejectors, antagonists, or people who may act in an erratic, unpredictable

fashion, aggression is likely; however, when reconnection is perceived as a possibility, prosocial behavior is likely.

Resource Redistribution

Shilling and Brown (2016) further suggest that it may be instructive to consider appraisals of evolutionarily adaptive needs, such as self-preservation, status, and belonging, as determinants of behavioral tendencies following social exclusion. They propose that appraisals of exclusion determine which goals are prioritized, initiating trade-offs in shared, limited-capacity mental resources in service of the person's most urgent goals. When the appraisal of the situation prioritizes belonging, resources are allocated towards behaviors and processes that aid in social reconnection and away from less-relevant processes. However, when self-preservation or status restoration is prioritized (e.g., when one is interacting with a rejector, Buckley et al. 2004, or when one perceives a decrease in status, Schoel et al. 2014), resources are instead shifted towards more aggressive or self-promoting behaviors in service of protecting the self or regaining one's social standing. Shilling and Brown's idea of resource redistribution thus makes inroads to a more comprehensive understanding of the cognitive and neural mechanisms of responses to exclusion.

Conclusion

When others do not pay a person attention or even explicitly tell that person that he or she is not valued as a relational partner, the person is, quite understandably, hurt. This social pain and decreased self-esteem is adaptive as an emotional alarm, and it is followed by a similarly adaptive appraisal. How the individual construes the episode of exclusion (or rejection or ostracism) results in a reprioritization of goals, followed by subsequent resource redistribution in support of those goals. Indeed, advances in neuroscience and social psychology have

revealed much about the link between self-esteem as a sociometer and specific adaptive behaviors.

Cross-References

- ▶ Adaptations to Avoid Ostracism
- ▶ Prosocial Behavior
- ▶ Self-Esteem Reflects Assessments of Valuation
- ▶ Tactics to Solve Adaptive Problems of Sperm Competition

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Changes in Self-Esteem: Social Pain

- ▶ Changes in Self-Esteem Motivate Behavioral Changes

Character

- ▶ Emotional Disposition

Characteristic

- ▶ Genetic Predispositions

Characteristics of Human Language

- ▶ Design Features of Language

Characteristics that Help One Stays Alive

- ▶ Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches

Charitable Giving (Peter Singer)

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Synonyms

Author; Donations; Morality; Philosopher

Definition

According to Peter Singer, people in affluent societies have a strong moral obligation to donate much, if not most, of their resources to charitable organizations that prevent death and suffering.

Introduction

Most of us believe that morality requires that we give, at best, a modest amount to charity. Giving beyond this requirement may be morally admirable but is not morally obligatory. In an influential early paper (Singer 1972), and numerous subsequent publications (Singer 1999, 2009, 2011), the Australian philosopher Peter Singer has challenged this widespread view. According to Singer, people in affluent societies – including academics reading these lines – have a strong moral obligation to donate much, if not most, of their resources to charitable organizations that prevent death and suffering.

To support his conclusion, Singer appeals to two separate arguments: an argument involving an analogy between particular cases (the argument from analogy) and an argument from general philosophical principles (the basic argument).

The Argument from Analogy

The argument from analogy, sketched in Singer's original paper and developed more recently by Singer and others (Unger 1996), invites us to consider our intuitive responses to the following scenario:

The Pond. As you walk past a shallow pond, you see a child drowning in it. If you wade in, your expensive suit will be ruined. If you don't, the child will die. Should you wade in?

Nearly everyone agrees that you are morally required to wade in. But consider, next, a different scenario:

The Letter. You receive a letter from a charitable organization. The letter asks you to donate an

amount sufficient to prevent a child from dying. This amount is equivalent to the cost of an expensive suit. Should you donate?

Here most people believe that you aren't morally required to donate.

According to the argument from analogy, these different responses are unjustified. If we believe that we should wade in and save the child in the Pond, even at the expense of ruining an expensive suit, we should also believe that we should make the donation and save the child in the Letter, at a comparable cost.

Critics of Singer have resisted the challenge by attempting to identify a relevant disanalogy between the two cases (Ashford 2011). Thus, some critics have pointed out that the child in the Pond is a member of our community, while the child in the Letter case isn't. Morality requires that we assist our compatriots, but it doesn't issue a similar requirement to help foreigners. One could imagine, however, a variant of the Pond in which the child drowning isn't a member of our community, and it seems that most people would still judge that morality requires that you rescue her.

Other critics have pointed out that only you can save the child in the Pond, whereas many others could in principle save the child in the Letter. But again, the details of the Pond may be slightly altered, to yield a variant where there are other individuals in a position to wade in. Supposing that these bystanders decide not to intervene, most people would agree that, just like in the original case, you are morally required to save the child.

Finally, critics have pointed out that, unlike the Pond, where we know that the child will be saved if we take action, the Letter involves considerable uncertainty surrounding the effects of our actions. It seems reasonable to be skeptical, given the lack of relevant information about the charity and the complex causal chain involved. Still, here, too, one can tweak the details and stipulate that the charity has an impeccable track record of effectiveness so that we can realistically expect our donation to have its intended effect. (As will be seen in the next section, such a stipulation is not unrealistic.) Yet even after these adjustments, most people persist in thinking that you are morally required to donate in one case but not in the other.

More generally, for any alleged disanalogy claimed to justify our different moral attitudes toward the two cases, Singer's strategy is to alter the details of one of the cases in such a way that this new pair of cases (1) no longer exhibits the disanalogy and yet (2) continues to elicit the same moral attitudes as the original pair.

The Basic Argument

Singer's basic argument consists of three premises:

First premise: We are morally required to prevent something very bad from happening if we can do so without thereby sacrificing anything of comparable moral importance.

Second premise: Death and suffering are very bad.

Third premise: We can prevent death and suffering without sacrificing anything of comparable moral importance.

From these three premises, Singer draws the conclusion that we are morally required to give much, if not most, of our money to charitable organizations that prevent death and suffering.

The second premise is uncontroversial, at least with respect to pain: even philosophers, who disagree with each other on just about everything, agree that (unwanted, undeserved) pain is intrinsically bad. The third premise may have been somewhat controversial back when Singer first presented his argument. At the time, it was hard to know what an individual could accomplish by donating a given amount of money to a charitable organization. This is no longer the case, however. GiveWell, a highly respected charity evaluator, estimates that a donation of about \$3000 to the Against Malaria Foundation will, in expectation, prevent a child from dying of malaria (GiveWell 2015). For people in affluent societies, giving \$3000 doesn't involve a sacrifice of comparable moral importance to saving a child's life.

Consider, finally, the first premise. It, too, seems relatively uncontroversial. It only requires us to prevent what is bad rather than to promote what is good, and subjects this requirement to the

proviso that the agent shouldn't be asked to sacrifice something of comparable moral importance. Furthermore, the premise could be significantly weakened, to require us to prevent something *very* bad from happening if we can do so without thereby sacrificing *anything* morally significant (Singer 1972, p. 231). Such a weakened principle would be even less controversial but would still issue very demanding requirements.

When considered in isolation, each of the premises thus appears plausible. Yet they jointly imply a conclusion that contradicts what most of us believe. In fact, Singer thinks that this conclusion is so radical that "the whole way we look at moral issues [...] needs to be altered, and with it, the way of life that has come to be taken for granted in our society" (Singer 1972, p. 230).

In response, some philosophers have argued that morality cannot demand so much from us and that therefore Singer's conclusion must be mistaken. As David Lewis remarked in discussing a variant of Singer's original argument, "even if we cannot diagnose the flaw, it is more credible that the argument has a flaw we cannot diagnose than that its most extreme conclusion is true" (Lewis 2000, p. 155). This response, however, assumes that we are justified in believing that morality is not as demanding as Singer's conclusion implies. Other philosophers have disputed this assumption (Sobel 2007).

Explaining Our Responses

As we have seen, Singer argues that our different responses to the Pond and the Letter are unjustified. A separate question concerns the explanation of these responses, to which we now turn.

Considerable progress has been made in the study of moral judgment and decision-making in recent years (Bartels et al. 2015). Perhaps the most influential account in the literature is Joshua Greene's dual-process theory of moral judgment (Greene 2014a). On this theory, the same contrast between implicit unconscious processes (System 1) and explicit conscious processes (System 2) that explains our thinking in most domains (Kahneman 2011) also explains our moral

thinking. Situations involving “up-close-and-personal” interaction, of the sort our ancestors in the environment of evolutionary adaptedness would have encountered on a regular basis, trigger rapid, unconscious responses. By contrast, situations involving distant, impersonal interaction trigger slow, conscious responses. Greene’s dual-process theory could thus explain people’s responses to the Pond and the Letter as resulting from the operation of these two cognitive subsystems.

This scientific explanation may have philosophical implications. So-called debunking explanations seek to undermine the justification of a belief by tracing back its causal origins to an unreliable process of belief formation (Kahane 2011). As Greene notes, “science may teach us that some of our judgments are sensitive to features that, upon reflection, do not seem to matter morally” (Greene 2016, p. 176). As an example, consider incest. Once we understand our negative responses to the thought of sexual intercourse between close family members as originating in selective pressures to avoid birth defects, we may cease to believe that incest is inherently morally wrong.

We may similarly be inclined to distrust our belief that there is a fundamental moral difference between the Pond and the Letter. If Greene’s account is correct, these two situations trigger different responses as a result of a historical accident. We feel that there is a strong moral obligation to save the child in one scenario, but not in the other, because in the environment of evolutionary adaptedness it was possible to help others in personal ways, like wading into ponds, but not in impersonal ways, like donating money. Singer himself favors this sort of debunking explanation. He writes: “What is the moral salience of the fact that I have killed [or saved] someone in a way that was possible a million years ago, rather than in a way that became possible only two hundred years ago? I would answer: none” (Singer 2005, p. 348).

One response to this argument is to challenge the scientific premise on which it rests. Although Greene’s dual-process theory is supported by an impressive body of evidence (Greene 2014b, pp. 700–708), it has attracted some criticism (Nagel and Waldmann 2013). Another response is to question the conclusion drawn from that

premise: even if one grants that this account is correct, and agrees that people’s moral responses are sensitive to irrelevant factors, it doesn’t follow that the conflict between these responses should be resolved in a way that favors Singer’s argument. Instead of concluding that we should save the child in both cases, one could conclude that we should save the child in neither case. To adjudicate between these two possibilities, a more sophisticated debunking argument would be required.

Conclusion

Singer’s arguments for the conclusion that people in affluent societies – including academics reading these lines – have a strong moral obligation to donate much, if not most, of their resources to charitable organizations that prevent death and suffering pose a serious challenge to some of our deeply held moral convictions. Recent developments in the neuroscience and evolutionary psychology of morality have further increased the theoretical appeal of those arguments, both to psychologists interested in explaining our moral beliefs and to philosophers interested in vindicating or undermining their justification.

Cross-References

- ▶ Evolved Moral Foundations
- ▶ Moral Concerns
- ▶ Moral Instincts
- ▶ Morality Is Cooperation

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Charity

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Synonyms

Aid; Alms; Contributions; Donations; Gifts; Offerings

Definition (Merriam-Webster)

Generosity and helpfulness especially toward the needy or suffering; aid given to those in need; an institution engaged in relief of the poor; public provision for the relief of the needy.

Introduction

Much research examines why individuals might give to charity. The outputs that charitable organizations create are generally considered public goods; that is, the benefits accrue to society as a whole. A potential donor values the output generated by charitable organizations, but this individual would have the greatest material benefit if others funded the charity. As such, the potential donor has an incentive to not contribute to a charity she values (i.e., the donor has an incentive to free-ride). Samuelson (1954) demonstrates because of this incentive, decentralized markets do not efficiently produce public goods. The strongest version of this hypothesis states that the vast majority of people will not contribute, leaving only the wealthiest individuals to provide all of the funding. Because this implication is easily falsifiable (Andreoni 1988), much research has been devoted to understanding the motivations for charitable giving as well as factors, such as choice architecture, that may affect the amount and likelihood of giving to charity.

Motives for Giving to Charity

Two major motivations for contributing to charity have been identified. The first is a concern for the output of charitable organizations. This motivation is referred to as “pure altruism.” A pure altruist cares only for the total amount of the public good, not how it is funded. An altruistic donor would have the greatest material benefit by free riding and letting others fully fund charity. (Inequality aversion (Fehr and Schmidt 1999; Bolton and Ockenfels 2000) is often identified as a separate motivation. Concern for those with a lower income can be a type of pure altruism, so we do not discuss inequality aversion in detail here.

Furthermore, much empirical evidence for inequality aversion is based on behavior in ultimatum games, dictator allocation tasks, and market competition games. These games match participants with other participants (Chowdhury and Jeon 2014 for example) as opposed to charities (Eckel and Grossman 1996 as discussed below.) The second motivation is the psychic benefit the donor experiences resulting from giving to charity, as opposed to personally benefiting from the production of a charity. This motivation is commonly referred to as “warm glow” or pure egoism (Andreoni 1989, 1990). Concerned only for the private psychic benefits he receives from his gift, a warm glow giver is, therefore, less inclined to free ride on the giving of others. Pure altruism and warm glow are not mutually exclusive motivations. A combination of a concern for the recipient and joy of giving is referred to as “impure altruism.”

Ribar and Wilhelm (2002) suggest that the free riding problem may be a function of the size of donor groups. That is, free riding by pure altruists may be incomplete in small groups of donors but becomes more severe and possibly complete as the number of donors grows. Observed charitable giving in small groups may be motivated by impure altruism; in very large groups it may be motivated solely by warm glow.

Evidence for Motives

List and Samak (2013) study the charitable motivations of children between three and five years old. Children were given five marshmallows and were paired in a dictator allocation task with either another child or a teddy bear. The children were told that teddy bears do not like marshmallows, but do enjoy eating cotton balls. In some treatments, marshmallows passed to the recipient were placed in a “magic box” that could turn marshmallows into cotton balls regardless of the recipient being a child or teddy bear. The design allows the researchers to determine if young children give to improve the well-being of the recipient (pure altruism) or give for the sake of giving (warm glow). Children are shown to be altruistic, as average giving is 25% of the endowment. Yet,

children rarely give marshmallows to teddy bears or cotton balls to other children, which suggests that the primary motive for giving at this age is pure altruism. The authors argue that preferences for warm glow are acquired later in life.

Because experimental studies typically involve giving to an established charity or other individuals (occasionally, but not always individuals in need), it is difficult to separate pure altruism from warm glow. Any amount passed to increase the well-being of others could create a warm glow effect. The warm glow motivation is isolated in experiments by Crumpler and Grossman (2008), Luccasen and Grossman (2017), and Gangadharan et al. (2017). In these experiments, a charity (or individual served by a charity) receives an endowment from the experimenter. A participant can pass from her own endowment to a charity, but any amount passed is known to reduce the experimenter’s contribution by an equal amount. Participants cannot therefore increase the amount received by the charity, but giving to charity in this context could create an impression that part of the charity’s fixed donation came from the participant. In these studies, approximately 40–60% of participants pass money to charity, giving 15–20% of their individual endowments.

Preferences for giving to charity are likely to depend on the characteristics of the charity. Vesterlund (2015) describes motives for giving to charity as analogous to demand functions. An understanding of the demand for one good does not generalize to the demand for all goods. Pure altruism may be the primary motivation for a donor to give to public radio, but warm glow may motivate the same individual to give to charity in the immediate aftermath of a natural disaster.

Ottoni-Wilhelm et al. (2014) identify motives by examining the responsiveness of individual donations to charity to changes in the donations of others, operationalized in their experiment by exogenously changing the amount donated by a foundation. Participants were given the opportunity to donate to an individual child who was not harmed but lost his or her house in a fire. Participants were told a foundation would also contribute to the same specific child the participant was

matched with, and the foundation contribution ranged from \$4USD to \$34. The sensitivity of donations to the foundation's contribution depends on the level of the foundation's contribution. The authors report 44% of participants are motivated by pure altruism, 39% by impure altruism, and 9% by warm glow.

Gangadharan et al. (2017) take a different approach to identifying motives for giving. Their design is a sequence of donation tasks that allows them to observe the subjects' warm glow and/or altruism motivations for giving. In their first (Warm Glow) task, participants donate to their specific recipient, the recipients were served by a private charitable organization, in an environment where the donations are fully crowded out. In the second (Altruism) task, subjects are given a second opportunity to donate (to the same recipient), but with all donations going to the recipient. The authors report that 26% of participants are motivated by pure altruism, 31% by impure altruism, and 15% by warm glow. A further 28% were non-givers.

Social norms or a concern for image may be another motivating factor to contribute to charity. Social norms influence the decision to give to charity and the amount to give to charity. One common social norm is to tithe, which is contributing a fixed percentage of one's income to charity. Rather than receiving a warm glow from giving, some donors have an aversion to declining the opportunity to give, and thus respond to social pressure (DellaVigna et al. 2012). Blood donors in an Italian town respond to symbolic prizes, but only if the prizes are publicly announced (Lacetera and Macis 2010). Izuma et al. (2008) employ fMRI brain imaging to show that positive social rewards activate the same "reward circuitry" in the striatum as monetary rewards. (We do not review the literature on charitable giving for explicitly extrinsic motivations or for signaling (for example, making a large donation to a university to influence an admission decision). Although we do discuss the role of social image, which could be considered a type of extrinsic motivation, for more on the signaling motive, see Blumkin and Sadka (2007).)

Factors Affecting Giving to Charity

Because of these different motivations for giving, policies designed to affect giving will vary in their effectiveness. Perhaps the most direct method to affect giving to charity is to alter the financial incentives. Many governments encourage donations to charity by deducting donations from taxable income, which reduces the price of giving (Andreoni 2001). Behavioral sciences have not only expanded the range of policies studied beyond purely financial incentives, but also have provided additional insight into traditional policy tools. For example, should a government choose a rebate subsidy or a financially equivalent matching subsidy? Eckel and Grossman (2003) show that although these policies are financially equivalent, in practice the matching subsidy significantly increases donations to charity. Benabou and Tirole (2006) argue that donors motivated by warm glow prefer the matching policy over a rebate because receiving a rebate emphasizes the personal gain, thereby reducing the joy of giving to others in need.

Individuals learn norms and appropriate behaviors by cultural assimilation. Bowels and Polania-Reyes (2012) identify mechanisms (not mutually exclusive) through which explicit economic incentives affect ethical norms, altruism, or other social preferences for prosocial behavior. While explicit incentives are often designed to encourage prosocial behavior, incentives can have the opposite effect because an incentive can signal (i) an activity is not pleasant or appreciated, (ii) most people do not engage in the activity without the incentive ("moral disengagement"), and/or (iii) the activity involves a loss of agency and self-determination. As an example, a policy of paying blood donors may reduce donations because the explicit incentive interferes with the ethical norm or social-preference signal (see also Mellstrom and Johannesson 2008). An individual may adhere to a social norm of charitable giving for a variety of reasons, ranging from avoiding social sanctions to a genuine concern for the recipient (pure altruism). To the extent that individuals observe norms to signal group identity, such charitable giving is consistent with the warm-glow motivation.

Religious beliefs could plausibly affect giving to charity, and relationships between religion and charity are a focus of academic research. Eckel and Grossman (2004) find no significant difference in the response of religious and nonreligious individuals to changes in subsidies to charitable giving. However, the religious are more sensitive to changes in income than the nonreligious. Controlling for wealth, income, education, and other family characteristics, Ottoni-Wilhelm (2010) finds no differences in giving among Black Protestant, Evangelical Protestant, Mainline Protestant, Catholic, and nonaffiliated families. Further, Jewish households are more likely to give to charity, and give greater amounts than Christian families. Parrett and Grossman (2011) conduct a field experiment to study religion and tipping at restaurants. Although the context is not a charity per se, the results do address prosocial behavior, a major determinant of charitability. The authors do not observe greater prosocial behavior among those with a religious affiliation.

Empathy or an internalized value of caring for others may be a stronger predictor of charitable giving than religious identity (Ottoni-Wilhelm and Bekkers 2010). Andreoni et al. (2017) report a field experiment involving the Salvation Army that provides insight into the link between empathy and charitable giving. The authors noted that their experiment is not a direct test of any theory of empathy but it is consistent with underlying empathy as a prerequisite to charitable giving. In the experiment, Salvation Army bell-ringers are stationed in front of either one or both entrances of a large retail store. With a solicitor stationed at only one of the two entrances, customers could have avoided solicitation. The authors find a significant increase in charitable giving when a solicitor is stationed at both entrances, and giving increases further if the solicitors verbally ask passing individuals to give. Andreoni, Rao, and Trachtman argue that those who avoid solicitation when possible are not uncharitable people, but rather are “passive givers” with a latent desire to give. To use the authors’ example, just as someone who enjoys cake does not eat cake at every meal, charitable donors also attempt to regulate their temptation to give at every opportunity. Empathy

precedes giving to charity, and the impulse to give can be easily triggered.

Giving to charity is also influenced by image concerns, including what others may think (social image) and one’s own self-image. Reporting both laboratory and field data, Ariely et al. (2009) examine the behavior of individuals raising money for charity. The study manipulates both the visibility of the individual’s fundraising and whether the individual receives financial compensation. In treatments without financial compensation, individuals exert more effort in public than in private. Offering financial incentives did not increase public effort, but did increase private effort. These results show that individuals care about how they are perceived by others. Self-image is also an important motivator. Grossman and Luccasen (2017) conduct a laboratory experiment in which participants can give to charity from their own endowment of \$15, or can take money from a charity’s endowment of \$5. Individuals in some treatments make this decision by distributing cash between two envelopes in private, then deposit the charity’s envelope in a drop-box as they exit the room. In this highly anonymous environment, the authors cannot link a participant to an allocation decision, but can infer from the amount in each envelope if an individual gave to charity or not. In treatments in which participants privately allocate cash between envelopes, nearly 40% of individuals donated money to charity. Moreover, the average donation of these participants resulted in the charity receiving more than half of the total money available. Giving to charity in this double-blind setting, in which participants could have easily taken money, suggests that many people act to maintain a self-image of charitability.

Gender differences in giving have received considerable attention. In the dictator game, with the recipient an anonymous other subject, women are often observed to be more generous but the difference is not always significant (see Croson and Gneezy 2009 for a survey of gender differences in dictator games). However, in real donation experiments (Eckel and Grossman 1996), where giving is to a good cause such as a charitable organization, studies more consistently find

that women donate significantly more than men (see, for example, Carpenter et al. 2008; Crumpler and Grossman 2008; Eckel and Grossman 2003; Eckel et al. 2007; Fong 2007; Li et al. 2011; List 2004).

Donors appreciate agency over the use of funds and the timing of donations. Eckel et al. (2005) study the effect of tax-financed donations. The authors find that a tax and transfer policy reduces voluntary giving if the forced donation is made apparent, but an opaque fiscal policy does not reduce giving. Eckel et al. (2017) conduct a field experiment at a public university in which donors have the option to direct their donations to a specific college. Donations are higher with the option to direct giving, although remarkably few donors use the option. Li et al. (2015) report that the opportunity to direct giving more than doubles both the likelihood of giving and the size of contributions. Andreoni and Serra-Garcia (2016) note that many donors exhibit time inconsistency. Some donors will pledge a future donation but often will not donate immediately, while others display the opposite behavior by donating immediately but would not commit to a pledge of future donations. Donors prefer flexibility regarding the timing of donations, and the authors show that a simple thank-you note can reduce renegeing among those who self-select into pledging future donations.

Conclusion

Charities generally pursue goals that benefit society. As an example, a charity that provides assistance to a low-income household so that the head of the household transitions out of poverty clearly creates benefits to the household. Moreover, such an outcome benefits all individuals who care about poverty and income inequality. Because the societal benefits are greater than the private benefits, individuals may attempt to free ride on the donations of others, resulting in an inefficiently low level of activities provided by the charities. Governments and charities wish to understand donor motives, and what policies increase charitable giving. Although models of charitable behavior have

been developed and the efficacy of many policies has been studied, to date little research examines the general equilibrium effects of any policy. A successful campaign by one charity may increase total giving to charitable organizations, or the increased donations from one organization may come at the expense of another.

Cross-References

- ▶ Altruism
- ▶ Altruism Advertises Generosity
- ▶ Altruism and Costs to Altruist
- ▶ Altruism and Watching Eyes
- ▶ Altruism Defined by Benefits Conferred
- ▶ Altruism Displays Cooperative Potential
- ▶ Altruism Norms
- ▶ Indirect Benefits of Altruism
- ▶ Ingredients of Reciprocal Altruism
- ▶ Nonhuman Reciprocal Altruism
- ▶ Prosocial Behavior
- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reputation and Altruism
- ▶ Theory of Reciprocal Altruism

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Charles Darwin

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Introduction

Charles Darwin (1809–1882) is rightfully known as the father of evolutionary theory. In his *Origin of Species*, published in 1859, he argued not only for the fact of evolution – the natural development of organisms from forms far simpler – but proposed a theory of change. Starting with the ongoing struggle for existence, he argued that some will be winners – they will be naturally selected – and this will lead not only to new kinds of organisms but to adaptation, the design-like features that hitherto had been ascribed to the direct intervention of an all-powerful god. This entry considers all aspects of Darwin's life and work, the predecessors, the influences, and the consequences, both in science and in culture more generally.

The Man and His Life

Charles Robert Darwin was born on February 12, 1809. He was the fourth child (of five) and the second son (of two) of Dr. Robert Darwin, a physician in the town of Shrewsbury, in the British Midlands close to Wales. His paternal grandfather was Dr. Erasmus Darwin, a well-known physician and inventor. His maternal grandfather was Josiah Wedgwood, the founder of the famous pottery works. Because his father was not only successful in his profession but also a very good financier, and because his mother received a very large dowry from her father, young Charles never had to work during his lifetime for his living (Browne 1995, 2002).

One thing we can infer immediately. Although Charles Darwin was a great revolutionary – in fact, one can truly say there are few human beings

who have had quite the effect on our culture that he has had – you should never expect to find him a rebel (Richards and Ruse 2016). He came from a very comfortable, moneyed segment of British society, at a time when Great Britain was the most powerful nation on Earth. He fell very comfortably into the role expected of him, that is to say a respectable, upper-middle-class Englishman. What this means, therefore, is that to understand Charles Darwin and his great achievements, we should never expect to start from scratch. Rather, we should expect to find that he takes the elements of the society around him, draws them into himself and rearranges, and then as it were puts them back on the cultural market. Darwin is going to be a bit like a kaleidoscope. Pieces come from all over, are broken down, and put together again, and we have a whole new picture. Always, when trying to understand Darwin, we should look for the influences around him. There is nothing new in Darwin's work. And yet the work itself was entirely new!

Before Evolution

Charles's father Robert was naturally concerned that his young son would become an idle wastrel. Therefore, when the lad was still in his teens, Robert pushed Charles toward the profession of medicine. However, after 2 years of study in the Scottish capital of Edinburgh, Charles Darwin realized that he simply did not want to become a doctor. Looking for an alternative, and somewhat in despair, Robert next directed Charles in the direction of the church. In order to become a clergyman (of the Church of England), one had to have a degree from a British university. In 1829, therefore, we find Charles Darwin enrolling at Christ's College, Cambridge.

He spent three happy years as an undergraduate. His formal courses were not onerous, and he had much time to pursue the study of biology, an interest that was growing strongly. However, Charles Darwin's first excursions as a full-time scientist came in the area of geology (Herbert 2005). In 1831, he had the offer to go as the captain's companion on board the British warship HMS *Beagle*. The ship, under the command of Captain Robert FitzRoy, was going down to the

Southern Hemisphere in order to map the coastline of South America. FitzRoy was looking for a gentleman who could pay for his own mess bills (that is to say, his food and drink) and who would be somebody outside the line of command with whom he could relax in his spare time. Charles Darwin fit the bill exactly.

Overall, the *Beagle* voyage lasted some 5 years. It went first across to the east coast of South America, starting with Brazil, and then worked its way down to the very bottom to the snowy lands of Tierra del Fuego. It then sailed up the west coast, past Chile eventually swinging out into the Pacific. It made a visit to the group of islands known as the Galapagos Archipelago, now belonging to Ecuador. After that the *Beagle* went southwest to New Zealand and in Australia. It then visited South Africa, made a quick trip back to South America, and finally returned to England in the autumn of 1836.

Charles Darwin very rapidly matured from the role of captain's friend to that of ship's naturalist. He made massive collections of rocks and fossils and animal and bird skins and plants. These were sent back to England for cataloguing and classification. At the same time, Darwin did a fair amount of geology in its own right, as well as studying in some great detail the flora and fauna of the lands that he visited. He proved to be a bad sailor, often being dreadfully seasick. However, most of the time during the *Beagle* voyage, Darwin was not on board the ship. He would get put off at a port and stay there or travel on land and then rejoin the ship at a later point (when it returned having done detailed surveying up and down the coast). Darwin kept detailed diaries, and shortly after the voyage was over, he worked these up into what was to prove a very popular travel book, what became known as *The Voyage of the Beagle* (Darwin 1845).

The greatest influence that Darwin had on the *Beagle* voyage was the newly published work on geology by the Scottish lawyer-turned-geologist, Charles Lyell (1830–1833). Darwin took with him the first volume of Lyell's *Principles of Geology*, and the other two subsequent volumes were sent out to him from England. Lyell was arguing for what came to be known as a “uniformitarian”

view of geology. Lyell claimed that, given enough time, all the varied geological effects that one finds in the world – mountains, valleys, oceans, rivers, volcanoes, and much more – can be produced by regular forces, of an intensity no more than those presently in action. In other words, snow, rain, deposition, silting, volcanic eruptions, earthquakes, and all the other natural effects can produce everything. Darwin was very impressed by this view of the Earth's history, one which incidentally requires a great deal of time. Although his mentors at Cambridge, particularly the geologist Adam Sedgwick (1831), had endorsed a view which came to be known as “catastrophism,” where one supposes massive upheavals every now and then in the Earth's history, Darwin rejected this entirely in favor of Lyell's alternative position.

In fact, the first piece of scientific work that Darwin did, for which he is still rightfully famous, was right out on the Lyellian system. Lyell argued that the Earth is a little bit like a waterbed (Rudwick 1969). That is to say, as one part subsides (perhaps because of deposition of silt from rivers), another part rises. The major puzzle, unsolved by Lyell in the *Principles*, was that of coral reefs. Why do we find these circular, island-like phenomena in tropical seas, with coral growing around their rim? Lyle had argued that these are the relics of now extinct volcanoes. Darwin reasoned that it was highly unlikely that the volcanoes would have come up to, and no further than, the ocean's surface. Rather argued Darwin, the coral had first grown around the edges of islands and then kept growing upward as the islands subsided. He showed this would lead to coral reefs (Darwin 1842).

The uniformitarianism of Lyell had two major effects on Darwin, one scientific and the other religious. On the scientific side, Lyell's insistence that everything be explained by regular laws of an intensity now in operation started to push Darwin toward an evolutionary perspective on organisms, meaning here the belief that organisms are naturally produced by regular laws from other forms perhaps far more simple, rather than by miracles (Ruse 2008). Lyell himself denied evolution, but it was certainly open for a young follower to start

thinking otherwise. On the religious side, Lyell started Darwin on the long path that led eventually toward the end of his life to skepticism or agnosticism. As a young man intending to join the clergy, Darwin had been a practicing and believing Christian – a member of England’s established Protestant church, the Anglican Communion. On the *Beagle* voyage, under Lyell’s influence, increasingly Darwin found himself unable to accept miracles. Therefore, this meant that the Bible stories could not be literally true. Darwin came to reject the idea that Jesus is the Son of God.

It is important to emphasize that Darwin did not now become an atheist – he never became an atheist – but he did start to move from Christian “theism” to what is known as “deism.” By this latter term is meant the belief in a God who is an unmoved mover that is one who works entirely through unbroken law. This deism stayed with Darwin right through his mature life and only toward the end did it start to fade into a form of non-belief. It goes without saying that the truth of evolution is, if anything, proof of the power of God rather than despite it. Everything, including organism life, is produced by unbroken law, without the need of intervention by the deity.

From Evolution to Natural Selection

Darwin did not become an evolutionist on the *Beagle* voyage. However, the visit to the Galapagos Archipelago in 1835 was probably the most important event in his whole intellectual life (Larson 2002). It was there that Darwin saw the giant tortoises of the archipelago as well as the teeming birdlife. To his great surprise, Darwin discovered that the reptiles and the birds differ from island to island. Moreover, although they are like the wildlife of the South American mainland, they are slightly different. Darwin was extremely puzzled how this could be. Yet, it was not until he returned to England and asked a leading authority to examine and classify his birds that Darwin made the move over to evolution. When Darwin was told that the birds from the different islands on the Galapagos are undoubtedly different species, he could see no way of explaining this fact except through a long

process of what he was to call “descent with modification.”

Early in the spring of 1837, Charles Darwin became evolutionist. It is worth noting that probably due to the Galapagos influence, Darwin always thought of evolution as a branching process, starting with an original form that then diverges as the descendants get separated and go their different ways. For this reason, a branching “tree of life” was the picture of organic history adopted by Darwin and from which he never deviated. He may have made a great discovery. Letting it go public was another matter. By this time Darwin was starting to make a name for himself as a very promising young scientist. His work on coral reefs was gaining him much respect. Darwin realized that to announce the fact that he was an evolutionist would be fatal to his professional success. Hence, although he opened some private notebooks and set out on a detailed course of inquiry, he kept his newfound beliefs very much to himself.

As a graduate of the University of Cambridge, that is, as a graduate of the University which had some 200 years before housed the great Isaac Newton, Darwin realized that it was not enough simply to become an evolutionist. As Newton had found the cause of the Copernican system – his force of gravitational attraction that exists between all bodies – Darwin likewise realized he had to find a cause for evolution (Ruse 1979a). It took him 18 months to hit on the solution. Very quickly, Darwin realized that the key to change lies in selection. Animal and plant breeders who want to produce better quality products, fatter pigs, beefier cattle, and fleshier vegetables had realized that the secret to success is picking those which, for whatever reasons, have desired characteristics. Breed from and only from these, very quickly one can effect significant change.

Darwin searched therefore for a natural equivalent to the breeders’ selection. The crucial move came at the end of September 1838 when he read a work by an Anglican clergyman, the Rev. Thomas Robert Malthus (1826). Malthus was interested in the problem of why human beings bother to work at all. Why do we not spend all our days playing and idling away the hours? Malthus’ answer was

that God has made our reproductive inclinations so strong that there is constant population pressure on the limited availability of space and food. This leads to an inevitable “struggle for existence.” Humans therefore must work, and work hard, in order to succeed. Otherwise, they will starve and die.

Darwin took this Malthusian idea and applied it to the world of animals and plants. He argued that for all organisms there is a constant outstripping of food and space supplies, by ever-increasing population numbers. Throughout nature, therefore, there is an ongoing struggle for existence or more precisely struggle for reproduction. Since new variations are always appearing, for whatever reason Darwin never knew, this means that in the struggle some will succeed and some will fail. Those that succeed will on average tend to be different from those that fail. It was Darwin’s great insight to see in addition that the differences are the things that matter. It is precisely because organisms have different features that some succeed and others do not. There will therefore be an equivalent to the breeders’ method of choosing, an equivalent that Darwin famously labeled “natural selection.”

In the course of time, natural selection will lead to change, that is, evolution. It is most important to recognize that for Darwin it was never merely change. It was always change of a particular kind. In particular, Darwin thought that natural selection leads to “adaptation.” By this is meant that the features of organisms are design-like: the hand, the eye, the genitalia, the leaf, the bark, the hunting tactics of the predator, and the evasive strategies of the prey. Why was Darwin so convinced of the importance of adaptation? This was a result of the training he received at Cambridge. Part of the curriculum was the work of the Anglican clergyman William Paley. Paley was the author of the celebrated work *Natural Theology* (1802), in which he gave the definitive exposition of the argument from design of God. The eye is like a telescope. Telescopes have telescope makers. Therefore the eye must have an eye maker, the Great Optician in the Sky.

Darwin accepted completely Paley’s premise, namely, that the world is “as if” designed. Indeed,

in these early years, he did think that the organic world was designed. But whereas Paley thought that God designed and created hands-on, as it were, that is miraculously, Darwin’s deistic god created through unbroken laws at a distance. The important thing is that Paley saw ubiquitous adaptation. Following Paley, Charles Darwin saw ubiquitous adaptation, brought about by natural selection (Ruse 2017a).

The Later Years

Darwin discovered natural selection in 1838. A year or two later, he wrote a sketch of a theory based on this mechanism and shortly thereafter a fairly detailed exposition of 250 pages (Darwin and Wallace 1958). For reasons that are not clearly understood, even now, Darwin did not publish. Probably the reason is that given above, namely, that he realized that were he to publish, he would alienate himself from powerful members of the British scientific establishment. Darwin had no desire to be a pariah.

In any case, by this time he had fallen desperately sick. Early in 1839, Charles Darwin married his first cousin Emma Wedgwood, another of Josiah Wedgwood’s grandchildren. They set about having a conventionally large Victorian family. In the end there were ten children, seven of whom lived to majority. After the *Beagle* voyage, Darwin lived first in Cambridge and then in London. Thanks to family money, he and Emma were able to buy their own house, which they did in the Kentish village of Downe. There they rather cut themselves off from society, mainly mixing with neighbors and making extended trips to family members.

Quite why Darwin fell sick is still unknown. Some have suggested that it was the psychological burden of becoming an evolutionist (Desmond and Moore 1992). However, this seems unlikely because Darwin never truly seemed weighed down by this. Others have suggested that it was a physical ailment, Chagas’ disease caused by infection from an insect bite high in the Andes during the years of the *Beagle* voyage. More recently the suggestion has been made that Darwin suffered from lactose intolerance – an inability to digest milk products (Dixon and Radick

2009). This last hypothesis is given some credence by the fact that whenever Darwin went to health establishments, where he was put on a restricted diet, his health improved dramatically. It declined when once again he rejoined his family and started again eating the very rich diet that a comfortable middle-class family like the Darwins would have enjoyed daily.

What did happen was that Darwin slowly started to build around himself, mainly thanks to a very extensive correspondence (Darwin 1985–) – the Penny Post fortuitously came into being in 1840 – a group of younger scientists who would have far fewer objections and prejudices to evolutionary ideas. Prominent among these were the botanist Joseph Hooker and then a little later the morphologist and paleontologist Thomas Henry Huxley. For many years Darwin worked on an extensive study of barnacles (Darwin 1851a, b, 1854a, b). Finally, in the mid-1850s, he turned again to evolutionary studies and started writing up his work for publication.

Then, in the summer of 1858, he received from a young naturalist, out collecting in the Malay Archipelago, an essay containing virtually the same ideas that he had himself conceived 20 years previously (Wallace 1858). Spurred by the arrival of this essay, written by Alfred Russel Wallace, Darwin dropped everything and wrote for 15 months frenetically. Finally, in the late fall of 1859, his great work was published. *On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* presented Darwin's thinking to the world.

We shall later look in some detail at the reception of Darwin's *Origin*. Suffice it here to say that, despite much controversy, very quickly people accepted the fact of evolution. Natural selection, however, was a different matter and much criticized. Darwin himself revised the *Origin* through some six editions. At the same time, he turned to other projects including a small book on orchids, issues to do with domestication, and then in the 1870s an array of works on plants including a study of insectivorous plants and another of climbing plants (Darwin 1862, 1868, 1875a,b). At the beginning of that decade, he also published

a major work on human evolution. *The Descent of Man and Selection in Relation to Sex* (1871) was nevertheless a rather odd book. Much of it was less about our own species and more about a secondary mechanism that Darwin had always endorsed (although hitherto not much discussed), so-called sexual selection. This is another matter we shall take up later, seeing why Darwin wrote as he did.

For all the controversy, Darwin was greatly respected as a scientist. Even those who differed most from him saw that he was a genius whose thinking had changed our perspectives entirely and irrevocably. He was also a thoroughly nice man, who was devoted to his wife and family, a good master to his servants, a loyal friend, and one who was always ready to offer help and advice (and, if necessary, a cash gift) to those in need. There is therefore little surprise that when Darwin died in 1882, by popular demand he was buried in England's Valhalla for its heroes, Westminster Abbey. There he lies for all eternity, next to the man whose work in physics Darwin had striven to emulate in biology, Isaac Newton.

Predecessors

The ancient Greeks did not believe in evolution. This refusal was not a matter of prejudice and certainly not a matter of religious prejudice. It was simply that they did not see how a blind process of law could lead to organisms. It was the great philosophers Plato and Aristotle who first realized that there is something distinctively design-like about the organic world, that adaptive nature which we saw in the last chapter Charles Darwin explained through his mechanism of natural selection (Ruse 2017a). Plato believed that there was a God who designs organisms (for that reason his position is often spoken of as one of "external teleology"). Aristotle believed that organisms have some kind of innate, vital force which leads to their design-like nature (for that reason his position is often spoken of as one of "internal teleology"). Either way, they thought that organic nature precludes creation through regular law. The pre-Socratic philosopher

Empedocles had argued that organisms come about through the cohesion of various parts, randomly. This is not really a full-blooded evolutionary position, but it is natural in the sense of proceeding according to and only to blind law. Aristotle was withering in his criticism, arguing with force that such a position is simply ridiculous. Evolution simply did not get off the ground in the world of ancient Greece.

The coming of Christianity did not help things very much either. For many years, Christians debated about whether or not they were committed to the books of the Old Testament. After all, this was the Jewish Bible, and the Jews had rejected their Savior. However, eventually, thanks particularly to the thinking of Saint Augustine around 400 AD, it was realized that in order to make sense of the Christian story of salvation, it was necessary to presuppose the Jewish story of creation, particularly inasmuch as it involved a fall of humankind necessitating the coming of Jesus. This meant that, with the acceptance of story of creation involving but 6 days around 6000 years ago, there were new reasons for rejecting evolution. Not that one has much sense that anyone had much inclination to accept evolution in the first place.

Progress

It was not until the beginning of the eighteenth century, the beginning of what historians now refer to as the Age of the Enlightenment, that we find the first stirrings of evolutionary speculation (Ruse 1996). By this time, although by no means universally widespread, there were more and more people starting to doubt the Christian story. The corrosive effects of philosophy had done its work. Although René Descartes died a good Catholic, he had supposed the possibility of an evil demon who makes all our beliefs false, including our Christian beliefs. For all that Descartes himself denied that this was definitive, and for all that his followers frenetically denied that this was definitive, a nagging worm of doubt continues to gnaw through the bud.

Then there were the quarrels between Christians themselves. Not just the differences between Protestants and Catholics, although these were

bad enough. There were also differences between Catholics and differences between Protestants. Indeed, in the century before, Britain had been torn apart by religious differences between Protestants. Even if one did not give up the belief in God entirely, increasingly there was space for speculation about whether any of these warring groups had a lien on the truth. Finally, voyages of exploration – particularly to Asia – had brought Europeans into contact with peoples who had sophisticated civilizations, including religions, yet who had never heard of Jesus Christ. Could it therefore be that Christian beliefs were just the cultural ephemera of a particular people rather than claims with deep insights into objective truth?

With Christianity no longer such an overwhelming force, there was space for evolutionary speculation. However, the problem of design or adaptation had not been solved. This was not to happen for a 150 years. If there was not yet a solution to adaptation, what then was sufficiently strong to motivate people into speculation about natural origins of organisms, the belief that there was a natural development from very primitive forms of to today's sophisticated forms? In a word, it was the ideology of *progress*.

The Christian believes in Providence. We can do nothing on our own. We are tainted, sinful, and condemned to death. Our only salvation lies through the blood of Jesus on the cross. Because of his great sacrifice, the possibility of eternal life is ours. To the contrary, the believer in progress claims that humans unaided can improve their lot through education, science, civic reform, and like activities. We can make Jerusalem here on Earth, without the direct aid of God. Although do note that back at the beginning of the eighteenth century, most progressionists were not atheists. They were rather deists (the position we have seen adopted by Charles Darwin). They believed that God set things in motion and then expected us to do things for ourselves.

Progress led directly to evolution. People believed in the possibility of upward change in the cultural realm. They then read this into the biological world. And then, equally promptly and in a circular fashion, they used biological progress

to confirm their beliefs in cultural progress! You might ask why people felt the need of progress to justify their evolutionism? The simple fact is that, at the beginning of the eighteenth century, there was nothing else on which to rest their beliefs. The fossil record was barely uncovered; the geographical distribution of organisms across the world was hardly hinted at; discoveries in morphology and embryology had to wait another century; theories of heredity were at the crudest level, to speak generously. Progress, however, was a heady ideology, and its enthusiasts were ever ready to extend it to other fields, most particularly the domain of the living.

One of the most interesting of the early evolutionists, coming toward the end of the eighteenth century, was Erasmus Darwin, British physician, inventor, agriculturalist, friend of industrialists, popular poet, and grandfather of Charles Darwin (Porter 1989; Ruse 1999). We are not quite sure exactly what sparked his interest in evolution, although it could be fossils that were being uncovered by laborers as they dug the channels and bored the tunnels for the canals that were now starting to crisscross England. What we do know is that he was an enthusiast for progress, an enthusiasm that extended to full-blooded support of the American Revolution (he was a good friend of Benjamin Franklin) and, in the early years, no less support for the French Revolution (until things started to go terribly wrong in that country).

Darwin wrote extensively about evolution, often in poetry. As can be seen from the following very typical passage, it was always evolution with a message. We start with the blob (what in those days was often called the “monad”). We end with the human (what in those days was often called the “man”).

Imperious man, who rules the bestial crowd,
Of language, reason, and reflection proud,
With brow erect who scorns this earthy sod,
And styles himself the image of his God;
Arose from rudiments of form and sense,
An embryon point, or microscopic ens!
(Darwin 1803, 1, 295–314)

Showing just how unsophisticated was Erasmus Darwin’s thinking compared to that of his

grandson Charles, there is virtually nothing in his voluminous writing about possible causes of evolution. There is however something that was to become particularly popular in the nineteenth century, although interestingly less so in Charles Darwin’s writings. This is the analogy between the development of the individual and the development of the group. Just as an organism grows from a speck up to the full-blooded adult, so likewise one supposes that the group grows from the speck to the sophisticated endpoint.

France

Many people read the poetry and prose of Erasmus Darwin. However, his influence was far eclipsed by that of the French, minor nobleman, Jean Baptiste de Lamarck. His *Philosophie Zoologique*, published in 1809 (the year of Charles Darwin’s birth), had tremendous influence, if only because it was often held up as a bad example of what not to do! Lamarck is famous for the mechanism named after him, Lamarckism – the inheritance of acquired characteristics. The blacksmith gets strong arms through working in forge, and, as a consequence, his son is born with strong arms even before he starts work. As it happens, this is but a minor part of Lamarck’s thinking, and it was a mechanism already endorsed by Erasmus Darwin (and, incidentally, was always to be endorsed as a secondary mechanism by Charles Darwin). Lamarck’s main picture of evolution was of an upward progressive drive, starting with chemicals in ponds which are the basis of the “spontaneous generation” of new organisms, thanks to lightning and other natural forces. Eventually, for Lamarck, as for everybody else, evolution ends with human beings (Burkhardt 1977).

Interestingly, however, since we today always associate evolution with a tree of life, Lamarck did not have this picture in mind at all. He believed rather in parallel lines of evolution, starting continuously down through the ages. Organisms follow the same predetermined paths, with occasional deviations due to the inheritance of acquired characteristics. Thus, whereas for someone like Darwin, if a species goes extinct, it will never return, for Lamarck, if a species goes

extinct, it is just a matter of time before it reappears all over again on a different, parallel, upward evolving line.

Lamarck was as enthusiastic about progress as was Erasmus Darwin. If you think about it, there had to be some reason why a nobleman would not merely survive the French Revolution but do well during it (as was the case with Lamarck). It was because he endorsed completely the philosophy which lay behind the tumultuous events. When the Revolution went wrong and led to the dreadful events of the Terror, both in England and in France, there was a revulsion against the ideology of progress. It was many years before it was to pick up again. And with enthusiasm for progress went any enthusiasm for evolution. In the early years of the nineteenth century, evolution was a much-derided notion. Note that this was not so much because it was regarded as anti-Christian, as because it was seen (truly) as an epiphenomenon on the back of a strongly disliked ideology.

No one opposed evolution more strongly than Lamarck's fellow Frenchman, George Cuvier (1813, 1817). He is rightly known as the father of comparative anatomy, thanks to the brilliant dissections he performed comparing and contrasting organisms of different species. He opposed evolution on many grounds, starting with the empirical. Thanks to Napoleon's expeditions to foreign lands, Egypt in particular, many specimens were being brought back to Paris. These included mummies of organisms long dead. When unwrapped and dissected, Cuvier could show that the mummified forms were of species which exist today. He therefore argued that there is no evidence of ongoing change (Coleman 1964).

Cuvier was also opposed to evolution on ideological grounds. He became a very important member of the French civil service. He was therefore deeply opposed to significant change and looked back to the years of the Revolution with horror. Progress leads to change; therefore, progress must be wrong. Evolution is connected to progress. Therefore, evolution must be wrong. Most overwhelmingly, however, Cuvier was opposed to evolution because he himself was

strongly committed to adaptation, the design-like nature of organisms. (He had studied the works of Aristotle in detail.) He could see no way in which blind law could lead to adaptation, or to use his term, to the "conditions of existence." In Cuvier's language, the conditions of existence preclude significant and ongoing development of evolution of organisms.

Britain

Cuvier articulated these ideas primarily in the second decade of the nineteenth century, and, until Darwin started publishing, for many this was definitive (Rudwick 1972). Cuvier was particularly influential in Great Britain. Although Cuvier was a Protestant, and thus more likely (than a Catholic) to base his thinking on the Bible, he was strongly opposed to the mixing of science and religion. The British felt no such delicacy. Although by the 1820s, none of the serious scientists were biblical literalists, they were all eager to see a close parallel between the science of origins and their reading of the Bible.

They realized by now that the Earth would be very much older than the 6000 years that one can calculate from the genealogies given in the Old Testament. But they were strongly committed to miracles, and they combined this with suggestions by Cuvier that there had in fact been upheavals in the geological past ("catastrophism"), to give a satisfying picture of origins. It was one which, as they thought, combined a serious interpretation of the now rapidly growing knowledge of the fossil record, with an active and ongoing role for the creative Christian God.

Naturally, these British scientists tended much more to the side of Providence than that of progress. However, by the 1830s, the horrors of the French Revolution were starting to recede in people's minds. At the same time, now that the Napoleonic wars were long gone, industry was starting to pick up. Expectedly, therefore, thoughts of progress started to emerge once again. And with thoughts of progress came thoughts of evolution. Most notably, in 1844, a Scottish publisher, Robert Chambers, writing anonymously, put out an evolutionary tract that rapidly became notorious for the daring nature of its speculations.

Vestiges of the Natural History of Creation left nothing to the imagination. Starting with thoughts of spontaneous generation – Chambers suggested that the frost ferns left by cold weather on windowpanes turned naturally into living plants – he saw an inevitable rise up from the primitive to the complex, from the monad to the man, and from the blob to the Britain. Combining a sketchy knowledge of the fossil record (most likely based on a misreading of Lamarck), with an equally sketchy knowledge of then-developing, Germanic studies of embryology, Chambers saw upward progress everywhere – in society, in the individual, and in the group.

Naturally enough, Chambers' ideas were strongly condemned by the British scientific establishment. Darwin's old geology teacher at Cambridge, Adam Sedgwick (1845), was particularly vehement, suggesting that such ridiculous ideas could only have been written by a woman and then taking back this suggestion because no woman could have speculated in so vile in fashion! Yet, for all the official opposition, it is clear that many in Britain and America and elsewhere responded favorably to Chambers' speculations (Secord 2000). One of the most interesting, for example, was the poet Alfred Tennyson. He was writing a long poem, *In Memoriam* (1850), dedicated to the memory of a friend who died too young. Despondent at the seemingly meaningless message of Lyell's *Principles* – things just keep going on and on without any progress – he then read Chambers. Tennyson found this particularly inspiring, even going to the limit of suggesting that perhaps his dead friend was a highly evolved being who had appeared before the time was right! A very odd idea indeed, but one that Tennyson's fellow Victorians (including Queen Victoria) found very inspiring.

By the 1850s, therefore, although Darwin was still sitting on his ideas, tucked away in the village of Downe, the idea of evolution was now becoming quite well known. It was still highly controversial and not at all accepted by professional scientists. It was seen, rightly, as the other side of the coin to hopes of social and cultural progress. In a way, therefore, one can talk of evolution as a "pseudoscience" (Ruse 1996, 2013a, b,

2016). It was not in any way a professional science, like physics and chemistry. And this was a status very much underlined by a new arrival in the field: Herbert Spencer.

A fellow Englishman of Darwin, Spencer, came from a much lower rung of the middle classes. He was not an establishment man. He felt no compunction about taking on the professional scientists of his day. Completely and utterly committed to the ideology of progress, Spencer started writing a great length in favor of evolution. Interestingly and almost paradoxically, Spencer (1852) hit on the idea of natural selection, but he rather dismissed it as trivial. For him, it was the Lamarckian process of the inheritance of acquired characteristics that was the main cause of evolutionary change. But truly, much like Erasmus Darwin 50 years before, Spencer was less interested in causes than in ideology. It was the upward chain, whether it be in culture or in biology, that really counted.

We see, therefore, that when Darwin published the *Origin of Species* in 1859, he was not working untilled ground. Ideas of evolution had been around for a 150 years. By the middle of the nineteenth century, they were well known and much discussed. However, they were not respectable. It was not so much that they were considered antireligious, although clearly there were tensions on this score – less on grounds of going against biblical literalists and more because evolution was seen as threatening thoughts of Providence – but because they were associated with a controversial ideology.

What therefore was needed to move the story forward was a work by a respected scientist, laying out a respectable case for evolution and its causes. It was this that Darwin set out to do in his *Origin*. In the next section, we turn to the case that he made.

The Origin of Species

In his autobiography, written toward the end of his life, Charles Darwin referred to the *Origin of Species* as "one long argument" (Darwin 1958). Let us take this comment seriously.

True Causes

The 1830s, the time when Darwin was coming to scientific maturity and making his great discovery, was a very important time in Britain for the methodology of science. Leading figures in the scientific community, most particularly the astronomer-philosopher John F.W. Herschel (1830, 1841) and the scientific polymath and historian and philosopher of science William Whewell (1837, 1840), were articulating and specifying the desiderata of the best kind of science. This was not an activity done in isolation. Men like Herschel and Whewell were working hard to professionalize British science and to make possible full-time careers in the field. It was necessary therefore to have an ideal against which work could be judged.

Naturally the labors of Isaac Newton were the great inspiration. His was the best science that had ever been produced. It followed naturally therefore that good science would share the characteristics of Newtonian science. But what were the characteristics of Newtonian science? Herschel and Whewell agreed that a scientific theory should be what we today call a “hypothetico-deductive system.” By this is meant an axiom system, where the initial premises or axioms are lawlike claims about the physical world. In the case of Newtonian mechanics, for example, one starts with the three laws of motion and the law of gravitational attraction, and then one can infer deductively Galileo’s laws about motions here on Earth and Kepler’s laws about the motions of planets.

It was also thought that good science is causal. After all, this was the great strength of the Newtonian system. It provided an underlying cause – gravitational attraction – to explain everything. Newton himself had referred to gravity as *vera causa* or “true cause.” There was some dispute about the exact nature of a true cause. Herschel (1830), who took a somewhat empirical attitude toward science, argued that a true cause is either something that one can sense directly or something for which one has good analogical evidence. For instance, he argued that we know there is a cause pulling the Moon toward the Earth because when we spin a stone at the end of the piece of string around our finger, we can feel the force down the string pulling the stone toward

us. Whewell (1840), who took a somewhat rationalist attitude toward science, argued that a true cause is not necessarily something we sense. It is rather something we infer from the evidence. If it can explain a range of phenomena, what Whewell called a “consilience of inductions,” then we have a true cause.

It should be noted that in the 1830s, this difference about true causes gave rise to a very lively debate. After a century of acceptance of Newton’s particle theory of light, scientific opinion had swung strongly toward Huygens’ wave theory. But why should one accept waves if one never sees them? Herschel offered all sorts of analogies with sound waves and water waves in order to convince people of the true-cause nature of light waves. Whewell dismissed all of these, arguing simply that light waves explain a broad range of evidence. For that reason alone, they should be accepted as a true cause. Geology also got involved in the debate. Herschel argued that Lyellian uniformitarianism, specifying as it did that we should explain the past in terms of causes of the present, satisfies the empiricists’ true-cause criteria. Whewell argued that catastrophism is a perfectly acceptable geological position. If there are geological phenomena, like mountain ranges, that demand the supposition of forces that we do not experience today, then it is acceptable to suppose them in order to get a full explanation. We have a true cause.

Artificial Selection

As an undergraduate, Darwin had known Whewell well, and then Darwin spent much time with Whewell in the early years after the *Beagle* voyage. He read Whewell’s writings with much care. Darwin had read Herschel’s little book on scientific methodology just before he left on the *Beagle* voyage and then met with Herschel during the voyage when the ship put into port in South Africa, where Herschel was spending several years mapping the heavens as seen in the Southern Hemisphere. Darwin therefore knew the positions of the two men. Eager to provide a theory that was methodologically sound, Darwin covered his options by trying to satisfy both the Herschelian empiricist demands for a true cause

and the Whewellian rationalist demands for a true cause! He left nothing to chance (Ruse 1975).

Thus, Darwin opened the *Origin* with a detailed discussion of selection as practiced by animal and plant breeders. In part, he was clearly doing this heuristically to lead the reader toward the main claims of his theory. He felt that if the reader could understand what is going on in the world of the breeder, then claims about natural selection and its evolutionary implications would be more readily grasped. In part, however, Darwin was preparing the way to use human selection as a form of support for natural selection. Darwin was arguing that the great successes breeders achieve, for instance, with pigeons, mirror the great success that natural processes achieve with wild animals and plants. In other words, the discussion of artificial selection was intended as a Herschelian, empiricist true cause. We have an analogy between something that we can see and work on ourselves and something that is not directly observable and that we must in some sense infer.

Note incidentally that Darwin presupposed (and indeed always presupposed) that natural selection is going to be a rather slow process. He never really envisioned the possibility that we might see natural selection actually taking place and having effects in an individual's lifetime.

Natural Selection

Next in the *Origin*, Darwin went on to introduce his chief mechanism of change. Nothing is possible without a constant supply of new variation. Darwin never had an adequate theory of heredity; but he was always fully convinced that, whatever the causes, any natural population of organisms will show considerable variation and that from generation to generation new variations will appear. (Darwin was always adamant that these variations are never directed toward an organism's needs. They are completely random, not in the sense of being uncaused – even though Darwin knew nothing about the causes, he was convinced that such causes do exist – but in the sense that they do not occur according to need.)

Then, with the variation, Darwin was ready to introduce first the idea of the struggle for

existence and then second the idea of natural selection. About the struggle, he wrote as follows:

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. (Darwin 1859, 63)

Then, Darwin went on to infer natural selection:

Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the whole organization becomes in some degree plastic. Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. (pp. 80–81)

Note that although these arguments are rather informal, Darwin was clearly intending some kind of hypothetical-deductive picture (Ruse 1971). We start with laws, for instance, about the tendency of organisms to increase in number geometrically and the impossibility of food and space supplies ever matching this tendency. We then go on to infer the struggle for existence. After this,

we include a premise about the existence of variation in all populations, combine it with the conclusion about struggle, and go on to infer natural selection. Nothing is very rigorous, but the intention is clear.

Along with natural selection, Darwin also introduced the secondary mechanism of sexual selection. Clearly influenced by practices in the breeders' world, Darwin divided sexual selection – resulting from competition between organisms of the same species for mates – into two kinds. First, there is sexual selection because of “male combat.” This occurs when males battle for mates, as when two stags fight over the herd. It leads to such physical characteristics as antlers and is obviously modeled on the results of breeders selecting for more ferocious fighting dogs or cockerels. Second, there is sexual selection because of “female choice.” This occurs when females choose, for their mate, what they regard as the most desirable male. It leads to such physical characteristics as the stupendous tail feathers of the peacock. It is obviously modeled on the results of breeders selecting for melodious songbirds and so forth.

Darwin also introduced what he called his “principle of divergence.” This is the process whereby organisms differentiate into new groups or species (meaning populations that are reproductively isolated from all other organisms). Darwin argued that it comes about because greater differentiation means greater opportunities to exploit the environment. If everything is exactly the same, then everyone is competing against everyone else. However, with differentiation, different organisms can exploit different ecological niches (to use more modern language). This leads to the tree of life, and in fact the only illustration given in the *Origin* is of the tree. It is given to back up the discussion of the principle of divergence.

Consilience

With the main mechanism now introduced, Darwin quickly covered some of the difficulties in his theory – most particularly, he acknowledged his ignorance about the true causes of heredity. Then, he was ready to apply the mechanism. Here it was the influence of William Whewell that was paramount. Darwin wanted to incorporate natural

selection in a consilience of inductions, showing it to be a true cause because it could explain different phenomena right through the spectrum of the life sciences. This is the project for the second half of the *Origin of Species*.

Darwin started with social behavior, most particularly focusing on the Hymenoptera, the ants, bees, and wasps. Darwin always recognized that behavior is as important in the struggle for existence as any physical feature. Hence, selection works to promote adaptive behaviors. Generally, this is of no great significance. The wolf gets faster, obviously, in order to catch the prey. The rabbit gets faster or better at maneuvering, in order to avoid the predator. However, Darwin saw that, when it comes to social animals, behavior starts to raise an interesting and difficult problem. Here we find that one animal will put much effort into promoting the well-being of another animal, as, for instance, when the workers in the hive devote all of their energies to the well-being of the queen and her offspring. Darwin always interpreted the struggle as being one organism against another, and hence he could not immediately see how it fits that selection could produce what we today call “altruism” (Ruse 2019a).

Hampered by the lack of an adequate theory of heredity, Darwin always had problems on this issue. He could see why the behavior of social insects is adaptive. For instance, he went to some considerable trouble to show that the hexagonal form of the honeycomb is by far the most efficient use of the wax. In other words, he showed that adaptation can extend from the organism itself to the objects the organism produces. (This is what the English biologist Richard Dawkins (1982) has called an “extended phenotype.”) But what about the behavior which serves the aims of others? One thing that Darwin was adamant about was that one could never simply have an organism working for the good of another, without either some kind of relationship or return. Eventually, Darwin decided that in some way it is appropriate to consider the group, the nest, and the hive, as one interrelated individual. Therefore, we should look upon the sterile worker less as an individual in its own right and more as a part of the whole. Just as in the individual human, the heart, lungs, and the brain

all work together because of the whole, so likewise in the hive the workers serve the cause of the whole.

Darwin then went on to discuss paleontology. You might think that this would be the easiest area of them all for an evolutionist to tackle. Darwin did not see things in this way. He was very much aware of such problems as gaps in the fossil record and no less aware that critics of evolution had seized on this as evidence that later forms (i.e., fossils found higher in the record) are not descended from earlier forms (i.e., fossils found lower in the record). He therefore devoted much time and effort to arguing that gaps in the fossil record are truly artifactual. Either they represent points at which we have incomplete knowledge, and linking fossils will be found later, or they represent points where we have incomplete knowledge and the gaps will never be filled because the needed fossilization never occurred. Either way, argued Darwin, it is more reasonable to suppose that the gaps are inadequacies in the record, rather than faithful reflection is what actually happened.

Obviously, paleontology was not just a matter of explaining deficiencies and problems. Going on the offensive, Darwin made much of the fact that we have a well-articulated progress in the record from more primitive forms to the complex forms we have around us today. More than this, Darwin pointed out that earlier forms often are more generalized, having features that are today shared by organisms that are otherwise very different. Darwin theorized that the earlier, generalized forms are the shared ancestors of today's diverse organisms. Darwin was aware that the early generalized forms are often similar to the embryos of today's forms. However, he never endorsed a simple picture of organisms going from the embryonic to the adult, in geological time as well as in individual time. Apart from anything else, this would seem to imply a kind of inevitable momentum to the course of evolutionary history. Darwin always thought that evolution, fueled as it was by natural selection, is a much more contingent and random phenomena. There is never any guarantee that one form will necessarily lead to another.

Darwin turned next to geographical distributions of organisms. Expectedly, given that this was the area that had first sparked his evolutionary inclinations – the reptiles and birds of the Galapagos Archipelago – Darwin felt very much at home here and argued strongly that one can explain distributions only on the evolutionary basis. One thing of which Darwin made much was the fact that the inhabitants of oceanic islands are almost always much closer in form to the inhabitants of the nearest continental mainland than they are to mainlands elsewhere. The Galapagos organisms look like South American organisms and are not at all like African organisms. Conversely, the organisms of the Canary Islands in the Atlantic, close to the coast of Africa, have a definite African tinge, rather than looking like inhabitants of South America.

From here, Darwin went on to look at systematics. It was in the eighteenth century that, thanks to the Swedish biologist Linnaeus, a proper order was imposed on the wide range of animals and plants to be found here on Earth. Among biologists concerned with classification, there was considerable debate about which criteria lead to natural or objective systems and which lead to artificial or subjective systems. However, by the middle of the nineteenth century, people were starting to get a real sense of what are truly natural orderings as opposed to just conveniences imposed on the organic world by the classifier. For instance, no one was about to deny that the sea mammals like whales are truly to be classified with other mammals rather than with fish or that flightless birds like the ostrich or emu belong with other birds, rather than with the mammals. Darwin proudly pointed out that there is a good reason for taking this classification as uniquely natural. It is simply that it represents the course of history. Whales are descended from other mammals and only at a distance from fish. The ostrich and the emu likewise are descended from other birds and not from mammals. Evolution through natural selection is the key to natural classification.

Next came morphology or anatomy. It had been known since Aristotle that there are isomorphisms between the bones of very different organisms. The forelimb of the horse, of the human, of

the seal, and of the mole – not to mention the wings of bats and birds – seem as if modeled on the same plan, even though the functions are very different indeed. Why should this be so? Was it simply that God somewhat capriciously decided to work from one pattern and molded everything accordingly? It was Darwin's argument that the similarities, now known as "homologies," are the result of evolution through selection. There was the ancestral, rather general, form, and then through the ages, selection turned the individual organisms to their different ends. One has a nice combination of what was known traditionally as "unity of type," meaning similarity of form, with "conditions of existence," meaning difference of function.

Drawing toward the end, Darwin turned with some pleasure to embryology. The German biologists, particularly Karl Ernst von Baer, had shown that there are significant similarities between the embryos of organisms very different as adults, the human and the chick, for example. Why should this be so? Darwin argued simply that it represents shared ancestry. Natural selection did not act to tear the embryos apart, because they are protected in the womb or the egg. Selection however did work on the adults.

At this point, Darwin made use of his Herschelian *vera causa* argument, showing that very similar phenomena can be found in the world of the animal breeder. Horse breeders and dog breeders care about the adults, not the young. Darwin found that, expectedly, the young of bulldogs and greyhounds are very much more similar than the adults. Likewise, the young of cart horses and racehorses are very much more similar than the adults. This was perfect confirmation of Darwin's position, especially since the breeders themselves had denied that this was so!

The consilience was completed. Darwin had shown how evolution through natural selection explains across the spectrum of the life sciences. Conversely, the explanations point to the truth of the Darwinian true cause, natural selection:

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp

earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other, in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction... a Rate of Increase so high as to lead to a Struggle for Life, and as a consequence Natural Selection entailing, a Divergence of Character and the extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been and are being, evolved. (pp. 489–490)

Reception

John Murray, Charles Darwin's publisher, printed 1250 copies of the *Origin of Species*. Darwin was worried that many would be left over. Murray knew better. On the first day of his half-yearly sale of books to booksellers, the *Origin* sold out completely. At once, Darwin was ordered to start preparing second edition. It was almost as if the world had been waiting. Evolution was a much-discussed, highly controversial idea. What was needed was a definitive work by a major scientist. The *Origin* was that work and Darwin was that scientist.

Fact Not Theory

There was certainly controversy. Famous, even today, is the clash between Thomas Henry Huxley, representing the side of science, and Bishop Samuel Wilberforce of Oxford, representing the side of religion. In the summer of 1860, they debated at the annual meeting of the British Association for the Advancement of Science, at Oxford. Supposedly, Wilberforce asked Huxley if he was descended from monkeys on his grandfather's side or his grandmother's side. Supposedly, Huxley responded that he would rather be descended from a monkey than from a Bishop of the Church of England! The story is almost surely

apocryphal (Lucas 1979). But even myths tell truths. Darwin's theory of evolution through natural selection did cause a major upheaval in Victorian Britain.

As mentioned in section "[The Man and His Life](#)," very quickly most people accepted the fact of evolution. It became almost commonsensical. Darwin had accumulated so much evidence; it became difficult to deny that organisms had emerged slowly and gradually by natural processes. And in fact, to tell the truth, most people were happy to accept evolution. It has been explained that, even when Darwin was a young man, people were well on the way to interpreting the early chapters of the Bible metaphorically. With exceptions to be discussed later, it was realized that the Earth is very old and most people are happy to opt for natural origins rather than miracles. In 1866, the examinations for students at the University of Cambridge even went so far as to say that the truth of evolution should be assumed and examinees should focus on discussion of causes. While it is hard to be definite about these things, and of course there are going to be exceptions to every rule, by about 1870 very few wanted to deny evolution. This applied even to religious people. They probably wanted to make some special exception to human souls, but natural origins was now a given (Roberts 1988).

As also mentioned, the fate of natural selection was very different. No one wanted to deny its existence completely. However, there were few who wanted to give it the importance that Darwin proposed in the *Origin* (Bowler 1983). For example, although Huxley was happy to debate evolution with everybody and anybody, he never was much of an enthusiast for natural selection. To the contrary, he thought that every now and then, there are jumps – what were called “saltations” – taking organisms from one form to another, in just one generation. Others continued to stress the importance of Lamarckism, the inheritance of acquired characteristics. We have seen that Herbert Spencer fell into this category. Yet a third group wanted to put some kind of God-driven guidance into the new variations. Asa Gray, the professor of botany at Harvard University and Darwin's great North American supporter, was

one who thought this way. And we find another set, often inspired by Germanic thinking, who thought that there is a kind of momentum to evolution, driving it ever upward. These were the people who were particularly keen on analogies between the development of the individual and the development of the group. Most famous was the German morphologist Ernst Haeckel, who incorporated these ideas in to his famous “biogenetic law”: “ontogeny recapitulates phylogeny” (Richards 2008).

Against Selection

Why was there this downplaying of natural selection? In part, it was negative. Darwin thought that the most important characteristic of the organic world is that it is highly adapted. Natural selection was promoted to explain this fact. However, by the 1850s, biologists were far less impressed with adaptation. They had moved away from naturalistic studies of organisms in the wild, the sorts of things that Darwin was looking at when he was in South America during the time of the *Beagle* voyage, to laboratory studies of dead organisms on the dissecting table. The big questions in the 1850s centered on homology and structure, that is to say unity of type. Questions of design and success in life, that is to say questions of conditions of existence, were relegated to the relatively unimportant. So in a sense, by the time the *Origin* was published in 1859, many thought that natural selection was a solution to a nonexistent problem.

In part, the rejection of natural selection was positive. It was felt that there were insuperable difficulties to its acceptance. For a start, as has been pointed out earlier, Darwin had no adequate theory of heredity. Without this, natural selection was always vulnerable. If you cannot show why new variations will be passed on from generation to generation without being diluted, then no matter how effective selection may be, there's always the danger that it will fade away in two or three generations. This was the objection of the Scottish engineer Fleeming Jenkin. Even Darwin thought he scored a good point (Hull 1973).

There was an even bigger obstacle in the way of natural selection. The physicists had devised various ways of calculating the age of the Earth.

These were based on such factors as the heat received on Earth from the Sun, the saltiness of the sea, the heat expected from the Earth's core based on increasing temperatures as one goes deeper and deeper into mines, and other such phenomena. The general estimate was that the Earth cannot be more than 400 million years old and that it could be as young as 25 million years. The favored middle figure was about 100 million years. But this was felt to be far too short a time for such an allegedly slow process as natural selection. Hence, other mechanisms would be needed (Burchfield 1975).

Of course, today we know that the physicists were wildly inaccurate in their calculations. They were ignorant of the warming effects of radioactive decay. Today it is thought that the universe as a whole is about 15 billion years old and that the Earth is about 4 1/2 billion years old. The earlier life seems to have appeared about 3 3/4 billion years ago. At the time of the *Origin*, however, this was unknown and consequently was a major impediment to the acceptance of natural selection.

Darwin was convinced that he was right. Interestingly, although in the light of what we have seen perhaps predictably, whenever he was challenged on selection, he invoked the example of the wave theory of light, arguing that since we accept it, we should on the same grounds accept selection. Also, at every opportunity, he seized on new, favorable information. For instance, early in the 1860s in Germany, they discovered the first specimens of archaeopteryx, the transitional fossil between the birds and reptiles. Darwin introduced this organism into one of the later editions of the *Origin*, trumpeting it as proof that gaps in the fossil record are a function of ignorance rather than genuine absence. Again, a young naturalist and sometime traveling companion of Alfred Russel Wallace came up with a very ingenious, selection-based explanation of the mimicry that one often finds between different species of butterflies (Bates 1863). Henry Walter Bates argued that some butterflies are naturally poisonous and thus have an adaptation against their predators, the birds. Other butterflies have no such poisonous taste, but have found it advantageous to mimic the poisonous butterflies. In a series of ingenious

experiments, Bates showed how one could reasonably infer that this was the end result of a selective process. Darwin was very excited by this explanation, and it found its way into a later edition of the *Origin*. Although, somewhat curiously, in line with what has been said earlier about Darwin's never believing that selection can actually be seen in action, he rather relegated to a secondary position at the end of the book. One might have thought that it would have been introduced early and made prize specimen in the evidential gallery. One has the nasty suspicion that Darwin himself was not entirely out of line with the non-Darwinians after the *Origin*! After all, his major contribution to regular biology had been on barnacles, where adaptation often is a bar to discerning morphology.

Interestingly, Bates was not alone, and in the years after the *Origin*, many working on insects turned to selection for explanation. Of particular interest was industrial melanism, where butterfly and moth wings get darker to provide better camouflage against predating birds against the ever-increasingly soot-covered trees. One enthusiast even wrote to Darwin about this.

My dear Sir,

The belief that I am about to relate something which may be of interest to you, must be my excuse for troubling you with a letter.

Perhaps among the whole of the British Lepidoptera, no species varies more, according to the locality in which it is found, than does that *Geometer*, *Gnophos obscurata*. They are almost black on the New Forest peat; grey on limestone; almost white on the chalk near Lewes; and brown on clay, and on the red soil of Herefordshire.

Do these variations point to the "survival of the fittest"? I think so. It was, therefore, with some surprise that I took specimens as dark as any of those in the New Forest on a chalk slope; and I have pondered for a solution. Can this be it?

It is a curious fact, in connexion with these dark specimens, that for the last quarter of a century the chalk slope, on which they occur, has been swept by volumes of black smoke from some lime-kilns situated at the bottom: the herbage, although growing luxuriantly, is blackened by it.

I am told, too, that the very light specimens are now much less common at Lewes than formerly, and that, for some few years, lime-kilns have been in use there.

These are the facts I desire to bring to your notice.

I am, Dear Sir, Yours very faithfully,
 A. B. Farn
 Letter from Albert Brydges Farn on November
 18, 1878 (Darwin 1985-, 26, 440)

Instead of bringing out a new edition of the *Origin* with this letter facing the title page, Darwin seems not to have replied to the writer, adding weight to the belief that selection studies were simply not regarded as fully professional. Farn was a civil servant, and Bates spent his career as an administrator for the Royal Geographical Society. Darwin was not unappreciative of Bates – he got him the job – but Darwin never really seems to have internalized this sort of approach into his science (Ruse 2017a, 2018, 2019a, b).

Human Beings

In the *Origin*, Darwin said very little about humankind. Before all discussions were swamped by a tsunami of controversy about human origins, he wanted to get the basic principles of his theory out in public. Hence, he made only a throwaway comment at the end, about the significance of his theory for our own species. And he did this simply that he not be accused of cowardice on the subject.

Reticence should not be confused with hesitation. There was no doubt in Darwin's mind about the applicability of his theory to *Homo sapiens*. Interestingly, in his private evolution notebook for 1838, the very first mention we have of natural selection in action is a speculation about how the human brain will grow under the actions of this mechanism. Darwin was always convinced that humans are part of the natural order of things. This fit in nicely with his deistic beliefs and probably was connected experiences on *Beagle* voyage. On a previous trip, the captain of the *Beagle*, Robert FitzRoy, had brought back to England three of the natives of the southernmost tip of South America, the already-mentioned Tierra del Fuego. These were being returned on the voyage that Darwin took. When they were put ashore, within a week or two, to the horrified amazement of the *Beagle*'s crew, these natives reverted quickly back to what the Victorians called "savages." It convinced the ship's naturalist that we humans are very close to animal nature. He learnt a lesson that he never forgot.

Darwin was reticent on the subject of human origins; others were far less cautious. Huxley, in particular, was pushing a materialist philosophy and made the natural origins of humankind a major plank in his world picture. He wrote a little book, *Man's Place in Nature* (1863), arguing strongly for our animal nature. Others did much the same. Yet, although Darwin was responsible for one of the biggest controversies of his age, by nature he always shrank back from violent confrontations. He preferred to tend his illnesses in the security of his family, tucked away in the Kentish countryside. Probably, he would have been happy to have left others carry completely the discussion about humankind. However, it was not to be. Alfred Russel Wallace, the co-discoverer of natural selection, spent the 1860s becoming more and more enthusiastic about spiritualism. Finally, he took to arguing that humankind could only have come about thanks to the intervention and guidance of spirit forces. In other words, Wallace (1870) gave up entirely on a naturalistic explanation of our origins.

Darwin was appalled. He thought, with good reason, that Wallace was doing his best to destroy the credibility of natural selection. Something had to be done. But what? The trouble was that, spiritualism or not, Wallace brought forward some good arguments against the all-conquering power of natural selection. In particular, he pointed out that many human characteristics almost certainly did not come into being thanks to natural selection. Human hair was one example, and human intelligence was another. Although Darwin had seen many natives during his years in and around South America, he had never really lived with them. Wallace, to the contrary, had done just that. He had spent some 4 or 5 years in South America collecting butterflies and then a year or two later went East to the Malay Archipelago, where he spent even more time.

Without the unlimited funds of a Darwin, Wallace had to live in a fairly simple way. This meant sharing accommodations with the native people that he encountered. Wallace was impressed by the extent to which the natives obviously underutilized their potential brain power.

Although he was sure that native people could be as intellectually developed as Europeans, in fact this rarely happens. Hence, pointed out Wallace, it seems that for many years humans had a huge amount of unused brain capacity. This is something that could hardly have been brought about by natural selection, because having a brain is clearly something which is biologically costly. Protohumans could not have afforded such a luxury, at least not on naturalistic grounds. There had to be a reason. Wallace's conclusion was that spirit forces prepared the brain's early form, something waiting to be used when European civilization got underway.

The Descent of Man

It is at this point that Darwin turned to sexual selection for help, and it is this that explains the already-mentioned rather odd balance of Darwin's book on humankind, *The Descent of Man*. Darwin argued that many human characteristics are indeed inexplicable on natural selection; however, they can be readily explained thanks to sexual selection. In particular, Darwin argued that human intelligence is something that could readily have emerged through a struggle for mates, whether this be through combat of males or the selection of females of the men that they preferred. To be frank, one rather feels that Darwin got carried away by this topic. He discussed sexual selection in the *Descent* very much in its own right and at great length. However, the overall intent was to develop and present a secondary mechanism, something that could then explain important aspects of human nature.

The *Descent* appeared in 1871. It is not, and does not pretend to be, a work of the staggering originality of the *Origin of Species*. By the time Darwin was writing, there had been a decade of inquiry and speculation about human nature and its evolutionary origins. Darwin, therefore, was able to draw extensively on the work of others. Nevertheless, the book could only have been written by the author of the *Origin*. Darwin gave a very detailed exposition of the path of human origins as best known at the time. At the same time, he tried to show how natural selection could account for the main aspects of our evolution.

(Although Darwin was to make much of sexual selection in explaining human evolution, he never doubted that natural selection overall was the main force of change.)

Expectedly, given his fascination in the *Origin* with social evolution in the insects, the *Descent* devoted considerable attention to questions of social evolution in humankind. Darwin was particularly keen to show that our moral sense is something which comes naturally and does not demand a supernatural explanation. Following the discussion almost exactly from earlier years, Darwin saw morality as something developing within a tribe and a tribe itself he considered to be something akin to the nest of the ants or the hive of the bees. Darwin never deviated from his belief that ultimately selection is always between individuals and hence adaptations must rebound to the benefit of individual, and only secondarily to groups, if at all (Ruse 2012; Richards and Ruse 2016).

Darwin also touched upon religion, although briefly. By this stage of his life, like so many Victorians, he rather inclined to think that traditional religion is superstition. As a discreet Englishman, he did not come out and say this bluntly. But his treatment shows that this was basically his position. He looked upon religion as something of a by-product, brought about by incidental factors. For instance, he likened religious responses to nature to the excitement shown by one of his dogs when a parasol fluttered in the wind. It was not so much that Darwin was anti-religious but that basically he no longer found religion particularly relevant to his life, nor could he see much reason why it had to be relevant to the lives of others.

Although Darwin was not the fanatic about progress that had been so often true of earlier evolutionists and was still true of people like Herbert Spencer, it is clear from the *Descent* that Darwin believed fully that we humans have come out top. Moreover, among humans, the Europeans have come out best of all. In later editions of the *Origin*, Darwin speculated that a form of progress could occur because better quality organisms are always beating out lesser quality organisms. Overall, this could accumulate until one gets

some kind of progress approaching absolute value. There is not much explicit discussion of any of this in *The Descent of Man*, but it is certainly presupposed.

Interestingly, however, Darwin was not much inclined to think that today Europeans triumph over native races because of their superior fighting or intellectual characteristics. It is rather because Europeans have better natural immunities to diseases than do natives. Hence, when the two groups mix and interact, it is much more likely that native peoples will succumb to common diseases like measles. It is clear also that Darwin thought that sexual selection will play a role here. Better quality males will emerge, thanks to the struggle for mates. Also, more attractive females will emerge thanks to selection for beauty and related features. Although Darwin was a great revolutionary, as I said earlier he was no rebel. This is shown very clearly by his natural assumptions about the superiority of Europeans with the natives and even more by his unquestioned belief that males are far more intelligent on average than of females, whereas females compensate by being creatures of emotion and sympathy. Brains for men; hearts for women!

From Pseudoscience to Popular Science

Charles Darwin entered the scene when evolution was a pseudoscience. Given his careful attention to the methodologies of his day, it had obviously been Darwin's hope that in the *Origin* he would elevate evolutionary studies to the level of a professional science, like physics and chemistry. He wanted natural selection could be a fruitful mechanism of inquiry. However, he failed in this aim. He convinced the world that evolution as a fact is true. What he did not do was convince his fellow professional scientists that natural selection is an active and valuable tool of inquiry, giving us insights into the nature of organisms and their histories. In fact, as we have seen, Darwin himself was a little reserved on this matter. One could have developed a whole field of selection studies – Darwin himself could have funded a group working in such a field – but he seems to have been rather cautious and unenthused. At most one can

say that one had professional science being done by nonprofessionals.

More generally, after Darwin, evolution was very much a topic to be found and discussed in the general domain. One major sphere of activity and influence tended to be in the new museums of natural history that were being built in Britain, on the continent, and particularly in the great cities of the United States. It was there that one went to see the wonderful panoramas of biological change, from primitive forms up through lesser animals until one reaches the primates with humans out peak. With the fabulous finds of fossil dinosaurs in the Western United States and Canada in the second half of the nineteenth century, museums became focal points of immense popular interest.

Natural selection – and even more sexual selection – also had a big presence in the popular domain. In literature – novels and poetry! From the first, creative writers seized on Darwin's mechanisms and showed how they work in human affairs (Ruse 2017b) or canine affairs, as is shown in Jack London's classic *The Call of the Wild*:

His teeth closed on Spitz's left fore leg. There was a crunch of breaking bone, and the white dog faced him on three legs. Thrice he tried to knock him over, then repeated the trick and broke the right fore leg. Despite the pain and helplessness, Spitz struggled madly to keep up. He saw the silent circle, with gleaming eyes, lolling tongues, and silvery breaths drifting upward, closing in upon him as he had seen similar circles close in upon beaten antagonists in the past. Only this time he was the one who was beaten.

There was no hope for him. Buck was inexorable. Mercy was a thing reserved for gentler climes. (London 1903, 24)

Interestingly, London – like most of the writers on the topic – saw fully that selection does not just lead to the success of the brute, the killer. It can – as Darwin stressed – lead also to harmony and altruism. No sooner has Buck taken over the pack than he turns into a headmaster! Everyone now benefits from Buck's success, dogs and men. “Highly as the dog-driver had forevalued Buck, with his two devils, he found, while the day was yet young, that he had undervalued. At a bound Buck took up the duties of leadership; and where

judgment was required, and quick thinking and quick acting, he showed himself the superior even of Spitz, of whom Francois had never seen an equal" (26). And slackers are pulled back into line:

Pike, who pulled at Buck's heels, and who never put an ounce more of his weight against the breast-band than he was compelled to do, was swiftly and repeatedly shaken for loafing; and ere the first day was done he was pulling more than ever before in his life. The first night in camp, Joe, the sour one, was punished roundly – a thing that Spitz had never succeeded in doing. Buck simply smothered him by virtue of superior weight, and cut him up till he ceased snapping and began to whine for mercy. (26)

In poetry too, this poem, "Natural selection," by the young woman (in her sex's interest in Darwinism, she was by no means atypical) Constance Naden, is really about sexual selection. But it makes the point.

I HAD found out a gift for my fair,
I had found where the cave men were laid:
Skulls, femur and pelvis were there,
And spears that of silex they made.

But he ne'er could be true, she averred,
Who would dig up an ancestor's grave—
And I loved her the more when I heard
Such foolish regard for the cave.

My shelves they are furnished with stones,
All sorted and labelled with care;
And a splendid collection of bones,
Each one of them ancient and rare;

One would think she might like to retire
To my study—She calls it a "hole"!
Not a fossil I heard her admire
But I begged it, or borrowed, or stole.

But there comes an idealess lad,
With a strut and a stare and a smirk;
And I watch, scientific, though sad,
The law of selection at work.

Of Science he had not a trace,
He seeks not the How and the Why,
But he sings with an amateur's grace,
And he dances much better than I.

And we know the more dandified males
By dance and by song win their wives—
'Tis a law that with *avis* prevails,
And ever in *Homo* survives.

Shall I rage as they whirl in the valse?
Shall I sneer as they carol and coo?
Ah no! for since Chloe is false
I'm certain that Darwin is true
(Naden 1999, 207–8)

In short, although there was some limited amount of evolutionary morphology in the universities, by and large evolution through selection was not a science for the professional scholar. In the public domain, the story was very different. Thanks to Darwin, evolution was transformed from a pseudoscience to a popular science, for all that it had yet to achieve the status of full-blooded professional science.

Today' Science

After the *Origin*, probably the most important event in the history of evolutionary theory was the work in the 1860s, on the principles of heredity, by the Moravian monk, Gregor Mendel, or, perhaps more pertinently, the rediscovery of his work at the beginning of the twentieth century (Provine 1971). People often regret that Darwin and Mendel were working independently. If only they had got together and collaborated, then, much earlier than it was, the course of evolution would have been advanced significantly. Or, at least, this is the supposition. In fact, Mendel was working on rather technical questions about plant breeding (Stern and Sherwood 1966). It is highly improbable that had Darwin read his work he would have grasped the full significance. Conversely, Mendel did in fact read the *Origin of Species*. But he never once thought that what he himself was doing contributed to the story. Instead, from Mendel's marginalia we can infer that the big question that the *Origin* posed to him was whether or not it was a theory acceptable to a Catholic priest!

Becoming a Professional Science

Once rediscovered, Mendel's ideas were developed quickly and fused with a growing understanding of the physical nature of the organic cell. By the middle of the second decade of the twentieth century, Thomas Hunt Morgan and his

students at Columbia University in New York City had developed the so-called classical theory of the gene (Allen 1978). This theory sees the unit of heredity, the gene, as a particle on one of those long, stringlike entities, chromosomes, in the center of the cell, the nucleus. Chromosomes come in pairs, so genes are paired, and the time of reproduction one of each gene pair gets passed on through the sex cells to the next generation. The important thing is that the genes remain unchanged from generation to generation, changing only occasionally when they spontaneously “mutate” from one form to another. As Darwin supposed, mutation is random in the sense that it does not occur according to need, but it is not random in the sense of being uncaused. Today, much is known about the physical causes of mutation.

Perhaps expectedly, when Mendelian genetics was first rediscovered, its supporters inclined to think that it offered a rival to a Darwinian picture of evolution through natural selection. For a while, there was a bitter controversy between the Darwinian “biometricians” and the Mendelian “geneticists” (Olby 1988). However, by the second decade of the century, biologists were starting to see that Darwinian selection and Mendelian genetics are not contradictories but complementary parts of the whole picture. Because selection is something which works only on populations not on individuals, it was necessary to generalize Mendelian genetics to cover populations. This was done by two researchers after whom the key premise, the Hardy-Weinberg law, is named.

In Newtonian mechanics, his first law (that bodies remain at rest or in uniform motion unless acted upon by a force) acts as an equilibrium law, against which one can now introduce intervening or distorting forces. In “population genetics,” the Hardy-Weinberg law has the same function (Ruse 1973). This law essentially tells you that in large populations with no impinging forces – no selection, no mutation, or no immigration or emigration in or out of the population – the gene ratios will stay constant. In other words, it is the background equilibrium against which one can now introduce distorting forces like mutation and selection.

Around 1930, several mathematically gifted biologists developed this theory, something that is the basis of evolutionary thinking even to this day. In England particularly important were Ronald A. Fisher (1930) and J. B. S. Haldane (1932). In America particularly important was Sewall Wright (1931). As it happens, although their theorizing was formally equivalent, the English and the Americans (Fisher and Wright particularly) had very different visions of the evolutionary process (Provine 1986). For Fisher, it was always Darwin’s mechanism first and foremost, as he saw populations being molded and shaped by natural selection occurring on working on new variations, mutations. For Wright, things were rather more complex. Although he gave selection an important role in his “shifting balance theory” of evolution, random forces or effects were highly significant. Wright pointed out that, in small populations, the vagaries of breeding might be expected to overcome weak forces of selection. Hence, one might get ratios of genes “drifting” from one level to another. Wright believed that this is very significant in the evolutionary process and that, consequently, whereas Fisher with his selectionism saw adaptation everywhere, Wright was much more inclined to think that many features are adaptively neutral.

We have here echoes of the differences at the time of the *Origin*, with Darwin ultra-keen on adaptation and Huxley somewhat indifferent.

With the theory spelt out, the empiricists moved in. In England, particularly important was the Oxford biologist E. B. Ford (1964). He was the founder of the school of evolutionists which he labeled “ecological genetics.” Ford and his collaborators worked extensively on organisms that reproduce rapidly, including butterflies, moths, and small invertebrates like snails. Particularly noteworthy were some studies done in the 1950s by A. J. Cain (1954) and Philip Sheppard (1958) on the ways in which snail-shell colors and markings provide adaptive camouflage against predators, mainly thrushes. In the United States, the most important figure was the Russian-born geneticist Theodosius Dobzhansky. He was the author of *Genetics and the Origin of Species* (1937), a work in which he showed how Wright’s

shifting balance theory could be applied to many problems, particularly variations in *Drosophila* (fruit flies). Dobzhansky was also important for encouraging researchers in other fields to turn to evolutionary problems. Significant were the German-born systematist Ernst Mayr, author of *Systematics and the Origin of Species* (1942); the paleontologist George Gaylord Simpson, author of *Tempo and Mode in Evolution* (1944); and then a little later the botanist G. Ledyard Stebbins, author of *Variation and Evolution in Plants* (1950). Thanks to the work of these people, their collaborators and associates, and above all their students, by the hundredth anniversary of the *Origin of Species* in 1959, finally Darwin's work had matured into a fully professional science. In England, it was generally known as "neo-Darwinism," and in America, paying tribute to Mendel as well as Darwin, as the "synthetic theory of evolution" (Maynard Smith 1958; Ruse 2006).

The last half-century has seen a huge amount of work, both theoretical and empirical, tackling evolutionary problems from a Darwinian perspective. To give a flavor of what has been produced, it will be convenient to follow the pattern of the argument in the *Origin*. In that way, we will get an idea not only of what has been done but how things have advanced since Darwin himself. Generally, the Darwinian belief in the ubiquity of adaptation has prevailed, although we shall see that critics do persist.

Artificial and Natural Selection

We start with artificial selection. There are now a many case studies showing how continued, systematic selection by human beings can have huge effects on the genetically based nature of animals and plants. To take but one example, justly famous is very long-term study (it started back in 1896) done at the University of Illinois on the oil content of corn (what Europeans call maize). At the beginning of the study, the oil content was in the range of 4–6%. By the end of the study, in the 1970s, thanks to continued selection, the oil content had increased threefold to around 16%. This is change in itself (Mangelsdorf 1974; Dudley 1977). However, one objection that

Darwin's contemporaries (notably Thomas Henry Huxley) often made was that artificial selection seems never to lead to new species, meaning separate groups of organisms unable to interbreed. Today we have such cases. One experiment started with yellow and white varieties of corn. Selecting intensely for individuals that mated with others of the same color, in a very few generations, experimenters produced two groups with very little cross-fertilization. It turned out that there was a good reason for this. The white variety flowered at an earlier time than the yellow variety, and hence pollination of the two varieties was kept quite separate.

Moving on to the key part of the *Origin* where natural selection was introduced, what evidence do we have today of this mechanism in action? It will be remembered that Darwin himself inclined to think that we would never have any direct observations of natural selection changing organisms. Remember though, although I am not sure that Darwin picked up on the significance, late in his life, one of his correspondents drew his attention to what today is probably the most famous example of evolution in action, so-called industrial melanism. Butterfly collectors cherish exceptional or strange forms. By the middle of the nineteenth century, in England, it was becoming clear that increasingly in some species of butterfly, there were dark or so-called melanic forms. Darwin's correspondent hypothesized that there is a reason for this: industrial pollution. By the end of the nineteenth century among students of butterflies and moths, industrial melanism was a well-recognized phenomenon, and researchers realized that natural selection was at work (Tutt 1891). However, it was not until the middle of the twentieth century that one of Ford's groups of ecological geneticists, H. B. D. Kettlewell (1973), working in areas around Oxford, finally showed definitively that the melanic forms of moths and butterflies are indeed sustained by selection for camouflage. Presciently, Kettlewell suggested that were pollution ever to be controlled, we might expect to find that the melanic forms would decline and the normal forms regain their ascendancy. Since the 1950s, in Britain there has been major overall drive to reduce air

pollution. Trees today are far less blackened than they were 50 years ago. And as predicted, we find that the lighter forms of butterflies predominate and the melanic forms are consequently significantly lower. A beautiful case of natural selection is being observed in action (Majerus 1998).

We need not dwell here at any length of the discoveries about heredity. We have seen already in this entry that the field has been transformed since the days of Charles Darwin. Of course, genetics itself has not stood still. The major event after the rediscovery of Mendelian genetics was obviously the deciphering of the structure of the DNA molecule in 1953, by the American James Watson and the Englishman Francis Crick. The double helix led to a huge amount of work uncovering the basic secrets of heredity at the molecular level. Repeating an earlier pattern, at first it was thought that the new genetics was a rival to Darwinian selection; but then, again repeating an earlier pattern, it was seen how in major respects molecular biology is a handmaiden to the evolutionist. Most notably, in the 1960s, the geneticist Richard Lewontin and his associates used their knowledge of molecular biology, combined with new experimental techniques, to peer in much greater detail into the nature of variation in wild animals and plants. It will be remembered how important it was for Darwin's theory that there be such variation. In its absence, natural selection is ineffectual. Using "gel electrophoresis," Lewontin and others showed just how much variation there is, leading to a level of understanding quite beyond anything that Darwin offered in the *Origin of Species* (Lewontin 1974).

Consilience

What of the consilience of inductions? We have seen how this was a crucial part of the argumentation of the *Origin*, as Darwin strove to show that natural selection is a true cause. Simply put, the consilience as such exists unchanged in today's evolutionary studies. But it has been transformed completely by new findings and new theories that have enriched our understanding of the different areas of the life sciences. Following Darwin, let us go briefly through social behavior, paleontology,

biogeographical distributions, systematics, morphology, and embryology.

The study of the evolution of social behavior has seen explosive growth in the past half-century. "Sociobiology," as the field is now called, has many, many exciting discoveries to report. Thanks to the work of leading exponents – particularly William Hamilton (1964a, b) in England and Edward O. Wilson (1975) in America – we have a detailed and sophisticated grasp of how natural selection has shaped and molded the behaviors of organisms in groups (Ruse 1979). Particularly important was Hamilton's insight that organisms need not reproduce directly themselves. It is enough that close relatives (that is to say, organisms sharing the same genes) reproduce, so one does it by proxy as it were. "Kin selection" has proven to be a very powerful tool of investigation (Maynard Smith 1982). Sociobiologists have been able to analyze the relationships existing within groups of ants, bees, and wasps (Hymenoptera). They point to the fact that sterile workers share the same genes as their fertile nest mates, and hence, inasmuch as they help these nest mates to reproduce, they are themselves reproducing, in the sense of passing on copies of the genes. In other words, today we can go a step beyond Darwin and show that nests need not be considered simply as united individuals. There can be different reproductive strategies even within the nest. Although, what is still emphasized is Darwin's prime insight that selection works for the benefit of the individual ultimately and not the group.

One of the biggest problems that Darwin had about the fossil record was that it seemed to start abruptly in the Cambrian. Darwin did not have absolute dates, but we know now that this occurred rather more than half a billion years ago. Adding to Darwin's worries, the earliest known organisms were invertebrates like trilobites, and these are extremely sophisticated. Where then were the simple Precambrian organisms that Darwin's theory presupposed? Darwin spent much effort offering ad hoc hypotheses to explain the absence. Today, however, it is not necessary to invent such hypotheses because we have full and detailed knowledge of the fossil record going back nearly four billion years

(Knoll 2003; Knoll and Carroll 1999). Moreover, as expected, the very earliest organisms are very simple, and then, coming up to the Cambrian, they get more complex (Benton 1990, 2009; Raup and Stanley 1978; Sepkoski 2012; Ruse 2006, 2013a).

In addition to speaking to all of this, we have been able to fill in many of the gaps in the later record (Wilford 2006). Some of the most exciting discoveries in the past half century or more have been in that area leading up to *Homo sapiens*. Equaling archaeopteryx and its importance, in the early 1970s, American paleoanthropologist (student of human origins) Don Johansson and his colleagues discovered “Lucy,” *Australopithecus afarensis* (Johansson and Edey 1981). This is a small primate, about four million years old, who lived in East Africa. She is humanlike in that she walked upright, and yet she had a brain the size of the chimpanzee (about 400 cc as opposed to modern humans who have brains about 1200 cc). Some of the most troublesome “missing links” are missing no longer. From being a worry to the Darwinian evolutionist, the fossil record has become one of its greatest sources of comfort.

The coming of continental drift, fueled by the mechanism of plate tectonics, has obviously transformed our understanding of the geographical distributions of organisms (Hallam 1973; Frankel 2017). We can today readily explain why it is that often we find fossils representing the same species in very different parts of the world – for instance, in Africa, India, and Antarctica. It is simply because, at some point in the past, these different landmasses were all joined together and their inhabitants could roam freely across. The lands started to drift apart, and the fossil remains of the earlier inhabitants were separated by vast tracts of ocean.

At the same time, thanks to more sophisticated understandings about how organisms can travel from one area to another, today’s evolutionists can throw considerable light on the relationships between the living organisms on different landmasses. For instance, there has been much successful effort devoted to the relationships between the inhabitants of North America and the inhabitants of South America. It is shown how there was an interchange when the lands were joined and how newcomers succeeded with greater or lesser

success when they traveled into new ecological surroundings. The overall theory is still very Darwinian, but in all details it has been completely transformed.

Systematics underwent a major revolution of its own about 30 years ago (Hull 1988). Thanks to new techniques, brought about in large part by the introduction of computers which were able to digest huge amounts of information, new ways of classifying organisms were devised. “Cladism” is a far more sophisticated way of working out genealogical relationships than anything that existed previously. It is true that some of the early enthusiasts for cladism were less than enthusiastic Darwinians. They were not much interested in adaptation – after all, by the time that the taxonomist gets to work the specimens are usually dead and hence not using their body parts – and so tended to downplay the need of selection. But, with the passage of time, it has become more and more apparent that the classifications of today represent not just evolutionary relationships but evolutionary relationships that were brought about by natural selection.

Some of the most exciting discoveries of all have occurred in morphology, considered in a broad sense. Thanks to molecular biology, we can now compare organisms right down at the most basic levels, far below the physical features known to Darwin and his contemporaries. Truly outstanding has been the way in which molecular biologists have been able to show that there are homologies in the DNA molecule between organisms very far apart, notably between humans and *Drosophila* (fruit flies) (Ruse 2006; Carroll 2005; Carroll et al. 2001). This does not disprove Darwinism. Anything but! What it shows rather is that nature does not build each organism from scratch, as it were. Rather organisms are built on modular principles, rather like Lego toys. We start with a set of different parts: building things one way we get fruit flies and building things another way we get humans. It is entirely analogous to Lego: building things one way we get the White House, and building things another way we get the Statue of Liberty. The important point is that it is selection that guides the process.

Finally, we come to embryology, or as it is known today “evolutionary development” (evo-devo). Again, there are echoes of the Huxley stand on adaptation. We find enthusiasts who suggest that selection is unimportant, merely acting as a garbage collector of failed new forms. Truly, this is far from the case. What today’s developmental biologists are able to show is that often change does not involve new genes making new characteristics as such. Rather, change comes about through adjusting rates of growth (Gould 2002). By stretching an organism or increasing the number of segments, you can often make something very new indeed, without the need of finding whole new body parts. But how it is determined which organisms survive and reproduce, and which do not, is of course a Darwinian matter. Selection monitors organisms in every generation. It never takes a break. In other words, as so often is the case, the new theories and Darwinian selection are complements rather than rivals.

Conclusion

The great Greek philosopher Heraclitus said “you cannot step into the same River twice,” meaning that everything changes. The equally great Greek philosopher Parmenides said “nothing changes.” The fate of Darwinian theory shows that both philosophers were right! Everything has changed since the days of the *Origin of Species*. Nothing has changed since the days of the *Origin of Species*. If Charles Darwin came back to Earth today, he would be delighted.

His Place in Culture

Charles Darwin’s theory of evolution through natural selection was always more than just a scientific theory. From the first, people recognized that it had major implications throughout culture. In this concluding entry, we shall consider some of these implications. Let us start with religion.

American Religion

We have seen that, for all there was some initial objection to the message of the *Origin*, by about 1870 even religious people (with exceptions to be

noted below) had taken Darwinism on board (Roberts 1988; Moore 1979). They had accepted the fact of evolution. Although, as with just about everybody else, there were serious questions about whether or not natural selection was that powerful and effective. One place where Christians generally wanted to make an exception was with respect to humankind. It was not that they were denying that our physical bodies had evolved but rather that when it came to immortal souls, special intervention was deemed necessary. However, given that everybody agreed immortal souls are not scientific notions, this was not terribly troublesome.

One important point where Darwinism did have a significant effect was with respect to natural theology, that part of theology that attempts to get to God through reason rather than through faith (Ruse 2018). Although Darwinism clearly challenges aspects of revealed theology – the part of theology, like belief in the Bible, that does center on faith – it was for most people not a big issue. The Genesis stories had long been considered metaphorical. Natural theology was different. Before Darwin, even skeptics like David Hume admitted that something extra seems to be needed in order to explain the design-like nature of organisms. After Darwin, even if natural selection was not all-powerful, it was realized that we were well on the way to providing natural explanations of the adaptive nature of organic life. This did not lead straight to atheism; however, it was realized that Darwinism was a severe blow against those who argued that the design-like nature of the organic world necessitates a belief in a God. As Thomas Hardy shows in his poem “Hap,” written in 1866 less than a decade after the *Origin*, it was not so much that God was nonexistent but that He was irrelevant, indifferent to our fate.

IF but some vengeful god would call to me
From up the sky, and laugh: “Thou suffering thing,
Know that thy sorrow is my ecstasy,
That thy love’s loss is my hate’s profiting!”

Then would I bear, and clench myself, and die,
Steeled by the sense of ire unmerited;
Half-eased, too, that a Powerfuller than I

Had willed and meted me the tears I shed.

But not so. How arrives it joy lies slain,
And why unblooms the best hope ever sown?
—Crass casualty obstructs the sun and rain,
And dicing time for gladness casts a moan. . . .
These purblind doomsters had as readily strown
Blisses about my pilgrimage as pain.
(Hardy 1994, 5)

One should say that here, as always, the discussion was not going on in vacuum. Many theologians independently of science were already feeling uncomfortable about natural theology. For instance, the great English religious thinker John Henry Newman, who started life as an Anglican but ended as a cardinal in the Church of Rome, always downplayed the importance of natural theology. He felt that the God of the natural theologians – the God of power and omnipotence – was not the God of Christianity, the God of love and compassion (Ruse 2015). So, he for one rather welcomed Darwinism rather than repudiated it. What Newman did not encounter, as he made his move from Canterbury to Rome, was much objection to the idea of evolution as such. By and large, the Catholic Church decided to sit this one out (Appleby 1999). At the end of the nineteenth century, it was much more concerned with the rise of modernism and like issues than with scientific theories. It is true that there was some opposition within the church to evolution, but it was far from universal. So long as evolution was not taken to be denying essential elements of faith, it was left alone.

Thus, things continued and would probably have continued down to this day had not other factors arisen. For a number of reasons, Americans saw the growth in the nineteenth century of a homegrown form of Protestant, evangelical Christianity (Noll 2002). This was a Christianity which was firmly Bible-based and that insisted on reading the creation stories of Genesis in a very literal fashion. There are many reasons for the development of this movement, not the least of which were the quarrels both before and after the Civil War. Particularly in the South, before the war the Bible was taken as justification for slavery. Then, after the defeat in the war, the Bible was used as

justification for the troubled state of the South. Sermon after sermon was preached on the theme that God afflicts those most whom he loves the most and explicit analogies were drawn between the Israelites in captivity in Babylon and the South pressured by outsiders from the North.

Evolution was added to this mix (Numbers 2006). After the war, in the North there was a great drive toward industrialism, education, and science generally. Evolution was taken to be the epitome of the underlying philosophy of progress and was embraced by the general population as well as by their leaders. After the war, in the South there was a longing for a mythical past and determination to slough off changes imposed from outside. Evolution was as important to Southerners as it was to Northerners, but in the South it was taken as a symbol of all that is wrong. It had to be disproved in every possible way.

As is well known, this conflict continued into and through the twentieth century. In 1925 in the state of Tennessee, a young schoolteacher John Thomas Scopes was prosecuted for teaching evolution to his students (Larson 1997). The offense was led by three-time presidential candidate William Jennings Bryan and the defense by the notorious, agnostic lawyer Clarence Darrow. Both sides claimed victory. Scopes was found guilty, but the conviction was overturned on a technicality. The South took the trial as a symbol of defiance. The North took the trial as a symbol of the importance of science and the crudity of thinking in the South. One chilling effect was that, after the Scopes trial, evolution was pretty much banished from textbooks and indeed from any teaching in the schools of the nation. Paradoxically, this happened as much in the North as in the South, because textbook manufacturers tended to produce one uniform edition, dumbed down to the lowest, acceptable level.

Creationism

Biblical literalism, particularly focusing on the absolute truth of the Genesis stories of Creation, revived strongly after the Second World War. Americans were terrified of nuclear conflict with the Russians. Thus, an evangelical religion that focused on cataclysmic events in the past –most

notably Noah's Flood – things taken as premonitions of Armageddon to come, found a ready market. *Genesis Flood*, published in 1961, authored by biblical scholar John C. Whitcomb and hydraulic engineer Henry M. Morris, was a runaway bestseller. Creationism, or as it was sometimes called Scientific Creation, found many adherents, paradoxically just at the time when Darwinian evolution was finally moving forward rapidly as a fully-fledged, professional science.

There were bound to be clashes. In 1981, in the state of Arkansas, a law was passed insisting that schoolchildren be taught Creationism along with evolution (Ruse 1988). Thanks to the US Constitution separating church and state, it was soon found illegal and overturned. However, nothing daunted, like the phoenix literalists rose again from the ashes, and by the 1990s a new version of literalism was being promoted. The so-called Intelligent Design Theory claimed that there are aspects of the organic world that are “irreducibly complex” and thus cannot be explained by natural means (Johnson 1991; Behe 1996; Dembski 1998; Dembski and Ruse 2004). The motor driving the tail, the “flagellum,” on bacteria was one example. One must therefore invoke a designer, and, although the proponents tended to be rather cagey on the subject, there was little doubt that this designer was to be identified with the God of the Bible. Creationism lite, perhaps, but Creationism nevertheless (Pennock 1998; Miller 1999). Again, a court case occurred and again literalism was pushed back (Pennock and Ruse 2008). But it continues to thrive today.

Interestingly, in recent years, evolutionists have gone in parallel directions to the Creationists, inasmuch as they have entered the public domain and started to argue strongly for the imposition of their views against all alternatives. Undoubtedly sparked by the horrors of 9/11, when Moslems flew planes into the World Trade Center and the Pentagon, these fanatics have argued vehemently not just for evolution but against all forms of Christianity and other religions. The so-called New Atheists, among whom one can name the British biologist and popular science writer Richard Dawkins (2006) and the English-born, American-residing,

journalist Christopher Hitchens (2007), argue that all forms of religion are not just false but socially dangerous (Also Harris (2004) and Dennett (2006)).

For better or for worse, just as in the late nineteenth century, evolution was taken as a banner for modernity and right-thinking, so today for the new atheists, evolution has a very similar role (Ruse 2019c). And we find a counter in the Intelligent Design Theorists, who usually cannot wait to move on from the fossil record to condemnations of modern life, including abortion on demand and gay marriage. The paradox is that, although Charles Darwin would almost certainly have agreed with many of the claims made by the new atheists, he would've drawn back with horror from their tactics. Ever the English gentleman, Darwin would have thought that it is socially crude and politically inopportune to attack Christianity in the open way advocated by Dawkins and Hitchens and associates.

This clash over evolution is continuing and no resolution is yet in sight. Up to recently, it was very much an American phenomenon. However, increasingly it is being exported to other countries (Numbers and Stenhouse 1999). For instance, Creationism of various kinds has found receptive ears in several Muslim countries, and there too evolution is taken to be a symbol of all that is wrong. Likewise, in Britain and in Australia, one finds enthusiasts for Creationism and attempts to introduce it into the schools. It is surely paradoxical that, at a time when evolutionary biology has matured into one of the most important areas of natural science, in the public domain, it should be under ever-increasing pressures.

One must add that complexifying the picture is the fact that many Darwinians make somewhat of a secular religion from their science, a sort of evolutionary humanism (Kitcher 2014). Picking up on what was said earlier about the Providential underpinnings of the Christian cause and the Progressivist underpinnings of the Darwinian cause, the latter is used as a basis for supplying all that one finds in conventional religions, especially Christianity – a story of origins, a special exalted place for humankind, moral directives (see more in the next section), and more (Ruse 2005, 2017b,

2018, 2019b). Darwinians are fully entitled to do this if they want – not all do want (having given up the spiritual religion of childhood they are loath to replace it with a secular religion of adulthood) – but it must be realized that this is an additional goad to the religious, especially the evangelical religious, and it is little wonder that there is opposition and bitterness.

Social Darwinism

Closely related to the debates about religion have been debates about the implications of Darwinism for moral and social behavior. As it happens, after the *Origin* Darwin was but a minor player in this movement, and, although later generations labeled the movement “Social Darwinism,” in many respects Darwin stayed on the sidelines (Ruse 2017b). The main proponent of bringing evolutionary thinking into the area of social and moral thinking and behavior was Herbert Spencer. He argued strongly that society should be based on an evolutionary foundation. Notoriously, he abstracted a version of the struggle for existence from the animal and plant world and applied it to the social world. He therefore argued for a rather extreme libertarian or laissez-faire form of society, where government at plays but a little role and individuals and organizations are allowed to battle it out for supremacy (Richards 1987). It is hardly surprising that some of Spencer’s most enthusiastic supporters were American industrialists, notably John D. Rockefeller the first and the steel baron Andrew Carnegie (Ruse 2009). As we have seen, this kind of thinking also found an enthusiastic response in several of the novelists writing around the end of the nineteenth century, notably Jack London and his *The Call of the Wild*.

However, as always – and as we have seen already – things are a little more complex than one might suspect from popular accounts. Not all who brought evolution to bear on social issues were enthusiasts for libertarian ways of behaving. For instance, Alfred Russel Wallace (1900) was always a socialist. He therefore emphasized what he took to be the group effects of natural selection, arguing that state support is in fact biologically justified. Spencer became much more holistic over the years – society as an organism – and

dropped many of the cruder exhortations (Spencer 1879). And then, somewhat off at a tangent, there was the Russian anarchist Prince Peter Kropotkin (1902). He argued that animals naturally evolved a sense of “mutual aid.” This applies also to humans, who would be best off in small societies without heavy government intervention. He thought that given such a social situation, human happiness would be maximized in a way that is not possible otherwise.

Today’s Creationists make much of links that they see between Darwinian theory and the National Socialist movement that swallowed Germany in the 1930s and 1940s (Weikart 2004). They argue that there is a direct line from the *Origin*, with its talk about struggle for existence, to Hitler’s demands for living room for the Germans at the expense of nations to the East. To be fair, something must have caused Hitler and his vile associates, and it would be naive to pretend that nothing in Social Darwinian theorizing (whether or not this was due to Darwin himself) had any effect in this respect. However, there were clearly many other factors leading to the national socialists, and these had at least if not more of an effect (Richards 2013). For a start, there was the volkish movement in Germany coming out of the nineteenth century, something obsessed with the glory in the past (think of all those Wagnerian operas) and looking forward to triumph in the future. Then there were issues to do with religion, and it is certainly not implausible to think that the anti-Semitism of Christianity had at least some effect on Nazi thinking. It is also worth mentioning that although one does sometimes find Hitler parroting Social Darwinian ideas, in many respects the Nazis were deeply opposed to Darwinian thinking (Ruse 2018). For a start, it is of the essence of evolution that all humans are related. Aryans and Jews and others are people of one blood. Nazi theorists realized this, and for this reason one finds that there was often a very distant attitude toward evolution. In short, one should be very wary of simple links between Darwin and the horrible social movements of the twentieth century.

Do we find Social Darwinism alive and well today? Certainly not by that name; however,

undoubtedly, there are those who promote ethical and social ideals in the name of evolution (Ruse 2005, 2019b; Ruse and Richards 2017). One of the best known in America today is Edward O. Wilson (1984, 2002, 2012), whom we met in the last entry as one of the founders of sociobiology. Wilson, who was raised as an evangelical Christian, is ardent in his belief that our evolutionary origins are highly significant, both explaining our ethical inclinations and pointing to the moral tasks that humankind faces today. In particular, he argues strongly that humans have evolved in symbiotic relationship with the rest of nature – a world of plastic would literally be fatal to us all – and he argues therefore that morally we have an obligation to preserve biodiversity. Faithful to his beliefs, in recent years Wilson has been much involved in campaigns to preserve and protect the Brazilian rainforests (Wilson 1992, 1998).

Knowledge

Moral issues are but one side to traditional philosophical inquiry. There is also the question of knowledge (Ruse 1986, 2009). If we are truly modified monkeys rather than modified mud, that is to say if we are truly the end result of evolution through natural selection rather than the creation of a good God miraculously on the sixth day, does this not have immediate and important implications for the ways in which we think and reason? Many today would argue that it does. In fact, this is a line of thought which goes back to Darwin himself, although (as with Social Darwinism) it was more in America that these ideas were picked up.

In the latter part of the nineteenth century and into the twentieth century, one has the so-called “Pragmatist” movement – Charles Sanders Peirce (1997), William James (1904), and then somewhat later John Dewey. They all acknowledged a great debt to Darwin. If the Darwinian process is one of putting up new variations and then subjecting them to the fire of the struggle for existence, then is not knowledge acquisition something very similar? One comes up with new ideas and puts them into the general discourse and then sees how they fare. Good ideas succeed, bad ideas fade from sight. It is not a matter of ultimate truth or falsity but much more a very pragmatic matter. What works? The

Pragmatists argued that if something is successful for a while, then that is the best we can hope for. It is all very Darwinian (Wiener 1949). There is no absolute truth, no trees falling in the forest and making a sound when no one is around.

There are still many who would argue this way today. However, increasingly as our knowledge of the human brain is developed and refined, more and more people take a slightly different tack. They argue strongly that the ways in which we think and reason are a reflection of adaptive strategies that proved successful in our past. Even scientific reasoning, it is argued, has its justification in evolution (Cosmides 1989). Why should we take something like a consilience of inductions to be a good form of reasoning? Simply because those protohumans who thought in consilient ways tended to survive and reproduce and those that did not. Those humans who took full account all the clues and reasoned (let us say) that they point to an unseen-but-hovering predator stood a better chance of living until tomorrow than those who simply ignored the clues. They may have been happy in their ignorance. One hopes so, because their lives would tend to be short.

Conclusion

As with religion, debates about ethics and knowledge are ongoing. There are those who are enthusiastic Darwinians. There are those who are not (Plantinga 1991; Nagel 2012; Fodor and Piattelli-Palmarini 2010). But for or against, no one denies that Darwin’s ideas stimulate and provoke. For that reason if for no other, no educated person today should be ignorant of the life and labors of Charles Darwin. In science and in culture, he is one of the seminal figures of all time. I hope I have shown you also that his ideas are not just important. They are incredibly interesting.

Cross-References

- ▶ [Adaptation](#)
- ▶ [Adaptation and Natural Selection](#)
- ▶ [Alfred Russel Wallace \(1858\)](#)

- ▶ Charles Lyell
- ▶ Evolved Moral Foundations
- ▶ Natural Selection
- ▶ Reproductive Value
- ▶ Richard Dawkins on Constraints on Natural Selection
- ▶ Sexual Selection
- ▶ Social Darwinism

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Charles Darwin: Theory of Natural Selection

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Synonyms

[Survival of the fittest](#)

Definition

Natural selection was the term Darwin used to describe the evolutionary process by which favorable or advantageous traits and characteristics are preserved and unfavorable or disadvantageous ones discarded.

Introduction

Natural selection was the term Charles Darwin (1809–1882) used for the main mechanism by which he understood evolution to work. Natural selection was first announced publicly in a joint reading of his and Alfred Russel Wallace's papers at the Linnean Society in July 1858 (Darwin and Wallace 1858) and first developed in published form in Darwin's most important book, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859). As the full title of the Origin indicates, natural selection was key to Darwin's evolutionary argument, and the fourth chapter of the Origin was devoted to an exposition

of its operation. Darwin's definition of natural selection was deceptively simple: "This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection" (Darwin 1859). Packed within the term, however, were a series of assumptions and implications which Darwin had taken over 20 years to work through and which critics of his thought subsequently sought to pull apart.

At its simplest, natural selection describes a process in which favorable or advantageous characteristics – physical or psychological – are preserved and unfavorable or disadvantageous characteristics are discarded. This is a "natural" process because it is said to occur without the conscious intervention of either the organism which is undergoing change or any external selector. The process of "selection" is in fact one of the preservation and discarding, determined by the utility or disutility of any given characteristic. What is useful is "selected," in the sense that it is preserved and strengthened across generations; what is useless is weakened and eventually discarded across generations. Natural selection, therefore, requires an extended time-scale and, like all evolutionary theories, depends upon inheritance.

Darwin's theory of evolution by natural selection is premised upon two prior conditions, a naturally occurring variation within species and an ongoing "struggle for life" among all organisms, in which the fittest survive and the weakest are eliminated. Natural selection occurs only as a result of variation and the "struggle for life" but is not synonymous with them. As Darwin explained in the *Origin*:

If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many

variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection. (Darwin 1859)

This process of natural selection is the core of Darwinism and constitutes the essence of Darwin's distinct contribution to science.

The Origin of Natural Selection

Darwin developed his understanding of natural selection even before he began to use that specific term. Although Darwin first developed a distinctive understanding of evolution in the late 1830s, it was not until the early 1850s that he came to regularly and confidently refer to his theory as "natural selection." So enamored of the term did he then become that after he began work on his never-to-be-completed "big species book" in 1856, he decided that it would be entitled *Natural Selection* (Stauffer 1975).

In his first unpublished "Sketch" of his species theory, however, written in 1842, the term "natural selection" appears only twice – once as a subheading and once in the main body of the text – in over 15,000 words. Despite the "Sketch" covering, in outline, much of the same subject matter that Darwin would later tackle in the *Origin*. The term is only slightly more prominent in Darwin's also unpublished 1844 "Essay": appearing 6 times in the 60,000 words that again anticipate the structure and argument of the *Origin* (Darwin 1909). One of the few aspects of the *Origin* that is not anticipated in these earlier renderings of Darwin's theory was the separate consideration of natural selection that formed the fourth chapter of his book.

The relative absence of the term, and the fact that neither the "Sketch" nor the "Essay" did Darwin trouble himself to introduce or explain the term, does not diminish the centrality of the underlying idea to both texts and the strong connecting thread between these two manuscripts and the *Origin*. Nonetheless, the fact that Darwin used the term

only sparingly in the early 1840s, compared with well over 200 times in the *Origin* is striking. What seems to have changed is that Darwin had become accustomed to the term during his studies of domestic breeding. After Darwin's publisher John Murray complained, upon receipt of the manuscript of the *Origin*, about the obscurity of the term "natural selection," Darwin wrote to the geologist Charles Lyell expressing some surprise. "Why I like the term," he told Lyell, "is that it is constantly used in all works on breeding, and I am surprised that it is not familiar to Murray: but I have so long studied such works that I have ceased to be a competent judge" (<http://www.darwinproject.ac.uk/DCP-LETT-2439>).

This remark is doubly illuminating: it confirms Darwin's derivation of the term and that his use of it grew out of his immersion in the world of animal breeders. This is significant because breeders used the term "natural selection" as convenient phrase to contrast unknown causes of changes in species with the deliberate changes which they actively sought to engineer. This contrast, and subsequently the analogy, between "natural selection" (changes that arose without any deliberate action or design on the part of the breeder) and "artificial selection" (changes that were actively sought, instigated, and accentuated by breeders) was integral to Darwin's understanding.

Modern readers of the *Origin of Species* are sometimes perplexed or amused by the first chapter, "Variation under Domestication," dwelling so long upon the subject of pigeon breeding, but in this chapter Darwin is both laying the foundations for an analogical argument and providing an insight into the development of his thought. Having established the principle of modification and selection in breeding, Darwin proceeds, in Chapters 2 and 3, to consider first the variability of species in the state of nature and then the ubiquity of a struggle for existence, before, in his fourth chapter, explaining how "it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected" (Darwin 1859).

In case any reader had missed, or doubted, the analogy, Darwin restated it clearly:

I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. We have seen that man by selection can certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art. (Darwin 1859)

In his *The Variation of Animals and Plants under Domestication* (1868) – the only part of his unfinished "big book" to be published in his lifetime – Darwin went further, distinguishing three types of selection: methodical selection, which arose from breeders systematically endeavoring to modify a breed; unconscious selection, "which follows from men naturally preserving the most valued and destroying the less valued individuals, without any thought of altering the breed;" and natural selection, "which implies that the individuals which are best fitted for the complex, and in the course of ages changing conditions to which they are exposed, generally survive and procreate their kind." Unconscious selection, Darwin noted, graduated into methodical selection and could rarely be distinctly separated, while natural selection was sufficiently strong to come, "to a certain extent into action, independently of, and even in opposition to, the will of man" (Darwin 1868).

The Strength of Natural Selection

Darwin's certainty of the strength of natural selection was rooted in his understanding of the forces underlying its operation. As already noted, natural selection was premised on two prior processes: naturally occurring *variations* and an intense *struggle for life*. In order for natural selection to make sense, that is, one needed to accept (i.) the mutability of life forms and (ii.) the universal prevalence of a competition for the means of survival. Neither idea was new: Darwin's

innovation was to bring them together as the foundation of his own, innovatory evolutionary mechanism – natural selection.

Darwin's notebooks show that by 1837 he was deeply immersed in the problem of the mutability of species and was trying to understand how the process of the transmutation of species might operate (Gruber 1974). At this point his growing conviction that evolution occurred was matched by a suspicion of the inadequacy of all previous attempts to understand transmutation (see Stott 2012).

His breakthrough came in autumn 1838, Darwin later recalled, when he read Thomas Malthus's *An Essay on the Principle of Population* (1803), "for amusement." Malthus's *Essay* argued that humans had an inherent tendency toward overpopulation, as they reproduced faster than the food supply could be increased, inducing regular struggles for subsistence. It was an argument Darwin encountered with a sense of recognition:

and being well prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable new ones to be destroyed. The result of this would be the formation of a new species. Here, then, I had at last got a theory by which to work ... (Barlow 1958)

Reading Malthus was not merely the midwife to the birth of Darwin's theory of natural selection; the Malthusian struggle was a key constitutive element in his understanding of its operation. Only if there was a "Struggle for Existence amongst all organic beings throughout the world, which inevitably follows from their high geometrical powers of increase," would Darwin be able to explain why some traits and characteristics were favored, and others eliminated, and this struggle, he told readers of the *Origin*, was "the doctrine of Malthus, applied to the whole animal and vegetable kingdoms" (Darwin 1859).

By making overpopulation key to the operation of natural selection, Darwin's theory of evolution was distinguished from that of his predecessors in several important respects. In particular, natural

selection made competition, utility, and extinction central evolutionary themes.

Prior to Darwin, the most fully developed theory of evolution was to be found in the writings of the French zoologist Jean-Baptiste Lamarck (1744–1829). Lamarck argued that the transmutation of species occurred by a process of inheritance of acquired characteristics and that new characteristics were acquired by species through the use and disuse of organs, leading structures to either develop or disappear. The prompt for the increased or decreased use of any particular organ was, in turn, an internal urge, rooted in an innate tendency to develop in a certain way. Lamarck's understanding, that is, was orthogenetic, with organisms developing toward a predetermined goal.

Evolution by natural selection, by contrast, occurred because certain variations proved advantageous or disadvantageous in the ongoing struggle for life. This made natural selection directionless. The key to which variations prospered or failed was their *utility* in the ongoing *competition* for scarce resources. There was no orthogenetic element to this, as there was no predetermined direction to natural selection, beyond whatever proved most useful. Natural selection was, in contrast to Lamarck's understanding, a brutal and destructive mechanism, which worked by the constant overproduction of organisms, and the recurrent elimination of those less fitted for the struggle for life. So brutal was this process, Darwin asserted, that *extinction* – which Lamarck's account had precluded – was a frequent occurrence under natural selection. Indeed, "extinction and natural selection," Darwin declared, "go hand in hand" (Darwin 1859).

Darwin's rooting of his theory of natural selection so firmly in the Malthusian population principle had two contradictory consequences for the reception of his ideas. On the one hand, notions of competition, struggle, and utility were so familiar, especially as adumbrated through the new social science of political economy, that natural selection would have echoed with an almost common sensical familiarity for many readers. On the other hand, however, it immediately threw up many of the same theological problems – not least why

would an omnipotent and benevolent deity depend upon a mechanism that entailed death, destruction, and apparent evil? – that had greeted Malthus’s theory (see Pullen 1987).

Darwin neatly sidestepped this in the *Origin*, arguing that there was “grandeur” in the view of life which saw “from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows” (Darwin 1859). This type of language, self-consciously deployed to give comfort to those with religious sensibilities, could not entirely soften the blow that Darwin had delivered. Taken to its logical conclusion, natural selection meant an end to teleology, an end to special interventions, an end to all notions of design, and an end to the natural theology associated the name of William Paley. Writing, toward the end of his life, in his “Recollections,” Darwin was clear:

The old argument of design in nature, as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered. We can no longer argue that, for instance, the beautiful hinge of a bivalve shell must have been made by an intelligent being, like the hinge of a door by man. There seems to be no more design in the variability of organic beings & in the action of natural selection, than in the course which the wind blows. Everything in nature is the result of fixed laws. (Barlow 1958)

Difficulties with the Term

Although Darwin himself had become increasingly enamored of the term “natural selection” prior to the publication of the *Origin*, his confidence in its appositeness received a blow from the initial reaction of his readers. Writing to Lyell in September 1860, a mere 10 months after the *Origin* was published, Darwin declared: “if I had to commence de novo I would have used natural preservation” (<http://www.darwinproject.ac.uk/DCP-LETT-2931>). The problem, he complained, was that too many readers seemed incapable of understanding the term.

In the third edition of the *Origin*, published in 1861, Darwin inserted an extra paragraph at the start of Chapter 4, to address those writers who

had “misapprehended or objected to the term Natural Selection.” In particular, he sought to correct those who understood natural selection to imply the need for active selection, either by the organism itself or by an external chooser. Part of the misunderstanding, Darwin acknowledged, arose from an ambiguity inherent to the term. “In the literal sense of the word,” he wrote, “natural selection is a misnomer,” which had allowed some readers to suppose that he understood nature to be personified into a “selector” and that natural selection itself was “an active power or Deity.” This, Darwin complained impatiently, was wrong: natural selection was no more an active power or deity than was gravity. When he referred to “nature” he meant only the aggregate action and product of natural laws. The problem, he concluded, was that his readers were failing to understand that “natural selection” was a metaphor “With a little familiarity,” Darwin concluded, “such superficial objections will be forgotten” (Darwin 1861).

This proved to be a rather optimistic assessment. Five years later, in July 1866, Wallace wrote to Darwin to say that he has been “so repeatedly struck by the utter inability of numbers of intelligent persons to see clearly or at all, the self acting & necessary effects of Nat[ural] Selection” and that he was forced to conclude “that the term itself” and Darwin’s illustrations of it were at fault. By comparing natural selection to artificial selection, and by personifying nature as “selecting” and “preferring,” said Wallace, Darwin had deployed a metaphor which, instead of aiding understanding, was proving to be a “stumbling block” (<http://www.darwinproject.ac.uk/DCP-LETT-5145>).

Wallace’s criticisms were well made. In basing natural selection upon an analogy with artificial selection, Darwin encouraged an anthropomorphic conception of selection in which the “power” which “acted” could be seen as an active deity. This was not Darwin’s intention. At the time he wrote the *Origin*, Darwin was, on his own account, still a theist. The agnosticism (and arguably atheism) of his later years was still some way off, but he did not entertain any notion of an active, interventionist god. For Darwin, nature

was a set of fixed laws, and natural selection was directionless beyond favoring whatever was best adapted. Yet his words frequently suggested something else. Thus when he wrote to the US botanist Asa Gray, announcing his new theory, he claimed: “I think it can be shown that there is such an unerring power at work in Natural Selection (the title of my book), which selects exclusively for the good of each organic being” (<http://www.darwinproject.ac.uk/DCP-LETT-2136>). Following this introduction to the concept, it is perhaps unsurprising that Gray became the principal champion among those who sought to reconcile natural selection and natural theology.

Wallace suggested a way out of such misunderstanding. Darwin, he advised, should abandon the term “natural selection” and replace it with the phrase “survival of the fittest.”

This latter phrase, which many now associate with Darwin, had been coined 2 years earlier as a synonym for “natural selection” by Herbert Spencer, in an installment of his *The Principles of Biology* (Spencer 1864). Wallace argued that Spencer’s term was “the plain expression of the facts” – nature did not “so much select special variations, as exterminate the most unfavourable ones” – and, as such, was less liable being “misrepresented & misunderstood” than Darwin’s metaphorical, “and to a certain degree indirect & incorrect,” natural selection.

Wallace’s letter had a limited effect. Darwin did agree to integrate Spencer’s phrase into his work. It was too late to make changes to the fourth edition of the *Origin*, which was already with the publisher, but Darwin used “survival of the fittest” 6 times in the *Variation* and 16 times in the fifth edition of the *Origin* (1869). Nor were these unimportant or incidental uses. Darwin even reworked the title of Chapter 4 of the *Origin* into “Natural Selection, Or The Survival of the Fittest” and in the text described “survival of the fittest” as “more accurate” than and “sometimes equally convenient” with natural selection.

Ultimately, however, Darwin was unwilling to give up his own term. In part this was a matter of practicality: the *Origin* had enjoyed such a wide circulation, and natural selection had “been so largely used abroad & at home,” (<http://www.darwinproject.ac.uk/DCP-LETT-5145>) that Darwin doubted whether its use could be eliminated, even if he had wanted that. And there is no evidence that he did, quite the contrary. Darwin continued to cling to the hope he had expressed to Lyell that in time his readers would come to understand his phrase. This had nothing to do with the obvious criticism that might be made of the term “survival of the fittest,” i.e., it is a tautology with little explanatory value. Rather, Darwin preferred the term “natural selection” precisely for the reason that Wallace questioned its use: it was a metaphor.

A number of scholars, principally Robert M. Young (1971), have made the case that the phrase “natural selection” had an important explanatory role both in the development of Darwin’s thought and in his efforts to persuade others to accept his theory. In the absence of any precise understanding of how inheritance worked, Darwin’s task in the *Origin* was not so much to show evolution in action, or to provide a complete example of the stages by which it occurred, but to stress the greater plausibility of his theory over all other explanations, principally Lamarckism and all notions of special creation. In those circumstances, language mattered: natural selection was more than just a phrase, convenient for summarizing a complex process. For Darwin, “natural selection” was a “theory-constitutive metaphor” (a metaphor which suggests future research strategies) and an “emphatic metaphor,” i.e., one which is bound up with the cognitive content of the theory it seeks to explain (Al-Zahrani 2007).

Difficulties with the Theory

Prior to Publication of the *Origin*

What troubled Darwin most when developing his theory was the need to square natural selection with some apparently awkward scientific facts. The need to work through possible objections, and reconcile his theory to the existing state of scientific knowledge, accounts, in part at least, for the otherwise extraordinary “delay” (van Wyhe 2007) between Darwin’s revelatory reading of

Malthus and the publication of the *Origin* some 21 years later. As a result of the time he took, one feature of the *Origin*, which helped to make it such a compelling argument, was that Darwin led his readers through his own initial doubts and their subsequent resolution. Thus the four middle chapters of the *Origin* are concerned with exploring and resolving various objections and difficulties, including the problems of hybrids, the imperfection of the fossil record, and the problem of producing complex outcomes by a series of insensibly fine gradations.

The “most serious special difficulty” posed to Darwin’s own acceptance of the sufficiency of natural selection, however, came in the form of neuter insects, especially sterile females such as worker ants:

with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection? (Darwin 1859)

Part of Darwin’s answer to his own question was to emphasize that natural selection applied to “the family” as well as “the individual” and that in the case of social insects, such as ants, it was entirely possible for fertile parents to transmit to their fertile offspring a tendency to produce sterile offspring, if that was beneficial to the community. Natural selection, that is, acted upon fertile parents to regularly produce neuter offspring.

The “climax of the difficulty,” however, as Darwin saw it, was not merely that neuters were produced but that the neuter ants themselves were specialized into two or three “different castes.” Among *Eciton* ants, for example, the neuters were divided into worker and soldier ants, “with jaws and instincts extraordinarily different.” To explain this by natural selection required Darwin to suppose that a graduated series had first been formed, “and then the extreme forms, from being the most useful to the community, having been produced in greater and greater numbers through the natural selection of the parents which generated them; until none with an intermediate structure were produced” (Darwin 1859).

It is obvious when reading the *Origin* that Darwin’s success in resolving this problem, with which he had wrestled for a considerable period, boosted his confidence in natural selection considerably. The fact that natural selection could explain the existence of neuter insects proved, for Darwin, the superiority of natural selection over Lamarckism: “For no amount of exercise, or habit, or volition, in the utterly sterile members of a community could possibly have affected the structure or instincts of the fertile members, which alone leave descendants.” Even in relation to instincts, he argued, there was in nature “one general law, leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die” (Darwin 1859).

Subsequent to Publication of the *Origin*

Although Darwin had satisfied his own doubts about natural selection prior to the publication of the *Origin*, problems remained. There were three principal scientific barriers to winning full acceptance for natural selection, each of which related to the question of inheritance.

First, as compelling as Darwin’s argument was, what the *Origin* offered was natural selection as a *hypothesis* for how evolution worked. The “preservation” of a trait and characteristic occurred by its transmission between generations, with each successive generation accentuating whatever advantage it offered. But, writing before modern genetics, Darwin was not able to explain precisely *how* inheritance worked. In the *Origin* he rather fudged the issue, by making natural selection refer to both the evolutionary *effect* (the favored trait or characteristic) and the *mechanism* (preservation in struggle and hereditary transmission).

In the *Variation*, however, Darwin did attempt to flesh out what he called a “provisional hypothesis” of heredity, which he called pangenesis. Pangenesis brought together an ancient tradition stretching back to Hippocrates with some of the latest thinking in cell theory, in an unconvincing amalgam. According to the pangenesis theory, all parts of the body produced tiny particles (gemmules) which circulated in the blood, but migrated to the gonads, and were passed on to

offspring, before developing as the offspring matured. Because these gemmules were continually produced, it was possible for both somatic and behavioral traits to be inherited (Darwin 1868).

Unfortunately, Darwin's attempt to shore up his theory of natural selection with pangenesis tended to weaken his own theory by opening up space for the very Lamarckian interpretation he had set out to counter. Pangenesis suggested that alterations to body parts would, in turn, alter gemmules and, therefore, that an inheritance of acquired characteristics would be possible.

From our perspective it is easy to see what was missing from Darwin's hypothesis: he lacked a particulate theory of heredity, a distinction between somatic and germ cells, and a concept of dominance, i.e., he lacked modern genetics and molecular biology. It was to take the rediscovery of Mendel's laws of inheritance in the early twentieth century, and their integration with evolutionary theory, to firmly establish the *mechanism* of natural selection. Ronald Fisher's *The Genetical Theory of Natural Selection* (1930) and Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937) were particularly important in this movement, which became known as the "modern synthesis," and gave us natural selection as it is now understood.

The second principal challenge natural selection faced was how to explain the preservation of favorable variations when inheritance was widely believed to involve "blending." The engineer Fleeming Jenkin (1833–1885) became a trenchant and troubling critic of Darwin on this point, arguing in an 1867 review of the *Origin* that any advantageous mutations would be swamped and diluted out of existence within a few generations. Certainly no change could survive across the hundreds or thousands of generations that would be required to bring about Darwin's process of evolution by natural selection (Jenkin 1867). As with inheritance more broadly, this problem would eventually be overcome by the integration of Mendel's theory of particulate inheritance, but Darwin's initial reaction was a concern and a hurried attempt to give a partial answer in the fifth edition of the *Origin*.

What gave Jenkin's criticism added bite was that it chimed with the third challenge to Darwin's theory of natural selection: doubts about the age of the earth.

As Jenkin noted, a process of incremental change required preservation across a huge span of generations, but in the years immediately following publication of the *Origin*, the depth of geological time necessary for natural selection was called into question. William Thomson (later Lord Kelvin) argued that the crust of the earth had solidified no more than 100 million years ago. Darwin was "rattled" by this claim, lamenting Thomson's work as "an odious spectre" and identifying it as "one of my sorest troubles" (Browne 2002). In response, the fifth and sixth editions of the *Origin* placed an increased emphasis on use and disuse explanations of evolution, alongside natural selection, as a means of accelerating aspects of the evolutionary process (Darwin 1872).

Natural Selection and Other Evolutionary Mechanisms in Darwin

This "speeding up" was possible because Darwin had always left room for other factors working alongside natural selection. As he reminded readers of the introduction to the 1874 edition of his *Descent of Man*:

even in the first edition of the 'Origin of Species,' I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind. I also attributed some amount of modification to the direct and prolonged action of changed conditions of life. Some allowance, too, must be made for occasional reversions of structure; nor must we forget what I have called "correlated" growth, meaning, thereby, that various parts of the organisation are in some unknown manner so connected, that when one part varies, so do others; and if variations in the one are accumulated by selection, other parts will be modified. Again, it has been said by several critics, that when I found that many details of structure in man could not be explained through natural selection, I invented sexual selection; I gave, however, a tolerably clear sketch of this principle in the first edition of the 'Origin of Species,' and I there stated that it was applicable to man. This subject of sexual

selection has been treated at full length in the present work, simply because an opportunity was here first afforded me. (Darwin 1874)

Darwin's defense here was a little disingenuous. With the publication of *The Descent*, in particular, a significant change had occurred in his thought.

In the first edition of the *Origin*, the overwhelming emphasis on natural selection was supplemented by a small section in the fourth chapter, which considered "Sexual Selection," and a brief discussion in Chapter 5 of the evolutionary effects of use and disuse. In both cases Darwin found these other mechanisms to be subsidiary and supplementary to the overriding importance of natural selection. Sexual selection, which Darwin defined as "a struggle between the males for possession of the females," was, he said, "less rigorous than natural selection" and, for the most part, merely reinforced its more powerful counterpart: "Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny" (Darwin 1859). It was the same with use and disuse. Darwin allowed that changed habits could produce an inherited effect and speculated that moles and cave-dwelling fish, for example, may have lost their sight this way, but Darwin also implied that natural selection was the underlying cause of every change and that use and disuse contributed only by accelerating a process that natural selection might have effected, albeit more slowly, on its own.

When Darwin turned to the question of human evolution, however, in *The Descent of Man, and Selection in Relation to Sex* (1871), he identified sexual selection as, in some instances, more powerful than an independent of natural selection.

Natural Selection and Human Evolution

Darwin had not addressed human evolution directly in the *Origin*, limiting himself to the gnomonic prediction: "Light will be thrown on the origin of man and his history" (Darwin 1859).

This deliberate omission certainly helped Darwin finish his book and probably helped to minimize the controversy that the *Origin* provoked. It also, however, meant that by the time Darwin was ready to publish his thoughts, others had already begun the process of applying his theory to human evolution.

Two ideas, in particular, had taken hold in the 12 years that elapsed between the *Origin* and the *Descent*. The first was Wallace's argument, outlined in his 1864 paper *The Origin of Human Races and the Antiquity of Man Deduced From the Theory of "Natural Selection"*, that the human brain effectively removed humans from the bodily effects of natural selection and that natural selection now operated exclusively on the human mind and intelligence. The second, promulgated most prominently by Darwin's half cousin Francis Galton, was that the trappings of civilization seriously impeded or completely prevented the operation of natural selection – physically *and* mentally – and that, in consequence, human evolution was threatened with a reverse process of degeneration (Galton 1869).

Darwin acknowledged this fear in a section of the fifth chapter of the *Descent*, entitled "Natural Selection as Affecting Civilised Nations." "We civilised men," he began, "do our utmost to check the process of elimination; we build asylums for the imbecile, the maimed, and the sick; we institute poor-laws; and our medical men exert their utmost skill to save the life of every one to the last moment." As a result, those who would have been eliminated by the free operation of natural selection were allowed to breed, and "this must be injurious to the race of man" (Darwin 1871). Despite this doom-laden language, which foreshadows the arguments of the later eugenics movement, Darwin's overall conclusion was positive. Whatever impediments society might erect to its operation, Darwin argued, much as he had in the *Variation*, that natural selection was always sufficiently strong to act "independently of, and even in opposition to, the will of man" (Stack 2012).

When explaining physical differences between different human groups, however, rather than

reasserting the primacy of natural selection, Darwin turned to sexual selection. “For my own part,” he wrote, “I conclude that of all the causes which have led to the differences in external appearance between the races of man, and to a certain extent between man and the lower animals, sexual selection has been by far the most efficient.” Darwin still thought that natural selection played the primary role in accounting for the development of man’s “intellectual and moral or social faculties” but doubted its ability to explain racial divergence. Natural selection, Darwin noted, depended upon utility, but “as far as we are enabled to judge (although always liable to error on this head) not one of the external differences between the races of man are of any direct or special service to him” (Darwin 1871). If racial differences were predominantly ornamental or aesthetic, Darwin concluded, they could be better explained by sexual selection.

Human groups, tribes, or races, Darwin suggested, had become their own selectors, breeding themselves to their own ideal:

We have seen that with the lowest savages the people of each tribe admire their own characteristic qualities,—the shape of the head and face, the squareness of the cheek-bones, the prominence or depression of the nose, the colour of the skin, the length of the hair on the head, the absence of hair on the face and body, or the presence of a great beard, and so forth. Hence these and other such points could hardly fail to have been slowly and gradually exaggerated from the more powerful and able men in each tribe, who would succeed in rearing the largest number of offspring, having selected during many generations as their wives the most strongly characterised and therefore most attractive women. (Darwin 1871)

It was a similar story when Darwin came to explain differences in the mental powers of the sexes. “With respect to differences of this nature,” Darwin wrote, “it is probable that sexual selection has played a very important part.” Again Darwin did not entirely discount natural selection: male intellect, he argued, had been honed both in the competition of natural selection (from which females had been relatively sheltered) and sexual selection, the struggle “for the possession of the females” (Darwin 1871).

The result, when supplemented with Darwin’s use and disuse argument that it was the age at which a characteristic was strengthened which determined when it would be transmitted (thus males inherited distinctively male, and females distinctively female, characteristics), was that Darwin’s mix of natural selection, sexual selection, and use and disuse explanations combined to produce an evolutionary basis for male “superiority.”

Male genius, Darwin maintained, had:

been developed in man, partly through sexual selection,— that is, through the contest of rival males, and partly through natural selection, — that is, from success in the general struggle for life; and as in both cases the struggle will have been during maturity, the characters thus gained will have been transmitted more fully to the male than to the female offspring. Thus man has ultimately become superior to woman. (Darwin 1871)

Here we can see that Darwin’s dilution of natural selection as the main mechanism for human evolution went hand in hand with arguments that gave a naturalistic basis to the social inequalities of the late Victorian world and tended to justify racial and sexual inequality (Goodman 2019). This may not have been his conscious intention, but it is striking that the normally cautious Darwin offered firm conclusions despite the fact that, by his own admission, his views “on the part sexual selection has played in the history, want scientific precision” (Darwin 1871).

A useful contrast can be made here with Wallace, an advocate of equality, who despite his misgivings about the term remained steadfast in his commitment to natural selection, to the exclusion of all other evolutionary mechanisms. In his rendering of their shared discovery, *Darwinism: an exposition of the theory of natural selection, with some of its applications* (1889), Wallace argued for the “overwhelming importance of natural selection over all other agencies” and rejected Darwin’s account of sexual selection. Indeed so unrelenting was he in his advocacy of a “pure Darwinism” that George J. Romanes characterized Wallace as a “neo-Darwinian” for “seeking to out-Darwin Darwin by assigning an exclusive

prerogative to natural selection” (Romanes 1895). This was never Darwin’s position.

Summary

Natural selection was the term Darwin used to describe both the mechanism and the effect of the evolutionary process by which favorable or advantageous traits and characteristics are preserved and unfavorable or disadvantageous ones discarded. The “selection” process is “natural” in the sense that it occurs without any conscious intervention (there is no “selector”) in response to an ongoing “struggle for life.” Traits and characteristics favorable to survival in that struggle are preserved and developed. This, for Darwin, is the basis of evolution. Key to the process is inheritance, but, as he was writing without knowledge of modern genetics, Darwin’s presentation of natural selection did not include any detailed understanding of how inheritance worked.

Although Darwin succeeded in winning acceptance for the general notion of evolution, the mechanism of natural selection remained controversial. Partly this was due to a lack of direct evidence. Besides the absence of any precise understanding of genetic inheritance, Darwin struggled against gaps in the fossil record, the elusiveness of transitional forms, and his inability to demonstrate direct instances of natural selection in operation.

His major work, *On the Origin of Species by Means of Natural Selection*, presented “one long argument” in favor of his mechanism, but critics pointed out that swamping, blending, dilution, and the uselessness of incipient structures would all tend against the process he described. A further challenge came from William Thomson’s work on the cooling of the earth, which suggested that the planet was too young to have witnessed the magnitude of species development, wrought by incremental change, which Darwin suggested. Other readers misunderstood what Darwin meant by natural selection and supposed an active selector to be at work. This led some of Darwin’s allies,

most notably Wallace, to suggest abandoning the term.

Darwin refused and continued to favor “natural selection” as a metaphor. Nonetheless, in his later works, and even in later editions of the *Origin*, Darwin was keen to stress that, although the most powerful, natural selection was not the only mechanism by which the evolutionary process occurred. Especially in the case of humans, discussed by Darwin in *The Descent of Man*, use and disuse and sexual selection were given greater prominence. One consequence of this was that although an acceptance of evolution flourished in the late nineteenth century, an understanding and acceptance of Darwin’s mechanism of natural selection were less widespread.

The success and prevalence of natural selection that we know today have its roots in the “modern synthesis” of the early twentieth century, which united Darwin’s hypothesis of natural selection with the understanding of genetics that he lacked.

Cross-References

- ▶ [Alfred Russel Wallace \(1858\)](#)
- ▶ [Lamarckism](#)
- ▶ [Sexual Selection](#)

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Charles Darwin: Theory of Sexual Selection

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Synonyms

[Evolution of secondary sexual characters](#); [Mate choice](#); [Mating advantage](#); [Reproductive success](#); [Selection in relation to sex](#)

Definition

Sexual selection is the form of selection that operates specifically on the reproductive success of individuals. Natural selection is associated with the struggle for survival (which includes reproduction), but sexual selection is entirely associated with an organism's ability to find a mate, successfully copulate, and produce offspring.

Introduction

Darwin's theory of evolution by natural selection is essential and is adequate to explain the diversity of life on this planet. The theory – based on genetic variation, adaptation, and inheritance – is all encompassing, and as the great evolutionary geneticist Theodosius Dobzhansky remarked, “nothing in biology makes sense except in the light of evolution.” Evolution is the string theory of biology. As a grand theory, its descriptors include genetic variation, selection, adaptation, speciation, and extinction. Since the theory applies to all organisms, the details of the organisms do not matter to the explanatory power of the theory. Fitness can be defined in terms of genes, not organisms, as it has been done in population genetics. However, if we want to understand how

organisms interact and adapt to their environment and how they live, mate, reproduce, and die, we need to look at organisms at the scale of their life, which varies from days to months and years. It is at this scale that the theory of sexual selection, along with natural selection, becomes essential.

To understand sexual selection, it is important to understand the context in which Darwin felt the need to propose this theory in a separate book *The descent of man and selection in relation to sex* (Darwin 1871), after publishing his book on the theory of natural selection (Darwin 1859). It is also important to understand how sexual selection is related to and yet is fundamentally different from natural selection. Hunger and sex are the two driving forces of evolution; organisms need to eat to survive and to reproduce in order to perpetuate themselves. Darwin's theory of natural selection included competition for food and sex as well as surviving challenges arising directly from the environment. Sexual selection centers more on sex and reproduction. Reproduction is part and parcel of natural selection except in one respect. If males and/or females exercise mate choice, which they often do, then one sex can induce changes in the other as a result of his or her mate choice habits.

Sexual selection, according to Darwin "depends on the advantage which certain individuals have over individuals of the same sex and species, in exclusive relation to reproduction" (Darwin 1871, p. 256). Darwin goes on to say that in all those cases where males have acquired a particular structure,

not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone, sexual selection must here have come into action. It was the importance of this distinction which led me to designate this form of selection as sexual selection. (p. 210)

Sexually selected traits can simultaneously be under natural selection, in which case the two forces will jointly act to regulate the outcome of the selection processes. The Peacock's unusually long tail is a classic example of such a process, where female choice lengthens the tail, and

natural selection, presumably due to pressures from predators, stops any further lengthening of the tail. Whereas "female choice and male modification" was the main mechanism offered by Darwin to explain how sexual selection operates, he did notice the active role of males in seeking mates through song, dance, and charm, which was accepted as part of the mating dance. Although Darwin was aware of male choice, he did not consider "male choice and female modification" to be an important mechanism, presumably because extreme cases of sexual modifications were more commonly observed in males, not in females.

Males and females make different investments into sex and reproduction. Males constantly seek mates, and females seem to be choosy about who they mate with. This difference is presumed to be the consequence of anisogamy. Anisogamy refers to differences in the size of male and female gametes or in the energetic cost of gamete production. Females expend large amounts of energy to produce fewer but larger gametes, whereas males produce smaller but plentiful gametes. Reproduction is therefore more costly for females, and it is in the best interests of the female to be choosy and select high-quality males to fertilize her few eggs. Males on the other hand have no such limitations and can mate frequently and indiscriminately. Gamete-based consideration of cost is not the only explanation for why females are more likely to exercise mate choice. An equally likely and probably a more correct explanation would be that male/female mate choices are two sides of the same coin. Males are always ready to mate before females, and are free to engage in frequent mating, which makes selection act stronger on males than females. Females may take longer time to get behaviorally/physiologically ready to accept mates. Also, one can question the assumption that male gametes are less costly to produce than female gametes. A single sperm may be less costly compared to an egg, but males do produce large amounts of sperm. In an energetic cost-based argument, it is the total cost of gametes that should matter, not the cost of individual gametes. As such, some fundamental issues regarding the sexual roles of males and

females and how the sexes interact to influence mating outcomes are debatable. Even after nearly a century and a half since Darwin, there still are discordant opinions on natural selection and sexual selection, such as what secondary sexual traits come under the category of sexual selection; how does male-driven sexual selection differ from female-driven (female choice) sexual selection; why do females choose or what is the basis of female choice, does sexual selection incur extra costs, do sexually selected traits evolve faster, and whether sexual selection is aligned with natural selection or does it oppose natural selection; and more.

Here an attempt will be made to shed light on these important questions, but it is not the intention of this entry to provide an in-depth review of all literature on sexual selection. Readers are directed to other entries that specifically deal with some aspects of sexual selection, sexual antagonistic coevolution, and sexual conflict.

Sexual Selection

Secondary Sexual Traits and Mate Choice

Darwin was convinced that many aspects of sexual dimorphism were the results of sexual selection. He began the chapter “Principles of sexual selection” by introducing and distinguishing between primary and secondary sexual characters (Darwin 1871, Ch. VIII). These terms were originally used by John Hunter, who described male and female reproductive organs, which are evident from birth, to be primary sexual traits, and secondary sexual traits were those that did not develop until animals approached breeding age. Darwin adopted Hunter’s terminologies but made some important functional distinctions. Darwin called primary sexual traits as those that are essential for and directly connected to the act of reproduction itself. Secondary sexual traits are not directly connected with the act of reproduction, but they are important to attract mates or to fight-off other members to gain mates, i.e., secondary sexual characters are central to the process of intra- and intersexual selection. By making this distinction, Darwin was able to explain how these

secondary sexual characters, such as elaborate antlers in deer or mandibles in beetles, by virtue of being used as weapons, evolved as a result of male-male competition. Similarly, he proposed that females may also choose the victors of male competition based on their strength and pugnacity or choose more ornamented males. He wrote:

There are many other structures and instincts [of males] which must have been developed through sexual selection- such as the weapons of offence and the means of defense of the males for fighting with and driving away their rivals – their courage and pugnacity – their various ornaments-their contrivances for producing vocal or instrumental music – and their glands for emitting odors, most of these latter structures serving only to allure or to excite the females. It is clear that these characters are the results of sexual selection and not of ordinary selection, since unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, but for the presence of better endowed males. We may infer that this would be the case, because the females which are unarmed and unornamented, are able to survive and procreate their kind. (Ch. VIII, p. 210–211)

Darwin supported his case by presenting substantial evidence to illustrate two major features; firstly, mating is nonrandom in most cases, and secondly, males of most taxa are more “modified” compared to females. Nonrandom mating implies that some individuals succeed more in finding a mate and reproducing more than others. Darwin attributed this mating advantage to be the outcome of two major processes – male-male competition, where males competed with each other, often severely, in order to gain access to mate, and female choice. In either case, Darwin’s idea of reproductive success was based on quality – higher-quality males and female leave more offspring. Male-male competition is easy to envision – victors of a competition are able to have more mates and, thus, more reproductive success. With female choice, Darwin explains that females appear to choose males with certain “preferred” traits. Such males will reproduce more and leave a greater number of offspring compared to males who do not possess the “preferred” trait. Thus through female choice, females can shape the nature of modifications that develop in males of a population.

Darwin was criticized that he was mixing two types of traits – weapons that males use to fight among themselves and structures that males use to attract females and induce them to copulate (Mayr 1942). The critics claimed that only the latter category of traits can genuinely be the product of sexual selection. This interpretation is not correct because male-driven sexual selection implies “attracting females,” which includes *fighting for females*. The term male-driven selection here corresponds to what Darwin called “male eagerness and vigor” (discussed later in the entry). While Darwin does not specifically say so, his writings imply that male-male competition for females is more pervasive and stronger than competition for food. Once a weapon or a means of defense has originated, it can be used for both purposes – fighting for sex (females) or fighting for food. It is a different matter that the fights may not actually involve physical contact and may occur largely by threats and bluffs. Regardless, the consequences remain unaltered.

In theory secondary sexual traits can arise as a result male- or female-driven modifications and can be found in either sex with varying frequencies. Darwin made a strong point of the development of the senses in higher organisms which allow interaction within and between sexes. He marshaled impressive evidence from a variety of taxa to demonstrate that secondary sexual characters are not restricted to morphological traits but extended to instincts, odors, as well as visual and acoustic signals (Darwin 1871). Even though he focused on female choice and male modification, in theory, there are four possible processes:

- Male-male competition and male modifications (e.g., weapon)
- Female choice and male modifications (e.g., male ornaments)
- Male choice and female modifications (e.g., female beauty)
- Female-female competition and female modifications for attracting males (e.g., female beauty)

In this entry, we will mainly discuss the first three possibilities.

Male-Male Competition and Sexually Selected Traits: Armaments Versus Ornaments

Male-male competition can occur in two ways – direct male-male competition and indirect male-male competition. Here, we will briefly describe direct male-male competition (see entry on ► [“Sexual Selection via Direct Male-Male Interactions”](#) for more details). Indirect male-male competition, such as sperm competition, which Darwin was unaware of, is discussed elsewhere (see entry on ► [“Sperm Competition”](#)).

Darwin’s understanding of male-male competition was essentially complete. He realized that direct male-male competition occurs in two ways; one way is when males physically battle one another in order to gain access to females (“the law of battle”). The other way is males will try to outcompete one another by engaging in visual, acoustic, or behavioral displays to attract females. Darwin realized that male-male physical competition was a major reason for the evolution of male weaponry or armaments, such as large antlers or tusks or even body size. Darwin envisioned a process where depending on the trait used in combat, e.g., antlers or body size, the males with larger antlers or large body size are most likely to be victorious. Using the analogy of how “...man could improve the breeds of his game-cocks by the selection of those birds which are victorious in the cockpit,” he deduced that the most vigorous or strongest males or those with the best weaponry have a distinct advantage in battles and thus reproduce more (Darwin 1871). The offspring of these victors will inherit the superior traits of their father and will be poised to be successful in their mating efforts. Male elephant seals are a classic example of male-male competition and body size evolution. Male elephant seals compete intensely for territory and for dominance over a harem of females, and larger males have greater success in accomplishing both.

Male-male competition by display is easily seen in birds, where rather than engage in direct battle, male of many species compete by displays of plumage, song, or dance. Darwin described how several species of birds would congregate, and males would “display with the most elaborate care, and show off in the best manner, their

gorgeous plumage; they likewise perform antics before the females, which standing as spectators, at last choose the most attractive partner” (Darwin 1859). This form of a more “peaceful” male-male competition, where the most attractive male leaves more offspring, results in the evolution of “ornaments” rather than armaments. Here “ornaments” is used as a general term to describe the color or morphology of plumage, acoustic signals such as songs or nonvocal sounds, or dance.

Other forms of male-male competition, such as alternative mating strategies, have also been documented. Males within some species avoid encounters with aggressive, dominant males and gain access to females by deviating from the customary mating strategy – they engage in “sneaky” mating behaviors. For instance, in the sexually dimorphic marine isopod *Paracerceis sculpta*, larger alpha morph males defend harems to monopolize females. Smaller beta morph males are about the size of females and gain access into harems by mimicking female behavior. In the horned beetle, nutritional differences cause some males to develop larger horns. These large-horned males defend females by guarding the entrance of the tunnel in which the female feeds. Smaller males that lack horns or have very small horns gain access to females by digging a new tunnel and bypass the guarding male. Such male-male competition via alternative mating strategies is not common but has been found in a variety of taxa.

Female Choice and Male Modification

One of the key observations Darwin made was that males were more “modified” relative to females across species. He was not only referring to the remarkable diversity of male secondary sexual characters, but he was also referring to the variation within males of the same species. Darwin had previously noted that variation was central to the evolutionary process by natural selection (Darwin 1859). Similarly the within species variation in male secondary sexual characters is the substrate for female choice. In fact, Darwin realized that the idea of female preference or choice would be moot if males did not vary in their efforts to pursue and/or if there was no variation in the traits that females preferred (Darwin

1871). The very fact that variation exists justifies that females have the opportunity to choose. As such, he deduced that male modifications were a result of female choice, if not by male-male competition. Just as the more vigorous males have the opportunity to select-out the less vigorous males through male-male competition, females have the opportunity to select males with certain modifications.

Darwin’s theory of female choice was received with some confusion and rejection by his contemporaries (including Wallace and Huxley) and was sidelined for the next several decades as well (Mayr 1942). The reason was that male-male competition was quite obvious, but female choice was not only unclear, but it was immediately linked to human-like esthetic behavior in animals despite Darwin’s assertions that female preference only reflects an arbitrary ability to discriminate. Another problem is that Darwin never really explained how female preference evolved. To begin with female choice, females will need to already possess or somehow acquire a “preference” for specific male traits or set of traits – this matter remains a conundrum.

Evolution of Female Preference

Several decades after Darwin, Ronald Fisher (Fisher 1915; Fisher 1930) proposed an ingenious explanation for the evolution of female preference. Fisher begins his verbal treatise by perceptively explaining that:

an animal’s struggle for survival is not only measured by the number of offspring which it produces and rears, but also by the probable success of these offspring. (Fisher 1915, p. 185)

So it would be important to select a mate that is more likely to produce successful offspring. In his verbal model, Fisher conceived of a heritable male trait that was initially favored by natural selection. He surmised that the male trait may or may not by itself have any value to a female, but a female may merely associate that trait with the male’s vigor. The male’s vigor could reflect his fitness as a potential mate who would produce successful offspring. A female that makes such a choice will then likely have more success and leave more offspring. The important idea here is that while a

female's preference for a male trait will modify the male trait, e.g., the male's tail gets longer; the female's preference is also modified such that females in subsequent generations will prefer males with longer tails. So in Fisher's model, the trait is firstly favored by natural selection, and is then additionally favored by sexual selection, which will reinforce that such a trait increases in frequency in a population. Moreover, as Darwin deduced, sons will inherit the father's trait and daughters inherit their mother's preference for the male trait. Thus, the evolutionary trajectories of these traits become correlated and will evolve in tandem. Such correlated selection can result in a rapidly accelerating process that will cause the male trait to become exaggerated until natural selection opposes its further elaboration.

However, Fisher was aware of traits such as the peacock's tail, and like Darwin, he too realized that such a trait would debilitate rather than facilitate the bird's survival. To explain the evolution of such exaggerated traits, Fisher (1930) proposed a second component to his theory, which he dubbed the "runaway process." He proposed that:

as long as there is a net advantage for further plumage development, there will also be a net advantage in favor of giving to it a more decided preference.

The two characteristics affected by such a process, namely plumage development in the male, and sexual preference for such development in the female, must thus advance together, and so long as the process is unchecked by severe counterselection, will advance with ever increasing speed. In the total absence of such checks, it is easy to see that the speed of development will be proportional to the development already attained, which will therefore increase with time exponentially, or in a geometric progression. Thus in any binomic situation, in which sexual selection is capable of conferring a great reproductive advantage, the potentiality of a runaway process, which, however small the beginnings from which it arose, must, unless unchecked, produce great effects, and in the later stages, with great rapidity. (Fisher 1930, p. 137)

In this argument Fisher deduced that persistent female preference is likely to counteract the limitations imposed by natural selection, thus displacing the sexual selection-natural selection equilibrium. So if female continued to prefer males with longer tails, then the process may

"runaway" unchecked by natural selection, and male tail lengths can reach exaggerated proportions in a short number of generations. Females will prefer males with exaggerated characters not because they are better in quality but because the sons of the female will be more attractive to females ("sexy sons"). Fisher's intuitive insights were largely ignored until decades later when genetic models explicitly corroborated the plausibility of Fisher's theories (O'Donald 1962; Lande 1980).

Cryptic Female Choice

Sexual selection via female choice became quite popular in the 1970s and 1980s, and substantial research revealed that female choice can be a major driving force that shapes the nature of male modifications in a species (Andersson 1994). Eberhard and Cordero (1995) proposed the idea of cryptic female choice, which they defined as "female behavior, physiology, or morphology that selectively biases paternity in favor of some conspecific males and against others, after copulation has already begun" (Eberhard and Cordero 1995; Eberhard 1996). Females can therefore modify the outcome of male mating success. Eberhard's idea of cryptic female choice was an important development in sexual selection research since it explained the remarkable diversity of not-so-easily observed male modifications, such as genitalia (see entry on [► Evolution of Genitalia, The](#)). Cryptic female choice also offers an explanation for how females may be able to overcome male coercion during mating, i.e., post-copulatory selection.

Why Do Female Choose?

Despite the strong theoretical framework that was established on the evolution of mate preferences, some questions remained unanswered. How did female preference arise in the first place and was then selected for? An explanation to this question has never really advanced beyond Darwin's and Fisher's broad assumptions. Furthermore, there is the question of why *do* females choose? Do they receive benefits from preferring certain males, or

is preference based on some sensory perception regardless of benefits to the female? These questions received considerable attention and spawned the development of distinct theories and models that have been under considerable debate for the last few decades. The models to explain how and why females choose may broadly be placed under four categories based on the mechanisms at play: direct benefits model, indirect benefits model, sensory drive model, and “other” models, each of which are driven by several processes.

The direct benefits model is the least controversial of all, given its relative simplicity. Under this model, females would prefer to choose mates who provide direct benefits to the females, such as territory, nuptial gifts, parental care, etc. Direct selection can occur in several ways, for instance, if females choose mates who are more conspicuous than others, they reduce time spent in finding mates and avoid predation risks or if female preference for particular males has other unrelated favorable consequences, such as producing more offspring (Markow et al. 1978). In general mate choice via direct selection will evolve if females prefer mates who increase female fecundity or survival.

Indirect benefits models apply to taxa where females do not receive direct benefits yet seem to show a preference for male ornaments. Indirect benefits models are more complex and can be divided in two major categories based on the adaptive and nonadaptive schools of thought – indirect selection via “good genes,” and indirect selection via coevolutionary processes, i.e., the Fisherian process. Before explaining the models, a brief mention of “indicator mechanisms” is necessary. Indicator mechanism derives from the widespread observation that costly secondary sexual characters are likely to be well developed in healthier individuals and thus may serve as “indicators” of male quality. Fisher (1915) included this idea in his theory but was largely ignored until Williams (1966) formalized the term.

The “good genes” hypothesis belongs to the adaptive school of thought and stemmed from (Zahavi’s 1975) handicap principle. Zahavi claimed that males with costly exaggerated characters must be of higher genetic quality since they have passed the test of natural selection, i.e., they are

able to maintain the exaggerated trait despite the fact that it reduces their chances of survival (i.e., their viability). This idea spurred the development of the condition-dependent indicator model. Under this model, the development of the male’s indicator traits is condition dependent, i.e., dependent on the male’s genetic quality and viability. The condition dependency makes the ornament a reliable indicator for females to judge male quality. One of the classic case examples for condition-dependent good genes indicator is Hamilton and Zuk’s (1982) study on birds. They postulated that healthier males will be more resistant to infections and thus be able to maintain elaborate plumages. Conducting an extensive survey of blood parasites in American passerine birds, they found that males with brighter plumage did have lesser parasitic infections. Such studies lend empirical support to the idea of the evolution of indicator traits and that perhaps females may use them to choose mates.

Fisherian process exemplifies a nonadaptive process, where female choice evolves by indirect selection via the Fisherian process (see above). It is interesting that despite the traditional dichotomy between the “good genes” and Fisherian model, both rely on female preference for an indicator trait, but in the Fisherian process, the trait may be random and mate choice evolves via females mating with “arbitrary” attractive males to produce “sexy sons.” Under the “good genes” process, the trait signals higher fitness, and mate choice evolves via mating with attractive males who have higher viability. Despite this dichotomy, the two may not be mutually exclusive, because if female preference and male trait have a heritable genetic basis, then a Fisherian process is implicit in any form of indirect-benefit model.

Sensory drive broadly refers to how selection on sensory systems can influence the evolution of traits (including mate choice). It comprises of several models such as sensory exploitation, sensory trap, receiver bias, etc. (Endler and Basolo 1998). Here, genes affecting female mating preferences may also influence other aspects of survival, such as predator avoidance, foraging etc. (i.e., via a pleiotropic effect). In such a case, selection on sensory perceptions that are not necessarily related

to mate choice but to other aspects of life (foraging, predation) can drive biases in mating and can be confused with the traditional “mate preference.” Essentially, females may associate male traits with predation or even food availability, or males may exploit these associations to attract the attention of females. Such sensory mechanisms have been implicated in the diversification of South American guppies, where female preferences coincide with predation intensity or even food coloration. For instance, females in high predation areas prefer males with inconspicuous color patterns and vice versa. Similar trends have been found in the African cichlid fish. Sensory drive can be quite powerful because it varies with the environment, spatially and temporally. Such sensory mechanisms may also initiate and drive the direction of mate choice evolution via Fisherian processes and even provide the foundational basis for the “good genes” system because in essence, the evolution of sensory systems, signals, and behavior are coupled and will coevolve.

Other models. Another class of models suggests that females may choose more genetically compatible males. This model proposes that by choosing genetically dissimilar males, females may receive benefits such as fitter offspring by increasing heterozygosity and/or silencing dominant deleterious alleles. A popular example is how new combination of MHC alleles can increase fitness. A more recent hypothesis suggests that female mate choice can evolve due to sexual conflict or sexual antagonism. Here, female choice evolves via the evolution of female resistance to males who try to entice or force females into mating. Males in turn may evolve additional strategies to manipulate female choice, which can lead to sexually antagonistic coevolution or sexual arms race, which may resemble a “runaway process,” or in this case, a “chase away process” (see entry on ► [“Sexual Conflict”](#)).

Male Choice, Female Modification, and the Theory of Male Sex Drive

The traditional popularity of female choice may have overshadowed the role of males in the

mating game. Even Darwin appeared to emphasize on how females choose males. However, Darwin repeatedly mentions the heightened sexual activity of males and remarked that “males with their superior strength, pugnacity, armaments, unwieldy passion and love songs, are almost always the more active and most often, the initiators of sexual interactions” (Darwin 1871). Darwin must have seen that male-male competition was the result of male’s “sexual drive” and that this drive will work even in the absence of direct male-male combat. He used the expressions male “vigor” and “eagerness” to describe the role of males but did not formalize these terms as traits that may be under selection. Fisher also invoked male “vigor” (see above) in his theory. Yet even though Darwin coined the term “female choice,” he failed to clarify male “vigor” and “eagerness” to be the male counterpart of “female choice.”

Darwin appears to divide males into two groups based on their mating behavior. In species with direct male-male competition, males may develop strength and weapons for fighting. In these species, the winner takes the female. The second category of males have showy traits that they presumably use to display and charm females. The latter is how Darwin visualized female choice to work, particularly in species with showy traits such as in the peacock. While Darwin noted the heightened activity of males during mating, he did not see that all males are alike in one respect, i.e., they are all driven by what a recent theory has termed male sex drive or male-driven sexual selection (Singh and Kulathinal 2005). While seeking mates, males, often unrelentingly, make use of all their resources – ornaments or armaments to secure females.

Male-male competitions and male displays are not two alternate states of mating strategy, but they represent two ends of the male lifestyle spectrum. Males can use their armaments or “showy” traits to intimidate other males just as they can use it to coerce females into submission. Physical strength and aggressive behaviors that males develop through male-male competition can also be used in male-female sexual interactions. From

the males' point of view, combining charm and coercion may be a winning strategy, and thus all male displays maybe viewed directly or indirectly as mixed with threats of physical force.

Male sex drive is described as the driving force behind the heightened, male-driven sexual activity during the course of mating. This would include, but is not limited to, sexual desire and libido, male-male competition for females, searching for mates, courting or even harassing females, song and dance, mounting and mating, controlling copulation, sperm quantity and quality, mate guarding, and readiness for remating. Male sex drive encompasses all efforts – physical, material, and psychological – made by males in order to procure mates. Since there is variation in these traits, they will be under selection via male activity or via female choice. As Darwin put it, the power to charm females has been in some instances more important than conquering other males in battles. Male charm and male aggression against females are invariably mixed and may range from pure charm to pure aggression. Male sex drive theory posits that sexual selection is stronger in males in all aspects of mating. Moreover, male sex drive and female choice together makes sexual selection a self-reinforcing, perpetual force of evolutionary change.

Sexual Selection and Adaptation

It is well understood that natural selection generally acts to increase all aspects of organism fitness, facilitating organisms to survive and reproduce in a given environment. The role of sexual selection, on the other hand, with respect to the general organism fitness remains controversial. As is evident in the previous sections, much of the intellectual debate in sexual selection is the evolution of maladaptive traits, such as the peacock's tail, and since Darwin, the opposing forces of sexual selection and natural selection have been implicated in theories and models. This has led to disputes whether sexual selection will eventually reduce population viability, and possibly cause extinction, or if sexual selection augments natural selection.

Under the “good genes” model, natural and sexual selection can complement one another since females choose males of higher fitness and thus produce high fitness offspring. This was also Darwin's (1859) thinking when he stated “Amongst many animals, sexual selection will give its aid to ordinary selection, by assuring to the most vigorous and the best adapted males the greatest number of offspring.” A fundamental requirement for this is that male secondary sexual traits must be “honest” indicators of genetic fitness (e.g., Hamilton and Zuk 1982). Under “good genes” and honest indicator conditions, several theoretical models show that sexual selection does increase overall fitness by increasing the spread of advantageous alleles, by removing unfavorable mutations in the genome, and by speeding up the process and the rate of adaptation (e.g., Lorch et al. 2003). These effects can increase population fitness and even confer advantages to maintaining sexual reproduction (Agarwal 2001). Empirical support, however, is mixed with some studies showing that sexual selection augments natural selection and others showing that sexual selection opposes natural selection and impedes adaptation to new environments. These contradictory reports raise the need for more comprehensive studies because the nature of sexual selection, and the costs and benefits of sexually selected traits can vary across environments and also change with changing environments.

Sexual Selection and Rapid Evolution

Gradual change is the hallmark of evolution by natural selection. This is generally thought to be due to the gradual nature of changes in the environment, biological and non-biological, but more precisely due to the limit on variance in fitness (Fisher 1930). The last 50 years of work in population genetics has shown that, excluding isolated-inbred populations, genetic variation is not a limiting factor in evolution. Evolution is driven by ecological opportunities as shown by the rapid response of beak sizes in Darwin's finches. Gradual evolution does not mean uniformity of rates over time, but instead variable/episodic evolution

in molecules and morphology is a norm and not an exception in modern evolutionary theory.

Sexual selection, on the other hand, provides a mechanism for rapid evolution. Even Darwin and Fisher realized this. Unlike viability, which follows environmental changes but within limits over time, sexual selection depends on mate choice and mating frequencies that involve sexual interactions between males and females – a feature that remains persistent generation after generation. All else being equal, the factors affecting mate choice (female choice, sexual arm race, and male sex drive) can illicit changes in every generation, which would make sexual behavioral characters, e.g., desire to mate, to become reenforced over time.

Evolutionary studies have shown that sexual selection is an important factor in generating sexual dimorphism in a variety of molecular, morphological, physiological, and behavioral traits. Molecular evolutionary studies are shedding light on how sexual selection has shaped male and female specializations in the genome. Recent studies have shown that sexual selection is an important factor in generating sexual dimorphism in patterns and rates of molecular evolution in genomes. Some of these observations are as follows: (1) A large proportion of the annotated genes in the genomes of *Drosophila* and other organisms show sex-biased expression, indicating that sex- and reproduction-related (SRR) genes represent a significant component of the genome; (2) SRR genes show elevated levels of tissue-specific expression compared to non-SRR genes; (3) a high proportion of SRR genes displays accelerated divergence in sequence and expression, as well in loss/gain of genes; and (4) male-specific molecules like testis-specific genes, seminal fluid proteins (SFP), and spermatogenesis genes show lineage specific bursts of accelerated evolution and positive selection. These trends have been recently demonstrated in an increasing number of taxa. These results show that sexual selection is an important force driving the rapid divergence of male SRR genes and that accumulation of “male-fitness enhancing” mutations are likely due to male sex drive. Note that, in birds and Lepidoptera, female-biased genes evolve faster

since they are the heterogametic sex. It is important to note here that not all SRR genes show higher divergence; for instance, genes involved in sperm and egg structures and functions remain constrained in their rate of evolution.

Sexual Selection and Speciation

Speciation is well recognized to be one of the fundamental processes that generate biodiversity and understanding how speciation occurs remains one of the greatest puzzles in evolutionary biology. Darwin was aware that sexual selection can play a potent role in the origins of species. Indeed, he dedicated an entire book explaining how sexual selection influenced divergence of sexual characters, creating “varieties,” “subspecies,” and “allied (closely related) species,” and how divergence and variations in man were a result of sexual selection (Darwin 1871). Post-Darwin however, the role of sexual selection in speciation, was considered secondary since divergence of sexual characters and the establishment of reproductive isolation was considered to evolve gradually when populations were geographically isolated from one another, i.e., in allopatry (Dobzhansky 1937; Mayr 1942). This was also a time when the mechanism(s) of sexual selection was intensely debated (see above), and mate choice, species-recognition, and speciation were viewed as fundamentally different, rather than a continuum as we see it today (i.e., all three phenomena incorporate the same processes).

Several studies later emerged and supported the idea that divergence of sexual characters due to sexual selection can be a powerful force that can not only initiate but also accelerate the process of speciation. The rapid origins of the remarkable diversity of the Hawaiian *Drosophila* attracted considerable attention to the possible role of sexual selection in speciation. Studies proposed that via concurrent evolution of male signal displays and female preferences, species can rapidly radiate into new behavioral niches, rather than into geographical niches (Ringo 1977). Lande’s work (e.g., 1980) was most influential in establishing the idea that sexual selection can cause speciation.

In his models, as long as there is genetic variation for male traits and female preferences for that trait, then assortative mating will lead to speciation in a Fisherian manner. West-Eberhard (1983) wrote an influential review and provided detailed arguments of how social evolution, including social competition for resources and mates, including intrasexual and intersexual selection, can lead to rapid divergence of social and sexual signals even in sympatry. She reasoned that under social evolution, sexual selection will be strong and that a runaway process can be initiated by any number of behavioral, genetic, or ecological factors. Thus sexual selection is certain to have played a role in speciation across animal groups.

One of the ways to test that sexual selection causes population behaviors to diverge to the point that speciation can occur is to show that (1) male signals must be divergent across populations and species, (2) females must prefer local signals to heterospecific signals, and (3) male signal divergence across populations must correlate with genetic divergence between populations. Ryan and coworkers made important contributions by demonstrating considerable variations in male signals and female preferences for these signals in anuran populations. Ryan and Rand (1993) demonstrated that sexual selection and behavioral isolation occur via similar processes. These processes were previously considered to be unconnected. They showed that female tungara frogs (*Physalaemus pustulosus*) respond to both heterospecific and intraspecific signals, but females nonetheless prefer the intraspecific signal. Later, Boul et al. (2007) demonstrated that all three test criteria in are met in *Physalaemus petersi* (a sister species to *P. pustulosus*) to substantiate that sexual selection does indeed drive speciation.

Comparative studies have traditionally played an important role in suggesting that sexual selection influences speciation. Two types of comparative tests have been useful. Darwin noted that (1) secondary sexual characters appeared most pronounced in species-rich (speciose) animal groups, and (2) sexual characters are the most divergent across closely related species (Darwin 1871). Tests of the first kind were done by

Barraclough et al. (1995), who compared 20 recently diverged sister species of passerine birds that either had different color patterns between males and females (sexual dichromatism) and those that did not (monochromatic). Sister species, in theory, have accumulated variations for a similar amount of time. If Darwin was right, then one would expect the sexually dichromatic species to be more speciose than the monochromatic birds – which is what Barraclough et al. (1995) found. This comparison was later extended to show that promiscuous bird taxa tend to be more speciose. However, recent tests of same issue across mammals, birds, butterflies, and spiders remain inconclusive with some supporting Darwin's observation and others finding no evidence for it.

Research on the second test – that sexual characters are most divergent across closely related species – has been far more consistent in supporting the role of sexual selection in speciation. Darwin (1871) himself gathered plenty of data to demonstrate that sexual characters are most divergent between species and emphasized on female choice as a driving force. Eberhard (1985) compiled an impressive array of data showing that male genitalia are one of the most divergent characters across the animal kingdom. He later attributed this trend to be primarily due to cryptic female choice (Eberhard 1996). Arnqvist and Thornhill (1998) argued that genitalia evolved rapidly and divergently due to sexual conflict. Jagadeeshan and Singh (2006) proposed an interaction between male-sex drive and female choice. The rapid evolution of male genitalia has been extended to a variety of taxa other than insects, but the evolution of female genitalia is only recently beginning to receive interest.

The advent of gel electrophoresis and subsequent advances in molecular methods revolutionized evolutionary research. Singh and coworkers were influential in bringing about interest into the molecular signatures of sexual selection (reviewed in Singh and Jagadeeshan 2012). In 1988 Coulthart and Singh published a series of papers showing that reproductive proteins showed little variation within species but large variation between species. Later it was demonstrated that

reproductive proteins evolved more rapidly and divergently compared to nonreproductive proteins. A long line of studies across taxa subsequently demonstrated that reproductive genes, particularly male SRR genes, evolved fast compared to nonreproductive genes. This trend also brought new light into Haldane's rule (Haldane 1922) that when hybrids are produced, the heterogametic sex is either inviable or sterile. New insights continue to emerge from comparative genomic studies. All of these studies provide a strong molecular foundation that sexual selection influences speciation. However, there is a lack of consensus regarding the mechanisms, and many important tenets of speciation by sexual selection remain to be demonstrated. There is emerging consensus, however, that in most cases, sexual selection will interact with natural selection and species ecologies in various ways to influence speciation.

Sexual Selection and the Problem of Males

Sexual selection by definition implies selection through mate choice performed by males and females and the two sexes are a given. In other words sexual selection does not pertain to the important question "Why males, or why are there males?" Why males, is part of the larger question: why there is sex? The answer, provided by population genetics, is that sex essentially means variation and variation is good for evolution. The advantage of variation must be large enough to compensate for what is called the twofold cost of sex (producing males and transmitting only half the genome to offspring) and to counteract the establishment of self-fertilizing mutations in populations. The problem of males is worse than the problem of sex because as opposed to asexuals or hermaphrodites, in species with males and females half of the population does not reproduce, other than contributing gametes. Given the high cost of sex, advantage of variation is not a satisfactory answer to why sex is so prevalent.

The twofold cost of sex is based on evolution in a closed population comparing unisexual (self-

reproducing) versus bisexual reproduction. If we move away from the advantage of variation argument and look at the sexual behaviors and lifestyles of males, then the evolutionary purpose of males becomes clearer. With their dominance, agility, and mobility to explore new territory and new resources, one wonders if males have found a way to invade the (asexual) genome, to induce molecular changes that make females dependent on male contribution, and to evolve an aggressive lifestyles that favors males often at the cost of females – all of which may add up to more than what is needed to compensate for the cost of producing males. Males, driven by their "eagerness" to mate may have turned themselves into nature's drivers of evolution by self-reinforcing, repeated evolutionary change; this occurs through selection for exaggeration of sexual desire, which in turn promotes mate seeking, competition, copulation, mate guarding, and everything else. Individually males get the benefits of mating; collectively they augment overall population and species fitness. Sexual selection through sex drive offers a powerful mechanism for the maintenance of males and for the success of higher organisms in general.

Cost of Sexual Selection

We are not concerned here about the cost of males or the maintenance of sexual reproduction but only about the cost of sexual selection or the cost of mating. Mating can be costly to females. Males and females are different and unequal in their biological endowment with respect to sex and reproduction. This is likely due to anisogamy and the associated difference in energetic requirements to produce gametes. Males can produce larger number of smaller gametes and engage in repeated mating. Females on the other hand produce limited number of eggs and do not mate as often as males do. Thus a male's fitness is directly proportional to the number of mates he can garner. The resulting sex differences in reproductive interest can be detrimental to females due to male harassment and the harmful effects of multiple mating.

Notwithstanding, it is important to point out that with respect to linking the origin of sexual dimorphism on anisogamy, it may not be the differences in gamete size per se that drives male-male competition. Indeed, egg sizes vary considerably between animals but so can sperm. *Drosophila bifurca* is only a few millimeters in size, but it produces sperm 6 centimeters long. The heightened male activity and male-male competition may originate from qualitative sexual differences in the transmission of genetic information between the sexes (excluding sex chromosomes or mitochondrial DNA). Life is an unbroken chain through females (or hermaphrodites), but not males; male contribution is necessary but limited to a reduced set of chromosomes. Females, on the other hand, transmit through their eggs, a haploid set of chromosome plus essential mRNA and proteins needed to kick start embryogenesis. Furthermore, gametes have to find each other. This is achieved through mate recognition, mate choice, and mating, followed by movement of sperms toward the eggs. Eggs are sedentary; sperm are mobile.

Aggressive male mating behavior means stronger selection on males since all males do not get to mate. Male-male competition provides a mechanism for the purging of male-deleterious mutations and the accumulation of male-beneficial mutations, even if they may be harmful to females. *Drosophila* male accessory gland proteins (Acps) are a good example of the latter. Male Acps are transmitted with the sperm during copulation. Many of these proteins are known to affect females in a variety of ways including modifications to female remating behavior, life span, egg-laying, and overall fitness (Wolfner 2007).

Female choice can also impose costs on sexual selection. Strong female choice linked to a trait such as the peacock's tail (irrespective of whether it is a condition-dependent or condition-independent indicator trait) will lead to its exaggerated expression and associated cost not only in energetic terms but also in terms of negative effects on the male's fitness. The cost of sexual selection is real, and it is irrelevant that males gain more mates and success. Even if disassociated from female choice, male-male competition for

mates can lead to exaggerated expression of a male trait as shown by the length of deer's antlers or the large size of elephant seals (Andersson 1994). Indeed, sexual reproduction is often wasteful and goes against the theory of optimality.

Beside the cost of mating, sexual conflict and sexually antagonistic selection (see chapter on these topics) can lead to unequal fitness of the sexes and lower overall population fitness. In theory both sexes should have equal fitness, but in reality this may not be possible due to the lack of mechanisms available for females to counter respond. Alternatively it may be possible to make up for such loss of population fitness through trans-generational gain of fitness that is driven by male reproductive longevity. For instance, loss of fitness due to death of females (caused by male harassment or toxic seminal proteins) can be compensated by males mating multiply with females from different generations, i.e., similarly aged females and with younger females from the next generations (Jagadeeshan et al. 2015).

Sexual Selection and Human Evolution

Darwin's theory of evolution by natural selection, or descent with modification, affected how humans view themselves, and the theory faced stiff opposition. Arguments were made by many to make humans exceptional, particularly in the area of language, art, and choice. Since Darwin did not believe in human exceptionalism, it is believed that one reason why Darwin pushed the idea of sexual selection (through female choice) was that he wanted to show that "choice" was not a prerogative of humans, a position promulgated by theologians, and that other animals can also exercise choice. Furthermore, Darwin did not believe that the origin of human races could be explained by natural selection alone, a position no evolutionist holds now. Darwin went on to conclude that "of all the causes which have led to the differences in external appearance between the races of man, and to a certain extent between man and the lower animals, sexual selection has been by far the most efficient" (Darwin 1871).

Darwin pushed the idea of female choice and esthetics even though he was aware, as were most of his contemporaries, that there appears to be little evidence for female choice in humans. And this is the reason why Darwin's theory of sexual selection was rejected by his contemporaries including Russell Wallace. Wallace suggested a utilitarian role for coloration and argued that the reason why female birds are dull is that dullness provides females and their eggs protection from predators. While Wallace's protective coloration became accepted, his theory did not explain why males were bright and conspicuous.

Darwin flip-flopped on men choosing women and wrote in *The Descent of Man*: "In civilized life man is largely, but by no means exclusively, influenced in the choice of his wife by appearance" and then contradicted himself, "Civilized men are largely attracted by the mental charms of women, by their wealth, and especially by their social position" (Darwin 1871, p. 338). While evolutionary psychology literature is full of examples of female choice, in which adaptationists argue that "it makes sense" from the female point of view, the original observations about men have not changed: that men have a strong *desire for sex*, that they have *innate feeling for beauty*, and that it is largely men who exercise *selection in choosing mates (women)*. The sexual axis of "desire-beauty-choice" is largely a self-reinforcing male-driven process.

Mating Systems, Mate Choice, and Female Beauty

To see if sexual selection has played an important role in human evolution, we need to look at the evolution of mating system. The role of sexual selection in human evolution can be partitioned into three phases that may reflect changes in mating strategies: preagriculture hunter-gatherers, agricultural-settled populations, and modern populations. Human mating system has evolved from being promiscuous to polygamous to monogamous. Promiscuity would have allowed room for mate choice and sexual selection to operate through both sexes. Polygyny would have been far more common than polyandry, and it would have allowed room for male choice

where resource-rich males would have monopolized beautiful females. Even monogamy allows room for male choice in the selection of brides in patriarchal societies. With the rising role of female choice in modern (western) populations, true sexual selection in the Darwinian sense has begun to play an important role, but male choice for brides still reigns in much of the world.

One of the most important aspects of human mating systems is the evolution of male desire (male sex drive) for younger females and female beauty. Male choice for younger females would select for early sexual maturity and early reproduction and male choice based on beauty would push for the concentration of "beauty traits" in younger females. Besides facial features, many of which would have evolved to become population, country/culture specific, sexual selection has played a major role in the evolution of skin color in mixed modern populations. While traits affecting survival evolve in response to changes in environmental elements, sexual desire evolves through repeated male-male competition and/or through male charm and/or coercion. This makes the evolution of sexual desire or male sex drive unlike any other trait.

Male Choice and Female Modification in Humans

The role of male choice and female modification extends beyond facial beauty and skin color. Evolutionary consequences of male-driven sexual selection can be costly to females, and it can potentially reduce female fitness. A recent study showed that male preference of younger mates would deprive older females from reproduction and its associated biology, which in turn would lead to the accumulation of deleterious mutations affecting female fertility, eventually giving rise to menopause (Morton et al. 2013). The important point of choosing younger mates here is that it not only provides a genetic theory of menopause, but it also shows that human (mating) behavior can make deleterious fertility mutations behave as neutral and accumulate in the population. Sexual selection by mate choice has been consequential to the evolution of female fitness by influencing the evolution of traits such as menopause,

maternal mortality, loss of estrus, breast size, hip size, and others.

Conclusion

Sexual selection, according to Darwin “depends on the advantage which certain individuals have over individuals of the same sex and species, in exclusive relation to reproduction” (Darwin 1871, Vol. 1, p. 256). Sexual selection is the result of competition for mates. Since males generally compete for females, Darwin thought that female choice is a major driving force of evolutionary change. The issue of how and particularly why female choose remains a contentious issue but by no means undermines the progress that has been made. Any trait that becomes the basis of mate choice, will for various reasons, come under selection as a result of changes in mating behavior. Animals have evolved a large repertoire of mate selection mechanisms or mating rituals in which males and females make use of various traits (song, dance, calls, size, color, plumage, and odor) to select mates. The development of several valid theories of mate choice or sexual conflict, male sex drive, etc. is evidence of the complexity of the field. The unresolved debates can only mean that the field of sexual selection is still wide-open and avails rich opportunities for research in a technologically advancing world. Due to the traditional popularity of female choice since Darwin (males fancy to be the object of female desire), male choice has been given little attention. Sexual conflict has provided an alternative, but the male’s role in sexual selection has been largely restricted to male-male competition. Yet Darwin himself was fascinated by the “eagerness” and “vigor” of males during mating. These qualities can themselves be under selection as Darwin and Fisher deduced – that the most vigorous males succeed or that females choose a trait that indicative of a male’s vigor. Research in this field is beginning to receive some attention and the results are promising.

Overall, a large variety of data now support the idea that sexual selection is responsible for many

of the spectacular sexual dimorphisms and species diversity across animal and plant groups. Molecular studies have uncovered the impact of sexual selection on the genome as a whole and have shown that sex- and reproduction-related genes have diverged faster than other genes and male-biased genes faster than female-biased genes. The molecular data support the conclusion that besides female choice, male sex drive has been a powerful force of evolutionary change. In the end, much progress remains to be made and much more to be learned, and Darwin’s intuitive framework laid out a century and half ago will continue to steer the exciting progress that will be made in sexual selection research.

Role of sexual selection in human evolution goes beyond mate choice and reproduction; sexual selection has become a permanent feature of human society and culture. All through history – particularly religious history – man has fought against sexual desire at every level and in every possible way while at the same time succumbing to it as an addict to his substance. Man has wrangled with his sexual nature by denying it, but advances in sexual selection and psychology have turned the tide. Religious and social stigma can no longer ignore the fact that man is driven by sexual desire and that male sex drive is a major force of evolutionary as well as social change. Sex defines man’s nature and sexual selection and mate choice are essential to the understanding of human nature – body and mind, individual and society.

Cross-References

- ▶ [Evolution of Genitalia, The](#)
- ▶ [Fisherian Runaway Selection](#)
- ▶ [Sex Differences](#)
- ▶ [Sexual Conflict](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Dimorphism and Sex-Biased Gene Expression](#)
- ▶ [Sexual Selection via Direct Male-Male Interactions](#)
- ▶ [Sexual Size Dimorphism](#)
- ▶ [Sperm Competition](#)

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Charles Lyell

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Charles Lyell was born at Kinnordy House, near Kirriemuir, a few km SW of Aberdeen, in Forfarshire (now Angus), Scotland, on

14 November 1797. He died in London on 22 February 1875 and was buried in Westminster Abbey. He was joined there 7 years later by his friend Charles Darwin. Significant pioneers of geological science and the study of evolution lie together. He was the oldest of ten children; the family moved south to the New Forest region, near Southampton where he lived when he was young. At the age of 19, he enrolled at the University of Oxford (Exeter College) and graduated BA in 1819 and MA in 1821. He was lured into geology, to a large extent, by Poulett Scrope and spent his life dispensing geological knowledge. His first paper, in 1825, was on a serpentinite exposure in Canty Burn along what is now known as the Highland Boundary Fault. The Canty exposure is only 3 km from Kinnordy. His great work was the *Principles of Geology* which commenced publication in 1830 and was produced in a variety of editions throughout his life (Lyell 1830–1833). The 12th edition was in print at the time of his death. He is associated with Charles Darwin; he wrote the famous letter to Darwin in 1836, just after the return of the *Beagle*, urging him to avoid all administrative tasks and to concentrate on scholarship. He also cooperated with Joseph Hooker, to have the outline of the theory of evolution, sketched by Darwin in 1844, published along with Alfred Russell Wallace's version of the same conception, by the Linnaean Society in 1858 (see Partridge 2015).

Biobibliographical Studies

There are several excellent biographies; Bailey (1962) presented him as a “British Man of Science” in the Nelson series. Wilson (1972) reported the early years (to 1841) in great detail and added useful accounts of Lyell in America (Wilson 1998). He also published a valuable study of Lyell's journals on the species question (Wilson 1970). The best appreciation of Lyell is perhaps that by Secord (1997). This appeared as the introduction to the Penguin edition of *Principles*. The Penguin edition is a superb version of the *Principles*; Secord has carefully edited the three-volume work down to a handy one-volume paperback; the

essence is retained, but some unnecessary detail is discarded.

The whole three volumes of the first edition have been reproduced by the University of Chicago Press – another impressive bibliographical achievement. volume 3 carries the bibliography of Lyell's sources by Rudwick (1991), an invaluable aid to the Lyell scholar. So the *Principles* is nicely available, and the life story carefully told. Lyell's more intimate moments are caught in the *Life and Letters, and Journals of Sir Charles Lyell, Bart* edited by his sister-in-law Kathleen Lyell (1881).

Poulett Scrope (1797–1876)

George Julius Poulett Scrope and Charles Lyell were secretaries of the Geological Society of London in 1825. Scrope was interested in the volcanoes of the Auvergne region and wrote quite extensively on this topic; his *Volcanoes of Central France* was reviewed by Lyell for the journal *Quarterly Reviews*, and this review is seen as a major pioneering geological work by Lyell. This review of more than 40 pages allowed Lyell to set out his basic ideas on geology – which he went on to develop throughout his life in the successive editions of the *Principles* (Lyell 1827).

Bailey (1962, p. 67) quoted a section of Poulett's writing which he offered as a sort of mantra for Lyell's approach to geology:

The leading idea which is present in all our researches, and which accompanies every fresh observation, the sound which to the ear of the student of Nature seems continually echoes from every part of her works, is- Time! –Time! –Time!.

The concept of time is key to the works of Lyell. He establishes the importance of time. Deep time – geological time – was more or less invented by James Hutton (1726–1797), but Hutton was an incoherent apostle for his great invention; Lyell was the great prophet of time, and the *Principles of Geology* presented to the world the concept that the world was very old and that deep time extended back an almost inconceivable distance. There was plenty of time for the processes of evolution to operate.

Uniformitarianism

The term “uniformitarianism” as used in modern earth sciences has been reviewed by Romano (2015). The term is essentially now synonymous with the entire theoretical system proposed by Lyell in the *Principles*: “the present is the key to the past.” The term was coined by Whewell in 1832 to indicate a specific part of Lyell’s hypothesis, but over the years, it has become the central part of the Lyell doctrine. Time – deep time – is required in which geological processes can operate.

Darwin Correspondence Project

The Darwin Correspondence Project has set out to collect and publish all of Charles Darwin’s letters, letters to Darwin and letters by Darwin. Since Darwin was a prolific letter writer, the list of correspondents includes many notables of the time. There is, of course, a considerable section of letters to and from Lyell. Letter DCP-LETT-4149F dated 9 May 1863 from Lyell to Darwin related the events around Lyell’s conversation with Queen Victoria; the Queen wished to talk about Darwin.

Letter DCP-LETT-335; dated 26 December 1836

From Lyell to Darwin

Will you come up on Monday January 2, and come and dine with us at half-past five o’clock, or come at five, and I will go over the paper before dinner? No one dines with us but Mr and Mrs Horner and one daughter, and Mr Horner will be glad to renew his acquaintance with you.

Soon after the return of the Beagle, a close, harmonious relationship between Lyell and Darwin begins.

Principles of Geology

volume 1 of the *Principles of Geology* was published by John Murray in London in 1830. The second volume followed in 1832 and the third in 1833. By the time that Vol. 3 appeared,

second editions of Vols. 1 and 2 were already published. For the rest of his life, Lyell updated the *Principles*, and a succession of editions appeared. The 12th edition was in press at the time of Lyell’s death. It remains in print in various editions; there is a very neat one-volume edition available as a Penguin Classics.

Secord (1997, p. x), the Penguin editor, observed that *the Principles of Geology* is often read as a Victorian work, but its origins are in the Romantic era, in the religious, political, and literary history of the Regency. The first edition (published by John Murray in 1830) belongs on the shelf with De Quincey and Scott, not Dickens and Darwin. Its foundational project marks the book as part of political debates that culminated in the 1892 Reform Bill. Secord (1997, p. x) noted that many readings of the *Principles* narrow its meaning, and it is often seen solely as a precursor to Darwin’s *On the Origin of Species* (1859) – a view that would have surprised Darwin himself.

Darwin took Vols. 1 and 2 with him on The Beagle, and Vol. 3 reached him at Valparaíso in Chile. Darwin was reading about Lyell’s new enthusiasm for loess as the Beagle headed north, on the return voyage.

In the default biography of Lyell by Wilson (1972, p. 376), volume 3 is described as the first volume to contain straightforward geology:

The third and final volume of the *Principles of Geology* was in a sense the first which dealt with geology proper, or what would have been recognized as geology before Lyell began writing. In it Lyell surveyed the whole series of geological formations beginning with the most recent and proceeding back through the succession of Tertiary formations, which had been revealed in part by the work of Desnoyers, but which Lyell himself now developed far more fully and completely. (Wilson 1972, p. 376)

Antiquity of Man

The great work of Lyell’s later life was the foundation book for anthropology and prehistoric studies. Bailey (1962, p. 198) suggested that among Lyell’s achievement in his later years, the *Antiquity of Man* (1863) surely ranks highest. If it

stood along, it would place him among the foremost of scientific authors. Its scope is amazing. Bailey gives a good review of the 24 chapters. Wool (2001) pointed out Lyell's role as a forerunner of modern ecology.

Lyell and Darwin

Secord has suggested that a valuable account of the relationship between Lyell and Darwin can be found in Browne (1995). She (Browne 1995, p. 348) proposed that Darwin was the first naturalist to use Lyell's "principles" effectively, his first and, in many ways, his only fully committed disciple.

Harriet Martineau (1877, p. 268) wrote:

There were the friends Lyell and Charles Darwin, after the return of the latter from his four years' voyage round the world:- Lyell with a Scottish prudence which gave way more and more as years passed on, to his natural geniality, and to an expanding liberality and freedom of speech; and the simple, childlike, painstaking, effective Charles Darwin, who established himself presently at the head of living English naturalists.

Harriet was a good friend of Erasmus, Darwin's brother, and was well placed to observe interactions with Lyell.

Wilson (1972, p. 433) quoted this passage at the head of his chapter on Darwin and Lyell (1836–1841). He went on to say that Lyell and Darwin met frequently to discuss geology. Seldom (he claimed) can there have been a more fruitful interaction of scientific minds. Darwin had found the *Principles of Geology* an indispensable guide in interpreting the geology of South America and one which illuminated the meaning of the country for him.

The Horner Family

Lyell had several links to the Horner family. He married Mary Horner in 1832. She was the eldest daughter of Leonard and Anne Horner. In the early 1830s, the Horner family lived at Bonn. Lyell made an excursion to the Eifel region in

1831 (Smalley et al. 2016; Smalley 2017), ostensibly to look at the volcanic phenomena of that region and also to visit the Horners. During that visit he became engaged to Mary Horner. They married in 1832 and made a trip down the Rhine for their honeymoon – during which Lyell was able to observe the loess deposits and talk to Karl Caesar von Leonhard and H J Bronn, the famous mineralogists at the Heidelberg.

The Horner's fourth daughter Katherine married Lyell's brother Henry and eventually edited the *Life and Letters, and Journals of Sir Charles Lyell, Bart* – an invaluable source for all Lyell scholars (Lyell K.M. 1872).

Leonard Horner was a committed geologist (Smalley and Kels 2018) and worked with Lyell in the Eifel region. He and Lyell made a famous field trip to the crater of the Rodderberg in 1832 and investigated the loess which had been deposited in the crater. He was present at the dinner in 1836, the famous post-Beagle dinner with Darwin. Two of the diners went on to become famous geologists. Horner spent his life as a social reformer and striver for worker's rights – one of the few people mentioned by name in *Das Kapital* by Karl Marx.

Lyell's Loess Legion

Lyell's fame rests essentially on his great study of all of geology, the ongoing *Principles* project, and his association with Darwin and evolution. This great blanket of fame has to some extent obscured other aspects of his geologizing and resulted in the neglect of several geological achievements. In particular his early (1830–1836) studies on loess material and loess deposits have been unappreciated for many years. Now there is a realization that Lyell was a major loess pioneer (Lyell 1834); in fact he is one of the two major loess pioneers, sharing that honor with Karl Caesar von Leonhard (Smalley et al. 2014, 2019).

In the preface to volume 3 of the *Principles*, Lyell wrote:

In the summer of 1831 I made a geological excursion to the volcanic district of the Eifel, and on my return I determined to extend my work to three

volumes, the second of which appeared in January, 1832. The last volume has been delayed till now by many interruptions, among which I may mention a tour, in the summer of 1832, up the valley of the Rhine, when I examined the loess. (Vol. iii, p. 151)

For much of the nineteenth century, Lyell's theory of water-deposited loess was the paradigm theory for loess deposit formation. It largely held sway until replaced by Richthofen's aeolian theory in the 1880s (Smalley and Markovic 2019). Lyell identified various key workers in the field of loess studies and listed them in Vol. 3 of *Principles*. In the first edition, they were von Leonhard, Bronn, Boue, Voltz, Steininger, Merian Rozet, and Hibbert; by the fifth edition Horner (father in law) had been added, together with von Meyer and Noeggerath. Lyell was following developments in the world of loess scholarship.

Lyell and Darwin Interact

Four aspects of interaction can be identified:

1. Darwin takes Lyell's books with him on the Beagle. They provide his geological support.
2. Soon after the return, Darwin and Lyell meet for dinner, and a cooperative relationship is launched.
3. Lyell and Hooker, determined to look after Darwin's interests, arrange for the first announcement of evolution by natural selection to be a joint paper by Darwin and Alfred Russell Wallace.
4. Lyell and Darwin never reach a proper agreement on all aspects of evolution, but they are close and always reconciled.

A final word from a historian, Richard Holmes (2008, p. 454), writes that the geologist Charles Lyell began in 1830 to bring out his classic work *Principles of Geology*, which would finally use scientific evidence to reject the Biblical account of short-scale creation of the earth, as maintained by every authority from Cuvier and Paley to Buffon and Buckland. Lyell's proposal of "deep time" corresponded to the "deep space" cosmology of William Herschel. It would ultimately provide the

supportive authority for Charles Darwin, his great friend, to accept the deep time necessary for evolution by natural selection to take place.

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Chase-Away Hypothesis, The

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Definition

A coevolutionary race between signals that access preexisting vulnerabilities in receiver sensory/endocrine systems in order to manipulate reproductive traits and resistance to those signals due to receiver costs.

Introduction

A long-standing question in modern evolutionary biology began with Darwin (1871), who hypothesized that “. . . ornaments of many kinds—their organs for producing vocal or instrumental music—and their glands for emitting odours. . . serv [e] only to allure or excite the female.” Why these traits succeed remains an open question. Their attractiveness may be an adaptation by the choosier sex resulting from the ornament having provided information about species identity or qualities associated with a prospective mate (e.g., genetic, resource, parasite presence) (see Andersson 1994, for an overview). Alternatively, ornament attraction may not be an adaptation. Instead, “preferences” may be pre-existing incidental sensory biases (Basolo 1990; Ryan 1990).

The chase-away hypothesis proposes that sensory biases are vulnerabilities of information processing that may be subsequently exploited by signals that induce reproductive trait changes away from the receiver’s optimum. Signals range from molecules (pheromones) to highly ornate sounds, tissues, and behaviors that may attractively stimulate the receiver. With respect to the fitness effects on receivers, these signals are no different than what is expected from brute force. Manipulated traits include the age of sexual maturity, mating frequency, and parental effort (fecundity and investment per offspring). Fitness costs select for resistance to the signals (e.g., increased cumulative stimulation required to elicit the same behavior), counter selecting increased signal magnitude. The coevolutionary race may last indefinitely and leave a trail of magnificent signals that may be of minimal value. In this model, the signal does not provide useful information to the receiver, but other models are not mutually exclusive.

Darwin-Bateman Paradigm

Most researchers agree that the source of sexual selection is described well by the Darwin-Bateman paradigm (see Parker and Birkhead 2013, for a recent introduction to sexual selection and sexual conflict). Bateman (1948) performed a simple experiment in which he assigned male and female fruit flies (*Drosophila melanogaster*) a specific number of mates. Female reproductive success increased modestly after the first mate (females can store sperm to fertilize eggs for several days), but male reproductive success increased approximately additively with each mate. Bateman proposed that female fitness was energy limited, while male fitness was fertilization limited. Trivers (1972) generalized Bateman’s analysis and identified relative parental investment (PI) as a critical organizing influence of sexual selection. PI is any investment (time, energy, etc.) in an offspring that reduces a parent’s ability to invest in other components of fitness. Sexual selection will tend to occur in proportion to the difference in PI between sexes. The fitness of

members of the greater PI sex is usually limited by their ability to convert resources into offspring, whereas the fitness of members of the lesser PI sex will tend to be limited by fertilization success. The lesser PI sex competes for the gametes of the higher PI sex. This article often uses “male” and “female” for simplicity. Because of the evolution of shared PI, or PI role reversal, it is a better predictor of reproductive strategies than sexual identity. One could also use operational sex ratio or potential rates of reproduction, rather than PI.

Life History Trade-offs

Individuals are selected to allocate investment in any activity in a way that maximizes fitness, given the innumerable trade-offs, such as between current parental investment and future capacity for parental investment. For example, when Gustafsson and Pärt (1990) randomly assigned collard flycatcher females an extra egg during their first clutch (increasing their number of eggs from approximately 5–6), their unmanipulated clutch sizes in subsequent years plummeted compared to control females who did not receive the extra egg at age one. A variety of experiments and theory produce consistent results. If life is a race, then the distance of the race determines the optimal speed. Females are selected to run a marathon, distributing their enormous parental effort optimally over time. Males are selected to manipulate females to sprint, to the extent that future offspring are likely to be sired by others.

Intersexual Conflict Over Female Optima and Sexually Antagonistic Coevolution

The foundation for the study of intersexual reproductive conflict begins with Darwin, 1871. The modern subject was reawakened by Parker (1970) and Trivers (1972). This article is concerned with intersexual conflict over female optima for reproductive traits, such as the age of sexual maturity, mating frequency, and rate and timing of maternal investment. In each case, the optimal value from a male’s fitness perspective

may differ. Such conflict can lead to sexually antagonistic coevolution (SAC), a type of arms race between other traits (e.g., pheromones and receptors) in males and females that mediate the value of the trait in question. SAC, as with that of ecological enemies, like parasites and hosts, may proceed indefinitely and occurs between traits that are produced by different genes (interlocus). For reviews, see Parker (1979), Rice and Holland (1997), Chapman et al. (2003), and Parker (2006).

SAC Over Hormonal Control of Female Reproduction

Internal fertilization and development create widespread opportunities for exploitation of maternal investment that result in costs to lifetime female fecundity and survival. Seminal fluid contains much more than sperm. Experiments with the model organism, *D. melanogaster* (a fruit fly), show that among the approximately 130 seminal fluid proteins include some that act as female hormones. For example, sex peptide (Acp70A) increases egg production, delays remating, and exacerbates the survival cost (discussed below) of mating in females (Wigby and Chapman 2005). In short, it increases male offspring production per copulation (Fricke et al. 2009) at an apparent long-term cost to female fecundity. Kuijper et al. (2006) manipulated *D. melanogaster* female remating frequency to measure dose-dependent effects of mating and found that losses in lifetime fecundity accelerated with each remating. Other polygamous insects show similar patterns. Male accessory gland secretions of the moth *Spodoptera litura* induce females to delay (polyandrous) remating and increase egg development and egg laying (Yu et al. 2014). Unfortunately, experiments do not always measure lifetime fecundity. Measuring anything less could easily lead to an opposite, incorrect conclusion about the effect of male SFPs on female fecundity in polygamous species, similar to stopping after season one of the fly catcher experiments.

Female counter evolution is sometimes harder to infer but appears likely in a number of

examples. Female *Drosophila* do not make sex peptide, which begs an explanation, given that it is a female reproductive hormone. It has been suggested that hormones might be a cue to the female that copulation is occurring and a form of assistance. This would be an invasive cue and would provide trivial energetic savings. The presence of a male on one's back and the filling of highly innervated sperm storage organs should be sufficient evidence of copulation. Further, females would have better access to information about their physiological condition and hormonal needs than would a copulating male. More likely, the ancestral state was for females to produce sex peptide, then followed a mutation, expressing sex peptide in a male's seminal fluid. The resulting increase in embryo production and delay in female remating were good for the male because his mate(s) used more of his sperm. In other words, the optimal amount of sex peptide present in a female, at mating, is greater for her mate than for her. This male-benefit trait spread. This counter selected females with decreased expression of sex peptide. SAC eventually minimized female expression of the peptide.

Another form of resistance is to decrease response to male deposited hormones. This appears to have been demonstrated by Sakaluk et al. (2006) who tested the resistance prediction of chase-away in a PI role-reversed species. *Gryllodes sigillatus* females benefit from remating because of a nutritional "gift" (spermatophylax) provided by males at copulation. Female *G. sigillatus* remate at the same interval whether or not they are allowed to eat the spermatophylax. *Acheta domesticus* is a non-spermatophylax species. When female *A. domesticus* were given the spermatophylax of male *G. sigillatus*, they accepted more sperm and took longer to remate than those not receiving the gift. The authors suggest that male *G. sigillatus* produce a substance within their spermatophylax that inhibits sexual receptivity, causing females to mate at a suboptimally low rate, and *G. sigillatus* females subsequently evolved resistance to the inhibiting substance.

In placental mammals, a parental contest over maternal investment occurs in the fetus. IGF-II is

a growth hormone that is sexually imprinted (the gene expression is reduced or silenced for one generation) in offspring, by their mothers in rodents, artiodactyls, and primates. The result is that during fetal development the only source of this growth hormone produced in the offspring (placenta) is from the paternal allele, reducing the dosage by approximately 50 %. The mannose-6-phosphate receptor is a sink for IGF-II (by binding and removing it from circulation) and is imprinted in the reverse direction in rodents and artiodactyls. That is, males turn it off in their offspring, while females do not (Burt and Trivers 2009). The logic is the same as with polygamous insects: fathers manipulate mothers to increase their investment in their shared offspring beyond what is optimal for mothers. Somewhat larger than average offspring have higher fitness and higher costs, which will be paid for by the number or quality of the mother's future offspring, sired by a different male. Females coevolved an imprinting response that moved their investment back toward their optimum.

Within each species, there is a trade-off between the age of onset of reproduction and future reproductive success through fecundity, survival, and/or offspring success. This is similar to trade-off seen with the fly catchers. This trade-off is generally inevitable or selection would favor quicker development. Pheromones within the urine of dominant, but not subordinate, male house mice can induce sexual maturation in pre-pubescent females. Prepubescent females avoid the urine of adult males. Around puberty, this avoidance stops. The above are consistent with male manipulation to hasten the sexual maturation of females that might not otherwise be reproductive during the tenure of the dominant male and behavioral resistance on the part of juvenile females to avoid the costs of prematurely entering into their reproductive phase of life.

The types coevolutionary conflicts exemplified above should be common. In general it is not possible for selection to favor males to improve female fitness through hormonal manipulations of female reproductive effort, investment per offspring, or timing of mating or sexual maturation: (1) they lack the information that females have

about their own condition; and (2) in polygamous species, the optimal *maternal* effort is higher for sires, who at the time of mating can only be selected to augment maternal effort and investment per offspring, to the extent that future offspring will be sired by other males. Males will inevitably be screened for traits that turn females into reproductive sprinters (i.e., maximize short term reproductive effort), and females will counter-evolve adaptations to minimize the manipulation and cost to their fitness.

Costs of Mating and Collateral Damage

The act of copulation has a number of substantial, direct costs to both sexes. STDs and lost energy and time are ubiquitous, and increased exposure to predation is common. In species with internal fertilization and polyandry, the perpetual coevolution among male reproductive traits will also generate collateral costs for females (Arnqvist and Rowe 2013). For example, SFPs appear to reduce female survival in a dose-dependent manner (Chapman et al. 1995) as a byproduct of sperm competition (Parker 1970). Sperm competition has selected proteins that displace any previous males' sperm and protect focal sperm from such displacement by any future seminal fluid. When a female *D. melanogaster* remates, the seminal fluid of the new mate displaces most of the stored sperm (Harshman and Prout 1994). The SFP Acp62F is a protease inhibitor that substantially reduces displacement of the focal male sperm by subsequent males' seminal fluid (Mueller et al. 2008). About 10 % of this deposited protein enters the female hemolymph, whereby it appears to reduce lifespan (Lung et al. 2002). Acp70A is also toxic in *D. melanogaster* (Wigby and Chapman 2005). Toxic SFPs have been found in two seed beetles, *Acanthoscelides obtectus* and *Callosobruchus chinensis* (Yamane et al. 2015). Seminal fluid of the moth *Spodoptera litura* also decreases female lifespan (Yu et al. 2014). The toxicity is not immediate, as that would be counterproductive for the inseminating male. The toxicity works more like an acceleration of female senescence.

In polygamous species, once a male's sperm are displaced natural selection cannot favor him to protect his former mate from collateral damage. Female adaptations may interfere with the original male adaptation, or not. However, the main point is that mating is costly and that internal fertilization creates additional costs for females. The perpetual arm's races among SFPs will sometimes generate collateral costs for females. In principle, females may recoup fitness through sons that have these same traits that reduced maternal survival. There is little theoretical support for this hypothesis (Paker 2006). In an experiment that measured female fitness and offspring fitness, the direct costs of conflict greatly outweighed the benefits in offspring (Orteiza et al. 2005).

Conflict Over Mating Frequency

The lesser PI sex generally benefits more from polygamous mating, while internal fertilization increases cost for females (e.g., hormonal manipulations and survival, discussed above). Both the benefits and costs generally favor a higher optimal polygamous mating frequency in males. Therefore, there will commonly be a conflict over mating frequency in polygamous species because it is a joint behavior with sex-specific optima. This does not imply that females cannot benefit from polyandry, as described below.

D. melanogaster has been the focus of much of the work on mating. It is a polygamous species with substantial courtship, and males provide no measurable nongenetic resources to females. Courtship throughout Drosophilids is complex, consisting of wing-song, touch, and pheromones. Wing-song in *D. melanogaster* is a pronounced display in which the male extends one wing toward a female and beats it in a species-specific rhythm while he walks in a semicircle in front of her. Males that provide altered song, or no song, suffer substantially lower mating success which is partially restored by playing an artificial song. Courtship is also stressful to females, reducing longevity (Partridge and Fowler 1990). Linder and Rice (2005) found that genetic variation for female susceptibility to all forms of male harm

comprises 17 % of the total genetic variation for female fitness. Variation in female ability to limit remating in response to persistent courtship was a major component of female susceptibility. The cost of mating to females rises nonlinearly with copulation frequency (Kuijper et al. 2006). The above findings do not appear to be a laboratory artifact. Observations in nature indicate that female mating frequencies are similar, if not identical, to those observed in laboratories (Kuijper and Morrow 2009) and mating decreases female lifespan in a variety of Diptera and Orthoptera insects (Simmons 2001).

Experiments in which populations were made monogamous over evolutionary time indicate that the load on female fitness specifically due to sexually selected conflict is substantial. In populations of fruit flies maintained under experimentally enforced monogamy with random mate assignment, and control populations that retained the opportunity for sexual selection, males evolved to court less and cause lower mortality per mating. Females evolved reduced defenses to male harm, implying that ancestral females possessed adaptations to resist male harm. Within 45 generations, these populations produced approximately 20 % more offspring per generation than controls, which is a substantial peace dividend (Holland and Rice 1999).

The above is meant to illustrate important points, not exhaust possibilities. There can also be benefits to polyandry: sterility, low gamete levels, genetic compatibility, and increasing the genetic variation among offspring are all important (and also important to males). Sometimes females benefit from remating because it generates protection from the current mate or otherwise reduces harassment, or they may be able “trade-up” to a mate of higher quality (see Parker and Birkhead 2013). The critical issue is relative optima. The cost:benefit ratio tends to favor a higher optimal mating frequency in the lesser PI sex.

In summary, there are innumerable conflicts that arise as a consequence of polygamy. Across taxa, males possess traits that in various ways manipulate female reproductive physiology and behavior and/or reduce survival, at a cost to

female fitness. Females possess adaptations to resist male manipulations. Endocrine reproductive manipulation and female resistance are one example of a coevolutionary struggle. Sensory systems may also be hacked.

Sensory Bias

The frog *Physalaemus pustulosus* includes chucks in its male mating calls and females are attracted to these chucks. This same attraction exists in females from a different group in which the males lack the chuck in their vocalization. Phylogenetic analysis indicates that the female attraction predates the male display (Ryan and Rand 1993). In swordtail fish, including *Xiphophorus helleri*, males possess ornamental extensions of the caudal fin (“swords”) which are sexually attractive to females (Basolo 1990). In a sister group, including *Priapella olmecae*, swords are absent. When artificial swords were surgically attached to males of the swordless species, females of that species were attracted to them (Sinervo and Basolo 1996). As with the frogs, phylogenetic evidence indicates that the female attraction predates the evolution of the male display. This is inconsistent with benefits models of sexual selection, which predict that the preferences are adaptive *responses* to the fitness gains associated with the display. Therefore, benefits models do not predict sister taxa with preferences for displays that they have never had a chance to benefit from.

Resistance to Sensory Bias

Using larger males from a closely related species, Ryan and Wagner (1987) demonstrated strong sexual selection by female pigmy swordtail fish, for larger male size. At that time, large body size was not known to occur in any natural pigmy populations. In 1988, large males were discovered in three adjacent, natural populations of the pigmy swordtail. The frequency of large males varied from common to rare along a distance gradient, possibly indicating the spread of large

males from a source population to two downstream populations. In 1988, female preference for large body size was found only in the population where large males were rare. This pattern was also observed in 1993, but the degree of preference for large male body size had diminished further. Both the absence of female preference in the two populations where large males were common and the diminishing preference in the population where large males were rare suggest that female resistance, rather than preference, was evolving for large body size.

McClintock and Uetz (1996) studied two species of wolf spiders. Only one species has evolved tufts of bristles on the forelegs. Phylogenetic analysis indicates that the tufts are a derived character (evolved after divergence from the lineage leading to the tuftless species). Females watched videos of courting males and were graded for sexual receptivity behavior. Manipulation of video images was used to add, remove, or enlarge the tufts on the same males (i.e., every other aspect of the male's appearance was identical). Sexual receptivity in females of the tufted species (*Schizocosa ocreata*) was unaffected (or so small as to be statistically indiscernible) by the presence, absence, or enlargement of tufts. However, in the tuftless species (*S. rovnneri*), the addition of tufts more than doubled the acceptance rate of females to their own, naturally tuftless males. In short, females were attracted to a male ornament more strongly when they lack an evolutionary history with it, indicating that females from the tufted species had evolved resistance to, rather than preference for, this sexual stimulant.

Alex Basolo (1998) also measured the strength of female preference for swords in *X. helleri* and the artificially sworded *P. olmaceae* (see above). Female preference was substantially stronger in the genus that has not evolved swords. Assuming the level of attraction to swords in the swordless species is representative of the primitive state in the sworded species, the strength of female preference for swords has declined in the sworded species, presumably following the evolution male exploitation of the female sensory bias.

Conclusion

The above findings suggest a conflict-based model for the evolution of male signals: (1) sensory and endocrine vulnerabilities in receivers, favor (2) mutations that create (and subsequently elaborate) signals that manipulate those vulnerabilities, resulting in (3) increased mating and fertilization success, and manipulation of maternal effort, and (4) increased cost in receivers due to fitness lost through mating too often/seldom, too early after sexual maturity, etc., and fecundity schedules (e.g., excessive rate of reproduction or investment per offspring), which in turn (5) counter-selects receivers who are relatively resistant to the novel (or elaborated) signals. Steps 2–5 recur in a coevolutionary tug of war between signals and receivers (Holland and Rice 1998).

Chase-away makes two predictions that distinguish it from other models of sexual selection: (1) signals reduce the net fitness of the receiver. For example, if there is variation in receiving sex for mating frequency, it predicts that individuals with below average attraction to the signal will also have below average mating frequencies and will have greater fitness through *lifetime* fecundity (barring PI role reversal, as with *G. sigillatus*), and (2) the evolution of decreased sensitivity/attraction for a signal following its evolution (Holland and Rice 1998; Sakaluk et al. 2006). Reviewed above are examples consistent with these predictions for hormonal, visual, and auditory stimuli. Counter examples were not found.

The opportunities for chase-away are broader than discussed in this article, which focused on PI and mating in polygamous species. For example, chase-away can occur in monogamous systems over mate choice. Once paired, conflict between monogamous mates ceases (assuming true life-long monogamy). If there is remating, for example, after a mate dies, then natural selection sees polygamy, regardless of what we may call it. See Rice and Holland (1997, 1999) and Holland and Rice (1998) for a broader discussion of SAC between genes that mediate intersexual reproductive behavior.

Cross-References

- Conflict Between Parents And Offspring
- Fundamental Tradeoffs
- Life History Theory
- Parental Investment Theory
- Parent-Offspring Conflict (Trivers)
- Sexual Coercion as a Mechanism of Sexual Selection
- Sexual Conflict In Nonhumans
- Sexual Conflict Theory
- Sexual Selection In Evolutionary Psychology
- Sperm Competition Theory

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Chastisement

- ▶ Evolution of Punishment
- ▶ Women Use Verbal Derogation to Be Included

Cheat

- ▶ Problem of Cheating

Cheater Detection

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Definition

The ability to detect non-reciprocators in social exchange scenarios, in which a cheater obtains a

benefit, without satisfying the condition given by the benefit provider

Introduction

Cheater detection, or the ability to detect individuals cheating in social exchange scenarios, is often seen as a branch of evolutionary psychology that shows great promise. The social exchange algorithm, or social contract theory, was developed in Leda Cosmides' now seminal paper (Cosmides 1989) and has generated much interest from those who generally support evolutionary reasoning, those who ardently oppose it, and all those in between. For Cosmides, and others (e.g., Cosmides and Tooby 1992), the enhanced ability of detecting cheaters in logical reasoning tasks, relative to more general reasoning abilities, represents evidence of an evolutionary selection on cognition and, more specifically, of an evolved module specialized for the purpose of detecting cheaters. Although some disagree with this implication, many would accept that, more broadly, this research program has succeeded in providing clear, testable hypotheses, as well as a prespecified paradigm to test them.

Cheater Detection and Social Exchange

Within evolutionary psychology, it is generally proposed that the mind is made up of mechanisms or “adaptations” that were “designed” by natural selection to solve recurrent problems faced by our ancestors in evolutionary history. One such problem likely involved social exchange or cooperation with others to allow for mutual fitness benefits. It is helpful to imagine the following conditional, typical of a social exchange scenario: “If you accept Benefit B from me, you must satisfy Requirement R.” Traits that led to cheating the system, that is, taking Benefit B and gaining the associated fitness benefits, without satisfying Requirement R, would have been selected for, as they allowed the cheater fitness benefits. As a result, the ability to *detect* these cheaters would

also have evolved over time. In essence, for the very act of cooperation to exist, without it being eradicated due to excessive cheating of the system, we must have developed the cognitive capacity to detect non-reciprocators in these scenarios. Based on a series of studies, Cosmides (1989) and Cosmides and Tooby (1992) have suggested that the problem of social exchange scenarios and the possibility of non-reciprocation have, through natural selection, led to the evolution of an automatic, domain-specific cheater-detection module, which is present and observable in human cognition today.

The Wason Card Selection Task

The paradigm that Cosmides (1989) used to support her social contract theory and the existence of a cheater-detection module was the Wason card selection task (Wason 1966). Initially developed to test conditional reasoning, the task involves detecting possible violations of a statement in the form “If P, then Q.” Participants are required to select which of four cards could, in theory, violate this rule, when turned to reveal the other side of the card (see Fig. 1a for an abstract example). The visible sides of the cards show instances of P, not-P, Q, and not-Q (although they are not labelled as such), and the *only* violations of the “If P, then Q” rule could be gleaned from turning over P (to show not-Q) and not-Q (to show P). Generally, performance is poor on the descriptive and abstract versions of this task, with only around 10–25% of participants identifying the appropriate cards to turn (e.g., Wason 1966; Cosmides 1989).

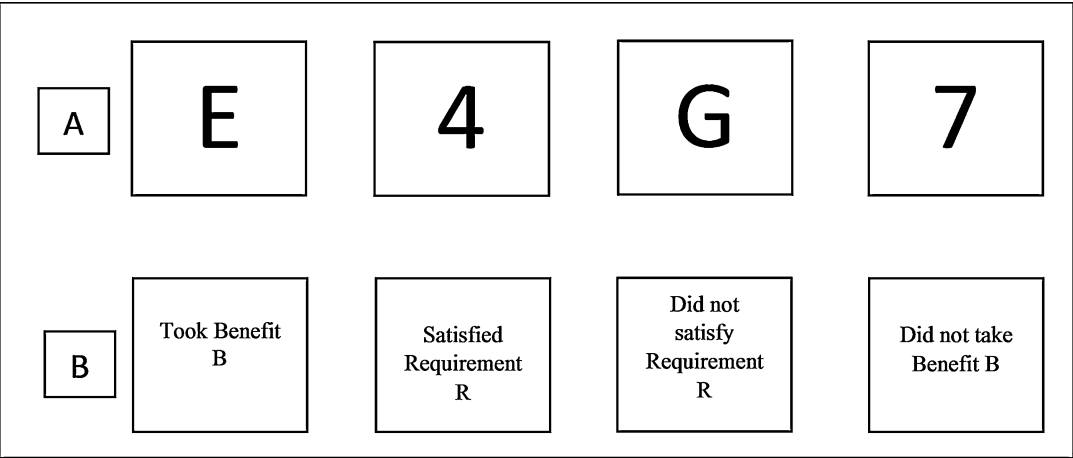
Crucially, when the task was couched in terms of social contracts, Cosmides (1989) found content-related performance facilitation. When presented in the form “if you accept a Benefit B, you must satisfy Requirement R,” reflecting a social exchange scenario, accuracy at detecting violations increased to around 65–80% (Cosmides 1989; Cosmides and Tooby 1992; see Fig. 1b for generic form of social contract task). An actual example of this conditional given in a social exchange context might be the following

rule: “If you use my car, you must pay for petrol,” such that P = using my car and Q = paying for petrol. To detect a cheater in this scenario, one must ascertain whether someone who used the car (P) did not pay for petrol (not-Q) and whether someone who did not pay for petrol (not-Q) used the car (P).

Supporting Evidence

Aside from performance facilitation in cheater-detection contexts already discussed (e.g., Cosmides 1989; Cosmides and Tooby 1992), further support for this purported domain-specific mental module can be derived from evidence of selective impairment in cheater-detection reasoning, relative to more general reasoning abilities. Stone et al. (2002) found that while control subjects performed similarly on both tasks, patient RM, who had extensive bilateral limbic system damage, performed much worse on a Wason card selection task involving social contract rules (“If you take benefit B, then you must satisfy requirement R”), relative to a problem regarding precaution rules (“If you engage in hazardous activity X, you must take precaution Y”). This selective impairment for cheater detection provides support for the existence of an independent, specified mechanism that drives performance and is less consistent with a domain-general mechanism supporting reasoning.

Cross-culturally, there appears to be similar performance facilitation in social contract scenarios, relative to general task performance, as found in a group of nonliterate horticulturalists in the Amazon (Sugiyama et al. 2002). Furthermore, van Lier et al. (2013) found that enhanced performance for cheater detection did not depend on age or cognitive capacity and that requiring participants to complete another task simultaneously, thus placing a burden on cognitive resources, had no impact on performance. This suggests automaticity to the mechanism, which is consistent with the modular view of the human mind advocated by many evolutionary psychologists, including Cosmides (1989) and others (e.g., Cosmides and Tooby 1992).



Cheater Detection, Fig. 1 (a) Abstract, descriptive example of the task, given the conditional rule: “If there is a vowel on one side (P), there will be in even number on the other side (Q).” Given that detecting violations of “If P, then Q” always relies on turning cards “P” and “not- Q,”

the correct items to turn would be E and 7. (b) Generic social contract version of the task, given the rule: “If you take Benefit B (P), you must satisfy Requirement R” (Q). The correct items to turn would be Took Benefit B (P) and Did Not Satisfy Requirement R (not-Q)

Controversies

Research on cheater-detection and social exchange scenarios has generated much debate within the scholarly community. One example comes from a study offering an alternative explanation for the findings. Sperber et al. (1995) argued that people generally use intuitions to solve the Wason card selection task and that there were differences in the accessibility and salience of these intuitions, depending on the conditional used. Crucially, for many of the cheater-detection conditionals, “P and not-Q” was easier to represent, more salient, and more relevant than “P and Q,” which, according to their relevance theory, accounted for correct card selection (“P” and “not-Q”).

Others have argued that the ability to detect cheaters could have developed through learning and that there is no particular reason why we must infer an innate, domain-specific module to account for content-related performance facilitation effects (Gray et al. 2003). These authors suggest that functional responses, that exist without awareness and occur automatically, need not be the result of an evolved module. To give their example: when riding a bicycle, if one begins tilting over to one side, one is able to right oneself. This ability is automatic, and we are typically not

aware of how we do it. Indeed, as Gray and colleagues suggest, many people give an incorrect response as to what they would do when in this predicament. However, there is no reason to assume that this automatic, functional response is the result of an innate, evolved “bike-riding module.” Thus, Gray and colleagues argue there is no particular reason to believe that the ability to detect cheaters relies on an evolved mental module, rather than simple learning mechanisms.

Conclusion

Research on cheater detection is often touted as a branch of evolutionary psychology that has delivered real insight into human cognition. Since the proposal of the social contract theory, there have been many studies demonstrating stark differences in performance on reasoning tasks, depending on the context in which the conditionals are placed. Specifically, detecting violations of conditional rules is easier, reflected in better task performance, when the scenario is given in terms of identifying cheaters of social exchange. For Cosmides (1989), this evidence is most parsimoniously explained by appealing to a cheater-detection module, which has evolved

through natural selection as a solution to the inherent problem our ancestors faced with social exchange scenarios. However, despite mounting evidence for cheater detection, the mere presence of this effect is not enough to convince some scholars of the underlying cognitive architecture that drives performance on the task. Regardless, the evidence on cheater detection has encouraged a range of researchers to debate what was previously assumed true, a feat that will surely contribute to our developing understanding of human cognition and the mechanisms that underlie it.

Cross-References

- ▶ [Mechanisms to Detect and Punish Cheaters](#)
- ▶ [Reciprocal Altruism and Group Living](#)
- ▶ [Social Contract Rule Violation](#)
- ▶ [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)

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Cheater Detection Adaptations

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Definitions

Cheater detection adaptations are evolved mechanisms that facilitate the identification and avoidance of cheaters.

Introduction

Cooperation has evolved in humans as a means to increase survival within groups. However, within cooperative interactions, there is always the possibility of exploitation wherein one party would receive the benefits of a cooperative social exchange but fail to reciprocate (Axelrod and Hamilton 1981; Trivers 1972). In these cases, cooperation fails to be adaptive and instead poses significant costs to the exploited individual. Given the costs, there may be cheating detection mechanisms functioning to minimize the likelihood of an individual being victim to a cheater (Cosmides 1989; Cosmides and Tooby 1992). These mechanisms may include a heightened ability to recognize and recall the faces of cheaters, and the same heightened ability to remember previous interactions with cheaters as a means to allow individuals to identify, recognize, and avoid potential cheaters (Cosmides and Tooby 2005).

Evidence for Cheating Detection Adaptations

Much of the research on cheating detection mechanisms has focused on assessing whether memory is heightened for faces that have been labeled as a cheater. Initially, studies found that recognition memory (i.e., the ability to assess whether you

have seen a person before) improved when identifying cheaters (Oda 1997; Mealey et al. 1996). However, recent studies have failed to replicate this finding (Barclay and Lalumière 2006; Mehl and Buchner 2008) calling into question its validity. However, further research suggests that although recognition memory may not increase with respect to cheaters, source memory may increase. In other words, individuals are better able to remember where or how they know someone from when the target has been labeled a cheater (Buchner et al. 2009). There is also evidence that individuals contain some ability to identify cheaters through facial photographs (i.e., cheater detection rather than cheater recognition; Verplaetse et al. 2007; Yamagishi et al. 2003). For example, there was a positive association between participants' ratings of an individual's honesty after looking at a picture of their face and that (pictured) individual's report of their willingness to deceive (Bond et al. 1994).

Although the previous studies are considered as support for the existence of cheater detection mechanisms, there are researchers who argue that these findings could be attributed to a general cost-avoidance mechanism rather than a specific cheater detection mechanism (Sperber et al. 1995). Alternatively, the increased source memory for cheaters may be due to heightened memory for potentially costly events or for events that violate social norms. Additionally, given that negative information is remembered better than positive information (Kensinger 2007), increased memory for cheaters may be due to cheating being perceived as a negative behavior (for further discussion on alternative explanations, see Bell and Buchner 2012).

Conclusion

In summary, evidence suggests that individuals have an increased source memory for cheaters and that individuals have at least some ability to discriminate between cheaters and noncheaters based on facial photographs. However, there is disagreement on whether these findings are due

to a specific cheating detection mechanism or due to a more general mechanism such as a cost-avoidance mechanism. Future research is needed in order to fully assess which theory has greater validity.

Cross-References

- Adaptations for Reciprocal Altruism
- Evolution of Reciprocal Altruism
- Problem of Cheating

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Cheater Memory Advantage

- ▶ [Memory Enhanced for Cheaters Versus Non-cheaters](#)

Cheating

- ▶ [Defection](#)
- ▶ [Egg Mimicry](#)
- ▶ [Rule Violations Checked If High Status](#)
- ▶ [Rule Violations Not Checked If Low Status](#)
- ▶ [Sex Differences for Pursuing](#)

Chew-Chew Theory

- ▶ [Ta-ta](#)

Child Abuse

- ▶ [Familial Violence](#)
- ▶ [History of Abuse](#)
- ▶ [Risk Variation with Parent Age](#)
- ▶ [Sex Differences in Death by Filicide](#)

Child Abuse and Bullying

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Synonyms

[Antagonizing](#); [Coercing](#); [Harassing](#); [Harassment](#); [Mobbing](#); [Oppressing](#); [Tormenting](#); [Child endangerment](#); [Child malnutrition](#); [Child maltreatment](#); [Child neglect](#); [Childhood trauma](#)

Definition

Child abuse is defined as aggression or negligence toward a minor (typically by an older individual, e.g., parent/guardian, caregiver, family member) that inflicts harm on the child or jeopardizes the child's well-being. Bullying is the repeated intentional use of aggression to harm a peer(s) and is characterized by an imbalance of power in which the bully has more power (e.g., more physical strength or size, higher social standing, more social capital) than the target.

Introduction

Aggression is broadly defined as behavior intended to cause harm, injury, or pain to others through physical, verbal, or indirect means. Bullying and child abuse are two forms of aggression in which the perpetrator has more power than the target. Child abuse can occur in a variety of ways such as physical, verbal, emotional, or sexual abuse. The power discrepancy in child abuse is generally implicit in the age difference between the perpetrator (i.e., adult) and target (i.e., child) in which the older perpetrator holds more power and control than the target. Bullying also occurs in different forms such as overt/physical, verbal, indirect/relational, or cyber aggression. The power discrepancy between peers in bullying is

most commonly due to physical size differences (e.g., the target being smaller in stature or weaker) or position in the social hierarchy (e.g., the target having less social capital/influence).

Forms and Prevalence

Bullying. Bullying occurs in several different forms including overt/physical (e.g., hitting, ruining possessions), verbal (e.g., name calling), indirect/relational (e.g., ostracism/exclusion), and cyber/electronic (e.g., texting, social media) aggression. Approximately 30% of youth self-reported being involved in bullying as either a bully, the target of bullying, bully victims, or bystanders (e.g., actively or passively supporting the bully or defending the victim). Although rates of bullying are highest during adolescence, bullying occurs across the lifespan starting as early as preschool and kindergarten to elementary, middle, and high school and continues into universities and the workplace in emerging adulthood, adulthood, and nursing homes during older adulthood (e.g., Rex-Lear et al. 2012; Vlachou et al. 2011). In their meta-analysis of 80 studies, Modecki et al. (2014) concluded that adolescents were twice as likely to engage in more traditional forms of bullying (e.g., physical, verbal, relational) compared to cyberbullying; however, cyberbullying was significantly correlated with traditional forms of bullying.

Child Abuse. Child abuse can also occur in a variety of forms that includes physical (e.g., hitting, punching), verbal (e.g., demeaning, hurtful comments), emotional/psychological (e.g., humiliation), neglect (e.g., abandonment, malnutrition), and sexual (e.g., rape) abuse. Physical abuse is the most commonly experienced form of child abuse that adults retrospectively report followed by sexual abuse and emotional abuse (e.g., Afifi et al. 2015; May-Chahal and Cawson 2005). May-Chahal and Cawson (2005) also found that children are at a higher risk for experiencing physical and emotional abuse in their homes, whereas out of the home, they are at higher risk for sexual abuse. However, less than 10% of adults who reported experiencing child abuse

recall having contact with child protective services/organizations (e.g., Afifi et al. 2015); people who reported experiencing physical abuse, sexual abuse, and exposure to intimate partner violence were most likely to have had contact with child protection organizations (rather than experiencing a single or two types of abuse).

Risk Factors

Bullying. People engage in bullying for a number of reasons. The stereotypical perception of a bully is of someone who is large in stature, has low self-esteem, and does not socially fit in with peers. This type of bully is typically physically aggressive rather than relationally aggressive and tends to be reactive and impulsive (i.e., likely to use hostile aggression). In contrast, according to Vaillancourt et al. (2010), the Machiavellian bully is an individual with strong social skills and high self-esteem who is well regarded and respected by peers and adults. The Machiavellian bully uses peer aggression in a calculated, manipulative way in order to gain benefits and to gain or retain power; this type of bully is often socially skilled and tends to have a high position in the social hierarchy. The Machiavellian bully is typically relationally aggressive rather than physically aggressive; he/she is likely to use peer aggression as a way of achieving personal gains (i.e., likely to use instrumental aggression).

Despite the research being correlational in nature, researchers have identified several risk factors associated with people who bully others. For example, youth nominated as bullies by peers were more aggressive, exhibited high motor functioning, and lower anxiety during preschool (as retrospectively reported by parents); youth peer nominated as bullies were also likely to come from families of lower socioeconomic status and have parents with more externalizing problems (i.e., substance abuse and antisocial behavior; Jansen et al. 2011). In addition, witnessing domestic violence during early childhood and experiencing child maltreatment predicted being identified as a bully. Boys are also significantly more likely than girls to be identified as a bully;

however, this sex difference does not appear to hold when examining relational aggression.

Child Abuse. Several risk factors predict whether an individual will abuse children. Parents who have been diagnosed with a mental health problem (e.g., psychiatric disorder, substance use disorder, or developmental disorder) are at a higher risk of abusing their children than those without mental disorders. In addition, parents who experienced child maltreatment during their own childhood, were placed in foster care, or experienced intimate partner violence are more likely to maltreat their children. Additional risk factors of perpetrating child abuse include living in poverty and having limited access to early childhood education and social services. In addition, babies who are considered fussy babies are at higher risk for being maltreated than babies with an easy temperament.

Effects on Target

Bullying. There are a host of negative mental and physical health ramifications on people who are bullied by their peers. For example, people who have been bullied are more likely to exhibit internalized problems such as depression, anxiety, loneliness, symptoms of post-traumatic stress disorder, and suicidal thoughts, as well as externalizing problems such as rule breaking, aggression, and substance use/abuse compared to people who have not been bullied. In addition to mental health problems, youth who are bullied are more likely to have physical health symptoms such as mouth sore, sore throats, stomachaches, and fatigue than youth who are not bullied. College students who are bullied are more likely to have bone and joint problems and have been told by doctors that they are at risk for heart problems compared to students who have not been bullied. This increased risk of physical health problems may be due to differences in physiological functioning; people who have been bullied tend to have lower morning salivary cortisol levels and an overall flatter diurnal cortisol pattern compared to people who have not been bullied. Children who are bullied in early elementary school are at higher

risk to be bullied later in elementary, middle, and high school than children who are not bullied in early elementary school.

Child Abuse. Children who experience child abuse are at a higher risk for mood and anxiety disorders such as bipolar disorders, anxiety disorder, phobias, and post-traumatic stress disorder than children who were not abused. Children who experience abuse are also at higher risk of developing behavioral and emotional problems such as emotional instability, depression, suicidal thoughts and attempts, and a tendency to be aggressive or violent than children not abused (e.g., Stirling et al. 2007). Experiencing child abuse can alter future stress responses (e.g., heightened sensitivity). Children who have been abused or neglected (especially children who were physically abused) were more likely to have arrest records for delinquency and crime as adolescents and adults compared to non-abused children. Maltreated children are also at higher risk of being injured by intimate partner violence in adulthood, whereas neglected children were more likely to be the perpetrator of intimate partner violence in adulthood (Widom et al. 2014).

Similar to the effects of being bullied, there is evidence that early trauma may affect neurological and physiological functioning. For example, according to Fonzo et al. (2016), adults who were emotionally maltreated as children displayed different brain activities (e.g., more amygdala activity and less right dorsolateral prefrontal activity) when viewing faces displaying fear or anger compared to adults who were not emotionally maltreated. In addition, adults who experienced abuse as children had altered salivary cortisol levels (both daily diurnal patterns and in response to an acute stress test). These physiological differences may increase people's risk of mental health problems such as depression and anxiety.

Conclusion

Being the target of others' aggression, whether by peers (i.e., bullying) or adults/caregivers (i.e., child abuse), can have lasting negative impacts on youth's development and health. As discussed

above, both bullying and child abuse are associated with more mental (e.g., depression, anxiety, suicidal thoughts, psychological disorders) and physical (e.g., stomachaches, fatigue) health problems. In addition to increased health problems, people who experience child abuse or who are bullied are at higher risk of developing behavioral and emotional problems compared to people who do not experience such trauma. Moreover, there is evidence that these negative outcomes may be explained by physiological differences (e.g., salivary cortisol, brain activity) among people who experience bullying and child maltreatment. Perpetrators of child abuse or bullying may have been victimized during their childhood or experience mental health problems; environmental characteristics (e.g., living in poverty, resources available in the community) are also risk factors in whether abuse will occur. Both child abuse and bullying are traumas that have long-term negative impacts.

Cross-References

- Anonymity of Cyberbullying
- Outcomes of Homophobic Abuse
- Peer Rejection
- Procedures for Dealing with Bullies
- Sex Differences in Cyber Bullying
- Sexual Abuse

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Child Care

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Synonyms

Alloparenting; Day care; Early care and education; Non-parental child care

Definition

Child care refers to any arrangement for taking care of young children when they are not with their parents, who may be working or studying.

Introduction

Before children start elementary school (or kindergarten), they typically require some form of day care by another adult if their primary caregivers are working or studying outside of the home. The settings of child care are rather diverse, ranging from informal arrangements of taking care of the child at the home setting by a relative, a neighbor, or a nanny to formal, center-based solutions offered by preschools, nursery schools, or day care centers employing providers with relevant education and training. While informal child care arrangements typically do not have set standards for their execution, professional child care centers usually group children by age and are required to meet certain criteria, such as child-to-provider ratio and health and safety standards. In the following sections, first evolutionary accounts of child care will be offered, then the need for child care in the contemporary context will be discussed, and finally the consequences of child care will be elaborated.

Evolutionary Accounts of Child Care

Child care has been an evolutionary need as the altricial nature of human infant necessitates rather laborious care for a long period of time due to extended childhood and adolescence in humans. This made raising a human offspring on one's own too costly and necessitated collective caregiving, resulting in humans being an exception to the mammalian norm that offsprings are primarily taken care of by the biological mother. In humans, it is typical for adults other than the biological parents to offer care for young children. These adults can be genetically related to the child, such as grandparents or members of the extended family

(e.g., aunts, uncles); or they can be non-kin, such as friends, neighbors, or professional caregivers. The care offered by these adults, termed *alloparents*, is argued to have evolved because this collective care increased the chances of survival of the immature child and their development into reproductive age (Hrdy 2009). Access to alloparenting has indeed been reliably linked to greater child survival (Sear and Mace 2008). Alloparenting is also an evolved solution to the trade-off between provisioning and child care parents face. Biological parents can rely on alloparents to take care of their children, while they seek access to resources (e.g., hunting/gathering or agriculture in traditional societies, higher education or work in modern life). This cooperative childrearing system is seen in both traditional and modern cultures (Sear and Mace 2008).

The most common form of alloparenting is child care offered by grandparents, particularly maternal grandmothers, which is theorized to have evolved to increase inclusive fitness through making sure one's genes survive into the generation following their own offspring's. The findings showing grandparenting effort is highest among maternal grandmothers, followed by maternal grandfathers, paternal grandmothers, and finally paternal grandfathers, provide support for this conjecture, indicating grandparenting effort decreases with risk of paternity uncertainty, hence potential for fitness (Euler 2011). The extended period of life after reproductive years in human females is also argued to be another adaptation evolved to increase inclusive fitness through helping offspring raise their offspring, also known as *the grandmother hypothesis* (Hawkes et al. 1998; Hrdy 2009).

Child care offered by non-kin, such as friends, neighbors, or professional caregivers, is also very common in both traditional and modern societies. This type of non-kin child care also has adaptive advantages, this time within a reciprocity framework, where these individuals gain access to either material resources, in the case of professional caregivers, or social resources in the form of receiving care for their offspring when they need it, in the case of friends and neighbors.

Need for Child Care in the Contemporary Context

In the modern context, child care serves two main functions: enabling parental employment and supporting school readiness in children. With increasing maternal employment and higher education pursuits of parents, child care has become one of the most important needs of contemporary life. Parents, especially mothers, with access to reliable and high-quality child care can contribute to the workforce more easily and efficiently, which has significant positive downstream consequences for economic welfare and gender equality. Day care also prepares the child socially and cognitively for primary school by providing a stimulating environment, therefore enabling a smoother transition to formal education with higher success. This growing need for child care has resulted in a rapid increase in the number of institutions that offer professional day care services all around the world. These center-based day care options are typically costly, sometimes even costlier than other family expenses such as food or rent, so family income becomes an important factor in whether children can have access to this form of caregiving.

Consequences of Child Care

At the earlier years of the expansion of child care services, there was a widespread concern that receiving care from someone else than the mother could lead the child to develop insecure attachment to their mother and hence experience negative downstream consequences in their development. This concern led to empirical research, chiefly carried out by the National Institute of Child Health and Human Development (NICHD) Child Care Research Network. The NICHD Study of Early Child Care and Youth Development, which was launched in the early 1990s, investigated thousands of children in day care over years and reached exciting results. One of the main findings of the study was that as compared to early child care experience, parenting is as a stronger and more consistent predictor

of children's developmental outcomes and non-parental care is not associated with the quality of infant-mother attachment. Yet, long hours of center-based day care were found to be moderately related with increased problem behaviors, especially in middle-income children. Higher-quality child care predicted higher cognitive (e.g., vocabulary, reading, mathematics) and social competence that seem to be maintained into adolescence and adulthood. Higher educational attainment and improved economic outcomes have also been linked with high-quality child care. The child-to-provider ratio has been identified as a crucial factor in determining the quality of care offered in day care centers, with lower ratios predicting better outcomes. The interested reader is directed to the papers by Belsky and colleagues (2007), Dearing et al. (2009), and Vandell and colleagues (2010) for the results of this large-scale multistate study and reviews of other studies investigating the links between child care and developmental outcomes.

It is worth noting that higher-quality child care seems to benefit children living in low-income families the most (e.g., Havnes and Mogstad 2015). Low-income children who has had the chance to attend high-quality day care show better academic outcomes, higher employment, and less criminal behavior as teenagers and young adults (e.g., Schweinhart et al. 1986). Higher-quality child care is thought to act as a buffer to dampen the negative effects of growing up in an otherwise impoverished environment through better access to resources; higher cognitive, social, and emotional stimulation; and social ties with providers and friends. There is even evidence to suggest that high-quality child care acts as a buffer against problem behavior for children with mothers who report depressive symptoms – typical of stressful parenting environments (Charrois et al. 2017). Hence, early education has been identified as one of the most cost-effective and efficient ways of enhancing the developmental outcomes of children from impoverished backgrounds. This led to increased governmental efforts in providing accessible child care to low-income families in many countries, such as the United Kingdom and Italy. The most well-known example of such

efforts is the federally funded Head Start Program in the United States. The benefits of the Head Start Program seem to be most prevalent in high-risk populations (e.g., foster children, children from families with lower levels of education), yet the effects are attenuated when the children move to public elementary schools, which probably have fewer resources.

Conclusion

Child care, an evolutionary necessity imposed on humans by the altricial nature of human infants, is playing an increasingly central role in child development with more parents joining the workforce and/or pursuing advanced education. Research shows that child care is not at all harmful for optimal child development – to the contrary, it contributes to positive outcomes, but only when it reaches a certain level of quality. So, organized efforts toward making high-quality child care affordable and accessible are crucial in achieving both optimal child development and a more productive labor force.

Cross-References

- ▶ Access to Alloparents
- ▶ Alloparenting
- ▶ Alloparenting and Grandparenting
- ▶ Day Care
- ▶ Grandmother Hypothesis, The

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Child Custody

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Divorce occurs in both industrialized and non-industrialized cultures (Anderson 2011). Following this dissolution, the decision of who receives custody may become an issue for parents and the

state. In industrialized nations, women are much more likely to be granted full custody of children (Anderson 2011). For example, in the United States, one study found that the majority of single-parent households (84%) were headed by mothers (Grall 2007). In some non-industrialized nations, the same child custody pattern occurs as well. For example, in the Hadza, a hunter-gatherer tribe, divorce is common, and when it occurs, the majority of the children live with the mother (Marlowe 2010). However, data from across 45 societies found 17.8% and 20.0% of the time children resided with mothers and fathers, respectively. From this same sample, 53.3% of those who received custody of the children were granted custody based upon a variety of factors (Frayser 1985). Factors that may play a role in who receives custody could be parental death, the role of kin as guardians, the age of the children of the parents who decide to divorce, the role that stepfamilies may play, the possibility of child abuse, and the biases inherent in the court system.

From an evolutionary theory perspective, it is not surprising that mothers are granted custody more often. Mothers more often receive custody due to relative parental investment. The relative time one parent may invest begins before conception given the vast difference in sex cells (Trivers 1972). Furthermore, given that fertilization and gestation are internal and that breastfeeding typically occurs after birth for 3–4 years, there is a greater duration of parental investment for women than for men. If a child needs to continuously breastfeed, it would be adaptive for the child to spend much more time with his or her mother than with his or her father. Due to the adaptive nature of spending more time with the mother, cross-cultural research shows that fathers do not spend the same amount of time or care for children to the same capacity that mothers do (Geary 2000). Additionally, women may also be more likely to receive custody because they are better able than men on average to control their emotional responses. Women on average can delay their own gratification and control aggression better than men (Kochanska et al. 1996), which are adaptive skills to have when raising offspring.

Taken together, these differences in parental investment and in women's behavior may contribute to why mothers may be awarded custody more often.

However, while women may receive custody more often due to the extended childhood of humans (Bjorklund and Shackelford 1999), fathers may also receive partial custody. This can also be explained from an evolutionary perspective. Men can engage in a flexible mating strategy in order to increase their own fitness by investing time in a limited amount of offspring (Buss and Schmitt 1993). Therefore in some cases, men may want to increase their fitness by caring for their child.

To conclude, while using evolutionary theory to explain child custody is useful in understanding typical scenarios, a further examination of other factors must be considered in real-life custody situations to determine the best outcome for children.

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Child Development

- ▶ [Early Childhood and Adolescence](#)

Child Endangerment

- ▶ [Child Abuse and Bullying](#)

Child Homicide

- ▶ [Filicide](#)
- ▶ [Marital Status and Infanticide](#)
- ▶ [Methods of Filicide](#)

Child Malnutrition

- ▶ [Child Abuse and Bullying](#)

Child Maltreatment

- ▶ [Child Abuse and Bullying](#)
- ▶ [History of Abuse](#)

Child Mortality

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Synonyms

[Under-5 mortality](#)

Definition

Child mortality, also known as under-5 mortality, refers to the deaths of children under the age of 5 and is often reported as the number of deaths per 1,000 live births.

Introduction

Child mortality, also known as under-5 mortality, refers to the deaths of children under the age of 5 and is often reported as the number of deaths per 1,000 live births. A special case of child mortality is infant mortality, which includes all deaths prior to 1 year of age. The majority of childhood deaths tend to occur during this first year, and after which there is a sharp drop in mortality risk, which ultimately levels out around the age of 10 to the low levels that characterize human adulthood. For most of human history and in many pre-epidemiological transition populations today, early childhood has been marked by elevated mortality risks, largely due to an increased susceptibility to infectious disease and, to a lesser degree, violence (i.e., infanticide). Under these circumstances, child mortality rates often exceed 200 per 1,000 births. However, in recent history, most populations have experienced a rapid reduction in child mortality risk, and developed countries often exhibit child mortality rates below 10.

Child Mortality in Traditional-Living Societies

Throughout the majority of human history, child mortality patterns were likely very different from those exhibited among modern developed populations and more similar to those observed among subsistence-level populations with little access to modern healthcare. Life tables for only a handful of such populations have been published. Among five modern hunter-gatherer populations, infant mortality rates average approximately 200 deaths per 1,000 births, ranging from 115 to 370. When looking at the first 5 years, child mortality rates average

approximately to 300, ranging from 190 to 450 (Blurton Jones et al. 2002; Early and Headland 1998; Gurven and Kaplan 2007; Hill et al. 2007; Hill and Hurtado 1996; Howell 1979). Infant mortality accounted for approximately two thirds of all child deaths, with annual mortality rates falling to around 50 per 1,000 in ages 1 through 4. Horticultural populations exhibit comparable child mortality rates and a similar pattern with infant mortality accounting for the majority of child deaths (Early and Peters 2000; Gurven and Kaplan 2007; Gurven et al. 2007; Neel and Weiss 1975; Wood 1980) (Fig. 1).

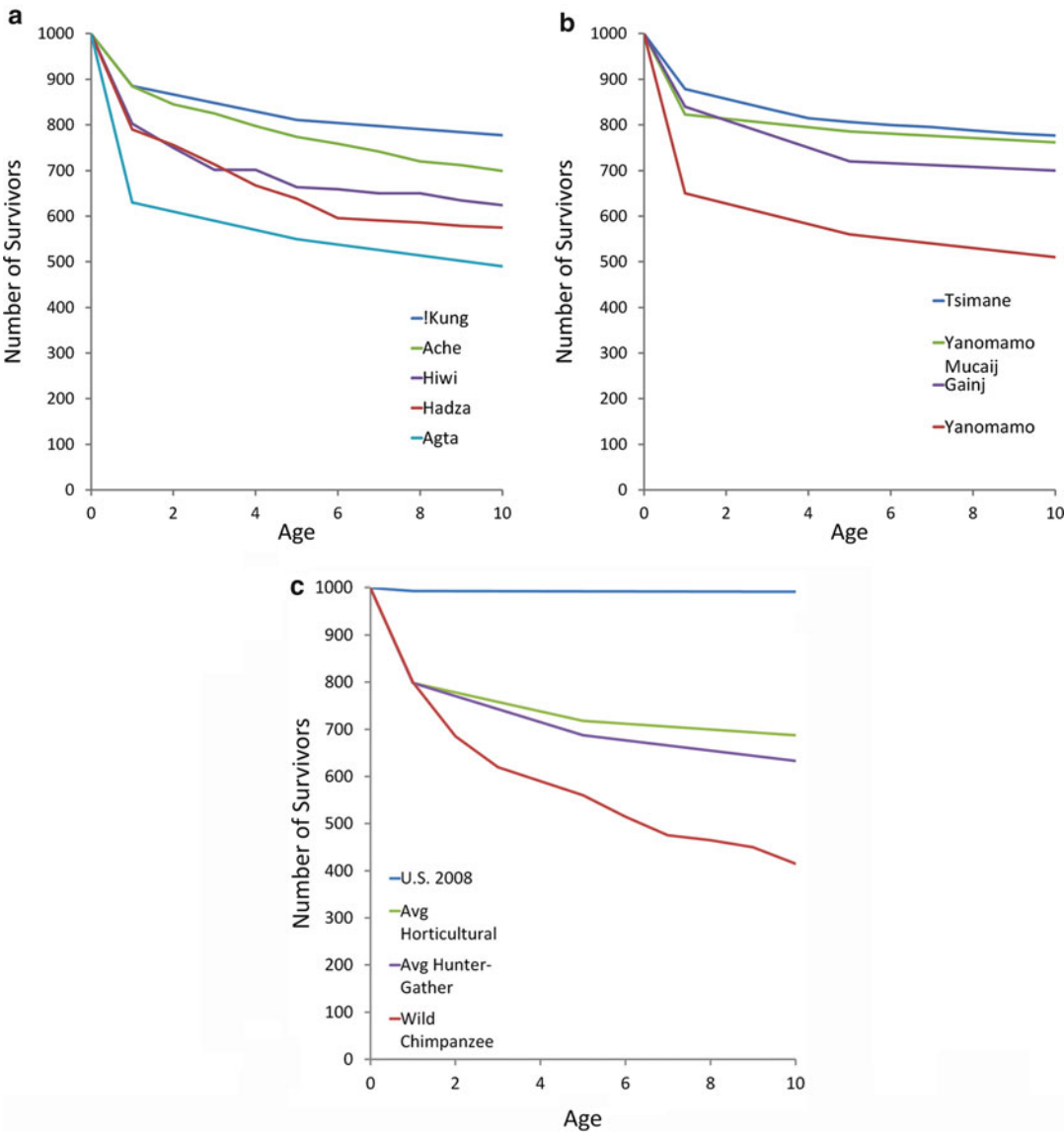
The similarity across subsistence-level populations suggests a human pattern that differs substantially from the extremely low mortality rates exhibited by populations with access to modern healthcare, as well as from the much higher rates exhibited by wild chimpanzee populations (Arias 2012; Hill et al. 2001). This pattern of reduced child mortality compared to other primates is likely a derived feature of the human life history pattern, which is realized through a variety of strategies. Human infants are born at about 6 % of average female body mass, larger than that of other great apes, and a larger percentage of this mass is composed of body fat (DeSilva 2011). However, mothers in natural fertility populations tend to wean their infants between 2 and 3 years of age, much earlier than the 4–6 years that is more typical of the other great ape species (Robson and Wood 2008). In other primates, weaning is associated with a cessation of caloric investment by the mother and an increased risk of nutritional stress in the offspring. In humans, however, nursing is replaced by provisioning. This decouples inter-birth intervals from length of investment, as mothers can continue to invest even after they give birth to subsequent children. Thus, human children can remain nutritionally dependent on caretakers for a much longer proportion of the lifespan compared to other primates.

In addition to enjoying a longer period of investment, children receive these investments from a number of different caretakers – mothers *and* fathers, grandparents, siblings, etc. In most

foraging populations, such caretakers rely on an even larger social network of producers who pool foraged resources, providing further nutritional stability to dependent children. Finally, caretakers can utilize their greater intelligence and cumulative cultural knowledge to manage the threats in the environments to a degree that is unachievable to virtually any other animal. All of these factors likely contribute to the reduction in mortality rates throughout childhood and, indeed, the entire lifespan.

Causes of Child Mortality

The causes of infant and child mortality vary across populations. Most demographic research among traditional-living populations relies on retrospective reports of past deaths, making the determination of exact causes of death challenging. Causes are therefore often grouped into broad categories, and a substantial portion typically remains unexplained. Congenital/birth afflictions and infectious disease tend to be the most common causes of infant mortality in these populations, with each accounting for comparable proportions of deaths (see references above for details). Neonatal deaths that occur shortly after birth due to congenital abnormalities and/or birth complications are often not specified beyond this general description. Regarding infectious diseases, respiratory diseases are reported as the most common cause of disease-related infant death in some populations, while in others, it is gastrointestinal disease (often accompanied by diarrhea). Infants are particularly susceptible to infectious diseases, as it takes time for the naïve adaptive immune system to mature and go through the process of clonal selection, so that it can become attuned to the local pathogen environment (McDade 2003). This process can be delayed by early pathogenic and nutritional insults, which were likely common in the low-energy balance, pathogen-rich socioecological conditions that characterized most of human history. During this early period of immunological naiveté, infants are buffered against infection by antibodies and other nonspecific immune defenses that are passed from mother to child via breastfeeding.



Child Mortality, Fig. 1 (a) Survivorship curves for hunter-gatherer populations. (b) Survivorship curves for horticulturalist populations. (c) Comparative survivorship curves.

Violence often represents another common cause of death of young children in traditional-living populations. Rates of infanticide, which can account for up to 40 % of infant deaths in some groups, vary substantially across populations and are largely affected by cultural trends. In many populations, infanticide is effectively nonexistent (see the section below on [Infanticide](#)).

During ages 1 through 4, infectious disease tends to account for a larger proportion of all deaths even though the rate of death by infectious disease itself declines. This is because the rates of death due to violence and congenital afflictions decline even more substantially. In some populations, however, violence remains a major cause of death (Hill and Hurtado 1996). Accidents

are often another major cause of death at this time, and rates of accidental death tend to be higher than those found among adults.

Kin Effects on Child Mortality

Human reproductive and parenting patterns are often characterized as a cooperative system, in which children receive investment from numerous caretakers (Hrdy 2005). These caretakers can reduce mortality risks in numerous ways. They can affect children's energy balances through provisioning and carrying, thereby reducing the risk of nutrition and immune deficiency-related deaths. They can provide protection from infanticide and environmental threats. They can watch over children to protect them from accidents. They can also provide aid to the mother so as to facilitate her ability to directly care for her children.

Many studies have explored the effectiveness of caretakers by calculating child mortality in the absence and presence of particular categories of caretakers (Sear and Mace 2008). Such studies are prone to issues of self-selection, as the absence of a common caretaker is often associated with other factors that also affect child mortality risk. Many of these challenges can be at least partly resolved through methodological and statistical means, however (Winking et al. 2011). All studies that have explored the impact of maternal presence on the mortality risks of infants and/or young children have reported significant effects, suggesting that maternal care is difficult to substitute. Similarly, a majority of studies exploring the impacts of grandmothers have found their presence to buffer children from mortality risks. Only a minority of those focusing on father presence have found such effects, however (Sear and Mace 2008).

Infanticide

In many populations, infanticide – the killing of an infant through active harm or willful neglect – is a common cause of child mortality, accounting for up to 40 % of infant deaths in some populations (Hill and Hurtado 1996). Cross-cultural reviews suggest that infanticide was historically practiced with some regularity in half to

two-thirds of the world's cultures (Daly and Wilson 1988). Infanticide is often perpetrated by the mother or other kin member because of a perceived inability to successfully raise the child to adulthood. Under extremely trying circumstances, neglect or infanticide might be considered the only viable strategy to ensure that limited resources are directed to those who can benefit from them (Scheper-Hughes 1993). In many of these populations, contraception and other means of family planning are unavailable, and infanticide is not viewed as an aberrant criminal act but a practice that is occasionally necessary for a family's survival. Methods of infanticide are varied but include deliberate killing (e.g., burying or smothering), placing the child in dangerous situations, and abandonment. Across cultures, the most commonly cited reasons for infanticide include circumstances that are unfavorable for rearing a child (e.g., short inter-birth interval, lack of male support), infant limitations (e.g., deformities, illness), and paternity issues (e.g., uncertain paternity, undesired paternity) (Daly and Wilson 1984).

In some populations infanticide is driven by gender preferences leading to vastly different rates of infanticide for male and female infants. This can be due to one sex being more likely to be deemed nonviable, as well as adults killing an infant because it is not the preferred sex. In most of these instances, female infants suffer higher rates of neglect and infanticide than male infants (Early and Peters 2000; Fuse and Crenshaw 2006; Hill et al. 2007; Hill and Hurtado 1996), although some populations do exhibit a preference for female infants (Cronk 1991).

Child Mortality in State-Level Populations

The demographic transition is the process by which populations move from a demographic profile characterized by high mortality and high fertility to one of low mortality and low fertility. The first stage tends to be defined by a rapid drop in mortality rates, which is often achieved via improved sanitation, nutrition, and access to healthcare. While this process began in the

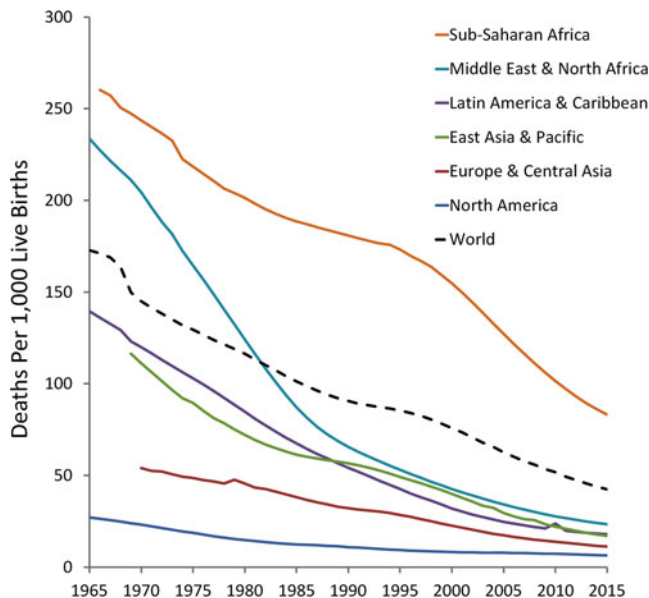
1700s for some European countries, many began the process in the past century. Every region of the world has experienced declines in child mortality over the past 50 years with the global child mortality rate dropping by over 75 % (The World Bank 2015). The seemingly higher global rate compared to the regional levels is due to the fact that fertility rates tend to correlate with mortality rates, such that high-mortality populations are contributing disproportionate numbers of births to the sample. Sub-Saharan Africa remains the outlier region, even though child mortality rates have dropped by nearly 70 % in this region over the past half century. Currently, of the 20 countries with the highest child mortality rates, 19 are within Sub-Saharan Africa. Global infant mortality, which accounts for roughly two-thirds of child mortality, dropped by a comparable level over the same time period, changing from 114.8 in 1965 to 31.7 in 2015 (The World Bank 2015) (Fig. 2).

It is difficult to determine the relative impact of the many factors that have contributed to the overall reduction, but likely factors include access to vaccinations, better sanitation and access to clean drinking water, improved nutrition, anti-malaria efforts, and access to healthcare systems (Ahmad

et al. 2000). The United Nations made cutting child mortality rates by two-thirds the fourth objective of its 1990 Millennium Development Goals (United Nations 2016). While it failed to meet this goal by the 2015 deadline, mortality rates dropped by over half, and there is still a substantial effort to continue this trend. In 2014, the United Nations Children's Emergency Fund (UNICEF) spent nearly \$5 billion on numerous efforts related to children's well-being, many of which undoubtedly contribute to the continued decline of child mortality (United Nations Children's Fund 2015).

Causes of Child Mortality

Infectious disease continues to be the most common cause of child mortality, accounting for 64 % of global deaths occurring under the age of 5 in 2010 (Liu et al. 2012). Pneumonia and diarrheal diseases are the most common among these, and nearly all of such deaths are now preventable given access to appropriate medical care. Preterm birth and other birth/congenital complications account for another 29 % of child deaths. Among more developed nations and through time globally, child mortality is increasingly



Child Mortality, Fig. 2 Child mortality rates through time

dominated by neonatal death (that taking place between birth and 28 days of age), which now accounts for the majority of under-5 deaths in some regions (Liu et al. 2012).

Gender Biases

Typically, male children suffer a higher mortality risk than female children (Fuse and Crenshaw 2006; Sawyer 2012). Globally, the male infant mortality rate is approximately 15 % higher than the female infant mortality, and in Western countries, the difference often exceeds 20 %. This difference is generally attributed to a host of genetic and biological factors that cause naturally higher male mortality throughout the lifespan. Therefore, infant mortality rates closer to parity are taken to reflect gender-biased investment and/or harm that disadvantage female offspring. Infant mortality rate ratios (male/female) trend higher in highly developed countries and have increased globally in developing countries through time (Sawyer 2012).

Of particular note are China and India, the two most populous countries and two countries that have some of the lowest male/female infant and child mortality rates (Fuse and Crenshaw 2006; Sawyer 2012). These patterns have driven a large literature exploring the causes of this phenomenon and the potential demographic consequences of the so-called “missing girls.” The types and degree of gender bias vary throughout each large country and seem to be due to many complex socioecological and family-specific circumstances. Gender inequities appear to be diminishing in some regions, although overall trends suggest continued (and even increasing) gender differentials in major measures of wellbeing (Singh 2013).

Conclusion

For most of human history, the first 5 years of life, and the first year in particular, marked a particularly dangerous period for children, mostly due to a greater susceptibility to infectious disease. However, humans’ reproductive patterns differ in

many respects from those of other apes in ways that buffer children from the even higher mortality rates that nonhuman apes experience. These differences include a longer period of parental investment, direct provisioning, a greater number of caretakers, and cultural inventions designed to neutralize environmental threats. The continued decrease in child mortality in state-level populations, brought about through improved sanitation, nutrition, and healthcare, is simply an extension of this overall trend.

Cross-References

- ▶ [Alloparenting](#)
- ▶ [Breast Feeding](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Father Absence](#)
- ▶ [Grandparental Investment](#)
- ▶ [Infant Survival](#)
- ▶ [Infanticide](#)
- ▶ [Maternal Investment](#)
- ▶ [Parental Investment](#)
- ▶ [Paternal Investment](#)
- ▶ [Trivers-Willard Hypothesis](#)

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Child Murder

- Risk Variation with Parent Age
- Sex Differences in Death by Filicide

Child Neglect

- Child Abuse and Bullying

Child Spacing

- Birth Spacing and Birth Order

Child Support

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Men and women have differing parental investments in their offspring and certainty of paternity plays a role in their parental investment (Trivers 1972). The sex with parental certainty is more likely to invest resources in their offspring than the sex with parental uncertainty. As a consequence of paternal uncertainty, men are more likely to leave their offspring and forego investment, shifting greater responsibility onto women to care for the offspring (Trivers 1972). Since it takes a considerable amount of resources to rear a child, women typically seek child support from men who do this. But, many men do not pay their child support. Consequently, child support enforcement policies were expanded and were more stringently enforced beginning in the twenty-first century in the hope of improving children's lives (Pirog and Ziol-Guest 2006; Wilson 2002). This shift is important because the mental and physical health of a child is impaired when the child does not live with both biological parents (Daly and Wilson 1985, 1986, 1988). But, many men are still reluctant to pay child support.

The US Census Bureau in 2011 stated that \$37.9 billion dollars in child support was owed during the year of 2011, and 53.4% of the individuals who were awarded child support were custodial single mothers (US Census Bureau 2013). Additionally, the percent of parents who reported receiving child support dropped from 52% in 2003 to 43.3% in 2011 (Grall 2013). This has continued with child support payment becoming less likely when a divorce occurs (Meyer et al. 2015). Evolutionary theory can provide an explanation or why this is occurring.

Researchers hypothesize eight evolutionary theory-based reasons why men refuse or reduce their child support payments (Shackelford et al.

2005, 2012). Men will refuse or reduce child support if (1) they are concerned that the custodial mother will use it to increase her attractiveness and fitness, decreasing the man's fitness. If a woman does this, the money may not reach the offspring and instead may be used to increase the mother's fitness, thus reducing the fitness of the male. A man will reduce child support (2) if the woman channels the resources to a new partner, if (3) he needs resources to obtain a new partner, and (4) if he needs resources to retain a new partner since women prefer men who can provide for them in the long-term (Buss 1989; Buss and Shackelford 2008). Therefore a male may reduce child support in order to show his new mate that he can provide for her. A man will also reduce child support (5) if he produces children with a new partner and this child lives with him (Manning and Smock 2000). Furthermore, reducing child support for noncustodial children could also be due to the child's age, since the cost of investing in an older child outweighs the benefits (Trivers 1974).

Furthermore, child support may be reduced (6) when confidence in paternity certainty is low or (7) when sexual access is terminated with the custodial mother. Finally, (8) men who engage in an affair or a short-term poach will refuse to pay child support when confidence in paternity of the offspring produced in the affair is low. This occurs because a man is at risk of investing in an offspring that is not his, and that decreases his fitness. Similarly, when a man does not resemble his offspring, he may be less likely to invest (Apicella and Marlowe 2004; Burch and Gallup Jr 2000; Gallup Jr et al. 2016) and consequently may be less likely to pay child support.

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Childcare

- ▶ [Access to Allopapants](#)
- ▶ [Parental Investment and Parenting](#)

Child-Centered Learning

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Synonyms

[Learner-centered education](#); [Student-centered learning](#)

Definition

A pedagogical practice that places the child's interests and learning needs at the center of education.

Introduction

The notion of child-centeredness can be traced in the writings of several “classic” Western developmental psychologists and educational philosophers of the eighteenth, nineteenth, and twentieth centuries including Jean Piaget, Lev Vygotsky, Urie Bronfenbrenner Jean-Jacques Rousseau, Johann Heinrich Pestolozzi, Friedrich Froebel, Maria Montessori, and John Dewey. Placing the child at the center, the concept of child-centered learning has multiple roots emerging from the fields of developmental psychology, philosophy, sociology, and education. In its contemporary pedagogical practices, child-centered learning has long been recognized as a progressive and innovative method for teaching students of all ages and learning abilities, ranging from early childhood, to primary, secondary, and tertiary education (Fallace 2015). To emphasize the

importance of placing the child/student at the center of education requires a radical shift in the teacher's self re-conceptualization and understanding of pedagogical practice about the child as a learner.

Narratives of Child-Centered Education: Multiple Constructions of Child-Centeredness

Child-centeredness has multiple origins and variations of theoretical orientation. Jean-Jacques Rousseau's novel, *Emile* (or *On Education*), coming from a European romantic construction of the child, outlined the nature of education and painted a particular cultural representation of the nature of the child as (s)he grows and develops into a (wo) man. Previously, before the eighteenth century, in Western civilization, the child was viewed as a miniature adult and was never the center of focus in sociocultural activities. However, in *Emile*, Rousseau depicted how a young boy should grow and develop under the adult's protection and guidance from early childhood, through adolescence, and into adulthood. In these early descriptions about the stages of learning and development, Rousseau's romantic narrative of *Emile* as a "noble savage" placed the child in the center of education, particularly in the early childhood years. Such a narrative about the child added new possibilities for a variety of sociocultural constructions of child-centeredness. Influenced by this romantic narrative of child-centeredness, several other prominent educational philosophers and theorists emerged to shape the (trans)formation of child-centered learning.

In the field of education, Johann Heinrich Pestolozzi's educational philosophy further amplified the romantic construction of the child and what his or her education should be to enhance development. As a student of Pestolozzi, Friedrich Froebel consolidated the idea of placing the child/person/student in the center of learning. Creating the concept of kindergarten, Froebel recognized and emphasized the importance of "seeing" all children as having unique learning needs and capabilities, placing the children at the center of education. His publications on educational

philosophy and method established the foundation of play and how teachers should understand the importance of children's play in order to facilitate children's learning and development. Froebel's creation of play materials (known as Froebel Gifts), designed to meet children's learning and development, was recognized as innovative and progressive. Froebel's work, as the father of kindergarten, established the notion of child-centered learning.

Maria Montessori's work in education follows a similar sociocultural construction of child-centered learning. With her medical background and through her early work with children of special needs in Rome, Montessori observed children's learning and development and drew on various physicians' and educators' work to classify children's development. Through the work of Jean Marc Gaspard Itard and Édouard Séguin, Maria Montessori developed her "scientific" approach to education and established a framework of child/human development to identify the child's developmental stages. Placing the child in the center of education, Maria Montessori's classroom design was meant to be a well-prepared and sequenced learning environment for the child. Conceptualizing the child as an active learner, a Montessorian perspective of a child-centered environment recognizes that the child is not passively waiting to be taught by the teacher or for knowledge to be transmitted from the teacher to the child.

Meanwhile, in the field of cognitive psychology, Jean Piaget's and Lev Vygotsky's cognitive developmental frameworks further pushed the (trans)formation of child-centered pedagogy in the field of education. Piaget's stages of cognitive development theory greatly influenced teachers' understanding of how children develop and learn in classroom settings. Similarly, Vygotsky's sociocultural cognitive development theory has broadened contemporary educational practices, shifting pedagogical practice in classrooms to facilitate children's learning and development. While their theoretical frameworks of cognitive development and constructivist approaches to the child's learning and development are very different, both Piaget's and Vygotsky's works significantly influenced the spread of child-centered

learning pedagogical practices in the field of education.

These multiple narratives of child-centeredness from different fields of study have all worked to legitimize the notion of child-centered learning as innovative and progressive pedagogical practice. Placing the child in the center of education has never been questioned of as a truthful, universal, appropriate, contemporary educational practice. Therefore, it is important to destabilize the popular conception of child-centered learning, for it has been a dominant Western narrative of learning and development for centuries. The need to unpack and problematize the cultural conflicts of child-centered pedagogy cannot be ignored.

Critical Reflections on Child-Centered Learning

The dominant constructions of child-centeredness across contemporary global education systems have primarily reflected Western sociocultural narratives of the child to form the basis of child-centered pedagogy (e.g., see Lee and Tseng 2008). While it is significant to place the child in the center of his/her education to support and facilitate the child's learning and development, it is also important to raise critical questions to unpack hidden sociocultural bias in the dominant narratives of child-centeredness. Critical questions such as "*whose child has been placed at the center of education*" should not be ignored, since most of the well-known pedagogical approaches in education that promote child-centered learning all have cultural roots of Euro-centric or Anglo-Saxon political and sociocultural assumptions (Dahlberg and Moss 2005). For example, Froebel's idea of child's play, Montessori's conception of child-centered pedagogy, Piaget's cognitive development theory, and Vygotsky's sociocultural cognitive developmental perspectives are related to Western sociocultural backgrounds (Burman 1994; Cannella 1997). These variations on similar constructions of child-centeredness are sociocultural inventions in that "the child" is a particular type of child through which the conceptual formation of child-centeredness and child-centered learning

can privilege certain group(s) of children only. Therefore, it is imperative to unpack the bases of the *kinds* of knowledge that come together to shape the specific sociocultural constructions of child-centered learning for all children.

While acknowledging the importance of child-centered learning to support children's development and learning, contemporary critical theories have not been taking the notion of "child-centered learning" at face value. For instance, to challenge the notion of "child-centeredness" as a progressive education and pedagogical practice, it is important to reconceptualize that knowledge is never neutral, but is constituted within complex webs of power relations with social, cultural, political, and historical influences (Apple 2000). The question of "whose knowledge counts" as the "universal" truth when it comes to shaping "our" understanding of child-centered learning has opened up possibilities to destabilize the grand narrative of child-centeredness. Additionally, if the notion of child-centered pedagogy is not problematized or reconceptualized, it is ironic that many children will be excluded from the center of education and their different learning needs and development may be silenced.

Conclusion

In the twenty-first century, child-centered learning is a much promoted educational philosophy and pedagogical practice. The main rationality of child-centered learning pedagogy is to place the child in the center of teaching and learning for the cultivation and facilitation of an active learner as well as to foster the child's/learner's autonomy and independence in his/her own learning process. Additionally, with strong roots in the field of cognitive psychology, child-centered learning acknowledges the child as an active learner who has a voice and agency in his/her learning process and development. In contrast to the traditional education approach that is teacher-centered, the notion of child-centered learning does not see the teacher as the primary source of knowledge. Rather, knowledge is co-constructed between the child and the teacher in child-centered learning pedagogical practice.

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Child-Directed Speech (CDS)

- ▶ [Interactive Language Development](#)

Childhood Co-residence Duration

- ▶ [Kin Recognition and Classification in Humans](#)

Childhood Fatalities

- ▶ [Methods of Filicide](#)

Childhood Maltreatment

- ▶ [Genetic Relatedness and Child Abuse](#)

Childhood Sexual Abuse

- ▶ [Sexual Abuse](#)

Childhood Sexual Victimization

- ▶ [Sexual Abuse](#)

Childhood Trauma

- ▶ [Child Abuse and Bullying](#)

Childless Women

- ▶ [Evolutionary Paradox: Women Choosing Not to Have Children](#)

Childrearing

- ▶ [Parental Investment and Parenting](#)

Child-Rearing

- ▶ [Socialization Processes](#)

Children and Sibs Share Same Proportion of Genes

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Synonyms

[Genetic relatedness](#); [Kin relations](#)

Definition

Individuals share approximately the same amount of genes with their biological children and with their full siblings.

Introduction

Biological parents share an average of 50% of the same genes with their children and step-parents share 0% of the same genes with their stepchildren. Adoptive parents can either share some genes with their adoptive children (in the case of within-family adoption) or not. In addition, individuals share approximately 50% of their genes with their full siblings, 25% of their genes with their half siblings, and 0% of their genes with their step-siblings. In the case of within-family adoption, siblings can be genetically related, but in the case of outside family adoption, they tend to be unrelated.

Although individuals share approximately the same proportion of genes with both their biological children and their full siblings, these relationships are substantially different from each other. Sibling relationships are typically horizontal because siblings are often close in age and therefore belong to the same generation. Relationships between parents and children, however, are vertical by nature because parents are always older than their biological children, meaning that parents and children do not belong to the same generation. Relationships between two siblings are usually equal and reciprocal, but parents invest much more time and resources in their children than they can ever assume to receive back (Del Giudice and Belsky 2011).

Across human societies, mothers have been the most important individuals to guarantee children's survival and well-being (Sear and Mace 2008). Older siblings can act as "allo-parents" and increase the survival of their younger siblings, but individuals' investments in siblings are far lower than parental investments in children. Moreover, compared to

parent-child relationships, sibling relationships include more competition by nature because siblings can compete with one another for parental resources (Salmon and Hehman 2014).

Relatedness and Kin Investment

Based on inclusive fitness theory, the degree of genetic relatedness explains how altruistically individuals act towards one another. Several studies have provided support for this prediction (see Volk 2011 for review). An increasing amount of studies indicate that fathers who have biological children invest more in their offspring compared to fathers who have children via their spouse. Stepfathers are also more likely to neglect their stepchildren than biological fathers are to neglect their biological children. However, in the case of adoptive children, parental investment can be as substantial as with biological children (Segal et al. 2015).

In the case of siblings, the degree of genetic relatedness influences sibling relationships (see Pollet and Hoben 2011 for review). Studies have reported that siblings who share both biological parents are closer to one another compared to step-siblings. Moreover, full-siblings tend to have closer relationships and more contact than half-siblings. Finally, some recent studies have detected that individuals may also have more conflict with their full rather than their half-siblings, at least when less severe conflicts are measured (Salmon and Hehman 2015; Tanskanen et al. 2016), indicating that small disagreements may forecast good rather than bad kin relationships.

Conclusion

Although the degree of genetic relatedness is similar between parents and biological children and between siblings who share both biological parents, parent-child, and sibling relationships differ from one another. In general, the net flow of resources tends to go from parents to their children. Although siblings are often emotionally

close to one another, parents and children form a special bond across societies. Perhaps the most important similar aspect between sibling and parent-child relationships is that in both of these kin relationships, the degree of genetic relatedness may make a difference. Individuals tend to invest more resources in their more closely related kin than in less or nonrelated kin.

Cross-References

- ▶ [Children Have Greater Reproductive Value than Sibs](#)
- ▶ [Helping and Reproductive Value of the Recipient](#)
- ▶ [Reproductive Value](#)

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Children Have Greater Reproductive Value than Sibs

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Synonyms

[Age-related reproductive potential](#); [Future reproductive capacity](#); [Reproductive potential](#)

Definition

On average, individuals share 50% of the same alleles with their children and with their full siblings. Because of age-related reproductive potential, however, it is often more evolutionary beneficial to invest time and resources in children than in siblings.

Introduction

Evolutionary theory predicts that kin investments are dependent on the potential fitness benefits of the investments that are related to recipients' current and future reproductive potential (Hughes 1988). For instance, although a 55-year-old mother shares 50% of the same alleles with both her 18-year-old daughter and 65-year-old sister, in terms of her inclusive fitness, it is more beneficial to invest resources in her daughter than her sister. This is because her 18-year-old daughter has a potentially high reproductive capacity, but her 65-year-old sister is already beyond her reproductive years. Investing resources in children at the beginning of their reproductive careers may maximize the investors' number of offspring in future generations.

In addition to age, reproductive value is also sex-specific. Although the fertility of both females and males declines with age after they have reached their sexual maturity, males can still reproduce until they die, but human females experience a long nonreproductive lifespan. The reproductive value of children is highest at the beginning of their reproductive years when their potential time to have their own children is long and they are most fertile (Trivers 1971).

Reproductive Value and Kin Investment

The reproductive value prediction has been tested in some previous empirical studies with respect to children and siblings. For instance, children with disabilities need more parental investment and are less likely to provide fitness benefits because they have a lower probability to reproduce if they even survive (Salmon and Malcolm 2011). Therefore, infants who are born with disabilities are more likely to become victims of parental infanticide compared to children without such disabilities (Daly and Wilson 1984). From a fitness perspective, it would be more beneficial to parents to abandon investment in children with disabilities and to invest in other offspring with higher reproductive potentials.

A set of studies has tested the reproductive value hypothesis in sibling relationships. These studies have found that childless couples more often take care of their siblings' children compared to couples with children (Pollet and Dunbar 2008) and that childless women have more contact with their siblings with children than their siblings without children (Pollet et al. 2006; Tanskanen 2015). These results indicate that individuals who do not have children of their own may try to increase their inclusive fitness by investing in their kin in descending order, providing evidence for the prediction that the recipient's reproductive value shapes human behavior (Pollet and Hoben 2011). Moreover, studies on non-human species have shown that reproductive value is associated with the time and the resources that individuals direct towards their kin (Emlen 1984).

Conclusions

Based on inclusive fitness theory, for childless individuals, investing resources in their siblings with children could be the most beneficial strategy to increase their own inclusive fitness, particularly when it is unlikely that these individuals will have their own children because of older age or some other reason. Reproductive value may also explain why individuals tend to invest more resources in their children than their siblings, although the degree of relatedness between them is similar. By investing time and resources in their offspring in descending order, individuals can maximize their number of descendants in future generations.

Cross-References

- ▶ [Children and Sibs Share Same Proportion of Genes](#)
- ▶ [Helping and Reproductive Value of the Recipient](#)
- ▶ [Reproductive Value](#)

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higher socioeconomic status in adulthood (Geary 2005). Though this research has established the generalized importance of paternal investment for both sons and daughters, some of the most reliable and pronounced associations revealed in this literature are those between low paternal investment and daughters' developmental, sexual, and reproductive outcomes.

Children Without Paternal Investment

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Synonyms

Father absence; Low-quality fathering; Paternal disengagement

Definition

Offspring who receive no (or low-quality) parental care, financial or emotional support, or other fitness-relevant resources (e.g., energetic, social) from their biological fathers.

Introduction

Social scientists have long recognized the importance of families, in general, and parents, in particular, in shaping children's outcomes (for better or for worse). Although past work has largely focused on the effects of joint parenting processes or maternal behavior on children's well-being, more recent investigations have examined the unique impact of a father's investment on sons' and daughters' outcomes. In general, this research suggests that for children across cultures, growing up with (versus without) the investment of one's father is associated with a wide range of social and physical benefits, including reduced mortality risk and illness, greater academic achievement, and

The Effects of Low Paternal (Versus Maternal) Investment

Research on the influence of physical father absence (including parental divorce) on daughters indicates that growing up without (versus with) one's biological father in the home is associated with accelerated pubertal development (James et al. 2012), early initiation of sexual activity (Ellis et al. 2003; James et al. 2012), increased risk of teenage pregnancy (Ellis et al. 2003), and increased risky sexual behavior, such as having sex with a greater number of partners and having unprotected sex (Coley et al. 2009; James et al. 2012). Although disparities between daughters from intact and divorced homes are apparent across development, some research suggests that these group differences are most pronounced when physical separation from the father occurs early in life (Ellis et al. 2003).

Low paternal investment that results from physical absence of the father is reliably associated with accelerated and unrestricted sexuality among daughters; however, low-quality father–daughter relationships may take on similar (if not greater) importance in shaping these outcomes. Low-quality fathering – whether indexed by low levels of warmth, emotional closeness, or involvement in children's lives – is associated with accelerated sexual development, early sexual onset, and increased sexual risk taking among daughters, even when the biological father remains in the home (e.g., Coley et al. 2009; Ellis et al. 2012; Rink et al. 2007). Importantly, such relationships persist when controlling for unmeasured genetic and environmental confounds (e.g., genetic risk for problem behavior, poverty) by comparing the behavior of biological sister pairs with differential exposure to their

fathers, suggesting a causal relationship between paternal behavior and daughters' sexual risk taking (Ellis et al. 2012). Accordingly, low-quality father–daughter relationships can be a more important risk factor for risky sexual behavior than physical father absence from the home.

Though a mother's investment undoubtedly influences adolescent outcomes, it may be fathers who exert a stronger, unique impact on daughters' sexuality. For instance, Rink et al. (2007) demonstrated that increased father – but not mother – connectedness decreased daughters' likelihood of engaging in early sexual behavior. Ellis et al. (2012) found that increased exposure to low-quality fathering (indexed by low warmth and high harshness) predicted increased risky sexual behavior among daughters from biologically disrupted families, even after controlling for the quality of the relationships that daughters had with their mothers. The reliable impact of fathers (versus mothers) on daughters' sexuality may derive from the information that paternal investment patterns provide daughters about the availability of male investment in their local environments (i.e., paternal investment theory: Draper and Harpending 1982; Ellis et al. 2012). On this view, receiving low (or no) investment from the father lowers daughters' expectations for receiving long-term investment from male relationship partners, instead shifting them toward relatively short-term (“fast”) reproductive strategies.

Low Paternal Investment and Adolescent Risk Taking

From the perspective of paternal investment theory, the effects of a father's investment on sexual behavior will be more pronounced for daughters relative to sons. However, this does not suggest that paternal investment has no impact on sons. Veneziano (2003) explored the effects of paternal warmth and physical presence on boys' interpersonal aggression (including theft and homicide) among a culturally diverse sample. The results of this research suggested a link between increased paternal warmth and decreased interpersonal aggression among boys. Other work has found

parental divorce/separation (including single parenthood) to be an equally strong predictor of early sexual behavior among adolescent boys and girls (e.g., Flewelling and Bauman 1990).

Despite evidence that fathers' behavior (or absence) can impact boys' aggressive and sexual tendencies, when directly comparing the effects of paternal investment on sons' and daughters' sexual outcomes, many studies suggest stronger fathering effects for daughters than for sons. For instance, Coley et al. (2009) revealed that increased paternal knowledge reduced sexual risk taking among daughters more than it did for sons. Similarly, James et al. (2012) found that father absence from the home directly increased the likelihoods of early sexual debut and risky sexual behavior among daughters but not among sons.

The logic of paternal investment theory also suggests that the effects of fathers on daughters should be most pronounced for risky *sexual* behavior and should not necessarily extend to influence other forms of risk taking. Despite some research suggesting that paternal disengagement can have implications for adolescents' willingness to take sexual *and* nonsexual risks (e.g., substance use; Flewelling and Bauman 1990), other studies have failed to reveal a strong or reliable effect of paternal disengagement on daughters' nonsexual risk taking. To illustrate, Mandara and Murray (2006) examined the effects of father absence on adolescent drug use and found that father-absent boys were more likely to use drugs than father-present boys. However, father absence (versus presence) did not significantly increase girls' reported drug use.

Further, whereas early father absence is a strong predictor of girls' increased risk of early sexual activity and teen pregnancy, Ellis et al. (2003) found that exposure... to father absence does not uniquely predict the occurrence of nonsexual problem behaviors (e.g., violent acts, externalizing behavior problems) after controlling for other risk factors (e.g., family life stress). In light of the mixed support for father absence being associated with different forms of nonsexual risk taking, it appears that the unique effects of fathers may be most pronounced and consistent for

daughters' engagement in early and unrestricted sexual behaviors.

Conclusion

Does a father's investment matter, and if so, how? The empirical evolutionary developmental literature has taken important steps in addressing these questions. In traditional societies, the investment of a father can mean the difference between life and death for a developing child. In modern, Western societies characterized by low child and infant mortality, a father's investment may provide other critical advantages, such as better health and the promise of future socioeconomic success (Geary 2005). Although these advantages are enjoyed by children regardless of their gender, paternal investment may be most influential in shaping daughters' mating outcomes. On this view, a father's investment provides information to daughters suggesting that men are able and willing to invest in reproduction, and as such, reproduction can be delayed until such investment is secured. Daughters may thus attend to cues such as the father's presence in the home and his behavior (e.g., his level of warmth and support directed toward them and their mother) in calibrating emergent reproductive strategies. From a functional perspective, this approach makes good adaptive sense, allowing females to avoid (or capitalize on) potential reproductive opportunities based on what they can reasonably expect from males within the local ecology.

Cross-References

- ▶ Early Childhood and Adolescence
- ▶ Ecology of Paternal Investment
- ▶ Father Absence
- ▶ Father Absence and Stress Reactivity
- ▶ Paternal Investment
- ▶ Paternal Investment Relative to Maternal Investment
- ▶ Reproductive Strategies
- ▶ Sexual and Reproductive Development

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Children's Antipredator Adaptations

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Synonyms

Threat avoidance

Definition

Numerous physiological, cognitive, and cultural cues help children avoid a range of threats and predators.

Introduction

Predator avoidance is greatly prioritized across humans and the animal kingdom. Furthermore, organisms that lack the ability to adapt to environmental demands will face casualties in the “war of nature” (Darwin 1871; Mobbs et al. 2015). Thus, researchers across several disciplines have studied the various adaptations protecting individuals – including infants and young children – from predators. Of these, physiological, cognitive, and cultural mechanisms are discussed.

Neuroanatomical and Physiological Mechanisms

Öhman's (1993) evolved fear module describes a neural system tuned to evolutionarily relevant threats. The module is selective, automatic, and independent of conscious cognition. Located in neural circuitry centered in the amygdala (within the anterior temporal lobe), the module mediates threats (e.g., detecting a snake or spider) and appropriate responses (i.e., fight or flight) before fearful stimuli are fully identified across regions of the cortex (Öhman and Wiens 2004).

One paradigm often used to support this neural system for fear involves measuring event-related potentials (ERPs) utilizing an electroencephalogram. ERPs reflect cortical activity, which can inform neural processing and responses to a variety of stimuli, for example, how soon a stimulus is detected after it is presented to a participant. Researchers have measured children and adolescents' early detection of fear in the amygdala (Monk et al. 2008). The amygdala operates as a quick detection fear module within the brain, which in turn enables the experience and perception of fear (Fox et al. 2007). Researchers have measured amygdalar activation from a range of

emotional stimuli across adults, adolescents, and children (Guyer et al. 2008; Hare et al. 2008; Passarotti et al. 2009). Additionally, both Gee et al. (2013) and Pfeifer et al. (2011) have demonstrated the amygdala's connection to emotion reactivity. Additional work with children, some utilizing ERPs, others utilizing functional magnetic resonance imaging (fMRI), supports the role of the amygdala (Forbes et al. 2011), hippocampus (Pagliaccio et al. 2015), and prefrontal cortex (Monk et al. 2008) in threat detection.

Arousal data also hint toward an evolved fear module, with various measures showing immediate physiological responses to threat. Fear is represented in a variety of physiological responses (i.e., rapid heart rate, skin conductance, pupil dilation). In one study, Weems et al. (2005) explored skin conductance and heart rate in 6–17-year-olds following exposure to a mildly phobic stimulus (e.g., a video of a large dog). Their findings suggest both physiological responses are linked to anxiety (a component of fear); however, the association for heart rate was higher. Weems et al. (2005) explained that, while both are reasonable measures to consider in these studies, heart rate is the better measure because the amygdala (where threat is detected) has a stronger influence on heart rate (Thayer et al. 2012). Field and Schorah's (2007) research further supports that notion. In their study, children between 6 and 9 years old were asked to place their hand into a box that contained fearful, positive, or neutral information about animals. Their findings revealed there were significant differences between heart rate among the boxes, including a significantly higher heart rate when children approached the box with threat-related information, relative to the box with neutral information.

Skin conductance responses (e.g., sweating) reflect changes within the sweat glands that then produce changes in the electrical conductivity of our skin. Because this reflects activity across the sympathetic nervous system, it further provides a useful metric for arousal (Jovanovic et al. 2014). In their research, Gao et al. (2010) investigated skin conductance responses in fear conditioning among children 3–8 years old. Results suggested fear conditioning increases in children at a very

early age, beginning between the ages of 5 and 6. Glenn et al. (2012) further showed that with conditioned stimuli, responses were elevated for 10–13-year-olds, again showing skin conductance can provide important insights for conditioned fear.

Adaptations to threat exist in children in the early stages of development, suggesting some responses to fear are not learned. Examples of these include immediate processing in their amygdalae, followed by strong sympathetic responses most evident in children's heart rate.

While children's physiological responses to threat detection can differ, researchers argue heart rate and skin conductance responses are the most common and reliable measures. Of equal importance, children ought to use these physiological signals to guide their behavior and responses to threat (Howle and Kazanas 2019).

Cognitive Mechanisms

Adults' attentional biases for threat-relevant stimuli are well-established in the cognitive literature (e.g., Öhman et al. 2001). Öhman's (1993) evolved fear module predicts adults and children should behave similarly, with both age groups needing to rapidly detect and avoid threats in their environment. To test this hypothesis with young children, LoBue and DeLoache (2008) modified the typical visual search paradigm with the addition of a touchscreen monitor. They asked 3–5-year-old children and their parents to detect targets from distractors, when targets were either snakes, flowers, frogs, or caterpillars. Participants identified targets by touching the single target embedded among the distractor stimuli. Across three experiments, adults and children performed similarly: each time, detecting snakes faster than each of the nonthreatening distractors (see Penkunas and Coss 2013b for a replication with snakes and lizards). They replicated these findings with 8–14-month-old infants, as well, when snakes were displayed among flowers and frogs (LoBue and DeLoache 2010). Importantly, infants detected snakes only *numerically* faster than frogs (i.e., this difference was not significant), hinting

toward the possibility of some generic animacy effect at this young age (c.f. Altarriba and Kazanas 2019), rather than an explicit mechanism for detecting snakes.

Nevertheless, the attentional bias for detecting snakes observed by LoBue and DeLoache (2008) has been tested with other groups of children. In one example, Penkunas and Coss (2013a) determined these patterns for threat detection replicate with non-Western populations, including 3–8-year-old children living in Southern India. In one particularly notable finding, the rural and urban children performed similarly: both with shorter latencies to locate the target when it was a snake or a lion than when it was a lizard or an antelope. Importantly, the rural children live in or near national parks (some even in tiger reserves), while the urban children do not regularly encounter these threats. Thus, it appears neither experience nor novelty played a role in these comparisons.

In one recent paper, experience *did* play a role in threat detection. Prokop (2018) asked parents to describe their child's recent medical history, identifying children as "vulnerable" if they had contracted some infectious disease in the past year. Then, 5–6-year-olds and 8–9-year-olds were asked to identify predators (e.g., wolves), disease carriers (e.g., mosquitoes), and animals aposematically colored (i.e., those warning off predators with their appearance, e.g., skunks) from control animals (e.g., zebras). Predators were identified most accurately, as we would expect from this literature, but, critically, children identified as vulnerable were especially successful at identifying disease-carrying animals. This particular finding suggests animacy, particularly predatory threats, helped shape important elements of human cognition (e.g., adaptive memory; Kazanas and Altarriba 2015, 2017; Kazanas et al. 2020). Perhaps, then, the more vulnerable react faster, thanks in part, to some connection to their behavioral immune system.

Other researchers have wondered *how* these biases occur, perceptually. LoBue and DeLoache (2008) reviewed earlier hypotheses from the visual search paradigm, such as Treisman and Gormican's (1988) important features, most

notably, curved lines. For example, perhaps a snake's tendency to slither or coil their elongated, limbless body somehow mattered in human evolution. Years later, they confirmed this idea, with children and adults detecting coiled wires faster than flowers, and no advantage for snakes when they were *not* presented in a coiled shape (LoBue and DeLoache 2011; see also DeLoache and LoBue 2009 for a similar argument with an emphasis on movement). We cannot be sure precisely why a curved shape garners this advantage, unless snakes shaped the far earlier primate visual system, too (Isbell 2006). Rakison and Derringer (2008) made a similar case for our tendency to rapidly detect spiders: Infants as young as 5 months old looked longer at schematic spider imagers than they looked at reconfigured versions of these images (while they do not appear to have any templates for flowers at this age). Thus, at such a young age, we can observe attentional and perceptual mechanisms shaped by threatening stimuli.

Hansen and Hansen's (1988) "face in the crowd hypothesis" predicts children will also demonstrate attentional biases for faces, particularly angry faces appearing among nonthreatening faces. LoBue (2009) sampled both adults and preschoolers, to see if experience conflates this hypothesis. She compared a variety of positive and negative facial expressions, testing whether (1) we are particularly sensitive to angry faces or (2) we possess something akin to a general negativity bias (Cacioppo et al. 1999; Smith et al. 2003). Her participants completed a number of visual search tasks, with targets and distractors comprised of angry, afraid, sad, and happy faces. Findings from the first three experiments supported a general negativity bias, with faster latencies to touch the target when it was an angry, afraid, or sad face, relative to a happy face, suggesting these negative expressions were easy to detect. Importantly, the next set of experiments compared latencies when both targets and distractors were negative expressions. Critically, participants detected angry and afraid faces the fastest, evidence of an attentional mechanism built to rapidly attend to danger in the environment.

Perhaps the strongest evidence of this mechanism lies in the similar patterns of data across adults and preschoolers. While adults *did* perform the tasks faster, both age groups displayed the same attentional biases to negative expressions and their latencies to touch the target were the fastest for angry and afraid targets. This broadly implies an evolved bias to rapidly detect threats – otherwise, young children without the experience (explicit or otherwise) would not have known to react this way to a threat, barring any novelty effects, of course. Additional research, perhaps with infants, could disentangle some of these additional explanations. For example, LoBue and DeLoache (2010) examined attention biases with 8–14-month-old infants, finding rapid orientation to angry faces (Experiment 2), but not to afraid faces (Experiment 2A), though they looked at them longer than they looked at happy faces. We can only surmise infants are using these moments to learn about potential threats in their environment. One final point worth mentioning: LoBue and DeLoache (2009) have also detected some (small) tendency for young girls to detect targets faster than young boys, but *only* when the targets feature emotional expressions. Moreover, this advantage occurs whether or not these expressions are categorized as threat-relevant (i.e., angry, afraid) or not (i.e., happy, sad). Replications can bolster the reliability of these trends in the literature.

In one final paradigm, Hoehl and Pauen (2017) examined fear acquisition in 9-month-olds with gaze-cueing. In this paradigm, researchers use ERPs – at key locations – to infer attentional biases, such as increased attention when a fearful face is shown looking at a spider. In this case, the authors measured attention by way of the negative central component: a measure of infant attention particularly sensitive to emotion (Hoehl et al. 2008). Fearful and neutral faces were presented next to threatening or nonthreatening stimuli (e.g., spiders and snakes vs. flowers and fish). For example, in Experiment 2, Hoehl and Pauen observed increased attention to snakes, regardless of the face paired with it. This further hints to an evolved fear for snakes (c.f. Poulton and Menzies 2002). Meanwhile, in Experiment 1, featuring

spiders and flowers, the authors observed only some increased attention when fearful faces were paired with spiders, though this interaction was not significant. This finding suggests infants may take cues from others' emotional expressions when learning about their environment, showing a particular sensitivity to their *fears*. Universal attentional biases – such as the ones observed with snakes – suggest some fears are more easily developed, whereas others perhaps develop after an experience or from some amount of social learning.

Cultural Mechanisms and Individual Differences

Cultural upbringing greatly shapes a child's interaction with a stranger. Cultural contexts including “the economy, social structure, settlement pattern, and household and family organization” shape a child's learning environment and influence their behavior (Whiting and Whiting 1975, p. 66). For example, Otto et al. (2014) studied Nso children in the South African country of Cameroon and in Germany to determine if the cultural contexts in which a child grows and learns in shape their interactions with strangers. To test this hypothesis, a stranger was introduced to a mother and year-old child in their family home. The stranger was instructed to hold and play with the child for 3 min with play including holding the child and interacting with toys and games. Overall, Otto et al. found significant differences in child interaction with the stranger. German children were less likely to comply with stranger wishes while Nso children were more likely to conform to the wishes and suggestions of the stranger. This significant difference in interactions with strangers is supported by the beliefs of each of the culture in the study. German caregiving is child-centered and German parents focus on child socialization to include assertiveness, individualization, and self-actualization (Keller et al. 2006, 2009; Keller and Otto 2011), while Nso mothers focus on teaching their children obedience, conformity, and a respect for authority (Otto and Keller 2015).

Another effect of culture on child interaction with strangers may stem from own-race bias and homogeneity of the area in which the child grows up. Bar-Haim et al. (2006) studied 3-month-old Caucasian Israeli children, African Ethiopian children, and Israeli-born infants of Ethiopian origin to assess preference for own-race faces versus other-race faces. In this study, children observed African and Caucasian face-pairs and researchers noted their direction of gaze and its duration. The results of the study showed Caucasian children looked longer at Caucasian faces than African and the opposite was found for African children. Interestingly, the Israeli-born infants of Ethiopian origin showed no face preference for either Caucasians or Africans. The children that showed a race-preference came from homogeneous race environments. This race-face bias may indicate children raised in homogeneous race environments may be averse to those who are from outside of their usual environment.

A similar study by Gaither et al. (2012) found Caucasian, Asian, and biracial Caucasian-Asian children in Los Angeles showed no race preference for faces. This result makes sense as Los Angeles is a very racially diverse area, meaning that these children are more likely to be exposed to other races at a higher rate than children in more racially homogeneous areas. The study found that when asked “What percentage of time do you spend with people not of your same race and/or culture?,” parents noted a high percentage of exposure to others outside of their own race. The results of these two studies broadly imply children from homogeneous locations are going to be more likely comfortable around those who look like them and their own family, with an aversion to those who do not share those same appearances. These children may become fearful of those from other races or cultures, unless they are socialized with those different than them later in life.

Other researchers have looked at the influence of parents on child responses to strangers. Trause (1977) studied 40 infant-mother pairs that were approached by a stranger, followed by the mother leaving the child and allowing a stranger and child interaction that included talking to the child, touching the child, and attempting to hold the

child for 30 s. Half of the mothers stayed with their child for 3 min and the other half stayed with the child 10 min before leaving. All the infants were alone with the stranger for 13 min. Once the mother left, stranger approach toward the child elicited significantly more negative reactions than it did when the mother was present. The presence of the mother moderated the child's response to the stranger.

Lamb et al. (1982) took a different approach than the previous authors and studied children's attachment to both their mother and father to determine the effects on stranger interactions. When the parents and children first arrived, child sociability was measured by their behavior in different scenarios, once with the father and once with the mother. Half of the children interacted with a male stranger and the other half a female, for both measures. After the child's sociability was measured, the Strange Situation (Ainsworth et al. 1978) occurred, which measured attachment to the individual parent. Children with secure attachment with high contact relationships with their fathers were significantly more sociable than those with avoidant attachments and secure attachments with low contact. Infants who were securely attached to their fathers were marginally more sociable than those children who were insecurely attached. Interestingly, there was no significant relationship between mother and child attachments and sociability with strangers. This finding is surprising, because previous studies found infants who are securely attached to their mothers are more sociable to strangers than those who are insecurely attached (Main 1974). Regardless of the differences in results according to the parent gender, children with an insecure or avoidant attachment are less sociable to strangers than those who are securely attached.

A final study of parental influence on children's response to strangers studied children in single- and two-parent families. Weinraub and Ansul (1985) aimed to determine if children from single- and two-parent households respond differently to male and female strangers, if maternal stress influences mother-child interactions and thusly affect child response to strangers, and if the quality of mother-child interactions affect child

response to strangers. Thirty-eight mother-infant pairs (19 single-parent family, 19 two-parent families) participated in this study. Child responses to male and female strangers, in the presence and absence of their mothers, were studied using a modified form of Ainsworth's Strange Situation (Ainsworth et al. 1978). Children from single-parent families showed more fearful behaviors toward both strangers than those from two-parent families. These children ignored requests to play or to be comforted by the stranger significantly more often than two-parent children. Single-parent children tended to cry more when left alone with the strangers and tended to express more negative verbalizations toward the strangers than their peers.

Each of these studies shows parents have a great effect on their children's response to strangers. Children who are not securely attached, in the presence of a parental/maternal figure, or those from single family homes are more likely to have negative responses to a stranger. These responses are often fearful and less sociable toward the stranger, with behaviors to ward off the stranger including crying, negative verbalizations, physically distancing themselves, gaze aversion, and refusal to play (Lamb et al. 1982; Trause 1977; Weinraub and Ansul 1985).

Finally, gender plays a large role in infant response to strangers. Gender differences in response to strangers have been identified in several studies. Boys are often more stable and positive in their interactions with strangers than girls, while girls engage in fewer social interactions with strangers, avoid the stranger more, and are more likely to show negative responses to the stranger as time or attempt at contact with the stranger increase (Shaffran and Decarie 1973; Trause 1977; Weinraub and Ansul 1985).

Gender of the stranger is even more significant in affecting the response from children. Overall, children respond more negatively to male strangers than to female strangers (Lamb et al. 1982; Shaffran and Decarie 1973). This male aversion was also shown in Weinraub and Ansul's (1985) study. Children made significantly more approaches and tended to remain in close proximity more frequently to their mother in the presence

of a male stranger than a female stranger. Significantly more exploratory behaviors were displayed in front of the female than the male stranger, with children engaged in more exploratory manipulation, such as playing with toys in the room. One explanation for this male aversion by children could be the height of the male versus the female stranger (Brooks and Lewis 1976; Lewis and Brooks-Gunn 1972).

Conclusion

Findings from several lines of inquiry support the role of threat in shaping children's responses toward predators. Those responses are evident in children's arousal, but also in their outward attention toward and fear of dangerous animals, angry faces, and adult strangers. Throughout our evolution, automatic, and almost universal, attention toward these predators, along with appropriate responses (e.g., avoid, rather than approach), has ensured our children's safety. However, these responses are also strengthened by a culture's or individual family's attitudes toward strangers. Together, these findings emphasize the importance of both innate and learned mechanisms in understanding an individual child's response. Further, the most fine-grained understanding comes from also considering a child's age, gender, and other dispositional characteristics, along with understanding that some findings may not generalize to all children, from all cultural contexts. Future research with these considerations in mind, paired with multimethod approaches, can further our understanding of children's inward and outward antipredator behaviors.

Cross-References

- ▶ Ability to Recognize Individuals
- ▶ Adaptation
- ▶ Associative Learning
- ▶ Attention
- ▶ Attention and Memory
- ▶ Attention and Perception

- ▶ Context, Environment, and Learning in Evolutionary Psychology
- ▶ Defending Against Predator
- ▶ Evolved Physiological Reactions
- ▶ Face and Object Recognition
- ▶ Facial Expressions
- ▶ Fear Affords Protection
- ▶ Fears
- ▶ Fears and Phobias
- ▶ In-Group–Out-Group Bias
- ▶ Out-Group Members
- ▶ Physiological Mechanisms
- ▶ Predators
- ▶ Predators as Attention-Grabbing
- ▶ Selective Attending
- ▶ Selective Attunement to Adaptive Problems
- ▶ Social Learning
- ▶ Understanding Human Gaze
- ▶ Universal Human Fears

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Chimpanzee Raiding

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Synonyms

Between-community raiding; Border patrols; Coalitionary killing; Conspecific killing; Gang attacks; Intergroup aggression; Intergroup conflict; Lethal raiding; Lethal violence

Definition

Lethal raiding is a form of coalitionary, intergroup aggression observed in chimpanzees in which a party leaves its core range to find and attempt to kill strongly outnumbered and isolated members of neighboring communities.

Introduction

While intergroup conflict is common in social animals, fatal aggression is rare and usually a result of accidental injury during escalated fights (Manson and Wrangham 1991). However, in some species, such as chimpanzees and humans, intergroup aggression appears to be marked by coalitionary, apparently deliberate attempts to kill conspecifics. In chimpanzees, this behavior is likely facilitated by their fission-fusion dynamics, male philopatry, and resource defense polygynandry. We review several proposed hypotheses on the adaptive function of this behavior, which are not mutually exclusive. Critics of this adaptive interpretation suggest that lethal raiding is caused or exacerbated by human disturbances to chimpanzees, though this is not strongly supported by the current evidence. Chimpanzee raiding shares several characteristics with human warfare and is therefore often part of the debate on the origins of human warfare.

Intergroup Conflict in Chimpanzees

Across social species, contest competition for access to limited resources can result in conflict between groups (e.g., Kitchen and Beehner 2007; Radford 2008). Such intergroup conflict may range from avoidance by one group or exchange of aggressive threats to sometimes fatal physical aggression between members of rival groups. Certain socio-ecological conditions, such as when resources are highly defensible and the relative power between the opposing groups is great, increase the likelihood of conflict (Enquist and Leimar 1990; Jaeggi et al. 2016). Aggressive intergroup conflict has been well documented in

primates (Majolo et al. 2016), in particular in chimpanzees where it is characterized by coalitionary attacks that involve apparently deliberate attempts to injure and kill the opponent (Glowacki et al. 2017; Manson and Wrangham 1991). The term “lethal raiding” refers to such unprovoked gang attacks on strongly outnumbered or isolated members of neighboring chimpanzee communities (Manson and Wrangham 1991). While the term is often associated with groups of chimpanzees making deep incursions into neighboring territories, often by stealth, this pattern of coalitionary intergroup aggression also occurs in the context of territorial boundary patrols as well as opportunistically, during chance intergroup encounters (Watts et al. 2006).

Chimpanzee Social Organization

Several features of chimpanzee social organization are thought to be related to the occurrence of lethal raiding, and so we first outline some of these aspects before providing descriptions and explanations of raiding behavior. Within chimpanzee groups, competition for access to food resources may be high at certain times of the year; however, fission-fusion dynamics allow individuals to respond adaptively to environmental variability. As a result, members of a chimpanzee community rarely gather together in a single, cohesive group, but rather travel, forage, and rest in subgroups, or “parties” that change in size and composition throughout the day in response to fluctuations in local resource availability (Wilson 2013). Typically, male chimpanzees remain a member of their natal group throughout their lives, a feature known as male philopatry, whereas female chimpanzees disperse from their natal group when they reach sexual maturity (e.g., Boesch et al. 2008; Pusey 1980). In chimpanzees, as in other primates, male philopatry is associated with remarkable levels of male-male cooperation (Boesch et al. 2008; Manson and Wrangham 1991), and male mating success may be increased through coalitions with other males (e.g., Watts 1998). Because, in most mammals, male fitness is primarily determined by access to fertile females,

while female fitness is largely determined by access to resources (Davies et al. 2012), chimpanzee males can maximize their fitness by defending a territory containing valuable food resources which increase the reproductive success of the females within the community and may attract additional females (Pandit et al. 2016). As chimpanzee males mate with multiple females and females mate with multiple males, this is known as resource defense polygynandry. Fission-fusion dynamics, male philopatry, and resource defense polygynandry are inherent to chimpanzee sociality and are crucial to understanding how and why lethal raiding occurs in this species.

Patterns of Lethal Raiding in Chimpanzees

Observations of Lethal Raiding

Intercommunity killings are mainly observed when large parties, consisting mostly of adult males, encounter isolated and/or greatly outnumbered individuals (Manson and Wrangham 1991; Wilson et al. 2014; Wrangham 1999). The most common context in which this occurs is during territorial boundary patrols into areas of range overlap with neighboring communities (Manson and Wrangham 1991; Watts et al. 2006). During these patrols, the males move cautiously and quietly, often in single file, stopping to listen intently and/or inspect signs of outgroup chimpanzees such as feces, nests, and discarded food wadges (Boesch and Boesch-Achermann 2000; Wilson 2013; Wrangham 1999). If the males encounter members of the neighboring community, their response depends on the size and composition of this outgroup party. Lethal intercommunity attacks most often occur when the attackers greatly outnumber their opponent, with a median ratio of eight to one (Wilson et al. 2014). If the encountered party contains two or more males, the raiders will typically retreat (Manson and Wrangham 1991). However, an isolated male, sexually unreceptive female, consorting male-female pair, or an infant may be stalked and attacked. Sexually receptive females without infants are potential immigrants and therefore

less likely to be aggressed by the raiding party (Boesch and Boesch-Achermann 2000; Pusey 1980). The targeted individual is often restrained or immobilized by the superior numbers of attackers, enabling the attackers to inflict potentially lethal injuries with little to no risk to themselves (Boesch et al. 2008; Manson and Wrangham 1991; Wilson et al. 2014). In fact, there are no reports of attacking parties suffering any major injuries (Manson and Wrangham 1991; Pandit et al. 2016). If members of the neighboring community are not found, the party may either return to their territory or penetrate deeper into the neighboring range (Manson and Wrangham 1991).

Intergroup killings also occur opportunistically, for example, during chance encounters between hunting or foraging parties, often after auditory contact (Boesch et al. 2008; Watts et al. 2006). The frequency of such chance encounters can be affected by food distribution, as observed in Kanyawara (Uganda) where chimpanzees spent more time near the southern border of their territory when fruits there were ripe (Wilson et al. 2012). The majority of observed intergroup interactions occurred during this seasonal fruit availability, likely because chimpanzees from different communities were attracted to the same area and ranges overlapped simultaneously (Wilson et al. 2012). Upon making auditory contact with members from a neighboring community, chimpanzees may silently approach them, after which the encounter follows a similar pattern to those that arose during boundary patrols. Regardless of whether the attack results from a patrol or chance encounter, once the victim is isolated, attackers often persist until the individual is dead, after which they may continue to drag, hit, kick, and jump on the body (Wilson 2013). Should the victim attempt to escape during the attack, the attackers may give chase and attempt to restrain them and/or inflict further harm (Watts et al. 2006). Inspection of the bodies reveals that male victims are frequently emasculated during the attack by removal of the testes and/or penis (Boesch et al. 2008; Watts et al. 2006). Attackers sometimes twist limbs, inflict wounds with their canines, remove extremities and appendages such

as fingernails and ears, and rip off strips of flesh (Watts et al. 2006; Wilson 2013). There are also many documented cases of intercommunity infanticide, following attacks on neighboring females with dependent offspring, after which the infant is often cannibalized (Boesch et al. 2008).

If, during an attack, auditory contact is made with nearby members from the attacked individual's community, the attackers may become wary of these potential supporters and retreat before killing the targeted individual (Watts et al. 2002, 2006). In these cases, the victim may still die in the following days, most likely from internal injuries (Watts et al. 2006).

Frequency of Lethal Raiding

Observations of lethal raiding in chimpanzees all come from long-term study sites (e.g., Gombe and Mahale in Tanzania), as the large ranges and low population densities of chimpanzees make intergroup encounters relatively infrequent (Wilson 2013). In more densely populated areas, such as Taï Forest (Côte d'Ivoire) and Ngogo (Uganda), encounters between communities occur around once or twice per month (Boesch et al. 2008; Wilson 2013).

The majority of intergroup interactions are limited to acoustic contact, where members of neighboring communities remain separated by hundreds of meters (Boesch et al. 2008; Wilson 2013). Chimpanzees use long-distance vocalizations, such as pant-hoots, to communicate with members of their community (Goodall 1986). When hearing calls from another community, chimpanzees might respond with their own chorus of pant-hoots (Watts et al. 2006; Wilson 2013). In some cases, however, the chimpanzees remain silent and either stay still, looking in the direction of the vocalization, rapidly retreat, or move toward the callers, potentially escalating the interaction to visual contact which, depending on the size and composition of the encountered party, could in turn escalate to physical contact, often leading to injuries or death (Wilson 2013). Most intergroup interactions are limited to acoustic contact. In the Taï Forest, for instance, only 27% of intergroup encounters included visual contact, of which 1.5% (0.4% of all intergroup encounters)

involved lethal aggression (Boesch et al. 2008; Wilson 2013).

Just over a third of all lethal aggression between chimpanzees occurs during aggression within communities (37%), while the remaining two-thirds occur (63%) during intergroup aggression (Wilson et al. 2014). The higher percentage of intergroup fatalities becomes even more prominent when the frequency of contact is considered. In theory, chimpanzees have the opportunity to lethally attack members of their own community every day, yet only rarely encounter members from other communities (Wilson et al. 2014). The two types of lethal aggression are also distinct in that most intragroup killings are infanticides, whereas lethal intergroup aggression often targets adults (Wrangham et al. 2006). Though relatively rare, intraspecific killing (including intragroup aggression) is a highly significant cause of death in chimpanzees, second only to dying from disease (Williams et al. 2008). When taking the low population sizes and observation times into account, a study of nine chimpanzee communities estimated that intraspecific aggression caused 271 deaths per 100,000 individuals per year (69 deaths per 100,000 individuals per year from intergroup aggression alone) (Wilson 2013; Wrangham et al. 2006). To put these numbers into perspective, the rate of intentional homicides in the United States in 2016 was 5.35 deaths per 100,000 individuals per year ("UNODC Statistics Online" n.d.). The relatively high percentage of intergroup fatalities, combined with the brutal and perseverant nature of the attacks, suggests that the killing of adult opponents is characteristic to chimpanzee intergroup conflict, rather than merely a consequence of escalated resource competition. If so, chimpanzee raiding shares one of the most important distinguishing characteristics of human intergroup aggression and warfare: the deliberate killing of conspecifics (Manson and Wrangham 1991).

Adaptive Explanations

In order for a behavioral strategy to be adaptive and evolve, the benefits of performing the

behavior must outweigh any potential costs to the animal, leading to an increase in reproductive success, that is, an increase in the number of direct and/or indirect descendants (Davies et al. 2012; Wilson 2013). It is difficult to test and evaluate the adaptive benefits of lethal intergroup aggression in chimpanzees, due to their relatively slow life histories (Watts et al. 2006). There are several adaptive hypotheses in the literature that offer explanations for lethal raiding in chimpanzees, and while they all share the ultimate function of increased fitness through greater access to resources and/or reproductive females, they differ in their emphasis on the proximate mechanisms and socio-ecological conditions that elicit lethal aggression. These explanations are not mutually exclusive and a combination of factors likely selects for lethal raiding (Watts et al. 2006; Wilson 2013).

Resource Defense Hypothesis

The resource defense hypothesis (Emlen and Oring 1977) suggests that intergroup aggression benefits the attacking community by allowing them to defend food resources, which, due to resource defense polygyny in chimpanzees, affect both the males' access to females and the reproductive success of these females, and therefore the fitness of the defending males (Williams et al. 2004). Performing raids in a particular area might induce the targeted community to avoid using that area and/or its resources (Pandit et al. 2016). This hypothesis is consistent with an observed increase in patrol frequencies with the availability of ripe fruit (Watts et al. 2006). Additionally, the resource acquisition hypothesis suggests that chimpanzees attack other groups, not just to defend their resources but to further expand their territories, gain access to more food, increase the feeding success of their community, and therefore potentially increase female reproduction (Mitani et al. 2010; Williams et al. 2004; Wrangham 1999). This is supported by observations of coalitionary attacks on a neighboring group, followed by territorial expansion into areas previously occupied by that group (Mitani et al. 2010). The resource defense hypothesis broadly explains the reproductive benefits of

intergroup conflict in chimpanzees, predicting that male philopatry should arise as a consequence of resource defense (Greenwood 1980; Ostfeld 1987). It can therefore provide the socio-ecological context in which male-driven lethal intergroup aggression is expected (Jaeggi et al. 2016; Pandit et al. 2016). It has been suggested that, while resource defense polygyny explains the reproductive benefits of intergroup conflict in chimpanzees, it is insufficient to explain why chimpanzee raiding appears to be aimed at killing their opponent, rather than merely displacing them from the contested area (Pandit et al. 2016). If so, lethal intergroup aggression in chimpanzees must be promoted by additional factors, as suggested by the fact that this behavior is not commonly reported in other primate species with a resource defense mating system (Pandit et al. 2016).

Imbalance of Power Hypothesis

Currently, one of the most widely accepted explanations for the lethal intergroup aggression in chimpanzees builds on this prior explanation of resource defense polygyny, to suggest that the behavior is promoted by their fission-fusion sociality and male philopatry, which create opportunities for intergroup encounters where one party has a superior number of cooperating males (Glowacki et al. 2017; Manson and Wrangham 1991; Pandit et al. 2016; Watts et al. 2006). By nature of numerical superiority, attackers can greatly reduce the costs of aggression (risk of injury) and more easily inflict injury on others. An important factor in this risk reduction is the cooperative, coordinated nature of the attacks, facilitated by coalitionary bonds between philopatric males, in which opponents are quickly subdued or immobilized, further minimizing potential costs (Manson and Wrangham 1991; Watts et al. 2006). The "imbalance of power hypothesis" therefore proposes that lethal attacks are promoted not by high benefits but primarily by low costs (Manson and Wrangham 1991; Wilson et al. 2014). Despite acknowledging the substantial benefits of lethal raiding, Manson and Wrangham (1991) highlight the fact that there is only one confirmed, and one suspected, case of

group extinction due to lethal raiding. They therefore conclude that the benefits, while potentially great, are likely to be much less important than the costs when considering the evolution of lethal raiding behavior. The hypothesis has been well-supported by observations that most lethal intergroup aggression occurs when large parties attack a greatly outnumbered individual and by the fact that there are no reports of major injuries incurred by the attackers (Manson and Wrangham 1991; Pandit et al. 2016).

It must be stated that, while most intergroup aggression has been observed to occur in low-cost situations, chimpanzees sometimes appear to accept large risks and engage in conflict with numerically superior communities, even when in very small parties (Boesch et al. 2008). In these cases, social factors, such as limited access to fertile females, may increase the potential benefits of attacking (or the cost of inaction) to exceed the potential cost of attacking, even without a favorable imbalance of power (Boesch et al. 2008).

Reduce Rivals Hypothesis

The benefits of killing an opponent, rather than chasing them off, could simply be to eliminate a potential competitor or reduce the coalitionary strength of the rival group (Boesch et al. 2008; Mitani et al. 2010; Watts et al. 2006; Wilson 2013; Wilson et al. 2014; Wrangham 1999). This “rival coalition reduction hypothesis,” also called the “dominance drive hypothesis,” is strongly linked to the imbalance of power hypothesis. The benefits of killing a rival hold true for any species with group-level conflict (Wilson et al. 2014). However, in species without a mechanism to facilitate a sufficient imbalance of power, this benefit is likely outweighed by the potential cost of killing (Wilson et al. 2014). In these cases, animals would likely not risk injury by pursuing and attempting to kill their opponent but would simply displace them from the contested resource (Wilson 2013). Enabled by the fission-fusion social system, gang attacks and lethal raids provide low-cost opportunities for chimpanzees to decrease a neighboring community’s competitive ability (Wrangham 1999). As males do not migrate between groups, killing a male reduces the coalitionary strength of

the targeted community until the male is replaced through births within that community (Wrangham 1999).

Female Recruitment Hypothesis

It has also been suggested that intergroup attacks serve to recruit new females, as young females have been observed to join the attacking community (Goodall 1986). Though this hypothesis has not yet been systematically tested, there are indications that emigrating females may select communities with large numbers of adult males, so these attacks could serve to advertise their community size (Boesch et al. 2008; Wilson 2013). The observed intergroup infanticides have also been suggested to be a strategy to increase males’ access to fertile females, as is the case in species such as lions, langurs, and gorillas (Boesch et al. 2008). However, there is currently no convincing evidence this behavior increases the likelihood of female chimpanzees joining the infanticidal males’ community (Boesch et al. 2008). As stated before, the proposed adaptive explanations are not mutually exclusive. Males may be able to attract new females by defending and expanding their resources (Manson and Wrangham 1991; Pandit et al. 2016). This territorial expanse could in turn be facilitated by the reduction of the rival coalitionary strength (Mitani et al. 2010; Watts et al. 2006), which is made strategically viable through the imbalance of power.

Female-Targeted Attacks

If chimpanzee raiding is a strategy by which coalitions of chimpanzee males are able to decrease the coalitionary strength of males from neighboring communities, as per the rival reduction hypothesis, this raises the question of why these attacks have also been observed to target adult females (see Marchant and McGrew commenting in Manson and Wrangham 1991). While female involvement in intergroup conflict has been observed to vary between populations, the killing of adult females also occurs in populations where females do not actively participate and is therefore not sufficiently explained by the rival reduction hypothesis (Boesch et al. 2008; Watts et al. 2006).

Furthermore, the female recruitment hypothesis proposes that lethal raiding benefits participating males via the recruitment of potential reproductive partners. This hypothesis would therefore predict that males would not target adult, sexually receptive females, but would rather predict attempts at affiliative behavior (Boesch et al. 2008; Watts et al. 2006; Wilson and Wrangham 2003). At Gombe, attacks on sexually receptive females were observed to occur less often than attacks on non-receptive females, but the question remains as to why females are attacked at all (Williams et al. 2004).

One possibility is that attacks on females may serve to weaken bonds between adolescent females and their mothers to induce the younger females to transfer communities and thus benefit the recruitment of females (Goodall 1986). A second possibility is that infanticide of the female's infant is the primary goal (Hiraiwa-Hasegawa and Hasegawa 1994), and a third is that aggression elicits mating with the female (Boesch and Boesch-Achermann 2000). However, there appears to be little evidence for such transfer of females after attacks (females transfer at adolescence due to female dispersal anyway), targeting of infants or post-attack mating (Williams et al. 2004). Of the adaptive explanations for lethal intergroup aggression in chimpanzees covered in this text, only the resource defense hypothesis offers an explanation for attacking adult females as it may be a way for chimpanzees to further induce a neighboring community to limit their use of certain areas or resources (Wilson 2013). If so, the killing of sexually receptive outgroup females should occur in cases where the potential expansion of territory provides greater reproductive benefits than the recruitment of a potential reproductive partner.

Further insight, into conditions influencing whether males should attack females in neighboring communities, is provided by a model that incorporates the degree of reproductive skew among males (Pradhan et al. 2014). When the highest-ranking male has priority of access to females, the addition of neighboring females to his community (while increasing birth rate) increases the number of females that have

overlapping periods of sexual receptivity. This in turn decreases the level of skew, as the dominant male(s) can no longer monopolize all females. Thus, high-ranking males should prefer to expand their territory, attacking females rather than tolerating them, whereas lower-ranking males can gain greater fitness benefits by tolerating new females. As the reproductive skew decreases, mating success is more equally distributed across males, and therefore both high- and low-ranking males benefit from fatal attacks on females. Current observations provide initial support for this model, but further data are required to test predictions in detail.

Influence of Human Disturbance

Critics of the adaptive interpretation of chimpanzee intergroup aggression have suggested that killing is merely incidental to intergroup aggression, exacerbated by human influences such as human encroachment (deforestation, hunting, etc.) and food provisioning by researchers (Power 1991; Sussman and Marshack 2010; Watts et al. 2006).

Several aggressive, territorial behaviors, including boundary patrols and intergroup killing, were first observed at Gombe and Mahale, contrasting with earlier reports from short-term studies at other sites that seemed to indicate peaceful chimpanzee communities with open membership (Goodall 1977; Goodall et al. 1979; Nishida 1968, 1979; Reynolds and Reynolds 1965; van Lawick-Goodall 1968; Wilson 2013). The Gombe and Mahale sites both used artificial feeding to facilitate observations, raising the possibility that the intergroup aggression was caused by food provisioning, rather than being part of a natural behavior repertoire (Power 1991). It was shown that provisioning impacted the chimpanzees' behavior, with increased aggression on days that food was provided, though this impact might not have extended to behavior away from the feeding station (Wilson 2013; Wrangham 1974).

This "human impact hypothesis" further expanded to include other human influences that could cause or increase aggressive behavior.

Human encroachment or disturbance of habitat (e.g., the conversion of forest into cropland) could affect intergroup aggression by increasing competition for the space available (Goodall 1977; Pusey et al. 2007; Wilson 2013). Poaching and human-transmitted diseases could decrease coalition sizes within a community and leave them vulnerable to attack (Goodall 1977; Pusey et al. 2007; Wilson 2013). However, since then, data from sites that were habituated without food provisioning do not support this “human impact hypothesis” and show that observed variations in rates of lethal aggression in chimpanzees were not explained by either provisioning by researchers or any other measured indication of human disturbance (Wilson 2013; Wilson et al. 2014). In fact, the highest rate of killing was observed at Ngogo, an unprovisioned and relatively undisturbed site (see Richard Wrangham commentating in Sussman and Marshack 2010). Current studies not only support the adaptive explanation of lethal coalitionary aggression as part of an evolved behavioral strategy but also indicate that the rate at which this behavior occurs is unrelated to the suggested human influences (Watts et al. 2006; Wilson et al. 2014).

Relevance to Human Warfare

Adaptive explanations of chimpanzee raiding as a natural behavioral strategy are central to the debate on the origins of human warfare (Gat 2006; van der Dennen 1995; Wilson 2013). It is often cited as evidence against the argument that war is a relatively recent cultural invention, originating within the past 12,000 years (Ferguson 2011; Gat 2015; Otterbein 1999).

The imbalance of power hypothesis predicts that lethal coalitionary attacks should occur in species where intergroup conflict is beneficial to reproductive success, party sizes are variable (facilitated by fission-fusion sociality in chimpanzees), and individuals form long-term coalitionary bonds (Glowacki et al. 2017; Wrangham 1999; Wrangham and Glowacki 2012). Human hunter-gatherer societies generally display coalitionary bonding between males, a fission-fusion social

system, and may often have hostile relationships with neighboring communities (Glowacki et al. 2017; Heinz 1972; Wrangham 1999; Wrangham and Glowacki 2012). Hunter-gatherer conflict often involves low-risk, coalitionary attacks on strongly outnumbered members of a rival community (Glowacki et al. 2017). These raids are performed by groups of men, who leave their territory with the intent to ambush, or otherwise surprise, small groups (Gat 1999), after which, the raiders quickly retreat to their own territory (Glowacki et al. 2017). They are relatively low-risk to the raiding party, though some injuries can occur (Chagnon 1997; Glowacki et al. 2017). Intergroup conflict appears to allow these male coalitions to defend and increase resources (e.g., territory and food) crucial to their reproductive success, as is thought to be the case for chimpanzees (Wilson 2013; Wrangham and Glowacki 2012).

Despite these similarities, several key differences distinguish raiding behavior in humans and chimpanzees. The use of weaponry, such as bows, clubs, and spears, introduces an unpredictability to the imbalance of power and therefore affects the potential cost of lethal raiding (Boesch et al. 2008; Kelly 2005). During surprise attacks on unarmed individuals, weaponry can greatly amplify the difference in instantaneous fighting ability and further reduce the cost of killing (Pandit et al. 2016). However, if an attacked individual also has access to weapons, they may seriously injure or kill members of the attacking coalition (Glowacki et al. 2017; Kelly 2005), greatly increasing the cost relative to chimpanzee raiding. Humans can also affect the imbalance of power through the strategic use of terrain, deception, and other relatively complex tactics (Wadley 2003).

The origin of human warfare is too complex to determine from chimpanzee data alone, but the similarities between the two species support the view that warfare in humans is a behavioral strategy by which coalitions of males increase their fitness as a result of defending and expanding relevant resources (Glowacki et al. 2017; Wilson 2013). War is likely not caused by a single instinct but is facilitated by several evolved psychological traits, such as xenophobia and parochial altruism

(Glowacki et al. 2017). As a result, the frequency and methods of warfare are heavily influenced by cultural differences, technological advances, and political and economic relations. Unlike chimpanzees, who can only benefit from intergroup interactions at the expense of the other party (e.g., by taking over parts of their territory), human intergroup interactions are not always a zero-sum game (Wilson 2013). Humans can trade with neighboring groups as an alternative, peaceful strategy to obtain their resources with a potentially lower cost than warfare.

It is important, therefore, to emphasize that the possibility of a biological basis for warfare in humans does not mean that this behavior is inevitable or even justifiable (Glowacki et al. 2017; Wilson 2013). There is no reason to believe that warfare cannot be reduced or even eliminated (Glowacki et al. 2017). Whether it is cultural or biological in nature, intergroup aggression is only a viable strategy if the benefits outweigh the costs. Throughout history, political institutions have increased the cost of violence and facilitated peaceful interactions within a certain region (e.g., a nation) and pushed warfare to the borders of that region (Glowacki et al. 2017). These zones of peace have expanded from small regions of allied communities to the borders of a single nation to large regions of friendly nations, such as the European Union. By expanding such regions in which the costs of warfare and/or the benefits of peaceful, mutually beneficial interactions are increased, global peace could be a practically achievable goal.

Conclusion

Current evidence indicates that the coalitionary killing of intergroup conspecifics in chimpanzees is an adaptive behavior facilitated by fission-fusion dynamics, resource defense polygyny, and male philopatry. The adaptive explanations presented in this text are not mutually exclusive and a combination of factors are likely to interact. For instance, fission-fusion dynamics and male philopatry create

opportunities in which the imbalance of power is such that coalitions of males are able to kill members from other communities with little to no risk of incurring serious injuries. The imbalance of power therefore makes it strategically viable for chimpanzee males to reduce the coalitionary strength of a neighboring group. This could be necessary for territorial expansion (Mitani et al. 2010; Watts et al. 2006), which, in turn, could increase their access to fertile females (Manson and Wrangham 1991). Contrary to the human disturbance hypotheses, lethal aggression in chimpanzees appears to be part of their naturally evolved behavioral repertoire. While raiding in human hunter-gatherer societies may have had a similar adaptive function, there is no reason to believe that warfare in humans is unavoidable.

Cross-References

- [Competition Between Groups](#)
- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Evidence of Intentional Killing](#)
- [Humans: Between-group Conflicts](#)
- [Nonhuman Primates: Between-group Conflicts](#)

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Chimpanzee Sexuality

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Chimpanzees (*Pan troglodytes*) are highly intelligent animals whose sexual behaviors occur in the context of a complex social environment: Chimpanzees live in multi-male, multi-female communities that can range in size from <10 to approximately 200 members. These communities exhibit a fission-fusion dynamic, where all community members are rarely, if ever, together at the same time; instead, individuals range and forage in fluid sub-groups whose composition changes over the course of hours or days (Goodall 1986; Nishida 2012). Males and females compete for rank in separate linear dominance hierarchies; all adult males are dominant to all adult females (Hayaki et al. 1989; Takahata 1990; Pusey et al. 1997; Muller 2002). Mating is promiscuous, paternity certainty is low, and there is no evidence of direct paternal care (Goodall 1986). Because infanticide by males is sometimes observed, promiscuous mating is most often interpreted as a female strategy to decrease paternity certainty and avoid infanticide.

Female sexuality in chimpanzees is characterized by swelling of a specialized anogenital sexual skin for a portion of the ~35-day ovarian cycle, which is also associated with behavioral estrus (Tutin 1979; Goodall 1986). Full swelling lasts for an average of 12–13 days but can vary with age and among populations (Wallis 1997;

Deschner et al. 2003; Matsumoto-Oda et al. 2007; Thompson 2013). These swellings are hormonally mediated: rising estrogen during the follicular phase leads to tumescence, while detumescence is triggered by progesterone in the luteal phase, following ovulation (Graham 1981; Dixson 1983).

Young females typically exhibit their first swelling around age 8, but these initial swellings are small and do not elicit attention or mating from adult males (Pusey 1990). Females are considered sexually mature upon their first mating with an adult male. However, they may then experience a period of adolescent sterility, cycling and mating for a period of years before conceiving. Juvenile and even infant males may play thrust and mount toward their peers and estrous females. Males show marked testicular growth and began ejaculating around age 9 but do not typically sire offspring until they are at least 12 years old (Pusey 1990).

In parous females, swelling resumes after a period of post-partum amenorrhea. Females are most attractive to males and receptive to mating during maximum tumescence, which corresponds approximately to the periovulatory period (Deschner et al. 2003, 2004; Emery and Whitten 2003; Emery Thompson 2005). Successive swellings tend to increase in size approaching conception, and males are also sensitive to this inter-cycle variation, mating more during the conception cycle (Deschner et al. 2004; Emery Thompson and Wrangham 2008). Female attractiveness increases with both age and parity, suggesting that males are most attracted to females with proven records of maternal care (Muller et al. 2006). High-ranking males are most likely to mate when the chance of conception is highest, while females may use proceptive behaviors outside of the periovulatory period to secure mating opportunities with lower-ranking, younger males and avoid monopolization by the alpha (Nunn 1999; Stumpf and Boesch 2006). Post-conception swellings may also occur, most frequently early in gestation, and females may mate during these swellings, but their functional significance is poorly understood (Wallis and Lemmon 1986; Wallis and Goodall 1993).

Female proceptive behaviors include grooming with males and presenting their swelling for inspection. Males inspect sexual skins, both swollen and non-swollen, by directly sniffing or by sniffing a finger that has been inserted into the vulva (Nishida 1997). These inspections may allow males to assess the fertility of a given female (Wallis 1992). Females may occasionally display proceptive behaviors more typical of males, such as a branch-shaking, to attract the attention of a desired mate (personal observation).

Males use a variety of courtship behaviors to solicit matings from sexually receptive females, including shaking branches, bipedal walking, piloerection, stomping or pounding on the ground or tree roots, and penile displays, which consist of the presentation of the erect penis, often in combination with a flicking motion (Goodall 1986). Copulation occurs with the male squatting behind the female, who crouches and lifts her swelling to facilitate intromission. Males may also use aggressive coercion, both at the time of mating and during non-swollen periods, to increase their mating success (Muller et al. 2007, 2010; Feldblum et al. 2014). Forced copulation has also been recorded (Goodall 1986). Males may attempt to restrict other males from mating by interfering in copulations or aggressively mate guarding an estrous female when the pair is in a larger group (Wroblewski et al. 2009). In a more extreme manifestation of mate guarding, pairs can also form consortships, leaving the group to range alone for a period of hours to months (Tutin 1979). Consortships lead to exclusive mating by one male and, as such, are often resisted by females, who may be aggressively coerced into leaving the group with a single male. Alpha males have the highest reproductive success during their tenures, but lower-ranking males sire a larger-than-expected proportion of offspring, suggesting that alternative strategies such as consortships and sneak copulations are also effective (Wroblewski et al. 2009). Because females often mate with most or all community males during a single cycle, sperm competition is high, and males have relatively large testicles (Tutin and McGinnis 1981; Hasegawa and Hiraiwa-Hasegawa 1990).

Chimpanzee sexuality is perhaps best understood as a set of male strategies for monopolizing females and the counter-strategies used by females to avoid monopolization. New lines of evidence add nuance to this picture, suggesting that females are more likely to conceive with unrelated males and that sires may recognize and bias behavior toward their own offspring.

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Choice of Sides

- [Robert Kurzban on Group Processes](#)

Chomsky and Language Evolution

- [Noam Chomsky and Linguistics](#)

Cinderella Effect, The

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Synonyms

[Discriminative parental solicitude](#); [Familial violence](#)

Definition

The increased prevalence of mistreatment, both lethal and nonlethal, of children by a biologically unrelated step-parent, compared to by a genetically related parent.

Introduction

Cross culturally, folklore and fairytales have portrayed step-parents as menacing and potentially life threatening to their unrelated offspring. Over the last 30 years, a body of literature has demonstrated that this portrayal is, in fact, reflected in the real world as a significantly increased risk for the child of an unrelated parent to be a victim to child abuse and homicide, a phenomenon referred to the *Cinderella Effect* (Daly and Wilson 1999). An evolutionary explanation of this fictional phenomenon, based on kin selection theory (Hamilton 1964) and the subsequent Hamilton's Rule, predicts that a lack of shared genes between a step-child and parent will discourage altruistic behavior and investment in this offspring.

Child Abuse

Kin selection theory is based on the idea that individuals having shared genes are more likely to invest in one another and display altruistic behaviors. For example, parents sharing the same genes as their biological children are more likely to interact with them in a healthy and positive manner. It should be expected that step-relationships would experience this same need to build relationships between one another. However, research has consistently found that these step-relationships involve less investment (by step-parents), tend to be more conflictual, and are less satisfying compared to the relationships between genetic parents and children (Wilson and Daly 1987). Step-parents are less likely to experience the need to invest in their step-children because they do not share the same genes. They tend to prefer their own biological children in any given situation. According to Daly and Wilson (1988), “genetic relatedness is a predictor of reduced conflict and enhanced cooperation because the genetic posterities of blood relatives covary (are promoted by common exigencies) in direct proportion to their degree of relatedness” (p. 519).

Violence towards non-kin, depends as evaluated through the occurrence of physical child abuse, exemplifies the discrepancy between kin-driven altruism for related and unrelated parents. Using over 20,000 reports of child abuse from the American Humane Association, Daly and Wilson found that “a child under three years of age who lived with one genetic parent and one stepparent in the United States in 1976 was about seven times more likely to become a validated child-abuse case in the records than one who dwelt with two genetic parents” (Daly and Wilson 1999, p. 27). This finding was further supported through research on child abuse in Canada, England, Sweden, and Korea, all of which provide evidence for trends of increased likelihood of abuse at the hands of a step-parent (1999).

Infanticide

Based on Hamilton’s Law, investment in a genetically unrelated offspring involves high costs, without associated inclusive fitness benefits. Those costs additionally create direct competition with the prospects and resource access for one’s own (genetically related) offspring. In some cases this can lead to the killing of an infant, or infanticide, which has been documented in both human and nonhuman contexts. A male African Lion, for instance, upon gaining access to a pride of potential female mates, will kill the female mate’s previous offspring. This behavior promotes the reproductive success and efficiency of their own reproduction.

The prevalence of infanticide among non-related parents and offspring has been evaluated in humans as well, with research finding that it is significantly more likely to occur when parent and offspring are unrelated. An early study of the homicide of infants in England, finding that a significant (and disproportionate to the general population) number of these killings was in fact committed by step-fathers (Scott 1973). This trend was more broadly supported by Daly and Wilson (1988), who found that

coresiding step-parents were about 70 times more likely to kill a child under two, compared than a genetic parent.

There are also other aspects influencing rates of infanticide: the mother’s age and marital status. According to the hypothesis proposed by Daly and Wilson (1988), younger women are more likely to engage in infanticide compared to older women. Burgos and McCarthy (1984) found that women (ages 15–19) were more likely to commit infanticide among the Ayoero Indians. Daly and Wilson (1988) also found similar findings in Canada; infanticide was more frequent among younger women. Marital status also influences the rates of infanticide. Women that were not married were less likely to deliver babies (approximately 12%), but they also accounted for a higher percentage of reported infanticides (Daly and Wilson 1988). Both of these variables interact with each other; younger women that are unwed are most likely to commit infanticide.

Discriminative Parental Solitude

Ornithologist Harry Power (1975) found that nonrelated Mountain Bluebird males would differentially refuse to feed the prior offspring of their mates, for which there was a discrepancy between parental investment based on the amount of shared genes. This selective investment can have similar consequences in the dynamics of human step-families, creating sentiments of less love and affection from both the step-child and step-parent, as well as a higher rate of conflict within the marriage over issues of children and resources.

These issues do not stem from the desire of step-parents to intentionally harm their step-children, according to Daly and Wilson. As mentioned above, step-relationships are less likely to have the same levels of affection and commitments as genetically related relationships (Wilson and Daly 1987; Doberman 1998). Step-parents also are less likely to experience the same type of emotions regarding unreciprocated

parental investment compared to genetically related parents (Daly and Wilson 1996). For example, these differences could contribute to explanations as to why step-parents may react violently toward step-children; the emotional barriers to violence are less strong.

Cross-References

- Familial Violence
- Kin Selection Theory
- Martin Daly and Margo Wilson (Founders of Evolutionary Psychology)
- Parent-Offspring Conflict

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Circadian Rhythm

- Sleep-Wake Cycles

Circumcision

- Genital Mutilation

Circumventing Mate Choice

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Synonyms

Mate guarding; Mate rejection; Mating sabotage; Relationship dissolution; Romantic rejection; Sexual rejection; Stalking

Definition

Disregarding or obstructing the sexual or romantic decisions of others or disregarding one's own previous mating decisions

Introduction

Mate choices fall into several different categories. One can choose a partner for sexual relations only, for a short-term non-committed liaison, for a short-term committed relationship, or for a long-term uncommitted or committed relationship. When an individual makes an overture to form or continue a relationship, the other can choose whether to accept or reject them for the proposed interactions, and an outsider can interfere with the process. Kelly et al. (2016) suggested that all the behaviors seen within human mating contexts could be classified along a continuum. The proposed spectrum ranged from active rejection (purposefully preventing mating attempts), followed by indifferent rejection (e.g., not selecting a partner), then mate selection (selecting and obtaining a

partner), and finally to mate retention (retaining the partner). The act of circumventing mate choice can occur at any of these relationship stages, including within existing or established relationships or during the first advances. It can involve denying mating attempts by a potential or actual partner or obstructing the attempts of peers, kin, partners, or a desired individual to mate with others.

Circumventing Mate Choice in Early Courtship

Mate rejection is easier in the early courtship phases, prior to a relationship being established (discussed in Kelly et al. 2016). At this time, one can circumvent the mate choices of others by simply denying potential partners access to their time or body (including their friendship or companionship), thereby circumventing sexual or romantic advances. Methods used to circumvent mate choice at this stage might involve avoidance, verbal rejection, physically stopping mating attempts (e.g., pushing, kicking, punching, assuming a fetal position), threats (similar to those seen in Kelly et al. 2015), and taking refuge among friends or family (discussed in Smuts 1992; for full discussion of potential mating avoidance strategies, see Duntley and Shackelford 2012).

On the flip side, a potential suitor might circumvent the mate choices of their target mate by obstructing the target's attempts to partner with someone else. In this situation, the perpetrator might use methods that include stalking, intimidation, and threats in an effort to isolate and coerce their chosen mate into a relationship or liaison (see discussion in Duntley and Buss 2012).

Parents, family, and friends can also circumvent mate choices, by disallowing their kin or friend to become sexually active or partnered with an individual that they deem inappropriate (Perilloux et al. 2008; discussed in Duntley and Buss 2012; see also Smuts 1992). The methods used by kin in these early stages can be physical (e.g., chaperoning or disallowing one-on-one contact, physically attacking the suitor), verbal (e.g.,

threats), and social (e.g., shaming or damaging the social standing of the suitor).

Circumventing Mate Choice in Existing Relationships

Circumventing mate choice is still possible even after mating decisions have been made: from the moment the relationship is established to within a deeply committed long-term relationship. Within a relationship, one partner can circumvent the mate choice of the other simply by denying copulation. Here, even though a mate choice has been accepted (by entering the relationship), a partner can still exercise control over his or her own mating and potential conception.

Terminating the relationship would also circumvent a previously established mate choice and can lead to genuine evolutionary challenges for the rejected party (Perilloux and Buss 2008) as well as the rejecter (Kelly et al. 2015; see also Kelly et al. 2016). Furthermore, established partners may circumvent their previous mate choice by remaining in a relationship yet engaging in extra-pair mating (e.g., infidelity). In this way, an individual can disregard their partner and any commitment of exclusivity they may have made to them and obtain additional sexual or romantic companions.

In response to this threat, couples may restrict the extra-pair mating attempts of their partner by engaging in various mate retention strategies. As established by Buss (1988; see also Miner and Shackelford 2010; McKibbin et al. 2007), these strategies might include positive approaches like kindness, helpfulness, and gift giving or unsocial strategies including exercising physical control (e.g., using violence) and emotional control (e.g., using threats or belittling the partner's self-esteem so that they will not seek alternate mates) or controlling their partner's time (e.g., booking out their schedule so that they cannot be apart or able to stray). Mate guards might even stalk their partner (e.g., following them, monitoring their social and online interactions; see discussion in Duntley and Buss 2012). Using these techniques, one partner might circumvent the

extra-pair mate choices of the other by restricting their ability to acquire another mate, gain access to that mate, or copulate with them.

Conclusion

It is possible to circumvent the mate choices of others in many different ways. One can avoid the advances of both potential and actual mates and can block the attempts made by peers, kin, or a desired entity to mate with others. One can even circumvent their own mating choices by engaging in mate rejection or extra-pair mating. The partners of these individuals might try to prevent their mate from leaving or cheating by engaging in various mate retention strategies, thereby circumventing their partner's new mate choices.

Cross-References

- [Daughter Guarding](#)
- [Direct Guarding](#)
- [Prevention of Infidelity](#)
- [Relationship Dissolution](#)
- [Violence](#)
- [Violence as Coercive Control](#)

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Civic Commitment

- [Civic Duty](#)

Civic Duty

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Synonyms

[Civic commitment](#); [Civic engagement](#); [Civic involvement](#); [Civic obligation](#); [Civic participation](#); [Civic responsibility](#); [Community interest](#); [Community involvement](#); [Community participation](#); [Political interest](#); [Social responsibility](#)

Definition

Social norms that produce a feeling of obligation to provide help or to grant the requests of others in the belief that the common good is thereby served; an action or responsibility expected of every member of a society.

In a society or community, in order to establish the well-being of their surroundings, people tend to act not only to pursue personal interests but also to pursue collective interests shared by the whole group. Generally accepted examples of civic duty include obeying laws, serving on juries, paying

taxes to the government, being active about politics, voting in elections, and doing volunteer work. Individuals with greater sense of civic duty tend to exhibit more civic participation and activities.

The Socialization of Civic Duty

According to political socialization theory (Steintrager 1968), which tries to explain how, when, and through what agencies individuals learn their political behavior, family constitutes one of the most important agencies regarding the establishment of individual's civic duty. Parents pass on the content and meaning of civic duty to their offspring through behaviors and discussions in the regular life. Children learn about the civic participation by observing their parents' actual engagement in civic activities and by listening to what they are talking about politics and current events (Zaff et al. 2010).

Political socialization can be regarded as a replication model in which adolescents simply copy norms and understandings of civic duty from the former generation. Research supported the frequency of parent-adolescent political discussions which could powerfully predict adolescents' civic involvement. For example, with a sample of 5579 adolescents coming from 7 countries, the study (Flanagan et al. 1998) indicated that family socialization on social responsibility could produce a significant effect on adolescents' public interest. Another study found that individuals growing up in homes where they discussed current events with their parents and saw parents taking part in civic activities tended to engage more in political activities (Brady et al. 1995).

However, some researchers argued this theory ignored the impact of ecological environment, which influenced the forming of adolescents' opinions and active role in interpreting the given rules (Zaff et al. 2010). Consist with this opinion, recent studies found mothers' observed civic duty information in terms of following the rules and obeying laws correlated negatively with adolescents' attitudes on engaging in social movement activities. This result supported the active role of

adolescents' in the political socialization (Oosterhoff and Metzger 2016).

In fact, developmental systems theories, which emphasize the collective contribution of genes, environment, and epigenetic factors on developmental processes, proposed that there was an interaction between adolescents' behaviors and beliefs about civic duty and their ecological context. Adolescents' opinions about civic duty are plastic, which could be shaped or modified by the experience or information they receive from the environment.

This viewpoint has been supported by quite a few studies. In addition to parents, discussion with peers or teachers on politics and social events could produce significant effects on adolescents' civic behaviors, attitudes, and skills (Andolina et al. 2003). And peers may shape each other's civic duty beliefs by exchanging thoughts and sharing civic experiences (Oosterhoff and Metzger 2016). Actually the influence coming from the environment could be explained in terms of the power of social norms. Research (Flanagan et al. 1998) indicated that in order to identify with peers, specific groups, and institutions, adolescents would take part in voluntary work and student solidarity at school.

Factors Influencing Individual's Civic Participation

Individual's notion about civic duty is relatively stable, but the age effect is still obvious across the life span. High school students always exhibited a higher level of civic volunteering than young adults (Kirby et al. 2011). The level of civic engagement decreased generally in the transition out of high school (Malin et al. 2017), and civic participation among young adults was lower than other age groups (Twenge et al. 2012). The civic involvement would increase at roughly age 26 (Snell 2010).

In addition, due to the limitation of cognitive abilities, young person usually could not completely understand the abstract meanings of civic responsibility and the consequences of one's action on others' until the early adult years. Their

understanding of civic duty continues to increase throughout the whole life. Apart from cognitive abilities, age can also have indications for fulfilling civic engagement (Tsai et al. 2009). For example, problems that come along with aging can reduce the amount of social engagement. Depression, illiteracy, cognition impairment and other issues can all be risk factors of poor social engagement in old groups. Despite all this, researchers usually believe that higher levels of social engagement are associated with wellbeing and longer survival in the elderly (Kiely and Flacker 2003).

In addition to age, other demographic variables also contribute to individual's civic involvement, for instance, in comparison with people who didn't attend college, those who did demonstrated higher levels of civic involvement initially and over time. In addition, research (Flanagan et al. 1998) also demonstrated females were more likely than males to be engaged in voluntary work.

Conclusion

Family and peer norms play important roles in the formation of individual's civic duty. Across the life span, individuals would show different levels of civic involvement at different life stages.

Cross-References

- Norms
- Peer Feedback and Norms
- Peer Groups

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Civic Engagement

- Civic Duty

Civic Involvement

- Civic Duty

Civic Obligation

- Civic Duty

Civic Participation

► [Civic Duty](#)

Civic Responsibility

► [Civic Duty](#)

Civil Archives

► [Public Records](#)

Civil Documents

► [Public Records](#)

Civil Records

► [Public Records](#)

Civilization

► [Decline of Violence](#)

Civilization Division

► [Guns, Germs, and Steel](#)

Civilized Norms

► [Evolution of Teaching](#)

Clan

► [Birthrights and Bloodlines](#)

Classical Conditioning

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Synonyms

[Associative learning](#); [Learning through associations](#); [Pavlovian conditioning](#); [Reflexive conditioning](#); [Respondent conditioning](#)

Definition

Classical and/or Pavlovian conditioning constitutes an automatic learning process that arises through the acquisition of an association between two stimuli. Through the acquisition of a classically conditioned association, a stimulus that prior to learning did not induce any particular response obtains the ability to induce a response that is qualitatively similar with the one that a biologically significant stimulus induces.

Introduction

Pavlovian and/or classical conditioning is a type of associative learning that involves the formation of new behavioral responses through the acquisition of new associations. Specifically, during the course of classical conditioning, an organism adjusts in response to the detection of sequential relationships between stimulus of environmental and/or proprioceptive nature (McSweeney and Murphy 2014). Classical conditioning has been discovered and methodologically described by a Russian physiologist named Ivan Petrovich Pavlov. This type of learning is named “conditioning” since its inventor, I. P. Pavlov, used the

term conditioned reflex to label and designate the learning outcome (Schachtman 2011). I. P. Pavlov assumed that new reflexive responses can be developed through the acquisition of classically conditioned associations between neutral stimuli, that is, stimuli which originally do not induce any particular response, and unconditioned stimuli, that is, biologically relevant stimuli which reflexively evoke an unconditioned response (Spence 1978). Through the acquisition of a classically conditioned association between a neutral stimulus and an unconditioned stimulus, the first turns into a conditioned stimulus and acquires the capacity to induce a conditioned response that is qualitatively similar to the unconditioned response (McSweeney and Murphy 2014). I. P. Pavlov examined various reflexes, yet his most widely known experiments revolved on responses to food. Even though early researchers in the fields of both human associative memory and behaviorism had studied mechanisms that nowadays would be considered to be similar to the ones that I. P. Pavlov described, I. P. Pavlov was the first who officially and methodologically described and designated the process of classical conditioning in the scientific community through the publication of conditioned reflexes in 1927 (Spence 1978).

The Study of Gastrointestinal System and its Role in Classical Conditioning

I. P. Pavlov discovered the associative mechanism of classical conditioning accidentally while examining the physiological processes of the gastrointestinal system. Specifically, I. P. Pavlov was examining the alternations of dogs' saliva and digestive fluid secretion through their mouth and stomach while feeding. At some point, during the experimental procedures that I. P. Pavlov set in order to observe the alternations of dogs' saliva and digestive fluid secretion in response to feeding, he observed that the subjects' (i.e., dogs) saliva and digestive fluid were also secreted every time he and his associates arrived in the laboratory. Consequently, I. P. Pavlov decided to experimentally examine the mechanisms and functional structures that let the dogs secrete saliva and digestive fluid in his presence as well,

rather than exclusively to the presence of food in response to which the dogs reflexively and automatically secrete saliva and digestive fluid (Spence 1978).

I. P. Pavlov and his associates systematically and methodologically administered for several times a neutral stimulus (i.e., sound of a bell) to the dogs just before they were presented to their usual food, that is, a meat powder. When this trial was conducted numerous times, I. P. Pavlov and his associates observed that the dogs were also secreting saliva and digestive fluid when the stimulus of the sound of the bell was administered alone, that is, in the absence of food (Shanks 1995). Ultimately, I. P. Pavlov came to the conclusion that the constant pairings of the sound of the bell and the food resulted in the formation of an association between the sound of the bell and the food. Specifically, the sound of the bell which at the beginning was neutral stimulus, a stimulus that does not elicit a response, acquired the capacity to elicit a response that is qualitatively similar to the one that the food naturally and automatically elicits. The dogs' response became classically conditioned and respectively the sound of the bell turned into a conditioned stimulus. Consequently, the new response that was learned as a reaction to the sound of the bell is termed a conditioned response (Schachtman 2011).

The Evolution of Classical Conditioning

The theory of classical conditioning has considerably evolved after the work of I. P. Pavlov in conditioned reflexes. The initial model of classical conditioning was operationally and theoretically elaborated by the work of several learning theorists in the USA. Specifically, theorists in the field of learning in the USA formed different techniques for assessing the functional qualities of associations between conditioned stimuli and unconditioned stimuli. In addition, they also found new conditioning processes and reinterpreted the fundamental processes of the conditioning that became known through the procedures that I. P. Pavlov proposed (Wills 2012).

A considerable factor that let to substantial modifications of the initial theory of classical conditioning is the integration of cognitive functions

in it. Specifically, even though the work of I. P. Pavlov on conditioned reflexes was widely spread in the USA, it received a considerable amount of criticism in 1950. Most of the criticism on his ideas was expressed in 1950 by the well-known Polish neurophysiologists named Jerzy Konorski and Stefan Miller. Jerzy Konorski and Stefan Miller initiated the primary cognitive conceptualization of respondent conditioning. Their work constitutes the precursor of the well-known and highly influential Rescorla–Wagner model of classical conditioning (McSweeney and Murphy 2014). In addition, at the same period, the psychiatrist Joseph Wolpe as well as the psychologists John Watson developed treatment plans that were based on the principles of classical conditioning so that to change dysfunctional behaviors into functional ones. This attempt to apply learning principles in the development of clinical interventions became known as behavioral modification and significantly increased the use of such interventions by psychiatrists and psychologists (Staddon 2014).

The theoretical conceptualization of classical conditioning has significantly changed with the introduction of the Rescorla–Wagner model in classical conditioning in 1972 (McSweeney and Murphy 2014). The Rescorla–Wagner model proposes that while living beings interact with their environment, develop causal expectations that enable them to estimate the relationships between environmental conditions. According to this model, learning involves acquiring knowledge related to the way that the environment is causally organized. Specifically, an organism becomes able to achieve learning by developing solid associations between environmental components (Rescorla 2008). Yet even if the environmental components become contiguous and in turn organisms form associations between them, the environmental components need to also allow the acquisition of knowledge related to causal relationships. In other words, the fundamental idea is the concept of contingency and how an organism perceives it (McSweeney and Murphy 2014). This model by integrating cognitive elements within the formation of associations indicated the acceptance of both cognitive functions

and associative processes in the brain, something that quickly earned the favor of experimental psychologists (Klein and Mowrer 1989).

Even though living beings sometimes form conditioned associations based only on a conditioned stimulus-unconditioned stimulus contiguity, there are numerous cases in which learning appears to enable living beings to anticipate the presentation of the unconditioned stimulus due to the presentation of the conditioned stimulus. In such cases, learning takes place through a contingency relationship that is probabilistically manifested (McSweeney and Murphy 2014). For instance, when the likelihood of the unconditioned stimulus being presented is equal with the likelihood of the conditioned stimulus being and not being presented, the conditioned association cannot be achieved. In contrast, when the likelihood of the unconditioned stimulus being accompanied by the conditioned stimulus is higher than the likelihood of the unconditioned stimulus being presented in the absence of the conditioned stimulus, a conditioned association could be achieved. For that reason, respondent conditioning is considered to reflect the ability of living beings to identify and learn possible associations between signals and important environmental conditions (Staddon 2014).

Nowadays, respondent conditioning is viewed as a multifaceted associative mechanism that involves many types of responses, rather than involving only glandular and visceral reactions, as it was initially considered. Respondent conditioning among other factors also relies on how relevant is the conditioned and the unconditioned stimulus, the appearance of other stimuli while conditioning takes place, and the degree of surprise that the unconditioned stimulus evokes (McSweeney and Murphy 2014). In addition, the evolution of the connectionist framework that models human cognition revived the attention in respondent conditioning as a productive technique for the study of associative learning. Therefore, nowadays, classical conditioning is most accurately defined and designated by its procedural method, which encompasses the preservation of firm control over the presentation of stimuli (Shanks 1995). In addition, it is highly

important to take into consideration that the principles that accurately differentiate classical conditioning between other forms of associative learning, such as operant conditioning and associative memory, are limited. Specifically, classical conditioning is most accurately differentiated by the extent to which the form of the conditioned response is determined by the choice of the unconditioned stimulus. Furthermore, a classically conditioned response is usually unaffected by instrumental contingencies. For example, pigeons cannot be easily prevented from pecking (conditioned response) at a separate key light (conditioned stimulus) which was paired with food (unconditioned stimulus) even if pecking stops the distribution of food (Wills 2012).

The Discrepancy Between Unconditioned and Conditioned Responses

I. P. Pavlov proposed through his work on conditioned reflexes that the same response that was elicited by an unconditioned stimulus could also be elicited by a conditioned stimulus through its association with the unconditioned stimulus (McSweeney and Murphy 2014). However, it quickly became clear that conditioned responses are of lower intensity than unconditioned responses. In addition, research related to classical conditioning after I. P. Pavlov's work has reliably proposed that the unconditioned response and the conditioned response are not the same responses, but they are usually qualitatively similar. Specifically, it has been cited that I. P. Pavlov's dogs did not confuse the sound of the bell with the meat powder, but they actually responded to the association among the sound of the bell and the meat powder which has consistently been presented right after the sound of the bell (Ramnero and Torneke 2011). In addition, the unconditioned response as well as the conditioned response is not limited to the secretion of saliva and digestive fluid. Specifically, the secretion of saliva and digestive fluid constitutes just a part of a multifaceted response through which the dog's body is being prepared for obtaining the meat powder (Staddon 2014).

Classical conditioning enables environmental components and/or conditions to acquire a

physiological capacity that did not have before. In other words, an environmental component and/or a condition that possessed other functions or none now acquires a new function, an acquisition that has adaptive significance for any species. Specifically, classical conditioning provides to a living being the chance to alter its behavior and thus increasing its capacity to adapt and survive (Ramnero and Torneke 2011). For example, a kid might jump on a road full of cars, lacking the association between such situations and threat. However, the kid possesses a physiological system that responds to specific unconditioned stimuli such as abrupt cries, screams, and violent acts with an unconditioned response of fear. In a plausible scenario where his/her mother or his/her father responds with a loud scream or exhibits a violent act when the kid tries to jump on the road, the road and/or other relevant stimuli would acquire qualitatively similar functions with the unconditioned stimulus of a loud scream, enabling the road and other relevant stimuli from then on (conditioned stimulus) to induce a conditioned response of fear. The acquisition of this new association would enable the kid to alter his/her behavior when it comes to a crowded road. A further example that depicts the way that classical conditioning could enhance the capacity for adaption and survival is a woman who is attacked on a remote parking place. One month later she goes to the same parking place and she begins to feel dizzy, chest pains, numbness in the hands, and a sense of terror and as a result she immediately leaves the place. In this scenario, the woman became classically conditioned to a previously neutral stimulus (remote parking) which has now induced a physiological response of fear due to its association with the unconditioned stimulus of assault, leading the woman to leave immediately from the remote parking and avoid a possible future attack (McSweeney and Murphy 2014).

The Relationship between Basic Affects and Conditioned and Unconditioned Responses

Human beings are endowed with a variety of responses and the environmental conditions in which they are induced rely on the individual's

learning history. A person's affective reactions of happiness, anger, or fear are governed by many factors. These affective reactions are not completely biologically endowed to humans, but they are formed to a high extent through the individuals' specific environmental experiences (Baum 2017). Meanwhile, it has been consistently cited that features of these affective reactions appear in people universally despite culture and ethnic variations. In addition, a significant amount of research proposes that people inherit either a small number of basic affects or a number of emotional mechanisms that are induced inevitably under specific conditions (Ramnero and Torneke 2011).

In 1870s, Charles Darwin proposed that human beings as well as other living beings are endowed with a set of basic affective responses that assist them to survive (Thines). Today, the research community did not reach a consensus when it comes to the exact amount of these basic affects and the responses that each one of them consistently induces, yet researchers agree that disgust, anger, sadness, fear, and joy constitute basic affects (Baum 2017). Each one of these basic affects is facially expressed in a specific way that is easy to be observed especially on the face. In addition, the basic affects could also be differentiated through the biological reactions they induce (Ramnero and Torneke 2011). Moreover, basic affects have the potential for certain types of behaviors and/or the predisposition for specific types of actions. For example, once an individual experiences the affect of fear her/his heart rate increases, specific muscles are stimulated, as well as blood flow is altered (Baum 2017). This sequence is considered to be an integral part of the basic affect of fear. For example, by the time an individual perceives that she/he is experiencing fear, her/his body had already activated biochemical reactions so that to prepare her/him for certain kind of actions such as fight or flight. In other words, the basic affective reaction of fear prepares humans for instant acts so that to be able to survive hazardous situations. Similarly, the basic affect of disgust prepares the body so that to move away from unwanted as well as dangerous smells and tastes such as poisonous food, and

anger entails bodily preparation for an attack. That is, by the time an individual perceives that she/he is experiencing anger, her/his body had already been prepared to attack (Thines 1987).

Affective Responses that Are Governed by Unconditioned Responses

Research related to classical conditioning has consistently suggested that affective responses are governed by unconditioned responses that have been shaped through evolutionary history so that to help humans to adapt and survive (Baum 2017). However, the research related to the mechanism and/or conditions (unconditioned stimulus) that induce such affective responses has not been yet fruitful. Specifically, the majority of research studies have included adults as participants, yet an adult person plausibly has a lengthy history of learning (McSweeney and Murphy 2014). However, it has been consistently cited that there are numerous stimuli that are not learned, yet induce a response of fear. Such stimulus includes sounds of high intensity, objects getting near fast, loud noises, and specific facial expressions of other individuals (Ramnero and Torneke 2011). Through the lens of an evolutionary perspective, it is not plausible to presume that there is just one kind of stimulus that is able to induce, for instance, fear or anger. That is, if these emotional responses ought to enhance adaption, and thus help an organism to survive, they must be triggered in numerous settings, yet the discrepancy between the stimulus would not have to be very high to have an influence early in a person's life (Baum 2017).

Classical Conditioning and Emotional Functioning

Classical conditioning could be used to gain an insight into the way that a person's emotive experience of the world is developed during childhood. For instance, despite the fact that only certain stimulus could induce fear responses early on in an individual's life, as the person grows up would acquire further associations which will obtain qualitatively similar operations with the ones that an unconditioned stimulus possesses, which would from then on induce fear responses

(McSweeney and Murphy 2014). Therefore, through classical conditioning, phenomena acquire new associations with external stimuli such as behaviors of other people, certain environmental conditions as well as internal stimuli, such as other emotions and interoceptive experiences. For example, a young boy who experiences sadness and is recurrently challenged by a father who is behaving in a manner which induces fear in the boy, via the process of classical conditioning, the father's behaviors could lead the young boy to develop an association between the affects of sadness and fear, and thus every time he feels sadness (conditioned stimulus), a response of fear is induced. In other words, this boy has learned through classical conditioning to experience fear every time he is sad (Thines 1987).

Classical conditioning shapes individuals' responses from early on in their lives and continues to influence the way in which a person relates to the world during the course of all of his/her life (Ramnero and Torneke 2011). The recognition that affective responses could also be induced by classically conditioned associations has its roots early in the development of behaviorism (Thines 1987). Specifically, John Watson, who is considered the father of "behaviorism," embraced I. P. Pavlov's work on conditioned reflexes and decided to implement its principles to investigate the way that the affective response of fear emerges in people. In addition, classically conditioned responses are fundamental to gain an insight in the way that individuals who experience trauma respond to a specific stimulus such as loud noises, fire, dark, or a preparator's perfume (Shanks 1995).

Stimuli of External and Internal Nature

Conventionally, behavioral psychotherapy has directed its attention on external stimuli, that is, stimuli that reflect alternations that occur outside the organism. However, the last few decades, researchers have also focused on internal stimulus (Klein and Mowrer 1989). Internal stimuli constitute alternations to the conditions within the body such as emotions, cognitions, hunger, thirst, and pain. Internal stimuli have the predisposition to also acquire conditioned associations, and the

term that is used to describe and designate such phenomena is called interoceptive conditioning (Schachtman 2011). Interoceptive conditioning is considered to be vital to the understanding and treatment of specific anxiety disorders such as panic disorder and phobias.

Biological Predisposition in Learning

Humans are endowed with a number of reactions to unconditioned stimulus, yet the responses that people exhibit are more complex than that. What is termed neutral stimulus, sometimes its function is not completely neutral (Ramnero and Torneke 2011). Specifically, stimuli could be differentiated in their ability to acquire conditioned associations and not all reactions could be induced by a previously neutral stimulus in the same time-framework and potency. For example, in order for a sound of a bell to acquire the capacity to induce an eyeblink to a human being, the sound of the bell and the puff of air have to be associated multiple times. Yet for instance, in order for a formerly neutral stimulus of a specific odor to induce a feeling of disgust and dizziness, a person has to experience once or maybe a few more times the association between the odor and a vomit (Spence 1978). Similarly, research related to affects proposes that it appears as if organisms inherited the capacity for specific types of leaning. For example, humans are more likely to exhibit fear towards a snake, height, and dark, rather than to a series of other stimuli. This is also true for conditions and circumstances in which people get scrutinized as well as abandoned by other people and in situations where people experience unfamiliar bodily sensations. Therefore, classical conditioning constitutes a mixture of genetically endowed elements and personal interaction with one's environment (Baum 2017).

Facilitating Factors

As already mentioned, conditioned associations constitute a response to the relationship between an unconditioned stimulus and another stimulus that was formerly neutral or unconnected to a certain setting. Accordingly, the nature of the exact relation between the associated stimuli is of ultimate significance (Schmajuk 2010). In

addition, there is a variety of factors that facilitate the acquisition of classically conditioned associations. Firstly, when the frequency with which a conditioned stimulus is presented together with an unconditioned stimulus is augmented, the likelihood that the conditioned stimulus would acquire the capacity to induce a conditioned response would be also augmented. For instance, if the frequency with which a sound of a bell accompanies the puff of air in a person's eye area is consistently augmented, the likelihood that the sound of the bell would induce a conditioned response of an eyeblink is augmented (McSweeney and Murphy 2014).

Secondly, when conditioned stimuli are constantly presented when the unconditioned stimuli are presented, the likelihood that a conditioned stimulus would induce a conditioned response would be higher compared to cases in which the unconditioned stimulus presents too in the absence of the conditioned stimulus (Schmajuk 2010). For instance, if the sound of the bell is permanently presented when the dog receives food, the likelihood that the sound of the bell would induce a classically conditioned response of saliva secretion would be augmented. In contrast, if the sound of the bell is presented only in specific times when the dog is receiving food, the likelihood that the sound of the bell would induce saliva secretion would be decreased. In addition, if a man engages in a consistent use of a specific cologne just in cases in which he engages in sexual intercourse with his wife, the likelihood that the aroma of this cologne would induce sexual arousal to the couple would be augmented (Ramnero and Torneke 2011).

In addition, classical conditioning necessitates a precise and a constant sequence of stimuli in which the unconditioned stimulus must follow the conditioned stimuli's presentation and not the other way around (Spence 1978). For example, in order for a tone to acquire the capacity of inducing an eyeblink, the tone must be presented just before or as the puff of air is received. If the tone is presented after an individual has received the puff of air around the eye area, this individual would never learn to classically respond with an eyeblink in the presence of the tone, despite the

number of times that this sequence of stimuli is repeated (Shanks 1995). A further factor that facilitates conditioning is the intervening time between the presentation of the conditioned stimuli and the unconditioned stimuli. Specifically, as the intervening time between the presentation of the conditioned stimuli and the unconditioned stimuli is increasing, the likelihood that the conditioned stimulus would induce a conditioned response is decreasing. For example, if a tone is presented a long time before an individual receives the puff of air, the tone would not acquire a classically conditioned association with the puff of air (McSweeney and Murphy 2014).

The definite relationship between the associated stimuli is not the only factor that governs conditioning. People possess potent biological tendencies that could alter this. For example, nausea could easily become conditionally associated with other stimuli (Baum 2017). That is, if an individual has a delightful plate of pasta and then a few hours later he gets a flu, the features of that plate of pasta such as its aromas and sense of taste could acquire classically conditioned associations with the sensations related to a flu and in turn induce a conditioned response of nausea regardless of the fact that a significant amount of time has passed between the presentation of the pasta's aromas and sense of taste, the flu (unconditioned stimulus and nausea (unconditioned response). That is, the pasta's aromas and sense of taste have become conditioned stimuli and acquired the capacity to induce nausea (Wills 2012).

Further Conditioning: Second-Order Conditioning, Generalization, and Discrimination

Second-Order Conditioning

Stimuli that have acquired conditioned associations can set the ground for further conditioned associations. For example, when a kid experiences fear in the presence of darkness resulting to the darkness being a conditioned stimulus that induce a response of fear, an additional stimulus that exists in the setting of darkness such as specific noises can acquire too qualitatively similar

operations with the conditioned stimulus and induce a fear response despite the fact that these noises did not accompany the stimulus that initially induced the fear response in the dark setting (Ramnero and Torneke 2011). This phenomenon is usually termed second-order conditioning. Once more, the stimulus of darkness is likewise one that is not so neutral, as humans are biologically predisposed to more easily associate it with fear than other stimuli (McSweeney and Murphy 2014).

Generalization

An additional and very significant functional process of classical conditioning is the propensity to react in a qualitatively comparable manner to similar stimuli, a process that is termed stimulus generalization (Staddon 2014). The term stimulus generalization when it comes to classical conditioning defines the process through which a specific response would spread in such a manner that other stimuli which have qualitatively similar traits with the initial classically conditioned stimulus would acquire the ability to also induce the classically conditioned response (McSweeney and Murphy 2014). For instance, a kid that has been scratched and wounded by a dog would not only respond with fear whenever sees that specific dog. Specifically, this kid is very well likely to respond with fear to the presence of dogs which are similar enough. However, if the kid was scratched by a large dog and the height of the dog is a dominant feature of the conditioned stimulus, it is likely that a very small dog would not induce a conditioned response of fear. Yet if the dog's barking is a dominant feature of the conditioned stimulus, then a very small dog's barking could operate as a conditioned stimulus and induce a conditioned response of fear. In other words, in order for an organism to respond in a qualitatively similar way to different stimuli, the stimuli must be similar enough (Ramnero and Torneke 2011).

Stimulus Discrimination

The opposite conditioning operation to generalization is a process termed stimulus discrimination. Stimulus discrimination is the capacity of

an organism to detect and respond to differences between stimuli, that is, the capacity to detect similarities among stimuli. For example, I. P. Pavlov's dogs at the beginning exhibited stimulus generalization since they were secreting saliva and digestive fluid in response to a variety of sounds that were different than the sound that was initially classically conditioned (Ramnero and Torneke 2011). However, if the dogs had consistently received only a specific sound before they were fed, their capacity to differentiate, that is, to discriminate, among similar stimulus would be enhanced and in turn, they would secrete saliva and digestive fluid only in response to the specific sound that precedes feeding (Shanks 1995).

The processes of generalization, discrimination, as well as the equilibrium among them are of vital importance for living beings in order to learn to adapt and survive (Baum 2017). Specifically, in some situations is of vital importance to exhibit stimulus discrimination and just respond to specific stimuli. For instance, a living being that must assess an area which is full of ice where a discrepancy in the white-color shows the degree to which is safe or dangerous to pass through the ice must have the capacity for stimulus discrimination. However, in other situations, stimulus generalization has higher adaptive and survival significance, such as the case of an organism which is chased by a variety of predators. In such a scenario, this living organism must respond to everything that presents in front of it.

Extinction

Classical conditioning and its derivative processes such as stimulus generalization and discrimination are dynamic in nature. Consequently, classically conditioned associations could be loosened and ultimately be extinguished, a process that is termed extinction (Ramnero and Torneke 2011). In classical conditioning, the term extinction indicates that the unconditioned stimulus does not any more accompany the conditioned stimulus, something which eventually leads to the termination of the conditioned response (McSweeney and Murphy 2014). For instance, in the experiment that I. P. Pavlov conducted, dogs were classically conditioned to secrete saliva and digestive fluid in

response to a sound of a bell. However, at some point in time, the sound of the bell was consistently occurred to the dogs in the absence of the food (unconditioned stimulus), leading to the extinction of the conditioned response of saliva and digestive fluid secretion. In other words, the sound of the bell did not any more operate as a conditioned stimulus due to no longer being followed by the unconditioned stimulus (food) which means that the sound of the bell lost its capacity to induce the conditioned response of saliva secretion (Shanks 1995). Yet as I. P. Pavlov indicated a classically conditioned response that became extinct is prone to reconditioning. Specifically, I. P. Pavlov got two of his dogs so that to test this assumption. The first dog was initially classically conditioned to secrete saliva, a response that then became extinct. The second dog had never learned the association between the sound of the bell and the food. Then he set the conditions so that both of them could learn the association between the sound of the bell and the food. The dog that once associated the bell with the food learned the association between the two stimuli significantly earlier than the other (Spence 1978).

Extinction is a multifaceted behavioral mechanism that has been recently found not to remove the initial learning experience (Ramnero and Torneke 2011). For instance, I. P. Pavlov indicated that a reaction that became extinct sometimes spontaneously reappears in the future, a phenomenon that is termed as spontaneous recovery. Subsequently, the phenomenon of spontaneous recovery has been experimentally verified in the field of both respondent and operant conditioning (McSweeney and Murphy 2014). However, the phenomenon of spontaneous recovery does not always appear and when it does appear is usually for a short period of time. In addition, when spontaneous recovery takes place the conditioned response is of lower intensity than it used to be (Schmajuk 2010).

Experimental Procedures

As mentioned above in respondent conditioning, an originally neutral stimulus acquires classically conditioned associations with biologically

relevant stimuli. In appetitive conditioning, the biologically relevant stimulus is positive for an organism such as food and originates behaviors of consummative nature in living beings. In contrast in aversive conditioning, the biologically relevant stimulus is negative in nature for an organism such as pain and initiates defensive responses like avoidance and escape (McSweeney and Murphy 2014).

Conventionally, research related to respondent conditioning has focused on excitatory conditioning (Shanks 1995). Excitatory conditioning occurs when a conditioned stimulus maintains a positive relationship with the unconditioned stimulus. That is, in excitatory conditioning, the conditioned stimulus acquires the capacity to predict the appearance of the unconditioned stimulus (Schachtman 2011). In contrast, in inhibitory conditioning, the conditioned stimulus acquires the capacity to predict that the unconditioned stimuli are not going to occur. Specifically, conditioned stimuli that acquire inhibitory qualities, when they present they indicate the nonappearance of either positive or negative unconditioned stimulus which in turn leads to the inhibition of the conditioned response by a living creature (Schmajuk 2010). This kind of conditioning was studied by I. P. Pavlov, and there has been a renewed interest for it the last few decades (McSweeney and Murphy 2014).

Conclusion

Due to the operational procedures of classical conditioning in which two stimuli are presented at the same time, it is considered that learning related to this associative connection relies on the dynamic characteristics of stimuli-stimuli associations. Additionally, research related to this hypothesis indicated that the conditioned stimulus acquires the capacity to trigger a representation of the unconditioned stimulus that has been associated with it (Shanks 1995). As mentioned above theorists and experimenters directed their focus on classical conditioning for various reasons. Firstly, classically conditioned associations acquire the capacity to fundamentally

influence organism's behavioral responses. Specifically, classically conditioned associations constitute a mechanism which enables organism to adapt to impending biologically important conditions (Schachtman 2011). Moreover, the operational principles of classical conditioning enabled mental health professionals to develop and implement effective treatment interventions for affective abnormalities and substance abuse. Last but not least, Pavlovian conditioning equipped learning theorists and researchers with an efficacious experimental design that enables for a significantly accurate analysis of the way that organisms form associations between environmental and interoceptive stimuli (McSweeney and Murphy 2014).

Cross-References

- ▶ Associative Learning
- ▶ Conditioned Response
- ▶ Conditioned Stimulus
- ▶ Conditioning and Association
- ▶ John Watson
- ▶ Unconditioned Stimulus
- ▶ Unconditioned Response

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Classical Twin Design

- ▶ Twin Studies

Classically Conditioned Stimulus

- ▶ Conditioned Stimulus

Cleaver

- ▶ Acheulean

Climacterium

- ▶ Menopause

Climate and Habitat Diversity

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Synonyms

Environmental heterogeneity; Ancestral environment; Evolving environments; Environment of evolutionary adaptiveness; Unstable environments

Definition

The various environmental conditions and forces that ultimately guided and shaped the evolution of humans.

Introduction

Environmental changes can be fatal to any biological life form. Each and every living organism is essentially a biological response to both its ancestral and present environmental pressures. Every facet of the environment and climate can influence an organism's nature, and many anthropologists claim that the human species is a result of an extensive and diverse environmental history. Evolutionary theory is founded upon an organism's ability to adapt to its environment, whether natural or artificial. Evolutionary psychology assesses both prehistoric and present environmental conditions, which contribute to the development of the field's hypotheses and theories.

General Climates and Habitats of Human Evolution

Prehistoric humans, also called *hominids*, evolved in Africa. Today, modern humans dominate every continent and reside within one of almost 200 different countries over the globe. Over millennia, various species of humans travelled across the world and encountered a wide variety of environments similar to those existing today, which include deserts, forests, woodlands, mountains, coasts, islands, and Arctic regions. Early humans have a long history of hunting and gathering, which demanded them to explore beyond their "homes" or "campsites" in order to collect necessary natural resources for survival. With drought and famine usually within weeks away, prehistoric humans had every right to abandon their original habitats (Harari 2015).

Hominid diasporas were a powerful force that drove human evolution. The fluctuating temperatures, sea levels, and animal and vegetable life made survival the most onerous task (National Research Council 2010). To an extent, scientists

are able to unveil prehistoric climatic and environmental conditions with measurements of oxygen isotopes (Elton 2008; Potts 2016). Following the ice age, tropical climates and vast expansions of vegetation intercepted hominids' journey across the globe (National Research Council 2010), which diversified all forms of life. Typical foods gathered and eaten by modern humans, or *Homo sapiens*, included berries; onions; mushrooms; roots; seeds; bugs; smaller animals, such as rabbits, fish, and turtles; and occasionally large predatory animals like bison and mammoths (Harari 2015), which all do not share a sole natural habitat.

Natural disasters – volcanic eruptions, hurricanes, floods, etc. – and other demographic pressures compelled *Homo sapiens* to settle for different and novel habitats. An organism's *environment* is not restricted to its physical surroundings; other organisms also serve as a selective force of nature. There were periods where *Homo sapiens* were not the only human species living on Earth; *Homo neanderthalensis*, often referred as the *Neanderthal*, once shared present-day Europe with *Homo sapiens*. Neanderthal deoxyribonucleic acid (DNA) is found in modern Middle Eastern and European humans. Some anthropologists and biologists claim that, on rare occasions, *Homo sapiens* and the Neanderthals were capable of producing fertile offspring (Harari 2015). Nonetheless, the time Neanderthals and *Homo sapiens* shared together was relatively short-lived. *Homo sapiens* settled in uninhabited habitats, like Australia, that was home to animals that did not evolve to fear humans, which led to the extinction of countless species. Neanderthals went extinct shortly after the arrival of *Homo sapiens*, giving *Homo sapiens* the reputations of being both the most adaptable species yet (Potts 2016) and the most widespread "ecological serial killers" (Harari 2015).

Effects of Environmental Diversity on Human Evolution

The biological evolution of humans merely coincides with major environmental and climatic change (Potts 2016). *Homo ergaster*, for example,

is believed to have a body that was highly adaptable to heat (Potts 1998). Hominids that adapted to colder climates often had shorter appendages and a wider torso, similar to the Neanderthals (Elton 2008). Although physical attributes acquired from environmental pressures may seem evident, adapting to novel environments requires a more versatile lifestyle. Organisms, including hominids, that do not adapt to climate and environment change are more likely to be exterminated than those with at least some ability to adapt habitual change. The desiccation of arboreal habitats produced thousands of square miles of open and flat land in Africa. Bipedalism, walking on two legs, is hypothesized to have evolved from this environmental change, which is also known as the *Savannah hypothesis* (Potts 1998; Elton 2008).

Physical attributes were not only acquired from the natural forces hominids endured. The ability to adapt to a novel environment requires new intelligences and skills, such as making tools and shelter, controlling fire, and establishing social order (National Research Council 2010; Harari 2015). Scholars argue that *Homo sapiens* inadvertently evolved to become dependent on tools and technology. The human diet, for example, would be drastically limited if there were not any means to cook food. Prolonged physical and mental maturation may also be results of humans' rich environmental history. Some scientists even hold environmental and climatic diversity responsible for the enlargement of the human brain, complex symbolic expression, and social structures similar to modern societies (Potts 2016).

Millennia ago, hunter-gatherers had to scrutinize their environment in order to discern cues that could predict seasonal and weather changes (Harari 2015). Today, human beings will somberly call a desert, mountain, forest, island, or Arctic region their permanent home unless under the constant threat of natural disasters (Elton 2008). Perhaps the most precious feature from human's evolutionary history is cultural diversity. The natural lifestyle of a band of humans was rarely identical to another that lived elsewhere (Potts 2016). Humans may have paid an irrevocable price while spreading across the world, but

they may also have acquired the finest survival skills and instincts Earth has ever witnessed.

Variation Selection and Habitat-Specific Hypotheses on Evolutionary Psychology

Like all other species, *Homo sapiens* have a fixed set of environments that they can survive and reproduce in, yet environmental instability is the best impetus for adaptation development. While some scientists consider *Homo sapiens* as a biological product of various and diverse environments, others consider them as a biological product of specific ones, the former being the *variation selection hypothesis* and the latter as the *habitat-specific hypothesis*.

The relatively large biological reaction norm, or phenotypic plasticity, is ultimately what permits human cultural and biological diversity. Body shape, stature, and skin, among other traits, vary between individuals with ancestors from different regions of the world. Human cultural and biological diversity supports the variation selection hypothesis; however, there are reported universal preferences for geographical landscapes and climates that resemble the African Savannah, which embody the popular *Savannah theory*, a habitat-specific hypothesis (Potts 2016).

Regardless of the two competing theories, the environments in which humans acquired their adaptations or their *environment of evolutionary adaptedness* (EEA) are at the forefront for the development of evolutionary psychological hypotheses. Given that adaptations resulting from natural selection can be both physical and mental, a sense of adaptive universality among humans across all cultures is fundamental in evolutionary psychology. Ruling out alternative explanations for universal psychological traits and tendencies is a current objective of empirical research within evolutionary psychology.

In spite of the endeavor to synthesize human paleoanthropology and psychology, most social and behavioral scientists advocate for theories that are independent of biological evolution. The *blank slate* theory posits that human behavior is solely a product of knowledge, will, and experience (Pinker 2016). Many social scientists often

view *nature* and *nurture* as conflicting explanations for human behavior, but accumulating evidence within evolutionary psychology may reconcile the two. After all, an environment-rich evolutionary history is likely to yield species with seemingly perfect and malleable minds.

Conclusion

The evolution of hominids encompasses a wide array of environmental pressures that make it difficult for anthropologists to summarize concisely. The famous hominid diasporas out of Africa presented hominids with novel habitats and ecosystems that served as catalysts for human evolution. Although only fossils and artifacts are what remain from human prehistory, measurements of oxygen isotopes, among other scientific and forensic procedures, allow scientists to estimate prehistoric climates and environments. Assessments of the diverse environmental conditions that existed during human evolution serve as the foundation for evolutionary psychological research. Every adaptation, whether physical or mental, is a response to a range of environmental pressures. The psychology and behaviors of *Homo sapiens*, indeed, exhibit the blank slate's assertions, but *Homo sapiens* also have a reputation for terraforming habitat after habitat, which necessitates a versatile mental capacity.

Cross-References

- [Habitat Change](#)
- [Reaction Norms and Tokens](#)
- [Savanna Hypothesis, The](#)

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Climate and Use of Spices

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Synonyms

[Spicy food in hotter countries](#)

Definition

Foods eaten with more spices are found more often in hot climates. Some suggest that the use of spices by humans may be an evolutionary adaptation to fight against food poisoning.

Introduction

Spices are “dried, fragrant, aromatic or pungent plant substances . . . that contribute flavor, whose primary function in food is seasoning rather than nutrition, and that may contribute relish or piquancy to food or beverages” (Farrell 1998, p. 17). Spices include pepper, onions, garlic, parsley, and so on. Although spices are now easily obtainable all over the world, there is a common tendency to relate spices to some cuisines more than others. A few notable examples are the “spicy” foods of India, Mexico, and Indonesia,

whereas Swedish, British, and Russian foods are not known to be particularly “spicy.” Even a cursory glance reveals an interesting pattern: there would appear to be some correlation between spiciness of the cuisine and the climate of its country. Indeed, there has been much discussion about why it seems that people who live in warmer climates use more spices in their cooking compared to those in colder climates.

One theory, by Billing and Sherman (1998), suggests that humans’ use of spices has evolutionary roots and that the link between climate and the use of spices could be explained by the spices’ antimicrobial properties.

The Antimicrobial Theory

The acquisition and consumption of food, although necessary, pose risks. Microorganisms and toxins that inhabit food can cause people to fall ill and may even result in death. This was an especially severe problem in the days before refrigeration and artificial preservatives were in wide use. The use of spices in food has been suggested as an adaptive solution to this problem. Spices, which are derived from plants, possess secondary compounds which act as the plants’ defense mechanism against harmful organisms.

In order to test the theory that spices have been used for their antimicrobial properties, Sherman and Billing (1998) studied 4578 traditional meat-based recipes from 36 different countries. Recipes from traditional cookbooks were used as considered by Billing and Sherman (1998) as artifacts of human behavior. Meat-based recipes were used because unrefrigerated meat spoils quicker than unrefrigerated vegetables, and there were more meat-based recipes available in traditional cookbooks. The use of 42 spices in these recipes was catalogued along with each country’s mean annual temperature. They set up several key predictions of their antimicrobial theory.

1. Spices used in cooking should inhibit food-spoiling microorganism activities.

If spices do inhibit the growth of harmful food-borne microorganisms, using spices would aid in the reduction of food poisoning. Of the spices located by Billing and Sherman (1998), half inhibited the growth of more than 75% of bacteria. Laboratory tests of the efficacy of spices against microorganisms have used concentrations of below 1000 parts per million or ppm, while the recipes in Billing and Sherman’s study roughly contained 250–1000 ppm of spices (e.g., Kivanc et al. 1991; Billing and Sherman 1998). This suggests that the concentration of spices used in everyday cooking is sufficient to inhibit microbial activity in food.

2. Use of spices should be greatest in hotter climates.

The rate of bacterial growth on meat increases drastically in a matter of mere hours if left unrefrigerated. This growth is further accelerated in hotter climates. Thus, if the antimicrobial theory holds true, there should be a positive relationship between the use of spices (in order to fight food spoilage) and hotter climates. The data was found to be consistent with the prediction: the number of recipes containing spices and the number of spices in a recipe both increase in positive correlation with the mean annual temperature.

3. Use of spices with the most potent antimicrobial properties should be greatest in hotter climates.

Country-specific uses of highly inhibitory spices such as onion, garlic, and oregano, which reduce bacterial growth by 100%, were found to correlate positively with countries’ mean annual temperature. This pattern also holds true for other highly inhibitory (i.e., inhibiting more than 75% of bacterial species) spices. Although the use of dill and parsley was found to be negatively correlated with temperature, neither has a significant inhibitory effect. Billing and Sherman (1998) also note that two of the most frequently used spices, pepper and lemon juice, do not positively correlate with mean annual temperature nor are they powerful

bacterial inhibitors. Instead, they suggest that pepper and lemon juice work in conjunction with other spices in order to increase the antimicrobial effects of other spices.

4. Within a country, recipes from areas of lower latitude (i.e., warmer climates) should have a higher number of and more potent spices than recipes from areas of higher latitude (i.e., colder climates).

Although information relating to recipes based on regional latitudes was scarce, they were able to collect data from China and the United States. Data from both countries are consistent with the prediction and show patterns that are similar but less dramatic than those between countries: southern regions of the United States and China use spices more frequently and more potent spices in their recipes compared to those in southern regions.

Sherman and Hash (2001) further predicted that, within the same country, vegetable-based recipes should have less spices compared to meat-based recipes because vegetable-based food are associated less with food-borne illnesses than meats. When plants die, their cell walls are harder to break down for many microorganisms unlike in meat. In contrast, the main inhibitor of microorganisms in animals is the immune system, a system which completely ceases to function upon the death of the animal. To test this, they carried out a similar study with vegetable-based recipes. Throughout the 36 countries in the study, traditional vegetable-based recipes used significantly fewer spices compared to meat-based recipes. From the 41 spices that were compared, 30 were used significantly less often in vegetable dishes compared to meat dishes. There were also fewer vegetable-based recipes that used more than one spice or extremely potent spice. As the recipes and spices compared were within the same countries, the accessibility of spices in the different countries cannot explain the difference in spice use in different climates – the spices used in the recipes were actively chosen by people rather than dictated by what spices were available.

In further support of the antimicrobial theory regarding climate and the use of spices, Ohtsubo (2009) found that the predictions made by Sherman and colleagues also hold true using Japanese spices. He additionally predicted that more spices would be used in recipes that contained unheated main ingredients than recipes with well-heated ingredients. This is because unheated ingredients are more susceptible to food-borne pathogens. Datasets provided by experts in traditional Japanese foods supported the predictions of the antimicrobial theory.

Cost of Spices

As spices aid in preventing food spoilage, one might expect that although spice usage would be more useful in warmer climates, it would also be beneficial in colder climates. Therefore, the infrequency of the use of potent spices in recipes found in colder climates – even though most spices are available there – suggests that spice consumption may have its drawbacks (Billing and Sherman 1998). Plant secondary compounds in spices inhibit microbial growth but they can also have mutagenic, carcinogenic, and other ill effects when consumed (Beier 2000). Therefore, while the benefits of spices' antimicrobial effects outweigh the risk in warmer climates, this does not seem to be the case in colder ones. The slower rate of food spoilage, the possible health risks of spice consumption, and the higher price of obtaining spices probably explain why countries with lower mean annual temperatures use far fewer and less potent spices than warmer countries.

How Did It Start?

Although using spices to enhance the flavor of food is often the go-to answer as to why we use spices, this explanation is insufficient to explain how humans began to use spices. This can be seen in children who react negatively when.

Sherman and Billing (1999) suggest that spice use may have begun with spices that were

tasty or caused desirable aftereffects. Individuals and families who spiced their food may, then, be less likely to fall ill due to food-borne illnesses compared to those who did not use spices, especially in warmer climates. This information would have been passed onto their offspring and may have been imitated by other families observing the habits of the healthier family.

However, these individuals may still have become ill due to microorganisms growing resistance or exposure to new food-borne bacteria. Humans tend to develop food aversions to the taste of foods that have once made them ill (Milgram et al. 1977). Adding different spices that could kill the microorganisms and also change the taste of the avoided food would perhaps allow the once avoided food to be consumable again. Eventually, humans would prefer the taste of spiced food compared to unspiced food, especially in hotter climates where the growth of food-borne microorganisms is faster. This may be reflected in the large number of spicy recipes found in warmer climates.

Modern Day Examples

Spices do not only seem to aid in protecting our ancestors from food-borne illnesses. Although Japan and Korea are geographically proximate with similar mean annual temperatures and climates, bacterial food poisoning affected only 3 per 100,000 Koreans, while it affected 29.2 per 100,000 Japanese (Lee et al. 1996). The difference in the prevalence of food poisoning between the two countries can be attributed to the fact that Korean recipes contained more spices and more potent spices than that of the more delicate Japanese recipes (Billing and Sherman 1998). The Japanese recipes' lesser use of spices may stem from the abundant availability of fresh seafood in Japanese history. However, due to an increase in population and overfishing, there is an increase in the delay between catching and consuming the seafood, allowing the growth of harmful microorganisms on the food.

Alternative Theories

Although the antimicrobial theory provides a good explanation for why hotter climates are associated with the use of more spices, other alternative explanations have been put forward. Some include:

- Spices help disguise the smell and taste of food that may have started to spoil (Barker 1982).

This theory, although consistent with the trend that more spices would be used in hotter climates as there would be more bad smells to cover, overlooks the evolutionary disadvantage of masking food that may be ridden with food-borne illnesses. Covering up foul smells and tastes would cause humans to be more likely to consume spoiled food.

- Spices increase perspiration and cool down the body (Bosland 1994).

This cooling pattern only seems to hold true for only some of the spices used like chilies. Hotter climates are linked with the use of many other spices that do not increase perspiration. Furthermore, cooling of the body via perspiration is metabolically expensive and would not be a sustainable cooling strategy.

- There are no benefits to eating spices and that people consume whatever spices they have locally.

This is unlikely because, as mentioned earlier, availability of spices cannot account for spice usage patterns. Additionally, many spices are not immediately pleasant to consume especially in children. Children consume spices usually after being encouraged by their parents, suggesting that there is a benefit to eating spices that outweighs the initial displeasure due to their taste.

Conclusion

In sum, the frequency of spice use, the amount of potent spices, and the proportion of recipes that contain spices increase as the mean annual temperature of a country increases. This has been suggested to be due to the antimicrobial properties of spices. By consuming spices, humans were able to reduce the likelihood of contracting food-borne illnesses. However, there are also risks associated with spice consumption. Thus, recipes from different climates and different eras represent “records of our coevolutionary races against food-borne diseases” (Sherman and Billing 1999). Practices that promoted the health of spice users may have spread as a cultural meme and were more beneficial for those in hotter climates and those in colder climates.

Cross-References

- [Access to Resources](#)
- [Climate and Habitat Diversity](#)

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Climate Change

- [Climate Fluctuations in the Last 200 Ky](#)

Climate Fluctuations in the Last 200 Ky

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Synonyms

[Catastrophes](#); [Climate change](#); [Global warming](#)

Definition

A change in global or regional climate patterns.

Introduction

Climate fluctuations are changes in the earth’s atmosphere due to an array of events that can temporarily or permanently change elements in the global or regional area. These changes can vary considerably, and climate fluctuations can be due to many potential causes. These changes can be from natural events such as earthquakes or volcanic eruptions, or more modern climate change can be seen as a result of human behavior and changes to the environment such as carbon emissions. However, in

order to understand what climate fluctuations are, it is very important to first discern two concepts that are often a point of confusion when talking about these changes – *temperature* and *climate*.

Temperature

Essentially, all that differentiates climate and temperature is a measure of time, and how long these effects go on for. Temperature is essentially a measure of atmospheric fluctuations in the short term that result in effects that we feel as humans in our daily lives. These are things that are much more noticeable to us, in general, rather than long-term climate fluctuations. Temperature is experienced every day simply by leaving one's home, and sometimes is even apparent by looking outside the window. In general, humans experience sensations such as hot weather, cold weather, rainy weather, humid and dry weather, heavy or light winds, snow, thunder and lightning, and so on. These are examples of short-term atmospheric changes that can have a profound effect on daily lives but can change quickly in a short period. For instance, there may be weeks whereby a stretch of some great weather comes that may be warm and dry, but soon followed by periods of heavy rain, winds, and humidity. These are all examples of weather fluctuations because of their short-term occurrence. Living in the northeast, for example, one might expect that in the months of December, January, and February to experience cold weather with snow as compared to months of June, July, and August whereby hot weather is typical. However, while unusual, it is not impossible to experience a very warm day in winter months, or a chilly day in summer months. These random fluctuations happen constantly and are a result of changes in our atmosphere. These are significantly different from something such as climate change, which can be exemplified by weather phenomena but are usually an accumulation or take place over a longer period of time.

Climate

While weather is usually defined as being the atmospheric changes within a short period of time (usually anything from within a few days to a few months, such as seasonal changes), climate is long term, typically over the course of years or decades. More specifically, it is usually indicative of *average* weather patterns over a period of time. For instance, back to the example of the northeast United States. Across anywhere north of the equator, one would expect that in the summer months (June, July, and August) warm weather would be typical as compared to the cooler months (December, January, and February). This is true across nearly every single region north of the equator, and south of the equator would be the opposite. However, the actual difference in this weather phenomenon is what is indicative of climate. Instead of “Is it cold?” or “Is it hot?” more importantly is the larger picture – more specifically, “How *much* colder?” or “How *much* hotter?” To once more refer to the northeast United States, one would expect that the difference between the coldest day in winter and the hottest day in summer would be pretty drastic, as compared to a place like the southeast United States, which in general typically has a warmer climate. As such, their difference between coldest and warmest day would likely be less drastic than that of the northeast United States. This difference is an example of climate – long-term temperature fluctuations or patterns that are often common to a specific area. The northeast United States, in general, experiences colder weather and more snow than do parts of the lower United States and other countries, especially as one gets closer to the equator. Therefore, the northeast United States has a colder climate than the southeast United States. There may be a day in a given year where Florida has a colder day on the same day than New York – this would be an example of a temperature fluctuation rather than a climate one, given that it is over the period of a day rather than decades. However, in the event that for 50 years, Florida has a successively warmer winter each year, then this is a result of climate change. The understanding of this difference is

essential in understanding why climate change and fluctuation was such an important part of our evolutionary past.

How Did Climate Fluctuations Impact Human Evolution?

Now that the differences between climate and weather fluctuations have been studied and understood, theories emerged that attempt to explain how major climate fluctuations began to impact early hominins, and how their being forced to adapt eventually paved the way for evolutionary changes we still see today. A major way to assess climate change is through the usage of oxygen isotopes. By looking at microscopic skeletons of certain creatures on the sea floors, it is possible to detect their oxygen isotopes that give a measure of how temperature has changed over time as well as rate of glacier melting, which also can show us forms of climate change. By looking at these oxygen isotopes, research has shown that there have been various climate changes as far back as we can detect (Behrensmeyer 2006). If this is the case, then we can determine that our ancestors such as early hominins were likely heavily impacted by these climate changes, and as a result likely had to make dramatic behavioral changes to accommodate to the changes in their environment around them to survive (Demenocal 2004). Modern research also shows that these climate fluctuations have become more dramatic the more hominins were evolving, suggesting that the most modern *Homo sapiens*, especially within the last few hundred years, have been a major contributor to the lasting and dramatic climate change that we see today (Potts 1996).

How Does Climate Change Affect the Environment?

All organisms experience the effects of weather-related fluctuations. For instance, looking outside a window and seeing that it is raining would typically invoke reaching for an umbrella. While an umbrella is obviously a more modern, human-

made creation, the point still stands that humans make small changes in daily behavior to account for the weather fluctuations that occur around us. All organisms do the same thing, especially with regard to seasons (for instance, certain animals changing fur colors to go along with a change in season). The difference between weather and climate fluctuations, however, is that the organism will continuously make these changes according to the weather. For instance, that same organism that changes fur color would only do so with regard to the weather phenomenon that it is experiencing. If there is no reason for a thicker fur, then it will not grow one as that would be maladaptive (a thicker fur would prevent cooling in warmer months, and so would be evolutionarily disadvantageous). It is only with climate change that we would begin to see permanent changes in an organism's behavior (Vrba 1995). For instance, if over the course of millions of years that fur-changing organism only experienced winter, it would eventually adapt to keep its winter coat on and avoid changing furs as there is simply no reason to. To use the umbrella example, if the climate changed such that it now rained every single day out of the year, humans would likely keep our umbrellas around constantly given that it is now reflective of the environment around us. This is an example of how climate change can drastically impact the behavior humans exhibit on a daily basis, and more specifically how our ancestors had to change their behavior in response to the climate change around them. When our behavior changes, and we have to adopt new behaviors to survive, evolution takes place over millions of years, whereby our physiological bodies will begin to adapt to whatever is necessary in our new environment to ensure survival (Ruff 1991).

What Kinds of Climate Change Did Early Hominins Experience?

Evidence shows that there were large-scale shifts in temperature and precipitation around 200,000 years ago that have only gotten progressively more variant over time (Stewart and

Stringer 2012). These changes can result in huge changes in their respective environments, affecting things such as vegetation and daily temperature. Living in trees may not have been suitable given these climate changes, especially if vegetation that was an essential part of our diet was no longer available. Our ancestors were then confronted with either dying because of the lack of resources, or changing their behavior to accommodate to their newly changed surroundings. As a result, the ancestors that did survive likely had to migrate closer to the forest floor, and begin looking for new vegetation that was not as heavily impacted by the climate change as were the things at higher elevations in the trees. In addition, different wildlife that represented prey would have been extremely valuable, ensuring survival. Therefore, the ancestors that failed to adjust would have died off, and those that did survive would continue to reproduce and raise children in the same environment, and they would emulate the same behavior. Over the course of long periods of time, this would become instinctive to early hominins and they would all begin to adjust to living life on the forest floor. From there, it is possible that the forest floor simply lacked sufficient resources or was too dangerous for these hominins, so they ventured out gradually until they found grasslands, which was eventually where they settled and developed more human-like qualities seen today. These qualities included things such as completely opposable thumbs, standing upright with a straight spine, usage of arms to do things such as throwing and creating weapons, bipedal locomotion, human speech and communication, and so forth (Trauth et al. 2007).

Other climate changes that may have drastically impacted the environment could have been things such as earthquakes or changes in tectonic activity. Earthquakes and shifting plates can completely change locations of lakes, rivers, mountains, valleys, and so on – also changing their respective environments and vegetation. When these changes occur, organisms face the dilemma of either dying or changing their behavior to survive, resulting long-term in evolutionary changes to adapt to their new surroundings (Füssel and Klein 2006). Other things include

volcanic eruptions and forest fires, which can change entire environments and even quality of breathing in certain areas, also drastically changing the way the organism can survive in that respective area.

Conclusion

The bottom line is that early hominins grew up in a time where environmental instability was very much prevalent (though not as prevalent as it is today). As a result, changes in the environment were very likely, such as changes in temperature, rainfall, tectonic plate shifts, earthquakes, forest fires, volcanos, and so forth. These events can cause changes in local environments, causing shortages of food, shelter, water, and other resources. When organisms such as early hominins are confronted with this change, they are forced to either relocate and find an environment that is more hospitable or be forced to survive in an environment that is inhospitable, and eventually evolutionarily change to adapt to their new environments. Alternatively, the organisms that cannot survive die off or fail to reproduce, resulting in endangerment and extinction of the species. The reason humans exist today is because these early hominins were able to adapt to their environment and move onto grasslands and out of trees to adapt to the climate fluctuations and changes to their environment, and thus resulted the physiological and biological changes seen in the human body to this day.

Cross-References

- [Climate and Habitat Diversity](#)
- [Climate Change](#)

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Climax

► Orgasm

Climax Disorder

► Orgasmic Disorders

Climbing Assists

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Synonyms

Climbing tools

Definition

Tools (*sensu* Shumaker et al. 2011) used as aids in ascending or moving the body up to or across

elevated substrates or objects. It includes vertical and angled climbing and clambering.

Introduction

The use of objects to assist in climbing was one of the first types of tool use reported in primates. A hundred years ago it was described in captivity for orangutans by R. M. Yerkes, and soon after for chimpanzees by W. Kohler, gorillas by R. M. Yerkes, and capuchin monkeys by J. A. Bierens de Haan (reviewed in Shumaker et al. 2011). Since then, the use of tools to aid climbing has been extensively observed in captive settings for these and other primate species. Comparatively, fewer observations of tools used as climbing aids have been reported for primates in the wild.

Evidence from the Wild

Chimpanzees

When infant chimpanzees become separated from their mothers by a large gap between trees, the mother pulls the branch where her infant is and holds it still until the infant crosses (Goodall 1986).

To access trees that they cannot climb directly, chimpanzees have been seen to use different types of tools. They prepared long sticks (including hooklike types) and, standing on a branch of a neighboring tree, used them to pull down one of the branches from the target tree, gripped it, and climbed into the target tree after several attempts (Sugiyama and Koman 1979). To access the same target tree, a chimpanzee detached several branches from a main branch of a nearby tree making it lighter; he then swung on it vigorously until he was able to grab a branch of the target tree and climb into it (Sugiyama and Koman 1979). To avoid the thorny branches when climbing in kapok trees (*Ceiba pentandra*), chimpanzees have been seen to place small branches under their feet (stepping sticks) or hands (“gloves”) (Alp 1997).

Once a wild chimpanzee used a human ladder abandoned on a tree to climb it (McGrew 2004),

but it was not described if the ladder was repositioned by the chimpanzee.

Bonobos

Bonobos use small trees as vehicles (bridges) to travel from one large tree to another, bending the small tree in a particular direction with their own body weight (Ingmason 1996).

Orangutans

Orangutans use flexible trees as vehicles to access target trees by swaying the vehicle tree in a specific direction until they get close enough to reach the target tree and climb into it. They remove lianas entangled on a vehicle tree by biting or pulling with their hands to release the tree and then sway it to reach a target tree (van Schaik et al. 2006). While swaying a vehicle tree, orangutans use long, hooklike sticks to bring a branch from the target tree closer, grab it, and climb into the tree (van Schaik et al. 2006). Orangutans use several leaves together as a cushion, transferring the tool several times between the hand and foot to aid in climbing the thorny branches of trees (van Schaik et al. 2006).

Gorillas

On one occasion, after trying to climb a bamboo thicket unsuccessfully, an infant mountain gorilla grabbed a pole the mother was holding vertically; then she turned toward the infant and seemed to intentionally hold the pole firmly while the infant used it to climb up to her (Grueter et al. 2013).

Western Red Colobus Monkeys

A female relocated and positioned an attached branch to aid her infant in crossing a canopy gap and climbing into the tree where she was (Shumaker et al. 2011).

Evidence from Captivity

Chimpanzees, orangutans, gorillas, bonobos, and capuchin monkeys have been reported to use four categories of tools as climbing aids for problem-solving in experiments, sometimes spontaneously

(reviewed in Shumaker et al. 2011). These categories are (1) balancing a vertical pole or other objects, (2) repositioning an object, (3) stacking objects in a tower-like construction, and (4) stabilizing and leaning an object against a vertical or inclined surface or other objects to use as a ladder. However, only chimpanzees have been observed to use a fifth category: employing sticks as “pitons” (McGrew et al. 1975). These climbing tool categories have been used by all five species to achieve the following goals: (1) to reach food or another desirable object suspended above the ground, (2) to access natural vegetation for exploration or ingestion, (3) to look through windows, or (4) to access elevated areas for exploration. Also, chimpanzees, orangutans, and gorillas have used climbing tools to escape from enclosures.

One group of chimpanzees spontaneously invented a surprising series of different climbing tools (Menzel 1973; McGrew et al. 1975). First, they made ladders by leaning sticks and poles firmly against walls, fences, and trees and then by setting up and stabilizing poles on top of the narrow edge of elevated structures. The goal was to access a window or to avoid electric wires before climbing into trees. Later, the chimpanzees used longer poles as ladders to escape their enclosure over a fence. At this point, caretakers removed objects that could be used as ladders from their enclosure. However, the chimpanzees detached parts of fallen trees, knocked down still-rooted tree stumps, up-rooted posts, from a former runaway system, detached planks by separating nailed joints, all to be used as ladders and escape their enclosure. They eventually broke apart planks attached by powerful iron screws and used them as ladders. Finally, when all objects large enough to be used as ladders were removed from their enclosure, the chimpanzees used straight, carefully selected sticks as pitons. They inserted them into seams or joints in the fence and climbed on them to escape tools stopped the escapades.

Orangutans have made “gloves” to avoid electric shocks by holding bunches of straw when climbing over an electric fence (Shumaker et al. 2011).

Macaques and baboons have also been reported to use tools as climbing aids (reviewed in Shumaker et al. 2011). Lion-tailed, Japanese, and Tonkean macaques spontaneously erected poles against vertical constructions to use as ladders, and chacma baboons were observed to balance sticks and shift a box to obtain overhanging food.

Conclusion

The use of tools to assist climbing by primates has a long history in captivity, but has been reported only rarely in the wild. Primates use climbing tools in the wild when (1) offspring need help to manage large canopy gaps or (2) climbing cannot be done directly because a tree trunk is too large for vertical climbing or has long spines or sharp edges that make climbing difficult. Wild chimpanzees and orangutans have invented similar tools to protect their hands and feet while climbing thorny trees and to reach target trees. But one of the most common types of climbing tools used in captivity, the ladder, has only once been reported to be used in the wild. Presumably, primates would benefit from using ladders to access trees full of fruits, flowers, or seeds that they cannot climb directly, (e.g. baobab, *Adansonia digitata*) but the importance of such difficult-to-climb tree sources has not been assessed in primate habitats.

The conditions that elicit the use of climbing assists may be more common in captive settings. Experiments in captivity facilitate the use of climbing tools to obtain rewards, access elevated targets, or escape. Most primate enclosures, even naturalistic ones, lack the complex three-dimensional world of wild primates, and boredom and curiosity may favor the invention of climbing tools in captivity.

Cross-References

- Evolution of Tool Use
- Primate Tool Use
- Tool Manufacturing
- Tool Use

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Climbing Tools

- Climbing Assists

Clinical Depression

- Depression
- Depression (Paul Gilbert)

Cliques

- Peer Groups

Close Kin

► Siblings

Clothing

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Synonyms

Clothing refers to items worn to cover the body; terms such as [apparel](#) are synonymous. Clothing however must be distinguished from terms such as dress, costume, adornment and fashion which embrace a wider range of items and activities such as body painting and cosmetics.

Definition

The origin of clothing reflects the loss of hair cover in hominin evolution and the resulting vulnerability of humans to cold stress during the global climate changes of the ice ages. Alternative theories about the origin of clothes suggest a universal human inclination to cover the naked body for reasons of decorative display or modesty, yet these motives are not corroborated by ethnographic data from recent naked hunter-gatherers. Despite an absence of actual clothing remains due to perishability, a thermal origin is supported also by archaeological evidence which links the development of clothing-related technologies in prehistory to past glacial cycles and environmental conditions. Thermal physiology was similarly responsible for the advent of textile garments after the last ice age in the context of global warming, as woven fabrics provided enhanced permeability to perspiration in the warmer and more humid conditions. Demand for textile fibers

was a key aspect of the agricultural revolution, encouraging the domestication of plants and animals. While biological factors were paramount with the origin of clothing, psychosocial factors such as modesty and the rise of fashion as the basis of habitual cover had a profound influence on social evolution and the emergence of modern civilized life.

Introduction

Clothes are what most visibly set humans apart from all other species. In fact no other technology plays such an intimate part in the everyday lives of modern humans. Yet of all our major inventions, the least is known about the origin of clothes. One reason is that clothes do not survive for long in the archaeological record. Another factor contributing to an academic neglect is a gender bias: Clothes are generally considered more a feminine concern.

Clothing originated as an adaptive behavioral response to biological nakedness which became a thermal liability during the Pleistocene ice ages. Findings from climatology and thermal physiology can reveal the prehistoric need for clothes as insulation from cold. While no garments have survived, archaeology yields evidence for clothing-related technologies in the paleolithic era (especially tailored clothes). The invention and improvement of clothes as protection from worsening weather conditions led to major technological innovations – toolkits with stone scrapers, blades, and bone needles. These technologies allowed hominins to conquer most of the world's environments and to finally enter the Americas from Siberia. Clothing was the most advanced technology developed by hominins in prehistory – and it is the only paleolithic invention that people still carry with them in the contemporary world.

Climate change was again relevant with clothes after the Pleistocene. Global warming made people change their clothes in many regions: They changed from wearing animal skins to woven fabrics. Textiles were a technological solution to the physiological problem posed

by sweating in warmer and more humid conditions. This effectively put the cloth into clothing, and production of textiles was a feature of neolithic agriculture. Clothes also acquired psychological and social functions relating to personal decoration and display, and also a new need to cover the naked body out of modesty. For these reasons, clothing finally came into fashion.

Evolution of Clothing

The oldest remains of clothing recovered by archaeologists are a few cloth fragments that date from 12,000 years ago at the end of the last ice age. However, clothing was invented much earlier, beginning perhaps a million years ago, and its prehistoric development was limited to populations in cool environments. Yet the habitual use of clothes is now almost a permanent and universal behavioral trait of humans: There is probably only one small group of Andaman Islanders in the Bay of Bengal who continue to live without any clothes. However, until recent historical times, many groups in warm climates wore little or no clothes on a regular basis. And while clothing now serves many psychological and social purposes, its origins reflect adaptive functions in the context of past climate change.

Origin Theories

The leading theories can be classified into three causes: display, modesty, and protection from cold. The first two suggest a universal human tendency to adopt clothes, which is refuted by ethnographic evidence from hunter-gatherer societies. Among many African and Australian groups, no garments of any kind were worn. For purposes of display and decoration, the naked body was adorned with paints, beads, feathers, tattoos, and scars (cicatrices). Early European explorers were often shocked by a complete absence of any need to cover the body for reasons of shame or modesty. Even in cold regions like Tasmania or Tierra del Fuego on the southern tip of South America, people used garments to ward

off the cold but otherwise they were naked (Gilligan 2008) – much to the astonishment of Darwin when he encountered the Fuegians in 1832 (Darwin 1839).

Protection from cold is the only motive consistent with all available data. A thermal model is supported by archaeological evidence despite a paucity of prehistoric clothing remains, and it allows the evolution of clothing to be delineated in considerable detail.

Scientific Evidence

The main sources of evidence are:

Ethnography – forager groups like Australian Aborigines, Andaman Islanders, Fuegians, and Bushmen (generally designated now as San peoples) were routinely naked prior to external contacts. Where clothes were worn, it was for thermal protection. In the case of the Bushmen, they had contacts with pastoralist groups in recent millennia and are often shown wearing loincloths, although early descriptions mention only the traditional antelope cape (kaross) worn in cool weather, used also as a rug and blanket (e.g., Sparrman 1785).

Biology – paleoanthropology can inform about the evolution of fur loss in hominins (Jablonski 2010), while thermal physiology delineates human cold tolerance and the physiology of clothing (Parsons 2014).

Climate science – paleoenvironmental research documents temperature regimes during the Pleistocene epoch from 2.6 million years ago to 12,000 years ago (Bradley 2015).

Archaeology – this encompasses data about the presence of hominins in cooler environments, technologies related to the manufacture of clothing, and artworks depicting clothes (Gilligan 2010).

Entomology – genetic studies of clothing lice can estimate when humans first adopted clothes, though the results relate more to the routine use of garments. Dates range between 84,000 and 107,000 years ago during the last ice age, or possibly as early as 170,000 years ago during the previous glacial cycle (Reed et al. 2015).

Prehistoric Technology

Hominins began to spread beyond Africa early in the Pleistocene, but they retreated from middle latitudes during the glacial episodes. From 800,000 years ago, *Homo erectus* was present in northern China throughout a couple of interglacials which also spanned a mild glacial period; clothing-related stone tools (scrapers and awls) were found at the cave home of Peking Man. From 400,000 years ago, hominins began to occupy northern middle latitudes during cooler phases and their toolkits contain more hide-scrapers, notably in the Mousterian industries of Neanderthals.

Homo sapiens evolved 200,000 years ago, but the earliest evidence for their presence outside Africa is 80,000 years ago in southern China. Signs of improved clothing technology appear in southern Africa during a cold phase 75,000 years ago, with stone blade tools and needles made from animal bones, which may have been used to make tailored garments. Eyed needles were invented as the global climate cooled again after 45,000 years ago, appearing first in southern Russia 40,000 years ago (Golovanova et al. 2010) and subsequently in northern China from 30,000 years ago (Zhang et al. 2010). Eyed needles appear a little later in Western Europe where conditions were milder; these quintessential clothing tools were common in the Solutrean industry around 22,000 years ago during the Last Glacial Maximum (LGM).

Simple and complex clothing refers to a distinction based on the thermal effectiveness of clothes and the technologies involved. Simple clothing has a single layer and is loosely draped, while complex clothing is fitted (or tailored) and can have multiple layers for added insulation. In terms of paleolithic technology, simple clothing requires scraper tools, whereas complex clothing also requires cutting tools (blades) and hide-piercing implements (awls and needles).

The archaeological evidence indicates simple clothing was invented multiple times by various hominin species from nearly a million years ago, whereas complex clothing was restricted to modern humans during the last glacial cycle. Only with complex clothes that fully covered the body

were decorative functions transferred onto garments, and the use of clothing then became more habitual. At the Russian site of Sungir near Moscow which dates to 26,000 years ago, two human skeletons were covered with thousands of beads made from the tusk ivory of mammoths. These beads were evidently sewn onto garments and arranged in two layers, documenting the presence of underwear (Bader and Bader 2000).

Textiles began to replace animal skins as the preferred material for clothes from the end of the last ice age 12,000 years ago, based on thermal properties of woven fabric which permit perspiration to escape more easily. Fabric was a practical and comfortable material for people who continued to use clothes in the warmer and more humid weather conditions. Production of fibers for textile clothes featured prominently in early agricultural communities (with wool, linen and cotton), which may have been an impetus for the transition to agriculture (Gilligan 2007). The oldest preserved woven fabrics were made from hemp-like fibers 12,000 years ago in Peru (Jolie et al. 2011), followed by linen fragments in Turkey around 9,000 years old (Hodder 2013).

Psychology

The evolution of clothing reflects the influence of biology and climate in prehistory, but psychological and social aspects have become more important during the historical epoch. Psychosocial factors are relevant to why people continue to wear clothes and also to how clothing has shaped modern human behavior and social evolution.

Motives for Wearing Clothes

Humans now take the thermal function of clothes for granted: People can choose warm apparel from their home wardrobes based on weather forecasts and purchase new garments in local shops based on the latest fashions. The main functions in the contemporary world are the contradictory motives of adornment and modesty: display and cover.

Fashion is almost synonymous with clothing. In sociology and dress studies, the role of clothing in adjusting appearance is paramount. However, a

focus on clothes as dress can distract from another fundamental function in the modern world: the paradox of needing to conceal the naked body from view.

Modesty likely began as a psychological consequence of wearing clothes, although its origins are shrouded in mystery. Initially it would have involved behavioral learning processes, with a combination of classical (Pavlovian) and instrumental (operant) conditioning. Nakedness was associated with exposure and vulnerability, and social reinforcement of covering behavior involved both rewards and punishment. The result was not only a new need for clothes as personal and social display but a sense of inadequacy and shame about lack of cover, transmitted to offspring as an independent psychosocial phenomenon. More intriguing, the social requirement for cover mandates concealment of sexual organs as a minimum.

Sexual shame and guilt likely emerged as a consequence of clothing, beginning with modesty. The initial psychological processes again would have been behavioral: Sexual behavior is associated with the naked body, especially the unclad skin surface. Once nakedness was sanctioned, sexuality became more problematic for society and sexual pleasure became socially subversive. Sexual display was increasingly transferred to clothes: Ironically, the main material instrument of sexual repression serves as a major means of sexual attraction.

Sexual repression happens within both the individual and society, and the crucial transition occurs when sexual restraint becomes useful and productive. This involves psychodynamic processes, notably sublimation (e.g., Valdrè 2014). The sexual drive is harnessed and transformed (often beyond recognition), providing a seemingly infinite and renewable source of energy to enhance cultural and intellectual activities and also to form intimate material attachments and promote technological innovation. Societies come to depend culturally and economically on these processes, and in this manner the modesty function of clothing becomes indispensable.

Modesty was established by the end of the last ice age among descendants of people who had

developed complex clothes. Archaeological evidence for modesty and sexual shame appears in artworks that depict people wearing garments covering the genitalia. One of the earliest is found at the 11,000-year-old megalithic site of Göbekli Tepe in Turkey: Images are carved on the stone pillars which show humans wearing loincloths. These were made from fox pelts, with fox bones among the commonest faunal remains at the site (Peters and Schmidt 2004).

Effects of Wearing Clothes

As cover and enclosure of the body and an agent for controlling sexuality, clothing has immense psychological ramifications.

Enclosure becomes generalized as a preference to construct external enclosures, separating the human world from the natural environment. One postglacial trend was sedentism, the shift from a mobile lifestyle to living in permanent settlements. Sedentism represents a withdrawal from open engagement with nature and it reflects the emergence of a dualistic mentality. The stone walls and enclosures of the early villages (like Çatalhöyük in Turkey) act as a form of externalized clothing, symbolic of a domestication process whereby humans as well as wild plants and animals were tamed and controlled (Hodder 1990; Ingold 2008).

Cover likewise is generalized as perception of the world as covered. The workings of nature are no longer apparent and immediately accessible to the senses; instead, they are perceived as concealed and accessible through a process of uncovering.

Science is the most productive expression of this covered perception of reality: an intellectualized desire to discover (dis-cover). Mind-body dualism and the development of geometry and mathematics are further products of a separation of the mind from the physicality of bodily existence in the present. Geometry and mathematics emerge as pure abstractions necessarily devoid of any temporal or sensual connection, as does the written word and the symbolic potential of language (Derrida 1974; Husserl 1939).

Materialism is another psychological trait accentuated among people who routinely wear

clothes. In becoming intimately attached to clothes as a fabricated material, a personal attachment is generalized to other materials and especially artificial fabricated objects. This spurs technological innovation and promotes an economic dependence on the production of material goods, visible in modern market economies and with the rise of consumerism. Conversely, naked foragers were distinctly disinterested in material possessions (e.g., Dampier 1729).

Human aggression and warfare is amenable to analysis as a psychological by-product of clothing. One of the challenges for evolutionary psychology is to explain why a taste for violence appears to be natural for humans. Rather than fabricating adaptive scenarios for this maladaptive trait, it can be understood as an outcome of the control and suppression of sexuality that accompanies clothing. Where sexuality becomes concealed and largely taboo, violence is sexualized through association as an evil or forbidden form of physical contact. As with all sublimated pursuits, it then acquires a capacity to deliver ostensibly nonsexual gratification, which has implications also for the philosophical – and psychological – problem of evil. This scenario can accommodate the troubling attraction of violence and the pleasure (and entertainment value) of war, without the ethological contradictions involved in portraying it as a vestige of humanity's animal nature. Moreover, it is compatible with the ethnographic and archaeological data, which point to an absence of warfare in naked forager societies and its relatively late prehistoric development among complex (particularly agricultural) communities after the end of the last ice age (Fry 2013; Pardoe 2014).

Social Evolution

The transition from egalitarian to hierarchical social structures based on wealth accumulation and inequality of access to resources is one of the major recent trends in human evolution. Its causes remain unclear and explaining its origins represents one of the great challenges for archaeology.

Hunter-Gatherers and Nakedness

Egalitarian social relations are a hallmark of naked forager societies. Sharing of food and material resources was actively promoted and defended, while any attempts by individuals to acquire or accumulate material wealth were actively discouraged and prevented. Egalitarian principles and group altruism probably evolved in hominins for adaptive reasons (Boehm 2012). Nonegalitarian societies emerged quite late – after the end of the last ice age – and only where clothes were present.

The routine presence of clothes acts as a barrier to casual tactile and sensual contacts between people. Among other primates, these tactile connections are almost constant from birth and serve to maintain social cohesion; they form the basis of connections between individuals and function as the main means of conflict resolution. In humans, cultural evolution is accompanied by a marked reduction in skin contact, whereas among egalitarian hunter-gatherers where little or no clothing is worn, tactile skin contact occurs almost constantly in infancy and childhood (Hewlett 2014).

Grooming and frequent tactile (including sexual) contacts in bonobos serve a key role in maintaining egalitarian group structure and forestalling violence (de Waal 1997). Once clothing is interposed between people, it prevents these routine skin contacts and discourages sexual encounters. Clothing thus sabotages the sensual basis of egalitarian social relations and promotes materialism and aggression, contributing to the collapse of egalitarianism.

Clothing and Social Complexity

The evolution of complexity has both a negative side (loss of naked egalitarianism) and a positive side whereby sexual repression and sublimation promote cultural development, culminating in the emergence of civilization. Freud saw repression and sublimation of the sexual drive as intrinsic to civilization (Freud 1930) although he neglected clothing, mentioning only how concealment of the body might enhance curiosity and the sublimation of sexuality into artistic pursuits. However, insofar as cover causes modesty and sexual guilt, clothing may play a more central role.

Cross-cultural research shows that clothing, modesty, and sexual restrictiveness correlate with various indices of complexity on a global scale (e.g., Murdock 1964; Stephens 1972). The civilizing potential of sexual repression and sublimation is underlined by the fact that the sexual drive is especially strong in humans: By any standards, *H. sapiens* is comparatively hypersexual (Ryan and Jethá 2010).

Conclusion

Clothing is a uniquely human innovation and its evolution reflects adaptation to unusual selection pressures. Biological nakedness may have first evolved as an adaptation to heat stress among bipedal ancestors, but it subsequently posed a survival challenge for hominins due to cold stress during the Pleistocene ice ages. Among various theories about the origin of clothing, those that claim a role for decoration or modesty as initial motives can be refuted by ethnographic evidence, whereas a thermal model is consistent with all available lines of evidence, including recent genetic studies of human clothing lice.

While there exists no direct archaeological evidence of prehistoric clothes in the Pleistocene, paleoenvironmental and physiological data can be harnessed to infer its development based on minimum thresholds of cold tolerance and the thermal properties of clothing. Archaeological evidence indicates that as hominins began to occupy cooler environments over the last million years, they developed technologies linked to the manufacture of clothing. These tools include stone hide-scrapers and blades for cutting hides, as well as awls and needles for sewing which first appeared during cold phases of the last glacial cycle from 100,000 years ago. Clothing was the most complex invention of the paleolithic era, and it promoted technological advances associated with the middle and upper paleolithic transitions.

The first clothes were simple loose garments which would have been discarded when no longer needed for warmth. The invention of fitted garments and multilayer assemblages – complex clothing – was restricted to *H. sapiens*. Complex

clothing differed from simple clothing in that once more complex clothing was adopted, it acquired nonthermal functions that encouraged the continued use of clothing after the end of the Pleistocene.

The postglacial onset of warm and more humid weather led to a major change in clothing material: the shift from using animal skins to woven fabrics. Textile garments became more common from the beginning of the Holocene epoch 12,000 years ago, and an increasing demand for textile fibers played a role in the transition to agriculture.

Modesty emerged as a psychological consequence of routinely covering the human body, and along with the transfer of decorative functions from the skin surface to using the surface of clothes for display purposes, modesty became a psychological motive for wearing clothes. Clothing is implicated also in the development of sexual shame and repression as uniquely human phenomena.

Sublimation of the sexual drive was a fundamental psychological process in social evolution and the emergence of civilization. The role of clothing in causing modesty and sexual shame thus makes it a key factor, but its psychological effects extend further and contribute to a host of modern psychosocial traits. These include separation from nature, construction of an enclosed artificial environment, the scientific mentality and the propensity for violence and warfare that dominates the historical era. In more ways than one, clothing is the fabric of civilized life.

Cross-References

- [Human Ornamentation](#)
- [To Afford Protection Against Climate and Weather](#)

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Clothing is Distinguished from Terms Like Adornment, Costume and Dress Which Encompass Body Painting, Cosmetics, Scarification and Tattooing

► To Afford Protection Against Climate and Weather

Coalition

► Cooperation Among Fishes

Coalition Alliance

► Gang Affiliation

Coalition Formation

► Cooperation Among Nonchimpanzee, Non-human Primates

Coalition Leaders

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Synonyms

Group leaders; Internal status hierarchy

Definitions

Coalition leaders take the responsibility of coordinating the efforts of group members. Such positions are both high-risk and high-reward and are therefore more likely to be occupied by men.

Introduction

Living in coalitional groups afforded many benefits to humans' hunter-gatherer ancestors, but in order to reap those benefits, individual members

of the group needed to be able to coordinate their efforts. This need for coordination likely led to the emergence of evolved mechanisms for leadership and followership. Individuals in leadership positions are likely to reap greater benefits from the efforts of the group but also incur greater risk. Given the high-risk, high-reward nature of leadership, it appeals most strongly to men, who owing to their minimal investment in offspring, benefit greatly from large investments in mating. Positions of leadership are likely to increase men's mating opportunities through the greater monopolization of the group's resources that women find desirable, as well as women's attraction to men who have earned high positions of status. As a result, men are likely to compete with one another, more so than women, for leadership positions. Below, this theoretical rationale is elaborated upon, and research examining the leadership tendencies of men and women, as well as the reproductive benefits bestowed to leaders, is reviewed.

Coordination in Social Groups

Humans are highly social animals that gain many benefits from living in groups (Baumeister and Leary 1995). Throughout evolutionary history, hunter-gatherers faced unpredictable environments that presented a variety of survival and reproductive challenges (e.g., preparing adequate shelter, navigating, hunting, fighting predators, attracting suitable mates, and nurturing offspring). Many of these problems are best addressed by groups and may be nearly impossible to deal with as a solitary individual. As a result, humans are likely to possess psychological mechanisms for promoting their membership in social groups.

Yet solving complex problems as a group is difficult unless the actions of individual members are well-coordinated with one another. This coordination may be best achieved by the presence of group leaders (Van Vugt et al. 2008). Research has indicated that evolved mechanisms for leadership and followership likely emerged within the Pleistocene period. Without such mechanisms among individuals, groups would not be able to so easily

coordinate efforts to solve complex problems, such as hunting large game, defeating predators, and raiding other groups for resources. Research consistent with the idea that humans possess such mechanisms for leadership includes that by Brown (1991) indicating that leadership is a universal characteristic of human societies. Additionally, research suggests that leaders naturally emerge in leaderless groups when a challenge arises that requires coordination (Van Vugt and De Crème 1999).

Sex and Leadership

Leaders of groups are in positions to gain increased benefits from group efforts. For example, leaders receive greater levels of prestige and dominance, as well as larger shares of resources acquired by the group. All of these benefits can be converted to increased mating opportunities. However, the benefits of leadership come at a cost. Leadership positions often entail many hardships associated with seeking and maintaining prestigious roles. Often it is a requirement of those seeking leadership to engage in dangerous acts of dominance, as has been observed in hunter-gatherer societies (Chagnon 1988). In pre-industrial societies, roughly 33% of men were reported to be killed while competing for status and resources (Daly and Wilson 1988). When status is threatened, men may be resistant to submitting to the threat as this would result in a loss of prestige as well as opening oneself up to attacks from others witnessing their submission (Felson 1982). However, status contests present a clear risk to physical safety, particularly when one is outmatched. Leaders also open themselves to risk by the very actions that define their leadership. Leading a hunting expedition or an attack on an outgroup entails large risks to those who make the first move (Hackman and Wageman 2007; Van Vugt et al. 2008).

Given the high-risk entailed in acquiring high-status and positions of leadership, it is expected that men will be more likely to gravitate toward such positions. In short, this is because men experience greater variance in their reproductive

outcomes and failing to compete for status and access to mating opportunities could result in reproductive oblivion. In contrast to women, men's obligatory investment in parenting is quite low, thereby freeing up time and energy for investment in mating. This incentivizes a male reproductive strategy that is oriented toward short-term mating with an emphasis on the quantity of mates.

In this context, women are a limiting resource because of their large investment in offspring and low reproductive ceiling. Given this large investment, women practice a more long-term oriented mating strategy that emphasizes mate quality, in particular, a mate's ability to help provision offspring with resources. The result of men and women's divergent reproductive strategies is that men must compete with other men to gain access to mating opportunities. A man's level of prestige or status provides a good indicator of their ability to provide access to resources desired by females. As a consequence, there are large incentives for men to compete for status, prestige, and positions of leadership that directly or indirectly increase their mating opportunities. Given the ability of one male to monopolize mating access to multiple females, some men face the prospect of reproductive oblivion. This leads to an increase in men's tolerance for risky behavior in the service of protecting or increasing one's status.

Leadership roles within hunter-gatherer societies are also male-oriented owing to the nature of the leadership tasks, sexual dimorphism, and the division of labor. With a largely egalitarian social structure, leadership in hunter-gatherers is largely task-specific and "earned" based on one's expertise and skill. Many tasks for which leadership is essential, such as hunting and warfare, are male-dominated tasks that require physical strength. Provided the physical differences between males and females, men were more likely to emerge as leaders in hunter-gatherer groups.

Still today, there is evidence that males are more likely to emerge as leaders in leaderless groups (Eagly and Karau 1991). Research has also shown that when asked to list characteristics for leaders, there was greater overlap with characteristics identified as descriptive of "men in general" versus "women in general" (Brenner et al.

1989; Schein 1973, 1975). Along similar lines, females are evaluated less favorably as leaders than are men (Eagly et al. 1992; Eagly and Karau 2002). Moreover, a meta-analysis provided evidence of a prejudice against women leaders, and that the preference for male leaders is heightened when the leadership role is a stereotypically masculine role (Eagly et al. 1992).

Leadership Benefits

Although leadership positions are risky in nature, many benefits come from the ability to control group resources and one's level of status and prestige within a group. For example, in tribal societies, research suggests that high-status men benefit from better nutrition (Chagnon 1990), thereby increasing their ability to successfully deter rivals and rise to positions of leadership. Across cultures, women also show a preference for high-status men with greater access to economic benefits (Buss 1989). Accordingly, individuals in high-status positions produce more offspring (von Rueden et al. 2011; Wilson and Daly 1985). These findings support the notion that intrasexual competition among men serves the function of increasing men's attractiveness to women by climbing the group social hierarchy (Buss and Shackelford 1997; Daly and Wilson 1978).

An examination of coalition leaders throughout history clearly illustrates the connection between leadership, status, and reproductive success. For example, Genghis Khan, leader of the Mongol Empire, has a long genetic lineage that still exists today. Research suggests that 8% of men residing within a large region of Asia are descendants of Khan and his male-line relatives (Zerjal et al. 2003) and that 0.5% of the world's population may be genetically related to Genghis Khan. In tribal societies such as the Yanomamö, high-status men typically have greater numbers of wives than low-status men in their polygynous society. Specifically, it has been documented that headman and warriors of the Yanomamö have more wives, more extramarital affairs, and more offspring (Chagnon 1988; Chagnon 2013). The

importance of high-status in acquiring mating opportunities is also well-illustrated by the plight of low-status men. For instance, in what is now considered northwest Germany, or Krummhörn, men of low status were four times more likely than men who were in higher social positions to have their genetic lineage extinguished (Klindworth and Volland 1995). Overall, these examples illustrate the connections between leadership and reproductive benefits for high-status males cross-culturally and throughout history.

Conclusion

As a social species, humans reap benefits from living in groups. However, extraction of such benefits requires coordination of efforts among members. Psychological mechanisms for leadership and followership were likely the result of a need for a leadership role to serve this function. Those who take on leadership positions tend to receive greater benefits obtained by the group. This includes tangible resources, as well as the indirect increase in mating opportunities as a result of high-status and resource access. Yet leaders must also tolerate greater risk, such as the consequences of physical dominance displays and conflict intervention. Given the high-risk, high-reward nature of leadership, and the task-oriented style of leadership that was pervasive among hunter-gatherers, men have been more likely to occupy positions of power and leadership. Indeed, provided the zero-sum nature of intrasexual competition for men, opting out of status competition is not a reproductively viable option. Evidence from both the modern labor market and tribal societies illustrates these principles in action, such that men are more likely than women to strive for positions of high-status and leadership.

Cross-References

- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)

- ▶ Reputation
- ▶ Sex Differences in Same-Sex Aggression

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Coalition Members

- ▶ Same-Sex Relationships

Coalitional Aggression

- ▶ War More Likely with Higher Likelihood of Success

Coalitional Hunting

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Synonyms

Cooperative hunting; Group hunting; Hunting strategies

Definition

The collaborative effort to pursue and kill animals for food and other natural resources necessary for survival.

Introduction

Typical diets of the species of early humans, or *hominids*, have oscillated since the rise of the first primates. Although modern humans, often referred as *homo sapiens*, like ourselves, are omnivorous and are not restricted to eat only meats or vegetables, famine was always a lingering threat. As populations of humans expanded exponentially, demand for food skyrocketed while food supply plummeted.

Hunting for game larger than rodents and other smaller animals, such as bison and mammoths, satisfies the basic need for a larger band of humans to eat and survive. The endeavor to hunt larger animals is facilitated when done in groups rather than done by a single individual. Coalitional hunting not only provides more food for larger bands of humans, it also provides a crucial advantage to those who practice it over those who do not.

The physical and mental traits to better hunt and cooperate are embedded in human's biological and cultural evolutionary history. Traces of the effects of the extensive history of coalitional hunting on modern *homo sapiens* are what define archaic *homo sapiens* as *hunter-gatherers* and these effects are under the scientific scrutiny of evolutionary psychology.

Evolution of Coalitional Hunting

The culture of carnivores and predators are founded on their hunting instincts and skills. Although humans today do not hunt or scavenge on a basis, meat is a central feature of the human diet (Bailey et al. 2012). Modern humans are offspring of profound *homo sapien* hunters; many features that characterize a human, such as the ability to run long distances, having eyes facing forward, and having predilections to commit

kill, are reasons to claim ancient humans as hunter-gatherers. This *Hunting Hypothesis* acknowledges the natural athleticism of *homo sapiens* and of earlier hominids and implies that hunting alone was far more dangerous than hunting with others (Ardrey 1976; Bailey et al. 2012).

For millennia, humans have been hunting and eating meat (Ardrey 1976), but small game like rabbits, ducks, and wolves were not sufficient to sustain a hundred or dozens of humans, especially right after the ice age or other major climate changes (O'Neil 2014). Hunting larger game like reindeer, horses, and mammoths is an extremely difficult feat for one hunter; henceforth, adopting a new hunting strategy was in order.

Homo sapiens are not the only primates to practice cooperative hunting. Chimpanzees are known to sometimes coordinate themselves while pursuing prey (Melis and Semmann 2010). Scholars consider coalitional hunting to be rooted so deeply in human nature that it contributes to some physical and psychological differences between the sexes. Anthropologists are in general consensus that male *homo sapiens* predominantly had the occupation of hunting and most of which were kin (Wrangham 1999; Bailey et al. 2012).

For the Ache tribe in Paraguay, *persistence hunting*, a form of coalitional hunting, usually includes two to four hunters, which sometimes yields more than three times the amount of game killed per hunt with one hunter (Liebenberg 2008). In Europe, *homo sapiens* domesticated wolves and hunted with dogs, which may have played a major role on the extinction of lions, hyenas, mammoths, bison, and even the Neanderthals (Shipman 2015; Liebenberg 2008). Coalitional hunting was a powerful asset to human evolution that it may even be held accountable for the evolution of cooperation and social order (Melis and Semmann 2010).

Effects of Coalitional Hunting on Homo Sapiens

Coalitional hunting was more than a means to obtain a larger food supply (O'Neil 2014; Harari

2015). Saving time and energy, especially during times with limited hunting opportunities (Bailey et al. 2012), could aid the survival of much more than a single individual. From a gene's perspective via inclusive fitness, related individuals who receive any survival benefit are evolutionary advantageous (Melis and Semmann 2010; O'Neil 2014) and *any* individual involved with the coalition is likely to receive similar fitness benefits (Bailey et al. 2012).

Over time, coalitional hunting has granted humans with opportunities to advance their tools, strategies, and skills. Spears and other weapons became more sophisticated and individualized (O'Neil 2014); homo sapiens evolved the ability to throw projectiles with precision and accuracy; and social structures became more complex as populations increased (Melis and Semmann 2010). Moreover, the illusion for nature to select individuals evolved to the illusion for nature to select groups of individuals.

Species that practice planned and intricate hunting strategies is very likely to possess a mentality that permits higher order cooperation. Communication of information such as the locations of food, water, and lethal predators can separate the ones that survive from the ones that do not (Bailey et al. 2012). Homo sapiens acquired functional linguistic skills, which inadvertently expanded their populations (Harari 2015). The humans were not the only species to interpret and display communicative signals, domesticated dogs evolutionarily benefit with the ability to interpret symbolic behavior from their human masters (Bailey et al. 2012).

Other prestigious cognitive traits that are considered to have evolved from human's coalitional hunting nature include: memory for mapping their territories (Harari 2015); mental capacities to learn or become classically conditioned in order to predict when and when not to invest time and energy wisely (Bailey et al. 2012); the ability for the coalition members to focus their attention in unison; and even empathy and theory of mind (Moll and Tomasello 2007).

Coalitional Hunting and the Evolution of Human Psychology

As populations of humans grew exponentially, traits that engender higher social and emotional intelligence become advantageous adaptations. Evolutionary psychologists claim, even outside of homo sapiens, that there are psychological mechanisms that reduce aggression between group members and promote information-sharing (Bailey et al. 2012).

Evolutionary social psychology embraces what Robert Trivers called *reciprocal altruism* (Melis and Semmann 2010). Cooperation requires coalition members to practice specific policy orders and even morals (Bingham and Souza 2012). Psychological mechanisms that (1) aid in the determination of who contributed what and (2) to whom are the contributions addressed to reduce instances of free-riding and enhance perceptions of one's coalition or in-group; however, such perceptions may produce undesirable behavior and actions towards those who belong to an out-group (Wrangham 1999). Being ostracized, having negative reputations, and other certain punishments has a universal effect on species as social and intelligent as homo sapiens. Some evolutionary psychologists theorize that there are mechanisms that help prevent such dangerous consequences like ostracism (Melis and Semmann 2010).

The traits that characterize a charismatic leader such as decision-making, communication, and understanding other's limitations in order to assign proper roles may have originated in circumstances similar to coalitional hunts (Bailey et al. 2012; Moll and Tomasello 2007). Arranging into a populated social structure that obeys one or a group of leaders is a prerequisite of political policy. Paul Bingham and Joanne Souza (Bingham and Souza 2012) also recognized that a tribe's population is likely to be of a certain kinship, which serves a motivation to belittle outsiders or nonkin. Coalitional hunting, in essence, appears to meet the criteria as being a powerful and natural force that drove the cognitive revolution of humans.

Conclusion

Linguistic skills, memory for kin and other members and their roles, cooperation, and other social intelligence skills are at the forefront of both traditional social psychology and evolutionary social psychology. The attributes that compose a virtuous leader, the social infrastructures that constitute democracy, and a basis of morality may be of heritage of the ancient occupation of coalitional hunting. Evolutionary psychology, among other disciplines, accepts and examines the influential role of coalitional hunting on human psychology. The attributes that embody a prosperous hunting coalition during prehistoric times can still be observed today in modern human behavior.

Our hominid ancestors have been hunting as a means to obtain meat long before the evolution of the first primates. While evolutionary anthropologists and psychologists accredit coalitional hunting with both the mass extinction of other species including the Neanderthals and the humans' domination of the globe, further research awaits in order to establish the deep relationship between coalitional hunting and cognitive psychology (Bailey et al. 2012).

Cross-References

► Male Coalitions for Hunting

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Coalitional Mate Retention

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Definition

Mate retention behaviors performed by allies (solicited or unsolicited) that function to reduce the risk of partner infidelity.

Introduction

A long-term partner's sexual or emotional infidelity inflicts costs on both men and women, such as increasing the risk of contracting sexually transmitted diseases and inducing psychological distress, such as depression and anxiety. In fact, partner infidelity is the leading cause of relationship dissolution.

Men and women also incur sex-specific costs from partner infidelity, stemming from asymmetries in reproductive biology. Due to

internal fertilization and gestation occurring in women, ancestral men were uncertain that they were genetically related to their romantic partner's offspring. Thus, men are at risk of investing resources into genetically unrelated offspring. In contrast, ancestral women had maternity certainty. However, when they were rearing children (e.g., nursing), women relied heavily on male-provisioned resources. A woman whose partner is unfaithful risks losing partner-provisioned resources to another woman. Over evolutionary time, the sex-specific costs of a romantic partner's infidelity have produced sex-differentiated mate retention behaviors that appeal to opposite-sex mate preferences. For example, men (more than women) display their status and resources, whereas women (more than men) highlight their reproductive value and attractiveness (Buss and Shackelford 1997).

Given the costs associated with a romantic partner's relationship defection, individuals have motivation to perform "mate retention" – behaviors that minimize the risk of partner infidelity or defection. Individuals use several different mate retention strategies concurrently (Barbaro et al. 2015). One mate retention strategy individuals use is *individual mate retention* – behaviors that are performed by the individual without assistance from others (Buss 1988). Another strategy is when individuals recruit a close ally, such as a friend, to perform mate retention behaviors for them. Recruiting an ally to perform mate retention is a strategy referred to as *coalitional mate retention* (Pham et al. 2015a).

Evidence of Coalitional Mate Retention

Individual mate retention behaviors (i.e., behaviors performed without the assistance from allies) have been investigated by social and evolutionary psychologists for several decades. Empirical investigation of coalitional-level mate retention behaviors (i.e., behaviors performed with assistance from allies), however, went uninvestigated. Examination of instruments designed to assess individual-level mate retention behaviors provides peripheral evidence that individuals do

request the assistance from others to aid in their mate retention efforts of their romantic partner. For instance, a widely used measure to assess individual mate retention behaviors is the Mate Retention Inventory (Buss and Shackelford 1997; Buss et al. 2008). Two items in the Mate Retention Inventory (e.g., "had my friend check up on my partner," "got my friends to beat up someone who was interested in my partner") suggest that individuals do request assistance from others to perform mate retention behaviors. Another widely used instrument that assesses mate retention behavior is the relationship maintenance behaviors inventory (Stafford and Canary 1991). Although this measure does not directly measure coalitional mate retention, this inventory focuses on how cooperation and social networks promote healthy romantic relationships. These social network behaviors (e.g., "focus on common friends and affiliations") suggest that allies are instrumental for mate retention.

Further evidence of coalitional mate retention comes from historical and comparative documentations. For example, kings regularly recruited guards to protect their harem (Lad 2011). Additionally, many nonhuman species recruit allies for coalitional mate retention. For example, in lions, a coalition of males is more successful than a single male at defending sexual access to a female against rivals (Grinnell et al. 1995). Male macaques may form coalitions to overpower higher-ranking males to secure sexual access to fertile females (Bissonnette et al. 2011). Males of other species also sometimes form alliances with other males to defend sexual access to females as has been documented in cheetahs (Caro 1994), chimpanzees (Watts 1998), and dunnocks (Davies 1992).

Benefits and Costs of Coalitional Mate Retention

Coalitional mate retention can potentially overcome some costs of individual mate retention behaviors. Excessive use of individual mate retention may cause one's romantic partner to perceive them as overbearing, excessively jealous, and

mistrustful – which can reduce relationship satisfaction and, potentially, relationship dissolution. Individuals can reduce their partner's perception of excessive individual mate retention by employing coalitional mate retention. A person using coalitional mate retention can appear more trusting to their partner – for example, by having a friend accompany their partner to a social gathering where rivals may be present – and simultaneously reduce the risk of partner infidelity.

Employing coalitional mate retention could also increase one's perceived mate value to their romantic partner. Individuals mated to a less desirable partner are more likely to terminate a romantic relationship or commit infidelity (Shackelford and Buss 1997). Individuals can request that an ally advertise their positive qualities to their partner for them, thereby avoiding the costs of appearing narcissistic if they advertise their positive qualities themselves.

There are potential costs to coalitional mate retention. Individuals who recruit same-sex allies to perform coalitional mate retention are at risk for their ally poaching their romantic partner. Mate poaching may be particularly problematic when requesting coalitional mate retention – this strategy may signal to an ally that one's relationship is unstable and sometimes requires that an ally spend time with a romantic partner. Individuals who recruit opposite-sex allies to perform coalitional mate retention risk being a target of their ally's mate poaching attempts. Individuals sometimes befriend opposite-sex friends with the intention of mate poaching (Schmitt and Buss 2001), and friendship is one strategy individuals use to poach individuals away from their romantic partners (Mogilski and Wade 2013).

The Coalitional Mate Retention Inventory

Indirect evidence suggests that allies, such as friends, play important roles in helping individuals retain a romantic partner. Formal investigation of coalitional mate retention behavior began

the development of a measure designed to assess the frequency with which coalitional-level mate retention behaviors are utilized. Across two studies, Pham and colleagues (2015a) developed and validated the Coalitional Mate Retention Inventory using data- and theory-driven methods. Study 1 (Pham et al. 2015b) utilized an act nomination procedure (Buss and Craik 1983), asking 100 participants recruited via social media websites to report up to ten acts that they (or someone they know) asked their friend or relative to do to prevent their partner from becoming interested in someone else.

The acts obtained in Study 1 were then given to a separate sample of 387 participants recruited via Amazon's Mechanical Turk in Study 2. These participants were instructed to think of one heterosexual man and one heterosexual woman that they considered a good friend. For each friend, participants reported (1) how often they *requested* their friend to perform each behavior during the past year and (2) how often they believed their friend *performed* that behavior during the past year. Similar to the Mate Retention Inventory developed by Buss (1988), the Coalitional Mate Retention Inventory utilized the four-point scale (0 = *never*, 1 = *rarely*, 2 = *sometimes*, and 3 = *often*) to afford comparison between the two mate retention strategies.

The Coalitional Mate Retention Inventory includes 44 coalitional-level mate retention behaviors across seven tactic categories. The *Manipulation* component includes behaviors in which an ally deceives the partner into admitting (e.g., “got my partner drunk to see what my partner said”) or demonstrating (e.g., “tried to ‘hook up’ my partner with someone else to see what my partner did”) the partner's propensity to commit infidelity. The *Praise* component includes behaviors in which an ally says positive things to the partner and to others (e.g., “said nice things about me when my partner and other people were around”), thereby increasing the romantic partnership's desirability. The *Vigilance* component includes behaviors in which an ally watches the partner's behavior (e.g., “observed how my

partner acted around people interested in my partner”). The *Monopolizing* time component includes behaviors in which an ally spends time with the partner (e.g., “accompanied my partner to a party”). The *Therapy* component includes behaviors in which an ally strengthens the romantic partnership by repairing relationship problems and listening to relationship concerns (e.g., “told my partner how much I liked my partner”). The *Gifts* component includes behaviors in which an ally secures information about appropriate gifts for the partner (e.g., “told me what gifts my partner wanted”). The *Violence* component includes behaviors in which violence is employed against potential mate poachers (e.g., “hit someone who was flirting with my partner”).

Empirical Research on Coalitional Mate Retention

Concurrent strategies. Research investigated the frequency in which individuals employ coalitional mate retention as a function of individual differences, and contexts in which coalitional mate retention may be more readily utilized. Initial investigation of coalitional mate retention behaviors centered on whether coalitional mate retention is used concurrently with other mate retention strategies or used as a compensatory mate retention strategy. Previous research has demonstrated that, for men, individual mate retention behaviors are positively correlated with in-pair copulation frequency (Shackelford et al. 2006) – another type of mate retention strategy employed by males to prevent the risk of cuckoldry (Barbaro et al. 2015). This work suggests that individuals may use mate retention strategies concurrently to exhaust all potential mate retention efforts to reduce the likelihood of partner infidelity. Initial research to further investigate the relationships between coalitional mate retention and other mate retention strategies largely supports the notion that individuals use various mate retention strategies concurrently. Specifically, tactics of coalitional mate retention are positively

correlated with tactics of individual mate retention (Pham et al. 2015a), suggesting that individuals who deploy more frequent individual mate retention also deploy more frequent coalitional mate retention. Similarly, coalitional mate retention is positively correlated with in-pair copulation frequency (Barbaro et al. 2015), suggesting that individuals who deploy more frequent coalitional mate retention also copulate more frequently with their romantic partner.

Friendship quality. Because coalitional mate retention necessarily involves an ally, the quality of a friendship with an ally is likely to influence the frequency of coalitional mate retention. Research investigated whether requests of coalitional mate retention and unsolicited performance of coalitional mate retention differed as a function of friendship quality involving male and female friendships (Pham et al. 2015b). Results from Pham et al. (2015b) indicate that requests for coalitional mate retention are positively associated with the quality of friendships involving women (i.e., male–female friendships, female–male friendships, and female–female friendships) but are negatively associated with the quality of male–male friendships. The negative relationship between friendship quality and coalitional mate retention in male–male friendships may result because men, relative to women, inflict heavier retaliatory costs on mate poachers. For example, a man who poaches his male friend’s romantic partner risks potentially fatal retribution by the man (e.g., Daly et al. 1982). Coalitional mate retention may be less likely to be deployed between male friends who are especially close friends because poaching – and even the mere appearance of poaching – is a potent violation of male alliance.

Personality. Requesting coalitional mate retention is further influenced by individual differences in personality. Research has investigated whether the personality traits that predict performance of individual mate retention performance (e.g., Holden et al. 2014) extend to coalitional mate retention (Pham et al. 2016). Individuals lower in honesty–humility and higher in extraversion report less frequent requests for coalitional

mate retention. Men (but not women) higher in emotionality and lower in openness more frequently request coalitional mate retention, suggesting that coalitional mate retention might be employed more frequently by men who are less willing to communicate with their partner. It appears, more generally, that dishonest individuals are more likely to request coalitional mate retention, suggesting that coalitional mate retention – as compared to individual mate retention – is associated with manipulative and deceitful personality types (Pham et al. 2016).

Parity. Coalitional mate retention may be more frequently used by romantic partners who share offspring. Humans – unlike other primates – form long-term pair bonds. Men and women may remain pair-bonded following their child's birth to promote offspring survival by provisioning resources and providing protection from infanticide. Barbaro and colleagues (2016) documented that mothers and fathers perform more frequent coalitional mate retention than individuals without children. Specifically, men and women who share genetic children with their current partner more frequently request coalitional mate retention behaviors – across all seven tactics – from both their male and female ally than men and women who do not share genetic children with their current partner.

Conclusions

Coalitional mate retention behaviors are performed, solicited and unsolicited, by an individual's ally (e.g., a friend) to reduce the likelihood of a romantic partner's infidelity or defection from a romantic relationship. Coalitional behavior in the domain of romantic relationships was not an explicit area of study until Pham et al. (2015a) developed the Coalitional Mate Retention Inventory to assess the frequency with which individuals request coalitional mate retention from their allies and how often an ally performs coalitional mate retention unsolicited. Coalitional mate retention encompasses the intersection of mate retention behavior and coalitional behavior: two ubiquitous features of human life. Research has

begun to investigate relationships between coalitional mate retention and individual differences and dyadic process. There remain open numerous profitable avenues of research regarding coalitional mate retention.

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► Mate Retention

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Coalitional Partner Choice

- [Mechanisms to Prefer Traits in Coalition Members](#)

Coalitional Psychology

- [Male Adaptations that Facilitate Success in War](#)

Coalitional Relationships

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Synonyms

[Alliance formation](#); [Intergroup competition](#); [Social support](#)

Definition

Coalitional relationship: coordinated and cooperative action among two or more individuals against some third party or parties.

Alliance relationship: reliable co-participation in coalitional action over time.

Introduction

Coalitions are ubiquitous among humans and nonhuman primates (Chapais 1995; Cheney and Seyfarth 2008; Macfarlan et al. 2014; Patton 2000; van Schaik et al. 2006; von Rueden et al. 2008; Watts 1998). Coalitions are an important component of social dynamics by altering how power is distributed across individuals within and between groups and importantly affects fitness outcomes. Human warfare, politics, and economic behavior are coalitionally based and operate in a social landscape populated by like coalitions comprised of and connected by alliance relationships. Importantly, primates exhibit considerable variation in patterns of coalition and alliance formation. This chapter first details the key configurations that alliance relationships and

coalitional action can take among primate species. Then the importance of coalitions and alliances in humans will be addressed as well as their connection to the topics of the evolution of egalitarianism, hierarchy and status-striving, and cooperation in group-based conflict.

Coalitions in Primates

Considering the ranks that can be occupied by different individuals in a dominance hierarchy, three types of coalitions had been described in the literature: (i) conservative, (ii) bridging, and (iii) revolutionary (Chapais 1995). Conservative (i.e., all-down) coalitions are established when two or more high- or middle-ranked individuals attack a lower-ranked target (Chapais 1995). The outcome of this coalition does not upset the hierarchical order but rather preserves it. In nonhuman primates, such as in chacma baboons (*Papio ursinus*), high-ranked females living in female philopatric societies may not only receive support from other high-ranked kin within the matriline but also from females ranking immediately below (Cheney and Seyfarth 2008). By receiving support from female kin and from unrelated dominant females, high-ranked matrilines display greater cohesiveness, relative to lower-ranked families (Cheney and Seyfarth 2008). Thus, whereas low-ranked females should choose to support either a high-ranking unrelated female or her low-ranking kin, dominant females do not face such a social dilemma (i.e., the Anna Karenina principle; Cheney and Seyfarth 2008).

Intersexual conservative coalitions have also been described. For example, in multi-male polygynandrous societies, exhibiting long gestation and lactation periods, middle- or high-ranking females may seek support from a male against an invading or rival male due to the risk of infanticide or other expressions of sexual coercion (e.g., sexual intimidation and harassment; Lemasson et al. 2008). In olive baboons (*Papio anubis*), the number of male supporters or friends has been found to be positively associated with the rank of the female in the dominance hierarchy (Lemasson et al. 2008).

Male conservative coalitions in male philopatric societies differ from those observed among females living in matrilineal associations. Due to paternal uncertainty, kin-based cooperative mechanisms, such as kin selection and inclusive fitness, may not be sufficient for the formation of coalitions and alliances among males living in polygynandrous societies (van Schaik et al. 2006). Hence, cooperation based on mutualism, reciprocity, and/or biological markets (e.g., negotiating the exchange of commodities in accordance with the current demand and offer in the market) may allow the supporter of a high-ranking male to obtain benefits by preserving the hierarchy. Male chimpanzees (*Pan troglodytes*), at Kibale National Park, in Uganda, have been observed to collectively guard periovulatory females, tolerating the copulations of male allies, and preventing estrous females from copulating with rival males outside the coalition (Watts 1998).

Different from conservative bonds, in bridging coalitions, the association is constituted by a high- and a low-ranking partner against a middle-ranking target (Chapais 1995). By joining forces with a high-ranking member, the low-ranking member attacks and deposes the middle-ranking target and ascends in the hierarchy. Rank inheritance, the ascent in the dominance hierarchy based on the rank occupied by a relative, is a correlate of bridging coalitions (Chapais 1995). Rank inheritance has been described in both female philopatric societies (Chapais 1995) and in societies with female dispersal.

Besides the effects of maternal social status in rank ascent, intersexual bridging coalitions between nonrelatives require future exploration. Some evidence regarding female dispersal and male policing would support its occurrence. Immigrant female chimpanzees, for example, are frequent targets of aggression from resident females after joining a new group (Kahlenberg et al. 2008). Furthermore, the high urinary cortisol and low-status ranking would indicate the precarious condition experienced by immigrant females. Affiliating with a protective male allows dispersing females to decrease the risk of aggression when joining a new group (a similar process has

been observed in mountain gorillas; *Gorilla beringei beringei*; Kahlenberg et al. 2008). It is worth noting, however, that additional evidence is needed to determine whether females do ascend in rank as a product of male policing or if male protection of immigrant females is an expression of a bridging leveling coalition.

Finally, in revolutionary (i.e., all-up) coalitions, a high-ranking target is attacked by two lower-ranking members. Revolutionary associations have been described in male philopatric societies (Chapais 1995). For example, in captive chimpanzees, middle- and low-ranking males had been observed to join forces and depose a high-ranking male allowing the allies to rise in the hierarchy (Chapais 1995). However, in contrast with conservative and bridging coalitions in matrilineal societies, revolutionary coalitions are considered to take place infrequently (Chapais 1995).

More recent analyses have further subdivided the latter coalitional classifications into rank-changing and leveling coalitions. In rank-changing coalitions, individuals may depose or displace rivals in hierarchy. In leveling coalitions allies may not ascend in their ranks but rather temporarily gain access resources or receive protection during an agonistic interaction (van Schaik et al. 2006).

Coalitions in Humans

Across human societies, alliances and coalitional processes underpin systems of dynamic social power, affecting the establishment of both more and less egalitarian social arrangements. Further, coalitional phenomena are fundamental to understanding intergroup violence in humans.

Interestingly, coalitional processes have been hypothesized to contribute to the unique egalitarianism that characterizes most extant hunter-gatherer societies. A distinguishing feature of human political and social organization in comparison to that of chimpanzees is the variance in hierarchical power across societies. This variance has been described as the U-shaped trajectory of egalitarianism in human evolution (Knauff et al.

1991). Where at one end of the U, it is presumed that the last common ancestor of humans and chimpanzees was highly despotic and hierarchical, like extant chimpanzee populations. The lower trough of the U represents the political egalitarianism that characterizes extant foraging societies and likely the types of societies in which most of human evolution occurred, with the rising right end of the U representing the increasing hierarchy and despotism common to more complexly organized types of human societies, i.e., chiefdoms, archaic states, and civilizations. This model exhibits the precarious egalitarianism in foraging societies, which is underpinned by coalitions that function as leveling mechanisms that quell aggrandizing individuals from establishing themselves at the top of an incipient dominance hierarchy (Knauff et al. 1991).

However, coalitional support can grant as well as deny social differentiation by augmenting relative differences in power between individuals in potential contest competition. Evidence shows that coalitional support is an important predictor of multiple forms of social status among Tsimane men, a forager-horticulturalist group in the Bolivian Amazon (von Rueden et al. 2008). Social status is broadly defined as relative access to resources within groups. This influence of coalitional support on status differences is important considering how robustly status is associated with male fitness across a large sample of societies (von Rueden and Jaeggi 2016), which suggests that this status-fitness association is a possible human universal.

Coalitions are also a crucial element of human intergroup violence (i.e., warfare) and our understanding of this context as a cooperation dilemma. Namely, why should individuals take on personal risk of injury and death which benefits unrelated individuals in their coalition or in a larger group from which their coalition is derived? Despite the importance and interest in this topic, there is yet no consensus view regarding the ultimate evolutionary explanation that accounts for coalitional conflict.

Individual benefits to warriors do seem important in some contexts, such as for Yanomamö *unokai* (men who are recognized as killing an

enemy in conflict). In comparison to non-unokai, unokai have twice as many wives and three times as many children. This relationship survives a more robust statistical approach (i.e., Poisson regression with robust standard errors controlling for age, number of wives, and headman status; Macfarlan 2015), alleviating the criticisms often targeted toward the primary research.

In parallel, Patton (2000) shows that Amazonian Achuar and Quichua men are allocated status to the extent that they are perceived as distinguishing themselves in coalitional conflict, conditional on coalitional membership, and alliance strength, i.e., the condition that status allocators are likely to benefit from a warrior's behaviors in future conflict. Therefore, engaging in individually risky intergroup conflict can be an adaptive strategy for status acquisition in coalitional contexts.

Alternatively, costly coalitional conflict could result from the operation of group-structured cultural selection. Evidence includes the importance of social norms among the Turkana pastoralists of East Africa, which favor the punishment of cowards in large-scale battle raids and that hostilities should be directed toward other ethnolinguistic groups and never toward other Turkana territorial sections (Zefferman and Mathew 2015). Further, the cultural group selection model of cooperation is supported by assessment of cultural and genetic F_{st} measures, which gives the ratio of between-group variability in traits to total population variability. Notably cultural F_{st} is much greater between small-scale societies than genetic F_{st} , which suggests that cultural variation is better able to structure large-scale cooperation within societies in service of conflict against other ethnolinguistic groups (Zefferman and Mathew 2015).

Conclusion

Coalitions are a fundamental aspect of human and primate sociality. Among primates in general, they determine access to critical resources via contests within groups at the interindividual level. Though as identified here alliance relationships are expressed in varying patterns across species and for different purposes. Importantly,

these patterns also occur on a much larger scale in humans. However, the specific nature of the selection pressures operating to augment basic primate coalition formation to produce these patterns in humans is an active and a yet unsettled topic of research.

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relating to frequency. Based on evidence from paleontological studies, cochlea seems to have been originated from the basilar papilla (hair-cell epithelium for hearing) of the stem amniotes such as lepidosaurs, archosaurs, and mammals. Further evidence of this statement is from a relative of the ancestors of land-living vertebrates, namely the “living fossil” coelacanth fish *Latimeria chalumnae*.

Coalitionary Killing

► Chimpanzee Raiding

Coalitions

- Cost of Same-Sex Friendships
- In-Group Versus Out-Group
- Male Coalitions for Hunting
- Peer Groups
- Same-Sex Friend

Cochlea

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Synonyms

Inner ear; Organ of Corti

Definition

An important structure in the inner that is responsible for the analysis of sound.

Introduction

The cochlea is a snail-shaped structure in the inner ear and it is responsible to separate sound

Structure of the Cochlea

The cochlea looks like a snail and is comprised of fluid-containing compartments in the form of a spiral, and it contains the organ of Corti, which is the receptor for hearing (Chang and Khana 2013). In humans the cochlea is about 2.5 turns and if it is uncoiled it reaches a length of 3.1–3.3 cm. Its height in humans is 0.5 cm and it is similar in small animals such as the chinchilla. Together with the vestibular organ, the cochlea is enclosed in the temporal bone (Moller 2013). More than 15,000 hair cells in each cochlea are stimulated by the vibrations of the inner ear fluid. This motion causes the inner hair cells to produce electrical signals that are perceived by the brain as hearing (Balkany and Brown 2017).

Function of the Cochlea

Specifically, the cochlea separates the sounds according to the frequency so that different sound spectra activate different auditory nerve fibers. This sensory transduction takes place in the inner hair cells. The outer hair cells are active micromechanical elements that help to reduce friction on the motion of the basilar membrane. They, also, increase the vibration breadth of the basilar membrane for the lower intensities of sound and increases frequency selectivity. Also, the intensity of sound plays a significant role here because the frequency selectivity decreases when the intensity of sound is increased which in turn causes the cochlea to function in a nonlinear way. This nonlinear function delivers amplitude compression of the sounds before the innervation of

the auditory nerve. This process serves to code sounds in the auditory nerve based on the sound intensities (Moller 2013).

Furthermore, the function of the cochlea is to produce various kinds of sounds which are directed through the middle ear, triggering the tympanic membrane, which subsequently produces sounds known as the optoacoustic emission (OAE). This is, essentially, a sensitive microphone in the ear canal that records produced sounds (Moller 2013). Moller noted that there are many kinds of OAE such as: (a) the transient evoked optoacoustic emission (TEOAE), which is provoked by a momentary sound and produced by a reproduction of the traveling wave on the basilar membrane; (b) the spontaneous optoacoustic emission (SOAE), which is a continuous sound that is produced without any applied sound to the ear; (c) the distortion product optoacoustic emission (DPOAE), which is a measure of nonlinear alteration in the cochlea. This is provoked by applying two tones to the ear, and measuring the breadth of the tone difference (Moller 2013).

Evolutionary Status of the Cochlea

Based on comparative and paleontological studies, there is a possibility that a specific hair-cell epithelium for hearing (a basilar papilla) already existed in stem amniotes (lepidosaurs, archosaurs, and mammals) but was very small (Manley 2010). Evidence of this statement is based on a relative of the ancestors of land-living vertebrates, namely the “living fossil” coelacanth fish *Latimeria chalumnae*. Fritsch (1987) noted that the basilar papilla seems to be the precursor of the cochlea in mammals. Mammalian ancestors and ancestors of other amniote clades inherited a small basilar papilla for low frequency processing sounds (Manley 2000). Therefore, hearing high frequency sounds is not ancestral in the amniotes, nor in mammals but it was developed during the early evolution of therians (marsupials and placentals). According to Köppl (2011) the basilar

papilla is the organ of Corti in mammals, and it is homologous between birds and mammals.

The features of the therian cochlea was developed over millions of years, resulting in the loss of the lagenar macula – something which led to the decrease in endolymph calcium levels. Apparently, this led to a structural revolution of the auditory physiology of the cochlea (Manley 2017).

Based on comparative auditory research, the ears of birds and mammals are similar in function (see Dooling et al. 2007, on the processing of harmonic complexes on a number of different species), but are different in terms of precise temporal resolution for complex sounds – a trait that favors the birds (Dooling et al. 2002). Specifically, one major difference between mammals and birds is related to cochlear dimensions, which result in a frequency-dependent cochlear response delay (Dooling et al. 2007).

Organ of Corti

Another structure located inside the cochlea is the organ of Corti, which is composed of a specialized structure containing the hair cells together with their nerve endings and supporting cells. The organ of Corti is located on the basilar membrane and it organizes the auditory transduction. It becomes rigid by an arch of rods or pillar cells across its length, with the upper ends of the rods ending in the reticular lamina, which forms the chemical reaction between the ions in the fluids of the scala media and the scala tympani. The arch of rods is enclosed by phalangeal cells. The inner phalangeal cells enclose the inner hair cells, and the outer phalangeal cells (known as Deiters' cells) hold the basal ends of the outer hair cells. The outer phalangeal cells extend their phalanges to the reticular lamina. Various supporting cells such as Hensen's cells form rows inside the organ of Corti (Pickles 2012, pp. 28–33).

Moreover, the organ of Corti is covered by a gelatinous and fibrous fold called the tectorial membrane, consisting of molecules and collagens

known as tectorins (Pickles 2012, pp. 28–33). These tectorins have a significant role for the hearing process (see Richardson et al. 2011, for a review).

In order for the organ of Corti to generate sharply tuned traveling waves, and for the transduction of sound in general, certain electrochemical reactions must take place. This is done by creating a place where the cochlear scala is divided into the endolymphatic and perilymphatic spaces. Seemingly, the high positive standing potential and high potassium concentration of the endolymph seems to have a significant role in cochlear function for mechanotransduction and amplification of the traveling wave (Pickles 2012, pp. 52–57).

The cavity of the labyrinth of the inner ear is consisted of two compartments. The larger compartment, composed of the scala vestibule and scala tympani, runs the length of the system and is filled with perilymph. The other compartment is smaller and also extends throughout the length of the system. It is made of the scala media and is filled with endolymph (Pickles 2012, p. 52).

Endolymph and Perilymph

The endolymph, measured by ion-selective electrodes, is composed of a high level of K^+ (150 mM) and a low level of Na^+ (1.3 mM). The chemical composition is compared to the ionic composition found intracellularly. The endolymph and endocochlear potential are both created by the stria vascularis, a structure of the outer wall of the cochlear duct (see Pickles 2012, p. 54, for a review). The chemical composition of the perilymph, which is located in the outer fluid compartments of the cochlea, is similar to the extracellular fluid or cerebrospinal fluid.

The perilymph seems to be partially produced by transcellular transport of solutes from blood plasma, through the capillaries in the walls of the perilymphatic space. The K^+ concentration of the perilymph is 4–6 mM and the Na^+ concentration is 140–150 mM.

Conclusion

The structure and function of the cochlea has been briefly reviewed. The evolutionary development of the cochlea has, also, been reviewed. Additionally, the organ of Corti was discussed, as well as the purpose of the endolymph and the perilymph fluid surrounding the cochlea structure.

Cross-References

- Inner Ear, The
- Organ of Corti

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Code of the Streets

- Sociocultural Theories of Violence

Co-development

- Dyadic Processes

Co-efficient of Genetic Relatedness (r)

- Alarm Calling upon Predator Detection

Coefficient of Relatedness

- Genetic Relatedness

Coefficient of Relationship

- Genetic Relatedness

Coercing

- Child Abuse and Bullying

Coercion

- Coercive Control
- Dominance and Threat or Use of Force
- Female Counter-Adaptations to Rape

Coercive Control

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Synonyms

Coercion; Coercive controlling violence; Intimate terrorism; Manipulation; Nonviolent coercive control

Definition

In intimate relationships, coercive control is a pattern of intimidation, isolation, and manipulation tactics used to gain and maintain power or dominance over a partner.

Introduction

Coercive control refers to a pattern of tactics, like intimidation, isolation, and manipulation, used by one or both partners in a current or former relationship. It is considered abusive on its own but can co-occur with physical violence or other forms of nonphysical abuse like emotional, verbal, and psychological abuse. Stemming from sociologist Michael P. Johnson's (2008) work on the typology of domestic violence, relationships involving coercive control and physical violence are classified in the scientific literature as intimate terrorism, patriarchal terrorism, or coercive controlling violence. The nature of these relationships mirrors what scholars have historically referred to as domestic violence, wife abuse, or wife battering, where sustained physical violence and psychological abuse are used by men against women. In relationships without a history of physical violence, coercive control is commonly called nonviolent coercive control or described as a form of psychological abuse in the social science literature. In general, violence and abuse against women is considered a major public health

concern in the United States, with about 1 in every 4 women experiencing some form of it in her lifetime (Centers for Disease Control and Prevention 2008). Male partners are much more likely than female partners to use coercive control and violence in heterosexual relationships. Relatively less is known about the nature, prevalence, and consequences of violence and abuse in same-sex relationships, but reports of coercive controlling abuse in same-sex relationships have begun to be documented (Frankland and Brown 2014).

Theoretical Explanations

Researchers of intimate partner violence have approached the study of coercive control and coercive controlling violence in heterosexual relationships from a variety of theoretical standpoints. Psychological and evolutionary scholars posit that mental illness and male proprietariness help to explain why some men may use violence and coercive control against women. Social learning theorists suggest that violence and coercive behaviors are learned within families and society, and feminist scholars believe that patriarchy and inequalities between men and women create the socio-cultural landscape and vulnerability for violence and coercive control against women to occur and be effective.

Evan Stark (2007) offers a conceptual model for understanding the four key elements of coercive control based upon multi-disciplinary research and direct practice with female survivors: violence, intimidation, isolation, and control. According to Stark, the violence used in coercive control may range in severity and frequency but is aimed at establishing and maintaining dominance and instilling fear. Partners use a variety of physical assault tactics, including but not limited to punching, choking, beating, raping, and using weapons or objects to produce physical harm and injury. Men may intimidate their partner in ways including but not limited to physical violence, for example by making threats and insults, creating shame and secrecy within the relationship, and stalking a partner or monitoring their daily activities. Intimidation and violent tactics

can also extend beyond the romantic relationship to involve or threaten close friends, family, and pets. A key feature of coercive control is isolation, as its success relies on women's inability to contact and receive support from others. Coercive controlling abusers may limit or deny access to friends, family, or even the general public. Last, coercive control involves the micromanagement of everyday life and control of resources, including one's access to money, transportation, and other necessities for independence and wellbeing.

Importantly, Stark (2007) emphasizes that coercive control is enacted in highly personalized and gendered ways. Indeed, given the intimate nature of romantic relationships, coercive controlling abusers are well-informed of their partner's daily routines, connections, and sources of strength and vulnerability that help make their entrapment of victims successful. In line with feminist scholars, Stark describes coercive control as gendered not only based on the typical perpetrator or victim but primarily based on patriarchal social norms and institutions that contribute to violence against women and the success of coercive control attempts. In fact, many coercive controlling abusers use gender as a tool of abuse, for example, by micro-managing household tasks traditionally assigned to women, or degrading and controlling a partner's appearance to diminish one's self-esteem and sense of identity as a woman.

Documented Consequences

Regardless of one's theoretical orientation, scholars across disciplines agree that coercive control has negative consequences for women, children, and families. A large body of research documents the particularly serious nature and impact of coercive control involving physical violence. When violence is aimed at controlling one's partner, it tends to occur more frequently, be of greater severity, and create more serious injuries than violence used situationally to resolve conflict (called situational couple violence; Johnson 2008). Coercive controlling violence is also associated with greater psychological consequences

than situational couple violence, including post-traumatic stress disorder, intense feelings of fear, and a sense of losing one's identity and self-worth. Women who leave coercive controlling and violent relationships remain at high risk for ongoing violence and intrusion by their former partners, particularly if they are mothers involved in coparenting (Hardesty and Ganong 2006).

Although less is known about nonviolent coercive control, it, too, appears to have damaging effects. Women with nonviolent but controlling, demeaning partners report having diminished self-esteem and symptoms of clinical depression (e.g., Lammers et al. 2005). Men's use of coercive behaviors in nonviolent relationships may also predict later use of physical violence. Johnson (2008) refers to this phenomenon as "incipient intimate terrorism." Despite these documented negative consequences, coercive control receives the most attention in research and identification and prevention efforts when it is coupled with physical violence. In fact, most researchers studying coercive control examine it only in conjunction with violence. Further research is needed to understand the nature and consequences of coercive control when used on its own to dominate a partner in relationships.

Conclusion

Coercive control has received increasing attention in research as a central component of abuse against women (e.g., Crossman and Hardesty 2018; Hardesty et al. 2015). Indeed, understanding coercive control helps to explain the damaging, long-term psychological impacts of abuse reported by women above and beyond physical abuse. Nevertheless, screening tools used today to identify women experiencing or at risk for abuse still rely heavily on reports of physical violence with less attention to psychological forms of abuse like coercive control. Thus, women in need of services and support may be overlooked by healthcare professionals, counselors, and other service providers, particularly when seeking help

to cope with or safely leave an abusive relationship characterized by nonviolent coercive control. Further research is needed to document the nature and consequences of coercive control, occurring both with and without violence, to help inform early identification, prevention, and intervention efforts that promote nonviolence and women's safety and wellbeing.

Cross-References

- ▶ Familial Violence
- ▶ Manipulation
- ▶ Men's Violence Against Female Partners: The Role of Culture
- ▶ Sex Differences in Intimate Partner Violence
- ▶ Sexual Assault and Intimate Partner Violence
- ▶ Sexual Coercion and Dating

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Cognitive Buffer Hypothesis, The

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Coercive Controlling Violence

► Coercive Control

Coevolution of the Sexes

► Evolutionary Arms Race

Co-evolution of the Sexes

► Genital Evolution

Cognition

- Attention and Memory
- Fish, Amphibian, and Reptile Tool Use
- Social Learning and Social Cognition

Cognitive Ability

► Intelligence

Cognitive Biases

► Selective Attunement to Adaptive Problems

Synonyms

Brain size; Environmental change hypothesis

Definition

The survival advantages of coping with environmental changes through behavioral adjustments should have been a major force favoring the evolution of large brains.

Introduction

The cognitive-buffer hypothesis (CBH) is an attempt to explain why some animals have evolved large brains despite substantial energetic and developmental costs. The hypothesis, first formulated by Allman and colleagues (Allman et al. 1993; Allman 2000), posits that the essential role of the brain is to buffer animals against environmental variation. Assuming that this buffering capacity increases with the size of the brain, the hypothesis suggests that brain expansions might have been an adaptive solution to environmental changes.

The mechanisms by which enlarged brains are supposed to enhance survival are cognitive, and include inventing new behaviors and adjusting old behaviors to new situations (Fig. 1). Thus, a large brain would primarily reduce extrinsic mortality by facilitating the construction of plastic behavioral responses to novel or unusual

problems (Sol 2009). The most obvious example of the importance of the brain as cognitive buffer is found in humans, whose large brain and advanced learning abilities allow them to survive in places that otherwise would be inhospitable.

Evidence that Large Brains Evolved to Buffer Against Environmental Changes

The CBH is sustained in the finding that animals with disproportionally large brains (relative to body size) tend to exhibit lower mortality rates and live longer lives. Although necessary, this evidence is nonetheless insufficient to demonstrate the hypothesis as other mechanisms like delayed maturation and physiological regulation can also explain the above links (Deaner et al. 2003; Sol 2009) (Fig. 1).

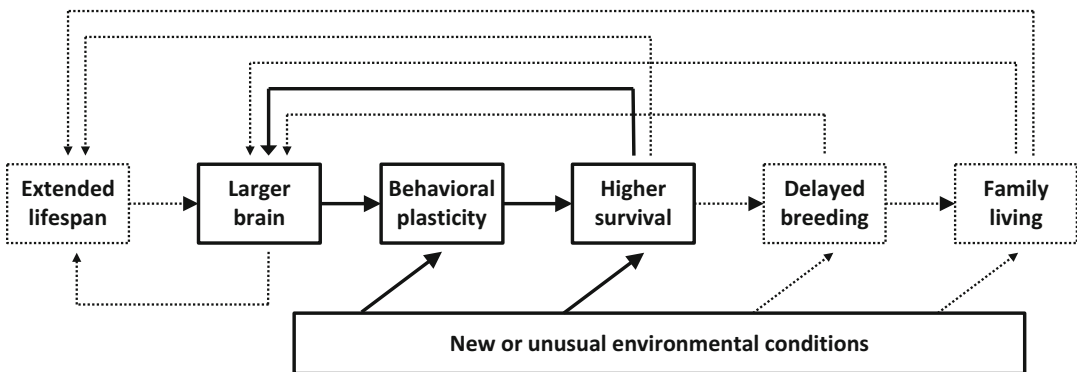
An additional source of evidence for the CBH comes from the analysis of human-mediated introductions of animals outside their native ranges. If a large brain buffers individuals against environmental changes, the likelihood of establishing a persistent population in the new region should be higher for big-brained animals. This expectation has been confirmed for

reptiles and amphibians (Amiel et al. 2011), birds (Sol et al. 2005) and mammals (Sol et al. 2008) but not for fishes (Drake 2007). Within the new regions, many successful invaders thrive in human-altered environments, where enhanced abilities for behavioral innovation and learning are known to be particularly important (Liker et al. 2008).

In contrast, historical evidence showing that environmental variation has shaped brain evolution is lacking. However, some indirect evidence exist. In parrots, brain size is larger in species occurring in climate-variable environments (Schuck-Paim et al. 2008). In passerine birds, resident species exposed to seasonal environments tend to be more innovative and have larger brains than migratory species (Sol et al. 2010). In lemurs, relatively larger brained species tend to experience less variation in their dietary intake than indicated by the seasonality of their habitat (van Woerden et al. 2010).

Mechanisms Underlying the CBH

The CBH links two previously suggested ideas, that larger brains enhance the capacity of animals to modify their behavior and that behavioral



Cognitive Buffer Hypothesis, The, Fig. 1 Life history framework representing the cognitive buffer hypothesis (solid lines) and alternative mechanisms and feedback (dashed lines). According to the hypothesis, a large brain functions, and hence may have evolved, to buffer individuals from extrinsic mortality by facilitating the construction of plastic behavioral responses to novel or unusual conditions. This in turn may favor extended life span and

delayed reproduction, further increasing the benefits of plastic behavioral responses. Family living can also buffer individual against extrinsic mortality and select for larger brain to facilitate social interactions. The link between brain and lifespan reflects that other mechanisms besides a cognitive buffer may also explain why the brain is closely related to long-lived life histories (Modified from Sol (2009))

adjustments allow them to cope with many challenges animals encounter during their life.

The notion that behavioral adjustments are an important mechanism by which animals respond to environmental challenges is now well-established. Behavior not only mediates how animals interact with their environment but, by virtue of their plastic nature, can modify the interactions. New Caledonia crows, which have brains that are substantially large for their body size, are able to construct and use a variety of tools to extract insects from crevices. This allows them to exploit an important food opportunity that most other animals are unable to exploit. Learning is particularly relevant in facilitating the production of plastic behaviors. There is for instance evidence showing that training captive-bred animals to avoid predators can improve the success of reintroduction programs (Griffin et al. 2000).

While the importance of behavioral adjustments as response to environmental changes is unquestionable, the notion that larger brains enhance the capacity of animals to modify their behavior remains more controversial. A main concern is that because the brain is structured in functional distinct areas, mosaic evolution could potentially lead to brains of similar size by increasing different brain areas. This would imply that a brain can be large for very different reasons, making comparisons meaningless.

However, recent studies contradict the above criticism, showing that large brains are the result of increases in the brain areas more closely involved in general-domain cognition (Sayol et al. 2016). Moreover, there is growing evidence that animals with larger brains, relative to their body size, exhibit higher propensity to innovate behaviorally when facing new challenges. For example, the likelihood of observing innovative behaviors in the wild is higher in species with disproportionally larger brains in both birds (Overington 2008) and primates (Reader et al. 2011). Experimental support is also growing. By presenting 39 mammalian carnivore species with a novel problem-solving task, obtaining food from a closed box, Benson-Amram et al. (2016) demonstrated that species' relative brain sizes predict problem-solving success.

Artificial selection experiments in the guppy (*Poecilia reticulata*) have revealed that brain size can evolve rapidly and that increases in the brain bring associated improvements in learning, at least in females (Kotrschal et al. 2013). Finally, it is increasingly recognized that behavioral responses require more than cognitive abilities. For example, the ability to innovate behaviorally also depends on how morphology and physiology affect the ability to explore novel opportunities and the diversity of motor patterns needed to manipulate objects. However, the debate continues over why it is relative brain size and not absolute brain size what matters to be better at innovation and learning.

Environmental Scenarios Selecting for a Cognitive Buffer

Unlike other hypotheses for the evolution of large brains, the CBH does not assume any particular selective force. As a result, it allows integrating a variety of hypotheses for the evolution of large brains, both social and ecological. This is the strength and, at the same time, the weakness of the theory as it makes less explicit which selective scenarios should be examined to test the hypothesis.

In any case, the CBH does not deny the possibility that some selective pressures are more important than others. It should be noted that most current evidence for the role of enlarged brains as cognitive buffers come from the foraging domain. In mammals, the size of brain and adipose depots are negatively correlated (Navarrete et al. 2011), which can be interpreted as encephalization and fat storage being alternative strategies to buffer against starvation. This line of thinking has led to propose that large brains might have particularly been favored in highly seasonal environments, which force animals to cope with the harsh conditions during some periods of the year. In human evolution, for example, brain expansions have been associated with the transition from rain forests to more seasonal environments (Allman 2000). Inhabiting cold regions requires not only higher daily energy

requirements, but food must be obtained under difficult conditions (e.g., snow) and in a shorter daylight period (Roth et al. 2010). This should select for adaptations that enhance food acquisition and increase the accuracy and speed of decision-making (Roth et al. 2010; Sol et al. 2010). In agreement with the expectation, black-capped chickadees (*Poecile atricapillus*) from harsh northern populations tend to have larger telencephalic regions relative to body mass than those in the south, and outperform them in response to novelty and problem-solving ability (Roth et al. 2010). As already advanced, however, general evidence that environmental variation has selected for enlarged brains is missing.

Although features of the external environment may be important in selecting for larger brains, often it is not the environment itself but the way the animal interacts with it that really matters to understand how larger brains have evolved. Lefebvre et al. (1997) suggested that opportunist-generalist lifestyles, where individuals interact frequently with new food opportunities, should have been a major pathway toward greater encephalization on the grounds that learning is essential to exploit new food opportunities. Behaviorally, physiologically, and morphologically unspecialized animals are less constrained to develop new behaviors, thereby often relying on behavior to solve ecological problems. Indeed, there is evidence that large-brained animals are more generalists than small-brained ones, at least in birds (Overington et al. 2009; Ducatez et al. 2014; Sol et al. 2016), although it is unclear what is the cause and what the consequence.

Brain Evolution and Life History Theory

The CBH fits well with life history theory. Organisms whose fitness depends on a long reproductive life (that is, that prioritize survival over reproduction) need buffer adaptations to ensure high survival. A large brain could be one of these buffering adaptations. Large brains and enhanced cognitive abilities might thus be part

of a slow pace-of-life strategy to deal with environmental changes (Sol et al. 2016).

Considering brain evolution within a life history framework allows understanding why many species thrive with small brains despite the benefits of large brains. The brain is energetically expensive to produce and maintain, and hence energy invested in the brain cannot be diverted to reproduction. Moreover, developing the brain and the behavioral skills needed to survive takes time, which may force to delay the onset of reproduction (Fig. 1). Consequently, only long-lived animals may pay the costs of investing in large brains.

A life history perspective also helps understand why the brain has evolved so rapidly in some lineages, like primates and corvids (Fig. 1). A long life gives more time to explore and learn how to use new ecological opportunities, and increases the likelihood that individuals are exposed to changes during their life. As a result, the benefits of increasing brain size are higher in slow-lived species, generating positive feedback that may potentially speed up the evolution of enlarged brains. Likewise, longevity can favor a delayed onset of reproduction and promote family living (Covas and Griesser 2007). The social environment might in turn reduce mortality and facilitate an increase in brain size if, as the social intelligence hypothesis suggests, individuals living in cohesive social groups face higher cognitive demands than individuals living alone. These processes may again favor rapid evolutionary increases in the brain.

Conclusion

The CBH provides a sound explanation for the function, and hence the evolution, of large brains by proposing that large brains are part of a life history strategy through which animals buffer themselves against extrinsic mortality. While many aspects of the theory remain little understood, growing evidence shows that a large brain may actually buffer animals from environmental changes. In absence of historical evidence, however, whether the advantages of a cognitive buffer

may have been an important pathway toward greater encephalization lacks empirical verification.

If the brain functions to cope with changes in the environment, big-brained species should be less prone to extinction risk. This does not occur, however. Some big-brained animals like big apes and many whales are highly endangered. One reason may be that other factors beside the brain are important in putting species at risk of extinction. Long-lived species, like those with enlarged brains, tend to occur at smaller densities and recover more slowly from population crashes, and are thus quite sensible to hunting pressure. This warns us that like other adaptations, the brain is part of an adaptive complex that can be useful in some contexts but costly in others, implying that when it comes to the brain larger is not always better.

Cross-References

- Adaptation
- Adaptation and Natural Selection
- Adaptations: Product of Evolution
- Adaptive Learning
- Adaptive Plasticity
- Advanced Tool Use
- Brain Size and Intelligence
- Climate and Habitat Diversity
- Cognitive Science
- Comparative Evidence
- Content Specificity
- Controversies
- Convergent Evolution of Hyena and Primate Social Systems
- Convergent Evolution of Intelligence
- Convergent Evolution of Intelligence Between Corvids and Primates
- Costs and Benefits of a Large Brain
- Darwin's Struggle for Life
- Development of Adaptations
- Domain Specificity
- Ecological Niche, The
- Environmental Harshness
- Environmental Harshness/Mortality
- Environmental Influences

- Environmental Risk
- Environmental Unpredictability
- Environmental Unpredictability and Bet-Hedging
- Evolution of Adaptations
- Evolution of The Brain, the
- Extrinsic Mortality
- Family
- Habitat Change
- Identifying Adaptive Functions
- Intelligence Versus Natural Selection
- Iteroparity
- Learning
- Life Expectancy and Reproduction
- Life History Strategies
- Life History Theory
- Modularity of Mind
- Natural Selection
- Nature Versus Nurture
- Nonhuman Primates
- Personality
- Phylogenetic Analysis Within Comparative Psychology
- Prey Availability
- Primates
- Problem Solving
- Social Context
- Social Intelligence Hypothesis, The

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Cognitive Capacities

► Intelligence Testing

Cognitive Changes in Adolescence

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Human adolescence is the transitional period from caregiver dependency to the autonomy of early adulthood. During this extended period, both sociocultural influences and physiological actions of hormones play an important role. They act

independently and synergistically to influence neural networks in a manner that increases cognitive flexibility and reorients an individual's social interactions to the psychological and social complexity of adult society and sexual maturation. Behaviorally, these changes are manifested in the individual by increases in their self-awareness and that of the perspective of others, as well as increased interest in peer interactions and sexuality (Blakemore 2008).

At the onset of adolescence, the child already has a well-developed cognitive foundation. Piaget's sensorimotor and preoperational stages are completed, and the concrete operational stage is well advanced. Thus, at this point in development, a level of structural brain organization and cognitive complexity already supports the basic cognitive skills essential to adult social interactions. These skills include concrete logical thinking, adult levels of syntactical language complexity and comprehension, complex emotional comprehension and expression, and spatial and arithmetic abilities. During adolescence, the neural foundation of these skills is expanded in ways that support mating and parental behaviors, as well as social interactions with adults outside the family.

Piaget proposed formal operations as the cognitive stage that emerges during adolescence, which is characterized by an intellectual capacity for employing abstract logic and hypothetical thinking as part of problem-solving. Research over the past two decades has modified this view because cross-cultural studies of formal operations show that it is poorly developed or largely absent in a majority of adolescents and adults (Moshman 2009). Thus, adolescence is now viewed as a period of integration and expansion of existing cognitive systems. The current empirical approach to adolescent cognition focuses on how social interactions, hormones and sex differences, motivation, and self-regulation influence this remodeling reprocess (Spear 2013).

Influence of Hormones. The average age of puberty onset is 9–10 years, occurring approximately a year earlier in females. Menarche and spermarche occur about 2 years later when circulating estradiol and testosterone reach adult levels.

The process continues with the further development of secondary sex characteristics, such as breast development, fat deposition patterns, or beard growth, which extends the pubertal period to an average of 4 years.

Hormonal influences on adolescent cognition arise from the pubertal process, and their actions amplify behaviors related to social interactions but are not causal. For instance, adolescent elevations in circulating testosterone increase the likelihood of aggressive behavior in situations of social conflict, but they do not cause the behavior. Rises in hormone levels are gradual, and the process of puberty begins a year or two before there are manifest signs of hormonal actions.

The normal pubertal process has a significant amount of variability in its onset and duration, with onset ranging from 8 to 13 years and duration from 2 to 5 years. This has important implications for cognitive and behavioral influences of hormones, because although neural connectivity is influenced by hormone levels, brain growth during the adolescent period is an independent process. Thus, a brain exposed to adult levels of testosterone or estrogen at 11 years of age is not the same as one exposed to adult levels at 12 or 13 years. This creates an interaction between brain development, time of hormonal exposure, and sociocultural influence factors. The sociocultural influences, especially among peers, are partly mediated by the individual's stage of sexual maturation. These complex interactions contribute significantly to the wide range of socio-emotional behaviors observed in the adolescent population (Mills et al. 2014).

Brain Development and Adolescence. From a physiological perspective, the interaction between physiology and environment on adolescent brain development is part of a recurring, nonlinear pattern of postnatal brain growth (Huttenlocher and Dabholkar 1997; Thatcher 1997b). Between birth and adolescence, structural maturation of different cortical regions shows cyclical periods in the production of new synapses, followed by synaptic pruning associated with environmental stimulation. These proliferation-pruning cycles provide a basis for the environment to modulate brain development and brain

organization. For example, the prefrontal cortex connections with posterior cortical areas in the temporal and parietal cortex show a cyclical proliferation-pruning that closely follows the transitional ages of Piagetian cognitive stages before puberty. This suggests that these physiological changes underlie a reorganization of higher cortical processing related to changes in conceptual cognitive complexity exhibited at each stage (Thatcher 1997b). As new connections are integrated into existing neural circuitry, cortical gray matter continues to increase until it peaks during the mid- to late adolescent period (Blakemore 2008).

The same general process of synaptic proliferation and pruning unfolds during adolescence but with the additional influence of hormones. At the average age of puberty onset, there is a wave of synaptic proliferation in the connections between the frontal lobes and posterior cortical regions (Thatcher 1997a). Gray matter volume peaks in the frontal and parietal cortex at the average age when circulating hormones reach adult levels and then decreases over the next few years. In both cortices, the peak occurs around 11 years in girls and 12 years in boys. The volume decrease that follows the peak is generally interpreted as a reflection of synaptic pruning and reorganization associated with neural efficiency (Lenroot and Giedd 2010; Paus et al. 2010).

Changes in adolescent socio-emotional behavior may be a result of gradual strengthening and remodeling of connections between the prefrontal cortex and other cortical and subcortical areas. Important aspects of prefrontal executive function include an assessment of the emotional significance of a stimulus and taking the perspective of another. The brain areas involved include prefrontal connections with the anterior cingulate cortex, superior temporal sulcus, amygdala, and inferior parietal lobule. Together they form a social cognition network that shows evidence of structural reorganization during adolescence. Changes in this social network are thought to underlie adolescent mood lability, increased risk-taking behavior, and heightened self-consciousness (Blakemore 2008; Spear 2013). Imaging studies are consistent with this view. Studies related to emotional

processing in the social network show increased activity during adolescence in the orbital region of the prefrontal cortex and the anterior cingulate compared to younger children and adults (Monk et al. 2003).

Behavioral Correlates. Longer reaction times are found in adolescents for making perceptual decisions involving socially relevant emotional stimuli (Choudhury et al. 2006). This is consistent with other evidence showing changes in reaction time to identify emotional facial expressions in a task that relies on the prefrontal cortex (McGivern et al. 2002). At 10 years of age, reaction times to make a correct decision were similar in males and females. However, by mid-puberty, reaction times increased by 10–20% in both sexes, without any change in accuracy. In girls, this rise in reaction time was observed at age 11–12 and in boys at age 12–13. After this point, there was linear decrease through age 15–16 when reaction times were similar to that observed at 10 years of age. The sex difference in timing of the increase in reaction time suggests that synaptic proliferation at the time of puberty may be influenced by rises in gonadal steroids and that reorganization of prefrontal circuitry initiated by the rise in hormones leads to a decrease in cognitive efficiency.

These reaction time studies measure perception, not intellectual skills. With respect to full-scale IQ, large, cross-sectional samples in adolescents from ages 11 to 18 years do not show sex or age differences (Makintosh 2011). However, greater variability has been observed in female scores measured at 12 or 14 years of age compared to retest scores at 40 years of age. For males, greater variability was observed at age 18 compared to retest scores at 40 years of age (McCall 1977). Adolescent volatility in test-retest IQ scores was also observed in a study comparing individual performance and verbal IQ scores in males and females measured between 12 and 16 years of age with scores obtained in each individual 5 years later (Ramsden et al. 2011). Results showed changes in the performance or verbal IQ scores of some individuals that increased or decreased by a standard deviation or more. Although average scores for the two time points did not differ, there was a significant

increase in variability between the two tests. Imaging studies were also conducted in the same individuals at both testing ages. Results showed that the amount of change in verbal IQ score was positively correlated with changes in the density of gray matter in Broca's area, while the amount of change in performance IQ score was positively correlated with changes in the density of gray matter in the cerebellum. The pattern suggests that reorganization occurring in the adolescent brain at the time of testing influences performance. However, the group size at each adolescent age was not large enough to assess the role of puberty status, age of onset, or hormone levels at the time of testing in adolescence. These are important issues that remain to be addressed before a clearer picture emerges of how neural changes during adolescence influence cognition.

Sex Differences. In addition to the frontal and parietal cortices, male and female adolescents show structural differences in other cortical and subcortical areas that are associated with pubertal rises in circulating estradiol or testosterone (Mills et al. 2014; Paus et al. 2017). This raises structure/function questions regarding how these structural differences might relate to well-established cognitive sex differences found in adolescents and adults. An organizational role for early testosterone is well established in enhancing adult skills related to space relations, but only recently has an organizational role for androgens on the adolescent brain been proposed as well (Schulz and Sisk 2016). If hormones during puberty have organizational influences on cognition, are they acting to enhance existing cognitive sex differences, creating new ones, or having no cognitive effects? Well-established cognitive skills that favor males include tasks related to space relations, abstract visualization, and tracking movement. Those that favor women involve verbal fluency, episodic and autobiographical memory, and implicit memory for objects (Handa and McGivern 2015). Hormonal actions on brain organization during the perinatal period are an important influence on spatial skills favoring males, but early hormonal actions on the "verbal" skills that favor females are less clear. One possibility is that tasks favoring females become

more pronounced by pubertal rises in estrogen levels. Another possibility is that tasks that already favor males become enhanced by the rise in testosterone.

Two large studies approached these questions using cognitive sex difference tasks, imaging, and/or physiological measures. Herlitz et al. (2013) studied individuals at several ages during adolescence using a variety of cognitive tasks that show sex differences. The expected pattern of cognitive sex differences was present at the onset of puberty and did not change in magnitude over time irrespective of pubertal onset, age, or circulating hormone levels. However, a cross-sectional study found that the age of pubertal onset influenced mental rotation in males (Beltz and Berenbaum 2013) but did not observe age-related change in other tasks. The broad pattern indicates that cognitive sex differences are well established by the onset of puberty and that pubertal steroids play only a small role. Importantly, none of these studies were designed to address potential changes in social cognition due to hormones and age. Further research may yet show a differential role for pubertal hormones across adolescent age in organizing social cognition.

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Cognitive Complexity

► Nonhuman Intelligence

Cognitive Control

► Executive Functioning

► Inhibition

Cognitive Decline

► Use It or Lose It

Cognitive Development

► Emergence of Social Reasoning About Hierarchies

► Resources for Brain Development

Cognitive Development in Non-human Primates

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Key Idea

Cognitive development

Synonyms

Cognitive developmental science

Definition

The study of change across the lifespan in the mental action or process of acquiring knowledge and understanding through thought, experience, and the senses.

Introduction

Cognitive development encompasses behavior, cognition, and the brain from birth until adulthood. As such, it is a varied and complex discipline with many areas of study and numerous perspectives and theories. Below is a summary of the main theories of cognitive development that historically and currently have impacted the field. This summary is, of course, not exhaustive but provides a first look at the variety of the field. Next, the development of three major cognitive abilities is described: attention, memory, and language. These are also not exhaustive; any number of abilities could have been chosen. But, these three cognitions, and their accompanying behaviors, are understood very well from infancy through childhood and are broad cognitions used throughout everyday of life.

Major Theories

Piagetian Stage Theory

Jean Piaget (1896–1980) was a Swiss clinical psychologist in the early twentieth century who crafted one of, if not the, most influential theories of cognitive development to date. Piaget viewed children as “little scientists” who construct meaning in the world by interacting with it and testing their intuitive theories about how the world works. He described cognitive development as the movement between four distinct and independent stages of thought: sensorimotor (0–2 years), preoperational (2–6 years), concrete operations (7–12 years), and formal operations (13–adulthood). Children do not linearly or gradually move from one stage to the next; rather, each stage represents a distinctly different way of thinking about and interacting with the world. The sensorimotor stage is defined by exploration

of the world through strictly sensory means. In the preoperational stage, children become representational and able to represent concepts or objects with words and images. Concrete operations introduce logical thinking and the ability to engage in rudimentary mathematics. Lastly, children in formal operations are able to think abstractly and hypothetically about the world, what Piaget saw as the pinnacle of cognitive abilities.

Piaget argued that children hold theories or “heuristics” about how the world works. When a child encounters a new experience or piece of knowledge, learning occurs through one of the two processes: accommodation or assimilation. Accommodation occurs when information is encountered that requires a child to change their theory or heuristic of the world. The new information trumps what the child previously thought and requires a change in their theory of the world. Assimilation occurs when information can be worked into the child’s current theory of knowing about the world. It is through this process that children learn and are constantly updating their theory, like a “little scientist.”

This theory, and subsequent work supporting and contradicting it (known as neo-Piagetian), laid the groundwork for the modern study of cognitive development and has generated decades of debate and inquiry. As a general statement, Piaget was correct about much of cognitive development but probably underestimated the abilities of newborns and infants due, in part, to his limitations in research methodologies with this population.

Vygotsky’s Sociocultural Theory

Lev Vygotsky (1896–1934) was a Russian psychologist who formulated a theory of development incorporating biological, social, cultural, and historical elements. He was an influential figure in Russia and Europe, but not so in North America until the post-humous translation into English of many of his works in the 1960s. He is primarily known for two major concepts, tools of intellectual adaptation and the zone of proximal development, both of which tout the importance of cultural and social influences on children’s cognitive development.

Vygotsky defined tools of intellectual adaptation as cultural and technological tools and advancements that assist children in their cognitive capacities. He argued that the historical and cultural availability, or lack of availability, of technologies such as mathematics, language, formal schooling, etc. are significant determinants of the cognitive abilities achieved by children. For example, in modern America and Europe, it is not unusual for high school students to learn calculus, a truly advanced system of mathematics. This is a virtually impossible achievement for children who grow up as members of the Ache tribe in Paraguay, whose cultural tools do not include words for numbers above 3. Using systems of technology, cultures can accumulate knowledge and methods of learning enabling increases in cognitive complexity across time. It is not that people and children are inherently more intelligent today than in the tenth century, but becoming an astrophysicist is certainly easier if you grow up with computers in twenty-first-century France.

The zone of proximal development is Vygotsky's major contribution to how direct social learning and assistance can impact the cognitive abilities and behavior of a child. Vygotsky argued that children have a baseline capacity in any ability that they can accomplish on their own (e.g., a 6-year-old can successfully add and subtract single-digit numbers independent of assistance). There is also a limit to their abilities both with and without assistance (e.g., this same 6-year-old is incapable of long division no matter the situation). However, between these two extremes is a middle ground, known as the zone of proximal development, in which children can extend their abilities with the assistance of a more capable helper. For example, the 6-year-old can successfully add and subtract double-digit numbers, but only with the assistance of a parent or teacher. This zone is where assisted learning occurs; children have the ability but need help to consistently achieve. Vygotsky called this help "scaffolding." By standing on the scaffolding of an adult (or older child), children can extend their abilities and learn.

Information Processing

An information processing account of cognitive development focuses on change in explicitly measurable and quantifiable cognitive abilities. This perspective construes cognitive development as the increases in capacity or sophistication of both general and specific capacities. For example, working memory, the ability to hold information in mind and manipulate it for application to problem solving, is a general ability because it can be used to hold many different types of information in many different contexts. Capacity and speed of processing can be measured and will vary between individuals and across development. Examples of more specific abilities are verbal fluency, vocabulary, or reading comprehension.

One of the major goals of information processing is to define, quantify, and measure the importance of intelligence. Typically, intelligence is defined as two constructs in this perspective: first, crystallized intelligence and second, fluid intelligence. Crystallized intelligence abilities are skill based and learning dependent, such as vocabulary or social skills. Fluid intelligence abilities are considered to be more biologically based and constrained, such as speed of processing or inhibition. Often, fluid intelligence is known as *general intelligence* (*g* or *Gf*) and defined as the ability to use deliberate mental operations to solve novel problems. In other words, crystallized intelligence is information you can memorize; fluid intelligence are the abilities used to solve problems with this information.

Gf is considered a multifaceted variable that is deduced from the assessment and statistical and overlapping of other measurable abilities. Common measurements used to define *Gf* are attention, working memory, and perception/speed of processing. High scores on measurements of *Gf* are associated with better school achievement, mathematical prowess, and verbal abilities across the lifespan (for more info on fluid intelligence and development, see Primi et al. 2010).

Core Knowledge

Core knowledge can be seen as a neo-Piagetian perspective on development, in that one of its consequences is to refute Piaget's underestimation

of the cognitive capacities of infants. This approach to cognitive development emphasizes evolutionarily relevant classes of information or abilities that are present early in life and are then built upon throughout the lifespan (Spelke and Kinzler 2007). Major areas of core knowledge are number, objects/physics, and people. Infants are said to possess implicit understanding or knowledge of these aspects of the world either at birth or shortly after birth. Much of this work became possible with technological and methodological advancements that allow for cognitive testing of infants and assumptions about their cognitions and knowledge. Common paradigms utilize eye tracking (measuring where and for how long infants look at a given location or object) and habituation/dishabituation (a general measurement of looking time that allows for assumptions about whether infants can tell a difference between two stimuli). From these methods the cognitive world of infants has been shown to be much richer and more complex than scientists thought in the early and mid-twentieth century. Young infants seem to understand differences between small numbers (1 vs. 2 objects or 2 vs. 3 objects), intuitively understand Newtonian physics and how objects should behave in relation to each other and gravity, and prefer attending to people and speech.

Developmental Contextualism

Developmental contextualism is an interactive theory of development that grew out of evolutionary biology and incorporates all levels of analysis: genetic, neural, behavioral, and environmental. Many academics and researchers adhere to this perspective, the most influential of which is Gilbert Gottlieb. Gottlieb demonstrated that development cannot be considered in a vacuum, whether genetics and neurology in the absence of environment or social and cultural influences in the absence of genetics and neurology. This theory argues that the nature versus nurture debate, in which deterministic developmental processes such as genetics and environmental determinants such as rearing environment are pitted against each other, is a fruitless and wasteful enterprise. Development and complex functioning can only

be properly understood by adopting a multi-level interactive approach.

For example, Gottlieb (1991) conducted an experiment using incubating but unhatched duck eggs. Typical behavior upon hatching is to find the mother duck, by both sight and sound, and follow her, through a process known as imprinting. New hatchlings are able to do this with no apparent previous behavior or exposure, suggesting a purely genetically determined explanation for the behavior. However, Gottlieb demonstrated that even this basic behavior is dependent upon environmental input. During the time of incubation when the chick's auditory system is organizing, Gottlieb removed the upper portion of the eggshell and shined a strobe-like light into the egg. This disrupted the organization of the chick's auditory system in favor of devoting neural resources to the visual system, in response to the novel visual stimulus. Upon hatching, the chicks could not discriminate between a chicken call and their mother duck's call and failed to successfully imprint upon the mother. This suggests that the process of auditory discrimination and the ability to imprint is dependent upon auditory development and stimuli prior to hatching. Unhatched ducks hear their mother and their nest-mates and learn "what a duck sounds like." Thus, what appeared to be a straightforward genetic effect is dependent upon appropriate timing of environmental stimuli and the prompting of neural development.

Evolutionary Developmental Psych

A relatively modern perspective on cognitive development is the application of an evolutionary perspective, termed evolutionary developmental psychology. Founded by a diverse group of psychologists coming together from a variety of original backgrounds, most notably David Bjorklund and David Geary, this perspective acknowledges that evolution by natural selection does not simply begin working on the adult; it molds and shapes children and the process of development itself. Given that the human lifespan delays consistent reproduction until roughly the age of 15 years, there must have been selection pressures that warranted this shift in developmental timescale.

Furthermore, considering that a lengthy childhood is both metabolically expensive and physically dangerous, there must be substantial compensatory benefits to its existence. Evolutionary developmental psychology seeks to understand these selection pressures, the adaptations that arose from them, and how they impact the development of the modern child.

This theory recognizes two types of development relevant adaptations. The first one is deferred adaptations, which are behaviors or cognitions in childhood that serve to prepare the child for adulthood. Their benefits are deferred to adulthood. For example, female children display greater interest in infants and spend more time interacting with them than to male children, most likely in preparation for child rearing as adults. Second, ontogenetic adaptations are those that serve an adaptive purpose during childhood itself; they help the child survive or flourish during childhood. Aspects of infant and childhood memory have been theorized to represent ontogenetic adaptations, such as context dependence in infancy, increased recall for negative stimuli, and attention to and recall of faces (Sellers II and Bjorklund 2014).

Developmental plasticity is another hallmark of evolutionary developmental psychology, which contends that natural selection has, in some instances, selected for responsiveness to environmental inputs. For example, harsh and unpredictable early environments have been found to lower the age of menarche (first menstrual cycle) in girls. This is most likely the activation of a contextually sensitive mating strategy to help women achieve reproductive viability in an uncertain environment.

Cognitive Abilities Across the Lifespan

Attention

Infancy

Controlled and directed attentions are probably very difficult for an infant. They are experiencing a plethora of stimuli that all beckon for attention, deciding what to attend to, and having the

cognitive fortitude to sustain attention are quite difficult endeavors for an infant. However, there are stimuli to which infants preferentially attend. Faces (ovals and triangles, for their face like qualities), dynamic or moving stimuli, and high contrasts are all more likely to attract and hold the attention of an infant.

As mentioned previously, attention, in the form of looking time and eye tracking, are some of the only tools for making assumptions about the internal cognitive lives of infants. The introduction of these attentional paradigms caused a significant shift in how experimental psychology viewed infants. Since the 1990s, substantial experimental evidence forces the acknowledgement that infants active cognitive participants in their environment, holding expectations, memories, preferences, and assumptions about the world.

Childhood

As children age, they gain more sophisticated abilities in attention, such as the ability to consciously and explicitly attend to a particular stimuli. The ability to direct attention is tied to inhibitory abilities, to stop oneself from engaging in a non-relevant or desired behavior. For example, in order to attend to a teacher, a first grader must be able to inhibit their desire to talk to their friend or run around the room. In preschool (ages 3–5) inhibitory and attentional abilities are relatively poor, especially in comparison to adult-like functioning. The famous marshmallow test (Mischel 2014) is a wonderful demonstration of children's lack of inhibition. Children are given one marshmallow and allowed to eat it. But, if they wait and inhibit this desire, they will be given two marshmallows at a later time. Despite the obvious benefit of waiting, young children are notoriously poor at delaying gratification; they feel compelled to immediately eat the one marshmallow. While this may seem trivial, the ability to delay gratification and then attend to appropriate material are skills at the heart of success in the modern educational and corporate worlds. As children age, these abilities increase substantially into adulthood until individuals can be reasonably expected to attend school or work diligently for 8 or more hours per day.

Memory

Infancy

Infant memory is a difficult area of study as they obviously cannot directly respond physically or verbally to commands. However, through looking time measures and reinforcement/associative procedures, psychologists have concluded that infants do in fact possess implicit memory systems (and perhaps explicit), perhaps even more sophisticated than one would assume. At the age of 2 months, children can remember information for a few days, by 6 months their memory retention increases to about 2 weeks, and 1 year children can remember for up to 8 weeks. Children will have difficulty expressing these memories due to their limited language abilities, but their responses indicate reliable and accurate memory.

Paradoxically, adults experience *infantile amnesia*, the inability to remember events from infancy. So, even though infants themselves can be demonstrated to have memories, they are not retained into adulthood. In fact, most adults' earliest memories are from between 2 and 4 years of age. Many factors contribute to this lack of long-term memories from early life, such as the inability for infants to create memories using language, changes in neurological development, and infants' lack of explicit self-awareness.

Childhood

Beginning around the age of 2, children begin to display all of the memory systems also present in adults, explicit long-term memory, implicit long-term memory, and short-term/working memory. Explicit memories are those that can be consciously and purposefully recalled of both an episodic nature (e.g., remembering what happened at the park yesterday) and semantic nature (e.g., knowing that bananas are classified as a fruit) across days or years. Implicit memories are practiced physical activities (e.g., knowing how to ride a bike) or conditioned associations (e.g., Pavlov's dogs salivating to a bell). Short-term memory is a brief holding store for information, and working memory is this holding information in mind while using it for complex operations and problem solving.

Capacity for short-term and working memory reliably increases with age, reaching adult levels in the teenage years. Explicit long-term memory has no known capacity; humans can remember an immeasurably large amount of information. However, the accuracy of those memories can be assessed. Young children are more susceptible to false memories and to memory errors; they make many mistakes through by adding elements that were not present and forgetting elements that were. This is often an issue in child interviews or legal testimony, and careful steps should be taken not to influence a child's memory.

Language

Infancy

Infants are obviously not capable of sophisticated, representational language. However, they do engage in both communication and language learning. Crying is an infant's primary method of communication, and they will use different cries to signal different needs (e.g., hunger, discomfort, pain, etc.). Infants also observe language, attend to its noises and the faces of those speaking, and begin attempting to imitate at a very young age. Around 2–4 months of age, children will engage in "cooing," the elongation of vowel noises (e.g., "oooooh," "eeeeoo"). Between 6 and 10 months, children begin "babbling" the repetition of common consonant-vowel pairings in their native language (e.g., "babababa," "dadadada," "mamamama"). Many parents take these noises to be first words, especially "dadada" and "mamama"; however, they are not words meant to represent concepts or convey information. The infant is simply playing with and practicing the noises they hear in their world.

At birth, infants are capable of learning any language equally well, regardless of their racial or ethnic origins. This ability is supported by a host of neurological and behavioral characteristics that are genetically dedicated to language learning. However, they require the input of language within a certain timeframe in order to function appropriately. For example, at birth infants are able to distinguish between all phonemes in every language. A phoneme is the smallest unit

of spoken language sounds (e.g., /ff/, /ch/, /sh/). Some phonemes sound very similar and can be difficult to distinguish. Native adult speakers can recognize all the phonemes in their spoken language but do not have the same ability for other languages. Infants possess this ability for all languages but lose it around the age of 6 months for all languages other than their native one (Saffran et al. 2006). This process is known as perceptual narrowing and is a product of infants beginning to learn the expected language input from their environment.

Childhood

Around 18 months of age, children continue to increase their database of usable consonant and vowel sounds to the point of forming their first words. When speaking words with harsh, stressed syllables, such as the /t/ in “water,” children will often drop the unstressed syllable (saying “wawa” in place of “water”). Furthermore, until children learn the complex rules associated with language (syntax and grammar), they will use single words to convey numerous meanings. The words “water” can be used to request water, ask if something is water, or point out the presence of water. There are substantial individual differences in this process with some children experiencing a vocabulary spurt around the age of 18 months, some gradually acquiring new words, and others experiencing a later spurt.

The next step in language development is known as telegraphic speech, because it resembles the type of communication done over telegraph when users were charged by the letter. For example, a child might say “Mama go store” by dropping articles and helping verbs, instead of saying “Mama went to the store” or “Mama is going to the store.” Children then gradually acquire syntax, grammar, phonemes, and vocabulary through the preschool and school years. One commonality in language development throughout childhood and adulthood is the difference between receptive language and productive language. Receptive language, the number of words a person can understand the meaning of when

listening to them, is consistently larger than productive language, the number of words a person can appropriately use in their own speaking, across the lifespan. By 18 years of age, the average adult speaker has a productive vocabulary of around 150,000 words.

An important point to make about language learning in childhood is the existence of a sensitive period for language acquisition. Perhaps the most influential modern linguist, Noam Chomsky, theorized the presence of a Language Acquisition Device that helps young children acquire language (Chomsky 1986). While a bit of a misnomer, it is not an actual “device”; language research has in fact confirmed that the behavioral, cognitive, and neurological suites of abilities that enable language learning are most efficient early in life and gradually taper off in effectiveness throughout childhood. This is why learning a second language is more difficult for teenager or adults than it is for toddlers or elementary school students.

Conclusion

It is tempting to discount development, especially in the study of evolutionary psychology, as children are unable to engage in the adult behavior of reproduction that ultimately drives natural selection. However, childhood should be viewed as the “crucible of evolution” in that it served as an evolutionary bottleneck for survival and preparedness so that adaptive adult behavior could be possible. Therefore, development must be ripe with evolutionarily relevant adaptations of behavior and cognitions. In fact, if the study of evolution is how genetics interact with individuals and the environment, then perhaps there is no better place to study it than in development. From a non-evolutionary perspective, the study of cognitive development is critical for many areas of basic science (e.g., how genes interact with environment, how neurons grow and change, what is typical language development) as well as substantial application (e.g., developmental disorders, education policy, parenting practices).

Cross-References

- ▶ [Developmental Milestones](#)
- ▶ [Duration of Childhood](#)
- ▶ [Lev Vygotsky](#)
- ▶ [Pinker's \(1994\) The Language Instinct](#)
- ▶ [Social Learning and Social Cognition](#)
- ▶ [Steven Pinker and Language Development](#)

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Cognitive Developmental Science

- ▶ [Cognitive Development in Non-human Primates](#)

Cognitive Enhancement

- ▶ [Use It or Lose It](#)

Cognitive Ethology

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Synonyms

[Cognitive science](#); [Ethology](#); [Study of animal minds](#)

Definition

A field that combines techniques from ethology and cognitive psychology to study animal cognition or animal minds.

Introduction

Giving a definition of “cognitive ethology” is difficult. In “Is Anyone a Cognitive Ethologist?” Colin Allen distinguished between two possible interpretations of what “cognitive ethology” might refer to (Allen 2004). It can be thought of, as many contemporary philosophers do, loosely as the general study of cognition in nonhuman animals (I shall follow the common practice in using “animal” to mean nonhuman animals). Marc Bekoff, a self-described cognitive ethologist, seems to have this more general idea in mind when he states, “cognitive ethology is the comparative, evolutionary, and ecological study of nonhuman animal minds including thought processes, beliefs, rationality, information-processing, and consciousness” (Bekoff 1995).

However, as Allen argues, this general conception ignores a number of important historical and methodological implications of the term. There is a core tension in the term between its constitutive parts; on one hand we have cognitive psychology, which pulls one toward the laboratory and controlled experiment, while on

the other we have ethology which values in situ observation of animals. Historically, it ignores the fact that the term was coined by Donald Griffin whose work focused, controversially at the time, on the conscious awareness of animals.

While the term “cognitive ethology” and the larger academic field it represents may be edged by some fuzzy borders, the study of animal cognition has made and will continue to make important contributions.

Text

History

Cognitive ethology is a combination of two separate traditions: ethology and cognitive science. Classical ethology is generally seen to be a continuation of the work done by Konrad Lorenz and Nikolaas Tinbergen. Their work encouraged observation of animal behavior within their natural environment. Tinbergen’s famous four questions (see Fig. 1), for instance, require that for any observed behavior to be understood, it must be placed in a context that includes both current and historical influences of the natural environment (Tinbergen 1963). On the other hand, cognitive psychology – which grew out of the cognitive revolution and general dissatisfaction with behaviorism in the post-World War II period – was highly experiment driven.

These two ideas were, at least in theory, brought together in a series of books and papers

beginning in the late 1970s where Donald Griffin coined the term “cognitive ethology” and laid the groundwork for the field’s eventual practice (Griffin 1978). Griffin’s initial work on the phenomenon of echolocation (a term he also introduced) in bats led to the controversial proposal that not only did animals have mental states comparable to those of humans, but that these mental states were valid objects of scientific inquiry. Griffin’s work was a critique of the behaviorist tradition, typically associated with B. F. Skinner, which dominated both American psychology and animal sciences in the early twentieth century.

Dangers of Anthropomorphism

One of the critiques that was leveled at Griffin is that by allowing animal minds as objects of research, one implicitly humanizes the animal and may be more likely to attribute complex, humanlike capacities where none actually exist. This is especially concerning in the context of evolutionary psychology as the cognitive continuity between humans and nonhumans is a central issue. These fears have been a concern within animal studies for centuries, but became formalized and popularized around the turn of the nineteenth century by Conway Lloyd Morgan in the form of Morgan’s canon:

In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development. (Morgan 1903, p. 59)

	Synchronic/Static: Looks at behavior in a point in time	Diachronic/Dynamic: Looks at behavior over a span of time
Proximate (How): Considers immediate influences on behavior	Mechanism (Causation) What are the mechanical or causal relationships that affect how the organism works?	Ontology (Development) How does the individual change over its lifespan?
Ultimate (Why): Considers role of behavior in the organism’s evolution	Adaptive Value (Function) How do the traits of the organism benefit it in terms of increasing fitness?	Phylogeny (Evolution) How does the species change over time, compared to others?

Cognitive Ethology, Fig. 1 Tinbergen’s four questions

There is currently debate over what, exactly, Morgan intended this statement to mean and how it should be used in the contemporary arena; however, the popular interpretation which has shaped much of contemporary comparative cognition studies is as a behaviorist Occam's razor, e.g., Griffin uses the cannon this way. We should, whenever possible, look for lower-complexity, nonpsychological, explanations for animal behavior and only resort to minds when behavior fails to enlighten us.

More recently, Sara Shettleworth's discussion of "killjoy" explanations in comparative psychology presents a slightly different take on the issue. A killjoy explanation is one that attributes the observance of complex behavior in an animal to a "lower" or nonmental process. Rather than being seen as boring, killjoy explanations should, in a sense, turn the tables and ask us to reexamine our assumptions about the complexity of human mental states. If an animal can exhibit behavior of humanlike complexity without relying on higher-order mental capabilities, it is at least possible that humans also rely on simpler, nonmental processes to exhibit these behaviors. Shettleworth claims that these killjoy explanations "contribute to a deeper, more truly comparative psychology" (Shettleworth 2010, p. 1).

Communication

Given the perceived importance of language to understanding the evolution of human cognition, it is unsurprising that a great deal of work had been done on communication in non-humans. Much of the modern work on animal communication and comparative communication can be linked back to Peter Marler. Marler's work on birdsong and primate communication, particularly his 1961 paper, *The Logical Analysis of Animal Communication*, laid the groundwork for much of the current literature (Marler 1961). Marler's model focuses on the receiver of a signal, using their behavior to indicate the content of the original message. While Marler's view is widely known and used, it is not the only one.

The popularity of Marler's model is due, partially, to its use by his successors. One of the most

widely cited studies on animal communication came from two of Marler's postdoctoral advisees, Dorothy Cheney and Robert Seyfarth. Their study on alarm calls in vervet monkeys (Seyfarth et al. 1980 and Cheney and Seyfarth 1980) shows that three distinct alarm calls are recognized by the monkeys – one for "eagles" and airborne predators, one for "snakes" and ground predators, and one for "leopards" and tree-dwelling predators – and that each elicits a different response.

The evolutionary implications of this came to a head in the debate between two groups. On one hand Marc Hauser, along with Noam Chomsky and W. Tecumseh Fitch, argues that the faculty of language can be seen in either a broad sense, FLB, which includes "a sensory-motor system, a conceptual-intentional system, and the computational mechanisms for recursion, providing the capacity to generate an infinite range of expressions from a finite set of elements" (Hauser 2002, p. 1) or a narrow sense, FLN, which includes only syntactic recursion. Further, Hauser et al. claim that FLN is the only uniquely human component of language and that, while it is ultimately an empirical question, FLN may have evolved for reasons other than human language, "for example, number, navigation, and social relations" (Hauser 2002, p. 1). On the other side of the debate, Steven Pinker and Ray Jackendoff have argued that the FLN-only approach is problematic (Pinker and Jackendoff 2005). They claim that it ignores a great deal of evidence from comparative anatomy and cognition, linguistics, and genetic studies that indicate at least one human speech and language gene that is not specific to recursion has been evolutionarily selected for.

Conclusion

Cognitive ethology is a young field which shows great promise of giving a better understanding on both human and animal cognition. The psychology (or at least cognition) of non-human animals is varied and complex, and the scientific study of this plethora will,

undoubtedly, be invaluable when thinking about human psychology, especially in an evolutionary context.

Cross-References

- ▶ Anthropomorphism
- ▶ Bird Tool Use
- ▶ Cephalopod Tool Use
- ▶ Cognitive Science
- ▶ Corvids
- ▶ Evolution of Tool Use
- ▶ Field of Comparative Psychology, The
- ▶ Marc Bekoff
- ▶ Nonhuman Intelligence
- ▶ Primates
- ▶ Primate Tool Use
- ▶ Vocal Communication

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Cognitive Map

- ▶ Spatial Mapping

Cognitive Modularity

- ▶ Modularity of Mind

Cognitive Neuroscience

- ▶ Cognitive Science

Cognitive Ornithology

- ▶ Convergent Evolution of Intelligence Between Corvids and Primates

Cognitive Primatology

- ▶ Convergent Evolution of Intelligence Between Corvids and Primates

Cognitive Psychology

- ▶ Cognitive Science

Cognitive Revolution, The

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Introduction

The cognitive revolution was an intellectual movement that began in the 1950s and exerted deep influence on psychology, linguistics, computer science, artificial intelligence, neuroscience, and philosophy. It was a reaction against the radical empiricist ways of behaviorism that had dominated the study of human and animal behavior since the early twentieth century.

Background

In the early twentieth century, psychology had wandered a long way from being the “study of mind” that William James had envisioned it to be. Quite the contrary, psychologists had all but given up on issues concerning the mind and the mental, focusing instead on behavior as responses to physical stimuli. The behaviorists argued that mental events, such as *beliefs* and *representations*, were not publicly observable. Since my internal beliefs, say “I like red cars,” are not objectively available to others for observation, independently of my introspective recollections, behaviorists argued that such concepts cannot be studied scientifically. Behavior, on the other hand, is very publicly observable and recordable. It is possible, for instance, to observe me repeatedly buying cars which are red and ascribe my decision to do so to similarly observable stimuli that reinforces my behavior, such as approving attitude of my friends and neighbors. As such recording observable behavior, documenting what factors in the environment (stimuli) correspond to them, and converting them to a behaviorist jargon were asserted by behaviorists to be the only means to bringing about scientific objectivity to the study of what living organisms do and

why (Miller 2003). Primarily an American phenomena, behaviorism had an overwhelming influence on experimental psychology. For many behaviorists, consequently, there ceased to be any meaningful dichotomy between *perception and discrimination*, *memory and learning*, etc. This, however, had the negative side effect of erasing any distinction between describing a phenomena (e.g., If dropped, a ball falls downward.) and causally explaining the precise mechanisms underlying said phenomena (e.g., the effects, and origins, of gravitational pull). In 1951, George Miller published *Language and Communication* (Miller 1951) a study of language and linguistic phenomena, acknowledging the well-established behaviorist bias of the time in his preface. Miller’s work, however, was much less radical in its behaviorism compared to B.F. Skinner’s soon-to-follow *Verbal Behavior* (Skinner 1957), which practically reduced language to operant-conditioned verbal behavior. It was Skinner’s book that sparked what has become, possibly, the most well-known criticism of behaviorism and one of the major manifestos of the cognitive revolution in the form of Noam Chomsky’s scathing review of Skinner (Chomsky 1959a).

Development

Behaviorism in psychology was a very influential movement in North America, dominating almost every aspect of the discipline and turning it into “a study of behavior.” The behaviorists had a narrow aim of predicting and controlling behavior, and in the case of psychologists like J.B. Watson, the latter took center field and equated all psychology with applied psychology. The motto of the methodological behaviorist was to deny all discussions of internal mental states or belief systems and focus simply on documenting observable behavior in order to isolate specific stimuli that could be used to either re-elicite, suppress, or modify said behavior in some shape or form. Watson’s insistence on using a stimulus-response approach resonated well with radical empiricists because of its reliance on the associative basis of all behaviors.

Allegedly, every behavior could be associated with some stimuli that could reinforce its learning. While the notion of “observable” was central to behaviorists in declaring their methodology as “science,” the history of science itself is rather sparse in endorsing such definitions of the term (Chomsky 1959a; Kuhn 1970; Whitehead and Russell 1912).

Watson’s influence was seminal in most aspects of psychology, flooding it with the standard stimulus-response approach; there still were notable exceptions found in E.C. Tolman’s “cognitive maps” and B.F. Skinner’s “functional behaviorism.” Skinner used a functional definition of stimuli and responses as eliciting/discriminative conditions and operant behavior (Skinner 1995), but not unlike stimulus-response behaviorists, much of his early work was focused on nonhuman behaviors. This was, directly and indirectly, a result of the theoretical failure of behaviorism in accounting for the complex cognitive functions found in humans (Miller 2003). As interest rose in explicating the biological basis of human cognition, and isolating the factor that creates a species boundary between *Homo sapiens* and other primates, the gaps in behaviorist reasoning started becoming more apparent. Having been banished from mainstream psychology for decades, the writing was on the wall for an oncoming paradigm shift in the study of mind and brain that was going to take *folk psychological* notions of *concepts*, *representations*, and *knowledge* with the seriousness it deserved and couch its defense in some form of physicalist naturalist framework, without regressing into a sort of Cartesian dualism.

New Beginnings

Breakthrough disciplines often bring about a transformation in science in general, and this was no less true of the cognitive revolution. A number of developments would ultimately result in the actual shift causing psychologists and philosophers to rethink what the object of inquiry in a scientific study of human nature

ought to be. This includes a growing realization of the shortcomings of the dominant paradigm of the day; the rise of then nascent disciplines like computer science, artificial intelligence, and neuroscience; and new developments in statistical and mathematical theories as well as breakthroughs in mainstream biology. The emerging developments in genetics and evolutionary biology were making it aptly clear that even in animals endowed with less complicated cognitive processes, a simple stimulus-response model could not account for their behavioral patterns. For instance, the works of biologists such as E.O. Wilson showed that an animal itself makes significant contributions toward curving out an ecological niche within which its experiential learning could take place. This contribution made by the organism is encoded in its genetic code, and a causal theory of behavior will then have to account for the ways in which the organism concerned interprets and represents its environment to itself (Wilson 2000). As exciting an adventure as behaviorism had been for psychology, it seemed poised not to succeed in attaining the goals it had set for itself.

Observing the obsession in psychologists of the day with recording a complete history of input stimulus and accompanying behavior, Chomsky (1959) writes:

Putting it differently, anyone who sets himself the problem of analyzing the causation of behavior will (in the absence of independent neurophysiological evidence) concern himself with the only data available, namely the record of inputs to the organism and the organism’s present response, and will try to describe the function specifying the response in terms of the history of inputs. This is nothing more than the definition of the problem. There are no possible grounds for argument here, if one accepts the problem as legitimate, though Skinner has often advanced and defended this definition of a problem as if it were a thesis which other investigators reject. The differences that arise between those who affirm and those who deny the importance of the specific “contribution of the organism” to learning and performance concern the particular character and complexity of this function and the kinds of observations and research necessary for arriving at a precise specification of it. If the contribution of the organism is complex, the only hope of predicting behavior even in a gross way will be

through a very indirect program of research that begins by studying the detailed character of the behavior itself and the particular capacities of the organism involved.

The premise of Chomsky's criticism here is rather simple – it is not enough to merely describe what an organism does and when, unless we have an account of how the circumstantial/environmental information of the event is filtered by the organisms' genetically limited processing abilities and the precise nature of the information extracted therein. In simpler words, if we observe that bats echolocate their ways around space, an explanatory account of the same should include the precise mechanisms that allow a bat to create sound waves and receive the echoed waves back in order to elicit spatial information from them. This ability is the bat's unique contribution to echolocation is independent of echoes as physical phenomena and cannot be inductively learned by a species unless they are born with it. What is difficult still, however, is coming up with such scientific accounts for infinitely more complex phenomena such as human mental processes (e.g., beliefs, desires, concepts, language, etc.).

The introductory lines of *Syntactic Structures* (Chomsky 1957/2002), a book that grew out of his initial attacks on behaviorism, aptly summarize Chomsky's intended alternative to approaching the psychological basis of mental processes:

Syntactical investigation of a given language has as its goal the construction of a device for producing the sentences of the language under investigation.... The ultimate outcome of [such] investigations should be a theory of linguistic structures in which the descriptive devices utilized in particular grammars are presented and studied abstractly.... One function of this theory is to provide a general method for selecting a grammar for each language, given a corpus of this language.

Unlike the behaviorists, Chomsky's rationalist approach is concerned less with attested patterns in behavior and more with the open-ended *creativity* with which children seem to manifest their linguistic abilities (Aarsleff 1970; Bever 2009; Chomsky 2009). This is reminiscent of Bertrand Russell's concern with how it is that human

beings, whose contact with nature is so brief and transient, come to learn so much of their environments? This would lead scientists of the day to look elsewhere in search of possible alternatives, and here Chomsky's seminal review of behaviorism comes to play an important role. Applying this general observation to linguistic phenomena, Chomsky asks how is it possible for a child to instinctively create new utterances to which it has never been exposed specifically, based only on exposure to a fraction of the possible sentences of a language. The conclusion that Chomsky drew from this line of thinking was already a staple in mainstream evolutionary biology (Mayr 1961, 1982) and amounted only to an acknowledgment that all epigenetic developments follow a trajectory that is genetically predetermined. In other words, to learn something properly, an organism needs to have at least a preliminary outline of what it is that needs to be learned and what constitutes evidence for such learning. Not unlike David Hume, Chomsky points out that though organisms no doubt derive much of their understanding of nature through experimental reasoning, that ability itself is something that they derive through the original hand of nature, and on this, they improve little to nothing throughout their lifetime.

All biological organisms are rather rigidly constrained in things that they can, and cannot, make sense of (Mayr 1982; Wilson 2000), and this constrain shapes and determines the way an organism would represent its knowledge of the world to itself. Psychologists of the day, however, were still reluctant to admit any notion of *representations*, as such talks were considered *mentalistic*, and being unobservable externally, mentalistic discussions were little more than mathematical obscurities to the behaviorist. This would change radically, however, with the rise of computer science and the growing realization that mathematical computations were in fact realized in nature on physical substrates. Here, at last, was a way to give a scientific expression within psychology to the link between cognition and behavior in a manner that was unlikely to fall short of biological complexity.

Computation and Cognition

The discussions so far have straddled various scattered bits and pieces of reasoning, with a common unbroken thread running through them – why do organisms behave the way they do, and what causes their behavior? The fundamental problem with behaviorism had been the problem of *causality*. It is not sufficient evidence of a causal relationship that event Y is often preceded by event X. Missing from such correlational observations, among other things, is the notion of levels of interaction that often lead to emergent phenomena. A scientific theory can only be evaluated at the appropriate level it is addressing, and while behaviorism flourished at locating correlations between X and Y, for example, its ability to tease apart whether the two events are correlated directly or as a result of intervening phenomena at levels not addressed by its stimulus-response methodologies was limited. This problem concerned not just linguistic behavior but held true for most issues concerning complicated cognitive phenomena of any kind. One of the first major empirical findings to put a finger on this issue involved Claude Shannon's information theory. Shannon's theory, based on Markovian processes, had an inherent allure for behaviorists and their stimulus-response methodology. Miller (1951, 1956b; Miller and Chomsky 1963) was among the first to illustrate that Shannon's theory was drastically lacking in explanatory prowess beyond elementary analysis of written sequences. Recounting his early efforts in this direction, Miller (2003, p. 1) writes:

But information measurement is based on probabilities and increasingly the probabilities seemed more interesting than their logarithmic values, and neither the probabilities nor their logarithms shed much light on the psychological processes that were responsible for them.

Miller's empirical findings would lead him to look elsewhere for explanatory accounts of cognition, and this would eventually lead him, and others, to Chomsky's syntactic theory. This shift in perspective, while slow, opened the door for reconnecting the two sides of the Atlantic and made possible meaningful collaborations with

research groups that were unaffected by the primarily American behaviorism. These would include, among others, Bartlett's works on memory in the UK, Jean Piaget's seminal research on child acquisition in Geneva, as well as A.R. Luria's foundational attempts at unifying the mind and the brain in Moscow. Being unaffected by the behaviorist aversion to abstractions, these researchers were willing to look beyond quantifiable behavior for explanations. Chomsky's syntactic theories seemed suited to become the strongest contender for an alternative framework, primarily because they were not statements of behavior but rather formal mathematical statements of cognition with *rules* of cognition proving the means for transformation of one cognitive state of affair into others.

This change in attitude would coincide with breakthrough developments in computer science. On the 10th of September, 1956, *The Special Interest Group in Information Theory* organized their seminal symposium at MIT, which directly led to some of the foundational concepts in computation and cognition being tabled for discussion. Newell and Simon (1956) discussed their *logic machines*, while Miller (1956) discussed the nature and organization of human memory architecture. Alongside these scholars, John McCarthy and Marvin Minsky (Minsky 1961; Minsky and Papert 2017) were laying the foundations of what would become *artificial intelligence*. Finally, while Chomsky was revolutionizing linguistics by demonstrating that language exploits all the precision of mathematics and explicating its computational nature (Chomsky 1959b, 1975), Bever, Fodor, and colleagues produced foundational research highlighting the cognitive subtleties of acquisition (Bever et al. 1965, 1969). Miller (2003) writes that computer scientists like Newell were primarily invigorated by Chomsky's exposition of the algorithmic beauty of language, as it was finally making available for formal mathematical investigation one of the most complex human behaviors. Other related developments included Szikali's experiments on perception and processing and Birdsall's work on application of signal detection theory to perceptual studies.

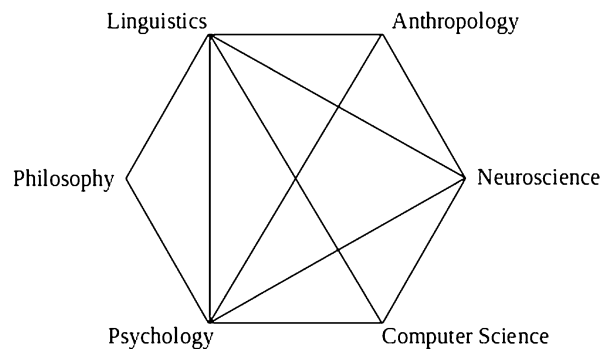
The major formal recognition of something akin to a scientific revolution involving multiple disciplines would come with the Sloan Foundation's interests in funding extensive research into what was by now being referred to as the *cognitive sciences*. Following the establishment of the cognitive studies group at Harvard, information-processing psychology at Carnegie Mellon, and an international meeting at MIT in 1974 organized by Massimo Piattelli-Palmarini bringing together biologists like the Nobel laureate Salvador Luria and linguists like Chomsky and Lenneberg, the foundation facilitated the formation of a highly interdisciplinary committee to summarize the state of the art in cognitive science. Miller (2003) writes that the driving concepts behind the emerging areas of research were summarized in a hexagonal figure, with the six corners representing the six major fields that would contribute expertise, while the lines joining them stood for an interdisciplinary methodology combining the tools of the disciplines. Thus, the union of computer science with the computational interpretation of linguistic phenomena would lead to computational linguistics, while computational methodologies would model neural functionings elucidated by neuroscientists to create cybernetics. The Sloan Foundation accepted the report in 1978 (Miller 2003), and subsequently, funding was made available to various universities for recruitment of scholars and facilitation of scholar mobility, seminars, and collaborations. This directly resulted in an outburst of scholarly works that pushed the limits in a multitude of disciplines and brought about methodological

paradigmatic shifts in all six disciplines. Linguistics rapidly matured from being the red-haired stepchild of philology to a proper scientific study of a biological phenomenon (Massimo Piattelli-Palmarini coined the term *biolinguistics* in 1974 to describe this emerging new field); philosophers left their armchairs and indulged in sophisticated empirical pursuits, while computational sciences established once and for all that computation was more than a mathematical convenience and constituted a fundamental natural phenomena. The study of thinking was no longer the domain of metaphysics and speculation, and the human mind was ready for a naturalistic inquiry into its functional and architectural limitations (Fig. 1).

Impact and Aftermath

The impact of the events that unfolded in the 1950s, and through the 1960s and 1970s, has been profound enough that the series of events have been termed *the cognitive revolution*. While the term revolution is prone to imply a somewhat violent detachment from all things past, a number of scholars have pointed out that in reality, it was more of a return to unanswered questions and unexplored problems yesteryears (Chomsky and McGilvray 2009; Fodor 2001). The cognitive revolution was primarily driven by a need to better understand the nature of information and the role of a biological organ, the brain, in packaging and storing it in a fashion that could feed cognitive processes. The foundational frameworks were laid by the works of Noam Chomsky

Cognitive Revolution, The,
Fig. 1 Cognitive science in 1978. (Source: Miller 2003)



(1965, 1975, 1980, 2002), Jerry Fodor (1975, 1981), David Marr (1982), and Eric Lenneberg et al. (1967) among others. Chomsky’s attack on behaviorism opened the door for a return to the old questions concerning universality of the human mind. In *Cartesian Linguistics*, Chomsky and McGilvray (2001) notes that the idea that there must be something universal about the structure of the human mind, and its unique abilities including language, date back to Descartes and featured prominently in the works of the Port Royal Grammarians. Chomsky’s formalist investigation of the information structuring of natural languages (Chomsky 1975), as well as his works on formal languages and logic (Chomsky and Schützenberger 1959), helped firmly establish the need to approach the functioning brain as a mathematically describable information processing system. Early research in computer science would then help establish that computations are, indeed, executable on physical substrates further lending credence to the plausibility that the brain could really be something akin to a computer. It was, however, the philosopher and cognitive scientist Jerry Fodor who would propose the most impactful analysis of the mind as a computer with his series of expositions of *the computational theory of mind* (Fodor 1975, 1981, 2001). Fodor argued that mental states, such as beliefs and desires, are relations between individuals and mental representations. He maintained that these representations can only be correctly explained in terms of a language of thought (LOT) in the mind. Furthermore, this language of thought itself is an actually existing thing that is codified in the brain and not just a useful explanatory tool. Fodor adhered to a species of functionalism, maintaining that thinking and other mental processes consist primarily of computations operating on the syntax of the representations that make up the language

of thought. For Fodor, significant parts of the mind, such as perceptual and linguistic processes, are structured in terms of modules, or “organs,” which he defines by their causal and functional roles. These modules are relatively independent of each other and of the “central processing” part of the mind, which has a more global and less “domain-specific” character.

Likewise, the neuroscientist David Marr was a pioneering influence in furthering the understanding of the biological basis of information processing (Marr 1970; Marr and Thach 1991; Marr et al. 1991). Marr’s seminal book, *Vision* (Marr 1982), argued for what is often referred to as *the tri-level hypothesis* – one must understand information processing systems at three distinct, complementary levels of analysis (Table 1).

The convergence of the sort of psychological nativism and computationalism advocated by Chomsky, Fodor, and Marr has been influential in, some senses, completely refocusing the research questions that concern scientists involved in understanding the biological basis of cognitive functions (Bever 1970; Bever and Poeppel 2010; Carey 2009; Embick and Poeppel 2015; Fodor 1998; Hauser et al. 2002). A complete review of its influences is beyond the scope of this chapter, but briefly, its effects have been dominant in four major strands of emerging research – the evolution of complex cognition, the realization of highly formal computations on physical/biological substrates, the constraints on such computations and their realizations stemming from general laws of nature, as well as in more applied researches into bioinformatics and artificial intelligence.

The discussion of evolution of cognitive abilities has a long and complicated history in the scientific literature. While curiosities and

Cognitive Revolution, The, Table 1 Marr’s tri-level hypothesis

Level	Description
1. Computational level	What problem does the system solve?
2. Algorithmic level	How is the problem solved, and what representations are used?
3. Implementational level	How is such a system physically realized?

speculations about the universal nature of the mind can be traced back to Plato (cf. *Plato's Problem*, in Chomsky and McGilvray 2009), with significant contributions by Kant, Descartes, and Hume (Chomsky 1959a, b), discussions of evolutionary origins of such abilities like language were declared taboo by the *Société de Linguistique de Paris* in 1866. With the advent of the cognitive revolution, however, a naturalist framework for such discussions was made available that did not have to regress to Cartesian dualism (Chomsky and DiNozzi 1972). This effect was not limited to linguistics in particular either, as the fundamental basis of the revolution was predicated upon the issue of mental representations. A representational system, linguistic or otherwise, is an algebraic system of symbolic variables (Gallistel 1981). The symbols are the representational primitives that form representations that are *isomorphic* to another system, the represented system. The isomorphism implies that the mathematical relations that hold between the symbols bear a similar form to the ones holding between the things being represented. Because the forms of the relations that the variables enter into are the same between the two systems, it ensures the validity of the conclusions drawn about the represented system through an analyses of the symbols of a representational system. Computational processes are algorithmic instructions that dictate the manipulation of representational symbols, leading to generativity. Accordingly, Gallistel and King (2009) have argued that the ability to represent numbers, and to recall them from long-term memory, is the most important mechanism that underlies higher cognition. In a similar vein, many researchers argue that a science of cognition is essentially the science of representational systems and their inner workings (Gallistel 2001; Marcus 2003).

The exact nature of the evolutionary process that led to such computational representational systems is still a hotly debated topic. While Pinker and colleagues have argued that the computational mind is a result of adaptation through natural selection (Pinker 1997; Pinker and Jackendoff 2005), yet others have criticized the adaptationist approach (Fitch 2005; Fodor 2001; Fodor

and Piattelli-Palmarini 2011; Hauser et al. 2002; Hauser and Spelke 2004). The growing interest has contributed significantly to the rise of evolutionary psychology as a major scientific discipline, with its insistence on a massively modular mind that is the result of specific adaptations to different needs (Pinker 1997). While maintaining its commitments to computational-representational theories, the evolutionary psychology approach has nonetheless attracted criticisms directed both at its conception of modularity and computationalism from other computationalists (Fodor 2001).

Effects of the cognitive revolution have been also prominently felt in neuroscience and psychology, especially with the advent of easily accessible neuroimaging tools. The ease of observing the functioning brain in action has led to a plethora of imaging studies that have shed light on the many intricacies involved in cognitive processing (Bosker 2016; Chow et al. 2014; Tettamanti et al. 2002, 2009; Wilson and Iacoboni 2006; Xiang et al. 2009). As useful and insightful as imaging studies of various kinds have been, however, the cognitivist perspective has exerted an even greater influence over theoretical neuroscience. For instance, David Poeppel and colleagues have argued in a series of influential publications that in order for cognitive neuroscience to be successful, appropriate linking hypotheses must be posited between cognitive and neural phenomena (Bever and Poeppel 2010; Poeppel et al. 2012). Because neuroscience and formal cognitive investigations operate on different sizes of conceptual granularity, the authors argue that there is no direct translation of phenomena from one domain in terms of the lexicon of the other. Two important factors are pointed out – (i) *the granularity mismatch* issue points out that the phenomena that concern the two disciplines, and their primitives, are not similar in their conceptual granularities, and (ii) *the ontological incommensurability problem* is a reminder against greedy reduction of cognitive primitives to neural substrates (Embick and Poeppel 2015; Poeppel and Embick 2017). Likewise, Krakauer and colleagues have argued that in order to attain a properly explanatory

account of the neural basis of cognitive processes, neural examinations should be informed by theoretical insights as well as thorough behavioral examinations (Krakauer et al. 2017).

A similar concern is seen in the refocusing of the goals of linguistic theory through the emerging biolinguistic program (Boeckx and Martins 2016; Chomsky 2007; Crain et al. 2017; Piattelli-Palmarini 2013; Piattelli-Palmarini and Uriagereka 2004, 2008). In a series of much-debated publications, Hale, Reiss, and colleagues (Hale and Reiss 2000, 2008; Isac and Reiss 2013; Reiss 2003, 2007) have argued for an *I-language* perspective, a speaker's implicit knowledge of her language, that which yields her observable utterances, is a system of computation that operates over symbolic variables. The rules of this computation constitute her knowledge of language, and a study of grammar constitutes an investigation of the shared properties of all such possible states of knowledge. Likewise, building on Reiss' arguments of modularity (Reiss 2007), Volenec and Reiss (2017) have proposed a framework for exploring the partial veridicality that holds between physical speech stimuli and mental representations of sounds and meaning. The authors argue that cognitive representation and processing of sounds of natural language are purely algebraic computations and that the primitives of such computations are independent of the stimuli that accompany their externalization. Similar arguments have also been made by cognitive scientists and psychologists exploring other types of information processing in the brain (Fodor and Pylyshyn 1988; Gallistel 2007; Gallistel 1981; Pylyshyn 1984; Marr 1982).

It is perhaps a sign that aforementioned developments have been able to bridge the gaps between the cognitive sciences and the more basic natural sciences, that in recent years there has been an increase in research activities focusing on the place of cognition within nature and the status of cognitive sciences as natural science. For instance, Medeiros and colleagues have reported that linguistic computations manifest putative universal patterns observed generally in nature (Carnie et al. 2005; Medeiros et al. 2016)

and that linguistic structures like the *x-bar* schema are results of optimal computations in a very general sense. Krivochen and Saddy (2018), likewise, report empirical evidence to support the same position. Further, Piattelli-Palmarini and colleagues (Piattelli-Palmarini and Vitiello 2017) have reported remarkable isomorphisms between various cognitive processes and field quantum theory, while seminal research in bioinformatics have recently reaffirmed the feasibility of classical computations on biological substrates (Green et al. 2017).

Conclusion

In the end, it remains a matter of perspectives whether or not the cognitive revolution was a single event localized to a single year in history, or a series of events over the years, and whether it had set for itself a fixed set of goals and agendas. What can be said definitively, however, is that a sort of Kuhnian paradigm shift has gradually come to pass and has exerted enormous influence across several disciplines (psychology, philosophy, neuroscience, linguistics, anthropology, etc.) and resulted in the prosperity of newer ones (artificial intelligence, cognitive science). It was marked by a shift in perspectives from observation of behavior and correlational stimulus-response behaviorism to more causally explanatory theories of cognition. It has not, however, been a uniform movement, having given rise to many contending frameworks (cf. Fodor and Piattelli-Palmarini 2011 and Hauser et al. 2002 vs. Pinker 1997 and Pinker and Jackendoff 2005; Prince and Smolensky 1993 vs. Hale and Reiss 2000), that nonetheless can be argued to share broad assumptions regarding the object of inquiry. As an intellectual movement, it was sparked by a break from a dominant paradigm, was inspired by newly emerging fields of research in computation, and has been fundamentally influential in refocusing several research questions even if it has not always provided conclusive answers. There are few conclusive ends in science, being that as a project, science is characterized by continually

evolving understandings of nature. However, to the extent that scientific inquiry is dependent on scrutiny and periodic readjustment of its methods and tools, the cognitivist phenomena have been nothing short of a revolution.

Cross-References

- Cognitive Science
- Information Theory
- Linguistics
- Noam Chomsky
- Universal Grammar

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Cognitive Schemas

► Gender Schema Theory

Cognitive Science

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Synonyms

Cognitive neuroscience; Cognitive psychology; Computational neuroscience; Neurophysiology; Neuropsychology; Neuroscience; Psychophysics

Definition

“Cognitive science” is an interdisciplinary field that focuses on the mental architecture of the mind and how it processes information, specifically how the brain functions with respect to emotion, attention and consciousness, language, perception, learning and memory, and executive functioning.

Introduction

The theoretical roots of cognitive science can be traced back to over 2,000 years ago. However, cognitive science as a formal discipline was established in the 1970s. Several “precursors” catalyzed the field of cognitive science being recognized as a legitimate field of study, namely, criticism toward behaviorism, computational and algorithmic mathematics, linguistic analysis, and models of information processing. Behaviorism contributed to our understanding of problem-solving (Tolman and Honzik 1930), learning (Tolman et al. 1946), and higher-order behaviors (Lashley 1951). Computational and algorithmic mathematics contributed to our understanding that the mind does not operate in a strictly mechanistic manner. Rather, the mind makes use of an *algorithm* to be used in a systematic manner across an array of situations and domains (Turing 1936, 1950). Linguistics taught

us that language also makes use of complex algorithms, specifically the ability to transform or convert sets of symbols into different strings of symbols (Chomsky 1957). Models of information processing demonstrated that the human mind tends to “bottleneck” in regard to how much information can be efficiently encoded, stored, and retrieved (Miller 1956). Lastly, the ability of one’s mind to function in such a systematic and complex manner is a product of how the brain has evolved over time; some processes are selectively reduced or eliminated, whereas others may be emphasized and preferentially expressed.

Components of Cognitive Functioning

Cognition can be conceptualized as a dynamic and interrelated set of functions that encompasses perception, emotion, executive functioning, learning and memory, language, and attention and consciousness. *Perception* refers to a person’s ability to detect the presence of a stimulus (novel or habitual). The process of perception can be conceptualized as a person’s ability to believe that “something” is a “certain way” based on set parameters or expectations (i.e., representational theory; Harman 1990; Loar 2002). In other words, perception is a modular approach to processing sensory-related information that is mediated by specific sensory-related algorithms (Fodor 1985; Marr and Nishihara 1978; Pylyshyn and Turnbull 1986). *Emotion* can both influence and be influenced by cognition. For example, one’s “appraisal” of a situation will facilitate a process, whereby the person evaluates its environment in relation to its goals and/or well-being, thus eliciting some type of emotional response to contend with the situation (e.g., depression; Arnold 1960; Lazarus 1991). Conversely, a person who experiences chronic depression may view future situations or interactions in a negativistic manner, thereby perpetuating a depressionogenic “schema.”

Executive functioning is comprised of several cognitive processes that allow a person to reason, problem-solve, make decisions, and engage in a goal-directed behavior. For example, reasoning

tends to be associated with how a person makes use of new information; mental representations of conditions can be modified as a result of previous knowledge (i.e., “semantic/pragmatic modulation”; see Johnson-Laird and Byrne 2002). Alternatively, decision-making focuses on how a person’s beliefs and values direct their choices; “prospect theory” asserts that in a value function situation, people tend to take risks when it is framed in terms of loss. Conversely, people tend to avoid risk when it is framed as a gain (Kahneman 1979).

Current theories of *learning and memory* assert that there are three types of memory: working, short-term, and long-term. Working memory describes a process where information is temporarily held to be manipulated in order to perform a task (e.g., seconds), which may later be transferred into short-term and ultimately into long-term memory (Miller 1956). The multicomponent theory of working memory by Baddeley and Hitch (1974) states that a stimulus registers on a sense organ and then transfers within several “subsystems,” the phonological loop, episodic buffer, and visuospatial scratchpad, all of which are mediated by the central executive. Conversely, short-term memory describes a process where information is temporarily retained over a period of brief delays (e.g., seconds to minutes; Murdock 1974). Alternatively, long-term memory describes a process where information is stored over a long period of time (Atkinson and Shiffrin 1968; Murdock 1974). Moreover, the process of memory involves four steps, initial encoding, storage, forgetting, and retrieval, although contemporary theories also include consolidation and reconsolidation as two additional processes, especially as the latter two facilitate long-term memory (Craig and Lockhart 1972; Ebbinghaus 2013; Müller and Pilzecker 1900).

Cognitive science has used the analogy of computers as a means to define how the human brain processes information or communicates within itself. With that analogy in mind, the primary method of communication within a computer is a binary or symbolic system of *language*. Language processing emerged from the physical symbol hypothesis, which states that

intelligent life transforms physical symbols as to act on it in some meaningful way (Simon and Newell 1975). This hypothesis was expanded upon by Fodor, who created the language of thought hypothesis, which states that basic symbols are stored in the mind. However, information processing is facilitated by transforming symbols into sentences and language of thought (Fodor 1985, 1987).

Attention and *consciousness* are interdependent cognitive processes; attention refers to one's ability to orient one's senses (e.g., visual, tactile, olfactory, auditory) to perceive and encode a stimulus. Types of attention include simple, focused, sustained, divided, and rapid alternating. Alternatively, consciousness refers to a person's awareness or ability to react to stimulation in the environment (Wolman 1989). Consciousness also refers to one's level of arousal and varies along a continuum ranging from coma, stupor, delirium, and normal consciousness (Inouye et al. 1990; Levin et al. 1979; Lipowski 1990). Both processes are integral in a person's ability to detect sound, position, shape, color, texture, and temperature of stimuli. Two state consciousness-based theories have shaped how consciousness is conceptualized: the higher-order perception (HOP) and higher-order thought (HOT) theories (Armstrong 1968, 1981; Bayne and Chalmers 2003; Dainton 2000; Lycan 1987, 1996). The HOP theory asserts that consciousness is achieved via higher-order representations of a stimulus, with internal monitoring/introspection of one's own mental/brain states. Alternatively, the HOT theory asserts that consciousness is achieved by simply having a thought, essentially removing the necessity for introspection or monitoring of brain states.

Collectively, cognitive functions such as emotion, attention and consciousness, language, perception, learning and memory, and executive functioning have served an evolutionary purpose. Over time, *Homo sapiens*' ability to attend to, perceive, and determine a course of attention (i.e., executive functioning) has evolved from experiencing threatening predators to experiencing the nuances of complex work environments. In either scenario, both pertain to the vital

longevity and security of the organism (e.g., staying alive vs. staying employed). Emotions have provided *Homo sapiens* the qualitative product of cognitive functioning. For example, emotions may be functional, whereby information is processed and acted on for a specific utility (e.g., jealousy as a means to alter a threatening relationship), and emotions may be constructive, whereby information provides the organism cues to the survival-related nature of a situation. *Homo sapiens*' ability to learn and remember information transcends human evolution as a means to remember past experiences and adapt them to relevant situations for optimal survival and prosperity. Lastly, language has facilitated the *Homo sapiens*' ability to convey thoughts and ideas among his/her peers for optimal tribal or familial functioning.

Evolution of Cognitive Science

Cognitive science has much in common with psychology, especially its philosophical underpinnings attributed to Plato's *tripartite theory of the soul* where he considered one's "psyche/soul" the essence of a person and that a person's psyche is composed of *logos* (the mind), *thymos* (emotion), and *eros* (desire). Moreover, Plato's *Meno* posited that humans are born with innate knowledge and that learning is a process, whereby a person seeks to recollect that knowledge (i.e., anamnesis). French philosopher René Descartes supported Plato's theory of multiple souls; however, he further asserted that the mind and body were separate entities, whereby the mind is non-physical and is responsible for consciousness and awareness (i.e., substance dualism), eventually leading to the present-day "mind-body" debate.

In contrast to Plato and Descartes, British philosopher John Locke would assert in his *An Essay Concerning Human Understanding* that the mind is a "blank slate" at birth, without parameters for information processing, and that such parameters are later added to guide information processing based on one's unique sensory experiences throughout life. While rudimentary, Locke's theory supports present-day neurobiological

evidence that the brain is designed to process unique, sensory-related information as a result of cytoarchitectural differences within the brain. In 1819, physician T. I. M. Forster coined the term “phrenology,” referring to a pseudoscientific discipline based on Franz Joseph Gall’s accountings of brain functioning. Phrenology espoused that one’s intellectual or mental abilities were proportional to a given brain region and that each brain region created a unique shape within the cranium. Thus, one could infer a person’s relative mental strength or weakness based on the relative indentations within a person’s cranium.

As medicine and science observed the flaws within phrenology, notable pioneers such as Fechner, Weber, and Helmholtz laid the foundation of the field of “psychophysics” considering earlier philosopher’s accountings of mental activities. As such, German physician Wilhelm Wundt expanded the findings from Fechner, Weber, and Helmholtz and would become the “father of psychology,” creating the first laboratory of experimental psychology that examined aspects of brain-related functions such as perception and memory. Another notable discipline would contribute to the founding of cognitive science: behaviorism. Skinner’s radical behaviorism emphasized the necessity for strict observation of behaviors, since mental processes or introspection had no place in psychology. Skinner’s diligence and structuring of experiments laid the necessary groundwork from which cognitive science would later develop. Moreover, while behaviorism took root in the United States, Gestalt psychology and the concept of “schemas” emerged in part due to the contributions of Sir Frederic Bartlett (memory distortions), Jean Piaget (organized stable systems), Lev Vygotsky, and Alexander Luria (language and thought). The schema concept appealed in large part because it succinctly described how sensory-specific information is encoded, retained, and utilized in context-specific interactions, a concept that would later be expanded on by computational models and neural network theories.

The “cognitive revolution” was born in the 1950s as a means to distinguish itself from the

field of psychology. However, the actual term “cognitive science” was coined in 1973 by Christopher Longuet-Higgins in his “Lighthill report” (Longuet-Higgins 1973). Leading up to the revolution was the advent of cybernetics in the 1930s and 1940s, which described the organizing principles of the minds within humans, animals, and machines. The 1940s provided the *Theory of Computation* with the “Turing machine” being the most famous example of a basic computer (Turing 1937). Moreover, the advent of the modern digital computer, or “von Neumann architecture,” in 1945 formed the basis of theories associated with both human and machine-based operations; it was composed of a processing unit, a control unit, memory, external mass storage, and an input and output mechanism (Von Neumann 1993).

In the 1950s, the concept of “generative grammar” demonstrated that language is governed by a set of rules that generate combinations of words for specific functions. This concept laid the groundwork for computational models that espoused a “universal grammar” or syntax that allow both animals and machines to communicate both within and between each other. The 1970s and 1980s brought about the age of artificial intelligence (AI) with advancements in understanding how humans and machines communicate, problem solve, and make decisions. The 1980s and 1990s brought about the age of artificial neural network models, most notably James McClelland and David Rumelhart’s parallel distributed processing (PDP). The PDP approach asserted that information is encoded across multiple systems, where localized information is synthesized across multiple domains or systems and translated into a user-specific function or product (McClelland et al. 1986). At the same time, the field of neuroscience made significant contributions to cognitive science with the use of neuroimaging techniques with high spatial resolution, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). Both imaging techniques have allowed scientists to identify blood flow-related cerebral changes in the context of a specific task. Moreover, the use of electrophysiological techniques such as

electroencephalography (EEG) to measure event-related potentials (ERP) have allowed scientists to identify temporal-related changes in the brain while engaged in a specific task. In sum, neuroimaging and electrophysiological techniques continue to alter how we conceptualize the architecture and functions of the mind.

Encephalization and Cognitive Science

Encephalization refers to expected brain growth/size in relation to a mammal's body size and is measured by calculating the encephalization quotient (EQ) (Jerison and Barlow 1985; Kappelman 1996). Higher EQs are associated with greater brain volume and reliance on higher-order intelligence, whereas lower EQs are associated with lower brain volume and reliance on basic intelligence. *Homo sapiens'* brain reflects a much larger brain in contrast to its australopithecine predecessor, thus reflecting a higher EQ by comparison. With larger brain sizes, *Homo sapiens* possess greater cortical "real estate" and increased diversity in neuronal cytoarchitecture, allowing them to acquire high-order skills (Jerison and Barlow 1985). However, contemporary research emphasizes the analysis of specific brain regions to determine relative cognitive capacities (Barton and Harvey 2000; Shultz and Dunbar 2010).

From Hominid to Artificial Intelligence

Hominid is a phylogenetic term used to describe a tribe of primates, of which human beings are members. Hominid is also a term used to describe the relative adaptive changes that have occurred across species within the tribe as a result of changing ecological and selective conditions. *Homo sapiens'* brain has evolved with the advancement in technology, placing a greater demand on what would be required for optimal functioning in one's environment. Moreover, culture has greatly influenced how *Homo sapiens* behave, from influencing one's ability to communicate with others, making inferences of others'

intentions, and appraising situations (McBrearty and Brooks 2000). As a result, cerebral organization has adapted over time to accommodate changes in its architecture. Contemporary theories emphasize that architectural changes were a necessary evolution in *Homo sapiens* for efficient information processing abilities, which is best measured by one's *fluid* or *general intelligence* (*g* or *Gf*), a statistical outcome that describes one's "crystalized intelligence" in an effort to problem-solve (Cattell 1963).

One of the more prevailing theories in cognitive science emphasizes a *dynamical systems* approach in understanding how intelligent life functions. This approach asserts that a dynamical system is any system that evolves over time in a law-governed way; this includes human beings as well as machines (Thelen and Smith 1993). As *Homo sapiens* have evolved, our curiosity about what makes intelligent life "intelligent" has also evolved. The advent of AI has sought to uncover such mysteries by transposing neurobiological and philosophical accountings of cognitive functioning into a man-made system or machine. Moreover, cognitive scientists have evolved in their conceptualization of AI, viewing AI organization from the perspective of *agents of architecture* where information processing is determined by (1) a simple reflex, (2) a goal, or (3) learning to viewing it as a series of cognitive subsystems with domain-specific processes (i.e., modularity of mind; Fodor 1983; Russell and Norvig 2003, 2009).

Conclusion

The evolution of cognitive science is very much reflective of the zeitgeist. With the advent of neuroimaging in the 1950s, much of our understanding of the human brain has shifted or has been completely altered. Moreover, we know that culture and society have greatly impacted the cerebral architecture of *Homo sapiens'* brains; as such, our understanding of "cold" cognitions (i.e., information processing-based) and "hot" cognitions (i.e., emotional arousal-based) has altered our understanding of intelligence. Consequently, our

“evolution” on how we have conceptualized cognitive functioning and intelligence has also shaped how we harness such newfound information with its application to AI. Evolution is an ongoing process, and with it, so is our understanding of the human mind.

Cross-References

- ▶ *Australopithecus africanus*
- ▶ *Australopithecus garhi*
- ▶ *Australopithecus* Group
- ▶ Cognitive Ethology
- ▶ Cognitive Neuroscience
- ▶ Domain Specificity
- ▶ Evidence of Brain Modularity
- ▶ Evolution of Intelligence, The
- ▶ *Homo habilis*
- ▶ *Homo heidelbergensis*
- ▶ *Homo neanderthalensis*
- ▶ *Homo rudolfensis*
- ▶ Human Tool Making
- ▶ Linguistic Evolution
- ▶ Linguistics
- ▶ Modern Theories of Language
- ▶ Why Humans Are Unique

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Cognitive Specialization

- [Specialized Cognitive Skills](#)

Cognitive Universals

- [Psychic Unity](#)

Cohabitation

- [Two-Parent Families](#)

Coition

- [Penile-Vaginal Sex](#)

Coitus

- [Penile-Vaginal Sex](#)
- [Sexual Intercourse](#)

Coitus Interruptus

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Synonyms

[Onanism](#)

Definition

Mating interruption due to male’s copulatory organ withdrawal previous to a forthcoming ejaculation.

Introduction

Coitus interruptus is a widely diffused practice in humans and is considered the most ancient form of birth control method, being firstly described in the Genesis. Nowadays, there are different lines of thinking in whether considering onanism as a contraceptive method or not. The perception of its effectiveness seems to vary depending on the sociocultural context or the age of the practicans

(Sznitman et al. 2009; Gilliam and Hernandez 2007; Higgins et al. 2014), and a common agreement on its efficacy seems to lack also among academics. Some studies pointed out that conception may occur during copulation (i.e., mating) before ejaculation, due to the presence of sperm in the seminal fluid, or that onanism requires experience to be effectively practiced, meaning therefore that coitus interruptus does not represent a valuable and reliable contraceptive method (Doherty and Stuart 2011; Gilliam and Hernandez 2007; Lampiao 2014). By contrast, other studies proposed that onanism should instead be considered as an efficient method for birth control, since it remains one of the most widespread to prevent pregnancy (Lampiao 2014; Sznitman et al. 2009).

However, this last idea finds little support while the general tendency is to consider coitus interruptus as a poorly efficient practice, responsible for several cases of “side” pregnancies, reaching a peak of 27 % among women users within the first year of use (Doherty and Stuart 2011). Also, it is normally associated to scarce education environments, poverty, and lack of information or other contraceptives (Doherty and Stuart 2011; Sznitman et al. 2009).

Interestingly, onanism occurs in different forms also in other organisms than humans, meaning that this sexual behavior is not exclusively adopted by our species and that there might be room for a broader *evolutionary* consideration. This fact is remarkable as from a biological point of view, a trait displayed by a higher number of organisms allows a better understanding of the causes triggering it.

Onanism Types

Coitus interruptus does not occur only in humans. Even though onanism from an anthropocentric point of view is assumed to be a male voluntary act, if we abide by its definition we can ascertain its occurrence also among other species. For clarity, it is important to remark that *coitus interruptus* should not be confused with a generic *copulation interruption*, as it defines a different moment of

the sexual intercourse, namely instants before ejaculation. Indeed, while copulation interruptions are more likely to happen due to a variety of possible factors, as for instance predatory attacks, the greater majority of copulations in nature is meant to reproduce, resulting in a restricted number of species performing coitus interruptus.

We can distinguish between two different types of coitus interruptus, *voluntary* and *non-voluntary*. Voluntary onanism occurs when a male interrupts copulation on purpose or allows female to interrupt it before ejaculation and is diffused in humans and a few other primates, as for example, Sichuan snub-nosed monkeys (Li and Zhao 2007). In this monkeys males are polygynous (i.e., they mate with multiple females), and when copulation occurs the mating couple is often harassed by an extra-pair female. This fact induces males to leave the first female they are copulating with, to mount the heckler female to complete the sexual intercourse in more than 50 % of cases (Li and Zhao 2007). The heckler female harassment may consist in staring at the couple only, therefore male’s decision to stop mating with the first female before ejaculating is entirely voluntary, as there might be no physical contact between the couple and the heckler. In this study system, coitus interruptus is thus performed with the first female only, while sperm transfer occurs during copulation with the heckler female.

Nonvoluntary coitus interruptus is instead nondependent on male intentions. For instance, it has been reported for dogs, where it simply seems to happen accidentally: When a male is not successful in locking to mount a female, a so-called phantom lock may occur, consisting of the male remaining in the mating position and rhythmically releasing sperm, even if the female has moved away (Beach 1970). Another example involves meadow voles, but in this case sperm release outside female reproductive tract happens as a consequence of her decision not to be fertilized. Females during mating may run away just before male ejaculates, resulting in sperm wasting (delBarco-Trillo and Ferkin 2006).

Evolutionary Meaning of Onanism

Coitus interruptus is voluntarily performed in humans in order to avoid unintended pregnancies. This behavior is preferred in certain cases to other contraceptive methods, since the “dopaminergic reward” (i.e., the general feeling of pleasure and satisfaction related to the orgasm) is perceived to be higher and more gratifying (Gilliam and Hernandez 2007; Free and Alexander 1976). However, coitus interruptus functional usage may have deeper roots. If we analyze the meaning of coitus interruptus from a cost-benefits perspective, we can contextualize it more properly in a biological scenario. For example, in species providing broods parental care, it would be advantageous not to reproduce if resources are limited. This idea is reinforced by the fact that the only species adopting voluntary onanism also have strong parental care. Regarding humans, for example, from an ecological point of view what is considered as an opportune moment to have children in our society, namely having a good and safe working position and a stable relationship, could also be seen as a resource-predictable stable environment, in which the costs of reproduction (general metabolic effort, food supply, broods care, etc.) appear sustainable. If resources are limited instead, it might be advantageous to simply benefit from the “dopaminergic reward” for both sexes, avoiding conception. Benefits in improving social relationships and avoiding contrasts might also be involved. For instance, it has been shown in Tibetan macaques, another social primate, that nonreproductive matings improve couples synergy, increasing foraging together and proximity, and reduce conflicts among group members (Li et al. 2007). Voluntary onanism might also involve costs. If we think about human relationships, it is reasonable to assume that a greater majority of couples uses some forms of birth control practices, meaning that independently from the chosen method, the number of nonreproductive matings (meant to benefit from the “dopaminergic reward”) vastly overcomes the number of the reproductive ones. Since it has been shown in variety of species that there is a negative correlation between number of

matings (in term of ejaculations) and life expectancy, meaning that multiple copulations speed up the aging process, pregnancy-avoidance behaviors involving ejaculation, including coitus interruptus, might therefore be costly for males. From a female perspective, matings in general are associated to the risk of diseases and parasites transmission, thus if the number of matings increases due to the possibility to avoid the costs of pregnancy by using contraceptive methods, the risk of infections is also likely to be more severe.

While voluntary onanism is likely to involve both costs and benefits for the two sexes, if we consider nonvoluntary coitus interruptus under the same cost-benefits light we realize that for males it is likely to only involve costs. For instance, males might face sperm wasting, lost paternity opportunities, metabolic effort in sperm reproduction, and failure in mate acquisition. On the other hand, females might instead acquire benefits. In the case of meadow voles it has been proposed that the induced coitus interruptus may function as an honest signal for males quality, allowing them to assess whether they are mating with a good partner or not. Indeed, higher quality males should be able to monopolize females holding them to prevent escape attempts (delBarco-Trillo and Ferkin 2006), with the females receiving the benefit to conceive with a sure value male. By contrast, meadow voles males only seem to pay costs related to this female strategy, as they suffer for reduced number of ejaculations, meaning that males that experienced coitus interruptus might be more careful in mating due to previous negative events and/or that females discriminate these males (delBarco-Trillo and Ferkin 2006).

Anyhow, it is reasonable to suppose from an evolutionary point of view, that the sex promoting onanism occurrence is the one receiving general benefits from this behavior, favouring therefore selection for the trait.

Conclusion

At a first glance, coitus interruptus may only seem an “easy and quick” way to avoid unintended

pregnancies. A deeper consideration reveals that it is not only widespread in humans but is also present in other species. There are two different types of onanism, voluntary and nonvoluntary. Voluntary onanism is diffused in primates including humans and is meant to prevent conception with a particular partner or to obtain a “dopaminergic reward” avoiding the costs of pregnancy. Different pressures are instead acting on nonvoluntary coitus interruptus, ranging from conflict of interests between sexes to accidental events, and it occurs also in nonprimate mammals.

Independently from its real efficacy, coitus interruptus is perceived in humans as a valuable contraceptive method, remaining also nowadays one of the most used.

Cross-References

- ▶ [Decreased Reproductive Success](#)
- ▶ [Effect of Birth Control on Women's Preferences](#)
- ▶ [Male Prudence and Sperm Limits](#)
- ▶ [Paternal Care](#)

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Collaboration

- ▶ [Primate Cooperation](#)
- ▶ [Selection for Cooperative Relationships](#)

Collective Action

- ▶ [Non-human Leadership](#)

Collective Efficacy

- ▶ [Sociocultural Theories of Violence](#)

Collectives

- ▶ [Human Groups](#)

Collectivism

- ▶ [Culture of Honor](#)

Collusion

► Prisoner's Dilemma Outcomes

Colonization Effects

► Postcolonialism

Colony Size

► Group Size

Color Red

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Synonyms

Badge; Sexual signal; Social signal; Status symbol

Definition

Red coloration is a highly salient visual signal caused by the light reflective properties of blood oxygen saturation in exposed skin and enhanced carotenoid levels in skin coverings. May be sexually or socially selected trait associated with enhanced reproductive success and dominance across a range of animals, including insects, birds, and mammals including humans.

Introduction

To the human eye, red stands out. It grabs attention. It signals romance... danger... stop! We

“paint the town red” when we celebrate and “see red” when we are angry. It is used widely in advertising and the media to attract the public increase product sales. In the animal kingdom, red coloration is evident across invertebrate and vertebrate species and, as in humans, may signal either a mating opportunity or danger (Osorio and Vorobyev 2008). The biological relevance of the color red has driven the evolution of trichromatic color vision (ability to distinguish red from blues and greens) in the visual systems of most anthropoid primates; argument remains about the extent to which this was driven by the adaptive benefits of better detecting ripe fruit, leaves, or sociosexual signals (Changizi et al. 2006; Osorio and Vorobyev 2008).

What Causes Red Color?

Red color in species with exposed skin (such as anthropoid primates) is caused by blood oxygen saturation and carotenoid levels, both of which reflect underlying physiology and signal health status (Changizi et al. 2006). The former indicates cardiovascular fitness and short-term emotion states such as anger or embarrassment, while carotenoids, which are pigments obtained from plants in the diet, indicate nutritional status. The property of “redness” emerges from the interplay between the biological characteristics of both a signaler and a receiver. A “receiver” must possess receptors and a visual system sensitive to wavelengths at the red end of the spectrum in order to detect the red color for it to become a “signal” (Elliot et al. 2015).

Red as a Sexually Selected Signal

Sexual dimorphism in secondary sexual characteristics containing red reveals a role of red in sexual selection, as originally proposed by Darwin. The evolution of red as a secondary sexual characteristic can be explained by Fisherian runaway selection: for example, a positive feedback mechanism involving female preference for red in males would result in increase in male red traits

and female preference for red in subsequent generations (Elliot et al. 2015).

Empirical evidence for red as a sexually selected trait comes from its association with enhanced reproductive success across a range of species. In humans, for example, when asked to manipulate pictures of faces to enhance healthy appearance, both men and women increase the red component of male and female faces (Stephen et al. 2009); women are more likely to wear red clothes during their fertile phase (Eisenbruch et al. 2015) and are rated as more sexually desirable by men than when they are dressed in other colors (Elliot et al. 2015); female rhesus macaques, *Macaca mulatta*, with redder faces have higher reproductive output and receive more attention and affiliative behaviors from conspecifics than paler females (Dubuc et al. 2014); male rhesus macaques undergo reddening of facial and anogenital skin when receptive females are present, for which females show a visual preference, and which is associated with enhanced male reproductive success independent of dominance rank (Dubuc et al. 2014). A similar relationship is seen in Darwin's ape, the brightly colored Mandrill, *Mandrillus sphinx* (Setchell et al. 2008). Color expression in primates has been linked to androgen (e.g., testosterone) levels, which act as an immunosuppressant (Setchell et al. 2008). Red color may therefore provide a reliable indicator of male immune strength and physical condition (Dubuc et al. 2014).

Red as a Socially Selected Signal

Red color may also be a socially selected trait that is associated with aggression and dominance across a range of species (Osorio and Vorobyev 2008). Red clothing is associated with an increased probability of winning in competitive sports, and men wearing red are rated as more aggressive and dominant than are men dressed in other colors (Wiedemann et al. 2015); men with redder skin are perceived as more dominant than men with paler skin (Wiedemann et al. 2015),

probably because skin reddens with dominance-related emotions such as anger and pales with non-dominant emotions such as fear (Changizi et al. 2006). It is no coincidence that red is almost universally accepted as the color to signal danger across cultures (Elliot et al. 2015).

Red skin also provides a salient and reliable signal of dominance and competitive ability across primates. Anthropoid primates in which males fight for access to females, such as the Mandrill and rhesus macaques, undergo testosterone-regulated reddening of facial and anogenital skin when receptive females are present (Setchell et al. 2008; Waite et al. 2003) which provides an honest signal to other males of current androgen status, dominance status, competitive ability, and willingness to engage in fights (Dubuc et al. 2014; Setchell et al. 2008).

Red in Context

To understand fully the biological significance of red coloration, we need to place color within individual and situational context. Red color is not a singular trait, but rather a potentially variable attention-capturing cue that maximizes the probability of the "signaler" gaining a receiver. In competitive contexts, therefore, red is most often perceived as a signal of aggression and dominance, signaling danger, and triggering avoidance behaviors in the receiver (Wiedemann et al. 2015). In affiliative contexts, red is associated with romance and attractiveness, signaling reward, and triggering approach behaviors in the receiver (Buechner et al. 2014; Waite et al. 2003). In laboratory computer tasks, a red distractor on the screen impairs performance on an ongoing task, and this effect is strongest for men, possibly due to the stronger sensitivity to dominance and avoidance signals in men (Elliot et al. 2015). An apparently evolutionarily old attention bias for red therefore draws attention toward red cues in the environment, enhancing the motivational message of the cue (threat or reward) and directing subsequent approach-avoidance response (Buechner et al. 2014).

Conclusion

From santa to satan, lipstick to warning signs, the color red is of great biological and cultural significance to humans. The evolutionary basis for our attention bias for the color red lies deep in our primate past. Pre-existing biases for detecting red afforded by the evolution of trichromacy in anthropoid primates, together with the reliable signal value of red for reproductive status, dominance, and aggression, would have afforded a fitness advantage to individuals able to better detect fertile mates and respond quickly to avoid aggressive individuals in the ancestral social environment. The saliency of the color red to the human visual system is further supported by its widespread use in coloration of artifacts across human cultures and symbolism for heightened emotional contexts ranging from danger to romance.

Cross-References

- Adaptations: Product of Evolution
- Advertisements
- Aggression
- Aggression for Sexual Access
- Attention and Perception
- Charles Darwin: Theory of Sexual Selection
- Dominance and Testosterone
- Evolution of Fighting Assessment Abilities
- Female Choice
- Female Mate Choice
- Fisherian Runaway Selection
- Male Mate Choice
- Nonhuman Primates
- Sexual Dimorphism
- Sexual Signaling During Ovulation

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Coma dépasse

- Medical Definitions of Death

Combat

- Anatomical Adaptations for Fighting
- Defending Against Attack
- Information About Likely Combat Success
- War

Combat Sport

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Synonyms

Combative sport; Contact sport; Fighting sport

Definition

A combat sport is a competitive activity engaged in by two individuals or teams that models actual combat wherein winning or losing is defined by agreed-upon rules and is substantially determined by physical contact and/or the use of real or simulated weapons by opponents.

Introduction

Play fighting is common among mammals, many birds, and members of some other taxa. It involves not only competition but also cooperation in that fighting is simulated but does not include injurious bites or blows or lethal bites as occurred in conspecific aggression or predation. Play fighting also involves play signaling and self-handicapping in one form or another. Among human children, play fighting is often referred to as “rough-and-tumble play” (RTP) which, when not suppressed by adults, involves approximately 10% of free play, particularly among males. RTP influences brain growth in rats, specifically in the number and complexity of cells in the prefrontal cortex, and animals deprived of play suffer from deficits in emotional regulation and social competence. Evidence from monkeys and apes is consistent with that from rats with the addendum that mother-child play is also critical. Among human children, positive play experiences with parents appear to enhance later peer-peer interactions. Children’s

RTP also seems to enhance social skills (Pellis and Pellis 2017).

Combat Sports in History

Wrestling is, in one form or another, the most widespread sport in human societies and probably a cultural universal. A wall painting at the Beni Hasan Tomb of the Egyptian official Baqet III (c. 2,000 BCE), for example, depicts wrestlers in a variety of positions, while *The Epic of Gilgamesh* (c. 2,100 BCE) describes a wrestling match between King Gilgamesh and Enkidu, a wild man created by the gods to challenge Gilgamesh because of his arrogance. The original Olympic Games lacked combat sports but added wrestling at the 18th Olympiad (708 BCE), boxing at the 23rd (688 BCE), and *pankration*, a sport somewhat similar to modern mixed martial arts, at the 33rd (648 BCE). In China, *jiao di* (“horn butting”) was a martial art dating to the third millennium BCE wherein contestants wore headgear adorned with horns and attempted to butt or throw opponents off raised platforms. It may have evolved into wrestling and other martial arts in China. Forms of grappling and wrestling were popular in Medieval Europe in addition to team activities known as “mob football” or “Shrovetide football” (Poliakoff 1995). Mob football is probably an ancestor of later forms of football but involved few rules and considerable violence.

Cross-Cultural Correlates of Combat Sport

In a 1973 publication, anthropologist Richard Sipes examined the absence/presence of what he termed “combative sports” among 10 extremely warlike and 10 largely peaceful societies in the anthropological record. For Sipes, combative sports are played by two opponents, either individuals or teams, and involve actual or potential body contact; may involve gaining playing field territory from the opponent, including the placing of a disputed object (often a ball) in a guarded location; or involve patently warlike activity. He

hypothesized that combative sports could either discharge innate aggressive urges among society members, rendering warfare less likely, or could be part of a culture pattern of aggressive behavior with warfare, therefore more common. Sipes found that warlike behavior and combative sports typically co-occur and that war tends to be rare where combative sports are absent. Chick et al. (1997) replicated Sipes' study with a larger sample ($n = 110$) and found modest for the culture pattern model. However, they uncovered much stronger support for the copresence of warfare and what they termed "sham combats," activities that are combative in that they may involve physical contact and, frequently, the use of real or simulated weapons. Unlike the usual case in sports, they typically lack winners and losers and rules for determining them. An unpublished replication using a 130-society sample with a multiple regression-based statistical method that accounts for missing data and Galton's problem, the possibility that two or more societies may have similar cultural traits due to a common history, diffusion, or both, does not support a relationship between the frequency of warfare societies and the presence of individual combative sports. The level of social and technological complexity of societies, but not the frequency of warfare, predicts the presence of team combat sports. The presence of sham combats, however, is strongly influenced by the frequency of warfare. These results do not support Sipes' (1973) claim that combative sports co-occur with frequent warfare, possibly because of the bivariate nature of his analysis, because of his inclusion of sham combats as combat sports, and because his data were composed of outliers.

Combat Sports and Gender

The appearance of female gladiators coincided with the rise in the popularity of the games during the late Republican era and reign of the first Roman Emperor, Augustus (i.e., 147 BCE – 14 AD) (Poliakoff 1995). However, participation in combat sports by females appears to have been rare, at least until recent years. In a cross-cultural sample of 50 societies, Deaner and Smith (2012)

found that 37 had combat sports. Males were the exclusive participants in 55 different combat sports, while none were exclusive to females. Both males and females participated in 2.

Female participation in modern combat sports, including wrestling, boxing, and martial arts, as well as team sports, including rugby and American football, has had periods of popularity. Competitive female boxing was first sanctioned at the Olympic Games in 2012, and the World Boxing Association created a unified women's boxing title in 2015. In recent years, however, professional women's boxing has been largely displaced by women's mixed martial arts. Several amateur women's American football leagues exist in the United States and elsewhere, but they have struggled to attract fans.

Combat Sport and Mate Choice

De Block and Dewitte (2009) viewed sports, at least in part, as culturally evolved signaling systems that function similar to courtship rituals in nonhuman animals. Thus, sports evolved, to some extent, via sexual selection. For De Block and Dewitte (2009), in order for sports to indicate fitness, they must, first, be informative with respect to qualities that are evolutionarily relevant. Second, they must be accurate in providing that information. That is, rules should ensure the highest positive correlation between a competitor's fitness and the likelihood that he or she will win. Third, the signal provided by winning should be transparent to possible recipients. As success in sport, especially combat sport, exhibits qualities, such as dominance and fighting prowess, which should be of interest to females, it should be important for males to demonstrate these abilities. Because it is rule-bound and standardized, sport offers a context that minimizes cheating as it is informative, accurate, and transparent.

Graves (2010) found that the average age of men who achieved championship status in international boxing, based on data from the World Boxing Association, was 26.44 years, while the mean age at which titles were lost was 28.35, suggesting that males reach their peak ability in this form of combat sport in their mid- to late

twenties and that this peak period lasts for just under 2 years. Graves (2010) noted that this is approximately the age where males have the highest reproductive success. Brewer and Howarth (2012) found that a sample of heterosexual women, aged 19–39, rated males depicted in photographs and described as “playing competitive sport aggressively” as more attractive and desirable for a date, relationship, marriage, and parenthood than when described as “playing sport on a casual basis.” The men were judged least attractive when described as “not playing sport.” Similarly, Lombardo (2012) hypothesized that sport originated as a context for men to develop skills needed in hunting and warfare and then display them to possible allies and rivals. In turn, champion athletes, particularly in combat sports, are accorded fame, status, wealth, and power, qualities that are attractive to women. Several empirical studies report that women are attracted to athletes, particularly those who play team sports, and that athletes have more sexual partners as well as greater reproductive success than nonathletes.

Deaner and Smith (2012) disputed the claim that sports serve as culturally invented courtship rituals, however, pointing out that females primarily advertise physical attractiveness and personal integrity when seeking mates, neither of which are particularly emphasized in sport. Moreover, to the extent that physical attractiveness, high status, and dominance are associated with sports participation, they accrue to males but not females (Brewer and Howarth 2012). Sports that involved judged display (e.g., gymnastics, figure skating) emphasize physical attractiveness but do not involve direct competition, let alone a combative component. Deaner and Smith (2012) attributed greater sports participation in males to several factors, including socialization, but also greater exposure to androgens prior to birth. The latter, if confirmed, would support evolutionary models that emphasize male-male competition in sport, including combat sport.

Modern Combat Sports

While many combat sports, such as wrestling, boxing, and other individual martial arts, are

ancient in origin, both individual and team events, such as jousting and the melee, were popular components of Medieval tournaments. Individual combat sports in the modern Olympics include boxing, judo, taekwondo, Greco-Roman and free-style wrestling, and fencing. Modern mixed martial arts (MMA), a combination of Brazilian jiu-jitsu and shoot wrestling, was introduced in the United States in 1993 and has developed into several subvarieties, the best known of which is the Ultimate Fighting Championship. Modern technology has resulted in new forms of combat sport, such as paintball and laser tag, both of which can be played either outdoors or indoors and by individuals or teams according to a variety of rules specified prior to commencing the activity. American football and rugby, two team combat sports with the former descended, to some extent, from the latter, are played widely and at both amateur and professional levels.

Conclusion

Sport likely evolved from juvenile mammalian play, including that of human children, as it incorporates behaviors, such as capturing, escaping, and fighting, that mimic adult survival skills (Lombardo 2012). Combat sports appear to be institutionalized and rule-governed descendants of play fighting among animals as well as human children's RTP. Most model some form of actual combat. Although combat sports are not exclusive to males, men watch and participate in them in much greater numbers and frequency than women. This suggests that combat sports may, to some extent, signal information to females regarding the fitness of participants while, among males, serve as competitions for status and reliably communicate qualities, such as strength and bravery, that characterize effective hunters and warriors (Apostolou and Athanasiou 2016).

Cross-References

- ▶ Boys' Rough-and-Tumble Play
- ▶ Contexts for Men's Aggression Against Men
- ▶ Female Choice and Sexual Conflict Theory

- ▶ [Male-Male Competition](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Sexual Selection via Direct Male-Male Interactions](#)

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Combative Sport

- ▶ [Combat Sport](#)

Combined Oral Contraceptives

- ▶ [Birth Control](#)

Comedy

- ▶ [Humor Production](#)

Comical

- ▶ [Humor Production](#)

Comicality

- ▶ [Neurology of Humor](#)

Commitment

- ▶ [Enlarge Shadow of Future](#)

Commitment Skepticism

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Commitment skepticism refers to a person's apprehension about their current or potential mate's commitment to the relationship, specifically regarding parental investment (Pillsworth and Haselton 2006). It is possible that commitment skepticism is an adaptation because it evolved as a way to screen for a reliable, long-term partner. *Error Management Theory* (Haselton and Buss 2000) (see entry), a middle-level evolutionary theory, has been used to explain commitment skepticism.

Generally, *Error Management Theory* explains why, in circumstances where a decision or judgment has an unknown outcome, people are more prone to making a *false positive* error in judgment (believe X is true when X is not true, also known as a *Type I Error*) or making a *false negative* error (believe X is not true when X is true, also known as a *Type II Error*). This theoretical model suggests that a tendency to make false positives or false negatives may have evolved if one error increased fitness benefits or minimized fitness costs. As an example, when detecting snakes, people are more prone to mistaking sticks as snakes (false positive) than mistaking snakes as

sticks (false negative) because the false negative would have been quite costly whereas the false positive would not. Applying this theoretical model to judging the intentions of a potential long-term mating partner, people can be wrong in one of two ways: believe the person will commit to the relationship when the person would not (i.e., false positive) or believe the person will not commit when the person would (i.e., false negative). In order to predict which type of error people are more or less prone to making, we need to consider both the net costs and benefits of either decision.

Choosing a mating partner is a rather important decision because it impacts the amount and quality of resources one gets for their offspring, so there may be particular costs to making the wrong decision about a potential mating partner. Because men and women differ on the costs and benefits of false positives and false negatives when predicting a potential partner's commitment, we also expect men and women to differ on the degree to which they show commitment skepticism.

Since women's reproductive success is strongly impacted by the quality and amount of parental investment from one's mate, the costs of choosing a partner who does not invest in offspring is much greater than the cost of losing a potential partner who would have invested. Since men's reproductive success is strongly impacted by mate number, the costs of selecting a partner who does not invest are not as steep if he continues to pursue additional short-term mateships. Under these circumstances, we would expect women to show a stronger tendency toward commitment skepticism (see *Sex Differences in Commitment Skepticism Bias* entry). Indeed, available data has shown that women are more prone to commitment skepticism than are men (e.g., Brown and Olkhov 2015; Haselton and Buss 2000), which is also consistent with theory and research that indicate women are "choosier" than men when selecting a mate.

Much more empirical and theoretical work is needed to fully understand the psychology of commitment skepticism. Some, for example, have challenged the pervasiveness of sex

differences in commitment skepticism and proposed alternative ways to consider the circumstances under which men and women show commitment skepticism (Al-Shawaf 2016; Brown and Olkhov 2015).

Cross-References

► [Sex Differences in Commitment Skepticism](#)

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Committal Practices

► [Burials](#)

Committed Relationship

► [Sex Ratio and Men's Long-Term Mating](#)

Common Knowledge

► [Norms](#)

Commonsense Psychology

► [Theory of Mind and Evidence of Brain Modularity](#)

Communal Breeding

► [Alloparenting](#)

Communication and Developmental Milestones

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Synonyms

[Gesture](#); [Language](#); [Pointing](#)

Definition

Watershed skills that human children develop early in life.

Introduction

Even before birth, children are making sense of the sounds they hear. The human ear is functional in the final trimester, and fetuses respond to a range of auditory stimuli from outside the womb. Evidence suggests that infants are in fact highly sensitive to the sounds they hear from within the womb and newborns can identify sounds from the language to which they have already been exposed while in the womb (May et al. 2011). De Casper and Spence (1986) asked pregnant women to read a short passage of text

aloud daily for the last 6 weeks of their pregnancy. At just a few days old, the newborn infants actively sought to hear the speech passage they had heard prenatally, rather than a novel passage. A control group of infants who had not been regularly read to during pregnancy showed no preference for either passage. Taken together, these findings suggest that language learning begins very early in human development.

Postnatally, infants continue processing the sights and sounds they encounter, showing a keen interest in faces and voices, as part of the social development which underpins later language learning. Infants only a few days old show a preference for looking at faces over other objects, and even newborns will orient toward the sound of a voice (Brazelton 1978), thereby providing the sensory information required to build the communication skills we see later in life. Although some researchers have dismissed early infant smiles as purely reflexive behaviours, there is evidence that, although rarer, smiles from newborns and very young infants do reflect early social engagement with caregivers (e.g., Oster 2005). Ultimately, the acquisition of typical communication skills requires the ability to both understand and produce both language and gesture. Here we consider the development of language comprehension, language production, and gesture and outline some key developmental milestones.

Language Comprehension

Every word starts out as a new word, so infants face enormous challenges in order to start decoding their own language (or languages). One of the first challenges for infants is to identify words from a stream of speech. Written language helps readers identify individual words by providing space between words, but this rarely happens in speech. In speech, words run into each other, and speakers often change the sounds of beginnings and ends of words to blend them with others (Ladefoged 2006). This makes identifying individual words particularly challenging.

Fortunately, infants can use a number of strategies to help them segment words from the speech stream. Cues such as prosody (e.g., the use of stress or rhythm in speech), intonation (e.g., changes in pitch), and even facial expressions (e.g., Mitchel and Weiss 2013) can support successful speech segmentation, suggesting that infants benefit from language exposure very early in development. Saffran et al. (1996) demonstrated that 8-month-old children could learn the statistical regularities of a nonsense language from as little as 2 min of exposure, even without any additional prosodic cues. This suggests infants can successfully integrate a range of cues, detecting those sounds which commonly occur together, and those which do not, to make judgments about where words begin and end, thus segmenting words from a stream of continuous speech.

Once a child has successfully identified a word, they need to attach some meaning to it. When hearing a word for the first time, children face the challenge of identifying its referent. A new word may have endless potential meanings; it may refer to an object, or any property of that object, a feeling, a time, or an action (Quine 1960). This *referential ambiguity* poses a challenge for the child, which they appear to solve rather effectively using a number of strategies.

The relative speed with which children appear to process the information required to map a new word to its meaning led to the coining of the term fast mapping (Carey and Bartlett 1978). Subsequent research, however, found this initial mapping to be rather fragile and suggests robust word learning takes place over time (Horst and Samuelson 2008). Markman (1990) suggested certain constraints guide young children through the mapping process. The *whole-object assumption* suggests that children interpret new words as labels for whole objects, rather than parts or other properties of objects. The *taxonomic assumption* suggests children extend words to taxonomically related objects rather than perceptually similar or thematically similar objects. Finally, *mutual exclusivity* refers to the way in which children map a novel word to a novel object, rather than an object for which they already know a label

(although children learning more than one language behave differently).

During early childhood in particular, caregivers typically support children's language development by adopting certain helpful styles of interaction. For example, adults typically speak to infants and young children using shorter sentences, repetition, slower speech, higher pitch, and hyperarticulation. This is referred to as infant- or child-directed speech, or motherese. Although cross-cultural research has found evidence of some cultural variation in infant-directed speech, the use of such supported speech toward infants appears widespread (for a review, see Saint-Georges et al. 2013). In addition to supporting children's language acquisition by adopting helpful speech styles, caregivers and other adults also use other means. Simple techniques such as use of ostensive naming can be helpful for word learning, but more simply, if caregivers wish to support language acquisition, they should provide the richest possible linguistic environment for their children. Children who are exposed to the widest range and volume of vocabulary are those who start school with the largest vocabularies. This means speaking directly to children or even exposing children indirectly to speech and reading to children are important activities. Infant-directed speech and storybook reading and talking to children all support emotional, social, and cognitive development, in particular, that of language comprehension and production.

Language Production

Language comprehension involves children processing what they see and hear and beginning to integrate this into their understanding of human behavior and communication. Children's language production typically lags behind their language comprehension. For example, children understand their first word long before they can produce their first word. Although language comprehension precedes production, infants begin to vocalize very early in life. Such vocal communication is shaped over infancy and childhood by many factors, not least those of experience,

motivation, and the development of the human child’s vocal anatomy.

The infant vocal tract is, of course, smaller than that of an adult but also proportionally shorter, due to higher placement of the larynx. A shorter pharyngeal cavity also leaves less room for tongue movement, and a lack of muscle control limits complex tongue movement. Anatomical differences between adult and infant vocal apparatus mean that certain sounds, for example, adult vowel sounds, rely on physical developments to take place before they can be performed (for a summary, see Vihman 1996).

Researchers have mapped children’s pre-linguistic sounds over development to provide a clear picture of children’s vocal development (e.g., Nathani et al. 2006; Oller 1980; see Table 1). Early production comprises reflexive or

involuntary sounds, such as crying, grunting, or fussing in a stage called phonation. Caregivers reward infants’ early cries with nutrition and comfort, and in the months that follow, despite a lack of vocal control, infants respond to adult vocalizations with vocal outbursts. In the months that follow, infants begin to have increasing motor control, enabling them to begin to experiment with the sounds they can produce. Infants produce cooing sounds and their first laughter at around 2–4 months of age. This is followed by vocal play or expansion, such as changes in pitch and volume, including long vowel sounds, until at around 6 or 7 months, infants begin to produce babbling sounds. Early babbling sounds include combinations of repeated consonant-vowel sounds (e.g., CV; \ma\ma\ or \ba\ba\) in what is termed canonical babbling. This is followed by variegated

Communication and Developmental Milestones, Table 1 Approximate ages at onset of communication

Age (mos.)	Vocalizations	Smiling	Gesture
1	Phonation ^a	Social ^c	
2	Cooing/gooing ^a		
3			
4	Exploration		
5	Expansion ^a		
6	Understand first words ^b		
7	Canonical		
8	Babbling ^a	Anticipatory ^f	
9			Understand pointing (near) ^g
10	Variegated		Showing off/produce pointing ^h
11	Babbling ^a		
12	Produce first words ^c		
13			Symbolic gestures ⁱ
14			Pointing with gaze alternation ^h
15			Understand pointing (far) ^h
16			
17			
18	Vocabulary explosion ^c		
19			
20			
21			
22	Two-word utterances ^d		
23			
24			

Notes. Representative studies: ^aOller (1980), ^bBergelson and Swingley (2012), ^cGanger and Brent (2004), ^dNelson (1973), ^eOster (2005), ^fJones and Hong (2001), ^gButterworth and Grover (1988), ^hDesrochers et al. (1995), ⁱAcredolo and Goodwin (1988)

babbling which includes a variety of consonant and vowel combinations (e.g., CV, VC, VCV; \ga \, \um\, \aba\), and at this stage infants vocal production begins to sound much more like adult language. Although there can be a great deal of variation in these linguistic milestones, children typically produce their first word at or around their first birthday.

Having mastered their first word, other single words follow. These first few words are likely to include words for family members, food, body parts, and other familiar objects or descriptive words such as “gone” or “dirty” as well as onomatopoeic words such as “woof” or “moo.” Early word acquisitions are likely to be single syllable and formed of simpler to produce sounds that do not require multiple consonant sound combinations, or more challenging pronunciations may result in some simplification (e.g., spaghetti might become a-ghetti). The pace of new word acquisition accelerates quickly during a child’s 2nd year, often termed the “vocabulary explosion,” even though most experts now agree this is a smoother and more gradual transition than the stage-like process described previously (Ganger and Brent 2004). Early accounts suggested children learn as many as ten new words per day (Bloom and Markson 1998) and marked a particular stage in development. More recent evidence points to more moderate gains of no more than two words per day for the 2nd year of life (e.g., Anglin 1993) and suggests more cumulative and generalized mechanisms may explain the exponential vocabulary acquisition (McMurray 2007) in the 2nd year of life.

Toward their second birthday, children have enough words in their vocabulary to combine two words, often a noun and a verb, enabling much richer communication. Then, shortly after, children begin to combine three or more words to produce telegraphic sentences. Telegraphic speech usually includes nouns, verbs, and adjectives but typically lacks articles, such as “the” or “a,” or prepositions such as “in” or “on.” At this point, children begin to demonstrate their knowledge of syntax (sentence structure) in the language they produce.

Competent language use requires more than just knowing words. Grammar plays an important structural role in language by providing a set of rules, which help impart meaning. Such structure can include syntax and morphology. Syntax describes change at the level of the sentence, so can be described as the order in which words are organized in a sentence. In English, for example, in a sentence such as “Ben pushed Jane,” the word order implies who carries out the action and who is the subject of the action. If the word order changes to “Jane pushed Ben,” this changes the meaning. Morphology describes changes at the level of the word. This includes, for example, changes to a noun to denote a plural by adding “s” or “es” or the addition of small units of meaning such as suffixes or prefixes to add meaning as in the case of adding “re” at the beginning of a word to mean “to do again.”

The most influential theoretical account for the origin of human language claimed that children have an innate, specialized ability to learn language. Chomsky (e.g., 1965) argued that children are born with a universal grammar, which sets out the possible “rules” for any language, and relied on language specific human evolutionary adaptations. Research examining many languages failed to find the consistency across languages needed to support Chomsky’s original claims. This led to subsequent modifications of the theory. A more recent alternative theoretical account is that of usage-based linguistics (for a review, see Ibbotson and Tomasello 2016). Usage-based theory suggests that language learning recruits more generalized brain systems and builds up knowledge of language from repeated exposure to it. This contemporary theory for language acquisition appears to better allow for the huge cultural variation in language and language development.

Gesture

Over the course of the 1st year of life, children begin to use gestures toward particular ends. Most readers will be familiar with the “reach up” gesture, in which babies raise both arms in apparent

requests to be picked up. Children adopt numerous culture-specific gestures that have conventional meanings within their cultures, but are not universal in meaning across cultures. Examples include waving bye-bye, sticking out one's tongue (a pejorative in some cultures, but a greeting in others), and various manners of pointing (Kirch 1979).

By the end of the 1st year of life, in Western cultures, babies can follow others' pointing gestures to close-by objects and, as they enter their 2nd year, to increasingly more distant entities (Adamson and MacArthur 1995). Usually within a few weeks of producing their first words, babies also start pointing, themselves. By the early part of their 2nd years, babies start to point to entities while simultaneously looking toward their social partners, thus displaying a parallel gestural/attentional deployment tactic that is often termed, "nonverbal reference" (e.g., Bates et al. 1975; Pechmann and Deutsch 1982). The developmental onset of pointing comprehension and production is the focus of considerable theoretical debate about the relationship between pointing and other nonverbal referential behaviors and the evolution of language. For many theorists, pointing permits states of psychological engagement unparalleled in the animal kingdom (e.g., Carpenter and Call 2013; Tomasello et al. 2007). According to this theoretical perspective, pointing signifies a human unique quality of psychological understanding between two people – (a) an appreciation that another has an independent visual perspective on the world that can be manipulated with pointing gestures, (b) that this visual perspective informs their understanding of the world, and (c) that this joint attention to some distal entity constitutes a shared psychological state of knowing together (e.g., Carpenter and Call 2013). As such, this capability for joint attention heralds a nonverbal mechanism for reference that is said to form a psychological foundation for the kinds of shared understandings of words (or symbolic reference) that occur with speech. One line of evidence for a supportive role of gesture in speech development is the finding by Goldin-Meadow and Butcher (2003) of increasing integration of gestures with speech over the 2nd and 3rd years of life: children

begin conveying different information in gesture and in speech, but eventually learn to convey two distinct topics in speech alone, and this is consistent with observations that children become less reliant on gestures as their speech skills improve throughout childhood (Pechmann and Deutsch 1982). For these and other reasons, some theorists have suggested that these gesture-initiated states of joint attention represent a biological adaptation that fosters language development uniquely in our own species. Consistent with this view, until fairly recently, it was widely believed that pointing with the index finger was both universal among humans and unique to humans among primates (e.g., Butterworth 2003; Povinelli et al. 2003).

However, now it is well-known that (a) pointing varies in its posture across cultures (Wilkins 2003) and (b) great apes (chimpanzees, bonobos, gorillas, and orangutans) readily adopt pointing gestures when they are raised in captivity (Leavens and Racine 2009). Rather than signaling uniquely human evolutionary cognitive adaptations, it may well be that pointing is a developmental response to linguistic communication environments in which much of social engagement is object-centered – about things – and that pointing reflects cognitive adaptations that are common to humans and their nearest living relatives, the great apes, when exposed to reference-rich environments. Evidence in support of this view is the observation that of the apes that have been raised like human children, in peoples' homes or as part of language-training projects, 100% of them display pointing, despite its extreme rarity among wild apes (Hobaiter et al. 2014; Leavens and Bard 2011). This evidence has supported the view of pointing gestures as a generalized hominoid (apes plus humans) response to the ecological effects of being raised in language- and artifact-dense environments. (A unique and subtle theoretical perspective on pointing has been developed by Juan-Carlos Gómez 2009: he argues that nonverbal reference and joint attention in humans rely initially on the same sorts of primitive cognitive mechanisms for understanding visual attention that we share with great apes but that a higher, representational capacity is eventually attained by humans, later in development.)

It seems likely that the ability to follow another's signals to focus on an object or location and the converse ability to direct another's attention (the two skills together are known as *joint attention*) assist babies in linking verbal labels with the objects of joint regard (Butterworth 2003). Many studies find that, for example, age at onset of pointing predicts later vocabulary size, as children develop (Colonnesi et al. 2010). From the standpoint of infants directing attention, they can elicit verbal labels for the entities that capture their interest. Conversely, from the standpoint of following directional cues, babies can use these cues to relate a visual object or activity to a verbal label.

Usually sometime after their first words, infants begin to adopt rich repertoires of conventional or symbolic gestures, such as waving “bye-bye” in some cultures (Acredolo and Goodwin 1988). During the 2nd year, children expand their expressive capacities by simultaneously using gestures with single-word utterances – this allows children to express more complex ideas than can be expressed in one word (Goldin-Meadow and Butcher 2003). As children's vocabularies begin to rapidly increase, usually near the end of the 1st year, and with their abilities to string successive words together, gestures tend to reduce in frequency with speaking, although of course we continue to gesture throughout our lives.

Conclusion

The developmental trajectories of language and gesture have been discussed separately here, but research suggests gesture and language are interdependent and jointly form human communicative interactions (e.g., McNeill 2003). This is the case both during the communicative interaction (e.g., gesture and speech are shaped by what we know about the communication partner) and over the course of development (e.g., early gestural use predicts subsequent language development). Traditional accounts of the development of communication in humans described such development as occurring in discrete stages, but more recent research

suggests children's acquisition of communication skills is much more fluid and features overlaps between the various milestones. It is therefore important to consider the inevitable individual variability that exists for each of the key milestones summarized in Table 1 during typical development.

Although we can now be relatively confident about the key milestones, which constitute early communication development, there remain many important unanswered questions. Understanding how humans acquire their distinctive communication skills, how and why these have evolved, and to what degree these reflect human unique skills are all issues that continue to prompt intense debate. Such questions make the topic of human communication development one of enormous importance when considering the place of humans in evolutionary history.

Cross-References

- Developmental Milestones
- Gestural Theory
- Language Acquisition
- Language Development
- Primate Gesture

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Communication and Social Cognition

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Synonyms

Nonverbal; Social thinking; Verbal

Definitions

Communication	the act of a message being sent by a communicator to a recipient; usually refers to aspects of spoken and nonverbal (e.g., facial expressions, gestures) language that enable message delivery and reception but may also refer to written language
Social cognition	mental processes that enable thinking about the self and others; key in navigating social situations and expectations

Introduction

Humans have evolved to communicate with one another through necessity and desire. After all, humans are social beings. In order to be successful group members, early humans communicated with one another within their social groups to coordinate efforts that promoted survival, such as hunting, gathering, and protection strategies. Communication was also used in early humans to warn of the approach of threats, such as predators. Later, written language developed throughout the world as a way to record historical events, important societal information, stories, and religious material.

Social cognitive skills such as perspective taking (i.e., theory of mind), empathy, pattern detection and recognition, interpretation of nonverbal and paralinguistic (e.g., tone of voice) signals, and others enable communication among individuals. One must be able to infer the intention of communication from others while also tracking in real time both the verbal and nonverbal signals being produced by the individual(s). Trust or mistrust for individuals may be garnered through communication. Indeed, such skills enable safe interaction among individuals, thus promoting survival. This, in addition to survival promoted within groups through shared language use, emphasizes the importance of the interconnectedness of communication and social cognition.

Aspects of Communication

Communication occurs when a message is conveyed through verbal, nonverbal, or other means from a message sender to a message recipient (Berlo 1960). Individuals communicating successfully with one another share a common ground regarding the topics of conversation, such that they are both relatively familiar with what is being discussed and are using a language or mix of languages that allow comprehension of information being exchanged (Clark 1996). Verbal communication contains linguistic and paralinguistic aspects, such as word choice and tone of voice, respectively (Prutting and Kirchner

1987). Another aspect of verbal communication is speech sound delivery. An additional paralinguistic characteristic may be an individual's typical volume of voice. Nonverbal aspects are the other major contributors to communication. These include gestures, facial expression, posture, and other body language. Indeed, some communication is carried out by solely using nonverbal signals (e.g., sign languages).

Verbal and nonverbal communication may be congruent or incongruent; that is, what a message sender is saying verbally may or may not match what their body language is portraying. For example, someone delivering a verbal apology may also wring their hands or show open hands or other common bodily signs of being regretful or sorry. The message recipient may perceive the message sender as genuinely apologetic, since these are nonverbal signals that one typically expresses when they are apologizing and asking for forgiveness. Conversely, the verbal apology may be paired with crossed arms and little eye contact, or even with aggressive body language, which would be incongruent with the expected sincerity of an apology. The results of incongruent verbal and nonverbal signals can vary (Morioka et al. 2016); the recipient may interpret the incongruence as insincerity (even if the verbal apology is present) due to the mismatch in what the person is saying and what their body language is portraying. Conversely, they may be put on alert as a result of the aggressive body language or gestures (effectively delivering the opposite of an intended apology).

Varying estimates have been postulated regarding how much information about a message is gleaned through verbal aspects compared to nonverbal and paralinguistic aspects. For example, Mehrabian and associates' (1967) historically well-cited work reflects a 55%/38%/7% breakdown of nonverbal, paralinguistic, and verbal aspects' contributions to communication, respectively. However, more recent research emphasizes various situational demands that may influence how a message is perceived (although nonverbal communication still tends to stick out as the major contributor). Thus, the manner in which a message is delivered is as important as the

message itself if one wishes to communicate effectively.

The way humans communicate and receive messages can signal prosocial or antisocial intentions to other individuals (Marzi et al. 2014). Consequently, communication can be viewed as a language-based way to test the safety or threat level of a person. An obvious example of a threat would entail an individual shouting and gesturing aggressively toward another person, which could engage the fight-or-flight response of the message recipient even if the verbal message was non-threatening. In fact, individuals identify "suspicious" nonverbal signals from others relatively quickly and easily, such as shifty eyes or nervous hand gestures. Research from the deception literature has demonstrated reliable effects of certain eye movements and microexpressions as signs of lying and deception (Matsumoto and Hwang 2018). Humans are able to quickly detect and process these types of signals, as they provide valuable information that may help determine whether the communicator is trustworthy, dangerous, etc.

Aspects of Social Cognition

Social cognition refers to the ability to think about oneself and others (Frith 2008). In particular, social cognition allows humans to function in social groups and societies through a shared understanding of social behavior and functioning. Much of what social cognition allows for is unconscious; that is, we automatically process many of the social cues that are presented to us in everyday life. For example, we automatically process facial expressions and the emotions they may portray. In many ways, this is how social cognition relates to human functioning and communication.

In the example of an individual attempting to deceive a conversation partner, nonverbal communication comprehension is seamlessly interwoven with social cognitive skills. Indeed, we create first impressions of people we are communicating with in a very short amount of time, and we tend to be quite accurate in our first

judgments about individuals (Ambady and Rosenthal 1993). Evolutionarily, this has been a survival skill when discerning intentions of others.

Social cognition is also involved in thinking about the self. Around 18 months of age, children begin to develop a sense of self-awareness and realize that they are an independent and different being from their caregivers and siblings (Brownell et al. 2007). They develop theory of mind by age 4–5, which allows them to know that not everyone possesses the same knowledge they do (Baron-Cohen 2001). Theory of mind also allows children to understand the emotional states and intentions of others, which are valuable skills for navigating social situations both early in life and throughout the lifespan.

While seemingly a skill relevant mainly to the self, theory of mind enables many aspects of communication. For example, knowledge of the self when communicating enables understanding of turn-taking and equal contribution with a conversation partner (Sacks et al. 1974). It also enables one to consider the feelings of another person when delivering difficult or sad news before communicating with them, allowing insight that can soften language. Here, empathy is also a central ability to communicative functioning. Therefore, knowledge of the self enables an individual to operate properly within the social realm.

Evolutionary Explanations for Social Communication

There has been much research into several specific effects of evolved social cognitive communication abilities in humans. The Chameleon Effect, for example, is housed under the skill set of nonconscious mimicry (Chartrand and Bargh 1999; Lakin et al. 2003). Nonconscious mimicry is a phenomenon in which an individual begins to mirror the verbal and nonverbal actions of another person, which creates positive feelings between the communicators. Indeed, the automatic processing of the mimicry on the part of the other

individual creates social bonding in that the individuals seem more similar to one another, signaling safety and belonging. The Chameleon Effect in particular is the human ability to utilize this skill set in social situations of many types in order to “blend in” with the nonverbal communication styles around oneself.

Another especially important instance of how social cognition and communication have evolved is the human ability to use context and inference to deduce meaning from a message (Lee and Harris 2013). In English, for example, homophones (i.e., words that sound the same but have different meanings and are spelled differently) such as “bear/bare” and “ate/eight” exist. In order to know which word is intended during spoken communication, one must utilize perspective taking and theory of mind to think about the context of the message that the communicator is attempting to create and then discern which word is being referenced. If a message about a camping trip is being communicated, the tendency is to interpret the homophone as the most relevant and likely word “bear.” This inferential ability is essential for gaining meaning from messages.

Another more organic example of how social cognition and communication have evolved is through the discovery of mirror systems in the brain. These systems are groups of neural networks that activate whether an individual performs an action or sees another person perform the action (Dickerson et al. 2017). For example, cooperation is an essential function in group maintenance and survival (Cosmides and Tooby 1992), and mirror systems allow for a platform of shared understanding when performing cooperative tasks and working toward a common goal. Moreover, mirror systems contribute to uniting factors such as empathy.

A final example of how social cognition and communication work together in an evolutionary sense is through the passing down of information, stories, and traditions with cultural themes (Kashima 2000, 2008). Historical information sharing and storytelling work to continue and strengthen cultural ties, enabling group

membership to increase in complexity as time passes. New generations of group members are told stories that may increase cultural understanding and dedication, thus increasing feelings of group belongingness.

Conclusion

The complexities of social cognition and communication enable some of the most essential functions of human bonding, group membership, and social belongingness. Neural network formation beginning early in life works bidirectionally in conjunction with automatic social information processing such as facial expressions and gestures, which continue to serve as the bases for social signal detection. Ultimately, efficient social cognitive skills facilitate communication, which can support such important factors as attraction, relationships, social belongingness, and group membership, thus increasing the likelihood of flourishing.

Cross-References

- Communication and Developmental Milestones
- Cooperation and Social Cognition
- Evolution of the Brain, The
- Language Acquisition
- Language Development
- Out-Group Members
- Social Cognition
- Social Skills

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Communication, Cues, and Signals

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Synonyms

Information exchange; Messaging; Signaling

Definition

All animals communicate. Communication involves an action or characteristic of one individual that influences the behavior of another individual in a noncoercive way. One key way individuals communicate is through the use of signals. A signal is a display or act produced by a sender that influences the behavior of receiver, wherein the signal and its response evolved in senders and receivers because, on average, senders and receivers benefit from the use of the signal. Another key way individuals communicate is through the use of cues. A cue is phenotypic variation in a sender that causes a reaction in a receiver that benefits the receiver even though the phenotypic variation in the sender has not evolved to cause that reaction. This entry provides an introduction to these three topics, as well as a discussion of the evolution of signals from cues.

Introduction

All animals communicate. In fact, by many definitions of communication, all living things communicate (D'Ettore and Hughes 2008). Communication is perhaps the key organic body-to-organic body interaction that makes essential biological processes possible. These processes include everything from biochemical

changes on the surface of one cell that alter the metabolic activity of a nearby cell to the production of a mating signal by one individual that alters the likelihood of reproductive activity of a nearby individual. It is an inherently social act, and even the most solitary organism must rely on communication to achieve key biological ends, such as attracting a mate, warding off a competitor, or evading a predator that has detected it. Communication is therefore largely about changes induced in a receiver by a signal, and is one of the most fundamental biological processes observed in nature.

In the pages that follow, communication is first defined and described. Part of this discussion involves notions of information, manipulation, and management. These terms have become important in recent controversies over the use, and usefulness, of the term “information” in understanding communication in nonhuman animals (hereafter, animals). Following this discussion, signals and cues are in turn defined and described. As part of this discussion, the major kinds of signals, as well as the notion of signal reliability, are described. Many of the subsequent entries will go into greater detail on these issues, so the coverage here will be brief. Although the ubiquity of communication to biological processes in general was raised above, from here on out the discussion will be limited to animal communication.

Communication

In its broadest sense, communication involves an action or characteristic of one individual that influences the behavior of another individual. The first individual here is typically referenced with terms like sender, producer, signaler, or manager; the term “sender” will be used hereafter. The second individual here is typically classified as the receiver, target, audience, or assessor; the term “receiver” will be used hereafter. The action or characteristic of the sender is a signal or cue and not the direct exertion of the body of the sender on the body of the receiver. A large dog biting and attacking a smaller dog to the point of the smaller

dog running away is not communication, but rather a coercive action (Scott-Phillips and Kirby 2013). Conversely, a large dog growling and bearing its teeth to a smaller dog to the point of the smaller dog running away is communication. Whether growling and teeth baring in this example are communication through *signals* or *cues* of the sender is a topic addressed below.

The modality of communication is the means by which a sender produces and transmits its signals or cues. Visual, chemical, and acoustic modalities are the common modalities that most animals use (or at least the ones most heavily studied), although tactile, vibrational, and electrical communication is crucial for some species (Bradbury and Vehrencamp 2011). Visual communication includes permanent body shapes, colors, and markings; changes in posture, orientation, or movement of certain body parts; and alterations to the physical environment. Chemical communication includes lightweight volatile substances that can travel easily in air but tend not to last long in the environment, and also nonvolatile substances that are heavy in molecular weight and that typically cannot travel far but can remain on the substrate for long periods of time. Acoustic communication includes sounds produced inside the bodies of animals that are generated through specialized vocal production organs and projected outward from the mouth or head, and sounds produced on or outside the bodies of animals by either bringing two different body parts together or by one body part contacting the substrate. Although the discussion above implies or explicitly describes communication through the air, communication can also occur through the backgrounds of water or solid material such as plant tissue or the ground. The physical background through which these displays and communicative acts travel to receivers is the medium. The physical properties of the medium (e.g., how dense the vegetation is through which a signal or cue must travel) can select for different kinds of structure or patterning to the communication. Finally, for both the sender and receiver of the signals or cues, there are often specialized organs that have evolved in their particular species to make the communication effective and efficient. As just

two brief examples, consider the two sides of the syrinx and songbird species that allow for the independent production of distinct sounds, and the specialized external morphology of the outer ears of many terrestrial mammals that allow for flexible and directional capture of sounds in the environment. Even within a single communicative modality (let alone across modalities), there is enormous variation across species in sender production mechanisms, the signals and cues that are produced, and receiver perceptual mechanisms.

Although there is a tremendous amount of variation in how and why different species communicate, there are some overarching themes that all animals share. Perhaps the most obvious principle is that animal communication is essentially social. Without both a sender and attending receiver, communication is impossible (including in autocommunication, such as echolocation, wherein the sender is also the receiver of the signal). Communication furthermore makes other types of social behavior possible – from competitive interactions over access to a food resource to courtship interactions leading up to mating. Another general principle of animal communication can be found in Morton's "Motivational-Structural Rules" (Morton 1977). According to this view, birds and mammals that rely heavily on acoustic signaling tend to use harsh, low-frequency sounds when displaying aggression and they tend to use relatively pure, higher frequency sounds when frightened, appeasing, or approaching without hostility (Morton 1977). Perhaps there are parallels to these motivational-structure rules for vocal sounds in signal production in other modalities and in other taxa beyond birds and mammals.

For decades, communication has been defined as the exchange of information from a sender to a receiver that affects the behavior or physiology of the receiver. In his seminal text on communication, Smith (1977) describes the diversity of messages of nonhuman (and human) animal sender displays, and the potential meanings to receivers. The sender produces a behavior or possesses a physical trait that sends a message to receivers. In other words, the behavior or physical trait (often, a signal) provides information that

receivers can use in making decisions. The meaning of the communicative interaction is typically understood from the standpoint of the receiver collecting information about the environment – the signal or cue provides one portion of the information available to the receiver. The receiver gains meaning from the combination of the signal or cue itself and the context in which the signal or cue is experienced. Contextual factors include sender or receiver characteristics (such as current behavioral activity or state), sender *and* receiver characteristics (such as the nature and longevity of the relationship between the two individuals), or the environmental situation itself (such as the recent presence of a predator or competitor). In an important extension of Smith's ideas here, researchers need to consider not just the meaning that a receiver generates from the signal/cue and the context, but the decision-making process used by the receiver to choose its response to the signal/cue and the context (Fischer 2013).

A common approach to describe “information” and this decision-making process is to utilize statistical models. Signals and cues predict (in a probabilistic sense) events or states on the part of the sender that are important to the receiver. Receivers continually update their understanding of the world based upon their own previously acquired information, but also upon the information they glean from senders (e.g., from the signals produced by senders). Statistical decision theory involving Bayesian updating of information provides a recent and powerful approach used by researchers to generate predictions about communication's effect on receivers (Kight et al. 2013). Receivers pay attention to senders' signals and cues because they are associated with biologically meaningful variation in sender and environmental characteristics. This association with biologically meaningful sender and environmental variation is one of the key meanings of the term “information” for researchers studying communication.

Another key notion of information comes from the “Mathematical Theory of Communication” of Claude Shannon – information transmitted from a sender to a receiver reduces uncertainty in the receiver (Shannon and Weaver 1949).

Information here is “a measure of one's freedom of choice when one selects a message . . . in the simplest cases, to be measured by the logarithm of the number of available choices” (p. 9). One important component of this general view of information is that information relates to diversity. The greater the variation in the number and type of signals and cues available to a sender and receiver in a communicative interaction, the more information resides in that communicative system. In short, in two comparable species, the species with the larger repertoire of signals and cues is the species with more information that can potentially be communicated.

The previous few paragraphs have revolved around the idea of communication as the transmission of information from senders to receivers. This notion of information in communication has been criticized for various reasons for nearly 50 years (Burghardt 1970; Rendall et al. 2009). One of the major criticisms of the use of information in the field of animal communication is that it is a term that comes from writing and thinking about human language and human cognition (Shannon and Weaver 1949), and so carries a lot of unnecessary (and perhaps even harmful) theoretical baggage into the field of animal behavior. Perhaps the key criticism that stems from this argument is the notion of encoding that comes from Shannon's “Mathematical Theory of Communication” (Shannon and Weaver 1949). According to Shannon's view, a sender detects a stimulus/source of information in the environment and encodes that information into a signal, which then transmits through the noise of the environment to a receiver, who then decodes the information in the signal to determine what the stimulus/source of information was. The notion of information encoding by a sender suggests to these critics an individual consciously and with intent choosing signal *A* over signal *B*, to impart information to a receiver in a way that benefits both.

These critics argue that a stronger and more biologically valid way of viewing animal communication is in terms of senders influencing the behavior of receivers with the use of their signals through terms like manipulation and

management. Senders produce signals that are in their own best evolutionary interests to manipulate/manage the behavior of receivers, whether those signals benefit receivers or not. Senders do not encode information into signals, but, as described above regarding Smith's view (Smith 1977), receivers gather and assess information about senders from both their signals and from the context of the signaling. It is interesting that much of the terminology used by critics of the information view also brings with it significant cognitive baggage from human interactions (e.g., manipulation, management, propaganda, advertisement, assessment). This baggage can lead to a view of senders taking higher-order cognitive approaches to their behavior and strategically using their signals in sometimes deceptive ways to get receivers to act in ways that benefit senders. The anti-information view also seems unable to account for a good deal of interesting and important animal communication, including signaling sequences by two or more senders (McGregor 2005) and consistency in signal use over time by senders (Botero and de Kort 2013). Nonetheless, critics of views of information in animal communication have helped sharpen and strengthen ideas about signaling and communication, and have moved the field forward. A recent volume is the key summary of these arguments and is highly recommended as a starting point to the "information debate" (Stegmann 2013).

Signals

Signals are displays or acts produced by senders that influence the behavior of receivers, and do so because (a) they have evolved for that communicative function in senders, and (b) receivers' responses to those signals have also evolved, because, on average, senders and receivers benefit from the use of those signals (Maynard Smith and Harper 2003). If the use of a signal brings no benefit to senders in a given population, that signal will be selected against. Similarly, a signal that brings benefits to senders but costs to receivers in a given population should result in selection pressure for receivers to assess and discriminate

signals more carefully, to ignore or avoid such costly or unreliable signals.

With animals living in isolation, the signals they employ need not be complex. A short, periodic call may be sufficient to ward off territorial intrusion or to attract a mate. However, as organisms increasingly interact within complex social structures, components of the communication systems are also likely to increase in complexity. Many species are social – individuals in these species spend large parts of their lives in social groups, in close proximity and often engaging in repeated interactions with specific conspecifics (and perhaps heterospecifics) over time. Living in social groups brings benefits such as an enhanced ability to detect and respond to predators and food resources. These benefits of group living are often thought to accrue to prey species, but predators clearly benefit from sociality as well. For both predators and prey, the benefits of living in social groups often critically depend on information encoded in signals (Bradbury and Vehrencamp 2011; D'Ettorre and Hughes 2008).

In many animal species, effective and efficient social living requires social cognition. Social cognition can include a wide range of processes, such as the ability to recognize group members, remember past interactions, and strategically influence the behavior of others (Shettleworth 2010). Increased social cognition has been documented in species with more complex social groups compared to species with less complex social groups (Shultz and Dunbar 2007). Part of this increased social cognition likely includes effective and efficient signaling abilities. Without the ability to signal, sustained social interaction would be impossible and so signaling is crucial to the understanding of the evolution of social cognitive abilities. More complex groups often demand increased social cognition in group members; therefore, strong selection pressure is expected for enhanced signaling systems that provide individuals diverse behavioral ways to assess and manage the behavior of others in their groups (Freeberg et al. 2012). What are some of these major types of signals used in communicative interactions? A few of the major classes of signals are introduced here; readers should consult the

key reference on animal communication for the full range of signal types (e.g., Bradbury and Vehrencamp 2011).

Index Signals Some signals used by senders are directly related to their specific physical characteristics. These are called index signals, and cannot be faked by senders because the signals are so tightly constrained by earlier developmental conditions or by current physical state of the sender. For example, in the field cricket *Gryllus pennsylvanicus*, larger males produce louder calls at lower frequencies (Hz) compared to smaller males (Harrison et al. 2013). In these species, sound production stems from two body parts rubbing together, and the larger the body parts for a particular species, in general the more intense and lower the frequency of the sounds produced.

Handicap Signals Like index signals, handicap signals involve communicative acts and displays that are very difficult to fake, and so are typically reliable. These are signals that are effectively produced by individuals in good condition or of good quality and are costly to produce (Zahavi 1975). These costs can be borne easily enough by individuals of good condition/quality but are much harder for individuals of poor condition/quality to bear. For example, in males of *Anolis* lizard species, the rate at which push-up displays are produced is positively correlated with sender physiological condition, and increased rate of visual displays makes conspecific male intruders less likely to approach the signaling male (Brandt 2003). In these cases of handicap signals, senders in poorer condition can produce the signals, but only senders in good condition can produce the signals repeatedly at high rates – assessment of such signaling over periods of time will thus reliably indicate to a receiver the relative qualities of senders.

Conventional Signals Although definitions of conventional signals have varied over the years (and these changing definitions have caused confusion), a general view of this class of signals is that it refers to signals that are arbitrarily related to

the entity or condition with which they are associated (Guilford and Dawkins 1995). If signals are independent of associated entities or conditions (such as a level of arousal due to a detected predator or the body condition of a male signaling in a breeding context), they are relatively cost-free for senders to produce, or at least the costs of signal production are unrelated to variation in the entity or condition about which the communication is occurring. In these cases, senders might be expected to be less reliable in their communication. Several largely receiver-borne processes exist to ensure conventional signal reliability, however, including retaliation by receivers, alignment of interest between senders and receivers, and reciprocity or reputation (Bradbury and Vehrencamp 2011; Searcy and Nowicki 2005).

Referential Signals Referential signals are signals that are specifically associated with certain stimuli in the environment (Bradbury and Vehrencamp 2011). Referential signaling is important to identify because it could indicate that the sender has voluntary control over what it communicates, as opposed to its communication being just an involuntary, affect-based response. It is also argued to be a step forward toward animal communication having more in the way of semantics – signals representing entities in the environment. Vervet monkeys produce acoustically distinct alarm calls when they detect three different classes of predator (eagle, leopard, and snake), and context-free playbacks of those alarm calls produce functionally appropriate escape or information-gathering information in receivers, supporting the notion of referentiality in these calls (Cheney and Seyfarth 1990). However, the concept of referential signals remains controversial (Wheeler and Fischer 2012). In many cases it is unclear if the animals are using different variants of calls to signal about aspects of their environment, or if the differences in these calls are a result of motivational changes in the sender as a response to environmental differences.

Multimodal Signals It has become clear that a great deal of animal communication involves senders producing changes in their behavior in

more than one modality simultaneously, with the result that receiver behavior can potentially be influenced by one or both components of the signal (Partan and Marler 2005). A well-studied example involves the physical changes to head and body postures when animals produce sounds, such as calls of anurans and insects, and songs of birds. Receiver behavior can potentially be influenced by the acoustics of the sound produced, the visual patterns of the sound generation and changes in body posture, or both. Importantly, the different modalities involved in a multimodal signal may influence receivers in nonadditive ways, suggesting an emergence of information from the different components generated by different modalities (Partan and Marler 2005).

Cues

In their normal activity, animals produce considerable variation in movement speeds, body postures, limb and head orientations, and so forth. This variation in body part orientation and movement can allow an observer (the receiver) to predict behavioral tendencies of the target individual (the sender). This is the meaning of a cue in animal communication – phenotypic variation in a sender that causes a reaction in a receiver, where that reaction's function is to be caused by that phenotypic variation even though the phenotypic variation itself does not function to cause that reaction (Scott-Phillips and Kirby 2013). In other words, sender variation in behavior did not evolve to communicate to the receiver, but the receiver gains information about the sender nonetheless. For example, sleeping behavior in human infants serves as a cue to likelihood of activity (or lack thereof) to others in the environment, even though sleeping behavior did not evolve to communicate to another individual the likelihood of the level of activity of the sleeping individual. Cues, unlike signals, have not evolved for the particular function they serve (Maynard Smith and Harper 2003); cues benefit the receiver and not the sender.

Cues are used by receivers for multiple reasons – social and nonsocial. Individuals use cues

from potential predators to determine predation risk. Predators produce cues that could indicate the level of risk that the predator may entail. For example, for many small mammals and birds, a detected hawk that is sleeping represents a different level of threat compared to a detected hawk that is awake, and both of these hawks are lower levels of threat than a flying, actively hunting hawk. It is likely not advantageous to the predator to reveal cues that could indicate risk to its intended prey, but the variation in body part orientation and movement related to variation in life's activities (hunting, resting, courting, etc.) cannot always be concealed. As one key example, many species are readily able to discriminate the head orientation of a predator. For example, both Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) avoid a feeder more and call differently if a potential predator has its head oriented toward a feeder rather than oriented away from the feeder (Kyle and Freeberg 2016). Beyond head orientation, many species seem to be especially sensitive to the eyes of others, including predators. Eye gaze is thought to be one of the most important cues used by prey species to determine what a predator is attending to and the level of threat posed by that predator. In predator species the eyes are especially salient, with most predator species having forward-facing eyes, as opposed to the lateral eyes of many non-predatory species. It seems that many species are able to pay attention to eye shaped objects more than other objects.

Assessment of eye gaze is not only important to identify predation risk but is also important in social interactions. In many primate species, individuals can identify whether another individual is visually paying attention to them or to an important stimulus in the environment. Experiments have revealed that numerous primate species can follow a conspecific's eye gaze toward a goal. Many have argued that the ability to understand where an individual is looking is a crucial step in the evolution of the theory of mind in humans (Calder et al. 2002). Humans also seem to be particularly fixated on the eyes and eye gaze of other humans. The fact that humans, nonhuman primates and birds all pay attention to eye gaze

suggests that it is an important communicative feature in perception of sender cues that should be examined more carefully.

Evolution of Signals

One of the most fundamental reasons why animals communicate is that it aids in their survival and reproduction capability. They need to find food sources, attract and compete for mates, fight with any intruders and competitors that threaten their resources, and avoid or defend themselves from predators. Many of these requirements result in changes in arousal and emotional state in animals, and many of these changes could also result in cues to receivers. Charles Darwin addressed the topic of communication chiefly through his examination of emotional expressions. Darwin argued that emotional expression was (at least at some point) beneficial for many types of animals (Darwin 1872). A growling dog may intimidate another dog into abandoning a food source without a fight. A distress call from a newborn chimpanzee would likely provoke the caregivers into both attending to the newborn and investigating the source of their distress. Thus, communicating about motivational states is assumed to be helpful to individuals in general.

Darwin provided three principles of emotional expression to help explain how they became part of evolutionary processes that result in communicative signals: *serviceable habits*, *direct action of the nervous system*, and *antithesis*. These principles have been extended by decades of subsequent research – particularly in the field of ethology. Beginning with *serviceable habits*, consider the classic example of a dog (or almost any terrestrial mammal, for that matter) attacking another individual. A key means by which a dog attacks another is by biting it. To bite another individual effectively, a dog must carry out two precursor movements. First, the dog must open its mouth to make the bite possible. Second, the dog must pull its lips back away from its teeth, exposing the teeth for the bite. Thus, a receiver not wanting to fight could benefit by paying attention to the sender's initial cue of an open mouth and bared

teeth in the short time period prior to an attack involving biting. The benefits gained by both parties not actually having to fight, but by solving the agonistic interaction through this “open mouth/teeth baring” cue, would generate strong selection pressure for that cue to evolve into an even stronger and less ambiguous signal of likelihood of attack. This evolutionary process is known as ritualization.

In his view of *direct action of the nervous system*, Darwin argued that many emotional expressions were rooted in the physiology of the organism. Each organism depends upon numerous homeostatic and nonhomeostatic processes to maintain biological functioning in response to a dynamic environment to achieve its biological goals. Some of the changes in the body that result from changes in neurophysiological functioning are observable, including erection of feathers or hair, dilation of pupils, yawning, sweating, and defecation/urination. Finally, the principle of *antithesis* explains how the opposite changes in neurophysiology (or serviceable habits, for that matter) are also likely to provoke opposite effects on the resultant behavior. For example, hormone-activated aggression causes muscles to become tense, whereas the opposing, nonaggressive states promote relaxed muscles to preserve energy. As raised above, cues stemming from these three principles of emotional expression can evolve into signals, often through the process of ritualization (Bradbury and Vehrencamp 2011). Through natural selection, these cues can evolve to become “sign stimuli” – more conspicuous and stereotyped signals to other animals that invoke specific behavioral replies. These cues and signals can be integrated into higher-order cognitive systems in receivers that control communicative salience (Dall et al. 2005). This integration between attention mechanisms and the sign stimuli can generate selection biases in the receiver.

The “sender-precursor model” described above has explained that signal evolution occurs by receivers detecting cues of producers that are beneficial to those producers (and often to the receivers) and processes like ritualization (Bradbury and Vehrencamp 2011). Alternatively, the “receiver-precursor model” posits that

receivers have sensory biases and prefer specific types of behaviors or physical appearance in others. These biases are shaped by natural selection in a number of ways – for example, in species that rely heavily on the ingestion of orange fruits, greater perceptual acuity for orange color as a food item may result in stronger preferences for and biases toward orange color in general. Sensory exploitation occurs when senders evolve traits that receivers prefer (Bradbury and Vehrencamp 2011).

Conclusion

Throughout this entry, the general topic of communication has been addressed in a few different ways. Distinctions between signals and cues were clarified, major types of signals used by senders were outlined, the use of “information” as a framework (or in some cases, measure) of communication was described, and the evolution of signals from cues was overviewed. However, despite the fact that communication is such an essential and pervasive phenomenon found throughout the animal kingdom, this entry leaves many important questions unresolved (a number of which are addressed in subsequent entries). For example, how similar, or dissimilar, is human communication compared to animal communication (D’Ettorre and Hughes 2008; Tomasello 2008)? In humans, much communication concerns objective information – such as the location or identity of a desired item. Some of this objective information can reflect sender emotional state – receivers can typically assess when senders are happy or angry, for example. In addition to objective information, human senders can communicate abstract and subjective information – individual thoughts, perceptions, sensations, and feelings about idiosyncratic experiences and personal understandings of the world. Human senders can also communicate about communicating, such as the request by management for an audience of people to silence their cell phones prior to the start of a performance, or the encyclopedia entries in the current volume. To what extent can animals communicate abstract information to

others in ways similar to human language and communication?

Along these same lines, is animal communication primarily or exclusively related to communication about affective states and propensity to engage in certain behavior? Or is some animal communication truly referential, whereby certain signals represent important classes of environmental stimuli, such as predators (Wheeler and Fischer 2012)? Animals can vary their signaling behavior depending upon the particular audience of receivers they detect in the environment. Are these “audience effects” indicative of volitional control and strategic flexibility in signal use by senders, or of signal production in response to changes in affective state due to variation in social environments? Do animals communicate about communication, such as through the use of a signal to alert a receiver that another signal is coming (Tomasello 2008)? To what extent do the more basic sender–receiver interactions described here capture the signaling interactions – and the information receivers can glean from such interactions – in complicated communication networks (McGregor 2005)? How flexible are signaling systems in animal communication, from both developmental and evolutionary perspectives? These are currently topics of intensive research, and this entry could not hope to do them justice here due to space constraints. Other entries in this volume will touch on these important topics, however, and if this entry has successfully communicated the fundamental role of communication in animal lives, readers of this entry should be encouraged to read on.

Cross-References

- ▶ [Communication and Developmental Milestones](#)
- ▶ [Communication and Social Cognition](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Costly Signaling](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Navigating Social Relationships](#)
- ▶ [Signal Reliability](#)
- ▶ [Social Cognition](#)
- ▶ [Social Intelligence Hypothesis, The](#)

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Comparative Evidence

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Synonyms

[Phylogenetic study of homosexual behavior](#)

Definition

Cross-species comparative analysis of same-sex sexual behavior.

Introduction

If sex is the engine that drives Darwinian evolution, why would a variety of animal taxa invest in nonconceptive sexual behaviors that do not directly contribute to reproduction? This section aims to address this evolutionary conundrum by focusing on the cross-species comparative analysis of homosexual behavior, in an attempt to shed further light upon the origins and evolution of human homosexuality.

Phylogeny of Homosexual Behavior

Despite its apparent lack of fitness benefits, same-sex sexual activity is broadly distributed across the animal kingdom. Descriptive reviews indicate that hundreds of species of mammals, birds, reptiles, amphibians, fishes, insects, spiders, mollusks, nematodes, and other invertebrates engage in extremely diverse homosexual behavioral patterns, including courtship displays, manual-genital, oral-genital, and genital-genital stimulations, and mounting interactions, with pelvic thrusting and even intromission between same-sex partners (Bagemihl 1999). However, the cross-species distribution and expression of same-sex sexual activity is uneven. First, the

frequent, prevalent, and enduring occurrence of homosexual behavior in some species contrasts with its seeming absence, or at least obvious scarcity, in others. Second, some species exhibit only female-female or only male-male sexual behavior, whereas other species exhibit both. Third, several proximate and ultimate hypotheses have been proposed to account for the diverse manifestations of same-sex sexual interactions in different species, such as the lack of opposite-sex sexual partners, the pursuit of immediate sexual reward, the practice by immature individuals for heterosexual sex, or the achievement of social goals (e.g., dominance demonstrations, alliance formation, or tension regulation; Poiani 2010; Sommer and Vasey 2006). Only systematic comparative research aiming to quantitatively examine the factors that contribute to the emergence and expression of homosexual behavior among animal taxa can provide some solutions to this evolutionary puzzle (Sommer and Vasey 2006; Vasey 2007).

One of the most powerful methodological tools to explore the origins and evolution of biological features is the phylogenetic comparative approach (Martins 1996). By superimposing the phenotypic trait of interest over a robust phylogenetic tree based on molecular data and encompassing many related species, researchers make parsimonious historical inferences about how this trait originated and changed in a step-by-step manner over time. Phylogenetic analyses are particularly useful to reconstruct scenarios for the evolutionary history of behavioral traits, which do not leave any direct fossil traces. They can be used to decide whether similar behavioral patterns are due to common ancestry or the result of independent adaptations to similar environmental pressures (Martins 1996). Such a comparative approach should be relevant to the evolution of homosexual behavior, because it can distinguish adaptive from nonadaptive traits by indicating which ones have predated, accompanied, or followed the modification of some of their structural and functional attributes. Moreover, just like play behavior (cf. Pellis and Iwaniuk 2000), the lack of functional constraints, and thus the flexibility and

versatility of same-sex sexual activity, makes it a good candidate for phylogenetic studies. In principle, reconstructing scenarios for the evolution of homosexual behavior requires well-established and often composite phylogenies that are not directly based on sexual characteristics.

Yet, comparative investigations of the evolution of homosexual behavior are extremely rare and limited to birds and mammals. A phylogenetic analysis of the frequency and form of same-sex courtship and mounting behaviors in 80 avian species showed strong associations between such homosexual interactions and both social mating system and developmental mode, but with marked differences between males and females (MacFarlane et al. 2007). More specifically, female-female sexual behavior mainly occurred in socially monogamous species that produce precocial offspring at hatching, whereas the frequency of male-male sexual behavior significantly increased with the degree of polygamy of the species, regardless of the developmental state at hatching. Another study conducted on 93 avian species showed a consistent relationship between sex-specific relative parental care and the frequency of both male and female homosexual behavior: When females provide less care than males, female-female sexual behavior is more frequent, and when males provide less parental investment than females, male-male sexual behavior is more frequent (MacFarlane et al. 2010). Poiani (2010) tackled the daunting task to examine the effect of social, life history, and ecological factors in the frequency of same-sex mounting across 72 bird species and 107 mammal species (including humans). In birds, he found that homosexual mounting was negatively associated with the size of the social unit and positively associated with adult male-biased sex ratio, increased sociality, and increased level of dominance. In mammals, he found that homosexual mounting was negatively associated with social unit size and relatedness between partners and positively associated with polygamy. In both birds and mammals, he found that same-sex mounting was

positively associated with social sexual segregation (i.e., spatial distancing between the sexes for part or even most of the year). Comparative tests showed that Poaini's (2010) *Synthetic Reproductive Skew Model of Homosexuality* fit better the avian than the mammalian data set, even though homosexual mounting is more prevalent in mammals than in birds. This suggests that same-sex mounting is more complex in mammals than in birds. The relatively higher prevalence of homosexual behavior in mammals is likely to be associated with a greater degree of sociality, polygamy, and cooperative breeding in this taxon (Poaini 2010). A recent phylogenetic study focusing on nonhuman primates showed that the frequency of same-sex genital contact was positively associated with social complexity, and this effect was stronger in males than in females (Fernandes et al. under revision).

Phylogenetic research on homosexual behavior is still hampered by several types of limitations that need to be overcome. The first type is both observational and theoretical: The validity of the comparative method rests on the ability of researchers to correctly detect, identify, and record this behavior in their study species when it occurs. This is not trivial because nonadaptive behaviors, such as same-sex sexual activity, are by definition devoid of major fitness consequences and thus tend to be dismissed as idiosyncratic, anecdotal, and not worth of research interest. As a result, the occurrence of homosexual behavior may be underreported in cross-species comparative reviews. The second type of limitation is logical: Absence of evidence is not evidence of absence. Because it is comparatively easier to prove the occurrence of a behavior than its absence, phylogenies of homosexual behavior are likely to contain false negatives (e.g., due to differential research effort when comparing species). The third type of limitation is methodological: The phylogenetic analytical tool kit is broad, and there is no universal consensus on whether the dependent variable (i.e., homosexual behavior) should be dichotomized (i.e., presence/absence) or classified on a frequency scale, divided by sex

(i.e., female-female versus male-male sexual behavior) or not, and superimposed on a specific cladogram to control for the evolutionary relatedness across species, as well as how phylogenetically independent contrasts should be calculated (cf. Martins 1996). All these decisions may affect the results of the interspecific comparison and their interpretations. Finally, it is important to remind the reader that these cross-species comparative analyses are based on homosexual *behaviors*, and there is currently very little to no evidence that homosexual *behavior* in nonhuman animals reflects homosexual *orientation*. Rather, it likely reflects animals' potential for bisexual behavior, which exists, for example, in several primate species (Dixson 2012). When considering how results obtained from animal research on homosexual behavior may apply to the evolution of human sexuality, one should keep in mind that although reproductive behaviors in humans and animals likely share some homologous features, nonconceptive sexual behaviors among different species may be analogous. For instance, exclusive same-sex sexual orientation has not been documented in any free-ranging nonhuman primate species. As such, the study of homosexual *behavior* in nonhuman primates may inform us about the evolution of homosexual *behavior* in humans but may shed only limited light as to why exclusive homosexuality evolved.

Conclusion

Overall, cross-species comparative studies suggest that same-sex sexuality is not an evolutionarily uniform phenomenon. Instead, it appears that multiple analogous forms of homosexual behavior have evolved, underlain by different developmental pathways, sociodemographic settings, motivational processes, functional outcomes, and phylogenetic histories both within and between species (Vasey 2007). Therefore, evolutionary explanations of homosexual behavior are contingent on the implementation and full integration of two complementary levels of

analysis, namely the phylogenetic (i.e., historical) and functional (i.e., adaptive) perspectives (Vasey 2007). Some forms of same-sex sexual activity may have no adaptive value whatsoever, while others may be nonsexual acts that are executed to serve social functions. As such, we should not expect any one evolutionary explanation for same-sex sexual behavior to account for the diversity of this phenomenon. Indeed, attempts to make unifying interspecies generalizations about the evolution of homosexual behavior may be misguided and misleading.

Cross-References

► [Cross-Cultural Studies](#)

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Comparative Neuroanatomy

► [Evolution of the Brain, The](#)

Comparative Phylogenetic Analysis

► [Hamilton's Rule and Genetic Relatedness](#)

Comparative Psychologist

► [Michael Tomasello](#)

Comparative Psychopathology

► [Psychiatry of Nonhuman Apes](#)

Comparative Psychopharmacology

► [Psychiatry of Nonhuman Apes](#)

Comparing Phenotypes

► [Holmes and Sherman \(1982\) on Ground Squirrels](#)

Comparison

► Social Comparison

Compensatory Mate Retention Tactics

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Definition

Compensatory mate guarding tactics are defined as mate guarding tactics such that the use of one tactic compensates for the lack of use another tactic.

Introduction

Once an individual secures a long-term mate or romantic partner, the individual has the adaptive problem of retaining the mate. As the word “retain” may be generally defined as “to keep possession or use of”, mate retention tactics might be considered to have as their aim the prevention of a mate from permanently defecting from or abandoning a long-term relationship. Although they do serve this purpose, mate retention tactics can also reduce the likelihood that a long-term mate will commit an infidelity or temporarily defect from a relationship by engaging in extra-pair copulations (EPCs). Mate retention tactics are, therefore, considered to be tactics that serve both purposes (e.g., Buss 1988; Shackelford et al. 2005). It follows that whether a particular mate retention tactic is aimed at preventing a partner from permanently abandoning a long-term relationship or engaging in EPCs depends on the motivation of the individual employing it.

In a seminal article, Buss (1988) devised a taxonomy of mate retention. His classification included two categories, subsuming six strategies, subsuming 19 tactics, subsuming 104 acts. For instance, the category *Intersexual Manipulations* subsumed strategies including *Negative Inducements* that subsumed tactics including *Threaten Infidelity* that subsumed acts including *He flirted with another woman in front of her*. Incorporating the acts, Buss devised a *Mate Retention Inventory* (MRI) to assess the frequency with which individuals employ the 19 tactics. Subsequently, Buss et al. (2008) developed a short form of the MRI (*MRI-SF*). The *MRI-SF* assesses the frequency with which individuals employ the 19 mate retention tactics but includes only two acts per tactic.

Notwithstanding Buss' (1988) taxonomy, there remains controversy over the classification of mate retention tactics. A notable example concerns whether *mate retention* is synonymous with *mate guarding*. Prior to Buss, taxonomies considered the terms to be synonyms as mate guarding was considered to comprise any tactic employed by an individual to prevent the individual's mate from being fertilized by intrasexual rivals (e.g., Thornhill and Alcock 1983). However, these taxonomies were based on non-humans, notably insects, and the tactics considered included female mimicry, mate plugs, and vibratory signalling; tactics not typically associated with humans.

Buss' (1988) taxonomy was the first to solely consider mate retention tactics used by humans. Unlike previous taxonomies, it subsumed *mate guarding* under *mate retention*. Buss argued that mate guarding may not reasonably be considered to encompass certain tactics of mate retention; “Tactics may be subtle, including dissuading potential competitors, luring one's mate with positive inducements, or even rendering one's mate less attractive or evocative to competitors. These tactics appear to fall outside the category of ‘mate guarding’ but are accurately subsumed by the category of ‘mate retention’” (p. 292). To support his classification, Buss used the term *direct guarding* to differentiate his definition of mate

guarding from the broader definition previously associated with the term. Under *direct guarding*, Buss subsumed the following tactics: *Vigilance*, subsuming acts including *He asked his friends to check up on her*; *Concealment of Mate*, subsuming acts including *He refused to introduce her to his same-sex friends*; and *Monopolization of mate's time*, subsuming acts including *He insisted that she spend all her spare time with him*. In light of Buss, it may not be reasonable to consider *mate guarding* as a synonym for *mate retention*. Alternatively, there may be value in following Buss and making a distinction between the inclusive term *mate guarding* and the more restrictive term *direct mate guarding*.

Although both sexes wish to prevent a partner from engaging in EPCs, for a man, a partner's engagement in EPCs may lead to him being cuckolded or unknowingly raising the children of other men. For men, therefore, mate retention tactics also serve as anticuckoldry tactics. Not all anticuckoldry tactics, however, are mate retention tactics as not all serve to prevent a partner from permanently abandoning a relationship or engaging in EPCs. Rather, certain anticuckoldry tactics serve only to reduce the likelihood that offspring will result from an EPC in which a partner has already engaged. For instance, Baker and Bellis (1993) found that the greater the length of time that a couple had spent apart since their last copulation, the greater the amount of sperm that men inseminated into their partners. Because the greater the length of time that a couple has spent apart, the greater is the likelihood that the woman will have engaged in EPCs, Baker and Bellis' finding suggests that the aim of depositing a greater amount of sperm is to increase the likelihood that the men's sperm will outcompete any rivals' sperm to fertilize their partners' eggs. Further, Shackelford et al. (2002) investigated if men have evolved psychological adaptations to reduce the likelihood that a partner's EPCs will result in offspring. They found that the greater the proportion of time that men had spent apart from their partners since their last copulation, men reported the

following: a greater attraction to their partners, other men found their partners more attractive, and a greater desire to have sex with their partners. Shackelford et al.'s findings suggest that these psychological adaptations serve anticuckoldry purposes by motivating men to, as soon as possible, place their own sperm in competition with any rivals' sperm that may already be in their partners' reproductive tracts. It follows that while men's anticuckoldry tactic of placing as much sperm as possible in their partners' reproductive tract as soon as possible serves to prevent extra-pair fertilizations, it serves neither to prevent a partner from engaging in EPCs nor to prevent a partner from permanently abandoning a relationship. It, therefore, cannot be considered to be a mate retention tactic.

Compensatory Mate Retention Tactics

Shackelford, Goetz, Guta, and Schmitt (2006) investigated the relationship between the frequency of men's use of the anticuckoldry tactics of mate guarding and in-pair copulations. They labelled as "compensatory," tactics such that the use of one tactic compensates for the lack of use another tactic. Shackelford et al. stated that there exists a negative correlation between the frequencies of use of compensatory anticuckoldry tactics.

Following Shackelford et al. (2006), the current article defines "compensatory" mate retention tactics as those such that the use of one tactic compensates for the lack of use another tactic. It is, therefore, assumed that there is a negative correlation between the frequencies of use of compensatory mate retention tactics.

The literature is not directly informative regarding the tactics that are used in a manner that is compensatory as defined here. Nevertheless, it is reasonable to speculate regarding factors that may lead particular individuals to employ particular mate retention in such a manner. For instance, some individuals may have insufficient resources to use the tactic "resource display" but

may be able to use the tactic “appearance enhancement” as a compensatory tactic. For those individuals, there will be a negative correlation between the frequency of use of “resource display” and “appearance enhancement.” Similarly, some individuals may not have the physical stature to use the tactic “violence against rivals” but may be able to use the tactic “resource display” as a compensatory tactic. For those individuals, there will be a negative correlation between the frequency of use of “violence against rivals” and “resource display.” Future research might, therefore, measure individuals along traits such as resources, physical attractiveness, and physical stature and ask them to report their frequency of use of various mate retention tactics. Tests might then be conducted to assess whether individuals who score low on particular traits have a low frequency of use of mate retention tactics associated with those traits and who score high on particular traits have a high frequency of use of mate retention tactics associated with those traits. As the intensity with which mate retention tactics are employed has been shown to depend on the relative mate values of partners and the length of a couple’s relationship (e.g., Buss and Shackelford 1997), there would be value in future research investigating if those factors moderate the use of mate retention tactics.

Conclusion

The literature on mate retention among humans is relatively new and the only taxonomy existing for it is that provided by Buss (1988). The primary aims of the current article have, therefore, been to clarify the following: the definition of the term *mate retention*, of which tactics mate retention is comprised, and the definition of *compensatory mate retention tactics*. By doing so, it is hoped that the current article will play a part in eliminating inconsistencies between future studies of mate retention and, therefore, lead to an improved understanding of the topic.

Cross-References

- ▶ [Coalitional Mate Retention](#)
- ▶ [Mate Retention](#)
- ▶ [Mate Retention After Children](#)
- ▶ [Mate Retention and Romantic Attachment](#)
- ▶ [Mate Retention Strategies](#)
- ▶ [Mate Retention Tactic](#)
- ▶ [Use of Mate Retention Strategies](#)

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Competition

- ▶ [Derogation of Rivals](#)
- ▶ [Dominance, Testosterone, and Cortisol](#)
- ▶ [Marital Status](#)
- ▶ [Meta-analysis of Sex Differences in Aggression](#)
- ▶ [Peer Competition and Cooperation](#)
- ▶ [Social Comparison](#)

Competition Between Groups

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Synonyms

[Between-group competition](#); [Intergroup competition](#); [Intergroup conflict](#)

Definition

Social behavior, in which individuals jointly fight for resources against another group of individuals or when social groups pursue mutually exclusive goals

Introduction

Cooperation and competition are two basic forms of social behavior. In the broad sense, competition relates to any types of conflict between agents. In a more narrow and strict sense, competition takes place only when agents strive to acquire the same resource or when achieving a goal means preventing others from achieving their goals. Margaret Mead, an American anthropologist, suggested that individualistic behavior, i.e., a goal-directed behavior not referring to others, is the third basic type of behavior typical for group life (Mead 1937, p.16). One has to note however that the behavior can be individualistic at the operational level, i.e., in terms of how the action is performed, whereas the goals can be either cooperative or competitive.

A number of influential theories, from Darwinian evolution theory and Hobbesian “war of all against all” to contemporary rational choice theories, consider competition as the core of all social behavior and the evolution itself. Altruistic or cooperative behavior in these approaches is often considered as a by-product of competition serving agents’ fitness and/or self-interest. By agents

these approaches typically mean individual agents. But for humans and some other species, social behavior is mainly organized around groups and is conditioned by group membership. As well as in the evolution theory where approaches stressing the group-based reality of social life (kin selection and group selection theories) appeared, the understanding of competition in human societies makes it necessary to consider competition between groups in addition to competition between individuals.

Evolution of Between-Group Competition

Although the most complex forms of intergroup competition are present in modern societies, its roots can be found in archaic human communities and nonhuman species. In nonhumans, individuals often form coalitions, both altruistic, e.g., in the form of protecting a related one against the third party, and more opportunistic, in the form of joining a stronger rival. However, competition between large groups is relatively rare in animals (Van Hoof 1990; Willems and van Schaik 2015). The most common types of between-group conflict are the competition of groups over territory, food, or access to mates. Same-specie groups may struggle for the territory when the population density increases but typically tend simply to avoid direct contact. The most shining examples of intergroup competition in nonhumans take place among the simplest species of social insects, on one hand, and the most developed species of mammals, namely, primates (Van Hoof 1990; Wilson and Wrangham 2003). Competition among males over territory, food, and females was found to be a form of social behavior in chimpanzees, thus indicating the possible roots of intergroup aggression in human societies (Wilson and Wrangham 2003).

In early humans the same types of intergroup competition became more common than in non-human species. Primitive wars, an extreme form of intergroup competition, are characterized by the great diversity. Some intergroup conflicts are

very similar to those of other species and can be directly related to increasing access to basic resources. At the same time, intergroup conflicts often take the form of “pure aggression,” in which no territory or other resources are conquered (Van Hoof 1990). Wars among primitive tribes can be rationalized by their members as having mystic- or “pride”-related motives. The diversity of forms and overt motives underlying intergroup wars, which are often very costly, leads to the hypothesis that humans developed specific psychological mechanisms supporting group-based forms of competition.

Between-Group Competition and Within-Group Cooperation

The distinctive feature of human intergroup competition is that it is possible only if the members of a group cooperate with each other. In other words, within-group cooperation is a necessary prerequisite for between-group competition. Moreover, human cooperation goes far beyond cooperation between closely related individuals typical in non-humans and explained by kin selection mechanisms. The exceptional ability of humans to cooperate with unrelated others is defined as their “ultra-sociality,” which is supported by psychological rather than genetic factors (Tomasello 2014).

These two distinctive features of human social life, prevalence of intergroup competition and exceptional intragroup cooperation, can be closely related to each other. More specifically, intergroup competition and conflict have been proposed to play the key role in promoting human cooperation within groups. A number of psychological experiments supported this view and described mechanisms preventing group members from violation of group norms and egoistic behavior. For example, a study by Burton-Chellaw et al. (2010) showed that introducing intergroup competition context increased within-group financial contributions. Individuals in these situations are more inclined to perceive other group members as cooperators rather than

competitors. This pattern of behavior is regulated by specific emotional reactions. Participants of an experiment felt more guilty when their contribution to the group was less than that of other group members and, on the other hand, felt more angry when their contribution was larger than that of others. Similar results were obtained in other psychological experiments (e.g., Puurtinen and Mappes 2009). These results support the view that when a higher-level competition between groups is introduced, it reduces costs associated with cooperative behavior and makes it more probable.

A more specific evolutionary explanation of relations between intragroup cooperation and intergroup competition was proposed within the so called Male-Warrior Hypothesis (Van Vugt et al. 2007). According to it, males and females evolutionary developed different psychological mechanisms supporting within- and between-group behavior. Males developed the ability to cooperate and coordinate their behavior to jointly increase their access to reproductive resources, i.e., females from a different group. Although engaging in overt conflict with an out-group is risky, for a group, male deaths are less important than female deaths, whereas access to additional reproductive resources is a valuable benefit. Male-warrior hypothesis is confirmed by numerous facts indicating that intergroup conflicts are mainly driven by males' behavior and that males are the primary targets of such conflicts (McDonald et al. 2012). The selection mechanisms underlying gender differences in intergroup behavior are supposed to produce different patterns of behavior between males and females and psychological reactions. For example, in response to out-group males, men are more suspicious, aggressive, and xenophobic and tend to strive for group-based social hierarchies, whereas women's reactions are more guided by fear and avoidance behavior resulting from the risk of sexual coercion (McDonald et al. 2012). Moreover, according to the theory, men should build stronger ties with in-group members than women.

The two approaches, described above, both stress the close link between intergroup

competition and intragroup cooperation although they differ in generality and supposed mechanisms. However, the first one is not limited by overt conflict relations between groups and more clearly states that the evolution supported a general psychological mechanisms for group-based cooperation and competition rather than more specific ones supposed by male warrior hypothesis. At the same time, the latter, stressing important gender differences in group-based behavior, doesn't necessarily mean that all intergroup competition should be considered as a war for reproductive resources available for a group. Rather, it stresses that this type of conflict was evolutionary crucial for the development of psychological mechanisms initiating and maintaining intergroup conflict.

Competition Between Which Groups?

Evolutionary explanation of group-based behavior is mainly driven by the kin selection theory. Concerning the problem of intergroup competition, it states that individuals may use the support of a group to increase their fitness and reproductive success. Even if an individual takes a risk of death during the intergroup conflict, the success of a whole group in obtaining additional resources will increase the probability of disseminating genes shared with close relatives. This theory however faces difficulties when cooperation between unrelated others are under considerations.

Indeed, in modern societies intergroup competition is very diverse and covers relations between small and large groups not related to kinship. Competition is common between nations, firms, sport teams, and research labs or even between arbitrary groups defined by very superficial and contextual features. Moreover, even in archaic societies kinship organizations could be very complex and provide opportunities to various patterns of group relations (Mead 1937). Competition and conflict between relatives are also a potential problem for kin selection theory (West et al. 2002).

The easiness, with which intergroup-competing emotions and behaviors can be induced in humans, indicates that the underlying

psychological mechanisms are very general and universal. The social identity theory argues that the mere social categorization, i.e., the distinction between in-group and out-group, is sufficient to trigger intergroup competition whatever the rationale for group boundaries is (Tajfel and Turner 1979). From the point of view of evolutionary psychology, the easiness and universality of intergroup-competing intentions and behaviors mean that the evolution of human sociality favored psychological mechanisms supporting general ability to cooperate with unrelated others rather than groups based on close kin relations. This view corresponds more to the group selection theory (Wilson 2006) and the theory of social cognition (Kinzler and Spelke 2007) stressing that humans developed specific abilities to form and recognize variety of group membership and intergroup relations.

Conclusion

Competitive behavior is common in nature and is directly explained by the key evolutionary mechanisms. A more specific form of competition is competition between groups, which is a distinctive feature of human societies. Even more importantly, intergroup competition in humans extends far beyond competition between close relatives and is supported by universal psychological mechanisms, which make it easy to trigger perception of social relations in terms of group membership and group-based competition. The basic explanation of such an evolutionary solution is that introducing intergroup competition context stimulates cooperation within a group, which is crucial for human sociality. Yet there are facts supporting the view that there are important gender differences in intergroup perceptions, emotions, and behaviors resulting from the different selection pressures in the past.

Cross-References

- ▶ [Cooperation](#)
- ▶ [Human Groups](#)

- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Reciprocal Altruism and Group Living](#)
- ▶ [Resource Competition](#)

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Competition for Mates or Resources Required to Mate

- ▶ [Sexual Behavior](#)

Competition for Parental Investment

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Synonyms

[Brother](#); [Sibling](#); [Sibling spacing](#); [Sister](#)

Definition

Parental investments are resources that a parent directs to the benefit of any single offspring at the cost of directing resources to other fitness-enhancing targets. Siblings, who share the same parents, represent competition for parental investment. Because an individual is always more related to herself than to her sibling, she will try to extract parental investment to herself at the cost of siblings. Competition for parental investments is a source of sibling rivalry.

Introduction

Through mutual parents, siblings share genes and parental resources. Humans have an exceptionally slow maturation process, and children are dependent on others long after weaning. In addition, humans have exceptionally short average birth intervals compared to our nearest relatives, great apes, resulting in multiple dependent offspring to be taken care of simultaneously. Hence, even though shared genes are likely to promote cooperation and altruism between siblings (see Hamilton 1964), siblings represent competition for

resources that are vital for survival and successful development.

Parental Investment and Parent–Offspring Conflict

Parental investment is defined as any parental actions or resources invested on the benefit of one child at the cost of investing in other fitness-enhancing actions (Trivers 1972). Parental investment is a limited resource, and additional offspring reduces investment in any single child. Parents are expected to always invest maximally, but from the offspring's point of view, any parental investment directed to siblings (50% relatedness) against investment in oneself (100% relatedness) is unbeneficial. Therefore, parents and offspring are in conflict on how much the offspring wants to extract parental investment and how much the parent is able or willing to invest (Trivers 1974). Siblings represent competition for parental investment. In addition, a parent may choose to invest disproportionately in offspring with greater perceived reproductive value (Jeon 2008), further intensifying the competition between siblings.

Birth Intervals as Components of Sibling Rivalry

Compared to great apes of similar body size than humans, humans have exceptionally short average birth intervals (Galdikas and Wood 1990). Short birth intervals combined with an exceptionally long maturation process result in having to take care of multiple dependent offspring simultaneously. Birth intervals affect the competition for parental investment and alloparental care (care provided by other people than the mother) between siblings to a great extent. In hunter-gatherer societies, birth intervals that fall short of 3–4 years, considered to be the species-typical interval for humans, are associated with increased mortality of both children defining the

short interval (e.g., Blurton Jones 1987). Short intervals supposedly hinder the mother to recover from previous pregnancy, leading, for example, to increased risks of prematurity and reduced fetal growth even in affluent industrialized societies (Conde-Agudelo et al. 2006). Short intervals also dilute care during the early years of intense needs of infants, affecting both the child born prior to and the child born after a short interval.

Especially in nutritionally challenged environments, lactational amenorrhea usually prevents a new pregnancy from beginning too early from a maternal perspective. However, from the previous child's perspective, an even longer birth interval than would be beneficial for the mother, is preferred. Infant's night waking, and continued nighttime breastfeeding, may be a sibling competition mechanism that increases birth intervals in the benefit of the infant (Haig 2014).

Indeed, shorter birth intervals seem to intensify sibling competition. Shorter intervals are associated with more affect-intense and conflict-burdened sibling relationships: siblings closer in age fight more (e.g., Minnett et al. 1983). Children of similar age have more similar needs and compete for parental (and possibly allomaternal) investment more than siblings who are of different ages. In addition, the number of siblings in general is inversely associated with individual's cognitive skills, academic performance, and adulthood income in postindustrialized societies (Steelman et al. 2002), and in high-fertility high-mortality societies, with child survival (Lawson et al. 2012). These negative effects of siblings on child development, however, are less pronounced with longer birth intervals.

Conclusions

Sibling rivalry is one consequence of competition for parental investments. Competition is intensified with more siblings and especially with closely spaced siblings. Individuals born prior to or after a shorter birth interval show signs of reduced

fitness, such as increased mortality or poorer reproductive quality.

Cross-References

- ▶ [C < Rb](#)
- ▶ [Parental Investment](#)
- ▶ [Parent-Offspring Conflict](#)
- ▶ [Reproductive Value](#)
- ▶ [Sibling Conflict](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)
- ▶ [Sibships](#)

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Competition for Resources Desired by Females

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Synonyms

[Female intra-sexual competition for resources and mates](#); [Male-male competition for resources](#); [Resource-defense polygyny](#)

Definition

Intra-sexual competition (in both females and males) for access to the resources necessary for female reproduction and parental investment.

Introduction

In the context of sexual selection, females compete more intensely for resources and males compete more intensely for mates. Females can compete with each other for access to resources and/or express biased selection for males that control resources. On the other hand, males can compete for mates by controlling the resources that females desire.

The nature and distribution of the desired resources can influence the institution of different mating systems (who mates with whom). In particular, males that can monopolize resources can also monopolize mates. This can establish a conflict of interest between males and females, as males benefit by having more mates and females benefit by limiting resource competitors. However, females can offset the costs of resource competition by investing in the quality of their offspring and their subsequent inclusive fitness. Thus, female competition for resources is best understood with a multigenerational framework.

Females Compete with Each Other over Resources

Female mammals need resources like food, shelter, and protection to reproduce. Competition for these resources is a significant selection pressure, and females possess a variety of adaptations to secure their needs. Behavioral strategies range from low to high levels of aggression but tend to be more indirect and lower risk than males. This is because mothers must survive to produce offspring and provide maternal care (at least for gestation and weaning). Females thus have plastic competitive strategies that vary with demographic and ecological factors (e.g., population density, socioeconomic conditions, group membership). Strategies can be highly aggressive when resources are especially valuable and during territory defense. But otherwise females (especially those in stable social groups) use dominance, threats, and coalitions to secure resources for themselves and their offspring (Fisher 2013; Liesen 2013; Stockley and Campbell 2013).

Competition among social females may also be balanced by the interdependent nature of their relationships. Females must compete among each other for resources and mates, but successful reproduction also involves their mutual cooperation. Thus, females may need to contend with a trade-off between fostering cooperative interactions while also competing over limited resources (Fisher and Moule 2013).

Females can indirectly compete over resources by mating with the males that control them. If males provide differential access to resources, care, and protection, then females can compete with each other over quality males – just as males conventionally compete with each other over females (Clutton-Brock 2009; Stockley and Bro-Jørgensen 2011; Stockley and Campbell 2013).

When females are allowed free choice in their mates, they act to maximize genetic quality and the quality of held resources. If males provide no resource value, females can select males with better quality genes, and better quality males accumulate more females. If males control

resources but there is no variation in value, then females can compete for the best genes but distribute monogamously for resources. However, if males vary in resource value, then females also shop for resource quality.

Males with many resources can support multiple females, and females may share their mates. But resource access decreases with additional female competitors. Thus, female selection may take place in relation to a “polygyny threshold”: the level of resources at which it is better to accept polygyny with a rich male over monogamy with a poor male. Even under polygyny, it is in the female interest to limit the number of other females that have access to a male’s resources and compete with those that do (Emlen and Oring 1977).

Males Compete with Each Other for Control over the Resources Females Want

Reproduction is cheaper for males and is limited primarily by access to mates. It is in the male’s interest to have multiple mates, and males can improve their reproductive success by controlling access to the resources that benefit females. Ideally, the more a male can monopolize access to resources, the more they can monopolize mating opportunities. This can lead to intense direct competition over resource control and the evolution of polygynous mating systems (one male mates with multiple females).

Gaining access to mates through resources is contingent on the defensibility of the resources. That is, the benefits of monopolizing resources must exceed the costs of defending them. The spatial and temporal distribution of resources is an important influence on resource defensibility. Resources are difficult to defend when they are evenly distributed or ephemeral. But the more resources are clumped in space and/or time, the greater their potential to be the subject of intra-male competition (Emlen and Oring 1977).

Males can gain status as an outcome of intra-sexual competition, providing them with priority access to resources. This can make high-status males more valuable to females. But status can

also limit female choice when high-status males have priority access to fertile females.

Males that are less directly competitive can gain access to females using mating strategies that don't involve resource control, such as sneaking. Females can benefit from mating with such males through indirect benefits, like increasing the genetic quality or variance of their offspring (Reichard et al. 2007).

The Institution of Resource-Defense Polygyny

A mating system describes who mates with whom. They develop as females and males act to maximize their fitness interests over resources and mates in a given context. Humans inhabit a wide variety of environments and express a diversity of social systems. Accordingly, humans display a variety of mating systems – from monogamy (one male/one female) to promiscuity (many males/many females).

Monogamy is believed to be the ancestral state due to the costs and benefits of foraging for resources. Provisioning offspring through foraging requires parents to cooperate (i.e., hunting and gathering), and resources are seldom economically defensible. However, farms and livestock are economically defensible resources that intensify male-male competition for their control. Males can also produce these resources with less dependence on cooperation from females. This coerces females into dependency on males for resource access. Males with more resources can accumulate multiple mates under these ecological conditions, which can ecologically or socially institute resource-defense polygyny (one male/many females). Other factors, including cultural norms (e.g., rules against polygamy) and the operational sex ratio (sexually active males/fertile females), also shape the resultant mating institution (Hartung et al. 1982; Kaplan et al. 2009).

Females in Polygynous Bonds Can Compete with Each Other

It is the male's interest to accumulate multiple mates because this increases his reproductive

success. However, it is in the female interest to limit resource competitors because this allows her to invest more in her offspring's quality. Females can achieve these fitness aims by selecting males that have fewer partners and influencing the selection of future partners. Females can also benefit by cooperating with a mate's other partners in childcare and resource exploitation, but only if this increases the gains of resource production (e.g., shared labor duties). Females can also form dominance hierarchies and benefit from the presence of subordinates (Mulder 1992).

Mother's Use Resources to Improve Their Children's Reproductive Success

Within a mating system based on resource control, wealthy males can improve reproductive success by having many mates and hence many children. However, female reproductive rate is limited by time and not the number of mates. Thus, females improve their own (inclusive) reproductive success by investing in the quality and reproductive success of their descendants. In this sense, female strategies to compete for resources often play out over multiple generations. The result is that competition between females over resources can more closely resemble a conflict of family lineages, as opposed to the individualistic and overt conflicts between males over mates (Stockley and Bro-Jørgensen 2011).

Reproductive success in males rich with resources can be many times greater than males with meager resources. Female reproductive success, by contrast, is less variable (even the most reproductive mother is limited by gestation time). However, female inclusive fitness may become more variable with successive generations. This is because mothers with very successful sons can achieve greater reproductive success than mothers with unmated sons. Thus, it is in the female interest to improve the reproductive quality of her sons with maternal investments and resource inheritance. Mothers can also reduce the competitive burdens on their polygynous

daughters by providing them with resources. Finally, females can inhibit the reproduction of other females, so as to ensure better resource access for their own children (Hartung et al. 1982; Mulder 1992; Stockley and Bro-Jørgensen 2011).

Conclusion

Females use aggression, social positioning, and reproductive inhibition to secure resources for themselves and their descendants. Males can gain access to fertile females by monopolizing these resources, thereby instituting female selection (and competition) for males based on both genetic and resource quality. However, the form and consequences of competition depend on the defensibility of the desired resources. Resources are easier to secure and defend when they are clumped in space and/or time, and this allows males to monopolize mates by monopolizing resources.

Ancestral humans relied on indefensible foraged resources and mostly had socially monogamous mating systems. However, crops and livestock are defendable resources that can lead to the evolution of “resource-defense polygyny.” In these systems, males with more resources can accumulate more mates, but females maintain an interest to reduce competition from other females.

Regardless of the mating system, females act to improve their inclusive fitness by using resources to improve their descendants’ reproductive quality. This multigenerational competition of lineages can be expressed in maternal resource investments, inheritance patterns, and inhibitions on the reproduction of others. When male reproductive success depends on resource quality, females can improve their inclusive fitness by investing in the resource quality of their sons. Similarly, mothers can provide resources to their daughters to reduce their competitive strain.

- [Intrasexual Male Competition](#)
- [Male–Male Strategies](#)
- [Sexual Selection via Direct Male–Male Interactions](#)

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Cross-References

- [Access to Resources](#)
- [Female–Female Competition](#)

Competitive Altruism

- [Costly Signaling Theory](#)

Competitive Mating

- ▶ Primate Sperm Competition
- ▶ Sperm Competition

Competitiveness

- ▶ Derogation of Attractiveness

Competitor Derogation

- ▶ Women Use Verbal Derogation to Be Included

Complete Family Unit

- ▶ Extended Kin Role

Complete Health

- ▶ Good Health and Stable Future

Completed Suicide

- ▶ Death by Suicide

Complex Problem Solving

- ▶ Problem Solving

Complexity

- ▶ Brain Size and Intelligence
- ▶ Differentiation

Components of Humor

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Synonyms

Humor; Incongruity; Laughter; Mirth

Definition

Humor as “nonserious social incongruity” has four prominent components: a cognitive, emotional, behavioral, and social one.

Introduction

Definitions of humor have changed considerably through the ages, and more recent attempts toward defining the term encompass a multitude of perspectives and are expanding quickly. Thus, definitions of humor either cover only distinct aspects of this multifaceted phenomenon or provide a broad framework for what is called an “umbrella-term” (Ruch 1998, p. 6). The definition proposed by Martin and Ford (2018) is an example of a rather comprehensive one, capturing the processes involved in the experience of humor:

Humor is a broad, multifaceted term that represents anything that people say or do that others perceive as funny and tends to make them laugh, as well as the mental processes that go into both creating and perceiving such an amusing stimulus, and also the emotional response of mirth involved in the enjoyment of it. (Martin and Ford 2018, p. 3; emphasis in original)

There are several components in this definition, which are (a) a cognitive aspect: the mental processes accompanying both the creation and the perception of humor; (b) an affective aspect: the emotional response of enjoyment (e.g., mirth);

(c) a behavioral aspect: the reaction to humor (laughter); and (d) a social aspect: a communicator and audience (Meyer 2000), also called producer/sender and perceiver/respondent/recipient. These four components cover important perspectives on humor.

Cognitive aspect: Humorous stimuli need to be perceived and processed in order to experience humor. Surprise or “a sudden unexpected change in events” (Gervais and Wilson 2005, p. 399) is fundamental for the initiation of humor. This aspect is also mirrored in script opposition as proposed by semantic and linguistic theories, that is, two sets of conditions are compatible (with a text) but the two conditions are contradictory (Attardo and Raskin 1991). The perception of incongruity is also the basis for major theoretical and empirical research endeavors.

Emotional aspect: Enjoyment or a state of amusement is a key ingredient of humor experiences and, thus, a defining feature of humor. Something has to be perceived as funny and elicit an emotional response such as mirth.

Behavioral aspect: Laughter as the vocal and physiological expression of humor is neither necessary nor sufficient for a humorous event; nonetheless it is often used synonymously with humor. Also, the extent of this behavioral reaction differs considerably between individuals.

Social aspect: Humor is a social phenomenon occurring in social contexts, based on the evolution of social play (Gervais and Wilson 2005; Martin and Ford 2018; Martineau 1972). Closely related are the functions of humor as lubricant or abrasive (Martineau 1972). In a more differentiated notion, humor functions in communications are, paradoxically, to unify or divide (Meyer 2000).

The causes of humor are very diverse, and most of them arise spontaneously. Accordingly, humor has a multitude of forms, with four broad categories introduced by Martin and Ford (2018) as the so-called performance humor, referring to the production of humor (e.g., sit-coms); jokes (e.g., riddles); spontaneous conversational humor (e.g., irony, teasing); and unintentional humor (e.g., physical or linguistic “accidents”). Also, functions of humor vary. Besides social-

psychological consequences for interpersonal relationships and broader group processes, humor has adaptive cognitive and social benefits for individuals like emotion regulation or coping with stress (Martin and Ford 2018).

Overall, the contemporary definitions of humor conceptualized as state usually include a “nonserious social incongruity” (Gervais and Wilson 2005, p. 399). But there are also approaches focusing on the way people use humor in their lives (e.g., humor styles, Martin et al. 2003), or conceiving humor as a rather stable trait (e.g., sense of humor, Ruch 1998). In the following, the four components of humor will be explained in more detail.

Four Components of Humor

The cognitive-perceptual component. Most humor researchers would agree that the core of humor is the perception of an incongruity (Forabosco 1992; Gervais and Wilson 2005; Scheel and Gockel 2017). Humor refers to a thought, statement, or event that is somehow incongruous or surprising and accompanied by humor cues that signal a nonserious mindset (Mulkay 1988). The essence of the humor process is the divergence from a cognitive model of reference and resolution as cognitive mastery (Forabosco 1992). Incongruity theory is the most widely accepted philosophical theory of humor and can be traced back to Aristotle and Kant. According to incongruity theory, “amusement is the enjoyment of something which clashes with our mental patterns and expectations” (Morreall 1989, p. 1).

To illustrate incongruity, take for example this joke: “Hear about the new restaurant called Karma? There is no menu: You get what you deserve.” When reading the sentence, you as reader activate one schema (in this example, restaurant) to interpret the statement and build logic expectations. The new information (“get what you deserve”) does not confirm the expectation. Instead you need to refer to other schemata (common idioms; Indian religions) to be able to resolve the incongruity. The new interpretation

can then lead to the emotional experience of humor. The awareness of an incongruity between two schemata and the resolution of this incongruity causes one to comprehend humor.

In a humorous mode of thinking, the rules of logic do not apply anymore. A thing can refer both, to a restaurant and not to a restaurant simultaneously (Mulkay 1988). Because this joke appears in a chapter about humor and is labeled as joke, you have probably read it in a nonserious mindset, interpreted it as funny, and experienced positive emotions.

The cognitive-perceptual experience of humor is based on characteristics of the humor stimulus and on the social context in which it occurs. First, the humor stimulus leads to the perception of an incongruity. Second, the comprehension of this incongruity occurs in a nonserious mindset (Martin and Ford 2018). The perception of incongruity in a nonserious mindset seems to be typical for all forms of humor that are mentioned above: performance humor, jokes, spontaneous conversational humor, and unintentional humor (Martin and Ford 2018).

The concept of incongruity offers a valuable basis for empirical research. Martin (1998) concluded in his review that there is considerable evidence for a close relationship between the ability to create humor and creative abilities. The creation and resolution of incongruence can even be regarded as creativity.

The emotional component. Positive emotions are widely considered to be among the consequences of humor. This assumption has received ample empirical support (e.g., Abel and Maxwell 2002; Szabo 2003; Tagalidou et al. 2018). However, the specific kind of emotion that is associated with the experience of humor is difficult to identify because this emotion is closely related to the humorous “aha-moment,” that is, the cognitive component of humor, and with laughter, that is, the behavioral component of humor. Martin and Ford (2018) suggest that the distinctive emotion accompanying the experience of humor is *mirth*. It is “gladness or gaiety as shown by or accompanied with laughter” (according to the Merriam-Webster dictionary). Mirth clearly denotes an emotion that is distinct from the

cognitive and behavioral component of humor and that can vary in intensity from mild to strong. Another suggestion for the specific emotion associated with humor is *exhilaration* (Ruch 1993). This word is related to *hilarity*, which means cheerfulness.

Empirical research about the emotional component has mostly focused on positive affect in general rather than specific emotions such as mirth. Participants who watched a humorous (as compared to non-humorous) video reported higher levels in positive affect – independent of participant gender, experienced stress, and trait humor (Abel and Maxwell 2002). In another study, participants reported their well-being after exercising, watching a humorous video, and watching a documentary (Szabo 2003). Humor and exercise increased positive well-being. A similar pattern of results was found in a test of a 7-week humor training in a subclinical sample (i.e., individuals with stress-related and other burdening symptoms; Tagalidou et al. 2018). Participants reported higher levels in cheerfulness immediately after the training and at follow-up one month later.

In interpersonal humor exchanges, the positive emotion can spread from one person to another (Attardo 2019). Speakers of humorous comments usually signal their humorous intent by using behavioral clues such as smiling or laughing. Because listeners often have a tendency to unconsciously imitate the behavior of their conversation partner (Chartrand and Lakin 2013), recipients of humorous comments should also smile or laugh – independent of their humor appreciation. They should therefore experience positive emotions because one’s facial expression directly influences one’s emotional experience (facial feedback hypothesis). This spread of positive emotions from one person to another can explain why and how humor is often followed by more humor in conversations.

Functional magnetic resonance imaging (fMRI) studies have identified key factors that are involved in the cognitive and emotional components of humor. This technique measures blood flow in the brain and can therefore identify the brain areas associated with particular tasks and

situations. Study results indicate that both components are associated with the activation of different, but connected areas of the brain (Shibata et al. 2014). Reading a punch line in a humor condition of an experiment elicited greater activation in the regions associated with comprehension and with the experience of positive emotions (Shibata et al. 2014). Another fMRI study (Amir et al. 2015) showed that humorous interpretation was associated with more brain activation than non-humorous interpretation. Participants first saw ambiguous drawings and then received a suitable caption leading to either a non-humorous or a humorous interpretation. After a humorous interpretation, more brain activity in the areas of the brain associated with the connection of remote concepts and with unexpected rewards was observed. Thus, the emotional experience of humor could be the result of combining remote ideas that lead to an unexpected activation in reward areas. This process is probably mediated by neurotransmitter activity.

The behavioral component. As the vocal-behavioral component of humor, laughter is the outward manifestation of mirth. Laughter has a distinctive “sonic signature,” which is “characterized by stereotyped features of note structure, note duration, inter-note interval and a decrescendo” (Provine and Yong 1991, p. 121). This vocalization is distributed species-wide and thus easily recognized (Provine and Yong 1991).

The intensity of laughter ranges from faint smiles to outbursts of guffaws. At high intensities, the whole body may visibly be involved, as indicated by reddened skin, bodily movements like rocking the body or throwing back the head, etc. (Martin and Ford 2018).

Also, the process of laughing has distinguishable (prototypical) components: First, the mouth widens and its corners are pulled up (like when smiling) (Berlyne 1972). An “unusual respiratory pattern, accompanied by vocalization” (Berlyne 1972, p. 51) is the second component. According to Fry (1994), this “stimulatory phase” is accompanied by an increase in physiological activities like heart rate, blood pressure, blood circulation, and pulmonary ventilation. Also, “skeletal muscles are exercised; the brain experiences

electrochemical activity” (Fry 1994, p. 114), thus, alertness rises, pain perception decreases, hormone production is stimulated, and the effectiveness of circulating immune substance increases (Fry 1994). Overall, these phenomena align with the arousal theory of humor (Berlyne 1972). Two further prototypical components, according to Berlyne (1972), are an opening of the mouth, bared teeth, a grin and a snarl, followed by a generalized tremor, sometimes up to convulsion. In the refractory or relaxation phase following laughter, the psychophysiological system “rewinds”, though all its elements do not reset at the same rate (e.g., immune system is resetting somewhat slower) (Fry 1994).

Laughter depends on motivational and emotional states as well as the social context (Martin and Ford 2018). When laughter is caused by humor, it is usually associated with pleasant affective states (e.g., mirth, exhilaration). However, there is humor without laughter, and laughter without humor. “Humor can be enjoyed without laughter” (Berlyne 1972, p. 51), eliciting far more discreet reactions like smiling. Also, sometimes humor fails. Besides humor, however, there are other causes for laughter including, for example, neurological disorders (e.g., Provine 2000), laughing gas, or tickling. Also, laughter may be provoked by triumph, contempt, and relief (Berlyne 1972).

Whether laughter is genuine or a smile is “faked” is indicated by is indicated by unique facial muscular movements. The so-called Duchenne display appears when both the lip corners are pulled backwards and upwards and the cheeks are raised in a way that causes eye wrinkles (Ruch and Ekman 2001). Put more technically, the joint contraction of zygomatic major and orbicularis oculi muscles indicates an “enjoyment” smile. The Duchenne smile is difficult to fake and thus seen as a reliable indicator of humorous emotions (Hurley et al. 2011). The importance of verifying the authenticity of a smile and the accompanying emotion becomes apparent when considering the interpersonal functions of laughter as stated by evolutionary theory.

Laughter is said to have important evolutionary functions as it communicates emotions.

According to Gervais and Wilson (2005), the Duchenne laughter serves as a “medium for playful emotional contagion” (p. 396). The fact that laughing is an inherited behavior (as indicated, e.g., by the ability of children who are born deaf and blind to laugh, Gervais and Wilson 2005; Provine 2000) supports evolutionary theories of humor. Also, the so-called play-face of higher primates (i.e., relaxed open-mouth face, Gervais and Wilson 2005) may resemble the origins of human laughter and occurs in similar social contexts (e.g., play, Martin and Ford 2018). Tickling of higher primates elicits a behavior “identified as paroxysmal, primarily expiratory, breathy respiration – much like human laughter” (Fry 1994, p. 113). Not only higher primates, but also rather tiny mammals seem to enjoy tickling. Findings from neuroscience indicate that rats “laugh” (Panksepp and Burgdorf 2003), that is, produce an ultrasonic vocalization pattern (50-kHz chirps) when tickled. Believed to indicate positive affect related to joy and social play, this sound may resemble primitive human laughter.

The social component. The experience of humor is strongly influenced by its social context. As mentioned above, humor can affect the emotional experiences of both sender and receiver. The wheel model of humor (Robert and Wilbanks 2012) highlights how humor and affect can spread in groups. A so-called humor wheel starts when people use and perceive humor and experience the resulting positive affect. The expression of positive affect through verbal and nonverbal cues such as laughter can spread from person to person through imitation or emotion contagion (Chartrand and Lakin 2013). This results in all people experiencing positive emotions in that situation, and thus, humor can evolve into a cyclical process. When a speaker says something humorous, listeners regard this as funny, experience positive emotions, and display their emotions by laughing. Positive affect can then bounce back to the speaker. In this way, humorous comments are likely to lead to even more humorous comments. According to the wheel model of humor, humor events have a cumulative impact. In other words, even minor events such as one humorous

comment can have a large impact in combination with other minor events.

The broaden-and-build theory of positive emotions (Fredrickson 1998) can explain the positive social consequences of humor. It postulates that positive emotions “broaden people’s momentary thought-action repertoires and build their enduring personal resources” (Fredrickson 1998, p. 219). In other words, positive emotions that arise due to humor can change individual cognition by broadening the scope of attention, cognition, and action. More importantly in this regard, positive emotions can help to create and maintain social bonds with others as a personal resource. When people share their positive emotions in humorous exchanges by smiling and laughing, they can strengthen their social ties with others (Fredrickson 1998). Similarly, the context of social play in children and apes – demonstrated by laughter or play-face – allows for playful interactions in a safe frame (Gervais and Wilson 2005).

However, humor does not only have positive social consequences in interactions. Robinson and Smith-Lovin (2001) developed a theory of humor and status in groups that predicts, among other things, when and how humor can strengthen or undermine social bonds in a group. Humor can strengthen social bonds, when the humorous comments refer to the group as a whole or to outsiders. Likewise, humor can undermine social bonds when humorous comments refer to one’s self or to another member of the group. This theory therefore highlights the duality of humor. Humor may on the one hand be used for identification (of communicators with their audiences) or clarification (of issues or positions); on the other hand, humor can be used for differentiation (of communicators from others) or enforcement (of norms in a delicate way) (Meyer 2000). Overall, the differentiation function of humor aligns with superiority or disparagement theories of humor (LaFave et al. 1976). According to these theories, individuals experience humor when they perceive another person’s shortcomings. Humor therefore helps to establish or maintain feelings of control, which, in turn, are pleasurable.

Four processes describe why friendly humor impacts social bonds (Cooper 2008). The first

process *affect reinforcement* means that humor can increase positive mood in social interactions. As mentioned above, friendly humor and laughing together create or reinforce positive affect. Second, *perceived similarity* means that humor can lead the sender and receiver to see themselves as similar because they both find the same thing funny. Third, *self-disclosure* refers to the expression of one's own attitudes and characteristics through humor. Finally, *hierarchical salience* highlights the fact that who uses humor and who reacts to it in what manner indicate sender and receiver status in a group.

Conclusion

Humor as a “nonserious social incongruity” has four prominent components: a cognitive, emotional, behavioral, and social one. Humor refers to a thought, statement, or event that is somehow incongruous or surprising and accompanied by humor cues that signal a nonserious mindset. Positive emotions are widely considered to be among the consequences of humor. The distinctive emotion accompanying the experience of humor is *mirth*. The behavioral expression of the humor experience is laughter, which is composed of a unique pattern of vocalizations and muscle movements. The main function of humor is to communicate the emotion humor elicits (most often enjoyment) as well as emotional contagion. This is especially important as humor and laughter are inherently social phenomena. Humor can strengthen or undermine social bonds in a group. The four components of humor are closely intertwined and inevitably overlap, hence making humor a challenging, but fascinating phenomenon for research.

Cross-References

- Evolution of Humor, The
- Humor Production
- Neurology of Humor

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Composition

- Gestalt Theory

Comprehensive Sexuality Education

- Sex Education in Schools

Compulsion

- Dominance and Threat or Use of Force

Computation

- Information Processing and the Interdisciplinary Perspective

Computational Neuroscience

- Cognitive Science

Computer Metaphor

- Information Processing and the Interdisciplinary Perspective

Concealed Estrus

- Concealed Ovulation and Pregnancy

Concealed Ovulation

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Synonyms

[Cryptic ovulation](#); [Hidden ovulation](#); [Sequestered ovulation](#); [Silent ovulation](#); [Undisclosed ovulation](#)

Definition

Concealed ovulation is understood as the lack of external signs of ovulation.

Introduction

In many primate species females have visual signals of ovulation and are receptive in relatively short period within a cycle. The fact that in humans there are no such conspicuous signs of ovulation prompted many scientists to consider this trait as an important factor of the hominization process. Being under specific selection pressures, the loss of visual signs of ovulation is also supposed to be a factor that could have driven important evolutionary changes in social and reproductive structure in human phylogeny. The lack of ovulation signs is also frequently linked to the “loss of estrus,” i.e., continuous female receptivity in the whole menstrual cycle. It is often emphasized that both the concealed ovulation and the loss of estrus are uniquely human traits. When first defined, “concealed ovulation” referred mainly to the anogenital visual signs of the fertile phase. Such visible signs in the form of swelling that extends from genitals to the anal region (“sexual skin”) are very pronounced in the fertile phase of the estrus cycle in chimpanzees. The difference between humans and chimpanzee has prompted many hypotheses about possible selection pressures acting on visual ovulation advertisement. The evolutionary adaptation

of concealed ovulation has been postulated to be linked with: (1) the increase of male cooperation within a group, (2) the emergence of monogamy, (3) the increase in paternal investments, (4) the increase in female acquisition of vertebrate proteins from male hunters, (5) the inability of males to attribute paternity, reducing the risk of infanticide by nonpaternal males, (6) the chance to preserve the best mate choice (with the stress on the best genes for an offspring) by females, or (7) to avoid aggression between females. There are, however, also hypotheses according to which concealed ovulation and constant receptivity were just side effects of other morphological or physiological changes in human evolution. For instance, bipedalism could have constituted a strong selection pressure against perineal swelling because the swelling might have disturbed bipedal locomotion. The other physiological hypothesis is that visually concealed ovulation was the consequence of the selection pressure for increased subcutaneous fat-tissue storage in the gluteofemoral region in females (Pawłowski 1999). This means that, according to different scenarios, it could have been either natural or sexual selection that was involved in the loss of visual signs of ovulation. There are, however, still many controversies over the meaning of changes in the level of ovulation disclosure and adaptation of these changes in human evolution (e.g., Haselton and Gildersleeve 2011, 2016; Havlicek et al. 2015).

Controversies on the Changes in Ovulation Signaling in Human Evolution

The chimpanzee and bonobo are our most closely related living species and therefore they are typically used as a model for a putative human ancestor. Since both these species have pronounced swelling of the perineum (“sexual skin”) that signals ovulation, it is assumed that our common ancestor also had the same trait. It is, however, possible that the common ancestor of chimpanzees and humans did not have very conspicuous ovulation. The pronounced “sexual skin” in hominoids might only have emerged a few million years ago, in the common ancestor of chimpanzee

and bonobo. There is no sexual swelling in orangutans and gorillas. The presupposition that human ancestors had at least small sexual swellings and have lost them over the course of evolution seems, however, to have also scientific support. First, it is the cladistic analysis of this feature in primates (Sillén-Tullberg and Möller 1993). A fully developed anogenital swelling is present not only in chimpanzees but also in many species of Cercopithecoidea and in small size in gibbons. Furthermore, its vestiges are also found in the pudendal lip swelling during ovulation in the gorilla and in pregnancy in the orangutan. The periodic estrogen-dependent peripelvic hyperemia (increase in blood flow) that occurs in humans might also be considered a vestige of swelling. The second argument can be long human penis. Penis lengthening took place mainly in primates that have anogenital swelling (e.g., chimpanzee, stump-tailed macaque, mandrill, yellow baboon). The swelling increases the depth of the vagina, and therefore an effective penetration requires a longer penis. In the case of hominines, however, this trait might have been also affected by bipedalism, resulting in the abdominal relocation of the female genitals.

The disappearance of human anogenital swelling is usually explained by sexual selection associated with monogamy and increased paternal investment. The majority of monogamous primates do not have conspicuous visual signs of ovulation. It is hypothesized that males, when they cannot easily determine the fertility of females, are prone to prolong mate-guarding and, thereby, increase the certainty of paternity. There are, however, a few nonhuman primates that have no swelling and live in nonmonogamous systems. The erect posture of hominines also influenced the position of the external female genitals and therefore made anogenital swelling a less visible signal. More importantly, swelling might have disturbed bipedal locomotion. Therefore, the pressure for efficient biomechanics could have constituted strong natural selection against sexual swelling.

Another controversial issue is the uniqueness of losing visual ovulation signals in the human lineage. A number of nonhuman primates lack

any visual signals of ovulation. Phylogenetic analyses indicate that sexual swelling has been independently lost more than once, and those losses did not coincide with a loss of sexual (behavioral) estrus. The fact that females of some species copulate outside their fertile period challenges the notion of the uniqueness of human constant receptivity.

If ovulation would be completely concealed, i.e., with not the slightest cues (morphological, olfactory, or behavioral) of the steroid hormonal fluctuation within the menstrual cycle (MC), sexual intercourse would be almost equally distributed across the cycle (barring during menstruation in particular cultural contexts). This does not seem to be the case even in hygienic, modern Euro-American populations.

A number of studies have shown various subtle changes in a woman's morphology (body and face), smell, and voice across the MC. The question is if they are just by-products of some physiological mechanisms or promoted by selection adaptation for signaling fertility state. It seems that in comparison to very subtle morphological changes, the most pronounced within MC and influencing a partner's sexual drive are olfactory cues. It has been shown that in the fertile phase a woman's scent is more attractive for men (Havlíček et al. 2006; Kuukasjärvi et al. 2004). This indicates that men are able to use olfactory cues to distinguish between ovulating and non-ovulating women and that steroid hormones influence these olfactory cues (no effect for contraceptive pill users has been found). There are also other potential cues of fertility that are perceivable; for example, changes in a woman's voice in the cycle. If the cues of fertility in the cycle are detectable, one should expect sexual behavior fluctuations within a cycle. Studies indicate that in the follicular and ovulation phase of the MC, women tend to masturbate more frequently, more often solicit sexual encounters (hetero and homo), and have more sexual thoughts and fantasies. In these phases, women also use more intensive makeup and dress more provocatively. The fact that they are perceived as more attractive in the fertile phase is also supported by the increase of male-initiated

heterosexual encounters and by the increased tips received by lap dancers in this phase (Miller et al. 2007). However, the results on the frequency of sexual intercourse across the MC are not conclusive. Some studies report that except menstruation phase it is relatively constant and others report that it is uneven (with an increase in the fertile phase). The first, methodological problem is that the results on sexual activity are different when data are collected soon after the events and when they are more distantly retrospective. The other problem is that majority of these studies were conducted in western societies, and inferring evolutionary explanations on the basis of such data is very controversial. This is because sexual signaling and behavior may be influenced by numerous environmental and cultural factors. Human traits evolved in completely different conditions than contemporary ones. Our ancestors did not use clothes and had a lower hygiene level. Furthermore, in warmer climatic conditions (as in Africa, where *Homo* evolved), semiochemical signaling was also stronger.

There are numerous controversies over the potential evolutionary meaning of such subtle and not easily detectable cues. In comparison with nonhuman primates, all mentioned changes within MC related to attractiveness and fertility should not be considered as evolved specifically to “signal” ovulation in humans. According to some (e.g., Thornhill and Gangestad 2008), the subtle cues of peak fertility in humans have not evolved for the purpose of signaling fertility. These cues are just inevitable side effects of estrogen level increase during the follicular and ovulation phases (“leaky cues hypothesis”). They claim that a completely hidden peak of fertility would be most adaptive for women, but the physiological costs of eliminating even the slightest morphological, olfactory, or behavioral cues due to sex hormones fluctuations would be very costly. Although we have abundant evidence indicating that fluctuations of the steroid hormone levels across the MC are related to perceivable cues of fertility, the question remains as to whether

evolutionary pressures promoted maintaining these hormone-related fertility cues or whether for some reasons removing these cues was impossible.

There is also other explanation for why men are able to perceive the shifts in women’s attractiveness and possibly detect their “current” fertility across MC. Since the difference in fertility and estrogens level is quite big between women, men could be rather adapted to discriminate the cues informing about this between-individual variance in sex steroid (reproductive related) hormones. Selection could have acted rather on detecting potential (overall) than on “current” fertility. This is “perceptual spandrel hypothesis” in which men’s benefit gains would be related to the discrimination of fertility between women, and the MC shifts would be just a by-product of men’s general preference for the cues of high estrogens level between women (Havlicek et al. 2015).

Conclusion

The ovulation concealment problem and the potential adaptiveness of the different cues shift across MC are still debatable. We do not even know if the ovulation was visually disclosed in our common ancestor with chimpanzees and therefore, if in our evolution there was strong selection against signaling ovulation. The evidences show that ovulation is not completely concealed (e.g., olfactory cues) in human, but what were evolutionary causes for only very subtle fertility level disclosure within MC is controversial and remain a challenge for the future studies.

Cross-References

- ▶ [Male Counter Strategies to Cyclic Shifts](#)
- ▶ [Ovulation](#)
- ▶ [Sexual Signaling During Ovulation](#)
- ▶ [Women’s Preferences During Ovulation](#)

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Concealed Ovulation and Multi-male Groups

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Definition

Concealed ovulation refers to the loss of ovulatory signals (visual, behavioral, pheromonal) in a species. Research suggests the loss of ovulatory signals occurs most often in multi-male mating

systems and may help maintain monogamous mating systems.

Introduction

Female mammals and other species are normally sexually receptive for only a circumscribed period around the time of ovulation, and both the ovulatory and receptivity period are advertised to males by distinct visual, behavioral, or pheromonal signals (Andelman 1987). Most species possess slight or overt ovulation, showing vulval swelling or reddening, while others have marked sexual swellings including perineal skin (Sillén-Tullberg and Moller 1993). The contrasting pattern of dampened or concealed ovulatory signals accompanied by sexual receptivity outside of the ovulatory period is frequently referred to as concealed ovulation. This is less common and understood (Andelman 1987).

Concealed ovulation does occur within species across the animal kingdom, although overt ovulation is much more prevalent. Typically, the female gives clear signs by pheromonal, morphological, or behavioral signals when she is ovulating and males focus their copulations on that period (Miller 1996). There is some amount of consensus in the literature that mating system and signs of ovulation are strongly correlated, if not involved in a causal relationship (Alexander and Noonan 1979; Hrdy 1979; Burley 1979; Daniels 1983; Turke 1984; Andelman 1987; Steklis and Whiteman 1989). Most of these hypotheses are based on the observation that sexual swellings, the major signal of obvious ovulation, mainly occur in a multi-male breeding system (Hrdy 1981; Hamilton 1984). Sillén-Tullberg and Moller in 1993 conducted a phylogenetic analysis using two behavioral characters; the presence of ovulatory signals and type of mating system (monogamous, multi-male, or uni-male). Through parsimony analysis of characters, Sillén-Tullberg and Moller found it possible to infer ancestral states and character transformations by mapping present-day ovulatory states and mating systems.

Emergence of Concealed Ovulation

Through their analysis of extant taxa, Sillén-Tullberg and Moller (1993) found that ovulatory signs are absent in every type of mating system in the Order Primate. They found that sexual swellings have evolved independently at least three times and the absence of ovulatory signs is inferred to have evolved 8–11 times overall: one to two times in platyrrhini, one to two times in cercopithecini, twice in macaca, one to two times in the Presbytis clade, once in the Colobus clade, and twice in Hominoidea.

In cases where ovulatory signs are inferred to disappear, it occurs many times in a non-monogamous context and at most once in a monogamous one. Sillén-Tullberg and Moller (1993) concluded that in the majority of instances, maybe all, when ovulatory signs have been lost it has been in a non-monogamous context. Sillén-Tullberg and Moller go on to state that of the extant monogamous taxa, none possess sexual swellings and most have no visual ovulatory signs, which would indicate a connection between monogamy and lack of ovulatory signals. According to the authors, monogamy has evolved four to six times in the absence of, and one to three times in the presence of ovulatory signs. The absence of signs is much more tightly coupled with monogamy than with any other mating system. They conclude that the absence of ovulatory signs could be an important, though not necessary, prerequisite for the evolution of monogamy if concealed ovulation evolved first. In the analysis of mating systems, the authors stated that it is often assumed that the ancestral states in our lineages are those of the chimp (multi-male mating systems with pronounced sexual swellings), but Sillén-Tullberg and Moller's parsimony mapping indicated that a multi-male system has evolved independently in the chimpanzee lineage and that the human ancestor was most likely a harem holder.

Mating Systems

A comparison of the phylogenetic analysis of mating systems by Sillén-Tullberg and Moller with the phylogenetic analysis of sexual

promiscuity by Strassmann (1996) showed a high correlation, as would be expected, of mating system and promiscuity. The behavioral ecology literature has long established the relationship between mating systems of species and cultures and their sexual behavior (Hamilton 1984; Stribley et al. 1987; Arnold and Halliday 1992). The multi-male mating system was associated with high promiscuity, while monogamy was associated with low promiscuity. This lends support to Sillén-Tullberg and Moller's (1993) hypothesis. There are slight differences in the phylogenetic trees of the respective studies that could be accounted for by the different experiments and observations analyzed in the respective studies.

Sillén-Tullberg and Moller's analysis was unable to discern which behavior developed first, concealed ovulation or monogamous mating system. Therefore, the questions of exactly how and when these traits occurred or were maintained remain. Even with all the data on extant taxa and analysis of the emergence of concealed ovulation, the subject that pervades the literature is why this trait would emerge or become adaptive.

Adaptiveness of Concealed Ovulation

The most cited hypothesis regarding the evolution and adaptiveness of concealed ovulation was put forth by Alexander and Noonan (1979) that females concealed ovulation as a strategy to obtain male aid in childcare. A female who provided clues to her ovulation would risk losing paternal investment for two reasons. First, her mate would suspect that other males had detected her ovulation. This would lower his confidence of paternity and consequently reduce his willingness to invest in his mate's offspring. Second, a male aware of his mate's ovulation might copulate with her only during that period and spend the remainder of his time seeking to impregnate other females. If he were successful the first female would run the risk that he might invest in the other children and not in her own. Turke (1984) added an important caveat to this and similar hypotheses: "natural selection probably could

not have favored males who increased paternal care until their confidence of paternity passed some threshold. Furthermore, given even high confidence of paternity, selection is expected to have favored promiscuous tendencies over paternal tendencies as long as promiscuity afforded males a high probability of impregnating many females" (p. 38).

Benshoof and Thornhill (1979) suggested that concealment evolved as a means whereby females could escape the consequences of being paired with a less fit male in a marriage system run by males. A female who concealed her ovulation could mate with a more fit male without attracting the attention of her mate and, because she did not signal ovulation, her mate would continue to invest in her offspring, having little reason to doubt his paternity. If the female were lucky, the majority of her children would be the outcome of matings with males who were more fit than her spouse. Freeman and Wong (1995) agree with this hypothesis stating that it is advantageous for females to conceal ovulation from males as it allows them to ensure that they mate with desirable males around their fertile period and gain benefits such as permanent male protection at all times. This hypothesis assumes that the monogamous mating system emerged prior to concealed ovulation. The majority of theoretical literature supports this timeline (Daniels 1983; Freeman and Wong 1995).

Hrdy (1979, 1981) took a different approach and hypothesized that prehomonid females who concealed ovulation and mated with a large number of males confused the issue of paternity and therefore reduced the possibility that her children by one male would be killed by another. Overt ovulation would create uncertainty in the male (if he can detect ovulation so could any other male and they would mate with her as well, eliminating his paternal certainty) and would also induce him to copulate with her during her ovulation and then copulate with others. A female with overt ovulation would then only have a limited amount of time with the male and would not gain any paternal aid. This hypothesis describes a multi-male mating system which is well-documented in primate literature (Schroder

1993; Halliday and Arnold 1987; Arnold and Halliday 1992; Baker et al. 1993; Chism and Rogers 1997) and Hrdy cites several behavioral ecology studies across species, from squirrels to chickens to primates, to support her hypothesis (Hrdy 1979). This hypothesis was not as widely supported by other socio-biologists, primarily because of the unusual amount of control Hrdy theorized females to have over their environment (Bixler 1986).

These studies and hypotheses are now classic in the realm of sociobiology. There have also been recent additions to this controversial topic. Daniels (1983) theorized that concealed ovulation had its origin in strengthening intragroup bonds during an evolutionary period when only reciprocal sharing and extensive cooperation allowed survival. Like other modern hypotheses Daniels assumes that monogamy was established prior to concealed ovulation. She also stated that the survival of an individual was dependent on sharing and cooperation with others, all of which were facilitated by the emergence of intelligence. Because revealing ovulation threatened monogamy, sharing, and cooperation, survival was also threatened. Self-deception became adaptive "so that certain interests could be excluded, such as selfish propagation, while other more critical activities could be attended to such as sharing and monogamy" (Daniels 1983, p.80). This type of hypothesis, the social bonding hypothesis, states that a trait would arise to increase harmony in the group. This implies that natural selection is acting at a level higher than possible. Natural selection molds behavior for reproductive success, not for social integration (Schroder 1993).

Conclusion

Biologists and bio-psychologists have implicated mating systems, increased intelligence, resource collection, and group harmony in the emergence of concealed ovulation (Alexander and Noonan 1979; Burley 1979; Benshoof and Thornhill 1979; Daniels 1983). Some have even implicated endurance running (Spuhler 1979, cited in Gray and

Wolfe 1983; Schroder 1993). None of these theoretical arguments have brought the scientific community any closer to discovering and/or understanding when and how the salient signals of ovulation have disappeared in hominids, or if there were any signals to disappear. The most thorough and revealing research to date was one study containing a phylogenetic analysis (Sillén-Tullberg and Moller 1993). The phylogenetic analysis by Sillén-Tullberg and Moller gained a great deal of insight into primate mating strategies and sexual behavior, searching for evidence of actual mating systems instead of theoretically constructing them. In order to adequately evaluate the various speculations on the loss of estrus or the concealment of ovulation, it is first necessary to collect such data and standardize the needed procedures. Using this data more specific and thorough phylogenetic analyses, observations of homology, and quantitative genetics can be conducted. Only then will research into the origin or extinction of a given behavior yield satisfactory results.

Cross-References

- [Concealed Ovulation](#)
- [Concealed Ovulation and Pregnancy](#)

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Concealed Ovulation and Pregnancy

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Synonyms

Concealed estrus; Fertility; Menstrual cycle; Mid-cycle; Ovulation

Definition

The inability of members of a species to detect the physiological state in which the females are capable of reproduction.

Introduction

A number of different species such as chimpanzees, rats, and gorillas display behavioral, physiological, or morphological cues that signal female fertility to male members of the species. These overt expressions of fertility are a form of honest signaling, which is observed among many species. Honest signaling is when individuals display their true qualities as a mate. However, not all species signal their reproductive status to potential mates. Instead, some species conceal their fertility status. Until fairly recently, it was believed that such was the case with human females. While humans generally cannot detect ovulation on a conscious level, a number of researchers have studied the effects of ovulation on male and female behavior. The findings of these studies suggest that women do in fact have the ability to subconsciously emit ovulation cues, and that men can subconsciously detect these cues. Such cues can be observed in the scent, voice, physical features, and a change in mate preference and behavior among ovulating women. For these reasons, it is now believed that ovulation is not entirely concealed in humans.

Honest Signaling and Fertility

Ovulation refers to the time during a woman's menstrual cycle in which an egg is released and is able to be fertilized by a male's sperm to create a zygote. In non-human species, this time of fertility is known as the estrus phase of the estrous cycle. According to Domb and Pagel (2001), in many species, males are able to detect fertility in females so that they know which females to mate with and can successfully reproduce their own genes. Many females from nonhuman primate species signal their fertility status through the swelling of genital areas during the estrus phase of the estrous cycle. In such species where fertility is not concealed, intrasexual competition among males increases a female's chance of successfully mating. Some of these cues, such as those seen in wild baboons, additionally signal a female's reproductive value so that males know the amount of mating effort that they should invest in a particular female, which is dependent upon factors such as her age and reproductive viability, and is an example of honest signaling (Domb and Pagel 2001). In addition to the signals seen in morphological features such as periovulatory swellings, other species show changes in their sexual behaviors, which can be seen when an animal is in heat. The time frame in which an individual can reproduce varies on the type of species as well. For example, the estrus phase in gorillas lasts about 3 days, whereas that of chimpanzees is approximately 12 days. Ovulation in human females lasts approximately 1 day; however, sperm can survive 3–5 days inside of the female reproductive tract. Essentially, this means that there is about a 3–5 day window in which copulation may result in pregnancy in human females. Unlike a number of other species, humans engage in copulation on approximately 23 out of the average 28 day cycle as a result of males not being able to detect when females are able to conceive (Marlowe and Berbesque 2012).

Concealed Ovulation in Humans

In the past, researchers have held the belief that ovulation in humans is fully concealed or

undetectable. From an evolutionary perspective, concealing one's ovulation status can be beneficial for female members of a species for a number of reasons. From an evolutionary perspective, female signaling of menstrual periods to males would allow for an estimate of when ovulation is taking place, which decreases the chances of a man being cuckolded and ultimately raising another man's offspring. Additionally, concealed ovulation prevents any one male in a group from dominating and mating with all of the females, due to the fact that the ovulatory period is unknown (Marlowe and Berbesque 2012). Human ovulation has been seen as unique because even women are unaware of their ovulation status. Self-concealment of ovulation is believed to be selected for along with concealed ovulation from conspecifics, despite the advantages of females being aware of their ovulation status, as having more information can lead to more strategic selection of a mate. Even though women generally report not knowing when they are ovulating, some argue that ovulation can be detectable, such as feeling pain when an egg is released, having an increased sex drive, or secreting higher amounts of cervical mucus due to an increase in estrogen (Freeman and Wong 1995).

Given the imbalance of parental investment between human males and females, such that parental investment on the male part is much lower than females, concealed ovulation is believed to have evolved as a result of it being especially beneficial to females. Oftentimes, females face the dilemma of choosing between a mate that possess better genetics to pass on to an offspring and a mate that will provide more resources but lower quality genes. From a Darwinian perspective, concealed ovulation in humans is advantageous for females because it allows them to copulate with mates that have desirable characteristics and good genes during the ovulatory period, while benefiting from protection and resources provided by males at other times of their cycle (Andelman 1987). By engaging in extra-pair copulations without males being able to detect her, a female could potentially be

able to cuckold her mate, or even get resources from multiple males who believe the child might be theirs. Such behavior essentially allows a woman to get the best of both worlds; genes and resources. However, while this may be beneficial for females, it can also create an adaptive problem for males who pursue long-term mating strategies, as they could potentially be devoting their time, energy, and resources to rearing offspring that are not their own. This is why paternal assurance tactics have evolved, as discussed in the section on paternal confusion.

To further examine the hypothesis of concealed ovulation in humans, Marlowe (2004) compared the behaviors of women in modern society and women of the Hadza tribe in Africa, a group of individuals who live a hunter-gatherer lifestyle that is more natural and similar to those of our human ancestors. The findings suggested that there is in fact no major differences between concealed ovulation in women living in westernized society and those living in a pre-westernized society, and that both groups of women were generally unable to distinguish the time period in which they were ovulating. This suggests that concealed evolution is not a result of more modern times and technology, but that it rather evolved during our semi-nomadic years.

Ovulation May Not Be Entirely Concealed in Humans

While humans appear to be one of the unique species who conceals ovulation, numerous researchers have begun to question whether or not ovulation is truly concealed in humans. Recent studies have provided evidence that women actually emit subtle cues that are instinctively picked up by males. In order to study ovulation cues, researchers have looked at the differences between women who are the peak of ovulation and women who are at a different stage of their cycle. The findings of these studies have shown that women near the peak of ovulation display significant behavioral and physiological changes, in addition to changes in mate preferences. Researchers argue that for these reasons, ovulation is

not fully concealed in humans, even if these behavioral and physiological changes are occurring at a subconscious level.

Ovulating women differ in their sexual behavior and the qualities that they look for in a mate. Whereas it is normally known that females prefer resources and social status over physical attractiveness, women who are near ovulation tend to show a preference for men with more masculine facial features and men who are more competitive (Thornhill and Gangestad 2008). Women who are in a relationship additionally show a preference for other men when their partner lacks these characteristics that are associated with increased masculinity near the ovulatory phase. An evolutionary framework would attribute this preference to an unconscious drive to mate with a male who possesses the best genes for survival in one's future offspring.

Research done by Gangestad et al. (2005) and Geher and Kaufman (2013) looked at additional changes in behavior, physical characteristics, and mate preferences in women who were at the peak of ovulation by reviewing the literature at hand. According to the findings, women near the peak of ovulation are more likely to initiate sex with partners, engage in sexual infidelity, be more attracted to the scent of males who were rated as more creative and more symmetrical in physical features, engage in risk-taking behaviors, dress in clothing that is considered more revealing, and be rated by others as having greater symmetry in their own body parts, such as their faces and breasts.

While these findings make it clear that female behavior seems to change in response to the time period of one's ovulatory cycle, research has also been done to study whether or not these subtle cues are picked up by male counterparts. Thornhill et al. (2003) looked at the difference in scent between women who were ovulating and women who were not. In this study, the "stinky T-shirt" paradigm was used to see if there was a difference in the odors emitted by ovulating and nonovulating females. Both groups of women were asked to wear t-shirts to bed for a couple of nights and avoid using any chemical substances that would alter their natural scent. A group of

men were then asked to rate the attractiveness of the smells of each shirt. Overall, t-shirts that had the odor of ovulating women were rated as more attractive. Similarly, Bryant and Haselton (2009) observed the effects of ovulation on the pitch and perceived attractiveness of female voices. The findings indicated that women's voices change in a way such that they are higher in pitch once a woman is near ovulation. Raters also rated women's voices as more attractive during this high-fertility phase of the cycle. Finally, Miller et al. (2007) looked at the differences in tips earned by exotic dancers during different phases of the menstrual cycle. At the end of the study, dancers who were ovulating earned a significantly greater amount in tips than those who were not ovulating and those who were taking contraceptives. The findings supported the idea that women emit signals that they are ovulating and that perhaps more importantly men are able to detect them. Such findings additionally provide evidence to support that men are willing to give more resources to ovulating women, possibly with the underlying drive that giving a woman more resources will increase the chances of her mating with him.

Conclusion

Ovulation cues are often emitted by females in a number of species. This has been effective in signaling when a mate should copulate with a female and the individual qualities of a potential mate. Humans were believed to be a species in which ovulation was concealed, as sexual patterns generally were not believed to change during the ovulatory cycle and no physiological or behavioral cues were believed to be signaled. However, more recent research has provided evidence to support the idea that ovulation is not entirely concealed in humans as researchers have documented physiological and behavioral changes in addition to change in mate preferences in women during the time of ovulation. Men also experience behavioral changes and find certain characteristics of ovulating women to be more attractive. Why concealed ovulation was selected

for in the first place may be explained by the fact that we are not an entirely monogamous species, and an individual female would benefit from extra-pair copulations with males that can provide better genes while staying with a male that can provide for her and her offspring. Concealing ovulation was advantageous for women, yet because men faced increased chances of paternity uncertainty, it is possible that they evolved their own set of mechanisms to detect the subtle hints that females emit during ovulation.

Cross-References

- ▶ [How Evolutionary Psychology Can Still Explain Behavior](#)
- ▶ [Menstrual Cycle](#)
- ▶ [Ovulation Suppression](#)
- ▶ [Paternity Confusion](#)

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Concealing Imitation

- ▶ [Masquerade](#)

Concealment

- ▶ [Camouflage](#)

Concentration

- ▶ [Attention](#)

Concept Discrimination

- ▶ [Concept Formation](#)

Concept Formation

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Synonyms

[Analogical reasoning](#); [Categorization](#); [Concept discrimination](#); [Concept learning](#); [Entropy](#); [Relation-between-relations](#); [Relational understanding](#); [Same-different concepts](#)

Definition

The process of forming mental structures within which categorical and relational information is stored.

Introduction

Animals live in complex perceptual and, in many cases, social environments, in which they encounter information that must be processed and stored in memory for later use. That information is then organized into units in order to reduce the amount of information that has to be processed, stored, and later recalled; these units are termed “concepts” (Rosch et al. 1976). Concepts are mental representations of information formed during the process of categorization. Through experience with the world, these concepts become more complex connected within themselves and more linked between each other. The links within and between concepts allow for painting a broader picture of the perceptual and social world. As an example, it could be easily reasoned that most, if not all, animal species somehow categorize food and nonfood (i.e., what can be eaten versus what cannot be eaten). The concept formation process starts with the distinctions between those two categories; then links between foods that can be eaten become linked with concepts for where to find those foods, if those foods are mobile (e.g., can run away); and so on. There has been a substantial amount of research done on the process of concept formation in both humans and nonhuman animals (e.g., Roberts and Mazmanian 1988; Rosch et al. 1976); however, no consensus has been reached regarding the mechanisms used by nonhuman animals during the process of concept formation or whether nonhuman animals’ abilities are truly comparable to humans. The following review will discuss research on conceptual understanding in nonhuman animals, emphasizing the framework proposed by Thompson and Oden (2000).

Thompson and Oden’s (2000) Framework

In a review article, Thompson and Oden (2000) discussed evidence of conceptual understanding, specifically in nonhuman primates. The ability to form concepts is both necessary and adaptive for animals in order to assess their environments and items in their environments. The formation of

these concepts, however, varies based on the mechanisms utilized to organize them and the complexity of the relationship between category members. At the most fundamental level, concepts can be formed based on shared perceptual features. Those commonalities can be sensory or physical in nature, for example, all birds being placed into the same category due to the shared features of feathers, beaks, and wings or all bluebirds being placed in the same category because of shared coloration patterns. These shared features can also be functional in nature (e.g., tools being placed in the same category because they all function in a similar manner). Thompson and Oden (2000) suggested another mechanism by which to organize categories as the members being associated or related to one another. This association can be that the items shared time and/or space with each other at some point in the past or present (e.g., a lamp being associated with a table because it is on the table) or it could be that the items are related to each other in some meaningful way (e.g., a cell phone and its charger). However, the ability to make categorical judgments based not on shared features or associative histories but on the conceptual similarity between the items forms the foundation more sophisticated reasoning abilities, such as analogical reasoning. This judgment of the relation-between-relations is argued to be the highest order of concept formation and, according to Thompson and Oden (2000), had only been definitively demonstrated in humans and chimpanzees, specifically symbol-trained chimpanzees, up to that point.

Conceptual Understanding in Nonhuman Animals

Given the above information, what is known about conceptual understanding in nonhuman animals? Broadly speaking, the ease at which nonhuman animals form concepts depends tremendously on the complexity of the concept (e.g., more abstract or necessitating understanding of the relation-between-relations) and the nature of the task they are asked to perform. In addition, with isolated exceptions, most of what is known about concept formation in nonhuman animals is

limited to pigeons and primates. That being said, gaining a full understanding of conceptual ability in nonhuman animals is far from being reached; however, as with all science, it is a process to be refined and expanded as time moves forward.

Same-Different Concepts

There are two main tasks that are utilized by most research on concept formation in nonhuman animals: same-different judgment (SD) tasks and relational match to sample (RMTS) tasks. Other tasks have been used less frequently, such as a two-alternative, forced choice (2AFC) procedure. In most SD tasks, the animals are shown two (or more) items and are to determine if they are the same or different. In some cases, the animals are reinforced for choosing either only same or only different pairs in a go-no go-type response (e.g., only peck/touch the screen if the items shown are different). Cook et al. (1995), however, utilized an altered SD procedure where the pigeon's same or different decision was made via choosing either the food hopper trained to indicate a same choice or the one trained to indicate a different choice. Overall, this task measured animals' ability to understand same-different concepts, which, according to Thompson and Oden (2000), forms the foundation for higher-level concept formation. The ability to make this judgment would facilitate abilities such as individual recognition in social groups and conspecific versus other species identification, both being evolutionarily prudent abilities for survival. However, the ability to judge same versus different can be done almost exclusively using perceptual cues and, in some cases, memorization of test images after repeated presentations (Thompson and Oden 2000). The same argument could be made for the use of 2AFC tasks where a concept must be inferred from repetitive pairings of two images from two different categories (e.g., animals versus nonanimals) with only one of the categories being reinforced (Vonk et al. 2013).

Both pigeons and primates have demonstrated relative success in forming same-different concepts using SD tasks, particularly with visually based object concepts. Cook and colleagues (1995) utilized their modified version of the SD task to investigate pigeons' abilities to

discriminate between uniform (same) or different textured visual displays. The different displays either contained a color difference or a shape difference within the array. The uniform displays all contained the same color or shape within the array. The pigeons demonstrated acquisition of the concepts of sameness or difference as measured by not just acquisition of the original stimuli but transfer and generalization to novel arrays. This idea of demonstrating *transfer* or *generalization* is important to rule out the simple memorization of the correct images as the discriminative cue instead of the understanding of the sameness or difference (Cook et al. 1995). Similar results were demonstrated by pigeons when their ability to make same-different judgments was investigated using textural differences (as seen in Cook et al. 1995), feature differences (contained a mismatching region of features not present in the rest of the array), geometric differences (contained a different geometric shape than the rest of the array), and object differences (contained a different natural object than the rest of the array [e.g., in an array of all the same birds, one different bird would be present]) (Cook et al. 1997). Additionally, Blaisdell and Cook (2005) used a variation of the SD procedure in which both a same two-item array and a different two-item array were presented simultaneously. Some birds were reinforced for choosing the array that depicted two same items, and some birds were reinforced for choosing the array that depicted two different items. Interestingly, the birds appeared to be more sensitive to differences than sameness, but both concepts were acquired successfully (Blaisdell and Cook 2005).

What may be of importance to note for these studies, as will also be seen in the vast majority of concept formation studies with nonhuman animals, is the large number of trials and sessions it takes the animals to reach criterion for acquisition of the concepts. Each session in Cook and colleagues' (1995) study consisted of 60 uniform and 60 different arrays. The birds, on average, took 22.25 sessions to reach criterion on the fastest acquisition phase of the experiment. Yes, the birds *could* form these concepts, but was it something done with *ease*? It would appear that while this task accurately measures their ability to learn

same-different concepts, it may not be measuring the same-different concepts that might be more ecologically and evolutionarily salient to the animals. In addition, the concept of *entropy* also may play an important role in *how* the birds acquired the concepts. Young and Wasserman (1997) described entropy as the level of variability within categories, where categories with no differences within category members have no entropy and categories where there is a greater amount of differences within categories have higher entropy. In most different arrays, there is a higher degree of entropy present than in the same/uniform arrays. Pigeons appear to be sensitive to this level of entropy when the arrays contain more images per array (e.g., 16 images per array). Both Cook and colleagues (1995) and Cook et al. (1997) utilized large arrays, making the different arrays contain more variability than the same arrays. In comparison, Blaisdell and Cook (2005) used two-image arrays, lowering the entropy within the images, but increasing the *perceptual* differences within the arrays, making the difference within the array more visually salient despite the low level of entropy present in the different arrays.

Evidence from nonhuman primates has also demonstrated mixed results in terms of rate of acquisition and impact of entropy on their performance in SD discriminations. Shields et al. (1997) utilized a slightly modified version of the SD task to compare human performance to that of rhesus macaques. The task paired two arrays of dots against each other with varying degrees of density of the dots in each array. In same trials, the dot arrays were of equal density. In different arrays,

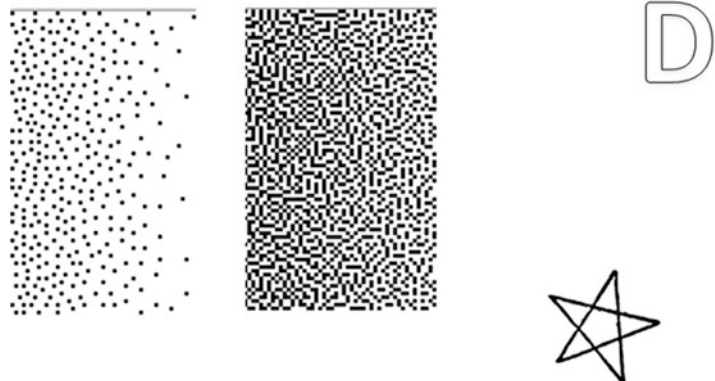
the dot arrays varied in density. In addition, the different arrays varied in degree of density difference as well, making some judgments of difference easier to make than others. The humans and monkeys then had to determine if the two dot arrays were the same or different by either moving the cursor (via a joystick) to the images if the two arrays were the same or to the letter D also displayed on the screen if the two arrays were judged as different. Of much interest is that they also allowed the participants to make a third choice, the choice of uncertainty, meaning that they could not tell if the arrays were the same or different. See Fig. 1 for an example of the trial structure for a different trial.

Both humans and monkeys were determined to be able to judge obvious same and obvious different arrays. In addition, both the monkeys and the humans used the uncertainty response only when they appeared to be actually uncertain about the same-different status. As the discriminations became harder to judge, the amount of uncertain responses tended to increase for both humans and monkeys. Entropy, in this case, would be hard to determine as both arrays contained the same image type (dots), just in different densities, but the results do provide evidence that when the same-different judgment is more explicit, monkeys can form those concepts and make the correct decisions (Shield et al. 1997).

Similar results were found when, again, comparing SD judgments in humans and rhesus macaques using single-item comparisons of polygons (Smith et al. 2008). Original prototype polygons were created via a computer program, and then they were distorted to varying degrees from

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Fig. 1 Example of a different trial configuration for Shield et al. (1997)



the original. In the same trials, the two polygons were identical (regardless of level of distortion); in different trials, the two polygons differed in the degree of distortion between the polygons (slight, moderate, or large disparities between shapes). In this study, the role of entropy appeared to be more clearly evident in human performance, with human judgments of difference showing a steeper increase as the level of entropy increased. The monkeys showed a more gradual increase in judgments of difference as entropy increased (Smith et al. 2008). Overall, these judgments, in addition to those discussed previously with both pigeons and monkeys, generally strengthen Thompson and Oden's (2000) claim that these same-different concepts are rooted in perceptual cues less than conceptual abilities.

Understanding the Relation-Between-Relations

In order to more fully understand the complexity of conceptual abilities in nonhuman animals, researchers began to test their abilities to understand the relation-between-relations, which form the basis for analogical reasoning. It has only been relatively recently that experimenters have attempted to study this ability in nonhuman animals. Premack (1983) suggested that without language (or some other symbol-based communication system) to guide concept formation, animals would be restricted to judgments of same-different relationships. Making judgments of the relation-between-relations would be restricted to humans and apes, specifically symbol-trained apes (in very specific terms, Premack's symbol-trained chimpanzee, Sarah). It should be noted, however, that what is considered a symbol system is not strictly defined. It could be argued that token economy system, where the animal is trained to give the researcher something (e.g., a rock) before it is given something else (e.g., food), is enough of a symbol system to facilitate success in RMTS tasks (Addessi et al. 2007). This "ape-only" assertion was upheld by failed attempts to demonstrate comprehension of RMTS tasks in monkeys (Washburn et al. 1997 as reported in Thompson and Oden 2000). RMTS tasks are a more difficult version of SD

judgment tasks in that they require the subject to make a same or different judgment based on *why* the two images are the same or different from each other, not just if they are perceptually similar/dissimilar. Typically, a sample image is shown first, and then two comparison images are presented, either with the sample image still present (simultaneous presentation) or without the sample images still present (delayed presentation) to add a level of complexity. The task requires the animal to then choose the array that is either the same as or different from the sample array, depending on which concept is being measured. As an example, two arrays could be judged as the same because they both contain a variety of different images *within* each array instead of having the same image within the array. In this way, the two arrays are the same because they both contain various images within the array, not because they are perceptually similar. One must infer, or abstract, the relationship between the two arrays in order to determine if they are the same or different; in other words, they must be able to tell *why* the arrays are the same or different to be successful in matching to the sample (Thompson and Oden 2000).

Supporting the idea that apes are capable of judging higher-order relation-between-relations, Vonk (2003) tested orangutans (*Pongo abelii*) and gorillas (*Gorilla gorilla gorilla*) on their abilities to judge what was termed *second-order relations*. The animals were given two-item arrays in an RMTS task where they first had to demonstrate first-order relations, matching individual items based on identity (same shape and same color), shape (same shape only), and color (same color only). Both species performed at levels significantly above chance and acquired these concepts after relatively little exposure, some in as little as one session (12 trials), which is in sharp contrast to the hundreds and thousands of trials necessary for pigeons, for instance. Interestingly, only the identity matching trials could be done purely based on perceptual cues alone as in both the shape and color matching trials, the animals would have to make same judgments based on a more conceptual-type rule (e.g., same shape despite

being a different color or same color despite being a different shape) (Vonk 2003).

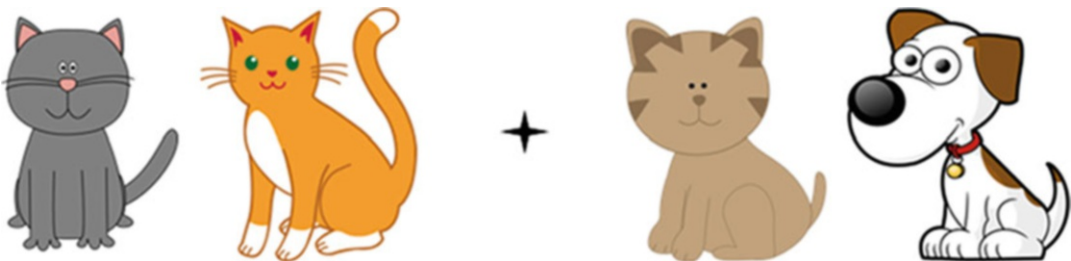
After successful completion of the first-order relation trials, the animals moved on to the second-order relation trials where they were of the same shape or the same color *between* arrays. For instance, the sample could be one blue circle and one yellow circle. The first comparison array could contain one blue triangle and one blue circle, while the other contained a red triangle and a green triangle. The latter choice would be considered the same choice as it contains the same shapes *within* the array as the sample. Both species successfully learned this discrimination, demonstrating the basis for understanding simple RMTS *despite* not being symbol-trained in any way, challenging Premack's (1983) belief in the necessity of some form of symbolic thought to be successful in RMTS tasks (Vonk 2003).

To test Premack's (1983) and Thompson and Oden's (2000) assertions that monkeys were incapable of understanding the relation-between-relations, baboons (*Papio papio*), Old World monkeys, have been tested on RMTS methods and have consistently been found capable of making judgments of the relation-between-relations (e.g., Fagot and Parron 2010; Fagot et al. 2001). However, baboons, like pigeons, appear to be sensitive to the level of entropy present in the arrays. Fagot and colleagues (2001) found that as the level of entropy within the different arrays fell from the highest possible level with 16 images per array to the lowest possible level with only two images per array, the time it took the baboons to learn the discrimination dramatically increased. Like pigeons in SD tasks, hundreds or thousands

of trials take place during the process of animals reaching criterion on these tasks. Indicating that while baboons can, indeed, successfully judge the relation-between-relations, a task once thought limited to humans and chimpanzees, it is an effortful process.

Fagot and Parron (2010) also discussed the impact of how the baboons are processing the stimuli as a possible factor that could impact difficulty in acquisition. In a typical task, the items within the array are spaced apart from each other by a small distance (see Fig. 2 for a hypothetical example).

Baboons (Fagot and Parron 2010), along with pigeons (Cavoto and Cook 2001) and capuchins (Spinozzi et al. 2003), appear to be treating each item in the array as distinct, individual units, making the task of comparing across arrays much more difficult. This finding is especially true if the space between items within the arrays is much larger than in the hypothetical image shown in Fig. 2. Thus, it appears that one other possible hurdle for the aforementioned species is their preference for local processing over global processing of the arrays. If they were looking at the array on the left as one image, they would more clearly be able to identify that the image on the left depicts the relation same (within array) and the image on the right depicts the relation different (within array), thereby allowing for the comparison to the sample image to require less cognitive resources. However, their focus on the images independently requires them to attend to each image individually before making SD judgments. The local processing bias has not gone unchallenged, though. Goto et al. (2004)



Concept Formation, Fig. 2 Hypothetical example of a two-item array RMTS trial with the center star indicating the initial fixation point

compared the abilities of humans and pigeons to classify geometric shapes based on a local feature or on global features. For both species, categorization based on global features was more rapidly acquired, challenging the use of local cues only.

Further evidence suggesting that monkeys are, indeed, capable of conceptualizing the relation-between-relations comes from work done with another Old World monkey species, rhesus macaques (*Macaca mulatta*), and a New World species, capuchins (*Cebus apella*), indicating that they have also been successful in RMTS tasks. Flemming (2010) made two methodological choices that stand out from those previously used in many studies: simple geometric figures as stimuli and gradually *increasing* the entropy within the arrays (from two-item up to six-item arrays) instead of decreasing as the monkeys progressed. Using simple geometric designs was specifically done to eliminate noise from the images commonly seen in clip art style images or complex patterns/geometric shapes. This decision helped to address the possible issue of local versus global processing of the images in the sense that it took out some of the perceptual noise, allowing the animals to more easily focus on the whole array and not just components of the array. Increasing the entropy, instead of decreasing it, as was necessary for the animals as they progressed through the trials worked as a kind of correction procedure or training if they could not understand the task (as demonstrated by failure to reach criterion) with the two-item arrays (Flemming 2010). The animals were only increased in level of entropy if they *failed* to reach criterion on the two-item arrays. It was found that most animals in both species groups rarely needed the increase in entropy in order to learn the discriminations with the two-item arrays.

Flemming (2010) concluded that it is possible that both species, but particularly capuchins, may be less affected by entropy than are baboons and pigeons. Like apes, rhesus macaques may also be more inclined to use global features in combination with local features when making visual classifications than either baboons or pigeons, especially when classifying more complex stimuli (Diamond et al. 2015). It should be mentioned,

however, that while rhesus macaques have demonstrated the ability to successfully complete RMTS tasks, the ease at which this occurs can be affected by outcome contingencies, with differential reward and punishment contingencies being the most successful combination (Flemming et al. 2011). It could be argued that without the proper outcome contingency, the animals' default processing might be to attend to the more perceptual features, hence the large amount of exposure, training, and number of trials typically necessary before criterion is reached in RMTS tasks (Flemming et al. 2011).

Conclusions

Given the above findings, Thompson and Oden (2000) appear to have been incorrect in their assertion that only humans and apes are capable of judging the relation-between-relations. Both Old World and New World monkeys, in addition to nonsymbol-trained apes, have demonstrated at least rudimentary abilities to understand this concept, which is commonly asserted to be the building blocks of analogical thinking. Taking that information into account, however, the impact of symbolic thinking on concept formation and conceptual understanding should not be dismissed. Wolff and Holmes (2011) suggested that one of the many roles that language, or any symbol system, could play is that of an *augmenter*. In this role of language as an augmenter to thought, and by proxy concept formation, symbols (in the case of language, words) act as a foundation upon which concepts can be formed. Having an ability to link symbols with concepts merely acts to help give a basis upon which to build and hold in place (anchor) those concepts. While having a symbol system is not *necessary* to understand more abstract relation-between-relations, it could definitely augment that process, making it less effortful (Wolff and Holmes 2011).

The literature, as a whole, provides a strong case for the argument that nonhuman animals at the minimum have the foundation for more abstract conceptual understating. Researchers are beginning to focus on the mechanisms that

underlie these abilities, including the neural basis of abstraction (Fabre-Thorpe 2003). Understanding these mechanisms will help to further elucidate the evolution of conceptual abilities in humans. It could be possible that humans share the same basic foundation for building and utilizing concepts as many nonhuman animal species, but the addition of more complex strategies (e.g., language) may allow for the greater ease of acquisition and use of abstract conceptual tools in humans as compared to other species (Fabre-Thorpe 2003). Possession of even the building blocks for abstract conceptual understanding could be beneficial in evolutionary terms for survival, allowing for more complex problem solving and analogical reasoning. It is of importance to continue to fill in the gaps in our understanding of not only how concepts are formed by nonhuman animals, but the breadth and complexity of their capacities, in order to gain a more complete understanding of human conceptual abilities. As has been demonstrated with other skills (e.g., tool use), as we gain more knowledge regarding concept formation in nonhuman species, we may discover that the way in which humans and nonhuman animals conceptualize, categorize, and frame the world may be more similar than different.

Cross-References

- [Nonhuman Intelligence](#)
- [Same-Different Categorization](#)
- [Unobservability Hypothesis, The \(Vonk and Povinelli, 2006\)](#)

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Concept Learning

► Concept Formation

Conception

► Ovulation

Conception Risk

► Women's Preferences During Ovulation

Conceptual Integration

- Adapted Mind, The
 - Metaphor and Analogy
-

Conceptual Mapping

- Metaphor and Analogy

Conceptual Representation

► Abstract Concept Formation

Concurrent Mate Retention Tactics

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Definition

Concurrent mate retention tactics are defined as mate retention tactics that are complementary, such that the use of one tactic supports the use of another.

Introduction: The Taxonomy of Mate Retention

Once an individual secures a long-term mate or romantic partner, the individual has the adaptive problem of retaining the mate. As the word “retain” may be generally defined as “to keep possession or use of”, mate retention tactics might be considered to have as their aim the prevention of a mate from permanently defecting from or abandoning a long-term relationship. Although they do serve this purpose, mate retention tactics can also reduce the likelihood that a long-term mate will commit an infidelity or temporarily defect from a relationship by engaging in extra-pair copulations (EPCs). Mate retention tactics are, therefore, considered to be tactics that serve both purposes (e.g., Buss 1988; Shackelford et al. 2005). It follows that whether a particular mate retention tactic is aimed at preventing a partner from permanently abandoning a long-term relationship or engaging in EPCs depends on the motivation of the individual employing it.

In a seminal article, Buss (1988) devised a taxonomy of mate retention. His classification

included two categories, subsuming six strategies, subsuming 19 tactics, subsuming 104 acts. For instance, the category *Intersexual Manipulations* subsumed strategies including *Negative Inducements* that subsumed tactics including *Threaten Infidelity* that subsumed acts including *He flirted with another woman in front of her*. Incorporating the acts, Buss devised a *Mate Retention Inventory* (MRI) to assess the frequency with which individuals employ the 19 tactics. Subsequently, Buss et al. (2008) developed a short form of the MRI (*MRI-SF*). The *MRI-SF* assesses the frequency with which individuals employ the 19 mate retention tactics but includes only two acts per tactic.

Notwithstanding Buss' (1988) taxonomy, there remains controversy over the classification of mate retention tactics. A notable example concerns whether *mate retention* is synonymous with *mate guarding*. Prior to Buss, taxonomies considered the terms to be synonyms as mate guarding was considered to comprise any tactic employed by an individual to prevent the individual's mate from being fertilized by intrasexual rivals (e.g., Thornhill and Alcock 1983). However, these taxonomies were based on non-humans, notably insects, and the tactics considered included female mimicry, mate plugs, and vibratory signaling; tactics not typically associated with humans.

Buss' (1988) taxonomy was the first to solely consider mate retention tactics used by humans. Unlike previous taxonomies, it subsumed *mate guarding* under *mate retention*. Buss argued that mate guarding may not reasonably be considered to encompass certain tactics of mate retention; "Tactics may be subtle, including dissuading potential competitors, luring one's mate with positive inducements, or even rendering one's mate less attractive or evocative to competitors. These tactics appear to fall outside the category of 'mate guarding' but are accurately subsumed by the category of 'mate retention'" (p. 292). To support his classification, Buss used the term *direct guarding* to differentiate his definition of mate guarding from the broader definition previously associated with the term. Under *direct guarding*, Buss subsumed the following tactics: *Vigilance*, subsuming acts including *He asked his friends to check up on her*;

Concealment of Mate, subsuming acts including *He refused to introduce her to his same-sex friends*; and *Monopolization of mate's time*, subsuming acts including *He insisted that she spend all her spare time with him*. In light of Buss, it may not be reasonable to consider *mate guarding* as a synonym for *mate retention*. Alternatively, there may be value in following Buss and making a distinction between the inclusive term *mate guarding* and the more restrictive term *direct mate guarding*.

Although both sexes wish to prevent a partner from engaging in EPCs, for a man, a partner's engagement in EPCs may lead to him being cuckolded or unknowingly raising the children of other men. For men, therefore, mate retention tactics also serve as anticuckoldry tactics. Not all anticuckoldry tactics, however, are mate retention tactics. Rather, certain anticuckoldry tactics serve only to reduce the likelihood that offspring will result from an EPC in which a partner has already engaged. For instance, Baker and Bellis (1993) found that the greater the length of time that a couple had spent apart since their last copulation, the greater the amount of sperm that men inseminated into their partners. Because the greater the length of time that a couple has spent apart, the greater is the likelihood that the woman will have engaged in EPCs, Baker and Bellis' finding suggests that the aim of depositing a greater amount of sperm is to increase the likelihood that the men's sperm will outcompete any rivals' sperm to fertilize their partners' eggs. Further, Shackelford et al. (2002) investigated if men have evolved psychological adaptations to reduce the likelihood that a partner's EPCs will result in offspring. They found that the greater the proportion of time that men had spent apart from their partners since their last copulation, men reported the following: a greater attraction to their partners, other men found their partners more attractive, and a greater desire to have sex with their partners. Shackelford et al.'s findings suggest that these psychological adaptations serve anticuckoldry purposes by motivating men to, as soon as possible, place their own sperm in competition with any rivals' sperm that may already be in their partners' reproductive tracts. It follows that while men's anticuckoldry tactic of placing as

much sperm as possible in their partners' reproductive tract as soon as possible serves to prevent extra-pair fertilizations, it serves neither to prevent a partner from engaging in EPCs nor to prevent a partner from permanently abandoning a relationship. It, therefore, cannot be considered to be a mate retention tactic.

Concurrent Mate Retention Tactics

Shackelford, Goetz, Guta, and Schmitt (2006) investigated the relationship between the frequency of men's use of the anticuckoldry tactics of mate guarding and in-pair copulations. They labeled as "concurrent," tactics that are complementary such that the use of one tactic supports the use of another. Shackelford et al. stated that there exists a positive correlation between the frequencies of use of concurrent anticuckoldry tactics.

Following Shackelford et al. (2006), the current article defines "concurrent" mate retention tactics as those that are complementary, such that the use of one tactic supports the use of another. It is, therefore, assumed that there is a positive correlation between the frequencies of use of concurrent mate retention tactics.

As the *Key Idea* article for this section outlines, the literature is informative regarding mate retention tactics that are used concurrently, such as men's concurrent employment of intersexual negative inducements, direct guarding, intrasexual negative inducements, and partner insults (Mckibbin et al. 2007). The *Key Idea* article also outlines the literature regarding personality traits that underlie individual differences in the concurrent use of particular mate retention tactics. There may, however, be additional factors that lead particular individuals to employ particular mate retention tactics concurrently. For instance, men who are of substantial physical stature may be especially likely to use the mate retention tactics "intrasexual threats" and "violence against rivals" concurrently. In contrast, men who are not of substantial physical stature may be especially likely to use the mate retention tactics "concealment of mate" and "monopolization of a mate's time." Women who are especially physically attractive may be

especially likely to concurrently employ the mate retention tactics "sexual inducements" and "jealousy induction." In contrast, women who are low on physical attractiveness may be especially likely to use the mate retention tactics "love and care" and "emotional manipulation" concurrently. Future research might assess these speculations by, for each factor, investigating between which mate retention tactics there is a positive correlation in the frequencies of their use. As the intensity with which mate retention tactics are employed has been shown to depend on the relative mate values of partners and the length of a couple's relationship (e.g., Buss and Shackelford 1997), there would be value in future research investigating if those factors moderate the use of mate retention tactics.

Conclusion

The literature on mate retention among humans is relatively new and the only taxonomy existing for it is that provided by Buss (1988). The primary aims of the current article have, therefore, been to clarify the following: the definition of the term *mate retention*, of which tactics mate retention is comprised, and the definition of *concurrent mate retention tactics*. By doing so, it is hoped that the current article will play a part in eliminating inconsistencies between future studies of mate retention and, therefore, lead to an improved understanding of the topic.

Cross-References

- ▶ [Coalitional Mate Retention](#)
- ▶ [Mate Retention](#)
- ▶ [Mate Retention After Children](#)
- ▶ [Mate Retention and Romantic Attachment](#)
- ▶ [Mate Retention Strategies](#)
- ▶ [Mate Retention Tactic](#)
- ▶ [Use of Mate Retention Strategies](#)

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Concussion

- [Specific Brain Damage](#)

Condemnation

- [Science and Morality](#)

Conditional Stimulus

- [Conditioned Stimulus](#)

Conditional Strategies

- [Making the Best of a Bad Job](#)

Condition-Dependent Mating Tactic

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Synonyms

[Condition-dependent variation in mating decisions](#)

Definition

Condition-dependent mating tactics are the differences observed on the typical expected sexual strategy affected by changes in the socio-environmental conditions.

Introduction

Several studies indicate that males and females have different sexual strategies in our species. Evidence indicates that different behavioral patterns have arisen because of the differences observed in the investment that each of the sexes makes in caring for the offspring. However, recent studies have revealed that the mating tactics used by individuals of the same sex are not constant and that part of these intrasexual variations can be explained by specific socioenvironmental conditions. This research addresses the variation observed in the expression of context-dependent mating tactics and shows examples of variation as a function of (1) changes in the operational sex ratio of the population and (2) environmental parasite load and (3) individual mate value in the local mating market.

Sex, Investment and Environment

For sexually reproducing organisms, offspring are a mixture of genes derived from each parent. One

of the indirect consequences of sex is the emergence of differences between males and females, originating from the gametes' specialization and the asymmetry of the costs associated with gametes' production. Due to differences observed, both primary sexual characters and secondary sexual characters evolved. Primary sexual characters are those with reproductive function required, while the secondary ones were modeled by sexual selection to increase success at copulation, such as the tactic used in mating.

According to the parental investment theory proposed by Trivers (1972), the differences in behavioral responses observed between males and females originated in response to the asymmetry of the energy investment that each of the sexes directs reproduction. On mammalian reproduction, females usually show costs associated with internal fertilization, such as placentation, gestation, and lactation. On the other hand, when compared to females, males have lower costs associated with investing energy in the offspring. It is believed that sexual selection favored an increased competition among males in order to increase their reproductive potential by access to a larger number of females, while the selective pressures that directed the adaptations in the females improved the criteria for choosing partners.

The theory of sexual strategies, proposed by Buss and Schmitt (1993), has shed light on the knowledge cited above to explain findings related to human behavior. In accord to the theory, the mating strategies of males and females were selected as a consequence of the different types of adaptive problems faced by our ancestors. The solutions that emerged from our male ancestors had resulted in a sexual strategy of lesser investment before sexual consent, a search for sexual access to a larger number of partners, and a search for partners who exhibit signs of reproductive health, such as high fertility and reproductive value. In the case of female subjects, the theory predicts that solutions originated to address adaptive problems include a more demanding criteria for partner selection and the search for partners willing to commit time, energy, and resources to women and in their children. Based on the theory

of sexual strategies, the expected appetite for relationships with low commitment and short duration is higher for males compared to females, and this would be the strategy typically expected for each sex.

A strategy implies a set of rules for behavior that is expressed by an animal, but it is important to keep in mind that the environment and even the organisms' abilities to cope with environmental challenges can change over time. In this sense, it is worth arguing that flexible strategies in response to signs of the environment or specific situations may represent greater benefits to individuals who have them. The researchers Gangestad and Simpson (2000) used this knowledge and proposed the strategic pluralism theory. According to this theory, sexual strategies would be conditional strategies, in which the sets of rules that individuals possess allow individuals to use different tactics according to environmental conditions. The authors argue that the intrasexual variation in the tactics used for mating is the result of conditional strategies and that variations in tactics were selected in our ancestors of both sexes, to optimize the energy allocation for parental care or mating effort. Context-dependent tactics are manifested in individuals' reactions to changes in the socioenvironmental context, which may affect their ability to reproduce.

Operational Sex Ratio

Operational sex ratio is an important factor in the environment that affects human mating tactics. The concept of the term represents the rate of receptive males per receptive female in a given period in time. The effect of this factor can be observed in contexts in which the number of men and women in a population is unbalanced. In a population in which the number of men exceeds the number of women, the relative value of the female subjects increases, which implies in the increase of the costs associated with the search of a partner by males. With relatively high value in context, females may be more discriminating in partner selection, i.e., they can more freely express the sexual strategy expected for females by imposing higher levels of investment from their partners before consenting to mating.

Conversely, in populations in which the number of women exceeds that of men, the female relative value decreases. In this context, female individuals are not in a position to impose high costs to potential partners, and male individuals can express the typical male strategy, which aims to reduce resource allocation in parental effort compared to resource allocation to mating (Moss and Maner 2016). Evidence of the effect of sexual ratio on the use of sexual strategies was observed in a cross-cultural study involving 48 nations (Schmitt 2005). The study revealed that in cultures where there are more women, the strategies used tend to focus on short-term relationships, through the acceptance of attitudes and behaviors linked to short-term strategies. Schacht and Mulder (2015) also found that male mating effort varies in predictable ways with the adult sex ratio, when men are in low number compared to women, they are more inclined toward short-term relationships.

Parasite Load

Parasites can be considered hostile forces that affect organisms that have long life cycle, affecting the chances of survival and reproduction. In the ancestral environment, it is possible to imagine that this factor can bring risk and uncertainty regarding the allocation of resources in the mating market. If parasite load was an evolutionary challenge faced by our ancestors that endangered reproductive outcomes, it is possible to imagine that sexual preferences, as a result of the expression of sexual strategies, should be sensitive to ecological variations in the prevalence of parasites. Penton-Voak et al. (2004) compared women's preferences in two societies, one with a lower incidence of parasites and another with a higher parasite load in which medical care is less common. The results indicated the tendency of women of the society with higher parasite load to prefer faces of more masculine men in their local populations. The authors argue that women's preferences may be associated with the characteristics of the environment and that environmental cues linked to the prospect of paternal investment may modulate women's decisions in the search for a partner. The prevalence of parasites may

compromise parental investment, since the intrinsic mortality rate may increase (Robson and Kaplan 2003). Hill et al. (2015) developed a study that examined the relationship between cues indicating that the rate of disease is increasing in their environment and women's desire for sexual variety. They found that women with a history of vulnerability to illness respond to the increase on perceived pathogen load by desiring a greater number of novel partners. Evidence shows that ecological variation in the prevalence of parasites can modify sexual preferences and the patterns of involvement in the relationship prior to consent for sexual access, which consequently affects the mating tactics expressed in the population (Gangestad et al. 2006).

Mate Value

In his work on parental investment, Trivers (1972) theorized that the best sexual strategy may depend on the mate's value and the local environment. Buss and Schmitt (1993) also suggested that individual mate value is important in determining sexual strategy; they argued that the higher the mate value, the greater the possibility of expressing the sex-typical strategy, i.e., the strategy that provides the greatest reproductive outcome. If we take the mating market as a biological market (Noë and Hammerstein 1995), it is possible to assume that the attributes that an individual possesses can be used to attract partners and allocate resources of rivals. In this context, the quality of the attributes of an individual can determine the sexual strategy expressed. Several papers support this understanding.

Surbey and Brice (2007) found that men with high self-perceived mate value endorsed casual sexual activity in contrast to committed relationships. On the other hand, Perilloux et al. (2013) found that women who perceived themselves with high mate value (more physically attractive) were more oriented toward short-term mating. Men with a high market value tend to have sex earlier and have more partners (Landolt et al. 1995); in addition, those with broad, muscular shoulders tend to short-term strategies, seeking more partners, engaging earlier in sex, and presenting more copulations out of the relationship (Hughes and

Gallup 2003). For women, one factor that has a strong influence on market value is age, which is related to fertility and reproductive value. Hughes and Gallup (2003) observed that female reproductive behavior may change with the woman's age, presenting a peak of sexual desire before the age of 30 years.

Conclusion

Condition-dependent mating tactics are the differences observed on the typical expected sexual strategy that are affected by factors present in the socioenvironmental conditions. These tactics are present in our species because those individuals who possessed the ability to adjust their mating strategies for local environmental context might had experimented greater reproductive return while allocating energy in parenting or mating. Evidence indicates that our mind is equipped with a set of mating tactics whose expression occurs in response to clues in the socioenvironmental conditions.

Cross-References

- Female Mate Choice
- Individual Differences
- Male Mate Choice
- Mate Value
- Operational Sex Ratio
- Reproductive Strategies

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Condition-Dependent Variation in Mating Decisions

- Condition-Dependent Mating Tactic

Conditioned Associations

► Associative Learning

Conditioned Emotional Reactions

► Little Albert

Conditioned Reflex

- Conditioned Response
 - Conditioned Stimulus
-

Conditioned Reflexive Response Classically Conditioned Response

► Conditioned Response

Conditioned Response

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Synonyms

Conditioned reflex; Conditioned reflexive response classically conditioned response

Definition

A conditioned response constitutes the product of learning through the acquisition of a new association between a previously neutral stimulus and a biologically relevant stimulus.

Introduction

Reflexive responses appear when an organism comes across stimuli which automatically trigger a reflexive response. For instance, a puff of air to the eye area automatically induces a reflexive response of an eyeblink (Spence 1978). In a scenario in which an originally neutral stimulus is associated with the puff of air, that formerly neutral stimulus turns into a conditioned stimulus and acquires functions that enable it to induce qualitatively similar responses (i.e., conditioned responses) with the reflexive ones (McSweeney and Murphy 2014). That is, in the field of Pavlovian/respondent conditioning, neutral stimuli refer to any stimulus that originally did not induce any particular reactions, yet through repeated pairings with a biologically relevant stimulus, obtain qualitatively similar functions with it. Respectively, responses that are induced by classically conditioned stimuli are referred to as conditioned responses (Schachtman 2011). That is, a conditioned response is formed through the acquisition of an association between a conditioned stimulus that precedes a biologically relevant stimulus. In other words, the key point that differentiates conditioned responses from unconditioned responses is that conditioned responses are the product of learning through the acquisition of new associations between previously neutral stimuli and a biologically relevant stimulus. In contrast, unconditioned responses are induced automatically and naturally by unconditional stimuli, requiring no previous learning (Shanks 1995).

Classic Example

Ivan Petrovich Pavlov came upon with the essential idea of the conditioned response by coincidence. Specifically, I. P. Pavlov was examining the alternations of dogs' saliva and digestive fluid secretion through mouth and stomach while feeding. At some point, during the course of the experimental procedure that I. P. Pavlov set in order to observe the alternations of dogs' saliva and digestive fluid secretion in response to feeding he observed that the subjects' (i.e., dogs) saliva and

digestive fluid were also secreted every time he and his associate arrived at the laboratory (Spence 1978). Consequently, I. P. Pavlov decided to experimentally examine the functional mechanisms and structures that let the dogs to also secrete saliva and digestive fluid in his presence, rather than exclusively to the presence of food in response to which the dogs reflexively secrete saliva and digestive fluid (Shanks 1995).

Specifically, I. P. Pavlov and his associates systematically administered for several times a neutral stimulus (i.e., sound of a bell) to the dogs just before they presented to the dogs their usual food (i.e., meat powder) (Spence 1978). When this trial was conducted numerous times I. P. Pavlov and his associates observed that the dogs were also secreting saliva and digestive fluid when the stimulus of the bell was administered alone, that is, in the absence of the meat powder (Shanks 1995). Ultimately, I. P. Pavlov came to the conclusion that the constant pairings of the sound of the bell and the food across time and space resulted in the formation of an association between the sound of the bell and the food. Specifically, the sound of the bell which at the beginning was a neutral stimulus, a stimulus that does not elicit a particular response, acquired the capacity to elicit a response that is qualitatively similar to the one that the food naturally and automatically elicits. The response of the dogs became classically conditioned and respectively the sound of the bell turned into a conditioned stimulus. Consequently, the new response that was learned as a reaction to the sound of the bell is named conditioned response (Schachtman 2011).

The Process of Acquisition and Its Role on the Functional Qualities of Classically Conditioned Responses

As mentioned above, a classically conditioned response is formed through the acquisition of an association between a formerly neutral stimulus that consistently precedes a biologically relevant stimulus (McSweeney and Murphy 2014). Yet, it must be noted that there are conditioned responses

that could be formed quicker comparatively to other conditioned responses and respectively there are classically conditioned responses of high and low intensity. The functional qualities of a classically conditioned response rely to a high extent on the conditions through which the process of acquisition took place. Specifically, classically conditioned responses are more efficiently developed when conditioned stimuli are presented just before the unconditioned stimuli, a procedure which is termed “delayed conditioning” because the unconditional stimulus is delayed when compared to the presentation of the conditioned stimulus. In contrast, in trials where the conditioned as well as the unconditioned stimuli are presented at the same time the conditioned responses that are induced are of low intensity (Wills 2012).

The Discrepancy Between Unconditioned and Conditioned Responses

I. P. Pavlov proposed through his work on conditioned reflexes that the same response that was elicited by an unconditioned stimulus could also be elicited by a conditioned stimulus through its association with the unconditioned stimulus (McSweeney and Murphy 2014). However, it quickly became clear that conditioned responses are of lower intensity than unconditioned responses. In addition, research related to classical conditioning after I. P. Pavlov’s work has reliably proposed that the unconditioned response and the conditioned response are not the same responses, but they are usually qualitatively similar. Yet, they can be considerably different. Specifically, it has been consistently cited that I. P. Pavlov’s dogs did not confuse the sound of the bell with the meat powder, but they actually responded to the association among the sound of the bell and the meat powder which has consistently been presented right after the sound of the bell (Ramnero and Torneke 2011). In addition, the unconditioned response as well as the conditioned response are not limited to the secretion of saliva and digestive fluid. Specifically, the secretion of saliva and digestive fluid constitutes just a part of a

multifaceted response through which the dog's body is being prepared for obtaining the meat powder (Staddon 2014).

Classical Conditioning and Emotional Functioning

Classical conditioning could be used to gain an insight into the way that a person's emotive experience of the world is developed during childhood. For instance, despite the fact that only certain stimulus could induce fear responses early on in an individual's life, as the person grows up he/she would acquire further associations which will obtain qualitatively similar operations with the ones that an unconditioned stimulus possesses, which would from then on induce classically conditioned fear responses (McSweeney and Murphy 2014). Therefore, through classical conditioning, phenomena acquire new associations with external stimuli such as behaviors of other people, certain environmental conditions, as well as internal stimuli, such as other emotions and interoceptive experiences. For example, a young boy who experiences sadness and is recurrently challenged by a father who is behaving in a manner which induces fear in the boy, via the process of classical conditioning, the father's behaviors could lead the young boy to develop an association between the affects of sadness and fear, and thus every time he feels sadness (conditioned stimulus) a classically conditioned response of fear is induced. In other words, this boy has learned through classical conditioning to experience fear every time he is sad (Thines 1987).

Further Conditioning: Stimulus Generalization and Stimulus Discrimination

In general, organisms have the tendency to exhibit classically conditioned responses to stimuli that have formal similarities with the conditioned stimuli, a phenomenon that is known as stimulus generalization. The converse conditioning operation to stimulus generalization is a process termed

stimulus discrimination. Stimulus discrimination is the capacity to detect and respond to differences between stimuli, that is, the capacity to detect similarities among stimuli (Ramnero and Torneke 2011). The processes of generalization, discrimination, as well as the equilibrium among them, are of vital importance for living beings in order to learn to adapt and survive (Baum 2017). Specifically, in some situations it is of vital importance to exhibit stimulus discrimination and just respond to specific stimuli. For instance, a living being that must assess an area which is full of ice where a discrepancy in the white color shows the degree to which it is safe or dangerous to pass through the ice must have the capacity for stimulus discrimination. However, in other situations, stimulus generalization has higher adaptive and survival significance, such as the case of an organism which is chased by a variety of predators. In such a scenario, this living organism must respond to everything that presents in front of it.

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Classical Conditioning](#)
- ▶ [Conditioned Stimulus](#)
- ▶ [Extinction](#)
- ▶ [John Watson](#)
- ▶ [Unconditioned Response](#)
- ▶ [Unconditioned Stimulus](#)

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of classically conditioned associations between neutral stimuli and biologically relevant stimuli (unconditioned stimuli). I. P. Pavlov examined various reflexes, yet his most widely known experiments revolved on responses to food (Spence 1978).

Conditioned Stimulus

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Synonyms

Classically conditioned stimulus; Conditional stimulus; Conditioned reflex

Definition

A conditioned stimulus is any stimulus that prior to learning did not induce any particular response. Yet, through the acquisition of an association with a biologically significant stimulus it acquires the ability to induce a response that is qualitatively similar with the one that the biologically significant stimulus induces.

Introduction

Pavlovian and/or classical conditioning is a type of learning that involves the formation of new behavioral responses through the acquisition of new associations. Classical conditioning has been discovered and methodologically described by a Russian physiologist named Ivan Petrovich Pavlov (McSweeney and Murphy 2014). This type of learning is named “conditioning” since its inventor, I. P. Pavlov, used the term conditioned reflex to label and designate the learning outcome. I. P. Pavlov assumed that a new reflexive response can be developed through the acquisition

The Study of the Gastrointestinal System and Its Role on the Concept of Conditioned Stimulus

I. P. Pavlov came upon with the concept of conditioned stimulus accidentally while examining the physiological processes of the gastrointestinal system (McSweeney and Murphy 2014). Specifically, I. P. Pavlov was studying the alternations of dog’s saliva and digestive fluid secretion through their mouth and stomach while feeding. At some point, during the experimental procedure that I. P. Pavlov set to observe the alternations of dogs’ saliva and digestive fluid secretion in response to feeding, he observed that the subjects’ saliva and digestive fluid were also secreted every time he and his associate arrived in the laboratory. Consequently, I. P. Pavlov decided to experimentally examine the mechanisms and the functional structures that let the dogs to also secrete saliva and digestive fluid in his presence rather than exclusively to the presence of food in response to which the dogs reflexively, that is, automatically, secrete saliva and digestive fluid (Spence 1978).

I. P. Pavlov and his associates systematically administered for several times a neutral stimulus (i.e., sound of a bell), a stimulus that originally did not induce any response to the dogs just before they presented to the dogs their usual food which constitutes an unconditioned stimulus that is a stimulus that reflexively induces a response from the dogs. When this trial was conducted numerous times, I. P. Pavlov and his associates observed that the dogs were also secreting saliva and digestive fluid when the previously neutral stimulus of the bell was administered alone, that is, in the absence of the food (Shanks 1995). Specifically, the constant pairings of the sound of

the bell and the food resulted in the formation of a classically conditioned association between the sound of the bell and the food. In other words, the sound of the bell, which at the beginning was a neutral stimulus since it elicited no particular responses, acquired the capacity to elicit a response that is qualitatively similar to the one that the food naturally and automatically elicits. The response of the dogs became classically conditioned and respectively the sound of the bell turned into a conditioned stimulus (Schachtman 2011).

Facilitating Factors

As mentioned above, classical conditioning takes place through the acquisition of an association between a formerly neutral stimulus and a biologically relevant stimulus that is, an unconditioned stimulus (McSweeney & Murphy, 2014). Yet, for a neutral stimulus to turn into a conditioned stimulus, specific conditions are required. Firstly, when the frequency with which a conditioned stimulus is presented with an unconditioned stimulus is augmented, the likelihood that a neutral stimulus would turn into a conditioned stimulus and induce a conditioned response would be also augmented. For instance, if the frequency with which a sound of a bell accompanies the puff of air is consistently augmented, the likelihood that the sound of the bell would acquire the capacity to induce a conditioned response of an eyeblink is also augmented (McSweeney and Murphy 2014).

Secondly, when the conditioned stimuli are constantly presented in trials in which the unconditioned stimuli are also presented, the likelihood that a neutral stimulus would turn into a conditioned stimulus and acquire the capacity to induce a conditioned response would be higher in comparison with a trial in which the unconditioned stimulus presents too in the absence of the conditioned stimulus (Schmajuk 2010). For instance, if the sound of the bell is permanently presented when the dog receives food, the likelihood that the sound of the bell would obtain the ability to induce a classically conditioned response of saliva

and gastric fluid secretion is augmented (Ramnero and Torneke 2011).

Thirdly, the neutral stimulus must always be presented just before the unconditioned stimulus is presented and not the opposite (McSweeney and Murphy 2014). For example, in order for a tone to acquire the capacity of inducing saliva and gastric fluid secretion, the tone must be presented just before or as the food is received. If the tone is presented after the dog has received the food, the tone would never turn into a conditioned stimulus and be able to induce a response of saliva and gastric fluid secretion because there is no functional significance in acquiring such capacity (Shanks 1995). A further factor that facilitates conditioning is the intervening time between the presentation of the conditioned stimuli and the unconditioned stimuli. Specifically, as the intervening time between the presentation of the conditioned stimuli and the unconditioned stimuli is increasing, the likelihood that a neutral stimulus would turn into a conditioned stimulus and be able to induce a conditioned response is decreasing. For example, if a tone is presented, a long time before a dog receives the food, the tone would not acquire the classically conditioned association with the food so that to obtain the capacity to induce a conditioned response of saliva and gastric fluid secretion (McSweeney and Murphy 2014).

Biologically Prepared Learning and Its Role on Conditioned Stimuli

Humans are endowed with a number of reactions to a variety of unconditioned stimulus, yet the responses that people exhibit are more complex than that. In addition, what is termed as neutral stimulus, sometimes is not exactly neutral (Ramnero and Torneke 2011). Specifically, stimuli could be differentiated in their ability to acquire conditioned associations and not all reactions could be induced by a previously neutral stimulus in the same time framework and potency. For example, in order for a sound of a bell to

acquire the capacity to induce an eyeblink, the sound of the bell and the puff of air have to be associated multiple times. In contrast, in order for a formerly neutral stimulus of a certain odor to acquire the capacity to induce a feeling of disgust and dizziness, a person has to experience once or maybe a few more times the association between that specific odor and a vomit for example (Spence 1978).

Further Conditioning: Second-Order Conditioning

Stimuli that have acquired conditioned associations with an unconditioned stimulus and become able to induce conditioned responses could set the ground for further conditioned associations. For example, when a kid experiences fear in the presence of darkness resulting to the darkness being a conditioned stimulus that induce a response of fear, an additional stimulus that is present in the setting of darkness such as specific noises can acquire too qualitatively similar operations with the conditioned stimulus and induce a fear response, despite that these noises did not accompany the stimulus that initially induced the fear response in the dark setting (Ramnero and Torneke 2011). This phenomenon is usually termed as second-order conditioning. Once more, the stimulus of darkness is likewise one that is not so neutral, as humans are biologically predisposed to more easily associate it with fear than other stimuli (McSweeney and Murphy 2014).

Conclusion

Classical conditioning enables environmental components and/or conditions (e.g., neutral stimuli) to acquire a physiological capacity that did not have before. In other words, an environmental component and/or a condition that possessed other functions or none when it turns into a conditioned stimulus acquires a new function, an acquisition that is vital for any species. Specifically, classical conditioning

provides to a living being the chance to alter its behavior and thus increasing its capacity to adapt and survive (Ramnero and Torneke 2011). For example, a kid might jump on a road full of cars, lacking the association between such situations and threat. Nevertheless, the kid possesses a physiological system that responds to specific unconditioned stimuli such as abrupt cries, screams, and violent acts with an unconditioned response of fear. In a plausible scenario where his/her mother or his/her father responds with a loud scream or exhibits a violent act when the kid tries to jump on the road, the road and/or other relevant stimulus would acquire qualitatively similar functions with the unconditioned stimulus of a loud scream, enabling the road and other relevant stimuli from then on (conditioned stimulus) to induce a conditioned response of fear. Therefore, the acquisition of this new association would enable the kid to alter his/her behavior in similar circumstances (e.g., crowded road) (McSweeney and Murphy 2014).

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Classical Conditioning](#)
- ▶ [Conditioned Response](#)
- ▶ [John Watson](#)

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Conditioning and Association

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Synonyms

Classical conditioning; Instrumental conditioning; Operant conditioning; Pavlovian conditioning; Respondent conditioning

Definition

Conditioning involves processes related to changing behavior (i.e., learning). Via the association of stimuli with other stimuli or with behaviors, organisms can effectively respond to their changing environment. Respondent and operant conditioning are two primary modes of behavior change.

Introduction

Processes associated with behavior change can be broadly classified in two categories: respondent and operant conditioning. Respondent conditioning involves the association between stimuli and responses such that a previously neutral (i.e., ineffective) stimulus can elicit an involuntary response that prepares the organism for a biologically significant event. Operant conditioning involves the change in the probability of an emitted voluntary response as a function of its consequences.

These processes involve the interplay between a behaving organism and environmental events with the end result of a change in the behavior of that organism. The ability to change behavior as a function of environmental events is an evolved adaptation. It is likely that some associations are

more easily formed than others. For example, Öhman and Mineka (2003) suggested that humans and other primates are particularly sensitive to learning to fear snakes, and Garcia and Koelling (1966) demonstrated that taste aversion learning is most likely to occur when rats experience nausea than when they experience pain. The evolution of the ability to learn is the ultimate adaptation, in that organisms can alter their behavior on a moment-by-moment basis and thus adjust to quickly changing environments. In addition, these adaptations may be further modulated depending on the particular evolutionary histories experienced.

Respondent Conditioning

The process of respondent (or classical or Pavlovian) conditioning involves the association between a biologically relevant stimulus and a reflexive reaction. The basic preparation involves presenting a *neutral stimulus* (NS) prior to the occurrence of a biologically relevant stimulus (the *unconditioned stimulus*, US). The US produces an involuntary response called the *unconditioned response*, UR. The predictive relationship between the NS and the US can cause conditioning to occur such that the previously neutral stimulus (now the *conditioned stimulus* or CS) elicits a response (the *conditioned response*, CR).

The prototypic example of this type of conditioning is the salivation that physiologist Ivan Pavlov was able to elicit in his dogs. In this example, a tone (NS) is paired with food (US), producing salivation (UR). After several tone-food pairings, the tone by itself (CS) produces salivation (CR). If the tone (CS) was presented several times in the absence of the food (US), the salivation response would decay, in a process known as respondent extinction.

Although the early focus of research in respondent conditioning was on the contiguity between the CS and US, later work has shown that conditioning is a much more complex and elegant process. Rescorla (1988) suggested that contiguity is neither necessary nor sufficient for conditioning

to occur. Instead, “information that one stimulus gives about another” (p. 152) is of greater importance. That is, the predictive relationship between the NS and the upcoming US is more important than the temporal relations between these two stimuli. In the blocking preparation, for example, a compound light-and-tone stimulus precedes a US (e.g., electric shock). If animals first experience the light alone as a CS, they will not become conditioned to respond to the tone (Kamin 1968).

Rescorla (1988) noted that respondent conditioning occurs when an organism “is surprised” by the “discrepancy between the actual state of the world and the organism’s representation of that state” (p. 155). Thus, respondent conditioning can occur with a single trial or across multiple pairings. The salience of the stimuli to be conditioned, the temporal relations between environmental events, and the complexity of the historical and immediate environment might all influence conditioning (Kamin 1968). Not only are the individual stimuli important, but so too is the context in which the stimuli are presented.

Rather than being a process that governs simple reflexive responding, Pavlovian conditioning is implicated in the processes associated with motivation and emotion. Additionally, this type of associationism is referenced with respect to the development of drug tolerance, analgesia, and immunosuppression (Rescorla 1988), as well as some of the physiological effects of placebos (Price et al. 2008). The responses that are a product of classical conditioning have potential survival value. Organisms that are able to respond not only to biologically relevant stimuli (i.e., the US) but also to associated stimuli (i.e., the CS) may be more likely to survive than organisms that fail to respond appropriately.

Operant Conditioning

Like respondent conditioning, operant conditioning provides a mechanism by which organisms

can alter their behavior in order to adapt to changing environmental conditions. Operant conditioning involves changing behavior by altering the consequences of voluntary behavior. *Reinforcement* and *punishment* are the two processes by which this occurs. A reinforcer is any consequence that increases the future likelihood of the response that produces it. For example, the behavior of driving at a high rate of speed may be reinforced by the consequence of arriving on time. A punisher is any consequence that decreases the future likelihood of the response that produces it. For example, the behavior of driving at a high rate of speed may be punished by the presentation of a speeding ticket, the associated fine, and insurance rate hike. As these examples suggest, behaviors can be simultaneously influenced by complex contingencies of both reinforcement and punishment.

Reinforcers and punishers (i.e., the consequences that strengthen or weaken behavior) can also be characterized as positive or negative. Positive reinforcers and positive punishers achieve their effect through the addition of a stimulus (e.g., presentation of food can serve as a positive reinforcer for the behavior of asking for food), whereas negative reinforcers and negative punishers achieve their effect through the removal of a stimulus (e.g., the removal of headache can negatively reinforce the behavior of taking medicine).

Several variables can influence the effectiveness of operant consequences. Immediacy is perhaps the most important: consequences are more effective when they immediately follow a response. Reinforcers can also be arranged according to *schedules*, which are simply rules that determine when a reinforcer occurs. Different *schedules of reinforcement* produce different patterns of behavior (cf. Ferster and Skinner 1957). For example, a continuous reinforcement schedule provides a consequence for every correct response, resulting in rapid acquisition. In contrast, intermittent reinforcement schedules (in which some correct responses are not followed by a reinforcer) produce slower acquisition, but

result in responses that are more likely to persist despite periods in which no reinforcement is available. Operant extinction is the process in which the reinforcement for a response is terminated. Initially, *extinction* may result in a temporary burst in responding, but if the reinforcer continues to be withheld, responding will gradually decrease in frequency until responding is eliminated.

Discriminative stimuli (also referred to as an S^D or S+) appear before an operant response and signal that particular contingencies of reinforcement are currently in effect. An operant response, however, is not caused by a discriminative stimulus, but rather the previous consequences of the behavior. A green light, for example, sets the occasion for safe passage through an intersection while driving, but does not cause this behavior.

Some consequences can serve as operant consequences without any previous learning being necessary, and these are referred to as *primary* reinforcers and punishers. For example, food naturally functions as a reinforcer for a hungry organism. Through the application of respondent conditioning, however, previously neutral stimuli can become reinforcers or punishers. For example, a clicker (CS) can be paired with a food reinforcer (US), so that the clicker becomes a *conditioned* reinforcer. Conditioned reinforcers and punishers can then be used as consequences to change behavior in the same way as primary reinforcers and punishers.

Together, the processes involved in operant conditioning allow organisms to successfully navigate their environment. Organisms sensitive to reinforcement and punishment can successfully produce desirable consequences (e.g., attention, food) and avoid aversive stimulation (e.g., pain, cold). Responding under the control of discriminative stimuli allows for efficient behavior, contacting reinforcers, and avoiding punishers. Individuals with a sensitivity to operant conditioning might be more likely to survive in their environment, making it advantageous to the species.

Conclusion

The processes described here, respondent and operant conditioning, are a result of the evolutionary development of species. Skinner (1984) suggested that organisms that are able to change their behavior as a function of environmental events are more likely to survive than organisms that are not sensitive to their environment. Respondent conditioning results in the development of new reflexive behaviors, while operant conditioning results in the development of new voluntary behaviors. Both processes operate simultaneously to generate, alter, and eliminate behavior depending on the conditions present in the environment. Such adaptations may make these organisms more likely to survive and reproduce.

Cross-References

- B. F. Skinner and Behaviorism
- Methods and Enduring Impact of Behaviorism

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Conditions Required for Evolution of Warfare Adaptations

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Definition

Describes the ancestral conditions that could allow for the evolution of adaptations for warfare in humans. The evolution of adaptations for warfare is possible when there are low-cost/high-benefit opportunities for violence, and it is also possible even if violence is costly, as long as fitness benefits can outweigh these costs in particular mating contexts. Additionally, in some species such as humans, the existence of warfare adaptations presumes the existence of a coalitional psychology able to track a broader range of group dynamics. In short, the evolution of adaptations for warfare is possible when reproductive benefits can outweigh the variable costs of violence and when those opportunities can be taken advantage of by an evolved coalitional psychology.

Introduction

Warfare is a prevalent feature of human social interaction. Given its significant and recurrent nature, scholars have sought to explain not only why particular wars are fought but also why humans organize into groups and fight each other in general. Some, such as the anthropologist Margaret Mead, have argued that war is a cultural invention and that it likely developed sometime between the agricultural revolution and the emergence of large sedentary proto-states. These authors claim that our evolutionary history and biological makeup can contribute little or nothing to our understanding of why humans fight. In

other words, historical, not biological, explanations for warfare are needed.

Others, however, have argued that group violence in humans is evolutionarily old and that the origins of collective violence can even be traced back to our chimpanzee ancestors, many millions of years ago (Wrangham 1999; Wilson et al. 2014). These authors further argue that the competitive coalitional nature of human evolutionary history had a unique impact on human psychology. Specifically, they argue that due to the fact that coalitional competition had such a significant and recurrent impact on our ancestors' reproductive success, we should expect to see adaptations in the human brain that enable us to reason adaptively in contexts of coalitional competition and violence. These scholars often refer to such adaptations as "adaptations for warfare."

Labels are useful because they help us categorize, define, and understand concepts and dynamics; however, research on the evolution of warfare is one area in which the labels themselves have been the targets of much dispute. Consequently, many disagreements about whether warfare is evolutionarily old or culturally recent actually hinge on disagreements about what warfare is and how it should be defined.

No consensus exists regarding the definition of terms such as "warfare," but definitional clarity at least allows one to evaluate the logical coherence of an argument on its own terms. Clearly defining terms such as "warfare" means disagreements about what warfare is can be momentarily put aside in order to ask a more specific question: given a particular definition of warfare, is there evidence that this behavioral pattern occurred ancestrally? This means that different definitions of warfare will result in different conclusions about its prevalence ancestrally and, by extension, different conclusions about the existence of adaptations for warfare. A logical implication is that some forms of warfare probably have no evolutionary explanation, while other forms of warfare probably do. In short, the importance of definitions is not to be overstated and is a necessary starting point.

Defining Terms: “Adaptation” and “Warfare”

What is an adaptation? Like the concept of warfare, there is much discussion on what a biological adaptation is, as well as whether adaptations in the brain should be studied in a fundamentally different way than adaptations in other parts of the phenotype (body). Evolutionary psychologists generally reject the proposition that adaptations in the brain (“psychological adaptations”) require different explanations than adaptations found elsewhere in the phenotype. Thus, evolutionary psychologists argue that the design and function of specific adaptations in the brain can be explained in much the same way as the design and function of adaptations in the liver or heart.

The brain is not one singular adaptation, but rather a collection of specialized adaptations that, broadly speaking, function to regulate the complex behavior of the organism. Indeed, a feature that distinguishes organisms that are capable of complex behavior from those that are not is the presence of a complex nervous system and brain. Therefore, the specific adaptations that compose the brain are generally designed to regulate some aspect of behavior by processing information from the organism’s environment in specific ways. This is why some evolutionary psychologists will also refer to psychological adaptations as “information-processing mechanisms.”

The process of natural selection explains the existence and design of biological adaptations (Williams 1966; Maynard Smith 1993). When some heritable trait emerges in a population, it can be favored by natural selection if it has a positive effect on reproductive success and when that effect is recurrent over evolutionary time. Resultant adaptations will tend to have certain characteristics; broadly, their design will represent a specialized solution to some reproductive challenge or opportunity faced by the organism. With some exceptions (e.g., frequency-dependent selection and “drift”), heritable traits that have a positive impact on the organism’s reproductive success over evolutionary time will tend to spread

in the population and become universal or near universal in the population.

As information-processing mechanisms, adaptations in the brain are often designed to produce a range of output (e.g., altered hormone levels) contingent upon a range of input from the environment (e.g., having won or lost a contest). The conditional – or “facultative” – nature of adaptations suggests that if there are adaptations that shape the way humans reason about fighting, then variation in the incidence of fighting across a population will not be evidence that adaptations for fighting are not universal or don’t exist. Rather, it is possible that this variation merely reflects the contingent logic of the universal adaptation.

What is warfare? A voluminous range of definitions of warfare exists, and there is no “right” definition of warfare, only myriad sets of behaviors that can justifiably be referred to as involving violence of some kind among groups. Consequently, much depends on one’s area of interest and expertise. Scholars of modern warfare, such as those who make use of the massive Correlates of War database, will (appropriately) define warfare as “sustained combat, involving organized armed forces, resulting in a minimum of 1000 battle-related fatalities within a 12-month period.” However, if this is our starting point, then the question of whether warfare has evolutionary origins must be “no” since no one would argue that this form of mechanized combat is anything but historically recent and evolutionarily novel.

Consider an alternative definition of war: “relationships in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group” (Bowles 2009; Wrangham and Glowacki 2012). This conceptualization opens up the possibility that “war” is an evolutionarily old human practice, which, in turn, opens up the possibility that adaptations for “warfare” exist. Whether one agrees that this is the correct definition of war is ultimately less important than whether a form of coalitional violence can be identified that *did* exist ancestrally, enabling specific inferences about how

adaptations designed in response to those specific ancestral challenges structure our beliefs and motivations in modern environments.

Conditions for the Evolution of Warfare

Given the above perspective on adaptation, and using the broader definition of war (i.e., Bowles 2009), a specific question can now be asked: what conditions must have held ancestrally in order for natural selection to favor psychological adaptations in humans that guide motivation and behavior in the context of warfare?

Reproductive Benefits

The first condition is simultaneously the least satisfying (due of its general nature) but also the most important. That is, the reproductive benefits of fighting in groups must have outweighed its related costs. This can be difficult to identify in the case of aggression – coalitional or otherwise – because of the significant physical costs involved in violence (Allen and Jones 2014). In other words, it is often easier to see the substantial risks and physical costs of coalitional violence than it is to see the benefits. However, there are two types of costs to consider in the context of violence: somatic costs and reproductive costs.

The somatic costs of violence refer to the physical damage that an individual or group sustains as a direct and immediate consequence of fighting, such as the loss of limb or the loss of life. In contrast, the reproductive costs of warfare refer to the reproductive opportunities lost as a consequence of fighting. In other words, one cannot reproduce if they are dead. An evolutionary analysis of warfare must attend to the question of its reproductive costs and benefits. Specifically, the reproductive benefits of warfare must outweigh the costs of participation in violence.

The fact that warfare can result in loss of life means that the theoretical challenge is to explain what reproductive benefits could make up for the costs of warfare when such costs entail loss of life and by extension a corresponding possibility of lost reproductive opportunities for the individual. There are two pathways by which the

reproductive benefits of collective violence can outweigh these costs. The first pathway intuitively occurs when both the somatic and reproductive costs of warfare are actually quite low relative to the reproductive benefits. The second pathway occurs somewhat counterintuitively when, despite very high somatic costs to the individual, the reproductive benefits of violence are even greater.

Pathway 1: Reproductive benefits of low-risk raiding. Collective violence can evolve in coalitional environments in which low-risk/high-benefit aggressive opportunities exist. When these opportunities exist, selection can favor raiding behavior between coalitions. Such behavior has specific characteristics and is well explained by the imbalance-of-power hypothesis (Wrangham 1999). Absent weaponry, success in aggressive encounters is often determined by relative strength, and thus, all else equal, the greater the size asymmetry between coalitions, the more likely the larger coalition is to prevail at low cost to its members. In combination with the element of surprise, the attacking coalition can virtually guarantee a low-cost, high-benefit outcome.

The low costs of asymmetric warfare for the attacking party are clear. However, what are the benefits? The first benefit is a direct consequence of the violence – the rival coalition loses one or more of its members, which constitutes a relative power loss. In an environment in which coalitions are small to begin with, the loss of even one individual would not be trivial. A loss of coalition strength can result in increased attacks from neighboring coalitions and an inability to defend the territory controlled by the coalition. Thus, not only is the rival coalition weakened, but the winning coalition can also obtain greater territory and with it the resources that it contains – both material and reproductive. The material and reproductive benefits of low-risk raiding have been well studied and measured (Wilson et al. 2014).

This “chimpanzee model” of warfare (Wrangham and Glowacki 2012) is a clear illustration of one set of conditions under which coalitional violence can evolve via natural selection, namely, where low-risk/high-benefit aggressive opportunities exist. This pattern can be seen in humans, although with important differences.

Human raiding, like chimpanzee raiding, occurs by stealth, is increasingly likely as the imbalance of power reaches a ratio of 3:1, and is accompanied by non-negligible material and reproductive benefits such as expanded territory (Johnson and Toft 2014). Unlike chimpanzee raiding, however, human raiding can be somewhat more risky due to the presence of weaponry and the cycles of revenge.

It may be the case that chimpanzee warfare offers a glimpse at the ancient “roots” of human warfare. However, while some aspects of human warfare resemble the chimpanzee model, other aspects do not. In a comprehensive review and comparison of chimpanzee and human warfare, Wrangham and Glowacki (2012) argue that there are two problems with the comparison of chimpanzee and human warfare. First, relations among human coalitions can range from hostile and violent to peaceful and cooperative. Second, human warfare seems to entail greater risks to attackers than the chimpanzee model, which returns us to the initial question of how evolution could explain psychological adaptations that motivate high-risk violence. Each is discussed briefly in turn.

The first problem (i.e., cooperative as well as combative coalitions) is not evidence that human raiding is not motivated by psychological adaptations that operate to seize low-risk/high-benefit aggressive opportunities. Rather, it suggests that this “raiding psychology” is part of an evolved coalitional psychology that is equipped with a broader toolkit of coalitional interaction. To oversimplify, one could say that humans have psychological adaptations not only for coalitional violence but also for inter-coalitional (as well as intra-coalitional) cooperation and alliance. This issue must be put aside and returned to in a subsequent section on coalitional psychology. For now, however, what can be said is that the conditional logic of psychological adaptations for intergroup violence in humans likely operates within a wider or at least different set of variables than it does in chimpanzees, encompassing opportunities for aggression as well as alliance and trade.

The second problem (participation in high-risk violence) must be engaged by careful

reconsideration of the reproductive costs and benefits of coalitional violence. The resolution of this second problem reveals the second pathway by which the reproductive benefits of warfare can outweigh its potentially significant costs.

Pathway 2: Reproductive benefits of high-risk battles. Collective violence can evolve despite the existence of significant somatic costs – even individual death – when reproductive resources in the coalition are subject to zero-sum distribution (Tooby and Cosmides 1988; McDonald et al. 2012; Lopez 2016). To understand this argument, the reproductive success of the gene or suite of genes that would benefit from the risk-taking behavior of its host must be examined.

All biological adaptations arise initially as a consequence of a random genetic mutation that is maintained in a population because of its positive effects on the organism’s ability to reproduce. Taken to the fullest extreme, therefore, Dawkins quips that “a chicken is only an egg’s way for making another egg” (Dawkins 1976). Put simply, natural selection describes the processes whereby a gene arises that has some effect on the body of its host, and when this effect causes more copies of that gene to make it into subsequent generations, this gene is under positive selection. Thus, natural selection can favor maternal altruism in part because a mother’s offspring is likely to share a significant fraction of her own genes (Hamilton 1964). Despite the fact that the “vehicle” in which the gene finds itself absorbs a cost to confer a benefit on another vehicle, the reality is that the genes in one vehicle are able to help copies of themselves in other vehicles. So what appears to be altruism at the level of the organism or “vehicle” is actually selfishness at the level of the gene (Dawkins 1983). This perspective can help to reveal the underlying genetic benefits of what often appear to be somatically costly behaviors, that is, behaviors in which one organism absorbs great personal costs to benefit another.

With this “gene’s eye perspective” it is possible to reexamine the reproductive benefits and somatic costs of warfare, beginning with some assumptions. First, assume a polygynous system in which male parental investment is relatively low and in which the primary limiting factor for

male reproductive success is access to females (Trivers 1972). Second, assume a world of two male coalitions that are roughly equal in size. Third, assume that these coalitions fight, resulting in the death of all males in the losing coalition, as well as the death of every male except for one individual in the winning coalition. Fourth, assume that reproductive resources and opportunities are allocated in a zero-sum fashion within the coalition. This means that the reproductive opportunities lost by the fallen equal the reproductive opportunities gained by the victorious survivors (Tooby and Cosmides 1988), which is made possible by the polygynous nature of the system. The result is that the reproductive benefits to the winning coalition are not diminished by its high mortality, but, rather, are reallocated among the survivor(s). The “last man standing” is therefore able to reap tremendously great reproductive benefits from this instance of coalitional aggression, despite the great somatic costs of the effort.

As Tooby and Cosmides argue, this situation therefore means that natural selection can favor a gene that motivates participation in somatically costly high-risk battles. Even if many individuals die from the effort, the zero-sum allocation of reproductive opportunities within the coalition means that the average fitness payoff to the members of the victorious coalition is not diminished by the death of one or even most of its members, assuming the above conditions are met. And since natural selection operates to favor strategies that are successful *on average* over evolutionary time (i.e., despite individual fitness reversals), a heritable propensity for participation in high-risk battles can spread in the population. Thus, even if the result is occasional death, the on-average reproductive benefits can outweigh serious and even fatal somatic costs to individual coalition members. This may be particularly true when a “veil of ignorance” exists regarding the prebattle distribution of risk among the coalition members.

The Strength and Existence of Selection Pressures. What has been shown is that it is possible for the reproductive benefits of risky battles to outweigh their related costs. The theoretical possibility on its own by no means implies that adaptations for warfare exist or that if they do exist,

they must be explained in this fashion. It is merely to suggest that adaptations for warfare can indeed be explained by natural selection operating at the level of the gene and the individual. The concluding section briefly engages the question of whether natural selection operating at other levels (e.g., the group) can explain the evolution of warfare adaptations.

First, however, a related question arises: given the possible ancestral existence of conditions that would have favored warfare adaptations, how strong must this selection pressure be in order for such adaptations to emerge? Recall that in order for selection to build adaptations, there must be some challenge or opportunity in the environment that is both recurrent and has fitness consequences for the organism. Thus, one common critique against the existence of adaptations for warfare is that even if there may be fitness benefits associated with coalitional violence, such behavior was actually extremely infrequent or even nonexistent ancestrally. In other words, one cannot claim that adaptations exist in response to an environmental event that was rare or nonexistent.

This challenge leads to two questions: (1) Did our ancestors engage in coalitional violence? (2) How frequently did they engage in coalitional violence? Unfortunately, the evidence does not allow a conclusive answer to either of these questions, forcing researchers to engage in methodological triangulation and to make educated guesses about the possibility and prevalence of ancestral coalitional aggression. Direct evidence of warfare, such as fossilized bone indentations, mass graves, and weaponry, is exceedingly rare and ultimately nonexistent as one peers further and further back in time.

Proponents of the evolution of warfare, however, point out that the absence of such evidence is not evidence of the absence of warfare; rather, the absence of direct evidence of warfare is instead the absence of the *instruments* of warfare, not of warfare itself. In that sense, the labeling of such evidence as “direct” is unfortunate and imprecise, since such evidence is actually indirect, not direct. Swords, mass graves, and fortresses, for example, are not requisites for coalitional violence, and

therefore their absence from the fossil record after a certain time period does not allow us to conclude that ancestral warfare was nonexistent. As Leblanc and Register wryly note: “The world was hardly peaceful until someone in China or Mesopotamia hammered out the first bronze sword” (2003).

This author has elsewhere engaged the question of the likelihood of ancestral violence, and it is a debate that has been vigorously argued on all sides (Pinker 2011; Allen and Jones 2014; Lopez 2016). However – and somewhat disappointingly for both sides in the debate – the very strongest claim that can be made regarding the existence of ancestral coalitional violence is that the evidence does not allow us to conclude that it did not exist. What seems clear is that unless it can be concluded (which it cannot) that ancestral coalitional violence was nonexistent, even the infrequent recurrence of coalitional violence could very well have provided enough of a selection pressure to favor adaptations for warfare. As has been well explored elsewhere, what appear to be quantitatively small selection pressures at one point in time can sum to very large impacts over evolutionary time (Dawkins 1986). Thus, claims that chimpanzee coalitional violence is not recurrent enough for selection to favor adaptations for warfare fail both theoretically and empirically. In theory, they underestimate the power of natural selection to operate on even the slightest fitness differentials. Empirically, clear evidence demonstrates that the rate of chimpanzee coalitional violence is sufficient to yield significant reproductive benefits (Wilson et al. 2014).

Coalitional Psychology

The previous section explored the structure of reproductive opportunities that could lead selection to favor the emergence of adaptations for warfare. However, in addition to the existence of opportunities, the right equipment is necessary in order to take advantage of such opportunities. Coalitional aggression is fundamentally a collective action problem, and participation in warfare therefore requires a degree of cognitive design for navigating a host of coalitional challenges. In short, adaptations for warfare presume the

existence of an evolved coalitional psychology that is designed to solve problems relating to the building, maintaining, and enforcement of within- and between-group relationships (Lopez et al. 2011).

The complexity of this task is not to be underestimated and requires cognitive mechanisms that perform a range of tasks, such as the following: identify and punish free riders; respond and yield to leadership; and regulate the distribution of resources. In short, collective action for aggression presumes cognitive machinery that quickly and reliably solves a range of related but distinct n-person challenges.

One characteristic of the inseparable link between the unique challenges of warfare and the broad toolkit of coalitional psychology is the immediate and reliable way in which the former triggers the latter. Experimental research in the lab and in the field has repeatedly and powerfully demonstrated the effect of intergroup conflict on within-group cooperation. Specifically, the prospect or actuality of intergroup violence is sufficient to trigger a host of within-group dynamics such as an increase in the overall level of cooperation, greater desire to reward participants and to see noncooperative individuals punished, as well as the associated emotional displays of within-group solidarity and shame or guilt among bystanders (Gneezy and Fessler 2011).

The effect of intergroup conflict on within-group collective action is twofold. First, warfare operates as an “effect multiplier” by enhancing many of the dynamics necessary for the prosecution of collective action in general, such as punitive sentiment toward free riders. Second, warfare triggers a unique set of psychological mechanisms designed specifically for intergroup competition and aggression, such as the tracking of in-group/out-group membership (Kurzban et al. 2001) and relative coalitional formidability (Parker 1974). These two effects of warfare on collective action dynamics mean that researchers must be careful to distinguish between those adaptations that are uniquely designed for warfare and those that are designed for collective action but triggered in the context of coalitional violence. The two sets of adaptations are necessarily integrated yet distinct.

As one example of the integrated nature of adaptations for collective action and adaptations for warfare, Tooby and Cosmides (1988) outline the “risk contract of war,” which outlines the psychological conditions that must be met in order for coalitional violence to be initiated against an out-group. The risk contract consists of two broad components: first, regulation of the individual’s decision to participate and, second, the enforcement of the agreement (or risk contract) on others. The individual decision of whether to participate is regulated by variables such as formidability, the degree of perceived risk, and its expected distribution within the group, as well as the expected distribution of spoils antebellum. The enforcement of the risk contract on others depends on an individual’s ability and willingness to pay costs to reward and/or punish others for the sake of labor recruitment and alliance maintenance. Thus, while the main challenge of the first component is one’s own willingness to participate, the main challenge of the second component is to manipulate the willingness of others.

In short, adaptations for warfare presume the existence of an evolved coalitional psychology that enables solutions to the complex coordination problems posed by intergroup violence. Taken together with the previous section, the overall discussion so far has explored the evolutionary feasibility of both low- and high-risk coalitional aggression, the power of even weak selection pressures to build complex adaptations for warfare, and the role of coalitional psychology for facilitating intergroup violence.

Auxiliary Observations Regarding the Uniqueness of Human Warfare

The above discussion outlines some general conditions that make the evolution of warfare adaptations possible. These conditions alone do not explain or attempt to describe the full range of psychological adaptations that possibly exist in humans for engaging in coalitional violence. Doing so would be the next logical step and requires careful adaptationist analysis of specific

reproductive challenges that is beyond the scope of this brief and general inquiry (McDonald et al. 2012; Lopez 2016). Nevertheless, some brief observations should be made that necessarily complement the preceding adaptationist inquiry into warfare.

Research on the evolution of war and its related psychological adaptations should not blind researchers to the very real and powerful “other half” of the story, namely, the evolved human capacity for peace. The existence of adaptations for warfare does not undermine the case for adaptations for cooperation, alliance, or reconciliation. Indeed, the psychology of cooperation and forgiveness among groups is well studied (McCullough 2008). The most fruitful way forward in these respective areas of research (on war and cooperation) is to examine the ebb and flow of motivations and dynamics related to each. For example, when and why do conflicts escalate or deescalate? Such a question can only be answered by acknowledging both the human capacity for violence and the human capacity for cooperation.

Researchers must also carefully examine sex differences in aggression. There is tremendous evidence of reliable and cross-cultural differences in the way males and females reason about and engage in warfare (Van Vugt 2009; McDonald et al. 2012). The theories of sexual selection and parental investment (Trivers 1972) provide a basis upon which to explain the distribution of sex differences within and between species, and these theories have also been used to successfully explain a range of sex differences in humans, particularly regarding individual and coalitional aggression (Van Vugt 2009). Importantly, the evidence does not show that females never fight; rather, the relevant distinction is to be found in the conditions under which males and females fight (Brooks and Valentino 2011; Lopez et al. 2011).

Research Note: The Levels of Selection Problem

The above discussion has focused on the fitness costs and benefits of warfare for individuals and genes. For instance, under certain conditions, genes that code for behavior-regulatory

mechanisms that motivate participation in warfare can spread either because of the associated benefits that accrue to the individual or *despite* significant costs – even death – to the individual. In the latter case, a gene can spread despite costs to the organism when the on-average result is genetic selfishness. This process is known as genetic selection and can result in patterns of behavior as seemingly dissimilar as maternal altruism and battlefield heroism. In the former case, however, a gene can spread simply because it produces direct positive fitness consequence for the organism in which it finds itself. This is known as individual selection and is the more commonly understood level of selection in evolutionary theory.

In addition to genetic and individual level selection, however, it is theoretically possible for a gene to spread in a population because of the benefits it generates for the *group* of organisms in which it finds itself. This is known as group selection. This is significant for the current discussion because warfare can be thought of as a process by which some groups survive and expand while others whither and perish. Warfare is, at least in this superficial sense, a process of group “selection.”

As a rough illustration, if a heritable trait emerges within the individuals of a group that has the effect of making that group more likely to win battles, then these genes would prosper, while alternative genes in the individuals whose group was vanquished would disappear. The result would be that directional change in gene frequencies is driven by its effects on group success, not individual success. This conceptualization led early critics of group selection to claim that this process can only work when there is no migration between groups and when the rate of group extinction is high (Maynard Smith 1976). Later proponents of group selection argued that both early conceptions of group selection and restrictions offered by critics were excessive or imprecise (Sober and Wilson 1999; Nowak et al. 2010). More recently, scholarship has focused on the possibility that the evolution of warfare has occurred via the simultaneous interaction of multiple levels of selection.

Game theoretic evidence has modeled the viability of warfare evolving via group selection

given what is known about the likely prevalence of ancestral intergroup conflict (Choi and Bowles 2007). Nevertheless, critics of group selection continue to make two points in particular. First, the conditions are rare or absent that would be necessary for group selection to build complex adaptations, and modern genetic data are inconsistent with predictions from group selection (Langergraber et al. 2011). Second, although group selectionists argue that behaviors such as “prosociality,” heroism, and other forms of social altruism can only be explained by group selection, critics argue that these are adequately – and more parsimoniously – explained by natural selection operating at the individual or genetic level (Williams 1966; Price 2012).

Conclusion

The foregoing discussion is an attempt to outline a set of conditions that may facilitate the evolution of adaptations for certain forms of intergroup violence. After defining the relevant terms, this effort consists of several components. First, it is necessary to carefully identify the reproductive costs and benefits of fighting and to identify the conditions under which the benefits of warfare would have outweighed its related costs. Second, if current or subsequent research can demonstrate that these conditions held ancestrally, then support is greater for the possibility that some features of human warfare can be explained as products of human adaptations for intergroup violence.

Adaptations for warfare can evolve when coalitions are faced with recurrent and reproductively significant opportunities for low-risk/high-benefit violence. Resultant adaptations should carefully monitor relevant variables such as relative coalition size, the element of surprise, and opportunities for escape – the ancestral analogue of the “exit strategy.” Indeed it is known that in chimpanzees such opportunities exist and are reproductively beneficial, and the pattern of raiding behavior conforms to this adaptive conditionality (Wrangham 1999; Wilson et al. 2014). Raiding in humans does not perfectly conform to the chimpanzee model due to the fact that human raiding

can entail higher physical risk to participants, and inter-coalition relationships are characterized by peaceful as well as agonistic relationships.

Adaptations for warfare can also evolve even in the face of steep somatic and reproductive costs, as long as the fitness benefits of coalitional violence are even greater. This is possible in a world in which reproductive resources and opportunities are allocated within the victorious coalition on a zero-sum basis. Although a high-casualty war of attrition between two large coalitions results in sizeable fatalities for both coalitions, the zero-sum allocation of reproductive resources for the winners means that the surviving victors stand to reap tremendous reproductive benefits. When selection is operating at the level of the gene, the result can be adaptations that motivate what appear to be individually irrational and even reckless participation in violent conflict. In other words, selfish genes can motivate risky behaviors in individuals when the reproductive benefits over evolutionary time outweigh the fact that such behavior can occasionally lead to individual death.

Warfare is a collective action problem and therefore presumes the existence of cognitive machinery that enables individuals to solve complex coalitional coordination problems. Thus, in order for warfare to evolve via natural selection, the reproductive benefits must outweigh the related costs of warfare, but individuals must also be able to navigate complex coalitional landscapes in the first place.

In addition to an elaboration of the conditions for the evolution of warfare and the search for ancestral evidence that such conditions existed, future research should continue to dissect the information-processing structure of adaptations designed for warfare by examining the adaptive logic of related motivations such as revenge, intergroup anger and reconciliation, xenophobia, morality and sacred values, and sex differences in aggression. Last, but not least, researchers must continue to develop models of multilevel selection to understand the complex interplay of selection pressures that operate not only at the level of

the gene but also at the level of individuals and groups.

Cross-References

- ▶ Aggression
- ▶ Chimpanzee Raiding
- ▶ Coalitional Relationships
- ▶ Competition Between Groups
- ▶ Cooperative Alliances
- ▶ Costs of Aggression
- ▶ Evolved Psychology of Warfare
- ▶ Lethal Violence
- ▶ Male Warrior Hypothesis
- ▶ Sex Differences in Aggression
- ▶ Violence

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Confidence

► Self-Esteem as Manipulative Status Communication

Confidence Judgments

► Metacognition

Configurations

► Facial Expressions

Conflict

► War

Conflict Between Parents and Offspring

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Synonyms

Interbrood conflict; Intra brood conflict; Mother-fetus conflict

Definition

The conflict of interest between parent and offspring that arises as a result of the differences in the optimal level of parental investment from the perspective of the parent and the offspring.

Introduction

L'Innocence, a popular eighteenth-century painting from French artist William-Adolphe Bouguereau, depicts a very young mother holding a sleeping infant affectionately nestled into her bosom. As its title implies, the painting's serene imagery connotes the supposed innocence of infancy, when offspring needs are eagerly fulfilled by mothers with no hint of conflict between parent and child. The notion of interminable harmony between parent and child is, however, wholly detached from the reality of parent-offspring relationships observed in nature. Conflict between parent and offspring is routine. An extreme illustration of this is infanticide – a behavior that is observed in a range of species including humans (Daly and Wilson 1988). From an adaptationist perspective, there should be contextual factors that influence the level of parental investment in any given offspring; not all situations are optimal for one to raise children. For example, young women who have many future opportunities to reproduce are more willing to sacrifice investing in a current child when environmental conditions

are poor. Across cultures, there is indeed a decrease in the rate of infanticide with increasing maternal age (Wilson et al. 1995). Concealed in the tranquility of Bouguereau's painting is the reality that the young mother portrayed is at greater risk of abusing, neglecting, or killing the infant she holds if the circumstances of raising this infant are not favorable (i.e., harsh ecology, low resources, poor infant health).

Why should conflict ever arise between parent and child? The idea of conflict between parent and child might seem, at a cursory glance, counterintuitive. After all, the ability of offspring to survive and eventually reproduce constitutes a parent's reproductive success. This brief review will start with the logic of parent-offspring conflict theory. The focus will then shift to a summary of the empirical work on parent-offspring conflict with a specific focus on the literature on humans. Readers interested in broader discussions of parent-offspring conflict theory are encouraged to read: Godfray (1995), Salmon and Malcolm (2011), and Schomler et al. (2011).

Parent-Offspring Conflict Theory

At the core of Trivers' (1974) original formulation of parent-offspring conflict theory (POCT) is Hamilton's rule, the fundamental formulation of kin selection theory (Hamilton 1964):

$$rB > C$$

This simple expression delineates the conditions under which altruistic behavior (behavior that benefits another individual at a cost to the actor performing it) is expected to be favored by natural selection. When the net benefits (in terms of reproductive fitness) gained by the recipient (B), discounted by the relatedness (r) between the actor and recipient, exceeds the fitness costs to the actor (C), then one can expect the costly action (i.e., altruism) to be performed. The relatedness coefficient (r) can range from 0 to 1. This coefficient, a representation of the probability that any two individuals share the same allele at any given locus, is critically important to POCT. The

relatedness between a parent and offspring is $r = 0.5$: an individual allele present in a parent has a 50 % probability of ending up in any of their given offspring. Parents and their offspring are expected to share the same alleles (across *all* loci) 50 % of the time. Critically, while a parent shares 100 % of its alleles with itself ($r = 1.0$), an individual parent only shares 50 % of its alleles with a given offspring. Herein lies the conflict: the optimal level of parental investment of resources from the parent's perspective differs from the optimal level of investment from the perspective of the offspring.

The intensity of conflict should depend on how much parent and offspring disagree (i.e., the “gap” between the two optima). Individual offspring values the benefits of parental investment twice as highly as their parents. How, then, should resources be allocated among offspring? This is a key adaptive problem that parents are confronted with (and have been confronted with across ancestral development). Resources can include calories (food), time, protection, attention, and anything that imposes a cost on the parent by reducing that parent's future reproductive success (see Bugental et al. (2012) for more examples). Resources are finite; any resource allocated to one offspring come at a cost to other offspring (current or future). All else being equal, mothers should be expected to distribute their investment equally among (current and future) offspring since mothers are equally related to each of their offspring ($r = 0.5$). An individual offspring is perfectly related to itself ($r = 1.0$), but its relatedness with each of its siblings is $r = 0.5$. From the perspective of an individual offspring, each can benefit by receiving a greater portion of investment (relative to its siblings) than parents would prefer to give. Mothers wish to allocate resources evenly, while each of her offspring is motivated to secure a disproportionate amount of the resources for themselves. Any allocation decision that results in a cost to the parent and a benefit to an offspring has the potential to become an arena of within-family conflict.

Models of parent-offspring conflict. These tradeoffs are not explicit calculations of fitness costs and benefits on the part of parent or

offspring. Predictions derived from POC models do not suppose that this conflict over resource allocation need be conscious and POCT does not exclusively refer to observable behavioral conflict. Within the framework of POCT, conflict is defined more broadly as the *conflict of interest* between parent and offspring. Early POC models provided the foundation for researchers to quantify the extent of conflict between parent and offspring. These “battleground models” focused on the opposing fitness interests of parent and offspring and helped explain how conflict might be expected to vary as a function of key environmental characteristics (e.g., resource availability, reproductive potential of offspring) (Godfray 1995). Subsequent models helped scientists form predictions regarding how these conflicts might be best resolved (i.e., who “wins”; when to expect compromises; how compromises deviate from the optima of parent and/or offspring).

POC theory is often framed as a battle over resources between a *single* offspring and its mother. As detailed above, the conflict is also a battle over the division of resources between current and future offspring (i.e., among siblings). Mothers not only seek to preserve resources for their own survival, but (ultimately) they also wish to retain sufficient resources to invest in the survival and reproductive success of additional offspring. POC models that focus more explicitly on sibling-competition fall into two overarching categories: interbrood and intrabrood conflict.

Intrabrood and interbrood conflict. In those species that produce multiple offspring concurrently (e.g., avian species that produce multiple offspring per clutch), *intrabrood* conflict among offspring selects for adaptations that can distort the distribution of resources in early development. Each individual offspring can benefit by skewing investment toward themselves and away from other siblings in the current brood. In such cases, each offspring can appeal directly to parents for a greater share of resources and, in essence, attempt to monopolize resources away from rival siblings who also need these to survive. Despite mothers being equally related to each of the offspring in a given brood, some offspring in the brood will

receive a greater share of investment, while other offspring will receive much less.

While POC in the intrabrood sense focuses on the division of resources among members of a current brood, these models are not appropriate for those species that raise multiple dependent children of different ages. In human families, each offspring competes for investment with current offspring and with future siblings. This *interbrood* conflict applies selection pressure to human parents specifically with regard to mechanisms that influence the total amount of investment supplied across a parent's reproductive career. From this interbrood POC perspective, one can expect that offspring will be selected to force parents to supply resources that the parent would otherwise prefer to withhold for future reproduction. Parents must then be equipped with mechanisms that can facilitate discriminative solicitude (Daly and Wilson 1988) to allow parents to make "informed bets" on a given offspring by assaying a wide range of relevant environmental cues such as the availability of resources and the reproductive value of any given child (detailed in a subsequent section).

Interbrood competition is a substantial source of POC in humans. Humans' families include multiple dependent children of different ages. Older children are competing with younger siblings for resources well before those younger offspring are born. However, due to the extended period of immaturity in humans, the resources that older and younger offspring compete for may not be identical. For example, an offspring in utero does not directly compete with her toddler-aged sibling for their mother's energetic resources (i.e., calories). However, a mother that invests energy toward fetal development does so at a cost to her older child. Her toddler may have benefitted from this additional energy in the form of additional vigilance or protection. In both the intrabrood and interbrood models of POC, conflict is often (ultimately) resolved by a compromise between parent and offspring. Parents will invest slightly more than optimal but still less than what would be optimal for a given offspring.

Life history theory. All organisms are expected to be equipped with adaptations shaped by natural selection that allocate resources optimally (within the constraints of the species) across the lifespan in accord with the specific demands of the environment. Life history theory provides a theoretical foundation from which to explore how parents might allocate resources among competing life tasks and how (and why) allocation strategies may differ across a parent's lifetime. Among the most fundamental tradeoffs that parents face in their lifetime is that of current vs. future reproduction. In viewing POC through the lens of life history theory, one can form specific predictions regarding the timing of reproduction and model the precise costs and benefits of reproduction and parental investment and how these costs and benefits may differ within an individual's lifespan (Schlomer et al. 2011).

Effort put into reproducing now will use resources that cannot be used for future reproduction. Parents face the risk of crossing an investment threshold, above which resources invested into current offspring would have produced greater (fitness) returns if these parents instead had allocated those same resources to future offspring. In terms of the *costs* of current reproduction, life history theory focuses on the factors that predict such costs as reduced offspring quantity, reduced offspring quality, and reduced somatic investment (a parent's own growth and survival). For example, those with a greater probability of reproducing in the future (i.e., an individual at the beginning of their reproductive career) will be expected to withhold resources from current offspring (potentially leading to reduced offspring quality) and thus the greater the potential for POC with current offspring. Thus, the intensity of POC is significantly influenced by life history relevant factors such as a parent's age, resource availability (e.g., calories, social support, time), and the level of harshness or unpredictability (i.e., rates of morbidity and mortality) in the surrounding environment. While the divergence of interests between parent and offspring (as well as between siblings) is omnipresent, the lens of life

history theory allows researchers to predict the shifting parameters of the zone of conflict across a parent's lifespan. Life history theory provides a broader context for POCT and allows scientists to formulate more concrete hypotheses about the influence of specific environmental factors on the intensity of POC.

Factors Influencing the Intensity of POC

From a biological standpoint, all children are important. Offspring are a parent's vehicle for getting genes into the next generation. The quixotic notion of a parent sacrificing one's self for offspring – no matter the cost or the situation – is at odds with the predictions of POCT. Decades of empirical work have uncovered some factors that shape the degree of conflict between parent and child and the stages in life (for both parties) that amplify or dampen the level of POC. These factors often influence the cost-benefit calculation of investing (or not) in a given offspring and can include age of parent, age of offspring, number of offspring, sex of offspring, an offspring's reproductive value, resource availability, and the degrees of relatedness between parent and offspring.

Child reproductive value. According to POCT, parents should discriminate among offspring according to markers of fitness. Fitness refers to the reproductive value of an offspring – the expected reproductive success of that individual. An offspring's fitness can be communicated through cues reliably associated with the probability of surviving and reproducing such as age (discussed below) and markers of the offspring's quality like size, health, and competitive ability. Resources are finite, and natural selection should have favored any mechanism that allowed parents the ability to gauge the probability of a child's expected future reproductive prospects. It is not likely that selection would have favored a mechanism that allocated resources to offspring indiscriminate of reproductive value. Across human ancestral development, a child that is unhealthy

or extremely unlikely to survive would have been a bad investment for a parent to make.

How likely is a child to convert each unit of investment into future reproductive success? This is the critical adaptive problem that parents have faced for millennia. Early cues of offspring quality should be of particular importance to human parents due to the exorbitant needs of neotenuous human infants. Infants who show early cues to low quality (e.g., disability, physical deformity) would have been unlikely to survive (much less reproduce) in the ancestral past. Thus, one expects parental solicitude mechanisms to be sensitive to offspring quality very early in a child's life. Indeed, infants born with severe physical deformities and disabilities are much more likely to be victims of abuse, neglect, and infanticide (Daly and Wilson 1984). Mothers with low resources are particularly at increased risk to abuse or neglect their low reproductive value offspring. Specific to human fathers, there is some indication that they also possess mechanisms sensitive to the reproductive value of young offspring: nonresidential fathers' willingness to provide financial support decreased as signs of early health issues increased (Hofferth and Pinzon 2011).

When resources are in short supply or when a parent's local environment is high in environmental risk, parental investment is more effective when restricted to children more likely to survive. There are special circumstances, however, in which parents may invest *more* resources into needier offspring. Parental investment has opportunity costs. Importantly, investment beyond a certain level results in less improvement in an offspring's potential return (quality) than the previous unit did. It is expected that a parent that possesses ample resources can receive greater fitness returns by allocating more resources to those offspring that need it most (provided that satisfying this greater need does not become deleterious to other offspring). Parents in higher resource environments can be assured greater reliability in their investment returns as parents in this context have greater direct influence on child survival and reproductive success. Prior work has provided

some support for this type of need-based investment strategy. For example, Davis and Todd (1999) conducted a computer simulation (with birds) in which a simple decision rule emerged as the most efficient feeding strategy: if resources are scarce, then feed healthiest chicks first; if resources are abundant, then feed neediest chicks first. Utilizing both experimentally varied levels and naturally occurring differences in parental resources, Bugental and colleagues (see Bugental et al. (2012) for review) found support for this model of investment among humans. Mothers who increased their cognitive-emotional resources (through an intervention) invested disproportionate amounts of resources in their needier children, while mothers that did not have these increased resources biased their investment toward healthier offspring. These researchers went on to demonstrate that maternal participation in this intervention predicted improved health of these “needier” children at older ages – an indication that the potential payoffs of investing in the neediest of offspring (when resources are abundant) can be realized in tangible fitness gains.

Genetic relatedness. POC is predicted to increase in intensity with a lower degree of relatedness between family members (i.e., between parent and child, between siblings). In the majority of mammals, females invest far more in offspring than males do. Due to internal fertilization and gestation, females have a distinct advantage over their mates when it comes to gauging relatedness: a female can always be assured that the offspring she believes to be her own are actually her genetic progeny, while males can never have this same degree of certainty. Males do however invest in children that they securely perceive to be their own. The costs of unwittingly investing in children that are, in reality, not a man’s own are substantial. Males then must be equipped with mechanisms that can alert them to cues of paternity. They must be prepared to invest in children only when such cues are present.

Prior work on human fathers has found support for the existence of cognitive processes that

evaluate offspring relatedness based on facial resemblance (e.g., Alvergne et al. 2010). Similarly, Daly and Wilson (1982) found that spontaneous comments about paternal facial resemblance following the birth of a child came more often from the maternal side (i.e., mothers and maternal grandparents) – potentially an attempt by a female’s family to help secure greater parental investment from her mate. In looking at investment in older children, Anderson et al. (1999) found that stepfathers invested substantially less financial resources in their stepchildren’s college education compared to that invested into biological children. A man’s genetic children were 5.5. times more likely to receive any financial assistance for college. In comparing just those stepchildren and biological children that received money for college, genetic children received much larger sums of money as well (on average, \$15,000 more).

Parents tend to be warmer and are more engaged in childcare activities with biological children than their stepchildren (O’Connor et al. 2006). Children living with one genetic parent and one stepparent are 40 times more likely to be abused than children living with both genetic parents (Daly and Wilson 1988). The rate of infanticide is correspondingly much higher in households where one parent is a stepparent (especially for very young children). These findings support the prediction from POC that a parent should wish to allocate resources preferentially toward children that are genetically their own.

Parent’s age. A parent’s age is expected to influence the degree of conflict between parent and child. Younger parents have more of their reproductive careers ahead of them, and thus, these parents should harbor resources in an attempt to maximize “reproductive success” (crudely, the number of healthy offspring that survive and reproduce). This should especially be the case if conditions for raising a child are suboptimal. Young parents, from an evolutionary perspective, can afford to be more discriminating in which offspring they choose to invest in and when to invest (or not).

Much of the evidence (in humans) has come from the work of Daly and Wilson (1984, 1988). The age of a mother was a significant factor in the likelihood of maternal infanticide. As POCT would predict, these young women (likely to have future opportunities to reproduce) appeared to be more willing to sacrifice a child when environmental conditions were poor (i.e., low resources). There is evidence to support the converse as well: older women were the *least* likely to commit infanticide. These women, closer to the end of their reproductive years, could not afford to pass up the opportunity to invest in their infants. Other work across cultures (e.g., Overpeck et al. 1998) also observed this decrease in the rate of maternal infanticide with increasing maternal age. These findings reflect the shifting costs-benefits of investing in a child as mothers get older. For mothers near the end of their reproductive window, foregoing an opportunity to raise an offspring becomes a much riskier bet.

Offspring age. The level of need from offspring does not remain static across development. In humans, for instance, infants require more time and attention than a child nearing the onset of adolescence. The decline in relative offspring need as children mature and the accompanying increases in the ability of older offspring to more immediately convert investment into fitness returns sets up the prediction that the value of offspring should *increase* as children near reproductive maturity. Older offspring (who have not yet reached sexual maturity) should be more valuable investment prospects than younger offspring.

Over the course of human history, mortality rates have been the most pronounced in early development, and this remains to be the case in developing societies. Volk and Atkinson (2013) estimate that approximately 27 % of infants failed to survive their first year of life and approximately 47.5 % of children failed to survive to puberty in environments that would have been similar to the environments that humans have inhabited through ancestral development. The average adolescent has a higher value than the average infant because so many infants do not even survive to become

adolescents. In Daly and Wilson's (1984) work, one again sees empirical evidence for a prediction from POCT: across cultures, it is the youngest offspring that are the likeliest casualties of murder at the hands of their parents. Infants are at a much higher risk of being killed by family members than any other age group, and the rates of children being killed *by parents* drops dramatically after the first year of life in spite of the finding that teenagers were the most likely to be killed at the hands of *nonrelatives*.

Number of offspring. The total amount of resources that a parent can allocate to offspring is finite, and, expectedly, these resources will be in shorter supply as the number of offspring increases in a given family. In humans, larger family size is indeed related to decreased levels of investment (of time) as parents in larger families were observed to be less involved in childcare activities (Lawson and Mace 2009). As family size increases, one also expects to see the downstream consequences of decreased investment such as smaller offspring size and decreased nutritional status. Larger family sizes are linked to decreased growth and decreased survival in humans (e.g., Hagen et al. 2006). If these developmental outcomes were consistently the result of decreased parental investment, one can predict that current offspring should be resistant to the prospect of a parent adding offspring to the existing family. Sulloway (2007) details some evidence to support this prediction: older children reverted to infant-like behaviors aimed at eliciting larger amounts of investment once a new infant was born.

Gender of offspring. Trivers and Willard (1973), using the logic of POCT, predicted that when one sex has a larger variance in lifetime reproductive success than the other sex and when there's variance between sexes in terms of access to valuable ecological resources, one can predict the context in which one sex would be "preferred" by parents. In humans, women have lower variance in reproductive success than men do. Mothers in poor conditions (i.e., low access to resources) are thus expected to prefer raising

daughters – a “bet” that carries less risk. In sum, parents in good condition will bias their investment toward sons, and parents in poor conditions will bias their investment toward daughters.

Evidence for the “Trivers-Willard effect” has come from historical data across cultures. For example, Bereczkei and Dunbar (1997) found that Hungarian gypsies (of lower status and correspondingly poorer access to resources in comparison to native Hungarians) had many more surviving daughters than sons. These gypsies also spent more time nursing daughters than sons and invested more in education for their daughters than sons.

In situations where possession of resources has a marked influence on male reproductive success, there should be a preference for sons over daughters. Among the affluent castes in India, a clear preference for sons can be observed (Gupta 1987). High caste families with sons that could marry women from any caste (as opposed to high caste women who could only marry from their own caste or higher) were more valuable as these sons had the potential to produce larger returns on parental investment. As a result, sons received a heavier share of investment than daughters. Infanticide among the higher castes was somewhat common before the twentieth century, and the victims were overwhelmingly female – adding support to the biased value of males over females in this specific environment.

Prenatal Parent-Offspring Conflict

The view of pregnancy as a time of agreeable cooperation between mother and fetus is incorrect. Any investment by a mother in an individual fetus’ development comes at a necessary cost to that mother’s ability to invest those same resources in other (existing or future) offspring. Investment in offspring survival and development starts well before offspring are born. It is expected then that POC should also begin at least as early in utero. A fetus’ best interests are served when it can increase maternal investment in utero beyond that of what a mother is selected to provide. A mother’s best interests are served when

investment in a fetus is close to levels in line with those that meet the minimum required for a fetus’ survival (thus leaving a greater share of resources for future fetuses). This conflict of interest over the optimal levels of investment in utero provides an arena for intense POC (Trivers 1974).

Pregnancy is a balance between a fetus’ attempts to procure disproportionate levels of investment from its mother and the countermeasures that a mother will employ to restrict the levels of resources allocated to the fetus (Haig 1993). The chief adaptive problem that a fetus must solve is that of survival in utero. The fetus must survive long enough to reach full term. Estimates of miscarriage vary across time and cultures, but a systematic review from Ammon Avalos et al. (2012) estimate that 11–22 % of pregnant women (from Western, industrialized nations) miscarry in weeks 5 through 20 of gestation. In spite of modern medical technology, early gestation continues to act as a type of sieve, where intense selection on the fetus has led to an audition of sorts where an individual fetus must meet a maternal threshold for quality or risk being eliminated.

Nutritional constraint. Fetal adaptations are designed to elicit large quantities of maternal investment across the full length of pregnancy. Mothers, equipped with adaptations designed to invest into each offspring more prudently, can limit nutrient availability to the fetus. Maternal nutritional constraint is estimated to contribute over 50 % of the variance in birth size (see Gluckman et al. 2005). In environments that are predictable and replete with resources, mother and fetus can resolve some of this conflict over nutritional resources through cooperating with each other (i.e., each can afford to compromise).

In those environments where the availability of resources is uncertain, however, this conflict can be disastrous for the mother and/or fetus. If the fetus survives, the restricted nutritional investment can cause enduring health complications well into adulthood. A deprived prenatal environment might calibrate a fetus to permanently develop a “thrifty phenotype” by being small and insulin resistant through the early postnatal period and into adulthood (Gluckman et al. 2005).

In turn, as an adult, the individual might be well suited to an environment in which nutrient supplies were limited (as their metabolic machinery “fits” with that of a resource-scarce environment). However, this individual would be more likely to be become unhealthy in a nutritionally *rich* environment – a scenario in which the postnatal environment is at a mismatch with the environment predicted from the prenatal period.

Blood glucose. For nonpregnant women, blood glucose levels rise after a meal but return to fasting levels once insulin is introduced from the pancreas. A pregnant woman’s insulin levels and her insulin response after meals remain typical until mid-gestation but rise considerably during the third trimester. It is noteworthy that, around this same time, insulin resistance develops, leading to a more prolonged elevation of blood sugar levels post meal. The high insulin levels combined with increasing insulin resistance in the third trimester appears paradoxical. Why would a mother’s body increase the production of insulin while simultaneously decreasing her body’s ability to utilize that insulin?

The answer comes down to intense POC in utero over nutritional resources. Once a meal is ingested, a mother and her fetus must then decide how to “share” the resultant increase in blood sugar (glucose). A mother can keep most of the blood sugar for herself if she can quickly produce sufficient levels of insulin to guide glucose into her cells (if she can reduce blood sugar levels quickly after eating). The fetus, having a vested interest in preventing maternal monopolization of glucose, can counteract this process by secreting human placental lactogen (HPL) – a hormone that increases maternal resistance to insulin (thereby maintaining elevated blood sugar levels for a longer duration which allows the fetus to acquire more glucose for itself). A mother, in response, can try to counterpunch HPL’s influence by further increasing her own production of insulin. The resulting POC escalation over glucose in the blood can have dire consequences for mothers. The benefits to the fetus (i.e., greater share of glucose obtained, increased birthweight) of increasing maternal blood sugar levels can come at cost to mother’s long-term health. If blood

glucose levels remain elevated, mothers increase their risk of developing gestational diabetes.

Maternal blood exchanges nutrients with fetal blood through the placental barrier. This process becomes another arena for conflict between mother and fetus. If the flow of maternal blood to the placenta is increased (e.g., through increasing maternal blood pressure), the quantity of nutrients allocated toward the fetus would also increase (Haig 1993). Mothers can combat “excessive” allocation of nutrients to the fetus by inducing the constriction of maternal blood vessels. The result of this tug-of-war over nutritional resources increases the risk of fetal-induced maternal hypertension. Chronically high blood pressure during pregnancy – a condition that would benefit the fetus thanks to the increased flow of nutritional resources – can result in preeclampsia, a condition that has the potential to cause permanent damage to a mother’s kidney and liver. In some cases, preeclampsia can lead to eclampsia, a potentially fatal condition. In terms of fetal development, it is clear that, despite a fetus’ reliance on the maternal circulatory system for all its needs, mother and fetus do not have completely overlapping interests.

Weaning Conflict

Following birth, the arena for conflict between mother and child shifts to the quantity of breast milk and the duration of breastfeeding. The duration of breastfeeding and the specific timing of weaning has significant relevance to the developmental outcomes of children.

In primates, it appears that weaning processes coincide with the resumption of mating (Maestripieri 2002). One expects weaning conflict to increase around the time when mothers begin to reallocate investment away from breastfeeding and toward producing new offspring. For example, some primate infants increase nipple solicitation when their mothers resume having fertile ovulatory cycles (Gomendio 1991). This strategy may be interpreted as an attempt by offspring to delay or prevent their mothers from reproducing.

Among the Turkana (of Kenya), conflict around weaning tends to be high when mothers resume sexual relations with their husbands (Gray 1996). Resumption of sexual relations represents a transition point where effort is being diverted away from parenting effort (cessation of breastfeeding) and toward producing additional offspring (renewal of fertile cycles). Young offspring should demonstrate particularly intense protest to the possibility of having their sole food source taken away and resist the addition of siblings to the mix. Haig (2014) proposes that disrupting a mother's sleep (i.e., night waking to suckle) is an adaptation of infants to extend their mothers' postnatal infertility (due to breastfeeding), thus delaying the birth of additional siblings. Breastfeeding suppresses ovarian function, and any adaptation that infants possess that can extend the duration of nursing (even for a few weeks) will be advantageous from the individual offspring's perspective.

Mate Choice

From an evolutionary perspective, parents should have a profound interest in their children's reproductive choices (e.g., *when* to commence mating, *who* to mate with). An offspring's choice of sexual partner and/or long-term mate can have a significant influence on the reproductive success of an entire genetic line for generations to come. Whether a society contains formally arranged marriages or individuals are essentially free to choose who to mate with, parents across cultures demonstrate varying levels of control over their children's mating partners (Apostolou 2011). Parents have their own reproductive interests at heart when evaluating an offspring's mate, but these interests, as mentioned throughout, do not necessarily overlap with offspring interests. The arena of offspring mate choice is one ripe with conflict between parent and child.

Parents may wish for their children to find a mate that complies with their own standards whereas their children will seek out mates that

are more compatible with their own preferences. Some evidence in humans suggests that parents and offspring disagree on timing of marriage, the age of an offspring's partner, and the importance of genetic quality in a mate (Apostolou 2011). While cultural differences do exist, offspring sometimes seek to compromise with their parents on the physical attractiveness, dependability, and family background of their mates. The data suggest that people are more willing to trade off physical attractiveness when selecting a partner for their children compared with a partner for themselves. In a sample of 443 young adults in Japan, parents and children disagreed on the acceptability of mating with a partner that had "poor" genetic quality (i.e., attractiveness, intelligence, creativity) – offspring viewed this as more unacceptable than did their parents (Dubbs et al. 2013). In terms of parental investment potential (e.g., family background, education) and cooperation with the in-group, however, being low on these traits was viewed as more unacceptable by parents than offspring.

Conclusion

The interests of parent and offspring only partially correspond. Natural selection favors adaptations in offspring that can help obtain resources beyond what parents are selected to give. Parents are equipped with mechanisms designed to resist providing resources too far beyond the optimum from their perspective. Whenever a given trait or behavior results in a cost to one party and a benefit to the other, parent and offspring are expected to disagree about the optimal levels of resource allocation. As demonstrated above, there are many arenas that one can expect to see POC. Conflict exists well before offspring are born and persists across the lifespan. Conflict between parent and offspring is ubiquitous across species and cuts across time and culture. The application of POCT to understanding the adaptive functions of specific decisions made by parent and child will be a fruitful area of research for generations to

come. Conflict between parent and offspring goes well beyond the conventionally researched parent-child skirmishes over chores, homework, behavioral problems, dating, or friendships. While the influence of POCT to evolutionary psychology has been pronounced, the impact of POCT to developmental psychology and other disciplines has only recently begun.

Cross-References

- ▶ Ecological Influences on Parent–Offspring Conflict
- ▶ Grandparental Investment and Genetic Relatedness
- ▶ Infanticide and Parenting
- ▶ Maternal and Offspring Condition
- ▶ Obligatory Parental Investment
- ▶ Offspring Diversity Hypothesis
- ▶ Parental Effort Versus Mating Effort
- ▶ Parental Investment and Parenting
- ▶ Parental Investment and Sexual Selection
- ▶ Parental Investment Theory (Middle-Level Theory in Evolutionary Psychology)
- ▶ Parent–Offspring Conflict
- ▶ Parent–Offspring Conflict (Trivers)
- ▶ Sexual Conflict and Sex Differences in Parental Investment
- ▶ Quantity Versus Quality of Offspring

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Conflict Between the Sexes

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Synonyms

Intersexual competition; Interlocus sexual conflict

Definition

A conflict between the evolutionary interests of individuals of the two sexes, mostly related to reproduction.

Introduction

Men and women's interests differ substantially in many areas of life – and where interests collide, there is the potential for conflict. From an evolutionary point of view, individuals' interests are almost exclusively related to reproduction. Thus, conflict between men and women is expected to arise when there is an asymmetry in reproductive interests and when the sexes pursue different mating strategies. These sex differences in reproductive strategies are largely explained by Trivers' (1972) parental investment theory, which states that there is a conflict for both males and females in how much time, effort, and resources to invest in mating versus parenting. The sex that makes the largest investment in offspring will also incur the highest costs from mating “mistakes” and as a result will be the most sexually discriminating, focus more on obtaining a long-term mate, and will be the sex in demand. In turn, the sex with the lower obligatory investment to compete more heavily with same-sex members for access to the higher investing sex and to adopt a more opportunistic, short-term mating strategy. In most mammals, including humans, one ejaculate during a sexual interaction suffices for males to pass on their genes to the next generation. For females, the minimally required investments are much larger. Should conception be successful, a female needs to invest in gestation and birth of her offspring, and after birth, lactation and childcare, causing females to be the more choosy sex. Thus, even though human males do invest heavily in offspring after birth (Geary 2000), women's obligatory or *minimum* parental investment is still larger than men's – causing intersexual conflicts. These conflicts – or rather, diverging reproductive interests – show themselves in mating strategies, mate preferences, and mate retention behaviors.

Mating Strategies

Among other things, discrepancies in minimum parental investments cause men and women to pursue qualitatively different *mating strategies* (Buss and Schmitt 1993), defined as the set of behaviors used by individuals to attract, select, and retain mates. If both sexes pursue their optimal mating strategy, conflict is likely to arise. Due to their higher physiological investments and the costs associated with these investments, women have evolved to be more discriminating about their sexual partners. Both a woman and her offspring would benefit most from a long-term, highly investing male, whereas men for men, short-term mating yields more reproductive benefits than long-term mating. Hypothetically speaking, a man mating with 100 women over the course of a year would likely have significantly more offspring than a woman mating with 100 men over the course of a year, which will likely only result in one pregnancy (Schmitt 2005). Indeed, compared to women, men report a greater desire for short-term relationships (Schmitt et al. 2001), have more permissive attitudes towards casual sex (Petersen and Hyde 2010), fantasize more about having sex with multiple partners (Malamuth 1996), and report desiring up to three times as many lifetime sexual partners (Buss and Schmitt 1993; Schmitt 2003). In a now-famous study, Clark and Hatfield (1989) showed that 75 % of the men but 0 % of the women approached by an attractive stranger of the opposite sex consented to a request to have sex that very evening.

However, just as long-term mating offers benefits to men, short-term mating may offer specific benefits to women. Greiling and Buss (2000) documented that women pursuing a short-term (extra-pair) relationship reported greater sexual benefits (e.g., having a partner willing to experiment sexually, obtaining greater arousal or being appreciated sexually), resource benefits (e.g., receiving expensive clothing or jewelry), and improvement of their attraction and seduction skills. Moreover, in addition to the differences between the sexes, there are also *within-sex* differences in the desire to engage in short-term

mating. Simpson and Gangestad (1991) introduced the Sociosexual Orientation Inventory to measure differences in people's willingness to engage in casual, uncommitted sexual relationships. Individuals can be classified on a continuum ranging from *restricted* – tending toward monogamy, prolonged courtship, and heavy emotional investment in long-term relationships, to *unrestricted* – tending toward promiscuity, quick to have sex, and desiring lower levels of romantic relationship closeness. Schmitt (2005) has shown that across 48 nations, consistent and large sex differences in sociosexuality appeared, with men generally being more unrestricted than women. Variation in sociosexual orientations, both between and within sexes, is likely to be partly influenced by environmental circumstances. For example, sex differences in sociosexual orientation are smaller in countries with more political and economic gender equality (Schmitt 2005).

As might be expected, the pursuit of qualitatively different mating strategies and the behaviors that follow from them might lead to considerable conflict between the sexes – after all, women might not be willing to consent to men's desires for casual sexual relationships, and men may not always give in to women's desire for commitment. Buss (1989b) focused on the specific emotions evoked by these kinds of conflict and showed that women were most likely to be upset and angered by men's greater sexual assertiveness and persistence. Men, on the other hand, were more likely to be angered and upset by women's tendency to require an emotional commitment before engaging in sexual behaviors. More recent studies have shown that men, particularly those who were focused on short-term mating and who rated themselves as attractive, tended to overperceive women's sexual interest (i.e., the overperception bias; Haselton and Buss 2000). Conversely, women tended to underestimate men's desire for a committed relationship (i.e., the commitment skepticism bias).

Conflicts over sexual access – men's greater desire and women's greater hesitation – can cause anger and frustration in men (Shackelford and Goetz 2004), which in turn increases the likelihood of sexual coercion. Sexual coercion can take

on more subtle forms – threatening to leave the relationship or withholding gifts if a partner does not consent to sexual intercourse – but may escalate to forcibly raping one's partner. As such, sexual coercion may be an extreme mate retention tactic, aimed at keeping the partner invested in the current relationship and keeping her (or him) from committing a sexual infidelity, and thereby reducing the risk of cuckoldry.

Mate Preferences

The type of mating strategy that is pursued also determines which characteristics are desired in a partner. Generally, the literature on mate preferences indicates that regardless of the type of relationship, both men and women value kindness, honesty, intelligence, and humor in a prospective partner (Buss 1989a), although there are also indications that these traits are considered luxuries rather than necessities (Li et al. 2002). Moreover, a long-term relationship requires both partners to make significant investments, which in turn causes both sexes to be more critical about a potential long-term partner's characteristics and to desire long-term partners with whom they can build a compatible and cooperative relationship (Li et al. 2002). Nonetheless, asymmetries in parental investments have caused sex differences in mate preferences, which are based on a prospective partner's reproductive potential – that is, the ability of an individual to invest in the growth, development, and competencies of offspring, and/or the genetic benefits he or she would confer to offspring. Thus, increased parental investment among men and women creates choosiness, which in turn causes the sexes to compete among each other in the domains the opposite sex values in a partner.

Women's Preferences

Given their larger obligatory investments in offspring and the associated higher costs of mating errors, it follows that women should be particularly choosy – for long-term mating as well as

short-term mating. Women's reproductive interests are served best from obtaining a long-term mate with the potential and willingness to invest social and material resources in her and their offspring (Buss 1989a). A man's reproductive potential is thus determined by his willingness to parent, his ability to invest material and social resources in his partner and children and genetic qualities which may increase his offspring's reproductive success. Because men with a higher societal status have better access to resources, women have evolved to value social status in long-term mates, as well as the internal attributes that signal the ability to attain high status or a leadership position – such as being a good judge of character, taking initiative, influencing people, and being assertive. Indeed, Li et al. (2002) showed that when mating decisions were highly constrained, women prioritized a minimum amount of social status before considering other mate characteristics. Thus, status seems a necessity rather than a luxury when women are choosing mates.

For short-term mates, women prioritize a male's physical attractiveness over his social standing (Li and Kenrick 2006), especially around the time of ovulation (for a recent meta-analysis, see Gildersleeve et al. 2014). Specifically, women require their short-term mates to be muscular, strong, fit, taller than they are, and masculine. Moreover, they tend to value bodily attractiveness over facial attractiveness for short-term mates (Li and Kenrick 2006). These preferences are in line with the strategic pluralism theory (Gangestad and Simpson 2000) which posits that given the trade-offs in mating and parenting, women are more likely to focus on desirable heritable qualities ("good genes") in situations where paternal investments are unlikely, such as in contexts of short-term or extra-pair mating.

Men's Preferences

For ancestral men, mating with a nonfertile woman would have been a reproductive dead-end. In women, ovulation is concealed, and female fertility peaks during their mid-20s and

declines afterwards. Men were thus faced with determining a woman's fertility based on external attributes and have evolved to focus on female physical qualities which signal fertility and youth due to their associations with high estrogen levels: full lips, soft hair, smooth skin, colorful cheeks, good muscle tone, and a low waist-to-hip ratio. Indeed, numerous studies have indicated that men place a premium on women's physical attractiveness, both for short-term and long-term relationships (e.g., Buss 1989a). However, similar to women, men prioritize bodily characteristics – particularly breasts and buttocks – over facial attractiveness in their short-term partners (Li and Kenrick 2006).

The search to attract the best possible mate causes sometimes fierce intrasexual competition, which is usually focused on the traits preferred by the opposite sex. That is, women compete within the domain of physical attractiveness, whereas men are more likely to compete over social status and resources. For most individuals, this competition causes a gap between what they ideally would prefer and what they can achieve. However, individuals with a high mate value are more likely to achieve their preferences and have greater reproductive success as a result. Indeed, high-income men report having more frequent sex and more biological children than men with a lower income (Hopcroft 2006), and highly attractive women are more likely to be married and have more biological children than less attractive women (Jokela 2009). In addition, men and women devote more effort to mate retention of high mate value partners than to lower mate value partners (e.g., Buss and Shackelford 1997).

Mate Retention

Once a partner has been successfully attracted, he or she needs to be retained. Some of the biggest conflicts between men and women can take place within a relationship, often causing the dissolution of the relationship. The loss of a partner inflicts costs on men and women, particularly a long-term

mate. One of the biggest threats to a relationship is a partner's infidelity, and worldwide, adultery is the leading cause of divorce and break-ups. To solve the adaptive problem of preventing a mate's infidelity, men and women have evolved sex-specific tactics to fend off intrasexual competitors and to retain their mate (e.g., Buss and Shackelford 1997). What the sexes have in common is a strong emotional response in the face of a threat to the relationship. *Jealousy* is evoked by the real or imagined presence of a romantic rival, and it involves feelings such as fear, suspicion, distrust, anxiety, and anger. Jealousy alerts the individual that the relationship is in threat, and it instigates a range of mate retention behaviors. Men and women differ in which aspects trigger their jealousy and the type of mate retention tactics they employ.

Jealousy Triggers

For men, a single sexual act of his partner with another male could result in a pregnancy, and thus, of him being cuckolded and unwittingly investing years of effort and resources in genetically unrelated offspring. Jealousy in men is thus hypothesized to be triggered more by his partner's sexual infidelity than by her emotional infidelity. In contrast, a woman's reproductive fitness is enhanced if she is able to monopolize her partner's investments and resources, and she must thus avoid her partner's redirecting these investments to another woman or child. Thus, a partner's emotional commitment to another woman – emotional infidelity – will evoke more jealousy in women than male sexual infidelity.

Indeed, when the two types of infidelity are pitted against each other and individuals are forced to choose the most upsetting element, more men than women select a partner's sexual infidelity as most jealousy-evoking, whereas more women than men report a partner's emotional infidelity as the most upsetting event (e.g., Buss et al. 1992). Similarly, men are more unforgiving of a sexual infidelity and more likely to break off the relationship because of it, whereas women found an emotional infidelity more unforgiving

and reason for a break-up. Since Buss et al. (1992) first reported these sex differences, this pattern of results has been replicated in numerous studies, across cultures and using different methods (for a meta-analysis, see Sagarin et al. 2012). Interestingly, these sex differences have been found to be enhanced in egalitarian societies (such as Norway) in which paternal investments are expected to be larger, and where the costs of a partner's infidelity are thus larger as well. Moreover, when there is *no* risk of conception – such as when an infidelity between an opposite-sex partner occurs with a same-sex rival – the sex differences in jealousy tend to disappear (e.g., Harris 2002).

Another sex-differentiated jealousy trigger is the rival itself. Specifically, the sexes differ with regard to the rival characteristics that are considered most threatening (for an overview, see Buunk et al. 2007). Specifically, since a woman's mate value is determined largely by her physical attractiveness, a romantic rival possessing such qualities will be attractive to men – and hence, threatening to other women. Indeed, studies have shown that women's jealousy is evoked most by physically attractive other women. Conversely, men's mate value is determined by his social status and economic potential, and it follows that for men, a rival displaying these qualities is most threatening. Indeed, these sex differences were repeatedly established, among heterosexual as well as homosexual individuals and across cultures.

Mate Retention Tactics

Once a threat to the relationship has been perceived, the necessity of mate guarding triggers behaviors aimed at retaining the partner. Men and women differ in the types of tactics they employ to retain their mate, as well as in the contexts in which these are employed. Among others, Buss and Shackelford (1997) showed that mate retention parallels mate preferences, such that men will attempt to retain their mate by engaging in resource displays like buying expensive gifts for their partner, whereas women are more likely to enhance their

appearance. Moreover, men more than women try to keep their partner away from other men and verbally and physically threaten their intrasexual rivals, whereas women are more likely to flirt with other men to evoke jealousy in their partners. More recently, research (e.g., Miner et al. 2009) has shown that a man's mate value is associated with specific types of mate retention tactics: Men with a high mate value are more likely to use mate retention behaviors that focus on enticing a woman to stay invested in the current relationship (e.g., by buying gifts), whereas low mate value men are more likely to engage in behaviors that function by inflicting or threatening to inflict costs on a woman for not remaining invested in the current relationship (e.g., by isolating her).

As the risk for infidelity increases, mate retention efforts are intensified. Having a mate with a high mate value increases the risk for infidelity and intensifies mate retention behaviors. Buss and Shackelford (1997) found that men married to attractive women and women married to high-income men reported more frequent and intense mate guarding. Also, men's mate retention efforts increase the more time they spend apart from their partners (Shackelford et al. 2007), and when their partner is near ovulation – a time when a female infidelity would be most costly (Gangestad et al. 2002).

Conclusion

Men and women differ in the obligatory parental investments necessary to ensure offspring survival (Trivers 1972), causing them to pursue qualitatively different reproductive interests. If both sexes pursue their own optimal reproductive mating strategy, conflict is thus likely to arise. This conflict is evident in (1) mating strategies – men desire and pursue short-term relationships, whereas women are focused on obtaining a long-term mate; (2) mate preferences – men place a premium on fertility and health, reflected in physical attractiveness,

whereas women desire a high-status, high-investing male; and (3) mate retention behaviors – men exhibit more mate retention behaviors when they are involved with an attractive female and when their partner is ovulating, whereas women perform more mate retention when their partner has a higher income.

Cross-References

- ▶ Coercion
- ▶ Cuckoldry
- ▶ Infidelity
- ▶ Interlocus Sexual Conflict
- ▶ Intersexual Selection
- ▶ Jealousy
- ▶ Mate Retention
- ▶ Mating Strategies
- ▶ Parental Investment
- ▶ Paternity Certainty
- ▶ Reproductive Strategies
- ▶ Sexual Conflict in Nonhumans

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Conflict of Mating

► Vigilance over Kin’s Romantic Relationships

Conflict over Parental Investment

► Parent-Offspring Conflict

Conflicts

► Controversies

Confluence Model

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Definitions

The Confluence Model is a general framework for understanding developmental processes by tracing the mutual influences between the individual and his or her social environment as they unfold over time to shape some characteristic of personality (Kihlstrom 2018). The general framework of the model has been applied to the study of sexual coercion that involve sexual behaviors whereby one of the individuals does not fully consent to the acts. Sexual coercion covers the use of physical force, threat, deception, or intimidation (Huppin and Malamuth 2016). Examples cover forced kissing and touching, verbal derogation, sexual rumoring, showing sexually explicit pictures or objects, threats to end relationship, and insisting on having sex. Similar terms are sexual aggression, sexual violence, and sexual harassment.

Introduction

Throughout history, the typical perpetrator of sexual coercion is a male. Self-reports show that men are far more often perpetrators, and women targets of sexual coercion, and that this sex difference holds up across cultures (Huppin and Malamuth 2016). The Confluence Model of sexual coercion combines evolutionary and feminist approaches in an attempt to cover more ground than any competing single factor models that stems from either feminist or evolutionary theory. In its most basic form, the model incorporates two developmental paths, each with relatively independent sets of characteristics that may interact or *mutually* influence each other to increase the risk of sexual coercion (Malamuth 1986, 1996). Men who experience harsh early environment

characterized by parental violence and/or child abuse may be at risk of coercive behavior toward women through two different paths. The first path proposes that delinquency/antisocial behavior leads to attitudes condoning violence that again leads to hostile masculinity (i.e., Hostile Masculinity Path). This multifaceted construct stems from feminist theory and covers a variety of ways men may relate to women. Men who believe interpersonal relationships are fundamentally exploitative; who are defensive, insecure, and distrustful towards women; or who get gratification from controlling and dominating women are at greater risk of behaving in sexual aggressive ways. The second path, stemming from evolutionary theory, proposes that delinquency/antisocial behavior leads to sexual promiscuity, characterized by emotionally detached (i.e., *impersonal*) and short-term oriented sexual relations (i.e., Impersonal Sex Path).

Theoretical Approaches

Feminists claim that sexual coercion is motivated by men's desire to assert power over women (e.g., Sanday 1981). Using group conflict as a framework, proponents of the feminist perspective claim that men – to preserve male supremacy – have constructed a patriarchal social system to dominate women. Within this perspective, sexual coercion is just one of several strategies that men apply to dominate and control women. Rape is considered the ultimate form of domination and serves to preserve the status quo in the power distribution of the two sexes. In explaining mechanisms underlying men's rape and sexual assault on women, feminists claim men are socialized to become aggressive and dominant, while women are socialized to become tender and empathetic, submissive, and dependent. Central to the feminist approach is that boys and girls are subject to parental and societal treatment that breeds sex differentiated attitudes toward the use of violence and sex roles, as well as sex differentiated emotional expression, sexual behavior, and desire. Also, pornography exposure and consumption are assumed to adversely and directly influence

boys' attitudes toward women and sexual violence.

Evolutionary psychology claims that cooperation between men and women has typically increased the survival of their common offspring. Prolonged childhood required sustained coordination of resources in our ancestors, and selection pressures has designed adaptations for love and attachment, along with adaptation for collaboration and cooperation. Still, conflicts are prevalent, and in evolutionary terms these typically stems from differences in reproductive interest between individual men and women known as sexual conflicts (Buss 2017). Trivers (1972) has shown that minimal parental investment is markedly higher for women than for men (e.g., pregnancy, childbirth, and nursing). (Pregnant or breastfeeding women need on average an additional 500 kilocalories each day (adding up to an equivalent of 50 kg fat over a period of 2–3 years). In ancestral times, these could only have been provided by a highly investing partner with sufficient resources.) The potential costs for woman mating with a man who provided low or no investment would be high. Furthermore, the potential reproductive benefits for women mating numerous men would be low compared to men who mated numerous women. This asymmetry of costs and benefits has through selection designed the human mind with numerous sex-differentiated adaptations or mechanisms. Preference for short-term sexual relationships is one. In general, men and women differ considerably in their orientation to sex that is void of affection or emotional bonds. Relative to women, men are cross-culturally generally more open to casual sex, they are more ready to accept one-night stands, and they desire casual sex more (Schmitt 2005). Other mechanisms include sexual exploitation tactics and sexual misperception, both assumed to affect the likelihood of men sexually coercing women. Sexual exploitation is gaining sexual access by bypassing women's choice (e.g., approaching women who are intoxicated, sleeping, or vulnerable in other ways). Sexual misperception involves a systematic overperception of ambivalent cues to sexual interest. Within the sexual conflict approach, the conflicting reproductive strategies

and tactics of the other sex may cause anger and hostility in both sexes.

Empirical Status

The Confluence Model has been subject to modification over the years, and the most recent form – the Confluence Mediation Model – underlines the combined effects of distal factors, specific risk factors, and proximate situational influences on sexual coercive behavior, and where the effects of individual factors may be mediated and/or moderated by other factors in the model (Malamuth and Hald 2016). While the central concepts Hostile Masculinity and Impersonal Sex have been subject to somewhat diverse operationalizations, the model – repeatedly being subject to empirical testing – has with few exceptions proven robust in cross-sectional, longitudinal, and laboratory studies. Further, support for the two paths of the model is found across samples of incarcerated and noncriminal men (for a review, see Malamuth and Hald 2016). Distal factors such as prior sexual violence (or intentions to do so), being subject to child physical or sexual abuse, delinquency or conduct disorder, or exposure to parental violence or family conflict are all found to be associated with men's sexual coercion of women in most studies (Tharp et al. 2012). In most studies, the effects of these distal factors are fully accounted for by the effects of specific risk factors and situational influences (Malamuth and Hald 2016).

In support of the Hostile Masculinity Path, Murnen et al. (2002) reported in their meta-analytic review that sexual aggression toward women was moderately associated with measures of acceptance of interpersonal violence, beliefs in interpersonal relationships being fundamentally exploitative, dominance/power, hostility toward women, and rape myth acceptance. The latter has also been reported to be significantly associated with sexual violence in two more recent reviews (Tharp et al. 2012; Yapp and Quayle 2018). Several of the studies covered by these reviews had examined the effect of hostile masculinity measures within the frame of the Confluence Model.

In support of the Impersonal Sex Path, Tharp et al. (2012) and Malamuth and Hald (2016) summarized that early initiation of sex (age at sexual debut), higher number of sex partners, casual sex relationship status, and number of casual sex partners all increased the risk of sexual coercion of women in nearly every study examined. It is predominately the casual, uncommitted aspect of the sex – not general sexual drive, desire, or fantasies – that increase the risk of sexual coercion (Malamuth 1996). Tharp et al. (2012) also identified a number of specific risk factors associated with sexual coercion including sexual risk taking, misinterpretation of sexual signals, heavy alcohol consumption, and extensive exposure to pornography. The latter appears to influence sexual aggression propensity even when other factors are accounted for in the Confluence Model, but the effect of pornography also appear to be moderated by personality factors such as agreeableness (for details, see Malamuth and Hald 2016). In younger samples of adolescent students, pornography exposure is clearly associated with unrestricted sociosexuality and not with hostility toward women or rape myth acceptance (Kennair and Bendixen 2012).

One of the core predictions of the model is the *mutual* influence of Hostile Masculinity and Impersonal Sex variables in predicting sexual coercion of women. The effects of factors from each of these paths are assumed interact to produce particularly strong predictive effects. However, this contention has not consistently received empirical support. Across studies, the interactive (i.e., multiplicative) effect of factors does not always contribute to the prediction of sexual coercion over and above the additional effect (e.g., Abbey et al. 2011). Further, through its recent developments, the added complexity of model has made it less testable. Finally, the Confluence model considers impersonal sex an outcome of delinquency and harsh parenting. However, preference for uncommitted short-term sexual relations may be considered an aspect of personality that has shown similar level of heritability (Bailey et al. 2000).

Conclusion

The Confluence Model represents the most comprehensive model for testing factors associated

with men sexually coercing women today. The central premise of the model is the convergence of several factors organized into two major constellations, or paths, the hostile masculinity and the promiscuous impersonal sex paths. The model combines evolutionary and feminist approaches to the understanding of sexual coercion of women and has received good empirical support.

Cross-References

- [Feminism](#)
- [Hostile Masculinity](#)
- [Sexual Coercion and Rape](#)
- [Sexual Harassment](#)
- [Sexual Violence](#)
- [Sociosexuality](#)
- [Types of Sexual Coercion](#)

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Conformity

- [Peer Pressure](#)

Confounding Use of Tools on Physical Tasks

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Synonyms

[Causal cognition](#), [Tool-use tasks](#), [Trap tasks](#)

Definition

Task manipulations that affect subjects' tool-use performance.

Introduction

Tool use is a widespread behavior among human and nonhuman animals (see Shumaker et al. 2011 for a review) and understanding which cognitive mechanisms underlie this remarkable behavior has been the subject of an important amount of research in the past decades (e.g., Sanz et al. 2013 for a review). Tool-use tasks that require subjects to overcome obstacles to get a reward have been important paradigms devoted to investigate causal knowledge in primates and birds (e.g., Call 2013). In this context, trap tasks – particularly, trap tube tasks – have been used extensively in recent years. Generally these tasks involve presenting subjects with a stick, a clear tube with a trap on its bottom part and a reward placed inside the tube next to the trap and outside of the subject's direct reach. Subjects have to use the stick to get the reward out of the tube while avoiding the trap in which the reward may fall (e.g., Visalberghi and Limongelli 1994).

Confounds in Trap Tasks

Strikingly, nonhuman primates perform quite poorly in trap tasks, and they require a large amount of trials to succeed. This poor performance has led some authors to argue that nonhuman primates fail to understand the causal relations between the different elements of this particular type of problem (i.e., tool, trap, and reward). Importantly, research has also shown that part of the difficulty of the trap-tube tasks is due to factors related to the specific presentation of the task. For example, the diameter of the tube and the tool might force the animals to push the reward out. This strategy might increase the difficulty of the problem, at least for nonhuman primates, since pushing the reward away increases

the distance between them and the food. In line with this observation, Mulcahy and Call (2006) presented great apes with a modified trap-tube task in which subjects could choose between raking the reward and pushing it out. Mulcahy and Call (2006) showed that subjects solved the task much faster than any other animals tested before. Another important finding was that in this modified trap-tube task great apes preferred to rake in rather than to push the reward out of the tube. Consequently, Mulcahy and Call (2006) suggested that forcing the subjects to get the reward by pushing it out might have caused the poor performance reported in previous trap-tube experiments.

While it is true that solving the trap task in few trials is consistent with the idea that subjects might have some level of causal understanding, it does not prove it. Other mechanisms – innate predispositions to avoid traps and learned heuristics (e.g., insert the tool in a particular location in relation to the trap position without understanding the effect that the trap has on the reward) – could produce equally successful behaviors. In this regard, previous studies have assessed the mechanism underlying performance in trap tasks by presenting subjects with the original trap task and a modified version of it. For example, Visalberghi and Limongelli (1994) used an inverted tube condition in which the trap was not functional because the tube was flipped 180°; therefore, the trap was above the tube and the bottom of the tube had no holes. The rationale behind this modification was that once the trap is nonfunctional, there was no need to avoid it. However, this modified version of the trap-tube task has been described as limited since there is no cost to continuing to avoid the trap. In order to circumvent this issue, Seed et al. (2006) developed a two-trap tube task in which a functional and a nonfunctional trap were located on the bottom of the tube. In two conditions, subjects – in this case, rooks – either had to push the reward into the nonfunctional trap to recover it from below or they had to avoid the functional trap and displace the reward over the nonfunctional trap in order to get the reward.

Although these conditions do control for some of the issues mentioned above, it is nevertheless vulnerable to criticism. This is because to succeed subjects could still be using learned heuristics rather than using the functional properties of the traps. Therefore, Seed et al. (2006) conducted two additional transfer tests, in which the causal relations integral to the task remained the same, but the appearance of the stimulus changed, thus preventing the use of certain perceptual features. Since one rook was able to transfer knowledge from the original trap problems to the two transfer problems, Seed et al. (2006) reasoned that the one subject might have understood something about the physical properties of the trap problem.

In a further attempt to investigate how successful performance is achieved in these tasks, Seed et al. (2009) presented great apes with two trap tasks: one that required the use of tools and one that did not. Strikingly, their findings showed that when eliminating the need for a tool, more subjects solved the task and they did so in fewer trials than subjects in previous trap task studies (e.g., Mulcahy and Call 2006; Povinelli 2000). The implications of this research are critical, and, as the authors argued, their findings suggest that “tool use is an activity that imposes cognitive demands of its own” (Seed et al. 2009, p. 33). In fact, Povinelli et al. (2010) have suggested that chimpanzees do not necessarily represent a tool as an extension of their body, and, therefore, tool use might require precise action monitoring. In this regard, trap tasks might be challenging problems because they involve not only having to avoid the trap but also monitoring the use of a tool. Therefore, when subjects only face one of these two problems (e.g., having to avoid a trap), their performance is remarkably improved.

More recently, Völter and Call (2014) presented great apes with a new trap task – a maze-like multilevel trap task. To succeed in this task, subjects were required to move a reward from the upper level of the maze to the bottom through open gaps placed at each of the three levels of the maze. Similar to Seed et al.’s (2009) study, Völter and Call (2014) investigated the role of tool use by presenting subjects with a condition

in which they could use a tool to move the reward and a condition in which no tool was needed – subjects could move the reward with their fingers. In addition, this new experimental paradigm allowed investigating the role that “planning” – defined as the anticipation of a series of sub-actions in order to achieve a final goal – played in trap tasks. Völter and Call (2014) argued that having to plan two actions (e.g., first, move the reward, and second, move the reward away from the trap) might have diminished subjects’ performance in previous tool-use trap tasks. Therefore, they expected that those subjects who had to use a tool to displace the reward would perform worse than those who did not – this would be particularly true when planning was required before making the first move. Völter and Call’s (2014) findings confirm previous studies showing that tool use imposes an extra cognitive load when subjects are asked to solve trap tasks (Seed et al. 2009). However, their results showed that tool use did not affect subjects’ planning abilities.

Theoretical Accounts

Thus far, research on tool-use trap tasks has shown that particular manipulations in the way the tasks are presented dramatically affect subjects’ performance. Strikingly removing a crucial component of these tasks – the tool – extraordinarily improves subjects’ performance. In an attempt to reconcile these findings, Frigaszy and Cummins-Sebree (2005) proposed a theoretical framework to help understand the mechanisms underlying performance in trap tasks. Their model incorporates the nature (i.e., egocentric or allocentric) and number of spatial relations, their temporal relation to each other (i.e., simultaneous or sequential), their specificity (i.e., prerequisite for a specific arrangement or orientation of one object to another or to a surface for efficient use), and their duration and stability over time (i.e., static or dynamic). What it is derived from this framework is that problems, such as trap tasks, are challenging because subjects have to consider two

concurrent issues – the use of the tool and the trap. Controlling the use of tool *and* understanding how the trap works might be a taxing cognitive activity when required to be performed in the same problem (Völter and Call 2014). Consequently, removing one of the actions from the problem (e.g., the use of the tool) facilitates subjects' performance (e.g., Seed et al. 2009; Völter and Call 2014).

Seed et al. (2009) have argued that at least three different factors could account for the cognitive load incurred by the use of a tool:

1. Splitting attention – the attentional load was suggested to depend not only on the complexity of the task but also on how familiar subjects are with particular action required in the task.
2. Cross modal matching – inferring functional information from visual appearance.
3. Response variability – individual preferences for certain actions (e.g., pushing away or raking in). While studies directly testing the role of tool use have offered empirical support for the first two factors (e.g., Povinelli et al. 2010; Seed et al. 2009; Völter and Call 2014), studies in which trap tasks presentation was manipulated provide some support to subjects' variability in tool-use preferences (e.g., Mulcahy and Call 2006).

Conclusion

Altogether understanding the cognition underlying animal tool use has been shown to be a complex enterprise. Contrary to what early studies on tool use, in general, and on trap tasks, in particular, had shown, some animal species can successfully solve these tasks when certain features are modified. Importantly, recent studies have also suggested that the use of tool imposes extra cognitive load, and, as such, it might hinder animals' successful performance. On this point, comparative studies on problem-solving abilities between tool-user and non-tool-user species will help to shed light on the role of tool use in cognitive evolution – since the few studies available on this issue are still far from being conclusive.

Cross-References

- [Nonhuman Tool Use](#)
- [Primate Tool Use](#)
- [Problem Solving](#)
- [Tool Use](#)

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Confusion Effect

- [Alarm Call Creates Confusion](#)

Congenital Adrenal Hyperplasia (CAH)

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Synonyms

[Adrenogenital syndrome](#); [Hyperadrenocorticism](#)

Definition

A genetic disorder present at birth characterized by a deficiency of the hormones aldosterone and cortisol and an overproduction of male sex hormones (androgens). In males this may manifest as enlarged penis, small testes, and early development of masculine characteristics. In females features include ambiguous genitalia, failure to menstruate, deep voice, and excessive hair.

Introduction

In 1932, the book *Sex and Internal Secretions* was published under the editorship of Edgar Allen. It represented a state-of-the-art compendium of work in the area of reproductive physiology and endocrinology. It went through three editions; the third and final was published in 1961, with W. C. Young as editor.

A quick check of the subject index fails to find a listing for “congenital adrenal hyperplasia.” There is, however, a listing for “hyperadrenocorticism,” and reference is made to pages found in chapters authored by J. Money and J. H. Hampson and J. G. Hampson. Today, if one googles “adrenogenital syndrome” or “salt-losing adrenogenital syndrome,” one will come up with 205,000 and 5,100 references, respectively.

Congenital adrenal hyperplasia (CAH) is the most prevalent cause of intersex for individuals with an XX karyotype. Its frequency of occurrence is reported as 1 in 10,000–18,000

(www.isna.org/faq/conditions/cah). The most common cause is a 21-hydroxylase deficiency. Affected individuals are exposed in utero to super-normal androgen levels as a result of excessive production of sex steroids, predominantly C19 steroids. In the case of genetic (XX) females, this androgen exposure may result in masculinization of the developing external genitalia, and such individuals were once referred to as “pseudohermaphrodites.”

The level of masculinization shows considerable variation. The neonates’ genitals can be rated on a five-stage progressive scale, developed by Andrea Prader and referred to as the “Prader scale.” The level of masculinization depends upon the timing of the exposure and the level of circulating androgens. The external genitalia develop during week 8–13 of gestation. This is often referred to as an embryologic “critical period.” If androgen levels are high between weeks 8 and 12, there will be labial fusion and the formation of a urogenital sinus. The genital tubercle, in rare cases, goes on to develop into a functional penis. If the exposure occurs after week 12 when the vagina and urethra have separated, only clitoral hypertrophy occurs. Genetic males (XY) with CAH don’t exhibit any hypertrophy of their external genitalia, as the fetal testis typically produces adequate testosterone, which is converted by 5- α reductase to dihydrotestosterone for genital development.

At early stages of embryologic development, embryos have both Wolffian and Mullerian duct systems. In genetic males, the fetal testes produce testosterone as well as Mullerian inhibitory factor (MIF); as a result, the Wolffian system proliferates and the Mullerian ducts regress. Genetic females don’t produce either testosterone or MIF, and the default developmental pathway for the human is that of Mullerian system proliferation, so the fallopian tubes, uterus, and upper vagina develop normally. In genetic females with CAH, the levels of adrenal androgen don’t appear sufficient to support Wolffian duct development, since, even in the most extreme cases, there is no obvious Wolffian development.

There are three different steroidogenesis enzyme deficiencies which may lead to

masculinization: (1) 3 beta-hydroxysteroid dehydrogenase deficiency (classic and nonclassic CAH), (2) 21-hydroxylase deficiency (salt-wasting, simple virilizing, and nonclassic CAH), and (3) 11-beta-hydroxylase (hypertensive classic and nonclassic CAH). All types of CAH require appropriate case management.

Early Work

According to Feder (2014), “examination of the history of CAH is a complicated matter. Though today it is clear that there is a close identification of genuine medical problems caused by CAH with the social problem atypical sex is taken to present, this was not always the case. Indeed, there is little evidence that ‘hermaphroditism’ . . . was associated with any condition we would regard as a disease or malady, as most forms of CAH obviously are now recognized to be” (Feder 2014, p. 25).

In the 1950s, Lawson Wilkens established a fellowship in pediatric endocrinology at Johns Hopkins Hospital. It was at this same time that John Money began his career at Johns Hopkins. Money joined John Hampson and his wife Joan; both of the Hampsons were psychiatrists and this couple, along with Money, was staff in Hopkins’ Psychohormonal Research Unit. It was this unit that developed an intersex care management routine, the “Hopkins Protocols,” as the five publications by this group, appearing between 1955 and 1956 in the *Bulletin of the Johns Hopkins Hospital*, came to be called.

In 1964, William Young, Robert Goy, and Charles Phoenix published a paper in *Science* in which they suggested that gonadal hormones had two specific forms of action in mammals. Fetal testosterone has an “organizational” action on developing organs, including the brain. The outcome of this action is anatomic and behavioral masculinization. The second gonadal hormone action is “activational” and begins at puberty. The hormones at this time bring about the development of secondary sexual characteristics and stimulation of species-specific sexual behavior. Work by Harry Harlow in 1965 established

that surrogate-reared and peer-socialized rhesus monkeys (*Macaca mulatta*) exhibit a number of sexually dimorphic behavior patterns during their prepubertal period. Goy provided validation of the “organizational hypothesis” by documenting the masculinization of the behavior of genetic female rhesus exposed in utero to testosterone propionate. More importantly, follow-up work by G. Eaton, R. Goy, and C.H. Phoenix with these pseudohermaphrodites as adults documented their ability to perform ejaculatory behavior with female partners when under testosterone treatment.

John Money, in his previously mentioned chapter, “Sex Hormones and Other Variables in Human Eroticism,” from *Sex and Internal Secretions*, reported on the situation of a total of 21 female hyperadrenocortical hermaphrodites who had been precociously virilized and then studied when feminized on cortisone therapy. Money stated that “only one of the older patients elected against, and none regretted a decision in favor of this feminizing procedure” (the surgical procedure referred to includes the reduction of clitoral hypertrophy) (Money 1961, p. 1398).

In their chapter, “The Ontogenesis of Sexual Behavior in Man” in Young’s book, the Hampsons cite work with 44 cases of hyperadrenocortical syndrome patients. In their final summation, they state, “one can conclude that an individual’s gender role and orientation as boy or girl, man or woman does not have an innate, preferred instinctive basis as some have maintained. Instead the evidence supports the view that psychological sex is undifferentiated at birth, a sexual neutrality in place of a Freudian bisexuality, and that the individual becomes differentiated as masculine or feminine, psychologically, in the course of the many experiences of growing up” (Hampson and Hampson 1961, p. 1413).

In 1972, John Money and Anke Ehrhardt published the book *Man & Woman, Boy & Girl* and in it presented data that he had collected on a group of 15 adrenogenital patients and their matched controls. In the chapter “Fetal Hormones and the Brain: Human Clinical Syndromes,” Money discusses not only sexual play but also

other behavior categories that appeared to be sex or gender dimorphic. These categories are: (1) Evidence of Tomboyism, (2) Expenditure of Energy in Recreation and Aggression, (3) Preferred Clothing and Adornment, (4) Maternalism, (5) Marriage, and (6) Romance. In the case of the presented data, there were significant differences of at least $P < 0.05$ on 9 of the 15 specific queries put to his subjects. However, Money doesn't discuss whether this seems consistent with the idea of androgen-related masculinization. Money discusses how cortisone treatment of this disorder began in the 1950s and thus prevented affected individuals from continuing postnatal androgen exposure. Money comments upon the situation of his androgenital cases in the following fashion:

There were some late-treated women with the adrenogenital syndrome who, even prior to cortisone treatment, manifested relatively little behavior that might be classified as more typically masculine than feminine. These women show that postnatally elevated androgen levels, persisting into adulthood, do not in and of themselves dictate a masculine gender role or gender identity. They also show that, if there is a permanent prenatal hormonal effect on a part of the central nervous system that mediates sexually dimorphic behavior, then it obviously is in some way selective. The selectivity may pertain to the timing and/or amount of fetal androgen exposure. An alternative explanation may be that postnatal gender-identity differentiation may be capable of overriding prenatal precursors, or at least of modifying them to an extensive degree. (Money and Ehrhardt 1972, pp. 104–105)

Money was a proponent of “sex neutrality” at birth, and The Johns Hopkins clinic treated intersex patients in a fashion consistent with this position. Money buoyed up this interpretation by referring to the success which had been achieved in the treatment of a genetic male who had suffered the loss of his penis during a botched circumcision. As John Colapinto (2000) points out, references to this case, which was under Money's management, are scattered across the introduction. Money suggested that any negative sequelae from his patient's gender reassignment were lacking. This would have been a medical success story if it had been accurate; however, Money was not truthfully presenting his patient's progress. In

reality, his patient experienced depression and instability and never felt himself to be female. There was eventually a second reconstructive surgery to re-masculinize his genitals as well as a name change from Brenda to David.

Paradigm Shift

The work carried out at John Hopkins is certainly important to a consideration of the organizational effects of gonadal hormones. In the case of humans, experimental work is ethically impossible, and so clinical cases, experiments of nature, become the appropriate approach. In the case of nonhumans, the identification of sexually dimorphic behaviors is fairly routine, and those that don't require concurrent hormonal support become most appropriate for a consideration of the validity of the organization hypothesis (e.g., canid urination patterns, prepubertal primate play, and sex behavior). The identification of appropriate sexually dimorphic behavior patterns for humans is more problematic. There are, however, a number of traits which seem to be commonly accepted, and these include (1) sexual behavior, (2) sex-typical, (3) spatial ability, (4) language facility, (5) aggression, (6) exploratory behavior, and (7) playmate preferences.

CAH is a clinical condition in which genetic females may end up virilized as a result of in utero exposure to abnormally high levels of adrenal androgens. Depending upon the timing and level of hormone response, the affected individuals should show behavior frequencies which are shifted in the direction of normal genetic males. In Money's first presentation of CAH psychosocial behavioral profiles, he included data on progestin-induced pseudohermaphrodites because he felt that the in utero androgen exposure the patients had received made them an appropriate comparison group for his CAH subjects. Perhaps an even more appropriate control subject group might be genetic female twins who were in utero with an opposite-sexed partner. There are studies that have examined possible sequelae from such exposure on a number of sexually dimorphic patterns, such as tooth eruption, attitudes, eating

disorders, and mental rotation performance. The paper by Vuoksima closes with the following assertion: “Finally, our results may reflect both prenatal hormonal and postnatal environmental factors, and these factors may be inextricably linked: Prenatal exposure to testosterone may subtly masculinize females, with the result that these girls may gravitate toward male-typical activities that enhance mental rotation ability” (Vuoksima et al. 2010, p. 1071).

Because of the in utero exposure to adrenal androgens, genetic female girls presenting with CAH should exhibit behavioral masculinization on those behavior patterns which have been identified as sexually dimorphic. In the case of humans, such validation of the organizational effects of prenatal androgen exposure has been reported for (1) aggression and activity and (2) toys and activities. Interestingly, work with vervet monkeys (*Cercopithecus aethiops*), as well as rhesus monkeys (*Macaca mulatta*), has provided data suggesting that a biological substrate may underlie the dimorphisms present in the play behavior and exploration shown in the nonhuman species. The biological basis for sexually dimorphic behaviors is certainly well-documented in nonhuman mammalian species. Studies of primates by Goy and others such as Melissa Hines and Kim Wallen have extended to a variety of topics. There are also data available relevant to the organizational hypothesis in the case of primates from a chacma baboon (*Papio ursinus*), caught in the wild as an adult, that presented as an XY male with gonadal dysgenesis (Bielert et al. 1980). This animal was deprived during development of the fetal testes outputs of testosterone and Mullerian inhibitory factor and as a consequence had a preadolescent female phenotype. When tested with appropriate sexual partners, it was clear that female behavior was exhibited at normal levels and that testosterone treatment was responded to in a fashion consistent with that of a genetic female (Bielert 1984). For human males presenting with complete androgen insensitivity, a female gender identity is adopted, and a female-typical sexual orientation (they are sexually attracted to men) was self-reported

(Wisniewski et al. 2000). Not unexpectedly, a report on the sex behavior of CAH females documented that most of the subjects were heterosexual but that the rates of bisexual and homosexual orientation were increased above controls (Meyer-Bahlburg et al. 2008).

Future Efforts

In the case of humans, it is relevant to consider cross-cultural differences in the view on and management of intersex conditions (Warne and Raza 2008). A study of young patients with CAH done in Malaysia confirmed reported increases in aggression for their CAH subjects, pointing out, however, that mean “T” scores of the children with CAH fell within the normal ranges of the normative sample, and closed with the suggestion that future studies be encouraged to insure a sample size sufficient to produce a rigorous study methodology (Idris et al. 2014). Studies on CAH have continued to receive detailed discussion in sources such as Cordelia Fine’s book *Delusions of Gender* and Robert Sapolsky’s recent volume, *Behave*. The suggestion made in Fine’s most recent book, *Testosterone Rex*, that studies focus on what particular features of boyish toys appeal to the male brain and what toy features might lead to nurturant activity, seems totally appropriate. Studies of this sort can build on work such as that by Corrine Hutt.

Conclusion

Future work in this area should be encouraged. It is time to approach sex and gender behavior differences in a more cautious fashion. Clinical studies on disorders of sexual development will continue to be important sources of information relevant to an appropriate consideration of the effects of in utero hormonal exposure as related to sexually dimorphic behaviors, and attention to their effective management should remain a concern (McCarthy et al. 2017).

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Conjugal Dissolution

- Relationship Dissolution

Conjugal Paranoia

- Jealousy: Psychiatric Diagnosis
- Sex Differences in Morbid Jealousy

Conjuality

- Benefits of Commitment and Marriage

Connection

- Eye Contact with Adults Versus Babies

Consanguineous Sexual Relationship

- Incest

Conscientiousness

- Five-Factor Model

Conscious Experience

- Self-Monitoring

Consciousness

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Synonyms

Awareness

Definition

An individual's awareness about self and its external environment

Introduction

The Cambridge English Dictionary describes consciousness as “*the state of understanding and realizing something*” (Dictionary 2017). A conscious state is characterized by access to a wide range of information to the brain at a point of time (Dehaene and Naccache 2001). Consciousness is a broad phenomenon. Attempts have been made to define various forms of consciousness. Self-consciousness is a form of consciousness where the awareness is focused on self (De Graaf et al. 2012). The individual who is aware of his or her physical, psychological, financial, social as well as spiritual state can be said to be fully self-conscious. An individual's self-consciousness varies from time to time. At a particular point of time, self-consciousness about physical well-being (e.g., health, body image) may be more evident, whereas at another point of time some other self-construct may be overemphasized. A form of higher-order consciousness makes humans aware of their past, present, and future (De Graaf et al. 2012). It helps in understanding the present and correlating or attributing it to the past and the future. It

also helps in making assumptions and predictions.

Consciousness: Perspective from Neuroscience

Consciousness is a fundamental brain activity. Consciousness is highly desired for performance of any cognitive task. Conscious activities need intactness of attention. Information processing and task performances operate at the conscious level as well as the subconscious level. Tasks operated consciously involve neuronal circuits that work coherently under top-down magnification of attention (Dehaene and Naccache 2001). The human brain contains various specialized neuronal networks for processing of information. Many of these networks process information that is readily available, whereas several other networks work in parallel to process information that is not readily available to conscious awareness, hence, referred to as unconscious processing of information (Wallace 2005).

Consciousness is predominantly (though not purely) an activity of the cerebral cortex. Cerebellum, though contains more neurons is not involved in regulation of consciousness (Tononi and Koch 2015). The prefrontal cortex, anterior cingulate cortex and their associated brain areas (reticular activating system) are responsible for maintaining consciousness (Dehaene and Naccache 2001). The working memory functions in close association with consciousness. The conscious state of mind readily accesses information from surroundings as well as from the memory stores (past experiences), which is required for task performance (Soto and Silvanto 2014).

Consciousness is a state. In a healthy individual, it fluctuates between fully awake state and deep sleep. In illnesses, it may get further diminished to the level of coma. Hence, it can be said that consciousness states range from comatose condition to fully awake state. These states are referred to as “state consciousness” (De Graaf et al. 2012).

A conscious state of mind carries many contents. These contents are mostly experiential (past

experiences stored in memory store) or factual. It refers to “content consciousness.”

Minimal consciousness is a state that refers to “individuals who show minimal evidences of consciousness and are unable to communicate” (Laureys et al. 2014). It is often seen in states resulting from extensive brain damage and during this state pain perception and emotional processing activities remain intact.

Consciousness is not merely being aware and responding to stimuli. An individual who is awake is not always conscious. Evidences support, that people with severe brain damage may have a state, where eye movements and opening are normal, as if the individual is awake but does not show any response to stimuli. A conscious individual is capable of experiencing stimuli, making prediction of events (anticipating), and will be capable of making decisions (Tononi and Koch 2015).

Consciousness: Psychological Perspective

In the brain, mental activities (e.g., information processing) occur continuously. Most of the mental activities are happening without the awareness of the individual, hence considered as unconscious in nature. Similarly, the brain receives information from multiple sources and attributes meaning to them, which do occur in a similar fashion (i.e., unconsciously) (Solms 1997). Conscious awareness results from the interaction between external perceptions (environmental stimuli), internal perceptions (experiencing emotion), and cognition (memory of life experiences) (Solms 1997).

Sigmund Freud had attempted to explain consciousness in his topographic theory of mind (Macmillan 2009). As per this theory, mind can have three processes: conscious, preconscious, and unconscious. Conscious process refers to the active awareness of mental activities and preconscious process refers to those ideas or mental activities that need effort to reach conscious awareness. Unconscious process is out of reach from the active awareness. The primary process “Repression” operates to conceal the unwanted or unacceptable ideas or thoughts (Macmillan 2009).

Unwanted interference of ideas or thoughts from preconscious state may affect the conscious state of mind, which is prevented by a mental force acting on the conscious–preconscious interface (Macmillan 2009).

Consciousness: From the Perspective of Spirituality

Explanatory models from spirituality explain consciousness as a journey that aims at expanding awareness from meeting the needs of sustainability to a state of flourishing (Heaton 2016). From a spiritual and philosophical perspective, consciousness has been one of the most difficult topics to address. Therefore, it has been aptly named by some as the “hard problem” (Shear 1999). The concept is too broad to be discussed in this brief chapter and hence, would be only superficially touched here. The Western philosophers describe consciousness in terms of either “dualism” or “materialism.” According to the theory of dualism, conscious mind is nonphysical in nature. Some may equate this “nonphysical” nature with that of spirit or soul, as described in various religious texts but the two views may not be necessarily similar. Further, this approach says that consciousness is nonphysical in nature and thus, not only is it invisible but is also beyond the reach of any physical instrument. Also, it is believed that the nonphysical consciousness and the physical/material body interact with each other in a complex manner and affect each other (Havlik et al. 2017; Sharma 2018; Gennaro 2019).

On the other hand, materialism believes consciousness is a by-product of neural activity of brain. This theory is easier to believe in light of the explosion of scientific knowledge and the invention of sharper scientific instruments that can record the most subtle activities of the brain. However, despite so many advances, there are significant explanatory gaps and materialistic theories are not able to explain all, thus leaving sufficient scope for other theories (Havlik et al. 2017; Gennaro 2019).

The Eastern philosophers have an entirely different view of consciousness. Here, it is believed

that consciousness is a matter of a different kind, i.e., *Prana*, or manifestation of cosmic energy. The Divine is the ultimate source of all cosmic energy and one could experience this divine energy within oneself through enlightenment. The state of enlightenment could be experienced through meditation and achieving a state of super-consciousness (Heaton 2016; Swift 2019). The Vedic philosophy, which has given birth to *transcendental meditation*, emphasizes on serial expansion of the horizon of consciousness through the meditative process in order to maintain harmony between mind-body-soul (Heaton 2016). The Vedas and the Upanishads clearly depict various levels of consciousness (lower consciousness: “ordinary state of wakefulness”; higher consciousness: “extra-ordinary state of awareness”). This extra-ordinary state is a state of harmony between existence, knowledge, and positive emotions (*sat-chit-aananda*) (Rao and Paranjpe 2016).

The Buddhist philosophy emphasizes on the state of consciousness (awareness). The mindfulness meditation, based on the Buddhist philosophy, encourages one to be conscious about the thoughts, emotions and behavior for their effective regulation (Rao and Paranjpe 2016).

Measuring Consciousness

The Glasgow Coma Scale (GCS) was developed to measure the level of consciousness, and over the past four decades, it has proved to be a useful tool for bedside assessment of depth of consciousness (Teasdale and Jennett 1974; Teasdale et al. 2014). It measures three different domains: best motor response, verbal response, and eye opening. It is simple and can give an accurate account of the depth of consciousness; hence, doctors as well as paramedics can use it without much assistance (Teasdale et al. 2014). The limitations of the GCS are: non-consideration of corneal reflexes, pupillary reaction, seizure or myoclonus into account. Similarly, in intubated patients, the verbal response score goes low, as a result of which the overall level of consciousness might be wrongly interpreted (Laureys et al. 2014).

Emergency Coma Scale (ECS) can be an alternative to GCS, for measuring the depth of consciousness (Takahashi et al. 2011). ECS quantifies the level of consciousness by taking eye opening, verbal response, motor response and orientation into account (Takahashi et al. 2011).

Consciousness: The Dilemma

In spite of the advancement in science, understanding the exact neural correlates of consciousness remains elusive. If consciousness is a matter of neuronal density and integrity, then cerebellum contains more neurons with integrity. If consciousness is all about awareness, responding, and predicting, then in this modern era, advanced computers and robots can do it faster and more accurately (Tononi and Koch 2015). But, is that all that accounts to consciousness? If yes, then something is missing unfortunately. If the answer is no, then extensive research is needed to understand the complex phenomenon of consciousness.

Conclusion

Consciousness is a basic function of the brain and is a complex phenomenon. With the help of consciousness, an individual meets the bare needs of life as well as the higher goals of life (spiritual enlightenment). Consciousness is a complex process in the brain that makes an individual aware of his/her body, mind, and soul so that the individual will be able to meet his/her survival needs as well as satisfying (pleasure) needs.

Cross-References

- ▶ Attention
- ▶ Attention and Memory
- ▶ Daniel Dennett: A Review of His Evolutionary Work
- ▶ Evolution and Self-Awareness
- ▶ Evolution of Self

- ▶ Meaning Making and the Self
- ▶ Self-Monitoring
- ▶ Self-Observation

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Consequences

- ▶ Positive and Negative Reinforcement and Punishment

Consequences of Imbalanced Sex Ratios

- ▶ Social Outcomes and Sex Ratio

Consequences of Possessing a Large Brain

- ▶ Costs and Benefits of a Large Brain

Consequent

- ▶ Selectionist Models: Implications for Behavior

Consequentialism

► Utilitarianism

such finitude that moral questions about how best to live one's life gain any traction.

A Strained Appeal to Divine Ends

Consequentialism and Suffering

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Synonyms

Pain/absence of pleasure; Utilitarianism

Definition

Consequentialism is a metaethical theory which requires that all the consequences of an action figure in determining whether it is right or wrong. The minimization of suffering and maximization of pleasure are the general desiderata for consequentialist moral evaluation.

Introduction

Suffering characterizes the human condition. This is evinced by the pivotal position it maintains in both the Christian doctrine of atonement and Buddhism's central focus on overcoming the suffering of oneself and others. From a general secular perspective, we recognize the breadth of possibility, the myriad courses of action open to us given our natural abilities, and despair in the knowledge that we can but satisfy relatively few of our desires. Nothing pains us more than our brute limitations, the stark fact of personal and collective potential unrealized. It is in the shadow of

Historically in the Western world, adherence to theism has provided a salve to this predicament. It is at least plausible that an omnipotent, omniscient, and benevolent deity (not unlike the God traditionally conceived of in Abrahamic religions) chose to create, as G.W. Leibniz suggests, "the most perfect world, that is, the one which is at the same time the simplest in hypotheses and the richest in phenomena" (Leibniz 1686, pp. 39). The perfection attributed to any such deity, following Isaac Newton's great discoveries in mechanics, was seen as inversely proportional to the need for miraculous intervention in the natural order. For a truly omniscient and omnipotent god would foresee the need to intervene and simply realize a different state of affairs if such a state was in any sense better for those supposedly created in the divine image. A deity that acts at a remove via natural laws or processes, or what are sometimes called "secondary causes," was considered more perfect than a god who must constantly intervene so as to correct or even alter aspects of its own creation. The lesson regarding the occurrence of human pain and suffering in this ideological framework was stark: Thank God it isn't worse!

Theological optimism of the foregoing variety, while not explicitly inconsistent, has nevertheless been strained to the breaking point in light of Charles Darwin's theory of evolution by way of natural selection. Darwin, a committed albeit liberal Christian throughout his early adulthood, labored mightily under the intellectual burden that accompanies accepting natural selection as the mechanism by which evolution proceeds. Nowhere is this struggle more forthrightly conveyed than in a 1960 letter he penned to one of his American contemporaries, the Harvard University botanist Asa Gray:

I own that I cannot see as plainly as others do, and as I should wish to do, evidence of design and beneficence on all sides of us. There seems to me too much misery in the world. I cannot persuade

myself that a beneficent and omnipotent God would have designedly created the Ichneumonidae with the express intention of their feeding within the living bodies of Caterpillars, or that a cat should play with mice. (Darwin 1888, pp. 105)

For Gray and Darwin alike, the problem was one of how to reconcile the idea of a beneficent deity with observations of atrocities transpiring in the biological realm. Nor was this exclusively a preoccupation of the nineteenth century mindset. With regard to the evolutionary process, philosopher Phillip Kitcher has recently remarked that, “Indeed, if we imagine a human observer presiding over a miniaturized version of the whole show, peering down on his “creation,” it is extremely hard to equip the face with a kindly expression” (Kitcher 2007, pp.124).

By far the most common way of responding to this “problem of natural evil” was (and for some still is) to depict the evolutionary process as ultimately progressive in spite of appearances to the contrary. This riposte predates Darwin’s elucidation of the mechanism behind evolution. Alfred Tennyson’s wildly popular poem *In Memoriam A. H.H.* (1850), a meditation on mankind’s place in the natural order and impact of scientific ideas like evolutionism on religious faith, is perhaps the quintessential example in this regard. In it he muses,

*Are God and Nature then at strife,
That Nature lends such evil dreams?
So careful of the type she seems,
So careless of the single life;
That I, considering everywhere
Her secret meaning in her deeds,
And finding that of fifty seeds
She often brings but one to bear,* (Canto LV, stanza 2–3)

The “single life” is presented to his Victorian readership as nothing but fodder for the evolutionary process. There is precious little grandeur in this view of life. If, however, such sacrifices are ultimately for the greater good, the consequences to which our all too human limitations blind us, hope remains:

*Who trusted God was love indeed
And love Creation’s final law –
Tho’ Nature, red in tooth and claw*

With ravine, shriek’d against his creed – (Canto LVI, stanza 4)

There is indeed a cosmic purpose or grand design if only we could but comprehend it. For the more sophisticated adherents of theistic evolution, then, the diversity of form and function in the living world can in fact be the result of evolution via natural selection conceived of as a secondary cause. Against those who would counter that careful scrutiny reveals natural selection to be a wasteful and cruel process, the theistic evolutionist appeals to human ignorance and limitation. We must judge the outcome and process from a blinkered perspective, one from which our world looks less like the product of perfection than it does the tinkering of a powerful but morally ambiguous entity. But if properly understood as a progressive goal-directed process, the ultimate purpose of which is to set the stage for human life and flourishing, evolution by means of natural selection is purportedly worth the titanic cost.

The Ends of Suffering Reconsidered

While such unfettered theological optimism may provide comfort to some, others find it badly wanting. Notice that it offers an unabashedly consequentialist justification. Consequentialism, a metaethical theory, requires only that all the consequences of an action figure in determining whether it is right or wrong. This leaves considerable room for differences of opinion over what makes for a *morally relevant* consequence. Pairing this permissiveness with a commitment to the idea that ends can justify means permits the theist’s construal of evolution as a genuinely progressive process (Ruse 1996). Suffering, especially of the nonhuman (animal or even early hominin) variety, is allegedly acceptable because it is presumed to be the means to a worthwhile outcome, namely human flourishing. For this conclusion to follow, human suffering would have to be of a fundamentally different qualitative kind or at least substantially different in terms of quantitative degree. Since Aristotle’s *De Anima* thinkers

the world over have urged it as a difference in qualitative kind. But establishing a mere difference in kind does not suffice to license unequal ethical consideration. It must also be shown that human suffering (and its complement pleasure) is of a kind which holds greater moral significance. That this is the crucial presupposition becomes all the more evident when noting that more than 99 % of all species that ever lived on Earth, roughly five billion species, are extinct (Stearns and Stearns 2000, pp.1921).

Justification for the inequality between human and nonhuman suffering is usually drawn from the work of philosopher John Stuart Mill. For Mill, the “higher” pleasures, such as those experienced when reading poetry or listening to Beethoven’s ninth symphony, are fundamentally different in kind from the “lower” human pleasures out of which they arise. Higher pleasures are more satisfying and, thereby, lend to greater overall happiness, which is the ultimate moral desideratum for a utilitarian consequentialist like Mill. While nonhuman animals might very well be sentient in the minimal sense that they have an interest in avoiding pain and suffering, the avoidance behavior that they exhibit is only instrumentally good as a means to satisfying the immediate base desires associated with survival and proliferation. Animals are not, according to this view, equipped for experiences like existential dread, anguish over the future prospects of their offspring, or lamenting the plight of genetically unrelated individuals at a geographical remove. Just as higher human pleasures are preferable to base human pleasures, so, too, is human pain and suffering supposedly superior to nonhuman suffering. Human sentiment was consequently thought to deserve more consideration in moral calculations. It was in this sense that Mill could claim that it is better to be Socrates dissatisfied than a pig satisfied (Mill 1861).

Roughly parallel thinking pervades the rationalizations of those who would accept the evolutionary sacrifice of countless nonhuman lives for human flourishing. But the problems facing this line of argument are daunting. First, it is less than obvious that the suffering

experienced by animals with sophisticated nervous systems merits any less moral consideration simply because it happens to be of a “lower” or instinctive variety. Animal rights and welfare advocates have offered cogent arguments to the contrary (Singer 1975). Second, even if one grants that the suffering of any token nonhuman is of a “lower” type and thereby of lesser moral worth relative to that experienced by a human, the sheer amount of animal suffering taken collectively over evolutionary time might well be enough to offset the happiness enjoyed by all current and future humans. A third problem is one of omission. While many find the trade of nonhuman suffering for human flourishing acceptable, intuitions diverge when the tradeoff involves the suffering of people in the past for the well-being of current or future humans. Human suffering has occurred on an epic scale. Only some of that human suffering can be attributed to evil or ignorant human acts. A good deal of human suffering has thus been due to natural causes. Theistic evolutionists must conclude that such past human miseries are collectively of lesser moral worth in the final reckoning: there is, or at least will be, greater human flourishing as a result. But this hedonic calculus involves more mystery than mathematics. For if nothing else, the legions of the tragically deceased continue to swell and will vastly outnumber the extant population at any foreseeable time. Perhaps just as worrisome is that our current (nature-induced) pain must also be worthwhile insofar as this suffering purportedly enables the well-being of future generations. At minimum, one can certainly understand why many remain unconvinced by the theological case for moral progress via suffering.

For others, it is nothing short of ironic that theistic evolutionists should resort to consequentialism as a way of addressing the issue of suffering. To see why, one must first understand how the maturation of population genetics and especially the advent of molecular genetics transformed questions about human suffering. If natural selection drives evolution via the differential survival and reproduction of heritable variations, favorable variations cannot be redistributed

randomly in subsequent generations. There must be some sort of transmission fidelity or inheritability between the fitness-enhancing phenotypic traits found in parental generations and the prevalence of such traits in offspring for cumulative adaptive evolution to occur. Discoveries involving the biochemical structure of genotypes revealed how and why transmission across generations is a more or less reliable and predictable process. But in so doing, it also engendered a new set of questions regarding the entities that are subject to the process of natural selection and the beneficiaries of selection, not to mention what it is that is being reliably transmitted from one generation to the next. Addressing these questions typically requires a distinction between “replicators” – entities which pass on their structure more or less intact through successive replications – and “interactors” – entities which bear traits and interact with their environment via those traits in such a way that their expected survival and reproductive success is determined partly by this interaction (Hull 1988). For most, molecular genes were obvious candidates for the role of replicators, while the individuals that bear phenotypic traits are better cast as interactors.

The implications of this division for the issue of human suffering could not be more profound. Within a theistic worldview, the “problem of moral evil” could be evaded by citing the existence and desirability of human free will. Morally evil acts and consequent suffering were cast as the outcome of error-prone humans acting in ignorance or with weakened resolve. This state of affairs was nevertheless preferable to a world in which initial conditions and natural laws determined all subsequent action on the grounds that cherished notions relating to moral responsibility are rendered seemingly irrelevant by hard determinism. But natural selection cares only for consequences measured in terms of the relative number and viability of the copies of genes (or gene combinations) produced in subsequent generations. The thoughts and intentional actions of human agents, when seen as evolutionary interactors, are of importance only insofar as these happen to coincide with the

survival and reproduction of the genes that they house.

Conclusion

At one fell swoop suffering’s role as one of the most intimate and powerful psychological motives in human history is reduced to its efficacy in directing the fleshy vehicles driven by our genes away from evolutionarily precarious situations. It is this “pitiless indifference” (Dawkins 1995) toward individual suffering and the apparent mockery it makes of free will that continues to disillusion human sensibilities. Theistic evolutionists were not so much wrong in thinking that consequences matter; it was just that in directing attention to the import of ultimate consequences they wound up undermining the relevance of those most precious to their own.

Cross-References

- ▶ [Charitable Giving \(Peter Singer\)](#)
- ▶ [Death](#)
- ▶ [Expanding Circle, The](#)
- ▶ [Free Will \(Philosophy\)](#)
- ▶ [Genetic Determinism](#)
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- ▶ [Science and Morality](#)
- ▶ [Selfish Gene, The](#)
- ▶ [Utilitarianism](#)
- ▶ [Western Perspectives on Death](#)

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Consolidating Familial Power

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Synonyms

Alloparenting
Family; Kin selection; Nepotism; Solidarity

Definition

In this context, consolidating family power refers to how adoption can help individuals support their kin and/or expand their familial social and economic resources.

Introduction

An important goal of evolutionary fitness is to ensure the passage of one's genes into future generations, including copies of one's genes that

are present in relatives (Hamilton 1963). One obvious way of doing this is to invest in one's own offspring so as to ensure the success of their shared genes (Trivers 1972). But parents can also increase their fitness by investing in copies of genes that reside in related, or even unrelated, children (Silk 1990; Volk 2011). There are two primary mechanisms at work under these circumstances: improving the success of non-offspring kin (kin selection) and improving familial access to social and/or economic resources (reciprocal altruism). These mechanisms are not necessarily exclusive of each other in enhancing familial power.

Kin Selection

Throughout history, raising offspring has been a challenging endeavor (Hrady 2011). Due to high mortality levels associated with adult lives (Volk and Atkinson 2008), the possibility of parents dying was quite real. In these cases, if the children were not of an age where they could independently support themselves (likely adolescence or beyond), those children would require substitute parental care (or alloparenting) in order to survive (Hrady 2011). Indeed, adoption of kin in contexts where the parents are still alive, but impoverished and/or incompetent, is found in many cultures including: modern Western countries, Brazil, and Peru; ancient Rome, medieval Europe, and Imperial China; and the Inuit, !Kung, Oceanic cultures, and West African cultures (Volk 2011). Thus this practice persists in modern cultures, in historic cultures, and in hunter-gatherer/agriculturist cultures. The benefits are relatively obvious as related by Hamilton (1963), such that investing in one's kin is beneficial so long as the net benefit to one's own genes (i.e., the costs to one's personal genes versus the benefit to shared kin genes) is positive. For example, a wealthy parent may face diminishing returns in continuing to invest in their own offspring versus investing in the offspring (i.e., nieces and nephews) of much poorer brother or sister. Finally, adoption may be a means

of promoting a family line when an adult lacks suitable offspring of their own due to infertility, death, and/or an inability to carry on the family lineage (e.g., Davis 2006).

Reciprocal Altruism

Another explanation for adopting kin or non-kin is reciprocal altruism. In this context adoption may be a way of securing economic assistance from the biological parents and/or adopted child (Demian 2004; Halbmeyer 2004). A relatively common arrangement is for the adopting parenting to care for a child when they are young and in return obtain labor and financial compensation from that child when they are older (Demian 2004). This arrangement is one way for wealthy adults to parlay their resources into benefits to their own genes at the expense of non-related genes.

Another form of reciprocal altruism that benefits the family is adopting for political or socially strategic reasons. These typically revolve around arranging future marriages and/or ending violent disputes (Halbmeyer 2004; Volk 2011). In these cases, the presence of the non-kin in the adopted family acts as a brake toward violence (e.g., adopting the son of one's enemy reduces their incentive to attack oneself) and/or as a catalyst toward marriage (e.g., adopting the daughter of an enemy or social rival increases their incentive to cooperate with you by arranging future marriages).

Conclusion

Adoption is a complex behavior that has roots in both reciprocal altruism and in kin selection. In either case, it can represent a significant benefit for the adopting family to expend resources in distantly related or unrelated children. The versatility of adoption in exchanging social and material resources for enhanced genetic fitness suggests that it was likely a widespread and viable

evolutionary strategy for promoting and consolidating familiar power.

Cross-References

- Adoption Preferences
- Evolutionary Paradox: Adoption
- Forms of Adoption
- Function of Adoption
- Resemblance

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Consonants

- Phonemes and Symbols

Conspecific Killing

- Chimpanzee Raiding

Conspicuous Consumption

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Synonyms

[Ostentatious consumption](#)

Definition

The acquisition of goods or services which have no purpose other than to display the possessor's ability to possess them.

Introduction

The Russian billionaire Roman Abramovich is said to have spent £285,000 for the purchase of the personalized car number plate "VIP 1". While for him this is a trivial sum, displaying it advertised his ownership of the car to potential vandals or, worse, to the international criminal community and therefore exposed him to some increase in personal risk. The benefits that outweighed this increase in risk are not immediately obvious. Surely not an improvement in the comfort or the performance of the car, which are clearly unaffected by the symbols on the plates, a remaining possible motive is the intention to inspire awe and admiration in those who understand the rarity and expensiveness of this object: conspicuous consumption

Thorstein Veblen

While the concept of conspicuous consumption goes back at least to John Stuart Mill (1848), Veblen's theory of the leisured class gave a solid conceptual foundation to this idea. His books are rich in examples. "The chief use of servants is the

evidence they afford to the master's ability to pay," rather than helping him in any useful manner (Veblen 1899, p. 62). Their cumbersome liveries and unwieldy uniforms are actually designed to prevent them from performing any useful or productive activity. Similarly, skirts persist tenaciously as fashion accessories because, not despite, they "hamper the wearer at every turn and incapacitate her for all useful exertion," thus unmistakably demonstrating that she does not need to work (p. 171). Corsets and top hats are among his other examples. The ostentation of these goods is intended to demonstrate that the owner has no need to spend time and energy pursuing the necessities of life. As Frank notes (2007, p. 30), understanding the principles of conspicuous consumption may provide strong clues to *prima facie* inexplicable quirky regularities of modern life, such as the different way men's and women's garments are buttoned. Like many things, buttons first appeared as a luxury, and displaying them had therefore an ostentation value, and they did appear at a time when wealthy men would carry swords and wealthy women would be dressed by their servants. Also, at the time when right-handedness was the (often forcibly enforced) norm. Unsheathing a sword worn on the left hip with the right hand would risk having the hilt caught by the fold of the jacket, if the latter had a women's button style. Conversely, a right-handed maid would find it easier to button her mistress' garment given the way the sides are buttoned. The position of buttons for men's and women's clothes was therefore the natural choice, and once a pattern is established and there are no strong reasons to change it, it persists by inertia.

The desire for conspicuous consumption is by no means exclusive to the western leisure class of the turn of the nineteenth century. While, as noted by Piketty among others (Piketty et al. 2014), the extremely rich nowadays work much harder than their predecessors, their pattern of consumption has changed only due to changes in technology: the 70-hour a week investment fund manager who collects expensive watches, drinks fine wine, and drives supercars is much more widespread than miserly Scrooge-like individuals. Economists have investigated the features of preferences that

allow the emergence of the Veblen effect, the willingness to pay more for functionally equivalent substitutes (Bagwell and Bernheim 1996): from diamond-studded smartphones and cufflinks to cruises to Antarctica or the outer space in addition to the Titanic style ones also available a century ago. The last example illustrates that to play their display role, items of conspicuous consumption, unlike diamonds, need not be forever. In fact, in societies where storage and security of durable goods might be a problem, these are replaced by the ostentatious destruction of perishable or vulnerable commodities, such as chiefs wastefully burning immense quantity of precious oil, in ceremonial feast among some Native American population (the so-called potlatch; similar events occur in New Guinea and among the Maori, the Koha, the Kula, the Moka; Ridley 1996, p. 122). That conspicuous celebrations become more so as the information about individuals' status becomes less reliable has been shown to be the case by Bloch et al. (2004) in their empirical analysis of wedding celebrations in rural India.

Going back in time much further, the widespread prevalence of the importance of decorative visible items unnecessary or even harmful to survival among preindustrial societies (Murdock 1967 and Murdock and White 1969), as well as the ease with which western explorers could acquire the friendship and trust of the indigenous leaders with trifles and other cheap but rare objects, suggests that the desire for conspicuous consumption is a universal trait of human behavior and has therefore been hardwired in the brain since before the dispersal from Africa 80,000 or so years ago. One of the earliest and most intriguing examples is hand axes, manufactured for over a million years. These axes are knapped in a highly symmetrical shapes and polished well beyond the necessity of practical use for butchering or hunting; and they are indeed often found unused and in large hoards (Kohn and Mithen 1999).

Conspicuous consumption is not only not exclusive to modern humans, but it is not exclusive to humans at all, with some evidence, in many animal species, of powerful males obtaining

and protecting large territories, much larger than it can be possibly be necessary to provide food and shelter to the family and subordinate individuals (Zahavi and Zahavi 1997, pp 28–29).

Status, Conspicuous Consumption, and Sexual Success

This universality of the desire for items of conspicuous consumption opens the question of its benefit to individual humans. Veblen (1899) identified a correlation between conspicuous consumption and a person status, defined loosely as the esteem in which society holds a person. Conspicuous consumption of goods such as luxury goods, which are “completely novel in evolutionary terms,” enhances status, and that desiring status is evolutionary hardwired to affect directly an individual's utility (Robson 2001, p. 24). Thus, in this literature, conspicuous consumption is seen as a way to achieve status, with the prevalent behavior being snobbism (attempting to display rare and unusual items, as theorized by Mason, 1981) or conformism (attempting to display items that indicate appurtenance to a group membership of which is hard to obtain). Corneo and Jeanne (1997) identify the number of consumers in society as one of the determinants of whether the desire for conspicuous consumption determines snobbism or conformism.

Of course attributing the universal desire for conspicuous consumption to the quest for status simply shifts the question. Why is status desirable? Given the ubiquity across time and cultures of this desire, this question can be reformulated more rigorously as “what is the evolutionary advantage of having a high social status?” If genes that make their bearer desire status, even at the potential cost in terms of reduced survival opportunities, as the time and effort spent acquiring conspicuous items are time and effort subtracted to survival activities, such as finding food and shelter, are to become established, then they must also confer some evolutionary advantage. It is widely recognized that status increases the availability and the quality of sexual partners and therefore confers a reproductive advantage

that might more than compensate for the survival costs incurred while trying to achieve status.

De Fraja (2009) is one of the papers that side-steps status and suggests that conspicuous consumption could emerge as a direct mechanism enhancing a personal reproductive success. The mechanism is the same as that proposed by Zahavi (1975) and described in detail by Miller (2009) and formalized by Grafen (1990): conspicuous consumption is a signal that members of one sex use to indicate to potential mates that they possess unobservable characteristics which are valuable to members of the opposite sex. To the extent that the ability to acquire items suitable for conspicuous consumption correlates with an individual quality as a parent, either because of a better genetic make-up or because it suggests the ability to provide food and shelter for children, choosing partners who can indulge in conspicuous consumption enhances fitness. The mechanism is essentially identically to that posed by Williams: “it is to the female’s advantage to be able to pick the most fit male available for fathering her brood. Unusually fit fathers tend to have unusually fit offspring. One of the functions of courtship would be the advertisement, by a male, of how fit he is. A male whose general health and nutrition enables him to indulge in full development of secondary [not physiologically necessary for reproduction] sexual characters [...] is likely to be reasonably fit genetically [...] In submitting only to a male with such signs of fitness a female would probably be aiding the survival of her own genes” (Williams 1966, p. 184). The hand axes mentioned above are a very apt instance of this, as well as being the earliest documented: the ability to manufacture these axes is a clear indication of dexterity, a genetic trait likely to be highly valued in potential mates (Kohn and Mithen 1999). The inherent danger in the activity, in an age where losing an eye or a finger seriously impaired a person’s survival chances, highlights the trade-off between survival and reproduction underlying the signaling theory of sexual selection: possession and display of many hard-to-make hand axes says to potential sexual partners “You should want my genes, because I am good with my hands, for me the risk of accidentally chopping a finger or losing an eye from a splinter is so low that it has

never happened, even though, as you can see, I spend a lot of time making these useless axes. And being good with their hands is something that you should want your offspring to be.” In modern days, Buss’s team systematically analyzed lonely heart columns and conducted surveys in 37 different societies and amply demonstrating how women prefer wealth in men, when men prefer youth in women (Buss et al. 1990). Ridley (2003, p. 54) argues that “men seek wealth because they know it attracts women,” as exemplified by Aristotle Onassis’s dictum that “if women did not exist, all the money in the world would have no meaning.” In her analysis of Murdock and White (1969) data, Betzig (1986) finds that “power predicts the size of a man’s harem” and wealth is a very good indicator of power. On the other hand, status and conspicuous consumption are not the only way to increase mate access: cultural displays may also play this role (Miller 1999), and Zahavi and Zahavi’s (1997, pp. 143 ff.) observe that, in some species, such as the birds known as Arabian warblers, prestige, as opposed to mere rank, determines the group’s dominant male’s degree of exclusivity of access to females.

Conclusion

In order to serve as a signal either to provide evidence of a more valuable genetic make-up or to establish status, the items a person displays need to be more valuable, rarer, and harder to acquire than those that are more easily available to the other members of society. This suggests that relative, rather than absolute, consumption should constitute the signal and hence valued by individuals, as argued long ago by Duesenberry (1949): we need to have more than our neighbor to be attributed a higher status. This has two consequences. Firstly, it pushes society in a rat race, with everyone having to run fast simply to “keep up with the Joneses.” It is a prisoner’s dilemma, whereby, if everyone were to reduce their consumption in the same proportion, everybody would be better-off, having the same relative position but with fewer of the costs (effort, risk, time) associated with the acquisition of items of conspicuous consumption, but from

each individual's viewpoint, acquiring more such items is beneficial because it enhances that individual's status. Evidence for the relative consumption hypothesis is mixed, however, whether from surveys (Maurer and Meier 2008; Kuhn et al. 2008) or from experimental evidence (Alpizar et al. 2005). Arrow and Dasgupta (2009) reconcile this evidence with the importance of relative consumption, by considering the role of future relative consumption.

Secondly, if individuals are willing to pay for items of no intrinsic value, then the structure of the optimal taxes in an economy, that is, of the taxes that minimize the loss of welfare of a country's citizens subject to raising a minimal level of income, is altered. If there are Veblen effects, that is, if the willingness to pay for a luxury item increases with the cost of the item, then adding to the cost with a tax also increases the consumer's willingness to pay, that is, the utility of owning it, so taxes can be raised without a corresponding reduction in welfare (Ng 1987). John Stuart Mill's preference for taxation of luxury goods was probably based on a mechanism of this kind. The structure of the optimal income tax is also changed when consumers care for status (Ireland 2001), with more emphasis for redistribution if the rich care more for status than the poor.

Cross-References

► Geoffrey Miller on Conspicuous Consumption

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Conspicuous Consumption (Marketing and Economics)

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Synonyms

Flashy consumption; Ostentatious consumption

Definition

Conspicuous consumption is the public consumption or usage of costly goods, services, or leisure activities out of the conscious or unconscious motive to display or enhance one's own social status, to indicate one's ability to pay for it and hence displaying one's own wealth despite the possibility to consume cheaper alternatives which yield the same functionality. So in principle conspicuous consumption is unnecessary (and often wasteful) consumption from a rational point of view which does not satisfy basic economic needs.

Introduction

Conspicuous consumption is not a new phenomenon. It probably has existed since humans use goods (e.g., cloth, weapons, music instruments). Remember the use of very expensive and hard to produce colorant purple by ancient roman

emperors or the luxury displayed publicly by most other aristocrats throughout our known history. But it was Thorstein Veblen's (1899) merit to provide the term *conspicuous consumption* by writing his analysis of the leisure class more than 100 years ago. All research in consumer behavior on this topic still refers back to Veblen's work although some scholars argue that it is indeed often cited but rarely read. While still at Veblen's times – and anymore in the ages before – conspicuous consumption was merely a phenomenon among the rich, industrialization, increasing prosperity for broader parts of the population, and the rise of the middle class lead to a spread of conspicuous consumption behavior in the century after Veblen.

Throughout the twenty-first century conspicuous consumption often was regarded to be irrational consumer behavior (cf. Shukla 2008). Homo economicus would not engage in conspicuous consumption, maybe that's why economists struggle to understand such behavior in its full depth. Mason (1984), who has also written two books (1981, 1998) on conspicuous consumption, provided a literature review about explanatory models for conspicuous consumption. His analysis of social psychological and rational economic models resulted in two points: (a) economists have not contributed much to a better understanding of conspicuous consumption up to that time, and (b) he suggested to utilize more psychological models in combination with economic ones to gain deeper insights. A more recent paper from Mason (2000) again criticizes economists' omission of extensive research on conspicuous consumption. His main objective for today's economy and politics is to find a way to stem the problem of wasteful consumption that comes hand in hand with mass conspicuous consumption behavior as well as to put our resources into "more productive economic activity" (Mason 2000, p. 123).

But at least one often used concept in consumer behavior research originates from economic research in the mid of the twenty-first century. Leibenstein (1950) coined the term *Veblen Effect*. This means that not only the quality or functionality of any product constitutes its value but also

its price. As a consequence products become more interesting for people who want to display their status through conspicuous consumption when their price rises – when the price falls (the product remains exactly the same) interest is decreasing. And Leibenstein made another explanatory note on the *Veblen Effect*: Indeed it will not be the price actually paid for a product that counts but instead the price, other people (the perceivers of the signal, the relevant reference groups, etc.) think was paid for the product. Such reflections will help to understand why today in wide parts of the world counterfeit products and branded goods are so often consumed.

In marketing probably a bit more research on conspicuous consumption was conducted (see next section). But within this field – not so in economics – several terms, such as prestige consumption, luxury consumption, and most often status consumption, are used similarly or sometimes even synonymously for conspicuous consumption. This may be due to the fact that there is no distinct definition of conspicuous consumption in the literature. Anyhow, such practice is not wise as some scholars note. Admittedly there is some overlap, but basically status consumption and conspicuous consumption are found to be two different constructs (cf. the discussion in Shukla 2008, pp. 26–27). Unfortunately also the relationship between these two constructs is unclear to some extent. While some scholars argue that one engages in conspicuous consumption first and then gains status, others have the opinion that it is the other way round.

Contemporary Research on Conspicuous Consumption in Consumer Behavior

In the twenty-first century, we notice that traditional consumer behavior research and evolutionary psychology are approaching each other which yields deeper insights and a more complete understanding of consumption phenomena. Geoffrey Miller and Gad Saad were among the first and most prominent scholars who analyzed marketing issues from an evolutionary point of view. Both have excellent chapters on conspicuous

consumption in their principal consumer behavior books *Spent* (Miller 2009) and *The Evolutionary Bases of Consumption* (Saad 2007). For Miller (2009, and Saad 2007 too) it is obvious that engaging in conspicuous consumption is a means of signaling fitness in the context of sexual selection. Referring to costly signaling theory the (high) price of a product is considered a benefit (and not a cost) in the context of conspicuous consumption. Not a small number of recent studies share this view of conspicuous consumption as a form of costly signaling.

To be regarded as a costly signal, a signal has to meet four criteria (cf. Nelissen and Meijers 2011). The signal (a) has to be easily observable by others, (b) has to be difficult to fake by others because of its high costs, (c) has to be associated with unobservable but desirable qualities of the signaler, and (d) has to entail some fitness benefit in the end. (a) and (b) could easily be fulfilled by publicly consumed expensive goods. (c) could indirectly be fulfilled since consuming such high-priced goods requires a certain level of wealth which may be acquired due to hard work, intelligence, competitiveness, long phases of good health in life, etc. Finally (d) is admittedly difficult to measure but could also be approached as shown by Nelissen and Meijers (2011) in the context of social interactions. So conspicuous consumption indeed could be regarded as costly signaling in an evolutionary sense.

Following Saad (2007) conspicuous consumption clearly has evolutionary roots. It is an universal and innate phenomenon. He discusses several empirical findings to underpin this point, among others the – from a traditional rational point of view – irrational fact that even poor people in all parts of the world try to enhance their status by engaging in conspicuous consumption (e.g., luxury apparel, watches, cars) although they cannot really afford it and should better invest their money in their daily needs. Often this ends up in buying and using counterfeit products (a topic of increasing importance in marketing and economics) to at least give the impression of being wealthy and having status. Understanding that acquiring and displaying status is a relevant human need leads to the conclusion that

conspicuous consumption is in principle not a typical irrational behavior (as older literature suggests) but a manifestation of some deeper (evolutionary) rationality.

Over the last years some lines of research in consumer behavior have emerged which are informed by evolutionary theorizing. To a great part that research focuses on intra- and intersexual competition. Among others Henninghausen et al. (2016) found that conspicuous consumption is a means for men to signal and enhance their status in intrasexual competition. Another male is a potential rival who should be outdone. The like was found for women (cf. Wang and Griskevicius 2014). Women engage in conspicuous consumption to signal other women that their actual partner shows high commitment to them (he cares for his wife, especially financially. A similarity to Veblen's (1899) vicarious consumption is evident). This is particularly valuable to prevent potential mate poaching by female rivals. Regarding intersexual competition, there is very interesting research such as a series of studies from Griskevicius et al. (2007). When mating motives are triggered both, men and women, tend to enhance their status and mate value by publicly engaging in conspicuous behavior. But differences occur in the way they do so. While men tend to increase their consumption of luxury goods, women tend to increase altruistic helping behavior. Private consumption (men) or private altruistic behavior (women) was not affected. So alongside the term conspicuous consumption, we may call this public altruistic behavior of women conspicuous altruism – it also qualifies as costly signal.

Further remarkable findings came from research on social benefits of conspicuous consumption. Nelissen and Meijers (2011) and others found that wearing luxury apparel results in more positive attributions from others and in preferential treatments in everyday social interactions. Surprisingly it also leads to the economically irrational fact that fundraisers on the streets receive more money from passersby when wearing luxury apparel than by wearing ordinary apparel (cf. Nelissen and Meijers 2011). And finally

there is research on so-called green consumption. Griskevicius et al. (2010) found that choosing green products may be due to status motives. When such products are costly and could be consumed in public (e.g., an ecofriendly but expensive Tesla car), they are best suited to display conspicuous altruism (the signaler shows that he cares for the environment AND can do so by using a really expensive product).

As a last point two small research streams in the field of marketing should be mentioned. As most concepts in marketing, scholars also want to measure conspicuous consumption in consumer behavior questionnaires. While most scales in that context were actually constructed to measure status consumption, Chaudhuri et al. (2011) developed an “11-item Conspicuous Consumption Orientation Scale.” They regard conspicuous consumption orientation as an “innate trait level, individualistic variable that motivates consumer to engage in visible forms of consumption in order to exhibit their uniqueness, as expressed through product selection and usage” (Chaudhuri et al. 2011, p. 217). Other marketing scholars found some changes in conspicuous consumption behavior by identifying *inconspicuous consumption* (Eckhardt et al. 2015), also known as subtle consumption. To some degree they attribute this shift – at least in wealthy industrialized parts of the world – to economic crises. Some consumers probably do not want to stand out to far from their community by engaging in ostentatious consumption. Implications for luxury brand manufacturers are, for example, to reduce their logo size on apparel. But the truth is that someone somehow must recognize what is worn – otherwise it probably won't make sense anymore to buy a more expensive product. The reference group will notice, and that is what it is all about in conspicuous consumption.

Conclusion

Present-day research taught us that conspicuous consumption is not the irrational behavior it once was considered to be but instead is basically an

evolutionary rational behavior. As Geoffrey Miller (2009) wrote, over the past 1000 years we have learned that we can display desirable traits by buying and consuming goods and services. Of course today's globalized market economy and consumer society could lead to maladaptations. All the more we should be sensible to the evolutionary roots of our consumer behavior.

Cross-References

- Conspicuous Consumption
- Costly Signaling
- Costly Signaling Theory
- Female Mate Choice (Intersexual Selection)
- Fitness Benefits of Costly Signalling
- Geoffrey Miller
- Geoffrey Miller on Conspicuous Consumption
- Intersexual Selection
- Intrasexual Male Competition
- Intrasexual Rivalry Among Men
- Intrasexual Rivalry Among Women
- Social Status and Economic Resources

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Conspicuous Leisure

- Geoffrey Miller on Conspicuous Consumption

Conspicuous Prosociality

- Altruism Displays Cooperative Potential
- Volunteering Publicly

Conspicuous Reputation

- Geoffrey Miller on Conspicuous Consumption

Conspicuous Waste

- Geoffrey Miller on Conspicuous Consumption

Construction Play

- ▶ Object Play
- ▶ Play and Tool Use

Consumption

- ▶ Feeding

Contact Sport

- ▶ Combat Sport

Contamination Vulnerability

- ▶ Sacredness/Purity/Disgust

Content Specificity

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Synonyms

Domain specificity; Functional fixity

Definition

The processing system and cortical correlates of encoding, storage, and recollection of learned information differ with the content of memories.

Introduction

Evolutionary processes cause each of multiple memory systems specialized to some degree, shaped by natural selection, to solve the adaptive problems posed by the environment which other memory systems cannot deal with. Humans have at least two qualitatively different systems of recollection based on the content, namely, declarative memory system and nondeclarative memory system. Declarative memory refers to the conscious storage and retrieval of information, and it can be declared by language, while nondeclarative memory involves implicit learning of skills, priming, and association (Squire 1992; Squire and Zola 1996). Declarative memory can furthermore be differentiated into two subcategories: episodic memory and semantic memory. Episodic memory is the memory of events, times, places, and associated emotions related to specific events, while semantic memory refers to the memory of concept-based knowledge independent of context and event (Tulving 1972). The taxonomy of memory systems provides an insight of functionally specialized, content-specific memory systems.

Biological Evidence of Content-Specific Memory

The study of functionally distinct cortical regions of recollection was first found in amnesic patients with brain damages. For example, the most-studied amnesic patient H.M. whose medial temporal lobes, especially the hippocampus, were removed can still learn new skills, but he cannot encode new episodic memories (Milner et al. 1968; Sherry and Schacter 1987). This lent the credence of two distinct memory systems (Squire 2009; Corkin 2002; Squire and Wixted 2011). Later on, the amnesia and animal studies found that the declarative memory largely depends on the medial temporal lobe (MTL) and its associated structures to encode and retrieve the information while nondeclarative memory system is independent of MTL (Squire 1992, 2004; Squire et al. 2004; Reber 2013). Additionally, the empirical

experiments conducted by Tulving and Thomson (1973) found episodic memory and semantic memory differ in encoding process, but not in retrieval process. The impairment of frontal cortex is related to the failure of encoding episodic memories (Janowsky, Shimamura and Squire 1989).

A growing number of neuroimaging and animal studies have investigated the cortical underpinning of recollection and provided strong evidence that the storage of different contents is associated with the activity in functionally distinct cortical regions. As for declarative memory, previous studies have found Wernicke's area for words (Wise et al. 1991) and distinct temporal cortices for memories of objects and faces (Wallis and Rolls 1997), showing that functional specificity exists in remembering different visual images. There are also pieces of evidences that brain-damage patients have content-specific deficits of lexical knowledge. For instance, patient M.D. cannot name fruits and vegetables but has no problem in naming animals (Caramazza and Shelton 1998). Meanwhile, the long-term storage of nondeclarative information is found associated with the cerebellum, basal ganglia, motor cortex, and premotor cortex (Reber 2013).

Adaptationism

In most memory studies, the stimuli that have emotional valence or adaptive importance are avoided (Klein et al. 2002). This experimental design does not take into consideration that our memory systems are designed to store the information which is critical for survival, such as offspring (Kendrick et al. 1992), the locations of food (Hampton et al. 1995; Hampton and Shettleworth 1996), environmental threat (Mineka and Cook 1993), and mating (Crews and Moore 1986). The content specificity of memory systems exists to permit encoding and retrieving appropriate content of memory efficiently in response to the adaptive demands from the environment (Tulving and Thomson 1973). Animals and humans, for instance, tend to avoid food which make them sick before. Semantic memory stores the extracted

invariant features from a series of events, whereas episodic memory has detailed information of an event. As Klein and his colleagues (2002) have mentioned, depending on the task, retrieval of memory can pull up content-specific information from episodic memory or semantic memory alone or both of these two memory systems.

Conclusion

Therefore, the content specificity may imply that multiple memory systems underwent distinct evolutionary paths and are designed to serve distinct functions (Sherry and Schacter 1987). The content specificity has its advantages. It can expedite information accessibility (speed) and retrieve relevant information to deal with the current task (accuracy) in multiple memory systems (Klein et al. 2002).

Cross-References

- ▶ Domain Specificity
- ▶ Functional Fixity

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Contest Assessment Strategies

► Evolution of Fighting Assessment Abilities

Contest Competition

► Intrasexual Violence and Aggression

Contests

► Dominance, Testosterone, and Cortisol

Contests of Aggressiveness

► Sexual Selection via Direct Male-Male Interactions

Context – Sensitivity

► Towards Methodological Pluralism in Psychological Sciences

Context, Environment, and Learning in Evolutionary Psychology

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Introduction

There is a widespread misunderstanding among social scientists that evolved psychological

adaptations are like reflexes or “instincts” – blind, inflexible, and insensitive to social and environmental circumstances. Nothing could be further from the truth. Evolved psychological mechanisms are environmentally sensitive and exquisitely context-dependent.

The purpose of this entry is to introduce the reader to the centrality of context in evolutionary psychology. To this end, we discuss: (1) the theoretical importance of context in evolutionary psychology, (2) the nature of evolved learning mechanisms, and (3) specific examples of context effects in evolutionary psychology.

The Importance of Context in Evolutionary Psychology

Environmental context plays a key causal and explanatory role in evolutionary psychology. Adaptations – the primary products of natural selection – require environmental input at every stage of their emergence. Indeed, environmental pressures (1) drove the evolution of the adaptations in the first place, (2) play a key role in their ontogenetic development, and (3) are responsible for activating them in the present (Buss 1995; DeKay and Buss 1992). In other words, adaptations evolve because of environmental challenges in the first place, they require specific kinds of environmental input to develop properly across an organism’s lifespan, and proximate contextual input triggers their activation in the immediate present. Far from neglecting environmental context, an evolutionary perspective places it center stage.

Another way to see the centrality of context in evolutionary psychology is by considering two facts: (1) the brain evolved to extract information from the environment and use that information to regulate behavior, and (2) different contexts carry different information. Context is central in evolutionary psychology not only in the sense that different contexts present different adaptive problems, but, crucially, environments also *carry the information needed to solve those problems*. Stated differently, an organism’s brain – its evolved on-board computer – must monitor the

environment for information relevant to the survival and reproduction of the organism.

In sum, context occupies center stage in evolutionary psychology for two broad reasons. First, adaptations require environmental input at every stage of their development, from initial evolution to current activation. And second, for an evolved information processor, context is central because it simultaneously poses key adaptive problems and carries the information needed to solve those problems.

Evolved Learning Mechanisms

There is a widespread misconception that “evolved” and “learned” are competing explanations. It might intuitively *seem* that “evolved” is the opposite of “learned,” but this is dead wrong. These two kinds of explanations are not in conflict for two reasons.

First, they answer distinct questions at complementary levels of analysis. Learning explanations are at the *proximate* level of analysis, whereas evolutionary explanations usually begin at the *ultimate* level of analysis (see Alcock 2012; Tinbergen 1963; Lewis et al. 2017, for a discussion of the relationship between ultimate and proximate levels of analysis).

Second, *learning* requires *evolved learning mechanisms* instantiated in the brain. This is why a brain can learn things a cauliflower cannot: the brain is equipped with evolved learning mechanisms but the cauliflower is not (Tooby and Cosmides 2015). Similarly, if you try to teach a young dog and a human child the same material in the same way, they will learn different things. This is because the puppy’s brain and the child’s brain are equipped with different learning mechanisms. Far from being in conflict, evolution and learning are explanatory partners. To explain psychological and behavioral outcomes, you often need to invoke both evolution and learning in the form of evolved learning mechanisms.

Specific examples of evolved learning mechanisms illustrate this point. Three prominent examples are (1) food aversion learning, (2) specialized fear learning, and (3) incest aversion learning.

An example of food aversion learning is the Garcia Effect, which refers to the discovery that rats will readily learn to associate nausea with food, but not with lights or sounds (Garcia and Koelling 1966). The Garcia effect occurs because in rats' natural environment and across their evolutionary history, nausea was caused by toxic or pathogenic food but not by lights or sounds. This phenomenon demonstrates that rats have evolved to learn some things (the relationship between nausea and food) more easily and more readily than others (the relationship between nausea and buzzers).

Specialized *fear learning adaptations* are common among primates. Fear learning in monkeys is a good example. If an observer monkey watches a target monkey react to a snake with fear, the observer monkey will learn a fear of snakes easily and rapidly – sometimes even in a single trial (Mineka et al. 1984). By contrast, if an observer monkey watches a target monkey react with the same fear to a rabbit or flowers, the observer will usually fail to learn a fear of rabbits or flowers. Monkeys are biologically prepared to learn a fear of snakes, but not of rabbits and flowers. It is also harder to get them to *unlearn* it: it is more difficult to extinguish a fear of snakes than a fear of rabbits or flowers (Cook and Mineka 1990). This “biological preparedness” supports the view that organisms are not equipped with a single, all-purpose learning mechanism. Rather, species have evolved problem-specific learning mechanisms that are specialized for learning information relevant to the particular adaptive problems they encountered over the course of their evolution. Species that have no evolutionary history of being preyed upon by snakes, for example, have not evolved this specialized fear learning mechanism.

Human also have specialized fear learning adaptations for snakes, spiders, heights, darkness, and strangers, but not for evolutionarily novel hazards such as cars, carcinogenic food additives, and cigarettes – despite the fact that these are more dangerous and kill more people in modern environments (Marks and Nesse 1994).

Incest aversion learning differs from both food aversion learning and fear learning adaptations –

in the adaptive problem it solves, the environmental input by which it develops, and in the information-processing machinery that produces its behavioral output. The adaptive problem in this case centers on avoiding mating with close genetic relatives. But humans are not born knowing who their genetic relatives are – this information must be learned. Incest avoidance mechanisms appear to take in at least two key inputs from the environment during development: (1) co-residence during childhood, and (2) maternal perinatal association (if you are the older sibling, seeing your mother breastfeed the other child). To simplify the process, if the mechanism in question receives sufficient levels of these inputs (e.g., shared habitation, observing a child nursing from one's own mother, etc.), it tags the co-resident as a sibling or other close kin and produces a lack of sexual attraction to that person as well as disgust at the mere thought of having sex with that person (Lieberman et al. 2007; Westermarck 1891). On the other hand, if the evolved learning mechanism *does not* receive sufficient levels of these two key inputs, it does not tag the other individual as a sibling and does not produce incest aversion toward that person. This is how we avoid having sex with our genetic relatives – through a learning mechanism that evolved because of its adaptive value in preventing inbreeding depression (Lieberman et al. 2007; Rantala and Marcinkowska 2011; see Al-Shawaf et al. 2018, for a discussion of the significance of these findings with respect to a key misconception about evolution and behavior).

Food aversion learning, hazardous fear learning, and incest avoidance learning all illustrate the importance of evolved learning mechanisms. These examples highlight the key point that for two reasons, evolution and learning should not be thought of as separate processes in zero-sum competition with each other for explanatory power. First, learning requires *evolved learning mechanisms* instantiated in the brain. Second, evolution and learning offer answers at different levels of analysis – ultimate for evolution and proximate for learning. There is no necessary conflict between the two (see Lewis et al. 2017).

Context Effects in Evolutionary Psychology

Specific empirical examples help to illustrate the centrality of the environment in evolutionary psychology. This section details context effects in four areas of evolutionary psychological research: emotions, cooperation and altruism, lifespan development, and human mating.

Some theorists draw a distinction between *context* effects and *condition* effects, emphasizing that context refers to the external environment, whereas condition refers to the internal environment (an organism's psychophysiological state). However, there is no fundamental distinction here: the external and internal environment are both critical to survival and reproduction, and evolved psychological mechanisms are sensitive to both. Broadly conceived, the terms "environment" or "context" therefore include elements of the ecological environment (e.g., parasite type and prevalence, flora and fauna, dangers from drowning), the social environment (e.g., local sex ratio, cultural norms about mating), and the internal environment (e.g., an individual's mutation load, strength of immune function). We touch on all three.

Emotions

Evolutionary psychological thinking suggests that emotions are heavily context-dependent, and that this context-dependence is systematic and predictable rather than arbitrary and random.

Disgust provides a good example. An adaptive disgust system would be designed to respond to pathogen-dense environments by downregulating personality traits such as extraversion and openness to experience. This would have the effect of reducing exploratory behaviors and intimate interactions with others, thereby decreasing the likelihood of infection. This is exactly what studies find: priming people with pathogen salience makes them regard themselves as less extraverted and less open to experience, while also prompting avoidant motor behavior (Mortensen et al. 2010). Experimentally inducing disgust reduces people's desire for short-term mating (Al-Shawaf et al. 2018). Cross-cultural data show a similar pattern:

people who live in regions of the world with higher pathogen density tend to be lower in extraversion, openness to experience, and proclivity for short-term mating (Schaller and Murray 2008). Research motivated by the hypothesis that masculine facial features are indicative of immunocompetence has shown that women who are more concerned with pathogens and disease show a heightened preference for masculine faces (DeBruine et al. 2010). Research based on the idea that out-group members tend to carry novel diseases that the immune system is not prepared to deal with suggests that priming people with the context cue of disease salience makes them more xenophobic (Faulkner et al. 2004). The contextual variable of pregnancy status affects levels of disgust in a principled and functional way, preventing the mother from ingesting teratogens that could harm the developing fetus (Fessler et al. 2005; Profet 1992). Studies show that mothers find their own baby's feces less disgusting than other babies' feces (Case et al. 2006). Finally, evolutionary analyses of disgust suggest a host of novel context-based hypotheses (Al-Shawaf et al. 2016; Al-Shawaf et al. 2017). These examples all highlight the context-sensitive nature of disgust: this emotion is designed to adjust our psychology, physiology, and behavior in response to different contextual cues in order to help solve the survival- or reproduction-relevant problem at hand.

Emotions such as anger show a similar pattern of context-sensitivity. For example, the welfare-recalibration theory of anger posits that an organism gets angry when it detects that another individual has not placed sufficient emphasis on its welfare. The victim then displays anger in an attempt to "convince" the perpetrator to upregulate the value that he places on the victim's welfare (Sell et al. 2009). Just as this welfare-recalibration theory suggests, the contexts that trigger anger are systematically predictable: people react with more anger when they have suffered a large cost, when the perpetrator only gained a small benefit, and when the perpetrator knew exactly whom he was harming. Relatedly, when a victim discovers wrongdoing, the perpetrator typically attempts to defuse the victim's

anger in a predictable manner: by asserting that the benefit he reaped was large, that he didn't realize how large the cost to the victim was, and that he didn't know exactly whom he was harming with his behavior (Sell et al. 2017). Finally, precisely as the theory predicts, context and condition affect individual differences in anger: more attractive women – and more attractive and more physically formidable men – anger more readily than their less attractive and less formidable counterparts (for a discussion of the logic underlying these predictions, see Sell et al. 2009).

The key point here is that an evolutionary psychological approach to the emotions emphasizes their context-dependence. Human emotions are activated by specific contexts, and these emotions subsequently regulate aspects of cognition, perception, physiology, and behavior in ways that are functional precisely because they match context. This is true not just of disgust and anger but also of pride (Sznycer et al. 2017), shame (Sznycer et al. 2016), jealousy (Buss 2000), envy (Hill and Buss 2006), sexual arousal (Al-Shawaf et al. 2016), hunger (Al-Shawaf 2016), love (Buss 2006), and, to our knowledge, all emotions. These emotions are functional precisely because they are so context-sensitive.

Cooperation, Altruism, and Group Living

The domains of *cooperation and altruism* nicely illustrate the centrality of context in evolutionary psychology. Key contextual variables in this area of research include how problems are framed, audience effects, and kinship.

One classic finding in this area of research is this: people perform poorly on abstract logical reasoning tasks such as the Wason Selection task when the problem is framed in terms of abstract letters and numbers, but they perform exceptionally well when the same problem is framed in terms of social exchange and cheater detection (Cosmides 1989). Because we have evolved to detect cheaters and rule violators in social exchange, but not to solve abstract logic problems involving letters and numbers, our performance on the former is much better than our performance on the latter. The remarkable thing about these

findings is that the two problems are logically identical. Our vastly different performance is due to the architecture of our evolved psychological mechanisms in conjunction with a key contextual variable (in this case, whether the problem is framed in terms of letters and numbers or in terms of detecting cheaters; Cosmides and Tooby 1989). Similarly, because we evolved in an environment in which we had to solve problems involving *frequencies*, but not *probabilities*, we are much better at solving problems framed in a frequentist format than mathematically *identical* problems framed in a probabilistic format (Brase et al. 1998; Cosmides and Tooby 1996; Gigerenzer 1991). The key idea here is the same: our evolved psychological mechanisms are built to process some contextual cues – roughly, those that were ancestrally ecologically valid – but not others. As a consequence, these mechanisms can produce radically different outcomes because of a change in a single contextual cue.

Another key contextual variable in the domain of altruism and cooperation is the presence of an audience. Studies suggest that we are more altruistic in public than in private, and that we choose to engage in more effortful altruism when we are being watched compared to when we are not (e.g., Bereczkei et al. 2010). Research shows that we are keener to mete out moralistic punishments when other individuals in the group are likely to find out that we engaged in costly punishment (which benefits the entire group; Kurzban et al. 2007). Experiments on the evolved psychology undergirding our moral evaluations of others suggest that we like and trust people more when their moral beliefs appear deontological (rule-based) rather than consequentialist (outcome-based; Sacco et al. 2017). This, in turn, suggests a novel hypothesis: that people may tend to present themselves as more deontological when they are being watched than when they are alone.

Kinship is another contextual variable that plays a central role in people's altruistic behavior. We tend to help and bequeath our assets to kin more than non-kin, and to closer kin more than distant kin (Smith et al. 1987). People's preferred solution to the famous trolley problem changes

when the potential victims are kin (Bleske-Rechek et al. 2010). We are more willing to sacrifice our weekends and a day's pay to search for perpetrators who victimized kin as opposed to non-kin (Lieberman and Linke 2007). We prefer harsher punishments for offenders when the victim is a genetic relative, as we do when a rule violator victimized an in-group member as opposed to an out-group member (Bernhard et al. 2006; Lieberman and Linke 2007). By contrast, we prefer *lighter* punishments when the *perpetrator* is a genetic relative. We are also more likely to attribute remorse to the perpetrator when he or she is a genetic relative (Lieberman and Linke 2007). Kinship is such an important contextual variable that people try to influence non-kin to induce higher levels of cooperation by invoking kin terminology: *brothers* in arms, a sorority of *sisters*, the *motherland*, and so on (Daly et al. 1997; Salmon 1998).

In sum, cooperation and altruism point to the same conclusion as that of emotions: context is crucial – and deeply embedded in the fabric of evolutionary psychological thinking.

Development

Lifespan development also exemplifies the importance of context in evolutionary thinking. We present a few examples from childhood and adulthood.

In infancy and early childhood, fears (e.g., fear of strange males) come online at the developmentally appropriate time – approximately when the developing organism begins to confront the relevant adaptive problem (in this case, coming into contact with strange adult males; Boyer and Bergstrom 2011). Later during development, some evidence suggests that father absence may channel children toward a path that includes earlier puberty, earlier reproduction, a stronger proclivity for short-term mating, and less investment in long-term relationships (Belsky et al. 1991; but see Comings et al. 2002, for a different explanation). Relatedly, the context of a harsh and unpredictable environment in early childhood appears to channel individuals toward greater future discounting, a stronger tendency to value immediate rewards over delayed gratification, and

less investment in committed long-term mating (Ellis et al. 2009; see Barbaro et al. 2017, for a different view and a cautionary note).

Other developmental work suggests that maternal care during infancy affects the development of neural systems involved in fear and stress reactivity. For example, the brains of rat pups who receive grooming, licking, and arched-back nursing develop in ways that lead to greater stress resistance, less fearfulness, and less behavioral reactivity to stress-inducing situations (Caldji et al. 1998).

Studies suggest that personality traits such as extraversion may be predictable on the basis of developmental context effects. High levels of extraversion can lead to increased mating opportunities by initiating more interactions with potential mates and by forming new friendships and valuable social alliances (Nettle 2005, 2006; Denissen and Penke 2008). Because more attractive individuals are more likely to reap mating benefits from the social interactions associated with high levels of extraversion, we should expect selection to have favored extraversion-calibrating mechanisms that are sensitive to an individual's own physical attractiveness. Indeed, studies show that both men's and women's physical attractiveness predicts their extraversion levels (Lukaszewski and Roney 2011). Because mates and positions of high social status are contested resources, high levels of extraversion can also expose individuals to competition and conflict, in particular among men (Lukaszewski and Roney 2011). Consistent with this, physical strength predicts extraversion among men.

The centrality of context continues to manifest itself throughout the lifespan. Men downregulate testosterone production after entering into a committed relationship, and downregulate testosterone further after having a child (Burnham et al. 2003; Gray et al. 2006). These changes are functional, as reduced testosterone facilitates deeper commitment to one's mate, reduced aggression, and greater investment in parenting. Evolved psychological mechanisms are – and indeed must be – exquisitely sensitive to context.

Mating

Like emotions, altruism, and development, the psychology of mating is highly context-dependent. We describe several examples, first from men's mating psychology and then from women's.

Men's Mating Psychology

Men who are satisfied in their romantic relationships tend to show less attentional adhesion to attractive women (Miller 1997; Maner et al. 2008). By contrast, men who are less satisfied and men with a stronger short-term mating orientation demonstrate more attentional adhesion to attractive women (Maner et al. 2007).

The temporal context of mating – short-term or long-term – also affects a variety of male mate preferences. For example, men's preference for intelligence depends on mating context (stronger preference in long-term mating), as does their perception of promiscuity (desirable in short-term mating but undesirable in long-term mating; Buss and Schmitt 1993; Goetz et al. 2012). Men interested in short-term mating display a heightened emphasis on bodily attractiveness relative to men interested in long-term mating, whereas those oriented toward long-term mating display a heightened emphasis on facial attractiveness (the body contains more information about current fertility, whereas the face contains more information about long-term reproductive value; see Confer et al. 2010). And many preferences and standards shift when men are pursuing short-term mating instead of long-term mating (e.g., standards are lowered for a variety of qualities during short-term mating; Buss and Schmitt 1993). Researchers have even hypothesized that the return to (pre-arousal) baseline after orgasm is different for men oriented toward short-term mating than for those oriented toward long-term mating (Al-Shawaf et al. 2016).

Men's own qualities affect their mating choices and proclivities as well. For instance, men higher in mate value tend to reduce their parenting effort and invest more in mating (Hewlett 1991). By contrast, those lower in mate value tend to invest more heavily in parenting (Smuts and Gubernick 1992). One's mate

value or physical attractiveness may even influence one's preferred mating strategy (e.g., Al-Shawaf et al. 2015; Gangestad and Simpson 2000). Preliminary molecular genetic evidence suggests that men with longer CAG repeats at the androgen receptor locus (i.e., men with reduced sensitivity to testosterone) are more likely to interpret ambiguous cues as indicative of their mate's infidelity and react with greater emotional upset to such cues (Lewis et al. 2018).

Studies also suggest that merely being exposed to attractive women causes men to declare that they are more ambitious and more interested in accruing wealth and succeeding in their careers (Roney 2003). Similarly, the mere presence of attractive female observers causes male skateboarders to experience a rise in testosterone, take more risks, and have more accidents (Ronay and Hippel 2010). And research suggests that looking at pictures of attractive models leads men to feel less committed to, less interested in, and less serious about their own partners (Kenrick et al. 1994).

Women's Mating Psychology

Women's mating psychology is also highly context-sensitive. For example, women of higher mate value have higher mating standards, demanding higher minimum levels of various attributes in their partners (Buss and Shackelford 2008; Waynforth and Dunbar 1995). Similarly, women with higher incomes and higher levels of education display a heightened preference for income, career, and educational attainment in their mates (Buss 1989).

Women, like their nonhuman female counterparts, engage in *mate choice copying* – a phenomenon whereby women find a man more attractive if he is already mated (Dugatkin 2000; Waynforth 2007), especially if his mate is highly attractive and appears to be genuinely interested in him (e.g., Place et al. 2010; Waynforth 2007). That is, women appear to use the social-contextual input of other women's choices to process information about a man's likely mate value.

Women's specific mate preferences also appear to depend on mating context, with increasing interest in traits such as muscularity, masculinity,

confidence, physical attractiveness, and facial symmetry during short-term mating (e.g., Buss 2016; Gangestad et al. 2007; Li and Kenrick 2006; Provost et al. 2008). Relatedly, women's desire for extra-pair affairs is highly context-sensitive: it is primarily women whose partners lack hypothesized cues of good genetic quality who exhibit a desire for extra-pair copulations (Gangestad et al. 2005). Furthermore, when they do have affairs, women appear to specifically pick men who possess these attributes (e.g., facial symmetry, physical attractiveness; Gangestad and Thornhill 1997). Even women's competitor derogation is exquisitely context-sensitive; the types of slurs women use to derogate their rivals vary systematically as a function of mating context (Buss and Schmitt 1993; Schmitt and Buss 1996).

One of the most striking context effects in the domain of mating is the effect of a country's sex ratio – a key dimension of the social environment (Schmitt 2005). Cross-cultural studies of more than 14,000 participants in 48 nations demonstrate that when there is a surplus of women, mating strategies shift toward short-term mating and casual sex. By contrast, when there is a surplus of men, there are observable nation-level shifts toward long-term mating, monogamy, and commitment. This can be understood in economic terms: the mating market is a kind of biological market in which whichever sex is less common is in greater demand and therefore has more bargaining power. Because women, on average, have a stronger desire for long-term mating than men, countries with a dearth of women tend to shift toward long-term mating. By the same logic, because men, on average, have a stronger desire for short-term mating than women, countries with a dearth of men tend to shift toward short-term mating (Schmitt 2005).

These findings highlight that, remarkably, global patterns of casual sex and committed mating can be predicted in advance on the basis of the key contextual cue of sex ratio. Human mating psychology, like the rest of our evolved psychology, is powerfully affected by key contextual cues in ways that can be predicted *a priori* from an evolutionary perspective.

The Breadth and Diversity of Context Effects in Evolutionary Psychology

We have focused on four domains – emotions, altruism, lifespan development, and mating – to illustrate key points about the ecological, social, and internal contexts to which our evolved psychological mechanisms are designed to respond. But even these examples fail to capture the breadth and scope of context effects in evolutionary psychology. In this section, we present a further sampling of context effects to give the reader a sense of how important and ubiquitous context is in evolutionary thinking.

Hunter-gatherer groups differ from one another in their degree of egalitarianism and food sharing. These group differences can be predicted on the basis of resource variability – a key contextual cue (Cashdan 1980). The perceptual bias known as *auditory looming* is heavily context-sensitive, with the bias appearing only for harmonic tones (e.g., sounds created by animate organisms) and disappearing for non-harmonic tones (e.g., background noise such as rain or leaves rustling) – precisely as evolutionary reasoning would predict (Ghazanfar et al. 2002). People tend to be more accepting of women's casual sex, and less moralistic about it, in societies where women are more financially independent (Price et al. 2014). More physically formidable men are more likely to endorse militaristic solutions to national and global problems (Sell et al. 2012) and are more likely to endorse a self-serving position regarding wealth redistribution: among poor men, strength predicts increased support for wealth redistribution, and among rich men, strength predicts increased opposition to wealth redistribution (Petersen et al. 2013). In line with evolutionary reasoning, fathers (but not mothers) show discriminative parental care as a function of facial resemblance between offspring and parent (Platek et al. 2002; Platek et al. 2005). Because parasites degrade physical attractiveness, people attach more importance to physical attractiveness in parts of the world with greater parasite density (Gangestad and Buss 1993). Even women's behavior toward their male kin may be affected

by the context variable of where they are in their fertility cycle (Lieberman et al. 2011).

These findings, across large swaths of content domains in psychology, capture only a fraction of the total set of context-based discoveries in evolutionary psychology. We include them here as a reminder that, despite having chosen to focus on four specific domains, context effects feature prominently in evolutionary psychology and permeate the entire discipline. The misconception that evolved psychological mechanisms are rigid and environmentally insensitive is pervasive, but deeply mistaken (see Al-Shawaf et al. 2018 for a discussion of additional widespread misconceptions about evolution and natural selection).

Conclusion

Our goal has been to demonstrate how essential context and environment are to evolutionary psychology. We think there are three main ways to appreciate this point. First, the environment is crucial to evolved adaptations at every stage of their emergence: their evolution, ontogenetic development, and immediate activation. Evolved adaptations would not exist without the environment, nor would the behaviors they produce. Second, *evolved learning mechanisms* simultaneously illustrate the centrality of context in evolutionary psychology and dissolve the fallacious (but common) dichotomy of “evolved versus learned.” Food aversion learning, hazard-specific fear learning, and incest aversion learning all demonstrate that *learning requires evolved learning mechanisms*, and that these evolved learning mechanisms are highly context-sensitive. Third, a long list of prominent context effects in domains such as emotions, altruism, lifespan development, and mating show that the centrality of context is not just an abstract theoretical point of passing interest, but rather pervades all the empirical work evolutionary psychologists do.

In sum, context is central to the theoretical framework of evolutionary psychology. Without it, evolved psychological mechanisms would not make sense – and would not exist.

Environmental pressures drove the evolution of these mechanisms in the first place, environmental inputs are the keys to activating them in the immediate present, and the primary function of said mechanisms is to extract information from the environment and use this information to adaptively regulate physiology and behavior (Tooby and Cosmides 2015). Looked at in this way, context lies at the heart of modern evolutionary psychology.

Cross-References

- Condition-Dependent Mating Tactic
- Early Attachment Experiences and Romantic Attachment
- Kin Recognition and Classification in Humans
- Life History Theory
- Sexual Strategies Theory
- Thirteen Misunderstandings About Natural Selection
- Tradeoffs in Mate Selection
- Trivers-Willard Hypothesis

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Context, Instrumental Behavior

► Selectionist Models: Implications for Behavior

Context-Dependent Self-Conceptualization

► Self-Concept

Contexts

► Factors That Influence Bullying

Contexts for Men's Aggression Against Men

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Synonyms

Aggression; Intrasexual competition; Mating effort; Sex ratio; Violence

Definition

Male-to-male aggression reliably arises in situations where men compete against other men for mates.

Introduction

One robust empirical observation is that men are more aggressive and violent than women. Aggression is behavior intended to hurt another person, and violence is aggressive behavior intended to cause severe physical harm such as death or injury (e.g., Anderson and Bushman 2002). Sex differences in physical aggression and violence are typically in the medium-to-large range (Archer 2009). Moreover, men are the primary perpetrators and victims of violence nearly everywhere in the world. Globally, men comprise 95% of all homicide victims and 80–97% of homicide perpetrators (UN Office on Drugs and Crime 2013). In other mammalian species such as chimpanzees (one of our closest primate relations), males are also the more violent sex.

Although aggressive behavior is often learned, evidence suggests that much male violence is caused by an evolved predisposition. Boys are more aggressive than girls even before 2 years of age, suggesting that men's tendency towards aggression is present before social learning can provide a reasonable explanation for behavior. After 2 years of age, aggression declines in both genders but rises again in 18–30-year-old men but not women. This peak in male violence coincides with men entering the mating market at a time when they have achieved their maximum size and strength (Archer 2009). Sex differences in aggression are also limited to physical aggression and do not include verbal (e.g., insults) or indirect aggression (e.g., gossiping; Archer 2009). These findings imply that physical aggression in ancestral men was adaptive (and may still be in some circumstances). It is these circumstances that elicit male-to-male aggression that this chapter is primarily concerned with.

In Wilson and Daly's (1985) classic article on male-to-male violence, they describe a murder

case from Detroit in which two young men are drinking together with other people. The perpetrator humiliates the victim by lifting him up between his legs. The victim asks to be put down while others laugh at him. The aggression escalates to hitting and eventually the offender shoots and kills the victim. To many observers, this type of violence and escalation of violence seems excessively disproportionate. But what if one of the onlookers was a romantic interest that the victim or both men were trying to impress? What if appearing weak in the peer group might elicit further victimization and loss of status? This chapter first introduces relevant work on men's adaptations for physical aggression. It then examines the contexts in which men are the primary victims and perpetrators of violence. These contexts will show that male-to-male aggression reliably arises in situations where men compete against other men for mates.

Men's Adaptations for Physical Aggression

Evolutionary scientists suggest that men possess adaptive psychological mechanisms and physical abilities that predispose men to fight other men when specific situations are encountered (Archer 2009; Buss and Shackelford 1997; Sell et al. 2012). One fundamental of evolutionary theory is that adaptations must have directly or indirectly solved an adaptive problem and thereby increased reproductive success in past generations. Buss and Shackelford (1997) proposed seven adaptive problems that aggression could solve. Of the seven, five are relevant to male-to-male violence: taking others' resources, defense, inflicting costs on other male sexual rivals, negotiating status hierarchies, and deterring other men from future attack.

To further elaborate on these adaptive problems, men often use violence to forcibly take resources from other men and also defend themselves against other men. This type of raiding and robbery has long been a part of human history and has been observed in chimpanzees. Inflicting costs on sexual rivals occur when men disparage

or weaken other men in front of a potential mate. In extreme cases, men often murder other men who have sex with their sexual partner. Depending on the type of status hierarchy, men who display aggression toward other men are often respected or hold more power than other men. Similarly, aggressiveness or even a reputation for swift and violent retribution can be an effective deterrent to violence from other men. Thus, violence likely solved many adaptive problems faced by ancient men. Such violence probably contributed substantial reproductive benefits to those men who were willing and able to use it effectively.

One putative adaptation that could solve these adaptive problems would be greater physical size and upper body strength (Sell et al. 2012). Upper body strength is important because fighting and using traditional weapons such as spears, clubs, bows, staffs, and swords required upper body strength. Because maintaining upper body strength and larger physical size is metabolically costly, it seems unlikely that these characteristics would have evolved had it not conferred fitness benefits. For men facing these adaptive problems, being larger and stronger than one's opponent would have been helpful in winning physical contests.

At the heart of whether a man behaves violently or not is the cost-benefit analysis. When directed against the right man at the right time, male-to-male violence could increase access to reproductively relevant resources (e.g., money, land) and social status and imbue a reputation for fierceness. These spoils of violence could then be used to attract or coerce women. In the wrong situation, however, enacting violence upon others can be a costly strategy. Psychological mechanisms for weighing the costs and benefits of engaging in violence in certain situations would thus offer men considerable reproductive advantage.

Men do indeed seem to "size up" other men to determine the costs associated with potential aggression. Men possess remarkable abilities to quickly determine the costliness of a potential violent conflict. Many other species also possess these abilities (see Sell et al. 2012). For instance,

people can accurately assess men's upper body strength and fighting ability from their faces, voices, and body (Sell et al. 2012). Moreover, in these studies, both male and female participants were better able to assess male upper body strength than female strength. The ratio of the facial width to height is also particularly important for influencing judgments of aggressiveness and dominance. Thus, the upper body strength and facial features of a male opponent is an important piece of information in the cost-benefit analysis of the decision to use violence or not.

In sum, throughout human evolution, much male-to-male competition has been violent and still is today to a lesser extent. It seems likely that this competition created strong selection pressures which produced physical and psychological adaptations that enhance the likelihood of using violence in certain contexts.

Male-Male Aggression Occurs When There Is Competition for Women

A compelling explanation for the prevalence of male-to-male violence comes from sexual selection theory (Trivers 1972). Sexual selection theory posits that the sex with the greatest minimum investment in producing offspring will be more cautious and choosy in mate selection (Trivers 1972). The maximum number of offspring that women can have is more limited than the number of offspring that men can have. This asymmetry is because women's minimum obligatory parental investment is greater, and women's reproductive success is physiologically limited by the frequency of ovulation and energetic cost of lactation. For these reasons, the cost of indiscriminate mating is greater for women. Thus, women tend to be the "choosier" sex when it comes to selecting a mate. As a result, men often compete against other men to enhance their chances of being chosen as a mate.

Male intrasexual competition is exacerbated by men's high reproductive variance (i.e., the variability in the number of offspring men produce). Men's reproductive variance is greater than that of women, meaning that some men produce many

children and others none. Polygyny, in which one man could monopolize reproductive access to many women, contributes to men's high reproductive variance. Historically, polygyny was common. More than 80% of cultures documented by anthropologists allow for polygyny. Under these conditions, winning mating contests provides the opportunity for reproductive access to a greater number of potentially fertile women and therefore more offspring in the next generation. As a result of this polygynous societal structure, many men will have no reproductive access to women and leave no descendants. Thus, mating competition is a potent selection force for men. High reproductive variability means that men are in competition with other men to accrue mates and reproductively relevant resources.

Aggressive and risk-taking phenotypes appear to increase men's reproductive success when mating competition is intense. Under polygynous mating conditions, men are larger than women and more muscular. In these conditions, men engage in more intrasexual competition and risk-taking behavior. These findings suggest a history in which physical strength, fighting ability, and risk-taking secured men a greater number of mates.

Although counterintuitive, there is good evidence to suggest that risk-taking increases men's reproductive success. In conditions where men have greater reproductive variance, the possibility of greater gains and greater losses increases the likelihood of taking risks to secure a mate. A good example of this proposition comes from an evolutionary simulation by Daly and Wilson (1988). In that computer simulation, each individual possessed low-, medium-, or high-risk competitive reproductive strategies. Competition took the form of fights between two individuals. The simulation showed that selection favored relatively risky competition strategies even when mortality costs were high, providing that the costs of losing and gains of winning were great (i.e., low or high reproductive success). Even though high-risk individuals experienced the greatest mortality, when the gains were associated with high reproductive success, high-risk individuals experienced the greatest fitness.

The finding that high-risk strategies are associated with greater fitness in polygynous mating conditions suggests that males should be most risky and aggressive when they are actively competing for mates. In men, this time period is usually young adulthood, and much evidence documents this heightened aggression. A meta-analysis of 353 studies found that sex differences in physical aggression peaked during the ages of 18–30 years (Archer 2004). Men are most violent when they are in venues where they can compete over women, such as bars and nightclubs. Men's involvement in male-male homicides also peaks during this age range (Daly and Wilson 1988), irrespective of the overall rate in the society.

Further support for the relationship between intrasexual competition and men's aggression comes from data on men's aggression when they are mated and unmated. Men's aggression and risk-proneness decline when they marry and invest in children. This decline is presumably because marriage secures a pathway for men to propagate their genes. However, when men get divorced or their spouse dies, their aggression and risk-taking reverts to levels comparable with single men in their age group. This pattern may result because upon marriage dissolution, men lose reproductive access to their former spouse. The increase in aggression and risk-taking presumably occurs because divorced or widowed men reenter the mating market.

Men's aggression in intrasexually competitive scenarios is selective. In traditional hunter-gatherer societies who are not at war, one of the most common reasons for male-male homicide was competition over a woman. In these instances, murder of a rival often led to securing a mate. This phenomena has been documented in the Tiwi of North Australia, the Inuit of North America, the !Kung of the Kalahari Desert in South Africa, the Siriono of Bolivia, and the Arapesh of New Guinea (Symons 1979). Thus, one effective method of removing a potential rival from the mating pool is homicide. These examples suggest that extreme forms of male-male violence such as homicide can function to increase men's reproductive success in certain contexts.

Male-Male Aggression Occurs When Status Is at Stake

Aggression and violence can also increase reproductive success by elevating male status. High status is ubiquitously preferred by women in potential mates (Buss 1989; Hill and Hurtado 1996). This preference is presumably because status usually confers the ability to provide resources. Resource provision can function as a form of parental investment (Trivers 1972), and men often display their resources to attract and retain mates. In a variety of societies, men who have higher status have greater reproductive success than those who are lower in status (Betzig 1994). High status men tend to obtain and marry women who are sought after and more physically attractive. High status men also have more female mates (Hill and Hurtado 1996). It has been estimated that 8% of modern Asian men have DNA linked to Genghis Khan, which is 0.5% of the male population worldwide. Similar findings have been reported for other “strong men” who ruled in Ireland and China centuries ago.

Successful intrasexual competition – especially when achieved through aggression and violence – is linked to higher social status in men. For example, young men in many tribal societies gained status and honor through homicide (Daly and Wilson 1988). Male warriors in these societies had more children, more sexual partners, and higher status (Chagnon 1988). In the Ache of Paraguay, men who had survived many battles attained status and power as a result of their aggression (Hill and Hurtado 1996). Similar findings are sometimes still observed in current times. In the United States, the most violent gang members are often bestowed the highest status and the most sexual partners (Campbell 1993). These findings suggest that high status confers direct reproductive success to men.

Inherent in these data is the notion that concerns about status drive men's aggression and violence. Indeed, in addition to revenge, competition for status is one of the most widely documented sources of violent conflict. The majority of alcohol-related violent episodes are related to pursuing social status. Experimental

social psychology research shows that men report a greater likelihood of aggressive or costly retaliation against others when their status was threatened (Geniole et al. 2015). Priming status competition in men also increases the likelihood of aggression against other men (Griskevicius et al. 2009). Winning an aggressive bout against a higher status man could yield greater gains by rapidly elevating the aggressor's place in the status hierarchy. For instance, monarchs experienced a much higher rate of homicide than the general population.

A good example of male-to-male aggression caused by status threat is observed in cultures where the rule of law is weak. Nisbett and Cohen (1996) argued that violent retaliation against status threats is adaptive for men in some conditions. When the rule of law is weak, resources such as livestock can be taken by force. In these conditions, cultivating a reputation for aggressive retaliatory ability is paramount as it dissuades potential competitors. Nisbett and Cohen (1996) suggest that a "culture of honor" emerges under these scenarios, in which even trivial slights escalate to violent aggression in an attempt to protect one's reputation. This phenomenon has been confirmed cross-culturally, with revenge and retaliation more prevalent in societies where livestock could be taken by force and where societal institutions are weak. The implication is that under conditions in which a reputation loss may result in resource loss, men are quicker to aggressively defend themselves against status threats.

Much male-male violence results from trivial altercations, which outside observers would declare petty or insignificant. However, threats to status are inherent in many of these altercations (Wilson and Daly 1985). These altercations usually involve one man challenging the status of another. When acquiescing might involve a potential loss of status and respect, neither man stands down. As a result, violence often erupts. In support of this notion, Wilson and Daly (1985) found that the majority of homicides between men concerned real or imagined threats to status. Insults and public humiliation have also been

shown to commonly provoke fights between young men.

The importance of status to men's reproductive success means that situations in which status gains or losses are at stake can elicit male-to-male aggression. Men who fare better in aggressive competitions gain status as a result. In contexts where status threats can result in a loss of resources, men are quick to aggressively defend themselves. The purpose of this aggression and violence is to ensure that their reputation for aggressive retaliation dissuades status challenges.

Male-to-Male Aggression Occurs When Men's Opportunities to Obtain Resources Are Bleak

Another condition that increases men's aggression is when their own social status is low. Women value high status in potential mates (Buss 1989), and when a man has low status (e.g., if he is unemployed or has a low-paying job), his likelihood of marrying drops. Because marriage is one pathway to securing reproductive success, relatively low-status men are at a reproductive disadvantage. Compared to mid- or high-status rivals, low-status men have fewer opportunities to gain status and resources through traditional means. In these circumstances, low-status men can seek out alternative routes for access to status and resources. These alternatives often involve taking more risks to out-compete rivals. For instance, stabbing a drug dealer in the neighborhood and stealing his car and money may help a low-status man garner resources to attract women and a reputation as a formidable opponent. Although this strategy is risky, men who feel they have little to lose might appraise this situation in a way that shifts the balance of the cost-benefit ratio toward violence.

In support of these notions, Wilson and Daly (1985) consistently find that male-to-male homicide perpetrators are more likely to be unemployed and unmarried. Many systematic reviews of the literature on crime and status also link low status with increased crime and homicide in particular. Violence also generally increases amongst

men who lack economic resources or prospects (Daly and Wilson 1988), yet decreases alongside men's opportunities for resource acquisition. As the gross domestic product, college enrollment, and educational opportunities for young adults increase, homicide declines considerably (Hiraiwa-Hasegawa 2005). This relationship is presumably because these factors allow men to focus on gaining status and resources through traditional, non-violent means.

A related scenario that escalates aggression is when income equality – rather than absolute income level – is low. Figueredo et al. (2012) explain that because sexual selection operates on relative reproductive fitness rather than absolute numbers of offspring, even a man with a steady income may feel he is losing out compared to his competitors. Income inequality thus escalates competitive tactics, with those at the bottom of the distribution feeling that they have little to lose from aggressive or risky strategies. In support of this notion, studies consistently demonstrate that the Gini coefficient (in which higher values index greater economic inequality) positively predicts national homicide rates even when controlling for relevant confounding variables (e.g., Walasek and Brown 2015). Income inequality also increases other intrasexual competition behaviors: when the Gini coefficient is high, men and women are more interested in acquiring luxury goods that are used to signal high status to competitors and potential mates (Walasek and Brown 2015).

Aggression and violent crime can ensure low-status men gain reproductively relevant resources that otherwise may not have been available. In this sense, aggression can be used to co-opt the resources of others (Buss and Shackelford 1997). For example, thieves can acquire valuable weapons or money from rivals, mates can be poached from existing relationships, and violence can be used to acquire territory rich with natural resources or other uses. Criminal and violent behavior can also be used to damage a rival's reputation (Buss and Shackelford 1997). By cheating another person out of a resource, the cheater acquires the resource and bestows upon the victim a reputation as someone who is easy to exploit (Buss and Duntley 2008). Such a

reputation could invite future exploitation attempts and diminish the social standing of the victim.

In sum, when men's opportunities to obtain resources are bleak – either because their social status or relative income is low – men are more likely to aggress against other men. In this context, male-to-male aggression can function as an alternative strategy to access status and resources.

Male-to-Male Aggression Occurs When There Is an Abundance of Women

Because men are more aggressive and criminally inclined than women, a seemingly logical conclusion is that when there are more men in a given society, there should be more aggression and crime. As it turns out, this statement is not generally true. Societies with an excess of men usually have lower rates of violent crime (Walsh 2003). Parental investment theory (Trivers 1972) provides one potential explanation for this surprising finding.

Parental investment theory (Trivers 1972) suggests that men's mating strategies are context dependent. In some scenarios, men engage in what is called *direct mating effort*. They compete against other men for access to fertile mates and avoid contributing to parenting. In other scenarios, men focus on *indirect mating effort*: They channel their attention to securing one mate by advertising their ability to parentally invest. Because direct mating effort involves more direct intrasexual competition, it also involves more male-male aggression and violence. By contrast, indirect mating effort often involves garnering economic resources and advertising them to increase the likelihood of securing a long-term partner. Thus, indirect mating competition can shift male intrasexual competition from direct male-to-male aggression to the economic arena.

The operational sex ratio is one environmental feature that influences men's mating strategies and associated aggression and violence. The operational sex ratio in humans is the ratio of sexually active men to fertilizable women. It depends on the reproductive rate of men and women, which is

influenced by the minimum obligatory parental investment and the age at which marriage is likely. When the operational sex ratio is high, there are more men than fertilizable women, making women a scarce resource. In these societies, women's ability to demand greater parental investment and resource potential in men increases. As a result, women are highly sought after as marriage partners, and men often focus on indirect mating effort to attract a wife.

Barber (2009) explains that when women are the scarcer gender, they are less likely to have sex outside of marriage. The implication is that premarital sex would damage a woman's marriage prospects. As a result, there is little direct mating competition between men over sexual access to women, and indirect mating effort is again emphasized. Thus, men in these contexts compete for long-term and marriage partners rather than short-term sex partners (Guttentag and Secord 1983). Because there is less direct mating effort, aggression is reduced.

In contrast, there are also situations where men are the scarce gender. After periods of wartime, for example, the death of many men in combat can result in an excess of fertilizable women compared to sexually active men (a low operational sex ratio). In these situations in which males are a scarce resource, females from a variety of species have been shown to engage in more intrasexual competition (Rosvall 2011). When men are scarcer, women advertise their sexuality, engage in more casual sex, and have more sex outside of marriage (Cashdan 1993). Indeed, there is an inverse relationship between the operational sex ratio and the rate of single parenthood and teen births (Barber 2005). Moreover, after World War II, shortfalls of men significantly increased the rate of out-of-wedlock births in the United States (Guttentag and Secord 1983). The implication is that fewer men make marriage more difficult for women. As a result, women engage in more premarital sexual activity to attract mates because an oversupply of women means that women's marriage prospects are reduced.

The result of this increased propensity towards sexual activity outside of marriage in women is

that direct mating competition increases among men. When fewer barriers exist for sexual access to fertilizable women, men directly compete against other men for mates. The opportunity for reward is high, yet so is the cost of failure (i.e., high and low reproductive success, respectively). Increased direct mating effort means that some men engage in more risky strategies in an attempt to monopolize the mating market and outdo their competitors (Wilson and Daly 1985). Men who were willing to take risks would have had an advantage directly competing for mates and seem to have been more likely to leave descendants (Kruger and Nesse 2004). As a result, male-to-male aggression and violence escalate. Indeed, there is a strong negative association between a society's operational sex ratio and its level of murders, rapes, and assaults (Walsh 2003). This finding has been documented cross-culturally even when controlling for economic development, form of relationships (e.g., polygamy), number of police, population density, drug trafficking, urbanization, infant mortality, and geographical region (Barber 2009).

A secondary mechanism whereby the operational sex ratio may increase violence is through parental investment. When men are the scarce gender and the operational sex ratio is low, marriages tend to be less stable (Guttentag and Secord 1983). There are higher rates of single parenthood and divorce, meaning that paternal investment in offspring is reduced. Again, this finding could reflect increased direct mating effort in men: instead of focusing on parental investment, men focus on directly competing for women. Barber (2009) suggests that research showing that children of single mothers are more criminally inclined is reflective of such conditions in which men are reproductively scarce. These conditions create rearing environments that normalize low-investment reproduction and facilitate antisocial or criminal tendencies in offspring.

Underlying these ideas is the notion that rearing conditions characterized by low paternal investment contribute to what evolutionary scientists call a "fast life history" (Belsky et al. 1991).

Life history theory proposes that an organism's behavior and reproductive strategies are influenced by their physical and ecological environment. When an environment is harsh or unpredictable, a fast life history ensues (Belsky et al. 1991). People with a fast life history have earlier sexual experiences and multiple sex partners, events characteristic of a focus on high offspring numbers and thus direct mating effort. Because the environment is unpredictable, high-risk strategies to attract mates as quickly as possible are more appealing. As a result, crime and aggression increases.

In sum, low operational sex ratios can facilitate violence by enhancing men's direct mating efforts and altering the rearing environment of their subsequent offspring. Offspring raised in these rearing environments are more likely to adopt a fast life history strategy. This fast life history strategy emphasizes direct over indirect mating effort, thus perpetuating the cycle of increased male-to-male violence.

Conclusion

Human evolutionary history has predisposed men to use violence against other men to obtain mates, status, and reproductively relevant resources. This chapter reviewed evidence suggesting that men have evolved physical and psychological adaptations to facilitate male intrasexual competition. Men are physically larger and stronger than women. They very quickly and efficiently use cost-benefit analyses to "size up" potential male opponents from minimal information such as tone of voice or facial features.

An integration of the existing research identified situations that promote violence between men. Because most human societies allow some form of polygyny, men must compete directly or indirectly to appeal to women. Indeed, violence between men peaks when men are part of the dating market and declines after marriage. As in other primate species, status is important for reproductive success. Thus, when men can obtain higher status or experience a threat to their status,

they may use violence to deal with these situations. Poor or otherwise low-status men are most likely to use violence because without status or wealth, men in most countries will have little opportunity to attract a mate. Perhaps the most counterintuitive finding is that a relative abundance of women can facilitate male-to-male violence. In these situations, men can engage in more direct and violent competition for short-term mates rather than in indirect, nonviolent competition.

Even though these situations tend to elicit greater aggression between men, they need not completely determine violent behavior. Human males do indeed have these basic tendencies and adaptations that enhance intrasexual violence in certain contexts and in response to certain types of provocations. However, cultural evolution has produced a substantial decrease in violence over the past few centuries and operates quicker than biological evolution. Thus, hope for reducing male-male aggression will be through the cultural route. For instance, men and boys could be educated about the severe consequences of making seemingly "trivial" status-threatening jokes.

Cultural changes at the institutional levels could also reduce male-male violence. Using sound government economic and social policies to increase wealth may reduce homicide because low-status, poor men tend to be the most common offenders. However, increasing absolute wealth alone may not reduce violence so long as substantial inequality exists in relative wealth. Thus, reducing inequality seems like a valuable means to reduce violence. In sum, although men are predisposed to hurt each other in certain contexts, with awareness and cultural change, they need not be beholden to violent tendencies.

Cross-References

- ▶ [Adaptation](#)
- ▶ [Condition-Dependent Mating Tactic](#)
- ▶ [Culture of Honor and Individual Differences](#)
- ▶ [Female Choice and Sexual Conflict Theory](#)

- ▶ Greater Risk-Taking and Status
- ▶ Indicators and Correlates of Status and Dominance
- ▶ Mate Value
- ▶ Meta-Analysis of Sex Differences in Aggression
- ▶ Observed Mating Behavior and Women's Long-Term Mating
- ▶ Operational Sex Ratio
- ▶ Reproductive Strategy
- ▶ Reputation as a Context for Men's Aggression against Men
- ▶ Sex Ratio and Men's Long-Term Mating
- ▶ Status and Dominance Hierarchies

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Contexts for Men's Aggression Against Women

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Synonyms

Homicide; Intrasexual competition; Physical aggression; Rape; Rivalry; Sexual coercion; Sexual jealousy; Violence

Definition

Evolutionary pressures on men and women result in sex-specific sexual strategies. Whereas men use physical aggression to secure sexual access and/or to deter rivals, men use sexual aggression to minimize their investment for sexual access and to thwart female sexual choice. Men use distinct forms of aggression against women, because, on average, these behaviors conferred ancestral benefits that exceeded the associated costs.

Introduction

In the context of mating, men and women have engaged in a co-evolutionary arms race. Specifically, reproduction and child-rearing often generate conflict between the sexes. Whereas men more than women pursue a relatively short-term mating strategy, by which they attempt to secure sexual access to multiple partners, women more than men pursue a relatively longer-term mating strategy, by which they attempt to secure resources for themselves and their offspring. One way in which men and women manage conflicting sexual strategies is through physical aggression and violence; an extreme manifestation of which is homicide. However, men commit the majority of instances of intimate partner violence and of

homicide, cross-culturally (Daly and Wilson 1988). Additionally, men use sexual aggression against women to bypass female choice and male-male competition. Similarly to physical violence, men, more often than women, are the perpetrators of sexual coercion and rape (Knight and Sims-Knight 2011).

Sex differences in violence perpetration emerge because of distinctive sexual strategies (Buss and Shackelford 1997). Men and women use aggression differently because of sex-differentiated minimum obligatory parental investment and associated sexual selection (Cross and Campbell 2011). Women, compared to men, invest more time and energy into their offspring, making women a valuable reproductive resource for men. Men, in contrast, invest much less in offspring (e.g., the physiological cost of an ejaculate and the time required to produce it). Because women engage in most of the child-rearing, for ancestral men to have been reproductively successful, they must have outcompeted rivals to secure the attention of high-investing females. Thus, our ancestors include those males who successfully used violence against rival males to gain sexual access to females. However, violence also may have been successfully inflicted on female mates, to thereby assure paternal certainty. More specifically, ancestral men may have used aggression against women and thereby thwarted them from deserting or committing sexual infidelity and are likely to have been more reproductively successful as a consequence (Buss 2014). Whereas it may have been ancestrally adaptive for men to be physically aggressive to combat paternity uncertainty or cuckoldry, female aggression is less likely to have been selected over evolutionary time. Given the investment that women contribute to their offspring, women may have evolved mechanisms, such as greater sensitivity to fear (Cross and Campbell 2011), that motivate them to avoid involvement in physical violence. In fact, research indicates that women engage much less frequently than men in extreme violence (e.g., homicide; Daly and Wilson 1988; Perilla et al. 2011). When women do aggress, this aggression is more likely than men's aggression to be nonlethal.

As with physical aggression, men use sexual aggression against women as a part of a sex-specific sexual strategy (Buss 2014). Sexual aggression (e.g., rape) is one tactic men may use to reduce the investment they trade for female sexual access. By exercising sexual aggression and circumventing female choice, ancestral men may have secured increased reproductive success while contributing fewer resources to the woman who rears their offspring. Thornhill and Palmer (2000) suggest that by sexually coercing women, men may succeed in competition for mates without having to be chosen by a woman or winning male–male competitions for sexual access. In contrast, nonevolutionary explanations of risk factors for sexual coercion or rape suggest that men perpetuate because they have rape-supportive attitudes, perceptual biases (i.e., believing that a woman's friendly behavior is sexual), high alcohol use, and high pornography consumption (especially aggressive genres of porn; Knight and Sims-Knight 2011). However, although it is important to acknowledge these individual characteristics and behaviors of sexually coercive men, those explanations do not engage ultimate causes of sexual aggression.

To avoid cuckoldry and to assure exclusive sexual access to a long-term partner, men's use of *physical* aggression against women is associated with male sexual jealousy, the age of the woman, and sexual rejection. Additionally, men's use of *sexual* aggression against women is associated with the age of the woman, male assessment of the vulnerability of the woman, and various individual differences in men (e.g., disadvantaged men and specialized rapists who are sexually aroused by violent or forceful sex).

Contexts for Men's Physical Aggression Against Women

Although some researchers argue that partner killing by men was not ancestrally adaptive and, therefore, not selected over human evolutionary history (Daly and Wilson 1988), other researchers

argue that men have evolved specialized mechanisms for partner-killing, designed to be deployed when it would have been ancestrally adaptive to do so (i.e., in the context of the threatened departure of a long-term partner; Buss 2006). Specifically, Daly and Wilson (1988) propose that partner-killing is an extreme manifestation of male sexual jealousy or "proprietaryness," unintentionally slipping from control to murder; the killing of a partner would not have provided sufficient reproductive benefits to the killer to outweigh the associated costs. Buss (2006), in contrast, suggests that men have an evolved psychology that motivates killing of a partner when killing produces benefits that exceed the costs. Consistent with both competing hypotheses, homicide and intimate partner violence are inflicted by men to deter partners from sexual infidelity or defecting from the relationship. Physically aggressive and homicidal acts that men commit against their female partners are often triggered by sexual jealousy (i.e., stemming from paternity uncertainty or the threat of cuckoldry), the age of the female partner, and/or experiencing romantic or sexual rejection.

Sexual Jealousy

First, lethal or nonlethal violence is regularly directed by men against their female partners in the context of male sexual jealousy (Buss 2000; Daly and Wilson 1988). In fact, male sexual jealousy is the most common cause of wife battery and a leading cause of uxoricide or wife-killing (Daly and Wilson 1988). Although jealousy is a common experience among both sexes, women report that they would be more distressed by a partner's *emotional* infidelity than *sexual* infidelity; whereas, the opposite pattern is reported by men (Buss et al. 1992). Specifically, men express greater distress by the prospect of or the actual act of a partner's sexual infidelity than by a partner's emotional infidelity. These sex differences in jealousy arise because of differences in evolved sexual strategies that men and women pursue; each

sex has its own set of goals and means of attempting to achieve them. In the conflict of interest between the sexes, women desire to secure long-term relationships in which they can secure resources for themselves and their offspring. However, women may sometimes “out-source” or copulate with other men to obtain higher quality genes for their offspring. If successful, women are assured the resources they need and have secured better genes for their offspring. In the process, they will have successfully deceived their long-term partner into raising and investing in offspring to whom he is not genetically related. Men, on the other hand, and relative to women, have evolved an interest in sex with multiple partners and with lesser investment in any one partner. To assure paternity, however, men may invest in a particular woman for the long-term, in which case they are motivated to thwart her attempts at infidelity. Sexual infidelity by a man's partner can result in the loss of time, effort, and resources in his partner, which could have been spent securing a different mate that would have been sexually faithful. If her sexual infidelity results in cuckoldry, her partner invests precious resources into a rival's offspring. In essence, women have evolved motivation to maintain their sexual autonomy, whereas men coevolved motivation to control their female partner's sexual behavior (Smuts 1992). To control female sexual behavior, male strategies range from physical violence to vigilance. The most extreme form of violence, homicide, occurs most often in the context of male sexual jealousy (Daly and Wilson 1988). In fact, men who kill their partners often do so because of suspected or discovered sexual infidelity, which embodies male concerns with paternity certainty and cuckoldry. Additionally, partner-killing by men most often occurs when the woman attempts to desert her partner and the relationship; in which case, the loss of a reproductively valuable woman to a rival motivates male proprietary aggression (Buss 2014). However, partner-killing by men does not inevitably follow suspected or discovered female partner infidelity or desertion; men

also use nonlethal violence to control their partner's sexual behavior.

Ancestral men recurrently faced the adaptive problem of paternity uncertainty because fertilization occurs within women. Whereas women are never unsure that their offspring are genetically their own, men face the problem of being deceived into providing resources and care for a rival's offspring. Given that men cannot account for their partner's sexual behavior at all times, the possibility of cuckoldry increases as time spent with one's partner decreases (Buss 2000). To combat the threat of cuckoldry, male sexual jealousy may have evolved as a mechanism of detection and as a motivator of subsequent (sometimes violent) action (Buss 2000). Further, male sexual jealousy plays a key role in intimate partner violence (Goetz et al. 2008). Specifically, male physical violence or aggression functions to punish or deter women from sexual infidelity; in these circumstances, violence against women functions as an anticuckoldry tactic. Because women have evolved as the less aggressive sex (due to internal fertilization and the need to protect reproductive and child-rearing capabilities), men can exploit women's interest in self-preservation for their own reproductive gain (i.e., women's fear of physical harm by men may stop them from deserting their partner, increasing their partner's opportunities to reproduce). The sexual jealousy arising from paternity uncertainty also manifests in the most severe form of violence, homicide. For instance, unemployment may influence men's aggression against women in the context of potential cuckoldry. Men who lack sufficient resources may be at a greater risk of cuckoldry than men in higher socioeconomic brackets (Buss 2006). One study found that of the men who killed their partners, 64% were unemployed at the time of the homicide (Easteal 1993). Given women's evolved interest in securing resources and support, it is not surprising that men with fewer expendable resources may be at greater risk of partner infidelity and cuckoldry. Although partner-killing is costly in terms of lost reproductive opportunities and time squandered securing

the murdered partner, the benefits of homicide might sometimes exceed such costs, with the result that selection favored male psychological mechanisms that motivates partner-killing, under particular circumstances (Buss 2006).

Motivated often by sexual jealousy, men attempt to stop women from deserting them through physical violence or killing. Male sexual jealousy is a frequent correlate of such controlling behaviors and violence. Men use both nonlethal (e.g., verbal threats) and more severe (e.g., homicide) forms of violence to control a woman's sexual behavior (Smuts 1992); many of these behaviors can be described as mate retention behaviors. One class of these behaviors is direct mate guarding; while engaging in this form of mate retention, men physically guard a mate and actively dissuade potential mate poachers. Direct mate guarding also includes more explicitly dangerous forms of control such as physical aggression. Men do not exclusively direct their aggression toward other men; violence as a mate retention behavior may include physical aggression against their partner (Shackelford et al. 2005). Specifically, direct mate guarding, monopolization of time, and punishment for a partner's perceived or actual infidelity predict female-directed violence. In sum, violence is closely related to autonomy-preventing mate retention behaviors. By using mate guarding tactics successfully, men inhibit or restrict their partner's sexual opportunities and stop them from deserting, becoming more confident that they are the sire of any offspring produced by their partner (Buss and Shackelford 1997). However, in cases which the woman does abandon her partner, the risk of homicide increases dramatically (Daly and Wilson 1988). Women are most likely to be killed by their estranged partner within the first year after a break-up (Buss 2006). Thus, when nonlethal violence does not prevent female infidelity or relationship defection, men may resort to homicide (Buss 2006). In such cases, a man might benefit from killing his partner, rather than simply letting her go, because she may offer reproductive opportunities to rivals, while he may not be able to replace the mate for his own reproductive endeavors. Further, and in connection with an

earlier point, men who are unemployed kill their partners more often than men who are employed, and these same unemployed men are more inclined to kill or attempt to kill their partner when she breaks off the relationship with them (Eastel 1993). This is because unemployed men typically lack the resources women desire and are less likely to secure a new mate in the future. By eliminating their partner, these men could thereby establish credit for their reputation (in certain cultures) and retain the resources that would have been allocated to the woman.

Age of Woman

The age of a woman predicts the likelihood she will be the target of intimate partner violence or homicide. Young women are more likely to be killed by their partner than are older women (Shackelford et al. 2000). Specifically, women aged 15 to 24 years, within the reproductive age bracket, are most likely to be killed by their partner (Daly and Wilson 1988). Women in the youthful, reproductive periods of their lives are more valuable to men as mates. Younger women are more sexually attractive and desirable to men because youth represents or indicates their fertility, which is important in male mate choice and ancestral male reproductive success. Additionally, males with a youthful and attractive partner gain social status from their mateship to this valuable reproductive commodity. Given the motivation and interest to secure as mates young, fertile women with high reproductive value, male sexual jealousy should be especially sensitive in the context of mateship to younger women. Because younger women are more desirable to male rivals, male sexual jealousy motivates men to defend their partners from mate poachers and sometimes motivates them to use aggression against their partner to stop them from deflecting. Men with younger, reproductive age partners are more likely to commit violence against them to control their sexual behavior (Smuts 1992). Because of the reproductive damage a younger woman (relative to an older woman) can cause her partner as the result of her desertion or sexual infidelity,

nonlethal and lethal violence are much more likely to be deployed by men against younger partners than by men against older partners. Additionally, researchers have investigated whether younger women are killed more often than older women simply because younger women are mated to younger and more violent men. The results of this research found that younger women are more likely to be killed across male partner age groups (Shackelford et al. 2000). In sum, younger women are at greater risk than older women of intimate partner violence and homicide.

Sexual Rejection

Sexual rejection may motivate men's aggression against women. Specifically, nonlethal and nonsexual aggression in response to denial of sexual access is a class of problems that women have faced recurrently over human evolutionary history. One study indicated that male rejection sensitivity is associated to perpetration of intimate partner violence (Downey et al. 2000). In particular, men who indicated a lower threshold for rejection negatively perceive and overreact to their partner's ambiguous or negative behavior, heightening their risk for responding aggressively. These researchers also found that, among college-aged men who indicated they are more invested in their intimate relationships, anxious expectations of rejection predicted their use of violence against their partner. In this context, it is possible that men respond anxiously and aggressively to rejection because they perceive that they have lost the opportunity to mate exclusively with a desired woman. Additionally, other researchers found that experiencing romantic rejection from a sexualized woman increases male aggression (Blake et al. 2017). In this study, when men were romantically rejected by a sexualized woman (sexualized through clothing in a profile picture and in response to sex-related questions) via an online dating platform, the men delivered more severe sound-blasts to the sexually-rejecting woman. Although these studies shed light on nonlethal aggression, sexual or romantic rejection may lead to serious consequences, such as

homicide. Consider desertion or abandonment, for example. Ending a relationship is, in effect, a permanent denial of sexual access and rejection of one's previous partner. When a man's sexual strategy is thwarted, discomfort and anger is expected to rise. Given how costly it is for a man to invest in a woman only to be denied sexual access, male violence may have been ancestrally adaptive in securing future mating attempts or in ending a woman's life to thereby deny rivals sexual access to that woman.

Contexts for Men's Sexual Aggression Against Women

US studies across the nation, criminal justice systems, healthcare systems, and college campuses indicate that men's sexual aggression against women is a widespread and prevalent problem (Knight and Sims-Knight 2011). From an evolutionary perspective, men may use sexual aggression against women to circumvent female choice and thereby to invest fewer resources for sexual access. By avoiding male-male competition for female sexual access and reducing the time, energy, and investment spent courting a desired woman, men may increase their sexual access by use of sexual aggression. Because women have an evolved sexual strategy in which they pursue long-term or committed and high-investing males, men who use sexual aggression against them expose them to undesirable circumstances (i.e., rearing an offspring without receiving resources from a mate). One study suggests that men's sexual aggression against women is extremely upsetting to women (Buss 1989) and much more upsetting than men estimate. Buss (1989) found that among college-aged women, sexual aggression was the single most upsetting act a man could commit out of 147 potentially upsetting actions. Given the conflict of interest between the sexes, a strategy of sexual aggression or rape may have evolved in men, while antirape defenses have co-evolved in women.

Rape refers to the use of force or the threat of force to secure sexual intercourse (penile-vaginal penetration) without a woman's consent (Buss

2014; Thornhill and Palmer 2000). There are two likely evolutionary hypotheses for why men commit rape: rape as a specialized male adaptation (Thornhill and Palmer 2000) and rape as a by-product of other male adaptations (Symons 1979). The human rape-adaptation hypothesis describes a specialized psychological adaptation in which the inclination to sexually aggress against women evolved in male psychology but is only deployed in particular circumstances. For a specialized rape psychology to have been selected, the benefits to ancestral men must have outweighed the associated costs (e.g., although ancestral men may face a physically aggressive husband or partner after committing rape against a woman, they may nevertheless have increased their reproductive success by copulating with an additional woman; McKibbin et al. 2008). In sum, rape may have been ancestrally adaptive when males were able to circumvent female choice and increase their mating opportunities.

In contrast, the by-product hypothesis of rape (Symons 1979) suggests that rape was not selected for but is a by-product of other male evolved psychological mechanisms. In other words, there is no male evolved psychological mechanism specialized to motivate rape because such a mechanism would not have produced net reproductive benefits ancestrally. Symons (1979) suggested that rape is a by-product of adaptations designed to secure sexual access from consenting partners. Specifically, deviations of male psychological mechanisms for desire for sexual variety/novelty, psychological sensitivity to mating opportunities, desire for uncommitted and minimal investment short-term mating, and the general inclination to use physical aggression may inadvertently and as a by-product lead to instances of rape.

The mate deprivation hypothesis of rape, which proposes that men who have little or no sexual access to desirable mates may be more inclined to use sexually coercive tactics, has received inconsistent empirical support (Lalumière et al. 1996). Other researchers suggest that there are several types of rapists (McKibbin et al. 2008), which may shed light on why there

has been inconsistent support of the mate deprivation hypothesis. McKibbin et al. (2008) identify five distinct categories of rapists: disadvantaged men who resort to rape, specialized rapists who are sexually aroused by violent or forceful sex, men who rape opportunistically, high-mating-effort men who exhibit psychopathic tendencies, and partner rapists motivated by actual or suspected risk of sperm competition (e.g., by female sexual infidelity).

It is important to note that although female choice may be thwarted by male sexual aggression, it is possible that women have evolved mechanisms that motivate them to prefer sexually aggressive men. Because men who use sexually coercive behavior may be more reproductively successful over human evolutionary history, women may desire that trait in their own male offspring. For example, one study found that sexually coercive men have consensual sex at an earlier age and have more consensual sex partners than do noncoercive men (Koss and Dinero 1988). This is not to argue that women generally prefer men who rape. In fact, women may also have evolved psychological mechanisms to defend against rape. For instance, Buss (2006) suggests that women's aversion to and intense fear of rape may have been selected because sexual aggression by men has been a recurrent adaptation women have faced over evolutionary history.

Rape Outside of the Context of Intimate Relationships

Rapist Types

First, regarding McKibbin et al. (2008)'s hypothesized rapist types, the fact that disadvantaged men sometimes resort to rape aligns with the description of the mate deprivation hypothesis. This type of rapist includes men who lack or have limited sexual opportunities or cannot access consenting women (Lalumière et al. 1996; Thornhill and Palmer 2000). Disadvantaged men who rape depend on a context-sensitive motivation for rape, engaging in sexual aggression when

deprived of mates by normal means. For example, men in lower socioeconomic status brackets commit a disproportionate number of rapes (Thornhill and Thornhill 1983). In this context, men who lack the resources to secure mates may resort to sexual aggression to achieve mating opportunities. Thornhill and Palmer (2000) suggest that an evolved psychology may motivate instances of rape when men lack resources and/or sexual access to mates.

Second, opportunistic rapists are men who may initially engage consensually with sexually receptive women but resort to sexual aggression when the woman changes her mind or if the possibility of retaliation for rape is low (McKibbin et al. 2008). Opportunistic rapists may be especially inclined to rape when the victim is vulnerable (e.g., during warfare). However, there is little evidence that supports the opportunistic rapist profile directly.

Third, high-mating-effort rapists are hypothesized to be sexually experienced rapists who are aggressive, dominant, have high self-esteem, and psychopathic traits (McKibbin et al. 2008). Unlike disadvantaged men who rape, high-mating-effort rapists do not have difficulty accessing consenting women. Specifically, psychopathic men use high-mating-effort strategies to gain sexual access without much investment, only resorting to sexual aggression when their other tactics do not succeed.

Lastly, McKibbin et al. (2008) discuss “specialized” rapists who report sexual arousal in response to violent or aggressive sexual stimuli. Specialized rapists may have an evolved psychology or arousal pattern in which they experience more rapid ejaculation during rape. Thornhill and Palmer (2000) suggest that a more rapid arousal and ejaculation pattern during rape may have been successful, compared to men who did not exhibit that pattern, because the rapist may avoid retaliation and other possible costs of detection. Additionally, specialized rapists may have evolved psychological adaptations which assess vulnerability of victims, preference for fertile women, and high quantity ejaculates.

Assessment of Vulnerability of Victims

Women who are targets of sexual aggression or rape may be chosen by men because of a psychological mechanism that motivate assessments of the associated risks and benefits of sexual coercion (e.g., “specialized” rapists; Thornhill and Palmer 2000). For example, during warfare, a woman might not have protection from kin or a long-term partner, and a prospective rapist might recognize this and target that woman. In this context, the rape as adaptation hypothesis suggests that men have evolved a vulnerability-detection mechanism specifically designed to assess potential rape victims (Thornhill and Palmer 2000). However, evidence suggesting that men have an evolved psychology that functions specifically to evaluate a woman’s vulnerability to rape is insufficient. In line with the by-product hypothesis of rape, it is possible that men evaluate potential rape victims according to an evolved cost-benefit evaluation mechanism that is not specific to rape (Thornhill and Palmer 2000). In sum, neither the rape-as-adaptation nor rape-as-byproduct hypothesis is uniquely supported by the evidence that women experience sexual aggression or rape in contexts in which they are more vulnerable.

Ejaculate Quality in Rape

Thornhill and Palmer (2000) suggest that there may be an increase in quality of rape ejaculates compared to ejaculates produced during consensual sex. Particularly, an adaptation in men to increase ejaculate quality during rape may be related to sperm competition. An evolved ability to influence ejaculate quality in the context of rape may increase the likelihood of fertilization. If men who rape are able to provide a higher quality ejaculate to the victim, their ejaculate would be better equipped to deal with the higher likelihood of sperm competition. For example, given that attractiveness and youthfulness in women are valuable to men, a highly desirable, young woman may already have a long-term partner whose sperm is already inside her. A rapist may increase their success in sperm competition by

introducing a higher quality ejaculate (e.g., more sperm) into the woman.

Age of the Woman

If rape is an adaptation that increased ancestral male reproductive success, one might expect that rapists would target fertile, reproductive-aged women, as opposed to nonfertile women. Similar to men's use of physical aggression against women, men who rape primarily target young women (Thornhill and Thornhill 1983). Fertility peaks in the mid-20s and women who are raped are disproportionately in that youthful, reproductive age bracket (Thornhill and Palmer 2000). It is possible that a victim-preference mechanism, such as a desire to copulate with younger, more attractive women, may have increased the ancestral reproductive benefits of rape. However, men's preference for reproductive-age women also aligns with the by-product hypothesis of rape given that the preference for young, reproductive-age women is exemplified in both men's choice of consensual partners and rape victims. In sum, the age of the woman is related to rape prevalence but does not address whether rape is motivated by specialized adaptation or as a by-product of other evolved mechanisms.

Rape in the Context of Intimate Relationships

Between 10% and 26% of married women report experiencing rape by their husbands (McKibbin et al. 2008). According to some researchers (Goetz and Shackelford 2006; Thornhill and Palmer 2000), partner rape may be motivated by sperm competition. In the context of suspected or actual sexual infidelity, men may rape their partners in an effort to successfully compete with a rival's sperm. Partner-rape may be an anti-cuckoldry strategy used by men to decrease their paternity uncertainty and risk of cuckoldry. In line with this hypothesis, women are especially at risk of rape by a partner who reports concern about the woman's sexual fidelity during or immediately

following a break-up (Thornhill and Palmer 2000). In this context, faced with potential desertion or abandonment to a rival, men may rape their partner (or ex-partner) to achieve fertilization of a woman who no longer grants them sexual access. Additionally, one study found that men mated to women who have committed sexual infidelity or were suspected to have committed sexual infidelity were more likely to use a variety of sexually aggressive tactics, including physical force and rape (Goetz and Shackelford 2006). Related to the possibility that a man might adjust his ejaculate in a rape context, partnered men also might produce higher quality ejaculates when they rape their partner (compared to ejaculates produced during consensual sex with their partner), in an effort to address perceived greater risk of sperm competition.

Conclusion

Men use distinct methods of physical and sexual aggression for particular reproductive reasons. Men use physical aggression against women to address recurrent adaptive problems of female sexual infidelity, paternity uncertainty, and exclusive sexual access. Although selection may have favored men's use of physical aggression, female aggression may have been mostly unfavorable to women's ancestral reproductive success. Additionally, men use sexual aggression against women to gain sexual access to young, reproductive-age women, to circumvent investment, and to avoid male-male competition. In instances of partner-rape, men use sexual aggression to combat the risk of cuckoldry by engaging in sperm competition. Women rarely use sexual aggression against men. Because women are a valuable reproductive resource that invests heavily in offspring, women do not compete as intensely for sexual access to men. We caution that although men's aggression against women may have been selected over evolutionary time, this does not mean that this aggression is morally good or defensible. It is not. Intimate partner violence, homicide, and rape are global problems

that affect women in devastating ways (e.g., contracting sexually transmitted infections, physical ailments, etc.). Some researchers suggest that further inquiry surrounding domestic violence and physical assault may assist in discovering solutions to combat it (Perilla et al. 2011). Additionally, other researchers suggest that rape prevention programs and policies must gauge proximate and ultimate causes of sexual coercion, as well as incorporate more comprehensive, multilevel strategies that incorporate genetic, social, and behavioral understanding (Knight and Sims-Knight 2011).

Cross-References

- Aggression for Sexual Access
- Female Age as a Predictor of Men's Aggression Against Women
- Female Infidelity
- Homicide Adaptation Theory
- Paternity Uncertainty

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Contexts for Women's Aggression Against Men

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Synonyms

Domestic violence; Intimate Partner Violence; Male victims; Violence; Women's Violence

Definition

There is a wealth of literature that demonstrates men's victimisation in intimate relationships, this paper explores explanations of women's aggression towards men. This includes exploring traditional models of intimate partner violence, evolutionary perspectives and critiquing the idea women's violence is only ever in self-defence.

Introduction

Women's violence remains a controversial and yet important topic in recent years for aggression research. For decades, the dominant discourse in the intimate partner violence (IPV) literature has been around historical and cultural social structures that have influenced violence against women. Despite evidence of women's violence in intimate relationships, an exploration of this topic has often been the recipient of accusations such as victim blaming and seen as an attempt to excuse men's violence. The aim of this entry is to explore the literature around women's violence including unpicking current gendered models and looking at the evidence for women's violence towards their partners. A further aim is to explore theoretical explanations for women's violence including evolutionary perspectives, risk factors for women's aggression, and the concept of the abusive personality. The conclusion of this entry will explore the implications for treatment and

intervention for violent women in a sector still rooted in feminist and gendered models of IPV.

Evidence of Women's Violence

Proponents of the gendered model of IPV posit that it is an asymmetrical problem of men's violence towards women and that women's violence does not equate to men's violence in terms of consequences, severity, or frequency. Feminist researchers, such as Dobash and Dobash (1979), believe that the cause of IPV is gender that violence is often used for socially constructed purposes, and by studying it in a different context the root of the problem is missed. For them, the correct interpretation of violence against women is that it forms the extension of the domination and control of wives by their husbands, control that is of historical and social construction. Many feminists acknowledge the statistics that detail women's violence against their partners but argue that these figures represent trivial acts such as a shove or push: they choose to use other statistics, such as police data, to support their argument believing that this adds support to the feminist view that men are much more likely than women to be the perpetrators of IPV.

Early research on IPV, and those examining typologies, only focused on male perpetrators. Within the last 40 years, the research uncovering the extent of women's violence towards their male partners has brought into question the view that the cause is solely to be found in the patriarchal values of society. One of the first researchers to publicize male victims of domestic violence was Suzanne Steinmetz. Her paper in 1978 entitled "The Battered Husband Syndrome" detailed the appearance of men being hit by their wives in comic strips across the world. She further mentions the "charivari," the post-Renaissance custom intended to shame and humiliate men who had "allowed" their wives to abuse them, in public, the target being behavior that was considered a threat to the social order of patriarchy. It involved individuals who violated social norms in the eyes of this patriarchal community and who were disciplined through humiliation and collective rule.

One of the first measures that revealed the frequency of women's violence towards men was the Conflict Tactics Scale (CTS; Straus 1979). It was designed to measure IPV by investigating which of a list of acts they had used in conflict resolution within a set period of time. It is usually used with community and undergraduate samples of married or dating couples and involves respondents completing for their own and their partner's behavior (Archer 1999). Criticisms of the CTS have mainly revolved around the lack of context; some researchers believe that the way the items are listed completely ignores their meaning and the situation in which the act took place. It has been criticized for reducing violence to a "check list of acts" that lack information around motives and consequences. Straus (1990) argued that these criticisms were based on a misunderstanding of the research design behind the use of the measure. He believes that the notion of the CTS ignoring context is based on the assumption that quantitative measures cannot accommodate context. In fact, the CTS does measure this by keeping the context and violence variables separate. The context is further set by asking participants to answer the questionnaire while thinking about a conflict they had had with their partner (or ex-partner). There is divided opinion on the issue of context as some researchers would suggest that violent acts are only those where there is an intent on the part of the perpetrator to cause harm, mainly those meant to injure and cause pain. Archer (1999) found that overall there was underreporting of aggression in both sexes for self-report measures on the CTS compared with victim-reports, and research has demonstrated that women's reports are likely to suffer the same biases that men are. Research has indeed found that women used self-defense as an excuse because they perceived that this was the demand characteristic of the situation, when they were aware this was not an accurate assessment of the incident; the claim of self-defense here was retrospective. The CTS has been used within many countries, but in 2004 Straus published a paper confirming its reliability and validity with high rates of internal consistency and low confounding with social desirability. Other scholars have cited

the creation of the CTS and the series of findings that indicate women are also IPV perpetrators, as two of the ten most important findings within the field of IPV research.

The gender-neutral surveying method of the CTS revealed the extent to which men were hitting women, but also, and more surprisingly, it found evidence that such violence was also bi-directional and female-to-male. Many studies within this field have now demonstrated that women are equally as aggressive to men if not more so. One of the most influential papers was John Archer's (2000) meta-analysis, which examined physical aggression within heterosexual relationships using 82 studies and a total of over 64,000 participants. Archer found that women reported perpetrating aggressive acts towards their partners more frequently than men. Other more recent studies have also found this difference (e.g., Bates et al. 2014), with other research suggesting that bi-directional violence is the most common type experienced in relationships. For example, Próspero and Kim (2009) studied the experience of IPV perpetration and victimization, coercion, and mental health problems, among 676 students. Their findings suggested that the majority of those who experienced IPV were classed as being in mutually violent relationships and that both men and women suffered mental health problems associated with it. Stets and Straus (1989) found that in couples where violence occurred, both partners were violent in around half the cases, then female-only and male-only in about a quarter of the time each. Females were more frequently the perpetrator in unilateral aggression in this and other studies (e.g., Gray and Foshee 1997).

An often-cited criticism of the research exploring and comparing rates of men's and women's IPV is that self-report measures do not capture the circumstances and so it is unlikely that women's violence towards men is particularly impactful. More recently, research has indicated that women's violence has serious physical and psychological consequences for men. For example, Hines et al. (2007) analyzed 190 male callers to the Domestic Abuse Helpline for Men (DAHMH), a national helpline for abuse men in the USA; they

found significant instances of physical aggression with the most common acts including hitting, kicking, and punching. The aggression was severe enough sometimes that the men called the police or sought medical attention. Over 20% reported violence that the authors considered life threatening (e.g., using a weapon such as a knife, or choking), and many men described their female partners targeting their genitals in physical attacks. Research does not currently exist exploring the different acts or patterns that are utilized by men and women within IPV perpetration, but what does exist demonstrates there is significant similarity and overlap.

When considering the impact of IPV on men, previous research has often compared outcomes for male victims compared to female victims; this is not an appropriate comparison as the literature suggests that men and women utilize different coping strategies when dealing with distress and trauma. Men may be more likely to externalize their behavior (e.g., by using alcohol and drugs) and women to internalize theirs, so that it is not a fair comparison (Hines and Malley-Morrison 2001). While there is significantly more research exploring the impact of IPV on women, the research that does exist for men suggests the outcomes are just as severe.

Women's Use of Coercive Control

Coercive control is a form of nonphysical aggression that includes behaviors such as humiliation, threats, degradation, and isolation (e.g., Follingstad and Dehart 2000), which are used to seek power over another in a relationship. Traditional models of IPV have seen control as a central tenant to men's domination of women within relationships; the focus on this patriarchal control has gone onto form the foundation of many perpetrator programs including the Duluth Model (Pence and Paymar 1993). Control is not always thought to be present within violent relationships; Johnson (1995) originally argued that incidents of IPV could be categorized into one of two types of physical aggression. The first he labeled situational couple violence (formerly

common couple violence), which encompasses the kind of violence that occurs when arguments get out of control: he did not believe it to be of any serious consequence and it was unlikely to escalate (Johnson 1995). Intimate terrorism (formerly patriarchal terrorism) involves the use of severe and coercive violence as part of a range of behaviors that men use to dominate and control their female partners. It is this violence found in shelter and prison samples, which is more likely to escalate into something more serious and to have more damaging physical and psychological consequences. His later work expanded the typology from an individual to a dyadic one to encompass all combinations of controlling aggression, noncontrolling aggression, and no aggression (Johnson 2006). Intimate terrorism represents a pattern of controlling aggression with a partner who either is not violent or uses noncontrolling violence. Johnson then added two new patterns of behavior: the first, named "violent resistance," represents violence of a noncontrolling kind in response to controlling aggression from the partner – this often encompasses violence in self-defense but is not confined to this. The other, labeled "mutual violent control," represents a destructive relationship where both partners use controlling aggression. To distinguish between these types of aggression would obviously mean collecting data about self and partner behavior.

Typically, Johnson (1995, 2006) suggested that men would be found within the intimate terrorism category with women being more likely to be in that of violent resistance. While there has been support found for the subtypes of this typology, there has been less support found for the predictors around sex and category membership. For example, Bates et al. (2014) found women were significantly more controlling towards their partners compared to men and that men and women were equally as likely to be categorized in all Johnson's categories. With feminist beliefs around the etiology of control being rooted in patriarchy, it has traditionally been studied just within the context of intimate relationships; the theory being that men's IPV is motivated by something different to when they are aggressive to other men. More recently though, research has

indicated that control is predictive of men's and women's same sex aggression (e.g., Bates et al. 2014) and rather than being a function of patriarchy, it could be more related to a generally aggressive and coercive interpersonal style (e.g., Corvo and deLara 2009).

Women's propensity to control could be seen as being related to their childhood bullying behavior. For boys, bullying is something that involves physical aggression, but for girls it is more indirect, they often use controlling tactics such as humiliation, isolation, and social ostracization to bully other boys and girls and manipulate the social hierarchy. While it was previously thought that the gender difference that existed between boys and girls was that boys showed a preference for physical aggression with girls showing more of a preference for verbal aggression, research has suggested that both boys and girls utilize verbal aggression and the actual differences lay in the use of direct versus indirect means of being aggressive.

Indirect aggression involves inflicting pain in a way that makes it seem as if there was no intention to hurt or harm at all; this leaves the aggressor as less likely to be identified and so consequently, not experience retaliation or punishment. This behavior encompasses acts to influence and often sabotage the social relationships of others, impact on the victims' self-esteem, often through directly expressed rejection, and can include nonverbal behaviors (e.g., facial expressions). Research has suggested that girls actually use more indirect aggression than boys, sometimes attributed to the fact girls' verbal and social skills (essential to utilizing indirectly aggressive tactics) mature earlier than boys (e.g., Bjorkqvist et al. 1992). However, more recent meta-analytic evidence suggests the differences in indirect aggression are actually quite small.

The overlap in behaviors that characterize a pattern of either controlling behavior or indirect aggression is very similar. They are often similar in their impact in terms of isolating the victim, impacting on their self-esteem and well-being and creating longer term issues with relationships and trust. For adult relationships, this can be part of a wider pattern of abuse that occurs, or it can be in

relationships where there is otherwise no violence. With an acknowledgment that both men and women have the proclivity to be psychologically aggressive and controlling, it changes the models of IPV that we have understood and should lead us to question the way IPV treatment and interventions work. It also leads to questions about whether all women's IPV could be considered as self-defensive.

Women's Violence as Self-defensive

Women's violence has also been researched much more since the sexual parity of IPV emerged in the literature. Feminists (e.g., Dobash and Dobash 1979) have suggested that women's violence is only in self-defense or quite trivial, but the literature does not support this. Studies examining IPV in community samples often find that it is mutual. For example, Gray and Foshee (1997) found that 66% of their sample reported being in a mutually violent relationship and that this violence was reciprocal, with participants reporting similar amounts of violence as perpetrators and as victims. When examining sex differences for the couples with only one violent partner, they found a higher proportion of males (26%) reporting being victims of violence only and a higher proportion of females (29%) reporting being perpetrators only. As mentioned above, a common misconception around women's violence is that it does not impact men to the same extent as violence affects women. There are a few studies that provide evidence on this, although the body of literature on the consequences for men is much smaller than that for women. Hines et al. (2007) in their study utilizing the DAMH found that all callers had experienced physical abuse from their female partners, over 90% experienced controlling behavior, and others reported being stalked. Some of the men reported being fearful of their partners' violence. Furthermore, they reported that the men had experienced frustrations with the domestic violence system in terms of seeking help.

O'Leary et al. (1989) examined IPV in a longitudinal study of a community sample and found

that women engaged in all forms of aggressive behavior at a rate equal to, or greater than, that of men. The most common types of aggression were pushing, grabbing, and shoving or slapping, as measured by the CTS. Women also perpetrated IPV in the absence of their partners being violent, which suggests that their aggression was neither exclusively self-defensive nor reciprocal. Studies that have examined which partner hit first have found that not only is the violence mutual in severity but also women more often than men strike the first blow. These studies not only indicate the presence of mutual violence, but also show women's greater perpetration in the absence of their partner's violence. This does not support the belief that their violence is mostly motivated by self-defense. In the UK, the majority of women who kill their partners claim self-defense; only a minority of these have their claim accepted however. Indeed, Christopher Nutall (the Director of the Home Office Research and Statistics Department 1992) stated "more than 90% of those accused of domestic homicide, whether male or female, were indicted for murder. At the trial, 22% of the women but only 5% of the men were acquitted of all charges. The data on the reason for acquittal is incomplete, but it appears that the most successful defence was one of self-defence." So, the majority of men and women who kill their partners appear not to be acting in self-defense. Of those convicted, similar proportions of men and women cite provocation (about a third), slightly more men cite diminished responsibility (around half of men and a third of women) and more women cite "no intent to kill" (a third of women and a fifth of men). These figures are consistent to those cited by authors such as Felson, who suggest police only attributed 10% of husbands killed by their female partners to be in self-defense.

Traditional models of IPV argue that patriarchy allows men to abuse their wives and that society does not reprimand them for doing so because they are upholding the patriarchal values within their home. Felson (2002) is one of the several researchers who have argued that patriarchy is not the norm that is relevant here; instead he suggested that norms of chivalry cause men to

inhibit their aggression towards women. When discussing chivalry, he refers to it as originating in a description of a code of behavior for knights in the middle ages that included protective behavior towards women. Felson argued that it is this norm of chivalry that protects women from men in society – he refers to the inadequacy of the word here also; it implies that this is just to protect women from men, when in fact it includes the protection of women from other men, other women, children, and nonhuman sources such as natural disasters (e.g., women boarding lifeboats first on the Titanic). This is supported by studies that indicate women are more likely to receive help from men with these sex differences often more pronounced when there are audiences present, suggesting that this chivalrous effect is normative.

Chivalry means that there is a greater moral condemnation of violence when the victim is a woman, and more serious punishments for the offenders. Felson believes that chivalry can reflect an exchange of submission, a sort of benevolent sexism (e.g., Glick and Fiske 1996). It is a controversial model as it portrays women as weak and is associated with traditional gender roles; however, Felson argued that there are two sources of evidence that support the chivalrous view that violence against women is viewed negatively. One is the finding that women perpetrate violence in relationships at a rate of that similar to men, and often more frequently (e.g., Archer 2000). Another source is research on reactions to violence against women. Many studies have examined evaluations of IPV and have found men's violence towards women is condemned more negatively than violence towards men (e.g., Sorenson and Taylor 2005). Felson and Feld (2009) analyzed a large representative sample of 810 American adults from a random telephone survey and found that participants were more likely to condemn men's assaults on women than any other gender combinations and they were more likely to report this type of assault to the police. They further found violence against a spouse, especially a female spouse, was condemned more harshly than violence against an acquaintance

of either sex, suggesting that violence is not normative within marriage.

Contrasting Patterns of Sex Differences in Aggression

Many studies have found that women are equally as likely to be physically aggressive towards their partner as men, if not more so (e.g., Archer 2000), including in longitudinal research (e.g., O'Leary et al. 1989). Furthermore, the literature (e.g., Archer 2004) and crime statistics that detail the propensity for men to be more aggressive than women to same-sex others suggests a contrasting pattern of sex differences dependent on the sex and relationship of the opponent. Few studies have studied same-sex aggression and IPV within the same sample, but those that have suggest this same pattern is found. For example, Bates et al. (2014) explored IPV and same-sex aggression in a large sample ($N = 1104$) and found women were significantly more aggressive to their partners, and men were significantly more aggressive to same-sex others.

The different pattern of sex differences found for aggression to same-sex others and to partners raises the question of whether men decrease their violence from same-sex to partner (as emphasized by Felson 2002) or whether women increase their aggression from same-sex to partner. Cross et al. (2011) noted that the usual sex difference (men as more aggressive) is not found within the home and they examined whether men inhibit their aggression to their partner or women increase their aggression, or if both occur. They presented participants with three conflict scenarios and asked them to rate the likelihood of using physical aggression, verbal aggression, explosive acts, and defusing acts against three opponents: a partner, a same-sex friend, and an opposite sex friend. This allowed them to separate out the effects of target sex and relationship, or intimacy. They used effect sizes to express the shift in the behavior from the different opponents. Women were more likely to say that they would use physical and verbal acts of aggression against a partner, and their increase of aggression to a partner appeared to be as a

function of intimacy. They found that when examining the difference in aggression for men, the diminution of their aggression from same-sex to partner was as a direct result of the target sex. This supports Felson's analysis, suggesting that norms of chivalry make men inhibit their aggression towards women. Cross et al. (2011) suggest here women's increase in their aggression to partners could be due to the knowledge that their partners would not hit a woman. This has also been expanded to be examined with self-report, rather than scenario studies with similar findings emerging (e.g., Bates et al. 2014). These findings support Felson's analysis (e.g., Felson 2002), suggesting that norms of chivalry make men inhibit their aggression towards their partner and that women increase theirs due to the lack of social sanctions associated with their aggression. Women are penalized less in both the legal system and judgments of the public.

Many authors have examined evolutionary perspectives on aggression (e.g., Campbell 1999). Sexual selection theory places the origins of the male directional sex difference in human evolutionary history (Archer 2004) with a focus on male competition. As with the majority of mammals, women have the higher parental investment pre- and postbirth, meaning their intrasex competition is less and their ability to be more selective in choosing a mate is greater. Consequently, men have less parental investment but greater male reproductive competition, the more men are able to offer (e.g., in terms of resources) the more attractive they will be to women. This increased competition between men also creates a short-term mating strategy with increased risk in attempting to gain social control over these resources, which would lead to a prediction of men being most violent to men, rather than to women. The magnitude of the sex difference in aggression will then follow that which poses the greater risk, with the greatest difference being for physical aggression and then less so for verbal and indirect aggression. Archer (2009) shows that this magnitude of sex difference in direct physical aggression can be best explained by using sexual selection theory than the alternative social role theory, arguing that male aggression is part of

a sexually selected adaptive set of behaviors. Competition between males is rife and the use of aggression in such competition is likely to make reproductive success more likely.

Campbell (1999) argues that the lower rate of female aggression is an adaptive strategy that is of huge importance in the mother's survival and reproductive success, and is not just an absence of masculine qualities such as risk taking. The greater importance of mothers than fathers to their infants' survival is supported through evidence of gestation periods, lactation, infant dependence, menopause, and the greater likelihood of male desertion. With this in mind, women should be less likely to perpetrate forms of physical aggression as these pose a risk of injury and endangering safety, leading women to weight the cost of physical aggression more highly than men. This in turn would lead to women experiencing higher levels of fear in situations that pose a physical threat, suggesting they may instead utilize a less risky form of aggression, such as indirect aggression, to minimize the possibility of retribution.

Status is less important to women, but they will still compete for resources; in studies with children, however, girls have been shown to prefer verbal behavior and cooperation to competition (the lower risk option). Campbell's (1999) discussion of intrasexual aggression among women indicates that when women resort to this sort of aggression it is to secure resources (e.g., a valuable male) rather than to maintain status within a dominance hierarchy. For example, Campbell et al. (1998) investigated explanations of female-to-female aggression and found support for the hypothesis that it is a function of female poverty in that it results in economic dependence upon men. This is reflected in a positive relationship between assaults and both female unemployment and AFDC receipt (Aid to Families with Dependent Children) with the latter being representative of men's desertion or abandonment of their female partners. Women will be aggressive in order to obtain the necessary resources for their own and their infants' survival.

This evolutionary account of women's propensity to avoid aggression that puts them in physical

danger is then shaped by society, culture, and social norms. For example, as Campbell (1999) suggests, women's aggression is then condemned as abnormal, masculine behavior and due to some sort of pathological disturbance or temporary insanity. She goes further to suggest that feminist researchers would explain this as originating in a patriarchal society that would condemn behavior of this sort by women where as other theories (e.g., Social Role Theory) see it as being related to culture and society when it may in fact be an innate protective mechanism by women. It leaves women with the need to explain and excuse their aggression in a way that men do not.

Campbell (2006) argued that this sex difference in direct aggression is not due to differences in experiences of anger, but due to different experiences of fear. Archer (2004) had already demonstrated there was no sex difference in anger, but other studies have found that women are more likely to experience greater levels of fear and fearfulness of potential danger. Again, fear driving the avoidance of aggression is an adaptive strategy to enhance survival of themselves and therefore their offspring. The sex difference in IPV seems incongruent with this explanation: if women were more fearful, it is unlikely that they would be perpetrating this type of aggression at the same rate as that of men. Their fear of physical injury must be less than for a same-sex or opposite sex stranger opponent, and indeed this is supported by studies suggesting there is a greater perceived danger from strangers than from intimates. A woman's awareness of the social norms that condemn violence against women could work to reduce the fear she may feel in a conflict situation with her partner. This could include the knowledge that if a woman was physically aggressive to her male partner there would be no physical reprisal, and so less, or no physical danger. This knowledge is one developed through knowing their male partners' behavior and values around women, something it is much less likely to know when the man is a stranger or acquaintance.

An alternative theory of the sex differences in aggression comes from Social Role Theory (Eagly 1987), which attributes sex differences in behavior, including aggression, as originating

from early socialization in terms of masculine and feminine sex roles. According to this theory, sex differences in social behavior have arisen historically from the positions and status men and women have held, which creates expectations about characteristics of each sex that are associated with their roles (e.g., women as homemakers, men as providers). Sex roles mean that women's aggression is viewed as incongruent with femininity and so women are more likely to use alternative forms of aggression. These expectations are then transformed into behavior with reinforcement of the differences, leading to different patterns of behavior developing (Eagly 1987). It is clear from developmental studies that boys prefer aggressive acts in play: for example, one study examined the development of preferential play for boys and girls among groups of four-, five-, six-, and nine-year-olds. They found that by 4 years of age, 50% of the boys (but less than 10% of the girls) rated that at least one of their favorite toys was used for inflicting harm through physical aggression on an inanimate object. This effect increased with age and filtered through into TV and media choices.

Archer (2004) performed a meta-analysis examining sex differences in aggression in real-world settings and related his results to both the evolutionary and social role theories. This study found that men were more physically aggressive than women were. The sex difference was smaller for verbal aggression, something that has been found in previous reviews of experimental laboratory studies. Sex differences were absent for anger and mostly absent for indirect aggression, something which is normally found in the female direction in studies of aggression in children. Elements of the results supported both theories, but Archer argued that the overall pattern was more consistent with sexual selection theory in terms of the fact that males were more likely to use risky forms of aggression when they are angry. This raises the question of what females do when they are angry: the most obvious form would be indirect aggression as it carries less risk.

Cross and Campbell (2011) describe the patterns seen in intrasexual aggression and explain that less is seen between women due to their

increased sensitivity to the costs of their aggression and an associated greater fear response. In discussing the contrasting pattern of sex differences, Campbell felt that the cultural norms may influence men's inhibition of their violence towards women, but that these norms would not be enough to reduce women's disinhibition; with an evolutionary mechanism that means women inhibit their aggression through fear of the consequences, it must be something more than this to make women overcome this barrier and allow their aggressive impulses to be enacted towards their male partners. Similarly, women's aggression is only inhibited towards partners, not men in general and yet the cultural and social norms dictate violence against all women is wrong. This fear reduction experienced by women who are violent in intimate relationships, is a fear reduction specific to their partners.

Campbell's work discusses the role of oxytocin in mitigating this issue. Oxytocin is a nonapeptide hormone and a neuromodulator which regulates a number of behaviors around reproduction, and in childbirth and new-born breastfeeding. In animal studies, it has been shown to be important in social behaviors such as partner bonding through sexual activity, and maternal and social bonding. It is also associated with a reduction of fear in animal and human studies; research with humans has shown oxytocin reduces amygdala activity in response to fearful stimuli and other aspects in response to threat.

Oxytocin may reduce inhibition generally, but release of this is context specific and is triggered by their intimacy meaning a partner-specific reduction in fear, so the increase risk of aggression is only directed towards their male partner. Campbell further points to this explanation going some way to understanding why women are aggressive to their male partners even in cultures where there is less gender empowerment for them. Typically, the research on oxytocin focuses on the positive social effects in terms of increased trust, and bonding, but Campbell states "it is a two-sided phenomenon" (p. 396) it increases mother's attachment to her infants but also reduces her fear (and so increases her chance of aggression) in defense of them.

Personality and Psychopathology

Many of the studies of risk factors of aggression and criminality, including those on IPV, have focused very much on male perpetrators. Addressing this issue, Farrington and Painter (2004) examined sex differences in risk factors based on conviction data. They used brothers and sisters in the Delinquency Developmental Investigation which is a longitudinal survey examining the development of offending and antisocial behavior in 411 males first contacted in the 1960s. The criminality rates were much higher for men than for women, with 44% and 12%, respectively, having convictions. There were similarities in predictive risk factors of criminality however: e.g., low family income, large family size, and having convicted parents and siblings (the probability of being convicted increased with the number of other convicted children in the family). However, there were differences, firstly in their choice of crime, with men being convicted more for burglary and theft and women more for shoplifting and crimes of deception. The most predictive risk factors included parental characteristics for men and socioeconomic status and child-rearing factors for women. This study shows that concentrating solely on one sex leaves a gap in understanding and limits the generalizability of the findings. Many of the risk factors that were identified for both sexes here develop early in life, and so this study is important for identifying those at risk and for intervention.

Medeiros and Straus (2006) reported a study of 854 university students and focused on whether risk factors of IPV were similar for men and women. They found that 8 of 21 risk factors were significantly associated with the increased risk of minor acts of IPV perpetration and that all eight were significant for both men and women. These included anger management, dominance, relationship conflict, and substance abuse. For severe acts, 12 risk factors were significantly associated, and nine of these were significant for both men and women – including jealousy, communications problems, and sexual abuse history. The authors suggested that the etiology of IPV is “mostly parallel” for men and women (p. 10) and

the finding that dominance was a risk factor for women as well as men contradicts the assumptions that male dominance alone is at the heart of the cause of IPV.

Ehrensaft et al. (2004) compared clinically abusive relationships (those causing injury, or requiring official intervention, or both), physically aggressive individuals without clinical consequences, and a control group who reported no abusive experiences. There were differences in the associations found, for example, men in these clinically abusive relationships had disinhibitory psychopathology and extensive personality disorders, whereas women had childhood family adversity and aggressive personalities. Similarly, other studies have compared men and women arrested for IPV and found (compared to men) that women were more likely to have higher levels of histrionic, narcissistic, and compulsive traits and were less likely than men to have dependent traits. Other studies have also found differences in risk factors associated with aggression for men and women, whereas some studies have also found similarities. The cross-sectional nature of many studies means firm conclusions about relationships and causality cannot be drawn, but the broad trends suggest that risk factors associated with men's and women's use of aggression are different.

There have not been many studies that have focused solely on women's violence, many focus purely either on men or on comparing men's and women's aggression. Often, with women being less likely to enter the criminal justice system as a partner violent offender, it presents fewer opportunities to work with female offenders. A recent review revealed that within this limited literature, common themes emerged including a high prevalence of trauma related symptoms, emotional dysregulation, substance misuse, attachment issues, and interpersonal dependency. This review also revealed that many perpetrators are also victims of violence, either historically or currently. This points to the complexity of the antecedents to women's violence.

Stressful or traumatic experiences in childhood, often referred to as adverse childhood experiences (ACE), are thought to have a negative and

detrimental impact in adulthood. Indeed, childhood interpersonal trauma has significant and longstanding impact on adult psycho-relational functioning (Dugal et al. 2016). Research has demonstrated the impact of ACE individually, but more recently it is thought that there is a cumulative impact of multiple ACE. Trauma impacts on neurological development that forms the underpinning of how children process and organize their experiences; where there is impaired functioning it forces individuals to find alternatively ways of coping with negative and emotionally provoking experience. ACE have been found to be associated with perpetration and victimization of IPV in adulthood.

Much of the ACE research has explored the impact for men and women using large-scale samples, for example, research indicating that men and women who experience childhood victimization are also at risk for adult violence victimization. Other studies have focused on women specifically; for example, ACE are associated with adolescent pregnancy, and negative outcomes associated with the adolescent pregnancy seem to be more likely related to the ACE than the age of pregnancy. Similarly, women with a higher frequency of ACE in their history were more likely to engage in risky sexual behaviors and more likely to be the victim of IPV.

The literature on risk factors and antecedents to women's aggression is scant in comparison to men's; however, the picture emerging is that men's and women's violence is predicted by a multitude of different factors. To be able to fully understand and intervene with violent women, there needs to be an understanding of what issues contribute to the cause of the violence. The controversy over women's violence and the implications for some gendered models of IPV has stalled the progression of research in this area.

The Abusive Personality: Influence of Attachment and Borderline Personality Traits

Dutton (e.g., 1998) discusses the influence of attachment and personality variables, specifically

traits of borderline personality, in the development of a so-called "Abusive Personality." Borderline personality disorder, or in a less extreme form borderline personality organization, has been discussed within the literature differentially, but there is some agreement around the key characteristics being: an unstable sense of self and issues with identity including experiencing abandonment anxiety, a pattern of intense and unstable interpersonal relationships characterized by issues of dependency, and intense anger and impulsivity which has been found to be tied to substance abuse and sexual promiscuity (e.g., Gunderson 1984). Dutton (e.g., 1998) described borderline personality organization as a continuum of these personality traits and issues that are characterized by issues around identity that manifest in intimate relationships. His work around this pattern of personality traits focused on a sub group of men who were only violent in these intimate relationships, and in which the violence seemed to appear cyclically, mirroring earlier work by other researchers. Here, attachment theory is used as a way of explaining that the interpersonal and relationship functioning of adults is linked to and related to early childhood experiences with caregivers that impact on the models developed of "self" and "other." Intimacy anger develops through a perceived threat of abandonment which is then directed to the person's attachment figure, their romantic partner. Their anger is matched then by their fear of abandonment and a cycle is created where anger is followed by violence and then contrition and dependency. As Dutton (1998) describes is: "These men are literally at their wives' knees or at her throat" (p. 94).

Research has supported this pattern in finding links between insecure attachment, borderline traits, and anger. Indeed, Dutton suggests that these traits are a component of abusiveness that are interacting with earlier learned cues around abuse in intimate relationships (e.g., witnessing IPV between parents). Due to their insecure sense of self and issues with being alone, these men are reliant on their partner to maintain their sense of self, but due to their inability to communicate this effectively to their partner, they appear demanding and often project anger on to their partner

when their needs are not met. After intense anger, there are often periods of contrition and regret which then characterize the cyclical nature of this behavior.

Dutton's work has been significant in understanding men's aggression in relationships, while it has not been explored as widely with violent women, the literature that exists shows promise. Research has previously demonstrated links between attachment anxiety and IPV perpetration as well as with issues such as emotion dysregulation, substance misuse, and interpersonal dependency to women's violence. Research has also demonstrated that women are more likely to possess borderline symptoms compared to men (e.g., Henning et al. 2003). In a study comparing 32 female offenders receiving treatment for their partner violent behavior, to a control group of nonoffending women who were engaged in psychological interventions, Goldenson et al. (2007) found significant differences between the two groups. The partner violent women reported experiencing less attachment security, more trauma symptoms, and more personality psychopathology (e.g., antisocial and borderline traits) compared to the control group. Introduction of trauma symptoms here links this body of literature with that of ACE described above.

Early childhood experiences can be key in influencing the development of later adult behavior including around IPV. Cumulatively, attachment anxiety multiple ACEs, personality and psychopathology are all influential; it is clear how this abusive personality could be mapped on to their violence as an explanatory factor. This personality type is not the only explanatory factor when considering women's aggression, and it indeed points to the development of more typologies of women's behavior that can help us understand the best way to intervene and provide treatment options. Typologies of women's aggression do exist; for example, Graham-Kevan and Archer (2005) investigated three explanations of women's IPV: that it is associated with fear, that it is reciprocal, and that it is coercive in nature. They found that each of the possible explanations received some support. Babcock et al. (2003) attempted to classify

women into Holtzworth-Munroe and Stuart's (1994) typology, using women who had been referred to a treatment agency for abusive behavior. The women were broadly categorized into either "partner only" or "generally violent." Generally violent women were reported to use more instrumental violence, have witnessed their mother's physical aggression, and experienced more traumatic symptoms than those who used IPV only. Babcock et al. posit that the generally violent women have learnt through socialization mechanisms that it is acceptable for women to use violence to resolve conflict.

Are There Sex Differences in Motivations for IPV?

The research discussed demonstrates the prevalence of women's aggression in intimate relationships and clearly highlights the complexity of men's and women's aggression in this context. There have been few studies that directly compare men's and women's motivations to use aggression; however, those that have have found both similarities and differences. For example, Campbell and Muncer (1987) proposed a theory to explain sex differences in aggression in terms of social representations of anger and aggression. They argued that men tend to use aggression in an "instrumental" way, to control other people, whereas women use it in a more "expressive" way, involving a loss of control. From this theory, they developed a measure, the EXPAGG, to assess the extent of instrumental and expressive beliefs about aggression. Studies using this measure have often found the predicted sex difference, in terms of expressive beliefs being higher in women and instrumental beliefs being higher in men. Other research has demonstrated similarities in motives for physical aggression; for example, Elmquist et al. (2014) found that with few exceptions, there were no significant differences between men and women in the motives they endorsed, which included self-defense, expression of negative emotions, communication difficulties, power and control, and jealousy. Other research has also demonstrated both men's and

women's propensity to use violence as a means to control, which could be driven through a fear of abandonment.

Langhinrichsen-Rohling et al. (2012) performed a review to explore motives for men's and women's IPV and noted among other findings that the "heterogeneity in methodology, measurement, and construct development" (p. 457) can make drawing conclusions difficult, which is compounded the fact that motivations are often internalized processes and are not often easy for perpetrators to label. Nevertheless, they found that power and control, self-defense, expression of negative emotions, jealousy, retaliation, and communication difficulties were all common motives, with few gender-specific effects being found. They further suggested motives differ based on the context in which the violence occurs and that more work is needed with more methodologically rigorous studies to fully understand why men and women aggress, as well as the motives to stop aggressing which could inform intervention.

Implications for Treatment and Intervention

Current interventions and treatment options for violent women are limited. Despite evidence of women's violence towards men, there are few women who enter the criminal justice system and are mandated treatment. When they are indeed referred, there are even fewer programs that are suitable for female offenders. Many current interventions still have their roots in the Duluth model of IPV that is about re-educating men about their male privilege and use of patriarchal control. With few options, many women are referred to victim services despite being an admitted aggressor. With so little research exploring the dynamic risk and protective factors associated with women's violence, then it is unlikely we will be able to develop effective, evidence-based perpetrator programs.

As with men's violence, there are complex histories and antecedents to women's aggression, and there is a need for interventions to include a more tailored approach to target individual

needs and comorbid issues (e.g., substance misuse). It would seem there are benefits to women completing programs, research has shown that completing a program as part of a criminal sentence, women showed less aggression towards their partner. The current programs available are not appropriate for women, but then the evidence suggests they are not appropriate for most men either. Rather than purporting the best way forward as being separate programs for men and women, some scholars (e.g., Carney et al. 2007) are highlighting the similarities between partner violent men and women (e.g., personality profiles, trauma, ACE) and that both groups have similar within group heterogeneity. From this, it would seem the design of a program should be tailored to individual need rather than being about gender.

A further issue arises in the way we construct IPV as primarily having a single aggressor and a single victim, rather than seeing the possibility that both people could fit into both groups at different times. Current services have a tendency to focus on "perpetrators" and "victims" separately in their support and intervention; the prevalence of mutual or bidirectional IPV provides a challenge to the way we currently intervene in IPV. As it stands, a bidirectional couple would be likely placed into perpetrator and victim services rather than approaching a couple based therapy, one that could tackle unhealthy conflict resolution strategies and encourage more appropriate means of managing conflict in the relationship.

Conclusion

A wealth of research demonstrates that women's violence in relationships is prevalent, serious, and has physical and psychological impact on male victims. We also understand more about the antecedents and motivations of women's violence than ever before, but with some still significant gaps in knowledge, there is also still a lack of evidence-based practice in the areas of interventions. A consequence of some sectors in society ignoring violence by women includes underfunded male victim support services and few options for women seeking help for their

aggressive behavior. It is also critical to develop methodologically rigorous evaluations to ensure that for both men's and women's programs, there is a commitment to evidence based practice rather than supporting ideological designs.

Evolutionary theory presents a more distal explanation of women's aggression but social theories (e.g., social learning theory, social role theory) also present evidence in understanding both the sex differences in aggression and the motivations behind them. As theories, they are not mutually exclusive and indeed they have been explored together to explore their respective contributions to our understanding of human aggression. For example, the suggestion that our evolutionary history has led men and women to adopt specific roles; these have then developed into social roles which have reinforced these adaptations. In the complexity of something such as human aggression, it can be seen that both approaches are important for understanding the nuances of different types of aggression. For example, IPV has been found to vary across cultures that have more traditional values around gender; cultures that have more gender equality in terms of societal power and gender empowerment see more women's aggression and tend to have the most parity in IPV perpetration (Archer 2006).

The research discussed here highlights that women's violence is sometimes motivated by self-defense, but that this cannot be assumed to be the motivation, more often than not there are other factors that explain more of the variance that exists. A common conclusion in this area is that more research is needed to understand aggression better; this is indeed the case here. There is more we need to understand about women's aggression before we can effectively tackle it as a social issue and, along with men's aggression, work towards reducing it.

Cross-References

- ▶ [Abusers: Husbands, Boyfriends, And Former Sexual Partners](#)
- ▶ [Aggression for Sexual Access](#)

- ▶ [Aggression](#)
- ▶ [Coercive Control](#)
- ▶ [Conflict Between the Sexes](#)
- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Contexts For Men's Aggression Against Women](#)
- ▶ [Contexts For Women's Aggression Against Women](#)
- ▶ [Female Age as a Predictor of Men's Aggression Against Women](#)
- ▶ [Female-Perpetrated Violence](#)
- ▶ [Indirect Aggression](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Partner Abuse and Homicide](#)
- ▶ [Physical Aggression](#)
- ▶ [Sex Differences in Aggression](#)
- ▶ [Violence As Coercive Control](#)
- ▶ [Women's Use of Direct Versus Disguised Social Aggression](#)

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Contexts for Women's Aggression Against Women

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Synonyms

Female intrasexual aggression; Female intrasexual competition; Female–female aggression; Female–female competition

Definition

The use of social and indirect aggression by women as a means to compete with other women, mainly in the context of mate search and mate retention.

Introduction

Both men and women face the challenge of deciding how much time, energy, and resources to invest in parenting versus mating efforts, but due to women's higher obligatory (or minimum) parental investments in offspring, men and women also face qualitatively different challenges to their reproductive success (Trivers 1972). These asymmetries in reproductive investments start at conception: for men, one ejaculate during a sexual interaction suffices for males to pass on their genes to the next generation. Should conception be successful, a female in contrast needs to invest in gestation and birth of her offspring and after birth, lactation and childcare. Moreover, it follows that the sex that makes the largest investment in offspring will also incur the highest costs from mating “mistakes,” and as a result will be the most sexually discriminating, focus more on obtaining a long-term mate, and will be the sex in demand. The sex with the lower obligatory

investment is expected to compete more heavily with same-sex members for access to the higher investing sex and to adopt a more opportunistic, short-term mating strategy. However, humans are among the few animal species in which both sexes engage in parental care, with both women *and* men investing heavily in offspring after birth. This high paternal investment causes men to be selective in their mate choice for long-term partners, and since available men are not all of the same mate value, women have to compete with each other for access to – and retention of – the most desirable men (e.g., Campbell 2013).

As will be detailed below, the way women compete with one another is different from the way men compete and will often take the form of indirect or social aggression. The remainder of this chapter will first focus on the types of aggression used by women, before detailing the contexts and contents of women's competition in the context of securing a mate, and the contexts and content of women's competition in the context of retaining a mate.

Types of Aggression

Direct aggression. Direct aggression involves acts to intentionally inflict injury or harm upon another person and it can be physical, verbal, violent, or nonviolent. Direct aggression is not anonymous: the perpetrator can be easily identified, and the target is therefore likely to retaliate, either immediately or at a later time. Therefore, direct aggression – in whichever form – is considered a high-risk activity. Both men and women are more likely to aggress against same-sex individuals, and whereas men are less likely to be aggressive the more intimately they know someone, the reverse is true for women (see Campbell 2013). Sex differences also emerge in victimization of aggression, with men being more likely to be the victim of aggressive acts – perpetrated by men and by women. However, as the risk associated with aggressive behaviors becomes lower, the sex differences tend to disappear. This can be explained by considering the differences in parental investments between men and women and the

qualitatively different adaptive problems they needed to solve during evolutionary history (e.g. Cross and Campbell 2011).

Given their high physical and economic investments, women incur high costs relative to the fitness benefits of engaging in direct aggressive competition with other females: across human societies, it has been shown that children's survival depends almost exclusively on the mother's continued investments. Moreover, a woman's survival benefits not only her own offspring but also her grandchildren. Being harmed during physical competition would negatively affect a mother's ability to provision for herself and her (grand) offspring, and her death would almost certainly have been – and often still is – fatal to her offspring. As a result of these selection pressures, women have evolved to be more risk-averse than men and are less likely to engage in physical or direct intrasexual competition with their rivals. Cross and Campbell (2011) argue that women are thus largely motivated by an avoidance of losses, and that women's lower fear threshold may be a proximate psychological manifestation of this motivation.

Indirect aggression. Indirect – or social – aggression refers to the purposeful, but often covert, manipulation of interpersonal relationships, and includes behaviors such as social exclusion, breaking confidences, spreading rumors, and gossip. Relative to direct (physical) aggression, these acts are less risky since there is a lower likelihood of retaliation or social consequences and are equally or more often employed by women than by men (see also Campbell 2013). The overall goal of the various forms of indirect aggression is usually to exclude rivals from one's social group, while simultaneously damaging their ability to form or maintain a social network of their own. Indirect aggression includes actions such as social exclusion, gossiping, spreading rumors, and defamation of the target. The overall goal of indirect aggression is to reduce a rival's desire, or ability, to engage in competition over mates; this goal may not always be the conscious driving force behind women's indirect aggression, however, but is likely to operate at an unconscious or implicit level. Research shows that indirect

aggression is the preferred way of women to compete with other women, and that it is mainly employed to intimidate rivals, diminish their mate value, or improve one's own mate value. Compared to men, women are more willing to engage in indirect aggression and are better able to pick up on subtle cues to social exclusion (Benenson et al. 2013).

Similar to direct aggression, women's indirect aggression is often targeted at other women, and in particular, at attractive or sexy women. The use of indirect aggressive strategies peaks during adolescence and young adulthood, when fertility is at its highest, and competition over mates is both most relevant and most salient. Research indicates that younger women report significantly more intrasexual competition than women who were past their reproductive peak. For example, in their study on one particular tactic of intrasexual competition, i.e., gossip, (Massar et al. 2012) showed that younger women gossiped more about their romantic rivals than older women did, and that this effect was mediated by younger women's higher mate value. Indeed, gossip as an indirect aggressive tactic is commonly used by women and tends to focus on topics like other women's appearance or sexual conduct. Gossip between females is more negative than gossip between men or mixed-sex pairs, and compared to men, women respond encouragingly and positively to gossip they hear from their female friends. More recently, Davis et al. (in press) established that individuals' intrasexual competitive tendencies predicted the use of gossip as an intrasexual competition strategy. Moreover, these authors report that women are more likely to gossip than men, in particular about physical appearance and social information.

There are also indications that indirect aggression is effective in eliminating the competition, for example, by suppressing a rival's sexual activity: whereas perpetrators of indirect aggression tend to reach sexual maturity at an earlier age, victims of indirect aggression mature later (see White et al. 2010). Moreover, being the victim of indirect peer victimization, including bullying, causes lower self-esteem in girls but not in boys. When discussing women's intersexual and

intrasexual competition in the remainder of this chapter, the implicit assumption will be that these forms of competition utilize indirect aggression, unless specified otherwise.

Competition in the Context of Securing a Mate

Female Intersexual Competition

Choosing the "right" mate is essential to reproductive success. Especially during the early years of life, human children are reliant on their caretakers for survival and require large amounts of care, food, and protection. Although women are capable of rearing children on their own, they may take longer to conceive a next child when they are the only caretaker. Biparental care thus greatly enhances reproductive success. Differences in the minimum obligatory investments in offspring between the sexes also cause a difference in emphasis on which traits are considered desirable – or even necessary – in a mate (Trivers 1972).

Given women's greater obligatory investment in offspring, their reproductive interests are served best if they are able to obtain a long-term mate with the potential and willingness to invest social and material resources in her and their offspring (Buss 1989). Because men with a higher societal status have better access to resources, women have evolved to value social status in long-term mates, as well as the internal attributes that signal the ability to attain high status or a leadership position – such as being a good judge of character, taking initiative, influencing people, and being assertive. Additionally, mates provide protection against (sexual) assaults by other men – i.e., they function as bodyguards – and research has shown that married women are overall less at risk of being victims of sexual assaults than single women (Wilson and Mesnick 1997). Women's fear of crime and feelings of vulnerability for victimization are associated with their preference for physically formidable and aggressive men. For men, the main challenge is finding a fertile mate. However, many of the characteristics which enhance women's mate value, including her

fertility status, are concealed and cannot be directly observed. Men are thus faced with determining a woman's mate value based on external attributes and have evolved to focus on female physical qualities which signal fertility and youth due to their associations with high estrogen levels: full lips, soft hair, smooth skin, colorful cheeks, good muscle tone, and a low waist-to-hip ratio. Indeed, numerous studies have indicated that men place a premium on women's physical attractiveness, both for short-term and long-term relationships (e.g., Buss 1989).

The search to attract the best possible mate causes sometimes fierce intrasexual competition, which is usually focused on the traits preferred by the opposite sex. That is, women compete within the domain of physical attractiveness, whereas men are more likely to compete over social status and resources. Individuals with a high mate value are more likely to achieve a mate with their preferred qualities and have greater reproductive success as a result. Indeed, high-income men report having more frequent sex and more biological children than men with a lower income, and highly attractive women are more likely to be married and have more biological children than less attractive women.

Female Intrasexual Competition

Intrasexual rivalry among females in socially monogamous species, including humans, is a well-documented phenomenon. Group social living substantially increases both male and female fitness, due to, for example, increased access to resources. However, group living also carries costs, such as an increased risk for pathogen infections, and increased competition over access to scarce resources and mates due to the presence of same-sex rivals. Intense intrasexual competition may cause group instability and evolve into intrasexual aggression. Indeed, in many socially living species, rates of female–female aggression increase as the proportion of (fertile) females in the group increases, with pregnant females showing the highest rates of aggression. Indeed, among, for example, wild chacma baboons, sexually receptive females received most aggressive attacks from other females, whereas pregnant

females initiated the most aggression against other females. These processes are likely driven by both mating competition – including suppression of other females' reproduction – as well as competition over access to resources (see Huchard and Cowlshaw 2011). Among humans, intrasexual competition similarly revolves around access to and retention of mates but also concerns status enhancement or avoidance of victimization.

As mentioned above, starting in early childhood, rather than engage in direct aggressive acts, women resort to less costly strategies of competition. In particular, women tend to use relational and indirect forms of aggression – which includes gossip, spreading rumors, and social exclusion (Archer 2004). These forms of aggression in turn may be seen as part of several intrasexual competition *strategies*. In the literature, generally two strategies of intrasexual competition are distinguished, which both men and women employ to compete with rivals: self-promotion and derogation of rivals (e.g., Schmitt and Buss 1996). Self-promotion refers to the enhancement of characteristics, such as physical attractiveness, to increase one's appeal to potential partners, relative to one's rivals, and as such increase one's own chance of winning the competition. Rival derogation on the other hand refers to acts which are intended to decrease one's rivals' appeal and thus decrease their chances of winning the competition (Fisher and Cox 2011). Women in particular are more likely to resort to self-promotion strategies than to competitor derogation (Fisher et al. 2009), but often these strategies are employed simultaneously. As well as advertising their own strong points through the enhancement of their appearance (e.g., by wearing make-up or tight clothes), women attempt to damage their rivals' reputation, mate value, and social standing (Campbell 2013). Fisher and Cox (2011) furthermore state that since there are costs for competing, individuals are likely to resort to strategies which reduce or even eliminate the need for competition. In a series of studies, these authors report that both men and women resort to two additional strategies to compete with others: mate manipulation and competitor manipulation. More specifically, mate manipulation relies on

redirecting a (prospective) mate's attention and activities away from rivals, hiding the latter from the mate, and thereby eliminating the need for competition altogether. Competitor manipulation involves trying to persuade a rival that the mate isn't worth the competition, thereby increasing one's own chances for success with this mate (Fisher and Cox 2011). Fisher and Cox (2011) have shown that after self-promotion, mate manipulation is the strategy most often employed by both men and women. These preferences might exist because of the lower costs of these strategies compared to the other strategies, which are aimed at a rival, but in could severely damage one's own reputation in the eyes of one's mate.

Self-Promotion and Ornamentation

Because men value attractiveness in their romantic partners, women often compete for mates by increasing their own attractiveness and sexiness, relative to the appearance of their competitors (e.g., Buss 1989; Campbell 2013). Women spend considerable time on their appearance, and Western women spend more than twice as much money on appearance-enhancing products – clothing, make-up, jewelry, or cosmetic surgery – than men. Like men, women also consume luxury goods – extravagant trips, jewelry, designer clothes, or expensive cosmetics – to signal their ability and traits to gather and waste such resources. For women, consumption of such luxury goods is however not used to attract mates but rather employed as a strategy to compete with other women. Hudders et al. (2014) showed that women who consume luxury goods were perceived by other women as more formidable rivals, since these women were perceived as more attractive, flirty, young, ambitious, sexy, and less loyal, mature, and smart. Women's desire to appear attractive to prospective mates and to out-compete other women sometimes has consequences which could be detrimental for mental and physical health. For example, Hill and Durante (2011) showed that women who were primed with intersexual courtship and intrasexual competition were more likely to indicate they would be willing to use dangerous diet pills or go sun tanning. Other research has shown that cues to intrasexual

competition cause women to be less satisfied with their bodies and to have lowered self-esteem, as well as to report increased favorability in their attitudes toward restricting their eating, whereas these effects were not found for men.

Several contextual variables influence women's tendency to enhance their attractiveness in response to intersexual and intrasexual competition. One such variable is the mate value of men and women in one's immediate surroundings. Hill and Durante (2011) suggest that women may calibrate their self-promotion efforts in response to the attractiveness of men and women in their social environment. For single women, this means that in order to decide the extent to which they should enhance their appearance, they should take into account both the attractiveness of same-sex competitors, as well as the quality of the potential mates. The presence of very attractive competitors and/or high quality mates in their environment should for single women thus cause increased efforts to engage in self-promotion – even at the expense of (future) health; it is likely however that such efforts at some point reach a “ceiling of effectiveness,” or optimum value. For committed women, these behaviors are more likely to be driven only by mate retention motives and therefore depend on the mate value of same-sex competitors (for similar arguments, see e.g., Fisher and Cox 2011).

Second, recently, researchers (e.g., Linney et al. 2017) have started to focus on *motherhood* as a specific context which both allows and instigates competition among women – termed competitive mothering. Linney et al. (2017) suggest that “Mothers should be prepared to invest energy, time, and resources in their offspring in order to nurture qualities associated with improved future fitness, such as intelligence, popularity, leadership skills, physical coordination, and physical attractiveness. This ‘extra’ investment that goes beyond ensuring mere survival can give a competitive edge to a woman's offspring, ultimately increasing the reproductive success of mother and child relative to their peers” (p. 94). Such maternal competition centers on mothers' assertions of their children's abilities, carrying the implication that they are superior to other mothers.

Competitive mothering shows itself in both specific and nonspecific bragging about one's abilities as a mother, and particularly, about the qualities and academic achievements of one's child, and causes anger, irritation, and annoyance in rival mothers (Linney et al. 2017). However, direct confrontation and hostility are avoided, and the "punishment" of such bragging mothers is more likely to take the form of avoidance, ostracism, or conversational indirect reprimands.

Furthermore, there are indications that the tendency to enhance one's appearance fluctuates throughout a woman's menstrual cycle. Given that the benefits for appearing attractive are highest around the time when conception is most likely, one would expect that women spend more effort to enhance their appearance around ovulation. Indeed, in photographs taken around ovulation, women were judged to want to appear more attractive than in photographs taken during the non-fertile phase (Haselton et al. 2007). Moreover, several studies show that near ovulation, women prefer to wear clothing that is more revealing and sexy and engage in more self-grooming (Durante et al. 2008). Furthermore, women tend to pay more attention to and buy more appearance-enhancing products near ovulation than at other time points during their menstrual cycle. Taken together, these studies thus suggest that particularly around ovulation, women ornament themselves for intrasexual competition.

Competitor Derogation

Although self-promotion is an effective strategy to enhance one's own mate value relative to that of a rival, actively trying to *decrease* a rival's mate value relative to one's own is another common strategy employed by women during intrasexual competition. Competitor derogation can be classified as a form of indirect aggression and takes on various forms, ranging from making quite subtle remarks or taking over conversations involving the rival to very blatantly pointing out a rival's flaws to a male in whom one is interested (Fisher and Cox 2011). There are indications that even though much of women's indirect aggression is covert or subtle, it is nevertheless effective at inflicting harm on rivals, in particular on female

rivals, since women are more likely to pick up on such subtle signals. For example, research has shown that merely receiving an averted eye gaze causes individuals to feel relationally devalued and negatively affects their self-esteem (Wirth et al. 2010). An individual receiving such a subtle social cue is likely to "get the message" and withdraw, particularly if the signal is sent by multiple females. Such subtle cues and indirect methods of aggressing against a rival are thus extremely cost-effective in the sense that it affects a rival's self-evaluations, without much effort on the side of the perpetrator. The main focus of women's competitor derogations is first, a rival's attractiveness and second, her sexual reputation.

Attractiveness. Although men also use competitor derogation, the focus of this derogation differs. Generally, as mentioned above, the intrasexual competitive acts are targeted at those characteristics which are valued in the opposite sex. Female mate value is largely determined by physical attractiveness, and therefore, when attempting to derogate their rivals, women focus mainly on facial attractiveness, weight, or body shape. Fink et al. (2014) report that in a context of intrasexual competition, the physical features men value the most in women are perceived by other women as most threatening: a very feminine face, larger breasts, and a low waist-to-hip ratio. As a way to counter the threat of such attractive rivals, women report often making derogatory comments about the unattractiveness of highly appealing other women. Compared to men, women also report feeling more *schadenfreude* over a same-sex friend's misfortunes, in particular when such events lower their physical attractiveness (e.g., got a bad haircut or developed acne).

Attractive women report being the targets of other women's social aggression more often than unattractive women, and for adolescent girls, being attractive increases the odds of being the victim of verbal derogation up to 35%. Among adolescent boys and girls, bullying is often targeted at body weight, but the specific aggressive strategies differ depending on whether a person is overweight or underweight. For example, Wang, Iannotti, and Luk (2010) showed that whereas overweight boys and girls were often

victims of (verbal) bullying, only the underweight girls were victims of indirect aggression – i.e., gossip and social exclusion. This makes sense in light of the value placed on thinness as a mate value enhancing characteristic for women. Interestingly, in addition to more often being the victim of intrasexual competition, attractive girls and women are also more likely to *use* competitor derogation as an intrasexual competition strategy (Fisher et al. 2009).

Sexual reputation. The second important domain in which women often derogate their rivals is her sexual reputation. Specifically, women's negative remarks about rivals' sexual reputation often center on her being too promiscuous ("a slut") or too chaste ("a tease"). For men, a woman's sexual reputation is important, especially in the context of long-term relationships. Since men who are looking for a long-term mate place a premium on finding a reproductively exclusive mate, accusing competitors of promiscuity and sexual availability may thus be a useful weapon (Campbell 2013). There are indeed indications that women simultaneously derogate a rival's promiscuity while strategically emphasizing their own chastity, for example, by underreporting the number of previous sex partners to a new partner.

A combination of being physically attractive and "easy" looking – i.e. *sexiness* – is then likely to be especially threatening to women, and Vaillancourt and Sharma (2011) showed that this is indeed the case. In their study, women were confronted with either a conservatively dressed or sexily dressed (i.e., wearing tighter and more revealing clothing) confederate. Their verbal and nonverbal responses were videotaped and showed that when the sexy confederate was in the room, women exhibited facial disgust reactions and made derogatory remarks. Moreover, when asked whether they wanted to befriend the confederate or introduce her to their boyfriend, they were more likely to refuse when she was provocatively rather than conservatively dressed. Women thus restrict other women's sexuality by using indirect means of aggression.

Derogation aimed at a rival's sexuality is particularly common in social contexts with a skewed

sex ratio, i.e., where suitable male partners are scarce. In general, women compete for mates by advertising qualities men find attractive, one of which is sexual exclusiveness or fidelity. Moreover, since past behavior is the best predictor for future behavior, challenging other women's sexual reputation is an effective way to influence perceptions of these women's future fidelity. Thus, when the sex ratio is female-biased, women often resort to gossiping and accusing other women of being promiscuous, "easy," or sexually unfaithful, simultaneously damaging a rival's sexual reputation and enhancing one's own. Indeed, experimental research (Arnocky et al. 2014) indicates that mere *perceptions* of mate scarcity – induced by a bogus newspaper article – increased women's intrasexual competitiveness, jealousy, and willingness to aggress indirectly against a same-sex rival. Similarly, women who are led to believe that their environment contains an abundance of rivals are more interested in relative compared to absolute gains in resource allocation tasks, emphasizing that these decisions are driven by a desire to out-compete one's rivals, even at costs to oneself. Finally, in mate-scarce contexts there is a risk that female indirect aggressive behaviors – including rival derogation – escalate into female–female direct (physical) aggression (see also Campbell 2013).

Menstrual cycle effects. Ovulatory shifts in women's use of competitor derogation have also been established. For example, Fisher (2004) showed that compared to nonfertile women, during ovulation, women derogated other women's facial attractiveness more. Moreover, during the ovulatory phase of their cycle, women tend to report increased dehumanization of other women – but not of men or elderly women – e.g., by describing others in animal-related words, and these effects may be driven by estrogen levels in particular (see e.g., Piccoli et al. 2014). In a study with women using hormonal contraceptives, it was shown that as the level of synthetic estrogen in these contraceptives was higher, the women's intrasexual competition also increased, in particular their tendency to objectify other women. Similarly, it has been established that among women using hormonal

contraceptives, higher levels of synthetic estrogen – but not synthetic progesterone – predict increased mate guarding tendencies. As mentioned above, women tend to ornament themselves around ovulation, and this seems especially the case when there is an abundance of rivals in the local environment: when women were told that there were many attractive women in the local environment and subsequently were offered the opportunity to select clothing items from a clothing website, women in the ovulatory phase were much more likely to choose sexy clothing items (Durante et al. 2008). In addition to their own menstrual cycle influencing intrasexual competition, a same-sex *rival's* fertility status might increase women's intrasexual competition and mate retention efforts. For example, Krems et al. (2016) showed that women in a relationship who were exposed to photographs of other women taken during their ovulatory cycle phase reported they would try to avoid or even socially exclude these women, but only when they rated their own partners as highly desirable.

Effectiveness of competition with rivals. Regarding the effectiveness of the intrasexual competitive tactics described above – self-promotion and rival derogation in particular – research has shown that attractive women have a credibility advantage over their less attractive peers. After hearing derogatory remarks about another woman's appearance, men tended to decrease their ratings of the facial attractiveness of this person when the remarks came from an attractive woman (Fisher 2004). Interestingly, Fisher et al. (2010) report that such derogatory comments not only cause men to devalue a woman's attractiveness but also her kindness, trustworthiness, and overall desirability as a mate. Thus, while rival derogation may be an effective strategy to influence perceptions of a rival's attractiveness or sexual permissiveness, it simultaneously decreases the perpetrator's reputation or mate value for men, as well as her appeal as a same-sex ally for women. Moreover, women are aware of the fact that direct, blatant, or unreasonable attacks on another woman's appearance are inappropriate and likely to be counterproductive (Fisher et al. 2010). Thus, although attacking

a rival and her appearance or sexual reputation may be a particularly effective way to reduce her mate value in the eyes of a (prospective) mate, it may backfire in the sense that one's own attractiveness and mate value are reduced as well. These relatively high costs are presumably the reason that women are more likely to resort to self-promotion than to competitor derogation in the context of intrasexual competition (see Fisher and Cox 2011).

Competition in the Context of Retaining a Mate

Female–female competition not only takes place in the context of mate search, but also, and no less intense, in the context of *mate retention*, also referred to as *mate guarding*. Maintenance of the pair bond is, as explained above, essential to a woman's reproductive success and the health and survival of her offspring. Therefore, to protect one's relationship, one needs to fend off potential mate poachers and prevent a mate from defecting. One of the biggest threats to relationship maintenance is a partner's infidelity, and it is threatening for different reasons for men and women. Whereas for men the main adaptive problem of a partner's infidelity is cuckoldry and paternity uncertainty, for women the largest threat is that a partner will divert his resources from her and her offspring to another woman. The threat of infidelity and the resulting emotions – in particular, jealousy – motivate individuals to undertake efforts to retain the partner for the pair bond. Such behaviors which are implicitly or explicitly aimed at maintaining the pair bond are termed mate retention tactics (e.g., Buss and Shackelford 1997). These tactics are often divided into benefit-provisioning tactics and cost-inflicting tactics (see Buss 1988). The former are used to reduce the likelihood of the partner's defection by focusing on enhancing the partner's satisfaction with the relationship and the partner, whereas cost-inflicting strategies focus on reducing a mate's self-perceived mate value, isolating them, and inducing fear of defection.

Variables Influencing Mate Retention Behaviors

Mate retention strategies furthermore can be aimed at the partner (intersexual mate retention tactics) but also at the rival (intrasexual mate retention tactics; Buss 1988). With respect to partner-directed mate retention, like their rival-directed tactics in the context of securing a mate, women's behaviors also follow from parental investment theory (Trivers 1972) and are attuned to the opposite sex' mate preferences. Given men's preference for young, fertile, and attractive women, women's mate retention efforts will be focused on making themselves appear more attractive in an attempt to please their partner – by wearing make-up, jewelry, tight-fitting clothes, or by engaging in weight-loss efforts. These self-promotion tactics simultaneously function to compete with rivals, as described above (e.g., Buss 1988). Another tactic women employ is to intentionally make their partner jealous, e.g., by flirting with another male when he can see it. The type of tactic used is influenced by, among others, cognitions and emotions about one's relationship. For example, committed individuals are more likely to enhance their appearance, whereas individuals in less committed relationships more often report they would intentionally evoke jealousy in their partner. However, in general, as a relationship progresses – and assumedly, commitment increases – the frequency of mate retention seems to decrease. The type of tactic that is used also tends to co-vary with an individual's mate value, such that lower mate-value individuals tend to engage in more cost-inflicting tactics, e.g., controlling behaviors such as isolation of the partner and may even resort to aggression. For example, women tend to engage in subtle indirect verbal aggressive behaviors as a form of mate retention, both towards their partners and their rivals.

Furthermore, women's fecundity – fertility, or the ability to produce offspring – is a predictor of more intense mate guarding: Younger (more fecund) women tend to employ more mate retention strategies (Buss and Shackelford 1997). Moreover, women's mate retention strategies are influenced by their *partner's* mate value. Buss and Shackelford (1997) report that women's mate

retention co-varies with their partner's status striving and income, such that they increased their mate retention activities if they were partnered with a high status male. Menstrual cycle effects have also been reported for the experience of jealousy, such that both partnered and single women report higher levels of jealousy during the fertile phase of their cycle than during non-fertile phases. However, using oral contraceptives caused increased overall levels of jealousy in partnered women, which were similar to the levels reported by fertile (normally cycling) women.

Jealousy and a Rival's Characteristics

Evolutionary psychologists generally agree that jealousy is the emotion that evolved as a response to the adaptive problem of infidelity (Buss and Shackelford 1997). The experience of jealousy thus signals a threat to the relationship and simultaneously motivates the individual to prevent the mate from abandoning the relationship. By definition, jealousy implies the presence of an imagined or actual rival. Overall, a rival who possesses qualities that are believed to be important to the opposite sex or to one's partner tends to evoke more feelings of jealousy than a rival who does not possess those qualities (e.g., Dijkstra and Buunk 1998). Given the sex differences in mate preferences, with physical attractiveness more valued by men, and status- and dominance-related characteristics more valued by women, from an evolutionary psychological perspective, one would expect women to feel more jealous than men when their rival surpasses them on bodily and facial attractiveness, and men to feel more jealous than women when their rival possesses status- and dominance-related characteristics. Research has repeatedly established that these sex differences in rival characteristics that evoke jealousy indeed occur (e.g., Dijkstra and Buunk 1998).

Interestingly, these sex differences in the jealousy-evoking effect of a rival's characteristics are also found in contexts other than mating: for example, in a work context, women tend to report higher levels of jealousy when confronted with physically attractive same-sex individuals than men, and in the context of personnel selection,

women would not hire a physically attractive woman – whereas men would welcome such employees. Interestingly, these results were found for undergraduate students but also for HR professionals. Conversely, not only do women seem to actively hinder attractive women's career advancement, but they also are affected with regard to perceptions of their own professional possibilities. A physically attractive rival in an organizational context caused women to attribute more unfriendliness to her, aroused more jealousy, and negatively affected their expectations for their own career advancement, presumably because women are aware of the fact that attractive individuals are more likely to receive promotions and achieve professional successes (i.e., the “halo” effect; see Buunk et al. 2016).

Massar and Buunk (2011) reasoned that for women, the jealousy-evoking effect of a rival's physical attractiveness is such a fundamental and adaptive process, that such evaluation of rival characteristics may be perceived outside one's conscious awareness. For example, in a study focusing on facial attractiveness, these researchers showed that exposure of mere milliseconds affects women's jealousy, such that they reported higher levels of jealousy after being subliminally exposed to an attractive female than when exposed to an unattractive female. Moreover, similar results were found when participants were primed with body shapes: an hour-glass shaped female figure with a waist-to-hip ratio of 0.7 – considered attractive and “ideal” for women – evoked significantly more jealousy in participants than a figure with an “average” waist-to-hip ratio (of 0.9). Similarly, Maner, Gailliot, Rouby, and Miller (2007) showed that priming individuals with jealousy increased “attentional adhesion” to physically attractive same-sex targets – but not average-looking rivals – particularly for individuals who were dispositionally more worried about intrasexual rivals.

Conclusion

Humans' high bipaternal investments in offspring cause both men and women to be selective in their

mate choice for long-term partners, which in turn causes considerable competition among members of the same sex to gain access to the best quality mates. Since available men are not all of the same mate value, women have to compete with each other for access to – and retention of – the most desirable men (e.g., Campbell 2013). As the current chapter has detailed, women's aggression against other women often takes on the form of indirect and social aggression, particularly, gossiping and social exclusion. Further, given men's preference for young and fertile partners, women's competition takes place mainly in the domain of physical attractiveness. Whether it is in the context of securing a mate or in the context of retaining a mate, competition is likely to take on the form of appearance enhancement or rival derogation. Furthermore, physically attractive rivals are especially threatening to women and evoke more jealousy and mate retention efforts than unattractive (or “average”) rivals, both in a mating as well as professional context. To sum up, the contextual – and hormonal – influences on women's intrasexual competition and aggression signify its dynamic nature.

Cross-References

- ▶ [Alloparenting and Female Same-Sex Behavior](#)
- ▶ [Derogation of Rivals](#)
- ▶ [Derogation of Attractiveness Among Women \(Intrasexual Rivalry\)](#)
- ▶ [Derogation of Promiscuity Among Women](#)
- ▶ [Desire to Be Included Among Desirable Women](#)
- ▶ [Female–Female Competition](#)
- ▶ [Female-Female Strategies](#)
- ▶ [Indirect Aggression](#)
- ▶ [Intrasexual Competition Between Females](#)
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- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Sex Differences in Jealousy](#)

- Social Aggression
- Use of Mate Retention Strategies
- Verbal Derogation Among Women

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Contextual Behavioral Science

- [Selectionist Models: Implications for Behavior](#)

Contextual Cues

- [Kin Recognition and Classification in Humans](#)

Contingencies

- [Positive and Negative Reinforcement and Punishment](#)

Contingent Cooperation

- [Contingent Reciprocity](#)

Contingent Reciprocity

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Synonyms

[Contingent cooperation](#); [Reciprocal altruism](#)

Definition

The contingent relationship between acts of giving and receiving among social partners.

Introduction

In evolutionary sciences, interest in contingent reciprocity mainly lies in its potential role in the evolution of cooperation and prosociality between genetically unrelated partners (Axelrod and Hamilton 1981; Trivers 1971). Specifically, selection should favor individuals who conditionally cooperate with others as long as future benefits scaled by the likelihood of future interactions outweigh the costs of cooperation (Nowak 2006). Evolutionary models have shown that strategies based on contingent reciprocity, such as tit-for-tat, can be evolutionarily stable (i.e., resistant to invasions of alternative, noncooperative strategies once constituting a significant proportion of a population) in the condition of repeated interactions with same individuals (Axelrod and Hamilton 1981).

These conditions for the evolution of contingent reciprocity can be extended to interactions in a sizable group resembling an n-person prisoner's dilemma (Boyd and Richerson 1988). More recent research also showed that when the degree of contingent reciprocity varies continuously, it is more sustainable than discrete, all-or-none reciprocity in sizable groups, and this sustainability increase with the efficiency of cooperation

(marginal per capita return; Takezawa and Price 2010). Trivers (2010) further identified the following broad conditions affecting the evolution of reciprocal altruism: (1) longevity (affecting the chance of repeated encounters), (2) dispersal rate (affecting the chance of interacting with same organisms), (3) degree of mutual dependence (affecting the benefit of cooperation and the cost of defection), (4) parental care, (5) dominance hierarchy, and (6) agonistic support.

Related Concepts

Contingent reciprocity is sometimes regarded as a synonym of *reciprocal altruism* or *contingent cooperation* (Gurven 2006; Trivers 1971). However, altruism is defined as actions that are beneficial to another organism but “apparently detrimental to the organism performing the action” (Trivers 2010, p. 124). This is not necessarily the case for contingent cooperation or contingent reciprocity in general. For example, humans not only exchange favorable treatment reciprocally, but they also exchange unfavorable treatment reciprocally. This *negative reciprocity* also constitutes contingent reciprocity (Narotzky and Moreno 2002). Nevertheless, most of the research on contingent reciprocity is focused on contingent cooperation and reciprocal altruism.

Reciprocal actions can occur when favors are exchanged over repeated encounters between the same two individuals. Alternatively, reciprocal actions of cooperation can also be contingent upon the reputation of third parties, which is derived from their prosocial actions, even if such actions do not benefit oneself directly. Such models of *indirect reciprocity* (Nowak and Sigmund 2005; See chapters in this book: Indirect Reciprocity; Indirect Reciprocity Theory) and, additionally, models of *generalized reciprocity* show that cooperation can be stable if cooperative individuals tend to associate with each other and if individuals respond cooperatively after they have been assisted by another group member (Barta et al. 2011; Rankin and Taborsky 2009).

Contingent Reciprocity in Other Species

Contingent reciprocity has been invoked to explain cooperation among non-kins in a few nonhuman species. Reciprocated actions in nonhuman animals include joint assaults on predators to save conspecifics by pied flycatcher (Krams et al. 2008), grooming among impala (Hart and Hart 1992), food sharing via blood regurgitation among vampire bats (DeNault and McFarlane 1995; Wilkinson 1988), and grooming, food sharing, and agonistic support in several primate species (De Waal 1997; Brosnan and De Waal 2002). Some of these instances might be explained by alternative mechanisms, including kin selection and mutualism (Clutton-Brock 2009). Nevertheless, contingent reciprocity is not necessarily mutually exclusive with other mechanisms in promoting altruism. Computer simulation based on the case of blood regurgitation among vampire bats, for instance, shows that even after accounting for genetic relatedness, reciprocal altruism might make major contributions to inclusive fitness beyond kin selection in a relatively large social group (Wilkinson 1988).

Experimental evidence for contingent reciprocity is limited even among our closest primate relatives. de Waal (1997) found some evidence that captive chimpanzees trade food for grooming or vice versa in a fashion of direct reciprocity. In an experimental task, Melis et al. (2008) found chimpanzees showed weak reciprocity in helping a familiar group member getting food by unlocking a door. However, chimpanzees failed to show reciprocity in tasks where other-benefiting actions appear effortless or costless (Brosnan et al. 2009; Yamamoto and Tanaka 2009).

The fact that natural instances of reciprocal altruism among genetically unrelated individuals is rare in nonhuman species might be explained by two major constraints. One is the cognitive demands to maintain reciprocity in a large group of individuals (Schino and Aureli 2010). Another constraint is that asymmetries in terms of dominance, resource-gathering abilities, or mate values are so common that the standard prisoner’s dilemma underlying many models of reciprocity

is problematic (Dawkins 2010). Within a dominance hierarchy, the capacity of the dominant individuals to coerce less dominant individuals into cooperation might remove the potential benefits of reciprocity, thus leading to nonreciprocal equilibriums (Dawkins 2010; Trivers 2010). Alternatively, dominance hierarchies might constitute reciprocal relationships if less-dominant individuals exchange their services for dominant individuals' nonaggression or protection. These constraints lead Brosnan and de Waal (2002) to distinguish three different types of reciprocity: (1) *symmetry-based reciprocity*, which is based on symmetrical dyadic relationships (e.g., mutual association, kinship), is the least cognitively complex and present in many nonprimate species, (2) *attitudinal reciprocity*, which relies on mirroring social attitudes of partners, is more cognitively complex and is exhibited by both capuchin monkeys and chimpanzees, and (3) *calculated reciprocity*, which requires mental scorekeeping, is the most cognitively demanding one and found only in humans and some chimpanzees.

The Ontogeny of Contingent Reciprocity in Humans

Compared with nonhuman animals, humans exhibit far more instances of contingent reciprocity. Anthropological studies showed in many small-scale societies, individuals and family units share greater quantities of goods with those that previously shared with them (Gurven 2006). Empirical evidence has also been accumulating regarding the development of the capacity of contingent reciprocity in children.

Early studies provided observational and correlational evidence of children reciprocating help and sharing with those who shared with them earlier. Fujisawa et al. (2008), for example, studied naturally occurring interactions among Japanese children of 3–4 years old and found that children's provision of help and toys to peers correlated with the peers' previous prosocial actions toward them, without explicit instructions. House et al. (2013) paired children aged

3–7.5 years in repeated face-to-face interactions of a Prosocial Game, in which they chose between (1) delivering resources to both oneself and the partner, and (2) delivering resources only to oneself. Results showed that the propensity of contingent reciprocity (in terms of prosocial resource sharing) consistently appear around 5.5 years of age. Finally, the age at which contingent reciprocity emerges seems to also depend on the tasks. Warneke and Tomasello (2013) experimentally manipulated helping and sharing behaviors of social partners before giving 2.5- and 3.5-year-old children the opportunity to help or share with the partner. Whereas previous helping did not influence helping among either group of children, 3.5-year-olds, but not 2.5-year-olds, are more likely to reciprocate previous sharing.

Reasons for the Variability in Contingent Reciprocity in Humans

Different societies differ in the degree or form of contingent reciprocity (Gurven 2006), due to factors such as resource abundance, type of subsistence, and population density. Situational factors that influence the ease of cheat detection, cost/benefit ratio of altruistic actions, and stability of social grouping are likely to differ through time in the same human population. This should cause natural selection to favor developmental plasticity in contingent reciprocity (Trivers 2010).

In some cases, reciprocity can be contingent on the exchange of equivalent services or goods of roughly the same value, whereas in other cases, reciprocal actions are only contingent on efforts (Trivers 2010). Indeed, anthropological evidence supported the claim that exchange imbalances in forager-agriculturalist groups tend to favor lower-producing families. Unequal reciprocity may also be accepted as long as the unequal exchange is better than no exchange (Gurven 2006).

Conclusion

Contingent reciprocity is crucial to understanding the evolution of prosociality among unrelated

organisms. In nonhuman primates and other species, evidence for contingent reciprocity is limited, likely due to the constraints of cognitive demands and/or asymmetrical relationships in dominance hierarchies. In humans, contingent reciprocity appears to emerge around 3–6 years of age, depending on the task involved. Contingent reciprocity might also differ in the form and fullness of the repayment of favors and is likely to show developmental plasticity in humans.

Cross-References

- Adaptations For Reciprocal Altruism
- Evolution of Cooperation
- Evolution of Reciprocal Altruism
- Prisoner's Dilemma and Cooperation
- Reciprocal Altruism
- Selection for Cooperative Relationships
- Strategies for Successful Cooperation

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Continuity

► Object Permanence

Continuous Breeding

► Reproductive Timing

Contraception

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Synonyms

Birth control; Contraceptive; Family planning

Definition

Preventing pregnancy through the use of a drug, device, or technique.

Introduction

While reproduction is critical for the continuation of a species, excessive reproduction can put strains on resources necessary for the survival of offspring. Availability of food and shelter and the need for support from adults during development are examples of these resources. Mechanisms that limit reproduction have evolved among many species. For example, clutch sizes among certain avian species emerged that resulted in the greatest number of surviving offspring who could subsequently reproduce (Lack 1954). Humans' relatively short history compared to other species and fast societal development have perhaps circumvented natural changes that would limit reproduction. Humans have developed technologies, such as in vitro fertilization, that ameliorate genetic and acquired characteristics that limit reproduction. Humans have also given much effort to preventing neonatal and infant mortality. There have also been great efforts to develop means for limiting reproduction, and these efforts have a long history across many societal structures. Contraceptives, means of preventing pregnancy, vary from behaviors and techniques to drugs and devices, many of which allow for copulatory behaviors to continue while avoiding pregnancy. In this section, the history of contraception and current methods are described.

History

There is a large volume of evidence that attempts to control reproduction throughout human history. The reasoning behind controlling reproduction during early history ranged from mysticism to preventing psychological trauma. Infanticide was a common practice of some preliterate societies to avoid infants born on days considered “unlucky” from bringing bad luck upon the family or village

(Himes 1936). Women of Easter Island often engaged in sexual intercourse with visitors and actively attempted to avoid pregnancy in such instances, possibly because of the temporary nature of the relationship (Himes 1936). The San Carlos Apache of North America would use herbal concoctions when women had multiple stillbirths or other pregnancy losses as a means of reducing the psychological strain on the mother (Hrdlicka 1908). Later in history, religious doctrines strongly influenced the development of contraceptives. The greatly influential Catholic Church forbade attempts at preventing pregnancy other than abstinence and more recently only allows for natural family planning as a contraceptive method, which will be discussed later. Talmudic-Rabbinical law was slightly more lenient, allowing for the use of contraceptives in select circumstances, like if pregnancy would put a woman's health at risk, and only if both the man and woman agreed to use a contraceptive. Islamic laws generally promoted the development of means for avoiding pregnancy. As a result, there are countless examples of contraceptives in ancient Islamic texts (Himes 1936). In modern times, the reasons for using contraceptives have changed from mystical rationalization and purely economic population control toward women's liberty. While there have been some moral objections to contraceptive use, such as the United States' Comstock Law of 1873 that forbade shipment of contraceptives until the 1936 court decision in *United States v. One Package of Japanese Pessaries*, and the Catholic Church continuing to forbid contraceptive use, contraceptives have grown to become more accepted and used across the globe. Along with these societal changes, medical knowledge and technology have rapidly advanced, and contraceptives have become more effective.

Mystical herbal concoctions and incantations aside, early societies perpetuated many somewhat effective methods of contraception. Chief among these was promoting abstinence from sexual intercourse. For example, the Tsonga tribes of Southern Africa forbade men and women from sexual intercourse after a woman delivered a baby until the baby began crawling, even after which sexual intercourse was allowed but not in a manner such

that pregnancy could occur until after the child has been weaned from the mother's breast (Junod 1927). In Madagascar, some tribes held a custom where a man and woman would not cohabit for 3–6 months after the birth of a child (Himes 1936).

Interrupting sexual intercourse prior to male ejaculation, called *coitus interruptus*, was commonly used throughout history and remains a popular method despite lacking efficacy. Many societies had rules and traditions that promoted *coitus interruptus*, including in the island nations in Oceania and many parts of Africa. Another historical means of preventing semen from entering the vagina was *coitus inter femora*, where the male rubs his penis between his partner's thighs. Despite their history and widespread use, these methods were taboo in some Western religions. The Book of Genesis tells a story of Onan, who was obliged to marry his brother's widow and decided their children would be illegitimately proceeded to "spill his seed on the ground" and was subsequently killed by God for this behavior.

Preventing insemination by expelling semen, using spermicidal douches, and blocking the vagina or cervix was also practiced in ancient history. One perhaps effective spermicidal douche of lemon juice in water was observed in tribal Guana and Martinique (Himes 1936). As early as 1800 BCE, the Egyptians wrote about the creation of pastes of honey and acacia leaves that were pressed against the cervix (Dickinson and Bryant 1931). The women of Easter Island similarly used algae and seaweed and in Japan barriers of disks of oiled paper (Himes 1936). Condoms grew in effectiveness and accessibility with the advent of rubber vulcanization in the mid-1800s CE but had existed in some form for hundreds, if not thousands, of years in Japan and Africa.

Early attempts at permanent sterilization were less common. In the Indian archipelago, a manual retroflexion of the uterus was occasionally conducted immediately after an abortion or live delivery in an attempt to prevent any future pregnancies (Himes 1936). This was not particularly effective, but represents one of a few plausible attempts at achieving permanent contraception. Permanent sterilization of males included castration and a process called subincision in parts of

Australia and New Zealand (Himes 1936). Subincision involved bisecting the urethra on the underside of the penis such that urine and semen exited the penis near the testicles instead of at the head of the penis. This redirection of semen may have prevented some pregnancies, but was not necessarily effective.

Many modern contraceptives share fundamental similarities with early methods and have improved as technology and medical knowledge have increased. A substantial advancement in contraceptive technology was the invention of hormonal oral contraceptive pills that became available in the 1960s. Since then, numerous hormonal and non-hormonal contraceptives that share similar mechanisms of action have been developed with increasing effectiveness.

Modern Contraceptives

Techniques

Abstinence The most obvious method for avoiding pregnancy is to abstain from heterosexual vaginal intercourse. Inhibiting behaviors so deeply rooted in evolutionary history is understandably difficult, requiring significant motivation to achieve.

Withdrawal Also known as *coitus interruptus*, it involves removing the penis from the vagina prior to ejaculation. Like abstinence, withdrawal involves inhibiting evolutionarily supported behaviors which can undermine the likelihood of it occurring. As a result, approximately 22% of sexually active women become pregnant in the first year using withdrawal to avoid pregnancy (Trussell 2011).

Fertility Awareness Methods Fertility awareness methods allow sexual intercourse to occur as normal but involve timing sexual intercourse such that it occurs during parts of the female's reproductive cycle when she is unlikely to become pregnant. Examples are the rhythm method and natural family planning. These methods involve monitoring a female's body temperature or cervical mucus characteristics and may also be used to

aid in achieving reproduction by timing sexual intercourse at peak fertility. Inconsistencies in menstrual cycles can undermine these methods and reduce their effectiveness.

Lactational Amenorrhea Method Following childbirth, consistent breastfeeding maintains hormonal levels that suppress ovulation for approximately 6 months. This method is highly effective but is temporary.

Barrier Methods

Condoms Condoms provide a complete barrier between the penis and vagina and as a result are the only contraceptive that can provide protection from both pregnancy and many sexually transmitted infections. The most common condoms are applied to the penis, but female condoms that are inserted into the vagina are also available and are similarly effective. Incorrect application of condoms significantly undermines their effectiveness such that 18–21% of women become pregnant in their first year of use (Trussell 2011). Combining condoms with spermicides, and especially with hormonal contraceptives, provides superior protection from both sexually transmitted infection and pregnancy.

Diaphragm and Sponge Diaphragms and sponges are barriers placed within the vagina that prevent propagation of semen within the vagina. A prescription is needed to obtain a diaphragm in order to ensure an appropriate fit and should be used in conjunction with a spermicidal agent to be effective. Diaphragms with spermicides applied before insertion remain effective for about 6 hours after insertion, and sponges containing spermicides are effective for up to 24 hours after insertion (Hatcher et al. 2011).

Hormonal/Biological Methods

Oral Contraceptive Pills Oral contraceptive pills deliver either progestins or some combination of progestins and estrogens. Administering these hormones systemically prevents pregnancy by inhibiting ovulation and thickening cervical mucus. Regimens may involve “placebo” pills to

allow menses to occur or may involve constant active doses to prevent menses.

Oral contraceptive pills can also be used for emergency contraception. Not to be confused with pills that induce abortions, emergency contraception pills contain high doses of progestins or progestins plus estrogens that disrupt ovulation or thicken cervical mucus to prevent sperm from reaching the egg. Given this mechanism of action, they must be taken within three days of unprotected intercourse to be maximally effective.

Transdermal Patch Systemic administration of combined progestins and estrogens is also available via a transdermal patch. The patch is replaced weekly for 3 weeks, followed by a week without a patch to allow for menses. Like oral contraceptive pills, the hormones delivered by the patch prevent ovulation and thicken cervical mucus.

Intravaginal Ring Intravaginal rings deliver a combination of progestins and estrogens through the mucous membranes of the vagina, which suppresses ovulation and may thicken cervical mucus. A ring is inserted into the vagina and remains for 3 weeks, when it is removed for a week to allow menses to occur.

Injection Injectable formulations of hormones, typically progestins although combined progestins and estrogens have been used in the past, gradually release for up to 3 months per injection. Like other systemic administration of hormones, injectable contraceptives inhibit ovulation and thicken cervical mucus. Unlike pills, patches, and rings, injections are administered by a medical provider instead of the individual.

Implant Subdermal implants are placed in the arm and slowly release progestins for up to 3 years. The steady release of progestins suppresses ovulation and thickens cervical mucus providing constant and highly effective contraception with minimal effort. A provider with specialized training is required to administer and remove the implant.

Intrauterine Devices Intrauterine devices (IUDs) are inserted into the uterus by a trained

provider and provide consistent, highly effective contraception for up to 12 years. Hormonal IUDs release progestins directly into the uterus, which thickens the cervical mucus and causes the endometrium to release substances that inhibit fertilization. Suppression of ovulation is not as consistent as with systemically administered hormonal contraceptives. Hormonal IUDs provide protection for up to 5 years. Copper IUDs increase levels of white blood cells, enzymes, and copper ions in the uterus and fallopian tubes, all of which prevent spermatozoa from surviving to fertilize an egg. Copper IUDs can provide protection for up to 12 years.

Permanent Methods

Female Sterilization Surgically obstructing the fallopian tubes is the most common method of permanently preventing future pregnancies. This minor surgical procedure can be conducted on an outpatient basis or immediately following an abortion or delivery. Pregnancy following such sterilization is extremely rare.

Vasectomy Physically separating the vas deferens, the vessel that carries sperm to the ejaculate, provides permanent sterilization to men. Impregnation of a female is extremely rare following vasectomy.

Conclusion

Contraception has developed over the course of human history, with modern medical and technological enhancements resulting in a multitude of highly effective drugs, devices, and techniques. Globally, acceptance of contraception has generally increased, fostered, and inhibited by cultural factors. One common thread throughout the history of contraception is that it has been predominantly focused on affecting females. Of a handful of potential candidates, no systemic contraceptive for males has been developed to the point of clinical use. This may be the next frontier for the continuing development of contraceptives.

Cross-References

- ▶ [Coitus interruptus](#)
- ▶ [Prevalence of STDs](#)
- ▶ [Sex education in schools](#)
- ▶ [Sexual intercourse](#)

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Contraceptive

- ▶ [Contraception](#)

Contraceptive Pill

- ▶ [Effect of Birth Control on Women’s Preferences](#)

Contraceptive Use

- ▶ [Goals](#)

Contralto

- ▶ [Music and Hormones](#)

Contributions

- ▶ [Charity](#)

Control

- ▶ [Dominance and Territory](#)

Control Education

- ▶ [Goals](#)

Controlled Attention

- ▶ [Selective Attending](#)

Controversial Issues in Evolutionary Psychology

- ▶ [Controversies in Evolutionary Psychology](#)

Controversies

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Synonyms

[Arguments](#); [Conflicts](#); [Discussions](#)

Definitions

Issues that provoke differing opinions in the study of animal behavior and cognition.

Introduction

Comparative psychology, perhaps more than any other domain of psychology, is fraught with controversy, most clearly in the realm of comparative cognition. Controversy centers around the fundamental question of whether Darwin was correct to postulate continuity in cognitive processes across species, including humans (Darwin 1871), or whether skeptics, known as “scoffers,” are justified in discounting the degree of continuity between man and other animals (Penn et al. 2008). Researchers sympathetic to the notion of continuity focus on results from studies investigating such topics as self-awareness, metacognition, episodic memory, imitation and culture, prosocial sentiments, causal reasoning, tool use, language, and, most notably, theory of mind (ToM). Over the last several decades, these researchers, known as “boosters,” have amassed a significant amount of data that purports to support the notion that animals share at least some elements of abilities previously thought unique to humans. However, a careful and critical read of such studies indicates that, even if animals share some components of traits such as ToM, the way in which these traits are expressed is fundamentally different from the manner in which the same traits are expressed in humans. Researchers, however, have been reluctant to accept such differences, often failing to appreciate that studying evolution is as much about acknowledging differences as it is about finding similarities (Vonk and Povinelli 2006). Thus, controversies exist because the same data is often viewed as supporting two completely different propositions depending on the bias of the researcher. Specific controversies are summarized in the following areas.

Self-Awareness

In the centuries following the famously misquoted Descartes declaration of “I think therefore I am,” (Descartes 1637), philosophers and psychologists alike have probed the question of whether any other species share the human tendency to reflect on their own existence. Gallup (1970) developed the mirror self-recognition (MSR) mark test for use with human children and nonhuman primates. Studies showed that human children investigate an otherwise inaccessible area of their face when in front of a mirror, indicating a recognition that the mirror image depicts themselves, at around the same age that they start using personal pronouns, further lending credibility to the notion that the test assesses self-awareness (Amsterdam 1972). The task, where behavior in front of a mirror is observed before and after an animal’s appearance is surreptitiously altered, typically with a small amount of paint on their face, has now been used with a variety of animals ranging from ants, birds, dolphins, elephants, and various primate species, with most researchers converging on the notion that MSR is shown by great apes but not by other primates. Research on non-primates is more controversial, as evidence for traits thought to be unique to humans found in species more distantly related to humans is often highly scrutinized. Even if one accepts evidence of MSR in non-humans, researchers have debated the extent to which the task measures self-awareness. For instance, some have suggested that successful investigation of the mark during the mirror test indicates mere body self-awareness, but not a true concept of self (Swartz 1997). In this light, the ability to pass the mark test cannot address whether an animal is self-conscious, nor can it determine whether species that are capable of MSR have self-conceptions identical or even similar to those in humans (Swartz 1997). Success on the mark test may simply indicate an animal’s ability to utilize its mirror image to differentiate itself from other features in the environment (De Veer and Van Den Bos 1999).

Metacognition

Similar to the studies on self-recognition, studies of metacognition – the ability to think about thoughts, including one’s own – aim to assess the extent to which other animals are self-aware. Studies of metacognition focus primarily on meta-memory – the animal’s awareness of the strength of its own memory and strategies that could be used to enhance performance in memory tests. Despite significant progress by comparative psychologists, arguments ensue over whether strategies used by nonhumans in experimental tests reflect true meta-memory versus associative strategies (Smith et al. 2006, 2009). To rebut such claims, researchers have devised ever more elegant paradigms to tap into nonhuman memory strategies.

One class of metacognitive tasks involves the use of uncertainty monitoring whereby animals can indicate whether they are uncertain of their own memory and can opt for an “uncertain” response, rather than being penalized for an incorrect judgment. Animals tend to use the uncertainty response judiciously and efficiently, opting out of trials for which memory would be weaker, such as at longer retention intervals, and when perceptual discriminations are more difficult. Researchers utilizing the uncertainty response paradigm suggest that an animal’s metacognitive capacities can be revealed by their adaptive use of the uncertain response option in difficult trials or when they lack sufficient information. However, skeptics have debated the extent to which such strategies are consciously controlled (Carruthers 2008). In the hotly debated area of animal metacognition, researchers should be wary of attributing animal behavior to sophisticated skills such as metacognition until low-level associate mechanisms can be ruled out (Smith et al. 2009).

Given controversies with the uncertainty response paradigms, researchers have more recently focused on information-seeking strategy tasks (Call 2012). In these types of tests, animals should be expected to seek information only when they know (or remember) that they have not been

provided with the relevant information with which to solve the task. As with other aspects of cognition, the data reveal strategies similar to those used by humans but not the full suite of capacities demonstrated by humans.

Episodic-Like Memory

Related to the issue of meta-memory and self-awareness, human memory was thought to be unique in that it involved auto-noetic consciousness (Tulving 2005). This auto-noetic or mental time travel component allows individuals to relive the subjective experience, as well as to recall the objective facts of a previous event. Comparative researchers have operationalized such memory as involving the binding of information about what, when, and where components of an event (i.e., the WWW memory phenomena). They have considered memory that integrates WWW information to be “episodic-like” because it is impossible to access the subjective experience of animals in the same way that one can query humans about the content of their memories. As is often the case in comparative psychology, the cognitive processes of nonhuman animals are deemed less sophisticated than those in humans, solely because researchers lack the means to irrefutably tap into an animal’s subjective experience. Work by Clayton and others has famously demonstrated that animals, such as scrub jays, can remember what type of food was buried in what location when. For example, jays search where they hid preferred wax worms at short delays but retrieve less preferred peanuts at longer delays, only if they have experience with the decay of worms (Clayton and Dickinson 1998). Whereas most psychologists accept the findings as indicative of episodic-like memory, they debate the extent to which such memories are reflected upon in the manner that humans might do when writing an autobiographical retrospective. Rather, animals may use information about past events simply to predict future occurrences. Researchers argue about whether it is possible to ever know the

content of a nonhuman's memories. In addition, researchers have debated whether animals show strong evidence of planning for the future.

Imitation and Culture

As with most of the topics that are hotly contested in comparative psychology today, early anthropologists and psychologists had an anthropocentric view of culture. This notion has been slowly changing in the last 70 years, since the concept of nonhuman animals having cultures was first proposed in 1952 by the Japanese primatologist, Kinji Imanishi, who posited that culture should exist in all group-living species (Huffman et al. 2008). Much of the debate surrounding nonhuman animal culture or behavioral tradition involves definitional disagreements for what truly constitutes culture. Essential to identifying culture is the presence of learning and social transmission of knowledge and skills among animals, leading to behavioral variation within and across species that cannot be accounted for by asocial learning, ecological, or genetic factors. Some animal behaviorists consider any socially transmitted modifications of behavior to exhibit cultural tradition, regardless of the underlying processes (Kummer 1971). However, other researchers such as Goodall and Galef emphasize that determining the presence of culture necessarily depends on how the information is transmitted, which in human populations is primarily through teaching or learning by imitation (Galef 1992). Many notable cases of purported animal culture can be explained by simpler mechanisms of transmission than pedagogy and imitation, two extremely contentious topics within comparative research. For instance, the famous case of various bird species in England learning to open milk bottles in the 1940s can be explained via stimulus enhancement, whereby another animal's attention was inadvertently drawn to the milk bottles by the action of one bird opening the bottle, ultimately leading to the observer learning to open the bottle faster (Galef 1992).

Whereas cultures within human populations typically expand and become more complex and efficient over generations, most supposed forms

of nonhuman animal cultures encompass behaviors that each animal could have learned independently (Galef 1992). Other well-known cases of purported animal culture are the propagation of washing sand off of sweet potatoes in streams by Japanese macaques and termite "fishing" by chimpanzees in Gombe National Park (Goodall 1971; Kawamura 1959). It has been argued that the extremely slow acquisition rate of the potato-washing behavior for other macaques (roughly 2 years after the first macaque began washing) is inconsistent with imitative learning, which is typically relatively quick, as trial-and-error learning is not needed (Galef 1992). Further, the method of fishing for termites was unable to be replicated. Despite the contention over whether imitative learning or teaching result in various behavioral traditions in animal groups, examples of non-imitative variations in behavior that resemble culture are found in rats, dolphins, fish, birds, and primates.

Prosocial Sentiments

Humans may be truly unique with regard to the extent to which they will assist others at some cost and no benefit to themselves. This question was poorly investigated until the groundbreaking work of Silk and colleagues (Silk et al. 2005), which incited hundreds of further comparative investigations. This seminal experiment found no evidence for other regarding preferences in chimpanzees, as the chimpanzees did not take advantage of a reward option where both the actor and the recipient chimpanzee would receive identical food rewards more frequently than the option where only the actor received an equivalent reward. Despite the explosion of empirical work on this topic, researchers have failed to come to a consensus as to whether other species also show prosocial motivations. Although they are often observed to assist others, such behavior can generally be attributed to kin selection, reciprocity, or mutualism. Even chimpanzees are unlikely to provide food to conspecifics even at no cost to themselves although they can be observed to help humans in helping contexts (Warneken and Tomasello 2006). Researchers have shown that

even rodents will release a trapped conspecific and even share a highly desired food with that rescued groupmate, (Ben-Ami Bartal et al. 2014); however, others have suggested that the rats were motivated by a desire to reduce their own distress rather than a truly prosocial concern for others.

Causal Reasoning and Tool Use

Tool use was also once deemed unique to humans. However, that notion has been dispelled, notably by Jane Goodall in 1960, when she observed a chimpanzee using a piece of grass to acquire termites from the ground. Later observations in other species confirmed the presence of tool use in nonhumans, with nonhuman primates, elephants, bears, corvids, and other animals using tools to gain food, relieve itching, or provide shelter. The current controversy stems from the question of whether animals make use of tools based on trial and error or whether they are capable of understanding the causal relation between various tools and aspects of the environment. Many studies have revealed that even chimpanzees tend to use visual cues, such as contact and proximity, rather than reasoning about support in an abstract and causal way when using tools to retrieve food (Povinelli 2000). Chimpanzees also struggle to invoke concepts of weight as a property of objects when weight can function to facilitate or hinder food retrieval (Povinelli 2012). New Caledonian crows, however, displayed an apparent causal understanding of displacement when they selected sinking objects more frequently than floating objects and solid objects more often than hollow objects to raise the water level for a reward in a study using Aesop's fable paradigm (Jelbert et al. 2014). Some, however, have shown that even humans fail to display causal reasoning in a variety of the same situations (Silva et al. 2005), suggesting that the tasks themselves are flawed.

Language

Early studies of language in nonhumans were also marred by faulty methodology. Studies in the

1960s of language in other apes first appeared promising; however, work in that area was all but squashed for many decades with Terrace's penetrating study of Nim Chimpsky (Terrace et al. 1979). Terrace showed that a chimpanzee could mimic human speech through rote memorization and operant conditioning but displayed no evidence of the hallmarks of human language use such as generativity, displacement, and arbitrariness. Terrace concluded that Nim had not acquired a skillset that deserved to be called language, as everything Nim was taught could also be acquired by pigeons via operant conditioning. Some researchers also question nonhuman apes' functional comprehension of language, as they rarely ask questions themselves, an ability that some believe distinguishes humans' capacity for language from that of nonhumans. Today, researchers have abandoned attempts to teach human-like language as a form of speech or sign language, instead using electronic keyboards presenting lexigrams to animals, such as Kanzi, the bonobo (Savage-Rumbaugh et al. 1986). Whereas some (Savage-Rumbaugh) believe that bonobos at least are capable of a human-like system of communication, most researchers are less generous in their interpretation of the results.

Theory of Mind

The question of whether nonhumans represent the mental states of other beings (i.e., ToM) is perhaps the most hotly contested topic in comparative psychology. "Scoffers" assert that no current studies can be diagnostic on the issue because all confound the use of behavior-reading strategies with the inference of mental states (i.e., mind-reading strategies) (Penn and Povinelli 2007; Povinelli and Vonk 2004). "Boosters," in contrast, have settled on the claim that many species understand at least some mental states, such as seeing, even if they do not pass false belief tests that would provide evidence of understanding knowledge states. False belief tests require the participant or animal to make an accurate prediction about how another individual will respond to a question based on what information was available to that individual. If ToM is present, the

participant will respond according to what information and experiences the other individual has, recognizing it as different from their own. However, given these limitations and qualifications, it seems clear that no other species has evolved a ToM capacity that rivals that wielded by humans to explain the actions of others. With the possible exception of experience-projection tasks, all other experimental paradigms allow the animals to predict another's behavior using behavioral cues that may or may not lead to an additional inference about underlying and unobservable mental states. Continuing to rely on such paradigms will prevent us from ever shedding light on this controversial issue, leaving comparative researchers with the onus of developing an ingenious method for testing ToM in nonhuman species in order for it to remain a viable issue within the field.

Conclusions

All of these topics are controversial because they allow researchers the potential to move the goal posts with regard to staking a claim for human uniqueness. If animals are shown to share the abilities previously attributed only to humans, humans will lose their special place at the top of evolution's metaphorical tree. However, if evolution is properly viewed as branching paths, rather than a hierarchy, the controversies will diminish. Instead of creating a dichotomy between animal minds and the minds of all other species, researchers should view each animal mind as unique and capable of its own amazing feats. Assuming that human performance should be the ultimate benchmark with which to judge the cognitive capacities of all other species leads to a slippery slope, where many species are denied the attribution of equivalent skills because researchers lack the means to inquire about their subjective experiences. Thus, many behaviors and cognitive features in nonhumans are described only as approaching those in humans, and any particular cognitive feature in nonhumans is rarely granted the full range of abilities as those granted to humans. Although highly contested in many areas, the general consensus in comparative

psychology suggests that Darwin was correct to presume some degree of continuity in mental processes between humans and other animals.

Cross-References

- ▶ [Abstract Concept Formation](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Cognitive Science](#)
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- ▶ [Theory of Mind and Nonhuman Intelligence](#)
- ▶ [Unobservability Hypothesis, The \(Vonk and Povinelli, 2006\)](#)
- ▶ [Why Humans Are Unique](#)

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Controversies in Evolutionary Psychology

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Synonyms

Controversial issues in evolutionary psychology

Definition

Controversies in evolutionary psychology attend two kinds of critique related to the field: *intrinsic* and *radical*. Intrinsic critiques originate from within the “Broad Church” of evolutionary psychology, and typically take the form of critiques of the Santa Barbara School, or “High Church” evolutionary psychology, with its emphasis on human universals and massive modularity and the primacy of cultural over biological evolutionary

change since the Pleistocene epoch. Radical critiques originate from outside of the field and are usually either implicitly or explicitly (in some cases) ideologically motivated. Radical critics often call into question the sufficiency of adaptationist accounts of the origin of the human mind and human behavior and frequently assert that such accounts are *ad hoc* and inherently untestable. Some radical critics substitute sociological mechanisms (such as social construction) for evolutionary ones in order to explain human behavior.

Introduction

Historically, skepticism about and controversies surrounding the prospects of evolutionary reasoning to yield a satisfactory account of the origin of human mental faculties did not relate only to proponents (and theories) of special creation, who considered evolution to be insufficient to account for the origin of any organic structure. This skepticism is also manifest in the writings of some of the earliest proponents of evolutionary theory, such as Alfred Russell Wallace (Smith 1991), who considered the “higher” faculties of the human mind too marvelous to have arisen via selection acting on variation. It is on objections to evolutionary psychology – which we define here as an empirical and theoretical approach to understanding the origin of human psychology and behavior, rooted in the idea that these phenomena are best conceptualized as outcomes of adaptations shaped by selection – emanating from ostensible evolutionists that we choose to focus this encyclopedia entry. Creationists, and their derivatives (e.g., advocates of intelligent design), while certainly qualifying as critics of evolutionary psychology (and indeed evolutionary theory writ large), simply lack sufficient representation in Western academia to be considered consequential; thus, critiques of evolutionary psychology idiosyncratic to creationism and its variants will not be considered here (for examples of these, see, e.g., Joubert 2012). Broadly speaking, the review taken up here will be subdivided into two parts. The first part will deal with intrinsic

critiques of evolutionary psychology, which originate in those who align with the objectives of the field but who have doubts about the standard model that is regnant among evolutionary psychologists. The second part will deal with radical critiques stemming from those who do not align with the goals of the field and whose criticisms are destructive, calling into question the scientific legitimacy of applying evolutionary models to the end of understanding the origins of the human mind and human behavior. As the latter set of criticisms is so large, we will examine it primarily through the writings of one adamant critic, Massimo Pigliucci, whose charges against the field are representative of standard radical critiques.

Review

Intrinsic Critiques of Evolutionary Psychology

Contemporary evolutionary psychology stems from the ethological and sociobiological movements of the twentieth century and their antecedents in the thinking of Charles Darwin, as expressed in his 1871 work, *The Descent of Man*. Evolutionary psychology has striven to distinguish itself from the human ethology movement, via its embrace of adaptationist logic, as opposed to the observational-behavioral account model, dominant in both human and nonhuman ethology (Lorenz 1965). Ethology, while evolutionarily informed, has not necessarily embraced adaptationist or *mechanistic* accounts of the origins of behavior (e.g., Tinbergen’s 1951 concept of *instinct*). Such accounts, it is argued, provide a more substantive *functionalist* explanatory framework for behavior, which in principle allows for a better understanding of the correlations among behaviors and their elicitors, in addition to the commonalities that exist among classes of behaviors. Further, positing distal mechanisms enables the construction of more rigorous hypotheses prior to the collection of data on a given behavior (be it in the context of experimental or observational work). For example, adaptationism makes sense of the phenomenon of *supernormal stimulus*, since it postulates the existence of

mechanisms that evolved to upregulate behavior in response to a specific elicitor on a dose-dependent basis; where *evolutionarily unfamiliar* levels of that elicitor exist (e.g., the stimulus is irregularly abundant in the environment), the mechanism can become overstimulated, leading to exaggerated behaviors (e.g., excessive consumption of sugar), with no throttling mechanism present to inhibit the action of the adaptation, because the elicitor was rare for the majority of a species' evolutionary history (Tinbergen 1951). By contrast, an ethological approach that restricts itself to the observation of behavior cannot explain the phenomenon of supernormal stimulus, because *post hoc* evolutionary accounts of behavior under supernormal stimulus (such as the idea that maladaptive behaviors, e.g., excessive sugar consumption, were somehow evolutionarily advantageous) absent an adaptationist-functional model are *prima facie* lacking in plausibly.

While evolutionary psychology initially very closely aligned with sociobiology (indeed the standard-bearing journal of the Human Behavior and Evolution Society was known as *Ethology and Sociobiology* until 1996), it is reasonable to consider the two as distinct fields. Sociobiology, in Edward Wilson's (1975) pioneering conception, focused broadly on the application of evolutionary and ecological thinking to understanding the origins of social behavior – not just in humans but in social organisms (such as ants) generally. Unlike early ethology, sociobiology embraced adaptationism as one of its theoretical foundations.

Conversely, contemporary evolutionary psychology more narrowly employs adaptationist logic to understand the origins of psychological modules, which are thought to have emerged in response to the presence of persistent selection pressures acting in phylogenetic time or otherwise in ontogenetic time. In order to optimize behavior, it is thought that a module must calibrate itself in response to signals stochastically sampled over the course of development (such as the modular systems that subserve incest-avoidant behaviors; Spain 1987). The multiplicity of recurrent selection pressures is said to have given rise to *massive*

modularity, i.e., the structure of the human brain as a set of modules, which are mental systems that each has a particular adaptive function (sometimes, and controversially, each such system is said to correspond to a functionally isolated neurological structure). This marriage of adaptationism and cognitive psychology is one of the hallmarks of contemporary evolutionary psychology, permitting the field to move beyond the relatively poorly articulated concept of instinct, as employed in ethology and sociobiology. The concept of modularity is intimately linked to the concept of *domain specificity*, which posits that modules require the presence of specific elicitors to produce a unit of adaptive behavior, much like the lock-and-key theory of enzymatic action, according to which an enzyme will only activate in the presence of a specific and compatible biochemical substrate. This modular specificity is necessary in order to avoid *combinatorial explosion* or the paralysis of action that would theoretically result if behavior were the product of *domain-general* processes. For it is argued that these processes would take in and combine multiple elicitors in the course of finding solutions to adaptive problems in a potentially boundless solution space, leading to exponentiation of permutation and concomitant behavioral inaction.

The Santa Barbara School

Massive modularity can rightly be considered a central tenet of the most prominent evolutionary psychology research program, specifically that which has been promulgated by John Tooby and Leda Cosmides (in particular). There are other elements associated with this so-called *Santa Barbara School* (or *High Church*; Heyes 2012) evolutionary psychology, which shape its distinctiveness as a body of theory. A key argument put forward by Tooby and Cosmides (1990) is that individual differences in personality essentially result from random quantitative variation around "species-typical" psychological adaptations, with such variation understood as a consequence of "genetic noise." One implication of this idea is that only the modules should be studied in evolutionary terms – the modules are basically

monomorphic and species-typical, having arisen due to the action of centripetal selection operating over the course of hundreds of thousands of years of exposure to recurrent domain-specific fitness challenges, unlike supposedly randomly occurring individual differences. Thus *human universals* are considered to be the optimal level at which to study human behavioral evolution. Consistent with this view, much of the foundational work in evolutionary psychology has focused on demonstrating the universality of grammar and syntax to language acquisition across cultures, in addition to factors such as kin recognition, cheater detection, and mate-choice criteria (Buss 2011).

A derivative of the human universals argument, also characteristic of the Santa Barbara School paradigm, is the *evolutionary stasis* argument. This is premised on the notion that adaptations take time to evolve since they are complex. Thus selection forming adaptations will tend to be stabilizing and centripetal (i.e., pulling inward to the mean), rather than directional or centrifugal (disruptive). Mutations are far more likely to disturb the functions of modular systems than to enhance them, and their capacity to enhance such systems diminishes in proportion to the degree to which the latter become optimized.

Humankind supposedly reached its highest point of adaptive optimization in the species' so-called environment of evolutionary adaptedness (EEA). Early on in the history of Santa Barbara School evolutionary psychology, this environment was identified with a specific time and place in the Pleistocene epoch (geographically corresponding roughly to what is today called the African Savanna; Barkow et al. 1992). More recently, the standard definition of the EEA has shifted somewhat to encompass an integrated set of spatially and temporally distributed environments in which different adaptations were acquired by different populations; but since they were universally fitness enhancing, these adaptations' fundamentals rapidly flowed to other spatially and temporally contiguous populations, ensuring their distribution all throughout the human species. There is little consensus as to when this process of universal adaptive optimization ended, though some evolutionary

psychologists suggest that it likely concluded at the start of the Holocene epoch (approximately 11,000–12,000 ybp; Kanazawa 2004). Those in the Santa Barbara School argue that evolution subsequent to this point has been purely cultural in nature but with such cultural evolutionary processes fundamentally reflecting the logic of underlying primordial adaptations. An excellent example of this thinking is found in the parasite-stress theory of values and sociality (Thornhill and Fincher 2014), which posits that many different facets of culture and inter-population variation in them, such as collectivism, conservatism, xenophobia, intellect, violence, religiosity, language, and ethnic diversity, stem ultimately from the fitness challenges posed by parasites and differential parasite burdens in and among human groups. Adaptations that were selected because of these challenges elicit in populations differing (consistent with variation in parasite burdens) degrees of *behavioral immunity*, with collectivistic, conservative, and other in-group-oriented behaviors serving to protect a cultural group from contact with members of outgroups, who may harbor novel parasites. Other behaviors, such as polygyny and consanguineous mating, may also serve to consolidate genetic capital (e.g., locally acquired immunities) within a specific group.

Explanatory models of the foregoing kind are predicated upon the idea that humans acquired a behavioral repertoire in the EEA that developed partially in response to variable exposure to parasites. Subsequent migratory radiation into different parts of the world faced distinct populations with different levels of parasite contact – thus evoking the execution of different adaptations acquired in the EEA to facilitate locally optimal behaviors. Thus, these evolutionarily informed models of cultural expression simply do not require populations in relatively novel environments to have acquired new and idiosyncratic adaptations in a relatively short period of time: their phylogenetic experience in the EEA was sufficient to biologically prepare them for a wide array of challenges, such that these populations arrived in unfamiliar environments genetically equipped to deal with (virtually) all eventualities.

Another (related) concept characteristic of the Santa Barbara School is *evolutionary mismatch*, which concerns instances in which a feature of an environment does not properly fit a given adaptive factor, such that resultantly dysregulated behaviors lead to maladaptive outcomes. Mismatch in turn depends on the idea of *evolutionary novelty* or the degree to which an environment contains potentially adaptively salient features that were either completely absent from, or were only rarely present in, the ancestral EEA. Civilization is believed to have amplified the evolutionary novelty content of environments in ways that may have led to maladaptive expression or suppression of (ancestrally) adaptive behaviors. In the Santa Barbara paradigm, the previously discussed phenomenon of supernormal stimulus may be used to explain the obesity epidemic as a consequence of evolutionarily novel availability of sugars and other “cheap” calories supernormally stimulating consummatory behaviors, along with the lack of need to hunt and forage encouraging sedentarism. Some evolutionary psychologists have applied the mismatch model to the end of understanding the origins of other diseases of modernity, both physiological and psychological (e.g., Hidaka 2012; Montgomery 2018).

Coupled to the Santa Barbara School core concept of evolutionary stasis is the concept of panmixia. As previously mentioned, genetic corridors are believed to have existed among the disparate populations living in different times and places in the EEA. The existence of these corridors permitted rapid intraspecific introgression among populations of variants that may have been universally fitness enhancing across all environments in which these populations existed (even though these variants of course originally arose at particular times and in specific locations). Variants that promote certain kinds of adaptive behavior under conditions of high parasite stress, for example, may also ultimately benefit and therefore persist in populations living under low stress, given that this parameter may vary in the future in unpredictable ways. This process would have had two primary consequences. First, it would have acted to resist *raciation* (the process by which distinct subspecies or races arise),

restricting the process to “superficial” characteristics (e.g., weak raciation producing variation in skin color across populations, adapting them to different levels of ultraviolet radiation exposure). As far as a population’s set of core psychological modules is concerned, there should exist no meaningful parametric variation among populations, in terms of either the numbers or the types of such modules (everyone recognizes kin in the same way, everyone acquires syntax in the same way, etc.). Cultural variation is therefore a consequence of differential adaptation execution under different patterns of elicitors (e.g., Thornhill and Fincher 2014). Proponents of the Santa Barbara School have even gone so far as to utilize the argument put forward by Richard Lewontin (1972) that the pattern of variance apportionment with respect to certain traits (such as blood groups) indicates greater within- versus between-race variation, to justify rejection of the possibility that disruptive selection, and resultant raciation, occurred in disparate human populations. Some Santa Barbara School proponents have also argued that the phylogenetic irrelevance of race to evolved human behavior can be demonstrated in experimental procedures that suppress the salience of race in coalition formation, once certain primes are used (Kurzman et al. 2001). The existence of panmictic patterns of gene flow in the EEA coupled with the seeming taxonomic meaninglessness of race are allegedly responsible for the apparent lack of any specialized ethnic coalition module or similar system involved in coalition formation.

Finally, another defining characteristic of the Santa Barbara School is its rejection of group and multilevel selection. The adaptationism of George Williams (1966), specifically his “ground rule,” posits that adaptive explanations of the origins of traits are “onerous,” and thus should only be utilized sparingly; similarly, individual- and gene-level selection should be favored as the most plausible mechanisms through which adaptive traits emerge, a stipulation that strongly influenced Richard Dawkins’ *selfish gene* model of selection, which in turn strongly influenced Tooby, Cosmides, and others, for whom (as with Williams) genic and kin selection constitute *sufficient*

driving forces behind the evolution of psychological modules.

Critiques of the "Standard Model"

The Santa Barbara School paradigm is sometimes described as the standard model of evolutionary psychology by its critics within the field (Winegard et al. 2017). Each of the core tenets of the standard model has in fact been vigorously and constructively critiqued by various researchers who align with the basic objectives of evolutionary psychology and who are here said to constitute the *Broad Church* of the field.

Massive Modularity on the Chopping Block

Massive modularity, and the adaptationist assumptions that undergird it, is one of the more frequently critiqued pillars of the standard model. It has been noted, for example, that the existence of *heritable* and substantial individual differences in the domains of personality and cognition along with the presence of genetic correlations among seemingly distinct sources of those differences (such that a *General Factor of Personality* [GFP] and a *general factor of intelligence* [g] seem to dominate the variance in "performance" among specific measures of personality and cognitive ability; Jensen 1998; Muek 2007) strongly militate against the particularist and monomorphic approach to understanding the origins of cognitive and conative faculties in the standard model. It has been noted that the definition of "module" appears to be elastic in such a way that permits the concept to simply be redefined so as to suit the needs of the field at any given time. This was the thrust of Jerry Fodor's (2000) critique of the standard model's massive modularity. Fodor (1983), who developed the mature form of the modularity concept, defined modules in a highly specific way, and argued that they exclusively appear in so-called peripheral mental systems (such as those subserving sensory perception). On Fodor's (1983) view, modules are characterized by (among other features) the quality of *encapsulation* or the specificity of a given module's association with a given eliciting stimulus. Fodor further argued that beyond this handful of very basic modules, there exist

domain-general systems that are responsible for all forms of higher-level processing. Fodor notes that subsequent attempts to "salvage" massive modularity appear to have moved beyond this more restricted conception of encapsulated modularity by recasting modules as entities that can interact with other modules in order to construct the more elaborate sorts of circuits needed for solving more complex problems based on context (e.g., Barrett and Kurzban 2006). David Geary (2005) observes that there is a decided lack of coherence in defining modules and reviews several seemingly distinct definitions in his seminal work on the evolution of general intelligence. Others (Fodor 2000; Panksepp and Panksepp 2000) have argued that if any mental system can be classified as a module, then the module concept is useless. Panksepp and Panksepp (2000) have even proposed a sort of *anti-modularity*, based on the idea that the brain is comprised of highly plastic and open-ended systems that did not evolve to solve specific tasks, but can nevertheless be organized into different systems that are optimized for producing certain behaviors or solving certain problems. It was this *domain-general* capacity of the brain that was primarily subjected to selective pressures across various adaptive contexts, rather than solution-generating subsystems, as the standard model posits.

It has been further argued that the dominance of general factors in distinct domains of life history, personality, and cognitive ability strongly evidences the existence of domain-general processing systems, which act to contextualize problem-solving via the use of learning and conditioning pathways, in addition to the establishment of hierarchical goals as guides to action (Chiappe and MacDonald 2005; Figueredo et al. 2006; Geary 2005). Systems such as working memory in the case of higher-order cognition and executive functions broadly in the case of higher-order conation have been put forward as solutions to both the combinatorial explosion and poverty of stimulus arguments against the existence of domain-general processing systems. These *executive* systems permit the solution space for a given open-ended problem (i.e., one for which there is no preprepared response) to be

restricted based on trial-and-error experience and concomitant learning and also intrinsically generated goal states, thus essentially throttling the ability for *representations* (i.e., the outputs) arising from more fundamental and specialized cognitive systems to proliferate and combine in uncontrolled ways. The resultant *meta-representations*, which guide behavior, can therefore be thought of as the equivalent of battle plans chosen by a general (the executive cognitive and conative systems) from among a set of potential plans, which in turn were prepared via consultation with military specialists (the lower-order, more domain-specific systems). The generals in this scenario are not inundated with countless battle plans, as ultimately they choose one from a subset, which is itself limited via a filtration process involving the general's staff consulting only the relevant specialists (e.g., if an enemy country possessed chemical weapons, then only chemical weapons specialists would be consulted, there being little point in talking to, say, nuclear weapons specialists). The failure of a given battle plan would occasion the development of new plans, only in this instance the particulars of the failure would be taken into consideration, imposing an additional constraint upon the solution space (a process analogous to trial-and-error learning). The general in this analogy further has a specific goal state (military victory), which imposes yet another constraint upon the broader solution space (the general would not, e.g., plan to build a circus in the town square if his objective is successfully defeating a foreign enemy). The goal state is flexible, however, as different strategies (sub-goals) can be tried and discarded based on their efficacy.

Some evolutionary psychologists have attempted to delimit these domain-general processes as modular in nature and therefore pertaining to specific adaptive problems. Dan Sperber (1994) has proposed the existence of a *metarepresentation module*, the function of which is to specifically deal with organizing the behavior of lower-order modular systems (akin to the general of the previous example). Satoshi Kanazawa (2004) has proposed that general intelligence is itself a module adapted to dealing with domain-

specific problems associated with evolutionary novelty. These attempts to modularize open-ended processes to a degree serve to highlight Fodor's and others' aforementioned objections – chiefly that if “everything” is a module, then “nothing” is, as there is now so much conceptual elasticity that the idea of a module loses coherence and thus scientific utility.

Such attempts furthermore suffer from the *poverty of stimulus* problem, as the sorts of problems that improvisation is needed to solve do not adhere to a specific domain *per se* but tend to straddle multiple domains. It is therefore unclear how stimuli related to such problems could be treated as pertaining strictly to a specific domain, and so it is difficult to see how these stimuli would yield dedicated systems for solving those problems. Put succinctly, the stimuli, by virtue of being indiscriminate with respect to domain, would not occur relative to *any specific domain* in isolation frequently enough to favor the evolution of specialized solution-generating mechanisms. The postulation of domain-general processes avoids the poverty of stimulus problem, however, as such processes simply act to impose boundary conditions upon the sorts of representations that can be usefully combined into units of behavior. Domain-general processes never evolved to deal with a given domain *per se*; instead, they confer a fitness payoff whenever a unit of behavior yields a successful solution to a given problem for which an organism is simply not prepared through some more specialized mechanism. The domain-general processes interact with the specialized ones but are not fully reliant upon their representations as guides to behavior (indeed systems of the former type can actively override *implicit* behavior originating from lower-level systems, when such overriding serves some explicit goal; a good example of this process would be the use of executive functioning in modulating impulsivity among those with low time preferences, facilitating delay of gratification; MacDonald 2008). This should not be taken to imply that there is some overarching *central executive* system in place that coordinates all behavior either; indeed, there is evidence for the existence of at least two broad executive

systems, one dealing with cognition and one dealing with conation (including life history and personality), which are largely genetically distinct from one another (Woodley of Menie and Madison 2015). This distinctness could be considered a kind of *metamodularity*, as it implies that the brain organizes behavior much like how the various branches of government organize the activities of a state: there are very broad but ultimately finite domains to which each domain-general system (or branch of government) pertains, which can be dealt with by each domain separately and largely without the need for interaction between them (Woodley 2011).

Supporters of the standard model (Cosmides and Tooby 2002) have also attempted a solution to the problem of the appearance of domain-general systems (at least as they pertain to cognition), by drawing a distinction between *dedicated* and *improvisational* intelligences – the former composed of modules and their domain-specific solutions to domain-specific problems and the latter representing the sum of the outputs of various modules that act in concert in response to all of the domain-specific components of a seemingly domain-general problem. Based on this model, behavioral units are consequences of an essentially harmonious interplay among the action of many modules, refined by selection. This solution obviates the need for domain generality, as (presumably) suboptimal behaviors, resulting from disharmonious interactions among modules, would have been selected out of the population. Behavior, furthermore, constitutes the level at which the representations are “integrated,” negating any necessity for “dedicated” domain-general systems to produce metarepresentations for guiding behavior. This model posits a process analogous to playing the piano. Each key is dedicated to the production of a limited range of sounds. The striking of keys is analogous to domain-specific elicitors, and the range of notes is analogous to the breadth of domain-specific problems. The resultant notes can be combined into either harmonious or disharmonious configurations, depending on which set of keys is struck and in what order. A key problem with this model is that it implies that the appearance of domain-general

mechanisms among psychometric measures of cognition and conation are illusory, resulting from the harmonious combination of modular “keys” being “played” by exposure to a given set of domain-specific problems. This implies that different problems yield only superficially similar latent factors, based on the different “scores” that characterize each problem domain. Thus we would not expect *g* factors, for example, to be measurement invariant across problems (which they typically are) nor would we necessarily expect hierarchical factor models to suffice for modeling higher-order variables among psychometric data (instead we would expect some kind of correlated factor model to be a better fit, which, at least in the case of intelligence, is not the case; Johnson et al. 2004). These psychometric observations imply the existence of distinct, higher-order, and domain-general processes, which regulate the production of behavior, and serve as an intermediary between more specialized systems downstream and behavioral action units upstream of them.

An additional problem with massive modularity issues from the observation that domain specificity implies species typicality, i.e., each species is adapted to the contours of a unique evolutionary niche or EEA. Thus behavioral differences among species should be differences of *kind* rather than *degree*. This has led to certain animal ethologists (e.g., Herrmann et al. 2010) positing that the patterns of domain-specific mechanisms involved in solving cognitive problems differ among species in such a way that makes them incomparable, when individuals of different species are challenged using common behavioral probes. Thus “intelligence” does not stem from some set of processes common across taxa but instead differs based on the unique phylogenetic experiences of different taxa. This claim has been countered with the observation that species differ from one another in problem-solving capacity primarily with respect to a latent general intelligence-like (*Big G*) factor, rather than relative to specialized problem-solving abilities (Fernandes et al. 2014). Furthermore individuals of different species manifest the largest differences in performance on cognitive measures that exhibit both high loadings

onto a common g factor and also high phenotypic variability, with the differences obscured by the presence of abilities that are modularized in one species but not in another (and thus impose floor or ceiling effects on performance, reducing variability; Woodley of Menie et al. 2017a). Highly G - and (at the individual-differences level) g -loaded measures exhibit the strongest signals of having been under directional selection (Fernandes et al. 2014; Woodley of Menie et al. 2015), so selection appears to have arrayed species differences in intelligence along a continuum of performance with respect to some overarching faculty (which derives from a quality common across taxa), rather than relative to specialized modules (species differences on such modules do exist; however, they are not the main locus of these differences in the context of cognitive performance). These findings raise further questions concerning the uniqueness of human modules. Implicit in the standard model is the assumption that humans acquired specialized adaptations to problems that were unique to human evolution. This is illustrated in the case of human language acquisition ability, which has been held up as an archetypal human species-typical module (Pinker 1994). But since this mechanism was first described in the literature, evidence has accumulated indicative of communicative ability and even primitive language use among other taxa and also prehuman ancestors (Clark and Henneberg 2017). This suggests that, while language use evolved in a particularly elaborate way in humans, the capacity to acquire and use structured language is something that an array of taxa potentially enjoys. Human species-typical modules therefore may not be uniquely human, strictly speaking, but may instead be derived from ancestral structures, which many taxa share (Panksepp and Panksepp 2000).

Individual Differences Are Evolutionarily Significant

One of the weakest features of the standard model is the claim that individual differences arise only from ontogenetic as opposed to phylogenetic processes, specifically resulting merely from “genetic noise.” This claim could be said to have

simultaneously stemmed from a desire to rhetorically highlight what Tooby and Cosmides perceived to be the major locus of human evolution, i.e., the fundamental architecture of the adaptive structures guiding behavior, coupled with the (now believed to be flawed) idea that adaptations should exhibit little heritable variation because selection has depleted it (Fisher 1930).

Nevertheless, many researchers believe that individual differences have adaptive significance. Certain evolutionary psychologists have attempted to square the existence of heritable individual differences with massive modularity, such as Geoffrey Miller, who considers individual differences, and also genetic correlations among different sources of individual differences, to result from the action of pleiotropic mutations, which jointly influence the efficiency with which multiple modules can act, bringing the resultant variations into correlation with one another. Different levels of these traits in different individuals would therefore reflect variation in mutation load. These differences serve as indices of genetic quality, guiding mate choice under sexual selection. The pleiotropic manifolds among traits not only potentially account for the presence of g and the GFP but also imply the existence of a broader general fitness factor (f) superordinate to multiple psychological and even physiological domains (Miller 2000).

Various evolutionary psychologists (most notably J. Philippe Rushton [1985] and Aurelio José Figueredo and co-workers [2007]) have also used life history theory to account for interindividual trait variation. Life history theory is based on the idea that organisms tradeoff bioenergetic and material resources among trait domains in order to optimize their fitness given exposure, over phylogenetic and ontogenetic time, to different degrees of environmental risk (harshness and unpredictability). Organisms living, and/or evolved, in environments characterized by high levels of, and/or random, mortality tend toward replacing lost offspring (mating effort) at the expense of investment into offspring (parenting effort), investment into condition-maintenance (somatic effort), and investment into inclusive fitness (communitarian effort).

Low and/or predictable mortality regimes on the other hand favor high levels of parental, somatic, and communitarian effort. Personality and another dimension of conation (the *K*-factor) that tracks variation in a number of psychological and behavioral components of life history cohere genetically into a continuum termed the Super-*K* factor, which also includes indices of physical and mental condition (collectively termed covitality). The *fast* life history pole of this continuum is reflected in poor general health and low social effectiveness, as well as risk-taking, promiscuity, weak attachment, poor executive functions, and concomitantly poor forward planning and impulse control. Those at the *slow* end by contrast are typically high in general health and social effectiveness, and are also altruistic, sexually and behaviorally restrained, prosocial (high need for attachment), future oriented, etc. Life history theory does not dispense with modularity (modules are ever present in the background). But unlike fitness indicators theory, which posits that individual differences are *purely* byproducts of variation in loads of adaptation-degrading mutations, which are acted on by sexual selection and with high *f* being *universally* favored over low *f* across environments, life history theory postulates that different levels of *Super K*, as reflected in patterns of variation and even degrees of coordination among modules (regulated through higher-level domain-general systems), yield different selective benefits under different regimes of environmental risk (Ellis et al. 2009). What both models have in common is the view that individual differences are ultimately maintained by various forms of stabilizing selection.

Woodley (2011) has taken the argument for adaptive individual differences even further by positing that the niche splitting that results from the presence of individual variation is itself highly favorable to the success of *competing groups*, as greater division of labor permits the sustainment of greater population densities, in addition to conferring upon groups a greater relative advantage in competition. Kevin MacDonald (2008, 2009) has elaborated this *anti-Williamsian* model further

still in his work on *cultural group selection*, which posits the existence of certain sources of individual variation that facilitate maintenance of the integrity of the extended phenotypes of cultural groups through suppression of free-riding behaviors. An example of such a source of variation would be *effortful control*, or the ability to use explicit processing to override implicit drives, which, if left unchecked, may promote behaviors that would undermine the integrity of a group's extended phenotype. Those high on effortful control can furthermore run strategic interference on those low in the ability, via the imposition of sociocultural conditions conducive to the fitness of those with group-selected (i.e., group-fitness enhancing) traits.

Race and Population

The broader debate about the role of group selection in human evolution ties into the related issues of whether (a) population structure (i.e., human racial and ethnic diversity) has played a meaningful role in human evolution and (b) whether environments that humans encountered after "leaving" the EEA were evolutionarily significant. If, as the standard model posits, racial and (biological) ethnic divisions were absent from the EEA, then ethnic conflict becomes difficult to explain. As Salter and Harpending (2013) demonstrated, kinship is a relative value: two randomly selected individuals from a single population may be only weakly related to one another in absolute terms, but relative to a third individual, selected from a more genetically distant population, they may be related to one another much more closely, when their coefficients of ethnic kinship are quantified with respect to their relatedness to the third individual. Thus potentially very large fitness pay-offs can accrue from the use of racial and other ancestral markers in the formation of coalitions for the purpose of intergroup conflict. These markers are typically highly correlated with one another, with only small numbers of them needed to infer ancestry with an extremely high degree of confidence. Edwards (2003) showed how using only small numbers of correlated traits it is

possible to highly accurately assign racial ancestry to individuals. He presented this finding in contrast to what he termed *Lewontin's Fallacy*, the idea that race is not a meaningful biological concept because there is more genetic variation within than between racial groups. Lewontin's (1972) "deconstruction" of the concept of biological race involved emphasis on single loci associated with systems that have been under persistent stabilizing selection (such as the ABO blood group system). In selecting such single loci, variation due to population structuring (racial or otherwise) will naturally be suppressed. These facts do not contradict Lewontin's accurate claim that as a general rule there is more genetic variation within than between racial groups (consistent with this, *Fst*, or the proportion of the variance among humans that is due to population structure, is around 15%; Cavalli-Sforza et al. 1996); but they do strongly counter his inference from this observation that race is not a valid biological or taxonomical category.

Some have also questioned the idea that race and population structure more generally have played no role in human evolution. Harpending (see MacDonald 2001, p. 70) has posited the *starburst model*, which is based on the notion that distinct populations repeatedly expanding, coming into conflict, and retreating were likely recurrent features of human evolution. Phylogenetic integration across these encounters should have prepared humans with adaptations that cause them to factor perceived genetic similarity into coalition formation. This is not to say that population-level variation and even context specificity do not play a role in how these mechanisms express in different groups. Some populations tend to be more collectivistic than others; thus, for these groups the salience of ethnic cues to coalition formation may be higher (MacDonald 2001). Ecological stress and pressures favoring endogamy for the purpose of boosting homozygote advantage, such as that experienced by populations under high parasite load, may also serve to epigenetically upregulate the salience of

ethnicity to coalition formation. That ethnicity matters to coalition formation across a very broad swath of *natural* contexts is a robust finding, however (Salter and Harpending 2013; MacDonald 2001).

Rapid Genetic and Cultural Variation: Beyond the EEA

Finally, the existence of genetic variation, across space and time, that is continuous with cultural variation (as studied under the rubric of *cross-cultural sociogenetics*) casts the standard model's concept of the EEA into doubt, since this variation implies that there were in fact multiple environments of evolutionary relevance for different populations and that the assumption of panmixia simply has not held throughout human evolution (otherwise *structured* population differences would not exist). This further indicates that cultural variation is not disconnected from genetic variation among populations, and may even be a motor for such change, as is posited by the theory of *culture-gene coevolution* (Cavalli-Sforza and Feldman 1981). Based on this model, culture changes in response to shifts in the gene frequencies of the populations responsible for generating it. As populations become more intelligent or more altruistic, for example, the contours of the culture change, reflecting such shifts. Those changed contours will in turn create additional opportunities for adaptive evolution, as the presence of certain cultural practices may impose fitness penalties upon one group of individuals with one set of traits while promoting the fitness of another group.

Cultural complexification was a hallmark of Eurasian populations living during the Holocene, for which genetic data indicate rates of adaptive evolution that were on the order of 100 times faster than those during the preceding Pleistocene epoch (Hawks et al. 2007). Evidence has been found that genetic variants associated with general intelligence were under particularly strong positive directional selection in the period covering the Bronze Age to approximately the mid-nineteenth century (Woodley of Menie et al.

2017b), with selection having subsequently disfavored these variants (due to the action of so-called *dysgenic selection* stemming from the use of contraception and fertility delays among those exposed to education for the longest amounts of time; Lynn 1996), starting in the mid-nineteenth century and continuing into the present day, at least in Western nations (Kong et al. 2017; Woodley of Menie et al. 2017d). The extremely rapid pace of culture-gene coevolutionary change and (resultant) cultural complexification among Eurasian populations in particular makes Holocene environments highly relevant to understanding human evolution (Frost 2011). Frost (2011) notes that the basic set of adaptive modules may have come to vary across populations – new ones having arisen rapidly via the process of duplication. He gives as an example of an outcome of this process the *visual word form area* of the brain, which permits written words to be easily recognized as such and likely arose as recently as 6,000 years ago, concomitant with the origins of written language among nomadic agriculturalists living in the Arabian Peninsula. The existence of these processes by which new adaptations can develop rapidly, essentially deriving from the duplication of already existing adaptations, furthermore contradicts a key assumption of the standard model, namely that such structures must take tremendous amounts of time to evolve, being fragile and sensitive to the action of deleterious mutations. In fact, these observations of apparently recent and rapidly evolved adaptations may pose the most profound challenge to the Santa Barbara School model, as the rapid emergence of entirely new adaptive systems in very small frames of time suggests that the basic claim of the universality of modular architecture among humans needs to be substantially revised. As Nicholas Wade has observed, “[n]ew analyses of the human genome have established that human evolution has been recent, copious, and regional” (2014; p. 2). It is therefore imperative for the Santa Barbara School of evolutionary psychology, if it wishes for its paradigm to survive, to consider ways of reconciling this profusion of new findings with its own position.

Radical Critiques of Evolutionary Psychology

Discussion of evolutionary psychology outside of the field is not infrequently critical. A significant subset of “external” critiques of the field is extreme, maintaining that evolutionary psychology, either necessarily or as standardly practiced (i.e., consistent with the Santa Barbara School model), is theoretically, methodologically, and/or empirically illegitimate. These are here termed *radical critiques* of evolutionary psychology. Pigliucci (2010, pp. 41–45) offers one such attack on the discipline, which he calls a “quasi-science” (p. 24), in other words a field of research that is located somewhere between actual science and pseudoscience. Pigliucci’s case against evolutionary psychology is exemplary of the larger class of radical critiques, insofar as it rests upon common and basic misunderstandings and mischaracterizations of research and methods and even upon unequivocally false claims about the nature of particular scientists’ work. In the way of outright inaccuracies, for instance, Pigliucci (2010, p. 41) insinuates that Herrnstein and Murray’s *The Bell Curve* (1994) is a work of sociobiology, which is in turn related to evolutionary psychology, despite the fact that the work involves almost no discussion of evolutionary theory and instead draws primarily on psychometrics; further, he asserts that *The Bell Curve* is “intellectually questionable” and makes “unsubstantiated claims about genetic determinism of human cognitive traits,” claims which are simply untrue (Herrnstein and Murray’s [1994] discussion of evolutionary theory is almost entirely relegated to a short section in an appendix, which discusses J. Philippe Rushton’s differential *K* theory of race differences. The discussion consists mostly of a general overview of Rushton’s theory and the controversy that has surrounded it, together with Herrnstein and Murray’s conclusion that “the theory remains a long way from confirmation” [1994, p. 643]. This hardly constitutes reliance on evolutionary theory. Furthermore, *The Bell Curve* contains minimal discussion of the genetic bases of intelligence, offering merely the view that variation of intelligence, among individuals [p. 292] and groups [p. 311], is due [or is probably due, with respect

to intergroup variation] to both *genetic and environmental* differences. At least in the case of individual variation, this is uncontroversial among experts [e.g., Plomin and Deary 2015]. Moreover, a report published by the American Psychological Association shortly after *The Bell Curve*'s publication largely supported the book's central claims [Neisser et al. 1996], indicating that Herrnstein and Murray's [1994] theses did not offend the mainstream of psychological research. In any case, Herrnstein and Murray [1994] clearly did not endorse genetic determinism as traditionally conceived, since they did not deny a role to environmental factors in the determination of individual and group differences. Even if they had, however, it should be noted that Pigliucci [2010] is mistaken in his apparent belief that the study of the relative contributions of genes and environment in determining human traits, cognitive or otherwise, is part of evolutionary psychology or theory. In fact, this is the province of a separate field: behavioral genetics [which is, to be clear, obviously compatible with evolutionary psychology, but is, as stated, independent from it].)

In tackling evolutionary psychology directly, Pigliucci (2010) employs the familiar gambit of averring that human behavior has been of course shaped by selective pressures, and yet concluding that it is nonetheless impossible to ascertain much about *how* human behavior evolved (Richardson 2007, p. 95 expresses the same sort of idea). He offers three arguments for this view. First, in criticizing Randy Thornhill and Craig Palmer's evolutionary account of rape, he argues, without evidence, that rape "doesn't pay," i.e., does not contribute to fitness, "in today's society" (p. 42). The fact that a behavior is not adaptive in a contemporary context does not imply that it was not adaptive in the past, however, and evolutionary psychologists, including Thornhill and Palmer, usually refer to conditions of the distant human past to explain the context in which human traits emerged because they were adaptive. Further, it is often not difficult for evolutionary psychologists to identify the features of modern environments that render maladaptive some trait predicted to have been adaptive, such that it

becomes clear that trait would be adaptive if not for those features (see, e.g., Kanazawa 2003). That notwithstanding, it would be very odd indeed for evolutionary theories of human behavior to focus exclusively on contemporary circumstances.

Apparently realizing this shortcoming, and implicitly acknowledging that his first argument is beside the point, Pigliucci (2010) then maintains that evolutionary psychological theories invoking evolutionarily relevant features of humanity's past, specifically in the Pleistocene, depend on mere "just-so stor[ies]" – such theories cannot find adequate empirical substantiation because "behaviors have an annoying tendency not to leave a fossil record, and neither do the details of the (largely social and cultural) environment under which [natural selection allegedly operated on humans]" (p. 43). The charge that evolutionary psychologists tell just so stories has been frequently advanced since the emergence of the field, and despite evolutionary psychologists' many refutations of the accusation (e.g., Andrews et al. 2002 and a number of commentaries on the piece), radical critics repeat the complaint, usually, as in the case of Pigliucci (2010), with no effort to rebut evolutionary psychologists' replies. Evolutionary psychologists, whether of the Santa Barbara School variety or otherwise, are in fact at pains to make their models of humanity's past circumstances consistent with available archaeological, anthropological, and paleontological evidence (e.g., Bowles and Gintis 2011), even if their emphasis on the Pleistocene is sometimes excessive and comes at the cost of ignoring recent human evolution (as was argued earlier in this entry). Beyond this, it must be noted that the idea that evolutionary psychology uniquely suffers from the problem of just so stories is grossly unfair. As Andrews et al. (2002) observe, a just so story is simply an inadequately empirically supported scientific claim. The non-biological social and human sciences and related fields, e.g., social psychology, cultural anthropology, sociology, and gender studies, are far guiltier of telling just so stories than evolutionary psychology has ever been. Specifically, they tell utterly implausible just so stories in which only social

and cultural constructions are treated as germane to and invoked to explain human behavior (or at least human behavioral variation), even though about half a century of quantitative behavioral genetics (Polderman et al. 2015) and in more recent years molecular behavioral genetics (e.g., Kong et al. 2017) have left no reasonable doubt that such sociocultural determinist models are untenable. Yet these non-biological behavioral disciplines are almost never met with the charge of telling just so stories. Pigliucci (2010) certainly does not claim that they are borderline pseudosciences. But in the judgment of Tooby and Cosmides (1992), these fields operate in the grip of the so-called *Standard Social Science Model* (or SSSM), a scientifically illegitimate, and thus critique-worthy, explanatory framework positing that biology is largely irrelevant to human behavior and culture or at least to variation in these phenomena. More precisely, the SSSM holds that human behavior should be understood as something developed and learned purely through environmental input – given the model’s assumption that the brain comes largely or entirely without predispositions toward the generation of particular behaviors – and further posits that society and culture should be analyzed exclusively on their own terms, meaning that biological factors should not be construed as if they undergird or give rise to social and cultural phenomena. It could be argued that Tooby and Cosmides’ (1992) description of the SSSM at times shades into caricature, since even the behaviorists did not deny that the human brain is equipped with certain psychological-developmental predispositions. Still, the tendency of social scientists to disregard pertinent research in the life sciences and its implications, and to stubbornly insist on the basic contingency and flexibility of human social and cultural activity with no or minimal explicit awareness of the limits that biology imposes on these domains, is repeatedly demonstrated by Tooby and Cosmides (1992), as well as by the contemporary academic literatures of the social sciences.

With respect to Pigliucci’s (2010) fossil claim, if it were indeed true that evolutionary accounts of human behavior cannot be reconstructed without

an appropriate fossil record, it would follow that evolutionary accounts of nonhuman animal behavior are impossible. This would invalidate a great deal of evolutionary biology, primatology, and entomology, to name a few fields. Pigliucci’s (2010) second argument clearly “proves too much,” then.

Yet again, however, Pigliucci (2010) seems to tacitly admit that an argument of his is not actually effective. For he notes that sound evolutionary theories of nonhuman animal behavior *can* be developed despite “lack of a relevant fossil record” (p. 45); but he also thinks that a special fact about humans entails that the same cannot be done for human behavior. This fact is that there are not enough surviving species of sufficiently close phylogenetic relation to humans with which humans can be compared, so as to gain insight into human behavioral evolution. The limited number of surviving related species means that the “statistical power” of such comparative efforts would be insufficient (Pigliucci 2010, p. 43). This is another argument that entails, if Pigliucci’s (2010) standard of close phylogenetic relatedness were applied, that much of the work in an established evolutionary science that Pigliucci does not criticize is worthless, for it would suggest that the evolution of primate behavior in general, an important area of study in primatology (e.g., Burkart et al. 2017), should be inscrutable.

Moreover, Pigliucci (2010) betrays a poverty of methodological imagination and theoretical sophistication in maintaining that evolutionary behavioral hypotheses can be tested only via interspecies comparison and experiments and observational studies in species’ EEAs (p. 45). First, the study of surviving hunter-gatherer tribes likely gives valuable, though imperfect, insight into the nature of human Pleistocene life (e.g., Diamond 2012) (note that the extent to which contemporary nonhuman animals’ environments are reflective of earlier environments in their phylogeny, to which they may be more optimally adapted, is not always clear; the existence of general intelligence, a capacity that is adaptive insofar as it allows organisms to deal with evolutionarily *novel* problems, across a number of species strongly evidences that they have not lived in completely

invariant environments over time [Burkart et al. 2017], as was discussed in the previous section). Second, the distorting effects of modern environments on human behaviors can be largely sidestepped by comparing various human *populations* inhabiting vastly different physical and sociocultural environments. When the same behaviors are found in sufficient frequency across these environments, and if they are shown to be generally adaptive, there is strong evidence that they are part of humans' *broadly* universal adaptive architecture (the case for evolutionarily tying such behavior specifically to the Pleistocene would require evidence that it emerged or at least existed among humans of that epoch for adaptive reasons, which may come from the sources indicated earlier, especially archaeological and paleoanthropological studies; see Gintis et al. 2015 for an example of a paper that builds a model of human behavioral evolution partially through application of such sources of evidence). Additionally, the seemingly anomalous behavioral phenomena seen in modernized human environments are not always as contrary to evolutionary psychologists' theories as some radical critics believe, meaning that they do not necessarily pose insurmountable obstacles to the application of evolutionary theorizing to modernized humans' behavior. For example, although social status is, contrary to some sociobiologists' and evolutionary psychologists' theoretical expectations, *negatively* associated with fertility in modernized women, certain data indicate that it positively relates to fertility in modernized men, and some have argued that these relationships between fertility and social status in men and women are not out of keeping with evolutionary models and observations of behavior in pre-industrial societies (e.g., Hopcroft 2015; cf Kanazawa 2003). Similarly, intelligence has a negative rather than the expected positive relationship with fertility in modernized populations; nonetheless, intelligence is still positively related to other measures of biological fitness, such as survival, in modernized humans (Burkart et al. 2017, p. 54). The anomalous negative correlation between intelligence and fertility in modernized populations nonetheless can be potentially

accounted for without violating the standard assumptions of evolutionary psychology (e.g., Kanazawa 2014). And contradicting the false but common charge that evolutionary psychologists think that all human behavioral phenomena can be explained in terms of adaptation, a theory has even been propounded to account for the fertility-depressing behaviors found under conditions of modernity with reference to the accumulation of *deleterious* mutations that specifically target and degrade adaptive behaviors and cultural structures (Woodley of Menie et al. 2017c).

Given Pigliucci's (2010) tendency to offer criticisms of evolutionary psychology that in fact call into doubt a number of evolutionary sciences, a further and more general point must be considered: Radical critics of evolutionary psychology are often not merely opponents of evolutionary psychology *per se* but of *adaptationism* as more broadly construed in biological science. Hostility to adaptationism was perhaps most famously expressed by Gould and Lewontin (1979), from whom Pigliucci (2010) borrows the just so stories criticism – in the case of the former, however, this criticism *explicitly* applies to adaptationist explanations in evolutionary science as a whole. Adaptationism can be defined as a mode of biological inquiry in which *some* features of organisms are hypothesized to be evolutionary responses to problems organisms' ancestors faced in the course of phylogenetic development. Without question, adaptationism is the most successful theoretical perspective on evolution in biological science, whereas non-adaptationist programs emphasizing genetic drift or Gould and Lewontin's (1979) "exaptations" have achieved nothing meaningful in advancing understanding of the evolution of life on earth (see Figueredo and Berry 2002; Krasnow and Truxaw 2018). As Figueredo and Berry (2002) ably show, the concept of an "exaptation," i.e., a trait that evolved to serve one adaptive purpose in one environment and then came to serve a different purpose in a different environment, reflects nothing other than basic misunderstanding of the concept of adaptation. Insofar as a trait's adaptiveness is always determined relative to some environment, the "exaptation" idea is already implicit in the original

adaptation concept. “Exaptationism” therefore adds nothing to biological knowledge. Adaptationism’s success is due to the fact that it alone (as an evolutionary paradigm) is able to produce novel predictions and theories that advance evolutionary understanding, for only adaptationism can link environment and ecology to phylogenetic development in such a way that the former can *explain* the latter (for a very similar point, see Krasnow and Truxaw 2018). At best, non-adaptationist perspectives can be applied when adaptationist hypotheses fail and in that case are merely part of the adaptationist program. At worst, non- (or even anti-) adaptationism is simply a way of retarding progress in biological science, often for political reasons, as when Levins and Lewontin (1985) sought to make evolutionary biology compatible with the pseudoscience of Marxism. Ironically, for all his objections to adaptationism as poor science, Lewontin’s non-adaptationist biology never advanced beyond a thin pretext for political advocacy (Wright 1998). In evolutionary psychology, adaptationism has proven remarkably successful, with a number of ambitious theories having offered testable predictions that have been found to be consistent with relevant empirical data (e.g., Loehlin et al. 2015; Woodley 2011). It is difficult to explain how such theories have made so many accurate predictions if the state of nature is such that, as Pigliucci (2010) claims, human behavioral evolution is simply beyond researchers’ grasps.

Conclusion

This entry has examined two forms of critique of evolutionary psychology, intrinsic and radical, and prominent controversies that are connected to them. Critiques of the former variety proceed from the premise that evolutionary theory can be successfully employed to elucidate the human mind and human behavior but maintain that particular forms of such evolutionary psychological science are flawed. Therefore intrinsic critiques are *constructive*, aiming to eliminate error in evolutionary psychology. Conversely, radical critiques of the field are *destructive*: their purpose

is to demonstrate that evolutionary psychology does not or even cannot qualify as a bona fide science. It is difficult to find fault in intrinsic critique *as such*, since it is an ordinary feature of all sciences. But radical critique requires substantial rational warrant, especially when its target is a well-established field of intellectual endeavor.

It is apparent that radical critics of evolutionary psychology have not met this burden, mostly because of their reliance on misrepresentations of the state and practice of evolutionary psychology and on standards of evidence that are unreasonable for all social scientific and some biological areas of study. Unless one is prepared to cast aside most or all of archaeology, paleoanthropology, environmental history, and so on, it is clear that approximately true reconstructions of the phylogeny of modern humans and their hominid ancestors can be and have been developed (see Bowles and Gintis 2011; Gintis et al. 2015). These reconstructions allow scientists to gain knowledge about the selection pressures that have shaped these phylogenetic pathways, and such knowledge in turn serves as the fundament of evolutionary psychological theorizing. When academics such as Pigliucci attempt to impose arbitrary standards of evidence that would have us ignore everything not known with a certain high level of precision, and thereby absurdly exclude as scientifically illegitimate multiple areas in the life sciences, one is rightly suspicious. Suspicion grows once it is observed that critics of Pigliucci’s, and by extension Gould and Lewontin’s, ilk never seem compelled to criticize strikingly empirically weak social sciences that endeavor to explain human behavior (e.g., sociology, social psychology, and political science). For reasons not made explicit, evolutionary psychologists are under obligation to test their claims using the highest-precision methods on offer in the evolutionary sciences, and if these methods cannot be applied in studies of humans, *nothing* less rigorous is acceptable (so says Pigliucci). On the other hand, sociologists and social psychologists are free to proceed, as they almost always do, on the (implicit or explicit) assumption that biological factors are either irrelevant to human behavior or are of such trivial import that they

can be safely ignored. But surely if Pigliucci were right, the inscrutability of the evolutionary, and therefore (to a great degree) biological, forces underpinning human behavior should lead to persistent and irresolvable doubt about why humans behave as they do. Sociological disciplines, by virtue of their inability to disentangle the evolutionary/biological from the social (given, again, that according to Pigliucci the former is scientifically inaccessible in the case of humans), should be just as powerless to illuminate human behavior as the evolutionary behavioral sciences. Perhaps limited proximate-level sociological and social psychological science would still be possible, but certainly the more encompassing and distinctive theories would have to be abandoned. So why have Pigliucci, Gould, Lewontin, and other such radical critics of evolutionary psychology abstained from attacking sociological theorists and scientists?

The most plausible answer to this question appears to be that radical critics are almost all allied to left-wing political causes, to an extent that has distorted their scientific work. Gould and Lewontin's Marxism and its deleterious effects on their "scientific" output are well known, and probably constitute the major reason that many biologists typically regard their pronouncements, as they pertain to human nature, with suspicion (e.g., Alcock 1998; Maynard Smith 1995; Queller 1995; for a philosopher's perspective, see Sesardic 2005). Pigliucci (2010) does not openly express any political biases; but in any case, his work certainly does not offend prevailing leftist academic opinion, e.g., via glaring misrepresentations of *The Bell Curve* discussed above. This is further seen in his evident sympathy to Gould and Lewontin's deeply flawed scientific theorizing. Whereas, again, the overall opinion of Gould and Lewontin among biologists is overwhelmingly negative, Pigliucci (2010) offers only tepid criticisms of Gould (but not Lewontin) and his attacks on evolutionary psychology are general enough to place him squarely in the non- or anti-adaptationist camp that Gould and Lewontin founded, or at least reinvigorated (see Sesardic [2005, p. 57] for more evidence of Pigliucci's positively slanted view of Lewontin; Sesardic

elsewhere [e.g., p. 166] highlights Pigliucci's basic alignment with Gould and Lewontin's research program). (As a general rule, those working in the philosophy of biology, e.g., Pigliucci, regard Gould and Lewontin more positively than do evolutionary biologists. This is perhaps due to Lewontin's academic relationships with many highly influential philosophers of biology of the twentieth and twenty-first centuries, such as Philip Kitcher, Peter Godfrey-Smith, and Elliott Sober.)

But why does leftism, including Marxism, generate among its adherents hostility to biological explanations of human behavior? The answer seems to be that leftism is typically aimed at social and political change or even revolution, usually for the sake of promoting certain forms of equality and freedom. Biological explanations of human behavior, insofar as they imply that there are limits to human behavioral change that cannot be surmounted without genetic change, threaten the social and political aspirations of leftists (Winegard and Winegard 2017). There are cases in which intellectuals on the left have been quite transparent about their fears that human biobehavioral science will have such implications. For example, in her book, *Testosterone Rex*, Cordelia Fine (2017), a feminist psychologist turned philosopher, although ostensibly taking up the *scientific* project of correcting inaccurate views about human sex differences in behavior, ends up revealing moral-political motivations early on in her effort: "Although scientific claims don't tell us how our society *ought* to be, that being the job of our values, they can give us strong hints as to how to fulfil those values, and what kind of arrangements are feasible. . . [I]f the sexes are essentially different, then equality of opportunity will never lead to equality of outcome" (pp. 20–21; emphasis in the original) (tellingly, she goes on to write that her critical target, an account of the biological bases of human behavioral sex differences that she terms "Testosterone Rex," "can appear undefeatable" [p. 22], a phrasing more at home in the world of ideological combat than of science). Anxiety surrounding the apparent tension between human behavioral biology and leftist political agendas has had the unfortunate effect of motivating deliberate (see Alcock 1998)

perversions and obfuscations of science. One of the more salient cases is Gould's corpus, which is largely an effort to restructure evolutionary theory so as to minimize the role of adaptationist explanation in the life sciences and which was also significantly motivated by Marxist politics. What makes this effort remarkable is its signal failure to produce anything resembling a legitimate alternative to adaptationism. As discussed earlier, there is no real "exaptationist research program," despite Gould and Lewontin's efforts, because non-adaptationist forms of evolutionary theory provide no basis for the development of scientific predictions (Figueroa and Berry 2002).

Taken collectively, these considerations suggest that radical critiques of evolutionary psychology, and the broader revisionist projects in evolutionary biology to which they are connected, are not intended to advance scientific understanding at all. Rather, they are efforts to retard or derail the development of science, for the sake of protecting theoretical models of human behavior that the political left favors. This is the most parsimonious explanation of the fact that Gould and Lewontin and related scholars only attack biosocial theories of human behavior, even as they (1) stress the supposed inability of scientists to understand the relative contribution of genetic, or at least evolutionary, factors to human behavior and behavioral variation (which necessarily leaves the *relative* importance of social factors unclear as well) and (2) uncritically present very poorly supported or discredited sociological hypotheses as superior alternatives to biologically informed theories of human behavior, alternatives which are always convenient for leftist causes. An example of this sort of tendentiousness comes from Lewontin et al. (1984): "Strong performance on IQ tests is simply a reflection of a certain kind of family environment" (p. 94). Years before Lewontin et al. published the book in which the foregoing statement appears, it was already known with great confidence, through behavior genetic studies of twins, that family environment accounts for none or virtually none of the variance in IQ among adults, whereas genetic factors were (and continue to be) found

to account for 70–80% of the variance (Jensen 1969; Plomin and Deary 2015). Jensen (1969) reviewed relevant evidence from twin studies well before the publication of Lewontin et al.'s (1984) book; Lewontin et al.'s (1984) attempt to critique Jensen's analysis reduces largely to attacks on the scientific integrity of Cyril Burt, on whose science Jensen partially relied (see Tredoux 2015 and Sesardic 2005 for defenses of Burt), and efforts to explain away the findings of twin studies that were at odds with and ignorant of the science of their day (see Nyborg 2003), and are still recognized as confused and baseless (see Sesardic 2005). Notably, Lewontin et al. (1984) offer no rigorous support for their environmental determinist view of intelligence differences, and subsequent research has borne out Jensen's estimates of the relative importance of the environmental and genetic variance components of IQ (see Plomin and Deary 2015). The only apparent explanation for such flagrant misrepresentation of the then state of intelligence research is that Lewontin et al. (1984) were writing explicitly for the purpose of advancing a Marxist agenda, and such a program for radical and egalitarian societal change is incompatible with genetically rooted inequality in a trait as socially important as intelligence.

Curiously, to the extent that Gould and Lewontin sought to safeguard leftist agendas from progress in the life sciences through their non- or anti-adaptationist program – and there is ample evidence that Gould especially sought to replace ultimate biological/adaptationist models of behavior with proximate environmentalist ones (Alcock 1998) – it is not clear that they would have succeeded in this effort even if their alternative takes on evolutionary biology had fared well. To take one example, Gould was fond of stressing the possibility that genetic drift might account for a great deal of evolutionary change that was allegedly wrongly attributed to selection. But some feature of an organism that comes about through genetic drift is no less rooted in genetics than a feature that emerges through selective processes. Thus if Gould hoped that explaining away selection and adaptation would

legitimately advantage environmentalist explanations of behavior, this was simply without sense. So, assuming that there was some rationality behind his project, it would seem that he really intended to thwart successful biological theorizing by obscuring the nature of evolution so thoroughly as to render it a muddle of causal processes that could not be disaggregated and comprehended. At worst (for Gould) and if it were successful, this would leave scientists in a sort of agnosticism about the role of evolved factors in human behavior; at best, it would have such scientists focus only on proximate and environmental models of human behavior (Alcock [1998] reaches a similar conclusion about Gould's intentions). The psychometrician Chris Brand (1999) identified the same basic strategy among environmental determinists in the IQ debate, who were (and still are) fond of using it to arrest scientific progress, or at least the recognition of such progress, in the camp of their hereditarian opponents: "Instead of seeing themselves as offering a competing social-environmentalist theory that can handle the data, or some fraction of it, the sceptics [i.e., anti-hereditarians or environmental determinists] simply have nothing to propose of any systematic kind. Instead, their point – or hope – is merely that everything might be so complex and inextricable and fast-changing that science will never grasp it" (p. 775).

The philosopher of science Imre Lakatos (1970) drew a distinction between what he termed "progressive" and "degenerating" research programs. Whereas the former generate novel hypotheses and predictions that enable the development of scientific knowledge, the latter merely offer ever more elaborate justifications of existing theories to guard them against disconfirmation; therefore, degenerating research programs do not produce knowledge, because they do not devise novel hypotheses and predictions and thus fail to advance scientific understanding. It should be patent from the details given above that radical critiques of evolutionary psychology are the products of a degenerating research program (or programs, depending on how one wishes to

carve up the pertinent academic terrain). Radical critics, like the skeptics of IQ hereditarianism characterized by Chris Brand, have no serious alternative to evolutionary psychology. They seek only to convince others that empirically impoverished and theoretically garbled, but leftist-friendly, sociocultural theories of human behavior are adequate (even though these have been shown to fail time and again; see, e.g., Boutwell and Connolly 2017; Figueredo et al. 2007; Woodley and Figueredo 2013), or at minimum to cast irresolvable doubt over biosocial explanations, so that the pure environmental determinist models can (appear to) be spared definitive refutation. Therefore it might be said that the radical opposition to evolutionary psychology is *necessarily* degenerative, because it is not in fact concerned with uncovering the true nature of human behavior. From the beginning, it is structured to reach morally and politically desired answers, or in other words to maintain the apparent (to some) integrity of a preconceived (leftist) worldview. While intrinsic critiques will continue to refine and improve evolutionary psychological science, the anti-scientific character of radical critiques will most likely lead to their eventual and unanimous rubbishing among the relevant academics, especially given that particular moral and political biases never retain intellectual hegemony in the long run.

Cross-References

- ▶ [Evolution of Intelligence, The](#)
- ▶ [Genetic Determinism](#)
- ▶ [Group Selection](#)

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Contusion

► Specific Brain Damage

Conventional Form-Meaning Mapping

► Arbitrary

Conventionalization

► Ritual and Speech Coevolution

Convergent Evolution of Cognition

► Convergent Evolution of Intelligence

Convergent Evolution of Dog and Human Social Cognition

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Synonyms

Comparative cognition; Human-dog symbiosis

Definition

The evolution of similar socio-cognitive traits in dogs and humans as a product of shared or similar selection pressures.

Introduction

Domestic dogs and humans have shared a close symbiotic relationship for at least 14,000 years (Nobis 1979). Both species entered into this relationship with complex social systems with a much longer evolutionary history. This likely enhanced mutual compatibility during early dog domestication.

While the details surrounding dog domestication remain an area of active debate, there is evidence that the early dogs were free-living scavengers that exploited a new niche – a nutrient source created by concentrated areas of human waste and refuse – that developed alongside stable human communities (Coppinger and Coppinger 2001). The majority of dogs around the world still exist within this niche. However domestic dogs have also become increasingly integrated into human societies and homes, with as many as 80 million pet dogs in the United States alone (APPA 2014). Dogs are also now employed in a wide range of working roles ranging from hunting, livestock management, and athletic partners to police and military aids, search and rescue, therapy, and service animals. Especially within the last several hundred years, these additional roles have increased the amount of intentional

trait selection imposed on dogs by humans. This long-standing symbiotic relationship between humans and domestic dogs, coupled with reported similarities in some socio-cognitive tests, has raised questions about possible convergent evolution of social cognition between these two species.

Support for Possible Dog-Human Convergent Evolution

Many aspects of human social cognition differ in important ways from humans' closest relatives. This is likely due to a combination of evolutionary and lifetime selection pressures. Certain traits such as the tendency to follow other's gestures and gaze, imitation, cultural practice, theory of mind (or the capacity to recognize that others have different knowledge states from our own), and the use of language are often considered hallmarks of human social cognition (Dunbar 2003). Consequently, much attention has been given to scientific pursuits designed to determine if our closest genetic relatives share some or all of these traits.

In the 1990s some of this focus shifted away from our closest relatives toward one of our closet companions, the domestic dog. While there has been a long history of scientific interest in the behavior of the domestic dog, research on human-dog interactions and canine cognition began expanding rapidly after several studies demonstrated that pet dogs' capacity to follow the pointing gestures of humans surpassed that of nonhuman primates (Hare and Tomasello 1999; Miklósi et al. 1998). These studies were quickly followed by more reports of pet dogs' social responsiveness, including sensitivity to human attentional state, emotional state, vocalizations, as well as an increased tendency to look at humans, especially in cooperative contexts (Udell et al. 2010). In 2005 it was proposed that the seemingly humanlike characteristics of pet dog's social cognition might be explained by convergent evolution with humans, based on the belief that chimpanzees and gray wolves did not share

this same sensitivity to human cues (Hare and Tomasello 2005).

Challenges and Other Considerations

The hypothesis that dog domestication resulted in a more humanlike social cognition has more recently been challenged by data demonstrating that many of these socio-cognitive traits are not unique to dogs or even domesticated species (Range and Virányi 2015; Udell et al. 2010). For example, wolves have been shown to excel on human-guided tasks and form functional attachment bonds to human caretakers if hand reared by humans (Udell et al. 2010). It is also now clear that experience, including socialization during early development and with specific human actions, is an important predictor of whether a dog will develop sensitivity to human actions and to what degree. Dogs with minimal human exposure, and those living outside of human homes in animal shelters or research labs, typically do not perform well on human-guided tasks without additional training (Udell et al. 2010).

Despite this, some findings related to differences in the social behavior and cognition of dogs and wolves have remain robust and appear to correspond with known behavioral, biological, and genetic changes associated with domestication. These differences include exaggerated proximity seeking behavior and extended gaze durations toward companions when compared to wild-type ancestors, elevated oxytocin levels as a result when in contact with human companions, and inhibition of independent problem-solving behavior under ambiguous or social conditions (Udell and Brubaker In Press). Many of these changes appear to correspond with developmental delays associated with the domestication syndrome more broadly, including morphological and behavioral neotony and shifts in the critical period for social development (Lord 2013). Coupled with living conditions that often reward, if not mandate, a pet or working dog's dependence on humans into adulthood, this evolutionary, developmental, and experiential relationships likely contribute heavily to the unique socio-

cognitive skills and depth of cross-species attachment reported within these populations.

Conclusions

While the domestic dog's social cognition has likely contributed to their success in human environments, the degree to which their socio-cognitive tendencies are uniquely comparable to adult humans is debatable. It may be more accurate to suggest that given early exposure to human environments, domestic dogs may retain (into adulthood) aspects of social cognition and attachment behavior more similar to the social cognition of human children than would be typical of wild-type species (Udell and Brubaker in press). This is consistent with what is known about the relationship between domestication and developmental delays. More mature aspects of human social cognition shared by dogs also appear to be shared, and in some cases surpassed, by the abilities of wolves (Range and Virányi 2015). Therefore, if convergent evolution contributed to similarities in dog-human social cognition, this may have occurred prior to domestication. However, research in this area is ongoing, and new developments are likely in years to come, especially given the recent vibrancy of research within this field.

Cross-References

- ▶ Cognitive Ethology
- ▶ Convergent Evolution of Intelligence
- ▶ Cooperation in Social Carnivores
- ▶ Symbiosis and Mutualism

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Convergent Evolution of Hyena and Primate Social Systems

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Definition

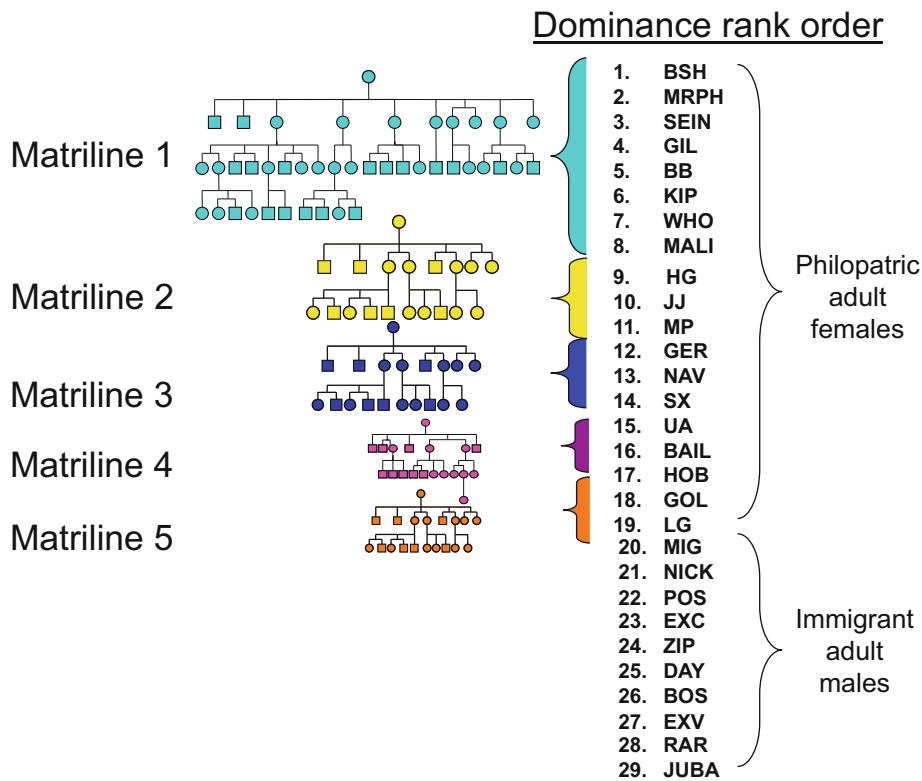
Societies of distantly related mammals may evolve in parallel fashion, along with the cognitive abilities that mediate social interactions, in widely divergent taxonomic groups.

Introduction

The societies of spotted hyenas (*Crocuta crocuta*) are remarkably similar to those of cercopithecine primates, which are old world monkeys such as baboons and macaques. Spotted hyenas are large mammalian carnivores that occur throughout sub-Saharan Africa. Although spotted hyenas last shared a common ancestor with primates roughly 90 million years ago, convergent evolution has produced the same social structures in these two distantly related mammals, and the same cognitive abilities needed to mediate social behavior. With respect to their size and complexity, the societies of spotted hyenas much more closely resemble those of primates than those of other terrestrial carnivores. Like old world monkeys, spotted hyenas live in permanent complex social groups, called clans (Kruuk 1972), which range in size from 20 to 130 individuals. On the prey-rich plains of eastern Africa, hyena group size does not differ appreciably from that of sympatric baboon troops. Furthermore, like most primates, hyenas within each clan can be ranked in a linear dominance hierarchy based on outcomes of agonistic interactions (Fig. 1). Although cercopithecine primates feed mainly on vegetable matter whereas spotted hyenas feed on carcasses of the herbivores they have killed, in both hyenas and monkeys priority of access to critical food resources varies with the social rank of individuals in the group’s dominance hierarchy (Holekamp et al. 2012).

Convergent Evolution of Social Structure

As in monkey troops, all members of a hyena clan recognize one another as individuals using multiple sensory modalities; they also cooperatively defend a common territory and rear their cubs together (Kruuk 1972). Like cercopithecine primates, spotted hyenas establish enduring relationships with clan-mates that may last many years, often spanning multiple decades. Like baboon troops, hyena clans contain multiple adult males and multiple matriline of adult female kin with offspring, including individuals from several



Convergent Evolution of Hyena and Primate Social Systems, Fig. 1 Dominance rank order of matriline within one cohort of adults present in a single large clan of spotted hyenas. As in a baboon troop, the dominance hierarchy of natal animals contains multiple matrilineal kin groups, shown at left; each matriline is represented by a different color. Squares in genealogies represent males and

circles represent females. Although only adult females are shown among the natal animals in the vertical listing at right, offspring are included in the genealogies shown at left; as in baboons, offspring slot into the hierarchy immediately below their mothers. In contrast to the rank ordering in monkey societies, however, all adult female hyenas and their young outrank all immigrant males

overlapping generations (Fig. 1). Breeding males in both taxa are usually immigrants born elsewhere. As in virtually all cercopithecines, male hyenas disperse voluntarily from their natal groups after puberty, whereas females are usually philopatric. As in many monkeys, relatedness is high within hyena matriline but, on average, clan members are only very distantly related due to high levels of male-mediated gene flow among clans. Thus both monkeys and hyenas interact on a daily basis with both kin and non-kin.

As in female cercopithecine primates, the social ranks of female hyenas in the clan's dominance hierarchy are not correlated with size or fighting ability; instead, power in both monkey and hyena societies resides with the individuals

having the strongest network of allies, and ally network size is highest in the highest-ranking matriline (Smith et al. 2010, 2011; Fig. 1). As they grow up in their natal groups, young spotted hyenas assume ranks in the clan's dominance hierarchy that are isomorphic with those of their mothers. As with young monkeys, young hyenas learn their positions in their clan's dominance hierarchy via a process of "maternal rank inheritance," and non-littermate hyena siblings assume relative ranks that are inversely related to age in a primate-like pattern of "youngest ascendancy" (Horrocks and Hunte 1983; Holekamp et al. 2012). Learning is a critical aspect of rank acquisition in both spotted hyenas and monkeys, and individuals clearly remember outcomes of

earlier encounters with particular group-mates. As in primates, coalitions play an important role in acquisition and maintenance of social rank in spotted hyenas (Horrocks and Hunte 1983; Smith et al. 2010). In both hyenas and cercopithecine primates, members of the same matriline occupy adjacent rank positions in the group's hierarchy, and female dominance relations are extremely stable across contexts and time. However, one interesting difference between hyenas and cercopithecine primates in regard to rank is that adult female hyenas dominate adult males (Kruuk 1972, Fig. 1), whereas male cercopithecines dominate females.

As in cercopithecine primates, all female spotted hyenas breed, but their reproductive success varies with social rank. The mechanisms mediating rank-related variation in reproductive success are remarkably similar between old-world primates and spotted hyenas. In both taxa, dominant females use aggression or displacement to gain better access to key resources. As in various primates, high-ranking female spotted hyenas start breeding at younger ages, produce more surviving offspring per unit time, and enjoy longer lifespans than do their low-ranking counterparts, and these differences have profound long-term fitness consequences (Hofer and East 2003; Holekamp et al. 2012). However, as in female baboons (e.g., Silk et al. 2010), the fitness of female spotted hyenas is strongly affected by sociability as well as by dominance rank. Life span is a major determinant of fitness in spotted hyenas, and highly gregarious females live longer than others. Like monkeys, hyenas can also use social strategies to offset certain costs of low rank. For instance, mid- and low-ranking hyenas who associate most closely with higher-ranking individuals are allowed to feed with them most often at ungulate kills (Smith et al. 2011).

Finally, patterns of intragroup cooperation in spotted hyenas are surprisingly similar to those documented among cercopithecine primates. Spotted hyenas often help both kin and non-kin allies defend their resources against alien hyenas or lions, and by doing so may risk serious injury or death (Kruuk 1972). As in baboons (Silk et al. 2010), female hyenas form long-lasting

affiliative relationships with a subset of other females in their clan, with the strongest bonds occurring among close matrilineal kin (Smith et al. 2011; Holekamp et al. 2012). Thus, as in many primates, hyenas have enduring cooperative relationships that affect survival and reproduction of individual group members.

Clearly, spotted hyenas share many aspects of their social biology with old-world primates, indicating that there has been strongly convergent evolution of their societies. Although some primatologists claim that primate societies are more complex than those of other mammals, the characteristics of hyena societies reviewed here suggest otherwise. The striking similarities in the social lives of monkeys and spotted hyenas have also promoted strongly convergent evolution of their abilities in the domain of social cognition (Holekamp et al. 2015).

Convergent Evolution of Social Cognitive Abilities

Cercopithecine primates possess well-developed cognitive abilities that make them unusually adept at predicting outcomes of behavioral interactions among their group-mates (e.g., Cheney and Seyfarth 1990, 2007). They recognize individual conspecifics based on their voices and faces, discriminate kin from non-kin, and may even be able to recognize paternal kin in the absence of paternal care. Nepotism is common in most primates, and kin also form stronger bonds than do non-kin (e.g., Cheney and Seyfarth 1990; Silk et al. 2010). As they mature, monkeys assume their places in the troop's dominance hierarchy through a protracted process of associative learning during interactions with group-mates (e.g., Cheney and Seyfarth 1990; Horrocks and Hunte 1983). They know that group-mates vary in their value as social partners, and they attempt to repair valuable relationships when those are damaged (e.g., Cheney and Seyfarth 1990, 2007). Monkeys clearly remember outcomes of earlier encounters with particular conspecifics, and they modify their social behavior on the basis of interaction histories (Cheney and Seyfarth 1990, 2007).

Furthermore, they possess knowledge about the social ranks of their group-mates and about the social relationships among their group-mates, and base their decision-making in social situations upon this knowledge. Due to convergent evolution, spotted hyenas share all these capabilities with cercopithecine primates.

Spotted hyenas can recognize individual group-mates using visual, acoustic, or olfactory cues (Kruuk 1972). For example, they can identify individual conspecifics and distinguish kin from non-kin, on the basis of their long-distance “whoop” vocalizations, and whoops also convey information about the caller’s age, sex, and motivational state. Hyenas also have a keen olfactory sense; each clan has a unique scent signature, mediated in part by volatile products of metabolism in the symbiotic microbes inhabiting the hyenas’ scent glands, and hyenas can distinguish scents of their clan-mates from those of hyenas from other clans. Spotted hyenas also use olfactory cues to discriminate sex, reproductive state, and familiarity of conspecifics.

Nepotism is common among spotted hyenas; social bonds are stronger among kin than non-kin (Holekamp et al. 2012; Smith et al. 2010), and individuals direct affiliative behavior most frequently towards kin. Although male hyenas do not participate in parental care, sires can recognize their offspring, and vice versa; this most likely occurs via phenotype matching. Furthermore, full sibling littermates associate more closely and direct more affiliative behavior toward one another, than do half-sibling littermates. When deciding whether or not to join on-going fights, female spotted hyenas support close kin most often, and the density of cooperation networks increases with genetic relatedness; nevertheless, as in primates, kinship fails to protect female hyenas from coalitionary attacks (Smith et al. 2010). As in monkeys, hyenas are more likely to attack the relatives of their opponents after a fight than during a matched control period, and after a fight they are more likely to attack relatives of their opponents than to attack other lower-ranking animals unrelated to their opponents.

As in monkeys, spotted hyenas recognize that their social partners vary in relative value to them and that they make adaptive choices regarding

with which clan-mates to associate. Although interactions between male and female spotted hyenas are almost exclusively initiated and maintained by males, females often mate with their closest male associates. Males prefer to associate most closely with the highest-ranking females, whose offspring survive far better than do offspring of low-ranked females, so this preference by males appears highly adaptive, although it is not known how males discriminate female rank. Adult hyenas of both sexes prefer to associate with non-kin holding ranks similar to their own. Furthermore, patterns of greeting behavior in spotted hyenas follow primate patterns of social grooming in which individuals prefer to spend time with, and direct affiliative behavior towards, high-ranking non-kin (Cheney and Seyfarth 1990; Smith et al. 2011).

Spotted hyenas use unsolicited appeasement and greeting behaviors to reconcile their fights. As is also true in many primates, victims in hyena fights are significantly more likely to reconcile than are aggressors. Furthermore, spotted hyenas can recognize third-party relationships among their clan-mates. Third-party, relationships involve interactions and relationships in which the observer is not directly involved. Like monkeys, hyenas can recognize third-party relationships based on either social rank or kinship, and they use this knowledge in adaptive decision-making. Hyenas clearly make flexible decisions regarding whether or not to cooperate or compete with conspecifics, modifying their behavior based on multiple types of information about their immediate social and ecological environments (Smith et al. 2010).

Conclusion

It is clear that convergent evolution has produced remarkable similarities between old-world primates and spotted hyenas, not only with respect to their social lives per se but also to the cognitive abilities that allow animals in both taxonomic groups to successfully navigate their large, complex societies. Although some social cognitive abilities known in primates have not yet been explored in spotted hyenas, the hyenas’ behavior

indicates that they can otherwise solve all the same social problems that primates can solve. Thus it appears that convergent evolution of social complexity promotes convergent evolution of social cognition.

Cross-References

- ▶ Ability to Recognize Individuals
- ▶ Access to Resources
- ▶ Convergent Evolution of Intelligence
- ▶ Cooperative Alliances
- ▶ Dominance and Health
- ▶ Dominance in Humans
- ▶ Status and Dominance Hierarchies
- ▶ Primate Dominance Hierarchies
- ▶ Resource Competition
- ▶ Resource Defense
- ▶ Status and Dominance Hierarchies
- ▶ Status and Redistribution of Resources

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Convergent Evolution of Intelligence

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Synonyms

Convergent Evolution of Cognition

Definition

When two or more distantly related species evolve similar cognitive adaptations in response to comparable environmental challenges.

Introduction

Convergent evolution occurs when two distantly related species evolve a similar trait as a result of experiencing similar environmental conditions. As cognitive traits are equally subject to evolutionary pressures as other biological traits, it may seem intuitive that natural selection would have produced comparable cognitive abilities in a range of species that occupy similar niches. However, the focus on convergent evolution in cognitive research is a relatively recent phenomenon. Instead, studies of animal intelligence have long tended to emphasize the importance of phylogenetic continuity – that is, cognitive similarities stemming from common descent – particularly in the context of understanding the evolutionary origins of human intelligence. Our closest relatives, extant nonhuman primates were long

assumed to be the most logical species group for investigating the evolutionary origins of intelligence (e.g., Byrne 1995). Only more recently has it become apparent that species from dissimilar taxonomic groups, such as corvids and cetaceans, share important aspects of intelligent behavior with primates (Emery and Clayton 2004; Marino 2002). Moreover, almost every cognitive trait present in primates has also been found in taxa ranging from fish to insects (Bshary et al. 2002; Chittka et al. 2012). This entry outlines what is known about the evolutionary pressures that contribute to convergent intelligent behaviors, while highlighting examples of species and behaviors that do not fit current evolutionary predictions. Despite having made progress on evolutionary theory surrounding intelligence, such anomalies illustrate how much more the field has to learn about the conditions that favor intelligence.

What Is Intelligence?

Animals routinely encounter uncertainty in their environments. Fluctuations in resources, in abiotic conditions, or in the behavior of others, can grant a fitness advantage to animals that make adaptive decisions in the face of uncertainty (Dall et al. 2005). From a broad perspective, intelligence involves the neuronally controlled means by which animals can make such adaptive decisions. While there is no consensus on precisely what constitutes intelligence, it is arguably best envisaged as an umbrella term for a range of cognitive abilities that allow animals to employ flexible behavior and extract generalizable rules, instead of having to rely on reflexive stimulus-response reactions or rote learning when conditions change (Byrne 1995; Mackintosh 1988). Under such broad terms, many types of cognitive traits can contribute to intelligence, and how this capacity manifests itself depends on the species and the type of environmental uncertainty they encounter. Evolution could favor specific cognitive adaptations to cope with a set of well-defined ecological challenges (Shettleworth 2010) or could favor more general abilities that could be

used across a variety of contexts, such as associative learning (Heyes 2012). Specific selection for convergent cognitive specializations can be seen, for example, in the enlarged hippocampus and greater spatial memory of food-caching birds (Olson et al. 1995) and scatter-hoarding rodents when compared to closely related, non-food-storing species (Barkley and Jacobs 2007). Meanwhile domain-general forms of intelligence, in which performance in a trait is correlated across multiple contexts, may stem from a variety of evolutionary pressures that are harder to pinpoint. The types of evolutionary questions that can be answered when comparing species' intelligence will be determined by whether investigators measure specific or general forms of intelligence.

How to Measure Intelligence

Since all cognitive traits stem from the brain, variation in brain morphology has clear evolutionary implications for intelligence. The brain is metabolically expensive, and neural tissue growth is evolutionarily conservative, at least in mammals (Finlay et al. 2001). Therefore evolving larger brains or brain regions should give species an advantage that warrants the increased metabolic costs of such structures (Byrne 1995; Herculano-Houzel 2011). Accordingly, greater absolute brain size and relative brain-to-body size have been found to correlate with cognitive ability within species groups (Deaner et al. 2007; Ratcliffe et al. 2006). A common alternative measurement involves comparing the relative size of brain regions that are thought to be linked with intelligent behavior, such as the mammalian isocortex and the avian hyperstratum ventrale (Lefebvre et al. 2004). In contrast to size-related assessments, it has been suggested that comparing the number of neurons within the brain or a brain region of interest better measures the computational power of the brain. This approach has yielded striking examples of convergent evolution in brain morphology. For instance, certain bird species, such as corvids and parrots, have a similar or greater number of neurons in their forebrains than primates have, despite their brain structures

being smaller in size. Therefore these birds may have been able to increase their cognitive capacity by packing a greater number of neurons in their forebrain instead of increasing these brain structures in size like primates did (Olkowicz et al. 2016).

While each of these brain measures are important for understanding the evolution of intelligence, none of them explicitly demonstrate what the brain does with any extra computing power it may have. Without a clear link to the behaviors that enhancements in brain morphology facilitate, it is difficult to connect changes in the brain to impacts on fitness and the evolutionary pressures that favor growth in the size or complexity of neural tissue. Therefore, tests of cognitive ability are a necessary component of comparing intelligence across species.

Since cognition occurs internally, intelligence cannot be assumed to underlie any given behavior without experiments to infer the cognitive mechanisms underlying the behavior. No single cognitive test can measure intelligence as a whole. Instead there are two different ways of assessing intelligence that differ depending on whether researchers focus on understanding cognitive specializations or quantifying domain-general intelligence. Studying adaptive specializations requires hypotheses about which evolutionary pressures would favor a specific cognitive domain, such as spatial memory, and then designing experiments to test that ability. For example, both salmon and sea turtles must navigate long distances in the open ocean in order to return to specific spawning or nesting locations. When tested on their homing abilities, both rely on the geomagnetic field to find their way, suggesting that this uncommon ability is a result of similar navigational challenges (Lohmann et al. 2008). Conversely, researching domain-general cognitive abilities involves conducting a battery of tests that capture a similar underlying trait (such as associative learning or discrimination ability) across multiple contexts. When conducted comparatively, this approach helps determine how much selection in one context, such as cooperative foraging, influences abilities in other contexts, such as spatial discrimination (e.g., Gingsins and Bshary 2016).

Even with a specific test or set of tests in mind, researches face challenges when comparing intelligence across species. Potential morphological or motivational differences between species can confound comparisons. For example, in tests of inferential reasoning abilities, elephants fail to choose the correct option when stimuli are comprised of the traditional auditory cues that are often used for primates, but succeed if the cues are olfactory in nature (Plotnik et al. 2014). Since experiments that are ecologically relevant are most likely to provide evidence for cognitive capacities (e.g., Gingsins and Bshary 2016), tests often need to be fine-tuned when deployed on a new species.

Evolutionary Pressures Favoring Intelligence

Food Availability

If intelligence serves to reduce uncertainty about an aspect of the environment, then increased intelligence should be favored by selection in environments that contain increased uncertainty. One source of uncertainty that all animals must face is in finding food. The reliability and distribution of food differs, which has been suggested to drive specific cognitive mechanisms depending on the type and amount of variability animals must overcome in finding their food. Foragers that must find patchily distributed or moving prey might gain fitness advantages for being behaviorally flexible, planning ahead, or remembering the location and value of particular resources. For example, animals that must remember the location of a specific food source in relation to how it changes over time, such as those that cache perishable food or forage on nonsynchronously ripening fruit, may do better if they are able to integrate such memories in an episodic way. Such theories have been used to explain episodic memory in Western scrub jays that cache food (Emery and Clayton 2004) and the ability of mangabey monkeys to account for the weather since they last visited fruiting trees (Janmaat et al. 2006). Prey distributions may not only influence selection for memory but also bias the way in which animals learn about their current environments. For example, nectar-feeding birds

and bees both face the challenge of maximizing foraging intake when feeding on rapidly depleting nectar sources, and thus both employ a “win-shift” cognitive strategy (i.e., learning to avoid rewarding places) which allows them to avoid visiting empty flowers (Demas and Brown 1995; Sulikowski and Burke 2007).

Seasonality and Habitat Heterogeneity

Abiotic aspects of the environment, such as the harshness of seasonal change, can also select for different cognitive capacities depending on whether an animal endures the changes or migrates to more benign climates. For instance, resident species typically demonstrate greater numbers of novel foraging behaviors, a trait sometimes considered to represent a species’ behavioral flexibility or innovation propensity (Sol et al. 2005). Conversely, migratory bird species commonly show increased long-term spatial memory capacities when compared to residents, enabling them to remember advantageous stop-over sites. Such abilities may, however, come at a cost, as they tend to be less exploratory at those sites and have smaller brains, presumably to help reduce energy consumption (Mettke-Hofmann 2016).

Other habitat variability that animals encounter, such as how quickly habitats change over short distances, can also influence evolutionary pressures on cognitive behaviors. The amount of habitat heterogeneity that species experience has been suggested to influence differences in spatial navigation and route learning, such that populations that occupy more stable environments such as lakes more readily rely on landmarks in navigating. Meanwhile, populations occurring in more variable habitats, such as rivers, appear to learn routes more quickly and rely more on egocentric navigation (Sheenaja and Thomas 2011).

The influence of the abiotic environment and habitat variability does not occur in isolation of other evolutionary pressures. For instance, spatial environmental variability coupled with group living would select for behavioral flexibility and social learning as groups move and adjust to varying environments (Rendell and Whitehead 2001).

This theory would predict that species with low travel costs and reduced territorial restrictions would particularly encounter these types of pressures (Knight 2001). Therefore, assessing the influence of the environment on the evolution of intelligence also requires an understanding of how animals interact with and within that environment.

Sociality

The social environment can generate substantial levels of uncertainty depending on how individuals interact with conspecifics. For instance, social animals may face challenges in responding to others, such as needing to recognize individuals, track relationships, deceive conspecifics, or avoid being deceived themselves. Moreover, individuals may also benefit from cognitive strategies to maximize the fitness gains obtained through learning from or cooperating with conspecifics. Abilities that allow animals to tackle these challenges or take advantage of these opportunities fit into the category of social intelligence or social cognition. Such abilities include being able to follow the gaze of others to determine where their attention lies, to imitate other’s behavior, and to understand what others may be thinking (Theory of Mind). According to the “Social Intelligence Hypothesis,” or the “Social Brain Hypothesis,” social environments that contain more of these challenges and opportunities select for such cognitive abilities (Humphrey 1976). For example, species such as primates, hyenas, and ravens all live in dynamic social groups that contain dominance hierarchies and would therefore be subject to similar evolutionary pressures. Accordingly, each of these species are able to understand relationships between two outside individuals (third party relationships) and to infer what those relationships mean for oneself (Engh et al. 2005; Massen et al. 2014). Moreover, the challenges of the social environment are not restricted to terrestrial animals, as different species of bony fishes display many behaviors indicative of social intelligence in primates, such as cooperative hunting, individual recognition, and social learning, arguably because they face similar social dilemmas (Bshary et al. 2002).

Despite the existence of examples where social systems seem to predict certain cognitive abilities, the “Social Intelligence Hypothesis” is still under scrutiny. Aspects of social intelligence, such as social learning, have been documented in solitary species such as a tortoise (Wilkinson et al. 2010). Additionally the generality of evolutionary pressures in the social domain is also contentious when subject to broader comparative analyses. For example, although the enlarged mushroom bodies (higher brain structures) of social insects have been suggested to stem from pressures of their colonial living, many other nonsocial insects share neuronal structures of a similar size or have similar learning abilities (Roth 2015). Moreover, phylogenetic analyses show that evolutionary pressures associated with a parasitoid lifestyle, such as host-finding behavior and central place foraging, better explain these brain morphology changes (Farris and Schulmeister 2010). Such anomalies and the current variation in intelligence seen across species with similar social structures indicate that social systems are not the only evolutionary driver of intelligent behavior, even in the social domain.

Life History Traits

Life history traits help determine whether animals would benefit from enhanced cognitive capacities, because they dictate how animals interact with their environments. An animal’s life span, and their length of juvenile development, for example, have both been implicated as having importance for intelligence. A long life-span coupled with menopause has been suggested to favor social learning, long-term memories, and group-specific or cultural behavior in orcas, short-finned pilot whales, and humans (Brent et al. 2015). A shorter lifespan, in contrast, could help explain why some species may not express traits predicted by their foraging ecology. For example, despite suggestions that nomadic species may experience convergent selection for long-term spatial memory to help remember foraging sites, such a memory would not be useful for species of seed-eating birds that do not live long enough to experience a full seed cycle (Mettke-Hofmann 2016). The duration of development during the lifespan is

also important. Prolonged infant development is necessary to support the growth of a large brain and extended period of learning. Therefore lengthy gestation and juvenile dependence (i.e., the lifestyle of *k*-selected species) often characterizes species with larger brains and those assumed to be more intelligent (Rushton 2004).

Convergence Across Multiple Cognitive Domains

Specific cognitive adaptations are much easier to explain in relation to the pressures of the ecological and social environment than examples of domain-general intelligence are. Although some species are considered to be “jacks of all trades” in their intelligence, they share many of the same environmental pressures which are often implied in influencing specific cognitive traits. For example, primates, odontocete cetaceans (toothed whales), parrots, and corvids all live in complex social groups, forage on spatially or temporally variable foods, have relatively larger, more complex or more neuronally dense brains, and have longer periods of development in comparison to closely related species. Moreover, all of these species show impressive performance in various cognitive tests in the physical and social domains (Emery and Clayton 2004; Marino 2002). Identifying what combination of evolutionary pressures triggered similar levels of intelligence in corvids, cetaceans, and primates would be useful in understanding what contributed to the evolution of human cognitive abilities. However, it is not yet clear to what extent selection in one domain – social intelligence, for example – influences cognitive flexibility in other domains, although social intelligence has been suggested to foster other aspects of intelligence (Humphrey 1976). Therefore, it is unknown whether a certain combination of ecological factors promotes domain-general intelligence and the lack of others facilitates modular selection for a specific cognitive trait.

The identification of broad convergence in intelligence across several taxa is useful for supporting the argument that intelligence may have evolved independently in multiple clades.

However, despite the discovery of these convergent traits across primates, cetaceans, and large-brained birds, the evolutionary explanations for their intelligence has been a largely post hoc process. Regardless of whether resource, climatic, or social uncertainty is under scrutiny, phylogenetically broad investigations are necessary for verifying hypotheses about the evolutionary mechanisms that favor intelligence (MacLean et al. 2012). Meanwhile, evolutionary theory has yet to catch up with the growing body of examples where cognitive traits appear in unlikely species. Incredible examples of intelligent behaviors in species with smaller brains and less “complex” social systems and environments prove there is much more to learn about the drivers of intelligent behavior. Therefore, investigations have yet to tease apart enough evolutionary mechanisms or study intelligence across enough species to fully understand the ecological drivers of intelligent behavior.

Conclusion

The growing evidence for convergent intelligence across diverse taxa highlights the importance of cognitive research in nonprimate species. Undue focus on phylogenetic continuity – concentrating research on the cognitive abilities of our primate relatives – may limit our understanding of human cognitive evolution when lesser related taxa may serve as better models for human traits. For example, human language learning arguably shares greater structural and genetic similarities with birdsong than with communication in apes (Berwick et al. 2011). In addition to understanding our own evolution, a convergent approach to intelligence will help uncover the common environmental drivers of intelligence across the animal kingdom. As the field continues to progress, the use of phylogenetic analyses will allow us to better discriminate convergence versus cognitive similarity due to common descent. Such an approach will likely reveal other evolutionary influences on intelligence that have not yet been considered.

Cross-References

- ▶ [Anthropomorphism](#)
- ▶ [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- ▶ [Evolution of Intelligence](#)
- ▶ [General Intelligence Factor *G* \(Reader, Hager, and Laland, 2011\)](#)
- ▶ [Individual Differences](#)
- ▶ [Inhibition](#)
- ▶ [Mirror Self-Recognition](#)
- ▶ [Nonhuman Intelligence](#)
- ▶ [Nonhuman Tool Use](#)
- ▶ [Relative Brain Size, Encephalization Quotient](#)
- ▶ [Social Intelligence Hypothesis, The](#)

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Convergent Evolution of Intelligence Between Corvids and Primates

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Synonyms

Cognitive ornithology; Cognitive primatology;
 Comparative cognition in corvids and primates;
 Evolution of intelligence

Definition

Convergent evolution describes the analogous (as opposed to homologous) acquisition of similar traits in phylogenetically diverse species facing similar selection pressures. Corvids and primates are often observed to exhibit highly intelligent behavior (with intelligence typically operationalized in this context as those behaviors that indicate the presence of advanced capacities once thought unique to humans or cognitive capacities which surpass those of humans). This led Emery and Clayton (2004) to identify primates and corvids as a case of convergent evolution of intelligence, citing the two groups' capacity for causal reasoning, cognitive flexibility, imagination, and prospection as the key ingredients of a shared cognitive toolkit.

Introduction

Primates and corvids comprise some of the most enigmatic study species in the field of comparative cognition. These two groups have produced some of the strongest claims of advanced intelligence among non-human animals. Wolfgang Köhler's *The Mentality of Apes* (1925) argued for a level of intelligence in apes that was primitive relative to that seen in humans but nevertheless sufficiently advanced as to justify the term *intelligent*, an adjective not afforded to any other non-human animal at the time. Nearly 100 hundred years later, Emery and Clayton (2004) published *The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes*, a clear reference to Köhler's seminal work. They observed the large brains (relative to body size) of both groups and argued that the cognitive feats observed in corvids were comparable to those previously celebrated in apes as indicative of advanced intelligence.

What Is Advanced Intelligence?

What constitutes advanced intelligence is a controversial and complex issue (Sulikowski and Burke 2015). Episodic memory, theory of mind, planning, and tool manufacture have all been nominated as feats of advanced intelligence. It is no coincidence that these same abilities are also those that have been indicated (at one point in time) as uniquely human traits. Reports of such advanced cognitive feats in non-human animals (such as the examples cited below) are thus frequently framed as breaking down the discontinuities between abilities (once) thought to be uniquely human and the cognitive abilities of animals more broadly. This anthropocentric perspective of what constitutes advanced intelligence derives from the study of intelligence in primates (described below).

When they first suggested that corvids and apes constituted a case of convergent evolution of intelligence, Emery and Clayton (2004) highlighted examples of corvid cognition from these categories to demonstrate that corvids

exhibited cognitive feats comparable to those seen in apes. They also referred to examples of transitive inference (being able to conclude that A is larger than C, based on knowledge that A is larger than B and B is larger than C) and the extensive spatial memory required to support cache recovery. They argued that four “cognitive tools,” present in both apes and corvids, were necessary and sufficient to support the evolution and development of such complex cognition:

- *Causal reasoning* (this includes reasoning about the physical causes of object-object interaction outcomes, such as occurs during tool use, and also to reasoning about the intentions and motivations of others, necessitating an attribution of agency to others)
- *Flexibility* (the ability to act on information flexibly by generalizing rules learned in one scenario to a novel circumstance or object)
- *Imagination* (the capacity to mentally perceive objects and stimuli that are not currently available to the senses, it would permit contemplation of problems not immediately present and may also support functions like cognitive maps, which require an integrated knowledge of disparate locations which are never simultaneously present)
- *Prospection* (somewhat related to imagination and potentially arising out of it, prospection describes the specific simulation of future events, permitting an individual to act purposefully in accord with future, rather than current, needs and motivations)

Therefore, intelligence in this instance is most appropriately operationalized as the cognitive feats (episodic memory, theory of mind, planning, tool manufacture, transitive inference) that provide evidence of Emery and Clayton’s cognitive tools (causal reasoning, flexibility, imagination, and prospection).

Intelligence in Primates

The study of intelligence in primates has unavoidably anthropocentric roots. Much research on the

cognitive capacities of primates focuses on the comparison between what humans do and what primates can achieve. Against the backdrop of an early twentieth-century presumption of a unique and superior human intellect that was qualitatively unlike that seen in any non-human animal, Koehler’s (1925) work was the first to suggest that another animal, the chimpanzee, may possess a mind capable of the flexibility, creativity, and insight (that was) intuitively recognized as intelligent (albeit not necessarily to the extent seen in man). Much latter-half twentieth-century primate cognition research was guided by a tacit agenda to deconstruct the notion of human uniqueness by closing the cognitive gap between humans and great apes (discussed in Povinelli and Bering (2002)). This was achieved via demonstrations in chimpanzees (and other primates), of cognitive abilities previously presumed to be unique to humans, including theory of mind (the capacity to appreciate that other individuals experience their own perceptions and goals that are independent of your own, reviewed by Call and Tomasello (2008)) and causal reasoning about the physical properties of objects (primarily as pertaining to tool use, reviewed by Call (2010)).

Intelligence in Corvids

Studies of corvid cognition rose to prominence much later in the twentieth century. They appeared against a backdrop of theoretical focus on ecologically adaptive specializations of cognition. Not anthropocentrically motivated, hypotheses were derived and tested based on the selection pressures species were presumed to face. In corvids, initial investigations focused on cognitive adaptations that may have arisen to support foraging. Clark’s nutcrackers recover tens of thousands of seeds, months after caching (necessitating exceptional spatial memory), and New Caledonian crows manufacture specialized hook twig tools and stepped-cut leaf tools to retrieve prey from holes and crevices, implying a causal understanding of the physical effects of the tools (reviewed in Taylor (2014)).

Observations of tool manufacture and use, in particular, invited comparisons between primate

and corvid intelligence (Emery and Clayton 2004; Lefebvre et al. 2004). This motivated further investigations of corvid cognition, focused on demonstrating the nominally intelligent behaviors to date observed only in humans and non-human primates. Subsequent evidence of episodic memory (termed episodic-like memory when observed in non-human animals, since episodic memory itself is a term reserved for human cognition and implies a subjective experience not necessarily observable in non-human animals, reviewed in Salwiczek et al. (2010)), planning (Raby et al. 2007), and theory of mind (reviewed in Taylor (2014)) emerged.

Selection Pressures Leading to Advanced Intelligence in Primates and Corvids

Two broad theories have been put forward to account for the advanced intelligence reported in apes and corvids. The first identifies ecological selection pressures (especially those derived from tool use and manufacture to support innovative foraging behaviors) as the primary drivers behind both larger brains and advanced intelligence (Lefebvre et al. 2004). Within both primates and birds (including but not restricted to corvids), innovative foraging behaviors predict larger brains (especially areas in the forebrain associated with higher-order integration of information) and greater propensity for tool use (Lefebvre et al. 2004). The need to innovate new foraging behavior and to create novel tools could create selection pressure for all four of Emery and Clayton's (2004) cognitive tools to emerge. Flexibility of behavior and prospection (foreseeing the consequences of novel actions) would both promote innovation. Causal reasoning (about the interactions between physical objects) and imagination (to support the insight required to use or fashion novel objects into tools) were argued by Clayton and Emery to be critical to the evolution of tool manufacture and use. Relationships between innovation, brain size, and tool use within other (non-corvid) avian clades suggest that the potential convergent evolution Emery and Clayton

described between corvids and primates may extend to other larger-brained and innovative avian species (including parrots and woodpeckers).

The second theory, known as the social intelligence hypothesis, identifies selection pressures derived from complex social interactions as the key driving force (Holekamp 2007). While social complexity predicts brain size and innovation well in primates, the same is not true for corvids (or birds more generally; Holekamp 2007). As such the applicability of the social intelligence hypothesis to corvids may be limited. Observations of hyenas, who live in complex hierarchically structured social systems, have relatively larger brains than other less socially complex carnivores, and use transitive inference to deduce social ranks of conspecifics, suggest that, within mammals, the social intelligence hypothesis may apply outside primates as well (Holekamp 2007).

These theories ought not to be considered as necessarily mutually exclusive. It is possible, even likely, that selection pressures derived from multiple sources have acted on the brains and cognition of both crows and primates to convergently produce advanced intelligence in these groups. Social complexity may have played a less prominent role in brain enlargement in corvids than in primates; corvids (western scrub jays) nevertheless exhibit evidence of advanced social cognition, in the form of theory of mind (reviewed in Taylor (2014)). As such, the relative contribution of selection pressures derived from social and nonsocial complexity may differ between primates and corvids, but the resulting advanced intelligence manifests comparable ways.

Conclusion

Claims of convergent evolution of intelligence in corvids and primates rest primarily on demonstrations of cognitive feats in both groups that meet intuitive (and somewhat traditional and anthropocentric) notions of advanced intelligence. These include demonstrations of planning, theory of

mind, tool manufacture and use, and episodic memory – all skills once considered unique to humans. Emery and Clayton (2004) proposed that these skills are supported by four cognitive tools (causal reasoning, flexibility, imagination, and prospection), which evolved convergently in corvids and primates. Selection pressures that may have led to these tools include those derived from innovative foraging behavior (especially that involving tools) and from the cognitive complexities involved in navigating social interactions within a large group of conspecifics. Broader comparisons, across other avian and mammalian groups and species, lend support to both possibilities and suggest that the convergent evolution of intelligence observed in corvids and apes may extend to other large-brained, innovative, and social groups of species.

Cross-References

- Bird Tool Use
- Causal Reasoning
- Convergent Evolution of Hyena and Primate Social Systems
- Convergent Evolution of Intelligence
- Corvids
- Non-Human Primates
- Nonhuman Tool Use
- Primate Tool Use
- Social Intelligence Hypothesis, The

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Convolution

- Metaphor and Analogy

Cooperation

- Alarm Callers Are Females with Greatest Genetic Representation
- Altruism
- Altruism Advertises Generosity
- Altruism Defined by Benefits Conferred
- Evolution of Human Sociality, The
- Evolution of Reciprocal Altruism
- Gossip and Indirect Reciprocity
- Group Living
- Indirect Benefits of Altruism
- Ingredients of Reciprocal Altruism
- Investment Versus Future Payoff
- Language and Economic Cooperation
- Male Coalitions for Hunting
- Moral Tribes
- Peer Competition and Cooperation

- ▶ Prosocial Behavior
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reputation and Altruism
- ▶ Significance of Helping
- ▶ Social Cognition and Communication in Chimpanzees and Bonobos
- ▶ Social Skills
- ▶ Wild Justice

Cooperation Among Fishes

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Synonyms

[Alliance](#); [Altruism](#); [Coalition](#); [Helping](#); [Mutualism](#); [Reciprocity](#)

Definition

Cooperation is the performance of a behavior by one individual that provides a benefit to another individual – thereby increasing the recipient's probability of survival or reproduction – and is selected for due to the actor receiving a benefit from the behavior's recipient. In fish, cooperative behavior has been observed in a variety of contexts – including group foraging, cooperative breeding, and anti-predator behaviors – and is maintained by a number of evolutionary mechanisms.

Introduction

The paradox of cooperation has proven to be one of the most enduring questions within evolutionary biology – that is, how can natural selection favor behaviors that may incur costs upon the performer while enhancing the relative survival and reproduction of another individual. An

enormous body of theoretical work has built up over the years proposing a variety of answers regarding both the evolutionary function of cooperation and the proximate mechanisms that maintain or promote it (e.g., Hamilton 1964; Trivers 1971; Axelrod and Hamilton 1981; Noë and Hammerstein 1994; Connor 1995; Ohtsuki et al. 2006; Clutton-Brock 2009; Kingma et al. 2014).

Over the past few decades, fish have become valuable model organisms for the study of cooperation within nonhuman animals due to several reasons. A vast diversity of social systems, morphologies, and life histories can be found within fish (Magnhagen et al. 2008) and many species have been shown to possess impressive cognitive abilities (Brown et al. 2011). Furthermore, fish species often lend themselves well to observation and experimental manipulation under both laboratory and field conditions (see examples within Brown et al. 2011).

Here, representative examples of cooperation among fish will be discussed in terms of the evolutionary mechanisms thought to maintain them. Following Clutton-Brock (2009), these mechanisms include: (1) kin selection, (2) reciprocity, (3) mutualism, and (4) manipulation. In each case, the evolutionary mechanism will be introduced and then relevant examples among fish will be presented. These evolutionary mechanisms are not mutually exclusive; frequently, more than one may help to explain the maintenance of cooperation within a given species or behavioral context. Nevertheless, the above categorization presents a useful framework that highlights relevant mechanistic distinctions while remaining broad enough to avoid over-emphasizing semantics.

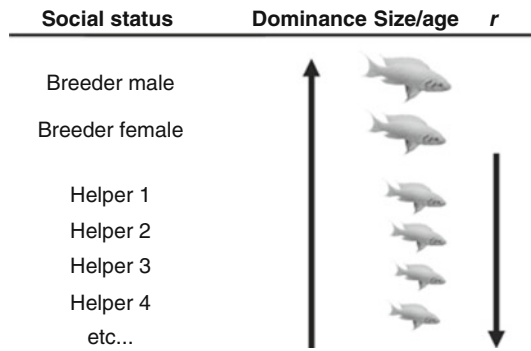
Kin Selection

The concept of an individual's inclusive fitness is critical to understanding the evolution of cooperation between related individuals (Hamilton 1964). Inclusive fitness partitions an individual's fitness – i.e., its genetic contribution to future generations – into direct and indirect sources. Direct fitness benefits are gained as a result of an

individual's own reproductive success, while indirect fitness benefits result from assisting non-descendant relatives who propagate genes identical by descent to the actor's own. Hamilton's rule proposes that cooperation will be selected for when $rB - C > 0$, where r is the coefficient of relatedness between the actor and the behavior's recipient(s), B is the benefit to the behavior's recipient(s), and C is the cost to the actor (Hamilton 1964). If a behavior involves some cost to the actor and it is directed at individuals beyond the actor itself, then the behavior must benefit an actor's blood relatives (who share some proportion of the actor's genes) for it to be favored by natural selection. For this reason, this evolutionary mechanism is known as kin selection.

For kin selection to operate, individuals must be able to differentially allocate assistance towards kin over nonkin. Kin recognition has been documented in a number of fish species, including Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Brown and Brown 1992). In both of these species, individuals display reduced aggression and greater levels of tolerance towards kin relative to nonkin, as well as establish smaller territories when their territories border those belonging to kin (Brown and Brown 1993). These cooperative individuals recoup the costs of increased competition through the indirect fitness benefits gained by helping their kin to survive and reproduce.

When animals live in stable groups with related individuals, kin selection can promote cooperative behavior between group members. Such stable groups often occur within cooperatively breeding species. Cooperative breeding is when subordinate individuals forgo reproductive opportunities and help to raise offspring of dominant breeders (Wong and Balshine 2011; Kingma et al. 2014). Within fish, the best studied cooperative breeder is the Lake Tanganyikan cichlid, *Neolamprologus pulcher* (Wong and Balshine 2011). Groups of *N. pulcher* defend small territories containing rocky terrain that provides shelters and breeding sites. On a territory, there is a pair of dominant breeders and anywhere from zero to 20 subordinate helpers (Fig. 1). Helping



Cooperation Among Fishes, Fig. 1 The social organization of a cooperatively breeding group of *Neolamprologus pulcher*. The pair of dominant breeders tends to be the largest individuals in a group. Subordinate helpers are arranged in a size-based dominance hierarchy below the breeders, where larger helpers are dominant over smaller helpers. Relatedness to the breeder pair, r , is on average higher in smaller helpers compared to larger ones (Reprinted with permission from John Wiley & Sons, Inc. © 2011)

in this species involves: (1) territorial defense against predatory fish, conspecific intruders, and egg predators, (2) territorial maintenance, such as excavating shelters, and (3) egg care (Wong and Balshine 2011).

Helping in *N. pulcher* is a complicated affair, where the costs and benefits of cooperative behaviors vary based on sex, body size and condition, relatedness, and opportunities for dispersal to nearby territories (reviewed in Wong and Balshine 2011). When helpers are related to breeders, kin selection may promote helping behavior by providing indirect fitness benefits to the helper. In *N. pulcher*, smaller, younger helpers are more likely to be related to the breeding individuals (Fig. 1; Dierkes et al. 2005). When subordinates were experimentally removed from their group – thus preventing them from helping – smaller helpers remaining with the group compensated for this absence by increasing their helping efforts, while the efforts of larger helpers remained unchanged (Brouwer et al. 2005). These results are consistent with the hypothesis that smaller subordinates are more likely to assist in caring for the breeders' offspring as a result of gaining indirect fitness benefits from facilitating the reproductive efforts of kin.

Reciprocity

While cooperation between related individuals can be understood in terms of inclusive fitness benefits, cooperation between unrelated individuals poses more of an evolutionary conundrum. One proposed solution which has received a great deal of theoretical and empirical attention over the past several decades has been reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Clutton-Brock 2009). Direct reciprocity – Trivers’ (1971) “reciprocal altruism” – models cooperation between unrelated individuals as an exchange of assistance. Individual A incurs a cost to itself in order to provide a benefit to individual B with the expectation that B will return the favor in the future by providing some benefit to A that outweighs the initial cost. However, reciprocity is not without risks, as the time lag between providing assistance and receiving benefits in return can be exploited by cheaters who benefit from receiving help but do not pay the costs to reciprocate the favor.

The evolutionary dynamics of direct reciprocity resembles the game-theoretic model known as the Prisoner’s Dilemma (Fig. 2). In this model, two players decide either to cooperate with the other player or to cheat via defection. This decision is made by each player without knowledge of

what their partner will choose. Mutual cooperation provides a greater payoff to both players than mutual defection. However, the greatest payoff occurs for a player if they defect when their partner chooses to cooperate, while the cooperator in this scenario receives the worst payoff. If partners play only one round of the game, the only evolutionarily stable solution is for both players to defect in order to avoid paying the costs associated with being cheated. However, in an iterated Prisoner’s Dilemma, in which players play several rounds of the game together, a number of cooperative strategies can emerge (Axelrod and Hamilton 1981).

Tit-for-tat (TFT) is the most well-known solution to the iterated Prisoner’s Dilemma (Axelrod and Hamilton 1981). The TFT strategy is to cooperate on the first round of the game and to copy your partner’s last move in subsequent rounds. In game-theoretic terminology, TFT is “nice” in that it starts out being cooperative, “retaliatory” in that it will defect in response to being cheated, and “forgiving” in that it will resume cooperation if its partner does. This combination of factors allows TFT to potentially reap the benefits of mutual cooperation, while avoiding unbroken strings of being cheated.

Several authors (e.g., Milinski 1987; Dugatkin 1991) have interpreted the dynamics of joint predator inspection in fish as matching those of an iterated Prisoner’s Dilemma (Fig. 2). Predator inspection occurs when one or more fish leave the safety of the shoal and approach a potential predator in order to assess the level of threat it represents. When two or more individuals engage simultaneously in this behavior, it can be viewed as an act of cooperation (Milinski 1987; Dugatkin 1991; Croft et al. 2006). Two individuals inspecting a predator together both receive the benefits of inspection – such as gathering information about the likelihood of an attack – while sharing the potential costs by decreasing the probability that any one inspector will be pursued by the predator. However, individuals that do not inspect a predator – or those that hang back during inspection and continuously allow their partner to take the dangerous lead position – are able to gain information from remotely observing inspection

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	R = 6 Benefit of mutual cooperation	S = 0 Cost of being cheated
	Defect	T = 9 Temptation to cheat	P = 3 Cost of mutual defection

Cooperation Among Fishes, Fig. 2 The payoff matrix for the Prisoner’s Dilemma from the perspective of Player 1. To satisfy the criteria of the Prisoner’s Dilemma, $T > R > P > S$. Mutual cooperation is more beneficial than mutual defection. However, the best payoff is obtained if Player 1 defects – i.e., cheats – in response to Player 2 cooperating, while the worst payoff is for Player 1 to cooperate when Player 2 defects

bouts. This allows for potential defection by allowing one's partner to bear the costs of inspection, while still benefiting from the information gained through their efforts. If no individual inspects, no information can be gained about the potential predator.

During joint inspection events, three-spined sticklebacks (*Gasterosteus aculeatus*) (Milinski 1987) and Trinidadian guppies (*Poecilia reticulata*) (Dugatkin 1991) adopt behavioral strategies that may represent a form of TFT reciprocity. When presented with a potential predator, Dugatkin (1991) found that pairs of guppies initiated inspection events at similar times to one another, lead fish within an inspecting pair were more likely to turn back from the predator than the lagging individual, and after retreating, these former leaders were more likely to wait for their partner to advance before once more advancing themselves. Dugatkin (1991) interpreted these patterns as representing the key qualities of the TFT strategy: "niceness", "retaliation", and "forgiveness," respectively.

Reciprocity is more likely to evolve if cooperators are able to associate preferentially with other cooperators and thereby avoid the potential costs of being cheated. Croft et al. (2006) quantified the social network of a wild guppy (*P. reticulata*) population and found stable, long-term associations between pairs of females that could persist for up to at least 1 month. When pairs of guppies from this population were observed within a predator inspection context, pairs of strongly associated females were more likely to act in a cooperative manner – e.g., more frequently exchanging lead positions during inspection – than weakly associated females. These results suggest that guppies may be able to preferentially associate with cooperative individuals and thereby reduce the potential costs of cooperation.

While joint predator inspection may represent a form of reciprocity, this interpretation has not been without criticism (Connor 1995, 2010; Clutton-Brock 2009). In particular, clear evidence is lacking that predator inspection behavior has been selected to provide benefits to a cooperator's partner(s) or that acting cooperatively in this context incurs net fitness costs to an individual at the

time it occurs (Clutton-Brock 2009). It has been suggested that joint predator inspection may be more parsimoniously viewed as a form of cooperation based on mutualism (Connor 1995).

Mutualism

Whereas reciprocity involves net fitness costs to an individual at the time that it offers assistance to another, cooperation based on mutualism generates inevitable shared benefits to all parties involved (Connor 1995; Clutton-Brock 2009). For example, cooperative foraging may increase the per capita success of each individual forager relative to that which they would experience when foraging alone. By garnering inevitable benefits from engaging in cooperative behavior, mutualism removes the temptation for individuals to cheat by withholding their cooperation. Cooperation based on mutualism may also be cognitively simpler to employ than reciprocity, as there is no need to remember the identities and past behavior of potential cheats. For this reason, mutualisms are predicted to be widespread in the animal kingdom (Clutton-Brock 2009).

Group foraging has been observed in numerous fish species and can range from fairly uncomplicated situations in which individuals travel together as a hunting group but do not coordinate with one another in terms of detection or capture of specific prey items (e.g., Arnegard and Carlson 2005) to more complex associations in which individuals coordinate to capture a particular prey item and can undertake different behavioral roles during a hunt (e.g., Bshary et al. 2006; Strübin et al. 2011).

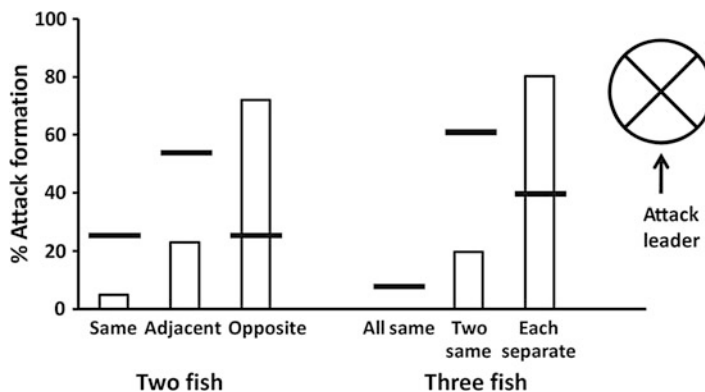
The weakly electric African mormyrid fish, *Mormyrops anguilloides*, form nocturnal hunting groups and detect their cichlid prey via distortions in self-generated electric fields (Arnegard and Carlson 2005). Foraging success was greater in hunting groups as compared to lone foragers, though *M. anguilloides* within groups did not appear to coordinate their hunting efforts during capture attempts. It may be that improved foraging success within groups resulted from failed capture attempts by one hunter generating capture opportunities for other group members.

Collaborative hunting has been observed in the yellow saddle goatfish (*Parupeneus cyclostomus*), where stable foraging groups hunt for piscivorous prey within coral reefs (Strübin et al. 2011). During a hunt, prey fish are often chased into crevices and other shelters within the reef. When this occurs, members of the hunting group are more likely to adopt positioning that maximizes the group's ability to cut off potential escape routes (Fig. 3). This level of coordination suggests individual goatfish adopt different roles during a hunt – i.e., directly chasing prey versus blocking off potential escape routes – and the role that an individual adopts in any given hunt varies depending upon context.

Both of the examples described above represent likely cases of individuals generating coincidental benefits for their group mates as a result of their own self-serving behavior (Connor 1995). For example, when a group of yellow saddle goatfish are chasing a prey item, the individual that initiated the chase is likely to be nearest to the prey and therefore most likely to succeed at capturing the prey via direct pursuit. Other group members are unlikely to overtake the lead fish. However, by deviating from the path of pursuit to cut off potential avenues of escape, they may on average enhance their own

capture probability. Such coordination is likely to increase the average hunting success of a group, thereby generating shared benefits for each hunter.

While cooperative breeding groups often involve individuals providing assistance to non-descendant kin, in which cooperation can be maintained by indirect fitness benefits (see above), unrelated individuals may also provide help in some cooperatively breeding species (Wong and Balshine 2011; Kingma et al. 2014). The group augmentation hypothesis may help to explain cooperative breeding under some of these circumstances. Group augmentation occurs when subordinate nonbreeders help to raise their group's reproductive success and gain direct fitness benefits, such as an increased probability of survival, by being part of a larger group (Kingma et al. 2014). For group augmentation to function, it requires that: (1) helpers contribute to greater reproductive success for breeders, (2) at least some offspring remain within the group, and (3) living within a large group provides benefits to its members. When these group-living benefits result from the inevitable self-serving behavior of other group members, helping behavior can be selected for even in individuals unrelated to the breeders.



Cooperation Among Fishes, Fig. 3 Hunting groups of yellow saddle goatfish that had cornered prey within a coral refuge were more likely to adopt positioning that maximized spatial distance between individuals and minimized probability of prey escape. A prey refuge is represented by a circle divided into equal quadrants, with the location of the individual who initiated pursuit indicated. In hunting groups made up of two fish, maximal

interindividual distance would constitute adopting positions 180° opposite of one another. In groups of three fish, individuals should position themselves each within a separate quadrant. Shown are the frequencies expected if individuals positioned themselves at random (black lines) and the observed frequencies (bars) (Reprinted with permission from John Wiley & Sons, Inc. © 2011)

Helping in the cooperatively breeding cichlid, *N. pulcher*, does appear to meet the general criteria required for group augmentation to function. Helpers in *N. pulcher* contribute to greater reproductive success for breeder individuals, in that groups with more helpers successfully reared more young (Balshine et al. 2001; Brouwer et al. 2005). Further, there is some degree of philopatry in this species, meaning that offspring often remain with the group for some amount of time (Dierkes et al. 2005). This is important in that some of the effort put towards raising offspring results in increased group size in the future. Finally, larger group size in *N. pulcher* correlates with reduced predation risk and increased survival for both breeders and helpers (Balshine et al. 2001; Heg et al. 2004).

By engaging in helping behavior, helpers in *N. pulcher* can generate benefits for themselves. In the short-term, some acts of cooperation generate immediate benefits to the helper individual, such as by reducing predation risk through shelter excavation (Heg et al. 2004). Eventually, those young that survived as a result of the helper's assistance can benefit the helper through dilution effects – i.e., providing safety in numbers – as well as engaging in predator vigilance and assisting in territorial defense (Balshine et al. 2001; Heg et al. 2004). While there is a time lag between the assistance provided to help rear young and the eventual benefits generated by those young, there is no risk of exploitation as there is in reciprocity-based cooperation. Offspring that remain in the group will enhance the fitness of the helper simply by acting in self-serving ways.

Manipulation

Manipulation involves inducing other individuals to engage in cooperative behavior that either increases the manipulator's fitness or avoids outcomes that conflict with the manipulator's interests (Clutton-Brock 2009). An excellent example of such manipulative tactics can be found by examining the relationship between the cleaner wrasse (*Labroides dimidiatus*) and its clients.

Cleaner wrasse establish cleaning stations on coral reefs throughout the tropical Indo-Pacific and consume the ectoparasites of client fish who visit these stations (Trivers 1971). However, the wrasse actually prefers to consume its client's mucus instead of its ectoparasites, thereby establishing a conflict of interest (Grutter and Bshary 2003). A wrasse that consumes its client's mucus instead of its ectoparasites is cheating from the client's perspective in that the client loses valuable – and energetically costly to produce – mucus without gaining benefits in exchange. In particular, nonpredatory client fish are presented with a dilemma in that they have no means to exploit a cheating wrasse in return – e.g., eating the wrasse itself. This creates an asymmetric interaction where cleaners have the choice of either cooperating with or exploiting their nonpredatory clients, while the clients lack such a choice.

Despite the potential for cheating, most cleaner-client interactions are largely cooperative. Clients employ manipulative control mechanisms that are effective in promoting cooperation in cleaner wrasse. Clients who have been cheated can respond by punishing the wrasse through chasing (Bshary and Grutter 2002), terminating the current cleaning session, and/or switching to a different cleaner station for future sessions (Bshary and Schäffer 2002). Given that cleaner wrasses generally feed against their preferences – i.e., consume ectoparasites instead of client mucus – these control mechanisms appear effective at stabilizing cooperation between cleaners and clients. Essentially, client fish manipulate cleaner wrasse to behave in ways that differ from how cleaners would act if their behavior was unconstrained. Further work in this system has examined cooperation between multiple cleaners simultaneously inspecting the same client – where if one cleaner cheats its client, its partner cleaner also suffers the resulting costs but without gaining any benefits – to better understand the cooperative dynamics of this system (Gingins and Bshary 2015).

Alternating exchanges of egg parcels in some hermaphroditic fish species may represent a manipulative tactic to promote reciprocal fertilization of each individual's valuable eggs. The

black hamlet (*Hypoplectrus nigricans*) is a simultaneous hermaphrodite in that it possesses both eggs and sperm simultaneously (Fischer 1988). These fish spawn during the last 2 h of the day, during which pairs join up together. A pair alternates courtship displays prior to one individual releasing a parcel of eggs to be fertilized by its partner. As the spawning interaction continues, individuals alternate between fertilizing their partner's eggs and releasing their own parcels. Over the course of a single spawning period, each individual on average releases about five such parcels.

When viewed solely within the context of a dyadic interaction between just two individuals, cooperative courtship interactions between *H. nigricans* pairs may represent an example of TFT reciprocity (see above). Eggs are more energetically costly to produce than sperm. As a result, black hamlets could be tempted to cheat by fertilizing its partner's egg parcel with cheap-to-produce sperm without subsequently releasing a costly parcel of its own. Evidence suggests that if a black hamlet fails to release an egg parcel when it is their turn to do so, their partner may "retaliate" by waiting longer before releasing another parcel of eggs to be fertilized (Fischer 1988).

Some authors have argued that egg parcelling represents a manipulative strategy that promotes cooperative behavior between courting individuals (see Connor 2010 and references therein). If individual A released all of its eggs at once, that would leave it vulnerable to having individual B fertilize its eggs and then leave to seek additional mating opportunities without providing eggs for A to fertilize in turn. By parcelling their eggs, black hamlets are manipulating the costs and benefits of their partner's options. It is generally more beneficial for their mating partner to stay and exchange parcels than to leave after fertilization and pay the time and energy costs of finding a new mating partner.

Helping behavior of subordinates unrelated to the breeding individuals within cooperatively breeding groups of *N. pulcher* was discussed above in terms of shared mutualistic benefits. Pay-to-stay models propose another mechanism that may promote helping behavior by unrelated

subordinates. As described above, belonging to a group enhances survival in *N. pulcher* (Balshine et al. 2001; Heg et al. 2004). Pay-to-stay models propose that subordinates trade helping behavior for being allowed to remain on the group's territory (Wong and Balshine 2011; Fischer et al. 2014).

One of the assumptions behind pay-to-stay models is that subordinates are costly to dominant breeders through competition over resources and/or reproduction. If so, then a key prediction of pay-to-stay is that subordinates that do not provide help should be punished and/or evicted by breeder individuals. Such a pattern was observed at least in small groups of *N. pulcher*, where subordinates who were physically present – but experimentally prevented from helping – received increased aggression from breeders (Fischer et al. 2014). In this case, dominant breeders induce subordinates to engage in potentially costly helping behaviors through the threat of punishment and/or eviction from the territory.

Conclusion

Examples of cooperation in fish are found in a wide variety of species and contexts, including mating, foraging, anti-predator, and territorial behaviors. This entry has provided a broad overview of the evolutionary mechanisms that maintain cooperation in nonhumans, as well as relevant examples within each category. Owing to their immense diversity in species, morphology, and behavior – as well as the relative ease of observation and experimentation for many species – fish will continue to represent valuable model systems going forward for examining both the proximate and ultimate explanations for cooperative behavior in nonhuman animals.

Cross-References

- Cooperation
- Cooperation Among Nonchimpanzee, Nonhuman Primates

- ▶ Cooperation and Social Cognition
- ▶ Evolution of Cooperation
- ▶ Kin Selection
- ▶ Nonhuman Reciprocal Altruism
- ▶ Prisoner's Dilemma and Cooperation

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Cooperation Among Nonchimpanzee, Nonhuman Primates

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Synonyms

[Alloparenting](#); [Altruism](#); [Behavioral Synchrony](#); [Biological Markets](#); [Coalition Formation](#); [Cooperative Breeding](#); [Food Sharing](#); [Grooming](#); [Kin Selection](#); [Mutualism](#); [Nepotism](#); [Partner Choice](#); [Punishment](#); [Reciprocal Altruism](#); [Reciprocity](#)

Definition

An actor performs a behavior which benefits one or more recipients; the actor may incur a fitness cost (altruism), the actor's fitness may remain neutral (byproduct), or the actor may gain a fitness benefit from the behavior (mutualism).

Introduction

Despite being vulnerable to exploitation, cooperation has been observed throughout the animal kingdom (Dugatkin 1997). The opportunity for a selfish partner to defect in a cooperative interaction by returning less than he or she received, or by not contributing as much effort as other partners and freeriding, raises the questions of how cooperation evolved and how it is maintained.

Human society is defined by complex cooperation, which scales from simple interactions (for example, familiar individuals sharing resources) to complex interactions on a global scale (for example, unfamiliar individuals working together to build the International Space Station). Therefore, the study of cooperation in close phylogenetically related nonhuman primates (hereafter,

primates) offers us the opportunity to explore the selective pressures that shaped cooperative behaviors and the social factors affecting the maintenance of cooperation.

Evolutionary theory predicts that cooperation can occur when it increases one's inclusive fitness (i.e., sharing benefits with kin; Hamilton 1964) or when the short-term cost of offering benefits to others is balanced when those benefits are returned by the partner through reciprocation (Trivers 1971; Axelrod and Hamilton 1981). Kin selection and reciprocity are two mechanisms underlying the evolution of cooperation among primates (Kappeler and van Schaik 2006). Historically, kin selection and reciprocity have been discussed in how they relate to altruism, in which a behavior is costly to the actor and beneficial to the recipient in terms of fitness consequences. Here, these mechanisms are discussed in the broader context of cooperation, in which a behavior benefits the recipient without explicit cost to the actor – the actor may or may not benefit from the cooperative interaction. Kin selection is pervasive among cooperative primate interactions (Silk 2002) and helps to explain cooperative breeding in the Callitrichidae (a family of New World Monkeys including marmosets and tamarins). There is abundant evidence for reciprocally patterned behavior in wild primates, but evidence for contingent exchanges in a laboratory setting is weak (reviewed in Hall and Brosnan 2016).

Primates' aversion to inequity underpins their understanding of the features that make another individual a good cooperative partner. If a primate can judge his or her own outcome relative to others', he or she can choose partners that distribute rewards fairly (reviewed in Hall and Brosnan 2016). If a partner does not distribute rewards fairly, primates can exert partner control mechanisms such as punishment. Partner choice and punishment are mechanisms that contribute to the maintenance of cooperative interactions.

Complementary studies of primates in both wild and laboratory settings will strengthen our understanding of the functions and mechanisms of cooperation.

Ultimate Mechanisms of Cooperation

Kinship

Kinship plays a large role in shaping the relationships of members of the highly social order Primates, including dominance hierarchies, coalitions, and the organization of social networks. Additionally, kinship can shape life histories: the presence of a father, grandmother, aunt, or juvenile sibling to care for new infants can affect an individual's reproductive performance. In this section, the role of kinship in cooperative interactions is described, particularly the roles of kin selection and nepotism and of cooperative breeding.

Kin Selection and Nepotism

Kin selection, first described by Maynard Smith (1964), is a mechanism by which costly acts that benefit others (altruism in particular, and cooperation more generally) can occur, when the actor shares a degree of relatedness with the recipient. Any social interaction which incurs an investment of time, such as grooming, can be considered costly because that time could be invested in other activities such as foraging. As most primates are female philopatric, it is common for females to become nepotistic in their interactions with others. For example, in macaques (*Macaca fuscata*, *M. mulatta*, *M. nemestrina*, *M. radiata*), baboons (*Papio cynocephalus ursinus*), and vervets (*Cercopithecus aethiops*), females tend to invest more time in grooming, resting with, and providing infant care to members of their matriline than to nonkin (reviewed in Silk 2002; Cheney & Seyfarth 1984). They also spend more time, and are more tolerant of, feeding with kin (*ibid.*). Additionally, these females are more likely to provide coalitionary support to kin (*ibid.*). These interactions directly benefit the recipient and also indirectly benefit the actor, because the two share a degree of relatedness due to common ancestry. Additionally, these cooperative interactions may also benefit the actor through symmetry-based reciprocity (described below).

Cooperative Breeding and Alloparenting

For primates of both sexes, but in particular for females, remaining in the natal group with generations of matrilineal kin confers reproductive benefits, even when considering the risks of inbreeding. In addition to increased vigilance for predators, and other fitness benefits of interacting frequently with kin (per kin selection theory, above), the enhanced social support of an aunt or younger sibling to help care for a newborn has a positive impact on the survival rate of both mother and offspring (Hrdy 2007). Alloparenting, or the providing of care to infants by individuals other than the infant's mother, comprises several behaviors: carrying or transporting infants, provisioning food and sometimes nursing, babysitting, support in agonistic interactions, and protection against infanticide. Genetically related nonbreeders increase their inclusive fitness by helping, and additionally, mothers allowing nulliparous daughters the opportunity to practice caring for younger siblings gives them the experience they need to be better mothers when the time comes (Hrdy 1999).

For obligate cooperative breeders in the family Callitrichidae (tamarins and marmosets), males carry the offspring – usually twins – up to 60 % of the time (e.g., common marmosets *Callithrix jacchus*), representing a significant energetic cost for the father, especially as the infants grow (Hrdy 2007). Male cotton-top tamarins (*Saguinus oedipus*) can lose up to 10 % of their body weight from carrying infants during the first 3 months after birth, though this is attenuated if additional helpers are available (Achenbach and Snowdon 2002). These parenting strategies allow for increased infant and mother survival as well as shorter inter-birth intervals.

Reciprocity

Cooperation among nonkin can evolve when partners take turns exchanging goods or services; this was formally defined as reciprocal altruism by Trivers (1971), but this is somewhat of a misnomer. As the actor ultimately benefits from the returned favor, there is a direct fitness advantage to cooperating, whereas to be defined as altruistic, the actor must incur a cost. In this section, the role

of reciprocity in cooperative interactions is described, in particular the types of reciprocity, and a discussion of biological markets theory.

Brosnan and de Waal (2002) proposed three levels of reciprocity. First, symmetry-based reciprocity suggests that reciprocity within a relationship exists simply because of the symmetrical nature of the relationship itself. For example, because A and B spend more time together, their actions will naturally benefit each other, without contingency between actions. Second, attitudinal reciprocity suggests that there is a contingent relationship between A's kind act towards B that elicits a feeling of good will in B towards A, thus increasing the likelihood that B will return a favor to A. Third, calculated reciprocity suggests that A and B cognitively keep track, in a tit-for-tat manner, the exchanged favors between them. However, it is difficult to distinguish between symmetry-based and calculated reciprocity from correlational data; data should be analyzed sequentially to determine whether an act by A towards B increases the probability of B acting towards A.

Grooming

In a meta-analysis of long-term grooming data from 22 primate species from both Haplorhini and Strepsirrhini, Schino and Aureli (2008) found that female primates preferentially groom the individuals that groom them the most, even when controlling for maternal kinship. Within a grooming session, there is a positive correlation between the durations of time that closely ranked chacma baboon (*P. c. ursinus*), bonnet macaque (*M. radiata*), and capuchin (*Cebus capucinus*) partners invest in grooming each other (Barrett et al. 1999; Manson et al. 2004).

Food Sharing

Feistner and McGrew (1989) define food sharing as when food-motivated individuals voluntarily transfer defensible food items to others, and they review examples of food sharing in wild primates. One hypothesis to explain food sharing among primates suggests that sharing only occurs reactively to relieve pressure from harassing conspecifics, whereas a second suggests that reciprocity

underlies a service economy in which food is one of many goods or services to exchange (see section on “[Biological Markets](#)”, below). Gilby (2006) found strong support for the harassment hypothesis in chimpanzees (*Pan troglodytes schweinfurthii*) but only mixed support for the reciprocity hypothesis: food possessors were more likely to share with frequent grooming partners but due in part to an effort to reduce their harassment. To compare the rates of reciprocal exchange of food between partners, Jaeggi et al. (2010) determined that food exchanges were reciprocal among tolerant chimpanzees but mainly unidirectional among despotic bonobos (*P. paniscus*). De Waal (1989) found a positive correlation between the rates of transfer of food in either direction between chimpanzee dyads, supporting the reciprocity hypothesis.

Evidence of the contingent reciprocal exchange of food between primates in a controlled laboratory setting, however, is weak. De Waal (2000) describes that capuchins (*C. apella*) passively transferred food through a mesh barrier in a reciprocal, but not contingent, manner. Even in low-cost situations, for example by choosing to pull a tray with food rewards for both partners versus pulling a tray with a reward only for the actor, chimpanzee and cotton-top tamarin subjects' behavior is not contingent on their partner's prior choice (Brosnan et al. 2009; Cronin et al. 2009).

Coalitions

Coalitionary support in agonistic interactions is another behavior thought to be costly to the actor and beneficial to the recipient. Among chimpanzees, rhesus and stump-tailed macaques (*M. arctoides*), there was significant reciprocity for beneficial interventions, but only chimpanzees significantly intervened in harmful ways, demonstrating a rudimentary system of revenge (de Waal and Luttrell 1988).

Biological Markets

Reciprocated exchanges need not be paid back in the same currency: often goods and services are traded in a biological “marketplace,” including grooming, food sharing, coalitionary

support, and mating access (Noë and Hammerstein 1994). There is continued debate as to whether primates must cognitively keep track of the value of multiple commodities over extended time or whether they behave based on current needs and the availability of the desired goods/services.

Hemelrijk (1994) confirmed that female long-tailed macaques (*M. fascicularis*) offer more support to other females who had recently groomed them than to those who had not, and that this outcome was directional: A supported B more after B had groomed A, but not after A had groomed B or if no grooming interaction had occurred prior to the agonistic interaction with C. In a meta-analysis of 14 species from both Haplorhini and Strepsirrhini, Schino (2007) showed that, in general, female primates direct their grooming efforts at higher-ranking individuals in exchange for their support in agonistic interactions.

Grooming can also be traded for food and vice versa: in naturalistic studies of chimpanzees and bonobos, it was found that both species showed short-term contingencies between the two commodities, but that controlling for long-term relationship characteristics diminished the effect for chimpanzees (Jaeggi et al. 2013). This result highlights the issues surrounding the timeframe of measurement; as evidence for short-term reciprocity is lacking, it is difficult to determine the span of time necessary for exchanges to become balanced.

Proximate Mechanisms for Maintaining Cooperation

Inequity Aversion

Brosnan (2006) proposed that aversion to inequity underlies the evolution of cooperative behavior. Primates' responses to inequity vary based on multiple factors: the presence of a task elicits a stronger response, dominance and certain personality traits predict a more adverse reaction to inequity, and responses are attenuated by the duration and quality of the partners' relationship (reviewed in Hall and Brosnan 2016). The inequity response

did not evolve through homology in the primates and is not an artifact of large brain size or living in a large social group, rather, it occurs in species that regularly cooperate with nonkin, including chimpanzees, bonobos, capuchins, rhesus, and long-tailed macaques but not in those that do not, such as orangutans (*Pongo spp.*), squirrel monkeys (*Saimiri boliviensis*), or cooperatively breeding tamarins, marmosets, and owl monkeys (*Aotus spp.*) (*ibid.*). Responding to inequitable outcomes allows primates to choose cooperative partners based on a more fair reward distribution (*ibid.*).

Partner Choice

In order to maintain cooperation in social groups and defend against defectors, primates exhibit partner choice. In cooperative interactions, primates pay attention to the characteristics of their partners, in addition to the relative reward outcomes. Due to the lack of partner choice in most laboratory studies (e.g., due to limited subject availability or lack of tolerance between partners), Molesti and Majolo (2016) introduced a cooperation apparatus – a string pulling task – into a group of wild Barbary macaques (*M. sylvanus*) to determine the factors affecting partner choice in an open-choice group scenario. They found that macaques had more success at the task when they chose partners with whom they were tolerant and shared a strong social bond (kin or not) and also found effects of similar rank, age, sex, and temperament.

Punishment

Another mechanism to deter defection and freeloading in cooperative interactions is punishment – whether by the abandoned partner or by a third party. Punishment, or the threat of it, can prevent individuals from defecting in future interactions. There is, however, limited evidence of punishment in primates, possibly due to the higher cost associated with punishment than with choosing a new partner from an available pool of multiple partners. Chimpanzees, for example, will punish those that steal food from them but will not punish based on unfair outcomes alone (Jensen et al. 2007).

Conclusion

Studying the underlying mechanisms of cooperation in primates can help us better understand the evolutionary path and function of the behavior, without the confound of human culture. When individuals interact with genetically related group members, cooperation is likely explained by the mechanism of kin selection: though the actor may incur a cost, ultimately he or she benefits from improved inclusive fitness. When unrelated individuals cooperate, reciprocity may be the underlying mechanism, whether symmetry-based, attitudinal, or calculated. It is not uncommon for these two mechanisms to share some overlap. By learning more about the selective pressures that may have molded a behavior, we can better tease apart the proximate motivations to cooperate from the ultimate functions of doing so. Understanding how these traits evolved, and how the mechanisms of partner choice and punishment help to maintain cooperation, can give us insight into the importance of cooperation for preserving social relationships.

Though there is good evidence of cooperation in primates, questions remain with respect to the influence of time on the balancing of given and received favors and the influence of cognition for tallying them. Short-term contingent reciprocity is difficult to show in a laboratory setting, and difficult to test with unfamiliar individuals, yet these concerns could be an artifact of the experimental setup, for example, lack of partner choice. Due to the difficulty in distinguishing symmetry-based and calculated reciprocity, the question of cognition remains sidelined.

Cross-References

- ▶ Access to Alloparents
- ▶ Adaptations for Reciprocal Altruism
- ▶ Genuine Altruism

- ▶ Adaptive Problem of Detecting Kinship
- ▶ Alarm Calling and Kinship
- ▶ Alarm Calling Predicted by Inclusive Fitness
- ▶ Alloparenting
- ▶ Alloparenting and Grandparenting
- ▶ Altruism
- ▶ Altruism Advertises Cooperativeness
- ▶ Altruism Advertises Generosity
- ▶ Altruism Among Nonkin
- ▶ Altruism and Costs to Altruist
- ▶ Altruism and Watching Eyes
- ▶ Altruism Defined by Benefits Conferred
- ▶ Altruism Displays Cooperative Potential
- ▶ Altruism in Kin Selection
- ▶ Altruism Norms
- ▶ Altruistic Punishment
- ▶ Altruistic Punishment and Strong Reciprocity
- ▶ Altruistic Punishment Enhances Reputation
- ▶ Barbara Smuts and Robert Smuts
- ▶ Behavioral Economics
- ▶ Benefit Group Relative to Other Groups
- ▶ Benefit to Another at Cost to Self
- ▶ Biparental Care
- ▶ Blood Sharing by Vampire Bats
- ▶ Cheater Detection
- ▶ Cheater Detection Adaptations
- ▶ Chimpanzee Raiding
- ▶ Coalitional Hunting
- ▶ Competitive Altruism
- ▶ Contingent Reciprocity
- ▶ Cooperation Among Fishes
- ▶ Cooperation and Social Cognition
- ▶ Cooperation in Social Insects
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Cooperative Alliances
- ▶ Cooperative Breeding
- ▶ Cooperative Foraging
- ▶ Cooperative Grooming
- ▶ Cooperative Hunting
- ▶ Costs of Punishing
- ▶ Costly Signaling and Altruism
- ▶ Costs of Punishing
- ▶ Defection
- ▶ Early Association Cue to Kinship in Primates
- ▶ Emotional Solutions to Free Riding
- ▶ Evolution and the Theory of Games

- ▶ Evolution of Cooperation
- ▶ Evolution of Morality
- ▶ Evolution of Punishment
- ▶ Evolution of Reciprocal Altruism
- ▶ Evolved Moral Foundations
- ▶ Fairness in Primates
- ▶ Females Remain with Natal Group
- ▶ Food Sharing
- ▶ Food Sharing and Nonhuman Reciprocal Altruism
- ▶ Fostering Values of Fairness
- ▶ Frans de Waal
- ▶ Frans de Waal's (1982), *Chimpanzee Politics*
- ▶ Free Riding
- ▶ Game Theory
- ▶ Genetic Relatedness Affects Aid to Kin
- ▶ Genuine Altruism
- ▶ Gossip and Indirect Reciprocity
- ▶ Great Apes
- ▶ Green Beard Effect, The
- ▶ Group Hunting
- ▶ Group Living
- ▶ Hamilton's Rule
- ▶ Hamilton's Rule and Kin Investment
- ▶ Helper at the Nest Among Nonhuman Primates
- ▶ Helping and Genetic Relatedness
- ▶ Helping and Inclusive Fitness Benefits to Helper
- ▶ Helping More Likely with Close Kin than More Distant Kin
- ▶ High-Cost Altruistic Helping
- ▶ Inclusive Fitness
- ▶ Indirect Benefits of Altruism
- ▶ Indirect Reciprocity
- ▶ Ingredients of Reciprocal Altruism
- ▶ Insist on No More than Equity
- ▶ Iterated Prisoner's Dilemma Model
- ▶ John Maynard Smith
- ▶ Jonathan Haidt
- ▶ Kin Selection
- ▶ Kin Selection Hypothesis
- ▶ Kinship
- ▶ Life History Strategies
- ▶ Living in Groups
- ▶ Male Coalitions for Hunting
- ▶ Mechanisms to Detect and Punish Cheaters
- ▶ Mechanisms to Prefer Traits in Coalition Members
- ▶ Moral Emotions
- ▶ Moral Instincts
- ▶ Moral Instincts and Morality
- ▶ Morality
- ▶ Morality is Cooperation
- ▶ Nonhuman Primates
- ▶ Nonhuman Reciprocal Altruism
- ▶ Observation of Altruism
- ▶ Partner Desertion
- ▶ Peter Kropotkin
- ▶ Primate Cooperation
- ▶ Primates
- ▶ Prisoner's Dilemma and Cooperation
- ▶ Problem of Altruism
- ▶ Problem of Cheating
- ▶ Psychology of Reciprocal Altruism
- ▶ Punitive Sentiment
- ▶ Puzzle of Altruism, The
- ▶ Recall of Cheaters
- ▶ Reciprocal Altruism
- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reciprocal Altruism and Group Living
- ▶ Repeated or Iterated Prisoner's Dilemma
- ▶ Reputation
- ▶ Reputation and Altruism
- ▶ Resource Defense
- ▶ Richard Wrangham
- ▶ Robert Axelrod's (1984) *The Evolution of Cooperation*
- ▶ Robert Trivers
- ▶ Sarah Blaffer Hrdy
- ▶ Sarah Brosnan
- ▶ Science and Morality
- ▶ Selection for Cooperative Relationships
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ Strategies for Successful Cooperation
- ▶ Strong Reciprocity
- ▶ Theory of Reciprocal Altruism
- ▶ Triggering Kin Selection

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Cooperation Among Non-kin

► Evolution of Cooperation

Cooperation and Social Cognition

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Definition

Cognitive processes and mechanisms underlying human ability to cooperate with others

Introduction

Living in groups implies the ability to cooperate and coordinate individuals' behaviors. In human societies, cooperation goes far beyond relations based on kinship, extending both in space and time. The human ability to cooperate with others, especially unrelated others, is a challenge for the evolution theory as it seemingly contradicts the notion of "self-interest" as the key driver of behavior. Cooperation implies behavior, which benefits others, often without immediate returns for an individual. Although evolution theory considers cooperation with little or no cognition at all, in human societies it depends on advanced cognitive abilities. To establish and maintain complex cooperation, individuals must be able to recognize others' identities as well as their states and intentions, monitor their actual behavior, keep memory for past interactions, calculate potential costs and benefits for long-term interaction, control one's behavior to receive a delayed reward, recognize deception, and others. Performing such tasks requires both general cognitive abilities and more specialized skills of social cognition, which is a crucial prerequisite for cooperation in humans.

Social Cognition

Social cognition is a set of abilities needed for social tasks, i.e., tasks which involve other

individuals and interaction with them. Although any cognitive process or ability can be related to social tasks, it is useful to recognize those ones which constitute the distinctive features of social cognition and its key functions. In a recent review, F. Happé, J. Cook, and G. Bird identified eight key components of social cognition all of which are important for cooperation (Happé et al. 2017, p. 247):

1. Social affiliation and motivation. The essential part of human cooperation is group-based cooperation, i.e., individuals prefer to cooperate with the members of their own group (ingroup). Such a tendency is a result of social motivation and the need of belonging. In terms of social cognition, social affiliation is based on processes of social categorization and social identity. Social categorization means that both oneself and others are perceived as members of social groups and categories rather than individuals, whereas social identity implies that individuals' group membership constitutes a part of self-identification. Identifying others in terms of group membership determines the readiness for others-oriented actions, expectations of others' group-directed behavior, and the decisions to cooperate.
2. Agent recognition, i.e., identification of social agents and their identity. As cooperation typically implies actual or potential repetitive interaction, agents must know with whom they have a deal and mutual obligations. In case of indirect reciprocity or unconditional cooperation, agents also must be sure their efforts are directed toward an appropriate other.
3. Biological motion perception, action recognition, and imitation. As cooperation manifests itself via observable action, agents must be able to identify and recognize what others actually do. Imitating others' actions, in turn, is an important part of social behavior, necessary for learning, collective cohesion, and understanding others' actions.
4. Emotion recognition. As behavior strongly depends on agents' affective states, they must

be timely and correctly recognized to maintain smooth interaction, predict others' behaviors, and determine their readiness for cooperation and reciprocity.

5. Empathy. The ability to experience the same affective states as that of others is not only a way to understand them and their intentions, but it also stimulates the readiness for other-benefiting behavior.
6. Social attention. Living in group means that individuals must constantly monitor the social environment and selectively focus on important social stimuli. Social attention is largely automatic and supports fast detection of social stimuli and recognition of their key social feature such as group membership or status.
7. Social learning. Learning from other individuals, either direct or by imitation, can also be related to cooperation, not only because it transfers skills and experience of cooperative behaviors but also because learning as a kind of social interaction is itself a form of cooperation.
8. Theory of mind (ToM). ToM, i.e., the ability to infer other's intentions and states of mind is probably the most important type of social cognitive processes as it helps to predict others' behavior and make strategic decisions. ToM implies the ability to take third person perspective and look at the situation by others' eyes. Understanding others' evaluation of the situation, possible benefits and losses of cooperation, as well as their preferences and attitudes helps to detect potential deception and decide whether it is worth cooperating with them or not.

The listed types of cognitive processes are not necessarily separate from each other. The ongoing discussions consider various scenarios of how they can be related to each other including partial overlapping, developmental relations, or even considering some of them as parts of the same process (Happé et al. 2017). However, the very idea of social cognition implies that humans as well as other social species have cognitive

abilities evolutionary developed and tuned to support social bonding and cooperation.

Two Types of Cooperation

There are two types of cooperation generally recognized by the evolution theory. The first one is largely unconditional and takes place among related individuals, e.g., kinship. Cooperation in this case depends on established relations with others and is generally explained by reference to kin or group selection. As this type of other-benefiting behavior depends on specific social markers of a partner, it can be termed group-based cooperation. This means that the decision to benefit other individuals is determined by their social affiliation with an agent, i.e., group membership. The second type of cooperation occurs between unrelated individuals and implies more strategic behavior. Decisions to cooperate in these cases are generally conditional, i.e., they depend on expectations of mutuality and returns, either direct or indirect. The decision to cooperate, unlike the first type, is a choice rather than imperative.

In regard to social cognition, these types of cooperation have important differences, which can be partially related to the dual-process cognitive theories. According to them, two types of cognitive processes exist in human mind and compete during decision-making (Kahneman and Frederick 2002). The first one is automatic, fast, and very efficient but less sensitive to contextual information. The second one is slower, more deliberate, rational, time-consuming, and sensitive to context. The dual-process approach was applied to the study of social cognition and cooperation, suggesting that intuitive (social heuristics) and deliberate decision-making are the two possible ways for making decisions in social dilemmas and providing different solutions (Rand 2016). Unconditional, group-based cooperation generally relies more on automatic processes, whereas strategic behavior is more associated with deliberate cognition. At the same

time, the distinction between the two types of cooperation as well as the idea of pure automation and deliberation are an idealization. In reality, the two types of cognition may act in parallel and interact with each other and are involved in each type of cooperation, so that, for example, automatic decisions (social heuristics) can favor cooperation with unrelated others and in the absence of reciprocity, due to their cost-efficiency (Bear et al. 2017). Despite this, various types of cooperation require different social cognitive skills and processes briefly described below.

Social Cognition in Group-Based Cooperation

The group-based cooperation is typically associated with kin selection mechanisms and needs only the minimal cognitive abilities or none of them at all, as it takes place, for example, among the social insects (Brosnan et al. 2010, p. 2699). The key feature of such helping behavior is that it is largely unconditional, i.e., doesn't depend on others' behavior. However, identification of co-species and the members of relevant social entity (e.g., a hive) is a necessary prerequisite for such cooperation. In species such as microorganisms or insects, identification of cooperators is typically based on chemical signals. In the most developed species, identification of appropriate recipients of helping behavior is more advanced and involves variety of psychological and cognitive mechanisms of self-categorization and social identity construction.

Human social identity is multiple and complex. Lay people identify their own and others' membership in various types of groups such as intimacy groups, social categories, task groups, and loose associations (Lickel et al. 2001). These types of groups differ in their personal significance, perceived homogeneity, and other characteristics, important for cooperative behavior. Individuals constitute their social identity from numerous group memberships of various types. Their own and others' perceived group membership is dynamic and constantly updating, different social categories become more or less salient in various contexts and overlap with each

other (Crisp and Hewstone 2006; Kang and Bodenhausen 2015). Some group memberships are considered to be especially stable and of highest priority. These include gender, age, race/ethnicity, and language (Kinzler et al. 2010). Recognition of these group memberships is fast and automatic although more controlled processes can also be involved in their representation. They are recognized by children and even infants, thus confirming that the human mind is evolutionary tuned to effectively manage the complexity of the social world.

Identification of group membership is the core cognitive process of group-based cooperation as it results with the differential perception, attitudes, and behaviors toward the members of the different groups. There is a general tendency to prefer and favor one's own group in various psychological domains such as attention, memory, attitudes, empathy, evaluations, social attribution, allocation of resources, or approach-avoidance behavior. Such preferences often occur very fast and are detectable on a neurophysiological level (e.g., Boksem et al. 2012; Bruneau and Saxe 2010; Cheon et al. 2011; Dickter and Bartholow 2007; Enge et al. 2015; Harris and Fiske 2006; Volz et al. 2009). The fact that social categorization affects many different cognitive and affective processes confirms the hypothesis that it constitutes a separate cognitive system, evolved to maintain the complex social relations (Kinzler and Spelke 2007).

Importantly, the tendency to favor cooperation with ingroup members is present in regard to various types of group memberships: racial/ethnic, nationality, age, gender, political affiliation, kinship, sports team fans, etc. It even occurs in the so-called "minimal group" condition, i.e., when group membership is very arbitrary and contextual (Tajfel et al. 1971; Otten 2016), and even in such situations the differences in responses to group membership information can be fast and automatic (Gamond et al. 2017).

Although such preferences for ingroup members can be counterbalanced by other processes such as social hierarchy perception or top-down control, they constitute the basis of

group-based cooperation, largely unconditional and automatic. The ability to make automatic decisions on cooperation can be evolutionarily advantageous because it reduces costs and allows to make multiple choices necessary to interact with many individuals. Recent studies showed that unconditional cooperation largely depends on specific neurohormonal mechanisms. More specifically, a neurohormone oxytocin is supposed to favor cooperating behavior by reducing stress and fostering social bonding and affiliation (Crespi 2016). Initially studied as a mechanism supporting mother-to-child relations, oxytocinergic system was found to be universally stimulating cooperation within various types of meaningful ingroups including kinship, ethnic, and cultural groups (Crespi 2016; De Dreu and Kret 2016). In humans, oxytocin promotes within-group cooperation by increasing empathy toward group members, compliance with group norms, and trust and discriminating against outgroup members (De Dreu and Kret 2016). Studies also confirm that oxytocin promotes intuitive cooperation with ingroup members rather than deliberate, i.e., is a part of unconditional, group-based cooperation (Velden et al. 2017). The question of how oxytocinergic system “chooses” the specific group membership and integrates with the cognitive mechanisms of social categorization, however, remains largely unclear.

Social Cognition in Strategic Cooperation

The second type of cooperation is between unrelated individuals and is not conditioned by group membership. It is a form of strategic behavior, depending on contextual information and expectations of future interactions. This type of cooperation is generally studied using theory of games approach and analyzes cooperative behavior in terms of potential costs and benefits associated with specific strategy. Although the notion of strategic cooperation can be applied to species without a brain, it is generally assumed to be very demanding in terms of partners' cognitive abilities (Brosnan et al. 2010). The need for these abilities results from several specific features

of strategic behavior. Brosnan et al. (2010) point to three factors contributing to the demand for specific cognitive ability needed for strategic cooperation. First, high mobility of partners and increasing number of interactions require good memory and ability to store and retrieve information on past interactions. Second, strategic behavior is often based on time delays between investments and rewards. When such delays take place in interactions, the probability of cheating increases. Individuals have to manage the problem of time delays, both by improving memory for past interactions and by developing skills to correctly anticipate future actions and events. Third, as sustainable strategic cooperation needs positive reinforcement (i.e., agents must receive rewards for their donations to others), temporal delays become a problem for associative learning. To manage this problem, individuals must develop abilities, which make possible behavior oriented toward a delayed reward.

In human societies, individuals are involved in numerous interactions with unrelated others, which don't imply immediate and automatic rewards. The abilities necessary to participate in cooperation with unrelated others are supposed to coevolve with the complexity of social organization itself (Dos Santos and West 2018). The unique human ability to cooperate in large societies with unrelated others and with significant time delays can be explained by reference to either general or specialized cognitive abilities. The general intelligence hypothesis assumes that larger brains allows humans to perform more sophisticated calculations, have better memory, plan for a long-term periods, and perform other cognitive operations more efficiently, whereas the social and cultural intelligence hypotheses state that human societies evolved due to specific needs of their sociality or even “ultra-sociality,” involving living in cultural groups (Hermann et al. 2007).

In accordance with the general intelligence hypothesis, larger brain and more efficient cognitive processing can indeed foster strategic cooperation. Abilities to calculate future outcomes and experience delayed rewards as actual reward and store and

retrieve information about partners and their past actions are universally supporting participation in strategic cooperation (Brosnan et al. 2010).

At the same time, there is strong evidence that humans evolved more specialized social skills necessary to handle strategic cooperation. These skills and abilities include:

- Effective social communications via language and nonverbal means, allowing to rapidly and accurately store and transfer a great amount of detailed information about other individuals, past interactions, and relevant contextual information.
- Fast and accurate recognition of social cues necessary to identify social position of partners and, consequently, to form expectations concerning their possible behavior in interaction.
- Action recognition.
- Fast and accurate recognition of other individuals' mental and emotional states, attitudes, and intentions, necessary to reconstruct their likely strategy and probability of cheating.
- Social signaling, i.e., using self-presentation techniques via control over bodily and facial expressions to demonstrate social status or intentions and to manipulate others' perception.

Studies in cognitive and neuroscience reveal the existence of specialized systems for performing these tasks. For strategic cooperation, correct identification of other's actions and intentions is crucial as it is directly related to decoding others' strategies, including the possibility of cheating, which is the key threat to cooperation. Three integrated neurocognitive systems jointly performing these tasks can be identified: social perception, action recognition, and theory of mind (Yang et al. 2015). The neural system of social perception is especially tuned for face processing and involves regions in the fusiform gyrus (FFG), posterior superior temporal sulcus (pSTS), orbitofrontal cortex (OFC), and amygdala. Action observation involves a mechanism of imitation, which is more self-referral and relies upon the so-called mirror neurons, i.e., neurons similarly

activated both during observation of others' actions and performing these actions by individuals themselves. The mirror neuron system is basically located in pSTS, inferior parietal lobule (IPL), and posterior inferior frontal gyrus (IFG). Theory of mind, i.e., the ability to reconstruct other's mental representations of themselves and their environment, is performed by a neural system typically associated with the temporoparietal junction (TPJ), medial prefrontal cortex (mPFC), and some other regions including pSTS, which was recently proposed to play the core role in integrating these three systems (Yang et al. 2015).

Conclusion

Although cooperative behavior is common among various species and is often regulated by genetic factors, in human societies it largely depends on cognitive abilities. Large size and complexity of social life require cooperation with both related and unrelated others, in a flexible manner and with significant temporal delays between other-benefiting behavior and potential future rewards. Both general-purpose cognitive abilities and more specialized mechanisms of social cognition coevolved with human social organization to maintain complex forms of cooperation.

Unconditional cooperation with related others, typical in nonhuman species and evolved by kin selection, becomes much more sophisticated in humans. The key element of social cognitive abilities underlying such group-based cooperation is social categorization. Ingroup-favoring behavior requires the ability to identify social affiliative relations, and in human societies affiliation involves multitude group memberships, flexible and interacting with each other. To navigate the multiple social categorizations and identities, humans developed advanced neurocognitive machinery, which helps to integrate information on group membership with attention, memory, evaluations, approach-avoidance predispositions, decision-making, and other cognitive processes relevant for cooperation.

Strategic cooperation, based on rational investments and expectations of future rewards, involves a wide set of cognitive mechanisms. Given the complexity of social organization, successful strategic cooperation with individuals outside strong affiliative relations needs both general cognitive abilities (efficient memory and computational resources, ability for long-term planning, and controlling immediate behavioral responses for delayed rewards) and specialized social cognition skills. The latter include social communication and signaling, status recognition, and especially the ability to detect and reconstruct others' internal states and intentions and predict their future behaviors.

All kinds of specific social cognitive processes necessary for cooperation have their neural basis and include both automatic and controlled mechanisms described by the dual-process theories. Although group-based cooperation relies more on automatic processes and strategic behavior more on controlled ones, they are often interacting and mixed. Group-based cooperation is driven by unconditional imperative to benefit ingroup, but due to the complexity of social categorization and individuals' strategic self-interests, it can be counterbalanced by controlled processes. In turn, deliberate cooperation with unrelated others can be downregulated and substituted by more cost-effective automatic responses used as social heuristics. The differences in individuals' social cognitive abilities, contextually available information, as well as other factors, such as culturally determined differences in social perception and normative orientations, produce variety of social situations in which cooperation and cooperative alliances establish, change, and dissolve.

Cross-References

- Alliances
- Benefit Group Relative to Other Groups
- Cooperation
- Social Cognition
- Strategies for Successful Cooperation

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Definition

Cooperation is a helpful act performed by one individual that benefits a second individual of the same species; here we focus on cooperative interactions between two or more individuals belonging to the same species in the mammalian Order Carnivora.

Introduction

Humans show an unprecedented capacity for empathy and prosocial behavior, but understanding the origins and maintenance of cooperation is an evolutionary puzzle. Why do individuals help others at a personal cost to themselves? Anthropologists have made excellent progress in tackling this long-standing question. To reveal the human origins of cooperation, traditional approaches include the study of the fossil record to reconstruct material cultures and tools used by our ancestors. Other workers study the behavioral patterns of living nonhuman primates to uncover the conditions shaping cooperation. In 1969, Schaller and Lowther proposed the novel idea that studying the lives of extant social carnivores might offer new clues about the origins of cooperation in early hominins beyond those available from these traditional approaches. Here, I synthesize the substantial information currently available about the ways social carnivores cooperate and then discuss how these insights inform our understanding of cooperation in mammals, including early hominins.

Cooperation in Social Carnivores

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Synonyms

Altruism; By-product mutualism; Carnivorans

Extent of Cooperation in Mammalian Carnivores

The mammalian Order Carnivora contains ~300 extant species that together are global in distribution, occupying a range of habitats and dietary niches (e.g., herbivores, omnivores, carnivores; Wilson and Reeder 2005). The vast majority of carnivores (~85–90%) are solitary, with conspecifics interacting only to mate or raise young. In contrast, the social carnivores interact regularly with each other, forming social groups or

societies. Although the social carnivores evolved from noncooperative ancestors, individuals within these extant species cooperate with group-mates to hunt large game, defend resources, guard against predators, attack others, and/or rear young (Smith et al. 2012, *In press*). Moreover, older and socially dominant individuals often emerge as leaders in the domains of group movement, food acquisition, within-group conflict mediation, and between-group interactions (Smith et al. 2016).

Because social carnivores are relatively elusive and long-lived, studies spanning one or more decades capture some of the best information about cooperation in social carnivores (Smith et al. *in revision*). Thus, for brevity, I focus on key examples from long-term studies to elucidate the ways this cooperation has coevolved with other traits across Carnivora (Smith et al. 2012). In doing so, I explain the clues that these species of Carnivora offer into understanding cooperation more generally.

Hunting of Large Game

Group life permits individuals in many of the social carnivores to improve their ability to acquire energy-rich prey that vary both spatially and temporarily in the predictability. Spotted hyenas (*Crocuta crocuta*), African lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and wolves (*Canis* spp.) are among the best-studied of the cooperative hunters. For these species, multiple hunters are often required to secure a single prey animal, each of which represents energy-rich food item that may weigh hundreds of kilograms. Across the Carnivora, additional meat gained from cooperative hunting appears to permit mothers to increase their investment in current reproductive effort by increasing offspring number and also to increase their own body size relative to that of males; cooperatively hunting species often produce more offspring and are less sexually dimorphic than species lacking cooperative hunting (Smith et al. 2012).

Natural selection favors individuals to hunt in optimal group sizes. Whereas spotted hyenas most often hunt alone or in pairs and lions hunt in intermediate groups, wild dogs gain the greatest per capita energy gain when hunting in the large groups (reviewed by Smith et al. 2012). Foragers must balance the benefits of group hunting with the ensuing costs of competition for access to food once prey is obtained. Intense feeding competition often favors groups structured by fission-fusion dynamics in most social carnivores. Individuals regularly break up (fission) from group-mates to hunt on their own or in small subgroups during times of food scarcity but then gather (fusion) into large subgroups to feed when food is abundant.

Coalition Formation and Defense of Resources

Despite their highly cooperative nature, within-group competition regularly occurs among social carnivores over limited resources. Intragroup coalitions form when two or more individuals join forces to direct aggression towards two or more members of their group. Among the carnivores, the patterns of evolutionary forces favoring coalition formation are perhaps best-studied for spotted hyenas living in female-dominated societies. Maternal rank is passed on from mother to offspring. As in many Old World monkeys, individual spotted hyenas learn their social ranks based upon a process of associated learning and repeated maternal interventions during fights (Holekamp et al. 2012). Spotted hyenas also bias their social support towards kin during intragroup disputes but gain direct benefits from reinforcing the status quo by attacking subordinates. Thus, kin selection and direct benefits appear to favor intragroup coalitions via the inclusive (direct + indirect) fitness benefits.

Intergroup coalitions involve multiple group-mates joining forces to direct attacks towards conspecifics belonging to a different social group. This behavior occurs in spotted hyenas, meerkats, and other species of the Carnivora. Interestingly,

although meerkat groups are comprised of closely related group-mates that cooperate in intergroup conflicts, group warfare in spotted hyenas involves kin and nonkin joining forces to attack members of other social groups. As such, spotted hyenas cooperate in group attacks against neighboring group despite their low levels of genetic relatedness with group-mates, presumably gaining direct benefits from their cooperative actions.

Predator Protection

Cooperative defense against predators includes mobbing of predators (e.g., group members collectively fend off potential predators by attacking them) or cooperative vigilance, defined here as any behavioral adjustments that reduces the risk of predation for members of the group. In general, mothers of species that cooperatively defend themselves from predators invest more in current reproduction, weaning offspring at later ages than do mothers of noncooperative species of the Carnivora (Smith et al. 2012). Species living in dense populations are most likely to cooperatively defend themselves from predators, presumably because cooperative defense is mainly a numbers game, requiring a large number of individuals to detect and cooperatively mob predators. Because their small body sizes make them vulnerable to predation, meerkats offer important insights into the evolution of cooperative defense against predators. Sentinels take turns looking out for predators and make alarm call to warn others of threats. Interestingly, meerkats gain both direct and indirect benefits from this behavior, with sentinels typically only assuming this role when they have feed and the costs to the caller are low (reviewed by Smith et al. [in revision](#)).

Alloparenting

Alloparental care is defined here as all aspects of care in which individuals guard, groom,

carry, play with, feed, or nurse the offspring of others (Creel and Creel 1991). As in many nonhuman primates, alloparenting is correlated with an increased brain size relative to body size in carnivores, suggesting that alloparenting enhances energy required to sustain neural tissue across the Carnivora (Smith et al. 2012).

Carnivores may engage in communal care of offspring that are not their own as members of plural or singularly breeding societies. Plural breeders with communal care include Artic foxes (*Alopex lagopus semenovi*), European badgers (*Meles meles*), banded mongooses (*Mungos mungo*), lions, and white-nosed coati (*Nasua narica*; Lukas and Clutton-Brock 2012). Shared communal dens allows for protection against infanticidal male lions (Packer et al. 1990). Similarly, spotted hyenas benefit from group defense of young from predation by lions (Smith et al. 2012). Singularly breeding carnivores in which only one member of a sex typically breeds is seen in many species belonging to the dog and mongoose families. In these groups, reproduction is typically restricted to one breeding pair and alloparenting is provided by nonbreeders, often including allonursing. One of the best-studied mongooses, the meerkat, has one breeding pair that actively evicts subordinate helpers if they attempt to breed (Lukas and Clutton-Brock 2012).

Conclusion

Although the extent to which early hominins ate meat is unclear, this article elucidates the numerous ways beyond group hunting that the social carnivores cooperate, all of which are also relevant to the ways that early hominins likely cooperated. Social carnivores therefore offer new interesting opportunities to study of convergent evolution in cooperation and will likely continue to shed new light on the origins of cooperation in early hominins. Species from both groups cooperatively hunt large game, defend resources, guard

against predators, and rear young. For example, early hominins were themselves likely hunted or otherwise killed by carnivores (reviewed by Smith et al. 2012). The evolution of cooperative defense of food and space, breeding, and protection from predators, as well as fission-fusion dynamics, in the Order Carnivora suggest that this taxonomic group continues to offer underexploited opportunities for testing hypotheses relevant to the evolution of hominins.

Large-scale comparative analysis of extant species of Carnivora indicates that multiple traits coevolved with the ability to cooperate; these correlates include a reduced sexual dimorphism, increased reproductive investment, high population density, fission-fusion dynamics, endurance hunting of big game in open habitats, and large brains (Smith et al. 2012). Similar traits may have also coevolved with cooperation in early hominins. Thus, studying the patterns of cooperation in social carnivores will surely continue to yield new and important insights that will contribute to our understanding of the evolution of cooperation more broadly for years to come.

Cross-Reference

- [Convergent Evolution of Hyena and Primate Social Systems](#)
- [Cooperation](#)
- [Cooperation Among Fishes](#)
- [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- [Cooperation and Social Cognition](#)
- [Cooperation in Social Insects](#)
- [Cooperation Varies with Genetic Relatedness](#)
- [Cooperative Alliances](#)
- [Cooperative Breeding](#)
- [Cooperative Foraging](#)
- [Cooperative Grooming](#)
- [Cooperative Hunting](#)
- [Division of Labor](#)
- [Evolution of Human Sociality, The](#)
- [Non-Human Primates](#)
- [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)

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Cooperation in Social Insects

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Many species of insects, such as ants, bees, wasps and termites, organize themselves into societies that parallel, and sometimes better,

human societies. They have impressive levels of social organization, communication, division of labor, cooperation and conflict, altruism and self-sacrifice, policing and punishment, and learning and teaching. They can accomplish feats in warfare with neighboring colonies or feats of internal cooperation such as the construction of sophisticated nests or mounds, which are impossible for individual colony members. They are organized into colonies whose sizes range from a few individuals up to a million or more, occupying from a few centimeters to hundreds of square kilometers (Fig. 1).

Consider a honey bee colony – perhaps the best known insect society (Winston 1987; Seeley 2010; Page 2013). Their colonies comprise tens

of thousands of individual bees, among which there is a single, large, and fertile female bee who is called the queen. Only the queen is mated, and with a store of sperm gathered from many males during her nuptial flight at the beginning of her life, she can lay thousands of eggs per day, both fertilized eggs that develop into females and unfertilized eggs that develop into males. Colonies may comprise a few male bees, also known as drones. The proverbially lazy drones do not take part in social life and do not contribute to domestic work. Instead, they leave their nests of birth and attempt to mate with virgin queens of other colonies. Drones successful in mating die in the act of copulation as their genitals are severed from their bodies and left hanging



Cooperation in Social Insects, Fig. 1 Examples of the major eusocial insects. Upper left, the tropical weaver ant, *Oecophylla smaragdina*; upper right, the Asian dwarf honey bee *Apis florea*; lower left, the best studied Indian

paper wasp *Ropalidia marginata*; lower right, the tropical mound-building termite (*Odontotermes obesus*). (Photos courtesy Dr. Thresiamma Varghese)

onto the females. The rest of the colony comprises smaller nearly sterile female bees, called workers. Workers have lost their genitalia over evolutionary time and cannot mate and cannot produce female offspring. They have small ovaries (much smaller than those of the queen), but these usually remain undeveloped in the queen's presence. Only upon the death of the queen and the colony not being able to rear a new queen do some workers develop their ovaries and lay a few haploid, male-destined eggs. In the presence of a healthy queen, workers refrain from reproduction and spend their whole lives working for the welfare of their colonies. Various tasks required for the functioning of the colony are performed in an orderly, systematic fashion through a process known as age polyethism. Young bees begin by cleaning the nest, after which they successively transition to perform the tasks of building the nest, feeding the larvae, guarding the nest, and finally venturing out to forage for pollen and nectar, which serve as the sources of protein and carbohydrate, respectively, for the growing larvae. The task a bee performs depends on its relative age in the colony. At the age at which they build the nest, they have active wax glands that convert the nectar consumed into wax, which is used for building the nest. As the worker bees get older, these wax glands degenerate, and their hypopharyngeal glands develop instead, secreting, many substances that are added to the diet of the larvae. Such relative age-based polyethism has a built-in flexibility permitting the colony to adaptively respond to unexpected changes in demography. Upon experimental removal of old bees, the relatively older of the intranidal workers becomes precocious foragers, leaving the nest at an abnormally younger absolute age than expected in normal colonies. Conversely, upon experimental removal of young bees, the youngest of the foragers become over-aged nurses, reverting to nursing, regenerating their already atrophied hypopharyngeal glands.

Division of labor is also modulated by the spatial distribution of tasks, and of the bees, and by their relative sensitivities of to the cues signaling the need to perform certain tasks.

Queens mate with several males and produce daughters of several patriline, contributing to the variability in the sensitivities of the bees to perform different tasks. For instance, bees differ in their response thresholds to the smell of dead bees so that undertaker bees are those that are most sensitive to the smell. If a colony is missing the most sensitive patriline, however, the intensity of the smell will soon be adequate for another patriline to remove the dead bees. Sources of pollen and nectar are located by some foragers, acting as scout bees; successful scouts return to the hive and recruit naïve bees to transport the pollen or nectar back to the hive. This they do by the well-known honey bee dance language. When the source is nearby, they perform a round dance motivating the bees to search nearby for the flowers with the expected smell. When the source is more than about 500 m, they perform a waggle dance, communicating specific information about the distance and direction of the food source. Bees estimate the distance and direction of the food source by the image motion on their eyes of the surrounding landscape (optic flow) and a process of dead reckoning called path integration, keeping track of their successive linear and angular displacements as they meander on their outward search flights (Wehner 1992, Mandal 2018). Worker bees thus devote their whole lives to the welfare of their colony and do not reproduce, even in the form of a few male-destined eggs that they can potentially lay. This is an extreme level of cooperation that we label as altruism. Even more impressive is their readiness to sting any marauder of their nest, an act that leads to their immediate death, as they cannot withdraw their stings from the bodies of their victims, owing to its outward-pointing barbs.

While there are some 10 species of honey bees worldwide, all belonging to the genus *Apis*, in the family Apidae, there are at least 15,000 species of ants, all belonging to the family Formicidae, found everywhere except in the Arctic and Antarctic poles. The ants have reached comparable levels of social complexity. Their species diversity permits the ants to embrace many lifestyles (Hölldobler and Wilson 1990).

For instance, leaf-cutting ants practice a sophisticated form of agriculture, cultivating fungi in their gardens and feeding a population of up to a million or more individuals only with the products of their labor – fungal spores. Medium-sized workers go out, locate, cut, and transport leaves back to their nests. These pieces of leaves of carefully chosen species are then ground into a fine paste and spread in the garden by even smaller workers. Fungal mycelia are then “planted” in the garden, and the spores eventually harvested. The fungi cultivated – certain kinds of mushrooms – are not known to exist outside the fungal gardens of the ants. Certain cultivars of the fungi appear to have been selected and passed down across generations of ant colonies and occasionally exchanged between colonies. The ants have elaborate adaptations for manuring their gardens with their feces and for keeping out weeds, with the help of a cocktail of antibiotics produced by bacteria they harbor on their own bodies.

In contrast, weaver ants dwell in nests on trees built by stitching leaves together with silk threads. While hundreds of ants use their combined effort to bend and maneuver leaves in alignment, some of them squeeze well-grown larvae to persuade them to donate some of their silk for the community good. Such donation of silk normally meant for their own pupation is costly to the larvae and constitutes an act of altruism even before the individual becomes an adult. Reminiscent of the lazy drones in honey bees, male ant larvae are less likely to contribute silk for nest building. Weaver ants are voracious predators in the tropical habitats of Africa (*Oecophylla longinoda*) and Asia (*Oecophylla smaragdina*) and build interconnected series of nests across several trees, with a single queen producing all the eggs required to maintain their colony populations.

In even greater contrast, ants of the genus *Diacamma* in Asia have permanently lost their queens. Their relatively small colonies (of a few hundred individuals) consist only of workers, one of whom is mated and functions as a gamergate (mated worker) and lays all the eggs for their colony. All workers are born with a pair of wing buds called gemmae, which appear to be

necessary for the female ants to attract males. The gamergate physically mutilates the gemmae of all eclosing workers and thus prevents them from mating and becoming reproductive. If the gamergate dies, the next worker to eclose retains her gemmae, becomes a gamergate, and mutilates all those who eclose after her. Mutilated workers perform all the tasks such as nest building, brood care, and foraging, required to rear the brood of the gamergate. *Diacamma* genus presents a unique method of reproductive regulation, leading to monogamy, i.e., reproductive monopoly by one egg-laying individual.

All social wasps are paper wasps because they construct their nests not with wax as honey bees do, not with leaves as some ants do, and not with soil as termites do but with paper. They manufacture their own paper by scraping cellulose fibers from plants, adding their own secretions to make a pulp and drying it. All social wasps belong to the family Vespidae. There is a very wide variation in the level of social evolution within the Vespidae. Species belonging to the subfamily Vespinae display advanced sociality resembling the honey bees, while species belonging to the subfamily Stenogastrinae are socially very primitive, bordering on the solitary. The subfamily Polistinae are intermediate and are considered primitively eusocial (see below). Their queens and workers are not morphologically differentiated, and most adults eclose being capable of taking on both queen and worker roles. Polistine wasps have been especially useful in investigating the evolution of social behavior because they display the transition from solitary to social life within the lifetime of individual wasps. New polistine wasp nests may be founded by a single-mated female who can, much like a solitary insect, build and guard her nest, lay eggs, forage, and bring her offspring to adulthood, all by herself. Her daughters from the first brood often stay back as sterile workers and assist her in producing more offspring, making the nest now a social unit. New nests may also be founded by small groups of females, in which case they are social units from the start. Female wasps may function as workers for some time and then transition to a queen status by leaving their

parent nests and starting new single foundress nests and new multiple foundress nests as their queens or may replace the queens of their parental nests. These transitions permit us to study the costs and benefits of solitary as well as social life and understand the ecological forces that mold the evolution of social behavior, despite the cost of non-reproduction (Gadagkar 2001).

Termites represent the fourth main group of insect societies. They are rather different in many ways. First, they do not belong to the insect order Hymenoptera like the ants, bees, and wasps but belong to a different insect order, the Isoptera. Second, unlike the Hymenopteran social insects which are haplodiploid (see below), they are diploid. They have both queens and kings that live together as a monogamous pair. Their workers are also of both sexes. In some species, the immature nymphs serve as workers and never complete their metamorphosis into adults. Workers ingest plant material, digest the cellulose with the help of gut microbiota, and feed the larvae and even the adult soldiers by regurgitating food to them by a process known as trophallaxis (Korb and Thorne 2017).

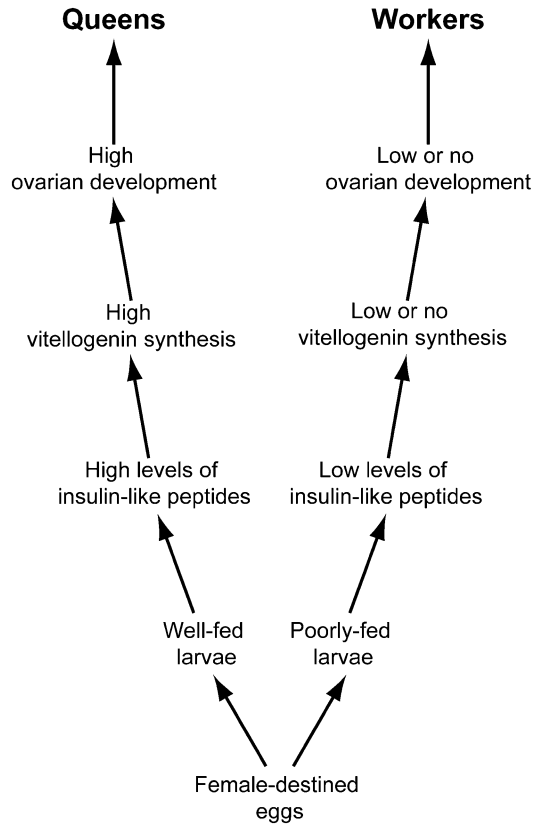
High levels of cooperation have made the social insects ecologically successful – in some tropical forest habitats, social insects, especially, termites and ants, may constitute three-quarters of the animal biomass. Biologists often use the terms cooperation and altruism interchangeably. In both cases, the reference is to behavior costly for the actor and beneficial to the recipient. As described above, social insects are replete with examples of such costly cooperation. However, their levels of social integration and division of labor vary greatly between different species so that they may be labelled as communal, quasi-social, para-social, semi-social, sub-social, or eusocial (Wilson 1971). The last label, “eusocial,” is considered the pinnacle of the evolution of social complexity. Eusocial species exhibit (i) cooperative brood care, so that individuals routinely care for offspring not their own; (ii) overlap of generations, so that caregivers can be younger than those who receive care;

and (iii) reproductive division of labor, so that only one or a few individuals in the colony reproduce, called queens or kings as the case may be, while the rest function as sterile helpers, often called workers. Among the eusocial species, it is customary to recognize two further sub-divisions, namely, the primitively eusocial and the advanced or highly eusocial. Until the 1970s, eusociality was thought to be restricted to ants, bees, and wasps in the insect order Hymenoptera and termites in the order Isoptera. In the last few decades, eusociality has also been discovered in thrips in the order Thysanoptera, aphids in the order Hemiptera, ambrosia beetles in the order Coleoptera, and shrimps, in the arthropod class Crustacea. Barring the case of the naked mole rat that lives in underground tunnels in Africa which curiously fits the definition, eusociality is restricted to insects and some shrimps. Despite this taxonomic range expansion of eusociality, advanced eusociality is restricted to ants, bees, wasps, and termites (Hölldobler and Wilson 1990; Gadagkar 2001; Rubenstein and Abbot 2017).

Biologists ask two kinds of questions about biological traits, the so-called proximate questions (sometimes called “how” questions) and ultimate questions (sometimes called “why” questions). In the context of cooperation in social insects, examples of the proximate kind include questions such as how do social insects recognize nestmates versus non-nestmates and maintain colony integrity; how do they divide colony labor among themselves; how does each member of the colony know what work to do when, and what not to do, so that they can function as an effective group; and how do they accomplish complex group tasks such as building elaborate nests, of locating, bringing, and processing food; etc. There is one overarching ultimate question, namely, how does natural selection favor the evolution of altruistic sterility by a process that is supposed to bring about survival of the fittest (fitness being usually measured as the number of offspring)? This can be split up into several sub-questions such as why does natural selection favor group living instead of

solitary living; why is the division of labor, the partitioning of tasks between different individuals, more efficient than each individual performing tasks independent of each other; and how does natural selection produce elaborate communications systems such as the dance language of honey bees, for example? (Gadagkar 1997).

We now have a fairly sophisticated understanding of the proximate mechanisms of social behavior and cooperation. These mechanisms may vary between the primitively and highly eusocial species. In primitively eusocial species, queens and workers are not morphologically differentiated. Queens and workers and sometimes even the sub-groups of workers that specialize in performing different tasks are referred to as castes. Caste differentiation in the highly eusocial species takes place in their early larval stages leading to the eclosion of differentiated adults that can no longer change their fate. In the primitively eusocial species, however, adults at eclosion are completely or nearly totipotent and can subsequently differentiate into queens or workers. Since the main difference between queens and workers is that of reproduction versus sterility, caste differentiation in highly eusocial species is developmentally regulated, while in primitively eusocial species, it is socially regulated. In highly eusocial species, the starting point of such differentiation is differential nutrition between queen-destined larvae and worker-destined larvae. The difference in nutrition may be one of the quality of the food, as in the case of the honey bee where queen larvae are fed with a sugar-rich royal jelly, while workers' larvae are fed with ordinary worker jelly. Or it may involve a difference in the quantity of food such that better-fed larvae become queens and poorly fed larvae become workers. Either way, differential nutrition channels larvae into alternate developmental pathways such that better-nourished larvae produce more insulin-like peptides, turn on vitellogenin synthesis, develop their ovaries, and become queens. Conversely, poorly nourished individuals produce less insulin-like peptides, produce little or no



Cooperation in Social Insects, Fig. 2 Our current understanding of the proximate mechanism of reproductive caste differentiation

vitellogenin, fail to develop their ovaries, and become sterile workers (Chandra et al. 2018) (Fig. 2). Further subdivision of workers into sub-castes can also be mediated by differential nutrition. In primitively eusocial species where caste differentiation is socially regulated, behavioral dominance-subordinate interactions modulate caste differentiation such that behaviorally dominant individuals become egg-laying queens and subordinate individuals become non-egg-laying workers. Further subdivision among workers into intranidal workers (those who work inside the nest) versus extranidal workers (those who work outside the nest) can also be mediated by similar aggressive interactions such that the relatively more dominant individuals among the workers, work at home, and the least dominant

Box 1 Hamilton's Rule

$$b \cdot r > c \quad \text{or} \quad b/c > 1/r$$

b = benefit to the recipient

c = cost to the altruist

r = genetic relatedness between the recipient and the altruist

or

$$n_i r_i > n_o r_o$$

n_i = number of relatives reared

r_i = relatedness to relatives

n_o = number of offspring reared

r_o = relatedness to offspring

Hamilton's rule defines the condition for the evolution of altruism. The upper forms of the inequality are useful to predict when an individual will be selected to sacrifice itself to help others. The lower form is useful to predict when a sterile individual who rears relatives will be selected over a fertile individual who rears its own offspring

individuals work outside, foraging for food and building material required by the colony.

Social insects accomplish many rather complex tasks both inside and outside their nests that appear to be inconsistent with their small brains and limited neural capacity. The secret of

their success in achieving complex outcomes incommensurate with the cognitive capacities of individual insects is that they use a process of decentralized self-organization – large numbers of individuals follow simple local rules, but there emerges a complex outcome due to their

collective behavior. This is sometimes called social intelligence and is the subject of intense investigations by interdisciplinary teams of biologists, physicists, and mathematicians (Camazine et al. 2003).

Understanding the ultimate causation of sociality, namely, the evolution by natural selection of cooperation and altruism, has been an even greater preoccupation of social insect researchers. The paradox of altruism referred to above was largely solved, at least in theory, by the realization that evolutionary fitness can be gained not only by producing one's own offspring but also by aiding the reproduction of genetic relatives. Indeed, one can combine the two kinds of fitness, direct (through offspring production) and indirect (through aiding genetic relatives), in a simple additive manner. The sum of these two kinds of fitness is known as inclusive fitness. Hamilton's rule predicts that natural selection can promote the evolution of altruistic behavior when the benefit to the recipient of altruism multiplied by the proportion of genes shared between the altruist and the recipient is greater than the cost incurred by the altruist (Box 1). This formulation of the solution to the paradox of altruism is known by several names – inclusive fitness theory, Hamilton's rule, or kin selection. There has been a great deal of effort to develop a sound mathematical foundation of this theory and some (but not enough) effort to see if animals actually behave as if they obey Hamilton's rule. Hamilton's rule can guide empirical researchers in the field and in the laboratory to ask the right questions and measure the right quantities. Nevertheless, very few studies have adequately measured all three parameters in Hamilton's rule to pronounce a clear verdict on whether altruists always obey Hamilton's rule or whether they sometimes get away without obeying the rule. The latter possibility suggests that there may be other ways of solving the altruism paradox. Selection at the level of the individual and also at the level of the whole colony (known as multilevel selection) is sometimes considered as promising avenues

for future research (Gadau and Fewell 2009). Meanwhile, the very validity of the inclusive fitness approach is being questioned by some prominent researchers, leading to a bitter controversy (Nowak et al. 2010). As a result, the study of cooperation in insect societies has gained a new vibrant dynamism, attracting much interest from theoreticians and empiricists alike, well beyond the traditional social insect community. Although many interesting phenomena have been discovered and their evolutionary logic is being worked out, many more phenomena surely await discovery. The study of cooperation in social insects is worthy of attention from practitioners of diverse disciplines, not only physics, chemistry, mathematics, and engineering in the natural sciences but also psychology, sociology, political science, and related disciplines in the social sciences.

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Cooperation to Solve the Prisoner's Dilemma

► Evolution of Cooperation

Cooperation Varies with Genetic Relatedness

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Synonyms

[Altruism](#); [Assortment](#); [Inclusive fitness](#); [Kin discrimination](#); [Kin recognition](#); [Kin selection](#)

Definition

A prediction from Hamilton's rule that altruism is more likely the more related the beneficiary is to the actor/donor. Here we briefly discuss the theoretical reasoning and focus on the empirical support for this prediction in humans.

Introduction

In the most general sense, cooperation occurs when one individual helps another. In evolutionary terms, helping means increasing the lifetime reproductive success of another individual. Genes are selected to produce behaviors that tend to increase their frequency in the population. They can do this via two routes, by inducing behaviors that increase either the reproductive success of their bearer (direct fitness), or the reproductive success of other individuals that tend to carry the same gene (indirect fitness). Hamilton realized this and that therefore natural selection, operating on genes, will lead to individuals that appear designed to maximize the sum of their direct and indirect fitness. Consequently, helping behaviors can evolve when helpers receive personal benefits in return that surpass their initial costs (increasing their direct fitness), e.g., through exchanging favors (reciprocity). Helping behaviors can also evolve even if helpers never receive any benefits, providing they direct their help toward other individuals that tend to carry the same helping gene (altruism, increasing indirect fitness). The easiest way to help individuals that tend to carry the same helping gene is to help close genealogical relatives, and therefore kin can be selected to cooperate altruistically (Kurzban et al. 2015).

Whether a helping behavior between kin will be favored by natural selection depends on three things: the costs to the actor/donor (in terms of reduced lifetime reproductive success), the benefits to the recipient (in terms of increased), and the probability that the recipient carries the same helping gene. In evolutionary terms, the probability that the recipient carries the same gene for helping at the same locus is termed Relatedness. Relatedness is a statistical coefficient genetic describing the similarity between the actor and recipient, relative to the rest of the population (see entry for 'R = Coefficient of Relatedness').

The relationship between these three terms is defined by Hamilton's rule, where $C < Rb$,

which means the benefits have to be greater than the costs, even when discounted by relatedness. Therefore, the more related the recipient is, the more costly the helping behavior can be and still be favored. Hamilton's rule leads to the prediction that cooperation will occur more often between closer relatives than distant relatives. Studies of how human cooperation varies with relatedness typically, for convenience, estimate relatedness on a scale from 0 to 1 by calculating the coefficient of relationship between two individuals, e.g., siblings are related by 0.5. Not that this estimate does not incorporate factors such as inbreeding (see entry for 'R = Coefficient of Relatedness').

Empirical Challenges

Although Hamilton's rule is supported in non-human studies, ethical considerations make it difficult to test experimentally in humans. Therefore human studies are often observational or survey based, and/or typically concern low-cost behaviors. This can be problematic because low-cost behaviors can be under less natural selection pressure, can be favored toward close and distant kin, and can be favored between nonkin for direct benefits (e.g., reputation). Strong tests of Hamilton's rule compare how cooperation varies with the degree of relatedness. Weaker tests only ask if humans cooperate more with kin than nonkin. Although how much people should discriminate between close and distant kin will depend on the costs and benefits and the cues of relatedness available. Note that studies which only measure cooperation toward nonrelatives do not invalidate Hamilton's rule, because they are unable to test the relative importance of Hamilton's rule. Indirect support comes from studies that show a psychological mechanism for recognizing kin, although this mechanism can also result from incest avoidance (Lieberman et al. 2007).

Survey Data

Survey responses, either on line or in the laboratory, often show that individuals expect to be more cooperative toward closer kin (Burnstein et al. 1994; Korchmaros and Kenny 2001; Stewart-Williams 2007), or expect to receive more cooperation from closer kin (Burton-Chellew and Dunbar 2015). For instance they report that they are more likely to donate a kidney to closer kin, although the effect sizes are modest (Stewart-Williams 2007). Burton-Chellew and Dunbar (2015) showed that individuals reported they *expected to receive* more help from closer kin than distant kin in times of crisis. While people still respond that they would help nonrelatives, mostly best friends, the key finding is that cooperation is increased toward close kin in support of evolutionary theory. Complementary data comes from studies that investigate the proximate, psychological, mechanisms governing these behaviors, and they typically show that feelings of "emotional closeness" are an important mediator of helping behaviors (Korchmaros and Kenny 2001).

Observational Data

Survey data has its limitations because the costs may never be realized. An analysis of real helping behaviors came from Smith et al. (1987) who analyzed patterns of giving by relatedness in 1000 wills. They found that when individuals made their wills, they allocated a greater proportion to their closer relatives. Specifically they gave 46% to close relatives ($r = 0.5$), and just 8% when $r = 0.25$ and 1% when $r = 0.125$. However as these transfers occur after death it could be argued they are noncostly. Another prominent nonexperimental study on real costs in real time was by Bowles and Posel (2005). They analyzed how much money male migrant workers sent "home" (remittances) and how this varied with the relatedness of the recipient to the migrant worker. Overall, they found that including relatedness in the model improved the model's accuracy to predict the value of

remittances, although other factors were important too. Likewise, many observational studies tend to find mixed support for the role of relatedness and other factors such as reciprocity in explaining human cooperation, but as explained above, cooperation can be explained by both direct and indirect benefits. The key prediction is that because indirect benefits vary with degree of relatedness, cooperation is greater or more likely with closer relatives.

Experimental Data

Perhaps the first experimental test of how cooperation varies with relatedness in humans was by Madsen et al. (2007). Across three crosscultural studies, participants were asked to adopt a painful posture (an isometric skiing exercise) in exchange for monetary benefits that went to their various relatives. Control treatments included benefits that went to themselves, nonrelatives, and charities. The posture involved supporting one's weight in a way that worked the thigh muscles and rapidly became intensely painful (after ~60 s). The pain may signal muscle damage and thus may indicate a genuine cost in evolutionary terms. A willingness to endure pain on behalf of relatives may also translate into a willingness to pay genuine costs. The longer the participant maintained the posture (cooperated), the more money their relatives got. The results were generally supportive. Cooperation did vary positively with relatedness, although in one study this arguably required including the control measure of help toward oneself, where relatedness = 1, and there were potential sex differences.

Other Factors

Finally, the indirect benefits of helping relatives also depend on other factors that ideally need to be controlled for. First, the indirect benefits of helping a recipient will be greater when they stand to gain more. This will occur when they have a

higher probability of future reproduction (more reproductive value), i.e., generally when they are younger, because the help is more likely to lead to increased reproduction. In both the studies of Madsen et al. and Smith et al., the results were more in line with theory once the reproductive value of the recipients was controlled for (Madsen et al. 2007; Smith et al. 1987). Second, competition occurs at different scales in populations, and relatives often have to compete, decreasing the benefits of kin-directed altruism. This is because helping one relative merely helps them to out-compete another relative, reducing the net gain (Borgerhoff Mulder 2007).

Conclusion

Studies generally find that very costly cooperation is greater toward kin than nonkin, which provides a weak test of Hamilton's rule. More studies are needed that directly test if and how individuals differentiate between close and distant kin.

Cross-References

- ▶ Altruism
- ▶ $C < Rb$
- ▶ Full Siblings Versus Half Siblings
- ▶ Genetic Relatedness
- ▶ Hamilton's Rule and Theoretical Implications
- ▶ Manipulative Use Of Kin Terminology

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Cooperation-Defect

- Prisoner's Dilemma, The

Cooperative Alliances

- Same-Sex Friendships
- Specific Friendships

Cooperative Breeders

- Access to Allopapents

Cooperative Breeding

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Synonyms

Primitively Eusocial; Quasisocial

Definition

Group living with allopaparental care

Introduction

Cooperative breeding is characterized by a combination of group living and allopaparental care, i.e., the care of others' offspring. Typically, young of previous broods remain in their natal territory and help raising subsequent offspring of dominant breeders. Hence, the characteristic of cooperative breeding is the joint occurrence of delayed dispersal of young with a propensity to help caring for offspring they have not produced. Such "helpers" may or may not participate in reproduction, but if they do, the majority of young is still produced by more dominant group members. In other words, the "reproductive skew" within groups is usually high.

There are numerous variations of this general pattern, which differs also systematically between taxonomic groups. In birds and mammals, for example, there are two prevailing patterns: either young that delay dispersal from their natal territory help raising their later born siblings, or several females produce offspring jointly and raise them cooperatively, which is usually referred to as "communal breeding" (Koenig and Dickinson 2016). In fishes, insects, and spiders, there are sometimes different variations of these patterns.

For instance, in fishes young delaying dispersal may help raising offspring of unrelated breeders that have replaced their own parents, or they may join forces to raise a brood that has been sired by several different males (Taborsky 1994). In some insects, several females jointly found a nest, in which only the dominant takes over the reproductive role, while subordinates help raising the latter's offspring irrespective of their degree of relatedness to them (Field and Leadbeater 2016). In social spiders, allofeeding of offspring that were not produced by the helpers may reach extreme levels, where helpers are consumed by these young even if they are unrelated to them (Lubin and Bilde 2007).

From an evolutionary perspective, cooperative breeding is of fundamental interest because it involves alloparental care, i.e., apparently altruistic behavior. This provides exceptional opportunities to ask under which circumstances selection will favor individuals accepting an apparent fitness cost at a benefit to the recipients of their helpful behavior.

Evolution of Cooperation

There are two principle ways how such behavior can evolve (Taborsky et al. 2016). Firstly, cooperative behavior may be mutualistic, i.e., the act itself has immediate fitness benefits to the actor; in this case, the behavior will be selected regardless of its beneficial effects on potential receivers. Secondly, cooperative behavior may be altruistic, which means that one individual helps another at immediate fitness costs exceeding the immediate fitness benefits of the act, i.e., the act bears immediate net costs. There are four possibilities how altruism, that is, cooperative behavior bearing immediate fitness costs, can be selected for.

- (1) Kin selection. If the donor and the beneficiaries of the helpful act share a common genealogy, i.e., if they are related by common descent, genetic predispositions for helpful behavior may be favored if the fitness benefits

to the receiver times the degree of relatedness between donor and receiver surpass the fitness costs to the donor. This algorithm has been termed "Hamilton's rule" after its originator William Hamilton (1964).

- (2) Green beard effects. If there is a genetic correlation between cooperative behavior and traits allowing individuals to identify carriers of such genetic cooperation predisposition, co-operators can exercise selective altruism towards other co-operators. Identifier traits can be arbitrary like a green beard, which is the reason why this potential mechanism has been coined "green-beard effect" by its originator (Richard Dawkins 1976).
- (3) Reciprocity. Altruistic behavior may be positively selected if it increases the chance of the actor to get something back in the future that overcompensates the immediate net costs of the act (Trivers 1971).
- (4) Coercion. Prospective receivers may enforce cooperative behavior on potential donors against the latter's fitness interests. As in this case the cooperative behavior reduces the lifetime fitness of donors, countermeasures against such exploitation will be selected. This can lead to an evolutionary arms race just like in brood parasite – host interactions.

Regarding the evolution of cooperative breeding, there is evidence for a role of both mutualism and altruism, and regarding the latter possibility, kin selection and reciprocity seem to be the most important underlying mechanisms (Taborsky et al. 2016).

Why Delay Dispersal?

There are two major ecological constraints that may select for delayed dispersal of offspring, i.e., for a prolonged stay in the natal territory.

- (1) Habitat saturation, which occurs when all areas suitable for breeding are already occupied by superior competitors. This constraint has been implied to explain cooperative breeding in many

bird species (Koenig and Dickinson 2016). (2) High risk, which may prevent dispersal if either the dispersal itself or the subsequent settlement entail exceptionally high risk. This ecological constraint has been identified in cooperatively breeding fishes (Heg et al. 2004).

Why Help?

Staying in the natal territory will usually lead to some form of family formation, but this does not compel individuals to help raising the dominants' offspring. As alloparental care usually entails fitness costs, there must be some benefits compensating for such seemingly altruistic behavior. As has been outlined above, there are in principle two evolutionary mechanisms responsible for costly helpful behavior shown by subordinate group members. (1) They may be related to the beneficiaries, i.e., to the dominant breeders and their offspring. (2) Alternatively, there may be reciprocal benefits to dominants and subordinates, i.e., some sort of trading of commodities between the different types of group members. In Lake Tanganyika cichlids, for instance, it has been shown that the brood care helpers benefit from being protected in the territory of dominants, and in turn they help caring for the latter's brood; in other words, they "pay-to-stay" in a safe territory. The amount of "rent" to be paid by subordinates depends on the need for help and on the demands of dominants, which are communicated to their helpers by restrained aggressive behaviors (Taborsky 2016).

Proximate Mechanisms

Important prerequisites for a proper operation of group living and cooperation in highly social species is the ability of individuals to recognize conspecifics by their group affiliation, rank, role, and/or relatedness. In some cooperative breeders, individuals specialize in different

duties. This is most prominent in animals continuing to grow after maturation such as fish, because this results in body size variation between group members; small and large individuals can perform diverse duties with different efficiencies, for instance direct brood care, digging out burrows, or territory defense. Such behavioral specialization of group members is most highly developed in eusocial insects, but it sometimes occurs also in cooperatively breeding vertebrates where individuals maintain their reproductive potential such as mole rats and cichlids (Taborsky 2016).

Most importantly, relatives should be distinguished from nonrelatives, because this allows differential allocation of altruistic help towards related beneficiaries. Such distinction has been shown to exist in several species of mammals, birds, and fish. While the cooperation propensity rises with increasing relatedness in many mammals and birds, there are cases where this does not hold. In vampire bats, for example, a blood meal is often donated to related young, but most blood donations depend on reciprocal exchanges and not on relatedness. In cooperatively breeding cichlids, relatedness even reduces the helpers' propensity to care for the eggs of dominants, as the latter demand more help from unrelated subordinates. If the alternative "outside options" of subordinates are bad, for instance, because of a high mortality risk outside of a territory, the helpers are prepared to pay a high price for protection and resource use in the dominants' safe territory (Taborsky 2016).

Some studies have shown that individuals may differ consistently in their propensity to cooperate, i.e., they show "helping personalities" which are heritable and hence subject to natural selection. Dominants may respond to such personality differences of subordinate group members.

The hormonal, genetic, and epigenetic mechanisms underlying behavioral decisions of dominant and subordinate group members are hitherto little understood. As many behavioral and physiological traits of several different individuals are involved, this topic features considerable

complexity, which makes it both challenging and rewarding to unravel these mechanisms. As the underlying neurophysiological and endocrine mechanisms seem to be deeply conserved among vertebrates, this allows to study general regulatory mechanisms in cooperative breeders that can be investigated under standardized experimental conditions, like cooperatively breeding cichlids (Taborsky and Taborsky 2015).

Conclusion

Cooperative breeding reflects the most complex form of social organization known among animals, featuring the highest degrees of cooperation and altruism. This applies particularly to its most extreme manifestation, eusocial organization, where individuals forego own reproduction for their entire lives to raise offspring of close relatives. The evolution of such altruism is explained through the action of kin selection or green-beard effects, as the genetic causes for lifelong reproductive abstinence can only be transmitted between generations by the offspring of individuals sharing the same genetic makeup with above average probability. In cooperative breeders that do not cross the line to complete celibacy, which is a social organization occurring in many different taxa, some form of reciprocity may also be responsible for cooperation and sharing of tasks among group members. This makes cooperative breeders a particularly useful target for studies of ultimate and proximate mechanisms of cooperation and social evolution.

Cross-References

- [Adaptation](#)
- [Altruism](#)
- [Alloparenting](#)
- [Brood Care](#)
- [Cooperation](#)
- [Cooperative Foraging](#)

- [Cooperation Among Nonchimpanzee, Nonhuman Primates](#)
- [Eusociality](#)
- [Evolution of Cooperation](#)
- [Food Sharing](#)
- [Helpers at the Nest](#)
- [Male-Male Competition or Male Provisioning?](#)
- [Nonhuman Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)

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Cooperative Childrearing

► Alloparenting

Cooperative Foraging

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Synonyms

By-product mutualism

Definition

The process through which two or more individuals benefit from working together to obtain food resources.

Introduction

Many species benefit from working together, in some form, for the purpose of locating and consuming food. Animals, from insects like the honeybee (*Apis* spp.) to carnivores such as the gray wolf (*Canis lupus*) and orca (*Orcinus orca*), benefit from not only foraging socially but cooperatively. This cooperation has been suggested to be one of the key drivers of evolution, sparking unique cognitive abilities (Wilson 2000).

Cooperative foraging, or by-product mutualism (Connor 1986), distinguishes itself from other social foraging styles (e.g., imitative foraging) in that it occurs when individuals are able to distinguish between group members and engage in altruistic self-restraint and complex communication. These abilities allow group members to coordinate behaviors to achieve a common goal,

thus increasing individual foraging efficiency (Wilson 2000).

Mechanisms Driving the Evolution of Cooperative Foraging

There are five mechanisms for the evolution of cooperative behavior: (1) kin selection, (2) direct reciprocity, (3) indirect reciprocity, (4) network reciprocity, and (5) group selection (Nowak 2006).

Kin Selection

According to Hamilton's rule, evolution favors cooperation when the donor and recipient of a behavior are genetically related to one another. In essence, when two individuals are related, they each benefit from the other's success through their shared genes. Therefore, cooperative behavior among relatives is an investment in one's own genes and is motivated by the individual's drive to promote its own genetic success (Hamilton 1964). Hence, most eusocial groups consist of closely related individuals (Boyd and Richerson 1989).

Direct Reciprocity

Despite the fact that individuals may be more likely to invest resources in a relative, individuals of various species also cooperate with nonrelated individuals, through direct reciprocity. Direct reciprocity results form a tit-for-tat strategy of cooperation between individuals. That is, if *Individual A* shares food with *Individual B* today, then *Individual B* will reciprocate tomorrow. Through this cooperative strategy, the two animals benefit over the long-term despite short-term losses in resources, thus increasing both individuals' overall fitness regardless of relatedness (Nowak 2006).

Indirect Reciprocity

For this strategy, the donor assists a recipient for no immediate direct gain in resources. Instead, in indirect reciprocity, *Individual A* assists *Individual B* who in turn assists *Individual C*, and so on, until another individual assists *Individual A* thus

returning the original investment. Humans are the only species to fully engage in indirect reciprocity likely because of the strong cognitive demands of such a strategy (Boyd and Richerson 1989). This strategy requires that individuals can remember their own actions, the actions of others, monitor group social structures, and the use of language to spread knowledge regarding the actions of others (Nowak 2006). For example, when an individual donates resources (e.g., food or money) to an individual in need, human social groups often hold the donor in high esteem. Indirect reciprocity may even be institutionalized in some societies, in the form of tax deductions for donating to charity. Indirect reciprocity promotes cooperation only when the probability of knowing an individual's reputation exceeds the cost-benefit ratio of the behavior in question.

Network Reciprocity

In a mixed group, where cooperators (individuals who suffer an intentional loss for the purpose of another's gain) and noncooperators (individuals who neither receive a loss nor benefit others) are combined, cooperators benefit their neighbors while noncooperators do not – thus enhancing the fitness of noncooperators while detracting from that of cooperators. To combat this phenomenon, cooperators come together to form a network cluster, excluding noncooperators, within which they can benefit one another. In humans, network reciprocity has been documented in cases when each individual within the network cluster both reports giving and receiving assistance from others within the cluster (Nolin 2012).

Group Selection

Because a group of cooperators has a higher rate of fitness than a group of noncooperators, it is likely that cooperators would reproduce at a higher rate. Thus, cooperators are likely to produce more offspring than do noncooperators, over time eliminating or reducing noncooperators through genetic sampling (Nowak 2006).

The Evolutionary Benefits of Cooperative Foraging

When a group consists purely of cooperators, the members of the group benefit from higher per capita fitness. Alternately, when a group consists entirely of noncooperators, the group members experience lower levels of fitness. However, in a mixed group (consisting of both cooperators and noncooperators), noncooperators experience increased fitness at the cost of the cooperators. Therefore, evolution strongly favors cooperation, but also rewards noncooperators, in the right environment (Nowak 2006).

The proposed causes of the increased rates of fitness, experienced by cooperative groups, include (1) increased vigilance and protection from danger, (2) increased information regarding the location of food sources, (3) increased ability to capture prey, (4) increased efficacy in defending resources, and (5) increased ability to exploit depletable resources (Clark and Mangel 1986).

Increased Vigilance and Protection from Danger

As group size increases, individual bouts of vigilance decrease proportionately. This phenomenon is described as the *group size effect* and results from the premise that as group size increases overall vigilance increases – thus reducing the vigilance required of each individual (known as the *many eyes hypothesis*), allowing individuals to devote more time to obtaining food (Lima 1995).

Increased Information Regarding the Location of Food Sources

Cooperative species benefit from the knowledge of the most experienced group members through imitation, observational learning, or communication. This allows group members to increase the efficiency with which they adapt to novel situations, systematically exploit resources. This is especially true when food resources are located in patches (Kurland and Beckerman 1985; Wilson 2000).

Increased Ability to Capture Prey

Through group cooperation, predators are able to maximize foraging efficiency by taking prey in either greater numbers or of a larger size than they would otherwise be capable of killing if hunting alone. Cooperative hunting requires that individuals are capable of coordinated behaviors. For example, African lions (*Panthera leo*), gray wolves, and orcas have demonstrated increased foraging efficiency through the coordination of movements to herd and contain prey animals by joining forces in order to overpower and kill large prey animals (Wilson 2000).

Increased Efficacy in Defending Resources

As individuals are working to obtain resources as a group, each individual has a similar investment in defending access to food resources against competitors. Thus, individuals benefit from an increased likelihood of maintaining access. For example, gray wolves in Yellowstone National Park actively guard a kill after group members have become satiated (e.g., Mech 1970).

Increased Ability to Obtain Depletable Resources

Cooperative foraging is most beneficial when food resources are unpredictable or scarce, as cooperative groups are likely to locate and exploit resources with greater efficiency than individuals (Wilson 2000). Solitary human foragers living on the savanna, for example, would have expended considerable energy attempting to procure patchily disperse food resources. Alternately, searching together, a group of people are much more efficient at locating and harvesting these resources. Therefore, selection favors those who cooperate with others in these environments (Kurland and Beckerman 1985).

Horn's Principle of Group Foraging

Some species, particularly flocking birds, may benefit from forming a cooperative group under certain circumstances. According to *Horn's*

Principle of Group Foraging, animals benefit from maintaining and defending individual territories when food resources are evenly distributed. However, when food resources are not evenly distributed, and unpredictable, animals benefit from foraging as a group. Groups benefit from the previous knowledge of individuals within the group, increasing the likelihood that any one group member will locate food on a given day. Therefore, some animals may not live as a cohesive group for the duration of their lives; instead they create microterritories located near a centralized location which then allows the animals to forage more or less as a group (Wilson 2000).

The Evolution of Communication and Cooperative Foraging

For communication to develop in the context of cooperative foraging, there must be two categories of individuals: signalers, who alert others to located food resources (i.e., cooperators), and non-signalers (i.e., noncooperators), who may respond to signals but do not signal to others. Individuals who receive emitted signals, and are not currently located in a superior location, will relocate in order to exploit the signaled resources. When altruistic communication directly benefits the recipient, but not the donor, it is considered to be cooperative communication, which is to be separate from inadvertent information sharing. Cooperative communication, which can be expressed in the form of recruitment calls, is issued when food resources are located. Despite the apparent benefit of keeping the resource to one's self, individuals recruit conspecifics to benefit from the located resource. Although this initially appears to be an altruistic endeavor, evaluations of this strategy demonstrate that through recruiting others, individuals effectively increase the number of animals issuing recruitment calls within a centralized area – thus increasing the efficiency with which resources are located and exploited within that area (Torney et al. 2011).

Conclusion

Cooperative foraging is considered to be a driver of evolution not only because of its cognitive requirements but also due to the resulting increase in individual fitness (Wilson 2000). Still, there are disagreements as to the relative benefits of cooperative foraging. Clark and Mangel (1986) argue that theories aimed at understanding cooperative foraging underemphasize group hierarchical structures, in-group competition, and environmental conditions which may mitigate the overall benefits of cooperation. For example, decreased individual vigilance within groups could alternately be explained as being a result of intragroup competition for food resources, area to cover, and variations in foraging ability rather than the assumed vigilance of other animals in the group (Vasquez 1997).

While there may be some merit to these concerns within certain contexts, complex species such as bottlenose dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*) demonstrate that social hierarchies may actually facilitate cooperative foraging as demonstrated by both a division of labor and a specialization of roles within foraging groups (Gazda et al. 2005) as well as food sharing (Gilby 2006). Similar observations have been made in Arabian babblers (*Turdoides squamiceps*). In this species, it has been observed that hierarchies not only play a role in selecting foraging strategies, but subordinate animals may even demonstrate more flexible behaviors in order to make use of novel foraging opportunities (Keynan et al. 2015). Clark and Mangel (1986) are correct in asserting a need to evaluate individual occurrences of cooperative foraging when determining how that behavior has evolved and its overall benefit to the organisms concerned.

Cross-References

- Communication and Social Cognition
- Cooperation in Social Carnivores
- Cooperation and Social Cognition
- Eusociality
- Nonhuman Reciprocal Altruism

- Primate Cooperation
- Psychology of Reciprocal Altruism
- Reciprocal Altruism
- Social Learning and Social Cognition

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imposes important costs to the donor, such as decreasing their predator vigilance or time spent foraging. Symbiosis, kin selection, direct reciprocity, and being part of complex social functions are the main mechanisms proposed through which donor individuals may gain benefits and increase their fitness via grooming a conspecific.

C

Cooperative Grooming

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Synonyms

[Allogrooming](#); [Allopreening](#); [Mutual grooming](#); [Reciprocal grooming](#); [Social grooming](#)

Definition

In contrast to autogrooming during which an individual cleans itself, cooperative grooming is defined as a social act during which an animal grooms a conspecific, usually implying costs to the groomer and benefits to the groomee.

Introduction

Grooming functionally serves different hygienic purposes such as removing dead skin and parasites. Therefore, it is an important part of hygienic routine in most animals and is strongly associated with survival. In many species, individuals do not only groom themselves but are also frequently observed grooming conspecifics (reviewed in Spruijt et al. 1992) or even individuals from other species (cleaning symbiosis; Poulin and Grutter 1996). Within species, besides increasing hygiene, allogrooming relaxes the receiving individual, serves as appeasement gesture to reduce aggression between partners, can be part of courtship behavior, and facilitates social bonds such as between mother and offspring or between individuals of a social group. However, allogrooming

Mechanisms and examples of cooperative grooming

When grooming themselves, individuals can not always reach all parts of their body and thus depend on the help by conspecifics or specialized symbionts (e.g., cleaner fish; Poulin and Grutter 1996). In the latter case, the cleaner removes and eats parasites, dead skin, and other material from the surface of a host organism (the client), and thus grooming is of mutual benefit for both the donor and receiver. However, allogrooming among conspecific can usually not be explained by immediate benefits for the donor but is still one of the most commonly observed social interactions in many animals (Spruijt et al. 1992). In fact, time spend in grooming a conspecific has to be traded off against predator vigilance or foraging, both which would increase the fitness of an individual. Similar to other altruistic behavior, allogrooming therefore is costly for the donor, and scientist have been searching for explanations on why this behavior evolved.

If animals groom individuals which they are related to, such altruistic behavior can be explained by kin selection (Hamilton 1964): An individual gains fitness by helping a conspecific sharing proportions of the same genes (i.e., siblings). After all, overall fitness or inclusive fitness is defined as the sum of own reproduction and the reproduction of relatives in comparison with the total reproductive output of the population. Thus, helping relatives promotes an individual's relative genetic representation in the gene pool in the next generation.

However, animals do not only groom relatives but also conspecifics which they are not related to. Direct reciprocity is one potential mechanism that may establish cooperative grooming among

nonkin. Impalas (*Aepyceros melampus*), for example, groom each other in the head and neck area (Hart and Hart 1992), a behavior which is directly reciprocated between individuals, i.e., the receiver of a grooming bout will return the favor to the previous groomer. Notably, in some species, grooming can not only be reciprocated with grooming but may be exchanges for other services. In the common vampire bat (*Desmodus rotundus*), for example, allogrooming is correlated with food sharing among individuals (Wilkinson 1986), and female baboons (*Papio ursinus*) can trade grooming for support during aggressive interactions and other valuable commodities (Barrett et al. 1999).

Thus, beyond hygiene, allogrooming may reflect the characteristics of the social relationship between donor and receiver and thus have important social functions. The structure and function of allogrooming relationships have mostly been studied in primates, such as in capuchin monkeys (*Cebus apella*; Bitetti 1997). Here, dominant males and females do engage more in allogrooming than subordinates, and females with infants are especially attractive grooming partners. Recently, potential social functions have been described in nonprimate species as well, such as in the cooperatively breeding meerkat (*Suricata suricatta*), where grooming may help to maintain beneficial social relationships and indicate the value of subordinate breeding helpers (Kutsukake and Clutton-Brock 2010). Through enhancement of the social position within a group, allogrooming individuals can thus increase their fitness via other benefits such as social support.

In humans, besides during child care, mutual grooming among is mostly directed to romantic partners, being of importance for courtship, developing trust, and as a potential indicator for parental investment (Nelson and Geher 2007).

Conclusion

Cooperative grooming is part of hygienic routine in many animals and is often reciprocated

between individuals. Besides, it has important social functions, such as during courtship or by establishing and maintaining social bonds. While cooperative grooming is common in other mammals, there are only few studies on humans where grooming is mainly observed as part of child care and between romantic partners.

Cross-References

- ▶ Adaptation
- ▶ Adaptation and Natural Selection
- ▶ Adaptations for Reciprocal Altruism
- ▶ Altruism
- ▶ Altruism Advertises Cooperativeness
- ▶ Altruism Advertises Generosity
- ▶ Altruism Among Nonkin
- ▶ Altruism and Costs to Altruist
- ▶ Altruism and Watching Eyes
- ▶ Altruism Defined by Benefits Conferred
- ▶ Altruism Displays Cooperative Potential
- ▶ Altruism in Kin Selection
- ▶ Altruism Norms
- ▶ Cheater Detection Adaptations
- ▶ Cooperation
- ▶ Cooperation Among Fishes
- ▶ Cooperation Among Nonchimpanzee, Non-human Primates
- ▶ Cooperation and Social Cognition
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Cooperative Alliances
- ▶ Cost-Benefit Analysis
- ▶ Costly Signaling and Altruism
- ▶ Discounting of Future Returns
- ▶ Evolution of Cooperation
- ▶ Evolution of Reciprocal Altruism
- ▶ Field of Behavioral Ecology, The
- ▶ Game Theory
- ▶ Genuine Altruism
- ▶ Gossip and Indirect Reciprocity
- ▶ Gratitude, Sympathy, and Empathy
- ▶ High-Cost Altruistic Helping
- ▶ Higher Status in Group
- ▶ Human Courting
- ▶ Indirect Benefits of Altruism

- ▶ Indirect Reciprocity
- ▶ Ingredients of Reciprocal Altruism
- ▶ Iterated Prisoner's Dilemma Model
- ▶ Kin Selection
- ▶ Living in Groups
- ▶ Non-Human Primates
- ▶ Nonhuman Reciprocal Altruism
- ▶ Peer Competition and Cooperation
- ▶ Primate Cooperation
- ▶ Primates
- ▶ Prisoner's Dilemma, The
- ▶ Problem of Altruism
- ▶ Psychology of Reciprocal Altruism
- ▶ Puzzle of Altruism, The
- ▶ Reciprocal Altruism
- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reciprocal Altruism and Group Living
- ▶ Reputation and Altruism
- ▶ Robert Axelrod's (1984) *The Evolution of Cooperation*
- ▶ Robert Trivers
- ▶ Strategies for Successful Cooperation
- ▶ Theory of Reciprocal Altruism

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Cooperative Hunting

- ▶ Coalitional Hunting

Cooperative Investments

- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)

Cooperative Returns

- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)

Co-opted Adaptation

- ▶ By-Products of Adaptations
- ▶ Evolutionary By-Products

Co-opted Spandrel

- ▶ By-Products of Adaptations
- ▶ Evolutionary By-Products

Coping Styles

► Personality, Gender, and Culture

Copulate

► Human Copulation

Copulation

- Penile-Vaginal Sex
 - Sexual Behavior
 - Sexual Intercourse
-

Copulatory Intrasexual Competition

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Synonyms

Reproductive competition among members of the same sex

Definition

Competition that takes place during coitus between members of the same sex to control fertilization and reproduction.

Introduction

Contrary to the impression that is created by the fact that men and women often have radically different reproductive best interests, males and

females do not typically compete with each other for fitness. When it comes to reproductive competition, males compete with other males for paternity, and females compete with other females to attract high quality mates who in the case of humans will enter into a long-term committed relationship (i.e., a pair bond) that includes protection and provisioning of the female and her offspring. In other words, reproductive competition among humans is often intrasexual rather than intersexual.

For most sexually reproducing species the males' role in reproduction is simply to provide a complementary set of gametes, and therefore insemination represents the end point in the reproductive process. However, for females, particularly mammalian females, insemination is the mere beginning of the reproductive process which in the case of humans can last for years or even decades (e.g., pregnancy, childbirth, breast feeding, child rearing).

In the strict sense of the term, copulatory intrasexual competition involves competition among members of the same sex that occurs in the context of copulation. Examples include evolved mechanisms related to sperm competition that enable males to adjust the contents of an ejaculation to take into account the possibility that the female may have viable semen in her reproductive tract left by former males, or that she may be likely to have sex with other males in the near future. Among females, copulatory intrasexual competition could include changes in the strength and frequency of orgasm and/or the timing of intercourse so as to make conception more or less likely when having sex with certain males (see entry on ► [“Female Copulatory Orgasm”](#)).

To illustrate some of the intricacies of intrasexual competition, a good example is the concept of human paternal assurance tactics, with particular emphasis on counter insemination tactics.

Human Paternal Assurance Tactics

When it comes to genetic assurance, females have an enormous advantage over males. Maternity is

always certain. Females have an iron clad guarantee of sharing 50 % of their genes in common with each of their children. But largely as a consequence of female infidelity, the probability of paternity is rarely certain and males have to contend with the prospect of being cuckolded; i.e., duped into caring for children sired by other males (see entry on ► [“Cuckoldry Risk”](#)).

Gallup and Burch (2006) identified and developed a refined analysis of four evolved strategies that men use to maximize the likelihood of paternity, or conversely to minimize the chance of being cuckolded. These tactics exist as a set of sequentially dependent strategies which begin with “Insemination Prevention Strategies” that function to preclude or at least minimize the likelihood that their committed partner will be inseminated by other males. These include mate guarding (Buss 2002), mate sequestering, mate monitoring, and male sexual jealousy (Daly and Wilson 1982). Other techniques used to discourage or preclude female infidelity include chastity belts and infibulation as barrier methods, or surgical removal of the clitoris designed to diminish any interest the female may have in engaging in sex with other males. It has also been suggested in this context that males who insist on having high frequency sex with their female partners do so to minimize the likelihood of partner infidelity by keeping their partners sexually satiated (Shackelford 2003).

However, should these tactics fail and the female is inseminated by another male, men then employ “Counter Insemination Strategies” which include sperm competition (e.g., Shackelford, 2003) and semen displacement (Baker and Bellis 1995). These function to reduce the likelihood of conception by the rival male (see entries on ► [Evolutionary Arms Race](#) and ► [Tactics to Solve Adaptive Problems of Sperm Competition](#)).

Should these mechanisms fail and the female is impregnated by another man, the next category of paternal assurance strategies involves “Pregnancy Termination Tactics” which can involve pregnancy-induced domestic violence that terminates the pregnancy (Burch and Gallup 2004), or vigorous sex that leads to coitus-induced uterine contractions which interfere with embryo

implantation (for details see Gallup and Burch 2006). Finally, if the pregnancy prevails and a child is born, the remaining class of paternal assurance strategies involves “Postpartum Investment Strategies” where the resident male adjusts his investments in the child in relationship to the probability that they share genes. These strategies can range from instances of genuine investment, to indifference, neglect, abandonment, child abuse, or even infanticide. There is growing evidence, for example, that males are sensitive to paternal resemblance and invest preferentially in infants with whom they share facial features (Platek et al. 2002). Recent evidence shows that in addition to shared physical features, shared interests and attitudes as behavioral phenotypes that may also be mediated by genes also appear to promote greater paternal investment by fathers (Gallup et al. 2016).

Semen Displacement

Sperm competition is the most frequently investigated form of intrasexual competition among males. In the case of humans, however, semen displacement has emerged to aid and abet more traditional instances of sperm competition. As suggested initially by Baker and Bellis (1995), there is now evidence that the configuration of the human penis has evolved to purge or displace semen recently left by other males from the female reproductive tract to enable the resident male to substitute his semen for those of his rivals (see entry on ► [“Evolutionary Arms Race”](#)).

Attempts to simulate sexual encounters under laboratory conditions using artificial genitals show that variation in penis morphology as it relates to the glands and the coronal ridge is related to semen displacement (Gallup et al. 2003). How the penis is used during sex also affects the magnitude of semen displacement; i.e., evidence suggests that the depth of insertion of the penis into the vagina is proportional to how much semen is removed. Consistent with the results of these laboratory simulations, follow-up studies (appearing in the same paper) of college students in committed sexual relationships

showed that under conditions that raise the prospect of female infidelity, males react by engaging in deeper and more vigorous thrusting.

The Topping-Off Hypothesis

Another potentially important dimension of copulatory intrasexual competition is emerging evidence in human males for context specific mechanisms that adjust the composition of the ejaculate on an occasion by occasion basis to fit the male's reproductive best interests (see entry on ► [“Seminal Plasma”](#)). For instance, the quality of semen samples obtained through masturbation (as measured by sperm count and sperm motility) is greater for males who watch sexually explicit videotapes than for those who have to rely on their imagination (Yamamoto et al. 2000). Higher quality ejaculates are also obtained from semen donors who watch sexually explicit films of novel as opposed to familiar women (Joseph et al. 2015). Moreover, in contrast to harvesting semen samples through masturbation, samples obtained using coitus interruptus are of greater quality (Zavos et al. 1994).

Rape may represent another instance in which there are changes in the chemical properties of the human ejaculate. In an attempt to explain the increased risk of conception as a consequence of rape as opposed to consensual sex, Burch and Gallup (2006) speculate that there may be mechanisms operating at the level of male reproductive biology that adjust the concentration of female sex hormones in seminal fluid to make induced ovulation as a result of sexual assault more likely. Rather than a matter of idle armchair speculation, Burch and Gallup identify what appear to be the hormones in seminal fluid that could trigger ovulation and outline several ways to test this hypothesis by conducting assays on semen samples obtained from rape victims or from semen donors who watch nonconsensual pornography (see entry on ► [“Seminal Plasma”](#)).

Conclusion

Reproductive competition among men typically takes the form of competition for paternity. Reproductive competition among women often involves competition for exclusive access to a high status/high quality man who will enter into a pair-bonded relationship with the women which will insure for the protection and provisioning of the woman and her children.

Cross-References

- [Cuckoldry Risk](#)
- [Evolutionary Arms Race](#)
- [Female Copulatory Orgasm](#)
- [Seminal Plasma](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)

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Copulatory Plugs

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Synonyms

[Mating plug](#); [Sperm plug](#); [Sphragis](#); [Vaginal plug](#)

Definition

Plugs consisting of coagulated semen or parts of male genitalia that are deposited in the female genital tract during or after mating.

Introduction

Copulatory plugs are taxonomically widespread, having been described in nematodes, insects, arachnids, amphibians, reptiles, and mammals. Copulatory plugs are often interpreted as male adaptations to male-male reproductive competition. Preventing or delaying female remating with rival males can increase the paternity success of males that deposit copulatory plugs. However, copulatory plugs may well serve other non-mutually exclusive functions.

Taxonomical Variation

There is great variation in the composition, size, and origin of copulatory plugs among animal taxa. Amorphous copulatory plugs are composed of seminal fluids that are excreted by male accessory glands, as is the case in the majority of taxa. The substances that form the plug are secreted by one or several of the accessory glands. Once transferred to the female, these seminal fluids coagulate into a gelatinous or waxy substance. In many taxa, copulatory plugs represent a considerable male investment. For example, in butterflies, males of some species transfer very large copulatory plugs that make up a large proportion of the ejaculate (Simmons 2001). In some spider species, males sacrifice parts of their genitalia or even their whole body (after dying a programmed death) in order to obstruct female genitalia (Uhl et al. 2010).

Paternity Protection

Research on copulatory plugs has strongly focused on their potential adaptive role in male-male reproductive competition. When females mate with multiple males, males may benefit from preventing or delaying female remating, especially when the last-to-mate male fertilizes the majority of a female's ova (Parker 1984). Copulatory plugs may represent a barrier to rival

males and reduce female attractiveness or sexual receptivity. However, selection on rival males to remove copulatory plugs and on females to resist chastity enforcement likely prevents copulatory plugs from being fully effective. For example, females may contribute secretions that degrade deposited plugs (Mangels et al. 2015), thus potentially influencing the male's fertilization success. Conflict between males and between the sexes thus leads to coevolutionary dynamics of plug effectiveness (Fromhage 2012), and extant species may represent snapshots of different stages of these dynamics. Indeed, while there is mounting evidence for a role of copulatory plugs in male-male competition from across species comparisons (Dixon and Anderson 2002; Ramm et al. 2005; Simmons 2001), direct experimental evidence is mixed and shows considerable variation in plug efficacy across different species. However, incomplete chastity enforcement does not mean that males do not benefit from depositing plugs, as partial prevention or temporal delay of female remating can represent a considerable paternity benefit.

Other Functions

In addition to paternity protection, copulatory plugs may serve other reproductive functions, such as promoting sperm transfer and transport, gradual sperm release, preventing sperm leakage, and triggering female physiological responses to mating (Avila et al. 2015). Depending on the effect of the copulatory plug, the interests of males and females may be opposing or aligned. In their extant state, copulatory plugs may be necessary for successful reproduction in many species, but understanding the evolutionary origins of copulatory plugs is a complex task. Recent research has started to elucidate the relative importance of copulatory plugs in male-male reproductive competition and the rather cryptic influence of females through assisting or resisting plug deposition, formation, and removal (e.g., Aisenberg and Eberhard 2009; Friesen et al. 2016).

Conclusion

Copulatory plugs represent a convergent male strategy for paternity protection against rival males in many animal taxa, but likely serve additional, nonmutually exclusive functions. Evolutionary dynamics of conflict and cooperation between males and females result in variation in the effectiveness of plugs for paternity protection.

Cross-References

- ▶ Conflict Between the Sexes
- ▶ Cryptic Female Choice
- ▶ Intrasexual Competition
- ▶ Intrasexual Male Competition
- ▶ Male Prudence and Sperm Limits
- ▶ Mating Systems
- ▶ Multiple Matings
- ▶ Polyandry
- ▶ Sexual Selection
- ▶ Sperm Competition
- ▶ Sperm Competition Risk and Partner Abuse
- ▶ Sperm Competition Tactics
- ▶ Sperm Storage

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Copulatory Wounding (pt.)

- [Traumatic Insemination](#)

Copying

- [Imitation](#)
- [Imitation and Mimicry](#)
- [Learning Versus Imitation](#)
- [Neonatal Imitation](#)

Core Design Principles

- [Strategies for Successful Cooperation](#)

Core Tool

- [Acheulean](#)

Coreidence

- [Adaptive Problem of Detecting Kinship](#)

Co-residence and Early Maternal Perinatal Association

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Synonyms

[Kin recognition](#); [The Westermarck effect](#)

Definition

Co-residence and early maternal perinatal association are two important kinship cues for identifying siblings.

Introduction

Although kin selection, inbreeding avoidance, and cooperation and conflict within the family do not necessitate an ability to identify another individual as a sibling, kin recognition is believed to be a central mechanism in the individual development of kin-directed social behavior in humans (e.g., Penn and Frommen 2004). Concerning siblings, two important kinship cues are co-residence and early maternal perinatal association.

The Westermarck Effect

Human kin recognition is thought to rest largely on environmental information, and this kin recognition can be direct (e.g., phenotype matching) or indirect. Co-residence and maternal perinatal association are two indirect kinship cues humans use to identify siblings. In 1891, Westermarck

hypothesized that two individuals living closely together during childhood will develop a sexual aversion toward each other. Because individuals living closely together during childhood tend to be genetically related (i.e., sibling or half-sibling), this aversion is, in most cases, an aversion toward sex with a sibling. There is a large body of evidence corroborating this hypothesis (see Rantala and Marcinkowska 2011 for a review). Studying arranged marriages in Taiwan, Wolf (e.g., 1970) compared two forms of marriages. In one type of marriage, the to-be couple lived together from childhood, and in the other type of marriage, the couple lived together only as adults. Wolf found that the divorce rate was higher and the fertility rate was lower when the arranged marriages included childhood cohabitation. Similar results of childhood cohabitation have been found in other populations. This includes unrelated individuals raised together in Israeli kibbutzim (e.g., Shepher 1971; Spiro 1958; Talmon 1964) and marriages between cohabiting patrilineal cousins in Lebanon (McCabe 1983) and Morocco (Walter 1997). Bevc and Silverman (1993) also showed that duration of co-residence between purported siblings was negatively associated with sibling incest. It has also been shown that moral judgment of third-party incest is harsher if the two incestuous individuals are described as having lived closely related in childhood (compared to living apart) and that this effect is particularly strong if there is no other evidence of genetic relatedness between the two individuals (Antfolk et al. 2012). In sum, childhood co-residence affects sexual behavior, decreasing sexual interest between individuals living closely together in childhood. As such, co-residence seems to operate as one mechanism leading to inbreeding avoidance between siblings.

Co-residence and Altruism

Shared co-residence also affects altruism (i.e., social behaviors that supports the well-being of another individual while coming at some cost to the altruistic individual). Altruism – contrary to

inbreeding aversion – is also affected by perceptions of reciprocity and trustworthiness. Because of this, altruistic behavior also includes other benefactors than kin. Nevertheless, costly altruistic acts are more likely to be directed to kin compared to close friends (Kruger 2003; Stewart-Williams 2007). In line with this, research suggests that when two individuals are raised together, and thus very likely to be related, feelings of emotional closeness no longer predict altruistic dispositions; between unrelated individuals, emotional closeness is, however, positively associated with altruistic dispositions (Lewis 2011). Also among unrelated individuals, duration of the co-residence habitation is positively associated with higher levels of altruism (Lieberman and Lobel 2012). Full siblings co-residing through childhood also show higher levels of investment in each other compared to half-siblings or non-related siblings (Pollet 2007; White and Riedman 1992). Bressan et al. (2009) examined how different types of altruism are influenced by different types of kinship cues. The authors found that both full siblings and half-siblings that had co-resided were more willing to help each other. The effect of co-residence with a half-sibling was independent of variations in emotional closeness (Bressan et al. 2009). Lieberman et al. (2007) even found that co-residence through childhood predicted altruism more so than siblings' consciously held beliefs about their genetic relatedness (Lieberman et al. 2007). In a recent study by Lieberman and Billingsley (2016), it was found that co-residence duration works as a proxy of shared parental investment, which, it could be argued, is the second most reliable kinship cue following early maternal perinatal association.

Co-residence Between Other Family Members

While co-residence originally was believed to be a kinship cue only used to identify siblings, some research also suggests it is used in other kin dyads as well. Here, studies have focused on paternal identification of their biological children. Studying men in the military, Williams

and Finkelhor (1995) found that involvement in caretaking, which usually prerequisites cohabitation, lowers fathers' incestuous attraction toward their daughters. Although this finding is in line with co-residence acting as a kinship cue also in father-daughter relationships, the study failed to effectively exclude possible confounds. For example, men in the military, who spend a lot of time away from their child's mother, will also be more likely to worry about cuckolding.

Interestingly, studying ethnographic information on fathers co-residing with either biological or stepchildren from a rural Trinidadian village, Flinn (1988) found that not only did fathers interact more frequently and less agonistically with their biological children: The duration of co-residence (and co-residence at birth) with stepchildren was associated with lower rates of interaction and higher rates of agonistic interaction (Flinn 1988). Hence, co-residence per se does not seem to act as an independent kinship cue for fathers. Two interesting possibilities remain. Firstly, co-residence might function as a dependent kinship cue, that is, provide information about relatedness if another cues are present simultaneously. Secondly, co-residence might directly increase altruism between two individuals, that is, affect social behaviors without affecting beliefs about relatedness. Regarding the first possibility, very little is known. Studies suggest that the perception of the mother's sexual fidelity (Apicella and Marlowe 2004) and phenotypic similarity (e.g., Alvergne et al. 2007, 2009; DeBruine 2004) are important kinship cues for fathers. Concerning the other possibility, studies suggest that co-resident fathers provide more parental investment (Carlson and Berger 2011). Quite naturally, co-resident biological parents have vital effects on children's well-being (e.g., Tooley et al. 2006). Furthermore, children co-residing with both biological parents receive more parental investment than children living with a single parent or a biological mother and social father (Carlson and Berger 2011).

Much less is known about whether co-residence is a kinship cue used by children to identify their parents. A retrospective study of adults, however, suggests that co-residence with adults may regulate children's perception of relatedness to adults and modulate social behaviors accordingly (Antfolk et al. 2014).

Early Maternal Perinatal Association

In most mammals including humans, internal gestation, birth, and breastfeeding provide a very reliable kinship cue between a mother and her offspring. If a child were to remember this early physiological and nutritional connection to their mother, the child could be fairly certain that the woman giving birth is the biological mother. An older sibling witnessing this early maternal perinatal association between the individual identified as a mother and a new child can, likewise, be fairly certain that this new child is a maternal sibling. For older siblings this cue provides very reliable information about maternal relatedness. For younger siblings this cue is not available. In 2007, Lieberman, Tooby, and Cosmides showed that co-residence regulates social behavior only in younger siblings. Older siblings, who can see their own mother caring for a younger individual, can use this as a kinship cue instead and do not need to rely on the presumably less valid cue of co-residence: Only in younger siblings was co-residence associated with sibling altruism and inbreeding aversion (Lieberman et al. 2007). In fact, if a sibling can use early maternal perinatal association as a cue, co-residence duration is no longer used. Co-residence duration strongly affects altruism and sexual aversion between siblings in the absence, but not in the presence, of maternal perinatal association. Maternal perinatal association significantly predicts altruism toward younger siblings, even when controlling for co-residence. Moreover, early maternal perinatal association predicts altruism toward younger siblings better than having the same mother or sibling co-residence beginning at the sibling's birth (Lieberman et al. 2007). Szynycer and colleagues'

(2016) cross-cultural study supports these findings: Both maternal perinatal association and co-residence are used as kinship cues in siblings.

Asymmetric Relatives

Co-residence but not maternal perinatal association can be used to identify paternal half-siblings. Simultaneously, maternal perinatal association is an equally strong cue for maternal half-siblings as it is for full siblings. Because of this, it is possible that not only the age difference between siblings (older vs. younger) modulates the effects of co-residence. It is also possible that lineage (full siblings and maternal half-sibling vs. paternal half-siblings) modulates the effects of co-residence. Unfortunately, to date, no study has been designed to specifically test this possibility. We predict that younger siblings depend on co-residence in both the identification of full siblings, maternal half-sibling, and paternal half-siblings, but that older siblings rest on maternal perinatal association when identifying full siblings and maternal half-siblings, but rely on co-residence when identifying paternal half-siblings.

Conclusions

Childhood co-residence is used as a kinship cue in younger siblings. It regulates inbreeding avoidance and altruism. Older siblings rely on maternal perinatal association. Alongside these two cues, other cues may also increase or decrease inbreeding aversion and altruism between siblings. It is currently unclear whether co-residence and maternal perinatal association are used as kinship cues in other relationship types. It is also currently unclear whether maternal perinatal association is employed only in the identification of full and maternal half-siblings.

Cross-References

- Kin Recognition
- Westermarck Effect

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Corporal Punishment

► Spanking

Correction

► Evolution of Punishment

Correlates

► Indicators and Correlates of Status and Dominance

Correlates of Fear

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Synonyms

Anxiety; Fear; Stress

Definition

Corresponding relationships between fear and different neurobiological and psychological constructs.

Introduction

Fear is an innate and universal emotion which, throughout development, generates adaptive responses to various situations. In this process, neurobiological mechanisms are activated in the face of threatening situations and/or stressors, and some individuals are more predisposed than

others to be reactive to these threats, and thus, to have a response to fear (anxiety).

Neurobiological Correlates of Fear

The amygdala, in addition to being related to the function of survival, is a key component for emotional processing and for the way we respond to the emotions of others. It is mainly associated with the processing and behavioral response to fear and threatening stimuli and, consequently, to anxiety symptoms (Moul et al. 2012). It is a component that acts in multiple circuits to give support to several psychological functions. In addition to its central role in the recognition of internal emotions and the emotions of others, the amygdala functions in a circuit related to the hypothalamus (HPA axis), responsible for mediating our responses in threatening situations. These responses are gradual, depending on how close the threat is, ranging from freezing, to flight, to fighting. Thus, when the threat is very close, making it impossible to freeze or escape, there is an increase in neural activity in this circuit, which leads to a more superficial cognitive processing, increasing the probability of reacting aggressively (Blair et al. 2014).

The activation of the HPA axis occurs from the perception of a threat, which is then processed in the limbic system by the amygdala and the hypothalamus, leading to the activation of the pituitary gland and then the adrenal gland, to produce cortisol. Cortisol is released into the cortex, and its function when faced with stressful situations is to suppress several metabolic processes, facilitating the use of coping strategies in front of the stressor (Corbett and Simon 2014).

Another point to be considered regarding responses to exposure to threat stimuli are the changes in the autonomic nervous system, which is one of the regulators of several physiological processes that allow fight or flight responses, and also responsible for bodily changes that are common responses to anxiety, such as dry mouth, sweating, and intestinal alterations.

The autonomic nervous system (ANS) consists of two systems: the parasympathetic nervous system (PSNS) and the sympathetic nervous system (SNS). The PSNS is involved in daily activities, promoting a calm behavior and vegetative and routine activities, while the SNS is activated when a stressor is perceived (Sapolsky 1998). When faced with stress, the vagus nerve is deactivated, suppressing metabolic demands and facilitating fight or flight reactions by accelerating the heartbeat and activating the sweat glands, increasing the level of skin conductance. In restful situations, the vagus nerve slows down the heart rate, facilitating engagement in social activities (Porges 2007).

The activity of the vagus nerve is measured by the variability of the heart rate, from the fluctuation of the intervals between beats. At stress peaks, variability falls because of the deactivation of the vagus nerve. Thus, the break from the variability of the heart rate allows individuals to select more actions to react to environmental demands, if necessary. Moreover, this is indicative of adequate self-regulatory skills (Porges 1992).

Cognitive Processing in Fear-Related Mental Disorders and Its Maintenance

Several hypotheses have tried to explain the cognitive processing involved in anxiety-related disorders. However, we will describe in more detail Beck and Clark's (1997) models for anxiety disorders and the Foa and Kozak's (1991) model for emotional processing. As previously mentioned, our body emits a fear response from the preappraisal of internal or external stimuli, which generates anxiety symptoms. Fight, flight, or freeze responses may be issued to maintain the physical and psychological integrity of the individual against the threat. Beck and Clark's (1997) cognitive model of anxiety describes the cognitive processing of high anxiety from the perspective of vulnerability. This perception would arise from the individuals' understanding that they are subject

to internal or external threats, which they have no control over, and they perceive themselves as unfit to deal with the threat (Beck and Clark 1997). Also, this first appraisal involves overestimating the possible danger of the threat. This, coupled with a second reappraisal, in which the individual considers himself or herself to be less able or to have few resources to cope with the threat, would result in high anxiety (Beck & Clark), which can reach clinical levels such as panic disorder, social anxiety disorder, generalized anxiety disorder, or post-traumatic stress disorder.

In general, the cognitive processing described by the authors involves a trigger situation or stimulus, such as an expression of anger or fear, which activates the primitive threat mode, involving the HPA axis, attentional bias, thoughts and images related to the threat (including memories), and immediate inhibitory or defensive responses (fight, flight, freezing), then a more elaborate reappraisal (distorted in highly anxious individuals), and finally, anxiety symptoms (Beck and Clark 1997). In turn, anxiety symptoms reawaken the fear activation mode, since the presence of anxiety is perceived as a threat, for example, in panic disorder (e.g., "I'm going to go crazy"), generalized anxiety disorder (e.g., "I'm very nervous, I won't be able to do anything"), and social anxiety disorder (e.g., "I'm anxious and everyone will notice").

One of the central mechanisms used by individuals with anxiety disorders for the immediate relief of symptoms and, consequently, their maintenance is avoidance. Avoiding trigger situations and anxious thoughts by itself already causes the individual not to initiate the process of appraisal and, consequently, of perception of increased danger and of low effectiveness against the threat. Processes such as cognitive avoidance, distraction, worry, and suppression of thoughts can be described as avoidance mechanisms. Still, it is described as having a central role for the disassociation of the stimulus to fear and the cognitive restructuring of the stimulus (Beck and Clark 1997).

Thus, avoidance maintains the association of fear with the stimulus or situation, since the individual is not exposed to it until the anxiety

naturally decreases, and then disassociation can occur between the stimuli and the physiological and cognitive habituation to anxiety. The avoidance process can even lead to an increase in trigger stimuli and in the anxiety generated by them, since it facilitates distorted thoughts such as generalization (Clark and Beck 2012). For example, an individual who was assaulted by a man in red might start by avoiding people with a face similar to the thief, evolving to individuals with red t-shirts; however, over time, he will avoid any red objects so as not to run the risk of activating his fear system and having anxiety symptoms.

The emotional processing theory by Foa and Kozak (1991) proposes that the cognitive structure of fear would be represented by a schedule so that it would be possible to escape danger. This programming would be based on "what" we are afraid of (the stimulus, trigger), its responses (e.g., accelerated heartbeat, trembling), and the associated meaning (e.g., trembling means I am afraid). The authors emphasize that in situations where appraisal of risk and of the ability to cope with the threat is realistic, fear is an adequate and normal reaction (Rothbaum et al. 2007). However, this reaction would become inadequate when the structure does not accurately represent reality, when fear and avoidance responses are elicited by simple and/or harmless stimuli, seen as dangerous, and when fear reactions interfere with the person's day to day (Rothbaum et al. 2007). Thus, it is emphasized that the activation of fear, and therefore of anxiety symptoms, is necessary for realistic information to replace nonrealistic ones in the structure of fear, for example, "I will not survive."

In the case of post-traumatic stress disorder (PTSD), the authors propose that the disorder would develop from a failure in the emotional processing of a traumatic memory; the recovery of a fear-generating memory in a safe environment would promote realistic information about the costs and consequences of fear, thus reprogramming the structure of fear. Thus, being exposed to traumatic memories can generate habituation to anxiety, and reformulate it as a single episode in space and time rather than

continuous in the present, increasing the individual's ability to survive it (Rothbaum et al. 2007).

Considering the theories of Beck and Clark (1997) and Foa and Kozak (1991; Rothbaum et al. 2007), it is possible to identify connections between both, and overlaps between anxiety disorders (Beck and Clark 1997) and specific fear-processing disorders resulting from traumatic events (Rothbaum et al. 2007). These aspects may allow a better understanding of the symptomatology related to the processing of threat stimuli, since it integrates environmental components, cognitive, psychophysiological and the necessity of exposure to them so that it is possible to restructure and reappraise the threat, coping skills to deal with it and its consequences.

Conclusion

From an evolutionary psychology perspective, this entry intended to describe fear and its adaptive function in human beings, as well as some of its neurobiological characteristics and the processing and maintenance of disorders related to threatening stimuli. The importance of early identification of situations of vulnerability and of early stress is emphasized, so that a hyperactivation of the HPA axis is avoided, which may be protective for the development of anxiety disorders and disorders related to trauma and stress throughout development and adulthood.

Cross-References

- Fears
- Increased Cortisol
- Stress Reactivity
- Universal Human Fears
- Victims of Violence

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Cortical Blindness

- [Blindsight](#)

Cortical Neurons and Conducting Velocity

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Synonyms

For “conduction velocity”: [Nerve conduction velocity](#); [Muscle conduction velocity](#)
For “cortical neuron”: [Cerebral cortex](#); [Cerebrum](#)

Definitions

Cortical neurons are the neurons present in the cerebral and cerebellar cortex.

Neurons or nerve cells are electrically excitable cells that receive and transmit impulses (such as action potential).

Conduction velocity is the velocity at which impulses are transmitted along an excitable tissue.

Introduction

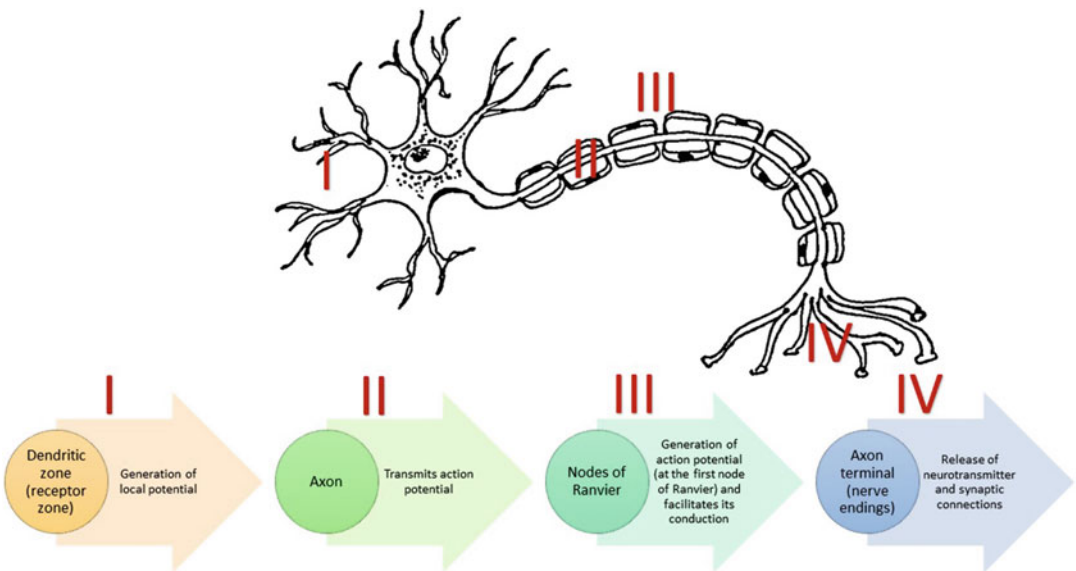
Neurons form the basic building blocks of nervous system. It is believed that neurons have evolved from primitive cells, which used to respond to various stimuli by contracting. Neurons have evolved and developed to perform the function of integrating and transmitting nerve impulses. Broadly the brain parenchyma contains two types of cells (neuronal cells and glial cells). The neuronal cells have a unique structure. Specific regions of the neuron deliver specific functions (Fig. 1).

The axonal processes of many neurons are myelinated. This means that the axon is covered

by a sheath of myelin which is a protein lipid complex. In the central nervous system, neurons are myelinated by oligodendrocytes. The oligodendrocytes send out multiple processes which are responsible for myelination on multiple neighboring axons (Barret et al. 2012).

Glial cells are non-neuronal cells, which have important roles as connective tissue (astrocytes), immune functions like phagocytosis (microglia), as well as myelination of neurons (oligodendrocytes). Myelination facilitates conduction of impulses, in addition to subserving functions like neuronal repair and metabolism of neurotransmitters. Glial cells have the ability to divide and proliferate in adulthood, unlike nerve cells. The glial cells myelinate axons, and this was a crucial step in the evolution of nervous system in vertebrates. They are responsible for maintaining the integrity of the axons in a long-term basis. The glial cells also perform key functions which are essential for normal neurogenesis, neuronal growth, and circuit refinement (Casano and Peri 2015; Nave 2010).

The cortical neuronal integrity is responsible for the cognitive functions, consciousness, as well as perception of senses (Molyneaux et al. 2007).



Cortical Neurons and Conducting Velocity, Fig. 1 Structure and function of the neuron

All these processes are carried out through functional connectivity of different brain regions with cortex as well as the amount of synapses established. Astrocytes help in formation of synapses between neurons (Farhy-Tselnick and Allen 2018). The electrophysiological characteristics of the cortical neurons are influenced by the degree of dendritic complexity (Zhu et al. 2016). Glial cells are closely associated with the functioning of the cortical neurons.

Conduction velocity is an important electrophysiological property of excitable tissues like neurons. In the brain, it is regulated through the neurons in coordination with glial cells associated with them.

Cerebral Cortex: Evolution and Development

The highly convoluted gray matter which forms the outermost part of cerebrum is what constitutes the “cortex.” Human brain has evolved over 300 million years, and the cortex has developed significantly in comparison other hominids, which is responsible for extraordinary cognitive capacity in humans. The cortex constitutes of billions of neurons and a larger number of glial (supporting) cells and other cells (Carter 2014). The cytoarchitecture of cerebral cortex comprises of distinct regions, which has become more complex during the human cerebral evolution; furthermore novel areas have also evolved. Gene regulation has played a crucial role in this evolutionary process. The *Homo sapiens* are in a higher stage of evolution and have well developed brain. Their brain’s extraordinary potential is attributable to the degree of cortical expansion during the early developmental stages through complex neural interaction, migration, and proliferation of neural stem cells (Kriegstein et al. 2006).

Mammalian cerebral cortex primarily contains two broad classes of neurons:

1. Pyramidal neurons which project to other regions of the brain.

2. Non-pyramidal neurons which are interneurons in the cortex.

Neurons in the brain develop from radial glial cells (located in ventricular zone) and intermediate progenitor cells (located in sub-ventricular zone). These neurons subsequently migrate to various zones including cortical plane in a sequential manner (Molyneaux et al. 2007; Noctor et al. 2004). The glutamatergic projecting neurons in the cortex develop from the progenitor cells present in the dorsolateral telencephalon, whereas the GABAergic interneurons in the cortex originate from the progenitor cells present in the ventral telencephalon (Molyneaux et al. 2007). This process of migration is very important for normal cerebral function. Abnormalities in neuronal migration can result in neurodevelopmental disorders (Geschwind and Rakic 2013; Parnavelas 2002).

Cortical Neurons: Types and Organization

The cortical neurons are organized within the cerebral cortex in horizontal layers and vertical or radial columns which form the cytoarchitecture of the cortex. Important cortical neurons include:

- (I) Pyramidal cells: These cells are the most common type of neurons in the cortex and constitute 65% of all cortical neurons. They are excitatory neurons and project out of their local area to distant target regions of the brain and hence also known as projection neurons. Their primary neurotransmitter is glutamate.
- (II) Spiny stellate cells: These neurons are also excitatory and are local interneurons. They make up 20% of cortical neurons. Glutamate is the primary neurotransmitter here too.
- (III) The remaining 15% is constituted by local inhibitory interneurons, and majority of them are GABAergic.

Typically the cortex is said to have six layers (Molyneaux et al. 2007):

- I. *The molecular/plexiform layer*: It contains very few cells. It is mainly composed of the axonal and dendritic processes of various cells including neurons outside the cortical area, cortical interneurons, and the pyramidal neurons in other layers of the cortex. In stained section, this layer appears as a narrow band of fibers lying horizontally.
- II. *The external granular layer*: It contains both pyramidal and non-pyramidal cells. On stained section, it shows vertically arranged fibers traversing the layer.
- III. *The external pyramidal layer*: It contains mainly pyramidal cells, along with scattered non-pyramidal neurons. Similar to layer II, myelin stain shows vertical fibers in this layer.
- IV. *The internal granular layer*: This is the narrowest layer. It contains a dense population of non-pyramidal cells. In stained section, a prominent band of horizontal fibers can be seen. This band is also known as *outer band of Baillarger*.
- V. *The internal pyramidal layer*: The size of pyramidal neurons increase from the superficial to deeper layers of the cortex, and this layer contains the largest pyramidal cells. This layer also contains non-pyramidal cells, and in stained section vertical fibers are seen. A prominent central band of horizontal fibers is also seen. This band is known as *inner band of Baillarger*.
- VI. *The multiform layer*: This contains neurons of different shapes, and the layer blends with the white matter below.

The interneurons in the cortex are responsible for interconnections between local (cortical) neurons, whereas the projection neurons in the cortex are responsible for connecting distant cortical structures as well as cortico-subcortical connections. The projection neurons also establish

connection with extra-cerebral structures (e.g., brain stem, cerebellum) (Molyneaux et al. 2007). There are some regional variations in the cortical structure, with some regions lacking certain laminae (layers); these are referred to as heterotypical variants. There are also homotypical variants, which have all the six layers (Standring 2008). Some recent evidences support the association of specific genes with the neurons of specific layers as well as their progenitors (Molyneaux et al. 2007).

Cerebellar Cortex

The cerebellum is the lower, rearmost part of the entire brain. Eighty percent of the total neurons of the brain are located in the cerebellum (Roostaei et al. 2014). The cerebellum has a similar layered microstructure to the cerebrum. The outer layer or cerebellar cortex is gray matter composed of nerve cell bodies and their dendrites. The distinct layers of the cerebellar cortex, from outside to inward are the molecular, Purkinje, and granule cell layer (Carter 2014). Cerebellar cortex receives excitatory inputs through two routes (Roostaei et al. 2014), which are:

1. *Climbing fibers*: These are olivocerebellar fibers which synapse directly on Purkinje cells.
2. *Mossy fibers*: They connect to Purkinje neurons via granular neurons.

The deep cerebellar nuclei (globose, emboliform, fastigial, and dentate nuclei) are connected with the collaterals arising from climbing and mossy fibers (Roostaei et al. 2014). The cerebellar cortex also contains inhibitory neurons called stellate cells, basket cells, and Golgi cells (Standring 2008).

Cerebellar neuronal integrity is responsible for coordination, balance, and execution of movements. Cerebellum exerts certain non-motor functions like cognitive control and affective regulation (Roostaei et al. 2014).

Conduction Velocity

The hallmark feature of nerve cell is its excitability. The various stimuli to which neurons respond include electrical, chemical, and mechanical stimuli. In response to these stimuli, two types of physiochemical changes are produced. These are:

1. Local potential which are non-propagated.
2. Action potential which are propagated.

Action potential is the main mode of interaction within the nervous system. It is produced due to movement of ions across the cell membrane. This impulse is conducted along the axon in an active and self-propagating manner and at a constant amplitude and velocity. This velocity is known as conduction velocity (Barret et al. 2012). Conduction velocity is also discussed in the context of other excitable tissues like muscle fibers; however we limited our discussion to neurons.

Factors Affecting Conduction Velocity

Action potentials travel down neuronal axons in an ion cascade. Larger diameter axons are able to send signals faster. This is because there is less resistance facing the ion flow. Therefore, conduction velocity is directly proportional to the diameter of nerve fibers. Myelination also increases conduction velocity. The spaces between the myelin sheaths have been traditionally called as the nodes of Ranvier. Myelin does the job of insulation and hence the current flow through it is almost absent. Therefore, in myelinated axons, depolarization takes in such a manner that it skips from one node of Ranvier to the next. This “jumping” of depolarization from node to node is called *saltatory conduction*. It is a swift process that allows myelinated axons to conduct up to 50 times faster than the fastest unmyelinated fibers.

Effects of other factors like age, gender, and temperature on conduction velocity have been studied (Stetson et al. 1992). Nerve conduction

velocity decreases with age due to decrease in number of nerve fibers, reduction in fiber diameter, and changes in the fiber membrane. Conduction velocity also decreases with decrease in temperature as cooling is thought to affect muscle and nerve membrane function, particularly the sodium ion channel. Studies have shown males have faster nerve conduction velocity than females, probably due to their faster increase of white matter in the brain during adolescence (Stetson et al. 1992).

Conduction Velocity: Implications

The cerebral cortex with its distinct organization of cortical neurons which is responsible for unique cognitive function is a basic requirement for intelligence. For a given brain design, the mean cortical nerve conduction velocity can affect the speed of information processing and, in turn, the level of intelligence. This is so because information can only be transferred from one cortical region to another along axons and across synapses. Therefore people with higher IQ, faster processing of information, and ability to analyze complex tasks may possibly have faster neural conduction velocity (Reed and Jensen 1992; Roth and Dicke 2005). Reaction time is an important determinant of processing speed. Conduction velocity also determines the reaction time. Faster conduction velocity reduces the reaction time (Vernon and Mori 1992). It has certain health implications, like individuals with mental illnesses and substance intoxication often have increased reaction times, which affects their cognitive performance, which can be traced back to impairment of conduction velocity due to the disease process.

Axons can be affected by a host of pathological conditions, most of which cause delay in conduction and ultimately to conduction block. Demyelination which occurs in multifocal manner affecting multiple tracts within CNS is seen in disorders such as multiple sclerosis. Though these diseases may typically cause

motor or sensory deficits, it may also cause cognitive dysfunctions seen in psychiatric conditions (Barret et al. 2012). Conduction velocities are adversely affected in peripheral neuropathy (Manganelli et al. 2016). Derangements in conduction velocity can be an early indicator for peripheral neuropathies (Kiziltan et al. 2007). Demyelinating neuropathies can be detected earlier and hence can be prevented from progression by screening conduction velocities.

Conclusion

Evidences support that density of cortical neurons and conduction velocity determine the level of intelligence of the individual (Roth and Dicke 2005). In the process of evolution, it was observed that the density of cortical neurons is higher in higher primates like humans, which makes humans the most intelligent among animals. Cortical neuronal integrity and conduction velocity are responsible for the optimal functioning of the brain. Mental well-being is determined by the cortical neuronal integrity and conduction velocity.

Cross-References

- Cerebral Cortex
- Nerve Conduction Velocity

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Cortisol Affords Immediate Action and Alertness

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Definition and Synonyms of Cortisol

Once in a “stressed” state, an individual will release a hormone called “cortisol.” Staufenbiel, Penninx, Spijker, Elzinga, and van Rossum describe cortisol as a glucocorticoid hormone. They define it as a regulator for many processes, such as: “fat and glucose metabolism, blood pressure, and inflammatory and immune responses” (2013, p. 1221). Generally, cortisol “awakens” the body to respond to an outside stimulus. Cortisol affects many systems of the body to put it into an alert state. One may feel an increased heart rate and respiration, muscle tension, and increased awareness to happenings around. Cortisol can stay at an increased level or can decrease to a baseline, depending on what the body senses. Any type of stressor can signal cortisol. An upcoming exam for a college student, a chronic illness, or excitement right before going on a roller coaster can trigger the release of cortisol, increasing an individual’s alertness.

Introduction

When an individual becomes “stressed,” the entire body reacts. A particular hormone, cortisol, is one of the many hormones that is released and utilized during that time. Cortisol can affect the body to aid in responding to that stressor. From sleep patterns to blood pressure, cortisol triggers the body to aid in preparedness.

How Cortisol Is Released

According to Chrousos (2009), change is detected by the peripheral nervous system and then within the central nervous system. Once within the brain, the hypothalamic-pituitary-adrenal axis, or HPA loop, is activated, and norepinephrine and epinephrine are released. Chrousos additionally mentions how stress activates the amygdala, nucleus accumbens, and the hippocampus. After the hormones are released, the hypothalamus is activated, which begins the loop. The hypothalamus signals the pituitary, which sends a signal to the adrenal glands, which release the cortisol into the bloodstream. Cortisol is released throughout the body and found “bound” and “unbound” or “free” (Lee et al. 2015). Cortisol is found in the bloodstream, but it can be released through urine and hair, which is how it is typically tested (Lee et al. 2015).

Effects on Immediate Alertness

Cortisol sets the body into a state which affects many bodily functions. It provides the key to help the body respond to whatever stimuli that was received from the peripheral nervous system. Each effect of this reaction plays a role in enhancing an individual’s appropriate response.

Effects on Arousal

Cortisol typically coincides with the circadian rhythm. Cortisol is normally highest in the morning and decreases throughout the day. When presented with a stimulus, cortisol can increase. Researchers have found that an elevated cortisol level can affect sleep patterns, even after cortisol has decreased. Glucocorticoids typically have an “excitatory” effect on the amygdala, prefrontal cortex, and hippocampus. This effect not only affects sleep patterns but also emotion and memory (Russo et al. 2013). Decreasing mechanisms that lower or “inhibit” cortisol may change sleeping patterns. Chrousos explains,

“Interestingly, sleep loss is also associated with elevated level of circulating IL6 in spite of the reduced stimulatory effect of catecholamines on IL6 secretion; this change possibly results from the currently decreased cortisol-mediated inhibition” (2009, p. 376). Commonly, an individual often feels less lethargic when cortisol is present.

Researchers have found that certain types of memory and emotion are affected by cortisol. Elzinga, Bakker, and Bremner explain in their 2005 study that specific stress exposure affects long-term memory storing and aids in immediate recall too. Another researcher, McEwen, describes a study explaining how emotional memories aid in already increased memory state when cortisol is present (2008).

Effects on Other Systems

Cortisol alerts many of the body’s other systems. An individual’s metabolism changes with increased heart rate and blood pressure along with gluconeogenesis and hepatic glucose secretion (i.e., producing sugar within the bloodstream). The body requires more energy during those states, so more sugar is released. Most thyroid and reproductive hormones have decreased, because energy is required elsewhere to keep one alert. The same is with the gastrointestinal function. It, too, decreases so energy can be used to attend to the stressor. An individual’s immune system is affected by cortisol as well. Depending on how long a stressor is present and the condition that an individual’s body is in, immunity could be enhanced or decreased (Chrousos 2009).

Conclusion

One hormone ignites an array of bodily processes that not only affect the neurological system but also the endocrine and many other systems. With cortisol’s presence, an individual is more prepared for stressors. Without it, one would respond to outside stimuli at an inappropriate state.

Cross-References

► Stress and Cortisol

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Cortisol Reactivity

► Increased Cortisol

Cortisol Response

► Increased Cortisol

Corvids

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Synonyms

Birds

Definition

Corvids are birds within the taxonomic family Corvidae and include crows, ravens, magpies, jays, and other species.

Introduction

The family of birds known as the Corvidae is an expansive family of over 120 species (including crows, ravens, magpies, and jays, among others; Clayton and Emery 2007). Many species within Corvidae are known for their sociality and intelligence (Clayton and Emery 2007; Seed et al. 2009). As such, they are an excellent target for studying the convergent evolution of social behaviors, in contrast to primates and other mammals. One area of social behavior of particular interest is morality; morality is an integral part of being human, yet whether it exists in other animals to the same degree as in humans is contentious.

Morality can be broken down into three levels of study: moral behavior, moral motivation or intent, and moral systems (Allchin 2009). Moral behaviors include altruistic behaviors such as cooperation and helping (regardless of whether this is “true” altruism, reciprocal altruism, or kin selection). Moral motivations include sympathy, empathy, and innate motivations for helping. Moral systems include social systems that enforce cooperation through reward or punishment. There is also the level of moral cognition: being able to

detect the intentions (positive or negative) of others (as either theory of mind or just behavior reading), being able to learn from and react to the behaviors of others (social learning), and being able to keep track the history of the behaviors of group members (reliability).

Reciprocal altruism in particular is considered a hallmark of human behavior, and many moralistic motivations appear to regulate it, such as friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, and guilt (Trivers 1971). At the level of the cognition involved in reciprocal altruism, fairness and reconciliation are behaviors that are currently of high interest in research of nonhuman animals. Although it is clear that some species of corvids have extremely complex social systems, the degree to which they have morality is less obvious. This entry will cover precursors to morality in corvids, such as their social systems and evidence for cooperation, social learning, and theory of mind.

Social Systems

Corvids span a huge range of social systems, from solitary to social living in groups almost as complex as those found in primates (Clayton and Emery 2007). Morality is essentially a social concept, so the first place to look for moral behaviors in nonhuman animals is in those with the most complex social groups. Clayton and Emery (2007) review some aspects of the sociality of various corvid species. Many of these species engage in what is called *fission-fusion dynamics*, a pattern that is common in primate societies, as well as some bat species, dolphins, elephants, and spotted hyenas (see Aureli et al. 2008, for review). Social groups with fission-fusion dynamics are composed of large groups that break into smaller groups and reform the larger group over time (hours, days, weeks, or months; Aureli et al. 2008). As this is one of the more complex forms of sociality, it is perhaps within these systems that we might expect to find rudiments of morality.

Rooks are perhaps one of the better-studied species with fission-fusion dynamics; rooks breed in extremely large colonies where mated pairs (forming lifelong pair-bonds) claim so-called micro-territories, but they disperse in other times of the year (Clayton and Emery 2007). Juvenile rooks form valuable relationships that mirror the pair-bonds they will form as adults (reviewed in Clayton and Emery (2007)). These relationships, typically between pairs of rooks, are characterized by affiliative behaviors (food sharing, allopreening [grooming each other], supporting each other in social interactions, caching food together, and bill twinning [holding their bills together]). However, affiliative behaviors are also directed at other individuals, and not all juvenile rooks form these pairs (Clayton and Emery 2007). Aggression never occurs between pairs, although rooks do direct aggression toward other rooks (including physical aggression, chasing, and displacing other rooks from perches), and pairs are much more likely to help each other (as opposed to others) during aggressive interactions (Clayton and Emery 2007). Rooks gain group benefits from being in pairs, beyond just food sharing; rooks in pairs increase their dominance within the group over time compared to non-paired rooks (Clayton and Emery 2007). In addition, affiliative behaviors are often part of a direct exchange, including giving and receiving food but also food for preening and vice versa, as well as bill twining and social support, indicating that these are reciprocal relationships (Clayton and Emery 2007).

Jackdaws, yellow-billed magpies, and pinyon jays also breed in pairs while nesting in colonies (Clayton and Emery 2007). Jackdaws in particular share many social variables with rooks. They form lifelong pair-bonds, and they share many of the same affiliative behaviors between partners that rooks do, and although they associate only with their partner during the breeding season, they live in large flocks the rest of the year, unlike rooks (Clayton and Emery 2007).

Pinyon jay groups are strongly characterized by fission-fusion dynamics, as individuals will not

only form subgroups within colonies but also move between different colonies altogether (Clayton and Emery 2007). Young pinyon jays live in crèches with other offspring where they are cared for by their own parents but also subsets of adults that are unrelated to them (Clayton and Emery 2007). This social complexity is accompanied by strong social cognition: pinyon jays are better at tracking multiple dyadic relationships more rapidly and more accurately than less-social western scrub-jays (reviewed in Clayton and Emery (2007)). These dyadic relationships were presented arbitrarily (as colored squares in a hierarchy) or socially (by observing interactions between other pinyon jays). A series of colors (or a group of jays) formed a hierarchy, and pinyon jays were able to infer and correctly respond to that hierarchy just from experience with the pairs (i.e., red beats blue, blue beats yellow; therefore, red should also beat yellow, called transitive inference). Thus, pinyon jays show high social complexity and awareness of social relationships (see Clayton and Emery (2007)).

Jungle crows do not live in colonies and instead defend territories in pairs. However, this behavior is not ubiquitous. In nonbreeding seasons, they will defend their territory during the day and roost communally off the territory (in breeding season, pairs remain at the nest all day and night), also reflecting fission-fusion social dynamics (Izawa and Watanabe 2008). Despite this flexible social structure, jungle crows form linear, stable dominance hierarchies determined by sex and aggressiveness, at least in captive populations (Izawa and Watanabe 2008). These hierarchies, once established, are maintained, implying long-term individual recognition of conspecifics (Izawa and Watanabe 2008). Long-term recognition has been confirmed by two newer studies: jungle crows recognize individual calls of different types (Kondo et al. 2010), and they match calls with visual presence of an individual (Kondo et al. 2012).

American crows also form lifelong pair-bonds and defend year-round territories in groups, but like jungle crows, some individuals form large

communal roosts for part of the year (Caccamise et al. 1997). American crows breed cooperatively, which means that they get assistance from related and unrelated individuals (helpers at the nest) also living within the territory. These helpers at the nest feed nestlings (Caffrey 1999). This behavior can be advantageous to the helpers in three different ways (Wiley and Rabenold 1984). First, there may be direct survival or reproductive benefits of staying, indirect benefits of increasing sibling survival, and delayed direct benefits of increasing later chances for acquiring a territory or mate (Wiley and Rabenold 1984). One interesting finding with regard to American crow sociality is their ability to form long-lasting memories of threatening humans (Marzluff et al. 2010). In addition, this learning is socially transmitted, both horizontally (to crows that observe a crow scolding a threatening human) and vertically (from parents to offspring; Cornell et al. 2012).

Carrion crows, Florida scrub-jays, and Mexican jays defend territories with a mate year-round (Clayton and Emery 2007). These species do not form colonies or roosts, but within their territories, they engage in cooperative breeding, like American crows. Carrion crows in particular are well known for their cooperative breeding habits, although they only engage in this behavior in some areas (see Clayton and Emery (2007), for review). Carrion crow, Florida scrub-jay, and Mexican jay territories are often also occupied by undispersed yearlings (adult offspring of the breeding pair) or unrelated immigrants to the territory (Clayton and Emery 2007). These extra occupants are helpers at the nest and assist with feeding nestlings, defending the nest, and detecting predators (Clayton and Emery 2007). Carrion crows also show attentiveness to traits of other crows and discriminate between reliable and unreliable conspecifics in terms of responses to alarm calls (Wascher et al. 2015). In addition, they can discriminate between familiar and unfamiliar human and jackdaw sounds, although the authors did not test their recognition of conspecific calls (Wascher et al. 2012).

Ravens, black-billed magpies, and Clark's nutcrackers form pair-bonds and nest inside their own large territories, without forming colonies

or engaging in cooperative breeding (Clayton and Emery 2007). However, juvenile ravens, before claiming a territory, live in larger groups and will aggregate at areas of surplus food (Clayton and Emery 2007). These groups do show fission-fusion dynamics (Clayton and Emery 2007). Juvenile ravens will form large flocks for feeding, roosting, and eating, but then break off into smaller and looser aggregations for other portions of the day, in which affiliative behaviors are common between pairs (Clayton and Emery 2007). Despite the tendency of breeding adults to occupy their own territory, this shows that ravens may also have complex social habits. Indeed, ravens have very good social memory: they can differentiate between individual ravens who have observed (or not observed) them hiding food (Clayton and Emery 2007). Ravens also differentiate between the calls of different ravens, including familiar and unfamiliar calls (Boeckle et al. 2012). They also have long-term memory about the calls of ravens that they have affiliated with and discriminate between not only familiar and unfamiliar calls but also calls from ravens with differing relationship qualities, even when the calls are from ravens they have not interacted with in years (Boeckle and Bugnyar 2012).

Like other corvids, New Caledonian crows form lifelong pair-bonds. However, they are less social than even other crows as they tend to live in small family groups with no unrelated individuals, and they do not defend territories (Holzhaider et al. 2011). While young crows stay with their parents for up to 20 months, they do not help with younger offspring (Holzhaider et al. 2011). New Caledonian crows are one species of corvid that is highly studied, but usually for their tool use-related cognition, rather than social cognition (see Holzhaider et al. (2011) for review). However, their tool-using behaviors are linked with interesting social cognition, such as social learning.

Social Learning

Social learning is the ability to enhance individual learning via observation of a conspecific. This can

result from mere stimulus enhancement (seeing a conspecific manipulate an object encourages the individual to manipulate that object as well), emulation (copying of the end result without copying the steps to get there), or imitation (copying the steps and the end result of a conspecific's actions; Whiten 2000). The ability to engage in social learning involves the ability to closely attend to the actions of others; although this is not a moral behavior in itself, it may be a precursor to more complex abilities that can involve moral-mental processes or behaviors.

Many corvid species demonstrate social learning. Rooks choose to forage near other rooks, and the roosts of ravens and hooded crows allow corvids to communicate the location of food sources to each other (see Seed et al. (2009) for review). New Caledonian crows, which use tools in the wild, appear to use social learning to learn how to make and use tools. Although much of their tool-using habits are genetically determined and emerge during development even without social influence, young crows prefer to use tools they have seen being manipulated, which enhances learning (Seed et al. 2009). In addition, the distribution of tool-making techniques across groups of New Caledonian crows suggests social transmission of these techniques (Seed et al. 2009).

Corvids have also been assessed for social learning in laboratory settings. Florida scrub-jays can learn foraging techniques via observation (Seed et al. 2009). Both Pinyon jays and Clark's nutcrackers were allowed to observe conspecifics solving a motor task (pecking a lid off a container to find food) and a discrimination task (learning which of two containers with different colored lids held food; Templeton et al. 1999). Pinyon jays learned both tasks faster when allowed to observe conspecifics solving these tasks, but Clark's nutcrackers did not seem to benefit from observation; as Pinyon jays are more social than Clark's nutcracker, this suggests an effect of living in large social groups on developing the ability to learn socially (Templeton et al. 1999). Jungle crows also show sophisticated social learning; they will copy techniques used by demonstrators to gain food from a puzzle box though this learning

appears limited to dominant individuals (Izawa and Watanabe 2011).

Cooperation

Cooperation is widespread in corvids. Carrion crows, Florida scrub-jays, Mexican jays, and other corvids engage in cooperative breeding, which can involve provisioning of (sometimes unrelated) offspring and cooperative territory defense from both predators and conspecifics (Clayton and Emery 2007). Other forms of cooperation in corvids are less well studied. Rooks, however, have been studied in a cooperative context, and although they can learn cooperative tasks (such as pulling two strings to draw in food), they do not appear to attend to their partner's actions and will pull their string even when the partner is absent (Scheid and Noë 2010). In addition, success at this task is not related to tolerance, as closely affiliated rooks do not perform better than those less closely affiliated (Scheid and Noë 2010). Instead, a bold temperament influences cooperation success; if at least one raven in a dyad is bold, they will succeed at pulling strings to reach food together (Scheid and Noë 2010). This may represent lack of physical knowledge, but could reflect a lesser degree of social knowledge than in species that succeed on this sort of task, like chimpanzees.

Ravens perform better than rooks on the same cooperative task (Massen et al. 2015); they needed no training to learn the task, unlike rooks. In addition, tolerance was an important factor influencing success, unlike rooks and like other species (Massen et al. 2015). But like rooks, the ravens did not appear to understand the necessity of a partner's actions as they pulled the string even when alone and did not always wait for a partner to appear (Massen et al. 2015). In line with ravens' inability to attend to other's actions in a cooperative task, ravens also do not cooperate in food reward distribution tasks (Di Lascio et al. 2013). When given the choice to receive a food reward, or receive a food reward and have food delivered to another raven, ravens did not appear to differentiate between these options. As ravens

do share food with partners in the wild and in captivity, the complexity of this task may have prevented cooperation.

Theory of Mind

Theory of mind is the ability to understand that another animal's behaviors are caused by mental states, such as beliefs and intentions (see Emery and Clayton (2009), for review). Many corvid species show some evidence of theory of mind, but these examples are still highly debated.

The debate around corvid theory of mind centers around food caching; many corvid species (pinyon jays, Mexican jays, scrub-jays, Clark's nutcrackers, ravens, rooks) will cache food for the purpose of eating later, and in response, these species will also pilfer the caches of conspecifics (Emery and Clayton 2009). Because of the risk of a cache being pilfered, those corvids involved in storing food take measures to protect their caches; these cache protection behaviors may result from multiple cognitive abilities, only one of which is theory of mind (Emery and Clayton 2009).

Scrub-jays are probably the best studied with regard to food caching (Emery and Clayton 2009). Scrub-jays with pilfering experience will re-cache food that was originally cached with a conspecific present (Emery and Clayton 2009). The ability to apply their own experiences to the behavior of other jays specifically could suggest the ability to attribute knowledge states (Emery and Clayton 2009). In addition, when observed, scrub-jays will re-cache food where other jays cannot see them, such as in shaded areas, rather than well-lit areas, and areas far or out of sight (behind barriers) from an observer, rather than close or in sight (Emery and Clayton 2009). These behaviors suggest the ability to take the visual perspective of others. Lastly, they can keep track of multiple observers and selectively re-cache food based on which observer watched what food is being cached (Emery and Clayton 2009). Ravens also prefer to cache far away and out of sight of conspecifics, and they will also re-cache food that was originally cached in the presence of another raven (Emery and Clayton 2009). Clark's nutcrackers

also cache less when observed and then later re-cache food that was cached under observation (Clary and Kelly 2011). Eurasian jays also prefer to cache food items out of sight of conspecifics (Legg and Clayton 2014). Overall, corvids show sensitivity to conspecific behaviors when caching food items, although whether this sensitivity demonstrates a theory of mind is still under debate. This sensitivity may be a precursor to moral-mental states, such as empathy.

Conclusion

Corvids have many complex and interesting social systems, some of which involve fission-fusion dynamics, a hallmark of primate societies. They also show some signs of cooperation involving kin selection and possibly reciprocity. However, they show few behaviors that could be classified as moral, and whether they understand mental states is still under debate. Despite this, they show many potential precursors to morality (the aforementioned cooperation and possibly the existence of theory of mind), so this is not a futile area of study for those interested in how morality evolves.

Cross-References

- Fairness
- Reconciliation

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Co-sleeping

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Synonyms

Attachment parenting; Bed-sharing; Mother-infant co-sleeping; Mother-infant proximity; Natural-parenting; Room-sharing

Definition

Co-sleeping refers to any situation in which a committed adult caregiver, usually the mother, sleeps within close proximity to her infant, so both parties can respond to the others' sensory signals, permitting mutual monitoring and regulation.

Introduction

For humans, mother-infant co-sleeping reflects adaptation for intensive parenting. Among mammals, co-sleeping with newborn offspring is universal as infants are born underdeveloped, typically without hair and therefore require mother for thermoregulation and continual nourishment. Social primates derive additional benefits from co-sleeping (i.e., mother-infant, but also group-sleeping with other kin) such as protecting an infant from predation, within-group competitive interactions, and infanticide (Nunn et al. 2009). Co-sleeping for humans in the early stages of infancy allows the mother to provide a suitable environment to promote healthy development, which is important due to the extreme immaturity of infant brain and body at birth. It is important to note, while co-sleeping has adaptive benefits, it is not known how much deviation from the prototypical pattern is possible without harming developmental outcomes, though such information has implication for cultural practices (Schön and Silvén 2007).

Exterogestation and Human Altriciality

Human infants are born remarkably altricial (i.e., underdeveloped), so much so that relative to other primates, the human infant appears incomplete at birth and the first year of life resembles continued gestation outside the womb (i.e., *exterogestation*) in which the unfinished brain and physiological systems (e.g., immune, digestive, thermoregulatory, respiratory, central nervous) require continual contact and feeding to reach their potential (Montagu 1961). Postnatally, the human infant has been characterized as being of a carried, rather than cached, type (e.g., Schön and Silvén 2007).

Carried infants require more frequent feedings due to the composition of breast milk, the hip and leg morphology as well as startle response promotes clinging, the fat distribution is reduced ventrally to allow mother-dependent thermal synchrony, and the infant cries when separated from mother. Maternal cues that indicate presence are soothing to human infants such as constant touch, smell, voice, movement, heartbeat, and warmth. Co-sleeping provides those cues when not being carried, reducing infant distress and potentially providing other benefits. For example, when human infants are born prematurely, kangaroo care is recommended (World Health Organization 2013), in which the infant is secured to the mother's chest in skin-to-skin contact for extended time periods. Kangaroo care provides maternal cues constantly and is associated with stabilization of infant physiology and behavior, regulation of sleep-wake cycles providing more alert time and more restful sleep, reduction of biological indices of stress, sensitivity and bonding between mother and infant, and increases the rate of neuromaturation (Feldman 2004). Of particular interest, is the synchrony of mother-infant sleep-wakefulness patterns, which is associated with reduced infant mortality (McKenna et al. 1990) and increases temporally matched interactive synchrony of care-solicitation and care-provision, which may affect parent-child attachment.

Social Development and Attachment

The evolutionary pressures that resulted in humans birthing such an altricial infant are debated, but the result is an infant with a unique developmental pattern, such that elaborate communication and social skills develop before physical capabilities (Flinn and Ward 2005). Beginning at birth, mother-infant interactive synchrony begins (Feldman 2007). The reliability and consistency of maternal response provides information to the infant about acceptance, cooperation, and availability. The sensitivity of the parental responses play an important role in organizing parent-infant attachment, such that secure

attachment results from the caregivers ability to perceive accurately and respond contingently to infant needs, providing a sense of security about the world (Ainsworth 1979). The security of attachment to the primary care provider becomes generalized and affects the developing humans' expectations, attributions, and responses to social situations and the world in general (Bowlby 1969). Co-sleeping during the nascent stages of attachment organization is likely important in promoting an attachment style characterized by trust and security, as opposed to exposing the infant to nocturnal maternal deprivation which introduces long periods of nonresponsive care provisioning.

Cultural Practices in Human Parenting

In modern humans, parenting practices are heavily influenced by culturally prescribed norms. In the case of infant sleeping location, cultural practices may be maladaptive. Biological evolution and thus basic infant needs are stable relative to the rapidity of cultural innovation (Schön and Silvéen 2007). In western-industrialized nations, cultural innovations facilitate parenting in an environment that differs from that of human evolutionary adaptedness. For example, the use of a breastmilk substitute allows mothers to remain in the workforce, but at the cost of optimal nutrition, bonding, and acquired immune defenses. In western cultures it has become commonplace to not only feed an infant formula but to sleep them away from their mother in a separate room, due to a separate room available and a cultural value of independence. Sleeping an infant in a separate room is associated with increased risk of infant mortality, as the mother is unable to monitor the infant. The American Academy of Pediatrics (AAP; Jones 2012) proposes to avoid increased risk of infant mortality associated with sleeping an infant in a separate room, the infant should sleep in the same room, but not in the same bed (i.e., room-sharing), as opposed to bed-sharing which is likely what humans evolved doing and is practiced in most cultures around the world. The AAP proposes the modern sleep environment may contribute to infant

suffocation and therefore caution should be taken. Ultimately, it is not known how much deviance from the evolved prototype is possible without compromising infant and parental well-being. Room-sharing or sleeping the infant in a separate room does not provide the same sensory cues (e.g., smell, movement, sound, warmth) that allow the mother's body to scaffold the infants development.

Conclusion

In the grander scheme of mammals which are born underdeveloped, and complete development externally being nourished by mother's milk, it is not surprising that for human mothers and infants, sleeping in close proximity is comfortable, safe, and beneficial. The length of time needed co-sleeping to meet the physical, social, and emotional needs of the infant is not clear, though during the early months skin-to-skin contact is beneficial and promotes secure attachment. Changes in cultural childrearing practices are much more rapid than biological evolutionary changes and as such may not be adaptive. Ultimately, the human infant is born more altricially than any other social primate, as such it is more extensively affected by its developmental environment. Most important to a human infant is the social environment, his approach to which is anchored by the security of early attachments. More research is need to understand the implications of variations in childrearing practices to ensure that infant needs are met in continuously changing and adapting human societies. Taking an adaptationists approach, an increasing number of parents are engaging in *instinctive parenting* (Schön and Silvéen 2007), assuming that any deviation from an evolved prototype has potential for harm.

Cross-References

- [Brain at Birth](#)
- [Brain Development](#)
- [Breast Feeding](#)
- [Breast Feeding and Mother-Infant Attachment](#)

- ▶ Breastfeeding Benefits
- ▶ Duration of Breast Feeding in Ancestral Environments
- ▶ Maternal Bonding
- ▶ Maternal Investment
- ▶ Offspring–Parent Attachment
- ▶ Parental Investment and Parenting

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Cosmetics

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Synonyms

Beauty aids; Beauty products; Makeup

Definition

Products applied to the body to enhance, change, or improve appearance

Introduction

A cursory glimpse at any television show or magazine depicting women will instantly cue the observer to the role or at least existence of cosmetics in the perception of female attractiveness. Women on TV, movies, in magazines are often covered in various cosmetics. Eyeliner and mascara make eyes look bigger, lipstick calls attention to the size and shape of a woman's mouth, foundation or face powder cover blemishes on the skin – all traits that are found attractive (larger eyes, red lips, clear skin). A somewhat recent beauty fad is “contouring” and “highlighting” the skin to accentuate specific parts of the face. Interestingly, some individuals use this technique to manipulate the shape of one's features. For example, by shading/contouring along the sides of the nose and adding a strong highlight down the center of the nose, it can create a modified nose shape without all the risks (and recovery) of surgery. From an evolutionary perspective, this is considered a form of *dishonest signaling*.

The Nature of Signaling

Sexual selection is comprised of two types of signals: honest and dishonest. Honest signals are when a specific trait reliably relates to underlying fitness and fertility, while dishonest signals may improve one's appearance and therefore mate value, but it is not linked to a person's reproductive potential (i.e., genetic code). Cosmetics fall under the category of dishonest signals – they may play up features found attractive due to their links to fertility or reproductive potential, but a bit of powder and/or ink cannot increase fecundity. Cosmetics can also be considered an *extended phenotype* (Dawkins 1999; Etcoff et al. 2011). In nature, animals use various techniques to bolster their position in the mating market, and in humans, cosmetics play the same role. By drawing attention to favorable characteristics (eyes, lips), it exaggerates important subtleties in sexual dimorphism that are often valued as indicators of fitness.

Facial attractiveness is often linked to symmetry (an overall cue to fitness), but it can also be broken down by individual parts.

Skin: Smooth, unblemished skin is a cue to a lack of mutations and overall fitness. While clear, evenly colored skin is an indication of health, sallow colored skin is often typical in those with diseases. Additionally, the presence of acne (in an adult) is usually indicative of an underlying hormone imbalance.

Eyes: Large, neotenous, clear eyes are a cue to fitness and are considered attractive, while “cloudy” irises and/or discoloration of the sclera is due to underlying health issues.

Lips: Full lips are considered attractive, and it has been suggested that there may be some similarities between the lips and the shape/color of the vagina.

Facial Shape: High, prominent cheekbones and a small lower face are considered attractive and are linked to higher levels of estrogen.

Conclusion

Cosmetics enhance signaling cues – they enhance various features while downplaying others. From an evolutionary perspective, cosmetics are dishonest signals of fitness but are good at the job they do – making naturally attractive features more apparent. While subtle use of cosmetics are typically used to highlight various features (e.g., mascara darkens and elongates eyelashes), other applications (like the layering of concealer to change the shape of the face) are more drastic in nature. All forms of cosmetics are considered dishonest signaling, yet the degree of dishonesty is dependent on the application.

Cross-References

- ▶ [Advertising](#)
- ▶ [Appearance/Beauty in Girls](#)
- ▶ [Art](#)
- ▶ [Body Modification](#)
- ▶ [Camouflage](#)
- ▶ [Competition Between Groups](#)
- ▶ [Culture of Honor and Individual Differences](#)
- ▶ [Extended Phenotype, The](#)
- ▶ [Facial Attractiveness](#)
- ▶ [Facial Disfigurement](#)
- ▶ [Good Genes](#)
- ▶ [Health Cues](#)
- ▶ [Individual Differences](#)
- ▶ [Male Ornamentation](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Peer Groups](#)
- ▶ [Peers](#)

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Cosmides & Tooby

► [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

Cost and Benefit Trade-Off

► [Daniel Nettle](#)

Cost Inflicting

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Synonyms

[Mate retention](#); [Domestic violence](#)

Definition

Cost-inflicting behaviors include those behaviors that cause physical or psychological harm to an individual and/or reduce an individual's access or perceived access to resources.

Costs of Intimate Relationship Development

Developing and maintaining an intimate relationship require the investment of resources, in terms of time, energy, finances, emotional commitment, and so on. If the benefits gained from being involved in an intimate relationship outweigh the costs of developing and maintaining that relationship, then the result is a net gain. If the costs

outweigh the benefits, on the other hand, the result is a net loss.

Males and females tend to bring different investments into a relationship and so may incur different costs for committing to such a relationship (Miller 2011). Males, for instance, are more likely to make investments of material resources. In effect, males can buy their way into a long-term relationship by demonstrating not only that they have money – or at least the potential to acquire money – but also that they are willing to use that money and the things that it can buy toward the benefit of a romantic partner and her offspring. Unlike males, the resource that females are most likely to invest in a romantic relationship is themselves. Rather than material resources, males are more likely to prefer that their female partners bring to the relationship sexual access and indicators of reproductive capacity (e.g., postpubertal youth, a low waist-to-hip ratio, facial symmetry, and attractiveness). In short, within the context of long-term intimate relationships, males' material resources are traded for access to females' embodiment of reproductive capability (Buss 1989). Of course, males and females provide many different benefits to one another in the context of an intimate relationship, and in a modern industrialized context, the roles of *provider* and *primary caregiver* are not resolutely sex specific. However, over the course of human evolutionary history, by virtue of sex differences in reproductive biology and all of the downstream consequences of those differences (Trivers 1972), males have been responsible for the heft of material resource investment, and females have been responsible for the majority of reproductive resources.

Typically, the investments males and females make toward the development and maintenance of an intimate relationship are given willingly. Males provide their partners with access to their material resources with the confidence that their female partners cooperatively will provide them with reproductive resources and vice versa. However, while both males and females can benefit from their investment in a long-term relationship, they

also both can potentially benefit from failing to provide a valuable return on their partners' investments, thus tipping the benefits in their favor and the costs toward their partners. In the context of a long-term relationship, many of these costs are inflicted on a partner via relationship defection.

Costs and Benefits of Relationship Defection

There are two main types of relationship defection, and both carry with them potential benefits for the defector and costs for the partner. The costs of a partner's short-term defection from a relationship, the type of defection often dubbed an infidelity, are most evident for male victims of a female's defection. Should a female engage in a sexual infidelity with a rival male, she could conceive offspring to which her long-term partner is genetically unrelated yet in which her long-term partner provides investments. That is, he could be cuckolded (Platek and Shackelford 2006). Cuckoldry, or the unwitting investment in genetically unrelated offspring, is evolutionarily devastating for males, in that it involves investing his finite resources toward the survival of a rival male's offspring while failing to ensure the survival of his own genetic line. The benefit to a female for subjecting her long-term partner to the risk of this cost is that she may gain high-quality genetic resources from her short-term partner. This benefit to females is evidenced in the fact that the risk of female short-term defection from a relationship seems to be highest at ovulation, which is precisely the time when that defection would inflict the most cost on her partner (Pillsworth and Haselton 2006).

Females, of course, cannot be cuckolded. But that does not mean that they incur no costs from a male long-term partner's short-term defection. A male who has engaged in an infidelity necessarily has expended at least some effort – in terms of time, attention, or material resources – in securing a partner with whom to engage in that infidelity, effort which otherwise could have

been allocated toward his long-term partner and her offspring. In effect, his short-term defection has cost her access to some of his resources. Additionally, both males and females who have been the victim of a partner's short-term defection face the additional risk that the short-term defection will be translated into a long-term defection.

Short-term defections from a long-term relationship are sometimes used as a method of "trading up." That is, if the benefit of being in a relationship with the new partner outweighs the cost of leaving the previous partner, then one may be likely to dissolve the previous relationship. When a long-term relationship dissolves, each member of that relationship loses whatever investment has been made into that relationship. In short, they incur the cost of having invested in that relationship without being able to receive the benefits that relationship could have provided.

In order to prevent incurring the costs of a partner's defection from the relationship, individuals may engage in mate retention behaviors. In short, mate retention behaviors include all of those things that an individual may do in order to encourage a partner's continued investment in the current relationship. Some of these behaviors function by enticing a partner's fidelity via the provision of benefits. These benefits might include gifts, compliments, or any other thing a person may appreciate receiving. Other mate retention behaviors function by punishing or threatening to punish a partner's defection from the relationship. These are called cost-inflicting mate retention behaviors (Shackelford and Buss 2000).

Cost-Inflicting Mate Retention

Cost-inflicting mate retention behaviors can take many forms. For example, a person might inflict financial hardship on his partner by restricting access to money or other material resources on which she relies. He also may attempt to restrict his partner's access to social resources by insisting

that she spend all of her time with him or otherwise preventing her from having meaningful contact with other family members or friends. In other cases, an individual may target his behaviors toward rivals who might otherwise entice a partner away from the current relationship. This could include anything from convincing the potential rival that the partner is in some way damaged and so not worth having to physically fighting the potential rival for appearing interested in one's partner.

In the examples above, an individual is attempting to maintain a partner's investment in the current relationship by removing opportunities to defect or otherwise establishing barriers to defection. However, another approach would be to lower a partner's *perceived* ability to defect from the relationship. For instance, successfully convincing a partner that she is of such low value that no other partner would ever have her and that she would be incapable of surviving in the world on her own serves the same purpose as actually removing her opportunities to defect. There would be no need to actually remove opportunities for defection if one has successfully convinced a partner that such opportunities do not exist.

The restriction of a partner's access to material and social resources, whether that restriction is actual or perceptual, is costly to that partner. The cost inflicted on a partner functions to protect oneself from incurring the costs of a partner's defection from the relationship. However, not everyone engages in these cost-inflicting mate retention behaviors with equal frequency.

Individual Differences

The use of cost-inflicting mate retention strategies is moderated by a variety of individual differences. In general, mate retention is positively related to one's partner's mate value, such that individuals with higher mate value are more likely to engage in mate retention behaviors (Buss and Shackelford 1997). In other words, a person with a valuable partner

is likely to want to keep that partner and so will engage in more behaviors that function to maintain that partner's investment in the current relationship. This is likely because the cost of a partner's defection from the relationship is greater when the partner could not be replaced easily. Similarly, the likelihood of the use of mate retention behaviors is increased when the risk of relationship defection is highest (Starratt et al. 2007).

In circumstances such as these, when one may be motivated to engage in mate retention behaviors, there are individual differences in the extent to which one chooses a cost-inflicting strategy. Specifically, individuals who are lower on the mate value spectrum are more likely than their higher-value cohorts to use cost-inflicting mate retention strategies (Miner et al. 2009). Generally, a person who is considered "high value" is one who has many of those traits that are prized by those who are seeking a mate, traits such as kindness, intelligence, attractiveness, and, at least for males, access to resources. A person with these high-value traits may have several advantages over lower-value rivals, including the ability to afford the investment it takes to engage in benefit-provisioning mate retention.

Enticing a partner into maintaining fidelity to the current relationship by providing that partner with benefits typically requires some manner of up-front investment. For instance, purchasing a gift requires the investment of financial resources. Providing social or emotional support, on the other hand, involves the investment of one's time, kindness, and potentially intellectual prowess. A person of low mate value is less likely to have any of these resources to invest – or may have the resources but is less likely to be inclined to use those resources toward the benefit of another, as may be the case for a partner with financial resources but without kindness or other such positive personality characteristics. Such low-value partners, though, still may have a need to engage in mate retention. Consequently, these individuals may be more likely to engage in those mate retention strategies that involve inflicting costs on their partners.

Conclusion

The development and maintenance of intimate relationships require the investment of a variety of resources. Should an individual's partner defect from that relationship, even briefly, one risks losing that investment, thus incurring potentially substantial costs. In order to prevent incurring such costs oneself, an individual may choose to inflict costs on his or her partner in the form of cost-inflicting mate retention behaviors. These behaviors function to maintain a partner's investment in the current relationship by inflicting or threatening to inflict costs for defection. The likelihood of one's engagement in cost-inflicting behaviors is highest under two conditions: (1) when the risk of a costly loss from a partner's defection is greatest and (2) when the individual is either unable or unwilling to maintain a partner's investment in the relationship through the provision of benefits.

Cross-References

- [Intimate Partner Violence](#)
- [Mate Retention](#)
- [Mate Retention Tactic](#)
- [Partner Abuse and Homicide](#)
- [Partner Rape](#)
- [Relationship Dissolution](#)
- [Sexual Coercion and Violence](#)
- [Use of Mate Retention Strategies](#)
- [Violence as Coercive Control](#)
- [Violence to Control Women's Sexuality](#)

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Cost of Same-Sex Friendships

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Synonyms

[Affiliative bonds](#); [Associations](#); [Coalitions](#); [Female-female](#); [Male-male](#); [Reproductive costs](#); [Social relationships](#)

Definition

Same-sex friendships are lasting coalitions between individuals who are the same biological sex. Friendships can have substantial fitness costs in terms of time budgets for maintenance, as well as costs associated with violation of rules of reciprocity.

Introduction

Friendships, characterized by long-term affiliative bonds between unrelated individuals, have an

association with evolutionary benefits of increased reproduction and survival. Evolutionary origins of friendships are best explained by reciprocal altruism, where reciprocity is sustained via proximate mechanisms of emotional closeness and high levels of trust. As well as bringing fitness benefits, friendships also have substantial costs connected to the maintenance of the bonds. As opposed to kin relations, the quality of the friendship bond is dependent on the frequency of the contact. Emotional closeness between unrelated individuals can evaporate over time if the contact with the friend is not maintained regularly (Roberts and Dunbar 2011a), which can result in dissolution of the friendship. The costs and benefits of friendships are different across the life course of the individuals. In this chapter, I will be focusing on the costs of friendships in adults of reproductive age. I will discuss this in terms of energetic costs (i.e., social time budgets), cost associated with violation of reciprocity (i.e., exploitative friendships), and intra-sexual competition and mate poaching.

Maintenance Costs

In order to meet the requirements of reciprocity, friendships have higher maintenance costs than kinships. Social networks are costly in terms of allocation of time budgets; energy allocated in one friendship limits the time available for maintaining other friendships. Indeed, close friendships are characterized by more frequent communication and contact (Roberts and Dunbar 2011b), which can take up a large part of an individuals' social time budget. Further, the costs of maintenance can differ as a function of the sex of the individual.

On average, women have fewer but closer friends in their networks than men do, and these friendships are often nurtured with intensity and intimacy. Women's friendships take more energy to maintain, and friendship conflict and dissolution in women are often caused by lack of care in the relationship by one of the parties (Dunbar and Machin 2014). The intimate same-sex friendship in women is likely to have an association with ancestral patrilocality (the propensity of males to

stay and females to migrate from natal groups when reaching maturity). Establishing non-kin-based close support networks was crucial for ancestral female fitness, which could be reflected in the high cost of maintenance. Ancestral males, in turn, could rely on the support of genetically related individuals, and did not require the costly time allocation in order to maintain the support network. Indeed, friendship networks of modern men are characterized by weaker ties and larger, activity-based groups, whereas modern women have fewer same-sex allies, but the relationships are more intimate and supportive (see David-Barrett et al. 2015, for further references and an interesting study on social media profile pictures).

Conflict, Competition, and Betrayal

Same-sex friendships bear substantial costs when the rules of reciprocation are violated. In some cases, friendships can be exploitative, where one person in the dyad gains benefits at the cost of the other person. Conflict in adult same-sex friendships is surprisingly little studied. Researchers suggest that exploitive friendships have a relationship with individual differences in personality. For example, those who are high on trait Machiavellianism use manipulative tactics in friendships (Abell et al. 2016), which could lead to imbalance in the costs and benefits within the friendship dyad.

Friendships can also be competitive, which is associated with dissatisfaction (Singleton and Vacca 2007) and reduced emotional attachment (Brewer et al. 2013). One common feature of competition is intra-sexual competition for mates (Bleske-Rechek and Lighthall 2010). Although friendships can be useful in terms of cooperation in acquiring and retaining mates, they can be costly when there is within-sex competition for the same mates.

Conclusion

Same-sex friendships can be costly because of high energetic requirements (i.e., social time

budgets) and intra-sex competition and rivalry. Overall, friendships are costlier to maintain than kinships and require a larger amount of an individuals' social time budget. Although friends can provide support in terms of mate acquisition and retention, friendships also pose a risk of intra-sexual competition for mates and losing a mate to poaching from a friend.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Friendship](#)
- ▶ [Kin Selection](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Same-Sex friendships](#)

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Cost-Benefit Analysis

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Synonyms

[Tradeoff](#)

Definition

A type of analysis that examines the potential costs of a decision compared to the potential benefits of the decision to determine the optimal choice.

Introduction

Every decision has associated costs and benefits to an organism. This is true for business decisions, parenting choices, and all areas in between. Evolutionarily, an organism's main objective is to successfully allocate resources to maximize fitness, and this is the ultimate goal of all decisions in all areas (Buss 1988). However, organisms do not have the resources necessary to maximize fitness in all areas of life and functioning (Ellis et al. 2009). As a result, organisms must make decisions that involve trade-offs: In order to maximize fitness in one area that is more important, resources must be not devoted to some other aspects of fitness. These decisions are dependent on various factors in the organism's environment that influence what is required to maximize fitness. Therefore, to make sense of all the factors that are involved in fitness-maximizing choices, organisms must perform cost-benefit analyses to determine optimal decisions for their individual situations.

Theory of Cost-Benefit Analysis

Cost-benefit analyses are used for many decisions. In order to make an optimal decision, an organism must examine both the costs and the benefits associated with the choices. For example, in many community project decisions, people must examine the monetary and nonmonetary (time, energy, work diverted from other projects) costs to the community and weigh those against both the monetary and nonmonetary benefits to the community in order to determine whether it is worthwhile to complete the project. For instance, if a community wanted to host a food drive, they would first need to calculate the monetary costs of publicity and worker reimbursement. Then, they would add these costs to the nonmonetary costs like the time and energy the workers would invest and the productivity lost by diverting helpers from their usual jobs to this project. Then, they would calculate the benefits to the community members in need of food assistance and the amount of food they are likely to raise. Finally, they would compare these costs against the benefits to decide whether or not to continue with the project. This type of analysis allows the community to make a productive decision and not invest resources in something that will cost more to implement than it would help after its completion. This same type of analysis can apply to all decisions, although the costs and benefits are not always monetary in nature.

The equation for cost-benefit analysis is as follows:

$$\frac{B \cdot Pb}{C \cdot Pc}$$

This equation multiplies the benefits (B ; usually the expected monetary value) by the probability or likelihood of achieving the expected monetary value (Pb), then divides this by the expected cost of the decision (C) multiplied by the probability or likelihood of keeping that cost (Pc). The rule of cost-benefit analysis says that organisms should choose the option with the highest benefit relative

to the cost when making decisions. Cost-benefit analysis has been used in evaluating many different things, including educational programs, various types of therapeutic interventions, and security and safety initiatives (Herman et al. 2015; Kliezt et al. 2010; Reynolds et al. 2011; Stewart and Mueller 2013). Although it is easy to see how this type of analysis applies to modern business decisions, it also plays an important role in evolutionary decision-making.

Application to Evolution

The fundamental evolutionary goal of any organism is optimizing resources, such as energy and its expenditure, to maximize fitness. The same type of cost-benefit analysis that is used in modern business decisions was also used throughout history and can be examined in many situations in ancestral time. For example, cost-benefit analysis can be seen in scenarios involving hunting a particular animal, such as a bison. For this scenario, there are potential costs to the organism including weapons, energy for the hunt, and risk of injury or death. However, potential benefits to the organism also exist, including the large amount of meat, large bones for tools, and the hide for clothes. In an unconscious manner, a cost-benefit analysis can be used to make the choice of whether or not to hunt a bison. Similarly, various costs and benefits can be examined for many evolutionary investments, including parenting, mating behavior, foraging, aggression, altruism, and more.

Natural selection favors the allocation of resources that are optimized over the lifetime across differing ecologies (Ellis et al. 2009). Natural selection prefers this because an adaptable organism is capable of surviving and reproducing in different environments. Across the lifespan, organisms encounter different problems to solve, and each individual organism will have access to different resources. Therefore, the costs and benefits associated with a certain choice differ based on the organism's specific environmental characteristics. For example, aggression has different

costs and benefits in different environmental situations (Georgiev et al. 2013). Life history theory can be used to understand how costs and benefits differ between and within species across different environments.

Life History Theory and Cost-Benefit Analysis

Life history theory can explain how individuals make different cost-benefit decisions within their environments. There are five main evolutionary trade-offs that require cost-benefit decisions to be made about resource allocation: maintenance versus growth, current versus future reproduction, growth versus current reproduction, survival versus current reproduction, and offspring quality versus quantity (Ellis et al. 2009). The environmental characteristics influence what decisions organisms will make within these realms. For example, in an environment with a high mortality rate, each day is unpredictable, and an organism does not know when vital resources can be obtained for survival. In this type of environment, an optimal decision would be to invest in current reproduction and have a large quantity of offspring. Having offspring earlier and more often will be more fitness-maximizing because life expectancy is shorter and the future is uncertain. When examining the costs and the benefits, this strategy has the higher payout in this environment because it increases the chances of survival for an organism's genes. Waiting to have offspring and having only a few are strategies with lower expected payout because the organism or its few offspring may die in a hazardous environment. In a different environment, however, this later strategy may have a higher payout because of the better probability of living to be able to see the future rewards of investments (such as in somatic growth or offspring quality).

An individual's investment in each of these trade-off categories can indicate their specific life history strategy. A slow life history strategy is characterized by decisions to invest resources in

the future, whereas a fast life history strategy is characterized by investing resources to receive benefits as soon as possible. Individuals can vary on this continuum, and their specific life history strategy influences the cost-benefit analysis associated with each of their decisions about resource allocation. Therefore, organisms use cost-benefit analyses within the contexts of their environment and life history strategy in order to make optimal decisions.

Conclusion

Various evolutionary decisions utilize cost-benefit analyses. Life history theory can be related to many areas that require trade-offs, such as the physiology of an organism, mating behavior, parenting, and reward orientations. Furthermore, all the different aspects of an organism's life can only use a portion of the individual's available resources, so an organism's resources must be divided up in a way that will increase fitness. One way to help make these important decisions is to perform a cost-benefit analysis of the current environment. Organisms using both fast and slow life history strategies utilize cost-benefit analyses to determine the most effective use of resources to increase fitness in their current individual environment.

Cross-References

- ▶ [Costs of Aggression](#)
- ▶ [Altruism and Costs to Altruist](#)
- ▶ [Benefit and Cost Asymmetries](#)
- ▶ [Benefit Group Relative to Other Groups](#)
- ▶ [Benefit to Another at Cost to Self](#)
- ▶ [Benefit to Another at Cost to Self](#)
- ▶ [Benefits to Kin](#)
- ▶ [Bridal Cost](#)
- ▶ [Cost of Same-Sex Friendships](#)
- ▶ [Costs and Benefits of a Large Brain](#)
- ▶ [Costs and Benefits of Mate Poaching](#)
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- ▶ Individuals That Impose Costs
- ▶ Life History Strategies
- ▶ Life History Theory
- ▶ Reproductive Benefits Must Outweigh Costs
- ▶ Sex Differences in Costs and Benefits of Mate Poaching

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Costly Apology Model of Suicidal Behavior

- ▶ Bargaining Model of Suicidal Behavior

Costly Displays

- ▶ Credibility Displays

Costly Punishment

- ▶ Altruistic Punishment
- ▶ Altruistic Punishment and Strong Reciprocity

Costly Rewarding and Punishment

- ▶ Strong Reciprocity

Costly Signaling

- ▶ Altruism Displays Cooperative Potential
- ▶ Handicap Principle, The

Costly Signaling and Altruism

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Synonyms

Handicap principle; Phenotypic quality advertisement; Signaling theory

Definition

An advertisement of one's phenotypic quality of cooperativeness, based on individually risky or resource-intensive displays of cooperation and/or selflessness.

In most social psychology traditions, altruism has tended to be examined in terms of the isolated situational factors which give rise to it on the part of individual altruists. Considerations like social norms and conventions, the proximity of the altruist to bystanders and confederates, the influence of rewards, and transient emotional states and much else have variously been identified as some of the major reasons why people tend to behave in an altruistic manner toward others. While examining these factors remains crucial to informing our understanding of the range-of-the-moment, proximal nature of altruism, adopting an evolutionary psychology lens allows us to assess *why* it is, in distal, ultimate terms, that these underlying motives and situational influences came to be so predictive of altruism (McAndrew 2002).

The proliferation of altruism was once a contentious issue by the lights of evolutionary theory. *Prima facie*, the notion that an individual would behaviorally perform in such a way that they incurred a personal cost (often a great one) only to benefit other individuals, was difficult to explain when invoking evolution by natural selection. It was not until Hamilton (1964) advanced the construct of inclusive fitness – through which altruistic behaviors were selected for through the vehicle of shared genes – that evolutionary theorists could employ an overarching framework through which altruism could be understood. In the intervening five decades since Hamilton's theoretical innovation in this space, a number of other theories – some competing and some complementary – have been advanced to provide additional or alternative grounding for the evolutionary rationale of altruism, including reciprocal altruism, competitive altruism, and multilevel-selection theory, among many others (Griskevicius et al. 2007).

Costly signaling theory (CST) is one such framework. CST operates by the principal that altruistic acts are a means through which individual people amass and mobilize social influence within their group and, as a result, increase their long-term reproductive fitness. People that perform altruistic acts self-interestedly fulfill their own individual objectives by publicly

broadcasting – often at great personal cost – instances of the qualities that underpin these acts, and do so in a manner for which the time, resources, risk, and energy inherent in them is apparent to those around them (Fehr and Fischbacher 2003). The reliability of the *signal* being broadcasted is contingent on its *costliness*, such as the case with instances of public generosity. The public provision of goods and services, instances of charity and philanthropy, and so forth, all imply a real and substantial personal cost in terms of what is sacrificed or spent by the altruist in performing the altruistic act. Such acts of altruism are unconditional, inasmuch as they are generally purposed toward assisting people for whom there is no expectation – both normative and practical – of them ever returning the favor in kind (Gintis et al. 2001; Zahavi 1975).

In performing such altruistic acts, CST predicts that the altruist themselves will benefit from developing a reputation for reliability within cooperative relationships and might thus be chosen as a strategic ally, romantic partner, friend, or mentor (Griskevicius et al. 2007). Obversely, it is not only the person broadcasting the costly signal that stands to benefit under such conditions. To the degree that the signal is reliable, those observing it benefit from high fidelity, useful information about the reputation of the altruist, and thus what the beneficial implications are of engaging in any kind of interpersonal relationship with them. In this sense, costly signaling is a reputation maximization mechanism: the more costly the act of altruism to whoever is performing it, the more effectively they themselves can convey their trustworthiness, and the more accurate their trustworthiness can be interpreted and understood by those around them (Jordan et al. 2016).

Experimental studies have demonstrated this phenomenon in action. The act of donating charitably to strangers has been shown to strongly influence the social attitudes of group members toward altruistic confederates. Among extant pre-industrialized societies, including the Ifaluk of Micronesia and Ache of eastern Paraguay, hunters reap substantial social and reputational

benefits from donating most (often all) of their catch to those within their society who have not incurred the palpable risk and onerous physical activity demanded of successful hunting expeditions that they themselves have. Those who lead such hunts, and who *publicly* share the spoils of them, take the opportunity to showcase not only their sense of charity and collective mindedness but their leadership skills and specialized understanding of local fauna; in the process, gaining both an esteemed reputation and the follow-on benefits of preferential access to high-quality mating partners – thus providing an evolutionary fitness calculus for the philanthropic results of their hunting prowess (Barclay 2012; Bird et al. 2001).

In addition to these revealing accounts of CST in pre-industrial cultural settings, additional empirical work (e.g., Bereczkei et al. 2010) has demonstrated a similar dynamic unfolding in modern, industrialized settings. Altruists have been shown to benefit from a payoff in social recognition, reputation, and group popularity when performing acts that were not only costly to the individual but performed publicly in such a way that the costliness of the acts were readily observable to those around them. Moreover, and as would be predicted by CST, the benefits of social recognition that accrue to the altruist increase proportionally with the inherent costs incurred by performing the act, such that the higher the investment made, the greater the commensurate gain in social reputation.

The notion that altruism ought to exist for its “own sake” – that altruism with any kind of self-serving utility function underlying it is ultimately not altruistic in some sharply definitionally demarcated sense – is a normative claim drawn from the most recent reaches of the human experience. *Why* altruism, and the performance of acts so costly to the individual yet so beneficial to others, came to exist at all within the evolved human neuropsychological architecture requires not just motives or situational explanations but a mechanism and an account of adaptive function.

CST, while not the only evolutionary theoretical framework marshaled to provide such an account, provides an explanation of how the costliness inherent in altruistic acts might be offset by the overall reproductive fitness benefits afforded by their public signaling.

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Costly Signaling Model of Suicidal Behavior

► Bargaining Model of Suicidal Behavior

Costly Signaling Theory

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Synonyms

Competitive altruism; Handicap principle; Honest signaling

Definition

“Costly signaling theory” proposes that animals (including humans) may send honest signals about desirable personal characteristics and access to resources through costly biological displays, altruism, or other behaviors that would be hard to fake.

Introduction

The existence of altruism was something of an obstacle for early evolutionary theorists, since an organism that engaged in behavior that came at a great personal cost and seemed to solely benefit other individuals appeared difficult for natural selection to explain. It was not until the introduction of the concept of *inclusive fitness*, also known as *kin selection*, by Hamilton in 1964 that evolutionists had a satisfactory theoretical framework for discussing altruism. The concept of kin selection, however, could not account for the many altruistic acts performed for individuals who are not genetic kin. An additional form of altruism, *reciprocal altruism* (Trivers 1971), explained why these important and socially necessary behaviors occur so frequently. Reciprocal altruism occurs when one organism provides a benefit to another organism at a cost to itself because it has received, or is likely to receive, a similar benefit in return from the other organism.

Neither of the aforementioned models of altruism, however, can explain large philanthropic

gifts, heroic self-sacrificial behavior, or handouts to beggars that will never be directly reciprocated. The most useful perspective on such behaviors has come to be known as “costly signaling theory,” which was first introduced by the Israeli biologist Amotz Zahavi in 1975. Costly signaling theory (Bliege Bird and Smith 2005; Grafen 1990; McAndrew 2002; Zahavi 1977) attempted to deal with these types of altruistic acts by proposing that such behaviors are a vehicle for individuals to advertise desirable personal qualities or resources. This may ultimately benefit the altruist by increasing the likelihood that he or she will be chosen as a mate or an ally and it may also be a way of positioning the individual for greater access to resources through direct or indirect reciprocation (Grafen 1990; McAndrew 2002; Nowak and Sigmund 2005; Roberts 1998; Zahavi 1977).

When the altruistic act is performed primarily for the purpose of advertising one’s own altruistic tendencies, it is referred to as *competitive altruism* because the signaler is effectively competing with individuals who are also attempting to establish altruistic reputations in the eyes of others (Barclay and Willer 2007).

The main distinction between competitive altruism and reciprocal altruism is that reciprocal altruism requires that the altruist is reimbursed by individuals who directly benefited from the original altruistic act, whereas costly signaling and competitive altruism can lead to future rewards from individuals who may not have directly benefited from the original act of altruism (Bowles and Gintis 2011).

Costly Signaling as Honest Signaling

The signals that conspecifics transmit to each other are only useful to the recipients of those signals to the extent that a signal communicates honest, reliable information about the sender. For example, a female who responds to misleading or false information about the quality of a mate may end up being saddled with low-quality offspring and a nonsupportive partner, both of which would

significantly impair her reproductive success. Consequently, there has been significant selective pressure to develop strategies for detecting honest signals of quality in others. In such a system, there must be a cost to the sender if a signal is discovered not to be honest (i.e., cheaters will be punished), and there will be a cost to receivers if dishonest signals are not detected (Higham 2014).

The “cost” of a signal to the sender is a reliable way of confirming the honesty of that signal, so costly signaling is very much about truth in advertising. A “low-quality” signaler who attempts to fake a high-quality signal will deplete whatever resources that he may have available, leaving the signaler in such a vulnerable position that the strategy will prove to be counterproductive. Conversely, a high-quality signaler has resources to burn and can easily afford a high-quality signal, so the adaptive benefits will outweigh the costs (Grafen 1990). Hence, costly signaling theory (CST) proposes that individuals often engage in behaviors that are very costly as a way of signaling honest information about themselves.

Smith and Bird (2000) have described the four qualities that a behavior must have to qualify as a costly signal. First, the behavior must be easily observable by others. Second, it must be costly to the actor in resources, energy, or some other significant domain. Third, the signal must be a reliable indicator of some trait or characteristic of the signaler, such as health, intelligence, or access to resources. Finally, the behavior in question must lead to some advantage for the signaler.

The term “handicap principle” has often been used interchangeably with “costly signaling theory.” This reflects the origins of this theory in research on animal communication where it has been established that some animals “handicap” themselves with extremely costly biological features that only individuals in excellent condition can afford to maintain. The brilliant plumage of the peacock’s tail and the impressive antlers of elk are classic (if a bit timeworn) examples of such handicaps. Many researchers no longer think of these terms as synonymous and believe that handicaps are neither necessary nor sufficient for honest signaling but may still be helpful insofar as

they prevent low-quality individuals from sending high-quality signals (Higham 2014).

Philanthropy as Costly Signaling

Public philanthropy is one of the most common costly signals of social status in humans, especially in Western cultures such as the United States. Universities, public television stations, museums, and the arts depend upon it for their very survival. CST suggests that such philanthropy is a conspicuous display of resources that reinforces the status, resources, helpfulness, and all-around quality of the benefactor. After all, if a person can afford to expend a great deal of money, energy, or time in a manner that seems to be irrelevant to his or her selfish interests, then the resources that are being held in reserve must be very great indeed.

This type of competitive altruism may be a way of positioning oneself for access to resources during unforeseen future times of need (Boone 1998), and there is in fact evidence to support the belief that individuals who have a history of being magnanimous are rewarded by others when times get tough. Among the Ache of Paraguay, for example, individuals who shared more than average with others in good times received more food from more people when they were sick or injured than did those who had been less generous (Gurven et al. 2000). Apparently, having everyone owe you for past unselfishness can be a good hedge against future calamities, and costly signaling may be an effective strategy for inducing reciprocal altruism.

Anthropological studies provide numerous examples of exaggerated displays of public generosity. For example, Smith and Bird (2000) described a form of costly signaling among the Meriam, a Melanesian society located on an island off the coast of Australia. Two to 5 years after a death, the family of the deceased puts on an elaborate feast to coincide with the erection of an expensive and showy permanent tombstone. Gifts are given to all guests, along with prodigious amounts of food. Ideally, one of the main courses is turtle meat obtained through a dangerous, time-

consuming turtle hunt. Successful turtle hunting requires careful coordination of effort and great physical agility, strength, and diving abilities because the turtle hunters have to jump from a boat onto moving turtles in open water. The ability to supply many turtles for the funeral feast serves as an honest signal of the physical quality of the males in the family. Everyone is invited to the feast, and no reciprocation of any kind is expected.

Laboratory studies by psychologists have also demonstrated that charitable donations and other acts of kindness are most likely to take place when the behaviors are easily observed and recognized by others (Bereczkei et al. 2010; Haley and Fessler 2005), and van Vugt and Hardy (2010) have even shown that people will make wasteful contributions in “public goods” situations, knowing full well that the contribution will not make a difference, as long as the contribution is publicly observed. The reason that this occurs is because the contribution is primarily a self-presentation strategy designed to increase the contributor’s status and prestige, with other outcomes of the philanthropy being less consequential to the donor.

Some researchers posit that conspicuous displays of philanthropy and benevolence can be triggered by mating motives, possibly as a way of advertising prosocial personality traits valued by prospective mates, and there are data to confirm that males are more likely to display altruism in the presence of attractive members of the opposite sex; the same does not hold true for females (Farrelly et al. 2007; Iredale et al. 2008). Griskevicius et al. (2007) found that mating motives are especially likely to encourage male generosity if the act of benevolence highlights a man’s prestige or his heroic nature.

The evolutionary roots of philanthropy as a costly signal may be found in the tradition of meat sharing by prehistoric hunters. Successful hunters signaled desirable physical qualities such as physical vigor and health, eye-hand coordination, and mastery of weapons, and by sharing meat they could also demonstrate cooperative, prosocial tendencies that would have been highly valued (Gurven et al. 2000).

Risk Taking and Heroism as Costly Signaling

It’s no secret that young men are notorious for engaging in foolish, risky behavior and that most people fear violent behavior by young men more than violent behavior by older men. In fact, the tendency of young men to engage in risky and/or aggressive behavior prompted the Canadian psychologists Margo Wilson and Martin Daly (1985) to give it a name: Young Male Syndrome. The results of the annual “Darwin Awards” competition support their position convincingly. The Darwin Awards feature those individuals who have lost their lives in dramatic fashion during the previous year by taking stupidity to a colossal new level. For the 5-year period from 2010 through 2014, the Darwin Award winners were skewed toward men by a margin of 38 to 5, with two of the five women who made the list getting there by being talked into having sex with men under less than rational circumstances (<http://www.darwinawards.com/>).

Why would this predilection for recklessness have evolved in young men?

For sound evolutionary reasons, younger men find themselves especially concerned with status and dominance. In early human societies, competitive success in early adulthood established a man’s standing in his social group for the rest of his life; it wasn’t possible to simply hit the “reset” button and join another group, so what happened during the teen years mattered a great deal. For this reason, high-risk competition between young males provided an opportunity for “showing off” the abilities needed to acquire resources, exhibit strength, and meet any challenges to one’s status. Consequently, heroic or even recklessly daredevil behavior was rewarded with status and respect – assuming, of course, that the young man survived the ordeal. Anthropologist Kristen Hawkes (1991) has developed the “show-off hypothesis” to explain the well-replicated finding that men in hunter-gatherer societies who are predisposed toward more risky hunting strategies end up with greater sexual access to women (Hill and Hurtado 1996; Smith 2004; Wiessner 2002).

Today, the widespread promotion of sport in our culture undoubtedly developed as a constructive alternative for dealing with the proclivities of young males that evolved in a very different time. In a legally sanctioned gladiatorial arena, young men are able to exhibit the same skills – throwing, clubbing, running, wrestling, tackling, hand-eye coordination – that would have made them successful fighters or hunters in the ancestral environment. Participating in team sports enables athletes to exhibit other qualities such as cooperativeness, loyalty, and planning ability – all of which are hard to fake (Kniffin and Sugiyama 2018).

This proclivity for recklessness may also be relevant to understanding why men are more likely to flout the conventions of polite society than are women (McAndrew 2018). In other words, why are men more disgusting than women?

Much of the time disgusting behavior is also risky behavior. By eating or drinking things that might be contaminated in some way or by risking social ostracism by flouting the rules of your group, you are putting yourself on the line. You are risking serious illness or excommunication from the group, both of which would have been deadly in the brutal prehistoric world of our ancestors. If you can take such risks and survive them, you are signaling to others that you have special qualities. Hence, behaving in a disgusting manner may in fact be a perverse form of costly signaling that demonstrates superior genetic or personal qualities.

Along these lines, a team of anthropologists at UCLA led by Dan Fessler tested what they called the “crazy bastard hypothesis” in a series of studies (Fessler et al. 2014). They gathered data online from thousands of Americans and in person from dozens of individuals in the Fiji Islands. They had people read short scenarios about individuals who engaged in risky, daredevil behavior or in more cautious, risk-averse behavior. They then asked them to make judgments about the characteristics that they thought the person in the story might possess. Among other things, the daredevil was perceived to be taller, stronger, and generally

more physically formidable than the cautious individual. Thus, risky male behavior may not just be about advertising genetic quality, but it may also advertise how one might behave as an adversary or an ally. If one sees a “crazy bastard” who behaves with apparent disregard for his own personal well-being by doing things that would scare ordinary men away, one might definitely end up wanting to have this person as a friend rather than as an enemy. Even though the crazy bastard’s behavior is not overtly aggressive, one can easily imagine the terror of dealing with such a reckless opponent in combat and the comfort that one might have going into battle with that individual as a comrade. Going back to the dawn of recorded human history, one can find rituals (often involving excessive consumption of alcohol) used by warriors to at least temporarily make themselves feel and appear to be formidable crazy bastards as a way of intimidating their enemies and taking the fight out of them before the battle even began.

A form of risky behavior that serves as an especially effective costly signal is physically risky altruistic behavior, which is the very definition of heroism. Evolutionary psychologists believe that even apparently selfless impulses such as true heroism must provide some adaptive advantage for individuals; otherwise, such behaviors would have been strongly selected against, and many studies confirm that people who sacrifice for the group by engaging in physically costly altruistic activities do in fact achieve elevated social status, respect, and recognition as a result of their public selflessness (McAndrew and Perilloux 2012; Willer 2009), especially when the behavior displays courage and physical strength (Farthing 2005; Griskevicius et al. 2007; Kelly and Dunbar 2001; Sylwester and Pawlowski 2011).

For example, on Ifaluk Atoll in Micronesia, males sometimes engage in torch fishing (luring flying fish into nets at night with torches) when other fishing techniques would actually be more efficient. Torch fishing is a difficult, time-intensive activity but also a highly visible activity that serves to advertise a man’s work ethic (Sosis 2000).

Displaying heroism in time of war is another powerful way for young men to acquire rewards from costly signaling, and historical data confirm that the proportion of a population made up of young men is one of the best predictors of when a society is most likely to go to war (Mesquida and Wiener 1996).

A team of European psychologists explored the proposition that war provides an arena for men to compete and impress both their male rivals and females who might be potential mates (Rusch et al. 2015). In one study, they found that 464 American men who had won the Medal of Honor during World War II eventually had more children than other US service men who had not been so heroically distinguished. This is consistent with the idea that heroism gets rewarded with greater reproductive success.

In a second study, 92 women rated the sexual attractiveness of men who had behaved heroically in war as being higher than that of soldiers who had served but not been identified as heroes. Tellingly, women did not show this increased attraction toward men who had behaved heroically in sports or business situations. A third study revealed that behaving heroically in war does not increase the attractiveness of female war heroes to men. In summary, heroism in time of war is sexier than any other kind of heroism but only for men. Similarly, enhanced access to females has been documented for males who join violent street gangs (Palmer and Tilley 1995).

Therefore, while there are certainly many examples of women behaving heroically, physically risky, self-sacrificial heroism is commonly perceived to be a stereotypically male behavior (Griskevicius et al. 2007; Iredale and Van Vugt 2009; Lyons 2005). If self-sacrificial altruistic behavior is indeed a “male thing,” it should be most likely to occur when males show off and compete directly with each other for status (and ultimately for mating opportunities). In a series of laboratory studies, McAndrew and Perilloux (2012) demonstrated that men were most likely to volunteer for physically costly experiences (experiencing pain and getting soaked in a dunk tank without any advance notice) so that their

group could win money when there was both a female *and* another male present in a three-person group. Their studies also confirmed that those who volunteered for such activities were liked better, were rewarded with more money, and were preferred as future work partners by their colleagues in the experiment.

Conspicuous Consumption as Costly Signaling

Perhaps the most readily observable form of costly signaling in capitalistic societies is wasteful spending on luxury goods that by definition are not essential for survival, or even for comfort, in daily life. This “conspicuous consumption” is driven by a desire for status and the clear signaling of this status to onlookers (Saad 2007). In a series of seven studies, Nelissen and Meijers (2011) confirmed that wearing brand label clothing does indeed increase perceptions of a person’s wealth and status, and that this perception leads to all sorts of advantages. Specifically, these studies demonstrated that individuals wearing expensive branded clothing are more likely to gain compliance to their requests, be recommended for jobs and higher salaries, achieve better outcomes in social dilemma and dictator games, and that they are more successful when soliciting charitable donations from others. Griskevicius et al. (2010) have also determined that people buy expensive, environmentally friendly products specifically to boost perceptions of status and to advertise their own altruistic tendencies.

A number of studies have highlighted how closely conspicuous consumption as a costly signal is tied to mating motives. Wang and Griskevicius (2014) found that the need to guard their mates and ward off mate poachers triggers displays of luxury goods by women who wish to deter rivals by demonstrating the depth of their mates’ devotion. Similarly, Hennighausen et al. (2016) found that priming men with concerns about competition with other men for status leads to an increased interest in acquiring luxury goods such as expensive cars, and that males are

predisposed to see other men who own luxury cars as potential rivals than as potential friends. Saad (2011) has even reported that men's testosterone levels increase after publicly driving an expensive Porsche automobile and decrease when driving a beat-up old Toyota sedan.

However, the mating advantages of conspicuous consumption are apparently limited. Conspicuous consumption by men primarily reflects an interest in short-term mating rather than long-term mating, and this is accurately detected by females who nonetheless judge conspicuous consumers to be more desirable as short-term (but not as long-term) mates (Hennighausen et al. 2016; Sundie et al. 2011).

Many anthropologists have studied how expensive cultural rituals such as wedding receptions translate into costly signals. For example, Bloch et al. (2004) examined how the notoriously over-the-top lavishness of Indian weddings (paid for by the bride's family) came to be. The dowry (bride price) and the wedding reception can cost the family up to six times their annual income, and it is one of the leading causes of debt among Indian families. Bloch and his colleagues interviewed many Indian families about just this issue. The status of Indian families is strongly linked to the importance of the people that they know and the size of their social network, and wedding receptions are an ideal venue for expanding and advertising the nature of this network. Their interviewees emphasized the importance of "making a good show" and they were keenly aware that the details of the wedding would be discussed by others. Marriage in general and the wedding in particular therefore become key ways of signaling prestige. Lavish weddings are especially important signals when the groom's family comes from a different village where the exact social standing of the bride's family may be unknown; they have less social impact when everyone in town already has in-depth knowledge of a family's economic situation. So, Bloch et al. (2004, p. 690) concluded that "wedding celebrations are a form of conspicuous consumption that signals the family's social status to the community."

Religious Commitment as Costly Signaling

Evolutionary psychologists have long thought of religion as a social mechanism for enforcing cooperation within cultural groups (Wilson 2002). One of the ways in which it may successfully accomplish is by using religious commitment as a costly signaling device (Henrich 2009). All religions have rituals, taboos, and other requirements that can be very costly in terms of time, money, or effort. Fasting, tithing, frequent and lengthy prayer and/or religious services, and dietary requirements that are difficult to maintain require a good deal of commitment. Thus, religious commitment can be a hard to fake signal of commitment to the group's values and a signal that one is likely to be a reliable, cooperative group member. Sosis and Bressler (2003) conducted a historical analysis of communal societies and discovered that the ones with the costliest membership requirements survived for the longest times but only if the commune had an underlying religious reason for existence. Soler (2012) found that religious commitment predicted generosity in economic games and self-reported acts of generosity among adherents to an Afro-Brazilian religion in Brazil.

Conclusion

Costly signaling theory provides a compelling rationale for altruistic acts that are not easily explainable by other mechanisms such as kin recognition or reciprocal altruism. Costly signaling occurs in a wide range of social situations such as consumer behavior, philanthropy, heroic action, and religious activity. Such costly signaling helps maintain social groups by providing honest information about the traits, resources, and behavior patterns of individuals who are members of those groups. All available evidence indicates that costly signaling does in fact result in rewards for the altruist in the form of increased mating opportunities, access to resources, and positive attention from others.

Cross-References

- Altruism
- Competitive Altruism
- Conspicuous Consumption
- Heroic Rescue in Humans
- Honest Signaling
- Men Riskier, More Aggressive
- Reciprocal Altruism
- Religion
- The Handicap Principle
- War
- Young Male Syndrome

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Costly Signalling

► Reliability and Deception in Language

Costs

► Living in Groups

Costs and Benefits of a Large Brain

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Synonyms

Brain evolution; Consequences of possessing a large brain; Incurrences of higher cognition; Privileges of the human brain

Definition

Humans are distinct from all other forms of life by the hub of their central nervous system, the brain,

which serves as both the most powerful and most exhausting human asset.

Introduction

It is critical to an organism's fitness to receive and to respond to information from its environments. The ability to process external information has become a driving force of evolution. As a result of various selection pressures over an extensive period of time, the most complex information processing system was engineered, the brain. Increased brain size and neuronal connections granted modern humans or *Homo sapiens* incredible perceptual capacities, such as consciousness and theory of mind. Although positioned as benefits in the context of being able to interact with the environment, there are also costs to operate the complex cognitive processes.

Evolution of the Mammalian Brain

The mammalian brain has a unique trait of changing shape as it matures. The cortical surface areas and volumes are relatively much larger than other species' cortical structures in the animal kingdom. Brains of mammals, especially primates, became more convoluted as it evolved a larger volume. The more the environmental challenges early humans or *hominids* faced became increasingly varied, the more varied their brain morphology became.

About 2.5 million years ago, *homo habilis* lived with an average brain size of 36 cubic in. (Harari 2015). *Homo erectus*, the first recorded humans to be completely bipedal, from almost 2 million years ago, had the privilege to practice hand dexterity. It is hypothesized that the freedom of hands gave rise to environmental manipulation, such as manufacturing tools to facilitate survival.

Today, the average adult *homo sapien* brain ranges from 73 to 85 cubic in. and comprises of billions of neurons (Harari 2015; Hofman 2014); however, it should be noted that *homo*

neanderthalensis or the *Neanderthals* possessed a brain size larger than the brains of *Homo sapiens* (Harari 2015). Although bigger is often better, a bigger brain is far from perfection.

Costs of the Human Brain

The brains of *Homo sapiens* account for 2–3% of their total body mass, yet it consumes about a quarter of the body's energy when at rest. Comparatively, the brains of several primate species consume about 8% of their body's energy when at rest. Given the size of the head relative to its body, combined with the fact that *Homo sapiens* are completely bipedal, its size and weight often are at fault of back aches and neck stiffness. With the increase in brain and skull size also came an increase in infant and mother mortality during childbirth (Harari 2015).

As a result of increased brain size, human offspring are born more underdeveloped compared to many other offspring of primates and mammals. Human babies are extremely fragile and require years of meticulous attention to grow into a healthy child. For instance, a baby's head is so large and heavy relative to its body that unless supported when being held, the baby's neck is at risk of breaking. Moreover, many baby health issues result from the brain's high demand for oxygen. Babies who do not meet this demand often acquire developmental disabilities via brain damage (Harari 2015). Modern human babies require years of being nurtured before becoming completely independent; a human brain takes almost three decades to mature (Arnett 2000).

Healthy brain development requires a substantial amount of energy and resources from the environment. Being deprived of a nutritious diet entails both physical and mental consequences. Infant and child mortality was not uncommon to early humans. Increased brain size within mammalian species is found to correlate with a decreased litter size, which suggests that quality was preferred over quantity (Isler and van Schaik 2009).

The adult human brain is so convoluted that there are a variety of factors that can stir its malfunction. A complex brain with the ability to perceive itself also has the ability to experience pain, negative affective states, and mental disorders (McManus 1997). One in four adults in the United States experiences a mental disorder every year (Duckworth 2013). Mental disorders are notorious for engendering a variety of negative emotions, which can escalate to homicidal and suicidal ideation.

Benefits of the Human Brain

The human brain is capable of possessing a variety of intelligences, some of which are exclusive to humans. Humans are exceptional learners; they are easily capable of solving a variety of problems and can learn from the successes and failures of others. The human brain houses spatial, kinesthetic, mathematical, linguistic, and social intelligences, which enable humans to simulate various scenarios in their environment, determine which foods are safe and unsafe to eat, carve stone, devise animal traps, take care of their young, and treat certain injuries (Harari 2015).

Along with higher intelligence, humans possess theory of mind and consciousness, which provides humans the ability to form mental simulations of others and themselves. Being able to attribute emotional states to others and being able to engage in extrapolation precedes making predictions of other's actions. The traits of precaution, refinement, and better decision-making, among others, are vital for humans to rise to the top of the food chain.

The brain's intelligences would be of little use if it lacked memory systems. Sensory, short-term, and long-term memories store bodies of information from the environment. Organisms that reside in ever-changing environments must find the means to store and retrieve previously processed information in order to adapt. Humans, like most animals, are exploratory creatures; being able to learn from mistakes is the most versatile evolutionary advantage.

Conclusion

The cerebral growth spurt from *homo habilis* to *Homo sapiens* is argued as the most rewarding and most debilitating development of the human. The human brain continues to baffle a wide range of scientists and is likely to remain an enigma for generations to come. It is a privilege to comprehend anything about the complex organ, especially about its impediments. Research in evolutionary psychology is driven by the mysteries of human behavior, which may always remain under the tutelage of the physical brain. Although it may be responsible for countless premature deaths, limited cognitive functioning, and mental illnesses, the brain is also responsible for granting humans the ability to learn, the ultimate adaptation.

Cross-References

- Early Stage of Brain Development at Birth
- Energy Consumption
- Largest *Homo* Brain
- Narrowing Birth Canal
- Neurons in the Cerebral Cortex

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Costs and Benefits of Mate Poaching

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Synonyms

Human mate poaching; Mate poaching; Sex differences in costs and benefits of mate poaching

Definition

Mate poaching is a behavior intended to lure someone away from their current romantic relationship to form either temporary or permanent relationships with them.

Introduction

Mate poaching appears to be a ubiquitous behavior found in various regions of the world. Schmitt et al. (2004) conducted a survey with 53 nations on 5 continents and found that more than half of men (56.9% for short-term relationships; 57.1% for long-term relationships) tried to poach a mate. The frequency of occurrences was somewhat lower for women (34.9% for short-term relationships; 43.6% for long-term relationships).

For both long- and short-term relationships, around 70% of men and women reported that someone attempted to poach them. The highest rates of mate poaching attempts in a long-term context were reported in the Americas and Europe (56.2–65.6% in men and 43.3–51.5% in women), and a similar pattern was observed in the short-term context (56.7–70.3% in men and 35.5–41.9% in women). In contrast, the lowest rates of mate poaching in the long-term context were found in South/Southeast Asia (38.9% in men and 17.4% in women), while lowest rates in

the short-term context were found in East Asia (29.5% in men and 14.9% in women). Overall, women tried to poach men for long-term relationships more than short-term relationships, while the opposite was true for men. These findings might suggest that mate poaching pays off more for men, in short-term mating.

The potential costs and benefits of mate poaching depend on the perspective of the individual involved. In other words, the perspective of mate poacher, poached one (i.e., the target of the poaching), and poachee (i.e., an individual whose mates were lured away) should be taken into consideration when assessing costs and benefits. For instance, taking pride in conquest is a potential benefit, while having a ready competition with the poachee is a potential cost exclusively for the poacher (Schmitt and Buss 2001). Fearing physical danger from the poachee, however, can be a potential cost for both the poacher and the poached one (Schmitt and Buss 2001; Wilson and Daly 1996). The poachee, on the other hand, might pay the cost of losing a partner.

The costs and benefits associated with mate poaching can be examined on the ultimate and proximate levels. The ultimate level cost-benefit analysis of mate poaching takes both the adaptive challenges that our ancestors may have faced and the adaptive solutions to those problems into account. This level of analysis urges to ask the “why” question to find the evolutionary function of the behavior. The proximate level analysis, however, has to do with the “how” question, and it encompasses immediate assessment of the behavior (Tinbergen 1963; Hladký and Havlíček 2013; Stephen and Sulikowski 2019). In this type of analysis, the flow of events (i.e., response to “how” question) is directly observable, unlike ultimate level analysis. The main aim of this entry is to provide an overview of ultimate and proximate costs and benefits associated with mate poaching. Several factors, such as type of the relationship desired by the poacher, sex differences, gender equality, socioeconomic status, and sex ratio, can potentially affect the costs and benefits of mate poaching. Costs and benefits linked with mate poaching will be explained and exemplified through these factors.

The Relationship Types and Sex Differences

Mate poachers aim to establish either short-term (i.e., temporary) or long-term (i.e., permanent) relationships with the poached. The type of desired relationships affects the potential costs and benefits of mate poaching. For instance, several proximate costs such as guilt feelings, deception issues, dating isolation (i.e., having to hide when on a date), and family rejection were reported as costlier in poaching for a long-term relationship compared to a short-term relationship for both sexes (Schmitt and Buss 2001).

Furthermore, the type of relationship that is being encroached on might also affect the potential costs and benefits of mate poaching. Davies and Shackelford (2017) found that the poached person expected more resources and physical attractiveness (compared to their current partner) when they were married as opposed to cohabitating and when they were cohabitating as opposed to dating. Similarly, Schmitt and Buss (2001) reported that both men and women were perceived as less successful in poaching women/men who have committed relationships as opposed to uncommitted relationships. Therefore, target individuals' current relationship status and investment affected their perception of the trade-off between the cost and benefit of being poached.

Together with the relationship types, sex differences also play a crucial role in the potential costs and benefits associated with mate poaching. An ultimate benefit of mate poaching is an increase in reproductive success. For men, the minimum parental investment required is only the copulation time, while for women, it is at least 9 months of pregnancy (Trivers 1972). Therefore, men can increase their reproductive success by having a higher number of partners. Relatedly, Schmitt and Buss (2001) found that enjoying sexual variety was labeled by the participants as a potential (proximate) benefit of mate poaching for men. In line with that idea, men might see more benefit in poaching for short-term relationships than for long-term relationships as compared to women. Schmitt and Buss (2001) found that the percentage of men (64%)

attempting to poach for a short-term relationship was higher than the percentage of women for the same purpose (49%).

More women (63%) than men reported to attempt poaching for a long-term relationship (52%). However, men, more than women, attempted to poach for both long- and short-term relationships in all regions (Schmitt et al. 2004). In line with this finding and compared to men, women perceived a higher cost of reputational damage and shame if they poach for short- or long-term sexual affairs or a new exclusive relationship (Davies et al. 2010).

Furthermore, Schmitt and Buss (2001) found that for short-term mate poaching, men perceived a greater benefit of taking pride in conquest, while women perceived the same benefit more than men in the long-term mate poaching context. Relatedly, men perceived more benefit of ego-boosting in mate poaching for a short-term relationship when compared to women (Davies et al. 2010). Consistent with their tendency for short-term matings with a lower commitment, men found more benefit in enjoying a lack of responsibility and always having time off from a relationship compared to women (Schmitt and Buss 2001).

Men can increase their reproductive success by having physically attractive partners. Previous studies showed that female physical attractiveness (e.g., waist-to-hip ratio and lumbar curvature) might indicate fertility (Singh 1993; Lewis et al. 2015). Therefore, having a physically attractive partner is a potential proximate benefit for men both as a poacher and poached.

Throughout human evolutionary history, the particular cost of fathering someone else's offspring has exclusively applied to men (Buss and Schmitt 1993). Therefore, to ensure their fatherhood, men might show sexual proprietariness (Buss and Schmitt 1993). One potential consequence of male sexual proprietariness might be murder, including wife killings (Wilson and Daly 1996; Buss 2005). In other words, having a physical danger might be a potential proximate cost for both the male poacher and the poached female.

The cost of fearing physical danger was rated more highly for men than for women by the

participants (Schmitt and Buss 2001). However, Davies et al. (2010) found that women who poached for an exclusive relationship saw a greater cost of being physically harmed by the poached partner. The difference between these two studies might be due to the variation in methods of perspective given (i.e., third-person perspective, Schmitt and Buss 2001; first-person perspective, Davies et al. 2010).

Women can increase their reproductive success by having men who are willing to and have the means to provide for themselves and their offspring. Therefore, gaining resources can be the proximate benefit for females. Schmitt and Buss (2001) found that gaining resources was attributed as a benefit for female poachers. Relatedly, resource depletion might be a proximate cost for men (Schmitt and Buss 2001).

For both sexes, most mate poaching attempts appear to result in success. Schmitt et al. (2004) found that over 65% of men and women reported successfully poaching a mate away as a short-term mate and a long-term mate. More than half of men reported to be either poached away as a short-term or as a long-term partner. Over 40% of women were successfully poached away as a short-term mate, except in South/Southeast Asia (28%) and Africa (26.9%). More than 42% of women were poached away as a long-term partner worldwide. Arnocky et al. (2013) found that the number of mate poaching attempts was a significant predictor of lifetime sex partners, lifetime casual sex partners, and lifetime dating partners. However, another study showed that relationships formed via poaching function rather poorly. There were lower levels of commitment and investment and less satisfaction, and the rates of infidelity were higher compared to the other relationships formed differently (Foster et al. 2014). The quality of the resulting relationships might also be affected by the friendship between the poacher and the poached. For instance, it was found that poachers were seen as less likely to commit infidelity when the poacher and the poached were friends. Furthermore, their relationships were considered more likely to last over a year (Mogilski and Wade 2013). Friendship might signal commitment. Therefore, the likelihood of experiencing

the proximate cost of future infidelity might be reduced.

Having a pre-approved partner can increase reproductive success, especially for women. As mentioned above, women can increase their reproductive success by being with men who can and are willing to provide resources for them and for their offspring (Schmitt and Buss 2001). These characteristics may not be readily available from the visual cues. Therefore, by copying the preferences of other women and poaching a coupled man, women can lower the cost of selecting a mate (e.g., time being spent and choosing a mate low in quality). On the other hand, the female body can signal fertility more readily than the male body (Perilloux and Cloud 2019). Therefore, men can use physical cues to assess women's mate value. Furthermore, preferring women with partner can lead to an unwanted consequence of misdirecting parental investment (Hill and Buss 2008). Therefore, having a pre-approved partner can be a proximate benefit of mate poaching for women rather than men.

The results of studies on female mate copying, however, have shown contradictory results. It was found that women perceive the male targets presented with females as more attractive (Gouda-Vossos et al. 2018) and that mate copying is more common among young women compared to older women (Anderson and Surbey 2014). However, Parker and Burkley (2009) found that only single women showed a preference for the attached men compared to single men. In another study, women did not perceive engaged or in-a-relationship men as more attractive or as having higher socioeconomic status (Uller and Johansson 2003).

A study conducted with male participants tested the mate copying effect. The findings suggest that men perceived the female images with the title "with a partner" as socially more distant compared to the female images with the title "without a partner" (Ueda et al. 2017). The two-thirds of the participants indicated a lower desire to have a romantic relationship with the partnered females in the images. They also show that this effect was accompanied by the parietal cortex activation. The parietal cortex is associated with social distance evaluation, the analysis of the

complex network of social relationships based on physical distance, such as close and distant friends (Yamakawa et al. 2009). The participants preferring females with partners, in contrast, had a higher orbitofrontal cortex activity (Ueda et al. 2017). This region of the brain is linked with risk-taking (Hsu et al. 2005) and with subjective ranking of visual objects (Lebreton et al. 2009).

In line with the studies discussed above, Davies et al. (2010) found that both men and women would be averse to mated individuals when they are equally attracted to single and already-mated ones. These findings collectively suggest that the costs of mate poaching might under many circumstances exceed the benefits for the poacher.

Cultural and Environmental Factors

Gender equality, socioeconomic status, and sex ratio might affect the cost-benefit assessment of mate poaching. For instance, Davies et al. (2010) found that the perceived cost of mate poaching was higher among women than men. This difference might explain why men attempt to poach more than women (Schmitt et al. 2004). In line with that logic, Schmitt et al. (2004) found that in gender-equal regions, sex differences tend to shrink for poaching a short-term partner. This finding mainly stemmed from the women's increased poaching attempts. Furthermore, there was a negative correlation between men's poaching attempts for long-term relationships and gender egalitarianism (i.e., equal access to political and economic power). Women's mate poaching attempts were, on the other hand, positively correlated with gender egalitarianism. Furthermore, both men and women showed increased poaching attempts when women have more political power indexed by the proportion of women in parliament. There was a positive correlation between political equity (i.e., equal access to political power) and women's both short- and long-term poaching attempts and their prevalence. Political equity was also positively associated with the occurrence of men's short-term mate poaching attempts.

Socioeconomic status can also have an impact on the potential costs and benefits of mate poaching. Schmitt et al. (2004) found that men who engage in short-term mate poaching attempts more had a higher socioeconomic status in many regions (i.e., North America, Western Europe, the Middle East, and Africa). Women also showed a similar tendency in certain regions of Southern Europe, South/Southeast Asia, and East Asia. Furthermore, for both sexes, the successful short-term mate poaching attempts were positively related to the socioeconomic status of the participants. Men's failure to resist short-term mate poaching attempts was also positively linked to socioeconomic status. Therefore, for both poacher and the poached, socioeconomic status affects the costs and benefits of mate poaching.

Lastly, sex ratio might also affect the costs and benefits associated with mate poaching. The available mating pool might shrink for the more prevalent sex when the sex ratio is skewed. This reduced availability might motivate mate poaching by potentially increasing the reproductive success of the more prevalent sex. In other words, the benefits of mate poaching might be higher for the more prevalent sex compared to the rarer sex. As expected, the prevalence of female mate poaching attempts was negatively linked to their sex ratio (Schmitt et al. 2004). However, when the male sex ratio was higher, men showed fewer attempts of mate poaching. Furthermore, in the regions where there is a surplus of women, mate poaching rates showed a trend to increase. Therefore, the potential effect of sex ratio on the cost-benefit assessment of mate poaching was only partially supported.

Future Directions

The number of studies on the costs and benefits of mate poaching is somewhat limited. Indirect evidence from uxoricide (i.e., wife killing), infidelity research, and mate copying research have been commonly used in the mate poaching literature. However, uxoricide or extra-pair affairs do not always encompass mate poaching. For instance,

if a married woman pursues a single potential partner and eventually has an affair, it falls into the definition of an extra-pair affair but not of mate poaching. Similarly, mate copying does not necessarily indicate mate poaching behavior. It might merely show the preferences of same-sex individuals. Therefore, future studies are needed in order to have a better understanding of the costs and benefits of mate poaching behavior. Furthermore, to our knowledge, none of the studies directly investigating the cost-benefits associated with mate poaching used the interview method. Qualitative studies with in-depth interviews might shed light on proximate costs and benefits further by exploring variation in contexts of mate poaching behavior.

Conclusions

Mate poaching appears to be a widespread human experience. Almost 70% of people claim that someone attempted to poach them, and nearly half of them reported to fail resisting it. Although it is a ubiquitous experience, the findings suggest that mate poaching may not be the first preference of most people when seeking a mate, possibly due to its potential costs.

There are various potential ultimate and proximate costs and benefits associated with mate poaching. Having a higher reproductive success is a potential ultimate benefit, while taking pride in conquest, gaining resources, and enjoying a sexual variety are among the proximate benefits. The potential ultimate cost of mate poaching is a lowered reproductive success; while future infidelity concerns, ready competition with the poachee, and resource depletion are the examples of the proximate costs.

Several factors affect the cost-benefit assessment of mate poaching for both the poacher and the poached individual. The types of relationships desired by the poacher and the type of target relationship being encroached on, sex differences, cultural and environmental factors (i.e., gender equality, socioeconomic status, and sex ratio) are among those factors. Future studies are needed to have more in-depth information about the context

of mate poaching. Having a detailed picture of the mate poaching context will lead to a better understanding of its costs and benefits.

Cross-References

- [Human Courting](#)
- [Infidelity](#)
- [Mate Copying](#)
- [Mating Rivalry](#)
- [Personality and Mate Poaching](#)

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Costs of Aggression

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Synonyms

Aggressive behavior; Violence

Definition

The price individuals pay when they behave aggressively toward others.

Introduction

Although aggression can serve many different functions, or no function at all, the function for which aggression presumably evolved, and which presumably accounts for most occurrences of aggression in modern human life, is competition.

In other words, aggression allows one individual to obtain a resource from another one; improve his/her status over another one; coerce another individual into an activity that is against his/her interests; reduce the competitive ability of another individual in physical, social, or psychological ways; or eliminate a competitor altogether.

By definition, competitive aggression toward another individual inflicts costs, and brings no benefit, to this individual (otherwise it would not be called aggression but punishment or something else). From an evolutionary perspective, the costs of aggression to the target or victim imply a reduction in this individual's probability to survive or reproduce. In everyday life, relatively minor forms of aggression may not necessarily impair another person's survival or reproduction but nevertheless can induce a variety of different costs: physical, social, psychological, reputational costs, or costs in terms of lost time or energy or missed opportunities to engage in other beneficial activities.

The analysis of aggressive behavior from an evolutionary perspective or the perspective of rational theory used by economists leads to similar predictions regarding the occurrence of aggression: aggression should occur only when it brings a competitive advantage to the actor (Georgiev et al. 2013). The competitive advantage to the actor can take two different forms, which correspond to two distinct forms of aggression: selfish and spiteful aggression. Selfish aggression, by the definition, entails costs and benefits to the actor and costs to the recipient. This form of aggression should occur whenever the benefits of aggression to the actor are greater than the costs of aggression to the actor. Spiteful aggression, instead, entails no direct benefits to the actor but costs to the actor and costs to the recipient. This form of aggression should occur whenever the costs of aggression to the recipient are greater than the costs of aggression to the actor.

In order to understand human aggression from an evolutionary or rational perspective, it is crucial to identify, quantify, and fully understand the benefits of aggression to the actor, the costs to the actor, and the costs to the recipient (Georgiev et al. 2013). The benefits of aggression

to the actor depend on what competitive aggression is about, including the value of the resource being contested. The costs of aggression to the victim may depend on many different variables including, among others, the intensity of aggression and the characteristics of the victim. The costs of aggression to the actor are typically independent from what competitive aggression is about or the characteristics of the victim. Instead, the costs of aggression to the actor largely depend on how aggression is delivered.

Whether aggression is selfish or spiteful, it is in the aggressor's best interests to always minimize the costs of aggression to himself/herself. Evolutionary theory predicts that the most costly forms of aggression, which involve the death of aggressor, can only evolve through kin selection (or, at least in theory, group selection) in relatively extreme and unusual circumstances. One of them is self-sacrifice to protect many highly related individuals: a good example is wasps or honeybees that die after they sting an intruder in order to protect the closely related members of their colony. Another rare and unusual circumstance would involve the use of highly devastating forms of spiteful aggression, such as suicide bombing. Individuals who self-sacrifice in this way can help their relatives (or members of their group) by eliminating large numbers of their competitors.

Whenever aggression is maintained by individual selection, rather than kin or group selection, there is selective pressure on the individuals (or incentives, in the framework of economists' rational theory) to keep the costs of aggression as low as possible. The extent to which the costs of aggression can be minimized is a crucial factor influencing the occurrence, frequency, and intensity of aggression. Other things being equal, the low costs of aggression can promote the occurrence of frequent and intense opportunistic aggression, while the high costs of aggression can act as a brake on the individuals' tendency to use aggressive strategies for competition.

A great deal of variation in the costs of aggression occurs both among different species and within the same species. Large differences in the

costs of aggression among species are associated with species differences in body size, weaponry, mobility, and social organization. Aggression is more costly in large mammals with horns, fangs, and claws than in the sedentary and peaceful polyps of the coral reef. Within species, some variation in the costs of aggression can be associated with age, sex, and body size. The costs of aggression are probably higher if it involves heavyweight boxing champions than 3-year-old kids. A great deal of interindividual variation in the costs of aggression within the same species, however, is strategic in nature, as it may depend on individual strategies regarding how and when to deliver aggression.

The rest of this chapter will be focused on interindividual variation in the costs of aggression in humans, with particular emphasis on the strategies people use to deliver aggression toward others, while minimizing the costs to themselves. For the sake of the analysis, a distinction can be made between situations in which aggression only involves two individuals, the aggressor and the victim, and situations in which multiple aggressors and/or multiple victims are involved. Some strategies for reducing the costs of aggression can apply to both types of situations, while some highly complex social strategies apply only to situations involving multiple aggressors or multiple victims. It is also useful to make a distinction between different types of costs of aggression, such as risk of physical injury or death; psychological pain or stress; retaliation against self, relatives, friends, or property; reputational damage; and waste of time and energy.

The Costs of Human Aggression

In direct one-on-one physical combat, one obvious way to reduce the risk of injury is to wear protective gear or armor. Whenever weapons are used, there is always the risk of accidental self-harm (e.g., an aggressor using a knife could accidentally cut himself/herself during combat, or a soldier could accidentally blow himself/herself up

with a grenade). All projectile weapons, however, reduce dramatically the risk that the aggressor may be harmed by the victim, by increasing the distance from the victim. This is true for anything that can be launched (a rock, a spear, a grenade) as well as for all firearms. Guns reduce greatly the costs of aggression relative to knives. One of the most effective ways to attack others at a minimal cost to the self is to launch a missile or drop or detonate a bomb from a great distance from the target by simply pressing a button. Hurting others from a distance can be very quick and effective; not seeing the victim while he or she is being hurt or killed can reduce dramatically the psychological costs of aggression, i.e., the notion that we are, under normal circumstances, naturally inhibited against harming others directly and/or suffer psychologically at the sight of other people being in pain.

While there is always a certain risk that a victim of aggression may hurt the aggressor during combat, there is also the risk that the victim will retaliate later against the aggressor himself, his/her relatives or friends, or even his/her property. One key strategy for the aggressor to reduce the retaliatory costs of aggression is to conceal his/her identity. In direct face-to-face combat, this can be accomplished by wearing a mask. When aggressor and victim are not in direct visual contact, the aggressor can ensure that the source of the attack remains anonymous. Anonymity can have a dramatic effect on the reduction of the costs of aggression and therefore enhance the probability of aggression itself.

The opportunity to deliver anonymous aggression is as advantageous as the opportunity to steal money or goods from others without any prospect of punishment.

Whenever multiple individuals are involved as aggressors, and one or more as victims, it always pays for the aggressors to outnumber the victims. The higher the number of aggressors, the lower the costs of aggression to them, for many reasons. If direct combat is involved, the victim's ability to hurt the aggressors is reduced if multiple aggressors are involved. The time and energy costs of aggression are also reduced with multiple aggressors. The psychological costs of aggression are

reduced because moral responsibility for hurting the victim and empathy for the victim's pain are shared and diluted among multiple aggressors. Finally, if retaliation from the victim, or the victim's relatives/allies occurs, the probability of being the target of retaliation is diluted among all aggressors. If aggressors act as a group, there may be no moral, social, or legal sanctions either, especially if that group itself is responsible for establishing or enforcing the moral, social, or legal norms. When a large crowd of individuals attacks one or more targets (mobbing), there is also further reduction of costs due to the anonymity of individuals within the crowd. For socially complex species, group aggression toward individuals or minority groups is highly significant, is likely to occur whenever favorable circumstances arise, and can have potentially devastating consequences including genocide.

Computer-based communication has provided new opportunities for expressing low-cost aggression, thereby promoting new, frequent, and troubling kinds of aggression. Emails may allow individuals to verbally attack others, including complete strangers, without incurring any significant costs. Sending offensive emails from anonymous accounts also minimizes the risk of later retaliation. Posting anonymous attacks on public Internet outlets, such as Amazon.com, where people can post book reviews as vehicles for personal attacks against the book's authors, also involves minimal costs. Given the current deregulated nature of Internet-based communication, blogs, including anonymous ones, provide a platform from which to launch low-cost attacks against individuals or minority groups. Given that posted material on the Internet is not easily removed and can be quickly and effectively retrieved by search engines such as Google, defamatory attacks are cheap but highly effective ways to inflict high reputational damage to individuals. Finally, social media such as Twitter and Facebook offer the opportunity to engage in mobbing, which has virtually no cost to the aggressors but potentially devastating consequences for the victim. To give an example of this mobbing and its consequences, an American woman named Justine Sacco, who made an inappropriate comment on her

Twitter account in New York while boarding a plane flying to South Africa on December 20, 2013, was the victim of rapid vicious attacks by thousands of Twitter users, some of which were addressed to the woman's employer and demanded her firing (Ronson 2015). When the woman's plane landed in South Africa and she checked her email and Twitter accounts again, she discovered that she had been fired by her employer and had been victimized on Twitter by thousands of strangers around the world. In addition to losing her job, the woman had to deal with the psychological trauma from the experience and the damage to her reputation that might potentially affect the rest of her personal and professional life. None of the Twitter aggressors paid any consequences whatsoever for their actions.

Given its characteristics, Twitter has become an ideal tool for low-cost ad hominem attacks. In fact, a category of professional Twitter aggressors, known as Trolls, has emerged, whose main activity is to insult, offend, and defame individuals who become someone's targets. While victims can limit the damage of this aggression by closing their Twitter accounts and limiting their presence on social media or other Internet outlets, reputational damages can still occur. Wikipedia profiles, which are typically reserved to individuals with positive accomplishments for society, are also frequently targeted by anonymous attacks and must be constantly and carefully patrolled by an army of Wikipedia editors, to prevent these attacks from emerging to the surface. These attempted attacks, however, leave traces on the "history" menu of the Wikipedia pages.

Conclusion

It is well established that human beings have a high potential for aggression but also that the expression of aggression is very sensitive to fluctuations in its costs and benefits. Human population on this planet has been growing exponentially, while natural and other resources remain limited. Increasing competition in human societies unfortunately means that the potential benefits of aggression will increase as well. For

example, we may hypothetically reach a time in future in which drinking water is so scarce and so valuable for survival to tempt people to kill each other over a bottle of water. The increased scarcity and value of resources, however, is not the only factor that can increase aggression. Reduced costs of aggression can produce the same outcome. Some social and cognitive characteristics of the human species and of human societies make it possible for us to express frequent and potentially lethal low-cost aggression. First, we are a highly social species and live in huge societies comprising millions of strangers. Although we are remarkable in our capacity to tolerate and to cooperate with strangers, this also means that we are able to form aggressive coalitions involving many strangers against our competitors. The low costs of group aggression in which aggressors largely outnumber their victims make group aggression, such as mobbing, potentially lethal for individuals and for minority groups who become targets. Second, in addition to our high sociality, our cognitive skills allow us to reduce the costs of aggression by concealing our identity or engaging in other forms of deception that may reduce the probability of retaliation. We also possess the cognitive skills to reduce the psychological costs of aggression, for example, by altering our moral and empathic inhibitions against hurting others. Finally, our technology can further reduce the costs of aggression by allowing us to protect ourselves while attacking others, attack others from a long distance and without visual contact with our victims, and attack others using technology-based communication such as the Internet, in which massive anonymous attacks against individuals can be quickly mounted at virtually no cost to the aggressors.

When Al Gore invented the Internet, he clearly had no idea that Twitter and other social media would lead to the creation of Trolls and the proliferation of online mobbing. New computer technology interacts with ancient aspects of human nature in novel and unexpected ways. The autistic geniuses of Silicon Valley should hire human nature experts such as myself as consultants.

Cross-References

- ▶ [Sex Differences](#)
- ▶ [Sexual Coercion and Violence](#)
- ▶ [Sociocultural Theories of Violence](#)

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Costs of Cooperate

- ▶ [Altruism and Costs to Altruist](#)

Costs of Punishing

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Synonyms

[Costs of retaliation](#); [Revenge](#)

Definition

The payoff or fitness reduction resulting from the punishment of norm violators.

Introduction

The willingness to punish selfish behavior is believed to play a key role in promoting cooperation in daily life. This entry provides an overview of what is known about the costs of punishing:

why they matter, what they imply for cooperation, and what they comprise of. The focus here will be on informal punishment, i.e., peer-to-peer punishment, a topic of intense investigation in the past decade. The case of formal or institutional punishment is not considered here. As it turns out, we know a fair amount about why the costs of punishment matter and what they imply for cooperation, but relatively little about what they comprise of.

Costs of Punishing

At the most fundamental level, the costs of punishing can be divided into two categories: those incurred by punishers and those incurred by the targets. Theoretical models and laboratory experiments clearly illustrate that both matter a great deal. From an evolutionary perspective, the costs incurred by punishers imply that punishers have a disadvantage in terms of fitness relative to non-punishers. Consequently, as these costs increase, the more difficult it is for the propensity to punish to evolve and be sustained in the long run (e.g., Dreber et al. 2008). In line with this, laboratory studies have shown that individuals are less willing to punish selfish (or antisocial) behavior as the monetary cost of punishment increases. On the other hand, the costs incurred by potential targets of punishment have the opposite effect, making selfish behavior less attractive. Laboratory evidence shows that as the monetary cost for targets increases, so does the level of cooperation. Taken together, this evidence suggests that the prospects for cooperation improve as the punishers' costs fall and that of the targets increase, that the costs incurred by punishers have to be substantially lower than that incurred by the targets for the threat of punishment to lead to high levels of cooperation (Egas and Riedl 2008; Nikiforakis and Normann 2008), and that punishers have a tendency to use the least costly forms of punishment (e.g., Balafoutas et al. 2014).

A natural question to ask is what these costs comprise of in daily life. In theoretical models and laboratory experiments, the costs of punishing take the form of a reduction in individual payoffs,

but what may be the cause behind these reductions in reality? To my knowledge, there has been no systematic attempt to answer this key question. Costs can be internal (e.g., guilt, shame) or external (e.g., retaliation, damaged reputation, severed relationships) and depend partly on the form of punishment: direct (i.e., confronting the target) or indirect (i.e., withholding a certain reward from the target). Arguably the main cost for punishers confronting directly their targets is the risk of counter-punishment, as documented both in the lab (e.g., Denant-Boemont et al. 2007; Nikiforakis 2008) and in the field (Balafoutas et al. 2014; Balafoutas et al. 2016). Perhaps surprisingly, punishing a selfish individual to promote cooperation may not improve one's reputation (Balafoutas et al. 2014; Rockenbach and Milinski 2011). On the other hand, punishment targets may suffer from a loss in reputation (Rockenbach and Milinski 2011), feelings of guilt or shame (Hopfensitz and Reuben 2009), and reduced self-image. The costs associated with indirect punishment have been so far less studied, but they are likely to be less substantial, at least for punishers who are unlikely to face counter-punishment (Balafoutas et al. *in press*). Of course this does not rule out that indirect reprisals may be used when indirect punishment is detected. In the long run, these can be quite costly (e.g., severed relations).

Conclusion

The importance of the costs of punishing is well established: the higher the cost for the target and the lower the cost for the punisher, the better the prospects of cooperation will be. There is however clearly a need for studies exploring systematically what the costs of punishing in daily life consist of and their relative importance. The literature suggests that the costs will differ considerably across situations (e.g., Balafoutas et al. 2014), cultures (e.g., Herrmann et al. 2008), and people (e.g., Hopfensitz and Reuben 2009). In any event, a careful analysis of the costs of punishing (alongside the potential benefits of punishment) will reveal when cooperation will be more likely to be achieved by peer-to-peer punishment and

when a different mechanism may be better in deterring free riding.

Cross-References

- [Altruistic Punishment](#)
- [Cooperation](#)

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Costs of Retaliation

- [Costs of Punishing](#)

Costs of Short-Term Mating for Women

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Synonyms

[Casual sex](#); [One-night stand](#); [Booty-calls](#); [Hook-ups](#); [Friends with benefits](#)

Definition

The term “short-term mating” typically describes a sexual relationship that is casual in nature, mostly focused on sexual pleasure, lacking commitment or longevity, and characterized by little emotional connection (Jonason 2013; Jonason and Balzarini 2016). The term “casual sex” is used as a catchall to refer to all kinds of short-term relationships, but these relationships can encompass one-night stands, booty-call relationships, hook-ups, and friends with benefits. While all of these relationships have their unique features, they share a common theme of creating a context where individuals have sex without any formal commitment.

Introduction

Casual sex is widespread in nature, with 38% of “adults” (Twenge et al. 2015) and 75% of college students (Jonason and Balzarini 2016) engaging in some form of casual sex relationship. Historically, casual sex has been viewed as a pathology, but this might not necessarily be the case if one takes an evolutionary perspective. Casual sex may be part of the naturally occurring variation in human sexuality.

Ancestrally and today, women (and female mammals) have a heavier obligation to offspring

than men (and male mammals) do, creating different costs and benefits for engaging in casual sex relationships in the sexes (Trivers 1972). This asymmetry has acted as a selection pressure shaping men and women's sexual psychologies differently and translates into men's greater willingness to have sex with a stranger (Clark and Hatfield 1989), to consume pornography, to pay for sex, to have lower standards in who they have sex with, to say "I love you" sooner, and to have more permissive attitudes about sex, findings that hold up cross-culturally (Buss and Schmitt 1993; Schmitt 2005) and over time (Petersen and Hyde 2010). Evolutionary-informed researchers point to the costs and benefits associated with casual sex for men and women as a way to better understand why people may engage in and avoid casual sex along with other relationships (Jonason 2013; Jonason and Balzarini 2016). Various benefits arise out of a short-term mating strategy such as gifts, protection, assessment of own mate value, assessment of a potential partner's characteristics, assessment of sexual compatibility, or gaining superior genetic benefits from a casual sex partner (Buss 2016). Despite these benefits, there are costs and risks to women for engaging in such a strategy. In the rest of this entry, we detail some of the costs women incur by engaging in short-term mating relationships. This is not to say that they do not experience benefits, but that is beyond our scope here.

Social Costs of Casual Sex

Men may be evaluated more favorably, and women are evaluated less favorably for engaging in similar sexual behaviors, an effect called the sexual double standard (Marks 2009). Typically, this double standard is framed in terms of social norms, but such a model fails to consider why those social norms exist in the first place and why women as opposed to men are saddled with the negative reputation for doing the same thing men do. Men's unfavorable evaluations may be driven by men's greater parental uncertainty, that is, their confidence that they are investing in a

biological child. Men who cared more about paternity certainty fathered more offspring than those who cared less. Men are reluctant to enter a relationship with a woman when her previous relationship has ended (Busche et al. 2013) which is claimed to ensure that he will not father a biological child from her previous relationship. Men will judge women with a high number of sexual partners as less desirable for a long-term relationship (Buss 2016) as this is thought to be a signal of future fidelity. These reputational costs may translate into men being less willing to invest in offspring and in her which, overtime, acts as selection pressure against female promiscuity in so much as resulting offspring survive and reproduce less often.

Women risk reputational costs for engaging in short-term mating behavior from women as well. Women engage in intrasexual competition and compete with other women to acquire and retain mates, for social status, and for resources to support their children (Benenson 2013). Furthermore, women engaging in short-term mating lowers the ratio of eligible men available to date (Baumeister et al. 2017). For these reasons, women view promiscuous women as threats to both dating and their relationships. Women disapprovingly evaluate other women with larger numbers of sex partners (Zaikman and Marks 2014). Even while being sexually active and viewing short-term mating as empowering, some women fear their sexual reputation and still believe casual sex is unacceptable for themselves. They will judge other women who engage in casual sex unfavorably even while engaging in the same behavior themselves (Farvid et al. 2017). As well as risking their reputational damage with other women, they forgo friendship opportunities with other women because women dislike sexually permissive women and are less inclined to be friends with sexually permissive women (Vrangalova et al. 2014). Even in cultures where short-term mating is normatively common and socially acceptable, such as Sweden, women who have a reputation for promiscuity will reputationally suffer (Buss 2016).

Health and Reproductive Costs of Casual Sex

If the only costs associated with casual sex in women were social in nature, reducing those costs would be a mere function of changing social norms around sex. However, there are also health and reproductive costs associated with casual sex that women predominantly face. These include sexual violence, sexually transmitted infections, and, also, the possibility of unplanned children. Dating partners may resort to tactics such as coercion, threats, and aggression, progressing ultimately through to rape if a woman does not agree to sexual activity. Women are at a greater risk of physical and sexual assault, with college students experiencing rates up to 27% of date rape, sexual assault, and sexual aggression over their lifetime (Rickert and Wiemann 1998). Sexual assault often results in psychological damage such as trauma, anxiety, depression, fear, guilt, and shame, which are mental health costs. Sexual assault has a reproductive success cost as it threatens women's reproductive choice. Sexual assault resulting in pregnancy dictates the choice of a father, resulting in a child that is fathered by a man whom she potentially would not have chosen and, therefore, may have inferior genes and traits than that she seeks in a partner. This man is unlikely to provide the greatest investment to her and her child. Furthermore, it may prevent a woman from finding a long-term partner willing to take on the parental role for another man's child (Buss 2016).

Methods of birth control such as condoms are required to prevent sexually transmitted infections and diseases. Contraceptives such as the birth control pill only prevent unplanned pregnancies. While contraceptives have allowed humans to separate the acts of sexual activity and reproduction, human psychological mechanisms lag our modern world and have not evolved fast enough to change our mating psychology (Buss 2016). Condom use in casual sex is low with only 47% of students (Lewis et al. 2012) and up to 55% of adults (Sanders et al. 2010) reporting use of a condom during the last casual sex act. This indicates sexual risk-taking, which may further be

exacerbated by the influence of alcohol (Lewis et al. 2012; Owen et al. 2011). Sexually transmitted infections and diseases can in turn affect women's future fertility (Bowden et al. 2002). Reduced fertility affects reproductive success, meaning that women will have lower rates of children or, at the extreme, remain childless and may ultimately threaten long-term relationships (Buss 2016).

Perhaps the largest reproductive cost that women face is unintended pregnancy. In ancestral and modern societies, women face the possibility (more than men) of having an offspring with no support of a father which will face increased childhood mortality risk and potentially maternal mortality as well (Buss 2016). If a modern woman finds herself pregnant from a casual sex encounter, she is stuck between a rock and hard place. She can have an unwanted/unplanned child and rear it as a single mother, remain in a potentially problematic relationship, or have an abortion. These come with costs that women suffer and have suffered asymmetrically more than men did. For example, women undergoing abortions have increased psychological distress such as depression, anxiety, self-judgment, guilt, and shame; experience social judgment from family, friends, and sexual partners; and are often less desirable as dating and long-term partners (Hanschmidt et al. 2016).

Alternatively, a woman may choose to keep the child and raise the child on her own. This will create hardship and stress for both her and her child as single parenting is challenging. Single parents experience financial strain, often resulting in physical illness and mental health difficulties (Stack and Meredith 2018). It is difficult for a woman to find a new long-term partner to invest in her and children from a previous relationship. Some men may not wish to invest their time and financial resources in another man's child. Both partners may face conflicts of interest over providing love and resources to each other or the stepchild. Stepparents are less emotionally invested and devote less time and resources than genetic parents. Furthermore, because the child represents a Darwinian cost to the stepparent, the risk of child abuse by

stepparents is 40 times higher than biological parents (Buss and Duntley 2013).

Mental Health Costs of Casual Sex

Casual sex can be a double-edged sword. Despite women's willingness to enter a short-term relationship (Schmitt 2005), some women experience postcoital psychological distress. Sex for extrinsic motives such as peer pressure, need for self-affirmation, or low self-esteem has been linked to psychological factors such as greater depression, anxiety, and lower self-esteem (Vrangalova 2015). One of the benefits of casual sex is the enjoyment, which is greater for men than women; however, women face greater risks in terms of mental health. For students with no prior depressive symptoms, casual sex has been associated with depressive symptoms over a long-term period (Owen et al. 2011).

Psychological effects can manifest in subclinical areas, for example, postcoital worries and self-esteem issues. Women regret engaging in short-term mating more than men and tend to worry more about factors such as having uncommitted sex, sex with a stranger, one-night stands, progressing relationships too fast sexually, losing virginity too early, or losing their virginity to the wrong person (Galperin et al. 2013). Adult and college student women report feeling used, rejected, embarrassed, reputational loss, self-disappointment, a loss of self-respect, and disappointment that the relationship did not progress to a long-term relationship (Campbell 2008; Lewis et al. 2012). Women who engage in casual sex experience more postcoital worry than men regarding their partner's intentions, being used for sex, and unwanted emotional attachments and experience vulnerability because they may form attachment bonds and are worried about future investment from their partner (Townsend and Wasserman 2011; Townsend et al. 2015).

Indeed, some women may only engage in some forms of casual sex to gain access to higher-quality partners (i.e., hypergamy by casual sex) for long-term relationships (Jonason and Balzarini 2016). That is, they leverage their sexual

availability as a lure to entice a man into a more serious relationship. This is a risky strategy in that couples who know each other better are less likely to use condoms (Sanders et al. 2010), thereby increasing STI and pregnancy risk, but may also translate into depression and postcoital regrets that can affect mental health. Given the postcoital effects of worry, loss of self-esteem, and feelings of rejection, this may have longer-lasting reproductive implications than typically considered. Women may experience a loss in self-perceived mate value and may, therefore, lower the quality of mates they are willing to date, mates who are likely to be less willing/able to invest and may provide lower genetic material to her offspring.

People with psychological conditions such as borderline personality disorder (BPD) are more prone to participate in casual sex, and women are dispositionally more likely to have BPD. Those with BPD are high on impulsivity, including sexual impulsivity. Individuals with BPD have higher rates of unplanned pregnancies and STIs, participate in unprotected sex, have a larger number of casual sex partners, and are more likely to have experienced rape and sexual assault (Frias et al. 2016). Women with BPD who participate in short-term mating may, therefore, be undermining their mental health.

Conclusion

A key insight from evolutionary models of sexuality is that there are reproductive asymmetries in men and women. Men tend to benefit more and pay fewer costs for engaging in short-term mating than women do. Women, in contrast, ancestrally and today, incur more costs for engaging in short-term mating, as summarized in Table 1. We have delineated some of these costs in relation to STIs, single parenthood, child-rearing constraints, mental health effects, and reputational issues. These costs are likely to have shaped women's sexual psychology toward long-term relationships where these costs are minimized. Nevertheless, the mating landscape is still fraught with these dangers, and not all women are disposed to engage in

Costs of Short-Term Mating for Women, Table 1 A summary of the costs of short-term mating in women

Social	Health and reproductive	Mental health
Men may be unlikely to view as desirable for a long-term partner	Physical and sexual assault	Depression, anxiety, lower self-esteem, increased worries
Single parents may face dating challenges	STIs	Vulnerability
Reputational damage from other women	Possible infertility from STIs	Self-respect
Loss of female friends and support network	Unplanned pregnancy	Shame and embarrassment
Less desirable as a future dating partner if having prior terminations	Single parenthood	Trauma from sexual assault
Social judgment from friends and family regarding terminations	Physical illness from financial strain of single parenthood	Anxiety, stress, and depression from financial strain of single parenthood
	Stepparents caring for child	Distress from possible terminations

serious relationships. For those women choosing to engage in short-term mating, they are likely to face these costs in their pursuit of other short-term mating motivations like sexual gratification, testing the waters, and calibrating mate value.

Cross-References

► Derogation of Promiscuity

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Counter Strategies Against Infanticide

► Infanticide in Nonhumans

Counteradaptations/Female Counterstrategies

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Synonyms

Intersexual competition

Definition

The female response to male attempts to control fertilizations through genital morphology.

Introduction

As stated in “genital evolution,” penises have been selected to confer reproductive benefits for males partially in response to intrasexual selection (competition between males for fertilization) and partially in response to intersexual selection (the

competition between males and females for control over fertilization).

Reproductive Strategies

Humans possess internal fertilization. This is a major factor in human reproduction, as males cannot be sure that fertilization (and therefore paternity) has taken place. This gives females a distinct advantage in confusing paternity, and in some species, expulsing the ejaculate of unwanted partners after coitus (Baker and Bellis 1995). Because of this (and male competition), male genitalia has evolved to overcome these obstacles and increase the probability of fertilization. For example, human penises are longer than other great apes and have a pronounced coronal ridge that assists in semen displacement (see ► [“Genital Evolution”](#)). This penile evolution is actually in response to female genitalia; the vaginas of females of a given species contain long twisted oviducts, enforced walls, acidic mucus, and other facets that help females control fertilizations. As female genitalia shifted to optimize female control over fertilizations, male genitalia evolved to match.

One of the most extreme examples of female genital evolution is in the Lake Duck. The male possesses the longest penis in vertebrates in relation to its body length. This long corkscrew shaped penis matches the female’s long corkscrew vagina. In addition, the female’s vagina contains dead-end sacs, where ejaculate deposition would result in the sperm never reaching its intended destination, and may make female ejection of the ejaculate much easier. This elaborate vaginal morphology appears to have coevolved with male phallus length, which in turn covaries with levels of forced extra-pair copulation. Females attempt to control fertilizations with elaborate genital morphology and behaviors such as ejaculate ejection, while males use elaborate genital morphology and behaviors such as coercion (Brennan et al. 2007).

In humans, females control fertilizations through various behavioral and physiological means. The most influential of these is concealed ovulation (see ► [“Reproductive Suppression and](#)

[Sexual Conflict During Mating”](#)). Due to concealed ovulation, males cannot determine when females are most fertile and must spend more time and invest in females to ensure paternity.

The female reproductive tract is also acidic. The acidity of the vaginal fluid and cervical mucous decreases the longevity of spermatozoa, making it more likely that if any sperm survive long enough to reach the egg, it will be younger, higher quality sperm. This increases the quality of the genes at fertilization. Females also shift risk-taking behaviors with their menstrual cycle (Chavanne and Gallup 1998), taking less risk when they are more fertile. Baker and Bellis (1993) also argue that when females orgasm the cervix uptakes and retains more ejaculate, increasing the probability of conceiving the offspring of males that make them orgasm. Thornhill et al. (1995) argue that these males are more likely to be more symmetrical and have higher quality genes. Baker and Bellis (1993) also argue that females can control fertilization through intercopulatory orgasms. Noncoital orgasms before and after coitus actually increase the acidity of the female reproductive tract, making it more difficult for sperm to survive; this includes both previously deposited sperm that have made it to the cervical crypts and sperm that are yet to be deposited at the next sexual encounter.

Conclusion

In summary, intersexual competition is played out both behaviorally and physiologically, and several strategies are displayed in the biological processes of the genitalia of men and women.

Cross-References

- [Evolutionary Arms Race](#)
- [Genital Evolution](#)
- [Intersexual Competition](#)
- [Reproductive Suppression and Sexual Conflict During Mating](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)

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Counterfactual Mental States

► False Beliefs

Countershading

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Synonyms

Dorsal pigmentary darkening; Obliterative shading; Optical flattening; Thayer's law

Definition

A form of protective coloration in which the body surface closest to the ambient light source is more darkly pigmented than the body surface furthest from the light source

Introduction

Countershading is a common pattern of coloration in terrestrial and aquatic animals (Rowland 2009). Among marine animals, countershading has been described in the common cuttlefish (*Sepia officinalis*), whale sharks, and the common octopus (*Octopus vulgaris*) and, among terrestrial animals, in moth and butterfly caterpillars, snakes, lizards, birds, amphibians, and mammals including gray squirrels (*Sciurus carolinensis*), naked mole rats (*Heterocephalus glaber*), and many primates.

Countershading is correlated with certain ecological traits (Allen et al. 2012). Small primates that spend more time in horizontal postural positions are more strongly countershaded (Kamilar 2009). Countershaded ruminants have stronger pigment gradients when they live in open lighting environments, live closer to the equator, and are smaller. A distinct demarcation between the dark dorsal side and the light ventral area is also more common in open lighting environments (Allen et al. 2012).

English naturalist Edward Bagner Poulton (1890) and American artist Abbot Thayer (1896) independently proposed that the function of countershading is to conceal. However, there are also other candidate explanations including thermoregulation, protection from ultraviolet radiation, and defense against abrasion.

Improving Background Matching

An animal may more closely match its background if countershaded, especially if it is viewed from different angles (Wallace 1889). For example, when viewed from above against a dark background or from below against a light background (e.g., the sky), a countershaded pattern of dark dorsum and a light ventrum conforms to the general principles of background matching. This could explain the patterning in pelagic fish and seabirds.

Counterbalancing Self-shadows and Disguising 3D Form

Countershading is also hypothesized to counterbalance self-shadowing and obliterate shape-from-shading cues, rendering a prey animal perceptually flat to a viewer. Because sunlight normally comes from above, a uniformly colored animal tends to appear lighter on its upper surface and to have a shadow on its underside. This pattern of differential illumination may diminish an animal's camouflage because it reduces the level of background matching and provides cues to three-dimensional (3D) shape. An inverse pattern of pigmentation to the natural shadows – a dark color closest to sunlight and light pigment on the surface furthest from the light – should cancel out the shadowing and result in a more uniform radiance distribution across the body and improve background matching and diminish 3D cues (Allen et al. 2012; Thayer 1896). Any visual system that relies on shape from shading can be fooled by countershading (Allen et al. 2012).

Evidence for the Camouflage Function of Countershading

The most convincing examples of countershading for camouflage are found in aquatic environments (reviewed by Rowland 2009). In terrestrial systems, countershading is common in lepidopteran caterpillars. Tinbergen (1958) argued that shadowing and the cylindrical shape of larvae would cause them to stand out on otherwise flat leaves, even if their color (before shadowing) matches the background. Rowland et al. (2008) tested the survival of countershading in caterpillars by recording attacks on artificial larvae placed on tree branches in a woodland with variable lighting conditions. The countershaded prey was attacked significantly less frequently than prey with control color patterns.

Other Explanations for Countershading

There are several non-camouflage explanations for countershading. The simplest is that countershading is an epiphenomenon resulting from selection acting on only one body surface because pigments are costly to produce (Ruxton et al. 2004). Functional non-camouflage hypotheses include protection from the damaging effects of ultraviolet (UV) light, thermoregulation, and abrasion protection (reviewed by Rowland 2009). Computational modeling has shown that for animals that can assume any orientation in space, countershading can assist crypsis and favor thermoregulation and UV protection (Penacchio et al. 2015).

Conclusion

There is still much to be tested about the evolution of crypsis through countershading. The effects of direct versus indirect sunlight, orientation, time of day, year, latitude, and background reflectance, as well as orientation behaviors of the countershaded animal, would uncover if countershading enhances crypsis. Furthermore, testing whether nonhuman animals perceive shape from shading cues is necessary. Such tests would show if the predicted predators of countershaded animals derive depth information from shading and if their visual system is fooled by countershading.

Cross-References

- ▶ [Camouflage](#)
- ▶ [Depth Perception](#)
- ▶ [Visual Illusions](#)

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Courageous Rescue

- ▶ Heroic Rescue in Humans

Courting

- ▶ Human Courting
- ▶ Perceiving Sexual Intent

Courtship

- ▶ Dating
- ▶ Human Courting
- ▶ Sex Differences in Attractiveness of Humor

Courtship Gift

- ▶ Nuptial Gift

Courtship Orientation

- ▶ Hormonal Component of Homosexuality

Covariance of Partner Phenotypes

- ▶ Specific Friendships

Covert Aggression

- ▶ Relational Aggression

Coyotes

- ▶ Canines

Creative Expression

- ▶ Art Production, Appreciation, and Fitness

Creativity

- ▶ Boredom as an Adaptation
- ▶ Tool Manufacturing

Credibility Displays

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Synonyms

Costly displays; Credibility enhancing displays

Definition

A costly display or behavior that provides other individuals with a reliable measure of a person's beliefs or degree of commitment to a group: an ideology, set of values, or beliefs. Ancestral humans faced the adaptive challenge of verifying culturally transmitted information from other people in order to avoid being exploited or misled. Therefore, individuals evolved the ability to attend to credibility displays because they are indicative of one's honest commitment to a group, or a group's beliefs and ideology. Credibility displays promote group cohesion and solidarity because they represent commitment to beliefs that may be collectively beneficial.

Introduction

Researchers have proposed a connection between credibility displays and levels of commitment to group ideologies, religious beliefs, and shared values that promote solidarity and cooperation within groups (Atran and Henrich 2010; Atran and Norenzayan 2004; Henrich 2009). Credibility displays are usually costly, and these costly displays can manifest as a wide variety of behaviors, ranging from charitable acts and extravagant adornment to ritual scarification, animal sacrifice, and self-mutilation. Although such behaviors are seemingly expensive, harmful, and otherwise detrimental to the individual, engaging in costly displays confers an overall benefit by signaling to others one's honest commitment to a belief system, reinforcing one's "credibility" within a

group, and promoting group cohesion between individuals. Natural selection shaped our cognitive processes in regard to cultural learning, such that certain kinds of displays or actions represent important cues of commitment, prestige, and group involvement (Henrich 2009).

The Evolution of Credibility Enhancing Displays

As humans acquired the ability to communicate and engage in cultural transmission using symbolic representations (e.g., language), individuals (i.e., cultural learners) became potentially exploitable by manipulators (i.e., cultural models), who could convey one symbolic, mental representation (i.e., belief), but actually believe something different. That is, manipulators could misrepresent their degree of commitment to a particular belief, provide misleading information, and exploit other individuals who are highly committed. As a result, cultural learners faced this adaptive challenge created by our capacity for symbolic cultural transmission. To address this adaptive challenge, cultural learners evolved the ability to attend to *credibility enhancing displays* (CREDs) – costly displays that provide the cultural learner with a reliable measure of the cultural model's actual degree of commitment to the beliefs that he or she has expressed (e.g., symbolically, verbally; Henrich 2009). The more costly the displays are, the deeper the degree of commitment. If cultural models were willing to incur great costs on behalf of a mental representation (i.e., belief), it would be unlikely that they would believe something different from what they expressed. Therefore, learners could use such displays to determine if they should commit to a particular mental representation, whether it is an ideology, a set of values, or a particular belief.

Credibility Enhancing Displays and Cultural Group Selection

Natural selection circumvented the emergent problem of manipulators by creating a

“cultural immune system” designed to assess a cultural model’s degree of commitment to a belief, judging by their displays (Henrich 2009). Cultural learners could look for displays that are most consistent with the expressed beliefs, as well as identify behaviors and actions that would not be performed by a cultural model who believed something different from what they expressed symbolically. This would in turn create a learning bias, where cultural learners are more likely to acquire culturally transmitted representations (e.g., practices, beliefs, values, strategies) if their cultural models perform costly acts that are both consistent with the underlying representation and inconsistent with alternative representations (Henrich 2009). Further, this learning bias is strengthened when certain CREDs facilitate the transfer of certain beliefs, when a belief favors specific CREDs, and when learners copy the CREDs of successful (e.g., prestigious) individuals. Reliance on CREDs can create stable cultural states, resulting in an interconnected combination of beliefs and practices (Henrich 2009).

Adaptive learning biases lead to the emergence of stable combinations of beliefs and corresponding costly displays. An interconnected system of beliefs could sustain costly practices that facilitate the commitment of other group members and the adoption of beliefs that promote group benefits, such as large-scale cooperation and group solidarity. Thus, CREDs promote success in competition between other social groups because social groups that are comprised of stable combinations of beliefs and practices (e.g., rituals) that favor in-group cooperation, as well as out-group competition, will be able to effectively out-compete other groups (Henrich 2009). The presence of multiple groups with stable combinations of beliefs and practices provides the conditions for *cultural group selection*. Social groups that have stable combinations of beliefs and practices that deliver group benefits (e.g., cooperation, solidarity) can spread at the expense of social groups who are less stable or cohesive. Taken together, costly actions and

rituals that facilitate larger-scale cooperation, solidarity, and success in intergroup competition may be a product of evolved cognitive adaptations suited for avoiding exploitation during social learning, in tandem with the process of cultural evolution.

Conclusion

Humans evolved to look for *credibility enhancing displays* that indicate a cultural model’s degree of commitment to, or belief in, expressed mental representations. Credibility displays are actions that are both consistent with a model’s professed beliefs and that would be unlikely to perform if he or she believed something different from what he or she expressed. Natural selection favored a reliance on CREDs in determining how much to commit to, or believe in, a particular representation. Participation in costly displays is associated with prosocial in-group behavior, because costly displays indicate commitment to beliefs that may benefit the group as a whole. Groups that require costly displays are favored by cultural evolution because costly displays are honest signals of belief commitment and thereby promote cooperation and success in inter-group competition (see Henrich 2009). *Cultural group selection*, then, spreads interconnected combinations of beliefs and practices, where stable combinations of beliefs and practices promote a group’s success over others.

The existence of credibility displays was presumably initiated by an evolved learning bias, which preferred costly displays because they signified greater commitment to a group, or a group’s beliefs and ideology. The more costly the displays are, the deeper the degree of commitment. The evolved psychological processes underlying the strong preference for credibility displays may illuminate a number of peculiar, costly aspects of group commitment. For example, religions often value individuals who make costly sacrifices, such as martyrdom, self-imposed poverty, celibacy, and sobriety (Atran and Norenzayan 2004).

Cross-References

- ▶ [Joseph Henrich](#)
- ▶ [Religion](#)
- ▶ [Religious Beliefs](#)
- ▶ [Scott Atran](#)

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Credibility Enhancing Displays

- ▶ [Credibility Displays](#)

Creolization

- ▶ [Spontaneous Language](#)

Crime

- ▶ [Female Counter-Adaptations to Rape](#)

Criminal

- ▶ [Monoamine Oxidase and Antisocial Behavior](#)

Criminal Acts and Criminal Behavior

- ▶ [Evolution of Crime, The](#)

Criminal Behavior

- ▶ [Criminals Are Made Not Born](#)
- ▶ [Criminology](#)

Criminal Behavior and Evolution

- ▶ [Evolutionary Forensic Psychology](#)

Criminal Justice System

- ▶ [State-Sanctioned Punishment as Deterrent to Violence](#)

Criminal Personality

- ▶ [Criminal Personality Variables](#)

Criminal Personality Variables

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Synonyms

[Criminal personality](#); [Individual aspects related to criminal behavior](#)

Definition

Criminal personality variables are understood as individual aspects that seem to influence involvement in criminal behavior.

Introduction

Criminal behavior is related to several variables, both environmental and individual. Several researchers point out different elements for the explanation of crime starting from the various theoretical points of view. Criminology has added most of these explanations to a field of study and practice as it constitutes an overlap of several sciences. Among these, psychology has made several contributions, both in theorizing and in intervening in criminal behavior. One of the main elements of study within psychology, more specifically investigations of criminal behavior, is personality.

In the field of psychology, personality is one of the most frequently studied and debated concepts. However, Allport (1955) already argued that personality is a very complex concept to be summed up. In general, for him, facets of personality guide specific behaviors and ideas, representing a more stable tendency to act, feel, and think. Variables of personality have long been used to explain criminal behavior. However, evolutionary psychology has not always assisted in the development of research in this area. However, personality has also been studied from the standpoint of evolutionary psychology, which has developed theories about this (life history theory, environmental heterogeneity in fitness optimal and frequency dependent selection), which is better explained throughout this chapter.

In this topic, the term crime is used as shorthand to refer to behaviors that violate laws and social norms. This choice is due to the complexity of the phenomena discussed here, crime and personality, as among these several forms of relationship are observed, depending on the variables of personality and the type of crime chosen. Throughout the topic we try to avoid too much explanation of specific crimes; the intention here

is to introduce the reader to this subject, which may lead them to study in more depth the crime or personality variables that are of interest.

Individual Differences

A major field in psychology, in a general way, is that which researches the differences that any person shows. In many approaches this interest has been present too, and evolutionary psychology is no different. For a long time, the main concern, and consequently the advances, of scientists was to understand, starting from evolution, what might explain many human behaviors. Areas such as sexuality and sexual conflicts, mating strategies, parenting, among many others, have gone through great advances, theoretically and empirically. However, the difference among individuals, and in this context, the personality, had been inadequately explored. More recently, this situation has changed owing to several researchers who have been dedicated to investigating the individual differences (Buss 2009; Del Giudice et al. 2015; Figueredo et al. 2015).

Buss (2009) has already emphasized the importance of investigating individual differences, and he lists four reasons for this. In the first of them he argues that the individual differences have been largely recorded, whether they relate to physical (body type, sleep rhythm, etc.) or psychological (dominance, pleasantness, intelligence, etc.) aspects. In the second reason he claims that most of these differences have hereditary components, besides presenting stability over time. For the third reason he declares that this stability has been revealed as an influencing element in central evolutionary issues, such as survival, mating success, production of offspring, etc. Last, Buss argues that individuals present significant differences between sexes in a feature that already shows differences between sexes. Mating strategies are an example of this. Some individuals may prefer long-term strategies, whereas others would prefer a short-term strategy, and yet others can prefer a mixed mating strategy.

Some of these explanations are presented in a summarized way, to facilitate the understanding of the relationship between personality and crime. The

purpose of this topic is not to discuss the different arguments related to individual differences; we refer the reader to the topic “Evolutionary Personality Psychology” of this encyclopedia, Buss (2009) or Figueredo et al. (2015).

One of the main explanatory theories of individual differences is life history theory. According to this theory, we possess limited resources during life, such as time, energy, the ability to strive, obliging us to trade off among life functions, and consequently resulting in various adaptive problems (Figueredo et al. 2015). Thus, relative to reproductive success, choosing to allocate energy to body development is to abandon developing parenting characteristics, or other types of kind investment, as resources are limited and allocating both requires more than can be offered.

The allocation of accessible resources happens according to several variables, such as qualities and defects of the individual, the life expectancy, the amount of energy available. In dealing with questions related to gene transmission, species that have a large life span end up allocating resources in the development of characteristics related to parenting, as is the case with mammals. However, species with a short life span seem to opt for effective strategies in the short term, experience high fertility with a large number of partners, to the detriment of characteristics associated with parenting, as is the case for most insects (Del Giudice et al. 2015).

In a first look, the life history theory can hold in a clear way the differences between species, as the individual intraspecies differences define an individual's life history orientation. The same way as the distinct environments produced differences among the species, they made differences within the species. If a non-human organism grows in a severe, unpredictable, environment, with a short life span, it is probable that this organism will engage in behaviors that can carry certain risks; furthermore, it will act impulsively and aggressively (Mishra et al. 2017). In the same way, a person who grows up in a social context marked by a short life expectancy can engage in risk behaviors, aimed at satisfying the needs of the moment, giving

scope for engagement in criminal behavior (Richardson et al. 2017).

From this point of view, the social context of the individual has an influence on the resources that the person possesses to invest in certain activities and characteristics of the personality. Thus, being poor, single, with low educational achievement increase the chances of engaging in strategies that present more immediate results, which are sometimes impulsive and involve risks. This context can provoke a short life span, considering that one consequence of this is the use of the previously described strategies. The context in which the individual is inserted is also considered to be fundamental for the explanation of individual differences by another approach, the environmental heterogeneity in fitness optima.

According to the idea of the environmental heterogeneity in fitness optima, the environment where the individual lives can favor different levels of certain feature. Some places would endorse particular characteristics of the personality as this level of a characteristic can guarantee more resources, as in the case of a risk-taking personality. By this logic, individuals raised in large cities end up developing personality traits distinct from those residing in small towns, to ensure maximum access to possible resources, in addition to survival.

Several other approaches are made to elucidate the mechanisms that support differences between individuals. Some start from the notion of genetic mutation, others believe that changes in the different levels of a characteristic would be distributed proportionally in the population, being maintained by frequency-dependent selection, among other forms. All of this is part of the same belief that the environment, especially the social environment, is somehow responsible for these differences. This understanding is widely accepted in research on humans and is gradually being explored with non-human organisms (Bridger et al. 2015). In general, what can be perceived is that the development of certain personality traits entails behaviors that may or may not cause harm to oneself or others. In this way, the relationship between personality and crime is palpable.

Crime and Personality

As mentioned before, several theories of criminology use the personality to explain criminal behavior (Akers 2017; Bonta and Andrews 2016; Gottfredson and Hirschi 1990). Since the first studies related to antisocial behavior, it has been possible to verify the strong relationship with the personality. However, the methods used to investigate this relationship have not accounted for the complexity of the phenomenon. Among the methodological weaknesses presented in these studies, the obscure definition can be highlighted of what would be the personality and validity of the instruments used for the evaluation of this construct. Subsequently, a confusing definition generates unreliable instruments (Brown 2015).

Theories that use the personality as key are prone to error, resulting from the use of large and multidimensional constructs such as “antisocial personality” and “psychopathy” (Brown 2015). Although these are correlates of antisocial behavior, their complexity is not covered by any theories, leaving several elements without explanation of their relation to criminal behavior. On the other hand, some theories indicate clear elements of the personality that would be associated with antisocial behaviors. Faced with this, some of these elements are presented, as we seek to highlight their relationship to crime.

However, before discussing the variables, it is necessary to emphasize that crime is a phenomenon that is presented in different ways and that has an intrinsic relationship with cultural issues. In this way, some crimes are explained by a certain set of variables, whereas another crime is explained by others. The purpose of this topic is to introduce the reader to the relationship between personality and crime, in its widest sense. For a specific type of crime, we recommend reading other topics in this encyclopedia such as “Rape (Evolutionary Forensic Psychology)” and “Assault and Murder.”

Among the various theories of personality, the Big Five model was one of the most widely used in the investigation of the most diverse phenomena, and with criminal behavior this would not be different (Allik and McCrae 2002; Bonta and Andrews 2016). In studies that relate this model

to criminal behavior, it is possible to observe a low level of agreeableness and conscientiousness in individuals who have committed some type of crime (Brown 2015; Walters 2018). Other studies also indicate that a high score in neuroticism would also be related to crime; however, this relationship is observed less frequently (Mishra et al. 2017). What can be perceived from the studies that use this model is a certain inconsistency in the results as many investigations explore specific crimes.

As stated, personality seems to influence in some way the type of crime in which an individual engages. This is not a clear and direct relationship as social elements and circumstances are fundamental for someone to commit a crime. However, the Big Five seem to interact with other personality elements, which in turn seem to establish clearer relationships with criminal behavior. In this way, the question “what features of the Big Five would explain more or less of the crime?” is still open, which until today has received different answers. The most correct statement to make about it is that it depends. It depends mainly on two elements, the first one is the type of crime requiring explanation and the second is the context in which this crime occurs.

Despite the disagreements about the relationship of the Big Five with crime, some other personality elements are extensively investigated and rely on several empirical research studies to indicate their relationship. When talking about crime, especially in research investigating opportunities and violent crimes, self-control appears to be one of the main explanatory variables. Since the publication of *A General Theory of Crime* (Gottfredson and Hirschi 1990), low self-control has been at the heart of criminology investigations, as one of the causes of delinquency and crime. The argument is that individuals who have low self-control tend to seek short-term reward, without taking into account the long-term consequences of their behavior. Thus, driven by a search for immediate rewards, individuals engage in criminal behavior.

What draws attention to this explanation is the origin of this low self-control, which according to the authors is the result of socialization, especially

that established by parents (Gottfredson and Hirschi 1990). Parental monitoring during childhood coupled with effective disciplinary practices has long been the main explanation for low self-control. However, some researchers have begun to present other elements that can be aggregated in this explanation, such as school socialization, peer groups, in addition to neural, biological, and genetic underpinnings (Meldrum et al. 2018). Generally speaking, the search for immediate rewards would lead to a person being impulsive, risk-seeking, physical, self-centered, short-sighted, and having a volatile temper, and as a result, they would end up engaging in criminal behavior.

Another personality element linked to criminal behavior is sensation-seeking, which is defined as “the seeking of varied, novel, complex, and intense sensations and experiences, and the willingness to take physical, social, legal, and financial risks for the sake of such experience” (Zuckerman 1994, p. 27). Most studies that investigate sensation-seeking adopt adolescents as participants, because until the beginning of adulthood various structures, neurological and cognitive, are still in formation (Shulman et al. 2015). Individuals with a high sensation seeking may engage in criminal behavior more easily when compared to those who have low sensation seeking. However, this relationship is not established in a simple way; it involves other elements of the personality, among them, impulsiveness.

Like sensation-seeking, low control of impulsivity is related to risk-taking behavior, such as the use of drugs, gambling, online gaming addiction, reckless driving, extreme sports. From risky behavior to criminal behavior there is a space that many texts do not address in which the complex relationship between personality and crime is present. Having a great desire for sensation-seeking and low control of impulse can explain the an individual’s taste for extreme sports, but cannot alone explain why an individual performs an armed robbery (Mishra et al. 2017).

As present earlier, the linear explanation of crime only through personality variables tends to fail, precisely because it fails to account for the complex interplay among them. At this point,

especially for the two variables presented above, sensation-seeking and impulsivity, evolutionary theory offers an explanation for engagement in criminal behavior. Again the search for resources and reproductive success seem to be the keys to understanding these two phenomena. Theories of sexual selection argue that males engaging in risky behavior indicate that they are able to provide resources and protection. Thus, to achieve a higher social position, and consequently increase the chances of reproductive success beyond resources, males would be involved in risk behaviors, and even in criminal behavior, such as homicide and robbery (Shulman et al. 2015).

This hypothesis accounts for other characteristics of the sensation-seeking, such as the fact that men tend to present a higher level of desire for this than women and the fact that it decreases in early adulthood (Zuckerman 1994; Shulman et al. 2015). In the first case, the literature indicates that a great desire for sensation-seeking in women, and consequently engaging in risk behaviors, causes a decrease in reproductive success; thus, there are no evolutionary advantages in this. In the second case, one of the possible explanations revolves around the stabilization of social status, as this seems to be experience-sensitive. In this hypothesis, some of the elements mentioned in the literature can be anchored, being protective of criminal behavior, such as marriage, children and formal employment, as the situation now requires the individual to have a less impulsive and safer behavior pattern to guarantee security and the level of resources.

In addition to these variables, some personality disorders are used as correlates of crime, such as antisocial personality disorder (ASPD) and psychopathy (Bonta and Andrews 2016). Criminology seeks to investigate the relationship between criminal behavior and possible psychopathological conditions that can increase the risk of engaging in criminal behavior. Just as in the cases of people without disorders who commit crimes, cases in which the individuals have some diagnosis of psychological disorders are complex and have multiple causes. However, depending on the disorder, it is possible to verify the incidence of certain crimes. In the case of ASPD, it is possible to observe a

greater frequency of violent crimes, such as aggression and homicide (Shepherd et al. 2018). This disorder is one of the most frequently investigated because of its prevalence in the prison population of several countries (Newbury-Helps et al. 2017).

In general, the pattern of behavior of individuals with this disorder tends to violate the rights and social norms, and this characteristic emerges in childhood with continuation in adult life (Black 2015). In addition, characteristics such as great impulsiveness, lack of security, the tendency to lie, among others, make up the ASPD framework, these being risk factors for engaging in risk behavior (APA 2013; Newbury-Helps et al. 2017). These same characteristics can be observed in another disorder, psychopathy. However, it is important to highlight that this presents other criteria for diagnosis, such as shallow affect, callousness, and an absence of empathy (DeLisi 2018; Hare 2003). Most psychopathic offenders satisfy the ASPD criteria; however, the opposite is not true (Black 2015; Shepherd et al. 2018). The relationship between mental disorder and criminal behavior is established in such a way that various diagnostic tools are used as indicators of risk of recurrence (Bonta and Andrews 2016). One of the main instruments is the Psychopathy Checklist–Revised, developed by Hare (2003) and used in several countries for predicting crimes (Gardner et al. 2018).

Conclusion

Criminology has already been associated with studying ways to explain criminal behavior. It has often been focused on social and contextual issues that could explain certain actions; however, the study of variables related to personality that could be connected has not been neglected. Personality, in turn, presents several explanatory theories of psychoanalytic, psychometric, and evolutionary biases.

In this sense, psychology contributes greatly to the advancement of studies of criminal behavior, and it is dedicated to exploring individual characteristics that can lead to crime. As discussed throughout the text, there are several aspects of personality that may be associated with engaging

in crime, such as impulsiveness and sensation-seeking. In this sense, evolutionary psychologists argue that the resources and evolutionary success may be found in the explanatory basis for cheating behaviors, for example. However, it is prudent to consider that, despite personality and crime characteristics, criminal behavior is emitted because of a complex combination of elements, involving, among other things, individual, social, and cultural aspects.

Cross-References

- ▶ [Criminals Are Made Not Born](#)
- ▶ [Evolution of Crime, The](#)
- ▶ [Evolutionary Personality Psychology](#)

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Criminals Are Made Not Born

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Synonyms

Causes of criminal behavior; Criminal behavior; Criminology

Definition

For evolutionary studies, criminal behavior is not only a conglomeration of psychological and individual aspects but a complex integration between distinct variables, with explanations involving the past and the present.

Introduction

Crime is multifaceted, with manifold causes, and requires a multilevel analysis to be understood. Essentially, humans' actions have multiple causes, and are influenced by macro and micro aspects that increase or decrease the chances of behavior (Durrant and Ward 2015). Considering that we observe and interpret the world as an ordered sequence of occurrences, what has happened previously reflects on current events. However, the causes are not linear (*a* causes *b*, which in turn causes *c*), which can be seen as a conglomerate of variables affecting nature, society, and

thus human behavior, in a feedback pattern (Bonta and Andrews 2016). Social and individual aspects are present in a complex circular explanation, that involves the past and the present, to make the crime occur.

Criminology is the area of science area investigates crime, searching for scientific explanations for the behaviors that violate social norms. In this field, numerous theories with this goal can be found, with diverse focus, epistemological bases, and methods (Akers 2017; Bonta and Andrews 2016; Durrant and Ward 2015). As there are many theories, the terms describing criminal behavior are varied. Antisocial behavior, offense, delict, among others, are used in the field of criminology to refer to the violation of the social norms and law (White et al. 2017). Thus, in this topic, the general term “crime” will be used as shorthand to refer to all elements explored by criminology.

In addition to the various terminologies used in referring to this field, there are several theories that seek to understand why individuals become involved in crime. Among the current explanatory theories about committing crimes are the Chicago School, Differential Association Theory, Anomie Theory, Labeling Approach and Critical Theory (White et al. 2017).

Crime theories usually elaborate assumptions about human nature, which, in general, are not articulated, considering man, for example, as essentially altruistic or selfish and self-oriented. On the other hand, criminological theories also affirm that human actions, including criminal behavior, would be expressly produced from the individual's relationship with the environment and with others (Durrant and Ward 2015).

In fact, explanations for criminal behavior generally focus on immediate factors, such as the psychological characteristics or the social context in which the individual lives (Akers 2017). On the other hand, despite the relevance of these theories for the administration and control of crime, the evolutionist approach focuses efforts on more distant causes from evolutionary history (Durrant and Ward 2015). It is believed that the integration of distal explanations and proximal explanations of the crime contributes to the elaboration of an explanatory framework of human nature, aiding in

the understanding of crime (Shryock and Smail 2011).

Distal Explanations for Crime

As presented by Duntley and Shackelford (2008), the crime, especially violent crime, reflects the conflicts between individuals. The authors suggest that the crime might have been favored by natural selection owing to the resource advantage to the offender. However, the sense of collectivity, which maintains the social structure, is also favored by evolution, in view of that the chance of group survival is increased when all members cooperate (Duntley and Shackelford 2008). In this context, those who not cooperate, or show behavior that infringes the group norms, are punished (Durrant and Ward 2015). In this way, evolution selects both altruism, which results in cooperative groups, and punishment, to guarantee social organization, in response to crime.

In this context, behavioral scientists have more than one way of understanding the evolution and adaptation of criminal behavior, and these ways are not necessarily exclusive (Durrant and Ward 2015). Among these methods of perceiving the mechanisms that seem to sustain the crime, two are highlighted. The first mode consists of crime as a direct product of evolution, favored by natural or sexual selection, as individuals who commit crimes end up raising more resources by increasing the chances of transmitting their genes (Duntley and Shackelford 2008). However, it is important to emphasize that this strategy seems to be currently at a disadvantage, given the way in which society responds to crime, with more precise methods of investigation and more effective punishments, leading to a decrease in crime rates, especially violent crimes (Bonta and Andrews 2016).

From this point of view, three explanations for crime can still be observed; again, they are not mutually exclusive, all being used in the research carried out in criminology (Durrant and Ward 2015). The first indicates that the adaptation would have worked in the best way possible, favoring criminal behavior. The second explanation expands on the understanding of crime by bringing

to the analysis the context in which it is observed, that is, the mechanisms underlying criminal behavior could also be the result of conditional adaptations that manifest in some individuals in a very specific social and ecological context. Last, the third explanation argues that it would be possible for criminal behavior to have been sustained by adaptations maintained by frequency-dependent selection, with criminal behavior being maintained in a reduced number of individuals in a population.

The second mode of understanding criminal behavior comprehends it to be a by-product of evolution (Durrant and Ward 2015). In this way, the adaptation of another mechanism would favor criminal behavior as a collateral effect. In this approach, the adaptation would be operating as it would have been; however, the crime would be a by-product of this adaptation. Moreover, another possible way of understanding the criminal behavior as a by-product would be that it would actually arise because of a pathological functioning of adaptation. However, it is important to highlight that this mode of understanding and explaining the crime assigns little importance to the context into which the subject is inserted.

Since the adoption of one of these explanations does not encompass the whole phenomenon, it is possible to think that certain crimes would have their mechanisms favored. The division of the specificity of crimes is common in criminology, the majority of authors classify crimes into two major categories, the “violent” and “non-violent” (Bonta and Andrews 2016; White et al. 2017). When the evolutionary explanations for these two categories of crime are observed, it is possible to perceive that the development of both categories travels different paths and is influenced by cultural elements to a greater or lesser degree.

Two concepts are central to understanding these crimes, and in a general way, the aggressive behavior, the notion of aggression and violence. Aggression is understood to be all behavior directed at hurting or injuring another living being (Allan 2017). Aggression is observed in many species of animals, for example, chimpanzees, mainly males, use aggression in diverse contexts, from competition with other males, to obtaining status and resources. Females also exhibit aggressive behavior, but less frequently (Campbell 2015).

The evolutionary logic behind the aggression is clear: it indicates that in any context of dispute (for resources, territory, power, etc.) the use of physical force will constantly be a reasonable strategy that can lead to an increase in reproductive success (Allan 2017). Another aspect is the ability to resist aggression, which also increases the chances of reproductive success, implying a greater transmission of this characteristic. Considering the boost in chances of survival and reproduction, biologists state that there seems to be a specific mechanism for the selection and adaptation of aggression (Durrant and Ward 2015). However, it is important to highlight that this strategy is considered potentially costly, seeing that the results lead to possible harm to the aggressor, who could be seriously hurt or killed. Any organism that consistently engages in violent behavior for a long period has fewer chances of survival (Campbell 2005). In the same way, even with a selection and adaptation process leading to aggression, it is sensitive to individual aspects (age, gender, physical conditioning, etc.) and contextual aspects (resources, social context, etc.) (Allan 2017; Campbell 2015; Durrant and Ward 2015).

On the other hand, violent crimes can be defined as those in which the offender aims to use aggressive behavior with the purpose of causing great injury to the victim (Loza 2018). By this logic, although robbery could be classified as aggressive behavior, homicide is classified as violent behavior. In addition to aggression, the violence can be observed in different species is also influenced by contextual and individual elements. The evidence points to violence also having undergone a specific process and selection in our species. Seeking to understand this phenomenon, Duntley and Buss (2011) proposed a theory that claims that homicide, violent behavior with greater lethality, went through a specific selection process. This theory became known as the homicide adaptation theory (HAT).

According to the HAT, humans possess specific psychological mechanisms for killing, which were selected because of the reproductive advantages that the ancestors obtained. The capacity for homicide would prevent humans from being the victim of possible violent behavior and would provide a certain reputation, guaranteeing social status and consequently security of territories,

resources, etc.. It would also allow the individual to eliminate those within the group considered costly individuals who are not genetically related, in addition to those who are relatives, but who do not present satisfactory conditions for the transmission of genes, such as children with disabilities, individuals with chronic diseases, etc. (Duntley and Buss 2008).

Even showing an reasonably valid argument, the HAT has many critics; some authors do not consider to be the best evolutionary explanation for an understanding of homicide (Durrant 2009; Durrant and Ward 2015). These authors agree with the idea of the mechanism of transmission of the capacity to kill; however, they disagree that the capacity to kill individuals of same species has a specific adaptive mechanism. For some, homicide would appear to be a by-product of the mechanisms of aggression and violence.

Distal explanations seem to be more relevant in the comprehension of aggressive and violent behavior and by consequence the crime in our sciences (Durrant and Ward 2015). Moreover, the distal explanations indicate, with strong evidence, that men are more likely to present physical aggression than women, this being observed in different cultures, historical periods, and at different stages of development (Campbell 2015). This difference between the sexes, which is an important subject in criminology, is greater when there is greater potential for lethal behavior, such as homicide. This difference could be due to a great evolutionary advantage received by men, whereas women would receive a disadvantage, in using physical aggression as a strategy to achieve their goals (Durrant and Ward 2015). However, the difference between men and women is smaller when compared with anger or indirectly aggressive behavior. This, because it does not entail so much damage, appears to be frequent in both, and presents similar advantages to other aggressive behaviors.

Explanations for violent and non-violent crimes work for a variety of criminal behavior, but some crimes are more effectively explained when other mechanisms are involved, such as sex crimes, white collar crimes, terrorism, etc. Considering the purpose of this topic, the distal explanations of all these crimes will not be presented; however,

for more detail, we suggest reading Bonta and Andrews (2016) and Durrant and Ward (2015).

Along these lines, the mechanisms behind the main categories of crimes were presented. In these explanations there are no arguments that individualize criminal behavior, that is, for each of the evolutionary mechanisms presented to explain the crime, the offender is not considered to be destined to commit crimes. From the distal point of view, there are mechanisms underlying the crime that were selected because they present advantages, but all species would, from this point of view, have the same chance of committing crimes (Durrant and Ward 2015). In this way, what differentiates between a criminal and a non-criminal, is precisely the specific, individual, and contextual aspects, which are mentioned in several theories. Thus, the following section discusses the individual aspects related to the crime.

Proximal Explanations for the Crime

Many researchers in criminology are looking for variables that can be classified as “increasing” or “decreasing” the risk of engaging in criminal behavior. More recently, the organization of risk and protective factors for the crime has been more organized and accurate (Singh et al. 2018). Studies that have a focal point in recidivism have spearheaded this field, primarily motivated by programs with the goal of reducing the risk of a return to committing crimes (Bonta and Andrews 2016). Several terms are used to refer to these variables, which can provoke some misunderstanding. Static and dynamic factors, risk and protective factors, criminogenic needs, among others, are terms easily found in research related to crime. In the end, all mention variables relative to criminal behaviors, but each one of them maintains a certain particularity.

Static and dynamic factors are related to the possibility of modifying a certain condition in relation to the individual (Ward 2016). In this way, static factors cannot be altered, e.g., an example of historic antisocial behavior or the fact that one or more members of the family has committed a crime, among others. On the other hand, dynamic factors would be those that can be modified, such as the relations that the person

establishes, their beliefs about crime, patterns of personality, etc. (Bonta and Andrews 2016; Ward 2016). At first glance, these look like “protective factors”; however, the first is about the increase or decrease of the chances of engaging in criminal behavior, whereas the second is about the capacity of modification of those variables. The group of factors considered dynamic can still be called “criminogenic needs.” This term refers to the essentially individual or social characteristics, related to criminal behavior, which when modified or managed at some level, cause a reduction in recidivism (Bonta and Andrews 2016).

Several theories and models of criminology use the risk and protective variables to understand and intervene in the crime (Singh et al. 2018). To this end, some empirical investigations have been undertaken with the goal of assessing the predictive power of those variables in criminal behavior. The main advances in this area come from longitudinal research, considering that they allow us to observe the social and individual changes that individuals undergo (Farrington 2015). Presented here are some variables considered risky, dynamic, and static, referring to most crimes. In the same way that it was possible to identify these variables, the studies also pointed out the effect of specific variables under certain types of crimes, such as sex crimes and white-collar crimes (Beech et al. 2015). As stated earlier, the purpose of this topic is not to discuss all types of crime, but to introduce the reader to this field. Reading Ward (2016) and Singh et al. (2018) can help further in understanding how these variables relate to specific crimes.

Much research classifies different risk and protective variables in criminal behaviors. This distinct allocation occurs according to the theory used by the author, in addition to the resources available for carrying out the research (Bonta and Andrews 2016). Our goal is not to explain each of these variables in detail, but to present this way of explaining the crime. The use of these variables in treatment programs has resulted in reduced crime rates, whether in adolescents or in adults (Singh et al. 2018). The results indicate that in fact these variables have an influence on criminal behavior, but they fail to explain their interaction. Among several groups of variables available in the

scientific community, we highlight the model risk need responsivity (RNR), which shows eight variables to be most explanatory of criminal behavior (Bonta and Andrews 2016).

The spotlight on RNR is due to the method used for its development. The authors conducted a series of meta-analyses, with data from various research from around the world. Thus, a history of antisocial behavior, antisocial personality patterns, antisocial cognition, association with deviant peers, family circumstances, schooling, work, leisure, and abusive use of substances, have been indicated as potential risk factors in behavioral engagements (Bonta and Andrews 2016).

However, the RNR is not the definitive model, or group of variables, in criminology. Several other variables that are not included in it have been presented by other surveys. Research has pointed to adolescence as the period when humans commit more crimes. The relationship between age and crime is bell-shaped, and the first to discover this was Quetelet (1833). The shape of this curve changes according to the type of crime, sex, and socioeconomic conditions. However, even with these differences, adolescents are more likely to commit crimes. Faced with this, criminology has sought to explain why some adolescents engage in crime and no longer do so when they are adults, whereas others continue to commit crimes.

Although the use of risk and protective variables by theories and models is common in criminology, this use is not exempt from criticism (Ward 2016). Some authors argue that the simple use of these variables in the explanation of crime, without worrying about understanding how the interaction occurs, can lead to a dead end (Durrant and Ward 2015). This situation is a product of the researchers' concern in the area of criminology in developing risk assessment tools to predict criminal behavior, regardless of the relation of variables in the real world. The risk factors described in the literature seem to be products, or by-products, of evolutionary mechanisms (Durrant and Ward 2015). Consequently, the explanation of crime assumes macro and micro dimensions, in which the proximal and distal factors interact. Thus, it is possible to explain why two individuals behave in different ways in the same context.

Conclusion

Despite the various ways of understanding the formation of criminal behavior and its evolution, explanations based only on evolution are not sufficient to encompass the whole subject. Consequently, although personality aspects have helped to advance research in this area, they do not provide an adequate explanation of criminal behavior either. Therefore, it is prudent to conceive of crime as a product of evolution without neglecting aspects related to culture.

For a time, criminology has focused on psychological characteristics to explain criminal behavior. Evolutionary psychology has presented advances in this field. In fact, it is possible to understand that a diversity of connected factors lead to criminal behavior; they are related to the evolutionary history of the human species, in addition to the current contingencies of the individual's life. Therefore, there is more than one way of understanding the evolution of criminal behavior.

Cross-References

- Criminal Personality Variables
- Criminology

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Criminology

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Synonyms

Criminal behavior; Social factors and crime; The psychology of crime

Definition

Criminology is an interdisciplinary field of study that focuses on crime and the responses to crime.

Introduction

As the study of crime and society's responses to it, criminology is an interdisciplinary field that brings together scholars, clinicians, and other professionals from all types of disciplines to seek an understanding of some of the behaviors that have deep and broad consequences for society. How has crime been studied in the past? How has it been conceptualized by different societies? Why are there inappropriate (i.e., criminal and illegitimate) codes of conduct in all societies where documentation exists? These are some of the questions we will pursue in this entry. First, we will describe what has been studied under the umbrella term "criminology," giving us an appreciation of the history of the field. Then, we will explore some of the more prominent theories in criminology from classical to critical perspectives. Then, we launch into an evolutionary explanation of why criminology exists as a field by framing what it studies – crime and the regulation of appropriate conduct – as evolutionarily relevant phenomena. We then examine how criminological observations of sex and age as important predictors reflect evolutionary principles and expectations of important predictors. Following this example, we more explicitly describe two prominent evolutionary models that attempt to frame criminological issues using evolutionary perspectives. Lastly, we give a brief overview of two varying criminal justice system approaches that frame the issue of *responses* to crime differently – rational-based approaches and honor-based approaches.

What Is Criminology?

Criminology is a field primarily interested in acts constituted as crimes and the subsequent social responses to these criminal acts. Though

sociological theories have played a prominent role in the development of the field of criminology, it is an interdisciplinary field organized around the study of law and crime, incorporating contributions from other disciplines such as psychology, anthropology, political science, and law (Durrant and Ward 2015; White et al. 2018). While there has been a general consensus among scholars and researchers that criminology should include the study of law, the causes of crime, and the responses of society (including responses by citizens, criminal justice professionals, and institutions) to criminal acts, there continues to be disagreement regarding what should be considered a crime and what specifically should be included under the purview of criminology (Durrant and Ward 2015; White et al. 2018).

The most fundamental definition of crime is any action that has legal consensus of being wrong or harmful, that is codified by law or legislation, and that has prescribed sanctions by the state for violation (Agnew 2011; Durrant and Ward 2015; White et al. 2018). That being said, criminologists have also recognized that what constitutes a crime is socially constructed and changes based on historical, cultural, and social conditions (Durrant and Ward 2015; White et al. 2018). For example, cannabis was initially criminalized in the United States in 1937; however, in recent years, many states have changed their laws to legalize the consumption of cannabis for both medicinal and recreational purposes (Adrian 2015). Therefore, many criminologists have argued that focusing on legal definitions of crime is "both too narrow and too broad" in that "it excludes many harmful acts while including many that result in relatively little or no harm" (Durrant and Ward 2015, p. 2). As an alternative, some criminologists have argued that the focus of criminology should not be crime as it is defined by the law but should also include other acts that draw social disapproval or nonlegal sanctions (e.g., ostracization) (Agnew 2011; Durrant and Ward 2015).

Hagan (1987; as cited in White et al. 2018) proposed different dimensions that could be used to define crime. In addition to the legal definition

of crime, he proposed that the definition of crime could be expanded to include social harms (i.e., causes harm to another individual), cross-cultural universal norms (i.e., patterns of crime observed across different cultures), labelling (i.e., actions that are labelled criminal, and are treated as such), and power dynamics (i.e., reflect unequal distribution of power and access to resources within a given society) (Hagan, 1987; as cited in White et al. 2018). Similarly, Agnew (2011) suggested that crime could be broadened to “acts that cause blameworthy harm, are condemned by the public, and/or are sanctioned by the state” (p. 187). While these theorists may differ regarding what to include in definitions of crime, they agree that legal definitions of crime do not capture the breadth of acts that can be considered a crime. Furthermore, while Agnew’s (2011) conceptualization of crime does not account for some of the important factors identified by sociologists (e.g., power differences between social groups), Durrant and Ward (2015) identify that it enables contributions to criminology from other disciplines, including evolutionary sciences. They identify that by advancing the definition of crime beyond legal forms of crime, it opens the field to include acts that threaten *biological fitness* and violate social norms in noncriminal ways, such as bullying or sexual harassment (Durrant and Ward 2015, p. 3).

Establishing an inclusive definition of crime is an important task in criminology given it will help to contribute to a more holistic and comprehensive understanding of crime and its responses. Scholars (e.g., Durrant and Ward 2015; Wright and Cullen 2012) have suggested that the study of crime could be improved if the field of criminology incorporated evolutionary sciences as a means of understanding “the more distal causes of criminal behaviour – those that reside in the evolutionary history of our species” (Durrant and Ward 2015, p. 1). That is, there is a greater role that biological sciences, specifically evolutionary psychology, can play in the understanding of crime since it has already made a significant contribution in parallel areas of interest to criminologists (see section on “[Evolutionary Models of Criminology](#)”) and can be integrated

into current criminological explanations to develop a more thorough understanding of crime (Durrant and Ward 2015; Walsh 2000; Wright and Cullen 2012).

Several researchers have identified that evolutionary theories and conceptualizations of criminal behavior have been overlooked in the history of the field of criminology (i.e., Durrant and Ward 2015; Wright and Cullen 2012). Durrant and Ward (2015) suggested that one of the possible reasons for why biological or evolutionary approaches have been avoided is the role they have played historically in justifying oppressive practices based on deterministic views of criminality, such as eugenics and institutionalization. For example, at the start of the twentieth century, many countries (e.g., the United States, the United Kingdom) implemented legislation that promoted the protection of society through the containment and elimination of persons considered *feeble-minded*. These individuals were considered morally defective and responsible for many social problems, such as alcoholism, prostitution, criminality, and poverty (Scheerenberger 1983). These beliefs were based on research, such as the *The Kallikak Family: A Study in the Heredity of Feeble-Mindedness* by Henry Goddard in 1912, which suggested that based on flawed measurements of intelligence, that feeble-mindedness was hereditary and, in turn, recommended the eradication and containment of persons considered a risk for contaminating the population and threatening the prosperity of the state (Scheerenberger 1983).

While historical uses of evolutionary and biological sciences have been used to oppress certain populations in the past and have been understood to endorse a deterministic view of crime, contemporary evolutionary and biological sciences do not condone oppression, and determinism is no longer a tenable position. Wright and Cullen (2012) suggested that criminologists need to move away from old attempts to integrate biological and evolutionary theories into criminology and recognize the role of a *biosocial paradigm of criminology*, which is “interested in genetic variation and tend[s] to focus on traits related to crime and antisocial behavior to understand how much variance in a specific trait can be attributed

to genetic and environmental sources” (p. 245). Durrant and Ward (2015) expand on this point, suggesting that contemporary developments in evolutionary biology and psychology are more aligned with existing criminological theories.

Current Perspectives of Criminology

As indicated in the previous section, criminology is an interdisciplinary field of study, and though its development has been led largely by sociology, it is composed of multiple disciplines identified in the previous section. As the social, historical, and cultural contexts have changed, several different and occasionally competing perspectives of criminology have developed (White et al. 2018). Each perspective attempts to understand crime and the responses to crime by asking different questions, focusing on different factors that contribute to the behaviors of the individual, society, and social institutions, explaining crime using different concepts, and constructing a different framework for analyzing and responding to crime (White et al. 2018). The four most common perspectives of crime are classical theory, positivism, strain theory, and critical criminology.

Classical Theories of Criminology

Prior to the Enlightenment period, codes of law (e.g., the Code of Hammurabi) existed; however, as Cesare Beccaria – an Italian philosopher and politician of the time – pointed out, the interpretation and execution of the law were inconsistent, and punishments were often disproportionately handed out (Hagan and Daigle 2018; White et al. 2018). As such, the social and political movement in the eighteenth century was characterized by the movement from feudalism to a system in which all citizens had rights that were not connected to their class. In addition, many institutions, including the criminal justice system, were influenced by Enlightenment thinkers that argued humans were rational beings capable of the choices associated with free will. Influenced by these philosophers and social thinkers, classical theorist argued that crime was the result of the individual’s choice or as a result of irrational

decisions (e.g., inebriation). In addition, given each citizen was prescribed individual rights, the state was empowered to develop and codify laws to ensure that all citizens are treated equally (Hagan and Daigle 2018; White et al. 2018).

Classical theorists argued that when a crime occurred, it was a violation of the *social contract*, an implied agreement that citizens will forfeit some of their individual rights in exchange for protection from the state. Cesare Beccaria argued that crime impacted all citizens and “society as a whole,” and therefore it was the role of the state to re-establish order (White et al. 2018, p. 28). In addition, philosophers such as Jeremy Bentham argued that all of human behavior could be reduced to the pleasure-pain principle that humans act in ways to maximize pleasure and to reduce pain. Therefore, classical theories of crime focused on punishments that were not vengeful but that acted as a deterrent to prevent both the individual from committing another criminal act and other citizens from committing offenses. Therefore, the role of the state was not only to decide what constitutes a crime but also what punishment was proportionate to the crime (Hagan and Daigle 2018; White et al. 2018). That is, by calculating the cost-benefit ratio of acting criminally, the state could ensure that the set punishment was painful enough to act as a deterrent and would nullify the reward for acting criminally.

While classical theories of criminology have been largely influential in many international criminal justice systems, critiques have identified that the law remains unequally distributed among citizens, with some populations being overrepresented. Furthermore, with regard to punishment, proportional sentencing may not be experienced the same by all citizens. For example, persons of lower socioeconomic status are more likely to experience monetary fines as more punitive than a person with more resources associated with higher socioeconomic status (White et al. 2018).

Positivist Perspectives of Criminology

In the nineteenth century, ideas regarding the nature of humans were being defined by the colonialism of European nations throughout

the world and the development of the natural sciences using the scientific method. Positivism developed as a way of understanding how the world worked and “ultimately provid[ing] a rational means of overcoming existing social problems and ills by using the scientific method” (White et al. 2018, p. 38). Criminology was no exception to this rule – how could the scientific method and a new understanding of the world (e.g., evolution) be used to understand crime and provide an effective response to crime? Two areas of interest become of interest to positivists: the individual differences that contributed to an offender deviating from the general population that caused crimes to happen and social contributions – mechanisms within society (e.g., the family unit) that no longer operated to ensure the “system was working as a whole” (White et al. 2018, p. 39).

Compared to classical theorists who focused on the law and the nature of the offense, positivists focused on the offender and the individual and social characteristics that contributed to the offense (Hagan and Daigle 2018; White et al. 2018). This shift in focus had a significant impact on the definition of crime, since it no longer focused strictly on legalistic aspects of crime but began to include deviations from the norm (e.g., mental illness, deviant social roles). One of the most well-known positivists was Cesare Lombroso, an Italian physician, who tried to categorize people based on Darwin’s theory of evolution (Hagan and Daigle 2018; White et al. 2018). He initially proposed that criminal behavior was the result of *atavism*, a regression to an earlier stage in human evolution; however, he later refined his classification to different typologies of the criminal (Lombroso 1911; White et al. 2018). For example, he suggested that female offenders were typified by characteristics traditionally ascribed to men.

Given the deterministic perspectives of the positivist criminological theorists, it is unsurprising that the responses to crime were limited (Hagan and Daigle 2018; White et al. 2018). While classical theorists emphasized the importance of sentences that suited the crime, positivists tended to recommend an indeterminate sentence that took into account the characteristics of the

offender. In addition, positivists focused on interventions such as treatment or containment to prevent further disruption to society.

Critics of positivist theories have identified that these theories have limited ability to explain all crimes (e.g., white-collar crime). Furthermore, as stated previously, many of these theories were misappropriated and used to oppress many populations (e.g., racism). Finally, it has been criticized for focusing too heavily on the individual and micro-level contributions (e.g., familial trauma) to crime and not accounting for macro social conditions that also contribute to criminal behavior (e.g., poverty) (Hagan and Daigle 2018; White et al. 2018). Nevertheless, some contemporary writers still ascribe positivist interpretations to criminal conduct (e.g., Raine 2014).

Strain Theories of Crime

With the development of sociology as a discipline and international changes following World War II observed in the twentieth century, criminologists became more interested in the distribution of opportunities throughout society, the ways individuals related to each other, and the impact of these variables on crime (White et al. 2018). Strain theories of crime were the first sociological theories of crime, which suggested that crime was a social phenomenon and the product of social processes and structures. While positivist theories of criminology assumed that crime resulted from individual deficits, strain theorists believed that crime represented a violation of social norms – the agreed-upon values and behaviors within a society (White et al. 2018). That is, crime was not a result of individual deficits or pathology but the result of social strains or tensions (Hagan and Daigle 2018; Walsh 2000; White et al. 2018). Strain theorists proposed that when citizens do not have equal access to resources (e.g., wealth), these individuals will seek out alternative, inappropriate opportunities to meet their needs. For example, Sampson and Laub (1993) examined how race and economic opportunities shaped the experiences of African-American youth being charged with an offense. They found that the experiences of African-American youth were indeed characterized by poverty, which in turn

influenced their confinement, especially when being charged with a drug offense.

One of the most influential strain theorists was Émile Durkheim, who proposed that crime was the result of *egoism* and *anomie* (White et al. 2018). Egoism is the state of society characterized by excessive individualism – “the unrestricted pursuit of individual desires;” whereas, anomie is “a state of normlessness, in which society fails to impose norms that inhibit such behavior” (White et al. 2018, p. 76). The importance of Durkheim’s contributions was that it drew attention to the fact that crime was the by-product of certain types of social order (White et al. 2018). Merton (as cited in White et al. 2018) further contributed to the idea of anomie by suggesting that crime could be understood in relation to two main variables – cultural goals shared by all citizens (e.g., wealth, status) and the different institutional means of achieving these goals. He proposed that “depending on the opportunities available to [citizens], people decide to accept or reject the cultural goals and to accept or reject the institutional means to attain commonly accepted goals” (White et al. 2018, p. 80). Merton would have argue that the youth in the Sampson and Laub (1993) study experienced greater barriers to accessing resources, which in turn influenced the decisions they made.

Strain theorists proposed that crime is best addressed by combining individual rehabilitation with institutional reform that increased access to social programs (Hagan and Daigle 2018; White et al. 2018). They recommend removing causes of strain by increasing access to social programs that target citizens at risk of experiencing strain (e.g., job finder clubs or afterschool programming) and that reduce the strain experienced by these individuals (Hagan and Daigle 2018; White et al. 2018).

Critical Perspectives of Crime

Finally, critical theories of crime are concerned with the structures of power within society and the ways that power is institutionalized to privilege certain groups of citizens. For example, critical feminist criminologists are concerned

with the ways that the law and the criminal justice system are structured so women face oppression. Thus, many critical criminologists concern themselves with revealing the underlying power dynamics that structure how different groups of citizens are treated and finding solutions to address them (Hagan and Daigle 2018; White et al. 2018).

White and colleagues (2018) identified that critical criminologists can be divided into two theoretical orientations – *structuralists*, who focus on power as something that is embedded in social institutions (e.g., the criminal justice system), and *postmodernists*, who examine how “knowledge production shapes human experience while simultaneously engendering conflict over meaning” (e.g., prostitute vs. sex trade worker) (White et al. 2018, p. 233). While structuralists view the marginalization of some social groups as the cause of crime, postmodern approaches identify that dominant discourses or popular beliefs are responsible for establishing what is a crime. Both structuralists and postmodernists are interested in revealing the underlying power relationships that contribute to the experiences of different social groups within the criminal justice system; however, structuralists focus on empowering disenfranchised groups and redistributing resources equitably, and postmodernists focus on building an inclusive society by defusing the power of dominant beliefs about criminalized groups of individuals (White et al. 2018).

While all of these perspectives have advanced the field of criminology, Durrant and Ward (2015) identified that evolutionary approaches have had limited influence in the field of criminology. Furthermore, several criminologists have identified that criminology is still a developing discipline and has yet to provide any solutions regarding how to prevent crime. Durrant and Ward (2015) proposed that the incorporation of the evolutionary approach into existing perspectives may lead to a more complete theory of crime and develop more effective laws and legal structures to address crime. The goal of this chapter is to explore how an evolutionary approach can be used to enhance criminology.

Evolutionary Logic of Criminology

The problems and issues that stimulate a study of criminology reflect both the prevalence and reality of crime in society *and* that there is something about it requiring and capturing our attention. In other words, criminology is not just the study of crime as a static reality in society, it is also revealing of our concern for the welfare of society. Humans are an obligate social species that depend on one another for their survival and well-being, making the idea that we should care about the welfare of society completely obvious. But what of criminal behavior? Why does criminal behavior emerge at all where it can begin to disrupt social welfare? And why do criminals not only face costs associated with their criminal activities but also tend to reap benefits? These are questions that are informed by an evolutionary perspective on criminology and are required if criminology is to maintain a nonarbitrary conceptualization of crime and criminal activity (Durrant and Ward 2012). Here, a nonarbitrary view provides a full explanation of why things are constituted as they are and not some other way and is a unique feature offered by evolutionary thinking for the social sciences (e.g., Buss 2009).

The law is an ever-present and structuring feature of modern societies. It embodies the criminal justice system that determines what constitutes a crime and upholds the law by responding to the commission of such crimes. But where does it come from? Yes, we can track the legal operation and history back to its recent origins in Greek and Roman – as well as other – societies (see section on “[Current Perspectives of Criminology](#)”), but where does it *really* come from? Why is there a law at all? What is it about humans that seem to compel us to create a law? Again, the logic provided by an evolutionary perspective is positioned to generate answers and explanations for these types of questions, suggesting that its inclusion in criminology is not only needed but desirable as well (Walsh and Jorgensen 2018).

The questions posed in the above paragraphs require more expounding. Crime and the law that defines it are concepts fundamentally important to criminology, but why should these things exist?

An evolutionary perspective is able to answer this by conceptualizing *crime* and *the law* as social constructs that reflect humans’ morality – what feels right versus wrong, seems fair versus unfair, and deemed just versus unjust – which constitutes them as an obligate social species shaped by and for these features (de Waal 2008; Haidt 2001). Most criminologists would easily recognize that this is the case that crime and the law are clearly morally infused. However, an evolutionarily minded criminologist appreciates that moral impulses and intuitions form the core of what has come to be called “crime” and the “law” that governs it. They acknowledge that these underlying moral impulses and intuitions have been shaped into us by selection because they have fitness consequences for individuals existing in those social groups. Thus, a deeper, nonarbitrary explanation is offered in using an evolutionary perspective toward problems of criminology, including the very framing of the discipline and its problems.

Another example that shows the nonarbitrary explanation that evolutionary perspectives offer criminology is understanding our different standards of conduct depending on who the victim of the crime is and the context surrounding it (Walsh and Jorgensen 2018). For instance, offenses committed against members of your own community were likely the primordial forms of criminal conduct that warranted punishment and/or correction. These crimes likely included cheating, theft, and assault against in-group members (Durrant and Ward 2012). What is interesting in using an evolutionary lens is that it becomes comprehensible why many societies do not punish acts against out-group individuals that might otherwise be considered criminal conduct. A particularly clear example of this is murder: killing in-group members is considered illegitimate and a supreme form of unacceptable behavior, whereas the killing of out-group members has legitimacy, particularly in the context of war (Daly and Wilson 1988).

Legal documents and codes of conduct have been prevalent in societies for thousands of years going back to Hammurabi’s Code. These codes of conduct, however, regulate the behavior

of individuals *within* a society, making their jurisdiction limited in scope to the group of people being governed. Even societies that do not have written technology abide by codes of conduct that monitor, regulate, and punish the behavior of in-group members not in the same way as out-group members. An example is the Yanomamö tribes in what is now Venezuela and Brazil. This diverse group of tribes strictly regulates and punishes in-group cheating, theft, and assault while condoning and sometimes encouraging out-group displacement and elimination (Chagnon 2013). It is expected that this should be the case from an evolutionary perspective; in-group codes of conduct should form the core of human societies, and out-group conduct should be separate, confined to a separate code of conduct involving intergroup relations. That international law has not become a preoccupation of individuals around the globe until the seventeenth century suggests codes of conduct regarding out-group members has not been as an important feature of how societies regulate wrongful behavior as have the codes of conduct within in-group contexts. In other words, evolutionary logic predicts that human societies should first be concerned with governing their in-group members because this most ostensibly had fitness consequences for the individuals abiding by those codes of conduct, especially in ancestral environments structured by nomadic and foraging conditions (Tooby and Cosmides 1992).

So we have seen that crime and the law reflect our moral impulses and intuitions, and this can be informed by an evolutionary perspective. But the final point to make in demonstrating the evolutionary logic behind criminology, as a discipline and in its subject matter studied, is to show why crime is classifiable as a concept at all. In humans' struggle for survival, status, and intimate relationships, individual desires can often come into conflict with the desires of other individuals within the social group. While humans are clearly an obligate social species dependent on each other, competition for scarce resources abound, especially in our ancestral environments where the traits and features of the mind were shaped (Tooby and Cosmides 1992). Disagreements

involving resource competition can progress to altercations, violence, and homicide (e.g., Daly and Wilson 1988); they can progress to stealing from or cheating a competitor; they can progress to harassment, abuse, and rape. What are these individuals even competing for that makes them so motivated to commit acts that their community will certainly punish? The answer is connected to resources that guarantee, or at least enhance, one's survival and reproductive success. Ancestors equipped with the capacity to engage in these acts – especially in certain contexts signaling unpredictability, harshness, and competition (e.g., Durrant and Ward 2012; Mishra and Lalumière 2008) – would have left versions of themselves more successfully than alternatives that could not engage in such acts given the *appropriate* context. Thus, crime exists because it underlies behavior that reflects the possibility of creating differential reproductive success in the competition for resources and mates.

This begs the question for some people not familiar with deploying an evolutionary lens of why everyone is not a murderous, cheating, thieving, and raping despot? Setting aside the fact that some humans who accumulated enormous and unconstrained power in history fit this bill (e.g., Genghis Khan, Ivan the Terrible), selection pressures have also abounded that shape prosocial, moral, and cooperative traits and features into the human mind. This is why we spent time discussing why crime and the law reflect moral impulses and intuitions. There is something about humans and other social species that demonstrate the survival and reproductive benefits of engaging in prosocial, empathic, and moral thoughts, emotions, and behaviors (de Waal 2008). It is not sufficient to conceive of competition for resources as a prerequisite to optimizing organisms for conflictual and individualistic thoughts, emotions, and behaviors. The benefits for survival and reproduction of engaging in more cooperative acts and forming cooperative networks must be immense; otherwise, they would not have come to structure human societies the way they have, giving rise to codes of conduct, legal systems, and morality (Haidt 2001). Cooperative thoughts, emotions, and behaviors facilitated by our moral

impulses have created a more *sustainable* way to survive and reproduce across generations. Thus, while competitively selfish individuals may benefit immediately and over one generation, this may not be sustainable multi-generationally, making the execution of such selfish and often “criminal” conduct more context-specific and responsive to certain cues in the environment (more on this in later sections; e.g., Mishra and Lalumière 2008). Thus, when cooperating, competition for survival as a group of individuals and as a species can warrant engaging in selfless acts promoting the well-being of the group over the individual. In acting selfless, one may also enhance their own reproductive success in gaining respect, status, and mates.

Especially in contexts where biological kin are prevalent as would have been the case in ancestral environments, selfless acts are often not fully selfless; instead, they reflect investing in reproductive success of closely related kin, suggesting a need to consider inclusive fitness as opposed to individual fitness (Hamilton 1964). Crimes in modern society, illustrated by the example of homicide, illustrate this kin-biased tendency. Estimates suggest around 6% of homicides in the United States involve biologically related victim-offender relationships, with the vast majority involving non-related individuals and a lesser amount involving spouses or friends who are also not related (Daly and Wilson 1988). For infanticide specifically, the risk increases approximately 100-fold when a stepparent is present than when the biological parents are present. These data illustrate the importance of using an evolutionary framework when examining criminal cases for a deeper, fuller explanation of crime and how to respond to it.

Criminological Problems and Evolutionary Principles: The Elusive Cases of Sex and Age

Why are men across cultures responsible for most of the violent, sexual, and even “petty” crime in societies (e.g., Krug et al. 2002)? Why does risk for criminal activity increase after puberty and decline thereafter? These two often-taken-for-granted demographic variables – sex and age – are some of the strongest and most reliable

predictors of engagement with crime (Hagan and Daigle 2018). Existing criminological theories have difficulty explaining the strength and reliability of either of these two variables’ prediction of crime, let alone providing a theory that accounts for and explains both variables’ involvement (Durrant and Ward 2015). Evolutionary principles, however, easily enable a conceptual understanding of both how and why sex and age should predict involvement in crime and, in addition to this, the types of crimes individuals at different levels of those variables are likely to commit (e.g., females vs. males, early adolescents vs. young adults). Evolutionary theory provides this conceptual understanding by examining three interrelated foundational principles that reveal its unique competence in explaining the involvement of sex and age in predicting crime.

The first evolutionary principle is *parental investment asymmetry* (Trivers 1972). The asymmetry here refers to the inherent differences that females and males as potential and actual parents exhibit in the ways they can invest in their offspring. Focusing on humans and other mammals, females are uniquely responsible for gestation, placentation, and lactation; even if males wanted to help with sharing the responsibility for ensuring these needs are met, they could only ever do so from a distance and in providing support for the female to do so (Hewlett and Macfarlan 2010). Males, on the other hand, are more likely to provide parental investment uniquely through acquiring food and other resources and ensuring security against predators and other threats (e.g., from other groups). Fathers, and other sources of social support, are also obviously likely to provide extended care of offspring, especially as children become more mobile and dependent on other sources of food besides breast milk (Hewlett and Macfarlan 2010). To illustrate the profound need of each sex to specialize in raising offspring, just imagine a mother of newborn twins in a foraging society faced with the task of breastfeeding both infants, maintaining social relationships, and gathering sources of food but *also* pressed with the task of finding high-calorie and high-protein food (e.g., hunting) and maintaining land and securing it against potential invaders and

predators. Or imagine a father of a newborn in a similar context whose partner passed away in childbirth. How will the child survive if they cannot yet eat solid food and he has no source of providing breast milk? These mental exercises demonstrate the need of both sexes working in concert on differentiated tasks to raise healthy offspring in the foraging environments of our ancestors (Friedl 1978).

This asymmetry articulates parental investment theory, and as this system reaches an evolutionary equilibrium (i.e., the evolution of mammalian strategies of gene replication), selection pressures would build and maintain this equilibrium. This is all to say that, evolutionarily, it is expected that males and females will be interested by and competent at different tasks, not absolutely but relatively. Criminal activity through this principle should differ based on sex and age. Younger mothers with less certainty about resource procurement and social support should be expected to engage in infanticide at a higher rate if they perceive they will not be able to raise the infant to reproductive age, a finding supported by research (Daly and Wilson 1988; Hrdy 1999). Young men who are not yet fathers are expected to engage in the highest-risk behavior in efforts to demonstrate usefulness and competence to climb the hierarchy of their male peers and appeal to putative opposite sex partners who may become the mothers of their children. This is also borne out in research, with young and unmarried men representing the highest-risk group for committing homicide (Daly and Wilson 1988) and other crimes (Krug et al. 2002).

The second evolutionary principle informing sex and age demographics in crime follows intimately from the first principle. The second principle, *reproductive success-from-multiple mates*, is that there is a reproductive limit imposed on females in mating with multiple partners that is *not* experienced by males (Bateman 1948). Putting aside morality, sustainability, or other constraints imposed upon humans, one man could impregnate many women within a relatively short time span. The same is not true if the women in this scenario had multiple men to

mate with. Women, even if they have multiple male sex partners, will become impregnated during *only one* of those matings, and any matings thereafter would not add to her reproductive success in a straightforward and reliable manner (cf. Hewlett and Macfarlan 2010; Hrdy 1999). This reality imposes selection pressures on the thoughts, emotions, and behaviors of males to be more likely to consider or pursue casual and multiple sexual partners that is not comparably found in females. In this framework, males should be more preoccupied with and engage in casual sex because it was more likely (but not definite) to enhance at least some ancestral males' reproductive success (Daly and Wilson 1988).

How does this second principle influence sex and age demographics involved in crime? Based on this principle, males are expected to engage in riskier, more impulsive, and more sexual thoughts, emotions, and behaviors. This could facilitate the engagement in extra sexual relationships that otherwise would not be acquired; the costs associated with risky and impulsive tendencies is offset by the potential reproductive benefits in males that is not the case for females. Thus, behaviors that involve risk and impulsivity such as showing off in dangerous situations, adventuring to unknown areas, and willingness to engage in anonymous sex are more common in men (Mishra and Lalumière 2008). These noncriminal but "deviant" actions reflect a sex-biased tendency to engage in criminal actions as well, including violent altercations, sexual harassment and assault, and homicide (Daly and Wilson 1988). Thus, the same tendency that may make men reduce their threshold for risky and impulsive actions because of their potential reproductive payoff may form the base for their over-involvement in crimes as well, helping to explain why men and not women are committing most crimes and especially sexual and violent crimes.

The third evolutionary principle of explaining sex and age demographics in crime is *reproductive variance asymmetry*. This principle relies on and follows from the first two principles and states that because women can spend lengths of time caring for existing and not producing new

offspring and men can father multiple offspring with different women, there is a greater likelihood that some men may not reproduce at all while others may reproduce an inordinate amount (Daly and Wilson 1988). This observation of greater variance in reproductive success should be less stark for women because they will have both many potential male partners interested in them and will not experience the same reproductive benefits in seeking out multiple partners (Bateman 1948). This principle observes that men who acquire more resources, dominance, and influence socially may translate their social and cultural capital into having many sexual partners, which subsequently enhances their reproductive success while making other men lose out. This is supported in foraging societies (e.g., Chagnon 2013) and in acute historical examples such as the life of Genghis Khan. Men in these and many other societies left no offspring in the next generation because one or a few men were reproducing with more of the women than a one-to-one ratio would suggest. This observation identifies a hidden anxiety that may structure the reproductive efforts of men, especially when environmental cues suggest the variance in reproductive success is skewed in favor of a few men (Daly and Wilson 1988).

This hidden anxiety and the evolutionary principle fueling it may be powerfully positioned to comprehend both the sex and age disparities in the commission of crime. Why do boys and young men seem so motivated to compete? Why does this competition often fuel violence, abuse, and even fatalities? If the stakes are, or could be, as high as being among the few who reproduce compared to the many who do not, then competition to be among the few could become fierce. Methods to be counted among the few may be stretched beyond “appropriate” limits – stealing to acquire resources, killing to gain status as a fierce fighter, and sexually coercing a woman against her will. As a male reaches puberty and is entering the reproductive pool, this competitive edge and feeling the hidden anxiety of male reproductive variance begin, explaining the age-crime curve that positions adolescent and young men as the most criminal. The important thing to consider with this

principle is that it is the *perception* of boys and young men growing up that can fuel this competitive mentality. If they perceive their environment as competitive where few males are succeeding and most are failing, this may be enough to orient them toward thoughts, emotions, and behaviors that facilitate or at least permit the illegitimate use of criminal conduct. This is why an evolutionary explanation is useful to criminology: it offers a conceptualization useful for formulating social policy that reduces the likelihood of crime by working *with* the desires of youth and, in this case, how to reduce the instance of young men committing criminal acts (see Durrant and Ward 2012; Walsh and Jorgensen 2018).

These three evolutionary principles – parental investment asymmetry, reproductive success-from-multiple mates, and reproductive variance asymmetry – provide a powerful framework for understanding the tendency of sex and age to be predictive of crime across societies. Appreciating not just *that* these variables are predictive but *why* they are as well requires a deeper explanation than what is currently on offer from criminological theories (see section on “[Current Perspectives of Criminology](#)”; Durrant and Ward 2015). An evolutionary perspective adds complementary, and not necessarily competitive, explanation to existing criminological theories and concepts (e.g., Durrant and Ward 2012). We will now turn to more fully articulated evolutionary models that have treated criminological issues as their central focus.

Evolutionary Models of Criminology

The two most prominent models in constructing an evolutionary argument of the problems of crime are life history theory (LHT; for a thorough review, see Del Giudice et al. 2016) and evolutionary neuroandrogenic theory (ENA; Ellis 2005; Ellis and Hoskin 2015). These theories are not mutually exclusive and have more similarities than differences. LHT and ENA are presented so that readers may get a different flavor for how evolutionary theory and its principles can guide research in criminology.

Life History Theory

A unique and fundamental observation made by LHT is that organisms make trade-offs during development in the different areas of growth, maintenance, and reproduction (Del Giudice et al. 2016). This observation brings to light that investment in some areas can preclude investment in other areas, particularly when resources and energy are scarce. Because our ancestral environments (and many modern environments) would have had long periods of resource and energy scarcity (e.g., Tooby and Cosmides 1992), evolution has likely instilled environmentally contingent strategies in organisms that vary the level of investment in these areas of development, leading to manifesting the capacity for what can be called different life history strategies. Fundamental trade-offs that organisms make include assessing current versus future reproduction, quality versus quantity of offspring, and parenting versus mating effort (Del Giudice et al. 2016). The resulting investment is considered an individual's life history strategy, and this strategy represents the embodied capital that an individual has, with the notion of "capital" implying currency in the capacity for survival and reproduction.

LHT proposes that organisms are fashioned within their genetic endowment to respond *flexibly* to their environments depending on different salient and recurrent environmental cues. This flexible responding allows organisms that have faced variable environments over the course of generations to have multiple pathways to ensure reproductive success. Or, different environmental pressures throughout a species history have led to different gene-environment adaptations (and the thoughts, emotions, and behaviors they produce) that facilitated reproductive success. LHT argues that the predecessors of these ancestral organisms have inherited a repertoire of adaptations that are "unlocked" and expressed when similar environments are faced by this new generation that shares this genetic endowment. From this perspective, LHT claims that evolution has "done the thinking" for organisms and provides them with different

developmental pathways that respond to environmental variability to optimize trade-offs in facilitating reproductive success (Del Giudice et al. 2016).

An LHT perspective conceptualizes engaging in criminal and antisocial conduct as representing a strategy that leans toward investment in current reproduction (not future), quantity of offspring (not quality), and mating effort (not parenting) (Wiebe 2012). In this model, investing in specific cognitive, emotional, and behavioral strategies that themselves may not constitute criminal conduct (e.g., anger, impulsivity, future discounting) may lead to increasing the risk of engagement in crime. Strategies that mark more crime-risk calibrations are described as *faster* life history strategies, whereas less crime-risk calibrations are *slower* life history strategies (Boutwell et al. 2015). The environment is a key component in this theory. LHT suggests that children (and even prenatal fetuses) are constantly monitoring their environments for cues that help them make optimal developmental decisions to ensure their survival and reproductive success. Environmental cues that signal unpredictability, harshness, and social competition are proposed to orient development toward more crime-risk life history strategies, making these types of environments important for criminologists to understand. Because of these concerns, LHT is similar to other criminological theories such as strain theory (Durrant and Ward 2012). LHT is one evolutionary framework that provides a unifying understanding of many variables that predict crime including sex, age, race, and socioeconomic status (Boutwell et al. 2015).

Evolutionary Neuroandrogenic Theory

ENA focuses on and provides an explanation of both the *how* proximate mechanisms associated with criminal correlates and *why* such correlates should exist (Ellis 2005). The *why* part of ENA encapsulates the evolutionary component, and the *how* part constitutes the neuroandrogenic component. The two components of ENA are intimately connected and conceptually represent a single

underlying construct formulated at different levels of analysis (Durrant and Ward 2012). The theory makes use of the concept of competitive/victimizing behavior, which describes a continuum of competitive actions that can vary on their risk or chances of victimizing another individual (Ellis and Hoskin 2015). Actions that are competitive but do not have a victim (e.g., competitive sports, games) are not considered criminalized behaviors, but competitive actions with victims are considered criminalized (e.g., sexual assault, theft). It is no surprise that these actions with victims tend to have consequences for survival and reproductive success of both perpetrator and victim.

The evolutionary component of ENA makes use of female mate choice to assist with explaining why competitive/victimizing behavior should exist in the first place and particularly in men. Connecting back to parental investment theory (Trivers 1972), ENA proposes that females have preferred and thus selected for males throughout humans' evolutionary history to be loyal resource provisioners for the successful raising of offspring. This idea suggests that ancestral females would have been more likely to mate with males who were proficient at provisioning resources for her and her offspring, making traits that facilitate resource provisioning more and more common in males. Some of these traits would include competitiveness, status-seeking, and hunting skills, of which men across cultures tend to manifest more than women (Ellis and Hoskin 2015). Along with this observation for more resource provisioning skills in men is the accompanying selection pressure for men to fake these skills and rely on deception to mate and, if deception fails, to potentially resort to coercion. Thus, ENA provides a framework for understanding why the patterns of crime exist and why men tend to exhibit characteristics that make them more likely to be counted among the criminals. How these characteristics get formed is the concern of the other component of ENA.

The neuroandrogenic component of ENA suggests that the way this differentiation of the sexes occurs is through masculinization of the brain and

body through androgen hormones, particularly testosterone (Ellis 2005). This component clarifies that in order for a male reproductive strategy to manifest, changes need to occur in the neural structures governing behavior, which can then facilitate more male-biased strategies. These are proposed to be (1) suboptimal arousal and (2) rightward shift in cortical functioning. These two proximal explanations of making a brain more male-like constitute a higher risk of engaging in competitive/victimizing behavior, since these mechanisms facilitate analgesic (pain-reducing), anxiolytic (anxiety-reducing), and emotion-attenuating functions (Ellis and Hoskin 2015).

ENA provides an explanation of why crime, as behavior that is competitive and victimizing, is more common in men than women and why age, particularly the onset of puberty in boys, predicts crime to such a great extent. With the relative enormous surge in testosterone at puberty in boys compared to girls, ENA clearly conceptualizes why crime increases after this age in boys and young men while also accounting for why this hormone-behavior link should occur to begin with. In other words, the link emerged because of selection pressures for the resource provisioning skills required and desired by females in the ancestral past to ensure the health and survival of their offspring.

Variations in Criminal Justice Systems

In this final section, we want to explore how evolutionary approaches can support alternative forms of justice. Just as criminology has developed, so too has the criminal justice system. While moral impulses and intuitions are expected to structure and guide the formulation and response to crime, humans also have a vast capacity to cognitively rationalize and reason which can impart substantial influence on moral judgments (e.g., Haidt 2001). To illustrate this difference in criminal justice system approaches, we will describe two systems that have different

underlying assumptions about “human nature” and that have influenced how crime and responses to crime are conceived. The first is the current dominant approach in much of the world, a rational-based retributivist and rehabilitative approach, while the second is more prevalent in indigenous communities and likely governed the behavior of much of human history, a relational honor-based system based on reparation (Little Bear 2000; Sommers 2018). We do not intend to treat these systems as oppositional or polarized nor to claim they are the only two possibilities but merely to explore alternative systems for crime and its regulation. Many modern jurisdictions have developed structures that blend these two approaches to justice (for a longer discussion of these systems, see Sommers 2018).

Much of the Anglo-American criminal justice system has developed based on the retributivist principles first introduced by classical theorists (such as Jeremy Bentham). That is, when an offense has been committed, the state is responsible for assessing culpability and imposing a fitting punishment. Once the punishment had been served, justice had been served (Wenzel et al. 2008). Wenzel and colleagues (2008) identified that there were two goals of punishment (1) deterrence, to prevent the likelihood of future offenses, and (2) retribution, a proportionate and just response to reduce the benefits associated with committing crime. Alternatively, another goal of the criminal justice system is rehabilitation of the offender, that is, to address the individual factors associated with the offense to be able to reintegrate the offender back into society (Wenzel et al. 2008). Durrant and Ward (2015) noted that from an evolutionary perspective, “we have evolved a set of motivational and emotional characteristics that, taken together, constitute a sense of justice and guide our decision-making when we encounter situations where individuals have violated moral and social norms” (p. 111). They also noted that people tend to be naturally motivated to punish others who violate group norms in retribution; however, as Walsh (2000) noted, a strict tit-for-tat strategy that is unforgiving once cheated may not garner the same benefits that occasional or situational forgiveness would permit. He

suggested that while tit-for-tat was effective in smaller groups, the addition of punishment is more effective in larger groups.

In contrast to these rational-based systems and their measures of correction, relational honor-based systems may constitute a primordial conceptualization of crime and its regulation, possibly tracing its origins to some of the first foraging societies and many modern indigenous communities (e.g., Little Bear 2000). This approach assumes that human nature is inherently relational and that people are seen as intimate extensions of their social group; the social group is the person, and the person is their social group. Following from these assumptions is that people have an inherent responsibility toward their society and are thus expected to make reparations when infractions against others within the society have been committed. These infractions (or crimes) are seen as relational injustices, and so they require a relational approach when formulating a model for correction and/or punishment.

In recent years, criminologists have started to pay attention to other models of justice that reflect an honor-based system, such as restorative justice. While scholars and advocates continue to debate whether this model of justice represents an alternative or addendum to the current criminal justice system, several legislations have started to incorporate restorative justice principles in their legislation (e.g., the Youth Criminal Justice Act in Canada) (White et al. 2018). Scholars of restorative justice (e.g., Zehr and Mika 1998) have outlined three key tenets of restorative justice: recognition that the offense does not only affect the victim and the offender but also members of the community; recognition that the offender has obligations and liabilities to the community as a result of their actions; and finally, recognition that the process promotes community empowerment and healing.

In restorative justice models, the focus is on reparation – repairing the relationship between the offender, the victim, and the community (Wenzel et al. 2008). While punishment can be part of the restorative justice, it is not the focus of the process. Braithwaite (1989; as cited in Walsh

2000) suggested that a critical process in restorative justice is *reintegrative shaming*, which communicates social disapproval and also provides an opportunity for the offender to make amends and remain a welcomed member of the community. Walsh (2000) suggested that this is akin to the tit-for-tat with forgiveness model, which highlights the importance of forgiveness since they can “transform a pattern of mutual cheating by not remaining permanently punitive but instead by cooperating, even when the other strategy cheats” (p. 857). That is, everyone (victim, offender, and community) benefit from forgiveness and the processes of restorative justice, and the risk of losing a valuable contributor that may help to secure survival is decreased. It is interesting that restorative justice models have been integrated into legislation targeting youth. Walsh (2000) identified that a strict tit-for-tat strategy with youth would be detrimental, especially given adolescence represents a period in which there is a discrepancy between skill and biology.

Conclusion

Criminology is an interdisciplinary study of crime, and the responses to crime have generated a wealth of knowledge surrounding the commission of crime, its predictors, social situations that elicit it, and many other topics. Its inherently interdisciplinary focus makes criminology a prime study for integrating an evolutionary framework governing human behavior into the realm of its focus. Equipped with the wisdom of time in producing and reproducing thoughts, emotions, and behaviors related to crime, evolutionary perspectives provide a complementary approach to expanding the scope of explanation afforded to criminologists.

Cross-References

- Criminal Personality Variables
- Criminals Are Made Not Born
- Evolutionary Forensic Psychology

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Crisis in Sociology

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Synonyms

Evolutionary sociology; Evolutionary thinking in sociology; Relationship of evolutionary behavioral sciences and social sciences

Definition

Crisis in Sociology is the title of a book written by sociologists Joseph Lopreato and Timothy Crippen. It was published in 1999 and demands a stronger consideration of evolutionary thought in the discipline of sociology.

Introduction

In 1859 Charles Darwin laid the foundation of modern evolutionary disciplines and thereby changed the way we thought about the position of our own species and its history. About 100 years later, the works of Richard D. Alexander, Richard Dawkins, Robert Trivers, George C. Williams, Edward O. Wilson, and others began to change also the way we think about our social behavior and social evolution, which were the main subjects of traditional social sciences like sociology up to that time. At the latest when Wilson published his book *Sociobiology: The New Synthesis* in 1975, a more or less adversarial debate arose (a) among evolutionary biologists, (b) between sociologists and evolutionists, and (c) most relevant for this entry, within sociology itself. The rise of new evolutionary disciplines like *sociobiology* in the 1970s or *evolutionary psychology* in the 1990s and their explanatory power when it comes to human social behavior represented a challenge for areas of sociology and their representatives.

Crisis in Sociology was neither the first publication from within sociology that calls for evolutionary thinking in the discipline nor is it the last. However already the book's title makes it stand out a bit from other likewise important and profound publications. Its title perfectly reflects the state of sociology (as early evolutionary sociologists would say) in the advent of modern evolutionary disciplines like sociobiology or evolutionary psychology. Out of the many relevant sociological publications on this topic, a few (due to the limits of this brief entry) will be presented subsequently.

The Debate Within Sociology

In the first years following 1975, the debate within sociology began. Van den Berghe, for decades one of the most vehement advocates of an integration of evolutionary insights into sociology, published an evolutionary informed sociology textbook as early as 1975. More than 40 years ago, he already discussed topics still highly relevant in today's sociology, like human families, inequality, politics, economics, religion, etc. from an evolutionary point of view. But most sociologists seemed to be reluctant to see the bigger picture at those times, so Ellis (1977) felt the need to publish a hypothetical paper about the decline of sociology between the years 1975 and 2000. Arguably an early wakening call towards sociologists before their discipline will possibly be absorbed by sociobiology. Ellis (1977, pp. 60–61) also provided his readers a comprehensive outline of evidence for evolutionary influences on diverse forms of human social behavior from the past two decades, such as aggression, altruism, cooperation, pair bonding, care for offspring, etc.

Moving forward almost 20 years to the 1990s, the situation doesn't seem to have changed. While new evolutionary disciplines besides sociobiology have emerged, especially evolutionary psychology, the debate within sociology was still the same. Nielsen (1994) gave another introduction to sociobiology and a review of its findings for sociologists, and shortly afterwards Ellis (1996)

predicts a bleak outlook for sociology if the discipline continues to refuse the biological factor. Ellis (1996) attributed sociologists "biophobia" to four causes, namely, semantic factors, a lack of training in biology, an exclusive focus on humans, and moral or political factors (p. 24). Most notably, he provides an extensive amount of literature sources and an overview of work already done by (who we today may call) evolutionary sociologists within the past two decades (p. 26–27).

In 1999 Lopreato and Crippen published *Crisis in Sociology*. They claimed to be "proud but concerned sociologists" (p. xi). The book was written out of the deep concern that sociology may not be able any more to meet real-world problems and should finally participate in the evolutionary revolution or otherwise will lead itself to "academic self-destruction" (p. xi) and get cannibalized by more up-to-date disciplines. Lopreato and Crippen granted sociology some more 25 years (cf. Ellis 1977) before it "risks deletion from the academia" (1999, p. xii) in case it will not pick up on modern evolutionary behavioral science. A few years later, Freese et al. (2003) gave an introduction to current disciplines like evolutionary psychology and behavioral genetics for their sociological audience. Then Machalek and Martin (2004) recognized the emergence of *evolutionary sociology*. But even though three decades of debate within sociology had passed and evolutionary disciplines made great progress in those years, both papers still had to discuss and dismantle misconceptions or misbeliefs like genetic determinism, etc.

In 2006 Barkow edited a book about *Darwinism for Social Scientists* with chapters from major social scientists, psychologists, and anthropologists, among them Ullica Segerstrale, whose work on the sociobiology controversy got famous. In its introduction, Barkow (2006) recommends that social scientists finally "come to grips with Darwin" (p. 44). By using the metaphor "sometimes the bus does wait" (p. 3), he shows some optimism that it is not too late for social scientists to integrate evolutionary thought, admittedly not in an unreflecting manner but critically and seriously. Another decade passed, and

Horowitz et al. (2014) published their investigation of 155 sociological theorists' thoughts about evolutionary biology. Their survey data clearly revealed the picture of sociology as a still divided discipline. For example, 40% of respondents found evolutionary explanations of male violent crime implausible (Horowitz et al. 2014, p. 498). Even higher rates of attributed implausibility of evolutionary explanations were found for male pornography use (50%) or virginity (53%). On the other hand, the highest plausibility of evolutionary explanations among their respondents was found for the taste for fats or sugars (60%). As others before, Horowitz et al. (2014) concluded that sociologists' acceptance or refusal of evolutionary explanations is significantly due to political reasons and worldviews.

The Need for Darwin

Sociology has met several crises in its long history – political, theoretical, and methodological ones. Lopreato's and Crippen's (1999) book *Crisis in Sociology* attempts to solve the recent crisis by integrating evolutionary theory into sociological theorizing and research. Both authors at that time already had a long record of publications which pursued the same objective. Their 1999 book received mixed reviews in sociological journals. A very positive one came from Badcock (2000) who obviously appreciated Lopreato's and Crippen's approach of overcoming sociology's crisis by picking up on evolutionary thought. *Crisis in Sociology* is structured in three main parts, each of which is divided into three (part one), two (part two), and four (part three) chapters.

Part one gives an overview of sociology's history from the early classics to the crisis of modern sociology. As students of sociology learn in introductory courses, sociology itself emerged out of crises. Changes in society and economy in the eighteenth and nineteenth century (industrialization, urbanization, societal conflicts, political turmoil, etc.) required a discipline to

understand those new challenges and maybe help to solve some issues. Chapter ("The Early Promise") of the book deals with some of those classical scholars of sociology, among them Auguste Comte, Karl Marx, Émile Durkheim, and Max Weber. All of them were great theorists who analyzed societal phenomena at their time. As Lopreato and Crippen criticize, they are rarely fully read and understood today. In principle such sketchy treatment of sociological theories may be one reason for modern sociology's crises. Chapters ("The Deepening Crisis") and ("Why the Crisis: A Sketch") are discussing the crisis in sociology as well as their reasons. Although there were great theorists like Robert K. Merton or Talcott Parsons in the twentieth century, sociology in general suffers on the one hand from still assuming that human behavior is solely due to socialization and on the other hand increasingly from its fragmentation, it is postmodern orientation, its mediocrity, and from overstated political correctness. While some sociologists may call that intellectual diversity and regard it as an advantage, Lopreato and Crippen may not.

Part two of the book presents an introduction to evolutionary theory (Charles Darwin: Theory of Natural Selection) through discussing natural and sexual selection and then gives an overview of key concepts like kin selection, fitness, altruism, parental investment, as well as a brief portrayal of the sociobiology controversy and the later debate between sociobiologists and evolutionary psychologists. Part two is especially helpful, since the book is written for a sociological audience and provides the relevant information in an accessible way. Finally part three may be considered to be the core of *Crisis in Sociology*. In its four chapters, the authors familiarize their audience with thinking evolutionary about well-known and utterly relevant sociological topics. Chapter (Sex Differences in Same-Sex Aggression) deals with sex differences, mating strategies, family structures, parenting, division of labor between the sexes, etc. Sociologists should become aware that there are biological influences to male and female behaviors and

strategies. Of course not a single evolutionist would deny that always both, genetic and environmental influences, interact. Genetic determinism is not what evolutionary behavioral science is suggesting – but often sociologists wrongly assume exactly that.

Chapter (“Fundamentals of Social Stratification”) discusses social stratification (a topic relevant to sociology at all times in its history). Drawing on primate dominance orders and human sexual selection, Lopreato and Crippen try to broaden sociological thinking and understanding of this phenomenon which has indeed always existed despite numerous attempts to mitigate it. The last chapter 9 is entitled “The Clannish Brain” and illustrates how ethnic conflicts – or more generally speaking, in-group versus out-group conflicts – happen and persist. Understanding that our species lived in small groups for the longest time in its history and that kin selection and altruistic behavior as well as in-group favoritism were relevant aspects may lead to a deeper grasp of such conflicts in today’s globalized and anonymous society. Needless to say that insight is relevant for solving real-world problems – what sociology certainly strives for. It is true for the last four chapters that the authors almost always try to integrate sociological and evolutionary views on those topics.

When reading the book, one clearly gets the impression that Lopreato and Crippen were sociologists, are sociologists, and will remain sociologists. They neither aim to reduce sociology to biology nor do they intend any dissolution of their discipline by completely shifting to any of those new evolutionary sciences. The authors instead obviously want to enrich their own discipline with evolutionary theory and insights from those disciplines so that sociology will remain a relevant and up-to-date social science. From the first sentence to the last one, the book is written with hope, profundity, and eloquence. One will hardly find a lot of books covering sociological and evolutionary knowledge and insight in such profundity in one place.

Conclusion

What better conclusion to give than Badcock’s final statement in his review of *Crisis in Sociology*: “By any standards, this is an outstanding and timely book, superbly written, faultlessly argued and unsurpassably well-informed. Sociology will ignore it at its peril, but whether Lopreato and Crippen will be able to do anything to resolve the crisis remains to be seen. Failure, however, will not be their fault.” (Badcock 2000, p. 600).

Cross-References

- Biosociology
- E. O. Wilson
- Sociobiology Wars, The
- Standard Social Science Model

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Critical Period

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Synonyms

Crucial time; Sensitive period

Definition

A maturational stage during the lifespan of an organism in which the organism's nervous system is especially sensitive to certain environmental stimuli. The organism is more sensitive to environmental stimulation during a critical period than at other times during its life.

Introduction

The phenomenon of critical period was first described by William James (1899) as “the transitoriness of instincts.” The term “critical period” was proposed by the Austrian ecologist based on his observations that newly hatched poultries, such as chicks and geese, would follow the object, usually their mother, if exposed to within a certain short time after birth.

According to Lorenz, if the young animal was not exposed to the particular stimulus during the “critical period” to learn a given skill or trait, it would become extremely struggling to develop particular behavioral pattern in the later life.

A vast of existing literature has identified the existence of critical period in vision, hearing, and auditory processing. Quite a lot of early interventions have been carried out to provide more beneficial environmental stimuli for early children.

Critical Period and Language Development

The critical period hypothesis, as a long-standing debate in linguistics and language acquisition, briefly states that the ability to acquire language is biologically linked to chronological age. According to CPH, the first few years of life are the critical period for an individual to acquire language. If not being exposed to the language during the critical period, the individual will never master the language fluently, especially the grammatical knowledge.

The evidence for the CPH is still limited. The support stemmed largely from theoretical arguments and analogies to other critical periods in biology, such as vision and hearing development. The existing literature is controversial on the nature of critical period in both first and second language acquisition. Though some research (Friedmann and Rusou 2015) supported the existence of the critical period in language acquisition, other literature (Vanhove 2013) still disputed this viewpoint. In addition, the duration of the period also varies greatly in different literatures.

Based on three central assumptions, Hurford (1991) proposed an evolutionary model of language acquisition in order to provide evidence for the evolutionary functionality of the critical period. Hurford believed language acquisition was an adaptation, which had a survival value for humans and was favored by natural selection. He indicated that knowing a language correlated positively with an individual's reproductive advantage. Because the experiment revealed no evolutionary advantage of acquiring more than one language, Hurford proposed the critical period has been evolved simply as a result of the lack of selection pressure. Hurford's research supported the existence of the critical period in language acquisition and pointed out it would end around the puberty.

Life History Theory and Critical Period

Quite a lot of research indicates the first few years of life were a critical period for children's social

development. John Bowlby proposed from birth to 3 years constituted the sensitive period for the establishment of children's attachment style (Bowlby 1969) and the deprivation of maternal care in the first few years of life would produce irreversible harmful effects on individual's ability to establish close emotional bonds with others (Bowlby 1951).

Based on the Life History theory several studies demonstrated the first 5 years of life might be a sensitive period for the development of individual's life history strategies due to at this stage young child would be most vulnerable to the environmental influences. For example, one study (Simpson et al. 2012) proved exposure to environmental unpredictability during the first 5 years of life, but not a later stage from 6 to 16 years old, could predict individual's sexual and risky behaviors at age 23 most powerfully. Those experiencing more unpredictable, rapidly changing early environments tended to adopt a faster life history strategy at ages 23. Study (Belsky et al. 2012) also demonstrated that environmental unpredictability during the first 5 years of life could predict more sexual partners at age 15 than unpredictability occurring later in childhood or adolescence. Another recent longitudinal study (Doom et al. 2015) found exposure to early greater environmental unpredictability, such as changes in residence, cohabitation, and parental occupation, from 0 to 5 years independently predicted externalizing behaviors in both adolescence (directly) and early adulthood (indirectly).

In addition, Draper and Harpending (1982) pointed out father absence at the age from born to 5 years old could predict most powerfully male's aggression, competition, low paternal investment and derogation of females and femininity at adolescence, and predict female's fast reproductive strategies. They believed this stage constituted the critical period for receptivity to fathering. Consequently they stated the first 5 years of life could be regarded as a developmentally sensitive period for being shaped by the absence of father. Similarly (Ellis 2004) also stated that the critical period for girls' learning of reproductive strategies, such as the timing of

pubertal maturation and sexual behavior, would be the first 5 years of life.

As a result, researcher (Susman 2006) believed young children's neural systems during early sensitive periods could be influenced by the inconsistent and unpredictable environments. This kind of early experiences could shape and "prepare" individual's brain for dealing with the similar situations later in life (Ellis and Del Giudice 2014).

Conclusion

The existence of critical period has been extensively evidenced. Though being widely known the CRH is still facing much controversy in the existing literature. Based on Huford's evolutionary model of language acquisition it would be reasonable to explain the existence of critical period from an evolutionary psychology. In line with Life History theory the first 5 years of life constitutes the sensitive period for the development of life history strategies, during which young child is most vulnerable to the influence of environmental unpredictability. Female's reproductive strategies can be powerfully shaped by the father absence during the sensitive period of from birth to 5 years.

Cross-References

- ▶ Bilingualism
- ▶ Evolution of Mammalian Vision, The
- ▶ Imprinting
- ▶ Life History Theory
- ▶ Parental Investment and Sexual Selection

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Critical Period of Acquisition

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Synonyms

Second language acquisition; Multilingualism

Definition

A developmental time interval that is optimal for experience-induced neural plasticity; with respect to bilingualism, this refers to a window of time during which the neural representation of the language system is malleable to second language acquisition, similar to first language acquisition.

Introduction

We begin life with biological systems that support the ability to acquire human language. Speech perception and ultimately the acquisition of language has been shown to be influenced by multiple critical periods (CPs) that open and close at different time points during development (Werker and Hensch 2015). The discussion of the CP of acquisition, as it relates to bilingualism, entails defining what is meant by “acquisition,” as well as what is meant by a “critical period.” This entry will discuss bilingualism within the context of the CP model, and how this phenomenon can be understood from an evolutionary perspective.

Acquisition Versus Learning

Krashen (1982) made a distinction between *acquisition* and *learning*, thereby distinguishing two distinct modes of developing competence in a second language. The first way is language *acquisition*, which refers to a subconscious process whereby one is not consciously aware of the rules of the language they have acquired, but instead having a “feel” for correctness (e.g., grammatical sentences “sound” right, or “feel” right, and likewise, errors feel wrong, even if the rule violated is unknown). This is similar to the way children acquire their first language and can be thought of as implicit or procedural learning. The second way to develop competence in a second language is via language *learning* or conscious knowledge of a second language (e.g., knowing the rules and being aware of them). In this case language-based knowledge is integrated into an existing system, through conscious purposeful

endeavor with persistent efforts (e.g., memorization, active participation). This second mode can be thought of as “knowing about” a language with respect to its grammar or rules and is equivalent to explicit or declarative learning. This entry will apply Krashen’s acquisition-learning distinction when discussing the CPs of bilingual acquisition, which in turn points to the implicit or procedural acquiring of language during infancy, which is automatic and effortless. When discussing CP of bilingual acquisition, this entry will rely on the distinction between implicit and explicit knowledge of language, as acquisition of semantic knowledge, which is declarative knowledge rather than procedural/implicit, remains less stringently bound to the effects of CPs.

Definition of Critical Periods

The conceptual definition of a CP refers to a window of time, typically in early development, during which neural representation of a particular system is open to experience-induced plasticity. This is considered an optimal time for rewiring of neural circuitry on the basis of input from the environment via sensory experience. While environmental influences can have an impact on a particular system at time points outside of the CP, the impact will not be as profound, as the system may be more resistant to reorganization outside of this “critical” or “sensitive” period. CP can therefore be thought of a period of time during which experience, or lack thereof, can induce significant changes in wiring. Biological mechanisms of CPs involve molecular triggers which shift a neural circuit from an immature to plastic state, thereby initiating or opening the CP; likewise, there are molecular brakes on plasticity that initiate the consolidation of the neural circuit from a plastic to stable state, thereby closing the CP. However, these critical windows may not close completely, and can reopen via targeted genetic, pharmacological, or behavioral manipulations, thereby reinstating plasticity later in life and enabling learning throughout the life span. For a review of the specific processes that open CPs, mediate their operation, and close

(or reopen) them refer to Werker and Hensch (2015).

Critical Period of Bilingual Acquisition

The CPs of language acquisition can be interpreted as windows of time that support perceptual narrowing of the speech sounds of infants’ native language(s). *Perceptual narrowing* refers to a developmental process that improves perception for socially relevant information of native stimuli experienced in the environment over foreign or nonnative ones (e.g., Lewkowicz and Ghazanfar 2009). Enhanced sensitivity to frequently encountered and meaningful environmental input is achieved by strengthening the neural representations that underlie such perceptual discrimination (e.g., Werker and Tees 1984). Through this process, an infant’s perceptual abilities become specialized for aspects of their social environment that has adaptive significance, helping them become more adept members of their community. Perceptual narrowing for native compared to foreign stimuli occurs across a number of socially relevant domains (e.g., faces, voices, music, etc.), including language and its various aspects (e.g., vowel and consonant contrasts, tone languages, visual language, and sign language).

The languages of the world have different collection of speech sounds that are used to form words and contrast meaning. For instance, many native Japanese speakers have difficulty with perceiving and producing English /r/ and /l/ in words such as “rate” versus “late.” This contrast is challenging for many Japanese speakers, especially those who began learning English later in life, because unlike English, Japanese groups phonetic units /r/ and /l/ into the same phonetic category (Japanese/r/), thereby treating any acoustic difference between the units as irrelevant (for a review, see White et al. 2013). While adults have difficulty discriminating some speech sounds that are not used in their native language, studies have shown that young infants, up to a certain age, can perceive and discriminate many native and nonnative phonetic contrasts, even without prior listening experience (e.g., Werker and Tees 1984).

Infants' first year of life is marked by CPs that support perceptual narrowing of various aspects of language that shift their phonetic perception from language-universal to language-specific by maintaining sensitivity only to native contrasts, as perception of nonnative contrasts declines (e.g., Werker and Tees 1984). While the CP of some aspects of language (e.g., vocabulary learning) remain open across the lifespan, the degree and timing of neuroplasticity for phonology and syntax are thought to be highly sensitive to the age at which language input occurs (e.g., Werker and Tees 2005). For instance, while English-speaking adults have difficulty discriminating two different "d" sounds that are used to contrast meaning in Hindi but not in English; however, 6–8-month-old monolingual English infants were as proficient as adult native Hindi-speakers at discriminating these Hindi (nonnative) phonemic contrasts. In contrast, 10–12-month-old monolingual English infants no longer succeed in differentiating this contrast, whereas Hindi-learning infants maintain sensitivity (Werker and Tees 1984). Previous studies have shown that perceptual narrowing for consonant discrimination is seen between 8 and 10 months of age, whereby infants reliably discriminate both native and nonnative speech sound differences by 8 months of age, but by 10–12 months of age they have difficulty discriminating acoustically similar nonnative contrasts (for a review, see Maurer and Werker 2014). Likewise, narrowing effects have been shown for vowel discrimination, for discrimination of lexical tone, and for discrimination of hand signs that are used in sign languages (for recent reviews, see Werker and Hensch 2015; White et al. 2013). Thus, while the nervous system maintains discrimination sensitivity, even for nonnative and never-before-heard speech sounds until 10–12 months, it is after this period that marks the beginning of consolidation period and a gradual decline in plasticity.

Up to 10 months of age, infant perception of speech sounds is fairly plastic and easily changed by means of minor exposure; however, after this window of time, double the exposure is necessary to bring about the same amount of change – this may be indicative of solidification of native sound

categories and a gradual decline in plasticity (for a review, see Werker and Hensch 2015). After this time point, successful learning of a second language has been generally agreed to be highly sensitive to the age at which second language learning begins, such that late compared with early learning of a second language is associated with lower proficiency, even though some individuals may achieve native-like proficiency (White et al. 2013). The wide variation observed in second language proficiency in adult learners has been attributed to attainment not being limited to age of second language acquisition, as other individual difference factors (e.g., working memory, intelligence, aptitude, developmental disorders, affective states, and memory systems, as well as auditory perceptual, neurophysiological, neuroanatomical, potential genetic factors, and noncognitive and nonlinguistic factors, such as motivation and sociocultural factors) play a part in second language development after the closing of a CP (for a review, see Morgan-Short et al. 2014).

Conclusion

The abovementioned perceptual narrowing of socially meaningful environmental input by 12 months of age appears to shape linguistic abilities by catalyzing a shift in phonetic perception from language-universal to language-specific (i.e., a shift from multi- or bilingual acquisition to a monolingual one). This developmental process goes hand in hand with a decline in discriminating other nonnative and therefore socially irrelevant information (e.g., other-race faces; for a review, see Friendly et al. 2013). From an evolutionary perspective, fast and easy identification of group and species members, supported by perceptual narrowing, may have conferred safety and survival benefits, as it enables one to easily discern in-group versus out-group members in order to help inform decisions such as whether to approach or withdraw from a situation. Thus, the ability to prioritize the processing of socially relevant environmental input may have facilitated the development of

becoming a fully functioning member of one's group.

While perceptual narrowing of nonnative speech sounds, or CP of second language acquisition, appears to be largely accomplished by 10–12 months post-birth, the human brain remains highly capable of plasticity beyond this age. However, reinstating sensitivity to a nonnative speech sound (e.g., learning a second language) and initiating plasticity, or reopening a CP beyond its initial closure, requires additional factors such as conscious learning and effort. This is in contrast to the effortless first language acquisition observed in children, which is an astonishingly rapid process. This may allude that the age-sensitive cognitive process of acquiring another language, post-CP, may have not been selected for propagation. The reasons for why acquiring a second language may not have been selected for can also be understood in the context of our ancestors interactions with their environment.

Evidence from the environment of our nomadic ancestors suggest that while mastering a language early in life was a highly useful evolutionary adaptation, acquiring a second language later in life may have not been as adaptive or advantageous, and consequently not selected for (Hagen 2008). As Hagen (2008) describes, this evolutionary assumption is based on the environmental circumstance of our nomadic, hunting-and-gathering human ancestors, who represent the vast majority of our past. When anatomically modern *Homo sapiens* began migrating from Africa into the Eurasian continent around 120,000 BCE, their diaspora was exceedingly sparse, compared to modern standards, and populations that averaged about 150 members (considered an ideal approximate group number in order to maintain group manageability) splintered when groups became too large. Splintering over time led to loss of contact with the former group, prompting language drift, and eventually new languages – a path that ultimately gave birth to the diverse languages that evolved across the African, Eurasian, and later the American continents (Hagen 2008). Moreover, several population bottlenecks in our past and subsequent

dramatic drops in our populations, in addition to a nomadic lifestyle, may have contributed to lack of sustained intergroup contacts among our nomadic ancestors. Given that the life expectancy of our ancestors was about 35 years, and considering that a child requires 3–4 years of exposure to a language to reach fluency, it is difficult to imagine circumstances in which all adult members of various nomadic groups to have had access to 3–4 years of steady exposure to a second language in adulthood. The transition from a nomadic to an agricultural lifestyle may have enabled intercultural contacts; however, these contacts would have been brief at most, and may have been marked by competition and aggression, as early human groups had to compete with other groups for scarce resources. It may have been therefore required less effort to ward off intruders or conquer enemies, than it does to expend effort to learn to communicate with them by acquiring a second language in order to negotiate and reach agreements with intergroup members. Considering the very recent globally interconnected and multicultural development in our history, and longer lifespan, our species may be progressing toward another evolutionary adaptation that may favor bi- or multilingualism.

Cross-References

- ▶ [Bilingualism](#)
- ▶ [Immigrant Parents](#)
- ▶ [Language Acquisition](#)
- ▶ [Language Acquisition in Infants and Toddlers](#)
- ▶ [Language Development](#)
- ▶ [Pinker's \(1994\) The Language Instinct](#)
- ▶ [Steven Pinker and Language Development](#)

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Criticisms of Darwin's Work on Natural Selection

► Gaps in Darwin's Initial Theory

Crocodilian Bait Hunting

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Synonyms

Crocodilians using hunting tools; Crocodilians using lures

Definition

Crocodilian bait hunting refers to crocodilians (crocodiles and alligators) using various lures to attract their prey.

Introduction

Use of objects as hunting lures is very rare among animals. Until recently it has been known only in captive capuchin monkeys, a few bird species, and one insect (Shumaker et al. 2011). There were a few observations of saltwater crocodiles (*Crocodylus porosus*) using fish prey leftovers as bait for birds (Shumaker et al. 2011) and of Orinoco crocodile (*C. intermedius*) using prey leftovers as bait for vultures (Dinets 2013), but in these cases it was unclear if baiting was intentional or accidental.

Dinets et al. (2013) found that at least two species of crocodilians use small sticks to attract and catch birds.

Mugger crocodiles (*C. palustris*) in India and American alligators (*Alligator mississippiensis*) in Florida were observed floating with sticks positioned across their snouts in pools where large numbers of egrets and other wading birds nested in trees (Fig. 1). Egrets that tried to pick up the sticks were caught and eaten.

Further observations in Louisiana found that alligators displayed this behavior predominantly



Crocodilian Bait Hunting, Fig. 1 A well-camouflaged mugger crocodile uses sticks on its snout to attract a bird looking for nesting material

in the vicinity of egret colonies and did so almost exclusively at the time of year when the egrets were building their nests and were actively looking for building material.

So far, this discovery is the only known case of reptiles using tools. It is unknown what stimulates stick-displaying behavior at particular locations and at particular times of year. The crocodilians might be reacting to large numbers of wading birds flying low over water, to the sounds made by courting birds, or to some other environmental clue. It is also unknown whether this hunting technique is an innate ability or a skill learned by observation. Hunting with sticks as lures by American alligators was probably more effective in the past, before the plume-hunting era of 1870–1910, when the numbers of wading birds in their range were much higher than today and huge egret colonies stretched for many miles (McIver 2003).

Conclusion

Using tools is just one of many complex behaviors recently discovered in crocodilians. Historically viewed as lethargic and dumb, crocodilians are now known to exhibit flexible multimodal signaling, advanced parental care, and highly coordinated group hunting tactics (Doody et al. 2013), as well as in various kinds of play behavior (Dinets 2015). These discoveries are interesting not just because they show how easy it is to underestimate the intelligence of even relatively familiar animals but also because crocodilians are a sister taxon of dinosaurs and flying reptiles; the behavioral complexity found in birds and crocodilians suggests that the behavior of non-avian dinosaurs and pterosaurs was most likely very complex as well (Dinets et al. 2013).

Cross-References

- ▶ Bait Fishing
- ▶ Bird Tool Use
- ▶ Cognitive Ethology

- ▶ Nonhuman Intelligence
- ▶ Nonhuman Tool Use
- ▶ What Makes a Tool

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Crocodilians Using Hunting Tools

- ▶ Crocodilian Bait Hunting

Crocodilians Using Lures

- ▶ Crocodilian Bait Hunting

Cross Sex Friend

- ▶ Opposite-Sex Friend

Cross-Cultural Comparisons

- ▶ Cross-Cultural Studies

Cross-Cultural Comparisons: Evolutionary Paradox of Male Same-Sex Sexual Attraction

► Paul Vasey

Cross-Cultural Differences

► Cultural Differences in Mate Preferences

Cross-Cultural Expression

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Synonyms

Cultural differences; Cultural evolution; Cultural learning

Definition

Cross-cultural expression generally refers to differences in the expression of traits and behaviors across cultures.

Introduction

Humans share many universals. However, culture plays an important role in influencing the way that behaviors and traits are expressed. There are many different cultures across the world. Is an experience for a person growing up in Central London the same as a person living in the slums of India, or the metropolis of Japan, or in a tribe in Africa? Clearly not. Individuals appear to shape and be shaped by their culture, thus influencing

psychological tendencies and behaviors. Therefore, what is applicable to one culture may not necessarily apply to another culture. Within this chapter, firstly I will provide a working definition of culture and will then highlight key evolutionary theoretical stances in the development and maintenance of culture, focusing largely on cultural variation. The latter section of this chapter will discuss the influence that cultural differences have on behavior and expressions, with examples of empirical research.

What Is Culture?

Culture is not easily defined. The single term “culture” encompasses a broad range of aspects. A widely accepted and inclusive definition of “culture” is the “sets of practices, beliefs, ideas, values, inventions, artifacts, and attitudes that characterise groups of people” (Gangestad et al. 2006, p. 78). Across the globe, people differ in their practices and heritage. Culture extends beyond food, crafts, and geography; it revolves around the central beliefs, behaviors, and the identity of a group. There are many indigenous cultural expressions, which can take the form of knowledge, practices, stories, rituals, music, art, and much more. Furthermore, mating behavior and parental styles differ cross-culturally. Therefore, culture has a pervasive influence on human behavior. Yet, despite the importance of culture to numerous disciplines, including psychologists, anthropologists, and biologists, it remains an underexplored and controversial research area.

Nonhuman and Human Culture

Cultural expressions and learning are apparent in both human and nonhuman species. However, they vary in complexity. Chimpanzees have excellent toolmaking skills; knowledge is passed between chimpanzees within groups. Some research has found, for example, that new methods (e.g. fo ant-fishing) can transfer from one chimpanzee community to another. However, there are many differences between humans and

primates, such as the capacity for imitation and language ability. These capacities in chimpanzees can be likened to “culture” in humans. When we consider human populations, the picture is much more complex. Some behavioral traits can be apparent in some cultures, but not others, like riding a bike. Alternatively, other cultural aspects merely differ in expression; one of the clearest examples of this is language. People in different cultures all possess language, yet the content and qualitative aspects differ.

Evidently, in both human and nonhuman species, culture is important. One main question that follows then is, how are these culture-specific expressions and behaviors integrated and maintained?

How Does Culture Develop?

This is no unified explanation for how culture develops. The cultural evolution approach applies Darwinian evolutionary theory to culture. Specifically, the transmission of culture has been analogized with transmission at a genetic level. In other words, human cultural expressions (e.g., knowledge, customs, languages) evolve and typically increase in complexity over time. Transmission and evocation are two proposed pathways that bring about cultural variation (Gangestad et al. 2006).

One proposed mechanism, by which cultural expressions are thought to be passed on between individuals and generations, is social learning and modeling/imitation (Henrich and McElreath 2007). Indeed, we frequently observe and learn from others. This method may be best exemplified which considering technological knowledge in cultures. For instance, individuals may impart agricultural knowledge onto other individuals which is passed on through generations and does not require individual learning. This is a form of cumulative cultural evolution (CCE) where beneficial traits are retained in populations, also labeled as a “ratchet effect” (Tomasello et al. 1993).

A second hypothesized process which may lead to specific cultural attributes being

passed on and maintained within cultures is the social and ecological conditions of a population, so-called evoked culture (Tooby and Cosmides 1992). For example, conditions of drought versus a plentiful source of water are likely to lead to different behavioral strategies within cultures. Following on from this idea, gene-culture coevolution theory (Richerson et al. 2010) posits a relationship between genes and culture. Specifically, culture frequently creates novel environments, which then apply selection pressures on genes. Put more simply, culture exerts an important influence on creating our human nature.

It is important to note that proposed social learning and environmental explanations are not mutually exclusive – it may be that both methods shape cultural expression. The next two subsections will provide examples of cross-cultural universals and differences.

Cross-Cultural Similarities

One of the most well-known examples that has created great debate over human universals across cultures is facial emotional expression. Early work by Charles Darwin suggested that judgments of emotional expressions are universal in humans. Following on from Darwin’s exploration, one of the most cited examples is the work by Paul Ekman and colleagues (e.g., Ekman and Friesen 1971), which typically highlighted universality in emotional expressions and recognition. This work found that six basic emotion categories (anger, disgust, fear, happiness, sadness, and surprise) were consistent across cultures – especially happiness and sadness. This ability to recognize emotional expressions was also found in illiterate tribes – hunter-gatherers in New Guinea and the Dani people of West Irian – with little or no previous interactions with outsiders. Hence, despite the diverse and rich cultures that we live in, emotional expression and recognition appear to be similar cross-culturally. However, not all studies support the universality of emotion (e.g., Crivelli et al. 2016). This highlights tentative conclusions when considering cross-cultural similarities in emotion perception.

Cross-Cultural Differences

Research has generally focused on investigating the similarities between groups. While this has been a fruitful exploration, it omits consideration of the diversity that cultures display. Indeed, there are evident and widespread differences in psychological realms across cultures, including attractiveness preferences. From an evolutionary stance, “true” universality is rare and often condition-dependent. Parasite threat and sex ratio, for example, create constraints that can in turn influence cultural behaviors.

An example that provides evidence for important differences across cultures is facial physical attractiveness preferences and parasite threat. Evidently, in some human cultures especially hunter-gatherer societies, pathogens can pose a risk to health. It is therefore advantageous for women to be attuned to signals of health and overall condition in potential mates. Indicators of poor health (i.e., open sores, yellow eyes) should be unfavorable when selecting partners, while high levels of physical attractiveness should be preferable as attractiveness is considered to be a marker of good health and parasite resistance (Symons 1979). Correlational analyses of cross-cultural data (Buss 1989) highlight that higher parasite occurrence is positively related to a preference for more physically attractive faces. Therefore, when considering facial preferences alongside culture, important differences occur. These differences are thought to arise from ecological and environmental factors. Unlike the example of facial expressions above, cross-cultural differences are apparent and appear contingent on cultural environment. Therefore, there are both similarities and differences in cross-cultural expressions and behaviors.

Conclusion

Culture is an integral part of human life. Although culture has been studied by many disciplines, most explorations are limited – focusing mainly on cultural similarities. Many debates still

surround culture, especially how culture develops and is then maintained across generations. Two methods of cultural transmission, proposed by evolutionary psychologists, are observation and environmental influences. Furthermore, the provided examples highlight important cultural universals as well as dissimilarities when judging expressions and attributes in faces. Overall, there appears to be great cultural and psychological variation amidst human universals. Going forward, culture remains a relatively new, contentious, and underexplored area. Thus, more explorations are required into how and why cultural variation exists while overcoming some key methodological challenges associated with exploring culture.

Cross-References

- ▶ [Evoked Culture](#)
- ▶ [Evolution of Culture](#)

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Cross-Cultural Pattern

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Synonyms

Cultural homicide patterns; Global homicide trends

Definitions

Extensive variability exists cross-culturally in the rates of homicide, however relatively invariant across cultures is the tendency for homicide rates to be predicted by inequality and to be primarily a male affair that peaks among men in their early twenties.

Introduction

Societies differ in their economic and political bases, and different cultures have different moral standards. Therefore, features of homicide such as rate of homicide per million individuals or apparent motives of the most frequent homicides differ greatly between societies in different cultures. However, there are several characteristics of homicide observed commonly across cultures, which can be explained from an evolutionary perspective.

Cross-Cultural Patterns in Homicide

Homicide rates per million individuals are extremely variable across countries and societies, as well as across time, for an individual society. Despite this variability, there is a strong trend toward the reduction of violence over the evolutionary history of humans. Evidence suggests that premodern, small-scale traditional societies may have had a higher homicide rate per 100,000 individuals than the worst homicide rates from modern societies (Kealy 1997; Pinker 2012). This trend toward greater non-violence may imply that the legal system in modern nation states have been effective in controlling for violence among individuals (Pinker 2012).

The homicide rates for modern, developed societies are determined by a complex mixture of social, cultural, and economic factors. Despite this, there are several culturally invariant patterns that can be detected in homicide patterns and predictors. First, a strong predictive factor of homicide is the degree of economic inequality among members of a society. This inequality, as measured by the Gini index, displays a very clear correlation with the homicide rate for many countries, states, and the same country through time (Daly et al. 2001; Hiraiwa-Hasegawa 2004). In all of the cases, the smaller the Gini index (i.e., the more equality across individuals in a region), the lower the homicide rate.

Another cross-cultural pattern that emerges is the tendency for homicides to be primarily perpetrated by men against men. Globally, the UN Office on Drugs and Crime (2013) reports that 80–97% of homicide perpetrators are men and 95% of the victims of homicide are men.

In addition to this, another, near universal pattern in homicide rate is its association with age, in which the rates of homicide by men rise sharply after puberty to a peak in the early 20s and then decrease afterwards (Daly and Wilson 1988). A study from Japan is interesting in this regard because no such age-related curve for homicide rate was observed cross-sectionally after the 1980s (Hiraiwa-Hasegawa 2004). Social and economic conditions for young men dramatically

changed after the Second World War in Japan. As the proportion of young men with higher education increased and Gini index decreased, the rate of homicide among young men gradually dropped. And when their rate of homicide was compared with those of older age categories, older men's homicide rates were higher than that of younger ones. However, when the age-specific homicide rates were calculated within each cohort, it revealed the age-homicide pattern described above, that is, the homicide rate was highest when men were in their early 20s and declined afterward.

Motivations for homicide across cultures also share some commonalities. For example, the motivations for male-on-male homicide is often based on competition for resources, status, and prestige, whereas the motivations for male-on-female homicide is often a response to sexual jealousy (Daly and Wilson 1988; Hiraiwa-Hasegawa 2004). Women commit homicide relatively rarely, but when they do, it is quite often the killing of their own baby, i.e., infanticide. In those cases, a mother kills their own newborn baby when she thinks that the baby's prospect of survival is very low, either because of the low physical fitness or no social support to rear the baby (Daly and Wilson 1988).

Conclusion

Homicide rates per million individuals are extremely variable across societies, but the global tendency is toward the reduction of violence. Although many factors are involved to determine homicide rate in a society, a strong predictive factor of homicide is the degree of economic inequality among members of the society: the smaller the inequality, the lower the homicide rate. In most societies, men are more often both the perpetrators and victims of homicide, and there is a strong age effect with a peak homicide rate in the early 20s. The motives for male-on-male homicide are often based on competition for various types of resources. Those patterns can be understood within the theoretical framework of sexual selection.

Cross-References

- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Women
- ▶ Meta-Analysis of Sex Differences in Aggression
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Violence to Control Women's Sexuality

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Cross-Cultural Psychology

- ▶ Language and Economic Cooperation

Cross-Cultural Punishment

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Synonyms

Altruistic punishment; Castigation; Retribution

Definition

Punishment mechanisms are crucial to understanding the processes of cooperation in groups and can be found in different societies; the level of punishment varies according to environmental, social, and cultural factors.

Introduction

Cross-cultural studies defend the idea that punitive sentiment may be universal among humans (Price 2005). Punishment is understood as a central element for explaining the phenomenon of group cooperation (Kurzban et al. 2007). For example, models of the evolution of costly punishment suggest that societies in which this type of punishment is common will have stronger norms of justice and prosociality because this punishment allows the development of stable rules to deter invading deserters (Henrich et al. 2006). Regarding moral punishment, it plays an important role in regulating an established moral system in which those who punish seek to identify and punish those who behave immorally (Hofmann et al. 2018).

Thus, it is important to discuss how punishment, so crucial to the understanding of cooperation processes, is identified in other societies. As Petterson and Vasey (2016) point out, cross-cultural studies depart from the principle of examining human behavior in various cultural contexts so that behavioral differences and similarities are elucidated.

Cross-Cultural Studies on Punishment

A study conducted by Henrich et al. (2006) in different continents (Africa, North America, South America, Asia, and Oceania) in different environments (e.g. urban, mountainous tropical forest, Savannah-woodlands), assessed second-party punishment through costly punishment and identified that costly punishment has a universal standard, despite differences in the level of

punishment among populations. In this study, some societies exhibited a high disposition for punishment, such as Tsimane, the Shuar, Yasawa, and the Samburu, sedentary and semi-nomadic societies whose basic economy is horticulture. However, most societies studied, which include societies living in urban, sedentary, wage-labor environments (e.g., Accra city, Missouri, and Dolgan/Nganasan), have shown a tendency to punish less.

In this sense, people from different cultures can give different attributions to the same situation because their beliefs are influenced by culture. Studies suggest that the intensity and form of control varies between Chinese and American culture, for example, with the Chinese being characterized by more punitive aspects. In China, the punishment or threat of it has a function of control over the behavior of individuals, so that they obey social norms; while in Western cultures, punishment functions as a means of justice for certain acts (Friedman et al. 2005).

Regarding religion, the belief in gods with moralistic and punitive characteristics, who may play a chastising role against those who do not cooperate with the social order, is characterized as a factor that explains human cooperation. These patterns can be explained from an evolutionary point of view, since with cultural evolution it is possible to establish patterns of self-reinforcing beliefs and practices, which remain because they are possibly associated with punishment (Purzycki et al. 2016).

Conclusion

Although it is an incipient area, cross-cultural studies can provide data on the universality of some behaviors and traits, facilitating the understanding of the factors that selected and maintained them. Regarding punishment, it is observed that its application is fundamental for the development of cooperation, but it should be emphasized that the level of punishment changes according to environmental, social, and cultural factors.

Cross-References

- [Altruistic Punishment](#)
- [Cross-Cultural Studies](#)
- [Evolution of Punishment](#)

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Cross-Cultural Research on Grandparental Investment

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Synonyms

[Grandparental involvement](#); [Grandparenting](#)

Definition

Grandparental investment refers to the various types of tangible or intangible resources (like time, energy, material, and solicitude) that grandparents, including maternal grandmother, maternal grandfather, paternal grandmother, and paternal grandfather, provide for grandchildren.

Introduction

In contemporary societies, increases in life expectancy and grandchild survival have enhanced the opportunities for grandparents to invest on their grandchildren (Coall and Hertwig 2010). The percent around the world is high. For example, in the USA two decades ago, more than half (60%) of grandparents provided occasional or more frequent grandchild care (Fuller-Thomson and Minkler 2001). Today in China, about three quarters of the children under age of 6 years old are routinely cared by their grandparents (Yue 2018). However, the investments or cares from different grandparent types (i.e., maternal grandfather, maternal grandmother, paternal grandfather, and paternal grandmother) are not equal but discriminative.

Evolutionary Perspectives

In explaining the discriminability in grandparental investment, evolutionary perspectives have provided considerable literatures. Kin selection theory (Hamilton 1964) is commonly acceptable. Investment from grandparents on their biological grandchildren can be seen as effective indirect strategy, as the results of genetic relatedness, to increase their inclusive fitness. The theoretical genetic relatedness between any grandparent type and grandchild is the same ($r = 0.25$ on average). As such, the average levels of investment from any grandparent type might be similar. However, human males have potential uncertainty in their biological relationship to their children (i.e., paternity certainty hypothesis; Euler and Weitzel 1996). The uncertain links of paternity

between grandparents and grandchildren render the ordered level of investment: maternal grandmother > maternal grandfather or paternal grandmother > paternal grandfather. Sex-specific reproductive strategies (Euler and Weitzel 1996) further the predicted rank order. In mammals, the production of eggs and the internal gestation render that females expend maximal resources on parental effort, whereas males reserve resources for further mating effort. Consequently, maternal grandparents ought to invest more in their daughters and daughters' children than paternal grandparents invest in their sons and sons' children. The combined effect of paternity uncertainty and sex-specific reproductive strategies thus predicts the clear rank order: maternal grandmother > maternal grandfather > paternal grandmother > paternal grandfather, representing as matrilineal biased (Coall and Hertwig 2010).

The abovementioned order is not supported by other hypotheses. The grandmother hypothesis proposes that menopause and the lengthened post-menopausal lifespan provide the evolutionary importance of grandmaternal investment (Alvarez 2000), while grandfathers are presumed to be more engaged in mating effort than nepotistic investment in grandchildren, leading to the order as maternal grandmother or paternal grandmother > maternal grandfather or paternal grandfather. The Trivers-Willard hypothesis (Trivers and Willard 1973) proposes that by providing investment to grandchildren, grandparents could facilitate their children's fertility; hence, the reproductive potential of the children plays a role in biased grandparental investment. In addition, the asymmetric genetic relatedness hypothesis (Chrastil et al. 2006) emphasizes that the genetic relatedness between grandparents and grandchildren is symmetric on autosomal genes but asymmetric on sex chromosomes. Granddaughters and grandsons have 50% chance of inheriting an X chromosome from maternal grandmother or grandfather. Granddaughters definitely do not obtain one X chromosome from paternal grandfather, whereas grandsons definitely inherit Y chromosome from paternal grandfather. Thus, paternal grandparents provide investment for granddaughters and grandsons more discriminatively than maternal grandparents.

However, the evolutionary perspectives are, to some degree, difficult to provide some specific and proximal explanations for biased grandparental investment in different cultures or societies (Coall and Hertwig 2010). In some WEIRD (Western, Educated, Industrialized, Rich, and Democratic; Henrich et al. 2010) societies, including the USA, Europe, and Australia, the biased pattern (maternal grandmother > maternal grandfather > paternal grandmother > paternal grandfather) has often been supported. For example, in the Netherlands, it was found that grandparental investment biased toward daughters' children (Kaptijn et al. 2013). However, in non-WEIRD samples, research has been relatively limited. Although that, limited studies have demonstrated that in traditional Western rural societies, it often showed high levels of patrilineal biased grandparental investment. For example, in rural Greece, paternal grandparents were found as the primary caregivers (Daly and Perry 2019). Besides, in Asian cultures, like China, the traditional patriarchal nature of filial piety prioritizes paternal above maternal relations, leading to more patrilineal than matrilineal biased grandparental investment (e.g., Chen et al. 2011). Therefore, the biased grandparental investment is more rooted in variations of specific sociostructural ways.

Cross-Cultural Research

Unlike the evolutionary perspectives, cross-cultural approach focuses on how different cultural values, like patrilineal or not, the norms of grandparental involvement, reciprocity, family obligations, and responsibility, shape the biased grandparental investment. The most salient cross-cultural difference is about patrilineal or not. Most published literature on grandparental investment relies on WEIRD samples (e.g., Danielsbacka and Tanskanen 2012; Danielsbacka et al. 2011). In these WEIRD societies, it doesn't favor patrilineal culture but mother-daughter bonds. And, paternity uncertainty is relatively higher than that in patrilineal societies; so, the matrilineal pattern of biased grandparental investment is often found (e.g., Bishop et al. 2009). However, in patrilineal

societies, it often shows high levels of paternal grandparental investment (Strassmann and Garrard 2011). China is a typical patrilineal country and often included as the object of cross-cultural research with Western ones (e.g., Burnette et al. 2013; Kaptijn et al. 2013). In China, the intergenerational transfers or ties are rigidly patriarchal. Historically, patrilocal extended family has been the dominant family form in East Asian and Southeast Asian countries, with adult sons (at least one of the sons), daughters-in-law, and descendants living in the same house (Mehta and Thang 2011). Parental preferring to invest toward sons than daughters lies in the patrilineal kinship system. For example, Wang and Chen (2019) asked a sample of childless female undergraduates to imagine being a grandmother and to report their biased investment on hypothetical grandchildren. The results revealed the strong preference to invest toward sons' children than daughters' children. Using the China Health and Nutrition Survey, Chen et al. (2011) reported that co-residence with paternal grandparents (high levels of grandparental investment) was about three times than with maternal grandparents on average (35% vs. 10%). Again, in Goh and Kuczynski's (2010) research, they reported a survey conducted in 2006 and that among 1301 grandparents from 738 households in Xiamen, 40% were paternal grandmothers, followed by maternal grandmothers (31%), paternal grandfathers (18%), and maternal grandfathers (17%).

The cross-cultural differential may be also from the heterogeneity among grandparents and ambiguity of the norms related to grandparenthood. Some anthropological researchers treated grandparental survival and senescence as the indicators of grandparental investment (Strassmann and Garrard 2011). In the psychology-related division, the roles of grandparents range from "uninvolved" to "occasional helper" or "long-term helper" or "long-term surrogate parent" or "custodial grandparent" in different studies. These different roles per se may reflect the different levels of grandparental investment. More importantly, the differential is usually covered by cultural differential. In WEIRD societies, state

welfare provisions substitute for some kin support in raising children. Investment for grandchildren is viewed as an option. The common norm of grandparental investment is "being there" but "not interfering" (Mason et al. 2007). That is, grandparental investment tends to be occasional and the level is relatively low. By the contrast, Black and Hispanic grandmothers tend to play a considerable role in caring grandchildren. The pattern does not only reflect varied cultural norms but also is the responses to socioeconomic disadvantage or parental difficulties (e.g., incarceration and mental illness) (Hayslip et al. 2019). In Asian families, grandparental investment is viewed as familial duty or obligation (Mehta and Thang, 2011) and the level is also very high (e.g., Chen et al., 2011). On the one hand, households rather than individuals or couples ought to overcome familial difficulties. Grandparents, especially grandmothers, are the optimal alloparents because of their low costs but enough time, energy, creditability, and experiences in childcare. Essentially, it is a family adaptive strategy, maximizing the well-being of the whole family. On the other hand, the elder generation holds a sense of "responsibility-oriented ethics." They fulfill their responsibilities and obligations toward their children and grandchildren. Accordingly, the Chinese context of grandparental investment is structural and functional, in which grandparents can provide matched or more caring and instructions for grandchildren than their adult children. For example, for some Chinese rural left-behind children, intergenerational investment is commonly from paternal grandparents; the grandparents are significant agents as same as their parents. In other Asian countries (e.g., South Korea, Vietnam, or Myanmar), the cultural norm is similar (Mehta and Thang, 2011), although the extent of grandparental investment may be discrepant (e.g., Knodel and Nguyen, 2015; Ko and Hank, 2014).

However, with the development of societies and integration of Eastern and Western cultures, the cross-cultural differential between patrilineal and matrilineal patterns of biased grandparental investment seems being weakening in some Asian societies, like China. In a recent survey conducted

in six cities of China, it was found that the proportions of maternal grandparents and paternal grandparents involving grandchild care were similar (49.5% vs. 50.5%), although grandmothers were always more than grandfathers (Yue, 2018). Decrease in fertility rate may be a predominant factor. In China, it was specifically driven by the One-Child policy. From 1978, Chinese government implemented the One-Child policy. The one-child generation started families from about 2000 and had a new generation of one-child. Although the policy was abolished from 1st January 2016, the national fertility rate is still at low level. In many families, it shows a “4-2-1” intergenerational pattern, i.e., four grandparents, two parents, and one child. Four grandparents had only a grandchild. The artificially controlled fertility may substantially confound the biased grandparental investment. And, with the development of urbanization, the average household size declines. The shift toward the nuclear family structure would result in the decline of grandparents’ co-residence. Statistics from the 2010 Census in China illustrate that the average household size is as low as 3.09, lower than 10 years ago (3.46). And, the number in urban areas is 2.71, lower than towns (3.08) and rural areas (3.34). The solution of whether or which one(s) of grandparents are required, invited, or voluntary to provide childcare in different families are various. The tradition of prioritizing paternal above maternal relations may be loosening. Besides, because of the gatekeeping role of mothers, maternal grandmothers might be more common in providing childcare than paternal grandmothers. Yet, no study has investigated the cross-cultural difference on biased grandparental investment between WEIRD and Chinese urban samples.

Conclusion

Humans are cooperative breeders. Investment from grandparents (or other alloparents) benefits children’s and grandchildren’s welfare. And, expanding urban market economies and fast-rising maternal employment across the globe

have amplified the need for families to find grandparental investment. Although the evolutionary perspectives have tried to ultimately interpret the biased grandparental investment, the socio-structural benefits of grandparental investment are culture-dependent. Cross-cultural approaches are complementary to evolutionary perspectives (Coall and Hertwig 2010); cross-sociocultural research on grandparental investment should be furthered.

Cross-References

- ▶ [Alloparenting](#)
- ▶ [Grandparental Investment](#)
- ▶ [Level of Grandparental Investment](#)
- ▶ [Maternal Grandmother Invests Most](#)
- ▶ [Paternal Grandfather Invests Least](#)

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Cross-Cultural Similarities

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Synonyms

[Biculturalism](#); [Cultural plurality](#); [Multiculturalism](#)

Definition

Culture has also been defined according to various dichotomies, e.g., individualism/collectivism loose/tight cultures; low-context/high-context communication. However, it should be noted that all cultures exhibit both ends of these continuums. All cultures exist along the entire continuum; therefore, all cultures show similarities in the broader scheme of culture. This broader scheme of culture is in essence human nature, human society, and human culture.

Introduction

Defining culture is a complicated endeavor given its variation across domains and purpose, which is embodied within a historical context. An anthropological definition of culture is “...that complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society” (Tylor 1871, p. 1). Culture has also been defined according to various dichotomies, e.g., individualism/collectivism (Gudykunst 2003; Ting-Toomey and Chung 2012; Triandis 2001); loose/tight cultures (Carpenter 2000; Gelfand et al. 2011; Parker et al. 2009; Realo et al. 2014); low-context/high-context communication (Brice 2002; Ting-Toomey and Chung 2012); and/or horizontal/vertical cultures (Triandis 2001).

The continuum of individualism/collectivism revolves around whether the culture places focus on the individual (“I” culture) vs. focus on the

group (“We” culture). Loose cultures display freer definitions of acceptable behavior and have higher tolerances for aberrant behaviors (Gelfand et al. 2011). Loose cultures are most often associated with individualistic culture. However, tight cultures display strong distinctions between in-group and out-group memberships and are most often seen in collectivistic cultures (Gelfand et al. 2011). Low-context communication relies more on messages conveyed (i.e., the words that are said or words in print) than environmental context, while high-context communication relies more on context and the clues for interpretation which can be tangential or indirect (Hall 1983). Meanwhile, horizontal cultures emphasize equalness and individuals holding similar status in society, while vertical cultures place an emphasis on rank and privileges of rank within society (Triandis 2001). However, it should be noted that all cultures exhibit both ends of these continuums. All cultures exist along the entire continuum; therefore, all cultures show similarities in the broader scheme of culture. This broader scheme of culture is in essence human nature, human society, and human culture.

Assimilation Versus Acculturation

Human nature, society, and culture all encompass the use of language to communicate, religion, education, government (or societal leaders), mores, and societal norms. All cultures exhibit traits from both ends of the above mentioned continuums (individualistic/collectivistic, loose/tight cultures, low-context/high-context communication, and horizontal/vertical cultural traits).

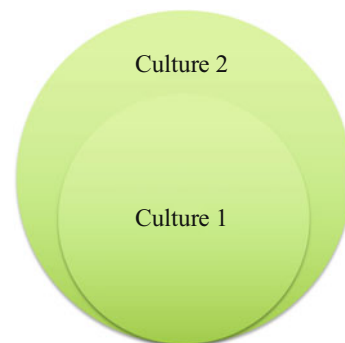
What happens when a person develops and grows up in one cultural context and immigrates into another cultural context (e.g., moving from one cultural group to another)? When a person immigrates to another country, two major forces are at play with regards to the degree to which an individual will change and conform to the dominant culture (assimilation) or retain their own cultural identity (acculturation) while accommodating to the dominant culture. Cultural similarities are those attributes which overlap and do not

cause cultural dissonance or cultural interference when the two cultures interact. Hence, this entry will further examine cross-cultural similarities with regard to acculturation and consonance.

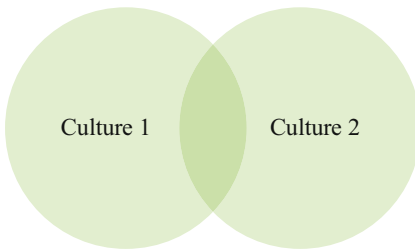
Cross-Cultural Similarities

According to Muhammad et al. (2016), stated that “... assimilation occurs when individuals reject their minority culture and adopt the cultural norms of the dominant or host culture” (p. 368). Acculturation comes about when individuals function in the dominant culture while retaining their original culture. Hence, there exists a continuum of cultural adaptation from assimilation to acculturation. Figure 1 illustrates assimilation, whereas, the prevailing culture two (C2) retains dominance over culture one (C1). This has also been referred to as an unidimensional model (Gordon 1964). Rhee (2019) stated that, under assimilation “...immigrants are expected to renounce their ethnic culture and get assimilated to the host culture” (p. 862). Whereas, under acculturation, no one culture retains dominance (See Fig. 2). Acculturation has also been referred to as a bidimensional model. In Fig. 2, the overlap of cultures one and two is evidence of cultural similarities.

Berry’s (1997) theoretical framework of acculturation is the leading theory that explains these processes and acculturation strategies that people employ when adapting to a different cultural environment. Berry (1997) delineates four strategies that a person or group employs when



Cross-Cultural Similarities, Fig. 1 Assimilation



Cross-Cultural Similarities, Fig. 2 Acculturation

acculturating to a new environment depending on whether: (a) the person belongs to the prevailing or to the non-prevailing group; (b) the extent to which the person maintains their cultural heritage referred to as cultural maintenance; and (c) the extent to which a person is in contact with other cultural groups or with their own cultural group referred to as contact and participation (Berry 1997).

The strategies are *assimilation*, *separation*, *integration*, and *marginalization*. *Assimilation* is when a person may conform to the mainstream culture at the expense of forgoing their own cultural identity. An example of *separation* is when an individual maintains their own cultural identity and avoids interacting with others from the dominant cultural group. Maintaining one's cultural identity while interacting with the prevailing group is referred to as *integration*. Rhee (2019) stated that, "Contrary to separation and marginalization, when immigrants effectively interact with the American society, their acculturation strategy can be defined either as integration with their adherence to their ethnic culture or as assimilation with low adherence to their ethnic culture" (p. 862). First generation immigrants are more likely to hold strong ties and adherence to their own culture (Rhee 2019). "*Integration*" is Berry's term; however, this is also referred to as acculturation by others. This entry will use the term "*acculturation*" since it is a more accepted and widely used term.

Marginalization is when an individual has no interest in maintaining their own cultural identity and interacts with the prevailing cultural group as a result of enforced cultural loss and discrimination. Of these strategies, research has documented that acculturation or biculturalism by others, is an

adaptive strategy associated with positive effects (Berry 1997). That is, one is able to maintain one's own cultural similarities and differences.

Employing an acculturation strategy depends on a number of factors such as whether the dominant cultural group is willing to accept non-prevailing groups into society, whereupon access to equal rights, such as education, healthcare services, job opportunities, are provided (Berry 1997). *Acculturation*, however, is only possible if the prevailing society values cultural and linguistic diversity, and also shows minimal prejudice, racism, and discrimination, i.e., positive mutual respect toward others and espouses a viewpoint that all cultural groups are part of a larger society (Berry and Kalin 1995). Also, the non-prevailing cultural group incorporates the values of the prevailing cultural group in their cultural schema. Consequently, a person from a non-prevailing cultural group that uses an acculturation strategy may show less acculturative stress and demonstrate more positive outcomes (Ehlers et al. 2009). Therefore, individuals from a nondominant cultural group may be less prone to depression and anxiety, and may be able to successfully maneuver between the dominant and nondominant culture (Mui and Kang 2006).

The least adaptive of these acculturation strategies is *marginalization* that has been linked to psychopathology and poor physical health outcomes, academic and work performance, as well as delinquency in immigrant youth (Ungar 2015). Acculturative stress occurs when a person experiences difficulties adapting to their new environment. This includes adapting to new standards, rules, behaviors, language, value system, dressing, eating, and ways of doing things. Typically, a person has a coping mechanism that allows them to overcome these difficulties and adapt to their new environment. However, when a person is marginalized or does not belong to either the dominant or non-dominant group (or in instances of high acculturative stress, i.e., stress encountered when changing from one cultural group to another (D'Anna-Hernandez et al. 2015)), clinical depression and anxiety may ensue (Burrow-Sánchez et al. 2015).

Research in acculturation points to the benefits of incorporating an integrative or bicultural

strategy in which a person integrates knowledge of cultural beliefs and values, positive attitudes towards both cultures, bicultural efficacy, bilingualism, and a repertoire of adaptive behaviors or roles (LaFromboise et al. 1993). Competencies in these various areas, a bicultural person is “grounded” or has developed a strong social capital that can be utilized in times of stress and adversity. Hence, the successful bicultural individual has reduced ambiguity, shown resilience, and is able to navigate between the two cultures with ease, i.e., able to navigate among culture one, the shared culture similarities, and culture two.

Conclusion

Cultural awareness and knowledge about the history, various institutions, social interactions, religious beliefs, gender roles, and practices of everyday life of both cultures allow one to navigate competently between cultures. Positive attitudes toward both groups facilitated by frequent contact and exposure reduce stress and conflict. This in turn builds self-efficacy to live within two cultures without losing one's own identity. In sum, biculturalism promotes cultural similarities to exist and to thrive.

Cross-References

- ▶ Culture of Honor
- ▶ Culture of Honor and Individual Differences
- ▶ Evolution of Culture
- ▶ Men's Violence Against Female Partners: The Role of Culture
- ▶ Personality, Gender, and Culture
- ▶ Relationship between Culture and Race

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present in a feminine/transgender manner and are recognized as members of a “third” gender, known locally as *fa’afafine* (see ► “Fa’afafine”). Here, quantitative research pertaining to two evolutionary hypotheses for male androphilia that have been tested in Samoa is reviewed (also see, ► “Kin Selection Hypothesis”).

Models of the Ancestral Form of Male Androphilia

VanderLaan et al. (2013) found that the conditions that typify the ancestral human sociocultural environment (e.g., small community size, dependence on hunting and gathering, egalitarian political structure, and animistic belief systems) were more prevalent in cultures in which androphilic males presented in a feminine/transgender manner, compared to cultures in which they did not. This suggests that the feminine form of male androphilia is evolutionarily ancestral to the masculine (“gay”) form. The outcome of evolutionary processes may be obscured when examining more derived forms of male androphilia (e.g., the masculine, “gay” form), which may reflect historically recent cultural influences. Consequently, feminine androphilic males likely represent better models for understanding the evolution of male androphilia.

Sexually Antagonistic Gene Hypothesis

Sexually antagonistic selection is a form of balancing selection that occurs when genetic factors that produce fitness costs in one sex result in fitness benefits in the other sex. The Sexually Antagonistic Gene Hypothesis for male androphilia (SAGH) posits that genes associated with the development of androphilia result in decreased reproductive output in male carriers, but the same genes result in increased reproductive output in female carriers. Given that kin share a disproportionate number of genes in common, the female kin of androphilic males should experience, on average, increased reproductive output than females with no androphilic male relatives.

Cross-Cultural Studies

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Synonyms

Cross-cultural comparisons; Cultural studies

Definition

Cross-cultural study involves examining human behavior across various cultural settings to elucidate human behavioral similarities and differences. Cross-cultural comparisons are particularly useful in the field of psychology, because they enable researchers to parse apart which features of human behavior can be attributed to unique social or environmental factors and which features reliably emerge regardless of context.

Introduction

A considerable portion of the cross-cultural evolutionary research on male androphilia (i.e., male sexual attraction to adult males) has drawn comparisons between Canada, Italy, and Samoa, a small Polynesian island nation in the south Pacific. In Samoa, androphilic males publically

In theory, the fitness benefits accrued to the female relatives of androphilic males balance out the fitness costs associated with male androphilia. Consequently, the sexual antagonistic selection of these genes occurs because of their fitness-enhancing properties in female carriers. A by-product of this sexually antagonistic selection is that male androphilia persists in populations over evolutionary time, despite its fitness-reducing consequences. Given all this, the basic prediction that flows from the Sexual Antagonistic Gene Hypothesis is that the female relatives of androphilic males should tend to produce more offspring than those of gynephilic males (males who are sexually attracted to adult females). Additionally, because females are conferred the benefit, it has been suggested that the genes underlying male androphilia should be present on the X-chromosome (Camperio-Ciani et al. 2004).

Samoa represents an optimal location in which to test the SAGH, because the population is characterized by higher fertility when compared to Western European and North American populations (Central Intelligence Agency 2012). Individuals in low fertility populations often employ methods to limit reproduction, which artificially lower women's fertility. In addition, the purported ancestral form of male androphilia – the transgender form – predominates in Samoa (VanderLaan et al. 2013).

Four studies have been conducted in Samoa that furnish data pertaining to the SAGH. Vasey and VanderLaan (2007) demonstrated that the mothers of *fa'afafine* produce more offspring than those of gynephilic men. VanderLaan and Vasey (2011) replicated this finding and Semenyna et al. (2017) replicated this finding a third time. VanderLaan et al. (2012) demonstrated that *fa'afafine's* maternal and paternal grandmothers exhibit elevated offspring production. Semenyna et al. (2017) replicated this maternal grandmother effect, but the paternal grandmother effect was not replicated. Due to the more robust sample size employed by Semenyna et al. (2017), which was 77 % larger than the one used by VanderLaan et al. (2012), it is possible that the previously reported paternal grandmother effect resulted from statistical error. If elevated offspring

production is limited to maternal-line female relatives, as Semenyna et al. (2017) study suggests, then it would be consistent with the assertion by Camperio-Ciani et al. (2004) that the purported sexually antagonistic genes influencing the development of male androphilia are located on the X-chromosome.

Elevated reproduction by the mothers and the maternal grandmothers of *fa'afafine* does not provide definitive support for the X-linkage of sexually antagonistic genes, because reproduction by these categories of female kin is naturally confounded with that of fathers and grandfathers, all of whom share genes with androphilic and gynephilic male probands. Instead, elevated reproductive output by androphilic males' maternal aunts, paternal aunts, or both would provide the clearest support for the SAGH, because androphilic and gynephilic male probands do not share genes with their aunts' male reproductive partners. To date, cross-cultural research in Samoa has consistently failed to find such aunt effects (VanderLaan et al. 2012; Semenyna et al. 2017). Further, evidence for this effect among aunts has been limited to samples of men pooled from Western Europe (e.g., Camperio-Ciani et al. 2004).

Balanced Polymorphism Hypothesis

The Balanced Polymorphism Hypothesis for male androphilia (BPH) takes as its starting point the assumption that male androphilia is not an isolated trait but, rather, is part of a larger package of gender-atypical traits. Ample empirical evidence exists to support this assumption (Bailey et al. 2016). Miller (2000) proposed that multiple genes influence the development of male androphilia, and these genes shift male brain development in a female-typical direction. Males who inherit a critical number of these genes become androphilic. Below this critical threshold, males who inherit some of these genes are gynephilic, but are feminized in terms of certain personality traits, which render them more sensitive, empathetic, tender, and kind. These personality traits, in turn, are thought to render

gynephilic males more attractive as mates. Indeed, ample empirical evidence exists to support this assumption (e.g., Buss and Shakelford 2008). Owing to their increased attractiveness, Miller (2000) argues that these males obtain more female sexual partners and father more children compared to gynephilic males who have no androphilic male relatives. These males are also hypothesized to be better fathers compared to fathers with no androphilic male relatives. The increased reproductive success experienced by androphilic male's gynephilic male relatives favors selection for the feminizing genes in question. As such, positive selection for these genes occurs despite the reproductive costs associated with male androphilia itself.

A number of predictions flow from the BPH. First, androphilic males are more likely to be feminine than masculine. Second, gynephilic males should be more feminine if they have androphilic male relatives, compared to those who do not. Third, gynephilic males should be more attractive if they have androphilic male relatives, compared to those who do not. Fourth, gynephilic males should obtain more female sexual partners if they have androphilic male relatives, compared to those who do not. Fifth, gynephilic males should father more children if they have androphilic male relatives, compared to those who do not. Sixth, gynephilic males should be better fathers if they have androphilic male relatives, compared to those that do not.

To date, two studies relevant to testing the BPH have been conducted in Samoa. VanderLaan et al. (2012) found that the maternal and paternal uncles of Samoan *fa'afafine* did not differ from Samoan gynephilic males in terms of their offspring production. In contrast, Semenyna et al. (2017) found that the paternal uncles of Samoan *fa'afafine* fathered more offspring than those of gynephilic males, but the effect size was small raising the possibility that this group difference may reflect statistical error. Taken together, these studies failed to furnish strong support for the Balancing Selection Hypothesis.

Conclusions

Cross-cultural comparisons have been used to study the evolution of male androphilia. This approach has helped establish the optimal population for testing evolutionary hypotheses. Hypothesis testing in relevant cultural contexts has furnished insights into the evolution of male androphilia. Overall, there is support for the SAGH, although more research in additional populations of transgender androphilic males would be beneficial.

Cross-References

- ▶ Comparative Evidence
- ▶ Evolutionary Cultural Psychology
- ▶ Fa'afafine
- ▶ Female Reproductive Variance
- ▶ Personality, Gender, and Culture
- ▶ Genetic and Prenatal Components of Homosexuality
- ▶ Homosexuality
- ▶ Homosexuality Paradox, The
- ▶ Human Sexuality
- ▶ Kin Selection
- ▶ Kin Selection Hypothesis
- ▶ Male Reproductive Variance
- ▶ Non-Western Homosexuality
- ▶ Paul Vasey
- ▶ Reproductive Strategy
- ▶ Reproductive Variance
- ▶ Same-Sex Relationships
- ▶ Sexual Orientation
- ▶ Sexual Orientation and Human Sexuality
- ▶ Sexual Reproduction

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Cross-Cultural Universality

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Synonyms

Human nature; Human universals; Universalism

Definition

Core mental attributes or psychological traits that are shared, to varying degree, by the vast majority of human beings (Norenzayan and Heine 2005)

Introduction

Despite some controversy (Geertz 1973; Norenzayan and Heine 2005), Donald Brown (1991) constructed a list of hundreds of universal characteristics (e.g., marriage, coalitions, rituals, fear of snakes, etc.) that are common to all known cultural groups. Although aspects of cultural behaviors are often learned, variations in ancestral ecologies across deep time ultimately gave rise to differences in the expression of innate human traits (Diamond 1997). Cultures are essentially adaptive responses to the environmental niche that they each evolved in (Cohen 2001; Boserup 1970; Gilmore 1990).

Cultural Universals

Determining what a cultural universal is depends on the operational definition of *culture* as well as the standards of evidence for such claims. The broader the definition of a psychological trait, like subjective well-being, for example, the greater the likelihood that the trait will be seen universally. However, if the operational definition is narrowly defined to exclude certain situations, the trait in question may be seen to a greater degree in some cultures than in others (English and Chen 2011; Suh 2002). There is no current consensus among researchers for what would methodologically strengthen the case for universality of a cultural trait (Norenzayan and Heine 2005). Generally, however, if the same psychological process exists in two widely divergent cultures, then the case for universality gains more traction. For example, if theory of mind exists in 4-year-old children in urban parts of Philadelphia as well as in 4-year-olds born in the rainforests of Cameroon, the case for universality is strengthened. Indeed, children sampled in Western populations are able to successfully understand another person's differing point of view in a false belief task around the same age as Baka children born in southeast Cameroon (Avis and Harris 1991), thereby supporting the case for universality.

The claim for universality of a cultural trait is further bolstered when multifactorial research methods are used in unison. Physiological studies (Way and Lieberman 2010), fMRI research (Hedden et al. 2008), self-reports (Miller et al. 2011), and animal studies (Nagell et al. 1993) have all been used to make the argument that cross-cultural universals do in fact exist. Take, for example, social facilitation or the notion that organisms tend to perform better on simple tasks in the presence of observers. Although disagreement about its innate origins exists (Do-Yeong and Junsu 2010), social facilitation has had supportive evidence in humans in a natural setting (Michaels et al. 1982), cockroaches (Zajonc et al. 1969), and macaques (Dindo et al. 2009).

Even in the presence of universality, there often exists a host of variations that some would rather not like to think of all too clearly. Incest avoidance is one such trait. From a genetic standpoint, it makes sense to avoid having sex with relatives (Westermarck 1922). This is one reason why it is standard practice in many households to separate girls' rooms from boys' rooms. But as universal as incest avoidance seems, the way bedrooms are set up differs in homes in Chicago compared to homes in Orissa, India (Shweder et al. 1995). Both populations value incest avoidance equally, but the next most important thing in Western homes is what Richard Shweder and his colleagues called "the sacred couple," whereas in Hindi homes it was "protection of the vulnerable."

The debate over whether incest avoidance is a human universal or not has led one researcher (DeMause 1991) to go so far as to make the exact opposite claim: that incest (and *not* its avoidance) is universal. The point here is that universals do exist, but what they are and to what degree they manifest themselves are often contentiously debated (Norenzayan and Heine 2005). The debate over the universality of psychological traits has lent itself to bitter acrimony over some of the most commonsense notions. Take, for example, when Paul Ekman showed that facial expressions are understood worldwide. He was called a racist and his idea (as unifying as it seems) was considered appalling by many. One of Ekman's own colleagues shouted at him in a

conference calling his ideas "fascist" (Pinker 2002).

Making the case for universality is often rife with friction when certain topics are investigated. Consider the research showing that male and female humans tend to guard their mates from mate poachers. In Western societies, methods of mate retention and guardianship vary within and between genders ranging from vigilance to violence (Buss 1988). In addition to this, there are cross-cultural differences seen as well. In many Muslim majority countries, for example, the hijab and other forms of guardianship have been used to keep poachers at bay and to preserve chastity and virginity. In fact, when environmental pressures increase, as one would predict (see next section), stricter mate-guarding practices are employed in the form of religious veiling (Pazhoochi et al. 2017). Mate guarding is seen throughout the animal kingdom as well including but not limited to giraffes (Bercovitch et al. 2006), jumping spiders (Elias et al. 2014), and the blue crab (Jivoff and Hines 1998).

To sum up, evidence from cross-cultural psychology as well as ethological studies support the idea that innate psychological traits exist in humans. It is clear that many hundreds of these human generalizations exist (Brown 1991), but what is also incontrovertible is the rich variation in the expression of these cultural traits.

Context Matters

There is a common misconception among social scientists who believe evolutionary psychology posits that psychological adaptations are solely determined by genes. Nothing could be further from the truth, and, in fact, many evolutionary theorists spend considerable portions of their careers refuting such misattributions. Evolution is not merely driven by incremental genetic mutation. Evolution is genetic mutation *plus natural selection* (Dawkins 1976). Similarly, evolutionary psychology is not simply about biological mechanisms; it is also about the environmental pressures that selected for these adaptations in the first place (Al-Shawaf et al. 2019; Cohen 2001). It was

not Darwin's "theory of evolution" but rather his "theory of evolution by natural selection" that he (and not Alfred Russel Wallace) was eventually given credit for (Schultz and Schultz 2012).

Indeed, the composite forces that shaped individual traits across deep time are discussed in such depth (Buss 1999) that evolutionary theorists have even provided specific nomenclature for it in order to test their hypotheses. The *environment of evolutionary adaptedness* (EEA) is the combination of elements that selected for certain traits (Tooby and Cosmides 1992). The EEA is not confined to one single place or time but rather refers to a host of environments of change. Whether the focus is on the evolution of bipedal locomotion, how humans moved from hunter gatherers to agrarian societies, or the many forms of eyes that evolved on our planet, evolutionary psychologists have long maintained that context plays a crucial factor in the selection of phenotypes – both physical and behavioral.

Cultural Variation

Why is it that some cultures, like the Sambia of Papua New Guinea, are still tilling the earth with stone tools while Europeans along the Franco-Swiss border are smashing subatomic particles at CERN? On the surface, this question may seem like a joke made in poor taste or a trope that could ultimately wax into unfalsifiability and the jingoistic rhetoric of Manifest Destiny. This is hardly a joke. In fact, this question is a complicated one and has been put forth in a different form by Jared Diamond in his Pulitzer Prize winning book, *Guns, Germs, and Steel* (1997). In it, Diamond investigated why it was the Spaniards who invaded the Americas and conquered the Incans and not the other way around.

To those who wrongly adhere to the Myth of the Noble Savage (Pinker 2002), the explanation would be that the Incans were peacefully living in harmony with nature and therefore had no desire to invade anyone. The evidence obviously contradicts this supposition when one takes even a cursory glance at the Incan's military campaigns (Espinoza 1981). On the other hand, a biological

determinist might say that the Incans had "inferior genes" and, as a result, were unable to develop the cultural tools necessary to cross the Atlantic and slaughter the Spaniards. However, this idea also collapses when scrutinized. The genetic differences between Incans and Spaniards are relatively small and could not by themselves account for such vastly disparate cultural adaptations (Heine 2008).

Learned Is Not the Opposite of Evolved

Given that the context a trait evolves in matters tremendously in the outcome of phenotypes (with "culture" being very broadly defined as a phenotype) and that variation in cultures exist around the world, questions arise: Why does culture vary at all?

It often is stated by anthropologists and cultural relativists that cultural variation exists simply because things are learned. But this is only partially correct. The mistake in labeling something as "learned" or "evolved" comes from ignoring whether one is looking at a psychological trait from a proximate lens or a distal one. For example, from a proximate point of view, we know that Pizarro defeated the Incans because his men had horses, rapiers, and muskets. From a distal point of view, the reason his men possessed these items (as well as resistance to certain germs) and Atahualpa's men did not, had to do with the abundance of wheat, grain, barley, and livestock that Pizarro's ancestors evolved in (i.e., their *EEA*) (Diamond 1997).

According to Diamond (1997), the origins of inequality have had less to do with simply having the right ideas as they have with the ancestral ecology one's people evolved in. Claiming that variation in cultural values and beliefs are simply the result of bad ideas versus good ideas would be committing the blank-slate error. Ecological variability in the environment, plus sociocultural input mechanisms, combined with the interaction of innate psychological primitives across deep time has yielded "if-then" strategies (Norenzayan and Heine 2005). In short, different environments have yielded different cultures

where innate psychological mechanisms were selected for by the environment. More specifically, the brain is a biological organ designed by natural selection to extract information from different environments ultimately giving rise to different cultures with similar core underpinnings (Al-Shawaf et al. 2019; Cohen 2001).

While common universal traits exist, ecological forces are known to have tailor-designed sociality across a broad range of biological taxa. For example, when cross-cultural psychologists have looked at gender and the division of labor across cultures and time, it is clear that those cultures that evolved in benign environments have more egalitarian gender roles than those that evolved in harsh environments (Alesina et al. 2013; Boserup 1970; Cohen 2001; Gilmore 1990). The environment has also played a key factor when researchers looked at culture of honor (Nisbett and Cohen 1996; Shackelford 2005), the varying degrees of penalty high moralizing gods mete out to transgressors (Botero et al. 2014), and human mating strategies (Buss 1999).

Conclusion

Thought experiment: imagine if we sent a spaceship with a load of microorganisms across the cosmos. This is precisely what Francis Crick and Leslie Orgel had proposed in 1973. Imagine this pod of genetic material landed on three different planets with slight variations in their ecologies. What would one expect to see over time? The most likely prediction from this is that organisms would evolve on those planets making them all alike and all different. They would be all alike because the origins of their genetic makeup were from a common source. And they would all be different simply because the ecologies that the genetic seeds evolved in across deep time allowed for variation in the affordances provided to those organisms. Hence, the environments on these hypothetical planets would select for different genetic traits ultimately leading to variations in culture. It would be erroneous to conclude that variations in cultures that existed on these planets

were simply due to learned behavior without taking into account genetic similarity as well as ecological variation.

Cross-References

- ▶ [Cross-Cultural Psychology](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Nature](#)

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Cross-Cultural Variation

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Synonyms

Cultural differences; Cultural heterogeneity;
Multi-cultural

Definition

Cultural variation is the degree that one culture differs from another on any continuum of comparison. It is best to think of these continuums as ranges of behavior; i.e., no one culture or person exclusively exhibits one end of the continuum. Variations may exist on any number of levels.

Introduction

Defining culture is a complicated endeavor given its variation across domains and purpose,

which is embodied within a historical context. Roseberry-McKibbin (2007) defines culture as, “Simply, culture is a dynamic set of values and belief systems that shape the behavior of individuals from various groups and communities” (p. 104). Hence, culture shapes how people live, interact, and interpret the world around them as well as what people value. For example, one culture may value independence and autonomy, while another values dependence and cooperation. Culture or shared patterns of behaviors, thoughts, feelings, attitudes, and values may differ according to membership of racial, ethnic, religious, or social groups (Zion and Kozleski 2005). Furthermore, culture can also differ between gender, class, physical and mental abilities, religious and spiritual beliefs, sexual orientation, and age.

What Is Culture?

Culture can be defined according to various continuums of behavior, individualistic versus collectivistic cultures, loose cultures versus tight cultures, low-context versus high-context communication styles, and horizontal versus vertical cultures (Triandis 2001). These continuums are not absolute; for example, individuals from collectivistic cultures can display behaviors that are individualistic. Cultural variation is the degree that one culture differs from another on any continuum of comparison. It is best to think of these continuums as ranges of behavior; i.e., no one culture or person exclusively exhibits one end of the continuum. Variations may exist on any number of levels.

Individualistic Versus Collectivistic Cultures

Individualism is the broad value of tendency of a culture to emphasize individual over group identities, individual over group rights, and the individual’s personal needs over a group’s needs (Ting-Toomey and Chung 2012), whereas collectivism, on the other end of the spectrum, refers

to broad tendencies of a culture to emphasize the value of the “we” group identity over the “I” individual identity. Group obligations dominate over an individual’s rights, and in-group-oriented needs are seen as more important than any individual’s wants and desires.

Individualistic cultures define the self apart from the group and as independent. The focus tends to be on the person and not so much on the group (Ting-Toomey and Chung 2012). Individualistic cultures explain one’s behaviors on personal attributes, e.g., Fernando seeks the teacher’s approval because he needs reassurance. Individualistic cultures tend to stress the “autonomous self” (Ting-Toomey and Chung 2012), where one portrays oneself outward, and face is self-oriented and self-driven (Triandis 2001). Individualistic cultures stress direct and overt communication. An example of overt and direct communication is seen in the “get to the point” style of speaking.

In comparison, collectivistic cultures value a more indirect style of communication, an emphasis on social interactions, and avoidance of confrontations. Confrontations are seen as loss of face. Belonging to the group is a main tenet of collectivistic culture (Gudykunst 2003; Triandis 2001). Cohesion and group participation are of utmost importance (Brice and Campbell 1999). Behaviors are explained by norms or standards of expected behavior, e.g., Fernando seeks teacher approval in order to belong to the group. “Face” is important in group cultures which emphasize group orientation (Gudykunst 2003). Membership in group cultures permits the right to be involved in the affairs of others; e.g., uncles, aunts, grandparents, teachers, or professionals may mediate on another’s behalf. Latino cultures, Asian cultures, Middle Eastern cultures, African cultures, and others exemplify collectivist cultures.

Loose Versus Tight Cultures

Cultures that have strong societal norms with low tolerances for aberrant behavior are defined as tight cultures (Carpenter 2000; Gelfand et al. 2011; Parker et al. 2009; Realo et al. 2014). Tight

culture and group cultures (i.e., collectivistic) have strong distinctions between in-group and out-group membership. Loose cultures typically have weak norms with high tolerances for aberrant behaviors (Gelfand et al. 2011).

Individualistic cultures are associated with loose cultures, whereas tight cultures are associated with collectivistic cultures (Brice and Campbell 1999). Looseness carries the substance of creativity. This is seen in language in word puns and humor. However, it should be noted that not all cultures will exhibit all behaviors consistent with either end of the individualistic/collectivistic or tight/loose continuums. For example, Cuban culture exhibits traits of creative language use with puns and witty language; however, Cuban culture tends to display itself along collectivistic and tight ends of the culture continuums (Brice 2002).

The USA is seen as a loose culture, while Japan is considered to be a tight culture (Gelfand et al. 2011). Whitting (1989) compares Japanese and US American in-group versus out-group cultures. He uses American versus Japanese baseball as cultural contrasts. Whitting (1989) stated that “All the managers manage differently here. I mean they manage Japanese style. And I do it more or less U.S. Style. So I’m the one that’s different really” (p. 143). Whitting emphasizes this point by stating that, “Many Japanese will argue that a foreigner should never be allowed to manage a Japanese baseball team” (p. 143).

Low-Context Versus High-Context Communication

The concepts of low-context and high-context communication were first introduced by Hall (1983). Low-context communication relies less on environmental context for interpreting the meaning of the message; instead, most of the message is in the spoken or printed words (e.g., print or formal communication such as speeches). Interaction between the speaker and listener tends to be minimal. Low-context communication is evidenced by logical and linear thoughts. Direct verbal and nonverbal interactions, overt

communicative intentions, and sender-oriented values are seen in low-context communication and typical in individualistic cultures (Ting-Toomey and Chung 2012). Low-context cultures tend to attribute behaviors to the individual’s personality, e.g., “That is just Charlie.”

High-context communication attributes behavior to an external locus of control or where one places responsibility for actions and to societal norms (Brice and Campbell 1999). One acts according to norms of how one is supposed to behave. High-context communication uses indirect styles of speech and includes multiple tangential, indirect conversations. The tangential conversations are seen to add to the big picture of the communication, i.e., relevant to the general message. Communication is achieved via verbal negotiations and use of subtle nonverbal nuances. Low-context communication messages are direct and “to the point.” Brice (2002) stated that Cuban-Americans exhibit a more indirect communication style. Discussion of family, friends, employment, etc. almost always precedes the main intent of the message.

Horizontal Versus Vertical Cultures

Culture can also be defined according to the horizontal versus vertical continuum. Group or individualistic cultures may either be horizontal or vertical on this continuum. The horizontal perspective emphasizes that individuals are similar and equal on most aspects especially that which involves rank or status; hence, this perspective emphasizes sameness. The vertical perspective emphasizes rank and privileges of rank even if inequalities associated with rank are present (Triandis 2001). Hence, this perspective emphasizes difference. Therefore, when the collectivistic-individualistic continuum is combined with the horizontal versus vertical continuum, then there are four possibilities: (a) collectivistic horizontal (group/same); (b) collectivistic vertical (group/rank and difference); (c) individualistic horizontal (individual/same); and (d) individualistic vertical (individual/rank and difference).

Individuals from a collectivistic horizontal (group/same) culture stress group values, social cohesion, cooperation, and equality among members. Israeli kibbutzim members both are group oriented and stress membership equality.

Collectivistic vertical cultures which are group/difference oriented show traits of belonging to a group yet maintain clear class and rank differentiations. In Japanese language and culture, the word and concept of “*giri*” signifies obligation, honor, duty, and burden. One is obligated to the group and also bound to superiors in completing one’s honor (i.e., especially to the family and to elder) over one’s individual wishes and desires. A rank model is also evident in language and the honorifics or etiquette in how one addresses others. One address others based on their rank, status, and/or hierarchy in relation to oneself. In Japanese, one may add the affix “*san*” to another person’s name that is at the same level as oneself. “*Sama*” is generally reserved for elders, especially family members (e.g., *otosama*, father; *okasama*, mother). “*Chan*” may be used as endearment for children. “*Sempai*” (mentor) is used for those with seniority, typically in workplaces. However, “*kouhai*” means the opposite of “*sempai*” denoting someone of a lower ranking. In addition, it is considered rude to employ such terms when speaking with those individuals.

Individualistic horizontal cultures (individualistic/same) place emphases on uniqueness and sameness. Sweden and Finland are examples. All individuals are seen as the same; therefore, there is no need for formal communication. What may be seen as intrusive in a rank-oriented culture is seen as typical in a horizontal culture. Living independently is a valued trait. Parents and grandparents do not live with their offspring children. Individual horizontal cultures are often seen in democratic socialistic governments (such as the Scandinavian countries).

Individualistic vertical cultures (individual/rank) focus on self-achievements and obtaining higher status. Individuals behave in ways to be recognized on one’s merits, especially if that places one at a higher social status. Taking

“selfies” and/or posting on social media illustrate the importance of the individualistic culture and how to stand out from others. Rank is evidenced in the form of titles (e.g., Instructor, Lecturer, Assistant Professor, Associate Professor, Professor). The CEO of a company or Dean of a College have the expected honor of having more “talk-time” in a meeting than employees or subordinates. Those in superior positions may be more direct or blunt in communications.

Culture and Language

The separation of cognition and language and how language is acquired is still debated. However, most researchers will agree that cognition and language are intertwined to some extent (i.e., whether a weak or strong connection exists). The role of language and culture has also been extensively disputed. The theory of linguistic relativity is discussed next.

The theory of linguistic relativity suggests that language affects how individuals see and construct their world (Hill and Mannheim 1992; Lucy 1997). Lucy defines linguistic relativity as, “The linguistic relativity hypothesis, the proposal that the particular language we speak influences the way we think about reality, forms one part of the broader question of how language influences thought” (p. 291). Linguistic relativity evolved from the earlier works of Benjamin Whorf (Whorf 1956). Whorf believed that difference in language grammars and how the languages are used affects the manner and way in which the speakers perceived the world and their environment. One can postulate that language is constructed and learned and, therefore, a reflection of culture (Lucy 1997).

Conclusion

Everyone possesses a unique cultural mosaic made up of different attributes. Whether one is collectivistic or individualistic; displays an internal versus external locus of control; is male or

female; is young, middle-aged, or old; is from low, medium, or high SES; or is short or tall makes everyone different. Our cultural mosaic makes us culturally unique. As educators, we need to realize the rich mosaic tapestry of who we are, and this is how culture should be viewed for everyone and not just for certain ethnically diverse individuals. This reminds us that stereotypes and biases can be reduced with greater awareness of cultural differences. However, it should be noted that no one culture or person exclusively exhibits one end of the continuums that have been examined (or any others) and that these continuums, as ranges of behavior, are not absolute.

Cross-References

- Culture of Honor
- Culture of Honor and Individual Differences
- Evolution of Culture
- Men's Violence Against Female Partners: The Role of Culture
- Personality, Gender, and Culture
- Relationship Between Culture and Race

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Cross-Cultural Variation in Intimate Partner Violence

- Unique Patterns in the United States

Cross-Sex Antagonistic Pleiotropy

- Intralocus Sexual Conflict
- Intralocus Sexual Conflict Across the Genome

Cross-Sex Friend

- Gender of Friend

Cross-Species Comparisons

► [Paul Vasey](#)

Crowds

► [Peer Groups](#)

Crows

► [Fairness in Corvids](#)

Crucial Time

► [Critical Period](#)

Crying

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Synonyms

[Bawling](#); [Blubbing](#); [Lachrymation](#); [Lacrimation](#); [Moaning](#); [Snivelling](#); [Sobbing](#); [Tearing](#); [Wailing](#); [Weeping](#); [Whimpering](#)

Definition

Welling of tears or shedding of tears from the eyes in response to internal emotional states, often accompanied by vocal emissions, irregular and interrupted breathing, and tremors.

Introduction

Tear or lacrimal fluid is produced in the lacrimal glands, situated above each eye and slightly askew to the side of the head. The tears moisture and lubricate the eye bulb, and their excess is drained into the nasal cavity through the *lacrimal canaliculi* at the upper and lower eyelids, close to the nose. Thus, both increased production and decreased evacuation of tear fluid result in visible wetting of the eye, eyelids, or cheek. To cry means literally to produce loud vocal sounds (from French *crier*, from Latin *quiritare*; to wail), while the term for shedding tears specifically to express grief or some other emotion is weeping (e.g., Chambers 2019), as noted by Bellieni (2017). To some confusion, crying colloquially and contemporarily designates weeping. These terms will be used interchangeably while noting that the term crying is more common and more explicitly implies the vocal emissions that are often and typically associated with weeping as an emotional expression. The pure shedding of tears regardless of cause and function seems therefore to be reserved for the technical term lacrimation, which may occur as a reaction to physical or chemical irritants, like smoke.

These functions and their etiology largely remain a mystery, although some general patterns have been established (for reviews see, e.g., Vingerhoets et al. 2001). Crying is very common throughout infancy and childhood and then drastically decreases in adolescence. Most people weep occasionally in adulthood, females much more often than males, but the individual differences are huge. In fact, the frequency of weeping may be the largest psychological sex difference, where females weep between four (Frey et al. 1983) and seven times more often (Kraemer and Hastrup 1986). Likewise, females tend to weep for longer periods than men and tend to be more prone to flowing tears and sobbing, whereas males more often become lachrymose without actually shedding tears (Bindra 1972). Another entry is devoted to sex differences in crying (Madison and Dutton 2019). Crying increases again in late adulthood and in old age, while the sex difference decreases. One study found that in their 40s, males

had cried on average 5.5 times and females 29.3 times in the last 12 months, whereas in a group approaching 70 years of age, the frequencies were 16.3 for males and 31.1 for females (Hastrup et al. 1986).

Crying is elicited by the sympathetic system, which prepares the organism for fight or flight and which typically also causes increased arousal, heart rate, and sweating, as well as slowed breathing. Side effects of crying are partly caused by the sympathetic response, such as quivering lips, cracking voice, and the sensation of a lump in the throat. This so-called globus sensation is caused by trying to close the *glottis* (ultimately to prevent food from entering the *larynx*), while the sympathetic response expands the glottis to increase airflow. Another side effect is that the flow of excess tears through the *lacrimal canaliculi* makes the nose run. The lacrimal system and its reflexive responses to irritants is present in many species, but in humans it also serves functions of emotional processing and social communication. There are anecdotal observations of lacrimation for some mammal species in situations likely to evoke emotions related to sadness and loss, but the evidence for weeping in nonhuman animals is weak (Frey and Langseth 1985).

Functions of Crying

One of the things we know is that crying is associated with sadness or grief, such as when mourning the death or illness of a loved one. The most important thing to know, however, is that crying is a complex, multifaceted phenomenon that exhibits many inconsistencies. Thus, people do not always weep when they are sad, and they do sometimes weep for quite different reasons. In a sample of 800 weeping episodes in typical women, 49% were associated with sadness, 21% with happiness, 10% with anger, and 7% with sympathy, and the remaining 13% were rather evenly distributed across anxiety, fear, and “other” (Frey et al. 1983). Inferred causes for crying in infancy include fatigue, hunger, fear, and loneliness (Catherine and Schonert-Reichl

2011), while self-reported reasons for adult crying include problems with interpersonal relations, sad thoughts, and media. Media refers mainly to fiction, such as movies and TV series, and accounts for about one third of all weeping episodes for both sexes (Frey et al. 1983). Four factors in particular should be considered in order to understand group differences in crying, namely, the exposure to emotional stimuli, the appraisal of these stimuli, social learning, and the threshold for beginning to cry (Vingerhoets et al. 2009, p. 451). Whether crying occurs in response to a certain event or emotional state furthermore depends on many other factors, such as one’s age, sex, being alone or in the company of others, one’s relation to those other people, and so forth (Vingerhoets et al. 2001). It is therefore not surprising that a range of quite different functions and theories for crying have been proposed.

Some of them focus on intraindividual functions, where the physiological processes of crying somehow lead to relief and recovery from distress, regardless of its origin being within or outside the individual (Frey et al. 1983; Stougie et al. 2004). More specifically, crying has been conceived of as part of a two-stage process, where it is preceded by a buildup of arousal, tension, or anticipation, which is then alleviated (Efran and Spangler 1979). Several reviews discuss these functions and the evidence for and against them (Rottenberg et al. 2019; Stougie et al. 2004; Vingerhoets et al. 2009).

Other theoretical explanations focus on inter-individual functions in terms of communication and social support, as reviewed by Bellieni (2017), Miceli and Castelfranchi (2003), and Vingerhoets et al. (2009). A recurrent theme is that crying ultimately signals helplessness and so prompts help and support from others (Miceli and Castelfranchi 2003). This should be seen in light of the fact that more than 70% of respondents rated that they were most likely to cry alone, at the same time as they were next most likely to cry in the company of a close female friend (said 53% of males and 86% of females) (Lombardo et al. 2001). Consistent with the help-seeking hypothesis, respondents reported that they would give more emotional support to and express less

negative affect toward a weeping person (Hendriks et al. 2008).

Finally, tears are elicited in response to certain profound experiences, such as religious fervor and appreciating the aesthetic beauty of works of art in painting, poetry, music, and sculpture, for example, although the explanation for this is unclear (but see Miceli and Castelfranchi 2003).

Etiology of Crying

As mentioned it is unclear if weeping occurs in any species except humans (Vingerhoets et al. 2009, p. 440). None of several suggested explanations has received convincing support. One example is that the smoke from fire used in funeral cremations or farewell ceremonies caused lachrimation, which led to associating tears with sadness and loss. This seems implausible because smoke would have occurred much more often in daily activities also associated with stress and stress relief, like cooking and keeping warm, without those becoming associated with tears (see Bellieni 2017).

Conclusions

Crying is a human universal and most likely an evolutionary adaptation, although its ultimate adaptive value and etiology remain poorly understood. Cross-cultural surveys exhibit similar patterns, most prominently that females cry more than males and that respondents report feeling better after crying (Becht and Vingerhoets 2002; Rosenblatt et al. 1976). The literature contains a wide range of empirical findings, relating crying and crying-related behavior to a host of other variables than those mentioned above. These variables include alexithymia, anhedonia, attitudes toward crying and people who cry, brain structure and brain activation, coping, depression, femininity and masculinity, hormones, individualism and collectivism, mood, and personality traits. They furthermore include shame, socioeconomic status, social connectedness (Vingerhoets et al. 2016),

and national estimates of gender equality/empowerment (Fischer et al. 2004), as well as specific constructs such as affective empathy, cognitive empathy, anxious attachment, and avoidant attachment (Denckla et al. 2014). This means that there exists a nexus of associations with crying and weeping, which taps a wide range of social dimensions, including friendship, family relations, social status, and power dynamics. Because of their large effect size, associations that involve sex differences would be particularly powerful. Thus, this rich nexus may be utilized for assessing evolutionary-based hypotheses that involve interactions between sex, crying, and other social behaviors (e.g., Vigil 2008).

Cross-References

- Communication, Cues, and Signals
- Manipulation and Dishonest Signals
- Sex Differences in Crying
- Types of Crying

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Crying Diversity

► Types of Crying

Crying Versatility

► Types of Crying

Cryptic Female Choice

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Synonyms

[Female-biased postcopulatory sexual selection;](#)
[Sperm choice](#)

Definition

A female mate choice occurring during or after copulation.

Introduction

Sexual selection, the selection pressure selecting for traits that increase reproductive success of individuals, can in principle operate through processes occurring both before and during/after copulations and being male or female driven. Prior to copulation, these are typically seen as male-male competition of access to females as mating partners and female choice of mating partners. When females mate with multiple males (i.e., are polyandrous), these processes can continue during or after copulations as sperm competition and cryptic female choice, respectively. The latter is a female postcopulatory mate choice where females bias

fertilization in favor of certain males, based on the phenotype of the male or his sperm (Eberhard 1996). The term is called “cryptic” because this form of female choice can be hard to observe, for example, in internal fertilizing species. Cryptic female choice is the part of sexual selection that to date is the least studied and is likely a consequence of this.

The research field cryptic female choice originated during the early 1990s, and the book that convincingly established cryptic female choice as an important component of sexual selection is the seminal book *Female Control: Sexual Selection by Cryptic Female Choice* (Eberhard 1996). With the development of techniques, the number of studies investigating and demonstrating cryptic female choice is increasing (but see below, [Defining and Demonstrating Cryptic Female Choice](#)). Females from all studied taxa have now been shown to be able to affect the outcome of a copulation and also to bias paternity, and in some cases the stage in the reproductive event in which this occurs is demonstrated.

Defining and Demonstrating Cryptic Female Choice

The definition of cryptic female choice diverges some, ranging from being general, such as “a female choice occurring during or after mating” (Thornhill 1983), to being very broad, such as “a female controlled process or structure that selectively favors paternity by conspecific males with a particular trait over that of others that lack the trait when females has copulated with both types of males” (Eberhard 1996) or be more specifically pinned down to be a mate choice carried out by a female, occurring at a postcopulatory stage disentangled from pre-copulatory processes and male adaptations to sperm competition (Birkhead 1998, 2000). Then again, due to the complex interactions that can occur between the sexes during and after copulation and because male adaptations

to sperm competition can be hard to disentangle from cryptic female choice, both processes have been suggested to jointly be called postcopulatory sexual selection (Birkhead et al. 2009).

As a consequence of what definition is used, how commonly cryptic female choice is demonstrated will differ. Based on Eberhard’s very broad definition of cryptic female choice, numerous potential mechanisms can take place by which females can conduct postcopulatory choice. These are ranging from female behavior during copulation to female physiology and morphology and to varying investment in offspring. Based on this definition, Eberhard claims that there are numerous examples of cryptic female choice in the animal kingdom (Eberhard 1996).

There is no doubt that there is great scope for females to potentially be able to have control on the outcome of mating and bias fertilization. Nevertheless, when using a more narrow definition of cryptic female choice, including only postcopulatory processes that are demonstrated to be female driven while ruling out pre-copulatory processes and male-driven processes (Birkhead 1998, 2000), the examples of when researchers have been successfully able to demonstrate cryptic female choice are reduced. This is because there are many and often complex ways in which males and females can interact both before and during copulation, in addition to how ejaculates and females, and sperm and eggs, can interact (Birkhead et al. 2009). It can therefore be challenging to separate pre- from postcopulatory processes and to separate the interaction of male adaptations to sperm competition and female influences on fertilization. If using paternity to infer cryptic female choice, variation in differential embryo mortality separated from female-induced biases in paternity should also be demonstrated (Birkhead 1998). This again highlights that separating cryptic female choice from other processes can be difficult, which in turn makes the study of cryptic female choice hard.

Mechanisms Used to Bias Sperm Use by Females

Independent of the applied definition of cryptic female choice, there are in principle four stages through which females have the potential to bias paternity: before, during, and after copulation (but before fertilization), or following fertilization (Birkhead and Møller 1998), and many stages in the female reproductive tract where biases can in principle occur (Birkhead and Brillard 2007). A cryptic female choice can thus in principle be explained in a range of behavioral, physiological, chemical, morphological, and genetic processes through which females can potentially bias paternity. For example, females can have control of oviposition and by biasing speed of oviposition, for example, to occur directly after a mating or delay it until she has remated can affect the paternity of the offspring. There is often a lot of variation in female reproductive tract morphology which in turn can explain a bias in paternity of offspring produced by these females. How actively females can use this in their favor is however less clear. Females of species as different as rodents, squid, and insects have been demonstrated to actively remove spermatophores, copulatory plugs, or ejaculates after copulation has occurred. Similarly, female differential ejaculate ejection (or sperm ejection) is observed in some mammals and birds (Birkhead and Pizzari 2002), while female sperm dumping is demonstrated in fruit flies (*Drosophila melanogaster*). Even if accepting an ejaculate, females may potentially have the ability to bias the transport of sperm to and from sperm storage organs in a manner that can affect female sperm use and bias paternity. Such biases have been demonstrated in insects to be explained by genetic relatedness between the male and female. In fishes, the ovarian fluid around eggs can affect sperm in ways biasing paternity, for example, by increasing sperm velocity of certain males. Sperm-egg interactions directly can also affect fertilization success, explained by genetic compatibility among the gametes. In external fertilizers, in other words

species where sperm and eggs are released into the water and fertilization is not occurring internally, cryptic female choice through gamete interaction can be the only way females may be able to affect fertilization. Finally, cryptic female choice can in principle also occur through a post-insemination pre-fertilization female bias meaning that the female may in some cases be able to perform a choice also occurs after insemination, before the pronuclei of males and females have fused (Carré and Sardet 1984, in Birkhead and Pizzari 2002). Although examples so far are from the animal kingdom, cryptic female choice can also occur in plants through similar processes as observed in animals, for example, gamete incompatibility and selection at the gamete level.

Conclusion

Females being able to bias fertilization through processes occurring during or after copulation enables females to increase control of paternity. There is a broad range of ways through which females may do this, ranging from behavioral to genetic interactions between individuals or gametes. Nevertheless, this cryptic female choice is often very hard to disentangle from processes occurring prior to mating, or that are male driven. As a consequence, studies clearly demonstrating this likely important and potentially widespread female mate choice are still relatively rare.

Cross-References

- ▶ [Avian Sperm Competition](#)
- ▶ [Circumventing Mate Choice](#)
- ▶ [Evolution of Female Resistance](#)
- ▶ [Female Choice and Sexual Conflict Theory](#)
- ▶ [Female Mate Choice](#)
- ▶ [Female Mate Choice \(Intersexual Selection\)](#)
- ▶ [Female Sneak Copulation](#)
- ▶ [Forced Copulation](#)
- ▶ [Insect Sperm Competition](#)
- ▶ [Male Qualities and Likelihood of Orgasm](#)

- ▶ Mate Choice effects
- ▶ Multiple Matings
- ▶ Non-Primate Mammal Sperm Competition
- ▶ Paternity Uncertainty
- ▶ Observed Mating Behavior and Women's Long-Term Mating
- ▶ Reproductive Strategy
- ▶ Sexual Coercion
- ▶ Sexual Coercion as a Mechanism of Sexual Selection
- ▶ Sexual Selection
- ▶ Sperm Competition
- ▶ Sperm Competition Risk and Partner Abuse
- ▶ Sperm Competition Tactics
- ▶ Sperm Competition Theory

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Cryptic Ovulation

- ▶ Concealed Ovulation

Cuckoldry

- ▶ Male Sexual Jealousy to Deter Partner Infidelity
- ▶ Men's Suspicions of Partner Infidelity and Women's Defection
- ▶ Paternity Certainty
- ▶ Paternity Confusion
- ▶ Paternity Uncertainty and Investment in Sons and Daughters
- ▶ Paternity Uncertainty Hypothesis
- ▶ Sexual Infidelity Versus Emotional Infidelity

Cuckoldry Risk

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Synonyms

Paternal uncertainty

Definition

The likelihood that a male is unknowingly investing in a child that he did not father.

Introduction

One of the most recent and by far most comprehensive attempts to examine the risk of being cuckolded among human males was undertaken by Anderson (2006) based on a meta-analysis of the world's literature on paternity testing comprising over 75 articles. The incidence of nonpaternity rates from paternity testing laboratories ranged from 14.3 % to 55.6 %. The problem of course is that men do not petition for paternity testing out of idle curiosity. So Anderson

partitioned the incidence of nonpaternity into males with high paternity confidence (i.e., males who had no reason to question their paternity) and those with low paternity confidence. Among those with high paternity confidence the incidence of nonpaternity was approximately 2 %, or one out of fifty. However, for those who had reason to question their paternity (men with low paternity confidence), the incidence of nonpaternity was 30 %.

Paternal Uncertainty

While the incidence of nonpaternity varies as a function of paternity confidence, Anderson argued that nonetheless the incidence of paternity remains higher than the incidence of nonpaternity under most circumstances. However, it is important to realize that the risk of nonpaternity (i.e., being cuckolded) among males with low paternity confidence was a staggering 15 times higher than those with high paternity confidence. Thus there would appear to be some pretty sophisticated evolved mechanisms operating that function to inform males about nonpaternity, i.e., males who harbor questions about paternity are far more likely to have been cuckolded.

The other way to think about these dramatic differences in nonpaternity as a function of paternity confidence is that nonpaternity is a proxy for female infidelity. Because the likelihood of conception as a consequence of a single random sexual encounter is low (some estimates put it at one in a hundred) it means that the incidence of nonpaternity is the mere tip of the iceberg when it comes to the underlying incidence of female infidelity. Women do not get pregnant every time they engage in infidelity. In fact, the majority of cases of nonpaternity are probably a by-product of one or more established, long-term extra pair liaisons between a woman in a committed relationship and one or more extra pair males.

Anderson's sample included data on the incidence of nonpaternity all over the world, and since he found that the incidence of nonpaternity did not vary as a function of geography, culture, or ethnic group status it seems reasonable to conclude that nonpaternity and

female infidelity are cross-cultural universals. Moreover, there are reasons to believe that these estimates of nonpaternity are relatively conservative since effective contraception was not an option during most of human evolutionary history.

Conclusion

Indeed, since the data Anderson used included cultures that have liberal attitudes concerning human sexual behavior along with those that are much more restrictive and conservative, it suggests that being "sexually liberated" affects what people say – but not what they in fact do.

Cross-References

- ▶ [Extrapair Copulation](#)
- ▶ [Infidelity](#)
- ▶ [Mate Guarding](#)
- ▶ [Paternal Resemblance](#)
- ▶ [Paternity Uncertainty](#)
- ▶ [Sperm Competition](#)

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Cues

- ▶ [Cues to Infidelity](#)
- ▶ [Fitness Benefits of Costly Signalling](#)
- ▶ [Observations of Sexual Dimorphism](#)

Cues of Being Watched

- ▶ [Altruism and Watching Eyes](#)

Cues of Female Estrous

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Unlike some other female primates, women do not display obvious sexual swellings during the high-fertility phase of their ovulatory cycles. This simple observation has led some researchers to assume that women's ovulatory status is completely concealed (Gangestad and Thornhill 2008). By contrast with this assumption, however, several lines of recent research suggest that women do display detectable cues of their ovulatory status, albeit ones that are considerably more subtle than those observed in some other primates.

For example, studies have presented evidence that women's clothing choices can act as a cue to their ovulatory status (Durante et al. 2008; Haselton et al. 2007). Women tend to display more bare skin and wear clothing judged by others as an attempt to look more attractive during the high-fertility phase of the menstrual cycle than they do during low-fertility phases (Durante et al. 2008; Haselton et al. 2007). Relatedly, women are more likely to wear red clothing (a color thought to increase women's sexual attractiveness, Elliot and Maier 2014) during the high-fertility phase of the menstrual cycle than during low-fertility phases (Beall and Tracy 2013; Eisenbruch et al. 2015). Although these results suggest that women's clothing can act as a cue to their ovulatory status, these findings have not replicated consistently in subsequent studies, suggesting they are not necessarily robust (Arslan et al. *in press*; Blake et al., 2017).

Further evidence that women display detectable cues to their ovulatory status has come from studies reporting that women's facial attractiveness increases during the high-fertility phase of the menstrual cycle (Roberts et al. 2004; Puts et al.

2013). These changes in facial attractiveness are not simply a consequence of changes in makeup use or hairstyle (Roberts et al. 2004) and do not appear to be due to changes in either skin coloration (Jones et al. 2015) or posture (Sulikowski et al. 2015). Similar fertility-linked changes in women's vocal (Puts et al. 2013) and body-odor (Gildersleeve et al. 2012) attractiveness have also been reported. Studies have also found that fertility-linked changes in women's body-odor attractiveness are sufficient to trigger changes in men's reported sexual desire and testosterone levels (Mondragón-Ceballos et al. 2013). However, the specific physical characteristics that underpin changes in women's facial, vocal, and body-odor attractiveness during the ovulatory cycle are currently not known.

The studies described above focused on identifying links between women's ovulatory status and specific aspects of their appearance. However, other studies have sought to demonstrate that women display cues to their ovulatory status by investigating changes in men's attitudes to their romantic partners across their ovulatory cycles. For example, women report that their partners engage in more mate-guarding behavior during the ovulatory phase of their menstrual cycle (Haselton and Gangestad 2006). Men also appear to become more attuned to physical cues in potential rivals, such as dominance, that women are thought to value more during the ovulatory phase than at other times (Fales et al. 2014). Findings such as these present converging evidence for the existence of detectable cues of women's ovulatory status.

Although evidence that women display subtle cues to their ovulatory status is accumulating, several important issues remain unresolved. For example, it is unclear whether fertility-linked changes in women's behavior and appearance are signals that evolved specifically to advertise their ovulatory status or are simply either imperfectly concealed cues (Haselton and Gildersleeve 2011) or a by-product of mechanisms that primarily signal between-women differences in hormone levels or fertility (Havlíček et al. 2015).

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Cues to Body Size

► Signals of Body Size

Cues to Height

► Signals of Body Size

Cues to Infidelity

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Synonyms

Cues; Extra-dyadic relationships; Extra-pair copulations; Or markers of adultery; Signals

Definition

Cues that signal one's engagement in a romantic/emotional and/or sexual relationship with someone external to the primary relationship.

Introduction

Infidelity is typically defined as an act that breaks the agreement of monogamy between two individuals who are dating, married, or in a committed relationship (e.g., Hertlein et al. 2009). Infidelity may be emotional and/or sexual in nature and entail involvement with someone outside of the primary relationship, such that there is a breaching of a subjective contract that the couple created (Fish et al. 2012). People engaging in infidelity typically define it themselves as "cheating" on their partner (Walters and Burger 2013).

Infidelity is a well-studied topic within the psychology literature. This attention is not surprising given that it may have harmful consequences for all parties (Altgelt et al. 2018). It is linked to declines in psychological health, increased probability of transmission of sexually transmitted infections and disease, and increased physical abuse, homicide, and suicides (see Jackman 2015). Betzig (1989) reports that it is the leading reason for relationship dissolution in 160 cultures around the world.

Prevalence of Infidelity

The overwhelming majority of people in the United States largely disapprove of infidelity, such that Gallup Poll results indicate 90% consider it immoral while 65% state it is unforgiveable (see Fincham and Way 2017 for a review). However, despite disapproval, rates of infidelity remain high. Therapists who see clients about interpersonal relationship issues estimate that over half of their practice pertains to couples coping with infidelity (Hertlein et al. 2009).

Actual prevalence rates vary dramatically across samples, partly in response to the

population examined, the methods used, and how infidelity is defined. For example, Walters and Burger (2013) review how researchers have labelled infidelity as extramarital involvement, extramarital relationships, extradyadic relationship, extradyadic activity, relationship infidelity, relational transgressions, and extramarital sex. In terms of prevalence, Wiederman and Hurd (1999) report 75% of men and 68% of women say they have engaged in extradyadic relational behavior, such as kissing or sexual intercourse. Mark et al. (2011) found 23.2% of men and 19.2% of women in heterosexual unions stated they had committed sexual infidelity in their current relationship. A far lower rate was found by Fincham and Way (2017), where between 2% and 4% of spouses reported having sex with a secondary partner in the past 12 months, with minimal sex differences in infidelity. Rates of infidelity may be far higher among dating than married individuals (see Jackman 2015). Generally, married individuals report lower rates of infidelity than those who are co-habiting or dating (Adamopoulou 2013). There also seems to be fluctuation due to seasonality: Infidelity peaks during the summer in the United States, which has been theorized to relate to increased travel to a different geographic area, leading to lower probability of the infidelity being detected by a partner (Adamopoulou 2013).

Linking Infidelity with Parental Investment Theory

Infidelity may be viewed from the perspective of lost investment, in that it signals the lack of a partner's commitment to the current relationship (Rusbult 1980). The lost investment can be best understood in light of parental investment theory, with an infidelity being considered primarily sexual or emotional in nature (e.g., Buss and Schmitt 1993). According to parental investment theory, it may be argued that men benefit most from establishing sexual contact with many fecund women. Men have a much smaller obligate parental role in children's lives than women, and therefore, it is thought that they should maximize their number of reproductive

partners and attempt to increase the number of children they sire. Thus, it may be most adaptive for men to have sexual relations with numerous women, including those outside of their committed relationship. However, simultaneously, men are presumed to be especially sensitive to a partner's sexual fidelity. Men are separate from the birth act (i.e., they do not give birth) and thus must rely on second-hand information to determine whether children are genetically related to them. They typically value sexual loyalty in their partners and attempt to avoid misallocated investments of time, resources, and energy into children of interlopers, especially when misplaced investments could harm their abilities to successfully invest in their own genetically related children. Consequently, men are thought to be more distressed by the thought of a partner having a sexual, as opposed to emotional, infidelity (Buss et al. 1992).

Contrariwise, women's obligate investment in parenting is far higher than men's, and consequently, they are argued to be most concerned with finding high-quality mates. Women have been considered reliant to varying degrees on men's resources, particularly when pregnant. Further, men's help with children and potential protection of their children (and the mother) is advantageous. Thus, women are thought to be particularly sensitive to a mate's emotional commitment and would be more distressed by it than sexual infidelity (Buss et al. 1992). Further, women have been reported to be more prone to emotional infidelity (i.e., falling in love or forming an emotional attachment to someone outside of their relationship) than sexual infidelity (Blow and Harnett 2005).

Motives for Engaging in Infidelity

There are various motives for engaging in an infidelity. Glass and Wright (1992) propose four main categories: sexual, emotional, love, and extrinsic (e.g., revenge, career advancement). They detailed that men report more sexual motives than women, while women report more

emotional motives than men. However, they found no sex differences for emotional or extrinsic motivations. Expanding on this idea, Omarzu et al. (2012) asked 22 men and 55 women currently engaged in an infidelity about their reasons for initiating such an arrangement and their perception of the emotional consequences of the infidelity. They largely replicated the earlier findings of Glass and Wright, in that they discovered motivations related to sex, emotional intimacy, love, revenge, and curiosity/excitement. Further, they documented that dissatisfaction with the primary partner (and relationship) was central to sexual, emotional, and love motivations, as was the opportunity for finding additional satisfaction. Both sexes were equivalent in saying that their infidelities were driven by sexual or emotional dissatisfaction with their primary partner. Men, though, were more likely to state they have accepted an opportunity to have more sex, while women were more likely to say they had accepted opportunity to find an emotional connection. Men, alone, said they engaged in infidelity due to sexually based curiosity or excitement.

Cues of Infidelity: Intentions

Detecting cues of potential infidelity is an important research topic for many reasons. At face value, it is informative to examine how individuals perceive subtle signals of other's behavior or intention. However, the detection of cues signaling infidelity may elicit emotions and behavior, specifically jealousy, in a partner. A man's experience of sexual jealousy, in particular, may be harmful toward a woman, as it is the most frequent cause of domestic battery and spousal homicide (Buss and Shackelford 1997). Therefore, detection of cues is a significant area of interest.

To start, infidelity may be detected via one's intentions. One could also examine intentions to commit infidelity. Actual behaviors have been linked to intentions to commit the behavior, which are in turn grounded by one's attitudes toward the behavior and subjective norms (e.g.,

the views or behaviors of those in one's social circles). Jackman (2015), in a study of 347 women and 165 men, found the most significant correlate of infidelity intentions were positive attitudes toward infidelity, which is influenced such that men, those low in religiosity, and individuals who have committed infidelity in the past are more likely to view it positively. Further, those with high self-efficacy and who have a social network that supports their infidelity is important.

Cues of Infidelity: Sexual Excitement and Performance Anxiety

A source of cues is revealed by work on the relational factors that may predict infidelity. Mark et al. (2011) studied predictors of sexual infidelity in 506 men and 412 women who were currently in heterosexual monogamous relationships. They found men's higher propensity toward sexual excitement, higher sexual performance anxiety, and an increased tendency to engage in sexual behaviors they may regret during times of negative affect all predicted sexual infidelity. The authors suggest that concern regarding sexual performance failure may be due to seeking high-risk situations to ensure arousal. It could also be due to participants believing that if their sexual performance is poor, there is no obligation to see the extradyadic partner again, and hence, they are protected from embarrassment or humiliation. For women, infidelity was predicted by higher sexual performance anxiety, but also low levels of happiness within the relationship, and low compatibility with their primary partner regarding sexual attitudes and values. The authors concluded that personality characteristics related to sexuality and for women, relationship features, are more important than other demographic variables such as relationship status, education, income, or religiosity. Returning to the topic of cues, identifying one's level of sexual performance anxiety, compatibility of sexual attitudes and values, and happiness within the relationship may be informative.

Cues of Infidelity: Personality

Cues of infidelity may also take the form of personality traits, in that one may predict the likelihood of a partner being involved in an infidelity based on whether they exhibit certain traits. For example, extraversion is linked to sensation seeking, seeking novelty, and sociability; it is also thought to be linked to finding sex more rewarding and seeking more mating opportunities, even if such activities entail high levels of risk. High extroversion has been associated with a higher propensity toward infidelity in a study of 545 British adults (Nettle 2005). Participants varied from those who had been loyal to their partner through to those with multiple occurrences of infidelity, and as extraversion increased in participants, so too did reported levels of infidelity. While this finding is accurate for both sexes, the effect size was larger and significant only for men, not women.

Further, in a large cross-cultural study of 52 nations in 10 world regions, low agreeableness and low conscientiousness were significantly related to infidelity for both men and women (Schmitt 2004). Individuals who describe themselves as being involved in an infidelity generally possess personality traits that are linked to a lack of trust, low empathy, a tendency to be disorganized, and are unreliable.

Individuals with high neuroticism, indicating emotional instability and high levels of worry, reported higher rates of infidelity in past and current relationships, an effect that appears to be stronger among women than men (see Altgelt et al. 2018 for a review). However, these connections between personality traits and infidelity are far from simple, and indeed the traits of the partner in the relationship also warrants attention. In their study of 108 newlywed couples over a 3-year timespan, Altgelt et al. (2018) documented that spouses with partners high in neuroticism or extraversion were more likely to engage in infidelity, and husbands with partners high in narcissism (i.e., feelings of superiority and low empathy) were more likely to engage in infidelity.

Cues of Infidelity: Attachment

Adult attachment may also matter; Attachment anxiety and avoidance significantly correlates with infidelity (Fish et al. 2012). Anxiety here refers to one's strong desire to receive positive attention from a partner, coupled with a fear that the partner or romantic relationship will fail to meet one's needs. Avoidance, alternatively, is one's difficulty in finding comfort in psychological intimacy or emotional connections and the need to maintain independence within one's romantic relationships. Therefore, one's attachment style may serve as a cue about their propensity to engage in infidelity.

Cues of Infidelity: Actual Behaviors

Shackelford and Buss (1997) sought to identify the behavioral cues that signal a partner's sexual and emotional infidelity. They performed two studies of college students. In the first study, participants nominated behaviors that may cause them to suspect a long-term partner was engaging in sexual or emotional infidelity. Thirty students of each sex were primed to think about a past, current, or future partner in a committed romantic relationship and imagine that partner was having sex with someone else or falling in love with someone else. Then, participants listed 10 cues that would lead them to suspect sexual or emotional infidelity, with cues being specific actions a partner may do, physical cues, sexual cues, emotional cues, behavioral cues, or verbal cues.

The results indicated that men and women overlapped considerably in the cues they provided for the two forms of infidelity, resulting in 170 distinct cues. Examples of the cues were: acting unusually angry when with their partner, being unusually critical of their partner, avoiding the topic of sex with their partner, spending less time on their appearance before seeing their partner, being bored with their partner sexually, breaking up with their partner, acting overly affectionate to their partner, avoiding dates with their partner, and avoiding a certain person as a topic of conversation with their partner.

In the second study, 114 men and 116 women examined the nominated behaviors from study 1 and then rated each act on how diagnostic it was for indicating sexual and emotional infidelity. Half the participants rated the likelihood that infidelity occurred based on the cues, while the remaining half rated the likelihood that the cue would be performed, given an infidelity occurred.

The 170 cues from the first study were grouped, using a factor analysis of ratings, to reveal 14 factors. These factors are as follows.

1. Angry, critical, argumentative toward partner. Here the person who has engaged in an infidelity is uncharacteristically angry or critical of the primary partner, less forgiving of the partner's mistakes, or seems to be seeking reasons to start arguments with the partner.
2. Apathetic toward partner. Cues for this factor are a general loss of interest in the primary partner, including less excitement about seeing the partner, not disclosing feelings to the partner, and claiming to be too tired to engage in sexual activity with the partner.
3. Relationship dissatisfaction and loss of love toward partner. This factor includes suggesting seeing other people external to the relationship with the primary partner, talking about ending the relationship with the partner, and reporting to have fallen out of love.
4. Passive rejection of partner and inconsiderateness. Here passive rejection of the primary partner occurs. Other behaviors are not saying "I love you" to the partner and failing to state any time spent together is enjoyed. Acting rudely toward the partner and being less gentle during sex is also included.
5. Reluctance to discuss a certain other person. Cues for this factor revolve around avoidance. The person who has engaged in the infidelity avoids talking about a particular other person or appears nervous if that person's name is raised in conversation with the primary partner.
6. Reluctance to spend time with partner. This factor includes cues where one avoids spending time with the primary partner, whether it be alone or together as a couple with family or friends.

7. Increased reference to, and time spent with, another person. Cues range from the person who engaged in the infidelity spending more time with another person, wearing an item of clothing belonging to another person which is noticed by the primary partner, calling the partner an incorrect name, or telling the partner about a desire to have sex with another person.
8. Acting guilty or anxious toward partner. The person who engaged in the infidelity is uncomfortable, nervous, or seems guilty when in close proximity to the primary partner.
9. Emotional disengagement from partner. Here the cues include forgetting the couple's anniversary or important dates, not making declaration of love to the primary partner, and providing minimal response to the partner's declaration of love.
14. Physical signs of sexual infidelity and disinterest in sexual exclusivity. Some cues include the recent contraction of a sexually transmitted infection or disease by the person engaged in infidelity or smelling like sex despite no sexual activity with the primary partner. This factor also includes the person committing infidelity stating they do not want to be sexually exclusive to the partner.

The remaining five factors directly contain cues regarding sexual behavior. They are as follows.

10. Sexual infidelity is revealed. The primary partner directly witnesses a sexual act between the person who engaged in the infidelity and another person, or the sexual infidelity is stated openly.
11. Changes in normal routine and sexual behavior with partner. Cues include changes in sleeping patterns or eating habits of the person who engaged in the infidelity. The person also tries new sexual positions with the primary partner or exhibits less orgasms during sex with the partner.
12. Increased sexual interest and exaggerated display of affection toward partner. Here there is a display of increased interest in sexual behavior with the primary partner, saying "I love you" more often than usual, and greater than normal displays of affection.
13. Sexual disinterest and boredom with partner. This factor includes cues such as boredom during sex with the primary partner, behaving mechanically during sex with the partner, or an inability to become or remain sexually aroused when with the partner.

Twelve of the 14 factors were found to be diagnostic of one form of infidelity relative to the other. There were the five factors listed for sexual infidelity. Being apathetic toward the partner (item 2 in the preceding list) and increased reference to, and time spent with, another person (item 7) did not differentiate between sexual or emotional infidelity. The remaining items were diagnostic of emotional infidelity.

Further, in the second study, Shackelford and Buss (1997) reported that the sex of the person doing the ratings and the sex of the person engaged in the infidelity mattered. Men and women rated performance of the cues within the factors as more diagnostic of infidelity when the person engaged in the infidelity was a member of the opposite sex. The authors concluded that people seem primed to infer infidelity more easily when it is an opposite-sex person who is displaying the cues as compared to a same-sex person. That is, men are more sensitive to cues of infidelity when they are displayed by a woman, and women are more sensitive to cues of infidelity when displayed by a man.

The cues for sexual infidelity incorporate a wide assortment of behaviors, ranging from obvious and overt signals such as revealing the infidelity, or physical signs of infidelity, to those that are subtler and covert, including changes in normal routines or increased sexual interest and exaggerated displays of affection. The weakest cue was sexual disinterest and boredom with the partner. Thus, the diagnostic value of the cues also varies accordingly, such that those that are more covert were rated as less diagnostic than those that were obvious.

Moreover, the authors posited that cues underlying emotional infidelity are not as clear-cut

as sexual infidelity due to the fact that it is a less identifiable form of infidelity. Emotional infidelity is less physically focused and instead pertains to the diversion of money, attention, support, or love and is typically accompanied with a reduction of time invested in the primary relationship.

Overall, women provided higher diagnostic ratings for the cues than men when the sex of the person committing the infidelity was not considered. The researchers contended that women tend to be more attuned to relationship dynamics than men, and given men are more likely to be involved in infidelity than women, it is possible that women have evolved a greater sensitivity to cues signaling potential infidelity.

Schützwohl (2005) extended these findings by examining the threshold at which participants reported feeling the first pangs of jealousy and then when the jealousy became unbearable. The cues were adapted from Shackelford and Buss (1997), such that they were listed in ascending order of diagnostic rank. A student sample of 95 men and 101 women completed the study. He found that the threshold for the first pangs of jealousy did not vary significantly by sex for emotional or sexual infidelity, as determined by the number of cues. However, after jealousy was experienced, men required fewer cues for sexual infidelity than women, and women required fewer cues for emotional infidelity than men, to reach the threshold where the jealousy felt unbearable. These results were replicated when reaction time was considered, instead of simply the number of cues.

Cues of Infidelity: Future Directions

Future work on cues of infidelity may include readily identifiable features that serve as accurate predictors of past infidelity behavior. Recently, Hughes and Harrison (2017) examined voice as a potential cue of infidelity. In their study, they used 10 voices of men and 10 of women, with half of the speakers self-identifying as having engaged in an infidelity at some point in their lives. Based on a brief recording (controlled for voice attractiveness, pitch), a student sample of 64 men and

88 women correctly identified those who had been involved in infidelity, signifying voice may contain signature cues of past infidelity behavior.

Future work may also incorporate social media. Cues of infidelity may occur on platforms such as *Snapchat*, where individuals receive messages from other users. Dunn and Ward (2019) reported that men imagined greater distress about a partner receiving a sexual *Snapchat* message revealing an infidelity than one revealing an emotional infidelity. The reverse trend was apparent for women. Therefore, the role of social media in infidelity, and in particular how it may provide cues as to potential or current infidelity, may be worth exploring.

Cross-References

- ▶ [Female Infidelity](#)
- ▶ [Frequency of Infidelity](#)
- ▶ [Infidelity Risk](#)
- ▶ [Male Sexual Jealousy to Deter Partner Infidelity](#)
- ▶ [Perceptions of Infidelity Cues](#)
- ▶ [Perceptions of Infidelity](#)
- ▶ [Prevention of Infidelity](#)
- ▶ [Relationship Dissolution](#)
- ▶ [Seeking Extra-Pair Partners](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)

Conclusion

Infidelity occurs within monogamous relationships where there is a social contract of exclusivity. It is related negatively to health and relationship outcomes, and is globally the main reason for relationship dissolution. Detecting a partner's infidelity, whether it be sexual or emotional in nature, presumably has strong evolutionary roots, given that misallocated time, energy, and resources may impact negatively on one's individual fitness. There are numerous cues of infidelity, with more research on how people detect sexual than emotional infidelity. Cues of infidelity may relate to personality traits, patterns of attachment, or actual

behaviors. Future work may examine the role of social media in providing cues or how some cues provide immediate, accurate information about past infidelity behavior.

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Cues to Size

► Signals of Body Size

Cues to Weight

► Signals of Body Size

Cuisine of the Fittest

► Darwinian Gastronomy

Cultural and Moral Relativism

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Synonyms

[Descriptive relativism](#); [Metaethical relativism](#); [Normative relativism](#)

Definition

Moral relativism refers to three distinct but related philosophical positions (Brandt 2001, pp. 25–28). *Descriptive relativism* is the hypothesis that there are pervasive and irresolvable moral disagreements between individuals or cultures. *Metaethical relativism* holds that moral claims can only be evaluated as true or false relative to a particular individual or culture's moral standards. Metaethical relativism thus denies that there are objective standards of moral truth that are universally applicable to all people and societies. *Normative relativism* is the prescriptive position that we should tolerate individuals or cultures with different moral standards. Such tolerance prohibits people from judging or imposing their moral standards on people or cultures with different moral standards. Each form of relativism can be cast at the individual level, i.e., that there are fundamental disagreements in individual moral standards, that moral truth must be evaluated relative to the standards of different individuals, and that we must tolerate individuals with different moral standards. *Cultural relativism* may refer to any of these forms of relativism cast as differences between cultures rather than individuals. (*Cultural relativism* may refer to other forms of relativism unrelated to morality, such as methodological and epistemic/cognitive relativism. Methodological relativism is the practice of suppressing enculturated biases when studying other cultures (Obeyesekere 1966). Epistemic relativism holds that different cultures or individuals employ radically different conceptions of knowledge, justification, or

reasoning (Boghossian 2006; Rorty 1991). Only moral forms of cultural relativism are discussed here (but see Brown 2008; Meiland and Krausz 1982).)

Introduction

This entry will not focus on the history of moral relativism or offer extensive discussion of arguments for and against relativism. Instead, it will provide an overview of each form of relativism and discuss their relationship with evolutionary psychology. (For more historical treatments of moral and cultural relativism, see Brown (2008) and Hollinger (2003, pp. 708–721).) Evolutionary psychology has important implications for all three forms of relativism. The extent to which moral judgment is constrained by evolved psychology plays a critical role in the possibility of deep and pervasive moral differences and could serve to circumscribe, falsify, or support some version of descriptive relativism. Evolutionary psychology is also relevant to metaethical and normative relativism. In part, this is because the practical significance of normative and metaethical relativism depends on the moral diversity postulated by descriptive relativism. However, philosophers also appeal to evolutionary influences on human psychology to support (Collier and Stingl 1993, 2013 Harman 2000; James 2009; Sterelny and Fraser 2016; Zamulinski 2007) or cast doubt on moral realism. Arguments in favor of moral realism are relevant to normative relativism insofar as the moral facts they purport to establish conflict with interpersonal and intercultural tolerance and may conflict with metaethical relativism if they purport to establish objective moral facts. Arguments against moral realism, on the other hand, are relevant to metaethical relativism insofar as they cast doubt on objectivist moral theories. The most prominent evolutionary arguments against moral realism are *evolutionary debunking arguments (EDAs)*. These arguments appeal to the evolutionary origins of moral judgment to undermine justification for moral beliefs (Kahane 2011). EDAs have become increasingly popular in the philosophical

literature and have spawned a growing debate over the relevance of evolutionary theory to metaethics. Evolutionary debunking arguments have received considerable support (Cline 2015; Fraser 2014; Griffiths and Wilkins 2010; Joyce 2006, 2013, 2016b; Lillehammer 2003; Mason 2010; Millhouse et al. 2016; Mogensen 2014b; Street 2006, 2008; Wright et al. 2014) but have also attracted many critics (Behrends 2013; Berker 2014; Bogardus 2016; Brosnan 2011; Carruthers and James 2008; Deem 2016; Enoch 2010; FitzPatrick 2014a, b, 2015; Kahane 2011; Mogensen 2014a; Peters 2012; Schafer 2010; Shafer-Landau 2012; Skarsaune 2011; Talbott 2015; Toner 2011; Vavova 2014; Wielenberg 2010). Even if these arguments fail on philosophical grounds, they all depend on specific claims about the evolution of moral cognition. Finally, while it is unlikely that evolutionary psychology could play any direct role in determining whether or not we ought to tolerate people or cultures with different moral values, it may inform normative relativism by providing practical insight into how to devise institutions, policies, and norms that facilitate tolerance.

Moral Relativism

Descriptive Relativism

Descriptive relativism is the empirical hypothesis that there are pervasive and fundamental moral disagreements between individuals (*descriptive individual relativism*) or cultures (*descriptive cultural relativism*). The most common source of evidence in support of descriptive cultural relativism is the prevalence of practices that are permissible or even obligatory in one culture, but prohibited in another, such as female genital mutilation, polygamy, cannibalism, and human and animal sacrifice. Analogous support for descriptive individual relativism draws on the existence of moral variation within a population. In either case, variation in moral belief is uncontroversial, so it may seem that descriptive relativism consists in the trivial claim that people often hold conflicting moral views. This is not the case. Descriptive relativism is committed to the

existence of *fundamental moral disagreements* or moral disagreements that cannot be resolved in principle because they express differences in basic moral beliefs and commitments (Moody-Adams 2009).

Many moral disagreements are not fundamental but are instead disputes over nonmoral facts or the result of misunderstandings or errors in reasoning. Two people with the same moral standards may hold conflicting views about gun control because they disagree about whether it reduces crime. Once both individuals were in full possession of the facts and knew whether gun control reduced crime, the disagreement would in principle dissolve. Errors in reasoning could also lead two people to disagree (or at least think they disagree) about a moral issue. Rational discussion could lead either side of a dispute to identify errors or inconsistencies in their position, modify their beliefs, and come to an agreement. If so, this dispute would involve misunderstandings that could in principle be corrected, not a fundamental moral disagreement.

Since it is possible that most or even all moral disagreements would dissolve once both sides of a dispute were in possession of the facts and were reasoning correctly, descriptive relativism must demonstrate that there would still be many moral disagreements even under such optimal conditions. In spite of this difficulty, empirical findings could vindicate descriptive relativism by providing compelling evidence that cultures or individuals really do have fundamentally different moral values.

Metaethical Relativism

Metaethical relativism is the philosophical position that moral claims are only true or false relative to an individual or group's moral standards. (There are other possibilities. Harman (1975) and Harman and Thomson (1996) argue that moral claims could be relativized to the shared context of the agent making a moral claim along with their intended audience (Joyce 2015). Moral claims could also be relativized to groups other than cultures, such as superordinate cultural groups (e.g. "the West") or different species.) Metaethical relativism does not deny

that there are moral facts; it only denies *metaethical objectivism*, the view that there are objective moral facts that are universally applicable to all individuals and cultures. Unlike metaethical objectivism, metaethical relativism allows the same moral claim, e.g., “slavery is wrong,” to be true relative to one moral standard but false relative to another.

It may seem absurd to suggest that the same claim can be both true and false, but ordinary language already incorporates linguistic features that permit expressions to have variable truth values. This is achieved by employing *indexicals*, linguistic expressions or behaviors (e.g., pointing) that allow statements to vary in meaning from one context to another or from one speaker to another. Common indexicals include “I,” “you,” “he,” “she,” “here,” “there,” “yesterday,” and “today” (Kaplan 1989). For example, if Alex says “I am at home,” she is referring to herself and her home, but if Sam says “I am at home,” she is referring to herself and her home, not Alex or Alex’s home. Indexicals also permit the truth of a claim to vary. If Alex is facing north and Sam is facing south, the statement “I am facing north” is true if Alex says it but false if Sam says it.

Metaethical relativism incorporates a similar indexical component into moral claims, such that each moral claim includes an implicit reference to a particular moral framework (Joyce 2015; but some object to this characterization, see Harman 2015). Since different people and cultures have different moral standards, the truth of a moral claim will depend on which moral framework is referenced. For example, Alex may live in a culture that prohibits slavery, while Sam lives in a culture that permits it. According to cultural metaethical relativism, when Alex says, “Slavery is wrong,” she implicitly refers to her culture’s standards. Since slavery is wrong in Alex’s culture, this statement is true. When Sam says “Slavery is wrong,” she references her culture’s standards. Since slavery is permissible in Sam’s culture, this statement is false. Thus, the same moral claim, “Slavery is wrong,” can be true when one person says it but false when another says it, because each claim implicitly refers to a different moral framework.

Although metaethical relativism treats moral claims as being true or false, critics often conflate it with moral skepticism (the belief that moral claims are unjustified or their truth is unknowable) or outright rejection of moral truth or warn that it inevitably leads to an egoistic or nihilistic view of morality (Wong 1998). For example, Pope Benedict XVI warned that “[W]hen policies do not presume or promote objective values, the resulting moral relativism . . . tends instead to produce frustration, despair, selfishness and a disregard for the life and liberty of others” (Ratzinger 2005). Pope Benedict may or may not be correct to worry that denying objective right or wrong has negative behavioral consequences, but a relativistic view of moral truth does not itself consist in a rejection of moral truth (unless moral truth is question-beggingly defined in such a way as to exclude relative truth) nor does it logically entail any normative implications, including the advisability of wanton indulgence. Furthermore, although metaethical relativism does deny that there are objective moral truths (at least in its most radical form), the denial of objective moral truth does not entail that the world is “without value,” unless the only legitimate values are objective, which would beg the question if it were offered as a criticism of metaethical relativism.

Admittedly, Pope Benedict does not necessarily intend to critique sophisticated philosophical positions that are careful to disentangle different forms of relativism, and he might concede that metaethical relativism, construed strictly as a metaethical and not a normative stance, is not subject to their concerns. Nonetheless, his remarks echo the common sentiment that there *is* a relationship between a denial of objective moral truth and the adoption of pernicious attitudes and behavioral dispositions (Kanarek 2013; Tasioulas 1998). Since metaethical relativism does not logically entail normative consequences, it could at best have only a contingent relationship with egoism, nihilism, or any other normative or behavioral consequences. Such a relationship *may* exist, but it would require empirical evidence to establish it. Researchers are beginning to explore this relationship, and preliminary findings suggest that

concerns about the deleterious consequences of relativism may be at least somewhat justified. Rai and Holyoak (2013) found that priming participants with relativism increased dishonesty and cheating, while Young and Durwin (2013) found that priming objectivism led to substantial increases in donations to charity but priming relativism did not.

Critics of metaethical relativism also argue that, because it does not privilege any moral systems over others, it is incapable of providing rational justification for condemning the moral practices of other people and cultures, even when those practices include genocide, torture, or other atrocities (Bennett 2002, p. 46; Pojman 2004; Rachels 2001). Defenders of metaethical relativism could respond by insisting that it does not have any normative implications, but others have responded by abandoning an entirely relativist metaethics and instead propose objectivist constraints that limit which moral systems can be legitimate. This *moderate metaethical relativism* can be distinguished from *radical metaethical relativism*, which asserts that all moral truth is relative and that no moral claims are objectively true or false (Carson and Moser 2001). This radical form of metaethical relativism does entail, as critics maintain, that all moral frameworks are equally true and that none hold any privileged status over others. It is this radical stance that has attracted harsh criticism. But metaethical relativism need not entail that *all* moral claims are relative. It is possible to regard some moral practices as relative but others as objective. Copp (1995), Brandt (1984), Velleman (2013), Foot (2001, 2002), and Wong (1995, 2009) have all defended moderate views of this sort.

Wong (1995, 2009) for instance, defends what he calls “pluralistic relativism” (cf. Xiao and Huang 2014). According to this view, conflicting moral frameworks could each be true, but human nature and local circumstances place constraints on which moral frameworks are legitimate (Gowans 2015). These constraints are based on the finite set of moral frameworks that, for instance, promote human flourishing and facilitate cooperation within a society. Since there are multiple ways to meet these conditions, mutually

incompatible moral systems could be equally consistent with moral truth. Any moral system that fails to achieve these standards, on the other hand, is objectively false. Wong’s pluralistic relativism, and views like it, is neither fully relativist nor fully objectivist. To proponents of more “pure” conceptions of relativism, this may be too great a concession. Nonetheless, moderate metaethical relativism offers a compromise that circumvents some of the difficulties faced by more radical forms of relativism.

Normative Relativism

Normative relativism is the prescriptive position that we must tolerate the moral practices of different people and cultures. Normative relativism does not require people to support moral frameworks that differ from theirs, but it does prohibit them from imposing their values on other cultures or judging them according to their own moral standards. The obligation to tolerate other cultures may be framed not as a principle of acceptance but as a principle of noninterference (Bennigson 1999; Gowans 2015). Few philosophers defend the notion that descriptive or metaethical relativism necessarily entail normative relativism (see Harrison 1976; Wong 2009; Williams 1972). Instead, contemporary debate concerns whether there is an indirect relationship between descriptive/metaethical relativism and normative relativism, such that descriptive and metaethical relativism in some way provide a rationale or a context in which a norm of intercultural or interpersonal tolerance is more likely, more desirable, or more philosophically defensible (see Bennigson 1999; Graham 1996; Ivanhoe 2009; Kim and Wreen 2003; McKinnon 2007; Rachels 2001; Prinz 2007; Tilly 1998; and Wong 1984).

Nonetheless, it is illustrative to examine a formal argument that tolerance follows directly from moral relativism. Pojman (2004) attributes one such argument to Herskovits:

1. If moral claims are only true or false relative to a particular culture’s standards, then there are no nonrelative justifications for members of one’s culture to morally judge the standards of another culture.

2. If there are no nonrelative justifications for members of one culture to morally judge the standards of another culture, then we ought to tolerate cultures with different moral standards.
3. Moral claims are only true or false relative to a particular culture's standards.
4. We ought to tolerate cultures with different moral standards. (Adapted from Pojman 2004, pp. 244–245).

This argument would have no practical significance if descriptive relativism was false, but the falsehood of descriptive relativism would not demonstrate that any of the argument's premises were false. The argument relies only on the hypothetical possibility of cultures with different moral standards. Nonetheless, descriptive relativism asserts only that there are fundamental moral disagreements. If true, this fact by itself would have no normative implications.

In addition, this argument fails to show that tolerance follows from metaethical relativism. As Pojman (2004) points out, "If morality simply is relative to each culture, then if the culture does not have a principle of tolerance, its members have no obligation to be tolerant" (p. 245). More importantly, we could not infer from the fact that moral truths are true relative to a particular framework that there is a universal, nonrelative moral duty to tolerate people who subscribe to different frameworks, since the very existence of such nonrelative moral facts is precluded by metaethical relativism. Even if the normative relativist endorsed a hybrid metaethical theory in which the obligation to tolerate others was objectively true, such a position would not follow from metaethical relativism itself. This suggests that the difficulty with this argument is the second premise. Even if there were no nonrelative way to condemn the practices of other cultures, this would not in any way entail that it were *morally wrong* to condemn the practices of other cultures. A culture could even include among its standards an obligation to be intolerant toward other cultures. Nothing about metaethical relativism precludes this possibility or suggests that it is less preferable than tolerance. Pojman makes this

point himself, concluding that, "[F]rom a relativistic point of view there is no more reason to be tolerant than to be intolerant, and neither stance is objectively morally better than the other" (p. 245).

Although normative relativism does not follow deductively from descriptive or metaethical relativism, they may provide indirect support for tolerating people or cultures with different moral practices. This could be achieved via inductive arguments, though Kim and Wreen (2003) consider and reject several attempts, and ultimately conclude that there is no inductive link either. Even if we accept their conclusions, there may still be a psychological link between descriptive or metaethical relativism and normative relativism. The belief that metaethical relativism is true, and that because of this there are no objective standards of moral truth, could induce a state of reflection and critical self-examination that would lead us to be more cautious in morally condemning others. Westermarck (1932) suggests this possibility, stating that "Could it be brought home to people that there is no absolute standard in morality, they would perhaps be on the one hand more tolerant and on the other more critical in their judgments" (p. 59). Baghrmian (2015) argues that such transformative experiences may not even require the belief that moral standards are relative but could instead result from exposure to and reflection on the sheer diversity of moral views that exist. Citing Knobe and Nichols (2007), she adds that such experiences may result in a crisis of faith similar to those experienced by children who, growing up in insular religious communities, discover that others do not share their religious beliefs, since circumstances like these may reflect instance of "contingency anxiety," as discussed in Mogensen (2015):

... [T]he discovery of religious diversity can prompt the thought that it's in some sense accidental that one happens to be raised in a Christian household rather than a Hindu household. This kind of arbitrariness can make the child wonder whether there's any reason to think that his religious beliefs are more likely to be right than those of the Hindu child. (p. 11)

(Westermarck's and Baghrmian's proposals could be correct, but if so, they would entail

only an indirect and contingent capacity for metaethical and descriptive relativism to encourage tolerance. They would be indirect and contingent in that any tendency for people to move from metaethical or descriptive relativism to normative relativism would not result from a rational chain of inferences or the logical deduction that the latter is a corollary of the former but of some further set of facts about the interaction of accepting the metaethical or descriptive relativism with other characteristics of specifically human psychology).

Even so, the discovery of a contingent empirical connection between metaethical or descriptive relativism and an increased tolerance for different moral practices would be fascinating and important. Some researchers have already found evidence consistent with this possibility. Goodwin and Darley (2012) found that, compared with relative moral beliefs, objective moral beliefs were associated with reduced comfort with people who disagreed, the judgment that people who disagreed were more immoral, and reduced willingness to reconsider that belief. Wright et al. (2014) found that objective moral beliefs were associated with greater unwillingness to date, interact with, or help people who did not share the same belief than nonobjective moral beliefs. These studies suggest that relativism is associated with greater tolerance of moral diversity than objectivism, but the correlational nature of these findings does not provide causal evidence that a change from objectivism to relativism would lead to greater tolerance. If such a relationship results from protracted reflection and critical self-assessment, as Westermarck and Baghramian suggest, such evidence may be difficult to acquire, since it is doubtful that priming participants with evidence of moral diversity or presenting an argument for metaethical relativism would induce anything approximating serious reevaluation of one's moral beliefs, especially if participants are evaluated immediately or shortly after the manipulations. Future research should investigate the causal impact of changes in metaethical beliefs and evaluate a broader range of behavioral consequences. Such research could also attempt to more closely replicate the impact of more serious

reevaluation of moral beliefs over an extended period of time to more specifically test Westermarck's and Baghramian's suggestions. Since it is possible that increases in tolerance are a specific instance of a global reduction in moral concern, one possibility is that reflection on moral diversity or relative moral truth increases tolerance via a global reduction in moral concern.

Evolutionary Psychology and Moral Relativism

Evolutionary Psychology and Descriptive Relativism

Even on the most uncharitable assumption of widespread exaggeration and misinterpretation, there is little doubt anthropologists have accurately documented an extraordinary degree of moral diversity. And there is no question that political, religious, and personal divisions lead people with similar cultural backgrounds to differ, often fiercely, over moral issues. All this would suggest that the case for descriptive relativism is settled. Yet descriptive relativism cannot be demonstrated by merely pointing to differences in moral beliefs, because it is unclear from the existence of such disagreements whether they result from differences in nonmoral beliefs, failures in reasoning or reflection, or genuine differences in fundamental moral values.

Descriptive relativism may be an empirical hypothesis, but it is not a hypothesis that could be confirmed or disconfirmed exclusively by observational research. Descriptive relativism holds that *even if* people were fully informed and reasoning properly, they would still disagree about a wide range of moral issues. But people are far from fully informed, and the human mind is riddled with cognitive biases that hinder people's ability to rationally evaluate information even when it is available (Tversky and Kahneman 1974). Descriptive relativism, as an explanation of moral diversity, rests on a conjecture about what would happen in a highly idealized hypothetical state of affairs that has not, and likely never will, come to pass. This does not invalidate it as a legitimate empirical hypothesis. Sufficient

evidence could show that the best explanation of available data is that extensive moral disagreement would likely persist under ideal circumstances, but establishing this claim is far more difficult than is commonly appreciated.

Descriptive relativism must overcome several theoretical and empirical difficulties to establish itself as the best explanation of moral diversity. It is subject to conceptual, normative, and methodological difficulties that make it difficult to precisely state, operationalize, and empirically evaluate. These difficulties make observational research alone inadequate to demonstrate widespread fundamental moral disagreement. As a result, a compelling case for descriptive relativism will require a sufficiently deep understanding of human psychology to reasonably conclude that many moral disagreements are irresolvable in principle. However, demonstrating descriptive relativism's dependence on psychological research and the importance of evolutionary psychology will first require an understanding of the particular theoretical and empirical obstacles the hypothesis faces.

Descriptive relativism, like every other empirical hypothesis, is vulnerable to the charge that it is underdetermined by available data (Newton-Smith and Lukes 1978; for discussion, see Acuña and Dieks 2014; Kukla 1996; Ladyman 2002, Chap. 6; Laudan 1990; Laudan and Leplin 1991). There is always a way to fit empirical evidence to a hypothesis provided an individual is willing to shift the rest of their beliefs accordingly. This means that for any scientific explanation of a given set of data, there will always be alternative explanations that are consistent with the data. As a result, we cannot interpret the implications of empirical data without implementing explanatory virtues that help us decide among competing accounts of the same data, such as simplicity, precision, scope, and conservatism (the minimization of changes to existing beliefs) (Lipton 2013; Sklar 1975). This by itself is not a significant cause for concern for any particular hypothesis, since the same general worry is applicable to science as a whole, but Michele Moody-Adams (2001) argues that descriptive cultural relativism is especially subject to concerns about

underdetermination, and some of these arguments may apply to descriptive individual relativism as well.

Moody-Adams (2001) notes that anthropological fieldwork often relies on limited access to a small number of interviewees, which raises questions about the representativeness of their responses. Sometimes this is justified on the grounds that members of a community are legitimate authorities on its beliefs and customs. Moody-Adams objects, noting that, "Any such confidence embodies a complex evaluative stance that will sometimes prove neither methodologically nor morally benign. Very often such confidence overlooks the possibility of internal conflict, as when a community practice has been subjected to criticism from within" (p. 95). Authority figures would not represent internal dissent and may not report on it. Yet dissent may represent an ongoing debate within the community that could reveal that some belief or practice is inconsistent with values that are more central to the culture's identity than the practice itself (p. 95). Communities may include subgroups that differ in important ways from designated spokespersons or typical members of the community. For example, interviewing the exclusively male leadership of a highly patriarchal society could overlook the critical and ongoing dissent among women and consulting the typical, reasonably well-off member of a highly economically stratified society may fail to capture the moral perspective of its most disadvantaged members. Attempts to provide a complete picture of the moral values of a given culture would require a more comprehensive analysis of its members and may require contestable appeals to evaluative judgments.

A complete and reliable picture of a culture's moral views is further impeded by linguistic and conceptual barriers that make intercultural interpretation exceptionally difficult. Any attempt to make cross-cultural comparisons will have to account for differences in local conceptions of what constitutes sex, slavery, consent, work, and other concepts relevant to morality, as well as differences in how people conceive of morality itself, including notions about justice, equality,

and purity, as well as differences in epistemic norms, religious beliefs, and a host of ancillary beliefs and practices relevant to their moral perspective. In many cases, this may make it difficult to determine what observations provide relevant information about a culture's moral beliefs and practices or if they even conceive of a given practice as moral at all. As Moody-Adams points out, "... [M]oral relativists seldom hesitate to assume that the natural languages of the groups they encounter contain a concept of morality ... [B]ut this assumption (however plausible) presupposes sophisticated judgment about a concept – the concept of morality – so complex that its content is [essentially contested] ... even by speakers of the same language" (p. 94).

A more pressing difficulty for descriptive relativism is disagreement itself. As previously noted, it is unclear how much moral diversity results from disagreements over nonmoral facts. Given extensive variation in education, cultural background, social class, religious belief, and political ideology, such differences are likely to be extensive both within and between cultures. More importantly, every person and every society are in a considerable state of ignorance about the consequences of their moral practices and of innumerable nonmoral facts that are potentially relevant to their moral systems. Even the most advanced nations have not reached consensus on the long-term consequences of their economic policies or criminal justice systems. Because of this, many moral disputes rest on disagreements about the impact of actions and institutions that everyone lacks adequate information about. People can disagree with impunity under these circumstances since nobody can appeal to evidence that decisively confirms their position. Even when evidence is available, disputes may remain unresolved, since any interpretation of that evidence will likely be tainted by motivated reasoning (Kunda 1990; Sunstein et al. 2016) and ideological commitments that impede rational evaluation (Cohen 2003; Kahan 2013; McCright and Dunlap 2011).

Even if factual disputes are set aside, moral diversity would still fail to unambiguously demonstrate fundamental moral disagreement, since

the same moral principles may be consistent with different local practices. One reason for this is that moral diversity is consistent with *local objectivism*. Local objectivism is the view that there is one universal set of objective moral principles, but differences in environmental conditions, psychological characteristics, or other factors may allow or even require that the same moral principle be satisfied in different ways by different individuals or cultures.

One way this can happen is if two cultures with the same moral values develop practices that differ due to local conditions but which conform equally well to their shared moral standards. An isolated island community with a limited food supply and small population may develop strict norms for regulating reproduction out of a necessity to conserve resources and minimize the deleterious effects of inbreeding. In the long run, failure to adopt these practices could otherwise lead to food shortages and poverty. Yet these practices may be inconsistent with the same moral values in communities with more resources and larger populations. Both the isolated island community and larger communities with more resources could place equal weight on the importance of reproductive autonomy and the collective welfare of the community, and agree sacrifices to the former must be made when necessary to promote the latter, yet only the isolated community would need to make this sacrifice in practice.

The same moral values may also be sufficiently general that a wide range of practices are consistent with them regardless of local conditions. If two people wanted to cross a river, one might achieve this goal by building a boat and the other by building a bridge. Provided these methods were equally effective, the same abstract goal (crossing the river) could be achieved by different concrete methods (e.g., a boat or a bridge). In much the same way, different cultures may conform to the same moral goals by developing different sets of beliefs and practices, even if those practices are not specific adaptations to local circumstance. Whether a specific moral practice conforms to the same set of abstract moral principles may also depend on its function in the context of the wider set of norms, beliefs,

and practices of the moral framework it is embedded in. This suggests that determining whether a particular practice is consistent with a given set of general moral values may require holistic evaluation of its interaction with other norms, beliefs, and practices.

It is also unclear what exactly it would mean to say that moral disagreements are sufficiently extensive that they entail descriptive relativism, since there are many ways of quantifying the total amount of agreement and disagreement or weighing the importance of particular norms or principles. We could emphasize judgments about first-order moral practices, like polygamy or abortion, but there may also be disagreements about the moral importance of character traits (e.g., courage, honesty) or differences in more abstract approaches to morality. For instance, Wong (1984) claims that some cultures adopt a moral system grounded in virtue and promoting the communal good, while other cultures ground morality in rights and emphasize individualism and liberty (Gowans 2015).

Morality can also be cast at different levels of generality. People can disagree about concrete moral practices but share the same commitment to abstract universal principles. Even apparent disagreement over relatively abstract moral values such as personal autonomy or promoting the good of the community could dissolve if morality were cast at an even higher level of abstraction. For example, people may value their culture's moral code because they believe it fulfills the more basic moral goal of promoting human flourishing. Disputes between societies that are more collectivist or more individualist may seem to represent quite abstract differences in a moral perspective and could present more viable candidates for fundamental disagreement, but even these may be due to disputes over which overarching perspective was best for the society on a largely shared understanding of what "best" entails. The purpose of even radically different moral systems, even ones that differ on relatively abstract moral values, could still be to promote even more abstract moral goals, e.g., to promote the well-being of its members (Kluckhohn 1955). Individuals or cultures may agree along some axes of morality

but disagree along others, and it is unclear which, if any, take priority, without drawing on contestable application of explanatory virtues and appeals to philosophical arguments or intuitions. This suggests that a given set of moral disagreements could be consistent with some conceptions of descriptive relativism, but inconsistent with others, and there may be no way to decisively argue that one account should be favored over another. If so, this could make the truth of "descriptive relativism" as a general thesis indeterminate.

In light of these difficulties, the prospects for descriptive relativism seem bleak. But the purpose of presenting them is not to show that they cannot be overcome, it is to justify the need for more comprehensive psychological evidence. At the core of descriptive relativism's claim is an empirical assumption that we are psychologically constituted in such a way that we can form mutually incompatible moral frameworks that could not be reconciled even in principle. If this is the case, it must be due at least in part to specific facts about how human minds function, and knowledge of these facts is critical to evaluating the possibility and extent of irresolvable moral differences. In other words, descriptive relativism is a hypothesis about human psychology. Psychological evidence of the conditions in which moral disagreements could be resolved would provide the most compelling evidence for or against descriptive relativism, since only these findings would allow us to determine whether two people or cultures with different moral beliefs would be likely to come to an agreement if they agreed on all relevant nonmoral facts. For instance, knowledge of how moral judgments differ from nonmoral judgments (or if they do), how moral beliefs are acquired, and what conditions are necessary for moral beliefs to change all inform the possibility that people could converge or fail to converge on the same set of moral beliefs if they agreed about the relevant nonmoral facts.

It is beyond the scope of this entry to survey all research relevant to this dispute, but one issue central to determining the extent and scope of moral disagreement is *moral nativism*. Moral nativism, as a general hypothesis, claims morality

is in some respect innate, but precisely what this means will depend on the particular nativist hypothesis (see Joyce 2016c). The most relevant way nativist accounts differ from one another concerns the traits purported to be innate. *Rule nativism* holds that we have an innate capacity for forming specific moral norms, rules, or judgments. This innate capacity consists of domain-specific psychological mechanisms that lead people to reliably develop particular moral judgments and beliefs, such as the belief that committing incest or harming innocent people is morally wrong.

A second, related view claims that certain moral *domains* are innate. These accounts claim that morality is innately constrained to a subset of domains that limit which behaviors and traits can be subject to moral evaluation. Haidt and colleagues have articulated the most widely developed and widely discussed form of domain nativism, *moral foundations theory* (MFT) (Graham et al. 2011, 2012; Haidt 2012; Haidt and Joseph 2004). MFT is typically characterized as having at least five domains: harm, fairness, loyalty, authority, and purity (as well as a proposed sixth domain concerning liberty and oppression, see Iyer et al. 2012; Graham et al. 2011, 2013). Norms in each of these domains may be triggered by distinct, domain-specific cognitive modules that evolved to meet a particular adaptive challenge relevant to that domain, though Graham and colleagues maintain that MFT can be sustained without any deep commitments about modularity or cognitive architecture (see Graham et al. 2013, p. 63). For instance, the *loyalty* domain evolved to facilitate cooperation with members of one's group, while the *purity* domain evolved as a "behavioral immune system" that encourages avoiding substances and activities that increase risk of infection (Schaller and Park 2011; Graham et al. 2013).

Moral foundations theory does not propose that all domains are equally active in every culture but that culture can amplify or attenuate the relative importance of a given domain. For example, Haidt and colleagues argue that American liberals tend to emphasize harm and fairness but assign relatively little importance to the domains of

purity, loyalty, and authority, whereas conservatives treat all five as important (Graham et al. 2009; Haidt 2012; Haidt and Graham 2007). Furthermore, the specific content of the domain is not specified in advance. Cultures may have standards of fairness but differ in their application, e.g., one culture's purity norms may include specific dietary or sexual taboos that differ from another culture. Finally, MFT incorporates Haidt's social intuitionist model (SIM) of moral judgment. According to the SIM, moral judgments are the result of rapid, automatic, relatively effortless intuitive processes (*system 1 processes*) rather than deliberative, effortful conscious reasoning (*system 2 processes*) (Kahneman 2011; Stanovich and West 2000). Moral reasoning that involves deliberative processes does occur, but it serves primarily to justify and explain our moral beliefs, not to enable us to seek moral truth (Graham et al. 2013; Haidt 2001).

Toolkit nativism holds that we have an innate capacity for thinking in moral terms and to employ *moral concepts*, but these concepts are not limited to any particular domains and do not specify particular moral norms or judgments. (Prinz refers to this form of nativism as *minimal* (Prinz 2009) or *weak* (Prinz 2014). Joyce (2013) objects to this characterization, arguing that it produces the rhetorical effect of making its proponents appear to have retreated from bolder nativist hypotheses and are desperately attempting to salvage a losing position.) Instead, "the individual's socialization process," as Joyce puts it, serves "as the sole determinant of to which subjects these concepts get attached" (p. 131). Concepts like "moral wrongness," "moral duty," and "moral praiseworthiness," may be innate, but whether we regard it as morally wrong to own slaves and morally praiseworthy to help strangers, or vice versa, will depend on our social environment (Joyce 2016c).

All three forms of nativism conflict with anti-nativist accounts. Anti-nativists accounts deny that there are any adaptations for distinctively moral thought or that moral norms, domains, or concepts reliably emerge as a result of innate psychological processes. Prinz articulates one such view. According to Prinz (2009), morality

is “a by-product of capacities that were evolved for other purposes. Morality is a spandrel. There is no mechanism dedicated to the acquisition of moral norms.” (p. 168). Such accounts may hold, like Prinz, that morality is a by-product of domain-general processes, though anti-nativist hypotheses do not necessarily endorse the view that the human mind is a *tabula rasa* or “blank slate” that consists *only* of domain-general processes (Barkow et al. 1992). For example, Machery and Mallon (2010) suggest that the human mind may lack an innate capacity for distinctively moral cognition, but there could still be an innate capacity for normative cognition in general. Machery and Mallon point out that normative thought is not restricted to morality. We also routinely employ normative judgments about rationality (“You should not believe everything you read”), aesthetics (“You should not wear that ugly sweater”), and social conventions (“You should not eat with your hands at the dinner table”) (p. 21). Even if moral norms or concepts in particular were not innate, the human mind could still possess an innate capacity for employing normative concepts, e.g., “oughtness,” with the social environment determining the specific normative domains a particular individual or culture employed. If so, morality would be a by-product of more general psychological processes, but these processes would still be canalized, species-typical traits that reliably emerged across cultures.

Each of these hypotheses has distinct implications for descriptive relativism. For obvious reasons, rule nativism presents the greatest potential threat. If the human mind is equipped with psychological mechanisms that reliably lead most people to adopt a shared set of moral principles, then, depending on how great of a proportion and how central these innate moral norms were to our moral systems as a whole, this could directly entail that descriptive relativism is false. However, rule nativism is not necessarily inconsistent with descriptive relativism. If only a few relatively specific moral norms were innate, other norms could be free to vary between individuals or cultures. If so, moral variation could still be sufficiently widespread to justify descriptive

relativism. A rule nativist account would also need to demonstrate that these innate moral rules are species-typical traits that are universal or nearly universal and that they reliably emerge in a wide range of contemporary social environments, since novel environments may lead some populations to develop different moral norms (Haraway and Maples 1998). As Joyce (2016c) points out, “[...] innate traits may well require substantial environmental input – input that may have been reliably present in the EEA [Environment of Evolutionary Adaptedness] but is absent, patchy, or distorted in the modern environment” (p. 132).

The generality or specificity of an innate moral rule also matters. If a handful of moral rules are innate but relatively specific, such as a norm against incest, these innate rules may fail to capture broad swaths of potentially variable judgment that doesn’t fall within their limited purview. However, a small number or even a single general moral principle could underlie all or nearly all moral judgment. Moral dyad theory (MDT) provides one such unifying account of morality (Gray et al. 2007, 2012a, b, Gray et al. 2014; cf. Crone and Laham 2015). According to Gray and colleagues, all moral judgments are the product of a dyadic template in which an agent intentionally causes suffering to a patient (Gray et al. 2012a). This cognitive template operates even when no obvious moral agent or patient is available by inserting an imagined perpetrator or victim into the act, a process Gray and colleagues refer to as “dyadic completion” (Gray et al. 2014). This allows MDT to explain seemingly “victimless” moral violations, such as homosexuality and masturbation. MDT seems to provide a direct challenge to descriptive relativism. Gray et al. (2012a) allude to this possibility when they state that viewing harm as the currency of morality implies that:

[T]here is not an unbridgeable gap between moral judgments across relationships [...] or cultures [...]. Just as Pesos can be converted to Euros, so too can moral violations across cultures be compared on perceptions of harm. Thus, liberals and conservatives may not fundamentally misunderstand each other’s moral judgments but instead simply disagree on what is harmful. (p. 209)

If so, then all moral disputes would be reducible to factual disputes about what causes harm, which suggests that all moral disagreements could be resolved in principle. Even so, it would remain an open question whether people possessed the psychological resources to resolve moral disputes in practice. Even if the cognitive processes involved to moral judgment were uniformly based in judgments about harm, concrete moral judgments about specific moral issues may be insensitive to this discovery or to information about how harmful an act is. If, for instance, the social intuitionist model or Prinz's anti-nativist view is correct, moral norms are acquired through mechanisms that would make rational resolution to moral disagreements difficult or impossible. Prinz (2009) argues for this explicitly when he states that variation between cultures "[...] may be impossible to rationally resolve. Moral norms are products of nonrational enculturation, not deliberation and deduction from shared first principles," which, he concludes, "amounts to a strong form of descriptive moral relativism" (p. 187). If moral norms are acquired this way, different populations will attach intrinsic importance to different concrete moral norms or otherwise develop rigid commitments to first-order moral beliefs. For instance, an individual raised in one culture may adopt that culture's condemnation of homosexuality, while someone raised in a different culture could adopt their culture's acceptance of it. Even if both of these beliefs were grounded in a harm-based template, information about the harmfulness of homosexuality may be insufficient to sway either individual to adopt the other's beliefs, since the mechanisms involved in norm acquisition would be insensitive to the domain-general processes involved in reasoning and philosophical reflection.

Domain relativism could also support descriptive relativism. If different cultures assign differential weight to or assign variable relevance to one or more domains, this could produce irresolvable intercultural differences in moral value. This possibility would be especially likely if the social intuitionist model is correct, since the SIM suggests that moral beliefs generated by intuitive processes are resistant to conscious revision.

While Haidt does not deny that we can reflect on and revise our moral beliefs, it is unclear whether such processes permit complete malleability in our moral commitments.

Toolkit nativism and anti-nativist hypotheses are consistent with descriptive relativism, though neither, if correct, would guarantee relativism. On either view, the moral content of different moral frameworks may vary between individuals or cultures, since the local social environment determines the content of an individual's moral beliefs. Yet this is consistent with the possibility that members of different social environments could converge on the same moral standards. Absent additional psychological facts about how moral norms are acquired and internalized, and how subject they are to change, views about the flexibility of moral beliefs could cut both ways. The very cognitive malleability that allows a person in one culture to develop a different set of moral beliefs than someone in another culture may also allow those individuals, under the right circumstances, and given further facts about the psychological mechanisms involved in moral judgment and moral disagreement, to reach agreement. FitzPatrick (2014b) points out that even if evolution played a substantial role in shaping the mechanisms involved in moral judgment "[...] This is entirely compatible with thinking that thousands of years of cultural evolution, including the development of sophisticated traditions of moral inquiry and reflection, have also allowed us to engage in largely *autonomous* moral thinking" (FitzPatrick 2014b, p. 242). FitzPatrick adds that we do seem to engage in this type of autonomous thinking when we pursue philosophy, mathematics, and science, and each of these areas of inquiry consists in the discovery of and convergence on a unified set of facts (FitzPatrick 2014a, b, 2015). If moral thinking falls within the ambit of domain-general processes, it is at least possible that the same capacities that permit convergence in math and science could also lead disparate individuals and cultures to converge on the same moral standards.

Descriptive relativism begins with the observation that there are significant moral differences across cultures or between individuals within the

same culture. The critical empirical question is not whether this is true or whether people are willing to fight and die on behalf of conflicting moral values. These issues have been settled with a decisive “yes.” Rather, it is whether the psychological mechanisms involved in the acquisition of moral belief and the resolution of moral disagreement involve a shared set of universal moral commitments, or a shared capacity to track the same set of objective moral truths, that would permit, at least in principle, all societies and all psychologically normal people to come to an agreement.

Evolutionary Psychology and Metaethical Relativism

Evolutionary psychology has both direct and indirect implications for metaethical relativism. Since most arguments for metaethical relativism rely on the claim that descriptive relativism is true, one way evolutionary psychology can play an indirect role is by supporting or casting doubt on the existence of fundamental moral disagreements (see Harman 1996; Prinz 2007; Wong 1984, 2009). One way of establishing metaethical relativism is to identify cases where people reach moral conclusions without any errors in their reasoning or mistaken judgments about the world. If conflicting moral perspectives can be rationally maintained, this suggests that neither position is objectively correct. Arguments along these lines rely on identifying plausible real-world instances of such “faultless” moral disagreements in which neither side of a moral dispute is demonstrably mistaken (Gowans 2015; Kölbel 2004). This reliance on descriptive relativism leads Gowans (2015) to suggest that metaethical relativism would lose most of its supporters if descriptive relativism were refuted. Metaethical relativism would not be decisively refuted even if descriptive relativism were rejected. Some arguments for metaethical relativism do not depend on the prevalence of moral disagreement (see Harman 2000; Rovane 2011, 2013; Velleman 2013). Others appeal to the hypothetical possibility of rationally defensible disagreement (Pojman 2004). If a single civilization came to dominate the world and impose the same cultural standards on everyone, there may be no moral disagreements, but moral

principles would not become objective merely because rival positions had been eliminated. If this were to happen, Pojman insists, “We could still *imagine* a culture that was an exception to the rule and be unable to criticize it” (p. 248). Metaethical relativists could also argue that intelligent extraterrestrial species would have faced different evolutionary pressures that would plausibly lead them to develop different moral values. This suggests that fundamental moral disagreements may be possible even if we cannot identify any among human populations.)

Evolutionary psychology also has important implications for moderate metaethical relativism. These hybrid accounts allow conflicting moral systems to be true but within objective limits imposed by human nature (among other constraints). Foot (2001, 2002), Nussbaum (1993), Wong (1995, 2009), and Velleman (2013) all ground objective moral constraints in empirical facts about what promotes a good human life. For example, Wong’s pluralistic relativism requires moral systems to promote cooperation and individual flourishing. Wong emphasizes that knowing which moral systems can achieve these ends in practice requires a detailed empirical understanding of the particular goals, needs, and desires imposed on the human species by its distinct biological and psychological characteristics, which leads him to explicitly conclude that moral theory must be integrated with empirical findings in evolution and psychology. Although Wong is hesitant to endorse specific evolutionary psychological accounts, empirical facts about human psychology float free of his particular stance and ultimately determine the conditions that optimize human flourishing. Wong is cautious not to explicitly endorse particular evolutionary psychological theories, however. He states that his “use of evolutionary theory [...] should not be confused with an endorsement of some of the most prominent theories of evolutionary psychology that do hold in central, universal psychological adaptations that evolved in the Pleistocene era and remain unchanged to this day” (p. 102). Wong cites Tooby and Cosmides’s (1992) “cheater detection module,” and Buss’s (2003) argument that men and women evolved

distinct preferences for different characteristics in mates as two examples, clarifying that “No argument in this book presupposes the truth of such assertions.” Nonetheless, Wong is confident that the liberal, Western conceptions of morality that dominate philosophy, such as Rawls’s *A Theory of Justice* (Rawls 1971), fail to account for the importance of community and family impressed upon us by natural selection. Aside from Wong’s account in particular, a persuasive case can be made that any attempt to limit moral systems on the basis of empirical facts about what promotes human well-being will depend heavily on evolutionary psychological insights into human motivation and behavior. Utopian dreams of abolishing familial bonds and parochial favoritism in favor of a more global, egalitarian social system may fail if familial affection and in-group favoritism are less susceptible to social conditioning than proponents of social constructivist approaches believe. Likewise, an evolutionary perspective can provide critical insight into the likely function, scope, and malleability of retributive impulses, feelings of jealousy, guilt, and shame, and virtually every other aspect of human psychology relevant to human well-being, insights that may be critical in prescribing norms and policies that do not backfire by failing to take proper stock of human limitations.

One critical response may be that these phenomena can be understood without adopting an explicitly evolutionary approach. However, the value of an explicitly evolutionary approach to psychology lies less in its formal necessity in understanding proximal psychological mechanisms than in understanding how these mechanisms are likely to operate under novel environmental conditions, in providing a deep well of theoretical resources for generating novel hypotheses and for its capacity to narrow the range of plausible hypotheses by providing a background of theoretical and empirical considerations that serve as a check on the plausibility of existing psychological theories, explanations, and phenomena.

To consider just one example of how evolutionary psychology can provide a novel insight into the conditions most likely to be conducive to

human well-being, Wright (1994) argues that conservative preference for traditional monogamous marriage and the nuclear family may reflect a deeper wisdom about human nature, even if progressive and liberal policies are usually more consistent with promoting collective human welfare. Men and women in ancestral environments faced distinct adaptive challenges with respect to mate selection, which culminated in an evolved preference in men for women who are young, healthy, and attractive and a preference among women for men who have high status and the ability to provide resources (Buss 1995). According to Wright, these differences influence the dynamics of the marriage market in polygamous and monogamous cultures. Wives will be less evenly distributed in polygamous societies, since many women benefit more from being a second or third wife to a wealthy, high-status man than the exclusive wife of a lower-status man with fewer resources. As a result, many men on the lower social rungs will remain unwed. Wright argues that this would have significant negative consequences for society, since marriage can exert a pacifying effect on men who would otherwise be more likely to engage in risky behavior and commit more violent and nonviolent crimes (Daly and Wilson 1990, 2001). Wright’s thesis is supported in part by evidence that a high male to female sex ratio is associated with increases in violent crime (Hudson and Den Boer 2004) and that marriage is associated with decreased crime (Burt et al. 2010). These effects may be quite dramatic. Sampson et al. (2006) found that “being married is associated with an average reduction of approximately 35% in the odds of crime compared to nonmarried states for the same man” (p. 465; but see Schacht and Kramer 2016 and Schacht et al. 2014 for more recent criticisms of the impact of sex ratios on crime).

Wright argues that contemporary liberal societies have become increasingly permissive of divorce, premarital sex, and a generally lax attitude about sexual behavior. The net effect has been an abandonment of traditional marriage and slide into serial monogamy, which has similar social consequences as polygamy, since serial monogamy allows high-status men to monopolize

the peak fertility of young women before moving on to younger mates (p. 101). In short, Wright argues that a strong norm of institutionalized monogamy would provide a bulwark against the socially destructive behavior of unwed men (pp. 101–102). Even if Wright is incorrect, his analysis reveals the potential for an evolutionary psychological perspective to uncover reasons to reevaluate the social impact of institutions we might have otherwise overlooked.

Findings in evolutionary psychology could also cast doubt on metaethical relativism by supporting forms of moral realism that are incompatible with it. At a minimum, moral realism holds that moral claims can be true or false, and at least some of these claims are true (Sayre-McCord 2015). (More specifically, moral realists hold that at least some first-order moral claims are true, e.g. “murder is wrong” (see Bennett 1998, p. 46). An anti-realist could acknowledge that some claims about morality can be true, e.g. “There are no moral truths,” but this does not constitute moral realism.) Not all conceptions of realism are necessarily incompatible with metaethical relativism (Harman 2015), and this minimal definition is consistent with metaethical relativism (see also Joyce 2015). (Joyce (2015) makes this point plainly, stating that “Moral relativism is sometimes thought of as a version of anti-realism but (short of stipulating usage) there is no basis for this classification; it is better to say that some versions of relativism may be anti-realist and others may be realist.”) However, moral realism is typically construed (and will be understood here) more narrowly as the claim that moral facts are “objective features of the world,” which we are capable of discovering and which are not dependent on or constituted by beliefs, preferences, or evaluative attitudes (Joyce 2016a, p. 5; Sterelny and Fraser 2016; Street 2006). Since moral realism in this narrower sense purports to establish the existence of a universal body of objective moral facts that are true for all people and cultures independent of their individual or cultural moral standards, any such account would entail an explicit rejection of metaethical relativism. Several attempts have been made to establish this more narrow conception of moral realism by appealing to human evolution (Collier and Stingl 1993, 2013;

Harman 2000; James 2009; Sterelny and Fraser 2016; Zamulinski 2007). Collier & Stingl refer to this approach as *evolutionary moral realism*, which they define as “the view that there are moral values with roots in evolution that are both specifically moral and exist independently of human belief systems” (p. 218). Sterelny and Fraser (2016) present one of the most developed accounts of evolutionary moral realism (Joyce 2016a). They argue that the moral cognition evolved primarily to identify “facts about profitable forms of cooperation, about social arrangements and cognitive dispositions positively and negatively relevant to the stable exploitation of those opportunities” (p. 10). The success of accounts like these depends critically on whether the facts of human evolution are consistent with them. If we did not evolve an innate capacity for distinctively moral cognition, or if we did, but this capacity does not function in part to detect facts about which policies, actions, and attitudes facilitate cooperation, Sterelny and Fraser’s account would fail for the simple reason that it rests on mistaken empirical presuppositions about the evolution of human moral cognition. But if they do correctly identify the facts of human evolution, one of these accounts could succeed at establishing an objective set of moral truths that would disqualify metaethical relativism as a viable philosophical position.

Even so, some of these accounts may provide an incomplete picture of morality that allows some room for fundamental moral disagreement. Sterelny and Fraser (2016) claim only that *one* of the primary functions of moral cognition is to track facts about cooperation. If, as they concede, our moral faculty only partially and imperfectly tracks facts about cooperation, this leaves open the possibility that there are other aspects of morality that cannot be fully incorporated into a realist account of morality. Sterelny and Fraser seem open to this possibility, rejecting the strict dichotomy between evolutionary influences on human moral thought either fully vindicating or fully debunking moral realism (p. 4). A moderate form of metaethical relativism could potentially escape partial realist accounts of this kind, if they can identify plausible instances of fundamental moral disagreement that fall outside the scope of

the truth-tracking aspects of moral cognition. (It also seems that evolutionary moral realist accounts may not escape being relativized to the *species* (see Harman 2000). If so, it is unclear how these accounts would manage interspecies moral disagreements. If moral facts *just are* the sorts of facts captured by human linguistic conventions, however, then one move may be to argue that another species with radically different values isn't really engaged in *moral* cognition but a conceptually analogous form of normative cognition that could similarly track its own independent set of normative facts.)

In contrast to arguments for evolutionary moral realism, *evolutionary debunking arguments* (EDAs) attempt to undermine moral realism by demonstrating that moral beliefs are false (Ruse 1986, 2006) or unjustified (Joyce 2006; Street 2006). Street (2006) presents one of the most widely discussed EDAs in the form of a dilemma for moral realists. Street begins with the premise that some form of moral nativism is true or at least that evolution has so extensive an influence on moral judgment that that "our system of evaluative judgments is thoroughly saturated with evolutionary influence" (p. 114). She then poses the following dilemma to moral realists: either there is no relationship between evolutionary influences on moral judgment and the independent set of objective moral facts posited by the realist or there is a relationship. If there is no relationship, then it would be an extremely unlikely coincidence if our moral judgments happened to track objective moral facts (Joyce 2016a). If there is a relationship, then moral judgments could track moral facts. Street refers to this second horn of the dilemma as the *tracking account*. Street believes that this is the more plausible of the two horns of the dilemma but that, unfortunately for the realist, available empirical data does not support it. Evaluating Street's argument is not critical here. The only relevant point is that both EDAs and evolutionary moral realism fail if they rest on mistaken assumptions about the evolution of human moral cognition. In short, these accounts rely on empirically falsifiable evolutionary psychological presuppositions, and to that extent they are all

fundamentally dependent on evolutionary psychological findings.

Fraser (2014) has criticized proponents of EDAs for failing to grapple with the relevant evolutionary details and proposes a minimal set of conditions necessary for the evolved cognitive mechanisms involved in moral judgment to reliably track moral truths. This represents genuine progress in identifying the empirical questions both moral realists and antirealists would need to answer. But the conditions Fraser identifies presuppose that we are adapted to engage in distinctively moral judgment. Machery and Mallon (2010) distinguish this strong nativist position from two alternative conceptions of what it would mean to say that "morality evolved." To say that morality evolved could mean that some of the underlying mechanisms involved in moral judgment (but not necessarily *only* moral judgment) evolved (p. 4). Likewise, normative cognition, understood as the "the capacity to grasp norms and to make normative judgments," may have evolved (p. 4). If so, there may be no specific evolved faculty for distinctively *moral* normative judgments. (Sinnott-Armstrong and Wheatley (2014) defend the even stronger claim that there is no conceptually unified domain of "moral norms" at all.)

Millhouse et al. (2016) argue that if a capacity for distinctively moral cognition did *not* evolve, this presents a significant obstacle for EDAs. If moral cognition results from a domain-general capacity for normative cognition, arguments that undermine moral truth may also undermine other evaluative truths, including the very epistemic norms that would permit people to make rational judgments in the first place. Any EDA that seeks to establish that *only* moral norms are threatened in this way must therefore either show that moral cognition is a distinct capacity or provide a principled means of debunking *only* moral judgments but not other normative judgments. Millhouse et al. refer to this as the *containment problem*. On the other hand, if some of the underlying components involved in moral cognition evolved, each may have a different evolutionary history and adaptive function. If so, debunking arguments that cast doubt on the reliability of specific mechanisms

will have to target each of these mechanisms separately to show that that mechanism in particular cannot reliably track moral facts. This opens up the possibility of more targeted evolutionary debunking of specific features of moral judgment. For instance, if Greene's dual process model of moral cognition is correct, then moral judgments may result from two relatively distinct psychological processes, each of which may have a unique evolutionary history and may have evolved to meet a specific adaptive challenge. An evolutionary debunking argument may succeed at undermining one of these domains without undermining the other. In short, if moral cognition is the result of a disunified set of cognitive processes, it may be possible to debunk some moral judgments without debunking others.

Evolutionary Psychology and Normative Relativism

The truism that one cannot derive normative conclusions from descriptive facts is no less applicable to the relationship between evolutionary psychology and normative relativism (Hume 1739; Schurz 1997). Although the moral duty to tolerate people and cultures with different moral practices cannot be derived directly from facts about the evolution of moral cognition, evolutionary psychology still has indirect implications for normative relativism. Arguments in favor of normative relativism are often predicated on the truth of descriptive relativism, metaethical relativism, or both. Insofar as evolutionary psychology supports or undermines either, it will have an indirect influence on arguments for normative relativism.

Evolutionary psychology also has the potential to provide practical insight into how to devise and implement policies and interventions that effectively promote intercultural and interpersonal tolerance of moral differences. Even if we arrive at the normative conclusion that tolerance of moral differences is desirable, the practical question of how best to conform to this norm will depend on relevant psychological considerations. Research on the developmental psychology (e.g., Aboud 2003; Bigler and Liben 2007; Cameron et al. 2001; Rutland et al. 2010), social psychology (e.g., Brown 2011; Devine 1989; Greenwald

and Banaji 1995), and neuroscience (e.g., Amodio 2014; Baumgartner et al. 2015; Ratner et al. 2014; Sellaro et al. 2015) of prejudice, stereotyping, and intergroup biases can and already has been usefully integrated with moral psychology (Van Nunspeet et al. 2014) and supplemented by an evolutionary perspective (Fiske 2000; Kaya 2015; Kurzban and Neuberg 2005; Kurzban et al. 2001; Mahajan et al. 2011).

Park (2012) has already made an explicit effort to extract practical guidance from an evolutionary psychological perspective on tolerance. An evolutionary perspective on prejudice suggests that there may be systematic differences between forms of prejudice related to intergroup interaction (e.g., racism) and forms of prejudice that are not (e.g., sexism) since the former may draw on evolved mechanisms uniquely adapted to coalitional psychology. If different forms of prejudice rely on different psychological mechanisms, understanding the evolutionary origins and likely function of these mechanisms may be relevant to devising effective interventions. As Park notes, "A broader implication of evolutionary perspectives is that there is unlikely to be a panacea for reducing every kind of prejudice. The best methods will differ for prejudices against ethnic out-groups, women, elderly people, gay people, obese people, disabled people, and non-human animals, because the roots of these prejudices differ" (p. 195).

Conclusion

The philosophical relevance of empirical data has become an increasingly contested topic in contemporary philosophy. The rise of experimental philosophy (Knobe and Nichols 2013), which utilizes social scientific methods to explore traditionally philosophical questions, has prompted widespread reflection and reevaluation of the methods and characteristics that make philosophy a distinct academic discipline. Recent attempts to draw philosophical conclusions from moral psychology (e.g., Greene 2003) have likewise challenged traditional assumptions about the relationship between moral psychology and moral philosophy. An

evolutionary psychological perspective will likely play a growing role in understanding the relationship between psychology and philosophy in general. In reviewing the relevance of evolutionary psychology to the different forms of moral and cultural relativism, this entry has outlined one small facet of this broader picture.

Cross-References

- Ethnography
- Franz Boas
- Misinterpreted as Cultural Relativism
- Modern Moral Relativism
- Relationship Between Culture and Race

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Cultural Cortical Recycling Hypothesis Applied to Money

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Synonyms

Cultural evolution; Monetary artifacts; Neural recognition systems

Definition

The cultural cortical hypothesis states that neural mechanisms, which were used in evolutionarily ancient environments for the recognition of natural visual categories like faces and food items, have now been recycled for recognition of more recent cultural artifacts, like money.

Introduction

Money is a recent institution – circa the seventh century BC, in Lydia for its apparition as coins (Kagan 1982; Pavlek et al. 2019) – fit to facilitate anonymous and out of group transactions. In shaping such transactions, money performs the function of shaping relationships with our conspecifics and, in turn, our social environments. But despite the ubiquity of money and economic institutions, it is evolutionarily ancient psychological traits like altruism, reciprocity, and cooperation which are most widely studied, both conceptually and empirically, to understand human social institutions. Little knowledge has been acquired on the biological anchoring of more recent economic institutions, like money and the social artifacts that support their functioning. A default hypothesis would be that they are a specific and autonomous development from our basic neurobiological and cognitive fabric. But it remains largely obscure as to *how* these biological mechanisms have been involved in the emergence of economic mechanisms that seem to lie far beyond their purview.

The Main Hypothesis

The hypothesis we advance here, in the particular case of monetary artifacts, is that of an epigenetic nature. Since one of the fundamental modes by which we relate to these artifacts is through perception and recognition, evolutionarily selected mechanisms in the visual system – dedicated to the perception of survival-oriented features in ancestral environments – are cortically recycled

to process these novel cultural items, vital in our modern economic environments. It must be noted that this does not exclude the role of social cognitive mechanisms driving monetary exchanges, which affect and bias the theoretically neutral use of money in important ways and are supported by modern artifacts like coins (Rumiati and Lotto 1996) and other monetary media. However, to be efficient, coins need to be efficiently and promptly identified, and the cortical recycling hypothesis can provide a biologically rooted, theoretical basis for the same.

The cultural cortical recycling hypothesis has hitherto been confined to other symbolic systems such as literacy and numeracy (Dehaene and Cohen 2007), which promote the idea that part of the human cortex is specialized for cultural domains such as reading and arithmetic. Though the apparition of these cultural domains is too recent to have influenced the biological evolution of the human brain, brain activations associated with these symbolic stimuli have been shown to demonstrate a reliably high degree of invariance. To account for this seeming paradox, the cortical recycling hypothesis is proposed, according to which cultural inventions invade evolutionarily older brain circuits and inherit some of their structural constraints. In this article, we speculate about the extension of this hypothesis to money and other symbolic aspects of our economic lives.

A Seminal Experiment

We briefly report on an experiment, demonstrating fast and automatic detection of the validity (or invalidity) of unfamiliar coins, in a subregion of the brain visual system – the fusiform gyrus. We show the existence of symbolic activities in the fusiform gyrus, associated with the visual categorization of monetary stimuli.

Tallon-Baudry and colleagues (2011) tested the perception of valid coins (euros and Australian dollars) versus invalid ones (French francs and Finnish marks, which have been out of circulation since 2002) using magnetoencephalography (MEG). Since coins are both material and symbolic objects endowed with economic properties by social agreement, abstract and

artificial features such as *coin validity* were expected to be analogous to words and their meanings. Moreover, since symbolic categories are conventional, they were expected to be differently processed than ecological categories which are based on visual similarities, like faces, food, and animals. It was expected that monetary stimuli would be decoded with a minimal 300 ms delay, similar to categorizing a letter string in one's natural language (Allison et al. 1994) and different from categorizing natural objects, which occur within a 150 ms delay (ibid.). Surprisingly, it was found that both familiar and unfamiliar coins were readily recognized and differentiated within 150–175 ms, similar to natural categories, indicating that there preexists a neural representation of money sufficiently generic and abstract to accommodate new instances. Thus, familiarity with specific categorical instances of valid or invalid coins was not a requisite for money recognition. These results suggested that the human ventral visual system is adapted to deal with symbolic environments, or at least certain objects such as coins, on the basis of general knowledge rather than long reinforced experiential channels.

Inter-species Comparison

This raises the question as to whether such mechanisms and observations are human specific or can be found in other species as well, with comparable visual neural organization. Do species, which flexibly use tokens in exchanges, display a similar ability to categorize the validity of these tokens on a mere perceptual basis? De Petrillo et al. (2019) studied six capuchin monkeys (*Sapajus* spp.), who were required to exchange valid/familiar tokens, valid/unfamiliar tokens, invalid tokens, and no-value items with the experimenter. They first exchanged a similar number of valid/familiar and valid/unfamiliar tokens, followed by exchanges of invalid tokens and no-value items. And just like humans, capuchins readily recognized token validity, regardless of their familiarity with these tokens. Time delays in the use of valid/unfamiliar versus valid/familiar tokens in the task were nonsignificantly different, evidencing the neurobiological capacity of non-human primates in promptly acquiring and

visually tapping into abstract monetary features, independent of long-term reinforcement.

In a sequel experiment, the authors evaluated the flexibility of the token–food association by assessing whether capuchins could engage in reverse food–token exchanges. This was done to study how rapid detection of monetary validity could be associated with actual proto-monetary behavior. Subjects spontaneously performed chains of exchanges in which a food item was exchanged for a token, and then the token was exchanged for another food item. Overall, capuchins recognized token validity and successfully engaged in chains of reverse and direct exchanges. This suggested that although non-human animals are far from having full-fledged monetary systems, for capuchins, tokens share at least some features with human money and can be promptly recognized as valid or invalid on a perceptual basis.

Adapting the Cultural Cortical Hypothesis

In order to explain such results, we put forward the idea that some specific cortical maps dedicated to basic perceptual functions could have been re-used at some point in relatively recent human history, for the purpose of processing novel cultural items (Dehaene and Cohen 2007). In other words, specific brain areas crucial for human survival in hunter-gatherer societies were recycled in view of optimal visual recognition of monetary stimuli. This would further suggest that there isn't a complete discontinuity between the cognitive and neurobiological mechanisms that bore upon exchanges in pre-monetary economics and the ones that prevail in modern times. From a neural point of view, our findings may indicate that the so-called ventral visual pathway, a system previously thought to analyze visual features such as shapes or colors in daily experiences, could also utilize conceptual features such as monetary validity in abstract economic exchanges.

The symbolic abilities of the posterior fusiform region suggested here could constitute an efficient neural mechanism to deal with culturally defined

symbols. Moreover, such a hypothesis also holds explanatory value for the success and cultural emergence of money as an extension of evolutionarily anchored and localized processing of natural items such as faces, food, or in the artifactual domain, tools (Stout et al. 2008). The main effect of validity versus invalidity has been documented to be concentrated in the fusiform gyrus. The speculation is thus that a special neural cortical map located in this area may have been selected through evolution to detect whether faces or foods, or anything contributing to the individual's survival in her environment, are of a "valid" or an "invalid" nature. This primitive cortical map may then have been reused in the processing of money stimuli and supported its emergence. Such a neural nesting of money would furthermore help to explain behavioral anomalies that have been often emphasized with respect to this culturally central human artifact, such as perceptual illusions in the guise of money illusion (Weber et al. 2009; Bourgeois-Gironde and Guille 2011).

Conclusion

The application of Dehaene and Cohen's (2007) cultural cortical recycling hypothesis to the visual processing of monetary artifacts is still speculative due to the lack of confirmatory experiments. Nonetheless our economic lives involve an array of symbolic activities, the emergence of which is contemporary with the cultural revolution leading to numeracy and literacy. In that sense it seems reasonable to investigate an adaptation of the cultural cortical recycling hypothesis to a domain of our human activities that has generated its own pervasive cultural items, such as, most centrally, money. A future refinement in the evolutionary approach to economic behavior would consist of an exploration of what we label "continuing temporal overlaps" in our cognitive and behavioral evolution. Using money in modern market transactions jointly taps into very anciently established neural circuits and to modern adaptations of these circuits. This temporal overlap may contribute an explanation to biases, including perceptual ones, that affects our economic behaviors.

Cross-References

- ▶ [Cortical Neurons and Conducting Velocity](#)
- ▶ [Early Perspectives on Evolutionary Change](#)
- ▶ [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)

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Cultural Determinism

- ▶ [Blank Slate, The](#)
- ▶ [Standard Social Science Model](#)

Cultural Development

► Evolution of Teaching

Cultural Differences

► Cross-Cultural Expression

► Cross-Cultural Variation

Cultural Differences in Mate Preferences

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Synonyms

Cross-cultural differences; Culturally variable; Partner preferences

Definition

Cultural differences in mate preferences refer to the variations that arise in preferred mate qualities as a result of cultural influences.

Introduction

Research has found that there are mate preferences that are found cross-culturally. For example, across cultures, symmetry is found attractive (Rhodes et al. 2001). However, studies have also found cultural differences in mate preferences (Batres et al. 2017; DeBruine et al. 2010; Penton-Voak et al. 2004).

Explanations for Cultural Differences in Mate Preferences

From an evolutionary standpoint, preferences are adaptations for mate choice. Therefore, mate preferences should vary depending on culture to reflect variations in the environment. Preferences for body mass index (BMI) have been found to vary cross-culturally since there are differing optimal weights for different environments. For instance, one study found that individuals from Uganda preferred heavier figures than individuals from Greece and Britain (Furnham et al. 2002). In environments with less food certainty, individuals with higher BMIs are found more attractive since they are better equipped to survive and reproduce.

Preferences for masculinity have also been found to vary cross-culturally. For example, one study found that Jamaican women preferred men with more masculine faces than British women (Penton-Voak et al. 2004). Similarly, DeBruine et al. (2010) found that across 30 countries, women's preferences for masculinity were higher in countries with decreased health. There is some evidence that masculinity in men signals health (Thornhill and Gangestad 2006), and therefore, it would be beneficial for women in countries with higher health risks to prefer more masculine partners.

Apart from an evolutionary perspective, urbanization has also been proposed as an explanation for cultural differences in mate preferences. Indeed, urbanization predicts changes in basic perceptual processes (Linnell et al. 2013). Individuals in environments with higher levels of urbanization have increased media exposure, and research has shown that this exposure influences partner preferences (Batres and Perrett 2014).

Lastly, a third explanation that has been proposed to explain cultural differences in mate preferences is familiarity. Studies have found that exposure to certain populations of faces increases the attractiveness of similar faces. For instance, Saxton et al. (2009) found that girls who attended single-sex schools preferred more feminized male and female faces than girls who attended mixed-sex schools. Similarly, another study found that

across El Salvador and Malaysia, individuals exposed to faces with higher adiposity preferred faces with higher adiposity (Batres and Perrett 2014). These results suggest that the visual diet of individuals also influences partner preferences.

Conclusions

Several explanations have been proposed to explain cultural differences in mate preferences. What is clear is that culture does indeed have an effect on preferred partner characteristics. Moreover, those preferences are quite malleable, with changes in the environment resulting in variations in partner preferences (Batres and Perrett 2017). Future research into cultural differences in mate preferences is still needed, but the growing concern about examining partner preferences outside of WEIRD (Western, Educated, Industrialized, Rich and Democratic) populations has already yielded many interesting insights.

Cross-References

- Evolutionary Cultural Psychology
- Mate Preferences

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Cultural Differences in Sexual Socialization

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Synonyms

[Sex education](#)

Definitions

Sexual socialization refers to the variable extent and many ways mating strategies are communicated and replicated along and beyond generational lines.

Sexual enculturation encompasses induction into any relatively patterned and durable system of elaboration of mating choices as socio-symbolic resources.

Introduction

Formal sex education has a distinct, if relatively short, global history, and although today near-universal, it exists importantly despite near-universal controversy (Zimmerman 2015). Evident cross-cultural differences in sexual socialization have been studied semi-systematically since the late nineteenth century. They triggered strikingly divergent valuations: by Victorian evolutionists, as vignettes of “primitive” promiscuity; by often psychodynamically oriented mid-twentieth-century sexual reformers, to denaturalize what was considered neurosis-inducing Western bourgeois sexual uptightness; by 1970s psychohistorians, claiming that most modes of sexual socialization recorded by historians and ethnographers entailed “child sexual abuse.” None of these readings enjoys much traction today; most controversy rather arises from interpreting comparative data in the light of evolutionary psychological theories of child development and child-rearing inspired by early 1970s “parental investment theory” (Draper and Harpending 1988; Belsky et al. 1991), and subsequently by early 1990s “sexual strategies theory.” Cross-contextual comparisons have been used to demonstrate both ubiquitously recurring patterns and high variability in lifetime reproductive challenges and outcomes. In these comparisons *sexual culture* is considered both to present, and to codify into sexological lore, specific reproductive challenges for parents, for their offspring, and for their prospective mates. These challenges reflect the responsive, yet differentiated, biological-reproductive outlooks of men and women. They simultaneously articulate the symbolic resources available to men and women within social systems providing gender, generational, kinship, and other frames for the allocation of status, resources, and identity.

Mating Contexts

Today, differences between parenting of boys versus girls are generally found to be minimal (Endendijk et al. 2016). In the area of sexuality, however, daughters are ubiquitously raised more restrictively than sons, arguably suggestive of culture-transcending fitness effects (Kuhle et al. 2015). Human and especially female mating strategies are considered highly contextual, in any case, requiring the development and lifelong fine-tuning of *mating intelligence* (Geher and Kaufman 2013) in any context, with usually well-recognized peer-group, parental, grandparental, or avuncular roles (Fisher et al. 2013). Parent-offspring conflicts over offspring mate choice are widespread across human cultures (Van den Berg et al. 2013). Such conflict can be said to create the need to socialize offspring in the direction of mating choices preferred by parents under specific environmental conditions. Enforcing of parental preferences can clearly also precede or otherwise obviate socialization of offspring mate-selection and mate-retention skills. Intrafamilial mating is subject to culture-specific rules, or in any case mechanisms, of avoidance. Other modalities of in-group mating may rather be subject to culture-bound rules of obligation, or less binding qualifications of convenience, appropriateness, or eligibility. These intrafamilial and intergenerational intrigues impress as ubiquitous among humans (Gray and Garcia 2013). They clearly also refer the anthropologist to cross-culturally and historically variable ways of being translated into lore and law. Parental control over mating has dominated most of what is known of human pre-industrial social evolution, and such control continues to exert an overriding sexual selection force, for instance across the Abrahamic religions (i.e., more than half of the world population).

Parental influence extends to a spectrum of key parameters of offspring mating, including mate preference, selection or exclusion (betrothal, arrangement of courtship, and mating trials) timing of mating and child-spacing; postmarital residence; and so on. These dimensions of *parental choice* are characterized by evident differences

between societies of different subsistence types (hunting-and-gathering, agropastoral, industrial and post-industrial economies), but also between and within societies of a similar subsistence type (Apostolou 2017). Child training patterns including those pertaining to sexuality have been shown to vary in ways predictable from evolutionary theory, especially between the sexes, and responsive to such factors as group size, marriage system, and stratification level (Low 1989). In preindustrial contexts, ritualization and coordination of reproductive “crises” (including especially menarche, marriage, and birth of, for instance, future male heirs) voice the interests of not so much *parents* as the wider scope of *fraternal interest groups* (Paige and Paige 1981), or overarching corporate entities such as lineages, clans, moieties, age sets, casts, and tribes. “Sexual socialization” here inclusively translates to all those formal and informal efforts to induct young people into these often starkly gendered and intricately allied political factions, which may in turn entail a dramatic delimitation or even determination of mate and mating choices. As a consequence, eventual mating choices may be interpreted as either articulations of corporate decision-making or as precarious attempts at defying such politics.

Mating Cultures

Parental choice is only one (a receding) facet of, or engine behind, what in twentieth-century Anglophone social scientific parlance was variably known as *sexual enlightenment*, *sexual socialization*, *sex training*, *sex education*, or *family planning*. Its purported objectives have shifted, reflecting a changeable encryption of pedagogical stakes and purviews: *sexual “well-being”* or *“fulfillment,”* *sexual agency*, *sexual self-determination*, unrestrained *“expression of one’s psychosexual identity,”* among other formulations. Living up to these familiar tropes is a uniquely human burden and requires what may more productively be called *sexual enculturation* (compare Konner 2010). It extends to culturally divergent concepts and indices of docility,

distinction, and discretion: beyond inculcation of often gendered traits such as “sexual restraint” or modesty, and including culturally belabored notions of shamefacedness, chastity, reputation, ignorance (“innocence”). In religious and ensuing medical conceptualizations, modes of satisfying the “reproductive drive” are abstracted across such time-honored juxtapositions as natural/unnatural, clean/polluted, and normal/perverse.

Much of this lore remains codified in medical consensus or law (often precariously both), though many contexts for adolescent mating are globally characterized by “stresses and shifts between concepts such as modernization/traditionalism, arranged marriage/free choice, love/family practicality, cohabitation/marriage, and collectivism/individualism” (Hamon and Ingoldsby 2003, p. ix). Within the course of a couple of generations, legislation has globally shifted from protecting the institute of the family from sexual liaisons and practices considered to undermine it, to protecting and disentangling the sex life of individuals from such corporate interference (Frank et al. 2010). In most of recent world history, most adolescents have not been known to cite, or indeed prefer, family as the primary resource for sexual instruction. Pre-adolescent sexual socialization is riddled with avoidance and anxiety, and even today poorly researched (Martin and Torres 2014). In the prolonged sphere of modern child-rearing and adolescent-coaching, makeshift cultural dichotomies reign, notably in the USA, between “good and bad” touch, “appropriate and inappropriate” comportment, “healthy and abusive” intimacies. *Sexual socialization* thus importantly entails not “mate choice” but the pancultural, and today variably international and global, projection and continual renegotiation of these binaries *regardless* of mate choice – unless choice of mates is declared, by cultural convention, impossible per se (such as where involving perceived power unbalances).

Conclusion and Implications

Though culture can be seen as providing solutions to common reproductive challenges, it can also be

said to create, entrench, or significantly complicate these challenges. This notably constrains scientific accounts of the problem. Sexual culture figures forth a socio-symbolic environment which frames reproductive problems in tendentious ways and offers resources for their resolution securely within those frames, with socio-symbolic payoffs and opportunities for some and hardship for others. Mating psychologists and behavioral ecologists might be thought of as decrypting and demystifying these frames. But since researchers and theorists are raised, and have to function, within some sexual culture or another, they typically steer clear of banalizing that culture's most critical sensibilities – today often precisely those gravitating around notions of “sexual and reproductive development” – and most end up crediting the status quo with accolades of presumptive functionality. In this way, *evolutionary psychology* can well function as yet another articulation, or framing device, of contemporary sexual culture, albeit an as yet marginally authoritative one.

Cross-References

- ▶ Adolescent Parenthood
- ▶ Arranged Marriages
- ▶ Conflict Between Parents and Offspring
- ▶ Cross-Cultural Studies
- ▶ Early Childhood and Adolescence
- ▶ Human Sexuality
- ▶ Mate Preferences
- ▶ Parental Investment and Parenting
- ▶ Peer Socialization
- ▶ Sexual and Reproductive Development
- ▶ Sexual Strategies Theory

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Cultural Display

- ▶ [Art Production, Appreciation, and Fitness](#)

Cultural Doctrines

- ▶ [Social Values](#)

Cultural Elements

- ▶ [Social Values](#)

Cultural Evolution

- ▶ [Cross-Cultural Expression](#)
- ▶ [Cultural Cortical Recycling Hypothesis Applied to Money](#)
- ▶ [Cultural Inheritance](#)
- ▶ [Cultural Transmission](#)

Cultural Evolution and Cultural Psychology

- ▶ [Evolutionary Cultural Psychology](#)

Cultural Heterogeneity

- ▶ [Cross-Cultural Variation](#)

Cultural Homicide Patterns

- ▶ [Cross-Cultural Pattern](#)

Cultural Inheritance

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Synonyms

[Behavioral evolution](#); [Behavioral inheritance](#); [Cultural evolution](#)

Definition

Cultural inheritance is an inheritance system characterized by the storage and transmission of information by communication, imitation, teaching, and learning.

Introduction

Cultural inheritance is an inheritance system characterized by the storage and transmission of information by communication, imitation, teaching, and learning (Peedicayil 2001). The communication can take place by different routes – visual, auditory, and other routes. The communication can occur by speech, by writing, by a tape recorder (Bonner 1980), and, in today's world, by television, cell phones, and the Internet. The communication can also take place over a considerable distance and over a considerable span of time (Bonner 1980). The communication can be fast or slow. This inheritance system was first proposed by the noted American geneticist and Nobel Laureate Thomas Hunt Morgan (1932). Cultural inheritance is widely present in the animal kingdom, especially birds and mammals. However, it markedly evolved and developed only during human evolution, with the marked increase in the size of the brain, which occurred both in absolute terms and in relation to body weight (Pilbeam and Gould 1974). The increase in size of the brain was associated with the emergence of language (Peedicayil 2002). Cultural inheritance is also referred to as cultural evolution

and behavioral evolution. It can occur by various routes (Jablonka and Lamb 1995): it can be transmitted from parents to offspring (vertical transmission), and to and from other members in the group (horizontal and oblique transmission).

When compared with genetic inheritance, cultural inheritance occurs faster, can occur between any two individuals, and is transmitted by the brain, and not by genes. However, cultural inheritance does have a genetic basis, the genes involved encoding proteins associated with the structure of the brain. Epigenetics, the study of heritable changes in gene expression not involving changes in DNA sequence, is considered to be the link between genetic inheritance and cultural inheritance during the evolution of cultural inheritance (Maynard Smith and Warren 1982).

Criteria to Be Fulfilled for a Trait to Be a Part of Cultural Inheritance

Modern evolutionary biology is founded on the Mendelian genetic model. However, now it is clear that this model is inadequate. Experimental evidence indicates that the environment can impose transgenerational effects and cause heritable variation for a broad range of traits (Bonduriansky and Day 2009). Danchin et al. (2011) have discussed the criteria that need to be fulfilled for a trait to be considered a part of cultural inheritance: (1) The expression of the trait must result from social learning, which is learning learnt from others. (2) Variation in information of the trait must arise from older to younger individuals, allowing the resulting variation in behavior to be inherited. (3) Social learning must modify the phenotype of the learning individual for enough time so that other individuals can observe the behavior and learn it. (4) The modification of the phenotype should be generalized to similar situations. The authors suggest that these criteria provide conceptual and practical tools for identifying cultural traits in order to study the ecological and evolutionary consequences of cultural inheritance.

Cultural Inheritance in Animals

As mentioned above, cultural inheritance is found not only in humans, but, to a lesser extent, also in animals. Obviously, cultural inheritance is only possible in animals with a considerable ability to change their behavior by copying and practice (Manning and Dawkins 1992). It is known that behavior can only evolve if animals differ in what they do and if the difference between them is transmitted from one generation to the next. In that case, natural inheritance can occur, favoring some variants, which hence spread, and eliminating others (Manning and Dawkins 1992). Cultural inheritance is unusual and unique because an animal can learn from its parents or others in its group. Later that animal itself can act as a model from which its own offspring can modify their behavior (Manning and Dawkins 1992). There are several examples of cultural inheritance in primates other than humans. For example, cultural inheritance manifests in the form of sweet potato washing, digging for peanuts, and placer mining of wheat grains in *Macaca fuscata* (found in Japan) (Wilson 2000). Examples among chimpanzees include fishing for termites using a twig, a leaf stalk, or a grass stem (Manning and Dawkins 1992). In orangutans in Borneo and Sumatra, several behaviors like gestures, tool use, and vocal signaling are also thought to be examples of cultural inheritance (Plotkin 2010).

There is now also increasing evidence for cultural inheritance in animals other than primates. A very good example of cultural inheritance in birds is the habit of blue tits to open milk bottle tops, a phenomenon first noticed in the United Kingdom (Manning and Dawkins 1992). Another example is young European blackbirds giving alarm calls to objects like a stuffed owl or a plastic bucket if they had heard their parents' alarm calls while looking at them (Manning and Dawkins 1992). Another example among birds is the maintenance of song dialects of many birds like the white-crowned sparrow (Manning and Dawkins 1992). Yet another example in birds is in New Caledonian crows which display significant cognitive skills in making tools for retrieving otherwise unobtainable food (Plotkin 2010). Cultural

inheritance is also thought to be at work in the phenomenon of vocal and motor imitation in bottle nose dolphins (*Tursiops*) and imitation and teaching in killer whales (*Orcinus orca*) (Rendell and Whitehead 2001).

Cultural Inheritance in Humans

Cultural inheritance is found predominantly in humans among all animals. This is because humans have two interrelated traits that distinguish them from other species: the first is a large brain in relation to body weight, and the second is the ability to communicate with other members of the same species by means of a very well developed language (Blackmore 1999; De Duve 2002; Buss 2008; Lieberman 2016). Language did not develop during human evolution all of a sudden. Before language evolved, a less sophisticated and developed form of language called protolanguage evolved (Jablonka and Szathmáry 1995; Szathmáry and Maynard Smith 1995; Nowak and Krakauer 1999). Protolanguage, when compared to language, is relatively simple, with a poorer grammar and lexicon. It is thought to have first appeared in *Homo erectus*, a precursor of our species *Homo sapiens*. *Homo erectus* appeared in the world about 1 million years ago (Foley 1995). The development of cultural inheritance was associated with an increase in the flexibility of behavioral responses, and was linked with the evolution of mental functions and abilities. It has been proposed that cultural inheritance underlies normal behavior and psychiatric disorders (Peedicayil 2002). Given below is a discussion of the evolutionary aspects of the role of cultural inheritance in normal behavior and psychiatric disorders.

Relevance of Cultural Inheritance to Psychology and Psychiatry

As mentioned above, language and a relatively large brain form the basis of cultural inheritance. The British psychiatrist and researcher Timothy J. Crow suggests that the human capacity for

language could be related to psychiatric disorders like schizophrenia and bipolar disorder. He suggests that such psychiatric disorders could be the disadvantageous spin-off of humans for having a large brain and the ability to communicate with one another by means of a well-developed language (Crow 1995, 2008). Indeed, it is well established that language is an essential and fundamental aspect of thinking and cognition (Fernald and Fernald 2007).

As referred to above, epigenetic mechanisms of gene expression were crucial in the development of language. Indeed, among all organisms, epigenetic mechanisms of gene expression play the greatest role in development in humans, and among all the organs in the human body, epigenetic mechanisms play the greatest role in the development of the brain (Peedicayil 2002). Moreover, there are abnormalities involving speech and language in psychiatric disorders like autism spectrum disorders and schizophrenia (Sadock et al. 2015), and there is a category of psychiatric disorders named language disorders. Language disorders present with difficulties in the acquisition and use of language across many modalities, including spoken and written, due to deficits in comprehension or production based on both expressive and receptive skills (Sadock et al. 2015).

Human beings are the quintessential social animal, and it is language that binds human beings together in any society. In this context, psychiatric disorders are well known to be influenced by psychosocial factors in their pathogenesis (Peedicayil 2004), and psychotherapy is a key component in the prevention and treatment of psychiatric disorders (Sadock et al. 2015). Moreover, it is known that psychosocial factors act by modifying epigenetic mechanisms of gene expression in the brain during the pathogenesis of psychiatric disorders (Peedicayil 2008), and epigenetic mechanisms of gene expression are thought to be the link between psychosocial factors and psychiatric disorders (Peedicayil 2015). There is also increasing evidence that psychotherapy exerts its therapeutic effect in patients with psychiatric disorders by modifying epigenetic mechanisms of gene expression (Peedicayil

2012). Thus, psychotherapy is thought to act by “undoing” what psychosocial factors have done during the pathogenesis of psychiatric disorders (Peedicayil 2017).

As discussed above, cultural inheritance is thought to underlie normal behavior and psychiatric disorders. As also discussed above, epigenetic mechanisms of gene expression were the link in the transition from genetic inheritance to cultural inheritance during the evolution of heredity. Hence, one can infer that epigenetic mechanisms are likely to play a major and crucial role in the pathogenesis of psychiatric disorders. Indeed, this is proving to be the case: there is increasing evidence that abnormalities of epigenetic mechanisms of gene expression underlie psychiatric disorders (Lee and Avramopoulos 2014).

Conclusion

Cultural inheritance is found in many animal species. However, it has only markedly evolved in humans. In humans, cultural inheritance underlies normal behavior as well as psychiatric disorders. Since cultural inheritance evolved from genetic inheritance by changes in epigenetic mechanisms of gene expression, epigenetic mechanisms also underlie normal behavior. Abnormalities of epigenetic mechanisms of gene expression predispose to psychiatric disorders.

Cross-References

► Evolutionary Social Psychology

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Cultural Intelligence Hypothesis, The

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Synonyms

Cultural quotient (CQ); Culture and intelligence

Definition

Cultural intelligence is understood as the capability to relate and work effectively across cultures.

Introduction

The initial proposal about cultural intelligence was presented by Earley (2002). Cultural intelligence has been defined as the individual's capacity to function and manage effectively in culturally diverse settings (Ng 2013). A concise definition of cultural intelligence was proposed by Thomas et al. (2008) as a system of interacting abilities that describe how these elements interact to produce culturally intelligent behavior and then identify measurement implications.

It can be hypothesized that from early in life, humans possess strong abilities for sociocultural

cognition; these abilities represent a framework for the further development of complex cognition. This is precisely the hypothesis known as cultural intelligence hypothesis (Herrmann et al. 2007).

Cultural Intelligence Characteristics

Cultural intelligence, sometimes referred as cultural quotient (CQ), is measured in a similar way to that used to measure the intelligence quotient (IQ) in general intelligence tests. People having a higher CQ are considered more successful when dealing with any cultural environment.

A cultural intelligence model composed by different dimensions has been developed (Earley and Ang 2003). According to this model, four different cultural intelligence dimensions (metacognitive, cognitive, motivational, and behavioral) and three intercultural effectiveness outcomes (cultural judgment and decision-making, cultural adaptation, and task performance in culturally diverse settings) can be distinguished. Diverse studies have demonstrated a consistent pattern of relationships where metacognitive cultural intelligence and cognitive cultural intelligence can predict cultural judgment and decision-making; while motivational cultural intelligence and behavioral cultural intelligence predict cultural adaptation, ultimately, metacognitive cultural intelligence and behavioral cultural intelligence predict task performance (Ang et al. 2007).

Furthermore, some relationships between cultural intelligence and personality have been demonstrated (McCrae et al. 1998). Using the Big Five personality model (Norman 1963), there have been significant associations between (a) conscientiousness and metacognitive cultural intelligence, (b) agreeableness and emotional stability with behavioral cultural intelligence, (c) extraversion with cognitive, motivational, and behavioral cultural intelligence, and (d) openness with all four factors of cultural intelligence. Therefore, the major and most important personality trait in cultural intelligence is openness to experience – a crucial personality characteristic that is related to a person's

capability to function effectively in diverse cultural settings (Ang et al. 2006).

Street et al. (2017) analyzed the question why primates vary in how much they use social learning. They found that both cerebral expansion and high reliance on culturally transmitted behavior coevolved with sociality and extended lifespan in primates. This coevolution is congruent with the hypothesis that the evolution of large brains, sociality, and long lifespans has increased reliance on culture and reliance on culture implies further increases in brain volume, cognitive skills, and longer lifespan in some primate groups.

Conclusion

Since the introduction of the concept of cultural intelligence in 2002, a significant amount of research has been developed concerning its measurement, definition, association with personality traits, and predictive capability. Furthermore, it has been observed that the evolution of larger brains and sociability is correlated with increased reliance on culture.

The concept of cultural intelligence has become an important concept in contemporary anthropology and psychology.

Cross-References

- ▶ Cross-Cultural Expression
- ▶ Cross-Cultural Similarities
- ▶ Cultural Universals
- ▶ Subcultural Theory

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Cultural Learning

- ▶ Adaptive Learning
- ▶ Cross-Cultural Expression
- ▶ Cultural Transmission

Cultural Plurality

- ▶ Cross-Cultural Similarities

Cultural Quotient (CQ)

- ▶ Cultural Intelligence Hypothesis, The

Cultural Studies

► Cross-Cultural Studies

Cultural Transmission

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Synonyms

Cultural evolution; Cultural learning; Social learning

Definition

The transmission of preferences, ideas, beliefs, and norms of behavior as a result of an interaction between biological predispositions and social interaction between and within generations.

Introduction

In his landmark work, *The Selfish Gene*, biologist Richard Dawkins describes living things as “survival machines” that do the work of our inherited genetic material (Dawkins 2006). Under this concept, these survival machines simply seek to survive and reproduce, a process that leads to the primary motivations of all living things, human, or otherwise.

If we are, as Dawkins says, merely survival machines for our genetic material, it suggests that we are not unique in any real way. However, that seems not to be the case, an admission that Dawkins makes freely. For Dawkins, “most of what is unusual about man can be summed up in one word: culture” (Dawkins 2006, p. 189).

Description

From a sociological perspective, culture is the language, beliefs, values, norms, behaviors, and even material objects that characterize a group (Henslin 2015). Cultural transmission occurs when those elements of culture are passed from one generation to the next. On its surface, it would appear that culture works independently of biological evolution but in a very similar format. However, this dualistic view represents a pre-modern approach to biology – an approach whose intellectual integrity has since been compromised (Cosmides and Tooby 1992). In fact, research has uncovered a symbiotic relationship between genes and culture (Bolwes and Gintis 2004; Gintis et al. 2008; Wind 1990), suggesting that culture and evolution work in concert to produce an interaction that determines either cultural or biological evolution or both (Bisin and Verdier 2005; Dick 2007; Jacobson 2009).

Where Dawkins speaks of culture as a uniquely human enterprise, others have found that it exists in chimpanzees (Whiten et al. 1999) with cultural transmission serving as a fundamental, albeit primitive, element of chimpanzee life. This suggests that the concept of culture is older than humans themselves – a concept that makes culture, or our ability to perpetuate it, of genetic origin.

Despite differences in complexity, culture in humans and chimpanzees works in a similar manner.

Darwinism holds that genes are self-replicating units that transmit biological data from one generation to the next. This is the bedrock of biological evolution. It can be seen as analogous to the hardware of a computer. But a computer requires software to run, software that requires updating from time to time throughout the life of the unit itself. Culture is that software and its basic unit of transmission is the meme, a term coined by Dawkins himself. Much like the gene, the meme is self-replicating, autonomous, and lacks foresight. The meme is tricky, however. It does not replicate well (low fidelity), like genes do, and is difficult to track, leading some to disregard the

concept altogether. It's important to understand that memes are a paradigm through which to understand the concept of cultural transmission.

Critics of evolutionary psychology often point to cultural adaptation and differences within cultures and between individuals as evidence that culture is not a biological universal, nor is it an adaptive trait. From early iterations such as Murdock (1932) to more recent arguments such as that of Lewontin et al. (1984) and Wood and Eagly (2002), critics often fail to recognize the symbiotic relationship between genetics and the environment in which they operate.

As humans we are born with a set of genetic material contributed by our parents. This material stays with us throughout our lives and determines a good deal of what we become, but it does not and cannot do it alone. Cultural transmission occurs when a social unit of replication (meme) is conveyed to us by someone. Historically, those transmitters were family and close friends, members of a group, tribe, community, etc. Sociologists call these conveyors our agents of socialization (Henslin 2015). With increased globalization, our world has gotten smaller, and our pool of transmitters has gotten much larger. As such, the memetic selection pressures are much different than they were even 25 years ago.

Conclusion

Cultural transmission is responsible for variations in language, diet, political ideology, social norms, fashion, and even part of our idea of what's attractive, offensive, or acceptable. In some extreme cases, cultural transmission can create ideologies that are difficult to alter, such as racism, religious beliefs, and political ideologies.

Cross-References

- ▶ Adaptive Learning
- ▶ Antimicrobial Hypothesis, The
- ▶ Cross-Cultural Universality

- ▶ Cultural Evolution
- ▶ How the Mind Works
- ▶ Living in Groups
- ▶ Memes
- ▶ Selfish Gene, The
- ▶ Social Exchange Theory
- ▶ Social Learning
- ▶ Symbolic Culture

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Cultural Universals

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Synonyms

[Anthropological universals](#); [Human universals](#)

Definition

Cultural universals are element, patterns, characteristics, or institution that are found in all human cultures worldwide.

Introduction

The idea that there are cultural universals has existed for a long time in anthropology and can be found in some classical anthropology literature, including authors such as Durkheim, Murdock, and Lévi-Strauss, and an idea that was further developed during the mid- and late twentieth century.

Several authors have referred to diverse cultural universals. However, the most influential and best-known proposal is Brown's proposal initially presented in 1991 and again later in 2000 and 2004. Brown refers to human universals as those features of culture, society, language, behavior, and psyche for which there are no known exception and are found worldwide in every cultural group. He presents a list of hundreds of universals divided in several groups, including language and cognition (for instance, color terms for black and white, antonyms, baby talk), society (such as, kin groups, cooperation, division of labor), beliefs (including, beliefs about death, belief in supernatural, beliefs about fortune and misfortune), and technology (such as, tool making, fire, weapons) (the complete list of the universals proposed by Brown can be found in Pinker's (2002) link

included in its reference). It can be assumed that those features, traits, and behaviors found in every human group represent fundamental evolutionary adaptations and have a significant survival value.

In his 2004 paper, Brown points out that in **cultural** realm, human universals include legends, myths, daily routines, rules, concepts of luck and precedent, body adornment, and the use and development of instruments. Furthermore, in the areas of **language**, universals include grammar, phonemes, polysemy, metonymy, antonyms, and an inverse ratio between the frequency of use and the length of words. Moreover, in the **social** dominion, universals include a division of labor, social groups, age grading, family, kinship systems, ethnocentrism, play, exchange, cooperation, and reciprocity. While in the **behavioral** realm, universals include aggression, gestures, gossip, and facial expressions; in the area of the **mind**, universals include emotions, dichotomous thinking, wariness around or fear of snakes, empathy, and psychological defense mechanisms. However, there are many universals that cannot be easily classified in one or another of these areas. For instance, kinship terminologies can be simultaneously interpreted as social, cultural, and linguistic. The concept of property is both cultural and social, where taking turns speaking in conversation is simultaneously linguistic, social, and behavioral.

It can be conjecture that diverse behavioral universals quite probably have distinctive, even specific, neural substrate, and consequently are also universals of mind.

Some anthropologists, however, have questioned the existence of cultural universals, taking a cultural relativist perspective. According to this perspective, behaviors and beliefs should be understood in relation to the individual's own culture, instead of being compared with other people's criteria. Some researchers consider that there are significant differences in perceiving and reasoning abilities among different cultural group; for instance, when comparing Asians and Westerners (Nisbett 2003), differences in reasoning strategies can be found. Other researchers insist that, regardless of apparent differences among different cultures, there are robust underlying

cross-cultural universals, observed in different areas, for example, classification systems (Atran 1998), color perception (Berlin and Kay 1969), and even basic emotions (Wierzbicka 1999).

Cultural Universals Characteristics

Proposals of cultural universals have been studied from different perspectives, in different areas, and including diverse research procedures. This is a research topic that has attracted attention not only in anthropology but also in psychology, sociology, linguistics, and other research areas.

Some universals in perception, classification systems, emotional terms, and the use of some specific terms will be examined below. Cross-cultural similarities in the way perceptual experience is conceptualized have been suggested. Vocabulary in each language represents the fundamental conceptualization system, and hence, not only differences but also similarities in word categorization should be recognized.

Kay et al. (1991) analyzed data from 111 languages in the World Color Survey and confirmed the main lines of the original Berlin and Kay hypothesis (1969, 1991), which assumes that there are semantic universals in basic color vocabulary. This analysis demonstrated that visual physiology plays a role in the evolutionary development of basic color lexicon, constraining the possible composite categories to a small number of those theoretically possible. One composite category, yellow/green, is clearly attested in the data, but the sequence leading to its emergence is not clear. Colors appear in language following a specific sequence, but the two universal colors found in every language are white and black (so-called achromatic colors).

Similarities in biological classification systems have attracted special attention. It has been observed that all cultural groups think about living elements – plants and animals – in highly structure ways (Atran 1998). Folk taxonomies are developed across cultures; these taxonomies are usually different, but they also present important

similarities. It may be assumed that such taxonomies are the results of human thinking strategies. Hence, similarities in classifications systems found when comparing different human groups are reflecting human basic cognitive schemas.

Other quite different types of universals have been pointed out. For example, frequently it has been assumed that there are universal emotions and in all the languages certain emotions are distinguished (Wierzbicka 1999). As an illustration, similarities in emotional terms across languages have been proposed. For instance, Romney, Moore, and Rusch (1997) analyzed the semantic structure of 15 emotion words for monolingual English-speaking and monolingual and bilingual Japanese subjects. A major question in this study was to contrast a single shared emotion model for English and Japanese versus culture-specific models for each language. Results supported a shared model for the semantic structure of emotion terms; nonetheless, some important differences were also found between English and Japanese structures. Interesting to note, the Japanese bilingual participants used a model more similar to English when performing tasks in English than when performing the same task in Japanese.

Cordaro et al. (2018) used a Facial Action Coding System coded over 2600 free-response facial and body displays of 22 emotions in China, India, Japan, Korea, and the United States to test five different hypotheses about the universality and cultural variations in emotional expression. The authors were able to identify cross-culturally some *core patterns* of expressive behaviors for each of the 22 emotions. They also demonstrated systematic *cultural variations* of expressive behaviors for each cultural group. These variations were shaped by the cultural resemblance in values. It was concluded that there are universal core patterns, and also variations on emotional expression in each of the studied cultural groups.

Scherer and Fontaine (2019) observe that the Component Process Model of Emotions claims that the different components included in the

emotion (i.e., action tendencies, physiological reactions, expressions, and feeling experiences) are basically the results of cognitive appraisals. The authors performed a secondary analysis of the large-scale data set with ratings of affective features covering all components of the emotion process for 24 emotion words in 27 countries. Profiles of emotion-specific appraisals, action tendencies, physiological reactions, expressions, and feeling experiences were constructed. The results of a series of hierarchical regression analyses to examine the prediction of the theoretical model are consistent with the assumption that appraisal patterns determine the structure of the response components, which in turn predict central dimensions of the feeling component.

Expression of gratitude is a special type of affective and linguistic behavior that has attracted special attention in the analysis of the cultural universals. Floyd et al. (2018) point out that gratitude has evolved to motivate and maintain social reciprocity among people. Gratitude is linked with diverse positive effects from different perspectives, including social, psychological, and even physical consequences. Current studies usually do not include cross-cultural elements of gratitude and have tended to consider gratitude as an emotion associated with a linguistic practice, as in English and other Indo-European languages. Floyd et al. raised the question, to what extent people express gratitude in different societies, by focusing on episodes of everyday life where someone seeks and obtains a good, service, or support from another. These episodes were compared across eight different languages from five continents. It was found that expressions of gratitude in these episodes are quite unusual, suggesting that social reciprocity in everyday life activities are based on implicit comprehension of rights and duties surrounding reciprocal collaboration. It also was observed in minor cross-cultural variations, with relatively higher rates gratitude expressions in Western European languages – English and Italian. Noteworthy, some Amerindian languages have few, if any, gratitude words, equivalent to “thank you.” For instance,

Guarani and Aymara languages use Spanish borrowings for “thank you”: *agradese* (from Spanish, *agradecer*, to thank) is used in Guarani language (spoken specially in Paraguay but also in Argentina, Bolivia, and Brazil); “thank you” in Aymara language (spoken specially in Bolivia, but also in Peru and Chile) is *yuspagará*, an adaptation of the Spanish expression *Dios pagará*, meaning “God will pay.” The expression “thank you” in many languages means “I give you my benefits”; for instance, in Spanish *gracia* from the Latin *gratia* means “grace,” and “charm.” In Russian, “thank you” can be *spasibo* (спасибо) but also *blagodaryu* (благодарю) which means “I give you the good.”

Naito and Washizu (2015) analyzed gratitude from an East Asian perspective. They conclude that the concept of gratitude has been studied under the universality hypotheses, which postulates the following: (a) gratitude is influenced by its antecedent factors, including gains of the beneficiary, cost to the benefactor, and the altruistic motivation of the benefactor; (b) gratitude implies positive feelings, such as attachment and respect for the benefactor and the wish to repay the benefactor; (c) gratitude may lead to particular behaviors such as expressions of the gratitude directed at the benefactor, repayments, and pro-social behaviors directed at other people in general; and (d) experience of gratitude is associated with positive attributes, such as well-being. But gratitude has many nuances, depending upon the language and the cultural context.

Universals in language have represented a major topic of analysis, as observed in Brown’s (1991, 2000, 2004) list of cultural universals. Universals in language during language development can also be conjectured. Ochs (1991) proposed that indeed there are cultural universals in the acquisition of language. He further proposed a model according to which (1) there are culturally universal trends in the linguistic marking of four language dimensions (epistemic and affective stances, social acts, social activities, and social identity); (2) language and culture universals basically consist in the “indexing” of stance and social

acts, the marking of which is more extended and conventionalized across social groups than the marking of other domains; and, finally, (3) language and culture particulars refer primarily to how stance and social acts are related to social activities and social identities. This model clearly recognizes that the universals in language can be observed not only in adult language but also during language development.

Conclusion

Since the earlier twentieth century, the idea that there are cultural universals has existed, meaning, elements, patterns, characteristics, or institution found in all human cultures worldwide. This is an idea that has become quite influential not only in anthropology but also in other scientific areas, such as psychology, sociology, and linguistics. Extensive lists of universals including hundreds of different elements have been proposed. Cultural universal cover different areas, including but not limited to language, social life, and cognition. However, some disagreement persists. Special interest has had the analysis of the cultural universal in classification/conceptualization systems, perception, emotions, and language.

Cross-References

- [Cross-Cultural Expression](#)
- [Cross-Cultural Similarities](#)
- [Cultural Intelligence Hypothesis, The](#)
- [Subcultural Theory](#)

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Cultural Variation

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Synonyms

[Human diversity](#)

Definition

The examination of differences in human behavior and development across contexts and cultures is crucial in appreciating human diversity.

Introduction

Although cultural universals are widely critiqued for the lack of emphasis on the diversity of human experiences and its Eurocentric principles (Ziai 2019), an examination of both variations and universals among cultures has been foundational in ethnography. Cultural universals are defined as similarities between human traits and attributes across cultures (Norenzayan and Heine 2005). For example, expressions of some emotions such as happiness, sadness, disgust, fear, surprise and anger (Ekman and Friesen 1971), sympathetic impartiality and communication (Wiredu 1995), arts, recreation, and social and economic organization (Cleaveland et al. 1979) appear to exemplify such universals.

Cultural variations, on the other hand, integrate diversity in development, behavior, and expectations across cultures as a result of human adaptation to their environment (Cohen 2001). Ethnographers, in their attempts to qualify cultural variations, have identified 30 dimensions. Examples of some of these dimensions are *contact vs. no-contact cultures*, *universalism vs. particularism*, *individualism vs. collectivism*, and more (Triandis 1982) and have concluded that cultural variations are an inevitable part of human life.

To illustrate, Ekman et al. (1987) reported that despite the universality of emotions, there are significant cultural variations in the intensity ratings of emotional expressions of happiness, surprise, and fear between Asian and non-Asian cultures. Asians tended to rate facial expressions to be of lower intensity, and the differences were particularly prominent in the ratings of fear. Ekman et al. applied Matsumoto's (1989) ideology and explained the pretext for lower ratings. Matsumoto suggested that decoding rules vary between individualist and collectivist cultures. Since, in collectivist cultures, negative emotions can be a threat to

group dynamics and cohesion, they are often downplayed. The justification provided by Matsumoto thus provides supporting groundwork to Cohen's explanation of cultural variations being adaptive and functional, thereby creating a sense of equilibrium within the members.

Functional Aspects of Cultural Variation

Hassan et al. (2019) advocated for the appreciation of "context-specific factors" (p. 11) while interpreting differences in the investment of mothers and fathers in their sons and daughters. In the Tanzanian sample of parents with children under the age of 5, Hassan et al. found that fathers discriminated among their children and favored sons over daughters, whereas mothers did not discriminate and invested equally regardless of their children's sex.

Abiding with the ideas of Cohen (2001) on the functional aspects of cultural behaviors, Hassan et al. (2019) asserted that Tanzania, being a patrilineal and patrilocal society, favors men over women. Thus, fathers are more likely to benefit from their sons as they will inherit the family property and continue the family name and legacy. Daughters, on the other hand, will be married and leave their parents' household, and therefore favoring them is not cost-effective. In contrast, mothers do not discriminate and favor both sexes because of obvious payoffs from sons and household chores and childcare help from daughters.

Cultural Variations and Implications for Research and Practice

Legare (2017, p. 429) suggested that most of the psychological research consists of "WEIRD" (Western, educated, industrialized, rich, democratic) participants resulting in a myopic view. As established above, cultural variation is adaptive and serves essential functions in a society and maintains equilibrium among its members. Moreover, cultures influence human development and behavior and their manifestations, motivations, directions, and constraints. Therefore, the

examination of the multidimensional aspects of cultural variation and its pretext is mandated to understand human diversity in all its forms. Although the influence of cultures on socialization, care, values, and beliefs is partially studied, cross-comparison investigations need to be further strengthened. The research can be strengthened through the development of culturally appropriate, valid, and sensitive screening and diagnostic measurement tools (Carlo and Maiya 2020) and designing culturally sensitive intervention programs.

Conclusion

Cultural variations are an integral part of human life, and therefore integrating cultural aspects in research will prompt us to ask more relevant and valuable questions and get meaningful information. The empirical evidence thus gathered can assist in designing and implementing culturally sensitive interventions (McClain et al. 2019).

Cross-References

- ▶ Cross-Cultural Universality
- ▶ Cross-Cultural Variation

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Culturally Variable

- ▶ Cultural Differences in Mate Preferences

Culture

- ▶ Adaptive Benefits of Matriliney and “Walking Marriages” in Mosuo Culture
- ▶ Social Learning and Social Cognition

Culture and Intelligence

- ▶ Cultural Intelligence Hypothesis, The
- ▶ Vygotskian Intelligence Hypothesis, The (Moll Et Al., 2007)

Culture of Honor

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Synonyms

Aggression; Collectivism; Dominance; Face; Masculinity; Pride; Reputation; Respect; Violence

Definition

Honor commonly refers to how others see an individual (usually a man) in terms of his respect, pride, dominance, and/or masculinity. Cultures of honor are those in which individuals strive to maintain their honor.

Introduction

The presence of a culture of honor is commonly used to explain differences in aggressive behavior of men from different regions, countries, or societies. The most prominent example of these differences comes from the pioneering research program by Richard Nisbett and Dov Cohen (1996). They compared male aggressive behavior in different US regions and consistently found that when the honor of men from the South was challenged they were more aggressive than were men from other regions (primarily the North). Similar results have been found in multiple other countries using many different measures of emotion, cognition, and behavior (for a brief review see Rodriguez Mosquera 2013).

However, men from cultures of honor are not found to be more aggressive in all situations, only in those in which their dominance or masculinity is challenged by another individual. For example, Cohen et al. (1996) had an actor physically bump into and insult a participant while observers assessed the participant's reaction. Those from a

culture of honor (Southern USA) reported feeling that their masculine reputation was more threatened, had higher levels of testosterone and cortisol, and responded more aggressively than individuals who were not from a culture of honor (Northern USA). Furthermore, men from cultures of honor have been shown to react more aggressively to a romantic partner's sexual infidelity (by attacking their partner or the other man) and sexual promiscuity of women in their family (Rodriguez Mosquera 2013). There are many explanations for why these situations evoke such responses from men in cultures of honor; three of them are outlined below.

Explanations for the Culture of Honor

One of the first explanations for societal differences in culture of honor was proposed by Cohen et al. (1996). They argued that the development of a culture of honor was associated with herding economies. In regions where herding was the main means of sustenance, there usually lacked governmental oversight, and an individual's resources could easily be robbed with little to no punishment. These circumstances increased the value of having a reputation for being dominant. Men who allowed others to publically insult them or otherwise question their dominance would be viewed as weak and more likely to become targets of theft. Those who were known to be dominant and able to protect their livestock were less likely to be victims of theft. Thus, a culture of demonstrating dominance and maintaining one's honor would develop as a means of protecting one's property. Furthermore, such a culture would be transmitted from generation to generation perpetuating its violent retaliatory practices, even after the advent of governmental authorities.

A different explanation for why cultures of honor develop was proposed by Thornhill and Fincher (2011). They argue that a culture of honor is more likely to develop in regions where there is a higher likelihood of contracting infectious diseases from other individuals. Because life-threatening parasites are more likely to come from individuals outside one's group, increased

parasite stress leads to an increase in collectivistic values, such as strong loyalty to the in-group (e.g., family), a sharp boundary with the outgroup, and respect for hierarchies. These collectivistic values in turn foster stronger reactions (e.g., honor killings) to offenses to one's family or challenges to one's dominance. To substantiate their explanation, Thornhill and Fincher (2011) analyze US-state level data on parasite stress, collectivism, and interpersonal violence. They find that states with higher levels of parasite stress have more cases of male-to-male and male-to-female violence associated with maintaining honor.

Shackelford (2005) offers yet another explanation for the development of cultures of honor. He argues that the violent behavior of honor cultures serves the evolutionary goal of retaining one's mate. Demonstrating aggression towards other males that might attempt to steal one's mate and discouraging one's mate from having sexual relations with other men decrease the odds that one's mate will court other males. Shackelford (2005) proposes that regional differences in honor aggression might be due to differences in the likelihood of mate infidelity – a topic for future research.

Conclusion

The explanations offered here do not exhaust the possible explanations for cultures of honor and they are by no means mutually exclusive. Cultures of honor may develop due to more than one reason, and different reasons may explain cultures of honor in different countries. Future research may shed light on the nuances of different cultures of honor and propose means of addressing the societal problems that are associated with them.

Cross-References

- ▶ Aggression
- ▶ Culture of Honor and Individual Differences
- ▶ Culture of Honor and Nepotism

- ▶ Culture of Honor and Retaliation
- ▶ Information About Likely Combat Success
- ▶ Reputation as a Context for Men's Aggression Against Men
- ▶ Sociocultural Theories of Violence

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Culture of Honor and Individual Differences

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Synonyms

Aggression; Masculinity; Phenotypic variance

Definition

Within culture individual level differences on reactions against threats to reputation.

Culture of honor has been defined as a specific cultural context in which individuals – predominantly males – react against threats to their reputation. Those reactions are in general aggressive and violent even if they are risky and costly (e.g., life-threatening) to oneself (Nisbett and Cohen 1996). Individuals in honor cultures prioritize their reputation against their safety and/or material gains. Even though it seems costly in the short run, individuals in honor cultures protect and preserve their self-worth in this way. In conflictual situations, individuals might deploy an “interest strategy” by avoiding risks or “rational strategy” by being aggressive when in an advantaged condition yet surrender when in a disadvantaged condition. As another option, individuals in honor cultures use “honor strategy” by striking back regardless of their current condition in that conflictual situation (Nowak et al. 2016).

Cross-cultural research on honor provides evidence for cultures as Mediterranean culture and southern states of United States valuing honor. There are also research aiming to explore the mechanism behind honor culture. For instance, low reliability of institutions, the toughness of the environment, herding cultures, and low-status compensation (e.g., Henry 2009) have been linked to honor cultures. Besides the research focusing on evolutionary and sociocultural correlates, a body of research has focused on the relationship between the culture of honor and individual differences.

Saucier and McManus (2014) argue that there is an individual difference in masculine honor beliefs regardless of the culture where individuals grew up. For instance, females scored higher on family and community masculine honor, while males scored higher on all other dimensions including courage, pride, virtue, protection, and provocation. Furthermore, individuals who scored higher on masculine honor beliefs also scored higher on trait aggression and benevolent sexism. For instance, it was found that masculine honor beliefs are associated with participation and action in sports such that

individuals with higher masculine beliefs prefer sports requiring physical contact (Saucier et al. 2016).

Furthermore, higher scores on honor values are correlated with rationalization and reinforcement of confrontational behavior against a hypothetical false accusation and disrespect (Cross et al. 2013). Likewise, individuals of honor culture are more sensitive to insults, immediately prepared for retaliation both physiologically and cognitively, and, as a result, more likely to express aggressive behaviors (Cohen et al. 1996). Regarding the close relationships, individuals who value honor favor loyalty of females and justify domestic violence by males (Vandello et al. 2009). Similarly, Vandello and Cohen (2003) found that individuals from honor culture perceive female infidelity as a threat to one's reputation and justify domestic violence and anticipate loyalty of females even if they are the target of domestic violence as a result of jealousy. Cohen and Nisbett (1997) also showed that honor culture is related to sympathetic reactions to violence as stabbing someone in response to family insult.

Thus, for individuals with high honor values, self-worth and social status are especially important. Moreover, research on individual differences yielded that honor is not only associated with protecting self-worth and social status, but it is also highly relevant for moral behavior (Cross et al. 2014). One study investigating individual differences on this topic revealed that higher endorsement of honor ideology predicted practice of extreme counterterrorism tactics above and beyond the right-wing authoritarianism and social dominance orientation (Barnes et al. 2012).

Culture of honor studies heavily focuses on culture differences. However, culture of honor beliefs and related behaviors such as aggression also shows individual differences. Therefore, it is also important to consider within-culture variation and individual differences to extend our understanding of culture of honor.

Cross-References

- [Culture of Honor](#)
- [Culture of Honor and Retaliation](#)

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Culture of Honor and Nepotism

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Synonyms

[Agropastoral cultures of violence](#); [Agropastoral honor cultures](#); [Blood feuds](#); [Herding culture of violence](#); [Honor cultures](#); [Nisbett-Reaves hypothesis](#); [Southern cultures of violence](#)

Definition

Cultures of honor are those placing a high emphasis on the importance of a man as willing and able to violently and lethally retaliate against anyone who insults his honor or the honor of his family. Thus, the defense of personal and family honor results in the favoring of kin for economic and socially valuable positions.

Introduction

The label “cultures of honor” refers to cultures placing a high emphasis on the importance of a man’s willingness and ability to violently and, even lethally, retaliate against anyone who insults his honor or the honor of his family. These insults typically involve accusations that a man’s male kin are cowards or that his female kin, wife, or female in-laws are not chaste. Such accusations may lead to the killing of the accuser and/or the killing of the accused female by her male kin, husband, or in-laws. These behaviors appear to be extreme forms of universal evolved aspects of human behavior. Thus, there has been an attempt to identify what social and ecological aspects of the environment may tend to produce these extreme forms (Shackelford 2005). The most well known of these studies was conducted by

Nisbett and Cohen (1996) on the US South; in it, the authors suggest that weak/ineffectual authority and the potential for complete theft of a man's livelihood (specifically livestock) lead to a culture of honor where violent, even lethal, retaliation is commonplace.

Key Factors in the Creation of Cultures of Honor

In addition to kin selection, the aspects of evolved human nature apparently contributing the most directly to cultures of honor are parental-investment theory, male sexual jealousy, and reputation management. Parental-investment theory holds that greater variance in male reproduction leads to males tending to pursue a life history of high mating effort that often includes high cost forms of violent competition with other males (Trivers 1972). The diversion of some of this mating effort to parenting effort is only evolutionarily advantageous when paternity certainty is sufficiently high, leading to selection of various forms of mate guarding and male sexual jealousy (Daly and Wilson 1988). In addition to evidence of infidelity being often followed by a lessening or termination of paternal investment, violence is often exhibited toward the mate. In addition to potentially deterring the female from infidelity, violent sexual jealousy can also influence other females who are potential mates and other males who may be deterred from pursuing sex with the man's mate or mates. These signals are part of the man's reputation management. Reputation management involves the influence of one's behavior on individuals who are not directly involved in that behavior, but are nonetheless influenced by it indirectly through observing the behavior or hearing about it. This is usually applied to indirect reciprocal altruism where an individual benefits from their altruistic acts because these acts are reciprocated, not by the recipient but by onlookers and/or those becoming aware of the individual's reputation for being an altruist. However, a reputation for many behaviors other than altruism can be created in the same way, and these reputations may also have significant evolutionary

consequences (Alexander 1987). Namely, solidarity with one's kin, through nepotism, creates an environment where honor can be defended by a coalition, and family reputation can be cultivated. Where men are isolated from kin, they lack the backing of a coalition for defending their honor, and lethal violence becomes much riskier.

All of these factors also influence the fitness of kin because kin selection predicts that individuals should value the behavior of their kin in accordance with Hamilton's rule (Hamilton 1964). This is most commonly applied to acts of altruism toward kin, but shared genetic makeup of close kin produces a more general common interest among close kin where not just altruism but behavior in general by one will have consequences for the other. Cultures of honor have been hypothesized to occur when the evolutionary concepts just described interact and take on an extreme form (Shackelford 2005). This extreme form is identified by high levels of violence toward both the impugner and the accused, especially the female kin accused of sexual impropriety. This in turn often leads to retaliation and the development of blood feuds.

US South

Although all of the factors that contribute to a culture of honor may be universal aspects of evolved human nature, they appear to be emphasized more in some cultures than others. Thus, hypotheses have attempted to account for this variation. Addressing the culture of violence in the US South, Nisbett and Cohen (1996) proposed that it was agropastoral environments (and heritage) combined with a weak governing body that produce cultures of violence due to the possibility of the complete theft of a man's livelihood and little recourse to authority. They supported this view with a series of experiments that compared men in the Southern United States (which was settled primarily by herdsmen from Ireland and Scotland), with men from the Northern United States (settled primarily by farmers from England). The factors contributing to an extreme culture of honor in such an environment are the

relative absence of external law enforcement and punishment, and easily stolen forms of wealth (Shackelford 2005).

Chu et al. (2000) conducted an independent analysis of the available data and found that after controlling for environmental variables, and then for poverty, there was either no relationship or one opposed to that found by Nisbett and Cohen (1996). Chu et al. did make an important distinction in their study: they separated the connection of herding-based societies producing cultures of honor from the connection of violence with cultures of honor. The two are not necessarily linked, and thus their analysis could be seen not as a rebuttal of Nisbett and Cohen, but as a refinement.

Other Cultures of Honor

Data on cultures of honor from other cultures around the world is largely limited to North Africa and Southern and Southwestern Asia. Here, cultures of honor are characterized by a quick recourse to violence, usually due to an insult of family honor or accusations that a female relation is not honorable/chaste/faithful. Honor killings of women are a relatively common occurrence in these cultures of honor. They appear to be closely related to nepotism and kin selection because they are commonly perpetrated by brothers and mothers of the accused (Kulczycki and Windle 2011). The circumstances that are present in this part of the world are highly variable, from nomadic herders to urban laborers, and thus do not always agree with what Nisbett and Cohen proposed for the US South. For example, Moritz (2008) argues that the various pastoralist cultures in Africa encompass substantial environmental and social differences and cannot be considered under a single analytical label. Further, similarly to Chu et al. (2000), Moritz argues that the “honor psychology” and “pastoral personality” (p. 100) are distinct categories that may overlap, but do not necessarily do so. This complicates the connection of cultures of honor and nepotism; connections beyond simple coalitional defense of reputation are unlikely to be the result of any single factor, but of some collection of possible

factors, interacting within different environments, that give rise to cultures of honor.

The current literature on honor killings is largely framed as violence against women or as a function of political economy/power, and thus further study is necessary to illuminate the specific evolutionary aspects of these cultures of honor. However, the simple fact that these cultures of honor exist in variable economic and social circumstances lends support to Shackelford’s (2005) idea that the evolved psychological mechanisms that lead to cultures of honor are not likely to be a result of relatively modern economies (i.e., herding) or lack of formal authorities but to the common problem of the theft of the reproductive value of a wife that was confronted by ancestral men (and the social consequences of this for kin).

Conclusion

Identifying the correlates of cultures of honor can have important practical implications, such as possibly identifying ways of lowering certain forms of violence. From a theoretical point of view however, cultures of honor develop not as an adaptation that has evolved in some human populations but not in others, but as one outcome of selection for a number of universal human adaptations found in all humans. This is because the specific environmental factors involved in the agropastoralism proposed to produce extreme cultures of honor are too recent to be an adaptation, and are thus best considered a by-product of a novel environment.

The nepotism that is associated with cultures of honor is a function of kin selection and reputation management and serves to create an environment where men have a ready coalition (especially in positions of power) that can be called upon to defend their personal and familial honor. Thus, one would expect increased nepotism in places where coalitions were/are necessary to defend one’s honorable reputation (perhaps due to weak/ineffective external authority) such as the US South and parts of Africa and Southern and Southwestern Asia. Although many aspects of cultures of honor involve kin who are so close

that kin selection may have been involved in their evolution, often the imperative to defend the honor of one's kin applies to one's very distantly related clan members. That is, one is expected to avenge an insult to individuals identified as kin by the inheritance of a traditional descent name inherited from a long-dead common ancestor. The inclusion of very distantly related kin among the individuals one is expected to avenge in some cultures of honor is an area in need of further study.

Finally, the vast majority of the literature focuses on men and male actions in creating and perpetuating cultures of honor and acts of nepotism. However, it is unlikely that the other half of the population, women, is uninvolved or oblivious to personal and familial honor, and the violent defense thereof. Whether women act as cultural repositories and serve to socialize their sons into cultures of honor (Nisbett and Cohen 1996) or if they take a more active role is an area that requires extensive study.

Cross-References

- ▶ [Male Sexual Jealousy](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Reputation as a Context for Men's Aggression Against Men](#)

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Culture of Honor and Retaliation

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Synonyms

[Honor-related violence](#)

Definition

Cultures of honor are cultures in which the concept of honor is thought to play an important role in everyday life. Retaliation is an action undertaken to harm someone else who has harmed oneself.

Introduction

“Culture of honor” is a label scientists from various disciplines (psychology, anthropology, sociology) use for cultures in which the concept of honor governs everyday behavior. These cultures can be found in the Mediterranean area (Spain, Turkey, Syria, Egypt), the Arabic peninsula, Central Asia (Afghanistan, India), the South of the United States, and in gang life (Horowitz and Schwartz 1974). Honor cultures are thought to arise when groups settle in harsh environments, lacking sufficient resources and law enforcement (Brown and Osterman 2012; Nisbett and Cohen 1996; Nowak et al. 2016; Shackelford 2005). As a consequence, honor codes – rules on appropriate

conduct (Stewart 1994) – start to govern social behavior. For example, it is thought that the culture of honor in the South of the United States is a remnant of the herding population that originally inhabited the Southern states (Henry 2009). Herding life relies on the ability to protect oneself and one's property from external threats. Responding violently to threats is then an adaptive strategy. Also in other honor cultures, for instance in Turkey, herders seem to be more sensitive to threats than farmers (Uskul and Over 2014). Even though harsh and lawless environments have largely disappeared in regions described as honor cultures, norms regarding violence seem to perpetuate. In the South of the United States, this seems to be the case due to pluralistic ignorance: Individuals falsely assume others to endorse norms in favor of violence and thus act accordingly themselves without personally valuing aggression (Vandello and Cohen 2004). However, pluralistic ignorance could not explain the perpetuation of positive attitudes toward violence in Western Turkey (Van Osch et al. 2013).

What Is Honor?

The multidisciplinary literature on honor has identified many differences in responses to honor threats between cultures considered high and low in honor (Uskul et al. *in press*). Most of this research is of a descriptive nature concluding that *x* is more often observed in cultures high than in cultures low in honor. Cultural differences have been documented in the extent to which people value the concept of honor (Martins Guerra et al. 2012) and how insults or affronts affect people's self-esteem (Rodriguez Mosquera et al. 2002) and emotional (Rodriguez Mosquera et al. 2008) and aggressive responses (Cohen et al. 1996; Van Osch et al. 2013). This research has provided a wealth of information on cultural differences between cultures high and low in honor, but has shed little light on the underlying psychological processes.

Here, honor is defined as a moral reputation. Honorable individuals are treated as worthy members of their community. Honor can be lost by

immoral conduct which has severe social consequences for the person and his or her associates. Humans are social beings and have a fundamental need to belong to groups (Baumeister and Leary 1995). Groups have rules that they want each group member to abide to. If members break the moral code, they are stigmatized and socially excluded (shunned, expelled). This is a functional response, because deviant behavior may threaten the survival of the group (Kurzban and Leary 2001) and responding to it strengthens the group's identity and "sense of common morality" (Jones et al. 1984). It is irrelevant whether the individual actually transgressed or is perceived as having done so, because the group will act based on their perceptions of moral deviance. The stigmatized who risk exclusion experience threats to their belonging, self-esteem, control, and meaning in life (Williams 2007) and have no choice but to defend or restore their moral reputation (Goffman 1963) in order to prevent social exclusion. Also, those who are close to the transgressor can be associated with the transgressor and suffer from a stigma by association requiring them to protect their own honor (Benavidez et al. 2016; Marques et al. 1988).

The psychological processes underlying responses to honor seem universal (Novin and Oyserman 2016; Shackelford 2005). Immoral conduct can result in stigmatization and social exclusion across cultures. What is considered immoral conduct however may differ across communities. Acts like rape, murder, or pedophilia are considered immoral almost everywhere. However, there are also acts that are considered immoral in some but not in other communities, for example, adultery (Erners 2007), premarital intercourse, or homosexuality (Matsumoto and Juang 2013). Cross-cultural differences in responses to misconduct may not only result from different perceptions of misconduct but may also result from differences in how salient the concept of honor is in a given community. Cultures high in honor, due to historical reasons (settling in harsh lawless environments), may have hypercognized the concept of honor. A psychological concept is hypercognized if it receives considerable attention, meaning that

there are many terms available to describe the concept (for instance, in Turkish there are at least four different terms available for honor; Ermers 2007), that members have a lot of explicit knowledge on the phenomenon, and that this concept is deemed important in the community (Levy 1973). Hyper-cognizing a concept does not imply differences in psychological experiences (Frijda et al. 1995; Parkinson et al. 2005) but may trigger (culture-) specific thought and action repertoires when activated, explaining why people in different cultures act in different ways when they commit or observe immoral behavior.

Threatened Honor

In line with the reasoning above, people can lose their moral, or good, reputation in roughly three ways. First, people can be the actors of immoral behavior. For example, if a Turkish woman engages in adultery, her honor is threatened. Adultery is not accepted in many communities in Turkey, and the accused will suffer the consequences. An adulterous woman is considered a bad, indecent woman and will no longer be trusted. She could be shunned or punished by her community and/or divorced by her husband (Ermers 2007).

Second, people can be associated with moral deviants. Stigmas do not only stick to the individual who misbehaved, but stigmas may transfer to those associated with that individual. This is called stigma by association or a courtesy stigma (Goffman 1963). Children can be stigmatized due to the misconduct of their parents (sex offenses) and have to deal with threats, differential treatment, and bullying (Levenson and Tewksbury 2009). Being friends with a stigmatized individual (e.g., homosexual) can already be enough of an association to suffer from a stigma by association (Neuberg et al. 1994). So, an adulterous woman in Turkey could be stigmatized and excluded herself, but also her parents, her husband, and her in-laws could become the targets of stigmatization and exclusion. They could have prevented her from misbehaving and thus can be held partly responsible for the misconduct.

Third, people's honor may be threatened because of a cowardice stigma. To prevent stigmatization and social exclusion and promote future cooperation, people should manage their reputation (consisting of both moral and nonmoral qualities such as social status) to ascertain their valued position in a community (e.g., Emler 1990). It is seen as honorable if people are willing and able to defend their reputation. If people fail to respond to messages that impact their reputation, or fail to respond strong enough, they may be seen as weak. For example, men in the South of the United States respond vehemently to insults in order to retain their reputation for toughness and protect themselves (Cohen and Nisbett 1994).

Honor and Retaliation

Retaliation is a potential reaction to all three types of honor threats. First, when the moral deviant is stigmatized, and marked as without honor, this negatively impacts someone's self-esteem (Major and O'Brien 2005). Apart from impacting one's self-esteem, being threatened with social exclusion also threatens other fundamental needs such as the need to belong and the need for control (e.g., Leary 2005; Williams 2007). Expecting or experiencing such threats can result in aggressive responses (Twenge et al. 2001; Warburton et al. 2006). Moral deviants may aggress and become vengeful toward those who confront them with their immoral behavior and thus humiliate them (Combs et al. 2010; Elison and Harter 2007).

Second, if people's honor is at stake because of their association with a moral deviant, they can aggress toward the accusers if the claim is unfounded (accusation rather than actual misconduct), or they can aggress toward the moral deviant to cleanse their own reputation. Research has shown that individuals distance themselves from deviants in order to decrease the chances of stigma by association (Eidelman and Biernat 2003) and sanction their deviant behavior (Chekroun and Nugier 2011). In more extreme cases, the moral deviant is killed. These so-called "honor killings" occur when the associates of the often sexual deviant kill

the deviant to reestablish or cleanse the honor of the group or family (Ermers 2007). In cases where sexual deviance affects the honor of a family, the family has two options. The first is to kill the man of the other family, if they consider the man “guilty” of damaging the family’s honor (for instance, in the case of rape; Ermers et al. 2010). This is considered an external settlement. The second option for the family is to kill their own relative, if the woman is held responsible for damaging her family’s honor (for instance, if she actively sought to deviate from the moral rules; Ermers 2007; Ermers et al. 2010). This type of internal settlement, and its underlying psychology, also seems to occur in Western societies in the form of violence against women by male relatives (Baker et al. 1999).

Third, if people are falsely accused of immoral behavior, they might aggress toward those who are falsely accusing them in order to prevent oneself from a cowardice stigma. Slander should be prevented, and the victims of the slander should undertake some form of action toward the source of the slander (Ermers et al. 2010). Using aggression to defend oneself can be functional as it protects resources and creates a reputation that deters future attacks (Buss and Shackelford 1997). In a recent laboratory study, it was demonstrated that Turkish students who were falsely accused of dishonesty (a moral quality) retaliated against their experimental partner, more so than students from the North of the United States (Uskul et al. 2015). Most research on the culture of honor in the South of the United States relies on this idea of a cowardice stigma, especially men protecting their reputation for toughness. Most research centers on examining differences in aggression between Southern and Northern parts of the United States. White males in the South are more prone to respond aggressively than those in the North of the United States, as evidenced in homicide rates (Messner 1983; Nisbett and Cohen 1996), school shootings (Brown et al. 2009), having people respond to offenses in experimental settings (Cohen et al. 1996), or measuring the approval of interpersonal violence for self-protection purposes (Hayes and Lee 2005; Nisbett and Cohen 1996).

A final form of retaliation, often related to honor, is called blood revenge and occurs across cultures (e.g., India, Turkey, the Middle East, Northern Africa, the Balkan Peninsula). Blood revenge is the killing of someone by others for having inflicted harm to someone from their group. For example, a man might be hurt or killed by another family because he hurt or killed someone from that family (Abu-Lughod 1985). The goal of such revenge is to reestablish a balance between two families or tribes (Ermers 2007).

Conclusion

Threats to one’s honor thus can result in retaliation. In general, people aggress toward those causing the honor threat. First, moral deviants themselves can become aggressive because of their loss of self-esteem and control. Second, those who suffer from a stigma by association may punish the person causing their stigma. Third, those whose reputation is challenged retaliate against those challengers in order to maintain their good reputation. These responses seem to occur across cultures but may be more explicit and present in communities in which the concept of honor is salient in everyday life.

Cross-References

- [Culture of Honor](#)
- [Culture of Honor and Individual Differences](#)
- [Intimate Partner Violence](#)
- [Partner Homicide](#)

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Culture Subdivision

► Subcultural Theory

Culture-Gene Coevolution

► Dual Inheritance Theory

Cunnilingus

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Synonyms

[Oral sex](#); [Sexual intercourse](#)

Definition

Oral sex act or stimulation performed by a person on the female genitalia.

Introduction

Cunnilingus is the stimulation of the female genitals by a partner's lips or tongue. One study of heterosexual female college students indicates that approximately 67% have been on the receiving end of oral sex while 99% of those same students have performed fellatio on a male partner (Bay-Cheng and Fava 2011). This sexual behavior is not only found in humans. For example, the Indian flying fox engages in cunnilingus, and those males who perform cunnilingus before copulation engage in longer copulatory sessions with their mate (Maruthupandian and Marimuthu 2013). It is also common in a number of insects (Gregorič et al. 2016). Although it does not appear to offer *direct* genetic benefits, performing cunnilingus can be advantageous to engage in for other reasons among humans.

Evolutionary Advantages of Cunnilingus in Humans

Engaging in cunnilingus in adolescence seems to be a proxy for sexual intercourse in the future and

may provide the individual with reputational popularity, but not likability from their peers (Prinstein et al. 2003). Additionally, when couples engage in oral sex more frequently, they tend to report more relationship satisfaction (Frederick et al. 2017). Women are also more likely to have an orgasm when they receive cunnilingus (Richters et al. 2006). Aside from positive affect, performing cunnilingus can be beneficial because it can function as a way to influence one's partner.

For starters, cunnilingus can be a way to combat sperm competition. Novel research methods – found via pornography coding – suggest that there is a positive relationship between attributes of male ejaculation and time spent performing cunnilingus among pornographic actors (Pham et al. 2016). Therefore, performing cunnilingus before copulation may, in part, produce more sperm which (1) could compete with other sperm in the reproductive tract or (2) produce more sperm to fertilize the ova. Furthermore, performing cunnilingus may be a way to taste or smell rival semen (Thornhill 2006). Although there is no empirical work on this, there is evidence that men who are at greater risk of infidelity and sperm competition report spending more time performing cunnilingus (Pham and Shackelford 2013a; Pham et al. 2013).

Engaging in cunnilingus can also be used to manipulate one's partner. For example, both men and women perform oral sex on their partner as a benefit-provision mate retention behavior (Sela et al. 2015). In addition, men who perform more mate retention behaviors and more benefit-provision mate retention behaviors report a greater interest in performing cunnilingus on their partner (Pham and Shackelford 2013b) which can alter their partner's behavior and can influence their relationship satisfaction (Frederick et al. 2017).

Conclusion

Cunnilingus can be a tool to facilitate satisfaction within the relationship and can be a tool to combat

sperm competition and retain one's partner. Future research should examine how women manipulate men into performing cunnilingus and how engaging in cunnilingus similarly benefits non-heterosexual couples (e.g., used as a mate retention tool).

Cross-References

- Oral Sex
- Oral Sex as Mate Retention

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Cunnilingus and Fellatio

► Oral Sex and Sexual Debut

Currency and Constraint

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Synonyms

[Optimal foraging models; Utility](#)

Definition

In optimality modeling of behavior, “currency” is the variable the model assumes is maximized by natural selection, while “constraints” are the hypothesized environmental, cognitive, or physiological limitations that shape the animal's ability to maximize currency. The currency and constraints of a model are best considered hypotheses that establish model predictions to be tested with behavioral data.

Introduction

Optimality models of behavior aim to develop testable predictions about the behavioral decisions of organisms under the assumption that natural selection has favored behavior patterns that maximize Darwinian fitness. These models and their

predictions arise from two sets of hypotheses that are implicitly or – more helpfully – explicitly described in the model as **currencies** and **constraints**. The currency in an optimality model is the net benefit of the behavioral decision hypothesized to be closely related to the animal's Darwinian fitness. Constraints are the environmental, physiological, or cognitive features that are hypothesized to limit the animal's ability to maximize the currency (Krebs and Davies 1984). For example, in a model that predicts the optimum amount of time that a male dung fly should mate with a female, the maximized currency could be the total number of eggs fertilized by the male (a variable closely related to Darwinian fitness), and the constraints include: the amount of time it takes to find and display to each female, the relationship between time spent mating and egg fertilization, and the ability of males to assess time.

Energetic Currencies

In optimality models, the currency is a measurable variable that is hypothesized to be closely related to Darwinian fitness. Fitness is difficult to measure directly as it accumulates over the entirety of the animal's lifetime and is dependent on population structure. In models of foraging decisions (the most well-developed models in behavioral ecology), the currency most frequently hypothesized to be maximized by natural selection is some measure of the net energy gained from food items. This is a reasonable starting point since energy will be used to improve the animal's ability to survive, find mates, and reproduce.

There are two major categories of energy currency typically used in optimal foraging models: rates and efficiencies (Ydenberg 1998). The rate of energy acquisition is typically modeled as the net energy acquired divided by the amount of time acquiring it. Energy efficiency is the amount of energy gained divided by the amount of energy expended. For example, within a minute, an animal could spend 1 calorie to acquire 10 calories (rate = 9 cal/min, efficiency = 10) or 10 calories to acquire 100 calories (rate = 90 cal/min, efficiency = 10). These

alternatives are equally efficient, but the latter provides an additional 81 calories per minute – a higher rate. The optimal choice might seem obvious in that example, so instead, imagine that the choice is between spending 1 calorie to acquire 10 calories (rate = 9 cal/min, efficiency = 10) or 50 calories to acquire 100 calories (rate = 50 cal/min, efficiency = 2). While the latter option still provides a much higher rate of return (an additional 41 calories per minute), it requires a very large investment of energy and is the less efficient option.

Several studies have directly tested which currency hypothesis is better supported by behavioral data. One of the first such studies revealed that starlings maximized the rate, not efficiency, at which they provisioned larvae to offspring (Kacelnik 1984). However, many studies since then indicate that animals make decisions that maximize efficiency instead of rate. In most of these cases, it appears that the efficiency currency may produce a better fit because it implicitly models hidden fitness costs experienced during foraging. Specifically, the amount of energy invested in foraging (the denominator of the efficiency equation) is frequently correlated to fitness costs such as exposure to predators, damage to feeding structures, or the build up of lactic acid in muscles (Houston and McNamara 2014). For example, feeding on larger mussels requires more energy, and that energy results in damage to the bills of oystercatchers. Therefore, while the rate of intake may be larger when feeding on large mussels, oystercatchers may instead maximize efficiency (and decrease damage) by selecting smaller mussels (Rutten et al. 2006). In general, it seems animal decisions maximize efficiency instead of rate when hidden costs limit their ability to expend energy.

fitness by avoiding predators, minimum energy requirements can be established as constraints and time spent foraging can be used as the currency. Moreover, diets consist of more than just calories; they also are the source of nutrients. The need for particular nutrients can result in diet choices substantially different than those predicted to optimize energy gains. In particular, narrow, high calorie diets may optimize the calorie currencies but not meet nutrient requirements, thus favoring broader diets not predicted by models maximizing calorie intake.

In socially complex species like humans, the social impact of behavioral decisions must also be taken into account. In a study on the hunting behavior of Ache men (Hawkes 1991), the subjects hunted more meat than predicted under the hypothesis that they were maximizing an energy currency. This indicated that an alternative or additional currency may also shape hunting behavior, such as potential mating advantages that arise from sharing meat.

Almost all optimality models start with the assumption that behavior should maximize genetic fitness. However, if the behavior of humans (or other animals) is influenced by cultural as well as genetic evolution, we might expect that models that maximize currencies related to both genetic and cultural fitness might better predict behavior. For example, imagine that the hunting meat and foraging for nuts provides approximately the same number of calories per unit of time or energy invested. However, the hunting of meat is somehow more memorable than foraging for nuts. While the genetic fitness associated with each diet is equal, the cultural fitness of hunting is higher, as each occurrence of hunting spreads the cultural traits more efficiently than each occurrence of nut foraging.

Beyond Energy and Darwinian Fitness

While the ability to gather energy is an important component of fitness, other components such as the ability to avoid predators might be better modeled by alternative currencies. For example, in a model hypothesizing that animals maximize

Constraint Assumptions

In economic models of behavior, “constraint assumptions” are hypothesized fixed properties of the environment (extrinsic constraints), the organism (intrinsic constraints), or their interaction. For example, in models of patch residence

(estimating how long animals should forage in a patch of resources before looking for another patch), the amount of time it takes to travel between patches is a constraint, as is the relationship between patch residency and resources received (the rate of resource accumulation is the currency in these models). The constraints can be thought of as the playing field on which the behavior occurs. Constraints are not necessarily invariable, but the behavior that the model is predicting does not change the constraint.

An approach pioneered by Belovsky (1978) illustrates how constraints establish the playing field on which foragers maximize a currency. In modeling the amount of aquatic and terrestrial plants included in an a moose diet, three constraints bound the potential diet composition: Each day, a minimum amount of aquatic plants must be consumed for sodium content, a maximum amount of plant mass can be consumed due to the limited size of the moose's gut, and a minimum amount of calories must be consumed. Data from moose indicate that their diet composition does indeed fall within the predicted space established by these constraints. Within that space, moose maximize caloric intake by only consuming as much of the bulkier aquatic plants needed to meet their sodium needs, and then choose the equally calorie-rich but less gut-filling terrestrial forage.

The predictive power of a model is dependent on how accurately it represents the actual constraints on the animal's behavior. When interpreting model fit, therefore, it is important to be aware of both the constraints that are explicitly described and those assumptions that are baked into the math or logic of the model. Giraldeau (2008) provides a useful list of both types of constraint assumptions. For example, models frequently explicitly assume that animals cannot handle prey and search for additional prey at the same time and that they encounter prey items one at a time. In contrast, constraints that often arise from the mathematical formulation of the model include the assumptions that all prey items within a particular category are equally valuable and that the encounter rate with prey items is constant.

Models with minimal intrinsic constraint assumptions are utilizing the "phenotypic

gambit;" the assumption that evolutionary or psychological constraints are so minimal that they are not required to effectively predict behavior. Cognitive ecologists have started to test models that explicitly model more limited cognitive constraints. For example, a typical assumption in prey selection models is that animals can immediately discriminate between the resources they are choosing among and that such discrimination is cost free. Psychological studies, however, reveal that animal "attention" is not unlimited, in particular when animals are engaged in difficult tasks, such as searching for inconspicuous prey. While animals searching for conspicuous prey are expected to include many prey species in their diet, animals searching for inconspicuous prey rely on search images and optimize their search by attending to one prey type at a time, even if other prey items are equally rewarding (Dukas 1998).

Conclusion

Evolutionary models of behavioral decisions aim to predict behavior based on particular hypotheses about the animal and its environment. Those hypotheses are the currencies maximized (or minimized) and the constraints acting on the organism. While empirical data occasionally tightly matches the predictions of optimality models, more often mismatch provides an opportunity to consider additional currencies or constraints that impact animal decisions. Most recently, cognitive ecologists have been able to use the rich comparative psychology literature to improve predictions by including hypotheses about constraints on cognition. Hopefully, the integration of cognitive constraints into these models might help bridge gaps between evolutionary psychologists and human behavioral ecologists.

Cross-References

- ▶ [Adaptation](#)
- ▶ [Adaptation and Natural Selection](#)
- ▶ [Benefits](#)
- ▶ [Cognitive Ethology](#)

- ▶ [Costly Signaling](#)
- ▶ [Evolution of Adaptations](#)
- ▶ [Food Preferences](#)

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Custodial Grandparents

- ▶ [Grandparenting](#)

Customs

- ▶ [Rituals](#)

Cutting

- ▶ [Scarification](#)

Cyber Harassment

- ▶ [Sex Differences in Cyber Bullying](#)

Cyber/Internet/Online Harassment

- ▶ [Anonymity of Cyberbullying](#)

Cyberaggression

- ▶ [Sex Differences in Cyber Bullying](#)

Cyberbullying

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Synonyms

[eBullying](#); [Electronic bullying](#); [Technological bullying](#)

Definition

Cyberbullying is a behavior conducted through technological means with an intention to hurt, is usually repeated and where there is an imbalance of power in the relationship.

Introduction

While bullying is a behavior which has occurred for most of human history, with the advent of technological communication, cyberbullying through this medium is now possible. There has been definitional controversy whether

cyberbullying is a form of bullying or another phenomenon. Further, there is disagreement about the severity of its consequences compared to face-to-face bullying. The roles involved in cyberbullying have been researched and the motives that lead individuals to conduct this behavior have been explored. However, prevention and intervention of cyberbullying is a consistent theme. To inform these efforts, the perspectives that cyberbullying is a maladaptive socially learnt behavior or an evolutionary adaptation need to be considered.

Definitional Controversy

Cyberbullying was first noticed late last century with the term used in a New York Times article in 1995. However, Bill Belsey, a Canadian, is widely credited with popularizing the term on his website. The controversy surrounds whether cyberbullying complies with the accepted definition of bullying or is a different phenomenon.

The traditional conception of bullying is based on Olweus' (1993) three pillars: the intention of the perpetrator to hurt or harm, that the behavior is usually repeated, and there is a power imbalance in the relationship by virtue that the victim cannot get the behavior to stop. Some researchers originally maintained that cyberbullying, despite its name, was a discrete form of aggression (Dooley et al. 2009). The arguments were that cyberbullied victims experienced more severe negative outcomes than face-to-face or traditional bullying (Campbell et al. 2012), although other studies have not shown this to be the case. The intention of cyberbullying to harm has not been questioned, however, there was debate about the repetitive nature of cyberbullying. This was based on the premise that a perpetrator might only bully once but the message can be redistributed or passed on causing a different kind of repetition (Dooley et al. 2009). It was also argued that the imbalance of power was not obvious in cyberbullying although some researchers have pointed to a technological advantage or the ability of the perpetrator to be anonymous. Other researchers have noted differences between traditional and cyberbullying in the

fact that in cyberbullying is 24/7 access, the permanence of the cyberbullying in cyberspace and the wide potential audience.

The argument against the view that cyberbullying is a different phenomenon is that physical bullying presents very differently from verbal bullying and social/exclusion bullying has its own manifestations. All forms of bullying are different from each other but all intend to hurt, are usually repeated and there is a power imbalance in that the victim cannot get the bullying to stop. In addition, victims of both traditional and cyberbullying have reported that being traditionally bullied is worse for them because of the embarrassment of being bullied in front of their peers (Corby et al. 2016). One of the most common arguments that cyberbullying is actually a form of bullying is the evidence that most victimized students were bullied both by traditional and cyber means (Cross et al. 2009) and that there are common predictors for perpetration of both forms of bullying (Kim et al. 2016). Most researchers now agree that cyberbullying is one of the four forms of bullying.

Prevalence

Although cyberbullying has been studied in the workplace, most research has been conducted with school students. There are unfortunately extremely different prevalence rates of cyberbullying reported among young people. Prevalence is usually measured by self-report, however, studies have been hampered by differences in participant recruitment, different data collection techniques, whether a definition is included (Ybarra et al. 2012) and if the behavior is measured by a global or behavioral question (Huang and Cornell 2015). Other issues include frequency cutoffs, the reference time selected, the age and country of the students (Selkie et al. 2016).

In a meta-analysis of 80 international studies, Modecki et al. (2014) found 15% of students were cyberbullied and 15% cyberbullied others. Katz and colleagues also in 2014 synthesized eight Australian studies reporting that approximately

20% of Australian students had been cybervictimized.

Consequences

Cyberbullying victims, similar to traditional victims have been shown to have increased anxiety, depression and social difficulties (Campbell et al. 2012), as well as decreased self-esteem (Chang et al. 2013) and substance abuse (Mitchell et al. 2007). It is not only those who are cybervictims who have negative outcomes but also cyberbullying perpetrators who also have depression, anxiety and social difficulties (Campbell et al. 2013) and high levels of stress symptoms (Cross et al. 2009). Those individuals who are both cyberbullied and cyberbully others have the most negative consequences with the worst scores on measures of physical and psychological health and academic performance (Kowalski and Limber 2007). Cyberbully victims are also more anxious, depressed and stressed, and less socially connected than those who are not involved in cyberbullying (Spears et al. 2016).

Motives for Perpetration of Cyberbullying

Many studies show that students who cyberbully profess the same motives as those who bully by traditional means. This is not surprising given the overlap between the two forms of bullying (Cross et al. 2009). The most widespread motive for cyberbullying is for the student to obtain dominance, power and social status. It has been suggested that bullying through technology can also lead to fast rewards such as the number of likes on Facebook. Cyberbullies can also strive for material gains and resources. Peer norms and peer pressure can also be motives for students to cyberbully.

Another motive that has been put forward for cyberbullying is that is fun and relieves boredom, it is something to do providing entertainment. Many adults believe that students who are found to be cyberbullying, excuse their behavior by

saying it was a joke, they were trying to be funny. However, it could be that with the absence of cues to elicit empathy and the peer norms of less polite behavior online, kidding around could be a genuine motive for some students to unintentionally hurt others. In addition, cyberbullying could be an act of revenge (Konig et al. 2010). With cyberspace providing a less physical environment than the schoolyard and with the ability to remain anonymous, it has been postulated that some traditional victims could cyberbully their playground bullies as they can obtain revenge without retaliation. Another motive has been suggested that it is easy to cyberbully and anyone who is different is fair game (Compton et al. 2014).

Theoretical Explanations of Cyberbullying Behavior

Two major theoretical perspectives of conceptualizing bullying are social learning theories and an evolutionary approach. These two explanations are not necessarily mutually exclusive and many of the solutions to bullying behavior seem very similar.

Social Learning Theory

To date most researchers explain cyberbullying behavior by social learning theories (Bandura 1986). Bandura's form of social learning theory, called social cognitive theory, comprises two main tenets that learning is by observation through modeling by the processing of information and by direct consequences. These basic concepts are an accepted part of most social learning theories.

The family is the main source of learning for children, especially in social relationships. When family dynamics are impaired and conflictual then children will tend to carry on conflictual relationships with peers including bullying perpetration (Low and Espelage 2013). Not only do children learn from the modeling of their parents about abuse of power, but harsh and conflictual parenting has been shown to influence young people's tendency to bully others (Bowes et al. 2009).

Sibling bullying within the family is also associated with more bullying of peers outside the family (Tanrikulu and Campbell 2015). In addition, low parental monitoring, especially on computers and mobile phones, allows children to engage in hurtful behaviors without negative consequences from their parents. Hinduja and Patchin (2013) found that young people who were punished for cyberbullying by parents were less likely to be involved in the behavior again.

Akers (1998) applied social learning theory to deviant behaviors of youth which he maintained were learnt by observation, imitation, differential associations (i.e., perceptions that the law can be violated), and differential reinforcement. Association with peers who are hurtful to others allows young people to conform to the group and engage in similar behavior. This behavior has also been found for youth who cyberbully (Holt et al. 2012). In addition, it has been shown that differential association was significantly correlated with cyberbullying behavior, that is, these young people thought there were no rules online and morally it was acceptable to write mean things (Li et al. 2015).

Evolutionary Explanations

Evolutionary psychology maintains that our behavior is shaped by genes that were evolved to be the most adaptive for humans in the past (Kolbert and Crothers 2003). One widespread behavior that has provided a competitive advantage in interspecies behavior is aggression. However, within-species violence is potentially nonadaptive. Thus, within cooperative species such as primates and humans it is argued that dominance hierarchies have evolved to restrain the negative effects of aggression and thus provide social stability.

This theory has been applied to childhood bullying which is postulated to be one of the central ways to establish dominance hierarchies in school systems (Kolbert and Crothers 2003). If there are stable hierarchies and young people know “their place” in the peer groups this is said to prevent destructive fighting in the group. Bullying is conceptualized as providing the perpetrator with social power to maintain the status quo.

Some recent research, however, has challenged this theory of bullying providing social stability in groups in young people. It has been found that there is actually much instability of bullying perpetrator roles (Le et al. 2017) where those students who self-reported bullying behavior at time 1 did not continue with this behavior at time 2 six months later. While it has been recognized that this changing of roles happens in very young children (Monks et al. 2003), these are the first studies to show changes of roles in bullying also occurs with secondary school students.

In considering cyberbullying from an evolutionary perspective it is necessary to decide if cyberbullying is an evolutionary adaptive tool. As previously argued, cyberbullying is one form of bullying, different in some of its manifestations from physical, verbal, and social bullying which are different from each other, yet all are forms of bullying. Therefore, the question becomes is bullying an evolutionary adaptive behavior? There are three major discussion points in this argument: is bullying heritable, is it goal related, and is it ecologically based (Volk et al. 2016).

The first point is heritability, is there an inherited component to this behavior? The genetic evidence is scant, with only Ball et al. (2008) providing some evidence with a twin study finding a heritability coefficient of 0.61. However, bullying is also very widespread and found in every country where it has been studied (Book et al. 2012) and throughout history (Rawson 2003). The behavior is also extremely hard to reduce (Ttofi and Farrington 2011).

The second point, is bullying goal-related? It has been shown that many students bully for social dominance (Reijntjes et al. 2013) or for physical resources such as food or money (Volk et al. 2015). Social dominance is particularly important in times of transition from elementary to middle school when peer networks are disrupted and need to be reestablished (Cross et al. 2009).

The third point is that adaptive aggression is conducted within a local ecology which influences how aggression is expressed (Hawley 2015). The argument is that societal toleration of bullying shows it is a sanctioned ritual for

establishing a dominance hierarchy (Kolbert and Crothers 2003). While this may have been the case previously since the work of Olweus and Smith in the last 40 years in demonstrating the negative outcomes from bullying societal attitudes in most countries have changed. As Hawley (2015) argues, however, because hierarchies are pervasive in nature does not make them morally correct or even healthy.

Prevention and Intervention Efforts

Examining cyberbullying through the two lenses of evolutionary psychology and social learning theory, it would seem cyberbullying behavior could, in part, be evolutionarily adaptive and maintained by social learning. Both theories offer explanations of why people behave as they do. How therefore, do the two explanations inform prevention and intervention efforts? Even if cyberbullying is adaptive evolutionary that does not mean it is acceptable (Hawley 2015).

It is known that bullying is widespread, historical and is very hard to reduce. This could be as the behavior is goal-directed with more benefits than cost then it is not easy to change. Ecologically if bullies are seen as lacking in social skills then by providing these skills this should reduce bullying, but this is not the case (Ttofi and Farrington 2011). This could be because most students who bully are socially popular (Reijntjes et al. 2013). There are probably two types of students who bully. Those who are socially skilled and popular (but often not liked), who adults would not see as being involved in bullying. Therefore, these students obtain the rewards with no costs associated, learn to abuse their power, and carry that into their working life to become workplace bullies. Then, there are those students who fit the stereotype of the maladaptive bully.

Evolutionary psychologists studying bullying have suggested two ways in which to reduce bullying in students. First, Volk et al. (2016) contend that bullies cannot be asked to relinquish their power and therefore one way to be able to accomplish this is by increasing the cost of bullying to

them. This would seem to indicate more negative consequences should be applied to these students showing this behavior, either from adults, such as parents or teachers, or from their peer group by ostracizing them. Motivational interviewing could also be a strategy to convince these students to change their behavior but only if there was costs to their behavior as well as rewards. The second suggestion by Volk and colleagues (2016) is to offer students who bully other ways of obtaining what they want, that is power and affiliation. Hawley (2015) advises substituting prosocial behavior for antisocial behavior for these students to maintain their power in the dominance hierarchy. Along the same lines, Kolbert and Crothers (2003) suggest using the concept of eminence instead of domination, that is, using the student's ability to influence their peers in positive and not negative ways.

At present, schools try to educate all students in the same way about bullying, which could work for prevention especially for the bystanders. However, it would seem more logical that as students who bully do so for various reasons within different ecological frameworks that intervention needs to be tailored to the individual as one needs to know their particular motives to address their needs to encourage them to change their behavior.

Conclusion

Cyberbullying is a worldwide public health problem, especially among young people. It is generally agreed that it is a new form of bullying with negative consequences for all involved. Most researchers conceptualize bullying in terms of social learning theories, where young people learn behaviors through modeling and operant conditioning. However, more recently evolutionary psychology has proposed an alternative framework that bullying behavior may be a biological predisposition. Whichever theory is proven to be more likely, the intervention strategies appear to be broadly agreed upon. Future research is needed to explore both these viewpoints.

Cross-References

- Adolescent Issues
- Anonymity of Cyberbullying
- Bullying
- Child Abuse and Bullying
- School Bullying
- Sex Differences in Cyber Bullying

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Cyberstalking

► Anonymity of Cyberbullying

Cycle of Violence

► History of Abuse

Cycle Variation

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Synonyms

Change in ovulatory cycle; Menstruation; Ovulation; Ovulatory cycle phases

Definition

Cycle variation is the different stages of the female ovulatory cycle, which occurs in fertile women.

Introduction

Human females have evolved ovulatory cycles that are different than the reproductive cycles of

other mammals. The ovulatory cycle in human females lasts 28 days on average. During different stages of the ovulatory cycle, physiological and behavioral changes can be observed. In the ovulatory stage, when a woman is capable of reproduction, females have exhibited a change in mating behavior and mate preference. Men also perceive women differently depending on which stage of the cycle females are in.

The Evolved Ovulatory Cycle

The reproductive cycle varies across species, with humans being especially unique. Most female mammals have estrous cycles, commonly referred to as being in heat. During the estrus phase of the cycle, females who are not taking care of infants display mating behaviors and signals to alert males of their ability to reproduce. These cycles are often related to external conditions, such as the time of year and prevalence of resources. Human females, on the other hand, evolved more regular cycles known as ovulatory cycles in which both ovulation and menstruation occur on a monthly basis, regardless of the time of year (McElroy and Townsend 2015).

Human females become fertile after the onset of menarche, or the first menstrual period, which generally occurs in adolescence, usually between the ages of 11 and 18. When females are no longer able to menstruate, they are no longer capable of reproduction, which is referred to as menopause. Menarche and menopause are often influenced by a variety of factors, including nutrition, overall health, and one's environmental conditions, or life history strategy. Unlike many other female primates, human females are able to live many years after the cessation of ovulation, which some researchers explain as the "grandmother hypothesis," originally contrived by Williams (1957). This idea posits that it is adaptive for older females who are not reproducing to help their own kin with child-rearing. There is also the "prudent mother hypothesis" which suggests that women lose the ability to reproduce in midlife because the developing fetus is at greater risk and it is more adaptive for women of this age to be

taking care of their kin (McElroy and Townsend 2015).

The human ovulatory cycle consists of two phases and is related to the various hormones present at each stage. The cycle begins with the follicular phase, which lasts from the first day of menstruation to ovulation. In this phase, estradiol levels rise until they reach their peak at ovulation, and an egg is released into the fallopian tube. If the egg is fertilized by male sperm, the female may become pregnant. In the luteal phase, the body prepares for pregnancy and releases progesterone and estradiol. If the egg is not fertilized, menstruation (i.e., blood withdrawal) occurs and the cycle repeats itself (Reed and Carr 2015).

The ovulatory cycle has been studied to have an effect on a female's behavior and additionally how she is perceived by males, as discussed more in depth in the section on concealed ovulation. A number of researchers have studied the effect of ovulation on behavior and female attractiveness. Schwarz and Hassebrauck (2008) found that women are perceived as more attractive at the peak of fertility in the ovulatory cycle by themselves and by men. Additionally, Puts et al. (2013) showed that females were rated as more attractive at the peak of fertility.

Conclusion

Ovulatory cycles are unique in humans in such a way that ovulation occurs in a cyclical pattern that consists of two phases, the follicular phase and the luteal phase, with ovulation occurring at the midpoint of an approximately 28-day cycle. During ovulation, females are perceived as more attractive and experience a change in behaviors that can be related to underlying sexual drives.

Cross-References

- ▶ [Birth Control](#)
- ▶ [Concealed ovulation](#)
- ▶ [Evolution of Adaptations](#)
- ▶ [Female Choice](#)

- [How Evolutionary Psychology Can Still Explain Behavior](#)
- [Ovulation Suppression](#)

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Cyclical Breeding

- [Reproductive Timing](#)

D

Daily Conception Risk

- [Problems of Assessing Fertility](#)

Daily Fecundability

- [Problems of Assessing Fertility](#)
- [Risk of Conception](#)

Danger

- [Environmental Harshness](#)

Dangerous Rescue

- [Heroic Rescue in Humans](#)

Dangers of Evolutionary Ethics

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Synonyms

[Darwinian ethics](#); [Ethical issues](#); [Evolutionary theory](#)

Definition

Evolutionary theory has been used to support a range of political ideologies and social policies, including unethical behaviors.

Introduction

Evolutionary theory, and natural selection in particular, has been utilized to justify a range of political ideologies and social policies, from conservatism to liberalism and individualism to socialism (Hodgson 2004). Consequently, while evolutionary theory may enhance scientific understanding and has been used to promote positive behavior, it has also been misappropriated to support a range of unethical acts. These include incarceration, discrimination, and genocide. The current entry outlines the misuse of evolutionary theory to justify Nazi ideology, with particular emphasis on the classification and separation of racial groups and the promotion or constraint of reproduction among those deemed to be superior or inferior, respectively. Throughout, the manner in which this ideology and subsequent social policy is inconsistent with evolutionary theory is emphasized. Indeed, the conclusions reached by those interpreting scientific (or pseudoscientific) theories are often more indicative of prior motivation and bias than the theories themselves.

Hitler and the Misuse of Evolutionary Ethics

Darwin focused on the manner in which evolution occurred rather than manner in which this should inform policy. He did, however, apply evolutionary theory to humans and acknowledge the manner in which prior struggle had contributed to the development of the species. In the *Descent of Man*, Darwin (1882) stated

Man, like every other animal, has no doubt advanced to his present high condition through a struggle for existence consequent on his rapid multiplication; and if he is to advance still higher he must remain subject to a severe struggle. Otherwise he would soon sink into indolence, and the more highly-gifted men would not be more successful in the battle of life than the less gifted. Hence our natural rate of increase, though leading to many and obvious evils, must not be greatly diminished by any means. There should be open competition for all men; and the most able should not be prevented by laws or customs from succeeding best and rearing the largest number of offspring.

Hitler, in contrast, focused on the manner in which evolutionary principles (and in particular the aforementioned struggle) should influence society (Weikart 2009). He believed that stronger and weaker members of a species exist, there is a struggle in which these individuals compete, and stronger members of the species survive leading to biological advancement of the species. Therefore, future development was assumed to be dependent on further struggle and the success of superior individuals. Factors leading to the improved health of the species were viewed as ethically good, whereas those leading to the stagnation or decline of the species were believed to be immoral. Specifically, “There is only one holiest human right, and this right is at the same time the holiest obligation, to wit: to see to it that the blood is preserved pure and, by preserving the best humanity, to create the possibility of a nobler evolution of these beings.” Social policies introduced included discrimination, eugenics, and population expansion, which it was argued would promote evolutionary progression and avoid biological deterioration. As stated by Hitler “It is absolutely true that first of all the law of

selection exists in the world, and nature has granted the stronger and healthier the right to life. And rightly so. Nature knows no weakling or coward, it knows no beggar, etc., but rather nature knows only those who stand firm on their soil, who sacrifice their life, and indeed sacrifice it dearly, and not those who give it away.”

Evolutionary theory and the description of intraspecies competition do not of course justify Nazi social policy. Though evolutionary principles have been employed to explain a range of negative behaviors such as rape (Thornhill and Thornhill 1983), homicide (Liddle et al. 2012, and abuse (Daly and Wilson 1985), we should not equate understanding those behaviors with endorsement of them. Furthermore, the “solution” does not necessarily follow from the identification of a social “problem.” For example, while apparent differences in IQ between racial groups have been used to justify prejudice and discrimination, they could be used to question the validity of the testing process or to promote equality of opportunity and education. Furthermore, though Darwin described the manner in which competition influenced the evolutionary process, he also advocated support for poorer sections of society. He stated “The aid which we feel impelled to give to the helpless is mainly an incidental result of the instinct of sympathy, which was originally acquired as part of the social instincts, but subsequently rendered in the manner previously indicated, more tender and more widely diffused. Nor could we check our sympathy, even at the urging of hard reason, without deterioration in the noblest part of our nature” (Darwin 1882).

Highlighting an alternate approach, Dickens et al. (2012) address the subject of teenage pregnancy in the United Kingdom (and in particular pregnancy among those from low socioeconomic groups) from an evolutionary perspective. The researchers do not recommend measures intended to reduce reproduction among women from these socioeconomic groups (who are more likely to experience poor health and lower educational success), as may perhaps be proposed by those adopting the traditional eugenics-based approach to evolutionary theory. Based on life history theory, it is instead suggested that those wishing to

lower teenage pregnancy rates among low socioeconomic groups focus on improving the environment in which these reproductive decisions occur. In poor quality environments, with few resources, individuals are most likely to produce a greater number of offspring with relatively low levels of investment in each. Those living in these environments are most likely to begin reproduction at an early age. Predictable well-resourced environments are associated with high levels of investment in a small number of offspring. The influence of environment type is referred to as r (growth rate of the population) and K (capacity of the environment) selection. From this perspective, teenage mothers from low socioeconomic backgrounds are following a fast life history appropriate to the ecological niche in which they exist. Hence, social policies intending to reduce teenage pregnancy should focus on improving the quality and stability of the environment, e.g., reducing deprivation and crime.

Racial Differences

While Darwin focused on the variation which occurs between individuals, Hitler argued that races of people were superior or inferior. This racial policy was fundamental to Nazi ideology. He argued that “nationality or rather race does not happen to lie in language but in the blood.” He reasoned that as these differences were biological in nature, education or similar interventions were not sufficient to address racial differences. For example, in *Mein Kampf* Hitler stated that it is “criminal lunacy to keep on drilling a born half-apie until people think they have made a lawyer out of him, while millions of members of the highest culture-race must remain in entirely unworthy positions.” The benefit of education was for Hitler in the reaffirmation of an inherent positive character rather than the reverse of biologically inherited traits. Hence, he promoted racial classification, separation of the races, and treatment according to racial category.

As part of his emphasis on group characteristics, the Aryan race was described as physically, intellectually, and morally superior to other races.

In contrast, Jewish people were particularly targeted by Hitler and often portrayed as sexually perverted, immoral, and selfish. For example, he stated “In his vileness he becomes so gigantic that no one need be surprised if among our people the personification of the devil as the symbol of all evil assumes the living shape of the Jew.” Hitler frequently dismissed individual human rights and freedoms in favor of the importance of group cohesion and sacrifice. For example, he stated “For evolution requires willingness on the part of the individual to sacrifice himself for the community.”

The identification of one individual (or group) of superior quality is of course problematic. The notion that fitness can be assessed on status or achievement implies that individuals compete from an equal position. There are however a range of social inequalities (such as access to an elite education, medical care) which influence the achievement of specific social groups. Similarly, racist ideology suggesting that Caucasian Europeans and those of European descent are stronger than other races (based on greater accumulation of economic wealth) neglects the importance of environment and the specific ecological niches occupied (see Diamond 1997 for a review). Further, there are multiple interpretations of fitness or quality, and we may be unaware of the benefits and costs associated with specific physical or psychological traits. For example, though sickle cell anemia is a serious disorder associated with stroke and pulmonary hypertension (thus likely to be interpreted as weakness under the Nazi regime), those carrying the gene display resistance to malaria.

Promoting Reproduction in Superior Races and Reducing Reproduction in Inferior Races

Hitler frequently referred to the struggle for existence and the importance of that struggle, which he regarded as central to the progression observed in all species. Hitler repeatedly warned that failure to adhere to these “laws of nature” would lead to stagnation or degradation of the human race. For example, he stated “We are all beings of nature, which – inasmuch as we can see it – only knows one harsh law, that gives the right of life to the

stronger and takes the life of the weaker. We humans cannot except ourselves from this law..." He introduced a range of measures based on this ideology intended to facilitate reproduction among those deemed to be stronger or superior and remove weaker or inferior members of a species in order to enhance the natural evolutionary process. Of course, the existence of evolution does not imply that we should seek to enhance the process via artificial selection.

Hitler frequently promoted reproduction among those deemed to be of superior race. For example, he introduced loans to facilitate marriage at an early age and further financial incentives for those producing large numbers of children. Indeed women could be awarded bronze (four children), silver (six children), or gold (eight children) medals for producing many children. He believed that increasing the German birth rate (and therefore the population) would promote the competition necessary for evolutionary progression. He also expected this to ensure the presence of a strong military presence in future generations. Similarly, Hitler opposed those practices believed to threaten the increased reproduction of the Aryan race such as contraception and abortion, though of course these were desirable for other "inferior" races. Essentially those behaviors which led to the production of healthy children of the superior race were believed to be ethically right, whereas those leading to no offspring or inferior offspring (as believed to be the result of mixed race relationships) were labeled immoral.

He stated "For as soon as procreation as such is limited and the number of births diminished, the natural struggle for existence which leaves only the strongest and healthiest alive is obviously replaced by the obvious desire to 'save' even the weakest and most sickly at any price, and this plants the seed of a future generation which must inevitably grow more and more deplorable the longer this mockery of Nature and her will continues." He was particularly critical of homosexuality, stating "The homosexual is always disposed to drive the selection of men toward the criminal or at least sickly rather than the useful in the selection of men. If one would give him free

rein, the state would in time be an organization of homosexuality, but not an organization of manly selection. A real man would defend himself against this endeavour, because he sees in it an assassination of his own evolutionary possibilities." There is however a wealth of evolutionary literature identifying the potential evolutionary benefits of homosexuality and existence of homosexuality in nonhuman species (e.g., MacFarlane et al. 2010).

In this context, the invasion of other countries can be conceptualized as an attempt to secure additional land and resources to support the expanding Aryan race. Hitler reasoned that these resources were there to support the stronger race and facilitate progression of the species. He stated

War belongs to those events that are essentially unalterable, that remain the same throughout all times and only change in their form and means. Nature teaches us with every insight into its functioning and its occurrences that the principle of selection rules over it, that the stronger remains victor and the weaker succumbs. It teaches us that what often appears to an individual as brutality, because he himself is affected or because through his education he has turned away from the laws of nature, is nonetheless fundamentally necessary, in order to bring about a higher evolution of living organisms.

In addition to introducing measures intended to increase birth rates among the Aryan race, Hitler also attempted to limit or eliminate reproduction among those deemed to be inferior. Those in poor health (chronic health conditions or disabled) and those from non-Aryan races were primarily targeted. Indeed, eliminating hereditary illness and preventing mixture of the races were primary objectives for Hitler and the Nazi regime. He believed that children of unhealthy parents or resulting from mixed race relationships would be of intermediate quality and were capable of slowing or reversing evolutionary progression. Hitler described the outcome of mixed race relationships

Such mating is contrary to the will of Nature for a higher breeding of all life. The precondition for this does not lie in associating superior and inferior, but in the total victory of the former. The stronger must dominate and not blend with the weaker, thus sacrificing his own greatness. Only the born

weakling can view this as cruel, but he after all is only a weak and limited man; for if this law did not prevail, any conceivable higher evolution of organic living beings would be unthinkable.

Hence, a number of policies were introduced such as relaxing criteria for abortions, prevention of “inappropriate” relationships, and sterilization. Hitler believed that this form of artificial selection was consistent with the action of natural selection and would improve the biological quality of the human race.

As previously stated, attempts to assess quality (characteristic of the Nazi regime) fail to capture the benefits associated with conditions such as personality disorders or may inappropriately emphasize qualities such as physical strength to the neglect of others, e.g., creativity. For example, while those with personality disorders have a lower life expectancy (Fok et al. 2012) suggesting that the disorders are maladaptive, some disorders are associated with increased mating success (Sansone et al. 2011). Hence, those with (at least some) personality disorders may achieve greater reproductive success, and the trait could be considered adaptive. Indeed, the notion that social policy should seek to reduce variation and improve the quality of the species by promoting a limited number of qualities is flawed. Variation within a species increases resilience and allows individuals to take advantage of different ecological niches. This is clearly demonstrated by the relative success of dark and light varieties of peppered moths (*Biston betularia*). Furthermore, sterilization programs may be criticized both from ethical and scientific perspectives. For example, defective genes are often recessive, with defects frequently occurring through mutation; hence, sterilizing those affected by visible abnormality would have little impact.

Conclusion

Hitler reasoned that behavior should be regarded as ethical or unethical according to the impact that the behavior had on the progression of the species. For example, while abortion was believed to be unethical for members of the Aryan race, it was

acceptable (and encouraged or required) for those believed to be of an inferior race. Though Hitler often used evolutionary theory to justify his actions, his conclusions represent a misunderstanding of evolutionary theory and the use of pseudoscientific research. The dangers arising from this approach are clear. It is important to advance our scientific knowledge, separate explanation of behavior from formation of social policy, and challenge those misappropriating scientific theory to justify their own political ideology.

Cross-References

- ▶ [Eugenics](#)
- ▶ [Moral Instincts](#)
- ▶ [Naturalistic Fallacy, The](#)
- ▶ [Science and Morality](#)
- ▶ [Social Darwinism](#)

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Daniel Dennett on Free Will

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Synonyms

[Freedom](#); [Self determination](#)

Definition

The ability of rational agents to act out of self-determination; to select actions from a broad set of possible alternatives based on rational expectations of their consequences.

Introduction

Daniel Clement Dennett, an American philosopher and cognitive scientist from Tufts University, is one of the most influential living thinkers on the topic of free will. According to Dennett, free will is an “ability to see probable futures – futures that seem like they’re going to happen – in time to take steps so that something else happens instead” (Closer to Truth 2014).

Dennett’s view on free will falls under the umbrella of compatibilism, which holds that free will is compatible with determinism. Whether the universe is deterministic or indeterministic, Dennett claims, has no practical implications for concepts of moral responsibility and is therefore irrelevant to the question of whether or not an agent has free will. He has argued extensively against libertarian thinkers, such as Robert Kane, who maintain that certain kinds of agents have free will in light of the fact that their actions are indeterminate, as well as against eliminativists.

Dennett has also criticized eliminativists, like Sam Harris, who deny that agents do or could have free will. While Dennett denies the existence of absolute free will, he maintains that the non-absolutist sense in which most humans have free will is sufficient for moral responsibility and serves as the conceptual bedrock of praise and blame as well as reward and punishment.

Compatibilism

The version of free will Dennett defends can exist in a deterministic world; one in which “all physical events are caused or determined by the sum total of all previous events” (Dennett 1984 p. 1). Opposing this view is incompatibilism, which states that free will and determinism are incompatible. According to incompatibilism, if all our actions are the product of physical causes – that is, all actions and the consequences thereof are determined – then no one can ever be said to have acted freely. The claim the free will can exist even if all actions are determined is *prima facie* paradoxical.

Dennett dispels this paradox by distinguishing the concept of *determination* from that of *inevitability* (Dennett 1984). Even if future states of the world were determined, they would not be inevitable – that is, they would not be unavoidable. Intentional agents (Dennett 1988) are capable of making accurate predictions about future states of the world conditional upon the performance of certain actions, and then selecting among possible actions to avoid the less desirable of these possible future states. For example, if someone were to see a brick being thrown at them, they could accurately predict that the brick would hit them conditional upon not moving (and that the brick would not hit them conditional upon ducking out of the way) and elect to duck in order to avoid being hit by the brick. In this sense, future states of the world may be “evitable” even if they are determined.

In the same way that determinism does not imply inevitability, Dennett claims that determinism does not imply that one “couldn’t have done otherwise” (Dennett 2003). The relevant

question to assess if an agent could have acted otherwise in a given situation is not whether the action was determined *per se*, but whether the action was determined *by factors external to the agent*. According to Dennett, the self can be roughly identified as the brain, or at least the part of the brain responsible for conscious action (Dennett 1992; Hofstadter and Dennett 1982). Actions are therefore the product both of one's self – that is, one's beliefs, desires, and capacity for rational action – and external factors. Considering an agent's decision retroactively, would changing some of the factors internal to the agent, along with slight variations in the external conditions, have led to her choosing a different course of action? If so, then she could have done otherwise.

Even in a deterministic universe, future states of the world would not necessarily be inevitable, nor would agents be incapable of having acted otherwise. Both evitability and the capacity to have done otherwise are requirements for having free will. In addition to the claim that indeterminism is unnecessary for free will, Dennett defends the stronger claim that indeterminism adds nothing valuable to our concepts of free will and moral responsibility (Dennett 1978). In his 1978 book *Brainstorms*, Dennett develops a two-stage “Valerian” model of an agent with free will in an indeterministic world. During the first stage, the agent's consideration-generator utilizes a randomized algorithm to generate a set of possible outcomes with probabilities conditional upon certain actions. During the second stage, the agent's reasoning processes select which actions to perform based on the output of the consideration-generator. The virtue of the Valerian model is that it incorporates indeterminacy into the decision-making process while allowing the agent to maintain control over its actions. However, such an agent would be no different in any morally or practically important sense from a deterministic agent whose consideration-generator operated according to a pseudorandom algorithm. Dennett claims more generally that pseudorandomness can be used as a morally and practically equivalent substitute for actual randomness in any libertarian model of free will.

A Free Will Worth Wanting

The criteria Dennett employ to construct his view of free will are based on the ethical and social function he envisions a concept free will fulfilling. In his own words, “Don't try to use metaphysics to ground ethics. . . ; put it the other way around: use ethics to ground what we should mean by our ‘metaphysical’ criterion” (Dennett 2003, p. 297). Specifically, the function of free will should be to ground notions of moral responsibility, praise and blame, and reward and punishment. Dennett is a consequentialist viewing punishment as a tool for discouraging bad behavior and reward as a tool for encouraging good behavior. The type of free will which can fulfill this function is a “free will worth wanting” (Dennett 2003).

According to Dennett, the primary utilitarian function of punishment is deterrence. However, only a certain class of agents are capable of responding to incentives such that deterrence would be effective for them. Dennett refers to this class of agents as the “Moral Agents Club” (Santa Fe Institute 2014). The threat of punishment provides reasons for not taking certain actions, and only agents capable of responding to these reasons can be held morally *responsible* for their behavior. In order for punishment to fulfill its role as a deterrent, it will be sufficient to punish only morally responsible agents. Extending punishment to morally irresponsible agents would be gratuitous insofar as it causes unnecessary harm for no utilitarian end. Accordingly, the concept of free will should be crafted to distinguish between morally responsible and irresponsible agents for the purposes of selectively assigning punishment in a socially optimal manner (Dennett 2003).

Dennett identifies six criteria which together are necessary and sufficient conditions for an agent to act freely (Santa Fe Institute 2014). The agent must:

1. Be well-informed
2. Have well-ordered desires
3. Be moved by reasons
4. Not be under the control of another agent
5. Be punishable
6. Be able to have acted otherwise

One desirable feature of a sense of moral responsibility based on these criteria is that it allows members of the Moral Agents Club to enter into enforceable contracts (Dennett 2003). For example, when signing a mortgage agreement, the mortgage lender can reasonably expect the borrower to repay her debt. If she refuses, she will face some sort of punishment and, as a morally responsible agent, the lender knows that the threat of punishment will motivate her to keep the contract. Another desirable feature of these criteria is that they do not require agents to be absolutely free in order to be responsible (Dennett 2003). Rather, free will and moral responsibility exist on a continuum, whereby an agent is free and responsible to the extent that she embodies these criteria. This allows Dennett to acknowledge that actions are partly determined by external factors while maintaining that most humans are free and responsible enough to participate in social contracts.

Finally, it is important to distinguish between a free will *worth* wanting and the free will most people *think* they want. Several studies in experimental philosophy suggest that people believe free will is incompatible with determinism, desire an absolutist contra-causal version of free will, and wish to use this absolutist free will to justify retributive punishment (Harris 2012). Dennett acknowledges that this sort of free will is indeed what people want and that it does not exist. However, he maintains that his version of free will both exists and is *worth* wanting, in the sense that the social benefits it produces are at least as substantial as those which could be guaranteed by absolute free will.

Freedom Evolves

As a naturalist and secularist, Dennett does not believe that free will is something granted by God (from the top down) but rather something that evolves through biological and cultural evolution (from the bottom up) (Dennett 2003). The history of evolution is the history of increasing “evitability,” as organisms develop better

mechanisms by which to optimally respond to their environment. Accordingly, Dennett maintains that the correct level at which to think about free will is not the physical level but the biological level (Closer to Truth 2014). Biological evolution has seen an arms race of evitability: for instance, predators evolve traits which allow them to avoid missing their prey, and prey evolve traits which allow them to avoid being eaten by predators. The evitability arms race may have been particularly important in the evolution of human social interactions, for example, as people evolved traits to avoid being cheated and cheaters evolved traits to avoid being detected (Byrne and Whiten 1988).

Dennett’s view of the relationship between biology and free will stands in contrast to that of B. F. Skinner, the father of behaviorism, who viewed psychology as having dispelled the idea of an inner free agent (Skinner 1971). In response, Dennett catalogued how, over the course of biological history, evolution has selected for creatures with increasingly greater levels of competence and freedom (Dennett 1996). One of the earliest and most basic creatures is the eponymous Skinnerian creature, which engages in trial-and-error learning absent of forethought, and does not have free will in any meaningful sense. Then came the more advanced Popperian creature, which exhibits forethought by selecting actions on the basis of their expected consequences (this creature is named after Karl Popper, who promoted the idea of falsificationism, as the Popperian creature allows its hypotheses to die in its stead). Later and more advanced still is the Gregorian creature, named after information theorist Richard Gregor, which augments its forethought by using thinking tools, such as language. Finally, the modern-day pinnacle of competence and freedom is the Scientific creature, which utilizes systematized social learning processes to improve its model of the world. Dennett contends that the level of competence and free will human beings enjoy as Scientific creatures results from biological and cultural selection pressures for advanced individual and social learning (Dennett 2003).

Criticism and Responses

Dennett's views on free will have been criticized in recent years by a number of scientists and philosophers, perhaps most notably Sam Harris (e.g., Harris 2012, 2014; Kane 1996; Pereboom 2001; Strawson 1994, 2003; Van Inwagen 1983). The main criticism is a terminological critique, which argues that Dennett's definition of "free will" disagrees so drastically with the commonplace notion of free will that his use of the term in public discourse is confusing and disingenuous. Harris has analogized the way Dennett justifies belief in "free will" to the way some theologians justify their belief in "God": by attaching idiosyncratic meanings to established terminology (Harris 2012). According to Galen Strawson, "[Dennett] doesn't establish the kind of absolute free will and moral responsibility that most people want to believe in and do believe in. That can't be done, and he knows it" (Strawson 2003).

Initially, Dennett replied by arguing that his definition of free will did have an established meaning within certain subdisciplines of philosophy (Dennett and Harris 2014). Criticizing him for using an established technical term, even if misunderstood by the general public, would be like criticizing scientists studying "color vision" for using the term in a way that disagreed with the commonplace concept of color vision. Furthermore, Dennett said, he was less interested in establishing the sort of free will that people want to and do believe in than establishing the sort of free will that is objectively worth wanting (see section "Introduction"). However, as a result of critiques by Harris, Strawson, and others, Dennett now believes the term "free will" engenders such confusion in intellectual and public discourse that it may be more useful to talk about moral responsibility in the absence of free will (Harris 2016; Santa Fe Institute 2014).

Conclusion

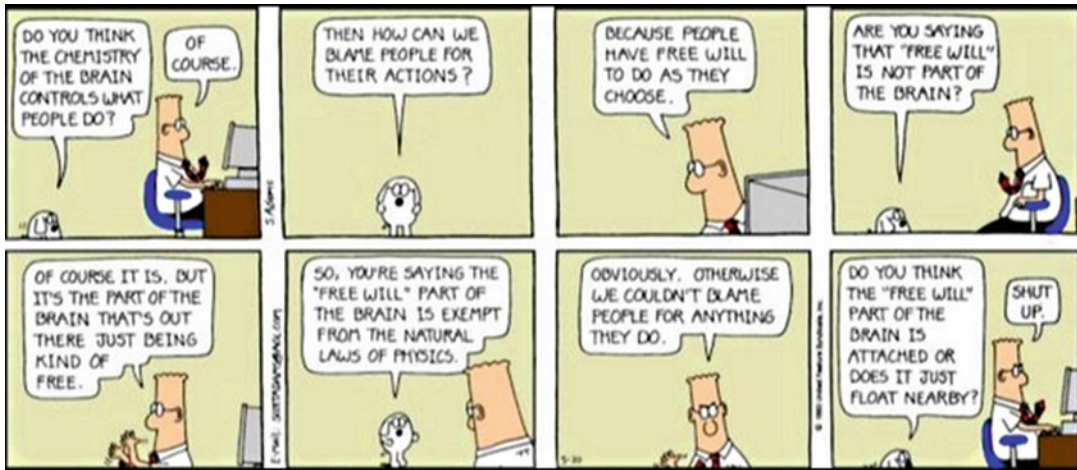
According to Daniel Dennett, free will is an "ability to see probable futures – futures that seem like

they're going to happen – in time to take steps so that something else happens instead" (Closer to Truth 2014). Dennett is a compatibilist, meaning that he believes free will and determinism are compatible. In a deterministic world – one in which all future events are determined by prior events – an agent's fate would not necessarily be inevitable nor would it be the case that she "couldn't have done otherwise" in a given situation. Moreover, Dennett claims that indeterminism does not add anything valuable to the notion of moral responsibility, making it practically irrelevant to the concept of free will.

Dennett believes that the metaphysical criteria used to determine whether or not an agent has free will should be based on the ethical and social function free will is supposed to perform; to ground notions of moral responsibility, praise and blame, and reward and punishment. Such a free will is a "free will worth wanting." From a utilitarian perspective, Dennett believes that punishment should serve as a deterrent by providing reasons against taking certain actions. Only agents capable of responding to these reasons can be held morally *responsible* for their behavior. Therefore, the concept of free will should be crafted to distinguish between morally responsible and irresponsible agents for the purpose of selectively assigning blame and punishment. (Similar logic applies when assigning praise and reward).

The history of evolution, in Dennett's view, has been an arms race of "evitability," as selection pressures have favored complex biological machines which are increasingly capable of anticipating and responding to possible future states of the world. Part of this history is the evolution of advanced cognitive capacities, such as augmented thinking tools and social learning mechanisms, the development of which can be viewed as the gradual evolution of freedom. These advanced cognitive capacities are especially pronounced in humans, who represent the modern apex of free will.

Dennett's views on free will have been criticized by a number of scientists, philosophers, and authors, whose primary concern is that using the term "free will" in public discourse ostensibly



Daniel Dennett on Free Will, Fig. 1 Daniel Dennett's favorite cartoon on free will

implies a belief in absolute freedom and retributive punishment. Though Dennett takes care to explicitly denounce this implication, he now believes that it may be more rhetorically pragmatic to focus on moral responsibility than on free will (Fig. 1).

Cross-References

► Free Will (Philosophy)

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Daniel Dennett: A Review of His Evolutionary Work

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Synonyms

Consciousness; Dual inheritance; Evolution;
Humor; Intentional stance; Memes

Introduction

Daniel Dennett is the codirector of the Center for Cognitive Studies, and the Austin B. Fletcher Professor of Philosophy at Tufts University. He is a philosopher in the analytic tradition but, unlike many of his contemporaries, has taken the trouble to familiarize himself with the nuts and bolts of empirical work. This has meant that over a six-decade career, he has made consistent and useful contributions to evolutionary scholarship, clarifying issues, generating research programs, and inspiring the next generation of scholars.

The Scope of Dennett's Philosophy of Science

"The aim of philosophy, abstractly formulated, is to understand how things in the broadest possible sense of the term hang together in the broadest possible sense of the term" (Sellars 1963, p. 35). This goal of pragmatist philosophy has been an explicit aim throughout Dennett's career. Sellars divided the world into the *scientific* image – for example, the world of particles and forces, and the *manifest* one – that this is the ontology accessed by commonsense, aided by logical reflection on the twin philosophical horns of necessary and contingent truths. The manifest image contains such things as colors, intentions, beliefs, and

(latterly) memes. A sensible way of summarizing one of the major themes of Dennett's work would be to say that he has achieved more than most in showing how these disparate elements can, or cannot, be made to live together coherently.

From the very inception of psychology as a science, a fundamental divide opened up in terms of seeing how much behavior could be explained by top-down mechanisms (such as social norms) versus that which could be explained by bottom-up mechanisms (such as stimulus–response schedules). Dennett is unusual in that he has argued consistently that both bottom-up and top-down approaches (which we would typically now call genes and culture, respectively) are subject to Darwinian selection. He thus embraces a dual-inheritance model.

Social constructionists (and others) are apt to make much of the fact that worlds of shared intentionality account for much of the so-called objectivity that we find in the world. Many thereby seek to undercut this sense of objectivity, by pointing out that humans could, if they wished, change this shared social space. Often the focus here is on language – and language change. However, objective reality is, in key ways, even more fragile than social constructionists can accept in their wildest dreams. Take a property like color. Naïve realism says that color is a real property of objects. However, naïve realism does not last long against optical illusions and neuroscience. However, a social constructionist might go further – by trying to link the perception of color to the use of color words in a culture, even to the extent of claiming that colors for which there are no words cannot be perceived (the Sapir-Whorf linguistic relativity hypothesis). Dennett's take on such phenomena is, in many ways, far more radical than this. For Dennett, color is a real property in the world, or, rather, a bewilderingly complex set of properties, but it is a very different set from the property we take it to be (see, e.g., Dennett 1991). However – those properties need to be defined in terms of a class of normal observers. And the fact that such a thing as a class of such normal observers exists at all should take people by surprise – especially

given the (superficial, but compelling) differences between cultures and individuals. What explains the fact that humans, more or less, despite individual and cultural differences, can be shown to be far more similar than they are different in their perceptions of the world? Evolution from common descent is the only non-magical process that can account for these otherwise miraculous facts. However, what processes are going on in each head is not the final word, and this phenomenology is not ineffable or private either. It is, on the contrary, to be understood in terms of representations. But representations of what? And, how are those representations to be compared with one another in ways that preserve our need for them to be truth-valued? Dennett's attempt is to draw these strands together, using a highly nuanced philosophy of mind that is clearly inspired by the metaphysically parsimonious insights of people like Willard Van Orman Quine (his undergraduate tutor, e.g. Quine 1951) and Gilbert Ryle (his PhD adviser at Oxford, e.g. Ryle 1949). This chapter will focus on the major themes of that program, especially those of particular interest to evolutionary scholars.

Content and Consciousness

The classic first essay set to analytic philosophy of mind undergraduates is "What is the mark of the mental?" Various options have been tried over the years but the dominant consensus is that mental states have "intentionality." This is a term of philosophical art that means that mental states are *about* something. What does it mean for a state to be about something? It might represent it in some way, for example. Dennett's position, consistent from his doctoral dissertation, is a form of functionalism: That what minds are is what they do. But, what is it that minds do? Here, there are various possible descriptions. At a bare minimum, minds must enable organisms to make (somewhat) reliable predictions about their ecology and responses to it. Minds inhere in brains. Plants do not need brains (although they can have rudimentary nervous systems) because they do not need to make predictions. Animals over a

certain level of behavioral complexity do need brains. Much of Dennett's earlier work (e.g., Dennett 1969) focused on what might be termed an enlightened behaviorism: A behaviorism that takes seriously a much fuller account of the functional properties of mental states, while still downplaying some of the more grandiose (yet commonsense) assumptions of minds being ineffable or being irreducible private. This sort of *heterophenomenology* (see Dennett 2003) takes the reports of experience seriously as objective facts (which is not to say that the experiences are themselves decisive of what is true). Thus, Dennett hopes to escape the Nagelian problem of how subjectivity can be part of an objective account of the world (see Nagel 1989). More latterly, Dennett (e.g. 2017) has started sketching out in more detail a dual-inheritance model of human evolution: one involving both genes and memes (see below).

The Intentional Stance

Dennett (1983) identifies three independent levels of description. The physical level, coterminous with what Sellars (1963) would call the scientific description, is the most parsimonious level: The level of particle physics. However, no amount of physical description of (say) an organism's trait will reveal its adaptive function: This level of description would be the design stance. Humans, and other organisms, are also steeped in predicting behavior. This requires an ascription of an intentional stance: This type of description takes in folk psychological concepts such as reasons for actions, Gricean (e.g. Grice 1975) accounts of meanings, and is more or less coterminous with a theory of mind (in its broadest sense). Dennett typically refuses to be drawn about the metaphysics of such stances, apparently being satisfied with their mutual irreducibility, and pragmatic requirement for all to be necessary for complete behavioral descriptions. These three levels map closely onto David Marr's (1982) famous distinctions between neurobiological hardware, a (functional) computational level (where this is to be understood in terms of problems solved) and

psychological algorithms. Note also that Tinbergen's (1963) distinctions between four types of biological cause (mechanistic, ontogenic, adaptive, and phylogenetic) while not being identical, can be readily seen as consilient with this way of carving up behavioral descriptions.

Here, and elsewhere, Dennett has shown a knack for "steel-manning": taking his opponents' strongest case onboard, agreeing with it, and then proceeding to show them how they were wrong to think it was an objection. For example, in Dennett (1983) he defends "panglossianism," a term intended to be abusive when first used by Gould and Lewontin (1979) in reference to the adaptationist program. He does this by sketching out precisely such a program for describing behavior at the level of goals, while being noncommittal about the content (or otherwise) of such goals. For example, a thermostat can be said to "want" to keep the temperature at a particular level without any commitment to said thermostat having a conscious state. However, without taking an intentional level description of it, no amount of physical level description will reveal this crucial feature. In a similar vein, he has embraced the "curious inversion of reasoning" (an intended slur on Darwin) that produces design without designers, and competence without comprehension (Dennett 2017).

Research Programs

A good example of the way that theory and practice feed one another in Dennett's work would be to note that his philosophical speculations have often guided psychological enquiry. For instance, the "Beliefs about Beliefs" commentary on Premack and Woodruff (1978) was foundational in generating research into autistic states using the Sally-Anne paradigm. Similarly, a lot of work on change blindness can be attributed to predictions made in *Consciousness Explained* (Dennett 1993).

A Universal Acid

Dennett's first encounter with the theory of Darwinian evolution was when playing bible seller in a theater production of *Inherit the Wind* (the play

about the Scopes Trial) as a teenager. He has been fascinated with it ever since. Evolution by natural selection has been noted as having that effect on people when they realize its implications. Not all scientific theories are on an equal footing. For example, it has been said that if your hypothesis appears to violate the second law of thermodynamics, then you may as well just pack up and go home, it is a nonstarter. In a similar way, evolution by natural selection is so powerfully evidenced by multiply converging lines of independent evidence, using a vast array of differently implemented investigative tools, that if your theory appears to contradict it, then you would be well advised to double-check your working. Some recent philosophers, notably Thomas Nagel (2012), and Jerry Fodor, have fallen foul of this, by attempting to refute evolution by consideration of some conceptual considerations – which usually turn out to be simple misunderstandings on their part. Professional philosophers sometimes make a virtue of not knowing the technical details of a scientific theory or a mathematical theory. Sometimes, this "not seeing the trees of the wood" strategy can work, but it runs the risk of resulting in an *ignoratio elenchi*, such as not appreciating that Xeno's paradox is solved by calculus. Dennett has regularly been seen as a champion of evolutionary theory in this regard. For example, Fodor (2008) states, "Contrary to Darwinism, the theory of natural selection can't explain the distribution of phenotypic traits in biological populations." (p. 11) Dennett's (2008) response is characteristic of his respect for the science over logic-chopping: "Now this really is absurd. Silly absurd. Preposterous. It is conclusions like this, built upon such comically slender stilts, that give philosophy a bad name among many scientists." (p. 25)

Why is evolutionary theory, in particular, something that philosophers are apt to misunderstand? Here is one set of reasons: Philosophy is about drawing of distinctions and this typically boils down to assessing the necessary and/or sufficient conditions for X's being Y's. "What makes these acts, 'acts of justice?'" "What is the correct way to pull the lever on a trolley, when the trolley is heading on tracks towards either five innocent

Kantians, or one really obese consequentialist?”, are typical analytic questions. Philosophers asking these sorts of questions are looking for essences – necessary and sufficient conditions. However, the scientific revolution was largely about replacing essences with processes. A set of key processes are laid out in the theory of evolution by natural selection and these are fatal to essentialist intuitions. An essentialist, like Fodor, asks “What is a species?” and expects to get an answer of necessary and sufficient conditions. Instead, an evolutionist is apt to answer this question with a set of processes with decidedly fuzzy boundaries, such as that species are “Guilds of genotypes committed to free, fair exchange of biochemical technology for parasite exclusion” (Hamilton, 1982). Biology is no friend to those who prefer hard clear conceptual lines.

An example of a more typical analytic problem would be that of the relationship of syntax to semantics. Let us take one example from Dennett’s (1995) Two Black Boxes. This is a thought experiment designed to short-circuit intuitions about whether semantics can ever be framed wholly in terms of syntax, or indeed whether examination of causes can ever elucidate reasons. Dennett’s take on this is that asking *why* questions – what he calls the intentional stance (and what evolutionists readily recognize as adaptive function questions) is unavoidable and that this should alert us to the fact that the problem as usually stated is badly framed, and, further, that only by adopting different descriptive levels will we gain philosophically satisfying solutions.

Why does Dennett hold evolution by natural selection in such high regard, given its propensity to offer fuzzy gradualist solutions to problems, where most philosophers want clear conceptual lines? One reason is that the process is, in his words, a “universal acid.” It takes mysteries of life that might otherwise appear to require divine intervention to account for them, and dissolves them into puzzles that empirical science can explain. The first mystery thus dissolved is the existence of apparent design in the world. Darwin (1859) solved this: The fittedness of organisms to their environments is explained, without the need for a designer, by descent with modification via

natural selection. The second big mystery is morality – not the details of how one should live – but the very existence of altruism. Hamilton (1964) explained this. If his axiomatic extension of natural selection, using genes as the substrate, $rB < C$, is satisfied then altruism can enter into the world. Thus, just in case the relatedness of an organism, multiplied by the benefit accrued by altruistic genes acquired by common descent is greater than the cost, then the behavior can be selected for. And, if altruism can enter, then all human – and other animal – morality can supervene on it. The final mystery to be turned into a puzzle is the human mind. Dennett thinks that this can be solved too, although here he is up against stiffer opposition. He thinks the solution here is also a Darwinian one – that humans evolved to be able to download not genes, but memes. And these semi-autonomous replicating agents use human brains for real estate. Before turning to a consideration of these memes, it is worth considering an example of Dennett’s application of this universal acid to a persistent problem in psychology – explaining how humor arose.

Humor

Why do we have a funny bone? Functions for humor – displaying intelligences, impressing the opposite sex, keeping yourself amused – are not hard to find. However, an *origin* for this ubiquitous sense has eluded scholars. Dennett, prompted by his graduate student Mathew Hurley, and a scholar of the history and philosophy of humor, Reg Admas proposed a fascinating idea, namely, that humor follows the pattern of other enjoyable activities that our genes needed to perform (Hurley et al. 2011). In this vein, it is easy to see why babies are cute, some of the opposite sex is sexy, and that cakes are sweet. But why is humor funny? Or, to put it another way – why has a reward system grown up around this sort of activity at all? Their solution to this is to note that human brains have a particular set of jobs to do that no other organism has to do: Curate incoming information. They would call these “memes” but this is not important at this stage. Humans are trying to drink from conceptual fire hoses of information and have no choice but to leap to

conclusions, and fill in gaps of knowledge and this means that we can make conceptual errors – confusing one thing with another. To triage this process, we require a gatekeeping system that is powerful enough to step in and identify errors in conceptual space. And a reward system for handling this (otherwise) tedious gatekeeping task is the result. In this way, humor is somewhat akin to the opposite of pain. Pain gets us to steer clear; humor gets us to pay attention to those errors, and even to enjoy them so that they do not mislead us. If this account is right, then other factors that might subsequently select for humor (such as finding funny people attractive) can *then* piggyback on this reward system. This account fits neatly with Dennett’s belief that what marks out human beings is their capacity for culture (which is fairly uncontroversial) and this means collections of memes (which is highly controversial).

Memes

Just as genes are packets of instructions for building bodies, memes are understood to be packets of instructions for building minds. Genes express themselves through phenotypes, and some of those phenotypes are more successful than others, leading to differential representation in the next generation. Just as Dawkins (1976) resisted the urge to pin down a gene to a set of necessary and sufficient conditions – leaving it as a replicator with sufficient longevity and power to create phenotypes – so too Dennett is unwilling to be completely nailed down as to what constitutes a meme. What count as memes? Words, certainly. Also snippets of tune, logos, habits that can be acquired, distinct likenesses. In short – something with sufficient longevity to be replicated across brains. Dawkins (1976) first drew on an analogy between the two in *The Selfish Gene*, and Dennett (1993) picked up this particular gage, especially in *Consciousness Explained*, and more recently (2017) in *From Bacteria to Bach and Back*. While the concept of memes has received short shrift in much of the evolutionary literature, work on cultural evolution has continued (see, e.g., Richerson and Boyd 2005). Thus, we have

accounts of evoked culture (Barkow et al. 1995), niche construction, and gene–culture coevolution (see those entries for full details). In short, (almost) everyone is sure that there is something happening besides genes, but the exact ontological status of such a thing is in still in doubt. Are they memes? This is highly controversial, but Dennett’s position is that it does not really matter what we call these elements, but if we accept that something that does the same work is needed for full descriptions then we probably ought to call them something. However, the word *meme* tends to raise defensive hackles in many scientists.

Dennett appears more than happy to respond to these raised hackles. This is probably because he is more than happy to see the connections between levels in scientific explanations, and thus be cognizant of a big picture. Memes, with their somewhat “mushy” associations, raise squeamish responses in those who believe that true reductionist science can only admit the existence of atoms and the void. But atoms and the void are high school physics. Even a cursory glance at quantum mechanics reveals that atoms are not the little billiard balls of high school physics. They are made up of things that can be given full expression in terms of information theory – that is to say, Shannon information. So, is Dennett saying that memes are information in that sense? No, because memes have informational content and Shannon information is content-free. We do not acquire memes per se – although Dennett makes frequent use of computational analogies – such as, memes as “apps” or “thinking tools.” It would be closer to the mark to say that Dennett’s position is not that we get culture – it is more or less that culture gets us. Our big species advantage is to be able to be the hardware for the software that are memes.

Whether this particular program will be fruitful remains to be seen.

Cross-References

- [Abstract Concept Formation](#)
- [Cultural Transmission](#)
- [Humor Production](#)

- [Memes](#)
- [Naturalism](#)
- [Why Humans are Unique](#)

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Daniel Nettle

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Synonyms

[Cost and benefit trade-off](#); [Evolutionary personality psychology](#); [Five-factor model](#)

Definition

Daniel Nettle’s proposal of a cost and benefit trade-off framework in personality entails that investment toward any personality domain is rarely fully adaptive or costly in the evolutionary paradigm and the optimum personality value is contingent on the varying adaptive problems present in each relevant ecology. Nettle’s contribution to evolutionary personality psychology had since provided researchers a direction toward the development of an evolutionary model of personality.

Introduction

Daniel Nettle’s research spans across a vast range of fields such as health psychology, individual

differences and personality, and evolutionary sciences as well as in topics such as social inequality, cooperation, deprivation, and biological aging. Among these include a series of studies leading up to Nettle's influential paper, "The Evolution of Personality Variation in Humans and Other Animals," which facilitated the progress of the academic study in personality within the evolutionary paradigm. This entry reviews the different theories that have been proposed to explain variations in personality and highlights how Nettle's work has contributed to the field of evolutionary personality psychology.

Explanations for Personality Variation

Since the conceptualization of the five-factor model (FFM), FFM taxonomies have demonstrated strong predictive abilities across various domains such as academic performance (Chamorro-Premuzic and Furnham 2003a, b; Poropat 2009, 2014), work-related performance (Barrick and Mount 1991; Barrick et al. 2001; Salgado 1998; see also Schmitt 2014, for a review), motivation (Judge and Ilies 2002), romantic partnership (Figueredo et al. 2006), and parenting style (Huver et al. 2010). Despite the breadth of its robust application, FFM and other forms of personality taxonomy remain largely descriptive and, by itself, cannot offer any explanation to the origin of personality variation.

Natural Selection

The process of natural selection favors traits that offer evolutionary advantages and creates selective pressure against those that do not. Accordingly, natural selection should eventually remove all but the highest-fitness variant at a particular locus (Fisher 1930; Tooby and Cosmides 1990), creating homogeneity in species-typical traits. Within this natural selection framework, individual differences were thought to originate from random sources and are irrelevant to the basic functioning of the universal psychological machinery – much like the colors of different wires in a car engine – and hence

lacked adaptive significance (Tooby and Cosmides 1990). Variances in traits persist because they are invisible to the selective forces of natural selection – a core proposition of selective neutrality.

Selective Neutrality

Selective neutrality proposes that trait variance results from the accumulation of fitness-neutral mutations, which are mutations that have no net effect on survival or reproductive success, averaged across all environments (Kimura 1983). In this view, being extraverted or introverted would not confer any fitness benefit nor impose any fitness loss on an individual in all environments. However, given the diverse evidence of personality traits influencing fitness-related outcomes such as life expectancy (Chapman et al. 2011), mating and relationship, and health (Ozer and Benet-Martínez 2006), selective neutrality is unlikely to explain the source of differences observed in personality.

Mutation-Selection Balance, Balancing Selection, and Nettle's Trade-Offs

Trait variance is influenced by two opposing forces: one being selection, which reduces variance, and the other being mutation, which increases variance. Since personality traits are consequential to fitness, according to the mutation-selection balance framework, variance in traits is therefore a result of the rate of mutation matching the rate at which natural selection takes place (Keller and Miller 2006; Lande 1975; Zhang and Hill 2005). Humans possess a relatively high mutation load (Eyre-Walker and Keightley 1999), and carrying non-neutral mutations tends to be harmful (Ridley 2000; Tooby and Cosmides 1990). While dominant deleterious mutations are often weeded out by selection, mutations carried by recessive genes persist over time (Zhang and Hill 2005). A mutation load of mostly recessive genes exists in an individual at any point in time (Penke et al. 2007). This mutation load may, therefore, account for the variation observed in fitness-related traits (Keller and Miller 2006; Zhang and Hill 2005) and personality (Lewis 2015; Verweij et al. 2012).

Where both selective neutrality and mutation-selection balance frameworks suggest that trait variance is maintained due to the lack of selective power to eliminate variance (traits either have no fitness impact or that new mutations are continuously introduced), the balancing selection framework postulates a mechanism in which trait variance is selected for (Penke et al. 2007). In this framework, trait variance is maintained when different levels of traits are optimal under different environmental conditions; selective pressures from different physical environments favor different levels of a trait (Buss 2009; Penke et al. 2007).

Nettle's contribution took into account the key pointers of both mutation selection and balancing selection; he recognized mutation as the process that produces differential traits and creates genetic polymorphism; this variance is then maintained by fluctuating environmental conditions (Nettle 2006a, 2011). Expanding on MacDonald's (1995) proposal that any normative range of observed personality variation represents a continuum of viable behavioral strategy, Nettle proposed a framework that alludes the concepts of trade-offs and demonstrates its application to the context of personality with the Big Five.

Origins of Personality and the Big Five

Nettle's approach to personality focuses on the fitness costs and benefits of possessing varying levels of each personality dimension such that these trade-offs shape personality variation. The benefits of possessing a particular trait depend on the adaptive problem the personality trait is designed to solve and how effective this trait is in circumventing the adaptive problem. The cost of a personality trait can arise from the cost intrinsic to the behavioral tendency as a result of possessing the personality trait or from opportunity cost where an individual would have benefitted if the individual had behaved differently.

Agreeableness

Agreeableness refers to the behavioral tendencies characterized by friendliness, consideration, modest

behavior, and propensity for nurturance. Its facets include trust, straightforwardness, altruism, compliances, modesty, and tender-mindedness (Costa and McCrae 1992). High scorers on agreeableness are more likely to be able to empathize with others (Nettle 2007), cooperate and engage in collective action (Denissen and Penke 2008), be accepted by peers and form friendships (Jensen-Campbell et al. 2002), share common resources, and thrive in joint cooperative ventures (Koole et al. 2001). Collectively, these findings seem to suggest that agreeableness serves an adaptive function of forming coalition and alliances that facilitate the cooperative task for the benefit of the collective.

Inasmuch as agreeableness facilitates social exchanges, being agreeable exposes one to social exploitation. Individuals high in agreeableness invest attention in the interests of others, to the detriment of their own, and, therefore, are vulnerable to social exploitation (Judge et al. 2012). When the majority of the population consists of individuals high in agreeableness and cooperation is widespread, cheaters and sociopaths may have considerable advantages to gain through their exploits (Nettle 2011). Hence, based on the trade-off principle, high agreeableness is favored when people live in small isolated groups that demand cooperative effort, whereas low agreeableness is favored when people live in loose social formation or when environment encourages solitary foraging (Nettle 2006b).

This trade-off principle can also be observed in intersexual dimorphism in agreeableness, where women are found to be significantly more agreeable than men (Costa et al. 2001; Schmitt et al. 2008). Women, who bear more childbearing fitness cost than men, often relied on social support and therefore stood to benefit more by better integration into their social network (Campbell 1999). Hence, the fitness benefits women have gained over human's evolutionary history by being agreeable, as opposed to men (Nettle 2011; Nettle and Liddle 2008), have been selected for and maintained.

Conscientiousness

Conscientiousness underlines orderliness, ownership of responsibility, and self-discipline

characterized by the facets of competence, order, dutifulness, achievement-striving, self-discipline, and deliberation (Costa and McCrae 1992). Being conscientious allows individuals in the modern context to excel in academic and work performance (Barrick and Mount 1991). Conscientiousness also enables individuals to delay immediate gratification in favor of longer-term benefits. In our ancestral condition, conscientiousness may benefit individuals facing tasks where adherence to repetitive schedules, forethoughts, or procedures is required to achieve the optimal outcome.

Despite the substantial benefits of high conscientiousness, individuals in the upper limits of conscientiousness incur opportunity cost by forgoing opportunistic situations in favor of their preferred routine. Conscientious individuals, held back by their inhibition and their avoidance of risky sexuality, have less short-term mates (Schmitt 2004). Certain circumstances in our ancestral condition may also be difficult to predict (e.g., unanticipated attack or opportunistic hunting), and failure to seize or act upon these scenarios would have led these individuals to incur fitness costs (i.e., failure to instinctively respond to survival threat or lower food resource; Nettle 2011).

Extraversion

Extraversion refers to the disposition toward social-seeking behavior and is characterized by the facets of warmth, gregariousness, assertiveness, activity, excitement-seeking, and positive emotions (Costa and McCrae 1992). Given extraverts' tendency to seek a variety of social partners, it comes at no surprise that there is a wealth of empirical evidence on the positive association of extraversion with the number of sexual partners (Alvergne et al. 2010; Heaven et al. 2000; Nettle 2005). Extraverts are more likely to engage in polygamy and partner switching, which suggests that there are more opportunities for them to acquire a higher-quality mate than introverts who tend to be more faithful toward a single mate (Nettle 2005). Extroverts are also more likely to initiate social behavior (Buchanan et al. 2005), engage in self-disclosure (Franken-

et al. 1990), and are more physically active (Kirkcaldy and Furnham 1991). On the flip side, in their quest to seek sexual diversity and physical activities, extraverts are more prone to injuries and accidents (Marusic and Musek 2001; Nettle 2005). They are also more likely to incite competitions and conflicts (Lund et al. 2007) and to be involved in criminal activities (Ellis 1987).

Extraversion is a behavioral strategy that is generally risky in nature; individuals with better physical attributes (e.g., attractiveness, formidability, and immunity function) are more likely to be able to bear the cost of an extraversion strategy going wrong (Nettle 2011). Hence, the optimum fitness values of extraversion are more likely to be observed in healthier individuals, an association that Lukaszewski and Roney (2011) support – attractiveness and strength predicted extraversion. Optimum fitness values of extraversion are also dependent on the ecological context. When social structures are fluid and the habitat is unfamiliar, there are considerable benefits to gain by being sociable. Extraversion would enhance group living that would aid survival and facilitate exploratory behaviors, which would allow one to achieve mastery over the new environment. In ecologies where stable and saturated social hierarchies with known environmental hazards exist, it may be more optimal to exercise caution instead (Nettle 2011). The fact that the long allele of the D4DR gene, which is associated with behaviors related to extraversion (Ebstein 2006), is more prominent among nomadic or migratory human populations (Chen et al. 1999) provides evidence to illustrate how the different local ecology produces variance in extraversion by selecting for varying optimum fitness value of extraversion.

Neuroticism

Neuroticism, the tendency to experience negative emotions, is characterized by its facets of anxiety, angry hostility, depression, self-consciousness, impulsiveness, and vulnerability (Costa and McCrae 1992). High neuroticism predisposes individuals to anxiety disorders as neurotic behaviors are manifested as a preventive strategy

that keeps one from facing and challenging their irrational fears from ambiguously threatening stimuli (Lommen et al. 2010). In general, high neuroticism is a risk factor for several psychopathologies, such as depression (Claridge and Davis 2001), schizophrenia (Van Os and Jones 2001), post-traumatic stress disorder (van Zelst et al. 2003), and eating disorders (Cervera et al. 2003). Individuals with high levels of neuroticism tend to experience chronic negative affect, as a result of their less adaptive coping strategies (Gunther et al. 1999), and chronic stress, which subsequently leads to poor physical health, marital instability and dissatisfaction (Kelly and Conley 1987), and sexual dissatisfaction (Fisher and McNulty 2008).

Given the well-detailed literature of the negative outcomes experienced by those high in neuroticism, its prevalence is paradoxical because high neuroticism would have been selected against and yet palpable variation is maintained. According to Nettle (2011), a potential explanation lies in the error management theory (EMT; Haselton and Buss 2000; Haselton and Nettle 2006) wherein the evolved decision-making psychological mechanism is selected to be biased toward the least costly error when the fitness cost of false-positive and false-negative errors was asymmetrical over evolutionary history. When the principle of EMT is applied to explain neuroticism, failure to detect threat in the social (e.g., mate rivalry) or physical environment (e.g., predator) would directly jeopardize reproductive odd and survival. Therefore, it is plausible that in ancestrally high-threat environment, bias toward a false positive (and therefore high neuroticism) is favored, and vice versa (Nettle 2011). High neuroticism in this view serves an adaptive function in threat detection, facilitating vigilance in threatening or competitive environments.

Openness to Experience

Openness, characterized by the cognitive disposition to creativity and aesthetics, comprises the primary facets of fantasy, aesthetics, feelings, actions, ideas, and values (Costa and McCrae 1992). Openness is positively related to artistic creativity (McCrae 1987), and creativity itself is

consequential to fitness as it reflects problem-solving ability. High openness to experience also appears to be a protective factor against age-related cognitive decline (Sharp et al. 2010) and memory impairment in multiple sclerosis (Leavitt et al. 2017). Individuals higher in openness are more actively engaged in cognitively enriching activities, combating decline and impairment with stimulation. Yet, high scorers of openness to experience are also more prone to psychosis and typically have an increased level of paranormal beliefs (McCreery and Claridge 2002; Thalbourne 2000; Thalbourne and Delin 1994), which may implicate fitness costs.

The distinction between the pathological and benign outcome of high openness to experience is not well understood; poets and artist have levels of openness as high as a schizophrenic individual but display no negative symptoms such as anhedonia and social withdrawal (Nettle 2006b). Nettle (2011) speculated that psychotic disorders might be the product of the interaction of a particular cognitive style with adverse general developmental conditions. In this case, openness is not so much selected by the different environment, but rather the optimum fitness value of openness may be contingent on other characteristics of the individual.

Conclusion

At present, although personality psychology has produced successful taxonomies capable of predicting several outcomes, the fundamental question of the origin of personality remains an unsettled science. Nettle's proposal outlined how each individual weights the cost and benefit of a personality strategy, which has fluctuating optimum values based on the local ecology of the individual. The cost and benefit trade-off principle is well supported by the proximate observation in both animals and humans (e.g., Boudreau et al. 2001; Friedman et al. 1995; Haselton and Miller 2006; Jensen-Campbell et al. 2002; Koole et al. 2001; Lukaszewski and Roney 2011; Nettle 2005; O'Steen et al. 2002) and is cited as the core conceptual pillar of recent

personality models (the condition-dependent, adaptationist model of personality; see Lewis 2015). Nettle's overall argument presents itself as a unitary force that brings together seemingly dichotomous concept that extends to the distinction between the genetic and environmental influence of personality.

In the 2011 reiteration of his proposal, Nettle turns toward an additional element in the discussion of cost and benefit trade-off: developmental plasticity. Nettle's case of developmentally induced individual variation is consistent with Buss and Greiling's (1999) concept of early environmental calibration, which states that individuals with a common evolved psychology can experience different development events that channel them into adopting different behavioral strategies. Given that it is not probable for a phenotype to be optimally adaptive in all ecological context and that it is costly to achieve complete plasticity in adulthood (Nettle 2011; Nettle et al. 2013), it is likely that individuals adopt behavioral strategies based on their formative experiences. Developmentally induced variations are either evolutionary responsiveness to specific early environmental cues available during ontogeny to forecast future ecological condition which facilitates the development of phenotypes adaptive in the anticipated ecology or a functional feature of an adaptive response to negative somatic state incurred with early life adversity (Nettle et al. 2013).

In essence, Nettle's framework postulates that each differential trait induced developmentally by environmental conditions has a cost and benefit value that differs cross ecology, and experiential factors funnel development toward a more ecologically beneficial level of a quantitative trait. It is this concept of trade-offs that is central to study of evolutionary personality psychology as it implies that trait variance is selected for; otherwise, natural selection would have selected for a specific value of the trait and reduced personality variance into a species-typical trait. The concept of cost and benefit trade-off in personality presents itself as a viable step toward the advancement of evolutionary personality psychology.

Cross-References

- Charles Darwin: Theory of Natural Selection
- Evolutionary Personality Psychology
- Five-Factor Model
- Personality
- Personality Development

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Daring Rescue

► Heroic Rescue in Humans

Dark Ages, The

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Synonyms

The Middle Ages

Definition

“The Dark Ages” is an historical label used to negatively characterize one period of time by contrasting it with another period, immediately before or after, which is alleged to be superior in some way.

Introduction

The Dark Ages is a label first developed by Renaissance humanists to characterize the Italian past between the fall of Rome and their own day. It has since been adapted to many different places and periods to suit different peoples’ perceptions (Nelson 2007). Wherever located in time, the Dark Ages is rhetorical shorthand variously used to characterize a period as crude, uncultured, barbaric, backward, irrational, violent, or stagnant.

Renaissance Origins

The first use of the term “Dark Ages” to refer to a period of history is usually attributed to the Italian scholar and poet, Francesco Petrarca (1304–1374). Petrarch lamented the political fragmentation of Italy in his lifetime and expressed the view that Italy had been in a state of darkness,

barbarity, and decay since the decline of the Roman Empire (Mommsen 1942). He expressed the hope, however, that a better age might arrive. The renewal of high culture through the careful study of the Classical past would, he believed, help inaugurate that new age. Subsequent generations of humanists adopted Petrarch's view, identifying their own activities with the age of rebirth, or renaissance. In doing so, Petrarch and the humanists adapted an older and essentially religious notion of "light" versus "darkness" to the sphere of culture and created the idea of a dark middle age between the ancient Roman past and their own day.

Reformation and Enlightenment Adaptation

The notion of the medieval period as a Dark Age was subsequently adapted by Protestants in the sixteenth and seventeenth centuries. In this case, however, the darkness was not perceived cultural decline but religious corruption. Reformers, dissatisfied with the state of Christianity in their own period, believed that the purity of the early Christian church had been lost. They attributed the corruption of that original Christianity to changes in the Medieval Latin church, particularly the role of the papacy. It was their belief that religious reform would remedy the corruption, ushering mankind out of the previous Dark Age and into a renewed Christian faith.

Enlightenment thinkers also perceived the period prior to their own as one of darkness, conceived of in their view as a society dominated by superstition and irrationality rather than reason. Writers like Voltaire and Edward Gibbon were broadly, though not uniformly, opposed to organized religion in their own time (McKitterick 2002). As a result, they perceived the medieval period as one of irrationality and zeal for religion, a barbarous Dark Age of credulous faith. This had, in their view, hindered the progress of history and could be remedied by the cultivation of reason. Edward Gibbon, in his *Decline and Fall of the Roman Empire*, attributed the political collapse of the Roman Empire to the spread of Christianity,

which he believed sapped the civic spirit of the Roman people, making them more focused on the afterlife than on the present (Pocock 1976).

Modern Scholarship on the Middle Ages and Late Antiquity

In the late nineteenth century, it was still common to write of the whole period from the decline of the Roman Empire to the Renaissance as "the Dark Ages." However, since then the term has fallen almost completely out of use by practicing historians. This has come about as consensus has built that labeling a period "the Dark Ages" inevitably implies a value judgment, fixing attention only on perceived negatives. "Medieval" and "Middle Ages" are still used by professional historians, because these terms refer more neutrally to a period of time, generally the fall or decline of the Roman Empire and the Renaissance (Robinson 1984). For a time, "the Dark Ages" was retained, but limited to only the Early Middle Ages, the period Edward Gibbon described as the *Decline and Fall of the Roman Empire*. Beginning around the publication of Peter Brown's 1971 *The World of Late Antiquity*, however, scholars have increasingly come to see the period from ca. 300 to 700 CE as a time of change and creative adaptation, rather than collapse and decline (Brown 2013). Thus, the more neutral label "Late Antiquity" has largely replaced "the Dark Ages," even for what used to be perceived as the darkest of the medieval centuries (James 2008).

Conclusion and uses in other areas

Despite these changes among professional historians, "Dark Ages" remains popular as a term of abuse and belittlement, alongside medieval, in popular culture. Policies or actions perceived as backward, irrational, or violent are met with cries that they threaten to bring about a new Dark Age or throw society back into the Dark Ages. Given the religious valence of the September 11 attacks of 2001, the use of "Dark Ages" as a term of condemnation has been given new

impetus, even on opposing political sides. For example, Jill Lepore, in *The New Yorker* in 2013 wrote about the policies of torture and interment characterizing George W. Bush's War on Terror under the heading, "The Dark Ages" (Lepore 2013). On the other hand, writers decry alleged Muslim "extremism" by alleging that Muslims or Islam are stuck in the "Dark Ages," as Julia Hartley-Brewer did in the *Telegraph* in 2015 (Hartley-Brewer 2015).

The Dark Age is also used in some limited contexts in reference to a period marked by the loss of large numbers of records. For example, it has been hypothesized that the possibility that digitally-recorded records might be lost due to changes in physical or electronic format could lead to a "digital dark age." In cosmology, the period between the big bang and the formation of stars is referred to as a Dark Age because it was literally dark. This usage is rarely retained among historians to describe medieval centuries with few surviving documents. However, the massive growth of archaeological study and alternative investigative methods, such as dendrochronology and ice core samples, has shed impressive light on previously invisible periods, rendering their characterization as "dark" obsolete (McCormick 2001).

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Darwin on Speciation

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Synonyms

[Darwin's principle of divergence](#); [Natural selection](#); [Origin of Species](#)

Definition

Charles Darwin's proposed mechanism(s) for the evolution of new species

Introduction

It is evident from the title of Darwin's seminal work that he sought to advance a theory of speciation – that is, to explain the causes and mechanisms of the origin of species. However, many historians of science hold that the question implicit in his title was never fully answered, primarily because he never concretely defined the concept of "species" in the first place and because he conjectured new species likely appeared in sympatry through the process of gradual divergence of characters. The theory of speciation as it is explained in *The Origin* and Darwin's later works is described here in full, and then it is placed in modern context to examine the cases for and against its accuracy and relevance to current evolutionary biology.

Darwin's Explanation of Speciation

Darwin described speciation as the "mystery of mysteries" (1959, p. 1): how do new species

appear? The essence of his answer is that “varieties” turn into new “species.” The specific meanings of these terms have been the subject of much modern debate (for a review see Mallet 2013) because they are used almost interchangeably, or so it seems. Darwin does define them as two nonequivalent but related units, and confusion arises because they are gradations of each other. Varieties are less discrete phenotypic clusters than species are. In other words, “...species are only strongly-marked or well-defined varieties” (1959, p. 55), but there is a degree of ambiguity regarding *when* a variety becomes distinct enough to be called a species: “...the amount of difference considered necessary to give two forms the rank of species is quite indefinite” (ibid., p. 59).

The two keystones of Darwin’s explanation of speciation were the principles of natural selection and divergence. Natural selection is the differential survival of organisms resulting from differences in phenotype: characters better suited to the environment will tend to confer selective advantages to organisms that have them. These characters are therefore more likely to be passed on to the next generation, resulting in evolutionary change in populations over time. Darwin’s principle of divergence holds that sympatric organisms will suffer less from competition with each other if they diverge in character. The interaction of these two principles, and how this results in varieties evolving into distinct species over time, is described in chapter IV of *The Origin*:

Only those variations which are in some way profitable will be preserved or naturally selected. And here the importance ... of divergence of character comes in; for this will generally lead to the most different or divergent variations ... being preserved and accumulated by natural selection. When ... a sufficient amount of variation is supposed to have been accumulated to have formed a fairly well-marked variety, ... [it] would be thought worthy of record in a systematic work. (ibid., p. 117)

In short, natural selection favors variation towards greater divergence. Over time, varieties diverge sufficiently enough from each other to produce distinct gaps in the distribution of phenotypes, warranting their categorization as separate species. Darwin then also draws upon the principle of extinction to explain the absence of

intermediate varieties between species: intermediate phenotypes are less able to compete with more diverged varieties and are driven to extinction. The same fate, for the same reason, awaited “parent-forms” or the ancestral phenotype.

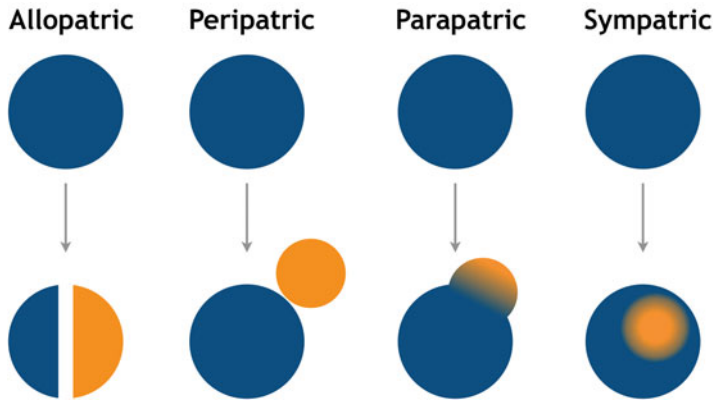
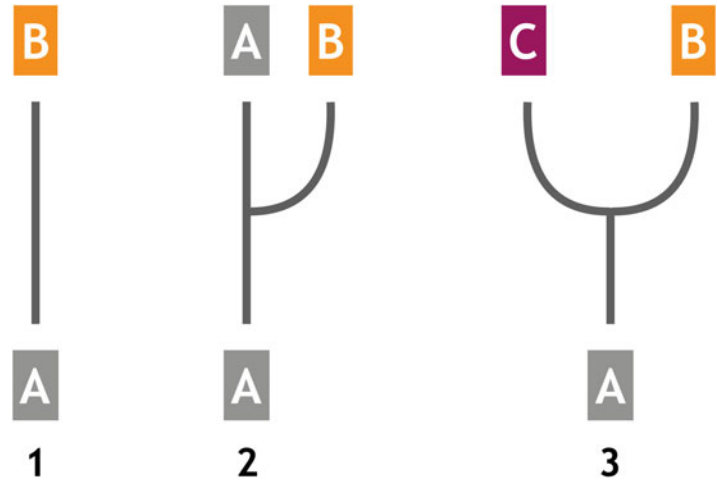
Darwin’s Theory in Modern Context

Modern models of speciation cover two important elements of the process: (1) phylogenetic pattern and (2) barriers to reproduction. Regarding the first, three broad “types” of speciation can be described (see Fig. 1). The first model is of continuous evolutionary change within a population, leading to an ancestral population (A) being replaced, over time, by a new population distinct enough to be classified as a new species (B). In the second, the ancestral population persists, but a new species buds off. In the third, the ancestral form goes extinct and produces two (or more) daughter species (B and C). Darwin’s model of speciation is not easily classified in this framework, because he describes both all models without distinguishing between them explicitly: he conjectures in very general terms that a new variety may diverge from its parental stock and replace it (model 1) or that a new variety can diverge from its ancestral form which persists because the new variety diverges sufficiently from it so that their ecological niches do not overlap (model 2) or that varieties that comprise an ancestral form diverge from each other, outcompeting their parental forms (model 3).

There are four main models describing the degree and nature of reproductive isolation during the process of speciation (see Fig. 2). From most to least isolated, these are allopatric, peripatric, parapatric, and sympatric speciation. In allopatric speciation, extrinsic barriers prevent gene flow between diverging populations. In peripatric, parapatric, and sympatric speciation, incipient species start occupying different niches, and the models differ in the degree to which these populations overlap in physical space. Darwin never explicitly describes the degree or type of isolation he expects to initiate speciation, although he does write that “...I do not doubt

Darwin on Speciation,

Fig. 1 Phylogenetic patterns of speciation. In model 1, the ancestral form (A) evolves into a new form (B) over time. In model 2, the ancestral form persists, and a new species (B) buds off this lineage. In model 3, the ancestral form goes extinct as it splits into two distinct new species (B and C)



Darwin on Speciation, Fig. 2 Types of isolation leading to speciation. Allopatric, or geographic, speciation occurs when an extrinsic barrier prevents gene flow between incipient species. Peripatric and parapatric speciation occurs when some members of an ancestral population begin occupying a new niche: these models differ in the

extent to which these niches and populations' ranges overlap. Sympatric speciation happens in the same area; this can be initiated by a genetic mutation that interferes with reproduction, or gene flow can be interrupted by diverging behaviors or mating strategies

that isolation is of considerable importance in the production of new species" (p. 105). His model is more mechanistic in nature, answering the question of *how* diverging varieties become established enough to be classed as distinct species, but not necessarily what extrinsic factors initiated divergence in the first place.

Darwin's description of speciation is frequently interpreted as an argument for sympatric speciation, and this is the basis of many of Mayr's allegations (e.g., Mayr 1992) that Darwin never

satisfactorily answered the question of the origin of species. Mayr's main point is that evidence for sympatric speciation through divergence is lacking or even absent and that the degree of variation inherently required within a population to supply the raw material for divergence is almost never seen. Consequently, "...intrapopulation variation does not supply the material for a multiplication of species" (ibid., p. 352). Mayr makes the case that allopatric speciation is the norm. Mallet (2008) disagrees with Mayr's criticism

and interprets Darwin as "...discussing the ecology of available niches for populations that have already become somewhat divergent, rather than arguing that the whole process of speciation is necessarily sympatric" (p. 8). Taken together, these views overlap in their interpretation that Darwin does not explicitly concern himself with proximate causes of divergence and rather describes a general process that establishes populations on independent evolutionary trajectories.

Conclusion

Darwin's explanation for the origin of species rests on two key processes: natural selection and divergence of character. He hypothesizes that varieties evolve into new species because natural selection favors divergence of character. This hypothesis is based on the intuitive logic that the more distinct populations are from each other, the less they overlap ecologically and therefore suffer less competition. The ambiguity of his definitions of "variety" and "species," as well as the lack of explicit discussion of proximate causes for initial divergence and consequent implicit argument that speciation occurs sympatrically, has been criticized by modern biologists.

Cross-References

- [Charles Darwin](#)
- [Charles Darwin: Theory of Natural Selection](#)
- [Gaps in Darwin's Initial Theory](#)
- [Impact of Early Theory on Charles Darwin](#)
- [Natural Selection](#)
- [On the Origin of Species](#)

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Darwin on the Origin of Language

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Synonyms

[The musical protolanguage model](#); [Theories of language](#)

Definition

Charles Darwin proposed theories of how language emerged. His theories availed for his observations on both animals and humans.

Introduction

In his book, *On the Origin of Species*, Darwin intentionally did not refer to human evolution in detail (Darwin 1859). Although it was perceived that this was a mere oversight, this was not true. Darwin carefully avoided to thoroughly refer to his hypothesis on human evolution because he knew that his theory would not be accepted, but rather it would probably provoke the existing insurmountable opposition. His rivals, however, emphasized the importance of human mind, and language in particular, to compete Darwin's work. Friedrich Max Müller, one of the reputed scholars of that time, was considered as Darwin's most intimidating rival on the linguistic front (Stam

1976). In 1861, Müller delivered lectures at the Royal Institution of Great Britain. These lectures, entitled as “Lectures on the science of language,” were published soon afterward, and Müller used his expertise in the “science of language” as a strong weapon to attack Darwin and Darwinism (Müller 1861). Müller’s hypothesis about the origin of human language in relation to how animals communicate provoked Darwin to further study language.

In 1871, Darwin published his second book *The Descent of Man, and Selection in Relation to Sex*. In this book, he raised the subject of human evolution, and he provided explanation of how language emerged. Darwin’s “musical protolanguage” model was a response to this propaganda and thus represented a combination of comparative data, evolutionary insight, and a biological perspective on language. His innovatory view of language and his models are still astonishingly applicable to contemporary arguments. Darwin proposed a complex model to explain the evolution of language in which he recognized the necessity of various mechanisms in order to produce vocal sounds. Most importantly, he observed that several components in vocal learning shared many biological capacities similar to birds in the production of sound.

Further, Darwin took advantage of a wide comparative collection of data, by using his insight of both nonhuman primate behavior and vertebrates. He proposed a broader theory of evolution that is applicable to insects, flowers, and birds. His purpose was to reveal through investigation general ideas, like sexual selection and shifts of function, to give more information about common and unique human characteristics. Darwin’s model suggested that language emerged only to humans since there is no progression of function between nonhuman primate calls and language (Fitch 2006).

Language as a Natural Aptitude

In his book *The Descent of Man and Selection in Relation to Sex*, Darwin discussed about the evolution of human mind. He suggested that animals have feelings, attention, memory, and

many other mental traits in common with human beings (pp. 34–52). Some of his opponents, however, and specifically Müller had already suggested the hypothesis that animals have memory, experience feelings, and so on. What was of paramount importance, however, was the subtitle “Language” (p. 53) in his book where he spoke for the first time about the evolution of language.

Theoretically, Darwin made some significant observations. First, he acknowledged the essential difference between the biological ability that enables humans to acquire language and specific languages (like Latin or English). Although he initially suggested language as an instinctive propensity shared by all humans, he later emphasized that language is not an instinct provided that every language has to be learnt. He suggested language as natural aptitude whose expression implies that both biological and environmental preconditions must be satisfied.

Second, in spite of the fact he was cognizant of the unique characteristics of the human vocal tract, Darwin supported that the human ability for language must be sought in the brain, rather than the peripheral vocal tract. He concedes that a unique characteristic of humans is the ability to speak fluently and coherently by controlled movements of their lips and tongue (p. 59). Nonetheless he repudiates that simple power of articulation is enough to distinguish human language, since as he explained parrots can talk as well. It is further stated that it is not speech, but humans who are largely capable of joining certain sounds with particular concepts that is definitive of language. This capacity apparently depends on the development of the mental abilities.

Finally, Darwin argued that there is a coherence of the evolution of language to the birdsong, which he thought it was similar to human language. Both humans and birds have fully instinctive calls that they have to learn. Also, he emphasized the fact that both birdsongs and speech form regional dialect depending on their place of residence.

The Musical Protolanguage Model

Darwin’s model of the evolutionary development of the language capacity assumes that various

features of language were obtained in specific order, inspired by unique selection pressures. The hypothetical arrangement that was classified by each addition was called as protolanguages (Hewes 1973). Darwin firstly hypothesized that the evolution of humans progress from an ape-like ancestor to the protohuman cognition. He proposed that some primates developed highly mental capacities even before any form of verbal expression come into use (p. 57). He also stated that both social and technological factors act as drivers of this superior cognitive ability.

Darwin later proposed the musical protolanguage model (Fitch 2006), after observing numerous resemblances in birdsong and human language. He precisely implies that there is an inherent ability to replicate vocals evolved analogously in humans as well as songbirds to express feelings such as love, jealousy, and success. He reasoned that sexual selection is mainly used as the main driver behind the evolution of spoken language.

What is crucial for further investigation, however, is the transition of the musical protolanguage model to a meaningful speech. According to Mithen (2005), the progress of the musical protolanguage model to a meaningful speech remains the greatest explanatory challenge for all musical protolanguage theories. Darwin, however, referred to Müller's writings, and he embraced the theory that language emerged from natural sounds, such as the imitation of the sounds of animals and man's own instinctive cries (Farrar 1870). It is important to note that once the protohumans had the ability to mimic sounds and translate signals into meanings, then the ability to produce speech evolved, including onomatopoeia and the imitation of human emotional vocalizations.

Sign Language

Darwin, in a clear and detailed manner, described the role of gestures in the communication among humans. He was aware of the practice of sign language as a mean of communication to deaf individuals (p. 58). He acknowledged the

importance of gestures in conveying meaning, and he emphasized the fact that in order for people to be able to communicate between them, they must see each other directly. Although he agreed that vocal communication can be aided by signs and gestures (p. 56), he criticized the gestural theorists. In his point of view, the vocal organs were significant to all mammals in the development of communication rather than the use of fingers. A major problem for gestural theories is to explain how such a system evolved from an initially iconic, holistic, meaningful system.

Sexual Selection in the Evolution of Language

Darwin's sexual selection theory states that sexually selected traits develop mostly in men who are considered to be more competitive and only at sexual maturity. Darwin, however, figured out that it is equally developed in males and females and is expressed very early in the biological development (Fitch 2005). There are few explanations to the difficulty that these facts pose. Firstly, during the musical protolanguage stage, sexual selection was the driving force, and song was expressed mainly in males at sexual maturity. After the evolution of language, Fitch (2004) proposed that a selective force appeared to aid women equally express language as men did, and that language develops in earlier stages of life. The communication among the members of the family can be a selective force. Parent's communication with their offspring is an important aspect of their upbringing. Moreover, this can explain the reason language evolves at an early stage in the life of human beings. Language at an early stage of life can help children absorbed their elder's knowledge and experience. Also, this kin-selective force can explain the reason that language evolved only to humans and not to animals. People are going through life stages where they gain knowledge and experience, with very small reproductive output in relation to animals, who can reproduce from their early stage of life (Fitch 2007).

A different approach proposed by Miller (2001) is that sexual selection was an important driving force in human intellectual evolution, including speech. This hypothesis suggests that both sexes can choose and compete for high-quality partners. It is of paramount importance, however, to understand that this hypothesis does not explain the early development of language in infants. Finally, it is considered that sexual selection never played a role in the evolution of language (Miller 2001).

Conclusion

Summarizing the compelling work of Darwin on the origins of language, it is important to note that Darwin proposed that the first step to language evolution was an increase in the mental capacities of humans. He agreed that both social and technological factors are significant in the selective roles. He used a wide comparative collection of data of nonhuman primate behavior and vertebrates, to propose his theories on the evolution of language. Darwin benefits from his studies on animals, and he used his observations to propose his theories on language development. Although he studied both the evolution of human and animals and described many traits shared between them, he concluded that language is unique only to humans.

Cross-References

- Early Theories of Language
- Evolution of Language

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Darwin's Beliefs

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Charles Darwin was born into a family in which both his father, Robert, and his grandfather, Erasmus, were medical practitioners. Erasmus had in addition been a poet and writer on what was then termed “natural philosophy” and whose ideas about evolution anticipated and no doubt influenced his grandson’s perspective. A theme

throughout Darwin's life was the contrast between the religious affiliations of the Darwin line as baptized members of the Church of England and those of the Wedgwood, including Darwin's mother and his eventual wife, Emma, who were Unitarians (Unitarians are egalitarian, protestant Christians who do not believe in the Trinity, but rather in a single divine being). Darwin's mother took him to the Unitarian chapel in Shrewsbury that also provided his initial schooling. She died when Charles was just 8, and Charles went on to the traditional Anglican establishment of Shrewsbury School and an education largely bound up in the Classics.

After the failure of his medical studies at Edinburgh, Darwin was sent by his father to Christ's College, Cambridge, where he attended King's College Chapel regularly due to the superiority of its choral tradition. He was to take a degree in Theology with the intention of becoming a priest. Little sense of calling was involved in this pragmatic decision, and there was no anticipation that Charles's studies would lead to a lifetime investigating the natural world. Indeed, "scientist" was barely a profession in the early nineteenth century, and most practitioners of the branches of science that Darwin encountered at Cambridge and elsewhere who influenced his initial career were themselves clergymen: notably William Paley, William Whewell, and John Henslow. Indeed, Whewell coined the term "scientist" in 1834 to denote the practitioner who relied on experimentation, measurement, and observation rather than abstraction – what we now call "evidence-based" science as opposed to "natural philosophy." Nevertheless, the new findings arising from the application of scientific method in geology placed a strain on thinkers whose world view needed to remain consistent with the faith they preached. Biblical accounts such as The Flood and other cataclysmic events influenced a trend in geology embraced by Whewell and his followers. They were dubbed *catastrophists* and were opposed to *uniformatarians* (note the implied link to the religious denomination) such as the leading geologist Charles Lyell, whose viewpoint was that the same forces acted interdependently on the earth over long periods of time (Ruse 2007, 3). Darwin

eventually sided with Lyell, taking the first volume of his mentor's *Principles of Geology* with him on the *Beagle* voyage. Application of Lyell's work to the phenomena he observed, especially in the Pacific, led to one of Charles's earliest scientific publications, on the formation of coral reefs (Darwin 1842).

The *Beagle* voyage had for the young Darwin many of the attributes we would now associate with postgraduate study. It involved scientific observation, exploration, and travel, permitting the examination of geological features, flora, and fauna as well as contact with people from markedly different cultures and environments to those Darwin would previously have encountered. The *Beagle* was Charles's graduate school, a community of scholars in which ideas were discussed and samples obtained for later analysis, while favored reading matter embraced both Lyell's geology and Milton's *Paradise Lost*. Above all, the *Beagle* voyage led both to immediate publication of the edited ship's journal (Darwin et al. 1839) and to the sequence of articles on coral, volcanic islands, and barnacles that would pave the way for *The Origin of Species* and for Darwin's eventual confidence to share its radical implications.

Almost immediately on his return from the *Beagle* voyage, alongside the preparation of publications and analyses of the copious and ground-breaking data he and his colleagues had assembled, Darwin initiated what was to become a parallel project, the systematic planning of family life: in short, his marriage prospects. He set out a list of the arguments for and against and the criteria that a suitable partner would furnish. While living like a hermit might provide the circumstances in which hard work could be achieved, he would miss companionship, music, and children (Darwin 1838). The woman whom Darwin, on deciding to marry, pursued was his first cousin, Emma Wedgwood.

Emma combined the fun-loving accomplishments of a young woman of her time, provided for her by her rich family, with a deep commitment to the Unitarian faith. She was a proficient linguist, well-traveled within the European cultural orbit that enabled her to take piano lessons from Chopin and Moscheles (Healey 2010). They

became engaged in November 1838 and wed just 2 months later. The marriage secured Darwin's financial status as well as providing him with the lifelong support that, as a virtual invalid, his considerable achievements were to depend upon.

When children came, the Darwins proved to be tolerant and active parents, sharing their interests and accomplishments. While the Bible was read at family prayers, and Emma remained true to her Unitarian upbringing, the children were baptized in the Church of England and attended the little parish church of the country home they established at Downe in Kent (Healey 2010, 199). The children followed their mother's Unitarian example in refusing to turn to face the altar during recitation of the creed (Keynes 2001, 115). Within Down House, they made music, like their mother, and went on to help their father with his experiments. But Charles himself participated less in their religious life and by his own account had ceased to believe in God by 1849: "disbelief crept over me at a very slow rate, but was at last complete" (Darwin 1969, 86). Despite reading a variety of recent interpretations of the Bible and its sources, he felt that the claims of Christianity were not supported by the evidence (Keynes 2001, 120). By contrast, his meticulous dissection and examination of living and fossil species was, at a similarly cumulative rate, convincing him of an alternative theory of creation.

The death from tuberculosis in 1851 of his daughter Annie at the age of just 10 came as a hammerblow. A week later, Darwin wrote a brief account of her life "as I think in after years, if we live, the impressions now put down will recall more vividly her chief characteristics" (Darwin 1985, 5.540–542). The eulogy movingly combines the expression of grief of the bereaved father with the scientific detachment and attempt to capture detail of the observant naturalist:

Her figure and appearance were clearly influenced by her character: her eyes sparkled brightly; she often smiled; her step was elastic and firm; she held herself upright, and often threw her head a little backwards, as if she defied the world in her joyousness. For her age she was very tall, not thin, and strong. Her hair was a nice brown and long; her complexion slightly brown; eyes dark grey; her teeth large and white. (ibid)

So began the decade that was to culminate in the publication of *The Origin of Species* in 1859. The long gestation of the work related partly to its sheer scale, representing the need to leave no available stone unturned in presenting an argument Darwin knew to be contentious. Darwin was conscious, too, of the impact on his wife and the believers among his circle of friends and relatives. *The Origin* barely mentions human evolution, let alone the interpretation of evidence for proposing it: this would emerge in his later work.

The eventual conceptual framework out of which the clarity of *The Origin of Species* emerged owed as much to the influence of farmers, pet breeders, and agriculturists as to biological theorists. The artificial selection they practiced provided a key insight into the potential of Darwin's theory of natural selection. Ever a practical man himself, capable of designing and building his own experimental resources in the garden of Down House, Darwin saw in the domestication of plants and animals a mechanism traceable in the natural world as species became shaped by the changing forces Lyell's geology revealed. Relating this to geographical distribution, as in the case of the Galapagos turtles and the finches whose unique characteristics were discerned in his laboratory by the ornithologist John Gould, enhanced the sense that speciation developed over time as organisms interacted with a particular environment. The mathematical model provided by Thomas Malthus – another Anglican clergyman – illustrated the means by which adaptation would favor the survival of those most fitted to their environment at the expense of the surplus it could not support (Ruse 2007, 9).

The theory of evolution – descent by modification – thus came to Darwin in a manner that paralleled the publication practice of contemporary novels by authors such as Dickens, whereby chapters appeared serially in magazines and the plot unraveled step by step: there was no opportunity to "look ahead" to future installments. Darwin and his closest circle were increasingly aware of the implications of his work but unsure of the impact of its dissemination. But science was beginning to replace religion in demonstrating ultimate causality (Ruse 2007, 9), and Darwin's

careful assembly of facts and cumulative argument were in danger of being gazumped by a journalistic whodunnit such as the 1844 publication on evolution by Robert Chambers. The more convincing and robust submission Darwin received from Alfred Russel Wallace in 1858 was what clinched matters, and Darwin shared with Wallace priority in the publication of the theory of natural selection.

As is widely known, the outcome was a counterblast from religionists, setting in motion the contrasting positions of science and creationism that continue to divide education and society in our own time. The model for this debate was the famous confrontation at Oxford between Bishop “Soapy Sam” Wilberforce and Darwin’s outspoken apologist Thomas Huxley. What is less well known is that Wilberforce (1860) had read the book in detail and brought out an extended review with Darwin’s own publisher, John Murray. The catalyst for Huxley’s withering condemnation was precisely that Wilberforce resorted to populist rhetoric in attempting to sway an audience less acquainted with what Darwin had actually written.

But the shorthand for Darwin’s theory, which we are descended from apes, became the principal image through which Darwin’s argument would be summarized. Benjamin Disraeli drew on this in a speech of his own in Oxford in 1863. As a Jew and thus a social outsider aspiring to high office within the traditionally closed community of the Tory party, Disraeli needed to position himself carefully in the eyes of the Bishops and the prevailing Anglican ethos of the two ancient universities. His own trope on Wilberforce’s remark was: “My Lord, I am on the side of the Angels” (Blake 1966, 505), an image later captured by the cartoonist Lalla Rookh (1874) with the caption *Paradise and the Peri*.

A social equivalent to the political competitiveness with which Disraeli had to contend is another common inference of Darwin’s theory of natural selection, one that conceals its author’s own personal interest in the relationship revealed in his later writing between human evolution and altruism. Spencer (1885) and Galton (1883) extrapolated versions of evolutionary thinking consistent with “survival of the fittest” –

Tennyson’s (1850) “nature red in tooth and claw” – and an interpretation applicable to ideas of social competition that in Galton’s case led to eugenics. By contrast, Darwin himself took a considerable interest in charitable work and the welfare of those less fortunate than himself, as well as in the cultures of the people of many different people he met on the *Beagle* voyage. His personal conscience aligned with that of his Wedgwood relatives’ strong stance against slavery, epitomized in the pottery cameo depicting a kneeling slave in chains with the slogan “Am I not a man and brother?” An indication of the enlightened political assumptions of the mature Darwin would be his organization of a letter arguing the need for political representation in South Africa to recognize the involvement of every citizen “without regard to color or race” (Darwin et al. 1877).

Darwin’s wide interests in several disciplines, both scientific and artistic, conferred the capacity for keen observation rendered in expressive language. His penchant for innovative connection permitted the imaginative leaps that exemplified his approach to the natural world, subsequently explained through carefully deduced logic. His liberation into religious “freethinking,” first through Unitarianism, thence agnosticism, and finally atheism, is inseparable from his questioning of prevailing authority. An example would be his noting of similarities in the appearance on the shoreline of sedimentary rocks in Tasmania and Tierra del Fuego, anticipating tectonic drift some 50 years prior to Wegener (Banks and Leaman 1999). Fittingly, his son George Darwin (1879) proposed on mathematical grounds the geological origins of the tides and their relationship with the moon; another son, Francis, went on to a Professorship in Botany while also pursuing a second career as a performer on historic wind instruments (Darwin 1914).

Darwin’s journey, from acceptance that his studies at Cambridge would lead to a life as a country parson to his becoming the leading scientist of his age and an icon of non-belief in divine creation, has left a legacy that resonates in evolutionary psychology today. His mentor William Paley’s presentation of the “argument from design” set up the conditions for which Darwin’s work provides the alternative. Paley (1802) asked

the reader to imagine the difference between encountering a stone while walking in the country and finding a watch on the ground. The latter requires us to accept that it:

... must have had a maker: that there must have existed, at some time, and at some place or other, an artificer or artificers, who formed it for the purpose which we find it actually to answer; who comprehended its construction, and designed its use. (Paley 1802, 6)

Paley's application of this conclusion to every complex structure in the natural world remains the basis of creationist argument in our own time and provided Richard Dawkins with the title *The Blind Watchmaker* (1986) of his guide to acceptance of the issue: "Darwin and Wallace solved it" (Dawkins 1986, xiii).

Two ironies emerge from the biographical and epistemological stories that are bound up in Darwin's legacy. The first is that the science of evolutionary psychology that descends from his theories of natural and sexual selection fully embraces a place for religion in the cultural development of *Homo sapiens*. The role of religion and the adaptive nature of spirituality inform work in the human sciences, art, music, and literature (Tylor 1871; Jung 1966; Lévi-Strauss 1966; Mithen 1996; Boyer 2001; Atran 2004; Pamcutt 2009; Lewis-Williams 2010). From an anthropological perspective, there need be no incompatibility between the application of evolutionary thinking and exploration of the origin and purpose of religion.

The second irony is that, contrary to his family's wish for Darwin to be buried in the country churchyard of his home, the public and political response to his passing favored his being laid to rest in Westminster Abbey with the full honors the state religion could afford (Ruse 2007, 2). There he lies, next to Isaac Newton, commemorated in a manner fitting to the scale of his achievement, if confusing to those who assume him to be an imposter in God's house.

Cross-References

- [Benefits of Commitment and Marriage](#)
- [Darwin's Education](#)

- [Emma Darwin](#)
- [Erasmus Darwin](#)
- [Marriage](#)
- [Religious Beliefs](#)
- [Religious Teachings](#)

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Darwin's Education

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Darwin's education, both at school and university, appears from a modern perspective to be surprisingly lacking in focused preparation for the scientific achievements that lay ahead of him. However, both his father and grandfather trained and practiced as doctors, and it was initially assumed that Charles would follow in their footsteps. His grandfather, Erasmus Darwin, combined his medical duties with philosophical and literary writings, including the two-volume *Zoonomia; or the Laws of Organic Life* (1794)

that embraced speculations about the evolution of life which must have been known to his grandson.

But education in the early nineteenth century largely comprised, in addition to mathematics, the translation and exegesis of Classical and biblical texts. Natural science, if studied at all, was engaged in a spirit of respect for the traditions of Greek philosophy and scriptural precedent. Attendance at church or chapel was as important as attendance at school, if a little less regular. Thus Darwin's earliest experiences included being taken by his mother to the Unitarian Chapel in Shrewsbury, though his mother died in 1817 when he was just eight, and he reported having very few memories of their time together, with the exception of a recollection of her, black-gowned, on her death-bed. Darwin's father thus brought up his young family as a widower, and proved a positive and respected influence on his son despite initial exasperation at the young Charles's apparent waywardness.

Lacking a mother, Charles developed a very close relationship with his older brother Erasmus, named for their grandfather. Five years older than Charles, Erasmus was the initially successful brother who followed the family tradition of studying medicine at Edinburgh and Cambridge and pursuing a career as a doctor. Charles later recalled Erasmus's influence with affection, including his leading chemistry experiments they set up together in the tool-house of their garden in Shrewsbury:

My brother Erasmus possessed a remarkably clear mind with extensive and diversified tastes and knowledge in literature, art, and even in science. For a short time, he collected and dried plants, and during a somewhat longer time experimented in chemistry ... He read much, even whilst a boy, and at school encouraged me to read, lending me books. (Darwin 1887, p. 12)

Charles first attended (1817–1818) a Unitarian day-school run by the Rev. G. Case, minister of the chapel that his mother had attended before her death. He later recalled: "I have been told that I was much slower in learning than my younger sister Catherine, and I believe that I was in many ways a naughty boy" (Darwin 1887, p.14).

Unitarianism was the denomination of his mother's Wedgwood branch of the family,

connection with which Charles was later to reestablish through marrying his first cousin, Emma. After his mother's death, Charles and Erasmus were baptized into the Church of England, possibly in order to remove some of the barriers to their future education that at that time nonconformism posed. The brothers went on to Shrewsbury School, one of England's august and historic private academies. Charles attended the school 1818–1825.

Charles's impressions of Shrewsbury School are vividly captured in his own words:

Nothing could have been worse for the development of my mind than Dr. Butler's school, as it was strictly classical, nothing else being taught, except a little ancient geography and history. The school as a means of education to me was simply a blank. During my whole life I have been singularly incapable of mastering any language. Especial attention was paid to verse-making, and this I could never do well. I had many friends, and got together a good collection of old verses, which by patching together, sometimes aided by other boys, I could work into any subject. Much attention was paid to learning by heart the lessons of the previous day; this I could effect with great facility, learning forty or fifty lines of Virgil or Homer, whilst I was in morning chapel; but this exercise was utterly useless, for every verse was forgotten in forty-eight hours. I was not idle, and with the exception of versification, generally worked conscientiously at my classics, not using cribs. The sole pleasure I ever received from such studies, was from some of the odes of Horace, which I admired greatly.

When I left the school I was for my age neither high nor low in it; and I believe that I was considered by all my masters and by my father as a very ordinary boy, rather below the common standard in intellect. To my deep mortification my father once said to me, "You care for nothing but shooting, dogs, and rat-catching, and you will be a disgrace to yourself and all your family." But my father, who was the kindest man I ever knew and whose memory I love with all my heart, must have been angry and somewhat unjust when he used such words. (Darwin, in Darwin 1887, p. 16)

At the age of only 16, in 1825, Darwin's father arranged for Charles to be admitted to Edinburgh University to study medicine. But the pursuit of medicine not to his liking: "The instruction at Edinburgh was altogether by lectures, and these were intolerably dull" (Darwin 1887, p. 17). After just 2 years of somewhat unfocussed studies

in Edinburgh, Charles transferred to Christ's College, Cambridge, with the assumption that he would prepare to become a vicar. Such a plan was by no means incompatible with his growing interest in natural history: some of the foremost natural scientists of the preceding generation and in his day, including Gilbert White, William Paley, William Whewell, and John Henslow, were ordained priests of the Church of England. All were to prove influential on the early career of Charles Darwin.

Time at Cambridge included attendance at Evensong in King's College Chapel and other musical events: "This gave me intense pleasure, so that my backbone would sometimes shiver" (Darwin 1887, p. 22). Darwin's interest in choral music was recalled with enthusiasm by his friend John Herbert, who was to present the young explorer with the microscope that served him so well on the *Beagle* voyage (Herbert 1832). Music was, by his own account (Darwin 1838; Stott 2003, pp. 75–76), to play a significant part in his choice of the pianist Emma Wedgwood as his wife. A clearer influence on Charles's future emergence as a scientist were the geology and botany field trips through which the hunter of his father's dismissive description began to acquire the observational skills and knowledge that were to serve him as an explorer. The process of Darwin's transformation into a serious scholar was nevertheless not immediate:

I was so sickened with lectures at Edinburgh that I did not even attend Sedgwick's eloquent and interesting lectures. Had I done so I should probably have become a geologist earlier than I did. I attended, however, Henslow's lectures on Botany, and liked them much for their extreme clearness, and the admirable illustrations[.] (Darwin 1887, p. 22)

The outdoor experiences that supplemented the dullness of the lecture theatre were what captured Darwin's imagination:

Henslow used to take his pupils, including several of the older members of the University, field excursions, on foot or in coaches, to distant places, or in a barge down the river, and lectured on the rarer plants and animals which were observed. These excursions were delightful. (Darwin 1887, p. 22)

Geological exploration under the guidance of Sedgwick was to follow, including a bracing trip to the mountains of North Wales.

The move towards a scientific focus commenced with small steps: "... no pursuit at Cambridge was followed with nearly so much eagerness or gave me so much pleasure as collecting beetles" (ibid.). The commitment to a scientific future essential to Darwin's selection for inclusion in the *Beagle* voyage began to take shape:

During my last year at Cambridge, I read with care and profound interest Humboldt's "Personal Narrative." This work, and Sir J. Herschel's "Introduction to the Study of Natural Philosophy," stirred up in me a burning zeal to add even the most humble contribution to the noble structure of Natural Science. No one or a dozen other books influenced me nearly so much as these two. (Darwin 1887, p. 24)

It was Henslow who made the initial connection that led to Darwin's opportunity to join the *Beagle* voyage as gentleman companion to the ship's captain, Fitz-Roy. The postgraduate pathway for a scientist was an uncertain one, probably to be followed in an amateur fashion alongside the study of Divinity. No such dedicated career path being available to him, the *Beagle* voyage could be viewed as Darwin's doctorate and post-doc rolled into one, both resulting in the opportunity to publish his immediate response to the encounters of the 5-year voyage and representing the basis for his lifetime's achievements in several fields.

Cross-References

► [Erasmus Darwin](#)

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Darwin's Principle of Divergence

► [Darwin on Speciation](#)

Darwin's Struggle for Life

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"Struggle for life" appears in the title of Darwin's epoch-making book, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859). However, Darwin also used "struggle for existence" in this and other writings. Both were used "in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny." Darwin's examples were clear:

"Two canine animals, in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a dearth is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which only one of an average comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The mistletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for, if too many of these parasites grow on the same tree, it languishes and die. But

several seedling mistletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the mistletoe is disseminated by birds, its existence depends on them; and it may metaphorically be said to struggle with other fruit-bearing plants, in tempting the birds to devour and thus disseminate its seeds. In these several senses, which pass into each other, I use for convenience sake the general term of Struggle for existence”.

Darwin then acknowledged his debt to the economist Thomas Robert Malthus' theory of human population growth inevitably pressing on the means of subsistence:

“A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase [...] As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdom; for in this case there can be no artificial increase of food, and no prudential restraint from marriage” (Darwin 1859, pp. 62–63).

Darwin's reading in Autumn 1838 of the 1826 edition of Malthus' *Essay on the Principle of Population* was a decisive step towards his theory of natural selection. Also Alfred Russel Wallace referred to Malthus as a source of inspiration for the theory of evolution he exposed in his essay “On the tendency of varieties to depart indefinitely from the original type” (Wallace 1858), a theory which impressed Darwin as bearing striking similarities to his own (but was not exactly the same: see Gayon 1998).

Words such as “struggle,” “battle,” and “war” had long been used when speaking of nature and human life, and were not uncommon in British social and political debates in the years before Darwin published his theory (Gale 1972). The philosopher and sociologist Herbert Spencer, who was to become the most popular philosopher of evolution of the late nineteenth century (and who later coined the phrase “survival of the fittest,” which Darwin adopted as equivalent to “natural selection”), described nature as pervaded by a “stern but beneficent discipline” preserving the species types by eliminating weak and unhealthy

individuals. He hoped that society would follow the same course, and that the improvident, lazy, and unable would be left unprotected by the State in a free-for-all competition (Spencer 1851).

By “war of nature” and similar expression, pre-Darwinian naturalists generally meant interspecific struggle, that is struggle between different species. Those who also considered intraspecific struggle, that is struggle between individuals of the same species, saw it as a factor of conservation, rather than transformation, of the species type: variations that were not “true” to it were eliminated (La Vergata 1990). By extending the meaning of “struggle,” Darwin emphasized the intricate network of relations between organic beings and between them and their environment, both physical and, above all, organic. This was the context in which natural selection operated, eliminating some forms while preserving others and favoring the accumulation of useful modifications along divergent branches. The most vocal supporter of Darwin in Germany, Ernst Haeckel, had exactly “all those complex interactions (*Wechselbeziehungen*) that Darwin indicates as the conditions of the struggle for life (*Kampf um's Dasein*)” in mind when he coined the word “ecology” in 1866 (Haeckel 1866: vol. I, 8, note; vol. II, 235–236, 286–287; 1878, p. 17).

Darwin's struggle for life ran contrary to the belief that a providential harmony, although ensured by apparently cruel means, reigned in the economy of nature, a view that had found its most well-known expression in the Swedish naturalist Carl Linnaeus. At the end of the *Origin*, Darwin warned the reader lest he forget that behind the beautiful scenery of a “tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth,” there raged “the war of nature, [...] famine and dearth,” from which “the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows” (1859, pp. 489–490).

Being an anthropomorphic metaphor, the struggle for life was easy to transfer (or re-transfer) to human affairs and to apply to social and political discourse. Darwin himself

used the phrase in the pages of *The Descent of Man, and Selection and Relation to Sex* (1871) in which he dealt with human races and “natural selection in civilized nations,” for instance, to explain the success of white colonizers all over the world (and of English colonizers of Canada over the French), and the decadence of nations and races which were “left behind in the struggle.”

Application of the struggle for life to individuals within society and/or to nations or races (the two terms were often used interchangeably) was a key element of the very complex phenomenon called “social Darwinism.” There were many, even contrasting varieties of it: individualistic, nationalistic, racist, even socialistic, depending on political biases and on which level of the struggle each author considered crucial for the progress of mankind. Others, however, appealed to Darwin’s own theory, in *The Descent of Man* (1871), on the origin of human morality in the social instincts of animals. They argued that mutual aid and cooperation were much more important factors in evolution, animal as well as human, than rivalry and aggression. The most well-known of these authors was the Russian anarchist Pëtr Alekseevič Kropotkin, who in his *Mutual Aid* (1904) rejected the description of nature as a “gladiatorial show,” to use the words of Thomas Henry Huxley (1888), Darwin’s main supporter in Britain. Anti-individualistic interpretations of the struggle for life became popular among socialists, especially in Germany and Russia (Kelly 1981; Todes 1989). In France, the idea prevailed that struggle did play a role in evolution, but it took place not between individuals but between groups of organisms and their environment – an “*association pour la lutte*” against adverse conditions, as the biologist and politician Jean-Louis de Lanessan (1881) called it. Most French biologists disliked Darwin’s natural selection acting on “spontaneous,” or “chance,” variations and preferred to think that the environment directly induced inheritable adaptations.

Karl Marx and Friedrich Engels criticized Darwin’s struggle for life on the grounds that it was imbued with class ideology. They praised Darwin for giving “the death blow to teleology”

but reproached him for accepting Malthus’ doctrine, which they hated. Writing to Engels in 1862, Marx found it “amusing” and “astonishing” how “Darwin recognises among beasts and plants his English society with its division of labour, competition, opening up of new markets, ‘inventions’ and the Malthusian ‘struggle for existence’ (*Kampf ums Dasein*).” “It is” – he went on to say – “Hobbes’ *bellum omnium contra omnes*, and it reminds one of Hegel’s *Phaenomenology [of Mind]*, where bourgeois society features as ‘the spiritual animal kingdom’, whereas in Darwin it is the animal kingdom that features as the bourgeois society.” Engels agreed: “Darwin did not know what bitter satire of people and particularly his fellow countrymen he was writing when he showed that the free competition and the struggle for life, which economists celebrate as the highest historical achievement is the normal condition of animal life.” Marx ridiculed the “ignorance and intellectual laziness” of those who claimed “to subsume the whole history under one great law of nature” – that is, struggle for life used as a “mere phrase” – “instead of analysing how the struggle for life manifests itself historically in different, particular forms of society.” Engels criticized the “infantile trick” by which the bourgeois view of society was first transferred by Darwin into the natural world and then re-transferred to society by bourgeois ideologists. “In this case” – he added – “the struggle for life merely consists in the productive class taking on the direction of production and from the hands of the class to which it has so far been entrusted, but which has by now become incapable to do it; and this means the socialist revolution” (Marx and Engels 1956-: vol. 30, pp. 249, 324; vol. 32, pp. 685–686; vol. 34, p. 170).

“Struggle for existence” and the like became popular catchphrases, and many biologists themselves ignored Darwin’s warning and took them in the most narrowly literal sense. For instance, the French physiologist, pioneer of serotherapy and eugenicist Charles Richet, Nobel prize winner for 1913, repeatedly wrote that in the “*combat pour l’existence*,” an “unceasing, relentless, merciless fight,” victory went to “the most able, the best armed, the most

numerous,” to wit, the “strongest,” that is the “best.” “Those that succumb deserve to succumb,” as “their inferiority explains, justifies and legitimises their being crushed.” A “primordial law dominates nature,” by which “the strong annihilate the weak, and the big eat the small;” it exacts “fratricidal struggles, ruthless fights, prey eaten alive, slaughter, massacre, suffering, illness, famine, savage death.” Richet believed that an “endeavour after life” (*effort vers la vie*) was the essence of the living being and the main cause of evolution and of “constant progress” (La Vergata 2018).

Especially in Protestant countries, Darwin's struggle for life was seen as further, decisive evidence and scientific confirmation that nature ensured progress – physical, moral, and spiritual – through overall strife, effort, endeavor, and self-help. It was generally believed that there was a continuity between biological evolution and human progress. However, it was also generally agreed that in the course of human evolution, the literal struggle for life slowly but increasingly took on the form of a competition of ideas, abilities, habits, and customs. Some went as far as saying that the meaning of the entire process lay in the “ascent of man” from a primordial hell to refined spirituality culminating in the “struggle for the life of others” (Drummond 1894), or in the triumph of “evolutionary love” (Geddes and Thomson 1889). But nature's lesson was clear: life must be strenuous (Thomson 1909).

The catastrophe of the Great War put an end to the equation of evolution and progress through struggle. The development of population genetics and the synthesis of Darwinism and Mendelism in the 1930s and 1940s, as it were, de-literalized and de-Malthusianized the struggle for existence by reformulating fitness in terms of gene frequencies and differential survival of variations. The struggle was, generally speaking, no longer considered as a cause of natural selection. Natural selection occurred whether or not resources were scarce. What mattered was that there were differences of fitness within a population (Gayon 1998; Radick 2003). The development of ecology, and the subsequent rethinking of competition and cooperation among organisms, did the rest.

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Darwin's Theory on Language Evolution

► Early Theories of Language

Darwinian Ethics

► Dangers of Evolutionary Ethics

Darwinian Gastronomy

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Synonyms

Cuisine of the fittest; Evolved food preferences;
Naturally selected seasonings

Definition

An evolutionary hypothesis for the culinary use of spices based on their antimicrobial properties.

Introduction

In their 1999 article, Paul W. Sherman and Jennifer Billing summarize their findings on the global patterns of spice use by humans and how country and regional differences in spice use may provide support for the hypothesis that, ultimately, spices are used to reduce foodborne illness and food poisoning.

The article is an extension of a review published in 1998 (Billing and Sherman 1998). It starts with a brief definition of *spice*, which is not a botanical category but a culinary term used to refer to various plant products sourced from different types of woody shrubs and vines, trees,

aromatic lichens, and roots, flowers, seeds, and fruits of herbaceous plants. Next, based on a survey of traditional cookbooks (93 books from 36 countries), the authors report the patterns of spice use in 4578 meat-based recipes across the globe. Vegetable-based recipes were less frequent in the sampled cookbooks and significantly less spicy than meat-based recipes (Sherman and Hash 2001). Finally, the authors show how differences in patterns of spice use between countries and within countries are correlated to temperature and may serve as evidence for their evolutionary explanation for this culinary practice. In addition to their obvious effect on food flavor, color, and palatability – the proximate explanation for the use of spices – the authors put forward an ultimate explanation based on the properties of the phytochemicals found in spices.

The Antimicrobial Hypothesis

Most of the “secondary compounds” found in spices are part of the defense repertoire of plants against predators, parasites, and other biological enemies. Since many of these, like bacteria and fungi, also attack meat and other food items, Sherman and Billing suggest that humans use spices to prevent foodborne illnesses and food poisoning. To support their antimicrobial hypothesis, the authors then present the evidence to satisfy five predictions:

Prediction 1: *Spices should exhibit antibacterial and antifungal activity.* Phytochemicals extracted from spices have been amply tested. All 30 spices – for which laboratory test results were available – killed/inhibited at least 25% of the bacterial species on which they were tested. Half of the spices tested killed/inhibited at least 75% of bacterial species, and four spices (garlic, onion, allspice, and oregano) killed every bacterium tested.

Prediction 2: *Use of spices should be greatest in hot climates, where unrefrigerated foods spoil especially quickly.* Considering all 36 countries sampled, mean annual temperature ranged from 2.8 °C to 27.6 °C (37.04–81.68 °F).

Within this range, as average temperatures increased among countries, significant increases were found in the proportion of recipes that called for at least one spice, the mean number of spices per recipe, and the number of different spices. Significant increases were also found when considering only spices with high inhibitory activity ($\geq 75\%$ bacterial activity inhibited).

Prediction 3: *A greater proportion of the bacteria should be inhibited by recipes from hot climates than from cool climates.* The mean proportion of traditional meat-based recipes that called for each highly inhibitory spice increases as mean annual temperatures increase. A positive significant correlation was also found between the number of bacterial species inhibited by each spice and the number of countries that use that spice. Although data on the local assembly of bacterial species of each country were not available, when considering 30 widespread bacterial species, the fraction of food spoilage bacteria inhibited by the spices used in each country also increased significantly in hotter climates.

Prediction 4: *Within a country, cuisine from high latitudes and elevations (i.e., cooler climates) should contain fewer and less potent spices than cuisine from lower latitudes and elevations.* Limited evidence was found for this prediction since regional cookbooks were available only for China and the United States. However, in both countries the total number of spices used, the number of recipes that included at least one spice, and highly inhibitory spices were greater in southern (hot) regions than in northern (cold) regions.

Prediction 5. *Quantities of spices called for in recipes should be sufficient to produce antimicrobial effects, and cooking should not destroy the potency of phytochemicals.* Despite the lack of data on the antimicrobial activity of spices in situ, the concentration of spices used in cooking are within the range (i.e., 30–2000 $\mu\text{g/ml}$) of the reported minimal concentrations of phytochemicals that were necessary to inhibit bacterial growth in vitro. In addition, most phytochemicals are

thermostable, although a few are destroyed by heat. The authors speculate that this could explain why spices like garlic, pepper, rosemary, and onion are added at the beginning of the cooking process, whereas others like parsley and cilantro are added near the end to prevent any loss in taste/effect.

Spices as Drugs

Many individual spices and blends have been used as medication to counteract a broad spectrum of conditions including impotence, dysentery, kidney stones, and high blood pressure. However, Sherman and Billing argue that the culinary use of spices differs from its medical use in three ways. On average, spices are included in very small quantities, to specific recipes, and are not correlated to the health status of the dinners. These differences would suggest that the targets of spice chemicals are on or in the food before it is consumed.

Alternative Hypothesis to Explain Spice Use

Sherman and Jennifer Billing also consider how well their spice use data fits into other, apparently proximate, explanations for this culinary practice. They concede that their finding that recipes from hotter places more frequently included spices, and more pungent spices, is consistent with the idea that spices are used to disguise the taste/smell of spoiled foods as food spoilage is faster and more frequent in hotter climates. However, they argue that this *disguise hypothesis* is flawed because it ignores the potentially strong negative effects, sometimes fatal, of ingesting contaminated food.

A second proximate alternative explanation inquired is that spicy foods are preferred in hot climates because they increase perspiration and help thermoregulation. The generality of this hypothesis, however, is limited since only a few spices, like chili, can cause sweating and does not contribute to explain the spice use in different temperatures. Furthermore, the human body

already has physiological mechanisms to regulate the organism temperature as needed.

Finally, Sherman and Billing consider three alternative ultimate explanations. The first is that spices, being difficult to obtain (expensive, rare, or both), could be used as honest signals of wealth and social status. A profligate use of spices would be possible only for wealthy or highly ranked individuals. Although this hypothesis could apply to rare spices with very restricted ranges, it does not explain the positive correlations between spice use and temperature and the patterns of use of common spices. In addition, Sherman and Billing draw attention to the fact the rarest spices tend to be used in the tropics, where they are endemic and often cheap. The second ultimate hypothesis is that spices supply chemicals that, in low concentration, have beneficial effects (e.g., micronutrients, antioxidants) other than inhibiting foodborne bacteria and fungi. The authors argue that the generality of this hypothesis, however, is also limited. Even if the phytochemicals found in spices like garlic, onions, and cloves can modulate metabolism and reduce free radicals, most spices do not have these properties. Moreover, it does not explain the positive correlations between spice use and temperature. Finally, Sherman and Billing consider the null ultimate hypothesis that spice use may not confer any benefits, other than enhancing food flavor. If this holds, they argue, spice use patterns should correspond to the local availability of spice plants. The relatively long history of spice trading and the extensive use of spices (e.g. pepper) in countries where they do not grow, however, suggest that the effect of local availability may be limited. The lack of correlation between the number of countries in which each spice plant grows (naturally or cultivated) and the number of countries in which it is used is presented as further evidence that the use of spices is not regulated by its local availability.

Origin of Spice Use

As an attempt to answer the question of how did spice use begin, Sherman and Billing hypothesized that people started using spices due to

their appealing flavors or possible digestive or vermicial effects. As a consequence families that created the habit of using spices would face food poisoning and suffer from foodborne illnesses less frequently than families that did not use spices, especially in hot climates. Additionally, spice-using families would have been able to store foods for longer, increasing their protection against energy shortages, a great advantage during periods of food scarcity. Observation and imitation of the culinary habits of these healthier families could have provided a fast way to disseminate spice use through societies.

Eventually, however, new microorganisms would immigrate, or local bacteria and fungi would evolve resistance to the local spices, and food would be potentially unsafe again. To solve this problem, and to circumvent newly learned food aversions, a different spice or set of spices could be added to the recipe. Over time, due to iteration of this process, the number of spices per recipe would increase, especially in climates favorable to microorganisms, where foods spoil rapidly. Consequently, spice synergism and variability could provide new antimicrobial benefits and improve the palatability of food again, helping to reinforce the conditioning between spicy dishes and safe foods.

Conclusion

Sherman and Billing collected evidence to support their hypothesis that humans seize the defensive compounds used by plants and put them to similar use in cooking, making food safer for consumption. Over time, our coevolutionary race with foodborne pathogens lead to a significant increase in the variety of spices used per recipe, particularly in hot places. In sum, the use of spices essentially contributes to the health, survival, and fitness of individuals and, hence, should be understood within an evolutionary perspective.

Cross-References

- [Antimicrobial Hypothesis, The](#)
- [Climate and Use of Spices](#)

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Darwinian Medicine

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Synonyms

[Evolutionary medicine](#); [Evolutionary mismatch](#); [Risk of illness](#); [Variation in disease risk](#)

Definition

Darwinian medicine can be defined as the application of principles of evolutionary theory in medical research and clinical practice. It utilizes and synthesizes various theoretical models and research from a variety of disciplines, including psychology, psychiatry, physiology, genetics, behavioral and health sciences, and anthropology. Symptoms or impaired functioning might represent evolved responses or, contrariwise, the absence of successful adaptation to a certain environmental factor. Accordingly, putting illness, diseases, or pathophysiological mechanisms in the evolutionary perspective can be helpful to understand the origin and significance of the symptoms and may provide some indication to deciding whether to offer symptomatic relief or not.

Introduction

Medicine is based on human biology, and biology at any organizational level can only be fully understood in view of evolutionary processes. Theory of evolution and related model provide a unifying and integrating framework for all biological processes and functions. Correspondingly, the knowledge of evolutionary processes contributes to a more comprehensive understanding of human biology, health, and diseases (Williams and Nesse 1991). Medical education and practice focuses largely on *proximate* causes, that is, pathological processes or anatomical distortions causing a disease, to develop diagnostic procedures and to promote therapeutic advances. Considering the *ultimate* aspects, namely, the evolutionary mechanisms which formed biological processes affecting the risks of developing a disease or the protective functions to avoid an illness, can be a significant addition to current models and practices in medicine (Stearns et al. 2010). The evolutionary framework can provide a more profound understanding of health problems or resilience, because it requires to analyze the ecological factors affecting the individual. Examining the effects of physical and social environment and other factors (i.e., ecological context) in regard to illness or health is a significant contribution to a more comprehensive view of why individuals get sick (Nesse and Williams 2012). However, Darwinian models of medicine do not state that diseases are caused by evolutionary processes, rather that these mechanisms alter the risk of developing symptoms or disease. Moreover, it is plausible to assume that multiple evolutionary mechanisms influence individual risk of illness (Gluckman et al. 2016). Simultaneously operating selection processes create trade-offs in adaptive systems or traits, and as a consequence, there will be inevitable restrictions in adaptive functions. This can be considered as one source of human vulnerability to illness.

Basic Principles of Darwinian Medicine

Analyzing the ultimate causes of diseases requires another perspective and the utilization of explanations on another level. The fundamental principles of evolutionary mechanisms have to be applied in medical models to gain more insights and new ways to interpret or understand pathological mechanisms or to better understand health and illness.

Most importantly, it has to be recognized that selective mechanisms benefit characteristics, which enhance the *inclusive fitness* of the individual. Survival and reproduction are the key elements of fitness suggesting that evolutionary processes do not promote health or longevity directly (Williams and Nesse 1991). Living longer or healthier might be advantageous in a more indirect way: increased period of parental investment can secure that the offspring reach maturity and its reproductive period. In biological context, resources are limited and not available for every individual. Consequently, the most vital task faced by all individuals is to successfully utilize resources (e.g., energy, time, etc.) toward survival and reproduction. Characteristics determining these trade-offs are the central elements of the individual *life history strategy* (also called as life history traits). Life history (LH) traits specify the patterns associated with survival and reproduction of the individual: growth, development, mating behavior, parental investment, and aging (Kaplan and Gangestad 2005). There are two significant environmental factors with essential impact on life history trade-offs: *unpredictability and harshness* (Ellis et al. 2009). These environmental factors reflect the availability of resources, morbidity-mortality rates, and the predictability of change of environmental factors. Mortality and morbidity up to the reproductive age were shown to be more impactful on inclusive fitness than age-specific fertility (Jones 2009).

The second key principle of evolutionary medicine is to clarify that beyond some single gene effects, the evolution of humans (i.e., phylogeny) and the individual developmental path (i.e., ontogeny) do not cause illness directly.

Evolutionary processes affect health rather in shaping individual susceptibility to certain diseases in particular environments (Gluckman et al. 2011). For example, to be exposed to a virus does not necessarily result in an actual illness, which is principally caused by the virus compromising the immune defense. Former infections can stimulate the immune system to protect the individual against subsequent similar infections. This *immunization* process is therefore context-dependent, which highlights the importance of environmental circumstances in adaptation.

This is the third major basic element of evolutionary models in medicine: most of the human characteristics are adaptive responses to challenges our ancestors faced in evolutionary past. However, human environment changed significantly and rapidly; thus, we face evolutionary novel conditions. The speed and extent of these changes challenges evolved human capacities (biological, physical, and psychological) and enhances disease susceptibilities (Nesse and Williams 2012). In the majority of human evolutionary history, individuals lived in small groups and changed their residence periodically leading to a diversified diet. This lifestyle enabled humans to be exposed more briefly to lower density of pathogens compared to modern individuals, living a more settled lifestyle mostly in densely populated areas boosting the risk of illness (Stearns et al. 2010).

These core principles help to understand and utilize Darwinian models in medicine and can provide a more comprehensive understanding of health-illness-related mechanisms in humans. Nevertheless, another significant contribution of the evolutionary perspective to medical education and practice is to highlight possible patterns how adaptive traits may lead to a disease or incapacity (Nesse and Stearns 2008).

The Effect of Evolutionary Environments on Disease Risk

As pointed out earlier, both the physical and social environments changed rapidly through *cultural*

evolution. Basic biological processes determining our traits and capabilities were adapted to different environments from our actual conditions. These *evolutionary* novel *environments* possess challenges to the individual and exceed their evolved capacity to adapt (Gluckman et al. 2011, 2016). For example, animal husbandry and agriculture transformed human lifestyle making individuals live in a more settled way. The proximity of each other and the animals together with the relative immobility increased the intensity of pathogen loads and made humans to be more susceptible to diseases. Other technical innovations (e.g., development of canals, means of transportation) enable parasites or toxins to travel long distance and be distributed in populations, where natural immunization did not occur in regard of these pathogens (Williams and Nesse 1991).

Another example of evolutionary environmental effects on health are *life history traits*. As discussed above, these factors form traits and behavioral strategies in order to maximize inclusive fitness of the individual. Resource scarcity necessitates decisions about resource expenditure (i.e., trade-offs) between actual and future reproduction or between to support offspring and rather to produce another (Kaplan and Gangestad 2005). The peak of investment in development (e.g., maturation, physical capabilities) and health-related functioning (e.g., repair functions, cellular and molecular maintenance) is selected to be utilized during the reproductive period and will be reduced in later life. Prolonged life span implies a longer post-peak reproductive period and a higher risk for illness or dysfunctionality in older age. Reduced ability to overcome infections or trauma and regeneration together with the aggregated harming effect of stress and exposure to pathogens for a long time period can cause disease or dysfunctionality. Health problems in the middle and older ages (e.g., osteoporosis, atherosclerosis, arthritis, neurodegeneration, and cognitive decline) can be characterized with similar features suggesting that these are the inevitable consequences of longevity (Gluckman et al. 2011, 2016).

Adaptions with Disadvantages

Evolved defense processes protecting the body against certain infections or toxins may become inappropriate or excessive and become potentially harmful for the individual. Adaptive biological responses of the body (e.g., pain, fear, or fever) are suppressed or unrealized until activated by the presence of threatening stimuli (e.g., toxins, environmental cues, or viruses). These regulation mechanisms are advantageous in situations where the energetic costs of activation do not exceed their benefits (e.g., health protection). However, defense processes can be activated in situations where they are less beneficial or even unnecessary and became detrimental. For example, fever – one of the most frequent accompaniments of infections – can be considered as a significant antibacterial reaction activating immune responses, but highly elevated fever for an extended time period can increase morbidity (Nesse 2005; Stearns et al. 2010).

A second pathway how adaptations may become disadvantageous is the *coevolution* of humans with microbes. Our body includes several symbiotic relationships with bacteria, microbiota, in particular in the gastrointestinal tract. Recently, it is increasingly recognized in medicine that the examination and interpretation of these mutual relations is important to better understand human health. On the other hand, there are numerous adverse pathogenic organisms our microbiome fighting against in an evolutionary arms race. The consequences of the biological relationship with the microbial world are mainly formed by the rapid generation time of these organisms, leading to an accelerated evolution of these creatures compared to humans. Quicker development and shorter life span enable the production of multiple generations in a shorter time period, creating the opportunity for pathogens to outcompete human defense mechanisms. For example, the intensive use of antibiotics is suggested to trigger the selection of resistant strains, and at higher rates of antibiotic cures, these strains can spread at high frequency and increase the risk of illness (Nesse and Williams 2012).

Evolutionary “design” compromises can be considered as another pathway of adaptive processes with possible pathological accompaniments. For example, the well-known case of the appendix can suitably illustrate this phenomenon: this small blind part of the human digestion system has no function anymore, but it was important in the evolution of the primate clade. The exclusively vegetarian diet required a much extended gastrointestinal track to provide a longer digestion time and to enable the adequate extraction of essential nutrients from the food. Humans still have the appendix despite the fact that it is superfluous and potentially dangerous (an infection leads to appendicitis), because to be selected out, the appendix is needed to shrink, which inherently stimulates appendicitis (Nesse and Williams 2012).

Evolutionary Selection Mechanisms Creating Adversities

In accordance with life history traits, it is plausible to suggest that harmful mutations affecting the health during the reproductive period should be selected out of the population (Jones 2009). Nevertheless, some recessive forms of diseases can be found at an increased frequency within the population, which suggest the effect of *balancing selection*. Types of selective processes referring to balancing selection can be accounted for maintaining higher frequencies of different alleles in the gene pool of a population. The main reason for this is if the heterozygous genotype represents a fitness advantage compared to the homozygote form (Gluckman et al. 2011, 2016).

Sexual selection is suggested to be essential in the evolution of many human anatomical features and gender differences. *Sexual dimorphism* in human traits and characteristics is represented by the shorter life expectancy and higher mortality of men compared to women. These differences can be understood as a result of sexual competition and mate-seeking: successive competition for a mate implies greater fitness payoffs for men. Characteristics enhancing mating success

also influence health: for example, higher level of testosterone can be advantageous in competition with other men (due to the increased body mass and aggressive behavior) but has some deteriorative effects in suppressing immune responses, making the individual more prone to infections (Gluckman et al. 2011, 2016).

More recent human history has also health-related consequences: *assortative mating* (homogamy) can result in a magnified prevalence of mutations within a population, which can be considered rather infrequent in other communities. This mating pattern (a certain form of sexual selection) is driven by similarity: individuals with similar phenotypes (e.g., body size, skin pigmentation, or age) mate with one another with a higher probability than random and increases the rate of genetic relatedness within the family (Gluckman et al. 2011, 2016).

Conclusion

Models of Darwinian medicine allow a broader range of explanation and interpretation of disease-related risks and have therefore implications for medical interventions and public health. However, to improve the comprehension of these models, gene-environment interaction selection processes and combination of gene-environment interactions should be examined in detail. Evolutionary medicine has overlapping domains with other contemporary evolutionary studies. Accordingly, to the further development of this research agenda, the diverse domains have to be integrated, and a new synthesis of medical practice and ultimate mechanisms is needed.

Cross-References

- ▶ [Darwinian Medicine and Survival Problems](#)
- ▶ [Evolutionary Medicine](#)
- ▶ [Evolutionary Mismatch](#)
- ▶ [Evolutionary Psychiatry](#)
- ▶ [George C. Williams \(Founder of Darwinian Medicine\)](#)

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Darwinian Medicine and Survival Problems

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Synonyms

Evolutionary medicine; Life expectancy;
 Longevity; Somatic maintenance

Definition

Darwinian medicine is the application of evolutionary principles to health and disease. In many instances, natural selection favors adaptations that improve the survival of individuals. In other occasions, however, natural selection can favor adaptations that have a negative impact on the survival, health, and well-being of individuals.

Introduction

One of the most striking features of living organisms is that they appear to have been designed for a purpose. A natural explanation of this phenomenon eluded scholars for centuries until the mid-nineteenth century, when Charles Darwin provided a solution to the problem. By carefully comparing different populations, their ecology, and geographical distribution, Darwin discovered that the appearance of design in living organisms is the product of a process he called evolution by natural selection (Darwin 1859). Natural selection sorts out the genetic variants that exist in populations of living entities; it weeds out those variants that are detrimental to the fitness of organisms but retains those that are beneficial. Because parents pass their genetic information on to their offspring, the beneficial variants slowly increase in frequency (Frank 1998). After thousands of generations, adaptations will accumulate in the population and organisms will appear as if they have been designed (Dawkins 1976).

This relentless Darwinian evolutionary process produces organisms with an extraordinary capacity to exploit resources, which they use to construct body parts and develop behaviors that improve their chances of survival and reproduction. Thermal insulation, binocular vision, and bipedalism are just a few examples of adaptations that allow organisms to outcompete their rivals in the constant struggle for survival. In some cases, however, organisms hold characteristics that work against their best interests but serve the interests of others. Honeybees body plan includes stings that they deploy in suicide missions against predators to protect their colonies. Ground squirrels are

willing to risk their lives to alert their social partners of a threatening predator (Trivers 1985). From a Darwinian perspective, such self-harming traits and behaviors are difficult to explain. William D. Hamilton, in his theory of inclusive fitness, provided the solution to this puzzle. He discovered that costly traits that increase the reproductive success of social partners can nevertheless evolve when these partners are close relatives and therefore share copies of their genes (Hamilton 1964). Thus, a trait can be favored either by increasing the reproductive success of its bearer (i.e., direct or Darwinian fitness) or by increasing the reproductive success of its bearer's relatives (i.e., indirect fitness). These two additive fitness components constitute the *inclusive fitness* of an individual, which is the target of natural selection.

Evolutionary theory thus answers a fundamental question regarding the purpose of organismal design: Organisms are designed to maximize their inclusive fitness. This principle of adaptive evolution has important consequences for the understanding of human health and disease. Our bodies contain copies of genes that increased the inclusive fitness of our ancestors, even if these copies predispose us to disease, misery, and decrepitude (Stearns and Medzhitov 2016). In other words, traits and behaviors that improve our ability to survive and reproduce can also have a negative impact on our physical and mental health. Natural selection solves the problem of survival and reproduction, not the problem of disease, happiness, or well-being.

Much of an organism's fitness depends on its ability to survive. Organisms need to fight off diseases, defend themselves against enemies and predators, while at the same time, maintain homeostasis, somatic integrity, and delay body deterioration. Because organisms can only access a finite amount of energy, they are unable to maximize all these functions simultaneously (Stearns 1992). Investment in one function can compromise investment in another function, and reproduction often has a negative impact on survival. Pregnancy can leave mothers susceptible to diseases, and maternal death during childbirth is not uncommon. Larger body size has survival and

health benefits but sometimes investment in the immune system compromises growth and adult body size. These and other constraints on organismal design often leave us susceptible to disease and poor health.

Survival, Life History, and Kin Selection

Before exploring the main ideas surrounding the problem of survival in evolutionary biology and Darwinian Medicine, let us first analyze the core concepts of adaptive evolution, which can be more precisely defined using the language of mathematics.

In mathematical terms, fitness is the maximand of natural selection. That is, traits that increase fitness will spread throughout the population, while traits that reduce fitness will tend to vanish from the population. While differences in fitness cause adaptive evolutionary change, not all evolutionary change occurs because of variation in fitness, where evolutionary change is defined as change in gene frequency. An important case of nonadaptive evolutionary change occurs because of class-effects. Class-effects happen when individuals find themselves in different conditions, and they occur in a vast array of scenarios. For instance, some individuals are born in privilege while others in poverty; some individuals are born females while others are born males; and some individuals are young while others are old. These differences in individual quality (or condition) matter for the calculation of fitness, which captures differences in the genetic make up of individuals, rather than differences in their quality or condition. For instance, the genes of individuals that are born in privilege may increase in frequency because of their privileged condition, even if their genes are inferior to the genes of those born in poverty. Thus, a general mathematical formulation of fitness needs to take the condition of individuals into account.

Let $w_i \rightarrow_j$ be the contribution of a class- i individual to the class j . To make the argument clearer, let us consider, for instance, that class represents the age of each individual. Then, when an age- i individual survives, its contribution

to the age- $i + 1$ class will be $w_i \rightarrow i + 1$. When an age- i individual gives birth to offspring, then its contribution to the age-1 class will be $w_i \rightarrow 1$. In this particular case, “class” represents the age of an individual, but “class” can be any other feature of an organism and its surroundings, such as body weight or number of social partners. The general equation that describes the fitness of an individual, denoted by w , is then given by:

$$w = \sum_i^{\omega} u_i \left(\sum_{j=1}^{\omega} w_{i \rightarrow j} v_j \right) \quad (1)$$

where u_i is the frequency of class- i individuals in the population, ω is the maximum age of an individual, and v_j is the reproductive value of a class- j individual (Frank 1998). Reproductive value is an asymptotic measure of fitness and is defined as the contribution of an individual to the gene pool of future populations (Frank 1998).

It is worth considering the specific case when classes represent the age of individuals. Assuming a stationary population, Eq. (1) can be written as:

$$w = \sum_{i=1}^{\omega} l_i f_i \quad (2)$$

where f_i is the fecundity of an age- i individual and l_i is the probability that the individual survives to age- i . Equation (2) tells us that an organism can increase its fitness either by improving its fertility rate, i.e., f_i , or by improving its survival, i.e., l_i . Further, because organisms are less likely to be alive at older ages, selection will act less strongly at older ages. This has implications for the type of genes that evolve in populations. For instance, genes that improve reproductive performance at age 20 (i.e., higher f_{20}) may be favored by natural selection, even if these genes have a detrimental effect of similar magnitude at age 45 (i.e., lower f_{45}). This type of selection regime may underlie the evolutionary origin of many later-life diseases, including cancer and other noncommunicable diseases, as we shall see in more detail below.

The analysis of social behavior is usually done through the lenses of Hamilton’s rule (Hamilton 1964), which is the condition that determines whether a social trait will increase in frequency. Hamilton’s rule partitions fitness into a direct and

an indirect component. The direct component gives the effect of the behavior on the personal fitness of the actor, while the indirect component gives the effect of the behavior on the personal fitness of the actor’s social partners. Hamilton’s rule follows directly from Eq. (1) and in its simplest form is given by:

$$-c + br > 0, \quad (3)$$

where c is the fitness cost of the behavior to the actor; b is the fitness benefit enjoyed by the recipient; and r is the relatedness between the actor and the recipient. The behavior will evolve if the condition holds. Hamilton’s rule allows us to classify behaviors into four types, depending on the sign of the fitness costs and benefits, as follows: if $c > 0$ and $b > 0$, the behavior is said to be altruistic; if $c < 0$ and $b > 0$, the behavior is said to be cooperative; if $c < 0$ and $b < 0$, the behavior is said to be selfish; and if $c > 0$ and $b < 0$, the behavior is said to be spiteful. Relatedness plays a pivotal role in the evolution of social behavior because it determines the value of benefits. All else being equal, the higher the relatedness between the actor and the recipient, the higher the probability that altruism evolves. This has an impact on the environmental and social conditions that favor the survival of individuals, as we shall see below.

When studying survival problems, it is useful to consider a different formulation of Hamilton’s rule:

$$-v_A C + v_R B r > 0, \quad (4)$$

where C is the survival cost of the behavior to the actor; B is the survival benefit enjoyed by the recipient; and v_A (or v_R) is the reproductive value of the actor (or recipient). This formulation of Hamilton’s rule highlights the importance of reproductive value to the evolution of social behavior. Lower (or higher) values of an actor’s reproductive value favor altruistic (or harming) behaviors. Lower (or higher) values of a recipient’s reproductive value favor harming (or altruistic) behaviors towards the recipient. Reproductive value gives a measure of individual

quality, and this quantity is especially relevant to the understanding of survival-related behaviors (Rodrigues 2018).

Forms of Survival

Traits that improve our survival prospects come in different forms. Although we can classify traits in many different ways, it is useful to classify them according to whether they are more or less flexible (Stearns 1992). At one end of the spectrum, we have traits that are constitutively expressed. That is, they vary little with environmental conditions. They can be expressed throughout the entire life of an individual, but their expression can also be limited to a certain age range, and they may depend on a few genes. Other traits, called plastic traits, depend on the environment. The capacity to adjust traits as a function of the environment is denominated phenotypic plasticity. Structural body size, for instance, largely depends on the nutritional intake between infancy and late adolescence. A common pattern in nature is that poor nutrition leads to smaller adult body sizes while good nutrition leads to larger adult body sizes. Traits like structural body size are plastic but irreversible. Once the growth period of an organism ends, structural body size becomes a permanent characteristic of the individual. The process that gives rise to these traits is called developmental plasticity. Other traits, by contrast, are reversible, and therefore, they show more flexibility. They may be temporary responses to environmental factors or to the state of individuals. Sun tanning, for instance, occurs whenever an individual is exposed to sunlight but fades as soon as the external stimulus ceases. Finally, some traits, such as behavioral responses, can be even more flexible, and they allow individuals to quickly react to changes in their physical and social environment.

Below, we will describe some of the adaptations that improve human survival. We will start by considering traits that are constitutively expressed. We will then describe how phenotypic plasticity allows us to cope with the challenges of the environment. We will consider developmental

plasticity but also behavioral traits, where we will emphasize kin selection. Finally, we will describe how psychological traits and decision-making processes provide a first barrier against pathogens and other threats, and how they can mediate behavioral and physiological responses.

Constitutive Traits

Many of our survival adaptations are built-in. That is, they are constitutively expressed, and therefore, they depend little on the environment. In some cases, it is possible to identify the genes that underlie these traits and mutations that disrupt their normal expression can lead (or predispose us) to disease. In this section, we illustrate how constitutive traits influence human survival, their function, and their impact on fitness.

Resistance to malaria is one of the most well-studied constitutive human traits. Malaria is an infectious disease caused by the *Plasmodium* parasite, which is carried in the saliva of insects – the vector – and injected into the red blood cells of humans – the host. Because the *Plasmodium* parasite targets red blood cells, the genetic variants that confer resistance to malaria, such as sickle cell or thalassemia, usually affect the shape of these cells. These genetic variants are not widespread among the human population. Instead, they predominantly occur in sub-Saharan Africa. Evidence that these genetic variants are adaptations that evolved through the selective pressure of the *Plasmodium* parasite is diverse, and it includes population genetics and physiological studies as well as statistical analysis of demographic parameters.

First, detailed genome-wide analysis has found a strong correlation between the frequency of the variants and the geographical areas where malaria is endemic, with a negligible presence of the variants outside these areas (Jallow et al. 2009). Further, statistical analyses of these populations have revealed that the mortality rate of infants and children that carry the genetic variants is significantly lower than the mortality rate of those who do not carry the variants (Aidoo et al. 2002). Moreover, blood tests found a lower density of parasites in children with the genetic variants (Komba et al. 2009).

While these studies show that the genetic variants that confer resistance to malaria can provide multiple benefits, they are not widely spread among the human population for good reasons. The benefits of resistance carry significant costs. For instance, the sickle cell form of resistance to malaria modifies the shape of red blood cells, which increases the risk of anemia (Rees et al. 2010).

Constitutive traits have also allowed human populations to extend their diet range. This has enabled humans to move into new ecological niches or to improve their ability to survive and adapt to changes that persist in the environment. The recently acquired evolved capacity to drink milk after infancy illustrates this scenario. The domestication of cattle and other animals and the advent of dairy farming had a dramatic and lasting impact on the environment of human populations (Durham 1992). Domesticated animals could be used as working animals and as a source of meat but at the same time, they also made milk readily available to humans. Until the domestication of animals, milk was only part of the diet of infants and young children, and it depended on breastfeeding. After weaning, no other reliable source of milk was available, and humans would lose their ability to process milk. These conditions changed with the domestication of animals, after which milk became available across the entire lifespan of an individual. Genetic mutations that allow humans to digest milk beyond childhood, a phenomenon called lactase persistence, have since spread in the human population. The rate at which lactase persistence has increased in frequency since it first emerged in the human population suggests that this trait is under strong selective pressure (Tishkoff et al. 2007).

Constitutive traits also protect humans against infectious diseases. The human immunodeficiency virus (HIV) was one of the most devastating infectious diseases in the late twentieth century. Prior to the discovery of a new generation of drugs, HIV infection was in most cases a death sentence. For a vast majority of the population, the life expectancy after an HIV positive diagnosis was limited to a few years. In a few rare cases, however, individuals were shown to be resistant to

HIV. The virus utilizes receptors to bind to and infect white blood cells. Individuals that are resistant to the virus carry a mutation that inactivates these receptors (Heeney et al. 2006).

Genetic variants have also allowed humans to expand their geographic range. For a vast majority of human populations, living in high-altitude Tibet and Andes would be nearly impossible. At high altitude, oxygen density is extremely low, and therefore, without acclimatization, high altitude is often fatal to humans. These adverse conditions, however, have not prevented populations of Tibetans and Andeans to live at high altitude. Genetic and physiological analyses have shown that these populations have several adaptations that enable survival at such high altitudes. Physiological analyses, for instance, have shown that Andeans have a higher blood flow, a mechanism that allows them to survive at high altitude (Gluckman et al. 2016).

We have seen how genetic variants allow individuals to improve their odds of survival, either by becoming resistant to infectious diseases, by increasing their diet range, or by allowing them to explore new ecological niches and environments. These variants often come at a cost and therefore they may also predispose humans to diseases.

Phenotypic Plasticity

Let us now turn the attention to traits whose expression depend on the environment. We will first consider traits that become fixed after early-life development (i.e., irreversible traits), and we will then consider flexible (or reversible) traits, where we will focus on kin selection and social behavior.

Developmental Plasticity

Early-life environmental conditions can impact later-life survival and susceptibility to disease. One of the most well-known cases of this phenomenon has been extensively documented in analyses of the Dutch famine cohort (Lumey et al. 2007). Typically, when individuals share identical environmental conditions, they are expected to express similar phenotypes. Thus, it is intriguing when individuals sharing the same

environmental conditions exhibit significant amounts of phenotypic diversity. This was the puzzling observation that motivated many of the Dutch cohort studies (Lumey et al. 2007). First, scientists found that the Dutch population showed a significant amount of variation in the incidence of noncommunicable diseases, such as diabetes or obesity. Second, they found that this variation did not show any apparent correlation with their current environments. High incidence of noncommunicable diseases was eventually traced back to the early-life conditions of the affected individuals. Individuals that were in utero when their mothers fell victim to the Dutch famine because of the German siege were significantly more likely to develop noncommunicable diseases later in life (Roseboom et al. 2006). Why detrimental conditions during early-life development affect later-life susceptibility to disease remains a major question and the subject of much discussion. There are two main hypotheses for an evolutionary explanation of this phenomenon.

The first hypothesis requires the anticipation of later-life conditions (Gluckman et al. 2005). It assumes that individuals use their early-life environment to predict their later-life environment. Individuals can then anticipate their later-life environment and prepare for it in advance by developing phenotypes that are adaptive in the predicted environment. For instance, let us imagine that higher reproductive rate is adaptive in harsher environments. If individuals are born in harsh environments, then the hypothesis predicts that they should develop physiological aspects of their phenotypes that facilitate higher reproductive rates later in life. There is, however, a problem with this mechanism. If there is a mismatch between early- and later-life environments, then individuals will end up expressing a phenotype that is suboptimal in their later-life environment. Thus, this hypothesis requires a strong correlation between early- and later-life environments. In the context of health and disease, later-life ill health would then be explained as a phenotype-environment mismatch that contributes to high levels of susceptibility to noncommunicable diseases later in life.

The second hypothesis proposes that early-life environment constrains the phenotype of individuals (Monaghan 2008). More specifically, early-life hardships constrain the range of phenotypes that individuals can develop, the best of which are still subpar. Under such scenario, later-life diseases do not occur because of a mismatch between early- and later-life environments but because of developmental constraints. Individuals born in poor conditions are simply making the best of a bad job.

It is still unclear which of these two hypotheses best explain abnormal levels of noncommunicable diseases among the Dutch cohort, and the significance of predictive adaptive responses in general. Comparative studies in animals provide little evidence for adaptive predictive responses to early-life environments (Uller et al. 2013), and a statistical analysis of a pre-industrial Finish population found no support for adaptive predictive responses (Hayward et al. 2013).

Behavior and Kin Selection

While our own genes and phenotypes are crucial for our survival, in many occasions, we rely on others to survive. During infancy, we rely on parents: they provide physical protection, nourishment, a cozy environment, and they even contribute to the development of our immune system. Such devotion of parents towards their children evolves for very good reasons: there is a one in two chance that parental genes have a copy located in the genome of offspring. Transmission of genes between parents and offspring aligns their interests, and therefore, parents are willing to provide substantial amounts of care to their children (Hamilton 1964). However, when we explore the repercussions of this argument further, we encounter a darker side of human behavior. As individuals become less and less related, the incentives for cooperation subside, and incentives for aggression may even creep in. This gradient of behavior as a function of relatedness can be seen in multiple aspects of our social lives. Frequently, both the nuclear and extended family are composed of highly related individuals, and therefore, most of the times, youngsters experience

harmonious interactions with those around them. In some cases, however, the composition of families departs from this kin-based structure, and when unrelated individuals are present, violence is more likely to break out (Daly and Wilson 1988).

Detailed statistical analyses have shown that the presence of stepparents increases the risk of violence towards young children, with Data showing, for instance, that the mortality rate of infants is higher when a stepparent is present (Buss 2019). Alongside kinship, there are several other factors that play an important role in the social lives of youngsters. For instance, the age and marital status of mothers has been shown to have an impact on the mortality of infants and children. Infants born to single young mothers are more likely to perish (Daly and Wilson 1988). Two underlying factors may contribute to this outcome. First, younger mothers have a longer reproductive life ahead of them, and therefore, they will have plenty of opportunities to become mothers again, which means that they “value” their current offspring less than older mothers. Second, the absence of a partner may impose additional economic and social stresses that compromise the survival of the offspring.

Parents are the main caregivers of infants and offspring, but grandparents also fill an important role. Grandmaternal care of offspring is intrinsically connected to an almost unique human trait: menopause. Menopause makes human life history trajectories significantly different from those of our closest relatives, such as the bonobos and chimpanzees. Female chimpanzees, for instance, reproduce until old age and therefore do not experience menopause. This suggests that the family lives of humans have undergone important changes since we first diverged from our most recent common ancestor. The most common evolutionary explanation for menopause is based on the evolution of grandmaternal care (i.e., the grandmother hypothesis; Hawkes et al. 1998).

The evidence for the grandmother hypothesis is diverse. While the average inter-birth interval of chimpanzees is 5–6 years, in humans it is 3–4 years (Galdikas and Wood 1990). Shorter inter-birth intervals allow humans to have babies

at a higher rate, and grandmothers may have been instrumental for this transformation. Research has shown that grandmothers collect food items that children are unable to collect, and food gathered by grandmothers constitutes an important part of a child’s diet (Hawkes et al. 1997). Further, a review of the literature has shown that the presence of grandmothers reduces the mortality rate of infants (Sear and Mace 2008). These and other findings strongly suggest that reproductive senescence (i.e., menopause) in humans is an adaptive trait that is associated with the redirection of a grandmother’s resources towards their grandchildren.

Above we have seen how kin selection explains some of the variation in human behavior. High relatedness explains parental and grandparental care of infants, children, and adolescents. Low levels of relatedness explain neglect, aggression, violence, and crime. As a result, family and group composition have an important impact on the survival of all individuals, but especially on those that are most vulnerable, such as infants and children.

Psychology, Decision-Making, and Survival

So far, we have seen how constitutive traits, developmental plasticity, and behavior all influence the survival of individuals throughout the course of their lifespans. Although organisms would certainly not survive without these adaptations, in many instances, the first line of defense is encoded in the brain.

Psychological traits are the first line of defense against predators, toxins, pathogens, as well as other aspects of the environment that threaten the lives of individuals (Buss 2019). Negative emotions and feelings like fear, anxiety, or disgust help us avoid dangerous substances or situations. Anxiety may work as an alert system that signals the presence of predators or aggressive conspecifics. Disgust may caution us against potential sources of viruses and pathogens. Positive emotions and feelings such as happiness, hope, or excitement can also improve our own survival prospects as well as the survival of our friends and relatives. Feelings of courage and love towards daughters and sons fill the lives of many mothers and fathers and are crucial to enact the

behaviors that improve the survival of these offspring.

The evolutionary biology of psychological traits is difficult to test. However, a growing number of experimental studies have been able to provide important insights about the adaptive role of psychological traits. Disgust, in particular, has been the focus of much attention. It has been shown that sensitivity to disgust increases during pregnancy (Buss 2019). In a web-based survey, researchers found that disease-relevant images were rated as more disgusting than disease-irrelevant images. Further, they found that female disgust sensitivity was higher than male disgust sensitivity across all ages, and bodily fluids of relatives were reported to be less disgusting than those of strangers (Buss 2019). These findings lend some support to the idea that disgust is a psychological trait that is involved in the avoidance of sources of pathogens.

Decision-making plays a crucial role in our survival. Our decision-making system is composed of different subsystems, which include emotions, feelings, instincts, intuitions, memory, and reasoning. These processes and states occur both at the conscious and subconscious levels, and they interact with perception during decision-making. The cognitive system works in conjunction with the physiological system and physiology can override our cognitive system. For instance, under severe nutritional deprivation, our physiological system shuts down the ability to conceive (i.e., amenorrhea). When resources become available and food intake increases, the reproductive system is turned on again, and the cognitive system takes over the decision-making processes that affect childbearing.

Our decision-making and perceptual systems are the product of natural selection, and therefore, they are designed to further our fitness. As such, they are particularly sensitive to fitness costs, and they often seek to minimize large survival costs, even when this leads to a higher rate of decision-making errors or to perceptual errors. For instance, when people are located at the top of a height, individuals can overestimate vertical height by as much as 29% in relation to a scenario where they are located at the bottom of the

height (Buss 2019). The perceptual error makes sense from an evolutionary perspective. Underestimating such height could lead to large costs due to injury, and it could even lead to death. In general, our decision-making and perceptual system tend to exaggerate features of the environment that can impose large survival costs.

Our decision-making system is highly contextual, and small changes in the environment can have a large effect on our behavior. For instance, when asked to assess others, people take into account subtle features of our environment, such as ambient darkness. In a darker environment, people tend to emphasize negative stereotypes. In a well-lit environment, by contrast, people tend to disregard negative stereotypes (Schaller et al. 2003). Cooperation and reciprocity are also highly sensitive to environmental conditions, in general, and to social environment, in particular. In a public goods game, the presence of a pair of “watching eyes” increases the contributions of individuals to a public good (Bateson et al. 2006). Most of these decision-making processes occur at the subconscious level. When participants are deciding the value of their contribution to the common good, they are not consciously and explicitly thinking: “if there is a pair of watching eyes, then I will make a more substantial contribution to the public good.” Likewise, when people are rating others, they are not explicitly making the calculation: “if it is dark, then rate your neighbors more negatively.” Despite occurring at the subconscious level, these decision-making mechanisms probably have an adaptive basis. A pair of watching eyes may be a cue for policing, which is probably an ancestral mechanism to enforce cooperation in small hunter-gatherer groups. Further, it is naturally more difficult to ward off an attack in darker places, a factor that may trigger an alert mechanism, which in the particular case of the aforementioned study may assume the form of negative stereotyping.

We have seen how our psychology and decision-making system are designed to improve our survival, rather than to provide an accurate description of reality. This explains why we exaggerate some features of the environment (e.g., height), why we exaggerate the intent or

personality of other individuals (e.g., aggressiveness), and why we are prone to errors (e.g., improve survival, but increase error rates). We have also seen how our psychology and decision-making system are highly contextual, how little changes in the environment can lead to significant changes in behavior, and how multiple subconscious cognitive processes contribute to our decision-making. This has implications for evolutionary approaches to public health, as we shall see below.

Survival and Medicine

Identifying and understanding the adaptive function of traits is a core objective of evolutionary biology. This understanding can be extremely powerful when applied to health and disease. Diseases have multiple effects on human bodies, and therefore, they are often described and diagnosed by a suite of symptoms and signs. Typically, symptoms are the target of medical treatment, either because they are seen as undesirable effects of a disease or because they are identified as the cause of the disease. In some occasions, however, symptoms can be the body's evolutionary response to disease. Thus, the treatment of symptoms that are identified as "undesirable," when they are in fact body adaptations to fight off disease, can aggravate the state of the patient.

There are some case studies in which the targets of medical interventions have now been shown to be a body's response to fight disease. Lower levels of iron have been typically seen as a homeostasis problem, and therefore, the target of medical therapies with the aim of restoring the homeostatic levels of iron. Recent findings, however, should caution us against this view. For instance, the growth of some pathogens and parasites depends on iron. Without iron, pathogens' growth rate slows down or stops altogether. Thus, increasing the availability of iron in the bloodstream can actually lead to an increase in the growth rate of the pathogen and therefore aggravate the disease (Gluckman et al. 2016). Fever is another symptom that has typically been the focus

of medical therapy. However, fever may be a strategy to fight off disease. Certain pathogens show lower replication or survival rates when temperature is raised, even if this is just by a few degrees (Gluckman et al. 2016). Thus, mild fever can lead to faster recovery times. In sum, an evolutionary perspective on disease can alter medical practices and ultimately improve the health and survival outcomes of medical interventions.

Implications for Public Health

The integration of evolutionary biology and public health is still in its early stages, and therefore, some progress is still needed to develop a fully functional evolutionary approach to public health. This barrier between the two fields arises because they emphasize different dimensions of human lives. Evolutionary biology aims to uncover the ultimate causes of human behavior and how they evolved in our ancestral environment. These studies are based on the main principle of natural selection, which states that individuals are fitness-maximizing agents, and therefore, they do not rely on principles of rationality or agency. On the other hand, public health researchers seek to promote health-related behaviors in the context of modern environments. This research program emphasizes human rationality and agency as the main drivers of behavioral change, and it does so within the constraints of the current social and cultural context.

Bridging this gap will require further interdisciplinary studies. Directly importing knowledge from one field to the other does not work. For instance, our ancestors lived in a low-calorie environment, and therefore, obesity was virtually absent throughout human history. However, proposing such low-calorie ancestral environment as a public health intervention to curb the current levels of obesity is certainly not an option. On the other hand, public health interventions often seek to raise awareness about the long-term consequences of health-compromising behaviors, with the aim of promoting the benefits of healthier behaviors. These lifestyle changes in behavior often assume rationality. However, as we have

seen above, rationality can be at odds with the evolutionary drivers of the targeted behavior, which perhaps explains the low efficacy of theory-based public health interventions (e.g., Kinmonth et al. 2008). Applying evolutionary biology to public health interventions thus requires a detailed analysis of how adaptations evolved in our ancestral environment, but also how they play out within the context of current physical, social, and cultural environments.

It is clear that human-driven environmental, social, and cultural changes often have long-term and unforeseen consequences for public health. Piped water, sewerage, and other technologies have reduced infant, child, and overall mortality to unprecedented levels, which contributed to an increase in life expectancy. At the same time, the means of production and distribution over the past few centuries have improved substantially, which has led to a shift from a low- to a high-calorie environment. These transformations have had positive but also negative effects on human health. While they caused a rapid decrease in the incidence of communicable diseases, they also caused a dramatic rise in the prevalence of non-communicable diseases (Corbett et al. 2018). The introduction of contraception has increased the number of menses per lifetime, which in some Western populations is three times more than in natural-fertility populations. This may have contributed to an abnormal increase in the incidence of later-life cancers (Gluckman et al. 2016). These problems are difficult to understand with current approaches to public health, which are often short-sighted, focus on single populations, and do not consider the evolutionary history of traits and populations. Evolutionary biology puts these problems in a broader evolutionary and historical context. Comparative studies allow us to assess the ancestral form of traits and therefore understand why these traits cause ill health in modern environments. Contraception, obesogenic environments, and fewer sources of mortality create a mismatch between our ancestral and current environment that leads to exaggerated and unhealthy forms of traits, a factor that underlies novel epidemics and diseases. This evolutionary understanding of the historical development of

diseases can provide new insights and suggest novel approaches to public health interventions.

An important theoretical tool that can be used to guide public health interventions is life history theory (Stearns 1992). Life history theory can predict the impact of environmental changes on population-wide traits, including health-related traits. Because of its predictive power, life history can caution us against our own cognitive and cultural biases, which sometimes underlie the failure of public health interventions (Kahneman 2011). Cognitive biases, such as the reverse naturalistic fallacy, can skew public health interventions that, despite their virtuous goals, can end up having unfortunate consequences for public health. This can be illustrated with a recent development initiative in Ethiopia. The goal of the initiative was to reduce the energetic expenditure of mothers in rural Ethiopia in order to improve the overall well-being in the community. This, however, had unintended consequences for infant malnutrition, which is already one of the major health problems in Ethiopia as well as in many other African countries. Unfortunately, the development initiative may have aggravated this problem. A statistical analysis of the population after the intervention revealed an increase in birth rate (Gibson and Mace 2006). If more babies are born, then, all else being equal, each baby will be less well nourished. From the perspective of public health researchers and others, the outcome of the initiative may be puzzling. Why, in some instances, would mothers and families inadvertently adopt a behavior that could harm their offspring? From an evolutionary perspective, however, there are circumstances under which this outcome is expected. As we have seen above, the target of natural selection is individual fitness, not well-being. Maternal or paternal fitness is sometimes maximized when more babies are produced, even when this carries a cost to each individual baby. This evolutionary trade-off between offspring number and offspring quality may explain the unintended, and unfortunate, consequences of the intervention. These outcomes could be cautioned if interventions include an evolutionary assessment.

Lifestyle diseases represent some of the most important and debilitating diseases in Westernized societies. To same extent, these diseases depend on the decisions and behavior of individuals regarding their diet and other health-related factors. Thus, the success of many public health interventions depends on the capacity to promote behavioral changes in societies. It is now well understood that small changes in the environment can drive significant behavioral change. Work on behavioral economics, experimental psychology, nudge theory, and cognitive sciences have shown that human decision-making deviates significantly from the rationality assumption that characterizes many studies of human behavior. This work has shown that humans can heavily discount future costs, that human decision-making often relies on heuristics, and that perception is often context-dependent. It is also becoming clear that evolutionary theory can provide a unifying explanation for these findings. In particular, many of these cognitive biases can be understood as mechanisms designed to minimize current survival costs at a cost to error rates and future survival or reproduction. Thus, evolutionary theory can provide a systematic method for identifying aspects of the environment that can lead to effective behavioral changes in the context of public health interventions. For instance, public health interventions that focus on the long-term benefits of behavioral change are less likely to be successful than public health interventions that focus on short-term benefits.

An important evolutionary concept that should be taken into account in the design of public health interventions is the idea of mismatch. As we have seen above, behaviors depend on several decision-making systems, on our perception, and on mechanisms that are tailored to solve specific problems. This cognitive apparatus works remarkably well in modern environments, despite having evolved in our ancestral environment. In some cases, however, there is a mismatch between our evolved problem-solving mechanisms and modern environments. In our ancestral low-calorie environment, a taste for sugar and fat

were crucial to prevent death and ill health during periods of nutritional deprivation. In a modern high-calorie environment, however, this problem-solving mechanism contributes to the ongoing obesity and diabetes epidemic. In evolutionary parlance, there is a mismatch between our evolved decision-making mechanisms and our current environment.

Because our decision-making system is designed to improve survival, an understanding of specific problem-solving mechanisms can lead to novel public health interventions. Further, we can apply evolutionary models to understand the population-level and long-term impact of public health interventions. To illustrate these points, let us consider the scheduling of reproduction, which is a major evolutionary problem of medical significance, and includes some of the most important decisions faced by men and women during their lifetime. Both man and women need to decide when to have the first baby, how many they should have, and the interval between each baby. At first sight, this is an extremely complex problem, as many factors can potentially affect these decisions. From an evolutionary perspective, however, there are a few key parameters that should mediate these decisions. In particular, life history theory predicts that reproduction should depend on extrinsic mortality, infant mortality, the cost of each offspring, maternal age, resource availability, food insecurity, and on several other factors (Stearns 1992). Indeed, a worldwide statistical analysis has shown that life expectancy alone can predict as much as 68% of the variation in age at first birth (Low et al. 2008). This finding, among others, strongly suggests that mothers take local mortality into account during their decision-making process. Still unknown, however, are the specific mechanisms that are driving such decisions. It may well be that multiple environmental and social cues shape our perception of mortality, such as crime rate, the health status of neighbors, local news, and others. Nevertheless, identifying these mechanisms is a crucial step towards the design of novel

evolutionary-based public health interventions. Decreasing the indicators of mortality rates can lead to a delay in motherhood, an improvement in education, and to many health benefits that these behavioral changes entail, both for mothers, families, and offspring.

Evolutionary biology can also help us identify mechanisms of survival, and this can be used to inform public health interventions. For instance, one can co-opt the neural circuits that mediate grandparental care. As we have seen above, later-life survival is thought to have evolved because of grandparental care. Thus, mechanisms that are associated with grandparental care are likely to trigger the expression of mechanisms and processes that affect later-life survival. For instance, bringing children and elders together may stimulate the neural circuits involved in the survival of elders and thereby improve their health and longevity. Some evidence supports this hypothesis. A statistical analysis of a contemporary population (i.e., the longitudinal Berlin Aging Study) has shown that the mortality hazards of grandparents that provided childcare were 37% lower than those that did not (Hilbrand et al. 2017). One can also hijack the mechanisms involved in the evolution of cooperation and reciprocity, such as familiarity (de Waal et al. 2008). For instance, writing more personal letters seems to improve the response rate of individuals. This may be because personal letters activate the neural circuits associated with reciprocity and cooperation, and therefore, people may feel compelled to respond more to personal letters than to impersonal letters (Scott and Edwards 2006). This approach can be used to improve the response rates of medical surveys and screening programs.

Conclusion

Natural selection favors those traits that increase the fitness of individuals. Over evolutionary time, this process leads to the accumulation of adaptations in the population and the appearance of organismal design. To a large extent, the fitness

of organisms depends on their ability to survive, and therefore, many adaptations are geared towards this purpose. Organisms need to find food, protect themselves against enemies and predators, and fight off parasites and pathogens while maintaining body homeostasis and somatic integrity. These traits are often mediated by psychological traits and decision-making processes, which constitute the first line of defense against pathogens, predators and other sources of mortality. Survival, however, is not always aligned with fitness, the primary target of natural selection. In such cases, survival can be compromised, and this can predispose organisms to disease and ill health. An understanding of adaptive survival mechanisms to fight off diseases can improve medical interventions. Moreover, an understanding of evolved survival mechanisms can elucidate the behavioral responses of individuals to environmental changes, which can be used to improve the efficacy of public health interventions.

Cross-References

- [Adaptation](#)
- [Darwinian Medicine](#)
- [Evolutionary Psychology](#)

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Darwinian Psychiatry

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Synonyms

[Ethological psychiatry](#); [Evolutionary psychiatry](#);
[Evolutionary psychopathology](#); [Psychiatric Darwinism](#)

Definition

A wide variety of hypotheses about the function and evolution of mental disorders.

Introduction

The Dutch ethologist Niko Tinbergen (1963) famously argued that to understand why organisms behave as they do, one needs to ask four different kinds of question. Firstly, *causation* questions are about the physiological mechanisms involved in causing a particular behavior. Secondly, *development* questions relate to the role of the behavior in the organism's ontogeny. Thirdly, *function* questions are about the adaptive value of the behavior, that is, its contribution to the organism's survival and reproduction. Finally, *evolution* questions relate to our understanding of the behavior's phylogeny, that is, the history of its changes throughout evolutionary time. The first two kinds of question are often bundled as proximate questions, while the latter are called ultimate or evolutionary questions.

Tinbergen's taxonomy can also help us make sense of the wide variety of research questions and explanations in the history of psychiatry. Biological psychiatrists have always asked questions about the causation of dysfunctional behaviors and mental states, hoping to find

answers in our DNA, our brain, or our blood. Others have taken a rather developmental perspective, identifying the internal (e.g., regression) and external (e.g., trauma) factors involved in developing mental illness. Mutations, brain abnormalities, antibodies, and traumas are all examples of *proximate* causes of mental disorders.

It is much less known, however, that many psychiatrists have also engaged with *ultimate* questions about mental disorders. In fact psychiatrists have been asking such questions since evolutionary theories became known. In recent years, research about the function and evolution of these illnesses has been brought together as "evolutionary psychiatry" or "Darwinian psychiatry." This entry opens with a brief history of Darwinian psychiatry. It then critically discusses four of its explanatory models of mental illness. Finally, it considers Darwinian psychiatry's relevance for both psychiatric practice and psychiatric research.

A Brief History of Darwinian Psychiatry

In the past 150 years, many psychiatrists have been tempted to put evolutionary theories to use in their efforts to understand and explain various aspects of mental disorders. Most of the initial attempts were based on now-outmoded "evolutionisms," such as Lamarckism and degeneration theory. Later attempts drew upon developments in orthodox Darwinian theory, such as ethology and the modern synthesis. From the 1990s onward, the latter attempts are collectively referred to as "Darwinian psychiatry" (McGuire and Troisi 1998) or "evolutionary psychiatry" (Stevens and Price 1996), while the former have been labeled as "psychiatric Darwinism" (Adriaens and De Block 2010). This section discusses two examples of each of these two strands in the history of Darwinian psychiatry.

Some contemporary Darwinian psychiatrists have credited Sigmund Freud as one of the founding fathers or pioneers of their discipline (e.g., McGuire and Troisi 1998, vii). Freud was indeed indebted to all sorts of biological theories of the day. In his posthumously published *A*

Phylogenetic Fantasy (Freud 1987 [1915]), for example, he attempted to link up our ancestor's vicissitudes during and immediately after the last Ice Age with our present day vulnerability to a series of mental illnesses. In his view, today's phobias bring back our ancestors' overwhelming fear when confronted with the privations of the Ice Age. Critics, however, have greeted Freud's evolutionary hypotheses with jeers, exposing them as textbook examples of the pervasive influence of Lamarckism and recapitulationism (or Haeckel's so-called biogenetic law). Freud has indeed always held on to these theories, and, openly so, considering his belief in "use inheritance" and the "biogenetic law" as "an audacity that cannot be avoided" (Freud 1939, p. 100). In this sense, Freud's evolutionary work fits in with psychiatric Darwinism, rather than with Darwinian psychiatry.

At the end of the nineteenth and the beginning of the twentieth century, Freud certainly wasn't the only scientist to consider regression, both in ontogeny and in phylogeny, as a key theme to understand mental illness. Darwin himself also believed that mental illness constituted some kind of regression to more primitive stages of human evolution, with psychiatric patients closely resembling children, "savages," and human ancestors in being able to experience the purity of emotions. In *The Expression of the Emotions in Man and Animals* (1872, p. 245), he approvingly quoted the British psychiatrist Henry Maudsley, saying that mental disorders are "a faint echo from a far-distant past, testifying to a kinship which man has almost outgrown." Darwin also expressed the view that emotions were based on involuntary and habitual actions which may or may not be, or have been, useful to the organism. Remarkably, in *The Expression* he discussed this usefulness mainly in terms of a Lamarckian use inheritance, rather than in terms of natural selection. It would be fair to say, then, that Darwin himself, like Freud, was a psychiatric Darwinist, rather than a Darwinian psychiatrist.

By contrast, contemporary Darwinian psychiatry originates in a series of theoretical developments in early twentieth-century evolutionary theory, including ethology and the modern

synthesis. The latter was itself in fact a series of syntheses – of Darwin's theories with Mendelian genetics, and of the resulting population genetics with other biological disciplines, such as ecology – resulting in a solidification of evolutionary theory. One of the many innovations of the modern synthesis was Theodosius Dobzhansky's theory of balancing selection. In the 1930s he noted that natural selection often maintains different alleles at a specific locus in our DNA, despite the fact that some of them are deleterious, and he hypothesized that natural selection favors heterozygotic forms because they are better at surviving and reproducing than homozygotes.

In the 1950s, geneticists substantiated Dobzhansky's hypothesis by revealing a trade-off between sickle cell anemia and malaria resistance in people of African and Mediterranean descent. The elegant logic of this case soon proved to be very inspiring in the realm of psychiatry. In 1964, biologist Julian Huxley collaborated with Ernst Mayr and two psychiatrists to hypothesize that schizophrenia may well confer some hidden fitness advantages to the relatives of patients suffering from schizophrenia, thus explaining how this heritable and highly prevalent disorder managed to escape natural selection (Huxley et al. 1964). The bottom line of their case was indeed that schizophrenia should be considered as part of a trade-off, in which it is somehow connected with an important adaptive trait.

Another school in contemporary Darwinian psychiatry reaches back to comparative ethology and the work of Konrad Lorenz and Niko Tinbergen. One of its seminal papers also dates from the 1960s, when the young psychiatrist John Price claimed, along Freudian lines, that many of today's mental disorders were in fact adaptive mechanisms in the social environment of our ancestors, enabling them to cope with the exigencies of a strict social hierarchy (Price 1967). Depressive symptoms, for example, would be excesses of behaviors related to a fall in that hierarchy. Price argued his case with a series of observations about similarities between human depressive disorder and the behavior of low-ranking hamadryas baboons and long-tailed macaques. The work of John Bowlby and

Harry Harlow belongs to the same tradition of ethological psychiatry, inspiring a number of psychiatrists in the later decades of the twentieth century to try to understand mental illnesses by relating them to analogical behaviors in non-human animal species as diverse as birds, reptiles, marsupials, and monkeys.

Darwinian Psychiatry's Explanatory Models

The distinction between psychiatric Darwinism and Darwinian psychiatry relates not only to a difference in the nature and validity of the evolutionary theories underlying them, but also to a difference in focus, where psychiatric Darwinists, including Darwin himself, had very little interest in functional accounts of (the mental states underlying) mental disorders. It was only with the advent of the modern synthesis that evolutionary scientists started to wonder why natural selection seems unable to eliminate genes involved in the etiology of mental disorders, given that many of these disorders are harmful to an individual's fitness and given that they are much more common than Mendelian disorders. Unlike the latter, mental disorders have frequencies that cannot easily be explained by means of a concerted action between mutation and selection (Keller and Miller 2006).

So how should we explain the occurrence and persistence of common, harmful, and heritable mental disorders? In answering this question, many Darwinian psychiatrists have followed some kind of (explanatory) adaptationist logic, assuming that adaptation (or complex design) is what needs to be explained in biology because it is simply the most interesting aspect of the evolutionary process (Lewens 2009). However, there are many ways to be an adaptationist about mental disorders. This section discusses three common adaptationist explanatory models in contemporary Darwinian psychiatry, contrasting them with a fourth and decidedly non-adaptationist explanation (for a more comprehensive overview of the many types of explanatory models in Darwinian psychiatry, see Faucher 2012, or De Block and Adriaens 2011).

The most controversial adaptationist explanatory model in Darwinian psychiatry is that mental

disorders are not disorders or dysfunctions at all. Rather, they ought to be considered as adaptations that, like all adaptations, have been spread over the population by natural selection because they confer some reproductive advantage to their bearers. Such adaptationist hypotheses have been and are still being defended in the literature today, particularly in relation to depressive disorders. Edward Hagen (1999), for example, has hypothesized that women affected by postpartum depression may signal that they are suffering an important fitness cost, either because they lack paternal or social support or because their newborn baby is in bad health. In this view, postpartum depression would be a bargaining strategy, enabling women to negotiate greater levels of investment from others.

Other researchers have proposed similar hypotheses for other mood disorders. Forty years after his seminal paper, for example, John Price teamed up with other psychiatrists and continued to argue that typical depressive symptoms, such as a loss of appetite and excessive ruminating, may have been designed by natural selection to signal yielding in a fierce social competition that cannot be won (Price et al. 2007), or to reconsider unfeasible ambitions and investments (Watson and Andrews 2002). The gist of these adaptationist hypotheses is that depression is not a disorder but a useful psychological mechanism that allows us to cope with the inevitable adversities of life, much like fever allows us to fight bacterial infections, and coughing and sneezing help us to keep our airways clear (Nesse 2001).

The idea that some mental disorders may have some functional significance is perhaps as baffling as it is alluring. Surely the persistence of depressive disorders across cultures and time must tell us something about their adaptive value. On reflection, however, this first kind of adaptationist explanation in Darwinian psychiatry lacks cohesion. For one thing, the analogy between depression and bodily defenses, such as fever and sneezing, does not hold. Fever may well be adaptive because it meets evolutionary biology's basic criteria for an adaptation. (That said, fever need not always be adaptive, since treating fever with Advil generally doesn't harm patients.)

For example, fever's form (raising the body's temperature) fits its function (to fight pathogens), since at least some pathogens, such as bacteria, do not like it hot. Also, most of the times, fever is evoked in appropriate circumstances, i.e., when and only when pathogens invade the body. Depression clearly does not meet these criteria (for an extensive account of this argument, see Nettle 2004). Many people become clinically depressed for no good reason at all. Moreover, the symptoms of clinical depression often obstruct its supposed function, as they make others more hostile and rejecting, and limit important social problem-solving skills.

Interestingly, though, many of the proposed functions of depression (bargaining, time-out, social navigation, etc.) do fit its normal counterpart, i.e., low mood, suggesting that low mood, rather than depression, could indeed be an adaptation. In this view, depression would be a dysfunction of low mood, or "adaptive behaviour gone wild," as Stevens and Price (1996, p. 94) have put it. More generally, even though negative emotions can be considered as useful reactions to situations with a negative cost-benefit outcome, they also tend to be oversensitive and prone to go off the rails. To account for this oversensitivity, Nesse (2001) has compared negative emotions with smoke detectors – their reliability requires them to express a number of false alarms, especially when the cost of such false alarms is low compared to the potential harm they protect against.

A second and somewhat less controversial adaptationist explanation of mental disorders brings us to the heart of contemporary evolutionary psychology. Evolutionary psychologists claim that our ancestral environment, i.e., our environment of evolutionary adaptedness (or EEA), differs substantially from our modern cultural environment. As John Tooby and Leda Cosmides (1992) once put it: "Our modern skulls house a stone age mind." As a result, they argue that we are much better at solving the problems faced by our hunter-gatherer ancestors than the problems we encounter in our modern world. Some Darwinian psychiatrists consider this mismatch to be the hotbed of many of today's

mental disorders. Some of these disorders may well have been adaptive once, but somewhere in the tempestuous transition from the world of our ancestors to our contemporary environment, they have lost their functional significance. Such explanations are commonly known as mismatch explanations of mental disorders.

It has long been known that human anxieties often involve natural threats, such as snakes, spiders, and heights. According to some Darwinian psychiatrists, these threats were probably common on the savannahs in Pleistocene East Africa, but they certainly aren't the most dangerous things in our contemporary environment. Thus it is that we do not fear guns the way we fear snakes, even though guns pose a much greater threat to our fitness today than snakes do (Ohman and Mineka 2001). Mismatch explanations have also been given for substance abuse disorders and eating disorders. Modern manufacture has created an abundance of substances that were as rare as they were vital in the world of our ancestors and for which natural selection carefully crafted intense cravings. As Steven Pinker (1997, p. 524) once noted: "We enjoy strawberry cheesecake, but not because we evolved a taste for it. We evolved circuits that gave us trickles of enjoyment from the sweet taste of ripe fruit, the creamy mouthfeel of fats and oils from nuts and meat, and the coolness of fresh water. Cheesecake packs a sensual wallop unlike anything in the natural world because it is a brew of megadoses of agreeable stimuli which we concocted for the express purpose of pressing our pleasure buttons." It may well have been adaptive to binge on certain substances whenever they were available, but that adaptive strategy has inevitably turned against ourselves in times of plenty.

The trouble with many mismatch explanations is that they are based on dubious assumptions. One of these assumptions is that the incidence of mental disorders is higher in modern environments than it has been in the past. However, we simply don't know anything about the mental health statistics of our ancestors, and while it is true that some contemporary epidemiological reports indicate an epidemic-like surge in clinical depression, for example, critics have objected that

such growing numbers are more likely an artifact of contemporary psychiatry's promiscuous diagnostic practices (Horwitz and Wakefield 2007). Another assumption of many mismatch explanations is that our bodies and brains have not been able to keep up with the dazzling pace of cultural evolution. By contrast, gene-culture coevolutionary theorists argue that we are a cultural species and that our brains have evolved to adapt to ever-changing cultural environments. Such adaptability explains how we were able to colonize nearly all continents and to adapt ourselves to climatologic, social, and ecological circumstances dramatically different from those encountered in the African savanna (Richerson and Boyd 2005). A third and final assumption underlying some mismatch explanations is that many of the mental mechanisms implicated in mental disorders are modular. Darwinian psychiatrists believe that our fear-regulating mechanisms, for example, are highly selective, automatic, and encapsulated. They are automatic because they escape cortical control; encapsulated because they are immune from the influence of ongoing cognitive processes; and selective because they are preferentially triggered by certain classes of stimuli, i.e., evolutionarily relevant threats, including snakes and spiders. Yet critics have shown that such threats produce the same effects on attention as evolutionary nonrelevant threats, such as ropes, syringes, and pens. More generally, they believe our fear mechanisms to be much more flexible than contemporary Darwinian psychiatrists would have us believe (Faucher and Blanchette 2011).

A third series of adaptationist explanations of mental disorders can be labeled as by-product explanations or, using a famous Gouldian term, *spandrel* explanations. In architecture, a spandrel is a spherical surface created by the crossing of a number of round arches. In biology, the concept of a spandrel is used to refer to a necessary by-product of some or other adaptive characteristic of an organism. An example of a spandrel is the snail's umbilicus, i.e., the cone-shaped hollow space within the whorls of a coiled shell. An umbilicus has no evolutionary function – it simply arises whenever one creates a shell by coiling a

tube around an axis (Gould 1997, p. 10754). At a later stage, some spandrels are co-opted by natural selection to fulfill a particular function. In some snail species, for example, the umbilicus is used as a brooding chamber to protect their eggs. Given that mental disorders themselves are (or were) unlikely to be adaptive, as argued above, the question is whether it makes sense to consider mental disorders as nonadaptive spandrels.

In Gould's own view, such spandrels are invisible for natural selection, neither enhancing nor subverting the fitness of their carriers. Spandrels, or so he believed, cannot possibly be maladaptive, as they would soon be eliminated by natural selection, regardless of the importance of the primary adaptation with which they are connected. Curiously, Gould seems to be oblivious here, both to his own admonishments not to overestimate the powers of natural selection (to break the connection between a spandrel and its adaptation) and to the fact that there are a number of cases in biology where the value of the primary adaptation is such that it offsets the disadvantages of its spandrels or by-products. Such examples are often conceptualized as package deals or trade-offs and include the classic and above-discussed example of sickle cell anemia.

Following Huxley's original 1964 hypothesis, many contemporary Darwinian psychiatrists believe that the sickle cell scenario may also apply to the evolution of some mental disorders. Schizophrenia is a good case in point. As Stevens and Price (1996, p. 146) note: "In a sense, schizotypic genes are like the genes responsible for sickle-cell anaemia, which enhance the well-being of carriers by protecting them from malaria while impairing those with greater genetic loading by afflicting them with anaemia." But what possible advantages could schizophrenia be associated with? While Huxley focused on physiological and particularly immunological advantages, most Darwinian psychiatrists believe that schizophrenia owes its evolutionary persistence to a genetic association with a highly valuable and (typically human) cognitive trait, such as language or creativity. Horrobin (2001), for example, has suggested that minor mutations in the genetic code of the fat metabolism of our

early ancestors, and the associated exponential increase of their cerebral capacities, have heralded the beginning of an amazingly creative new species: us. Yet the very same mutations also made us vulnerable for schizophrenia. In a sense, schizophrenia is the price we pay for our very humanity.

By-product or spandrel explanations imply that mental disorders have never been adaptations, even though they do have some kind of evolutionary history, more particularly as sidekicks or spandrels of highly valuable traits. As noted before, spandrel explanations are rather popular in contemporary Darwinian psychiatry, and yet they are the object of much criticism, even from within the discipline. According to Matthew Keller and Geoffrey Miller (2006), for example, it is highly unlikely that the evolutionary persistence of mental disorders is due to their being part of a trade-off, and for various reasons. Interestingly, their critique draws in part on the work of Gould.

First of all, they claim that most adaptationist explanations of mental disorders, including trade-off explanations, smell of panglossianism: “Evolutionarily oriented mental health researchers, such as Darwinian psychiatrists and evolutionary psychologists, often go to torturous lengths to find hidden adaptive benefits that could explain the evolutionary persistence of profoundly harmful mental disorders such as schizophrenia or anorexia, but these accounts are often frustratingly implausible or hard to test” (Ibid., 386). When charging evolutionary scientists with panglossianism, Gould and Lewontin (1979) did not only criticize their overly optimistic (or empirical) adaptationist view of the powers of natural selection (Lewens 2009). They also criticized them for being lazy in testing the predictions that follow from their hypotheses. Anyone can easily come up with stories about the function of, say, male baldness or being homesick, but there is an important difference between just-so stories and real science. Even Dennett agrees with this point: “To the extent that adaptationists have been less than energetic in seeking further confirmation (or dreaded disconfirmation) of their stories, this

is certainly an excess that deserves criticism” (Dennett 1995, p. 245). Now it may be true that some spandrel explanations of mental disorders amount to nothing more than just-so stories, but this certainly isn’t true for all of them. Nettle and Clegg (2005), for example, established that those artists who score high on particular components of a mild form of schizophrenia, i.e., schizotypy, also display enhanced mating success. Thus they suggest that by fancying male schizotypic artists, women would ensure the evolutionary persistence of a minor variant of schizophrenia. By providing evidence of a link between creativity and psychopathology, Nettle and Clegg have shown that spandrel explanations need not necessarily be Panglossian.

Secondly, Keller and Miller acknowledge the existence of trade-offs in nature, such as sickle cell anemia, but they also argue that such trade-offs are very rare. Moreover, given natural selection’s vigor and given the sweeping reproductive disadvantages involved in mental disorders, Keller and Miller expect trade-offs to be highly provisional phenomena, awaiting a better solution: “[S]election would strongly favour genetic events that overcome the costs of producing homozygotes, such as unequal crossover events that position both S and s [in the case of sickle cell anaemia] on the same chromosomal arm, so they can be passed on together without disruption, or mutations that reduce the fitness costs of either homozygote” (Keller and Miller 2006, p. 395). Basically, the authors would agree with Gould’s argument that strongly maladaptive features will soon be eliminated by natural selection. However, this argument is a probability argument which, in a sense, begs the question about adaptationism: exactly how omnipotent and ubiquitous is natural selection, especially when it has to deal with highly integrated organisms? Assuming that sickle cell anemia and schizophrenia are intricately connected to adaptations of primary importance, how likely is it that selection will break the correlations involved and come up with a better alternative?

Keller and Miller’s criticism brings us to their own attempt to make sense of mental disorders, which is part of a fourth and final series of

evolutionary explanatory models of mental disorders. In Darwinian psychiatry, these explanations are known as breakdown explanations or medical explanations, and they are explicitly non-adaptationist. As Dominic Murphy notes, for example, adaptationist explanations seem to assume that “none of our psychopathology involves something going wrong with our minds,” even though “nobody should deny that our evolved nature suffers from a variety of malfunctions and other pathologies” (Murphy 2005, p. 746). It may well be, for example, that low mood has some functional significance, but low mood, like any other trait or capacity, can also *dysfunction*, thus resulting in “malignant” sadness or clinical depression. From the perspective of breakdown explanations, it may well be useful to look for ultimate causes in explaining *normal* mental states, but mental *disorders* are proper dysfunctions caused by proximate causes.

Examples of such proximate causes are lesions and infections but also mutations. Keller and Miller’s explanatory model is based on the observation that the human genome is indeed particularly vulnerable to genetic mutations, i.e., tiny errors in our DNA’s xeroxing. These errors are the main source of genotypic variation. Most harmful mutations quickly disappear from the gene pool, but the bulk of genetic mutations have so little effect on reproductive success that they easily hold out during a number of successive generations. Thus the average human being is provided by his parents with five hundred up to two thousand slightly harmful mutations, half of which affect the construction and maintenance of the brain. Like many other traits, mutation load is continuously distributed across the population, so some individuals probably carry a few thousand brain-related genetic mutations, while others only carry a dozen. And the general principle seems to be that the more mutations one carries, the higher the chance of deviant behavior: “Individuals with an especially high load in mutations that disrupt a particular configuration of brain systems will tend to act in aberrant, harmful ways that provoke social comment and psychiatric categorization” (Keller and Miller 2006, p. 404). On this view, mental disorders are not veiled adaptations.

Rather, they are genuinely harmful dysfunctions, stemming from the immense mutational target size of the human brain.

Darwinian Psychiatry in Psychiatric Practice and Research

The evolutionary explanatory models discussed in the previous section go some way toward resolving the evolutionary paradox of common, harmful, and heritable mental disorders. In doing so, they may perhaps add to the solidification of contemporary *evolutionary theory*, but one wonders about their added value for contemporary *psychiatry*. What does psychiatry gain from its courtship with evolutionary theory? Traditionally, psychiatry has always been a hybrid discipline, dividing its time between research and practice, so our question can be further specified: what does Darwinian psychiatry have to offer to psychiatric patients and psychiatric researchers? This section discusses three examples of the discipline’s relevance for these target groups.

Many contemporary Darwinian psychiatrists are practicing psychiatrists, and their theoretical background indeed filters through to their therapeutic views and interventions. Firstly, Darwinian psychiatry can be instrumental in emphasizing that not all kinds of mental suffering are symptoms of an underlying dysfunction. Suffering may be as inevitable as it is useful. Anxiety and low mood, for example, are helpful defense mechanisms, enabling us to react efficiently and appropriately to adverse life events, such as losses and impending dangers. Extreme reactions to extreme events can still be normal. Secondly and relatedly, Darwinian psychiatrists can help change mere negative and stigmatizing views of mental illness, for example, in highlighting its connection to highly valued traits, such as creativity. Finally, some Darwinian psychiatrists, and especially ethological psychiatrists, have advocated more intense observation of patients in their social environment, arguing that suffering never takes place in a vacuum: “Psychiatric evaluation and treatment take place in offices and hospitals, rarely in patients’ natural environments, and the constraints that such practices introduce into diagnostic and treatment efforts are significant.

There is a not-so-subtle arrogance in the view that one can accurately understand patients' social environments simply by discussing these environments within the confines of one's office" (McGuire and Troisi 1998, p. 278).

However, Darwinian psychiatry's main contribution to contemporary psychiatry lies in its implications for psychiatric research. From the very beginning, Darwinian psychiatrists had high hopes of breathing new life into psychiatric research, particularly by bringing unification, sophistication, and solidification.

Firstly, Darwinian psychiatry promised to make an end to the incessant theoretical splintering of psychiatry (McGuire and Troisi 1998). Plagued by decades of trench warfare between competing theoretical frameworks, including psychoanalysis, biological psychiatry, phenomenology, and behaviorism, contemporary psychiatrists tried and tested two basic solutions, though without much success. One solution consisted in promoting the so-called biopsychosocial model. The model prescribes that all three levels – the biological, the psychological, and the social – must be taken into account when explaining mental disorders and treating patients, but it gives no guidance about how to prioritize choices, and so in practice it often devolves into eclecticism (Ghaemi 2010). Another solution consisted in giving up on theory altogether. Since 1980, contemporary psychiatry's ubiquitous *Diagnostic and Statistical Manual of Mental Disorders* (DSM) has steered an explicitly atheoretical course, hoping to bring unity to the field by focusing solely on clinical phenomenology, i.e., manifest symptoms. The problem with this solution is that the unity it generates is rather shallow and that it leaves unanswered the question how to connect the DSM's phenomenology with scientific research on the etiology of mental illness.

Darwinian psychiatrists believe that their discipline can provide a more successful solution to the problem of theoretical fragmentation in psychiatric research. As they point out, evolutionary theory has a track record in bringing together various domains in biology, including embryology, morphology, paleontology, and behavioral ecology. It did so by providing a theory about the interplay between on the one hand traits and

the genes involved in constructing them, and their environments on the other. Traits can only become (mal)adaptive in a particular environment at a particular time. The adaptive value of anxiety, for example, is always relative to the intensity of the adverse life event it relates to. Darwinian psychiatry could bring unity to contemporary psychiatry by overseeing the process of constructing both proximate and ultimate explanations of mental disorders.

Secondly, Darwinian psychiatrists can help refine contemporary psychiatry's methods and results. Thus they contend that good evolutionary explanations can provide the heuristic means to refine proximate explanations. Randolph Nesse and Matthew Keller's work on low mood is a case in point. In their attempts to demonstrate that low mood can be adaptive, they were able to confirm their prediction that different adverse life events correlate with different patterns of low mood features (Keller and Nesse 2006), even though they couldn't demonstrate that different feature patterns increase fitness in different adverse situations. Such research can help substantiate the search for more fine-grained mental disorder categories, the urgency of which is directly proportional to the mounting evidence against traditional disorder categories.

Thirdly, Darwinian psychiatry or, more broadly, evolutionary thinking in mental health care can help solidify contemporary psychiatry by contributing to the definition of its general concept of disorder. One of the most pressing problems of contemporary psychiatry is indeed its lack of consensus about how to define the concept of mental disorder. Jerome Wakefield attempted to tackle this issue by providing a hybrid evolutionary account of the concept in question. He argued that all and only mental disorders are harmful dysfunctions (Wakefield 1992). A mental mechanism is dysfunctional when it fails to fulfill the function for which it has been selected (by natural selection) in the past. A dysfunctional mental mechanism becomes a mental disorder when (and only when) it is experienced as harmful, either by the patient or by his or her environment. Depression is a mental disorder because it is both harmful and

dysfunctional, as it involves an evolved mental mechanism, i.e., low mood, that does no longer fulfill its function (whatever that is).

Wakefield's definition has been hailed by many psychiatrists as an important contribution to the field, but it brings its own problems. Wakefield claims, for example, that the function of a mechanism is related to its evolutionary history, rather than its contribution to the overall functioning of an organism. The problem with this view is that it is often impossible to find out the evolutionary function of a mental mechanism. Lacking such knowledge, we are thrown back on our own intuitions about the function of mechanisms – intuitions that often reflect our own petty values and prejudices (Faucher 2012). Wakefield (1992, p. 386) himself acknowledged the deadlock: "Because of the complexity of the inferences involved in judgments of dysfunction and our relative ignorance about the evolution of mental functioning, it is easy to arrive at differing judgments about mental dysfunction even on the basis of the same data."

Conclusion

There is ample evidence in the foregoing that Darwinian psychiatry is in fact a house of many mansions. Its advocates draw on a variety of traditions both in psychiatry, ranging from psychoanalysis to its sworn enemy, namely, biological psychiatry, and in biology, ranging from population genetics to ethology. Also, and testifying to the imaginative power of Darwinian psychiatrists, there is certainly no lack of hypotheses purporting to explain the occurrence and persistence of mental illness. Many Darwinian psychiatrists are adaptationists, arguing either that mental disorders are in fact adaptations, or that they are somehow genetically connected to an adaptation, or that they used to be adaptive. Some Darwinian psychiatrists also allow for non-adaptationist explanations, arguing that mental disorders are, and have always been, maladaptive. Some of these hypotheses have been tried and tested; others are little more than just-so stories. Given this heterogeneity, to hail

this wonderful discipline as the final turnabout in mental health care would be as presumptuous as to dismiss it altogether.

Cross-References

- [Anxiety Disorders](#)
- [Darwinian Medicine](#)
- [Depression](#)
- [Eating Disorders](#)
- [Evolutionary Clinical Psychology](#)
- [Evolutionary Psychiatry](#)
- [Fears and Phobias](#)
- [Freud's Psychoanalytic Theory](#)
- [Mismatch](#)
- [Mutation](#)
- [Phobias](#)
- [Postpartum Depression](#)
- [Schizophrenia](#)
- [Simon Baron-Cohen \(Darwinian Psychiatry\)](#)
- [Social Anxiety](#)
- [Substance Use Disorder](#)

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Darwinism

- [Alfred Russel Wallace \(1858\)](#)

Data

- [Advertising](#)

Data Analysis

- [Qualitative Versus Quantitative in Evolutionary Science](#)

Date Rape

- [Rape and Dating](#)

Dating

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Synonyms

[Courtship](#)

Definition

To be actively pursuing a romantic relationship with another individual.

Introduction

Courtship has been documented in many species (Moore 2002) and is commonly referred to as dating in humans and leads to mateship in all cultures (Greer and Buss 1994). Adolescence is the time period in which humans become increasingly interested in forming romantic relationships (Connolly et al. 1999). In fact, most North American adolescents have had at least one romantic relationship by late adolescence (Carver et al. 2003). By the 12th grade, boys spend approximately 5 h each week with girls, and girls spend an average of 10 h each week with boys, with each sex spending between 5 and 8 additional hours each week thinking about or talking with same-sex friends about the opposite sex when they are not together (Furman 2002). Connolly et al. (1999) found evidence for a series of transitions in adolescent social groups, changing from same-sex peer groups to mixed-sex peer groups, then to dating as part of the peer group, and finally leading to a dyadic romantic relationship that exists independently of the peer group. In college-age individuals, the romantic relationship is the most supportive relationship for men and one of the most supportive relationships for women (Furman 2002). Culture has an influence on the transitions between adolescent dating stages (Ha et al. 2010; Connolly et al. 2004). It has been hypothesized that romantic relationships in adolescence contribute to the development of an identity, the development of close friendships and family relationships, the development of sexuality, and the educational achievement and career planning (Furman and Shaffer 2003). Courtship rituals and behaviors are common in most cultures, and although the rituals vary between cultures, the ultimate goal of mateship stays consistent (Werner et al. 1992). These rituals may also serve as protective factors in the progression toward serious relationships, a concept investigated by Halpern-Meekin and Tach (2013),

mentioned in further detail in section “[Courtship Rituals and their Importance in Relationship Development](#)”. In order for courtship to occur, individuals must be able to signal interest in a potential suitor, and men and women have developed tactics to nonverbally communicate interest through body language (Grammer 1990) and can gain important insight to an individual’s potential as a mate using kissing as a cue (Hughes et al. 2007; Wlodarski and Dunbar 2014). A common modern approach to dating is through the use of online dating platforms. With access to a plethora of potential mates, individuals can use online dating websites and mobile apps to find a mate in a way that coincides with a busy schedule (Hobbs et al. 2017). Although online dating creates an easy way to meet new people, it is not without risks. People engage in a variety of forms of deception in an online dating context, many of which will be discussed in the following sections. The topic of dating and courtship will be discussed in detail in the following areas of research: (1) adolescents’ transition into dating, (2) courtship rituals and their importance in relationship development, and (3) the modern world of online dating.

Adolescents’ Transition into Dating

Adolescence is a time of many changes, including the transition into dating. It is understood that young adolescents understand the dynamics of romantic dating (Connolly et al. 1999) and it is a central topic of discussion (Simon et al. 1992), even if they have little personal experience. Through the years of adolescence, individuals become increasingly invested in romantic relationships, and much of adolescents’ social world becomes engrossed in romance and potential romantic relationships (Furman 2002). One accessible way for these young teenagers to learn about the world of romance is the portrayal of romance through various forms of media (Connolly et al. 1999). Perhaps one of the most influential sources of knowledge concerning romance comes from the development of mixed-sex peer groups (Connolly et al. 2000). Connolly et al. (2000) explain that through these mixed-sex groups,

individuals can meet potential romantic partners and have the opportunity to watch interactions between their peers. Adolescent romantic relationships do not reflect adult romantic relationships immediately; rather they go through a series of transitions to become familiar with the world of dating (Connolly et al. 2004). Stage models of adolescent dating propose two levels of romantic activities that take place before the dyadic romantic relationship stage. The first stage is the development of mixed-sex peer groups, followed by some peers forming pairs in the group and date while still participating in the group activities (affiliative dating), and the final stage is the formation of the dyadic romantic pair independent of the peer group (Connolly et al. 2004). While these stages exist, it is believed that adolescents do not follow a strict pattern of development and adolescents become interested in forming romantic relationships at their own pace (Furman 2002). Connolly et al. (2004) suggest development through the aforementioned stages of dating exists because social groups are of utmost importance in adolescence. Early romantic stages that encourage being a part of the mixed-sex social group and forming romantic pairs that function as part of the group will be favored by adolescents instead of immediately forming a dyad that functions independently of the group because this will draw an individual away from his or her social group. To further confirm the notion that social and romantic activities coexist in early adolescence, Connolly et al. (2004) examined the romantic activities and interest of young adolescents. They found that mixed-sex affiliative dating increased romantic interest in the young adolescents and led to romantic relationships. Further, their results supported a fluid model of romantic development that supports the stage model theory but explains that romantic development and interest do not replace mixed-sex peer groups and social activities, instead romantic interest and dating coexist with social groups and the activities the group partakes in (Connolly et al. 2004). In a study conducted to examine whether young adolescents have the same conceptions as adults regarding romantic relationships, Connolly et al. (1999) found

adolescents understand the core differences between friendships and relationships. The adolescents, aged 11–14, characterized opposite-sex friendships in terms of affiliation and relationships in terms of passion (Connolly et al. 1999). Adults, on the other hand, include emotional closeness in friendship and relationships, as well as commitment in relationships. Connolly and researchers speculate this could be because the age group in the study may be too young to conceptualize commitment and emotional closeness, as these are not yet important factors in their relationships with peers or romantic partners (1999). As adolescents mature, their opinions shift toward an idea similar to adults of what a romantic relationship is. Their findings also suggest there are cultural differences in the discussions regarding romance that takes place in friend groups, such that norms and expectations of romantic relationships vary depending on the cultural definitions of romantic relationships and how they should develop (Connolly et al. 1999). Even though early adolescent romantic relationships are based primarily on affiliation, older adolescents form relationships similar to adults, begin to seek out a partner to support their social and emotional needs, and turn to a romantic partner for support (Furman 2002). Furman (2002) states that this is due to maturation and continuous experiences as adolescents learn.

While adolescents can learn from the media and from peers about the nature of romantic relationships, teenagers can use their relationships with family members and same-sex peers to develop expectations for romantic relationships (Furman 2002). A study conducted in the Netherlands looked at indigenous and ethnic Dutch adolescents' romantic development and highlights the influence of parental and best friends relationships on romantic relationships (Ha et al. 2010). Ha et al. (2010) found that ethnic Dutch teenagers showed more commitment in romantic relationships when their relationship with parents was poorer, and they showed more passion in their romantic relationships when their relationships with their best friends were poorer. The researchers speculate these ethnic adolescents could be compensating for their poor-quality

friendships and parental relationships by investing more into their romantic relationships (Ha et al. 2010). They also explain that since the ethnic Dutch teenagers have cultural backgrounds from Turkey and Morocco where Islamic traditions are practiced, the collectivistic culture is dominant and influences parental decisions regarding their children's dating habits (Oyserman et al. 2002). Collectivistic cultures put emphasis on family and romantic relationships and rely heavily on interconnectedness and interdependence with one's family (Oyserman et al. 2002). To elaborate, ethnic parents tend to set more limits for their children in terms of who they date and set strict rules for dating which in turn can create tension between an adolescent and his or her parents (Ha et al. 2010). On the other hand, indigenous Dutch families follow a more individualistic culture (Oppenheimer 2004), and so these adolescents have the freedom to choose their partners based on their own standards, and parents let their children have the freedom to make their own decisions (Dion and Dion 1993). Ha et al. (2010) showed this could explain the lack of compensatory behavior toward romantic relationship partners of the indigenous Dutch teenagers. This study emphasizes the importance of familial relationships and the impact they have on adolescents' developing romantic interests and relationships.

Similar to the study conducted by Ha et al. (2010), Furman and Shomaker (2008) examined adolescents' romantic relationships relative to their relationships with close friends and their mothers. The researchers found that the affect of adolescents was more positive with their peers and romantic partners than with their mothers, even though their mothers had more positive affect than romantic partners. Further, the teenagers perceived more support in their romantic relationships than with their friends and mothers (Furman and Shomaker 2008). Furman and Shomaker (2008) speculate that adolescents try to avoid negative encounters with their friends and romantic partners because these relationships are more egalitarian compared to typical authoritarian parental relationships. Connolly et al. (2004) found a pattern similar to Ha et al. (2010)

regarding differential romantic activity based on cultural differences. Asian-Canadian adolescents engaged in less romantic activities, were less interested in romantic relationships, and had more same-sex friendships than the other groups of adolescents in the study, suggesting a cultural influence over romantic activity (Connolly et al. 2004).

Courtship Rituals and Their Importance in Relationship Development

Courtship can involve many different rituals and can encompass many different behaviors. Some of the more common examples of initiating a courtship or relationship are (1) the partners are chosen by family members without input from the couple, (2) the family makes the choice but the couple can decline, (3) the couple can select each other but the family can decline, and (4) the couple can decide whom they wish to date and the family has little say in the matter (Stone 1977). In some cases of courtship, there is very little courtship at all: in arranged marriages, there is no courtship; instead there are negotiations between the families of the individuals involved regarding prices and trades (Werner et al. 1992). In cultures where the couple and their families are both involved in the decision of marriage, gifts are exchanged, bride prices and dowries are discussed, and exchanges are made between families. These negotiations typically involve feasts and celebrations and gifts of money, jewelry, land, or animals, which are used to signal wealth. Further, in cultures where couples decide on their relationship, gifts are given to the couple, and little is exchanged between their families. Couples who have the freedom to decide whom they wish to marry do not usually involve their family until the relationship is more serious and there is a stronger commitment, and courtship usually takes place in public areas until the relationship is serious enough to involve family members. In terms of wedding ceremonies, western cultures adopt the tradition of the bride and groom coming together and meeting at a wedding ceremony, which signals they are equals entering into their

relationship. Other cultures have a different approach to marriage, with the groom, accompanied by his friends and family, picking the bride up at her family's house and bringing her to the ceremony: this is symbolic of the bride leaving her family and joining his (Werner et al. 1992).

In instances where couples must mutually agree on whom they wish to enter a relationship with, there are behaviors individuals can use to signal interest to another individual. For example, laughter has been defined as a courtship signal (Moore 1985) and is used to signal sexual interest in another individual (Duncan and Fiske 1977). Grammer (1990) conducted a study on laughter and body language and the messages they can portray. Grammer (1990) found that women use laughter as a tool more often than men do, and women use nonverbal cues more often than men. Specifically when interested, a woman will open her body up by extending her arms to seem engaged and look away from a man to highlight her profile from the side and accentuate her neck and breasts (Grammer 1990). This is consistent with male mate preferences, such that men prefer women who are young and fertile, as large breasts and smooth skin signal good health and fertility in women (Buss 1989). When men are interested in a woman, they will turn their bodies toward her and sit or stand with an open posture to imply he is intent and interested in her (Grammer 1990). This is consistent with female mate preferences for a man who is committed to her (Buss 1989). Interestingly, Grammer (1990) reported that women used their signalling postures only when a male was looking at her, and when he was looking away, she was watching him with her head tilted toward him with her arms and legs crossed, even if she was interested in him. While laughing, women use head tossing, an averted gaze, a protruded chest, and hair flipping to communicate interest in a male, and men tilt their heads and lean in while laughing to communicate interest in a female (Grammer 1990). Once interest has been signalled, one must decide if a certain individual is suitable enough to potentially begin a relationship with. Kissing is an important milestone in the courtship process, and Hughes et al. (2007) looked at romantic kissing as a sign of a good

partner. Females consider chemical cues like breath and taste, and the look of one's teeth when considering kissing someone, since these can cue health quality (Durham et al. 1993). Females reported a male being less attractive and less desirable if he was a bad kisser, and women are less likely to have sex with someone without kissing them first. This finding suggests women use kissing as a mate assessment tool (Hughes et al. 2007). This is in line with mate preferences in women, such that they look for mates with cues to good health and signs of commitment (Buss 1989). On the other hand, men prefer wetter kisses with more tongue, which could act as a signal for sexual receptivity (Hughes et al. 2007). When men were told a woman was a good kisser, they were more likely to rate her as attractive and more willing to date, engage in casual sex, and enter a long-term relationship with her (Wlodarski and Dunbar 2014). The effect of a woman being good kisser on a man's willingness to enter a long-term relationship with her from the study conducted by Wlodarski and Dunbar (2014) is consistent with findings from the study by Hughes et al. (2007) such that men and women think kissing a long-term partner creates greater emotional closeness and creates a stronger bond after sex when compared to a short-term partner.

Sex is important for courtship, and men and women have strategies in order to increase the likelihood of sexual encounters. A study conducted by Greer and Buss (1994) analyzed some tactics used by men and women to determine which tactics were used most often by men and women and which were most effective. Some of the strategies women use most often include directly requesting sex, increase sexual contact, indicate sexual attractiveness of their target, go to a private area, and dress and act seductively. A selection of the most commonly used tactics by men include verbal desire for sexual contact, directly requesting sex, imply commitment, increase attention toward their target, and imply sexual attractiveness of their target. In terms of which strategy proved most effective, men rated a woman directly asking for sex as most effective, and women rated a man telling her he loved her, was committed to her, and cared about her deeply

as most effective (Greer and Buss 1994). These tactics are consistent with mating preferences, such that men prefer a short-term mating strategy when possible (Buss and Barnes 1986), so perhaps women directly asking for sex is most appealing to men. Men's strategies are also consistent with women's mate preferences, as they prefer a long-term mating strategy and will choose a mate who is committed to her and will be emotionally supportive toward her (Buss and Barnes 1986). Women are more likely to dress seductively and enhance their physical attractiveness (Greer and Buss 1994), consistent with male mate preferences for a physically attractive mate (Buss 1989). Men use more tactics than women to increase the likelihood of sexual encounters (Greer and Buss 1994), consistent with the notion that women are the choosy sex in relation to mating (Buss 1989). When it comes to facilitating sex, men and women rely on tactics that exploit mate preferences. Other important milestones in the courtship process include giving one's partner a key to his or her apartment, moving in together, and engagement (Stanley et al. 2010). Couples who "slide" into these important milestones might experience greater relationship turmoil and poor relationship outcomes because these courtship milestones play a key role in relationship development (Vennum and Fincham 2011). Stanley et al. (2010) state that rituals like engagement are important in relationship development and may act as protective factors in a relationship because of how clear, mutual, and public the information is and that couples have a shared understanding of their relationship status. If these clear milestones act as protective factors, perhaps discordance between couples' reports of relationship progression indicates they "slid" into a more serious relationship instead of mutually deciding on meeting the next milestone, Halpern-Meekin and Tach (2013) postulated. They conducted a study to examine couples' reports of their relationship progression to see if discordance in reports was linked to marital quality. Halpern-Meekin and Tach (2013) determined discordance in relationship progression was linked with lower marital quality, and it is an indicator of "sliding" rather than mutually

deciding to progress in a relationship. This study shows that courtship rituals are important and also that mutual decisions from both partners are important for a healthy relationship.

The Modern World of Online Dating

Online dating has become an increasingly popular approach to searching for a mate. Bauman (2003) argues that romance and the courtship process have become a form of entertainment due to computer dating, since people will always have access to the mating market. Mobile dating apps are different from online dating websites in the experiences available due to the ability to take these apps wherever you take your smartphone (Hobbs et al. 2017). Many people enjoy using mobile dating apps because of how easy it is to use in a modern, busy schedule, and individuals now have access to many new potential suitors they may not have had access to before these mobile dating apps existed. Interestingly, Hobbs and colleagues conducted a study (2017) in which participants were asked how they would prefer to meet a partner, and over half stated they would choose meeting a potential romantic partner the traditional face-to-face way, and just under half of the participants said they would prefer to find a sexual partner the traditional way. Further, participants reported feeling embarrassed to tell someone if they had met a romantic or sexual partner online (Hobbs et al. 2017). Interestingly, Rosen et al. (2008) found people who prefer traditional dating have differing views on which characteristics are most important in a potential date from those who prefer online dating. People who prefer face-to-face dating value personal information, personality, and education to be most important factors in a potential mate, whereas people who prefer online dating stress the importance of communication style and physical attractiveness in a date (Rosen et al. 2008). The researchers speculate this could be because traditional daters have the opportunity to assess physical appearance immediately and must learn about an individual's personality and preferences as the courtship progresses. On the other hand, online daters can get to know a

person's personality and preferences from their profile or through email exchanges but must wait until meeting in person to assess physical appearance, since profile photographs can be deceiving (Rosen et al. 2008). Further investigation by Botnen et al. (2018) into the individuals who use mobile dating apps found that the use of these apps is associated with an unrestricted sociosexual orientation (looking for a casual sex partner rather than a long-term romantic partner) (Buss and Schmitt 1993). Specifically, an unrestricted sociosexual orientation explained the effects of looking for a casual sex partner and being comfortable picking up strangers (Botnen et al. 2018), which is consistent with the short-term mating strategy typically adopted by individuals who have an unrestricted sociosexual orientation (Buss and Schmitt 1993). Some individuals use mobile dating apps for casual hookups only (Hobbs et al. 2017), with findings that men use mobile dating apps for sex rather than a relationship and women use the app for to feel good about themselves because the attention makes them feel confident (Botnen et al. 2018). Hobbs et al. (2017) found similar results for mobile dating apps like Tinder, such that matching with someone works to boost one's self esteem because the apps are based on photographs of individuals. Hallam et al. (2018) found similar results in their study looking sociosexual orientation (preference for long-term or short-term mating) and online dating strategies. Hallam and colleagues concluded that individuals with an unrestricted sociosexual orientation prefer to use online dating for casual sex only, and individuals who adopt a restricted sociosexual orientation (preference for a committed, long-term partner) prefer to use online dating to look for a long-term partner and are motivated by romantic interest (2018). A study conducted by Blackhart et al. (2014) examined other factors that influence the individuals who use online dating sites. The researchers determined people who were highly sensitive to rejection were more likely to use online dating sites, perhaps because they could avoid rejection more easily through the Internet than it would be to avoid rejection in person. They speculate these individuals can more easily change aspects of their personality online and

can therefore feel more comfortable when interacting with potential romantic partners. These individuals who scored high in rejection sensitivity were also less likely to tell friends and family about meeting an individual online to avoid judgment (Blackhart et al. 2014). Hallam et al. (2018) found age influences the preference for mobile dating apps or online dating websites. Specifically, older individuals prefer to use websites, whereas younger people prefer to use mobile dating apps. They speculate this could be influenced by the preference for newer technology in younger adults, as younger adults are more open to new technology compared to older adults (Hallam et al. 2018). Individuals who engage in self-monitoring (altering one's personality based on reactions from one's audience) intentionally lie to prospective dates about their personality and interests so they appear to be more similar to their prospective date than they are (Rowatt et al. 1998). These self-monitoring individuals believe it is acceptable to alter aspects of themselves to increase interest from a potential partner, and there is a potential link of the tendency to self-monitor to high scores of neuroticism. The researchers believe the insecurity and anxiety experienced by individuals high in neuroticism may lead them to alter their personalities to impress a potential partner and to avoid rejection. Further, individuals who use self-monitoring techniques tended to alter characteristics related to personal preferences, attitudes toward love, and their own attractiveness, which can be considered trivial and are typically used to initiate interest in another person so courtship can continue. For example, if an individual alters small details about him- or herself to create similarities with a prospective date, it is seen as slightly more acceptable than lying to a long-term partner or lying to harm another individual (Rowatt et al. 1998).

While online dating does increase the dating market (Hobbs et al. 2017), there is an increased risk for danger and deception regarding potentially important details because there is no initial face-to-face interaction. Couch et al. (2012) conducted a study regarding potential dangers of meeting an individual online. These participants recalled the deception they encountered and

expressed their concerns. Participants recalled the most common lies they received were about relationship status, the intentions toward individuals they were talking to, and inaccurate profile photos. Many participants experienced exploitation of their emotional vulnerability, being lied to about others' intentions for the courtship, and the level of commitment the individual was interested in pursuing. Some participants recalled violence they had experienced from someone they had originally met online: a woman had her drink spiked for not sleeping with the man she met online, and another woman was stalked by someone she had recently began chatting with (Couch et al. 2012). Blackhart et al. (2014) expand on this by looking at personality factors and concluded people who score high in conscientiousness are less likely to meet in private with someone they met online, possibly due to their increased levels of caution. In the study conducted by Couch and associates, most individuals were concerned about people who were untrustworthy or dangerous, including prostitutes, scammers, and people from overseas, and a selection of participants recalled interacting with someone asking for money or to pay for a passport/travel visa (Couch et al. 2012). Aside from the attempt to receive money, it is puzzling why individuals decide to lie online, especially when research has shown that the first face-to-face meeting between individuals who originally met online does not fare well when an individual has been lied to (Sharabi and Caughlin 2019). Specifically, individuals who had been lied to experience a decrease in social and physical attraction, and have low expectations for future dates with this person, and also feel this person has low expectations too. Sharabi and Caughlin (2019) explain that when there is deception early in the formation of a relationship, it may cause individual to expect disappointment in the relationship and hinder potential progression toward a strong relationship. Research done by Ellison et al. (2011) revealed that some discrepancies are tolerable in an online dating context. Specifically, discrepancies in characteristics that are easy to change in the near future, like a hairstyle, were deemed acceptable, whereas characteristics that could not easily be

changed in the near future, like height or age, were not acceptable. The magnitude of the lie also affected the acceptability of a lie, such that smaller differences between what is presented and the truth are okay, but large differences are not. For example, lying about your age by 1 year is acceptable, but a difference of 8 years is not (Ellison et al. 2011).

A common area of deception in online dating involves physical attractiveness (Toma and Hancock 2010), and many people report that they are not completely honest online (Drouin et al. 2016). Since attractiveness is important to many individuals in a romantic context, it is common for less attractive individuals to attempt to enhance their physical appearance by selecting photos to share that increase their physical attractiveness (Toma and Hancock 2010). Toma and Hancock (2010) also report that women enhance their photos more often than men, consistent with the notion that men value physical attractiveness more than women (Buss 1989). Consistent with mate preferences (Buss 1989), men and women who were considered to be more physically attractive both received more emails from prospective dates, as well as women who had a lower body mass index (BMI) which is valued, and men with higher incomes (Hitsch et al. 2005), since a low BMI is valued by men and a high income is valued by women when considering potential suitors (Buss 1989). Another common area of deception involves self-presentation, defined as the alteration of one's personality or appearance to increase attractiveness in a certain situation or environment (Toma and Hancock 2010). It is common for individuals to exaggerate aspects of themselves to increase their attractiveness to a potential partner (Guadagno et al. 2012). Consistent with this notion, men change their personality characteristics and physical appearance when they wanted to meet an individual in person. Men exaggerated their agreeableness when communicating with potential dates over email and lowered their neuroticism to give the impression they would be a more emotionally stable partner than what may be true (Guadagno et al. 2012). Guadagno et al. (2012) explain this is consistent with the notion that females tend to be more

selective when choosing a mate (Buss 1989), so men would be more willing to change their characteristics to look more appealing.

Conclusion

Dating and courtship become a central aspect of humans' social lives beginning in adolescence (Connolly et al. 1999). As adolescents mature and learn about the concepts of dating, courtship rituals become important for signalling interest to another individual to determine if they reciprocate interest (Grammer 1990). Courtship rituals seem to be imperative in the development of a strong relationship because of the seriousness and clarity these rituals demonstrate (Halpern-Meekin and Tach 2013). Online dating platforms have increased in quantity and popularity over recent years, and the use of these platforms ranges from looking for casual sex partners to seeking a long-term romantic partner. The risk of these online dating platforms is that there is a lack of initial face-to-face interaction, leaving room for people to alter characteristics about themselves, like physical appearance or their intentions for seeking a partner. The dating world has evolved over the past decades and will undoubtedly continue to evolve over the coming decades, so it is important to continue to research this socially relevant topic of dating for new theories regarding dating and courtship processes.

Cross-References

- Adolescent Issues
- Human Courting
- Incest Avoidance and Dating
- Perceiving Sexual Intent
- Rape and Dating
- Sexual Coercion and Dating

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Daughter Guarding

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Synonyms

Daughters/females and mate selection; Evolution and guarding behavior; Offspring mating behavior; Parental influence; Parental monitoring; Parent-offspring conflict in mate selection; Protection and evolution; Sex differences in guarding behavior; Sex-biased parental investment

Definition

Daughter guarding highlights the tendency of parents to monitor and control their daughter's mating behaviors in order to protect reproductive success.

Introduction

Ancestral perspectives regarding sexual traits and behaviors have evolved and serve as a function that has persisted throughout time. From an evolutionary perspective, mate selection and reproduction is a way to carry on fitness advantage (the ability to survive generation to generation) (Voland 1998). Today, parents often attempt to influence their children's mating behaviors through various methods and strategies, such as parental monitoring. Reproduction compromises a female's survival in regard to the physiological risks associated with pregnancy. As such, parental investment in their offspring's reproduction protects the offspring's sexual fitness. Evolutionarily, in hunter-gatherer populations, parents needed to ensure that their daughters were selecting mates that had the ability to support them, such as being proficient at hunting. Because of the physical costs associated with pregnancies, parents did not want offspring to be produced with mates that lacked the ability to secure resources. The purpose of ensuring reproductive success is to maintain positive genetic variation in a population and protect against the extinction of future generations (Voland 1998).

In modern day, daughter guarding through messages such as limiting sexual activity "when ready" and "not too early" serves to ensure the best mate for their daughter and further propel the passing of genes. Parental investment has existed throughout time and is exhibited through sexual selection. From an evolutionary perspective, behaviors exist because they serve a purpose in survival. Thus, daughter guarding behaviors strive to ensure the survival of the fittest.

Sexual Selection Theory

Sexual selection theory attempts to explain what factors drive mate selection. Various researchers have argued which factors comprise the establishment of this theory. This theory distinguishes between three main factors: female choice, male-male competition, and parental choice (Apostolou 2014). Within hunter-gatherer cultures, male-male competition was a means to compete for female access, attention, and reproduction, leading to the increased likelihood of ultimately being selected by the female. Both female choice and male-male competition coincide to ensure reproductive success. Although all factors are arguably important, parental choice best supports the daughter guarding hypothesis (Apostolou 2014).

Daughter Guarding Hypothesis

The daughter guarding hypothesis describes the phenomenon of parental investment in monitoring and/or controlling their daughter's mating behaviors in order to facilitate reproductive success (Perilloux et al. 2008; Kuhle et al. 2015). Through this lens, the daughter guarding hypothesis describes the adaptations parents possess that function to defend their daughter's sexual reputation, prevent unwanted pregnancy, preserve her long-term mate value, and protect her from sexual victimization (Perilloux et al. 2008; Kuhle et al. 2015). Parents developed the personal responsibility to protect them their daughters from sexual victimization because in the past, there was no law enforcement to prevent it.

Historically, in order to preserve lineage, consensual sex was seen as genetically beneficial; however, if the preservation of future generations was placed in jeopardy, males chose the action of force (i.e., rape) in order to increase generational survival and reproduction. For women, rape comes with a burden to bear in relation to future partner choice, harm to status, and the risk for unwanted pregnancy (Gottschall and Gottschall 2003). Damage to a daughter's mate value may prevent her from obtaining a high-quality mate

who can support her. This may result in economic and/or social strains on the parents (Perilloux et al. 2008). Because males (e.g., sons) do not bear children, parents are less restrictive regarding their son's sexual encounters (Perilloux et al. 2008).

Current Implications

Parents are more likely to control offspring behavior if parent-daughter opinions differ, thus creating a cycle of conflict specific to daughters. This cycle may lead to daughter guarding and monitoring of behaviors (Bovet et al. 2018). Furthermore, there is a causal relationship between parental monitoring and daughter sensitivity. The phenomenon of daughter sensitivity has occurred as females, in comparison to males, have evolved to be more sensitive to their parents' approval and opinions regarding future mates. Women experience parental monitoring at higher rates, and this direct relationship implies that women who were more sensitive toward parental opinion were also highly monitored. For instance, women report allotting greater emphasis than men on their parents' wishes (Dubbs et al. 2012). This relates to parental acceptance as well as the significance placed on parental approval (Apostolou 2009). Moreover, parental investment was also believed to be of significance in a potential partner, as females would report experiencing hurt feelings if their parents did not approve of their partner and would even contemplate "cutting off" the relationship (Dubbs et al. 2012).

Research indicates that parents are more likely to control their daughters' mating decisions than their sons and parents reported dissatisfaction over their daughter's sexual activity (Perilloux et al. 2008). Both parents and their daughters described mechanisms by which daughter guarding is implemented in their daily life, including control over behavior, approval of behavior, emotional upset over sexual activity, approval of mate choice, control over curfew, and control over clothing (Perilloux et al. 2008). Parents are less likely to allow their daughters to engage in

romantic relationships (compared to sons) in order to decrease the opportunity of sexual contact and to reduce the chance of sexual victimization. With these two objectives in mind, parents may object to their daughters engaging in physical intimacy at higher rates than their sons (Perilloux et al. 2008). Parents of sexually active daughters may feel compelled to monitor her sexual activity with more vigilance in order to protect her sexual reputation and mate value. Approaches parents utilize to monitor their daughter's behavior include enforced curfews to limit sexual contact, decreased time away from parental observation, and restricted choice of clothing to be less provocative (midriff tops, low cleavage, etc.) (Perilloux et al. 2008).

Within a developmental context, parents typically facilitate sex conversations with their children with the intended purpose to possibly encourage abstinence, highlight being selective with regard to whom they allow sexual access, to possibly delay sexual contact until she reaches older age, and to deter from a potential partner's sexual advances. These reasons are established in conversations with daughters rather than sons. On the other hand, sons are more likely than daughters to receive messages that sex should be fun (Kuhle et al. 2015). Parents also suggest to daughters that they should not partake in or mimic sexual activities illustrated in media.

Thus, daughter guarding is a strategy parents use to socialize their daughters to foster reproductive success and preserve mate value (Kuhle et al. 2015).

Conclusion

Daughter guarding may have been a significant evolutionary force in order to withstand reproductive pressures. Throughout history, daughter guarding has attempted to protect from untimely pregnancies in regard to physiological reproductive costs, including rape and sexual victimization. At present, daughter guarding behaviors continue to exist and are exhibited in influencing not only offspring's mate selection but also the

conversations parents have regarding sex with their offspring. Across cultures, parents may implement robust control over the mating decisions of their offspring. Daughter guarding has also served its purpose in defending a daughter's sexual reputation and value in the long term.

Cross-References

- [Parental Investment and Sexual Selection](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)

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Daughter-Guarding

- [Violence from Women's Kin](#)

Daughters/Females and Mate Selection

- [Daughter Guarding](#)

David Benatar

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Synonyms

[Author; Philosopher](#)

Definition

David Benatar is a philosopher known for his writings about ethics, particularly involving procreation. He is considered one of the foremost authorities and proponents of anti-natalism.

Introduction

David Benatar is a South African philosopher, professor, and chair of philosophy at the University of Cape Town. He is the author of *Better Never to Have Been: The Harm of Coming into Existence* (2006), a treatise on anti-natalism, and *The Second Sexism: Discrimination Against Men and Boys* (2012), which chronicles wrongful discrimination against men, in the interest of advancing gender equality. While he is perhaps best known as a proponent of anti-natalism, he is also noted for writing about ethics, including topics in sexual ethics, male circumcision, female genital

mutilation, fetal pain, euthanasia, humor, and affirmative action. An opponent of speciesism, he has strongly advocated the ethical treatment of all sentient beings, including refraining from consuming animal products.

Anti-Natalism

Professor Benatar has gained prominence for his advocacy of anti-natalism, which opposes procreation. He has argued that coming into existence is always harmful, and thus it is immoral to bring new life into existence. This argument stems from the discrepancy between pain and pleasure, such that the presence of pain is always undesirable and the presence of pleasure is always desirable. In contrast, whereas the absence of pain is considered positive, the absence of pleasure is not necessarily a negative state and is better characterized as neutral. Missing out on pain by not being born is not equal to missing out on the pleasures of living. According to Benatar (2006), this basic asymmetry produces other asymmetries. For instance, bringing into existence, a child who will suffer can be considered regrettable, yet failing to bring into existence, a child who would lead a happy life produces no regret because of the lack of a person to lament it, or to be lamented. Since there is no person associated with not being born, no person exists to wish that they would be born to experience pleasures in life, because being is necessary for mental states such as a desire to be born. Further, even if a potential being might live a subjectively “good” life, it may not, and that risk outweighs the benefits of that life because the alternative – failing to be brought into existence – causes the nonexistent no harm while avoiding inevitable suffering in life.

Apart from the asymmetries of pain and pleasure, humans have a tendency to exaggerate the quality of their lives, underestimating past pain and suffering and overestimating pleasure and happiness. Such retrospective biases have empirical evaluation and support, such as the tendency of older adults to more readily recall pleasant memories and give more positive evaluations of autobiographical information (e.g., positivity

effect; Mather and Carstensen 2005). Although Pollyannaism (Matlin and Stang 1978) is psychologically powerful in retrospection, it does not change the fact that human lives are filled with suffering moment to moment. Thus, Benatar has surmised that procreation should be avoided because new life is new pain, as it is certain that every new person will suffer to some degree. Since there is no moral imperative to reproduce, humans have no reason to procreate new suffering. Acknowledging how deeply reproduction is entrenched in human evolved psychology, Benatar does not set the expectation that people stop reproducing immediately. He has set forth a plan for a “phased extinction” (Benatar 2006), with the goal to reach the ideal human population of zero, because it is the only way to ensure zero suffering. Phased extinction calls for the species to wean off reproduction across several generations, allowing the death rate to exceed the birth rate until humanity ceases to exist. He has favored this “dying off” plan to being “killed off” because of the potential suffering that could be brought about by killing already living humans en masse. To fill individual psychological drives for parenthood in the meantime – the primary practical impediment to his plan – Benatar has suggested adoption as a viable option. This might not be a perfect alternative to genetic offspring, however, given the evidence indicating that children tend to suffer greater domestic abuse and neglect from genetically dissimilar stepparents than from genetically related parents (e.g., Daly and Wilson 1980). However, Benatar has pointed out that humans have similarly evolved gratification delays which render the species uniquely capable of selecting its own extinction. Furthermore, humans are capable of culling their reproduction as modern contraceptive techniques have made pregnancy all but completely avoidable.

It is important to note that Professor Benatar has drawn a distinction between coming into existence and continuing existence. Although it is preferable not to have existed, once a person has been brought into existence, that person has a justifiable interest in continuing to exist and minimizing the suffering in his own life and those around him. In other words, “life may be

sufficiently bad that it is better not to come into existence, but not so bad that it is better to cease existing” (Benatar 2006, p. 212). Anti-natalism has often been misinterpreted as advocating suicide, and indeed, Professor Benatar (2006) has acknowledged that in some circumstances, taking one’s own life is a reasonable response, yet it need not follow the acceptance of anti-natalism. He has been careful to recognize that the costs of continuing to live must be high enough to outweigh the cost of taking one’s own life, including the impact on others. He has thus set the threshold for beginning new lives much higher than the threshold for continuing lives in progress, because those in existence have an interest in continuing to exist, where in contrast, no such interest in coming into existence is present in the nonexistent.

Although he has advocated anti-natalism on philanthropic grounds – that it is better for the potential new person not to be brought into existence – Professor Benatar has also presented an argument against procreating on misanthropic grounds. He has suggested that humans should not reproduce because of the tremendous harm that the species causes other sentient beings, both human and nonhuman (Benatar 2015). This premise portrays humans as both victims and perpetrators of tremendous harm in the world. As such, humans should not only refrain from creating new victims of suffering but also new causes of suffering. For both philanthropic and misanthropic reasons, Benatar has proposed that sexual intercourse is most ethical when it is non-procreative. He has thus bypassed the ethical debates surrounding many reproductive technologies, instead indicating that women are morally obligated to avoid impregnation and, when necessary, to terminate pregnancies as soon as possible, preferably before the fetus can feel pain (at about 27–28 weeks of gestation; Benatar and Benatar 2001). He has thus put the onus on defending procreation, and not abortion, taking a pro-death position (Benatar 2006). Because anti-natalism contradicts psychological drives that have promulgated modern humans into existence, it has been met with much criticism, and he has gone to great lengths to respond to them. He has furthered the debate on the ethics of procreation

coauthoring an anti-natalism–pro-natalism debate with David Wasserman, *Debating Procreation: Is It Wrong to Reproduce?* (Benatar and Wasserman 2015), and coediting *Procreation and Parenthood: The Ethics of Bearing and Rearing Children* (Archard and Benatar 2010).

The Second Sexism

Professor Benatar’s (2012) book *The Second Sexism: Discrimination Against Men and Boys* has also courted much controversy. In it, he presents the case that there are ways that male humans suffer unjust and unfair discrimination (the second sexism). Accordingly, what makes the second sexism so hazardous is how ubiquitous it is and yet how oblivious people are of it. The second sexism, as Benatar conceptualizes it, is not the result of some intentional malignant effort or design, but has come about as a secondary consequence of the evolutionary process from which the species has emerged and is thus fundamentally a manifestation of sex differences.

The bedrock of this argument is the undervaluing of male lives, as demonstrated by several examples, such as the historical and present exemption of women from conscription into the vast majority of the world’s militaries, higher rates of violence against men (perpetrated by both women and men), preferential placement of women in lifeboats on sinking ships, education disparities favoring women and girls, less severe criminal punishments for women including lack of corporal punishment, favoring of maternal rights over paternal rights in child custody cases, and near universal shorter life expectancies for males (Benatar 2012), especially in times of resource scarcity (e.g., Grayson 1993). These can be considered social manifestations of evolved mechanisms that value female lives over male lives. This depreciation of male lives is likely the product of the minimal reproductive investment required by males compared to females. Males have greater potential reproductive outcomes (in terms of sheer quantity of offspring) than females because of the differing required investments to reproduce. Given an

equal but uncapped number of mates, one man, due to his minimum reproductive investment, could produce many more genetic offspring than one woman. Thus, females have greater mate discretion and receive greater protection because of their lower individual reproductive potentials. This is consistent with the discrepancy between the male–female birth ratio (slightly favoring males) and the male–female population demographic (favoring females).

Although Professor Benatar has carefully crafted the case demonstrating the second sexism, he has not been free from significant criticism. He has fully acknowledged the presence of wrongful discrimination against women and girls and the harm that it has caused and prefaces his book as purposed toward forwarding egalitarian gender equality. To acknowledge wrongful discrimination against one sex is not to deny the existence of wrongful discrimination against the other sex. At this juncture is where much opposition exists, mostly from “partisan feminists” (Benatar 2012, p. 15), whom he contends are interested primarily in advancing and benefiting women and girls rather than promoting gender equality. Benatar has attempted to advocate the complete equality of sexes by acknowledging all instances of wrongful discrimination, against both sexes. Uncontroversial as this premise has been presented, it has not been consequently reflected in the response to the work.

Inconsistencies in Sexual Ethics

Other work in sexual ethics includes a comparison of a promiscuous (or casual) view of sexual ethics and pedophilia and rape. Benatar (2002) has outlined the logical inconsistencies between endorsing a promiscuous view of sex and condemning pedophilic sex and rape. Benatar has carefully elucidated how regarding sexual intercourse as a pleasure to be pursued as any other and not according it special consideration leaves insufficient grounds for condemning iterations of sex (in this case, pedophilia and rape) as abhorrent. Accordingly, if one takes a casual view of sex, no form of sex need be accompanied by

stigma or even condemnation. By his reasoning, if sex is not ascribed romantic or other significance beyond pleasure, as a casual view would imply, then sexual deviations need pose no greater condemnation than gastronomic preferences. In providing evidence to support this conclusion, Professor Benatar has also deflated counterarguments that attempt to reconcile these inconsistent opinions. For instance, the claim that pedophilic sex is condemnable because it can physically hurt the child can be dismissed by focusing on non-penetrative forms of sexual interaction or contact with willing children. Although there are empirically documented effects of childhood sexual abuse on children (e.g., Kendall-Tackett et al. 1993), evidence is also inconclusive about the extent of psychological harm to the child and whether it is due exclusively to the act itself, or rather from secrecy and societal mores prevailing the activity (e.g., Malón 2015; Rind and Tromovitch 1997), or some combination thereof. Indeed, much less evidence is available about the impact of sexual encounters between “consenting” children and consenting adults (although debate surrounds the definition and veracity of “consent” in adult–child sex, e.g., Abel et al. 1984; Ehman 2000). However, if a child is a willing participant, Benatar concludes that a casual view of sex should permit this as parents would permit a child to engage in other activities that they enjoy with adults that carry some risks, such as playing sports.

All of this considered, Benatar furthers the argument that for a person who holds the casual view of sex, rape might be an unnecessarily inflated concept, as it is not taking anything more important than one who deprives gastronomic pleasures. While rape can be considered wrong according to this sexual ethic because it is still bypassing the victim’s desires, it is no more serious than forcing someone with an aversion to tomatoes to eat a tomato. Although he initially does not mention how long-term consequences of rape, such as the possibility of unwanted pregnancy, injury, and disease, increase the consequences (and thus seriousness) of rape even according to the casual view, these additional considerations do not make the rape itself more

condemnable, but only in ad hoc evaluation of the event as subsequent tangential harms. For this argument, rape might thus be better juxtaposed to a nonsexual physical assault that causes lasting physical damage. Rape could thus be considered condemnably as it is opposing the physical rights of another person, but not to any greater degree than a robbery and battery. Insofar as both crimes are serious, according to the casual view of sex, one need not be considered more grievous than the other unless it causes greater bodily harm. Thus, a rape is considered more serious than battery when it results in impregnation or the transmittal of a disease and the battery results in only minor contusions. Similarly, a battery could be considered more serious than a rape when it results in broken bones and the rape results in no major physical injuries. When making such specific evaluations in concert with a casual view of sex, Professor Benatar has indicated it would also become necessary to scrutinize the sexual history of the victim to understand the value she places on sex and thus the magnitude of the rape to her. Thus, a rape might be considered worse for a woman who holds a significant view of sex than a casual view. In this way, only in the significant view of sex, in which sexual intercourse is accorded additional consideration as a special pleasure, can pedophilia and rape be considered particularly immoral as violations of this special act. This view assigns a value to sexual acts that makes condemnation of variations, with either unwilling parties, individuals incapable of appreciating the romantic aspects that make it a special kind of pleasure (e.g., children), or even casual consenting adults, consistent. Whether this condemnation is warranted, Benatar has left up to individual interpretation.

Nonhuman Animals

Professor Benatar is a noted vegan and advocate of animal rights. He has forwarded many arguments that eating meat is morally wrong and should be avoided. Benatar (2001) has surmised that many humans place a greater value on the gastronomic pleasures of meat eating than on the

suffering inflicted upon animals commercially bred, reared, and killed for consumption. It follows that the relatively minor pleasure of eating meat is not commensurate to the pain experienced by the consumed animals. Although he acknowledges that being omnivorous was certainly an important evolutionary development, meat is no longer a necessary part of the modern human diet as the nutrients abundant in meat can also be found in other food sources. Lacking the dietary compulsion to consume meat, Benatar has argued that humans continue to eat meat primarily for culinary pleasure, made possible by a devaluing of the suffering of nonhuman animals. This devaluing of animal suffering has produced subsequent blanket approbation for experimentation on animals. He contends that humans have evolved a priori acceptance of animal consumption leading to de facto acceptance of animal experimentation, with the tendency to make speciesist evaluations of the value of suffering to the animals (Benatar 2000). Thus, he has pointed out that because humans continue to underappreciate the suffering of nonhuman animals, the benefits to humans versus the immediate costs to laboratory animals must be more carefully weighed when evaluating the morality of animal experimentation.

Affirmative Action

In addition, David Benatar has written extensively about affirmative action in his native South Africa, arguing against the inclusion of race as a criterion for determining preferential consideration, especially in hiring or admissions to universities. He has outlined four types of affirmative action: “equal opportunity affirmative action,” which seeks to guarantee that discrimination (especially by race) does not inhibit opportunities for any individual (which he believes no reasonable person would oppose); “tie breaker,” whereby all other qualifications being equal, preference is given to the candidate from a designated (usually racial) category; “strong preference,” where deficiencies in other qualifications can be overlooked when candidates possess the

designated racial designation; and “quotas,” whereby a certain number of positions are set aside and only open to candidates who meet the designated racial criterion (Benatar 2007). The more weight one assigns race, the less weight can be afforded to other more relevant qualifications. While acknowledging the need to address historical wrongs that have left some individuals unjustly disadvantaged, Benatar argues that race is a poor proxy for disadvantage and that considering it as such continues to perpetuate the very apartheid-era stereotypes it exists to counter. For instance, he has argued that “black” academics need no preferential hiring at universities because their abilities have already conferred on them the desired qualifications for employment (Benatar 2007). Even if they were previously disadvantaged, having secured doctoral training and degrees, they no longer need the assistance of affirmative action to achieve positions in academia. He has participated in a lengthy written and panel debates on the subject at the University of Cape Town.

Conclusion

Although controversial, Professor Benatar’s commentaries have appeared in many popular media including the *Cape Times* and online and radio media such as “The Species Barrier” and “Politicsweb.” He has published in many academic journals, including *The Lancet*, *QJM: An International Journal of Medicine*, *American Philosophical Quarterly*, *Ethics*, *American Journal of Bioethics*, *Social Theory and Practice*, *British Medical Journal*, *Public Affairs Quarterly*, and *American Journal of Bioethics*, among others. He remains active in conducting research and publishing about the philosophy of ethics.

Cross-References

- [Anti-Natalism](#)
- [Debating Procreation \(With David Benatar\)](#)
- [Evolutionary Paradox: Women Choosing Not to Have Children](#)

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David Buss

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Definition

One of the founders of evolutionary psychology, author of *The Evolution of Desire: Strategies of Human Mating* and *Evolutionary Psychology: The New Science of the Mind*.

Introduction

David Buss is one of the founders of the modern field of evolutionary psychology. He is the most heavily cited evolutionary psychologist in the world, according to Google Scholar (48,773 scholarly citations as of December, 2016). He is widely known for his scientific contributions to understanding human mating strategies, subsumed under the label *Sexual Strategies Theory*. He has made contributions to personality psychology, personality and social interaction, adaptive individual differences, tactics of manipulation, sexual conflict, stalking, sexual violence, and homicide. He authored or co-authored three other evolution-based theories: *Strategic Interference Theory* (Buss 1989a), *Error Management Theory* (Haselton and Buss 2000), and *Homicide Adaptation Theory* (Buss and Duntley 1998; Duntley and Buss 2011). He created these interdisciplinary scientific bridges during an era when evolutionary biology was almost entirely absent from the field of psychology.

Buss's Personal Journey to Evolutionary Psychology

Buss's fascination with understanding human nature – what motivates people and how to characterize their basic mechanisms of mind – began as an undergraduate at the University of Texas at

Austin (1971–1976). He opted to major in psychology, believing that this was the discipline that offered the greatest promise for his quest. Over the course of several years, he became discouraged. All existing theories in psychology seemed somewhat arbitrary. Why, for example, would the human mind be designed to experience cognitive dissonance, intolerance of ambiguity, a desire to enhance self-esteem, or any of the dozens of “effects” or phenomena psychologists had documented? The proliferation of dozens of mini-theories in psychology, none connected to any of the others, seemed scientifically unsatisfying. Lacking was a non-arbitrary set of fundamental premises on which a science of the mind could be built. This quest for explanations anchored in deeper origins ultimately led him to evolutionary theory.

Buss first encountered evolutionary theory in an undergraduate geology class, and theories of cosmology and stellar evolution in an astronomy class. They captured his intellectual imagination. He was awed by the fact that there existed theories designed to explain the origins of things, life in the first case and the universe in the second. During this period, Buss read a book called *The Imperial Animal* written by Lionel Tiger and Robin Fox (Tiger and Fox 1971). Although anchored in a now-outdated theory of group selection, Buss saw for the first time that evolutionary theory might offer a non-arbitrary set of foundational premises for the field of psychology. His undergraduate term paper, titled “Dominance/Access to Women” (written in 1975) posited that men have evolved a status-striving motive, the sole reason being that elevated rank gave them increased sexual access to women. Simplistic perhaps, but a start.

In 1976 when Buss sought a PhD program, there existed no evolutionary psychologists and no field called evolutionary psychology. So Buss began graduate school in personality psychology at the University of California, Berkeley, in 1976, believing that this field had as a central goal the development of grand theories of human nature. During his first year, he conducted a study designed to test the hypothesis advanced in his undergraduate paper, although he never published those results. While completing his graduate work

at Berkeley, he focused the bulk of his empirical work on developing *The Act Frequency Approach* (with Ken Craik, his main graduate advisor), but also published articles with Jack Block and Jeanne Block (two of his other mentors) on personality development, and as sole-author (on dominance and activity level). He continued in his spare time to read widely in evolutionary biology and population genetics, including E.O. Wilson's now classic tome *Sociobiology* (Wilson 1975).

His mainstream work in personality psychology made enough of an impact to land Buss his first post-PhD job as assistant professor at Harvard University in 1981. In teaching his first large undergraduate course, *Human Motivation*, he used evolutionary theory as the overarching framework. He also discovered Trivers' (1972) theory of parental investment and sexual selection (in a book on sexual selection theory that he stumbled across at a used bookstore in Cambridge) and Donald Symons' (1979) book, *The Evolution of Human Sexuality*. At the time, Buss was designing an empirical study of married couples and decided to test predictions about mate preferences based on Trivers' theory and articulated in Symons' book.

Around this time (1981–1982), Leda Cosmides, then a graduate student at Harvard in psychology, heard that Buss was teaching a course on human motivation using evolutionary theory. She introduced herself to Buss, and then to her husband, John Tooby, a graduate student in biological anthropology. Cosmides and Tooby were in the process of developing the conceptual foundations of evolutionary psychology, although at the time their only publication was on the evolution of intragenomic conflict (Cosmides and Tooby 1981). Buss's friendship with Leda and John, and his intellectual connection to them and their magnificent work, endured during the subsequent decades and continues unabated. This friendship, in turn, led to meeting Martin Daly and Margo Wilson when they spent a sabbatical year at Harvard. Buss was influenced by Daly and Wilson's (1983) book, *Sex, Evolution, and Behavior*, which contained many novel insights and testable hypotheses unknown to mainstream psychologists (Daly and Wilson 1983).

In 1984, Buss published his first paper on evolutionary psychology, entitled "Evolutionary Biology and Personality Psychology: Toward a Conception of Human Nature and Individual Differences" in the prestigious journal, *American Psychologist*. Although naïve and ill-informed in many ways, it signaled Buss's enduring commitment to understanding species-typical psychology and profound individual differences within a unified conceptual framework.

When Buss was invited to give a talk at Yale in 1984, he decided to take a chance – he presented his first professional talk on the evolution of human mating. In the audience there happened to be the editor of the prestigious journal, *American Scientist*. On his return to Harvard a few days later, he received from him an invitation to write an article on human mating. This led to the lead article, "Human Mate Selection," published in *American Scientist* in 1985. Requests for reprints of this article poured in from all over the world. Buss responded by inviting scientists from 37 cultures to join him in conducting parallel research under the banner "The International Mate Selection Project." Invitations coming on Harvard University stationery probably helped produce the overwhelming positive response from what ended up to be 50 international research collaborators.

In 1984, Harvard promoted Buss to Associate Professor, but he simultaneously received an offer from the University of Michigan of Associate Professor. At the time, the Michigan Psychology Department was ranked as the best in the country. Buss was mostly known for his work in personality psychology. Had Michigan known that Buss's entire research program was in the process of shifting in an evolutionary direction, it is possible they would not have extended the offer. On the other hand, they were well aware of his evolutionary interests and arranged meetings with key evolutionary scientists at Michigan – Barb Smuts, Richard Wrangham, Dick Alexander, Warren Holmes, Bobbi Low, and Randy Nesse.

Shortly after starting his position at Michigan in 1985, he joined this interdisciplinary group and together they formed the *Evolution and Human Behavior* (EHB) group in 1986, funded with a

generous internal grant from a prescient dean. This rich intellectual environment provided Buss with exposure to primatology, evolutionary anthropology, work on nepotism in ground squirrels, and a stream of evolution-minded scientists who saw Michigan as intellectual hub. Yearly EHB meetings became testing grounds for this emerging interdisciplinary science. In 1986, for example, Buss was honored to chair a symposium with the invited speakers W.D. Hamilton, George C. Williams, Mildred Dickemann, Martin Daly, and Napoleon Chagnon. These yearly meetings eventually led to the formation in 1989 of the *Human Behavior and Evolution Society* (HBES) with W.D. Hamilton serving as its first president.

In 1987, Buss was elected to be a fellow at the *Center for Advanced Studies in the Behavioral Sciences* at Stanford. Elected fellows had the opportunity to spend a year at the center and could, if so inclined, propose a special project involving other scientists. Buss proposed “Foundations for Evolutionary Psychology” and proposed that Leda Cosmides co-lead the project with him. The project was one of only the two approved by the center, and in 1989–1990 it came to fruition with Buss reuniting with Leda Cosmides, John Tooby, Martin Daly, and Margo Wilson. One of our goals was to co-author a book on the foundations of evolutionary psychology, and they made some progress in the form of draft chapters. Although that collaborative book never came to fruition, the project morphed, leading Buss to sole-author the first textbook in the field: *Evolutionary Psychology: The New Science of the Mind* (first published in 1998; its 5th edition was published in 2015). At the center, Buss also began to work on his first book, *The Evolution of Desire: Strategies of Human Mating* (published in 1994; revised editions published in 2003 and 2016). Both books, translated into many languages, continue to be widely used in college courses throughout the world.

Evolved Mate Preferences

Although he found initial support for some key hypotheses about evolved mate preferences based

on studies conducted in Cambridge, Massachusetts, Buss was keenly aware that the work, when published, would be controversial. So he delayed publication and spent 5 years gathering additional data from what turned out to be known as the 37-culture study, involving 10,047 participants from six continents and five islands. Participants included those from all major religious groups, political systems, and geographical locations. Although he had advanced the evolution-based hypotheses prior to the study, Buss did not know what to expect. No one had ever conducted a study of that magnitude (now such large-scale studies are more common due to the internet). Prior to the study, when he asked a dozen non-evolutionary scientists from different disciplines to make predictions, not a single one predicted universal sex-differentiated mate preferences. Most expected that perhaps they might occur in western cultures, or perhaps in capitalist cultures, but certainly not universally. Buss regrets not obtaining signed predictions from these scholars, for once the results were published, one common reaction was “I could have predicted that.”

The first wave of results was published in a target article in *Behavioral and Brain Sciences* in 1989 (Buss 1989a). It received 29 commentaries from diverse scholars. Buss found universal desires for some mate preferences – love, mutual attraction, intelligence, dependability, kindness, emotional stability, and good health. The priority people universally placed on love and mutual attraction surprised Buss, since he had been taught that love was a culture-specific emotion invented by some European poets a couple hundred years ago. This finding was a heart-warming surprise, not predicted in advance of the study, and reinforced the importance of science conducted in the context of discovery in addition to the context of hypothesis testing.

The study also discovered some striking cultural variability. The most variable mate preference was for virginity in a potential spouse. The Swedes and French, for example, did not prioritize virginity at all. The Chinese, in contrast, viewed virginity as indispensable in a spouse. Countries such as Ireland and Japan fell in

between these extremes. Although Buss had predicted universal sex difference in the desire for chastity (defined as no prior experience with sexual intercourse), based on the adaptive problem that men, but not women, face regarding paternity uncertainty, men valued it more than women in only 62% of the cultures. The other 38% showed no sex differences. In no cultures did women value virginity more than man. So Buss's evolution-based hypothesis received only partial confirmation, certainly not robust confirmation, which would have required universality or near universality. The findings also showed that evolutionary psychological hypotheses can be falsified, contrary to the oft-repeated but scientifically inaccurate criticism of evolutionary psychology (see Confer et al. 2010).

By far the findings that received the most attention were the discoveries of universal sex differences, precisely as predicted. Men more than women valued cues to fertility. They placed greater importance on physical attractiveness. Appearance contains a bounty of cues to fertility, which, unlike in chimpanzees, cannot be evaluated directly due to ovulation being relatively concealed or cryptic in women. Men also desired younger spouses, supporting a second evolution-based prediction. Fertility is steeply age graded among women, more so than among men, so youth is a powerful cue to fertility and future reproductive potential. Women more than men universally prioritized financial resources, economic prospects, and nearly universally prioritized cues that lead to resources, such as ambition/industriousness and social status.

These basic findings provided the first massive cross-cultural support for a key set of evolutionary psychological hypotheses. In 1989 when they were published, evolutionary hypotheses were widely regarded as speculative, lacking an empirical basis. These findings rendered that view no longer tenable. Since 1989, these basic findings have been replicating in dozens of other cultures using multiple methods. They remain among the most robust psychological sex differences ever documented across cultures. It was an early "success story" for the emerging field of evolutionary psychology and helped spur others to get into the

field. The study became a "citation classic" and as of 2016 has received more than 3,600 scholarly citations.

Tactics of Attraction

Preferential mate choice represents one component of Darwin's theory of sexual selection. The second is intrasexual competition. Qualities that lead members of one sex to best same-sex rivals gain preferential mating access to the other sex. Although Darwin viewed intrasexual competition as primarily one of "contest competition," such as two stags locking horns in combat, it is now widely recognized that the logic is more general – whatever qualities lead to success in intrasexual competition, be they physical brawn or superior social skills, increase in frequency (evolve) because of the preferential sexual access gained by the victors. Moreover, the mate preferences of one sex should theoretically establish the ground rules for intrasexual competition in the other. If women prioritize athletic prowess in a mate, for example, men should compete with each other to beat other men in athletic displays. If men prioritize physical attractiveness and youth, then women should compete with other women to enhance their appearance and display cues to youth.

Buss tested these hypotheses, not in 37 cultures, but in more limited studies involving college students and married couples. The results again robustly confirmed the hypotheses. Moreover, Buss developed the first taxonomy of tactics of mate attraction, which includes 23 distinct tactics, including displays of kindness, devotion, resources, grooming, physical strength, and so on (Buss 1988a; Schmitt and Buss 1996). These studies also discovered unpredicted tactics, such as the display of humor, a topic that has subsequently receive much research attention and theorizing. Although the key sex-differentiated hypotheses received robust support, the unpredicted findings intrigued Buss as well and convinced him of the importance of conducting studies in a "bottom-up" manner in the context of discovery, in addition to the "top-down" manner in the context of testing *a priori* hypotheses.

Derogation of Competitors

Because mate competition is a zero-sum game in which one person's gain in mating comes at a loss to a rival, one can conceive of two general strategies – enhancing one's own attractiveness relative to rivals (tactics of attraction) and rendering rivals less attractive to mates relative to oneself. This logic led Buss to conduct the first empirical studies of derogation of competitors – the tactics that people use to impugn the desirability of their rivals. He developed the first taxonomy of derogation of competitor tactics, which included 28, such as questioning a rival's fidelity, spreading false rumors about sexually transmitted infections, derogating a rival's intelligence, and questioning a rival's sexual orientation (Buss and Dedden 1990). The studies supported the evolution-based predictions about sex-differentiated tactics. Men more than women derogated their rival's resources (e.g., "He drives a poor car.") and physical prowess (e.g., "He told others that his rival was physically weak."). Women more than men derogated their rival's physical appearance (e.g., "She made fun of the size and shape of her rival's body.") and ability to remain sexually loyal (e.g., "told others that her rival slept around a lot").

Other interesting findings, however, were not predicted in advance. Women were more likely than men, for example, to call their competitors emotionally unstable. Men were more likely than women to question their rival's hygiene. Again, this reinforced for Buss the utility of conducting studies simultaneously in a bottom-up manner that allowed discoveries unanticipated, as well as a top-down manner to test *a priori* hypotheses.

Tactics of Mate Retention

Mates gained must be retained to reap the reproductive potential inherent in long-term mate selection. While reading a book called *The Evolution of Insect Mating System* (Thornhill and Alcock 1983), Buss got the idea to study the tactics by which humans guard and retain mates once they have successfully attracted them. This led to the

first set of studies on tactics of mate retention in dating couples and married couples, as well as the first taxonomy of mate retention tactics (Buss 1988b; Buss and Shackelford 1997). Tactics ranged from *vigilance* (e.g., "He called her at unexpected times to see who she was with.") to *violence* (e.g., "He hit the guy who made a pass at his girlfriend.").

Studies of the use and perceived effectiveness of mate retention tactics supported evolution-based predictions about sex differences. Men more than women retained mates through resource displays and gifts; women more than men retained mates by enhancing their physical appearance. But Buss also discovered unexpected and unpredicted findings. Men (both in dating couples and in married couples), for example, were more likely to use the submission and self-abasement tactic, contradicting the stereotype that women are generally more submissive than men. Moreover, tactics involving displays of commitment, love, kindness, and caring were perceived as much more effective at mate retention for men than for women. These two early publications, the first to break ground on human tactics of mate retention, have received more than 1,000 scholarly citations. A short form of the Mate Retention Inventory (Buss et al. 2008) is now widely used in scientific studies and has been translated into other languages (e.g., de Miguel and Buss 2011).

Mate Poaching

Mate poaching – attempting to lure someone who is already in a mating relationship for either a short-term sexual encounter or a long-term relationship – turns out to be quite common (Schmitt and Buss 2001). This should not be surprising in that desirable potential mates are often the objects of intense interest, and so often end up in relationships. Relationship status, however, does not seem to deter all others from attempting to attract them. Together with David Schmitt (Buss' student, then colleague in a collaboration that has now spanned more than two decades), they conducted the first studies of human mate poaching and developed a taxonomy of its main

tactics. Many tactics turned out to be similar to tactics of attraction. But some are unique to the mate poaching contexts, such as befriending the couple in a platonic guise. Another is derogating one partner to the other (e.g., “He doesn’t appreciate you.” or “You are too good for him.”), implying a mate value discrepancy. Mate poaching represents a domain previously unexplored prior to the Schmitt and Buss (2001) study, and the term “mate poaching” has now entered the mainstream scientific lexicon (http://tierneylab.blogs.nytimes.com/2009/08/27/why-poach-anothers-mate-ask-an-expert-or-brangelina/?_r=0).

The Emotion of Jealousy

Jealousy is a commonly experienced emotion in romantic relationships. Yet it was largely ignored by emotion researchers when Buss began studying it. The pioneer emotion researcher Paul Ekman told Buss that jealousy was not really a “basic emotion,” such as fear, anger, and disgust. Instead, it was a “blend” of different emotions. Moreover, jealousy lacks a distinctive facial expression, and this criterion was central to Ekman’s theory of emotions, a view that can be traced back to Charles Darwin himself. Buss argued that criteria for an emotion being “basic” should not require a distinctive facial expression. Indeed, only emotions whose function is signaling or communication should have distinct facial expressions (Buss 2013). Moreover, if an emotion evolved for specific functions, that of contributing to the solution to specific adaptive problems, and shows convergent evidence of “special design” for those functions, then it should qualify as “basic.”

The hundreds of prior studies published on jealousy contained two key problems, according to Buss. First, most scientists viewed jealousy as a character defect, a sign of neurosis or insecurity, or as a profound pathology. Second, almost none of the hundreds of studies on jealousy had explored whether its psychological design differed between men and women. The two exceptions were the writings of Donald Symons (1979), who argued that sexual jealousy was a universal

and obligate emotion in men, whereas it was as “facultative” or context dependent in women (e.g., less strongly activated in the context of polygyny due to the need to get along with co-wives). And Daly et al. (1982) argued that men’s jealousy should focus heavily on the sexual aspects of a partner’s infidelity, whereas women’s should focus more on cues to the loss of commitment and resources.

Following these functional views, Buss sought to test hypotheses about different functional design of jealousy. He collaborated with Drew Westen, Randy Larsen, and Jennifer Semmelroth, and together they discovered strong evidence for hypothesized sex differences in the weighting given to triggers of jealousy. They posited that emotional infidelity was a cardinal cue to the loss of a partner’s commitment for women, whereas sexual infidelity as a key cue to compromised paternity certainty. Although both sexes are clearly upset about both sexual and emotional infidelity in a partner, when forced to choose which is more upsetting the predicted sex differences emerged. Moreover, men showed greater physiological distress to imagining a partner committing sexual infidelity, whereas women showed greater physiological distress to imagining a partner committing emotional infidelity (Buss et al. 1992).

The publication created a firestorm of reactions. Some proposed alternative theories, although the original author of one later abandoned his alternative theory and instead argued that the sex differences were methodological artifacts. Another offered an incoherent “social cognitive” theory that failed to explain known findings, failed to generate novel predictions, led to no new empirical research, and failed to generate any empirical support subsequently. The sex differences in the design of jealousy have been replicated using multiple methods – forced choice, continuous, physiological, fMRI, and behavioral, and among individuals who have and who have not experienced an actual infidelity in their relationships (Buss and Haselton 2005). The sex differences even show up in verbal interrogations of partners suspected of cheating, such as “Do you love her?” and “Did you have sex with him?” (Kuhle 2011). It remains among a small

handful of the most robust psychological sex differences ever documented across multiple methods and multiple cultures. The original 1992 article has become a “citation classic” and currently is one of the 30 most heavily cited article over the past 30 years in all *Association for Psychological Science (APS)* journals.

Strategic Interference Theory

Buss saw the functional emotion of jealousy as part of two larger theories. The first was strategic interference theory (Buss 1989b). He proposed that emotions such as jealousy, anger, and upset become activated when a person’s strategy for achieving a goal was impeded or blocked. A strategy of securing a partner’s sexual fidelity, for example, was impeded by attempts by mate poachers or rivals trying to lure one’s partner for sex or romance. To take another example, a woman’s strategy of exercising “female choice” about when and with whom she consents to having sex would be impeded by a man who pursued a strategy of sexual force or aggression. Strong negative emotions such as anger, jealousy, and upset serve several key functions, according to strategic interference theory: (1) they alert someone to the source of the interference, (2) motivate action to curtail the interference, (3) help to store interfering events in memory, which in turn functions to (4) avoid future episodes of strategic interference.

Error Management Theory

Jealousy turned out to be illuminated by error management theory (EMT), originally developed by Martie Haselton, Todd DeKay, and Buss (Haselton and Buss 2000). EMT is a theory of selection, so it can be applied to any domain of psychology from perception to social interaction. EMT logic can be stated syllogistically as follows:

1. We live in an uncertain world.
2. We experience cues that are only probabilistically related to cost-inflicting or benefit-bestowing events.

3. There are two ways to err – by inferring the existence of an event when it has not in fact occurred and by inferring the nonexistence of an event when it in fact has occurred.
4. If there are recurrent cost-benefit asymmetries in making these two types of errors, selection will favor adaptively biased inference procedures that function to minimize committing the more costly error, even at the cost of experiencing more frequent inferential errors of the less costly variety.

Jealousy illustrates EMT logic. Buss argued that the cost of missing a sexual infidelity that has occurred is typically greater than the cost of mistakenly suspecting an infidelity when none has occurred (Buss 2000). Because infidelities are typically conducted underneath a cloak of intentional secrecy, their existence must be inferred from probabilistic cues. Empirical evidence supports EMT logic applied to jealousy and infidelity (e.g., Buss 2000; Andrews et al. 2008). Haselton and Buss also used EMT to illuminate design features of the male sexual over-perception bias and the female commitment skepticism bias (Haselton 2003; Haselton and Buss 2000). And EMT logic has been used to illuminate a raft of other psychological phenomena, such as the auditory looming bias, the vertical descent illusion, and adaptive biases in a number of domains of social functioning (for a recent review, see Haselton et al. 2016). EMT logic has also been invoked to explain inferential biases about homicidal intent (Buss 2005).

The Evolution of Aggression and Murder

Because differential reproductive success necessarily hinges on reproductive competition, conspecifics are necessarily rivals, albeit in the context of some levels of intertwined reproductive fates and win-win situations (“gains in trade”) that select for adaptations for cooperation in certain contexts. Enhancing oneself relative to rivals is one generic strategy. A second is inflicting costs on rivals. Buss documented these two generic strategies in the context of mate

competition – tactics of attraction and derogation of competitors. In collaboration with Joshua Duntley, Buss extended this argument to murder. They argued, contrary to the Daly-Wilson claims that murder is a by-product of adaptations designed for nonlethal ends (Daly and Wilson 1988), that humans have adaptations for murder (Buss 2005; Buss and Duntley 1998; Duntley and Buss 2011).

Homicide Adaptation Theory (HAT) proposes that humans have evolved a number of distinct homicide adaptations, such as infanticide, intrasexual rival murder, and coalitional killing (warfare). Simply put, killing a rival, killing a rival's offspring, or killing a rival's kin have been extremely effective ways of inflicting massive costs on intrasexual competitors. The accumulating evidence of adaptations for conspecific killing in chimpanzees (Wrangham 1999) leads to the conclusion that some of these homicide adaptations predate the evolution of *Homo sapiens*.

Being killed inflicts severe costs on rivals, far more than merely harming them nonlethally. It terminates any future access to their current mates and future mating opportunities. It harms their children, since lack of an investing parent leaves children vulnerable to abuse and exploitation, sexual and otherwise. It harms the entire kin group of the victim, which becomes weakened. So as soon as homicide entered the human arsenal of strategies of reproductive competition, selection would immediately favor adaptations to prevent becoming a homicide victim. HAT argues that this set into motion a dramatic coevolutionary arms race, with finely fashioned anti-homicide defenses evolving in ratcheting fashion with ever more sophisticated adaptations to commit murder and ever more sophisticated defenses to prevent being murdered.

Buss and Duntley recognized that their theory is controversial; that the existence of coevolved homicide and anti-homicide adaptations does not rule out the likely possibility that some homicides are by-products of “slips” as Daly and Wilson put it, and that the current empirical evidence cannot definitively determine the precise number and full design of homicide adaptations. Nonetheless, they believe that there is sufficient evidence – from the

paleontological skulls and skeletons riddled with unmistakable marks of murder to the psychological and behavioral footprints of “special design” for murder – to conclude that it is far more likely than not that humans have experienced a long coevolutionary arms race that created adaptations for murder and defenses to prevent being murdered.

The Evolution of Personality and Individual Differences

Although most evolutionary psychologists have focused on universal or species-typical adaptations, Buss has made contributions to understanding personality and individual differences within the broader metatheory of evolutionary psychology. He has argued that humans have evolved difference-detecting adaptations, personality assessment mechanisms, that help to solve problems such as determining who will be a good cooperator (e.g., those high on agreeableness), coalition member (e.g., bravery), or hierarchically ally (e.g., those high in surgency or dominance). These difference-detecting adaptations also help individuals to avoid those who are dispositionally cost inflicting, such as those low on agreeableness or high on dark triad traits such as Machiavellianism or narcissism. Those high in narcissism and impulsivity, for example, are more likely to inflict the costs on their partners through infidelity and costs on their friends through poaching their mates. The personalities of other individuals, in short, partly define the “social adaptive landscape” that must be navigated (e.g., Buss 1991; Buss and Penke 2014).

Buss was among the first to highlight the possibility that personality traits might represent “adaptive individual differences” (Buss 1991; Buss and Greiling 1999), reflecting variation over time and space of which strategies are effective. High sensation seekers, for example, might thrive in migratory or novel environments, whereas low sensation seekers might thrive in more sedentary environments.

Finally, two key issues have eluded mainstream personality psychology – how to define

“situations” and how to conceptualize “person-situation interactions.” Buss contributed to both of these issues by defining situations as adaptive problems, the only non-arbitrary way to define situations from an evolutionary perspective (Buss 2009a). The “situation” of confronting cues to a partner’s infidelity can be illuminated by identifying those cues, detecting the presence of a mate poacher, gauging the relative mate value of the mate poacher compared to self, and so on. In short, situations are defined as the adaptive problems encountered and the corresponding evolved psychological mechanisms that render some clusters of cues psychologically salient and other information invisible.

This formulation, in turn, provides a powerful way to conceptualize person-situation interactions. Person-situation interactions come in two main forms: (1) the ways in which person variables, through the processes of selection, evocation, and manipulation, lead to nonrandom exposure to different suites of adaptive problems and (2) individual differences in the strategies deployed toward solving the adaptive problems that people nonrandomly encounter. Buss believes that a more comprehensive evolutionary psychology must include a deep understanding of the evolution of personality and individual differences and anticipates that these formulations may provide starting places for doing so.

Authored Books

In an effort to reach a broader audience for evolutionary psychology, Buss has authored several books. These include *The Dangerous Passion: Why Jealousy is as Necessary as Love and Sex* (2000), *The Murderer Next Door: Why The Mind is Designed to Kill* (2005), and *Why Women Have Sex* (2009, co-authored with Cindy Meston) (Meston and Buss 2009). His two most influential books are *The Evolution of Desire: Strategies of Human Mating* (1994, 2003, 2016) and *Evolutionary Psychology: The New Science of the Mind* (1998, 2004, 2008, 2012, 2015).

The Evolution of Desire. This book represented the culmination of a decade of research by Buss

and a conceptual synthesis of hundreds of studies on human mating by other scientists. It elaborated on Sexual Strategies Theory (Buss and Schmitt 1993) and included chapters on what women and men wanted in long-term and short-term mates, strategies of casual sex, tactics of attraction, causes of sexual conflict and breakups, mating over the lifespan, and harmony between the sexes. The book was first published in 1994; two new chapters were added to a new edition published in 2003; and the book was totally revamped in a thoroughly updated and revised edition, published in 2016. It has received more than 2,000 scholarly citations, has been translated into ten languages, and continues to be widely used in college courses worldwide.

Evolutionary Psychology: The New Science of the Mind While evolutionary psychology began to emerge as a cogent metatheory for psychology in the late 1980s and early 1990s, professors began to offer courses in it. There existed no textbook. One was urgently needed. After getting encouragement from a handful of people to write such a text, and being approached by publishers, Buss signed a contract. He produced the first textbook in the field in 1998. The text provided historical reviews of evolutionary theory and psychological science that converged on their synthesis (Chapter 1: The Scientific Movements Leading to Evolutionary Psychology) and a chapter on the conceptual foundations of this new science of the mind, heavily influenced by the theoretical work of Leda Cosmides and John Tooby (Chapter 2: The New Science of Evolutionary Psychology). Subsequent chapters were organized logically around adaptive problems – challenges of survival, mating, parenting, kinship, and social group living (e.g., cooperation, aggression, status hierarchies). The final chapter called for the evolutionizing of all subdisciplines within psychology, such as cognitive, social, personality, developmental, and clinical; reviewed evolutionary empirical work within each; and ended with a call for a unified field of psychology that eventually could dissolve these somewhat artificial subdisciplinary boundaries.

Adoptions of this text increased with each successive edition, despite roughly a dozen competing texts appearing since 1998. Buss' *Evolutionary Psychology* text remains the most widely used textbook in evolutionary psychology worldwide. It has entered into its 5th edition in 2015 (Buss 2015), with a 6th edition underway. It has been translated into half a dozen languages, including German, Chinese, and Arabic. And it has become a citation classic, with more than 4,000 scholarly citations as of 2016. Through this text, Buss helped the field of evolutionary psychology to grow and flourish, educating undergraduates, informing professors, and attracting new scholars to the field.

Edited Volumes

Buss has edited six volumes, including *Personality Psychology: Recent Trends, Emerging Directions* (Buss and Cantor 1989); *Biological Approaches to Personality* (Buss 1990); *Sex, Power, Conflict: Evolutionary and Feminist Perspectives* (Buss and Malamuth 1996); and *The Evolution of Personality and Individual Differences* (Buss and Hawley 2011). His most influential edited volume, however, is *The Handbook of Evolutionary Psychology* (Buss 2005), logging in at more than 1,000 double-column pages and some 35 chapters. This led to a 2nd edition of the *Handbook* (Buss 2016), which expanded to more than 50 chapters. Both editions contained a foreword by Steven Pinker, a special essay by Don Symons, and an afterword by Richard Dawkins.

The *Handbook* documented the rapidly expanding use of evolutionary psychology in empirical research. It has received nearly 1,000 scholarly citations and helped to document the utility of evolutionary psychology in leading to insights and discoveries about the human mind previously unknown to social scientists. It also documented the utility of evolutionary psychology for far-reaching branches of sciences and humanities, including business and marketing, literary analysis, political science, and the legal profession.

Teaching and Mentoring PhDs in Evolutionary Psychology

Throughout his career, Buss has devoted considerable effort to mentoring the future generation of scientists. Of his 27 PhD students, roughly two-thirds have obtained tenured or tenure-track professorial positions. The Association of Psychological Science (APS) honored Buss with the 2017 *Mentor Award for Lifetime Achievement*. His former students such as Todd Shackelford, Martie Haselton, and David Schmitt, in turn, have produced a number of PhDs in evolutionary psychology and themselves have made major contributions to the field.

Conclusion

The quest for a true science of the human mind has been Buss' lifetime mission. Although more about the human mind remains unknown than known, some of the key foundations for a science of the mind are now in place. Buss likes to believe that he has contributed to the emergence of evolutionary psychology through his conceptual and empirical work, his authored and edited books, and, importantly, through his students.

Cross-References

- ▶ [Act Nomination Method](#)
- ▶ [Error Management Theory](#)
- ▶ [Evolution of Desire, The](#)
- ▶ [Evolutionary Psychology, The Handbook of](#)
- ▶ [Founders of Evolutionary Psychology](#)
- ▶ [Homicide Adaptation Theory](#)
- ▶ [Sexual Strategies Theory](#)

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David Edmonds

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Synonyms

[Author](#); [Journalist](#); [Philosopher](#)

Definitions

David Edmonds is a philosopher, journalist, author, editor, senior research associate, and documentary maker.

Introduction

David Edmonds was born in 1964. He graduated from Oxford University and went on to earn a PhD in philosophy from the Open University. He subsequently had fellowships in the University of Chicago and University of Michigan. He has since become an influential philosopher and has written, cowritten, and edited 10 books. Additionally, he is a contributing editor for *Prospect Magazine*, a senior research associate at Oxford's Uehiro Centre for Practical Ethics, and an award winning documentary maker for BBC radio.

David Edmonds

David Edmonds' work lies within the philosophy subgenre of practical ethics (Edmonds 2016a). One of his recent books, *Would you Kill the Fat Man?*, which was picked for Editor's Choice in the New York Times, describes the Trolley Problem and its many variations. Beyond simply describing the moral puzzle, Edmonds discusses what the responses to this dilemma indicate about human morality (Edmonds 2013). Edmonds has also written a book called *Caste Wars: The Philosophy of Discrimination* (Edmonds 2006), which discusses the emotional reactions to discrimination and the complexity of "rational discrimination," which is discrimination based on statistical evidence.

Edmonds has also coauthored a number of best-selling books with John Eidinow depicting historical events that impacted the field of philosophy and society more generally. *Wittgenstein's Poker* (Edmonds and Eidinow 2014) describes the 10-min argument between Karl Popper and Ludwig Wittgenstein in Cambridge, and the consequences of this argument for both the field of philosophy and history. *Bobby Fischer Goes to War* (Edmonds and Eidinow 2011) describes the chess match in 1972 between an American, Bobby Fisher, and a Russian, Boris Spassky, which has often been called the most famous chess match of all time. *Rousseau's Dog: A Tale of Two Philosophers* (Edmonds and Eidinow 2007) focuses on the argument between Hume and Rousseau that turned the two philosophers into mortal enemies. Edmonds has also compiled and edited the essays of over 40 philosophers into a single book labeled *Philosophers Take on the World* (Edmonds 2016b). These essays cover topics such as guns, abortion, hatred of sports, and the morality of drinking alone.

Edmonds also produces and co-runs a number of podcasts with Nigel Warburton, a philosopher and freelance writer. *Philosophy Bites*, which has over 30 million downloads, interviews different philosophers for 15–20 min on a specific topic. Past featured philosophers include Peter Singer, Simon Blackburn, and Martha

Nussbaum. Other podcasts that he is involved with include *Free Speech Bites*, which tackles issues of free expression, and *Social Science Bites*, which includes interviews with leading social scientists such as Stephen Pinker and Kate Picket. Interviews from different podcasts have been compiled into a number of books, including *Philosophy Bites*, *Philosophy Bites Back*, *Philosophy Bites Back Again*, and *Big Ideas in Social Science* (Philosophy Bites n.d.).

Conclusion

David Edmonds is a prolific writer whose work has made significant contributions to the field of philosophy, as well as numerous fields of social sciences. His books manage to be digestible for the general public while remaining interesting to other philosophers and academics. If interested, further information on David Edmonds can be found at <http://davidedmonds.info/>.

Cross-References

- [Trolley Problem, The](#)
- [Would You Kill the Fat Man?](#)

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David F. Bjorklund

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Definition

David Bjorklund is an evolutionary developmental psychologist and Professor of Psychology at Florida Atlantic University.

Introduction

David Bjorklund was born in Worcester, Massachusetts, in 1949. He earned his Bachelor of Arts in 1971 from the University of Massachusetts – Amherst. He continued his education by earning his Master of Arts from The University of Dayton in 1973. He earned his Ph.D. in Developmental Psychology in 1976 from the University of North Carolina – Chapel Hill. After earning his Ph.D., Dr. Bjorklund joined the faculty of Florida Atlantic University. He has also served as a visiting professor at several prestigious institutions – including Emory University, The University of Georgia, James I University, and the Max Planck Institute for Psychological Research.

Career and Contributions

His current research interests include children's cognitive development and evolutionary developmental psychology. Over the past 40 years, Dr. Bjorklund has been awarded over \$700,000 in grants to aid in his research in developmental psychology. His research has focused on a variety of subjects, including cognitive development in children, suggestibility, false memories in children, and mental representations in nonhuman primates.

Dr. Bjorklund has been publishing empirical psychological research for over 45 years. He has published over 130 peer-reviewed articles in the areas of cognitive and developmental psychology.

He has also authored and co-authored several books on the subject of evolutionary developmental psychology – including *Children's Thinking: Cognitive Development and Individual Differences* (2012) and *Why Youth is Not Wasted on the Young: Immaturity in Human Development* (2007) which has been translated into Dutch and Korean, *Child and Adolescent Development: An Integrative Approach* (2012), *The Origins of Human Nature: Evolutionary Developmental Psychology* (2002), and *Looking at Children: An Introduction to Child Development* (1992). Dr. Bjorklund has also edited and co-edited many volumes on this subject as well, such as *Children's strategies: Contemporary Views of Cognitive Development* (1990), *Origins of the Social Mind: Evolutionary Psychology and Child Development* (2005), and *False-memory Creation in Children and Adults: Theory, Research, and Implications* (2000).

Dr. Bjorklund is currently the editor of the *Journal of Experimental Child Psychology*. He was also the associate editor of the journal *Child Development* from 1997 to 2001. He has also served on the editorial board for several peer-reviewed evolutionary psychology journals, including *Evolutionary Psychology*, *Journal of Comparative Psychology*, and *Evolutionary Behavioral Sciences*, as well as many peer-reviewed developmental psychology journals, such as *Developmental Review*, *Journal of Cognition and Development*, *Cognitive Development*, and *Educational Psychology Review*.

Conclusion

Dr. Bjorklund continues to conduct evolutionary developmental psychological research at Florida Atlantic University. He has remained an active professor, scientist, author, editor, and peer reviewer. He currently is the head of Florida Atlantic University's EvoDevo Laboratory, which focuses largely on how the environment interacts with one's genes to influence perceptual development in children. He also continues to teach undergraduate and graduate courses in cognitive development and evolutionary psychology.

Cross-References

- ▶ [Cognitive Changes in Adolescence](#)
- ▶ [Cognitive Ethology](#)
- ▶ [Development of Adaptations](#)

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David Haig

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Synonyms

[Evolutionary biologist](#); [Geneticist](#); [Researcher](#); [Theorist](#)

Definition

David A. Haig is an evolutionary biologist and the George Putnam Professor of Organismic and

Evolutionary Biology at Harvard University. He received his undergraduate and graduate degrees from Macquarie University in his native Australia and later held fellowships at Oxford and Harvard. His work in evolutionary theory spans a wide range of topics, including meiosis, human pregnancy, plant life history, the genetic code, gene selectionism, genetic conflicts, and genomic imprinting.

Introduction

We typically assume that each one of us is just that: a *one*. David Haig's work in evolutionary genetics exposes the flaw in this assumption. His evolutionary theories show how at the genetic level one isn't really *one* so much as *two*. Two genomes, one from mother and one from father, paired together transiently, each an object of natural selection. Although under certain conditions natural selection may favor cooperation between the two genomes during the development of the organism, under others it may foment conflict between them, for what is best evolutionarily for one is not necessarily best for the other. Haig has focused on these internal genetic conflicts and chronicled how natural selection acting at cross purposes on the two halves of the *one* has shaped our genetic system, our development, and our behavior in unexpected ways. He is perhaps best known for his work on the evolution of genomic imprinting and the evolution of imprinted genes in response to such evolutionary conflicts. Haig's perspective, that an individual is divisible into genetic factions, is necessary both for understanding why genomic imprinting evolves and for understanding the forces that have guided the evolution of the human brain and behavior.

The Kinship Theory for the Evolution of Genomic Imprinting

Genomic imprinting is an epigenetic phenomenon known to occur in dozens of genes in the genomes of flowering plants and mammals (Ferguson-Smith 2011). An imprinted gene has a different

expression level depending on its parental origin, which most often manifests as complete silencing of the maternally derived allele and expression exclusively from the paternally derived allele, or vice versa. Imprinted expression is found predominantly in genes expressed in the placenta and brain of mammals and in the endosperm of seed plants. Imprinted genes influence a diverse range of phenotypes, most notably growth and social behavior.

In the late 1980s, these were the known facts of genomic imprinting, and a motley collection of seemingly unrelated facts they were. Haig introduced his kinship theory for the evolution of genomic imprinting, which at once made sense of the various phenotypic effects, the narrow tissue-specificity, and the disjunct taxonomic distribution of imprinted genes (Haig and Westoby 1989; Haig 1997, 2000). He emphasized that in both mammals and seed plants growth depends on resources provided by a mother and comes at the expense of her ability to raise more offspring. Growth is itself a kind of social behavior in both taxa in that it indirectly affects the fitness of kin, and any organ – be it a brain, a placenta, or the endosperm of a seed – that can influence the allocation of limited resources among kin can therefore be an arena for genomic imprinting.

The kinship theory relies on a few reasonable premises to arrive at the evolution of imprinted expression: first, genes of maternal and paternal origin within an individual organism are not equally related to the individual's kin group; second, the optimal phenotypes – i.e., the behaviors or growth patterns that maximize inclusive fitness – are different for maternally and paternally derived genes; third, these phenotypes are sensitive to the gene's total expression level; and fourth, owing to epigenetic cues of parental origin, genes can achieve a different expression level when they are maternally versus paternally derived. If these premises hold, natural selection will favor genes with parental origin-specific expression levels. It is as though the two alleles at a locus take sides according to their parental origin and debate the total expression of the gene through the course of evolutionary time. When one evolves an increased expression level, the

other counters by evolving a decreased expression level. This evolutionary debate proceeds until natural selection has produced a gene that silences itself when inherited from one parent but expresses itself when inherited from the other, at which point the debate ceases (as an allele's expression cannot go any lower than zero).

For example, consider a gene for a growth factor produced by the fetal placenta during a mammalian pregnancy. The gene's increased expression confers growth on the offspring that expresses it at a cost to the mother who provisions him; in other words, the current offspring feeds but future siblings starve. Because of partner switching, the paternally derived allele is less likely than the maternally derived allele to be found in identical copies in these future siblings and so values this mother's future reproduction less than the maternally derived allele does. Natural selection will therefore favor higher gene expression when paternally derived than when maternally derived. In contrast, the maternally derived allele would be passed to the next generation in more identical copies – via the bearer's own reproduction plus that of future siblings – were it to temper the current offspring's growth somewhat. Thus, slight decreases to this gene's expression level when maternally derived would be favored and slight increases when paternally derived would also be favored. The kinship theory predicts that imprinted genes silenced on the maternally derived copy are those that generally enhance growth at the expense of kin and, vice versa, imprinted genes that temper growth are silenced when paternally derived, a prediction that is broadly supported by the data (Haig 2004).

Conflict in the Evolution of Human Behavior

But growth is not the only phenotype over which there may be conflict between the two genomes nor are proteins that pass between fetal and maternal tissues the only armaments available to genes in conflict. A wide range of social phenotypes – e.g., sleep duration (Haig 2014), impulsivity (Dent et al. 2018), and mentalizing ability

(Crespi 2008) – may entail different fitness effects for genes of maternal and paternal origin, and individuals' brains can affect their kin's fitness just as much as individuals' growth. A complete understanding of the human brain therefore requires recognizing that conflict may be widespread during its development and may have been a potent force in its evolution.

Much can be learned about the development and evolution of the human brain through the study of imprinted genes and imprinting disorders. Haig, for example, has studied Prader-Willi syndrome (PWS) to understand features of human behavior and life history (Haig and Wharton 2003). PWS is characterized by low muscle tone, a weak suck, high fatness, excessive sleep in infancy, and hyperphagia starting by about the age of four and a half. It is also associated with an increased risk for psychosis (Buiting 2010). PWS results from an absence of paternally expressed imprinted genes on one small region of human chromosome 15. Interpreted in light of Haig's kinship theory, the PWS phenotype is an overshoot of the maternally derived genome's optimum for these traits (equivalently, PWS can be viewed as an undershoot of the paternally derived genome's optimum); maternally expressed imprinted genes are naturally selected to promote decreased muscle tone, increased fat deposition, prolonged sleep, increased motivation for seeking supplemental foods, and an increase in the mentalizing abilities that become pathologically exaggerated in schizophrenia. Angelman syndrome (AS) is another imprinting disorder that, in contrast with PWS, results from the absence of a maternally expressed imprinted gene from the same region of chromosome 15. Children with AS display almost the opposite traits as those with PWS. They are hyperactive and hypertonic, they sleep less than normal children, and they have an increased incidence of autism (Buiting 2010).

That there are diametrical disorders such as these, which result from the over- or under-expression of imprinted genes, lends support to the kinship theory for the evolution of genomic imprinting (Úbeda and Wilkins 2008); the kinship theory ably predicts the opposite effects resulting

from the loss of expression of maternally or paternally expressed imprinted genes. Further, these disorders have inspired a view of the normal brain as lying on a spectrum between two extremes, each of which corresponding to a disease state that results from the overshoot of some genomic faction's optimum (Crespi 2013).

The novel perspective that emerges is one of genes clashing evolutionarily over how the brain should develop. The kinship theory, with its emphasis on the asymmetric relationships between maternally and paternally derived genomes to other kin, provides the evolutionary rationale for why there would be such battling within the individual during development, and it identifies the warring factions. It leads to the view that normal development results when these warring factions reach not a détente – for harmonious conflict resolutions are difficult to evolve – but rather an impasse. A normal brain is one where the opposing hostilities balance each other. Perhaps the most intriguing extension of Haig's kinship theory logic is to normal variation among humans. In principle it is possible that normal variation in human behavior and personality is the result of slight imbalances in the expression of genes that when greatly imbalanced lead to disease states (e.g., Goos and Silverman 2006; Crespi et al. 2018).

Conclusion

Haig's kinship theory does more than offer an explanation for a seemingly obscure epigenetic phenomenon. Like natural selection itself, it provides a new lens through which to view nature and bring into focus the logic of its design. The implications of Haig's kinship theory for evolutionary psychology are far-reaching. The theory suggests that normal behavioral phenotypes result only when a balance is achieved between the opposing pushes and pulls of maternally and paternally expressed imprinted genes during development. The theory also underscores how the evolution of these phenotypes and others has been shaped not only by selection on the organism itself but also by selection on the genes within it. We should recognize that each one of us contains genetic

factions, each of which are the targets of natural selection, and that the individual that results has been designed with their interests in mind as much as ours.

Cross-References

- [Genetic Relatedness Affects Aid to Kin](#)
- [George Williams](#)
- [Hamilton's Rule and Kin Investment](#)
- [Hamilton's Rule and Theoretical Implications](#)
- [Kin Selection](#)
- [Life History Theory](#)
- [Parental Investment Theory](#)
- [Parent-Offspring Conflict](#)
- [Robert Trivers](#)

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David Wasserman

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Definition

David Wasserman is the former Director of Research at the Center for Bioethics at Yeshiva University. He is currently on the faculty at the Department of Bioethics of the National Institutes of Health. He specializes in ethical issues related to reproduction, reproductive technology, genetics, neuroscience, and disability.

Introduction

David Wasserman began working in the Department of Bioethics at the National Institute of Health in 2013. He serves on the editorial boards for the journals *Ethics* and *Journal of Applied Philosophy* and is a Fellow of the Hasting Center for Bioethics (National Institute of Health 2019). He is also the Vice President of the Society for Philosophy and Disability and a member of the American Philosophical Association, the APA Committee on Law and Philosophy, the American Society for Bioethics and the Humanities, and both the District of Columbia and New York Bar Associations. He was previously the Director of Research at the

Center for Ethics, Yeshiva University (National Institute of Health 2019). Wasserman has made significant written contributions to the field of bioethics, with particular attention paid to ethical issues in reproduction, reproductive technology, neuroscience, health care, genetics, and disability. His many publications include two co-authored books (*Disability, Difference, Discrimination: Perspectives on Justice in Bioethics and Public Policy* (Silver et al. 1998) and *Debating Procreation: Is it Wrong to Reproduce?* (Benatar and Wasserman 2015)) and four co-edited volumes (*Genetics and Criminal Behavior* (Wasserman and Wachbroit 2001); *Quality of Life and Human Difference: Genetic Testing, Health Care, and Disability* (Wasserman et al. 2005); *Harming Future Persons: Ethics, Genetics, and the Nonidentity Problem* (Roberts and Wasserman 2009); and the *Oxford Handbook of Philosophy and Disability* (Wasserman and Cureton in press)).

Education and Career

David Wasserman earned a Bachelor of Arts in Philosophy from Yale University in 1975. He went on to earn a Juris Doctorate at the University of Michigan in 1978 and a Masters of Arts in Psychology at the University of North Carolina in 1984. Thereafter, he was an Assistant Professor and Director at the University of Connecticut School of Law (1984–1985), a Senior Staff Attorney in the Criminal Appeals Bureau for the Legal Aid Society (1981–1986), a Fellow at the New York University School of Law (1986–1988), a Fellow in Ethics and the Professions at Harvard University (1988–1989), a Research Scholar at the Institute for Philosophy and Public Policy at the University of Maryland (1989–2007), and the Director of Research at the Center for Ethics at Yeshiva University (2007–2014; Wasserman 2019). He is currently on the faculty at the Department of Bioethics of the National Institutes of Health, where his work focusses on the ethics of reproductive technology, genetic research and technology, health care, and disability.

Books and Edited Volumes

In addition to numerous articles and book chapters, David Wasserman has co-authored two books and has co-edited four books (three published, one forthcoming). Along with Anita Silvers and Mary Mahowald, Wasserman outlines current issues in bioethics in *Disability, Difference, Discrimination: Perspectives on Justice in Bioethics and Public Policy* (Silver et al. 1998). Specific topics, covered in the context of the Americans with Disabilities Act of 1990, include genetic discrimination, the so-called heroic treatment of impaired neonates, and euthanasia and assisted suicide among the severely disabled. The book includes three essays (one each by Silver, Wasserman, and Mahowald) where each author takes a different philosophical stance (libertarian, liberal, and egalitarian feminist, respectively) and where each essay is followed by criticisms by each of the other authors. Wasserman argues in favor of distributive justice approach that aims to balance the social tasks of either correcting people's disabilities or accommodating them in order to accomplish equality and full social participation of all people.

Wasserman followed his initial book with three edited volumes that similarly debate ethical issues related to genetics, disabilities, and reproduction. In 2001, he co-edited, along with Robert Wachbroit, a volume titled *Genetics and Criminal Behavior* (Wasserman and Wachbroit 2001). Contributing philosophers discuss important ethical considerations raised by genetic research into criminal behavior. Wasserman followed this edited volume with another titled *Quality of Life and Human Difference: Genetic Testing, Health Care, and Disability* (Wasserman et al. 2005), which discusses health policy, ethics, and social issues raised by prenatal testing for disability over nine essays. A third edited volume, titled *Harming Future Persons: Ethics, Genetics, and the Non-identity Problem* (Roberts and Wasserman 2009), is comprised of 16 chapters that cover the ethical obligations we have with respect to future persons and offspring and the ethical implications of our actions on future generations. Contributors specifically discuss the nonidentity problem, which is a paradox within population ethics involving the

inability to hold three views simultaneously: (1) that an act can be wrong only if that act makes things worse for or harms an existing or future person (i.e., the person-affecting view), (2) that an act that confers on a person a flawed existence is not bad for that person if the person could never have existed without that act, and (3) some acts that bring a person into existence are wrong even if not wrong for someone (see Roberts 2019).

Continuing his work on ethical considerations surrounding procreation, Wasserman teamed up with David Benatar to co-author *Debating Procreation: Is it Wrong to Reproduce?* (Benatar and Wasserman 2015). In this book, Benatar and Wasserman take contradictory views on the ethics and permissibility of reproduction. Benatar takes an anti-natalist perspective by arguing that reproduction is always morally wrong because, according to Benatar, coming into existence in and of itself always causes a serious harm to the individual. Benatar further contends that even if existence were not always harmful, the risk of harm is sufficient as to make procreation always wrong. Moreover, he asserts that because humans are defective and cause harm on a large scale (e.g., environmental harm, pain, and suffering to other living beings) that it is unethical to create more of them. In contrast, David Wasserman defends procreation with a series of moderate pronatalist arguments that describe procreation as permissible, but not required. Wasserman begins by criticizing what he views as the overreliance of anti-natalists on the argument that the avoidance of harm is more important than the accrual of benefits. He goes on to outline several pronatalist arguments that he believes should be only somewhat constrained based on the well-being of the future child (see also, e.g., Wasserman 2005). Wasserman maintains that the expected good of a future child and of the parent-child relationship can justify procreation, even in the face of expected adversity (e.g., disabilities).

Most recently, Wasserman co-edited the *Oxford Handbook of Philosophy and Disability* (Wasserman and Cureton in press). This edited volume features contributions by several prominent philosophers who summarize and discuss

ethical views of disability. Example topics include social inclusion, justice, reproductive choice and technology, moral and social status, neuro-technologies, discrimination, and parental autonomy, among others. This most recent work expands on the topics Wasserman specializes in (e.g., reproductive technology, bioethics, disabilities) by applying philosophical and ethical perspectives to contemporary issues.

Conclusion

David Wasserman has made and continues to make important contributions to the field of bioethics and related disciplines. His extensive written work on ethical issues surrounding disability, reproduction, genetics, biotechnology, neuroscience, and health care advances discussion on these topics in ways that can potentially inform public policy (e.g., Wasserman 1998) and encourage discourse (e.g., Benatar and Wasserman 2015).

Cross-References

- [Permissibility of Reproduction](#)
- [“Debating Procreation” \(With David Benatar\)](#)

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Day Care

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Definition

A place, facility, program, or organization that takes care of children during the day, usually while their parents are at work.

Synonyms

[Daycare](#); [Nonparental childcare](#)

Introduction

The number of US children who spend time in daycare has risen markedly in the past four decades (Johnson 2017). Currently, six million children under three-years-old are in nonparental care. A majority of US children will spend time in some form of nonparental care before age five (Zero to Three 2017).

While nonparental childcare is, statistically speaking, a current cultural *norm*, it has not

quite eclipsed stay-at-home parental care as a cultural *ideal*. Therefore, while 62% of mothers with infants are in the labor force, working American mothers still contend often with ambivalence, guilt, and social attitudes that may characterize them as less warm and committed than stay-at-home mothers (Brescoll and Uhlmann 2005).

As nonparental childcare has grown, child development researchers have become increasingly invested in learning about the implications of this form of care for children, their parents, and society at large. Early daycare research focused mostly on comparing home-reared and daycare children, looking to address fears that nonparental care might harm young children by disrupting their attachment relationships with their parents, undermining parental influence, or stunting their emotional and intellectual development. Early researchers were also interested in whether professional child caregivers could develop deep, nurturing bonds with the children in their care to provide them with quality interpersonal experiences necessary for healthy development.

In recent decades, with accumulating evidence showing that the “home-reared” and “daycare reared” labels were not in themselves predictive of developmental outcome, research has begun to focus on mapping how child and parent characteristics, environmental conditions, and the cultural milieu interact to produce developmental outcomes in children across care arrangements. We understand today that child development occurs and should be understood and studied in a multidimensional context, where both proximal (e.g., the home and daycare environments) and distal (e.g., governmental childcare policies; parental work stress) conditions interact to shape developmental trajectories. Concurrently, the old *nature vs. nurture* formulation has been supplanted by the understanding that children’s development and adjustment are shaped by *both* genetic and environmental influences in a complex, interactive dance (Shpancer 2006).

Daycare Research: Methodological Difficulties

Daycare research is not easy to conduct or interpret. True experimentation is not usually feasible due to ethical constraints (researchers cannot force a group of parents, chosen at random, to care for their children in a particular way). In the absence of true experimentation, cause and effect relationships are difficult to discern. In addition, genetic and environmental influences on child development are often correlated, which makes the task of teasing them apart challenging. For example, highly anxious parents may transmit the genetic make up for anxiety to their child and also practice an overprotective caregiving style. Moreover, different individual children select different environmental niches based on their temperamental tendencies. A hyperactive child will not likely choose to spend time in the library. His poorer academic performance may correlate with low library attendance, but his genetic makeup may be the cause for both his low attendance and his poor academics.

To complicate matters still, recent studies have suggested that children are differently predisposed genetically to being influenced by their environment, including the daycare environment. Some children are thus more prone to suffer adverse effects in daycare because their genetic endowment renders them more reactive to environmental stress. Such genetic individual differences may explain some of the inconsistency of findings in research on children’s adjustment in daycare (Belsky and Hartman 2014).

Finally, the results of daycare research are often open to competing interpretations, some of which may be guided by sociopolitical considerations far removed from – and at times hostile to – the jurisdiction of science (Crosnoe and Leventhal 2016). For example, if maternal employment is found to place some infants at higher developmental risk, how much child risk is our society willing to accept in the name of protecting mothers’ right to pursue financial independence and professional fulfillment (both of which may

confer benefits on their children later on in development)? No surprise then that daycare research has been at times both a contentious and a mad-deningly inconsistent field of inquiry.

Daycare Research: Consensus Findings

Still, the literature has converged onto several consensus conclusions. First, an emerging consensus in the literature is that daycare attendance does not inherently disrupt optimal child development and parent-child attachment relationships (Belsky et al. 2007; NICHD Early Child Care Research Network 1997). Second, family variables are, by and large, more predictive of child development than daycare variables, even for children who spend significant time in daycare (Shpancer 2006). Third, caregivers can indeed develop close, secure attachments with the children in their care, independent of parent-child attachment (Goossens and van Ijzendoorn 1990).

Another consensus for daycare researchers has crystalized around the importance of care quality. High-quality daycare has been shown to improve early learning, cognitive, language, and socioemotional development, as well as school achievement, with some effects lasting into adolescence and beyond (Child Care Aware of America 2017; Vandell et al. 2016; Zero to Three 2017). High-quality nonparental childcare may also serve as a protective factor for children from disadvantaged, chaotic home environments (Berry et al. 2016). High-quality care, of the kind that is associated with developmental gains for children, includes warm, responsive, and engaged caregivers; a safe and stimulating environment; and structured educational activities (Brooks-Gunn 2017).

Daycare: Lingerin Concerns

At the same time, concerns and challenges remain for daycare children (and their parents). First, research has shown quite consistently that under

some circumstances, particularly maternal insensitivity and low-quality daycare, extensive non-parental care in infancy predicts higher risk of disrupted mother-child attachment (Hazen et al. 2015).

Another cause for concern has been the persistent suggestion from the research that children who spend much time in daycare exhibit more externalizing (noncompliance) problems, particularly if they spend many hours in low-quality care and in large groups of peers (McCartney et al. 2010). These increases, it should be noted, tend to be mild, and they do not replicate well in non-US samples and when more rigorous designs are used (Dearing and Zachrisson 2017).

Daycare children, particularly younger ones, also experience a rise in respiratory tract and other infections, mostly upon entry to daycare (Schuez-Havupalo et al. 2017). Research has also found elevated levels of the stress hormone cortisol in children attending daycare (Groeneveld et al. 2010). Higher cortisol is of interest in part because of its association with poorer executive function in children. The long-term developmental implications of this finding are not yet clear, but research has suggested that multiple factors, such as daycare quality, caregiver competence, parent-child attachment, and parental social support may moderate this pattern (Wagner et al. 2016).

Another point of concern emerging from the research is that while parents by and large report satisfaction with their daycare arrangements, most daycare programs in the US today do not meet criteria for high quality (Child Care and Health in America 2016; NICHD Study of Early Child Care and Youth Development 2006). The mediocrity of daycare quality in the USA is troubling particularly in light of accumulating evidence showing that developmental gains for daycare children occur quite exclusively in high-quality settings (Peisner-Feinberg et al. 2001).

Alongside persistent concerns about quality, another fundamental concern regarding the daycare system in the USA is affordability.

Daycare in the USA – particularly formal, center-based high quality care of the kind that is associated with developmental gains for children – is pricy, costing as much as 12,000 dollars per year depending on the state. The average cost of infant day care may be as high as \$17,000 per year (the younger the child the more expensive the care, in part because caregiver-child ratio is smaller for younger children). The average cost of keeping an infant in center-based care is higher than college tuition in most states (Zero to Three 2017). Cost is the most commonly reported obstacle for families seeking childcare. Daycare costs have risen roughly 70% between 1985 and 2012 (Child Care and Health in America 2016; Laughlin 2013). High-quality daycare is currently out of reach for many poor and even middle-income families (Whitehurst 2017). Families therefore often must rely on relative care or a patchwork of informal unregulated arrangements of middling quality.

Conclusion

Daycare for infants and young children is normative in today's America. A majority of families with young children will at some point choose to use nonparental childcare services. Working parents need and want – and their children surely deserve – high quality, accessible, and affordable daycare. Spending time in safe, stimulating, and stable environments with properly educated, caring, and fairly compensated daycare professionals will facilitate most children's progress on the path to becoming well adjusted and productive adults (Brooks-Gunn et al. 2016). Thus, high-quality daycare is a sound social investment, and the return on investment in the early years is greater than what we typically get for intervening in later years (Brooks-Gunn, 2017; Karoly 2016). Unfortunately, the current state of American daycare is far from optimal. Too many daycare facilities lack in quality. Too many families lack education about, and access to, high-quality daycare. Figuring out how to solve these problems is an urgent challenge to which our society is yet to rise.

Cross-References

► Child Care

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Daycare

► Day Care

de Clérambault's Syndrome

► Erotomania

Death

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Synonyms

Extinction; Fatality; Mortality; Phenoptosis; Senescence; Thanatology

Definition

The irreversible cessation of all biological functions in individual organisms. A high degree of consensus focuses on cessation of pulse, breathing, brain activity, and personhood as defining characteristics of clinical death in human beings.

Introduction

Death is a phenomenon most human beings above the ages of about 4–7 “understand” and think about somewhat (Talwar et al. 2011), and medical science is largely clear about it, if with some caveats (Laureys 2005). But we retain diverse cultural and religious views on the theory and actuality of death and dying, while its universality is reflected unevenly in interdisciplinary sources on the topic. In one of the first edited, interdisciplinary, systematized collections on the subject, Feifel (1959) remarked how little was known; this was despite Weismann’s (1889) seminal work on programmed death. Death here is taken to be the complete and irreversible cessation of biological functions, indeed all functions of the individual. Religious and hypothetical concepts of an afterlife or “noncorporeal continuance” are not considered extensively but recent work in resuscitation science suggests loss of vital signs may not be accurately deemed the customary “moment of death” (Parnia 2014).

In the interests of semantic and developmental clarity, we might argue that *dying* is first characterized by massive sperm elimination before conception. Miscarriage and stillbirth remain significant losses, as do experiences of sudden infant death syndrome. For those who grow old and have a “standard death,” a life entails a chronic process of risks from early intrauterine existence onward, and apoptosis that accompanies the entire life course (Shields 2008), punctuated by individual biomarkers of aging and major transitions like menopause, accelerated molecular damage (Salinari and De Santis 2015), and finally to terminal diagnosis and end of life care. In the final stages, breathing slows, death rattle (terminal respiratory secretions) may occur, heart stops

(*clinical death*), and minutes later brain death signifies the moment of expiry, when urination or defecation may occur. Confirmation of loss of vital signs is given (*legal death*), and decomposition by autolysis (self-digestion) proceeds within minutes.

Just as biological age differs from chronological age between individuals (Simm et al. 2008), subjectively we may all feel younger or older than the supposed norm for our age, and the sense of mortality varies (Diehl et al. 2015). The “oldest old” (over 95) are often very ready for death or welcome it (Fleming et al. 2016), and even many younger but depressed, or badly disabled, people confront religious or statutory prohibitions on seeking assistance with voluntary dying.

Worldwide, approximately 57 million human beings die annually (Spellman 2014) and by most estimates about twice as many are being born. Causes of death worldwide are categorized in specific medical etiologies and circumstances, including cardiovascular disease and cancers, through infections, malnutrition, accidents, suicide, murder, executions, and mass disasters (Lozano et al. 2012). Average lifespan in the Paleolithic was 33; in early modern England (sixteenth to eighteenth centuries) 33–40; in the 1950s worldwide it was 48; and in 2010 it was 67.2. Today life expectancy varies by gender, ethnicity, region, and other factors but in the USA in 2014 was 78.94 (76.6 male to 81.4 female). In the USA in the 1850s infant deaths (below age 5) ran at an estimated 216 per 1000 but in 2014 were recorded as 582 per 100,000. The oldest documented person worldwide was Jeanne Calment (1875–1997) who lived to 122. Fogel (2004) charts the rise of life expectancy across the past 400 years. The *Hayflick limit* and other measures suggest a natural upper limit to human life spans based on telomere shortening in chromosomes (Burnet 1974; Dong et al. 2016; Mueller and Rose 1996). Volk and Atkinson (2008) estimate that prior to the last 200 years, approximately 50% of children died by the age of one and 80% by the age of 18.

In the widest context, the universe had a beginning and will have an end dictated by entropy (Impey 2010). All forms of matter are subject to

change and it is estimated that the vast majority of species have become extinct. Indeed, constant biological turnover from cells through to all species is unavoidable. *Homo sapiens* are subject to the same principles but appear to be the first species in which each individual is aware of his or her unavoidable future death. One estimate of how many people have ever lived (and therefore died), taking *Homo sapiens* to commence 50,000 years ago (this figure is often put at 200,000 years), is 108 billion.

Scientific Aspects of Death

Sometimes known as thanatology, the scientific study of death includes aspects of physics, chemistry, biology, and medicine. Howard (2016) after Schrödinger, reminds us that animals convert solar energy (light) into heat, as part of a universal entropic principle: animals must work to survive, to exist instead of succumbing to nonbeing, and in this process life generates constant turnover, complexity, and chaos. Clark (1996) charts a path from unicellular organisms about four billion years ago, through multicellular evolution from two billion years ago. Human cells are vulnerable to damage, and dead cells are disposed of by macrophages (cells with an “undertaker” function), which decompose and recycle them. This process of necrosis or accidental damage is one of about seven theories of aging. Another is the simple “wear and tear” or mutation accumulation (Goldsmith 2014). Another, known as programmed cell death, or phenoptosis, explains why all organisms must die. Vertebrate embryos display “almost uninterrupted cell growth” (Clark, op cit., p. 29), a pattern that changes, however, for humans as the cells for the evolutionary remnants of gill and web structures, for example, are forced to die at around eight weeks in the womb. Indeed, this has been referred to as “the [programmed] act of suicide by a cell” (Clark, op. cit., p. 32). Cells so affected undergo the process of apoptosis or gradual disintegration.

Clark places the origin of programmed death at one billion years ago, distinguishing between unicellular reproduction by fission and multicellular reproduction by sex. Sexual reproduction has the advantages of genetic variation which enhances

adaptation and of repair and removal of defects. But it is also intimately associated with the “clock of senescence,” as well as the gene-centered view of evolution. Clark here refers to “the irrelevance of our somatic selves” in the universal scheme of things, and here we are faced with the controversy of the scientifically endorsed indifference of nature versus the precious human individuality championed by most religion, social and human sciences, or evolutionary humanism in Chisholm’s (1999) terms.

Disease has always been with us, and human history is partly defined by the terrors and fatalities associated with the black death, syphilis, smallpox, typhus, cholera, tuberculosis, malaria, and others. Dense communities, agriculture, migration, wars and other opportunities have helped diseases to spread. Recent life-threatening epidemics include avian flu, dengue fever, swine fever, AIDS, Ebola, and the Zika virus. Anthrax is but one deadly disease that occurs naturally, can spread among cattle, and can be used as a weapon; in order to preserve its own life cycle, anthrax has no alternative but to kill its human host. Epidemiological research is ever alert to outbreaks; our predators are now rarely visible. The developing field of evolutionary medicine addresses the distal origins of health and disease (Gluckman et al. 2016). In what we might call an ecology of death, monitoring of mortality related to contemporary climate change also shows some positive correlation.

In general, larger animals live longer lives but there are exceptions. Typical maximum lifespan of bats is 2, the mouse 3, canary 24, bear 30, lion 30, gorilla 40–50, chimpanzee 50, elephant 60–80, golden eagle 80, giant tortoise 170, bowhead whale 211. A female Greenland shark has been carbon dated to an age of approximately 400 years, and it is believed the slow-growing species only becomes fertile at an age of 150. Different species of jellyfish live from a few hours to several months, and the unique species *Turritopsisdohrnii* is said to be potentially immortal, at least in laboratory conditions, since it can reverse its aging process. Factors of temperature, calorific intake, metabolic rate, sleep and hibernation, environment, and predatory niche, all

account for differences in longevity. Notable too are those creatures whose deaths are very closely associated with sex: migrating salmon that die after spawning; female spiders that devour their male mates during sex; female toads that drown after breeding events with multiple males (Howard 2016). Many animals use camouflage or displays of false ferocity to deter predators, and some feign death as a strategy for escape (Trivers 2011) as part of a “co-evolutionary struggle between deceiver and deceived” (p.30). Such “thanatomimesis” is sometimes enacted by soldiers on the battlefield in order to deceive enemy combatants and avoid death. As far as we know, humans are rare in their awareness of and emotional responses to the deaths of conspecifics, but some dolphins and whales have been rigorously documented as supporting and carrying their dead young in what appears to resemble mourning behavior (Reggente et al. 2016).

It has been a long-accepted practice to experiment on and dissect animals in order to understand pathological processes. Human cadavers may be dissected to determine cause of death or for medical research. The natural and induced chemistry involved following a death is predictable: coagulation of blood, drop in temperature, rigor mortis, cell death, breakdown of enzymes, putrefaction, the embalming process using formaldehyde, draining of stomach contents, decomposition accompanied by foul odors, dehydration, bloating, and shrinking. Few of us ever witness this process, but Roach (2004) presents an account made palatable by some humor.

Death and Technology

Taylor (2010) argues contentiously that human evolution has long transcended susceptibility to natural selection pressures, by virtue of tool and weapon making, discovery of fire, cooking, the plough, and so on, up until present day sophisticated technology. One way of looking at this unstoppable technological trend is as a *thanatophobic treadmill*, whereby the sense of cognitive and practical mastery of the hazardous environment inflates neural activity (the “runaway brain”), which in turn generates further problem-solving, technology-creating activity. Many of

these discoveries and creations directly enhanced survival odds as well as conviviality, and continue to do so. By and large, we have few natural predators. Our food supply is regulated, indeed for urban dwellers is outsourced to farmers, abattoir workers, and butchers, so that most of us see little death in reality. Similarly, our conflicts against national out-groups are subcontracted to military agents; criminal justice systems where necessary to engage specialist staff to execute murderers; the sick and dying are frequently hospitalized and tended by health and care professionals; and human corpses are transported, embalmed, and disposed of by funeral professionals (Mitford 2000). Of course this pattern does not apply to all cultures, but it is increasingly the dominant trend.

Medical technologies have become very sophisticated, so that perinatal deaths and infant mortality have sharply declined. Many of us experience lifelong medical monitoring, are duly investigated, medicated and treated, and when deemed necessary kept alive on life support machines beyond the point at which we could survive unaided. Dialysis for kidney failure is one of these. Individuals in a coma or persistent vegetative state (PVS) (or “unresponsive wakefulness syndrome”) may be on life support systems for months or years. The PVS is characterized by brain damage rather than brain death, hence the legal and ethical controversies surrounding it. These show the lengths we go to maintain compromised human life, and a charge of institutionalized thanatophobia (i.e., an abnormal fear of death) may be leveled here, but we should remember that the now standard practices of defibrillation and cardiopulmonary resuscitation came into being only in 1899/1947 and 1904, respectively. Medical technology has thereby challenged the parameters of the “irreversibility” of death. Similarly, the lengthy care of those Alzheimer’s patients who lack memory (a major ingredient of personhood) can be seen as challenging another sign of death. In all these ways, independent vitality-compromise or disability is compensated for in a medical-technological war on morbidity which can be read as either compassion-driven or thanatophobic. Alternatively,

it may be read as resentment that creaturely death interrupts our ambitious life projects.

Many of us have minor handicaps such as myopia and hearing difficulties and need artificial aids to function normally, even more so in the case of people with mobility problems and serious health concerns who require prosthetics, painkillers, surgeries, and other medical aids. In a natural (nontechnological) environment, many of us would be unable to survive, that is, we would die. Paradoxically, often our technologies cause accidents, addictions, pollution, and so on, which may in turn cause illnesses, trauma, and sometimes fatal injuries and diseases. Technology is increasingly the human milieu and is inescapable. Most of us now die in unfamiliar settings, usually on acute hospital wards, often uncomfortably and with little control over our own deaths (O'Mahony 2016; Shuland 1997); and grief and bereavement too are forced into an unnatural medical mould (Bandini 2015).

Given internet access, including lifespan calculators, most people have a conscious awareness of their mortality and approximate lifespan prospects. DNA home testing kits are also available which can suggest inherited pathological conditions and genetic risks. Health promotion research and popular dissemination of results affect lifestyle choice and mortality. The actuarial profession uses mathematical models to predict risks of critical diseases and mortality. Lancaster (2009) charts a historical decline in fatal accidents (extrinsic mortality) due to improvements in skillful navigation of the technological environment (see Koopman et al. 2015 for an alternative view), which may mirror the claim of a historical decline in violence, war and their casualties as measured by death rates associated with multiple causes and contexts (Pinker 2011).

Technology does not stop at death, however. Organs of the dead can be transplanted into others' bodies, and some body parts grafted. Beyond the post mortem (and increasingly the digital autopsy), we now have some strenuous research efforts underway to understand senescence and slow it down, so that even if death cannot be defeated it can be significantly

postponed. De Grey (2008) is one of the many gerontologists refusing to accept normal aging and dying parameters. Scientific research on robotics, nanobots, and artificial intelligence also seeks to enhance technologies in the service of slowing senescence, postponing or transcending death in a so-called posthuman future. Thomson (2016) reviews progress in cryonics, the meticulous process of cooling a recently dead body (or, in many cases, only the head) to -196°C and keeping it stored in hypersecure conditions until a future, hopeful scientific breakthrough allows for full resuscitation, and hence a much extended lifespan. Cryopreservation is already used successfully for storing body parts, including stem cells as part of regenerative medical procedures. Posthumous reproduction also throws up many new challenges and possibilities (Brede and Sabanegh 2013).

Cultural and Historical Perspectives

Estimates vary as to the first human awareness of death resulting in the construction of burial sites and rites. Taylor (2003) puts it at 120,000 years ago. This is significant when set against the dating of the first primitive tools at 2.6 million years ago. Val (2016), however, discusses dating uncertainties surrounding the discovery of *Homo naledi's* putative deliberate body disposal in deep caves in South Africa that may indicate a practice of hominid funerary caching (hiding of remains) dating to three million years ago. The earliest Egyptian pyramids and ziggurats were built about 5000 years ago, and Stonehenge and surrounding burial mounds in southern England date to 4500 years ago. A combination of archaeological evidence and speculation suggests that around 4000 years ago in Britain some corpses were laid out for birds to partially devour, the large bones then being buried in a communal barrow. But such deliberate practices are historically marked by fear of souls of the dead and respect, with ample evidence of ceremonial burial dating back to 26,000 years ago. Rivers have also been used for disposal of the dead and still are today in some parts of the world. Taylor's (2003) sweeping archaeological and cultural analysis of death and the practices around it show a multiplicity of

religious and other views, including vampirism, cannibalism, mummification, human sacrifice, and near-death experiences. The archaeologically attested scale of ancient ritual violence and killing in Peru is enormous, where human sacrifice was conducted as part of a belief in communication with supernatural forces.

Some of the earliest literature such as the *Epic of Gilgamesh* (approximately 2100 BCE) portrays encounters with death and quests for immortality. Religion and theology necessarily include prescientific explanations for death, indicating that it has long preoccupied and troubled human beings. Religious and folk psychological beliefs about death dominated until the advent of biology and medicine. We cannot say with certainty that a majority have been afraid of death and averse to discussing it, but there are ample reasons to regard Western civilization today as “thanatophobic,” wary of thinking about and discussing it freely. Attitudes toward death have changed significantly over the centuries (Ariès 1972). Until 1960, the Amazonian Wari’ Indians were known to practice endocannibalism (also known as funerary cannibalism and practiced in other cultures and times), or dismembering, cooking and eating their dead relatives as a mark of respect and affection (Conklin, 2002). The Wari’ have a highly nuanced understanding of death but such practices would be greeted with disgust by Westerners. But consider by contrast, the modern American funeral industry in which death is impersonal, outsourced, and part of the nexus of capitalism (Mitford 2000). Going even further than this, Gunther von Hagens provides an example of the corpses of humans and animals being skinned, preserved, plastinated, and arranged in poses for public exhibition, education, and entertainment.

While many Western funerals have become “clinical,” managed, and minimally emotional, Jinkinson (Jinkinson 2005) reports on death rites in a small Greek island village. Crying and singing may follow the news of death, the corpse is viewed, and the face kissed before burial; after forty days a wake is held; after 5 years the remains are exhumed and the clean white bones are taken, the skull may be kissed; then all is wrapped in linen and stored in an ossuary; this may be

repeated after another year or two to ensure the journey of the dead person is complete. Villagers believe that the dead communicate with the living.

Stearns (2007) reports that in eighteenth century France, older fathers were the most common murder victims, due to sons being unable to gain economic independence while their fathers retained possession of farming land. Within the USA, significant cultural comparisons can also be made (Kunitz 2014). Warner and Swisher (2015) show that adolescent immigrants’ expectations of survival according to race, ethnicity, and nationality (Mexican, Puerto Rican and Cuban) are often characterized by pessimism. Notably, death in the developed world occurs mainly in association with senescence, whereas in the developing world much higher rates of extrinsic mortality are associated with infectious disease, hunger, and dehydration. Mortality rates within developed countries also vary by region, class, and ethnicity, according to several but uncertain factors of nutrition, economics, and life chances. See Rogers and Crimmins (2011) for a comprehensive review.

Religion and Death

The topic of death is found centrally in all religions and it is often claimed that religion, or theistic religion, originated in early humans’ struggle to accept and understand the death of loved ones and the inevitability of their own deaths (see also Varki and Brower 2013). By constructing myths and rituals and embellishing existing narratives, religion evolved to bind groups together to sweeten somewhat the horror of the sight of a corpse, to pacify the imagined deities responsible for death, and to ease the dead on their onward journey to heaven, Valhalla, or paradise. The *Egyptian Book of the Dead*, originating in 1550 BCE, is a funerary text containing spells for assisting the dead on their way to the underworld, or *Duat*.

The monotheistic religions share the theology of the fall, which holds humans responsible for death due to sin: “the wages of sin is death” (Romans 6.23). Humans are “mortals” while gods are immortal. Judaism, Christianity, and Islam depart from each other over the meaning of Jesus Christ but all retain visions of an

afterlife. Christianity distinctively places punitive, sadistic public death at its centre in the crucifixion of its messiah. The claim is made in Christian theology that Jesus raised Lazarus from the dead, was himself riser after being crucified and dying and that his loyal followers would also enjoy physical resurrection. Belief in an afterlife of one kind or another quells fear of death and promises immortality based on keeping the faith or living a good life. Tombstone inscriptions typically include religiospatial metaphors (passed, called away to rest, gone to a better place, “fell out of the sight of men,” and religious hopes (“so he giveth him his sleep,” and “promoted to glory”). The monotheistic tradition also advances various eschatologies, or theories about the expected end times, or annihilation of the entire human species.

Hinduism and Buddhism promulgate a different metaphysics entailing cycles of existence and reincarnation, again closely associated with living virtuously or skillfully. One Hindu group, the Aghoris, worship the deity Shiva, associated with destruction and practice overcoming fear and disgust by frequenting cremation grounds, drinking from skulls, and eating from human corpses. Buddhism is based on the empirical observation that “all life is suffering” and the Buddha’s four noble truths which expound a view that birth, aging, illness and death create suffering, resistance to which reinforces suffering. Afterlife is not the goal, but acceptance without craving a different kind of life: the Buddhist *maranassati sutta*, meditation on death, serves such an end. It is notable that most religious beliefs, including Buddhism, can inspire some followers to risk death in diverse ways, for example undertaking suicide missions (Liddle and Shackelford 2014) or burning oneself to death as a protest against injustice. They can, likewise, sometimes inspire murderous actions against perceived infidels. More routinely, religion provides comfort to the dying and bereaved, and clear practical guidance for disposal of the corpse. A common mystical interpretation of death is that our births are contingent, time is illusory, and the ego that frets about death is also illusory; properly understood in meditation, death cannot

trouble anyone who exists in the pure, animalistic present.

Psychological and specifically evolutionary-psychological analyses of religion are by no means in agreement on this topic, although in principle EP is bound to explain the evolutionary origins of religious behavior: what caused collective beliefs and rituals to arise that were costly in terms of energy output with no discernible immediate payoffs? Theories range across religion as an advantageous adaptation, for example, increasing group bonding against adversity and boosting optimism, spreading like memes or cognitive viruses, or alternatively as being a byproduct of other survival strategies. Although religious belief is often inferred from grave markings up to 100,000 years ago, most formalized religion dates back to only about 4000 years. Interpretations vary enormously and no straight forward, satisfying account has yet emerged. Evolutionary psychology like most contemporary science is skeptical, if not atheistic, and may be inclined to connect decline in religious belief partly with the growth of scientific and technological benefits. Meanwhile, a majority of the world’s population remains religious and holds beliefs in an afterlife.

Gender and Death

Kastenbaum (2000) noted few distinctive gender differences in attitudes toward death, apart from speculatively contrasting the presumed greater emotional openness and communicativeness of women with male machismo and disinclination to show weakness. Some studies suggest gender differences in grief responses and disgust sensitivity, however (Bassett 2015). Causes of death mark some differences by gender, for example, breast cancer and heart disease, and suicide in females more often involves overdose and unsuccessful outcomes, contrasted with more violent methods such as shooting and hanging used successfully by males. Women have tended to live longer lives than men by a margin of a few years, which appears to contradict evolutionary assumptions that sexual fecundity is the key to individual survival. In the European Union in 2014, for example, women in the Netherlands outlived men by 3.5 years, and in Lithuania by

10.9 years. In almost all species, females outlive males, with, for example, adolescent male macaques often dying much younger and female sperm whales sometimes living longer by as much as 30 years. It is inferred that African male lions have higher mortality rates than females, whether due to being hunted or for other reasons.

Menopause normally spells the end of female reproductive usefulness, whereas men remain fertile into old age. It is speculated that various factors point to menopause being protective for women, especially in connection with fecundity at relatively advanced ages. Menopause may also underlie investment in grandmothers' childcare based on the lengthy development of human offspring. Additionally, estrogen has beneficial health effects. By contrast, testosterone is associated with high rates of death due to risk-taking (reckless driving, violence, etc.) in the 15–24-year-old age group (Wilson and Daly 1985) and in midlife due to suicide, alcohol consumption, and heart disease, as well as having immunosuppressive effects (Bribiescas 2016). While males tend to be taller, stronger, heavier, and faster, women's slower metabolism may protect them better from fatal diseases. Kruger and Nesse (2004) conducted a detailed analysis of mortality by gender, age, and cause of death across several countries which confirms the sexual selection thesis favoring female longevity. Contrarily, from a feminist perspective, Kruger, Fisher, and Wright (Kruger et al. 2014) predict that greater social equality leads to decreased male mortality and hence a narrower gap in the traditional male and female mortality ratio.

Philosophy of Death

Socrates asserted that all philosophy is preparation for death but the best-known “philosopher of death” may be Epicurus. It is here that analysis of fear of death finds its most cogent Western expression. Epicurus's famous reasoning was that while we exist, our death does not exist, and where death exists we are nonexistent. In neither case are we co-existent with death and we therefore need not fear it. Epicurus and his followers did not regard the idea of any form of posthumous survival as compatible with embodied life and continuous

memories which constitute human being. To some extent, this kind of logic is found in present day espousers of “amortality,” and cognitive behavioral psychotherapy that addresses death anxiety clinically (Furer and Walker 2008). Others including Nagel (1970) have disputed this reasoning, arguing instead that death, our annihilation, deprives us of the goods of life. Examples of highly creative but relatively short-lived people are used to illustrate this claim.

Bradley, Feldman, and Johansson (Bradley et al. 2013) demonstrate the sheer number and complexity of philosophical questions stimulated by death. These include specificity of time of death; loss of personality; the nature of the corpse; survival of death; immortality; emotion and rationality; the wrongness of killing; abortion; war; capital punishment; and animal death among others. These lie in the analytic and ethical tradition, but one of the best known continental “philosophers of death” is Heidegger, whose existentialism focuses on the authentic requirement to factor death into one's daily awareness. It is one's own death that counts, we do not know when we will die but it could be at any moment, we die alone, our lives are “being toward death,” and it is our attitude to death, not physical demise, that is important – these are some core Heideggerian principles.

One branch of moral philosophy that is both uncomfortable in its own right and potentially fruitful for evolutionary psychology is summarized by Broome (2004) in his highly technical book *Weighing Lives*. This confronts us with comparing good with arguably less good lives, and with cases like terminal illness where decisions must be made between palliative care and aggressive medical intervention. Drawn to considerations of longevity, we may easily ignore the contrasts between the qualities of lives (Small 2010). However, even today, it is unlikely that the majority of people employ careful analytic methods for addressing such problems; rather, evolved, rapid computational (heuristic) affect and compromise guide most such judgments and actions. Suicidal ideation, for example, may be construed in philosophical terms, or psychoanalytically, or even parasitologically, say, but an EP

analysis may explain it in terms of altruism to increase inclusive fitness for kin or as a byproduct of malfunctioning evolved mechanisms (Aubin et al. 2013). Another interesting philosophical challenge comes from a bioethical stance which refuses to accept normative “bravery” in the face of life-threatening illness, instead recognizing the reality of “antiheroic” experiences (Diedrich 2005).

Criminology and Death

Crimes involving death most obviously center on murder but there are many categories of killing, from a one-off crime of passion or drug-related felony, through killings by organized crime syndicates to serial murders with sexual motivations or associated with mental illness, mass killings in the name of terrorism, and necrophilia. Killing is taboo in almost every society, and an examination of death must ask what motivates inflicting death on others and risking harsh social sanctions. Buss (2005) presents evidence that although 87% of murders are committed by men, fantasies of killing others have been experienced by 91% of men and 84% of women. Buss argues on the basis of many interviews that the capacity to kill in certain circumstances is rooted in our nature, specifically associated with reproductive competition. Rather differently, Thornhill and Fincher (2011) apply parasite stress theory and collectivist identity to cases of homicide. Some writers have argued that human nature retains a cannibalistic capacity, and indeed this is observed in some extreme survival scenarios.

Necrophilia is the act of sex with a corpse. Widely treated as a crime and psychiatric disorder, necrophilia can entail motives of attraction to corpses, power, enjoyment of sex without rejection, and reunion with a deceased lover. It is of particular interest because, unlike “simple” murder which is taboo, necrophilia also overcomes the common taboo against disrespect and disgust with corpses. Serial killers well-known for necrophilia, such as Jeffrey Dahmer, Dennis Nilsen, and Ted Bundy, are not necessarily the typical culprits, however, since opportunistic necrophilia is documented among some partners of the dead and individuals who work in the death industries.

Incidence of necrophilia is unknown but assumed to be rare and is unlike the examples of homicidal fantasy given by Buss (2005). Since sexual coitus with the dead has been observed historically and transculturally, and in a variety of animals (including ducks, doves, penguins, and sea lions), it may be inferred to be a relatively uncommon but cross-species phenomenon (Finbow 2014).

Acts of killing in self-defense, killing (and dying) in the line of duty (police, military personnel), and mass killings in war are not usually regarded with the same sense of taboo or disgust. War *crimes*, however, are defined differently, which leads to questions about justifying killing in the name of one espoused ethics while demonizing those in the ethical out-group. Close encounters with sudden death often lead to post-traumatic stress disorder, given the relatively rare experience of witnessing horrific, disgusting fatalities that can create chronic shock (Engelhard et al. 2011).

Psychology of Death

Little specific literature existed prior to the 1970s on the psychology of death, unless we include works such as Freud’s (1917/1957) *Mourning and Melancholia* in that genre, Lindeman’s (Lindemann 1944) focus on the time taken to process acute grief and Kubler-Ross’s (1969) stages of grief model. Kastenbaum (2000) remains a key resource, which begins with the child’s progressive understanding of death. He points out the significant differences between observing a hamster die (“it is dead”) and internalizing the lesson that “I will die.” The child learns about absence, abandonment, separation, and nonresponsiveness in connection with death, but the sense of time develops slowly. Indeed, across the lifespan, the sense of time and distance from death develops quite slowly.

Early exposure to others’ deaths impresses on children features of coldness, immobility, and nonresponsiveness, and memories of death often focus on “thanatic fetishism” or small details (Hall 1922). As Kastenbaum (2000) speculates, parallels between sex and death can be inferred here, recalling psychoanalytic interpretations; some

have also speculated on connections between sex, death, taboo, and pornography. The expression *la petite mort* (little death), corresponding with orgasmic surrender, connotes brief loss of consciousness and, like sleep, depicts us at our most defenseless in these domains; sleep is also a common metaphor for death. We should perhaps not be surprised at the “polymorphous perversity” of cultural and individual ideas and practices about death. We might also infer a parallel between the child’s formation of memories, emotions, and ideas about death, and those of primitive humans first exposed to the sudden death of others, and human corpses, perhaps experiencing some of what we now call post-traumatic stress disorder (PTSD), and able to vividly understand their own mortality, and to unconsciously deny it (Varki and Brower 2013).

It may be that the neurology and psychology of PTSD, obsessive compulsive disorder, and some phobias hold important clues to the evolution of chronic death anxiety. These conditions recall or anticipate vivid life-threatening events and appear to be rooted in an ancestral environment in which sudden death followed bites by spiders and snakes, falls, eating toxic foods, or deadly encounters with animals or other humans, bequeathing hardwired states of defensive hyper vigilance, avoidance, and ritual compulsions. Close associations are also seen between conspecific deaths, mourning, and depression. The developing field of evolutionary psychiatry captures such phenomena (Brune 2015) and the evolutionarily ancient amygdala is often implicated.

Kastenbaum (2000) discusses the “mature view of death,” which rests on acceptance of mortality as universal, personal, inevitable, and irreversible. This emphasis on logic and de-emphasis of belief is disputed by many with different cultural and religious views of death and returns us to the question of denial. Other “extreme” refusals of the mature view, however, include death anxiety and calculated or impulsive risk-taking in the face of death. Death anxiety is pervasive in life and in the literature on death, and attitudes toward death are well summarized by Neimeyer, Wittkowski, and Moser (Neimeyer et al. 2004).

Kubler-Ross (1969) initiated one of the first and best-known models of stages of grief which applies to grieving relatives but also to other loss situations including a terminal diagnosis. The stages are denial, anger, bargaining, depression, and acceptance. While aspects of the model can be readily accepted, it is referred to as a myth by many since empirical evidence is lacking as to any linear “journey” across the five stages. Nevertheless, it remains influential in popular terms. Acute grief triggered by another’s suicide can also lead to so-called copycat, cluster or contagion suicides, and some natural deaths too apparently trigger heartbreak intense enough to lead to associated partner death. Potential behavioral contagion of this kind is sometimes given as a reason to prohibit euthanasia. Suicide prevention initiatives by psychiatry, legal systems, and voluntary organizations in mass populations require explanation beyond mere thanatophobic hysteria or uncritical pro-life assumptions, which may lie in the psychology of voodoo or nocebo effects.

Another, mainly discredited theory is Freud’s death drive, or instinct, which purports to show that humans are driven not only by *eros* but by an urge towards aggression, death, and self-destruction. The finding that a 13.8% chance of day of death coinciding with date of birth, proposed as an “anniversary reaction” (Ajdacic et al. 2012), might support Freudian theory. Yet at the same time, Freud had argued that the unconscious cannot imagine its own death. Certain psychotherapies utilize such life-and-death themes conceptually and clinically. Weatherill (1998), Razinsky (2014), and others have built further on Freudian psychoanalytic principles, and some theorists retain a psychosomatic etiology linking mind, illness, and mortality. A stoical-existentialist view can be found, while Furer and Walker (2008) commend cognitive behavior therapy. Kellehear (2014) is a relatively rare account of the dying person’s own experience, which includes some uplifting material.

Terror management theory (TMT) places death, or mortality salience, at the heart of psychology, offers a rival explanation to EP for human motivation and behavior, and ongoing tension exists between TMT and EP. Becker (1973)

speculated, drawing on the work of philosophers and psychologists among others, that fear of death drives all human endeavors, with humans behaving heroically to deny the fact. This led eventually to TMT, which is now supported by a wide range of situational applications and associated empirical research (Greenberg et al. 2004; Burke et al. 2010; Solomon et al. 2015; Harvell and NIsbett 2016). Buffers against the terror induced by thoughts of one's own mortality include self-esteem, religion, worldviews, different attitudes to health, and other defensive behaviors.

Navarrete and Fessler (2005) argue that TMT is incompatible with evolutionary biology, that mortality salience is not the all-powerful force it is deemed to be, and that coalitional psychology offers a better explanation for defense of in-group ideologies than TMT. They argue that although a fear and avoidance of predators exists, no fear of "death as such" exists. Humans have no generic 'survival instinct' but an emphasis on reproduction along with cognitive modules for addressing specific threat situations in the environment. Landau et al. (2007), however, appealed for compatibility. Tritt et al. (2012) suggest that TMT "runs counter to prevailing views in neuroscience" (p. 721) and offer a biological understanding of mortality where "death is not so special" (p. 728) but simply another instance of an uncertainty to be resolved by an ancient brain-based anxiety system. Kirko (2016) argues that unconscious death awareness is a better explanation than conscious death anxiety, which would be a more costly defense. This might go some way toward harmonizing TMT, EP, and related theories of mortality salience (Varki and Brower 2013). For Varki and Brower, however, mortality salience and its appearance in human evolution is more than a large and troublesome motivational force: realization of the meaning of personal death and the self-deception required to live with it, in order not to succumb to perilously morbid preoccupation, is here the explanation for the emergence of distinctive human consciousness itself.

Evolutionary Psychology of Death

Death is often treated tacitly in the literature of evolutionary psychology, for example, as the

ultimate cost of failure to adapt or simply the end point of evolved senescence. Darwin (1859/1968) in his epochal *The Origin of Species* barely mentions death. Rather, he speaks of how "Natural Selection almost inevitably causes much Extinction of the less improved forms of life" (p. 68). "Each organic being . . . has to struggle for life, and to suffer great destruction" (p. 129). "Unless we believe that the number of specific forms goes on perpetually and almost indefinitely increasing, numbers inevitably must become extinct" (p. 153). Darwin's focus here was on species death, and we now know that the vast majority of species that have ever existed have gone extinct (and not usually in dramatic extinction events), with the rate of anthropogenic extinction today accelerating. But we can infer from this that so far all discrete life forms, ourselves included, are destined to perish.

The publication of Dawkins' (1976) *The Selfish Gene* also lacked significant attention to death. However, Dawkins speculated that senescence may result from "deleterious copying errors and other kinds of gene damage" (p. 42). He also builds a little on Medawar's (1952) work to suggest that "lethal genes" and "semi-lethal genes" that are late-acting survive because they do not interfere with sexual reproduction earlier in life. Williams (1957) postulated about senescence that in terms of survivorship among early humans about half of infants came to sexual maturity: late life fitness had no value for natural selection. Peak fertility from around puberty is most valued by natural selection. Senescence is a "steady decline in adaptive performance" (op.cit., p. 172), resulting from antagonistic pleiotropy, whereby genetic processes trade-off early fertility for later morbidity. Natural selection does not produce perfection but pragmatic functional adaptations. While much controversy and uncertainty exist in this area, Wolpert (2009) is unequivocal: "The blame must fall on evolution, which is interested only in reproduction and not in health once we have reproduced" (p. 146). A contrary view is put by Shostak (2006), who argues that our technologically extended and lifestyle-extended existence is boosting juvenile features which via evolutionary forces acting on cellular activity is lengthening the

lifespan and delaying death. Werfel et al. (2015), using stochastic modeling, argue that limited spatiotemporal resources favor shorter, not longer, life spans, and hence that classic evolutionary theories of senescence are insufficient.

Suicide presents an acute challenge to evolutionary psychology if killing oneself is naively regarded as contrary to a “survival instinct.” However, sexual reproduction and successful care of the young, and not survival *per se*, are the evolutionary objective (DeCatanzaro 1991). Early life suicides can be seen as removal of an unfit individual from the gene pool. Altruistic suicides may include putting others first in order to prioritize scarce resources or removing oneself if a burden on others. Nevertheless, few other animals are known to commit suicide on the scale of humans (Ramsden 2010), and we may have to conclude that some humans experience distress so acute or chronic, accompanied by the cognitive expectation that no relief is forthcoming, that suicide seems the only solution. To say that someone “died by his own hand” also underlines evolved, distinctive human dexterity. Technology usually facilitates it, with pills, poisons, hanging, guns, knives, railway tracks, and tall buildings all available.

Similar to suicide, filicide superficially appears to have no adaptive value if passing on genes is the “purpose” of life. Infanticide by step-parents or others, however, may sometimes show a brutal genetic logic. Indeed, in the Paleolithic era, it is estimated that up to 50% of female infants may have been killed and significant infanticide to offset scarcity of resources may have continued until the Neolithic Revolution and the advent of agriculture (Milner 2000). Religious sacrifice of children also had a logic for its time. Infant mortality in eighteenth century France was so high that streets were “littered with the corpses of dogs and babies during famine periods” just prior to the demographic transition in which mortality and fertility both started to decrease in the developed world (Barret et al. 2002, p. 159). Even today in some cultures, infanticide is practiced, with more girls than boys being killed or abandoned. Volk and Atkinson (2008) argue for a better evolutionary understanding of the problems of child mortality, particularly the costly failure of gene transmission.

So-called social Darwinism is bitterly attacked for propounding views derived from Spencer and Galton placing emphasis on the “survival of the fittest” and “rational selection.” In this account, natural selection is replaced by the decisions of human planners and eugenic technologies. Darwinism was expropriated by Nazism and racial science to justify genocide on the grounds of eliminating human specimens and groups perceived as weak or degenerative from the gene pool. This was to ignore entirely human rights, the benefits of co-operation and the perils of pseudoscience. Nevertheless, EP is bound to have to address matters of the mass psychology of contemporary xenophobia and genocide (Smith 2012). Similarly, Malthusianism, framing death as an unfortunate “positive check” on continuing population growth in relation to limited resources, invites ongoing political controversy.

Life history theory (LHT) links genetic variation and mortality with scarcity of resources and an evolutionary underpinning. Based on cross-species mathematical analyses of the age schedule of birth, maturity, size, timing of reproduction, number of offspring, senescence and death, and environmental uncertainty, LHT embraces the notions of slow and fast life histories corresponding with life expectancy, not only in humans but mammals generally (Dobson and Oli 2007). Some studies of dates of death (e.g., Ajdacic et al. 2012) and evolutionarily driven circadian rhythms affecting time of death (Lim et al. 2012) are also suggestive here. In the case of contemporary calculations based on socioeconomic status, some individuals over-estimate the likelihood of premature death (“you have to live for the day”) and engage in high-risk activities with self-fulfilling properties (Griskevicius et al. 2011). Another area of potential for EP is provided by Gorban et al. (2016) who draw on Selye’s stress model to develop an evolutionary, hypothetical “adaptation energy” model of fitness optimization supported by mathematical work.

Evolutionary mismatch theory helps to explain some of the diseases of modernity, including breast cancer, obesity, and diabetes. Human longevity has been increasing, most lives are no longer nasty, brutish, and short, indeed we face new diseases of old age. In addition, psychosocial

factors such as loneliness, particularly in the developed, secular world, account for some increase in premature deaths (Holt-Lunstad et al. 2015). It may be important to consider evolutionarily recent and contemporary population and behavioral genetics, and increasing resistance to some diseases (Cochran and Harpending 2010). Simultaneously, with greater public acceptance of Darwinism and challenges to religious denial of mortality, more people are faced with the problem of finding strategies for sustaining morale. Growth in antinatalist awareness, for example, alongside various catastrophe scenarios, makes for demoralization, while improvements in health care, increasing longevity, and advances in technology make for hope (Chisholm 1999). An evolutionary psychology trained on more recent adaptations might well make useful predictions regarding this latter challenge.

Conclusion

Death is inevitable and necessary even if the lifespan may be stretched: to be born is to die (Shields 2008), or “life, thus death” (Volk 2002). Humans are aware that they must individually die, whether “prematurely” or by senescence, but this universal fact of life remains an unpleasant prospect, often feared and minimized in conscious common discourse. Science, however, continues to make unsettling discoveries such as Chen et al. (2016) which, taking over 13,000 individuals from three ethnic groups, finds that “epigenetic age” predicts death better than chronological age, lifestyle, and common risk factors. Human evolution and culture have brought about momentous changes distinguishing the human from the animal world, notably advance awareness and religious denial of personal annihilation, technology that extends life, and some degree of apparent free will. While it is true that we share some vulnerabilities with wild animals, we have escaped much of the “nature, red in tooth and claw” aspects. At any given time, “thousands of animals are being eaten alive, others are running for their lives, whimpering with fear; others are being slowly devoured from within by rasping parasites; thousands of

all kinds are dying of starvation, thirst and disease” (Dawkins 1995, p.154).

Responses to human mortality are culturally, historically, and disciplinarily highly pluralistic. The domain specificity of EP addresses important human functions of social and sexual interaction but does not accord mortality a particular place in its canon, as TMT does; it looks instead at aspects of life history theory, senescence, mismatch and trade-off theories of disease causation, disgust sensitivity, and sexual selection for fitness. The enormous energy costs demonstrated throughout human history, of propitiating the gods, denying, and postponing death, however, heavily imply a collective need to address mortality, an onus on academics to engage in an interdisciplinary focus, and a nuanced explication of the proximal-distal discrepancies in accounts of contemporary life and death.

Cross-References

- ▶ [Assisted Suicide](#)
- ▶ [Child Mortality](#)
- ▶ [Death in Christianity](#)
- ▶ [Death in Islam](#)
- ▶ [Disgust](#)
- ▶ [Disposable Soma Theory](#)
- ▶ [Extinction of Neanderthals](#)
- ▶ [Extrinsic Mortality](#)
- ▶ [Homicide](#)
- ▶ [Infanticide](#)
- ▶ [Life History Theory](#)
- ▶ [Reproduction, Suicide, Euthanasia](#)
- ▶ [Senescence](#)
- ▶ [Suicide](#)
- ▶ [Western Perspectives on Death.](#)

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Death by Suicide

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Synonyms

Completed suicide; Self-annihilation; Self-destruction; Self-murder; Suicidal enactment; Suicidality; Suicide

Definition

Suicide constitutes the intentional act that is actively causing one's own self-destruction.

Introduction

Death by suicide is the voluntary and explicitly deliberate engagement of an individual in a series of operational, external, as well as internal activities that result in her/his death. Suicide is a complex, multifaceted, and multifactorial phenomenon, and, while it is considered a global epidemic, it is a preventable cause of death (WHO 2014). Specifically, the suicidology literature has consistently indicated that high levels of suicide risk are frequently short term and are triggered by a specific stressful situation. Although suicidal ideation might reappear, it is not a permanent symptomatic condition, and the formerly affected person, given multidimensional support (medical, psychological, social), can live a long-lasting and meaningful life (Torres 2016). Additionally, while there are incidents of suicide that manifest without warning signals, most of the cases of completed suicide have been preceded by idiosyncratic warning signs (e.g., cognitive, emotional,

or behavioral). Therefore, identifying the warning signals which indicate that a person is experiencing a suicidal crisis could help the individual receive appropriate early treatment, which in turn could increase her/his possibility of surviving the suicidal crisis (Sadek 2019).

According to the World Health Organization (2014), suicide is considered to be the tenth leading cause of death across the globe and the second leading cause of death in the age group 14–29 years old. Nearly 750,000 individuals die by suicide annually, and it is estimated that in 2020 deaths by suicide will significantly increase across the globe to nearly 1.5 million per annum (WHO 2014). Moreover, it has been consistently indicated that approximately 10% of the general population has a history of a suicide attempt. That is, for every person who died by suicide, multiple individuals have attempted to take away their own lives each year with incidents of suicide attempts being approximately 25% higher compared to the incidents of completed suicide (Torres 2016).

Furthermore, it has been observed that suicide is a global phenomenon (Sadek 2019). However, it is widely cited that it manifests in significantly higher rates in low-income as well as in middle-income countries. In particular, 79% of deaths by suicide that occur globally usually manifest in countries with low- and middle-income economies. Generally, the sociopolitical geographical area of Eastern Europe exhibits the highest overall levels of suicide. The Central and South American geographical regions, as well as the countries of the Mediterranean, manifest the lowest levels and the United States, the west European countries, the Asian countries, and Africa somewhere in between (WHO 2014). Nonetheless, there is a significantly high variation among sociopolitical geographical areas concerning reporting incidents of suicide (Torres 2016).

The Multifaceted and Heterogenous Phenomenon of Death by Suicide

Suicide constitutes a multidimensional outcome. Specifically, there is a wide range of cultural, sociological, psychological, physiological,

genetic, and psychiatric factors that can contribute to the manifestation of death by suicide either independently or in interaction with one another. Thus, suicide is a complex phenomenon, with every incident reflecting an idiosyncratic mixture that consists of a dynamic interplay between qualitatively distinct contributors (Pompili 2018).

Additionally, the most widely accepted motivational factor of suicide in the clinical literature is considered to be the long-term frustration of psychological needs (e.g., sense of safety, autonomy, secure attachment system, belongingness, and self-efficiency and sense of purpose, control, orientation, and meaning in life). Specifically, the driving force of most suicides is the long-term frustration of an idiosyncratic mixture of basic psychological needs that are necessary for a healthy, meaningful life (Torres 2016). Therefore, clinical interventions that aim to help people cultivate and solidify their capacity to nourish and, thus, adequately satisfy their psychological needs could prevent suicide. Over and above that, most suicidal individuals who have the opportunity to safely explore their experience with an empathetic other are ultimately able to contain their emotions, feel interpersonally supported, and attain a viable degree of psychic equilibrium (Maris 2019). This often can lead them to reconsider their decision to commit suicide. Therefore, the availability of emotional support has the potential to prevent suicide.

However, due to the stigmatization that revolves around suicidal crises, individuals who are affected often do not feel safe to express their thoughts and feelings to their significant others and even seek professional help (Wasserman and Wasserman 2009). Stigmatization related to suicidal experiences inhibits suicidal recovery. Specifically, it has been consistently found that encouraging suicidal individuals to openly talk as well as freely explore their experience could provide them the opportunity for emotional containment, problem-solving, and decision-making something that, in turn, might enable them to reconsider their choice (Maris 2019). This is in contrast with the misconception that encouraging talking about suicide could reinforce the person's intention to commit suicide (Torres 2016).

Risk and Protective Factors

The clinical literature has consistently shown that there is a significant association between previous suicide attempts and completed suicide in the future. Nearly 45% of people who had attempted to take their own lives ultimately die by suicide. Therefore, a history of suicide attempts represents one of the major risk factors for death by suicide (Maris 2019). Furthermore, a substantial amount of research has found a significant association between mental disorders and suicidality (Karthick and Barwa 2017). Specifically, clinical depression, substance abuse and related disorders, trauma- and stress-related disorders, psychotic disorders, eating disorders, and conduct disorders have been consistently associated with a higher risk for death by suicide (Hirsch et al. 2019). However, while psychiatric disorders constitute significant contributors associated with suicide, neither all individuals who have a mental illness experience a suicidal crisis nor all people who die by suicide met the criteria of a psychiatric disorder (Lennon 2019). Thus, psychiatric disorders alone cannot explain the factors that contribute to the manifestation of suicide.

Furthermore, a family history of suicide has been consistently found to increase the risk of suicide. This implies that there is a genetic predisposition that contributes to the manifestation of suicide (Maris 2019). Moreover, knowledge and access to lethal means significantly increase the risk of suicide. Additionally, gender seems to be a significant risk factor, with females exhibiting higher rates of suicide attempts and males higher rates of fatal suicide attempts (WHO 2014). Further risk factors that are significantly associated with suicidality include unemployment and age, as older people exhibit significantly higher rates of suicidal behaviors. Moreover, the clinical literature has consistently found significantly higher rates of suicidal behaviors in people that exhibit chronic pain and functional deficits (Wasserman and Wasserman 2009).

Additionally, research related to suicidality has designated various protective factors regarding suicide. Specifically, some of the most cited protective factors for suicidality include education,

employment, access to medical care services, secure attachment system, marital status, social and communal integration, self-efficacy, emotion regulation, gratitude, hopefulness, cognitive flexibility, sense of purpose, orientation and meaning in life, and problem-solving and decision-making skills (Maris 2019).

The Suicidal States of Mind

A suicidal crisis is governed by profound psychic pain, which is characterized by floods of intolerable affect. Additionally, the main objective of suicide is to find a solution that would free people from the emotional drama, dilemma, as well as a life crisis that they might be experiencing. In other words, people who contemplate suicide think that death is the only feasible solution at their disposal that will ensure the end of their suffering (Pompili 2018). Furthermore, suicidal individuals often report that they experience a sense of entrapment and aloneness in a state where they feel defective and hopeless. This dynamic often triggers despair, rage, self-hatred, and existential anguish that involves disintegration anxiety and a powerful urge for immediate relief (Barzilay and Cohen 2017).

Moreover, one of the major qualitative functions of contemplating suicide is to alleviate the unbearable psychophysiological distress. Notably, during the experiential process of fantasizing and organizing suicide, the affected individuals feel that they have restored some of their sense of power and control over their suffering. That is, they feel that they can actively stop their ongoing suffering, which in turn decreases to some extent their sense of entrapment, hopelessness, and uselessness (Barzilay and Cohen 2017).

Additionally, when suicidal individuals feel imprisoned in an internal and/or external condition where they experience hopelessly intolerable psychophysiological pain, they are usually reacting with rage of high intensity (Maltsberger et al. 2018). In some cases of completed suicide, this reactive rage of being helpless constitutes the driving force that enables people to overcome the fear that is being activated by their survival and

reproductive instincts and thus proceed to kill themselves. Consequently, the suicidal states of mind are significantly associated with the affected individuals' inability to function adaptively in times of intolerable distress (Kapur and Goldney 2019).

A core characteristic of the phenomenological experience of suicidality is the quality of ambivalence (Maris 2019). That is, people who are contemplating suicide are also experiencing an inherent intrapsychic conflictual dynamic. Specifically, there is an intrinsic conflict between their instinct for survival as well as reproduction and their belief that indicates to them that the only feasible solution for escaping their psychophysiological pain is self-destruction (Barzilay and Cohen 2017).

Moreover, most people who experience a suicidal crisis exhibit a transient perceptual constriction, which prevents them from recalling the internal representations of themselves, others, and the world that could enable them to mentalize, and thus make sense of their experience (Sharma and Fowler 2018). Moreover, suicidal individuals experience difficulties in accessing their problem-solving and decision-making abilities effectively (Maris 2019). These deficiencies usually lead the affected individuals to rely on dichotomous cognitive-affective functioning (e.g., black/or white emotions and thoughts) as they experience a perceptual splitting between the past, the present, and the future. Consequently, they often feel trapped in the present moment of their suffering, which reinforces their suicidal ideation (Maltsberger et al. 2018). Moreover, people who experience a suicidal crisis exhibit a deterioration of their ability to recall autobiographical memories. This diminishes considerably their capacity for positive future thinking, which is one of the major capacities which facilitates the formation of positively oriented experiences (Hirsch et al. 2019).

Trauma and Death by Suicide

Mental trauma usually results when people experience intolerable levels of psychophysiological

arousal, which transcends their ability to endure and integrate their sensory, affective, and perceptual experience into symbolic representations that could have enabled them to contain their emotions and make sense of their experience (Maltsberger et al. 2018). However, the ability to endure externally as well as internally distressing conditions is the result of a dynamic interplay between genetic, psychological, and environmental factors and varies among individuals. Additionally, there is generally a consensus that the distressing stimuli which can trigger a traumatic experience can either be external (e.g., environmental) or internal (e.g., neuropsychological states, traumatic affects) (Maris 2019).

The cardinal feature that governs traumatic experiences is the inadequacy of the mind to process, regulate, and adapt to mental disequilibrium that is triggered by an external and/or internal stimulation. This stressful dynamic between the inner and the outer world often leads to a sense of entrapment and feelings of helplessness and hopelessness (Maris 2019). Also, there is a substantial amount of research studies that indicate that suicidal crises sometimes reflect the internal re-experience (e.g., flashback) of overwhelming neurophysiological distress, which was initially experienced in past traumatic events (Wasserman and Wasserman 2009).

Additionally, persistent and repeated suicidal crises might have long-term re-traumatizing effects. It should be pointed out that suicide attempt survivors are considered survivors of attempted murder as they are the perpetrator and the victim at the same time. Therefore, the suicidal act has the quality of a violent and potentially lethal assault (Maltsberger et al. 2018). Furthermore, recurrent and persistent traumatic experiences that trigger unbearable psychological pain disrupt the capacity to form and maintain secure attachments, something that often leads to the deterioration of ones' ability for hopefulness during life crises. This adverse type of mental trauma might also severely disrupt the affected individuals' capacity of distress tolerance during stressful times in the future. Specifically, recurrent and/or persistent mental traumas have been significantly associated with increased levels of

anhedonia, despair, existential, and disintegration anxiety. This implies that people who experience recurrent and persistent traumatic experiences find it challenging to hold on to hope and maintain their attachment bonds, which have essential life-preservative qualities (Pompili 2018).

Furthermore, the clinical literature has consistently found a significant association between childhood mental trauma (e.g., neglect, sexual, physical, and psychological abuse) and post-traumatic stress disorder as well as increased suicide risk in adolescents (Kapur and Goldney 2019). Moreover, there is a substantial amount of research that indicates that traumatic experiences influence the phenotypic expression of the operational mechanism of emotional self-regulation during childhood (Fonagy et al. 2002).

In addition, traumatic mental experiences can disturb essential operational properties of explicit memory and perception (Maris 2019). That is, following a traumatic experience, a functional somatosensory organization (e.g., outside of the symbolic realm) of the traumatic experience is immediately formed, which is, to a great extent, rigid and resistant to modification. Intolerable affective states lead to traumatic experience because they interfere with the process of assimilating the experience into existing mental schemas. Precisely, intolerable affective states lead to the dissociation of perceptions and memories of specific events which in turn are stored as visceral, visual, and olfactory sensations (Maltzberger et al. 2018). As a consequence, affected people tend to experience fear that has the quality of an unexpected assault in reaction to all the stimuli that have been somatosensory organized due to their association with the arousal-related bodily sensations. Thus, their perceptual lens predisposes them to be in a state of constant alertness waiting helplessly, an assault that would make them suffer. This dynamic elicits cognitive confusion and a sense of being entrapped and hopeless that is increasing the risk for suicide (Pompili 2018).

Moreover, suicidal people who have experienced attachment trauma during their early years of life do not sufficiently develop the capacity for self-object constancy (e.g., capacity to perceive the self and others as whole and constant)

(Maltzberger et al. 2018). Insufficient capacity for self-object constancy makes it extremely difficult for them to retrieve their internal representations of themselves in relation to the nurturing and soothing people that are currently in their lives (e.g., attachment bonds) in times of distress and thus be able to elicit the sense of their presence when they are physically absent (Sloate 2016). Consequently, even minor interactional conflicts often lead them to feel that they have been abandoned, misunderstood, and maltreated. The sense of abandonment and maltreatment increases their suicide risk as it gives rise to extremely intense feelings of dependency, rage, despair, worthlessness, alienation, aloneness, hopelessness, and helplessness that have their roots in their traumatic experience during their early childhood (Maltzberger et al. 2018).

On the contrary, there is a general consensus within the developmental psychology field that people whose parents were good enough during their early stages of development are more likely to develop and maintain the life-preservative capacities for basic trust, autonomy, interconnectedness, emotion regulation, self-compassion, and hopefulness that are negatively associated with post-traumatic stress disorder and risk for suicide (Allen 2013). This is to some extent due to an identification with stable, resilient, empathetically attuned, and nurturing parental models. That is, the identification with good enough parents enables children to subsequently internalize the capacities that their parents exhibit in order to provide for them a good enough environment in which they can survive, grow, reproduce, and flourish. Therefore, good enough parenting can facilitate the expression of constitutional resilience and the internalization of life-preservative capacities and, thus, lower the risk for mental trauma and death by suicide (Barzilay and Cohen 2017).

Theoretical Conceptualizations of Death by Suicide

Mentalization-Based Therapy

Humans rely to a high extent on relational attachments to survive, grow, reproduce, and

find meaning in life (Allen 2013). Mentalization is a functional construct that enables humans to make use in an integrate way their perceptual, inferential, and imaginative capacities in order to reflect on and comprehend the qualitative operations that influence peoples' idiosyncratic mental functioning (e.g., belief system, incentives, feelings) (Sharma and Fowler 2018). The ability to mentalize is crucial in the formation and maintenance of the operational mechanisms that render people capable of adaptive functioning in their everyday lives. Moreover, there is a substantial amount of research studies that indicates that the ability to mentalize is of vital significance in the development and maintenance of stable and mutually beneficial relationships (Fonagy et al. 2002).

Furthermore, it has been consistently cited that there is a significant association between suicidality and a dysfunctional family system of origin that do not sufficiently meet the neurodevelopmental needs of the affected person (Allen 2013). Additionally, it has been consistently found that a dysfunctional family of origin is associated with insecure attachment systems and a disordered ability for mentalization and emotion regulation (Sharma and Fowler 2018). This is in accordance with data indicating that people with an insecure attachment system and a disordered ability for mentalization find it very difficult to rely on the people that surround them in times of distress. This can lead them to experience aloneness, which in turn can trigger feelings of despair and terror that increase their risk of suicide (Maltsberger et al. 2018).

Over and above that, people who fall into a suicidal crisis manifest a series of common alexithymic features such as externally oriented cognitive functioning, low emotional intelligence, and constricted imagination (Lester 1991). That is, most suicidal individuals exhibit difficulties in recognizing and distinguishing their emotional states from their neurophysiological sensations and the neurovegetative symptoms that they exhibit during times of stress. Specifically, their capacity to symbolize affects and neuropsychological sensations is significantly diminished, and thus, they do not adequately regulate, explore, and express their subjective experience.

Consequently, their cognitive-affective lens through which they regulate their internal and external experiences is shaped mostly by external stimuli (Allen 2013).

Moreover, people who exhibit a disordered capacity for mentalization and emotion regulation often try to contain their emotional experiences through the psychophysiological mechanism of somatization and thus acting it out. Hence, conflictual relational dynamics usually lead to the manifestation of quick and intense shifts in their emotional state of mind, which is, in turn, manifested in the form of neurophysiological disequilibrium. This neurophysiological disequilibrium is often regulated through self-injury and suicidal preoccupation (Sharma and Fowler 2018).

In addition, mentalization-based therapy (MBT) has been found to significantly decrease the risk of suicide in adolescent and adult population (Sharma and Fowler 2018). MBT for suicidal individuals is designed in such a way as to cultivate a therapeutic environment in which the focus is on the immediacy of the interactional dynamics that emerge in the context of the therapeutic relationship (Allen 2013). This modality of treatment has developed clinical interventions that aim to build or restore the affected peoples' capacity for secure attachments, mentalization, emotion regulation, and impulse control. Specifically, through empathetic mirroring of peoples' neurophysiological, affective, and cognitive states as well as psychological needs, the therapist aims to help them conceptualize the suicidal crisis in terms of a breakdown in their capacity for mentalization (Sharma and Fowler 2018).

Subsequently, suicidal individuals are helped to develop and maintain the functional mechanisms needed to differentiate their own mental experiences from that of others and, thus, become mindful of how the quality of their state of mind influences their behaviors. Therefore, this therapeutic modality aims to provide a safe environment where suicidal individuals can securely identify, explore, and modify their distorted and dysfunctional perceptual lens. This phenomenological exploration and perceptual modification can help them to organize, regulate, process, and

stabilize their mental and interpersonal functioning (Fonagy et al. 2002).

Cognitive and Behavioral Therapy

According to the cognitive-behavioral theory (CBT) of psychopathology, suicide is significantly associated with depressive symptomatology (Routledge 2015). This theoretical model proposes that depressed individuals who also experience a sense of hopelessness about their future are vulnerable to suicide risk. Specifically, suicidal people believe that suicide is the only feasible way out of their unbearable suffering due to their distorted core beliefs that indicate to them that they live in a world in which there is no possible relief for them either now or in the future. Moreover, CBT indicates that these negative core beliefs about the future interact with additional core beliefs about the self and the world (Wenzel and Beck 2008). For instance, a suicidal individual might be thinking that he is a useless and unprotected person who lives in a dangerous world in which he will never find inner peace. That is, the perceptual lens of affected individuals predisposes them to expect more hardship and suffering as they continue to be alive. Consequently, the possibility of immediate escape from their suffering through suicide is perceived to be more desirable than being alive.

CBT is a therapeutic modality that is goal-oriented. It is brief and is methodologically and strategically structured. CBT helps people to understand the functional and disordered associations between their cognitions, emotions, actions, and neurophysiological sensations (Wenzel and Beck 2008). CBT models of suicidality teach the affected people emotion-regulation and problem-solving skills through distraction-related interventions (e.g., mindfulness), thought-suppression interventions, and cognitive-reappraisal interventions. This enables them to cultivate their capacities for distress tolerance and impulse control and then proceed on to work on their suicidogenic core beliefs (Wenzel and Beck 2008).

CBT educates suicidal individuals how to cultivate the capacities needed in order to engage in an operational procedure of cognitive

restructuring through the methodical assessment of the validity and the utility of their dysfunctional cognitive biases. In addition, through a series of behavioral techniques (e.g., behavioral activation, in vivo and in vitro exposure therapy), CBT aims to help suicidal people to change their dysfunctional patterns of behavior with more adaptive ones. A substantial amount of research studies has indicated that CBT is significantly effective in the treatment of the suicidal states of minds as well as in suicide prevention (Bryan and Rudd 2018).

Ideation to Action Theories of Suicide

Fluid Vulnerability Theory

The fluid vulnerability theory (FVT) has been invented and methodologically described in 2006 (Rudd 2006). The FVT provides a theoretical framework that aims to shed light on the underlying processes that contribute to the temporal manifestation of death by suicide risk in the short term as well as in the long term (Rudd 2006). FVT conceptualizes the suicidal risk as an idiosyncratic mixture of acute and baseline factors. Baseline risk factors constitute factors that are generally stable, such as biological predispositions and demographics, which are contributing to the persistence of increased suicide risk in the long run (Bryan and Rudd 2018).

On the contrary, acute risk factors consist of a dynamic interplay between external factors (e.g., environmental stressors), psychological factors (e.g., mental disorders), and operational dynamics that govern the suicidal states of mind. Thus, acute risk factors contribute to the predisposition of suicide risk in the short term (Routledge 2015). According to FVT, the risk for suicide is governed by dynamic features that are fluctuating in reaction to external and internal stimuli. Therefore, the frequency, intensity, and duration of suicidal crises depend on the emergence of an idiosyncratic dimensional mixture of constitutional and psychological vulnerability factors, which is triggered by environmental stressors (e.g., divorce, unemployment) (Rudd 2006).

FVT has incorporated and extended the core theoretical and conceptual principles of CBT regarding the functional formulation of suicidal states of minds as well as attempted and completed deaths by suicide. Precisely, the conceptual framework adopted by Rudd (2006) is termed the suicidal mode. The suicidal mode is an operational construct that integrates functionally and systematically the association between suicidogenic cognitions and dysfunctional emotions, behaviors, and neurophysiological reactions (Bryan and Rudd 2018). More specifically, suicidogenic cognitions represent mental schemas about the self, the world, and the future (e.g., I am defective, the world is a dangerous place, the future is hopeless), conditional beliefs (e.g., if things get terrible and dangerous, I will kill myself), and negative automatic thoughts.

Besides, these suicidogenic cognitions lead to unbearable emotional states (e.g., rage, shame, anhedonia) that are followed by cognitive and behavioral-based dysfunctional strategies (e.g., experiential avoidance, substance abuse, isolation) and neurophysiological states (e.g., vegetative symptoms) (Bryan and Rudd 2018). Furthermore, the underlying functional vulnerabilities that govern the suicidal mode constitute emotion-regulation deficits, perceptual distortions, and cognitive inflexibility that lead to deficient executive and affective functioning. Therefore, clinical interventions should target both of these functional vulnerabilities in order to prevent the transition from suicide ideation to its enactment (Bryan and Rudd 2018).

Additionally, the FVT has presented a series of proposed assumptions that enable the conceptualization of the intensity, frequency, and duration of suicidal crises. In particular, this model proposes that the qualitative nature of a suicidal crisis is time-limited and that the level of distress that could trigger a suicidal crisis differs among people. In addition, following the remission of a suicidal crisis, people are usually returning to their idiosyncratic baseline level of suicide risk (Rudd 2006). This implies that the risk of suicide is also governed by qualitative factors that are resistant to modification over time.

Interpersonal Theory of Death by Suicide

The interpersonal theory of suicide proposes that people are at high risk for suicide when they exhibit an intense urge to kill themselves and they have also cultivated the capacity to act on that self-destructive urge (Joiner and Staff 2015). Therefore, this theory differentiates people who experience suicidal ideation from people that engage in suicide attempts. According to this theoretical model, the driving force of the urge for self-destruction is fueled by two distinct but intertwined intrapersonal constructs, that is, perceived burdensomeness and thwarted belongingness (Joiner and Staff 2015).

Perceived burdensomeness designates the sense of being a burden to other people which is governed by an ego-dystonic (e.g., highly distressing) and distorted sense of being a human parasite. The phenomenology of this experience leads to the formation of a schematic representation that indicates to affected people that the world and its people would be much better if they die and, thus, cease to exist (Joiner and Staff 2015). Thwarted belongingness reflects a sense of intrapersonal isolation and alienation that significantly decreases the sense of orientation, purpose, and meaning in one's life. Moreover, thwarted belongingness implies that the affected individuals feel that they have failed to satisfy their fundamental need for human connectedness, which has life-preservative qualities (Ribeiro et al. 2013).

The simultaneous experience of both perceived burdensomeness and thwarted belongingness has been associated with high-intensity suicidal ideation (Joiner and Staff 2015). Nevertheless, this dynamic is not sufficient enough in order to overcome the primitive instinct of self-preservation and thus enable the transition from suicidal ideation to suicidal action. That is, for a completed suicide to result, the development of the capacity for self-destruction is necessary (Ribeiro et al. 2013).

Humans can develop the capacity for self-destruction, which is governed by high levels of tolerance to physiological pain and significantly low levels of death anxiety. Specifically, suicidal individuals develop the capacity for suicide due to habituation in fear of death, and

psychophysiological pain, and the simultaneous stimulation of opponent operational mechanisms that manifest in reaction to a systematic exposure to fear and pain-inducing stimuli of neurophysiological and psychological nature (Joiner and Staff 2015). For instance, the suicidology literature indicates that repeated exposure to pain through self-injury lowers the inhibitory threshold for suicidal actions at a later time due to habituation to the fear and pain and thus significantly increases the possibility of suicide (Joiner and Staff 2015).

Integrated Motivational-Volitional Model of Suicidal Behavior

The integrated motivational-volitional (IMV) model of suicidal behavior integrates existing data and well-researched operational constructs of different theoretical models of suicidality. IMV provides a conceptualization of the dynamic interaction between distal and proximal vulnerability factors, which contribute to the transition from suicide intention to death by suicide. Precisely, this model consists of three functional phases that conceptualize the multifaceted and dynamic interaction between internal and external vulnerability factors that contribute to the transition from suicidal ideation to suicide attempts and completed suicide (O'Connor et al. 2016).

The pre-motivational phase designates the various vulnerability factors (e.g., mental trauma, divorce, unemployment) that due to their interaction with one another, the biopsychosocial context of suicidality is formed and leads to the transition to the motivational phase in which the phenomenon of suicide intent emerges (O'Connor et al. 2016). For instance, numerous distressing experiences, whether internal or external, can contribute to a sense of defectiveness, failure, and humiliation. When perceptual distortions, and deficient capacities for emotion regulation, problem-solving, and decision-making, mediate such a distressing experience, a sense of entrapment emerges. In the context of further mediators such as the inability for future thinking and a sense of being a burden, disconnected, and alienated from the world and its people, the sense of entrapment intensifies and leads to the perception of suicide

as a feasible solution to ones' suffering (O'Connor et al. 2016).

In the volitional phase, the model conceptualizes the sequential relationship between suicidal intention, suicidal behavior, and death by suicide. Specifically, in this phase, the theoretical model presents cognitive, behavioral, and emotional factors (e.g., impulsivity, rage, capacity for death by suicide) that significantly contribute to the transition from suicide intention to its enactment and, thus, death (O'Connor et al. 2016).

The Three-Step Theory

The three-step theory of suicidality suggests that an overwhelming amount of psychological and/or physiological pain in conjunction with a sense of hopelessness leads to the emergence of suicidal ideation. Furthermore, the intensity of the suicidal ideation significantly intensifies when the phenomenological experience of pain and hopelessness exceeds the affected individuals' connectedness with the living world and its people (Klonsky and May 2015). Specifically, this theory proposes that when people experience high levels of misery, aversion, and pain in their lives, they perceive their engagement with the living world as highly punitive. This leads to the withdrawal of their investment to the living world and its people and, thus, the disengagement with life, which, in turn, leads to further escalation of suicidal ideation (Klonsky and May 2015).

The third step of this model conceptualizes the operational mechanism that enables the transition from suicidal ideation to its enactment and, thus, death. Specifically, this step designates three distinct functional contributory factors that govern the transition from suicide ideation to action. That is, dispositional, acquired, and practical factors contribute to the development of the capacity for suicide, which distinguishes people who exhibit suicidal ideation from people who exhibit suicidal ideation and behavior (Klonsky and May 2015). The dispositional contributors designate genetic factors – for instance, constitutionally low inhibitory threshold, low level of death anxiety, and high pain threshold. The acquired contributors reflect the habituation in death anxiety and psychophysiological pain due to a systematic

exposure to aversive stimuli (e.g., self-injury, victims of chronic abuse). Finally, practical contributors are among others information about, expertness at, and access to lethal means (Klonsky and May 2015).

Evolutionary Perspectives on Death by Suicide

The Altruistic Hypothesis

The kin selection theory proposes that peoples' sequential patterns of behavior have a nepotistic quality. This, in turn, increases the probability that their genetic material would survive through its transmission to the subsequent generations through offspring but also through non-offspring kin (Aubin et al. 2013). The altruistic hypothesis proposes that when the quality of peoples' living existence is perceived (e.g., inaccurately or accurately) to decrease the probability of their kin to pass on their genes, then self-destruction might reflect a sacrifice in the service of a net genetic benefit (Soper 2019).

Moreover, according to De Catanzaro (1984), human beings are most probably to cause their own self-destruction when their reproductive potential is low (e.g., terminal illness, severe psychopathology) and at the same time they perceive that their living existence significantly decreases their inclusive fitness by impeding with their overall genetic kin's reproduction. Therefore, an altruistic death by suicide reduces the reproductive fitness of the victim while increasing the inclusive fitness.

The Bargaining Hypothesis

A substantial amount of research studies related to suicidality has proposed that the manifestation of suicidality reflects costly yearnings for help which could have a functional quality for the people that are enmeshed in conflictual interpersonal dynamics. Specifically, some cases of suicidality might constitute a warning strategy that the affected individuals implement in the context of their interpersonal conflictual bonds (e.g., attachment relations, social group). That is, it might reflect a desperate attempt to communicate to their

significant others or to the members of a social group that they might experience significantly negative consequences if help or change is not offered (Aubin et al. 2013).

Additionally, this warning strategy can function as a genuine (e.g., not manipulative) signal for help, which in turn could motivate caring others to provide appropriate help to the person in need. Precisely according to this hypothesis, people who are exhibiting suicidal behaviors are gambling with their lives. People in need win in a scenario where they survive the suicide attempt and are then beneficially helped, and they lose when they do not survive. This hypothesis finds some support in the widely cited data indicating that most suicide attempts do not have a fatal outcome (Soper 2019).

Pain and Brain Model of Suicide

This model proposes that the phenomenon of suicide among humans might constitute a maladaptive side effect (e.g., negative by-product) of evolved mechanisms whose fitness properties were so powerfully effective that they were worth the cost of suicide. That is pain and cognition (Soper 2019).

Pain is an operational system which aids self-preservation by enabling the human mind and body to immediately and adaptively react to an aversive stimulus. The phenomenological experience of this reaction to aversive stimuli is a strong urge (e.g., affective sensory) to immediately escape from pain and/or experience relief (Soper 2019).

Additionally, psychological pain is intrinsically intertwined with physiological pain motivating humans to react adaptively to threatening stimuli that emerge in the context of their attachment relationships and meaning systems (e.g., cause and effect relationships, internal schematic representations of the word, the self, and others). Psychological pain is widely considered to be as distressful as physiological pain and thus motivates humans to act immediately in order to escape it. That is, aversive stimuli due to their potential damage (e.g., life-threatening, interpersonally threatening) elicit psychological and/or physiological pain that leads to a

psychophysiological disequilibrium (Soper 2019). Consequently, the organism is motivated to immediately find a solution that would lead to the regulation of pain and, thus, to psychophysiological and/or interpersonal homeostasis that significantly increases the probability of survival and reproduction. Thus, the overall adaptive benefit of psychological pain may have been so potent that it outweighs even such a maladaptive by-product as suicide (Soper 2019).

Furthermore, the intellectual mechanisms of the human brain are consensually considered among its most adaptive properties as they have enabled people to create tools, language systems of communication, civilization, and medical and psychological treatments. However, the intellectual capacities of the human brain (e.g., self-consciousness, intentional and logical reasoning, problem-solving) also provide the means to escape pain through self-destruction. For instance, when humans experience intolerable levels of psychophysiological pain triggered by a highly aversive condition (e.g., terminal illness, severe psychopathology) from which escape in the living world is perceived as impossible, they experience a sense of entrapment, defeat, helplessness, and hopelessness. The perception that there is no possible relief from intolerable levels of psychophysiological pain might lead them to use their otherwise adaptive intellectual capacities to escape pain through suicide (Soper 2019).

Conclusion

Death by suicide is a complex, multifaceted, and multifactorial phenomenon, and while it is among the leading causes of mortality globally, it is a preventable cause of death. Nonetheless, due to stigmatization that revolves around suicidality, people in need feel insecure to talk about their experience to their significant others and even seek professional help. That is, usually, suicidal people often suffer in silence, thinking that if they seek professional help, they would be negatively judged and/or considered dangerous. This, in turn, usually triggers feelings of guilt, anxiety, mental

confusion, and, thus, further self-disturbance that increases their risk of death by suicide (Maris 2019). Consequently, there is a need to identify and communicate through every means possible that there are clinical, social, and community interventions that can provide substantial help to the affected people.

Cross-References

- [Reproduction, Suicide, Euthanasia](#)
- [Suicide](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide as Kin-Directed Altruism](#)

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Death in Christianity

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Synonyms

Body disposal; Burial; Death; Western perspectives on death.

Definition

In Christianity, the concept of death is tied to the death of Jesus: Christians typically believe that Jesus sacrificed himself to pay for the sins of mankind and those who believe in him will be forgiven for their sins and gain an eternal life in heaven.

Introduction

A general understanding of Christianity is a prerequisite to exploring the concept of death in this religion. Christianity is considered a monotheistic religion that centers on the life and teachings of Jesus of Nazareth as portrayed in the New Testament, the second major component of the Christian Bible. The Hebrew Bible, called the Old Testament in Christian theology, comprises the first section of the Christian Bible. Although they may differ in the book order, most Christian denominations define the New Testament as 27 books, which include the four gospels, the book of Acts, the 21 epistles, and the book of

Revelation. Christianity is the largest religion practiced in the world. Christian populations make up roughly one third of the world's total population. There are five major branches of Christianity, i.e., Orthodox, Catholic, Protestant, Anglican, and Restorationism. The Roman Catholic Church is the largest church with approximately more than one billion participants. Protestants comprise the second largest group with approximately 500 million adherents. Although the term *Christian* encompasses diverse religious ideas and practices, this entry highlights the shared beliefs regarding crucifixion of Jesus of Nazareth and the role of his death in Christian views.

Most of Christian beliefs are based on the life and death of Jesus. Most Christian groups revere Jesus as the son of God and the incarnation of God. He is the Messiah, or one who is anointed. Followers of Jesus are known as Christians, since they believe that Jesus is the anointed one. According to Christian theology, Jesus died for humanity's sins. His birth, crucifixion, resurrection, and ascension into heaven were required to open the gates of heaven, or salvation, to human beings. Without this sacrifice, people would not be able to join God in eternal life. The traditional Christian understanding of Jesus' birth emphasizes that he was conceived by the Holy Spirit and by Mary of Nazareth, who was a virgin at the time of conception. Beyond his birth, little is known about Jesus' life before he began his public ministry. Jesus started his work as a teacher and healer when he was around 30 years old and spent approximately 3 years doing this work. According to the gospels, he drew large crowds as he traveled and taught in Galilee and Perea. Jesus' final meal with the apostles, the 12 people chosen to spread the word of Jesus' teachings, before his execution is a key event in Christian traditions. During the meal, which is commonly known as the Last Supper or the Lord's Supper, Jesus explained that one of the apostles would betray him. He also shared bread and wine and told his disciples that these were his *body* and *blood*. The gospels of Matthew, Mark, and Luke and the First Epistle to the Corinthians discuss this dimension of the final meal. For example, the Gospel of Matthew (26:26–29) notes:

Now as they were eating, Jesus took bread, and blessed and broke it, and gave it to the disciples and said, 'Take, eat; this is my body.' And he took a cup, and when he had given thanks he gave it to them, saying, 'Drink of it, all of you; for this is my blood of the covenant, which is poured out for many for the forgiveness of sins. I tell you I shall not drink again of this fruit of the vine until that day when I drink it new with you in my Father's kingdom.'

After the final meal, Jesus prayed in the Garden of Gethsemane. Temple guards arrested Jesus, while he was in the garden. Judas Iscariot, one of the apostles, is said to have betrayed Jesus by identifying him to the guards. Jesus was eventually charged with treason and brought before the Roman procurator Pontius Pilate who offered the crowd a choice between Jesus and Barabbas, a political prisoner charged with insurrection. The crowd opted for the freedom of Barabbas and Jesus was sentenced to death. Jesus died in Calvary (also called Golgotha) after being crucified on a wooden cross.

The books in the New Testament explain how Jesus was crucified, died, and buried within a tomb. Three days after his death, Jesus was raised from the dead. The gospels of Matthew, Mark, and Luke all tell of the resurrection of Jesus. Each text, however, emphasizes different points and varies in the details. Christians typically believe that Jesus sacrificed himself to pay for the sins of mankind. Those who believe in Jesus will be forgiven for sins as a result of Jesus' sacrifice and gain an eternal, satisfactory life in heaven. The emphasis of Christianity on heaven (vs. hell) and forgiveness (vs. punishment) may, to some extent, account for lower death anxiety among Christians (also see Krause and Hayward 2014; Lester et al. 2007; Templer 1972).

Although multiple versions of the Ascension exist, accounts emphasize how Jesus bodily ascended into heaven 40 days after resurrection. After ascending to heaven, Jesus sits at the right hand of God, comprising part of the holy Trinity. The Trinity doctrine states there is one God, who is the Father, Son, and Holy Spirit. The bodily ascension of Jesus represents the union of human beings and God and also highlights how Jesus embodies both the divine and the human. The Ascension is discussed at length in Mark 16:19, Luke 24:51, and in the first chapter of the Acts of the Apostles.

Christians remember Jesus' actions at the final meal with disciples in weekly services through the act of Holy Communion, or the Eucharist. The word *Eucharist* can refer to the act itself and/or to the bread and wine used during the act. During Holy Communion, the priest or minister blesses bread and wine (or grape juice) through a series of prayers and actions. After the bread and wine are consecrated, churchgoers leave their seats and go to the front of the church to receive a piece of bread and a sip of wine (or grape juice). This ritual re-creates the moment during the final meal when Jesus gave disciples bread and wine, explaining that these were his body and blood. It reminds Christians of how Jesus "poured out his blood" during crucifixion so that people could be restored to grace.

Evolution of Supernatural Beliefs Regarding Death

Overall, the abovementioned supernatural aspects of death in Christian viewpoint may be explained by evolutionary accounts on supernatural beliefs. The anthropologist Guthrie (1993) observed that humans tend to interpret ambiguous stimuli as having been produced by agents. He further suggests that this perceptual bias is adaptive because it makes humans more wary in their interactions with their environment and consequently reduces the risk of encounters with predators. Guthrie (1993) juxtaposes this finding with the context of a broader theory of religion. Barret (2000) tried to specifically identify the cognitive mechanisms that produce such perceptual biases. Barret coined the term "hypersensitive agency detection device" (HADD) and elaborated: "when HADD perceives an object violating the intuitive assumptions for the movement of ordinary physical objects and the object seems to be moving in a goal-directed manner, HADD detects agency." HADD could contribute to the *formation* of religious concepts (regarding death) by making people identify ambiguous objects as intentional agents (e.g., ghosts or spirits). Additionally, HADD could potentially

reinforce religious concepts regarding death. For example, people who survived a serious illness often reported presence of supernatural entities in their account of what actually happened.

Suicide in Christianity

It is important to present an overall idea of suicide and its ramifications in Christianity. There has been heated debate over the Christian view on suicide (Torgler and Schaltegger 2014). Early Christians believed that committing suicide is sinful and an act of blasphemy. The most notable pro-suicide group was the Donatists, who believed that by killing themselves they could be regarded as martyrs and go directly to Heaven. They were finally declared heretics. Most early theologians of the Catholic Church considered suicide as murder and thus a moral sin in the absence of circumstances that could potentially mitigate the sinfulness of the act. Yet, more recent accounts contend that suicide may not be as wrong as previously regarded. Some Christians posit that one cannot repent of suicide as praying and asking for forgiveness are not possible after death. Higher religiosity in Christian populations may decrease suicidal ideation; however, much of this association may be explained by the social support typically inherent in religious affiliations (e.g., Rasic et al. 2009).

Funerary Rituals

All religions have specific rituals regarding disposing the body of the deceased. Different branches of Christianity (e.g., Protestant vs. Catholic) have different burial rites that may have been evolved in response to different cultural contexts and ecological features. Christians typically believe that Jesus sacrificed himself to pay for the sins of mankind. Those who believe in Jesus will be forgiven for their sins as a result of Jesus' sacrifice and gain an eternal life in heaven. According to these religious teachings, funerary rites should typically

include: (1) an opening statement lead by the priest or minister, (2) prayers and hymns, (3) scripture reading, (4) a remembrance given by a close friend or a family member, and (5) praising Jesus and prayers for the soul of the deceased. Christian burial rituals mainly focus on the deceased entry into Heaven and God's ability to give the grieving strength to cope with their loss. The deceased person is usually placed in the grave on its back. Early Christians adopted the custom of putting the feet toward the east so that at resurrection the reborn can hurry toward sunrise. Wearing black is usually a sign of mourning (see Bedikian 2008). This dress code may be regarded as a social signaling. For example, widows of the deceased are usually, in many cultures, expected to wear black for long periods of time. To remove the black costume early after the death of the deceased husband was considered disrespectful.

Conclusion

In all, Christian beliefs and traditions are diverse and varied. Nevertheless, across denominations Christians share a belief in the importance of Jesus' crucifixion, resurrection, and ascension as the cornerstone of their faith. These phenomena are supernatural beliefs that may be explained using evolutionary psychological theories on supernatural beliefs. For Christians, Jesus' death and resurrection allow the salvation of humanity. Without his death and rebirth, human beings would not be reconciled with God and would be unable to enter heaven or eternal life after death.

Cross-References

- [Body Disposal](#)
- [Death](#)
- [Death in Islam](#)
- [Death in the Eastern Religions](#)
- [Religion](#)
- [Suicide](#)
- [Western Perspectives on Death](#)

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Death in Islam

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Synonyms

[Body disposal](#); [Burial](#); [Death](#); [Death in the eastern religions](#)

Definition

In Islam, death is the transition from life in this world to a truer eternal life in the next world.

Introduction

A nearly universal aspect of human existence addressed by religion is that of death and its meaning. In order to fathom the concept of death

from an Islamic perspective, one should have an understanding of what Islam actually is. There are various definitions and descriptions of Islam. Rather than providing a single definition, one can infer what Islam is, based on what Muslims have made of it in different cultural contexts, social statuses, and historical circumstances. Perhaps, the most robust way to introduce Islam is Quran, the holy book of Islam, which is believed to be a collection of revelations from *Allah* (the Arabic for “God”) as delivered via the angel Gabriel to Muhammad while he was living in western Arabian towns of Mecca and Medina. The Quran consists of 114 chapters and over 6200 verses and describes Islam as: “Upholding equity, Allah, his angels and those with knowledge have witnessed that there is no god but him, the mighty and wise. Indeed, religion in Allah’s eyes is Islam. Those who received the book disagreed among themselves out of jealousy only after knowledge had come to them. Whoever disbelieves in Allah’s sacred verses, (let him know that) God is swift in reckoning” (Quran, 3:18–19).

The Quran emphasizes belief in one just God and posits that disbelief incurs God’s anger. Broadly, the Muslims are those who believe in God’s revelation and submit to God’s will. Much of the contemporary disagreement among Muslims lies under the instances of “God’s will.” By honoring God’s will in this life, Muslims are promised inexhaustible rewards both in this world (*Dunya* in Quranic terms) and the next (*Akhira* in Quranic terms). Many verses of the Quran describe afterlife and death experience. For example, those who fulfill God’s will are expected to directly go to paradise after death. Moreover, a number of verses commend martyrdom and martyrs (*Shahid*), those who die on the path of Islam: “And never think of those who have been killed in the cause of Allah as dead. Rather, they are alive with their Lord, receiving provision” (Quran, 3:169).

Most of the Islamic documents on death and afterlife are based on teachings of the Quran. Death has been mentioned in 36 chapters of the Quran. Despite the diversity of the contexts in which death and afterlife are discussed, the themes of returning to *Allah* and taking full

responsibility for one’s actions are central in these documents. The Quran explicitly contends that one has only one chance, this life (*Dunya*), to prepare for the next life (*Akhira*). Thus, one should do good deeds to be prepared to go to paradise. The dead are believed to be resurrected on Judgment Day for an evaluation of people’s deeds and whether they will go to paradise or hell.

Different interpretations of death in Muslims’ texts have been accumulated throughout the centuries and have produced a complex eschatology that can be divided into the “widely accepted Muslim perspective” and the “Gnostic mystical perspective.” The former view adheres to the teachings of the Quran, guiding believers to stay away from sin. Furthermore, the Quran strongly encourages good deeds (e.g., helping others) and reminds Muslims that each person will be held accountable solely for his or her own acts in this world. The latter view, however, maintains an esoteric conceptualization of death that is direct, experiential, and unmediated. This view is attained by means of mystical practices and through supernatural discoveries.

Notwithstanding the abovementioned complex eschatology and the cited perspectives, there are still enormous variations in Muslim beliefs and practices about death, dying, funerary rituals, burials, and commemorations, some of which derive from differences within the religious tradition, but most of which derive from variations in national, ethnic, tribal, and folk cultures. The diversity of grieving traditions, afterlife beliefs, and burial manners may be explained by the notion that there are no homogenous beliefs in the texts. “Subspecies” of Islam have emerged, possibly because of different selection pressures in different groups that submit to this ideology.

In sum, life and death are interconnected for Muslims and this world is “just the beginning.” Short life of people in this world is a test period in which Muslims are taught to behave correctly, so they are prized with an immortal life of joy and prosperity. Evolutionary psychology has provided insightful findings on religion. The majority of the evolutionary psychologists currently argue that religion originated as a by-product resulting from the interaction of several evolved

psychological mechanisms, and with that initial foundation interacting with cultural evolution, religions are what they are now (Atran 2002). The evolutionary psychological study of death in religious context, specifically Islam, should be pursued using this framework. In what follows, two broad conceptualizations of death in Islam (i.e., widely accepted Muslim perspective and the Gnostic mystical perspective) are shortly discussed from an evolutionary psychological perspective.

First, the *widely accepted Muslim perspective on death* can be explained by its social and individual functions. The thought of being at presence of Allah after death can potentially relieve death anxiety. An enormous amount of social support is also provided for the grieving individuals. This social support is conducive to mental health and facilitates coping with the death of loved ones. In addition, funerary rituals and Islamic rules on body disposal are conducive to disease avoidance and public health. Therefore, Islamic teachings on death, besides being supernatural, provide the society and its individuals with lower death-related anguish, paired with better health in disposing the bodies of the deceased.

Second, *Gnostic mystical perspective on death*, which mostly accentuates supernatural experiential aspect of death, can be partly explained by “hypersensitive agency detection device” (HADD; see Barret 2000) and “minimally counterintuitive” (MCI; see Barret 2004). Barret (2000) has coined the term HADD as “when HADD perceives an object violating the intuitive assumptions for the movement of ordinary physical objects and the object seems to be moving in a goal-directed manner, HADD detects agency.” The by-product account of religious beliefs highlights the importance of the HADD and MCIs (i.e., concepts in which a relatively small number of assumptions are violated, thus grabbing our attention) in religious beliefs regarding death. Specifically, supernatural agents arise as a by-product of HADD and susceptibility to MCIs. Many supernatural, esoteric explanations of death and near-death experience in Islamic texts may be explained by these psychological mechanisms.

Suicide in Islam

It is important to note the Islamic perspective on suicide as well as its psychological analysis. Suicide – the willful taking of one’s own life – is often considered to be morally wrong and an offense against *Allah*. Muslims believe that suicide victims will be punished in the afterlife (Gearing and Lizardi 2009). This is broadly consistent with the finding that suicide attempts are significantly lower among religious individuals (Burshtein et al. 2016). Besides religious teachings on suicide, this topic has become an urgent matter in the past few decades because of the significant increase in the number of incidents in which Muslims have conducted deadly attacks on military and civilian targets that also took the attacker’s life. While religious ideology has been, to some extent, involved in recent suicide attacks, the degree to which it has been a decisive factor is hotly disputed. In fact, some Muslims say that these attackers are not even Muslim and hold unrealistic, brainwashed ideas about the true nature of Islamic teachings. What is almost obvious is that the attackers must think that they are doing God’s work and will be directed to paradise (for an evolutionary account on religiously motivated suicide terrorism, see Liddle et al. 2011).

In Islam, paradise is depicted in several verses, and those who die for a sacred cause (i.e., martyrdom) are welcomed in paradise right after they pass away. For example, paradise is depicted in these verses: “That will neither make the head throb, nor intoxicate. With fruits of their own choice and any flesh of fowl that they desire. And, [for them are] fair women with large, [beautiful] eyes, like hidden pearls, a recompense for all that they did” (Quran, 56: 19–24). It is important to note that religiosity, either Islam or other religions, cannot predict willingness to commit suicide attacks to kill others (e.g., nonbelievers). In fact, Islamic teachings also stress the virtues of humbleness, endurance, gratitude, patience, and obedience to *Allah*. Empirical work also shows a positive correlation between humbleness, honesty, and religiosity in a sample of Muslim individuals (Aghababaei

2012). It is the very subjective understanding of “God’s will” that forms a continuum within Muslims ranging from absolute endurance to suicide attacks.

Funerary Rituals

In Islamic communities, as in Jewish and Christian ones, funerary rituals involve various activities: preparations for death and burial, interment of the body, mourning, and memorial. These rites combine practices prescribed by religious tradition and local cultural customs. Islamic texts have set forth ritual requirements and taboos that Muslims are expected to observe. According to these religious teachings, funerary rites should include: (1) pronouncing the testimony of death, usually in Arabic language (*Shahada* in Arabic), prior to death and turning the dying person’s face toward Mecca; (2) washing and shrouding the corpse in accordance with ritual requirements; (3) performing funeral prayers; (4) conducting the body to the cemetery; (5) burial of the corpse on its right side, with the face turned to Mecca; (6) mourning following religious teachings and local traditions; and (7) visiting the grave. Burial should be performed within 24 h of death. The body is placed in the grave without a coffin and the body is usually wrapped in a piece of white textile. In some cultures, the corpse may be dressed in ordinary but not expensive clothing. It can be clearly seen that culture plays a crucial role in funerary rituals. This also highlights the interaction between the evolution of religious beliefs and cultural evolution. People usually pronounce prayers, while the body is being buried (e.g., “From it [the earth] we created you, then we put you back into it, and from it we will bring you forth again” [Quran, 20:55]). Wearing black, as a sign of mourning, is quite common, but exceptions exist in some areas.

Conclusion

In Islam, death is the transition from this world to the next. In other words, life in this world is a

small but critical part of a larger human existence. The holy book of Islam, the Quran, frequently mentions death, afterlife, and the Day of Judgment. What humans do in this life, the Quran says, will be evaluated and people will be directed either to paradise or to hell. The widely accepted Muslim perspective and the Gnostic mystical perspective on death were discussed. Islamic perspective on suicide and Islamic burial rituals were also shortly described.

Cross-References

- [Body Disposal](#)
- [Death](#)
- [Death in Christianity](#)
- [Death in the Eastern Religions](#)
- [Suicide](#)

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Death in the Eastern Religions

- [Death in Islam](#)

Death of Healthy (vs. Sick) Child Followed by More Grief

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Synonyms

Bereavement following a child's death

Definition

Parental grief – the suite of emotional and behavioral responses, including deep sorrow, that follows from a child's death.

Introduction

The death of one's children is perhaps one of the most painful experiences humans endure. Although incredibly painful, this experience can still be examined through the lens of evolution. Why did humans evolve to experience such profound distress at the loss of a child? All else equal, would not the parents who recovered seamlessly from their child's death outcompete their suffering counterparts for resources and social partners? Do bereaved parents experience equal levels of grief, or does the intensity of the grief response follow theoretically consistent patterns?

Grief Tracks Inclusive Fitness and Propagation Potential

At first glance, the emotional pain following the death of one's child appears to follow logically from such a substantial loss to inclusive fitness. Children, who share roughly 50% of genes by common descent with their parents, offer a mechanism through which parents can transmit copies of their genetic material to subsequent generations (Hamilton 1964). Indeed, many evolutionary theories of parental attachment are based in the logic that parents invest substantially into caring,

providing for, and protecting offspring precisely because children are vehicles through which parents propagate their genetic material. Parents who lose a child are thus losing an opportunity to transmit their genes. Moreover, parents will not reap subsequent inclusive fitness benefits for any investment (e.g., resources, time) they have already allocated to that offspring.

Given that kin, including offspring, offer mechanisms for individuals to enhance their inclusive fitness, early researchers contended that the human grief response is a natural consequence of these strong attachments (Archer 1999; Parkes 1972). If attachments generally track a social partner's ability to enhance one's inclusive fitness, then grief should be calibrated to the strength of the attachment the bereaved had with the deceased. In the case of a lost child, by this logic, parents should feel immense distress, given that children are one of the primary mechanisms by which parents enhance their inclusive fitness.

However, when allocating investment towards offspring, parents face a series of trade-offs. Because effort, resources, and time are limited, parents who allocate resources to one child are expending effort that might be directed towards other fitness promoting goals, such as investing in the survival of other children or pursuing additional mating opportunities (Trivers 1974). Indeed, parents cannot invest too many of their resources towards one offspring because such ample investment may jeopardize the survival of other offspring or the parent's potential to produce additional offspring in the future. Due to such constraints, parents may calibrate their investment based on offspring's probability of enhancing their inclusive fitness. Offspring who are ill, for example, are less likely to survive and reproduce than offspring who are in better health.

Littlefield and Rushton (1986) contended that the extent of parents' grief following the death of a child should correspond to the probability the child would have reproduced or the child's propagation potential. In a test of this hypothesis, they recruited 263 bereaved parents and demonstrated that grief was more intense following the death of an otherwise healthy child compared to following the death of an ill child. These hypotheses are further supported by pattern of infanticide or the killing of one's young

child. Compared to their healthier counterparts, infants who suffer poor health, exhibit physical deformities, or are born underweight are more likely to be killed by their parents (Ball and Hill 1996). Taken together, these results are consistent with the interpretation that grief intensity is calibrated to the deceased child's propagation potential.

Although the foregone inclusive fitness benefits of losing one's child suggest one explanation for the profound parental grief response, the immense costs of grief still may have severely harmed the fitness of bereaved parents. That is, to explain parental bereavement in terms of lost residual reproductive value commits the sunk cost fallacy because a parent's investments have already been allocated. The time and effort parents already invested in children cannot be compensated by the time, resources, health, and social relationships devoted to grief.

Accounting for the Costs of Grief

The large decrements in grievers' well-being must be offset by other fitness-relevant benefits (Winegard et al. 2014). Otherwise, the protracted and deleterious suite of responses during grief should have been winnowed out by natural selection. All else equal, parents who quickly overcame their child's death would have better competed for resources, status, social partners, and mates than those who allocated greater energy and resources to their sorrow.

Thus, evolutionary-minded researchers have attempted to forward adaptive advantages to exhibiting profound grief at a loved one's death. Archer (1999) argued that the human grief response is a by-product of humans' investment in close relationships. According to his logic, individuals feel distress when separated from loved ones because that distress motivates them to seek out their absent social partners, reunite, and foster their bond through continued investment. In the case of death, however, this distress is in vain. That is, the distress individuals experience during a partner's absence was generally adaptive insofar as it motivated reunion and continued provisioning. In the case of a loved one's death, on the other hand, the individual still experiences this distress response, but the distress is not adaptive.

Archer's (1999) logic assumes that the human cognitive system could not disentangle sources of a loved one's absence. According to the by-product explanation, humans exhibit the same suite of responses (i.e., grief) when a living partner is absent as they do when a partner is dead. However, emotional responses are often quite specific, prompting behaviors that generally would have been advantageous for that particular circumstance (Nesse 1990). Imagine, for example, your child storms out of the house after an intense argument. While they are away, you might feel worried for their safety or upset that they left. Imagine that a day or two later, you learn your child was killed in a car accident the night they left. Your emotional response would likely shift immediately from concern to despair. Or imagine instead you learned your child had left to reside with their friends' parents, with whom you have always felt a sense of rivalry. Your emotional response would quickly shift to relief and perhaps jealousy or moral outrage. These anecdotal examples suggest that emotional responses are quite responsive to cognitive attributions of a loved one's absence.

Indeed, human grave sites extend as far back as 10,000 years ago (Solecki et al. 2004) suggesting human ancestors have long had a cognitive awareness of death. If the human mind is capable of discerning sources of social partners' absences, then this cognitive distinction should have offered a mechanism through which natural selection could weed out the costly misfiring of the separation response. All else equal, individuals who displayed prodigious distress at a living loved one's absence, but not in response to a loved one's death, should have outcompeted those who displayed prodigious distress both when it provided benefits (i.e., in response to mere absence) and when it did not (i.e., in response to death).

More recently, evolutionary-minded researchers have forwarded a novel explanation of the human grief response which posits adaptive advantages to grievers displaying emotional distress and the associated behaviors (e.g., funerary practices) following the death of a loved one. That is, grief serves as a costly, hard-to-fake signal of a person's commitment to the deceased and, thus, the griever's

capacity to form enduring and committed bonds (Winegard et al. 2014). In a sea of potential social partners, humans must decipher which individuals will prove reliable and loyal from those who would abandon the relationship when self-interest favors defection. Because it is very challenging to ascertain individuals' underlying levels of loyalty, human psychology should aim to ascertain predictors of who will likely be a devoted social partner.

Grief may serve as one such cue of these underlying inclinations, precisely because it is so costly. Grievers who are truly distressed forego other fitness-enhancing opportunities (e.g., pursuing resources or mates), thereby honestly signaling their devotion to the deceased individual, who can never repay the devotion. According to the signaling perspective of grief, social partners should perceive individuals who display more intense grief as more trustworthy and prefer them as cooperative allies, compared to those who experience little to no grief at the death of a loved one. Empirical research supports these predictions. Indeed, across a series of experiments, people selected more over less intense grievers as friends and partners for trust games (Reynolds et al. 2015). These findings suggest the human grief response was extended over the course of human evolution because social partners preferred those who exhibited honest displays of their pro-social tendencies through grief.

According to the signaling explanation of grief, bereaved parents may be signaling not only their capacity for loyalty but perhaps also their inclination to be a devoted and nurturing parent. If individuals prefer kindness in both their cooperative alliances, friends, and romantic partners, then the grief response of parents may be treated as diagnostic of such traits. Whether more versus less intense grieving parents are preferentially selected as long-term romantic partners (a context where parenting ability is emphasized) is an open question for future research.

Conclusion

The death of a loved one, including a child, is an incredibly heart-wrenching experience. However, it does not have to be. Although children are one of

the primary mechanisms through which individuals enhance their inclusive fitness, the substantial decrements in fitness due to grief should render intense grief fitness-harming. Thus, evolutionary explanations of the human grief response must account for the immense costs of the suffering to the griever. According to by-product accounts of grief, grief is the misfiring of an attachment response that generally prompted reunion in the case of a loved one's absence. This explanation rests on the assumption that natural selection had no opportunity to winnow out maladaptive separation responses from adaptive ones. However, according to the signaling account of grief, the intensity of grief provides valuable information about the cooperative traits of the griever. That is, parents experience profligate distress following the death of their children because social partners could use these responses to inform their social and romantic choices.

Cross-References

► Inclusive Fitness

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Deaths from Famine

► [Calculating Starvation Risk](#)

Debating Procreation (With David Benatar)

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Synonyms

[Antinatalism](#); [Natalism](#); [The Procreation Debate](#)

Definition

Antinatalism is the philosophical position that procreation is unethical. David Benatar and David Wasserman debate this perspective in the book *Debating Procreation*.

Introduction

The permissibility of procreation is a subject that is not often debated, but David Benatar and David Wasserman take on this task in *Debating Procreation* (Benatar and Wasserman 2015). Benatar, an antinatalist, and Wasserman, a natalist, each present arguments supporting their positions and offering critiques to the opposing argument in an effort to answer a philosophical question: Is it wrong to reproduce?

The Procreation Debate

Antinatalism is based on the premise that it should never be permissible to reproduce. However, Benatar distinguishes between the ethics of procreation and the regulation of procreation. He asserts that the moral assertion that one should not procreate cannot be equated to advocating for the removal of the individual's right to

reproduce. Antinatalism is based on the premise that procreation causes harm, and, by not reproducing, harm can be attenuated. Antinatalists argue that being born is always harmful to the individual and others, and that the opposite, not being born, is better. Therefore, Benatar's task is to convince readers of the harmfulness of procreation. In order to do this, he introduces three arguments: (1) the asymmetry argument, (2) the quality of life argument, and (3) the misanthropic argument.

The asymmetry argument contrasts both the harm and the benefit associated with existence and nonexistence. Weights (i.e., positive, negative, or neutral) are assigned to each category, with Benatar contending that being born is always harmful (i.e., that the negatives outweigh the positives). The quality of life argument looks to extend this premise to conclude that all life is harmful enough to equate procreation with unethical behavior. Benatar argues that (1) humans are not good assessors of the quality of their own life because of psychological mechanisms like the optimism bias (i.e., that we are inclined to see positives more than negatives; Andrews and Withey 2012), (2) that there are many small inconveniences in everyday life (e.g., hunger) that are often overlooked, and (3) that there is risk for large-scale harm in every individual's life. He equates the combination of these three factors, particularly combined with the absence of harm that he links to nonexistence, as sufficient evidence that all life is harmful. Finally, the misanthropic argument contends that, not only is procreation harmful to the individual who is being born but also to other humans, other species, and the environment. These three arguments are the foundation of Benatar's premise that procreation is never permissible under any circumstances.

Wasserman begins his natalist argument by critiquing a fundamental assumption used in many antinatalist beliefs; he believes that the overreliance on weighing the avoidance of harm as more compelling than the accrual of benefits weakens the overall antinatalist arguments. Ultimately, he believes that the benefits one can accrue over a lifetime, such as the expected good from the parent-child

relationship, can offset the harm. However, Wasserman stresses that, while he believes there are benefits to procreation, it is never obligatory to procreate nor is it ever harmful to not procreate. Wasserman's pronatalist stance on procreation is more moderate than some other pronatalists and the general public (see Benatar and Wasserman 2015). While he does not believe that procreation is always wrong, he does believe that there are many circumstances where it should not be permissible to procreate.

Conclusion

Without being born, one cannot suffer. Without being born, one cannot experience the joys of life. These are the foundations on which Benatar and Wasserman build their arguments for natalism and antinatalism. While various philosophers have contributed to this discussion, Benatar and Wasserman's *Debating Procreation* provides an excellent overview of the arguments for those new to this philosophical debate.

Cross-References

- ▶ [Better Never to Have Been](#)
- ▶ [David Benatar](#)
- ▶ [David Wasserman](#)
- ▶ [Permissibility of Reproduction](#)

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Deceased

- ▶ [Medical Definitions of Death](#)

Deceit

- ▶ [Human Deception](#)
- ▶ [Reliability and Deception in Language](#)
- ▶ [Self-Deception](#)

Deceit and Self-Deception

- ▶ [Robert Trivers](#)

Deception

- ▶ [Egg Mimicry](#)
- ▶ [Information About Likely Combat Success](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Self-Deception](#)
- ▶ [Violation of Long-Term Mate Preferences](#)

Deception Kinship Psychology Manipulation

- ▶ [Manipulation by Others](#)

Deceptive Alarm Calls

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Introduction

Although there are potential benefits to be gained through deceptive communication, animal signals overwhelmingly are reliable indicators of some salient property of the signaler or its environment. One reason that honesty tends to prevail is that selective pressures should act on receivers to ignore signals that do not convey reliable

information (Searcy and Nowicki 2005). Thus, in order for there to be an evolutionary advantage for receivers, the benefit of responding to the signal should on average outweigh the cost of ignoring it (Kokko 1997). Because this is *on average*, however, some level of dishonest signaling can be evolutionarily stable in most signaling systems (Johnstone and Grafen 1993). In cases in which the costs of ignoring an honest signal are high relative to the those of responding to a deceptive one, high rates of deceptive signaling can be evolutionarily stable (Searcy and Nowicki 2005). Such a scenario characterizes alarm calling systems: acoustic signals emitted in the presence of a predator alert nondetectors to the predator's presence and allow them to take appropriate action to minimize their risk of a successful predatory attack, while a deceptive caller could elicit the same action in the absence of a predator in order to gain an advantage over receivers in competitive contexts. Because the costs of ignoring alarm signals given in the presence of a predator (potentially death or serious injury) are likely to be much higher on average than those associated with responses to false alarms (energy expenditure plus lost access to a resource), deceptive false alarm calling has the potential to occur at high rates (Wheeler 2009). This provides the rare opportunity for systematic study of both the behavioral ecology of deceptive signaling as well as the proximate mechanisms underlying the behavior.

The Behavioral Ecology of Deceptive Alarm Communication

The use of alarm calls in the absence of predators have been demonstrated in bovids, sciurid rodents, primates, and a number of avian taxa in two main competitive contexts: feeding and mating. In cases in which a food resource goes to the first individual to arrive (scramble competition; Koenig 2002), a false alarm may distract a competitor long enough to give the caller a competitive edge. This has been suggested to be the case in mixed-species flocks of Amazonian birds, wherein sentinel species regularly give alarm

calls that warn of hawk attacks, but also compete with nonsentinel species to be the first to capture flying insects flushed out during foraging; while both species fly toward the prey, the sentinels regularly produce calls that are acoustically similar to those given when hawks are seen, and these typically cause the listener to flee from the non-existent predator and give up the pursuit of the prey (Munn 1986; but see Satischandra et al. 2010). Similarly, fork-tailed drongos (*Dicrurus adsimilis*) in the Kalahari regularly forage in association with other birds and mammals, providing these other species with some antipredator benefits by producing alarm calls when raptors and mammalian carnivores are detected, but also kleptoparasitizing food of the associated species (Ridley et al. 2007). While such kleptoparasitism is sometimes achieved by direct attacks by drongos, false alarms are common in cases in which an attack is a less viable tactic, such as when the target species is relatively large and thus more likely to win a physical contest (Flower and Gribble 2012). Intriguingly, drongos not only deceptively use their own alarm calls to cause other species to abandon their food, but will also mimic the associated species' own alarm calls in the absence of predators to kleptoparasitize their food (Flower 2011).

Deceptive false alarms have also been shown to be an effective foraging tactic for relatively low-ranking individuals competing against dominant conspecifics, who enjoy greater feeding success because they monopolize access to contestable food resources to the exclusion of subordinates (contest competition; Koenig 2002). Among both great tits (*Parus major*) and tufted capuchin monkeys (*Cebus [Sapajus] apella nigrilus*), low-ranking individuals produce deceptive false alarm calls when feeding in association with higher-ranking individuals, causing the dominant to abandon the food patch long enough for the caller to obtain at least some of the contested food (Møller 1988; Wheeler 2009). High-ranking individuals do not need to use deceptive alarms because they can simply displace lower-ranking individuals from the contested food resource (Møller 1988; Di Bitetti and Janson 2001). Likewise, when food is less clumped, lower-ranking

individuals can obtain food by feeding away from dominants; in both tits and capuchins, the use of false alarms decreased when food was less clumped and thus less easily monopolized by dominants.

The use of deceptive alarm calls has also been shown to be a tactic used by males of some species to reduce the chances that females with which they have mated will mate with other males. Male barn swallows (*Hirundo rustica*), for example, are more likely to give false alarms if their mate is absent from the nest during periods of egg-laying, when extra-pair copulations and fertilizations are common, than they are during other periods; they are especially likely to call in this context if another male was recently seen in the vicinity of the nest (Møller 1990). Male Formosan squirrels (*Callosciurus erythraeus*) produce long bouts of false alarms after mating, which cause both the female and neighboring males to freeze, thus increasing the chances of multiple copulations with the female and likely providing an advantage in sperm competition (Tamura 1995). Similarly, male topi antelopes (*Damaliscus lunatus*) produce false alarms when a female attempts to leave his territory after mating (Bro-Jørgensen and Pangle 2010). These deceptive alarms typically cause the female to remain in the calling male's territory and engage in additional copulations with the deceptive caller before finally leaving the territory.

Although these studies show that production of false alarms are often successful in eliciting costly responses in receivers that are to the benefit of the caller, there is also some evidence that receivers may mitigate these costs through counter-deceptive "skepticism" of false alarms. Among tufted capuchins, listeners are less likely to employ antipredator escape reactions to alarm calls given during competitive feeding, when alarms are more likely to be deceptive (Wheeler 2009), than they are in less competitive contexts (Wheeler 2010). The fact that recordings of false alarms played back in noncompetitive contexts elicit antipredator responses at high rates suggests that the decreased response rate may be due to listeners being skeptical of calls given in contexts

in which deception is most likely (Wheeler and Hammerschmidt 2013). Rhesus macaques (*Macaca mulatta*) similarly are more likely to ignore alarm calls from subordinates than from dominants, which the authors suggest may be due to skepticism of callers that are more likely to call deceptively (Gouzoules et al. 1996). Likewise, when drongos repeatedly attempt to deceive individuals of associated species by repetitively mimicking the target species' alarm calls, the targets respond more weakly to successive false alarms (Flower et al. 2014). The drongos, however, are able to take advantage of the fact that the associated species recognize the alarm calls of additional species that the drongos can also mimic; by switching to the alarm call of yet another species, drongos can decrease the targets' skeptical responses to repeated false alarms (ibid.).

Mechanisms of Deceptive Alarm Calling

Due to the potential cognitive implications of deceptive behavior (Byrne and Whiten 1992), the proximate mechanisms underlying deceptive alarm calling have been subject to considerable speculation, but little direct study. In the examples given above, the evidence that false alarms function to deceive listeners is strong, insofar as the calls make listeners behave as if something that is not true is in fact true, which benefits the caller but is costly to the receiver (Searcy and Nowicki 2005). Whether or not callers produce these calls intentionally is less clear. Because intention to manipulate what a receiver believes requires an understanding that other individuals have beliefs at all (second-order intentionality or "Theory of Mind"; Shettleworth 2010), and because of the lack of evidence that these species have such cognitive abilities (Penn and Povinelli 2007), it seems extremely unlikely that the calls are produced with the intention to deceive. However, it is possible that the calls are intentionally produced with the goal of changing receiver behavior, without understanding that the change in behavior is a consequence of the changed mental

state of the target (first-order intentionality; Shettleworth 2010). Evidence for either first- or second-order intentionality would suggest that the calls are not merely functionally deceptive, but in fact are examples of tactical deception (Byrne and Whiten 1992).

While it seems plausible that calls may be produced with first-order intentionality due to relatively simple associative learning (Shettleworth 2010) of the fact that call production is associated with a competitor fleeing or a mate remaining nearby (Wheeler 2009; Flower 2011), in most cases it is difficult to rule out that call production is an unintentional, hardwired response to a given situation. Among the documented cases of deceptive alarm calling, intentional production seems most likely in the case of the false alarms by drongos; the mimicked calls themselves are not innate but develop only with experience (Goodale and Kotagama 2006), and such learned call types are likely under voluntary production (Jürgens 1995). In contrast, in nonvocal learning taxa like nonhuman primates, sciurid rodents, and bovids, vocalizations are species-specific and individuals appear unable to voluntarily choose in which context to produce a given call type because each call type is linked to particular affective states (Jürgens 1995). Thus, the production of false alarms in at least these mammalian species may not be intentional, but an involuntary vocal reaction to the affective state elicited by the competitive context (see Wheeler et al. 2014), which may but need not necessarily be the same state elicited by predators. It is possible, however, that even with this limitation that individuals can voluntarily choose to produce an alarm call when in the appropriate state, although deceptive calling may not be an option for individuals not experiencing such a state.

The only study to date to examine possible mechanisms underlying the production of deceptive false alarms tested whether such calls among tufted capuchins are associated with increases in production of glucocorticoids (“stress hormones”) among subordinates involved in competitive feeding (Wheeler et al. 2014). The study found no support for this hypothesis, although a follow-up

study found that deceptive callers show signs of anxiety in the contexts in which they produce false alarms (Kean et al. [in press](#)). However, because some noncallers similarly show signs of anxiety, it seems unlikely that anxiety simply leads individuals to call involuntarily. It is possible, instead, that certain individuals experiencing anxiety choose to call, perhaps because they have learned that doing so leads to food rewards. Further research is needed, however, on the ontogeny and mechanisms underlying deceptive calling in order to better understand the potential cognitive, emotional, and physiological underpinnings of this behavior. The study systems described above provide an ideal opportunity to study the mechanisms underlying deceptive communication systematically, although it seems likely that there are many cases of deceptive alarm calling that are yet to be documented.

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Decision Attributes

► Value Attributes

Decision Making

► Rejection Thresholds

Decision Theory

► Game Theory as a Foundation of Evolutionary Psychology

Declarative Communication

► Understanding Human Points

Declarative Knowledge

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Synonyms

Episodic memory; Factual information; Semantic memory; Single trial learning; Symbolic knowledge; Verbal knowledge

Definition

Declarative knowledge is proposed as the system containing memories of events and factual information.

Introduction

Declarative knowledge is subdivided into semantic and episodic memory that render it as symbolic knowledge system. It affords the individual the capacity to store associations in a single trial and contains knowledge that can be thought and spoken explicitly. Interestingly, declarative knowledge lies outside conscious awareness, until it is retrieved by cues from within the environment. The individual can only become aware of the outcome products of such process since the retrieval process cannot be accessible voluntarily.

Evolution and Declarative Knowledge

Phylogenetically, it can be argued that declarative knowledge appeared later than procedural knowledge. This can be shown by the fact that declarative learning only occurs in higher animals, if not human beings (Ornstein 1991). Ontogenetically, it is demonstrated by the fact that children begin to learn and remember procedures before they do facts (Bloom and Lazerson 1988). Also, natural selection has shown that procedural skills are more important for survival than declarative facts (Dudai 1989). Hence, it is not reasonable to assume that knowledge of facts evolved before the knowledge of skills. It is not clear how evolution of brains and brain modules proceeds. However, it cannot be assumed that the evolution of memory and of the visual system has the same background, for these faculties are concerned with quite different tasks (Gibson 1979). Taken together, the present theory states that in both vision and memory, a declarative subfaculty is part of the outcome, and that both systems are far more procedural in nature than it has been assumed so far. A tentative conclusion that can be made considering all this is that the procedural/declarative distribution is a feature of certain brain modules that exist independently of the content of those very brain modules. The distribution is a principle that supposes an organization of a certain kind in certain brain modules. If this hypothesis is valid, then an imbalance in the attention of cognitive

psychologists and neuroscientists given to the procedural subsystem and the declarative subsystem can be found in the visual system as well as in the memory system (Goodale 1992).

Brain-Damaged Patients

Declarative memory stems from the phenomenon of category-specific impairments in semantic memory. A double dissociation has been found in brain-damaged patients between their knowledge of respectively living, for instance animals and fruits, and nonliving, such as tools and clothes. Saffran and Schwartz (1994) argue that this deficit actually reflects not a distinction between living and nonliving things but a distinction between perceptual and functional characteristics of members of the impaired categories. The ground for distinguishing between two animals as similar as a leopard and a panther is the difference in visual characteristics, while the ground for distinguishing between two tools is their different functions. Once more, a difference between action and perception is found in a presumably single system. Category-specific impairment for functional attributes of objects is not a deficit of procedural memory since tool use is intact. In terms of the present theory, this could imply that even within semantic memory of declarative system, procedural aspects are a fundamental part of the system (Bechtel and Abrahamsen 1991). However, to draw any conclusions from this speculation would be premature until it becomes clearer what memory system exactly is damaged in these cases and how it connects with other systems.

One-Trial Learning

In the context of human declarative memory, one-trial learning implies that a fact is comprehended after one presentation (Johansson 1973). But it is also possible to know how to do something after one presentation (Baddeley 1990). For instance, patients who suffer from Korsakoff's syndrome, a form of amnesia typically associated with alcoholism, when they experience a physical painful event, their brain tends to store the unpleasant

outcome in declarative memory. In future situations of the same nature of events, the patient will avoid the event, but they will not be able to justify why, as they will not be able to remember the background information which have caused their outcome behavior.

Conclusion

It has been argued that declarative memory evolved from procedural memory and it constitutes a part of it. Some of its aspects might be reduced to procedural memory. It is both phylogenetically and ontogenetically younger than procedural memory; it is shown to be possible to model declarative knowledge in procedural systems and neural networks, and in some cases one-trial. Learning can function within the procedural system. This notion suggests that declarative knowledge is made possible by procedural knowledge; interpretively, declarative knowledge could be considered a special case of procedural knowledge.

Cross-References

- [Episodic Memory](#)
- [Evolution of Memory, The](#)
- [Evolution of Teaching](#)
- [Procedural Knowledge](#)

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Declarative Memory

- [Different Functions of Memory](#)
- [Episodic Memory](#)
- [Multiple Memory Systems](#)

Decline of Violence

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Synonyms

[Civilization](#); [Pacification](#); [Self-domestication](#)

Definition

A great deal of evidence indicates that human society has experienced a slow and steady decline in both interpersonal and intergroup violence as cooperation, empathy, and peaceful resolution of conflict have become more dominant.

Introduction

The emergence of *Homo sapiens sapiens* was a watershed moment in the natural history of the planet. Highly mobile populations of modern

humans quickly replaced all of the other contemporary hominins they encountered, probably through a combination of violent and nonviolent means, and dramatically reshaped every environment they entered. However, human social groups are marked by extensive intraspecific cooperation, empathy, and nonviolent resolution of conflict, at least compared to our closest relatives, the other extant apes. There are several theories that have been developed to explain the decline of violence in the human species that are not mutually exclusive; in fact, synergy among them is likely.

Intelligence, Communication, and Language

Intelligence and sophisticated communication are necessary preconditions for prosocial cooperation. While true referential communication – nouns and adjectives – has been observed in several nonprimate mammal species (and may also exist in birds), complex social communication is a hallmark of primates (Slobodchikoff 2012). The apes have taken this further to include body language and gestural communication that exhibits personal variation and regional dialects (Byrne et al. 2017). A phylogenetic analysis has revealed that, in primates, the size of the vocal repertoire is closely associated with both group size and time spent in close social contact (McComb and Semple 2005). The evolution of intricate sociality and sophisticated communication seems to be linked, perhaps inextricably.

Esther Herrmann and colleagues take this idea further and propose the *cultural intelligence hypothesis*, which holds that the key difference in intellectual capacities between humans and other animals is not in general intelligence, but in specific cognitive abilities related to our sociality (Herrmann et al. 2007). This includes our social intelligence, the ways in which we communicate, understand, and interact with our fellow humans, but also our *meta-social* intelligence, that is, the ways in which we form hierarchical subgroups, communities within communities. The activation and ecological shaping of innate

abilities is of key concern to this question because primate behavior is not strictly programmed, but rather extensively learned, and socially so.

In 1993, Frans de Waal and Denise Johanowicz performed a pioneering cross-fostering experiment that demonstrated the connection between prosociality and learning. They took juvenile rhesus macaques, which are fairly aggressive and not prone to displays of apparent social reconciliation, and allowed them to be raised with stump-tail macaques for 5 months, a species known for peaceful conflict resolution. The results were dramatic. In addition to acquiring various food preferences and strategies, etc., the cross-fostered rhesus macaques also picked up the behaviors described as “peaceful reconciliation.” These habits persisted long after they were returned to their original troop of conspecifics. This study demonstrates that primate behaviors are not purely genetically encoded but take shape through learning within a social milieu. That the reduced aggressiveness persisted even after they lost other learned habits hints that sociality may involve non-genetic (e.g., hormonal) mechanisms of self-reinforcement. In sum, elaborate communication and social collaboration is a driving force of intelligence across diverse clades of birds and mammals and culminated in apes and hominins.

Competition Drives Cooperation

It has been known for some time that, among primates and possibly other mammals, there is a rough correlation between group size and brain volume and this has led to the “social intelligence” theory of primate intelligence (Reader and Laland 2002). However, Byrne and Whiten (1988) emphasize that social intelligence is not always prosocial and may just as frequently be “Machiavellian” in nature. Importantly, these two notions are not necessarily in tension (Stewart et al. 2016). In fact, prosocial behaviors and manipulative behaviors involve many of the same cognitive abilities related to the interpretation of behaviors and mental states, understanding the past in order to predict the future, etc. Whether we strive to successfully work *with* or *against* someone, the necessary interpersonal skills overlap considerably.

Gavrilets (2015) has modeled the role of collaborative and competitive skills in the evolution of the human brain and found that the two are not just overlapping, but reinforcing. Conflict *between* groups sets up strong selective pressure for the emergence of within-group cooperation leading to an evolutionary arms race of “cooperative competition.” Groups of hominins competing against one another led to groups of humans cooperating with one another.

Cultural Group Selection

Although cooperation is a successful strategy for survival, flourishing, and biological fitness, it can nevertheless be purely self-directed in nature. Human cooperation goes beyond this into true prosociality in which individuals act for the benefit of others without regard for the immediate benefit to oneself. The extensive prosociality of humans, not to mention human altruism, has been a conundrum for evolutionary science since Darwin first proposed natural selection as the primary mechanism of adaptation. The problem of deception, cheating, and free-loading often overtakes cooperation in attempts to model the evolution of cooperation in animal species. Leticia Avilés (2002) has proposed that freeloaders can theoretically be kept rare by frequency-dependent group-level selection. This selection process may similarly function to restrain the proliferation narcissistic sociopaths (Lents and Trivers 2018). Christopher Boehm (2009) and others have argued that collective action to enforce rules and punish cheaters has resulted in the evolution of an egalitarian social structure among human societies dating back to at least the Paleolithic.

Nevertheless, however much between-group competition drives within-group cooperation, the emergence of collaboration, collective action, and altruism is difficult to model without the invocation of group-level selective forces. Although first fully articulated by the political and economic theorist Friedrich Hayek (Henrich 2004), a phenomenon called Cultural Group Selection (CGS) has its root in *The Descent of Man* (Darwin 1871). Darwin noted that the biological differences

between groups of humans are negligible compared to the differences in cultural practices and therefore latter are far more determinant of success when the groups clash. Because this phenomenon does not appear true in other species, human may have evolved in a unique selection environment, rendering obsolete selection models based on data from other animals. Not surprisingly, CGS has met with strong criticism (West et al. 2011).

Recently, Richerson et al. (2016) have mounted a vigorous defense of CGS as a key selective force in the emergence of human cooperation. This defense is predicated on the assertion that cultural traits, i.e., memes, can evolve in a Darwinian fashion (Dawkins 1976). To function in this way, CGS requires that a species meet the following criteria: (1) possesses high capacity for social learning, (2) exhibits conformist behavioral tendencies, (3) gains strong selective advantage from cooperation, (4) engages effective punishment of social deviants, (5) reputation (prestige) leads to reproductive success, (6) groups marked by symbolic, non-biologic differences, and (7) has established “institutions” through which collective action can bring group benefits. Interestingly, CGS relies on the actions of gene-level elements to facilitate group-level selection, a point underscored by Richard Dawkins’ coinage of the term *cultural meme* within a larger defense of the gene-centric view of natural selection (Dawkins 1976). It is worth noting that most scholars of human cooperation agree with many of the individual tenants of CGS, if not the entirety of the theory (Singh et al. 2016; and for a comprehensive discussion of some the counter-arguments to CGS, see West et al. 2011).

Self-Domestication: Survival of the Friendliest

An even more specific theoretical framework for the emergence of highly cooperative and nonviolent social structures in humans is the notion of self-domestication. This theory holds that the behavioral changes that occurred in animals as they were domesticated, such as increased docility, are similar to the “civilization” of human beings over the last 200–500 ka. Although this possibility was obliquely mentioned by Darwin (1871), it was first fully articulated by Franz Boas (1901). In the time since then, the possibility has

been raised that animal domestication may have been less something that humans intentionally did to other species, and more something that those animals did to themselves by pursuing the unique ecological niche of mutualistic cohabitation with humans. The very specific selective pressure of that niche resulted in what could fairly be called self-domestication (Zeder 2006, 2012).

Some of the features of domestication that cut across many species are reduced external ears, snouts, teeth, and brain size; curly tails, floppy ears, and skin depigmentation; as well as the all-important behavioral changes of increased docility, feminization, and neotany. That such specific features appeared in such divergently domesticated species argues for a common mechanism and has been called *domestication syndrome* (Wilkins et al. 2014). The search for this common cause has implicated deficits in neural crest cells during embryonic development and a host of candidate genes (Sánchez-Villagra et al. 2016).

The notion that modern humans are the result of self-domestication syndrome is rapidly gaining support. The anatomical evidence alone is striking: modern humans have a reduced jaw, brow, nasal projection, teeth, and cranial capacities, compared to our archaic forebears (see Fig. 1). In addition, Theofanopoulou et al. (2017) have identified a suite of candidate genetic changes for domesticated species, including humans, that may have mediated this transition.

Central to the theory of self-domestication is the notion that reduced aggression brought gains in biological fitness. Despite the nuance brought by the theory of cultural group selection, fitness, inclusive or otherwise, must be the output for adaptive natural selection. Whether mammals cuddling for warmth or hominins working together to hunt megafauna, personal benefit is key to the decline of aggression. Inspired by the theory of endosymbiosis that made her famous, Lynn Margulis remarked that “Life did not take over the globe by combat, but by networking” (Margulis and Sagan 2000). When applied to the emergence of modern human behavior, this idea is frequently expressed as “survival of the friendliest,” a term that, tellingly, grew out of research into intergroup contact theory (Pettigrew 1998).

In the past 10 years, substantial progress has been made in fields as diverse as developmental biology, comparative behavior, neuroscience, paleoanthropology, cognitive psychology, and of course evolutionary psychology, toward supporting the notion that reduced aggression, enhanced cooperation, and in-group prosocial behaviors were *naturally selected features* in the emergence of behavioral modernity (Hare 2017).

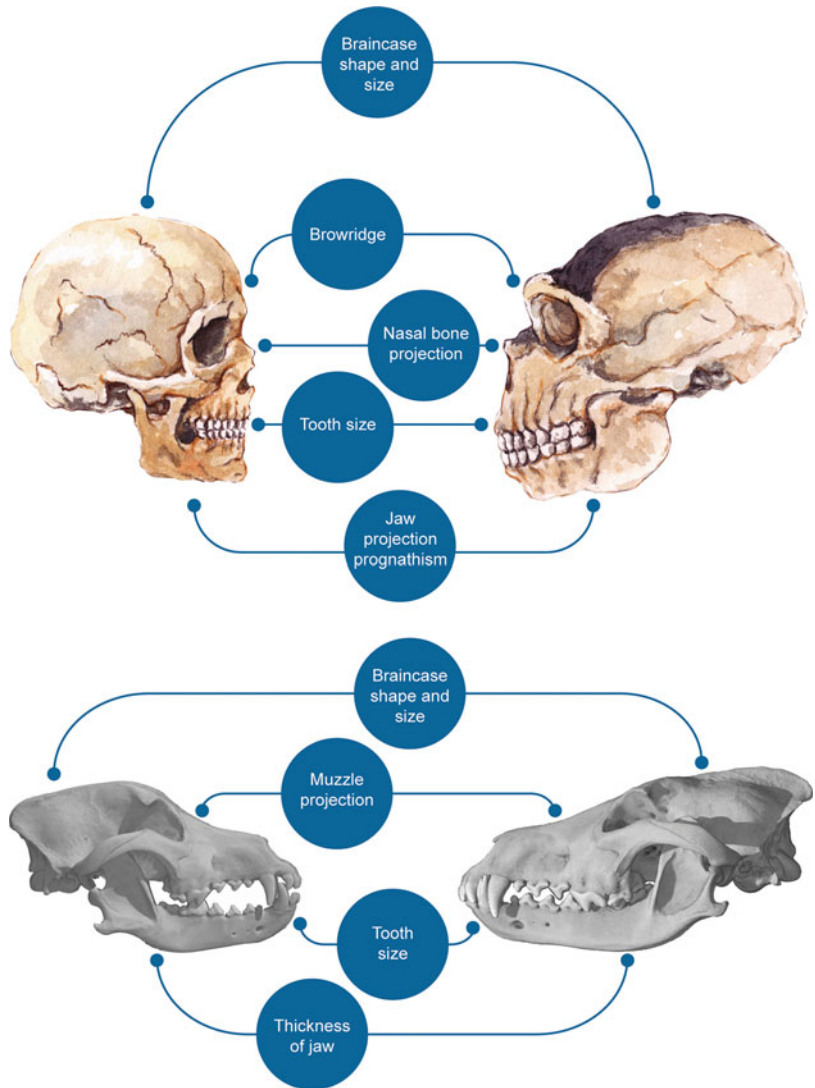
Aggression and Testosterone

The elephant in the room with the survival of the friendliest paradigm is the reality that human aggression and violence almost always aligns well with adaptive benefits (Buss and Shackelford 1997; Shackelford and Weekes-Shackelford 2012). However, the realization that aggression is actually comprised of two very different behavioral modes, proactive aggression and reactive aggression (Poulin and Boivin 2000), may allow a breakthrough of this apparent paradox. Wrangham (2018) has recently argued that these two modes of aggression may have been differentially shaped by natural selection over the last 200–500 ka. While proactive aggression (sometimes called predatory attack) refers to the willful, planned attack focused on obtaining or achieving a goal with clear survival benefits, reactive aggression (sometimes called affective violence) is a response to an immediately threatening stimulus and is directed only at escaping or neutralizing the threat. Under this model, the recent natural history of our species has seen a decline of reactive aggression, not proactive aggression. This can be expressed as gains in self-control, peaceful conflict resolution, etc. Intriguingly, calculated proactive aggression may have even contributed to the decline of reactive aggression through capital punishment. As Boehm (2000) has argued, the majority of the victims of capital punishment in traditional societies are those who fail to control their reactive aggression.

At the same time, there may also have been a turn away from direct physical violence toward subtler forms of social manipulation collectively referred to as *indirect aggression* (Ingram 2014). While it remains to be examined if the switch to indirect forms of aggression is more of a cause or

Decline of Violence,

Fig. 1 Salient craniofacial differences between modern humans and Neanderthals (top) and between dogs and wolves (bottom). Figure taken from Theofanopoulou et al. 2017



an effect of the decline of violence, the phenomena of reputation, status, gossip, and coercion enact some of the same social functions in humans as aggression does in other species. In summary, it seems plausible, then, that a combination of domestication syndrome and cultural group selection acted to reduce reactive aggression and promote self-control in humans, while cognitive advances allowed more sophisticated forms of proactive aggression, which can either promote or restrain violence, depending on context.

While a great deal of solid theoretical work has been done on the decline of violence, most is focused on the ultimate adaptive gains, with

comparatively little progress on the proximate mechanisms (the exception being recent work on the genetics of domestication syndrome in humans, see Theofanopoulou 2017 and references therein). However, new insight into the mechanism of cooperative prosociality has emerged from the study of behavioral endocrinology. Specifically, average levels of circulating testosterone have been linked to aggression in several mammal species including the African apes (Book et al. 2001). There is evidence that circulating testosterone has steadily decreased in modern humans over the last 100 ka, and possibly extending back 1–2 Ma (Cieri et al. 2014). This evidence comes

from the study of emerging skull features that have been linked to lower testosterone including the reduced prominence of the brow and jaw, smaller teeth and eye sockets, and rounding of the face. While it is not currently possible to measure testosterone in fossilized remains, the evidence for “craniofacial feminization” in our recent ancestry is compelling.

The careful analysis of Wardecker and colleagues (2015) adds important nuance to the role of testosterone and estrogens. For example, “in species where social dominance is integral to mating success, testosterone is very tightly linked to mating effort; in species where social cooperation is essential for mating success, testosterone is more loosely linked to mating effort.” (Wardecker et al. 2015). In addition, while testosterone is linked to dominance toward sexual rivals in human males, it is also associated with affiliation and cooperation with males that are *not* sexual rivals. Testosterone also seems to play a different role in short- versus long-term mating, although, as noted by Wardecker et al., the causal arrow could also point the other direction. Hormones don’t just influence social behaviors, they are influenced by social behavior.

While a great deal of work remains to parse out the role of the respective ultimate and proximate causal mechanisms, the social and cultural milieu of the last 200 ka of human history has been marked by increasing empathy, prosociality, altruism, and in-group cooperation. While violence has always been a part of our culture, it has been in steady decline as our species transitioned to so-called behavioral modernity, a transition that continues to the present (Pinker 2011). Understanding the social, cultural, genetic, and hormonal roots of this decline offers great promise for continued progress on the pacification and long-term success of our species.

Cross-References

- [Moralizing Gods and the Rise of Civilization](#)
- [Sociocultural Theories of Violence](#)

- [State-Sanctioned Punishment as Deterrent to Violence](#)
- [State-Sanctioned Punishment as Substitute for Tribal Vengeance](#)
- [Violence](#)

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Decolonialism

► Postcolonialism

Decoloniality

► Postcolonialism

Decreased Chance of Predation

► Predator Confusion Hypothesis

Decreased Reproductive Success

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Synonyms

[Fitness](#); [Reproductive fitness](#)

Definition

Estimates of offspring number of homosexual individuals.

Introduction

Nearly all literature on the evolution of human homosexuality refers to the lowered reproductive success of homosexual individuals. According to Potts and Short (1999, p. 74) “homosexual behavior is the antithesis of reproductive success.” Such emphasis is understandable, given the crucial importance of decreased reproductive success for what is often dubbed “the evolutionary paradox” or “the evolutionary puzzle” of homosexuality. Yet, it is striking how little research has been done to determine the actual reproductive fitness of homosexual men and women. For that reason, Ehrlich (2000) speaks of the “putative direct negative effect on fitness.” Others have also called the empirical evidence for the relative fitness relation between homosexual and heterosexual individuals weak. Moreover, the estimates in the existing studies do diverge.

Empirical Evidence on Offspring Number

Before discussing the main findings on offspring number of homosexual individuals, it is useful to outline why the topic has not been researched more thoroughly. First, many researchers seem to think there is no need to study extensively that what is obvious to any thinking person, namely that the reproductive success of homosexual individuals is lower than that of heterosexual individuals. Hence, it is assumed rather than shown that homosexual individuals have a reduced reproductive success. Often, scholars write that homosexual men have fewer children than heterosexual men, but without referencing this claim. Usually, it is acknowledged that some homosexual people have biological children, but it is also argued that this does not do away with the fact that their reproductive success is on average lower than that of heterosexual people.

Second, it is also assumed that the need for an evolutionary explanation for homosexuality does depend on the decreased reproductive success of homosexual people, but that it does not depend on how much lower this reproductive success is, at least as long as it is substantially lower, which it is usually assumed to be. So the evolutionary study

of human homosexuality does not directly motivate the search for precise estimates of the reproductive success of the homosexual population. Of course, this can change in the not too distant future, but until now, no evolutionary theory needs to establish how strong the selection pressure is; they only need to know that the selection pressure is strong.

Third, changes in reproductive behavior in the West since the early nineteenth century make it difficult to use Western samples for determining the historical fitness effects of human traits and behaviors. For instance, socioeconomic status in the West negatively correlates with reproductive success (Skirbekk 2008), whereas it is supposed to have a positive effect on reproductive fitness in other parts of the world. Likewise, quite a few researchers think that the reproductive success of homosexual individuals differs across time and cultures (Vander Laan et al. 2012), in large part because Western cultures may be outliers with regard to social norms about reproduction, and how these norms impact on the reproductive behavior and choices of homosexual individuals. If they are right, this is a good reason to be cautious about the generalizability of the data gathered in Western cultures. At the same time, it can also deter from doing research on the reproductive success of Western homosexuals (the most accessible population for most researchers), since the findings of these studies may not be very relevant for evolutionary hypotheses (Vander Laan et al. 2012).

Still, some research has been done. Many evolutionary hypotheses on human homosexuality invoke kin selection and inclusive fitness and hence they rely on the reproductive success of the relatives of homosexual individuals. This entry will not deal with data on indirect reproductive success, but focus solely on the direct reproductive success of homosexual individuals.

An Australian study from the early 1970s found that 95 homosexual men above 40 had 37 children in total, which is significantly lower than the number of children one can expect for a group of heterosexual men of the same age (the fertility rate in Australia was in 1972 around replacement level). Twenty-five years later, Van de Ven et al. (1997) reported similar numbers in

Australia, at least for older homosexual men (defined here as men above 49). A little more than 50 % of these older homosexual men had children. However, younger homosexual men were much less likely to have children. This may be evidence of a change in reproductive success among gay men in the West at the end of the twentieth century, something that others had already hinted at. The hypothesis that such a change occurred was corroborated by studies in the USA. In 1978, researchers estimated that the reproductive success of homosexual men was one fifth of that of heterosexual men (Bell and Weinberg 1978). Less than twenty years later, a new study found that the reproductive success of homosexual men was even lower: only 10 % of that of heterosexual men (Hamer and Copeland 1994). In 2005, the participants of an English study reported direct reproductive success that was only 1 % of the reproductive success of heterosexuals (King et al. 2005). The very few studies done in other cultures also show lower reproductive success for those men who are primarily attracted to men. According to Vander Laan et al. (2012), the reproductive success of the Samoan fa'afafine (men primarily or exclusively sexually attracted to men) is very low. However, it is important to note that on Samoa most men who identify as gynophilic do have sex with the fa'afafine. The homosexual behavior of these "heterosexual" men does not seem to affect their reproductive success (Vander Laan et al. 2012).

So, all available studies consistently show that homosexual men have fewer children than heterosexual men, although there are not many studies and nearly all studies have been done in Western societies. Still, reproductive success among homosexual men seems to vary considerably. Some of this variation is geographical, other variation is historical. Compared to older studies, recent studies indicate lower numbers of biological offspring in homosexual men, which may be caused by greater tolerance toward homosexuality in Western cultures and a general decline of the fertility rate in the West.

There is a huge literature on the evolution of *male* homosexuality. Human *female* homosexuality is less theorized about. The very few studies

that do address that issue again tend to assume that the reproductive success of homosexual women is lower than that of heterosexual women, although theoretical arguments are advanced for why the reproductive success of homosexual women will probably be higher than that of homosexual men (more fluidity, less freedom of choice, possibility of sexual intercourse without sexual attraction) (Apostolou 2010). While the data on reproductive success of homosexual men are already scarce, the data on homosexual women's reproductive success are even scarcer. A recent report from the Williams Institute (Gates 2013) shows that homosexual women are more than four times more likely to have biological offspring than homosexual men, even though their reproductive success is still considerably lower than that of heterosexual women. Still, the evolutionary relevance of these numbers is not clear, given the obvious involvement of new reproductive techniques (IVF and other forms of donor insemination).

Conclusion

It is widely assumed that homosexuality leads to decreased reproductive fitness. The empirical evidence for this assumption is weak regarding the reproductive fitness of homosexual men and very weak for the reproductive fitness of homosexual women. Still, it seems that the few studies that looked into the offspring size of homosexual people do point in the direction of a decreased reproductive success.

Cross-References

- [Ancient Homosexuality](#)
- [Differential Reproductive Success](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Medically Assisted Reproduction](#)
- [Offspring Diversity Hypothesis](#)
- [Paternity Uncertainty](#)
- [Reproduction](#)
- [Same-Sex Relationships](#)

- Sexual and Reproductive Development
- Sexual Orientation

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Defection

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Synonyms

Cheating; Exploitative; Free riding; Noncooperative; Selfish

Definition

An action that can increase an individual's payoff but that results in a socially inefficient outcome.

Introduction

In social interactions, there is often a conflict between what is immediately good for the individual as opposed to what is good for the group of interacting individuals as a whole. Such situations are known as social dilemmas (Dawes 1980) and arise because actions that immediately benefit one individual may nevertheless lead to inefficient outcomes. Consider trade or exchange, for example. Cooperation would involve fairly representing the goods being offered and honoring the terms of the exchange by, for example, not simply taking the goods of the other party by force and giving nothing in return. Defection, on the other hand, would involve misrepresenting the goods being offered or taking the goods of the other party by force. Although the total payoff to the pair of traders is maximized by cooperating, either individual can immediately gain by defecting. This occurs even though defection leads to an inefficient outcome in which each individual is worse off than if they had cooperated.

But yet no society would function if individuals always defected and did not cooperate. This problem occurs across biological taxa, from microorganisms through to social insects and humans. A vast body of research in anthropology, computer science, economics, evolutionary biology, and sociology, as well as evolutionary and social psychology, is concerned with finding conditions that take away the benefits of defection and promote cooperation.

Formalizing Defection Using Game Theory

The outcomes of defection for the actor and for the group are commonly formalized using game theory, which uses mathematical models to analyze the outcomes of strategic interactions between individuals. Table 1 shows the payoff matrix for a single-shot two-player interaction, in which each individual may either cooperate or defect. The game is symmetric, meaning that the identity of the players can be swapped without affecting the outcome.

Defection, Table 1 The payoff matrix for two-player symmetric games. Payoffs shown are for Player 1

	Player 2 chooses cooperate	Player 2 chooses defect
Player 1 chooses cooperate	R	S
Player 1 chooses defect	T	P

The payoff that a player receives is a measure of reward. This reward could correspond to a psychological reward or the economic concept of utility, or to biological or cultural fitness. Individuals are therefore assumed to try to choose actions that maximize their own payoff, whether this is through learning the consequences of actions, or through genetic or cultural evolution.

In this payoff, matrix R represents the reward for mutual cooperation; S represents the sucker’s payoff that the actor receives when it cooperates but its partner defects; T represents the temptation to defect – the payoff the actor receives when its partner cooperates but it defects on that cooperation; and P represents the punishment payoff for mutual defection. When $R > P$, mutual cooperation leads to a higher payoff for each player than mutual defection. If $2R > S + T$ and $R > S$, then mutual cooperation yields the highest total payoff for the pair and is hence the most efficient outcome. Given that these inequalities hold, social dilemmas occur when (1) unilateral defection gives a higher payoff to the defector than mutual cooperation ($T > R$) and/or (2) mutual defection gives a higher payoff than unilateral cooperation ($P > S$). Where only condition 1 holds, this is known as a snowdrift or chicken game. Where only condition 2 holds, this is known as a stag hunt game. Where both conditions 1 and 2 hold, the situation is a prisoner’s dilemma. In all of these games, there is a tension between defection, which can give a higher payoff to the individual, and cooperation, which gives a socially efficient state. This leads to the question of why individuals would not defect.

Theories for Why Individuals Would Not Defect: Kinship and Reciprocity

Much of evolutionary psychology is concerned with the evolved psychology of human hunter-gatherers. The hunter-gatherer social environment of living in small, mobile foraging groups (Boehm 1999) corresponds to the Environment of Evolutionary Adaptedness in which our species has spent most of its evolutionary time. In this environment, individuals relied heavily on cooperation with their group mates in order to obtain food for themselves and their families. This would have resulted in a value of R in Table 1 much greater than P . Evolutionary psychology then draws upon two classes of theory for why defection would not be favored.

The first is kinship. Individuals would often interact with their extended families. In such cases, the theory of kin selection from evolutionary biology (Hamilton 1964) tells us that a genetic predisposition to cooperate rather than defect can be favored due to the fact that relatives share genes. This means that when interactions are between relatives, a gene to cooperate helps copies of itself in other individuals and so spreads in the population. In other words, when interactions are between genetic relatives, then individuals in cooperative families will enjoy the payoff R , whereas individuals in families that defect will receive the smaller payoff P . The same argument can also apply when the tendency to cooperate or defect is transmitted culturally through social learning, rather than genetically. In that case, we can speak of the cultural relatedness between interacting individuals (Boyd et al. 2011).

The second, and complementary, theory is reciprocity. This theory originates from classical game theory in economics. It arises from the observation that social interactions are typically not one time only, single shot. Rather, most interactions are in fact repeated. Formally, the game in Table 1 then represents a stage game that is repeated for a number of rounds.

Repeated games allow for conditional strategies in which individuals condition their own actions on the past actions of their partner. A

strategy specifies the action that an individual will take for a given history of its partner's actions. The folk theorem of game theory (see, e.g., Binmore 2005) tells us that if the interaction is repeated for an indefinite length of time, and if individuals have sufficient knowledge of the past actions of their partners, then any strategy which gives more than the minimax payoff can be an equilibrium. The minimax payoff is the payoff that a player receives when its partner tries to minimize that payoff. In Table 1, the minimax payoff would be the payoff that an individual receives if its partner always defects. Consequently, any strategy in which individuals do not always defect results in a higher payoff to each individual. Such a strategy can therefore be an equilibrium even when individuals are concerned with only maximizing their own payoffs. The reason is that any individual who deviates from the strategy can be punished by having its payoff reduced to the minimax payoff through defection by its partners. If an individual defected, then it would subsequently always receive defection from other individuals, limiting its future payoffs to P or S , which are both smaller than the payoff R from mutual cooperation. The threat of being defected against can therefore stabilize cooperation when interactions are repeated.

This theory of cooperation under repeated interactions was later popularized in evolutionary biology by Trivers (1971). The tit-for-tat strategy advocated by Axelrod (1984) is one example of a conditional strategy. However, in general there will be a very large number of other strategies that give more than the minimax payoff and so which can also be equilibria.

What is needed for this result to apply in a real-world scenario is that the game is indefinitely repeated and that individuals have sufficient information about the past actions of their partners. In hunter-gatherers, interactions were effectively repeated for an indefinite number of times. This is because individuals relied on interactions with their group mates to survive, and no individual could predict the time of its death. Individuals also lived in close-knit communities where they repeatedly

interacted with the same individuals. This made it easy for them to obtain information about the past actions of other group members.

The Effect of Defection on the Evolved Psychology of Humans

The social environment of hunter-gatherers would have selected for psychological traits to detect defectors. Individuals would be selected to have a propensity to obtain and spread information about the actions of other group members, for example, through gossip. The spread of information would be facilitated by certain institutional rules that groups developed (North 1990). An example of this is the institutional rule of the whole group discussing around a campfire each evening. Individuals would also become sensitive to what other individuals thought about themselves, i.e., their reputation.

Because the folk theorem demonstrates that there will be a large number of possible equilibria, individuals would also be selected to coordinate their actions to ensure that they reached an equilibrium that yielded a high payoff to them. In other words, each individual would benefit from its group coordinating on an equilibrium in which cooperation was frequent and defection rare. This would select for individuals to create institutional rules and norms that coordinated actions onto a high payoff equilibrium. For example, by using low-cost coordinated punishment against acts of defection, such as ridicule and ostracism (Boehm 1999).

Defection in Large-Scale Societies

The origin of agriculture led to individuals living in much larger social groups. This meant that there was a lower genetic relatedness between interacting individuals. It also meant that it became harder for individuals to obtain information about the past actions of group members. Why, then, is defection not more frequent in large-scale societies? Some scholars argue that defection would actually be individually advantageous but that

individuals do not defect because they still carry the evolved psychological traits from our past hunter-gatherer environment. Under this account, our evolved psychology is “misfiring” in the new environment of large-scale societies. This “misfire” argument was popularized by Dawkins (1976). Other scholars contend that defection is not advantageous even in large-scale societies, because groups have created institutions that still allow the conditions for cooperation under the folk theorem to be satisfied (e.g., Greif 2006).

Conclusion

The possibility of defection threatens the potential gains from cooperation. The ecological and social environment of hunter-gatherers would have selected for traits that supported cooperation through kinship and reciprocity. This would include equipping individuals with a psychology that made them sensitive to their own reputation and the reputation of others. It would also have favored traits that facilitate the spread of information about the past actions of group members, such as gossip. To what extent these traits continue to be adaptive in the new environment of large-scale societies is a current research question.

Cross-References

- [Cooperation Varies With Genetic Relatedness](#)
- [Environment of Evolutionary Adaptedness](#)
- [Evolution of Cooperation](#)
- [Game Theory](#)
- [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reputation and Altruism](#)
- [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)

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Defector

- [Problem of Cheating](#)

Defectors/Sanctions/Violation of Social Contract

- [Mechanisms to Detect and Punish Cheaters](#)

Defending Against Attack

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Synonyms

[Combat](#); [Fighting](#); [Martial arts](#); [Personal protection](#); [Self-defense](#); [Situational awareness](#)

Definition

Biomechanical and psycho-physiological defensive response by the human body to a close quarters physical attack.

Introduction

All attacks and assaults on human beings are dangerous; however, the most dangerous attack is one a person doesn't see coming. Because predators stalk their prey, they often decide where, how, and when they will engage their target (Meadows 2007). This creates a dynamic where a victim is surprised by sudden violence given a lack of awareness of the attack and the subsequent and overwhelming psychological, emotional, and physical trauma during the critical incident. A blitz-style or ambush-style attack is one without a person's consent and is a common method used by nearly all offenders while they prey on a victim's perceived vulnerabilities (DeBecker 1997). An attack will create a fight or flight response as well as a state of inertia (freeze) depending on a victim's awareness and self-defense skills. Successfully navigating the best defense to sudden, interpersonal human aggression requires an examination of psycho-physiological and biomechanical processes of a victim during times of critical stress.

Evolution of Self-defense

For many years, much debate has centered on the best models for achieving proficiency in armed and unarmed human conflicts. With a lack of similar and interchangeable defensive tactics and firearm programs for civilians, non-universal laws, and an ever-increasing field of commercial use of force systems, discerning the best defense against an attack by a violent offender is difficult (Kinnaird 2014).

Most unarmed self-defense techniques learned today have a historical lineage through war and military engagements over thousands of years (Grossman 2008). From our prehistoric ancestors to soldiers of the early twentieth century, fighting

tools and tactics were primitive and limited. Since the 1950s, however, martial arts techniques such as kung fu, karate, tae kwon do, jiu-jitsu, and aikido had gained significant momentum as staples in self-defense programming all over the world (Kinnaird 2014). Originating mostly from Asia and taught to those who lived or served in the war theaters of that region, the ability to fight largely with close-quarters orientations such as punches, kicks, and grappling techniques became popular in both sport and street combat (Siddle 1995).

From karate and kickboxing tournaments, law enforcement and military recruit academies to the lone vigilante on television and films who have made them popular, hand-to-hand fighting skills have taken on various forms over the years. Most recently, mixed martial arts techniques demonstrated in television and pay-per-view events such as the *Ultimate Fighting Championship* have been more narrowly transformed for close-quarters engagements and are widely renowned in military, law enforcement, and self-defense communities throughout the world (Kinnaird 2014).

According to research conducted by pioneers in contemporary personal protection, survival through effective self-defense has transitioned through yet another iteration. Blauer (2006) and Siddle (1995) explained that while traditional martial arts are great for fitness, discipline, focus, meditation, respect, and other valuable outlets, they do not always prepare a person for real street violence. Dogmatic self-defense examines mostly weapons and technique-based training: firearms, non-lethal devices, pressure points, wrist grabs, holds, and escapes (Miller 2011). If weapons are not available, a person is forced to use their body and fight in close quarters when they are attacked suddenly. While pain compliance techniques, for example, are effective, they are only effective in certain situations and circumstances (Blauer 2006).

Through studies of crimes against people, historical research into the functionality of warfare & combat, and along with new research that deconstructs the anatomy of a real attack, experts have made scientific correlations that highlight the validity and reliability of various self-defense systems. In doing so, a holistic model that accounts

for behaviors related to fear and performance enhancement creates awareness in how a person feels when threatened or attacked (Artwohl and Christensen 1997; Blauer 2006; Grossman 1996; Murray 2004; Siddle 1995).

Behavioral Defense

Emotional and psychological arousal comprises the first component of holistic self-defense. A psychomotor skill is generally defined as a body movement resulting from mental processes (Siddle 1995). Blauer (2006) explained that mental arousal is the first attack and therefore the mind navigates the body. In a stimulus-response environment, how you think determines how you feel and how you think and feel affects what you *do*. Because humans are attacked psychologically and emotionally before they are ever attacked physically, awareness through visualization and expectation are positive behavioral strategies for defense against the attack (Blauer 2006). This includes good confidence by looking people in the eye, being assertive through choice speech, rehearsing a violent attack ahead of time, and expecting to successfully defend yourself from it.

Using words or verbal defuses help to de-escalate a hostile situation (Meadows 2007). Because attackers will often talk and physically posture, all potential attacks can be observed by understanding the feelings behind the words and observing the postures that go with it. By offering compliant words to the aggressor or *redirecting* any words the attacker, the self-defense comes from an interruption in thinking patterns and provides time to escape or time to think of another strategy (Blauer 2006).

DeBecker (1997) explained that fear management is another tool for increased awareness and modern personal protection. Will, the power of indignation, tenacity, and primal instincts are natural and organic responses to survival that do not include rote memory and complicated training. Furthermore, observing the behavior and pre-contact cues of an aggressor will help establish an intuitive radar that can be accessed

immediately and into the future. This “gut instinct” is born out of continuous observance of stimuli and responses to stimuli and is the quickest and most accurate way for your brain and body to sense trouble. This sensation is derived from a total accumulation of past experience, knowledge, and what a person can anticipate happening and then use it to inform a choice under stress (DeBecker 1997).

Grossman (1996) explained that because interpersonal human aggression is a primary human phobia, the lack of awareness and acceptance of predatory and attacking behavior (denial) can create significant barriers to mental processing and slow the scenario down in a negative way. Artwohl and Christensen (1997) offered that organic fear happens when a person sees someone who is angry, when they aggressively encroach personal space, or when they make threats or use vulgar or abusive language. These translate into physical responses that lead to tactical choices of escape (flight) or defense (fight).

Physical Defense

Physiological arousal is the last component of understanding the biomechanics of confrontation and utilizing holistic self-defense strategies. When attacked in close-quarters, the situation is tense, evolving, and uncertain. Because the situation is out of control, researchers agree that the behavioral aspects of organic fear and awareness through training and experience will increase or decrease the physiological arousal in both perceiving the attack and using effective strategies to survive it (Blauer 2006).

Key points about how the body responds to stress from psychological and emotional precursors have been examined and reviewed through motor control and learning as core training rhetoric for the physiology of skill acquisition (Artwohl and Christensen 1997; Grossman 2008; Siddle 1995). This includes rudimentary skill classifications and taxonomies such as fine, complex, and gross motor skills. The body will have a neurophysiological response to fear and,

even if managed well, fear and survival instincts will kick in. This includes the adrenal gland “fight or flight” response to stress such as automatic pilot, diminished sounds, tunnel vision, increased heart rate, increased blood flow, dissociation, slow-motion time, memory loss, and short bursts of strength (Artwohl and Christensen 1997).

As stress during an attack increases, fine and complex motor skills decrease including dexterity and coordination (Siddle 1995). Retention of learned self-defense techniques that do not account for this psychomotor loss will not be palpable tools during a sudden, aggressive attack. When a stimulus such as a punch, grab, or shove is introduced quickly, it will by-pass the cognitive, muscle memory systems in the brain and will create a startle-flinch response. According to a research by Blauer (2006), the human body’s flinch to danger is a hard-wired, reliable, and protective bio-mechanic process. These survival behaviors work in concert with the body’s autonomic and somatic nervous systems whereby the limbic system of the brain takes over the forebrain and larger, cognitive processes.

During this close-quarters encounter, the body is left with gross motor functions and will instinctively shield the head and upper body with arms and hands while turning away from the danger simultaneously (Blauer 2006; Siddle 1995).

While all humans respond the same to being startled, their perception and awareness of danger (and subsequent fear management) is variable and both can compound the ability to defend and survive a close-quarters attack (DeBecker 1997). Therefore, the use of gross motor tactics such as slapping, pushing, shoving, biting, clawing, and the use of elbows and knees to strike the vulnerable areas of an attacker are now universally accepted and shaped into modern self-defense programming (Siddle 1995).

Conclusion

Defense against an attack requires a functional and realistic response for survival. Because the human body and mind are connected, a holistic self-defense program captures both. Rather than

relying on spiritual or mystical foundations and primitive fighting models, contemporary defensive tactics programs are now field tested and modified for dangerous environments and legal redress based upon how the mind and body respond to danger and violence. Effective self-defense is best examined through psychological and physical stressors on the body during a real or perceived attack. Because a critical event is often outside a person’s control, new research on the psychophysiology of confrontation illustrates how organic fear and stress affect human responses to interpersonal human aggression and, ultimately, the best tactics for preparation and defense during a close-quarters fight.

Cross-References

- [Defending Against Predator](#)
- [Predators](#)
- [Self-defense](#)
- [Survival and Death](#)
- [Violence as Coercive Control](#)

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Defending Against Predator

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Synonyms

Killer; Self-defense; Situational awareness

Definition

Human, protective response to aggression and victimization through psychosocial and situational awareness.

Introduction

The role of predator and prey has long been studied through the animal kingdom of behavior, survival, and adaptation; however, only in recent decades has the concept been applied to human conditioning against predatory violence. Defending against a predator requires understanding the interactive dynamics of predator and prey and its intersection of violence and victimization. The psychological constructs of power, control, and the need to dominate another human being against permissive vulnerabilities when entering a human lion's den are all parts of a larger formula in examining the attractiveness of a victim and ultimately defending against a predator.

Victimization and Predatory Dynamics

Violence and victimization have traditionally been understood as random acts perpetrated upon unknowing people. Research into social and psychological dynamics is evolving, and recent findings have shifted from examining just cultural regression and active or passive *victims* to the *predator* and what they bring to the equation (Thomas 2013).

In examining deviant use of power, control, and domination of another human being, men have largely been identified as a predator. Inherent in predatory aggression are sociopathic and psychopathic tendencies evidenced by men where *survival* is their chief motivation. Wolman (1999) has explained that elation and depression originate from exaggerated feelings of strength and weakness. "Elation carries the message of power; depression is a psychological corollary of feeling weak and the angry at oneself for being weak" (Wolman 1999, p. 40). Suspending individual responsibility, they obliterate feelings of guilt and remove moral inhibitions, thereby launching violent or potentially violent behavior. The main attractiveness is power, and the predator will seek conditions where power and control are easily attained.

The Duluth Model or "Power and Control Wheel" exemplifies this unhealthy power through a circular and pervasive trait pattern demonstrated by male abusers of women (Pence and Paymar 1993). Not unlike a shark that circles a fish or a spider that spins a web and waits in the middle, the predator is often patient and pings his territory through continuous and observatory actions that box the victim in. The predator then wears the captive down until they are solely dependent upon them. This is an important distinction as run of the mill, rag-tag criminals do not pose the same strategies nor are they as effective in carrying out a crime (Thomas 2013). Because predators are largely ruled by impulses, they are incredibly sensitive to incentive structures and make informed decisions on whether an opportunity will pay off (Wolman 1999).

Victimization and Prey Dynamics

The concept of *victim* dates back to ancient civilizations and cultures originally, meaning to take the life of a person or animal to satisfy a deity (Karmen 1990). Today, victim and prey are used simultaneously as words that refer to different types of people: victims of domestic and sexual violence, hate crimes, workplace violence, and so forth. Victims are individuals

“who have suffered injury and harm by forces beyond their control and not related to their personal responsibility” (Karmen 1990, p. 5). Beyond just a cursory definition and sociocultural context, there are many different ways in which individuals can become victimized which requires an examination of behaviors and situations relative to the predator.

On a personal level, a victim of crime sustains the brutal reality of a deliberate violation of one human being by another (National Center for Victims of Crime 2004). Whether a murder, rape, robbery, or theft, an essential internal injury is the same, and the process, itself, induces a psychological trauma. The selection of prey by a predator is predicated on a reciprocity that exists between the “killer and the killed” (Meadows 2007). Modern theories are simply revised versions of earlier theories that studied victimization and produced victim classification systems. This includes higher-risk groups such as women, children, young adults, immigrants, minorities, elderly, and the disabled (Meadows 2007). These groups are often more prone to victimization given a diverse demographic field and large, male population. *Personal* factors such as immaturity, inexperience, lack of physical mobility, and mental illness are several variables that offer a direct line to predators, while *situational* factors including lifestyle, abuse of drugs and alcohol, spatial relationships, and associations with high-risk places further precipitate predatory victimization (McDevitt and Sgarzi 2003).

Cultural factors are another dynamic when examining typologies of victims who fall prey to interpersonal violence and human aggression. Galtung (1996) observed cultural trappings such as values, norms, and attitudes about race, gender, socioeconomic status, sexual orientation, and even child-rearing contribute to violence and victimization. A lack of familiarity with a different culture and rejection (or objectification) by a dominant population creates conditions where individuals and groups are specifically targeted. In these instances, dysfunctional families and perceptions of what is good or bad promote negative cultural values where survival and recognition are

necessary (Galtung 1996). In particular, African-American and Hispanic females from a low-income, inner city are highly prone to stalking behaviors and violent partners where those behaviors are observed as normal and necessary among families (Meadows 2007).

Putting It All Together

There are considerable exceptions and overlap when attempting to understand the best theory of victimization, and, historically, they are not intended to explain all types of predatory aggression or prey behaviors. With that in mind, a holistic model of self-defense against a predator is one that encompasses opportunity reduction strategies.

Crime prevention through environmental design is clearly articulated with the defensible space theory (Newman 1972). In it, effective defense requires detection strategies related to the physical environment. This includes understanding clearly defined territories, natural surveillance, and the general image of protection (Newman 1972). The most widely accepted adaptations from that foundation are the broken windows theory and crime triangle. Where individual people or structures like homes, buildings, and vehicles appear disorderly, it conveys a visual message that the associated culture and community are out of control and are thus attractive to predators (Kelling and Coles 1996). The use of adequate lighting, camera and other security systems, unobstructed windows, and employees trained in deterrence and safety provides signals to the predator. The non-enforcement of building codes, overlooking minor criminal conduct by law enforcement, and increasing locations that sell alcohol are additional factors that influence incivility and disorder in the eyes of a predator (Kelling and Coles 1996). Spatial relationships with other people also contribute to victimization where, ultimately, for crime to occur, there must be three variables present: a motivated offender, a susceptible target, and the absence of a capable guardian (Kelling and Coles 1996).

Conclusion

Defending against a predator in the world of interpersonal violence and human aggression requires a holistic understanding of psychological and social variables that create a high risk for victimization. Society has largely been trained that just learning physical defensive tactics is the best offensive mechanism for protection (Thomas 2013). A dynamic triad, however, that includes a study of the predator, the prey, and the environment in which both interact is a comprehensive and conclusive strategy for defense. It examines why the predator is attracted to potential victims and the high-risk places where these individuals have an exchange relationship.

Cross-References

- ▶ [Domestic Violence](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Predators](#)
- ▶ [Self-Defense](#)
- ▶ [Survival and Death](#)
- ▶ [Violence as Coercive Control](#)

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Defense Against Attack

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Synonyms

[Bidirectional violence](#); [Domestic violence](#); [Female-perpetrated violence](#); [Intimate partner violence](#); [Self-defense](#)

Definition

Despite similarities in physical IPV perpetration rates among men and women, researchers have noted that the context of men's and women's violence may be very different. For example, men's IPV perpetration is more likely than women's to be driven by power and control motives, while women's violence is more likely to be motivated by self-defense. In fact, of the potential motivational differences for men's and women's physical violence, self-defense is among the most commonly cited.

Introduction

A relatively large body of research indicates that women perpetrate physical intimate partner violence (IPV) at rates comparable to men (e.g., Kaufman-Parks et al. 2017; Swan et al. 2008). Yet research also finds that women's violence usually occurs as a reaction to violence initiated by male partners, while men's violence is more often motivated by a need to control or exert power over partners (e.g., Langhinrichsen-Rohling et al. 2012). For example, in a study of

men and women court ordered to attend abuse treatment counseling, 83% of women, compared to 49% of men, reported their partners used violence first in the relationship (Hamberger and Guse 2002). Relatedly, in a sample of college undergraduates, frequency of victimization accounted for almost 50% of the variance in women's IPV perpetration, but accounted for only 12% of the variation among men (Cercone et al. 2005).

Gender-based disparities in motivations for IPV perpetration are especially likely to exist in clinical-based samples, where couples experience, on average, more severe acts of violence. Conversely, in community-based samples that typically exhibit less severe and less frequent acts of violence, men and women are equally likely to perpetrate IPV simply due to conflict and negative emotions (Cascardi and Vivian 1995). However, even among clinical-based samples, not all reactionary violence is alike. Rather, women may respond to their male partner's violence in order to protect themselves or their loved ones, as a result of heightened levels of fear, or as retaliation for previous victimization.

Violence as Self-Defense

The need to protect one's self or one's children is commonly cited in the literature as a motivation for female-perpetrated IPV (e.g., Flinck and Paavilainen 2010; Hamberger et al. 1997; Langhinrichsen-Rohling et al. 2012; Swan et al. 2008). For example, in a study of male and female court-referred perpetrators, Hamberger et al. (1997) found that women were more likely than men to report violence perpetration to protect themselves or to escape a situation in which their male partner was being violent. Likewise, in their meta-analytic review of women who use violence with intimate partners, Swan et al. (2008) noted that children whose mothers are battered face a significant increased risk of being abused as well. Thus, women may react violently toward male partners in order to protect their children from physical or sexual abuse.

Importantly, self-defense as a motive for female-perpetrated IPV may be defined either narrowly or broadly. As a narrow definition, and as legally defined, self-defense is limited to protecting one's physical self when there is an imminent threat of bodily harm. More broadly defined, self-defense may be viewed as a response to ongoing victimization through not only physical violence, but also emotional and verbal abuse, as well as experiences of coercion and intimidation (Dasgupta 2002). When considering self-defense more broadly, greater gender disparities in men's and women's motivations for violence are likely to emerge. As concluded in a meta-analytic review conducted by Swan et al. (2008), although women may be perpetrating as much or more physical violence as their male partners, their partners may be committing other types of abuse that are not always assessed, such as sexual abuse and coercive control. Thus, women may be responding violently to abuse other than physical IPV. Providing support for this notion, a study assessing violence in dating relationships among undergraduate students found that the two most common reasons for self-defensive aggression as reported by females were to stop emotional abuse or to stop a situation that was becoming emotionally abusive (Shorey et al. 2010). Likewise, in a study of couples receiving marital treatment, Cascardi and Vivian (1995) noted that wives reported that their husbands engaged in significantly more psychological abuse and coercion than they did during conflicts, leading to either spouse's use of physical violence. The authors concluded that, consistent with other research (Kernsmith 2005; Shorey et al. 2010), women may perceive psychological abuse as more personally damaging than partners' physical aggression. As a result, women may become violent to defend against a hurt ego or to protect their self-esteem.

Violence as Fear Response

In line with the notion that women may be responding with violence to IPV that is not necessarily physical in nature, women may strike out

preemptively when they sense impending violence from their partners. For instance, findings from a recent meta-analysis (Hamberger and Larsen 2015) suggested that female perpetrators were more highly victimized, injured, and fearful than male perpetrator in clinical samples; and more women than men felt intimidated by their partners' size and the potential injury they could cause during physical conflict. Similarly, in a study of men and women attending batterer intervention counseling, Kernsmith (2005) found that women were significantly more likely than men to report feeling scared, powerless, and weak when they perpetrated violence.

Women may also experience fear and react violently as a result, even if they have not been victimized by their current relationship partner. Rather, such fear may be the result of victimization in earlier life that is then carried over into future relationships. More specifically, prior research has found that women who perpetrate IPV report significantly more IPV victimization in prior relationships than men, as well as higher levels of sexual abuse as children and adults (Hamberger and Larsen 2015). Thus, even when violence is not objectively imminent, women may perceive threatening cues in the environment, whether due to prior victimization from their current relationship partner or others in earlier life, which indicate they are in physical danger. Once these cues are perceived, violence initiation may be seen as an appropriate strategy for preventing an impending attack or securing personal safety.

Violence as Retaliation

Within the literature on women's motivations for IPV perpetration, researchers have noted that it is oftentimes difficult to distinguish between self-defense and retaliation (e.g., Langhinrichsen-Rohling et al. 2012), whereby retaliation implies a violent act that extends beyond the need to protect one's self and also includes an aspect of retribution for something a partner has said or done. Distinguishing between these two concepts may be particularly important in assessing female-perpetrated IPV, as a number of researchers have

argued that rather than protecting themselves, women are oftentimes simply fighting back for the abuse they have endured (e.g., Hamberger and Larsen 2015). For example, among a sample of men and women attending batterer intervention counseling, Kernsmith (2005) found that women reported perpetrating IPV in response to their partner's prior abuse and were significantly more likely than men to report revenge and retaliation as their primary motives for engaging in such violence.

Women's retaliatory violence may not necessarily be a reaction to physical victimization either. In a recent study (Elmquist et al. 2014) of motivations for IPV among men and women arrested for domestic violence, retaliation was defined to include not only getting back at a partner for being hit first, but also punishing a partner for wrong behavior; retaliating for being emotionally hurt; to hurt a partner's feelings; because a partner provoked the respondent; and because a partner cheated. Moreover, of the seven potential motivations for IPV perpetration that were included in the study, significant gender differences existed only for reasons of expressing negative emotions and retaliation, with women endorsing both of these motives more often than men.

It has also been found that even when both men and women endorse retaliation as their primary motivation for engaging in IPV, the reason cited for their retaliation may be different. For example, Kernsmith (2005) found that women were significantly more likely than men to endorse "getting back at partner for emotional hurt" as an explanation for their violence. Similarly, Follingstad et al. (1991) found that retaliation toward a partner who had initiated violence was more likely to explain males' IPV perpetration, while retaliation for being emotionally hurt by a partner was more likely to explain female-perpetrated violence.

Conclusion

Women may be just as likely, if not more so, as men to perpetrate violence against intimate

partners. However, the context in which men and women engage in IPV perpetration is likely to exhibit a notable degree of variation. In particular, research indicates that men are significantly more likely to use violence to gain and maintain power and control in the relationship, while women's violence is often a reaction to that which is initiated by their male partners (Swan et al. 2008). Whether enacted to protect self and children, as a result of heightened levels of fear, or to retaliate against male partners' words and actions, women's violence can largely be understood as a defense strategy against partners' attacks, whether these attacks be real or perceived, and violent or nonviolent in nature.

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Defense Regulation

► Anxiety Disorders

Defense System

► Immune System Benefits

Deferred Adaptations

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Synonyms

Non-transient ontogenetic adaptations

Definition

Deferred adaptations are behaviors or learning selected through evolution to facilitate later adult

functioning. They are often viewed as childhood preparations for adulthood. Examples of deferred adaptations are play (in which children simulate and rehearse adult roles and behavior), developing gender differences in behavior and motivation (which prepares for gendered adult responsibilities), and the young mind's orientation to novelty (which facilitates rapid learning). As these examples illustrate, deferred adaptations can have adaptive functions during the period in which they develop as well as in adulthood.

Introduction

Childhood and adolescence are typically viewed as a period in which the characteristics and skills necessary for adult functioning are prepared and rehearsed. This is true in evolutionary terms. Evolutionary adaptations have evolved to equip species with reliably developing characteristics that help to facilitate reproductive success, and many of these adaptations develop during the years of immaturity (Bjorklund 1997). This is important because, although the focus of evolutionary psychology is on how evolutionary adaptations function during adulthood when pair bonding, reproduction, and child rearing take place, adaptations also characterize childhood (see entry on ► [“Development of Adaptations”](#)). This makes the experiences of childhood significant for life-long development and the evolutionary adaptations influencing development. This is especially true of *deferred adaptations*, and this entry discusses deferred adaptations, provides several examples, and compares deferred adaptations with ontogenetic adaptations in childhood. In addition, examples of when deferred adaptations are also conditional adaptations, yielding a range of possible outcomes, are considered as an illustration of the flexibility or plasticity that can occur in evolutionary adaptations.

Evolutionary Adaptations in Childhood

There are two kinds of adaptations that emerge during childhood (see entry on ► [“Ontogenetic](#)

[Versus Deferred Adaptations”](#)). One kind, called *ontogenetic adaptations*, facilitates reproductive success by selecting for specific kinds of learning or behavior that facilitate development during a particular stage of growth, but have no necessary later significance (see entry on ► [“Ontogenetic Adaptations”](#)). An example is the umbilical cord and placenta that develop prenatally to support fetal development but are discarded when they are no longer needed after birth. Postnatal examples of ontogenetic adaptations include neonatal reflexes and the facial morphology of baby faces, each of which attract and keep caregivers nearby to provide nurturance, protection, and guidance. Ontogenetic adaptations are, in this sense, temporary or disposable adaptations.

Deferred adaptations, by contrast, have enduring significance because they are adaptive preparations for adult skills and characteristics. In some cases, these adaptations serve to promote adaptive functioning both when they are developing and in adulthood. In this respect, they are not temporary but have life-long significance.

Deferred Adaptations

Deferred adaptations are behaviors or learning selected through evolution to facilitate later adult functioning. However, these adaptations can also support children's adaptive functioning as they are developing. Children's play is often regarded as a deferred adaptation in which children simulate and rehearse adult roles and behavior, including adult work, parenting, and aggression. But children's play also facilitates early social development and integration into the peer group. The development of some behavioral and psychological differences between boys and girls can also be regarded as deferred adaptations to prepare children for the gendered roles they will assume as adults. Other likely deferred adaptations are the infant mind's orientation to novelty (from which rapid learning can occur), certain forms of innate or very early learning (including rapid early learning about gravity and physical causality), and the generally slow pace of early development in humans compared with other species. Each of

these adaptations promotes competent functioning in childhood but also prepare adult skills and competencies.

Whether behavior is interpreted as deriving from an ontogenetic adaptation or a deferred adaptation is quite important. Consider the development of infant-parent attachment (Thompson 2013a). On one hand, attachment could be viewed as an ontogenetic adaptation to help keep infants protected and nurtured by their parents (usually mothers) during their vulnerable early years. Viewed in this light, these attachments have no necessary long-term significance after children reach maturity. On the other hand, attachment could be viewed as a deferred adaptation that also prepares children for the close relationships they will depend on as adults. From this perspective, the strength or quality of these attachments could have enduring significance throughout adulthood.

Plasticity in Developmental Outcomes: Conditional Adaptations

Deferred adaptations sometimes result not in a single adaptive developmental outcome, but rather a range of possible outcomes, the choice of which depends on environmental conditions. This has the benefit of conferring flexibility or plasticity to these adaptations depending on the circumstances in which the individual lives. This illustrates a process called adaptive phenotypic plasticity: the selection for a range of behavioral outcomes depending on environmental conditions and other influences. This is a kind of deferred adaptation called a conditional adaptation (Boyce and Ellis 2005).

Consider again infant-parent attachment. Infants develop attachments to their mothers but they also vary in the security of those attachments: some become secure in their mother's care, others become more avoidant, others anxious. These variations in the security of attachment derive, in part, from differences in the quality of care. Securely-attached children tend to have responsive mothers, while those who are avoidant have mothers who are generally nonresponsive,

and anxiously attached children have mothers who are inconsistently responsive (Thompson 2013b). If attachment is interpreted as a deferred adaptation, then these variations also suggest that attachment is a conditional adaptation, in which the most adaptive attachment pattern that develops depends on the quality of care the child has received. In a sense, the adaptation commits the child to a particular developmental course only once relevant signals have been received from the environment – in this case, the quality of care the child receives.

The different patterns of attachment that result may, in turn, have longer-term significance for adult functioning. According to several theorists, these patterns of attachment evolved because they were adaptations to different amounts of maternal responsiveness that reflected differences in the safety and resources of the environment into which child had been born. In an environment of scarcity, for example, when mothers are unresponsive because danger is high and food is scarce, an avoidant pattern frees the child to seek support and assistance elsewhere (Belsky 2012; Chisholm 1999). That avoidant pattern may also, later in life, cause the adult to be cautious with others and sensitive to resources and stress. There is some supportive evidence for this view, although more research is needed (Ellis et al. 2009).

Conclusion

Evolutionary adaptations influence development throughout life. Deferred adaptations provide developing individuals with preparation for the capabilities and skills necessary for adult functioning, while usually also providing benefits during the period they are developing. When deferred adaptations are also conditional adaptations, they provide a range of possible behavioral outcomes that depend on environmental conditions and other influences. This provides developing persons with greater flexibility (or plasticity) in accommodating in necessary ways to the conditions in which they have been born.

There can be debate over whether certain developing capacities (such as infant-parent

attachment) constitute deferred adaptations or not, and this debate is important for understanding the potentially life-long significance of these early-developing capacities. As the catalogue of likely deferred adaptations (and ontogenetic adaptations) grows, understanding of the significance of early experience for life-long adaptive processes also grows.

Cross-References

- [Adaptation](#)
- [Development of Adaptations](#)
- [Ontogenetic Adaptations](#)
- [Ontogenetic Versus Deferred Adaptations](#)

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Degenerate

- [Use It or Lose It](#)

Degree of Relatedness

- [Helping and Genetic Relatedness](#)

Degrees Celsius

- [Regulation of Body Temperature](#)

Degrees Fahrenheit

- [Regulation of Body Temperature](#)

Deindividuation

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Synonyms

[Anonymity](#); [Behavior in groups](#); [Situational behavior](#)

Definition

Loss of individuality and a sense of anonymity that make individuals more likely to take part in antisocial behaviors.

Introduction

While an individual may display certain explicit attitudes, patterns of behavior, etc., when an individual holds a unique position within a group, a group can work successfully, and the ideals of the individual within the group may not show a significant shift as when they are alone. However, when an individual loses their sense of uniqueness

or identity within a group, deindividuation occurs. Deindividuation is the loss of individual accountability within a group setting.

Deindividuation and Antisocial Behavior

Stanisław Jerzy Lec once said, “No snowflake in an avalanche ever feels responsible.” Once deindividuation occurs, these individuals are much more likely to commit antisocial behaviors and not always feel responsible for their actions. History has shown time and again the way that deindividuation can influence people. Fascist movements held that the individual should submerge themselves into the group and that self-interests should be secondary to that of the interests of the group. One major example of this was the German Nazi Party. They were impressive in rebuilding their bedraggled nation. They were able to stand against the great powers of the world; however, their inner workings fell into a debauched society of shocking cruelty and evil that went well beyond what had been seen in other countries. Another example is that of the Ku Klux Klan. Members of this group would don hoods and robes, hiding their individual faces, and then commit violent acts on members of groups that they viewed as inferior. Diener et al. (1976) ran a study on stealing Halloween candy committed by trick-or-treaters. Some children were observed trick-or-treating alone, while others would go in groups. For this study, children that were randomly assigned to groups were set up so that one group could be easily identified and the other group had their identity remain hidden. Those in the identifiable group were asked their names and where they lived. The experimenter would repeat the names and addresses given to show they knew the children’s identity. Those in the anonymous group were asked nothing. These same principles applied to children that were tested alone. The experimenter then told the children that they were allowed to take one piece of candy and that the experimenter had to leave the room and go back to work. Children were monitored to observe how many pieces of candy each actually took

from a large bowl of candy. The results showed that alone and identifiable children stole extra candy less than 10% of the time. Anonymous and alone, as well as identifiable and in groups, stole extra candy roughly 21% of the time. Anonymous and in group children, however, stole extra candy almost 60% of the time. This study inarguably shows that anonymity in groups drastically increases antisocial behavior. The children that felt most accountable were the most unwilling to steal, while the children that had the least accountability stole well over half the time.

Reducing Deindividuation

The effects of deindividuation can be reduced. The best way of doing is to make individuals feel accountable for their actions. Taking away the anonymity of the individual within a group can easily alter their perceptions and behaviors. An example of this is from the Harper Lee’s novel *To Kill a Mockingbird* (1960). From pages 153–154, Lee describes a scene where a group is coming to the jailhouse to lynch Tom Robinson, an African-American falsely accused of a crime, and his lawyer, Atticus Finch, is there to stand between the mob and the jail. Scout, Atticus’s 8-year-old daughter, walks into the crowd and starts naming members and asking them personally why they are at the jail and what they intend to do to her father. Once the crowd shifted from a faceless group to a collection of individuals, they disseminated and no longer threatened violence. They reduced the anonymity and the effects of deindividuation dissolved. In his book, *The Lucifer Effect*, (2007) Philip Zimbardo brings up the idea of creating a better situation. He suggests that by celebrating those they break away from the crowd and retain their individuality, other persons will be less likely to accept the anonymity of a crowd.

Internet and Deindividuation

With the wide availability and use of the internet as a way of communication with others,

deindividuation is very common. While this form of deindividuation may not always take the form of physical groups, cyber groups can do a lot of harm. Hacking, identity theft, and cyber bullying have become very common online. Catching these individuals can be difficult in this arena; it makes attempts to reduce deindividuation extremely difficult as well.

Conclusion

Deindividuation is very powerful. When individuals lose their self-awareness and sense of accountability, negative behaviors tend to emerge. While group behavior can be highly effective, getting lost within a group can be very dangerous. Measures need to be taken to create better accountability and acceptance of personal responsibility, even when the individual plays only a small role in the overall process.

Cross-References

- [Anonymity](#)
- [Child Abuse and Bullying](#)
- [Cyberbullying](#)
- [Self-Concept](#)
- [Sex Differences in Cyber Bullying](#)

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Delayed Discounting

- [Discounting of Future Returns](#)

Delayed Disengagement

- [Predators as Attention-Grabbing](#)

Delayed Ejaculation

- [Orgasmic Disorders](#)

Delayed Reciprocity

- [Helping and Inclusive Fitness Benefits to Helper](#)

Delinquent

- [Antisocial](#)
- [Monoamine Oxidase and Antisocial Behavior](#)

Delusional Disorder - Jealous Type

- [Jealousy: Psychiatric Diagnosis](#)

Delusional Jealousy

- [Sex Differences in Morbid Jealousy](#)

Democratic Party

- [Political Left, The](#)

Dendrites

- [Early Stage of Brain Development at Birth](#)

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Introduction

Denys deCatanzaro is Professor of Psychology, Neuroscience, and Behavior at McMaster University. He received his Ph.D. from the University of British Columbia. His research interests and publications span the topics of reproductive toxicology, reproductive biology, neuroscience, and behavioral endocrinology. deCatanzaro developed the inclusive fitness model of suicide, which posits that suicide evolved to benefit genetic kin when an individual has low reproductive potential and is burdensome on their kin (1981, 1984, 1991, 1995).

Overview of Evolutionary Theoretical Research

In a series of papers published over the course of two decades, deCatanzaro outlined and tested a model of suicide that frames the act in a socio-biological perspective (1978, 1981, 1984, 1991, 1995). This model sees suicide as a means of increasing one's inclusive fitness when one has low reproductive potential and is imposing net costs of genetic kin, such as in the case of a debilitating illness. However, based on the evidence for the role of negative affect in precipitating suicidal ideation and suicidal behavior, deCatanzaro argued that emotion effectively acts as an interface between evolutionary catalysts (i.e., low reproductive potential and burdensomeness) and suicidal gestures (1995). Unlike alternative evolutionary models that focus on costly signaling and nonlethal suicidal behavior (e.g., the bargaining model, see Syme et al. 2016), the goal of suicidal behavior within the framework of the inclusive fitness model is death.

There is some support for the inclusive fitness of model from different areas of research including deCatanzaro's own investigations. Self-sacrifice through death is evidenced in a variety of species such as sterile castes of the order Hymenoptera for the purpose of colony defense (Preti 2007). Similarly, in *E. coli* self-sacrifice might function to limit the transmission of a bacteriophage to related organisms (Refardt et al. 2013). In Western, predominately white populations, the risk of suicide death tends to increase as a function of age, especially among males as reproductive potential decreases (Shah 2007). A survey administered by deCatanzaro (1995) found that measures of poor reproductive potential and low valuations of one's worth to their family correlated with suicidal ideation. In a test of the inclusive fitness model against 53 cultures in the ethnographic record, Syme et al. (2016) found that evidence for deCatanzaro's inclusive fitness model increased as a function of latitude. Thus, there was greater evidence for inclusive fitness model suicides in resource-scarce environments such as the Arctic where the provisioning of nonreproductive and infirm kin can be costly. Finally, according to Brown et al. (2009), low measures of health and low satisfaction in romantic relationships were associated self-destructive motivation among college students. In this same study, the researchers also found an inverse relationship between maternal age and self-destructive motivation, indicating that the reproductive value of kin might moderate the desire for suicide.

deCatanzaro (1995) attested that all instances of suicidal behavior are not necessarily adaptive, especially in the modern environment. Novel technology such as guns and cars, for instance, might create contexts where individuals with otherwise high reproductive potential are more susceptible to die by suicide, as the putative evolutionary mechanisms for suicide would not account for methods with such high lethality. Social learning might also factor into suicidal behavior as is evidenced by copy-cat suicides (1995).

deCatanzaro's more recent work focuses on the impact of endogenous and exogenous estrogens on reproduction in mice.

Conclusion

deCatanzaro's model of suicide is well supported by empirical evidence in some cases. A sense of burdensomeness is a risk factor for suicidal ideation, and in some environments, incurring costs on close kin likely facilitates suicide as is evidenced by specific cultural models of suicide in some Arctic cultures. Nevertheless, not all instances of suicidal behavior appear to fit under a single model.

Cross-References

- [Benefits to Kin](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide as Kin-Directed Altruism](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Denominalization and Nominalization

► [Verbing and Nouning](#)

Depression

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Synonyms

[Clinical depression](#); [Depressive episode](#); [Major depressive disorder](#); [Unipolar depression](#)

Definition

Major depressive disorder (MDD) is a mood disorder characterized by either depressed mood or loss of interest nearly every day for at least 2 weeks. Five or more of the following symptoms must also co-occur for a diagnosis to be made: significant weight loss or weight gain;

insomnia or hypersomnia; psychomotor agitation or retardation; fatigue or loss of pleasure; feelings of worthlessness or excessive guilt; diminished ability to think and concentrate, indecisiveness; and recurrent thoughts of death and suicidal ideation (American Psychiatric Association 2013).

Introduction

Why are melancholic states of mind so common? Most people have the capacity to experience sadness, for example, after experiences of loss. Nonhuman mammals portray sadness-like behavior, suggesting low mood has a long evolutionary history. Further, depression is also a diagnosable disorder with remarkable costs to its sufferers. Typical symptoms of clinical depression are lack of motivation, sleeplessness, loss of appetite and sexual desire, loss of psychomotor functions, failure to concentrate, and suicidality. People with depression also tend to spend a lot of time ruminating; they brood about their symptoms and its consequences (Nolen-Hoeksema 1991). It is an evolutionary mystery why humans are prone to this condition. The evolutionary adaptationist approach has offered an original approach to depression: Do depression symptoms serve any evolutionary advantages?

The current chapter will review evolutionary perspectives as to why depression exists. Some of these postulate that depression itself is an evolved adaptation with specific functions. Others argue for depression being a side effect of other evolutionary processes, while others still view depression as a maladaptive condition that is maintained by mutations and mismatches.

Why Does Normal Sadness Exist at All?

Emotions are evolved psychological adaptations. Fear, sexual arousal, jealousy, and disgust exist for specific evolutionary reasons. Broadly speaking, emotions assign behavioral priorities, or motivation, to different fitness-related situations. Different behavior patterns are required

depending on whether an organism is responding to a threat or to a mate.

Unpleasant emotions like sadness might function as a human defense similar to vomiting and physical pain (Nesse 2012). However, we still do not know why sadness exists and what its evolutionary functions might be. The only thing that is clear is that understanding maladaptive extremes of sadness is likely to be improved by understanding their normal function.

Humans tend to have optimistic outlooks on themselves and the world, and it might be useful to downregulate these tendencies in some situations. For instance, happy people are impulsive and tend to think less deliberately about the consequences of their actions, and people in a negative mood also tend to produce more persuasive arguments on controversial topics compared to happy people (see Forgas 2013). Further, sadness might help us detach from significant others or valued objects (Nesse 2012). Results like these give us some hints toward particular advantages sadness might bring to specific situations.

Evolutionary Theories of Depression

Social Competition Hypothesis

The social competition hypothesis postulates that depression is an involuntary strategy that is elicited during hierarchical encounters (Price et al. 1994). The idea is that depression is an “involuntary defeat strategy” which is activated in humans after losing in competitive social struggles (Gilbert 1992). If this social struggle remains unsolved, this defeat strategy can become dysregulated and manifest itself as symptoms of major depressive disorder. This theory is partly based on observations of nonhuman animals, whereby depressive behaviors such as a stooped posture and a downturned facial gaze are observed after losing a battle for resources or mates (Price et al. 1994). The depressive behaviors hence serve as reliable signals of “I am no threat” and “I am out of action” (Gilbert 1992). The social competition hypothesis postulates that depression serves the same evolutionary function in humans. Depressed humans, hence, are predicted to accept their situation and to be viewed by others as

nonthreatening. This hypothesis also predicts that depression will effectively inhibit aggression from others and the depressive will decrease the chance of being ostracized from their group.

Behavioral Shutdown and the Resource Conservation Hypotheses

The behavioral shutdown hypothesis states that an individual should decrease its energy expenditure when under chronic stress or when the goals of an individual become unreachable (Henriques 2000; Nesse 2012). These models of depression therefore predict that depression is activated when continued effort is futile or dangerous (Nesse 2012). For example, when obstacles to goals become impossible to manage, low mood is activated in order to encourage disengagement and reassessment of goals. Again, if the individual fails to give up the goal (e.g., by being overly ambitious or stubborn), the response can become dysregulated and manifest itself as depressive disorder.

Analytical Rumination Hypothesis

The analytical rumination hypothesis is a radical and comprehensive adaptive explanation of depression. According to the analytical rumination hypothesis, the most important aspect of depression is depressive rumination, which is considered to be an analytical tool designed to solve complex fitness-related problems (Andrews and Thomson 2009). Ruminative responses typically focus inward on feelings of distress rather than taking action to feel better, and it is a way of responding to distress by repetitively and passively focusing on the fact that one is depressed, the symptoms of being depressed, and the causes and consequences of having these symptoms (Nolen-Hoeksema 1991).

Other symptoms of depression are secondary and interpreted as orchestrated mechanisms designed to reserve limited cognitive resources for analytical rumination. The analytical rumination hypothesis states that a depressive episode is triggered by severe complex problems that require sustained analysis. Anhedonia removes rewarding emotions from previously pleasurable activities and thoughts, thus freeing up valuable cognitive resources for rumination. Various

psychomotor changes like loss of appetite and desire for social isolation further reduce exposure to distracting stimuli. In essence, depressive episodes are tailored to prioritize attention and resources toward the goal of solving the triggering problem, over more immediate short-term goals. The most central prediction of the analytical rumination hypothesis is that encouragement and facilitation of rumination should lead to shorter depressive episodes, and, inversely, cessation of rumination should have harmful effects in the long term.

Bargaining Hypothesis

The bargaining hypothesis postulates that depression serves the function of eliciting help from others (Hagen 2003; Watson and Andrews 2002). Depression is uncontrollable by the depressive. This is crucial from the bargaining perspective because it forces other people to act. Hence, depression functions as a worker's strike: I am unable to do anything, and this will result in me involuntarily withholding any resources that I could share, before I receive the help I need. A key prediction from the bargaining hypothesis is therefore that genuine help from people important to the depressive (e.g., a husband, family, or a close friend) will relieve the depressive symptoms.

Social Risk Hypothesis

According to the social risk hypothesis, mild depressive symptoms reduce social risks such as exclusion from social groups (Allen and Badcock 2003). Under the social risk hypothesis, depression serves the function of making the depressive hypersensitive to potential social (but not nonsocial) losses and hence becomes a more accurate social perceiver. This is based on the theoretical argument that social organisms should be able to calculate their own social value and social burden and incorporate appropriate behavioral strategies. The key part of human depression is that it works as an emotional mediator of behavior that reduces social risks when someone view their burden/value ratio to be unfavorable. A prediction from the social risk hypothesis is that perceptions and actual threats of social exclusion should lead to

depressed affect. A key prediction is that depression will actually help; depression should reduce the risk for social exclusion. Another interesting prediction from the social risk hypothesis is that individual humans who are unable to calculate their social value and burden should not have the capacity for depression (Allen and Badcock 2003).

Badcock et al. (2017) have elaborated their social risk view of depression based on a perspective on the brain as a prediction machine. People have models of the world, and brains are designed by evolution to reduce the errors the models make. The point is to reduce uncertainty and prediction errors. Under this view, normal low mood is an “adaptive prior,” meaning that the depressed person avoids interpersonal interactions that ancestrally were associated with aversive social outcomes. The depressed brain predicts aversive outcomes and therefore behaves in a risk-averse manner. Under the social risk hypothesis, clinical depression is likely to be the dysregulation of these adaptive processes (Allen and Badcock 2003).

Infection Prevention: Pathogen Host Defense Hypothesis

Pathogens are dangerous to humans. The evolutionarily ancient battle between pathogens and humans has resulted in a vastly complex immune system. Raison and Miller (2013) observed that many of the risk genes associated with depression are also involved in inflammatory responses. Hence, their main claim is that alleles associated with depression are maintained in the human genome because they help fight off attacks from pathogens. Depression is a by-product of this process. Raison and Miller (2013) postulate that the benefits of the immunological response outweighs the costs of depression.

A key prediction from the pathogen host defense hypothesis is that depression should be associated with increased inflammation and that inflammation is associated with increased depression. Further, allelic risk variants for depression should increase survival during infection. A good test of one of its predictions would be to look at depressed and nondepressed infected individuals

and see whether the depressed people are on average less likely to die from an infection.

The link between the immune system and psychological symptoms of depression appears to be robust (Miller and Raison 2016). And some of the predictions of the pathogen host defense hypothesis have been supported, for example, that psychological symptoms of depression are associated with greater immune activation (Stieglitz et al. 2015).

Sex Differences in Depression

It is a robust finding in psychopathology that women are affected by depression twice as often as men (Nolen-Hoeksema et al. 2003). Studies show that the sex difference in depression peaks in adolescence and declines and remains stable in adulthood (Salk et al. 2017). That the symptoms have their onset during sexual maturation suggests that sex-differentiated adaptations might play important roles in depression.

A variety of proximate factors are assumed to play a part in the sex difference in depression, including brain chemistry and genetics, dysfunctional ways of thinking, abusive relationships, financial issues, as well as cultural and social roles for men and women (Clarke 2006). Women’s tendency to ruminate more than men in response to depressive moods is also considered an important factor when explaining sex differences in depression (Nolen-Hoeksema et al. 2003).

The adaptationist theories of depression propose some ideas on why the sex difference exists. The social competition hypothesis views the sex difference in depression as a by-product of modern societies and not a functional one (Price et al. 1994). The bargaining hypothesis views bargaining strategies as more important for females because it is a relatively safe strategy, especially because lower upper-body strength hinders females from using anger instead of depression (E. H. Hagen and Rosenström 2016). The analytical rumination hypothesis proposes that females have been under greater selection pressures to spend more cognitive resources on avoiding social strains.

Problems with Adaptive Theories of Depression

Psychological adaptations are complex evolved structures that have been designed by selection to solve particular adaptive problems. In order for a trait to be considered a psychological adaptation, the trait must (1) show evidence of good design, (2) have appropriate activation, and (3) lack heritable variation (Nettle 2004). Depression does not meet any of these criteria.

Most humans experience fear in situations that are appropriate (e.g., while being threatened by an aggressive, formidable, and dominant male). If depression is adaptive in similar ways as fear presumably is, we would expect most people to become depressed in relevant situations. This is not the case. Depressive episodes do seem to be triggered by negative life events, although notably this is predominantly true of the first few episodes. Thereafter there is no obvious precipitating event. Further, the effect of negative life events is typically mediated by genetic factors (Kendler and Prescott 2006). And most people who experience similar life stress do not become depressed, and hence depression seems unlikely to be part of the evolved, universal human repertoire. Another problem is that depression does not show reliable evidence of “good design.” For example, the best predictor of a depressive episode is *past* depressive episodes. In other words, if depression is an evolved adaptation to solve social problems, for example, it does not seem to be effective at solving it because depression keeps recurring.

The bargaining hypothesis and analytical rumination hypothesis share the bold claim that symptoms of major depressive disorder often are the manifestations of underlying evolved adaptations rather than being the result of dysregulated processes.

A theoretical challenge for the analytical rumination hypothesis in particular is the efficacy of meta-cognitive therapy (MCT). MCT is based on theoretical underpinnings that consider rumination to be a harmful driving force of depression, which maintains and prolongs depressive episodes and symptoms. MCT consists of techniques designed to cessate rumination and dispel positive

beliefs about rumination (such as “I need to ruminate on my problems in order to find solutions”). If anhedonia and psychomotor changes and other symptoms of depression function to maintain rumination, targeted cessation of rumination should not relieve symptoms of depression, especially when patients are measured at 6 months follow-up (Hagen et al. 2017).

We do not know why the robust sex difference in depression exists either, and the adaptive theories do not give this problem the attention it deserves. The adaptationist approaches also typically fail to explain why male levels of depression vary so much across cultures, which might in itself be an important reason why we see a sex difference (Schmitt 2014). Nevertheless, there are many known sex differences in normal social cognition whereby females portray superior abilities in empathy, language, and emotional expression. Hence, evolved cognitive sex differences might serve as the basis for understanding sex differences in maladaptive pathology also (Martel 2013).

The Problem of Heterogeneity

Depression is a complex disorder. It is the DSM and ICD that bring together the cluster of symptoms that make up major depressive disorder. But depressed patients are remarkably heterogeneous: Some sleep less, some more. Some are suicidal, some are not. Some have strong feelings of guilt but not worthlessness and so on. So when researchers are looking into “depression” as a phenomenon, they are by definition looking at clusters of symptoms. An adaptationist look at depression needs, therefore, to know what symptoms are relevant for the proposed function. The ARH is one of the adaptationist approaches that addresses most different aspects of depression in general.

The Problem of Genetic Variation

Genetic variants that contribute to the design of psychological adaptations will over time spread throughout the population and become part of the universal genetic design within the species. For this reason, evolutionary psychologists assume that the heritability of evolved traits should approach zero. A finding across twin

studies on depression is that major depression is estimated to have a heritability of 31–42% (Sullivan et al. 2000). This variance is a challenge for adaptationist hypotheses of depression.

Three different evolutionary forces are responsible for maintaining genetic differences over time (Zietsch et al. 2015). The first is *mutation-selection balance*, whereby selection is a balance between new deleterious mutations that arise in the population and their eventual removal by purifying selection. The second is *neutral mutation drift*. Here genetic mutations are completely, or nearly completely, neutral to selection so their fixation or removal in the genome is caused by chance. The third is balancing selection, which is a group of different processes whereby genetic variance is actively maintained by selection because their relative fitness depends on the genetic and environmental context (Zietsch et al. 2015). Adaptationist hypotheses often do not address the crucial problem of why risk alleles for depression persist at all, or they assume that balancing selection adaptively maintains depression risk or that the alleles were neutral during human evolution and is not anymore.

Can Mutation Selection Balancing Explain Why Depression Alleles Are Maintained in the Population?

If depression is an evolved psychological adaptation, we would expect that the genetic variance underlying it is adaptively maintained by selection. That is, some force of balancing selection keeps the genetic variance in place. However, this is unlikely to be the case, because traits being maintained by balancing selection are actually very rare in nature. For example, with frequency-dependent selection (a form of balancing selection), the genetic variance is often caused by few genes with large effect sizes (Zietsch et al. 2015). Genetic psychiatry would have found these by now (Keller and Miller 2006).

A more plausible solution is that the genetic variance underlying depression is maladaptive. There is a constant influx of new deleterious mutations into the human genome. Some of these mutations are catastrophic and are removed quickly from the population (e.g., leading to

nonviable fetus or to early death). However, many have only a very slight negative impact on fitness. Therefore, by definition, it takes a while for selection to remove those harmful mutations. About half of human genes are involved in the construction and maintenance of the human nervous system. The human brain therefore has a large “mutational target size,” meaning that the many functions of the human brain are vulnerable to mutations (Keller and Miller 2006).

Consistent with the mutation-balancing selection view of major depression, the risk for developing depression is greater on islands where inbreeding rates are higher (Rudan et al. 2003). Inbreeding is harmful because deleterious recessive alleles are more likely to express themselves in offspring when both parents are genetically similar. If the prevalence of a trait increases as the degree of inbreeding increases, it suggests that the trait is caused by mutations and is not an evolutionary adaptation.

The Future of Evolutionary Psychopathology of Depression

All of the adaptive theories of depression are testable. They sometimes overlap in predictions and sometimes directly contradict each other. This is not a problem in itself because low mood and depression might have several functions. There is also some reason to consider several subtypes of depression, which may be an umbrella term for several mood pathologies. The greater problem is that the hypotheses are rarely tested. Rigorous attempts at actually falsifying and comparing all of the hypotheses together will be an important focus in the future.

Another key part in the future of the evolutionary psychology of depression is to develop high-resolution understanding of the evolved architecture responsible for low mood in order to understand the environmental contexts that activate vulnerabilities for depression and, further, to combine that knowledge with the usage of evolutionary-genetic frameworks in order to understand why the risk alleles for depression persist in the population and what happens when

the evolved architecture is disrupted. Evolutionary mismatches such as post-industrialization diets, lack of sunlight exposure, and sleep deprivation (Hidaka 2012), economic inequalities, and the life history strategies of individuals (Giudice 2014) are important fields for empirical development within the field. Evolutionary psychopathologists will also need to pay attention to developments within evolutionary behavioral genetics (Zietsch et al. 2015) and modern psychiatric genetics. Finally, the functional aspects of empirically supported therapeutic interventions that discontinue maintaining and possibly maladaptive coping behaviors need to receive more attention by evolutionary psychopathologists.

Conclusion

The counterintuitive nature of adaptationism used to test seemingly maladaptive traits, and suggesting possible functions for them, provides science with both original and testable hypotheses. However, none of the evolutionarily theories on depression have really influenced psychiatric or clinical psychological practice or mainstream theorizing about depression. This is in stark contrast to anxiety treatment where the functional understanding to fear informed most anxiety therapists understanding of irrational and maladaptive levels of aversive activation and maladaptive safety behaviors.

A current major discussion within the evolutionary psychology of depression is whether rumination is adaptive or maladaptive (Kennair et al. 2017). Paul Andrews and colleagues are developing specific measures to study the benefits of rumination, while other groups are studying the role of specific types of rumination for depression. Currently the evidence for the beneficial effects of discontinuing rumination outweighs evidence in favor of promoting rumination, and there are reasons to fear detrimental patient effects of increasing rumination. It is too early to conclude anything about any evolved problem-solving function of rumination, but no matter what future research will show, this is an important new development within evolutionary clinical psychology.

After being primarily a theoretical discipline for many years, the evolutionary psychopathology of depression is increasingly becoming an empirical science while providing important synthesizing theoretical frameworks. Our hope is that the field will ultimately benefit suffering patients.

Cross-References

- [Evolutionary Clinical Psychology](#)
- [Loneliness in Modern Life](#)
- [Phobias](#)
- [Social Phobia](#)
- [Stress Reduction and Mental Health](#)

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Depression (Paul Gilbert)

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Synonyms

Clinical depression; Major depression

Definition

“A common mental disorder characterized by persistent sadness and loss of interest in activities that you normally enjoy, accompanied by an inability to carry out daily activities, for at least two weeks” (World Health Organization 2019).

Introduction

Professor and clinical psychologist Paul Gilbert utilizes an evolutionary approach toward

the study of depression through social rank theory (SRT). This model views depression in terms of adaptive and maladaptive functions. In the context of social conflict, depression functions to tone down a subordinate's positive affect, accept defeat/loss (i.e., not meeting one's goals), and submit to the dominant and to signal to the dominant that the subordinate is not a threat (Price 1972). This process could be seen as adaptive, if it allowed individuals to disengage from negative environments and seek new sources of support (Gilbert 1992; Gilbert and Bailey 2014). Instead, depression blocks these adaptive responses, leaving the stress system in a prolonged state of arousal and the depressed person feeling demobilized (Gilbert 2000b).

Toning Down of Positive Affect

Pathways to the toning down of positive affect are explained through the arrested defenses model (Gilbert 1992, 2001). This model states that the body's defense system (e.g., fight or flight) in response to stress or perceived threats can become blocked. For example, one may feel a heightened urge to escape but feel trapped or feel anger but suppress negative expression of emotions. This pattern of arousal and blocking of defenses can become chronic, which can lead to the toning down of positive affect. Indeed, depression has been associated with feelings of entrapment (Gilbert et al. 2004) and suppressed anger (Allan and Gilbert 2002).

Defeat/Loss

An early study by Gilbert and Allan (1998) found that subjective reports of defeat were more predictive of depression than hopelessness. Moreover, subjective defeat has also been strongly linked to experiences of anhedonia (i.e., loss of pleasure) and feelings of inferiority (Gilbert et al. 2002). This component of SRT highlights the ruminative aspect of depression wherein individuals may harass themselves

repeatedly by their own negative self-appraisals (Gilbert 2004; Gilbert and Irons 2005).

Submissive Behavior

Submissive behavior is typically associated with perceived lower social rank and can involve inhibition of one's negative emotions, lack of self-advocacy or assertiveness, and denial of one's own feelings to appease others (Gilbert and Allan 1994). These subordinate behaviors and self-perceptions may perpetuate heightened physiological responses to stress (Gilbert and Allan 1998; Gilbert and McGuire 1998).

Conclusion

In sum, depression emerges due to the chronic activation of the defense systems in response to stressors, which results in a toning down of positive affect. Particularly when people see themselves as inferior, feel trapped, or suppress their own negative emotions, depression can follow.

Cross-References

- [Depression](#)
- [Depression \(Randolph Nesse\)](#)

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Depression (Randolph Nesse)

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Synonyms

Hopelessness; Melancholy; Misery; Sadness

Definition

A mood causing feeling of severe sadness, loss of interest in desirable activities, and inhibiting the way one may think or act.

Introduction

As defined in evolutionary psychology, humans have evolved mechanisms that help to defend themselves against disease and/or various defects, which for the sake of this entry is narrowed to psychological and/or physical defects within the body. Human bodies oftentimes have ways of protecting themselves which are viewed as beneficial. These can be things such as fighting a disease by inducing vomiting, whereas some defects have no advantage, such as seizures. Physiologically speaking, it is proactive to correct a defect within the body; however, interfering in such matters by utilizing a defense mechanism has shown to be destructive (Nesse 2000).

Depression (Randolph Nesse)

Depression symptoms have been shown to have been aroused by various traumatic stimuli when adapting to particular situations. Within the same subject, each depressive episode has shown various symptoms (Keller and Nesse 2006). Researchers have hypothesized that our bodies use different depressive symptoms as an adaptive condition to cope with, oftentimes, severely difficult life situations. The question then must be asked: Is depression an evolved adaptation to the issues we cannot or have difficulties facing? According to Randy Nesse, an adult depressive episode is an attempt at adaptation that has failed due to either help not being available or the feeling as though one cannot ask for help (Nesse 2000). However, Nesse (2000) also points out that when one has experienced endogenous depression for a third and fourth time, it could be that depression may not be a defensive mechanism at all. Additionally, Nesse (2000) also inputted that by applying natural selection, we can begin to see

difficulty in explaining mood disorders as adaptive response is difficult to do as natural selection does not shape diseases, but that it is the reason for an individual's body to be left to vulnerabilities that result in diseases (Nesse 2006). This has led Nesse to questions of why natural selection did not develop the body to be more "resilient"; "why do we have wisdom teeth and an appendix?" and "Why do so many people experience debilitating episodes of depression?" (Nesse 2006). The question now however has evolved to this: "How does depression arise? Is depression a sudden onset like a stroke or cancer due to a malfunction or is it like pain or a fever in response of protection?" (Nesse 2006). If looking at depression offhand without background research, the answer is clear; depression comes from a defect within the body (Nesse 2006). When looking at depression without background research, the answer seems apparent; depression comes from a defect within the body (Nesse 2006).

However, another outlook we can have is that depression does not necessarily have to be a disadvantage. Depression can offer a particular advantage. For instance, let us imagine that our subject is experiencing a time of loss. By providing motivation to regain a sense of fulfillment to fill the void of loss or by directly replacing the loss, the subject learns to avoid similar situations, they learn ways to protect oneself or others and they also learn how to prevent similar situations (Nesse 2006). Additionally, depression can another way of a subject calling out for help by showing signs of low mood or even breaking down and crying in front of peers. Based on the perceptions of depression, both socially and in one-on-one situations, researchers can see how depression influences how subjects seek treatment and/or help. Looking at distinctions between psychologists and psychiatrists on how depression is defined, we see that psychologists will depict depression as "habits of negative thinking, or social factors," whereas psychiatrists see depression as "a brain disease" (Nesse and Ellsworth 2009). Therefore, individuals may either seek psychotherapy to discover some sort of understanding in what they're feeling, or they

may possibly try seeking medications to balance their mood.

Conclusion

All in all, there are consistant psychological theories over the evolved mechanism of depression and it is necessary to continue further research to investigate emotions and how they may be adaptive responses that have branched off of natural selection.

Cross-References

- [Anxiety](#)
- [Anxiety Disorders](#)
- [Anxiety \(Randolph Nesse\)](#)
- [Death by Suicide](#)
- [Depression](#)
- [Depression \(Paul Gilbert\)](#)
- [Emotional Disposition](#)
- [Emotions](#)
- [Suicide](#)

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Depressive Episode

- [Depression](#)

Depth Perception

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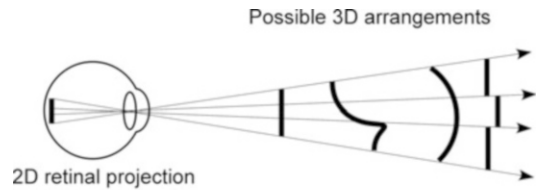
Definition

Depth perception is a process of recovering distances to and between objects from a two-dimensional retinal projection or from a two-dimensional image depicting a three-dimensional scene.

Introduction

Depth perception is a classic case of an ill-defined problem in vision: In principle, an infinite number of three-dimensional configurations can produce the same two-dimensional retinal projection (Fig. 1; Lowe 1985; Marr 1982; Palmer 1999). To cope with this “inverse optics” problem, human visual system makes a number of assumptions about the likely arrangement of 3D objects given a specific 2D input (e.g., that the occluding object is usually located closer to an observer than the occluded object). These assumptions, together with information contained in retinal projection (or projections) are then used by visual system to recover position of the objects in depth.

Depth perception cues can be classified as binocular (requiring a comparison of retinal input from both eyes) or monocular (available from a retinal projection of a single eye). Furthermore, they can be dynamic (requiring movement of an observer or an image) or static (available in absence of any motion). Finally, depth perception cues can be ocular (based on the mechanics of the eye) or optical (based on the information obtained from retinal projection). Table 1 provides these classifications for several important depth cues. The relative importance of different depth cues for evaluating depth perception depends on a species, although experimental evidence in many cases is either mixed or incomplete.



Depth Perception, Fig. 1 An illustration of ambiguous nature of depth perception. A two-dimensional projection of a straight line on a retina could be produced by a straight line in a three-dimensional environment, or by an infinite number of other configurations aligned to produce the same two-dimensional projection

Ocular Depth Cues: Accommodation

Vertebrate eye can maintain a clear view of an object through the process of *accommodation* that involves changing either the shape of the lens (mammals, birds, and reptiles) or the distance between lens and retina (fish and amphibians). Correspondingly, information about tension of the muscles controlling these changes can be used to derive distance to the object in focus. This cue is unavailable in compound eyes with fixed-focus optics.

Although in humans this cue is used only at close distances, it is a crucial source of depth information in the African chameleon. When chameleon prepares to strike its prey, the distance of the tongue flick is determined exclusively by information obtained from accommodation (Harkness 1977). The limited use of accommodation for depth perception at close distances has also been documented in many other vertebrate species. For example, under monocular conditions toads can use accommodation cues to judge distance to the prey (Collett 1977; see a review by Land 2015). Similar mechanics exist in the single-chambered eyes of cephalopods, but whether these animals use accommodation cues to recover depth information is currently unknown.

Binocular Depth Cues: Binocular Disparity

See ► “Binocular Disparity.”

Depth Perception, Table 1 Classification of classic depth cues (see text for more details) (After Palmer (1999))

Depth cue	Ocular or optical?	Binocular or monocular?	Static or dynamic?
Accommodation	Ocular	Monocular	Static
Binocular disparity	Optical	Binocular	Static
Motion parallax	Optical	Monocular	Dynamic
Linear perspective	Optical	Monocular	Static
Texture gradient	Optical	Monocular	Static
Occlusion (interposition)	Optical	Monocular	Static

Dynamic Monocular Depth Cues: Motion Parallax

See ► [“Motion Parallax.”](#)

Static Monocular Depth Cues: Pictorial Depth Cues

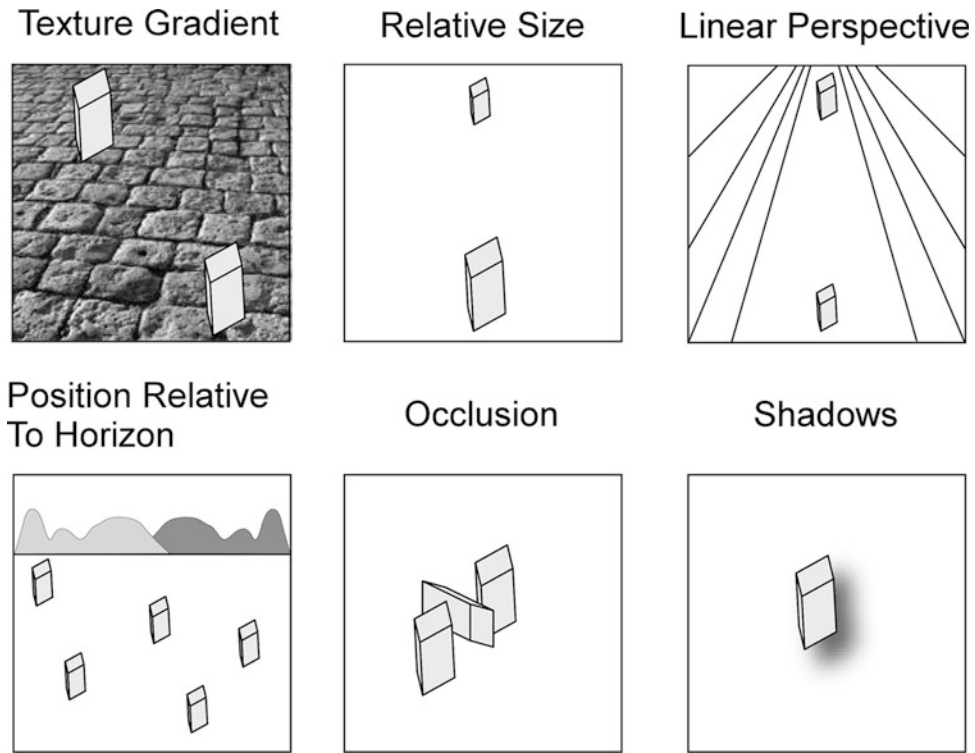
Even in the absence of binocular information or motion cues, human observers are able to perceive depth in two-dimensional photographs and paintings by using cues such as occlusion, shading, or linear perspective. Despite their name, pictorial depth cues are not confined to pictures of the three-dimensional world: A person who keeps their head perfectly still and one eye closed would still be able to perceive depth in their surrounding environment (Palmer 1999). Moreover, under certain circumstances pictorial depth cues can override depth information provided by binocular disparity (e.g., when using pseudoscope; see Palmer 1999, for more details) indicating their powerful role in depth perception.

More than a dozen of different pictorial depth cues have been described for human vision. For example, the size of elements in naturally occurring textures, such as pebbles on a beach, can be used to judge the distance to the different parts of texture because this size decreases with the distance (Fig. 2; *texture gradient*). Relatedly, larger objects are perceived to be closer to the observer than smaller objects (*relative size*). Because parallel lines in a three-dimensional environment project on a two-dimensional retinal image as lines converging toward a single point on a horizon, such converging lines can be used to induce

perception of depth in a two-dimensional image (*linear perspective*). The position of the objects relative to horizon also induces perception of depth such that objects located closer to the horizon line are perceived to be farther away from the observer (*position relative to horizon*). Objects that partially block another object are perceived as being closer to the observer (*occlusion* or *interposition*; see ► [“Occlusion”](#)). Finally, *shadows* cast by the objects also induce strong perception of depth in a two-dimensional image. In humans, the ability to use these cues for ordering objects in depth develops during first year of life (Kavšek et al. 2012).

Only a few experiments explored the presence of pictorial depth cues in nonhuman animals. Horses, baboons, pigtailed macaques, and chimpanzees have been shown to use linear perspective cues for estimating depth (Barbet and Fagot 2007; Gunderson et al. 1993; Imura et al. 2008; Timney and Keil 1996). The ability to use shading cues to extract three-dimensional information about objects has been demonstrated for chimpanzees and starlings (Cook et al. 2012; Imura and Tomonaga 2003; Qadri et al. 2014). Pigtailed macaques also use relative size for ordering objects in depth (Gunderson et al. 1993).

Although multiple studies have explored the use of monocular depth perception cues in pigeons, their results have been mixed. On one hand, pigeons appear to be unaffected by linear perspective cues (Cerella 1977; Nagasaka et al. 2007); on the other, they are sensitive to the Ponzo illusion which is presumably mediated by linear perspective (Fujita et al. 1991). Multiple studies have demonstrated that pigeons appear not to recognize occluded objects in two-dimensional



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Depth Perception, Fig. 2 An illustration of classical monocular depth perception cues. A perception of depth can be induced by a systematic change in the size of texture elements (texture gradient); a larger size of object located nearby in comparison to more distant objects (relative size); a presence of parallel lines converging on a single

point (linear perspective); a relative distance to the horizon line (position relative to horizon); a blocking of a more distant object by an object located closer to an observer (occlusion); or by presence of shadows and/or variations in shading of a surface of an object (shadows and shading)

displays (Sekuler et al. 1996; Ushitani and Fujita 2005), possibly because of the failure to separate an object from an occluder (DiPietro et al. 2002; Lazareva et al. 2007). Yet, Cavoto and Cook (2006) reported that pigeons can use occlusion, together with relative size and relative density, to extract information about relative location of the objects in depth. Recent research has also demonstrated that pigeons can recover shape of the object from information provided by its shading, again suggesting the use of monocular depth perception cues similar to that of primates (Cook et al. 2012). It is likely that some of the disparate results can be attributed to different stimulus material or different training approaches; more research is needed to address this possibility.

Among the invertebrates, cuttlefish has been shown to respond to changes in texture density

(Josef et al. 2014) and to shading cues (Zylinski et al. 2016), but the use of other monocular depth cues in single-chambered eyes of invertebrates remains largely unexplored.

Unique Static Monocular Cues: Retinal Defocus and Retinal Blur

As an observer's eye focuses on a specific point in the environment, the focused object falls on the fovea but the parts of the visual environment away from fixation point become gradually blurred. This retinal blur can then serve as another static monocular depth cue in human vision, although it is mostly useful for recovering depth information at very close distances (Vishwanath and Blaser 2010).

In contrast to human eyes that experience retinal blur temporarily as a side effect of focusing, two invertebrate species appear to have permanent retinal defocus in a large portion of their retina. The rear portion of retina in young oval squid has a bulge, or a retinal bump, that results in permanently myopic image due to closer distance to the lens in comparison to the rest of retina. The squids use this cue in conjunction with a bobbing movement of their head to bring the potential prey into a focus (Chung and Marshall 2014). Interestingly, the retinal bulge disappears with age allowing sharp vision across the entire retina in the older animals.

Jumping spiders also use retinal defocus for evaluating distance to the objects. These animals possess several pairs of individual single-chambered eyes serving different functions (Harland et al. 2012). The large principal eyes have a complex, four-layer retina, with two deepest layers containing high concentration of photoreceptors sensitive to green light. However, this light is only focused on the deepest, fourth layer, with the third layer receiving defocused images; the contrast between the focused image in fourth layer and defocused image in third layer can then be used as a depth cue. Consistent with this hypothesis, spiders underestimated a distance to a prey under pure red light and overestimated it under pure green light (Nagata et al. 2012). Water-beetle larvae have been hypothesized to use similar depth cue although direct experimental evidence supporting this idea is currently unavailable (Stowasser and Buschbeck 2014).

Unique Static Monocular Depth Cues: Retinal Elevation with Respect to the Ground

Many vertebrates including humans use retinal elevation, or the distance from the retina to the ground, to adjust their estimate of the distance from the observer to the object. In many species, however, retinal elevation is used as a reference frame for evaluating distance produced by other cues rather than on its own. For example, visual system of frogs estimates the distance to the prey

under the assumption that its eyes are located approximately 3 cm above the ground; if this assumption is no longer correct because the frog has artificially been lifted above the ground, then it underestimates the distance to the prey (Collett and Udin 1988). Similarly, human visual system takes into account retinal elevation when evaluating the distance to the object (Ooi et al. 2001), although some argue that postural cues rather than retinal elevation per se plays more important role in determining eye height (Leyrer et al. 2015).

In contrast, a fiddler crab (*Uca vomeris*) apparently relies exclusively on retinal elevation to evaluate a distance between an intruder and its own burrow. Fiddler crabs possess two compound eyes that sit on top of the long vertical stalks; as is typical for compound eyes, they provide a relatively poor resolution for their size. In a series of elegant experiments, Hemmi and Zell (2003) have shown that fiddler crabs keep tabs on the location of the burrow by positioning themselves so that its entrance always falls on the same horizontal position on crab's retina irrespective of whether this entrance is actually visible. The vertical location of the projection then provides the crab with information about the distance to the burrow; the farther away the burrow is, the closer its projection to the horizon. Whether other species with compound eyes also use similar cues to evaluate distance is currently unknown.

Conclusion

Human observers use multiple ocular and optical cues to accurately recover distance to the objects in the three-dimensional environment from the two-dimensional retinal projection. Some of these cues, such as motion parallax, appear to be used widely across many different species with extremely different anatomical eye structures while others seem to be limited to specific eye type (e.g., accommodation in single-chambered eyes) or specific eye arrangement (e.g., binocular disparity in frontally placed eyes). In addition, recent research uncovered unique depth perception cue, retinal defocus, the presence of which in other species remains to be explored (Nagata et al.

2012). Still, it is clear that despite dramatic differences in eye anatomy, number of eyes, location of eyes, and mechanics of neural processing of visual information, many principles of depth perception remain remarkably similar across different taxa. Further research in this area will be essential to our understanding of the basic principles of constructing a successful visual system and to our appreciation of how the properties of a visual system change as a result of its adaptation to a specific environment.

Cross-References

- [Binocular Disparity](#)
- [Motion Parallax](#)
- [Occlusion](#)

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Derogation of Attractiveness

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Synonyms

Competitiveness; Indirect aggression; Intrasexual competition; Mating strategies

Definition

Devaluing a woman's mate value relative to one's own mate value by criticizing her physical appearance.

Introduction

When people compete against same-sex peers for romantic partners, they typically compete to embody traits that the opposite sex finds attractive (Buss 1988). Consequently, the areas in which women compete with one another are dictated by men's preferences. One trait that men find highly desirable in a potential partner is physical attractiveness (Buss 1988). Sometimes, women's strategy is to enhance their own physical appearance to compete for partners. However, another strategy that women use to compete for romantic partners is to derogate other women's attractiveness. In other words, women attempt to devalue other women's physical appearance relative to their own physical appearance (Buss and Dedden 1990).

What Is Derogation of Attractiveness?

Derogation of attractiveness takes many forms, most of which can be described as indirect aggression (Vaillancourt 2013). Some examples of these behaviors are laughing at or criticizing a woman's appearance, gossiping about a woman's appearance to men or other women, ostracizing or refusing to befriend a woman, or using derisive body language toward another woman (Buss and Dedden 1990; Leenaars et al. 2008). Sometimes, the derogation is subtle and can happen at very low levels of perceptual processing. When chronically jealous women were asked to imagine their partner engaging in infidelity, they exhibited more implicit negative biases toward attractive women than unattractive women (Maner et al. 2009). Specifically, women were quicker to respond when the task required categorizing attractive women with “negative” and women were slower to respond when the task required categorizing attractive women with “positive.” The ease in which women associated attractive women with “negative” and the difficulty they had associating attractive women with “positive” provided evidence of a negative implicit bias toward attractive women.

To Whom Does It Happen?

Many of the characteristics associated with women's attractiveness are also associated with women's fertility (Singh 1993). Targets of derogation tend to be women who are in a fertile stage of their life (i.e., postpuberty, but premenopause). In a sample of high school students, girls who rated themselves higher in attractiveness were more likely to be the targets of indirect aggression than girls who rated themselves lower in attractiveness (Leenaars et al. 2008). The effect of the girls' attractiveness on indirect aggression decreased as the girls' age decreased. This suggests that girls who were less likely to be sexually active (i.e., younger girls) may not have been viewed as rivals and consequently were not targets of sexual jealousy.

Ovulatory effects on women's derogation of attractiveness provide further support that this phenomenon is particularly relevant to women who are at peak fertility. When women are in the fertile phase of their ovulatory cycle, other women may pose substantial threats if they block mating opportunities. A lost mating opportunity when a woman is ovulating is far more detrimental to reproductive success than a lost mating opportunity when a woman is not ovulating. Women's derogation of female rivals is more pronounced when the perpetrator is in the fertile phase of her cycle. For example, women who are in the fertile phase of their ovulatory cycle rate pictures of other women's faces (but not men's faces) lower in attractiveness than women who are not in the fertile phase of their cycle (Fisher 2004).

Effects Outside of Mating Contexts

Derogation of attractiveness is likely motivated by mating motives, but a mating context is not necessary to activate this phenomenon. Not only are women less likely to accept an apology from an attractive woman than they are to accept an apology offered by an unattractive woman, but apologies given by attractive women are evaluated as lower in quality than those given by unattractive women (Phillips and Hranek 2012). Women are also less inclined to hire an attractive woman than

an unattractive woman (Agthe et al. 2011). Finally, women are more likely to attribute attractive women's successes to luck, but they attribute unattractive women's successes to ability (Forsterling et al. 2007). Notably, attributional biases do not occur when female targets are pre-pubescent and thus unlikely evaluated as sexual rivals.

Conclusion

One strategy women use to compete for romantic partners is derogation of other women's attractiveness. Derogation of attractiveness occurs when women attempt to devalue another woman's appearance relative to their own appearance. If women successfully derogate a rival's appearance, they enhance their desirability to potential partners and consequently enhance their reproductive value. Derogation most often takes the form of gossip and dirty looks, but it can also affect a woman's inclination to forgive another woman or approve a woman's job application.

Cross-References

- [Contexts for Women's Aggression Against Women](#)
- [Derogation of Promiscuity](#)
- [Derogation of Rivals](#)
- [Female-Female Competition](#)
- [Intrasexual Rivalry Among Women](#)
- [Verbal Derogation](#)

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Derogation of Attractiveness Among Women (Intrasexual Rivalry)

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Definition

The disparagement of a rival's degree of physical attractiveness and the circumstances in which this type of derogation is most common.

Introduction

Intrasexual competition is the rivalry that occurs between members of the same sex in an attempt to secure prospective mates. Both men and women intrasexually compete; however, the manner in which they compete varies drastically. Unlike men, women compete for mates in primarily nonphysical ways. One of the most common forms of

nonphysical female competition is the verbal derogation of other women, particularly in relation to their physical attractiveness. This type of derogation has been shown to negatively influence a man's judgment of a target woman's attractiveness and, consequently, her mate value (Fisher and Cox 2009). This tactic is effective because it provides information relevant to an adaptive problem faced uniquely by men over human evolutionary history: identifying fertile mates. This adaptive problem produced selection pressure on men to find traits predictive of fertility as attractive. These traits include, but are not limited to, a small chin, full lips, large eyes, high cheekbones, a small waist paired with relatively large hips, and large breasts (Gangestad and Scheyd 2005). Consistent with this logic, a vast amount of research shows that men from regions and countries across the globe place great importance on the physical attractiveness of a potential mate (e.g., Buss 1989). Women are therefore expected to derogate the attractiveness of intrasexual competitors to lessen their desirability to potential mates (Fisher and Cox 2009). This behavior has evolved as a prominent strategy for the attraction, acquisition, and safeguarding of high-quality mates (Darwin 1871; as cited in Fisher et al. 2010).

Contexts that Elicit Attractiveness Derogation

The nonphysical, and oftentimes indirect (i.e., not requiring face-to-face confrontation), nature of competitor derogation makes it an especially appealing form of intrasexual competition for women. Campbell (1999) argues that because children are much more reliant upon care from their mothers than their fathers, women evolved to be apprehensive about engaging in situations that threaten the safety of their physical body, and by extension, their offspring. Thus, in many circumstances, women perceive the risk of engaging in physical forms of intrasexual competition as exceeding the expected benefits. It may also be that women avoid physical confrontation to preserve their own attractiveness and maintain their mate value. To date, this alternative explanation has yet to be explored.

Research has shown that while members of both sexes engage in competitor derogation, the focus of their derogation differs dramatically (Buss and Dedden 1990). Whereas men tend to call attention to a rival's lack of resources, women are likely to emphasize a rival's degree of sexual promiscuity (► [Derogation of Promiscuity](#)) and attack the weight, body size and shape, and facial features of other women (Buss and Dedden 1990). This is especially likely to occur at ovulation. Fisher (2004) showed that women were more likely to derogate (i.e., assign lower attractiveness ratings to competitors) during times deemed most critical for the derogators to secure a potential mate, namely, when their estrogen levels, and thus probability of conception, were highest. Additionally, derogation is more likely to occur when the target woman is scantily dressed. Vaillancourt and Sharma (2011) examined interactions between female participants and modestly or sexily dressed female confederates and found that participants were more likely to mock and derogate the sexily dressed confederate's appearance than the modestly dressed confederate's appearance following their interaction. Thus, it appears that when a rival woman is perceived to be highly threatening (e.g., displaying cues of sexual accessibility), women are more likely to derogate her attractiveness.

Women can increase their reproductive success by derogating the attractiveness of competitors (Fisher and Cox 2009); however, what derogating women might not consider is how other women, as well as the potential mates they are attempting to influence, perceive their behavior. Indeed, after listening to a derogator slander another woman, men revised their initial assessment of the derogator to be less benevolent, loyal, and as having less overall appeal as a potential mate (Fisher et al. 2010). These findings are consistent with those of Schmitt and Buss (1996), showing that female derogation strategies were relatively ineffective when compared to female self-promotion strategies. It is therefore reasonable to suggest that in contexts in which potential mates may be firsthand observers of the derogation, self-promotion may be a more effective strategy for female competitors. Nevertheless, derogation can be an influential and advantageous form of intrasexual competition.

A profitable avenue of future research would be to investigate the nature of competitor derogation in different contexts. One key factor might be the sex composition of the audience. Women are expected to be more discreet when derogating other women in the presence of potential mates, given findings that suggest that men find such behavior unattractive (Fisher et al. 2010). Other contexts to explore are those in which the rival woman is clearly and objectively attractive as opposed to ambiguously and subjectively attractive. Presumably, derogation specifically about a woman's attractiveness would be less effective in the case of the former, given that there is undeniable evidence to refute the derogator's claims. Relatedly, future researchers may wish to observe whether the nature and intensity of derogation is influenced by the attractiveness of the potential mate.

Conclusion

Much remains to be discovered about the conditions that trigger intrasexual competition among women, and, in the case of attractiveness derogation, the physical traits that are most likely to be the target of women's derogation. The evolutionary perspective that forms the basis of much of this research will continue to provide novel insights about the motivations, contexts, and consequences of women's attractiveness derogation.

Cross-References

- [Derogation of Promiscuity](#)
- [Fertility](#)
- [In-pair Female Attractiveness](#)
- [Mate Value](#)
- [Reproductive Value](#)

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Derogation of Promiscuity

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Synonyms

Aggression; Female-female competition;
Intrasexual competition; Intrasexual rivalry

Definition

Condemnation of a woman's casual sexual behavior in an attempt to devalue her mate value relative to one's own mate value.

Introduction

Women should compete with one another to embody traits that men find highly desirable in a potential partner (Buss 1988). Men desire sexually promiscuous behavior from short-term partners, but men do not like for their long-term partners to be sexually promiscuous (Buss and Schmitt 1993). This preference against long-term partners who are sexually promiscuous is a defense against cuckoldry. Before genetic testing was possible, men rarely could be completely certain of a child's paternity. By seeking long-term partners who are not sexually promiscuous, men can increase certainty that they are investing resources into genetically related offspring. Because men's preference for promiscuous women varies depending on the type of relationship they pursue, derogation of promiscuity may not always decrease men's attraction to derogated women. Nonetheless, evidence suggests that women consistently derogate other women's promiscuity.

This effect may be best explained by evidence that women are responsible for the suppression of female promiscuity (Baumeister and Twenge 2002). Women may use sex as a resource to negotiate with men. If women make sex too readily available, the value of sex diminishes. Consequently, women may wish to stifle other women's sexuality if they offer it too easily.

When a woman derogates another woman's sexual behavior, she may achieve two goals. First, derogation may decrease a woman's desirability to men as a long-term partner if the derogation prompts men to question the woman's fidelity. Second, derogation may help maintain the value of sex if the threat of being derogated against prevents women from freely offering sex to men. It is also possible that men could lose interest in some women as short-term partners if they feel that sex is off the table. Although the reasons for women to derogate promiscuity differ depending on the theory, both theories suggest that women should be motivated to derogate other women's sexual behavior.

What Is Derogation of Promiscuity?

Derogation of promiscuity occurs when someone condemns another woman's casual sexual behavior in an attempt to devalue the woman's mate value relative to one's own mate value. Women may gossip to other women or men about a woman's sexual history, they may refer to a woman with derogatory names such as "slut" or "whore," they may call into question another woman's fidelity, they may give another woman a dirty look or other negative body gestures, or they may physically threaten another woman if she seems sexually available (Leenaars et al. 2008; Vaillancourt 2013). In a sample of school girls and prison inmates, women reported that derogation of promiscuity was one of the most common reasons why they engaged in physical violence with another woman (Campbell 1986). The perpetrators were the women defending their reputations from the derogatory remarks.

Women are also less inclined to befriend women whom they deem to be too sexually available (Bleske and Shackelford 2001). Ostracism of promiscuous women may be driven by a fear of "guilt by association," or it may be driven by a fear that a promiscuous woman could lure away one's partner. Indeed, women are particularly upset upon imagining another woman acting sexually available to attract their partner (Bleske and Shackelford 2001).

To Whom Does It Happen?

A woman's sexual history is associated with derogatory actions toward her. Upon reading the description of a promiscuous woman, women report less desire to befriend someone like the woman described (Bleske and Shackelford 2001). In a sample of high school girls, as the number of recent (i.e., within the last month) sexual partners increased, their odds of being derogated against significantly increased (Leenaars et al. 2008). Derogation was measured by self-reports of how often they had received hurtful notes, had been excluded from activities, had

rumors spread about them, or had been physically threatened by another student. Notably, these effects were not present for the younger high school students. This finding supports the idea that derogation is an intrasexual competition strategy. Sexual activity is less common in younger adolescents compared to older adolescents, so the younger students were probably in less direct competition with each other relative to the older adolescents.

People rarely have direct knowledge of other people's sexual behavior, so derogation of promiscuity is not always triggered by *actual* promiscuous behavior. Quite often, derogation is triggered by cues that someone *may* be promiscuous. For example, women wearing red are evaluated as more sexually receptive than women wearing white or green (Pazda et al. 2014). Women are more likely to call into question a woman's fidelity when she is wearing red than when she is wearing white.

Women also derogate women who are wearing sexy or revealing clothing, presumably because women may suspect that choice of dress advertises sexual availability. Compared to women who interact with a conservatively dressed woman, those who interact with a sexily dressed woman display more negative facial expressions, more dismissive behavior, a more sarcastic tone of voice, make more negative comments about the woman, and are more likely to laugh about the woman behind her back (Vaillancourt and Sharma 2011). Even when a sexily dressed woman is overweight, women are less inclined to introduce the sexily dressed, overweight woman to their boyfriend than a thin, conservatively dressed woman. Further, women are less likely to befriend women who are dressed sexily than women who are dressed conservatively.

Conclusion

Derogation of promiscuity may be driven by two motives: to decrease other women's mate value and to maintain the value of sex as a resource. Strategies used to derogate promiscuity range from gossip and dirty looks to ostracism and

threats of physical violence. A woman's recent sexual history may make her the target of derogation, but simply wearing red or provocative clothing may also prompt derogation in the absence of actual promiscuous behavior.

Cross-References

- [Contexts for Women's Aggression Against Women](#)
- [Derogation of Attractiveness](#)
- [Derogation of Rivals](#)
- [Female-Female Competition](#)
- [Intrasexual Rivalry Among Women](#)
- [Verbal Derogation](#)

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Derogation of Promiscuity Among Women

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Definition

Disparaging a rival's sexual promiscuity as a form of intrasexual competition among women.

Introduction

Intrasexual competition is the rivalry between members of the same sex in an attempt to secure a potential mate. One manner in which women compete for mates is the verbal derogation of rival women. This behavior can take many forms (e.g., attractiveness derogation; ► [Derogation of Attractiveness](#)), one of the most common being the derogation of a competitor's sexual promiscuity. The effectiveness of this tactic is rooted in an adaptive problem faced uniquely by men: paternity uncertainty. Women's concealed ovulation paired with internal fertilization presents an opportunity for women to cuckold their partners, resulting in a nonzero chance that offspring are fathered, not by a woman's primary partner but by an intrasexual rival (Symons 1979). As a solution to this adaptive problem, men seek qualities in a potential mate that increase their probability of paternity, such as premarital chastity and post-marital sexual fidelity (Buss 1989; Buss and Schmitt 1993; ► [Preferences in Long- Versus Short-Term Mating](#)). Thus, by calling attention to or misrepresenting a rival's degree of promiscuity, women decrease the desirability of competitors.

The Costs and Benefits of Derogating a Rival's Promiscuity

Women have been shown to disclose information that a target woman is sexually promiscuous in an attempt to influence a potential mate's evaluation of that woman (Baumeister and Twenge 2002; Buss and Dedden 1990). This tactic produces a twofold effect: it casts doubt about the future fidelity of a rival woman while simultaneously suggesting that the derogator would remain faithful in a future relationship. Relatedly, disparaging rivals has been argued to increase the derogator's self-esteem, potentially increasing the probability that she initiates a romantic relationship or advertises herself as having high mate value (Fisher and Cox 2009).

While effective, women might not derogate another woman's promiscuity because of the potential for this behavior to decrease the derogator's overall desirability in addition to the target woman's desirability (Fisher et al. 2010). Furthermore, derogators run the risk of directing the attention of potential mates to rival women, whom they might not have otherwise noticed or considered romantically. The effectiveness of derogating a competitor's promiscuity is therefore expected to be context specific and deployed only in situations in which the probabilities of the intended benefits are high and the unintended consequences are low. Consistent with this logic, Schmitt and Buss (1996) found that denigrating a rival's sexual history was more effective in the context of a long-term relationship than a short-term relationship, as men find cues of sexual accessibility more desirable in the latter than the former (Men's Preferences in Long- Versus Short-Term Mating). In sum, women seem to be aware of what men desire in both long-term and short-term relationship contexts and may shift their derogation tactics accordingly in order to effectively decrease the perceived mate value of rival women.

An interesting direction for future research would be to compare the relative effectiveness

of various forms of derogation. Some traits, such as a competitor's physical attractiveness (► [Derogation of Attractiveness](#)), may be less effective targets of derogation because they are more easily observable – and therefore, refutable – than other traits, such as a woman's purported degree of promiscuity. In addition, researchers should explore how a woman's relationship status affects the nature of her derogation tactics. Women in committed relationships, who seek to prevent their mates from switching partners, risk enticing their mates into having a short-term affair by sharing information that a rival woman is sexually accessible. Clearly, much remains to be discovered about the costs and benefits of competitor derogation and the contexts in which one form of derogation takes precedence over others.

Conclusion

In the competition for mates, women have been shown to derogate an intrasexual rival's degree of promiscuity; however, this tactic decreases the desirability of rival women in some circumstances more so than others (e.g., long- vs. short-term relationships). Future research that applies an evolutionary perspective will bring the context-dependent motivational structure that underlies women's derogation into focus.

Cross-References

- [Cues to Infidelity](#)
- [Derogation of Attractiveness](#)
- [Frequency of Infidelity](#)
- [Infidelity](#)
- [Paternity Uncertainty](#)
- [Perceptions of Infidelity Cues](#)
- [Premarital Sexual Permissiveness](#)
- [Prevention of Infidelity](#)

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Derogation of Rivals

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Synonyms

Competition; Lack of respect

Definition

If an individual derogates another, it means to perceive or treat them as being of low worth and with no respect. If an individual behaved like this with a rival, it would be a person who seems equal or comparable to them and a potential competitor at any given task, for example, if they were applying for the same job.

Introduction

Following from the previous chapter, this entry focuses on how individuals may use manipulative communication with others via derogating rivals in order to protect or enhance their self-esteem. It will also demonstrate how the specific personality construct, narcissism, may accentuate this from an evolutionary perspective.

Competition and Derogation

The process of attracting a mate is competitive, sometimes because numerous individuals can be simultaneously attracted to the same person (Alexander 1979; Buss 1988). One way to compete with rivals in order to create better evaluations from potential mates is to derogate the traits and attributes of other competitors. Buss and Dedden (1990) investigated the forms of derogation tactics both males and females use. They found that tactics such as spreading rumors about the competitor, calling the competitor boring, and derogating their intelligence was equally common in both males and females. In addition, males were more likely to use tactics that derogated the competitor's achievements, financial resources, and strengths, whereas females were more likely to use tactics the derogated their competitors' appearance and sexual fidelity.

This behavior is particularly likely in those individuals with high levels of narcissistic traits due to their manipulative and self-enhancing behavior they present to preserve and protect their self-esteem (Goncalves and Campbell 2014). Bushman and Baumeister (1998) conducted a study investigating narcissism and competition by measuring participants' responses when given the opportunity to aggress against someone who had insulted them, praised them, or against an innocent third person. They found that the combination of narcissism and insult produced very high levels of aggression toward the source of the insult.

In addition, Goncalves and Campbell (2014) investigated the relationship between the dark triad (psychopathy, Machiavellianism, and narcissism) and derogating mating rivals. They found

that psychopathy was linked with endorsing tactics that damaged their rival's reputation. Machiavellianism was associated with a rude derogation style, and narcissism was associated with a derogation style where individuals tried to outperform their competitor in different situations such as sports, strength, and dominance. These findings for narcissists are not surprising due to their domineering need to succeed and be seen in a position of superiority compared to others.

Conclusion

An individual can derogate another when they feel in competition, particularly when it concerns attracting a mate. Research has found that this behavior is particularly likely in those individuals with high levels of narcissistic traits. This competitive behavior seen in narcissists could be viewed as manifestations of a short-term mating strategy as it could elevate them to a top position in a social hierarchy (Holtzman and Strube 2011). The derogation of rivals is another example of manipulative communication with others in order to protect or enhance self-esteem.

Cross-References

- [Projected Confidence](#)
- [Self-Esteem as Manipulative Status Communication](#)
- [Self-Esteem Reflects Assessments of Valuation](#)
- [Sociometer Theory](#)

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Descended Larynx

- [Laryngeal Descent](#)

Descent Illusion, The

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Definition

The Descent Illusion is the tendency to overestimate a vertical height more while standing on top of it than while standing at its bottom. Predicted from *Evolved Navigation Theory* to have evolved in response to greater falling risks on descent than ascent, it is ostensibly the largest known distance illusion.

Introduction

I predicted the Descent Illusion from my Evolved Navigation Theory (Jackson 2005; *Evolved Navigation Theory*, this volume). Evolved Navigation Theory specifies how natural selection can result from navigational consequences.

The Descent Illusion

A major source of selection resulting from navigational consequences over evolutionary

time is the act of falling, which continues to kill and injure modern humans more broadly than any other accidental source (Verma et al. 2016). One predictor of the likelihood and severity of falling is the direction of travel, where descent results in falls more often and more severe than ascent (see Jackson and Cormack 2007).

Many of the reasons that descent is riskiest derive from human biometry. Descent, compared to ascent, places our eyes farther from the navigated surface. Our bodies lean away from the primary traction source and the direction of travel. Forward momentum coincides with gravity, making acceleration easily overwhelming. Descent limits the efficacy of our hands to interact with the surface, opposite to the natural posture during steep ascent. Additionally, the movements of descent are comprised of short, guided falls consisting of negative muscle contractions that are more difficult to control than the movements of ascent. Many of these aspects of descent occur for other, nonhuman, animals.

Paired with the identification that falls are more common and severe on descent than ascent, Evolved Navigation Theory also identifies that distance perception is one of the cognitive mechanisms targeted by such selection over evolutionary time. For starters, distance perception generally features high variation upon which selection can act. Further, there is a strong Preference for the Nearest (PfN) of otherwise equal navigational goals (Jackson 2013). Selection on distance perception for specific surfaces would thus make overestimation adaptive for biasing navigational choices against navigation of those surfaces. Evolved Navigation Theory predicted that the greater mortality resulting from descent than ascent should have produced an overestimation of vertical surfaces more from above than below. This is exactly what we find.

The Descent Illusion consists of overestimating the vertical extent of an environmental surface more while standing at its top than bottom (Jackson 2005; Jackson and Cormack 2007; Jackson and Gómez de García 2016). This includes overestimating the vertical, in

comparison to an equal horizontal, from both the top and the bottom of the vertical surface (each of which separately constitutes an Environmental Vertical Illusion [Jackson and Cormack 2008]). Standing at the top or bottom of a vertical surface does not induce general distance overestimation: Observers estimate horizontal surfaces accurately or with slight underestimates, on average (Jackson and Willey 2011). The formula for the Descent Illusion is $\frac{(et - eb)}{eb}$, in which *et* is the estimate from the top and *eb* is the estimate from the bottom (Jackson and Cormack 2007).

The average magnitude of most distance illusions is roughly 10–15%. The average magnitude of the Descent Illusion is roughly 25–30%. Further, Descent Illusion observers' overestimates of a vertical surface while standing on top of it, compared to their estimates of an equal horizontal surface, exceed 80% on tall surfaces. This is ostensibly the largest known distance illusion.

This phenomenon is ubiquitous in everyday vision and yet humans are largely unaware of experiencing it (Jackson et al. 2013). It has been replicated across different real-world (Jackson 2005, 2009) and virtual environments (Jackson 2017), as well as across cultures and groups that include indigenous people selected explicitly for their disparities with previous samples (Jackson and Gómez de García 2016). This illusion redefines acrophobia as a normal fear of overestimated distances, rather than an abnormal fear of standard perception (Jackson 2009).

Conclusion

Competing theories failed to predict the Descent Illusion (Jackson and Cormack 2007), which is but one of many illusions and other cognitive mechanisms predicted by Evolved Navigation Theory (*Evolved Navigation Theory*, this volume). Although visual illusions are one of the earliest and most robust topics in psychological science (see Jackson and Cormack 2007; *Visual Illusions*, this volume), it was not until we utilized evolutionary psychological science that we were able to predict the largest among them.

Cross-References

- [Depth Perception](#)
- [Evolution of Mammalian Vision, The](#)
- [Evolved Navigation Theory](#)
- [Visual Illusions](#)

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Descent of the Larynx

- [Laryngeal Descent](#)

Descent with Modification

- [Evolutionary Change](#)

Descriptive Relativism

- [Cultural and Moral Relativism](#)
- [Misinterpreted as Cultural Relativism](#)

Design Features of Language

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Synonyms

[Characteristics of human language](#)

Definition

Distinctive qualities of human language

Introduction

Some general conclusions apply to all communication among living organisms. Communication, even in nonhuman animals, has unexpected complexity; it is a form of cooperative behavior; it includes individual recognition and categorization; and it requires the development of associations and thus memory. Furthermore, noise in communication is inevitable. Critical terms, such as information, signal, and noise, require operational definitions (for more on these topics, see ► [“Evolution of Communication”](#)).

These conclusions change basic assumptions about the relationship between nonhuman and human communication. Communication by nonhumans is more complex than expected and

communication by humans, as presented in the following sections, perhaps less so. There is clearly a large difference in brain size, cognition, and communication between humans and most other animals. Nevertheless, overstating a difference hinders comprehension just as much as understating it.

For centuries people have sought objective criteria to separate humans from other animals, and language has often taken first place among these criteria. Once Darwin and the early ethologists made it clear that nonhuman animals also have elaborate communication, the focus has narrowed to the properties of language that distinguish humans. Each such proposal has spurred students of animal behavior to probe deeper for parallels among nonhuman animals. Some organization in this process came when Charles Hockett (1960) presented a set of 16 “design features,” or distinctive properties, of human languages. Some of these features, such as a vocal-auditory channel (with its concomitants, broadcast transmission, directional reception, and rapid fading), interchangeability, and specialization are easily identified in diverse nonhuman animals. The remaining design features have more problematic parallels in nonhuman animals. Some of the issues they raise invite applications of the general conclusions listed above. The following discussion focuses on illustrative examples, rather than a general review, of these parallels.

Cultural Transmission

Culture is widespread in species with persistent associations of parents and offspring, but it is also prevalent in many species with less complex social behavior. Culture develops when patterns of behavior are acquired by young individuals as a result of experience with older ones. Prevalent examples in nonhuman animals include migration routes, territory boundaries, mating preferences, food selection, and predator recognition. Cultural transmission in humans as well as in other animals includes relatively unconstrained learning. Possibilities for learning have broad scope within wide predispositions. Nevertheless, the

study of nonhuman animals has revealed that even impressively open forms of learning have constraints that guide learning in adaptive ways. For rapid acquisition of complex traits within adaptive boundaries, learning within constraints is perhaps the optimal method. Such constraints (or predispositions) can for instance ensure that learning occurs within species, a particularly clear example of which is song learning by oscine birds. In this case, predispositions must affect responsiveness as well as production. Nevertheless, identifying predispositions for acquisition of human language remains contentious.

Animals other than humans rarely, if ever, appear to engage in teaching, in which an experienced individual directs the attention of an inexperienced audience to a task. Cultural transmission instead appears to result predominantly from observational learning by young individuals in the presence of adults performing routine activities (Matsuzawa 1999). A recent experiment with great tits reveals that observational learning can produce persistent cultural traditions in the feeding behavior of birds, even when the tradition is maladaptive (Aplin et al. 2015). In contrast, schools or apprenticeships are perhaps universal in human cultures. Nevertheless, it is possible that much, perhaps most, of human culture is instead transmitted by observational learning.

Cultural traditions in the songs of passerine songbirds, parrots, and hummingbirds illustrate one of the usual consequences of culture, the differentiation of dialects or traditions among nearby populations. All species of songbirds appear to learn at least some features of their songs. With few exceptions these species develop prominent geographical variation in their songs, whereas songs of other species vary only slightly, in line with variation in morphology. When the individuals of a species sing a single song pattern, all those in a limited geographical area often learn the same distinctive pattern. When individuals have repertoires of songs, dialects often intergrade as the frequencies of different acoustic patterns change progressively but incoherently with location (Marler and Slabbekoorn 2004; Kroodsmas 2005; Podos and Warren 2007). When individuals

sing only one pattern each, the formation of dialects is perhaps simplified. Nevertheless, distinct dialects in the vocalizations of some parrots and cetaceans include coherent repertoires of patterns.

Geographic differentiation of culture depends on the relationship between two periods in an individual's life: when a young individual learns the relevant behavior and when and where it moves before it eventually settles. The formation of distinct dialects requires either that young birds usually settle within the area of their natal dialects or that learning after settling predominates over earlier learning. In the case of coastal populations of white-crowned sparrows in California, individuals usually sing only one pattern, and dialects occupy nearly distinct areas with irregular shapes 2-20 km across. It remains uncertain whether the songs a young sparrow eventually masters are influenced by experience predominantly before or after dispersal. Conversely, it is also unclear whether or not a young sparrow's decision about where to settle is influenced by early experience.

Furthermore, it is also unclear whether or not dialects in birdsong are evolutionary adaptations (Podos and Warren 2007). Adaptation is a result of natural selection, the spread of alleles associated with advantages for individuals' survival or reproduction. In one possible scenario, dialects might result from adaptations for efficient signal detection in different environments. Alternatively, dialects might promote local adaptations for survival or reproduction in general, by restricting gene flow to populations in distinctive environments. Another possibility is that dialects might arise as collateral effects of the evolution of learning, if, for instance, complex learning was in itself important for mate choice. Or dialects might arise as side effects (pleiotropy) of local adaptations for noncommunicative purposes in structures also used for communication, for instance, if the structure of birds' bills adapted to the characteristics of their food but also constrained the kinds of sounds they could produce. In the latter two situations, the formation of dialects would in itself have no influence on individuals' survival or reproduction. In any case, dialects might promote the genetic divergence of populations and ultimately contribute to the origin of separate species.

All of these issues about dialects apply to human cultures as well. The maintenance of human languages and dialects indicates that individuals learn from older individuals within their natal area and then predominantly settle nearby. The increasing frequency of exceptions in recent centuries is presumably changing the geography of human languages. Each individual's choices of mates and places to settle are no doubt to some extent influenced by their natal language. Important but infrequent exceptions are the abduction of individuals and the translocation of populations as a regular consequence of warfare between culturally distinct groups. No doubt the boundaries between languages are influenced by interactions across these boundaries, but differentiation of languages in turn influences the nature of these interactions.

In contrast to birdsong, human language is distinguished by two levels of geographic differentiation. At one level, there are mutually incomprehensible "languages," which in their geographic pattern resemble the distinct dialects of songbirds. At another level, human "dialects" within a language intergrade more or less progressively, like geographic variation in the frequencies of song patterns of birds that have repertoires. Perhaps more study of songbirds would also reveal multiple levels of geographic differentiation.

A related design feature, learnability, refers to the human ability to learn more than one language. In songbirds with vocal dialects, individuals usually respond to dialects other than their own, although sometimes less so to distant dialects (Searcy et al. 1997). Furthermore, just as children are adept at learning any human language, songbirds acquire any dialect of their species-specific song with apparently equal facility. Bilingual individuals also occur among songbirds. Although careful comparisons are lacking, bilingual proficiency is perhaps as frequent as it is in human populations. Bilingual competence is hard to confirm when individuals sing multiple patterns that vary incoherently with location. When dialects are distinct, on the other hand, persistent study often reveals the presence of bilingual individuals. Most white-crowned

sparrows that settle near a dialect boundary sing only the pattern appropriate for their dialect, but some individuals near a boundary are indeed bilingual, with two song patterns, one matching each nearby dialect (Baptista 1977). To clarify these parallels between human and nonhuman cultures, the spatial and temporal properties of the transmission of signals and responses, in relation to the dispersal of individuals, need more attention, both in humans and nonhumans.

Despite these open questions about the process, geographical differentiation is one of the salient features of culture, both human and non-human. This differentiation requires errors in cultural transmission and thus reveals a crucial effect of noise in communication. Even if cultural traits have adapted to particular social or physical environments and even if migration of individuals introduces novelties in new areas, nevertheless errors must initiate the process of cultural change somewhere. Errors in cultural transmission are analogous to genetic mutations, insofar as both are transmitted to subsequent cohorts, although the rates of innovation and mutation can differ. Migration is similar in the two also, except that migrating individuals can abandon cultural traits but do not change genes (although the expression of genes might change). Cultural and natural selection, on the other hand, lack close analogy. The plasticity of individuals' traits, the rates of transmission, and the recipients all can differ markedly. Nevertheless, in the case of human languages, the stability and restricted acquisition of language might approach that of genetically canalized phenotypes. Close relatives usually play a predominant role in transmitting language. Language proficiency by humans requires years to develop and then, after the lapse of sensitive periods for acquiring some features of language, changes with great difficulty.

The transmission and innovation of culture depend on communication. Unless completely arbitrary, without advantages or disadvantages for signalers or receivers, this communication evolves by the same process of mutual optimization that applies to the evolution of all communication (see ► [“Evolution of Communication”](#)).

The advantages for signalers depend on the behavior of receivers, and the advantages for receivers depend on the behavior of signalers. Errors, from multiple sources, are inevitable. Even perception evolves by optimization with errors. The crucial role of errors, in other words noise, in all communication and perception means that culture, in humans or other animals, cannot be understood without studying errors. In studying the evolution of birdsong, the variation in learning is as important as the norm. The same is true of all human culture, including language. Yet studies of culture have usually focused on the norms, to the exclusion of the errors. Understanding communication requires attention to exceptions as well as norms.

Semanticity, Displacement, Arbitrariness, and Discreteness

This set of Hockett's design features refers in one way or another to how signals are related to situations. Many animals use discrete signals. Discrete signals are likely to improve discrimination by receivers and thus could have advantages in noisy situations such as long-range communication. In line with this expectation, discrete articulation might be more pronounced in long-range speeches by humans than in close-range conversation. This variation in discreteness would exemplify the scaling of exaggeration in signals with the level of noise, as predicted for the evolution of all communication in noise (see ► [“Evolution of Communication”](#)). More study of variation in signals with contexts could clarify this issue.

Arbitrariness refers to separation of a signal from direct resemblance to or evocation by its referent. Warning calls, for instance, do not resemble the sounds of predators. On the other hand, the pitch or tonality of sounds in some cases directly reflects an individual signaler's overall physiological state, such as its tendency to flee, fight, or freeze (Morton 1977; Reby et al. 2005). Arbitrariness is intended to denote a signal's association with a more cognitive internal state, a specific neurophysiological state rather than a general

physiological or emotive one. These alternatives, of course, are the ends of a spectrum of possibilities. Each case lies somewhere between a scream of fear and an abstract notion. Human speech conveys information about a speaker's general states, or emotions, in addition to and concurrently with specific states or abstractions. Any signal has some degree of arbitrariness and some degree of abstraction. No doubt human language includes more cognitive complexity than other animals' signals. An unanswered question though is whether or not it might also include more emotive complexity. This continuum between emotive and cognitive applies to the next two design features also.

Note in passing that arbitrary signals in discussions of sexual selection are defined differently. They have zero utility for receivers and, as argued elsewhere, seem highly unlikely in noisy communication (see ► [“Sexual Selection”](#) and ► [“Evolution of Communication”](#)).

Semanticity and displacement are related to information in signals about the external environment. Some of the best examples of semanticity in nonhumans are warning calls and food calls. Semanticity applies to signals associated with external referents in contrast with those expressing the signaler's internal states. This distinction is just as untenable here as in the previous paragraph. Recall from previous sections that all of an individual's actions are influenced by both its internal and its external state, by both its current constitution and its impinging sensations. Rather than a distinction between signals that are emotive versus cognitive, there is instead a continuum from more emotive to more cognitive. The question is where particular instances of calls lie on this continuum from emotive to cognitive.

Playbacks show that individuals respond appropriately to alarm or food calls even in the absence of an actual predator or food. Furthermore, some birds and mammals have distinct calls for two or more predators that pose different threats, and playbacks of these calls evoke the appropriate responses. The associations with different predators are in some cases learned. Young vervet monkeys reliably

produce the correct calls only after prolonged practice (Cheney and Seyfarth 1990). Many birds in contrast easily learn experimental associations of predator calls with various improbable objects. It is thus clear that some nonhuman animals can learn to produce, and to respond to, signals associated with specific external situations, and in some cases these associations are learned easily.

On the other hand, in normal circumstances these calls are produced and evoke responses, only in the presence of actual predators. Displacement, in contrast, refers to separation of a signal and its referent in space and time. This separation requires memory. With displacement, the cognitive rather than emotive associations of signals, and thus their semanticity, often seem clearer. Furthermore, relatively more cognition is suggested by two forms of noise in communication: unreliable and deceptive signals. Adult vervet monkeys, for instance, learn to ignore the unreliable calls of young individuals (or unreliable adults) (Cheney and Seyfarth 1990). Furthermore, some monkeys and birds produce predator warnings deceptively in the absence of a predator, as discussed further below. Errors in communication, the apparent exceptions, provide intimations of cognition.

Displacement is also attributed to the waggle dances of honeybees. These dances in a hive or a swarm indicate the location of food or potential nesting sites by means of two transpositions. The direction to the goal with respect to the sun becomes the direction of a waggle dance on a vertical surface with respect to gravity, and the total energy expended in flight to the goal becomes the instantaneous expenditure of energy in the dance. The levels of arbitrariness and semanticity are both low. The mapping of direction and distance onto the signaler's overall behavior and the limited memory remove this case from typical human cognition. Arbitrariness, semanticity, and displacement again contribute to a continuum between emotive and cognitive behavior. All are widespread in communication. All are disrupted by noise. Yet their use in noise sometimes reveals a degree of cognition.

Prevarication

Hockett's final design features are at the top of his proposals for human specializations. Nevertheless, there are reports of prevarication, or deceptive use of signals, in many birds and mammals. Predator calls, in particular, can serve to distract higher-ranking opponents so that low-ranking ones have a chance to obtain food or matings. Analysis of communication in noise shows that opportunities for such deception are expected in all forms of communication (see ► [“Evolution of Communication”](#)).

Nevertheless, linguists often balk at attributing true prevarication to nonhuman animals, in the absence of evidence for the signalers' intention. Intention becomes one of the definientia of deception. Does the signaler expect or plan to deceive the receiver? How does a person expect or plan to take advantage of another person? Presumably the actor anticipates a personal advantage based on anticipation that the recipient is vulnerable. In the case of deceptive communication, the signaler thus anticipates that a particular receiver is likely to respond in a way that yields an advantage to the actor despite a disadvantage to the receiver. This anticipation is tantamount to mind-reading or having a “theory of mind.” There is a circularity here: an actor has intentions provided it can read another's mind, and primary evidence that an actor can read a mind is provided by thoughts such as intentions.

Such circularity in discussions of mental phenomenon excludes not only nonhuman animals from a thinking person's mentality but also all other humans. An operational definition of deception, which avoids such circularity, is a system of signals directed specifically (nonrandomly) at receivers from which a response, on average, has advantages to the signaler but disadvantages for the receiver. Such signals require some preliminary strategy. Because responding to signals should evolve to increase a receiver's advantage in reproduction or survival, deceptive signals, which have the opposite effect, must in general occur infrequently. Consequently, deception often reveals evidence of a cognitive ability by signalers to adjust the frequency of attempted deceptions by

itself and others. For instance, a deceptive signaler might anticipate a particular receiver's probable response; in effect it might read its mind, from the temporal context of signaling.

Reports of deception by nonhuman animals indicate that this behavior is, as expected, usually dependent on the circumstances of the audience. Signals that call attention to the presence or location of food often depend on whether the audience is likely to be a competitor or a partner. Recognition (categorization) of individuals, not just broad classes of individuals, is often critical. Anticipation of the state of the audience is of course widespread in nonhuman signaling, but this attribution applied to specific individuals matches the kind of behavior associated with intentions, as just defined. It presumably occurs in many sorts of social interactions, from anticipatory cooperation to strategic aggression (Cheney and Seyfarth 1990, 2007; Seyfarth and Cheney 2014). It applies to roosters advertising food to attract hens (Gyger and Marler 1988), to subordinate males courting females without drawing the attention of dominant males (Smith et al. 2011), and to territorial warblers challenging specifically those neighbors that have trespassed (Godard 1993). The complexity of an organism's “theory of mind” depends to a large degree on the complexity of its categorization of the individuals it interacts with. Furthermore, intentions in the form of signals adjusted to contexts, whether human or nonhuman, are subject to errors.

Duality of Patterning and Openness

These final, and most problematic, design features are closely related. Openness in human language, an ability to rearrange units of sound to produce new phrases, depends on duality, the organization of speech into at least two hierarchical layers. Elements of a lower layer, which in themselves have little or no meaning, are arranged to produce units of higher layers, which do have meaning. As previously suggested, the operational definition of the “meaning” of a signal, in a particular context, is the receiver's usual response, overt or covert, immediate or remembered. Language is often described with three layers, phonemes,

morphemes, and phrases (sometimes with syllables of phonemes interposed), of which only phrases convey meaning. Duality of patterning requires two layers arranged so that recombined discrete components of one layer are nested within components of the other.

Many nonhuman animals have substantial repertoires of discrete signals (see ► [“Evolution of Communication”](#)). In those species that produce sequences of signals, some recombine signals into larger performances. Some songbirds use the same components in different sequential patterns of song, but some use different components in each sequential pattern. There is sparse evidence that the different sequential patterns in these repertoires convey different information, for instance, by association with different contexts or internal states, or evoke different kinds of response (Wiley et al. 1994). An absence of evidence is particularly inconclusive here, because finding significant associations with complex patterns of recombining elements becomes statistically challenging. Anthropologists have a big advantage in deciphering a previously unknown human language, as a result of their preconceptions about what humans are likely to talk about. Humans, in other words, have an anthropocentric theory of mind, one that provides much less help in deciphering communication of other species. Humans perhaps should not underestimate other animals.

Despite these possibilities for other species, human language no doubt has remarkable capability to recombine components of signals to convey a vast complexity of information. Nevertheless, components of language are not nearly so distinct in actual speech, in all its various contexts, as they are often presumed to be. Contextual and individual variation in phonemes and morphemes is well known. Furthermore, everyday conversation might depend heavily on phrases as units, learned for production and response as units, rather than as recombined components. All languages are beset with idioms and pat phrases, particularly for routine communication, phrases learned as units rather than by rules. In English, few people know the expressions “thin as a rail” or “what’s up,” for instance, as anything other

than “thin-as-a-rail” or “whats-up,” single units of expression, not recombining units. Another example is the instability of prepositions (and grammatical cases). Across and within languages, association of prepositions with contexts often defy consistent definition and instead become erratic or idiosyncratic. Most of these associations are presumably learned and deployed as units without parsing. Proficiency thus might often depend on mastering associations of these unitary phrases. Even when some parsing of recombined components is necessary, the associations of phrases can depend on common underlying metaphors (Lakoff and Johnson 1980). Indeed, morphemes raise the same questions. Many words are sequences of two or more syllables, which in combination evoke unitary associations. Etymological stems for syllables are rarely parsed. Even then underlying metaphoric associations dominate. Thorough study of the variability of human speech at all levels might reveal that duality of patterning requires a dose of grammatical fantasy.

The deployment of writing in itself changes communication. Writing allows much greater permanence than does neural memory alone, and this permanence allows a reader, as a receiver of signals, to examine and even to review the structures of phrases more carefully than is possible in conversation. With time available, humans can indulge their drive to categorize, by abstracting, cataloguing, and eventually prescribing patterns of usage. In reality both human and nonhuman communication are permeated with unexpected variation, as a result of errors in production, transmission, or reception of signals, but also just idiosyncrasies in usage by individuals or small groups of communicating individuals. The irregularities, idioms, idiosyncrasies, and errors are an inescapable part of language.

Openness is an abstraction or exaggeration of reality as well. Although linguists often claim infinite possibilities for language, the components of language are finite, the human brain is finite, and the practical possibilities for combinations are finite. Speaking humans do not produce stereotyped phonemes that recombine to form stereotyped morphemes and then phrases with unlimited possible meanings. The number of possible

associations is no doubt large, but the number of associations humans make in using language might not exceed the number of associations they make in categorizing other humans (Wiley 2013). Errors also limit associations of attributes with other objects.

Furthermore, limited evidence is a temptation for simplification of nonhuman animals' behavior. For instance, songbirds are usually thought to have repertoires of distinct patterns of notes, from one to several hundred such patterns. Careful inspection, however, reveals much variation in details, little or none of which has any current explanation. Perhaps even greater complexity in sequences of sounds occurs in cetaceans. The difficulties of investigating complex signals include the impediment of lacking an appropriate theory of mind on which to base hypotheses. Nevertheless, much variation is no doubt meaningless, just as it presumably is in human speech.

A promising way to investigate variation consists of looking for dependence in recombinations of components. A simple example is provided by displays of the Carib grackle (Wiley 1975). Males perform conspicuous displays to females and other males. Each display involves raising wings, tail, and bill to varying degrees. Elevated wings show some association with displays toward females, elevated bills with those toward males. Because these displays are easily observed, a large number can be scored for each element. Analysis reveals that wing and tail elevation are independent of each other, so in this case this species has the potential to generate infinite gradations of wing and bill elevation, each presumably related to neural and mental states while interacting with females and other males. This example of insipient duality and openness indicates how difficult it can be to decide whether complex variation in signals is relevant, erroneous, or simply adventitious.

Hierarchical Organization

As awareness of the complexities of nonhuman communication has accumulated, attention has focused on hierarchical organization as the key

to the relative openness of language. Although responses to "sign stimuli," simple sensations, occur widely, especially in the initial responses of young organisms or in the quick avoidance of predators, nevertheless, responses to more complex stimulation are also widespread. For instance, many vertebrates, but not humans, have neurons that act as movement detectors, even at low levels of sensory processing. Recognizing patterns is not an unusual capability of many other animals. Although birds and mammals soon after hatching or birth have reflex (highly canalized) responses to simple stimulation associated with predators, they often quickly learn more complex associations. Object constancy, an ability to recognize (form associations with) a set of sensations as a unique object despite varying perspective and occultation, does not differ in principle from other forms of recognition, including recognition of individual conspecifics or recognition of verbal sequences. Recognition of patterns, spatial or temporal configurations of components, is thus a mental capability that occurs widely in animals as well as humans.

Much recognition is potentially hierarchical. Any particular instance of a set of sensations could be recognized as belonging to one or more progressively more inclusive and complexly embedded or overlapping categories. A territorial neighbor can be recognized, for instance, despite singing multiple different song patterns, at different locations and distances, under different environmental conditions. Furthermore, it might be recognized more specifically as one that had recently trespassed or one known from a previous year (Godard 1991, 1993; Wiley et al. 1994; Godard and Wiley 1995). Hierarchical categories are recognized by Aristotelian definition, with consistently defined features. Alternatively, categories might be recognized by family resemblance, with inconsistently shared features. In the first case, all members of a category would share an inclusive set of features, as in a phylogenetic tree. Membership in categories would be unambiguous. In the second, members of a category would each share some but not necessarily the same set of features with every other, as in an actual family. Ambiguity might occur.

Chomsky (2005) recognized the importance of categorization when he proposed that merging is the crucial cognitive operation of language. Merging, in the usual sense of simple combining, is nevertheless too simple for his examples, which require combining elements from two separate categories, subjects and predicates, in order to produce a phrase with meaning. In more physiological terms, Chomsky's merging is not just association of perceptions but association of elements from two categories of perception. Associating perceptions from two categories is cognitively similar to associating individuals with different contexts. It is a matter of common experience that contexts affect recognition of individuals, presumably because objects such as individuals become associated with their contexts. Thus each context merges, in Chomsky's sense, more easily with some individuals than with others, just as each verb merges more easily with some nouns than others. In this way, parsing social interactions might require cognitive abilities that could be coopted for language. Yet it is not clear whether the relevant categories are recognized by definition or by family resemblance. Furthermore, both in language and social interaction, associations might sometimes be recognized as units, without any parsing, in other words, without any analysis and merging of parts, at all.

Consequently it seems unlikely that either language or social interaction is organized entirely hierarchically. Nevertheless, this particular form of organization has received special attention as a possibly fundamental feature of language. Hierarchy connotes two distinct kinds of organization. Human institutions are hierarchical in the sense of a chain of command, with each individual overseeing a set of subordinates. The organization is like a multidimensional pyramid, with lower sets embedded (nested) within higher sets. In contrast, tennis players and perhaps society mavens are ranked unidimensionally, in a ladder. In non-human social organization, dominance hierarchies take the latter form. An example of such a pattern is $(A > B > C > D)$ where A through D are individuals ranked on a single dimension. Embedding in this case consists of pairs of closely ranked individuals inserted between pairs of distantly related

individuals, $(A > (B > C) > D)$. Human language is also linearly ordered in time (speech) or space (writing), with similar nestings of components, where A through D are words (morphemes). Several experiments have suggested that birds can recognize sequences like (AABB) or (ABBA), although it is not clear that they can generalize such a pattern to new exemplars (Van Heijningen et al. 2009). The second sequence superficially matches a pattern of embedded phrases in language. On the other hand, the first, not the second, sequence matches complex dominance hierarchies that result when individuals' rankings are embedded within families' rankings or when dominants create coattails for familiar subordinates. There are indications that baboons and birds can "parse" a dominance hierarchy with embedded clusters (see ► ["Evolution of Communication"](#)).

Embedding of phrases in language (often confusingly termed recursion) is more complicated than either diagram above. Each phrase consists of components with different roles, for instance, nouns and verbs, or more generally objects and attributes. The exact relationship of these two types of components in a phrase is marked either by their sequence or by tags (inflections), and the relationships of phrases are also marked by their sequence or by tags (conjunctions). A more accurate diagram of embedding in language is thus $(A1(B1B2)A2)$, where A and B are phrases and 1 and 2 designate appropriate objects and attributes within each phrase (Corballis 2007). A human receiver associates A1 with A2 and B1 with B2. These associations are either temporal (for a listener) or spatial (for a reader). The cognitive issue is whether or not nonhuman organisms can respond reliably to $(A1-A2)$ regardless of whether these two components are separated in time or space by analogous phrases, such as $(B1B2)$.

Sensations evoking responses by animals are often (perhaps always) composed of multiple elements in particular arrangements. Thus it is not surprising to find that animals can master associations like $(A1-A2)$ regardless of some interruptions. An ability to respond to the associated sensations despite interruption comes

close to object constancy, discussed above. The experiments mentioned above, which show that birds fail to generalize such patterns (Van Heijningen et al. 2009), perhaps miss the point. Object constancy is probably not generalized either; instead each object is learned by family resemblance of its particular features, despite various interruptions, and eventually evokes a unitary response. Furthermore, as discussed above, it is not clear that using language requires parsing of components.

Embedding in language is even more complex, because in this simple case, (B1B2) modifies A1, so that (A1B1B2A2) becomes in effect ((A1(B1B2))A2). The phrase “The cat that the dog attacks hisses” does not merely merge two phrases “The cat hisses” plus “The dog attacks.” Instead the inner phrase changes the meaning of the outer phrase; the conjunction makes the connection. Can some nonhuman animals recognize an association of two signals, each of which associates components from two categories, regardless of whether one signal is interposed between the components of the other signal? Perhaps.

As important as embedding is for human language, the relationship established by an action also seems critical, as in a phrase such as “The dog attacks the cat.” The relationship between the “dog” and “cat” is in part specified by the action “attacks” but also by marks that indicate the relationship of each object to the action. This latter relationship is marked in English primarily by sequence: (A1 B1 A2). In Russian, and many other languages, the relationships are marked by modification of each noun (the case of each noun, either nominative or accusative): (A1n B1 A2a). In Russian, sequence has less salience (and determinatives are usually absent), so this inflected phrase would elicit a similar response in the sequence (A2a A1n B1) or in any other sequence. Can animals recognize a three-component signal in which the components have particular relationships specified either by arrangement in time or space or by at least one modifying (case) component. Despite the complexity, this challenge is nevertheless met by some nonhuman animals (Herman and Richards 1984; Marino et al. 2007).

Language as Criteria for Responses

The forgoing discussion has failed to identify a key to language. It has made little progress in isolating any qualitative requirement for the use of language that nonhuman animals do not already have, in some cases to a considerable degree. Yet it seems clear that no other species engages in communication approaching the complexity of human language. Nor have they achieved the levels of technological competence that language has catalyzed among humans. Before suggesting a solution to this paradox, this section first provides a different way to conceptualize the use of language. Recent thinking about language has usually started from the top, from idealizations by grammarians and linguists (Hauser et al. 2002; Chomsky 2005; Tomasello 2010; Fitch 2017; Seyfarth and Cheney 2017). The following starts from the bottom, from basic neural mechanisms for all communication.

Language consists of clusters of perceptions. Categorizing clusters of perceptions to form components of language is fundamentally the same as categorizing sensations to form primary perceptions. Sensations have inherent variability, as a result of variation introduced by their sources (including human signalers, speakers, writers, or signers), their receivers (including human listeners, readers, or sign readers), and the medium in between. This variability is noise in the perception of signals. All receivers of signals in noise make decisions to associate sensations with responses by means of criteria for response (Wiley 2015, 2017; see ► “[Evolution of Communication](#)”). These criteria associate particular sets of incident sensations with particular sets or levels of responses, either overt or covert, in action or memory. Classification of sensations is thus a result of their associations with responses. Initial perceptions are the first responses to sensations.

The criteria for each decision, like all other features of living organisms, develop in the course of each individual’s life as a result of an interaction between its genetic constitution and its environmental conditions. At any moment these criteria depend on the individual’s current physiological and anatomical state. The association of

sensory input with response thus results from the individual's current state and the impinging sensations.

Classification of sensations is the preliminary stage in the eventual classification of perceptions into the components of language. Initial perceptions are the fundamentally meaningful categories of sensations. At each subsequent stage of categorization, the process of association divides perceptions into progressively more specific perceptions or other responses. At each stage, the criteria for categories might combine definitions and family resemblances, and the criteria might change, with developing familiarity, from sequential or inflectional parsing of relationships among components to immediate unitary detection. The inherent variation in sensations at the root of the process propagates into variation in perceptions at every higher stage. Noise permeates all stages in the processing of language. It requires neural decisions to recognize categories of sensations or perceptions at each stage. The variation and exceptions are as important as the norms.

This perspective of language does not preclude human cognitive criteria that quantitatively exceed those of nonhumans. Yet it has not identified a qualitative cognitive capability that nonhumans entirely lack. Combinations of associations in time and space admit great complexity. Increased complexity no doubt can lead to a "great leap forward." It is a truism that quantitative change can lead to qualitative change. Indeed humans have a nearly inexhaustible impulse to categorize, so any change, no matter how small, can invite categorization as a qualitative change. Yet it is not clear whether or not such a "leap" requires any innovations beyond one small step at a time on the same path. Nevertheless, something extraordinary happened when human language developed. It might not have required any advance in cognition.

From Nonhuman to Human Language

Chimpanzees, bonobos, bottlenose dolphins, grey parrots, and other nonhuman animals have

demonstrated surprising capabilities (Savage-Rumbaugh and Lewin 1994; Marino et al. 2007; Pepperberg 2004). They easily master the use of abstract symbols, reference, displacement, and sequential recombinations. They can both produce and respond appropriately to symbols. They can use symbols to communicate with conspecifics to solve problems. They can to some extent acquire these capabilities from other conspecifics.

Despite some animals' language-like abilities, there is no clear evidence that these abilities are used for communication in natural situations. It is interaction with language-capable humans that reveals the inchoate capabilities for language in apes, parrots, and dolphins. This situation recalls a repeated result of all mathematical models for the evolution of communication. The initiation of communication, of whatever simplicity or complexity, must surmount a hurdle. Rare alleles associated with response to a new signal are unlikely to spread in the absence of individuals producing the signal. Conversely, rare alleles associated with producing a new signal are unlikely to spread in the absence of individuals responding to the signal. As seen in the models for the evolution of communication in noise and for the evolution of traits and preferences by sexual selection, the benefits of signaling depend on responses, and the benefits of responding depend on signals. The frequencies of signals and of responses must reach some threshold before the benefits of signaling and responding begin to spread (see ► ["Evolution of Communication"](#) and ► ["Sexual Selection"](#)).

This conclusion invites application to these language-capable but language-deficient populations. Chimpanzees have evolved enough mental capabilities to provide the advantages of language, yet in natural situations language among chimpanzees is, by all evidence, absent. There could well be advantages for apes to have language to assist in coordinating cooperation within their groups and competition between groups. They appear to have enough of a start in mental competence. Perhaps, so far, neither the frequency of gestures nor responses have reached the necessary threshold. Who knows? Perhaps a

fortunate coincidence, just one small group with by chance a few gesturers and a few responders, a few individuals with just the requisite predispositions, such as Kanzi seemed to have, and overnight a new kind of chimpanzee society based on new possibilities for communication would sprout. Subsequent natural selection would enhance these incipient predispositions for specialized learning.

After that leap forward, natural selection would result in evolution toward optimal signaling and responding. Perhaps it would evolve rapidly, accelerating as expected for sexual selection but also for any frequency-dependent selection of mutualism in communication. The increase in size and complexity of society with the introduction of agriculture might contribute to selection for greater complexity in language. The concurrent invention of writing would almost certainly increase the potential complexity, as a result of the greater storage and review of language. Then there would come printing and eventually the Internet and computers to assist with storage, search, translation, and associations of language. Perhaps even tools and fire might have affected the evolution of language, or, perhaps more likely, language affected them.

It is easy to imagine how increasing competence with language could improve thinking, which is after all internal communication. It presumably would require higher levels of association and memory. In contrast, a proposal that language-like thought might *precede* language for external communication with other individuals seems unlikely. Private language would lack the stability acquired from consilience in the process of communication with other individuals (Wiley 2015). Instead the evolution of language is likely to have promoted the evolution of thinking.

Conclusion

This scenario supposes that the advantages of complex hierarchical societies with some incipient forms of cooperation and monitoring of other individual's social relationships might have favored the initial evolution of advanced mental

capabilities. The advantages of multiplicity and specificity in individual recognition might be enough to promote the evolution of complex associational learning. The requirements for criteria based on complicated family resemblances and for object constancy in challenging conditions might produce enough cognitive complexity. The ultimate form of cooperation, language, would then just need the impetus to get past the impasse of signalers without receivers and receivers without signalers. A boost in frequencies of signals and responses might come with a random perturbation during a bottleneck in population size. After crossing the initial hurdle, natural selection on the predispositions for language could take hold. Perhaps faster than so far imagined, the use of language would flourish.

Cross-References

- [Evolution of Communication](#)
- [Evolution of Culture](#)
- [Sexual Selection](#)

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Designation

► Names and Titles

Desire and Arousal Disorders

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Synonyms

Erectile disorder; Erectile dysfunction; Female sexual interest/arousal disorder; Hypoactive sexual desire disorder; Impotence; Inhibited sexual desire; Low libido, female sexual arousal disorder; Low sexual desire

Definition

Sexual desire is a motivational state that is characterized by heightened interest in sexual stimuli and a drive to seek, initiate, and/or continue sexual activity. *Sexual arousal* is the bodily and mental sexual response to sexual stimuli during or in anticipation of sexual activity. *Hypoactive sexual desire disorder* (HSDD) is a persistent deficiency or absence of sexual/erotic thoughts and fantasies and desire for sexual activity that induces distress in the subject. *Female sexual arousal disorder* (FSAD) is an inability to attain or maintain sexual arousal during sexual activity and/or to have inadequate genital lubrication-swelling response during arousal and sexual activity, and that induces distress in the subject. *Erectile dysfunction* (ED) is the marked difficulty in obtaining and/or maintaining an erection during sexual activity and/or a marked decrease in penile rigidity.

Introduction

The manifestation of sexual desire and arousal is dependent upon two separate but interacting systems: a sexual excitation system and a sexual inhibition system (dual control model of sexual response; Janssen and Bancroft 1996). These opposing systems are differentially activated based on the presence of internal and external stimuli, internal state, and the expectation of reward and of negative consequences. The net activity determines the presence and strength of sexual desire and arousal and, ultimately, sexual behavior. Sexual stimuli or cues automatically trigger the sexual excitation system, which is necessary but not sufficient for a sexual response. The expression of a sexual response is dependent upon the potency of the erotic stimulus, the internal state (e.g., a satiated or non-satiated state), and other stimuli and/or cognitions signaling the immediate and delayed consequences of sexual responding. A potent sexual stimulus can activate the sexual excitation system (but also a weaker stimulus in an extremely non-satiated state), but if the consequences of sexual responding are perceived as negative, the response is dampened or

prohibited by activation of the sexual inhibition system. This allows adaptive responding and ensures that sexual behavior is less likely to occur when the consequences of such behavior are negative. Imbalance of these systems can lead to sexual dysfunction. Men and women who have a low propensity for sexual excitation or a high propensity for sexual inhibition are more likely to develop sexual dysfunction. However, by definition, these individuals do not yet *have* a sexual dysfunction, as such a diagnosis can only be made when absent/decreased desire and/or arousal induces substantial distress. When someone has a low propensity for sexual excitation, a potent sexual stimulus will have a reduced chance of inducing a sexual response. When someone has a high propensity for sexual inhibition, a sexual stimulus may induce activation of the sexual excitation system, but this activity (and the concomitant sexual response) is then quickly reduced by (continuous) over-activation of their sexual inhibition system. Either way, the net effect is decreased or no sexual desire and decreased or no sexual arousal. A differentiation based on this division has been operationalized for women with sexual desire and arousal problems (Bloemers et al. 2013), but the model likely holds for men with desire problems and psychogenic erectile dysfunction as well. In this model, women with a low propensity for sexual excitation are characterized by their low sensitivity of the brain for sexual stimuli, possibly due to altered function of their androgen system. Women with dysfunctional over-activation of their sexual inhibitory mechanisms are characterized by over-activity of their dorsolateral prefrontal cortex in response to sexual stimuli. The dorsolateral prefrontal cortex mediates inhibitory control of (motivated) behavior. The inhibitory neurotransmitter serotonin plays a key role herein. Unfortunately, it is not readily apparent to which category a patient belongs because the symptoms, low desire and/or low arousal, are the same for both these subgroups. A demarcation formula using both biological as well as psychological variables is needed to determine if a patient is low sensitive or high inhibitory (Tuiten et al. 2018).

Sexual desire and arousal problems often coexist. The sexual excitation and sexual inhibition systems influence both desire and arousal, so either excitatory or inhibitory dysfunction can then also easily impact both desire and arousal simultaneously. However, sexual desire problems can also exist without concomitant sexual arousal problems and vice versa. This separation between low sexual desire and low sexual arousal has been the topic of an ongoing debate ever since the development and launch of the 5th edition of the *Diagnostic and Statistical Manual for Mental Disorders* (DSM5; APA 2013). In this latest DSM edition, the DSM-IV (APA 2000) diagnosis of female hypoactive sexual desire disorder (HSDD) and female sexual arousal disorder (FSAD) are merged into a single diagnosis of female sexual interest/arousal disorder (FSIAD). This merged category has merit, because it is consistent with the premise of the dual control model that dysfunction on the excitatory or inhibitory side can impact both desire and arousal. It contradicts evidence, however, that HSDD and FSAD can exist separately without the other. Although not the intention of this entry to discuss the validity of FSIAD versus HSDD and FSAD, all that is outlined further below applies to both diagnostic categorizations unless otherwise stated.

Sexual Desire Disorders

Hypoactive sexual desire disorder (HSDD) is characterized by a persistent deficiency or absence of sexual/erotic thoughts and fantasies and desire for sexual activity. For a formal diagnosis according to the *Diagnostic and Statistical Manual for Mental Disorders* (4th edition, text revision; DSM-IV TR), the complaints must have persisted for at least 6 months, cause clinically significant distress in the individual, and cannot be attributed to other mental disorders, relationship distress, other significant stressors, a medical condition, or drug use/abuse. The prevalence of HSDD in women is approximately 8–19% (Goldstein et al. 2017), although many studies indicate a higher prevalence. Estimations of

prevalence of HSDD in men also vary greatly, ranging from approximately 3% to 16% (Krakowsky and Grober 2016). Problems in low desire can negatively impact the quality of life (Laumann et al. 1999).

The neural regulation of sexual excitation (and thus desire), even though it is far from being fully elucidated, can be split into several functional domains. Sensitivity to sexual cues reflects the brain's responsiveness to sexual stimuli. This is in part mediated by (among others, androgen functioning in) the amygdalae, which are known for their role in attributing salience to a stimulus, and the mesolimbic dopaminergic pathway that projects dopamine to the nucleus accumbens through the dopaminergic cells of the ventral tegmental area. The mesolimbic system mediates incentive salience and innervates the amygdalae, and functioning of this circuit is therefore key in someone's sensitivity to sexual stimuli. Other areas that play an important role in sexual excitation are, for example, the medial preoptic area, locus coeruleus which contains noradrenergic neurons, and the arcuate nucleus. Sexual inhibition has the more executive role as opposed to the sexual excitation system which is more automatic. The inhibition system "ascertains" if the consequences of the automatically turned on excitation system (i.e., sexual responses) are advantageous. The prefrontal cortex plays an important role in the inhibition of sexual behavior, especially the dorsolateral prefrontal cortex. A key neurotransmitter in this inhibitory control is serotonin. A propensity for increased activation of the sexual inhibition system may be caused by increased serotonergic activity in the prefrontal cortex. Indeed, drugs that augment serotonergic action in the prefrontal cortex (e.g., selective serotonin reuptake inhibitors) often induce severe sexual dysfunction as a side effect (Clayton et al. 2002). Other inhibitory modulators are opioids, endocannabinoids, and oxytocin, which are released following orgasm and play a role in satiation.

The insula and anterior temporal cortices also play an important role in the perception of a sexual response. The insula mediates the perception of physiological response (interoception).

Interoceptive stimuli are reprocessed with increasingly complex information, in a posterior to anterior gradient, accumulating in the anterior insula and forming subjective awareness of the (sexual) response. The anterior temporal cortices integrate this information with visceral-emotional information from multimodal association areas, giving a global (sexual) emotional state.

There are several social/psychological and pharmacological treatment options for HSDD. Psychotherapy and cognitive behavior therapy typically address beliefs, thoughts, emotions, behavior, and relationship communication and interaction that are counterproductive in developing, experiencing, or maintaining sexual desire. For example, patients may learn to “stay in the moment” and not stray in distracting thoughts that typically inhibit the sexual response or unlearn negative thoughts that stem from cultural or religious beliefs. Sensate focus therapy and many other forms of sex therapy emphasize the importance of (sexual) communication in the relationship and employ sensual touching exercises to gradually improve sexual intimacy. To date, there are no approved pharmacological therapies for HSDD for men and only one for women. There are several drugs in different stages of development and several off-label options that have been shown to have some merit. Agents that enhance dopaminergic functioning (e.g., bupropion, cabergoline, ropinirole) may be used. Theoretically, these should increase incentive salience and sexual motivation by mimicking actions of, or facilitating, the mesolimbic dopamine system. Agents that alter serotonergic function, and thereby target inhibitory control, may also be used, like flibanserin, which is the only regulatory approved drug in the USA for HSDD in premenopausal women. Flibanserin is a serotonin 1a receptor agonist and serotonin 2a receptor antagonist with a once-daily dosing regime. It has been shown to decrease serotonin levels in the brain but also increases dopamine and noradrenaline levels. Theoretically this is a sound approach, but the efficacy of the drug in women has been criticized because of the meager difference in its efficacy versus placebo (Jaspers et al. 2016). Bremelanotide, an on-demand melanocortin

receptor agonist administered by injection, has shown promising efficacy in women with HSDD. Two other on-demand drug combination products have also shown promising efficacy in women with HSDD/FSIAD. One is a combination tablet that combines the sublingual administration of testosterone with delayed release of oral sildenafil. This method of administration ensures the overlap of the pharmacodynamic effects of both compounds and is designed specifically for women with HSDD/FSIAD who show lower neural sensitivity for sexual stimuli. The second on-demand combination tablet has been designed for women with HSDD/FSIAD due to dysfunctional over-activation of sexual inhibition. It combines sublingual administration of testosterone with delayed release of buspirone and transiently decreases sexual inhibition. Chronic testosterone therapy is also used off-label in men and women, with mixed results especially in women (Khera 2015).

Sexual Arousal Disorders

Female sexual arousal disorder (FSAD) is characterized by the inability to attain or maintain sexual arousal during sexual activity and/or to have inadequate genital lubrication-swelling response during arousal and sexual activity. It causes marked distress or interpersonal difficulties that cannot be attributed to another mental disorder, relationship distress, other significant stressors, a medical condition, or drug use/abuse. The prevalence of FSAD ranges from 6% to 28% of women, and prevalence is likely tied with increasing age (Giraldi et al. 2013). Erectile dysfunction (ED) is the marked difficulty in obtaining and/or maintaining an erection during sexual activity and/or a marked decrease in penile rigidity. The complaints must have persisted for at least 6 months and cause clinically significant distress in the individual and are not caused by other mental disorders or as the result of relationship distress, other significant stressors, a medical condition, or drug use/abuse. The prevalence of ED is strongly tied to age, with approximately 2% of men in their 40s, rising to 25–30% of men in their

60s who suffer from ED (Boyle 2009). Problems in low sexual arousal/erectile dysfunction can negatively impact the quality of life (Laumann et al. 1999).

For adequate sexual arousal, the central mechanisms described under section, “[Sexual Desire Disorders](#)” also need to be functional. Peripherally, the genital sexual arousal response is largely determined by the engorgement of the genitalia with blood. The mechanism underlying genital engorgement is comparable in men and women because the genitalia share the same embryological origin. Genital engorgement leads to an erection in men and to erection of the clitoral complex in women, which subsequently induces vaginal lubrication. The cavernosal tissue that allows this swelling response consists of many small balloon-like arteries that are lined with smooth muscles. Most of the time, these muscles are constricted through sympathetic innervation so that the arteries themselves remain narrow. Under condition of central sexual stimulation (see above), the parasympathetic division of the autonomic nervous system triggers nitric oxide (NO) release from nerves and endothelium which induces production of cyclic guanosine monophosphate (cGMP). cGMP is a key mechanism in the relaxation of the smooth muscles. When the smooth muscles relax, the corpus cavernosa fills with blood, while at the same time the veins are constricted, limiting the outflow of blood. Factors that interfere with this process interfere with the peripheral sexual response. For example, if a central sexual response is dampened (see section “[Sexual Desire Disorders](#)”) parasympathetic activation will not be triggered, or will be triggered insufficiently, so that the entire process is not set in action. Psychological factors that induce sympathetic activation (e.g., anxiety) can also decrease the genital response through heightened or persistent sympathetic activation that outweighs the parasympathetic innervation. Also, diseases or substances affecting arterial functioning like diabetes mellitus and smoking can negatively affect genital arousal. Moreover, the hormonal milieu in men and women are also important for a functional genital response. In men and women,

testosterone is needed for the production of NO, and estrogens thicken and moisten the vaginal epithelium in women. Decreasing estrogen levels, for example, during and following the menopausal transition, or decreasing androgen levels in aging men and women can result in impaired genital arousal (Dennerstein et al. 2002; Araujo and Wittert 2011).

Arousal disorders can be often be treated like desire disorders because of the common etiology it shares with desire disorders. When arousal problems stem from a noncentral cause, peripherally acting drugs may also be beneficial. ED is often successfully treated with phosphodiesterase 5 (PDE5) inhibitors (e.g., sildenafil, vardenafil, tadalafil). PDE5 breaks down cGMP, so by inhibiting this inhibitory factor by the use of a PDE5 inhibitor, genital engorgement is facilitated. PDE5 inhibitors are effective in some women with FSAD, but it is not approved for this indication and thus remains to be prescribed off-label. Hormone replacement therapy (e.g., testosterone supplementation or estrogen replacement therapy) can also help with arousal problems in people with lower levels of the respective hormone.

Conclusion

Sexual desire and arousal disorders have a heterogeneous etiology, and much is still unclear. Truly effective psychotherapeutic and pharmacotherapeutic options are still lacking but very much needed as these disorders can have a detrimental impact on quality of life.

Cross-References

- [Evolution of Desire, The](#)
- [Four-Stage Model of the Sexual Response](#)
- [Human Sexuality](#)
- [Penile-Vaginal Sex](#)
- [Sexual and Reproductive Development](#)
- [Sexual Arousal](#)
- [Sexual Behavior](#)
- [Sexual Intercourse](#)

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Desire to Be Included Among Desirable Women

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Synonyms

Appearance enhancement effort; Attractiveness effort; Epigamic display; Intersexual selection

Definition

Women's desire to be considered among “desirable” women involves motivation and effort toward displaying attributes that enhance their desirability as either a mating or social partner.

Introduction

Men, more than women, prefer physically attractive and sexually faithful mates. Women and girls who are high on these desired traits might also be more popular within their same-sex peer networks. Accordingly, women, more than men, are

motivated to display and accentuate these mate-value and peer-valued characteristics, which are, in part, signals of reproductively and socially relevant information. Social-cognitive mechanisms such as social comparison, as well as emotions such as envy, appear to underlie some behaviors associated with women's desire to be considered among desirable women.

Across diverse human cultures, men's and women's mate preferences have been shown to diverge in reproductively important ways. One of the most consistent sex differences is men's greater expressed preference for physically attractive partners. For instance, Buss (1989) found that in each of 37 cultures studied, men more than women desired partners who were youthful and physically attractive. Moreover, men are remarkably consistent in the specific features that they find attractive in a mate. These features typically include lustrous hair, clear skin, full breasts, feminine and symmetrical facial features, and a low waist-to-hip ratio (i.e., an hourglass figure) (Buss 1989; see Arnocky et al. 2014 for review). A growing body of evidence suggests that such physical features may have evolved, in part, as relatively honest cues to reproductively important aspects of women's phenotypic condition, including youth (i.e., being of reproductive age), underlying health, and/or fertility (Arnocky et al. 2014). Ancestral men who happened to be attracted to these features would therefore have out-reproduced those who did not share their preferences (Arnocky et al. 2014). To the extent that mate preferences for condition-linked physical features are heritable, such preferences would proliferate and become prevalent in the population.

Another mate preference along which men and women sometimes differ is the desire for fidelity in a long-term partner. In the Buss (1989) study, 23 of 37 cultures expressed a sex difference whereby men more than women preferred a chaste partner. As with physical attractiveness, a mating partner's chastity also bears more heavily on men's, relative to women's, reproductive success. Due to concealed ovulation and the internal fertilization process of human reproduction, men can

never be certain of their paternity. Indeed, genetic cuckoldry continues in contemporary human society, although estimates of its frequency vary considerably. Accordingly, ancestral men who valued fidelity in a partner may have been less susceptible to cuckoldry (i.e., unwittingly investing parental effort toward offspring that are not genetically one's own) and thus may have been more reproductively successful relative to men who did not value chastity.

Given men's preferences for youthful, attractive, and faithful partners, it is intuitive that intersexual selection (i.e., mate choice) would favor women who best display these features. For example, physically attractive women are more likely to be asked out on dates (Walster et al. 1966), are more likely to be approached by men at social gatherings such as parties (Prestia et al. 2002), are more successful at poaching mates (i.e., stealing a partner from an already established mating relationship) (Sunderani et al. 2013), become sexually active earlier in life (i.e., have a longer period of reproductive potential), and have more long-term dating partners compared to less physically attractive women (Rhodes et al. 2005). Not surprisingly, physically attractive women are thus able to express greater choosiness for who they mate with. Similarly, women who are perceived as chaste (i.e., easy to mate with within the relationship, but hard for other men to mate with) are more desirable as dating partners than either uniformly hard or uniformly easy-to-mate-with women (Walster et al. 1973). The mating advantage afforded to women who best typify men's mate preferences serves as a powerful force in directing women's social-cognitive functioning, emotions, and behavioral efforts toward being considered desirable as a mate.

Evidence of Women's Desire to be Physically Attractive

Whereas features of physical attractiveness may have evolved as honest cues to mate value, there exists abundant historical and cross-cultural

evidence that women have long attempted to augment their physical appearances in ways that coincide with men's mate preferences. To a degree, women can influence the honesty of the cues associated with phenotypic features and in doing so benefit their mating success. When women are asked how they attract mates (i.e., successful intersexual selection), they often report attempting to explicitly enhance their physical appearances, such as through wearing makeup, wearing stylish clothes, keeping clean and well-groomed, as well as using skin-tanning products and applying nail polish (see Arnocky and Vaillancourt 2014 for review). Western women spend nearly ten times more money than men on products meant to enhance their physical appearances and are twice as likely to work on their appearance for more than 1 h per day (see Arnocky and Vaillancourt 2014). Three lines of evidence stemming from (1) explicit surveying and manipulation of mating motives and (2) ovulatory shifts in fertility, and (3) effects of differential mate availability, converge to suggest that women's use of appearance-enhancement behaviors are broadly linked to their mating motives.

First, mating motives have been shown to predict a range of appearance-enhancement behaviors among women. Hill et al. (2012) showed that although spending on most products decreases during an economic recession (or when experimentally primed with recession cues), women nevertheless increase spending on appearance-enhancing products (termed "the lipstick effect"). Moreover, the researchers found that women's reported preference for attracting mates with resources mediated this effect. Further experimental evidence suggests that women's appearance-enhancement motives are often linked to a desire to be viewed as attractive to members of the opposite sex. For instance, Hill and Durante (2011) found that single women who were primed with mating motives (versus control) were more interested in skin tanning and taking risky diet pills, highlighting the disconcerting fact that women sometimes engage in appearance-enhancement efforts that are risky to their health as a function of their mating motives. For example, eating disorders are significantly more

common among those who are most likely involved in intersexual selection and intrasexual competition. Heterosexual women in their prime reproductive years, compared to men, older women who are outside of reproductive age, and homosexual women, are more likely to exhibit eating disorder symptoms (e.g., Abed et al. 2012). Eating disorder behavior has also recently been shown to be predicted by a fast life history (characterized by greater reproductive and mating effort) among college-age women (Abed et al. 2012). It is important to note that physical appearance enhancement is not only a function of women's initial mate-attraction efforts but is also reported by women, more than men, as an effective mate-retention tactic (see Arnocky and Vaillancourt 2014 for review).

Second, shifts in appearance-related efforts occur throughout the menstrual cycle. When women are in the fertile phase of the cycle, they are more likely to wear more revealing clothing; an effect that is enhanced among those women higher in sociosexuality (Durante et al. 2008). Women also report an increase in self-perceived attractiveness and feelings of sexiness during ovulation (see Durante et al. 2008 for review). During ovulation, women have been shown to increase their behaviors associated with intersexual selection (i.e., outcompeting rivals for the favor of desired males). Haselton and colleagues (2007) showed that partnered women who were photographed at high and low fertility points in the menstrual cycle were rated as "trying to look more attractive" during high fertility phases, and the closer women were to ovulation when photographed, the more frequently their fertile photograph was classified as attempting to enhance their appearance. This hormonally regulated effect appears to be driven by a desire to outdo attractive rival women. For instance, women have been shown to choose products that enhance their physical appearance (e.g., "sexy" rather than more conservative clothing) more frequently during ovulation. Importantly, this ovulatory shift in behavior occurs when women view photos of attractive intrasexual rivals, but not after viewing unattractive rivals, attractive, or unattractive men (Durante et al. 2011).

Third, where men are scarce, women have been found to wear more revealing clothing, relative to where men are abundant (Barber 1999), suggesting that increased ecological pressure on securing a mate may increase women's efforts in the realm of intersexual selection.

Social-Cognitive and Emotional Influences on Women's Appearance Enhancement

Competing for mates depends not only on individuals' own attributes but also on the attributes of intrasexual competitors (Arnocky et al. 2016). From this perspective, women who are best able to compare their mate-value characteristics to those of their nearest rivals would be better able to determine the requisite level of investment in ornamentation necessary to outcompete rivals for desired mating opportunities, without over-investing. Moreover, unfavorable social comparisons on dimensions of physical attractiveness may result in an emotional response of envy (i.e., the unpleasant experience of hostility, inferiority, and resentment toward those who possess something desirable), which may in turn motivate appropriate compensatory behavior(s) aimed at augmenting that characteristic. To test this hypothesis, Arnocky et al. (2016) randomly assigned women to one of two conditions: an appearance-based social comparison condition, where women viewed magazine ads containing female models and were asked to compare their appearance to the target, and a control condition where women viewed different magazine ads from the same companies, but which did not feature a female model prominently in the ad. Following the priming condition, women reported on their state feelings of envy, followed by measures assessing a host of appearance-enhancement motives. Their results indicated that women who were primed to make physical appearance comparisons to models expressed more envy compared to controls, and the envy in turn predicted more favorable attitudes toward having cosmetic surgery, more

intended use of facial cosmetics, and more willingness to use a risky diet pill. These findings suggest that women's mating-relevant ornamentation efforts are sensitive to environmental inputs in terms of the relative quality of their same-sex conspecifics, as well as the emotional outcomes of such comparisons.

Evidence of Women's Desire to be Perceived as Chaste

When men invest in offspring, women behave in ways that will ensure or reinforce greater paternity confidence. Following births, hospital room videotapes indicate that mothers (and other relatives) allege paternal resemblance of the newborn much more often than maternal resemblance, supporting the hypothesis that women behave in ways to promote paternity confidence (i.e., enforce their chastity) to male partners. Women also generally report having fewer sex partners than men, and confusion has existed in the literature as to whether this is a function of male overreporting, female underreporting, or perhaps both. This is complicated by the fact that as many as 60 % of undergraduate men and women report having acted deceptively with their representation of their number of previous sexual partners (Horan 2015). One recent study sought to address this differential disclosure by having half of the sample's participants complete a questionnaire on sexual and social behaviors while connected to a lie detector (which was, unbeknown to the participants, nonfunctional). Results showed a significant gender by lie detector interaction, whereby women (more than men) were more likely to report not having engaged in sexual intercourse when disconnected from a lie detector compared to women who were connected to the lie detector. Women in the lie detector condition reported having more lifetime sex partners than women in the no lie detector condition. Importantly, self-reporting of other types of male or female-typical behaviors did not vary as a function of being attached to a lie detector (Fisher 2013). This suggests that women may underestimate when disclosing information about their sexuality, perhaps

as a mode of preserving a reputation of sexual restrictedness.

Taken together, evidence suggests that women attempt to augment their physical appearances and sexual reputations in a manner that conforms to the mate-preferences of men. Yet beyond intersexual selection, individual differences in these characteristics can also influence desirability within the broader social network, with mating-relevant implications.

Attractiveness, Sexual Behavior, and Social Status and Affiliation

Both physical attractiveness and sexual reputation have been linked to girls' and women's social statuses, friendships, and affiliations. Ancestrally, social acceptance would have played a vital role in acquiring food, shelter, protection, and mating opportunities (Brown et al. 2009). Moreover, females' relative to male's same-sex affiliations are characterized by greater emotional and informational support (Hall 2011). Women report that their same-sex friends provide mating advice and assist in mate-acquisition (Bleske and Buss 2000). Brown et al. (2009) argued that in achieving social acceptance, individuals are able thus to focus more of their attention and efforts toward mating. Across two studies, the authors showed that cues to social acceptance (e.g., being included in a ball-tossing game) increased participants' interest in mating with targets whose faces were presented on a screen.

The influence of physical attractiveness upon the lives of women begins at an early age, including having effects on social affiliation. For instance, Krantz (1987) found that for girls, but not boys, those rated as being most physically attractive prior to beginning kindergarten were more likely to be considered popular in school. In adolescence, longitudinal research has shown that physical attractiveness correlates with peer-rated popularity within the social group (Arnocky and Vaillancourt 2012). Even socially rejected girls are less likely to be overtly victimized by their peers if they happen to be physically attractive (Knack et al. 2012). Among young-adult

college students, attractive individuals are perceived to have more socially desirable personalities. Attractive women may be ascribed with higher social status and exert more social influence compared to less attractive women (see Arnocky et al. 2014). Moreover, attractive individuals (both men and women) are more likely to receive social help. Benson et al. (1976) left a completed graduate school application form, a photograph of the applicant, and an addressed, stamped envelope in a telephone booth. The picture varied by attractiveness (high and low) and ethnicity (black and white). The applicant's physical attractiveness predicted whether or not the application was delivered. However, some research suggests that the importance of physical attractiveness to friendships and overall social acceptance may be primarily relevant in cultures where individual choice in the establishment and maintenance of social relations is the norm (Anderson et al. 2008). Nevertheless, there is some research to suggest that females explicitly understand the importance of physical attractiveness to their social status: When asked to describe popularity, girls more than boys identified being attractive as an important component of being popular (Closson 2009).

Sexual behavior has also been linked to girls' popularity and friendships. Considering females' significant obligatory parental investment, female sexuality is a scarcer resource than males'. Baumeister and Vohs (2004) have argued that women would thus benefit from regulating the value of their sexuality by artificially restricting the supply via placing "pressure on each other to exercise sexual restraint" (Baumeister and Vohs 2004, p. 344). Such pressure may be exerted via social affiliation, whereby less sexually restricted females may become socially isolated and/or chastised by other females. Because of this, it has been argued that adolescent girls experience and express firm social norms that sexual behavior should not occur outside of dating relations (see Arnocky and Vaillancourt 2012 for review). Prinstein et al. (2003) found that adolescent sexual activity correlated positively with reputation-based popularity, but not likeability among peers. Moreover, increasing number of sex

partners correlated with lower popularity. Kreager and Staff (2009) found that girls with many sex partners reported having fewer friends – a relationship that did not exist among male participants. Moreover, women who are low in sociosexuality (i.e., have a more monogamous orientation toward sexual activity) are more sensitive to the popularity impacts of various dating risk situations (Rinehart 2012). Recently, Vrangalova et al. (2013) surveyed 750 undergraduates about their sexual behaviors and attitudes. Then, participants read a short description of a hypothetical person of the same sex who had either 2 or 20 past sex partners. Participants then rated this hypothetical persona as a potential friend. Results showed that women, regardless of their own sexual histories, overwhelmingly preferred the potential friend with fewer past sex partners. Given the adaptive significance of social acceptance, women who exhibit characteristics that are associated with receiving social acceptance, friendship, and status are likely advantaged in a variety of reproductively relevant domains.

Conclusion

Over human evolutionary history, the establishment and maintenance of long-standing peer and mating relationships would have been impactful upon women's reproductive success. Yet not all women are desired equally for these important relationships – and some women exhibit morphological and behavioral characteristics that improve their success in domains of interpersonal desirability. In considering two such characteristics, physical attractiveness and sexual reputation, both of which impact interpersonal attraction and interaction, research suggests that women who typify these and other important mate-value and/or peer-valued characteristics are often more desirable as romantic partners and same-sex friends. Unsurprisingly, women, more than men, express psychological and behavioral tendencies toward augmenting and displaying these characteristics, which may benefit their success in intersexual sexual selection and social relations.

Cross-References

- [Body Attractiveness](#)
- [Eating Disorders](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Intrasexual Competition Between Females](#)
- [Intrasexual Rivalry among Women](#)
- [Men's Mate Preferences](#)
- [Peer Competition and Cooperation](#)
- [Reproductive Potential](#)
- [Sociosexuality](#)

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Desires in Mating

► Mate Preferences

Despotism

► Primate Dominance Hierarchies

Destitute

► Redistribution Preferences and Low Socioeconomic Status

Detecting Infidelity

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Infidelity refers to a violation of sexual or emotional exclusivity within a pair-bond. Emotional infidelity is when a person allocates their time, love, and attention to someone other than their significant other, whereas sexual infidelity is when a person engages in sexual activity with someone other than their significant other (Shackelford and Buss 1997).

Infidelity is a universal behavior, occurring in all known cultures and times. In the United States, marital infidelity estimates vary from 26% to 70% for women and 33% to 75% for men (reviewed in Shackelford and Buss 1997). Though infidelity may have reproductive benefits (e.g., increase men's reproductive success by increasing the number of mateships), infidelity is associated with various negative outcomes. Women's sexual infidelity is costly to men due to cuckoldry (i.e., raising non-genetically related offspring) or possible loss of a mating partner to a rival, whereas men's emotional infidelity is costly to women due

to loss of parental investment (i.e., time and resources that are redirected to a rival). Infidelity and jealousy are also implicated in many cases of intimate partner violence. Due to the steep costs of infidelity, the ability to detect such acts or risks of such acts may have evolved.

Both men and women appear to be sensitive to cues of infidelity. Men more often recall cues signaling their mates' sexual infidelity whereas women more often recall cues regarding emotional infidelity (Schützwohl and Koch 2004). Shackelford and Buss (1997) identified 170 cues to emotional and sexual infidelity that loaded onto 14 factors. These factors were: (1) angry, critical, argumentative of partner; (2) sexual infidelity revealed; (3) changes in normal routine and sexual behavior with partner; (4) apathetic toward partner; (5) increased sexual interest/exaggerated affection toward partner; (6) sexual disinterest/boredom with partner; (7) relationship dissatisfaction; (8) passive rejection of partner; (9) reluctance to discuss a certain person; (10) reluctance to spend time with partner; (11) increased reference to and time spent with another person; (12) acting guilty, anxious toward partner; (13) physical signs of sexual infidelity; (14) emotional disengagement from partner.

Shackelford and Buss identified some interesting patterns with these cues to infidelity. Participants rated some of these factors as more diagnostic of sexual infidelity, such as sexual boredom, whereas other factors were rated as more diagnostic of emotional infidelity, such as relationship dissatisfaction. These cues are more likely to be considered a cue to infidelity when applying that cue to members of the opposite sex, suggesting the presence of a cognitive bias to perceive acts as signs of infidelity when it is performed by members of the opposite sex.

These factors have been used in other studies to test hypotheses about the effects of infidelity on intimate partner conflict. For example, Camilleri and Quinsey (2009) found that these cues were associated with self-reported propensity for intimate partner sexual coercion. More recent work has found that women are generally more sensitive to partner infidelity, are faster and more accurate in

detecting infidelity, and focus their attention on the rival, whereas men focus more on the intent of their partner (Ein-Dor et al. 2015). Other researchers are addressing how people process cues to infidelity (see Schützwohl 2004, 2005).

Cross-References

- Cues to Infidelity
- Female Infidelity
- Frequency of Infidelity
- Infidelity Risk
- Jealousy and Infidelity
- Male Sexual Jealousy to deter Partner Infidelity
- Men's Suspicions of Partner Infidelity and Women's Defection
- Perceptions of Infidelity
- Perceptions of Infidelity Cues
- Prevention of Infidelity
- Sexual Infidelity Versus Emotional Infidelity

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Detecting Romantic Cheating

- Perceptions of Infidelity Cues

Detestation

- Disgust

Developing Infant

- Fetus Development

Development

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Synonyms

Growth; Individual evolution; Maturation; Ontogeny

Definition

Series of self-constructive and transformative processes that lead to new, eventually more complex states of organismal organization.

Introduction

In the first pages of *The Strategy of the Genes*, Conrad H. Waddington wrote that “the main respect in which the biological picture is more complex than the physical one, is the way in which time is involved in it” (Waddington 1957,

p. 5). While an image of continuous flux is congenial with both ancient and present-day conceptions of the physical, the way in which change, the most distinctive seal of time, enters into the picture when one approaches the organic certainly underlines the breach which exists between the two realms. According to Waddington, this difference becomes even more noticeable when one considers that three different time-scales appear to be relevant when considering the latter realm. At one extreme, one finds (1) the minute, the daily time-scale of metabolism and function; at the other extreme, (2) the geological time-scale of evolution; and in the middle, (3) the individual-life encompassed time-scale of development (Waddington 1957, pp. 5–8). This intermediate developmental time-scale raises some controversial issues which are specific to the natural sciences (Robert 2004, Chap. 1), including their psychological ramifications (Michel and Moore 1995). These questions have mostly to do with the boundaries of the developmental perspective with the other two time-scales, but also with its scope within the whole life-cycle of an organism and with the delimitation of the entity, to which particular development processes must be properly ascribed (Minelli and Pradeu 2014).

Development: The main puzzles

For a long time, probably extending from Aristotle (384–322 BC) to the late nineteenth century, the study of development was basically equivalent to the study of the embryo (Amundson 2005). The entailment thus existed that development, as a matter of scientific interest, reached a somehow meaningful upper limit at the moment of birth. From that point on, the life of an organism entered the realm of physiological research. Such a viewpoint was clearly too closely centered around complex animals and delimited by the certainly relevant, but, ultimately, arbitrary milestone of their life-cycle. The alternative, which gained rapid acceptance (Burian and Thieffry 2000), widened the research scope of developmental studies to the point where organisms become endowed with their own capacity for generating new,

descendant organisms. Such an alternative was not, however, without shortcomings. To start with, it appears to equate “fecundity” and “maturity,” which is by no means a straightforward equation at all. Moreover, it appears to entail an all-or-nothing view of development, according to which the different aspects of the entire mosaic-like developmental process (Schlosser and Wagner 2004) point to the same, synchronous point of termination, where development comes to an end and the adult (reproductive) life of the organism starts.

Irrespective of the point of termination issue, traditional views of development like the ones thus far commented on shared some other problematic stances. For example, they all took for granted that there is a certain “something” that develops but never clarified sufficiently the ontic issue of what exactly that something is. The very meaning of “development” (lit. “un-wrap,” or “un-fold”) appears to entail a preexistent entity, which is modified throughout, rather than brought into existence by, a process of transformations. In any event, the scientific concept of “development” has historically swung between these extremes, routinely referred to as “preformationism” and “epigenesis” (Maienschein 2017) and, indeed, the debate is far from having been satisfactorily resolved.

Historically, research into developmental processes have mostly been conducted from a mechanism-oriented philosophical perspective (Love 2015), nowadays updated as a molecular-computational paradigm (Davidson 1990). This paradigm tends to privilege the internal milieu of the organism as a self-sufficient receptacle of constructive materials and guidelines for development, correspondingly downgrading the environmental contribution to a merely enabling role, which may certainly lead to disruptive effects if not present, but which appears to add nothing in terms of the specificity of the pathways or the intermediary and steady forms. In most cases, however, no clear criteria are offered supporting the ensuing hierarchy (Oyama 2000). Moreover, there exist (nonmarginal) cases in which the environment provides crucial determinants to nontrivial traits (e.g., sex determination

by temperature in fishes, amphibians, and reptiles; Gilbert and Epel 2015, pp. 48–50), or in which environmental and organism-internal products may interchangeably contribute to the attainment of identical phenotypic outcomes (e.g., wing dimorphism in beetles either by a Mendelian-single locus or temperature and food supply; West-Eberhard 2003, pp. 119–121).

Considering these and other similarly powerful arguments, issues of causality, agency, and ontology regarding development have undergone dramatic changes in recent decades. The following, mutually intercrossing points are aimed at offering a more nuanced account of these problematic issues and a necessarily schematic but hopefully informative enough image of an emergent and increasingly supported concept of development in the life sciences, in general, and in psychology, in particular.

1. Temporal Delimitation

Maturity, or adulthood, is customarily thought of as the segment of a life cycle in which a more or less steady form is attained by an organism. According to one interpretation of this viewpoint, maturity is reached when the different organ systems that compose a particular organism have all attained such a plateau phase, relative to prior stages. According to another, alternative interpretation, parallel, but different, developmental cycles are to be considered regarding a single organism, each with a different point of termination. Both interpretations are, however, somewhat problematic, in that steadiness is an extremely relative category. No single organic system ever attains anything like absolute steadiness. While alive, organisms are ever-changing entities, despite differences in the rate of observed change at different moments of their life cycles. Even maturity is a rather relative term, if only because what counts as a juvenile structure in one organism, may count as a mature structure in another similar one (e.g., the external gills and caudal fin of salamander larvae are features typical of mature axolotls; Alberch and Alberch 1981).

The issue appears to be one that cannot be solved but positing some kind of “clock model,”

like the one famously suggested by Stephen J. Gould (1977, pp. 246–262). Such models crucially rely on standardizing a certain stage as a reference point, which may prove an excellent strategy for comparative and evolutionary concerns, but merely an artifact from the point of view of development itself. These kinds of considerations have led some to conclude that even if one decides to keep alive the “segment” metaphor, development must be conceived of as “open-ended” (Minelli 2011). According to a more extreme interpretation, the concept of “development” and the concept of “life” ultimately conflate into one, without much (if any) explanatory loss (Minelli 2003). Conrad Waddington was clearly aware of all of this and he concluded that “to speak of the adult condition as a steady state is to some extent an oversimplification, since developmental change continues at a slow rate throughout adult life, leading eventually to senescence” (Waddington 1957, p. 33).

As for the particular case of psychology, a strong bias has existed towards a “point of termination” view on the development of psychological functions, which kept apart development (or ontogeny) proper, responsible for a basic set of natural cognitive functions, and later processes of cultural development that grow on top of the former (Vygotsky 1978). According to Jean Piaget, for example, cognitive development proper climaxes with the “formal operational stage,” only followed afterwards by lifelong knowledge accumulation or “intellectual development” (Piaget 1962). Thus, both the Vygotskian and the Piagetian traditions appear to agree in endorsing a view of psychological development as a natural process that both precedes and guarantees the acquisition of the cognitive contributions of society and culture by qualitatively different means. Within these classical perspectives, culture is somehow envisioned as an outer, late and increasingly dominant layer of cognitive development, giving grounds to a view where the biology/culture divide appears to assume a limiting role similar to the juvenile/adult distinction.

The biology/culture divide, however, is one viewed with suspicion by current psychobiological approaches (Michel and Moore 1995). It is

ultimately one particular aspect of the strong organism/environment divide, which is also increasingly being contested as supporting a bona fide biological boundary (Gilbert and Epel 2015; Oyama 2000; Sultan 2015). Organic systems incorporate structures that protect them from aggressions or help them to acquire a certain advantageous form, but the “limit” category does not appear to be plausible in biological terms. Organisms are more porous than that. The same applies when one moves to the life-cycle perspective, including the mental life and its specificities. Thus, Minelli’s tenet regarding the “open-ended” character of development appear to be a reasonable conclusion (Balari and Lorenzo 2015). The position entails the conflation of the developmental and the physiological perspectives, including developmental psychology and what some authors have named “cognitive physiology” (Anderson and Lightfoot 2002).

2. Spatial Delimitation

In parallel to the conception that a well-delimited segment of life is accomplished when an organism reaches adulthood, one strongly entrenched position conceives such a segment as the dynamic manifestation of constructive and directive resources internal to the organism. Such an internalist conception does not deny, of course, that the environment makes crucial contributions that help or strengthen development (nutrients, light, gravity, etc.), but it considers them of secondary importance, in that they are not seen as determinants of the attained forms. The idea usually adopts the preformationist stance that everything that is of primary importance for the timely accomplishment of adult designs is a priori given in the genome, as a plan or a program that is simply waiting to be read by extra-genomic intermediaries, both organism-internal and environmental (Mayr 1982). Alternatively, internalism adopts an epigeneticist standpoint, namely one that contends that development is not exactly preformed or planned, but unfolds as the organic conditions are created along the way. Nevertheless, each new stage is determined by the preceding one, so in the end the adult form is

determined by the materials already given at the very start of the process (see Gottlieb 1992, for distinctions within the epigeneticist camp). Both the preformationist approach and the deterministic-epigenetic one share a strong bias towards viewing the organism as the receptacle of the determinants of forms and, as such, as an entity to be set apart from the environment.

This kind of strong, dualistic divide between the inner and the outer (organism/environment, biology/culture, nature/nurture) has notably receded in recent decades (Moore 2001). On the one hand, there seem to be no strong reasons for ascribing to the genome a more central causal profile than to other concurring factors (extra-genomic imprints, RNA sequences, hormones, already attained tissular geometries, etc.), in the absence of which genes are “among the most impotent and useless material imaginable” (West-Eberhard 2003, p. 93). On the other hand, factors of external provenance (nutrients, symbionts, etc.) and dynamics held through the apparently isolating membranes and sensorial systems of an organism (the impact of temperature, of the size of the population, etc.), prove to be crucial for the attainment of forms to no lesser an extent than other factors and dynamics, with the result that ranking the former as secondary relatively to the latter loses any clear motivation (Oyama 2000).

In agreement with the preceding observations, a view on development has emerged based on a plethora of heterogeneous, partially overlapping, complementary or redundant factors, capable of generating, in the absence of any kind of central controller, the material conditions for the timely achievement of successively new states of organismal organization (Griffiths and Hochman 2015). An entailment of this position is that if an underlying developmental system is an inherent property of the organism as an individual entity, and if developmental systems spread out the environment, then the organism itself is not as clearly delimited by, for example, its skin as commonly thought. An interesting derivation of the resulting view leads us back to the preceding point (1), for it is well-known that factors crucial for the successful accomplishment of a certain developmental pathway are of maternal provenance, in the form

of preformed membranous structures, olfactory signals, bacteria, etc. Thus, the entailment also appears to follow that a clear-cut delimitation between developmentally well-defined identities in the temporal axis is not as straightforward as normally assumed (Minelli 2003). In this sense, inasmuch as successive life-cycles appear to overlap, rather than showing clear-cut limits, the boundary between the time-scales of ontogeny and phylogeny appears to become an extremely fuzzy one.

The impact of the previous ideas on the particular area of psychological development is especially clear. Going back to the biology/culture issue, sociocultural stimuli are not just the subject matter of a merely cumulative process of acquisition, as they also act as factors that actively contribute to the growth of neural tissue and structures. The mind of an organism embedded within a more or less rich cultural environment thus becomes a sort of developmental hybrid (Griesemer 2014), an idea that applies equally to humans and nonhuman species, as behavioral patterns transmitted by traditional inheritance are much more widespread than previously thought (Avital and Jablonka 2008).

3. Agency and Causality

The emergent views on development thus far commented on also have an impact on complex metaphysical issues, such as those regarding agency and causality. On the one hand, the kind of pluralism and causal democracy that is increasingly being privileged introduces a rupture with a long-held tradition, according to which development is the quintessence of a directive, goal-oriented or teleological process. However, the strong factorization and the lack of a central controlling instance that are favored by the “developmental system” concept run against such an entrenched teleological tradition. Alternatively, a view is favored according to which developmental processes are contingent, yet reliable and predictable (Gottlieb 2007). Development depends upon many different factors of diverse provenance and, correspondingly, exposed to many potentially perturbing fronts. The directedness of

development, however, is more in the eye of the beholder than an inherent quality of the processes. In other words (with obvious Kantian echoes), development works “as if” it were a goal-oriented process, but it is not.

What will prove to be ultimately responsible for such intuition is one of the central explananda for developmental studies. Current theoretical models increasingly rely on certain organizational properties of systems of development as the key to satisfactorily answering the question. On the one hand, the evolutionary process may be deemed responsible for recruiting factors and creating the most efficacious closeness relations between them; on the other hand, by recruiting mutually reinforcing and partially overlapping and redundant factors, a quality customarily referred to as “robustness,” systems may protect themselves against common perturbations or unexpected failures (Bateson and Gluckman 2011). Such an interplay of historical and systemic properties appears to be the most promissory arena where the mysteries of development can be expected to receive new and more satisfactory answers.

Conclusion

Development is at the center of any possible understanding of what being a piece of living matter means. It is a crossroads of sorts of concepts like organism, individuality, design, environment, plasticity, variation, evolution, purposiveness, robustness, and so on, which are to be currently understood as the key component pieces of the conceptual puzzle of life. While no consensual perspective exists regarding all these issues yet, an emerging and particularly promising one envisions them as leading to a view of development as a nondeterministic, yet robust kind of process, which in the absence of any kind of prefixed goal and central controlling unit replicates the properties of teleological, orchestrated constructive processes, similar to those leading to man-made technological contrivances.

Development is, in all likelihood, life itself and indistinguishable from evolution.

Cross-References

- Cultural Transmission
- Developmental Milestones
- Duration of Childhood
- Ecological Factors and Rape
- Ecological Niche, The
- Embryo
- Environmental Influences
- Gut Microbiome
- Human Nature and Biocultural Evolution
- Life Expectancy and Reproduction
- Life History Strategies
- Nature Versus Nurture
- Nurture Assumption, The
- Observed Mating Behavior and Women's Long-Term Mating
- Ontogenetic Adaptations
- Puberty in Boys
- Reproduction
- Sexual and Reproductive Development
- Social Development
- Social Learning
- Stages of Development

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Development of Adaptations

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Definition

The concept of *adaptation* is central to evolutionary psychology. Three types of developmental adaptations are described: *ontogenetic adaptations*, *deferred adaptations*, and *conditional adaptations*. Adaptations develop and are based on the highly plastic nature of infants' and children's behavior/cognition/brains. The concept of *evolved probabilistic cognitive mechanisms* is introduced, defined as information-processing mechanisms evolved to solve recurrent problems faced by ancestral populations that are expressed in a probabilistic fashion in each individual in a generation, based on the continuous and bidirectional interaction over time at all levels of organization, from the genetic through the cultural. Early perceptual/cognitive/affective biases result in behavior that, when occurring in a species-typical environment, produce adaptive changes in behavior and cognition, yielding stable and adaptive outcomes. Examples from three domains, the development of face processing in infancy, prepared fears, and tool use, are

provided illustrating the development of adaptations via evolved probabilistic cognitive mechanisms.

Introduction

Central to Darwin's idea of evolution by natural selection is the concept of *adaptation*, traits that promote survival and reproductive success. Needless to say, the concept of adaptation is also central to evolutionary psychology. Following Buss and his colleagues (1998), "An adaptation may be defined as an inherited and reliably developing characteristic that came into existence as a feature of a species through natural selection because it helped to directly or indirectly facilitate reproduction during the period of its evolution" (Buss et al. 1998, p. 535). Although mainstream evolutionary psychologists quite understandably focus on adaptations during adulthood – this is where the mating, competition for social dominance, and child-rearing take place, after all – adaptations also characterize childhood. In fact, until relatively recent times, childhood mortality was about 50%, making childhood the "crucible for natural selection" and thus likely the source of many adaptations.

In addition to describing different types of developmental adaptations in this entry, the developmental origins of adaptations will also be examined. Adaptations may be inherited, as claimed by Buss and his colleagues in the aforementioned quote, but they do not arise fully formed. Rather, from a developmental perspective, adaptations develop in a species-typical way when the organism experiences a species-typical environment (Bjorklund 2015). Infants and young children are biased by natural selection to process some information differently from other information, and such biases contribute to the development of adaptive species-typical behavior when children grow up in species-typical environments. Also to be discussed is how the plasticity of children's brains and cognition permits a range of potentially adaptive outcomes, dependent on the specific environments that children experience.

Adaptations of Infancy and Childhood

Not all adaptations are created equal. Evolutionary developmental psychologists have identified three types of adaptations associated with infancy, childhood, and adolescence: ontogenetic, deferred, and conditional.

Ontogenetic Adaptations

Ontogenetic adaptations serve an adaptive function at a specific time in development and disappear when they are no longer functional (Bjorklund 1997). They function essentially to keep the organism alive or to help it adjust to its current environment rather than preparing it for life in a future environment. Many aspects of prenatal functioning are good examples of ontogenetic adaptations. For instance, the yolk sac of birds and the placenta and umbilical cord of mammals serve obvious adaptive functions when the animal is in the egg or the uterus but are discarded after birth, being replaced by other adaptive physiological functions for respiration and nutrition. Newborns' tendency to copy facial expressions of adults (neonatal imitation, Meltzoff and Moore 1977) has been interpreted by some, not as a "true" form of social learning, but as reflexive-like behavior that serves to promote social interaction between an infant and its mother during a time when the infant cannot control its own social behavior. Support for this position comes from evidence that copying a models' facial expressions decreases to chance levels by about 2 months of age and that infants who displayed higher levels neonatal imitation show better social interactions with their mothers 3 months later (see Bjorklund 1997).

Ontogenetic adaptations are not limited to infancy but can be seen in older children as well. For example, preschool-age children consistently overestimate their physical, social, and cognitive abilities, thinking that they are smarter, stronger, and more popular than they really are, and such overestimation has some positive consequences. For example, in one study, preschool children who overestimated their imitative abilities had higher verbal IQ scores than more accurate children (Bjorklund et al. 1993), and preschool and

early school-age children who overestimated how many items they had remembered on early memory trials had higher levels of memory and strategy performance on later trials than more accurate children (Shin et al. 2007). Children's overly optimistic opinions of their own abilities presumably enhance their self-efficacy, causing them to persist on tasks and in situations where a child with a more accurate assessment of his or her less-than-stellar functioning might quit. (See the entry on ► ["Ontogenetic Adaptations,"](#) in this volume.)

Deferred Adaptations

In contrast to ontogenetic adaptations are deferred adaptations, which serve to prepare infants and children for life as an adult or for the acquisition of important skills that will be useful throughout life (Hernández Blasi and Bjorklund 2003). Sex differences are clear candidates for deferred adaptations, with boys and girls having different biases that direct them to different activities that will prepare them for life as an adult (or would have prepared them for adult life in the environment of evolutionary adaptedness). For example, in traditional environments, children learn much about how to function as an adult through play with age-mates. Play itself can be viewed as a deferred adaptation, for both boys and girls. However, although there are many similarities between the play of boys and girls, there are also differences. For example, boys engage in more vigorous rough-and-tumble play than girls, which some scholars have proposed prepared ancestral boys for adult fighting. Both boys and girls engage in fantasy play during childhood. Such play involves counterfactual thinking, and Nielsen (2012) proposed that fantasy play, along with imitation, was responsible in part for the evolution of the modern human mind. However, there are sex differences in the themes of play, with girls across cultures engaging in more play-parenting and nurturing roles, whereas boys' play is usually centered on aggression and domination themes. Such play, in addition to helping children navigate social hierarchies and develop relationships (which serve both immediate and deferred functions), helps children learn the roles they will likely play as adults or would have played in ancient

environments. These adaptations should not be viewed as being impervious to experience or as producing inevitable outcomes. Rather, they are better viewed as biases that can be modified by experience, reflecting the high degree of neural, cognitive, and behavioral plasticity characteristic of childhood (see further discussion to follow).

Conditional Adaptations

Conditional adaptations can be thought of as a type of deferred adaptation, but ones that emphasize the importance of children's plasticity and sensitivity to local environments and children's ability to adjust their developmental trajectories in anticipation of future contexts. Boyce and Ellis (2005) defined conditional adaptations as "evolved mechanisms that detect and respond to specific features of childhood environments – features that have proven reliable over evolutionary time in predicting the nature of the social and physical world into which children will mature – and entrain developmental pathways that reliably matched those features during a species' natural selective history" (p. 290).

Perhaps the most studied topic from this perspective is the effect of early rearing environment on the rate at which children (especially girls) attain puberty and subsequent mating and parenting strategies. For example, Belsky et al. (1991) proposed that economic and social-relational (e.g., parental warmth, dependability) conditions during the first 5–7 years of life are good predictors of subsequent environments and direct children to develop either a "fast" (early attainment of puberty, early sexual debut, relatively little investment in partners or children) or a "slow" (later attainment of puberty, delayed sexual activity, greater investment in partners and children) *life history strategy*. Although following a fast life history strategy may be seen as maladaptive from a societal or mental-health perspective, it may be adaptive from a biological/evolutionary perspective, or would have been for our ancestors. Children growing up in harsh and unpredictable environments may be better served by reaching maturity early, not depending on long-term support from mates, and having a greater number of children in whom they invest

relatively little (i.e., a "quantity vs. quality" approach). The opposite pattern would likely be adaptive for children growing up in supportive, predictable, and high-resource homes. More than two decades of research has generally confirmed this hypothesis (see Ellis et al. 2009, 2012), highlighting the importance of developmental plasticity as a function of early rearing conditions. Such adaptive plasticity is even found before birth, with researchers reporting that prenatal experiences can influence postnatal taste preferences, caloric metabolism, and attachment patterns (see Gluckman and Hanson 2005). As Del Giudice (2012, p. 1615) suggests, "The developing fetus can use this information as a 'forecast' of the environmental conditions it will eventually face after birth, and start adjusting its physiological and behavioral profile to match the requirements of the world it will probably encounter."

Although the concepts of ontogenetic, deferred, and conditional adaptations provide valuable ways for thinking about how natural selection may have operated over the life cycle and how contemporary children are prepared by natural selection at different points in their development, the distinctions are not always clear-cut. Moreover, even if an adaptation does prepare a child for adulthood, for example, it also likely provides some immediate benefit. For instance, most forms of social play help children learn how to navigate social hierarchies, settle disputes, and solve problems, all great preparation for adult life. However, the same social play also helps children deal with their immediate environment, and similar arguments could be made for some ontogenetic and conditional adaptations. For example, although certain aspects of attachment seem clearly well suited to foster a child's immediate survival, individual differences in attachment-related behaviors may help children anticipate future environments, as proposed by Belsky and his colleagues.

What Are Psychological Adaptations Made Of?

Unlike adaptations such as an umbilical cord or an opposable thumb, there are no easily identifiable

physical manifestations for psychological adaptations. Evolutionary psychologists have proposed that what underlie psychological adaptations are *evolved cognitive mechanisms* – information-processing mechanisms shaped by natural selection over evolution to solve recurrent problems faced by our ancestors associated with reproduction and survival. According to Tooby and Cosmides (1992, p. 277), evolved cognitive mechanisms “in interaction with environmental input, generate manifest behavior. The causal link between evolution and behavior is made through psychological mechanisms.” Such mechanisms are described as being *modular*, consisting of domain-specific cognitive abilities that evolved in response to specific recurrent adaptive problems.

One problem that some developmental psychologists have with the concept of evolved cognitive mechanisms is the implication of *genetic determinism* – such mechanisms are perceived as reflecting innate processes that are activated at appropriate times and in specific contexts to produce adaptive outcomes, leaving little room for the role of experience in shaping adaptive phenotypes. Although mainstream evolutionary psychologists rightly chafe at the label “genetic determinist,” the standard notion of evolved cognitive mechanism fails to capture the substantial role of plasticity that is seen in the development of adaptations. In response, Bjorklund et al. (2007) proposed the concept of *evolved probabilistic cognitive mechanism*, defined as

information-processing mechanisms that have evolved to solve recurrent problems faced by ancestral populations; however, they are expressed in a probabilistic fashion in each individual in a generation, based on the continuous and bidirectional interaction over time at all levels of organization, from the genetic through the cultural. These mechanisms are universal, in that they will develop in a species-typical manner when an individual experiences a species-typical environment over the course of ontogeny (p. 22).

Evolved probabilistic cognitive mechanisms share most features with evolved cognitive mechanisms as mainstream evolutionary psychologists define them; the major difference being that a cognitive mechanism’s expression is explicitly

probabilistic, dependent upon bidirectional interactions between all levels of the organism-environment system. From this perspective, what are inherited are perceptual/cognitive/behavioral biases or dispositions that interact with a child’s environment, producing a pattern of, usually adaptive, thinking or behavior. Children are sensitive to specific types of information at particular times in development, resulting in a choreographed dance between gene-influenced neural maturation and species-typical experience. This is why most members of a species, be they monkeys, geese, or humans, grow up to be much alike one another – they inherit both a species-typical genome and a species-typical environment. However, because of the high level of neural plasticity of infants and children, developmental outcomes are not predetermined but can vary, often in adaptive ways, as a result of variations in early experiences. Such sensitivity to early experiences and the ability to modify one’s developmental trajectory are critical for a species, such as humans, who live in a vast range of both physical and social environments. From this perspective, evolved probabilistic cognitive mechanisms are not viewed as encapsulated modules, but rather as emerging from initial perceptual and information-processing biases in interaction with species-typical environments. Thus, evolved probabilistic cognitive mechanisms, and the adaptations they underlie, develop, with the eventual form of an adaptation being dependent upon a history of experience.

The following sections provide some examples of how evolved probabilistic cognitive mechanisms may develop in the domains of infant face perception, prepared fears, and tool use, leading to adaptive outcomes. For a more in-depth discussion, please see Bjorklund (2015).

Infants’ Development of Face Processing

For a social species such as ours, with infants who are highly dependent on adult care, few stimuli can be of more significance than the human face. Newborns begin life with perceptual biases that attract them to faces, and they give special

processing priority to faces. For example, shortly after birth, neonates (1) show a bias to look at face-like stimuli (e.g., schematic stimuli with two dots placed over a single dot within a headlike figure vs. when the dots in the figure are inverted); (2) are especially attentive to faces with eyes open and gazing at them; (3) look longer at right-side-up versus inverted faces, but only when they can see the eyes; (4) spend more time looking at their mothers' faces than at faces of other women; and (5) discriminate between human and nonhuman faces (see Bjorklund 2015). This pattern does not necessarily mean that newborns understand the conceptual meaning of faces. Rather, faces appear to have certain perceptual features that attract young infants' attention, including movement and areas of high contrast, such as eyes. By 3 or 4 months, infants show a bias to attend to curvilinear stimuli and vertically symmetrical stimuli (i.e., the right and left sides of a stimulus are symmetrical) and have biases to attend to "top-heavy" stimuli (i.e., up-down asymmetry), with this bias being found even in newborns (see Bjorklund 2015).

Infants' abilities to discriminate among faces improve over the first 5 or 6 months of life and become especially good for the types of faces they see on a regular basis. For example, at 6 months of age, infants are able to discriminate between upright and upside-down faces of both humans and monkeys (Pascalis et al. 2002). By 9 months, infants are increasingly able to discriminate between human faces but now process upright monkey faces no differently than inverted monkey faces (Pascalis et al. 2002), reflecting more specialized processing with experience. Similarly, infants are better able to distinguish among the more-familiar females faces than the less-familiar male faces, unless fathers are the primary caretakers. According to Pascalis and his colleagues (2002, p. 1321), "the ability to perceive faces narrows with development, due in large measure to the cortical specialization that occurs with experience viewing faces. In this view, the sensitivity of the face recognition system to differences in identity among the faces of one's own species will increase with age and with experience in processing those faces."

A similar pattern of development is found for infants' ability to tell the difference between faces of people of their own race versus those of another race (the *other-race effect*). For instance, in one study (Kelly et al. 2007), 3-month-old Caucasian infants were able to discriminate adult faces from among four ethnicities (African, Middle Eastern, Chinese, Caucasian). By 6 months, infants were able to distinguish between Chinese and Caucasian faces but not between African or Middle Eastern faces, and at 9 months, they performed greater than chance only for the Caucasian faces. That experience with specific classes of faces was the primary reason for the development of the other-race effect is demonstrated by research that exposed infants to photos of faces from other races or other species and reported subsequent abilities to discriminate "foreign" as well as same-race (or same species) faces (e.g., Anzures et al. 2012). Thus, infants are initially able to make discriminations equally well for faces of different species, sexes, and ethnicities, but with experience, their processing narrows, increasing their ability to discern differences among faces they see regularly, whereas they become relatively less facile making discriminations among faces they see less frequently.

Newborns seem to know nothing about faces, per se, although they are attracted to and process more efficiently lower-level features that happen to be associated with faces. With experience, they become increasingly able to discriminate faces, especially those from groups of individuals with which they regularly interact (humans, women, members of their own race), while at the same time reducing their ability to process the types of faces they encounter only occasionally. Yet, infants retain enough plasticity that developmental trajectories can be modified, permitting Caucasian infants, for example, to maintain (or regain) their ability to differentiate between faces from a different race or even a different species.

Developing Prepared Fears

There seem to be some things that infants fear, or show heightened levels of distress for, with little or

no previous experience. These include loss of support and loud noises. Other fears seem to develop somewhat later but appear to be nearly universal, including fear of snakes and spiders. But do people actually have an innate fear of snakes or, like the processing of faces, do initial perceptual bias make acquiring such fears more likely?

Much as rats seem prepared to associate nausea with previously eaten food, monkeys that initially show no fear of snakes are more likely to respond fearfully after watching another monkey respond with fright to a snake than to a rabbit or a flower (Cook and Mineka 1989). Research indicates that adults, children, and infants identify snakes (and spiders) more quickly from an array of flowers than vice versa (see LoBue 2013). Such biases seem to extend to sounds as well. For example, in one study, 9-month-old infants were more attentive to evolutionarily fear-relevant sounds (e.g., crackling fire, hissing snake) than to modern fear-relevant (e.g., tires screeching, bomb exploding) or pleasant (e.g., Beethoven or rock-and-roll music, horse neighing) sounds (Erlich et al. 2013). Other research shows that people more easily acquire fear responses for evolutionarily relevant objects, such as snakes, than for objects that may be more dangerous in contemporary environments, such as guns, knives, and automobiles.

Yet, rather than being innately fearful of snakes and other evolutionarily relevant stimuli, it seems that humans (and monkeys) have a tendency to learn to associate such stimuli with fearful responses. For instance, in one study (DeLoache and LoBue 2009), 7- to 9-month-old infants and 14- to 16-month-old toddlers viewed videos of snakes and other animals (rhinoceroses, giraffes). Although the children initially displayed no fear of the snakes (in fact, infants and young children without previous negative experience with spiders and snakes are often highly interested in these animals, see LoBue 2013), when they saw short video clips of snakes and other animals paired with either a fearful or happy voice, they looked longer at the snakes when listening to the fearful voice than the happy voice. There was no difference in looking time to the two voices when they watched videos of other animals. Similar patterns

were reported for infants with respect to angry/fearful faces: infants more readily identified images of angry faces than happy faces (LoBue and DeLoache 2010), and 11-month-old girls more easily associated a spider or snake with an image of a fearful face than an image of a happy face (Rakison 2009).

It seems highly unlikely that infants enter world fearing snakes, spiders, or angry/fearful faces. Rather, such fears are learned, as much as fear for other stimuli is learned. However, primate infants appear to possess perceptual biases increasing the probability that fearful responses to these evolutionarily relevant stimuli will be learned.

Children as Tool Users

All animals must learn to deal with objects in their physical world, but many, perhaps most, of the objects that humans encounter are *cultural artifacts*, things made by people for a specific purpose. One large category of cultural artifacts is *tools*, devices used for “doing work” or solving specific problems. As soon as infants have sufficient motor dexterity, they begin to manually explore objects (“What can the object do?”), discovering their affordances (i.e., functional relationships between objects and the environment) along the way. This is followed beginning around 9-months of age by manual play (“What can I do with the object?”) (Belsky and Most 1981). Although estimates vary, approximately one-third of preschool-aged children’s activity involves playing with objects, with similar values being reported for children in hunter-gatherer societies (Bock 2005).

One purported purpose of object play is to allow children to discover the affordances of objects, which may facilitate subsequent tool use. For example, researchers reported that 5- and 6-year-old children were more likely to appropriately modify a tool (bend a pipe cleaner so it can be used as a hook) when they were given the chance to explore the properties of the object beforehand, in conjunction with observing a model using the tool, than children not permitted

to manipulate the materials (Cutting et al. 2014). In other research, Gredlein and Bjorklund (2005) measured the amount of object-oriented play in 3-year-old children during a free-play session, and then, in a separate session, assessed children's ability to select and use a proper tool to retrieve an out-of-reach toy. They reported that boys performed the tool-retrieval task better than girls (although girls performed comparably after a simple hint) and that there was a positive correlation ($r = 0.59$) between the amount of object-oriented play during the previous free-play sessions and performance on the tool-retrieval task for boys, but not for girls, causing Gredlein and Bjorklund (2005) to suggest that boys may be more sensitive to such environmental experiences than girls.

Infants and young children are not only motivated to interact with objects, but early in development, they learn that an artifact that is used to solve a problem was in fact designed for a specific function, referred to as the *design stance*. Children acquire the design stance for new tools relatively early. For example, when shown a new object and told of its function (e.g., a boxlike object used for catching bugs), 3-year-old children are less likely to see an alternative use for the object (e.g., collecting raindrops), associating it with its originally designed purpose. Their prior knowledge of what spoons are "for" resulted in what is referred to as *functional fixedness*, a lack of flexibility when it comes to using a familiar tool. Functional fixedness is generally thought of as a "mental block" that hinders effective problem solving. However, the design stance, though sometimes resulting in overly rigid behavior, more typically results in adaptive outcomes. By identifying what a particular artifact is "for," children (and adults) can more efficiently use tools that were in fact designed for a specific purpose.

Children's biases to manipulate objects, to discover their affordances, and their early design-stance orientation are associated with social-learning abilities in acquiring proper tool use. From at least 3 years of age, children readily learn how to use novel tools from watching models (e.g., Flynn and Whiten 2008). In fact,

preschool children tend to copy *all* behaviors associated with a model, whether relevant or not, which has been referred to as *overimitation*. Children assume that all of a model's behavior are normative and assume (usually correctly) that someone would not purposefully perform unnecessary actions.

Effective tool use in humans is nearly inevitable, but it is not based on an innate "tool-use" adaptation unique to our species. Rather, infants have biases to manipulate objects, with the purpose of both seeing what objects can do (exploration) and what they can do with the objects (play). In the process, they discover affordances of the objects and develop action plans for using these objects. As children become able to mentally represent objects, their general tendency to see purpose in the objects and events in the world make it increasingly likely that they will learn to use objects as culturally prescribed. This is further facilitated by social-learning biases that result in children viewing the actions of others as normative and worthy of often precise imitation.

Conclusion

The concept of adaptation is central to evolutionary psychology. However, due to the high levels of children's behavioral, cognitive, and neural plasticity, the final form (most) adaptations take will depend on the early and continuous experience of children on their way to adulthood. Infants and children with species-typical genomes possess low-level perceptual or cognitive biases or abilities, which, in interaction with their environment, lead most children to process effectively faces from their own species or ethnic group, to acquire fearful responses to specific evolutionarily relevant stimuli, or to develop a facility with tools.

Although the examples provided here may more easily fit the definition of evolved probabilistic cognitive mechanisms than others, the process is a general one, reflecting how many adaptive

behaviors and cognitions are acquired and have been acquired over the course of human evolution. For example, there are a number of low-level perceptual and cognitive traits that underlie social relations in infancy, in addition to the face-processing mechanisms discussed earlier. These include neonatal imitation, discussed previously as an ontogenetic adaptation, a bias to attend to biological motion, and baby-like facial features that promote caregiving. Similarly, the social-learning biases that foster rapid acquisition of tool use via observation are preceded by more basic abilities such as infants viewing others as intentional agents – individuals whose actions are performed to achieve some goal (Tomasello 2009) and are reflected by the development of perspective taking, social referencing, and shared attention.

From the current perspective, evolutionary adaptations are emergent properties, arising from low-level perceptual and cognitive biases, with children themselves playing an active role in these adaptations' development (and evolution), through continuous interaction with their physical and social environments.

Cross-References

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- [Play and Tool Use](#)
- [Play Fighting in Boys](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Tool Play](#)
- [Universal Human Fears](#)

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Development of Aggression

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Synonyms

Aggressive behavior; Etiology of aggression; Proactive aggression; Reactive aggression

Definition

Aversive behavior that may harm another organism.

Introduction

Aggressive behavior is ubiquitous across species. While animal models present a clear definition of aggression as any behavior that is aversive and may inflict harm on another organism, human aggression proves more difficult to define. The challenges of defining human aggression result from a combination of philosophical differences among academics, the difficulties associated with defining a complex behavior, and the challenges of assigning motivation that cannot be readily observed (Olivier and Young 2002). Human aggression is typically classified into two categories: *reactive aggression* and *proactive aggression*. Reactive aggression, or *affective aggression*, is theoretically rooted in Berkowitz's (1993) frustration-aggression model and is described in the literature as defensive and angry behavior in response to provocation. Proactive aggression, or *predatory aggression*, is theoretically rooted in Bandura's (1973) social learning theory and is described as deliberate, goal-directed, and often unprovoked.

Is Aggression Adaptive?

While the adaptiveness of aggression is subject to much debate, perhaps this question is best answered by clarifying what is meant by *adaptive*. According to Darwin's theory of evolution, variability in reproductive success within a population is necessary for natural selection to occur. The extent to which an organism is reproductively successful is referred to as *genetic fitness* (Silk 1986). Given the frequency and prevalence of aggression, it is likely an adaptation that conferred some sort of reproductive advantage to those who expressed it. Thus, if aggression improves reproductive fitness, it is considered adaptive.

Animal Models of Aggression Development

Aggression is expressed ubiquitously across the mammalian animal kingdom (Veenema 2009). *Offensive aggression*, which is similar to proactive aggression among humans, may be displayed by adult males who are defending resources such as food, mates, or territory. Similarly, predatory aggression is a form of goal-directed aggression displayed by animals while hunting for prey. *Defensive aggression*, which is similar to reactive aggression among humans, is displayed when animals are attacked by predators or conspecifics. *Maternal aggression* is a type of defensive aggression and is displayed by females to protect their young from potential intruders (Veenema 2009). These types of aggression are functionally and phenotypically distinct from each other and likely are associated with differing activation of underlying neuroendocrine systems (Veenema 2009).

Among captive groups of rhesus monkeys and pigtail macaques, there is a 5–10% rate of child abuse or neglect. Among pigtail macaques, incidents of abusive behavior increase following a stressful event, such as an attempted kidnapping of a child or intergroup aggression (Maestriperi 1998). Similarly, abusive mothers among Japanese macaques display higher levels of anxiety

than their non-abusive counterparts. Furthermore, abusive behavior decreases or ceases after the administration of anxiolytic medication (Troisi et al. 1991). Early experience appears to play a fundamental role in the etiology of abuse and neglect of one's kin that is demonstrated by a pattern of early experience accounting for more variation in abusive behavior than genetic inheritance (e.g., Veenema 2009). Taken together, these results suggest that early abuse contributes to a pattern of emotional dysregulation that may be exaggerated under conditions of stress (such as motherhood), which contribute to the development of aggression and neglect of one's kin.

Classic experiments conducted by Harlow & Harlow (1965) demonstrated the immense impact of early separation on typical development, leading to an increased likelihood of inappropriate displays of aggression later in life. The typical paradigm of maternal separation in animal experiments is "repeated maternal separation," which consists of removing a child from their mother for 3 hours a day, every day for the first 2 weeks of life. Experiments that utilize this paradigm with rodents have demonstrated that maternal separation leads to increases in aggressive behavior later in life. For example, male Wistar rats that experienced repeated maternal separation as infants displayed increased play-fighting as juveniles and intermale proactive aggression as adults (Veenema et al. 2007; Veenema and Neumann 2009). Similarly, while these results were not replicated among C57B1/C mice, repeated maternal separation as an infant did appear to contribute to increased maternal aggression during the first 2 weeks of lactation as an adult (Veenema et al. 2007).

Development of Aggression Through the Life Span

Prenatal Factors

Broadly speaking, the environment may interact with individual differences to produce aggressive responses. As such, displays of aggressive behavior represent a host of interacting biological,

psychological, and social factors. The adaptive perspective posits that aggression is highly context-specific and is only elicited in situations in which specific adaptive problems are confronted, for example, to defend against attack, inflict costs on intrasexual rivals, or negotiate power status (Buss and Shackelford 1997).

From a neurological perspective, researchers suggest that aggression is influenced by a system of glands in the nervous and endocrine systems that regulate stress responses called the hypothalamic-pituitary-adrenal (HPA) axis. Factors that negatively affect the development of the HPA axis include fetal exposure to environmental toxins, maternal substance use, and prenatal maternal stress. As a result, these factors are associated with long-term consequences on HPA functioning, including increased stress reactivity, negative emotionality, and behavior problems across the life span (Labella and Masten 2018).

Early Childhood

While controversial, some developmental scientists view early aggression as a developmental milestone (e.g., Hay 2017). Displays of aggression begin as early as an infant is able to control their bodily force in a productive manner. By the midpoint of the second year of life, infants are able to reach out to touch and grasp objects and people intentionally (Moszkowski and Stack 2007). Around the same time, they begin to express frustration and distress through facial expression and vocalizations (Stenberg et al. 1983). Soon after, infants can be observed forcefully touching objects, tugging and pulling toys away from others, and pushing, biting, pulling, and hitting (Eckerman et al. 1975). By 2 years old, toddlers can be observed using physical force against peers to attain goals, such as securing a toy to play with, in conflicts (Hay et al. 2011). While mal-intent cannot be ascribed to these actions, the instrumentality demonstrated by visual guiding and direct movement implies goal-directedness and volition in this behavior (Campos et al. 2000). Furthermore, aggression in children as young as 6 months old appears to be stable, as it predicts clinically significant conduct problems and aggression at 3 years old (Hay et al.

2014). Similarly, the first signs of relational aggression begin to appear around 3 years old and become more sophisticated throughout childhood (Crick et al. 2007). As such, early incidents, such as tugging, pushing, and hitting, may be indicative of a long-term developmental pattern of serious aggression (Hay 2017).

Childhood

Postnatally, environmental stressors continue to impact the development of aggression. According to Labella and Masten (2018), familial adversities such as poverty, family stress, disorganization, single parenthood, large family size, and household conflict are all linked to the development of aggression. Furthermore, the impact of environmental stressors on aggression extends beyond the family unit. Witnessing or experiencing violence, personally or through the media, is related to the development of aggression in multiple ways. For example, there are significant links between community violence exposure and increased aggressive behavior (Labella and Masten 2018). Specific interpersonal relationships impact aggression as well. It is well documented that affiliation with antisocial peers is a risk factor for aggression (Lansford 2018). Not only do such environmental factors undermine secure attachment, bias social information processes toward threat detection, and contribute to the dysregulation of the stress response system, but they also offer models of aggression to be imitated and promote the normalization of aggression (Labella and Masten 2018).

Temperament

Temperament appears to be a highly heritable trait, as children who have irritable temperaments may have inherited this trait from their parents. Moreover, an irritable temperament may evoke harsh parenting from a parent who may also have a predisposition toward irritability. A difficult temperament as a child is predictive of reactive aggression later in life. Similarly, children who responded with more negative emotionality than their peers to social and physical disturbances in their environments were more aggressive as preteens (see Vitaro et al. 2006 for review).

The development of aggression is influenced by factors such as self-regulation (effortful and reactive control), emotion states, and personality. There appears to be a salient relationship between aggression and self-regulation, which can be understood as one's ability to accomplish goal-directed behavior when impulses, desires, and habitual patterns of behavior compete for attention (Tirabassi et al. 2017). Research suggests that self-regulation is primarily associated with reactive aggression as a result of deficits in behavioral regulation and future-oriented problem-solving (Tirabassi et al. 2017).

The relationship between self-regulation and aggression may be, in part, a result of low levels of effortful control. Effortful control refers to the regulation of attention and negative reactivity as well as the inhibition of automatic cognitive and behavioral responses. Research suggests that arousing events (prevalent in stressful environments, such as those mentioned above) may make it difficult for individuals to develop the necessary regulatory mechanisms, such as effortful control, to regulate reactive emotions (Esposito et al. 2017). As a result, it may be difficult for individuals with poor effortful control to find non-aggressive solutions to interpersonal problems, including those that are emotionally driven (Loeber and Hay 1997).

The decreased ability to regulate negative emotions is related to the presence of environmental stressors. The resulting emotion dysregulation is predictive of increased levels of aggressive behavior (Lansford 2018). Labelle and Masten (2018) propose that the often emotionally unsupportive nature of early stressful environments contributes to higher levels of distress without a corresponding increase in emotion management (Labella and Masten 2018).

More generally, individuals with poor self-regulation often lack emotional control and may display aggression out of impulse (Wilson and Ray 2018). Likewise, aversive emotional triggers, such as anger or sadness, may elicit fight (i.e., behaving aggressively in response to the emotional stimulus) or flight (i.e., ignoring or retreating from the emotional stimulus) responses (Wyckoff 2016). Specifically, research suggests

that aggression is related to the regulation of negative emotions such as anger, sadness, and frustration. Dane and Marini (2014) suggested that proneness to frustration is associated with an increased risk of aggression, and in individuals with high levels of effortful control, the related behavioral inhibition and planning abilities may actually facilitate aggressive behavior in relational contexts. Furthermore, higher levels of fearfulness appear to play a role in relational aggression, as children who are more fearful may opt to employ more covert forms of aggression such as rumor spreading or exclusion (e.g., Volk et al. 2012). In terms of more positive emotions, research suggests that one's ability to experience and demonstrate empathy influences one's level of aggression (Wilson and Ray 2018). Empathy may act as an influence on aggression in that it facilitates the understanding of others' emotions, thereby potentially inhibiting one's desire to engage in aggressive behaviors directed at others.

Social Information Processing

Crick and Dodge's (1994) social information processing (SIP) model describes a sequence of cognitive processes that are posited to influence social behavior, such as aggression, in children. The five overlapping steps of the SIP model are (1) encoding of external and internal cues, (2) interpretation of those cues, (3) choosing a goal, (4) selecting a response to attain that goal, and (5) performing the response decision (Crick and Dodge 1994). Aggressive children are more likely to demonstrate differences at each of these steps of cognitive processing, such that they may (1) encode social cues as less benign, (2) demonstrate a hostile attribution bias to ambiguous behaviors, (3) select goals that are more likely to damage relationships with others, (4) generate fewer and less prosocial responses, and (5) evaluate aggressive responses that are favorable and expect aggressive behavior to have a positive outcome (Li et al. 2013). Lemerise and Arsenio (2000) extended Crick and Dodge's (1994) model to include the role of emotion and latent cognitive structures in the cognitive processing of social information. They suggested that a critical component of how a child evaluated social behavior is

their emotional style or emotionality. For example, a child who is easily overwhelmed by negative emotion may be more likely to interpret ambiguous behavior as threatening (i.e., Step 2) or choose self-focused responses to these cues (i.e., Step 4). Similarly, internal working models (i.e., mental representations of the self, attachment figures, and how they relate) inform the assumptions aggressive children may hold about their peers. Last, underlying moral knowledge structures are influential in at the response-generation (i.e., Step 4) and response-selection (i.e., Step 5) steps, as the decision on how to proceed will be subject to how the child views the response as impacting future relationships, what extent the perceived provocation is meaningful, and to what extent they will be able to recover from harm (Lemerise and Arsenio 2000).

The aforementioned environmental factors act in conjunction with cognitive distortions to elicit aggression. Cognitive distortions (e.g., hostile attribution bias, evaluating aggressive responses favorably) facilitate aggression by providing individuals with justifications for the ongoing use of aggressive behavior. Koolen et al. (2012) found that in both delinquent and nondelinquent samples, the presence of cognitive distortions was associated with aggressive, offending, and antisocial behavior. Specifically, their research supported that (a) proactive aggression is predicted by egocentric biases (i.e., the belief that one's own needs supersede those of others) and (b) reactive aggression is associated with the misinterpretation of social cues (i.e., hostile attribution bias).

Parental Influence

Reactive aggression appears to be predicted by a harsh and unpredictable environment and abusive or hostile parenting. Retrospective studies on aggressive youth have linked reactive aggression in adolescence with childhood experiences of physical abuse or harsh discipline. However, this is not the case with proactively aggressive youth. Proactive aggression appears to be predicted by supportive environments that allow for aggression to be implemented as a means to achieving one's goals. Similarly, exposure to family members who

model and endorse aggression, and use it to solve conflicts or advance interpersonal relationships, is predictive of later proactive aggression (see Vitaro et al. 2006 for review).

Parents who have traditional attitudes toward gender roles are more likely to reinforce gender role-consistent behavior. This includes reinforcing aggressive behaviors in boys. A study conducted by Endendijk and colleagues (2017) provided evidence to suggest that fathers and mothers with strong stereotypical views on gender roles were more likely to treat their sons and daughters differently in regard to their aggressive behavior. Specifically, parents used more physical control strategies with their sons than with their daughters. As such, boys may come to associate physical control with power and, consistent with social learning theory, may be socialized into traditional male gender roles that emphasize assertiveness and dominance as a consequence (Endendijk et al. 2017; Bandura 1973).

Aggression in Adolescence

From an adaptive perspective, adolescents may be using aggression as an instrumental tool to obtain socially relevant resources. For example, research conducted by Prinstein and Cillessen (2003) suggested that aggressive behavior is associated with higher social status, but lower levels of likability among peers. That is, while adolescents who are aggressive may not necessarily be liked by their peers, they may be choosing to engage in such behavior to attain social status. In other words, any costs associated with aggressive behavior may be outweighed by these benefits (Hawley 2003). Prinstein and Cillessen (2003) also found that there were differences among the subtypes of aggressive behavior. Adolescents who engaged in proactive aggression were more popular, while adolescents who engaged in reactive aggression attained lower levels of social preference. Therefore, it appears that the type of aggressive behavior an adolescent utilizes may be important in determining whether peers reinforce or reject the behavior (i.e., increased social status versus being disliked by peers).

If adolescents who choose to engage in aggressive behavior are rewarded, it may encourage these individuals to continue to utilize aggressive behavior as a means to achieve goals such as social dominance. Recent research has implicated personality as a strong predictor of an individual's willingness to employ aggressive behavior for personal gain across cultures (e.g., Volk et al. 2018).

Personality

Research has suggested that personality factors related to an individual's propensity to exploit and manipulate others for personal gain, unwillingness to cooperate with others, and tendency to favor short-term gains over long-term goals are associated with higher levels of both proactive and reactive forms of aggression (Knight et al. 2018). Similarly, research by Dinić and Wertag (2018) has replicated the result that individuals who are less inclined to cooperate with others are more likely to engage in both subtypes of aggression. Additionally, this research also suggested that individuals who are emotionally detached from others are more prone to engaging in reactive forms for aggression.

A frequent avenue for expressions of aggression, especially among adolescents in the school context, is bullying. A growing body of research is implicating personality as a key predictor of aggressive and antisocial behavior in adolescents (e.g., Volk et al. 2018). Specifically, individuals with personality profiles that include traits associated with the exploitation of others for personal gain and a tendency for reckless and inconsiderate behavior are more likely to engage in bullying behavior in samples of Canadian and Chinese adolescents (Volk et al. 2018). Furthermore, this research supports the evolutionary theory of bullying, which posits that bullying is a facultative adaptation that is used to obtain resources that will ultimately increase genetic fitness, such as material wealth, increased social status, and access to high-quality dating partners, under conducive environmental conditions (Volk et al. 2014).

Aggression in Adults

The way in which aggression manifests and is utilized may be different across the life span, particularly in adulthood. Whereas previous research has suggested that aggression is often stable from childhood to adulthood, other research has proposed that a considerable number of aggressive youth decrease in their aggressive behaviors over time (Loeber and Hay 1997). For example, longitudinal research by Moffit et al. (2002) that examined trajectories of antisocial behavior suggested that there were some differences in the progression from aggressive to delinquent behavior in males. This research found that while engaging in aggressive behavior during adolescence often progressed to delinquency as an adult, there was also another group of men who were low-level offenders as adults and who were aggressive as children but did not engage in delinquent behavior as adolescents. This demonstrates that the trajectory of aggressive behavior during childhood and adolescence to delinquent behavior in adulthood may not always be linear and emphasize the importance of early intervention at the onset of antisocial or aggressive behavior.

It might also be important to consider that certain combinations of gene and environmental interactions during childhood have the potential to result in adults who engage in antisocial behavior. For example, not all children who experience abusive parenting become aggressive adults; however, children who are born with an active monoamine oxidase A (MAOA) gene (an X-linked gene known to inhibit brain chemicals associated with aggression) and experience abuse as a child are more likely to engage in aggressive behavior as an adult than those who experience maltreatment but had an inactive gene (e.g., Byrd and Manuck 2014). Overall, while it is true that some individuals who are aggressive as children may be aggressive as an adult, this type of behavior may be more plastic than earlier research has proposed, and the trajectory may not be linear depending upon the genetic predisposition and experiences of the individual.

Conclusion

Aggression is related to a number of negative outcomes. For children, those that exhibit aggressive behaviors are at an increased risk for continued externalized and problematic behavior (Wilson and Ray 2018). Dane and Marini (2014) posit that aggressive behavior in childhood is related to such negative developmental outcomes as substance dependence, mental health problems, unemployment, inter-partner violence, and criminal offending. However, the frequency and prevalence of aggressive behavior in populations suggests that it would have increased our ancestors' evolutionary fitness – that is, engaging in aggressive behavior would have somehow increased one's chances of propagating their genes onto the next generation. As such, it may be reasonable to suggest that future research endeavors to employ the evolutionary perspective in further understanding the etiological pathways toward aggressive behavior and in designing effective prevention and intervention programs that improve the future outcomes of aggressive children and youth.

Cross-References

- Aggression
- Costs of Aggression
- Physical Aggression
- Relational Aggression
- Sex Differences in Aggression
- Social Aggression
- Variability of Aggression

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Development of Civilizations

► Guns, Germs, and Steel

Development of Differences Between Males and Females

► Development of Sex Differences

Development of Sex Differences

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Synonyms

Sexual differentiation, development of differences between males and females; Development of sex differences in brain and behavior

Definitions

Activational effects	Transient effects of hormones that occur throughout life.
Asexual reproduction	Offspring produced from a single organism that inherits the entire genome of the parent organism.
Diploid	Having two sets of chromosomes or double the number of chromosomes in the germ cell.
Eusociality	Cooperative breeding strategy in which usually one female and a few males are reproductively active, whereas the rest of the nonbreeding members provide care for the offspring of the colony and gather food and resources for the colony.
Haploid	Having a set of chromosomes equal to the number in the germ cell.
Heterogametic	Refers to the sex of a species that has two different sex chromosomes.
Homogametic	Refers to the sex of a species that has two of the same-sex chromosomes.

Intersexual competition	Mate choice, occurs when an individual is choosing between mates.
Intrasexual competition	Occurs between same-sex individuals competing for a mate.
Monogamous	Mate strategy in which an individual has only one partner at any one time.
Natural selection	Differential survival and reproductive success of individuals due to differences in heritable traits. Key mechanism of evolution.
Organizational effects	Permanent effects of hormones associated with critical developmental periods.
Polygamous	Mate strategy in which an individual has multiple partners at any one time.
Sexual determination	A biological system that determines the sex of an individual. In many species, including mammals, sex determination is genetic.
Sexual differentiation	The development of differences between males and females.
Sexual reproduction	Two organisms generate distinct reproductive cells that fuse together to produce offspring.
Sexual selection	Differential reproductive success due to preferential mate choice of the opposite sex.

Introduction

The development of sex differences is studied by evolutionary psychologists at two levels of analysis: the proximate and ultimate. The proximate level of analysis addresses the ontogeny of sex differences at the level of individuals within a species. At the ultimate level, reasons for the adaptiveness of sex differences and the evolutionary circumstances that lead to sex difference

development are addressed. Both the proximate and ultimate level of analysis will be addressed in this entry, including the evolutionary benefits of having two sexes, as well as evolutionary perspective behind sex differences in size and function.

The Evolution of Sexual Reproduction

Species reproduce in one of two ways, or occasionally in a combination of the two: (1) asexual reproduction by which offspring are produced from a single organism, and (2) sexual reproduction that requires two organisms to generate distinct reproductive cells, called gametes, that fuse together to produce offspring.

The evolutionary advantages of sexual reproduction eluded evolutionary biologists for over a century after the theory of natural and sexual selection was first proposed. Asexual reproduction has many advantages – chiefly, an organism, which has successfully survived to reproductive age in a given environment, produces offspring that inherit all of the parent’s genes with no wasted effort and resources spent on mating. Offspring from asexual reproduction are genetically identical to the single parent, unless any mutations occur during mitotic division. In contrast, with sexual reproduction, only half of the offspring’s genetic material came from each parent. Also, there is the “twofold cost of sex” problem: The offspring output per capita is halved with sexual reproduction because it inevitably requires two individuals, whereas, theoretically, each individual in a species reproduces with asexual reproduction. Furthermore, theoretical analyses suggest that genome mixing is risky, as resulting combinations of genes can be maladaptive. Sexual reproduction also requires a substantial amount of energy and resources devoted to acquiring mating partners.

One advantage of sexual reproduction is that evolution can occur more rapidly with the continuous recombination associated with sexual reproduction, whereas with asexual reproduction the evolution of a species relies on spontaneous mutations. Evolutionary psychologists have found

substantial support for the “Red Queen” hypothesis that explains how recombination through sexual reproduction can be advantageous for the individuals within the species to respond to changing environments, and also to evade evolving predators. Specifically this hypothesis explains that there is an arms race (or co-evolution) between parasites and hosts, and predators and prey, in which genetic recombination allows sexually reproducing species to dispose of deleterious mutations more rapidly and keep mutations that promote survival (For review of this “Red Queen” hypothesis, see Liow et al. 2011). Although evolutionary biologists continue to explore the ultimate reasons for the maintenance of sexual reproduction, it has been proposed that once sexual reproduction arises, it is difficult for a species to then secondarily evolve asexual reproduction (Hörandl 2009), and therefore, most higher order organisms reproduce sexually (For review, see Agrawal 2001; Otto and Thomas 2002).

Proximal Development of Sex Differences

Many species that reproduce sexually have two sexes that contribute to the genetic make-up of their offspring, including genetic information that determines sex. Sex chromosomes are responsible for the cascade of events that determine whether an animal develops into a female or male – a process called sexual determination (For an example of an exception to genetic sex determination, see Holleley et al. 2016). For haplodiploid sex determination, the number of chromosomes determines the sex of the species; males possess a haploid chromosome number, whereas females are diploid. In other species including mammals, birds, and many insects, in which both sexes reproduce through sexual reproduction, both males and females are diploid. When both sexes are diploid, one of the sexes is homogametic (i.e., have two of the same sex chromosome), whereas the other sex is heterogametic (i.e., have two different sex chromosomes). For example, in

birds as well as some fish, insects, and reptiles, females have two different sex chromosomes (Z, W), whereas males have two of the same sex chromosomes (Z, Z). In mammalian sex determination, as well as some other insects and vertebrates, females have two of the same sex chromosomes (X, X), whereas males have two different sex chromosomes (X, Y; For review, see Adkins-Regan 2012).

Sex-determining genes present on the sex chromosomes are responsible for sex-typical development. However, even between species with the same system of sex determination, gross differences exist in the sexual differentiation process. For example, *Drosophila* (common name: fruit fly) and mammals have X, X or X, Y sex chromosomes. However, in *Drosophila* sex is determined by a balance of female determinants on the X chromosome and male determinants on the autosomes. In mammals and some other vertebrates, however, it is the presence of male-specific genes on the Y chromosome that determines the sex of the animal (For review, see Adkins-Regan 2012).

Insect sex development has primarily been thought to depend exclusively on cell-autonomous expression of sex-specific genes. By contrast, in vertebrates, sex determination is decided by the presence of the Y chromosome, from which the sex-determining region of the Y chromosome (*Sry*) triggers the development of the testes in males. In the absence of *Sry*, ovaries develop. Once gonadal development is underway in vertebrates, the hormones produced by the gonads are responsible for subsequent sexual development – a process known as sexual differentiation. The process of sexual differentiation is well conserved among vertebrate clades, although recent evidence indicates that the sexual differentiation of both vertebrates and insects rely on both sex hormones and cell-autonomous mechanisms, rather than one or the other (For review, see Bear and Monteiro 2013).

The traditional theory of sexual differentiation posits that vertebrate sexual development is dependent on hormones produced by the testes (i.e., testosterone and its metabolites, and anti-Müllerian hormone). The production of these

hormones in males stimulates the growth of male-typical external genitalia and internal reproductive structures, and inhibits the development of female-typical reproductive structures. In females, the ovaries produce very little hormones during early development; female-typical genitalia and internal reproductive structures develop in absence of the male-typical hormones. In addition to these sex differences in gross physiology, the nervous system and behavior are influenced by these hormones: Gonadal sex hormones organize the structure of the nervous system during this critical developmental period (Phoenix, Goy, Gerall & Young, 1959; for review see, Wallen 2009). These permanent changes to the nervous system allow for the potential of male- or female-typical behaviors in adulthood. During puberty and adulthood, gonadal hormones further organize and activate these sex differences, promoting male- and female-typical anatomical growth as well as sex-typical mating behaviors. Both organizational and activational hormones are required for full sex-typical sexual differentiation.

Although sexual differentiation of vertebrates is largely dependent on sex hormones (e.g., the absence of sex hormones or sex hormone receptors greatly impedes male-typical sexual differentiation of physiology as well as the brain and behavior), more recent advances have indicated a role for sex chromosomes beyond its role in gonadal development (McCarthy and Arnold 2011). For example, *Sry* has a role in the expression of dopaminergic neurons in the substantia nigra, and is thought to play a role in the 1.5-fold increase in male incidences of Parkinson's disease in humans (Dewing et al. 2006). Additionally, males are more prone to X-linked diseases: Females possess two X chromosomes, whereas males have one X chromosome and a Y chromosome. In each cell of males and females only one X chromosome is expressed. In females one of her X chromosomes is silenced via the gene *X-ist*. This process called X-inactivation compensates for the additional genetic material. If a female possesses a defect on one X-chromosome, her other X-chromosome steps in and counteracts any negative effects of the defected X-chromosome. However, because

males only have one X-chromosome, any X-linked disease will be expressed in males (For review see, McCarthy and Arnold 2011).

The role of sex chromosomes has been further delineated by advanced genetic engineering of mice. Briefly, the Four Core Genotype model allows the generation of XX genetic female mice with male gonads (i.e., testes) as well as XY genetic males with female gonads (i.e., ovaries). Comparisons between these mice and their wildtype siblings confirm the importance of hormones on sexual differentiation of the brain and behavior in mammals. However, these models have also indicated important interactions of hormones with sex chromosomes, as well as sex chromosome-independent effects on sex differences in social behaviors, aggression, parenting as well as susceptibility to neural disease (For review see, McCarthy and Arnold 2011).

In addition to the new evidence of a role for sex chromosomes in sexual differentiation of mammals, recent studies have also indicated that female sexual differentiation is not a default that occurs in absence of *Sry* and male-typical gonadal development, as originally described by the traditional theory of sexual differentiation. Similar to male differentiation, recent genetic studies suggest that two pathways simultaneously repress male-specific gene activation and activate female-specific genes in typical female sexual differentiation (Baillet et al. 2010). Furthermore, although estrogens are not synthesized by female gonads until much later in life compared to testicular hormone synthesis (e.g., 2 weeks postnatal in female mice compared to prenatal hormone synthesis in male mice), organizational effects of maternal estrogens during the early critical period of development are necessary for full female-typical neural development as well as for the full display of copulatory behaviors in adulthood (Bakker and Brock 2010).

Ultimate Development of Sex Differences

In addition to the theory of natural selection, Darwin (1871) proposed the theory of sexual selection to explain sex differences observed across species. Advantages in intrasexual competition (i.e., competition with members of the same sex

over mates) and intersexual choice (i.e., discriminative choice of mating partners) determine the reproductive success of individuals within a species. Briefly, traits that are beneficial to gaining access to and/or attract mating partners increase reproductive success, and thus are maintained throughout evolution.

The traits that are sexually selected depend on the reproductive strategy of a species. Generally, intra- and intersexual selection pressures will affect the sexes differently. As explained by parental investment theory, the reproductive strategy (i.e., discriminatory mate choice vs. promiscuity) often depends on the number of offspring each sex can produce (Trivers 1972). The sex with lower rates of reproductive ability invests more in parenting and is more selective in mate choice; intersexual competition is typically displayed by the sex with higher parental investment. Conversely, the sex with greater potential for high numbers of offspring invest less in parenting, is less selective in mate choice, and exhibit intense intrasexual competition.

In more than 95% of mammalian species, females are limited in the number of offspring they can produce; whereas males are limited only by the number of mates they can gain access to (Clutton-Brock 1989). Typically, females are restricted by the number of eggs/ova they possess, by the relatively small window of fertility, and more prominently, by the number of pregnancies they can have as a consequence of long gestational periods. In contrast, males produce sperm quickly and in large amounts, and can impregnate many partners in the same amount of time that a female can only sustain one pregnancy. Thus, females will tend to select mates carefully, and will try to find a partner with healthy genes and resources to promote the success of their limited number of offspring. Conversely, males tend to spend their efforts attempting to gain access to as many mates as possible to increase their reproductive success. Traits that favor the sexes reproductive strategy will persist, as well as sex differences result in the underlying neuroendocrine systems that maintain these behavioral differences.

Parental investment theory predicts that the greater the sex difference in mating strategies,

the more sex differences the species will exhibit. In line with this hypothesis, monogamous species, in which males and females have a single mating partner and both parents participate in parental care, display fewer sex differences than polygamous species, in which males and females have multiple mating partners and females are typically the primary caregivers (Trivers 1972). A compelling example is observed in two highly related species of voles – the monogamous prairie vole displays fewer sex differences in both brain and behavior compared to the polygamous montane vole (Shapiro et al. 1991; Wang et al. 1999).

Few species display strict monogamy and thus sex differences can be found in almost every species, including humans. Although monogamy among humans is generally the aspiration of many societies, polygynous marriage occurs in the majority of societies (~83%). Even in societies in which monogynous marriages are typical, men are likelier to reproduce with a new partner following divorce. Therefore, men have higher reproductive variance in humans, and accordingly, there is evidence of sexual selection pressures in humans.

Ethnographic and archeological data indicate that compared to women, men are overall physically larger, more muscular and display higher rates of physical aggression, evident by the history of male production and use of weapons against each other and the participation in violence and warfare (Puts 2016). Furthermore, cross-cultural investigations indicate sex differences in humans according to mating strategies predicted by parental investment theory: males tend to prefer characteristics of reproductive capacity in females (e.g., youthfulness, physical attractiveness), whereas females prefer mates with resource acquisition potential (e.g., industriousness, ambition; Buss 1989). However, female mate choice (i.e., women's ability to freely choose mates) was likely limited in ancestral societies by men's social power and force. In line with this idea, recent work suggests that male secondary sex traits are less related to female mate choice and more effective for intrasexual competition (e.g., beards and robust faces are more effective at intimidating other men rather than attracting females; Puts 2016). Finally, there is evidence of

sperm competition in humans (i.e., competition within a single female between the sperm of multiple males). Humans are intermediate between the highly polygamous macaques and the highly monogamous gorillas in terms of sperm motility, such that it can take multiple days for sperm to meet the ovum of a female (Reviewed in Puts 2016). This delay allows time for healthier, faster-swimming sperm to reach the ovum first, and is a trait found in polygamous species. Evidence suggests that humans evolved in primarily polygamous societies and were subject to sexual selection pressures, although the high variance suggests that other factors have promoted a certain degree of monogamy.

Since Trivers (1972) proposed parental investment theory, other factors that can alter mating strategy and thus sex differences have been evaluated. For example, changes in mating strategy can occur due to a skew in the sex ratios of a species population (e.g., due to biases in the sex ratio at birth or in juvenile/adult survival). Under these circumstances, sex role reversals can be found such that females can become less selective and display increased intrasexual competition when few male mating partners are available, and males can become more selective in choosing from the relatively high number of available female mating partners. Furthermore, if there are factors that create large differences in the health of one sex, mating strategies can be adjusted. For example, males can become more selective when there are large numbers of females with variation in mating quality, that is, if reproductive success is diminished to the extent that selecting superior females will increase the number of offspring (For review, see Clutton-Brock 2007).

Species that evolved in extreme environmental conditions, in which the survival of both sexes are endangered, can develop unusual mating strategies that may be accompanied by unusual displays of sex differences. For example, the *Heterocephalus glaber* (common name: the naked mole-rat) is one of a few mammalian species that have developed an extreme form of cooperative breeding, called *eusociality* (For review, see Holmes et al. 2009). One breeding female and 1–3 breeding males are the only reproductive

members of colonies that on average are composed of 60–80 animals. All other nonbreeding members in the colony are reproductively suppressed; these animals, termed subordinates, do not undergo pubertal changes, and do not make attempts at mating. Subordinate members lack sex differences in external genital morphology, body size, gonadal steroids, or sex-typical behaviors (i.e., both sexes participate in parental care, colony work, and predator defense). However, sex differences can develop in subordinates if removed from their colony and housed with an opposite-sex conspecific. While transitioning from subordinate to a reproductively capable animal, sex differences emerge in the level of sex hormones, as well as in the expression of steroid hormone receptor messenger RNA in the brain (Swift-Gallant et al. 2015). Cooperative breeding is likely necessary for this species' survival; food is challenging to locate in the subterranean burrows where the naked-mole rat resides, and during dry season the soil becomes difficult to burrow, making food retrieval especially challenging. Many colony members are required to successfully reach food sources (Holmes et al. 2009) and thus eusociality likely evolved for this adaptive advantage.

The development of complex social structures within species can also gravely influence sexual selection pressures. For example, in some species, sex-reversal developed such that females are more aggressive/competitive than males. One extreme example is the spotted hyena. In this species, the male-typical endocrine mechanisms that underlie the sexual differentiation of aggression seem to have been co-opted by females to support the display of aggression and competition for rank within their social hierarchies. Gross aberrations in the female spotted hyenas' genitalia support the idea that females are exposed to male-typical endocrine influences. Specifically, female spotted hyenas have pseudopenises that resemble the external genitalia of males. Although the exact mechanisms underlying the genital growth in females is disputed, there is evidence that androgens, such as testosterone and its metabolites, are responsible for both the display of aggression in these animals as well as the male-typical genitalia in females (Glickman et al. 2006; McFadden et al. 2006).

In many cases, traits that are seemingly counter to a species' survival and/or reproductive success develop due to sexual selection pressures. For example, in some species males offer a nuptial gift to secure a mating opportunity, which are highly costly in terms of energy and resources of the male (Gwynne 2008), and in some cases the male himself is the nuptial gift as the female cannibalizes him, terminating his future reproductive success (Bilde et al. 2006). In many other species, males have flamboyant displays (i.e., that project health/propensity for survival) to attract mates, at the cost of also catching the attention of predators (Clutton-Brock 2007) – an obvious example being the vibrantly colored male peacock. In the case of the spotted hyena, the evolution of the pseudopenis in females appears to *decrease* reproductive success – more offspring are produced by female hyenas treated prenatally with anti-androgen that produce a smaller pseudopenis (Glickman et al. 2006), and thus it appears that the increased aggression displayed by females with a pseudopenis supersedes the reproductive downfall of the male-typical external genitalia. Although many of these costs seem counterintuitive to the theory of sexual and natural selection, research indicates that these traits may have evolved to ensure reproductive success.

Together, environmental conditions, sex ratios, gestational length, and social structures all contribute to mating strategies that work best for the reproductive success of various species. Depending on the mating strategies that develop, sex differences in physical morphology and neurodevelopment evolve to support each of the sexes' mating strategy. This accounts for why sex differences across species range from large and numerous to few and small, and why in some species a trait can be more male-typical while the same trait will be more female-typical in another species.

The Functional Significance of the Magnitude of Sex Differences

Sexual dimorphism and sex differences are terms that are often used interchangeably. However, it

has been argued that a meaningful distinction should be made, and this distinction relates to the evolutionary function behind the sexual differentiation of the trait in question.

Sexual dimorphism is the term typically used when two distinct forms exist, with little overlap between the sexes (review by McCarthy et al. 2012). It can also be used when the trait is present in one but absent in the other sex. These types of sex differences are often directly associated with reproduction, i.e., courtship behaviors (e.g., male bird courtship singing) or copulatory behaviors (e.g., insertive vs. receptive; mounting vs. lordosis). Brain regions associated with sexually dimorphic behaviors are often obviously different in the number, shape, and biochemical make-up of neurons and glial cells. For example, the sexually dimorphic nucleus of the medial preoptic area (subdivision INAH3 in humans) is larger, contains more and larger neurons, and shows neural activational differences between males and females (Hendricks and Scheetz 1973; Arendash and Gorski 1983; Allen et al. 1989; Savic et al. 2001). The functions of this brain region include many basic sexual behaviors and preferences in males.

The term sex difference is often used for differences between the sexes that are not as binary. Many sex differences fall along a continuum: Males and females can land on either extreme of the continuum; however, sex differences exist in the overall averages. At the neuroanatomical level, these differences are not as distinct as sexual dimorphisms, although some sex differences are still observed in neuron/glial number and/or size, and/or neural responses. These sex differences are not always directly related to reproduction, but often result due to downstream effects of genes, hormones, and environment associated with reproductive success. For example, female humans display increased empathy on average compared to males. This sex difference in empathy has been associated with reproductive hormones such as testosterone (fetal testosterone decreases ability to empathize; for review, see Christov-Moore et al. 2014). Although empathy may not be directly linked with reproductive function or mating, it may have evolutionary

advantages; empathy, the ability to understand and share in the internal states of others, has advantages for building social relationships. Females, being the primary caregiver in many species, may have an increased benefit from the display of empathy for the purpose of understanding the needs of their offspring (Christov-Moore et al. 2014).

In addition to sex differences that likely evolved due to sexual selection, De Vries has proposed that some sex differences may exist to *compensate* for the sex differences in physiology. Sex differences in brain structure may prevent sex differences in overt functions and behavior, while in other instances no sex difference may be observable in a particular behavior, but the underlying neuroanatomy and/or neurophysiology may differ between the sexes. For example, parental care is relatively equal among the monogamous male and female prairie voles; however, differences exist in the underlying mechanisms leading to parental care in this species – hormones produced during pregnancy facilitate the display of maternal care in females, but in males a neuropeptide, vasopressin, underlies paternal care behavior (De Vries 2004).

Conclusion

Research in comparative evolutionary psychology indicates that the development of sex differences across species can largely be traced to sex-specific effects of genes and hormones. However, the sexual selection pressures on a given species determine the nature and extent of the sex differences that develop. Sex-specific genes and hormones are well conserved throughout vertebrate evolution; however, the function of these genes and hormones are co-opted to produce sex differences that contribute to the reproductive success of a species. Through the use of comparative psychology approaches and by studying the evolutionary history of species, evolutionary psychologists continue to expand our understanding of why sex differences develop as well as how the mechanisms underlying sexual differentiation evolve to allow for sexual selection.

Cross-References

- [Charles Darwin: Theory of Sexual Selection](#)
- [Commitment Skepticism](#)
- [Copulatory Intrasexual Competition](#)
- [Female Mate Choice \(Intersexual Selection\)](#)
- [Intrasexual Selection](#)
- [Observations of Sexual Dimorphism](#)
- [Parental Investment and Sexual Selection](#)
- [Sex Differences](#)
- [Sex Differences in Same-Sex Aggression](#)

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Development of Sex Differences in Brain and Behavior

► Development of Sex Differences

Developmental Correspondence Between Childhood and Romantic Attachment

► Romantic Attachment and the Prototype Hypothesis

Developmental Milestones

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Synonyms

Maturation achievement

Definition

Behaviors that develop throughout infancy and childhood, such as crawling, walking, and talking.

Introduction

As infants enter the world, their awareness and perception of their environment are experienced through their response to external stimuli. At the time of birth, infants possess functional sensory skills including audition, haptics, olfaction, gustation, and vision. These skills enable infants to obtain information and stimulation from their environment while also maturing these senses to further gain perceptual knowledge in their later years. After birth, humans continue to develop and achieve new functions as they grow. This development of a new function is considered a milestone in human development. As one grows into adulthood, he or she will undergo multiple cognitive and physical milestones, including critical developments in language/communication and motor/movement skills.

Although every individual endures his or her own unique course of development for approximately the first 15 years of life, most people experience developmental milestones at approximately the same age in their lives. Generally, delay in developmental milestones is associated with a subsequent diagnosis of learning disabilities (Murray et al. 2007). It is critical for healthcare professionals and parents to maintain close attention to the development of their children as routine developmental surveillance (both clinical clues and developmental milestones) can be signals to indicate the need for in-depth assessment which can detect possible developmental conditions (Romanczyk et al. 2005).

The Five Senses: Vision

Every individual relies on the development of his or her five senses. Every second of every day at least one of the five senses is firing; these senses are even working when one is asleep. The five senses are a fundamental component to consciousness and help one understand the world around them, collaborating to ensure the individual maintains a safe and healthy lifestyle. One's senses impact the way in which humans live by creating a major influence on the development throughout one's lifespan.

At the time of birth, an infant's visual perception is still developing but is capable of viewing objects up close. In comparison to the vision of an adult, infants are unable to see images of small diameter at a distance due to the underdeveloped muscles, lenses, and nerves (Santrock 2011). An infant's visual perception is "estimated to be 20/240 on the Snellen chart used for eye examinations, which means that a newborn can see at 20 feet what a normal adult can see at 240 feet" (Santrock 2011, p. 135). However, the lack of 20/20 vision gives them just enough visual perception for one's role as an infant. Human primates depend heavily on the sensory system with more than half of the brain dealing with the processing of visual information (Slater 1998). By approximately 6 months old, one should perceive the world with 20/40 vision. However, satisfactory vision requires coordination of sensory vision (i.e., form, motion, color, and pattern with precise eye movement) (Slater 1998). It is important for an infant to seek visual stimulation early in life. Visual development is comprised of a variety of sensitive periods for distinctive visual functions. If one is visually deprived early in life, he or she will often fail to develop full visual capabilities (Slater 1998).

One's ability to perceive light involves an interaction of mechanisms at the retina in order to perceive the wavelengths of light in the visible spectrum (Slater 1998). Specifically, it is crucial for an infant to develop the two types of photoreceptors known as *rods* and *cones*. Rods are light-sensitive cells located within the retina of the eye and allow one to see objects in dim lighting. On the other hand, cones allow one to perceive color and objects in bright lighting. There are three different cone types in the normal human: S-cones, which see short-wavelength light (e.g., blue); M-cones, which see medium-wavelength light (e.g., green); and L-cones, which see long-wavelength light (e.g., red). Failure to develop these three different cone types can result in color blindness (Slater 1998).

As a child develops, not only does he or she undergo the process of developing vision, but simultaneously developing color vision as well. The average child can distinguish between

various colors by 8 weeks old, although some evidence indicate they may be able to distinguish various colors by 4 weeks (Santrock 2011). However, other scientific evidence has indicated 1-month-olds often fail to make some color discriminations (e.g., green vs. yellow) that one would expect they should be able to make if they had all four functional photoreceptors (rods plus three cone types) (Slater 1998). However, by 2 months, evidence suggests that normal infants can make most discrimination, particularly if stimuli are large and differences between stimuli are marked.

An important development in vision is the development of perceptual constancy. Perceptual constancy allows for an infant to perceive an object as the same at different distances or different orientations. There are multiple types of perceptual constancy, including shape constancy and size constancy. Humans experience shape constancy when viewing moving objects. When an object moves, there is a change in its spatial orientation; however, when one views the moving object, these changes in the object's spatial orientation do not affect the person's visual perception of it (Slater 1998). For example, if a person views a closed door, he or she may view the door as a rectangle. However, if the door is opened, the shape of the door (from the angle of the viewer) changes to something more trapezoidal in shape, but the viewer will still see the door as its original shape (i.e., rectangular). It has been found that infants at 3 months possess shape constancy, but do not have shape constancy for irregular shaped objects (Santrock 2011).

Size constancy is the awareness of an object's size as one moves toward or away from the object. Hence, the size of an object on the retina does not tell the viewer the object's actual size (Santrock 2011). For example, as objects move farther away from a viewer, the object appears smaller, but the viewer is aware that the object has not actually changed in size. Infants display some size constancy at 3 months old, but it is not fully developed until 10 or 11 years of age (Santrock 2011).

Once an individual reached adulthood, they have perception of occluded objects, whereas during infancy, one cannot perceive an object as a

whole when it is blocked by another object in front of it. By approximately 3–5 months of age, an infant has the capability to track temporarily occluded moving objects, and around 5–9 months of age, infants have the ability to trail moving objects that disappear progressively behind an obstructed barrier, disappeared abruptly, or collapse, although an individual is more capable of predicting a moving object when it disappears gradually rather than abruptly or collapsing (Santrock 2011).

Depth perception also plays a vital role in one's life, as it allows for one to accurately recognize the location of objects in one's environment, which is essential for efficient movement within one's environment. Depth perception, also referred to as stereopsis, is "when specialize cells in the brain's visual cortex compare the inputs from the two eyes and abstract a signal that conveys very small depth differences for targets that are relatively close – within arm's length" (Slater 1998, p. 34). In a landmark study, Walk and Gibson (1960) assessed infants' depth perception by constructing a miniature cliff with a drop-off covered by glass to give the illusion of an actual cliff. As infants were placed on the edge of the visual cliff, mothers coaxed them to crawl onto the glass; however, most infants would not crawl past the shallow side onto the glass. This was an indication that infants could perceive depth from 6 to 12 months of age (Santrock 2011). However, due to the inability to crawl at a young age, it is difficult to detect whether younger infants perceive depth. An alternative study was conducted on younger infants due to the incapability of crawling. The researchers monitored the infants' heart rates to measure their ability to perceive depth. Between 2- and 4-month-old infants, there were differences found in heart rate when they were placed on the deep side of the visual cliff instead of on the shallow side (Santrock 2011). However, this was not a valid acquisition but rather a display of differences between younger and older infants' visual characteristics, with no definite knowledge of depth. It can be concluded that infants of about 3–4 months of age develop the ability to use binocular cues to depth (Santrock 2011).

The Five Senses: Audition

Humans' sense of hearing develops while in the womb. Hearing is one's ability to recognize sound by the current of vibrations entering the ear. Within the last 2 months of pregnancy, the fetus has the ability to hear sounds such as the mother's voice or music (Santrock 2011). The changes in an individual's hearing are due to the perception of a sound's loudness, pitch, and localization. At the time of birth, infants do not have the capability to hear soft sounds, so they require communication to be spoken at normal conversation level rather than soft whispers. Pitch is the perception of the frequency of a sound. Infants are less sensitive to deeper low-pitched sounds and are more likely to hear high-pitched sounds (Santrock 2011).

At 1 month old, infants begin to show interest in the sound of human voices – specifically, the voice of their parents (James 2009). By 2 months old, infants become interested in the exchange of communication between two individuals. Infants can differentiate between sounds' pitches and intensities (James 2009). Infants also have the capability to generalize the location where sound is coming from (Santrock 2011). As sound is produced, an infant will turn his/her head in the direction the sound is coming from (James 2009). At 4 months old, infants develop the ability to hear soft sounds. Around 5 months old, infants have the ability to develop his/her understanding of language (James 2009).

Six to ten months is a major stepping stone in the development of an infant's understanding of sound. As infants are able to identify certain sounds, they may imitate those sounds and/or respond to their names (James 2009). Moreover, this time frame develops an infant's ability to link words with gestures (waving goodbye and saying goodbye mean the same thing). When approaching 10 months old, an infant can identify the difference between a male voice and a female voice (James 2009). Before an infant reaches 1 year, he/she will have the capability to participate in a conversation. However, they can understand more words than they can speak (James 2009).

The Five Senses: Smell and Taste

Individual's olfactory sense allows for one to identify between different odors and be consciously aware of one's external environment. Olfactory sense also plays a key role in his or her gustation perception and can have linkage to other somatic systems (respiratory and/or neurological) (Wittmann-Price 2010). The olfactory sensory epithelium is composed of a few million olfactory sensory neurons (OSNs), which are generated in situ from stem cells (Mombaerts 2001). Facial expressions are reliable indicators of the portrayal of smell. For example, a face of disgust represents smelling something repulsive, and a face of delight represents smelling something sweet or savory. With this, one can identify if a newborn has developed an olfactory sense. The expressions on an infant's face tell one that the infant enjoys sweet smells, vanilla and strawberry, but dislike the scents of odd or foul foods such as fish or rotten eggs (Santrock 2011).

Additionally, olfactory and gustatory senses begin developing in utero, which has great implications for lifelong nutritional habits (Wittmann-Price 2010). As one begins to eat, their taste buds are highly linked with sense of smell; this is "because olfactory receptors are stimulated from both the nostrils and nasopharyngeal passages" (Wittmann-Price 2010, p. 2546). Between 8 and 9 weeks in fetal development, the taste buds begin to develop, while the olfactory system is developed between 16 and 18 weeks. By 28–29 weeks, olfactory receptor neurons are mature (Wittmann-Price 2010).

As a mother is pregnant, her diet has a key impact on the child's lifelong taste preference because of certain dietary selections (Wittmann-Price 2010). Research found that 6-day-old infants who were breastfed displayed a higher preference for smelling their mother's breast pad over one that was clean. Although once the infant was 2 days old, there was no indication of this preference suggesting that recognition of scent requires several days (Santrock 2011).

Gustation and olfactory senses are closed linked (Breslin 2013). Taste is stimulated when nutrients or other chemical compounds activate

specialized receptor cells within the oral cavity. Individuals have the capability to differentiate between the four basic tastes of sweet, sour, salty, and bitter. One's preference to taste is influenced by diet and nutrition. In order for the sense of taste to develop, papillae – taste receptors inside taste buds – must develop. Taste has a heavy influence on the body as it allows humans to evaluate food for nutrition as well as harmful toxins, allowing humans to decide what to ingest. It also helps the body prepare for the metabolizing of foods once they have been ingested (Breslin 2013).

It is important for an individual to be able to identify taste to be aware of toxins going into the body. Human taste abilities have been shaped by the ecological niches our evolutionary ancestors occupied and by the nutrients they sought (Breslin 2013). Additionally, it allows for one to properly develop by ingesting the necessary nutrients and avoiding harmful substances.

The Five Senses: Haptics

The sense of touch – known as somatosensory function – is defined as the detection, discrimination, and recognition of touch sensation and proprioception (Dunn et al. 2015). The process of sensation is conveyed by sensory receptions in the skin, joints, tendons, muscles, and viscera (Dunn et al. 2015).

Somatosensory has been measured on four levels: detection (noticing stimuli), discrimination (distinguishing among stimuli) affecting the quality of movement, scaling (grading stimuli), and object recognition (knowing what the object is by touch) (Dunn et al. 2015). Not only does somatosensory allow one to experience touch sensation and proprioception, it makes possible for one to experience pleasure and satisfaction, learn and adapt, and experience the touch of others (Dunn et al. 2015). At the time of birth, a newborn has the sensation of touch, as a touch to the newborn's cheek can result in the turn of the head and a touch to the lips initiates the rooting reflex (i.e., sucking movements) (Santrock 2011).

Children between 3 and 4 years of age display the most inconsistency and failure among detection, discrimination, scaling, and object recognition. However, accuracy improved as the child got older, which is consistent with the rate of development of the somatosensory cortex in the children's brains (Dunn et al. 2015). As one gets older (over 70 years), their haptic recognition (recognizing an object simply by touch) and sense of touch in their feet become significantly less accurate. This decline is more pronounced in aging females than males (Dunn et al. 2015). This difference is probably due to age-related changes in the nervous system.

Physical Development: Gross Motor Skills

Gross motor skills are large general movements that require development of muscle tone and involve large muscle activities. For example, controlling one's posture – the ability to sit upright and/or stand – is a gross motor skill that is foundational in the development of other gross motor skills like crawling and walking (Santrock 2011). The start of postural control starts at infancy. Within the first few weeks of life, an infant can hold their head erect and not long after can lift their heads (Santrock 2011). By 2 months old, infants have the ability to sit in an infant seat or on an adult's lap with support, and between 6 and 7 months, an infant can sit independently without support. From the development of postural control, an infant develops the ability to stand between 8 and 9 months by pulling oneself up and being supported. Between 10–12 months, an infant can stand alone (Santrock 2011). This leads into 1 year of age, the time where the development of crawling and walking beings.

Much like an individual's five senses, the development of motor skills goes through a step-by-step development over the course of one's lifespan. Arnold Gesell, a developmental psychologist, discovered that there is a fixed order and time frame where children progress between rolling, sitting, standing, and other motor skills (Santrock 2011). This structured development Gesell argued is preprogrammed by one's genes.

Conversely, later research has indicated that one's motor development is not as congruent as Gesell had claimed. Esther Thelen proposed an influential counter theory – known as dynamic systems theory – which argued that perception and action are connected, as an infant uses his/her perception in the environment to seek an object or person of interest. This motivates the infant and develops one's motor skills (Santrock 2011).

Researchers in the 1930s claimed that there were two main factors impeding achievement of walking: leg strength and balance control (Adolph et al. 2011). It is important for one to be able to gain muscle strength and maintain balance in order for an individual to develop one's motor skills. An infant needs to be able to sustain body weight and balance on one leg at a time, "prior to independent walking, infants exhibit several transient upright skills that mitigate the requirements of single limb support" (Adolph et al. 2011, p. 306). Additionally, infants need the ability to control their muscles. Infants learn to walk once maturation of the nervous system allows them to gain the ability to have this sense of control. Starting at a very young age, the neural pathways that control leg alteration are developed (Santrock 2011).

Infants look for support when learning to walk, whether it is a parent's hand or nearby furniture. At roughly 14 months old, an infant has the ability to hold onto furniture to pull up to an upright position. Also at this age, infants have the strength to stand alone, walk forward, or cruise sideways with the support from furniture (Adolph et al. 2011). Cruising is the process that infants may develop prior to crawling – it involves the infant walking in a shuffling manner while holding on to furniture. Cruising has been linked to the development of leg strength as well as increases in sensitivity to perceptual information for balance and coordination (Adolph et al. 2011).

Different milestones involved in walking happen at different times for individuals but are developed within the same age range. Most infants cannot walk until their first year of life. From birth to about 6 months, however, infants engage in kicking movements while on their back. By approximately 9 months, an infant is capable of

judging the depth in front of him or her in order to learn forward in a sitting position (Adolph et al. 2011). When learning to walk, an infant's process changes each time they attempt to walk as by walking continuously; each walking step is slightly different from the last. This is because of the different locations and grounds that one covers and the "continually varying biomechanical constraints on the body, may help infants to identify the relevant combination of strength and balance required to improve their walking skills" (Santrock 2011, p. 128).

Although the first year is a major milestone due to the development of walking, the second year of life a child becomes more comfortable and mobile. Once infants approach 1 year, the developmental process time span expands giving infants more range in which they reach various milestones. Between 18 and 24 months, children begin the process of walking quickly or a variation of running for a short distance (Santrock 2011). Additionally, during this age range, infants learn to balance on their feet while squatting to play, walking backward without losing balance, kicking a ball while standing and not falling, throwing a ball, and jumping in place. From here on, infants continue to grow and master the skills of walking, and running eventually becomes more automatic and less conscious (Santrock 2011).

Cognitive Development: Piaget's Four Stages

The development of cognitive abilities throughout childhood allows children to begin developing schemas – which are cognitive frameworks that help people organize information that they learn in a way that helps them make sense of the world (Santrock 2011). Therefore, when a child has a thought regarding a certain aspect of the world, all of the information regarding that aspect is comprised in a schema, and that allows for an understanding of that aspect of the world. For example, let us say that a child has an idea of a cat. The child's schema for "cat" contains information like "small, furry, fluffy tails, meow, and smell nice." Whenever the child interacts with something that

possesses these qualities, the child understands that he/she is interacting with a cat. This is considered a state of equilibration – in which the child's understanding of *cat* is consistent with what he/she currently perceives as *cat*. However, now let us imagine that the child interacts with a skunk for the first time. The child may initially attempt to categorize the skunk in the *cat* category because they are both small and furry and have fluffy tails, but the child quickly realizes that this new animal does not meow and does not smell nice. This new information does not fit with the child's current understanding of the world, which leads to disequilibrium – a state of confusion that the child wishes to resolve. The child then attempts to resolve through processes known as assimilation and accommodation.

Assimilation is a process through which people interpret new experiences in terms of existing schemas. For example, children may learn that a skunk is not a cat because it does not meow, and it can emit a very foul smell that cats cannot. Therefore, the child develops an understanding of what a skunk is by understanding how it is different from a cat. This assimilation can allow for a new understanding of the world, which is a new state of equilibration.

Accommodation is a process of modifying one's current schemas in order to account for new experiences in one's environment. For instance, if a child has a schema for dogs that is based on his/her experiences with very small dog breeds like Chihuahuas or Pomeranians, but sees a large dog (e.g., Great Dane, St. Bernard, etc.), the child may have to change his/her schema in order to account for the new animal. Thus, the schema of *dog* changes from "small, furry, and barks" to something like "furry, barks, and size varies."

Piaget's theory of cognitive development focuses on how children use these techniques to develop these schemas and how children utilize their environment to help understand the world around them. Piaget also posits that children are active agents in their environment who are trying to obtain knowledge about the world around them. However, this ability to think and understand the world is something that develops over time and goes through some radical changes during that

process. These changes are marked by four stages of cognitive development, with each stage containing more complex abilities than the previous one.

The first stage is known as the sensorimotor stage. This stage occurs approximately during the first 2 years of one's life. During this stage, an infant will construct an understanding of the world by coordinating his/her sensory experiences with his/her motor movements. In other words, they learn by directly interacting with their environment in very basic ways, such as listening to sounds and touching objects. This allows infants to learn which sounds are desirable (e.g., pleasant sounds, like basic musical tones) and which sounds are undesirable (e.g., loud sounds that may startle the infant, such as breaking glass or a hammer hitting a wall). This also allows infants to learn which textures are pleasant to touch (e.g., soft things such as pillows, blankets, teddy bears, etc.) and which textures are unpleasant to touch (e.g., hard surfaces such as concrete, sharp objects, etc.). This stage marks the first understanding of one's surrounding environment.

The information that infants gather during the sensorimotor stage allows them to begin developing schemas. However, the sensorimotor occurs so early in life that the cognitive processes occurring in this stage are somewhat primitive when compared to the latter stages of Piaget's theory of cognitive development. For example, according to Piaget infants in this stage tend to not have object permanence yet – which means when they stop looking at an object, that object no longer exists (Piaget 1954). However, some research has shown that infants as early as 3 months old may possess some rudimentary form of object permanence (Baillargeon 1987).

Infants' actions within the sensorimotor stage begin with physical reflexes to one's environment. These reflexes eventually develop into more controlled motor movements and sporadic imitation (in which infants imitate basic motor movements that they see), which develops into more complex forms of imitation in which infants begin imitating words and facial features that they hear and see (Piaget 1951). These basic forms of movement are illustrated in children's play. During this stage,

Piaget (1951) noted that children begin engaging in practice play. This type of play consists of repeated body movements, such as putting objects in one's mouth or playing peekaboo.

The crowning achievement of the sensorimotor stage is the development of object permanence and symbolic thought. This means that the children are able to think about things (e.g., objects, people, animals, etc.) and use language, images, and gestures to articulate their thoughts about these things (Piaget 1954). At this point, these children progress to Piaget's second stage – the preoperational stage.

The preoperational stage occurs approximately between the ages of 2 years old and 7 years old. At this point, children begin to manifest their environment through talking about their home and drawing pictures of their family (Piaget 1954). However, children in this stage still have difficulty with logical thought. Specifically, preoperational children have difficulty solving conservation and classification problems. For example, if someone were to take a glass of water and pour the water into a taller, thinner glass container, children younger than 6 or 7 years old typically do not understand that the volume of liquid has not changed (i.e., it is conserved). In the case of classification difficulties, children in this stage lack class inclusion, which is the ability to relate a whole class (e.g., furry animals) to its subclasses (e.g., dogs, cats). For instance, if a researcher gives a preoperational child a drawing of seven dogs and three cats, then asks the child "are there more dogs or more animals in this picture?" the child tends to think the correct answer is *dog*.

Play in the preoperational stage increases in complexity from the sensorimotor stage. Preoperational children will often engage in make-believe role play. They may dress up as another individual (e.g., police officer, fireman, etc.). Their newly acquired ability of symbolic thought allows them to use objects to symbolize something other than the intended function. For example, they may use a ruler or stick as a pretend sword.

Children in the preoperational stage tend to be egocentric. This means that these children have a tendency to view the world solely from their own perspective. They have difficulty recognizing other people's points of view in an environment.

The three-mountain task has been used to examine this. A child is placed at a table with a model of three plastic mountains sitting side by side on it – one with a pole on it, one with a cross on it, and one with nothing on it. The child is then asked to draw the mountains the way that he/she sees it. After that, a doll is seated at the opposite side of the table, and the child is asked to draw the mountains the way that the doll sees them. Often-times, the child draws the mountains the same way as he/she sees them and does not take into account that the doll is seeing the mountains from opposite side of the table, which would reverse the order of the three mountains (e.g., the mountain with the cross on it may be on the far left from the child's perspective, which would make it look like it is on the far right from the doll's perspective).

Once children have mastered conservation and classification – and are able to understand that people see things differently from different angles and perspectives – they move on to the concrete operations stage, which is Piaget's third stage of cognitive development (Piaget 1954). This takes place approximately between the ages of 7 years old and 11 years old.). During this stage, play develops into games with rules. In other words, play becomes more structured with rules. This may also cause the development of teams and competition (Piaget 1951). Also during this stage, children are able to understand that properties such as mass, weight, and volume do not change when an object changes form. For example, if an ice cube melts, it still contains the same amount of water. Children in this stage also tend to be successful with classifying objects by a varying number of classes (e.g., weight, size, color, etc.). However, in this stage of cognitive development, children tend to only do well with concrete examples – not abstract ones. In other words, physical examples are needed for these children to understand the concepts of conservation and classification. Trying to reason with abstract principles tends to be too difficult for children in this stage (Piaget 1954).

The fourth and final stage of Piaget's theory of cognitive development is known as the formal operations stage. This stage takes place from 11 years old to adulthood (Piaget 1954). It is in this stage where children are able to develop

rational thought regarding abstract ideas and principles – no physical examples are needed anymore. Many forms of complex thought begin to develop in the formal operations stage. For example, metacognition begins to occur. This is the ability to think about one's own thoughts. This allows for adolescents to ponder the purpose and utility of their thoughts and emotions. This helps develop self-regulatory learning, which is the ability to monitor one's own thoughts and behaviors in order to reach a specific goal. For example, John is an eighth grade student who realizes his grades have begun to decline. After thinking about it for a while, John realizes that he is easily distracted by his best friend who sits next to him in class. John likes his best friend and has a lot of fun talking to him, and that is why he sits next to him, but John has a goal of making the honor roll this year, so he has decided to sit in a different seat so that he can complete his work and improve his grades.

This complex thinking also leads to hypothetical-deductive reasoning, which is the ability to develop predictions/hypotheses and test them. This ability is often examined using the pendulum task. Adolescents are asked one question: "Which of the three things contributes to how much a pendulum swings: the weight of the pendulum, the length of the pendulum's string, or the force at which the pendulum is pushed?" The adolescents are then given three strings that vary in length and three different weights. The point of the task is to see how the participants reason through it. People who are not engaging in hypothetical-deductive reasoning tend to grab strings and weights at random, whereas those who are engaging in hypothetical-deductive reasoning tend to grab one weight, then systematically vary the string length, and vary the force at which they push the pendulum in order to see if variations in length or force affect the swing of the pendulum (Siegler et al. 1973).

Cognitive Development: Attention and Memory

Cognitive functioning is an important development process for an individual as it is the makeup

of memory, attention, and reasoning to develop one's knowledge. Attention is defined as the focusing of mental resources on select information (Santrock 2011). Attention allows one to fixate on a task or object and not get distracted. One's attention process determines the information selected for subsequent perception, action, learning, and memory (Amso and Scerif 2015).

During infancy one's visual attention is strongly influenced by eye movements. At 3 months old, when pointed to by a parent, infants can rapidly change his/her visual attention, but it is not until between 4 and 6 months old that an infant can suppress competing information during attention-orienting shifts (Amso and Scerif 2015). This involves being able to direct attention to important locations and object features such as color and/or shape (Santrock 2011).

Another type of attention is called *sustained attention* or *focused attention* which allows infants to learn and remember attributes of a stimulus as it becomes familiar (Santrock 2011). Sustained attention can be found within infants as young as 3 months old and develops substantially in the second year of life (Santrock 2011).

At approximately 7 to 8 months old, an infant develops another aspect of attention known as *joint attention*. Joint attention is the process of focusing on the same object or event, which requires the ability to track another's behavior (e.g., following someone's gaze), directing the behavior of another, and common interactions (Santrock 2011). Then, by an infant's first year of life, he/she has the capability to direct adults' attention to objects or images that grasp their concentration (Santrock 2011). Attention in an individual continues to develop throughout childhood and improves significantly within the preschool years.

There are two areas of attention that children develop during the preschool years: *executive attention* and *sustained attention*. Executive attention includes goal-directed behavior that allows the child to pay attention to goals, planning, and even errors that impede goal achievement. Executive attention is also utilized to help the child understand how to deal with difficult situations. Sustained attention, on the other hand, allows for

extended focus on particular objects, events, or other aspects of one's environment (Santrock 2011). During the preschool years, the more a stimulus stands out in their environment, the more attention children will pay attention to it. When an infant or child has the inability to fixate on an object or task, it could be the result of atypical visual attention development. Atypical visual attention development is an abnormal attention span which can be indicative of a variety of disorders including attention deficit hyperactivity disorder (ADHD), autism spectrum disorder (ASD), and/or fragile X syndrome (FXS) (Amso and Scerif 2015). One's attention correlates highly with working memory capacity and his/her short-term and long-term memory.

Infants between 2 and 6 months old have the capability to remember certain experiences through 2 years of age. However, this can be the cause of infants only using implicit memory rather than both implicit and explicit memory according (Santrock 2011). Implicit memory is memory without conscious recollection, such as procedural memory – memories of skills and routine procedures that are preformed automatically. Explicit memory, on the other hand, is memory that requires conscious attention, such as the memory of facts (semantic memory) and experiences (episodic memory). In infancy, one's explicit memory of brief experienced visual information can be stored for up to 2 weeks (Schneider and Ornstein 2015). A longitudinal study of infants within their second year of life found that “older infants showed more accurate memory and required fewer prompts to demonstrate their memory than younger infants” (Santrock 2011, p. 158). Researchers have acknowledged that 6-month-old infants have a better ability of remembering information for 24 h. Infants by the age of 20 months have the ability to remember information they encountered 12 months earlier (Santrock 2011).

When given enough exposure and appropriate cues, infants can retrieve information after extended periods of time. This retention increases linearly between 2 and 18 months of age (Schneider and Ornstein 2015). However, most individuals cannot remember any events that occurred prior to the age of 3–5 years old. This

memory loss, known as *infantile amnesia*, is caused by the lack of a fully developed prefrontal cortex and hippocampus (the so-called memory center of the brain) during these early years of life (Santrock 2011). Therefore, during individual's younger years, their memory is rather brief and requires time and development to become substantial.

Cognitive Development: Language and Communication

Language is a way for individuals to communicate with others, which can manifest verbally or visually (in the form of writing or images). The community one lives in defines both written and spoken languages. The variation of dialect the community uses also affects the way written language is utilized. The use of language is important in one's life because individuals utilize language to share and/or exchange information, news, and ideas.

All languages are comprised of phonological development. Phonology is the study of sound systems – specifically how sounds are used and combined – referring to the system of a distinct language (Stoel-Gammon 2006). At birth, infants have their own way of communicating through babbling, crying, smiles, and gestures (Renzi et al. 2017). Language development begins with the recognition of different sounds. For an infant to develop speech, they must effectively monitor and assess their own self-generated speech (Masapollo et al. 2016).

Infants are able to identify the differences in sounds in multiple languages only during the initial months of life. By 6 months old, infants become more successful at detecting the sounds and changes in the language their parents or guardians speak to them. As an infant reaches 5 months old, they have the ability to vastly develop their vocal skills by viewing an adult pronouncing vowels and sounds on a television (Masapollo et al. 2016). Infants have the ability to link sensory patterns with what they see and hear with sensorimotor patterns that they are trying to construct. Infants pay close attention to

phonological features, which allows infants to recognize permissible sequences of these phonological features as well as their frequency of occurrence within the language input the infants receive (Stoel-Gammon 2006). The input that infants often retain and learn language through differs from that of “normal speech.” Infant-directed speech is also known as “motherese,” characterized by reduced speed, elevated pitch and affect, and unusual prosody (Eaves et al. 2016).

The first 3 years consists of “prelinguistic” vocabulary (Stoel-Gammon 2006), which includes variations of sounds that are not actual words but resemble actual speech. For example, variations of “mama” and “dada” are not actual words yet they resemble the attempts to produce the words “mommy” and “daddy”; however, it illustrates that the infant has sound-meaning relationships of conventional adult-based words (Stoel-Gammon 2006). An infant's prelinguistic vocabulary is a production of speech containing some of the phonetic features found in adult languages, which then progresses through developmental stages. This progression begins with vowel-like utterances at 2 months old and continues through a period of vocal play toward sequential productions of consonant-vowel strings around the end of the first year (Stoel-Gammon 2006).

Linguistic development can be divided into five stages (Stoel-Gammon 2006). Stage one – known as *phonation* – takes place during the first 2 months of life. This first stage consists of verbal pronunciations that have little resemblance to adult speech due to involuntary motor patterns. Vocal behaviors during this stage involve mostly reflexive (sometimes called *vegetative*) dialogues, such as crying, fusing, coughing, sneezing, and burping.

Stage two – *cooing* – takes place between the ages of 2 and 4 months (Stoel-Gammon 2006). Intentional communication begins during this stage via expressive vocalizations and smiles. As infants become familiar with their capabilities as a communicator, they become more mindful of their parents' behaviors and the impact the infant can have on those behaviors (Renzi et al. 2017).

This stage is the production of vowel-like sounds called *coos* and “are characterized by nasal resonance and are generally perceived as containing vowels and consonants produced at the back of the mouth (velars, uvulars) and back vowels” (Stoel-Gammon 2006, p. 643). As an infant attempts to pronounce consonant-vowel syllables in stage two, he or she may struggle with timing of opening and closure gestures that are within syllable timing in adult communication (Stoel-Gammon 2006).

The third stage – known as *vocal play* – takes place during the ages of 4–6 months. During this stage, infants begin producing nonsensical vowel-like sounds such as shouting, squealing, rumbles, and raspberry sounds. Producing these sounds suggests that the infant is exploring their vocal capabilities and producing consonant-vowel syllables. Additionally, the earliest an individual can recognize their name when spoken is at 5 months.

From the ages of 6 to 10 months is considered stage four – *canonical babble*. This is the alternation of consonants and vowels. The infant’s syllables consist of single syllables or repeated syllables, such as “mama.” This is due to the “timing and phonetic characteristics of these syllables which are similar to those of adult speech” (Stoel-Gammon 2006, p. 644) and resemble words of the adult language. This is vocal progression of multisyllabic utterances and reduplicated babbles (the string of identical syllables) as well as variegated babbles (syllable strings with varying consonants and vowels). Both utterances occur in stage four (Stoel-Gammon 2006); however, variegated babble increases after the infant reaches 9–10 months (Stoel-Gammon 2006). Within approximately 8–12 months, an infant understands basic linguistics and begins using gestures to communicate. Gestures may include waving to say “goodbye,” nodding to say “yes,” and pointing to an object to acquire it or to draw attention to it.

The fifth and final stage begins at 10 months and older. This stage – known as *jargon babble* – is the stage of babble, also referred to as *intonated babble*, that is “characterized by strings of sounds and syllables uttered with a variety of stress and

intonational patterns” (Stoel-Gammon 2006, p. 644). During this stage, infants begin to use their own language instead of that of older children and adults in their environment. By 13 months old, they understand approximately 50 words. However, they cannot pronounce this many words until 18 months. Therefore an infants’ *receptive vocabulary* – the number of words they can understand – exceeds one’s spoken vocabulary (Santrock 2011).

Research on American children has found that the first words infants can recite have not changed for at least 50 years. These first words tend to be *dada, kitty, car, ball, milk, eye, hat, clock, and bye* (Stoel-Gammon 2006). By the age of 2 years old, infants’ can speak approximately 200 words. This dramatic increase in the number of words they can speak is known as a *vocabulary spurt* (Stoel-Gammon 2006). This also includes attempts of two-word speeches; therefore, a child learning the English language can produce multiple-word sentences.

Conclusion

Individuals experience a variety of changes over their lifespan that involve development in all areas and aspects. Proper development ensures individuals a healthy and proactive lifestyle that will later determine the adult he/she will become. It is important to monitor an infant and child’s development to understand if one meets the proper milestones at the given age, as there are extensive changes between birth and adolescence. Failure to reach these milestones can result in permanent underlying developmental dysfunction later in life.

Cross-References

- [Cognitive Development](#)
- [Communication and Developmental Milestones](#)
- [Duration of Childhood](#)
- [Eye Contact with Adults Versus Babies](#)
- [Humans Crawl: Species Atypical Movement](#)

- Imitation
- Language Acquisition in Infants and Toddlers
- Learning Versus Imitation
- Mobility: Crawling and Walking
- Object Permanence
- Social Development
- Social Learning
- Special Case: Autism
- Theory of Mind

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Developmental Noise

- Environmental Unpredictability and Betting

Developmental Plasticity

- Adaptive Plasticity

Developmental Psychologist

- Michael Tomasello

Developmental Psychology

- ▶ [Age of Parent](#)
- ▶ [Jay Belsky](#)

Developmental Stage

- ▶ [Duration of Childhood](#)
- ▶ [Stages of Development](#)

Deviant

- ▶ [Antisocial](#)
- ▶ [Monoamine Oxidase and Antisocial Behavior](#)

Device

- ▶ [Advanced Tools of Neanderthals](#)
- ▶ [Waterspouts \(Archerfish, Sharks, Rays\)](#)

Diabetes

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Synonyms

[Diabetes mellitus](#); [DM](#)

Definition

Diabetes is a group of metabolic disorders that are characterized by high blood sugar levels over an extended amount of time.

Introduction

Within the realm of evolutionary medicine, diabetes is often thought of as a form of maladaptation to the conditions of modern society. This modern ailment is often considered to be a prime example of an evolutionary mismatch.

The Evolutionary Relevance of Diabetes

In modern society, there are three major types of diabetes, type 1, type 2, and gestational diabetes. Type 1 diabetes is characterized by the pancreases' inability to produce insulin due to different potential issues regarding beta cells. Type 2 diabetes is hallmarked by insulin resistance; the cells in the body are failing to properly react to the presence of insulin. Lastly, gestational diabetes can be found uncommonly in pregnant women with no prior history of high blood sugar levels. This type of diabetes typically resolves after the conclusion of the pregnancy.

Diabetes is often considered an evolutionary maladaptation for several reasons. For example, in ancestral conditions, coming across foods with high sugar content was exceedingly rare, with the primary source being different fruits. The consumption of foods high in sugar had huge benefits, such as increased energy, which could potentially lead to the production of additional resources. This, in turn, would help the individual survive and pass their genes onto the next generation. However, after the industrialization of society, foods high in sugar are very common and easy to purchase and consume. This leads to the problem that is the overconsumption of sugary foods, which is one of the factors that directly correlates to the development of type 2 diabetes (Lean and Morenga 2016). The overconsumption of sugary foods paired with a largely sedentary lifestyle has given rise to the modern medical problem that is type 2 diabetes. The treatment for this form of diabetes consists of dietary restrictions and an increase in exercise.

Further, research into the evolutionary background of type 1 diabetes has shed new insights onto this form of the disease. Researchers Moalem et al. state "Recent animal research has uncovered

the importance of the generation of elevated levels of glucose, glycerol and other sugar derivatives as a physiological means for cold adaptation. High concentrations of these substances depress the freezing point of body fluids and prevent the formation of ice crystals in cells through supercooling, thus acting as a cryoprotectant or antifreeze for vital organs as well as in their muscle tissue. In this paper, we hypothesize that factors predisposing to elevated levels of glucose, glycerol and other sugar derivatives may have been selected for, in part, as adaptive measures in exceedingly cold climates” (Moalem et al. 2005). This finding would suggest some evolutionary advantage to the development of type 1 diabetes, particularly for those that lived in the extreme cold, as it would have temporarily aided in survival.

Conclusion

In conclusion, diabetes is a serious medical issue within the developed, industrialized world. This disease is best considered to be a classic example of evolutionary mismatch within the realm of evolutionary medicine.

Cross-References

- [Evolutionary Medicine](#)
- [Evolutionary Mismatch](#)

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Diabetes Mellitus

- [Diabetes](#)

Diamond Rings

- [Engagement Rings as Modern Commitment Cue](#)

Diane Ruble

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Introduction

Diane Nelesen Ruble is a social developmental psychologist who has contributed innovative research and theorizing across a broad array of topics relevant to evolutionary psychologists. This chapter begins with a description of her background and training, then an overview of her research interests and theoretical contributions, and ends with a brief conclusion about the contributions to the field of psychology.

Background and Training

Dr. Ruble was raised in Phoenix, Arizona, by a sports-loving family consisting of a mother, father, and three daughters. She excelled in academics as well as in sports, and those talents were apparent in her undergraduate time at Stanford University. Stanford provided the training and classes that set Dr. Ruble on her path of interest in social and developmental issues. In one of these classes with Eleanor Maccoby, her interest in gender was first peaked. She also was successful in sports being a member of the Stanford tennis team. In 1967, she graduated with honors and received a B.A. in Psychology. She then moved to University of California, Los Angeles, and was awarded a Ph.D. in Psychology in 1973.

Dr. Ruble's first academic position was at Princeton University but spent much of her

career in the Psychology Department at New York University where she was promoted to Associate and then Full Professor. Prior to settling in at NYU, she also spent a year at the University of Toronto, several years at Indiana University, and a year at University of California, San Diego. Each of these universities provided unique experiences with colleagues from social and developmental psychology, and these experiences colored Dr. Ruble's research and thinking about how children develop.

Dr. Ruble's research and theorizing led to her being asked to be Associate Editor of *Personality and Social Psychology Bulletin* and to act as Consulting Editor for the top journals in developmental (e.g., *Child Development*, *Developmental Psychology*), social psychology (*Journal of Personality and Social Psychology*, *Journal of Personality*), and women's studies (*Psychology of Women Quarterly*). Furthermore, Dr. Ruble was involved in committees for the major psychological associations including APA, APS, SRCD, and SESP. As a successful grant recipient at NIMH, she was also asked to serve on the Behavioral Science Panel for 3 years and was involved in a committee associated with NSF. Two working groups played an important role in connecting her with like-minded colleagues who were able to provide important direction for the field: one involved a Working Group on Social Identity (funded by MacArthur Foundation and Russell Sage Foundation) and the other was the MacArthur Foundation Network on Pathways through Middle Childhood.

Federal grants supported the research that Dr. Ruble conducted with a large cohort of successful graduate students. She received funding from NIMH, NIH, NSF, Spencer Foundation, Health and Welfare Canada, USA-Israel Binational Science Foundation, MacArthur Foundation, and Russell Sage Foundation. In addition to R01s from NIH/NIMH, the value of her research was acknowledged with NIMH Research Scientist Development K Awards (1984–1993), Research Scientist Award, and NIMH Merit Award.

Research and Theorizing

Two early themes marked Dr. Ruble's research, and both of these themes were carried throughout her career: gender roles/gender-related attitudes (e.g., Ruble and Higgins 1976) and understanding how children learn to use social categories and make social comparisons (e.g., Ruble et al. 1976).

Little was known about how children use social categories or other individuating information to make social comparisons prior to Dr. Ruble's research on this important issue (e.g., Rholes and Ruble 1984). Many social psychologists have been interested in the study of people's connections to and mental representations of social categories and their consequences for intergroup relations, personal choices, and well-being. It is well documented how identification with a particular social category can promote a sense of belonging and connectedness while also sometimes leading to feeling stigmatized when one's group is devalued by others. However, despite the wide-ranging importance of social category beliefs and group belongingness, until Dr. Ruble's research, little was known about when and how they develop and become linked to individual motivations and behaviors (Cameron et al. 2001; Feldman and Ruble 1977). This theme of being interested in the acquisition of such social knowledge and its implications for children's identity development trajectories and behaviors (Ruble et al. 1988) continued throughout her research career and played out in interest in social identities as well as in exploring the emergence and consequences of being a typical or atypical member of two influential social categories of race/ethnicity and gender (e.g., Rogers et al. 2012; Halim et al. 2011, 2014). Her work applying a social cognitive approach has facilitated a broader conceptualization of the nature and consequences of social identity development.

Interest in issues of how individuals change as they adopt new identities was also central to Dr. Ruble's body of research. Based on her research on this topic, she developed a phase model of transitions that accounts for the cognitive and motivational consequences that accrue with any type of social, occupational, or role

change (Ruble 1994). The phase model has been successfully applied to provide better understanding of the transitions involved in becoming a mother, taking on new occupations, and fluctuations in rigidity and flexibility in children's gender development (Trautner et al. 2005) among many other topics.

Dr. Ruble's interest in gender has been wide-ranging. She has explored a number of diverse topics as well as conducted in-depth explorations into specific gender-related topics. For instance, the range of gender-related topics she has covered and ages involved include how toddlers learn to label gender and its consequences (Zosuls et al. 2009), the development of gender concepts in children (e.g., Martin et al. 2002; Ruble et al. 2007), the development of gender stereotypes and attitudes in children and adults (e.g., Halim et al. 2012), menstrual experiences and attitudes in adolescents, and transition to motherhood (Hackel and Ruble 1992). Not surprisingly, given this range of interests, her studies include toddlers, children, and adults. Notably, one of her articles on menstrual attitudes was published in the very prestigious journal, *Science* (Ruble 1977). Although these research topics and target populations seem diverse, the questions and issues were directed by social identity theories and from cognitive/constructivist theories of gender development. Turning her social psychological lens that is informed by knowledge of significant social processes on questions of developmental importance such as the origins and trajectories of change illustrates the best of how research combining these two fields of study can inform one another, to the benefit of both.

Conclusion

Few psychologists have explored with such success the boundaries of social and developmental psychology as has Dr. Diane Ruble. Her social cognitive theoretical perspective has richly enhanced how social identities are conceptualized in the field and has broadened their investigation to include trajectories of change and transitions. Her research has illuminated the nature of and

consequences associated with being typical or atypical members of a group as well as exploring different variations in identification with social identities for children and adults. These themes and contributions relate to tenets of evolutionary psychology that cognitive processes are important in how individuals view others and ultimately how they navigate the social world.

Cross-References

- [Categorization By Sex](#)
- [Development](#)
- [Gender Schema Theory](#)
- [In-Group Versus Out-Group](#)
- [Menarche](#)
- [Social Development](#)
- [Socialization Processes](#)

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Dichogamy

► Sex Switching

Die Reichertsche Theorie

► Reichurt-Gaupp Theory

Diet

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Synonyms

Dietary; Fare; Food selection

Definition

The usual food and drink consumed by an organism or a group.

Introduction

Human diet is important for human survival, due to the need of food and water to stay alive by getting the necessary amount of calories and nutrients to maintain the organism's functions. Thus, the capacity to discriminate what can be ingested from what need to be avoided was beneficial over evolutionary time; those who fail to discriminate what is edible can get poisoned, for example, or be killed trying to capture the food intended (Tooby and DeVore 1987). Modern humans have very little obstacles to acquire food with adequate nutrients and food free of toxins. Over human evolutionary history, that wasn't so easy. Our ancestors devoted energy and time into food acquisition, recognizing whether a food was harmless, and then capturing, collecting, consuming, and digesting it (Buss 2015).

Food selection, sharing, and consumption in humans are major social activities (Rozin and Todd 2015). For example, sharing resources, such as food, may serve as a courtship and mating

strategy (Buss 2015). There are several hypotheses regarding whether and how the evolution of food preference, acquisition, sharing, and consumption in humans ancestrally promoted health and helped securing social bonds.

The Hunting Hypothesis

Securing food is an important feature of human evolution. For example, the hunting hypothesis states that large game hunting was fundamental to securing food (Tooby and DeVore 1987). This hypothesis states that humans face a unique challenge to obtain the adequate amount of nutrients from an exclusive vegetarian diet. Therefore, meat consumption would take a central feature in human groups for thousands of generations, corroborating previous research indicating that humans ingest more meat than all other primate species (Tooby and DeVore 1987). Some consequences of this specific method of food acquisition include improvement of tool making and use, the expansion of human brain, and the development of language skills for the communication necessary for cooperative activities (e.g., hunts).

The hunting hypothesis is associated to the intense parental investment in humans (i.e., provisioning hypothesis). For example, high male investments among mammals are related almost exclusively to a carnivorousness diet (Tooby and DeVore 1987). Therefore, the preference for meat consumption may also be explained by the provisioning hypothesis: the benefits of high-calorie food ingestion reflect on the efficiency to provide food for the offspring, reducing the odds of energy shortages.

The Gathering Hypothesis

The gathering hypothesis also provides a possible explanation for the evolutionary history of human eating habits (Buss 2015). This view suggests that the tools observed on the emergence of modern human were not initially for hunting but for a more secure and economical way of digging and gathering food (e.g., plants, seed, and fruits).

Evidences that the diet of human primate relatives was mainly of plants provide support to the gathering hypothesis (Buss 2015). In addition, most of the diet of modern hunter-gatherers consists of gathered plant food (Marlow 2005).

The Scavenging Hypothesis

Another hypothesis adds to the understanding of human eating habits: the scavenging hypothesis. This hypothesis states that our ancestors engaged in scavenging behaviors, that is, they seized the food remains of other predators as a method for food acquisition (Dominguez-Rodrigo et al. 2014). This method would secure the high-calorie diet but with far less energy cost. This form of food acquisition incurs a cost: meat left for some time can proliferate harmful microorganisms and quickly rot. The costs associated with eating rotten food therefore selected for psychological mechanisms in humans that motivated efforts to develop an important technique in human evolution: cooking (Tooby and DeVore 1987).

Cooking

Cooking is a technique that increases the possibilities of food manipulation. For example, cooking optimizes the digestive process because it is easier to digest cooked (vs. raw) food. Humans are the only animal species that cook or manufacture their food (Krebs 2009).

This technique improves the digestibility of the food, by increasing the absorption of nutrients and reducing the energetic cost of this process (Carmody and Wrangham 2009). This method can also help to solve the pathological consequences of toxic substances that may be found, for example, in some roots and in rot meat from scavenged remains (Carmody and Wrangham 2009).

Food Preferences

Although food preference may be influenced by individual differences, social norms, and cultural contexts, food preference is mostly shaped by

evolution (Buss 2015). Although individuals may respond differently to similar types of food (e.g., some like vegetables, and some do not), some preferences remain stable throughout human evolutionary history (e.g., preference for sweet foods). The preference for food that provides greater protection against energy shortages, while reducing the likelihood of choice for potentially hazardous foods (Starratt 2016), solved the adaptive problem of low food availability.

Several factors may affect human preference for food and include food's nutrition content and the energy cost associated to its acquisition (Rozin and Todd 2015). One important factor that affects human preference for food is palatability. Humans evolved five senses of taste: sweet, sour, salt, bitter, and umami. These senses are important for adequate consumption of essential nutrients for human survival, and it also helps to avoid toxic and rotten food (Krebs 2009).

Despite the diversity of food available, individuals maintained a preference for sweet and fatty foods. It is possible to think that natural selection operated in favor of individuals who had a preference for high-calorie foods, as these kinds of food allow longer between-meal intervals and greater energy supplies, which are specially advantageous in restricted food environments (Starratt 2016). Additionally, a preference for sweet food may be associated with the identification of ripe fruits, which is advantageous, because ripe (relative to non-ripe) fruits are more calorie dense. Moreover, human and nonhuman milk is fatty and sweet (e.g., rats, nonhuman primates), suggesting that a preference for a sweet and fat diet may be an evolved trait (Rozin and Todd 2015).

The preference for a sweet and fatty diet and the mismatch in the energy expenditure associated with food acquisition in the hunter-gatherer and modern environments have led to the emergence of obesity (Rozin and Todd 2015).

Moreover, salt is essential for the body to function properly. Because individuals lose a large amount of salt through sweat, it is advantageous for humans to prefer salty (over non-salted) food (Breslin 2013). However, similar to sweet and fatty food preference, a predisposition to choose salty (over non-salty) foods present current risks

to the modern human health. The overconsumption of salt has caused serious chronic diseases (e.g., hypertension).

Humans also presented a predilection to sour taste. Bitterness may serve as a proxy to high concentrations of vitamin C, an essential vitamin that has a great nutritional value (Breslin 2013). In addition, sour tastes are markers of fermentation, and the combination of sweet and sour tastes was more efficient for the identification of ripe fruits.

Moreover, humans can taste umami, which is associated with the presence of amino acids and ribonucleotides (Rozin and Todd 2015). Umami taste is an indicator of easily digested nutrients, pointing out to a preference for fermented foods, including cooked meats (Breslin 2013). A preference for fermented foods therefore improves and facilitates access to nutrients and probiotic bacteria.

On the other hand, alcohol, coffee, and some vegetables are examples of bitter foods. The fondness for bitter foods represents a controversial preference, once there is an innate avoidance of bitterness, due to the association with high levels of toxins such as cyanide (Rozin and Todd 2015). Another example of food that humans supposed to be averse is spicy food. However, these elements have some nutritional benefits – spices, for example, tend to hold antioxidation and antibacterial properties (Krebs 2009).

Another essential source of nutrition in mammals is milk, which has lactose as the major component. Humans need the enzyme lactase to properly absorb lactose. Most humans become lactose intolerant after weaning; some humans, however, continue to produce lactase during adulthood. It is possible that continued production of lactase during adulthood was particularly beneficial after the emergence of agriculture and livestock (Krebs 2009).

Indeed the percentage of individuals who continue to produce the enzyme lactase varies between geographical areas (Ingram et al. 2009). This variation may be due to the intense selective pressure under communities with pastoralist nomadic habits (Ingram et al. 2009). In contrast, even though the lactase persistent phenotype can represent an evolutionary advantage, the

environmental pressures for absorbing lactose were not so strong that groups of humans that were not in a context with this specific selective pressure continued to be lactose intolerant, such as most modern humans and their primate relatives (Rozin and Todd 2015).

Conclusion

The evolutionary history of the development of eating habits has a direct effect on humans. Over human evolutionary time, food preference evolved to optimize cost-benefits trade-offs of specific food ingestion (e.g., ripe vs. rotten), energetic content (e.g., high vs. low calorie), amount of available resources, as well as environmental and cultural pressures (e.g., availability of sweet foods). These elements allowed the development of specific food preferences that helped humans to behave more efficiently in regard to food selection and consumption. The diet of an organism is intrinsically linked with its survival. Moreover, a successful acquisition of food requires the ability to avoid deadly threats (e.g., harmful toxins) and recognize adequate food with the necessary nutrients (e.g., ripe fruits, fresh meat). Food acquisition also facilitates the development of social bonds (e.g., cooperation in hunting), helping humans to overcome the hostile pressures of nature.

Cross-References

- Body Reserves and Food Storage
- Brain Evolution Resulting from Cooking
- Darwinian Gastronomy
- Food Aversions and Cravings
- Food Preferences
- Obesity

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Dietary

- Diet

Dietary Preferences

- Food Aversions and Cravings

Dietary Shifts

- Food Aversions and Cravings

Difference Judgements

► Same-Different Categorization

Differences in Viral Infection

► Evolution of Virulence

Different Functions of Memory

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Synonyms

Declarative memory; Encoding; Episodic memory; Implicit memory; Learning; Localization of memory substrates; Multiple memory systems

Definition

Memory, as an information processing system, encodes (function 1), stores (function 2), and retrieves learned information (function 3).

Introduction

Our memory has three major functions. It (1) encodes new information through our five senses, (2) stores information in the short-term (minutes) or long-term (hours to years) memory systems, and (3) retrieves that information when the need arises (McDermott and Roediger 2016;

Melton 1963). These three memory functions are visited in this order below.

Encoding

“Encoding refers to the initial experience of perceiving and learning information” (McDermott and Roediger 2016). In our everyday lives, we come across stimuli/information that we are already quite familiar with them and stimuli that could be either just familiar, at varying degrees, or completely unfamiliar to us. New stimuli or information that come across, in our environment, and catch our attention will be **encoded** in our memory systems and be associated with older information or concepts or upgrade these already existing cognitive concepts. For example, seeing for the first time a new model of a well-known car brand is encoded as information that is associated with the style and look of this car brand, which is already in store. Alternatively, new information or concepts may not associate with older knowledge and create novel concepts and memories, which are not related to what we already have in store (Hunt 2003); this is called distinctiveness. For example, seeing a new car model from an unknown brand, with which you never came across, will be encoded as brand new car-related information.

Encoding could take at least three forms:

- (a) Semantic Encoding, where we encode words and sentences
- (b) Visual Encoding, where we encode visual spatial information
- (c) Auditory Encoding, where we encode sounds, voices, songs
- (d) Haptic Encoding, where we encode touch sensations
- (e) Olfactory Encoding, where we encode smells and tastes

Therefore, encoding is mainly the sensory input (of information) into our memory system.

Storage

Encoded information will move into storage, which is the next level within the memory system (Smith 2014). Retaining and storing information, which was previously encoded, is a process that is reinforced or hindered by our emotional state during encoding, our emotional attachment to the information being encoded, the environment where encoding took place, the competing information present during the encoding of information, and many other internal (related to the person) and/or external (environmental) factors.

Newly encoded information could be lost if deemed irrelevant by us or if any of the aforementioned internal and/or external factors interfere during encoding or immediately after encoding. If the information is not lost, then it moves onto the next levels of processing.

There are three empirically identified stages that the encoded information could follow if not lost:

1. As the information is encoded through our senses, it makes first impressions and registers very briefly to our sensory memory (very short-term memory). Sensory memory has a very short duration of less than a second.
2. If we pay attention and concentrate on this new input of sensations then we could move this newly encoded information into our short-term memory systems. Our selective attention will select the sensory memories that are important enough to be registered into our short-term memory system. The duration of short-term memories is a matter of dispute among scientists, and it is said that they could last from seconds and minutes to hours.
3. If the information is rehearsed, reencountered, or it is important for us, then the information could move into our long-term memory system, where the process of information decay is harder to happen. Long-term memories could last for hours, years, or our entire lives. Our long-term memory is divided into explicit (includes episodic and semantic memories)

and implicit memories (included procedural and emotional memories).

Retrieval

“Retrieval is the use of learned information, induced by sensory or internal cues” (Ben-Yakov et al. 2015). The retrieval of information from our short-term memory or long-term memory systems could be rather automatic (e.g., easy to remember information, such as the name of your mother) and called **recall**. In recalling, there is no need for cues to retrieve information. Retrieval is also automatic when we recognize information that we previously learned or encountered (e.g., in a multiple-choice question or when we run across a person only for second time and recognize them). This retrieval process is called **recognition**. Both of these retrieval processes require little cognitive effort.

On the other hand, the retrieval of information could involve varying degrees of cognitive effort and called effortful recall. For example, it is probably hard to remember the name of a person you met once, a month ago, but it is even harder to remember the name of a person that you met a year ago. In both instances, you may have to remember first the location, the date, and other details before the name of the person “pops up” from your memory storage (if it ever does).

A third form of retrieval is called relearning and it involves learning information much faster when you re-encounter the same information. For example, if you memorize all of the definitions in this encyclopedia entry for a test and remember them for next week’s test, the definitions may decay if you never use these definitions again for the years to come. Later in life, however, you may reencounter and relearn this information when you are starting a new Masters Degree in Cognitive Psychology and find out that you can memorize the material faster now.

Conclusion

Encoding information through one of our senses (smell, touch, vision, hearing, or taste) leads to storing that information either for less than a second (sensory memory) or for a short period of time lasting a few minutes to a few hours (short-term memory). Long-term memories are formed if the information is rehearsed, reencountered, or it is important enough for us (e.g., emotional attachment to a piece of information). Long-term memories are then retrieved either automatically, without much cognitive effort (e.g., the name of your dog) or with varying degrees of cognitive effort (e.g., the directions to a place that you have not visited for a long time).

Cross-References

- [Evolution of Memory, The](#)
- [Inceptive and Derived Memory](#)
- [Personal Memory](#)

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Differential Male Reproductive Success

- [Male Reproductive Variance](#)

Differential Parental Investment

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Synonyms

[Intrasexual competition](#); [Intersexual selection](#); [Obligatory investment](#); [Parental investment](#); [Sex differences](#)

Definition

Differences in minimum obligatory parental investment contributed by men and women lead the sexes to diverge in their sexual strategies and affective experiences, although under certain conditions, men's mating preferences converge with women's.

Introduction

A general principle underlying mate choice is that the greater the amount of parental investment required for offspring survival, the more stringent criteria will be for potential mates (Trivers 1972). This chapter first describes necessary or obligatory parental investment, examines the origins of sex differences in obligatory parental investment, describes examples of such differences across a range of species, and highlights the consequences of these differences in terms of human sexual strategies, conflicts, and affective experiences. This chapter next describes nonobligatory parental investment that can also be beneficial for offspring survival and the implications of male parental investment in humans.

Parental Investment

Parental investment refers to any expenditure, such as time, energy, or resources, from a parent

that benefits its offspring's fitness at the expense of the parent investing the resources in other fitness components, such as the parent's own survival or mating opportunities (Trivers 1972). Parenting, in the form of provisioning and offering protection from predators and conspecifics (i.e., member of the same species), is generally associated with lower offspring mortality (Clutton-Brock 1991). As a result, offspring have a higher chance of growing into healthier adults and are better able to compete for mates who in turn produce viable offspring themselves. Thus, in species where offspring that receive parental investments are significantly more likely to survive and reproduce, evolution shaped parents who pay the cost of investing in offspring such that net-positive genetic benefits accrue to the parents.

Obligatory parental investment more specifically refers to parental investment that is *required* for offspring to be produced and survive (Geary 2005). In mammals, for instance, offspring can only be produced through a process of internal gestation in the mother, and the offspring's early nutritional and developmental needs are also vitally dependent on milk produced by the mother after birth. Pregnancies and postpartum suckling therefore represent forms of obligatory investment by mammalian females to produce and develop offspring. On the other hand, while mammalian males can provide significant parental investments (e.g., Clutton-Brock 1991), their obligatory investment consists minimally of their sperm and a few minutes for copulation; any additional paternal investment is considered a luxury rather than a necessity.

Differences in Obligatory Parental Investment

The relative contribution that male and female parents make to offspring care varies by species. In amphibians, male-only and female-only parental investments express themselves fairly equally, while biparental investment is less common. Among reptiles that exhibit parental investment, either only the female or both parents provide the investment. The majority of bird species

demonstrate biparental investment, but on average, females invest more heavily than males. In invertebrate species with parental care, the majority have female-only investment and biparental investment is uncommon. In arthropods, male parental investment exists only in eight independent lineages which constitutes a small minority. Finally, among mammals, male-only investment is completely absent, and females raise and nurture offspring alone in more than 90% of species (Clutton-Brock 1991).

Although the forms of parental investment that are required for offspring production and survival manifest differently across various sexually reproducing lifeforms, females of most species tend to demonstrate relatively greater obligatory parental investment than males. For example, in mammals, offspring's fitness is crucially dependent on internal gestation and postpartum suckling by the mother. These physiological requirements of females but not males constitute the significantly greater female obligatory parental investment and care relative to males in mammals (Trivers 1972; Clutton-Brock 1991). Humans follow this general pattern of sex differences in mammalian obligatory parental investment – women's minimum obligatory parental investment includes approximately 9 months of pregnancy and is often followed up with years of nurturance in the child during his or her formative years. In comparison, men's minimum obligatory investment is a single sperm and can end with a single act of sexual intercourse. Any additional investment from the father during the child's formative years is beneficial but not essential for the survival of the child to reach adulthood (Goetz and Shackelford 2009; Trivers 1972).

Differential parental investment provides an important general principle underlying evolutionary hypotheses of mate choice by specifying that the greater the level of obligatory parental investment required of one sex relative to the other, the more stringent that sex should be when selecting potential mates in order to avoid costly errors associated with mating and production of offspring (Trivers 1972). Sex differences in obligatory parental investment also lead to differences in variability of reproductive success, or reproductive variance, between males and females (Brown

et al. 2009). As competition over the scarce and valuable sexual and parental resources of females results in some males being more successful than others, males often experience greater reproductive variance than females, therefore providing the evolutionary impetus for competitiveness, risk-taking, and gambling for mating success in males (Hawkes 1990) and conversely selectiveness and cautiousness in females (Buss 2006). As a result of these differences, the mating strategies of males and females diverge in order to increase the benefits and reduce the costs of mating for each sex: The high minimum obligatory parental investments required of females mean that having sex with more mates does not increase (and may even lower) their reproductive success, whereas placing a premium on the *quality* of mates is the preferred strategy. In contrast, the low minimum obligatory parental investments required of males mean that males are capable of increasing their reproductive success by focusing on obtaining greater mating *quantity* (Brown et al. 2009).

Parental investment theory elucidates two important components underlying Darwin's (1871) sexual selection theory, namely, intrasexual competition where members of one sex compete for access to the valuable higher-investing opposite sex and intersexual selection where the higher-investing sex exerts selective preferential mate choice over members of the other sex. The costs associated with fast and indiscriminate mating are therefore generally higher for females than for males. For many species, including humans, because females are the higher-investing sex, they evolved to be more careful, discriminate, and stringent during mate selection and are more likely to engage in intersexual selection by exercising greater preferential mate choice over mates compared to males. This in turn drives behaviors that facilitate greater intrasexual competition in the lower-investing males to contest other similarly eager conspecific males for sexual access to selective females (Buss 2006), greater risk-taking to exploit the odds of reproductive variance (e.g., Reaney and Backwell 2007; Wilson et al. 2010), and greater preference for sexual variety to increase the quantity of mates (e.g., Brown 1974), compared to females.

Examples of Parental Investment Theory

Sex differences in intersexual selection and intrasexual competition can be observed across a wide variety of species. For instance, elephant seal pups are nursed solely by females, while males do not invest in the care of offspring. Male elephant seals have also been observed to accidentally kill their own pups when they attempt to copulate with mates in the harem. The high value of the sexual and parental resources provided by female elephant seals drives fierce competitiveness among males, as only one third or less of the males can secure a mate during any breeding season (the highest-ranked males acquire at least half of all the matings; Le Boeuf 1974).

The greater reproductive variance of males relative to females also drives behaviors in males that maximize mating quantity through aggressiveness and risk-taking. For instance, risk-taking was found to predict aggression and mating success in male fiddler crabs, and this was independent of their body size (Reaney and Backwell 2007). Likewise, aggressiveness and exploratory behavior is correlated with mating success among European house crickets (Wilson et al. 2010).

The Coolidge effect is a phenomenon seen in mammalian species that facilitates the pursuit of sexual variety, where males (and to a lesser extent females) exhibit renewed sexual interest if introduced to new and receptive sexual partners. A study of rats found that males that were allowed to copulate to exhaustion were more sexually rearoused by novel females as compared to familiar females, indicating that reduced desire to copulate was not due to exhaustion but rather familiarity (Brown 1974). In fitness terms, fertilization becomes fairly likely after several consecutive copulations, so continued sexual activity with the same female likely faces sharply diminishing returns.

Intrasexual competition also drives the evolution of exaggerated traits and displays in the males of various species, as can be observed from the antlers of stags, tusks of elephants, and plumages of peacocks. Male satin bowerbirds do not partake in offspring care nor associate with the female after mating, but males compete by expending

significant time and energy to build large, specialized, and highly elaborate nest structures known as bowers to attract females (Borgia 1985).

Whereas male intrasexual competition tends to be more prevalent than female intrasexual competition, the evidence for female choice is more often observed than male choice in species that have greater obligatory parental investment in females than males. In the earlier example of satin bowerbirds, females exercise selectivity based on the males' bower-building prowess (Borgia 1985). During the mating season for koalas, females exercise selectivity over which males are capable of emitting the most low-pitched mating calls that signal large body mass, which is an indicator of high mate value. In insect species such as the water strider, females have evolved abdominal spines that serve to thwart the advances of sexually eager and harassing males and reduce the frequency of costly matings (Arnqvist and Rowe 1995).

Although obligatory parental investment is often greater in females than males, the males of some species contribute a larger obligatory parental investment than females. In these cases, the sex role is reversed, and the males of those species are the more selective sex, while the females intrasexually compete for the males (Trivers 1972). Among pipefish and seahorses, the females transfer their eggs onto specialized egg-brooding structures located on the males' tails during mating, where they are nourished throughout the entire duration of gestation. The females thus evolved to be brightly colored in order to compete intrasexually to be selected by the males, while the males preferentially choose the most attractive and brightly colored females as their mates (Wilson et al. 2003). In a bird species known as the *Phalaropus lobatus*, the female phalarope's obligatory parental investment only consists of laying the eggs in the nest. In contrast, the male phalarope builds the nest himself, incubates the eggs, and looks after the young alone. As predicted by parental investment theory, the females aggressively court the males and compete with each other to be selected by the males. Sex-role reversed species therefore strongly validate parental investment theory, as the theory specifies that

greater levels of minimum obligatory parental investment correspond with greater selectiveness, rather than specifying that females should always be more selective than males (Trivers 1972).

In sum, sex differences in the amount of obligatory parental investment toward offspring drive the underlying components of sexual selection. The high-investing sex (with greater mating cost) evolves to be stringent and choosy over mates, while the low-investing sex (with lower mating cost) evolves to be competitive with members of their own sex for mating opportunities, that is, access to the high-investing and thus more valuable opposite sex (Buss 2006).

Implications of Differential Parental Investment for Human Sex Differences and Mating

The general principle of differential parental investment that guides sex differences in mate choice among nonhumans provides important insights for understanding human sex differences and mating. This section highlights a few of the key sex differences between men and women as predicted by their relative obligatory parental investment.

Sexual Strategies

Asymmetries in obligatory parental investment between the sexes incentivize distinct sexual strategies differently such that mating costs are decreased and mating benefits are increased for each sex, therefore serving each sex's unique reproductive interests. For ancestral women who lived without modern food production, public health, and social welfare, being impregnated or having children without the commitment of a reliable mate carried heavy costs (Daly and Wilson 1983). Thus, in reproductive terms, the costs of noncommitted, casual sexual relationships typically outweigh the benefits for women more so than for men. Accordingly, women evolved to prefer a selective, long-term mating strategy to procure the lasting commitment of a good quality mate who can provide protection and resources, while men evolved to be more eager than women

to engage in casual, short-term sexual relationships in order to increase their quantity of mates (Buss 2006).

Risk-Taking

As men experience greater reproductive variance than women given that they can sharply increase their reproductive success by increasing mating quantity, men generally stand to benefit more than women from being open to risks and uncertain opportunities (Hawkes 1990). A study of road crossing found that males are more likely than females to put their safety at risk and cross a busy road to catch a bus, and males are also more likely to attempt risky road crossing when they perceive the presence of females in the vicinity, but females do not show a comparable effect in relation to the presence of males. Indeed, studies have found that women have generally lower appetites for risk than men, and this is partly due to men experiencing less distress than women when placed in risky situations (Campbell 1999). An experimental study of male skateboarders also found that the presence of an attractive woman elevated their testosterone levels and produced an increase in risky stunts attempted and completed (Ronay and von Hippel 2010). Sex differences in mating outcomes as indicated by differential parental investment and reproductive variance may therefore dictate that, on average, men will be paid more handsomely than women to have a higher risk appetite.

Aggression

Differential parental investment predicts that men are more likely than women to be physically aggressive in order to win at intrasexual competition and emerge dominant over intrasexual competitors (Campbell 1999). As high-investing females also carry valuable sexual and parental resources, the cost of losing these resources as a result of physical aggression is also high. While some researchers have argued that both men and women have the same capacity to aggress, female aggression consists mainly of subtle and indirect verbal behaviors, such as ostracism, as opposed to males' direct verbal and physical assaults, and when weapons are used, women use less physically harmful tools than men (Campbell 1999).

Sexual Conflict

Conflicts arise because the ways in which each sex distributes their limited reproductive resources are not always in the best interest of the other sex. As men have a stronger preference for short-term relationships and stand to benefit more from maximizing mating quantity than women, men will have a stronger desire for sexual variety and will be more sexually persistent, whereas women, who have a strong preference for committed long-term relationships, will be more sexually restricted than men (Buss 2006). This difference in preference thus predicts that men are more likely than women to sexually harass the opposite sex, while women are more likely than men to downplay, thwart, or frustrate the sexual advancements of the opposite sex. Goetz and Shackelford (2009) therefore argue that historically and cross-culturally, men are more likely than women to be the perpetrators of sexual coercion and rape, while women are more likely than men to be the targets.

Sexual Misperception and Commitment Skepticism

Men and women's differing awareness and assessments of the opposite sex's intentions also arise from differences in mating and parenting costs. Studies have found that men are more likely than women to perceive the presence of sexual interest in a woman based on minimal cues such as a smile, a touch on the arm, or mere friendliness (Haselton and Buss 2000). On the one hand, this relative overperception on the part of men is likely an adaptation to facilitate the enactment of a short-term mating strategy, given that, for men more so than for women, inferential errors leading to missed sexual opportunity carry greater reproductive costs compared to mistakenly inferring sexual interest. This male bias likely contributes to women's experience of unwanted sexual advances (Goetz and Shackelford 2009). On the other hand, just as women underreport their number of sexual partners (Smith 1992), they may be underrepresenting their sexual interest in ambiguous situations. Additionally, there may be other adaptive female biases at work. For instance, women, more than men, report falsely leading

on members of the opposite sex to believe that they are sexually interested when they are not (Haselton et al. 2005). Friendly behaviors toward men may, consciously or subconsciously, be adaptive ways for women to encourage interest from a wide number of male suitors and to extract resources and encourage demonstrations of value and commitment from such men. Furthermore, the incentive to be choosy compels women to be skeptical about a man's commitment even when it may be sincere, as the reproductive costs to women of wrongly inferring that a man is committed are immense (Haselton and Buss 2000).

Jealousy

Jealousy is an emotional state that is aroused by a perceived threat to a relationship and motivates behaviors to counter such threats (Buss et al. 1992). As fertilization and pregnancy occur in women, they are guaranteed full certainty of maternity. In contrast, men cannot be certain that the offspring is theirs (Geary 2005). As a result, men experience intense jealousy from acts that signal sexual infidelity by their female partners, as sexual infidelity from partners put men at risk of having their mating effort and resources redirected to another man's offspring, thus unknowingly assisting the reproductive success of another male at the expense of their own (Buss 2006). Indeed, the experience of jealousy from a partner's sexual infidelity has been found to be less severe for a woman than a man (Buss et al. 1992). Instead, women experience more jealousy when their mates are involved in emotional infidelity, as this translates to the man channeling his parental efforts and resources away from her and her offspring toward mating rivals and their offspring (Buss 2006).

Sexual Regret

When asked about their regrets in life, men are more likely than women to report wishing that they had slept with more partners, whereas women are more likely than men to wish they had tried harder to avoid poor choices of sexual partners (Roesse et al. 2006). Various forms of sexual regret (Galperin et al. 2013; Roesse

et al. 2006) can also be derived from the distinct errors that the sexes sought to avoid but ended up committing. Women, more than men, regret indiscriminate sexual actions, such as having a one-night sexual encounter or having sex with someone who led them to believe they were interested in a relationship but in fact turned out to be only interested in having sex (Galperin et al. 2013). Conversely, men, more than women, regret sexual inaction, such as failing to respond to a sexual invitation or missing a sexual opportunity (Roesse et al. 2006).

Evolution of Nonobligatory Male Parental Investment

The biology of internal gestation and obligatory postpartum suckling, as well as the associated sex differences in the opportunity and potential benefits of seeking multiple mating partners (Brown et al. 2009; Trivers 1972), account for the large sex differences in observed intrasexual and intersexual competition and mating behaviors in mammals. Although these factors give rise to a greater preference for casual and short-term sexual relationships in men than women, human males are unique among mammals for also having a preference for long-term relationships and investing significantly in offspring. When humans select mates for a long-term relationship, both sexes are intersexually choosy, and females also demonstrate intrasexual competitiveness for males who are willing to contribute significant (though nonobligatory) investments to offspring. The phenomenon of human paternal investment is therefore exceptional and extraordinary.

While uncommon in mammals, obligatory paternal investment is found among many bird, fish, and insect species (e.g., Thornhill 1976). In humans and other species, because paternal investment is not always required for offspring survival, it is nonobligatory and facultatively expressed; that is, it varies with proximate conditions. Nonobligatory paternal investment in a species can arise when such investments significantly improve offspring survival rates and when there is a high degree of paternity certainty (Geary 2005).

The facultative expression of male parenting in humans thus reflects trade-offs between the costs and benefits of parental investment in the ecological context of the male, and males may evolve to invest significantly in offspring if doing so increased their own fitness.

Offspring Survival

As the brain size needed for effective survival increased in the hominin lineage, childhood periods became progressively longer due to the longer duration needed by human offspring to develop their mental faculties. Children are thus altricial (i.e., helpless and dependent at birth), and long-term pair bonding and paternal care enhanced the fitness of the men engaging in it. By providing protection and nurturance to offspring, men can increase the likelihood that offspring can reach reproductive age, are capable of acquiring mates, and can produce viable offspring (Geary 2005). In many forager societies, children without an investing father have lower survival rates than those with one (e.g., Hill and Hurtado 1996). In industrial societies, one trait that is strongly associated with social competitiveness and mate value is educational achievement. Paternal investment, including income provided to the family and direct care, is correlated with better academic skills and upward social mobility in children, even when controlling for maternal investments (Amato 1998). Paternal involvement in play also helps develop the social competence of offspring. For instance, children whose fathers regularly play with them are more likely to be socially accepted and liked than children who lack such fatherly involvement (Carson et al. 1993).

A man's fitness can also be indirectly increased through parental investment regardless of increments to offspring survival. Men who demonstrate a willingness to commit and invest in children are regarded as desirable and can therefore raise their own mate value and attract mates themselves (Buss 2006). A man who shares the costs of parenting with his mate can also reduce her workload and calorific costs associated with raising offspring (Marlowe 2001), which may increase her fertility and accordingly enhance the man's fitness.

Paternity Certainty

In reproductive fitness terms, a male that invests in another conspecific rival's child suffers large costs to himself and his own legitimate offspring. As discussed earlier, men experience intense jealousy in response to their partner's actions that signal sexual infidelity, thus serving as an evolved affective defense against such reproductive costs (Buss 2006). Correspondingly, men are also more likely to invest in offspring when they have confidence in those offspring being theirs – in other words, when paternity certainty is high (Geary 2005).

For many species, cuckoldry is a gamble on the part of females that typically involves trade-offs between the risk of losing a primary mate's investment (upon his discovering that she is having sexual relations with someone else) versus the opportunity of gaining additional social and material support from extra-pair males, higher-quality genes for her children, or both (Geary 2005). In species where the investment provided by males is obligatory, these investments are virtually guaranteed, and hence there is low variance in male investments to offspring. Cuckoldry rates are thus low as females have no incentive to gamble for additional investments from other males and risk losing the investment of their primary mate. Conversely, for species where male investment is nonobligatory, cuckoldry rates vary with male quality; females paired with low-quality mates often risk the loss of their primary mate's investment and attempt to copulate with better quality mates when the opportunity arises. A similar variation in cuckoldry rates is reflected in human societies (Anderson et al. 2007). The significance of paternity certainty to male reproductive fitness is evidenced by the rise of marital arrangements and the universality of the paternity presumption in marital arrangements (i.e., the legal determination that a man is "presumed to be" a child's biological father without additional supportive evidence) across cultures, which serve to establish and enforce men's exclusive access to their mate's reproductive capacity and, ultimately, to ensure their paternity certainty.

Thus, contrary to most mammals, human males form long-term pair bonds and invest significantly in offspring insofar as paternity certainty is high and paternal investments can increase men's fitness. Paternal investment has evolved because it contributes to the reproductive fitness of offspring (and thus, to both parents) and women have evolved to look for signs of a man's ability and willingness to invest in offspring when they seek long-term mates.

Conclusion

Differential parental investment guides the evolution of preferred sexual strategies and mating behaviors of reproductively successful parents to optimize their own reproductive fitness. Across many species, including humans, females have a greater minimum obligatory parental investment than males to ensure offspring survival, which has tended to select for sexually choosy and discriminating females and sexually eager and competitive males. The different costs associated with parenting and mating for males and females have implications for intrasexual competition and intersexual selection which lead to differences in their preferred sexual strategies, aggression and risk-taking, perception of potential mates, and the mating conflicts they experience. While these sex differences in mating preferences do exist, men may also pursue a long-term mating strategy and provide nonobligatory parental investments under facultative circumstances where their fitness can be increased.

Cross-References

- ▶ [Commitment Skepticism](#)
- ▶ [Cuckoldry](#)
- ▶ [Error Management Theory](#)
- ▶ [Female Manipulation of Men](#)
- ▶ [Female Mate Choice](#)
- ▶ [Female-Female Competition](#)
- ▶ [Intersexual Selection](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Long-Term Mating](#)

- ▶ [Male Mate Choice](#)
- ▶ [Male-Male Competition](#)
- ▶ [Maternal Investment](#)
- ▶ [Obligatory Parental Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Paternal Investment](#)
- ▶ [Paternity Certainty](#)
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- ▶ [Sex Differences](#)
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- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)
- ▶ [Sex Differences Versus Gender Symmetry](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)
- ▶ [Sexual Selection](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Short-Term Mating](#)
- ▶ [Sociosexual Orientation](#)

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Differential Reproductive Success

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Definition

A measure of the number of offspring (or replications) a particular individual, group, or gene left behind relative to others.

Introduction

Differential reproductive success consists of a statistical analysis of the outcome of a class of mechanisms that, according to Darwin's Theory of Evolution by Natural and Sexual Selection, produces changes in the distribution of variants within populations. According to the essence of Darwin's theory, *differential selection* acts on *variations in fitness*, which produces *differential reproductive success* over time. To clarify our

concept of differential reproductive success, we must first define both differential selection and variations in fitness.

Differential Selection and Variance of Fitness Are Devices to Achieve Greater Differential Reproductive Success

Differential selection refers to a class of selective pressures that disfavor (or favor) some members of a population over others. The mechanics of differential selection may differ with any given level of analysis.

Variation in fitness consists of two interrelated concepts: variation and fitness. *Variation* is a descriptor for differences that exist within a population. *Fitness* is a measure, the gold standard of which is set relative to a dynamic set of causal factors that favor some variants in a population over others (differential selection). Taken together, *variation in fitness* provides a measure of the success or failure (differential success) of any given variant in a population. (The term “*fitness*,” as used here, is a moving average measure of how well an individual member of a population solves extant adaptive problems leading to reproductive success relative to other members of the same population. Hence, *fitness* is a moving average that provides an estimate of an entity (and its copies) that, when compared to the competitor fitness, quantifies progress toward *differential reproductive success*.)

Working together, differential selection operates on variations in fitness in a way that produces differential reproductive success over time. *Differential Reproductive Success* involves at least three components. The first component consists of the abstract construct *reproduction* – defined as the production of one or more copies of an entity. The second component consists of the measurable construct *reproductive success* – defined as actualizing one or more copies of an entity or event. The third component, *differential reproductive success*, consists of several measurable subcomponents – (a) an individual, by whatever means, actualizing one or more copies of

itself that (b) outnumber the actualized copies of individuals in direct reproductive competition, that (c) engage in the same process during each subsequent generation.

Taken together (i.e., over generations), *differential reproductive success* documents an increase in percentage of the population occupied by successfully copied entities and their characteristics.

These measures make no reference to the survival of the strongest individual or to individuals outliving others. Instead they are measures of success, relative to competitors, in leaving copies of individual replicators in future generations. For example, how likely genes will successfully replicate relative to other genes (Barash and Wilson 1982). In this example, genes with the greatest fitness relative to the mechanisms of extant differential selection – replicate through generations of individuals (sometimes referred to as “vehicles”) via each successive generation of individual differential reproductive success. Those genes with the greatest fitness, by definition, out-reproduce the genes of less fit genes. Over generations, genes that out-reproduce less fit genes come to represent a greater proportion of a species population (Buss 2012).

Conclusion

These inherited fitness variations are byproducts of natural selection; variations in fitness leads to greater reproductive success for some than for others – which equals greater differential reproductive success relative to others in the same group. The idea of fitness resulting in differential reproductive success applies to individual entities and to higher- (e.g., groups- or species) and lower- (e.g., gene or replicator) level entities.

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Differentiation

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Synonyms

Articulation; Complexity; Individuation

Definition

Differentiation refers to a process of change in a system toward greater complexity or the result of such a process (i.e., the complexity of a system's structure); in a somewhat narrower sense, differentiation is concerned with the number of specialized elements in a complex system.

Introduction

The concept of differentiation has long been central to several psychological theories. Witkin et al. (1962) discuss the notion of *psychological differentiation*, viewed as an organism-wide process of development toward greater psychological complexity. At the core of Bowen's (1978) family system theory and therapy is the concept of *differentiation of self*, considered as a key aspect in the process of emotional development and maturing. Child psychology and psychoanalysis use the term differentiation interchangeably with the term *individuation* to denote a process through which a child develops a self (e.g., Mahler et al. 1975). In all the above theoretical approaches, differentiation is conceived of as the developmental task. The idea bears resemblance to the use of the term in biology, where organismic differentiation is assumed to increase phylogenetically and ontogenetically. Greater differentiation is expected to be associated with increased specialization of elements and functions of a given psychological system, and carries implications ultimately for the relations with the environment –

a more differentiated system is characterized by separation between what is recognized as internal and external to the self. Implied here also – as the organizing response to increasing differentiation – is an increasing degree of integration. Indeed, this relationship between differentiation and integration may be seen as the basic law of development, best known as the orthogenetic principle. It states that “Wherever development occurs, it proceeds from a state of relative globality and lack of differentiation to states of increasing differentiation, articulation, and hierarchic integration” (Werner 1957, p. 126).

The three theoretical conceptualizations outlined above as well as other meanings of the concept of differentiation are briefly explored below.

Witkin's Psychological Differentiation

The concept of psychological differentiation has its origins in Witkin's (1949) earlier work, which focused on the stylistic tendencies that cut across perceptual and intellectual functioning. Using various perceptual tasks such as the body-adjustment test (BAT), the rod-and-frame test (RFT), the rotating-room test (RRT), and the embedded-figures test (EFT), Witkin and his coworkers demonstrated that consistent individual differences exist in the tendency to overcome embedding contexts. These individual differences account for the dimension of cognitive style called *field dependence-independence*. Studies of the field dependence-independence have led Witkin to the conclusion that these cognitive styles are linked to a variety of personal characteristics, all of which are manifestations of a broader dimension of personality functioning, namely psychological differentiation (Witkin et al. 1962).

The main indications of psychological differentiation include mode of structuring experience, extent of definition of the self-concept, articulateness of body concept, and mechanism of impulse regulation. Highly differentiated individuals maintain an analytical approach to problem solving, have a sense of separate identity, experience their bodies as having definite

boundaries, and are more likely to employ more specialized defenses (e.g., rationalization, isolation). Conversely, those low in psychological differentiation have a global cognitive style, lack clear body boundaries, rely on external sources for definition of their beliefs and of their views of themselves, and tend to use more primitive defenses (e.g., repression, denial; Witkin et al. 1962).

Small but consistent gender differences were found in the area of psychological differentiation, with men being more differentiated than women. Also, some ethnic groups, like Mexican-Americans and Eastern Europeans, are believed to have cultural backgrounds which favor lesser differentiation qualities (Witkin and Berry 1975).

Bowen's Differentiation of Self

Differentiation is defined by Bowen as an instinctually rooted force "that propels the developing child to grow to be an emotionally separate person, an individual with the ability to think, feel, and act for himself" (Kerr and Bowen 1988, p. 95). At the same time, there is a counterbalancing force – togetherness – that spurs the child and family to think, feel, and act alike. Well-differentiated families are characterized by interaction patterns that facilitate an age-appropriate balance of the two forces.

According to Bowen (1978), differentiation of self is a multidimensional construct. On an intrapsychic level, it is viewed as the ability to separate thinking and feeling. Individuals who are able to choose between being guided by their intellect or their emotions are those whom Bowen believed to have an enhanced sense of *solid-self* (also called basic, real, or differentiated self). Conversely, those prone to let their emotions override their thinking are those believed to be operating out of *pseudo-self* (also called pretend or fused self). The solid-self is made up of firmly held beliefs, convictions, and life principles, while the pseudo-self lacks beliefs and convictions of its own and reacts to others around it. On an interpersonal level, differentiation of self entails comfort with both intimacy and autonomy in relationships.

Differentiated individuals are capable of taking the I-position in relationships, meaning they are able to adhere to a clearly defined self without the need to conform to others' expectations. On the other hand, those who struggle with the differentiation process tend to remain fused in or emotionally cut-off from their relationships.

The Bowenian concept of differentiation has been operationalized with several self-report measures. However, only the Differentiation of Self Inventory (DSI; Skowron and Friedlander 1998) can be said to capture all aspects of differentiation (i.e., emotional reactivity, fusion with others, emotional cut-off, and taking the I-position).

Mahler's Self-Object Differentiation

Within the Mahlerian scheme of development, differentiation refers to the process, in which the child becomes able to "separate out and to differentiate his self-representations from the hitherto fused symbiotic self-plus-object representations" (Mahler 1967, p. 749). The process takes place from about 5–9 months and is considered to be the first subphase of an overall process known as *separation-individuation* process (the three remaining subphases being practicing, rapprochement, and constancy). According to Mahler, at the time children have completed the separation-individuation stage, they arrived at psychological birth, marked by a sense of being a separate individual entity. Clinical evidence implicates disturbances in the separation-individuation phase in the later development of adult psychopathology, particularly borderline personality disorder and schizophrenia (Mahler et al. 1975).

Characteristic features of the differentiation period include customs inspection (i.e., examining the mother's face and hair), a double sensation of touch (a single sensation in the child's fingers is produced by touching the mother's body, whereas all own-body exploration produces a double sensation), the peek-a-boo game, and craning (i.e., supporting own head and neck when carried; Pine 2004). These activities are believed to produce the experience of self-mother differentiation. An important marker for the latter is the 8-month

anxiety (also called separation or stranger anxiety), often emerging in children at this age.

Other Applications of the Concept of Differentiation

Theorists and researchers have made extensive use of the concept of differentiation. It has been invoked in several fields of research into cognition. Originating from Kelly's (1955) personal construct theory, the concept of *cognitive differentiation* (or complexity) is understood as the "relative number of different dimensions of judgment used by a person" (Tripodi and Bieri 1964, p. 122). Operationally, differentiation in an individual's construct system is usually defined as the number of nonidentical ratings of various interpersonal figures (e.g., mother, brother) along a set of bipolar construct dimensions (e.g., friendly vs. aloof). Several studies have demonstrated that individuals with greater cognitive differentiation fare better than less differentiated individuals when exposed to information-overloaded environment and when confronted with contradictory information (e.g., Press et al. 1975).

Social-cognitive research on the self-concept has used the term *self-concept differentiation* to refer to an individual's tendency to view oneself as possessing different personality characteristics across different roles or contexts (Donahue et al. 1993). Of note, the authors posit that high self-concept differentiation is indicative of a divided self and unresolved intrapsychic conflict. A related line of research has focused on yet another feature of the self-concept structure, namely, *evaluative differentiation* (also referred to as compartmentalization). It is defined as the extent to which positive and negative information is clustered within one's self-aspects, with high evaluative differentiation being associated with high, although unstable, self-esteem (Showers 1992).

Applied to the study of emotion, *differentiation of emotional experience* refers to the propensity to make subtle distinctions within emotion categories. It is termed as an aspect of emotional complexity, the other aspect of which regards the

range of one's emotional experiences. Emotional complexity is conceived as a product of cognitive complexity, personality dispositions (such as private self-consciousness and openness to experience), and life experiences, and has been shown to lead to empathic understanding of others' feelings and greater interpersonal adaptability (Kang and Shaver 2004).

In addition, the concept of differentiation has been used by social psychologists to describe the diversity of functions, roles, ranks, cultures, and interests in a society (i.e., *social differentiation*).

Conclusion

There is a plethora of psychological literature that addresses differentiation. Some authors treat differentiation as a general personality trait that extends across various areas of psychological functioning. Other researchers deal with it as a domain-specific psychological state. All these applications seem to share the notion that differentiation serves structuralization and specialization of psychological functions and systems.

Cross-References

- Identity
- Self-Concept

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Digit Ratio

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Synonyms

2D:4D; Estrogen; Finger length; Prenatal sex steroids; Testosterone

Definitions

Effects of prenatal sex steroids on fertility, behavior, and health.

Introduction

Digit ratio (or 2D:4D), i.e., the relative length of the 2nd digit ("index finger"; 2D) and the 4th digit ("ring finger"; 4D) has attracted the attention of scholars for many years (Baker 1888; Minami 1952; Phelps 1952). At the center of this interest lies the sex difference and ethnic variation in 2D:4D, and the appearance of the sexual dimorphism in 2D:4D at a very early stage in ontogeny.

Digit ratio is sexually dimorphic with males typically having longer 4th digits relative to 2nd digits than do females (male 2D:4D < female 2D:4D). The sex difference in 2D:4D suggests an involvement of sex steroids (primarily testosterone [T] and estrogen [E]) and a developmental origin that predates puberty and may indeed extend back to the 1st trimester of pregnancy. In 2D:4D, we may have a relatively fixed record of the influences of T and E during a narrow developmental window in early pregnancy. If this is so, we can use 2D:4D to address many questions regarding the etiology of sexually dimorphic abilities (e.g., speed, stamina, strength), behaviors (e.g., aggression, criminality, risk-taking), disorders of development (e.g., autism, attention deficit hyperactivity disorder, dyspraxia), and major diseases (e.g., heart disease, many cancers, osteoarthritis). There are differences in mean 2D:4D across large ethnic groupings (Caucasians, Blacks, East-Asians) in the fetus and adults (Minami 1952), and across smaller groupings such as the nation-states of Europe (Manning and Fink 2011a). They hint at in utero hormonal variation in humans, which may be driven by sexual selection and contribute to group differences in, e.g., marriage systems and susceptibility to sex-dependent diseases. Furthermore, the group and sex differences in 2D:4D may have a reach beyond that of *Homo sapiens* to other taxa within the primates (Nelson and Shultz 2010) and could indeed map on to other

mammalian groups including the rodents (Zheng and Cohn 2011).

Measurement of Digit Ratio

The most accurate measure of digit length is from radiographs that include the three phalanges. However, experimenters are often unable to take X-rays of the hand, and where there is a pre-existing archive of X-rays, it has often been of the left hand only. Soft-tissue measurements of digit length are more common and are usually taken from the ventral surface of the digit. There is a limitation with this approach as the proximal measurement point excludes approximately half of the proximal phalanx. Direct measurement of digit length has acceptable repeatability, but is more time-consuming than indirect measurement (e.g., from photocopies or scans). However, the latter method causes a reduction in 2D:4D, which is influenced by sex (greater in males than females). The effects of indirect digit measurement are a matter of debate (Manning et al. 2005), and there are concerns regarding the “clarity of report” regarding these effects (Ribeiro et al. 2016).

Sex differences in Digit Ratios and Their Stability

Digit ratio shows sex differences (2D:4D males < 2D:4D females) with low-to-medium effect sizes (Cohen's *d* from about 0.20 to 0.60; Manning 2002). Some of this variation is influenced by measurement protocol (greater for indirect than direct 2D:4D; Hoenekopp and Watson 2010) and by variation in the strength of sexual selection across populations (Manning et al. 2014a). However, we must also bear in mind that 2D:4D is a composite trait and that effect sizes for sex differences may vary across the phalanges (e.g., in the mouse, Zheng and Cohn 2011).

Finger lengths grow rapidly in children. If 2D:4D is to be used as a correlate of prenatal sex steroids, it is necessary to establish whether it

remains stable over periods of rapid growth. Manning et al. (1998, 2013) have measured sex differences in right and left 2D:4D (boys < girls) in a sample of 680 Caucasian children from 2 years to 18 years. There was no significant change in mean 2D:4D or in the sex difference across year-groups. Trivers et al. (2006) have reported stability of right 2D:4D with growth in Afro-Caribbean children, but less stability in left 2D:4D. McIntyre et al. (2005) found a tendency for radiographic left 2D:4D to increase with growth in Caucasian children, but sex differences in 2D:4D within year groups remained stable. The stability of 2D:4D is enhanced because it is underpinned by bone (the phalanges; e.g., Robertson et al. 2008) and its maintenance during rapid growth is a remarkable example of the homeostasis of form.

Human Comparative Differences

There are significant differences in mean 2D:4D across the major ethnic groups such that Caucasians have higher 2D:4D than Blacks or East-Asians. This pattern has been noted in fetal ratios (Minami 1952) and in adults (Manning 2002). Within ethnic groups, there is also evidence for between-nation variation in 2D:4D. For example, in the BBC internet study (Reimers 2007) with $n > 200,000$ participants, the mean 2D:4D (across sex and hand) per ethnic group was 0.978 for Chinese participants, 0.981 for Blacks, and 0.989 for Caucasians. Within the Caucasian sample, there were significant between-nation differences that map on to variation in national values for personality scores (Manning and Fink 2011a), consumption of alcohol and cigarettes (Manning and Fink 2011b), and gender inequalities (Manning et al. 2014a).

Digit Ratios and Sex Steroids

Manning et al. (1998) suggested that 2D:4D correlates negatively with prenatal testosterone (PT) and positively with prenatal estrogen (PE). In support of this model, they reported that (i) 2D:4D was sexually dimorphic

(males < females), (ii) the dimorphism was stable across age groups 2 years to 25 years and was not affected by puberty, and (iii) low 2D:4D (particularly right 2D:4D) was associated with efficient spermatogenesis. Since the publication of Manning et al. (1998), it has become apparent that the sex difference in 2D:4D is determined by the end of the 1st trimester of pregnancy (Galis et al. 2010; Malas et al. 2006; Szwed et al. 2017) and is in general stable in postnatal growth.

Fetal Testosterone and Estrogen

There is evidence that PT levels correlate negatively with postnatal 2D:4D. Thus, children with congenital adrenal hyperplasia (CAH), a trait associated with high PT, have been reported to have lower 2D:4D than controls (Brown et al. 2002; Ciumas et al. 2009; Okten et al. 2002). Another study reported no association (Buck et al. 2003), but overall a meta-analysis found significant associations between low 2D:4D and CAH (Hoenekopp and Watson 2010). In contrast to CAH, men with Klinefelter's syndrome (47, XXY; which is accompanied by low PT) have higher 2D:4D than population norms (Chang et al. 2015; Manning et al. 2013; Savic 2014). It is to be noted that insensitivity to T should remove variation in 2D:4D that is related to PT, but leave the variation that is linked to PE. Berenbaum et al. (2009) and van Hemmen et al. (2017) reported that T-insensitive individuals had increased mean 2D:4D, but variation in 2D:4D was still present. Their result is supportive of a PT:PE link with 2D:4D.

In studies that assessed hormonal concentrations in amniotic fluid, PT:PE ratio and PT were found to be negatively correlated with 2D:4D (Lutchmaya et al. 2004; Ventura et al. 2013), and T in maternal serum was reported to be positively correlated with children's 2D:4D (Barona et al. 2015; Ventura et al. 2013). With regard to perinatal cord blood, we should not expect to find correlations between 2D:4D and T and E because sex-dependent variation is established some 6 months before birth. However, associations were reported between low 2D:4D and high-functioning T-producing prenatal

Leydig cells that have their origin early in gestation (Mitsui et al. 2015).

The Ancient Origin of 2D:4D

Manning (2002, 2008) suggested that the sexual dimorphism of 2D:4D is an ancient trait, which may have its origin in the evolution of four-limbed animals. Sex differences in 2D:4D are present in birds (Nagy et al. 2016) and mammals (Nelson and Shultz 2010). In rodents, inactivation of the androgen receptor (AR) gene increases 2D:4D, whereas inactivation of the estrogen receptor (ER) gene lowers 2D:4D. The administration of exogenous PT or the blocking of ERs lowers 2D:4D, whereas administration of PE or blocking ARs increases 2D:4D (Auger et al. 2013; Talarovicová et al. 2009; Zheng and Cohn 2011). These experimental data confirm that 2D:4D is fixed by PT:PE in a narrow prenatal window and it is linked to the activation of "skeletogenic" genes by PT:PE. The genes, some 20 in number, have multiple functions, which include the morphogenesis of the skeleton, reproductive organs, and the brain (Zheng and Cohn 2011).

Digit Ratio and Sensitivity to Testosterone

A number of studies have investigated the link between low 2D:4D and high sensitivity to T. This includes studies of associations between 2D:4D and the structure of the AR and those that have reported associations between 2D:4D and administered T. Modifiers of AR function include polymorphisms in its coding sequence (e.g., variable numbers of CAG repeats), interaction with cofactors, intracellular trafficking of the T-bound complex, and interaction with general transcription factors. Over 170 proteins possess AR coactivating or corepressing characteristics, indicating that a multitude of signals converge on the AR to regulate its function (Heemers and Tindall 2007; Heinlein and Chang 2002). Some studies have reported a negative relationship between 2D:4D and CAGn, and one study found that 2D:4D in neonates was dependent on CAGn and circulating levels of T (see Hoenekopp 2013 for a meta-analysis). However, most reports have not found a correlation between CAGn and 2D:4D.

The importance of this null-finding for the putative association between 2D:4D and PT is a matter of debate. Hoenekopp (2013) has suggested that CAGn has a weak effect on AR transcription rates, and no or little or inconsistent effects on traits that are known to be strongly influenced by T. An alternative view of the correlations between 2D:4D and the AR is given by Voracek (2014). Clearly the link between 2D:4D and PT would benefit from an experimental rather than a correlational approach.

A more powerful experimental method of considering sensitivity to T is to administer the hormone and note whether 2D:4D modulates the response. It has been reported that 2D:4D modulates the effects of exogenous T application on empathy, moral judgment, cooperation, trust, preference for status goods, aggression, and brain activity associated with mental rotation task scores (Buskens et al. 2016; Montoya et al. 2013; Pintzka et al. 2016; van Honk et al. 2011, 2012 for women; Carré et al. 2015; Wu et al. 2017 for men). The direct manipulation of T itself makes this experimental procedure more powerful than correlational data. The link between 2D:4D and sensitivity to T is potentially further amplified by associations between low 2D:4D and production of T in competition-induced circumstances (Manning et al. 2014b). Thus, men with low 2D:4D, and those with lower right 2D:4D relative to left 2D:4D, tend to produce high levels of T and high T:C ratios when challenged with intense exercise and/or aggressive stimuli (Crewther et al. 2015; Kilduff et al. 2013a, 2013b).

Digit Ratios, Target Traits, and Effect Sizes

Masculinized and feminized traits are generally associated with low and high 2D:4D, respectively. Effect sizes for associations vary. The strongest correlations with 2D:4D are found for performance in sport and developmental disorders and the weakest among personality traits. Autism is a severe developmental disorder that is strongly sex-dependent such that the male-to-female sex ratio is 4 to 1 across the full IQ range, and rising to

9 to 1 in children with normal IQ. Children with autism are often unresponsive to people and lack awareness of the feelings of others (“mind-blindness”; Baron-Cohen 1995). The sex-dependent pattern of autism has led to the suggestion that it may result from the influence of high levels of PT, the “extreme male brain theory” (Baron-Cohen and Hammer 1997). Thus, it has been proposed that PT effects of hypermasculinization of the brain may cause autism.

Manning et al. (2001) considered the relationship between 2D:4D and autism in 72 children (Asperger’s Syndrome [AS]; of these, 23 participants had normal IQ), 210 unaffected relatives (88 fathers, 88 mothers, 34 siblings), and a matched normative control sample. In comparison to controls, children with autism and children with AS had lower 2D:4D, and fathers, mothers, and sibs from affected families had lower 2D:4D. These findings have been the focus of a number of replications and two meta-analyses (Hoenekopp 2012; Teatero and Netley 2013). Both studies were supportive of a correlation between low 2D:4D and autism spectrum disorder. More recently, Barona et al. (2015) reported an association between low 2D:4D and emotional and communication difficulties in a large community-based sample. However, this relationship was restricted to the lowest 10% of male 2D:4D ratios. Currently, it is unknown whether associations between low 2D:4D (high PT) and symptoms of “mind-blindness” are present throughout normative populations (as predicted by the extreme male brain theory) or whether these effects are found only among males who have been exposed to very high PT.

Digit Ratio and Sports Performance

Manning and Taylor (2001) reported a negative relationship between 2D:4D and performance across a range of sports and extended this analysis to a detailed consideration of professional soccer players. Since this initial report, there have been similar findings for other sports such as running, skiing, surfing, rugby, rowing, basketball, and Sumo wrestling, and for measures of fitness and strength. A meta-analysis confirmed the initial finding of Manning and Taylor, and found

substantial relationships but with some heterogeneity in effect sizes such that endurance sports tended to show the strongest effects (Hoenekopp and Schuster 2010).

Digit Ratio, Aggression, Risky/Criminal Behavior

The associations between 2D:4D and aggression and rule breaking show sex differences, with higher effect sizes in men compared to women (e.g., Hoenekopp and Watson 2010). There is evidence that T influences such behavior, with greater intensity of expression associated with high T (Mehta et al. 2015). It is to be expected that 2D:4D would be related to aggression, risky/criminal behavior, and dominance because 2D:4D modulates the action of T (Carré et al. 2015; Montoya et al. 2013; van Honk et al. 2011, 2012). PT is associated with neuronal loss and there is evidence of a positive relationship between 2D:4D and brain morphological features. Darnai et al. (2016) reported significant positive correlations between 2D:4D and volume measurements such as total cerebral cortex, total cerebellar white matter, and total cerebellar cortex in men but not women. Gorka et al. (2015) found low 2D:4D was associated with reduced anterior cingulate cortex gray matter volume (a brain region supporting conflict monitoring and behavioral inhibition).

Aggression

There are reliable negative relationships between 2D:4D and sports performance and many of these sports involve aggressive/competitive interactions (Hoenekopp and Schuster 2010; Manning and Taylor 2001). This pattern of significant 2D:4D effects in sports that provide intense challenge conditions is what we would expect if 2D:4D were a proxy for sensitivity to and amplitude of T-spikes. Therefore, it seems reasonable to assume that 2D:4D and aggression is negatively associated. However, the effect size of the 2D:4D and aggression relationship has proved difficult to quantify.

A meta-analysis of studies concerning 2D:4D and aggression revealed no significant relationship for women ($n = 19$ studies) and a

small but significant negative relationship for men ($n = 18$ studies, $r = -0.06$; Hoenekopp and Watson 2010). Subsequent large-sample studies have reported male effect sizes of about $r = -0.10$ (Butovskaya et al. 2013; Hoenekopp 2011).

Correlations of $r = -0.06$ to -0.10 for male 2D:4D associations with aggression are small. However, aggression is not invariant across situations but is context-dependent (Millet 2011). Thus, an interactionist perspective is necessary to understand its relationship with T. Baseline differences in T from individual to individual do not correlate strongly with between-individual variation in aggression. Rather, it is variation in spikes of T in response to challenge situations that correlate with levels of aggression (Carré and Olmstead 2015). Low 2D:4D (particularly low right-left 2D:4D) individuals tend to produce marked T-spikes on challenge with aggressive stimuli and/or intense exercise (Crewther et al. 2015; Kilduff et al. 2013a, 2013b). They are also sensitive to high concentrations of T (Carré et al. 2015; Montoya et al. 2013; Pintzka et al. 2016; van Honk et al. 2011, 2012) and show negative correlations between 2D:4D and aggression in challenge conditions (Kilduff et al. 2013b; Millet and Dewitte 2007).

Therefore, it may be that the 2D:4D and aggression correlation is significant in men when in challenge conditions, and weak in contexts other than challenges (Kilduff et al. 2013b; Manning et al. 2014b; Millet and Dewitte 2007). Support for this suggestion comes from real-world studies. Thus, in professional soccer players, there is a negative correlation between the number of yellow and/or red cards per match and 2D:4D in junior and elite players (Mailhos et al. 2016; Perciavalle et al. 2013). Similarly, patients with “boxer’s” fractures (of fourth or fifth metacarpals) acquired during street-fighting have lower 2D:4D ratios than controls (Joyce et al. 2013).

Risky/Criminal Behavior

The relationships between 2D:4D and risky/criminal behavior appear to show higher effect sizes than those found for the relationship of 2D:4D and

aggression. For example, Hoskin and Ellis (2015) reported a mean correlation of about $r = -0.40$ between 2D:4D and criminality. Hanoch et al. (2012) found a correlation of $r = -0.24$ between 2D:4D and impulsivity among offenders and non-offenders. Schwerdtfeger et al. (2010) reported a correlation of $r = -0.36$ between 2D:4D and traffic violations. Furthermore, large internet samples of 2D:4D enable us to consider risk avoidance across nations rather than individuals. In the BBC internet study, Manning and Fink (2011a) reported significant correlations for mean male 2D:4D per nation and national values of uncertainty avoidance (23 nations: right hand $r = 0.58$, left hand $r = 0.59$).

Personality

It is generally thought that 2D:4D is only weakly associated with aspects of personality such as the “Big-Five” constructs (Austin et al. 2002; Fink et al. 2004; Lippa 2006). This view may be correct. However, the field would benefit from a consideration of the context in which personality is examined. For example, in conditions such as aggressive challenge, the relationships between 2D:4D and traits such as neuroticism may change (Manning and Fink 2018).

Sexual Orientation

Interest in the relationships between 2D:4D and sexual orientation came shortly after the publication of Manning et al. (1998). Unfortunately, the first papers (Robinson and Manning 2000; Williams et al. 2000) used indirect methods (photocopies) to measure finger lengths. This practice has continued such that most studies show this limitation. A meta-analysis concluded that lesbians showed lower mean 2D:4D than heterosexual women, but the 2D:4D of gay men did not differ from that of heterosexual men (Grimbos et al. 2010). This is a surprising result which should be treated with caution. Homosexuality in men is thought to be primarily determined by early genetic and hormonal influences while homosexuality in women may be more influenced by later-life effects. Finger lengths in almost all the studies considered by Grimbos et al. (2010) were measured indirectly. The BBC

internet study concluded that lesbians and heterosexual women did not differ in their 2D:4D but gay men had significantly higher 2D:4D than heterosexual men (Manning et al. 2007). Further work on 2D:4D and sexual orientation would benefit from the use of direct digit measurement.

Digit Ratios and Health

There are possible applications for 2D:4D and diagnosis, prognosis, and response to therapeutic interventions in a number of diseases and developmental disorders.

Sperm Production

Manning et al. (1998) reported negative relationships between 2D:4D and spermatogenesis. However, this was in a sample from a fertility clinic and the participants included a proportion of men who were producing few or no sperm. The links between 2D:4D and spermatogenesis in the normative population are more controversial and need to be clarified (see Auger and Eustache 2010 for data and discussion).

Heart Disease

There is accumulating evidence that low 2D:4D in men is associated with protection against early myocardial infarction and coronary heart disease (e.g., Manning and Bundred 2001; Wu et al. 2013; Zhenghao et al. 2012). However, the correlation between 2D:4D and heart disease in women requires clarification.

Cancers

There is now much interest in links between 2D:4D and cancers that are dependent on sex steroids. We feel this is particularly important as there is the possibility that 2D:4D may be useful in prediction of susceptibility and also disease progression where the inhibition of sex steroids may be part of the treatment (e.g., Li et al. 2017). We include here cancer of the breast (Muller et al. 2011) and prostate (Rahman et al. 2010). There are now 19 papers concerning 2D:4D and susceptibility to various sex-dependent cancers (Bunevicius 2018). In order to focus attention on

Digit Ratio, Table 1 The relationships between national means of 2D:4D and age-standardized DALY's by 100,000 in 29 countries and 16 malignant neoplasms. For cancer of the breast, cervix, uterus, and ovary, the mean of female right and left 2D:4D was used, and for cancer of the prostate, the mean of male right and left 2D:4D was used

Malignant neoplasm	r	r^2	p	Adjusted p
Mouth	0.35	0.12	0.06	
Esophagus	−0.19	0.04	0.31	
Stomach	0.57	0.32	0.001	0.02 (2-Tailed)
Colon/rectum	0.05	0.003	0.79	
Liver	0.56	0.31	0.002	0.03 (2-Tailed)
Pancreas	0.23	0.06	0.22	
Lung	0.51	0.26	0.005	0.03 (2-Tailed)
Melanoma	−0.41	0.17	0.03	
Breast	−0.50	0.25	0.005	
Cervix	0.48	0.23	0.008	0.04 (1-Tailed)
Uterus	−0.11	0.01	0.57	
Ovary	0.08	0.007	0.67	
Prostate	−0.53	0.28	0.003	0.02 (1-Tailed)
Bladder	0.47	0.22	0.01	
Lymphoma	−0.07	0.004	0.73	
Leukemias	0.58	0.33	0.001	0.02 (2-Tailed)

those cancers that may be linked to 2D:4D, we present associations between overall mean 2D:4D per nation and DALY's (disability adjusted life years; [Global Health Estimates 2015](#)) of a number of cancers, including those for the stomach, liver, lung, cervix, prostate, and various forms of leukemia (Table 1).

Osteoarthritis

The relationship between low 2D:4D and risk for osteoarthritis of the knees seems to be firmly established (e.g., Ferraro et al. [2010](#)). This correlation appears to be independent of wear-and-tear consequent on engagement in sport or other physical activity (Haugen et al. [2011](#)). Further work is indicated regarding 2D:4D and prognosis and response to treatments.

Smoking and Alcohol Choices

Smoking and the consumption of alcohol are major public health issues. In the BBC internet study, Manning and Fink ([2011b](#)) reported correlations with 2D:4D such that low 2D:4D was linked to high alcohol intake and smoking to high 2D:4D. These correlations applied to individuals and to mean 2D:4D per country and

national levels of consumption of cigarettes and alcohol. Further work is necessary to identify the relationships between 2D:4D, health (heart disease, lung cancer, respiratory conditions), and consumption of tobacco and alcohol).

Conclusion

In humans, 2D:4D is a sexually dimorphic trait (male 2D:4D < female 2D:4D) that is more or less fixed by the end of the 1st trimester of pregnancy, and which is little affected by puberty. It is a composite trait such that the sexual dimorphism may differ between the phalanges. The sex difference in 2D:4D is ancient among the four-limbed vertebrates with similar sex-dependent ratios in mammals (rodents and primates). There is experimental and correlational evidence for the influence of prenatal sex steroids on mammalian 2D:4D. Low 2D:4D is associated with high PT low PE and high 2D:4D is related to low PT and high PE. Digit ratio is determined in a narrow fetal time-window and the effect sizes of correlations with target traits depending on whether such traits are influenced in that time-window.

There are large effect sizes in the relationships between 2D:4D and sport (particularly sports that are dependent on endurance) and developmental disorders. Effect sizes are smaller with regard to complex sex-dependent behavioral traits that are difficult to measure. A potentially important aspect of 2D:4D are its links with sex-dependent diseases such as cancers, heart disease, and osteoarthritis.

Our understanding of 2D:4D has advanced considerably since the late 1990s. However, the speed of this advance has been affected by the many methods that have been used to measure finger length. The lack of clarity of report concerning this issue means that we still do not understand the properties of various indirect methods of digit measurement. This apart, we feel that the diverse program of research into 2D:4D will continue to reveal the importance of the prenatal hormonal environment on behavior, physiology, and predisposition to disease.

Cross-References

- [Bernhard Fink](#)
- [Biology of Human Gender, The](#)
- [Hormone Effects on Human Fetal Development](#)
- [John Manning](#)
- [Robert Trivers](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)

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Digital Age

- [Loneliness in Modern Life](#)

Dignity

- [Self-Esteem as Manipulative Status Communication](#)

Diminish

- [Use It or Lose It](#)

Ding-Dong

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Synonyms

[Imitation of sounds](#); [Onomatopoeia](#); [Origin of language](#)

Definition

The ding-dong theory constitutes an early theory of the origins of spoken language postulating that the meaning of the words derives from what things sounded like.

Introduction

The idea behind the early speculative theory of ding-dong theory is sound symbolism which is a nonarbitrary connection between phonetic features of linguistic items and their meanings. Max Muller at the early stages of his work on the evolution of language proposed the ding-dong theory by stating that meaning comes from sounds. According to this hypothesis, the origin of language emerged evolutionary with the names our ancestors gave to objects, activities, and natural occurrences after an identifiable sound associated with it in real life (Mandavilli 2016). An important characteristic of this notion is the fact that words having high front vowels were used to name small or jagged objects in comparison to words having round vowel which were used to name large or round-shaped objects. It is suggested that people used sound symbolism to give meaning to words through onomatopoeia, which is the formation of a word by the imitation of a sound made by or associated with its referent in real space and time. “Boom,” for example, was the word given for explosion (Mitchell et al. 2013).

A major drawback of this theory is that onomatopoeic words are not the same in every country because the sound and pronunciation of the words are not similar among the different languages. People in different nations used their onomatopoeic words which are formed in regard to how they interpret different sounds. These words are a very limited part of their vocabulary since many ideas such as love, hate, harmony, and the sea do not make any noise. For this reason, this theory was later abandoned by Max Muller (1877).

Conclusion

According to the ding-dong theory, a connection was established between language and the

quality of the things which were part of our ancestors. It refers to the concept that there was a relation between the sounds made and the comprehension of the surroundings. The origin of language, therefore, emerged by the connection between the meanings of words and the sounds that were made by the early human beings.

The limitation of this theory is that it does not explain the origination of different ideas or things that do not produce any sound. This results to a limited vocabulary of the languages. Thus, there cannot be an explanation of the origin of names of such concepts, if this theory is chosen as the origin of language. Besides, the relationship between meaning and sound is not established by any convincing evidence.

Cross-References

- [Bow-Wow](#)
- [Pooh-Pooh](#)
- [Ta-Ta](#)

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Direct Bullying

- [Girls Psychological Bullying](#)
- [Same-Sex School Bullying](#)

Direct Familiarization

► Kin Recognition and Classification in Humans

Direct Fitness

► Limited Reproductive Potential

Direct Guarding

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Synonyms

[In-pair mate retention](#); [Sex as a mate guarding strategy](#)

Definition

Using sexual intercourse as a form of mate guarding, keeping partner from straying, and reducing risk of extra pair copulation.

Introduction

Mate guarding refers to strategies that seek to preserve access to mate, hinder reproductive rivals in gaining access to partner, derogate rivals and competitors, and keep the partner from defecting the relationship (Buss 2002). While there are various forms of mate guarding tactics utilized within relationships (see, e.g., Arnocky et al. 2014; Buss and Shackelford 1997), here frequency of intercourse as a mate guarding strategy within couples is presented.

Frequency of in-pair copulation and mate guarding behaviors have been found to be positively associated (Shackelford et al. 2006), both self-reported by men in relationships and from women reporting on mate guarding behavior from partner. This suggests that men's mate guarding behavior and in-pair copulation function concurrently as anti-cuckoldry tactics, and other studies have found such association to be moderated by mate value of partner (e.g., attractiveness in Kaighobadi and Shackelford 2008) and own mate value (e.g., height in Brewer and Riley 2009). Women who reported more frequent in-pair intercourse also performed other retention tactics (such as enhancing appearance) at a higher frequency (Barbaro et al. 2015). While couples seem, to some extent, to have the same perception of what kinds of tactics are being used to mate guard within a relationship (Shackelford et al. 2005), and mate guarding behavior and intercourse frequency is linked, motivation for sexual intercourse in itself is also related to mate guarding.

Both sexes use intercourse to increase partners' sexual satisfaction, hence increasing relationship commitment (Barbaro et al. 2015), reducing the chance of mate defection. Engaging in intercourse has also been found to be a means of keeping partner away from potential rivals or consolidate a relationship. At least two studies investigating reasons for having intercourse found that women and men use sex in order to keep partners in relationships, to keep partner happy, to reduce the likelihood for partners to cheat by having sex with her/him and having sex with someone due to fear of him/her having an affair if sex was not had, and to "trap" partner into a new relationship (Meston and Buss 2007; Kennair et al. 2015). These are all reasons that are linked to mate guarding and potentially function to reduce possibility of mate poaching and relationship defection. While there are few sex differences in the reasons for engaging in sex related to reduction in mate poaching, there are suggestions of sex differences in ultimate explanations for frequency of in-pair copulation.

Multiple studies have shown that men increase sexual interest toward partner, increase distress and persistence in response to partners sexual

rejections, and even increase forced in-pair copulation, as a function of time spent away from current partner (e.g., Shackelford et al. 2007; Starratt et al. 2007; Goetz and Shackelford 2006). This has been suggested to be behaviors that evolved in response to increased chance of infidelity and sperm competition (for a review of sperm competition in humans, see Shackelford and Goetz 2007). Women seem to a larger degree to engage in in-pair copulation in order to increase partner's commitment to the relationship in order to reduce partner investment in rivals (e.g., Barbaro et al. 2015).

Conclusion

Sexual satisfaction is associated with relationship satisfaction (e.g., Byers 2005; McNulty et al. 2016), and by definition in-pair frequency of intercourse is identical between women and men in relationships. However, there are suggested sex differences in how frequency of intercourse is used as a mate guarding tactic, with sperm competition and eliciting relationship investment differing between men and women.

Cross-References

- Fitness Benefits of Mate Guarding for Males
- Mate Retention
- Mate Retention Strategies
- Sexual Behavior
- Use of Mate Retention Strategies

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Direct Reciprocity

- [Nonhuman Reciprocal Altruism](#)

Direct Reciprocity and Group Formation

- [Reciprocal Altruism and Group Living](#)

Direct Sexual Coercion

- [Types of Sexual Coercion](#)

Directed Attention

- [Selective Attending](#)

Direction of Sounds

- [Evolution of Auditory Perception, The](#)

Directional Odor

- [Directional Smell](#)

Directional Smell

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Synonyms

[Directional odor](#); [Olfactory navigation](#); [Oriented smell](#)

Definition

The ability of humans to discriminate between odorous stimuli perceived either from the right or from the left side.

Introduction

Our sensory systems have developed in order to allow us to identify stimuli in the environment, evaluate them, and make sensible decisions about them (Kringelbach and Stein 2010). Olfaction is of great importance for food selection and reproduction (Porter et al. 2007). Olfactory sensory neurons can detect a large variety of odors and process the information by sending them through their axons to the olfactory bulb. The human perception of an odor is usually associated with pleasant or unpleasant emotions (Mori et al. 1999). The question that has been researched widely in the past decades is whether humans are able to define the direction of an odor, in other words, the ability to discriminate between odorous stimuli perceived either from the right or left side.

Kobal et al. (1989) define directional smell as:

the ability to localize an odor source in space by perceiving the differences of the odor's concentration reaching both nostrils, with a higher odor concentration on the nostril closer to the odor source stimuli with accuracy.

Is There Directional Smell?

Since a sound source can be localized because emitted pressure waves reach each ear at a slightly different phase, one might also assume that a source of smell could also be localized by differences in time or intensity with which the different odors reach the nostrils (Kobal et al. 1989). Von Békésy's research experiment (1964) indicated that if the time difference and the difference in sensation intensity of an olfactory stimulus is used, the direction of an olfactory source can be determined between the two nostrils as the air surrounding the odorous object is inhaled.

Therefore, according to Von Békésy (1964), the direction of a smell can be determined with precision in spite of the small distance between the nostrils and human sense of smell process, an equivalent to the phenomenon of directional hearing. More recent research (Van Toller et al. 1980; Prah and Benigus 1984; Hummel et al. 2003; Wysocki et al. 2003; Frasnelli and Hummel 2005; Villarreal et al. 2012) supports odor localization mediated by the olfactory nerves and a strong consensus that humans can localize olfactory/trigonal exists.

Various research experiments have been conducted to date, in order determine the existence of directional smell. Contradictory to von Békésy's findings, Skramik stated that substances that merely stimulate the olfactory nerve cannot be localized, but if the substances additionally excite the trigeminal nerve, then it is possible to distinguish between right and left side (Von Skramlik 1925 in: Kobal et al. 1989). The trigeminal nerve is connected with the sense of pain, cooling, warming, or pressure; hence, if the odors elicited such effects, distinction between right and left was possible. In their experiments, Schneider and Schmidt (1967) obtained similar results when they used coffee, *n*-butane and ammonia presented to both sides of the nose in two different concentrations and again with two different arrival times. Because in their experiment less than half the participants were able to localize either the strong odors or the odors presented first, they added head rotation to the sniffing procedure and all three odors were accurately localized as to left, right, and center. They concluded that directional smell requires additional information from the trigeminal and/or the position sense.

In the last decade, research seems to be supporting the existence of olfactory localization. Despite the evidence that localization of an odor is possible only if the odor stimulates the trigeminal nerve, some evidence that active sniffing may affect this ability and facilitate the localization of pure odorants exists. Frasnelli et al. (2008) tested the ability of participants to localize a pure odorant and a mixed olfactory/trigeminal stimulus under two stimulation conditions, active or passive. The results indicated that subjects could only localize the mixed olfactory/trigeminal stimulus, but there was significant interaction between

stimulation condition and nature of the odorant. What was interesting in their findings was that participants had more correct answers after stimulation of the right nostril than of the left nostril, which may suggest laterality effects (Zatorre and Jones-Gotman 1990; Frasnelli et al. 2010). Although the activation of olfactory receptors is essential to the smell process, most odorants simultaneously stimulate the trigeminal system (Doty et al. 1978). Kleemann et al. (2009) investigated the human sensitivity and ability to localize hydrogen sulfide, which in low concentrations stimulates the olfactory system, and trigeminal substances including carbon dioxide. Their results demonstrated that humans are not able to localize substances which only activate the olfactory system independent of their concentration despite of their aware perception, but they possess an ability to localize odorants that additionally excite trigeminal system. Moessnang et al. (2011) investigated olfactory localization using implicit spatial cueing which suggested the existence of spatial information processing in the olfactory system. They concluded that humans are unable to explicitly localize the odorant under immobile conditions with passive stimulation, but they suggested that odor localization has implicit effects on behavior, thus supporting directional smelling in humans (Moessnang et al. 2011).

Additionally, a number of studies argue that human phylogenetic heritage has not entirely disappeared. Porter et al. (2005) contrasted olfactory left versus right localization with olfactory identification during brain imaging, by delivering odorants to the left or right of the nose. They found nostril-specific neural activity in primary olfactory cortex that was predictive of behavioral localization accuracy. The same region has been implicated in auditory and visual localization as well (Calvert et al. 2001). According to Moessnang et al. (2011), these findings imply increased sensitivity of implicit tests for spatial abilities in human olfaction, which may help to reconcile the conflicting results concerning directional smelling in previous studies. Research points to evidence that the nature of an odor influences the ability of humans to localize it (Brand and Jacquot 2001; Brand et al. 2001). Porter et al. (2005) found that regions that are classically

understood to be visual processing centers are also activated during olfactory identification. From their findings, they concluded that humans can spatially localize an odorant to the left or right, when behavioral conditions are optimized (Porter et al. 2005).

Conclusion

Research to date has shown that when pure odorants are used as stimulants localization is random (Kobal et al. 1989). On the other hand, stimulation of the trigeminal somatosensory system simultaneously can lead to directional orientation. Research (Kobal et al. 1989) shows that directional smelling exclusively mediated by the olfactory nerve does not exist. Olfactory localization can be allocentric, egocentric, trigeminal, or pure olfactory. According to Porter et al. (2005), in any occasion it must be subserved by neural substrates that research is yet to explore. Future research should aim to establish the existence of directional smelling through the investigation of patients with olfactory or trigeminal deficits.

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Directionally Random Morphological Asymmetries

► [Fluctuating Asymmetry](#)

Directory or Catalog of Behavior

► [Ethograms](#)

Disabilities

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Synonym

[Impairment](#)

Definition

Conditions that inhibit the learning educational material and/or social interaction with peers in the classroom.

Introduction

In 1975, Congress passed the *Individuals with Disabilities Education Act* (IDEA). Originally called the *Education for All Handicapped Children Act*, IDEA mandates the provision of a free and appropriate public school education for eligible students ages 3–21. The primary goals from IDEA is to protect the rights of children with disabilities, and to give parents a voice in their child's education. Children that have a disability that need special education and related services also receive a Free and Appropriate Public Education (FAPE). FAPE believes that students with

disabilities are entitled to an education that is appropriate for them, and must be provided to every eligible school-age child with a disability. All students with disabilities who are eligible for FAPE will be educated at the public expense, and FAPE will also be implemented in the public-school system that the student is in. Public-schools are required to provide special education in the least restrictive environment which means that they must teach the students with disabilities in general education classrooms whenever it is possible. Under the *Individuals with Disabilities Education Act* (IDEA), this law gives parents specific rights and protections, which is called procedural safeguards, to make the educational decisions for their child. IDEA covers Autism, deaf-blindness, deafness, emotional disturbance, hearing impairment, intellectual disability, multiple disabilities, orthopedic impairment, other health impairments (including ADHD), specific learning disabilities (including dyslexia, dyscalculia, and dysgraphia), speech or language impairment, traumatic brain injury, and visual impairment (including blindness) (Lee 2014).

From 2014 to 2015, people who are receiving special education services from the ages 3 to 21 years-old were 6.6 million, or about 13% of students with special needs as public-school students (National Center for Education Statistics 2017). Among those students receiving special education services from public-school, 35% had specific learning disabilities (National Center for Education Statistics 2017). Even though a student has a disability, it does not guarantee the child getting special education services unless the result of that disability needs special education services to make progress in school. For instance, a student with ADHD can be doing well in school and would not be covered by the IDEA. A child who is not eligible for support under the IDEA can still be eligible for support under the *Section 504 of Rehabilitation Act*. The *Section 504 of Rehabilitation Act* is a federal law that requires a school district to provide a free and appropriate public education to each child with a disability in the district and this federal law can provide accommodations to help children in school (Lee 2014).

Evaluating Disabilities

To be able to get a child the help he or she needs, first the child must go through the evaluation process called a Comprehensive Educational Evaluation. The evaluation process will be conducted by either a psychologist or a special education teacher where they will either evaluate or observe the child. Then a case manager, or sometimes called an IEP coordinator, will coordinate all the testing to see if the child needs an Individualized Education Program (IEP). An IEP is a plan that details the support and services at the school that will provide to meet the individual (the child) needs of a student with a disability who qualifies for special education. The parents, one of the child's general education teachers, at least one special education teacher, school district representative, a school psychologist or other specialist, and the child (when the child is 16 years-old) will be at the IEP meeting to talk the Present Level of Performance (PLOP), annual goals, and individualized supports and services. PLOP is a statement about a child's current levels of academic and functional performance, which includes social, behavioral and motor skills, and goals. The IEP will need to be revised as the child makes progress and faces new challenges each year, and then the new instruction techniques and technology become available (Morin 2014).

Learning and Social Disabilities

Individuals with Disabilities Education Act (IDEA) covers learning and social disabilities, and some disabilities can flow through both learning and social disabilities (Lee 2014). Disabilities that are learning include Auditory Processing Disorder (APD), Dyscalculia, Dysgraphia, Dyslexia, Language Processing Disorder, Non-Verbal Learning Disabilities, Visual Perceptual/Visual Motor Deficit, and related disorder include, Attention Deficit Hyperactivity Disorder (ADHD), Dyspraxia, Executive Functioning, and Memory. IDEA also uses the term Specific Learning Disability (SLD) which is a disorder in one or more of

the basic psychological processes involved in understanding or in using language, spoken or written, which disorder may manifest itself in the imperfect ability to listen, think, speak, read, write, spell, or do mathematical calculations. SLD includes a range of disabilities including, but not limited to, dyslexia, aphasia, issues with perception, and brain damage (American Speech-Language-Hearing Association 2017). Some children who have learning disabilities can be less observant in their social environments, misinterpret the social behavior of others at times, and may not learn as easily from experiences of social cues as their classmates. While other children who have learning disabilities, they can exhibit an immaturity and social ineptness due to their learning disability. Learning disabilities arise from neurological differences in the brain structure, function, and can affect a person's ability to receive, store, process, retrieve or communicate information. Learning disabilities are still undergoing considerable progress to map some of the characteristics but people believe that it could be a consequence of developing brain before or during birth, involving such factors as significant maternal illness or injury, drug or alcohol use during pregnancy, maternal malnutrition, low birth weight, oxygen deprivation and premature or prolonged labor. Early recognition for children that may be at risk with a learning disability can prevent years of struggle and self-doubt.

Social disabilities include Autism Spectrum Disorder (ASD), Specific Language Impairment (SLI), Learning Disabilities (LD), Language Learning Disabilities (LLD), Intellectual Disabilities (ID), Developmental Disabilities (DD), Attention Deficit Hyperactivity Disorder (ADHD), and Traumatic Brain Injury (TBI). Social communication disorder can include problems with social interaction, social cognition, and pragmatics that can be either a distinct diagnosis or occur within the context of other conditions. Social communication behaviors that include eye contact, facial expressions, and body language, are influenced by the sociocultural and individual factors of the person (Learning Disabilities Association of American 2017).

Laws Protecting Disabled People

The *Americans with Disabilities Act* (ADA) is another civil rights law that protects people with disabilities from discrimination in schools, work-place, and other environments. ADA protects people who have a physical or mental impairment that substantially restricts one or more major life activities, this also includes learning. This law prohibits employers from using unnecessary qualification standards to weed out applicants with disabilities, but no requiring employers to hire unqualified applicants with disabilities. Employers are also prohibited from referring to inaccurate job descriptions to determine that an employee with a disability can no longer perform his or her job, and failing to provide reasonable accommodations that do not cause undue hardship to them (Cortiella and Horowitz 2014).

The *Elementary and Secondary Education Act* (ESEA) is another federal law focusing specifically on disability that includes students with disabilities. The ESEA was first passed in 1965 as part of the President Lyndon B. Johnson's war on poverty, and in 2001, is known now as the *No Child Left Behind Act* (NCLB). The ESEA requires schools to meet standards for educational content and student achievement, schools to measure student achievement and progress annually in reading and math, and schools must provide data on overall student performance as well as on programs made by discrete student group, including students with disabilities (Cortiella and Horowitz 2014).

The National Assessment of Educational Progress (NAEP) is the only nationally administered measure of student academic achievement in reading math that is given to students in fourth and eighth grade. The NAEP has three levels, Basic, Proficient and Advanced, that measure what students should know and are able to do at each grade assessed. The NAEP also reports the proportion of students whose scores place them below the Basic achievement level. It shows a wide and persistent achievement gaps between students with and without disabilities in both reading and math but there has been no significant improvement seen in

NAEP for students with disabilities from 2009, 2011, to 2013 administrations (Cortiella and Horowitz 2014).

Risk Factors for Children with Learning and Social Disabilities

Children with disabilities are faced with many challenges that include protective and risk factors. Some common risk factors in a child's developmental path with disabilities include temperament, developmental delay, early antisocial behavior, disturbed peer relationships, and biological/genetic factors. There are environmental risk factors for delay and psychopathology, which include chronic poverty, lack of parenting skills, parental psychopathology, chronic family discord, and lack of social support for the child and the family members. There are also risk factors that have been identified in relation to school failure, school dropout, and substance abuse (Morrison and Cosden 1997).

"Researchers have also identified protective factors, or variables associated with resiliency, for a variety of outcomes" (Morrison and Cosden 1997, p. 45). No one factor has been directly associated with the development of later problems, even though there are many risks and proactive factors that have been identified (Morrison and Cosden 1997). Protective factors can ameliorate problems that are often associated with learning disabilities that can also reside in the person's other skills or temperament or in the responsiveness of the environment to the individual and the ecocultural fir of the individual to the environment. The presence of learning disabilities is a risk factor because of the wide variations in the emotional and social adaptation with people that have learning disabilities (Morrison and Cosden 1997).

Risk factors can be internal, like the function of a specific neurological characteristics that can affect behavior, or it can be external, like the structure of family, peers, and societal environments which can result in frustration. On the other hand, protective factors can ameliorate problems that are often associated with learning disabilities,

which can reside in the individual's other skills, temperament, responsiveness of the environment to the person, and the ecocultural fit of the person in the environment. The ecocultural fit acknowledges learning disabilities by the affected person, with his or her family, and other people in the environment. So, a person can see their disability as all-encompassing or discrete in ecocultural fit. Social expectations and values can put a person with learning disabilities at risk for failure at school and in other social environments, or can help protect that person (Morrison and Cosden 1997).

People with learning disabilities tend to score higher on the scales of anxiety and depression than do other people who do not have known disabilities. People with learning disabilities that have anxiety and depression are found to have self-esteem and self-awareness. They can have higher levels of self-awareness and self-esteem which is correlated with lower levels of anxiety thus self-awareness and self-esteem is a protective factor. Many people with learning disabilities do not have significant emotional problems but there is a correlation with people who have learning disabilities appear to have a greater risk for depression and anxiety. Family environment can be a different story because having a child with a learning disability may add to the family stress in several ways. Parents will have different types of interactions with their children because of problems of information processing at home and school with their children who have learning disabilities. Parents are required to interact more with the school personnel where their child attends which can add more stress on the family (Morrison and Cosden 1997).

Children that have hyperactivity have also been noted as a risk factor for the family functioning because it can be associated with less support and less control for the family with a child that has a learning disability. A parent's goal with having a child that has a learning disability is understanding the nature of the child's disability, and not generalizing the child's disability to the whole child. Protective factors in families with a child who has a learning disability, are more effective in

responding to their child's needs, both cohesive and flexible, demonstrate affective support for the child, and utilize coping skills to use at home and with their interactions at the school (Morrison and Cosden 1997).

Academic performance of students with learning disabilities is compromised by their high rate of disciplinary removals. One in two students with learning disabilities experiences a suspension, in or out of school, or expulsion, but students with emotional disturbance receive more disciplinary removals (Morrison and Cosden 1997). Disciplinary removals will continue to be problematic for students with learning disabilities until school implement evidence-based practices proven to reduce problem behavior. Dropping out of school is a major societal problem with both the impact on the person who drops out and as a general indicator of educational and economic decline. People with learning disabilities have a significantly higher rate of school drop than students without disabilities. The drop-out rate for students with learning disabilities has dropped to 19% in 2011 versus 35% in 2002, but the drop-out rate varies widely across states (Cortiella and Horowitz 2014). People with learning disabilities who have also dropped out of school are at risk for extended economic and social disadvantage. Risk factors that include students with disabilities that drop out are prior school attendance, discipline problems, reading ability, socioeconomic status, family intactness, school transfers, and suspensions and/or expulsions. Any type of school practices that lead to student alienation, disengagement, and loss of commitment to children with learning disabilities also contribute to the dropout problem. Adjustment problems, an experience of school failure, peer problems and/or family disruptions are associated with subtypes of people with learning disabilities that dropout of school. Some people with learning disabilities can successfully negotiate their work environments, make friends, and gain alternative educational credentials outside of the school environment after dropping out of school. Within the special education programs, having small class sizes with low student-teacher ratios, responsive

educational programs, individual attention, basic skill instruction, and parental involvement have helped with the successful dropout prevention for children with learning disabilities. Increasing the graduation rate and reducing the drop-out rate continues to a high priority for parents and educators, especially with the importance of a regular high school diploma, and detrimental and lifelong effects of dropping out of school.

Transitioning from post-school life is a required part of every student's Individualized Education Program (IEP) from the IDEA. According to Cortiella and Horowitz (2014), 54% of students with learning disabilities had the goal to attend a 2 or 4-year college, 43% would like to attend a vocational training program, 57% wanted to obtain competitive employment, and 50% wanted to live independently in 2013 (p. 22). Parental expectations are important, as they are associated with levels of student achievement and general post-high school outcomes (Cortiella and Horowitz 2014).

Conclusion

Disabled children are exposed to the same societal challenges as other children but the existence of a learning disability can put the disabled person at a greater risk for negative emotional, familial, and societal outcomes. Risk factors for people with learning disabilities can have internal factors that make the person more vulnerable to negative outcomes which include certain types of nonverbal learning disabilities, impulsivity, hyperactivity, and denial of a person's disability. Schools can provide the supportive environment and skills necessary for positive coping strategies for children with learning disabilities, but higher levels of school disruptions, unsuccessful school performances, and family separations often lead to school dropout for people with learning disabilities. Many interventions have focused on the remediation of academic problems associated with people who have a learning disability. When a child is diagnosed with a learning disability, they are set into

motion for a set of academic and school structure modifications to help the child with their academic needs. However, understanding the impact of these factors for children with learning disabilities will help enable other people to reduce many of the secondary problems associated with having a learning disability.

Cross-References

- [Child-Centered Learning](#)
- [Learning](#)
- [Maria Montessori](#)
- [School Environment](#)

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Discipline

- [Evolution of Punishment](#)

Discounting of Future Returns

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Synonyms

Delayed discounting; Temporal discounting

Definition

The decrease of perceived value of a particular item as time passes.

Introduction

All types of organisms are constantly making choices throughout their lives. Some of these choices are simple, with one alternative clearly better than the other. However, other choices that must be made are less clear-cut. When human beings and other organisms make decisions, how do they actually analyze and decide between two alternatives? When faced with the choice between two items that differ only on one factor, individuals should pick a larger value over a smaller value, a reward available sooner over a reward available later, and a more certain reward over a less certain reward (Green and Myerson 2004). These are the basics that determine how organisms make the best possible choices. Nevertheless, this only explains one simple type of choice; in reality, most choices are much more complex and differ on many factors. When multiple conditions are examined together, individuals must make tradeoffs to make their decisions.

Perceived Value Changes as a Function of Time

When organisms must make decisions with multiple conditions to consider, the determining factor is the value that they assign to individual components of a choice. The changes in this value for various reasons allow organisms to select one choice over another when neither are wholly better than the other. The perceived value of an item declines as a function of temporal distance, or time, from the present moment. This is called the discounting of future returns. To illustrate: \$100 now is the same monetary value as \$100 in 30 days; the amount has not changed. However, according to temporal discounting, an individual will perceive the \$100 as less valuable 30 days in the future. This helps to explain how organisms make decisions when multiple factors are involved. Various changes to the two options in delay discounting tasks can result in different choices – and different perceived values assigned to the objects – on the part of participants. For instance, making the later reward a larger absolute value or reducing the delay for receiving the larger reward will both result in a higher perceived value for the later reward when all other factors are kept the same. This change is often referred to as choice reversal and is the interest of study in many research areas. One way to look at how organisms discount future returns is by mathematically describing it.

Economists often use an exponential discounting function to explain how the subjective value of an option decreases by a constant percentage per time unit. The equation is as follows:

$$V = Ae^{-bD} \quad (1)$$

In Eq. 1, V is the perceived value of a future return, A is the amount of the return, D is the delay of receiving the return, and b is a parameter that is the rate of discounting. Equation 1 is often criticized because by itself it cannot predict the choice reversal. However, Green and Myerson (1993) have stated that this model can predict the reversal

if the discounting rate for a larger amount is assumed to be lower than the discounting rate for a smaller amount.

There is another popular equation used to study discounting. This equation is referred to as a hyperbolic function. In delayed discounting, a hyperbolic function is often used to model how the values of two choices differ as temporal distance increases (Mazur 1987).

$$\frac{V = A}{(1 + kD)} \quad (2)$$

In this equation, V is equal to the present value of the reward, A is the value of the reward, D is equal to the time of the delay of the reward, and k is the discounted parameter rate of decrease in value (Mazur 1987). This equation can often lead to one of the lines depicted in Fig. 1.

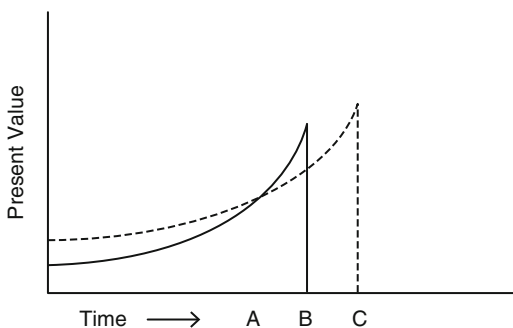
As time increases, the present value of the two rewards will change according to a hyperbolic function. In Fig. 1, there are two different hyperbolic functions. The solid line represents the smaller reward, and the dotted line represents the larger reward. At point B is the reception of a smaller, sooner reward, and at point C is the reception of a larger, later reward. At point A, the two lines intersect, and the smaller reward becomes more valuable than the larger reward. This reversal of the options is because the time has increased, and the second option is now preferable after a significant amount of delay.

This reversal is often the focus of many studies to see at what specific point participants will

prefer each individual reward and at what point that preference shifts. Research on the discounting of future rewards is applicable to many areas of psychology because individuals discount the future more or less steeply depending on certain characteristics. For instance, some research has examined discounting rates in loan borrowers and nonborrowers, finding that loan borrowers discount the future more steeply than nonborrowers (Mahoney and Lawyer 2016). The application of the discounting of future returns has also been studied as it relates to shopping, such as for CDs in an online marketplace (Hantula and Bryant 2005). All of these areas of research are easily linked to the explanation of how organisms discount the future. However, one link that may not be readily apparent is the relationship between the discounting of future returns and evolutionary psychology.

The Discounting of Future Returns and Evolutionary Psychology

Evolutionarily, organisms also have to make tradeoffs when making decisions. For example, reproductive decisions in ancestral time can be examined for evidence of temporal discounting. Over time, organisms have had to make many decisions regarding immediate versus delayed rewards, and these decisions have varied across different ecologies. To return to the previous example, an organism in an unstable environment may discount future returns more steeply and may choose to have offspring sooner because the value of future offspring decreases due to the higher chances of death before future reproduction can take place. During the life of an organism, there are many decisions that can be deemed as having a benefit in the distant future or the immediate future. The benefits of a decision for an immediate or delayed reward are specific to whether that choice would be advantageous in the current environment. In addition, some individual differences exist in individuals' decisions to receive items sooner rather than later, and, therefore, in the amount that individuals discount future returns. An organism will have an overall preference for



Discounting of Future Returns, Fig. 1 Two rewards discounted as a form of delay

now or later, and this preference can be beneficial or harmful depending on the environment of the individual. These preferences are theorized about in life history theory, which differentiates these preferences as a fast strategy (immediate rewards) and slow strategy (future rewards). Life history theory has been used to explain many different aspects of behavior, but more importantly for this chapter, it has been used to explain how specific tradeoffs are made in many aspects of behavior (e.g., time versus money) (Griskevicius et al. 2010). This theory also helps explain individual differences in the discounting of future returns.

The Discounting of Future Returns and Life History Theory

An individual's life history strategy has been shown to influence how that organism discounts future returns. Life history theory says that all individuals must make tradeoffs when deciding how to allocate resources to maximize fitness, but environmental factors, particularly in infancy, influence how organisms make these decisions throughout their lives (Ellis et al. 2009). Life history strategies vary both between and within species; humans have a slow life history relative to many other species, but humans can also have relatively slower and faster life history strategies based on their own personal environmental characteristics and experiences. The harshness and unpredictability of the environment an individual experiences when they are young predicts whether an individual will select a fast or slow life history strategy, and this strategy influences how they make decisions about the present versus the future. Some factors related to life history theory have been found to reliably influence future discounting across populations, including sex and age.

An individual's sex and age have been shown to influence how he or she discounts future returns. For example, children and adolescents value the present and discount the future much more steeply than older adults (Daly and Wilson 2005). They are less likely to wait for a reward in

the future, choosing instead to receive gratification immediately. Additionally, males have been shown to discount future returns at higher rates than females (Kirby and Marakovic 1996). Life history theory suggests that this happens because males' life history strategy is faster and higher-risk; in other words, males have achieved reproductive fitness by using short-term strategies more than females across evolutionary history, so they have evolved to use short-term strategies in other areas as well, discounting the future more steeply than females in favor of more immediate rewards. Further, life expectancy for males is lower than for females, and this also influences their life history strategy and their discounting of future returns, because they need to select a choice that will benefit them while they are likely to be alive to receive those benefits (Daly and Wilson 2005).

Life history theory says that slower life history strategies should be associated with a preference for less risk and a higher value for the future, while faster life history strategies should be associated with more risk and a lower value for the future (Griskevicius et al. 2011b). This is because organisms with faster life history strategies expect to have a shorter life span, and the payoff for the future reward may not be realized. If an organism is unlikely to live to collect a reward, investing in the future is not a fitness-maximizing decision. Therefore, organisms with fast life history strategies should prefer more immediate rewards over future rewards, while organisms with slow life history strategies can safely invest in the future. This influence is not only present in monetary decisions; life history theory can be applicable to many different areas of life in which an organism is required to make decisions about present rewards versus future rewards.

Various empirical studies have tested the relationship between life history and future discounting across many types of decisions. For example, individuals with a slower life history strategy have been shown to prefer low risk and future-oriented financial options and express less positive attitudes toward early reproduction (including a desire to postpone reproduction to obtain more education or work experience), while individuals with a faster life history strategy

prefer high risk and present-oriented financial decisions and show more positive attitudes toward early reproduction as a response to mortality cues (Griskevicius et al. 2013; Griskevicius et al. 2011a; Griskevicius et al. 2011b).

Conclusion

Organisms take many variables into consideration when making choices, including whether it is fitness-maximizing to receive a smaller, immediate reward or a larger, future reward based on their specific situation and environmental characteristics. Life history theory can help explain some variations in the ways that individuals discount future returns; this theory can be applied to many different areas of life in which decisions must be made, from monetary choices to reproductive timing decisions to educational options. Researchers will always be interested in the various factors that influence how organisms make various decisions in the real world and in the laboratory, and this specific research can apply to decisions that organisms have made across assorted times in both the past and present.

Cross-References

- [Access to Resources](#)
- [Benefits of Short-Term Mating](#)
- [Cost-Benefit Analysis](#)
- [Environmental Unpredictability](#)
- [Fundamental Tradeoffs](#)
- [Investment Versus Future Payoff](#)
- [Life Expectancy and Reproduction](#)
- [Life History Strategies](#)
- [Life History Theory](#)
- [Reproductive Benefits must Outweigh Costs](#)

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Discrepancy

- [Mismatch](#)

Discriminative Care

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Discriminative Grandparental Solicitude

- ▶ [Level of Grandparental Investment](#)

Discriminative Parental Solicitude

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Disease Avoidance

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Synonyms

[Behavioral immune system](#); [Immunity](#); [Parasite avoidance](#); [Pathogen avoidance](#); [Psychoneuroimmunology](#)

Definition

Behavioral disease-avoidance processes help animals maintain safe distances from sources of

contagious disease, thereby reducing the need for physiological immune responses.

Introduction

Threats to survival have been a major driving force in evolution, shaping a wide range of specialized defensive adaptations. Some of the threats come in the form of the many hazards in the physical environment. Other, perhaps more potent threats come in the form of exploitation by other organisms. Predators are an obvious example, as are other members of the species competing for limited resources. Although less conspicuous than typical predators, tiny organisms that infiltrate larger organisms and cause somatic damage have posed a recurrent and pernicious threat. These tiny organisms include microbes such as viruses, bacteria, and protozoa, as well as relatively larger organisms such as hookworms. What unifies them is that they have evolved to spend at least a part of their lives within a host organism in order to complete their life cycle. When they cause disease in their hosts, they are known as *pathogens*. The effects of pathogens are wide ranging. Highly potent pathogens can seriously debilitate or kill their hosts within days, whereas less harmful ones may linger around for years, gradually undermining the host organism's ability to survive and reproduce (in the latter case, they are more commonly referred to as *parasites*).

When species face a recurrent threat across generations, evolutionary theory predicts the emergence of adaptations designed to thwart the threat or minimize the damage. So, what adaptations did host organisms evolve to deal with pathogens and parasites? From plants to animals, most organisms have evolved various internal defenses whose function is to detect and eliminate harmful microbes, and attenuate their harmful effects. In addition, animals – organisms with the ability to move spontaneously – appear to have evolved behavioral defenses against pathogens as well. These behavioral defenses involve specialized perceptual systems (vision, olfaction, gustation) and psychological processes (emotions, beliefs,

attributions), which ultimately increase the likelihood that the animals will stay away from sources of pathogens (Murray and Schaller 2016). In humans, these defenses have implications that go beyond maintaining health. Several lines of research have examined the ways in which disease-avoidance processes may influence various aspects of social life, shedding new light on topics such as physical attractiveness, intergroup prejudice, and cultural variation.

Why Did Behavioral Defense Evolve?

When it comes to natural defenses against infectious diseases, we humans are most familiar with the vertebrate immune system, which is our primary defense against pathogens. This system comprises multiple layers of physiological defenses involving specialized cells and bodily fluids, and specific responses such as fever and inflammation. Perhaps the most impressive component is the adaptive immune system (“adaptive” in the sense of adapting to different pathogens within a lifetime), involving tailored reactions to different kinds of pathogens in the body (Clark 2008). Not only does the adaptive immune system efficiently rid the body of the multitudes of pathogens that gain entry on a daily basis, it can also form a “memory” so that future invasions by the same pathogen are dealt with even more swiftly (this capacity is what makes vaccination possible). This incredibly complex and efficient immune system – which scientists have yet to fully understand – serves as a compelling example of the creative power of natural selection operating over expanses of time.

As useful and impressive as these physiological defenses are, they have a number of shortcomings. First, they are mostly reactive, doing their work only after pathogens have breached the body (although recent evidence suggests that mere perception may activate physiological defenses prior to actual contact – see below). Second, they are physiologically costly, consuming large amounts of metabolic resources, and sometimes entailing sickness behaviors which may come into conflict with other adaptive behaviors such as foraging

and mating. Third, they are not perfect, sometimes succumbing to infection (when a new, exotic pathogen enters) and sometimes overreacting to non-pathogenic agents (such as pollen, in the case of seasonal allergies). Finally, pathogens themselves evolve over time to better overcome the hosts’ immune defenses – and with much shorter generations, pathogens can evolve at a quicker pace (which can, at times, be deadly for the host species). For these reasons, in addition to behaviors for managing sickness following infection, behaviors that function to prevent pathogens from entering the body in the first place would have been highly adaptive for animals (Hart 2011). And it appears that this selection pressure shaped the evolution of animal behavior: Growing evidence indicates that animals possess behavioral defenses against pathogens. In the human literature, the suite of psychological and behavioral processes involved in disease avoidance has come to be known as the *behavioral immune system* (Schaller and Park 2011).

The behavioral immune system has two key characteristics in common with the physiological immune system: It tends to be overinclusive (responding to nonthreats more often than failing to respond to threats), and it is functionally flexible (responding more vigorously when the threat is registered to be more imminent). These characteristics will be further explicated below and will feature throughout the discussion of various aspects of disease avoidance.

Perception and Cognition

The first step in avoiding dangers is their detection, thus introducing the first key engineering problem in the evolution of danger-avoidance adaptations. For most animals, detecting bigger predators such as lions and snakes is relatively straightforward – you can usually see them, sometimes hear and smell them. In fact, it is likely that the sights and sounds of bigger predators are specifically what prey animals have evolved to respond to. But microscopic pathogens (which are essentially very small predators) elude our senses for the most part. In fact, people were

unaware of their existence until the seventeenth century, when microscopes opened up the world of microbes and helped scientists to eventually develop the *germ theory of disease*, which is the idea that some diseases are caused by microorganisms. Obviously, neither direct observation of pathogens nor an understanding of germs was necessary for the evolution of the behavioral immune system. This is because pathogens often leave behind a trail of aftereffects that can be used as cues for their detection – for example, they may change the sight and smell of food, or cause infected people and animals to exhibit overt symptoms. Also, harmful amounts of pathogens tend to be reliably found in certain objects (e.g., feces), and certain animals are especially likely to be vectors of pathogens (e.g., cockroaches). Adaptive disease avoidance can be accomplished by making use of those cues that tend to reliably co-occur with pathogens.

The cue-based nature of disease detection helps make sense of the underlying perceptual and cognitive processes. There are many examples of things that people generally do not want to touch, due to an intuitive sense that some sort of contamination may occur – moldy fruit, maggots, mucus, feces. Symptoms of disease that may usefully serve as perceptual cues include physical and behavioral anomalies such as skin lesions, fetid smells, and abnormal gait. Animals (including humans) appear to have evolved to be sensitive to these disease-connoting cues (Schaller and Park 2011). In humans, there is evidence for efficient cognitive processing of disease-connoting cues involving enhanced attention and recall, and when faced with seemingly conflicting information, people seem to be swayed more strongly by visually conspicuous abnormalities than by rational knowledge regarding the presence or absence of disease (Murray and Schaller 2016). The face may be a particularly important interface through which underlying disease is detected, as many contagious diseases alter features of the face, and observers seem to show especially strong aversion to facial abnormalities (Oaten et al. 2011). In short, ancestral humans and animals that responded with specific aversion to observable correlates of pathogens were more

likely to survive and reproduce, thus propagating those tendencies. We are descended from a long line of humans (and prehuman ancestors) who never died from contagious disease before reproducing at least once.

Relying on cues to detect pathogens is useful and has served animals well, but it does need to overcome a crucial problem, with important ensuing implications: Not all pathogens produce detectable cues (e.g., some pathogens do not produce any symptoms, especially in the earlier incubation period), and things that appear very similar to disease-related symptoms (such as burn scars) may in fact be harmless. This means that inferences based on cues will inevitably be imperfect, sometimes under-inferring disease (failing to detect actual pathogens) and sometimes over-inferring disease (“detecting” pathogens where they do not exist). In the absence of perfectly reliable cues, it is impossible to eliminate errors, but the system can be calibrated toward making one type of error, in order to reduce the likelihood of the other type of error (much like household smoke detectors that are deliberately calibrated to be hypersensitive, leading to many annoying false alarms, but, presumably, very few misses – no alarm when there is a fire – which can be highly costly). Many evolutionary psychologists have argued that under-inferring disease is much more costly than over-inferring disease in terms of survival and reproduction, and so perceptual systems should have evolved to be biased toward errors of over-inference, which will minimize errors of under-inference (Haselton and Nettle 2006; Kurzban and Leary 2001). As a result, much like smoke detectors prone to false alarms, humans will quite often “detect” diseases where none exists – that is, show a tendency to be over-inclusive in cue-based inferences regarding disease. Furthermore, because the tendency to be over-inclusive will have greater payoffs when the probability of actual infection is higher, this tendency is expected to be functionally flexible, being heightened in response to perceived vulnerability to disease – which has been empirically documented (Miller and Maner 2012). The over-inclusive nature and the functional flexibility of disease detection have interesting implications not

only for social perception and cognition but also for emotions and motivations.

Emotion and Motivation

We do not usually question our intuitions regarding things that are alluring or repugnant – it is simply obvious to us, for instance, that babies are cute and feces are revolting. Even Charles Darwin (1872) could not fully shake off this intuition-driven circularity when he defined disgust as a reaction to “something revolting, primarily in relation to the sense of taste, as actually perceived or vividly imagined” (p. 250). It is thus a somewhat underappreciated insight that the adaptive logic of disease detection and avoidance explains *why* unsightly symptoms and fetid smells are subjectively experienced as unsightly and fetid – ancestral animals and humans who found these stimuli aversive (and thus were motivated to avoid contact with sources of pathogens) would have outcompeted those who found the stimuli appealing (and had no motivation to avoid sources of pathogens). Of course, some learning does take place with regard to associating specific locally available cues with aversion (with the result that there is some cross-cultural variation in what things are considered repulsive and need to be avoided), but the basic negative response itself is unlikely to be a product of learning. There is increasing evidence that disease avoidance constitutes a distinct motivational system (Murray and Schaller 2016) and that the key emotional experience associated with disease avoidance is *disgust* (Curtis 2013; Oaten et al. 2009).

What kinds of things are disgusting? In recent decades, several groups of researchers have compiled massive amounts of data to address this question. Although it appears that human disgust has evolved to serve multiple functions (Tybur et al. 2013), a commonality running through most of the things that reliably elicit disgust across cultures and time periods – rotting food, skin lesions, maggots, bodily fluids, dirty hands – is the potential for transmission of parasites and pathogens (Curtis 2013). In other words, disgust may be an innate emotion that is reliably activated

in the presence of sources of pathogens. Or, as Pinker (1997) put it, “disgust is intuitive microbiology” (p. 383). And this intuition seems well attuned to the nature of microorganisms. Unlike toxins with safe dosage levels below which they may be harmless, many pathogens have no safe dose, because they can proliferate very quickly. This may explain why people have the sense that “anything that touches a yucky substance is itself forever yucky” (Pinker 1997, p. 383). As a result of this (perceived) association, people will find their favorite foods inedible after it has come into contact with something that is typically associated with disgust (such as a fly swatter, even if it is brand new and obviously clean). This sort of response appears to be further exaggerated in people with anxiety disorders centered on contamination fears. (By contrast, certain toxins like caffeine and alcohol are, despite their bitter taste, avidly consumed by many people.)

Interestingly, disgust may act as a psychological complement to the physiological immune system, being dialed up in response to the physiological system being compromised – for instance, due to recent infection or pregnancy. In other words, when our bodies are more susceptible to pathogenic infection, the behavioral immune system may compensate by heightening our disgust response, making it more likely that we will stay away from potential sources of pathogens. This process appears to be mediated by specific hormones, indicating that the behavioral and physiological systems are closely intertwined. Furthermore, studies have shown that disgust (or the mere perception of disease cues) can directly prime the physiological immune system, seemingly preparing the body for potential infection (reviewed in Murray and Schaller (2016)). The close relationship between the physiological and behavioral components of disease avoidance is further discussed below.

Before leaving the topic of emotions and motivations associated with disease avoidance, it is also important to mention *nausea*, which is a more specific physiological response related to disgust. Nausea is the sensation of uneasiness associated with the urge to vomit, and this response may function to quickly rid the body of

harmful substances (which includes, but is not limited to, pathogenic substances). Thus, nausea tends to occur in situations in which something has been ingested, whereas disgust has a much wider array of triggers.

Behavior

What specific behaviors evolved as part of the behavioral immune system? Some pathogens are transmitted via waste products or vector organisms. Therefore, management of such pathogens would be facilitated by some sort of hygiene behavior (e.g., keeping fecal waste out of nesting sites), which has been documented in humans and nonhuman animals (Curtis 2013). Many other pathogens are transmitted via contact with the body or bodily secretions of infected individuals. Thus, minimizing the probability of infection by other individuals requires physical avoidance, particularly avoidance of direct contact. Indeed, there are many examples of such avoidance behavior in nonhuman animals (e.g., Kavaliers et al. 2005). Chimpanzees, the closest living relatives of humans, have been found to exhibit disease-avoidance behavior: Jane Goodall (1986) observed chimpanzees maintaining physical distance from other chimps who walked abnormally as a result of polio.

In humans, most of the research has focused on the internal psychological processes (thoughts, feelings) presumed to underlie disease-avoidance behavior, partly because such research is easier to conduct and also because people are able to verbally report how they might behave in hypothetical scenarios, with at least some degree of accuracy. Nevertheless, examination of overt behavior is crucial, and there have been a few studies looking directly at disease-avoidance behaviors in humans. One study focused on an aspect of behavior that lies mostly beyond conscious control: Participants' reaction times were measured as they engaged in arm flexion (i.e., approach) or arm extension (i.e., avoidant) movements in response to visual stimuli. Consistent with expectations, participants who had been experimentally primed with information

regarding germs and diseases showed relatively quickened extension movements (Mortensen et al. 2010). In another study, participants were given a task of handling various props that they believed had just been handled by other participants, some of whom exhibited flu symptoms or a facial birthmark (as seen via video recordings). The task required participants to make different kinds of contact with the props which became progressively intimate (involving the hands, head, face, then mouth), and the researchers measured the number of participants willing to complete the task at each stage. Participants were also video recorded so that their nonverbal reactions could be assessed. The results showed that participants were far less willing to handle the props and showed stronger facial expressions of disgust when they believed that the props had previously been handled by someone exhibiting flu symptoms or a facial birthmark (Ryan et al. 2012).

This is not to say that people only avoid individuals exhibiting conspicuous markers. Today, we have a better understanding of diseases and the mechanisms of disease transmission, with the result that people also show tendencies to avoid known disease carriers (such as people with HIV) who may not exhibit any overt symptoms – although this understanding may be highly susceptible to extraneous information and bias.

Implications for Social Behavior

Animal species vary in the extent to which they are social, with solitary animals at one end (e.g., tigers) and eusocial animals at the other (e.g., ants). Sociality does not come for free, and it appears to have evolved within species when the benefits sufficiently outweighed the costs. Humans, like many other species, have evolved to be a highly social species, reaping the myriad survival and reproductive benefits of group living (e.g., greater protection against predators, mutual gains via cooperation, ease of mating). Group living generally requires physical proximity, and some interactions (e.g., mating, parenting) require highly intimate contact, all of which leave individuals more vulnerable to pathogen

transmission. Therefore, the benefits of being close to other individuals and engaging in intimate contact must be balanced against the costs of possible pathogen transmission (among other costs of group living, such as possible exploitation by other members). Clearly, the benefits have been substantial enough to put humans on an evolutionary path toward sociality – apart from rare exceptions, humans do not live solitarily, despite the fact that solitary living would be the best defense against pathogens that are transmitted interpersonally. Of course, not all individuals in our surroundings pose equally high levels of pathogen threat, and some situations are more conducive to pathogen transmission than others. Accordingly, it appears that psychological defenses against disease have evolved the capacity for discriminate and flexible sociality, allowing people to reap the benefits of group living and intimate relationships while simultaneously minimizing the potential costs.

Antisocial Implications

One obvious implication of possessing disease-avoidance processes that respond to disease cues is that, rather than harboring a blanket wariness regarding interpersonal contact, humans may have evolved to selectively avoid and exclude individuals who are more likely to be infected – which may be based on explicit knowledge and/or disease-connoting cues. As noted above, avoidance of infected others appears to have deep evolutionary roots, and Kurzban and Leary (2001) argued that this evolved tendency is likely to be one of the bases for stigmatization in human societies – that is, when people systematically avoid others who are (or appear to be) diseased, the targets experience what we refer to as stigmatization. While contagious disease is not the only reason people stigmatize others (criminals, for instance, are also highly stigmatized), there appears to be a long history of humans ostracizing other individuals with highly visible diseases and keeping them isolated (Oaten et al. 2011). Leper colonies and other instances of disease-related quarantine are examples of such exclusion.

Stigmatization involves consensual (widely agreed upon) exclusion, and so it is a more

permanent phenomenon than temporarily staying away from someone who has a fleeting infection or an illness. Indeed, disease-based stigmatization is usually reserved for those individuals who bear stable morphological markers (e.g., lepers with skin lesions) or harbor diseases believed to be permanent (e.g., AIDS). As noted above, the behavioral immune system is expected to be over-inclusive in classifying anomalous features as disease symptoms. Based on this reasoning, it has been predicted that a number of common visually conspicuous features – physical disability, obesity, facial disfigurement, birthmarks, facial features associated with old age – may be perceived as disease cues, even if people are fully aware that those features are benign. Many studies, using a wide range of methods, have found support for this conjecture. For instance, people appear to implicitly think of those physical features as being sources of contagion, and negative responses to individuals bearing those features tend to be heightened when people feel more vulnerable to disease. These findings have provided deeper insights into the psychological bases of stigmatization of morphological abnormalities (Murray and Schaller 2016).

Similar processes may underlie some instances of prejudice against members of ethnic outgroups (i.e., people of other nationalities, cultures, races). In addition to visible physical differences, ethnic outgroup members may engage in behaviors that seem “wrong” with regard to hygiene and food preparation (as different cultures have developed their own unique norms in these domains), which may trigger concerns about disease transmission. A number of research findings imply that concerns about contagious disease may underlie prejudice against ethnic outgroups (e.g., Faulkner et al. 2004). Of course, because there may be multiple reasons for excluding others, for many common prejudices, disease concerns may sit alongside other concerns and amplify negative attitudes and motivations for behavioral avoidance.

Disease-avoidance processes can contribute to antisocial tendencies even without the presence of any obvious disease cues. Sexual contact, for instance, can potentially transmit contagious

diseases, many of which may not give rise to any overt symptoms among carriers. Therefore, it can be predicted that motivations to avoid disease may be associated with reduced inclinations for sexual contact. Indeed, individuals with chronically heightened concerns about disease tend to report less promiscuous sexual behavior. Similarly, temporarily heightened concerns about disease inspire more cautious sexual behavior (Murray and Schaller 2016). More general personality traits may serve as defensive tendencies against pathogen transmission. For instance, greater neuroticism and introversion (two of the “Big Five” personality dimensions) are associated with higher anxiety about threats and reduced sociability, respectively, and so it is not surprising that chronic concerns about pathogens are associated with neuroticism and introversion (Duncan et al. 2009). There is also evidence that such personality tendencies can be temporarily primed by the apparent salience of disease (Mortensen et al. 2010).

People frequently form negative attitudes toward others on the basis of physical unattractiveness. Although not necessarily a cue for pathogenic disease, physical unattractiveness may be perceived to be associated with ill health. This can be due to an overgeneralization effect, the result of an overinclusive system that responds to any deviations from the population average (i.e., lack of a “healthy” appearance). Also, because physical attractiveness may actually serve as a signal for health in terms of resistance to pathogens and parasites (i.e., good genes, developmental stability), it makes sense that the absence of attractiveness may be perceived as a cue for the presence or the potential for disease. One way to test this would be to examine whether individual differences in pathogen disgust sensitivity (but not pathogen-irrelevant disgust sensitivity) are correlated with perceptions of attractiveness in relatively unattractiveness faces. Indeed, one set of studies found that higher pathogen disgust sensitivity was associated with perceiving relatively unattractive faces as especially unattractive; moreover, the relationship was found to be specific to disgust regarding pathogen-connoting situations (Park et al. 2012).

Prosocial Implications

Sociality is not just about physical proximity or congregating in large numbers – it is about the formation of lasting relationships. Indeed, there are many evolutionary reasons to expect animals to form strong and stable bonds. The bond between parents and offspring, for example, can be predicted from evolutionary theory: Parents who incurred costs to promote the well-being of their offspring would have been more likely to have surviving (grand)children, who would inherit those same parental tendencies (the same evolutionary process explains other forms of nepotistic altruism). One implication relevant to the present topic is that such strong bonds may dampen aversive feelings associated with disease avoidance – indeed, it has been found that mothers find their own baby’s feces less disgusting than those of other babies (Case et al. 2006).

Also, the effect of disease concerns on negative sentiments toward ethnic outgroups described above may be coupled with increased positive sentiments toward ingroup members. This may be due to the objectively lower risks posed by ingroup members (as people are more likely to be immune to local diseases); also, ingroup members may become more salient sources of support in the event of being debilitated by disease (Navarrete and Fessler 2006). Thus, although discriminatory, disease-avoidance processes can promote positive attitudes toward other people. Disease concerns may also influence views regarding the ingroup by increasing the emphasis people place on moral values pertaining to the welfare of the group (as opposed to the welfare of individuals), for example, loyalty to the ingroup and obedience to authority (Park and Isherwood 2011). Furthermore, heightened concerns about disease may translate into greater social conservatism, which also tends to be associated with exaggerated positive sentiments regarding the ingroup (Terrizzi et al. 2013). Of course, as noted above, these “prosocial” responses toward the ingroup are often coupled with antisocial responses toward outgroups, as well as toward individuals perceived to deviate from the ingroup mainstream (such as homosexuals).

Disease avoidance is associated with another type of interpersonal affection – perceptions of physical attractiveness. As already discussed above, physical attractiveness may serve as a signal for health in terms of resistance to pathogens and parasites. One contributor to facial attractiveness is bilateral symmetry, so it can be predicted that preference for symmetrical faces (over subtly less symmetrical faces) may be especially strong when concerns about pathogens are heightened. Also, such an effect would not be expected for nonsocial objects, and studies have shown evidence for this. Symmetry (as a signal for health) is important not only with regard to immediate disease avoidance, but also because it indicates the potential to produce similarly healthy offspring. For this reason, the preference for symmetry may be particularly strong in mating contexts (e.g., in heterosexual judgments of opposite-sex faces, but not same-sex faces), and there is evidence for that as well. Facial masculinity in men may be a signal for immunocompetence, and it has been found that pathogen disgust in women is associated with preference for masculinity in male faces – in other words, women especially sensitive to the threat of disease show a stronger preference for male faces displaying features associated with disease resistance (for a review of the findings described in this paragraph, see Murray and Schaller (2016)).

Culture and Cultural Differences

The operation of disease-avoidance processes discussed above may shed light on certain aspects of cross-cultural differences. The principle of functional flexibility, which helps account for the variable deployment of disease-avoidance responses (i.e., stronger responses when the threat of disease is greater), may also operate at the level of geographical regions and associated cultural groupings. To understand this, one key premise to note is that regions vary substantially in pathogen prevalence – the level of threat posed by infectious diseases. Another key premise is that many cultural norms and practices – prejudicial attitudes toward individuals who deviate from

“healthy” standards, more discriminatory attitudes regarding ingroup–outgroup relations, norms regarding eating and hygiene, and, indeed, the importance of conforming to norms – may be functional adaptations (emerging through biological and cultural evolution) that guard against disease transmission (Murray and Schaller 2016).

Putting those two premises together may explain not only why certain cultural norms exist in the first place, but also why their strengths and expressions vary across different cultures. Social scientists have noted for decades that cultures vary in the extent to which they have norms promoting individual autonomy versus group cohesion, a dimension commonly referred to as *individualism–collectivism*. Notably, higher collectivism is associated with greater social pressure against deviating from group norms and stronger ingroup–outgroup boundaries, both of which may ultimately protect against pathogens. Interestingly, research has shown that regions with greater pathogen prevalence have more collectivistic cultures (Murray and Schaller 2016). Similarly, people living in regions with higher pathogen prevalence tend to more strongly endorse moral values that promote the welfare of the group (Van Leeuwen et al. 2012). More broadly, cultures vary in how “loose” or “tight” they are, in terms of the existence of norms regulating behavior and the importance of adhering to those norms. It has been hypothesized – and empirically documented – that cultures that have historically faced higher levels of threat (including pathogens) tend to be “tighter” (Gelfand et al. 2011). Similar logic can be applied to cultural variation in personality traits (Murray and Schaller 2016).

Also, to the extent that physical attractiveness serves as an indicator for health (signal for immunocompetence, cue for lack of early-life illness), it can be predicted that physical attractiveness in prospective mates may be more strongly prioritized in regions characterized by greater pathogen prevalence. This cross-cultural variation has been documented (Gangestad and Buss 1993).

Although these findings are interesting, it must be noted that studies linking pathogen prevalence to cultural variation face important theoretical and methodological challenges, as voiced by a number of researchers (e.g., Pollet et al. 2014).

Conclusion

In this review, a distinction has been maintained between physiological and behavioral defenses, reflecting the recent evolutionary psychological research on the processes underlying disease avoidance and their implications. Clearly, the treatment of the behavioral immune system as a distinct phenomenon has been theoretically useful and empirically fruitful, generating research on previously undocumented cognitive processes, emotions, and behaviors, particularly with regard to many topics in social psychology. Of course, no psychological or behavioral process can exist in a physiological vacuum, and future research on defenses against disease will require greater integration of physiology and psychology in order to move forward. Indeed, for quite some time, many researchers have been interested in the effects of social and psychological factors on the functioning of the physiological immune system, in a field known as *psychoneuroimmunology*. Given the demonstrable ways in which the behavioral system interacts with and complements the physiological system, it has been argued that the research on the behavioral processes identified by psychologists should actually be situated within psychoneuroimmunology (Clark and Fessler 2014) and that researchers ought to think of the physiological and behavioral defenses as constituting a single integrated immune system (Gangestad and Grebe 2014). These views set the agenda for future research: It seems likely that a more sophisticated (and more accurate) picture of defenses against disease will emerge in the upcoming decades.

Cross-References

- [Disease Avoidance Hypothesis](#)
- [Disgust](#)

- [Facial Disfigurement](#)
- [Nausea](#)
- [Sex-Differences in Disease Avoidance](#)

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Disease Avoidance Hypothesis

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Synonyms

Behavioral immune system; Disgust; Infection; Pathogens

Definition

The disease avoidance hypothesis refers to the set of psychological processes that promote detection of, and aversion to, temporary or chronic pathogen threats as a means of reducing infection risk.

Introduction

Pathogens and parasites have long represented critical threats to human survival and wellbeing. In fact, management of infectious disease is one of the most fundamental problems humans have confronted over their evolutionary history (Ackerman et al. 2012). Even in modern times, pathogenic agents infect hundreds of millions of people, causing approximately 9,500,000 deaths (over 16 % of all deaths) worldwide per year (World Health Organization 2008). In turn, natural selection has shaped sophisticated defenses against invading pathogens such as the complex biological mechanisms comprising the physiological immune system. Although this system is remarkably effective at managing disease threats, it is metabolically costly and imperfect in that it requires initial infection and it must continually adapt to the co-evolution of germs themselves. To address these problems, humans have evolved additional safeguards that help mitigate the probability of initial infection. The psychological collection of these defenses is termed the *behavioral immune system* (BIS; Murray and Schaller 2016).

Behavioral Immune System

The behavioral immune system consists of a suite of psychological mechanisms which functions both to improve detection of potential pathogenic threats and to defend against infection from these threats (Schaller and Park 2011). Concern about such threats directs the mind to seek out specific types of cues and, upon detecting these, to react appropriately by avoiding, expelling, or otherwise managing the danger of infection. For instance, many illnesses produce external symptoms such as sores and lesions, and accordingly, perceivers' reactions to these features are often strongly negative (e.g., Kurzban and Leary 2001; Park et al. 2003).

Behavioral immune responses can be triggered from exposure to at least three distinct sources of information. The first of these involves aspects of the environment that have been historically or ecologically linked to heightened infection risk. Regions around the world vary in terms of their pathogen prevalence, with hotter, wetter climates facilitating breeding and transmission of germs better than colder, drier climates (Murray et al. 2011; Schaller and Murray 2008). Societies that inhabit ecologies with greater pathogen prevalence exhibit differences in psychological detection and defense mechanisms compared to societies inhabiting less pathogen-rich ecologies. Second, situational cues can prompt behavioral immune activity, much as salient cues in the immediate environment influence a wide variety of social psychological outcomes. Pathogen-relevant cues include informational media (e.g., news reporting, advertising) as well as signs that other people may be infected (e.g., sneezing, coughing, bodily sores, face masks). Finally, intrapersonal elements may lead people to exert more or less effort on the detection of and defense from disease. These may involve chronic individual differences such as perceived vulnerability to disease (Duncan et al. 2009) and disgust sensitivity (Tybur et al. 2009) or temporary state changes arising from felt emotions and recent illness (e.g., fighting off infection can reduce the effectiveness of physiological immune activity, leading to

compensatory behavioral immune activity; Miller and Maner 2011).

Although having frontline defenses against infection would clearly be useful for the maintenance of bodily integrity and for survival, the behavioral immune system is particularly interesting from a psychological standpoint because of its wide-ranging implications for interpersonal and intrapersonal phenomena. These implications rest on certain key principles underlying the functioning of the behavioral immune system. The first such principle is grounded in a classic signal detection dilemma. Accurate perception of pathogen threat is inherently problematic. Outside of medical settings, humans cannot see most disease-causing organisms, and thus people must rely on indirect indicators of their presence. For example, when considering whether a person represents a germ transmission risk, two forms of error are possible. A perceiver may infer that a risk is present when it is in fact not (a false positive error), or a perceiver may infer that a risk is not present when it actually is (a false negative error). In the context of this example, a false positive error is unlikely to be especially costly for the perceiver (e.g., one might not spend much time or effort on social interaction). A false negative error, on the other hand, could lead to direct contact with an infected person and thus transmission of germs to the perceiver. As with many other signal detection problems, the mind has evolved to minimize the more costly perception error. Consistent with this, people commonly presume that more cues indicate the presence of disease threat than is truly the case. This overgeneralization bias is termed the “smoke detector principle” (Nesse 2005)—a smoke detector is designed to sound the alarm whenever it detects smoke (a minor annoyance if no fire exists) and not wait for the presence of fire (which would incur greater damage). Similarly, activation of the behavioral immune system occurs in response to cues that are heuristically, but not necessarily, related to disease threat. For example, people concerned about disease react negatively to many benign cues, including physical abnormalities such as disfigurements, obesity, and

disabilities (Ackerman et al. 2009; Miller and Maner 2011; Park et al. 2003; Park et al. 2007), and membership in outgroups (e.g., being of a different race, nationality, or sexual orientation than the perceiver; Faulkner et al. 2004; Huang et al. 2011). From the standpoint of infection risk, the costs to these reactions are relatively low.

A second key principle highlights the costs associated with activating the behavioral immune system. BIS responses do require energy and effort, although these are often less metabolically draining than physiological immune responses. One way evolutionary processes have fine-tuned these psychological mechanisms to reduce unnecessary costs is by introducing “functional flexibility” (Murray and Schaller 2016). This flexibility refers to the context sensitivity expressed by the behavioral immune system. The BIS is not universally triggered in response to a given cue; it takes into account factors from the proximate context in regulating cognitive, affective, and behavioral expression. Specifically, contextual cues that indicate one has low vulnerability to infection produce relatively little BIS activity, whereas cues indicating one has high vulnerability produce especially strong BIS activity. For example, reactions to pathogen threat can depend on individual differences in perceived vulnerability to disease (Duncan et al. 2009) and on state-based differences, such as being in an early stage of pregnancy, when physiological immune responses are naturally suppressed (Navarrete et al. 2007).

A last important feature of the behavioral immune system is that it includes both avoidance- and approach-based action tendencies. Although pathogen avoidance is the end goal of this system, sometimes the best defense is a good offense. Thus, perceiving infection vulnerabilities may motivate actions intended to resolve those perceived problems. These actions could be as simple as seeking medical or social support, or an increased attraction to signals of safety (e.g., familiar people or objects), but they can also extend to aggressive attempts to remove perceived carriers of disease from one’s environment. For example, chimpanzees encountering another obviously sick or injured chimp may first exhibit

fear (an avoidance reaction) and subsequently perform aggressive displays and attack behaviors (approach reactions) toward that individual (Goodall 1986). In humans, seeing a news report about a flu outbreak may trigger concerns about catching the flu and thus rouse hygienic behaviors. As with chimpanzees, though, stereotypic associations between certain people and disease/disgust can also prompt expression of negative attitudes and aggression toward those people (e.g., gay men; Terrizzi et al. 2010). Therefore, it is useful to construe the behavioral immune system as incorporating the full spectrum of action tendencies that serve the underlying function of preventing infection.

Products of the Behavioral Immune System

Just as the physiological immune system is comprised of many distinct but interwoven biological mechanisms, the behavioral immune system draws on a range of psychological mechanisms in the service of pathogen avoidance. These include emotions, early-stage cognitive processes, preferences, personality dispositions, intergroup attitudes, and behaviors. Emerging research suggests that a diversity of outcomes commonly considered to be deliberative in nature (and thus less influenced by incidental cues such as indicators of pathogen threat), including morality, political attitudes, invention and innovation, and consumer behavior, may also be shaped by BIS processes. Next, several categories of BIS outcomes are reviewed.

In order for the behavioral immune system to function effectively, individuals must detect (true or heuristic) signals of pathogen threat. Much of this detection activity occurs through rapid recruitment of early-stage cognitive processes. For instance, when actively concerned about infectious disease, people focus their visual attention longer on faces with physical disfigurements, even when those features are not true indicators of infection (Ackerman et al. 2009). Further, interpersonal categorization is affected such that perceivers set lenient thresholds for categorizing people along dimensions heuristically linked to disease (e.g., obese weight, old age; Miller and Maner 2012). These biases do not translate into

better memory for individuals, however, because perceivers confuse targets for other targets bearing similar heuristic cues (Ackerman et al. 2009; Miller and Maner 2012). Such effects may be accompanied or driven by the rapid onset of particular emotions, most prominently, disgust (Tybur et al. 2009).

Subsequent to these early-stage processes, a number of forms of interpersonal behavior are influenced by activation of the behavioral immune system. All of these behaviors share the common features of downregulating interaction with people who present relatively higher pathogen risks and upregulating interaction with people who are relatively safe (as with other BIS processes, the cues used to indicate risk or safety are often heuristic in nature). Most generally, chronic and active concerns about infection are associated with lower dispositional extraversion, agreeableness, and openness to experience (Duncan et al. 2009; Mortensen et al. 2010). Together, these traits indicate that people worried about disease exhibit lower sociality. This does not mean that such people simply want to hide from the world, however. Researchers have found that infection concerns are also associated with greater endorsement of social norms and conformity to those norms (Murray and Schaller 2012). Normative behavior requires ingroups with members that adhere to those norms, suggesting that people worried about disease preferentially wish to interact with ingroup members relative to outgroup members. This type of selectivity is found in studies of interpersonal attraction as well. Physical attractiveness is largely based on features indicating health and freedom from infection, namely, symmetry and lack of disfiguring marks (Kurzban and Leary 2001; Murray and Schaller 2016). Behavioral immune activity therefore should attune people to the attractiveness of others and increase the selectivity with which others are judged. Indeed, a number of studies show that people who are chronically or temporarily concerned with infection exhibit exaggerated judgments of attractive and unattractive individuals as well as heightened preference for symmetrical, opposite-sex faces (e.g., Little et al. 2011; Park et al. 2012; Young et al. 2011).

In addition to interpersonal cognition, BIS activation has implications for intergroup attitudes. Much of the research in this area focuses on expression of prejudicial attitudes and discrimination toward groups which are heuristically associated with infectious disease. Such associations can stem from the implicit content of group stereotypes and from a more general neophobia, or fear of the new and unfamiliar, which itself may be grounded in a motivation to avoid exposure to novel and dangerous pathogens (Huang et al. 2011; Kurzban and Leary 2001). For instance, disease concerns both correlate with and cause stronger prejudicial cognitions about physically disabled and obese others (Miller and Maner 2011; Park et al. 2003, 2007). Such concerns also contribute to ethnocentric and xenophobic attitudes, as well as endorsement of behaviors that would limit contact with people from other races or groups (Faulkner et al. 2004; Huang et al. 2011; Navarrete and Fessler 2006; Terrizzi et al. 2010).

Finally, a more recent approach to understanding the broad impact of the behavioral immune system has considered whether cultural attributes and practices may stem, in part, from the threat of pathogen transmission. Much of this work has examined the connection between pathogen prevalence within societies (and their local ecologies) and population-level characteristics. Many of the findings mentioned previously scale up to cultural differences, including preferences for attractive others, traits such as extraversion, and conformist tendencies (Murray et al. 2011; Schaller and Murray 2008). Researchers have also found links between pathogen prevalence and cultural values such as religiosity, political attitudes, and the classic cultural variable of individualism/collectivism (e.g., Fincher and Thornhill 2012; Fincher et al. 2008). More work remains to be done at this level of analysis, but the strong selection pressures exerted by pathogens and parasites along with the wide variety in BIS-linked psychological outcomes suggest that behavioral immune research may yield more exciting insights into many of the commonalities and differences that exist across cultures.

Open Questions in Pathogen Avoidance Research

Despite the breadth of evidence for a suite of psychological pathogen avoidance mechanisms, open questions persist about integration of the BIS with other research areas and on ways of addressing potentially undesirable outcomes of BIS activity. On the latter point, the behavioral immune system appears finely tuned to flexibly respond in the presence of pathogen threats, but it also can produce a number of pernicious cognitions and behaviors that impede social connection, cooperation, multiculturalism, and so on. This is especially problematic if we consider the tendencies of people to overgeneralize perception of cues to pathogen threat and to treat others who represent no such threat as potential sources of germ transmission. For example, the heightened ethnocentrism following disease cue exposure (e.g., Faulkner et al. 2004) may have once served a useful, protective purpose, but in the age of modern medicine, the benefits of avoidance may no longer outweigh the societal costs. Helpfully, though, an understanding of behavioral immune processes offers potential means of controlling such outcomes. If people react by distancing themselves from others perceived to be associated with infection risk in order to mitigate vulnerability to that risk, then interventions to BIS activity could target either those interpersonal and intergroup associative cognitions or the vulnerability perceivers infer in themselves. Some evidence addressing the latter possibility exists. Huang et al. (2011) examined two methods of altering perceived vulnerability—vaccination and handwashing. Whereas recently unvaccinated people expressed prejudicial attitudes toward outgroups following exposure to pathogen threat cues, consistent with work cited earlier (e.g., Faulkner et al. 2004; Navarrete and Fessler 2006), people who had recently received a flu vaccination (and especially people reminded of this event) expressed fewer such negative attitudes. The vaccine conferred some sense of invulnerability to disease, which translated into decreased BIS activity, despite the fact that this vaccine conferred protection only against influenza. A similar effect occurred when people were asked to wash their hands (an even less rational outcome given that

handwashing protects only against current, not future, germ exposure). Research on behavioral immune interventions is sparse, however, and much more work remains to be done.

Another unresolved question with both theoretical and practical importance involves the connection between the behavioral immune system and the physiological immune system. The BIS has the potential to act both as a complementary system, in which behavioral and physiological systems reflect a common underlying immune quality (e.g., as a function of genes, developmental stability, or proximate somatic integrity), and as a compensatory system, in which individuals engage behavioral mechanisms in response to weakened physiological mechanisms and vice versa. Current research does indicate that some degree of compensation occurs between these systems. For instance, during pregnancy, suppression of women's physiological immune functioning is strongest during the first trimester, and this is the same period marked by a high level of behavioral immune activity (e.g., food disgust, ethnocentrism; Navarrete et al. 2007). Other work has shown that when recovering from recent illness, physiological immune efficacy is compromised, and again this period features exaggerated BIS responses (Miller and Maner 2011). An intriguing line of research also suggests that the systems may be complementary as well. Several studies have found that observing pathogen threat cues (e.g., sneezing people) not only activates behavioral avoidance strategies but also may trigger a physiological immune response, perhaps in preparation to fight off infection (Schaller et al. 2010; Stevenson et al. 2011). These investigations are quite new, and often feature relatively small sample sizes, indicating the need for additional research to verify exactly how and when the two systems are connected.

Conclusion

A number of open questions exist about the functioning of psychological pathogen avoidance mechanisms such as those described here. When

do emotions like disgust play a central role in behavioral immune activity and when do they not? How specialized is the behavioral immune system in terms of responsivity to pathogen threat vs. nonpathogenic forms of bodily threat? Should the behavioral immune system be entirely integrated within the larger field of psychoneuroimmunology? Given the active state of research on these topics, such questions may not wait long to be answered.

Cross-References

- [Disease Avoidance](#)
- [Disgust](#)
- [Error Management Theory](#)
- [Facial Disfigurement](#)
- [Parasites](#)
- [Pathogen Disgust and Perceptions of Attractiveness](#)
- [Pathogen Load and Attractiveness](#)
- [Pathogen Protection](#)

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Disease Cues and Immune Response

- [Immune Response to Disgust and Disease Cues](#)

Disguise

- [Camouflage](#)

Disguised Aggression

- [Gossip, Rumors, and Social Exclusion](#)

Disgust

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Synonyms

[Abhorrence](#); [Detestation](#); [Grossed out](#); [Repulsion](#); [Revulsion](#)

Definition

A feeling of intense displeasure or revulsion in response to an offensive or revolting object, person, or behavior.

Introduction

An evolutionary perspective on emotions holds that the physiological, psychological, and behavioral characteristics of a specific emotion, such as disgust, should be seen as evolved features that have been useful to humans at some point during our evolutionary history. Individuals equipped with a genetic makeup that enabled them to respond to a certain stimulus or situation by experiencing a certain emotion were better able to cope with and respond to recurring challenges and opportunities and subsequently increased their reproductive success (e.g., Cosmides and Tooby 2000). Seen from this perspective, the advantages that disgust has offered to ancestral humans are likely to have been communicative, motivational, physiological, and influential for future behaviors. In the following paragraphs, the experience and expression,

functions, and individual differences in disgust are discussed, followed by a short conclusion.

The Experience and Expression of Disgust

The emotion of disgust is experienced as a strong feeling of revulsion, often accompanied by nausea, and causing a motivation to withdraw from, avoid, or push away the disgust-eliciting stimulus (Rozin et al. 2000; Oaten et al. 2009). Darwin (1872) considered disgust as one of the six basic emotions: “Disgust [...] refers to something revolting, primarily in relation to the sense of taste, as actually perceived or vividly imagined; and secondarily to anything which causes a similar feeling, through the sense of smell, touch, and even of eyesight” (pp. 256–257). Rozin et al. (2000) argue that from this original toxin-based distaste system aimed to reject tainted foodstuffs, disgust gradually expanded to multiple domains and stimuli and primarily motivates the avoidance of pathogens. In the current literature (e.g., Curtis et al. 2004; Rozin et al. 2000; Oaten et al. 2009; Chapman and Anderson 2013; Tybur et al. 2013), disgust is recognized as playing a key role in motivating behavior that reduces exposure to and contamination with bacteria or viruses.

A feeling of nausea often accompanies disgust and is elicited independently of the ingestion of the disgust-eliciting stimulus, thereby serving to prevent consumption. If such preventative measures fail, vomiting may help to expel the ingested substance. However, although nausea is often seen as the prototypical physiological concomitant of disgust, not all disgusting stimuli elicit nausea. For example, skin-transmitted pathogens such as disease transmission or venom injection via contact with a parasite carrier, venomous insect, or reptile produce a skin-crawling sensation and an urge to protect the skin (the “heebie-jeebies”; Blake et al. *in press*). Additionally, exposure to one’s own and other people’s moral transgressions produces a need for physical cleansing – literally, to wash away one’s sins (Zhong and Liljenquist 2006).

The experience of disgust is accompanied by a typical facial expression which includes slightly narrowed brows, a wrinkled nose, a curled upper lip, and protrusions of the tongue. The wrinkling of the nose restricts airflow through the nose, narrowing the brows reduces the exposed surface area of the eyes, and the curled upper lip and protrusion of the tongue prevent infected substances from entering the mouth (e.g., Rozin et al. 1994). Although different elicitors may cause variations in its expression (Rozin, et al. 1994), the prototypical disgust expression is recognized across cultures (Darwin 1872; Sauter et al. 2010). Brain imaging studies have shown that both experiencing disgust and seeing another person making a disgust face activates the same sites in the anterior insula and to a lesser extent in the anterior cingulate cortex (e.g., Wicker et al. 2003).

The Functional Domains of Disgust

Across cultures, disgust is reliably elicited by stimuli that are associated with the presence of pathogens – such as feces, dead bodies, and sexual fluids (Curtis et al. 2004). This type of disgust, elicited by concrete physical stimuli, is termed *physical disgust* (Chapman and Anderson 2013) or *pathogen disgust* (Tybur et al. 2013). In addition, disgust is elicited by stimuli that are not associated with the presence of pathogens, but rather by abstract social and moral transgressions – e.g., lying, theft, and fraud. This type of disgust is referred to as *moral disgust* (e.g., Rozin et al. 2008; Chapman and Anderson 2013). Its function is to regulate social interactions and particularly to coordinate condemnation and punishment. For some authors (e.g., Chapman and Anderson 2013; Rozin et al. 2008) the transgressions which elicit moral disgust also include certain sexual activities which are condemned by modern society – such as bestiality or incest. However, Tybur et al. (2013) argue that a fully functionalist approach to disgust should take into account the selection pressures which shaped the emotion of disgust, that is, the domains of survival

and reproduction. Thus, in addition to pathogen and moral disgust, *sexual disgust* is thought to be elicited by threats to the functional domain of reproductive success, that is, sexual activities or behaviors which might negatively affect one's long-term reproductive success. The three distinct functions of disgust are detailed further below.

Pathogen Disgust

Pathogens posed a constant threat to survival and reproduction in human ancestral and modern environments. It is likely natural selection favored perceptual systems which could reliably detect those properties associated with pathogen presence (Tybur et al. 2013). Cues to the likelihood that pathogens might be present can be visual (e.g., a slimy texture), olfactory (e.g., the smell of feces), gustatory (e.g., sour-tasting foodstuffs), or tactile (e.g., moisture content). Indeed, cross-culturally, disease-salient stimuli such as unhygienic or ill-looking individuals, bodily fluids (blood, slime, or feces), and skin lesions reliably evoke disgust (e.g., Curtis et al. 2004; Oaten et al. 2009; Tybur et al. 2013). Pathogen disgust is thus thought to have evolved specifically to serve the function of avoiding such sources of infectious agents (Curtis et al. 2004).

Pathogen disgust is sensitive to "false alarms," meaning it is also elicited by objectively non-infectious stimuli such as severe skin burns, amputated limbs, or insects resembling maggots or parasites (Oaten et al. 2009; Park et al. 2003). This bias toward having a relatively low threshold to detect and avoid possibly infectious stimuli is hypothesized to be the result of a cost-benefit computational analysis (Tybur et al. 2013), where the costs of not avoiding a stimulus which does contain pathogens (a type II error, a miss) are higher than the costs of falsely avoiding a stimulus which does not contain pathogens (a type I error, a false alarm; e.g., Oaten et al. 2009). Moreover, such a computational account would also predict that the amount of disgust experienced by certain stimuli is the result of specific trade-offs of avoiding pathogens versus obtaining other benefits (expected value of contact; Tybur et al. 2013).

Indeed, pathogen disgust is moderated by a variety of variables: strangers evoke more disgust than kin (Curtis et al. 2004), and being food deprived decreases the disgust response to unpalatable foods (Hoefting et al. 2009).

Sexual Disgust

Choosing the right mate to reproduce with was – and is – a significant challenge to humans, and choosing wrongly significantly decreases the chances of producing multiple healthy offspring, and as such is reproductively costly. Moreover, the time and energy spent on courtship, copulation, and the raising of offspring are generally restricted to one individual at a time, prohibiting the pursuit of alternative mating opportunities, producing opportunity costs. To avoid these costs, both men and women are choosy about the individuals they mate with and look for high-quality mates. Quality is assessed on various dimensions, most notably on the dimensions of intrinsic quality and genetic compatibility (Tybur et al. 2013). Intrinsic quality can show itself in features that influence objective physical attractiveness (e.g., Grammer et al. 2003), and both men and women assess a possible partner's attractiveness on features like facial attractiveness, body symmetry, and body shape. For example, fluctuating asymmetry is a reliable visual marker for genetic quality and developmental stability (Gangestad and Simpson 2000), and individuals with symmetrical faces are judged to be both healthier and more attractive than individuals with asymmetrical faces. Genetic compatibility can be influenced by genetic relatedness or major histocompatibility complex similarity, and generally humans prefer mates with a genetic makeup that differs from their own. For example, men prefer the smell of MHC dissimilar women compared to MHC similar women (Thornhill et al. 2003).

Low-quality mates might negatively affect one's reproductive success, and sexual disgust is thought to have evolved to stimulate active avoidance of such individuals (Tybur et al. 2013). For most individuals, sexual interactions with an individual with whom we share a significant proportion of our genes – siblings, parents, and

offspring – evoke strong disgust reactions, and sexual relationships between siblings with a history of cosocialization are highly condemned by third-party observers (e.g., Fessler and Navarrete 2004). Additional evidence for a specific function of sexual disgust comes from research showing that disgust and disgust-induced avoidance decrease subsequent sexual arousal, especially in women (Borg and De Jong 2012), and in young males, sexual arousal differentially affects the experience of sexual disgust, but not general disgust (Stevenson et al. 2011).

Moral Disgust

In addition to concrete stimuli-eliciting (pathogen) disgust, abstract moral and social transgressions reliably elicit disgust as well (Chapman and Anderson 2013; Tybur et al. 2009). Moral disgust is elicited by moral transgressions which contain references to pathogens or sexual acts, such as eating rotten meat or engaging in incest. Additionally, this type of disgust is also elicited by transgressions that have no connection to pathogen or sexual disgust, particularly by acts which violate the autonomy and rights of others, and violations or moral rules related to harm or fairness, such as lying, cheating, and stealing (Chapman and Anderson 2013). Individuals who engage in such socio-moral transgressions are often seen as “tainted” or “impure,” making people hesitant to touch them or the objects they have touched and instigating a need for physical cleansing (Zhong and Liljenquist 2006). Moral disgust is experienced by adults as well as young children (Danovitch and Bloom 2009), and brain activation patterns associated with disgust are also visible in a number of moral judgment tasks (Schaich Borg et al. 2008).

An evolutionary account of moral disgust emphasizes that moral transgressions pose direct and indirect costs to individuals and their social groups (Tybur et al. 2009, 2013). From an evolutionary perspective, it would have been beneficial to avoid or punish free riders, rapists, or cuckolds. Moral disgust is hypothesized to facilitate social distancing from and avoidance of individuals who have committed serious moral transgressions (Tybur et al. 2009). Additionally, the facial

expression of disgust functions to broadcast the detection of a violation and may persuade others in one’s social group to condemn the transgressor as well (Tybur et al. 2013).

Individual Differences

Individuals differ in the type of stimuli which elicit disgust as well as the intensity of disgust once it is elicited, that is, they differ in their *disgust sensitivity*. In general, women are more sensitive to disgust than men, and they perceive greater disease threat in disease-related images (Curtis et al. 2004). Women are also more accurate in recognizing the facial expression of disgust, both in male and in female faces (Rotter and Rotter 1988). Although the sexes differ in disgust sensitivity in all three domains, the difference is largest for sexual disgust (Tybur et al. 2009). This sex difference can be explained by the sex differences in the costs and investments associated with reproduction (Trivers 1972). Compared to men, women’s biological investments in offspring are larger, and making poor choices with regard to sexual partners and sexual practices is more costly for women than for men. In order not to jeopardize their chances of producing healthy offspring, compared to men, women are less likely to take sexual risks (e.g., have casual, uncommitted sex; Gangestad and Simpson 2000) and more likely to be disgusted by sexual practices (Tybur et al. 2009).

Moreover, disgust sensitivity has been associated with several personality traits. For example, individuals who are more prone to pathogen disgust also score higher on measures of neuroticism (Olatunji et al. 2012), whereas individuals who are sincere, fair, greed avoidant, and modest are more sensitive to sexual and moral disgust (Tybur and De Vries 2013). In addition, higher disgust sensitivity – in all three disgust domains – is related to lower levels of trait aggression as well as lower daily aggressiveness (Pond et al. 2012). Additionally, higher disgust sensitivity, particularly in the moral domain, has been associated with susceptibility for religious obsessions (Olatunji et al. 2005).

Conclusion

Disgust is a negative emotion, evoking a feeling of revulsion and a desire to distance oneself both psychologically and physically from the disgust-eliciting stimulus. Evolutionary psychologists propose that disgust has three functions, corresponding to domains relevant to human survival and reproduction: pathogen avoidance, sexual decision-making, and condemnation of socio-moral transgressions (see, e.g., Tybur et al. 2013). Individuals differ in the extent to which stimuli elicit disgust and the magnitude of their disgust response. Differences in disgust sensitivity are thought to play a central role in contemporary intra- and interpersonal social processes, such as (obesity) stigmatization (Lieberman et al. 2012).

Cross-References

- Behavioral Immune System
- Disease Avoidance
- Disease Avoidance Hypothesis
- Mating
- Morality
- Nausea
- Pathogens
- Pathogen Risk
- Pregnancy
- Randy Thornhill

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Disgust and Immunity

- [Immune Response to Disgust and Disease Cues](#)

Disgust Sensitivity

- [Pathogen Disgust and Perceptions of Attractiveness](#)

Disliked

- [Rejected Children](#)

Disorders of Sexual Preference

- [Sexual Pathology](#)

Disorganized Attachment and Reactive Attachment Disorder

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Definition

Disorganized-disoriented attachment denotes an insecure category of attachment characterized by an inability to maintain an organized strategy of behavior in relation to the caregiver following activation of the attachment system. Disorganization is thought to stem from an unsolvable approach-avoidance conflict of simultaneously being motivated to approach the caregiver for comfort and being alarmed by the caregiver, a phenomenon termed “fright without solution.” Disorganized attachment has been predicted by abuse and maltreatment and by frightening/frightened behaviors and hostile/helpless states of mind on behalf of the caregiver. Disorganization is behaviorally shown in a variety of fearful, odd, and inexplicable behaviors in relation to the caregiver, including simultaneous or sequential contradictory behavior, freezing and stilling, and direct signs of fear and apprehension of the caregiver. Reactive attachment disorder (RAD) denotes a very rare phenomenon whereby children develop profound difficulties in forming selective attachments to others. RAD stems from a lack of a specific and continuously available

caregiver, is typically observed in children growing up in some institutions, and manifests in two types (inhibited/socially withdrawn and disinhibited/indiscriminately social).

Introduction

John Bowlby, a British psychoanalyst and child psychiatrist (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), was unsatisfied with the explanations of attachment available at the time, which deemed children’s attachments to their caregivers secondary to other mechanisms, such as children’s drives and/or feeding (see ► [“Psychodynamic Foundations”](#)). Seeking an alternative explanation, Bowlby founded attachment theory by drawing from multiple scientific traditions, most notably ethology, cybernetics, and cognitive theory (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)).

Specifically, Bowlby (1982) argued that humans come into the world endowed with an attachment behavioral system (and attachment behaviors), which function is maintain proximity to caregivers and which was retained through natural selection as it was associated with increased chances of survival against predators and other natural dangers (see ► [“Infant Survival”](#)). Thus, children (the weaker, smaller part) form attachment bonds to caregivers (the stronger, wiser part) who are sufficiently available and responding to their signals (not the other way around; see ► [“Offspring–Parent Attachment”](#)).

Bowlby, having to contest the theories of attachment available at the time, and formulate a new scientifically based explanation, devoted a great deal of effort into the normative aspects of attachment. Although he believed that there are individual variations in the “quality” of children’s attachment, manifested in cognitive affective representations of self and others (termed “internal working models” [IWMs]; see ► [“Individual Variations in Attachment”](#) and ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#); Bowlby 1982), he did not get around to systematizing these variations. Lacking an

empirical method for examining variations in the quality of attachment, he focused his efforts on the need for a continuously available and responsive caregiver and the negative effects following separations from and loss of caregivers (Bowlby 1982).

Attachment theory therefore owes much to his close collaborator Mary Ainsworth and her colleagues and students, most notably Mary Main, for the subsequent mapping of systematic individual differences in attachment quality and organization (Ainsworth et al. 1978; Main and Solomon 1990). Drawing on Bowlby’s ideas about the interaction between the attachment system and other behavioral systems, most notably the exploratory system and the fear system, Ainsworth devised a semi-structured laboratory observation method called the “strange situation procedure” (SSP), which enabled examination of the organization of behavior that children (aged 12–18 months) strike between their attachment needs and those of exploration. That is, the quality of children’s attachments to their caregivers cannot be indexed by any single behavior but is seen in the organization of behavior in relation to the caregiver (see ► [“Individual Variations in Attachment”](#)).

Ainsworth and her colleagues discovered three organized patterns of attachment, varying in quality. Secure attachment is considered the optimal organization of behavior (e.g., of highest quality), due to these children’s ability to use the caregiver as a secure base and a safe haven (see ► [“Secure Attachment”](#)). Insecure-avoidant attachment (e.g., a minimizing strategy) and insecure-ambivalent attachment (e.g., a maximizing strategy) are considered less optimal (e.g., insecure) yet organized patterns (see ► [“Organized-Insecure Attachment”](#)).

Mary Main (Main and Solomon 1990) subsequently discovered a fourth category of attachment, “disorganized-disoriented” (“D”). The display of D behaviors in relation to the caregiver made these impossible to classify using Ainsworth’s coding scheme. Disorganized attachment is discussed below. Reactive attachment disorder (RAD), a very rare clinical condition, is also discussed below.

Disorganized Attachment

Behavioral description. A minority of children from normal populations were impossible to classify using Ainsworth's coding scheme to the SSP, since they, for example, behaved as an avoidant child in one reunion and as an ambivalent/resistant child in the other, or showed inexplicable, bizarre, or fearful behaviors in the presence of the caregiver. Mary Main (Main and Solomon 1990) discovered that children showing these disparate behaviors had one thing in common: an inability to maintain an organized strategy of behavior in relation to their caregiver (hence the label "disorganized"). Disorganization is, as outlined by Main and Solomon (1990), classified through marked displays of any of seven different classes of behaviors: (I) sequential display of contradictory behavior patterns; (II) simultaneous display of contradictory behavior patterns; (III) undirected, incomplete, and interrupted movements and expressions; (IV) stereotypies, asymmetrical movements, mistimed movements, and anomalous postures; (V) freezing, stilling, and slowed movements and expressions; (VI) direct apprehension regarding the parent; and (VII) direct indices of disorganization or disorientation. Thus, D attachment differs from the organized-insecure patterns in the form of a breakdown in behavioral and attentional strategies (Hesse and Main 2000), and D attachment is accordingly even less optimal.

Relational predictors of disorganized attachment and developmental correlates. Mary Main and her collaborator Erik Hesse have theorized that an important antecedent to D attachment is fear in relation to the caregiver and that D attachment follows from frightening/frightened behaviors from the caregiver (Hesse and Main 2000). Disorganized children are, upon activation of the attachment system, thought to become stuck in an unsolvable approach-avoidance conflict of both being motivated to approach the caregiver for protection and support and simultaneously being alarmed by and motivated to avoid the caregiver. The reason for this paradox and why it is unsolvable is as follows: activation of the attachment system triggers a

change in the attachment system's "set goal" (the momentary instruction regarding desired spatial distance to the attachment figure) so that children are motivated to increase the degree of proximity (e.g., use the caregiver as a safe haven), since proximity to caregivers (i.e., the predictable outcome of activation of the attachment system) has been associated with increased chances of survival in our evolutionary environments (i.e., the species-typical functional consequence; see ► ["Evolutionary Foundations of the Attachment System and Its Functions"](#)). However, if children are simultaneously being alarmed by the caregiver (the very object to which the attachment system is programmed to increase proximity), the attachment system receives highly contradictory instructions that it cannot handle (e.g., it cannot settle upon a set goal regarding spatial distance), ultimately leading to a characteristic breakdown in behavior. Being attached and thereby motivated to approach, the caregiver upon activation of the attachment system is therefore a prerequisite for D attachment.

D attachment is common in abused and maltreated children, supporting Main and Hesse's theoretical proposal of fear as key in D (Cyr et al. 2010). However, and in contrast to a common misconception, not all children assigned a D classification have been maltreated. An estimated 15 % of children in normative samples are classified D (van IJzendoorn and Sagi 1999). Indeed, unresolved traumatic experiences in the caregivers can lead to momentary frightening/frightened parenting behaviors in the absence of maltreatment, which in turn predicts D attachment (Schuengel et al. 1999; see ► ["Attachment in adulthood"](#) for a discussion of disorganization in adulthood). Disorganized attachment is the attachment category that shows the strongest association with concurrent and later behavior problems, particularly externalizing problems such as aggression and symptoms of oppositional defiant disorder (see ► ["Effects of Attachment Quality and Organization"](#)).

Temporary overstress, neurological vulnerability, and disorganized behaviors: a word of caution. It cannot be stressed enough that one cannot infer a characteristically disorganized

attachment system merely from observing D behaviors. Research has, for example, found that temporary overstress and neurological vulnerability, such as having early difficulties regulating attention and emotion at birth, are risk factors for disorganized behaviors (Granqvist et al. 2016; Padrón et al. 2014). Thus, children may display D behaviors without these behaviors stemming from a disorganizing relational history.

Reactive Attachment Disorder

Behavioral description. A (small) minority of children do not show clear signs of attachment behaviors in relation to their caregiver and can therefore neither be captured with the main dimensions of attachment quality and organization nor the usual coding scheme to the SSP (Dozier and Rutter 2008). One cluster of children show a marked unresponsiveness to the caregiver in the SSP, neither initiating interactions with the caregiver nor responding to the caregiver's bids for interaction and/or bids to comfort the child. Another cluster of children fail to check back with the caregiver in the unfamiliar setting of the SSP and exhibit a lack of age-typical social reticence by showing a willingness to go off with and approach the stranger as if it were an attachment figure. These patterns are considered two subtypes of reactive attachment disorder (RAD): an emotionally withdrawn/inhibited type and an indiscriminately social/disinhibited type, respectively (Zeanah et al. 2011).

Predictors of reactive attachment disorder.

RAD is mainly found in children who have experienced severe social deprivation, being rare to nonexistent in low-risk samples but among the most common problem found in children who have experienced institutionalization (Zeanah et al. 2011). RAD is therefore thought to stem from a lack of a consistently available caregiver to direct attachment behaviors toward, with a severe lack of species-typical experience compromising the development of the attachment system.

Attachment disorders often remit when caregiving conditions improve, such as following

adoption, attesting to the resilience of the attachment system, but attachment disorders can persevere long after adoption, possibly indicating that the attachment system may have a sensitive period for typical development to occur (Dozier and Rutter 2008). Research to date indicates that the emotionally withdrawn type may be more responsive to intervention than the indiscriminately social/disinhibited type, with children found to display indiscriminate behaviors long after having formed attachment bonds to their foster/adoptive parents (Zeanah et al. 2011). Length of institutionalization and timing of removal also seem important, with children spending more than 6 months in institutional care and being removed from institutional care after 12 months of age significantly more likely to develop problems (Dozier and Rutter 2008; Zeanah et al. 2011).

Conclusion

Disorganized attachment denotes an inability of attached children to maintain an organized strategy of behavior in relation to the caregiver following activation of the attachment system and is predicted by having experienced frightening/frightened behaviors on behalf of the caregiver. However, disorganized behaviors can also be the result of temporary overstress and neurological vulnerability, not representing a disorganizing relational history. Disorders of attachment in the form of profound difficulties forming selective attachments to caregivers, as captured in reactive attachment disorder, are reserved for children who have not had any consistently available caregiver to direct attachment behaviors to, typically children growing up in institutions.

Cross-References

- ▶ [Adult Attachment](#)
- ▶ [Effects of Attachment Quality and Organization](#)
- ▶ [Evolutionary Foundations of the Attachment System and Its Functions](#)
- ▶ [Individual Variations in Attachment](#)

- [Infant Survival](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Offspring–Parent Attachment](#)
- [Organized-Insecure Attachment](#)
- [Psychodynamic Foundations](#)

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Disparity Between the Prehistoric Environment and the Current One

- [Benefits of Profound Kinship Connectedness \(and Problems from a Lack Thereof\) Through an Evolutionary Mismatch Lens](#)

Dispersal

- [Alarm Callers Are Females with Greatest Genetic Representation](#)

Displaced Reference

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Definition

The use of language to refer to entities and events that are spatially and temporally removed from the context of language use.

Introduction

A defining characteristic of human language is the ability to communicate about entities and events that are spatially and temporally displaced from the communicative act (Hockett 1960). Species-typical communication of non-human animals concerns the immediate present. Species-typical communication in humans, by contrast, frequently evokes entities and events

that are unrelated to the context of communication. Human language even allows individuals to refer to purely imaginary and even impossible events. Investigations of this function of human language inform scientific debates about language development as well as the cognitive and social determinants of the human language capacity.

Development of Displaced Reference

The ability to make displaced reference provides enormous evolutionary advantages. Humans can transport their communication partners to any time, place, or mental state with a few well-chosen words. Evidence of this function of human language begins to emerge as early as the first year of life, after infants have achieved essential cognitive and social milestones. Precursors to communicating about the non-present include the ability to form mental representations of entities and events, the ability to engage in joint attention, and the ability to gauge an interlocutor's intentions. Note, however, that each of these so-called precursors is also continuing to change well after the onset of displaced reference.

Comprehension of reference to absent entities develops between 12 and 18 months of age but varies with the stability of the infant's representation of the referent. For example, infants comprehend a reference to an entity that is highly familiar, such as a family member, at a younger age than a reference to a recently introduced stranger. Further, infants respond to a reference to someone who just left the room at a younger age than to a reference to someone who left the room a while ago (Ganea and Saylor 2013). This variable skill stabilizes by the middle of the second year of life.

Production of displaced reference is first seen in requests for absent objects. After several months of reaching, grunting, and whining, toddlers begin using language around 17 months of age to request something they cannot see (Sachs 1983). Sachs painstakingly describes the gradual changes in the use of the word "Where" in parent-child discourse, from parent requests for the child

to point at a present object to the use of the term by either parent or child to initiate a search for an object – either present or absent – to a more sophisticated usage at 22 months in which parent and child simply exchange information about the location of an absent object. Morford and Goldin-Meadow (1997) document a stable pattern of the extension of displaced reference from communication about absent objects to other referential domains. Children move from referring to absent objects, actions, attributes, and locations to talking about the recent past and future and then finally begin to talk about the distant past and future as well as imaginary events. Even deaf children who communicate primarily through self-created gesture systems, called *homesigns*, follow this developmental path, albeit with a delay of a year or more for each expansion relative to children who are learning language from their parents.

Is Displaced Reference a Linguistic or a Pre-Linguistic Capacity?

An ongoing debate about displaced reference as it relates to the origins of human language is whether it is a pre-linguistic, symbolic capacity that preceded the emergence of language or whether displaced reference was only possible by virtue of human language. On the one hand, Liszkowski et al. (2009) argue that displaced reference is a social-cognitive function that may have preceded language in human evolution. They demonstrate that pre-linguistic infants can request an absent object through a pointing gesture, whereas chimps will only point to a location of an occluded object, but not a location previously associated with an object that is no longer there. They argue that chimps lack the human capacity to share common ground with an interlocutor. Further, deaf children without access to linguistic input from their hearing parents can nevertheless make displaced reference with their homesign gestures (Butcher et al. 1991). On the other hand, Cuccio and Carapezza (2015) contend that infants who use pointing gestures may well be preverbal but are not pre-linguistic. By one year of

age, infants comprehend a great deal of language. They argue that when infants produce points with the intention of drawing the interlocutor's attention to the absence of an object, these points are a linguistic and symbolic act that will eventually develop into the ability to express nonexistence and complex negation. Likewise, they argue that homesign systems are an expression of the human faculty for language and, thus, do not provide convincing evidence that displaced reference could have preceded language in human evolution.

While this debate continues, Butcher et al. (1991) point out that even when linguistic modeling of displaced reference is absent, modern day homesigners are surrounded by cultural products that index the non-present – pictures in books of absent objects – and photographs of events the child participated in at other times. Further, homesigners and their parents share social routines that enable them to recognize the referent of nonconventionalized communicative bids. For example, one homesigner was playing with a toy school bus and moving toy figures into the bus. When his mother tried to join his play by enacting their morning routine when she waves good-bye to him, he shook his head at her then gestured that the toys are small, but she and he are both big. He then pointed between his mother and a small Mickey Mouse figurine and then showed how the action figure waved “good-bye!” to the toy children on the school bus (Morford and Goldin-Meadow 1997, pp. 427–428). Hence, while linguistic forms of displaced reference do not need to be modeled for children to devise a way to communicate about the non-present, the symbol-rich and socially structured environments that children inhabit today clearly support the development of this function of human language.

Socializing Children into Displaced Reference

The social dimension of displaced reference is emphasized in research that investigates whether

caregivers' talk influences mastery of this function. Much early research was invested in showing that caregivers' talk about the here and now promotes language development. Specifically, children of caregivers who link their talk very closely to the child's focus of attention tend to develop language more quickly than children of caregivers who persist in talking about something after their child's attention has shifted to something else. Veneziano (2001) points out that a sole focus on the here and now could theoretically inhibit acquisition of the ability to make displaced reference. However, her in-depth investigations of caretaker speech indicate that caretakers actually take advantage of context-linked conversation to introduce displaced reference to their children. While talking about the child's focus of attention, they link the current context to past experience, to potential outcomes that did not happen, to absent entities, and so forth. More than a third of utterances that are focused on the here and now nevertheless reference a displaced entity or event.

Between 30 and 36 months of age, typically developing children begin initiating talk about the past and future. Parents scaffold their children's participation in such conversation, raising their expectations of their children's contributions as they become more linguistically adept (Lucariello and Nelson 1987). Fivush and Nelson (2006) show how conversation about the past is fundamental to the child's developing conception of self and to the discovery that representations of past events are distinct from one person to another. In this way, there is a dialectic between the use of displaced language and an individual's representation of past and present. Likewise, for parent-child talk about imaginary topics, which begins at a similar age, there is a strong interplay between engagement in displaced fantasy talk and the development of cognitive abilities including creativity, decision-making, and self-regulation. As Sachs (1983, p. 25) concludes, adults “do not deliberately structure their language to teach, but in the course of quite ordinary everyday talking, they use what the child already knows to provide opportunities for the child to learn something new.”

Conclusion

The ability to refer to the non-present is a hallmark of human language. Development of this function of language emerges in the earliest stages of verbal interaction, but with considerable support from caregivers. Scientific investigations of the development and use of displaced reference reveal that cognitive, social, and linguistic skills interact in complex ways to allow humans to evoke the non-present in the minds of others.

Cross-References

► [Language Acquisition in Infants and Toddlers](#)

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Displays

► [Facial Expressions](#)

Disposable Soma Theory

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Synonyms

[Evolutionary theory of aging](#); [Trade-off between reproductive fitness and longevity](#)

Definition

Organisms must devote limited resources either to produce more offspring or to live longer. Evolutionarily, it is beneficial to sacrifice the latter for the sake of the former.

Introduction

Senescence is the decrease in an organism's ability to reproduce and the increase in the chances it will die as it ages. Explaining why senescence evolved at all has long been an issue for evolutionary theory, because any decrease in an organism's ability to reproduce should be selected against, and senescence – which always ends in death – completely eliminates reproductive potential and occurs in all organisms. Disposable soma theory (DST) was first proposed by Kirkwood (1977) as an evolutionary explanation for this. It posits that a trade-off between reproductive fitness (i.e., an organism's ability to produce offspring) and longevity (i.e., the number of years an organism lives) is what causes aging. Organisms must divide limited energy resources between reproduction and maintaining their bodily tissues (i.e., somatic maintenance). Theoretically, an organism could devote

all of its energy to preventing aging and live forever, but because most animals in the wild die from extrinsic causes (e.g., being preyed upon, dying of infectious disease, etc.), preventing aging would not benefit organisms, because it is likely that they would still die of non-age-related causes even in the absence of aging. It is therefore adaptive to devote only the minimal amount of energy needed to reach the average life expectancy of their species in the wild (which is set by levels of extrinsic mortality) and to devote the remaining energy to reproduction. This reduction in energy focused on somatic maintenance which causes defects in the replication of cells, which with time accumulate enough so that they become harmful. After many years, this leads to aging and eventually death. This is what the DST proposes causes aging (Kirkwood and Rose 1991).

An Example from Kirkwood (1977)

As an example, given that the vast majority of deaths in the wild are due to extrinsic mortality, an organism might be a member of a species whose average life expectancy in the wild is 20 years. This organism could theoretically invest enough resources in somatic maintenance such that it would never age, but this would mean that it would have almost no resources to devote to reproduction. This would destroy its ability to pass on its genes, which is maladaptive, and would not reduce its chances of extrinsic mortality (e.g., even if an organism does not age, it can still be preyed upon, etc.). Therefore, it would be beneficial for the organism to reduce its level of somatic maintenance to such a level that it would die of old age at a maximum of 20 years old. This would allow it to reproduce more while not truly reducing its longevity. Thus, DST predicts that the rate of senescence should increase with increases in extrinsic mortality.

Gender Differences in the Trade-Off Between Fertility and Longevity

According to DST, there should be sex differences in the relationship between longevity and

reproduction. Both sexes experience costs to reproduction, but the nature of the costs differ. Females experience more direct costs from reproduction than males, because females must carry children for several months, experience the trauma of childbirth, and use additional energy for creating milk. Therefore, the decrease in longevity for females for each additional child should be greater than that for males, whose cost for reproduction is mainly seeking mates and fending off rival suitors (Chereji et al. 2012). Travers et al. (2015) found this in female *Drosophila melanogaster*, a species of fruit fly; Nussey et al. (2006) found this effect in red deer, and studies on archival data of the number of children and age of death of seventeenth and eighteenth century aristocracy have found that number of children was negatively correlated with age of death (Chereji et al. 2012).

However, males also face a greater challenge in passing on their genes. Although males have a greater chance to pass on their genes to a huge number of offspring, owing to the fact that they can easily impregnate many females, they also face greater competition from other males (i.e., intrasexual competition). Therefore, it is also more likely for males to fail to reproduce due to intrasexual competition. Thus, it is common for males to pursue “live fast, die young” strategies as seen in higher levels of risk taking. This may cause selection for a shorter life span on average for men, because of the accumulation of wear and tear on their tissues at a greater rate than females. Females, on the other hand, have much lower levels of intrasexual competition and therefore much less variability in how many offspring they have; that is, there is a great chance that any given female will have at least a moderate number of offspring. Therefore, females tend to pursue lower-risk strategies for mating and child-rearing, and this would lead to selection for longer life span. In summary, females should experience a greater decrease in their longevity with each additional child, while males’ general longevity is shorter due to intrasexual competition (Bonduriansky, Maklakov, Zajtschek, & Brooks, 2008).

The Effect of Mating Cost and the Abundance of Food

Using a mathematical model, Shokhirev and Johnson (2014) investigated the combined effects of the rate of extrinsic mortality and mating resource costs on senescence. They found that when mating costs are high but energy (e.g., calories) is abundant in the environment, an increase in the rate of extrinsic mortality increases average longevity. This is because when the mating costs are high and extrinsic mortality increases, the population decreases, because for a species to reproduce at a rate that will keep up with the reduction due to the increase in extrinsic mortality when mating costs are high will be immensely difficult (due to the costs). But this means that there is more energy available for each organism that does survive due to the decrease in the population, which allows them to devote more time to accruing resources and makes it easier to avoid extrinsic mortality. Furthermore, this increase in available resources allows individuals to obtain a lot of energy resources before reproducing. This will reduce the rate of death from intrinsic causes (e.g., aging), meaning the organisms should invest more in the repair of their tissues, thereby decreasing senescence and increasing longevity.

When mating costs little energy and when little food is produced, an increase in extrinsic mortality will decrease longevity in a species. Shokhirev and Johnson (2014) speculate that this is likely because, when there is little food and mating is easy (i.e., does not cost much energy) and extrinsic mortality increases, organisms begin to spend more time on mating (because it is easier) and less on acquiring food and maintaining bodily tissues. This then leads to the accumulation of tissue defects, which leads to rapid aging.

Life History Theory and the Disposable Soma Theory

DST can be further understood in the context provided by life history (LH) theory. LH theory deals with how organisms allocate time and energy to tasks and traits in ways that maximize

fitness (Del Giudice, Gangestad, & Kaplan, 2015). One of the fundamental trade-offs is between present and future reproduction. According to LH theory, growth is the process by which organisms increase how much energy they store, which increases their life span and their future potential for reproducing by virtue of the years that they add to their life span. Maintenance is the process through which organisms repair tissues and devote energy to keeping their immune system functioning. Reproduction is the process of creating offspring. How organisms balance these three processes is referred to as LH strategy. The loss in future reproduction potential and the loss in life span caused by current reproduction are called the cost of reproduction. The optimal amount of energy organisms should devote to maintenance decreases as the quantity of tissue of an organism (i.e., as it grows from infancy to adulthood) increases, because maintenance becomes ever costlier. Furthermore, in the case of the aforementioned “life fast, die young” strategy that males ought to pursue, the greater investment males put into intrasexual competition over mates means that they will have less energy to devote to maintenance, which causes them to age faster than females. So although female longevity should decrease to a greater extent with each additional child, males will generally age more rapidly.

Challenges to the Disposable Soma Theory

There is much compelling evidence for DST in nonhuman animals, but results are mixed when applying DST to humans. DST predicts that the more children humans have the earlier they should die; however, many studies have found no such effect – or a reverse effect – and many of the studies corroborating this prediction have not been methodologically sound. For example, one study looked at the relationship between number of children and longevity in British aristocrats born between the seventeenth and nineteenth century. But other researchers have pointed out that much of those data are inaccurate and that

the sample is not representative due to the great wealth of the aristocracy. Furthermore, Chereji et al. (2013) found, in a sample of 15,622 twins, that having children *increased* longevity. Moreover, Gavrilova and Gavrilov (2005), in a review of past literature on the relationship between fertility and aging in humans, found that the *majority* of studies done on humans have found a positive correlation between fertility and age at death. Furthermore, Gavrilova and Gavrilov (2005) did their own study in which they looked at the life span of people who had no children at all and found that childlessness had no predictive value for the age at which women would die. Finally, it is impossible to conduct an experiment on humans with regard to the DST, as it would be unethical; thus, it is impossible to ever know for certain whether DST applies to humans in a direct way.

Conclusion

DST states that aging occurs as a result of the trade-off between devoting energy to tissue maintenance and reproduction. Because it is evolutionarily beneficial to direct energy away from maintenance to reproduction, this allows tissue defects to build over the years, eventually leading to aging. DST remains an influential evolutionary theory of aging. However, results have been mixed when researchers have tried to find evidence of its applicability to humans. Future research is needed to find whether the mathematical model of Shokhirev and Johnson (2014) and LH theory's predictions can be reconciled with studies of the relationship between fertility and longevity in humans that find no correlation or even a negative correlation between the two variables.

Cross-References

- [Extrinsic Mortality](#)
- [Life History Strategies](#)
- [Life History Theory](#)
- [Longevity](#)

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Dispositional Theories

- [Trait Theories](#)

Disruptive Camouflage

- [Disruptive Coloration](#)

Disruptive Coloration

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Synonyms

Disruptive camouflage; Disruptive pattern

Definition

Disruptive coloration is a set of high contrast markings that creates false edges and boundaries and thereby hinders the detection or recognition of an object's true outline and shape.

History and Mechanisms

Disruptive coloration is a camouflage technique in which concealment is attained using high contrast markings. These markings create false edges inside an object and/or obscure existing ones, and thereby disrupt the detection or recognition of the object's true outline. Thus disruptive coloration combines two methods of concealment: (i) creating the appearance of false edges and boundaries within an object and (ii) concealing the real object boundary (Stevens and Merilä 2009).

Disruptive coloration is seemingly widely employed in animal kingdom, and the approach has been exploited in a variety of fields including the military and art. Although the phenomenon was eluded to by the prominent naturalist the Henry Walter Bates, disruptive coloration was formally recognized and described by artist and natural historian Abbott H Thayer (1909), in his book *Concealing Coloration in the Animal Kingdom* (page 77):

“Markings... of whatever sort, tend to obliterate, – to cancel, by their separate and conflicting pattern, the visibility of the details and boundaries of form...”

Thayer's principle of “ruptive coloration” influenced the design of camouflaged military uniforms and vehicles during World War I.

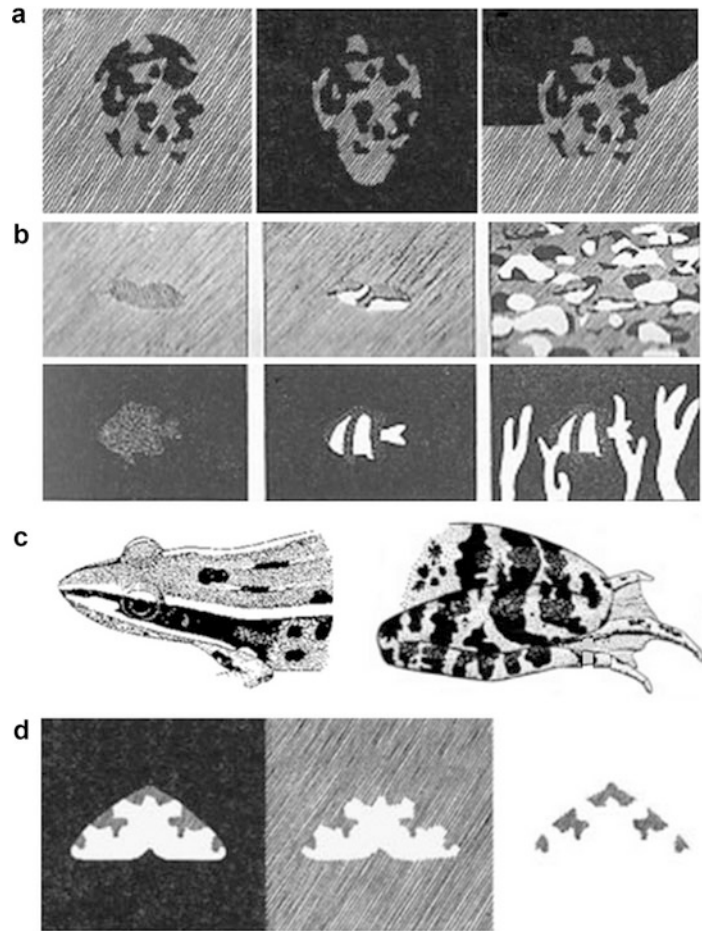
In 1940, a British zoologist Hugh B Cott expanded the theory of disruptive coloration and classified several mechanisms that organisms employ to achieve disruption of edges in his book *Adaptive Coloration in Animals* (Cott 1940):

- (1) “Differential blending” arises when some color patches in an animal have the same color as their background while the other patches stand out, which blends the animal outlines into background and creates the false boundaries (Fig. 1a).
- (2) “Maximum disruptive contrast” predicts that highly contrasting, thus seemingly conspicuous, patterns between adjacent patches within an animal actually conceal by disruptive effect (Fig. 1b).
- (3) “Coincident disruptive coloration” conceals characteristic features, such as eyes or limbs, by having the color patterns on different, but adjacent, body parts aligned to match those features (Fig. 1c).
- (4) “Disruption of surface through false edges” works by breaking up the continuity of outlines through markings that are touching the animal outline and thereby make “gap on the surface” which creates the false outlines of non-regular shapes (Fig. 1d).

Several of Cott's principles were rigorously tested in the early twenty-first century by exposing disruptively patterned (or otherwise patterned for comparisons) artificial moth-like targets to birds under field conditions and estimating their “survivorship.” This artificial moth prey system has provided empirical support for Cott's principles and revealed that concealment through disruptive coloration can be attained mainly via the color patterns that touch the outline of animals, while highly contrasting colors enhance this effect (Cuthill et al. 2005; Stevens et al. 2006). Subsequent eye-tracking experiments with human subjects showed that computer generated moth targets with more edge-intersecting patches were looked at for longer periods prior to attack, and passed-over

Disruptive Coloration,

Fig. 1 Examples of subprinciples of disruptive coloration: (a) differential blending, (b) maximum disruptive contrast, (c) coincident disruptive coloration, and (d) disruptive of surface through false edges (All photos adapted from Cott (1940))



more frequently during search tasks (Webster et al. 2013).

Although disruptive coloration is a conceptually different mechanism from background matching (which is a widespread camouflage mechanism achieved by the resemblance in color and patterns with the object's background), they are not mutually exclusive and animals often use both background matching and disruptive coloration simultaneously. Indeed, since some of the principles of disruptive coloration (e.g., differential blending) require the color matching between an object and its background, disruptive coloration seldom occurs alone, but usually accompanies (or requires) background color matching to give disruption effect. Nevertheless, the adoption of disruptive coloration can sometimes involve a trade-off in which high contrast

marks reduce the probability of an object being detected, even at the expense of reduced background matching (Webster et al. 2013). Moreover, background matching can achieve camouflage without disruption effect, particularly on uniform surfaces (see Fig. 1b).

Many animals have disruptive patterns that have evolved for camouflage including isopods, frogs, butterflies, birds, avian eggs, and cephalopods. One of the best examples of disruptive patterns can be found in cuttlefish. Notably, cuttlefish dynamically change their body patterns dependent on their visual background: they adopt disruptive patterns only when they are against highly contrasting visual backgrounds while, when they are against a plain background, they adopt uniform/stipple patterns (Hanlon et al. 2009). This suggests that disruptive patterns may be more

effective ways for camouflage against visually complex/contrasting backgrounds while background matching can be effective against plain backgrounds.

Conclusion

Disruptive coloration is a form of camouflage that prevents detection and (or) recognition by breaking up the true outline of an object through conspicuous internal contrasting patterns. This camouflage mechanism is widely used in many animals and adopted in many disciplines such as art and military services.

Cross-References

- [Adaptations](#)
- [Aposematism](#)
- [Camouflage](#)
- [Natural Selection](#)

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Disruptive Pattern

- [Disruptive Coloration](#)

Disruptive Selection

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Synonyms

[Divergent selection](#)

Definition

A mode of selection in which individuals with extreme trait values have higher fitness compared to those with intermediate values.

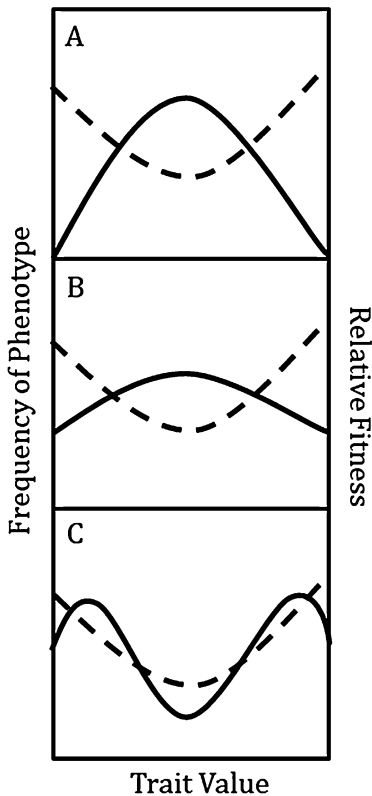
Introduction

Although the popular view of natural selection evokes directional change – bigger, faster, smarter, more colorful – there are modes of selection that can lead to evolutionary change of a trait without directional shifts in its distribution. One example of this is disruptive selection, in which individuals with trait values close to the mean have lower fitness than those exhibiting more extreme values. Disruptive selection can lead to a bimodal distribution of trait values and therefore can result in an increase in the variance of a trait without a change in its mean.

Disruptive selection, also known as diversifying selection, refers to a selective regime in which extreme values have higher relative fitness than values closer to the mean. In a population genetic context in which a trait is influenced by a single locus with two alleles, disruptive selection would occur when there is underdominance – i.e., if both homozygote genotypes have higher fitness than the heterozygote genotype. Underdominance can lead to an unstable equilibrium, with one allele

typically going to fixation (Fisher 1922; Wright 1931), unless additional factors such as negative (i.e., inverse) frequency-dependent selection or interactions with other genetic loci can increase the relative fitness of the less common homozygous genotype.

Continuous traits under the influence of multiple loci can also experience disruptive selection. In these cases, intermediate forms are less competitive than (i.e., have reduced fitness compared to) forms at the extremes of the trait distribution. Provided the trait is sufficiently heritable, disruptive selection can lead to trait divergence (Fig. 1). Several examples are briefly reviewed below.



Disruptive Selection, Fig. 1 disruptive selection over time, with the frequency of a particular value of a phenotypic trait (solid line) and selection (depicted as relative fitness, dashed line). In panel a, the unimodal trait distribution before selection has acted. Initially, selection will likely cause the trait distribution to broaden with increased variance around the mean (panel b). Over repeated episodes of disruptive selection, the trait may assume a bimodal distribution (panel c)

Divergent selection on gamete size: Anisogamy refers to a species producing gametes of different size (e.g., small sperm and large eggs). Many models exploring the evolution of anisogamy rely on disruptive selection to explain the transition from isogamy (gametes of uniform size). In one formulation of the model, imagine cumulative gamete size determines zygote survival with a diminishing returns function (larger gametes survive better, but an increase in size has more of an effect on small compared with large zygotes). Additionally, reproducing individuals have a set amount of resources they can dedicate to gamete production, such that gamete size trades off against the number of gametes produced. If a population starts out as isogamous with intermediate-sized gametes and if gametes compete against other gametes for fertilization, models predict that the population should eventually evolve to a bimodal distribution of gamete sizes. Individuals that make lots of small gametes will be favored because of increased fertilization success, while individuals who make very large gametes will also be favored by ensuring their offspring are competitive. Individuals who make intermediate-sized gametes will lose on both accounts (Lehtonen and Kokko 2011; Parker et al. 1972).

Disruptive Selection for Avian Plumage Maturation: A classic example of disruptive selection has been found in behavior and plumage brightness in a small songbird, the Lazuli Bunting (*Passerina amoena*) (Greene et al. 2000). Males in their first breeding season show a bimodal distribution of fitness based upon plumage brightness, with males of intermediate brightness exhibiting reduced fitness. Brighter males were able to claim high-quality territories of their own, while duller males were sufficiently non-threatening that older territorial males permitted them to settle nearby. These older males apparently benefit by using the young, dull males as buffers against nearby older competitors seeking extra-pair copulations. Males with intermediate plumage brightness were unable to settle on good territories by means of either of the above routes and had the lowest mean reproductive success of any males in their age class.

Ecological Character Displacement: Disruptive selection is thought to play a role in generating and maintaining much of observed phenotypic diversity we see. Ecological character displacement results partially from frequency-dependent competition for resources. For example, some lake-dwelling populations of three-spined stickleback fish (*Gasterosteus aculeatus*) show intraspecific trophic and habitat specialization; lakes can host morphologically and behaviorally distinct benthic and limnetic forms. The two forms can interbreed, yet in field experiments, Bolnick and Smith (2004) found that when fish density was increased, forms with intermediate morphology appeared to face a fitness cost when experiencing the increase in competition. These intermediate forms had smaller body size and relative gonad size compared to conspecifics with more typical benthic or limnetic morphology, a pattern also found in many natural populations (Bolnick and Lau 2008).

Reproductive Character Displacement: Reproductive character displacement occurs when isolated populations experience secondary contact and selection acts on traits related to mating or fertilization success. For example, consider two species of chorus frogs (*Pseudacris feriarum* and *P. nigrita*); secondary contact has led to sympatric populations in which the two species interact. These species show character displacement in male call attributes, with call pulse rate and/or pulse number of *P. feriarum* differing between populations depending on whether they are sympatric with *P. nigrita*; female preferences of the rarer of the two species also differed in sympatric compared with allopatric populations (Lemmon 2009). Furthermore hybrids suffered substantial fitness reduction compared with non-hybrid offspring. The majority of the fitness cost could be attributed to female preference for species typical calls rather than the intermediate calls of hybrids (Lemmon and Lemmon 2010). Thus disruptive selection, in this case against hybrids in the hybrid zone, can explain much of the observed diversification in reproductive traits between these two species.

Conclusion

Selection can take a variety of forms, and fitness functions may not be limited to any one of the primary modes (directional, disruptive, or stabilizing). For example, selection could be simultaneously directional (increasing or decreasing the mean) and also stabilizing or disruptive (changing the variance). Disruptive selection is an important driver of diversification, particularly for generating diversity within a population. As such, it is responsible for many of the dazzling array of adaptations we see in the natural world.

Cross-References

- [Frequency-Dependent Selection](#)
- [Natural Selection](#)
- [Sexual Selection](#)

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begins. The acoustic information – distinguished in intensity (loudness) and frequency (pitch) – travels from the outer ear to the structures of the inner ear through the structures of the middle ear. A process known as binaural hearing helps to clarify sounds in noisy environments.

Dissimulation

- [Response Bias](#)

Distinction According to Genealogical Level

- [Kinship Distinctions According to Generation](#)

Distinguishing the Direction of Sounds

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Synonyms

[Sound generation](#); [Soundwaves direction](#); [Transmission of sound](#)

Definition

The way the sound is directed.

Introduction

To better comprehend the direction of sound, we must consider how sound is directed. When sound is traveling through the air it eventually reaches the ear; there is where all the processing

The Direction of Sound

Sound is generated when an object vibrates and creates soundwaves traveling through the air as a pattern of pressure changes heard as sound (Moore 2001). Air is one medium for the traveling sound to be heard. According to the pressure of the environmental medium (called impedance), the associated pressure will be needed for the soundwave to travel (see Pickles 2012, pp. 1–19). Specifically, when the molecules of the air are drawn together, pressure is generated leading to a process named compression. When the opposite happens, the pressure from the molecules decreases, leading to a process named rarefaction (Oghalai and Brownell 2012). Sound is described in sinusoids, and each sinusoid is called a Fourier component of the sound – based on a theorem by Fourier. A magnitude plot of the components based on frequency is described as a spectrum. Fourier analysis of sound is to produce the spectrum of the soundwaves by slicing the waveforms to sinewaves of various frequencies (Moore 2001; Pickles 2012). In each soundwave, there are two variables: frequency (number of waves measured in hertz) and intensity or loudness (magnitude of movements formed measured in decibels).

Hearing the Traveling Sound

Once sound is generated, our outer ear captures the soundwaves which reach the eardrum, causing it to vibrate. The structures of the middle ear are then activated, that is, the ear bones transform the vibrations into fluid-borne vibrations in the cochlea, activating the structures of the inner ear

to transform the soundwaves into bioelectric signals in the auditory sense cells (Hoy 2012). Sound is then analyzed into the structures of the inner ear, using spectral and temporal analyses. Spectral analysis is used to extract and define the frequency components of the acoustic information. This is done inside the cochlea, where the amplitude and temporal components of the sound is analyzed. This constitutes the first processing of auditory information, with further processing happening in the auditory pathway to the brain (Seikel et al. 2010).

To distinguish between high and low sounds, the basilar membrane closer to the vestibule is vibrated. This structure is the basal end of the cochlea. The basilar membrane is responsible for the analysis of sound frequencies as demonstrated by a series of experiments by von Bekesy (1948). The low frequency sounds are processed in the apex of the basilar membrane. The traveling wave always travels from the base to the apex of the basilar membrane according to the membrane gradient (Seikel et al. 2010).

Localization of Sounds

The location of sound is based on the process of a binaural hearing, in which the sound is analyzed by the central auditory pathways from the auditory information that were sent by the two cochleae to the hearing structures of the brain. Consequently, there is a process of segregation and localization of the sound signals in order to separate the acoustic messages from noisy environments (see Moore 1991). There is an evolutionary advantage for this type of hearing that lead to the survival of species (Avan et al. 2015). Binaural hearing take place at three levels of the brain: the Superior Olivary Complex (SOC), the Nuclei of the Lateral Lemniscus (NLL) and the Inferior Colliculus (IC) (see Moore 1991).

Conclusion

The direction of sound moves from a vibrating object to produce soundwaves through a medium,

usually the air. According to the frequency (i.e., number of waves measured in hertz) and the intensity (magnitude of movements formed measured in decibels) the sound is directed to the structures of the middle ear, through the structures of the outer ear. The sound then travels to the structures of the inner ear and the auditory areas of the brain for further analysis along with the aid of binaural hearing process.

Cross-References

► [Hearing](#)

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Distress Calling

► [Alarm Calling](#)

Distributive Justice

► [Insist on No More than Equity](#)

Divergent Selection

► [Disruptive Selection](#)

Diversified or Conservative Bet-Hedging

► [Environmental Unpredictability and Bet-Hedging](#)

Divided Attention

► [Selective Attending](#)

Division of Labor

► [Sex Differences in Navigation](#)

Divorce

► [Relationship Dissolution](#)

DM

► [Diabetes](#)

Docosahexaenoic Acid (DHA)

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Synonyms

[Essential fatty acids](#); [Omega-3 fatty acids](#)

Definition

Docosahexaenoic acid (DHA) is one of the major polyunsaturated fatty acids and a metabolite of the omega-3 family fatty acids. DHA is the most prevalent polyunsaturated fatty acid in the central nervous system, located in the membrane phospholipids of the mammalian brain, particularly in the phosphatidylethanolamine portion of cell membranes, and retinal cells. DHA accounts for 40% of the membrane phospholipid fatty acid in the brain and is found at rates of more than 30% in the whole retina and up to 60% in the discs of the rod photoreceptor cells. DHA is a very long-chain fatty acid, made up of a 22-carbon backbone and six double bonds. The large side chain and a high degree of unsaturation are properties that appear to grant properties to cell membrane phospholipids that are unique in function and structure, particularly to those in the retina and neuronal synapses in the brain.

Introduction

Neurons are not able to metabolize DHA in vivo, so they must make use of dietary omega-3 fatty acid. The diet of Paleolithic humans was characterized by a relatively equal amount of omega-6 and omega-3 polyunsaturated fatty acids (Crawford 1968). This balance is important because it protects against inflammation, which in turn is helpful in terms of gene expression, the metabolism of leukotriene and prostaglandin, and the production of interleukin-1 (IL-1; Simopoulos 2008). The excessive consumption of omega-6

fatty acids, such as arachidonic acid, is one factor leading to an imbalance between omega-6 and omega-3 fatty acids. In this instance, not only are omega-6 fatty acids being consumed in greater amounts than omega-3 fatty acids, but arachidonic acid also displaces DHA from membrane phospholipids, reducing plasma DHA levels.

Over a short period, significant changes in the human diet have occurred, creating a new phenomenon in human evolution. The western diet is now characterized by disproportionate consumption of omega-6 fatty acids, and it is estimated that the majority of individuals in these regions are DHA-deficient (Simopoulos 2008). The agricultural era is one contributor to the decrease in omega-3 polyunsaturated fatty acids. Because livestock is largely fed an omega-6-rich diet of grain, their carcasses contain far less omega-3 polyunsaturated fatty acids than they would if the animal consumed grass. In comparison, wild animals that feed on wild plants are very lean and contain much more polyunsaturated fatty acids than that of domesticated livestock (Crawford 1968). The difference in omega-3 content between wild and cultivated fish and chicken eggs has also been detected (Raper et al. 1992). Public fear of saturated fat and subsequent government recommendations to substitute vegetable oils (omega-6 fatty acids) in their stead has also become a contributor to low DHA consumption in western populations.

Because the advice to consume more vegetable oil is inconsistent with human evolution, it may lead to maladaptation in those genetically predisposed (Simopoulos 2011). Suboptimal consumption of omega-3 polyunsaturated fatty acids, especially DHA, leads to increased inflammation and is correlated with many diseases common in the western world (i.e., coronary heart disease). For example, deficiencies in alpha-linolenic acid, a precursor to all omega-3 polyunsaturated fatty acids, lead to a slew of symptoms that include paresthesia, blurry vision, leg pain, general weakness, and an inability to walk (Holman 1971).

DHA is crucial for brain development. The developmental period from birth to 2 years of age is when humans experience the greatest brain growth, in which DHA plays a major role.

DHA is known to affect neurotransmitter pathways, synaptic transmission, and signal transduction (Carver et al. 2001). It has a unique structure, including multiple double bonds, which allows DHA to increase the effectiveness of cell signaling. Levels of DHA in the neural membrane impact the maturation of cortical astrocytes, as well as cortical glucose uptake and metabolism. Importantly, myelination of the frontal lobes continues throughout childhood and adolescence, and DHA is vital to this growth (Brown and Jernigan 2012). The frontal lobes are not only rich in DHA, but are also responsible for cognitive processes such as planning, problem-solving, and focused attention (Anderson et al. 1998). Indeed, there is evidence that a child's IQ is increased for every 100-mg increase of maternal DHA (Cohen et al. 2005).

DHA and the Evolution of the Modern Human Brain

Given the importance of dietary DHA in the central nervous system, the discovery of high quality and easily digested nutrients from marine sources is likely to have been an important turning point in human evolution (Newman 2001; Bradbury 2011). Using fossil records combined with stable isotope values of the bone collagen of human remains allows for an estimate of the proportion of protein attained in the diet from aquatic versus terrestrial sources in the 10 years before death (Richards et al. 2001). This technique provides evidence that the Neanderthals main source of protein came from land-dwelling creatures such as wolves and hyenas. These food sources would have had very low levels of alpha-linolenic acid or DHA. There is no sign of aquatic-based protein being part of the Neanderthals diet according to their bone collagen samples. In contrast, there is evidence that early modern humans made aquatic-based protein a staple of their diet. Aquatic sources of protein accounted for between 10% and 50% of the diet, depending on the region to which the sample was attributed. This marked increase in consumption of aquatic sources coincided with a rise in the use

of crafts, such as personal ornamentation, pottery figurines, and textiles (Bradbury 2011). It also coincided with the rapid expansion of gray matter in the cerebral cortex (Broadhurst et al. 2002).

DHA and Sexual Selection

The rapid expansion of brain size in the modern human is likely to have been accompanied by other changes in processes to support the development of such a large brain. Given the incredible importance of long-chain polyunsaturated fatty acids in neurodevelopment, adaptations to acquire, store, and appropriately invest such a resource emerged in females (Lassek and Gaulin 2008). This is apparent in the sexually dimorphic nature of fat storage. Human females tend to have higher gluteofemoral fat stores than human men, and gluteofemoral fat is a main source of long-chain polyunsaturated fatty acids, DHA in particular. Further, abdominal fat appears to have a negative effect on the availability of the essential fatty acids that are essential for infant brain development.

The fact that lower-body fat *increases* the supply of neurodevelopmental resources, such as DHA, and upper-body fat *decreases* these resources is an indication that a low waist-to-hip ratio is an important evolutionary trait. Indeed, a lower waist-hip ratio is correlated with higher blood-DHA levels (Karlsson et al. 2006), and the majority of long-chain polyunsaturated fatty acids found in human breast milk come from maternal fat stores instead of maternal diet (Del Prado et al. 2000). Women's waist-hip ratio is also negatively associated with her own and her offspring's cognitive ability (Lassek and Gaulin 2008). Because of this, the essentiality of DHA for early brain growth, and the human evolutionary history of rapid brain expansion, it is possible that there was once a considerable demand for these brain-building resources, creating a male preference for lower waist-hip ratios. In fact, there is substantial evidence that waist-hip ratio is a significant gauge of female attractiveness, as indicated by a strong

male preference for lower waist-hip ratios in potential sexual partners (e.g., Singh 1993; Tovee et al. 2002; Wilson 2005).

Impact on Animal Behavior

There is evidence that omega-3 polyunsaturated fatty acids play a major role in animal neural development and behavior. When rats that are fed diets rich in DHA for two generations, they produce offspring that respond correctly to a cognitive task at significantly higher rates than the offspring of rats that are fed DHA-deficient diets for two generations (Yamamoto et al. 1987). Similarly, feeding either DHA-deficient or DHA-enriched diets to mouse mothers and their offspring produces significant changes in the ratio of omega-3 to omega-6 brain phospholipid acetyl chains, and these changes lead to changes in performance on learning and memory tasks (Nakashima et al. 1993). For example, compared to mice fed diets high in linoleate oil (source of omega-6 fatty acid), mice fed diets high in alpha-linoleate oil (precursor to omega-3 long chain polyunsaturated fatty acids DHA and eicosapentaenoic acid) were able to reach a safe platform in a water maze test significantly quicker than linoleate oil-fed mice, and they outperformed the linoleate oil-fed mice in an elevated plus maze task. These mice also demonstrated differences in sensitivity to drugs that are known to affect behavior, such that the linoleate oil-fed mice demonstrated a significantly higher degree of sensitivity to an anesthetic and scopolamine injections than the alpha-linoleate oil-fed mice did. Further, DHA has been shown to play a protecting role in the impact that prenatal stress typically has on learning and cognitive development in mice. For example, pregnant rats that experience restraint stress tend to produce offspring with cognitive impairments, among other problems (Feng et al. 2012). However, if pregnant rats are fed DHA-rich diets, the negative impact of restraint stress is buffered. Therefore, DHA appears to play a role in preventing prenatal stress-induced brain dysfunction in animal models.

Impact on Human Behavior

DHA also appears to play a role in human cognition and behavior, beginning in the earliest days of infancy. Evidence suggests that early infant sleep/wake patterns are an indication of the functional expression of the central nervous system and are highly correlated with future behavioral outcomes. A significant relationship between prenatal DHA consumption and infant sleep/wake cycles has been demonstrated. Infants whose mother took a 300 mg per day DHA supplement had more stable sleep-wake cycles within the first 2 days of parturition than infants whose mothers received a placebo (Judge et al. 2012).

In contrast, self-reported low or no prenatal consumption of fish is associated with subsequent offspring deficiencies in communication skills, verbal IQ, fine motor skills, and social communication (Hibbeln et al. 2007). The same associations are not seen among the offspring of mothers who report consuming three or more servings of fish per week while pregnant. Similar deficits were found among the offspring whose mothers had low blood-DHA levels at the time of birth, as measured by cord blood (Kohlboeck et al. 2011). Importantly, mothers with high blood-DHA levels produced offspring who scored higher on measures of cognitive ability, but the effect dissipated after age seven.

Lower omega-3 polyunsaturated fatty acid blood levels have been linked to depression. In young boys (ages 6–12), low blood plasma phospholipid levels of omega-3 polyunsaturated fatty acid are associated with more behavior problems, temper tantrums, and sleep problems than their normal-DHA-level counterparts (Stevens et al. 1996). Similarly, another study demonstrated that college students who took DHA-rich oil capsules for 2 months during a particularly stressful time in the semester were significantly less aggressive than college students who took a placebo during the same timeframe (Hamazaki et al. 1999). Though there is not a wealth of studies looking at the association between DHA and aggression, one recent meta-analysis found a significant negative relationship

between omega-3 polyunsaturated fatty acids and aggressive behavior (Gajos and Beaver 2016).

DHA supplementation appears to have an impact on cognition and behavior. At first glance, the role that DHA plays in the learning and behavior of healthy children seems mixed. Several studies that use pre- and postsupplementation cognitive tests report no significant differences in performance postsupplementation (Kuratko et al. 2013). However, nearly all of these studies also report ceiling effects, where the participant had relatively normal DHA levels and high performance presupplementation.

DHA supplementation appears to be beneficial to those who are most DHA-deficient. For example, although the impact of DHA supplementation in healthy children tends not to lead to significant postsupplementation performance boosts on cognitive tests, there are exceptions. One such exception occurs among children from low socioeconomic status backgrounds (Kuratko et al. 2013). Presumably, these children would be lacking dietary DHA in comparison to higher socioeconomic status children. Attention deficit-hyperactivity disorder is also associated with essential fatty acid deficiency, and DHA/eicosapentaenoic acid supplementation generally has a positive impact on cognitive and behavioral outcomes of children with attention deficit-hyperactivity disorder (Richardson 2006).

Conclusion

DHA is critical in neurodevelopment and likely played a major role in the evolution of the modern human brain. That DHA is a valuable resource may be reflected in the association between DHA and waist-hip ratio, given that waist-hip ratio plays a significant role in female attractiveness and male choice. However, the agricultural era and dietary recommendations to consume more vegetable oil has led to an imbalance in the human diet of the ratio of omega-6 to omega-3 fatty acids favoring the former. This recent underconsumption of DHA is a potential contributor to several diseases common in western

civilizations (i.e., coronary heart disease), behavioral disorders, and deficits in attention and learning.

Cross-References

- [Brain Development](#)
- [Metabolism](#)

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Doctor

► [Jack Kevorkian](#)

Does the Chimpanzee Have Theory of Mind?

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Definition

A landmark paper in the philosophy and science of animal minds. David Premack and Guy Woodruff (1978) describe a series of innovative experiments with an adult chimpanzee, Sarah, whom the authors conclude can attribute mental states to her trainers.

Introduction

Premack and Woodruff's "Does the Chimpanzee Have a Theory of Mind?" was published in 1978.

It is amongst the most anthologized papers in the wide variety of disciplines that constitute contemporary animal studies. In the article, a single adult chimpanzee named Sarah is the subject of a series of experiments designed to assess her ability to attribute mental states such as goals, intentions, knowledge, and ignorance to humans. This general ability is indicative of a *theory of mind* or *mindreading* – a capacity long thought to be unique to our species. Premack and Woodruff concluded that Sarah did, in fact, possess a theory of mind. While the author's methods were widely respected, their conclusion was subject to extensive critical scrutiny that continues to this day.

What Is a Theory of Mind?

According to Premack and Woodruff (1978), "An individual has a theory of mind if he imputes mental states to himself and others. A system of inferences of this kind is properly viewed as a theory because such states are not directly observable, and the system can be used to make predictions about the behavior of others." Mindreading hypotheses are commonly contrasted with explanations for animal behavior indicative of *behavior-reading*, a process of social cognition which does not entail mental state attribution. Behavior-reading hypotheses explain the social behavior of an organism strictly in terms of mere associationism or learned behavioral rules acquired through repeated experiences in like-situations. A mindreader, by contrast, goes "beneath the surface to an understanding of the goals, perceptions, knowledge and beliefs that guide action" (Call and Tomasello 2008). To infer another's *mental states* means that one is interpreting that individual's behavior in terms of their underlying intentions, beliefs, doubts, knowledge, and so forth.

Premack and Woodruff's Experiments

In order to determine whether chimpanzees attribute mental states to others, Premack and Woodruff (1978) showed the chimpanzee Sarah a

collection of videos wherein a human actor is attempting to solve a series of problems. These problems ranged from quite simple, such as attempting to find or reach hidden or inaccessible fruit, to relatively complex, such as escaping from a locked cage. The authors paused each 30-s video during the final 5 s, at which time Sarah was shown a multiple photographs, one of which representing the solution to the problem. For instance, in a video where a human actor attempts to attain out-of-reach food, the photographic options consisted of the actor (a) laying on his side and reaching outside the cage with a stick, (b) moving a box, (c) piling concrete blocks into a box, and (d) standing on a box (the correct answer). Essentially, Sarah's task was to select the photograph that completed the sequence of events – a task that Premack and Woodruff suggested was indicative of understanding the goals or intentions of the human actor.

In the more complex scenarios, Sarah was shown videos of an actor attempting to free himself from a cage, shivering next to a faulty heating unit, unable to wash a floor because the hose was not attached to the faucet, and attempting to play a record on a turntable that was not plugged in. Sarah had previously observed humans interact with these objects but had never used them herself. What is more is these complex sequences were never clearly segmented for her. As Premack and Woodruff (1978) claim, they never “made a little ceremony” out of the numerous steps involved in washing the floor or playing a record. In the same manner as the simple cases, the video was paused and Sarah was then shown multiple photographs. This time, the photographs depicted various objects known to her, one of which representing the solution to the problem at hand. For example, in the instance of the faulty heater, the correct photograph was of a lit wick, and in the instance of the caged human, the correct photograph was a key. Sarah scored perfectly on this series. On a more complicated version, more photographs were added, including keys that were intact, twisted, and broken, lit and unlit wicks, and hoses and power cords that

were both damaged and in normal condition. Here, Sarah made only a single mistake, which the authors attribute to the quality of that particular photograph. The purpose of these second tests was to rule out simple physical matching hypotheses.

Finally, “Does the Chimpanzee Have a Theory of Mind?” was the first paper to describe a popular experimental paradigm used to test mindreading capacities: the “knower-guesser protocol.” In this test, in order to retrieve a food reward that is under one of two containers the chimpanzee is asked to discriminate between a trainer who was present during the baiting and a trainer who was not present. The idea is that the chimpanzee should choose the knowledgeable helper over the one who is merely guessing. In a later paper, Premack (1988) conducted this experiment and found that the majority of chimpanzees will, in fact, choose the trainer with knowledge over the guesser.

In sum, Premack and Woodruff (1978) interpreted their findings in the following sense: Sarah not only understood the specific problem represented in each video, she also understood the *goal* or *intention* of the human actors in relation to the problems they were struggling with. As a result of these experiments (as well as others included in the paper but not covered in this entry), Premack and Woodruff concluded that because Sarah had no prior experience with any of these tests, and since she passed the vast majority of the tasks on her first try, hypotheses indicative of behavior-reading or associative learning – while *possible* – are unlikely, and as such the most parsimonious explanation for Sarah's behavior was mindreading.

Critical Commentary: Past and Present

In three independent reviews of this paper at the time of publication, Gil Harman (1978), Daniel Dennett (1978), and Jonathan Bennett (1978) all highlighted what has become arguably the most tenacious and well-known philosophical problem in mindreading debates, commonly referred to today as the “logical problem.” The logical problem boils down to the following: since all we

observe is an animal's behavior, and mental state attribution is an unobservable process, coming up with experiments that can truly distinguish between cases wherein an animal is employing a theory of mind or a behavioral rule when interacting with others is exceedingly difficult – if not impossible.

The most influential proposal to “solve” the logical problem came from Harman's (1978) review, which suggested that if chimpanzees could pass a false-belief test we could be almost certain that they possess a theory of mind. The idea was that if a chimpanzee could correctly predict another's behavior on the basis of that individual's *false* beliefs about the world, rather than what the chimpanzee actually knows to be the case, behavior-reading hypotheses would be ruled out as the chimpanzee would clearly be demonstrating the ability to attribute mental states of belief and knowledge. It took many years for the false-belief test to be tried on chimpanzees. In recent decades, chimpanzees have been evaluated on, and have consistently failed, nonlinguistic variations on the standard false-belief test (see Krachun et al. (2010) for a review).

A critical sea change in experimental paradigms for assessing mindreading in chimpanzees occurred around the turn of the twenty-first century. In an attempt to design experiments in such a way that more closely represented scenarios chimpanzees regularly experience in the wild, experimenters began to garner results highly suggestive of mindreading hypotheses. Arguably the most powerful evidence that chimpanzees possess a theory of mind has come from a series of experiments based on food competition paradigms (e.g., Hare et al. 2001). Rather than testing chimpanzees' abilities to cooperate for food, which is a rarity in their natural habitats, these experiments provided opportunities for chimpanzees competing for the same food to employ deceptive tactics. This was accomplished by placing various occluders between the test subjects, controlling what each chimpanzee could and could not see. Experimenters found that during competitive trials, the actions of subordinate chimpanzees are certainly

affected by what dominant chimpanzees can and cannot see, as well as whether their opponent possesses or lacks prior knowledge of the food source (e.g., Hare et al. 2001).

Conclusion

In the twenty-first century, mindreading remains central to debates over human uniqueness in social cognition. Premack (2007) has claimed that he still defends the view that chimpanzees are capable of attributing intentions to others, though he is highly skeptical of the existing evidence suggesting that chimpanzees can also attribute beliefs or knowledge. Claims of this nature have led many contemporary scholars to describe different *kinds* or *levels* of theory of mind, most commonly in the form of “minimal mindreading” (e.g., Butterfill and Apperly 2013).

On the 30th anniversary of Premack and Woodruff's original paper, Josep Call and Michael Tomasello (2008) published an oft-cited companion-piece summing up much of the relevant experimental research to that date. They note that there is still strong disagreement over whether the logical problem will ever be truly solved, “In a broad construal of the phrase ‘theory of mind’ [...] the answer to Premack and Woodruff's pregnant question of 30 years ago is a definite yes.” By this they mean that despite the fact that chimpanzees consistently fail false-belief tests, there is currently overwhelming evidence that they understand others' goals, intentions, and perceptual states.

While “Does the Chimpanzee Have a Theory of Mind?” did not introduce the question as to whether mindreading is a uniquely human capacity, the extraordinary influence of this paper lies in the ingenuity of its empirical research and the wealth of productive commentary that it engendered. It is fair to say, for instance, that the origins of the false-belief test, the knower-guesser protocol, and the logical problem in animal minds are all directly tied to Premack and Woodruff's landmark article.

Cross-References

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Dogs

- [Canines](#)

Domain Specificity

- [Carruthers on Massive Modularity](#)
- [Content Specificity](#)
- [Language Modularity](#)
- [Modularity of Mind](#)

Domain-Specific Reasoning About Dominance Hierarchies

- [Effect of Status on Social Reasoning \(Cummins 1998\)](#)

Domestic Violence

- [Contexts for Women's Aggression Against Men](#)
- [Cost Inflicting](#)
- [Defense Against Attack](#)
- [Evolutionary Psychology and Intimate Partner Violence](#)
- [Familial Violence](#)
- [History of Abuse](#)
- [Men's Violence Against Female Partners: The Role of Culture](#)
- [Sex Differences in Intimate Partner Violence](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Unique Patterns in the United States](#)

Domestication

- [Silver Fox Domestication Experiment](#)

Domestication Hypothesis

- [Understanding Human Points](#)

Dominance

- [Appearance/Beauty in Girls](#)
- [Baringa's \(1996\) Crayfish](#)
- [Culture of Honor](#)
- [Female Choice for Men High in SDO](#)
- [Higher Status in Group](#)

- [Indicators and Correlates of Status and Dominance](#)
- [Individuals that Impose Costs](#)
- [Men in Positions of Power](#)
- [Play Fighting in Boys](#)
- [Primate Dominance Hierarchies](#)
- [Procedures for Dealing with Bullies](#)
- [Reputation as a Context for Men's Aggression Against Men](#)
- [Social Authority](#)
- [Social Dominance Orientation \(SDO\)](#)
- [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)
- [Social Status and Economic Resources](#)
- [Status Competition and Peer Relationships in Childhood](#)
- [Status Hierarchies](#)

Dominance and Health

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Synonyms

[Prestige](#); [Social status](#); [Status](#)

Definition

Dominance is the rank of an individual relative to conspecifics, which predicts the outcomes of social interactions and has consequences for access to resources and influence. Perhaps unsurprisingly, dominance rank has consequences for health.

Introduction

Dominance rank has consequences for health, not only due to the access to valuable resources

afforded to high-ranking individuals but also to the stress experienced as a consequence of rank. Depending upon the social system, stress could be highest in the most or least dominant individual, or those in the middle of the hierarchy, and can depend upon the stability of the hierarchy. This may explain the health differentials seen in human populations across socioeconomic status strata.

Dominance and Health

If dominance confers access to resources such as preferential nest sites and nutritious food resources, it makes sense that high-ranking individuals should experience better health than their lower-ranking conspecifics. While this is often the case, there is an additional link between rank and health in the form of the experience of stress. Sapolsky (2005) reviews evidence that high-, low-, and mid-ranks can all be associated with stress and that this is dependent upon the social structure. While some of the highest levels of stress are seen in subordinate members of despotic hierarchies, there are cases (e.g., ring-tailed lemurs and African wild dogs) where the top-ranking individual must aggressively defend their position. Here, physiological measures of stress are very high. Where social ranks are relatively stable, subordinates tend to have physiological indicators of higher stress. When the hierarchy becomes unstable, this pattern may be reversed. He argues that strong and enduring relationships between socioeconomic status and health in humans, such that individuals experiencing socioeconomic deprivation have a greater likelihood of suffering from multiple conditions, including cardiovascular disease, may stem from similar processes.

There may, however, also be health costs to at least some aspects of dominance. In humans, traditional masculinity encompasses traits that likely lead to dominance and is linked to a variety of psychological problems. Positive correlations have been found between masculinity and, for example, stress and suicide attempts (reviewed in Coleman 2015).

Conclusion

Dominance rank predicts health, both as a consequence of differential access to resources but also due to the experience of stress as a result of achieving and maintaining a rank. This may translate into health differences in socioeconomic strata in humans.

Cross-References

- ▶ Abusers: Husbands, Boyfriends, and Former Sexual Partners
- ▶ Access to Resources
- ▶ Adaptations for Navigating Social Hierarchies
- ▶ Aggression
- ▶ Aggression for Sexual Access
- ▶ Alpha, Beta, and Gamma Males
- ▶ Anatomical Adaptations for Fighting
- ▶ Assessment of Fighting Ability
- ▶ Biology of Human Gender, The
- ▶ Biosociology
- ▶ Biosociology of Dominance and Deference
- ▶ Boys Bully More than Girls
- ▶ Boys Physical Bullying
- ▶ Boys' Rough-and-Tumble Play
- ▶ Bullying
- ▶ Categorization by Sex
- ▶ Competition for Resources Desired by Females
- ▶ Conflict Between the Sexes
- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Men
- ▶ Contexts for Women's Aggression Against Women
- ▶ Costs of Aggression
- ▶ Cross-Cultural Variation
- ▶ Defense Against Attack
- ▶ Development of Aggression
- ▶ Development of Sex Differences
- ▶ Differential Parental Investment
- ▶ Differential Reproductive Success
- ▶ Division of Labor
- ▶ Dominance and Territory
- ▶ Dominance and Threat or Use of Force
- ▶ Dominance Hierarchies
- ▶ Dominance Hierarchy
- ▶ Dominance Theory (Cummins)
- ▶ Evolutionary Social Psychology
- ▶ Facial Width to Height Ratio and Dominance
- ▶ Factors that Influence Bullying
- ▶ Female Choice and Sexual Conflict Theory
- ▶ Female-Female Alliances
- ▶ Female-Female Competition
- ▶ Financial and Hierarchy Maintenance
- ▶ Forced Copulation
- ▶ Function of Dominance
- ▶ Girls Psychological Bullying
- ▶ Group Living
- ▶ Group Size Optimality and Stability
- ▶ Height and Dominance
- ▶ Higher Status in Group
- ▶ Hostile Masculinity
- ▶ Humans as Social Primates
- ▶ Indicators and Correlates of Status and Dominance
- ▶ Indirect Aggression
- ▶ Intersexual Competition
- ▶ Intrasexual Competition Between Females
- ▶ Intra-Sexual Competition
- ▶ Intrasexual Male Competition
- ▶ Intrasexual Rivalry
- ▶ Intrasexual Rivalry Among Women
- ▶ Male Adaptations that Facilitate Success in War
- ▶ Male Adaptations to Assess Fighting Ability
- ▶ Male Coalitions for Hunting
- ▶ Male Dominance Hierarchies
- ▶ Male-Male Competition
- ▶ Male-Male Competition or Male Provisioning?
- ▶ Male-Male Strategies
- ▶ Mating Rivalry
- ▶ Men but Not Women Will Have Adaptations for War
- ▶ Men in Positions of Power
- ▶ Men Riskier, More Aggressive
- ▶ Murder
- ▶ Nonhuman Primates
- ▶ Partner Abuse
- ▶ Physical Aggression
- ▶ Polygyny and Male Risk-Taking for Status
- ▶ Primate Dominance Hierarchies
- ▶ Primates
- ▶ Reputation as a Context for Men's Aggression Against Men

- ▶ Resource Competition
- ▶ Resource Defense
- ▶ Secondary Sexual Characteristics
- ▶ Sex Differences
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Sexual Contact and Sexual Disgust
- ▶ Social Dominance and Sexual Access
- ▶ Social Dominance Orientation (SDO)
- ▶ Social Dominance Reduces Fighting
- ▶ Social Hierarchies
- ▶ Social Status and Economic Resources
- ▶ Status and Dominance Hierarchies
- ▶ Status and Redistribution of Resources
- ▶ Status and Reproductive Success
- ▶ Status Competition
- ▶ Status Competition and Peer Relationships in Childhood
- ▶ Tactics to Solve Adaptive Problems of Sperm Competition
- ▶ Testosterone
- ▶ Stress
- ▶ Vocal Indicators of Dominance
- ▶ Women's Prosocial Dominant Acts

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Dominance and Territory

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Synonyms

Control; Influence; Power

Definition

Dominance can be described as a pattern of behavior that results in a consistent outcome with one individual gaining priority to access resources.

Territory can be described as a fixed space or location from which an individual may actively exclude competitors from a specific resource.

Introduction

Territory has long been considered to be a spatial area or location that provides access to resources. These resources can include shelters, access to nutrient-rich food patches, or potential mates. Dominance can be described as the relationship established following inherent displays of aggression between individuals, resulting in the retreat of one. Social dominance is found to be closely related to the acquisition of resources, and territoriality can be described as a form of social dominance (Kaufmann 1983). Assertion of dominance, particularly in acquisition of territory, can translate into control of resources within that territory. This assertion of dominance commonly manifests in dyadic or multiparty contests. The escalation of any given contest is dependent on several intrinsic and extrinsic factors. Intrinsic factors that affect aggression and consequent contest escalation are the size, sex, reproductive status, as well as previous social experience of the individual. Extrinsic factors are the status of the individual within a social hierarchy, the value and availability of a given resource, as well as prior residence. While aggression in an individual has been closely tied to establishing territories, the interaction of both the intrinsic and extrinsic factors will dictate the outcome of the contest to determine which individual would be able to acquire a particular territory and thus the resources associated with the territory.

Examples of Territorial Dominance

Competition for access to resources can result in agonistic interactions between individuals,

whether between conspecifics or between individuals of other species. By asserting social dominance, individuals are able to gain or retain access to resources which can have both direct and indirect fitness consequences. Aggression in crayfish has been extensively studied due to the highly ritualized fighting behavior that exists as well as the development of social dominance hierarchies. Shelters within a particular territory prove to be vital for the survival of individuals by directly reducing the risks associated with predation (Figler et al. 1999). Additionally, the acquisition and retention of shelters housed within a particular territory are often a result of aggressive interactions between crayfish. In many species, males tend to be more aggressive than females; however, in females of *Procambarus clarkii* reproductive status appears to play a role, with “maternal” females having an advantage over others (Figler et al. 1999). Thus, the intrinsic factors can play a role in determining the status of dominance.

There are several factors that play a role in determining the outcome of any given agonistic interaction, with the dominant individual or “winner” gaining access to critical resources such as territory (Moore 2007). The size of the individuals interacting often determines who the “dominant” individual will be, with larger individuals establishing and maintaining dominance. However, another essential determinant is which individual can claim prior residence to a given area. There is evidence of a prior residence effect in which contestants that are residents seem to have an advantage over other individuals. Therefore, the value of a resource as well as prior social experience also influences the outcome of any given agonistic interaction. In studies where food and shelter is present, increased levels of aggression are exhibited by crayfish (Moore 2007). This has been extensively studied in adults but also in juveniles. In contests of male and female juveniles of *P. clarkii*, larger individuals were at an advantage similar to contests between adult crayfish. However, residents in size-matched contests appeared to not only initiate aggressive encounters but also won a greater proportion of the bouts. The prior residence effect in

crayfish combined with the initiation aggression can be attributed to territoriality.

In addition to intraspecies competition for resources such as territory, there are often different species of crayfish competing for the same resources. Several reasons for this interspecies competition can be attributed to the success of one species in displacing another. Primarily, species of crayfish with larger chelae or greater body size tend to win more aggressive interactions and thus are able to acquire access to a particular territory more readily. Another species-specific attribute that lends to resource acquisition through dominance is “intrinsic aggression” (Usio et al. 2001). Interspecies aggression and dominance has been examined particularly in the context of invasive and native species. Research on the invasive North American crayfish *Pacifastacus leniusculus* a larger, fast-growing species when compared to the European native *Austropotamobius torrentium* found that access to the shelter was determined by aggressive encounters, and this dominance was found to be size dependent (Vorburger and Ribi 1999). Additionally, when the use of shelters was examined in each of these species, shelter usage was higher in *A. torrentium* when compared to *P. leniusculus*. This maybe a result of *P. leniusculus* excavating burrows that serve as shelters and thus demonstrating a reduced preference for artificial shelters in a lab setting. In mixed competitions, *P. leniusculus* occupied shelters more frequently. Similarly, comparison of yet another native species (*Procambarus acutus acutus*) to an invasive (*P. clarkii*) demonstrated increased aggressiveness and established dominance. *P. clarkii* demonstrated lower preference for shelters but continued to evict *P. acutus* from shelters. These findings are consistent with the hypotheses that when there is competition for shelter, aggression and social dominance (often dictated by size of the individuals) in invasive species would potentially outcompete the native species. Additionally, the value of a resource such as a shelter is considerably enhanced in an environment where there is a greater threat of predation.

Common crayfish shelters are usually larger rocks or submerged logs; however, some crayfish

species construct their own shelters by burrowing. Studies using the secondary burrowing species, *P.clarkii*, which constructs simple burrows to be used as shelters have found that burrowing behavior is inhibited following aggressive encounters. Construction of burrows is an energetically costly process. Inhibition of this process in the presence of a dominant individual is advantageous when the resident has “lost” recently. Additionally, the inhibition of burrowing behavior can be reversed when the subordinate crayfish is no longer in the presence of the dominant individual. Thus, the formation of a social hierarchy in crayfish tended to affect nonagonistic behaviors as well (Herberholz et al. 2003). As mentioned previously, establishment of dominance by an individual can lead to acquiring greater territory and possibly more resources associated with the territory (Fero and Moore 2008). In crayfish, the establishment of a social dominance hierarchy has a more profound impact than just the acquisition of the immediate resource in question (Martin and Moore 2008). Firstly, as individuals continue to win encounters they are more willing to initiate contests rather than retreat from a contest (Goessmann et al. 2000). Secondly, individuals that are established as dominant appear to initiate and engage in more escalated bouts. Lastly, the “loser” effect appears to persist, with these individuals being more likely to retreat. While crayfish dominance hierarchies maybe shifting, if an individual is established as dominant the “loser” is more likely to lose access to its territory and consequently any resources associated with the territory.

As extensively as crayfish aggression has been examined, the majority of the work has been conducted in artificial laboratory settings. In comparison to fighting within a lab setting, contests in a naturalistic environment tend to be shorter and less intense. Examination of intra-specific aggression in three different habitats, two with varying food resources and one with the presence of shelters, were examined in two species of crayfish (Bergman and Moore 2003). The results were consistent with the hypothesis that in the presence of resources, more inherent displays of aggression would be observed.

Consistent with laboratory studies, fights that occurred in the presence of a shelter were found to be more intense and of a longer duration, signifying the value of the resource. Similarly, of the two different food resources the overall intensities of fights were greater in the areas of the preferred nutrient. However, in comparing the fight intensities within these three habitats, those in the presence of the shelter were most intense. Additionally, when the abundance of a resource decreases in a given area the perceived value associated with that resource increases. Consequently, the competition for the resource increases as do the intensity of aggressive interactions.

Conclusion

Competition for resources often results in agonistic interactions with displays of social dominance resulting in acquisition of a resource. Crayfish tend to exhibit and maintain social dominance hierarchies which in turn translate into control of resources such as a territory with shelter and/or nutrient-rich food patches. Dominant individuals will reinforce their status and thus maintenance of these hierarchies is critical in determining which individual will retain the resources. These hierarchies are dictated by both intrinsic and extrinsic factors with the interactions between these factors playing a significant role in determining which individual can establish dominance and subsequently retain a territory.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Baringa's \(1996\) Crayfish](#)
- ▶ [Dominance Hierarchies](#)
- ▶ [Function of Dominance](#)
- ▶ [Resource Defense](#)
- ▶ [Resource Limitation](#)
- ▶ [Shifting Dominance](#)
- ▶ [Social Dominance Reduces Fighting](#)
- ▶ [Status and Dominance Hierarchies](#)
- ▶ [Status and Redistribution of Resources](#)

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Dominance and Testosterone

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Synonyms

Social status; Status; Prestige

Definition

Dominance is the rank of an individual relative to conspecifics, which predicts the outcomes of social interactions and has consequences for access to resources and influence. The sex steroid testosterone is linked to aggression and dominance rank and may play a proximate role in dominance behaviors.

Introduction

Testosterone is a steroid hormone secreted primarily from the testes and in smaller amounts from the ovaries. It is responsible for the development of primary and secondary sexual traits in males, and levels surge during male puberty when these traits undergo rapid development. The classic model of testosterone’s relation to dominance was based on early animal experiments showing that administration of exogenous testosterone resulted in increased aggression. While, as discussed in the section *Dominance in Humans*, there are cases in which dominance rank is decided via overt aggression, there are also many instances where this is not the case. It is clear, then, that testosterone alone cannot predict dominance rank in all systems, but there is certainly evidence that it plays a role – albeit a complex one.

Dominance and Testosterone

Under the challenge hypothesis, testosterone levels rise in response to competition for status (Wingfield et al. 1990). Here, the function of elevated testosterone is to promote the aggressive behavior required to win a dominance contest. During a period of instability in the hierarchy, for example, high-ranking rhesus macaques under attack from lower-ranking males had the highest and most variable testosterone levels (Higham et al. 2013). There are also relationships between testosterone and rank in females. In hybrid baboons, for example, females with the highest ranks were also those with the highest testosterone (Beehner et al. 2005). Archer (2006)

concludes that results of human studies are fairly consistent with the challenge hypothesis. There were weak, but significant, positive relationships between testosterone and leadership, toughness, personal power, and aggressive dominance across studies. Both women and men responded to competition with elevated testosterone. Contests, however, as we have seen, do not take a single form, do not occur in isolation, occur in males and females, within and between sexes, and during different seasons, and therefore testosterone is likely to be an imperfect predictor of rank.

There is evidence that relationships between testosterone and dominance are reciprocal, with dominance rank influencing testosterone and testosterone influencing dominance rank. Mazur (2005), for example, reviews evidence from humans that testosterone rises in expectation of a face-to-face dominance challenge such as athletic competition, and post-competition, the testosterone of the winner stays elevated for significantly longer than for the loser. Interestingly, the same patterns are shown in nonphysical contests (e.g., chess matches).

That a number of physical traits correlate both with testosterone and dominance further implicates the hormones' role in predicting dominance rank. Recent work has revealed potential physical cues to dominance in humans, many of which are proposed to develop under the action of testosterone such as facial and vocal masculinity, facial hair, height, and muscularity (see Hill et al. 2013 for a review). Among the most heavily researched of these modalities is facial structure. The degree of masculinity in male faces is positively related both to circulating testosterone and to perceived dominance and actual dominance (reviewed in Valentine et al. 2014). Specific facial dimensions have been proposed to mediate the link between testosterone and perceptions of dominance. Facial width-to-height, for example, has recently received attention due to its relationship with testosterone reactivity to a threat. Results demonstrate that men with greater width-to-height ratios have better financial performance (among chief executives; Wong et al. 2011), are less

likely to die from contact violence (Stirrat et al. 2012), and have higher lifetime reproductive success (Loehr and O'Hara 2013).

Testosterone, however, may also come at a cost, since its effects on behaviors associated with dominance also put the individual at risk of reduced longevity. Global figures demonstrate that men comprise the majority of early and accidental deaths, dangerous and violent crimes, substance abuse, and completed suicides. As Cross et al. (2011) review in their meta-analysis of sex differences in impulsivity, men were significantly more impulsive than women (i.e., less punishment sensitive and more sensation seeking). Since there is some evidence that impulsiveness is linked to testosterone, it is possible that sex differences in testosterone contribute to sex differences in impulsivity and its consequences for longevity. It is important, again, to consider the roles to which men and women are allocated and the expectations and behaviors that come with these. Women, for example, as well as having lower levels of testosterone, are taught to exercise greater self-control in line with a traditional female gender role and men to be more adventurous.

Conclusion

There is evidence to support the challenge hypothesis in humans, with weak relationships between testosterone and measures of dominance such as leadership. The relationship, however, is reciprocal, with testosterone rising in response to a challenge. Testosterone underpins the development of traits which may signal dominance and aggression, such as facial dimensions and vocal masculinity. Finally, testosterone comes with a cost, with links to reduced longevity.

Cross-References

- ▶ [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- ▶ [Access to Resources](#)
- ▶ [Adaptations for Navigating Social Hierarchies](#)

- ▶ Aggression
- ▶ Aggression for Sexual Access
- ▶ Alpha, Beta, and Gamma Males
- ▶ Anatomical Adaptations for Fighting
- ▶ Assessment of Fighting Ability
- ▶ Biology of Human Gender, The
- ▶ Biosociology
- ▶ Biosociology of Dominance and Deference
- ▶ Boys Bully More Than Girls
- ▶ Boys Physical Bullying
- ▶ Boys' Rough-and-Tumble Play
- ▶ Bullying
- ▶ Categorization by Sex
- ▶ Competition for Resources Desired by Females
- ▶ Conflict Between the Sexes
- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Men
- ▶ Contexts for Women's Aggression Against Women
- ▶ Costs of Aggression
- ▶ Cross-Cultural Variation
- ▶ Defense Against Attack
- ▶ Development of Aggression
- ▶ Development of Sex Differences
- ▶ Differential Parental Investment
- ▶ Differential Reproductive Success
- ▶ Division of Labor
- ▶ Dominance and Territory
- ▶ Dominance and Threat or Use of Force
- ▶ Dominance Hierarchies
- ▶ Dominance Hierarchy
- ▶ Dominance Theory (Cummins)
- ▶ Evolutionary Social Psychology
- ▶ Facial Width to Height Ratio and Dominance
- ▶ Factors That Influence Bullying
- ▶ Female Choice and Sexual Conflict Theory
- ▶ Female-Female Alliances
- ▶ Female-Female Competition
- ▶ Financial and Hierarchy Maintenance
- ▶ Forced Copulation
- ▶ Function of Dominance
- ▶ Girls Psychological Bullying
- ▶ Group Living
- ▶ Group Size Optimality and Stability
- ▶ Height and Dominance
- ▶ Higher Status in Group
- ▶ Hostile Masculinity
- ▶ Humans as Social Primates
- ▶ Indicators and Correlates of Status and Dominance
- ▶ Indirect Aggression
- ▶ Intersexual Competition
- ▶ Intrasexual Competition Between Females
- ▶ Intra-sexual Competition
- ▶ Intrasexual Male Competition
- ▶ Intrasexual Rivalry
- ▶ Intrasexual Rivalry Among Women
- ▶ Male Adaptations That Facilitate Success in War
- ▶ Male Adaptations to Assess Fighting Ability
- ▶ Male Coalitions for Hunting
- ▶ Male Dominance Hierarchies
- ▶ Male-Male Competition
- ▶ Male-Male Competition or Male Provisioning?
- ▶ Male-Male Strategies
- ▶ Mating Rivalry
- ▶ Men But Not Women Will Have Adaptations for War
- ▶ Men in Positions of Power
- ▶ Men Riskier, More Aggressive
- ▶ Murder
- ▶ Nonhuman Primates
- ▶ Partner Abuse
- ▶ Physical Aggression
- ▶ Polygyny and Male Risk-Taking for Status
- ▶ Primate Dominance Hierarchies
- ▶ Primates
- ▶ Reputation as a Context for Men's Aggression Against Men
- ▶ Resource Competition
- ▶ Resource Defense
- ▶ Secondary Sexual Characteristics
- ▶ Sex Differences
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Sexual Contact and Sexual Disgust
- ▶ Social Dominance and Sexual Access
- ▶ Social Dominance Orientation (SDO)
- ▶ Social Dominance Reduces Fighting
- ▶ Social Hierarchies

- ▶ [Social Status and Economic Resources](#)
- ▶ [Status and Dominance Hierarchies](#)
- ▶ [Status and Redistribution of Resources](#)
- ▶ [Status and Reproductive Success](#)
- ▶ [Status Competition](#)
- ▶ [Status Competition and Peer Relationships in Childhood](#)
- ▶ [Stress](#)
- ▶ [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- ▶ [Testosterone](#)
- ▶ [Vocal Indicators of Dominance](#)
- ▶ [Women's Prosocial Dominant Acts](#)

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Dominance and Threat or Use of Force

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Synonyms

[Coercion](#); [Compulsion](#); [Power](#); [Superiority](#); [Supremacy](#); [Ultimatum](#); [Violence](#); [Warning](#)

Definition

The acquisition and use of authoritative power over another individual or group reinforced through the signaling or implementation of emotional, physical, or other forms of coercion or compulsion.

Introduction

Humans, like many social species, have a tendency to sort themselves into dominance hierarchies within groups. Functions of these hierarchies include the distribution of authoritative power and determining which individuals are allowed access to resources, alliances, and mates. Dominance hierarchies can include millions of individuals, such as in nation-states and cities, but only two individuals are necessary to create a power differential. For humans, dominance hierarchies can exist in groups such as friend circles or business management and in situations such as interactions with authority figures. There are many behaviors and tactics that humans use to increase their status in these hierarchies, from successfully navigating social situations, to buying their way up with money, to using physical dominance.

Dominance and Force

Physical dominance can be described as a measure of physical behaviors or traits that are used to increase an individual's status within a hierarchy, usually by influencing the behavior of others. A simple example of this is that the trait of being a taller person affords the "right of way" in brief dyadic interactions. When two people approach each other while walking in opposite directions, more often than not, the shorter person will move out of the way to let the taller person pass by (Stulp et al. 2015). Although the physical size of an individual is a salient indicator of their ability to inflict harm on others, it is not necessarily an indicator of the likelihood that they will behave in a dominant way. However, when judging an individual's level of physical strength and level of dominance based on their facial appearance, both judgments correlate highly and may be considered as functionally the same (Toscano et al. 2016). Humans use cues like these as a means of determining the likelihood of the use of force when navigating hierarchies.

Humans use more explicit signals as well. Gestures like facial expressions, vocal cues, and eye gaze are sufficient behaviors to affect changes in power structures. For example, behaviors such as tilting the head down in pitch while maintaining eye contact are seen as an indication of anger (Toscano et al. 2018) and thus can imply the increased probability of an impending dominance challenge by physical force. These signals, and the benefit that the ability to interpret them provides, are likely evolutionary adaptations. This is due to the risks involved when using physical force. Dominance signals allow for the mutual avoidance of engaging in actual physical violence while maintaining status quo. Although these signals likely developed in the more combative ancestral past of humans (Sell et al. 2009), the threat or use of force still has utility in modern times.

As mentioned above, nonverbal cues can be used to signal the threat of the imminent use of force in an attempt to dominate others. However, nonverbal behaviors can also be used as behavioral indicators for targeting potentially

submissive individuals to dominate. In film-based stimuli, those who were rated as being vulnerable to victimization moved in ways that were systematically different from those who were not rated as vulnerable. This finding has been supported in a variety of ways including the use of point-light kinematics and videotaped walking styles/gait (Book et al. 2013). For the most part, the sending and receiving of these social signals serve to establish and maintain social dominance hierarchies. However, sometimes social interactions result in the threat or use of force.

Force is a broad concept, and the variation in types of threat or force used in obtaining or reinforcing dominance reflects this. The armed services and police forces of nation-states use an escalation of force model and train their members vigorously in its use. This model is used to assess threat and assert dominance in order to control social situations, often involving large groups. In the case of state versus state interactions, force can range from direct or indirect communication between leaders to full military engagement. In the case of policing the general public, officers' use of force can range from the mere presence of a soldier or police officer to the use of deadly force (Bagwell 2008). A similarly broad range of behaviors can be used to threaten or instigate physical force in individual interactions. These include verbal and nonverbal cues, coercion/manipulation, threats of violence, reputational coercion through violence to others, and the direct use of violence.

Verbal threats can be used to ward off rivals and establish dominance in order to cope with the threat of others. Verbal behaviors can also be used to manipulate and coerce and may include verbal pressure, emotional and physical threats, and deception (Finkelstein 2014). Manipulation and coercion use nonverbal, verbal, and physical cues to instigate the giving of some benefit to a conspecific without the intention or expectation of reciprocation (Clutton-Brock 2009). Manipulation and coercion are often used in close interpersonal relationships as a method of establishing and maintaining dominance. Buss (1992) found that the use of manipulative and coercive tactics

is more common in closer interpersonal relationships (i.e., romantic partners are manipulated/coerced more than friends). Further, the use of manipulative/coercive behaviors is related to high levels of the personality traits boldness and disagreeableness. These personality traits and the use of manipulation/coercion are also related to psychopathic behaviors, a socially exploitative phenotype that utilizes a mixed strategy involving both cheating, intimidation, and violence to increase access mating and resources (Book and Quinsey 2004). A key sex difference in psychopathic behaviors and the use of threat or force in order to establish dominance is that females tend to rely more on verbal aggression, manipulation, and coercion, whereas males more regularly threaten and/or instigate violence (Carabellese et al. 2019).

Interpersonal and intergroup physical violence can be used to establish dominance and facilitate social exploitation, this occurs because to the receiver(s) of violence the loss of reputation or resource is less detrimental to their fitness than the cost of incurred violence (Buss and Duntley 2008). For the perpetrator(s) of violence, it serves to not only increase their access to resources and mating opportunities but confer long-lasting benefits through reputation by increasing social dominance and in turn social capital. Dominance through the use or threat of violence begins during childhood and adolescence, with schoolyard bullying commonly occurring. Mynard and Joseph (1997) found that in 8- to 13-year-old schoolchildren, bullies had lower levels of self-esteem and higher levels of neuroticism than controls but targeted victims who had high levels of introversion and lower levels of self-esteem than themselves. In this way bullies could use violence to increase their reputations by establishing dominance over others.

Secondary victimization occurs as the result of damage to an individual or group's reputation following interpersonal violence. The physical dominance of the victor(s) is established and serves as a signal to others. As a result the reputation of physical dominance of the perpetrator of

violence increases, while the reputation of the victim is harmed (Duntley and Shackelford 2012). One reason that reputational coercion is so effective at establishing and maintaining dominance in a group is that human memory is biased toward the recall of distressing events. Lalande and Bonanno (2011) had participants' self-report events over a period of 4 years by responding weekly to a survey assessing whether events from a list of 50 options had occurred. Events fit four categories; potentially distressing events, academic or financial stressors, interpersonal stressors, and lifestyle changes. At the end of the 4-year period, participants estimated how many times each of the 50 events had occurred. Participants generally underestimated the frequency of each event but gave more accurate responses for potentially traumatic events. Further, distress at time of recall was related to the number of events recalled only for potentially distressing events. One of the most accurately remembered events was the experience of robbery or mugging.

Conclusion

Dominance plays an important role in human social hierarchies and social interactions at both a group and an individual level. Dominance can be established in multiple ways including social manipulations, control, and distribution of resources and physical superiority. The possible use of force as a way of establishing or reinforcing of dominance is signaled between individuals and groups using methods that range from subtle signals (facial expressions, vocal tones, etc.) to overt signals (direct or indirect violence). Force can also be used in forms ranging from manipulation and coercion to primary and secondary physical violence.

Cross-References

- [Communication and Social Cognition](#)
- [Dominance in Humans](#)

- [Primate Dominance Hierarchies](#)
- [Problem of Cheating](#)
- [Social Aggression](#)
- [Social Authority](#)
- [Social Hierarchies](#)
- [Social Reputation](#)
- [Status and Dominance Hierarchies](#)
- [Victims of Violence](#)

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Dominance Hierarchies

- [Emergence of Social Reasoning About Hierarchies](#)

Dominance Hierarchy

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Synonyms

[Peck order](#); [Social dominance hierarchy](#); [Social hierarchy](#)

Definition

Dominance hierarchy is a social structure of a society or a family. Within this structure some individuals are more dominant than others and as such have access to greater (or better) resources (i.e., food, mates, etc.). Dominance hierarchy enables to decrease number of conflicts between individuals because some give way to the others and let them have resources without fighting. This behavior is mostly based on their experience from previous interactions. Moreover, the higher ranking ones restrict the lower ranking individuals.

Introduction

The term *dominance hierarchy* (McFarland 1981) refers to hierarchical ranking of individuals in a society (in a group, a family, a clan, or a pack). Terms such as *social hierarchy*, *social dominance hierarchy*, and *peck order* (McFarland 1981; Manning and Dawkins 2009; Veselovsky 2005) have similar meaning. The concept of dominance hierarchy is widely used and has been explored in depth in animals, including primates. In humans, the same feature is expressed by socioeconomic status, social status, or power.

The dominance hierarchical rank influences the probability of an individual's survival. The likelihood of getting food, space to rest or hide from predators, the chance to mate, or the quality of a sexual partner – all these facts depend on the hierarchical rank. An individual's rank within the dominance hierarchy strongly influences the life of both humans and animals.

How it Works

Dominance hierarchy refers to the way the society or the family is organized (Veselovsky 2005). The relationships in a dominance hierarchy are called *dominance-subordination relationships*, or *dominance-submission relationships*. The higher ranking individual is considered a *dominant* individual, while the lower ranking individual is called *submissive* or *subordinate* (Jozifkova

2014). Individuals are frequently ranked and named according to the Greek alphabet. The most dominant individual is titled the alpha (α); the second highest ranking individual is the beta (β), followed by the gamma (γ); and the most submissive one, subordinate to them all, is the omega (ω) (Veselovsky 2005).

The rank ordering decreases the number of conflicts between individuals (Manning and Dawkins 2009) and increases the cohesion between members of a group (Veselovsky 2005). When individuals compete for the same resources, conflicts arise. Even genetically related individuals are not spared from mutual conflicts in the competition for the resources. However, the conflicts are costly (the individual may lose energy that otherwise could be used for survival and/or reproduction) and may result in injuries or deaths. Based on their previous experience, the individuals living together in the group remember those who beat them in the conflict or recognize features of those who are likely to defeat them. The individual may identify such rivals by cues (e.g., body size) and/or badges of status (e.g., the black bibs of male house sparrows). Thus, the individuals are able to predict the outcome of the conflict. So the lower ranking individuals retreat to the stronger members (Manning and Dawkins 2009). Dominance hierarchy means that social *ranks* are established in the group, so that some individuals yield to others and allow them to have scarce resources without fighting (Alcock 2013). Mostly, lower ranking individuals let the higher ranking individuals feed first and leave them safe places for rest and sexual partners (Manning and Dawkins 2009). Lower ranking individuals are restricted by higher ranking individuals. The dominance rank is maintained by higher ranking individuals, who threaten the lower ranking individuals in a specific way, i.e., direct gaze, upright posture, showing teeth or “weapons,” etc. (Manning and Dawkins 2009; Veselovsky 2005).

The lower ranking individuals try to avoid the conflict with the higher ranking ones (McFarland 1981). They display submissive behavior to signalize their lower rank (McFarland 1981). A *submissive posture* (McFarland 1981) stops or

slows down aggression between the same species of individuals (Veselovsky 2005). *Appeasement behavior* (McFarland 1981) helps to manage the situation in a way it unblocks another kind of behavior (e.g., a shift to parental or sexual behavior).

The dominance hierarchical rank of the individual in a society depends primarily on his ability to fight (and/or to be supported by those who are able to fight). Dominance hierarchy is a strategy how to survive in a given environment. The form of social hierarchies differs depending on the natural conditions (Manning and Dawkins 2009). The dominance hierarchy is defined by both the mating systems (polygyny versus polyandry versus monogamy) and social organization.

In detail, the environment (namely, the distribution of the resources) impacts the size of a group and thus influences both the social organization and the mating system which can be considered behavioral adaptations. A species survives under given environmental conditions because of behavioral adaptations. Species of weaver birds which live either in forests or savannahs are the example of such an adaptation. The forest species live solitarily because the resources of food are dispersed. The savannah species live in bigger groups because the resources of food are clumped together. While the forest species are monogamous, the majority of the savannah weaver birds is polygynous (Davies et al. 2012).

The males tend to have bigger body size than females and ranked higher than females in species with polygyny mating system, while the females may be bigger and may rank higher than males in polyandry mating systems. But there are some exceptions: in ring-tailed lemur, all adult females rank higher than males despite that the ring-tailed lemurs have polygynous mating system.

The higher ranking animals guarantee the stability within a group; they protect the group (the group primarily includes their sexual partners and offspring, and by their protection the higher ranking individual increases its fitness) and secure resources which are important for the group. Frequently they make decisions. Their experience often brings benefits to the group (Veselovsky 2005).

Living in the group allows the lower ranking ones to survive, participate in reproduction, or increase their fitness indirectly by supporting their relatives (Jozifkova 2014).

Different Dominance Hierarchy Structures

Peck order in poultry is an example of *linear hierarchy*. The higher ranking hen pecks the lower ranking individuals (McFarland 1981). The most dominant animal (alpha) is not pecked by any other animal. The second higher ranking (beta) is pecked only by the alpha. The third animal is pecked only by the alpha and beta, but it can peck everybody else except the alpha and beta. The lowest ranking animal is pecked by all other animals (Manning and Dawkins 2009).

Individuals of large groups may not know each other in person. In these groups, an *incomplete hierarchy* occurs frequently. The higher ranking animals are easy to spot, while the hierarchy between members of the base is unclear (Franck 1996).

The hierarchical structure is sometimes more complex. An alpha rank is higher than beta, and beta dominates the gamma, but the alpha may not dominate the gamma (Manning and Dawkins 2009). This is example of *angular* (Franck 1996) or *circular hierarchy*.

The society can be governed by more than one individual. Frequently, more experienced individuals make a coalition so that they can control the society accordingly (Veselovsky 2005; Franck 1996).

A society has either one dominance hierarchy that includes all members of the society or separate hierarchies for males and females (Veselovsky 2005). The hierarchy separates when males and females compete for different resources. In free-living rabbits, the males compete for the females, while the females compete for a place to make a burrow, and therefore there are *separate hierarchies*. However, the sibling group of a domesticated rabbit which lives in the small space under artificial conditions forms a single linear hierarchical structure, including both male and female (Vervaecke et al. 2010).

The hierarchies differ in rigidity of rules which control mutual behavior between members of a group and between groups. Animal species can be classified as tolerant (small hierarchical disparity) and despotic (big disparity). The terms *dominance gradient* (Jacobs et al. 2011) and *steepness of the hierarchy* (Vervaecke et al. 2010) describe the gap between the higher and the lower ranking individual.

The “vote” of the higher ranking animal is of higher value when the group makes a decision (Jozifkova 2014).

A leader (the individual in the head of the group on the move) or an initiator (an animal which starts with an activity first) might not be the higher ranking animal (Ihl and Bowyer 2011), i.e., it could be an elderly or middle-aged animal who knows the landscape. Lead animals may differ in different situations (Jacobs et al. 2011).

How the Dominance Hierarchical Rank Is Determined

The dominance hierarchical rank is determined by factors which help to win the interaction (usually fight or ritualized fight). The important factors, either individually or combined, involved body size, condition (health, rutting/pregnancy, age), gender, experiences, hierarchical rank of parents (some species inherit a rank from the mother), family or clan, partnership (having a partner), rank of partner, ability to change behavior of the others (manipulation and cooperation), and personality, including aggression and inherited tendency to dominate or subordinate (character dominance) (Veselovsky 2005; Jozifkova 2014).

An individual reaches the higher rank by winning either the real fight or a ritualized fight (McFarland 1981), or via positive interactions (Manning and Dawkins 2009). Grooming is an example of the positive interaction (Manning and Dawkins 2009).

Individuals clash in the ritualized fights under inborn rules which are inherited from generation to generation. These animals usually have special physical structures (such as antlers)

which decrease the probability of an injury (Veselovsky 2005).

Notably, the interactions between individuals who are closely matched in their levels of a specific trait/characteristic (e.g., battle between the same strength in deer, the conflict between women of the same attractiveness, etc.) are most severe, whereas the individuals who differ markedly in the specific characteristic give up the fight quickly.

Aggressive behavior or this tendency can help to increase the rank of an individual, especially when the hierarchy is still establishing. The aggressiveness helps one to reach a higher position if the rival is unsure and backs off.

How the Hierarchical Rank Influences the Life of an Individual

Dominance hierarchical rank directs the life of an individual. The rank predicts the probability of survival and reproduction; in terms of evolutionary biology, it impacts inclusive fitness, i.e., how an individual participates in reproduction or supports its relatives who reproduce (Jozifkova 2014).

The higher ranking individuals have higher probability of survival because dominant individuals get priority access to resources, such as fine food, safe places to rest, space distant from predators, places which are free of parasites, and other suitable environmental conditions. The higher ranking individuals have better chances to mate. Moreover, they can mate with higher Quality partners. This fact, together with better access to resources, causes the offspring of the higher ranking individuals to be stronger, more numerous, and survive better. Thus the higher ranking individuals achieve higher fitness. On the other hand, there are costs. These individuals have to invest a significant amount of energy to reach and defend their higher rank.

When unable to compete with higher ranking males, a lower ranking male can use alternative Reproductive tactics to steal the opportunity for reproduction from higher ranking ones (Alcock 2013).

The lower ranking individuals lose in the interaction with the higher ranking ones, which results in hormonal changes, such as an increase of the cortisol level. These changes have a negative impact on their health. The higher the number of high ranking individuals, the more stressed the lower ranking individuals are (Jozifkova 2014).

The ways and options how the individual can behave in a society or a family are influenced or even determined by his or her hierarchical rank. The hierarchical rank also shapes communication between individuals, such as the quantity and quality of information transferred between humans. For example, the submissive individual tends to agree and suppress his/her opinion and gives the dominant individual more information than is necessary, while the dominant individual controls the topic and the length of the communication, asks questions, and hides information. Rank plays a crucial role during courtship and partner choice. Women do prefer higher ranking men. While the higher rank increases attractiveness of men, physical attractiveness of women increases their rank. On the other hand, a portion of women is sexually aroused by lower ranking men.

Partner violence, bullying, and mobbing may be seen as an extreme manifestation of dominance hierarchy in which the perpetrator repeatedly slashes down the hierarchical rank of the victim (Jozifkova 2014).

Conclusion

A society or a family is hierarchically organized on the basis of probability of winning or losing an interaction between members of the group. It is a way how group members can avoid repeated fighting. Therefore, an individual usually behaves in agreement with his or her hierarchical rank. Higher ranking (dominant) individuals restrict the lower ranking (submissive, subordinate) ones and have priority access to resources, spaces, and sexual partners. Thus, the higher ranking individuals have increased fitness. A lower ranking individual has a chance to survive by staying in the society. They can support their relatives who

reproduce, but circumstances may even bring them opportunity to participate in mating directly. The rank of an individual changes according to his or her ability to win interactions. Dominance hierarchy is an adaptation of a society to local ecological conditions. Therefore, the structure of hierarchies differs under different conditions. Hierarchy can be linear or circular, can be markedly distinct or indistinct, may include both genders or may be gender-divided, may be led by the highest ranking individual or a dominating coalition, and may be tolerant or despotic with a severe slope. The hierarchical rank determines the behavior of an individual. These facts should be borne in our minds when observing or analyzing human behavior.

Cross-References

- [Dominance and Testosterone](#)
- [Dominance in Humans](#)
- [Dominance, Testosterone, and Cortisol](#)
- [Facial Width to Height Ratio and Dominance](#)
- [Height and Dominance](#)
- [History of Dominance Theory](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Nonverbal Indicators of Dominance](#)
- [Size and Dominance](#)
- [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)
- [Vocal Indicators of Dominance](#)

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Dominance in Humans

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Synonyms

Status; Social status; Prestige

Definition

Dominance is the rank of an individual relative to conspecifics, which predicts the outcomes of social interactions and has consequences for access to resources and influence.

Introduction

An individual's rank relative to its conspecifics is a predictor of behavior, health, and reproductive output across the animal kingdom. When talking about animal societies, this is typically described in terms of dominance rank, which is determined by the outcome of contests for access to resources such as food or mates. In humans, the picture is far more complex and dominance is the product not only of direct physical contests between individuals ("physical dominance") but of prestige,

group membership (e.g., based on gender or ethnicity), and situation within large-scale "formal hierarchies" such as socioeconomic status.

Dominance in Humans

Wherever social groups exist, a dominance hierarchy will inevitably emerge, with unequal access to resources such as food and mating opportunities. The relative rank of an individual amongst its conspecifics can depend upon, for example, its size and strength, age, experience, aggression, matriline (i.e., the status of its own mother), or the quality of its coalitionary relationships. Hierarchies differ in their fluidity and linearity, the top spot may be occupied by a single individual or shared, and the hierarchy may be established and regularly enforced in the case of permanent groups or only become relevant occasionally, such as during the breeding season.

Taking primates as a case study (while acknowledging that the patterns reported are seen in the animal kingdom more widely), there are examples of societies in which reproduction and access to prime territories and food resources is dominated by a single individual. This is the case in, for example, gorillas, ring-tailed lemurs, and blue monkeys, where there is a single top-ranking individual to whom the rest of the group defers. In these despotic hierarchies, there are usually few status differences amongst the rest of the group. In contrast, in an egalitarian hierarchy, dominance relationships are "transitive": each individual can beat all those ranked below her but none of those ranked above her (e.g., chimpanzees, lion-tailed macaques, and squirrel monkeys).

Dominance rank is usually estimated via observation of associated behaviors, such as who is approached or avoided by whom, gestures, and access to mates, food, or nest sites. Most commonly, rank is assessed by observing "contests" between all dyads in a group and recording the outcome (who is successful and who retreats). From these data, a matrix can be developed which allows the researcher to rank individuals on the basis of outcomes in contests across all

dyads. These dyadic interactions, however, do not occur in isolation and there is a growing body of work which shows that the wider social context influences behavior and outcomes in these interactions. Laporte and Zuberbühler (2010), for example, report that the “pant-grunt” signal of chimpanzees, which is used as a greeting signal to higher-ranking individuals, was expressed more often by females to males if the alpha male and/or female were absent and was further inhibited the greater the size of the audience of bystanders.

Dominance in humans is much more complex than the primate cases described above and is the product not only of direct physical contests between individuals (‘physical dominance’) but of variables such as prestige, group membership (e.g., based on gender or ethnicity), and situation within large-scale “formal hierarchies” such as socioeconomic status. Furthermore, humans do not – usually at least – exhibit such obvious dominance behaviors and displays as the other primates. There are, however, markers to status with, for example, high-status individuals dominating conversation by talking longer, louder, and interrupting more often (Dunbar and Burgoon 2005). Humans are also reasonably good at telling us who, in their group, is a leader and who is a follower, thus providing an estimate of “influence.” Furthermore, we assign status on the basis of a myriad of physical (e.g., beauty, strength, ethnicity, gender) and behavioral (e.g., humor, leadership, intelligence, personality, social class) traits, regardless of whether there is validity to the assumption that some groups deserve to be positioned in higher ranks than others.

Physical Dominance

Physical dominance can play out in the context of face-to-face interactions and can take the form of both overt physical contest (as in the case of fights) but can also take more subtle forms such as verbal and nonverbal signals (e.g., body posture and lean; Dunbar and Burgoon 2005). Furthermore, physical dominance can be expressed via large scale, formal contests such as warfare. As Mazur (2005) argues, while these play out on national- and international-scales, often with

considerable loss of life, and usually over competition for power and resources, there is often a personal motivation underlying these extravagant dominance contests.

Prestige

As is the case in the primate examples discussed above, status can be ascribed on the basis of access to resources, but in addition to this, the extent to which an individual is popular and exerts influence (or their “prestige”) is closely linked to status in humans. Prestige is earned by the expression of skill, rather than the ability to win physical contests or otherwise coerce others to one's will, and is associated with prosociality and leadership across traditional societies (see Henrich et al. 2015 for a review). Cheng et al. (2013) demonstrate that coercion and prestige are also distinct pathways to status in laboratory group tasks involving undergraduate Canadian students. Here, participants were able to attain status either via coercion via force and intimidation or via sharing of knowledge and expertise (prestige). Interestingly, popularity was not linked to status, with those following the route of “prestige” securing significantly greater popularity.

Official Hierarchies

Human dominance in face-to-face dyads and groups is situated within a structure of “official hierarchies” such as governments and socioeconomic strata (see Mazur 2005 for a review). These broad, formal, ranks organize access to resources, power, and influence, with a small number of “leaders” atop a series of levels of decreasing status and increasing numbers. Individuals may or may not know others in the levels above or below them, so here the formal status conferred by level in the official hierarchy interacts with the informal status derived from face-to-face interactions with those within one's immediate group. Occupation of positions in these official hierarchies has profound effects on our psychology. An extreme example of this comes from Zimbardo's classic “Stanford Prison Experiment,” in which groups of students were arbitrarily allocated to the role of “guard” or “prisoner” with consequent manifestations of extreme dominance behavior by

the guards and deference by the prisoners (but see Haslam and Reicher (2012) for evidence that these effects can be mediated by, for example, permeability between roles).

Sex, Gender, and Status

One way in which we organize ourselves, and which has profound effects both on attributions of status and on the ways in which status is negotiated, is by sex. Men and women look and act differently from one another in a number of ways. Men's larger size and greater upper body strength, and women's greater investment in gestation and early infant care, are argued to have evolved under conditions of mild polygyny with greater competition amongst males for mates than amongst females (Archer 2009; Puts 2010). These biological sex differences likely predisposed men and women to efficient performance of different tasks which, over time, were attributed with different "status." While men had a physical composition better suited, perhaps, to hunting, women's biology provided the conditions for heavier investment in early offspring care. This not only set the scene for different selection pressures for men and women (who, to an extent, occupied separate ecologies as a result of their biology), but may also have resulted in the adoption of tasks which not only furthered the divergence in male- and female-ecological niches, but also conferred different levels of status to the two groups. The meat won through hunting is a valuable nutritional resource which can be traded and, therefore, confer status. In their biosocial model, Wood and Eagly (2012) argue that biological differences between men and women predisposed them to different social roles within communities which, in turn, influenced many of the traits and behaviors which we consider to be "male/masculine" and "female/feminine" today. For example, the greater assertiveness, aggression, and agency of the male gender role is certainly consistent with the requirements of competing for valuable physical resources. The nurturing and social traits of the female gender role are, in contrast, perhaps the result of a history in investment in caregiving. These pathways that flow from biological sex differences to the allocation of distinct tasks and

responsibilities to men and women, to the behavioral and psychological traits required to fulfill these gendered social roles, likely had multiple consequences for the ways in which men and women establish dominance amongst same-sex conspecifics and also for the dynamics of between-sex interactions.

Male dominance is reported to be expressed via physical displays and contests more often than is the case for women and this. Men are more likely than women to respond to threats with aggression, particularly when there is an audience of other men (i.e., future potential competitors) and to participate in inter-group conflict (see Buss 2015 for a review). In addition, men score more highly on measures of "social dominance orientation," which assesses preference for unequal status across groups. This is, perhaps, not entirely unsurprising given the likely stronger intrasexual selection on men to compete for mates due to an asymmetry in investment in gametes and, at minimum levels, in offspring (Archer 2009). Male dominance, however, is not as straightforward as success in physical contests. von Rueden et al. (2008), for example, investigated male status in a population of Amazonian Tsimane hunter-gatherers. The authors argue that this community provides a meaningful case study for conditions under which social life likely evolved over much of our evolutionary past. They report that physical size and social support predicted the outcome of dyadic physical contests amongst men: being larger and with more coalitionary support resulted in greater physical dominance. Social support also predicted "influence" and "respect," as did hunting ability. The authors argue that male status is multidimensional and is dependent not only upon physical individual differences, such as a man's size and age, and also upon the strength of one's coalitionary support. Furthermore, status differentials in this population are related to proxies of reproductive success, with high-status men having more extra-marital relationships than those of lower status (von Rueden et al. 2010).

There is evidence to suggest that women use indirect aggression to a greater degree and direct physical aggression less, than do men in order to influence their own status and that of others.

Perhaps the most classic example of this is accusations of witchcraft, in which an individual's reputation is degraded by untestable accusations, with women more commonly accused (see Hess and Hagan (2006) for a review). This may be due to the high costs to women's fitness of direct physical aggression (due to investment in needy offspring), and therefore more indirect forms of aggression may have evolved (see Stockley and Campbell 2013, for a review). Much as male status via acquisition of resources necessary to invest in offspring may be desirable to the opposite sex, perhaps female status is bound up in the traits which make her desirable to men, such as physical attractiveness and chastity. Vaillancourt (2013) suggests that women use two broad strategies to appear attractive to mates: self-promotion (displaying physical attractiveness) and rival derogation (disparaging appearance and fidelity). Hess and Hagan (2006), for example, report that women in a laboratory task were more likely to express desires to retaliate to a threat by attacking reputation than were men.

As argued, however, the behavior of men and women cannot be interpreted in light only of their biology. Biology exists within, and interacts with, a social context. Archer (2006), for example, reports that sex differences in physical aggression against a partner is correlated societal gender equality, such that the size of the sex difference was reduced under conditions of greater equality.

Dominance and Reproductive Success

Across species, high-ranking individuals obtain more food and have greater reproductive success. In primates, for example, high-ranking males tend to have more offspring than do those of lower ranks. This, however, is not a straightforward linear relationship and is most likely influenced by factors such as the numbers of male competitors and receptive females, male coalitions, female choice, female reproductive synchrony, and alternative male mating strategies (see Clutton-Brock and Huchard. (2013) for a review). The relationship between rank and reproductive success is equally variable in female primates. In order to interpret variation in the magnitude of the

relationship between rank and fitness, Clutton-Brock and colleagues call into question the assumption that that status and fitness should be more closely linked in males than females, due to the asymmetry in minimal investment in reproduction by mammalian males and females. The interpretation and application of this classic model has come to treat the proposed dichotomy of competitors (typically males) and choosers (typically females) almost literally, with a greater research focus on competition for resources and status amongst males than females. In their review of a growing body of evidence that females can compete for resources and status to the same extent, or more vigorously, than males, Clutton-Brock and Huchard (2013) show that there are relationships between the degree of reproductive competition and physical traits associated with attracting mates and with intrasexual competition in both sexes. They argue that sex differences in effects of status on fitness (i.e., that status is often more closely linked to fitness in males) may have been over-estimated due to differences in the breeding lifespans of males and females and that without direct comparisons of relationships between rank and fitness of males and females, it is not possible to conclude that selection pressures on traits associated with status vary between the sexes.

As a case study of the above, status and reproductive success are correlated in both men and women, albeit the strength and direction varies. Various measures of status are positively related to number of men's surviving offspring in traditional societies (see Hopcroft 2006 for a review); high income men have more biological children in the contemporary USA whereas years of education is inversely related to reproductive success in both men and women (Hopcroft 2006). Nettle and Pollett (2008) report positive selection for male wealth due to higher childlessness amongst low-income men across eight societies but a negative relationship between income and reproductive success in women. Fieder and Huber also show that income is associated with fewer children for women and more for men (2007). Here it seems likely that interactions between the biology and social-role occupation of men and women are at play. It is interesting to imagine, for example,

whether in a hypothetical society in which there was full gender equality in the opportunity to balance education, employment, and childcare, inverse relationships between wealth and reproductive success would exist to the same extent for women or between education and reproductive success for men and women.

Conclusion

There are sex differences in the expression of aggression across species, and of direct and indirect aggression in humans, stemming from divergent intrasexual selection pressures. This, however, is qualified by evidence that sex differences may not be as large as previously assumed and vary with context, such as societal level of gender equality in humans. Dominance in humans is perhaps best viewed as the status that results from the relative positioning of an individual within their local groups and communities (negotiated via either prestige or coercion) which, in turn, is situated within – and interact with – the context of large, formal, status hierarchies. While there are many remaining unknowns, what is clear is that an individuals' rank has profound implications for his or her life history.

Cross-References

- ▶ Abusers: Husbands, Boyfriends, and Former Sexual Partners
- ▶ Access to Resources
- ▶ Adaptations for Navigating Social Hierarchies
- ▶ Aggression
- ▶ Aggression for Sexual Access
- ▶ Alpha, Beta, and Gamma Males
- ▶ Anatomical Adaptations for Fighting
- ▶ Assessment of Fighting Ability
- ▶ Biology of Human Gender, The
- ▶ Biosociology
- ▶ Biosociology of Dominance and Deference
- ▶ Boys Bully more than Girls
- ▶ Boys Physical Bullying
- ▶ Boys' Rough-and-Tumble Play
- ▶ Bullying
- ▶ Categorization by Sex
- ▶ Competition for Resources Desired by Females
- ▶ Conflict between the Sexes
- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Men
- ▶ Contexts for Women's Aggression Against Women
- ▶ Costs of Aggression
- ▶ Cross-cultural Variation
- ▶ Defense Against Attack
- ▶ Development of Aggression
- ▶ Development of Sex Differences
- ▶ Differential Parental Investment
- ▶ Differential Reproductive Success
- ▶ Division of Labor
- ▶ Dominance and Territory
- ▶ Dominance and Threat Or Use Of Force
- ▶ Dominance Hierarchies
- ▶ Dominance Hierarchy
- ▶ Dominance Theory (Cummins)
- ▶ Evolutionary Social Psychology
- ▶ Facial Width to Height Ratio and Dominance
- ▶ Factors that Influence Bullying
- ▶ Female Choice and Sexual Conflict Theory
- ▶ Female-female Alliances
- ▶ Female-female Competition
- ▶ Financial and Hierarchy Maintenance
- ▶ Forced Copulation
- ▶ Function of Dominance
- ▶ Girls Psychological Bullying
- ▶ Group Living
- ▶ Group Size Optimality and Stability
- ▶ Height and Dominance
- ▶ Higher Status in Group
- ▶ Hostile Masculinity
- ▶ Humans as Social Primates
- ▶ Indicators and Correlates of Status and Dominance
- ▶ Indirect Aggression
- ▶ Intersexual Competition
- ▶ Intrasexual Competition Between Females
- ▶ Intra-sexual Competition
- ▶ Intrasexual Male Competition

- Intrasexual Rivalry
- Intrasexual Rivalry Among Women
- Male Adaptations that Facilitate Success in War
- Male Adaptations to Assess Fighting Ability
- Male Coalitions for Hunting
- Male Dominance Hierarchies
- Male-Male Competition
- Male-Male Strategies
- Mating Rivalry
- Men but not Women will Have Adaptations for War
- Men in Positions of Power
- Men Riskier, More Aggressive
- Murder
- Nonhuman Primates
- Partner Abuse
- Physical Aggression
- Polygyny and Male Risk-Taking for Status
- Primate Dominance Hierarchies
- Primates
- Reputation as a Context for Men's Aggression Against Men
- Resource Competition
- Resource Defense
- Secondary Sexual Characteristics
- Sex Differences
- Sex Differences in Ability to Assess Fighting Ability
- Sex Differences in Same-Sex Aggression
- Sexual Contact and Sexual Disgust
- Social Dominance and Sexual Access
- Social Dominance Orientation (SDO)
- Social Dominance Reduces Fighting
- Social Hierarchies
- Social Status and Economic Resources
- Status and Redistribution of Resources
- Status and Reproductive Success
- Status Competition
- Status Competition and Peer Relationships in Childhood
- Stress
- Tactics to Solve Adaptive Problems of Sperm Competition
- Testosterone
- Vocal Indicators of Dominance
- Women's Prosocial Dominant Acts

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Dominance Theory

- ▶ [Rule Violations Checked If High Status](#)
 - ▶ [Rule Violations Not Checked If Low Status](#)
-

Dominance Theory (Cummins)

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Definition

A theory proposed by Denise D. Cummins that interprets specific social cognitive functions as adaptations to the exigencies of living in a dominance (or status) hierarchy.

Introduction

Eight decades of empirical investigation have unequivocally demonstrated that human reasoning performance varies as a function of problem content. Problems with identical formal properties but different subjective contents often produce vastly different levels of performance, a phenomenon referred to as *content effects*. The most

robust performance differences are observed when people are asked to reason about rules that describe constraints on behavior, such as permissions, obligations, prohibitions, or warnings. When asked to test the truth of such rules, people invariably and wrongly adopt a confirmation bias strategy, choosing to investigate cases that could prove the rule true rather than those that could prove the rule false. The latter strategy is the only one that can provide incontrovertible proof concerning the truth status of the rule (Popper 1959). In contrast, when asked to test compliance with the rule, people invariably and correctly choose to investigate cases of possible non-compliance, that is, to seek to discover whether someone is doing something that is not permitted or is failing to do something they are obligated to do. Permissions, obligations, and prohibitions are called deontic concepts, and reasoning about what one may, must, or must not do in a given set of circumstances is called *deontic reasoning* (Hilpinen 1981). The superior performance elicited by deontic content is called the *deontic advantage* in human reasoning.

Several explanations have been offered for the deontic advantage. One of the most influential is social contract theory, which was proposed by psychologist Leda Cosmides (1989). According to the theory, social contracts are cases of reciprocal cooperation for mutual benefit. When a reasoning problem is interpreted as a social contract, a genetic “look for cheaters” algorithm is spontaneously triggered that causes people to investigate individuals who have accepted benefits (to ensure they have paid the required cost) and individuals who have not paid the cost (to ensure they have not accepted the restricted benefit). The difficulty is that problem contents that elicit a violation detection strategy do not always define opportunities for two individuals to participate in mutually beneficial cooperative transactions. Instead, they typically describe deontic rules that are more appropriately described as *social norms*, constraints created by authorities that dictate what is permitted and obligated when specific conditions apply. For example, the cassava root scenarios used by Cosmides (1989) describe a rule created by village elders or a chief named “Big Kiku” that

restricts the eating of cassava root to members of a particular tribe. Scenarios like these do not describe a reciprocal exchange between two individuals. They instead describe a social norm created and enforced by village authorities. “Cheating” does not take the form of failing to reciprocate a benefit. Instead, it takes the form of failing to comply with an obligatory rule that is imposed by authorities on subordinates. Stanovich and West (1998, Experiment 1) found that adult performance plummeted from approximately 80% to 30% when reference to authority was removed from “social thematic” problem descriptions. Compliance with norms – not reciprocation – is expected and required. Moreover, social norms may or may not be mutually beneficial. Indeed, social norms may have as their goal the exploitation or subjugation of one group of individuals by another, privileged group.

Dominance Theory

To address this discrepancy, psychologist Denise Cummins proposed *dominance theory* (Cummins 1996a, b, c, 1998, 1999, 2000, 2001, 2002, 2004, 2005, 2013a, b, 2016a, b; Cummins and Cummins 1999, 2003). The core tenet of the theory is that social cognition (including the deontic advantage) was shaped by the continual need to survive within dominance (or status) hierarchies, the social organization that is ubiquitous in the societies of humans and nonhuman animals throughout evolutionary time. High-status individuals are essentially authorities in this type of social organization, monitoring and controlling the behavior of subordinates in order to maintain priority of access to competitive resources (such as food and mating opportunities). Dominance theory posits five main cognitive functions that were shaped by the exigencies of living within status hierarchies: rank discrimination, acquiring social norms, monitoring compliance with social norms, monitoring reciprocity, and flouting social norms through deception.

Evolutionary theory is based on the assumption that there is a causal relationship between the adaptive problems a species repeatedly

encounters during its evolution and the design of its phenotypic structures, including cognitive and behavioral traits. Solving problems of social competition and cooperation has direct impact on survival rates and reproductive success. The ubiquitous social structure that evolved from this pressure is the dominance (or status) hierarchy, a social organization in which some individuals have regular priority of access to resources and fertile mates in competitive situations. These individuals are referred to as high status (or high ranking). Individuals who have lower priority of access are called subordinate or low status.

From a cognitive standpoint, status hierarchies can be interpreted and analyzed as systems of implicit social norms that impose constraints on what is permitted, obligated, or prohibited based on one’s status within the group. Surviving within a dominance hierarchy depends crucially on the capacity to learn these constraints, the capacity to recognize violations of these constraints, and the capacity to use deceptive strategies to flout these constraints in order to garner a larger share of resources. Failure to do so carries a high risk of eliciting agonistic encounters or ostracism. According to the theory, the deontic concepts of permission, obligation, and prohibition are primitives (innate concepts) in the cognitive architecture of social animals that were selected for because they were crucial for survival within status hierarchies. It is these primitive concepts that confer the deontic advantage in reasoning performance.

Support for the theory comes from six sources: comparative psychology (particularly primatology), developmental psychology, anthropology, behavioral economics, neuroscience, and cognitive psychology.

Primatology. *Homo sapiens* is a primate species whose ancestors diverged within the primate line a scant five million years ago. Because evolution builds upon existing structures, studying nonhuman primates can provide insight into the characteristics of human reasoning that reach deep into our evolutionary past, prior to the splitting of hominids within the primate line. The most striking of these characteristics is that, like human reasoning, the reasoning of nonhuman primates

is subject to content effects, and social content provides the most robust effects. For example, nonhuman primates readily make rank discriminations among individuals in their social groups, even when all possible dyadic interactions are not directly witnessed (Cheney and Seyfarth 1990, pp. 91–96): They readily infer that A is dominant to C if they witness interactions in which A is dominant to B and B is dominant to C. In contrast, they can perform transitive inference on object-oriented tasks only after considerable drilling with paired stimuli (Gillan 1981).

Primate status hierarchies are replete with “implicit social norms” that dictate who is allowed to groom, sit next to, play with, share food with, and mate with whom. In order to avoid punishment (or ostracism, which can mean death due to predation or starvation), individuals must learn what is *permitted*, *forbidden*, and *obligated given their place in the hierarchy*. High-ranking individuals monitor the behavior of subordinates in order to protect their privileged access to resources. They also frequently take on the role of enforcing norms, aggressing against those who violate them and breaking up disputes between lower-ranking individuals (Boehm 1999).

The hierarchies that characterize primate groups are rarely static structures. Instead, individuals continually vie for control of resources. Higher-ranking individuals defend their privileged access to resources by detecting and punishing acts that threaten privileged access, while lower-ranking individuals attempt to engage surreptitiously in forbidden activities in order to secure a larger share of resources. Individuals move up in rank to the extent that they form alliances with dominants through the formation of reciprocal obligations. Rank within primate dominance hierarchies is acquired and maintained through dyadic aggression, and alliances typically determine the outcome (Harcourt and de Waal 1992; Uehara et al. 1994). Alliances are formed on the basis of reciprocal obligations, such as reciprocal grooming or food sharing (Schino 2007). Alliances are also terminated when an individual fails to reciprocate in giving aid, grooming, or food sharing (de Waal 1992). Cosmides’ social contract theory addresses the

reciprocal nature of these interactions. It does not address, however, the impact of social rank on reciprocation. The terms “despotic” and “egalitarian” have been applied to animal social groups to describe end points on a continuum of the degree of bias in which benefits are distributed (Vehrencamp 1983). A recent analysis of hierarchies falling on the extreme ends of this dimension indicated that the rate of reciprocity and prosocial behavior varies considerably as a function of the steepness of the hierarchy (Kaburu and Newton-Fisher 2015): In chimpanzee groups that show steep rank relationships, dominants provide more agonistic support than subordinates, males direct grooming up the hierarchy, and the rate of reciprocation of grooming is lower for dominants than for subordinates. These observations are best explained as strategies employed by subordinates to obtain rank-related benefits from dominants. In contrast, within shallow hierarchies, high-ranking individuals do not offer agonistic support more frequently than low-ranking males, and dominance rank does not affect grooming distribution, with males of similar dominance rank showing stronger reciprocity than those who hold more distant ranks. Even in steep hierarchies, other research has shown that among chimpanzees, for instance, dominants may trade meat for coalitionary support or mating, as long as they cannot obtain these commodities by force (Jaeggi and Gurven 2013). In fact, primatologists have noted that the most generously sharing individuals are often fully dominant (de Waal and Brosnan 2005).

Lower status individuals also frequently engage in deceptive behaviors that improve their access to resources (Byrne 1995). They conceal objects or behaviors from others by hiding them from view, acting quietly so as not to attract attention, avoiding looking at desirable objects themselves, and distracting attention away from a desired object (such as fruit) or forbidden behaviors (such as mating with non-dominants). For example, dominant males monopolize reproduction opportunities by aggressing against females and subordinate males who are caught socializing or consorting. Because of the high risks involved in such forbidden liaisons, females

and subordinate males often engage in deception, such as concealing their trysts from the view of dominants and suppressing their copulation cries (Kummer 1988; de Waal 1988).

Finally, the neocortex ratio expresses the relative volume of the neocortex compared to the volume of the rest of the brain. It correlates with the mean group sizes that characterize primate species, with larger group sizes corresponding to greater neocortical volume. This ratio correlates with the prevalence of tactical deception observed across primate species (Byrne 1995, pp. 219–221).

Developmental Psychology. Since the 1980s, developmental psychologists have used techniques borrowed from comparative psychology to investigate the cognition of preverbal infants and very young children. They have discovered that infants and toddlers possess an astonishing wealth of knowledge about agents and objects long before there is sufficient time to induce such knowledge from experience. The best explanation for this state of affairs is that these techniques have provided a window into human cognitive evolution, showing us the types of cognition that were shaped by evolutionary pressures.

Infants as young as 6 months of age infer the social dominance relationship between two competing individuals based on the size of the group to which they belong and expect individuals from a numerically larger group to get their way (Pun et al. 2016). By 10 months of age, they can transitively infer dominance relations, just as other primates do (Gazes et al. 2015). Yet, like other primates, children can perform object-based transitive reasoning only if they are extensively drilled on the object pairs upon which the inference is to be performed. Truly content-free transitive reasoning does not reliably appear until 6 years of age.

Status hierarchies are apparent in the playgroups of preschool children as young as 2 years of age (Strayer and Trudel 1984). As early as 3 years of age, preschoolers are able to infer dominance not only from physical supremacy but also from decision power, age, and resources (Charafeddine et al. 2015). They expect an individual who imposes his choice on another

to exhibit higher competence in games and to have more resources. Children also prefer to associate with and imitate high-status as opposed to low-status individuals (La Freniere and Charlesworth 1983).

Children also show a marked *precocity* for acquiring social norms and monitoring compliance with them (Cummins 2013a, b). By the age of 3 years, children's reasoning performance is characterized by a deontic advantage as large as that seen in adults: They rightly seek violations when testing behavioral compliance with a rule but wrongly seek confirmation when testing the truth of a rule, just as adults do (Cummins 1996b). Children as young as 3 years of age do not just follow social norms; they actively enforce them on others – even when serving as spectators rather than players in the game (Schmidt and Tomasello 2012).

The ability to deceive is closely tied to theory of mind, that is, the ability to understand that individuals have inherently private intentions, desires, and beliefs and will act accordingly (Bartsch and Wellman 1989). Deception relies on this ability because to deceive, individuals must understand their target's mental state – what the target knows, wants, or believes. Within the first year of life, infants engage in subtle manipulations that succeed in deceiving others at least temporarily, and the bulk of these deceptions have as their goal hiding activities that are forbidden by adults (dominants) (Reddy 2007). For example, they will hold eye contact with an adult in order to draw attention away from a forbidden activity, such as discreetly throwing disliked food or objects onto the floor. They will also do forbidden things quietly so as not to draw attention to their behavior, wait until a parent leaves the room before rushing to engage in a forbidden activity, and turn their backs or use their bodies to screen a forbidden activity or object from other's view (Reddy 2007). By the second year of life, infants can reason not only about the actions of agents who hold false beliefs but also about the actions of agents who seek to implant false beliefs (Scott et al. 2015).

Anthropology. The egalitarianism of small-scale societies is often misconstrued as an absence

of dominance motivations (or status striving) on the part of group members. Yet leaders in these societies may orchestrate collective actions that produce goods more beneficial to themselves and their kin (von Rueden and van Vugt 2015). Instead, small-scale society egalitarianism is better understood as an active leveling of would-be dominants through norms compelling humility and coordinated punishment of aggrandizers (Boehm 1999). These norms strongly impact decisions members of small-scale societies make in economic games. Henrich et al. (2005) conducted a cross-cultural study of decision-making in 15 small-scale horticultural, foraging, and pastoral cultures in Africa, South America, and Asia. Their results clearly showed a pattern of behavior best described as status seeking and alliance formation through gift giving, which is common throughout Melanesia. The authors concluded that economic behaviors emerge from “a set of basic human psychological mechanisms involving fairness and resource distribution, constrained in different ways by kinship, age, status, and other biologically meaningful variables.”

Behavioral Economics. A cornerstone of economic theory is that rational agents are self-interested agents. When making choices about allocations of resources, rational agents will choose to maximize benefits to themselves. More than a decade of research in experimental economics, however, has shown that people do not always behave this way, often choosing to be more generous or stingy than predicted by rational self-interest. In the dictator game, dictators have full control over allocation of a windfall resource between themselves and another individual. Rational dictators should keep all of the resource for themselves, but experimental results indicate that, on average, dictators freely give away about 15–35% of the resource to their partners (Camerer 2003). In the ultimatum game, one party proposes how to divide a sum of money, and the other party chooses whether to accept or reject the proposed division. If the offer is rejected, the entire sum is forfeit. From a rational standpoint, any amount (no matter how small) should be accepted since something is always better than nothing. But

results indicate that proposers tend to be more generous in their offers, with 40–50% comprising the modal range, while recipients tend to be choosy, with offers of less than 20% being routinely rejected. Here, proposers appear to behave strategically, taking into consideration which offers are likely to be acceptable to their partners.

Importantly, several studies have reported that perceived relative status strongly impacts behavior in both dictator and ultimatum games (Ball and Eckel 1996, 1998; Eckel and Wilson 2007; Hoffman et al. 1994, 1996). Dictators offer less to their partners when they are told that they scored higher on a trivia test than their partners did. Ultimatum proposers also offer less when they believe they ranked higher than their partners, and responders are willing to accept lower offers when they believe proposers ranked higher.

Neuroscience. In the last decade, studies involving fMRI and ERP technology have revealed broad brain regions that detect and process social dominance and social rank, indicating that recognition of relative social rank occurs quite rapidly – within 200 ms (Chiao et al. 2008). These regions include the amygdala, hippocampus, striatum, and various cortical networks such as the prefrontal and parietal cortices. The amygdala and anterior hippocampus have been implicated in tracking social rank but also in expressing signals that code for social rank (Kumaran et al. 2012). Additionally, it has been found that neurotransmitter systems, such as the dopaminergic and serotonergic systems, modulate and are modulated by the formation of the social hierarchy in a group.

Cognitive Psychology. When asked to monitor compliance with a social rule, adults are more likely to look for rule violations when they adopt a high-status position relative to the individuals whose behavior they are monitoring (Cummins 1998). But when engaged in reciprocal exchanges, adults instead exhibit noblesse oblige, that is, greater generosity and greater tolerance for non-reciprocation when they adopt a high-status perspective, even when the lower-ranking partner was described as having a higher income than the higher-status partner (Fiddick and Cummins

2001, 2007). This pattern of behavior has been reported among participants from seven countries that vary along hierarchical and individualist/collectivist social dimensions; participants were more tolerant of non-reciprocation when they adopted a high-ranking perspective compared with a low-ranking perspective (Fiddick et al. 2013). The best explanation for these status effects is costly signaling theory which states that costly, altruistic acts may benefit an altruist indirectly by establishing a “reputation” that enhances alliance formation, a factor that is crucial for acquiring and maintaining a high-status position (Bird et al. 2001).

Criticism of Dominance Theory

The main motivation for dominance theory is explaining the “deontic advantage” in human reasoning. But other interpretations of the “deontic advantage” have been offered that reject evolutionary accounts. Most of these explanations focus on studies employing the Wason card selection task in which participants are asked to choose which cards must be turned over to test the truth of a rule or compliance with the rule (Wason 1968). Oaksford and Chater (1994) have argued that people view the deontic (rule compliance) and truth-testing versions of these tasks in terms of optimal data selection and shift their strategies from maximizing expected information gain on the truth-testing version to maximizing expected utility on the deontic version. Manktelow and Over (1995) and Evans and Over (1996) also explain performance on the deontic version of the selection task by modeling it as a process in which subjects seek to maximize subjective expected utility. In the deontic version, reasoners are purported to construct a model of the rule along with possible outcomes and to evaluate these outcomes in terms of costs (negative utility) and benefits (positive utility). In contrast, on the truth-testing version of the task, reasoners purportedly try to maximize expected epistemic utility by choosing evidence that will reduce their uncertainty about some particular claim relative to another.

While researchers differ in terms of their explanations for marked performance differences on deontic and truth-testing reasoning tasks, the larger question is why people perform exceptionally well on the deontic version of the task regardless of general intellectual ability or level of education, while performance on the truth-testing version correlates positively with intelligence (Stanovich and West 1998). Is it something about the nature of the tasks, or is it something about the nature of human cognition?

Dack and Astington (2011; Astington and Dack 2013), among others, argue that the extant data on the deontic advantage cannot speak to the issue of innateness or evolutionary impact on cognitive architecture. Instead, they argue that expertise in deontic reasoning is due to experience: The ubiquity of social rules in everyday life leads to the development of deontic reasoning schemas. These ubiquitous encounters with social rules facilitate conceptual development during the preschool years through explicit instruction and social enculturation. The difficulty is that these explanations fail to address the fact that children are exposed to lies and falsehoods as frequently as they are to social rules (Heyman et al. 2009, 2013), yet they infer no efficient strategy for testing the truth of statements (Cummins 1996b, 2016c).

Conclusion

According to dominance theory, the evolution of social cognition was shaped by the continual need to survive within dominance (or status) hierarchies, the social organization that is ubiquitous in the societies of humans and nonhuman animals. Five main cognitive functions arose from the evolutionary pressures imposed by this social structure: rank discrimination, acquiring social norms, monitoring compliance with social norms, monitoring reciprocity, and flouting social norms through deception. Support for the theory comes from six sources: comparative psychology (particularly primatology), developmental psychology, anthropology, behavioral economics, neuroscience, and cognitive psychology.

Cross-References

- [Access to Resources](#)
- [Cooperative Alliances](#)
- [Dominance and Health](#)
- [Dominance in Humans](#)
- [Emergence of Deontic Reasoning](#)
- [Higher Status in Group](#)
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- [Social Status and Economic Resources](#)
- [Status and Dominance Hierarchies](#)
- [Status and Redistribution of Resources](#)
- [Status and Reproductive Success](#)

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Dominance, Testosterone, and Cortisol

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Synonyms

Competition; Contests; Hierarchy; Sex steroid hormones; Social status; Status; Stress hormones

Definition

Testosterone and cortisol are steroid hormones that have effects on dominance behavior and are in turn influenced by dominance-related social interactions.

Introduction

Dominance status is an important factor in the structuring of many animal and human societies.

Dominance is the state of having high social status relative to one or more group-mates, who react submissively to dominant individuals. High status within hierarchical societies provides important benefits to individuals, including priority of access to resources, enhanced influence over subordinates, and ultimately, increased fitness. Lower-ranking individuals are therefore often motivated to improve their position in the hierarchy, whereas higher-ranking individuals strive to maintain their current status. Dominance relationships are often established by fight or threat displays, perhaps most commonly observed during agonistic competitive interactions between group-mates. Dominance displays also function to maintain social rank, once it has been acquired.

Research into the biological factors that affect dominance in animal and human groups suggests that dominance behavior is importantly influenced by two steroid hormones, testosterone (T), a reproductive hormone, and cortisol (C), a stress hormone; concentrations of both these hormones can be measured in blood, saliva, urine, feces, or hair. Two axes in the body, the hypothalamic–pituitary–gonadal axis and the hypothalamic–pituitary–adrenal axis, produce T and C, respectively; each of these axes inhibits the other at several different levels. Together these axes create a complex network regulating aggressive and dominance behavior, although the direction and strength of these hormonal influences are still being assessed. Several hypotheses have been put forward to explain the relationship between dominance and these hormones in a wide variety of animals.

Cortisol and Dominance

The relationship between C and social dominance varies both across and within species (Creel et al. 2012). Several studies have indicated that socially dominant animals have relatively low concentrations of C, whereas subordinate individuals have relatively high C levels. Often, these differences are particularly striking during times of social instability. In other

species, however, dominant individuals have elevated C concentrations compared to those in subordinate animals. Thus, in some cases, it is stressful to be at the top of the social ladder, and in other cases, being at the bottom of the hierarchy is stressful. These differences probably reflect species-specific factors such as social organization, stability of the hierarchy, resource allotment, frequency of agonistic and conciliatory behaviors, and the ability of subordinate animals to avoid dominant individuals (Sapolsky 2005).

The Challenge Hypothesis

The “challenge hypothesis” (Wingfield et al. 1990) was originally proposed to explain intra- and interspecific variation in T secretion in birds in relation to aggressive, sexual, and parental behavior. Here we will focus on dominance and aggressive behavior, about which the challenge hypothesis predicts that behavioral stimuli and social context can alter endogenous hormone concentrations. Behavioral cues, such as territory establishment, agonistic “challenges” from males, and sexual behaviors from females, stimulate the secretion of T. In turn, this increase in T leads to a rise in territorial and mate-guarding aggression. By adjusting T production to the social environment, individuals can exhibit flexible behavioral responses that fit the specific challenge and can also avoid the fitness-reducing costs associated with chronically elevated T levels. A recent meta-analysis found that T was positively correlated with both dominance and aggressive behavior in mammals, although there was no strong pattern when observed across the diverse mating and parental care systems of all vertebrate taxa (Hirschenhauser and Oliveira 2006).

Archer (2006) applied the challenge hypothesis to humans, reasoning that T levels should increase in any competitive situation, particularly in males. In Archer’s meta-analysis, both men and women demonstrated a small but positive association between T and aggression, and a larger positive correlation between T and measures of dominance behavior such as toughness, leadership, and aggressive dominance.

The Biosocial Model of Status

Focusing on humans and other primates, the “biosocial model of status” supplements the challenge hypothesis by making explicit predictions regarding T in relation to changes in status (Mazur 1985). Like the challenge hypothesis, this model predicts that T concentrations change during competitive interactions, increasing in winners and decreasing in losers. T should rise shortly before a competitive encounter, increase further in winners at the end of the competition or after a rise in status, and decline in losers or after a reduction in status. Feedback between T and the dominance outcome reinforces a continuation of that behavior, such that these changes in T influence an individual’s future competitive behavior. Thus, this model suggests a relationship of mutually reinforcing feedback between T concentrations and social dominance.

Hormonal Correlates of Competition

Winner and/or loser effects have been observed across a wide range of animal taxa. Individuals that have recently won generally exhibit more aggressive behavior toward a new opponent and have a better chance of winning again (the winner effect), whereas individuals that have recently lost frequently display more submissive behavior and have a higher likelihood of losing again (the loser effect) (Hsu et al. 2006). In many species, the outcome of the competition influences T concentrations, with increased levels in winners and reduced levels in losers (Hirschenhauser and Oliveira 2006). In some species winning a contest is not sufficient to increase the probability of winning future contests unless the victory is associated with an increase in T (Carré and Olmstead 2015). Evidence for the physiological basis of the loser effect is more variable, although elevated levels of C are often discovered in individuals that have recently lost a fight (Hsu et al. 2006).

In humans, T rises in anticipation of a competition and increases during competition; these increases in T are higher during sports competitions than during nonphysical forms of competition

(Archer 2006). Athletic competitions are usually also associated with an increase in C in both men and women, regardless of the competition outcome. Winning an athletic competition is associated with an increase in T in both sexes across a variety of sports, although there is no consensus on the effects of losing on T (Casto and Edwards 2016).

However, the winner-loser effect is much more variable when evaluated across all types of human competition, from laboratory paradigms to political elections, including athletics. In a recent review, Carré and Olmstead (2015) found that, although many studies reported that winners had elevated T levels relative to losers, nearly as many studies failed to find this effect; other reviews have found similarly inconsistent results in regard to C (Casto and Edwards 2016). This heterogeneity in results is possibly due to individual differences in personality and contextual differences between competitions. In humans, the T response to competition is more important than the actual contest outcome in predicting future competitive and dominance behavior. Thus, a postcontest rise in T predicts increased competitive behavior in the future, whereas a decrease in T predicts less competitive behavior in both winners and losers alike (Carré and Olmstead 2015).

The Dual-Hormone Hypothesis

One probable explanation for the variable findings described above is that T and C interact to regulate dominance, such that neither hormone alone predicts competitive behavior. The “dual-hormone hypothesis” instead suggests that the positive relationship between T and dominance pertains only to individuals with low levels of C, with C blocking the effect of T on dominance (Mehta and Josephs 2010). Thus, T should only increase dominance behavior and encourage higher status when C is low. There has been significant empirical support for the interaction between C and T in both men and women with respect to leadership, social status, and risk-taking in both athletic competitions and laboratory paradigms (Casto and Edwards 2016). Although there have been a few

studies in nonhuman animals of the competition dynamics posited by the dual-hormone hypothesis, it is evident that T and C levels vary between dominants and subordinates according to each species’ social system, reproductive strategy, and the allostatic load distribution within the dominance hierarchy.

Conclusion

Research has shown that dominant and competitive behavior is associated with changes in both T and C. In mammals, T positively correlates with dominance and with aggressive behavior, whereas C and its relationship to dominance vary across and within species. The challenge hypothesis, one of several put forward to explain hormone-behavior relationships, suggests that social and environmental factors affect changes in T concentration. The biosocial model of status expands the challenge hypothesis to predict that T concentrations should increase in winners and decrease in losers in human competitions, allowing individuals to quickly adjust to changes in their social status. In competitive situations, C has also been shown to moderate the psychological effects of T, and more recent research has suggested that the relationship between T and dominance is only true for individuals with low levels of C. This dual-hormone hypothesis may explain individual differences in dominance behavior that remain unexplained by single-hormone studies of dominance.

From an evolutionary standpoint, these divergent hormonal responses may allow for rapid adjustment in social behavior relative to changes in the social environment. In winners, the increase in T may promote the competitive, aggressive behavior necessary to defend their status, and the decreased T levels in losers may promote submissive behaviors that permit avoidance of physical injury and prevent further loss of status. Overall, the short-term changes in hormone concentrations modulate social behavior and dominance and likely have far-reaching fitness implications for individuals. This idea remains relevant as researchers work to develop a deeper understanding

of the variety of hormonal mechanisms that underlie dominance and aggression in human and animal societies.

Cross-References

- [Biosociology of Dominance and Deference](#)
- [Dominance and Health](#)
- [Dominance and Testosterone](#)
- [Dominance Hierarchies](#)
- [Dominance in Humans](#)
- [Function of Dominance](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Male Dominance Hierarchies](#)
- [Primate Dominance Hierarchies](#)
- [Serotonin and Dominance](#)
- [Social Hierarchies](#)
- [Status and Dominance Hierarchies](#)
- [Status Competition](#)
- [Stress and Cortisol](#)

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Dominant

- [Serotonin and Dominance](#)

Dominant Acts Expressed (Buss 1981)

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Synonyms

[Aggression](#); [Power](#); [Sex differences](#); [Status](#)

Definition

Psychological research suggests men and women employ sex-specific strategies for expressing dominance, and dominant acts are perceived differently based on the sex of the actor. The nature of sex differences in dominance-based behavior, variation in personality and dominance, and ethnographic accounts of dominance in leadership positions are discussed.

Introduction

The role of dominance in the formation of hierarchy is an ancestral feature of social organization

humans share with nonhuman primates as well as social animals generally. As a strategy for achieving influence, dominance is likely a cross-cultural universal, yet there are stark sex differences and cultural variation in the universal expression of dominance.

Dominance consists of gaining authority through the use of coercion, fear, aggression, or agonistic threats by social superiors to subordinates (Cheng et al. 2010; Henrich and Gil-White 2001). Patterns of deference behavior follow a semi-stable ranking in a transitive and linear fashion. Within human social hierarchies, there is immense variation in the expression of dominance, and the formation of dominance hierarchies does not necessarily involve direct aggression. Culture, ecology, personality, age, and sex can all influence the ability of and means by which an individual pursues a dominance-based strategy for achieving influence within a group.

Buss (1981) investigates the expression of dominance and the evaluation of dominant acts in reference to established psychological models and reports sex differences in both the desirability and expression of dominant acts. Over the past 35 years, dominance, contrasted with prestige, has become a prominent theoretical framework in models of social status and hierarchy (see Cheng et al. 2014). Here Buss' seminal study is reevaluated, and findings are framed in the context of relevant contemporary literature.

Conceptualizing Variation in Dominance

Symbolic and complex cumulative culture presents humans with a range of opportunities for expressing dominance, and individuals can adjust dominance-based strategies for specific situations. Variation in phenotypic expression and personality type can render certain expressions of dominance more amenable for different individuals. For example, dominance can be expressed very directly relying on physical size and agonistic threats or more subtly through prosocial behavior and tactful displays. Buss (1981) tested the expression of dominance in reference to Bakan's (1966) dualistic model of human existence, which suggests human existence – behavior – can take one of two forms; individuals can act agentically,

or in masculine fashion with egocentric aims, or individuals can act communally, or in feminine fashion with group goals shaping behavior. In this context, Buss (1981) addresses whether there is a sex difference in the desirability of dominant acts, if dominant acts are perceived to be more desirable when performed by a male, if males and females differ in frequency of performing dominant acts, and if males and females differ in regard to the nature of expressing dominant acts. In addition to identifying important sex difference in the expression of dominance, Buss (1981) seeks to provide evidence counter to the stereotype that dominant behavior is an exclusively male trait. Following Bakan's model, Buss (1981) predicts that the expression and evaluation of dominant acts by males will follow the agentic mode, whereas the evaluation and expression of dominant acts by females will follow the communal mode. Buss (1981) tests these predictions using a two-study design and a sample of undergraduates rating 100 dominant acts on their social desirability and a self-report measure of how often they performed them.

The Expression of Dominance

Despite individual variation in the expression of dominance, evidence suggests males and females have sex-specific adaptations for expressing and assessing dominant behavior. Buss (1981) found males rated egotistic and manipulative acts as more socially desirable than females. Similarly, females rated prosocial, group-centric expressions of dominance as more desirable than males. This profound sex effect reveals men consider more self-serving and egotistical dominant acts as more desirable than women.

To investigate if perceptions of dominance manifest in expressions of dominance, Buss (1981) uses psychometric measure of dominance in comparison to self-report measures of the performance of dominant acts. Among men and women, those who score high on psychometric measures of dominance tend to also report greater frequencies of performing dominant acts. However, the study revealed sex-specific trends in reported expressions of dominance. Dominant men reported performing egoist, self-serving acts of dominance at greater

frequencies than women, whereas women's reported acts of dominance were more likely to be prosocial and group focused. According to Buss (1981), the expression of dominance among men is more likely to serve immediate individual level goals; for women, dominant behavior is more likely to increase within-group cohesion.

Buss (1981) revealed women do engage in dominant behavior but tend to do so in a gendered way. Egoistic and prosocial dominance behaviors represent two strategies for achieving social influence within a group, and despite general sex-specific trends, the two strategies are not mutually exclusive or necessarily sex specific. Hawley et al. (2008) suggest there is less distinction between male and female expressions of dominance than previously described and both males and females employ egoist and prosocial strategies for achieving social influence, independent of aggressiveness. Using a sample of German children and peer-report, self-report, and psychometric data, Hawley et al. (2008) measured the propensity to engage in coercive or prosocial strategies, the ability to control group resources, individual dominance and aggression, and social standing. Similar to Buss (1981), key sex differences emerged.

Among children, boys are more likely to value social influence, employ coercive and aggressive strategies in attaining influence, and report success in their attempts at gaining social influence (Hawley et al. 2008). This distinction also manifests in peer reports with children reporting boys are more controlling, coercive, and aggressive than females. However, contrary to perspectives emphasizing sex differences in expressions of dominance, several important similarities were documented between boys and girls scoring high on measures of dominance and resource controlling ability.

Children demonstrate a preference in play for bistrategic controllers or those who employ both prosocial and coercive strategies of control (Hawley 2003). Both males and females are perceived as equally effective at controlling resources when using both coercive and prosocial strategies (Hawley et al. 2008). Additionally, bistrategic controllers are equally likely to be male or female, limiting the ability of males to disproportionately

control group resources and dynamics when prosocial strategies are considered (Hawley et al. 2008). However, when overt physical aggression is the principal mechanism by which individuals strive to achieve social influence, females are at a disadvantage. Considering relational aggression, girls are perceived to out rank boys (Hawley et al. 2008), a trend that continues across development (Hess and Hagen 2006). These sex differences are widely supported in the psychological literature (Campbell 2002) and in at least one study among hunter-gatherers (Hess et al. 2010).

Females are able to compete with males during childhood through employing a bistrategic approach to social influence. A similar phenomenon emerges among postmenopausal women. Several ethnographic accounts reveal that after their childbearing years, women in small-scale society are more likely to surface as major political agents and achieve positions of leadership in prosocial arenas. This has been termed a "coming of age" for women's sociopolitical influence (Brown and Kerns 1985). Traditionally, during their reproductive years, women are limited in their ability to pursue positions of social influence, and their ability to express social dominance through coercive or prosocial strategies is ineffective.

Dominance and Personality

The propensity to pursue a dominance-based strategy is not solely related to physical size and aggression. Whereas Buss (1981) related the expression of dominance to agentic and communal behavior, contemporary studies have investigated the expression of dominance in the context of variation in personality. In a predominately female sample of undergraduates, Cheng et al. (2010), using a series of psychometric measures, contrast hubristic pride, which is driven by antisocial behavior, arrogance, and conceit, with authentic pride, which is driven by individual accomplishments, success, and confidence. Based on self-report measures, hubristic pride was positively and strongly related to dominance as predicted. Unexpectedly, authentic pride demonstrated a weak positive relationship to dominance as well, independent of other relationships (Cheng et al. 2010). Additionally, dominance was positively related to narcissism, aggression, and

extraversion and, to a lesser degree, conscientiousness. Conversely, dominance was negatively associated with agreeableness, social acceptance, and self-esteem (Cheng et al. 2010).

In the described study, the authors do not focus on sex differences. These results reveal patterns in the expression of dominance across personality types independent of sex. Despite variation in the expression of dominant acts, males and females more prone to pursue dominance-based strategies of social influence are likely to share common personality profiles.

Cultural Variation in the Expression of Dominance by Males and Females

The expression of dominance and dominance-based strategies for achieving positions of social influence are very likely universal features of an inherited leader-follower psychology. However, ecological and sociocultural features contribute to variation in the expression and utility of dominance-based behaviors in unique ways for males and females. Contrasting ethnographic examples from egalitarian populations, or populations which lack inherited status differences, have little wealth disparity and are generally characterized by greater gender equality, with stratified populations, which are characterized by graded differences in inherited status and wealth and demonstrate increased gender inequality and reveal the influence of cultural systems on sex-specific expressions of dominance.

In egalitarian societies, leaders and high status individuals have limited direct authority over subordinates, and overly assertive expressions of dominance can be subverted through group-wide resistance, deposition, or physical retaliation (Boehm 1999). Egalitarian societies tend to lack expressions of dominance in sociopolitical organization and among the Mbuti, Turnbull (1965:187) relates that, "it is plain, then, that while any movement toward individual authority, conscious or otherwise, is sharply countered, and while individual authority is virtually nil, there is nonetheless a clear basic framework to support the values of the hunting band. There is the division of leadership, according to field, throughout the entire band, yet there is the midcamp site from

which anyone may harangue all present." With dispersed and contextual leadership, Mbuti society accomplishes effective organization yet maintains and promotes an openness of dissent. The ability of any one individual to effectively employ dominance-based strategies in leadership positions is limited.

Within the egalitarian system of the Iban, men engage in ruthless between-group competition and head-hunting which leads to within group positions of influence based on respect but also fear, intimidation, and threats of physical aggression. Counter to these egoist expressions of dominance, women are expected to provide a more prosocial service among couples with considerable social influence. Sandin (1967:56) describes, "wives of these heroes should also try to excel other women in various skills. Without these qualities, they could neither have the position to receive the human heads which their husbands hunted. . . nor could they become leaders of other women if they are bad, greedy and jealous. All women who are married to such prominent persons should, therefore, initiate good deeds in order to match with the courage and qualities of their husbands." Egalitarian societies both reward and resist expressions of dominance. Dominance-based strategies can secure group interests in between-group competition but must be resisted or balanced with prosocial investments in the context of within-group collective action and social organization.

The emergence of inequality and social stratification is linked to an increase in dominance-based strategies for social influence. With an increase in monopolization over resources and social influence and a reduction in equality, leaders are able to expand the domains through which dominance can be expressed (Kaplan et al. 2009). By exploiting followers and exercising dominance across social relationships, including kin groups and in marriage patterns, in economic systems, using organized military forces, and across broad ideological values, leaders effectively maintain and control positions of authority and are able to pass on these positions to their offspring (Earle 1997). Amhara chiefs are known to strategically and preemptively act to

maintain their social control, and in one example, it was noted that the chief, “expects to see his tenant-followers quite often. If they stay away for more than a reasonable period of time, he will suspect that they are plotting against him or currying the favor of some other important man” (Hoben 1963:182). Cultural systems and socio-political organization grant chiefs excessive power and ample opportunities to employ dominance-based strategies. Among the Bemba, Richards (1940:106) describes, “the sanctions for a chief’s authority are numerous, and they were still greater in the old days. . .much of his power also rested in the old days on force. A chief practised savage mutilations on those who offended him, injured his interests, laughed at him or members of his family, or stole his wives. A number of these mutilated men and women still survive in Bemba country today. Command over the army and over the supply of guns also lays in the chief’s hands, and there is no doubt that the greatness of the Bena nandu rested to a large extent on fear. The people explain that the royal family were named after the crocodile because ‘they are like crocodiles that seize hold of the common people and tear them to bits with their teeth’.” With authority over wide social domains and the sanctioned use of force at their disposal, leaders in highly stratified societies maintain near divine positions of power and wield this power absolutely, instilling fear in followers through threats, aggression, and deadly force.

Though opportunities for dominance-based strategies for achieving social influence among women are rare in stratified traditional societies, they are not universally absent. Among the matrilineal Trobriands, Austen (1940:272) mentions that, “Botabalu lives in a high-chief’s house, and has women and girls for her companions, who keep the house clean and tidy. . .she is a stout woman and does not walk about. Most of her time is spent in the village, and because she is a great chieftainess, with many kinsmen and numerous villages under her rule, she is greatly feared by all.” In the context of hereditary social stratification, female leaders, though to a lesser degree than males, also employ dominance-based strategies to achieve and maintain positions of influence.

Conclusion

Buss (1981) provided a framework for understating and investigating sex differences in dominance behavior. Most notably, males tend to use dominance-based strategies to achieve personal, egocentric goals, whereas females tend to use them to achieve group-level goals.

Further research in the field both supported this distinction and revealed caveats. Among Western children, when both dominance-based and prosocial strategies are considered, there is little distinction between high-ranking males and females (Hawley et al. 2008). Additionally, the personality profiles of males and females who employ dominance-based strategies in social interactions are likely very similar, with both trending toward narcissism, extroversion, and aggression (Cheng et al. 2010).

Across a diverse range of leaders in traditional societies, expressions of dominance are associated with positions of social influence. However, the nature of expressions of dominance varies greatly between egalitarian and stratified societies and between sexes. Cultural context and sociopolitical organization influence the viability of specific types of dominance-based strategies, but do not completely prevent them.

The dominance model adopted from ethology and animal social hierarchies has been incredibly influential within the social sciences investigating leadership, status competition, and social influence. Buss’ seminal work remains an important foundational study in this field.

Cross-References

- [Men’s Egoistic Dominant Acts](#)
- [Women’s Prosocial Dominant Acts](#)

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Dominant Hemisphere

► Language and Handedness

Donation

► Prosocial Behavior

Donations

► Charitable Giving (Peter Singer)

► Charity

Donner Party Disaster: Scarce Resources and Illness

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Synonyms

Donner-Reed Party; Group mortality during environmental stress

Definition

The Donner Party disaster is one example of how children, the elderly, males, and individuals in smaller kin groups tend to die at the highest rates during periods of scarce resources and illness.

Introduction

Evidence taken from the records of historical disasters, such as the abortive Donner Party expedition in the American West, suggests that periods of scarce resources and illness within a population generally produce varying mortality rates between its constituents. Preadolescent children (including and especially infants) and the elderly are usually the first members to perish. Within adult populations at lower risk for death, males die at higher rates and more quickly than females. Further, larger family groups produce higher survival rates than smaller groups.

Factors Predicting Mortality

In his review of the records from the Donner Party, Grayson (1993) provided confirmatory evidence that scarce resources predict illness and differential survival patterns in human groups such that mortality during environmental duress generally follows a prescribed plot. Typically, a curvilinear pattern is observed in mortality, with children and the elderly dying more quickly, and in greatest numbers. Death rates are usually highest between 1 and 5 years of age, decreasing until around age 35 years, at which point mortality rates begin to increase again. This trend has been well documented in other historical disasters, such as during the 1974–1975 famine in Bangladesh (Watkins and Menken 1985). Thus, age is a major predictor of survival during times of famine and climatic hardship.

Similarly, sex differences have been observed in survival patterns during periods of environmental stress. Females tend to have higher survival rates than males, which also reflects the general longer life span of females relative to males worldwide (World Health Organization 2014). In fact, cross-culturally, males have near universally higher mortality rates at all periods of life, beginning at infancy (e.g., Pongou 2013). Many behavioral and proximate factors may contribute to higher mortality among males, such as the tendency toward

aggression and risk-taking behavior (i.e., young male syndrome; Wilson and Daly 1985). These dispositions seem to be exacerbated during periods of scarce resources and illness.

One biological difference proposed to be related to the disparity in survival between sexes is body fat reserves and metabolic rates. In general, females have higher fat reserves as well as lower metabolic rates than men, meaning their lower energy requirements and higher energy reserves may help buffer against starvation. Although men may be thus disposed to higher mortality, this model may be inadequate to completely explain differential survival patterns seen during periods of duress (Speakman 2013). Males are also more often exposed to grueling or dangerous conditions, causing greater risk for fatality especially in times of scarce resources (Grayson 1993). These conditions can include performing more labor-intensive (and thus calorically costly) tasks, such as clearing vegetation impeding travel as in the Donner Party, and can also carry risk of physical injury. Thus, some combination of biological disposition and proximate factors likely combine to produce a higher mortality rate among male members of communities facing environmental duress. Evidence from the Donner Party supports this conclusion, where males died at about twice the rate of females (Grayson 1993).

Finally, larger kin groups may provide a buffer against mortality during periods of scarce resources. Because cooperation can increase resource procurement and allocation within a group, and since cooperation is more likely among genetically similar individuals (e.g., West et al. 2002), even if these individuals are not kin (Sinervo and Clobert 2003), it follows that larger kin groups would also promote cooperation and, consequently, survival. This pattern was found among the Donner Party, with the surviving members travelling with larger average kin groups than deceased members (Grayson 1993). When resources are scarce, cooperation may be fostered by living among a larger group of genetically similar individuals, which may, in turn, provide social support in many forms such as sharing food,

nursing when injured, morale, and even higher immune system functioning (Grayson 1993).

Conclusion

When human groups are exposed to hardships, including disease and lack of resources, elderly and children tend to die first. Further, men tend to perish at much higher rates than women. It is proposed that the differential survival pattern between the sexes is due to many causes, including differences in body composition, caloric expenditure, and more frequent exposure to pathogens and dangerous activities. Finally, larger kin groups may buffer the risks posed to members of a community struggling against environmental hardships.

Cross-References

- [Cooperation Varies with Genetic Relatedness](#)
- [Kinship](#)
- [Stress](#)

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Donner-Reed Party

- [Donner Party Disaster: Scarce Resources and Illness](#)

Dopamine

- [Music and Hormones](#)

Dorsal Pigmentary Darkening

- [Countershading](#)

Dorsal Stream, The

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Synonyms

[Dorsal visual pathway](#); [Superior longitudinal folliculus](#)

Definition

A parallel, hierarchically organized series (i.e., “stream”) of interconnected cortical structures in the occipital and posterior parietal cortex (PPC).

Introduction

The dorsal visual stream refers to a parallel series of cortico-cortical projections that arise chiefly from extrastriate visual areas of the occipital cortex, which innervate structures in and around the intraparietal sulcus (IPS) of the PPC. Many cortical structures of the dorsal visual stream are

reciprocally connected, send horizontal and feedback projections to structures within the same level and those within lower levels of the hierarchy, and show close homologies across human and nonhuman primates (Kravitz et al. 2011). Dorsal stream structures, like all others in primate cortex, are typically delineated according to their morphology, connectivity, and functional properties along microscopic and macroscopic scales of observation. However, unlike cells in “early” areas of the occipital cortex, visually-sensitive cells in the PPC, including those structures comprising the dorsal stream, possess relatively large receptive fields and the retinotopic organization of dorsal stream structures in the PPC is not as prominent. Furthermore, many cell responses in the dorsal stream require some level of volitional task engagement that involves the movement of effectors, such as the eyes or upper limb, or somatosensory stimulation of different parts of the body.

Subcortical Visual Input to the Dorsal Stream

Geniculostriate Visual Pathway

The dominant source of retinal input into both the dorsal and ventral streams comes through early visual cortex via the dorsolateral geniculate nucleus (dLGN). The dLGN receives visual input directly from retinal ganglion cells and indirectly via another direct recipient of retinal ganglion cell input, the superior colliculus (SC). Visual input from the dLGN to the occipital cortex arises from different populations of neurons. The best studied of those populations are the parvocellular (P) and magnocellular (M) cells, which occupy different layers of the dLGN (Kaplan 2004). Relative to P neurons, M neurons possess faster conduction velocities and their responses are more transient. Furthermore, M neurons are largely insensitive to chromatic difference, possess larger visual receptive fields, and are more sensitive to low-contrast visual stimuli (Kaplan 2004). The M and P cells send parallel convergent and divergent projections to striate (primary) visual cortex (V1). This pattern of connections continues on

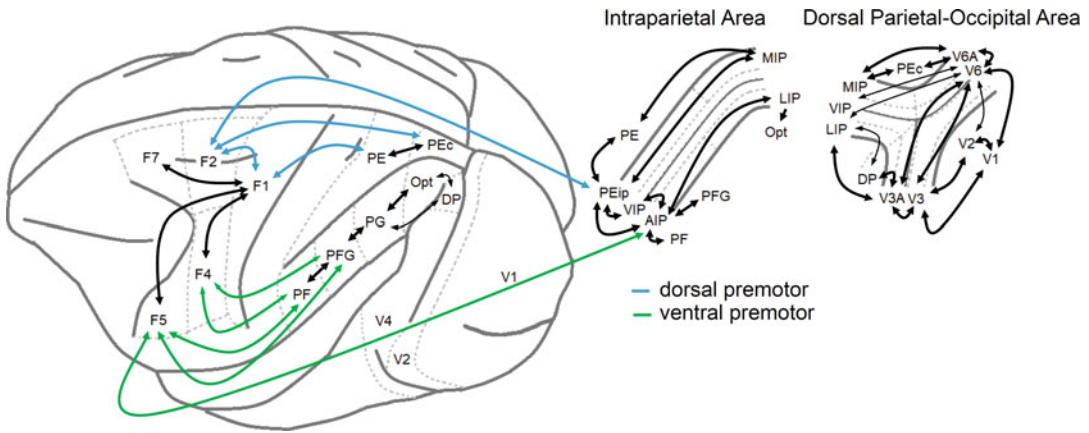
through the many extrastriate cortical areas, forming parallel, though interconnected, subpathways within the dorsal and ventral streams (Ferrera et al. 1994; Kaplan 2004). The dorsal stream predominantly receives input from the M subpathway, whereas the ventral stream receives a more balanced input from the P and M subpathways (Ferrera et al. 1994). A major target of the M pathway are cells in layer 4Ca in V1, which send projections to cells in layer 4B in the same area. Neurons in layer 4B are strongly connected to two of the major “tributaries” to the dorsal stream, V5 and V6 (Ferrera et al. 1994; Gamberini et al. 2015).

Extrageniculostriate Visual Pathway

A second visual pathway to the dorsal stream involves the SC and pulvinar. The medial, central, and posterior nuclei of the inferior subdivision of the pulvinar receive direct visual input from retinal ganglion cells. The posterior and central-medial nuclei of the inferior pulvinar receive a secondary source of retinal input via the superficial layers of the SC. The medial, central-medial, and posterior nuclei of the inferior pulvinar project to extrastriate visual cortical areas that are located in and around the posterior middle temporal sulcus, including V5. The central-medial nucleus of the inferior pulvinar projects to another dorsal stream tributary V3A (Kaas and Lyon 2007).

Extrastriate Visual Cortical Area “Tributaries” to the Dorsal Stream

The extrastriate visual areas that send major projections to PPC structures of the dorsal stream are V3, V3A, dorsal prelunate gyrus (DP), V5, and V6 (see Fig. 1). V3 is a heavily-myelinated region that occupies the fundus of the lunate sulcus (LS) extending medially into the occipital-parietal sulcus (OPS). V3 lies in the posterior bank and fundus of the LS. V3A lies anterior to V3 on the anterior bank of the dorsolateral aspect of the LS and on toward the juncture of the LS and OPS. Both V3 and V3A receive visual input from V1 and V2. V3A predominantly projects to dorsal



Dorsal Stream, The, Fig. 1 Dorsal stream structures in the occipital and posterior parietal cortex and their connections to motor and premotor cortical structures in the frontal lobe. Not shown are the connections that involve V5 and its satellites, a dorsal stream tributary structure buried

in the caudal aspect of the superior temporal sulcus. Two major frontoparietal pathways of the dorsal stream, the dorsal and ventral premotor connections, are color coded blue and green, respectively

stream structures, whereas V3 innervates structures in both the dorsal and ventral stream (Felleman et al. 1997). V5 is located in the posterior aspect of the superior temporal sulcus and is characterized by dense myelination and its reciprocal connections with V1. V5 is part of a complex of additional neighboring visual areas which include the medial temporal sulcus (MST) and the fundus (floor) of the superior temporal sulcus (FST; Born and Bradley 2005). Area V6, another densely myelinated area, is located in and around the juncture of the OPS, IPS, and the LS, occupying the fundus and lower anterior bank of the OPS and posterior to the medial bank of the IPS toward the medial wall of the occipital cortex. Approximately half of its connections are with V1, V2, V3, and V3A; the remaining connections are with dorsal stream structures in the inferior and superior parietal lobule (IPL and SPL, respectively). There are no known direct connections between V6 and any ventral stream structures. Similar to V5, the heavy V1 projection to V6 originates in the M-dominant layer 4B (Gamberini et al. 2015). Thus, the connections of areas V3A, V5, and V6 can deliver visual input relatively quickly to two subpathways in the dorsal stream of the PPC, a dorso-lateral pathway in the IPL and a dorso-dorsal pathway in the SPL.

Reciprocal Subpathways Between Premotor Cortex and the Posterior Parietal Cortex

Dorso-Lateral Pathway

The dorso-lateral pathway is comprised of a number of structures in the IPL and IPS. The lateral surface of the IPL is parcellated along a posterior-anterior axis into areas Opt, PG, PFG, and PF. Medial to PG on the lateral bank of the IPS sits area LIP, and medial to PFG and PF, again on the lateral bank of the IPS but anterior to LIP, sits area AIP (Rizzolatti et al. 1998). Generally, each area within the IPL is strongly reciprocally connected with their immediate neighbor and less well connected with IPL areas beyond that neighbor. Areas PG, PFG, and PF are heavily interconnected with the parietal operculum, but Opt is not. LIP is not connected to its medial neighbors PG or PFG (Rozzi et al. 2006). LIP is reciprocally connected with its anterior neighbor, AIP. AIP is well interconnected with its neighbors PF and PFG. V3A sends a major projection to LIP and a minor projection to the ventral bank (fundus) of the IPS (VIP) (Nakamura et al. 2001). V5 and MST project to VIP and to Opt (Born and Bradley 2005; Rozzi et al. 2006). V6A projects to areas PG, Opt, and LIP (Gamberini et al. 2015).

The IPL structures of the dorso-lateral pathway form a ventral-premotor (PMv) cortical circuit. PMv lies posterior to the inferior branch of the arcuate sulcus and anterior to primary motor cortex (F1). PMv is comprised of two major subregions positioned along dorsoventral and rostro-caudal axis, F4 and F5, both of which are reciprocally connected with F1 (Rizzolatti et al. 1998). Areas PF and PFG are more heavily reciprocally connected with F5 than with F4 (Rozzi et al. 2006). Areas F5 and PF possess mirror neurons that respond to object-directed grasps performed by the self and those performed by others (Rizzolatti et al. 1998). AIP, along with its medial neighbor, PEip in the SPL, is predominantly connected to F5, whereas VIP is predominantly connected with F4 (Rizzolatti et al. 1998). LIP is reciprocally connected with the supplementary eye fields of F7 and the frontal eye fields, both of which are premotor structures in the frontal cortex (Rizzolatti et al. 1998; Nakamura et al. 2001).

Dorso-Dorsal Pathway

The dorso-dorsal pathway is comprised of a number of structures in the SPL and the medial bank of the IPS (MIP). V6A receives much of its visual input from V6 and is a major input node to its neighboring dorsal stream structures in the SPL which includes the medial bank of the IPS (MIP), area PE, which occupies much of the dorsal SPL, and the mesial side of area PG (PGm) anterior to V6A (Gamberini et al. 2015). Although the dominant PPC projection of V3A is to LIP, it also projects to the medial bank of the intraparietal sulcus (MIP). V6A projects to MIP, PGm, and the posterior subregion of PE (caudal PE or PEc). PEc is reciprocally connected to the neighboring somatosensory-related subregion of PE, located anterior to PEc, and the posterior cingulate area on the mesial PPC (area PEic; Gamberini et al. 2015).

SPL structures of the dorso-dorsal pathway form a dorsal-premotor (PMd) cortical circuit. PMd is located above the superior branch of arcuate sulcus and is comprised of two major subregions along an anterior-posterior axis, F7 and F2. PMd is reciprocally connected with F1 (Rizzolatti et al. 1998). SPL area PGm is reciprocally connected with F7,

whereas SPL areas PEc, PE, and MIP are reciprocally connected with F2 (Gamberini et al. 2015; Rizzolatti et al. 1998). Area PE is also reciprocally connected with primary motor cortex, area F1 (Rizzolatti et al. 1998).

Function

Many dorsal stream structures contain sensory, motor, and sensorimotor cells. Sensory cells are often sensitive to motion, orientation, or shape, whereas motor cells are often sensitive to different configurations of particular effectors such as the eyes, mouth, arm, wrist, or hand. For example, the response of some cells in V3A, V6A, and LIP depend on the position of the eyes in their orbit (Gamberini et al. 2015). Sensorimotor cells are often sensitive to both sensory and motor task features. Cells in areas V5 and V6 are sensitive to the direction, orientation, and speed of moving stimuli (Born and Bradley 2005; Gamberini et al. 2015). Cells in VIP are sensitive to stimuli moving toward or away from the viewer, arm movements toward and away from the body, and tactile stimulation to particular areas of the face (Rizzolatti et al. 1998). Cells in V6A are sensitive to the arm and hand movements performed when reaching for targets or grasping objects (Gamberini et al. 2015). Cells in AIP is sensitive to particular combinations of object shape and the hand and finger configurations recruited during grasping (Rizzolatti et al. 1998). Cells in the haptic areas PE and PEc are sensitive to combinations of joint configurations and tactile stimulation and are thought to provide F1 with information about body position necessary for the control of limb and body movement (Rizzolatti et al. 1998).

Conclusion

The dorsal stream is a hierarchical network of parallel cortical structures in the occipital cortex and PPC of the primate brain and receives major sensory input from visual and somatosensory cortex. Proposals concerning the nature and content of the operations performed in the dorsal stream

have been an area of active research for decades. Contemporary accounts focus on a number of different roles which are perhaps best summarized as *sensorimotor* and *sensorispatial* and would include goal-directed and object-interactive movements, spatial navigation, spatial working memory, action observation and recognition and movement planning (Kravitz et al. 2011; Rizzolatti et al. 1998).

Cross-References

- [Frontal Cortex](#)
- [Mirror Neurons](#)
- [Nonhuman primates](#)
- [Retina, The](#)
- [Ventral Stream, The](#)

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Dorsal Visual Pathway

- [Dorsal Stream, The](#)

Douglas Kenrick

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Synonyms

[Author](#); [Evolutionary psychologist](#); [Psychologist](#); [Researcher](#); [Social psychologist](#)

Definition

Douglas Kenrick is a president's professor of social psychology at Arizona State University (ASU). He received a BA in psychology from Dowling College (1970) and a PhD (1976) in social psychology from Arizona State University under the tutelage of Robert Cialdini. Kenrick then served as an assistant professor of psychology at Montana State University before coming back to ASU. In 2018–2019, Kenrick served as president of the Human Behavior and Evolution Society. He has authored over 200 highly cited academic articles, 2 textbooks, and 2 popular books – *Sex, Murder, and the Meaning of Life* (2011) and *The Rational Animal* (2013, with Vlad Griskevicius) – as well as numerous edited volumes and invited book chapters. He is well

known among colleagues, students, collaborators, and anyone who has attended any of his talks, as being extremely insightful and funny. His wit and guts are undisputedly unmatched by any academic. In a now-legendary 2000 Human Behavior and Evolution Society plenary presentation, Kenrick delivered the entire 45-min talk in a deeply-southern Baptist preacher's accent and left a standing-room-only audience rolling with laughter in their seats and in the auditorium aisles.

Introduction

A favorite Kenrick quote is from Oscar Wilde, "We are all in the gutter but some of us are looking at the stars." A glimpse of his past indicates how a particular fondness for this quote may have come about. Douglas Kenrick was born in Queens, New York, into a family and environment hardly befitting to a future eminent scholar. As Kenrick openly recounts, his friends were switchblade-carrying greasers, and his father and brother both rightfully earned places in Sing Sing maximum security prison. Kenrick himself avoided life imprisonment by keeping in check his fantasies about killing his stepfather (but later used insights gained from this experience to investigate homicidal fantasies; Kenrick and Sheets 1993). He was, though, expelled from two high schools and put on academic probation at a community college. Somehow, in the midst of this unpromising life path, Kenrick developed a determination to break from family tradition and environmental influences and developed a keen interest in academics.

In this entry, we cover some of the many areas in which Kenrick has contributed important insights.

Personality

In his earlier work, Kenrick published an influential paper addressing a major debate on personality and the situation and how personality traits do actually meaningfully predict behavior (Kenrick and Funder 1988). Another paper challenged the

presumption that personality traits were weak predictors of behavior, by showing that traits which people rated high in self-rated observability and consistency yielded high agreement among self, parent, and peer ratings (Kenrick and Stringfield 1980).

Age Preferences

Together with former graduate school classmate Richard Keefe, Kenrick published several papers detailing people's minimum and maximum age preferences as indicated in their personal advertisements (Kenrick and Keefe 1992). They found that while women of all ages tend to look for mates at their own age or up to a few years older, men tended to want mates who are increasingly younger compared to their own age. Marriage statistics, as Kenrick found, fit this pattern quite nicely. Of particular note, teenage boys found women older than them to be most attractive, despite that those women did not have any interest in them (Kenrick et al. 1996). This finding countered the sociocultural notion that age preferences reflect men wanting to control women and younger women are simply easier to control. Instead, the entire pattern of findings on age preferences was consistent with an evolutionary psychological explanation that sex differences in age preferences reflect males having evolved to value female fertility and reproductive value, which peaks at age 23, and females having evolved to value men's social status and resources, of which older men have more.

Mate Preferences

Aside from age preferences, Kenrick has also investigated mate preferences for other traits, finding support for an important qualification on applying parental investment theory to humans. Using a minimum percentile preference paradigm, Kenrick investigated mate preferences across various types of relationship durations (Kenrick et al. 1990, 1993). Of particular note, he found that while men and women tend to have

similarly high minimum requirements across various types of relationships for traits like intelligence, they differ sharply when the relationship is purely sexual. That is, while women retain their high standards, men relax their standards considerably. As Kenrick pointed out, this sex difference reflects minimum differences in obligatory parental investment (Trivers 1972), where women but not men bear potential costs of pregnancy so women have evolved to be more selective and cautious than men for casual sexual partners. However, when men and women have evolved to invest similarly high as in committed, long-term relationships, both sexes are equally selective about their partners.

Another interesting and relevant line of work featured contrast effects. That is, when men view pictures of attractive, naked women – as in *Playboy*, *Penthouse*, or *Hustler* centerfolds – they subsequently find normal people and their own mates to be unattractive (Kenrick et al. 1989). Importantly, such effects are not limited to nude erotica, and the implications extend beyond high school boys giving lower ratings to their peers or wife. In a series of insightful follow-up studies, Kenrick and colleagues found that when exposed to facial photos of attractive women, women feel worse about their own mate value, and men feel less committed to their current partners. Similarly, when exposed to descriptions of socially dominant men, men feel worse about their own mate value, and women feel less committed to their current partners (Kenrick et al. 1994; Guttieres et al. 1999).

Together, these findings support the idea that people's view of themselves, their mating standards, and their relationship commitment, are indexed on – and can be sabotaged by – the perceived value of people in their environment. Furthermore, what constitutes value is sex-differentiated according to what traits are most adaptively beneficial to have in oneself as well as in one's partner. While this process would have been adaptive in the ancestral environment where anyone that one encountered was an actual potential mate or competitor, in the modern world, it leads to problems. Specifically, we now encounter thousands of still or moving images of beautiful

models and individuals. As if that's not enough to make us feel really bad about ourselves and our mates, technology now allows photos to be instantly beautified, thereby intensifying the effects of our automatic social comparison mechanisms (Yong et al. 2017).

In yet another line of work on mate preferences, Kenrick and Li solved a paradox in the literature. Evolutionary theorists have argued that physical attractiveness is a cue to female fertility and that a man's social status is a cue to his ability to provide resources critical for offspring survival (e.g., Buss 1989; Symons 1979). Without these traits, reproduction and offspring survival in an ancestral environment are not possible, respectively. Yet, although empirical work shows sex differences in the predicted directions for mate preferences regarding physical attractiveness and social status, numerous mate preference surveys indicate that these traits are not considered to be particularly important. To resolve this paradox, Kenrick and Li introduced a budget allocation methodology to constrain people's selection of traits (Li et al. 2002; Li and Kenrick 2006). When budgets are low and choices are highly constrained, men prioritized physical attractiveness above other traits, and women prioritized social status above other traits for long-term mates. However, when budgets were higher and choices were less constrained, men and women favored other traits. Thus, for long-term mates, men regard physical attractiveness as a necessity, and women regard social status as a necessity. Other traits are considered luxuries – they are important only after necessities can be obtained in sufficient quality.

Dynamical, Complex Systems

Kenrick's foray into dynamical systems reflects his unique ability to see connections at the big-picture level and the courage to go forward with one's convictions. Kenrick uniquely saw how evolutionary psychology, social psychology, and dynamical systems (complexity theory) could be meaningfully combined. At the time, many individuals doubted these ideas. But

Kenrick persisted, and these ideas were endorsed by founders of evolutionary psychology at the 1999 HBES conference and made for a highly cited *Psychological Review* paper (Kenrick's second at this very top journal; Kenrick et al. 2003). The article theorized and demonstrated through simulations that many of the social patterns found at the group level stem from individuals following simple decision rules but interacting with other individuals using the same decision rules. The decision rules are subject to laws of natural selection and process as input the social environment. In turn, the evolved decision rules and how they play out in this space influences the group-level patterns that emerge in the social environment.

Fundamental Motives

In that *Psychological Review* paper (Kenrick et al. 2003), Kenrick identified six major social domains that characterize human life and broadly represent what humans evolved to do: coalition formation, social status, self-protection, mate choice, relationship maintenance, and parental care. Across several papers published with various former students including Joshua Ackerman, Vaughn Becker, Jessica Li, Jon Maner, Jill Sundie, and Vladas Griskevicius, Kenrick examined how activating fundamental motives like mating can influence a host of decisions in seemingly unrelated areas such as conspicuous consumption (Griskevicius et al. 2007; Sundie et al. 2011), conformity (Griskevicius et al. 2006b), creativity (Griskevicius et al. 2006a), economic decisions (Li et al. 2012), facial recognition (Ackerman et al. 2006), interpersonal perception (Maner et al. 2005), and threat perception (Becker et al. 2010). Much of this work is summarized in one of Kenrick's popular books, *The Rational Animal: How Evolution Made Us Smarter Than We Think* (Kenrick and Griskevicius 2013).

More recently, Kenrick took on the ambitious task of rewriting Maslow's hierarchy of needs from an evolutionary perspective (Kenrick et al. 2010). In this highly cited and controversial work, Kenrick replaced the original need levels with

fundamental motives, arguing that parenting, not self-actualization, occupies the very top level.

Conclusion

Douglas Kenrick started out on a path leading nowhere at best and death row at worst. Yet, he went on to become a one of the most influential social psychologists and evolutionary psychologists. On this journey from the gutter to academic stardom, Kenrick has published many important works, leading the world in providing interesting and important big ideas and insights into human behavior and human nature. This entry has covered some of the major areas that Kenrick has examined, but there are many other important papers and topics not mentioned here. Much of Kenrick's work and the surrounding background and inspiration for the work can be found in Kenrick's book *Sex, Murder, and the Meaning of Life* (Kenrick 2011). Just as importantly, Kenrick has induced countless individuals to laugh out loud along the way, whether in papers (e.g., Kenrick 1995), academic talks (e.g., Kenrick 2000) and speaker introductions (Kenrick 1994), or office meetings. At this point, the learned world awaits Kenrick's next big idea as well as his next stand-up routine. In the meantime, readers can tune into Kenrick's insightfully entertaining blog at Psychology Today. Here is one to check out: www.psychologytoday.com/us/blog/sex-murder-and-the-meaning-life/200912/how-the-dawkins-stole-christmas.

Cross-References

- Age Differences in Marriage Partners
- Evolutionary Hierarchy of Needs
- Evolutionary Social Psychology
- Fundamental Motives
- Lowering Partner Standards in a Short-Term Mating Context
- Men's Mate Preferences
- Older Men
- Preferences in Long- Versus Short-Term Mating

- [People's Responses to Personal Ads](#)
- [Women's Mate Preferences](#)

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Downfall of “Tall Poppies”

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Synonyms

Envy; Inferiority; Resentment; Schadenfreude; Status-leveling

Definition

A status-undermining misfortune suffered by another or others of higher relative status, or “tall poppies.”

Introduction

Higher-status people enjoy greater access to high-quality mates and other resources than those of lower status (Buss 1999). Thus, people have evolved to maximize their status relative to competitors, as natural selection favors people with greater reproductive success than others in the local environment (Buss 1999, 2000). One way people of lower status can decrease the status gap between themselves and their rivals is prestige-enhancing skill building – that is, they can “build themselves up.” Another way to accomplish the same status-leveling goal, however, is by promoting status-decreasing misfortunes among one’s rivals, thereby leveling the others down (Buss 1999, 2000; van de Ven et al. 2009; van de Ven et al. 2014). The focus of this entry will be on the latter route to narrowing fitness-jeopardizing status gaps between the self and others – as Buss (1999) noted, “The pleasure people feel in a rival’s misfortunes may act as a motivational mechanism to promote those misfortunes” (p. 367), an idea later supported empirically by social neuroscience research (e.g., Cikara et al. 2011).

“Tall poppies” are high-status people whose outstanding achievements and talents make them stand above the rest of the crowd. Given the crucial role of relative status in determining reproductive success, it is little wonder that literary references to the *downfall* of such tall poppies date to at least the lifetime of the Roman historian Livy, who referenced the story of King Tarquinius decapitating the heads of the tallest poppies in his gardens. That symbolic message was relayed to his son, who proceeded to bring the rebellious state of Gabii to heel by ridding it of its leaders, or tall poppies (Feather 1994). In part as a response to the widespread belief in Australia that Australians particularly enjoy seeing tall poppies fall, Australian social psychologist

Norman Feather (1989, 1994, 2012) pioneered research on people's reactions to tall poppies being cut down to size via a number of different sorts of misfortunes under varied circumstances. This research led to the identification of key determinants of reactions to misfortunes befalling high-status people, such as the perceived deservedness of those misfortunes.

As evolutionary psychological thinking and abundant empirical research across many different cultures suggests, "tall poppy syndrome," or the desire for exceptional, high-status people to suffer misfortunes, is far from a uniquely Australian phenomenon. A common Japanese aphorism, for example, states that "The nail that stands out gets pounded down." Interestingly, Feather and McKee (1993) found that Japanese people expressed a greater tendency toward favoring the downfall of tall poppies than did their Australian counterparts, who tend to have relatively more independent self-construals and thus a greater comfort with those whose outstanding achievements distinguish them from others.

A number of different reactions to the downfall of tall poppies are possible, including feelings of sympathy or pity. This entry, however, will focus on *schadenfreude*, or joy over the misfortune, and primary antecedents of it suggested in the empirical literature. These will include (1) inferiority, (2) hostility, (3) unfairness and deservingness, (4) envy, and (5) perceived gain.

Inferiority

Self-esteem likely evolved as a "sociometer," or indicator of one's social value and chances of social exclusion, which can have negative consequences indeed for one's fitness (Leary et al. 1995). As such, people are exquisitely attuned to signals of their social value, which is reflected in part by their position in the status hierarchy (Smith 2013). Relative inferiority in self-relevant domains is likely to threaten self-esteem and lead to painful feelings of inferiority, especially when the advantaged person is both similar and psychologically close to the disadvantaged person (van Dijk et al. 2011a). That painful

inferiority, however, should motivate status-leveling corrective action, as one's status may be genuinely threatened, and a self-relevant goal (e.g., of status-enhancing professional achievement) has been frustrated by the other's superiority (DelPriore et al. 2012; Floyd et al. *in press*; Frijda 1988; Hill and Buss 2006).

Van Dijk and colleagues (2011b) found that students felt threatened following failure on a self-relevant test of academic ability, priming them for joy over the academic failure of a high-flying, star student. In line with evolutionary theory, however, prior failure (as opposed to success) on the test led to increased *schadenfreude* *even when the domain of the misfortune was unrelated to the domain of relative inferiority*. Both domain-relevant and domain-irrelevant misfortunes can reduce painful status gaps, as status is often based on excellence or superiority in a variety of domains, such as interpersonal popularity, intelligence, athleticism, or physical attractiveness. The downfall leads to happiness because it can help repair threatened self-esteem – one's social value has increased relative to an erstwhile superior, similar other.

In addition to acute self-esteem threat, chronically low self-esteem sets the stage for increased *schadenfreude* when a "taller" poppy suffers a misfortune, although self-affirmations (e.g., reflecting on one's values or important aspects of one's life) can substantially weaken that tendency (van Dijk et al. 2011b). One reason self-affirmations might reduce self-threats (whether acute or chronic, domain-specific or global) is that they may help people convince themselves that their standing is not particularly threatened by relative inferiority to taller poppies, whether or not that perception reflects reality.

Inferiority's effects on *schadenfreude* are not limited to interpersonal situations; inferiority, and indeed other antecedents of *schadenfreude*, such as disliking, deservedness, and resentment, has also been found to operate at an intergroup level (Hoogland et al. 2015; Leach and Spears 2008). For example, in a study of students' reactions to the performance of their university quiz bowl team, Leach and Spears (2008) found that when the students' team was defeated, an emotional

process called *ressentiment* occurred, whereby inferiority feelings were later transmuted into vengeful, hostile feelings toward teams who were not involved in their team's defeat. As a result of *ressentiment*, when a third-party team lost, *schadenfreude* resulted despite that team's having had nothing to do with their team's loss (Leach and Spears 2008). Notably, this suggests the possibility that, at a deeper level, the *schadenfreude* toward the third-party team was driven by a perceived reduction in the status of a possible future competitor and thus a perceived increase in the relative status of the students' own group.

Hostility

Ill-will engenders *schadenfreude* in both intergroup (Hoogland et al., 2015; Leach and Spears 2008) and interpersonal (Feather 1994; Hareli and Weiner 2002) situations. For example, hostile feelings of anger, dislike, and hatred are each other-directed negative emotions that predict *schadenfreude* in reaction to both mild and severe misfortunes suffered by average and superior others alike (Hareli and Weiner 2002; Smith and Kim 2007). That hostility and subsequent *schadenfreude* may or may not be driven by envy (van de Ven et al. 2009, 2014). For example, even during a strong year for a perennially excellent college basketball team, in-group identification-based hatred of a rival basketball team was positively associated with *schadenfreude* following a very severe misfortune – an excruciatingly painful, career-ending injury suffered by a player on the rival team (Hoogland et al., 2015). Given such findings, it may come as no surprise that hostility-based *schadenfreude* is related to both passive and active status-leveling behaviors, including withholding of help (Hareli and Weiner 2002) and negative gossip and interpersonal rejection (Duffy et al. 2012).

Perceived Unfairness

People with poorer relative outcomes often believe them to be unfair, a judgment frequently

coupled with the appraisal that others with superior deserts enjoy them unjustly. Such unfairness judgments can be classified as either objectively or subjectively unfair, although objectively unfair advantages are, by that fact, also subjectively unfair. Objectively undeserved advantages are those that, by social consensus, are considered to be unfair, such as advantages gained by cheating, while subjectively undeserved advantages feel unfair despite being considered fair by most others in one's culture (Smith and Kim 2007). Subjectively unfair advantages include those largely outside of personal control, such as greater intelligence and physical attractiveness, often making them seem unfair to a disadvantaged person despite being "objectively" fair in others' eyes. That is, the perceived controllability of a (dis)advantage often drives subjective fairness judgments (Floyd et al. [in press](#)).

Making a distinction between objectively and subjectively unfair advantages can be useful to understanding and predicting the consequences of such justice-related judgments on *schadenfreude*. When another's advantage is perceived to be objectively and subjectively fair, the resulting reaction is likely to be a hostility-free motivation to move oneself up, and sympathy, not *schadenfreude*, should result if the justly advantaged other suffers a misfortune (van de Ven et al. 2014). Appraising another's advantage as objectively unfair, however, is especially likely to foster resentment, a robust predictor of *schadenfreude*, along with relatively open actions against the person with the unjust advantage, including public expressions of righteous indignation (Feather 2012; Krizan and Smith 2014). Judging that advantage as subjectively unfair, on the other hand, is likely to engender hostility-tinged, malicious envy and more secretive actions aimed at cutting down the unfairly advantaged tall poppy. To openly oppose another's "objectively" fair advantage would risk negative consequences, such as being branded "envious" by others, counterproductively widening the status gap between the self and the *subjectively* unfairly advantaged other. In short, the perceived objective and subjective fairness of a tall poppy's relative advantage partially determine which emotions

and behavioral tendencies follow from that advantage. These include the extent to which schadenfreude and refusing to help, rather than sympathy and helping, will characterize the disadvantaged person's emotions and actions following the downfall of the tall poppy.

Perceiving another's relative advantage as unfair and therefore undeserved (e.g., because he or she did not expend much effort to attain that advantage) enhances schadenfreude and dampens sympathy following the fall of tall poppies, as do judgments of personal responsibility for the misfortune itself (Feather and Sherman 2002; Feather 2012). In fact, the perceived deservedness of both the tall poppy's advantage and the misfortune may be influenced by a multitude of factors, and deservedness perceptions frequently mediate links between schadenfreude and its antecedents, including envy, dislike, and resentment (Feather 2012). Deservedness may therefore play a central role in many, if not most, instances of schadenfreude following the downfall of a tall poppy.

Envy

Despite the intuitive link between envy and schadenfreude, envy's role in reactions to the downfall of tall poppies has been a topic of perennial controversy in the empirical literature, in part because some empirical studies have yielded an association between envy and schadenfreude, while others have not (Hoogland et al. *in press*). The seemingly puzzling null results were likely a consequence of the widely varying ways in which envy has been conceptualized. For example, Smith and Kim (2007, p. 46) defined envy as "An unpleasant, often painful emotion, characterized by feelings of inferiority, hostility, and resentment caused by an awareness of a desired attribute enjoyed by another person or group of persons." When envy includes hostility and resentment, along with a motivation to pull the other down, it is considered "malicious envy," which does predict schadenfreude; however, another type of envy, which occurs equally frequently, is "benign envy," which, though painful, includes no ill-will and instead inspires self-improvement efforts (van

de Ven et al., 2011, 2014). Not surprisingly, benign envy does not predict schadenfreude following advantaged-others' misfortunes – such unpleasant events are not seen as deserved, the advantages themselves are perceived to be fair, and perceptions of personal control over the situation tend to be high, as self-improvement seems possible. Notably, that self-improvement need not be in the domain of perceived relative inferiority, supporting the evolutionary psychological hypothesis that the pain of envy exists to motivate people to improve their relative status, whether via pulling others down (malicious envy) or by building themselves up (benign envy), irrespective of whether such status-leveling actions impact the domain of inferiority itself (DelPriore et al. 2012; Hill and Buss 2006; van de Ven et al. 2009, 2014).

Both advantaged and disadvantaged parties incur envy-related costs in ways tending to maximize their long-term relative outcomes. Tall poppies, for example, are well aware of the possibility that others envy them, and therefore take steps to prevent others from either (1) actively attempting to cut them down to size or (2) failing to provide assistance should they suffer a misfortune. Behaviors aimed at obviating such undesirable outcomes, however, often entail personal costs. They are therefore only performed when perceived as necessary. For instance, fear of malicious envy, but not harmless, benign envy motivates costly prosocial behaviors benefiting lower-status people, thereby reducing their invidious hostility (van de Ven et al. 2010). Just as placating the less fortunate can be costly, *expressing* envy in the hopes of receiving a larger share of a resource can also be costly. For example, envy will be especially pronounced when another possessing an easily shareable resource is nonetheless *not* expected to share it (Inoue et al. 2015). In such instances, the benefits of making envy-driven demands for divisible resources from people otherwise reluctant to share them are relatively likelier to outweigh the costs (e.g., possible reputational damage) than when such demands are either expressed toward (1) someone who already appears inclined to share a divisible resource or (2) someone who simply cannot

share a resource because it is very difficult or impossible to do so (Inoue et al. 2015). In sum, both tall poppies and those looking up to them from below modulate their behaviors to maximize benefits while minimizing costs.

Gain

A final determinant of schadenfreude in response to the downfall of tall poppies is perceived personal or in-group gain. For example, sex-specific differences in joy over the mate-value-reducing misfortunes of potential intrasex competitors suggest that one of schadenfreude's functions may be as a mate-value-tracker (e.g., Colyn and Gordon 2013; see entry ► ["Schadenfreude"](#) for a review). Further, across several studies of reactions to minor and severe misfortunes suffered by an outgroup member, Hoogland and colleagues (2015) found that perceived in-group gain was an even more powerful and consistent mediator of schadenfreude in response to those misfortunes than dislike and resentment of the outgroup. Moreover, when competition and hatred are particularly intense, as is so often the case in political matters, perceived-gain-based schadenfreude may even occur in response to extreme misfortunes. For instance, many highly identified Democrats experienced some degree of schadenfreude when they learned of US troop deaths during the Second Iraq War, as they hoped those tragic losses would lead to Republicans' losing power and, ultimately, an end to the war (Combs et al. 2009).

Conclusion

Factors playing major roles in the degree to which people feel malicious joy or empathic sympathy when tall poppies fall include perceived inferiority to and hostility toward the tall poppy, the perceived unfairness of the tall poppy's advantage, the perceived deservedness of the misfortune itself, envy, and perceived personal gain as a result of the tall poppy's downfall. The operation of these factors, moreover, can be predicted on the

basis of evolutionary psychological theory. Accumulating empirical evidence suggests that schadenfreude is a cross-culturally universal emotion that evolved to motivate adaptive responding when misfortunes befall others, perhaps especially those of higher status.

Cross-References

- [Schadenfreude](#)
- [Self-Enhancement Relative to Others](#)

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Dowry

- [Bridal Cost](#)
 - [Nuptial Gift](#)
-

Drama

- [Fiction](#)
-

Drug Abuse

- [Substance Use Disorder](#)
-

Drug Addiction

- [Substance Use Disorder](#)
-

Drug Dependence

- [Substance Use Disorder](#)
-

Drug Misuse

- [Substance Use Disorder](#)

Drug Sensitization

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Synonyms

Sensitization

Definition

An increase in drug effect upon continual exposure to a drug in the organism, which was previously exposed to the drug.

Introduction

Drug sensitization is a process frequently encountered in the literature of the field of addictions and pharmacology, and it is an essential process towards the understanding of drug action and use.

Drug Sensitization in Substance Abusers

With repeated drug administration, gradual and incremental neuroadaptations are produced that make animals hypersensitive to the specific drugs. Even though users or abusers will be keeping the same dosage levels, drug effects will be greater and greater, therefore they would become intoxicated even in small doses. Using repeatedly a drug but with some pauses in between causes greater sensitization compared to taking a single dosage or even taking repetitively the drug. Moreover, sensitization is promoted if periods of use are alternated with periods of abstinence. When a person who is sensitized let's say to cocaine and abstains from use for some time, he/she is at risk of fatal overdosing at reuse (Steketee & Kalivas 2011;

Robinson & Berridge 2008). Known addictive substances, that sensitization has been observed in, are cocaine, amphetamines, morphine, nicotine, and even alcohol; importantly, not all drugs subject to sensitization, mostly stimulants. In addition, the selected route of drug administration as sensitization is influenced by the speed or the time it takes for a drug to reach the brain. Sensitization in the case of drugs is long lasting with its effects on behavior and cognition lasting for years even with abstinence; however, factors such as the time lapse between dosages, the choice of drug, the age and sex of the user, and genetics influence the strength of sensitization. Due to these factors, vulnerability to sensitization differs between individuals Steketee & Kalivas (2011). That provides an insight into the long-asked question of why some users become addicts while others do not get addicted. The sensitization of behavior and other psychological or psychomotor functions implies neural sensitization. Drugs seem to alter or reorganize neural systems and neurotransmitters, and even though causal relationships are yet to be established, neuroadaptations seem permanent. The permanency of changes in neurotransmitter circuits have crucial implications on the matter of cravings and relapse. Of special importance is the sensitization of the mesolimbic pathway of the mesotelencephalic dopamine system. Since dopamine is responsible for the motivation to go after pleasure and happiness and fulfill our “wants,” drugs come to jeopardize this process by making dopamine hyperreactive, consequently increasing the prominence of drug cues, hence the intense cravings Robinson & Berridge (2008). The aforementioned comprise the “Incentive Sensitization” theory of addiction developed by Berridge and Robinson (1998) and is noteworthy of further reading.

Conclusion

Drug sensitization is a complex process influencing drug users in a cellular level and in consequence in a behavioral level.

Cross-References

- [Kindling](#)
- [Non-associative Learning](#)
- [Sensitization](#)

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Drugs and Rape on College Campuses

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Definition

The association, on and about college campuses, between psychoactive substance use and the use of force or threat of force to achieve penetration of an individual without their consent.

Introduction

The association between alcohol use and rape on college campuses is addressed in ► [“Alcohol and Rape on College Campuses”](#). This brief entry presents an evolutionary perspective on the possible role of other psychoactive substances in rape on and about college campuses, attending to potential interactions between the psychoactive

effects of these drugs and hypothesized rape and rape avoidance adaptations. As reviewed in *Alcohol and Rape on College Campuses*, surveys of college students suggest that among the types of sexual assault, unwanted sexual contact and coercion are most common, followed by incapacitated rape (i.e., completed rape while the victim was intoxicated) and then forcible rape (Fedina et al. 2016). Estimates of the prevalence of sexual assault, including rape, vary widely. Prevalence estimates for incapacitated rape have ranged from 1.8 to 14.2% for females and been observed at 1.9% for males, while forcible rape estimates have ranged from .5 to 8.4% for females and from .6 to .7% for males (Fedina et al. 2016). Fedina et al. (2016) contend that this variance stems from measurement and definitional differences. It is important to note that these estimates rest largely on samples of White, heterosexual, female students in traditional colleges – the prevalence of sexual assault among minority females may be higher and rape incidence is likely underestimated generally due to underreporting.

Drug Use and Rape

High profile cases of drug-assisted rape, along with high profile antispiiking campaigns, might give the impression that rape via spiking (i.e., administration of a psychoactive substance to a person without their consent) is relatively prevalent. However, research on toxicology consistently suggests that there are very few cases in which rape is occasioned by nonvoluntarily consumption of substances (Lovett and Horvath 2009). For instance, analyzing a large sample of suspected drug-assisted rapes, Scott-Ham and Burton (2005) found that 45% of cases involved alcohol, 32% involved illicit substances, and only 2% involved a sedative or disinhibiting substance that could be tied to nonvoluntary consumption. The results of studies across Europe, USA, and Canada indicate that alcohol is the substance that most often occasions sexual assault, running counter to media representations of the psychoactive substance-sexual assault connection (Horvath and Brown 2006; Lovett and Horvath 2009).

Notably, one study of college students in the USA found that only about 13% were aware of this fact (Crawford et al. 2008). Horvath and Brown (2006) raised the question of whether drug-assisted rape is in fact a misnomer – it brings to mind nonvoluntary consumption, but in most cases, drug-assisted rape actually implies self-intoxication through alcohol use and offender targeting of victims on the basis of their alcohol consumption.

Evolution, Drugs, and Rape

As noted in *Alcohol and Rape on College Campuses*, rape has been observed across all human cultures and males in many nonhuman species have evolved strategies to sexually coerce and rape females (McKibbin and Shackelford 2011). As in nonhuman species, human perpetrators of sexual assault are nearly always male and victims are most often female (Testa and Livingston 2009). Many psychoactive substances (e.g., cocaine and marijuana), like alcohol, can be disinhibiting and also sensitize salience through their effects on activity in the prefrontal cortex and dopamine transmission, respectively (George and Koob 2010; Robinson et al. 2013). Thus, the consumption of psychoactive substances other than alcohol may also increase the likelihood that some males will commit sexual assault by modulating brain activity such that cues to the execution of adaptations contributing to rape are amplified (for further discussion of this, see *Alcohol and Rape on College Campuses*). This might occur via effects on the perceived biological value of potential victims, diminished ability to shift attention away from perceived sexual opportunities, reduced capacity for inhibiting sexual arousal, and reduced awareness of the costs that could stem from rape. Also like alcohol, the consumption of other substances could inhibit the execution of rape avoidance adaptations in females (for discussion of female rape avoidance adaptations, see McKibbin and Shackelford 2011), making some females less likely to avoid strange men, avoidant of being alone, aware of their surroundings, and able to resist forcible rape.

Consistent with the possibilities raised above, consumption of drugs other than alcohol is also associated with sexual offending (Kraanen and Emmelkamp 2011) and prospective studies suggest that consumption of drugs such as marijuana also increases the risk for experience of rape (Messman-Moore et al. 2008).

Conclusion

Rape on college campuses has been linked to psychoactive substance use. This brief entry presented an evolutionary perspective on the possible role of drug use in rape on and about college campuses, reviewing evidence suggesting that drugs other than alcohol may similarly contribute to rape through their effects on the brains of would-be male rapists, as well as by interfering with the functioning of rape avoidance adaptations employed by potential female victims. This entry also attended to evidence that rape via spiking is quite rare and thus drug-assisted rape should generally be understood as offender targeting of females self-intoxicated through their consumption of alcohol and/or other drugs.

Cross-References

- ▶ [Alcohol and Rape on College Campuses](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Rape](#)
- ▶ [Rape and Dating](#)
- ▶ [Rape Avoidance](#)
- ▶ [Rape in Warfare](#)
- ▶ [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- ▶ [Sexual Coercion and Rape](#)
- ▶ [Victims of Violence](#)

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Dry Nurse

► Bottle Feeding

Dual Inheritance

► Daniel Dennett: A Review of His Evolutionary Work

Dual Inheritance Theory

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Synonyms

Culture-gene coevolution; Gene-culture coevolution; History of natural selection; Natural selection

Definition

Dual Inheritance Theory is a theoretical framework positing that human biology and behavior are influenced by two lines of inherited information: a genetic line, which all species inherit from their biological parents, and a cultural line, unique to our species, which we inherit from other members of our society.

Introduction

Dual Inheritance Theory was first developed by two population geneticists (Cavalli-Sforza and Feldman 1981) and an anthropologist and an ecologist (Boyd and Richerson 1985) as a set of formal mathematical models to describe the transmission and evolution of culture – beliefs, values, behaviors, technology, and other socially transmitted knowledge possessed by societies around the world. Both pairs of scholars drew on the rich toolkit of evolutionary biology that had so nicely described the rest of the natural world, extending it to explain humans as a new kind of animal. The theory identified the conditions that

lead any species to rely on social learning (learning from conspecifics) over individual or asocial learning (figuring things out by oneself); the ways in which social learning could transmit cultural information, copying biological parents (vertical transmission), peers (horizontal transmission), or other members of the parents' generation (oblique transmission); and the biases on what to learn and who to learn from – including payoff biases (e.g., copying successful individuals) and frequency biases (e.g., copying the majority). These models described how culture met the criteria for an independent adaptive evolutionary system: variation, transmission, and selection. Humans, they argued, have two lines of inheritance: (1) a genetic line, which all species inherit from their genetic parents, and (2) a cultural line, unique to humans, which we inherit from our societies. The secret to human success is cumulative cultural evolution – a package of knowledge, know-how, technology, beliefs, and behaviors, adapting and accumulating generation by generation, often outside conscious awareness, and beyond what even the brightest individual could create alone in a single lifetime.

In developing this framework, Cavalli-Sforza and Feldman and Boyd and Richerson expanded evolutionary biology to include the human animal and its social world; offered a formal mathematical toolkit that allowed scientists to develop theories about human behavior, psychology, and society in a manner consistent with the other natural sciences; and laid the foundations for a formal and general “Theory of Human Behavior.” In the following decades, the next generation of researchers expanded the set of models and compiled and created anthropological, archeological, economic, and experimental psychological evidence testing the various formal predictions (Chudek et al. 2015; Henrich 2016; Laland et al. 2010; Mesoudi et al. 2006; Muthukrishna and Henrich 2016).

Theories falling under the Dual Inheritance Theory framework have offered explanations for a wide range of phenomena, from infant cognition, norm psychology, and in-group ethnic biases at an individual level to the source of cross-cultural differences, relationship between

sociality and cultural complexity, and transitions between stable equilibria at a societal level. In an act of self-reflection, recent theories have also tackled the problem of innovation, offering an explanation as to why at least two groups of independent researchers developed Dual Inheritance Theory (Muthukrishna and Henrich 2016). Before discussing these processes, it would help to have some perspective on the history of evolutionary biology and psychology.

History

In 1859, Charles Darwin published *On the Origin of Species* laying out the theory and evidence for evolution by natural selection. The theory was far from universally accepted, and Darwin faced a great deal of hostility, not only from the religious but also from members of the scientific community. In 1864, physicist Lord Kelvin used the rate of cooling to calculate the age of the Earth as no more than 400 million years, an estimate which left insufficient time for evolution by natural selection. Given such opposition, evolution by natural selection did not become a dominant paradigm for some time, particularly in the psychological and behavioral sciences. Wilhelm Wundt, the father of experimental psychology, rejected the evolutionary approach altogether. However, evolution's impact was visible in some schools of early psychology. For example, the relationship of humans to other animals was assumed in George Romanes' work on comparative psychology and William James' search for human instincts.

In 1903, the heat released by radioactive decay was discovered, setting the stage for a revision of Lord Kelvin's calculations by an order of magnitude, leaving enough time for Darwinian evolution. Evolution by natural selection gradually became the bedrock of the biological sciences. The early twentieth century saw the mathematical formalization of evolutionary theory, most notably spearheaded by Ronald A. Fisher, Sewall Wright, and J.B.S. Haldane. During the 1930s, apparent inconsistencies between macroevolution and microevolution, between the rediscovered

discrete Mendelian genetics and both continuous population distributions (e.g., height) and gradual changes, were reconciled, creating a theoretical synthesis across a wide range of subfields of biology: *The Modern Synthesis*.

The Modern Synthesis was a milestone in the biological sciences, but the human and social sciences – including economics, anthropology, and psychology – were missing from this synthesis. As psychology transitioned through the behaviorist and then cognitive revolutions, the biological sciences, with evolution at its core, were largely ignored (with ethology as a notable exception). The psychological sciences had yet to fully incorporate the logic of evolution, biological approaches, and the formal mathematical toolkit.

Evolutionary approaches began to reenter psychology during the 1970s and 1980s. John Bowlby, as part of his work on attachment theory, coined the term *environment of evolutionary adaptedness* (EEA). The EEA referred to the environment to which organisms had adapted. Evolutionary psychologists have since explored in great detail the mismatch between the modern world and the human ancestral environment in Africa (human EEA). Evolutionary approaches also reentered psychology in testing the predictions of evolutionary logic that applied broadly to animals, including humans. For example, the implications of Robert Trivers' *Parental Investment Theory* (1972) was tested by several researchers including Martin Daly and Margo Wilson (Cinderella Effect) and David Buss (sex differences in jealousy). This early work relied on testing predictions from evolutionary biology generated using its standard toolkit. In 1992, anthropologists Jerome Barkow and John Tooby and psychologist Leda Cosmides edited *The Adapted Mind*, laying out additional research and new methodological approaches to identifying further human-specific adaptations to the human EEA.

Earlier attempts to directly expand the modern evolutionary synthesis to the social sciences more generally can be traced to biologist Edward O. Wilson's 1975 book *Sociobiology: The New Synthesis* that brought together a growing body of work to explain the evolutionary processes underlying social behaviors such as

communication, dominance, and altruism. In 1981, Wilson, along with his then postdoc, Charles J. Lumsden, published *Genes, Mind, and Culture*, an attempt to formalize some of the ideas Wilson had laid out in sociobiology as a step toward unifying the biological and social sciences (In a twist of history, Boyd and Richerson applied to spend time in Wilson's lab at around the time Lumsden was a postdoc. Wilson responded that his lab was full and their efforts ended up being independent.). It was in the same year, 1981, that Cavalli-Sforza and Feldman published their classic. In their book, the core tenets of evolution such as mutation, selection, and drift, along with the process of transmission, were used to create formal mathematical models of cultural transmission similar to those used in population biology. These models examined the conditions and factors facilitating cultural transmission and demonstrated its possible forms – namely, vertical transmission from one generation to the next and horizontal transmission between conspecifics. Soon after, in 1985, Boyd and Richerson took a similar approach, once again noting the similarities and differences between cultural transmission and biological transmission. Their research laid out the conditions and implications of biased cultural transmission – the role that learning biases have in the transmission of culture. Perhaps due to the independent disciplines in which they originated, throughout the 1990s, the traditions laid out by Boyd and Richerson and Cavalli-Sforza and Feldman proceeded largely independently from that laid out by Barkow, Tooby, Cosmides, and other evolutionary psychologists.

Dual Inheritance Theory and cultural evolution began to influence psychology through comparative and developmental work from figures such as Andrew Whiten and Michael Tomasello and their collaborators, as well as through the theoretical and experimental work of figures such as Joseph Henrich and Kevin Laland and their collaborators. The key aspects of Dual Inheritance Theory are an evolved psychology that undergirds our capacity for culture, the dynamics of cultural evolution, the selective pressure culture has exerted on our genes (culture-gene coevolution), and cultural-group selection.

Cultural Evolution and the Capacity for Culture

Dual Inheritance Theory is an extension of evolutionary theory (rather than an analogy) into the realm of culture. An adaptive evolutionary system, be it genes or a computer scientist's genetic algorithm, requires three factors: variation, transmission, and selection (Or more generally, variance reduction, such as genetic or cultural drift. While this is still evolution, for evolution to be adaptive, the variance reduction needs to be in an adaptive direction.). Humans have evolved abilities and proclivities that give our cultural system these three properties. Variation is easy – individuals do all kinds of things for all kinds of reasons: mistakes in copying, differential access to information and life experience, blind luck, and so on. The key lies in transmission and selection. The starting point is the tendency to rely on social learning.

In their 1985 classic, Boyd and Richerson laid out the environmental conditions that lead to any species relying on social learning. The answer lies in environmental variability. When the environment is highly stable, genes can adapt well. Consider the average amount of sunlight as a function of latitude. Although there is seasonal variability, as you move North the average amount of sunshine decreases. Rather than relying on culturally acquired information or individual learning, human skin color has genetically adapted to provide the appropriate amount of protection while also providing enough vitamin D through UV exposure. In the modern world of distant migrations, dark-skinned individuals in Northern latitudes generally require vitamin D supplementation, and lighter-skinned individuals in Southern latitudes generally require sunscreen. At the other extreme, when the environment is highly unstable, genes are unlikely to evolve at a rate fast enough to match the environmental change. In such unstable environments, genes for individual learning are favored, since the long-term past is not a good predictor of the future. Between these extremes is a Goldilocks zone where your parents and grandparents have knowledge worth paying attention to. As an example, consider a cyclical

drought. You may never have experienced a drought, but your parents and grandparents remember the last time there was a drought and where the village found water and what else they did to survive. In this Goldilocks zone of intermediate environmental variability, social learning is favored. These predictions were formally modeled in 1985, but the data to test this theory didn't emerge till ice core data was made available in the next two decades. The data fit nicely – climate variability increased around 3 million years ago, just as the *Homo* genus emerged. Of course, this argument predicts widespread social learning (which is what we observe; Hoppitt and Laland 2013). Social learning alone is not sufficient.

One form of social learning is imitation: humans tend to copy with *high fidelity*, often with an absent or incomplete causal model. An experiment by Victoria Horner and Andrew Whiten (2005) nicely illustrates this proclivity. Chimpanzees and human children were presented with two versions of a puzzle box with a reward inside. The experimenter presented a series of causal and irrelevant actions to access the box. When the box was opaque such that both chimpanzees and children couldn't distinguish between the causal and irrelevant actions, both imitated all experimenter actions. But when the box was transparent and the irrelevant and causal actions were easily distinguishable, the chimpanzees only copied the causally relevant actions. The children, in contrast, continued to copy all actions. More recent evidence suggests that children can distinguish between instrumental behaviors where all that matters is the outcome and conventional behaviors that are either normative or where a causal model isn't apparent. However, life is mostly made up of a world too complex to fully understand, and understanding is often not required – from cooking by copying family recipes without the need to understand the underlying biochemistry to using a computer without the need to understand the computer science and physics which drive it. Research by Herrmann et al. (2007) further illustrates the abilities and proclivities that underlie the capacity for culture through cognitive tests with human children,

chimpanzees, and orangutans. In the physical domain of space, quantiles, and causality, humans were no better than the other primates. But in the social domains of Theory of Mind, communication, and most clearly social learning, they thoroughly outcompeted their primate cousins.

Humans are highly reliant on high-fidelity social learning, but we don't copy arbitrarily; we learn selectively from successful, self-relevant and reliable sources of information. Much theoretical and experimental research in cultural evolution has identified a constellation of strategies and biases through which we acquire information. For example, we tend to copy experts with greater skill, those who are generally successful, and those who others are paying attention to (prestige). When these payoff biases exist, over time, the population acquires a package of the most adaptive beliefs and behaviors, so we also copy majorities and pay attention to changing frequencies (trends) in the population. Not all information is equally relevant; sometimes someone is a better model for you. We moderate these selective biases on self-similarity, such as sex and ethnicity. Children will often copy children only slightly older than themselves, since they provide behaviors more relevant to their personal ecology. Since not all sources of information are equally sincere, we also seek out costly and credibility-enhancing displays (CREDs) that increase our trust in the information. And because not all domains are equally important, we focus on certain content over others, such as dangers, mating-relevant information, reputational information and norms (Chudek et al. 2015).

The world in which we now find ourselves is more complex than any one of us can understand or recreate. Culture adapts to the local environment, including to aspects of the environment that are genetic. For example, our species gives birth to large-brained, helpless infants that require extra care. There are many cultural solutions to this core problem, from controlling female sexual access and forcing fathers to look after their children to the fatherless societies where brothers are expected to look after their sisters' children to societies with multiple fathers and corresponding partible paternity beliefs (Henrich 2016;

Muthukrishna and Henrich 2016). Similarly, genes will adapt to features of the environment that are highly stable, sometimes over short periods. Many of these features to which genes adapt are part of the cultural environment, leading to culture-gene coevolution.

Culture-Gene Coevolution

The classic case of genes adapting to cultural practices is lactase persistence, the uniquely human ability to process lactose beyond infancy. Drinking milk in infancy is a typical mammalian trait, but the ability to process lactose in adulthood is a uniquely human ability but found in less than a third of humans. The domestication of animals, a cultural practice, provided the selection pressure for such variation – milk is a rich source of calories and nutrients, and the ability to process it is highly advantageous, offering an evolutionary advantage to members of a society who could process it beyond childhood. Lactase persistence nicely tracks the domestication and herding of livestock. In an exception that proves the rule, lower levels of lactase persistence are present in populations that turned milk into lower-lactose products, such as cheese and yogurt, using culturally evolved milk-processing technologies. Other examples of culture-gene coevolution include processing of alcohol and other food types, and immunity and pathogen defense. Other human features, including language and our social learning abilities and proclivities, may also have been products of culture-gene coevolution adapting to ever-increasing levels of information (Laland et al. 2010).

Cultural-Group Selection

Cultural-group selection is one of the most misunderstood aspects of Dual Inheritance Theory (Richerson et al. 2016). The main sources of misunderstanding are perhaps the problems associated with genetic-group selection, what people think is being selected, and conflation between equivalence of mathematical accounting systems and causal processes.

Genetic-group selection is the idea that natural selection might act at the level of the group as well as at the level of the individual. Group selection would allow for behaviors that were good for the group at the expense of the individual. While in theory group selection might be possible, one key problem is that genetic groups often struggle to maintain their genetic boundaries, such that in the long run, even small amounts of migration (from, e.g., individuals with genes that favor themselves over the group) will eventually make interacting groups genetically similar. Such migration destroys between group differences, and without sufficient variance between groups relative to the variance within groups, intergroup competition can't select between genetic groups.

Some researchers have proposed that cultural-group selection can overcome this problem. Cultural-group selection as a force can be considered a consequence of various aspects of our cultural psychology, most notably our ethnic and norm psychology. That is, our ability to identify the cultural groups to which we belong and to assimilate new members, and our capacity to represent norms and tendency punish violators. We know which groups we belong to and the norms associated with belonging to those groups. As long as migrants are assimilated into the group norms (e.g., immigrants following the laws of their new country or newcomers speaking the group language), group boundaries are maintained. Cultural groups with packages of norms that cause the groups to grow and outcompete neighboring groups can be favored by selection. Empirical research supports the idea that cultural groups can maintain their boundaries. For example, at a country level, cultural differences between neighboring countries far outweigh genetic differences. Similarly, at small-scale societal level, neighboring groups of hunter-gatherers have larger between-cultural-group variance relative to within-cultural-group variance. These group differences allow for selection between cultural groups. This leads to the second misunderstanding of what is under selection.

Cultural-group selection refers to selection among cultural groups (rather than a cultural variety of standard "group selection") – that is,

differences in traits between cultural groups may give one group, and the members therein, a selective advantage over a competing group. But what is a cultural group? In the anthropological literature, the cultural group is often defined as the ethnolinguistic group, individuals with a shared cultural history who speak the same language. While this is a strict cultural group, humans belong to multiple embedded and overlapping groups. We can talk about differences between East Asian and Western culture, but equally between Chinese and Japanese culture, or rural and urban regions within China and so on. Similarly, we can belong to overlapping groups such as Boston Catholics and Belfast Catholics. What is really being tracked in a mathematical model and what defines the group are a package of cultural traits – the norms, values, beliefs, and behaviors of the group. That is, cultural groups can be thought of as groups of cultural traits possessed by clusters of people; it's important to distinguish between the cultural traits and the population. Since cultural-group selection is often used to help explain the extraordinary levels of human altruism – groups made up of altruistic individuals would outcompete groups made up of selfish individuals – the cultural traits that often define the cultural group of interest are altruism norms and behavior. But depending on the question of interest, many cultural traits or packages of traits may constitute the cultural group. There are mechanisms and combinations of mechanisms for competition between groups of cultural traits, for example, direct competition, such as warfare between groups; demographic swamping, whereby one set of traits grows at the expense of another; migration, whereby individuals move between groups bringing with them traits that match the new group (assortative migration) or taking on the traits of their new group (assimilation); and prestige-biased cultural-group selection, whereby entire groups of people take on the attributes of a more prestigious group (such as the spread of democracy).

The final misunderstanding lies in the equivalence of the mathematical models of group selection compared to inclusive fitness or individual fitness. These approaches are simply different, but

mathematically equivalent approaches to partitioning the variance when modeling the evolutionary process. Which accounting system makes the most sense (in terms of making it easy to model and understand the selection process) depends on the degree to which the differences between groups contribute to the evolutionary process. The mathematical equivalence does not mean that the causal processes are equivalent, but especially in modeling cultural-group selection, a group selection framework is often the most useful.

Conclusion

Dual Inheritance Theory is an extension of evolutionary biology into the human realm of culture and society. By making precise formal predictions about human physiology, anatomy, and psychology, it offers a potential “Theory of Human Behavior.” And in using the toolkit of the biological sciences, it allows us to synthesize the psychological and social sciences with the biological sciences. It is no surprise then that the models of Dual Inheritance Theory, particularly those associated with social learning, have proven useful in biology and in understanding social learning in other animals. As a theoretical framework, it may do to the psychological and social sciences what the periodic table did to chemistry and what natural selection did to biology. Offer a lens through which thus far disparate empirical findings suddenly make sense.

Cross-References

- [Altruism Norms](#)
- [Cognitive Science](#)
- [Cooperation](#)
- [Cultural Evolution](#)
- [Cultural Intelligence Hypothesis, The](#)
- [Cultural Transmission](#)
- [Examples of Group Selection](#)
- [Group Selection](#)
- [History of Natural Selection](#)

- [Joseph Henrich](#)
- [Lactose intolerance](#)
- [Michael Tomasello](#)
- [Multilevel Selection Theory](#)
- [Natural Selection](#)
- [Social Darwinism](#)
- [Social Learning](#)
- [Theory of Mind](#)

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Dual-Mating Hypothesis

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Definition

The **dual-mating hypothesis** is an important guiding perspective in evolutionary psychology that posits how women may have evolved to develop two overlapping strategies when choosing mates: (A) a short-term strategy that prioritizes men who are high in physical attractiveness and therefore possess “good genes” and (B) a long-term strategy that prioritizes men who are more likely to invest resources in potential offspring (Gangestad and Thornhill 1998; Pillsworth et al. 2004).

Introduction

These strategies are often at odds with each other, as the potential mate who possesses the highest-quality genes is often not the same potential mate who is most likely to invest resources in potential offspring. From the dual-mating hypothesis, researchers have highlighted how women who are faced with this trade-off manage their strategies accordingly, i.e., when they are likely to prioritize genetic fitness versus resource provision from their partners.

Short-Term or Long-Term Strategies?

According to the logic of adaptiveness, both mate-choice strategies (i.e., the preference for good genes in the short term and potential investment in the long term) should be in service of maximizing the likelihood of survival of future offspring (Cosmides and Tooby 1994). Potential offspring are more likely to survive if they have “good genes” that allow them to be resilient to

environmental stressors, as well as caregivers who are willing to invest resources (e.g., time, money, etc.) in ensuring their survival.

However, parental investment theory (Trivers 1972) indicates that men and women should have differing concerns when it comes to mate choice. According to parental investment principles, there are fundamental differences between men and women in mating behavior, due largely to differential parental investment in offspring. For humans in particular, initial female parental investment is much greater than initial male parental investment, given how women and men reproduce. Human gestation occurs within the woman, and a woman typically releases only one ovum per month for a limited period of her life. As a result, it is more costly for women to choose unworthy mates, given the costs of spending 9 months gestating that otherwise could have been spent pursuing better mates. Men, on the other hand, have billions of sperm cells that are viable across their lifespans, and they do not gestate. From an evolutionary perspective, men suffer fewer consequences from an unwise choice of mates.

One implication of this reality is that women tend to be more oriented toward long-term mating strategies, whereas men tend to be more inclined toward short-term mating strategies (Buss and Schmitt 1993). Women should be more discriminating when choosing mates, and they should tend to prefer mates who are more inclined to provide for their offspring, even if they must sacrifice genetic fitness as a result. On the other hand, men should be relatively less choosy when selecting mates, especially short-term mates, and can focus primarily on genetic fitness without worrying about implications for long-term investment.

Famously, Buss (1989) examined the mate preferences of individuals in 37 different cultures (ranging from the United States to Zambia) and found cross-cultural evidence for this sex difference in mate-choice strategies. Men, relative to women, were more attracted to markers of health and fertility (e.g., physical attractiveness), attributes that are not highly correlated with

investment of parental effort. In contrast, because they invest relatively more in each offspring, women were more attracted to markers of a man's ability and willingness to provide resources (e.g., financial wealth and social status). A rich body of literature has further established this relative sex difference in mate-choice strategies, in which men are more inclined toward short-term mating and thus mindful of immediate reproduction goals, whereas women are more inclined toward long-term mating and thus mindful of long-term reproduction goals (e.g., Perilloux et al. 2012).

However, researchers who have adopted the dual-mating framework argue that it is overly simplistic to argue that women universally adopt a long-term mate-choice strategy (Pillsworth et al. 2004). Consistent with the modularity assumption, i.e., that human beings have developed domain-specific evolved mechanisms to solve different problems of adaptation (Barrett and Kurzban 2006; Tooby and Cosmides 1992), it is believed that women prioritize both short-term and long-term mate-choice strategies, with the situational context influencing which strategy is relevant at any particular time. This is somewhat at odds with the idea that the ideal mate-choice strategy for women is to sacrifice good genes in favor of the likelihood of investment. Instead, under this logic, the ideal mate-choice strategy for women should be to choose a long-term partner who is willing to invest in offspring while simultaneously (and perhaps secretly) obtaining good genes via sexual intercourse with a short-term mate (Pillsworth et al. 2004). It is usually impractical to obtain good genes from a short-term sexual encounter while finding a cuckolded partner to invest in the offspring after the fact. In most cultures, there are usually strong social norms that encourage strict monogamy and discourage infidelity (e.g., Conley et al. 2013). Moreover, from an evolutionary perspective, men should be motivated to reduce paternity uncertainty as much as possible, meaning that they will be highly attuned to the threat of sexual infidelity (Buss et al. 1992) and engage in mate-guarding behavior when the threat of infidelity is especially salient (Buss 2002). Nonetheless,

although external pressures may prevent women from enacting this strategy, this still allows for the possibility that women will exhibit a short-term preference for good genes given the right environmental cues.

Trade-Offs Between Strategies

Women could theoretically find a partner who will both transmit good genes and be likely to invest in resultant offspring, but this is difficult to accomplish in reality due to the unavoidable fact that time and energy are limited resources. Gangestad and Simpson (2000) emphasized the importance of trade-offs, i.e., that any adaptation is necessarily going to come with an "opportunity cost" because effort allocated to one adaptive domain could have been allocated to another adaptive domain instead (see also Kaplan and Gangestad 2005). Specifically, they used the example of mating effort versus parenting effort, by highlighting how time and energy devoted to parenting is time and energy that is no longer available to seek out sexual encounters with other potential mates. In regard to the dual-mating hypothesis, this explains why men who have the highest-quality genes are unlikely to be the same men who are most likely to invest in offspring. Likely due to their value as short-term mates, physically attractive men (i.e., men with markers of good genes) have more lifetime sexual partners and are more likely to engage in non-monogamous behavior (e.g., Frederick and Haselton 2007). However, this focus on mating effort means that they may not have the remaining time and energy to put into parenting as a result. Conversely, because less physically attractive men have relatively fewer opportunities to engage in mating effort, they may invest that time and energy into parenting instead, thus increasing their value as long-term mates (Gangestad and Simpson 2000). Moreover, less physically attractive men may be more likely to invest effort in building status and/or wealth in order to further signal their ability to invest in offspring (Kaplan and Gangestad 2005).

Research indicates that women have different criteria for mates depending on if they are asked

to think about short-term or long-term mating concerns. Consistently, researchers have found that women are more likely to use physical attractiveness as a criterion for judging short-term partners and potential extra-pair mates (e.g., Buss and Schmitt 1993; Scheib 2001). Specifically, Frederick and Haselton (2007) found that women perceived muscular men (relative to non-muscular men) as being sexier and more attractive as short-term mates but also less likely to be committed to a romantic relationship, meaning that women are sensitive to the trade-off that men must make between mating effort and parenting effort. Furthermore, Roney et al. (2006) collected measures of both testosterone levels and implicit attitudes toward infants from a sample of men and then asked women to explicitly rate them from their photographs on their attractiveness (A) “as a short-term romantic partner (e.g., for a brief affair)” and (B) “as a long-term romantic partner (e.g., for a committed relationship such as marriage).” In fact, attractiveness as a short-term mate was predicted by testosterone levels (i.e., a marker of good genes), while attractiveness as a long-term mate was predicted by positive implicit attitudes toward infants (i.e., a marker of interest in parenting).

Ovulation and the Dual-Mating Hypothesis

The most compelling evidence for the dual-mating hypothesis comes from research on the ovulatory shift, which is the phenomenon where women show increased attraction toward mates who demonstrate markers of “good genes” (i.e., high physical attractiveness) when they are ovulating and thus at peak fertility (Gangestad and Haselton 2015; Gangestad et al. 2002). In one of the earliest and most noteworthy studies on the ovulatory shift, Gangestad and Thornhill (1998) had female participants smell clothing worn by men of varying fluctuating asymmetries (i.e., a marker of physical attractiveness and good genes) and then indicate their attraction toward the men based only on scent. Despite not actually knowing the fluctuating

asymmetry of the men in question, high-fertility women were more attracted to scents from men who were lower in fluctuating asymmetry, while fluctuating asymmetry had no significant influence on the olfactory preferences of low-fertility women. Therefore, this provided an initial sign that, even if women generally show a preference for long-term mates, they may temporarily shift to a short-term strategy when obtaining good genes is more of a priority (i.e., when conception through sexual intercourse is especially likely).

A plethora of literature has replicated the basic finding that women show an increased cognitive preference for markers of good genes when they are ovulating, but not necessarily markers of long-term investment (see Gildersleeve et al. 2014, for a review). Moreover, it has been shown in multiple studies that women during high fertility are more likely to engage in behavior that should theoretically be more effective in attracting a short-term partner with good genes. For example, ovulating women are more likely to pay attention to physically attractive men (Anderson et al. 2010), express increased interest in attending events where men are likely to be present (Haselton and Gangestad 2006), are more likely to wear clothing that is seductive in nature (Beall and Tracy 2013; Durante et al. 2008), behave more flirtatiously in the presence of available partners (Cantú et al. 2014), and are even more likely to consider infidelity if they are currently in a romantic relationship (Gangestad et al. 2002). In an especially illuminative study, ovulating women in romantic relationships were more critical of their partners when their partners were perceived as sexually undesirable, but felt closer to their partners when their partners were perceived as more sexually desirable (Larson et al. 2013). However, ovulation status did not predict actual commitment to the relationship, providing support for the dual-mating hypothesis by showing that commitment to a partner could be buttressed by both short-term and long-term mate value. Correspondingly, men appear to be sensitive to the ovulatory shift and more likely to engage in mate-guarding behavior when their romantic partners are ovulating (e.g., Fales et al. 2014), providing indirect evidence for the

dual-mating hypothesis by demonstrating that men are perhaps aware of how women are adjusting their mate-choice strategies depending on their ovulatory status.

Conclusion

There have been notable challenges to the dual-mating hypothesis. For example, Buss and Shackelford (2008) pointed out that cuckoldry of a long-term mate, i.e., the ideal mate-choice strategy according to the dual-mating hypothesis, is actually a relatively rare phenomenon (see also Thompson and Muller 2016). As such, they argue that the dual-mating framework is fundamentally flawed and that human females have likely evolved to find the best combination of short-term and long-term mate value in a single partner, rather than attempting to find different partners to maximize each domain. Although researchers using the dual-mating framework already acknowledge that cuckoldry is a difficult mate-choice strategy in practice, Buss and Shackelford (2008) argue that such a strategy is so impractical for most women that it calls into question the extent to which it can really be considered the ideal strategy at all. From this logic, when extra-pair mating actually does occur, it may be better explained by the mate-switching hypothesis, in which women are exploring the possibility of taking on a new partner with greater overall mate value, rather than attempting to maintain relationships with two partners at once (Buss et al. 2017).

Furthermore, although the most compelling evidence in support of the dual-mating hypothesis comes from research on the ovulatory shift, researchers have debated the robustness of these effects, with meta-analyses by Gildersleeve et al. (2014) and Wood et al. (2014) resulting in differing conclusions. However, the body of research on the ovulatory shift as a whole is additional evidence that the narrative of women valuing investment over good genes may be overly simplistic. Future research on the dual-mating hypothesis will likely focus on establishing the robustness of ovulatory effects (Gildersleeve

et al. 2014; Harris et al. 2014; Wood and Carden 2014) as well as determining the particular women for whom and situational contexts in which the dual-mating strategy is especially likely (Buss and Shackelford 2008; Scelza 2013).

Cross-References

- [Costs of Short-Term Mating for Women](#)
- [Good Genes](#)
- [Ovulation](#)
- [Ovulatory Shifts in Psychology](#)
- [Parental Investment and Sexual Selection](#)
- [Sexual Strategies Theory](#)
- [Women's Mate Preferences](#)

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Dual-Mechanism Morphology

► Words and Rules

Dual-Route Model

► Words and Rules

Dunnock Breeding System

► Study of Dunnock Mating, The

Duplication

- [Function of Reproductive Strategy \(Kurzban\)](#)

Duplicity

- [Human Deception](#)

Duration of Breast Feeding in Ancestral Environments

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Synonyms

[Age of weaning in human evolutionary history](#);
[Evolved infant feeding behaviors in humans](#);
[Nursing duration in human evolution](#);

Introduction

Contemporary studies reveal widespread global variation in breastfeeding patterns, providing a fascinating example of human behavioral flexibility (Sellen 2009). However, human infant behavior and physiology evolved under environmental conditions that differ notably from those in which most humans live today. Current evidence places the origin of *Homo sapiens* at ~200,000 years ago (Conroy and Pontzer 2012). Ancestral *Homo sapiens* were hunter-gatherers for most of the species' existence until agriculture, urbanization, and industrialization emerged—all within the past ~11,000 years (Ellis et al. 2013). Under ancestral conditions of hunting, gathering, and high infant mortality, infant survival depended on the immunological, hormonal, and nutritional factors in maternal breastmilk (Hinde and Milligan 2011; Volk 2009).

Prolonged breastfeeding is the norm in most contemporary hunter-gatherer populations, and biological patterns of infant digestive and masticatory development similarly suggest that this pattern is also the human ancestral norm (Sellen 2009). Mean age of introduction of solid foods and total breastfeeding durations were 5.0 ± 4.0 months and 29.0 ± 10.0 months, respectively, in an analysis of 113 nonindustrialized populations; cultural groups with “extractive” (hunter-gatherer) economies had longer overall breastfeeding durations than pastoralists and agriculturalists (Sellen and Smay 2001). In stark contrast, breastfeeding rates are low and durations short in many contemporary, industrialized settings, perhaps because technology and medicine minimize selective pressures that have shaped infant biology throughout human evolutionary history (Ball 2008; McKenna and McDade 2005). Life history theory, a branch of evolutionary ecology, provides a useful framework for analyzing population differences in breastfeeding durations, and for inferring breastfeeding patterns throughout human evolutionary history.

Theoretical Approach

Life history theory (LHT) posits that the behavior and life schedules of organisms are shaped by natural selection to maximize biological “fitness” or reproductive success – usually defined by proxy as “the surviving number of offspring of an individual” (Wilson 1975). Biological fitness maximization occurs when energetic resources are optimally allocated to competing life history functions (brain and body growth, survival/maintenance, and reproduction) (Smith and Fretwell 1974; Charnov and Berrigan 1993; Charnov 2004). Organisms have fixed energy budgets, so energetic “trade-offs” occur between competing life history functions (e.g., upregulated survival effort diminishes growth effort) (Stearns 1989) and are most pronounced under conditions of resource scarcity (Tschirren and Richner 2006).

According to LHT, many parenting behaviors are shaped by natural selection. Parental investment is defined as “resource allocation to one

offspring that diminishes a parent's ability to invest in another" (Trivers 1972). In mammalian mating systems, females bear the energetic burdens of gestation and lactation; in most human societies, mothers are higher investing than fathers and provide the majority of offspring care (Konner 2005). Lactation represents a particularly energetically costly form of maternal investment, and as such it "trades off" with other maternal life history functions (e.g., time and energy for self-maintenance, production of food resources, care of other existing offspring, and production of additional offspring) (Prentice et al. 1996). Weaning (the gradual cessation of breastfeeding) can therefore become a source of conflict between mothers and infants (Trivers 1974).

Maternal–Offspring Conflict

Weaning conflict exists due to asymmetry in genetic relatedness between mothers and offspring (Trivers 1974). Mothers are entirely related to themselves, and equally related (by ~50%) to each of their different offspring. Infants are entirely related to themselves, but share fewer common genes with their mothers, and any existing or future (nonidentical twin) siblings. Mothers must therefore partition investment optimally between multiple (current and future) offspring, and between self-maintenance and reproductive effort, to efficiently maximize individual lifetime reproductive success (Lee 1996). However, in accordance with Hamilton's rule, offspring should prioritize their individual fitness over that of their kin; weanlings may adopt behavioral tactics to continue to extract maternal resources (e.g., breastmilk) (Hamilton 1964; Trivers 1974). Common behaviors include smiling, nuzzling, begging, crying, and tantrums, with weanlings sometimes demanding more than mothers are willing to provide (Haig 2014; Trivers 1974). Continued suckling is associated with maternal lactational amenorrhea (postpartum anovulation), which improves weanling fitness by delaying conception and birth of a younger sibling (Haig 2014). Compelling new research suggests that maternal physiology may, in turn, be evolved to modify offspring behavior; for example,

"bioactive components in maternal milk may be influencing the infant microbiota to shift the infant phenotype toward the mother's optima for investment" (Allen-Blevins et al. 2015, p. 117).

Phylogenetic Context of Human Infancy

Life history theory is also used to make phylogenetic comparisons across animal taxa (Charnov and Berrigan 1993; Lee 1996). Several distinguishing human life history traits (slow fetal growth, infant altriciality, short infancy durations, prolonged juvenility, and high fertility) likely evolved in the past ~2 million years, in conjunction with rapid increases in human brain size (Bogin 1998). The human fetus grows somewhat slowly in utero compared to fetal growth in other ape species; humans are born with ~30% of their adult brain size (compared to ~40% for chimpanzees), and human newborns are neurologically altricial compared to other newborn primates (DeSilva and Lesnik 2006). Human infancy – defined here as the period of maternal lactational provisioning – is also fairly short (~1–3 years) in comparison to other great apes (~3–8 years) (Kennedy 2005; Lee 1996). In contrast, human childhood and juvenility are prolonged in comparison to other apes (Bogin 1998).

In nonhuman primates, the end of infancy is marked by the eruption of first permanent molars; in humans, weaning occurs roughly 3–5 years the first permanent molars erupt (Smith and Tompkins 1995). In concordance with a broader pattern characteristic of mammalian species where mothers birth altricial, singleton infants, human weaning tends to be a protracted process in most nonindustrialized populations (Whitehead 1995; Sellen 2009). Notably, in most human societies, nonmaternal group members (fathers, grandparents, siblings, extended kin) assist with provisioning of recently weaned children (Kramer 2010). This practice accelerates the resumption of maternal ovulation post birth, shortens human interbirth intervals relative to other great apes, and facilitates high fertility rates that have come to characterize the human life course (Humphrey 2010).

Breastfeeding and the Weaning Process

Human infants are born immunologically naïve and face pronounced growth–maintenance trade-offs in the first years of life (McDade 2005). Human breastmilk contains nutritional, immunological, and hormonal components that meet the complex demands of developing infants (Hinde and Milligan 2011). Breastfed infants experience lower rates of diarrheal and respiratory morbidity compared to non-breastfed infants, which is especially important in low-income settings where sanitation and medical care access are inadequate (Kramer and Kakuma 2012). Due to these and many other benefits, the World Health Organization (WHO) recommends 6 months of exclusive breastfeeding, and partial breastfeeding for 2 or more years (WHO 2011). The term “weaning” is often used to refer to the complete cessation of breastfeeding but has also been defined as a “more or less gradual process by which milk is first supplemented, and then replaced, by other foods” (Haig 2010). The entire human weaning transition may be broken down into the following three stages:

1. *Exclusive breastfeeding*: The period in which infant nutritional and immunological needs are met exclusively through consumption of mother’s milk. The relative benefits of breastfeeding decline as infants approach 6 months of age, because maternal milk output is limited and infant energetic requirements increase continuously (McDade and Worthman 1998). Although exclusive breastfeeding is not practiced in some settings (in lieu of formula and other breastmilk substitutes), it is essential to infant survival in most past and present socio-ecological contexts.
2. *Partial breastfeeding*: This stage is marked by the introduction of liquid and solid weaning foods that are regularly consumed by infants in conjunction with breast milk. Because increased gastrointestinal infection is associated with the introduction of infant foods, they may be specially prepared to facilitate digestion and minimize antigen exposure (Fouts et al. 2005). Throughout this protracted weaning process,

nonmaternal group members often support young children through nutritional provisioning of processed weaning foods (Humphrey 2010). Partial feeding may last until a child is two or older in nonindustrialized populations (Sellen and Smay 2001). In contrast, initial infant food provisioning is often synonymous with cessation of breastfeeding in some very modernized contexts (Whitehead 1995).

3. *Nutritional independence*: In most mammals, by the onset of nutritional independence (end of the weaning transition) offspring have attained sufficient physical maturity and competence to undertake independent traveling, foraging, food processing, and digestion (Lee 1996). Because human weanlings are not capable of successful independent foraging, they continue to receive foods provisioned by mothers, other kin, and unrelated alloparents (Bogin 1998; Kramer 2010). Provisioned post-weaning foods tend to be energy dense, and provide nutrients required to fuel children’s brain growth, which continues up to 7 years of age and beyond (Kennedy 2005).

Threshold Model of Weaning

Phylogenetic life history comparisons reveal positive correlations between adult and neonatal body weight, adult and neonate brain weight, and interbirth intervals (a proxy for weaning age) (Harvey and Clutton-Brock 1985; Lee 1996). In large-bodied mammals, offspring are typically weaned by a maximum “threshold” body size, which is achieved when the infant grows to roughly quadruple their birth weight (Lee 1996). According to this model, a human neonate born at 3.3 kg will be weaned at 13.2 kg (10.6–16.2), which “corresponds to an age of 2.5 years (1.3–3.9) for breastfed male babies on the 50th growth centile” (Humphrey 2010). Weaning is often thought to occur at this threshold because infant energetic requirements come to exceed the upper limits of maternal metabolic capacity (Lee 1996). It has also been suggested that slow infant growth leads to longer breastfeeding durations in nutritionally and epidemiologically risky

environments (Hochberg 2011). In general, infant growth rates are rapid in the early postnatal phase, decelerate across infancy, and then abruptly accelerate at the onset of the biologically salient transition into childhood. In hunter-gatherer populations, this transition occurs near the mean weaning age (2–3 years) whereas in affluent Westernized countries, it occurs at ~6–12 months (Hochberg 2011).

Facultative Model of Weaning

The “shifting weaning optima” model states that weaning age is facultative and occurs when the maternal costs of prolonged lactation outweigh the infant benefits (Sellen and Smay 2001). A conceptually similar “evolutionary trade-offs” model was proposed by Tully and Ball (2013), more explicitly incorporating Trivers’ (1974) model of parent–offspring conflict. According to these models, prolonged breastfeeding will persist in settings where its benefits to infants are high (e.g., environments of high infectious disease morbidity) and/or when actual and/or perceived maternal time, energy, social, and opportunity costs are low (McDade and Worthman 1998; Tully and Ball 2013; Veile and Kramer 2017). Support for a “shifting weaning optima” has been at least partly supported through qualitative assessments of costs and benefits of breastfeeding in different environments (Veile and Kramer 2017), though it should be noted that the costs and benefits of breastfeeding are challenging to operationalize.

Conclusion

The duration of breastfeeding in human ancestral environments can be inferred through investigations of ancient human fossil remains, extant and extinct nonhuman primates, and contemporary hunter-gatherer populations. Human breastfeeding durations are simultaneously shaped by divergent mother–infant fitness interests, local ecologies, and cultural norms. Despite substantial intraspecific variability in breastfeeding patterns,

combined bodies of evidence suggest that breastfeeding for 2 or more years is the human ancestral norm (Sellen 2009). Though the biological fitness costs of not breastfeeding are reduced in many contemporary modernized settings, prolonged breastfeeding is still an economical, nutritional, and hygienic strategy for maximizing infant survival in many parts of the world.

Cross-References

- [Breast Feeding](#)
- [Breast Feeding and Mother-Infant Attachment](#)
- [Breastfeeding in Modern Environments](#)
- [Breast Milk Composition](#)

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Duration of Childhood

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Synonyms

Developmental stage; Immaturity

Introduction

The period of immaturity is known to be more protracted in humans than in other primates.

This text sets out to compare the various developmental stages of the immaturity period in mammals in order to more specifically explore the adaptive value of each stage for human beings, with special emphasis on childhood.

The Four Stages of the Immaturity Period in Human Beings

Most mammal species progress from infancy to adulthood without any intervening stages (Bogin 1990). The infancy stage ends when breastfeeding stops (Bogin 1997). Highly social mammals, such as wolves, wild dogs, lions, elephants, and the primates, delay puberty with a period of juvenile growth between infancy and adulthood (Bogin 1997). Juveniles are defined as “prepubertal individuals that are no longer dependent on their parents for survival” (Pereira and Altmann 1985). Presumably, adolescence later emerged, by natural selection, among the apes. Adolescence is a period of rapid and profound physical, hormonal, and behavioral change leading up to the full reproductive and social maturity characterizing the adult years (Kraemer et al. 1982). In chimpanzees, adolescence begins at approximately 8 years of age and ends around age 14 for females and 15 for males (Pusey 1990) whereas in human beings, adolescence spans ages 10–18 for girls and 12–21 for boys. Puberty begins in chimpanzee males with significant testicular growth and ejaculation, and in chimpanzee females, with slight swelling during ovulation (Pusey 1990). Human puberty begins with the appearance of the secondary sexual characteristics, then the development of breasts in girls, the enlargement of the testes (less than in chimpanzees) and penis (more than in chimpanzees) in boys, and the onset of interest and activity in adult patterns of sociosexual behavior. Moreover, human adolescence also involves a growth spurt of skeletal and muscular tissue that produces sexual dimorphism in size and physical strength in favor of males, to a greater extent than in chimpanzees. These differences in sexual dimorphism between humans and chimpanzees can be explained by the species’ contrasting

reproduction types. In chimpanzees, intermale competition for access to females is mainly spermatic because of the species’ sexual promiscuity: although the dominant male has a greater likelihood of copulating first, females have sexual relations with many partners. In humans, males are in greater direct competition with one another for access to females within a system of reproduction that features a mix of union types. Although polygynous marriages can be found in most human societies, monogamy remains predominant across the globe given that, in most polygynous societies, only a small portion of men have more than one wife (Chapais 2008).

Given the absence of growth spurts in non-human primates, Bogin (1997, 2011) considers adolescence to be a developmental stage specific to humans. However, this sole criterion seems insufficient, in our view, to deny the existence of adolescence in other animals. Indeed, chimpanzees, too, display an adolescent growth spurt, albeit only in individuals who exhibited delayed growth in the juvenile period as a result of severe environmental pressure (Hamada and Udono 2002). Moreover, the above-mentioned differences between the two species, in terms of sexual organs and sexual dimorphism, should also be taken into account.

According to Bogin (1997), human physical growth from 3 to 7 years of age indicates that childhood, likewise, is a unique developmental stage of humans. Childhood is the period following weaning, when youngsters still depend on older individuals for feeding and protection (Bogin 1997). Children evidence a relatively larger disproportion between brain size and body/gut size than adults (Bogin 1997). They require a special high-energy diet owing to their rapid brain growth, the continued presence of their deciduous dentition, and their small digestive tracts. The eruption of their first permanent molars and the completion of their brain growth (in weight) mark the transition to the juvenile stage. Juvenile humans have the physical and cognitive abilities needed to acquire much of their own food and to protect themselves from environmental dangers such as predation and disease (Blurton-Jones 1993). Cognitively speaking,

the age of seven in human children equates with the beginning of Piaget's concrete operational stage (Piaget 1983).

Hence, the protracted immaturity period in humans can be explained by the extension of the juvenile and adolescent stages and the addition of the childhood stage. However, the duration of the infancy stage in humans has shrunk compared to that observed in our closest cousin, the chimpanzee. Apes, like, chimpanzees, show a pattern of brain growth that is rapid before birth and relatively slower after birth, whereas humans exhibit rapid brain growth before and after birth (Bogin 1997). Young nonhuman primates' weaning age, in days, is equal to 2.71 times their mother's body weight in grams (Dettwyler 1995). Interpolating from comparisons among nonhuman primates, human should have an average weaning age between 2.8 and 3.7, as opposed to 4.9 years old in chimpanzees. The average age of weaning is 3 years old in non-Western traditional societies, namely small-scale horticultural and hunter-gatherer populations (Johnson 2012). It is important to keep in mind that humans lived in hunter-gatherer societies for over 99% of the evolutionary history of the *Homo* genus (Chapais 2011). Among traditional human subsistence societies, infancy lasts from birth to 30–36 months of age, childhood, from 3 to 7 years old, the juvenile stage, from 7 to 10 for girls and 12 for boys, and adolescence, until 18 for girls and 21 for boys (Bogin 2009). According to UNICEF, half of the world's population continues breastfeeding until at least age two. Contrastingly, fewer than 15% of Americans (and 25% of Canadians) continue nursing their infants after only 6 months of age (Johnson 2012).

The average period between successful births is 5.6 years in wild chimpanzees and 3.6 years in the !Kung, a traditional hunting and gathering society located in southern Africa (Bogin 1990). In theory, humans can have one child per year since breastfeeding is an unreliable ovulation-suppression mechanism in our species. Even if humans mature later than chimpanzees both sexually and socially, their smaller gap between births and longer lifespan give them greater fertility than apes.

Adaptive Value of the Childhood Stage

Three reasons are traditionally cited to explain childhood (Bogin 1997), namely (1) an extended period for brain growth; (2) time to acquire techniques and skills (tool making, food processing, etc.); and (3) time for socialization, play, and the development of complex social roles and cultural behavior. However, as Bogin (1997) notes, these functions could be covered by any of the other stages. Bogin instead posits childhood as an evolutionary strategy to elicit caring from others (juveniles, adolescents, adults, grandmothers, etc.), thus enabling children to develop new skills suited to their environmental conditions while freeing up their mothers for reproduction, hence diminishing the interbirth interval and increasing reproductive fitness. In terms of allometry, as they grow, human children maintain an infantile appearance (large cranium with a small face and body) that prompts nurturing and caregiving behaviors in older individuals (Lorenz 1971). This care for children by other members of the community in hunter-gatherer societies is not observed in other primates (Lancaster and Lancaster 1983).

The hypothesis set forth here is that childhood (3–7 years of age) is the period during which individuals' interaction with peers and education from adults allows them to learn the cultural rules pertaining to, and develop the skills needed for, cooperation. Human beings considerably set themselves apart from other primates by their ability to cooperate with others. This cooperation is central to all human activities, from the division of social roles to searching for food, caring for children (by other members of the community), and even war.

One of the hallmarks of primates is their large brain in relation to their body size. The traditional explanation for this trait is that a larger brain increases cognitive capacity, thus granting the ability to solve the problems encountered in primates' physical environment. A more recent explanation called the "social brain hypothesis" instead suggests that having a larger brain makes it possible to live in larger organized groups. Hence, humans live in more extended groups than do other primates. After all, collective action

is more effective than individual action. One of the main advantages of large groups is the greater protection they provide against predators. Among our ancestors, large groups also enabled the emergence of collective large-game hunting – our ecological niche. However, this coordinated activity raises the problem of how to fairly portion out the meat after the hunt. Indeed, fairness is a prerequisite for continued cooperation. To address this, it became helpful for humans to develop an understanding of the actions, intentions, and beliefs of others of their kind. The ability to step into others' shoes to try to grasp their intentions helps not only detect cheaters, but also mislead and manipulate others while avoiding detection. This manipulation and misleading ability has been referred to by primatologists as Machiavellian intelligence. The ability of social animals, and humans in particular, to catch onto clues enabling them to form a mental picture of what is going on in other people's minds is referred to by psychologists as "theory of mind." The strong correlation observed between neocortical ratio and group size in non-human primates has helped determine, by extrapolation, that humans are capable of memorizing and understanding interrelationships (family ties, alliances, etc.) between 150 individuals (Dunbar 1993). Children's more frequent interactions with other members of the community within a caregiving context offer an ideal setting in which to safely acquire many social skills of all kinds.

Although nonhuman primates are also able to imagine the mental states of their fellow primates, in Tomasello's (2014) view, humans have a more sophisticated theory of mind and can better picture the goals and intentions of other members of their species. According to Tomasello's shared intentionality hypothesis, humans' significant capacity for cooperation relies on the ability to engage in joint attention to achieve joint goals and collective group goals. Chimpanzees have individual intentionality: they are individualistic and competitive, and focus on getting food for themselves rather than engaging in joint attention. Chimpanzees understand that others have goals, and sometimes even help others achieve them, but they do not collaborate with others through a joint goal. Environmental circumstances have forced

humans to become more cooperative and to coordinate to achieve joint goals and collective group goals. Tomasello (2014) refers to joint intentionality when the cooperation is dyadic, and collective intentionality when it involves the cultural group. Collective intentionality likely emerged when human populations began growing and competing with one another. The development of cultural conventions, norms, and institutions would thus have been made possible by language, which enables a higher degree of abstraction.

Still according to Tomasello (2014), in order to solve concrete problems of social coordination, joint intentionality requires the development of specific skills: new forms of cognitive representation (perspectival and symbolic), inference (socially recursive), and self-monitoring (regulating one's actions from the standpoint of a cooperative partner). Chimpanzees make intuitive inferences about their experience (simulating the causes and outcomes of physical and social situations), but not inferences about what others are thinking about their own thinking. The socially recursive inferences begin when humans attempt to coordinate their actions and attention with others in collaborative activities with joint goals and attention.

Linguistic communication in humans paved the way for the development of skills specifically geared toward collective intentionality, i.e., reflective inferences and normative self-monitoring (Tomasello 2014). Reflective inference has to do with the discursive process by which each individual presents, justifies, and argues their ideas or beliefs to others with a view to a common action to be undertaken by the group. This process of cooperative argumentation, of taking into account diverse potential perspectives, leads to a truth considered as an objective part of external reality, in turn justifying the establishment of social norms that will help better regulate decision-making in the future.

Joint attention and cooperative communication are already present during human infancy. As early as 12 months old, human infants are already cooperative and helpful in an array of situations (Tomasello 2009). Before even being able to speak, infants use pointing and pantomiming to direct others' attention perspectively

and/or symbolically toward items relevant to their joint activity, following which the partner makes cooperative inferences about what was intended. Early helping behavior is an expression of natural inclination to sympathize with others in strife, and is mediated by empathetic concern as opposed to resulting from socialization practices. "After their initial period of a kind of indiscriminate altruism mixed with some selfishness about valuable things, young children become more discerning based on various characteristics of potential targets of their altruism. Several recent studies have shown that children begin to make these judgments about others from around 3 years of age. . . . Children of this age more often help those who have been helpful to others" (Tomasello 2009, p. 29). In other words, it is at the age of three – i.e., the beginning of childhood, according to Bogin – that children begin to incorporate cultural norms and values through modeling, communication, and instruction. Genuine social norms based on reciprocity emerge in the late preschool period, as children shed their egocentrism and start to view others and themselves as coequal autonomous agents.

Already during infancy, children have a predisposition for competition (aggression) and a predisposition for helpfulness and cooperation (informing and sharing). Clearly, these tendencies in young children are later shaped by socialization. They learn to be selective about who to help, inform, and share with, and to manage the impression they make on others (their public reputation and self) as a way to influence others' actions toward themselves. Children develop joint intentionality skills during infancy, and then collective intentionality skills during childhood when they first begin to understand social norms and other conventional phenomena as products of a collective agreement of sorts.

With the exception of self-recognition in a mirror, which seems to emerge during infancy (around 18 months of age) and is assumed to be a prerequisite for assigning independent mental states to others, most skills required to understand complex social situations, such as perspective-taking, can be observed starting from 4 years of age in humans, which is earlier than in apes.

Adaptive Value of the Juvenile Stage

We hypothesize that humans' longer juvenile phase can be explained by the need to organize the skills learned during childhood into flexible structures so as to be able to adapt to the many and varied social contexts found in different human cultures.

Experience with multiple playmates in a variety of contexts enables children to develop the behavioral flexibility they need to successfully forge alliances and cooperate in groups. Although social skills appear in most humans at preschool age (3–5 years old), the same cannot be said of social competence. Acquiring social competence requires the individual to combine and regulate skills in order to achieve the flexibility to meet goals across a great number and variety of social contexts. Flexibility, then, appears to be the main advantage of humans' protracted growth. A prolonged period of immaturity would allow humans to acquire skills (4–6 years of age) and especially to organize them into flexible structures (7–12 years of age). Behavioral flexibility is the chief characteristic of social competence; it implies a mastery of basic skills, a strong knowledge of social contexts and, ultimately, self-mastery in the face of the choices to be made. Whereas most specific social skills are believed to be developed during childhood, children only seem to integrate these skills into social competence during the juvenile phase. Social competence is an organizational construct in which specific mental skills are developed and regulated in order to be able to perceive and interpret behavior or mental states of self and others to pursue goals in social contexts. A single skill taken alone – for example memorizing the social status of each member of a group – is a poor indicator of future adaptation. Rather, what enables the individual to meet current and future challenges is proficiency with activating, inhibiting, or coordinating their own skills or those of others depending on social information (Waters and Sroufe 1983).

Friendships are a good way to develop social competence. Children with friends are more socially competent than those without; they tend

to be more sociable, cooperative, altruistic, and self-confident (Hartup and Stevens 1997). Starting from 2 years of age, friendships essentially consist in sharing common activities; it is at preschool age (3–5 years) that friendships support the acquisition of new social skills, particularly in the areas of cooperation and conflict resolution. Beginning at school age, both friendship networks and time spent with friends tend to expand (Hartup and Stevens 1997): friends share interests and exercise self-disclosure. Children 6–12 years old spend more time understanding themselves and others within increasingly complex systems of kinship that lead to more or less stable friendships between peers. Indeed, researchers have noted that more than half of friendships among children 6–7 years old are unstable, and this rate of instability holds steady all the way to adult age (Poulin and Chan 2010). Although the stability and quality of friendships during the juvenile stage are a good predictor of adult social adaptation, researchers point out that this developmental period leading to adolescence affords multiple social experiences in which friendships are forged and maintained in accordance with maturation needs: children first seek out friends with which they can share common activities, before searching for more loyal friends toward adolescence. Given that the instability of friendships increases with group size (70% instability in cliques of 2–9 children) (Chan and Poulin 2007), the challenge of creating the stable ties required for survival and reproduction in adult humans, such as managing alliances in large-group settings or forming lasting couples, increases in complexity as the child grows older. Humans are also believed to require more time to hone their skills and to become socially competent before reproduction age.

Adaptive Value of Adolescence

Finally, we hypothesize that humans' protracted adolescence compared to chimpanzees can be explained by the greater variety and complexity of power relationships and alliances among humans. In most animal species, power

relationships are dyadic (involving only two individuals) and based on coercion (aggression and social dominance). A third party's interference in the power relationships of others (politics) is a relatively rare phenomenon observed only in social species with very highly developed brains such as wolves, lions, and the primates (Chapais 1988). The complexity of strategic alliances among chimpanzees even inspired Frans de Waal to write his famed book *Chimpanzee Politics* (de Waal 1982).

In humans, at adolescence, friendships continue to play a significant role in forging a mutual relationship, with an increase in self-disclosure between friends (Hartup and Stevens 1997). Adolescents compete less with friends than with non-friends, and share more than in the juvenile stage (Hartup and Stevens 1997). We suggest that adolescence is a period for experimenting with and forging power relationships and alliances with peers, before competing with adults. Although rough-and-tumble play does not correlate significantly with aggressive interactions in young chimpanzees and young children, it does in adolescence, for both species (Paquette 1994). This means that adolescents' rough-and-tumble play is a mechanism enabling them to establish dyadic dominance while avoiding harm or the intervention of a third party.

Adolescence is the phase during which intrasexual competition for sexual partners begins. Testosterone is the hormone of both libido and social dominance. The dominance hierarchy is most often shaped by a series of aggressive interactions, but once established, it automatically determines priority of access to resources without requiring further attacks between opponents, as each individual knows their place in the hierarchy. Although testosterone increases in both sexes during adolescence, the spike is greater in boys. Boys' more extensive risk-taking (including aggression) compared to girls can be explained by the mechanism of sexual selection; boys are prepared to take significant risks to achieve a higher social standing that will give them access to a greater number of sexual partners. Women, too, compete among themselves for social standing and sexual partners. Women prefer to mate

with men of high status and good reputation and with men with more resources (Paquette 2015). Based on testosterone and risk-taking curves (Paquette 2015), intrasexual competition is more pronounced during adolescence and early adulthood (until 25 years old) than before or after this period. In addition to dominance, leadership also plays a crucial role in humans. According to a review of the literature by van Vugt (2006), no association can be found between dominance and leadership, as they are different forms of power, the first resulting from coercion and the second from influence. Leadership is a form of cooperation between a group and an individual which gives the group a structured approach to achieving a common goal. Finally, in humans, power is not exercised only through coercion (punishment-based control) but also through differential control of goods and services (power of compensation), information (power of knowledge), and symbolic rewards (normative power) (Chapais 1988). These three last types of power depend on individuals' competence in controlling the resources required by others. The most powerful individuals are those boasting the largest number of people who depend on them to meet their needs.

Sex Differences

From 3 years of age, girls and boys interact with same-sex peers more frequently than with opposite-sex peers (Rose and Rudolph 2006). At this age, boys engage in more rough-and-tumble play and war games than girls. Rough-and-tumble play is the most evolutionary ancient and widespread type of social play found among social mammals (Panksepp 1998). It is a proximal mechanism conducive to developing dyadic fighting skills while avoiding culmination into genuine aggression (Paquette 1994). War games are a specificity of humans, and include both play with guns and "pretend" play or role-playing between warriors or superheroes (Costabile et al. 1992). Whereas rough-and-tumble play first and foremost entails physical contact between two partners without requiring objects, war games are above all symbolic and may or may not involve multiple

partners (solitary or social play), with or without toy weapons. The function of this play is not known, but one possibility is that it allows children to engage in higher-level political or strategic learning that teaches them about intergroup power relationships (us vs. them).

Moreover, also at 3 years of age, boys begin to use more physical aggression than girls, and girls to use more relational aggression and to be more prosocial than boys (Paquette et al. 2013). Relational aggression is a form of aggressive verbal behavior used by children to isolate a peer with the goal of expanding the initiator's own network of influence; this type of aggression peaks at puberty (Vaillancourt 2005). Paquette et al. (2013) have also shown that preschool-aged girls are just as competitive for local resources as boys on two competitive dimensions (other-referenced competition and maintenance of dominance hierarchy), and more competitive than boys on task-oriented competition. Other-referenced competition consists in comparing oneself with the aim of outdoing others and winning, whereas task-oriented competition means striving to surpass oneself in achieving a goal.

By 6 years of age, another sex difference emerges: boys develop the tendency to play in large groups (Rose and Rudolph 2006). Rough-and-tumble play between peers peaks between the ages of 8 and 10 (Pellegrini and Smith 1998).

Intimacy and self-disclosure heighten in both sexes as individuals move toward adolescence (Buhrmester and Prager 1995; McNelles and Connolly 1999). Several studies have shown that adolescent girls report higher levels of intimacy in their friendships than boys at approximately age 12–14 years (Buhrmester 1996; Shulman et al. 1997). Bauminger et al. (2008) emphasize the importance of self-disclosure in establishing and maintaining both intimate friendships and romantic relationships. Some researchers have also demonstrated that shared activities lead to intimacy in adolescent boys (Camarena et al. 1990; McNelles and Connolly 1999). Empathy and intimacy, which are linked to both prosociality and leadership (Bauminger et al. 2008; Garaigordobil 2009; Radmacher and Azmitia 2006), are undoubtedly key to the development of mutual trust and

loyalty, and hence important to reciprocal altruism. The theory of reciprocal altruism (Trivers 1971) puts forward an explanation for cooperation and helping behaviors between nonrelatives of the same species. Such altruism consists in a non-simultaneous exchange of services between two unrelated individuals. It evolves in species capable of individual recognition and remembering past events. This behavior is selected over the course of evolution in cases where both individuals receive more than they contribute, e.g., the cost of supporting an ally against an adversary is low compared to the benefits of holding high dominance status.

Conclusion

To sum up, our comparison of different stages of physical growth in mammals has uncovered a typical human stage that distinguishes our species from the other primates, namely childhood – a period between the infancy stage and juvenile stage, spanning the ages of 3 and 7 years – in today's hunter-gatherer societies. This period may connect with the childhood of our nomadic ancestors who lived as hunter-gatherers for nearly two million years, in contrast with most human societies which became sedentary and agriculturally based only 10,000 years ago – a blip in the evolutionary scale.

Based on the theory of social brain and research showing that humans are highly cooperative compared to the other primates, we have also postulated that the adaptive value of childhood is that it enables young people to develop the basic skills needed for cooperation thanks to interaction with peers, and to learn social rules and moral codes thanks to more frequent contact with the other adults in their community.

Drawing inspiration from psychology research, we have suggested that the adaptive value of the juvenile phase (7–11 years old) lies in the integration of previously acquired social skills into social competence, i.e., flexible structures enabling the individual to adapt to an array of social contexts, especially thanks to friendships, which are relatively unstable throughout

human development. Finally, we concluded that the adaptive value of adolescence resides in experimenting with and forging power relationships and alliances with peers, before competing with adults.

Finally, the sexual differences noted in human development have underscored that power relationships take on different forms depending on the sex. Men more strongly tend to exercise hierarchical power among themselves to acquire prestige and self-esteem, whereas women are gradually primed for more egalitarian relationships focused on cooperation with other women. This cooperation between women may take on various forms such as mutual assistance in searching for food, social support, and, very likely, collective caregiving for the community's youngsters during childhood (3–7 years old) to enable young women to invest in new offspring. Males, too, exhibit various forms of cooperation, such as collective hunting and protecting the community against predators and other groups, but probably above all within alliances during conflicts over social status.

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During Ovulation

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Synonyms

[Estrus](#); [Fertile window](#)

Definition

Ovulation occurs when an egg is released from the ovaries and becomes available for fertilization.

Introduction

Conception is most likely to occur within a window of time ending on the day of ovulation (Wilcox et al. 1995). During this time period, evolutionarily advantageous, or sometimes disadvantageous, circumstances arise – for both the woman ovulating and the individuals interacting with the woman who is ovulating.

During Ovulation

A window of peak fertility is a time when the female member of the species makes significant

changes – explicitly or implicitly – to her behavior to increase her odds of conceiving. For example, Beall and Tracy (2013) found that women who were at high conception risk were three and a half times more likely to wear a red or pink shirt than women who were at low conception risk. Present in nonhuman primates and once present in early humans, ovulation is advertised through various mechanisms of coloration – facial redness and hindquarter redness (Jones et al. 2015). Thousands of years later, red and pink are still associated with sexual arousal and romance. The increased likelihood of wearing red or pink during ovulation, while not an explicit choice, suggest that ovulating females would like potential mates to be aware of their fertility status.

While behavior choices made during ovulation can foster favorable interactions with the opposite-sex, the female body undergoes variations that are seemingly perceptible. In a seminal paper in 2007, Miller et al. (2007) discovered lap dancers earned up to US\$170 more during ovulation than any other menstrual phase. Patrons of the venue seemingly were able to distinguish between ovulating, nonovulating, and contracepting females – visual cues of ovulation can be perceived and acted upon by interested males. Further studies have investigated whether women are perceived differently during ovulation. Cobey et al. (2013) using a within-subjects design discovered that men rated their partner as more attractive when she was fertile, more so than when she was nonfertile or using hormonal contraception. Even further, participating women did not rate themselves significantly different throughout the study – perhaps indicating that their male partner's perception of their attractiveness is not reliant on the woman feeling more attractive herself during ovulation.

If conception risk is high, females can be put on the defensive – they must avoid the consequence of unintended pregnancy via rape or sexual assault. Petralia and Gallup had female participants read a sexual assault scenario and found only the ovulating females exhibited an increase in handgrip strength after reading the passage (Petralia and Gallup 2002). This

rape-avoidance mechanism serves to protect females from conceiving with an undesirable mate.

When women are fertile, their preferences for sexual partners is distinct. For example, women prefer the scent of a man with high testosterone (Thornhill et al. 2013); testosterone is the driving hormone in the masculinization of the face, growth of skeletal muscle, increased intrasexual competition abilities, and overall increased sexual fitness (see Thornhill et al. 2013). Therefore, when women are assessing potential mates during ovulation, they are showing increased preferences for characteristics *directly* affected by an increased level of testosterone. Ovulating women prefer high masculinity in the body, voice, and face (see (Thornhill et al. 2013)). Further, fertile women generally prefer taller men, in addition to preferring men exhibiting social behaviors that lend to the ability to compete with other men – and emerge victorious (see (Thornhill et al. 2013)). This preference is so distinct that these preferences vanish in women who are not ovulating – specifically women who are utilizing hormonal contraceptives (Roberts et al. 2013). Hormonal contraception ceases the normal ovulation cycle to prevent unwanted pregnancy. With that cessation in cycling comes an interruption of the adaptive changes in behavior and preferences. However, the changes can resume once the woman discontinues hormonal contraceptive use.

Women at high conception risk engage in various behaviors that either put them in situations that lend to producing high-quality offspring or avoid situations that would result in low-quality offspring. Antfolk and colleagues found women were most disgusted at the idea of an inbreeding description, specifically for situations when they were described as a *participant* in the activity, when they were most fertile (Antfolk et al. 2014). Ovulating females regulate their behavior accordingly to avoid the genetic, and social, consequences of inbreeding. On the contrary, ovulating women show greater sexual interest and fantasize about extra pair copulation during ovulation, compared to the nonovulation phases (Gangestad et al. 2002). This interest in mates aside from their primary partner hints to the notion that the

ovulating female is more inclined to reap the genetic rewards of mating with a male of increased quality, as described above. Further, the same female participants indicated their partner was more likely to exhibit mate-guarding behaviors when they were ovulating, versus other times in their cycle – the partners of normally cycling women regulate their behavior accordingly to prevent the consequences of extra-pair copulation.

Conclusion

During ovulation, females exhibit a cascade of changes to their behavior, their body, and their preferences to further the likelihood of successful conception. Ovulating women have maintained the ability to leak cues of estrus to interested partners, and thousands of years of successful mating strategies shaped preferences for the most desirable mate at the most imperative time.

Cross-References

- Cuckoldry
- Mate Preferences
- Rape Avoidance

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such as two romantic partners who form a couple, two friends, teacher-student couples, or two co-workers. Their type of relationship can differ, for example, in the degree of intimacy, time spent with each other, situations in which they meet, or their closeness. Such characteristics might affect relationship-related outcomes such as relationship quality (romantic relationships and friendships) or job satisfaction (e.g., employee-supervisor characteristics). Direct and indirect interactions of behaviors of members of the dyad (e.g., reactions in conflict situations, inclination to spend time with the respective dyad member) and characteristics of each dyad member (e.g., expressions in personality traits) are associated with individual and dyadic outcomes (e.g., attraction or relationship satisfaction). Such *dyadic effects* help to understand the relationship between members of a dyad; for example, how two partners deal with a stressor (e.g., *dyadic coping*) affects external criteria beyond the individual's coping behavior.

This entry gives a short overview of theoretical considerations on why dyadic processes play a role in understanding individuals, methodological challenges in the study of dyadic data, and statistical approaches to study dyadic processes. Finally, we will present key findings on three main topics from the field of dyadic research.

Dyadic Processes

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Synonyms

Co-development; Interpersonal perception; Relationships; Similarity

Definition and Introduction

A dyad is composed of two people who are interdependently connected by a relationship

Why Studying Dyadic Processes Matters

While psychology aims at describing, explaining, and predicting behavioral, cognitive, and emotional aspects of individuals, humans coexist and interact with others throughout the life span. The social environment contributes to shaping stable dispositions of thoughts, feelings, and behaviors (approximated as personality traits) in private and professional contexts over time – from birth (e.g., interactions with caretakers, siblings) throughout life when dealing with peers, romantic partners, teachers, or colleagues across all domains of life. As people do not exist independently from each other, relationships and dyad members' interdependence have consequences; for example, a robust finding in romantic life is that romantic partners have assortative mating preferences

(i.e., above chance similarity in partners' phenotypes) and show similarity in numerous physical and psychological variables (e.g., Conroy-Beam et al. 2019; Luo 2017). Also, there is strong evidence that one's own but also the partner's personality have an impact on romantic life (e.g., relationship quality) and that joint characteristics of the dyads also play a role. For example, partner similarity contributes positively to relationship satisfaction (i.e., similar couples are happier than dissimilar couples, although usually with small effect sizes; Luo 2017; Weidmann et al. 2016). Overall, social interactions play a role across all life domains (e.g., at work, in the classroom) and for any type of relationship that people form and maintain in those domains (e.g., Chow et al. 2013; Ireland et al. 2010; Liden et al. 2016).

Dyadic interactions have been studied on different levels using various data sources. Studies have examined associations of verbal and nonverbal dyadic behaviors such as the similarity in partners' language use and their inclination to romantic interest (Ireland et al. 2010), the occurrence of couples' joint laughter, and relationship satisfaction (Kurtz and Algoe 2015) or whether mimicking a partner's nonverbal behaviors (e.g., smiling, crossing arms, or hand movements) is associated with liking one's respective partner (Kurzius and Borkenau 2015). Other studies have examined the influence of relatively stable dispositions in dyadic systems such as romantic couples when studying the associations between broad and narrow personality traits, dyadic effects (e.g., partner similarity), and romantic outcomes (e.g., relationship satisfaction; e.g., Brauer and Proyer 2018; Weidmann et al. 2016).

Theoretical considerations on why and how dyadic interactions affect individuals and their relationships have been proposed. For example, in the line of research on adult playfulness, Chick (2001) suggested in his *signal theory of play* that being high in playfulness communicates underlying characteristics such as low aggressiveness in men and high fecundity in women to their potential long-term partners. Therefore, playfulness could be one characteristic that impacts sexual selection. Moreover, potential partners need to accurately perceive and interpret traits in others,

which is also subject to dyadic research, as it seeks antecedents and consequences of interpersonal perception (Connelly and Ones 2010). Indeed, empirical evidence supports Chick's suggestions, as there is evidence that (a) playfulness can be accurately perceived by others, even upon minimal information (i.e., short textual self-descriptions, Proyer and Brauer 2018), (b) romantic partners demonstrate similarity in their playfulness, and (c) individual and dyadic levels of playfulness are related to partners relationship satisfaction (Proyer et al. 2019). This example shows that theories on dyadic processes and their empirical examination are complex and demand multimethodological approaches.

Dyadic interactions can also have negative consequences; for example, peer aggressiveness (*bullying*) is a dyadic phenomenon between the aggressor (bully) and the victim. To understand the conditions under which bullying and victimization occur, it is important to study the individuals involved and their dyadic interactions (see Salmivalli 2010). Consequently, one might argue that interventions should be more effective if they target not only an individual but the dyad (or larger systems; e.g., classrooms, families, work teams).

There are theoretical accounts of how and why social interactions affect both the individuals in the social situation and their relationship reciprocally. For example, the *dynamic interactional paradigm* describes the co-development between individuals' personality and their relationships over time and assumes that people create and maintain their relationships in a way that suits their personality (e.g., Neyer and Asendorpf 2001; Neyer et al. 2015; also see Deventer et al. 2019). However, the social environment might also affect the individuals' personality involved in the relationship over time. Thus, a dynamic process between the individual and its social environment exists that indicates bi-directional effects in the way that the person affects his social environment and how he/she is affected by his/her social environment (so-called *personality-relationship transactions*; Neyer and Asendorpf 2001). There are differential relationships between traits of the individuals, dyadic

interactions, relationship types (e.g., friendship vs. work), and outcomes.

The study of dyadic processes needs specific methodological approaches that account for the interdependent structure of dyadic data. In the following section, we will give a short overview of four statistical approaches to analyze dyadic data, namely, the *Actor-Partner Interdependence Model* (APIM; Cook and Kenny 2005), the *Common Fate Model* (CFM; Ledermann and Kenny 2011), the *Social Relations Model* (SRM; Kenny 1994), and *Response Surface Analysis* (RSA; Edwards 2002).

Statistical Approaches for the Analysis of Dyadic Processes

Unit of analysis. Research on dyadic processes considers data of both dyad members; thus, the unit of analysis is the dyad instead of the number of individuals. The latter are nested into dyads (e.g., two romantic partners form a couple). Therefore, the sample size is defined as $k = N/2$. For example, when collecting data from 400 supervisor-employee dyads, the sample size for the study of the dyadic data is defined as $400/2 = 200$ dyads (see also Kenny et al. 2006). It must be noted that the nested nature of the data affects the statistical power and the degrees of freedom when testing the statistical significance of effect estimates (for an overview on statistical and methodological consequences, see Kenny et al. 2006).

Actor-Partner Interdependence Model. The APIM considers a predictor (e.g., extraversion) and an outcome variable (e.g., satisfaction) for each dyad member. Further, the interdependence of the dyad members' predictor and outcome variables and their error terms is considered. The APIM allows for estimating the association between predictor and outcome variables by two effects: the *actor effect* (i.e., association between partner A's trait expression and partner A's satisfaction; same for partner B) and the *partner effect*, which describes the association of the predictor variable of partner A with partner B's outcome. For illustration, one might think of studying the relation between extraversion (predictor) and

relationship satisfaction (outcome); the actor effects describe the association between partner A's extraversion and his/her own satisfaction as well as the relation between partner B's extraversion and his/her own satisfaction. More interestingly, the partner effects describe how partner A's extraversion is related to partner B's satisfaction as well as the association between partner B's extraversion and A's satisfaction, which allows for examining how each dyad member contributes to their own satisfaction while also considering the partner's contribution under control of their interdependence (e.g., similarity in predictors and outcomes). Overall, the literature has shown that partner effects are typically numerically smaller than actor effects but show incremental value (Weidmann et al. 2016).

Further, researchers might be interested in how partners affect each other. Kenny and Ledermann (2009) proposed a method to examine the existence of particular *dyadic patterns*: the *actor-only* pattern (i.e., only actor effects but no partner effects exist within the dyad), the *partner-only* pattern (i.e., only partner effects but no actor effects exist within the dyad), the *couple* pattern (i.e., actor and partner effects exist), and the *contrast* pattern (i.e., actor and partner effects exist but are in the opposite direction; e.g., positive actor but negative partner effects).

The APIM also allows for adding dyad-level variables such as an interaction term (e.g., interaction of partner A's and partner B's extraversion) or an index of similarity (e.g., absolute differences between partners' extraversion or profile similarity across a number of traits) to estimate the magnitude of dyadic effects over and above each member's contribution to their respective outcomes. This overcomes methodological fallacies that might bias the findings, as ignoring the main effects of actors' and partners' predictors leads to overestimation of dyadic effects. For example, previous literature on the role of dyadic similarity (e.g., in personality, attitudes, and values) overestimated the role of similarity for relationship satisfaction (see Luo 2017; Weidmann et al. 2016). Thus, dyadic research should utilize methods that partition variance into effects of actors, partners, and their relationship.

Finally, the APIM can be extended to implement mediator variables (*Actor-Partner Interdependence Mediation Model*, APIMeM; Ledermann et al. 2011). The APIMeM allows for examining the effects of both partners' mediator variables and estimates how they affect partner A's and partner B's actor and partner effects. The APIMeM has helped to extend knowledge on which mechanisms and processes underlie dyadic interactions and their associations with external outcomes (e.g., the mediating role of interpersonal competence for the association between empathy and relationship quality in friendships; Chow et al. 2013).

Overall, the APIM is a popular and useful approach to study dyadic relationships, and its extensions allow for modeling the complexity of a variety of research questions when investigating dyadic processes. Researchers can choose whether the APIM is estimated by means of structural equation modeling or multi-level modeling (Kenny et al. 2006).

Common Fate Model. In comparison with the APIM, which examines the dyad in terms of each member's predictors and outcomes separately, the CFM allows for analyzing variables that are composed of both members' views (Kenny and Ledermann 2012). For illustration, one might think of the construct of *dyadic coping*, which describes how romantic partners deal with stressors in their relationship. Since both members contribute to how they jointly cope with stress, the construct should cover the views of both partners, and thus ratings of each partner are needed. The CFM treats a dyad-level construct as a latent variable, which is estimated using both members' responses as manifest indicators (Kenny and Ledermann 2012).

Further, the CFM can be utilized to describe dyadic processes over time (e.g., estimating change in dyadic coping between two time points) as well as effects of a dyadic predictor on a dyadic outcome (e.g., how does understanding each other affects relationship harmony; see Kenny and Ledermann 2012). Further, researchers might be interested in examining relationships between individual- and dyad-level variables, for example, when testing how each dyad member is affected

by a jointly experienced life event (e.g., child loss). In this case, hybrid models combining the APIM and CFM are available. Interested readers are referred to Kenny and Ledermann 2012), who discuss applications and examples for the usage of the CFM and its distinctions from the APIM. The CFM is computed by using structural equation modeling.

Social Relations Model. The SRM allows for analyzing three components of interest in dyadic research questions (As a technical note, it must be mentioned that an error term is computed as a fourth effect in the SRM, but this is not considered in further detail here. See Back and Kenny (2010) and Kenny (1994) for more information.), namely, the actor and partner effects and a relationship effect, which characterizes the unique interaction between an actor and his/her partner. In contrast to the previously described approaches, the SRM is based on more than one interaction of participants. Hence, each participant rates k partners and receives a reciprocal rating by each partner.

While the SRM allows for studying numerous variables (e.g., ratings of personality or behavioral acts), we will illustrate its effects with a study on interpersonal liking. Consider a group of four participants who meet for the first time and interact with each other for 5 min. Afterward, each of the four participants (Denis, Franz, Kira, and Maria) give ratings on how well they like their respective group members (A research design in which all participants provide and receive reciprocal ratings is called *round-robin design*. An alternative design is the *block design* that considers asymmetric combinations of participants (e.g., only reciprocal ratings between males and females).). Thus, there is data on how every participant is liked by their group members as well as how every member likes his/her respective group members. The SRM estimates three effects for each actor, each partner, and each interaction between two members. For example, the actor effect of Kira describes her general tendency to like others, whereas her partner effect describes how she is liked on average by the other three members. Similarly, actor and partner effects can be computed for Denis, Franz, and Maria. To capture the dyadic component of each interaction

between the four participants, a *relationship effect* is computed. This dyadic effect indicates how much variance is explained by the unique dyadic process between two persons while general tendencies of viewing others (actor effect) and being viewed by others (partner effect) are controlled. Thus, the three variance components give a first impression of the explanatory value of actors, partners, and their unique dyadic relationship.

The SRM allows for extending analyses toward the dyadic process of *reciprocity*. Firstly, the *generalized reciprocity* is computed as the correlation between actor and partner effects. Considering our example of liking, the generalized reciprocity informs how well liking others (actor effect) converges with being liked by others (partner effect) across the sample. A positive correlation would indicate that, on average, people who like others are also liked by others while participants who dislike others are also disliked by others. Hence, this describes trends across all studied dyads. Secondly, *dyadic reciprocity* is the correlation between dyad members' relationship effects. This allows for estimating the convergence of the unique liking between two members. While the description and example illustrated the SRM when studying a single variable (liking), the model can be extended to bivariate analyses. For example, one might be interested in how liking is related with the willingness to enter a romantic relationship with an interaction partner (see Back and Kenny 2010; Kenny 1994). Overall, the SRM estimates dyadic processes in complex ways and helps to understand the role of individuals and their relationship characteristics.

Response Surface Analysis. Finally, researchers might be interested in the *interplay* of two dyad members' attributes (e.g., expressions in personality traits, attitudes, values, etc.) to predict an outcome of one dyad member (e.g., one partner's satisfaction) or the dyad (e.g., dyadic coping). RSA allows for a fine-grained analysis of such effects on a third variable by using *both* dyad members' data in a polynomial regression model that describes a three-dimensional space (i.e., X/Y-axis = scores of partner A/B and Z-axis = outcome variable). RSA is often utilized to examine the convergence between members'

scores (e.g., similarity or agreement) and its effects on outcomes. A merit of RSA is the usage of the full information of both members' instead of transforming them into a dyadic index by means of an algebraic, absolute, or squared difference (Edwards 2002). This approach overcomes psychometric disadvantages of difference scores (e.g., loss of reliability, untested constraints, confounded main effects; see Edwards 2002) and describes the complexity of dyadic congruence and incongruence and its effects on criterion variables. While the standard RSA considers both dyad members' predictor scores, only one outcome can be predicted. Since researchers are often interested in how dyadic convergence affects both members' outcomes, the *dyadic response surface model* (DRSA; Schönbrodt et al. 2018) has been introduced to allow for the full dyadic analysis of predictors and outcomes by combining RSA with the APIM. Examples and computation guidelines can be found in Barranti et al. (2017) and Humberg et al. (2019).

Key Findings of Dyadic Processes

The methods described above have been utilized for a broad range of studies on dyadic processes using numerous methods and designs (e.g., behavioral measures, self-, peer, or partner reports). We will give a short overview of key findings from three major lines of research in dyadic research: the study of dyadic similarity (i.e., how dyad members resemble each other), interpersonal perception (i.e., how accurately dyad members perceive others' traits), and co-development (i.e., does the individual affect its social network and/or does the social network affect the individual that is embedded in its social network).

Similarity. As mentioned previously, the role of similarity has been studied in dyadic research across types of relationships with respect to two key issues: (1) describing the similarity between two people and (2) testing whether similarity affects outcomes (e.g., are similar couples happier than dissimilar couples?). In sum, the literature supports the notion that relationships are

characterized by partner similarity instead of complementarity across a wide range of variables such as age, intelligence, attitudes, personality traits, and habitual behaviors (e.g., hobbies; for an overview see Luo 2017). Recently, this robust finding has been replicated across 45 countries (Conroy-Beam et al. 2019). It has been suggested that similarity contributes to low disagreement in couples, as they share similar views and behave accordingly, which reduces the potential for disagreement, facilitates satisfaction, and thereby contributes to healthy and positive relationships. However, the literature shows that similarity has only small effects on outcomes beyond the contribution of actor and partner effects (Luo 2017; e.g., Brauer and Proyer 2018; Proyer et al. 2019; Weidmann et al. 2016).

Interpersonal Perception. When people interact, they form impressions about others (e.g., their personality traits or intelligence) in order to predict and estimate their future behaviors. Such judgments occur across life domains and types of acquaintanceship – for example, when teachers form impressions about students, supervisors about their employees’ performance, or when making judgments about potential partners. Thus, perceptions of others concern a typical dyadic research question. In this line of research, the dyad is composed of a *target* person who is judged by an *observer* (also called *perceiver* or *judge*). Overall, the literature has shown that people can infer others’ traits accurately and above chance, even when making inferences about strangers at zero acquaintance (e.g., Proyer and Brauer 2018; for an overview see Connelly and Ones 2010). While most interpersonal perception studies analyze the overlap between targets’ self-ratings and observer ratings (*self-other agreement*), there is robust evidence that judgments possess predictive validity for naturalistic outcomes such as academic achievements or job performance (Connelly and Ones 2010; also see Ambady and Rosenthal 1992).

Overall, it is suggested that accurate judgments about others facilitate everyday decision-making across all domains of life and have consequences for both the judge and the judged person as mate choices, hiring decisions, or student evaluations

are based on interpersonal perceptions. Finally, the field has provided evidence that moderating variables such as the length of the acquaintanceship, the evaluativeness and observability of traits, as well as characteristics of targets and judges affect the goodness of perceptions (Connelly and Ones 2010). Taking previously mentioned findings into account, accurate perceptions of others are the prerequisite to finding partners who show desired characteristics and/or are similar to oneself.

Co-development. Since people are embedded in social systems in private and work life, it has been argued that dynamic transactions between the social environment (e.g., peers, teachers, or romantic partners) and the individual exist (cf. “Why Studying Dyadic Processes Matters”). There is robust evidence for this assumption, as longitudinal studies examining the dynamic relationships between the individual and its social network support the notion that people choose and maintain relationships that suit their personality (i.e., selection effects) and that the social environment affects the individuals over time (i.e., socialization effects; Neyer et al. 2015 and Wrzus and Neyer 2016). The findings indicate that changes in personality traits predict changes in social network characteristics and vice versa. Thus, social interaction and its underlying dyadic processes affect how personality is shaped, while the personality of those within the social network contributes to shaping and maintaining the social relationships.

Conclusion

The description and study of dyadic processes is a complex topic because researchers are faced with additional methodological challenges to account for the interdependent nature of dyad members’ predictor and outcome variables while accounting for their unique dyadic relationships. Within the realm of available methods, researchers must choose the appropriate analysis procedure depending on their research question and design.

However, the presented findings underscore that people exist and develop within social

networks across all areas of life. There is broad evidence that actors' outcomes, such as happiness and satisfaction, are also uniquely affected by their partners (e.g., peers, romantic partners, family members) or characteristics of the relationships (e.g., similarity, length of acquaintance). Thus, to truly meet psychology's core aims of describing, understanding, explaining, and predicting humans' patterns of behaving, thinking, and feeling, it is advisable to extend studies toward people's interpersonal relationships and examine their role for the individual.

Cross-References

► Dyadic Relationships Versus Group Processes

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Dyadic Relationships Versus Group Processes

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Synonyms

Group living; Marriage; Pair bonds

Definition

A dyadic relationship comprises two individuals who are more or less interdependent and who need one another to facilitate their survival and reproductive goals. Groups comprise three or more similarly interdependent individuals who may or may not be related, and who cooperate with one another to achieve common goals. Both dyads and groups may experience conflict when self-interest trumps mutual benefit. Groups also compete with each other for control of resources.

Introduction

From the moment of birth, humans have been crafted by evolution to desire relationships with those who are best placed to meet their needs, and to find happiness and security in the company of those who value and care about them. Further, and in the interests of successful reproduction, humans possess powerful motivations to establish committed pair-bond relationships that facilitate the survival of offspring. From an evolutionary perspective, then, humans are equipped with the psychological mechanisms required to successfully engage with their social world and to meet its challenges and opportunities.

To what extent might these mechanisms be specific to particular kinds of relationship and group contexts? Unlike social groups, for example, pair-bond relationships are characterized by proximal, mating-relevant interests and goals, such as the need to secure partner commitment, negotiate relationship threats such as the availability of attractive alternatives, and successfully manage the exigencies of raising offspring. On the other hand, a variety of processes occur within and between social groups such as stigmatization, social exclusion, prejudice, and warfare that would seem to have little relevance to either pair bonds or other types of dyadic relationships, such as friendships. However, there are aspects of both dyadic and group relationships that present the same, basic challenges to their successful functioning, such as competition for resources, the need for cooperation, and the costs of betrayal. It

seems likely that some of the adaptive psychological mechanisms that have helped humans meet these and other social challenges over the course of their evolutionary history operate in both dyadic and larger group contexts. Our aim in this chapter is to briefly discuss some of the unique and shared aspects of dyadic relationships and group processes, and to examine the critical role of emotions as evolved psychological mechanisms that facilitate both dyadic and group functioning.

Dyadic Relationships: The Formation and Maintenance of the Pair Bond

Social psychologists have long been interested in the phenomenon of interpersonal attraction, and what draws people to one another (Berscheid and Reis 1998). There is now a large body of research demonstrating the fundamental features of social selection amongst humans, each of which is potentially adaptive for their welfare and survival (Barclay 2016). One important feature is familiarity, signaling safety and predictability, while another is perceived similarity, signaling rewards such as reciprocity of attraction and, potentially, genetic relatedness (see Kurland and Gaulin 2005). A third feature is physical attractiveness, including facial symmetry and signs of good health (and potentially, fertility). This latter feature is particularly relevant in the context of sexual selection, but also plays a more general role in social selection, with cross-cultural research demonstrating that physically attractive individuals (including children) tend to enjoy higher status and attract preferential treatment from others (Langlois et al. 2000). One explanation for this evolved preference is that people implicitly associate physical attractiveness with other positive qualities such as intelligence, kindness, and success in life. At a proximal level, these qualities enhance the desirability of attractive individuals both as friends and mating partners. At a more fundamental level, it appears that humans possess an evolved psychological mechanism that drives both affiliative and mating preferences towards others who, on the basis of their physical

attractiveness, are relatively “good bets” with respect to also possessing superior health and resources (Fitness et al. 2003).

There are, however, aspects of mate selection that distinguish it from other kinds of social selection. Specifically, and as Buss (1989) demonstrated in his cross-cultural research, both men and women place primary importance on emotional stability and kindness in a potential mating partner. These are important safety signals given the risks of exploitation and betrayal in a sexually intimate relationship. However, men and women differ with respect to the importance they place on the desirability of physical attractiveness and the possession of resources, including status. Specifically, and in line with their reproductive interests, men’s mating preferences tend toward relatively young, physically attractive (and likely fertile) women, while women’s mating preferences tend toward older men with the resources to support their offspring. Even so, there are important caveats to these general preferences, depending on context. For example, women who are seeking short-term rather than long-term mating opportunities, may, like men, place relatively more importance on “good genes,” signaled via physical attractiveness, than on resources (Buss and Schmitt 1993).

Another mating-specific psychological mechanism that effectively switches off mate-seeking motivations and switches on commitment to the current mate is the intense and sometimes overwhelming experience of romantic love (see Fletcher et al. 2015). Romantic love is theorized to comprise two evolved systems with discrete functions. The first system, passionate love, integrates sexual desire with deep longing for, and obsession with, a mating partner. The evolved function of passionate love is to motivate mating, the ultimate outcome being the successful transmission of an individual’s genes to the next generation. The second evolved system, attachment love, may be further divided into two subsystems. The first is nurturing, or care-giving love, the primary function of which is to provide offspring with the unconditional commitment they require to survive and thrive. However, romantic lovers also nurture and care for one

another when necessary, and powerful feelings of tenderness may be aroused by a partner's perceived vulnerability (Fitness 2015). The second subsystem of attachment-love is intimate, or "companionate," love characterized by strong emotional bonds and commitment, the function of which is to facilitate the maintenance of the pair bond over time and provide an environment conducive for successful reproduction and child-rearing (Berscheid 2010).

It has been proposed that the human attachment system is the "*sine qua non*" of both parent-child relationships and adult pair bonds (see Gillath et al. 2016, for a review of the voluminous literature on this topic). Further, attachment processes are also active within close, platonic friendships, particularly during adolescence, when young adults may shift some attachment functions from their parents to one or more close friends (Gillath et al. 2016). This may be especially true for young women, whose same-sex attachment bonds are frequently emotionally intense, intimate, and long-lasting. It has been proposed that these intimate bonds between women are adaptive psychological mechanisms derived from an evolved history of exogenous mating; i.e., women have frequently had to leave their own kinship groups and join their mates' groups (Vigil 2007). Under these circumstances, and in the potential absence of adequate partner support, women needed (and arguably still need) the care and support of one another for successful child-rearing (Sear 2016). Support for this hypothesis is strengthened by the observation that in general, men's friendships with one another tend not to involve the same kinds of emotional intimacy and companionate love as women's closest friendships (Fehr 1996). As will be discussed later in this chapter, men tend to have different requirements for friendships that involve the coordination of shared goals and activities (see also Kurzban and Neuberg 2005). At any stage of life, however, both men and women may develop close, same-sex friendships characterized by nurturance, intimacy, and trust, with the warmth and love associated with these relationships providing a significant source of ongoing, mutual support.

Conflict in Dyadic Relationships

As discussed above, close relationships such as the pair-bond, close friend, and parent-child relationships are the source of some of our most powerful and positive emotional experiences. However, as noted by Shakespeare, "the course of true love never did run smooth," and these close relationships also provide the context for some of the most painful emotions that humans can experience (see Fitness 2015). Romantic jealousy, for example, is a powerful emotion experienced by individuals in every culture in response to the perceived diversion of resources (including sex and love) to a rival. Further, and in line with their reproductive interests, there are reliable sex differences with respect to the events that trigger the most intense jealousy. Specifically, and in line with the threat of paternity uncertainty, men are most incensed by a partner's sexual infidelity, whereas women are most threatened by a partner's deep emotional attachment to a rival that might, in turn, lead to the loss of commitment and resources (Buss 2018). Similarly, sex differences have been found with respect to the types of deception that men and women find most upsetting. For example, women are more upset and angry than men by their partner's concealment of an emotional bond with other women, while men are more upset and angry than women when their partner is sexually unfaithful in the context of a long-term relationship (Haselton et al. 2005).

Clearly, romantic love and romantic jealousy are potentially adaptive psychological mechanisms, shaped by natural selection to facilitate mating and mate-guarding. However, humans possess a range of other discrete emotion systems that motivate potentially adaptive behaviors in the close relationship context. Ellis and Malamuth (2000), for example, demonstrated that feelings of love and anger in married couples operate independently of one another, with love tracking strategic facilitation (how well is my partner meeting my needs?) and motivating continued commitment, and anger tracking strategic interference (my partner is blocking my desires and goals) and motivating behaviors to remove the blockage,

some of which may involve aggression and violence.

Perhaps the most potent sources of anger in dyadic relationships derive from perceived exploitation and acts of betrayal. Close relationships are characterized by both partner interdependence and communal norms and values, such as mutual responsiveness to each other's needs. In communal relationship, partners do not keep close track of costs and benefits as they would in an exchange or quid pro quo relationship (such as with the plumber in an employment relationship). Rather, they trust that their partners are committed to their welfare and will act in their best interests (Clark et al. 2001). However, high trust also means high risk, and vulnerability to the possibility that one's partner may cheat (e.g., by taking more resources than they invest; see Shackelford and Buss 1996). Such perceived inequities are a major cause of anger and marital dissatisfaction (Sprecher 2018).

Acts of betrayal, too, may range from the relatively minor, such as ignoring a partner's wishes or failing to consult about what should be a joint decision, to physical and/or sexual abuse, infidelity, deception, and desertion (Fitness 2001). Such violations of relational "rules" and expectations may generate not just anger but a range of other powerful emotions such as fear, grief, or even hatred, depending on how the injured partner appraises the threat to their welfare. Hurt, for example, tracks partners' perceived investment in the relationship and is elicited in response to behaviors signaling that one's partner does not value the relationship as much as had been assumed (Fitness 2015). The pain of relational hurt may be experienced as traumatic, with the devalued partner experiencing the shame and fear of being found unlovable and unworthy in what was meant to be a secure, safe haven.

Once a relational rule has been violated, an injured partner can choose either to maintain the relationship or terminate it, and this decision depends on a number of factors. For example, if the violation has been appraised as relatively severe and/or re-occurring, then termination may be seen as the most adaptive option (particularly if there are attractive alternatives available). From

an evolutionary perspective, however, it may also make sense to "kiss and make up" if partners are heavily invested in the relationship and there are still tangible benefits, such as security or shared child-rearing responsibilities, that outweigh the costs, such as emotional pain. An evolved propensity to forgive and reconcile with close others clearly has adaptive value and plays an essential role in the maintenance of important relationships, especially among kin and between pair bonds. However, forgiving also involves the risk of further offending and exploitation of the forgiver; hence, the process of forgiveness does not imply that there are no costs imposed on the offending partner (see Fitness and Peterson 2008). Indeed, one of the defining features of anger is the motivation, not just to remove an obstruction to one's goals but also to punish the perceived cause of the obstruction.

From an evolutionary perspective, punishment serves a behavioral deterrence function, signaling aversive outcomes of repeat offences. In the proximal context, punishment restores some power to the punisher and importantly, may feel good, even when personally costly (e.g., cutting off one's nose to spite one's face). In a study of marital betrayal and forgiveness, Fitness (2001) found that a range of punishments had been imposed on offending partners, from the relatively mild (e.g., regular reminders of the offence, publically telling family and friends about it) to the more serious (e.g., exclusion and "the silent treatment," verbal and physical abuse). Some of the latter punishments became hurtful relational transgressions in their own right foreclosing possibilities of reconciliation as partners become trapped in escalating cycles of conflict (see also Gottman and Driver 2005).

In summary, couples in close relationships are challenged by the need to deter exploitation and future harm via punishment, with restoring relationship benefits via forgiveness. Different emotion systems can help them to do that. Being in love, for example, helps partners to put a "positive spin" on each other's shortcomings and facilitates charitable explanations for partner offences (Fitness et al. 2003). Similarly, genuine displays of an offending partner's guilt and remorse may

motivate empathy and compassion and facilitate forgiveness (Fitness 2001). However, there is still much to be learned about the ways in which dyadic partners manage these delicate negotiations in the interests of recalibrating their relationships, and the potential role of powerful avoidance emotions like hatred, contempt, disgust, and shame, in shutting down such negotiations entirely.

Group Processes and Intergroup Conflict

Just as no individual or dyad can survive alone, so too do humans need the support of groups within which they can share resources for their mutual benefit and protection (Van Vugt and Schaller 2008). It has been proposed that, just as humans have evolved psychological mechanisms to facilitate pair bonding and parental care, so too have they evolved psychological mechanisms that facilitate their capacity for living in groups (Kurzban and Neuberg 2005). For example, one of the most important aspects of group living involves the willingness of group members to cooperate with one another and to reciprocate valued resources. Given that the willingness to co-operate necessarily entails some self-sacrifice, it is important when advertising oneself as a potentially desirable group member to demonstrate qualities of unselfishness, trustworthiness, and commitment to the group. As noted previously, these qualities are also highly attractive in the dyadic context, whether one is “in the market” for a mating partner or a close friend (Barclay 2016). Similarly, in both social contexts there is the risk of false advertising, and in both contexts humans are finely attuned to the identification and punishment of cheats who threaten the welfare of the dyad or the group (Shackelford and Buss 1996; Van Vugt and Schaller 2008).

Further, in the course of group formation and maintenance, group members become increasingly interdependent with the associated benefits and costs that such interdependence entails. For example, being accepted into valued groups is rewarding, and collaborative group interactions have the potential to generate happiness and joy,

emotions that build and strengthen friendships and attachment relationships (Fitness 2015). However, and as noted above, to the extent that group members develop broad and deep interdependencies, so too do they become vulnerable, just as dyadic partners do, to the risks of betrayal. Further, just as such violations of relationship “rules” generate powerful emotional responses in dyadic relationships, so too within groups do such threats activate emotional responses such as anger, with its corresponding motivations and behaviors, including punishment of offending group members. Indeed, the motivation to punish traitors who are perceived to have acted against the interests of the group (and potentially delivered them to a hostile outgroup) is especially powerful (Kurzban and Neuberg 2005). The Italian poet Dante, for example, assigned traitors to the lowest and coldest regions of Hell, to be forever frozen up to their necks in a lake of ice as punishment for having behaved so heinously. In line with the theme of “freezing out,” one of the most frequent punishments for perceived offences by an in-group member is social exclusion and ostracism. These are particularly severe penalties given the fundamental human needs for belonging and protection. As noted previously, close relationship partners may also use this form of punishment, with “the silent treatment” having been described by some relationship partners as worse than abuse (which at least reminds them that they exist; see Williams et al. 2005).

Perhaps one of the most powerful group contexts that exemplifies the rewards and costs of group living is the family. Families are prototypically communal contexts, characterized by complex interdependencies and shared responsibilities for each other’s welfare. Further, the benefits and costs of family life are particularly potent because family members typically are genetically related to one another by varying degrees and so must frequently negotiate conflicts between the competing demands of self-interest (e.g., when a child would prefer to monopolize parental resources) and self-sacrifice (e.g., when the same child is required to share resources to facilitate the survival of a brother or sister (see Kurland and Gaulin 2005)). One important implication of this conflict

is that for self-sacrifice to be worthwhile, family members must be sure that they are, in fact, genetically related to one another. In one investigation of favored and disfavored family members (Fitness 2005), respondents reported that the primary reason for their “black sheep” status was either explicit genetic unrelatedness (i.e., they were adopted) or that they were perceived by other family members to be “different” and to not “fit in.” This was in contrast to favored family members, who were more likely to report talent, “goodness,” likability, and similarity to the parent as reasons for their favored status. As noted in the discussion of interpersonal attraction, similarity is a fundamental feature of acceptability to others, signaling mutual rewards and in the context of kin selection, likely genetic relatedness. Further, just as social exclusion is a prominent feature of dyadic and within-group punishment, so too the consequences for familial black sheep were frequently severe, ranging from total exclusion to “chilly” politeness, reminding them of their “outsider” status. Clearly and despite the mythology of the family as a “safe haven” characterized by unconditional love and forgiveness, like every other group, families have rules, boundaries, and punishments. The costs of exclusion are decidedly higher, however, than expulsion from one’s book club and may contribute to lifelong feelings of shame, anger, and depression (Fitness 2005).

Just as competition for scarce resources can generate within-group tension and conflict, so too can competition *between* groups generate intense rage, hatred, and contempt, unmitigated by any history of cooperation or shared fate. Based in part on the strength of these emotional responses, Kurzban and Neuberg (2005) suggested that there may be specific adaptations serving group-based competition functions, such as enhanced within-group cooperation when under threat from an outgroup, and the formation of strong coalitional bonds amongst men, motivating aggression and warfare. Importantly, they also noted that the most severe forms of antisocial behavior tend to be targeted toward groups that are perceived to be internally coordinated and cooperative, implying that tightly-knit kinship groups may be perceived by other kinship groups,

or tribes, to represent the most threatening categories of “outsiders.” Cottrell and Neuberg (2005) further argued that a threat-based framework is useful for predicting the emotional responses of in-group members, such as fear or outrage, to particular outgroups, with specific emotions activated in response to specific kinds of perceived threats. Outgroups that are perceived as threats to physical safety, for example, will elicit fear within the in-group; those that threaten in-group resources will elicit anger; and those that appear to threaten health or in-group morals will generate disgust. In this way, the same fundamental emotion systems that operate within dyadic and in-group contexts may be co-opted for service in the context of out-group hostility, derogation, and even genocide.

Conclusion

As noted throughout this chapter, the emotional responses of humans in any kind of social relationship provide a rich source of information about their perceptions, interests, and goals. It should be noted, however, that the emphasis in much of the work on within-group and intergroup processes has focused on threats and challenges, leaving gaps in our understanding of the potential roles other emotions may play in both enriching within-group relationships and encouraging more conciliatory relationships with outgroups. For example, and as discussed previously, emotions such as liking, love, and joy feature prominently within dyads and groups, signaling that needs and goals are being facilitated, and strengthening bonds. Further, couples, family members, and close friends may frequently experience the relationship-enhancing emotions of pride, admiration, and gratitude in relation to one another (Fitness 2015). Unfortunately, the corollary to these warm, within-group feelings may be cold, hostile feelings toward outgroups. Researchers are speculating on the potential roles of compassion, guilt, and empathy as ways of breaking down perceptions of “other-ness” and acknowledging out-group members’ common needs and interests (e.g., see Goetz et al. 2010; Karaçanta

and Fitness 2006). However, much of this work is still speculative, and given the ancient imperatives of kin selection, it is likely that intergroup conflict will always constitute a challenge for scholars to fully understand, and for humankind to ameliorate.

Cross-References

- Cooperation
- Emotion
- Group Living
- Pair-Bonding
- Romantic Attachment

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whether a trait is socially desirable or not may be influenced by the role played by that trait in *multi-level selection*, with traits deemed desirable or eugenic having typically been the ones that were historically promoted during periods of intergroup competition and expansion via group selection. By contrast, traits that solely promote individual-level selection at the expense of group-level fitness, or pathologies that result from mutational accumulation, are the ones that are typically deemed to be undesirable and dysgenic.

D

Dyads

► Peer Groups

Dysfunctional

► Antisocial Behavior

Dysgenic Concerns

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Introduction

The idea that certain patterns of fertility are dysgenic or eugenic is intimately coupled with normative considerations of social desirability. Further muddying the waters of this discussion are the ethical issues associated with the sorts of counteractive measures proposed by eugenicists to mitigate dysgenic concerns (i.e., sterilization, marriage licencing, financial incentives toward low or high fertility, etc.). Recent work has attempted to strip concepts like dysgenics and eugenics of their normativity by linking them (and their valancing in terms of social desirability) with multilevel selection, thus permitting these terms to be used objectively. This article will consider this recasting in detail before moving on to a discussion of whether patterns of fertility and other genetic changes actually justify dysgenic concerns historically.

Synonyms

Cacogenics; Genetic deterioration

Definition

Dysgenic concerns stem from the tendency for the genes underlying traits deemed *socially desirable* to decrease in prevalence as a consequence of selection pressures disfavoring their reproduction and the accumulation of mutations that degrade their function. In the West, the perception of

Review

Overview

The term *dysgenics* describes the tendency for the carriers of certain traits deemed socially undesirable to reproduce or otherwise proliferate to excess, and was first coined by Caleb Williams Saleeby (1913). This concept was expounded upon by Galton (1868), who identified three major classes of traits, high levels of which were considered to be socially desirable and necessary for the maintenance of civilization. Galton's three trait classes were *intellect*, *good character*, and *health*. To counter the

existential threat to civilization that Galton perceived to stem from the high fertility rates of those with low levels of these traits, a system of artificial selection known as *eugenics* (meaning good breeding) was proposed as a means of ensuring human betterment via the control of heredity.

Multilevel Selection

The idea that some traits (such as intelligence, altruism, etc.) are socially desirable is a value judgment; hence terms like dysgenic and eugenic are intrinsically normative and thus nonscientific, given that selection has no preferred direction in nature. Eugenic attributions of higher “fitness” to the carriers of traits like high intelligence (e.g., Lynn 2011) are no less problematic, especially given that the carriers of such traits seem to be at a fitness disadvantage in modern societies.

Recently however the case has been made that terms like eugenic and dysgenic might be empirically grounded when used as descriptors of the consequences of shifts in the relative strengths of individual vs. group selection in multilevel selection (Woodley and Figueredo 2013). High intelligence and altruistic disposition would seem to feed into group-level fitness, especially in the case of the sorts of unusual cognitive and personality combinations that characterize the *genius phenotype* – such individuals being capable of significantly increasing group-level fitness via *disruptive innovation* (e.g., innovations in cartography aiding colonization, engineering innovations aiding weapons manufacture, etc.) (Hamilton 2000). Consistent with this inference, despite having a large impact on group-level fitness, historical data indicate that geniuses typically fail to achieve replacement-level reproduction at the individual level (Simonton 2003). Another critical component of group-level fitness as it pertains to human populations is the presence of conditions that reduce the *relative fitness* of those exhibiting low levels of intelligence, poor social skills, etc., such as high extrinsic morbidity and mortality stemming from environmental (i.e., cold, famine, disease) and social (i.e., violence and warfare) harshness. Such conditions historically enhanced the relative fitness of those exhibiting higher intelligence,

lower time preferences, greater impulse control, and so on, facilitating the eventual *embourgeoisement* of Western populations via the downward social mobility of the elite reproductive surplus (Clark 2014). This would have simultaneously increased the probability that rare group-selected phenotypes will arise via population growth, who can further enhance this growth via their innovations (Hamilton 2000; Woodley and Figueredo 2013).

Conditions conducive to group selection prevailed throughout much of the West up until the nineteenth century, when reductions in the relative frequency and intensity of intergroup conflict diminished consistent with the period known as *Pax Britannica*, which spanned the nine decades from the end of the Napoleonic Wars to the First World War. Rising global temperatures coupled with advances in medicine and social innovations (such as welfare) released Western populations from many sources of ecological stress, which would have had the effect of reducing reproductive constraints on large segments of these populations. The rise of education and increased economic competition among individuals within Western populations would have furthermore imposed constraints on the relative fitness of the carriers of higher levels of intelligence and other bourgeoisie phenotype components, thus establishing gradients of dysgenic fertility with respect to these traits. This would have the effect of lowering the aggregate population levels of these traits with time (Lynn 2011; Woodley of Menie et al. 2018a).

Thus, when considered in terms of multilevel selection, the idea that certain patterns of fertility are objectively “good” or “bad” makes empirical sense, as fertility patterns can either *enhance* or *undermine* group-level fitness. The folk notion of social desirability therefore seems to be implicitly linked with considerations of cost-benefit trade-offs at the level of group fitness. Scrutiny of the writings of eugenicists from the early and mid-twentieth centuries indicates that they were cognizant of this, as they placed a premium on the promotion of traits clearly necessary for group selection such as selflessness and communal orientation, which they in turn saw as necessary for

the enhancement of society (Woodley and Figueredo 2013).

Coupled to alternating patterns of group- vs. individual-level selection is the idea of *mutation accumulation*, which results from the relaxation of purifying or mutation-eliminating selection on populations. The rate at which *de novo* mutations accrue in the germ lines of humans is around 100 per diploid genome per generation (Lynch 2016). The *mutation load paradox* postulates that such a rate of accumulation should lead to around 80% of the population failing to reproduce with reproductive surpluses among the remaining women of 16 or more children being necessary in order to ensure population viability (Kondrashov and Crow 1993). While reproductive failure and surplus of this magnitude are not observed among modern Western populations, pre-reproductive death and reproductive failure rates were and indeed still are extremely high (>50%) in premodern populations, likely because the negative pleiotropic impact of these mutations on aspects of cognition, personality, and health would have had higher fitness costs in the context of the harsher physical and social environments that characterized the West historically and still characterize much of what is termed the developing world today. The mutation load paradox can therefore be solved in part by stipulating that under modern conditions, the reduced fitness cost to having these mutations is permitting them to accumulate, which in turn is engendering subtle, cumulative fitness losses, both directly at the level of fertility and indirectly through their pleiotropic effects upon behavior (Lynch 2016, see quasi-empirical simulation in Woodley of Menie et al. 2018b), which may have implications for the maintenance of group-level fitness also. This is especially the case if some of these variants induce behavioral changes that significantly disturb group-selected cultural formations that engender fitness enhancing norms (Woodley of Menie et al. 2017a).

Actual Dysgenic Consequences

It has recently been found that selection operating on factors such as height, BMI, and age of menarche can produce meaningful changes in the

population means of these traits in just a handful of decades (Stearns et al. 2010).

The trait that has been most closely studied by those interested in dysgenics is intelligence. The *co-occurrence model* (Woodley and Figueredo 2013) posits that genetic selection and environmental enrichment have opposing effects on different variance components of intelligence, with selection effects being largest on the more heritable and more general intelligence (*g*)-loaded intelligence measures and the effects of the environment being largest on the less heritable and more specialized intelligence measures. Hence *g* may be declining in populations as a consequence of genetic selection, whereas specialized cognitive skills may be growing as a consequence of the Flynn effect (the secular increase in IQ of three points per decade). The growth in the latter is larger than the decline in the former; hence at the level of aggregate intelligence, IQ scores appear to be rising. Certain intelligence indicators may by virtue of very high or cross-temporally stable *g*-loading and high heritability, be declining nonetheless, when considered in isolation. Consistent with this dysgenic selection directly predicts the decline in usage frequencies of hard-to-learn vocabulary items across 100 years of sampling from a large textual corpus, even when controlling for rising literacy, word age, and serial autocorrelation effects. Usage of easy-to-learn words is increasing in frequency however in response to rising literacy, consistent with the Flynn effect (Woodley of Menie et al. 2015). A similar pattern has been noted in the case of digit span performance, where more highly *g* loaded working memory measures show signs of having declined over time, whereas the less *g* loaded short term memory measures show the opposite pattern (Wongupparaj et al. 2017). Parallel secular declines in factors such as processing speed, the per capita prevalence of macro-innovations and indicators of 'social intelligence', starting in the mid-nineteenth century, may also result from genetic selection on *g* (Woodley of Menie et al. 2017b). Consistent with this, it has been found that approximately 25% of the variance in the decline among these indicators can be predicted using polygenic scores that are predictive of both education

attainment and g and are declining over time in certain populations (Woodley of Menie et al. 2018a, see also Kong et al. 2017).

Concerning possible trends toward reduced *developmental stability* potentially resulting from mutation accumulation, Rühli and Henneberg (2013) list six medical abnormalities that have increased in prevalence throughout the twentieth century. There are parallel secular increases with respect to sinistrality (left-handedness) and certain measures of fluctuating asymmetry which may also track an underlying decline in developmental stability (Woodley of Menie et al. 2017b). It is also possible that the increase in the prevalence of neurodevelopmental disorders such as autism may, in part, be driven by mutation accumulation, although properly conducted longitudinal studies are required in practice to confidently make this inference (Lynch 2016).

Conclusion

Dysgenics can usefully be thought of as any genetic change, which either increases individual fitness or causes degradation of function, in both cases at the expense of group-level fitness. Dysgenics thus defined can be said to objectively correspond to a measurable negative outcome – i.e., reduced group-level fitness. The special emphasis placed on certain classes of trait historically by eugenicists, high levels of which have the potential to boost group-level fitness, suggests that folk notions of social desirability are intimately connected with the perceived costs and benefits of these traits to group-level fitness. This conceptualization also reduces the potential for *fact-value conflation*, as a pattern of fertility that has empirically deleterious consequences for group-level fitness, does not necessarily entail any particular course of *meliorational* political action – dysgenics in these instances simply becomes an empirical description of an objective phenomenon.

It is clear also that patterns of selection and mutation accumulation, starting in the mid-nineteenth century, may justify dysgenic concerns with respect to several traits.

Cross-References

- [Eugenics](#)
- [Mutation Accumulation Theory](#)

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Dyssocial

► Antisocial

E

E. O. Wilson

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Synonyms

Author; Biologist; Entomologist

Definition

Edward Osborne Wilson is an American biologist recognized as one of the foremost authorities on the study of ants. He is also widely considered as the father of sociobiology.

Introduction

Edward Osborne Wilson (born June 10, 1929) is an American entomologist, biologist, naturalist, and researcher. He graduated in biology at the University of Alabama, and, in 1956, he started to be part of Harvard University. In 1996, Wilson officially retired from the faculty of Harvard, but he continued to hold the seat of Professor Emeritus and Honorary Curator in Entomology. Edward O. Wilson is the author of books like *The Insect Societies* (1971), *Sociobiology: The New Syntheses* (1975), *On Human Nature* (1978),

The Ants (1990), and *The Diversity of Life* (1992). In this context, he is best known for studying *Sociobiology* and *Biodiversity* and for his relevant contributions in ecology – with the *Theory of Island Biogeography*. Moreover, Wilson is recognized for his biological specialty of the study of ants, what is called *myrmecology*.

Sociobiology

Wilson (1978) defines *Sociobiology* as the systematic study of social behavior focusing on biologic aspects. It is emphasized that this branch of knowledge covers all kinds of organisms, including humans. Regarding this, Wilson (1978) states that *Homo sapiens* is a species that exhibits a great genetic diversity that affects its behavior. Thus, for him, it will soon be possible to identify and locate specific genes that influence social behavior, even the most complex ones.

Moreover, it is relevant to say that the exposure of *Sociobiology*, brought by Wilson, instigated criticism from scientists, especially because the author includes the human species on his studies, along with the other animals. About it, Wilson (1976) affirms that it is possible to extend the sociobiological methods to humans, even if their behaviors are more complex and flexible. Beyond that, many social scientists do not recognize *Sociobiology* because they believe that culture has no genetic basis (Wilson 1978). However, the author exposes that geneticists have already

shown that several traits that affect social behavior have hereditary influence (Wilson 1978).

“Lord of Ants”

As previously stated, Edward O. Wilson is known for his studies on insects, focusing especially on ants. In 1990, Wilson and Hölldobler published the book titled *The Ants*, in which ideas such as the importance of the abovementioned species, its origin, its social behaviors, and the form of organization of its colonies are approached. In this sense, Wilson and Hölldobler (2005) assert that “ants are especially notable among the insects for their ecological dominance as predators, scavengers, and indirect herbivores” (p. 7411). Thus, the authors expose that the evolutionary history of the ants is relevant, since the ants demonstrate to have an extremely advanced social organization, besides the environmental influence at world levels (Wilson and Hölldobler 2005).

Biodiversity

According to Ehrlich and Wilson (1991), biodiversity studies refer to the systematization of all types of organisms, including the study of ways to preserve diversity and how it can be used for society’s benefit. In this sense, these authors affirm that the diversity of life can be considered a central theme on biology and that biodiversity studies “combine elements of evolutionary biology an ecology with those of applied biology and public policy” (Ehrlich and Wilson 1991, p. 758).

Regarding the progress of the knowledge about Earth’s biodiversity, over the past 250 years, Raven and Wilson (1992) explain that it has been rather slow because of the vast diversity on this planet – since it allows that many species live together in the same place (Wilson 1994). In this context, Wilson (1994) affirms that “the study of biodiversity is one of science’s greatest challenges, and humanity’s greatest needs” (p. 7). On the one hand, this enormous diversity shows itself as a source of wealth, promoting benefits for society – such as pharmaceuticals, petroleum substitutes, and other products useful to humanity

(Raven and Wilson 1992). However, on the other hand, all this biodiversity seems to be fading away at a rapid pace, mainly because of habitats’ destruction, deforestation, and pollution (Raven and Wilson 1992).

Concerning what has been previously stated, Wilson (1994) suggests that for thousands of years, human activity has been reducing the biodiversity of the Earth. To solve this problem, he says that the excessive growth of the human population must be controlled and proposes that each country should create a population’s control policy, calculating the ideal size of population for the preservation of biological wealth (Wilson 1994).

Island Biogeography Theory

In 1967, as a result from the partnership between Robert MacArthur and Edward Wilson, *The Theory of Island Biogeography* was published, representing a transition, in the context of ecology and biogeography, from studies with a descriptive perspective to studies with analytical approaches (Losos and Ricklefs 2010). In the first chapter of the aforementioned book, the authors highlight the relevance of an island as a study object, once it is the most appropriate unit for the beginning of scientific comprehension (MacArthur and Wilson 1967).

The authors understand insularity as a universal feature of biogeography, insofar the principles displayed in remote archipelagos apply in a certain degree to all natural habitats (MacArthur and Wilson 1967). Therefore, the purpose of *The Theory of Island Biogeography*, as stated by the authors, was to perform an examination of the possibility of a biogeography’s theory at the species level (MacArthur and Wilson 1967). The development of such theory took place by relating species distribution with population ecological concepts (MacArthur and Wilson 1967).

Among the contributions brought by the theory was a graphic which indicates the MacArthur-Wilson equilibrium model (Losos and Ricklefs 2010). Thus, the theory’s remarkable implication was that the biota of an island has a system by which species disappear, being replaced by new individuals at an equal proportion, assuming

a dynamic steady state (Losos and Ricklefs 2010). MacArthur and Wilson's development of ideas over ecology, population biology, evolution, and paleontology brought remarkable implications for conservation of species (Losos and Ricklefs 2010).

Biophilia

Biophilia is "the innate tendency to focus on life and lifelike processes," as defined by Edward O. Wilson, in his book *Biophilia*, published in 1984 (p. 1). Later, in the first chapter of his work, *The Biophilia Hypothesis*, Wilson (1993) explains the concept of biophilia, in other words but in the same sense, as "the innately emotional affiliation of human beings to other living organisms" (p. 31).

In fact, while developing the concept, Wilson (1993) explains that the term "innate" must be understood as "hereditary," as part of human nature. In this context, the author postulates that biophilia should be assimilated as a complex of learning rules able of being individually studied and should not be simplified as a single instinct. The author clarifies also that the emotions which surrounds the biophilia hypothesis, being defined by its learning rules, range from positive feelings to negative feelings or, as the author illustrates in his book: "from attraction to aversion, from awe to indifference, from peacefulness to fear-driven anxiety" (Wilson 1993, p. 31). It is possible to infer from this perspective that biophilia is based in learned behaviors which results from the fact we are connected to nature.

Thereby, Wilson (1993) concludes that when *Homo sapiens* separate themselves from the natural environment, interrupting his direct contact with nature, biophilic learning rules continue to influence strongly humanity over the generations. Biophilia, therefore, is expressed in the most diverse peculiarities of the new way of life artificially created by man (Wilson 1993). As the example brought by the author, it is interesting to observe how appealing attractions like zoos are for people all over the world.

It is also remarkable the influence biophilia has over humanity's cultural expressions. With the

development of language, the myths, for example, were created strongly affected by metaphors with living organisms (Wilson 1993). Myers and Saunders (2002) state that the various expressions of nature – such as plants, weather, landforms, and waters – represent something surpassing, singular, and remarkable for people's life. But above all those segments of the natural world, the most special case of human's biophilia is the experience with animals (Myers and Saunders 2002). The existence of a great quantity of pet owners all over the world proves the emotional connection humanity has with animals (Myers and Saunders 2002).

Wilson (1993), inquiring how biophilia's evolution could have happened, concludes that the likely answer is biocultural evolution or gene-culture coevolution. Therefore, the genes which determinate learning propensities were spread by natural selection, influencing the elaboration of culture (Wilson 1993).

In conclusion, defining himself as a conservationist, Wilson (1993) understands that biodiversity is at risk and, because of the disappearance of the living part of the environment, becomes necessary the development of a more sophisticated environmental ethic.

Conclusion

The undeniable relevance and admirable extent of E. O. Wilson's work make him one of the greatest scientists alive. He is considered a pioneer in important areas, as sociobiology and biogeography, having made remarkable contributions for the progress of science. He has been recognized by the scientific community, awarding many medals and prizes, among them, two Pulitzer Prizes. Furthermore, his work has a tremendous influence in the conservation movement; as an example, the E. O. Wilson Biodiversity Foundation is a nonprofit organization created to use education, technology, and business strategies to further the preservation of biodiversity. Being himself an advocate of the preservation of habitat and biodiversity of species, his work inspires people all over the world to join the cause.

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Early Association Cue to Kinship in Primates

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Synonyms

[Kin bias](#); [Kin recognition](#)

Definition

Kinship can be defined strictly as genetic relatedness above a certain threshold or broadly as describing genetic or social relatedness including

both consanguineal and affinal kinship. In primate research only the former is considered as “true” kinship, and the degree of relatedness is estimated based on a probabilistic proportion of shared genes. Due to the overlapping generation length in most primates, kin relations tend to consist of grandparent-parent-offspring relationships, sibships, half-sibships, and aunt-uncle-cousin relationships.

Kin recognition is the process of recognizing maternally or paternally related individuals. The mechanisms of kin recognition include direct genetic recognition via a cue, phenotype matching, and association-based learned recognition.

Introduction

Kin recognition is beneficial, even necessary: nepotism, kin-biased cooperation, mate choice, and parental behavior are all influenced by recognition of who is a relative. Most non-human primates (henceforth: primates) live in social groups, in which recognizing relatives from nonrelatives is highly relevant. There is ample evidence in primates for kin-biased behavior from preferential association to selective cooperation (Berman 2015). For example, kin are often the most preferred grooming partners and conflict allies. This indicates that primates indeed recognize at least their closest kin. How do they do that?

The mechanisms of kin recognition can be categorized as cue based and association based. The former are shown in species that use particular phenotypic features to recognize kin, such as cuticular hydrocarbon components in ants and odors in golden hamster’s scent-marking. Association-based recognition includes learning by imprinting and learned recognition due to close and consistent co-presence. Primates appear mainly to learn who is kin by associating with them (Rendall 2004). This is shown by cross-fostering studies and other experimental and observational studies that test whether interactions among unfamiliar relatives differ from those among unrelated individuals. They do not. For example, in captive monkeys raised in peer groups, separated from their mothers and other adults, social affiliation as adults is best predicted by early familiarity instead of paternal or maternal relatedness (Rendall 2004).

Maternal Kin Recognition

In most primates, males are the dispersing sex. Females remain in their natal group and, thus, associate with one another from birth. Such a system allows for the formation of matriline, in which maternally related females grow up in close association with their mothers, sisters, aunts, and even grandmothers. In many cercopithecines, matriline are the primary context in which cooperation and close association takes place: maternally related females are the most frequent and durable grooming and support partners. Maternal recognition in a matrilineal system is based on learning to know kin due to consistent and close co-presence, likely weighted by the type and frequency of interactions (Rendall 2004; Kapsalis 2004).

Matrilineal bonding does not determine behavior as strongly in certain other female philopatric species. Capuchins, for example, have less consistent tendencies to cooperate and associate with maternal kin despite female philopatry and strong affiliative bonds among females.

In species in which females disperse and males remain in their natal group, the dynamics of kin-based bonding are different. Now it is the males who remain in the natal group and may form brother-networks. In muriquis, which is a male philopatric species, maternally related males form cooperative bonds as adult, and juveniles seek to associate with their older brothers. However, maternally related brothers do not always prefer each other as partners. Similarly, in male chimpanzees, the strongest male-male bonds are not exclusively due to kinship (Mitani 2009). This may be due to maternally related (half-) brothers having a relatively large age-gap: adolescent and adult males rarely associate with their mother beyond reproductive age (with bonobos as a notable exception: Surbeck et al. 2011), which means that adult males do not spend time in association with their younger siblings who are still in mother's care.

Interestingly, primates can recognize maternal kinship also among their group members: They recognize group members' matriline membership, relative dominance rank, and mother-offspring relationship (e.g., Bergman et al. 2003).

Allocentric kin recognition is beneficial for successful navigation of a network of relationships characterized by kinship, friendship, and competition. For example, aggressive conflicts and their aftermath often involve opponents' relatives, who provide support, are targeted for redirected aggression, and may provide indirect reconciliation on behalf of their kin (e.g., Das 2000; Wittig et al. 2007).

Paternal Kin Recognition

Learning to recognize kin by association does not work equally reliably for paternal kin. When a single male fathers several offspring in one age cohort, age mates have a high likelihood of being paternal siblings. Age similarity thus may become a cue for kinship recognition among paternal siblings. However, recognizing kin by age similarity may nevertheless operate through familiarity, since half-sibs have formed peer relationships as juveniles. Age similarity is used for paternal kinship recognition in rhesus macaques and possibly also in baboons, where age-mate females and males have reduced likelihood of consortship (Widdig 2007).

Age similarity is an increasingly unreliable cue of kinship when multiple resident males have a possibility to father at least some of the offspring. Recent research is uncovering paternal kin recognition through other mechanisms. For example, rhesus macaques appear to use phenotypic matching of acoustic features to recognize their paternal kin (Pfefferle et al. 2014).

Conclusion

The most prevalent mechanism of recognizing relatives in primates is familiarity that is acquired through frequent association. This method is relatively crude and prone to lead to errors, yet it appears to provide a sufficient mechanism to identify relatives for the purposes of kin-biased cooperation, nepotism, and inbreeding avoidance in primates.

Cross-References

- ▶ [Adaptive Problem of Detecting Kinship](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [C < Rb](#)
- ▶ [Ego-Centered Kin Terminology](#)
- ▶ [Emotional Closeness Predicted by Relatedness](#)
- ▶ [Facial Resemblance and Kinship Detection by Strangers](#)
- ▶ [Full Siblings Versus Half Siblings](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
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- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Helping and Genetic Relatedness](#)
- ▶ [Helping and Inclusive Fitness Benefits to Helper](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
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- ▶ [Kin Recognition and Classification in Humans](#)
- ▶ [Phenotypic Resemblance and Kinship Detection](#)
- ▶ [R = Coefficient of Relatedness](#)
- ▶ [Rescuing Friends and Relatives](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)
- ▶ [Sibships](#)
- ▶ [Special Case: Autism](#)
- ▶ [Universal Aspects of Kinship](#)
- ▶ [Universal Grammar](#)

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Early Attachment Experiences and Romantic Attachment

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Synonyms

[Attachment theory](#); [Internal working model](#); [Parental investment](#); [Reproductive strategies](#)

Definition

Conceptualized as an evolved behavioral system, attachment has been said to lead a “double life” such that it serves two complementary yet distinct functions: (1) to elicit proximity to and care from caregivers in infancy and childhood and (2) to

regulate the complex dynamics of adult pair-bonding and reproductive strategies (Chisholm 1996; Del Giudice 2009).

Introduction

The pioneering work of John Bowlby (1973, 1982) and his colleague, Mary Ainsworth (1964, 1989), along with more recent theoretical extensions and contributions by Belsky et al. (1991), Hazan and Shaver (1987), and others, forms the basis for attachment theory as it is understood today. This middle-level evolutionary theory is reflected universally in humans as a behavioral system that is initiated in infancy and persists throughout adulthood, aiming individuals toward greater inclusive fitness (i.e., successful passing of one's genes to the next generation) in the anticipated environment. Developmental considerations include: patterns of attachment as a marker of variation in life history strategies; early experiences with caregivers shaping initial patterns of attachment; the restructuring of attachment during middle childhood; and the influence of attachment on adult romantic relationships.

Attachment and Life History Strategies

Though Bowlby's attachment theory was based in Darwin's theory of adaptation, subsequent attachment research programs did not always emphasize its evolutionary roots. Belsky et al.'s (1991) evolutionary theory of socialization brought this basis back into focus. Building from Draper and Harpending's (1982) work, Belsky and colleagues proposed that developmental pathways toward adaptive reproductive strategies are initiated by experiences in childhood. In particular, Belsky and colleagues emphasized the first 5–7 years of life as providing important cues to the developing individual, including cues about the social context in which they live. These cues speak to the availability and trustworthiness of others and guide development toward life history strategies that optimize survival and reproduction given environmental demands. Life history strategies are comprised of suites of traits that influence how organisms allocate time and energy to competing

demands across the lifespan, including growth, mating, and parenting (Del Giudice 2014; Ellis et al. 2009). Harsh and unpredictable environments favor “fast” life history strategies characterized by early and unrestricted sexual activity, unstable interpersonal relationships, and early reproduction. Safe and predictable environments, on the other hand, tend to favor “slow” life history strategies and the opposite pattern of behaviors (Ellis et al. 2009). In addition to predicting individual differences in self-regulation, risk taking, and sexual behavior, variation in life history strategies is reflected in different patterns of attachment to caregivers and romantic partners (Belsky et al. 1991; Del Giudice 2014; Del Giudice and Belsky 2010). Thus, early interactions (i.e., between caregiver and child) influence developmental trajectories and life history strategies aimed at meeting ultimate goals. As such, attachment patterns constitute adaptive behavioral strategies that are contextually driven and serve the ultimate goals of survival and successful reproduction (Belsky et al. 1991; Chisholm 1996).

Early Attachment Experiences as the Foundation

The initial function of the attachment system during the first 5–7 years of life is to elicit proximity to and care from caregivers (e.g., mothers) during an extensive, vulnerable period of infancy and childhood. Humans are born quite immature and therefore are entirely dependent on their caregivers early in life. Thus attachment, as a behavioral system, equips infants with strategies that minimize mortality risk (Bowlby 1982). Attachment behaviors include signaling behaviors (e.g., smiling, cooing), aversive behaviors (e.g., crying, screaming), and active behaviors (e.g., clinging, following; Bowlby 1982). As children become more mobile, the caregiver serves as a secure base who can be returned to as needed during play and exploration (Ainsworth 1964, 1989).

The attachment behavioral system is conceptualized as reflecting the caregiving behavioral system such that once a child's attachment system is activated, it initiates the caregiver's

caregiving system (George and Solomon 1999). Various experiences, but particularly experiences of salient danger (either real or perceived), activate the attachment system and corresponding attachment behaviors (i.e., aversive and/or active behaviors). A child's enactment of attachment behaviors in response to threat or danger (e.g., crying and reaching toward the caregiver) serves to elicit caregiving behaviors (e.g., picking up, soothing, and protecting the child from harm). Both systems are subsequently deactivated once proximity between caregiver and child is achieved and the threat diminishes (George and Solomon 1999).

Building from Ainsworth's Strange Situation paradigm (i.e., an infant attachment assessment paradigm; Ainsworth 1964), early attachment measurements categorize a child's attachment pattern generally as secure, insecure, or disorganized. Insecure attachment patterns are further delineated into anxious/ambivalent and avoidant patterns of attachment. Each of these patterns is derived from the quality of repeated caregiver (un)responsiveness to the needs of the child. Caregiving quality is based on the accurate reading of and timely, sensitive response to a child's attachment behaviors (Belsky 1999). A caregiver's ability and willingness to provide quality care depend on a host of influences including the caregiver's own psychological attributes, health, social support, and reproductive strategies (Belsky 1999). Although bidirectional influences of mother and child characteristics (e.g., temperament) may contribute to the quality of interactions, attachment is formed in the presence of a power differential in the child-caregiver relationship (Belsky 1999). Accordingly, attachment is regarded as the close, emotional bond that the child forms toward the caregiver and not the reverse (Bowlby 1973, 1982).

Children of each attachment pattern (i.e., secure, anxious/ambivalent, avoidant, or disorganized) tend to display a corresponding set of attachment behaviors. Put simply, children with secure attachment patterns generally find their caregiver's ability and willingness to respond to

their needs predictable and thus engage more easily in normative exploration and learning opportunities (via the exploratory behavioral system). Children with anxious/ambivalent attachment patterns find their caregiver's ability and/or willingness to attend to their needs unpredictable and thus tend to be more clingy and demanding. This elevated behavior corresponds to hyperactivation of the attachment system (Mikulincer and Shaver 2012) which may serve to increase an unpredictable caregiver's proximity and responsiveness (Chisholm 1996). Children with avoidant attachment patterns find their caregiver to be unresponsive, harsh, and/or rejecting and therefore tend to withdraw and become self-reliant. This behavioral pattern corresponds to deactivation of the attachment system (Mikulincer and Shaver 2012) which may allow the child to maintain minimal proximity and avoid instigating harshness and/or rejection from a caregiver (Chisholm 1996). Finally, children classified as disorganized attach to their caregiver but not in a coherent, organized fashion. Disorganized attachment patterns are less frequently observed and most often associated with children who have experienced severe abuse or trauma. Associated behaviors include fluctuating (i.e., disorganized) use of avoidant and anxious behaviors, as well as freezing or trance-like responses to fear situations (Hesse 2016).

Dependency of attachment patterns on the quality of caregiving does not preclude variation in attachment among children in the same family. Caregivers may invest differentially in their children (i.e., favor one child over another) based on their own reproductive strategies (Trivers 1974), thus resulting in attachment variation among siblings. Additionally, some children may be more genetically predisposed to one pattern of attachment over another or may be more sensitive to environmental influences on development (i.e., differential susceptibility; Boyce and Ellis 2005), both of which contribute to individual differences in attachment even when receiving similar caregiving quality. Further, the intergenerational transmission of attachment and caregiving

behaviors is an area of research still not fully explored but may be an important piece in the puzzle (Belsky 1999).

During the early childhood period, attempts to identify sex differences in attachment patterns have generally been unsuccessful (Del Giudice and Belsky 2010). Given attachment during this early developmental period aims toward survival, sex-differentiated attachment patterns and associated behaviors may not be necessary until later developmental stages. In sum, it is the interplay between nature and nurture that guides early development of an individual's attachment system.

Hierarchical System of Attachment

While the term "caregiver" is used consistently here, the majority of attachment research programs (including Bowlby and Ainsworth's foundational work) emphasize the mother-child relationship. This focus is due to caregiving behaviors historically being carried out disproportionately by mothers (biological or otherwise) across cultural contexts. However, attachment is not limited to mother-child relationships (Belsky 1999; Bowlby 1973). Fathers, as well as additional caregivers (e.g., stepparents, family members, professional caregivers), are also included as attachment figures in what was described by Bowlby (1982) as a hierarchical system of attachment.

The primary caregiver is the individual who most frequently attends to the child's basic needs (often the mother). Additional caregivers with whom the child develops a close, emotional bond can hold a place in the attachment hierarchy as well. Placement within the infant attachment hierarchy may depend on frequency and quality of care and the strength of the child-caregiver emotional bond. Different patterns of attachment organization can develop between the child and individual caregivers as the types of interactions and quality of caregiving provided by each individual may differ (Howes and Spieker 2016). The development of multiple attachment relationships of varying attachment patterns is likely further complicated for children in foster care and

adoption systems where there may be increased inconsistencies (Howes and Spieker 2016).

Internal Working Models (IWMs)

Bowlby (1973) proposed that the early, recurring experiences a child has with a caregiver contribute to the child's IWM, a mental representation of the social world and him/herself in it. These IWMs allow for predictions about one's environment and support the capacity for goal-corrected behavior (i.e., the ability to adjust behavioral strategies based on the immediate context) in the attachment system. Specifically, one's IWM represents both (1) the child's expectation about the availability of caregivers (i.e., ability and willingness to provide care and love) and (2) the child's understanding about his/her worthiness of and ability to receive care and love. Children who developed secure attachment to their caregivers based on consistent, responsive caregiving develop IWMs of others as dependable, caring, and loving and of oneself as worthy of and able to be cared for and loved. Children with the opposite recurring experience (i.e., having developed an insecure attachment) generally develop IWMs of others as undependable and uncaring and of him/herself as unworthy of and/or unable to receive care and love. (Note that IWMs are more nuanced than explained here as they are based on a range of child-caregiver experiences and more specific attachment classifications.) Variations in recurrent experiences with multiple caregivers over time lead to more complex IWMs which are revised and updated throughout development. These IWMs become the filters through which relationships and interactions are initiated and interpreted and remain salient throughout the lifespan.

In sum, infants are equipped with an attachment system that functions to maintain proximity to caregivers during a vulnerable developmental period. Early attachment patterns are shaped by the quality of caregiving received and contribute to IWMs about oneself and others. These IWMs affect (and are affected by) subsequent attachment relationships and continue to be updated across development.

Attachment Is Restructured During Middle Childhood

Following the initial calibration of attachment and IWMs that takes place during infancy and early childhood, the attachment system is restructured during middle childhood. Middle childhood generally takes place between ages 6 and 11 (Colle and Del Giudice 2011; Del Giudice 2014). Although physical growth of the body is slowed during this developmental stage, middle childhood remains a time of profound change. In the brain, new neural connections proliferate (i.e., synaptogenesis), and white matter increases as neural circuits become functionally mature (Del Giudice 2014). These changes support increasingly sophisticated cognitive abilities, emotional competencies, and social behavior. During this time, children's social contexts are also rapidly changing. Relationships with peers take on increased importance as children no longer depend exclusively on their parents for survival (Del Giudice 2009). Intense social learning occurs as children play and begin to practice adult skills and behaviors (Del Giudice 2014). Important social challenges include learning to navigate peer dominance hierarchies, honing skills related to cooperation and competition, and forming stable friendships (Colle and Del Giudice 2011). Although not yet sexually mature, this period is characterized by a strong separation of gender roles, as segregation into same-sex peer groups peaks prior to adolescence (Colle and Del Giudice 2011; Del Giudice 2014).

Adrenarche as a Developmental Switch Point

Also known as "adrenal puberty," adrenarche is the hormonal event that signals the transition to middle childhood (Del Giudice 2009, 2014; Del Giudice and Belsky 2010). Between ages 6 and 8, glands in the adrenal cortex begin to release increasing amounts of adrenal androgens into the bloodstream (Del Giudice 2009; Del Giudice and Belsky 2010). On average, boys and girls begin adrenarche around the same time; however, there is variation in when individual children experience this event (Del Giudice 2014). The timing of adrenarche may be accelerated or delayed based

on cues to harshness or support in the early childhood environment, including the availability and quality of parental care and levels of marital conflict (Ellis and Essex 2007). Children who begin adrenarche relatively early (or late) tend to begin puberty similarly early (or late; Del Giudice 2014).

Although adrenal androgens do not produce many visible bodily changes, they exert powerful effects on brain development and function (Del Giudice 2014; Del Giudice and Belsky 2010). However, the brain's response to adrenal androgens may differ for boys and girls. Adrenal androgens can be converted into estrogen or testosterone in the brain, sending brain development and function down sexually differentiated pathways (Del Giudice 2014; Del Giudice and Belsky 2010). Indeed, middle childhood is characterized by emerging sex differences in affect regulation, responses to stress, aggression, and conduct problems (Del Giudice 2009; Del Giudice and Belsky 2010).

Still years away from attaining sexual and reproductive maturity, differences between boys' and girls' "prereproductive" behavior and relationship patterns become evident during middle childhood, with adrenal androgens likely playing a key role (Del Giudice 2009). Adrenarche may be responsible for the onset of romantic and sexual attractions around ages 7–10 (Del Giudice 2009). Further, hormonal changes during this phase may induce, and provide a biological basis for, emerging sex differences in attachment (Del Giudice 2009).

Some researchers consider adrenarche to be a critical switch point in the development of sex-differentiated life history strategies, including patterns of attachment. According to Del Giudice (2014), a "developmental switch" is a hormonally driven regulatory mechanism that "turns on" at a specific point in development (or during a sensitive period). Such a mechanism is posited to integrate information from an organism's physical and social environments with information about their current state to guide developmental trajectories toward strategies that promote survival and reproduction under these conditions (Del Giudice 2014; Ellis 2013). Developmental switch points

are likely critical in the context-dependent development of alternative (fast vs. slow) life history strategies and their associated behavioral patterns.

Emergence of Sex Differences in Attachment

Relative to earlier developmental stages, an individual's fitness becomes less dependent on parental care and investment during middle childhood. As such, the attachment system can prepare to take on more mature functions, including directing pair-bonding and reproductive activities (Del Giudice and Belsky 2010). Middle childhood thus serves as a critical transition period between attachment system functioning during infancy and adulthood, leading to a partial reorganization of attachment patterns initially calibrated in response to early caregiving (Del Giudice 2009). According to the "psychobiological hypothesis," this hormonally mediated recalibration of the attachment system co-occurs with adrenarche (around age 7) and results in sex-differentiated patterns of attachment (Del Giudice and Belsky 2010). Unlike infants who face largely similar survival-related challenges regardless of biological sex, an evolutionary framework predicts sex-based differences in adult attachment because men and women have recurrently faced different mating-related challenges throughout human history (Del Giudice and Belsky 2010). Therefore, it is posited that sex differences in attachment emerge during middle childhood to prepare individuals to adopt reproductive strategies that are most likely to optimize fitness for members of their biological sex in adulthood (Del Giudice and Belsky 2010).

Specifically, males and females are expected to develop different patterns of insecure attachment in environments characterized by moderate levels of stress or danger (Del Giudice 2009). Early stress and insecure attachment should favor reproductive strategies that prioritize mating (over parenting) effort and early reproduction. Under these conditions, males with insecure attachment should adopt avoidant strategies to facilitate successful intra-sexual competition and attraction of multiple sexual partners. Whereas avoidant attachment among boys may be characterized by increases in aggression, externalizing behaviors, and inflated self-

esteem (integral to seeking and attaining status among same-sex peers), in men such patterns may display as low commitment to romantic relationships and increased promiscuity (Del Giudice and Belsky 2010).

Females with insecure attachment, on the other hand, should adopt anxious/ambivalent attachment patterns within moderately stressful environments. Such care-eliciting strategies may function to maintain closeness to a mate (particularly an avoidant one) and to maximize the amount of investment received within that partnership (Del Giudice 2009). Whereas girls with anxious attachment may demonstrate passivity and internalizing symptoms, as women they may display increased impulsivity, early and unrestrained sexual behavior, and a strong desire for intimate and committed relationships with men (Del Giudice and Belsky 2010). However, females may adopt more avoidant interpersonal orientations within extremely harsh or dangerous environments (Del Giudice 2009).

Research suggests that the predicted sex differences in insecure attachment emerge during middle childhood. Unlike studies of infants and younger children, studies of children ages 7–11 reveal consistent sex differences in insecure attachment patterns on attachment questionnaires and doll-play tasks (although not on attachment interviews that focus on past experiences with caregivers). In research revealing sex differences in insecure attachment, boys are more likely to display avoidant (vs. anxious/ambivalent) attachment, whereas girls' attachment is more likely to be categorized as anxious/ambivalent (Del Giudice 2009; Del Giudice and Belsky 2010). Relatively few studies have tested for sex differences in attachment in middle and late childhood; however, this pattern has been revealed in research conducted in the United States, Canada, Israel, and Italy (Del Giudice 2009).

The sex-dependent distribution of insecure attachment in middle childhood is consistent with patterns of romantic attachment observed among men and women in adulthood (Del Giudice and Belsky 2010). This suggests that information used to calibrate sex-differentiated attachment patterns at adrenarche may carry over

to the next developmental switch point at gonadarche (i.e., the transition to adolescence), providing an opportunity to further adjust reproductive strategies and attachment before achieving reproductive maturity (Del Giudice 2014; Ellis 2013).

The Role of Paternal Caregiving

Evolutionary developmental models emphasize the importance of parental behavior in transmitting information to children regarding levels of environmental harshness and support (Belsky et al. 1991). However, mothers and fathers may shape the behavioral and reproductive strategies of their children in qualitatively different ways. For instance, unlike maternal investment, paternal investment levels reflect the amount of male-male competition, character of the mating system, and availability of paternal care within the local environment (Del Giudice 2009; Draper and Harpending 1982). On this view, low paternal investment (including father absence) suggests to offspring that their environment is relatively polygynous, pair-bonds do not last, and men preferentially allocate resources toward attracting multiple mating opportunities at the expense of investing in offspring (Ellis 2004). Sons and daughters are posited to use this information to guide their development and behavior in different ways. For instance, low paternal investment is expected to promote increased aggression and hypermasculinity among sons to promote successful intrasexual competition, and early sexual development and short-term sexual relationships among daughters (Del Giudice 2009). Consistent with this view, research demonstrates unique effects of fathering quality in shaping daughters' pubertal timing, with high-quality paternal investment predicting delayed sexual development among daughters (Ellis 2004). Further, research by Chisholm et al. (2005) has shown that women growing up without their father in the home experience earlier menarche and first birth and are more likely to be insecurely attached than other women. This research suggests that when monogamy is not perceived to be the norm (such as in contexts characterized by low paternal investment), insecure attachment patterns can facilitate women enacting fast reproductive strategies, even

if they retain a preference for long-term commitment (as may be the case with anxiously attached women; Del Giudice 2009).

In sum, middle childhood is a critical transitional period between a survival- (and caregiver-) focused attachment system calibrated in early childhood and the mature attachment system that regulates mating behavior in adolescence and adulthood (see section "[Romantic Attachment in Adolescence and Adulthood](#)"). Insecure attachment patterns become sex-differentiated at a hormonally mediated switch point, as boys and girls develop patterns of attachment that promote successful intrasexual competition and reproduction in moderately stressful environments. Consistent with this view, the sex-biased distribution of insecure attachment that emerges during middle childhood is consistent with patterns of insecure romantic attachment observed among adult men and women.

Romantic Attachment in Adolescence and Adulthood

As noted, the mature function of the attachment system in adolescence and adulthood is aimed toward regulating the complex dynamics of adult pair-bonding and reproductive strategies (Chisholm 1996; Del Giudice 2009). Bowlby (1982) conceptualized the attachment system as persisting throughout the lifespan, and Ainsworth (1989) proposed sexual pair-bonding as among the types of attachment relationships beyond infancy. Hazan and Shaver (1987) were the first to fully explore romantic relationships as an attachment process. In their empirical studies of adult romantic attachment, they found that the attachment patterns of child-caregiver relationships present similarly in adult romantic relationships and that romantic attachment patterns correspond to IWMs of self and others. It is important to note, however, that their study was less conclusive regarding the relation between retrospective reports of early attachment and current romantic attachment patterns in adulthood. This lack of clarity has been the source of ongoing discussion and research regarding aspects of

continuity and change in attachment across the lifespan, which is considered next.

Continuity and Change

The attachment system evolves across development in ways that exhibit both continuity and change. While there are enduring aspects of attachment for which early childhood is the foundation, important differences also emerge as the function of attachment shifts toward an emphasis on pair-bonding and reproduction (Del Giudice 2009). As argued by Figueredo et al. (2009), adult romantic attachment relationships likely require different behavioral approaches as they serve different primary purposes (i.e., reproduction) than child-caregiver attachment relationships (i.e., care and protection). Hence, attachment behaviors evident in childhood (i.e., signaling, aversive, and active behaviors) may be facultative in that they are specific strategies aimed at solving the problems of an extended, vulnerable childhood (Figueredo et al. 2009). Attachment patterns in adulthood, on the other hand, correspond to an increased complexity in the attachment hierarchy which becomes multidimensional beginning in adolescence. In addition, romantic attachment patterns should be sexually dimorphic given different reproductive pressures facing males and females (see section “[Emergence of Sex Differences in Attachment](#)”; Del Giudice and Belsky 2010).

Adult pair-bonding involves coordination of three behavioral systems: attachment, caregiving, and reproductive (Ainsworth 1989). Adult romantic attachment serves in part to increase reproductive fitness by increasing paternity certainty (e.g., limiting the likelihood that a father invests fully in offspring that are not his), allowing for shared parental investment during an extended period of child dependency, and therefore increasing the likelihood of thriving offspring (Zeifman and Hazan 2016). While the emphasis here is on the ultimate goal of reproduction, the romantic attachment system may also continue to serve survival purposes for humans, a vulnerable, ground-living species (Zeifman and Hazan 2016). In this sense, maintaining proximity to a caring, dependable partner is useful in times of threat (such as intense illness). Unlike childhood,

adult attachment and caregiving roles are interchangeable between partners.

Continued Shifts in Attachment During Adolescence

Adolescence is the transition from childhood to adulthood (i.e., roughly ages 10–19 years) and, as such, involves developmental processes that guide behavior toward increased autonomy and decreased dependence on caregivers. According to Del Giudice (2009), adolescence allows for childhood influences from caregivers (e.g., attachment) to be modified and replaced as one transitions into adulthood. This is evident in changes to the attachment hierarchy that continues in adolescence.

The attachment hierarchy in adolescence evolves through a process of expansion and revision. This evolution is considered in the Important People Interview (IPI; Rosenthal and Kobak 2010). Peers are central to the daily experience of adolescents and, in many cases, become more accessible and knowledgeable about the dilemmas experienced by the adolescent (Rosenthal and Kobak 2010). This results in increased support-seeking and affiliative behaviors among peers which provide the backdrop for the potential formation of peer attachment relationships (i.e., enduring bonds with peers who are sought out in times of danger or threat; Rosenthal and Kobak 2010). Additionally, increased social interactions of mixed-gender peer groups (as opposed to more prominent same-sex peer groups in childhood) and the emergence of dating behaviors likewise set the stage for the formation of romantic pair-bonds (Ainsworth 1989). Romantic attachment becomes increasingly prominent during the transition into adulthood, as the reproductive behavioral system becomes more salient at the onset of puberty.

The attachment hierarchy can also be revised as adolescents mature. While childhood caregivers (i.e., parents) often remain primary attachment figures (Rosenthal and Kobak 2010), the attachment relationship itself may shift. One initiator of hierarchy revision is the developmental shift toward autonomy. In response to this shift, the goal-corrected partnership (i.e., caregiver and adolescent) may renegotiate the balance between

responsive caregiving and promoting autonomy and increased self-reliance (Allen and Tan 2016). Further, maturing metacognitive functions provide an opportunity for adolescents to reevaluate their caregiver attachment relationships in a process of resolution. In this process, adolescents are able to see their caregivers in both positive and negative lights. This “deidealization” of caregivers allows an adolescent to reevaluate and revise not only their attachment hierarchy and behaviors but also, importantly, their IWMs (Allen and Tan 2016). This is particularly important for adolescents who had negative early attachment experiences (i.e., insecure attachment with caregivers). For those unable to resolve IWMs, establishing healthy friendships and forming enduring bonds are difficult (Allen and Tan 2016).

Overall, attachment in adolescence has potential for both continuity and change. The role of the caregiver as a secure base is often maintained, though there is a developmental shift toward increased autonomous exploration. In addition, attachment hierarchies and corresponding IWMs are open to expansion and revision as additional bonds are formed with friends and romantic partners and as mature metacognitive functions allow for resolution of negative early attachment experiences.

Measurement of Romantic Attachment and IWM

Adult romantic attachment is considered a “person by situation” construct such that it can be activated differentially based on the attachment relationship and the specific context (Mikulincer and Shaver 2012). On the one hand, attachment can be thought of as self-sustaining such that individuals both approach and interpret relationships from the perspective of their IWMs, which then become validated. On the other hand, adult romantic attachment relationships in particular are dynamic, and the context can be complex. An attachment pattern with one partner in a particular social context may not mirror that with a different partner and/or different social context (Mikulincer and Shaver 2012). Additionally, individual and environmental factors such as heritable dispositions and the local sex ratio impact reproductive

strategies and, thus, the attachment system (Del Giudice 2009). In this sense, romantic attachment in adulthood reflects a complex biopsychosocial process.

Initial measurements of adult attachment focused on patterns established in infancy under the premise that early attachment experiences serve as the foundation for attachment behaviors and IWMs in adulthood. The Adult Attachment Interview (AAI; Hesse 2016) focuses on retrospective self-reports of early attachment relationships and the coherence of those relationships based on “states of mind” (i.e., IWMs). These comprehensive interviews channel individuals’ organized attachment patterns into the three categories (i.e., secure-autonomous, insecure-dismissing, and insecure-preoccupied) which closely align with descriptions of their early childhood attachment pattern counterparts (i.e., secure, avoidant, and anxious/ambivalent, respectively). For individuals not able to be categorized (i.e., their attachment behaviors are not observed in an organized pattern), the categories of “unresolved/disorganized” and “cannot classify” were added subsequently. As conceptualized by Bowlby (1973, 1982), attachment later in life is subject to subsequent interactions and experiences and therefore does not remain static. Thus, the AAI opened the door for relationship researchers to consider ways to assess the complexity and multidimensionality of adult attachment patterns.

To measure adult romantic attachment, Hazan and Shaver (1987) developed a forced-choice, three category (i.e., secure, anxious/ambivalent, avoidant) measure. Though these categories are reminiscent of infant attachment patterns, the questionnaire included both retrospective reports of early attachment as well as a recent romantic attachment relationship and current IWMs. As interest in romantic attachment gained momentum among relationship researchers, measurement of this construct continued to evolve. One measurement trend conceptualized romantic attachment as two dimensional, such as in Griffin and Bartholomew’s (1994) Relationship Styles Questionnaire (RSQ). Based on earlier versions, the RSQ is a 30-item inventory that considers two dimensions: IWM of self and IWM of others.

Individuals fall into four possible categories (i.e., secure, preoccupied, fearful-avoidant, and dismissing-avoidant) based on a positive/negative classification on both dimensions. The Experiences in Close Relationships Scale (ECR: Brennan et al. 1998) is another such 36-item measure which considers attachment along two dimensions. In the ECR, individuals are categorized based on their scores on avoidance and anxiety scales, and individuals scoring low on both scales are classified as having a secure attachment style. Updated versions of the adult romantic attachment measurements mentioned support current romantic relationship research as well as research using a life history framework (Chisholm et al. 2005).

Conclusion

The theory of attachment, as originally developed by Bowlby and elaborated on in the seminal works of Ainsworth and others, has been integrated into a modern life history framework (Belsky et al. 1991; Del Giudice 2009). Early parent-child attachment relationships (e.g., secure vs. insecure) are central to life history models of the development of alternative reproductive strategies. Adolescent and adult romantic attachment relationships are also theoretically relevant to life history models, and increasing efforts have been made to incorporate attachment patterns during these later developmental periods into a life history framework. In particular, modern evolutionary developmental research integrating attachment theory and life history theory elucidates the role of emergent sex differences in attachment as mediating sex differences in reproductive strategies.

Cross-References

- Attachment Theory
- Life History Theory
- Parental Investment
- Sex Differences

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Early Brain Development in a Child

► Brain Growth in the First Year

Early Care and Education

► Child Care

Early Castration

► Music and Hormones

Early Childhood and Adolescence

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Synonyms

Child development; Infancy; Juvenility; Puberty; Youth

Definition

Early childhood and adolescence are stages of human development that precede adulthood and are bridged by a juvenile period.

Introduction

Evolutionary developmental psychology (EDP) applies the principles of evolutionary biology to understand human developmental norms and variability (Del Giudice and Ellis 2016). On this view, stages of human development (and their characteristic physiological, cognitive, and behavioral patterns) have been shaped by natural and sexual selection throughout the history of our species. This perspective emphasizes the interactional influences of environmental and genetic factors in shaping individual developmental pathways. Accordingly, an understanding of early childhood and adolescence requires consideration of (1) the role of past, current, and future expected environments in guiding development; (2) functional phenotypic plasticity that occurs in response to varying environmental conditions; and (3) behavioral outcomes that are adaptive in context yet may be labeled “maladaptive” from other perspectives.

Early Childhood

Early childhood (considered here as the first 5–7 years of life) is a period of considerable somatic growth and brain development and, as such, of high energy demand. Trade-offs must be made when allocating limited energetic resources to the competing needs of brain, body, and reproductive development, particularly within deprived environments (Bjorklund and Ellis 2014). For example, in impoverished conditions, preservation of vital organs (e.g., the brain) may be favored over other somatic growth. This allocation pattern can improve immediate survival outcomes but increase one’s likelihood of developing metabolic syndrome within food-abundant adult environments (thrifty phenotype hypothesis; Hales and Barker 2001). Thus, early childhood is not only an important time of discovery and play for the purpose of stimulating critical social and cognitive skills. This period also has long-term implications for an individual’s developmental trajectory that can impact their adult phenotype and fitness-relevant outcomes

(Bjorklund and Ellis 2014). The ability to receive multiple reliable cues (i.e., information) from the physical and social environment during early childhood is therefore imperative.

Harshness and unpredictability are unique and fundamental dimensions of the environment to which children are sensitive that influence development of life history strategies and promote associated suites of behaviors and preferences (Ellis et al. 2009). Environmental harshness refers to extrinsic (uncontrollable) factors that increase one’s risk of disability or death. Salient proximate indicators include local exposures to violence and premature death. Environmental unpredictability refers to high variability in local morbidity-mortality rates and is reflected by frequent changes in residence, parental figures, and socioeconomic conditions (Ellis et al. 2009). Together, cues of harshness/unpredictability communicate information to developing individuals regarding their likelihood of a long life given the social and energetic resources available in their local ecology. As such, presence (or absence) of these cues direct individual development toward relatively fast (or slow) life history strategies, which serve to match one’s phenotype to his/her expected environment.

Infants enter the world already having received environmental harshness/unpredictability information from maternal hormones that pass through the placenta and help calibrate the naïve stress response system (Bjorklund and Ellis 2014). Once delivered from the womb, the infant enters a physical and social environment that is host to a multitude of novel stimuli (e.g., hormones in mother’s milk; touch during caregiver interactions). Many of these stimuli have, over generations, served as reliable cues to anticipated environments (i.e., the environment expected in adulthood) ranging in harshness/unpredictability and warmth/supportiveness. During childhood, the majority of such cues are provided by the behavior of caregivers.

According to Belsky and colleagues (1991), experiences in early childhood provide critical information regarding the availability of social resources (e.g., the ability to trust others and maintain enduring relationships). The development of

attachment to one's parents may reflect a child's earliest cues regarding the degree to which trusting and enduring relationships can be expected. Specifically, secure and insecure (anxious/avoidant) attachments are expected to develop in response to high and low levels of parental investment, respectively. Children often develop secure attachment when they receive consistently high levels of sensitivity, availability, and emotional warmth from the parent(s). Insecure attachment, on the other hand, reflects inconsistent and/or low levels of such relationship qualities (Belsky et al. 1991). These contrasting forms of attachment likewise correspond to the continuum of possible life history strategies, with relatively fast strategies developing in response to an anticipated environment that is characterized by heightened competition for scarce resources and minimal parental investment in offspring (Belsky et al. 1991; Bjorklund and Ellis 2014). Within this context, individuals who demonstrate high impulsivity, aggression, and opportunistic interpersonal orientations may enjoy better fitness outcomes than individuals whose developmental trajectories did not prepare them for such conditions. Consistent with this view, evidence suggests that aversive early life interactions and experiences (e.g., rejecting and/or inconsistent parenting) predict behaviors indicative of faster life history strategies, including earlier sexual debut and first reproduction (Bjorklund and Ellis 2014).

In sum, early development is sensitive to multiple reliable cues that forecast the environments that children will inhabit as adults. These cues (e.g., hormones from maternal milk, parent-child attachment) guide developmental trajectories in ways that function to match individual phenotypes to their expected future environment and promote instantiation of life history strategies along the slow-to-fast continuum. However, it is important to note that the extent to which an individual is influenced by the myriad stimuli to which they are exposed in early childhood may critically depend upon their level of differential susceptibility to context (Belsky et al. 1991; Bjorklund and Ellis 2014). That is, some individuals may be more (or less) attuned to specific environmental cues, elucidating why we can observe striking differences in outcomes among

individuals from similar backgrounds (including children from the same family).

The Juvenile Transition and Adolescence

Following early childhood is a period of juvenility ("middle childhood"; approximately ages 7–11) that precedes adolescence. Middle childhood is characterized by the onset of adrenarche (involving secretion of adrenal androgens), appearance of adult molars (enabling independent foraging for food), decreased dependency on parents, brain maturation, and increased social play and learning (Hochberg and Belsky 2013). Sex differences in attachment also emerge during this time. Importantly, this is a period of slowed growth in humans, which serves as a distinct contrast with adolescence.

Adolescence is a uniquely human stage of development that generally takes place between ages 11 and 17 (Hochberg and Belsky 2013). This stage is largely defined by puberty-specific changes, including gonadal maturation and a rapid growth spurt in height and weight, and broadly entails physiological, behavioral, and motivational changes that prepare males and females for adult social roles and reproductive activities (Ellis et al. 2012; Hochberg and Belsky 2013). Although parental investment often continues into early adulthood, the influence of parents decreases during adolescence, as the importance of peer relationships simultaneously increases. Other puberty-specific changes include maturation of primary and secondary sex characteristics, shifts in sleep patterns, increased caloric intake, and increased sensation seeking (Ellis et al. 2012). As sexual motivation and competition increase in intensity, adolescents begin to assess their desirability as mates, form mating-relevant preferences, and practice mate attraction tactics (Ellis et al. 2012). From the perspective of EDP, strong selection has historically occurred during adolescence due to the implications of competition for fitness-relevant resources (including mates and social status). As such, adolescents experience pronounced emotional and behavioral responses to their social successes and failures (Ellis et al. 2012).

From an evolutionary viewpoint, developmental trajectories functionally vary in response to environmental conditions. Adolescence is no exception. Adolescence is posited to be a sensitive period for change that is regulated by hormonal switches (Ellis et al. 2012). In addition to heritable variation, the timing (and duration) of puberty is susceptible to the influence of individuals' physical and social environments (e.g., family stress; Hochberg and Belsky 2013). Accelerated maturation serves as a component of a fast life history strategy that is adaptive under harsh/unpredictable conditions. Specifically, accelerating the transition from juvenility to adolescence (and adolescence to adulthood) under stressful conditions may increase one's probability of reproducing before death, especially for girls (although this transition may be delayed when access to calories is inadequate; Hochberg and Belsky 2013). Under conditions of harshness/unpredictability, taking risks that jeopardize long-term health and well-being may provide better immediate outcomes than "playing it safe."

Importantly, functional sex differences in morphology and behavior manifest during this period. Adolescent boys achieve fertility approximately 2 years after their growth spurt begins (around ages 14–15). However, they appear juvenile in terms of their body hair, stature, muscularity, and voice. As such, adolescent males are able to learn adult social roles while sexually mature, but not yet seen as competition by more dominant adult males (Hochberg and Belsky 2013). During pubertal maturation, testosterone activates courtship behavior and increases social dominance among boys (Ellis et al. 2012; Hochberg and Belsky 2013). Adolescent boys may enact a variety of behavioral strategies to gain social status and mating opportunities, including physical aggression (e.g., bullying; Hawley 2011). In addition, boys' engagement in potentially hazardous risk behaviors (e.g., fighting, reckless driving) increases during this time, with potential implications for fitness. Indeed, male risk-taking increases when being viewed by same-sex peers of similar status or after viewing images of attractive females (Ellis et al. 2012). From a fitness perspective, males have more to gain and less to

lose (relative to females) by engaging in risky behaviors, and research suggests that such strategies are effective. For instance, bullies often begin dating at a younger age than their same-sex peers, and social status achieved by adolescent boys can persist into adulthood (Ellis et al. 2012).

Girls achieve menarche approximately 1 year after their peak growth in height (Hochberg and Belsky 2013). In contrast to males, adolescent females appear feminine and show signs of sexual maturity (e.g., subcutaneous fat deposits in their thighs, buttocks, breasts), which can aid in mate attraction (Hochberg and Belsky 2013). However, human females remain infertile until approximately age 18, when ovulation reaches adult frequency and the birth canal achieves adult size. This gap between menarche and reproductive competence allows girls to learn adult social roles and practice mating skills without conceiving (Hochberg and Belsky 2011). As noted earlier, environmental factors may affect the pace at which girls reach these development milestones (and promote associated life history traits). For instance, the timing of female pubertal maturation is influenced by early environmental conditions, including exposure to family disruption/father absence (Hawley 2011). Girls are posited to encode father absence (or low-quality fathering) as suggesting that male investment in reproduction is not likely to be available when one reaches reproductive age. Under such conditions, girls can increase their reproductive success by accelerating maturation and engaging in earlier sexual activity, getting pregnant earlier, and having multiple short-term relationships (Hawley 2011). Under more supportive and benign conditions, however, a relatively late transition to adolescence allows for greater preadolescent growth, which can increase somatic, social, and psychological capacity for girls (favoring future over current reproductive success; Hochberg and Belsky 2013).

Conclusion

When considering variability in adult outcomes, one must look back to experiences

during early childhood and adolescence to see the full picture. It is here that evolutionary psychology takes a developmental approach. During early childhood and adolescence, individuals receive proximal cues (e.g., through parent-child interactions or family transitions) that interact with more distal cues and genetic factors to shape developmental trajectories in functional ways.

These changes function to match the individual to their anticipated future environment. While plasticity (the capacity for change) in some domains may persist into adulthood, childhood and adolescence constitute sensitive periods for structuring brain, body, and reproductive development via hormonal switch points (Bjorklund and Ellis 2014). As such, what happens during these stages can have long-term implications, and adult outcomes viewed as “maladaptive” from a societal perspective may reflect an individual “making the best of a bad situation” when confronted with circumstances that are less than ideal (Ellis et al. 2012).

Cross-References

- [Development of Adaptations](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Fast Versus Slow Strategies](#)
- [Fundamental Tradeoffs](#)
- [Life History Strategies](#)
- [Reproductive Strategies](#)
- [Sex Differences in Attachment](#)
- [Sexual and Reproductive Development](#)

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Early Definitions of Species

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Synonyms

[Pre-Darwinian species definitions](#); [Species concepts](#); [Species definitions](#)

Definition

Pre-Darwinian concepts of “species”.

Introduction

The attempt to partition a continuous evolutionary process into discrete units is the essence of the “species problem,” the unresolved question of *what*, if anything, “species” are. Modern (here

defined as post-Darwinian) definitions of species comprise upwards of 30 distinct concepts (Zachos 2016) emphasizing different diagnostic biological features. “Species,” however, was not an exclusively biological concept until around the nineteenth century; it has a long philosophical history with roots in Platonic and Aristotelian thinking. Here, two types of species definitions are traced from their philosophical origins to Darwin’s time: first, conceptions of the species *category* or *rank* (i.e., the entire class of units known as species), and second, early approaches to defining species *taxa* (specific units within the category, e.g., *Homo sapiens* or *Cavia porcellus*). The latter, in particular, has been the subject of recent debate, with scholarly approaches falling into two camps: the conventional “essentialists” and the “non-essentialists.” Finally, the impact of Darwin’s work on species definitions is examined to conclude he did not necessarily revolutionize taxonomy, as is often assumed, but rather altered the analytical framework in which it was conducted and interpreted.

Application of the Concept

The concept of “species” did not have a purely biological meaning for much of its history. The idea of definable types or categories of biological and nonbiological entities alike stretches back to antiquity, with the most well-known works being Plato’s *Theory of Forms* and Aristotle’s *Categories*. Plato and Aristotle sought, in the broadest terms, to classify things by defining their “essences,” and Aristotle referred to “eidos” (species) in both his biological and logical works. Aristotelian philosophy formed the bedrock of much Medieval thought, and “species” continued to be applied to classify biological and nonbiological things alike. According to Wilkins (2009), the first definition of “species” in a specifically biological context was published in 1686 by an English naturalist, John Ray. It remained routinely used to classify nonliving objects until the nineteenth century, however: indeed, Linnaeus classified minerals alongside plants and animals in his *Systema Naturae*.

Defining the Species Category

The term “species” has at least two meanings: species *taxa*, and the species *category* to which all species taxa belong. Definitions of species taxa are applied to discern discrete groups in nature, so they describe the boundaries between these groups; the species category, on the other hand, is a rank in the taxonomic hierarchy and therefore outlines the characteristics species taxa share that mark them as members of the category.

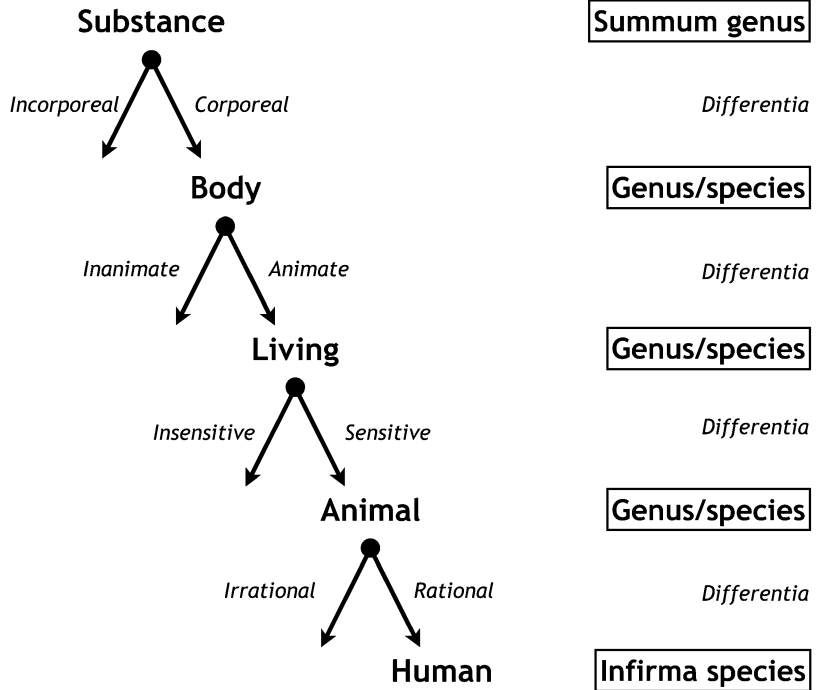
“Species,” in the category sense, was a relative term in classical and early modern scholarship, unlike the fixed rank it occupies today. This is best illustrated by what became known in the Middle Ages as *Porphyry’s tree* (Fig. 1), a scale of classification by the third-century Greek neoplatonist philosopher Porphyry. The tree is a nested classificatory hierarchy of dichotomous divisions where all levels (except the highest and lowest) are “genus” to the level below it and all levels are “species” to that above it. By contrast, the species category occupied an absolute rank in Linnaeus’ *Systema Naturae*, first published in 1735. His taxonomic hierarchy comprised five levels, with species occupying the lowest; this system is still in use today with additional ranks above and below the species level.

Defining Species Taxa

More than 30 definitions of species taxa are in use today (Zachos 2016), but despite this diversity they are all based on what Mayr (1959) has called “populationist” thinking. This approach is characterized by a belief that the “type” (the average) “is an abstraction and that only variation is real” (p. 2, *ibid.*). The traditional interpretation of the history species taxa definitions is a clear dichotomy with Darwin at the center: before him the standard approach to classification was essentialism, and he revolutionized taxonomy by pioneering population thinking. In the essentialist or “typological” (Mayr 1959) approach, species are conceived of as Platonic types with necessary and sufficient properties that defined them. Thus, the “type,” defined by properties that must always be present,

Early Definitions of Species,

Fig. 1 Explanatory text: Porphyry's tree, with a classification of humans to illustrate its use. Each level of classification is "genus" to the level below it and "species" to the level above it, except for the highest and lowest levels, which are the summum genus and infirma species, respectively. Classification proceeds dichotomously: each genus is split up into species according to a "differentia" with two options. (Adapted from Fig. 2.1 in Zachos 2016)



is real, and variations around it are illusions. The established view holds that the stranglehold of essentialism produced “two thousand years of stasis” (Hull 1965), principally because it does not allow the essential characters to vary in a population while evolution by natural selection requires them to.

This view has been increasingly successfully challenged. The essence of criticisms is as follows:

1. The practice of pre-Darwinian taxonomy was not restricted to an essentialist paradigm (even if taxonomists adhered to an essentialist worldview in theory).
2. Essentialism was not the sole theoretical approach to taxonomy, and other species taxon concepts emphasizing genealogy rather than essential defining features were in use before Darwin.

Regarding the first point, Winsor (2003) makes the case that the pre-Darwinian practice of classifying organisms more frequently followed a polythetic approach in which species were delineated

according to common but not *essential* shared features. She describes two widely applied approaches. “Chaining” involved acknowledging the continuity of features between groups in nature: “each species or genus was linked to the next by clear similarities, but by the end of the chain all the characters of the first link had been lost” (p. 392). The method of “exemplars” defined groups with reference to a “typical” member, analogous in some ways to today’s type specimens in taxonomy; potential members of the group were then compared to the typical member and excluded if they were distinct enough. Even if early taxonomists theoretically conceived of species in an essentialist paradigm, this did not necessarily inform the practice of classifying organisms. Instead, classification was largely pragmatic and taxonomists acknowledged problematic “fuzzy boundaries” between groups in nature.

That is not to say that an essentialist theoretical conception of species was universal, however. Wilkins (2009) claims a “generative” conception of species, which emphasized common descent rather than the need to exhibit essential and

sufficient features, was actually the most commonly used species taxa definition. There are numerous examples to support his case, including the first species definition in a purely biological context by John Ray (“...No matter what variations...if they spring from the seed of one and the same, they are accidental variations” (Ray 1686 quoted in Zachos 2016) and Kant’s (1775) assertion that “In the animal kingdom the division of nature into... species is grounded on the general law of reproduction” (p. 11). Regarding Linnaeus, commonly conceived of as the archetypical essentialist, Richards (2010) writes that “if he was an essentialist, it was of a genealogical kind. Essences were passed on in reproduction via the transmission of medullar matter...” (p. 58). There were, of course, pre-Darwinian theoretical essentialists alongside those who prioritized descent, but the variety of early species concepts has been severely underestimated in the traditional account.

Darwin’s Contribution

In the traditional view, Darwin liberated biology from the shackles of essentialism by promoting “population thinking.” It is clear that this narrative lacks support in the reevaluated interpretation. Indeed, Darwin never produced a clear species definition and his view on species remains debated (Zachos 2016). His fundamental impact, instead, lies in the overarching philosophical framework in which taxonomy was interpreted: the relationships between organisms classified in the pre-Darwinian Linnaean system are now understood in terms of shared descent.

Conclusion

“Species” referred to living and nonliving entities for much of the history of the concept. Biologically speaking, “species” refers to at least two concepts: the species category and the species taxon. The species category was a relative term in classificatory hierarchies in classical and early modern scholarship, but occupied a fixed rank

from the publication of Linnaeus’ *Systema Naturae* onwards. The traditional view with regard to early definitions of the species taxon is that Platonic essentialism dominated taxonomic theory and practice until Darwin pioneered population thinking, but this view is increasingly challenged. The established view, at the very least, underestimates the variety of species definitions in use in pre-Darwinian times; a shared feature of many early species definitions emphasizes shared descent and genealogy. It is likely that many early taxonomists employed more pragmatic definitions in the actual practice of classifying organisms. In light of this reinterpretation, Darwin’s contribution to species definitions is not so much that he revolutionized taxonomy, but rather that he altered the fundamental framework in which species were interpreted.

Cross-References

- Charles Darwin
- Impact of Early Theory on Charles Darwin
- On The Origin of Species

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Early Homo

- ▶ *Homo floresiensis*
 - ▶ *Homo rudolfensis*
-

Early Life

- ▶ [Fetus Development](#)
-

Early Male and Female Socialization

- ▶ [Sex Differences in Social Development](#)
-

Early Perspectives on Evolutionary Change

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Synonyms

[Pre-Darwinian evolutionary ideas](#); [Philosophical antecedents of Darwin](#)

Definition

The idea of evolution existed in the writings of various philosophers and scientists for many centuries before Charles Darwin produced a formal theory consistent with a large body of scientific evidence.

Introduction

Though Charles Darwin is the individual most closely associated with evolutionary theory

in the public imagination, evolutionary perspectives on the origin of life had been a topic of discussion among philosophers and scientists for millennia. Among the pre-Socratic Greek philosophers, for example, Anaximander of Miletus (c. 610-546 B.C.E.) thought that the first animals were aquatic, with land-dwelling forms developing later. The first terrestrial ancestors of modern humans were amphibious, according to Anaximander, born in water and spending only part of their lives on land. Empedocles (c. 490-430 B.C.E.) speculated further that new species arose accidentally from the disjointed parts of deceased animals, mixing and intermingling in new configurations. When the new combinations were well-suited to their environments, those survived to breed and became new species.

Classical Greek Perspectives

Plato and Aristotle both wrote about the origin of species as well, though they went in a different direction than the pre-Socratics. Plato argued that the Creator (Demiurge, in Plato's terminology) created the world in a complete and perfect form, with all conceivable forms of life already present, because if any of them were missing, the world would be incomplete; thus, the creation would be less than perfect, as would be its Creator as well. Aristotle, Plato's student, expanded on this view by proposing that all species were created to occupy a particular place, as a step in a *Scala Naturae*, or Ladder of Nature, later also commonly referred to as the Great Chain of Being. Like most ladders, the Ladder of Nature has a top and a bottom, and Aristotle proposed that organisms are arranged hierarchically, so that the world contains both higher and lower forms of life. This idea would remain influential all the way up to Darwin's time.

Early Christian Perspectives

The early Christian thinkers in Rome, most notably the fourth-century bishop Augustine of

Hippo, also speculated on the possibility of evolutionary change, in ways that might surprise modern readers. In Augustine's book *The Literal Meaning of Genesis*, he taught that worshipers should not take the Biblical account of creation literally but rather that living things were not created in a state of final perfection. Instead, they were made in a state of potentiality, and they transform slowly over time. In keeping with Aristotle's ladder, these changes involve development toward higher forms, but only the angels and the human soul were already perfect and in their final form at the moment of creation. Augustine also allows that the many species of insects, worms, and other small animals not mentioned in the Bible were not created by God on the fifth and sixth day, but rather emerged on their own through spontaneous generation from rotting organic matter. This idea was quite influential; well into the nineteenth century, it was widely believed that maggots emerge spontaneously from spoiled meat, for example.

Post-Roman Islamic Perspectives

Following the fall of the Roman Empire, the Greek and Roman philosophical and scientific traditions were interrupted for a number of centuries, but Islamic scholars continued to consider evolutionary ideas. Ibn Khaldun, in his *Muqaddimah* (1377), for example, speculates that humans developed from other primates, including monkeys, through a process by which species became more numerous. Well-acquainted with Aristotle, Ibn Khaldun reiterates the idea of a Great Chain in which species are arranged hierarchically as lower and higher forms, but he also asserts that some forms change into others, in an ongoing and endless process.

The Medieval Period

In the Early Middle Ages, as the works of Aristotle and Plato were reintroduced into the European universities, religious scholars like Peter Abelard and St. Thomas Aquinas made

Aristotle a centerpiece of their speculations on the natural world. Aquinas in particular held Aristotle in such reverence that when he cited him as a source, he referred to him simply as "The Philosopher," as no further identifying information was needed. The medieval view of biology is simply an updating of the Great Chain of Being, in which species occupy a hierarchical ranking in a perfect creation, with hell at the bottom of the ladder and God at the top. In a perfect hierarchy, there are no gaps and no unfilled positions, and thus there is no way that an organism would alter its position and therefore no evolutionary change. Although this perspective would greatly influence the eventual rise of seventeenth- and eighteenth-century biology, Aquinas was actually open to the possibility of evolution. Like Augustine before him, he cautioned that the account in Genesis should not be taken literally, or at least not in way that conflicted with what natural philosophers (scientists) were learning about the natural world. Aquinas argued that there is no necessary conflict between the idea of a divinely created universe and the concept that, via natural processes, it may have changed over time.

Eighteenth-Century Science

Although the idea of a fixed hierarchy of species remained influential for centuries, in the eighteenth century, several influential philosophers began to question it again. In France, Georges-Louis Leclerc, Comte de Buffon, wrote that modern species were modifications of earlier forms, changed by environmental factors. He used cats as an example, suggesting that leopards, tigers, and domestic cats plainly share a common ancestor. Buffon speculated that the approximately 200 species of mammal known at the time were actually modifications of only 38 original animal forms. This idea was quite influential in European scientific circles, unfortunately, so was Buffon's idea that those earlier forms had arisen through spontaneous generation. His fellow Frenchman, Denis Diderot, also wrote that living things arise through spontaneous generation,

though he added an early attempt at describing natural selection: new forms are spontaneously generated all the time, and they either survive or fail to survive based on how well-suited they are to their environment, by a process of trial and error.

Meanwhile, in England, James Burnett wrote in 1792 (perhaps borrowing from Ibn Khaldun) that man had descended from other primates and that over long periods of time, species would change their characteristics in response to changes in their environment. He gave no indication of what processes might be involved in such change, however.

Into the Nineteenth Century: Erasmus Darwin and Jean-Baptiste Lamarck

In the late eighteenth and early nineteenth century, Erasmus Darwin, Charles Darwin's grandfather, also wrote about the origins of life in a remarkably prescient manner. In *Zoonomia* (1796), he speculated that all warm-blooded mammals must have a common ancestor in the distant past. In his best-known work, the epic poem *The Temple of Nature* (1802), Erasmus Darwin writes that this common ancestor of all animals must have originated in the sea, and he does so in verse (*Canto I*):

Ere Time began, from flaming Chaos hurl'd
 Rose the bright spheres which form the circling
 world;
 Earths from each sun with quick explosions
 burst,
 And second planets issued from the first.
 Then, whilst the sea at their coeval birth,
 Surge over surge, involv'd the shoreless earth;
 Nurs'd by warm sun-beams in primeval caves
 Organic Life began beneath the waves.

Shortly after the publication of Erasmus Darwin's epic, the less-poetic Jean-Baptiste Lamarck became the best-known evolutionary theorist prior to Charles Darwin with the 1809 publication of *Philosophie Zoologique*, in which he introduced the influential notion of the *inheritance of acquired characteristics*. Lamarck dispensed with the idea of a common ancestor, instead following Buffon and Diderot's notion

that new life forms are continuously emerging via spontaneous generation. These new species then adapt to their environment by changing their use of their organs and muscles in response to environmental pressures, and they then pass along these structural changes in their own bodies to their offspring. A Lamarckian explanation of the giraffe's long neck, for example, would focus on the idea that during its life, a giraffe had to stretch frequently to reach leaves, and because of this stretching, its offspring will inherit a slightly longer neck. The inheritance of acquired characteristics became widely known as Lamarckism, and it influenced subsequent discussions of evolution, including Darwin's own deliberations on his data, throughout the nineteenth and into the twentieth century.

One last pre-Darwinian theorist deserves mention here: Robert Chambers, whose best-known work, *Vestiges of the Natural History of Creation* (1844), was published anonymously, with the author's identity only confirmed posthumously, when the eighth edition was published in 1884. The book was quite popular with the public but widely derided by the scientific community for its simultaneous embrace of both the latest scientific findings and a distinctly unscientific religious notion of predestination. Chambers acknowledged that the fossil record clearly reveals evolutionary change over time, but this change follows a progressive, ascending path that leads inevitably, inexorably to man at the top of the Great Chain of Being. In this view, natural processes do operate on the development of species, but only as part of a preordained master plan that leads to humanity as the highest organism. *Vestiges* was extremely popular; both Abraham Lincoln and Queen Victoria are known to have read it, along with Alfred Lord Tennyson, Elizabeth Barrett Browning, and William Gladstone. The book stirred up so much controversy and was so reviled by members of the Royal Society that its publication is frequently cited as one of the reasons that Darwin chose to delay the publication of *On the Origin of Species* for another 15 years, lest his own work receive the same contemptuous dismissal by the scientific community.

Cross-References

- [Erasmus Darwin](#)
- [Jean-Baptiste Chevalier de Lamarck](#)

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Early Relationship Processes

- [Sex Differences in Social Development](#)

Early Stage of Brain Development at Birth

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Synonyms

[Apoptosis](#); [Axons](#); [Brain development](#); [Dendrites](#); [Fetal](#); [Infant](#); [Maturation](#); [Necrotic cell death](#); [Neonatal](#); [Neonate](#); [Neurons](#); [Postnatal](#); [Prenatal](#); [Synapse](#)

Definition

Apoptosis	Distinct form of cell death that reflects a highly regulated sequence of physiological events
Axons	Principal means of sending signals from the neurons

Dendrites	Major sites for receiving inputs from other neurons
Fetal	Week 9–week 40 gestation
Necrotic cell death	Pathological process that follows insult or injury to a population of cells
Neonatal	1–28 days living
Neurons	Specialized nerve cells that communicate with one another using electrical and chemical signals
Infant	1 month–12 months living

Introduction

The human brain develops in a predictable sequence but not at an even pace. Early experience during the postnatal period undergoes processes that underlie plasticity and capacity for adaptation in brain development. The human brain will double in size in the first year with the prefrontal cortex being the last brain area to mature. The prefrontal cortex houses our most advanced cognitive functions such as attention, motivation, and goal-directed behavior. Human brain development involves gene expression and environmental influence. Genes begin the process of brain development, and experience furthers the process. Development of the human brain remains incomplete until the age of 25.

Early Stage of Brain Development at Birth

A neonatal brain must first undergo development within the prenatal stage in utero. The neural tube is the first well-defined neural structure within the brain. The neural tube will eventually form the ventricular system of the brain. The structural and functional identity of the sensory and motor cortices remain malleable to the effects of input and experience into early postnatal development. Most neurodevelopmental events involve the proliferation of neural elements (Stiles and Jernigan 2010). Most neuron production takes place on the walls of the ventricles during brain development. The brain has almost all the neurons it ever will at birth, and most neurons are still immature that

connections between neurons are weak or have not yet been formed. They possess the characteristics of post-mitotic cells; once formed, they are no longer capable of dividing and producing new cells. Neurons need to become a part of the information processing networks and do so by developing axons and dendrites to communicate with other neurons. Synapses allow for the transmission of electrochemical information essential to communication in the brain by passing messages between neurons. Early in the postnatal period, the number of synapses plateau at levels nearly 200% as observed in the adult brain and form at a faster rate than at any other time between the ages of birth and 3. According to the neurotrophic hypothesis, neurons that establish effective connections are able to obtain more neurotrophic factor and are more likely to survive. There are two processes that involve a substantial loss of neural elements. A normal loss of 50% or more of the neurons within a brain will be due to a natural occurrence of cell death. Natural cell death occurs mostly in the prenatal period, whereas pruning occurs in large scales in the postnatal period. Necrotic cell death is a mechanism for eliminating damaged tissue from the biological system. Apoptosis is a cell-intrinsic process ultimately resulting in the breakdown of DNA and supports proteins and fragmentation of the cell. Apoptosis can reach up to 70% in some regions across the cortex and peaks during prenatal life. A systematic elimination of up to 50% of connections following a large scale of excess production occurs as a result of pruning. Microscopically, rapid formation and retraction of connections of individual neurons over time periods of minutes or hours can be observed. Cell death and pruning play essential roles in establishing complex networks of the developing brain. Important to cell death in brain development is the role played in regulating the establishment of effective and functional neural circuits. Substantial evidence has shown that cell death plays an essential role in eliminating cell populations that serve only a transient function in brain development (Stiles and Jernigan 2010). Proliferation and migration of glial progenitors (specifically oligodendrocyte progenitor cells (OPC)) continue for a protracted

period. Unlike neural progenitors, glial progenitors continue to proliferate as they migrate. OPC begins to differentiate by extending processes and increasing myelin protein expression. They synthesize a number of trophic factors that appear to contribute to the maintenance of axonal integrity and neuronal survival. Newer evidence has suggested that a subset of the OPCs dispersed throughout the brain form excitatory and inhibitory connections with neurons, potentially contributing actively and directly to neural signaling (Stiles and Jernigan 2010). Early in the postnatal period, transient connections form throughout the brain, which are unobservable in adults.

Experience in Brain Development

During the postnatal period, the mature organization of the neocortex emerges over a protracted time and requires diverse forms of input via all of the major sensory systems (Stiles and Jernigan 2010). The specific experience of the organism plays an essential role. Alternative patterns of brain organization will emerge when input specific aspects are lacking. Greenough's "experience expectant" and "experience dependent" offer constructs for the importance of early postnatal input. Enrichment and deprivation can alter input and have dramatic effects on structural and functional organization on the developing brain. Environmental changes influence neonatal behavior after birth which enables continuity between prenatal and postnatal behavior (Satnojevic et al. 2012).

Conclusion

The early events in the prenatal period provide an initial pattern that is underspecified and malleable. The mature human brain has a characteristic pattern of folds and ridges. This enfolding is thought to be an adaptation to the dramatic growth of its size during the course of evolution. Brains do not develop normally in the absence of critical genetic signaling or of essential environmental input (Stiles and Jernigan 2010). The regularity of developmental processes of the brain follows genetic, factored constraints.

The developmental process relies on the right neural elements presenting at their appropriate developmental time.

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Early Theories of Language

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Synonyms

[Darwin's theory on language evolution](#); [Muller's theories on language evolution](#); [Origin of language](#)

Definition

The early theories of language refer to the early theories addressing the evolution of language.

Introduction

The origin of language in the human species is a topic that has received increased attention over the

centuries. Due to the scarce evidence, there are difficulties in studying how language emerged. Therefore, researchers who wish to study the emergence of language need to draw inferences from other kinds of evidence such as historic petrified and physical remains and studies of language acquisition and evaluate the differences between human language and systems of communication existing among other animals.

On the 8th of March 1866, the Linguistic Society of Paris prohibited any existing or future discussions on the topic, and this ban continued its legacy in the West until the late of the twentieth century (Stam 1976). The absence of empirical evidence has led many researchers to consider the entire subject as inappropriate for further research examination. In our days several theories address the evolution of language (Tallerman and Gibson 2012). Many scholars in the field of linguistics, psychology, anthropology, and others have endeavored to explain the commencement of language in the early 1990s (Christiansen and Kirby 2003). It is of paramount importance, however, to consider the contribution of early theorists, such as Friedrich Max Müller and Charles Darwin, whose legacy was significant to further research in language acquisition in later years.

Friedrich Max Müller and His Early Theories on the Evolution of Language

Müller was a German philologist who proposed some early theoretical formulations concerning the origins of language. After the publication of *The Origin* in 1859, Müller was fascinated of the idea of human evolution. The tradition of giving disparage names to the theories regarding how language evolved commenced by him, and this was an important factor in his campaign against Darwin's evolutionary theory. Müller (1877) established associations between Darwin's evolution on humans and many other ideas about development, and he concluded that languages are subjected to historical radical change. However, he later realized that he underestimated Darwin's arguments and his suggestions concerning the history of human evolution. In 1864, Müller

presented his *Lectures on the Science of Language*. In this period of time, he started to reevaluate Darwin's theory. In his book "The Descent," Darwin had a section about Language, in which he proposed his own theories about the evolution of language. Müller had different ideas about how language emerged, and therefore, he talked in public about "Mr. Darwin's Philosophy of Language" in 1873 (Knoll 1986).

In these talks, Müller suggested that the language faculties of humans are distinguished from other creations; therefore it was impossible that the human development evolved from a lower form without language acquisition. His point of view was supported by his opinion that the linguistic roots are considered the original building blocks of language. In his *Lectures on the Science of Language*, he proposes that Indo-European verbal communication had developed from hundreds of verbal "cells." Müller hypothesized these linguistic roots as fundamental of the theory of mind. He assumed that they establish the principles for the Kantian intellectual classifications used by the mind to establish cognizance out of raw sense of perception. This capacity of the individual's mental structure separated man from animals since it formed the basis of man's exclusive capacity to form a concept and think rationally. Without these capacities, neither language nor thought was possible. Müller concluded that because animals do not have this intellectual structure, their evolution into humans was impossible (Müller 1877). In 1861, Max Müller published a list of theoretical concepts concerning the origins of language. He later abandoned most of his theories which include the bow-wow theory, the pooh-pooh theory, the ding-dong theory, the yo-he-ho theory, and the ta-ta theory.

Bow-Wow Theory

The overall idea of the bow-wow theory is that the beginning of language can be linked to the era when the progenitors begun to mimic the sounds in their natural environment, a process called "onomatopoeia." The natural world was of paramount importance in the origination of language since the sounds of animals played a significant role in the invention of the vocabulary used in

verbal communication. On the one hand, Thorndike (1943) was doubtful about the credibility of this theory as the beginning of language. On the other hand, recent studies support that being able to mimic sounds in the natural environment was of paramount importance in the evolution of language (Malle 2002).

A major drawback of this theory is the fact that people use different words to describe the sounds of animals according to their country and more specifically due to their language. For instance, the sound of a pig can be translated differently across the countries. In English a pig makes the sound "oink-oink," and in Russian it makes the sound "hyru-hyru," while in Chinese it makes the sound "oh-ee-oh-ee." Therefore, the sound and pronunciation of the words are not similar among the different languages. Another challenge is that there are few onomatopoeic words in the languages worldwide. In case the theory was credible, then it should have plenty of words out from the basic rule of onomatopoeia. The hypothesis that language is determined by how a person interprets a sound was rejected, since there are many languages and nobody can suggest that human vocabulary arose from these sounds (Thorndike 1943).

Ding-Dong Theory

The idea behind the ding-dong theory is sound symbolism which is a nonarbitrary connection between phonetic features of linguistic items and their meanings. Max Müller proposed the ding-dong theory by stating that meaning comes from sounds. According to this hypothesis, the origin of language emerged evolutionary with the names our ancestors gave to objects, activities, and natural occurrences after an identifiable sound associated with it in real life (Mandavilli 2016). An important characteristic of this notion is the fact that words having high front vowels were used to name small or jagged objects in comparison to words having round vowel which were used to name large or round-shaped objects. It is suggested that people used sound symbolism to give meaning to words through onomatopoeia, which is the formation of a word by the imitation of a sound made by or associated with its

referent in real space and time. “Boom,” for example, was the word given for explosion (Mitchell et al. 2013).

A major drawback of this theory is that onomatopoeic words are not the same in every country because the sound and pronunciation of the words are not similar among the different languages. People in different nations used their onomatopoeic words which are formed in regard to how they interpret different sounds. These words are a very limited part of their vocabulary since many ideas such as love, hate, harmony, and the sea do not make any noise. Thus, the relationship between meaning and sound is not established by any convincing evidence. For this reason, this theory was later abandoned by Max Müller (1877).

Pooh-Pooh Theory

The early speculative language theory of pooh-pooh refers to the notion that language emerged from unintentional vocal responses to agony, fright, astonishment, enthusiasm, satisfaction, or other emotions (Barber 1965). Although animals produce sounds as well, language is unique only to humans. “Ouch!,” “Aaah!,” and “Wow!” are some examples of the unintentional vocal responses that emerged from this hypothesis. This theory can be found in the literature as “the expressive theory,” “*the interjectionist theory*,” or “the expressions of emotions theory” (Barber 1965). Max Müller supported the pooh-pooh theory for a while, but later he abandoned it (Müller 1877).

The notion of the pooh-pooh theory that language has many emotional exclamations has been widely criticized by many reviewers. It has been argued that the explanations provided by this theory constitute a very limited part of the vocabulary of different languages. Further, the various languages worldwide have different interjections. For instance, in English pain is “ouch,” while in Greek it is “aou.” Therefore, it is indicated that sounds could have been different if their origin was from interjections. To conclude, although early human beings could use words based on interjections, these may have been ultimately overruled by more sophisticated and abstract

terms (Mandavilli 2016). Finally, it is important to emphasize that although animals react to the sudden feelings they experience using sounds, they didn’t develop language as human beings did.

Ta-Ta Theory

According to Richard Paget, who was specialized in speech science and the origin of speech, the ta-ta hypothesis supported that speech and the development of sound was produced to endorse the hand and body movements of the individual. So as to better demonstrate the meaning behind the gestures, these sounds developed different words or combinations of sounds unavoidably leading to speech patterns (Paget 1930). For instance, when a person would say ta-ta, he was basically saying good-bye with his tongue. At some point, this theory was even supported by Charles Darwin (Mandavilli 2016). In the literature, there are several theories such as the oral gesture theory and the chew-chew theory that support the idea that the origin of language begun from early human gestures made from their mouth. It is of paramount importance, though, to understand that it is not feasible to explain the origin of some words using the ta-ta theory.

A major drawback of this early theory on the origins of language is the fact that in order for people to be able to communicate between them, they must see each other in person. Also, there must be daylight, or firelight, and with nothing blocking one’s view. In the case of hand gestures, it is important that hands are free from doing something else (Crowell Meir et al. 2010). Last but not least, in order for this hypothesis to be the origination of communication, it required a number of gestures be in place already for humans to imitate with their mouth gestures, but it didn’t explain how these gestures arose in the first place.

Yo-He-Ho Theory

Verbal communication commenced as growls, moans, and rhythmic chants which occur from the overwrought efforts of ancient menfolk to move a boulder or heave a rock, as it is suggested by the yo-he-ho theory (Mandavilli 2016). Every

time these people were working hard to move something heavy, they produced a sound which slowly developed into words such as “heave” and “lift.” Therefore, if they didn’t want to memorize their favorite growl-sound and use it over and over again, this sound would seem to be random. However, these growls would not be accounted as words in a lingual meaning since they would seem unlikely to fall into consonant-vowel patterns (Rice 1976). The yo-he-ho theory does, however, have a benefit since it is responsible for the inducement, the cause, and the aim of the language. It describes language as emerging from a need to communicate and for making the engagement among men possible in organized activity, rather than seeing language resulting from a cave dweller imitating an animal’s howl to assist him while he was away for his dinner (Barber 1965). The yo-he-ho theory can be found in the literature as “yo-heave-ho theory” and “Social interaction source,” all of them proposed that the origin of speech begun as growls and moans (Mandavilli 2016).

Notwithstanding the above, evolution plays an important role since it claims that human society developed gradually because men began thinking of new things to do and began doing them collectively. What makes this theory interesting, however, is the query of what motivates the speechless cavemen move a boulder in the first place since language emerged from the growls and moans of their teamwork. Unfortunately, the origin of grammatical structure is not explained or how a social system got started void of language (Rice 1976).

To summarize, it is a matter of fact that language is a human trait. All efforts to explain how language emerged have failed because of the absence of knowledge concerning the origin of any language. An important factor for the inability to acknowledge the origin of language is because none of the animals possesses any transitional form of communication. As a consequence, Müller could not differentiate between humans’ linguistic faculties and the growls or sounds of animals. Also, the cultural roots of various hand gestures did not suggest verbal communication. Last but not least, most of his theories did not explain the origination of different ideas or things

that do not produce any sound, and this resulted to a limited vocabulary of the languages. As a result, there could not be an explanation of the origin of names of such concepts, if his theories were chosen as the origin of language.

Charles Darwin’ Work on the Origin of Language

In his book, *Origin of Species*, Darwin intentionally did not refer to human evolution in detail (Darwin 1859). Although it was perceived that this was a mere oversight, this was not true. Darwin carefully avoided to thoroughly refer to his hypothesis on human evolution because he knew that his theory would not be accepted, but rather it would probably provoke the existing insurmountable opposition. His rivals, however, emphasized the importance of human mind, and language in particular, to compete Darwin’s work. Müller, one of the reputed scholars of that time whose work on evolution of language was summarized above, was considered as Darwin’s most intimidating rival on the linguistic front (Stam 1976). In 1861, Müller delivered lectures at the Royal Institution of Great Britain. These lectures, entitled as “*Lectures on the science of language*,” were published soon afterward, and Müller used his expertise in the “*science of language*” as a strong weapon to attack Darwin and Darwinism (Müller 1861). Müller’s hypothesis about the origin of human language in relation to how animals communicate provoked Darwin to further study language.

In 1871, Darwin published his second book *The Descent of Man and Selection in Relation to Sex*. In this book he raised the subject of human evolution, and he provided explanation of how language emerged. Darwin’s “*musical protolanguage*” model was a response to this propaganda and thus represented a combination of comparative data, evolutionary insight, and a biological perspective on language. His innovative view of language and his models are still astonishingly applicable to contemporary arguments. Darwin proposed a complex model to explain the evolution of language in which he recognized

the necessity of various mechanisms in order to produce vocal sounds. Most importantly, he observed that several components in vocal learning shared many biological capacities similar to birds in the production of sound.

Further, Darwin took advantage of a wide comparative collection of data, by using his insight of both nonhuman primate behavior and vertebrates. He proposed a broader theory of evolution that is applicable to insects, flowers, and birds. His purpose was to reveal through investigation general ideas, like sexual selection and shifts of function, to give more information about common and unique human characteristics. Darwin's model suggested that language emerged only to humans since there is no progression of function between nonhuman primate calls and language (Fitch 2006).

Language as a Natural Aptitude

In his book *The Descent of Man and Selection in Relation to Sex*, Darwin discusses about the evolution of human mind. He suggested that animals have feelings, attention, memory, and many other mental traits in common with human beings (p. 34–52). Some of his opponents, however, and specifically Müller had already suggested the hypothesis that animals have memory, experience feelings, and so on. What was of paramount importance, however, was the subtitle “Language” (p. 53) in his book where he spoke for the first time about the evolution of language.

Theoretically, Darwin made some significant observations. First, he acknowledged the essential difference between the biological ability that enables humans to acquire language and specific languages (like Latin or English). Although he initially suggested language as an instinctive propensity shared by all humans, he later emphasized that language is not an instinct provided that every language has to be learnt. He suggested language as natural aptitude whose expression implies that both biological and environmental preconditions must be satisfied.

Second, in spite of the fact he was cognizant of the unique characteristics of the human vocal tract, Darwin supported that the human ability for language must be sought in the brain, rather

than the peripheral vocal tract. He concedes that a unique characteristic of humans is the ability to speak fluently and coherently by controlled movements of their lips and tongue (p. 59). Nonetheless he repudiates that simple power of articulation is enough to distinguish human language, since as he explained parrots can talk as well. It is further stated that it is not speech but humans who are largely capable of joining certain sounds with particular concepts that is definitive of language. This capacity apparently depends on the development of the mental abilities.

Finally, Darwin argued that there is a coherence of the evolution of language to the birdsong, which he thought it was similar to human language. Both humans and birds have fully instinctive calls that they have to learn. Also, he emphasized the fact that both birdsongs and speech form regional dialect depending on their place of residence.

The Musical Protolanguage Model

Darwin's model of the evolutionary development of the language capacity assumes that various features of language were obtained in specific order, inspired by unique selection pressures. The hypothetical arrangement that was classified by each addition was called as protolanguages (Hewes 1973). Darwin firstly hypothesized that the evolution of humans progress from an ape-like ancestor to the protohuman cognition. He proposed that some primates developed highly mental capacities even before any form of verbal expression come into use (p. 57). He also stated that both social and technological factors act as drivers of this superior cognitive ability.

Darwin later proposed the musical protolanguage model (Fitch 2006), after observing numerous resemblances in birdsong and human language. He precisely implies that there is an inherent ability to replicate vocals evolved analogously in humans as well as songbirds to express feelings such as love, jealousy, and success. He reasoned that sexual selection is mainly used as the main driver behind the evolution of spoken language.

What is crucial for further investigation, however, is the transition of the musical

protolanguage model to a meaningful speech. According to Mithen (2005), the progress of the musical protolanguage model to a meaningful speech remains the greatest explanatory challenge for all musical protolanguage theories. Darwin, however, referred to Müller's writings, and he embraced the theory that language emerged from natural sounds, such as the imitation of the sounds of animals and man's own instinctive cries (Farrar 1870). It is important to note that once the protohumans had the ability to mimic sounds and translate signals into meanings, then the ability to produce speech evolved, including onomatopoeia and the imitation of human emotional vocalizations.

Sign Language

Darwin, in a clear and detailed manner, described the role of gestures in the communication among humans. He was aware of the practice of sign language as a means of communication to deaf individuals (p. 58). He acknowledged the importance of gestures in conveying meaning, and he emphasized the fact that in order for people to be able to communicate between them they must see each other directly. Although he agreed that vocal communication can be aided by signs and gestures (p. 56), he criticized the gestural theorists. In his point of view, the vocal organs were significant to all mammals in the development of communication rather than the use of fingers. A major problem for gestural theories is to explain how such a system evolved from an initially iconic, holistic, meaningful system.

Sexual Selection in the Evolution of Language

Darwin's sexual selection theory states that sexually selected traits develop mostly in men who are considered to be more competitive and only at sexual maturity. Darwin, however, figured out that it is equally developed in males and females and is expressed very early in the biological development (Fitch 2005). There are few explanations to the difficulty that these facts pose. Firstly, during the musical protolanguage stage, sexual selection was the driving force, and song was

expressed mainly in males at sexual maturity. After the evolution of language, Fitch (2004) proposed that a selective force appeared to aid women to equally express language as men did and that language develops in earlier stages of life. The communication among the members of the family can be a selective force. Parent's communication with their offspring is an important aspect of their upbringing. Moreover, this can explain the reason language evolves at an early stage in the life of human beings. Language at an early stage of life can help children absorb their elder's knowledge and experience. Also, this kin selective force can explain the reason that language evolved only to humans and not to animals. People are going through life stages where they gain knowledge and experience, with very small reproductive output in relation to animals, which can reproduce from their early stage of life (Fitch 2007).

A different approach proposed by Miller (2001) is that sexual selection was an important driving force in human intellectual evolution, including speech. This hypothesis suggests that both sexes can choose and compete for high-quality partners. It is of paramount importance, however, to understand that this hypothesis does not explain the early development of language in infants. Finally, it is considered that sexual selection never played a role in the evolution of language (Miller 2001).

To summarize the compelling work of Darwin on the origins of language, it is important to note that Darwin proposed that the first step to language evolution was an increase in the mental capacities of humans. He agreed that both social and technological factors are significant in the selective roles. He used a wide comparative collection of data of nonhuman primate behavior and vertebrates, to propose his theories on the evolution of language. Darwin benefited from his studies on animals, and he used his observations to propose his theories on language development. Although he studied both the evolution of human and animals and described many traits shared between them, he concluded that language is unique only to humans.

Conclusion

The origin of human language despite its long history will probably remain uncertain. Nowadays, most scholars consider the early theories of how language emerged as invalid. These theories were the beginning for later researchers to develop their concepts on how language emerged, a topic that up until today it remains controversial. All these years, the evolution of language is one of the hardest topics under investigation, since there is not enough empirical evidence to adequately address the factor/s that initiated speech in our ancestors.

Cross-References

- [Darwin on the Origin of Language](#)
- [Müller's Language Hypotheses](#)

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Ears of Mammals

► Mammalian Ear, The

Eating

► Feeding

Eating Disorders

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Synonyms

Anorexia nervosa; Binge eating disorder; Bulimia nervosa; EDs; Fear of weight gain; Food restriction

Definition

Eating disorders are a category of psychological disorders characterized by abnormal eating and related thoughts and emotions. People with eating disorders often have a preoccupation with food and their body image.

Introduction

Eating disorders (EDs) are a category of psychological disorders. The three main classifications in

the category of feeding and eating disorders are anorexia nervosa (AN), bulimia nervosa (BN), and binge eating disorder (BED). A fourth category is “eating disorders not otherwise specified,” in which individuals have eating-related problems but do not meet the diagnostic criteria for anorexia, bulimia, or binge eating. Eating disorders are characterized by abnormal eating behaviors and related thoughts and emotions (Parekh 2017). People who suffer from eating disorders are often preoccupied with food and their body image or weight and tend to be perfectionists who are extremely critical of themselves and their bodies (Parekh 2017). Eating disorders can be detrimental to one’s overall health and, in some cases, they can be life-threatening conditions. For example, anorexia is associated with increased risk of osteoporosis, anemia, and damage to the heart and brain (Brownell et al. 2011). Research has shown that individuals with anorexia have a mortality rate 18 times higher than peers who do not have eating disorders (Steinhausen 2009). Bulimia can result in mouth damage, gum disease, esophageal tears, and gastric ruptures (Parekh 2017). Furthermore, eating disorders are associated with an increased risk of suicide and increased rates of other psychological disorders such as depression and anxiety (Walden Behavioral Care 2019). Approximately 90% of those diagnosed with eating disorders are females (Hudson et al. 2007). However, the number of males diagnosed with eating disorders has been slowly increasing. When it comes to binge eating disorder, males and females are equally as likely to be affected (Brownell et al. 2011). Over recent decades, researchers have been studying the potential adaptive underpinnings of psychological characteristics which at nonclinical thresholds or in different ancestral environments may have conferred a survival or reproductive advantage, but which in their extreme form contribute to maladaptive eating behavior in contemporary humans. This chapter will describe the symptoms and diagnostic categories of eating disorders, discuss major hypotheses surrounding the evolution of the psychological and behavioral features of AN and BN, and highlight the role of food preferences and consumption behavior that evolved in ancestral environments that contributes to binge-eating disorder in a modern food environment.

Anorexia Nervosa and Bulimia Nervosa

Anorexia nervosa is an eating disorder specifically categorized by significantly low body weight, an intense fear of gaining weight or becoming fat, and disturbances in body image (Parekh 2017). The disorder can take one of two forms: restrictive subtype and binge-eating/purging subtype (National Institute of Mental Health 2018). The disorder typically emerges in adolescence, primarily between the ages of 15 and 19, and has the highest prevalence among females in Western societies (Brownell et al. 2011). However, eating disorders can affect people of all ages, racial/ethnic backgrounds, and genders (National Institute of Mental Health 2018). Bulimia nervosa, on the other hand, involves episodes of binge eating excessive quantities of food in a short amount of time and subsequent compensatory behavior to prevent weight gain by vomiting or using laxatives, enemas, or diuretics (Walden Behavioral Care 2019). This disorder can also be classified further into two types: purging and non-purging. Purging type is the most common form of bulimia and involves the abovementioned compensatory behaviors (Walden Behavioral Care 2019). The nonpurging type involves excessive exercise or fasting after a binge eating episode (Walden Behavioral Care 2019). Individuals with bulimia and anorexia share many features such as an extreme fear of fatness, a distorted body-image, a preoccupation with food and eating, and both primarily affect females of reproductive age in Western societies.

Since the mid-1970s, researchers have been interested in explaining the cause of eating disorders from a variety of perspectives. Some of the predominant theories are rooted in psychoanalytic approaches, sociocultural approaches, and biological approaches (see Salmon et al. 2009 for review). For example, one common sociocultural explanation attributes the cause of eating disorders to exposure to western ideals of female beauty and the internalization of a thin ideal (Salmon et al. 2009). Another set of studies from a biological approach have focused on the influence of genetics due to high heritability rates. Yet, despite the various theories that attempt to explain these disorders, they all face major limitations and

thus the causation of eating disorders still remains poorly understood (Faer et al. 2005; Salmon et al. 2009).

Recently, some researchers have approached the problem from a Darwinian perspective and developed evolutionary hypotheses in an attempt to better understand these disorders. Guisinger (2003) proposed the adapted to flee from famine hypothesis, which suggests that anorectic symptoms are manifestations of adaptive mechanisms to conditions of famine faced in our evolutionary past. These symptoms include restrictive food intake, denial of starvation, and hyperactivity, the latter of which has been evidenced by laboratory findings on rodents. Aside from this and some other minor theories, a few distinct evolutionary hypotheses can be identified in the current literature, all surrounding the ultimate causation of eating disorders. These include the Reproductive Suppression Model (Wasser and Barash 1983; Voland and Voland 1989), and theories that fall under the evolutionary concept of intrasexual competition, which includes the Sexual Competition Hypothesis (Abed 1998, 2012), and the theory that anorexia is a manipulative strategy imposed on subordinates by females (Mealey 2000).

The Reproductive Suppression Model (RSM)

We first consider the Reproductive Suppression Model (RSM) proposed by Wasser and Barash (1983). This theory rests on the assumption that not all conditions are equally favorable for investment in reproduction (Wasser and Barash 1983). For example, poor mental and physical health, social and psychological stressors accompanied by a perceived loss of social support, or the expectation that future conditions will be better than present conditions should trigger the suppression of reproduction. Individuals under this type of stress might be unsuited to pregnancy and raising offspring since these are cues of unfavorable environmental conditions (Wasser and Barash 1983). In these circumstances, the ability to delay reproduction is adaptive because it allows females to avoid reproduction when environmental conditions are not conducive to her offspring's survival,

and thus the benefits of suppressing reproduction often outweigh the costs. Females of many species including rabbits, elephant seals, and chimpanzees appear able to suppress or delay reproduction when environmental conditions are unfavorable. These mechanisms for “deciding” not to reproduce include suppression or delay of ovulation, delay of sexual maturation, and fetal miscarriage (Wasser and Barash 1983).

Other scholars have built on this initial theory and applied the RSM to humans to try to explain anorexia. They argue that it could be beneficial for human females to suppress reproductive potential when conditions are not favorable for investment in reproduction, and that body fat is minimized in situations when it would be disadvantageous for a girl to become pregnant (Surbey 1987; Voland and Voland 1989). By becoming anorexic, females can manipulate the timing of reproduction and stunt development. Research by Juda, Campbell, and Crawford (2004) supports the Reproductive Suppression Hypothesis, as they found women who perceived less support from their families have higher levels of dieting and decreased perceptions of parental readiness. They felt less prepared to raise a child and had more disordered eating attitudes and behaviors. Dieting is a mechanism that can be used to suppress reproduction; thus, these results lend support to the idea that dieting symptoms and perhaps eating disorders may be associated with an ancestral reproductive suppression mechanism (Juda et al. 2004).

This is highly relevant in modern day society which favors late maturation. Anorexia is a way to delay a female’s natural developmental trajectory by reducing fat through strict dietary behaviors. Most women require adipose tissue to make up approximately 22% of their body weight to maintain ovulation (Salmon et al. 2009). Women with anorexia approach a dangerously low weight to the point that their bodies often become incapable of supporting reproduction. Women with anorexia often experience cessation of their normal menstrual cycle (amenorrhea), since their body fat levels drop significantly below the average (Surbey 1987). Surbey (1987) concludes that it is unlikely that anorexia itself is the result of selection. Rather, what might have been selected

for is the ability of females to alter the timing of reproduction and anorexia nervosa appears to reflect this ability in response to environmental conditions (Surbey 1987). Voland and Voland (1989) noted that the patient’s age, initiating events, and the developmental context of AN seem to support the connection between reproductive suppression and AN. For example, 95% of AN cases had an onset under the age of 25, which corresponds with the ages at which women are most fecund (Voland and Voland 1989). The authors also incorporate kin selection theory to explain reproductive suppression in anorexic females. It has been proposed that the reproductive suppression that occurs in anorexic individuals may be adaptive since it allows for an increase of familial helping behavior at the cost of her reproductive suppression (Voland and Voland 1989). This could allow for an increase in her inclusive fitness, as noted in an analysis of female anorexic case histories by Voland and Voland (1989). Some studies have found that anorexic individuals are constantly and excessively worried about the welfare of their families and feel responsible for protecting their family members, and this worry, coupled with excessive helping behavior, was apparent in one of the case studies (Voland and Voland 1989).

Although the reproductive suppression model has received some support, it fails to address many key features of anorexia. For example, it cannot be used to explain why anorexia exists in postmenopausal women, why a less costly method to suppress reproduction would not have been selected for, and the distorted body image of those who have eating disorders. Furthermore, it fails to explain eating disorders in males and the mechanisms associated with other eating disorders.

Intrasexual Competition

Another evolutionary hypothesis surrounding eating disorders attempts to address some of these gaps and limitations faced by the previous explanations. The Sexual Competition Hypothesis (SCH) is based on Darwin’s (1859) theory of sexual selection, which has shaped systems

designed for mate attraction and retention. This theory explains that eating disorders, as well as the pursuit of thinness more generally, stem from the process of female intrasexual competition. Specifically, eating disorders are considered to be a state of “runaway” female intrasexual competition whereby the drive for thinness, which in moderation may be a useful and even adaptive strategy, instead spirals out of control in response to a range of genetic and/or environmental factors and becomes maladaptive (Abed 1998, 2012; Faer et al. 2005). Whereas men usually engage in more direct, physical forms of competition, women tend to engage in indirect forms of intrasexual competition. This often invokes the exclusion of rivals from the peer group, disparaging the competitor’s appearance and gossiping or spreading rumors about the rival’s fidelity or level of promiscuity (e.g., Davis et al. 2018). The goal of this form of intrasexual competition is to reduce the mate value and lower the desirability of a rival in the eyes of potential mates while simultaneously raising one’s own standing within the social network.

One other competitive mechanism women might employ within this domain, which bridges intersexual and intrasexual selection is the achievement and preservation of a nubile, sexually appealing body shape, as modeled by a low waist-to-hip ratio (WHR). Reproductive potential reaches its maximum 3–4 years after puberty, and this is also the time the nubile female body takes its full shape (Abed 1998). Men exhibit preferences for women of intermediate weight with a low WHR (Singh 1993). From this, it can be inferred that the extremely low body weight of those with anorexia is not an ideal imposed by men (Mealey 2000). Research demonstrates that the most attractive female WHR was judged to be 0.7–0.8 by both males and females (Singh 1994). Conversely, males with a low WHR were considered undesirable (Singh 1995). This gender specificity of the ideal WHR suggests that this trait is fundamental to mate attraction and could have evolved via sexual selection. A low WHR in women is viewed as an honest signal of a woman’s health and reproductive potential; it putatively indicates a higher estrogen ratio and

greater fecundity (Jasienska 2004). Thinness has also been shown to correlate with youthfulness (Singh 1993). Thus, the pursuit of thinness can be an adaptive strategy for mate attraction and retention, but only to a point. Once the female reaches a state of being clearly undernourished and emaciated, this is no longer attractive to males and is a threat to the woman’s health and wellbeing. The bodies of women with anorexia do not represent the attractive ideal, since their WHR is far from the 0.7 to 0.8 range. Furthermore, obvious malnutrition is a visual cue that can signal a woman’s inability to bear children. For example, having very low body fat can result in amenorrhea, the absence of ovulation and menstruation. The SCH is also able to explain pathological by-products such as reproductive suppression. The theory proposes that amenorrhea arises as a by-product of maladaptive runaway intrasexual competition (Abed 1998). Thus, for women with eating disorders, this drive for thinness becomes extreme and maladaptive.

There has generally been more empirical support for this hypothesis relative to the others reviewed thus far. For example, Faer et al. (2005) recently demonstrated that intrasexual competition for mates had positive direct relationship with body dissatisfaction and drive for thinness. Furthermore, it was a predictor of disordered eating behavior, suggesting that eating disorders are fundamentally linked to female intrasexual competitiveness (Faer et al. 2005). In an extension of this study by Abed et al. (2012), results demonstrated an association between female intrasexual competitiveness, status, and disordered eating behavior. This consistent finding lends more support to the SCH. In a study by Li, Smith, Griskevicius, Cason, and Bryan (2010), researchers found that for heterosexual women, but not homosexual women, intrasexual competition cues led to greater body image dissatisfaction and more restricted eating attitudes after exposure to competitive vs. noncompetitive cues of same-sex individuals. Specifically, this occurs after being exposed to a photo of a high-status competitor (Li et al. 2010). This study emphasizes the role that cues of high status competitors might be playing in the relationship between intrasexual competition and unhealthy eating behaviors.

More recently, Arnocky et al. (2016) showed that when women made social comparisons to attractive intrasexual rivals (measured either as an individual difference trait or by experimental priming task), females reported being more envious and in turn were more willing to use risky diet pills in order to lose weight.

One theory that strongly supports the SCH speculates that dominant women may attempt to inhibit the reproductive capacity of other women in order to diminish resource competition (Mealey 2000). In this case, anorexia is a tactic of reproductive suppression of subordinates by dominant females which manifests as an intense form of female intrasexual competition. It has been suggested that the reproductive manipulation of subordinate women by dominants is a type of competitive reproductive suppression (Wasser and Barash 1983). Mealey (2000) hypothesizes that anorexia could be a result of increases in female intrasexual competition, specifically through the media, whereby socially successful and dominant women manipulate young women who are potential competitors for good mates and other resources. From this perspective, anorexia is a consequence of social manipulation rather than a tactic for outcompeting rivals.

Another existing theory that lends support to the SCH is life history (LH) theory. Fast life history strategies are associated with greater risk-taking and short-term thinking, whereas slow life history strategies are associated with long-term thinking and careful consideration of risks (Abed et al. 2012). The SCH predicts that intense intrasexual competition for mates is associated with disordered eating behaviors, which has been supported by research (Abed et al. 2012). Further, recent research has shown that disordered eating behavior is predicted by a fast life history strategy (Abed et al. 2012). A fast life history strategy is associated with increased effort toward propagating one's genes in the short term and involves greater mating effort compared to a slower life history strategy. Thus, a fast life history strategy is consistent with the increased mating effort involved in high levels of female intrasexual competitiveness, and slow life history strategies are incompatible with increased levels of intrasexual competitiveness. Indeed, a slow life

history strategy was found negatively correlate with intrasexual competitiveness (Abed et al. 2012). Furthermore, it seems that a slow life history strategy incorporates increased behavioral regulation or self-control, which plays a protective role against female intrasexual competitiveness and the development of disordered eating behavior (Salmon et al. 2009). Thus, these results categorize eating disorders as pathologies of deficient behavioral regulation and indirectly associate disordered eating behaviors with faster life history strategies and high intrasexual competitiveness.

The SCH has recently been applied to a wider range of eating disorders, since the drive for thinness is apparent in both individuals with bulimia and anorexia. This hypothesis proposes that intense female intrasexual competitiveness is the ultimate cause of both eating disorders (Abed et al. 2012). However, this hypothesis does not come without its own limitations. Namely, it still makes it difficult to explain the existence of eating disorders in males; however, sex differences in response to intrasexual competition may explain why dietary restriction and AN is substantially more common in females. Additionally, this hypothesis rests upon the assumption that concern about physical attractiveness is universal. Since the Sexual Competition Hypothesis and the process of reproductive suppression both involve female intrasexual competition, it is also possible that both mechanisms might be working together in some cases (Abed 1998). This growing body of evidence suggests that the psychological and behavioral aspects that make up AN and BN have roots in evolutionary concepts such as intrasexual competitiveness and potentially the process of reproductive suppression in response to less than ideal environmental conditions, and that this lens can provide a more comprehensive understanding of the ultimate factors contributing to these disorders.

Binge Eating Disorder

Binge eating disorder is an eating disorder characterized by out-of-control episodes of binge eating in which individuals consume excessive

amounts of food in a short period of time (Striegel-Moore and Franko 2003). Individuals with BED eat until feeling uncomfortably full, eat much more rapidly than normal, eat large amounts of food even when they are not hungry, eat alone due to embarrassment, and experience marked distress regarding their behavior (Parekh 2017). The binge eating is not associated with the use of compensatory behaviors as in anorexia and bulimia. Compared to individuals with anorexia nervosa and bulimia nervosa who are usually underweight (AN) or normal to slightly overweight (BN), those with binge eating disorder are often overweight. Although binge eating disorder affects males and females at similar rates, men are significantly less likely to be diagnosed. This is because men are less likely than women to report distress over binge eating, which is a symptom required for diagnosis of BED (Striegel-Moore and Franko 2003).

Evolutionary theory can also help to inform the prevalence of this eating disorder. In our evolutionary history, foods high in fats and sugars were very hard to come by; therefore, it was advantageous to be able to store fat and sugar effectively and to develop psychophysiological mechanisms that motivate their consumption. It was also advantageous to overeat occasionally, since there were periods of food shortages that humans had to account for (King 2013). This was often due to seasonal variations in food, which resulted in both periods of food shortage and abundance, so it was adaptive to consume as much animal fat as possible when it was available (King 2013). Since then, the human diet has changed dramatically. Now, fats and sugars are widely available and easily accessible, which is contributing to widespread obesity and early loss of life (King 2013; Mealey 2000). Research has also found that it is not necessarily about physiological hunger signals that drive humans to seek out and consume large amounts of food; rather, it is the large variety of highly palatable foods (King 2013). Indeed, research shows that individuals with binge eating disorder consume more dessert and snack-food items than obese control subjects during meals, and highly palatable foods with a greater percentage of fat (Yanovski et al. 1993). Foods high in sugar and fat activate reward centers of the brain,

and thus we are driven to eat foods that are now widely available to us, yet can be very dangerous for our health in large quantities (King 2013). Binge eating disorder has been linked to severe obesity, diabetes, hypertension, and cardiovascular disease, and in general, a high body mass index can be detrimental to health and fertility (Parekh 2017). Today obesity constitutes a serious global epidemic in industrialized countries (Kardum et al. 2008).

Conclusion

Because the understanding of eating disorders constitutes a relatively new area of research, especially from an evolutionary perspective, it is important for evolutionary psychologists to continue to research the ultimate underpinnings of eating disorders and how these interact with more proximate causal and contributing factors to better inform clinical practice and treatment. For example, assessments may incorporate measures of intrasexual competitiveness. Further, a majority of the work to date has been conducted on individuals with anorexia nervosa, whereas the bodies of literature on bulimia, binge eating disorder, and other related eating disorders still require significantly more attention from an evolutionary psychological perspective.

Cross-References

- [Anorexia Nervosa](#)
- [Desire to Be Included Among Desirable Women](#)
- [Evolutionary Clinical Psychology](#)
- [Intrasexual Competition Between Females](#)
- [Obesity](#)

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Eating Disorders (EDs)

► Anorexia Nervosa

eBullying

► Cyberbullying

E-Bullying

- ▶ [Anonymity of Cyberbullying](#)
 - ▶ [Sex Differences in Cyber Bullying](#)
-

Echoing

- ▶ [Imitation and Mimicry](#)
-

Echolalia

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Synonyms

[Verbal mimicry](#)

Definition

The repetition of speech sounds, usually in a meaningless way

Introduction

The word *echolalia* is derived from the Greek words of echo (to repeat the sounds) and lalia (to speak). In Greek mythology, Echo was a talkative mountain nymph tasked with distracting Hera so that her husband Zeus could continue to enjoy his pleasures. Hera cursed her with the voice of the echo to speak only the last words of others.

Clinical Causes

In clinical practice, echolalia is recognized to be a symptom of a range of conditions, including

autism spectrum disorder, Tourette's syndrome, schizophrenia, and frontal brain damage caused by dementia or stroke. It is also a feature of typical early language development. It is a very common feature of autism, but a much less infrequent symptom of the other disorders. It is described in most detail in the manual of the Autism Diagnostic Observation Schedule (Lord et al. [2012](#)) where it is used as a diagnostic indicator.

Phenomenology

Echolalia may be delayed or immediate. As immediate echolalia, it usually consists of a repetition of the last words of someone else's speech. Echoing in this form can be a part of normal conversation if the listener is clarifying what has been said or is confirming that he or she has heard correctly. Immediate echolalia is characterized as being nonfunctional speech, being spoken without any purpose.

When echolalia is delayed, the repeated phrases occur sometime after they have been heard. They are more likely to be whole phrases and are often copied from television or other media sources, as well as from adults. The tone and inflection of the speech may be copied as well as speech content. Delayed echolalia may also be called "stereotyped speech." The phrases are often nonfunctional but not necessarily so. Sometimes they are incorporated into functional speech and may only be evident by seeming "odd," out of character, out of context, or being used in a repetitive way. For example, a child may use language which has a very adult-like or over formal quality. Sometimes children with autism spectrum disorder will adopt odd accents. For example, children in Scotland with autism may adopt an American accent through watching American television even though people around them are Scottish. There is no clear demarcation between normal patterns of repetitive speech and stereotyped speech or delayed echolalia, and many people have speech habits which include the use of repetitive elements that do not serve an effective function. For example, people might use a word or

phrase repetitively to preface the beginning of a sentence (e.g., “actually . . .,” “to be honest . . .”), or they might use certain words excessively (e.g., awesome, cool).

In autism, immediate echolalia tends to occur in association with little verbal ability and poorly developed language. Similarly, in brain damage such as stroke, it is likely to occur in association with other forms of aphasia where major speech centers have been damaged. In schizophrenia it is usually considered a feature of the catatonic subtype, which is relatively uncommon these days. In Tourette’s syndrome, schizophrenia, and autism, echolalia may be associated with *echopraxia*, involving the copying of limb movements and postures, or *mannerisms* and *tics* which are stereotyped patterns of movement which range from being very simple (tics) to complex (mannerisms). *Vocal tics* in association with echolalia are also repetitive patterns of vocal behavior but are not linguistic and may consist of grunts, coughs, or screams. Echolalia may also overlap with *coprolalia* in Tourette’s which is the compulsive expression of obscene language.

Evolutionary Aspects of Vocal Mimicry

In the animal world, humans were thought to be relatively unique along with songbirds, hummingbirds, and parrots in having the ability for vocal learning and speech mimicry (note that echolalia is often referred to as “parroting”). More recently, vocal learning is described in bats, cetaceans, elephants, and seals (Chakraborty and Jarvis 2015). Most animal species have a limited range of vocal expression which is largely innate (the chicken is a good example), and they are unable to mimic speech. A capacity for vocal learning in birds is evident by the presence of regional differences in vocalization which are independent of genetic differences. For example, in the United Kingdom, the chaffinch song differs across the country, showing evidence of dialect. In addition, chaffinches that are reared in isolation sing an impoverished song (Slater et al. 1984).

It is suggested that similarities between bird-song and human speech have emerged through

evolutionary convergence and that songbirds provide a model system for the study of speech acquisition in humans (Chakraborty and Jarvis 2015). This suggestion presupposes that immediate echolalia can be understood within a spectrum of social learning that ranges from “blind copying” or mimicry to intentional (goal-directed) imitation.

In the imitation literature, action copying more generally has been classified in this way, and a distinction has been made between imitation learning and mimicry (Whiten 2006). Mimicry involves perception of an action (whether visually or as a vocalization) which elicits execution of a previously learned motor program for the same action (or vocalization). In imitation, inference of the intention or motor plan associated with the action (including its purpose or “meaning”) occurs, and the action is reenacted in an intentional way to serve that same purpose. In birds, mimicry occurs but not imitation. The difference between typical functional speech and echolalia or stereotyped speech may therefore be best understood as whether it is directed and purposeful or whether it is nonfunctional. The caveat to this is that the phenomena of “over-imitation” is well recognized in typically developing young children, who will often copy a model’s behavior even though that behavior serves no useful purpose (Whiten et al. 2009). Therefore, as already mentioned, echolalia may be part of normal development.

Neurology of Echolalia

Speech control involves the coordination of about 40 muscles involved in respiratory, laryngeal, and articulatory control (Jürgens 2002). The motor neurons controlling this behavior are located in various brainstem nuclei providing output through the cranial nerves that include the vagus, glossopharyngeal, and hypoglossal. Like other aspects of voluntary motor control, control over the acoustic structure of vocalizations is carried out in a hierarchical manner, with behavior at a higher level encoded by the laryngeal motor cortex, and planning of speech encoded by Broca’s

area. Connections with sensory feedback mechanisms and mechanisms serving extrapyramidal control serve important regulatory functions. A second pathway involving anterior cingulate and periaqueductal gray matter (PAG) appears to serve the production of involuntary and innate motor behaviors such as the grunts or coughs that are characteristics of vocal tics in Tourette's syndrome (Jürgens 2009).

Echolalia would appear to reflect disinhibition of the neural pathways that serve to enact learned voluntary motor behaviors. The coexistence of echolalia with vocal tics suggests that anterior cingulate cortex (ACC) in medial prefrontal cortex may be important in regulating vocal mimicry as well as rates of innate utterances. Neuroimaging evidence indicates that the ACC mediates effects of social influences on action mimicry (Wang et al. 2011), as well as encoding the reward values of actions in humans (Lockwood et al. 2015). In animal studies bilateral lesions to anterior cingulate abolish the capacity to enact learned associations between vocal behaviors and rewards, providing further evidence that it regulates enactment of learned motor behaviors (Jürgens 2009). The supplementary motor area (SMA) is similarly implicated in both the control of imitation behavior (Koski et al. 2003) and amount of vocalization (Jürgens 2009), suggesting that it could also play a role. Echolalia in neurodevelopmental and neurodegenerative disorders suggests that it occurs when frontal lobe functions are damaged or undeveloped. Occurrence when Broca's area is damaged by stroke suggests it may occur when speech-planning mechanisms are damaged.

Conclusion

Echolalia is a word used to describe repetitive patterns of speech that mimic others. Echolalic speech can be delayed or immediate and fits within a spectrum of vocal and manual behaviors that range from features of typical social learning to pathological symptoms of neurological impairment.

Cross-References

- Autism
- Imitation
- Imitation and Mimicry
- Special Case: Autism
- Stereotyped Vocalizations

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Ecological Demands

► Ecology

Ecological Factors and Rape

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Synonyms

Sexual abuse; Sexual aggression; Sexual coercion; Sexual violence

Definition

Rape may be defined as the use of force, or the threat to use force, to obtain sex. Ecological factors include any individual, social, biological, etc. factors that influence a living organism.

Introduction

Females are the choosier sex, in that they get to be choosier about with whom they copulate. This is due to females having bigger gametes than males, being born with a limited number of gametes, and having to carry the fertilized gamete (the zygote) until birth (Buss 2016). A female's reproductive success is contingent on her ability to choose to only conceive children that can be raised, to select the best father for her children, to persuade males to aid her and her children, to maximize the return on sexual favors she supplies, and to minimize the risk of violence or withdrawal of support by her partner and kin (Symons 1979). Rape circumvents female mate choice and thereby interferes with a central component of female reproductive strategy (Buss 2016). Determining the factors, both proximate and ultimate, surrounding rape may aid researchers in concluding how to extinguish this behavior.

Proximate Versus Ultimate Causes

Proximate causes of behavior are those that can be defined as the immediate causes of behavior. Proximate causes include factors such as environment, physiology, hormones, and genes. While proximate causes have to do with how developmental or physiological mechanisms cause something to happen, ultimate causes of behavior have to do with why particular proximate mechanism exist. According to Thornhill and Palmer (2000), "no aspect of life can be completely understood until both its proximate and its ultimate causation are fully known" (pp. 5). Regarding sexual coercion, rape appears to occur in all human societies, even modern ones, and is quite common during wartime. Its universality indicates that rape has likely arisen from ultimate causes, or adaptations, and that studying evolved differences between the sexes will aid in identifying the proximate causes (Thornhill and Palmer 2000).

The Thornhill Theory

Two leading theories exist in the evolutionary literature concerning why rape continues to be an existing human behavior. These theories, constructed by Randy Thornhill and Craig Palmer (2000), suggest either that rape evolved as a male sexual strategy or that rape is better understood as a by-product of male's sexual strategy of seeking out low-cost casual sex. Thornhill proposes that men have evolved a rape adaptation or specialized psychological mechanisms in which forced sex on unwilling women is a reproductive strategy that exists in all men's sexual repertoire (Buss 2016). Thornhill's theory proposes six specialized adaptations which include an assessment of vulnerability of the potential victim, a context-sensitive adaptation that motivates rape by men who lack sexual access to consenting partners, a preference for maximally fertile victims, an increase in sperm count in forced sex ejaculations compared with those occurring in consensual sex copulations, male sexual arousal and female

resistance, and context-specific marital rape when sperm competition might exist through infidelity. Support for Thornhill's hypothesis comes from research that suggests men are sexually aroused when exposed to sexual scenes, regardless of whether consent is involved (Buss 2016). However, evidence against this hypothesis comes from research that indicates that the presence of violence, evidence that the victim is in pain, and a disgust reaction from the victim all inhibit male sexual arousal (Malamuth 1986).

The Palmer Theory

Palmer proposes that rape is a by-product of other evolved male psychological mechanisms such as the desire for sexual variety and the capacity of men to use physical aggression to achieve a wide variety of goals (Buss 2016). Palmer draws from Symons' (1979) original rape as a by-product hypothesis which suggests that the primary adaptations responsible for rape include male's greater visual sexual arousal, greater autonomous sex drive, reduced ability to abstain from sexual activity, a greater desire for sexual variety, greater willingness to engage in impersonal sex, and less discrimination in sexual partner criteria. Palmer argues that many human behaviors are by-products of the intense sexual desires of human males and the sexual choosiness of human females. Some examples include child sexual abuse which can be seen as a way for males to gain access to individuals who are too young to control sexual access and masturbation which can be taken as a means of obtaining sexual gratification without meeting criteria for female's mate choice. To reject this hypothesis, a phenotypic feature of the human male analogous to rape-specific phenotypic features of other species, such as the notal organ in male scorpionflies, is needed (Thornhill and Palmer 2000). This feature would include some aspect of rape that cannot be accounted for by differences in male and female sexuality as described above. No such feature has yet to be identified. Thus far, no conclusion can be reached as to whether Thornhill or Palmer is correct.

Perpetrator Characteristics

Perpetrators of rape are almost invariably men, while most victims are women, though victims can also include children and men (Buss 2016). Other characteristics of perpetrators include hostility toward women, an endorsement of the idea that women secretly want to be raped, impulsiveness, low agreeableness, low empathy, hypermasculinity, and a high degree of sexual promiscuity (Malamuth et al. 1991). Age seems to play a role for the perpetrator as well. About half of all men arrested for rape between 1994 and 2010 were age 30 years and older, 34% were between the ages of 18% and 29%, and 15% were 17 years old or younger (Planty et al. 2013).

Mate value. In some instances, women are raped by "low mate value" men or men who are not willing to commit, have little to no resources, have low genetic quality, or are incapable of or unwilling to provide protection (Buss 2016). For these males, coercion may represent a desperate alternative (Thornhill and Palmer 2000). This concept is often referred to as the mate deprivation hypothesis (Lalumiere et al. 1996). If this forced copulation results in a pregnancy, the female is forced to bear and rear a child of someone who is not going to be helpful to her. Additionally, the child may be sickly or have genes that will make him or her unattractive to mates in the future. This is detrimental to the woman's reproductive fitness. In this scenario, the low mate value male reaps the benefits by forcing a mate ship that would not otherwise exist. Furthermore, if the woman is in a relationship with another man, or even if she is single, she risks being blamed or even punished for the rape. Her partner may then choose to leave, resulting in her having difficulty attaining a mate in the future (Buss 2016).

The mate deprivation hypothesis (Lalumiere et al. 1996) may be supported by the fact that much sexual coercion is committed by men in lower socioeconomic groups (Thornhill and Thornhill 1983). However, this finding may be misleading as men in lower socioeconomic groups commit all crimes at a higher rate (Thornhill and Palmer 2000). Additionally, lower rates of reporting may occur when the

rape is committed by men in higher social groups or because higher status men may be able to better evade arrest and conviction due to the ability to afford superior legal guidance (Buss 2016). Conversely, other research suggests that men who have a lot of sexual partners are more likely to use force (Lalumiere et al. 1996), and men who report higher future earning potential also report more physical coercion tactics in their mating relationships (Buss 2016).

Findings from a study done by Blake and Brooks (2018) propose that men who perceive themselves as disadvantaged in sexual competition (low mate value) are less likely to endorse acts of intimate partner violence (IPV) in conditions of gender equality, while this same condition evokes endorsement for IPV in high mate value men. Blake and Brooks hypothesized that the lack of endorsement is due to the low mate value men's fear that their reputation, which may be all that they have to offer a mate, will be destroyed if they are supportive of IPV and will lessen their chances of finding a mate. It is thought that when gender conditions are equal, men who are advantaged are at risk of their mates engaging in infidelity at work and have less control over their mates. Conversely, in conditions of gender inequality, high value men are less likely, and low mate value men are more likely to express attitudes accepting of IPV. When gender conditions are unequal, men with low mate value appear to capitalize on oppressive social norms and low female structural power, seeking to maintain dominance over their intimate partners through coercive violence, while high value men have little reason to support jealousy violence when conditions are in their favor.

Development. Development may also play a factor in why men commit acts of sexual violence. Men, who grow up with reduced parental investment and in environments in which social relationships tend to be short and uncommitted, tend to exhibit more sexually coercive tendencies in adulthood (Malamuth 1998). These men may have an expectation that sexual relationships should be brief and have a reduced ability to invest in women they are involved with. They also exhibit coercive sexual attitudes toward women and accept that aggression is a viable tactic for obtaining their goals, both sexual and

otherwise. Like the mate deprivation hypothesis, this developmental model suggests that men in disadvantaged groups may use violence as a last resort effort to attain mates.

Other Factors

Other factors that influence rates of rape include war time in which young attractive women are unprotected and punishment is unlikely (Thornhill and Palmer 2000), polygynous societies in which males are taught to be especially competitive, and societies with a high ratio of males which tend to experience more wars (Buss 2016). These contexts seem to suggest that male competition intensifies in times of a surplus of males.

Research supports the hypothesis that women who have protection from kin or male friends and mates are less likely to be raped (Buss 2016). High status men seem to have greater ability to prevent rape between their mates and other men (Thornhill and Palmer 2000). While women who are married may be subject to rape, married women, regardless of age, are less likely to be raped than same-age unmarried women (Buss 2016). Additionally, statistics on the occurrence of date rape, which may be between 15% and 20% of all college women, reveals that women not in long-term relationships are at considerable risk (Buss 2016).

Women who exclusively utilize short-term mating strategies are at a greater risk of both physical and sexual abuses (Buss 2016). Dating, it seems, is a common context for rape. A study containing over 10,000 victims of rape found that women between the ages of 16 and 35 were more likely to have been raped than any other age category (Thornhill and Thornhill 1983). Other research suggests that 85% of all rape victims are less than 60 years old (Buss 2016). Likely, the reason women of these ages are at a higher risk is due to being fertile. If rape is an adaptation or by-product, it seems reasonable that women who have the greatest chance of conceiving a child would be targeted most often. One startling statistic that evidences this theory is that pregnancy rates resulting from rape among reproductive-age women may be as high as 6.42% (Gottschall and Gottschall 2003). This

is highly shocking considering the consensual per-incident rate is only 3.1% (Gottschall and Gottschall 2003). This seems unlikely to be due to chance, especially with the advent of modern birth control.

If a woman is raped by her husband or long-term partner, it is likely a result of sexual jealousy and worry over real or imaged sexual infidelity (Buss 2016). Marital rape is also more likely during or immediately following a breakup. This finding may support the theory of rape as a sperm competition adaptation though there does not seem to be ample evidence yet to determine if there is a rape adaptation in human males (Symons 1979).

Conclusion

As David Buss (2016) concludes in his work *The Evolution of Desire*, it seems that a simple version of the mate deprivation hypothesis of rape is not likely to be correct. More likely is it that two context-specific rape adaptations have evolved: one that is contingent on when a male experiencing a mating failure and one in which the costs are so low that he can get away with it. Buss also notes that there are probably distinctive reasons for different scenarios (such as wartime versus date rape). Lumping these together will not help to determine the causes, proximate or ultimate.

Cross-References

- [Life History Theory and Rape](#)
- [Rape](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Conflict in Mating Strategies](#)

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Ecological Influences

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Synonyms

[Ecology and behavior](#); [Environmental contingencies](#); [Environmental effects](#)

Definition

How environmental/external conditions affect behavior.

Introduction

Local ecology has tremendous ultimate and proximal influence on human behavior through both evolutionary and developmental processes.

A number of theories predict a number of specific ecological influences for a variety of human behavior. Thus, a complete account of ecological influences is not possible. However, one theory in particular deserves special attention for the variety of diverse ecological conditions that it can bring together to explain a wide range of human behavior, life history theory. Here, life history theory is explained, the logic of life history theory is used to discuss specific environmental conditions and how they affect behavior, and evidence is presented that shows the theory-consistent impact of our local ecology on behavior. Finally, potential mediators of the effects of ecological conditions on human behavior are discussed.

Life History Theory

Life history theory has gone through substantial changes since its early focus on *r* versus *K* strategists and a focus on population density as a driving force in *r*-*K* selection (McArthur and Wilson 1967; Pianka 1970). Typical modern approaches using life history theory use a mix of evolutionary biology and behavioral ecology. At its core, life history theory is a theory about how organisms allocate their finite amount of bioenergetic and material resources (Figueredo et al. 2004; Stearns 1992). The two points on this continuum are somatic effort (the energy and resources allocated to the continual survival of an individual organism) and reproductive effort (the energy and resources for the production of new organisms). Reproductive effort can be further partitioned into mating effort (resources allocated to obtain and retain sexual partners), parental effort (resources allocated to enhance offspring survival), and nepotistic effort (resources allocated to enhance genetic relative's survival). These bioenergetic and material resource allocations represent trade-offs, as investment in one area (e.g., reproductive effort) means that the same effort cannot be allocated toward another area (e.g., somatic effort). To understand trade-offs in resource allocation, it is useful to contrast the strategies that result from these trade-offs.

Individuals who trade off reproductive over somatic effort and mating over parental/nepotistic effort exhibit a fast life history strategy. Individuals who trade off somatic over reproductive effort and parental/nepotistic over mating effort exhibit a slow life history strategy (Promislow and Harvey 1990; Figueredo et al. 2004, 2005, 2006). These life history differences are realized as a set of coordinated traits or behavioral responses that facilitate certain reproductive strategies and solve adaptive problems. These different strategies affect key variables such as the timing of reproductive events and the amount of investment in offspring. By coordinated, it is meant that traits should be consistent and reinforcing rather than inconsistent and interfering. For example, high sensation seeking and impulsivity are generally consistent and reinforcing traits, and life history theory would predict these traits to be related to a fast rather than slow life history strategy. Indeed, there has been research on individual differences in life history strategy from numerous disciplines including evolutionary biology, genetics, anthropology, and psychology. Psychological evidence, for example, indicates that fast life history strategists tend to have short-term mating, low parental investment, low group altruism, and higher criminality and are more prone to risky behaviors (Ellis 1988; Figueredo et al. 2004, 2005, 2006). Although life history theory predicts that traits like criminality and risky behavior will be related to a fast life history strategy, the theory does not predict that all fast life history strategists are criminals. Again, the coordinated traits should only generally be consistent with each other, and a fast life history strategy merely permits behavior like criminality.

Life History Theorized Environmental Contingencies

Although genetic influences are important (see Figueredo et al. 2004), specific changes in the local ecology are also theorized to affect the evolution and development of life history strategy. For brevity, these environmental contingencies were referred to by Reynolds and McCrea

(2015) collectively as life history contingencies. Ellis et al. (2009) extensively detail the variety of environmental conditions that compose these contingencies and grouped them into two main influences: harshness and unpredictability. Harshness is the rate of external factors that cause death and disability (i.e., extrinsic mortality). A variety of ecological conditions can fit under this umbrella, including pathogen stress, warfare, predation, and weather. The rate of death and disability, that is harshness, can also vary over time and space. In other words, it is not only the degree of harshness that is important, but how predictable or unpredictable it is. One reason life history theory is so useful when discussing ecological conditions is the ability of the theory to take seemingly separate ecological influences, like weather and warfare, and bring them together in a coherent manner.

Another reason the theory is useful is that it discusses a variety of ecological conditions and how they interact with each other to influence behavior. Additional ecological factors that interact to influence behavior include population density, intraspecific competition, and resource scarcity. Resource scarcity refers to the availability of nutritional and economic resources or lack thereof. Intraspecific competition is when members of the same species compete for limited resources; however, this can take multiple forms, one being a scramble competition and the other being contest competition (Ellis et al. 2009; Rogers 1992; Danchin and Cézilly 2008). In scramble competition, individuals have equal access to limited resources. As individuals consume resources, fewer resources are available to others. The competition is therefore indirect (Rogers 1992; Danchin and Cézilly 2008). In contest competition, individuals do not have equal access to resources. Some individuals suffer less or not at all in terms of growth and reproduction. This is due to evolved competitive adaptations for obtaining disproportionate amounts of resources. The distinction between these types of competition is important as it is contest competition that tends to characterize humans (Rogers 1992; Ellis et al. 2009).

All of these combined ecological conditions are theorized by LHT to lead to the development

and evolution of life history strategy. Certain combinations will lead to a slow life history strategy, whereas a different combination is predicted to lead to a fast life history strategy. Life history theory predicts that low harshness of the environment when combined with low population density, low resource scarcity, and low intraspecific competition should result in a fast life history strategy (Ellis et al. 2009). A reproductive over somatic effort trade-off is more advantageous in this case because the population is not near the carrying capacity. There are an abundance of resources available to the population. As a result, investing in somatic maintenance is not as valuable. Apportioning more energy and resources toward mating and reproduction effort, on the other hand, has valuable fitness effects.

However, low harshness of the environment combined with high population density, high resource scarcity, and high intraspecific competition should result in a slow life history strategy (Ellis et al. 2009). Here, resources allocated toward mating and reproductive effort is disadvantageous. These conditions require somatic maintenance, because the population is near its carrying capacity, meaning the environment, and hence the amount of resources available, can no longer sustain the number of individuals of that particular species in the population. In addition, intraspecific competition is high, which means conspecifics must engage in greater competition to gain access to resources including food, territories, and mates. According to life history theory, this should result in a more energetically sparring phenotype and the trade-off of somatic over reproductive effort. In these circumstances, selection would favor development of a slow life history strategy.

Life history strategy is also related to the link between the mortality rates among juveniles in the population. A high mortality rate among juveniles should result in a slow life history strategy. Under these conditions, parental effort can be translated into increases in offspring quality and resistance to environmental stressors. If the mortality rate is linked specifically with the adult proportion of the population, or the mortality rate is distributed throughout the population, a fast life history

strategy should develop. Here, parental effort cannot be translated into increases in resistance, because the environmental stressors are not juvenile specific. These examples demonstrate how using an LHT analysis results in the consideration of multiple environmental influences.

Unpredictability or the spatial-temporal variation of harshness in the environment results in similar predictions. For example, life history theory predicts that high environmental unpredictability and high variance in adult mortality-morbidity should lead to a fast life history strategy. To understand the reason for this prediction, it is useful to contrast this with a slow life history strategy trade-off. If an organism is making a somatic over reproductive effort trade-off in an environment characterized by unpredictability, they will be investing more heavily in themselves phenotypically. Thus, they will have offspring later, and if they have offspring, invest more heavily in them. However, due to the variation around the mean for adult life expectancy, the individual may perish before reproducing. Thus, a strategy with a reproductive over somatic effort trade-off will result in greater fitness. The organism's genes will be more likely to be passed down because they are more likely to reproduce before dying.

Empirical Evidence: Nonhumans

Research supports life history theory predictions in multiple species. Although the present work is focused on humans, research by Reznick and colleagues is briefly discussed as it is some of the most well-executed research and uses methods that would be untenable in the case of humans. For example, Reznick and colleagues conducted research on populations of guppies in low versus high predation areas. Results indicated that guppies in high predation areas display an FLHS and have traits like faster growth, earlier age at sexual maturation, and larger litter size (Reznick 1982; Reznick and Ghalambor 2005). As predicted by LHT, the high degree of nonage-specific environmental harshness is associated with phenotypic changes indicating a trade-off of

reproductive over somatic effort. As an extension of this research, guppies in high predation areas were moved to low predation areas. Eleven years and several generations later, the guppies had shifted to a slower life history strategy, displaying traits like later age at maturity and fewer offspring per litter (Reznick et al. 1996; Reznick and Shaw 1997).

The studies by Reznick and colleagues focus on nonhuman species and on the life history traits of body growth, age at sexual maturation, and litter size. Although many researchers agree on what the core life history traits are, such as timing of reproduction, there is less agreement regarding whether psychological traits should be considered life history traits. However, many psychological traits have been considered life history traits by some researchers, and some of these traits (e.g., criminal behavior and religiosity) can only be studied in humans (Ellis 1988; Figueredo et al. 2005). Research on humans also supports the hypothesized ecological effects on behavior.

Empirical Evidence: Humans

Research employing a variety of methodology has shown how ecological effects are associated with changes in a variety of important behavior. Longitudinal evidence comes from Brumbach et al. (2009) who investigated the role of harshness and unpredictability experienced early in life and how those conditions influence later life history strategy and deviant social behavior. Brumbach et al. (2009) used data from the National Longitudinal Study of Adolescent Health. Harshness was operationalized as self-reported exposure to violence from conspecifics and unpredictability as frequent changes or ongoing inconsistency. Using a structural equation modeling approach, the results showed that both environmental harshness and unpredictability during adolescence were associated with a number of important outcomes including health, sexual restrictiveness, and social deviance. Specifically, increased environmental unpredictability was associated with decreased health and increased social deviance. Increased environmental harshness was

associated with less sexually restrictive behavior and greater social deviance.

Similarly, Belsky et al. (2010) found a relationship between early maternal harshness, daughter's age of menarche, and risk taking. Using a subset of the families from the NICHD Study of Early Child Care and Youth Development, Belsky et al. (2010), using path analysis, found that greater maternal harshness at 54 months directly predicted social risk taking including using alcohol, drugs, and delinquency. Greater maternal harshness also directly predicted earlier age of menarche, which in turn predicted sexual risk taking.

Finally, also using a longitudinal design, Hampson et al. (2016) investigated the effects of harsh environments experienced in childhood and how these environments affect adjustment in emerging adulthood. Five cohorts of children (grades 1–5) from the Oregon Youth Substance Use Project were sampled and assessed through 1 year post-high school. Measurements of harshness included neighborhood quality and family poverty. Using structural equation modeling, results indicated that greater harshness experienced in early childhood directly predicted decreased parental investment in later childhood, and indirectly predicted favorable beliefs about substance use and willingness to use substances (such as alcohol and marijuana) at grade 9, and later use of substances and risky sexual behavior (grades 10–12).

Griskevicius et al. (2011) used both existing data and an experimental design to understand how environmental conditions influence reproductive timing. First, using data from the Uniform Crime Report, the US Census (2000), and the US Centers for Disease Control National Vital Statistics System (2004), Griskevicius et al. (2011) examined correlations between crime, socioeconomic status (SES), and reproductive timing. Results showed that violent crime was related to the age that people had children, even when controlling for SES. That is, in areas with higher violent crime rates, people tended to have children sooner. This pattern is consistent with LHT because adult mortality rates were related to having children sooner, an indication of a reproductive versus somatic effort trade-off. Griskevicius et al. (2011) further examined the relationship

between environmental contingencies and reproductive timing using experimental methodology. Harshness and unpredictability were manipulated via story primes. In the mortality prime condition, participants read a supposed news article about the increasing violence in the United States and how there are many random violent deaths (e.g., shootings in residential and commercial areas). The control condition was also formatted to look like a news article but it was about losing and finding a set of keys. Researchers also asked participants about their perceived resources (e.g., if they felt they were wealthy compared to others) as children and at present. Results showed a prime by perceived resource availability in childhood interaction. For people who grew up relatively poor, the mortality cues were associated with them wanting to reproduce sooner. A number of other experimental studies from multiple laboratories have shown a relationship between harshness and unpredictability with exploitative strategies and related variables such as short-term mating.

Exploitative strategies are one of the three fundamental strategies humans use to acquire reproductively relevant resources, and they consist of depriving other people of a resource while simultaneously enhancing one's own (Buss and Duntley 2008). In a within-subjects design with a sample of college students, Dunkel and Mathes (2011) used life expectancy manipulations to understand the effects on sexual coercion. The life expectancy manipulation involves having participants imagine different levels of mortality. Specifically, it consists of participants imagining that a doctor has just told them they have 5 months, 5 years, or 50 years left to live. Results indicated that the shorter life expectancy manipulation was related to an increased willingness to engage in sexual coercion. Also using the life expectancy manipulations, Dunkel et al. (2010) found that when participants imagined shorter life expectancies, they showed a greater interest in short-term mating. Finally, Dunkel et al. (2010) found shorter life expectancies were related to an increase in participants' inclination to express anger and be aggressive. Research by Reynolds and McCrea (2015, 2016a) extends this work.

Reynolds and McCrea (2015) used both a self-report measure called the Exploitative and Deceptive Resource Acquisition Strategy Scale (EDRASS) and a behavioral measure called the Dot Game to investigate the effects of a number of environmental contingencies. The EDRASS asks participants to imagine a scenario containing an exploitive behavior and rate how tempted they are to engage in the behavior. The Dot Game is a behavioral cheating game that can be played online and involves competing against another participant (fake participant) for money. Using some of the same primes from Griskevicius et al. (2011), in a between-subjects design, the results indicated that participants who read about the world being a dangerous uncertain place (i.e., harsh and unpredictable) engaged in greater exploitative behavior on the Dot Game. However, there were no effects of the prime that communicated that the world was high in population density, intraspecific competition, and resource scarcity. In a similar study, but using the EDRASS, Reynolds and McCrea (2015) could not replicate the effect of the harshness and unpredictability prime and continued to find non-significant effects of population density, intraspecific competition, and resource scarcity. To determine the reason for this discrepancy in findings, Reynolds and McCrea (2016a) conducted three studies in multiple populations. Results of the three studies found reliable effects of the harshness and unpredictability prime and the population density, intraspecific competition, and resource scarcity prime. However, contrary to predictions, participants who read about population density, intraspecific competition, and resource scarcity were more likely, compared to control, to be tempted to engage in exploitative behavior. Age was the most likely factor that caused the discrepancy in the previous findings, as Reynolds and McCrea (2016a) were able to replicate all effects with a younger college sample but not an older sample. This leads to an important question concerning the effects of ecology on behavior, is age one of the key moderators for ecological effects?

Evidence on this question is somewhat unclear. Simpson et al. (2012) found that unpredictability

experienced in early childhood (age 0–5) *but not* in later childhood (age 6–16) predicted sexual and risky behavior at age 23. Simpson et al. (2012) argued that the evidence suggested the first 5 years of life represented a developmentally sensitive period for environmental unpredictability. Griskevicius et al. (2011) also only found effects on timing of reproduction for the mortality prime, which communicated harshness and unpredictability, for people who grew up relatively poor. However, Hampson et al. (2016) found effects of harshness on children grades 1–5. Dunkel and colleagues and Reynolds and McCrea have found consistent main effects of specific environmental contingencies for college-aged people. As discussed above, Reynolds and McCrea (2016a) did find that less reliable effects are likely in older populations. Collectively, this evidence would seem to indicate that at least some behaviors are amenable to influence from some environmental contingencies at least until early adulthood, but other behaviors may show a different developmental sensitivity range. In other words, environmental contingencies can affect behavior, depending on the specific contingency, the specific behavior, and age.

Another important question for understanding ecological influences is what are the mediating psychological processes between environmental contingencies, like harshness, and behavioral strategies? According to life history theory, environmental influences like harshness, unpredictability, and resource scarcity should affect a suite of traits from intelligence and criminality to emotions and social skills. Traits should be generally mutually consistent with other traits, for example, high parental investment by a father should correspond with lower risk taking. However, while environmental influences are argued by multiple theories to affect a wide range of behavior, some traits may play a key role in mediating further change. Although there are many candidates, two potentially strong mediators include inhibitory self-control and time perspective.

Inhibitory self-control or inhibition regulation is the ability to inhibit responses motivated by short-term rewards in order to pursue more long-term benefits (Fujita 2011; Reynolds and McCrea

2016b). According to the dual component theory of inhibition regulation (DCTIR), self-control is an adaptation in the form of a computational module that monitors for certain impulsive mechanisms and inhibits them until the inhibition model has met its tolerance level or threshold. According to the DCTIR, specific environmental influences such as harshness and unpredictability interact with this mechanism in functional ways. Specifically, the DCTIR argues, consistent with life history theory, that high harshness and unpredictability lower threshold. As a result, it will be less likely a behavior will be inhibited for a long period of time, and the temptation of certain behaviors (such as risky behavior) may increase. In other words, one way that the environment may have such an impact on a wide range of behaviors is by not only directly changing certain traits like aggression or risk taking, but by changing regulatory mechanisms such as self-control. By affecting regulatory mechanisms, influence is exerted over all the systems to which the regulatory mechanism controls. There is some evidence already suggesting just such a role for self-control. There is extensive work demonstrating the relationship between self-control and criminal behavior, for example (Pratt and Cullen 2000). Most importantly, Dunkel et al. (2013) manipulated life expectancy and found that, under conditions of short life expectancy, there was a decrease in self-control and an increase in criminal intent. This relationship was further moderated by differences in life history strategy. Although there is much work to be done on the relationship between environmental influences and self-control, this may be a promising area of future research.

Another promising area of work involves the relationship of environmental contingencies with time perspective. As in self-control, time perspective is argued by some to be a mediating psychological process between environmental influences and behavior. Kruger et al. (2008) argued that individuals raised in unpredictable environments will have a more present oriented time perspective and thereby exhibit riskier behavioral strategies. To test this, Kruger et al. (2008) used items from the Monitoring the Future study from urban middle school students ($N = 607$). Positive and

negative aspects of social developmental environment, including physical safety, positive socialization neighborhood threats or harassment, witnessing fights, and being a victim of theft, were measured. Time perspective, including future and present orientation, was measured using items involving delay of gratification, planning for the future, importance of hard work, attitudes toward risky behavior, and the arbitrariness of goal-related outcomes. Behavioral strategies included measures of interpersonal aggression and illicit resource exploitation. Structural equation modeling results indicated that positive social developmental environment was associated with a future time perspective which then negatively predicted aggression. Negative social developmental environment was associated with a present oriented time perspective which then positively predicted aggression and resource exploitation. Thus, time perspective mediated the relationship between social developmental environment and phenotypic strategies.

Schechter and Francis (2010) found similar results in a population of Native American youth aged 10–19. Specifically, environmental risk and uncertainty were associated with internalizing these characteristics as mechanisms such as time perspective, which then predicted attitudes about risky behavior and investments in education. Although neither Schechter and Francis (2010) nor Kruger et al. (2008) discuss the computational structure of time perspective and how it is effected by environmental contingencies, as is the case with self-control (see Reynolds and McCrea 2016b), these studies clearly show an important mediating relationship that is only just being understood.

Conclusion

Ecological influences on human behavior can vary from harshness to population density. These contingencies have complex relationships that demand not only an understanding of how the contingencies interact with each other, but an understanding of the moderators (e.g., age) and mediators (e.g., self-control). The work by

Reznick and colleagues has demonstrated strong evidence of the influence of ecology on behavior. Research on humans is of course limited by ethical constraints in conducting similar experiments. However, research on humans is advantageous because psychological mediating processes are arguably easier to measure. Although there is considerable research on humans for environmental contingencies such as harshness and unpredictability, there is less on contingencies such as population density. Although there is much work to be done in this area, understanding ecological influences represents a critical piece to understand the mind and will continue to be a successful research area.

Cross-References

- [Ecological Factors and Rape](#)
- [Ecological Influences on Parent–Offspring Conflict](#)
- [Ecological Niche, The](#)
- [Life History Strategies](#)
- [Life History Theory](#)

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Ecological Influences on Parent–Offspring Conflict

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Synonyms

Conflict between parents and offspring; Environmental effects; Environmental contingencies

Definition

The environmental conditions that affect conflict between parent and child.

Introduction

To understand parent–offspring conflict and its ecological influences, Hamilton's rule is presented, which provides the basic logic for these conflicts. Life history theory is then briefly discussed, and the logic of these two approaches is used to understand how multiple ecological influences can affect parent–offspring conflict. Hamilton's rule defines the parameters by which altruistic behavior can evolve by natural selection. Thus, Hamilton's rule is a foundation for kin selection theory (Hamilton 1964a, b). Hamilton's rule states that altruistic behavior can evolve if $rB > C$, where C is the cost to the altruist, B is the benefit to the recipient, and r is the coefficient of relatedness. The coefficient of relatedness can range from 0 to 1 and represents the probability that, at any given locus, two individuals will share the same allele. Thus, for parent and offspring

$r = 0.5$, for siblings $r = 0.5$, and for half-siblings $r = 0.25$. A consequence of this relationship is that the higher the coefficient of relatedness, the more individuals can afford higher costs in order to benefit the other individual. In the case of parent–offspring relationships, parental investment involves resources that increase offspring chance survival, including time and food (Trivers 1972). For example, if a mother has two children and we assume equal costs and benefits, the mother should allocate her parental investment resources equally among the children. However, both the offspring and the mother are more related to themselves ($r = 1.0$) than with each other ($r = 0.5$). Additionally, not all offspring are equally good fitness vehicles. Some offspring will be more likely to survive and reproduce, and some offspring are more likely to benefit from certain types of parental care. This sets the stage for parent–offspring conflict because the offspring desires a disproportionate amount of parental investment resources (Schlomer et al. 2011). In other words, there are different levels of optimal parental investment from either the parent's or offspring's perspective, which leads to conflict. Parent–offspring conflict is thus viewed as general conflict of interest, rather than an observable instance of physical or verbal conflict. For example, there can be a conflict of interest in the mother–fetus relationship concerning fetal nutrition. According to parent–offspring conflict theory, conflicts of interest over the allocation of parental investment will be maintained by natural selection (Parker et al. 2002; Trivers 1974). There are a multitude of factors that can influence these conflicts, for example the age of the parents, the age of the child, the number of offspring, paternal certainty, step parenthood, and adoption. Here, the focus is on ecological influences, including environmental harshness, unpredictability, pathogen prevalence, resource scarcity, and dispersal.

Life History Theory

Life history theory focuses on the relationships between growth, reproduction, and survival

across the life cycle (Chisholm 1993). Life history theory predicts that there are trade-offs between investment in somatic effort (i.e., investment in development, growth, and body maintenance) and reproductive effort (i.e., investment in producing new organisms). Reproductive effort can be subdivided into mating effort (i.e., investment in obtaining and retaining mates) and parenting effort (i.e., investment in offspring). Trade-offs are fundamental because time and energy invested in one arena necessarily means that less can be invested in another. Ecological factors such as harshness determine which trade-offs are optimal for survival and reproduction.

Most trade-offs can be categorized as either a trade-off between current and future reproduction or a trade-off between offspring quantity and offspring quality (Chisholm 1999; Sterns 1992). For example, effort devoted to reproducing now means that the energy and resources cannot be used for future reproduction, the cost of which comes in the form of reduced number of future offspring, quality of future offspring, or survival of future offspring, as well as reduced parental growth and survival (Chisholm 1999). If the parent can be expected to engage in future breeding, the more resources are withheld from current reproduction. This naturally creates greater potential for conflict with existing offspring. Thus, different parental reproductive strategy trade-offs lead to different investments in offspring. These differences then lead to offspring solicitation for investment and create the potential for conflict (Schlomer et al. 2011). Therefore, conditions that affect parental reproductive strategy trade-offs can affect parent–offspring conflict.

Ecological Conditions

Harshness and Unpredictability

Ecological conditions that may affect parent–offspring conflict through parental reproductive strategy trade-offs include pathogen stress, warfare, predation, and weather cycles. What these ecological conditions have in common is that they are external causes of disability and death (i.e., extrinsic mortality). As an additional dimension,

these ecological conditions can vary over time and space. Life history theory summarizes these ecological conditions as harshness and unpredictability. Harshness is the rate of external factors causing disability and death. Unpredictability is the rate at which harshness varies over time and space (Ellis et al. 2009). Harshness and unpredictability can be relatively insensitive to the adaptive decisions of the organism. Although basic parental care benefits offspring, conditions of harshness and unpredictability create diminishing returns for parental investment (Pennington and Harpending 1988; Quinlan 2007). When there is high harshness and unpredictability, optimal levels of effort are lower because offspring are less likely to survive and reproduce. When harshness and unpredictability are low, parental investment can more successfully influence offspring survival and reproduction.

Although life history theory offers interesting predictions concerning ecological conditions and parent–offspring conflict, there has actually been little empirical work in this area. There is research on environmental conditions and aspects of life history that are related to parent–offspring conflict, such as the relationship between harshness and reproductive timing (e.g., Chisholm et al. 2005). However, much of this empirical work has focused on animal rather than human behavior. Nonetheless, existing human research supports the hypothesized relationships between ecological factors and parent–offspring conflict.

Belsky et al. (2012) investigated the relationships between both harshness and unpredictability experienced in families and parenting and early life history strategy. They examined 1,364 mothers and their offspring using longitudinal data from the NICHD Study of Early Child Care and Youth Development study. Belsky et al. (2012) measured a number of variables and modeled them using structural equation modeling. Of most significance to the present discussion was maternal sensitivity, defined as the ability of the mother to infer signals from the infant and respond appropriately to them (Ainsworth et al. 1974). Maternal sensitivity can be viewed as reflecting parental investment and thus has a

direct relationship to parent–offspring conflict (see Schlomer et al. 2011). Maternal sensitivity was measured through mother–child interactions during short videotaped sessions of semi-structured tasks. These data were collected when the children were between approximately 6 and 8 years old. Multiple coders then rated the interactions on supportive presence, respect for autonomy, and hostility. These scores were summed to create a general measure of maternal sensitivity. Results indicated that both harshness and unpredictability were uniquely related to maternal sensitivity.

Quinlan (2007) studied the relationship between extrinsic mortality factors, such as pathogen stress and warfare, with parental investment. One measure of parental effort was maternal care, which was measured as body contact with the infant, response to crying, and sleeping proximity. Results indicated that as the prevalence of warfare increased, maternal care decreased. Quinlan (2007) also measured weaning as a form of parental investment, which is particularly interesting from a parent–offspring conflict perspective. Following offspring birth, breastfeeding becomes the center of the mother–child relationship. There is good reason for this, as beyond basic nutritional needs which the mother provides to her offspring, breastfeeding contributes to the survival and overall health of the infant (e.g., health benefits include reduced risk of infections; Cunningham et al. 1991). Therefore, breastfeeding decisions such as duration and timing of weaning are important. This sets the stage for conflict because resources that the mother invests in breast feeding cannot be spent later on future reproduction. Thus, the optimal duration of breast feeding will differ from the parents' and the child's perspective, with longer durations advantageous from the perspective of the child and shorter durations advantageous from the perspective of the parents. Conflict due to the weaning dilemma should increase when maternal investment is allocated from breastfeeding toward producing new offspring. Multiple ecological and social conditions can influence weaning, and therefore potential conflict, such as social support, maternal workload, the availability of non-breast milk foods, and

socioeconomic status (McDade and Worthman 1998; Wander and Mattison 2013). In terms of harshness, the relationship with weaning can be complex. Quinlan (2007) found that higher pathogen levels were related to earlier weaning. In other words, when there is high pathogen load, which is a type of extrinsic mortality or harshness, offspring were weaned earlier. This is an expression of the current vs. future reproduction trade-off.

Using a longitudinal design and a structural equation modeling approach, Hampson et al. (2016) studied how harsh environments effect adjustment in emerging adulthood through parenting. Participants included five cohorts of children (grades 1–5) from the Oregon Youth Substance Use Project. Participants completed both interviews and questionnaires through 1 year post-high school. Hampson et al. (2016) measured harshness through neighborhood quality and family poverty. Parenting was assessed using three scales (monitoring, inconsistent discipline, and positive parenting) from the Alabama Parenting Questionnaire. Beliefs about substances (e.g., alcohol and marijuana) were assessed at grade 9, and risky sexual behavior and substance use were measured at grades 10–12. Adjustment 1 year post-high school was measured using life satisfaction, self-rated health, sociability, and depressive symptoms. Results indicated that harshness experienced in grades 1–6 directly predicted adjustment 1 year post-high school as well as parental investment at grade 8. In turn, parental investment at grade 8 predicted both beliefs about substances at grade 9 as well as risky sexual behaviors and substance use at grades 10–12. This evidence demonstrates that not only do harsh environments relate to parental investment, but that parental investment remains an important mediator for a number of life history relevant variables.

Resource Scarcity

In addition to ecological conditions that affect harshness and unpredictability, factors such as resource scarcity and dispersal may also affect parent–offspring conflict. Resource scarcity, that is, lack of nutritional and economic resources, can have a profound effect on parent–offspring conflict. One of the main effects is that resource

scarcity can limit how much can be invested in each child. As the number of offspring increases, investment in each offspring tends to decrease. Thus when resources are scarce, parents are forced to strategically allocate their investments. It is strategic because there is not equal division of investments among offspring; some offspring are favored. What determines being favored is partly due to the reproductive value of the offspring, i.e., their fitness. Offspring that have high fitness require less investment than do offspring with low fitness. Therefore, there should be greater conflict between low fitness offspring and parents. If the environment is rich in resources, then parents can afford to invest in needier offspring (Kushnick 2009). But when there is resource scarcity, this forces tough decisions. These decisions can even culminate in one of the more extreme examples of parent–offspring conflict, infanticide. Infanticide is common. For example, between 1995 and 2002 in England and Wales, infants had the highest homicide rate of any age group (Brookman and Nolan 2006). Fitness of the offspring may relate to infanticide. In cultures like the Ayoreo, when an infant is born, it is inspected for signs of deformity. If signs of deformity are evident, it is put in the hole and buried. In Brazilian shanty towns, which evidence significant resource scarcity, healthy infants are given preferential care, while less healthy infants are neglected (Scheper-Hughes 1992). In other words, parental investment is strategically allocated disproportionately to higher fitness infants. Again, there should be greater conflict between the offspring who are invested less in and the parents because the offspring are needier which increases demand for parental investment. Interestingly, historical events provide useful data on the relationship between resource scarcity and parent–offspring conflict.

The historical record is filled with incidences of famine. Famine, which is an extreme case of nutritional resource scarcity, has been linked with one of the earliest forms of parent–offspring conflict, that of between the mother and the fetus. The majority of fertilized eggs are not brought to full term. The majority of them are spontaneously aborted, with the most common cause likely

being genetic abnormalities (Simpson 2007). One of the most important environmental determinants of pregnancy outcomes is nutrition, and pregnancy is a time of increased nutritional needs, with fetal growth depending completely on the mother (King 2003). Historical cases of famine have been linked in many countries, across time, to an increase in intrauterine mortality. In Leningrad, 1942, citizens of the former Soviet Union endured one of the longest and costliest sieges in history via a military blockade by the German army. Increased levels of fetal wastage were observed during this period (Antonov 1947). On the German side, following food shortages after the war, there was a large increase in miscarriages reported in Frankfurt (Wynn and Wynn 1993). In the Netherlands, during the Dutch Hunger Winter (1944–1945), there was an increase in the number of stillbirths (Stein et al. 1975). In China, during 1959 to 1961, the Chinese people suffered through what has been called the Three Years of Great Chinese Famine, as well as the Great Leap Forward Famine. This was a period in China marked by drought, poor weather, and some unfortunate political policies that resulted in widespread famine. Using survey data that covered almost a quarter of a century, from a large number of pregnancy histories, Cai and Feng (2005) found an increase in miscarriages and stillbirth during the Great Leap Forward Famine. More recent studies continue to support the relationship between fetal wastage and famine.

In rural Varanasi, India, a longitudinal study of 49 villages from 1988 to 1992 found that low socioeconomic status and chronic undernutrition were associated with an increase in fetal wastage (Agarwal et al. 1998). Particularly interesting was that, whereas Agarwal et al. (1998) found that poor maternal nutrition was linked with an increase in still births, this was somewhat alleviated by a pregnancy interval of over 2 years. One way to interpret this is that the greater pregnancy interval period represented a life history trade-off of future over current reproduction. As a whole, the historical relationship between famine and fetal wastage supports the predicted life history theory relationship of resource scarcity and parent–offspring conflict.

Dispersal

Finally, ecological conditions such as spatial population structure may affect parent–offspring conflict. For example, dispersal involves the tendency of offspring to separate from locations where they originated (Mitteldorf and Wilson 2000). When there is limited dispersal, the spatial population structure is referred to as viscous. When the population is viscous, the correlation between average genetic relatedness and geographic proximity increases. There is not a large body of research currently on how dispersal affects parent–offspring conflict in humans. However, this may change with several new theoretical models predicting complex effects between the two. In terms of complexity, sometimes evolutionary conflicts are intensified as in parent–offspring conflict over sex allocation, whereas other times evolutionary conflicts are lessened, as in sexual conflict over mating rate (Rankin 2011; Kuijper and Johnstone 2012). In a recent extension of conventional models, Kuijper and Johnstone (2012) develop an evolutionary demographic model that involves the impact of limited dispersal on the intensity and resolution of parent–offspring conflict. According to Kuijper and Johnstone (2012), limited dispersal can increase local competition, including competition among related young. This competition can then reduce the cost of decline in maternal productivity. Kuijper and Johnstone (2012) argue that this favors greater offspring selfishness. In terms of resolving parent–offspring conflict, Kuijper and Johnstone (2012) argue that costly begging (a behavioral tactic for soliciting extra resources) is important, particularly the relationship between parental investment (supply) and begging (demand). The model developed by Kuijper and Johnstone (2012) predicts an interaction between these factors. When there is greater supply and less demand, parental investment should be higher in viscous populations, whereas when there is both great supply and demand, parental investment should be reduced in viscous populations. Considering that the advancement of technology has led to a greater potential for extremes in dispersal, such an approach has interesting implications for human behavior today.

Conclusion

This work discussed a range of ecological conditions, from pathogen stress to dispersal, and how they relate to parent–offspring conflict in humans. What should be evident is that there are a number of theoretical frameworks, such as parent–offspring conflict theory and life history theory, that make predictions about how ecological conditions affect parent–offspring conflict and resolution (see also Schlomer et al. 2011). Although some evidence for these predictions was discussed, it should be clear that there is a need for more empirical work directly investigating ecological conditions and parent–offspring conflict. Part of the problem stems from the difficulty of studying humans, who produce fewer offspring and have long lives. Nonetheless, with no shortage of good theory in this area, a major focus of empirical work should be on ecological conditions that influence parent–offspring conflict.

Cross-References

- [Conflict Between Parents and Offspring](#)
- [Early Childhood and Adolescence](#)
- [Ecological Factors and Rape](#)
- [Ecological Niche, The](#)
- [Life History Strategies](#)

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Ecological Niche, The

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Synonyms

Habitat

Definition

The ecological niche corresponds to the sum total of unique ways in which a species is accommodated by and interacts with both biotic and abiotic factors in its surrounding ecology. Niches can be modeled as n -dimensional hypervolumes, whose dimensions correspond to the distribution of a species along abiotic and biotic gradients. Niches are idiosyncratic to species, with no two species sharing the same niche, although considerable overlap among niches can exist within a given ecosystem owing to competition.

Introduction

The term niche was first utilized in an ecological context by zoologist Joseph Grinnell (1917); however a rigorous quantitative definition of niche was not forthcoming until the 1950s. The concept has had a tumultuous history, having become unfashionable in ecology in the latter decades of the twentieth century owing to criticism from the philosophy of science and the rise of competing models. The concept has started to make a comeback in recent years however. This entry will first outline the early history of the concept before proceeding to discuss the quantitative ecological foundations of niche theory, as described by G. Evelyn Hutchinson. Criticisms leveled against niche theory will then be reviewed, and the recent

revival and expansion of the niche concept will be considered. Finally, in the conclusions, the applicability of niche theory to evolutionary psychology will be discussed.

Review

Early History

The term “niche” appears to have been first applied to ecology in 1917 by Joseph Grinnell. The Grinnellian niche essentially corresponds to the species’ *habitat*, or its physical location within an ecosystem. A subsequent attempt was made by the zoologist Charles Sutherland Elton (1927) to define the niche in relation to a species’ trophic interactions with other species, i.e., its associations with predators and prey. The Grinnellian niche can be considered analogous to a species’ *address* within an ecosystem, whereas the Eltonian niche can be considered analogous to a species’ *profession* or to its impacts on other species within an ecosystem. Both niche theories were descriptive or qualitative and made little impact on the development of ecology as a discipline.

The Hutchinsonian Niche

In the 1950s, limnologist G. Evelyn Hutchinson set out to answer the question “why are there so many kinds of animals?” (Hutchinson 1957, 1959). In doing so, he devised a novel quantitative model of the ecological niche that was based on the idea that a given species exhibits an idiosyncratic range of ecological requirements, which can be expressed in terms of the distribution of that species with respect to various environmental gradients. These gradients encompass factors, such as temperature, pH, salinity, pressure etc. Each gradient can be modeled as an axis in an n -dimensional graph, the species’ niche being the resultant hypervolume or centroid described by its distribution throughout this n -dimensional space. Thus Hutchinson’s solution to his question was that because environments contain many different gradients, they can sustain many different species – with no two species being described by precisely the same hypervolume or centroid. This

model allows for competition and coexistence among species to be more precisely described also. In considering this, Hutchinson partitioned the species niche into *fundamental* and *realized* niche space, with the former corresponding to the entirety of environmental gradients that are suitable for a given species and the latter corresponding to the portion of the niche actually realized by a particular species and that is unshared with other species. In practice a species never realizes its fundamental niche as *competition* between species for resources prevents this from occurring. A species’ realized niche therefore results from *character displacements* and *trade-offs* that facilitate *coexistence*. To illustrate this, Hutchinson emphasized the role played by limits imposed on the degree of morphological similarity between closely related species sharing the same habitat, such as size, which keeps the two species from *competitively excluding* one another. Hutchinson proposed a theory of *limiting similarity*, which could be expressed as a ratio of morphological similarity between species corresponding to 1.3:1 (i.e., two closely related species can coexist if one is 1.3 times the size of the other). This came to be known as *Hutchinson’s ratio*.

Criticisms

In the 1970s, niche theory came under considerable criticism, which eventually led to the concept falling out of favor in ecology. The initial criticisms were philosophical in nature. The Popperian school of scientific philosophy emphasizes the significance of being able to falsify scientific hypotheses to the process of sorting among competing theories. Niche theory, it was claimed, had not been tested in such a way that could theoretically lead to its falsification. It was also noted that biogeographical models, which deal with ecological processes at large spatial and temporal scales, could predict species diversity and abundances using only *metapopulation dynamics* (i.e., the assumption of equal rates of immigration, emigration, births, deaths, etc.), without assuming the existence of species-specific niches (Simberloff 1978; Strong et al. 1979). In applying these biogeographical modeling

assumptions to smaller spatial scales – the traditional domain of niche theory – the ecologist Stephen Hubbell (2001) developed the *neutral theory of biogeography and biodiversity*, which can be considered an effective null hypothesis to niche theory as species abundances and diversities within a given community are predicted based on the explicit assumption of strict ecological equivalence among species.

Revival and Expansion

Hubbell's neutral theory has not been received uncritically by ecologists, and while it has enjoyed some measure of empirical success in predicting species abundances in ecosystems at equilibrium, in non-equilibrium ecosystems, it has had far more limited success (Chase and Leibold 2003). Alternative *idiosyncratic models*, making the assumption of absolute species ecological uniqueness (an extreme form of the niche assumption), have also been found to predict species abundances at least as well as neutral models (Pueyo et al. 2007), indicating the existence of a large family of predictive models, among which model selection might profitably be based on the degree to which they make realistic assumptions. Ecologists Jonathan M. Chase and Mathew A. Leibold (2003) have pushed for a revival of the niche concept, arguing that further evolutions of the definition of ecological niche should take into consideration both the requirements of species – this being central to the Grinnellian and Hutchinsonian niche concepts and their impacts on other species – this being central to the Eltonian “feeding” niche concept. The concept of the *evolutionary niche* has also been proposed. Unlike the ecological niche, which is essentially a snapshot of competition pressures operating on a given species at a particular point in time, the evolutionary niche takes as its dimensions the sum of selection pressures operating a species, which have shaped the species' present ecological requirements and impacts (Chase and Leibold 2003). A closely related concept is *niche construction* which is based on the idea that species are not passive with respect to their environments but ineptively modify or construct their niches so as to suit their idiosyncratic needs, and in so doing the

constructed niche becomes part of the species' *ecological inheritance system*. This can be seen in the case of pocket gophers (Geomyidae family) whose social and reproductive ecology involves the creation of elaborate networks of tunnels, which can be “transmitted” across multiple generations (Odling-Smee et al. 2003). In this model, changes in the way in which a species constructs its niche can alter its ecological inheritance in such a way that feeds back onto the species' gene frequencies (i.e., exploitation of a new resource bringing two species into competition); thus a species' evolutionary niche coevolves with and ultimately drives the evolutionary trajectory of that species.

Conclusion

The niche concept, and in particular the concept of the evolutionary niche and niche construction, has significant implications for evolutionary psychology. In many respects that concept of the *Environment of Evolutionary Adaptedness* from “classical” evolutionary psychology (Tooby and Cosmides 1990) has the characteristics of an evolutionary niche, with the sum of the places and times of adaptive relevance in the Pleistocene constituting its dimensions and the various cognitive modules being adaptations to its contours. *Evolutionary mismatch* occurs when a feature of the human mind adapted to a particular dimension of the evolutionary niche interacts with an evolutionary novel feature of the contemporary built environment in such a way that yields an evolutionarily suboptimal behavioral manifestation. This has been challenged however by proponents of niche construction (Odling-Smee et al. 2003), who argue that *Homo sapiens* is an aggressively niche-constructing species by virtue of its high intelligence and that far from being removed from evolutionary relevant environments, niche construction has played and continues to play a critical role in the evolution of the species, such as in the case of *culture-gene coevolution*, where gene frequency change-initiated alterations to the contours of the *cultural niche* create novel selection pressures, which feed back onto

the cultural niche via their impacts on gene frequencies, leading to runaway selection (as in the case of the spread of lactase persistence). Better understanding of the dynamics of mutual transaction between biological and ecological inheritance in niche-constructing taxa might therefore pave the way for a post-neo-Darwinian evolutionary ecology (Odling-Smee et al. 2003).

Cross-References

- [Adaptation](#)
- [Ecology](#)
- [Resource Competition](#)
- [Resource Limitation](#)
- [Resources](#)

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Ecological Rationality

- [Bounded Rationality](#)

Ecological Trap

- [Maladaptive By-Product Hypothesis](#)

Ecological Validity

- [Towards Methodological Pluralism in Psychological Sciences](#)

Ecology

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Synonyms

[Ecological demands](#); [Environment](#); [Evoked culture](#)

Definition

Ecology: The relationships between living organisms (including humans) and their environment.

Introduction

Most research on sociosexuality has focused on the individual level of analysis, investigating either between-person differences or differences between men and women (e.g., Simpson and Gangestad 1991). Other work suggests that sociosexuality also varies extensively across cultures around the globe (e.g., Schmitt 2005) and that this variation – far from being stochastic – is at least

partly due to predictable variation in different ecological demands.

Cultural Variation in Sociosexuality

In the largest systematic investigation into sociosexuality around the world to date, Schmitt (2005, as part of the International Sexuality Description Project) administered the Sociosexual Orientation Inventory (Simpson and Gangestad 1991) in 26 languages and 48 countries to over 14,000 people around the globe. This investigation revealed extensive cross-country variation in sociosexuality scores across countries: On average, Bolivians reported being more sociosexually unrestricted than Belgians and Slovenians more unrestricted than South Koreans. These differences attest to the substantial plasticity in human sociosexuality. Despite this large variation across countries a notable consistency also emerged: Consonant with parental investment theory (Trivers 1972), men in each of the 48 countries reported a significantly less restricted sociosexuality than women. Although the magnitude of the sex differences varied across countries they were generally large, with an average effect size of $d = 0.74$ across the entire sample.

Schmitt was also able to test potential causes of this cross-country variation. One demographic variable that emerged as a strong predictor was sex ratio. Sex ratio theory predicts that relatively more men than women in a country would be associated with more restricted sociosexuality, given that increased competition for women allows them to have greater influence than men over sociosexual norms. Indeed, Schmitt found that higher ratios of men were associated with more restricted sociosexuality in a country. Second, Schmitt tested the impact of ecological demands on sociosexuality. Consistent with Strategic Pluralism Theory, which stresses the higher adaptive value of biparental care and restricted sociosexuality in harsher ecologies (Gangestad and Simpson 2000), analyses revealed that people were more sociosexually restricted in countries characterized by more demanding ecologies (characterized by factors such as higher infant mortality and child malnutrition).

Finally, Schmitt tested potential causes of the variability of magnitude of sex differences between countries. Again consistent with Strategic Pluralism Theory, which predicts that women's sexuality should be more facultatively calibrated to demands within the local ecology, results revealed that women's sociosexuality was much more influenced by ecological demands than was men's. Results also revealed the influence of a social variable: Increased levels of gender equity (assessed by variables such as percentage of women in politics and divorce rates) were associated with much smaller sex differences in sociosexual orientation within a country.

Disease Threat and Variation in Sociosexuality

Infectious disease has posed one of the largest threats to human welfare and survival throughout human history, likely accounting for more deaths than any other factor (Inhorn and Brown 1990; Wolfe et al. 2007). The magnitude of this threat, however, varies between regions and ecologies. Along with evolved physiological adaptations to mitigate this threat (such as the immune system), humans have also developed culture-specific behavioral norms and practices that serve as defenses against infectious disease which are often evoked by the local ecology.

Sexual behavior provides much opportunity for disease transmission, and more sexually promiscuous behavior is associated with an increased risk of contracting diseases and spreading these diseases to others. However, a more unrestricted sociosexual orientation can also have specific kinds of adaptive benefits – providing, for example, the opportunity to produce more offspring (see Gangestad Sociosexuality). These benefits must be weighed against the disease-related costs, and this cost/benefit ratio varies depending upon the prevalence of disease-causing pathogens. Where pathogen prevalence is higher, the costs of unrestricted sexuality are more likely to outweigh the benefits, whereas in places characterized by lower pathogen prevalence the benefits

are more likely to outweigh the costs. This logic leads to the hypothesis that greater pathogen prevalence predicts more restricted sociosexuality.

Cross-national evidence provides support for this hypothesis (Schaller and Murray 2008). In places with a higher level of historical pathogen prevalence, both men and women report being more sexually restricted (r 's for men and women were -0.27 and -0.62 , respectively). This effect is stronger for female scores, and this sex difference in effect sizes fits with the cost/benefit framework and with Strategic Pluralism Theory more generally (Gangestad and Simpson 2000). Men have a lower minimum level of parental investment than do women (see Gangestad Sociosexuality); thus, the fitness benefits associated with unrestricted sexual behavior are likely to be greater among men than among women. Therefore, for men only, these benefits may outweigh the costs (disease transmission) even at relatively high levels of pathogen prevalence. Among women, however, the benefits of unrestricted sexuality are relatively minimal and so are more likely to be outweighed by disease-related costs as pathogen prevalence increases. Consistent with the conceptual framework, additional results revealed that cross-national variation in women's unrestricted sexual attitudes were predicted especially strongly by the prevalence of human-transmitted non-zoonotic diseases, compared to the prevalence of zoonotic diseases (Thornhill et al. 2010). All of these relationships were robust when controlling for other potential causes of variation in sociosexuality, such as economic development and inequality, and other ecological demands.

Recent additional results from analyses of Pew survey data from 40 countries (www.pewglobal.org/2014/04/15/global-morality) also speak to the influence of disease threat for cultural variation in sociosexuality. This survey found that the acceptance of nonmarital sex differs widely across cultures: Whereas 97 % of Indonesians say that premarital sex is wrong, for example, only 11 % of Italians do. Murray and Schaller (2016) tested whether acceptance of premarital sex was associated with disease threat. Indeed, they found that historical pathogen prevalence strongly predicts the percentage of people within a country who

state that premarital sex is morally wrong ($r = 0.65, p < 0.001$). Consistent with the causal interpretation, acceptance of premarital sex was more strongly predicted by historical rather than contemporary pathogen prevalence.

Other work at the psychological level also indirectly supports the influence of disease threat for sociosexuality. First, chronic *perceived* risk of disease transmission is negatively associated with promiscuous sociosexuality (Murray et al. 2013). Of more inferential utility is the finding that people high in worry about disease became *more* sociosexually restricted when the threat of disease (but not a disease-irrelevant threat) was made salient (Murray et al. 2013). Additional analyses suggested that these effects were especially strong for women. These results also provide further evidence for adaptively flexible mechanisms which respond to immediate ecological circumstances.

Conclusion

Taken together, this work highlights the importance of ecological factors in the calibration of sociosexuality. The existing evidence clearly shows that neither gender is rigidly predisposed to a single mating strategy. However, these data also suggest that, at present, no ecological or social pressure is strong enough to make women on average more sociosexually unrestricted than men.

Cross-References

- Behavioral Immune System
- Disease Avoidance
- Evoked Culture
- Factors That Influence Bullying
- Parental Investment Theory
- Strategic Pluralism Theory

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Ecology and Behavior

► Ecological Influences

Ecology of Pair-Bond Stability

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Synonyms

Environmental factors associated with marital harmony

Definition

The study of physical and social environmental factors influencing pair-bond stability and dissolution.

Introduction

Humans are a pair-bonding species, and this is reflected in our behavior and physiology (Quinlan 2008). While their form and duration varies, pair-bonds exist in all human societies—and there are very few, if any, exceptions to this rule. To understand the stability of pair-bonds, it is useful to look at the contexts under which they are unstable, to examine the factors that increase the probability of divorce or dissolution. These factors have been well studied by scholars in sociology, psychology, anthropology, medicine, and law. Despite this, the *ecological* factors driving pair-bond stability and divorce have received much less attention in humans as they have in studies of other pair-bonding organisms, such as birds.

This entry will provide a selective and brief account of (1) the behavioral ecological approach to pair-bond stability in humans; (2) mate desertion theory, the primary theoretical approach used in studies of human pair-bonding, and empirical tests of the idea; and (3) studies that have gone beyond the limitations of mate desertion theory.

Behavioral Ecology and Pair-Bond Stability

Human behavioral ecology is the study of human behavior in evolutionary and ecological context. Under the assumptions of this framework, humans are viewed as actors whose behavior is shaped by genetic and cultural evolutionary mechanisms to maximize inclusive fitness given the constraints of prevailing ecological conditions. Adopting the wording of Winterhalder and Smith (2000), a typical HBE hypothesis might take the following form:

- In context X, stay in a pair-bond because it maximizes inclusive fitness.
- In context Y, leave an existing pair-bond because it maximizes inclusive fitness.

These hypotheses are often derived from mathematically or graphically formulated optimality models. When the payoffs are frequency dependent (i.e., one actor's payoff depends on what the other actors are doing), as is often the case with pair-bonding, game theory provides the best-fitting analytical tools. The idea of an evolutionarily stable strategy (ESS) comes from this body of theory and can be defined as "a strategy such that if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection" (Maynard Smith 1982, p. 10).

Pair-bonds can dissolve via divorce, abandonment, or death. The first two causes of dissolution should occur when one or both in the pair can increase their fitness by doing so, for instance, by having a reasonable probability of finding a better mate. The third cause, mortality, is out of the actors' control (except, perhaps, in the case of spousal homicide). Despite these fundamental differences, both should be influenced by ecological conditions.

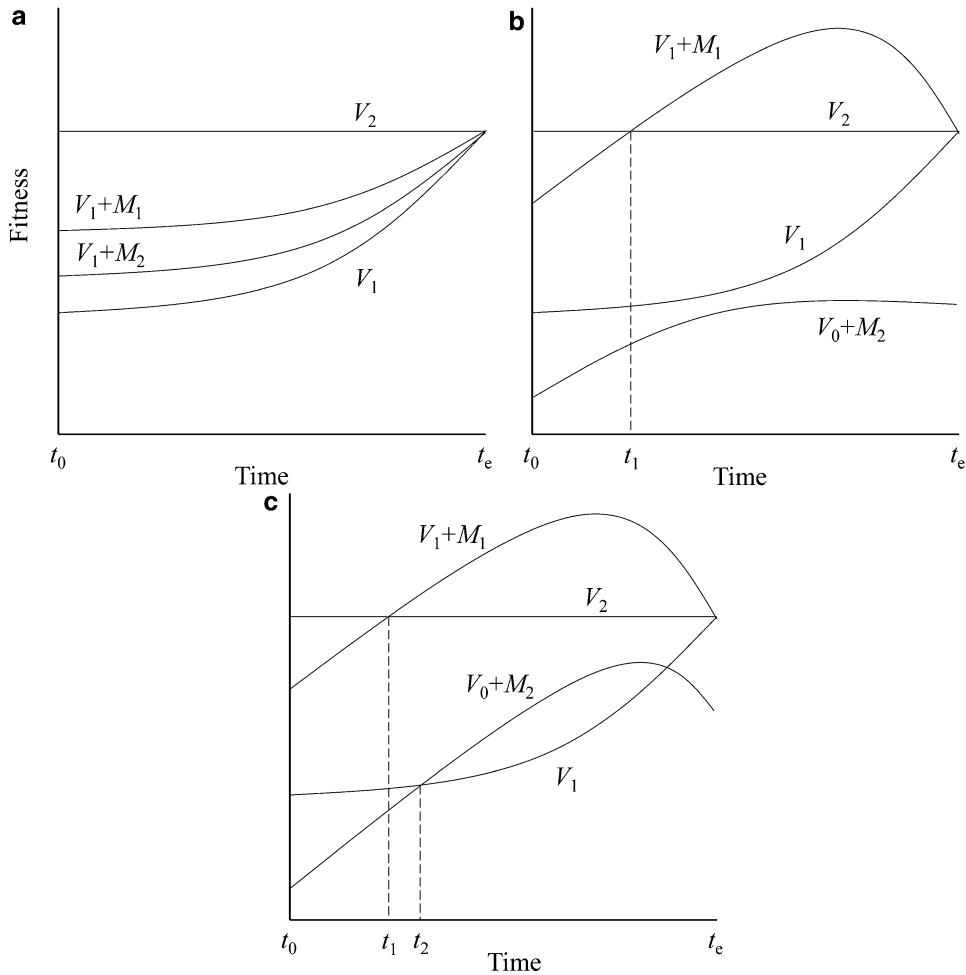
Mate Desertion Theory

Maynard Smith (1977, 1982) can be credited for bringing game theory to bear on the problem of mate desertion. In his models, the decision to stay or desert depends on the *frequency-dependent* fitness payoffs for staying (parenting effort) as traded off against a *fixed* payoff for seeking additional mating opportunity (mating effort). While the prospective nature of the models improves on existing ones that viewed past investments as reasonable drivers of future ones, they are now viewed as having a serious shortcoming (Houston et al. 2013). The mating benefits of desertion should be a frequency-dependent, rather than fixed, function of how many opposite-sex individuals have left their own pairing in favor of the mating pool. More recent models of mate desertion account for this.

The major conclusions drawn from these models are as follows. First, mate desertion will occur when the fitness benefits of seeking additional mates outweighs the decrease in offspring survival caused by reducing the number of individuals providing parental care. Second, desertion by none, both, or one partner can be an evolutionary stable strategy. This is illustrated graphically in Fig. 1 using examples from Lazarus (1990). In these illustrations, the fitness accrued between the start (t_0) and end (t_e) of the period of parental care for biparental care is V_2 , uniparental care is V_1 , and no care is V_0 . The fitness accrued in searching for another mate is M_1 for the partner with the higher marginal gains and M_2 for the partner with the lower marginal gains. In (a), neither partner deserts because $V_1 + M_1 < V_2$ and $V_1 + M_2 < V_2$. In both (b) and (c), the first partner deserts at t_1 because $V_1 + M_1 > V_2$. In (b) the second partner does not desert because $V_0 + M_2 < V_1$. In (c) the second partner deserts the offspring at t_2 because $V_0 + M_2 > V_1$.

Harpending and Draper (1986) argued for the application of mate desertion theory to the problem of human pair-bond stability, identifying specific aspects of the socioeconomic environment that shape the payoffs. They pointed to fertility rates as a measure of the potential payoffs for mating and care-dependent child mortality rates as a measure of the potential payoffs for fathering. In relatively good environments, where increases in paternal care lead to increases in offspring survivorship, more stable pair-bonds are expected compared to relatively bad environments where paternal care is unlikely to increase offspring survivorship. The focus on payoffs to males was due in large part to males being the ones with higher marginal payoffs to mating (M_1 in Fig. 1) and, thus, the more likely to desert for these reasons.

Hurtado and Hill (1992) tested hypotheses derived from mate desertion theory using data from two South American foraging societies, the Ache and Hiwi. Blurton Jones et al. (2000) extended the analyses to include two African foraging societies, the !Kung and Hadza. They argued that societies with higher pair-bond stability should have (a) higher payoffs for fathering effort, measured as differences between



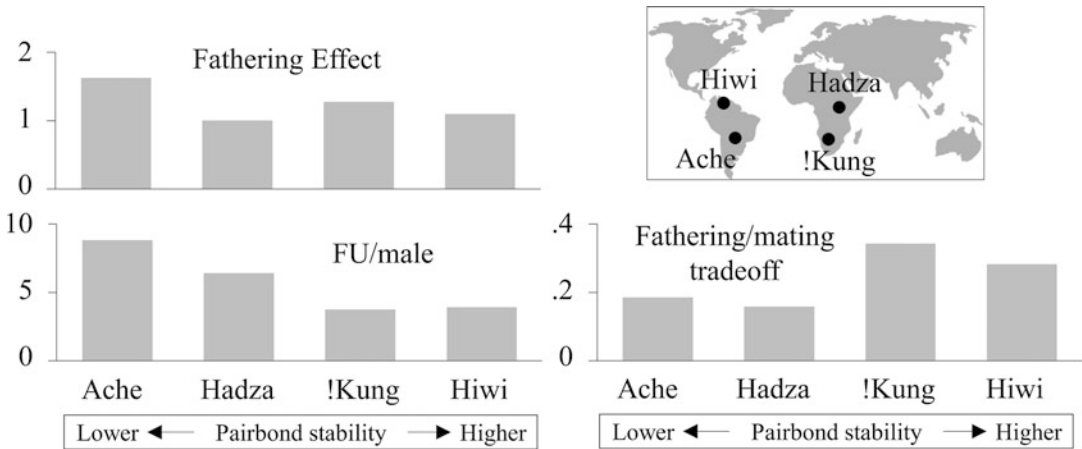
Ecology of Pair-Bond Stability, Fig. 1 Illustrations adapted from Lazarus' (1990) model of mate desertion, depicting scenarios where (a) neither partner deserts, (b) one partner deserts, and (c) both partners desert. The following parameters describe fitness payoffs: V_2 is the payoff for biparental care, V_1 for uniparental care, V_0 for no care;

M_1 is the payoff to looking for an additional mate for partner 1, and M_2 is the payoff to looking for an additional mate for partner 2. The labels on the time axis describe the following: t_0 is the start and t_e is the end of the period of parental care, t_1 is the timing of desertion for partner 1, and t_2 is the timing of desertion for partner 2

father-present and father-absent child mortality rates (i.e., the “fathering effect”); (b) lower pay-offs for mating effort, as measured by fertility rates (i.e., fertility units per male or FU/male); and (c) a higher value for the trade-off between the two, as measured by the parenting/mating index. As shown in Fig. 2, they found that the payoff for mating was a better predictor of pair-bond stability than the payoff for fathering. The trade-off measure was also supported, albeit not as the predicted gradient. Blurton Jones et al. (2000)

argued that their results cast doubt at previous accounts of the primacy of provisioning for the evolution of human pair-bonding (Quinlan 2008).

While paternal care may have an important function in supporting lactation (Marlowe 2003; Quinlan and Quinlan 2007, 2008), it does not covary as predictably with environmental uncertainty as does maternal care (Quinlan 2007). In Sear and Mace's (2008) review of studies of the effect of fathers on offspring survival, they found markedly mixed results with less than half



Ecology of Pair-Bond Stability, Fig. 2 Fathering effect, FU/male, and their trade-off in four societies ordered by pair-bond stability, the inverse of divorce rates. Only the measure of payoff for mating effort, and less so the trade-

off measure, approximates the predicted gradient by pair-bond stability (Created using data from Table 4.4 in Blurton Jones et al. (2000, p. 78))

showing a clear positive fathering effect. Studies of longer-term effects of fathers on offspring success appear mixed as well (e.g., Winking et al. 2011). This may be, in part, because children are cared for by a variety of kin, and this may buffer children against father absence. Indeed, Quinlan and Quinlan (2007) showed that availability of helpers led to higher incidence of divorce in a study of 58 small-scale societies. Taken together, the evidence supports Blurton Jones et al. (2000) contention that mating may outweigh fathering in the evolution of human pair-bonding.

One of the most important aspects of the socio-ecological environment shaping the payoff to mating effort is the operational sex ratio (OSR) — a measure of the number of males to females currently available for mating. With a male-biased OSR, competition for mating opportunities is much more intense, and thus, males do better to stay in existing pair-bonds; with a female-biased OSR, on the other hand, males may increase their fitness by deserting their mate in favor of the increased possibility of acquiring a mate of better quality (Blurton Jones et al. 2000; Ellsworth et al. 2015). These hypotheses were overwhelmingly supported in a recent comparative study of pair-bonding birds (Liker et al. 2014), and there is accumulating evidence

along the same lines in humans (e.g., Barber 2003; Kruger 2009).

Other Costs and Benefits in Ecological Context

The major shortcoming of mate desertion theory is that the actual benefits of pair-bond stability go beyond the immediate parental care ramifications, and the actual costs go beyond the current breeding attempt. Pair-bond dissolution should be favored any time one or both in the pair can increase their fitness by seeking another mate. As Choudhury (1995) puts it, pair-bond dissolution should be “viewed as a reproductive strategy by an individual to maximize its own fitness” and to ascertain an individual’s “net benefit from divorce one must compare the expected future gain in fitness with the new mate versus the expected gain with the old mate” (p. 414). Winking and Gurven (2011) measured these quantities with data from Tsimane hunter/horticulturalists from Bolivia and concluded that males can increase their fitness via divorce.

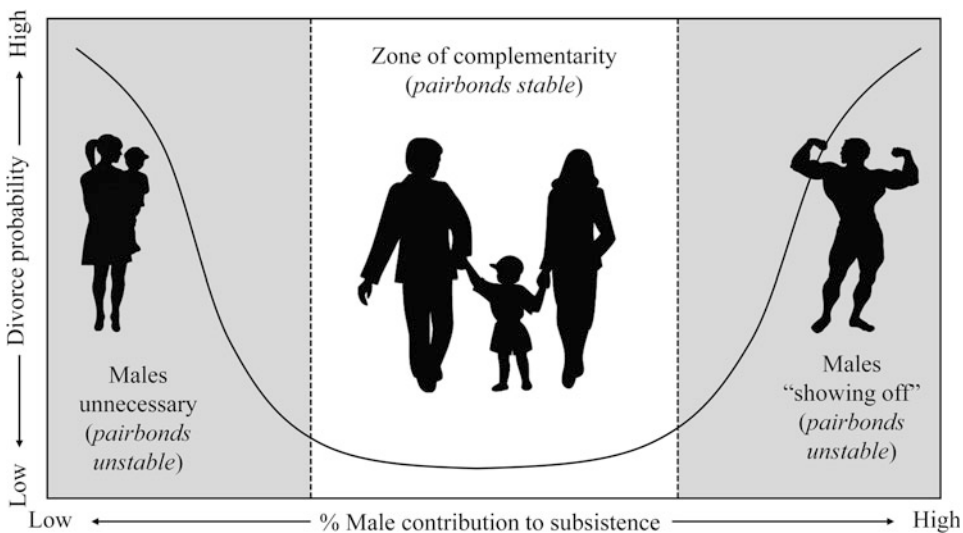
Once one moves beyond mate desertion theory, however, little work has been done in developing quantitatively precise models of divorce that account for ecology. McNamara (1999), for

example, built an ESS model of divorce, but it focused on intrinsic qualities of the partners rather than extrinsic qualities of the environment. The model predicted that high-quality individuals should be more likely to seek greener pastures than low-quality individuals and that the most stable pair-bonds will be between individuals of similar quality. This suggests that sexual conflict theory may be necessary to understand divorce, as the fitness increase enjoyed by the initiator is a fitness decrease for the abandoned. This appears to be true in at least some cases in humans. Käär et al. (1998), for instance, showed that divorce led to increased reproductive success in males but not females in the eighteenth- to twentieth-century Sami populations from Finland.

Marital satisfaction appears to hinge on ecologically variable factors that are closely tied to fitness (Shackelford and Buss 1997; Dillon et al. 2015). Further, in a study of divorce using the standard cross-cultural sample — a database of 186 small-scale societies each coded for more than 2000 variables describing various aspects of typical behavior, beliefs, and environment — Betzig (1989) found that a handful of factors were associated with divorce, but most commonly infidelity and sterility. Both factors appear to cause

divorce in industrialized societies as well (e.g., Barber 2003), and both should also vary with socioecology. Economic opportunities were also associated with divorce in Betzig's (1989) study, a result similar to those in industrialized societies (e.g., Barber 2003). This mirrors trading-up territories as a cause of pair-bond dissolution in birds (Choudhury 1995), which should occur in environments with marked variation in territory quality.

Economic considerations are central to Quinlan and Quinlan's (2007) finding that subsistence complementarity was strongly related to pair-bond stability in a multivariate study of data from the standard cross-cultural sample. In other words, divorce is a curvilinear function of percent male contribution to subsistence. As shown in Fig. 3, when either males or females do the majority of subsistence work, there appears to be little reason to remain pair-bonded, though the reasons for this vary for the two non-complementary zones (Quinlan 2008). When females do the majority of the subsistence work, there may be no reason for males to stick around. When males do the majority of work, it may be that the work is geared toward "showing off" for potential future mates. Ellsworth et al. (2015) suggest their finding



Ecology of Pair-Bond Stability, Fig. 3 A schematic illustration of Quinlan and Quinlan's (2007) discovery of, and explanation for, a strong association between pair-

bond stability and subsistence complementarity in societies from the Standard Cross-Cultural Sample

of a latitudinal gradient in marital stability, but a lack of association with subsistence type may be due to latitudinal gradients in subsistence complementarity. Another possibility is that latitudinal gradients in pathogen distribution shape the fitness payoff for genetically diverse offspring, which could also lead to higher divorce rates (Low 1990).

Resource predictability is another ecological factor that has been hypothesized to lead to pair-bond instability. Weinrich (1977), for example, used evolutionary logic to ascribe contrasts in pair-bonding strategies among US ethnic groups as a function of income predictability. Studies of pair-bonding species might provide clues. For instance, Botero and Rubenstein (2012) found that environmental fluctuations and unpredictability were associated with divorce in a study of 163 bird species, suggesting that such flexibility in mating behavior may serve to minimize the negative fitness consequences associated with ecological crossovers – i.e., where the fitness payoffs for one mating strategy are drastically reduced with sudden, unpredictable environmental changes. Other studies of humans, however, suggest that there is not such a simple link between the two. For instance, Cohen (2014) found that divorce rates *decreased* in the USA during the Great Recession of 2008–2011, the most drastic economic crisis of the twenty-first century.

Conclusion

Human behavioral ecology brings evolutionary logic to bear on the problem of the ecology pair-bond stability. Most work has centered on mate desertion theory, and its emphasis is on the trade-off between mating and parenting in males. This perspective is limited, however, as the costs and benefits of mate desertion go beyond the immediate effects on current offspring survival and the probability of finding a new mate. Models with a broader scope need to be developed, models incorporating a wider range of costs and benefits.

Cross-References

- [Child Mortality](#)
- [Evolution of Long-Term Pair-Bonding in Humans](#)
- [Human Behavioral Ecology](#)
- [Relationship Dissolution](#)

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Ecology of Paternal Investment

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Synonyms

Paternal care

Definition

The activity of expending time, energy, or resources on one's offspring

Introduction

One of the primary drivers of animal behavior is successful reproduction. In humans, as with all mammalian species, and most avian and fish species, this involves considerable time and effort engaging in parental care. This expenditure, which often poses a risk to the animal's own survival, was coined “parental investment” by Trivers (1972). For the majority of mammalian species, parental investment is primarily undertaken by females. However, humans exhibit biparental care; that is, care by both biological parents (Woodroff and Vincent 1994). Given the importance of parental care for physical and psychological well-being in humans, a considerable body of research has been conducted to explain the conditions under which biparental care develops and the proximal factors that maintain it.

Female-Dominated Care

Before looking at the factors that have led to biparental care in humans and other, largely non-mammalian, species, it is necessary to examine why female-dominant care is the norm for mammals. Even prior to conception, in many species,

females have a larger gametic investment, with female gametes being exponentially larger than male gametes and limited in number from birth (i.e., differential gametic potential). In all live breeders, reproductive potential is also limited by the length of the gestational period. For mammals, newborn young are wholly reliant on nourishment from their mothers, which often delays the onset of post-reproductive conception. In combination, these factors lead to a decreased reproductive potential in females. This has two consequences: at any given time, there are fewer females capable of reproducing, meaning that females can afford to be choosier during mate selection, and males face a quality or quantity dilemma, whether to care for present offspring or to focus on seeking out additional mates elsewhere. Moreover, for animals that breed internally, paternal investment puts the male at risk of cuckoldry. Indeed, recent advances in DNA analysis have shown that extra-pair paternity is much more common than previously assumed, even in species which were previously thought to be monogamous (e.g., Dillard 2016). For these reasons, therefore, biparental care is not adaptive for the majority of mammals. However, the opposite pattern is found in fish species, where the costs of parental investment are often much higher in females than in males (Balshine-Earn 1995; Clutton-Brock and Parker 1992). This shows that parental investment is largely dependent on the life course of the species under examination.

Environmental Factors

Just as with cooperative breeding, environmental factors can arise that make it not only adaptive, but necessary for biparental care to occur. Indeed, Markham et al. (1995) has posited that biparental care will only occur when environmental conditions necessitate. These conditions may take the form of extreme weather conditions (Mongolian gerbils), high predation rates (raptures versus passerine birds), or scarce resources (penguins). When such environmental pressures are present, the relative cost-to-benefit ratio of engaging in parental care is altered, such that failure to invest in offspring decreases

overall fitness, even though some fitness is lost by forgoing current reproductive opportunities. Another factor of importance is how altricial offspring are, as opposed to precocious; it is believed that this may be the main factor driving biparental care in humans (Cartwright 2016; Hrdy 2011). That is, human offspring, unlike the majority of living organisms, are wholly incapable of survival without care and are much more vulnerable to predation or injury than other mammalian species, most of whom are mobile within hours or days of birth. Humans also have a protracted development, such that they are not capable of any real degree of independence for more than a decade after birth. The combination of vulnerability and the extent of care required for human offspring to survive necessitates care by more than one individual.

Proximal Factors

A second explanation for the development of biparental care in humans is the proposal that it may have first arisen as an alternate mating strategy (Meynard et al. 2001). It is well-established that testosterone is positively related to aggression and negatively related to parental investment across species and sexes (e.g., Holecamp's Hyena Project). Subordinate males may find it particularly difficult to find a mate or hold a territory and may, therefore, choose to engage in cooperative parenting with a female who already has offspring, thereby gaining reproductive potential following successful rearing (Meynard et al. 2001). The advantage of the care-then-mate strategy may be that it decreases the risk of cuckoldry (Meynard et al. 2001). This shows that hormones and other psychobiological factors may be a proximate cause of parental investment decisions. In addition, research has indicated that the probability of future reproductive opportunities (e.g., mortality risk) and indicators of health of both offspring and mate also play a role in determining how much parental investment, if any, will occur (e.g., Laczi et al. 2017). This is because there is a certain degree of parent-child conflict inherent in parental investment; it is often in the child's best interest to receive more care than would be in the best interest of the parent(s).

Conclusion

Parental investment is dependent upon the life-course history and the environmental factors present in the reproductive environment. While the majority of animals engage in some form of parental investment, the extent of this investment will be dependent on the costs involved (i.e., to one's own survival/fecundity) and the likelihood that the offspring will survive and reproduce. For humans, recent research using an evolutionary game approach suggests that a high infant mortality rate resulted in the predominant reproductive strategy in humans being monogamous care, though extra-pair reproduction did occur (Alonso and Rodríguez 2017). However, despite decades of scientific inquiry, understanding of parental investment, especially in humans, remains limited. This is problematic given the importance of the family unit to well-being. It is, therefore, in our best interests to continue striving to understand the place of parental investment, including its ultimate and proximate causes, to our human family.

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Economic Deprivation

► Economic Hardship

Economic Hardship

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Synonyms

Economic deprivation; Financial distress; Financial pressure; Perceived income inequality

Definition

Economic hardship refers to psychological distress that results from a perception of relatively low economic resources (Barrera et al. 2001). Hardship is contrasted with poverty, which is simply the lack of economic resources. Economic hardship does not need to involve an actual lack of economic resources, but simply a perception of this deficit. Economic perceptions are heavily influenced by comparative processes (Kraus and Park 2014). Consequently, economic hardship is closely related to how one's economic resources

compare to others. Hardship is also related to *competitive disadvantage*, which describes when an individual is disadvantaged relative to competitors in hierarchical social structures. When one perceives themselves as having fewer resources compared to their competition – due to such factors as economic hardship – they may infer competitive disadvantage.

Introduction

Economic hardship describes a perceived lack of extrinsic resources, with resultant consequences for selection: Individuals with more resources generally tend to survive and reproduce more effectively. Individuals who possess greater resources are also more able to provide higher levels of parental investment, increasing the probability of genes being successfully transmitted to the next generation. Economic hardship may in part act as a barometer of competitive disadvantage indexed by the possession of extrinsic resources. Those who suffer from economic hardship – that is, those who perceive themselves to be competitively disadvantaged relative to others – likely engage in different patterns of conflict and cooperative behaviors. Conflict behaviors allow individuals to gain access to resources through nonconventional means. Cooperation is a tool that allows those experiencing economic hardship to receive resources from resource-rich individuals in an exchange, or as a form of insurance against poverty. We review these consequences of economic hardship in more detail below.

Conflict

As a result of experiencing economic hardship, an individual may believe that they are not able to gain sufficient resources through normative means (and thus perceive themselves to be competitively disadvantaged). Those who are competitively disadvantaged, still need resources to survive, attract mates, and ensure offspring survival. Therefore, they may decide to reduce their disadvantage by engaging in antisocial acts

against others in their environment (Wilson and Daly 1985). Through these acts, they may gain resources or status, and competitors may lose resources or status. In both cases, the antisocial actor's competitive disadvantage relative to the victim is reduced or eliminated, which may in turn reduce relative economic hardship and competitive disadvantage.

Wilson and Daly's (1985) conception of *young male syndrome* is a key example of the relationship between competitive disadvantage and antisocial conduct. Evidence clearly indicates that young men commit a disproportionate amount of antisocial and criminal acts. Wilson and Daly (1985) explain this cross-cultural fact by arguing that young males experience intense competition. Those who are competitively disadvantaged may turn to need-based risk-taking, such as antisocial behavior and crime, in an attempt to gain outcomes that may otherwise be unattainable through nonrisky or nonantisocial means. Economic inequality – that is, steep disparity between “haves” and “have nots” – has been robustly linked to increased risk-taking and crime, providing further evidence of the link between competitive disadvantage and conflict behaviors (reviewed in Daly 2016). Importantly, economic inequality is a much more robust predictor of conflict behaviors than is simple poverty, suggesting that competitive disadvantage (i.e., perceived economic hardship compared to others) is more important than simple lack of resources.

Cooperation

Based on the behaviors of contemporary hunter-gatherer societies, Gurven (2004) argued that many societies have a cultural bias toward helping the needy (i.e., those who are competitively disadvantaged). Evolutionary pressures have likely supported this development, although the relative contribution of different selection pressures to cooperation is still being debated (see Cooperation). For example, givers may provide resources to those experiencing economic hardship to get something else in return (reciprocal altruism), leading to increased fitness in the long run. Giving

to competitively disadvantaged individuals may also signal to other members of the society that givers have enough resources to survive *and* give away to others. Such giving may indicate that the giver holds higher relative position (social status) compared to those that have enough resources to survive but not enough give to others, with resultant positive survival and reproductive consequences. In a social game that measures cooperation, participants with higher intelligence scores were more likely to give resources to a public pool compared to those with lower intelligence scores (Millet and Dewitte 2007). The authors argued that intelligence is associated with a greater ability to acquire resources, and high-intelligence individuals signal this ability through cooperation.

Fear of economic hardship may have also influenced the evolution of cooperation. Cashdan (1985) posits that altruistic norms may have developed as a form of insurance against need. Individuals may invest resources into helping others with the expectation that they would in turn receive financial aid should they need it. Just like insurance, individuals often pay a small amount of their resources to a communal fund used to help those experiencing economic hardship. If others in their society do the same, these givers should expect that if they were to experience economic hardship, they would receive some of these communal funds. Thus, factors that would reduce their fitness through a loss of resources (even uncontrollable factors like natural disasters) would now not have as deep of an effect on them; they can rely on their neighbors to provide for them. In support of this hypothesis, Suleiman, Aharonov-Majar, and Luzon (2015) demonstrated in an experimental study that people are more likely to join groups and share resources when facing environmental risks (in this study, losses in a game of chance). Further evidence for the social insurance hypothesis comes from an examination of sub-Saharan African water resellers. Compared to households connected to water that do not resell water, those who do resell water were generally in a more precarious economic situation (Zuin et al. 2014). Many of these resellers, however, do not enter this business for financial reasons and may lose money by

engaging in water reselling. Instead, Zuin et al. (2014) argued they resell water with the expectation that buyers would help them if they were to need help in the future; facing economic hardship encouraged resellers to share water with others as a form of insurance against this hardship.

Conclusion

Economic hardship refers to the perception of a deficit of resources compared to others. Those who suffer from economic hardship are competitively disadvantaged, with resultant consequences for survival and reproduction. The perception of economic hardship may motivate individuals to adopt different behavioral strategies including both increased conflict behaviors and increased cooperation.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Antisocial Behavior](#)
- ▶ [Competition for Resources Desired by Females](#)
- ▶ [Cooperation](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Risky Behavior](#)
- ▶ [Social Status and Economic Resources](#)
- ▶ [Status and Redistribution of Resources](#)

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Economic Resources: Wealth

► Social Status and Economic Resources

Economically Vulnerable

► Redistribution Preferences and Low Socioeconomic Status

Economists and Evolutionary Psychology

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Definition

Economics has traditionally been defined as a subject concerned with those aspects of human behavior that are involved in the application of scarce resources to produce, distribute, and consume goods and services for the satisfaction of human wants. However, evolutionary psychology has increased the scope for understanding the

“human behavior” component of economic activity by positing that the human brain contains a large number of evolved psychological mechanisms that play a key role in framing this economic behavior.

Introduction

Over the last two centuries or so, many economists have exhibited an ambiguous attitude towards psychology and evolution as disciplines, even while sometimes borrowing isolated concepts from them, but a few economists have embraced both of these subjects and fruitfully utilized them within the economist’s conventional remit.

The most well-known economist to do this was the American institutionalist Thorstein Veblen, but this entry will demonstrate that many other economists have attempted to import concepts from what can be called evolutionary psychology in its broadest meaning into their analyses. Moreover, less recognized is that evolutionary psychology itself has economics-related concepts embedded within in, which could be used to partially reformulate the basic principles of economics as a discipline, if such a reformulation was so desired.

This entry is structured as follows. It will first consider the work of one nineteenth-century and two twentieth-century economic thinkers who employed aspects of past incarnations of evolutionary psychology to a degree, Gabriel Tarde, Veblen, and F.A. Hayek, before it then examines the work of a number of contemporary economists who have employed a modern version of it more directly. Finally it will examine the implications of two central concepts developed by contemporary evolutionary psychologists for economic analysis: the existence of evolved cognitive architecture for social exchange, and the functioning of biological markets.

Gabriel Tarde (1843–1904)

Tarde has a direct link to the further development of Charles Darwin’s theory of evolution by natural selection as his work was actively considered by

James Baldwin, the initiator of the well-known Baldwin effect whereby learnt behavior is posited to become innate (Weber and Deprew 2007). Tarde was the author of *The Laws of Imitation* and he also wrote a book devoted to economic psychology. Tarde asserted that social evolution was composed of two basic elements, innovation and imitation, and the latter often involved a form of adaptation. Baldwin employed the concept of imitation to develop a theory of individual mental growth through imitation that led directly to the idea of organic selection or the Baldwin effect (Richards 1987, 470). Baldwin distinguished between social and psychological imitation, the latter providing the raw materials for learnt habits to become instinctive via organic selection, or what he called accommodations to the local environment.

The Baldwin effect is still controversial in the scientific literature, but it is a logically possible means for some psychological mechanisms to have evolved. Darwin posited that many new instincts evolved by means of random variations to preexisting ones, but he also allowed that habits could influence instincts (Darwin 1873, 418). This latter mechanism is conventionally interpreted as mistaken Lamarckism, but the Baldwin effect would be one way for it to occur through neo-Darwinian means.

Thorstein Veblen (1857–1929)

If the psychological mechanisms of evolutionary psychology are equated with the older concept of instinct, then Veblen's book *The Instinct of Workmanship and the State of the Industrial Arts* can be highlighted as the first major work by an economist to explicitly employ a version of evolutionary psychology (Veblen 1914). Here, Veblen distinguished between tropismatic urges, simple instincts, complex instincts, habits, and institutions, some of these concepts having equivalents in contemporary evolutionary psychology (Barnett 2017; Buss 2004). Veblen had obtained his initial understanding of psychology from four authors of the period, William James, William McDougall, C. Lloyd Morgan and Jacques Loeb, the first two of whom are embraced as pioneers by

today's evolutionary psychologists (Tooby and Cosmides 2005, 7), although Veblen developed his understanding of instinct in a unique way.

Veblen hypothesized the existence of a significant number of instincts including the workmanship instinct, the parental instinct, the predatory instinct, the emulation instinct, the beauty instinct, and the curiosity instinct, the latter generating in modern times the scientific spirit. One of Veblen's most significant innovations was to distinguish between simple and complex instincts; the latter being (in part) evolved structured combinations of simple instincts and other tropismatic urges. Veblen deployed these simple and complex instincts to explain how human behavior was driven by various teleological goals, to understand how different instincts could come into conflict or contaminate each other, and to explain how habits and institutions that had evolved on the cultural plain could act to modify and develop these instinctive proclivities.

Explicitly employing a version of the environment of evolutionary adaptedness concept (but without labeling it as such), Veblen located the origin of instincts as adaptive solutions to problems of survival and reproduction that had faced human beings across the Paleolithic period of prehistory, although he located the origin of the predatory instinct in *Homo sapiens* in a more recent period: alongside the Neolithic origins of agriculture and the concomitant processes of animal domestication (Barnett 2018).

Veblen explicitly championed the application of Darwin's theory to economics. In his article "Why is Economics not an Evolutionary Science?" Veblen advocated the employment of what he termed a post-Darwinian method of cumulative causation in economics, rather than the conventional utility maximization approach of mainstream economic theory. As he explained: "The economic life history of the individual is the cumulative process of adaptation of means to ends that cumulatively change as the process goes on, both the agent and his environment being at any point the outcome of the last process" (Veblen 1919 [1898], 74–75). He also implied that economic methodology should be rehabilitated using what he called modern anthropology, ethnology, psychology, and "the biological sciences proper."

One of the most well-known concepts that Veblen developed in his work was conspicuous consumption, or the purchase and display of extravagant products that were much more expensive than their basic equivalents. He argued that conspicuous consumption functioned as a status display mechanism and as a means to indicate social group membership; evolutionary psychologists would add that it also functions in relation to intrasexual competition as a means to attract mates.

Ever since Veblen, there has existed a group of institutionalist economists who have developed his legacy, but – ironically – Veblen’s most penetrating insight – that an understanding of economic behavior must be framed by means of an evolutionary conception of psychology – was discarded by most institutionalist economists on the mistaken assumption that Veblen’s instinct psychology quickly became out-of-date. In fact, it is the behaviorist critique of instinct psychology that is now recognized as mistaken.

F.A. Hayek (1899–1992)

Hayek is somewhat less recognized than Veblen as a contributor to an evolutionary understanding of psychology, but in *The Sensory Order: An Inquiry into the Foundations of Theoretical Psychology and Knowledge, Evolution, and Society*, Hayek did develop some themes that are also found in evolutionary psychology. For example, in the latter, he explained that: “our innate moral emotions and instincts were acquired in the hundreds of thousand years – probably half a million years – in which *Homo sapiens* lived in small hunting and gathering groups and developed a physiological constitution which governed [their] innate instincts” (Hayek 1983, 29). He also argued that cultural selection as a process was analogous to biological selection.

Hayek is one of the few economists to have written a substantial book on the workings of the human brain. In *The Sensory Order*, he argued that identifying basic human urges and drives was essential for an accurate explanation of purposive behavior (Hayek 1952a, 81). He proposed

as the central thesis of his book that sensory or mental qualities were not an attribute of individual physiological impulses, but that instead these qualities were determined by the system of connections by which the impulses were transmitted from neuron to neuron; it was the position of the impulse in the whole system of connections which distinguished it; and this system of connections was acquired both in the course of the development of the species (i.e., by evolution) and also in the individual’s own life-experience (Ibid., 53). This in turn required the development of a biological theory of the evolution of adaptive and purposive processes. Current understanding of neural networks is of course much more sophisticated than Hayek’s, but systematic interconnections are still a prominent feature of them (Nolte 1999, 18).

Elsewhere Hayek proposed the notion that: “all the ‘physical laws of production’ which we meet, e.g., in economics, are not physical laws in the sense of the physical sciences but people’s beliefs about what they can do” (Hayek 1952b, 31), implying that a main focus of economics should be on mental capacity. Moreover the objects of economic activity could, for Hayek, only be defined with reference to evolved human purpose and the terms of view that people held about particular commodities and money, i.e., through an evolutionary understanding of psychology. Hayek is one of the most well-known economists of the twentieth century but his work emphasizing the importance of the psychological foundations of economic behavior is sometimes unfairly overlooked.

Contemporary Economists

There are a number of contemporary economic thinkers who employ aspects of modern evolutionary psychology in varying degrees in their work, including Vernon Smith, Gad Saad, P.H. Rubin, Jason Potts, Nigel Nicholson, Stephen Lea, and others.

Gad Saad has focused much of his research on the evolutionary foundations of consumption and marketing (Saad 2007), for example,

explaining compulsive buying and other consumption-related addictions as maladaptive behaviors caused by the “misfiring” of evolved psychological mechanisms that have positive functions when deployed in the correct way and/or in the correct context. Geoffrey Miller has also considered evolutionary consumer psychology, in particular how costly signaling theory developed by evolutionary biologists can be applied to product branding and advertising techniques (Miller 2009).

Vernon Smith has imported the concept of ecological rationality, as elsewhere developed (Todd and Gigerenzer 2007), from evolutionary psychology to economics, defining it as relating to an ecological system that had emerged from both biological and cultural evolutionary processes (Smith 2008a, 36). Smith contrasted two different types of rationality that he termed constructivist as against ecological rationality. The former related to the conscious, deliberate, deductive processes that were conventionally believed to underlie human reason by economists. The latter related to the unconscious, automatic, neuropsychological processes that enabled human beings to function effectively without the employment of conscious constructivist reason (Smith 2003, 466–68).

However, Smith’s version is an adaptation: “*Ecological rationality* refers to emergent order in the form of practices, norms and rules governing action by individuals, groups and institutions that are part of our cultural and biological heritage, created by human interactions, but not by conscious human design” (Smith 2008b, 139). Emergent practices were seen as higher-order consequences of human interactions as structured by cultural and biological heritage, a form of nonconscious intelligence embodied in rules and traditions that had formed out of the “ancient history of human social interactions” (Smith 2003, 470).

Evolutionary psychologists have developed a parallel definition of ecological rationality which, while it overlaps with Smith’s definition, differs from it in some ways. Ecological rationality is defined by evolutionary psychologists as encompassing all the problem-focused

psychological mechanisms that have evolved in response to specific statistical regularities – ecological structure – that had been encountered in ancestral environments (Buss 2004, 377).

One important area where evolutionary psychology differs strongly from the assumptions of mainstream economics is sex differences. In this regard, Paul Rubin and Chris Paul have developed an evolutionary model of risk taking and risk aversion in relation to an individual’s age and sex: adolescent males are more risk seeking and mature males are more risk averse. Moreover, they posited that, in environments where only those males with incomes higher than a certain level (or with access to a certain level of resources) are attractive to females, noticeable sex differences in risk preferences would evolve (Rubin and Paul 1979). The wider consequences of this latter point are something that evolutionary psychologists understand well, but most economists do not, naively assuming that the risk profile and men and women are identical, or at least very similar.

In fact, men and women (on average across large numbers of individuals) exhibit a very different attitude to risk, one indication of this being that young men are much more likely to engage in physical altercations with each other than young women (Byrnes et al. 1999). This difference in attitude to risk has consequences for how men and women choose to make financial and investment decisions across their lives and with respect to their offspring. It also has important consequences for understanding differences in rationality in general terms when comparing men and women. If women and men have evolved (in some respects) different psychological mechanisms for responding to distinct life-tasks and social situations, then this is likely to have important consequences for the attempt to understand male and female economic behavior.

Another subfield of economics where evolutionary psychology has fruitfully been applied is the nature of money. Stephen Lea has developed an evolutionary account of purchasing and shopping behavior and also of money motivation, distinguishing between “tool theories” and “drug theories” of money. In the former, money is

understood as simply a means to an end and its value is seen as purely instrumental; in the latter, money is conceived in addition as plugging into ancient evolved motivational systems, and as being desired for more that it can deliver in purely material terms. Lea argued in turn that any “tool theory” was incomplete and had to be supplemented by a version of the “drug theory,” the ancient motivations involved being evolved psychological mechanisms relating to both reciprocal altruism and object play (Lea and Webley 2006). Following on from Lea, Vincent Barnett has suggested that money most likely first came into being as the solution to the “cheater” problem of the potential for social exchange partners involved in reciprocal altruism to defect at a future date (Barnett 2015).

One area of economic analysis is particularly well-suited for the application of concepts from evolutionary psychology: understanding the organizational structure of companies and business management systems. Various concepts developed by evolutionary psychologists such as dominance hierarchies, status striving, cooperative alliances and collective behavior, the consequences of group size, the evolution of organizational structures in prehistory, and others have been applied to assist in understanding how company organization and personnel management operate.

For example, some companies modeling their structure around the “family, village, and tribe” system of organization that operated in human hunter-gatherer prehistory have been identified (Nicholson 1998). Elsewhere, how individuals attempt to bias periodic tournaments for advancement (e.g., company promotion opportunities) in their favor so that their own power is preserved/advanced has been identified. This can be accomplished by denigrating opponents and exaggerating their own achievements for example, in contrast to what has been specified as the false theory of the prevalence of a meritocracy within business structures.

Finally, Jason Potts has developed an evolutionary theory of *homo aëconomicus* by positing that the nomadic lifestyle of our distant ancestors had important consequences for the cognitive

adaptations that evolved, in particular, the fact that resource-availability in the African savanna was only semistable over both time and space: nomadism is here defined as a behavioral strategy within a space. Potts then linked these evolved nomadic instincts with their hypothesized modern behavioral descendants such as business entrepreneurship and innovation (Potts 2003).

Social Exchange

A key concept developed by evolutionary psychologists of direct relevance to economics is that “the enduring presence of social exchange interactions among our ancestors has selected for cognitive mechanisms that are specialized for reasoning about social exchange” (Cosmides and Tooby 2005, 585). These psychological mechanisms, if they do exist, “would ground economics in the evolutionary and cognitive sciences, cross-connecting economics to the rest of the natural sciences” (Ibid.). Obviously, this is a controversial claim for economists to accept, as it would mean that their subject would have to be at least partly reconstituted, but it is certainly one worth exploring in more detail.

Deferred cases of exchange – or reciprocal altruism – take place among all human beings while they are adhering to an implicit and accepted set of rules, or an implied form of social contract, e.g., those relating to the nature of the reciprocity, to the value of the items or services being exchanged, and to cheater detection. It is this set of rules that evolutionary psychologists assert are present as specialized in-built features of the human mind. As evidence that such psychological mechanisms do actually exist, the fact that people routinely choose to cooperate with others rather than defect, sometimes even when defection gives a higher payoff, is cited, as well as empirical findings that individuals do not follow the standard precepts of rational choice theory when making related calculations (Ibid., 618). In addition, the fact that children develop social exchange abilities at an early age is also cited as evidence that this capacity is in-built.

This type of evidence, while it has very definite value, is not conclusive: it is logically possible that social exchange skills are acquired by learning at an early age, although the mechanism for this learning would need to be clearly specified. It is also possible to suggest that social exchange skills are simply one set of skills provided by a more general cognitive system. In response to the latter suggestion, the argument is made that social exchange skills are very specific and natural selection would therefore favor the evolution of a set of specialized mechanisms devoted to this task.

If human beings do possess evolved cognitive architecture for social exchange, then this could have significant consequences for many aspects of economic behavior, such as how traders make buy/sell calculations and how financial investment decisions are made. When money is being exchanged for a good or service, then the individual involved is invariably making some type of mental calculation regarding their preference for having the good or service rather than retaining the money. This calculation would necessarily employ some of the social exchange architecture hypothesized as existing by evolutionary psychologists.

For instance, the notion that the cognitive architecture of social exchange contains mechanisms for evaluating the relative worth of goods and services is an idea that is of direct relevance to economics. In hunter-gatherer societies, food items obtained by individuals were shared amongst others on a regular basis. The hypothesis is that this process, over the very long run, facilitated the evolution of psychological mechanisms for evaluating the relative value of specific items, e.g., food or other supplies. If one individual with a supply of meat gives a portion of this meat to someone else at a given point in time, then this other individual will be obligated to return the exchange at a future date.

Suppose further that at this future date the second individual reciprocates when they have a supply of fruit, but how much fruit was the meat previously received worth? There needs to be a shared method of evaluation so that the pair can agree that a fair exchange has been made. The hypothesis is that cognitive architecture would

evolve that facilitated such judgments as to what a fair exchange would be in such instances, relating perhaps to labor/time expended; or, more likely, *Homo* cognitive capacity in this regard is an evolution of previously-evolved great ape capacity, as reciprocity behavior has been detected in chimpanzees and monkeys (Cosmides and Tooby 2005, 589). This would mean that human beings have an innate sense of the relative value of certain goods and services, something that would be of definite significance for economics.

Biological Markets

For evolutionary psychologists, the gamete market for a reproductive partner is the most important market that any animal participates in, including human beings: this hypothesis is at odds with some of the central tenets of mainstream economics. Although some economists have analyzed the marriage market, the principles used to analyze this market are different from the principles used by evolutionary psychologists to analyze the gamete market. In the gamete market, there is a central asymmetry between the value of what the male animal provides (sperms) and what the female provides (ova), which has consequences for the associated behavior of the participants. Economists do not fully recognize the significance of the biology involved and the associated evolved psychology, instead emphasizing the economic gains from marriage and financial issues such as the costs of raising children.

One reason why the gamete market is central for evolutionary psychologists is that the associated psychological mechanisms that have evolved to deal with behavior related to it have significant consequences for other areas of behavior as well. In addition, the individualistic conception of personal utility maximization used by economists as a foundation for understanding behavior contradicts the evolutionary psychologist's use of inclusive fitness (or close family interest) and kinship relationships as a foundation for their analyses, the latter being linked to the gamete market. The evolutionary biologist's assertion that all animals

have both selfish and altruistic traits also contradicts the more narrow view of individual self-interest used by many economists.

The evolutionary approach can be widened to create the more general concept of “biological markets,” where animal “traders” exchange biological and other commodities (e.g., nuptial gifts, nectar) and services (e.g., alarm calls, shelter) for mutual benefit. Biological markets are characterized by competition within trader classes by contest or outbidding, preference for partner value in reproduction, conflict over the exchange value of goods as the law of supply and demand operates, and mechanisms for determining the composition of trading groups (Noe and Hammerstein 1995). Biological markets encompass mating markets (the gamete market), mutualism between members of different species, and also cooperation among conspecifics.

The “biological markets” model is in contrast with the marriage market model presented by economists such as Gary Becker, which focuses on the allocation and distribution of resources within marriage and also on chosen partner characteristics (Becker 1973). Bizarrely for evolutionary psychologists, economists do not consider the biological factors involved, assuming that both sexes behave in the same way in their mating decision-making, as if their biology was identical. The impact of sex differences on behavior is perhaps the most significant difference in the underlying assumptions of economics and evolutionary psychology: both subjects cannot be correct. The fairly well-documented case of sex differences in spatial ability – males perform better in most tasks, except for female advantage in object-location memory – is a standard example in the literature (Puts et al. 2007, 334), but the consequences of these type of differences for economic behavior have not properly been considered by economists.

Conclusion

Ever since Tarde and Veblen, economists have had an ambiguous relationship with evolutionary accounts of psychology. A good example of this

ambiguity is Hayek. Even though he explicitly undertook a detailed study of brain processes for his book *The Sensory Order* and explicitly highlighted that economic laws should be conceived at least in part in psychological terms, most of his well-known works in pure economics such as *The Pure Theory of Capital* contain hardly any consideration of psychology, let alone of evolutionary psychology. This apparent contradiction can perhaps be explained in part by the significant degree of inertia in the conventional content of economics and the difficulty in Hayek’s time of going against the grain vis-à-vis the use of a Veblen-style instinct psychology in an era of behaviorism.

A similar phenomenon can be found in the work of Henry Sidgwick, a late-nineteenth-century economist and author of *The Principles of Political Economy*. Sidgwick explicitly considered Darwin’s work and recognized the importance of instincts to understanding human behavior in an article on the theory of evolution (Sidgwick 2000 [1876], 22), but he then virtually ignored instincts and evolution across his main economic output, as if economic behavior occurred in a realm entirely divorced from evolutionary influence.

However, in the more recent period, various economists have successfully employed evolutionary accounts of psychology in their work, as have been considered above. In addition, two basic concepts of evolutionary psychology discussed here – social exchange architecture and the gamete market – are of direct relevance to developing new foundations for a subject that might tentatively be called evolutionary economic psychology (EEP). EEP would place center-stage an understanding of how economic behavior is framed both by evolved cognitive architecture and sex differences in cognition.

For example, conspicuous consumption of luxury items as a signal is, at least to a degree, interpreted differently by men and women. Women interpret the display more in terms of the indicated resource-giving potential of the man who owns the item, whereas men interpret the display more as a test of the purchasing judgment of the woman who owns the item, although both

sexes see multiple other meanings as well. As another example, it can be hypothesized that successful traders must possess sophisticated cognitive social exchange architecture, perhaps in a more developed form than is found in the average individual. This would not mean that social learning processes would have been unimportant to these successful traders, only that such learning would have been partly framed by preexisting social exchange architecture.

One final existential problem might seem to face the economist who wants to incorporate evolutionary psychology into their work. If evolutionary psychology is everything that it claims to be, such as providing the means to understand the cognitive foundations to all social exchange behavior, then why not dispense with economics entirely and become an evolutionary psychologist? One plausible answer is that economics does ask some distinct questions that differ from those of conventional evolutionary psychology, and hence it offers space to develop original contributions that might not get produced under the latter subject's standard remit. What is certain is that the crossover between economics and evolutionary psychology will continue to be fruitfully mined in the future.

Cross-References

- [Behavioral Economics](#)
- [Evolution and the Theory of Games](#)

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Ectothermic Animals

► Fish, Amphibian, and Reptile Tool Use

EDs

► Eating Disorders

Edward Hagen

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Definition

Edward Hagen is a biological anthropologist who specializes in the evolution of depression, self-harm, psychoactive drug use, among other topics.

Introduction

Edward Hagen is a Professor of Anthropology at Washington State University where he has taught since 2007. He received his Ph.D. in Anthropology from UC Santa Barbara in 1999 under the supervision of John Tooby and took a postdoc in

Peter Hammerstein's group at the Institute for Theoretical Biology, Humboldt University, Berlin, from 2001 to 2007. Hagen has published on numerous topics in evolutionary psychological theory, but his work predominately centers on evolutionary approaches to noninfectious disease, particularly mental health. He is best known for his evolutionary theoretical research on depression and psychoactive drug use. His publications defending the field of evolutionary psychology against its critics are also widely cited.

The Bargaining Model of Depression, Self-Harm, and Suicidal Behavior

Most major depressions are caused by adversity, but most people who experience adversity suffer sadness, grief, or other negative emotions, but not major depression. Major depression is nevertheless common in adults of all ages. Hagen has developed theoretical models rooted in costly signaling theory in an attempt to explain the function of major depression (Hagen 1999, 2002, 2003) as well as nonlethal suicidal behavior and self-harm in an evolutionary framework (Hagen et al. 2008; Syme et al. 2016).

In many cases, individuals can adequately respond to adversity with little help from others. In other cases, however, individuals need help, yet, due to *conflicts of interest*, help might not always be forthcoming. Informed by game theoretic models, Hagen posited that both depression and suicidal behaviors could effectively serve as bargaining strategies that function to elicit support from social partners (e.g., genetic kin or a mate) who are reluctant to provide it. According to these models, the symptoms of depression and/or self-harm reduce or eliminate an individual's investment in joint cooperative endeavors that benefit her social partners as a strategy to compel them to provide her with more help. In other words, the behavioral correlates of depression and suicidality are evolved mechanisms that function to protest exploitation.

Hagen first outlined the bargaining model of depression in the context of postpartum depression (PPD), which serves as a case for the model

more generally. The bargaining model of PPD proposes that depression during this vulnerable period might be an adaptation that arises when a new mother is suffering a fitness cost (Hagen 1999, 2002). Low mood, anhedonia, and psychomotor retardation, among other symptoms in effect, function to reduce or eliminate the mother's investment in her infant such that social others who might share a concern for the infant (e.g., the father, mother's kin) would have to increase their share of investment in correspondence to their stake in the infant's survival. This theory accounts for the major risk factors of PPD, namely, marital discord; a lack of social support, particularly from the father; and poor infant health (see Hagen 1999 for an exhaustive list of sources). For most of human evolution, these conditions would have severely impeded the fitness of the mother and her infant. If the mother does not receive the support she needs, then she might eliminate investment entirely resulting in infant death at which point she can redirect investment toward mating and future offspring.

More broadly, depression is a bargaining strategy that emerges when cooperation imposes a net cost, but constraints make defection impossible. For instance, social partners might monopolize a resource (e.g., a mating opportunity). The depressed individual goes "on strike" by withholding their investment in the cooperative enterprise. Furthermore, the depressed individual sends a costly signal that informs the social partner of their true valuation of the endeavor, which is low due to the fact that he or she is not receiving their fair share of the benefits (Hagen 2002).

Hagen and Rosenstrom (2016) developed the unified bargaining model of depression and aggression. They argue that when social partners are imposing high fitness costs for little reward, those who are physically strong will be more aggressive – a confrontational strategy – to negotiate, while those who are physically weak will be more depressive, a withdrawing strategy. Since almost all males are more physically formidable than almost all females, this model might help explain the sex difference in depression, and Hagen and Rosenstrom found evidence to support this hypothesis.

Hagen applied the bargaining model to self-harm and suicidal behavior (Hagen et al. 2008; Syme et al. 2016). As with the bargaining model of depression, according to Hagen, self-inflicted harm could act as a means of signaling social need. The goal of some suicidal behavior, according to this model, is not death, but rather this behavior represents a last resort to elicit aid in otherwise hopeless situations. The bargaining model of suicidal behavior was supported in a test of two evolutionary models of lethal and nonlethal suicidal behavior against 53 cultures in the ethnographic record. The study found that across cultures suicidal behavior frequently occurred in response to social conflicts that posed a fitness threat to the victim (e.g., forced marriage); the victim was often powerless relative to those whom they were in conflict with; and, a victim who survived a suicide attempt could influence others to act in accordance with his or her valid interests (e.g., preventing a forced marriage) (Syme et al. 2016).

Research on Psychoactive Drug Use

In a series of papers, Hagen and colleagues investigated tobacco and cannabis use among Aka foragers in the Congo Basin (Roulette et al. 2014, 2016a, b). In a 2014 paper, the researchers reported the results of a test of a novel evolutionary hypothesis that recreational use of tobacco can defend human hosts against parasitic infection. The researchers write, "Plants have evolved an enormous variety of toxins to deter herbivores, and herbivores have co-evolved to use plant toxins to defend against their own parasites, a phenomenon referred to as self-medication, zoopharmacognosy, or pharmacophagy" (Roulette et al. 2014). Hagen and colleagues argue not that humans evolved to consume tobacco or any other specific plant toxin, but instead that humans, like other vertebrates, evolved mechanisms for regulating the consumption of psychoactive plant toxins (Hagen et al. 2009, 2013; Sullivan et al. 2008). The researchers found evidence to support the hypothesis that tobacco is protective against helminthic infection. Among the 260 Aka males

in the sample, there was a negative correlation between cotinine, a nicotine metabolite, as measured in saliva and worm burden as measured in stool samples. Moreover, they found that treating helminthes with a commercial anthelmintic reduced cotinine concentration 2 weeks following administration compared to controls, suggesting that tobacco use covaries with the degree of worm burden. These findings among others support the hypothesis that humans use tobacco as well as other psychoactive plant toxins to defend against parasitic infection. In a separate study, Hagen and colleagues found a negative correlation between THC levels and parasitic infection among the Aka (Roulette et al. 2016b).

Hagen and colleagues have also investigated sex differences in drug use (Roulette et al. 2016a; Hagen et al. 2016). Globally, females use drugs recreationally less often than males, which many have attributed to gender inequality. Hagen et al. (2016) found that cross-nationally women's total fertility rate and measures of gender inequality are independently associated with female tobacco smoking prevalence. Throughout most of human evolution and in modern natural fertility populations, females spend most of their reproductive years pregnant or lactating. Thus, fetal protection is a likely source of women's lower drug use prevalence. This evidences differential benefits in the use of plant neurotoxins for the purposes of pharmacophagy.

Defense of Evolutionary Psychology

Hagen is an adamant defender of evolutionary psychology (EP) against critics who attack the field on political and philosophical grounds (Hagen 2005, 2014). He eschews the pervasive delusion among the critics of EP that humans will be moral and selfless if we imagine them to be that way in favor of a more realistic view of human nature based on evidence and facts. To summarize Hagen's standpoint, the most pragmatic means of limiting behaviors such as infanticide, exploitation, sexual assault, suicide, and other harmful acts is to identify the human propensity toward these behaviors and the environmental

circumstances that are most likely to trigger them (Hagen 2005). Since the laws of the physical world govern the mind, pretending otherwise could never produce real social change.

Other Research

Hagen in conjunction with colleagues has published on a wide array of topics in evolutionary psychology including pregnancy cravings and aversions (Placek and Hagen 2013, 2015, Placek et al. 2017), indirect aggression and informational warfare (Hess and Hagen 2006; Hess et al. 2010), parental investment (Hagen et al. 2001; Hagen et al. 2006), game theory (Hagen and Hammerstein 2006), and music and dance as coalitional signaling (Hagen and Bryant 2003; Hagen and Hammerstein 2009).

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Effect of Birth Control on Women's Preferences

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Synonyms

[Contraceptive pill](#); [Hormonal contraception](#); [Oral contraception](#)

Definition

Birth control relates to any method of preventing conception while engaging in sexual intercourse. This can include avoiding intercourse while the woman is fertile (e.g., rhythm method), pre-ejaculatory withdrawal, and barrier methods (e.g., condom, uterine cap) which prevent sperm from reaching the egg. So far as we know, choice of these methods has no effect on women's mate preference. This entry is instead concerned with modern hormonal methods of birth control (especially the oral contraceptive pill) which achieve contraceptive function by manipulating women's reproductive physiology and function.

Introduction

Birth control (BC) is one of the most successful and widely used of all medical interventions. More than one-fifth of women of reproductive age (15–49) and in a relationship use the “pill”, injectable or implant BC methods across the world, and these rates are typically even higher among younger and unmarried women (United Nations 2015). BC has undoubtedly improved women's quality of life, giving women control over their reproductive lives and enabling them to postpone childbearing and pursue other important goals. Nonetheless, given the prevalence of use in younger women, at a life stage where most are seeking to establish life-long partnerships and begin families, any unintended effect on the success of those family units warrants rigorous attention. There is accumulating evidence that use of BC may indeed have just such effects, by exerting subtle changes in mate preferences.

Hormonal Contraceptives and Women's Mate Preferences

Some previous studies suggest that women's preferences for male traits exhibit an increased periovulatory preference for traits that appear to signal high mate quality (e.g., Roberts and Little 2008). It is argued that stronger preference for such traits as facial masculinity when conception probability is high suggests a mechanism by which women maximize quality of mating partners (Penton-Voak et al. 1999). If these cyclic shifts are shaped by changing hormonal levels associated with ovulation, then they should be absent in BC users.

Consistent with this suggestion, Little et al. (2002) showed that a stronger preference for facial masculinity in attractiveness judgments for short-term than long-term partners, which was present in normally cycling women at ovulation, was absent in women using BC. Another study showed that users of BC have weaker changes in masculinity preferences for both faces and voices (Feinberg et al. 2008). Similarly, while normally cycling women show increased ovulatory

preference for the odors of symmetrical over asymmetrical men, this preference is absent in BC users (Thornhill and Gangestad 1999). These studies indicate that BC use is associated with reduced demand for male characteristics that ovulating women typically display.

Other studies show that BC users have qualitatively different preferences compared with non-users. For example, they appear to have stronger preferences for health, which is also characteristic of women with high progesterone levels, such as during the luteal phase of the menstrual cycle or in pregnancy (Jones et al. 2005). Furthermore, in contrast to normally cycling women who were more attracted to odors of men who are genetically dissimilar at genes in the major histocompatibility complex (MHC), BC users display the opposite trend, preferring odors of more MHC-similar men (Wedekind et al. 1995). Among vertebrates, preferences for MHC-dissimilarity are thought to be usually favored because this may increase offspring heterozygosity and in turn to enhance the ability to fight infectious diseases.

Although such studies indicate that BC may influence women's mate preferences, it might be argued that differences between users and non-users are simply a product of between-group behavioral or attitudinal characteristics, rather than a direct consequence of BC use. To address such concerns, Roberts et al. (2008) used a longitudinal design to compare odor preferences for MHC-similar/dissimilar men before, and 3 months after, initiating BC use. Consistent with a direct BC effect, women's preferences shifted after initiating BC towards MHC-similar odors, compared with a nonuser control group tested across the same 3-month interval. This study provided the first direct evidence of a causal link between BC use and disruption of partner preferences.

One other study has demonstrated a similar effect. From a sample of the same women tested in Roberts et al.'s (2008) study, preferences for facial masculinity were also tested using the same design. Whereas there was little change in the control group, women's preference for masculinity was reduced after initiating BC use, and this effect was observed in male but not female faces, suggesting a mate choice-specific effect rather

than one that affects general face perception (Little et al. 2013). Not only this, but in a separate sample, it was found that, in women who used BC when the couple met, the male partners had more masculine faces compared with partners of women who were not using BC when the couple met (Little et al. 2013). Although this latter result could be due to between-group differences, it raises the possibility that changes in mate preferences could have real-life effects on actual mate choice.

Implications of Altered Mate Preferences

The clearest implications of altered mate preference choice due BC come from the studies on MHC-correlated mate preferences. If preferences of nonusers are typically for MHC-dissimilar partners but BC use brings about a preference for MHC-similarity (Roberts et al. 2008), then we might expect couples who meet while the woman is using BC to be comparatively MHC-similar. One possible consequence of this would be direct health consequences for any offspring due to their lower heterozygosity. Such consequences could include higher rates of miscarriage (Beydoun and Saftlas 2005) and lower resistance to infectious diseases in offspring (Carrington et al. 1999). Furthermore, reduced heterozygosity and hence perceived poorer health may additionally influence the perceived attractiveness of offspring (Roberts et al. 2005).

It is also likely that alteration of mate preference, for any given preferred trait, will directly influence a woman's attraction towards her partner when she changes BC use. Imagine, for example, a woman who is using BC when she meets her partner, and presumably finds him very attractive. If she ceases BC use, then both her hormonal levels and her preferences will revert to their normally cycling states, and she may subsequently no longer find her partner as attractive as she did. Alternatively, if the same woman began BC use *after* meeting her partner, she might experience the reverse pattern of changes, but ultimately with the same kind of outcome: a preference *now* that is different (or noncongruent) to what it *was* when

she met her partner. Both these examples have been captured in what has been termed the *congruency hypothesis* for BC effects on women's sexual desire for, and satisfaction with, their partner (Roberts et al. 2013).

The first evidence for the congruency hypothesis comes from a comparison of approximately 2500 women who were BC users or nonusers when they met their male partner, but who were all nonusers when they were surveyed. Although women who were using BC when they began their relationship were more satisfied with their partner's level of support, they reported lower attraction towards him and lower sexual satisfaction with him (Roberts et al. 2012). In another sample of about 350 couples, women's sexual satisfaction was higher if their current BC use was congruent with that at the time they met their partner, compared to noncongruent women, although BC congruency did not affect levels of nonsexual satisfaction (for a replication, see Russell et al. 2014), nor either kind of satisfaction among the male partners (Roberts et al. 2014). Similarly, levels of sexual but not other kinds of jealousy were higher in women if their current and previous use of BC was congruent (Cobey et al. 2013). Other studies that simply compare BC users and nonusers report comparable differences in not just sexual jealousy (Cobey et al. 2011) but also other related aspects of mate-guarding behavior (Welling et al. 2012). Ultimately, such sexual dissatisfaction and mistrust may have consequences on relationship survival; indeed, Roberts et al. (2012) found that in couples who had subsequently separated, women who more likely to have initiated the separation if they met their partner while using BC.

Conclusion

There is growing evidence that use of hormonal contraceptives influences women's mate preferences and has consequences on subsequent relationship satisfaction. Cross-sectional studies may be strongly influenced by between-group differences, and more longitudinal studies are needed in the future.

Cross-References

- [Attraction During Ovulation](#)
- [Dual-Mating Hypothesis](#)
- [Male Perception of Cycle-Related Fluctuations in Women's Attractiveness](#)
- [Menstrual Cycle](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Sexual Signaling During Ovulation](#)
- [Women's Preferences During Ovulation](#)

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Effect of Status on Social Reasoning (Cummins 1998)

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Synonyms

[Domain-specific reasoning about dominance hierarchies](#)

Definition

The effect of social hierarchy and status position on the evolution and implementation of social reasoning abilities.

Introduction

Sociality, the formation of social groups by a species, is often seen as an evolved solution to some of life's most basic problems, such as how to obtain food, how to successfully reproduce and care for young, and how to avoid predation long enough for these prior concerns to be issues at all. While helping to solve many of these problems, sociality also presents a unique challenge: how are limited resources, such as food, to be distributed among group members? In response, many social species, including humans, developed social hierarchies wherein higher-status individuals typically have priority access to resources. Therefore, while sociality and social hierarchy helped solve some evolutionary problems, they themselves produced unique evolutionary pressures. In this context, Cummins (1998) hypothesized that key components of reasoning developed in response to the demands of competing and cooperating within social groups and social hierarchies. More precisely, she argued that domain-specific reasoning capacities (e.g., cheater detection) evolved to recognize and respond to the social rules concerning necessary (obligatory or prohibited) and permissible behaviors found in social hierarchies. Evolutionary, behavioral, and neuroimaging evidence in support of these claims is reviewed as well as investigations and literature suggesting the need for further research.

Hierarchies, Evolution, and Social Reasoning

Put simply, a social hierarchy means that in social groups certain individuals maintain regular and priority access to key resources, such as food and mates (Cummins 2006). In turn, these high-

status individuals are more likely to survive and are more likely to have offspring (Ellis 1995). Importantly, in many species, most notably primates, social hierarchy is not stable, nor is it simply a matter of pure physical dominance (i.e., physical size or strength) (Harcourt and de Waal 1992). In this context, survival and reproductive success depends on the amount of time one is able to spend in positions of relatively higher status, which in turn depends on a number of nonphysical factors (Altman et al. 1996). In this regard, it is likely that natural selection would favor psychological and neurological mechanisms to effectively navigate status hierarchies. Evidence in primates suggests that key among these mechanisms are a collection of social reasoning abilities, including the capacity (i) to learn the rules around necessary (obligatory or prohibited) and permissible behaviors, (ii) to detect and remember those who violate these rules (cheaters), (iii) to form and monitor reciprocal relationships (cooperation and reciprocity), and (iv) to read and understand the intentions of others (theory of mind) (for a review see Cummins 2000). In other words, the better you are at these abilities, the more likely you are to successfully navigate the social hierarchy, achieve and maintain high-status, and thus survive and reproduce. In this way, sociality and status hierarchies are seen to provide evolutionary pressures and context for the development of foundational social reasoning capacities in many social species.

Hierarchies and Social Reasoning in Humans

Far from being a primitive feature of nonhuman social species, social status and hierarchy appear to be universal across human cultures (Brown 1991). Indeed, while the signs and impact of status and hierarchy are easily identified in many cultures (e.g., income inequality, caste systems), hierarchy and status also appear to be among the first and most stable characteristics seen in human peer groups (Strayer and Trudel 1984). For example, the development and recognition of status hierarchies are found in children as young as two

and continue to play a major role in social structure throughout the life-span (Frankel and Arbel 1980). Moreover, the ability to understand and report on the structure of a social hierarchy appears to develop in children well before the ability to describe similarly complex content in nonsocial domains (Smith 1988). This developmental trajectory may suggest that humans are predisposed to attend to and develop social skills in reference to social hierarchies. This sensitivity to social status is even found at the neuroendocrine (e.g., cortisol, adrenalin, testosterone) and physiological levels (e.g., heart rate, blood pressure; Knight and Mehta 2014). For example, when allowed to retaliate against an aggressor of lower status, heart rate, blood pressure, and cortisol indices, initially elevated by the frustration of the situation, return to baseline levels. In contrast, if the aggressor is a higher-status individual, these stress indices remain at their original, frustration-induced, levels (Hokanson and Shetler 1961). In other words, social hierarchy appears to be an integral part of human societal structure, developing early and impacting not only our cognition but our physiology as well.

While humans and nonhuman primates differ in many regards, it is clear that human social structures were, and are, subject to many of the same hierarchy pressures seen in nonhuman primates. In this context, it is unsurprising that many of the same social reasoning abilities used by primates to successfully navigate hierarchical social structures are seen, and expanded upon, in humans. Indeed, decades of research demonstrates that, just like nonhuman primates, human's success at navigating social structures depends on the capacity (i) to learn the rules around necessary (obligatory or prohibited) and permissible behaviors, (ii) to detect and remember those who violate these rules (cheaters), (iii) to form and monitor reciprocal relationships (cooperation and reciprocity), and (iv) to read and understand the intentions of others (theory of mind) (see Cummins 2000 for review). While each of these skillsets is seen as important, much research has focused on people's ability to (i) learn social rules and (ii) detect cheaters, as these skills are not only seen as foundational for more advanced social

reasoning skills (e.g., reciprocity, and theory of mind) but also appear to be intimately linked to one another.

In countless studies across numerous disciplines, researchers have consistently demonstrated that humans appear to be more effective at reasoning in some domains than others, with one of the largest and most well-established differences being seen in social reasoning. Most often this difference is studied in regard to the deontic-indicative distinction. Deontic reasoning is concerned with social rules or what is permitted, obligated, and forbidden. When engaged in deontic reasoning, individuals appear to spontaneously look for and identify violations of these social rules. Importantly, in both functional and cognitive terms, social hierarchies can be conceptualized as a collection of specific social rules imposed on lower-status individuals by those of higher status. In this way, deontic reasoning is directly tied to many of the social constraints (rules) seen in social hierarchies. Indicative reasoning, in contrast, is concerned with what is true or false and triggers a confirmation-seeking strategy. Importantly, although indicative reasoning can be related to social content, it is not related to social rules. Notably, humans consistently perform significantly better on deontic tasks (60–90% correct on deontic tasks vs 10–30% correct on indicative versions of the same tasks; Cummins 2000). In other words, people perform consistently and systematically better on social reasoning tasks when they entail social rules concerning what is permitted, obligated, or forbidden. While abundantly clear in adulthood, this difference also appears to be present in early development. For example, by age 3, children appear to preferentially check for and determine whether a social rule has been violated and are able give specific reasons why a behavior represents a rule violation (Cummins 1996; Harris and Nuñez 1996). Importantly, mirroring what is seen in adults, this skill does not appear to transfer to nonsocial problems of similar complexity. This advantage for social rule-based reasoning is seen at even younger ages as well. At 16 months, children are already preferentially noticing and attending to violations of social rules (Cummins

1999a), and by 24 months, they use social rules to justify their behavior (Dunn 1988). Overall, these results seem to indicate that humans are uniquely skilled at social rule-based reasoning, that this advantage develops early, and that it continues to impact reasoning throughout the life-span.

Importantly, the broader literature on this social reasoning advantage, and more specifically the deontic effect, is not without controversy (see Cummins 2000 for a brief review). Indeed, over the years, numerous theories have been developed to explain the deontic effect, with some arguing in-line with the domain-specific process already introduced, while others advocate a more domain-general approach. For example, some argue that the deontic effect is simply due to familiarity with social content rather than any unique or evolved advantage for social reasoning. Despite decades of inquiry, consensus around the best-fitting theory is still lacking.

Regardless of this debate, a crucial component seen in the potential social reasoning advantage is the tendency to spontaneously check for rule violations when considering social rules. While violation-detection is equally appropriate of other types of reasoning, such as evaluating whether a statement is true, it appears to be rarely used outside of situations focused on social rules. In this regard, detecting and remembering those who (intentionally) violate rules, cheaters, is seen as a crucial component to forming and enforcing the rules necessary for even a basic level of sociality. While cheater detection is obviously important for social rules in general, this bias may be particularly important in reference to status hierarchies. Specifically, in order to maintain priority access to resources, high-status individuals often need to maintain the status quo, which entails checking for, remembering, and penalizing cheaters. While there is a wealth of examples to support the impact of status on cheater detection in nonhuman primates, evidence is currently equivocal in humans. Specifically, while there is some evidence to suggest that individuals are more likely to check for and remember cheaters of relatively lower status (Cummins 1999b; Mealey et al. 1996), more recent studies have failed to replicate these results (Barclay and Lalumière

2006; Mehl and Buchner 2008; Buchner et al. 2009). In this regard, two aspects are important to note. First, in all of these studies, status was manipulated in a relatively narrow fashion focused on occupation or income. In contrast to this, literature and research on social status in humans indicate that an individual position in the social hierarchy is determined by a variety of connected, yet independent, constructs, such as power, socioeconomic status, dominance, prestige, influence, and leadership (Blader and Chen 2014). Further complicating this picture, while social status is often discussed as a dispositional attribute, it is also highly situational, such that an individual may be of high status in one environment (e.g., friend group or family) but low status in another (e.g., occupation). Second, numerous studies indicate that cheater detection is influenced by a host of individual and situational variables, such as subjective importance of detecting cheaters (Chiappe et al. 2004) and the relative number of cheaters (Barclay 2008), meaning that cheater detection is not a static phenomenon. Thus, more research is needed to untangle the potential impact of status on cheater detection in humans, with a special focus on the numerous ways human status can be determined and conceptualized.

Evolution of a Neural Architecture for Social Reasoning

A key concept in Cummins proposal is that evolutionary pressures not only helped to shape key aspects of social reasoning but that a similar and mirrored development occurred in neuroanatomy. In her original manuscript, four points were addressed to support this idea. First, the development and role of the neocortex compared to the evolutionarily older structures found in the limbic system. In general, the limbic system is responsible for relatively basic socio-emotional functions, such sexual behavior, aggression, and emotion. In contrast, the neocortex, is responsible for higher-level cognitive and social functions, such as thought and language. The variation in function and the later development of the neocortex are seen as evidence that higher-level social functions

evolved in a commensurate fashion with specific and evolutionarily newer neural architectures.

Second, prefrontal lobe syndrome in humans and bilateral prefrontal ablations in primates suggest that there are specific neural substrates responsible for crucial components of social reasoning. In prefrontal lobe syndrome, bilateral damage to the ventromedial prefrontal cortex produces impairment in socio-emotional stimuli, typically without producing similar impairments in broader intellectual functioning (Damasio 1994). In primates, bilateral prefrontal ablations of the ventromedial or dorsolateral prefrontal cortices result in similarly dramatic changes in social functioning, with these changes not typically seen from damage to other cortical areas (Cummins 1998).

Third, autism, a neurodevelopmental disorder, is characterized by selective impairment in the social domain. Specifically, individuals with autism find it difficult or impossible to reason, especially automatically, about the mental states or beliefs of other individuals, which makes it exceedingly difficult for them to engage in cooperative or reciprocal social interactions (Baron-Cohen 1995). Despite this, however, individuals with autism typically do not display impairments in other nonsocial domains of cognitive functioning. Mirroring prefrontal lobe syndrome and the bilateral prefrontal ablations, this selective impairment of social reasoning suggests a unique and separable neural architecture for social reasoning.

Lastly, in primates, the neocortex ratio, the relative volume of the neocortex to the rest of the brain, correlates positively with social group size (Dunbar 1993). This suggests that larger groups, and thus more complex forms of sociality (due to the increased number of relationships), require greater cognitive resources. Moreover, given the evolutionary trajectory of the neocortex, this suggests that more complex forms of sociality developed alongside the necessary neural architecture (i.e., larger neocortex).

More recent advances in neuroimaging also appear to detail a neural architecture adapted for social reasoning (Barbey et al. 2009). Indeed, converging results from numerous studies suggest that the lateral prefrontal cortex enables the representation of evolutionarily adaptive social rules,

with each of its three major subsections supporting particular types of reasoning necessary for various degrees of sociality. Specifically, the ventrolateral prefrontal cortex is tied to reasoning about necessary actions (rules about obligatory or prohibited behavior), the dorsolateral prefrontal cortex is involved in reasoning about possible (permissible) actions, and the anterolateral prefrontal cortex is recruited for higher-order reasoning that incorporates both necessary and possible actions. Importantly, research also demonstrates that the lateral prefrontal cortex initially evolved from the ventrolateral prefrontal cortex, followed by the dorsolateral and then the anterolateral regions. Given the functional significance of each area, this developmental trajectory makes evolutionary sense. The foundation for basic sociality is being able to create, understand, and enforce necessary (obligatory and prohibited) social rules, which are instantiated in the ventrolateral prefrontal cortex, which evolved first. Following this, social rules around permissible behaviors enable a greater range in possible behaviors and thus more complex social relationships. Mirroring this trajectory, these abilities are found in the dorsolateral prefrontal cortex, which developed second, after the ventrolateral regions. Finally, representing and reflecting on rules governing both necessary and permissible behaviors foster even more complex social relationships, with these abilities being facilitated by the dorsolateral prefrontal cortex, which developed last. Thus, current data suggests that social reasoning around rules may have evolved in a commensurate fashion with specific neural architectures supporting particular abilities.

Recent data also suggests that social status may play an important role in the development and function of this architecture. In a hierarchy, rules created and enforced by members of a higher social status represent necessary rules that an individual of lower rank must follow. Given this it is not surprising that areas for identifying others' social status are anatomically connected to ventrolateral prefrontal regions, which are crucial for reasoning about necessary rules. This link between status and necessary rules was supported by a recent study by Marsh et al. (2009), which

demonstrated selective recruitment of the ventrolateral prefrontal cortex when processing status poses for high-status individuals. Future studies leveraging various conceptualizations of human status hierarchies could provide further clarity about the role of social status on the development and function of social reasoning neural architecture.

Importantly, however, it must be noted that advances in neuroimaging also demonstrate that social reasoning and status hierarchies are not exclusively dependent on areas in the lateral prefrontal cortex. Indeed, countless studies have implicated a host of diverse areas in social reasoning and social hierarchy, including the parahippocampal cortex, the ventral striatum, the sensorimotor cortex, the supplementary motor area, the amygdala, the anterior insula, the anterior cingulate, the inferior parietal lobe, and the inferior parietal sulcus (Pornpattananangkul et al. 2014). Moreover, the lateral prefrontal cortex and its subsections are not solely implicated in reasoning about social concepts. For example, the ventrolateral prefrontal cortex is implicated in motor activity, such as walking, as well as the ability to detect and retain spatial information from visual cues. Thus, while there is strong evidence to suggest a neural architecture for social reasoning, it remains unclear whether this network was evolutionarily adapted specifically and uniquely for reasoning about social content such as status hierarchies and cheating.

Conclusion

Evidence to date provides equivocal support for much of Cummins' (1998) hypothesis that key components of reasoning developed in response to the demands of competing and cooperating within social groups and social hierarchies. While there are certainly results and data from evolutionary, behavioral, and neuroimaging contexts supporting key aspects of this hypothesis, questions remain. Indeed, there are inconsistencies in and failures to replicate key results, an important debate around the interpretation of the deontic effect, and a need for more nuanced and

detailed investigation into the neural architectures supporting social reasoning. Future research can provide clarity in many of these areas through continued replication attempts, acknowledgement and investigation into the numerous ways social status is determined in human hierarchies, and continued consideration of competing theories.

Cross-References

- ▶ [Domain-Specific Reasoning About Dominance Hierarchies](#)
- ▶ [Dominance Hierarchies](#)
- ▶ [Dominance in Humans](#)
- ▶ [Emergence of Deontic Reasoning](#)
- ▶ [Emergence of Indicative Reasoning](#)
- ▶ [Emergence of Social Reasoning About Hierarchies](#)
- ▶ [Rule Violations Checked If High Status](#)
- ▶ [Rule Violations Not Checked if Low Status](#)
- ▶ [Social Learning and Social Cognition](#)
- ▶ [Status and Dominance Hierarchies](#)
- ▶ [Status and Redistribution of Resources](#)
- ▶ [Status Competition](#)
- ▶ [Status Competition and Peer Relationships in Childhood](#)

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Effect on Attachment

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Synonyms

Attachment opportunity; Attachment security;
Caregiving; Quality of attachment

Definition

Attachment is the strong, affectionate bond we feel for individuals who provide pleasure when we interact with them and comfort by their proximity when under stress.

Introduction

Attachment is something that many creatures develop with those that provide care for them. Typically, infants form attachments by the second half of their first year of life. Infants will form an

attachment to individuals that respond to their needs. These needs can be items such as food and shelter, or they can be more emotional as in providing comfort when we are in a stressful situation. While most infants will form an attachment with their parents, this may not always be the case.

Attachment Based on Food or Touch

It was thought by behaviorists that a mother would satisfy an infant's hunger, which was a primary drive, and this is what leads to attachment. Because of this feeding, the infant would prefer the comfort and closeness of their particular caregiver. Harlow and Zimmerman (1959) put this idea to the test. They provided baby monkeys with surrogate mothers, one made of wire that provided the baby monkey with food and the other wrapped in terry cloth. What they found was that even though the wire mother provided food, the baby monkeys preferred to cling to the terry cloth mother. This shows that just because one provides food, the tactile sense of touch is extremely important when forming an attachment.

Styles of Attachment

Mary Ainsworth and her colleagues (1978) were pioneers in the domain of attachment styles. They created the strange situation so that they could objectively observe the infant-parent attachment style. In the strange situation, infants are allowed to play in a room while the caregiver is present. A stranger would enter the room and the caregiver would exit the room. They monitored the stranger attempting to comfort the infant as well as the interaction of the infant with the caregiver once they returned to the room. Ainsworth and colleagues found a few different styles of attachment. The most common was called secure attachment. In this style of attachment, infants used the caregiver as a secure base and explore the area. When the caregiver left the room, the infant became visibly upset. The stranger was unable to calm the infant; however, when the caregiver returned, the infant would actively seek them out and crying

was reduced quickly. The infants were upset because the caregiver was absent and preferred them to the stranger. The next attachment style found was avoidant attachment. Infants with this attachment style were not very responsive to the parent, while they were present and not usually distressed when the parent left, reacted to the stranger in a similar fashion as they did to the parent, and were slow to greet the parent when they returned. When the parent would pick them up, oftentimes they would fail to cling to the parent. The third attachment style is known as resistant attachment. These infants sought closeness with the parent and would not explore the area. When the parent left, they would become visibly distressed. When the parent returned, they would blend clinginess and resistive behavior. Infants appeared to be angry with the parent as they would often hit or push away from them when picked up. Also of note, these infants were not easily calmed as they would continue to cry even though the parent had returned. The fourth and final attachment style found is disorganized attachment. Infants in this attachment style showed a multitude of confused and contradictory behaviors when the caregiver returned to the room. Infants would sometimes look away while being held and show their disorientation with a dazed facial expression, and a few would begin to cry without warning after they had been calmed. These four styles of attachment were major discoveries and have helped shape the way we view infant-parent interactions.

Effects of Opportunities for Attachment

René Spitz (1945; Spitz and Wolf 1946) observed what happened to infants when they did not have an opportunity to produce a close bond with a caregiver. He observed infants that were given up by their mothers and institutionalized. These infants shared a nurse with at least seven other babies, and their pre-separation happy demeanors turned into more withdrawn demeanors after separation. When a consistent caregiver did not replace the mother, the infants lost weight and had difficulty sleeping. Tizard and Rees (1975) followed adopted children who were placed in homes after

the age of 4. They found that many of these children were able to form their first attachment as late as the ages of 4 to 6 years. However, these children did tend to display social and emotional problems. Some children excessively sought out adult attention, while others would become overly friendly toward unfamiliar adults and peers.

Conclusion

From previous research it is easy to see that forming an early attachment is extremely important for humans. Daycare may be easy for parents, but it could prove to be harmful for kids if there is a large ratio of children to those taking care of them. The children could become more depressed and withdrawn or start aggressively seeking adult attention. Some parents may feel that they have no choice in the matter and are obligated to go back to work. It is possible that these children could form more of an attachment with the individual taking care of them at daycare than with their parent. It does appear that as long as the parent creates sufficient comforting, physical contact, they can form an attachment with the child. The main cause for concern is to make sure that the child has an opportunity to form an attachment, either with their primary caregiver or have a consistent alternative.

Cross-References

- [Parent influences](#)
- [Peer socialization](#)
- [Personality development](#)
- [Social development](#)

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Effective Breeding Populations

- [Mating Systems](#)

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Effects of Attachment Quality and Organization

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Definition

John Bowlby argued that attachment, beyond the main biological function of increasing infants' chances of survival, is important for psychological development. A robust association has subsequently been established between children's attachment quality/organization and psychological development, particularly as regards socio-emotional functioning (e.g., internalizing and externalizing behavior problems, social competence), with secure attachment linked to favorable development and insecure attachment to increased risk for suboptimal development. Important research questions pertain to the factors that mediate (e.g., internal working models, emotion regulation, executive

functioning) and moderate (e.g., attachment quality to other adults, child temperament, factors related to social context) the relation between attachment quality and subsequent development. Another question is whether variations in attachment quality are specifically important for particular aspects of development or constituting a protective vs. risk factor in general. Yet another one is to what extent, and for which developmental outcomes, variations in children's attachment quality contribute to developmental outcomes when other aspects of caregiving that may covary with caregiver sensitivity are taken into account.

Introduction

John Bowlby, the founder of attachment theory (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), contested the theories of attachment available at the time since they defined attachment was secondary to other processes (e.g., “drives” and feeding, see ► [“Psychodynamic Foundations”](#)). Bowlby therefore devoted a great effort into finding an alternative and scientifically sound explanation for attachment, and he eventually formulated the core tenets of attachment theory by drawing from multiple scientific disciplines, including ethology, cybernetics, and cognitive psychology (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). This work includes the conceptualization of the attachment system as a behavioral control system with a specific function of continuously monitoring and maintaining proximity to caregivers, retained through evolution as it served an adaptive function of increasing chances of survival against predators and other natural dangers (see ► [“Infant Survival”](#) and ► [“Offspring–Parent Attachment”](#)).

Bowlby was also convinced that children develop individual variations in attachment quality, depending on how consistently available the caregiver(s) have been and how effectively the caregiver(s) have responded to the children's signals (i.e., caregiver sensitivity). He was moreover convinced, in line with psychodynamic object

relation theories (see ► [“Psychodynamic Foundations”](#)), that children's attachment quality is important for subsequent psychological development and mental health; “what is believed to be essential for mental health is that the infant and young child should experience a warm, intimate and continuous relationship with his mother (or permanent mother-substitute) in which both find satisfaction and enjoyment” (Bowlby 1997, 1982, p. xi–xii).

However, Bowlby lacked an empirical method for examining individual variations in attachment quality and could therefore neither “systematize” these differences nor conduct detailed mapping of relations to personality development. He instead examined effects of child-caregiver separations, which he regarded as a possible pathogen for children's personality development (i.e., a form of trauma) and which were readily observable in the post-World War era, and, for example, found that delinquent and aggressive children had experienced more frequent early separations from their caregivers (Bowlby 1944). In explaining such findings, Bowlby argued that “the young child's hunger for his mother's love and presence is as great as his hunger for food, and in consequence, her absence inevitably generates a powerful sense of loss and anger. . . loss of mother-figure, either by itself or in combination with other variables yet to be identified, is capable of generating responses that are of the greatest interest to psychopathology.” (Bowlby 1997, 1982, p. xiii).

Bowlby was therefore grateful to his close collaborator Mary Ainsworth who, by conducting extensive naturalistic observations of children's attachment development and developing a laboratory observation procedure for examining individual differences in attachment quality (the strange situation procedure (SSP)), discovered three organized patterns of attachment together with relational antecedents (Ainsworth et al. 1978; see ► [“Individual Variations in Attachment”](#)). Briefly, the three patterns are secure attachment, associated with sensitive caregiving and denoting a flexible ability to use the caregiver as a secure base from which to explore the environment and as a safe haven to return to for

comfort (see ► [“Secure Attachment”](#)); insecure-avoidant attachment, associated with rejecting and intrusive caregiving and denoting relative minimization in the expression of attachment behaviors when distressed; and insecure-ambivalent/resistant attachment, associated with inconsistent caregiver sensitivity and denoting relative maximization of expressions of attachment behaviors coupled with anger/ambivalence and difficulties being soothed by the caregiver’s overtures (see ► [“Organized-Insecure Attachment”](#)).

Mary Main (a student of Ainsworth) later discovered a fourth attachment category, insecure-disorganized/disoriented attachment, denoted by an inability to maintain any of the three organized patterns following activation of the attachment system (Main and Solomon 1986; see ► [“Disorganized Attachment and Reactive Attachment Disorder”](#)). Disorganized attachment is behaviorally manifested in, for example, odd, inexplicable, and simultaneous and sequentially contradictory behaviors in relation to the caregiver (Main and Solomon 1990), and is relationally predicted by frightening/frightened and dissociative caregiver behaviors (e.g., Schuengel et al. 1999). However, disorganized *behaviors* have also been predicted by temporary overstress (Granqvist et al. 2016) and neurological vulnerability (e.g., Forslund et al. 2016b; Padrón et al. 2014). A disorganizing relational *history* can therefore not be inferred merely from observations of disorganized *behaviors*.

The “patterns of attachment” and the SSP-enabled systematic assessment of relations between individual variations in attachment quality/organization and subsequent development. This research was further strengthened by “the move to the level of representation,” which enabled examination of individual variations in attachment in older children, adolescents, and adults using representational measures in which participants are interviewed about attachment-related situations and experiences (Main et al. 1985; for research in adults, see ► [“Adult Attachment”](#)). Research examining effects of variations in quality/organization of attachment was largely in its cradle at the end of Bowlby’s active career, but he noted two general insecure socio-

emotional patterns; “on the one hand a tendency to make excessive demands on others and to be anxious and angry when they are not met. . . and, on the other, a blockage in the capacity to make deep relationships” (Bowlby 1997, 1982, p. xiv). In delineating the problems yet to be solved, Bowlby rhetorically asked, “. . .how is each pattern related to subsequent personality development and health?” (Bowlby 1997, 1982, p. 331). The work pertaining to this question, which has largely been undertaken after Bowlby’s retirement and termed the “competence hypothesis” (van IJzendoorn and Sagi-Schwarz 2008), is the focus of the current discussion.

Elaboration of Bowlby’s Notions

Environmental programming of the attachment system and goodness of fit between its early programming and the later environment.

Bowlby argued that the attachment behavioral system is moderately stable and, within limits, open to learning from experience for adaptive functioning in children’s particular environments. Although Bowlby emphasized the benefits of the system’s flexibility, he also highlighted its downsides; “. . .a design that permits of modification according to environment is likely to result in equipment that is better adapted and more efficient in its workings than equipment based on a general purpose and fixed design can ever be; although with modifiability goes also the risk of curious twists of development. . .” (Bowlby 1997, 1982, p. 46). Using machines and cars as metaphors, Bowlby argued that no system can be programmed to suit every environment equally well; a car that is constructed (i.e., programmed) to suit the streets of London is hardly as adaptive in difficult countryside terrain (and vice versa). Thus, if the attachment system becomes programmed to function adaptively within a certain environment (aiding survival and reproductive success), it may be inefficient if it needs to operate in a different environment. Bowlby argued that such understanding would be of importance for the understanding of psychopathology (Bowlby 1997, 1982).

Applied to the “insecure patterns,” avoidant attachment may, for example, be adaptive for a child growing up in an environment wherein the caregiver(s) do not have the ability to respond sensitively. By minimizing expressions of attachment behaviors, and thereby not taxing the caregiver, the child may decrease the risk of further rejection (Main 1981) and, in evolutionary terms, the risk of being abandoned (Simpson and Belsky 2008). However, the “insecure strategies,” which are regarded as less flexible than secure attachment, may result in lower relationship quality and maladjustment when children grow older and form relationships beyond their immediate family context, for example, with peers and romantic partners. Hence, links between variations in attachment quality and psychosocial maladjustment may indicate a suboptimal fit between the early calibration of the attachment system and the environments in which children later operate (cf., “goodness of fit”). As such, secure attachment (i.e., expecting others to be available and responsive) may in fact be disadvantageous in some environments.

Secure attachment, which is the most frequent pattern across cultures, has from a developmental psychology perspective tended to be regarded as “normative,” as the “primary strategy,” and as the “optimal” calibration of the attachment system, with the insecure patterns regarded as suboptimal compromises (van IJzendoorn and Sagi-Schwartz 2008). For example, Main (1990) argued, following Bowlby’s reasoning, that the insecure patterns are psychological adjustments representing a gradual shift of attentional process (i.e., psychological defenses; see ► “[Psychodynamic Foundations](#)”) away from the baseline (i.e., secure attachment), necessitated by suboptimal responses from the caregiver in order to protect the infant from anxiety and contextually maladaptive behaviors.

Evolutionary psychologists have taken another stance, arguing that there is no primary strategy or “optimal” programming of the attachment system. According to this line of reasoning, there have been multiple evolutionary environments of adaptedness (EEAs), and the patterns of attachment may constitute various programs that are

triggered by different environments, wherefore no pattern of attachment should be considered more or less optimal (Simpson and Belsky 2008). The experience of physical abuse (linked to disorganized attachment) has, for example, been linked to expertise in identifying anger in other’s facial emotional expressions, arguably adaptive in these children’s immediate environment (Pollak et al. 2009). Naturally, if there were no advantages with “insecure” attachment in any contexts, it would be difficult to account for why approximately 40% of children and adults are insecure (with cross-cultural and contextual variations; van IJzendoorn and Sagi-Schwartz 2008). Evolutionary perspectives are however only partially considered in the literature, as the predominant position has been a more standard developmental/clinical psychology perspective.

Internal working models of self and others as the mediator between the environmental programming of the attachment system and psycho-social development. Bowlby (1973) emphasized, drawing from artificial intelligence theory (e.g., Craik 1943; Young 1964), that individual variations in attachment-related experiences are manifested in cognitive-affective representations of self and others which he termed internal working models (IWMs) (see Bretherton and Munholland 2008). The IWMs are thought to include expectations of others’ behaviors in relation to the self and the availability of others (particularly in attachment-related situations), as well as expectations on the self and its effectiveness in affecting the environment (including others). Importantly, Bowlby argued that IWMs of self and other are complementary as the child gets to know him/herself as a person through how (s)he is responded to by the caregiver.

Drawing from information processing and memory theories, Bowlby also argued that experiences of insensitive caregiving lead to the creation of incoherent (or multiple) IWMs, whereby the later emerging explicit (conscious, declarative) layer of the IWMs differs from the implicit (unconscious, procedural) layer. Thus incoherence stems, in Bowlby’s view, from the usage of psychological defenses, such as defensive exclusion, to protect the individual against anxiety

(Bowlby 1973; see also ► “[Psychodynamic Foundations](#)”). Importantly, Bowlby stressed that once IWMs are formed, they will guide children’s attention, behavior, and displays of emotion in future attachment-related situations (with the caregiver and others), and children therefore become active cocreators of their subsequent experiences.

In other words, Bowlby regarded the IWMs as a (partially) mediating factor between variations in attachment quality/organization and later functioning and development. The workings of the IWMs have often been inferred from the different patterns of behavior shown by children in attachment measures (i.e., the SSP). However, Bowlby’s claim has also received empirical support from, for example, eye-tracking research, showing that secure children attentionally expect (other) caregivers to respond sensitively to distressed children, whereas insecure children expect caregivers to respond insensitively (e.g., Johnson et al. 2010).

Empirical Research on the Association Between Attachment Quality and Developmental Outcomes

Since attachment theory is at its core a relational theory, a particularly large body of research has examined attachment quality in relation to socio-emotional functioning, as indicated by broad indices of social adaptation (e.g., social competence) as well as by distinct socio-emotional competences (e.g., emotion regulation).

Individual variations in attachment quality and organization in relation to broad indices of social adaptation. A series of meta-analyses have recently demonstrated significant and robust links (of small-to-moderate magnitudes) between attachment security and several broad domains of socio-emotional functioning. First, secure attachment has been linked to lower levels of internalizing behavior problems (e.g., anxiety, sadness, fearfulness, withdrawal; Groh et al. 2012). Second, secure children have been found to show lower levels of externalizing behavior problems (e.g., aggression, conduct problems;

Fearon et al. 2010). Third, secure children have also been found to be higher in social competence (e.g., peer acceptance/rejection, popularity, prosociality; Groh et al. 2014). The meta-analyses found that the associations between attachment quality and externalizing behavior problems and social competence were stronger than with internalizing behavior problems. However, examination of internalizing behavior problems may be particularly difficult since these problems are not as readily observable.

The meta-analyses moreover highlighted insecure-avoidant attachment as the pattern most strongly associated with internalizing behavior problems and disorganized attachment as the one most strongly associated with externalizing behavior problems. Importantly, associations between attachment quality and psychosocial adjustment have been obtained by parent ratings, teacher ratings, observations, and children’s self-reports (e.g., Bohlin et al. 2000). In sum, these findings support the competence hypothesis (van IJzendoorn and Sagi-Schwartz 2008). However, the magnitude of the effects are “only” small to moderate, suggesting that the strength of the associations may, in part, be dependent on interactions with other variables conveying risk or protection (see section on moderators, below).

Individual variations in attachment quality and organization in relation to specific socio-emotional competencies. Socio-emotional competence includes multiple distinct abilities (e.g., Saarni 1999), which have been grouped into three general abilities: emotion identification, emotion understanding, and emotion regulation (Colle and Giudice 2011). The subsequent selective review follows this structure with the addition of empathy. Conflicting findings have been reported, and more research is warranted in relation to each of these components, but a general pattern is emerging.

Several studies have reported links between attachment and the ability to identify facial emotional expressions in others. For example, Steele, Steele, and Croft (2008) found that school-aged children who had been coded as secure in infancy were better at identifying facial emotional expressions. Forslund et al. (2016a) moreover found a

generally diminished ability to identify facial emotional expressions in children with disorganized attachment representations, and Peltola et al. (2015) found that infants who were later classified as disorganized in the SSP lacked an age-typical attentional bias toward fearful faces. Effects of attachment on facial emotional expressions have been argued to stem from the importance of facial emotional interactions between children and their caregivers in the interactions leading to the formation of attachment (see Forslund et al. 2016a).

Several studies have also linked individual variations in attachment quality and organization to emotion understanding. For example, Barone and Lionetti (2012) found a diminished ability to understand emotions in preschoolers with disorganized attachment representations. Moreover, Laible and Thompson (1998) reported a higher ability to understand emotions in securely attached preschoolers, particularly for negative emotions. These findings have been discussed in the context of caregiver(s) being of special importance in children's early learning about emotions, and the process of forming attachments has even been termed emotion socialization (De Oliveira et al. 2004).

Lastly, multiple studies have reported links between attachment quality and emotional reactivity and regulation, as measured in overt behavior as well as in physiological responsivity. For example, Colle and Giudice (2011) found that children with secure attachment representations reported higher knowledge of adaptive emotion regulation strategies, with a linear effect indicating the least developed knowledge in disorganized children. Using parental reports, Contreras et al. (2000) also found more constructive coping mechanisms in secure children. Moreover, Nachmias et al. (1996), using laboratory tasks designed to trigger the fear system, found higher levels of constructive coping (e.g., social referencing, affective sharing) in secure children. Infants classified as secure have also been found to show lower levels of negative emotionality as toddlers, to be less oppositional, and to show more positive affect in relation to their caregivers in laboratory problem-solving situations and free play sessions (Matas et al. 1978).

As regards physiological responding, studies have reported heightened cortisol reactivity in insecure children in both the SSP and other situations designed to induce stress, though results have been conflicting regarding the insecure pattern(s) driving the effect. For example, whereas some studies have found elevated cortisol reactivity in resistant children (e.g., Luijk et al. 2010; Spangler and Schieche 1998), other studies have reported elevated cortisol reactivity in disorganized children (Hertsgaard et al. 1995; Spangler and Grossman 1993). Yet other studies have suggested that the relation may depend on an interaction with temperament, with elevated cortisol reactivity seen specifically in insecure infants who are *also* temperamentally inhibited (e.g., Nachmias et al. 1996; Spangler and Schieche 1994). Caregiver presence has also been found to buffer against or prevent cortisol elevations for secure children in situations designed to elicit fear (e.g., Nachmias et al. 1996; Spangler and Grossman 1993), and securely attached infants have been found to show lower cortisol levels than insecure children during adaptation to childcare settings (Ahnert et al. 2004).

Attachment quality and organization have also been associated with empathy. For example, Kestenbaum et al. (1989) found that secure children responded more empathically to a distressed peer and were rated as more empathic (see also Van der Mark et al. 2002). Panfile and Laible (2012), who also found a positive association between secure attachment and empathy, further found that this association was mediated by secure children's better emotion regulation and lower levels of negative emotionality. Indeed, becoming overwhelmed by negative emotionality (i.e., "personal distress") in relation to others' displays of distress is thought to compromise empathic responding. In this vein, disorganized children have been found to react with aggression toward cues of distress in others (Main and Goldwyn 1984), and disorganized attachment representations have been linked with an increase in callous unemotional traits in middle childhood (Bohlin et al. 2012).

Individual variations in attachment quality in relation to cognitive development. Attachment quality has also been linked to children's

cognitive development and intelligence (IQ). For example, Matas et al. (1978) found that secure children were more persistent and effective in problem-solving situations. Similarly, attachment security has been linked to children's executive functioning (EF; inhibitory control, working memory/updating, and set shifting; Miyake and Friedman 2012), concurrently (e.g., Bohlin et al. 2012; Forslund et al. 2016b), as well as prospectively (Bernier et al. 2012). Children experiencing prolonged separations from their main attachment figure due to the attachment figure working overseas have also been found to show impeded EF development (Hewage et al. 2011). Attachment security has also been found to predict higher school engagement via low attentional impulsivity and higher self-control (Drake et al. 2014). Attachment security in infancy has also been prospectively linked to IQ in preschool (van IJzendoorn and van Vliet-Visser 1988), and caregiver sensitivity has been found to predict children's general cognitive development (Lemelin et al. 2006).

Important Research Questions Regarding the Link Between Variations in Attachment Quality and Subsequent Development

As described above, empirical research has established a robust link between inter-individual variations in attachment quality and subsequent development, in line with Bowlby's hypothesis. There are however, as elaborated below, multiple remaining questions.

The specificity of individual variations in attachment in relation to developmental outcomes and the need for developmental integration

It is at present unclear whether systematic variations in attachment quality and organization should be viewed as important for specific aspects of children's development, or as a general risk vs. protective factor for adaptive/maladaptive development. One reason for this ambiguity is that most of the research undertaken to date has

investigated attachment quality in relation to only one or a few aspects of children's development at a time. For example, levels of externalizing and internalizing behavior problems and social competence may often covary, and research examining whether attachment quality is *specifically* associated with any of these domains of social adaptation would therefore need to control for the other domains.

As an illuminating example, interest has grown in disorganized attachment as a possible pathway to attention-deficit/hyperactivity disorder (ADHD), with concurrent as well as longitudinal associations reported (e.g., Pinto et al. 2006). However, disorganization is robustly associated with externalizing behavior problems such as oppositional defiance, which are highly comorbid with ADHD symptoms. The association between disorganized attachment and ADHD symptoms may therefore depend on a primary association between disorganization and externalizing behavior problems which causes a secondary elevation in ratings of ADHD symptoms. Indeed, examining disorganization in relation to both ADHD symptoms and conduct problems, and accounting for their overlap, Forslund et al. (2016b) found a specific association between disorganization and conduct problems but not between disorganization and ADHD symptoms.

Second, few studies have examined whether attachment quality contributes to different developmental outcomes when accounting for the role of various caregiver behaviors that may correlate with caregiver sensitivity and child attachment and in of itself constitute predictors of the pertinent developmental outcomes. For example, caregivers who are sensitive (the primary predictor of secure attachment) may also tend to be good at cognitive scaffolding (pedagogical support), which is an important predictor of children's development of executive functions. As such, research examining whether attachment quality per se is important for children's EF development should account for the role of caregiver's scaffolding. More studies examining (I) the specificity of links between attachment quality and different developmental outcomes and (II) which developmental outcomes attachment is predictive of beyond factors covarying with

caregiver sensitivity are clearly needed for developmental integration.

Factor(s) Mediating the Association Between Attachment Quality and Developmental Outcomes

Bowlby's (1997, 1982) notion of IWMs as a mediator is still popular, and the importance of IWMs has been acknowledged by scholars outside the attachment field, for example, in relation to conduct problems (Dodge and Pettit 2003). However, theorizing and empirical research have seen multiple proposals of alternative and/or complementary mediators, some of which overlap theoretically and/or are construed on different levels of analysis (i.e., on a level affecting the conditions for children's learning, or as influencing children's development of specific competencies).

Learning conditions as mediators

van IJzendoorn et al. (1995) reviewed and discussed four different hypotheses regarding learning conditions. First, according to the "attachment-teaching hypothesis" (cf., Fonagy and Campbell's [2015] *epistemic trust* idea), children's attachment quality may influence the caregiver's ability to teach their children, through attachment quality affecting how much resources children can devote to learning. That is, insecure children may have to devote more resources to attachment-related aspects of situations, consequently limiting the resources that remain for learning. Second, the "attachment-exploration hypothesis" (cf., Aber and Allen [1987] on *Readiness to Learn*) proposes that attachment quality might affect children's own ability to learn from the environment through effecting their exploration. According to this hypothesis, secure children, who are thought to have internalized a model of their caregivers as available if danger should arise (i.e., felt security), may be more free to explore the environment and learn from it. Third, according to the "social network hypothesis," secure children may develop more frequent, harmonious, and stimulating social relationships from which they can learn adaptive skills, with insecure children thought to be hampered by

defensive processes and anxiety. Fourth, according to the "attachment-cooperation hypothesis," secure children may be more cooperative with others as they may be less defensive and anxious.

Further, similar to the attachment-teaching/epistemic trust hypothesis, attachment quality may affect internalization of parental norms, with secure children found to heed parent's directives more in situations of do and don't (Kochanska 1995). Possibly related to several of these hypotheses, attachment quality may affect further development through effects on the stress response system, with increased stress reactivity possibly hampering insecure children's ability to explore on their own as well as their ability to learn from others.

Specific competencies as mediators

Regarding attachment quality and the development of specific competencies, the various patterns of attachment have been conceptualized as different strategies for emotion regulation, with secure attachment thought to facilitate flexible and open emotional communication (Cassidy 1994; Mikulincer et al. 2003). Moreover, children's EF has been proposed as a possible mediator, for example in relation to externalizing behavior problems, with disorganization and insecurity hypothesized to impede EF development (Fearon et al. 2010; see also Bernier et al. 2012). In line with Bowlby's account, attachment-related experiences and memories have also been discussed as potentially influencing social information processing (e.g., hostile attributional biases, Crick and Dodge 1994).

Research to date has not examined multiple proposed mediators simultaneously, and it is therefore unclear whether any one mediational hypothesis should be regarded as superior to the others. Indeed, it is also possible that attachment quality influences children's development through effects on multiple mediating factors simultaneously, for example influencing both children's exploration, their caregiver's ability to teach them, and their development of distinct competencies. More research is clearly needed to disambiguate these questions.

Factors Moderating the Link Between Attachment Quality and Developmental Outcomes

From the onset, Bowlby (1997, 1982) reasoned that attachment quality might assert its influence through interactions with other variables. Yet, attachment research has, for most part, tended to focus on simple effects, for example through examination of concurrent or longitudinal associations between variations in attachment quality and developmental outcomes. When other variables have been included, it has often been as controls, for example to show that associations are not due to temperamental differences. However, just as the prevalence of the attachment patterns varies depending on factors such as socioeconomic status, with contextual variables thought to affect caregiver sensitivity, the association between attachment quality and developmental outcomes varies in strength depending on contextual and individual factors.

First, children typically have more than one caregiver and may have qualitatively different attachment relationships with different caregivers. As such, being secure with one caregiver may buffer against the risk from being insecure with another. Though relatively few studies to date have examined this issue, Boldt et al. (2014) found that attachment security with fathers in toddlerhood moderated the link between attachment security with mothers in toddlerhood and later behavior problems in school age. More specifically, children having low security scores with both mother and father showed the highest levels of behavior problems.

Second, other child characteristics, such as temperamental dispositions, may interact with attachment security in relation to subsequent development. As reviewed by Vaughn et al. (2008), research on interactions between these two domains, particularly in relation to interpersonal outcomes, started as late as during the 1990s. However, multiple findings now indicate that interactions between these two domains may be important, so that high temperamental reactivity together with insecure attachment increases the risk of maladjustment (Vaughn et al. 2008).

Third, contextual factors should be taken into account as moderators. As reviewed by DeKlyen and Greenberg (2008), multiple studies have found that attachment insecurity constitutes but one of many factors influencing further development, and associations between attachment insecurity and behavior problems may magnify substantially given the presence of contextual risk factors such as family adversity and additional unfavorable aspects of parenting. As such, insecure attachment may convey relatively little risk for a child who grows up with the presence of buffering factors such as a stable two-parent home, a sufficient and functioning social network, good access to peers, and access to good day-care.

Conclusion

Attachment theory has become a highly influential theory in psychology. Variations in attachment quality and organization have, in line with Bowlby's hypothesis, been robustly linked to broad measures of social adaptation and is linked to distinct aspects of social competence. However, we hasten to add that children's development is determined by so much more than attachment quality and therefore caution against simplified reasoning.

First, the amount of variation in developmental outcomes explained by individual variations in attachment quality is typically small, and particularly so in low-risk contexts. Second, and relatedly, associations between individual variations in attachment and developmental outcomes are moderated by contextual and individual factors. Attachment quality must therefore be seen in interaction with other aspects of development which magnify or buffer against risk, rather than as deterministically associated with subsequent development. Third, it is still unclear whether the various patterns of attachment are specifically linked to particular developmental outcomes, or if attachment quality (e.g., security/insecurity, organization/disorganization) constitutes a general protective vs. vulnerability factor. Fourth, most research conducted thus far has not accounted

for effects of other aspects of parenting, which may covary with caregiver sensitivity and child attachment and independently constitute predictors of the pertinent developmental outcomes. As such, it is still unclear to what extent attachment quality per se contributes to children's development beyond these aspects of caregiving. Fifth, several sets of mediators have been proposed, and it is at present unclear whether any of those are superior to the others, if effects of attachment are mediated by a number of different factors, or whether different mediators are implicated in relation to different developmental outcomes.

Although a challenging task, intensified examination of these issues represents important avenues for future attachment research in order to clarify the role of attachment quality in relation to children's development. Research following Bowlby has supported his general hypothesis that attachment quality is important for children's development, but there are still many unanswered questions.

Cross-References

- [Adult Attachment](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Infant Survival](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Offspring-Parent Attachment](#)
- [Organized-Insecure Attachment](#)
- [Psychodynamic Foundations](#)
- [Secure Attachment](#)

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Egg Ejection

► Egg Rejection

Egg Mimicry

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Synonyms

Cheating; Deception; Manipulation

Definitions

An evolved resemblance of host eggs by the eggs of avian brood parasites, resulting from Darwinian natural selection.

Introduction

The interactions between avian brood parasites, such as cuckoos or cowbirds, and their hosts have emerged as model systems to study coevolutionary processes under natural conditions. Instead of building a nest and tending their offspring, brood parasites lay their eggs in the nests of other birds and abandon the care of their young to the host. Adult parasites tend to remove or damage host eggs when depositing their own and parasite chicks generally eliminate the rest of the host's brood after hatching. Consequently, hosts evolve defences against brood parasites, which select counteradaptations in parasites, further counteradaptations in hosts, and so on. While evidence of reciprocal adaptations and counteradaptations in hosts and brood parasites are evident at all stages of the host's nesting cycle (Feeney et al. 2014b), the exquisite mimicry of host eggs by the eggs of some brood parasites comprise among the most charismatic and iconic examples of deception in the animal kingdom.

Egg Mimicry in Avian Brood Parasites

Mimicry as an adaptation to increase the likelihood of successful parasitism has evolved numerous times in the avian brood parasites (Feeney et al. 2014b). Best studied in the Eurasian common cuckoo (*Cuculus canorus*), it is most notably recognized as a counteradaptation to host discrimination (Brooke and Davies 1988). Preference for and coevolution with different hosts species can result maternally inherited host-specific egg phenotypes (Fossøy et al. 2016) that mimic those of their respective host species (i.e., host-specific egg “genres” or “races”; Gibbs et al. 2000), allowing for host specialization without speciation. Correspondingly, studies have empirically demonstrated the link between the degree of color (Stoddard and Stevens 2011) and pattern (Stoddard and Stevens 2010) matching and host discrimination across common cuckoo lineages and host species, when accounting for the host's visual perspective.

Outside of the common cuckoo and its hosts, studies have shed insights into other agents of

selection for egg mimicry by brood parasites, other kinds of mimicry resulting from brood parasite–host coevolution, and the amount of time it can take for these phenotypes to evolve under natural conditions. For example, in the dark nests of their crevice-nesting hosts, African greater honeyguides (*Indicator indicator*) produce eggs that mimic the size and shape of those of their hosts. However, rather than mimicry being a product of coevolution with their hosts, egg mimicry in this system is a product of selection imposed by competing honeyguides, which destroy nonmimetic eggs in order to maximize the likelihood of their own young surviving (Spottiswoode 2013).

In Australia, numerous small songbirds build dimly lit dome-shaped nests and produce white eggs with varying degrees of speckling. Rather than producing an egg that closely resembles that produced by any particular host, the Horsfield's bronze-cuckoo (*Chalcites basalis*) appears to have circumvented the defences of multiple host species, as well as the need to diverge into host-specific races, by producing an egg that generally resembles those of its multiple hosts (also known as “compromised,” “generalist,” or “jack-of-all-trades” mimicry; Feeney et al. 2014a).

Finally, the interactions between the African cuckoo finch (*Anomalospiza imberbis*) and its tawny-flanked prinia (*Prinia subflava*) host provides an elegant example of coevolution between the eggs of a brood parasite and its host, as well as unique insights into the timespan over which these kinds of evolutionary changes can occur. Unlike the common cuckoo, in which female-lineages are host-specific, selection imposed on the prinia eggs by cuckoo finches has selected numerous egg-races in prinias, which allows to more easily identify and reject cuckoo finch eggs that do not closely match their own. However, cuckoo finches have responded by evolving eggs that resemble those of the different prinia lineages (Spottiswoode and Stevens 2010). Further, Spottiswoode and Stevens (2012) used an egg collection that spans over 40 years to track the coevolution of egg phenotypes in prinias and cuckoo finches. They demonstrated that the pressure imposed on hosts by brood parasites can

select new phenotypes (i.e., egg colors) within this time period and that parasite egg phenotypes closely track those of their hosts.

Conclusion

Brood parasites commonly evolve egg mimicry in response to pressures imposed on them by either their hosts, or by other parasites competing for access to hosts. Selection imposed on brood parasites can select for host or host-race specific egg phenotypes, providing a clear and elegant example of naturally occurring coevolution.

Cross-References

- [Egg Rejection](#)
- [Rejection Thresholds](#)

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Egg Recognition

- [Rejection Thresholds](#)

Egg Rejection

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Synonyms

[Egg ejection](#); [Nest abandonment](#)

Definitions

A well-studied defense against avian brood parasitism in which a host “rejects” a brood parasite’s egg – either through physical ejection, burying the egg in the nest lining, or abandoning the nest.

Introduction

The interactions between avian brood parasites, such as cuckoos or cowbirds, and their hosts have emerged as model systems to study coevolutionary processes under natural conditions. Instead of

building a nest and tending their offspring, brood parasites lay their eggs in the nests of other birds and abandon the care of their young to the host. Adult parasites tend to remove or damage host eggs when depositing their own and parasite chicks generally eliminate the rest of the host's brood after hatching. Consequently, hosts evolve defenses against brood parasites, which select counteradaptations in parasites, further counteradaptations in hosts, and so on. While evidence of reciprocal adaptations and counteradaptations in hosts and brood parasites are evident at all stages of the host's nesting cycle (Feeney et al. 2014), rejection of foreign eggs by hosts is a well-studied defense that acts as a catalyst for subsequent coevolution between these species.

Egg Rejection as a Defence Against Brood Parasitism

Despite hosts employing an array of defense to prevent brood parasites laying eggs in their nests, it often occurs, which select adaptations in hosts that aim to minimize the cost of parasitism. Of these various adaptations (reviewed in: Feeney et al. 2014), rejection of foreign eggs often emerges as a key defense.

Iconic field experiments demonstrated that egg rejection behaviors are widespread, but not ubiquitous, among hosts of brood parasites (Brooke and Davies 1988; Rothstein 1975). Rejection of foreign eggs selects egg mimicry by parasites (Brooke and Davies 1988), which makes discrimination more difficult and increases the likelihood of hosts mistakenly rejecting its own egg. Hosts can decrease the likelihood of parasites laying eggs that match their own with individually identifiable "egg signatures" (i.e., female or race-specific egg phenotypes; Stoddard et al. 2014). Additionally, they can counter-egg mimicry with cognitive mechanisms that increases the likelihood of them accurately identifying and rejecting the correct egg (or eggs) in their nest (Stevens et al. 2013) and weigh the decision to reject an egg against their

perceived risk of parasitism (Thorogood and Davies 2016). Unlike other defensive adaptations, such as recognizing and responding to adult parasites near the nest, egg rejection behaviors appear to quickly become conserved after evolving, and can persist for at least hundreds of years after the pressure imposed by parasites has been removed (Lahti 2006).

Counteradaptations by brood parasites, or external ecological pressures, can generally explain why some species do not reject foreign eggs. For example, in the United States, brood parasitic brown-headed cowbirds (*Molothrus ater*) employ "mafia tactics" to ensure that hosts do not reject their eggs and increase the likelihood of successful parasitism. Unlike many parasitic cuckoos, cowbird nestlings do not always eliminate the host's entire brood, which allows for a circumstance where cowbirds monitor parasitized nests and repeatedly destroy the nests of egg rejecters until they succumb and accept the compromised, but not entirely diminished, reproductive output associated with hosting a cowbird nestling (Hoover and Robinson 2007). Similarly, despite Jacobin cuckoo (*Clamator jacobinus*) eggs being large and conspicuous in cape bulbul (*Pycnonotus capensis*) nests in sub-Saharan Africa, the combined effects of them being difficult to effectively eject with high external predation and the relatively low likelihood of the parasite's egg hatching in sync with the host's own eggs makes acceptance of the parasite's egg optimal in this species (Krüger 2011).

Conclusion

Egg rejection represents the best-studied counteradaptation that hosts employ to minimize the cost of brood parasitism. Research into the interactions across diverse parasite–host pairs highlights how ecological circumstances, available information, and the particular characteristics of the involved species shape this unique behavior.

Cross-References

- [Egg Mimicry](#)
- [Rejection Thresholds](#)

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Eggs

- [Production of Eggs and Sperm](#)

Ego-Centered Kin Terminology

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Synonyms

[Kin system](#); [Kin terms](#); [Kin term system](#); [Kin terminology](#); [Kin vocabulary](#)

Definition

Ego-centered kin terminologies are when kinship terms are organized relative to the self, also known as ego. For example, if an individual says “(my) brother” that relationship is reckoned with respect to them, and the referent will not be the same as the listener’s brother (unless the ego and listener are siblings).

Alternatively, ego-centered kin terminologies show the genealogical relationships between individuals and are used as a visualization tool for representing kinship terminologies within languages, or within families/clans.

In Regard to Kinship Terms

The bilateral kinship network formed as the result of procreation is often used as the basis for kinship organization, and hence encourages the use of ego-centered kinship organization. That is, when a couple has a child, it creates a unique kinship network for that child, connecting both the father’s and mother’s family lineages. Societies impose cultural ideas on how an individual should behave toward various kin, e.g., who should be respected, and which kin have (or do not have) sexual taboos. Kinship terminologies provide a template of kinship categories that reflect these ideas, which can be applied to any individuals’ kin. However, there are suggestions that the

ego-focused basis of kinship studies imposes a European ethnocentric approach to kinship terminology and the understanding of societies' kinship organization (Schneider 1984).

The alternative to an ego-centered kinship organization is *sociocentric* organization, where individuals are organized based on a social category, as opposed to individual relationships (Dousset 2011). Here a group of individuals will all be referred to with the same term, based on their affiliation to a kin-based social category. These categories are often defined through lineage patterns, and are sometimes described as “skin” relationships, rather than kin (McConvell et al. 2018).

A second example of when kinship terms are not egocentric can be seen in the use of triangular kinship terms, commonly found throughout Australia, but also seen in Brazil and Patagonia. This is where a specific kin term is used by a speaker who addresses someone with whom they have a connecting relative. For example, a son speaking to his mother about his uncle, who is also the mothers' brother would use a specific term. In Biniñ Kunwok, a language from the Australian Northern territories, this term is *na-djumu* (Garde 2013). The mother would use a different term for the reciprocal relationship between her, her son, and her brother, since this covers a different set of relatives. These kinship terms are unique in that they are semantically denser than the traditional dyadic kinship terms, by taking both the speaker's and addressee's perspective on kin into account.

As a Visualization Tool

Ego refers to the central person in the terminology, to whom all relationships are extended from (Parkin 1997; Stone 2014). The ego can be gendered or gender neutral depending on whether the kinship language is dependent on the sex of speaker or not. For example, in Tongan, the term *ta'okete* means elder same-sex sibling, making the labeling of the terminology dependent on the gender of ego. English is an example of when ego is gender neutral. Typically, consanguineal (or blood) relatives are indicated by a single line, and parallel

lines indicate affinal relatives (or relatives by marriage). Men are often indicated by triangles and women by circles. However, this is not a universal custom and readers should take note of the author's legend or notes.

Cross-References

- [Kin Recognition and Classification in Humans](#)
- [Kinship Distinctions According To Generation](#)
- [Kinship Distinctions According To Sex](#)
- [Manipulative Use of Kin Terminology](#)

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Egocentrism

- [Narcissism](#)

Einmensen (German)

- [Anting](#)

Einfühlung

- [Gratitude, Sympathy, and Empathy](#)

Ejaculate

- ▶ [Seminal Plasma](#)

Ejaculate Adjustment

- ▶ [Physiological Evidence for Human Sperm Competition](#)

Electronic Aggression

- ▶ [Anonymity of Cyberbullying](#)

Electronic Bullying

- ▶ [Anonymity of Cyberbullying](#)
- ▶ [Cyberbullying](#)
- ▶ [Sex Differences in Cyber Bullying](#)

Elementary Technology

- ▶ [Primate Tool Use](#)

Elimination

- ▶ [Extinction of Neanderthals](#)

Embodied Language Processing

- ▶ [Modern Theories of Language](#)

Embryo

- ▶ [Fetus Development](#)

Emergence of Deontic Reasoning

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Synonyms

[Practical reasoning](#); [Social reasoning](#)

Definition

Reasoning about what one may, ought, or must not do in a given set of circumstances.

Introduction

Deontic reasoning is reasoning about what one *may*, *must*, or *must not* do in a given set of circumstances. Virtually all of our social institutions presuppose a capacity to understand and reason about what is *permitted*, *obligated*, *prohibited*, or *advised*. Failure to reason effectively about deontic concepts can have disastrous consequences, including social rejection, punishment, and even incarceration.

Deontic reference emerges quite early in children’s speech, appearing in children’s justifications of their behavior as early as 24 months of age.

Toddlers use terms such as *must* and *may* to talk about obligation and permission (e.g., “*You must stay*”), while epistemic uses of the same terms (e.g., “*It must be raining*”) do not reliably emerge until the 4th or 5th year of life.

Deontic reasoning is closely related to the concepts of *social norms* and *social contracts*. Social norms differ from social contracts in much the same way as laws differ from

Denise D. Cummins has retired.

contracts; norms (like laws) are prescriptive rules established by authority that dictate what is permitted or obligated under specified conditions, whereas contracts are agreements entered into freely by agents who promise a conditionalized exchange of benefits. Violating a norm means engaging in proscribed behavior, and there need not be any direct or immediate benefit to the agents controlled by the norm (other than avoiding punishment). In fact, many systems of social norms are enacted and enforced precisely to benefit some members of society over others. A violation of a social contract, on the other hand, is simply failure to reciprocate a benefit received that was given conditionally on reciprocation.

Emergence of Social Norm Reasoning

Beginning around 3 years of age, young children do not just follow social norms, they actively enforce them on others, even in situations in which they are not directly involved. They do not need to be explicitly instructed about the rules by an authority; they simply need to see an adult engage in it. For example, 3-year-olds will actively correct and admonish a puppet that interacts with an object in a way that is different from the way that an adult previously interacted with it, and they will use deontic/normative language to do so (e.g., “You have to do it this way”) (Schmidt and Tomasello 2012). Cummins (1996a) found that children as young as 3 years of age perform as well as adults when asked to monitor compliance with a norm. Children were shown toy mice, some of which squeaked when squeezed. Children were told either “*The Queen Mouse says all the squeaky mice are in the house*” (epistemic) or “*The Queen Mouse says all the squeaky mice must stay in the house*” (deontic). They then had to choose whether to squeeze toy mice that were inside or outside of a toy house to “*make sure no one is disobeying the rule*” (deontic) or “*find out if she’s wrong*” (epistemic). Across two experiments, two thirds of 3-year-olds correctly chose to squeeze the mice that were outside the house in the deontic case, but only one third chose to do so in the epistemic (truth-testing) case. Similarly,

Harris and Nuñez (1996) showed children cards that illustrated compliance with or violation of social rules such as “When Julie rides a bicycle, Julie wears a helmet.” Children were required to find the picture that showed either that the sentence was wrong (epistemic) or that Julie was doing something wrong (deontic). Preschool children were found to perform nearly optimally on the deontic versions of the task but frequently made errors on the epistemic versions of the task.

Emergence of Social Contract Reasoning

Within the first year of life, infants engage in reciprocal turn-taking behavior with caregivers, and by at least the third year of life, children are selective in their distribution of altruistic acts, preferring to aid those who have aided them in the past. Children as young as 4 years of age reason effectively about reciprocal exchange, correctly identifying instances of contract compliance as well as instances of cheating (Harris et al. 2001).

Explanations of Early Emergence

Differences in learning opportunities. One explanation for the ease and speed with which children induce deontic reasoning strategies is the frequency and urgency with which deontic reasoning situations present themselves during early childhood. In other words, there is ample opportunity to induce a schema for reasoning about deontic situations given their ubiquity. Yet children are exposed to instances of lying (epistemic violations) as frequently as instances of misbehavior (prescriptive violations).

Despite this, we induce no efficient schemas for testing truth. Children and adults agree on what constitutes a violation of a social rule, but considerable disagreement exists among theorists concerning how the truth of statements should be tested. Moreover, both adults and children frequently employ deficient strategies (e.g., confirmation bias) when asked to test the truth of statements (see Cummins 1996b for a review).

Differences in the complexity of meta-representations and satisfaction conditions.

Some researchers have argued that epistemic reference emerges later than deontic reference because the former is more demanding of meta-representational cognitive resources. But epistemic sentences do not require more complex operators than deontic sentences to capture their logical forms. Deontic sentences usually include modals to express permission (“You *may* do that”) and obligation (“You *must* do that”). Epistemic sentences use the same modals to express possibility (“You *may* be right”) or necessity (“You *must* be the one who did it”). Epistemic sentences also need not make use of modals (“It is raining”) and hence are syntactically simpler than deontic sentences.

The same can be said about task complexity. Deontic and epistemic versions of reasoning tasks require children to detect discrepancies between a mental representation of what should be (e.g., “Squeaky mice must stay/are in the house”) and the actual situation (e.g., “Squeaky mice are not in the house”). In both cases, the state of affairs described and the actual state of affairs must be compared in order to assess whether their satisfaction conditions have been met.

Despite this, epistemic tasks appear to impose greater cognitive load than deontic tasks. Van Lier et al. (2013) found that reasoning about deontic content does not depend on cognitive capacity or age and is unaffected when cognitive resources are burdened by performing a concomitant secondary task. In contrast, performance on a non-deontic version of the same task was found to depend on available cognitive capacity. This suggests that it is something about our cognitive architecture that makes it easier for us to understand and process deontic tasks.

Evolutionary explanations. Evolutionary accounts explain early emergence in deontic reasoning by arguing that this type of reasoning was a target of selective pressure. The first researchers to offer an evolution-based explanation were Cosmides and Tooby (1989), who proposed **Social Contract Theory**. They argued that performance improves only when people interpret the materials as social contracts with reciprocal benefit structures. An offer to engage in social

exchange can be expressed by a rule of the form: If Benefit [to Party X, from Party Y] then Benefit [to Party Y, from Party X]. Subjects encountering such a rule should perceive that individuals who have accepted a benefit without returning a benefit are cheating. Cosmides and Tooby argued that algorithms for reasoning about social exchange evolved in protohumans during the Pleistocene, making them species-specific cognitive architecture.

Cummins and Cummins (1999) offered an alternative evolutionary explanation which they call the **Learning Bias and Canalization View**. Learning bias refers to attentional biases for social stimuli (e.g., the preference of newborns to look at faces as opposed to equally complex stimuli). Canalization refers to the degree to which the development of a trait is robust across normal environmental variations. According to this view, all infants are “primed” to rapidly acquire social rules due to an attentional bias toward social stimuli, but *which* rules are acquired depends on the norms characterizing their particular social groups (canalization).

They further argue that this kind of cognition is not unique to humans but instead reflects cognitive functions that were shaped over evolutionary time by the exigencies of living in social groups. Numerous primatologists have noted that primates are endowed with cognitive abilities that are especially well suited to tracking social information. They are able to recognize individuals, identify kin, keep track of past interactions with group members, discriminate between cooperators and defectors in reciprocal interactions, and form alliances based on reciprocal obligations (such as grooming and food sharing) (Silk 2007). These characteristics of primate cognition have measurable fitness consequences, that is, measurable impact on the frequency of an individual’s genes in the gene pool via differential reproductive success. It is difficult to defend the position that humans were exempt from this evolutionary pressure.

These accounts are bolstered by neuroimaging of reasoning pathways. For example, in a study conducted by Canessa et al. (2005), the effect of content on brain activation was investigated with functional magnetic resonance imaging (fMRI)

while people solved the truth-testing and deontic versions of the Wason selection task. They found that both tasks activated a left-hemispheric fronto-parietal network, which is consistent with a number of studies that report left hemisphere involvement in deductive reasoning. But deontic content was also found to recruit activity in right-hemisphere frontal and parietal regions while truth-testing content did not. This selective recruitment of right hemisphere areas is consistent with other studies showing a major role of the right hemisphere in the processing of social content.

Conclusion

Thriving in a complex social environment depends crucially on deontic reasoning. Humans and other social animals appear to be biologically prepared to rapidly learn what is permitted and what is forbidden in a social group, and readily detect transgressions of social norms and contracts. They also readily form alliances based on reciprocal obligations, and monitor transactional imbalances. These basic social cognitive functions are, in a very real sense, what the social brain evolved to do.

Cross-References

- Adaptations for Reciprocal Altruism
- Adapted Mind, The
- Altruism Norms
- Cheater Detection
- Cognitive Development
- Cooperation and Social Cognition
- Emergence of Indicative Reasoning
- Evolution of Cooperation
- Evolutionary Cognitive Psychology
- Fairness in Primates
- Ingredients of Reciprocal Altruism
- Judgment and Decision-Making
- Language Development
- Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)
- Nonhuman Reciprocal Altruism
- Psychology of Reciprocal Altruism
- Robert Trivers
- Social Learning and Social Cognition

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Emergence of Indicative Reasoning

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Synonyms

Discursive reasoning; Epistemic reasoning;
Theoretical reasoning

Definition

Reasoning to determine what is true.

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Introduction

Reasoning about what is true is referred to in philosophy as *theoretical* reasoning or *discursive* reasoning. It is also referred to as *epistemic* reasoning in developmental psychology, and *indicative* reasoning in psychological research that studies the way people reason about indicative statements. Indicative statements are simple assertions such as “*I am tall*,” as opposed to statements that describe subjunctives such as “*If I were taller*” or include modals such as “*It must be raining*.”

Research has shown that development of the capacity to reason about truth is quite protracted compared to other types of reasoning. For example, toddlers use modals such as “*may*” to express permission (“*You may do that*”) and “*must*” to express obligation (“*You must do that*”). Epistemic sentences use the same modals to express possibility (“*You may be right*”) or necessity (“*You must be the one who did it*”), but these types of utterances do not reliably emerge in children’s language until the 4th or 5th year of life (Ozturk and Papafragou 2015). It is not until this age that children also begin to reliably pass versions of theory of mind tasks that tap children’s understanding of epistemic states such as true and false beliefs, and tasks that depend heavily on frontal lobe executive functions, such as switching rules by which objects must be sorted (Henning et al. 2011). Second-order mental state understanding (e.g., *Peter knows that Sally thinks it is raining*) does not emerge until about 6 years of age, and it undergoes steady development well into adolescence (Sullivan et al. 1994).

While reasoning about true and false beliefs in the social realm undergoes development, reasoning about truth and falsity on nonsocial tasks remains uniformly low throughout the lifespan. For example, 3 year olds perform poorly on reasoning tasks that require them to test the truth of indicative conditional rules. Cummins (1996a) showed 3- and 4-year-old children toy mice, some of which squeaked when squeezed. Children were told either “*The Queen Mouse says all the squeaky mice are in the house*” (epistemic) or “*The Queen Mouse says all the squeaky mice*

must stay in the house” (deontic). They then had to choose whether to squeeze toy mice that were inside or outside of a toy house to “*make sure no one is disobeying the rule*” (deontic) or “*find out if she’s wrong*” (epistemic). Across two experiments, two-thirds of 3-year-olds correctly chose to squeeze the mice that were outside the house in the deontic case, but only one-third chose to do so in the epistemic (truth-testing) case. Four-year-olds correctly chose the outside mice over 80 % of the time in the deontic condition, but performance on the truth-testing version remained unchanged at 33 %. Adults show the same magnitude differences on adult versions of deontic and truth-testing selection tasks (Cummins 1996b).

Similarly, Harris and Nuñez (1996) showed children cards that illustrated compliance with or violation of social rules such as “*When Julie rides a bicycle, Julie wears a helmet*.” Children were required to find the picture that showed either that the sentence was wrong (epistemic) or that Julie was doing something wrong (deontic). Preschool children were found to perform nearly optimally on the deontic versions of the task but frequently made errors on the epistemic versions of the task.

Theoretical Explanations

Differences in learning opportunities. One explanation for deficient epistemic reasoning strategies relative to social reasoning strategies is that there is ample opportunity to induce schemas for reasoning about deontic situations given their ubiquity in the child’s everyday experiences. Yet children are exposed to instances of lying (epistemic violations) as frequently as instances of misbehavior (prescriptive violations).

Despite this, we induce no efficient schemas for testing truth. Children and adults agree on what constitutes a violation of a social rule, but considerable disagreement exists among theorists concerning how the truth of statements should be tested. Moreover, both adults and children frequently employ deficient strategies (e.g., confirmation bias) when asked to test the truth of statements (see Cummins 1996b for a review). Moreover, normative theories of hypothesis-testing are

relatively recent developments in the history of science (see Cummins 2012, chapter 7). The importance of adopting a falsification strategy was articulated as recently as the mid-twentieth century.

Differences in the complexity of meta-representations and satisfaction conditions. Some researchers have argued that epistemic reasoning emerges later because it is more demanding of metarepresentational cognitive resources. But indicative sentences do not make use of modals, and hence are syntactically simpler than deontic sentences.

The same can be said about task complexity. Deontic and epistemic versions of reasoning tasks require children to detect discrepancies between a mental representation of what should be (e.g., “*Squeaky mice must stay/are in the house*”) and the actual situation (e.g., “*Squeaky mice are not in the house*”). In both cases, the state of affairs described and the actual state of affairs must be compared in order to assess whether their satisfaction conditions have been met.

Evolutionary Explanation

Psychological investigations have repeatedly shown that adults and children perform better when evaluating compliance than when evaluating truth, and this difference has been replicated in dozens of experiments using a variety of experimental tasks over the course of 30 years (Cummins 1996b). Adults and children typically find the truth-testing version much more difficult than the deontic version of the task, even when the tasks require identical responses and even though they do not differ in representational or strategic complexity.

It should also be noted that while there is agreement among logicians concerning normative treatments of deontic conditionals, no consensus has been reached on how to capture the truth conditions of indicative conditionals (Edgington 2014). This suggests that it is something about our cognitive architecture that makes it easier for us to understand and process deontic tasks, a conjecture that is supported by two lines of evidence.

First, epistemic tasks appear to impose greater cognitive load than deontic tasks. Van Lier et al. (2013) found that performance on a nondeontic task declined when reasoners were burdened by performing a concomitant secondary task while deontic versions of the same task were unaffected.

Second, deductive reasoning typically activates a left-hemispheric frontoparietal network. Canessa et al. (2005) found that both deontic and truth-testing reasoning tasks activated this network. But deontic content also recruited activity in right hemisphere frontal and parietal regions, areas that play a major role in the processing of social content. The recruitment of this additional network apparently facilitates understanding and reasoning about social content.

Conclusion

Reasoning about truth depends on executive functions that are applied broadly across domains and develop slowly over the course of brain maturation and development. In contrast, deontic reasoning appears to benefit from specialized cognitive architecture that develops quite quickly in childhood to facilitate cognizing the social world.

Cross-References

- [Cognitive Development](#)
- [Cognitive Science](#)
- [Development](#)
- [Emergence of Deontic Reasoning](#)
- [Judgment and Decision-Making](#)
- [Language Development](#)
- [Theory of Mind](#)

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Emergence of Social Reasoning About Hierarchies

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Synonyms

Cognitive development; Dominance hierarchies; Social status

Definition

The development of the ability to use cues to dominance, such as physical power, social power, or access to resources, to reason and make inferences about species-specific social hierarchies.

Introduction

Social hierarchies, defined here as organizational structures in which certain individuals or groups have greater social power and/or access to resources than others, are ubiquitous across cultures and species (Cheney and Seyfarth 2007). These hierarchies shape many aspects of life, from one's desirability as a social partner or mate, to overall health and well-being (Marmot and Sapolsky 2014). Social hierarchies serve to reduce the need for physical aggression, maintain group stability, and enable predictability in social environments; by knowing each individual's position in the hierarchy, one can predict the likely outcomes of interactions with group members and behave accordingly.

Given the ubiquity and importance of social hierarchies, it is not surprising that species from fish (Grosenick et al. 2007) to nonhuman primates (Bergman et al. 2003) can reason about hierarchies. For example, Hamadryas baboons expect dominance relations to be stable, and can infer – based on vocalizations alone – when unexpected dominance interactions occur (e.g., when a subordinate individual gives a threat-grunt – signaling dominance – to a more dominant individual: Bergman et al. 2003). Although social hierarchies are present in many species, most research in nonhuman species has only examined the *consequences* of hierarchies, such as investigating how an individual's rank in a hierarchy shapes physiological functioning, mortality rate, or access to food or mates (see Cheney and Seyfarth 2007; Marmot and Sapolsky 2014). The question of *how* individuals develop the ability to reason about hierarchies has largely been asked only in humans. Therefore, this entry reviews the literature on the emergence of reasoning about hierarchies in humans, shown to be capable of this type of social reasoning before reaching their first birthday.

Hierarchies: Simply Complicated

Dominance hierarchies are simultaneously simple and complicated. They are simple because the

defining trait of a hierarchy is an asymmetric relationship. In other words, hierarchies arise when two individuals are in a zero-sum situation where only one can achieve the desired outcome. For example, if two children both want to play with a toy, but there is only one toy, then a hierarchy is formed between those two children, and the child who gets to play with the toy is the dominant individual and the child who does not get the toy is the subordinate.

Hierarchies are also complicated. First, although each individual dominance relation is established between two individuals, hierarchies are often constructed at the group level and therefore include more than two individuals. Thus, to learn the larger, group-level hierarchy, group members must keep track of dyadic (i.e., one-to-one) dominance relations and then construct the group-level hierarchy from each of these dyadic relationships. Importantly, individuals can construct the group-level hierarchy by observing some (but not all) of the dyadic dominance relations, inferring unseen dyadic relations through transitive inference. In this context, transitive inference is the ability to derive an unknown dominance relation between two actors based on knowledge of the dominance relations each of those actors has with a shared, third actor. In other words, after observing A prevail in an asymmetric interaction with B, and B prevail over C, transitive inference would lead one to expect A to prevail over C, even without seeing any prior interactions between A and C. Second, hierarchies can be constructed both within a single group (*intragroup* hierarchy, as described above) as well as between groups (*intergroup* hierarchy). Therefore, in addition to constructing intragroup hierarchies based on interactions between two individuals, individuals must also develop the ability to see groups as cohesive units and construct intergroup hierarchies based on the interactions of two groups. Third, asymmetries can be based on a wide variety of factors, from access to resources, to social power, to influence over others. Thus, children must learn how to detect cues to asymmetric dominance relations using each type of factor; for example, being able to represent concepts such as “more” versus “less”

(for asymmetric resource-based relations). Fourth, and relatedly, the factor that a given hierarchy prioritizes is likely to vary across different contexts. For example, while playing in their neighborhood, children might form a hierarchy on the basis of the number of toys each kid has (prioritizing access to resources). In contrast, when at school, children might form a hierarchy on the basis of power or prestige (prioritizing influence over others), putting the school principal at the top of the hierarchy, teachers in the middle, and students at the bottom (for a detailed review of reasoning about dimensions of status hierarchies in adults, see Mattan et al. 2017). Despite the sometimes complicated nature of hierarchies, humans – even from infancy – are remarkably good at identifying cues to dominance that signal hierarchies.

Learning Cues to Dominance

In fact, humans seem predisposed to organize the world in a hierarchical fashion from an early age. Infants as young as 15-months-old learn and remember dyadic dominance relationships and use these to construct linear dominance hierarchies (e.g., where $A > B > C > D$, and so on: Mascaro and Csibra 2014). When presented with two actors that infants have seen interact separately with a third actor, but not interact with each other, 10-month-olds use principles of transitive inference to predict the outcome of this novel interaction (Gazes et al. 2015). A predisposition toward hierarchical organization continues into adulthood. Adults can better perceive, remember, learn (and even prefer) asymmetric relationships (in which one actor is dominant to the other) than relationships in which both actors are equal in status (Zitek and Tiedens 2012). Finally, although it has yet to be examined in infants, 5-year-old children have spatial representations of hierarchy, representing dominance in a vertical space where the powerful are higher than the weak (Lu et al. 2017).

In infancy, one particularly salient cue to dominance is size (reviewed in Pun et al. 2017). Ten- (but not eight-) month-old infants expect

bigger individuals to be dominant to smaller individuals (Thomsen et al. 2011). When shown a video where two blocks – one larger and one smaller – vie for the same goal, infants expect the larger block to prevail, exhibiting surprise when the larger block bows down (acts subordinate) to a smaller block, but not when the smaller block acts subordinate to the larger block. By 12 months of age, infants expect these dominance relations to be stable across different contexts; when shown a video where one actor (A) wins a physical contest over another actor (B) in one context (i.e., gaining access to a contested space), infants then expect actor A to prevail over B in a new context (Mascaro and Csibra 2012). However, when infants are shown A interacting with a new actor (not-B), the infants do not expect A to prevail in this new interaction context, suggesting that infants view dominance relations as specific to a given pair of individuals (in this case, specific to A and B, and not generalizable to A and not-B). Even younger infants are sensitive to cues of dominance, using numerical group size to infer dominance. Employing a similar paradigm of contested interactions as described above (in Mascaro and Csibra 2012; Thomsen et al. 2011), Pun et al. (2016) found that 6-month-olds expect groups with fewer members to be subordinate (and defer) to groups with a greater number of members.

Infants and children are capable of using even more subtle cues, such as facial physiognomy (i.e., facial structure or features), to detect dominance. Faces with more masculine and mature features (e.g., rated as looking aggressive and older by adults) are perceived as more dominant by adults, as well as by children as young as 3-years-old (Cogsdill et al. 2014). Even infants are sensitive to these types of cues; 13-month-olds differentiate between scenarios where puppets with more masculine faces prevail from scenarios in which puppets with less masculine faces do (Hartstein et al. *under review*).

Young children can use more dynamic cues to infer dominance relations as well, although this ability has only been documented later in development (i.e., after infancy). By 3-years-old, children can use a variety of cues to detect dominance,

including physical supremacy (e.g., who prevails in a physical fight), number of resources (e.g., who has more toys), and age (e.g., who is older: Charafeddine et al. 2015). Five-year-olds (but not 3- or 4-year-olds) can infer which actor is dominant based on nonverbal cues such as body posture (e.g., standing with shoulders back vs. hunched over, head up making eye contact vs. head down with no eye contact, etc.: Brey and Shutts 2015). Providing multiple cues to dominance appears to simplify the task; when given verbal input in addition to seeing nonverbal cues (i.e., when the dominant individual gave instructions and the subordinate asked for instructions), then even 3-year-olds are able to identify who is in charge (Brey and Shutts 2015). In contrast, a separate research study conducted on 4- to 9-year-olds found that children were incapable of understanding that the one who gives instructions is dominant to the one who accepts them before the age of 7 (Gülgöz and Gelman 2016). Some of the variation across studies in the age at which children have the ability to detect and infer dominance from various behavioral cues is likely to be due to methodological differences. Thus, more research studying how and when children come to use different cues to construct social hierarchies will help clarify the developmental trajectory of this aspect of cognitive development. In sum, when presented with a variety of cues to dominance in dyadic interactions, children are remarkably accurate at inferring who is dominant and who is subordinate, and even infants are capable of using dyadic interactions to construct group-level hierarchies (Mascaro and Csibra 2014).

Applying Dominance Hierarchies to Real-World Social Groups

Understanding how children come to organize the people and social groups around them into social hierarchies is important. Children, and adults, often prefer people and groups at the top of the hierarchy (Bigler and Liben 2007), perhaps due to the fact that high-status individuals have preferential access to resources as well as social capital and thus are likely to be beneficial social or

coalitional partners (Cheney and Seyfarth 2007). This preference for high-status groups is evident even among individuals who belong to stereotypically low-status groups (e.g., a pro-White bias among Black children in the USA, see Raabe and Beelmann 2011). Much of the work on children's ability to reason about hierarchies and to apply hierarchical organization to the social groups around them has focused on two social categories that are important in much of western culture – race and gender.

In cultures where race and socioeconomic status co-vary, children begin to view racial categories in a hierarchical fashion during early childhood, and children make inferences about status using a variety of cues to dominance. When given information about occupations that differ in prestige, 6-year-old children in the USA believe Black people are more likely than White people to have low-status occupations, and expect novel occupations to be lower status when they are described as held by Black people (Bigler et al. 2003). When presented with differences in resource holding (by being shown possessions that vary in quality or quantity), preschool-aged children expect White people to have higher quality and quantity of resources than Black people in both the USA (Elenbaas and Killen 2016; Mandalaywala et al. [under review](#); Shutts et al. 2016) and South Africa (Shutts et al. 2011).

Resource holding might be a useful cue to dominance for racial categories, given the types of input children are likely to be exposed to (through media, in their daily interactions, etc.). However, information about resources might be less informative when considering how status hierarchies map onto gender categories. For instance, although the gender pay gap is well discussed among adults, wealth differences between men and women might not be salient to children, particularly those growing up in heterosexual two-parent households. Indeed, previous work found that 3- to 9-year-old children in South Africa did not use gender to predict who had nicer possessions, although they did use race in this manner (Olson et al. 2012). In contrast, when presented with prestige-based cues to dominance, such as occupation, 5- and 6-year-

olds organize gender categories in a hierarchical fashion, rating stereotypically male-biased professions (e.g., scientist) as higher status than stereotypically female-biased professions (e.g., teacher: Liben et al. 2001). When given information about symmetry in social power (i.e., differential ability to make decisions for others), children as young as 3.5-years-old say that males are higher in the social hierarchy than females (Mandalaywala et al. [under review](#)). Less work has examined how young children reason about hierarchies outside the context of race or gender, for example, in the context of the caste system in India (but see Dunham et al. (2014) for evidence that children as young as 9-years-old are aware of the relationship between caste and wealth, rating Brahmins as wealthy and Dalits as poor).

Applying Hierarchies to the Self

Although children are aware of the dominant stereotypes about status, at least as they are applied to culturally-relevant social groups, they do not readily apply these stereotypes to themselves. This suggests a disconnect between knowledge of stereotypes and internalization of stereotype content. Although children between the ages of 3.5- and 7-years-old display awareness of culturally relevant stereotypes about status hierarchies, these same children do not apply societal stereotypes about status hierarchies to themselves. At these ages, even children who belong to groups that are stereotyped as lower-status (e.g., female or African-American children) perceive their own status to be high (Mandalaywala et al. [under review](#)). In other words, children's subjective social status (e.g., their perception of their place in a social hierarchy) does not shift in accordance with their objective social status (e.g., their status based on group-membership is a stereotypically higher or lower status social group). This is an important point, as subjective social status is a strong predictor of health and well-being. Although socioeconomic status (SES, often determined through a combination of educational attainment, occupational prestige, and income) is obviously important for determining

access to resources and opportunities, among adults, subjective status can differ from SES. Importantly, people who feel lower in the hierarchy than their SES would imply (i.e., having lower subjective status) have more health problems and are likely to die at a younger age than their SES-matched peers who do not feel low in the hierarchy (Singh-Manoux et al. 2005). Whereas young children seem relatively immune to the potentially pernicious consequences of subjective status, by 10-years-old, children's subjective status assessments begin to match family SES (Mistry et al. 2015). Better understanding exactly when and why children begin to view their subjective status as lower, and when they start to view themselves as members of group-based social hierarchies more generally, will help us understand the development of reasoning about hierarchies.

Conclusion

From an early age, humans are able to use a variety of cues to infer dominance and can use these cues to construct social hierarchies. Although this work sheds light on the types of dominance cues individuals use to determine social standing, it is unclear how infants and children determine what cues to dominance are the most relevant and informative in their environment and to the particular hierarchy in question. A cue such as being physically larger in body size is used to signal and infer dominance relations across a broad swath of non-human species and thus is likely to have ancient evolutionary roots. Therefore, we might expect among humans that larger body size is cross-culturally understood as signaling dominance and that individuals infer dominance based on larger body size from early in development. However, other cues, especially those based on culturally-specific concepts of prestige, are likely to be culturally dependent (e.g., being a priest may be prestigious in Italy, a predominantly Catholic country, but not in Saudi Arabia, a predominantly Muslim country). To best understand the role of cultural input on the development and consequences of children's reasoning about hierarchies, cross-cultural work looking directly at the types of

input about status hierarchies that children are exposed to will be necessary. Finally, although very little work has examined the development of reasoning about dominance relations in non-humans, comparative research would shed light on the cognitive adaptations underpinning the evolution of humans' rather remarkable (but not unique) abilities to structure complex societies into stable, informative hierarchies.

Cross-References

- ▶ [Domain-Specific Reasoning About Dominance Hierarchies](#)
- ▶ [Dominance Hierarchies](#)
- ▶ [Function of Dominance](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)

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Emergent Literacy

► Language Acquisition in the Home

Emergentist Approaches to Language

► Modern Theories of Language

Emesis Gravidarum

► Pregnancy Sickness

Emma Darwin

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Introduction

Emma Darwin is best known not so much for who she was or what she did but for being the wife of Charles Darwin. However, “wife of Charles” does not begin to address her importance or her life.

She was intelligent, well-read, and had strong opinions which she was not afraid to state. She was an outgoing woman with many friends and family members who enjoyed the quiet of country life. She was a devoted wife and mother who also pursued her own interests. In short, she was as complex as any modern woman and deserving of a closer examination of her life.

Early Life

Emma Darwin (*née*: Wedgwood) was born on May 2, 1808, and was the youngest child and fourth daughter of Josiah Wedgwood II. From a young age, she was known for her high spirits and general lack of tidiness. Emma grew up in a very liberal household. The Wedgwoods were a family of readers. They encouraged liberal thinking, education, an intellectual lifestyle, free speech, and respect for all people. They were also very active in their support for the abolition of slavery. Emma knew French, German, and Italian. She also rode, danced, was an archer, and was gifted at playing the piano. Reportedly, she received some lessons from both Moscheles and Chopin (although the latter remains unverified). Emma developed a love of politics early and followed political news closely throughout her life. Much of what we know about Emma is through copies kept by herself and her family members of her frequent correspondence and through a journal she kept from the age of 16 until her death (Litchfield 1915a, 1915b; Loy and Loy 2010).

Marriage to Charles

As a Wedgwood and part of the extended and intertwined Darwin-Wedgwood family, Charles and Emma knew each other for most of their lives. Charles proposed and Emma accepted on November 11, 1838. There followed many letters between members of the two families expressing their delight at the pairing. Charles worried that he was not good enough and did not deserve a wife such as Emma. He also worried that she would find life with him far too quiet and dull after growing up in a lively household. He stated in a letter to her that he hoped to prove himself worthy

of her and, perhaps foretelling the future, that he needed her to take care of him. In a letter to her aunt, Emma remarked that one of Charles' traits that made her happy was his lack of fastidiousness; however, she was unhappy that he did not enjoy attending plays. They married on January 29, 1839 (Litchfield 1915b).

Emma's primary concerns regarding getting married were leaving her sister, Elizabeth, to be the sole care-taker of their mother and father who both had failing health when they had been sharing those duties and Charles' dwindling or lackluster Christianity. The latter, to Emma, meant they could not be together in the afterlife. All indicators are that Charles and Emma fell deeply in love with one another – if not before the wedding then certainly afterwards – and she obviously married him despite her worries (Litchfield 1915a, 1915b; Loy and Loy 2010).

Josiah Wedgwood and Robert Darwin, Charles' father, both contributed to the new couple's financial well-being on the announcement of their betrothal. Emma brought into the marriage £5000 in investments and a £400 annual allowance while Charles received a £10,000 investment with £600 per year expected in dividends. Combined, in today's terms, this equates to a net worth of \$1.25 million with an annual income of approximately \$83,000. They were quite well-off when first married and continued to accumulate wealth and property over the years via investment, inheritance, and earnings from Charles' publications. By today's standards, they were multimillionaires by the time they were 50 years old (Loy and Loy 2010).

Middle Life

By the middle of 1844, Emma was in her mid-30s and Charles had finished a 230-page draft of his "species theory." He wrote Emma detailed instructions on what to do with the draft, who to have edit it, what publishers to approach, etc. in case he died before doing anything with it himself. Despite their differences when it came to religion, he completely trusted Emma to fulfill his wishes regarding the document. Additionally, he had her act as his first editor – reading, commenting upon, and correcting the manuscript wherever she

encountered grammatical issues, unsupported assumptions, or questionable conclusions. By all accounts, she was a meticulous taskmaster. Charles then put the manuscript aside. Emma's role here was important as this was one of the first steps leading to the publication of Charles' evolutionary work (Loy and Loy 2010).

Emma was also very social – far more so than Charles – and placed great stock in lively conversation. When not pregnant, she would make frequent trips to London to socialize, attend concerts, and see plays. Sometimes Charles would go with her, other times he would not. Though social, Emma also tended to be very matter-of-fact in her approach to life. When Charles received the Royal Medal for Natural Science in November of 1853 – a high honor – Emma's only comment in her diary was that he had gone to London (Loy and Loy 2010).

Emma's final pregnancy of ten, in 1856, occurred when she was 48 years old. She had suffered from pregnancy sickness through them all. For the last, she took "blue pills," which contained mercury, to help with the sickness. For her last few pregnancies, she used chloroform during the birthing process. Her last child, Charles Waring Darwin, may have had Down's Syndrome or may have had some level of retardation due to mercury poisoning in utero from the pills (Loy and Loy 2010).

Emma's nursemaid skills were called upon throughout her life. Not only did she take care of Charles through his many bouts of recurring and debilitating illness but also most of her children were ill to very ill at various points. The Darwins lost their first daughter, Annie, when she was only 10 years old to what may have been tuberculosis. Some of the children contracted but survived scarlet fever while her last baby, Charles Waring, died of that disease at only 18 months of age. Others, such as Henrietta, were sent off to hydropathists for "water treatments" (the same as those Charles endured) for months at a time in an attempt to address their ailments. It has been suggested that there may have been a "cult of ill health" at Down House fostered by an overly solicitous mother (Emma) that, at some level, encouraged invalids. However, it is also very true that there was serious illness after serious illness (e.g., diphtheria, scarlet fever, tuberculosis, measles, typhus/typhoid fever)

within the family and all members seem to have suffered from perennial dental problems requiring extractions (Loy and Loy 2010).

Late Life

In 1859, Emma again worked with Charles on what had become *The Origin of Species* by helping him to read and correct the proofs from the publisher. Although she did not agree with the ideas presented therein and continued to worry about Charles' soul, Emma was willing to accept what she considered the "bad" with the "good" of being with Charles Darwin in their 20th year of marriage. She did, in fact, rejoice with him over the positive reviews and commiserate over the negative ones. In the following years, Emma would also function as Charles' personal secretary, helping him to deal with the high volume of correspondence he both sent and received (Loy and Loy 2010).

Despite their very different opinions regarding religion early in their marriage, Emma's views changed significantly over the 43 years that they were married. Not long before Charles' death on April 19, 1882, Emma remarked to one of her children that her opinions, like those of Charles, differed significantly from those of her son's very religious fiancée. Emma was too ill to attend Charles' funeral and did not view his gravesite at Westminster Abbey until almost one year later. Following Charles' death, Emma split her time between Down House and a residence in Cambridge with her daughter, Bessy. Two of her sons, Horace and Frank, built houses on either side of the Cambridge house, thus creating a Darwin compound there (Loy and Loy 2010).

By her 77th year, Emma's strength and stamina were on the decline and she spent more and more time in her "bath chair" – an early version of a wheelchair. Her hearing was also diminishing. She was, however, still a voracious reader and spent much time following the political scene. That same year, 1885, her son Frank was working on *The Life and Letters of Charles Darwin*, which included the short autobiography Charles had written as a memento for the family. Emma worked with Frank to edit Charles' comments

on religion, removing passages she thought might be offensive to others or that she felt not worthy of his memory. It was not until 1958 that an unabridged version of the autobiography was published by Charles' and Emma's granddaughter (Loy and Loy 2010).

Conclusion

Emma Darwin does not really have a "claim to fame." Charles was the famous member of the family. However, she formed the core of their family, kept the household functioning, suffered though many births and deaths, entertained the minions who flocked to Charles like moths to a lantern, and facilitated Charles' ability to write and publish. Without her, it is doubtful that Charles could have accomplished all that he did. She was, in short, the steady foundation upon which Charles built his opus.

Cross-References

► [Charles Darwin](#)

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Emotion

► [Sex Differences in Emotional Communication](#)

Emotion Detection

► [Selective Attunement to Adaptive Problems](#)

Emotional

► [Genetic Relatedness and Child Abuse](#)

Emotional Bond

► [John Bowlby and Attachment Theory](#)

Emotional Closeness Predicted by Relatedness

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Synonyms

[Altruism](#); [Bonding](#); [Empathy](#); [Kin](#); [Prosociality](#); [Relationship closeness](#); [Social closeness](#)

Definition

Emotional closeness is used to measure the strength of a relationship. Humans tend to feel emotionally closer to genetically close kin compared to more distant relatives or non-kin. Emotional closeness is also high between spouses and affinal kin, who share a reproductive interest in mutual offspring.

Individuals feel more compassion for and provide more help to emotionally close others. Among close kin, however, emotional closeness explains only part of the willingness to help.

Introduction

Emotional closeness is a kind of magic wand for scholars of sociality. Close dyadic bonds are the foundation for primate cooperation, and a seemingly trivial question – “how close do you feel to ‘x’?” – taps deep also into human behavior.

Charles Darwin (1871, p. 308) was the first to link the “all important emotion of sympathy” to social behavior and family relations. Emotional closeness has since been confirmed as a crucial factor in assessing relationship strength, alongside other factors such as contact frequency, geographical proximity, and the types of activities engaged in together (Dunbar and Shultz 2010). Today, emotional closeness is commonly used in surveys and experiments to assess the quality of a dyadic social bond at a particular moment. Emotional closeness can be assessed verbally or visually through the inclusion of other in self (IOS) test (Aron et al. 1992).

Feeling emotionally close is associated with trust, commitment, empathy and compassion, and a willingness to help and support the concerned individual (e.g., Korchmaros and Kenny 2001). Its function may be to enhance the smoothness of interactions between individuals. Since processing all past interactions in each social encounter would be cognitively encumbering and slow, mammals including humans appear to rely on a feeling of “bondedness” to guide their actions. Thus feeling close may provide a psychological shortcut to whether a particular individual should be helped or trusted.

Closeness and Kinship

Kinship is one of the most robust predictors of emotional closeness. Bondedness between family members extends beyond the functional tasks of mating and parenting: it characterizes human sociality across the life course (Emlen 1995). Emotional closeness is also typically higher towards members from an individual’s own group, between individuals who have a shared history of coresidence, reciprocal support or interaction, and among females.

Close genetic relatives are known to preferentially associate with each other across the life course. This behavior is partly explained by emotional closeness among kin. Based on inclusive fitness theory, emotional closeness can be expected to emerge among individuals who are closely genetically related and of high

reproductive value to each other (Hughes 1988). Indeed, empirical studies have consistently found emotional closeness to correlate with degrees of genetic relatedness in different societies. For instance, aunts and uncles who are monozygotic twins are socially closer to their nieces and nephews, to whom they are 50% related, compared to aunts and uncles who are dizygotic twins and on average 25% related to their nieces and nephews (Segal et al. 2007). Korchmaros and Kenny (2001) found that emotional closeness accounted for around 30% of the effect that genetic relatedness had on helping behavior.

Emotional closeness cannot, however, fully account for altruistic behavior towards close kin. Nepotistic tendencies are to be expected among kin also irrespective of emotional closeness. Close relatives are helped even when they are not particularly liked, and the relationship includes strain and conflicts. This effect has been called the “kinship premium” (Curry et al. 2013). Among non-kin, by contrast, emotional closeness is more strongly correlated with altruistic helping, as well as more easily taxed by arguments or loss of trust (Stewart-Williams 2008).

Closeness and Reproductive Interest

Two additions should be made to the general and positive association between genetic relatedness and emotional closeness. First, emotional closeness among kin can coexist with or be superseded by kin competition. For many years after weaning, human infants are exceptionally dependent on the resources provided by others. Since the flow of these resources is usually from the older generation to the younger, resource competition is likely to be especially severe between members of the same generation, such as siblings and cousins (Hughes 1988). This can explain why the closest friends typically score higher on emotional closeness in Western societies than siblings do (Stewart-Williams 2008).

Second, it is not so much genetic relatedness in itself, as investment in shared and dependent offspring that characterizes the social dynamics of cooperative breeders such as humans (Emlen

1995). Emotional closeness among adults can therefore be predicted to be highest among individuals who cooperate to protect and rear shared descendants (Hughes 1988), for example, among the parents and grandparents of a child. This is the ultimate reason for why emotional closeness tends to be strong between spouses, who are usually not closely genetically related, and why having a child may strengthen the emotional bond between a couple and their parents-in-law (Danielsbacka et al. 2015).

Conclusion

Emotional closeness varies with gender and age, so that females experience it more, and it is more often directed towards subjects of higher reproductive value, who usually represent the younger generation.

As the saying “blood is thicker than water” denotes, the greater their genetic relatedness or shared reproductive interest in offspring, the closer individuals become. Thus genetically close relatives, as well as spouses and affines, tend to feel emotionally closer to each other than to non-kin. Their mutual sympathy can also stand more strain and conflicts than other relationships can. The tendency for higher emotional closeness among close kin can be reduced by kin competition. Emotional closeness does not fully account for altruism among close kin.

Cross-References

- [Kin Altruism](#)
- [Reproductive Value](#)
- [Resource Competition](#)

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Emotional Communication

- [Sex Differences in Emotional Communication](#)

Emotional Contagion

- [Empathy in Rats](#)
- [Gratitude, Sympathy, and Empathy](#)

Emotional Disposition

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Synonyms

[Character](#); [Nature](#); [Temper](#); [Temperament](#)

Definition

The tendency to have a particular type of affective experience, most often toward the type of experience the person has already had.

Introduction

Consciousness is considered to be the state of being aware of an external object (van Gulick 2004) or something within oneself (Farthing 1992). An emotion reflects the current state of consciousness and influences behavior (Schwarz 1990). Thus, an emotional disposition is an important part of the mechanism of consciousness as a persistent tendency to feel a specific kind of emotion in the presence of a certain object. Although the original states of emotion arise under certain general types of situation rather than specific individuals, living creatures, or things, they come to be associated with certain individuals or nonliving things while obtaining personal experience. After being formed this way, emotional dispositions manifest themselves in the form of actual emotion on specific occasions.

Importantly, the term “emotional disposition” is not the same as an “emotional mood.” While mood is an actual affect of consciousness, emotional disposition occurs even when either the mood or the emotion itself is not being felt. Therefore, such broadly used words as “like” and “love” generally suggest emotional dispositions rather than emotions currently felt. As pointed out by William McDougall (1932), “on the higher levels of mental life, where ideas and concepts play a prominent part, emotional dispositions are very complex, and are called Sentiments or Interests.”

Emotional Dispositions and Character Traits

Emotional dispositions are often compared with character traits, since some individuals may be more prone to experiencing certain emotions. Sensitive people can start feeling anger sooner when their personal boundaries are being violated than less sensitive individuals (Novaco 1986). Paul Ekman, an American psychologist who is a pioneer in the study of emotions and their relation to facial expressions, suggested to classify the following emotions as basic: anger, disgust, fear, happiness, sadness, surprise. He subsequently

added ten more basic emotions to his list: amusement, contempt, embarrassment, excitement, guilt, pride in achievement, relief, satisfaction, sensory pleasure, and shame (Ekman 1999). All of these emotions are linked to personality traits and are thus related to emotional dispositions.

Emotional Dispositions and Personality Characteristics

Personality research shows a link between dispositional positive and negative affect and the Big Five factors such as extraversion, conscientiousness, agreeableness, openness to experience, and neuroticism (McCrae and Costa 1991; Shiota et al. 2006). For example, extraversion is positively correlated with predicted frequency and intensity of felt positive emotion, as well as reactivity to positive feedback representing positive emotional predisposition (Bachorowski and Braaten 1994; Wilson and Gullone 1999). These results also suggest that relationships between dispositional positive emotionality and the Big Five personality variables are far more complex than previous research indicates, opening new horizons in future studies to fully understand the relationships between human personality and emotional dispositions.

Regulation of Altruism by Emotional Disposition

Robert Trivers, an American evolutionary biologist and sociobiologist, proposed the theory of reciprocal altruism – i.e., contingent cooperative investments between non-kin individuals that are based on the cooperative returns (Trivers 1971). He stated that certain emotional dispositions linked to social structures and cultural traditions are important in explaining the tendency to cooperate or cheat. Trivers suggested that people differ in the degree of tendencies and responses based on emotional dispositions. These dispositions are crucial for creating friendships/partnerships, and they affect human culture and the structure of societies. Robert Trivers proposed the following

emotional dispositions that are evolutionarily linked to reciprocal altruism in humans:

1. Friendship and emotions of liking and disliking. These emotional dispositions are important for an act of altruism to take place.
2. Moralistic aggression. This instrument is a part of the mechanism to protect an altruist against cheaters. The moralistic altruist functions to instruct/punish a cheater.
3. Gratitude and sympathy. Receiving gratitude can encourage altruistic responses by a receiver.
4. Guilt and reparative altruism. Guilt may prevent the defector from defecting/cheating again.
5. Subtle cheating. This type of cheating was used to explain the existence of adaptive sociopathy.
6. Trust and suspicion. Measures to control for cheating and subtle cheating.
7. Partnerships. Kind of altruism to create partnership and alliances.

Emotional Dispositions in Social and Political Life

Anger and fear as dominant aspects of modern political life are considered as emotional dispositions/emotional states often being exploited by domestic or international elites and mass media for political purposes (Lupia and Menning 2009; Hatemi et al. 2013). A considerable part of political science deals with the methods by which the public is manipulated through the activation and escalation of fear and anger (Brader 2005; Abramson et al. 2007). An interesting study by Skitka and colleagues (2004) demonstrated that in response to 9/11, individuals who were angry but not fearful supported expanding the war beyond Afghanistan, while fearful but not angry individuals supported deporting Arab Americans and first-generation immigrants out of the country. Importantly, a significant heterogeneity in fear disposition was found between individuals (Neale and Fulker 1984; Kolassa et al. 2008), which is partly due to genetic differences

(Olsson et al. 2005; Santos et al. 2010). This shows that dispositions such as fear are malleable but can be manipulated only to a certain extent. This is a significant finding in light of the role that genetic and other biological factors have on formation of political attitudes (Schreiber and Iacoboni 2012).

Conclusions

Emotional dispositions are important for understanding behavioral decisions that humans and other organisms make as individuals, groups, and societies. Some emotional dispositions and their evolution can be understood in terms of regulation of altruism. Emotional dispositions are linked to personality and thus are dependent on genetic and physiological factors. Multidisciplinary research is therefore of major importance in this field.

Cross-References

- [Altruism](#)
- [Consciousness](#)
- [Emotion](#)
- [Mood](#)
- [Reciprocal Altruism](#)

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Emotional Jealousy

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Definition

An emotional state that occurs in response to a perceived or real threat to one's intimate relationship, specific to when a partner directs time and resources to another person.

Emotional Jealousy

Jealousy is defined as an emotional state that occurs in response to a perceived or real threat to a social relationship (Buss et al. 1992). When a perceived or real threat occurs, people respond in a way that counteracts the threat in order to protect the relationship, suggesting jealousy is an evolved adaptation (Buss et al. 1992; Buss and Haselton 2005). Jealousy in intimate relationships takes one of two forms: *sexual jealousy* and *emotional jealousy*. Sexual jealousy occurs in response to a partner's sexual involvement with another person (see ► [“Sexual Jealousy”](#)), whereas emotional jealousy occurs in response to emotional involvement with another person. Men and women both experience sexual and emotional jealousy, though data and theory suggests the sexes may differ on the degree to which they respond to either type.

Several studies have examined the underlying factors that lead to emotional jealousy within relationships. Traditionally, psychologists considered jealousy a pathology that manifests itself identically in both men and women. However, evolutionary-informed research has suggested that men are more likely to find sexual infidelity more distressing due to cuckoldry risk, (i.e., cuckoldry risk is the risk of unknowingly raising unrelated offspring; male sexual jealousy in response to cues to partner infidelity is hypothesized to have evolved in response to such a risk, Buss et al. 1992). whereas women are more likely to find emotional infidelity more distressing due to

Emotional Distress

► Girls Psychological Bullying

the potential loss of commitment and resources (Buss and Haselton 2005; Buss et al. 1992). This latter situation is particularly salient to women because a barrier to women's fitness is mate quality, which includes accessing their partner's resources to assist with raising and protecting offspring. Men who pursued long-term emotional relationships with other women posed reproductive costs to their partner due to a loss in parental investment. These actions are not as costly to men because their reproductive success increases through mate number. Thus, it has been argued that women are more sensitive to emotional jealousy because it identifies a reproductively relevant threat and motivates them to minimize such a threat.

Consistent with this hypothesis, Buss et al. (1992) found that 60% of men reported greater distress over their partner's sexual infidelity whereas 83% of women reported greater distress over their partner's emotional infidelity. Use of alternative operational definitions also found converging evidence. For example, using Electrodermal Activity (EDA) to measure autonomic arousal, men showed a significant increase in EDA when imagining sexual infidelity compared to imagining emotional infidelity, and women showed a significant increase in EDA when imagining emotional infidelity.

Although many studies have replicated these sex differences in emotional jealousy, the magnitude of these differences varies across cultures (e.g., Buunk et al. 1996), and some have suggested the effect is not robust (Harris 2003). For example, some have been critical of using forced choice options (i.e., participants need to choose which of sexual and emotional infidelity is worse), finding that sex difference effects disappear when using continuous measures of emotional and sexual jealousy (DeSteno and Salovey 1996). There were, however, methodological issues with these studies (Sagarin 2005), and a follow-up meta-analysis using more appropriate methodology found evidence supporting sex differences on types of jealousy, even when using continuous measures (Sagarin et al. 2012).

Psychometric investigations of emotional jealousy require greater attention. There does not appear to be a clear method for independently assessing emotional jealousy. Most measures

consider other psychological responses to emotional infidelity, which may or may not be valid indicators of emotional jealousy, such as outrage, sadness, worry, among many others (see Sagarin et al. 2012). Specifically, Shackelford et al. (2000) identified 103 possible emotional responses to infidelity, and these items factored in 15 components: undesirable/insecure, hostile/vengeful, depressed, helpless/abandoned, happy, shocked, nauseated/repulsed, blameworthy, content/relieved, humiliated, sexually aroused, tired, homicidal/suicidal, anxious, and forgiving. Although Shackelford tested to see if these outcomes varied by sex and infidelity type, it is still not clear if some psychological responses are specific indicators of emotional jealousy or if they are outcomes from it. This literature would benefit from psychometric research on the validity of quantifying emotional jealousy by testing for its content validity and discriminant validity from sexual jealousy. Developing psychological assessments specific to quantifying variation in emotional jealousy will assist with further research on evaluating its causes, consequences, and function.

In the psychological literature, emotional jealousy varies in its operational definition because it can also refer to its affective response, which differs from cognitive jealousy and behavioral jealousy. A psychometric study found that items in a measure of jealousy fell into one of these three factors, and that emotional jealousy was positively associated with relationship love, whereas cognitive jealousy was negatively associated (Pfeiffer and Wong 1989). This literature has some inconsistent findings – although emotional jealousy is associated with relationship love, others found that it is negatively associated with happiness and relationship satisfaction (Pfeiffer and Wong 1989; Anderson et al. 1995). Further theoretical and empirical works on understanding emotional jealousy as an affective component are needed.

Cross-References

- Jealousy
- Jealousy and Infidelity
- Sexual Jealousy

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Emotional Solutions to Free Riding

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Synonyms

Emotions; Free rider

Definition

A free rider is an individual who benefits from accessing a public resource, but does not contribute toward the sustainability of that resource. The core logic of an emotional solution to the free rider problem centers on the idea that emotions can provide powerful incentives for an individual to cooperate in sustaining a public good as well as powerful incentives to punish those who fail to cooperate in sustaining a public good.

Introduction

The classic example of free riding is Hardin's (1968) *tragedy of the commons* in which the unregulated grazing of cattle on a parcel of common land leads to the eventual depletion of that resource through overuse. The role of emotions as solutions to the free rider problem can be illustrated by combining behavioral economics methodologies (e.g., modeling social interactions as bargaining games) with insights from evolutionary psychology (the idea of emotions as strategic decision-making devices).

The core logic of how emotions might solve the free rider problem centers on the idea that emotions can function as strategic commitment devices that compel individuals to pursue strategies that maximize long-term payoffs rather than pursuing strategies that promise spuriously attractive immediate rewards (see Nesse 2001; Ketelaar 2006 for reviews). The sentiment of gratitude, for example, can compel an individual to repay an act of kindness even when the cost of repayment exceeds the initial benefit bestowed upon the actor (Hirschleifer 1987). While costly acts of gratitude-inspired reciprocity may provide no immediate rewards, the benefits of such acts (e.g., stronger alliances, increased social capital) can be reaped in future social encounters. Similarly, the emotion of guilt can compel a person to redress a harm that they have inflicted upon another party, even when there is little chance of immediate retaliation from the offended party. As such, guilt functions to maximize the long-term benefits of immediately

redressing such harms (or signaling your willingness to do so) by repairing the damage done to a relationship with a potential long-term social interaction partner.

So, how can emotions such as anger or guilt function as commitment devices that solve the problem of free riding? One mechanism by which anger can function as commitment device is by serving as a guarantor of threats directed toward under-contributors in collective actions (see Hirshleifer 1987, 2001 for a more general discussion of emotions as guarantors of threats). The *ultimatum game* studied by behavioral economists, for example, provides a nice environment in which to study anger and social decision-making. The *ultimatum game* consists of a social bargaining game in which a communal resource is split between two parties. One party (the ultimatum-giver) proposes how the resource is to be divided, but the final decision regarding whether the resource is actually divided (in the manner proposed by the ultimatum-giver) lies in the hands of the recipient of the ultimatum. In one study of the ultimatum game, it was observed that feelings of anger (reported by the ultimatum recipient) were associated with rejections of unfair ultimatums (Pillutla and Murnighan 1996). Other studies have found that participants make greater concessions in negotiations when they believe that their negotiation partner is angry than when they believe that their partner is happy (Van Kleef et al. 2004). In another study that is more directly related to the free rider problem, one third of the participants in a repeated public goods game consistently punished group members who made deviant contributions. Of particular relevance to the role of emotions in solving the free rider problem, it was observed that these costly acts of punishment were directed toward low contributors and were linked to feelings of anger on the part of the punishers (Fehr and Gächter 2002).

Through a somewhat different psychological mechanism, guilt can also serve as a commitment device that solves the problem of free riding. Consistent with the notion that guilt provides a powerful incentive to cooperate when there is a

temptation to behave in a self-interested fashion, one study found that 57% of participants in a repeated ultimatum game reported feelings of guilt after proposing an unfair division of the money in the first round of play. More important, these feelings of guilt were predictive of increased cooperation in the second round. More specifically, 91% of the participants who felt guilty after proposing a selfish offer made a subsequently generous offer in the second round. By comparison, only 22% of the participants who felt no guilt after making a similarly unfair offer made a generous offer in the second round (Ketelaar and Au 2003). The link between feelings of guilt after engaging in self-interested behavior was also demonstrated in a study of the iterated prisoner's dilemma where increased cooperation was associated with feeling guilty after behaving non-cooperatively. This study found that individuals who felt guilty immediately after defecting across several rounds of the iterated prisoner's dilemma subsequently displayed 25% more cooperation compared with those who reported felt no such feelings of guilt after defecting (Ketelaar and Au 2003).

Conclusion

Emotions can “solve” the free rider problem by functioning as commitment devices that compel individuals to contribute to a public good and to punish those who fail to cooperate in sustaining a common resource. Certain emotions – such as guilt – can compel an individual to cooperate even when it is not in their immediate self-interest to do so, whereas other emotions – such as anger – can compel an individual to punish those who fail to cooperate in sustaining a public good (Ketelaar 2006).

Cross-References

- Behavioral Economics
- Cooperation
- Emotion

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Emotional Unfaithfulness

- [Jealousy and Infidelity](#)
- [Sexual Infidelity Versus Emotional Infidelity](#)

Emotions

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Definition

Emotions are phenomena that emerge from more basic biological and psychological ingredients, which represent the relationship between the

function of a person's physiological systems, past experiences that the person has had, and the context in which the person is in the moment, to provide granular, context-specific information that organizes experience and can be used to guide action.

Introduction

An emotion is an emergent phenomenon that represents the relationship between the function of a person's physiological systems, past experiences that the person has had, and the context in which the person is in the moment to provide granular, context-specific information that can be used to guide action. Emotions – such as anger, happiness, sadness, and fear – emerge from more basic or fundamental biological processes within individual people, as well as basic or fundamental social processes created by groups of people. Neither the individual-level nor social group-level processes are specific to emotions, but rather those processes serve many functions, of which supporting the generation of emotions is one. That is to say, emotions are not circuits in the brain or body, nor do they arise from discrete dedicated biological circuits. Neither are emotions sociocultural programs or modules that are exclusively learned in, or exist solely as a result of, social contexts and experiences. Rather, human emotions arise from the interplay between complex biological systems which are embedded into human social systems.

Definitions of emotion as emergent phenomena arise from a variety of academic traditions including philosophy, anthropology, psychology, sociology, and neuroscience. As a result of this variability, different perspectives focus on different features which are necessary, sufficient, or simply important for the emergence of emotion. Even within a discipline, there is variable focus on particular ingredients. For example, psychological perspectives tend to focus on concepts, language, social relationships, and/or physiology (Barrett 2017b; Clore and Ortony 2013; Cunningham et al. 2013; Lindquist 2013; Mesquita and Boiger 2014; Russell 2003). However, psychological perspectives consistently

suggest that one component is thought to be critical for emotion to emerge – affect (sometimes called “core affect”; see Barrett and Bliss-Moreau 2009; Russell 2003) – in order to distinguish it from the generic term that refers to emotions, moods, feelings, etc.

Affect is discussed in the literature as both a biological phenomenon and a psychological phenomenon. Biologically, affect is a signal that results from an integration of interoceptive (processing of sensory signals arising from the body) and exteroceptive (processing of sensory signals arising from the environment) information and thus serves as a barometer representing an individual's place in the world (Barrett 2017b). In humans, this biological summary is available to be experienced as a psychological state. Psychologically, affect is a mental state characterized by some degree of valence (or hedonics, ranging from very good to very bad) and some degree of arousal or activation (ranging from very activated to very deactivated) (Barrett and Bliss-Moreau 2009; Russell 2003). In organisms that have the capacity to represent internal body states as “feeling,” affect is available to be felt consciously as feelings of pleasantness and unpleasantness or activation or deactivation. Importantly, human affect is not necessarily conscious (for a discussion of affect and consciousness, (Russell 2005)) – biological systems are always in action even if a person is unaware of his or her affective state. Major shifts in affective state (e.g., from neutral to positive or between degrees of positivity or negativity) capture attentional resources, allowing affect to be experienced consciously in some organisms. Directed top-down attention can also bring affect into conscious awareness – for example, asking oneself or being asked, how do you feel? Affective states provide the individual with global, agranular (or fairly nonspecific) information about its relationship to the world – e.g., this is bad for me, this is good for me – and produce course behavioral responses that subserve survival-related goals (e.g., move away, move toward). As a result, the presence of affect is sufficient to meet basic evolutionary challenges (e.g., survive long enough to reproduce) (Bliss-Moreau 2017; Bliss-Moreau et al. 2018).

Humans have long been the primary species for the study of affect – and in particular the conscious experience of affect – but humans are not the only species to have affect, although its nature and complexity may vary across the animal kingdom. For humans, physiological signals from the periphery generated by the autonomic nervous system are critical for affect (Barrett and Bliss-Moreau 2009; Craig 2011; Critchley and Nagai 2012) because they are interoceptive signals and they also mediate exteroceptive processes. Thus, we have hypothesized that nonhuman animals that share homologous (or nearly homologous) autonomic nervous systems with humans will have similarly structured and functioning affect (Barrett and Bliss-Moreau 2009; Bliss-Moreau 2017). Both functional and anatomical evidence from nonhuman primates speak to these homologies (e.g., Bliss-Moreau et al. 2013; Kawashima et al. 2005). Note that nonhuman animals need not have the capacity to consciously represent affect as feelings of pleasantness and unpleasantness or feelings of activation for the biological signals to impact behavior. In fact, the evolutionary roots of affect are thought to be present even in organisms that do not have nervous systems (e.g., chemosensing in bacteria which allows bacteria to move toward food sources and away from chemical environments that have the potential to kill them (Wolanin and Stock 2004).

While affect may provide the foundation for emotion and has been hypothesized to be a critical ingredient of emotion (i.e., without affect, there is no emotion), emotions cannot be reduced to affect (Bliss-Moreau 2018; Russell 2003). That is to say, happiness is not reducible to pleasantness, nor are fear, disgust, and anger reducible to intense physiologically activated unpleasantness. Fear, disgust, and anger – whose foundation is in the prototype case an intensely unpleasant negative aroused state – differ from each other in terms of the contexts in which they arise, the behaviors and thoughts associated with them, their functions, and even how they are experienced consciously.

Other components, processes, or “ingredients” must be added to affect in order for emotions to emerge. New approaches grounded in neuroscience and physiology adopt what is called

a predictive coding framework (Clark 2013) to understanding this emergence. The predictive coding framework specifies that animals' brains constantly generate models of the interplay between their internal (interoceptive) and external (exteroceptive) worlds in order to anticipate what resources are needed to take action at some point in the future (Barrett 2017b). In this view, the brain predicts what is coming next using information about the past, contextual information, and present sensory and physiological information, rather than only responding to present needs, thus engaging in allostasis (predictive or anticipatory regulation of physiology) rather than homeostasis (reactive regulation of physiology) (Barrett 2017b). Physiological processes associated with allostasis (via the autonomic nervous, endocrine, and immune systems) form the basis of interoception (Craig 2003). In humans (and likely in some other animals), all of this information is represented as mental states characterized by valence and arousal – affect.

Psychological approaches suggest that emotions come to be when what we know about emotion (conceptual knowledge) and a linguistic representation of that concept are linked to an affective state via attention resources (Lindquist 2017; Russell 2003). These approaches inherently recognize that the context in which emotions emerge contributes to their emergence, in part because conceptual knowledge includes contextual information. As a result, emotions are contextually bound, although the contextual information that helps to create an emotion need not be physically present at the time of the emotion – it can be represented as conceptual information and remembered or imagined. Some of these psychological approaches particularly emphasize the importance of social contexts for learning conceptual information and language (thus emphasizing the importance of social culture) and also creating a context in which emotions emerge (thus emphasizing the importance of interpersonal relationships).

Both biological and psychological approaches emphasize that emotions provide more granular information about the world and the individual's place in the world than does affect, allowing for more efficient navigation of both the physical and

social environments (for a similar argument, see Barrett 2017b). That is, when activated unpleasant affect which signals “this is very bad for me” is transformed into fear or anger or disgust, those discrete emotions include specific conceptual information from both the individual's culture (e.g., what contexts generate each emotion or when it is appropriate to have each emotion, words for the emotions) and the individual's past experience (e.g., early socialization about which emotions happen when, specific instances that have generated similar sensation before in similar contexts) that allow the generation of context-specific behavioral responses. As a result, discrete emotions are thought to have specific functions (e.g., Fischer and Manstead 2008).

Emotions sometimes, but not always, are associated with observable outputs. Outputs include vocalizations, facial behaviors, and other overt behaviors like body postures or movement, as well as physiological signals. It has long been believed by some scientists and the general public alike that these outputs map to emotions in a predictable discrete way – such that a particular facial behavior (e.g., a smile, crinkled eyes) either is generated as a result of a particular emotion or is part of that emotion (e.g., happiness), such that behaviors can be “read” to understand the emotion state of another person (hence the phrase “facial expression” which inherently assumes that the face expresses something specific) (e.g., Shariff and Tracy 2011). A robust literature, however, demonstrates that while people having emotions do sometimes generate behaviors or peripheral physiological changes, there is tremendous variance in the extent to which they generate outputs and the nature of those outputs and how those outputs are perceived (e.g., see these meta-analytic reviews on the face in emotion (Nelson and Russell 2013) and on physiological signals in emotion (Siegel et al. 2018). Context is such a powerful force that can even override the valenced (positive or negative) meaning of outputs (e.g., Kayyal et al. 2015). Context-dependent meaning of emotion-related outputs also appears to be evolutionarily old (for a review, see Bliss-Moreau and Moadab 2017). For example, rhesus monkeys (who share a lineage with humans some 25 million years ago) use their “silent bared

teeth display,” sometimes referred to as a “fear grimace,” in both agonistic and peaceful contexts, and the meaning of the signal (either “I submit to you just in this moment” or “I submit to you in perpetuity”) is dependent on the context (Beisner and McCowan 2014). Nevertheless, people’s strong intuitive sense that their perception of emotion in others results from “reading” emotion-related outputs most likely arises from the innate ability of healthy humans to make mental inferences about others (i.e., to ascribe mental states to other agents (Mitchell 2009)) rather than the generation of discrete emotion outputs themselves.

The evolutionary roots of human emotions are present in a variety of nonhuman animals and other living organisms, allowing for both comparative study and empirical study of the evolution of emotion (what we call *EvoEmo* (Bliss-Moreau 2017; Bliss-Moreau et al. 2018)). To date, thinking about *EvoEmo* has been dominated by the view that discrete human emotions (e.g., disgust, fear, happiness, etc.) evolved meet survival and reproductive goals (Tooby and Cosmides 2008). Basic survival and reproductive goals can be met by affect alone, however, as it provides an integrated representation of interoceptive and exteroceptive information at a given moment signaling what is good or bad for the individual (including representing information about intensity or magnitude). This view is consistent with the observation that many of the most successful species on the planet (e.g., bacteria, jellyfish, cockroaches) lack brains or brain structures that would be necessary for allowing emotions to emerge from affect and other ingredients. The hypothesis that affect is sufficient to meet survival and reproduction goals of seeking food and reproductive partners (good), and avoiding predators and poisons (bad), means that the evolution of affect can be studied in many different animals.

Conclusion

Considering affect as sufficient for basic survival raises new questions about how and why human emotions evolved emerged. One possibility is that human emotions supported, were supported by,

coincided with, or were required for the development of complex and large social groups that are characteristic of human societies – and violate many of the principles of optimum group size (for a discussion, see Bliss-Moreau 2017; for a similar argument, see Tomasello 2014). In this view, affect may have been sufficient to navigate finding calorie-rich food sources and avoiding poisonous foods, but affect was not sufficient for navigation of complex social interactions such as choosing a hunting partner who would consistently share his or her spoils without trying to steal your reproductive partner (Bliss-Moreau et al. 2018). Complicated social transactions benefited from more granular information about people and experiences – including the ability to integrate past information and make predictions about future situations – that could not be represented as associations and required abstraction. Thus, the emergence of emotions in evolutionary history may have coincided with the emergence of a particular type of conceptual information that was not bound by perception of statistical regularities in the physical environment into which interceptive information was integrated – abstract concepts about internal states (for discussions of abstract concepts and human evolution related to emotion, see Barrett 2017b; and in general (not specific to emotion) see Tomasello 2014).

Cross-References

- ▶ [Emotional Disposition](#)
- ▶ [Emotional Jealousy](#)
- ▶ [Emotional Solutions to Free Riding](#)
- ▶ [Evolution of Emotion in Social Context](#)
- ▶ [Moral Emotions](#)
- ▶ [Music and Hormones](#)
- ▶ [Sex Differences in Emotional Communication](#)

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Empathic Concern

- ▶ [Empathy in Rats](#)
 - ▶ [Gratitude, Sympathy, and Empathy](#)
-

Empathy

- ▶ [Emotional Closeness Predicted by Relatedness](#)
 - ▶ [Wild Justice](#)
-

Empathy in Rats

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Synonyms

[Emotional contagion](#); [Empathic concern](#); [Pro-social behavior](#)

Definition

Empathy is the ability to understand and mentally experience an event from another being's (human or nonhuman) frame of reference.

Introduction

In humans, prosocial behaviors (actions undertaken to benefit another person) require empathy. Empathy can be defined as an emotional reaction that occurs in response to the perception of need in another (Bartal et al. 2011). While there is clear evidence of empathy in primates (Yamamoto and Takimoto 2012), the evidence for empathy in other nonhuman species, such as rodents, is considered far more controversial.

Empathy can be thought of as existing on a continuous spectrum, with various subclasses

such as “emotional contagion” (in which an individual is affected by a conspecific emotional state). Langford et al. (2006) found evidence for emotional contagion in mice. They used the “writhing test,” in which either two mice were given injections of a solution to induced abdominal pain or one mouse was given saline while the other was given the painful injection. The mice were then placed into an apparatus where they could observe one another. They found that when both were given doses of the painful injection, the mice displayed significantly more behavioral indicators of pain compared to when only one mouse received the painful injection. These results imply that there was emotional communication of pain from one mouse to another resulting in a greater display of pain behaviors. Bartal et al. (2011) provided a new paradigm designed to test empathy in rodents through goal-directed behaviors. In their study, they investigated whether rats were motivated by empathic concern to release a conspecific from a physical restraint. Free rats were tested in an open arena which contained a restraining tube within which was a trapped cagemate. Researchers found that within approximately a week, the free rats had learned to consistently lift the door to the restrainer, releasing the trapped cagemate. Free rats were tested in three conditions: one in which the restrainer contained a trapped cagemate, one in which it contained a plush rat toy, and one in which the restrainer was empty. Bartal et al. (2011) found that the free rats were significantly more likely to open the door to the restrainer if it contained a trapped cagemate. To test whether the rats were only motivated to release the trapped cagemate as a way of attaining social contact, researchers ran the rats through another condition in which they prevented social contact after release of the trapped rat and they found that the free rats continued to release the trapped conspecific regardless. Lastly, researchers investigated the value of liberating a cagemate compared to the value of obtaining a preferred food reward. In this condition, the free rats were placed into an arena which contained two restrainers, one of which always contained a chocolate reward whereas the second

either contained a trapped cagemate or was empty. When the second restrainer was empty, the free rats opened the chocolate containing restrainer significantly faster. When the second restrainer contained a cagemate, there was no significant difference in the latencies to open the two restrainers. Furthermore, the free rats would often share the chocolate reward with their liberated cagemate even though the amount available was small enough for a single rat to consume in one sitting. These results provide strong evidence that rats will behave prosocially when faced with a familiar conspecific experiencing distress.

There is some controversy surrounding the interpretation of these results, however. Silberberg et al. (2014) suggested that the behavior of the rats in Bartal et al.'s (2011) study may have actually been due to a combination of neophobia and the pursuit of social contact. In their modified replication of Bartal et al.'s (2011) study, Silberberg et al. (2014) found that given enough time after release, trapped rats often return to the empty restrainer tube (which had been presumed to be aversive) in order to maintain a closer proximity to the free rat. Furthermore, when trained to touch the door of the restrainer to open it, the free rats continued to do so even when the restrainer did not contain a trapped cagemate. They further suggested that the trapped rats' behavior (immediately leaving the restrainer) in the earlier sessions may have been a neophobic reaction to restrainer itself and the act of the door opening. As time went on, the rats grew accustomed to the apparatus and the movement of the doors, explaining why the formerly trapped rats would then return to the restrainer in later sessions.

Conclusion

While there has been some support for both the empathy hypothesis and the social contact hypothesis in some experimental situations, neither hypothesis has been able to account for the behaviors of rats in these experiments across all

conditions. Vasconcelos et al. (2012) suggest that in order to infer empathic intent, researchers must be able to demonstrate that the apparently empathetic behavior of the animal is psychologically directed to reduce the distress of the trapped individual. One way to accomplish this task is to design a new paradigm which would ensure that the only outcome of the "empathic" behavior would be to reduce the stress of the trapped individual and not to cease the stress signals displayed by the trapped individual.

Cross-References

- [Empathy](#)
- [Prosocial Behavior](#)

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Empirical

- [Falsifiability](#)

Employer Versus Employee

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Synonyms

Leadership vs. followership; Servant leadership;
Work relationship legitimation

Definition

The interface between people in relative positions of hierarchy and influence within the context of an employment relationship.

The construct of leadership likely has a long evolutionary lineage. It may have arisen, in part, as a psychological and structural solution to the challenges inherent in complex group coordination: conflict resolution, coalition formation, collective nomadism, and so forth. It could be argued that an individual's fitness would have been improved as a result of living in groups with effective leaders (Bastardo and Van Vugt 2018). If one were to imagine two largely identical groups of ancestral humans – both inhabiting the same physical environment and beholden to the same climatic and environmental parameters – with one governed by effective leadership and thus optimized decision-making and reduced group discord and the other not, then, all else equal, those fortunate enough to be part of the former will be better positioned to survive and reproduce. Thus, there is likely an ancient selective advantage for some variation on effective leadership (Van Vugt 2006).

However, leadership (and by logical extension followership) in this adaptive, ancestral sense – which was functionally bound up in immediate and salient survival objectives for vulnerable hunter-gatherers on the savannah of antiquity – is rather distinct from the kinds of social

relationships that characterize modern employer-employee relationships. In this context, survival-related goals are almost never a consideration (much less the major driving force) in these relationships, and the central interpersonal exchange in question is tied to the kinds of evolutionarily novel cultural artifacts that are typical of modern organizational life: productivity, remuneration, career progression, company values and objectives, and so on. As such, there is considerable scope for discordance between the adaptive faculties – both psychological and socio-structural – which gave rise to effective leadership in ancestral times, and the modern business contexts in which they are presently pressed into service (Van Vugt and Ronay 2014).

For one, the idea of formalized roles, job titles, and a granular delineation of responsibility which are characteristic of present day employee-employer relationships were simply not a factor in ancestral times. There were no “colleagues” as such, and no effective distinction to be made between “work life” and “home life.” Leaders were not recognized because of a codified position that could be understood as an abstraction and followers did not participate in their assigned tasks because an explicit contract formally rewarded them to do so. Again, all coordinated activity for which leaders took the reins was governed by the group's most immediately pressing survival demands (Li et al. 2018; Nicholson 2005).

While a return to a kind of “work life” where mere day-to-day survival is the group's principal aspiration would be neither practical nor preferable; there are varieties of employer-employee relationships which might better reflect and utilize our evolved capacities for leadership and followership, while also minimizing the potentially harmful impacts of evolutionary mismatch in this domain (Li et al. 2018). The idea of employees contributing in substantive, meaningful ways to the effective functioning of their organization might be one such solution. Employees tend to flourish in circumstances where they are actively involved in organizational life, and their personal

contributions to organizational outcomes are salient and apparent – a modern reimagining of the motivation to promote group survival. Smaller and flatter organizational structures that reduce hierarchies and anonymity within companies might be another solution: structuring organizations to more closely mimic the intimate and egalitarian social systems of ancestral humans, and harnessing the evolved psychological preferences of humans to work in smaller groups with people whose personalities and reputations one can keep track of (as opposed to the faceless impersonality of mega-corporations with thousands of employees, for example) (Van Vugt 2017).

Whatever potential solutions that organizations might operationalize in the service of structuring themselves along less evolutionarily discordant lines, the overarching message is that the employer-employee relationships of today's world are distinct from the leadership-follower relationships that have long been a part of the history of humanity. Recognizing this distinction, and where evolutionary mismatches might arise from it, ought to be of principal concern in any attempt to understand employer-employee relations through an evolutionary lens.

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Employment Status

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Synonyms

[Aggression](#); [Homicide](#); [Young male syndrome](#)

Definition

Men compete with other men for access to mating opportunities. Unemployed men who cannot appeal to women on the basis of their resource access may resort instead to violent competition. This provides an explanation for why young, unemployed men are the primary perpetrators of homicide.

Introduction

Acquiring the resources necessary for survival is a main focus of all living beings. Those with greater access to resources increase their ability to survive and reproduce. For males, resource access is essential both for their own survival, as well as their ability to attract mates. This leads to fierce competition among males. For humans, and most other animals, this competition can sometimes have a violent ending, with the main participants being those with the least to lose and the most to gain. This entry describes the violence and aggression resulting from this competition in unemployed men.

Evolutionary Background

Parental Investment Theory. Owing to sex differences in reproductive physiology, females have

a greater obligatory parental investment in offspring than do males (Trivers 1972). Among humans, successful reproduction requires that females produce the energy to sustain a 9-month gestation, as well as a long period of lactation following birth. The large investment of females limits the number of offspring they can have over their lifetime, leading them to choose their mates carefully, holding out for the highest quality suitor. This in turn has caused males to compete with one another for females and their parental investment (Trivers 1972). With males' parental investment being less than females, their fitness is limited only by their ability to secure mating opportunities with females. This incentivizes a short-term mating strategy that more strongly prioritizes quantity of mates over quality, allowing them to be much less selective in their mate choice relative to females.

Sexual Selection. The emphasis on short-term mating among males creates intense intrasexual competition among males for access to females. This competition may take the form of contests for direct sexual access to a female, as well as contests over access to resources that indirectly increase one's appeal to females. This competition produces selection pressure on males for traits that increase their likelihood of success. This provides an explanation for observed sex differences in height, physical strength, and violent and aggressive behavior. Males who opted out of this competition left behind fewer offspring than those who were successful, leading to the evolution of stronger and more aggressive males. Indeed, for males, it is either join the competition or be left with nothing.

Status and Reproductive Success. A key trait that predicts men's ability to successfully outcompete rivals for mating opportunities is their status. Men of high status typically have greater access to resources and are therefore preferred mates by women. Throughout history successful and high status men have deterred their rivals and increased their fitness. This is particularly true in polygamous societies where one man can have many wives, whereas other

men may have no wives at all. Betzig (1982) has documented the worldwide generality of absolute power and extreme polygamy. In Africa, harems have exceeded 1000 women, as they also have in India, China, and the Muslim world. As an extreme example, Mulay Ismail Ibn Sharif, the one-time emperor of Morocco, is estimated to have had 888 children (Daly and Wilson 1988). Similarly, estimates suggest that 0.5% of the world's population, and 8% of men in a large region of Asia, are descendants of Genghis Khan and his male-line relatives (Zerjal et al. 2003). In societies where one man has the means to do so, a large number of concubines are often kept (Daly and Wilson 1988). Indeed, men of high social rank have more wives, greater access to other men's wives, more children, and their children are more likely to survive than men of lower social status (Daly and Wilson 1988).

With their vast access to resources, women view high-status men as high-quality mates who are capable of providing for their offspring. Additionally, men may treat higher-status men with greater deference given their ability to control large shares of the group's resources. This has been the case in foraging, pastoral, horticultural, and state societies (Daly and Wilson 1988). The monopolization of mating opportunities by one or a few men creates fierce competition between men of lower social status, which may result in deadly violence as men with little to lose, and much to gain, struggle to gain access to mating opportunities.

Patterns of Violence

Wilson and Daly (1985) reported on a landmark study examining predictors of homicides in Detroit in 1972. The study revealed a pattern of violence supporting the theorizing that most homicides are motivated by competition for status among men.

Types of Homicide. Wilson and Daly (1985) discuss two types of crimes committed in 1972 Detroit, "crime specific homicides" and

“social conflict homicides.” As defined by Wilt (1974), crime specific homicides are cases where homicide was incidental to the omission of another crime (e.g., robbery) where the offender did not initially intend on killing the victim. Social conflict homicides are described as heat of the moment actions taken by the offender and not incidental to the omission of another crime. Social conflict homicides are a struggle for social resources that men deem valuable for their positive fitness consequences, including power, respect, and status. In contrast, crime specific homicides are a struggle for more tangible resources (e.g., money). The primary perpetrators of both types of violence are young men, particularly those who are unemployed.

Unemployed Men. The harsh reality of being a man of low social status is that mating opportunities are limited and the competition is more intense for you than it is for men of higher social ranking. Competition for females is the fiercest at the bottom of the scale where the male on track for total reproductive failure has nothing to lose and will therefore resort to violent tactics to improve his mating prospects (Daly and Wilson 1988). This may lead unemployed males to commit crimes, such as robbery, to gain the resources necessary to improve their fitness and deter rivals. Evidence of this comes from the research of Wilson and Daly (1985) who demonstrated that unemployed males in Detroit were more represented in crime-specific homicides (e.g., robbery 43%) than social conflict homicides (e.g., bar fights 39%). This may reflect a motivation of unemployed men to improve their social status through the acquisition of resources (Daly and Wilson 1988).

The prospect of reproductive failure may lead men to risk death in order to improve their reproductive success. This may explain why men who participate in risky criminal behavior or predatory violence have different time horizons, weighing the near future more heavily against the long term (Daly and Wilson 1988). This means that a man in a low status position will focus on what he has now (or does not have), instead of what he will have in the future. In comparison, men of higher status are more likely to make decisions

about how to act based on the future rewards or repercussions of those actions. The shorter time-horizons of unemployed men mean that the benefits gained from committing a crime (immediate increase in access to resources) outweigh the potential future consequences of that action. For instance, in Detroit in 1972, 43% of homicide victims and 41% of homicide offenders (across homicide types) were unemployed, as compared to 11% of all men in the city (Wilson and Daly 1985). The drive to improve fitness leads to risky decision-making and may cause men to participate in activities that put them at risk of ending up in prison, or dead.

Employed Men. In contrast to the unemployed, employed men have longer time horizons and focus more on how much they have to lose from engaging in risky, violent behavior. Engaging in violent behavior and/or criminal activity puts them at risk of losing the position that grants them high social status. Employed men are better served to compete for mating opportunities by conspicuously displaying their resource earning capacity to women, as opposed to putting that status in jeopardy by engaging in violent or criminal behavior.

Men with good jobs may deter rivals and attract mates as a function of their high status, making violence as a means to gain mating access unnecessary. A man with a good job or high social status may choose to walk away from a situation where his reputation is being tested and suffer no loss of respect from witnesses. Indeed, engaging in violent altercations may present more of a risk than walking away. In contrast, a man of low social status has only his reputation for toughness and therefore must respond to even minor insults in order to protect that reputation.

Conclusion

Unemployed men are more represented in crime specific homicides compared to social conflict homicides and are overrepresented in both types of crimes compared to the population of unemployed men in Detroit (Wilson and Daly 1985; Daly and Wilson 1988). Evolutionary theorizing predicts that men with low status and limited

reproductive opportunities will take drastic measures to increase their fitness. Men of low status are more likely to resort to violent crime in order to gain access to the resources necessary to attract mates, whereas men of high status have less to gain and more to lose by using violence as a way to improve their fitness.

Cross-References

- [Contexts for Men's Aggression Against Men](#)
- [Culture of Honor](#)
- [Marital Status](#)
- [Meta-Analysis of Sex Differences in Aggression](#)
- [Most Perpetrators Are Men](#)
- [Physical Aggression](#)
- [Reputation](#)
- [Same-Sex Homicide](#)
- [Sex Differences in Same-Sex Aggression](#)

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Emulation

- [Imitation](#)
- [Imitation and Mimicry](#)

Encephalization

- [Brain Evolution Resulting from Cooking](#)
- [Neurons in the Cerebral Cortex](#)

Encoded Memories

- [Inceptive and Derived Memory](#)

Encoding

- [Different Functions of Memory](#)

Encoding and Sleep

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Synonyms

[Acquisition](#); [Learning](#)

Definition

Encoding can be defined as the neuronal activity which takes place in the brain during the acquisition or learning of a new task.

Introduction

Sleep is a type of behavior exhibited by numerous species on this planet, and although there is some variability in its individual characteristics across species, there are common patterns found in all mammals (Siegel 2009). Sleep is characterized by regularity in its occurrence around the circadian cycle. In diurnal animals such as humans, it

usually takes place during the dark whereas in nocturnal animals such as rats and mice, during the light phase of the 24-h period. The duration of sleep varies depending on the type of animal, with predators enjoying more hours of sleep compared to animals that are prey. Humans are placed in the middle of this continuum, with a duration of about 8 h of sleep per night. The use of electroencephalography in the study of sleep has allowed us to discover some of its intricate attributes, such as the different stages of sleep characterized by different patterns of electrical activity. Although numerous functions for sleep have been proposed over the years, the most prominent one seems to be its role in synaptic plasticity (Born et al. 2006). The discussion in this review will focus on the various processes that take place primarily during acquisition (encoding) and postencoding processes that promote learning and memory.

Sleep and Its Role in Encoding and Long-Term Memory

Sleep is characterized by different patterns of neuronal activity in the brain as measured by recordings of electrical activity using electroencephalography (EEG). The onset of sleep is characterized by increasing reduction of brain activity (stage 1) followed by further decrease in brain activity which is characterized by sleep spindles and K complexes (stage 2). This stage leads to further slowing of brain activity known as slow wave sleep (SWS) or deep sleep (stages 3–4) which is more evident at the beginning of the sleep period. A distinct phase of sleep, known as rapid eye movement (REM) or paradoxical sleep, is characterized by a high level of brain activity as well as rapid eye movements in combination with muscle atonia or paralysis. The REM episodes are rather short in the first part of the night but get increasingly longer as the night progresses. During this stage, most of our dreaming is thought to be taking place although dreaming may also occur during non-REM sleep (Stickgold 2005).

Although we have learned a lot about sleep in the past 50 years, there are still some important questions that are either unanswered or are

answered partly. The most intriguing question which is yet to be fully answered is in regards to its function. Numerous hypotheses have been proposed, such as conservation of energy, reduction of oxidative stress, and maintenance of optimal immune system function (Siegel 2009). Yet, the hypothesis which is gaining increasing support in the last few years is the role of sleep in learning and memory (Born et al. 2006).

Encoding can be defined as the neuronal activity which takes place in the brain during the acquisition or learning of a new task. Encoding itself is of course very important but even more critical is the neuronal activity which follows this initial encoding and allows for the establishment of new knowledge. Initially reported in rat hippocampal place cells, increased firing during exploration (wake) continued when the animals went to sleep. Thus, during sleep, the neurons replayed the previous experience perhaps in order to retain the information (Wilson and McNaughton 1994).

Studies done in humans were initially focusing on the overall role of sleep on learning and memory by applying a basic approach of allowing participants to sleep or not before taking a memory test, showing an advantage for the participants that were allowed to sleep before testing (Mednick et al. 2003). Both REM and SWS have been implicated in the enhancement of learning and memory. REM sleep has been more closely associated with the enhancement of nondeclarative tasks as well as the integration of new memories within existing semantic networks. SWS has been associated with the enhancement of declarative memories (Mednick et al. 2003; Born et al. 2006).

Following acquisition, a process known as consolidation must take place, in order for the newly acquired material to be kept for long-term use. The idea of consolidation has been proposed in 1900 by Müller and Pilzecker and was later supported by research evidence, demonstrating that the consolidation process involves the synthesis of new proteins and the formation of new synapses (see review: Born et al. 2006). Although the “seat” of memory creation is the hippocampus, especially for declarative memories, the memory traces themselves are not stored in the hippocampus itself. Following an initial phase of

strengthening the memory trace in the hippocampus, the memories are transferred to areas in the neocortex which were active during encoding, so that they can be available for future use. This process of redistributing information to the neocortex is known as systems consolidation, which not only allows for the distribution of memory traces across the cortex and thus the storage of long-term memories throughout the brain, but also for the emptying of the hippocampus so that new learning can take place (Born et al. 2006).

Sleep is thought to play an important role in this process, since accumulating evidence suggests that these important processes of consolidation mainly take place during sleep. For many years, the idea was that sleep strengthens the connections that are formed during learning; however, this may be half of the story. Sleep is not adaptive only because it helps strengthen the synapses formed during encoding but also because it helps to actively remove old memory traces from the hippocampus (Norimoto et al. 2018), in order to either transfer them to the neocortex for long-term storage (Khodagholy et al. 2017) or to eliminate them (Davis and Zhong 2017).

The idea of synaptic pruning during sleep was proposed by Tononi and Cirelli (2014). The synaptic homeostatic hypothesis (SHY), which they proposed, suggests that during wake there is increased firing due to encoding of new information; thus, synaptic pruning during sleep probably helps to reinstate the brain so that it can be able to function and learn more the next day. Indeed, recent studies in mice have shown that this may be an important function of sleep. During SWS, hippocampal neurons which were active during encoding continue to display increased firing whereas neurons which were previously active (remote traces) decrease their activity, most likely in a process which promotes the removal or weakening of remote memories which can be redistributed to other areas of the brain or to be erased altogether. This aspect of “weeding out” of memories may become possible by a characteristic pattern of neuronal activity during SWS, the sharp wave ripples (SWRs) which may transfer information from the hippocampus to the areas of the neocortex (Khodagholy et al. 2017).

Thus, during sleep, the brain is continuing to work in order to enhance prior learning, to help distribute learning that has been already established to other areas for long-term reference (long-term memories) as well as to remove information which is judged to be not needed. Although the intricate mechanisms by which the brain decides on how to select which neuron should be doing what have not been identified yet, it is a rather fascinating time as the secrets of the most basic mechanisms of learning and memory are beginning to become clearer. Sleep has an important role to play as it is the main platform during which this “tagging” of memories is taking place and during which the brain is constantly updating its “archives” in order to optimally reflect experience (Stickgold and Walker 2013).

Conclusion

It seems that an amazing story is unfolding when it comes to the role of sleep in learning and memory. During acquisition, the neurons implicated in learning enhance their firing in order to encode the information in a neural code, but the story does not end there. During sleep, the consolidation of memory takes place in the hippocampus via reactivation of the neurons involved, but as time passes these neurons will pass on their information to neurons in other cortical areas. In addition, memories which are deemed to be redundant are most likely erased in order for synapses to be available for new learning to take place. These complicated processes which have such an impact on our lives are taking place during this “offline” time, when we sleep. We may not feel it but when we sleep, our brains are orchestrating numerous processes which are crucial for our ability to learn and remember.

Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Episodic Memory](#)
- ▶ [Long-Term Potentiation](#)
- ▶ [Multiple Memory Systems](#)
- ▶ [Working Memory](#)

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Enculturation

- [Social Development](#)

End of Reproductive Ability

- [Menopause](#)

Endocrine Changes

- [Women's Preferences During Ovulation](#)

Endocrinology

- [Testosterone](#)

Endogamy/Exogamy

- [Assortative Mating](#)

Endosymbiosis

- [Mitochondrial DNA](#)

Energy Balance

- [Body Reserves and Food Storage](#)

Energy Consumption

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Synonyms

[Brain energy absorption](#); [Brain metabolic costs](#);
[Food ingestion](#); [Metabolism](#)

Definition

The process of converting natural resources into fuel for bodily function and maintenance.

Introduction

What unites all of life that has ever existed is what Charles Darwin called in *The Origin of Species* (1859), *The Struggle for Existence*. Every organism experiences various pressures against their ability to survive and/or reproduce. The most basic fuel for all organisms is nutrition, which may be in the form of a single nutrient or an entire animal. Mammals, especially humans,

require a large amount of energy in order to grow, survive, and reproduce. As diet and means of obtaining food evolved, early humans or *hominids* rose to the top of the food chain with their rapidly developing brain. Using an evolutionary psychological perspective, the higher functioning regions of the human brain can be traced back to its natural origins.

Biological Functions of Energy Consumption in Mammals

All contemporary mammals require food and water in order to live and maintain proper bodily function. At a cellular level, nutrients from plants or other animals are synthesized into a molecule called adenosine triphosphate or *ATP* by the cells' mitochondria (Magistretti et al. 2000). Processing food into energy, or *energy metabolism*, serves to regulate and maintain stable conditions in all bodily systems (Brandt 2008; Magistretti et al. 2000).

The fuel to synthesize nutrients or chemicals requires energy while the mammal, for example, maintains its body heat or locomotive power (Brandt 2008). The mammal's body is modulated by its central nervous system, the brain, which commonly requires some time in order to become completely functional. Today, *Homo sapiens* brains require almost three decades in order to completely develop (Del Giudice et al. 2015).

Evolution of Human Brain Energy Consumption

Early humans already had complex nervous systems, but the difference between modern and early hominid brains was mainly due to an increase in neuron circuitry rather than an increase in neurons (Hofman 2014). The catalysts of the brain's evolution remain under investigation, but Rachel Carmody and Richard Wrangham (2009) argue that cooking food is responsible for humans' world domination. Cooked food is generally more digestible than uncooked food; thus

its metabolization becomes more efficient. Potential pathogens within the food are significantly reduced, allowing humans to develop a more eclectic cuisine with a reduced risk of getting sick. The surplus of energy resources from cooked food is suggested to have enhanced the fitness of the human brain and body. Cooked food usually has a longer shelf life than raw food; henceforth, the task of feeding multiple humans became simpler (Carmody and Wrangham 2009).

Although cooking quickly became a human phenomenon, gathering was humans' main activity for food acquisition. Food from the vegetable kingdom was more abundant in the human diet than food from the animal kingdom. The more complex the human brain evolved, the higher its metabolic costs became. Although the general human *body* consumes most of the consumed energy, the human *brain* consumes a disproportionate amount of energy. The modern human or *Homo sapiens* brain accounts for about 2–3% of its body weight, yet it consumes about 500 calories per day, which is about a quarter of what the entire body needs on average (Harari 2015).

The brain's cerebral cortex distinguishes *Homo sapiens* from other hominid species. Its function and maintenance have become the predominant source of energy allocation within the brain. For neural networks to remain active and efficient, glucose and other resources are processed. When the human is active, all sensory functions simultaneously process information from the environment (Magistretti et al. 2000), which is not metabolically cheap.

A relatively recent discovery of the brain's energy expenditure is the *default mode network* (DMN). When the human brain is at rest or when it is not concentrating on a particular task, DMN activity *increases*. Current scientists who study the DMN observe that different regions of the brain become active when other regions become inactive. It is hypothesized that the purpose of the DMN is to nurture the brain and to organize newly processed information, which would account for the disproportionate amount of energy it consumes (Raichle 2015).

The Role of Cerebral Energy Metabolism on Evolutionary Psychological Research

Humans burn their calories 27% faster than what chimpanzees can burn. Other primates also do not have as high metabolic rates as humans (Gibbons 2016). In understanding what it means to be human as a recurrent theme of evolutionary psychological research, the nuances of the brain's functions are not ignored. For other animals, hibernation is hypothesized to allocate time for the organism to conserve its energy when its energy resources are scarce (Benington and Heller 1995). Although humans do not hibernate, numerous scientists believe that sleep is an evolutionary adaptation.

It is fairly common for humans to take short and long naps during the day. Both physical and mental exhaustion engenders the desire to rest the body and mind. From an evolutionary perspective, sleep can be as beneficial to the mind as it is to the body. Processing countless information each day depletes cognitive resources, which are suggested to revamp during sleep. Conserving cognitive resources is a valuable asset to human psychology. A complex brain that runs on a quarter of the body's consumed energy requires extensive maintenance, even when at rest or asleep (Del Giudice et al. 2015).

Evolutionary psychologists acknowledge that bodily services to the brain's overall fitness is as crucial as the body's overall fitness. The ultimate adaptation humans evolved is the ability to think, which may be argued as the most biologically expensive feature. The ability to reason, make pivotal decisions, communicate with others, simultaneously process information from the environment, and learn is founded upon the human's mental capacity. Although the occupations of hunting and gathering appear to be ancient, the *Homo sapiens* brain was engineered from ancestral pressures and conditions. Evolutionary psychologists strive to learn more about human psychology with the brain's natural functions and biological origins.

Conclusion

Every organism cannot survive without its energy resources. Food provides the organism with the most basic resources for all biological systems to operate long enough for it to reproduce. It is necessary for the mammalian brain to be equipped with higher cognitive functions in order to adapt to a diverse array of environments. Consuming cooked food is still debated to be the most unearthing treasure of the human brain. As long as the brain's functional origin remains a mystery, the science of evolutionary psychology will be relentless in its pursuit to understand human behavior.

Cross-References

► [Costs and Benefits of a Large Brain](#)

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ring may convey information about an individual's financial resources, commitment to the relationship, or preferences for certain features, such as for youth and nubility in women (Cronk and Dunham 2007). The custom of giving engagement rings provides opportunities for testing evolutionary hypotheses about mate preferences and mate guarding. Engagement rings may also signal other features, such as the aesthetic sensibilities of the couple or their beliefs about traditionalness, that are not easily related to evolutionary hypotheses (Dunham 2010).

E

Engagement Rings

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Definition

An engagement ring is a ring given by a suitor around the time of a proposal of marriage. Although some engagement rings are family heirlooms, more often they are purchased either by the suitor alone or by both members of the betrothed couple. In the United States, an engagement ring is conventionally worn on the third finger of a woman's left hand. Engagement rings often include one or more diamonds. Following the marriage ceremony, the engagement ring may be worn in combination with a wedding band.

Introduction

In many human societies, the exchange of property or money around the time of marriage is socially expected and may take many forms (Fortunato et al. 2006). In the United States and some other industrialized economies, engagement rings are a form of marriage-related property transfer, usually from a man to a woman, that is conspicuous, financially costly, and socially meaningful. Beyond serving as a de facto signal of a woman's relationship status, an engagement

Engagement Rings as Signals

Engagement Rings as Signals Within the Relationship

Diamond companies and jewelers encourage the idea that a man should spend the equivalent of 2 months' salary on an engagement ring. Even when men do not follow that advice, the high cost of engagement rings has the potential to make them good opportunities for a prospective bride to assess her suitor's wealth. However, although it is true that wealthier men tend to purchase more expensive engagement rings than do their less wealthy counterparts, the relationship between male income and ring cost is not strong or consistent enough for it to serve as an effective signal of male wealth. Wealthy men often purchase rings that cost less relative to their income than do poorer men. Poorer men, on the other hand, often purchase rings that cost more relative to their incomes due to the baseline expense necessary to purchase an engagement ring at all and the availability of credit. Thus, anyone using an engagement ring to assess a male's resource control is likely to underestimate the wealth of a rich man and to overestimate the wealth of a poor man, making them rather misleading indicators of male resource control (Cronk and Dunham 2007; Dunham 2010). Fortunately, for prospective brides, women are likely to have plenty of other opportunities to assess the wealth of their suitors by the time that a proposal of marriage is made. In

cases in which an engagement ring is purchased from a couple's joint financial holdings, which happens frequently, the issue of the value of the ring as a signal of male resource control is moot (Dunham 2010).

Another possibility is that men may use engagement rings to enhance their desirability as marriage partners. This is supported by a recent study in which women indicated that they would be willing to accept an engagement ring of smaller size and lower cost in a hypothetical proposal of marriage from a man who was rated as highly attractive, in comparison to the size and cost of a ring that they would expect from a man who was considered less attractive (Cloud 2015). In another experimental study, participants expected men to spend more on engagement rings in settings with a male-biased sex ratio, consistent with the hypothesis that women can afford to be more choosy or can expect greater investment when single men are relatively plentiful (Griskevicius et al. 2012).

Camerer (1988) suggested that the high cost of an engagement ring may signal a man's commitment to the relationship. Thus, if long courtships are one signal of commitment to a relationship, an expensive ring might be particularly useful following a short one. Testing this within actual courtships, Cronk and Dunham (2007) found that shorter courtships were not associated with more expensive rings and thus that ring cost is unlikely to reassuringly signal commitment in the absence of a lengthy courtship.

The cost of an engagement ring may be associated with a woman's perceived desirability. Female youth is classically seen as a marker of fecundity and desirability, and research among the agropastoralist Kipsigis of Kenya demonstrated that younger women attracted larger bridewealths than did older women (Borgerhoff Mulder 1988). Similarly, younger women in a US sample received engagement rings that were proportionately more expensive, relative to male income, than did older women (Cronk and Dunham 2007). Furthermore, men in a psychological study indicated that they would hypothetically choose a more expensive engagement ring to propose to a woman who was considered highly

attractive than they would choose for a less attractive woman (Cloud 2015).

Engagement Rings as Signals Outside of the Relationship

In addition to signaling information between members of a couple, the gift of an engagement ring may signal information to outside parties. These parties include the kin and close social contacts of both members of the relationship, along with potential romantic rivals. Engagement rings may potentially serve a mate-guarding role wherein the conspicuousness of the ring signals to potential suitors that the wearer is in a committed relationship. Because the gift of an engagement ring creates an asymmetric signal in a heterosexual courtship, an engaged woman's relationship status can be ascertained simply by looking at her hand, whereas an engaged man's relationship status is only visually apparent if the members of the couple are seen together.

The gift of an engagement ring may signal the seriousness of the giver's intention to marry – and conversely, receiving the engagement ring may signal the recipient's intention in committing to her suitor – to social contacts who are invested in the well-being of the members of the couple, such as their kin and close friends. It may then serve a role of reassuring members of the couples' broader social circle and of facilitating multigenerational ties.

Marketing and Changing Norms

The convention of giving engagement rings upon a proposal of marriage may be affected by changing social norms. Jewelry wholesalers and retailers have a financial incentive to seek out new potential markets. One such opportunity comes through marketing fine jewelry to women to purchase for themselves. While the conventional notion is that an engagement ring is purchased by a man and presented to a woman at a surprise proposal of marriage, 16 % of couples in one study used the woman's funds to pay for part or all of the cost of an engagement ring, and women participated in the selection of the ring 42 % of the time (Dunham 2010). An advertising campaign launched in 2003 exhorted women to

“raise your right hand” and sought to increase purchases by women of diamond rings. The campaign promoted conspicuous consumption within the language of celebrating female empowerment, success, and self-worth and in doing so decoupled the association between diamond ring purchases and heterosexual marriage proposals (Crymble 2012).

Engagement rings are not exclusive to heterosexual relationships; indeed, among same-sex couples engaged to marry, two-thirds of female couples and nearly one-fifth of male couples purchased engagement rings (Wells 2014). In the aftermath of the recent US Supreme Court decision legalizing same-sex marriage nationwide, a possible further increase in same-sex marriage may involve further shifts in the engagement ring industry.

Conclusion

Engagement rings are considered to be a significant financial investment, yet have little intrinsic worth and a poor resale value. They are valuable because of what they signal and what they symbolically represent, rather than due to any advantage they confer to a couple embarking upon a new marriage. As a ritualized component of American courtship, engagement rings offer social scientists numerous remaining opportunities to test evolutionary hypotheses.

Cross-References

- [Mate Preferences](#)
- [Signaling Theory](#)

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Engagement Rings as Modern Commitment Cue

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Synonyms

[Diamond rings](#); [Pledge to marry](#); [Wedding rings](#)

Definition

A ring that one partner gives to another when they become engaged to be married as a sign of their commitment.

Introduction

It is a common practice for a man to buy a relatively expensive engagement ring, usually including a diamond, to give to his fiancée when they become engaged as a symbol of their commitment and impending marriage. Engagement

rings are often donned for the mere intent to make public a couple's relationship commitment, and the woman, specifically, is to wear an engagement ring to display that she is "taken" and out of the dating market (Schweingruber et al. 2008). There seems to be no sex difference placed on the importance of an engagement ring before marriage (Ogletree 2010).

Signaling Mate Quality

The practice of giving and wearing a ring can also communicate a kind of social achievement (Parsons 2008) such that an engaged person possesses certain desirable attributes such as stability or maturity (Black and Monteverde 1975) that makes them a suitable, long-term mate. Some theorists have even proposed the so-called "wedding ring effect" whereby engaged individuals are thought to be preferred because being engaged signals their high mate value (Dugatkin 2000). Further, in cultures where it is customary for men to wear their wedding rings during their engagement, engaged men may be seen as attractive partners because it signals their willingness to commit to family life and invest time and effort in their children (Uller and Johansson 2003). Although there is mixed evidence that suggest wearing a ring makes a person more attractive to the opposite sex (Dugatkin 2000; Uller and Johansson 2003), wearing and advertising an engagement ring is still commonly exercised.

Cost-Benefit Analyses

The practice of giving engagement rings follows a reproductive cost/benefit analysis often seen in human mating strategies. A young male suitor will likely expend the costs of a diamond engagement ring against the expected gains of a joint union with a faithful mate and subsequent reproduction (Camerer 1988). A short-term relationship would not yield as much gain, and therefore, a man could not afford to make such a costly investment in those situations. Thus, premarital

gifts can be considered a way of sorting potential partners according to their intentions like investment plans.

In the past, marriage obligated women to bear children, which is very costly. A woman would have to determine who would be a worthy mate willing to invest and provision in her and her offspring, and the engagement ring can offer investment intent. Giving premarriage gifts such as engagement rings is thought to be analogous to the nests that male birds build to pledge their fidelity to female birds (Camerer 1988). Thus, presenting and accepting an engagement ring is a symbolic exchange that signifies commitment and trust from both partners (Haas and Deseran 1981). Despite the fact that marriage in modern times no longer obligates a woman socially or physically to bear children (due to changing mores, modern birth control, legalized abortion, etc.), gifts like diamond rings still send a resonating signal of intent and commitment.

Historically, engagement rings were given as long ago as the Middle Ages (Brinig 1990), but have become popular only recently. The custom of engagement rings in the United States has been traced back to the 1840s, but it was not until the early decades of the twentieth century that the practice became widespread (Rothman 1987). Before this time in the days of "Breach of Promise to Marry" laws, in most states it was possible for a woman to sue for damages in the event of a broken engagement (Brinig 1990). A woman would not only have lost her husband but it was thought that her mate value would have diminished if she relinquished her virginity to her fiancé before the wedding occurred. Hence, if a man did not fulfill his obligation to marry, the woman had legal recourse. The man did not have to pledge collateral since the law provided the woman with something akin to bankruptcy protection. Brinig (1990) argued that the elimination of such breach-of-promise actions in the mid-twentieth century created a demand for another bonding device, and she suggested that diamond engagement rings fulfilled that need. Women wanted upfront financial assurance, or collateral, from men so that if she never made it down the aisle, she would be left with something.

However, further reforms in family law began to insist that the ring is given conditioned on marriage and that it has to be returned if the marriage fails to materialize regardless of fault (Tushnet 1998). Thus, a woman's engagement ring became legally contractual and any breach of promise to marry requires the return of said engagement ring. Both the shift in mandatory ring-return rules and the denial of women's claims for restitution have made premarital law unfavorable to women, and engagement rings have spurred much litigation after the dissipation of an engagement before marriage (Tushnet 1998). To this day, more women than men, support the idea that women should be able to keep the ring after a break-up (Ogletree 2010). As a result of legal reformations, the diamond engagement ring has undergone a transformation and no longer stands for security but is meant for signaling commitment. As such, engagement rings have remained popular in the United States with more than three quarters of all first-time brides receiving them (Brinig 1990; Rothman 1987).

Diamond Engagement Rings

Modern opinions about the quality of a couples' relationship continue to be shaped by whether a man follows the traditional practice of bestowing a *diamond* engagement ring, in particular, to a woman. The wedding industry has bolstered the motto that "diamonds are forever." When surveying over 2,000 college students, participants perceived other couples' relationships as stronger when a diamond ring was presented during the proposal rather than another kind of ring or no ring at all (Schweingruber et al. 2008). Not presenting a diamond engagement ring, or giving another type of ring during a proposal, even if the woman wanted it, seemed to have caused confusion among a secondary audience evaluating another's proposal. The man was expected to present the woman with a diamond ring, and an absence of a diamond ring had casted doubt on whether the proposal was genuine. Interestingly, however, participants in the study did not perceive the strength of the relationship

differently based on the size of the diamond and had evaluated a relationship as stronger when the couple picked out the ring together as opposed to the man selecting the ring by himself.

The Expense of Engagement Rings

The lucrative wedding industry has also long promoted the norm that spending a large amount of money on an engagement ring is a true sign of commitment and is helpful for a marriage to be successful. However, there is no evidence to suggest that marriage duration is associated with the cost of the engagement ring or wedding ceremony. In fact, when examining more than 3,000 ever-married persons in the USA, it was found that after controlling for income and other characteristics among male respondents, relatively high spending on the engagement ring was *inversely* associated with marriage duration (Francis-Tan and Mialon 2015). The only positive factor associated with the cost of an engagement ring in proportion of male salary was with courtship duration, suggesting that engagement ring cost simply reinforces a signal of commitment already conveyed by a lengthy courtship (Dunham 2011).

Several factors related to a woman's mate value contribute to the amount a man will spend on an engagement ring. For instance, men who proposed marriage to younger women spent significantly more money on an engagement ring than men who proposed to older women (Cronk and Dunham 2007). The effect of female youth on ring cost is in line with many other studies that emphasized the importance of female age on male mate preferences (e.g., Grammer 1992), which makes evolutionary sense since female age is related to reproductive potential. Further, as men become older and acquire a higher income (and can likely afford more expensive engagement rings), they tend to seek younger mates (Grammer 1992).

While engagement ring cost is negatively associated with female age, it is positively associated with both male and female income (Cronk and Dunham 2007). That is, men who earned more money and whose fiancées earned more

money also spent more on engagement rings, further indicating that engagement ring cost may reflect both male and female mate value. Many studies (e.g., Hughes and Aung 2016; Pawłowski and Dunbar 1999) have found male income of primary importance for female mate preferences, which is consistent with the evolutionary hypothesis that females seek mates who have resources and are willing and able to invest in offspring. The effect of female income on ring cost suggests that female resource control also influences male mate choice similar to how bride wealth and dowry payments do in other societies (Gaulin and Boster 1990). Men may view female resource control as part of her mate quality, responding to the female's income itself, characteristics associated with income (e.g., her willingness and capacity to work hard), or some combination of the two (Cronk and Dunham 2007).

Because younger, uncommitted women value long-term mates who show wealth potential and provide them with romantic gifts (Hughes and Aung 2016), one can assume that the cost that a man spends on an engagement ring signals his economic accrual. Indeed, male income has the strongest effect on engagement ring cost (Cronk and Dunham 2007). While the price a man pays for a ring might not tell a woman anything more than she already knows about a man's income after a period of courtship, considering a man's overall spending habits relative to cost of the engagement ring he offers might give a woman valuable information about his willingness to invest in her and her offspring. Thus, bestowing an expensive engagement ring is revealing of not only his resources but also his generosity as a mate. In fact, men with low mate value can increase their own chances of attaining a higher mate value woman if they are capable and willing to share their resources (Grammer 1992).

Population Sex Ratios

Population sex ratio rates also affect spending patterns of engagement rings. A higher operational sex ratio (i.e., an abundance of eligible men in comparison to eligible women) permits women to become choosier and causes men

to invest more in mating effort. Thus, a male-biased sex ratio is associated with higher marriage rates, fewer out-of-wedlock births, greater paternal investment, and higher costs of engagement rings (see Griskevicius et al. 2012). When tested experimentally, both men and women expected men to spend more money on mating-related products such as engagement rings when women were scarce (Griskevicius et al. 2012). The authors concluded that a male-biased ratio should not only motivate men to exert more mating effort but also motivate women to increase their thresholds for what they consider is acceptable male spending on engagement rings.

Gender Roles

Lastly, stereotypical gender role attitudes play a part in the expectations of cost and value of commitment indicators such as engagement rings. It has been shown that traditional gender role attitudes were associated with the ideas of spending greater money on engagement rings rather than spending money more wisely elsewhere, and with the idea that only diamonds should be in engagement rings (Ogletree 2010). On the other hand, more egalitarian gender role attitudes were associated with less desire for high-cost engagement rings and weddings, yet did not devalue or eliminate the overall practice of having an engagement ring serve as an indicator of commitment.

Conclusion

An engagement ring is a piece of jewelry advertising that the person wearing it is engaged to be married. In many Western cultures, engagement rings are worn primarily by women and rings tend to feature diamonds or other precious gemstones. In some cultures, both men and women wear matching engagement rings and engagement rings are also used as wedding rings. Historically, a woman's engagement ring is presented as a token of a man's betrothal to his prospective spouse and represents a formal agreement to future marriage. The cost spent on

an engagement ring is related several to factors such as income level, age of the prospective bride, population sex ratios, and stereotypical gender roles.

Cross-References

- [Benefits of Commitment and Marriage](#)
- [Engagement Rings](#)
- [Marriage](#)

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Enhancing Women's Competitiveness

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Synonyms

[Improving competition in women](#); [Increasing competitiveness of women](#); [Increasing women's willingness to compete](#)

Definition

The process of increasing women's willingness to engage in competition

Introduction

Competition among different species is one of the main structuring forces in the living world, shaping different ecological communities, while intraspecific competition is the main driving mechanisms behind natural selection in Darwin's theory of evolution, leading to fitness-enhancing

(Darwin 1872). However, individuals between and within species differ significantly in how much they invest into their competitive ability. While some individuals are very competitive in order to get access to high-quality resources, others prefer to avoid competition and make the most of lower-quality resources that are left over for them (Baldauf et al. 2014).

Competition levels also vary across sexes. Among humans, males are more competitive than females, reflecting different environmental pressures that both men and women have faced throughout human evolutionary history. Those differences have been addressed as a potential reason for the wage gap between men and women in which women receive less than men to perform the same function, when they are as qualified as their male pairs. Therefore, men would be better off if they were less competitive, whereas women would be better off if they were more competitive (Niederle and Vesterlund 2011). Increasing women willingness to enter competitions has been a challenge; however some scholars have presented some interventions that can enhance women's competitiveness, which would be addressed in this entry. Before discussing intervention strategies, I will first present potential evolutionary explanations to the difference between male and female competition levels, following with some empirical data comparing competitive behavior across sexes.

Women and Competition: Using the Past to Explain the Present

Darwin (1872) described man as "the rival of other men," adding that they delight in competition. In contrast, women are tenderer and less selfish, directing these qualities not only toward their infants but also probably toward their fellow creatures. Sexual selection is expected to have played an important role in shaping those differences. Because men have been forced to compete more fiercely for mating opportunities, considering that they have slightly greater reproductive gains to obtain from them, selection has not only shaped physical traits that favor men in contests

but also a psychology that makes them more willing to compete (Apicella and Dreber 2015). In contrast, although women do not lack motivation to compete, since they need resource as much as men do, especially when they have an offspring that depends on them, if they had competed as ferociously as their male pairs, they would have exposed themselves to death or injury, risking their ability to raise their children. Thereby, the ancestral women who avoided direct aggressive competition would have had more chances to raise surviving offspring (Campbell 2013). These different environmental pressures lead men and women to adopt different strategies to pass their genes ahead; while men had to compete in order to reproduce, women had to stay alive to raise their offspring, even if that meant giving up competing for better resources. Paraphrasing Campbell (2013), the message for women was clear "stay alive, at all costs."

Confirming those assumptions, the recent experimental economics literature has identified that men are more eager to compete and actively seek competition, whereas women tend to avoid it. For example, Buser (2012) found women less prone to enter a competition than men and identified biological differences as an important factor to explain gender preferences for competitiveness. More specifically, the results showed that women are substantially less competitive when taking contraceptives containing progesterone and estrogen and during the periods of their natural cycle in which the production of these hormones is higher. Consistent with an evolutionary explanation, these findings demonstrate that competitiveness is less desirable during infertile phase when the levels of these hormones are high than during the fertile phase when the hormones levels reach a low level.

Although men seem to be substantially more prone to compete than women, it is premature to conclude that women do not engage in competitive behavior. As stated previously in this entry, women have enough reasons to compete as much as do men. However, while competition among males is well documented, far less is known about female competition. The first reason for that is the already mentioned emphasis that sexual selection has attributed to male competition. Additionally,

when competing, women tend to do it in a subtler way in comparison to males whose competition tactics are overly expressed (Hardy 1981). For example, when competing for mates, having other women as opponents, to attract the desirable partner, differently from men, they would use strategies such as indirect aggression to decrease potential rivals' mate value (Vaillancourt and Sharma 2011). Indeed, overall, it seems that women are willing to engage in competition with other women, but on the other hand, when it comes to direct competition against men, they shy away from it even when they are high skilled. Perhaps the explanation for that lies on their own evolutionary past, because men tend to adopt more aggressive competition tactics, competing against them would be riskier than competing against other women.

In turn, although women compose the largest part of the population with a high education degree, men are still the ones who occupy the leadership positions, also receiving higher salaries than women to perform the same function. Traditionally, the explanation for that lies in gender roles and the discrimination women suffer in the labor market; however, as previously stated, the recent literature has also suggested that whereas men are eager to compete, women tend to avoid it. Many experimental and correlational studies have given support to that assumption, and even high-ability women choose not to compete, which is costly for the society that does not get to have their best members allocate into the positions they are suited for. However, as shown previously, the fact that women do not shy away from competition with other women suggests that they actually do not dislike competition; they perhaps only need the right motivation to display competitive behavior. In the next section, I will consider potential intervention that could improve women's competitiveness.

Strategies to Enhance Women's Competitiveness

Having that in mind, there is room for enhancing women's competitiveness. Analyzing the state of

the art of the gender competition gap, Nierdele and Vesterlund (2011) concluded that men would be better off if they were less competitive, whereas women would be better off if they were more competitive. Therefore, in order to increase women's competitiveness level, men's preferences for competitiveness should also be taken into account. A potential change would be to implement team competitions instead of single player competitions. An experiment showed that competing in teams reduces about two-thirds of the gender competition gap while at the same time reduces women undercompetition and men overcompetition since women prefer competing in teams, whereas men prefer competing individually.

Another potential intervention would be the adoption of affirmative actions to increase the engagement of women in tournaments and inhibit the interest of men. Nierdele and Vesterlund (2011) found that women were more willing to enter a tournament with multiple winners that guaranteed a minimum percentage of female winners. At the same time, the inclusion of the affirmative action did not affect negatively the participation of the best candidates, given that it encouraged particularly high-performing women to take part in the tournament. Another experiment also demonstrated that both offering women a preferential treatment by giving them a head start over men and the implementation of quotas contribute to increase women's willingness in engaging in a competition. Again, these actions did not affect negatively the entry of high-performing candidates.

Conclusion

In nature, enough resources are rarely available to fulfill the needs of the organisms. When resources such as food, mates, shelter, and safety are available in a short supply, competition arises. The same logic applies for humans, since men and women are constantly required to compete for several resources. However, in the evolutionary past of the species, those women who opt out direct contests could raise a larger number of children, whereas the male winners of

competition were the ones who had a higher reproductive success. As a result, avoiding competition was desirable for females, if they wanted to stay alive to raise their offspring, while for males, competing was crucial to acquire better mating opportunities and reproduce. Nowadays, the environment is not as harsh as was in the past, women can easily avoid a pregnancy, and in most countries, they can count with support from the state to raise their children. On the other hand, men are no longer required to engage in aggressive contests to obtain a mate or to guarantee other resources. These environmental conditions, however, have not been in motion for long enough to disrupt the long evolutionary chain, and as such, humans still express traits that helped their ancestors to survive thousands of years ago. Women are still avoiding direct competition, yet men are more prone to compete.

While in the past avoiding competition benefited women, nowadays this can bring some disadvantages that, as stated in this entry, have been shown in the literature to reflect in a wave gap between men and women. A substantial experimental evidence has demonstrated that women shy away from competition, whereas men tend to seek for it. Women, however, do not avoid competition when their opponents are other women, perhaps because women competition tactics are less ferocious than men's, which suggests that women actually do not dislike competition as thought for many researchers, but they evaluate the risks before they decide to engage in a competition. In fact, women need resources as much as men do; however they seem to be more cautious and evaluate the risks and benefits before competing.

Based on that, some actions can be adopted in order to increase women's competitiveness. The actions suggested in this entry were the implementation of team competition instead of individual competition and the adoption of affirmative actions such as requiring a minimum percentage of female winners or giving women a start advantage over men. All these actions seem to be useful to increase women's competitiveness and, at the same time, in selecting high-performing individuals to enter competitions. Such strategies could be implemented, for example, by companies to assure that qualified individuals from both sexes

fill in the vacancies they are suited for and, as such, decrease the wave gap between sexes.

Cross-References

- [Women and Competition, The Oxford Handbook of](#)
- [Women's Use of Direct Versus Disguised Social Aggression](#)
- [Working Women](#)

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Enlarge Shadow of Future

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Synonyms

[Commitment](#); [Reciprocity](#)

Definition

“Enlarge the shadow of future” is one of the recommendations given by Robert Axelrod (1984) to help promote cooperation in social dilemmas, based on evolutionary models.

Introduction

Based on evolutionary models of cooperation and computer simulations, Axelrod (1984) proposed three mechanisms to promote cooperation between selfish individuals: (a) make future outcomes more important than the present ones, (b) change payoffs of possible outcomes in an interaction, and (c) teach people to care about others. This entry concerns the first of these mechanisms, which refers to the increase of the likelihood of future interaction with others and is called “the shadow of the future” by Axelrod and others (Axelrod 1984; Axelrod and Dion 1988; Bó 2005; Oates et al. 2010b; Sebastián-Enesco and Warneken 2015).

Evolutionary Models of Cooperation

Cooperation, or altruism, has long been considered an evolutionary puzzle (Nowak 2006). If one assumes that natural selection will tend to favor selfish strategies in a population, how could cooperative strategies have evolved? A solution to this problem was the kin selection theory (Hamilton 1964) which demonstrated that individuals will tend to cooperate with closer kin, because the cooperators’ genes will be transmitted indirectly through their relatives. However, this theory does not fully explain why some animals, and specially humans, cooperate with nonrelatives. Thus, a second solution to the puzzle of cooperation was the theory of reciprocal altruism (Trivers 1971). This theory proposes that cooperation can evolve if there is a high chance that the individual’s actions will be reciprocated in the future. The theories of indirect reciprocity (Alexander 1985) and network reciprocity (Nowak 2006) contribute to this framework by adding that this return can come from third

parties and not necessarily from the individual who benefited from the altruistic act in the first place.

Axelrod (1984) modeled repeated pairwise reciprocal interactions to investigate whether and how cooperative strategies would evolve among a variety of other strategies. He and his collaborators (Axelrod 1984; Axelrod and Dion 1988) ran a series of computer tournaments in which several game theorists submitted their strategies to compete against each other in repeated rounds of an economic game called the prisoner’s dilemma. This game simulates a social dilemma in which an individual is always better off in the short term if he chooses to not cooperate with others. This dilemma is illustrated in the following way: two accomplices are arrested, hence becoming prisoners. They are put in separate rooms and cannot communicate with each other. They can either confess and receive a lighter sentence or remain silent and receive a harsher one. Regardless of which one decides, the confession always remains the best choice, if the individuals involved will never meet again. However, when there is a high chance of future interaction, remaining silent, and therefore cooperating with the other criminal, might be more important for the long term.

In Axelrod’s tournaments, the programmed strategies interacted repeatedly with each other, with some of them choosing always the same strategy (e.g., always defect or always cooperate) and some of them using some sort of decision criteria. The strategies could win points by either choosing to cooperate with or defect against their partners in each round, and the payoffs were dependent on both their decisions and those of their partners. The strategies that won more points in the long run would survive and reproduce more than (i.e., out-compete) the other strategies. The winning strategy in the first tournaments was the tit for tat, which had a simple heuristic: always cooperate in the first move and replicate the other player’s previous move – that is, cooperate when someone had cooperated previously and retaliate when someone had defected previously. Thus, in a mixed strategy population, tit for tat can survive and spread. But this will only happen if the shadow of the future is large enough, so that tit for tat can capitalize on the risk of cooperating

with potential defectors. Other tournaments (Axelrod and Dion 1988; Wedekind and Milinski 1996) also showed that tit for tat loses to other more forgiving strategies, but only after winning over all the other previous ones. Thus, the better strategy for cooperation in repeated social dilemmas with the same partners involves a combination of being a bit generous, thus giving others the chance to change their strategy and engage in cooperation while still eventually punishing those who refuse to cooperate.

There are two main types of models that attempt to explain the evolution of cooperation: partner control models, in which cooperators can attempt to control their partners by cooperating with other cooperators and cheat or punish noncooperators (Axelrod 1984; Trivers 1971), and/or partner choice models in which cooperators can choose their partners, thus preferring to interact with other cooperators (Baumard et al. 2013; Noë and Hammerstein 1994). The shadow of the future is especially relevant to the former type of model, which accounts for situations in which individuals technically can't choose with whom they interact. Thus, if the probability of encountering the same partners is relatively high, making future interactions more predictable, and in the long run the benefits of cooperating with others surpass those of cheating, individuals will tend to cooperate with each other. Moreover, in real-world situations similar to the prisoner's dilemma, increasing the chances of meeting the same people in the future increases the probability of cooperating with them, more specifically when these repetitions appear infinite – that is, with no clear indication of when the last interaction between partners will occur (Bó 2005). Thus, enlarging the shadow of future is a recommendation applied to contexts in which cooperation is not always desirable, and individuals cannot choose with whom they interact with based on past interactions or any other judgment.

For the shadow of future to be effective, individuals must be able to respond to environmental or social cues that hint on the likelihood of meeting their partners again. This can happen through simple mechanisms, such as territoriality (individuals interact with others in fixed territories, thus

ensuring that the same individuals will meet periodically, Axelrod and Hamilton 1981) or cooperation with partners that are similar to themselves in some manner (Axelrod and Hamilton 1981; Riolo et al. 2001). However, more sophisticated skills are required for more complex interactions, such as the ability of recognizing others and remembering past interactions (Stevens et al. 2005). In all of the cases outlined above, the shadow of future can maintain cooperative relationships because these mechanisms ensure that noncooperators can be retaliated by desertion or punishment. The following sections present examples of the influence of the shadow of the future on nonhuman animal and human social interactions and lay out the limitations of the shadow of the future as a mechanism to promote cooperative behavior.

The Shadow of the Future in Nonhuman Animals

There are several examples of reciprocal interactions among nonhuman animals which are affected by the shadow of the future (Axelrod and Hamilton 1981; Buss 2008; Oates et al. 2010b; Trivers 1971). The vampire bat is a classic example of reciprocal altruism (Carter and Wilkinson 2013; Trivers 1971; Wilkinson 1984). Vampire bats live in small communities of females and their offspring and feed themselves in the night, by sucking the blood of other animals. Feeding is very costly to them, due to higher rates of failure. To overcome this, vampire bats regurgitate blood and share it with those that had given blood to themselves previously, hence favoring reciprocal interactions. In addition, bats only share blood with individuals with whom they had frequent interactions previously and share more often with those who helped them recently. Thus, it pays off for them share blood with those in need, because the chances that the favor will be reciprocated in the future are high.

The mutualistic relationship between the cleaner fish and its clients is another good example of reciprocal altruism, which occurs between species, and it is kept by means of territoriality cues (Axelrod and Hamilton 1981) and indirect reciprocity (Bshary and Grutter 2006). Cleaner fish feed themselves off parasites they remove from

other fish's and reptiles' bodies; large fish are potential predators for the cleaners, which are very small, but the clients avoid eating them because of the benefits of the removal of parasites. A species of cleaner fish that remains in small areas (called cleaning stations) tend to cheat their clients less than another species that rovers over a larger area, which makes it possible for them to desert clients more often (Oates et al. 2010a,b). Despite that, the latter also has preferred areas for interacting with specific clients, more specifically where there is a higher probability of future repeated interactions, which indicates that they also establish stable reciprocal relationships and are affected by the shadow of the future (Oates et al. 2010b).

The Shadow of the Future in Humans

The social contract theory (Cosmides and Tooby 1992) proposes basic adaptations for reciprocal cooperative interactions in humans. Based on findings from experiments with a logic task applied to social contexts, Cosmides and Tooby (1992) proposed that humans have psychological adaptations to detect cheaters in social exchanges. They identified the risk of being exploited by cheaters as the main source of evolved adaptations for cooperation; in response to that, humans have developed: the ability to recognize different individuals, to remember past interactions, to communicate their values, to model others' values, and to represent costs and benefits across different kinds of items. In other words, human have evolved a set of skills necessary for engaging in more sophisticated cooperative reciprocal interactions than other animals.

Humans engage in reciprocal interactions very early, more specifically by turn-taking interactions initiated by parents (Trevvarthen 2011). There is evidence that these interactions increase prosocial behavior in young children (Cortes Barragan and Dweck 2014; Rabinowitch and Meltzoff 2017), which can be an indication of an early mechanism that responds to cues of future interactions. In other words, repeated interactions might hint at future probability of interactions, thus functioning as a cue for prosocial behavior. However, reciprocal prosocial behavior, such as taking turns in sharing goods with a partner, only seems to fully emerge during middle childhood. Five-year-old American

children are able to delay gratification and share more goods with a partner in anticipation of future reciprocal interactions (House et al. 2013; Sebastián-Enesco and Warneken 2015). Eleven-year-old American children increased their donations in repeated prisoner's dilemma games compared to one-off games (Blake et al. 2015). However, when in repeated interactions within a group, children's donations tend to decrease with time when they are anonymous but not when they are public, especially among children older than 8 across different cultures (Dutra et al. 2018; Zbaratany et al. 1985) and similarly to adults (Bó 2005; Wang et al. 2017). Thus, the shadow of the future increases human prosocial behavior, but particularly when individuals make public decisions.

Limitations to the Shadow of the Future

Enlarging the shadow of future refers to the increase of frequency of interactions and commitment between partners. However, this recommendation is based on models of reciprocal altruism which often assume that players have similar levels of power, cannot communicate with each other, and cannot opt completely out of the game (Buss 2000). Whenever one of these conditions is not met, enlarging the shadow of the future might not be as effective or even necessary. For instance, Ostrom (2000) found that communication can increase cooperation in collective social dilemmas similar to the public goods games, up until the last interaction, being more effective than external incentives or norms in similar settings.

Conclusion

Empirical evidence supports classical theoretical predictions that enlarging the shadow of the future – that is, increasing the probability of interacting with others in the future – is one significant factor in the increase of cooperation among partners in the long run. However, the influence of future interactions is constrained by certain conditions, such as individuals' abilities to detect and interact with cooperative partners, environmental conditions that limit social interactions to certain areas and increase contact among individuals. Many human

interactions are either one-off, or future interactions are uncertain, particularly in contemporary societies; other mechanisms such reputation and social control from institutions are in place to enforce cooperation among humans. Nevertheless, whenever the shadow of the future is large enough and individuals are able to retaliate by not cooperating with noncooperators, cooperation thrives.

Cross-References

- Iterated Prisoner's Dilemma Model
- Reciprocal Altruism
- Robert Axelrod's (1984) *The Evolution of Cooperation*
- Robert Trivers

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Ensemble Representation

- ▶ [Summary Representation](#)

Entombment Customs

- ▶ [Burials](#)

Entomologist

- ▶ [E. O. Wilson](#)

Entropy

- ▶ [Concept Formation](#)

Environment

- ▶ [Ecology](#)
- ▶ [Social Context](#)

Environment of Evolutionary Adaptedness

- ▶ [Climate and Habitat Diversity](#)
- ▶ [John Bowlby](#)

Environmental

- ▶ [Factors That Influence Bullying](#)

Environmental Adversities

- ▶ [Environmental Risk](#)

Environmental Aesthetics

- ▶ [Three Stages of Habitat Selection](#)

Environmental Change Hypothesis

- ▶ [Cognitive Buffer Hypothesis, The](#)

Environmental Contingencies

- ▶ [Ecological Influences](#)
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Environmental Effects

- ▶ [Ecological Influences](#)
- ▶ [Ecological Influences on Parent–Offspring Conflict](#)

Environmental Factors Associated with Marital Harmony

► Ecology of Pair-Bond Stability

Environmental Harshness

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Synonyms

Danger; Rate of death and disability; Risk

Definition

Environmental harshness: externally caused levels of morbidity and mortality in a population.

Introduction

Environmental harshness is one of the major components of an ecology implicated in guiding an organism's life history decisions. As such, an organism's experience with cues of harshness in an environment during critical periods of ontogeny is capable of modifying developmental trajectories and energy budget tradeoffs (Ellis et al. 2009). In humans, encountering harshness and unpredictability has also been revealed to predispose an individual to a suite of psychological tendencies: impulsivity, risk-taking, and the propensity to discount delayed rewards (Griskevicius et al. 2011b, 2013). Harshness emerges as a principal characteristic of an ecology's profile that predicts both between-species and within-species variation in life history strategies (Ellis et al. 2009).

Extrinsic Threats Versus Intrinsic Threats

The external threats of morbidity and mortality that together comprise an environment's level of harshness can be either extrinsic or intrinsic. This definition is not solely determined by the source of death and disability (e.g., violence, disease, or famine), but rather an organism's ability to overcome such threats by optimally investing resources and effort (Ellis et al. 2009). For extrinsic threats, allocating additional resources towards mitigating the impact of environmental harshness through parental effort or somatic development fails to reduce morbidity and mortality. As a result, organisms inhabiting a harsh ecology dense in extrinsic threats typically display phenotypes representing tradeoffs that favor reproductive investment, such as reproducing at a younger age, a greater quantity of offspring, a smaller size, and reduced parental effort (Kaplan and Gangestad 2005; Mittal and Griskevicius 2014). This faster strategy is employed to maximize the probability that at least some of the many – albeit lower quality – offspring will reach reproductive age. Conversely, environments dominated by intrinsic threats in which rates of morbidity and mortality are sensitive to somatic investment might actually select for slower life history strategies. In this case, increased parental investment and a longer adolescence yield a lower quantity of high-quality progeny better equipped to survive and reproduce.

Harshness in Nonhuman Animals

Many characteristics of an ecology can influence rates of death and disability in a population. Among these are predation, pathogen density, and bioenergetic resource availability, alongside other sources of environmental stress (Ellis et al. 2009). The effects of harshness on life history strategies in nonhuman animals have been verified both in the wild and under controlled laboratory conditions. For example, organisms inhabiting regions of high predation – an extrinsic threat – exhibit traits at the faster end of the life history continuum than conspecifics in areas with less predation (Reznick

and Endler 1982). In contrast, intrinsic threats that can be diminished by investment in traits, like a larger size, facilitate resource allocation towards higher quality offspring, driving slower life history strategies (Gosselin and Rehak 2007).

Harshness in Humans

The ancestral environments of humans have likewise demanded the evolution of mechanisms for overcoming harshness. External threats to survival and reproduction in human ecologies resemble those of other species, including disease, conspecific violence, and resource scarcity. For instance, crosscultural research has found that parental investment is lower when pathogens in a region are extremely dense (Quinlan 2007). In addition to the threat of disease, comparison of crime and reproductive age in different counties of the United States confirmed that mortality risk by violent crime rates predicted an earlier age at first reproduction, also demonstrative of a faster life history strategy (Griskevicius et al. 2011a). Elaborating upon this finding, experimental studies have supported the impact of mortality threats on human life history strategies. For example, priming individuals with environmental danger led those having experienced a lower childhood socioeconomic status (SES) – a proxy measure of environmental harshness and resource scarcity – to report a desire to reproduce sooner than individuals with a higher childhood SES.

Psychological Effects of Harshness in Humans

In addition to changes in reproductive behavior and physical maturation, levels of environmental harshness can further impact human psychology. Much research has explored psychological and cognitive shifts that might accompany or mediate changes in development and behavior induced by harshness. When faced with mortality cues, individuals having experienced a lower childhood SES tend to prefer riskier decisions for larger

payoffs and discount the future compared to their higher childhood SES peers (Griskevicius et al. 2011b). Priming another facet of environmental harshness, resource scarcity, similarly led individuals from a lower childhood SES to prefer risk, respond more impulsively, and more quickly approach temptation (Griskevicius et al. 2013). In the same way an organism may forgo extended development to maximize fitness by reproducing earlier in a harsh ecology, these psychological reactions to mortality threats may serve an adaptive function. Although impulsivity and risk-taking could be considered harmful or counterproductive in modern environments, they may have been integral in maintaining adequate bioenergetic reserves and escaping danger in the past.

Critical Periods

The effect of context in calibrating life history strategies appears to be most influential during critical periods of development. Many of the changes in behavior and psychology predicted by childhood conditions are not replicated when considering only adult environments (Ellis et al. 2009; Griskevicius et al. 2011; Simpson et al. 2012). This window of susceptibility during which environmental harshness is most important in adjusting life history strategies appears to exist during early childhood, resembling critical periods of development for other important functions, such as language acquisition.

Unpredictability

Unpredictability in environmental harshness is defined as the temporal-spatial variation in levels of harshness (Ellis et al. 2009). In addition to total harshness in an ecology, instability in conditions impacts parental investment, reproductive behavior, and other components of a life history strategy. Research suggests that this role of unpredictability in shaping life histories is independent of absolute harshness. For example, experimentally generated volatility of foraging

conditions in nonhuman primates reduced parental investment more than mere foraging harshness (Rosenblum and Paully 1984). Further evidence in humans using a longitudinal analysis of environmental unpredictability in childhood and adult outcomes revealed that sources of early life unpredictability, such as number of residential transitions and mother's employment status changes, predicted risky behavior in adulthood (Simpson et al. 2012). Psychological responses to unpredictability likely appear because risks that cannot be anticipated cannot be minimized through appropriate somatic investment. Therefore, stochasticity in an ecology itself presents an extrinsic challenge to survival and reproduction.

Conclusion

Environmental harshness and unpredictability are key factors in the calibration of life history strategies for humans and other organisms. Threats of morbidity and mortality in an ecology necessitate mechanisms of diverting resources towards investment in allaying risk if possible, or expediting reproduction if not. The formative years of early childhood represent a crucial window for role of harshness in developmental programming. Further research is warranted into the budget tradeoffs that are made in different domains when an organism is faced with varying levels of environmental harshness. Future lines of inquiry will also examine the pathways through which organisms receive cues about the quality of the local ecology.

Cross-References

- [Environmental Risk](#)
- [Environmental Unpredictability](#)
- [Extrinsic Mortality](#)
- [Life History Strategies](#)

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Environmental Harshness/ Mortality

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Synonyms

[Environmental scarcity](#)

Definition

Environmental harshness is the surrounding condition an individual is living in, which can be measured, for example, by local mortality/morbidity and availability of the resources.

Introduction

There are many influences on pair-bonding in human and nonhuman animals alike, and one of them is the harshness of the environment the pair is living in. Environmental harshness and local mortality can affect an individual's mating strategy, which is closely intertwined with pair-bond stability. In harsh environments, reproductive strategies are often characterized by prioritization of mating over parenting effort (Ellis et al. 2009), which can result in infidelity and relationship dissolution. It is possible that relationship instability, and a greater need for biparental care in harsh conditions, relates to what individuals find initially attractive in a prospective mate as well, shifting the preference away from what is stereotypically considered as attractive.

Life History Theory, Mating Strategies, and Pair-Bond Stability

Non-evolutionarily informed research has found that poverty, low educational levels, and unemployment are important risk factors for divorce (Amato 2010). From evolutionary point of view, all of these can be used as an indicator of the harshness of the surrounding environment. The effect of environmental harshness and mortality on pair-bond stability can be understood within the life history theory (LHT) framework. According to LHT, in harsh, high mortality environment, it may be more adaptive to follow a fast life history strategy (LHS), with early sexual maturation, early sexual activity, and a larger quantity of offspring that receive less parental care.

The effects of environmental harshness can have a sex-specific impact on a mating strategy. For men, fast LHS is often associated with a higher likelihood

for deserting their partner while looking for new mating opportunities elsewhere. For women, fast LHS may relate to an earlier age of childbearing and bringing up children without a stable, long-term father figure in the household (Nettle 2010). Indeed, when looking for long-term partners, environmental harshness is associated with a preference for a mate that is less likely to be unfaithful.

Research on long-term mate preferences has found that in harsh environments, both sexes prefer partners that do not exhibit exaggerated sexually dimorphic traits that are attractive to the opposite sex. For women, this may indicate a preference for lower levels of facial masculinity in men, and for men, lower levels of facial femininity in women (e.g., Little et al. 2007; Lyons et al. 2016; Marcinkowska et al. 2014). It is possible that preferring a lower-quality but higher investing partner could work as an insurance policy against desertion in harsh conditions.

Conclusion

Environmental harshness can affect pair-bond stability via a shift in mating strategies, where individuals may prioritize mating effort over parenting. Fast LHS can be adaptive in high mortality environments, with the cost of reducing the stability of a pair-bond. In harsh conditions, children are more likely to grow up in a household where the biological father is absent, as fast LHS in men is associated with promiscuous mating strategies. Environmental harshness has also an impact on mate attraction, where less attractive individuals are preferred as partners, possibly due to a lower likelihood of infidelity.

Cross-References

- ▶ [Environmental Harshness](#)
- ▶ [Fast Versus Slow Strategies](#)
- ▶ [Father Absence](#)
- ▶ [Female Mate Choice](#)
- ▶ [Life History Strategies](#)
- ▶ [Life History Theory](#)
- ▶ [Male Mate Choice](#)

- [Parental Investment and Parenting](#)
- [Sex Differences in Parenting and Parental Investment](#)

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Environmental Heterogeneity

- [Climate and Habitat Diversity](#)

Environmental Influences

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Synonyms

[Milieu](#); [mise-en-scène](#); [Setting](#); [Surroundings](#)

Definition

The external circumstances, objects, or conditions that influence one's pubertal maturation.

Introduction

There is a large and growing body of research on the environmental influences affecting pubertal maturation, leaving little uncertainty regarding its significant role in pubertal onset. Research on secular trends regarding puberty has shown a steady decrease in the age of onset from the mid-nineteenth to the mid-twentieth century in developed countries (Parent et al. 2003). Research such as this indicates that environmental factors must play a role in pubertal maturation, given the short time frame for such drastic changes. This entry focuses on the environmental influences regarding the topic of pubertal maturation through aspects pertaining to (1) energetics, (2) psychosocial stressors, and (3) endocrine disrupting chemicals. It is important to note, however, that due to the limited research on male pubertal maturation and difficulties associated with it, this entry will focus mainly on the environmental influences affecting the pubertal maturation of females.

Energetics

Energetics theory hypothesizes that the degree of nutritional availability in one's environment affects one's pubertal development (Ellis 2004). As such, “children who experience chronically poor nutritional environments will experience late pubertal development. . . , whereas children who experience chronically rich environments will experience early pubertal development. . . ” (Ellis 2004, p. 925). Although the theory holds that the greater the surplus of metabolic energy that can be garnered then the greater the surplus for development and reproduction, it has little effect on sufficiently nourished populations (Ellis 2004). However, prepubertal females from less developed countries who were adopted (or migrated) into first-world countries tend to experience menarche at an earlier age (Parent et al. 2003). This phenomenon is speculated to be a result of one moving from an underprivileged environment to a privileged one, causing the body to undergo a period of *catch-up growing*, which triggers sexual maturation

(Karapanou and Papadimitriou 2010). In a somewhat similar manner, one's socioeconomic status (SES) may also influence the onset of one's pubertal maturation. For instance, females from "higher social classes experience earlier pubertal development than do girls from lower social classes" (Ellis 2004, p. 926). Generally, however, this is only evident in societies where significant differences in health and nutritional status between low- and high-SES individuals exist (Ellis 2004).

While there are many possible compounding factors that may be responsible for the association between SES and the onset of puberty, it is likely that the two associated with nutrition – diet and exercise – play an influential role. Typically, individuals lower in SES, among other things, are limited in their options regarding diet and exercise. Research has shown that prepubertal females between the ages of 3–5 years old, whose diets are high in animal protein, tend to experience earlier menarche than those whose diets are high in plant protein (Karapanou and Papadimitriou 2010). Similarly, prepubertal females whose diets are high in fiber have also been associated with delayed onset of puberty (Ellis 2004). Additionally, diets high in soybean products, fortified products with supplements like dietary fiber, calcium, and vitamin D may also be influential in the timing of female sexual maturation (Yermachenko and Dvornyk 2014, p. 5). In addition to diet, a child's weight has also been found to be correlated with pubertal timing (Karapanou and Papadimitriou 2010). In females, early menarche becomes increasingly likely the greater their subcutaneous fat levels and BMI are during prepubertal ages. On the other hand, leanness has been correlated with earlier puberty in males (Karapanou and Papadimitriou 2010).

A factor worth noting, when considering nutrition and diet, is energy expenditure. Exercise, which plays a crucial role in the body's allocation of caloric intake, has been shown to delay the onset of menarche in females (Karapanou and Papadimitriou 2010). However, this typically only occurs with those who conduct at least 2 h of daily physical activity, such as athletes (Karapanou and Papadimitriou 2010).

Psychosocial Stressors

Since 1991, when Belsky and colleagues published the evolutionary theory of socialization, there has been a great deal of research conducted into the associations between various psychosocial stressors early in life and pubertal timing (Ellis 2004). While there is a general consensus regarding the most sensitive period of exposure to psychosocial stressors being the first 5–7 years of life, there is conflicting findings on the degrees of significance. These contradictory findings may be attributable to likely co-occurrences between many of the stressors (Ellis 2004), possible cumulative effects of co-occurrence (Li et al. 2014), other variations in the environment and/or racial/genetic dispositions (Ellis 2004; Li et al. 2014), or differences in study methodology (Ellis 2004). Nonetheless, most converging empirical research seems to be indicative of reasonable, yet incomplete, support for a number of psychosocial stressors influencing puberty (Ellis 2004).

Converging empirical evidence, viewed as supportive of psychosocial stressors' influence on puberty maturation, pertain to various aspects of familial environment and childhood adversities (Li et al. 2014; Ellis 2004; Yermachenko and Dvornyk 2014; Karapanou and Papadimitriou 2010). Based on his comprehensive literature review, Ellis found "Empirical research to date had provided 'reasonable, yet incomplete. . .' support for [psychosocial acceleration theory] 'warm, cohesive family environments slowing down pubertal development'" (Ellis 2004, p. 935). Although he found an association between greater frequency of parent-child interactions being predictive of later puberty, he failed to find adequate methodologically sound research suggesting the opposite true of dangerous or conflictual family environments predicting earlier pubertal development (Ellis 2004). Studies on the roles of various forms of familial conflict and their association with the timing of puberty exposed great gaps in knowledge leaving research riddled with inconsistent findings (Li et al. 2014).

Some of the more consistent and accepted associations among familial environments and childhood adversity for the onset of female menarche are seen with marital dissatisfaction,

parental mood disorders and illness, sexual abuse, parental investment, neglect, physical abuse, father presence/absence, stepfather presence, step-brother presence, family size, number of older sisters, urban or rural environment, and many others (Ellis 2004; Karapanou and Papadimitriou 2010; Li et al. 2014; Yermachenko and Dvornyk 2014). Some of these instances have also been associated with accelerated pubertal development in males (Li et al. 2014). Depending on an individual's genetic predisposition to stress, the age of occurrence, duration, and frequency, psychosocial stressors such as sexual abuse have been thought to have associations with both late and early puberty. Further evidence for genetic disposition is seen in research showing father absence having less of an effect on African-American females, regardless of age of occurrence, indicating the significance of race. Combinations of psychosocial stressors can also alter data as seen by prevalence of early menarche becoming "...even higher when stepfather presence is combined with a stressful family environment and with maternal mood disorders" (Karapanou and Papadimitriou 2010, p. 5).

Specific factors like severe socioemotional stress or war are thought to largely include prolonged psychological stress. While there is little doubt of the association between times of war and pubertal delay, there is some regarding the specific causes of the delay. Many of the confounding variables (food rationing, increased physical activity, prevalence of disease, etc.), make it difficult to ascertain the mechanisms for this delay (Ellis 2004).

Endocrine Disrupting Chemicals

Since the 1940s, there has been an exponential increase of synthetic chemicals found in the environment, with roughly more than 84,000 different chemicals in commerce (Meeker 2012). Many of these synthetic chemicals, as well as natural chemicals found in nature, can interfere with hormonal pathways through a variety of mechanisms that interfere with endogenous endocrine action

(Zawatski and Lee 2013). These endocrine-disrupting chemicals (EDC) can "compete for estrogen receptor binding and activation, interfere with post-receptor signaling pathways, and modulate synthesis, bioactivity, or degradation of hormones, receptors and cofactors" (Zawatski and Lee 2013, p. 3). Through these mechanisms, and their influence on a range of different hormones responsible for the development of reproductive organs (e.g., estrogens, androgens, and gonadotropin-releasing hormone), it is speculated that EDCs can affect pubertal maturation, among other aspects of human development (Zawatski and Lee 2013; Meeker 2012; Özen and Darcan 2011). The cause for concern and relevance to pubertal development comes from the degree to which the average person is exposed to EDCs. Many EDCs are commonly found in consumer goods, personal care products, food, water, contaminated soil, and air (Zawatski and Lee 2013; Meeker 2012). Some of this EDC exposure is due to highly toxic chemicals, such as Dichlorodiphenyltrichloroethane (DDT) and Polychlorinated biphenyls (PCBs), which were banned in industrialized nations in the 1970s, but are still detectable in the environment (Zawatski and Lee 2013). These persistent organic pollutants (POP) are "lipophilic chemicals with long half-lives that bioaccumulate up the food chain" (Meeker 2012, p. 953). POPs, along with most other EDCs, accumulate in fat tissue, are difficult to deactivate and are likely to stay within the human body for long periods of time which may have deleterious effects (Özen and Darcan 2011). Dose, duration, and age of exposure also have roles in the possible effects EDCs may have (Özen and Darcan 2011). Evidence of this is found in research affecting females who experience prenatal exposure as well as exposure via lactation to polybrominated biphenyls (PBB) and DDE/DDT (Özen and Darcan 2011; Den Hond and Schoeters 2006). Further compounding onto the complexity and difficulties associated with EDCs are the long latency periods between exposure and effect, multiple mechanisms a single chemical can use, individuals' genetic susceptibility, exposure to multiple chemicals, and other environmental influences.

Although limited, human studies pertaining to the effects of EDCs on puberty have been documented and supported by evidence gathered in animal studies (Karapanou and Papadimitriou 2010; Meeker 2012; Özen and Darcan 2011; Yermachenko and Dvornyk 2014; Zawatski and Lee 2013). Due to animals' serving as a baseline and reference point, it is reasonable to conclude that a relationship between EDCs and pubertal timing exist (Zawatski and Lee 2013). Several studies on postnatal female exposure have shown the risk of early menarche to increase with high exposure to PCB, DDE, and other EDCs, while delaying age of menarche with high levels of lead exposure (Den Hond and Schoeters 2006; Yermachenko and Dvornyk 2014). Findings pertaining to some exposures in prepubertal males found similar results. There is an association between earlier pubertal onset and exposure to DDE and PCB (Zawatski and Lee 2013), while lead and certain pesticides (specifically, endosulfan) have been associated with delayed puberty and decreased penile length (Hond and Schoeters 2006). Although many of these findings have been confirmed in animal studies, the various confounding influences still pose a significant challenge for uncovering the effects of EDCs on pubertal development.

Conclusion

A general consensus among various nations attributes approximately 50% of the variation in age of menarche to environmental influences (Ellis 2004). These influences pertain to energetics (e.g., nutrition, weight, diet, exercise), psychosocial issues (e.g., family environment, childhood adversity, and war), as well as EDCs (e.g., DDT, PCB). Additionally, environmental influences such as SES, migration, war, several psychosocial stressors, premature birth and birthweight (associated with greater risk for menarche), and illness covary with multiple aspects.

Research into associations between various environmental influences each have their own difficulties. Dose, duration, and age of exposure also play crucial roles in the possible energetic

(e.g., energy expenditure), psychosocial (e.g., length of abuse), and EDC effects. Additional challenges regarding EDCs are the long latency periods between exposure and effect, multiple mechanisms a single chemical can use, individuals' genetic susceptibility, exposure to multiple chemicals, and other environmental influences. These problems increase the difficulty of understanding how various environmental factors affect the human pubertal process. Further research is needed in many areas of environmental influence on pubertal maturation.

Cross-References

- Family
- Genetic Influences of Puberty
- Menarche
- Peers
- Puberty
- Puberty in Boys
- Puberty in Girls
- Sexual Stigmatization

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Environmental Instability

► Environmental Unpredictability and Bet-Hedging

Environmental Risk

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Synonyms

Environmental adversities; Environmental threats and challenges

Definition

Within the life history theoretical framework, environmental risks refer to depleting or low levels of resource and high rates of extrinsic threats, such as predation, famine, disease, and intraspecific violence, that are insensitive to the survival effort of the individuals and that cause mortality and morbidity of the population, as well as stochastic variations of the resource levels and mortality–morbidity rates.

Introduction

Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. (Darwin 1859/1979, p. 117)

In the chapter entitled “Struggle for Existence” of *The Origin of Species*, Darwin points out a critical assumption about evolution – that there will always be more lives than there are resources to support them. This results in constant intra- and interspecies competition in which only the fittest survive. The competition or struggle for existence occurs at the individual or organism level and, fundamentally, at the genetic level. However, advancements in knowledge since Darwin’s seminal work was published have shown further evidence that an individual’s life is composed of characteristics called life history (LH) traits. Limited resources and resource competition manifest as a limited energy budget that cannot support all LH traits, and the strategic allocation of limited energy results in trade-offs between different LH traits. Similarities and patterns derived from LH trade-offs form LH strategies, which are aimed at optimizing the struggle for existence at the individual level. One such broad pattern of LH trade-offs is the fast–slow LH strategic continuum (Promislow and Harvey 1990). A fast LH strategy involves trade-offs characterized by early maturation and reproduction, squandering rather than conserving energy and resources, and high mating and low parenting. By contrast, a slow LH strategy involves late maturation, delayed reproduction, slow development, and a longer lifespan, all of which facilitate amassing and conserving resources, learning and developing skills, and parenting and training fewer, high-quality offspring who are equipped for intra- and interspecies competition in the struggle for existence. The fast–slow continuum and other intraindividual strategic LH trade-offs respond to and are shaped by the struggle for existence at the individual level. This chapter addresses the relationship between the

environmental risks or constraints that make individuals' lives a struggle and the intraindividual LH strategic trade-offs individuals employ to optimize the conditions of the struggle for existence.

Environmental Harshness

What is essential for life and subsequently responsible for the struggle for existence? The answer must be food and safety, the levels and variations of which also shape LH trade-off strategies. For most species and for humans of the evolutionary past, the main safety concern is predatory risk, which is the main cause of mortality. Other extrinsic causes of mortality include famine, disease, and conspecific violence. Because these causes may also lead to injury, illness, and disability, in addition to death, Ellis et al. (2009) coined the term "mortality–morbidity" to encompass all of these negative consequences of such extrinsic risks as predation and disease. Food, or more generally, resources are essential for life. Their shortage and scarcity is responsible for the struggle for existence. In the evolution literature, resource scarcity and mortality–morbidity are defined as constituting the harshness dimension of the environment that regulates fast–slow LH strategies (Ellis et al. 2009).

Resource Scarcity

Resources were first studied as a density-dependent selection condition in relation to population density and competition (MacArthur and Wilson 1967). When resources are sufficient to carry or support organisms living in a habitat, organisms tend to freely exploit them for fast development and early reproduction, producing high numbers of offspring who receive little parental investment in teaching and learning about survival because they can survive and thrive in resource-rich and competition-free environments (Pianka 1970). This is known as r selection, where r represents the maximal reproductive rate of a species (MacArthur and Wilson 1967). When the high reproductive rate increases

the population density to the point that resources become depleted, species adopt slow strategies, also known as K selection, where K represents the carrying capacity of the environment. Slow LH strategies trade fast development and mating for slow development and parenting; they raise few, high-quality offspring who can compete for and monopolize the depleting resources of their environment (Pianka 1970). The K -slow strategy is particularly relevant to humans who rely on skills and knowledge to monopolize resources in contest competition, where resources are unevenly distributed to K strategists; this is in contrast to scramble competition, where resources are evenly distributed, leading to fast LH strategies (Rogers 1992). Cross-cultural data on preindustrial societies suggest that resource scarcity arising from high population densities and related energy limitations favor the development of slower LH strategies involving paternal presence and comparatively high biparental care of offspring (Hewlett 1992; Katz and Konner 1981).

Rushton (1985) was among the first to apply the density-dependent r – K framework to the study of human LH strategies. However, research on resource scarcity as a type of environmental harshness has not flourished partly because other factors, such as age-specific mortality and environmental unpredictability (discussed in the following section), play more important roles than resources alone in shaping LH traits (Ellis et al. 2009). Another reason is that there is no reliable measure for resource availability or scarcity at the individual level. In modern life, the putatively representative indicator of available resources is family income or socioeconomic status (SES) at the individual level and per capita income at the population level. However, SES is an inadequate indicator of the evolutionary concept of resource availability or scarcity for several reasons. It has the floor effect in that even a low SES in resource-rich, developed societies does not approach the resource depletion point below the environment's carrying capacity. It is also potentially confounded with two other LH concepts. First, in most metropolitan areas, a low SES is

associated with an environment that is high in crime and violence, which represents a separate mortality–morbidity component of environmental harshness and unpredictability. Because of this potentially confounding measurement, low rather than high SES has been shown to be associated with fast LH strategies (e.g., Belsky et al. 1991) against LH predictions. Second, it is potentially confounded with intraspecific competition, with higher SESs representing success in intraspecific competition. The opposite effects of competitiveness and resource abundance on LH strategies nullify the potential effect of SES.

Mortality–Morbidity

Whereas resource levels seem to influence LH strategies uniformly across the lifespan, the effect of mortality–morbidity on LH is age and stage dependent (Ellis et al. 2009): “Indeed, extrinsic morbidity–mortality is not defined by the source of death or disability but rather by which members of the population are affected” (p. 219). In general, if extrinsic causes of mortality–morbidity are insensitive to the survival efforts of the able adults of a population, high frequencies of such extrinsic risks lead to fast LH strategies because natural selection favors accelerated development and reproduction before extrinsic mortality–morbidity strikes (Promislow and Harvey 1990). If such mortality–morbidity as that derived from endemic disease exposures mainly affects the young and weak of the population, natural selection tends to select slow LH strategies because LH trade-offs that favor body repair and maintenance, including immune competence over mating, should enable individuals to escape disease attacks (Ellis et al. 2009). In species where juveniles suffer from high rates of mortality–morbidity, the affected fast–slow LH strategies depend on whether mortality–morbidity responds to parental investment, as well as juvenile investment (Ellis et al. 2009). If parental investment reduces extrinsic risk for the juveniles, natural selection should favor slow LH strategies by increasing physical development to build stronger disease or predatory defense mechanisms. If mortality–morbidity is insensitive to parental investment, natural selection should favor fast LH to accelerate growth and

development to outlive the age-specific extrinsic risks.

Low levels of extrinsic mortality–morbidity, however, do not necessarily lead to slow LH strategies (Ellis et al. 2009). Under the conditions of low environmental harshness that characterize human evolution, density-dependent factors, such as resource and intraspecies competition, become more relevant determinants of LH strategies (Pianka 1970). Low mortality–morbidity combined with low resource availability and high competition should lead to slow LH strategies, whereas low extrinsic risks accompanied by high resource availability and low competition should lead to fast LH strategies. However, few human LH studies have examined resource levels or competition. Conducted primarily in the West, extant studies have examined exposure to violence, crime, and antisocial activities (Brumbach et al. 2009) and rundown neighborhood conditions (Crowder and Teachman 2004), including the presence of gangs, abandoned cars, and graffiti (Upchurch et al. 1999), as indicators or proxies of environmental harshness. These proxies generally correlate with fast LH strategies.

Environmental Unpredictability

Stochastic spatiotemporal variations in resource levels and mortality rates are defined as environmental unpredictability, which shapes fast–slow LH strategies (Ellis et al. 2009). These random fluctuations between good times and bad times are caused by such uncontrollable factors as predatory behavioral idiosyncrasy, weather change, or pathogenic breakout and disappearance. Unpredictable environmental fluctuations increase the variance and decrease the mean of fitness (Phillippi and Seger 1989). Because the geometric mean is negatively affected by the variance, reducing the variance increases the geometric mean despite it also reducing the arithmetic mean. In fluctuating environments where fitness is calculated with the geometric rather than the arithmetic mean, phenotypes with reduced variance are favored over those of higher variance and higher mean fitness (Phillippi and Seger 1989).

This trade-off between having a more variable number of offspring across time (with a higher arithmetic mean) and having a more constant number of offspring over time (with a higher geometric mean) is called “bet-hedging” (Phillipi and Seger 1989), for which there are two types: conservative and diversified bet-hedging. In conservative bet-hedging, animals reduce the variance of fitness across time and on specific occasions by decreasing the number of offspring in good times or in stable environments so that the number of offspring is closer to the mean. In diversified bet-hedging, animals reduce the fitness variance across time and space by increasing the number of offspring during bad times or in unpredictable environments. The two types of bet-hedging achieve the same end result, which is reduced variance of fitness across the lifespan or across generations (Phillipi and Seger 1989). Because conservative bet-hedging trades off offspring quantity for quality, it can be regarded as a slow LH strategy. Diversified bet-hedging, which increases offspring quantity at the cost of quality, can be considered a fast LH strategy.

According to Ellis et al. (2009), short-term environmental unpredictability (e.g., within generations) that causes variations in juvenile mortality predicts diversified bet-hedging to reduce fitness variance. Fitness variance is reduced by producing more offspring, reproducing with different partners, or extending the age schedule of reproduction, all three of which potentially diversify offspring phenotypes so that some offspring may survive environmental adversity. When variations in juvenile mortality are due to long-term environmental fluctuations across generations, natural selection favors conservative bet-hedging. Fitness variance is reduced by reducing the quantity and improving the quality of offspring so that, despite the overall number of offspring being lower than what would be optimal in good times or stable environments, the improved quality promotes offspring survival across the range of environmental fluctuations from good times to bad times. When environmental unpredictability affects adult mortality and morbidity, natural selection favors fast LH strategies: “Both high absolute levels of adult mortality

(harshness) and high variation in adult mortality (unpredictability), therefore, select for fast LH strategies” (Ellis et al. 2009, p. 229).

Central to the discussion of environmental unpredictability is the age of a population in which large variations of mortality–morbidity occur. Age-specific mortality–morbidity implies different effects or extents of an effect depending on the age or developmental stage of individuals when they experience environmental unpredictability. A robust and consistent finding from numerous human LH studies is that early childhood experiences of unpredictable environments lower the age of sexual maturation and increase the frequency of sexual activity. In such studies, early environmental unpredictability was represented by microenvironmental proxies from the childhood or early childhood environment. These include family SES (e.g., Belsky et al. 1991), residential mobility (e.g., Crowder and Teachman 2004), family and parental change (e.g., Belsky et al. 2010), disruptive and coercive family relationships (Byrd-Craven et al. 2007), maternal history of psychopathology (e.g., Ellis and Garber 2000), divorce (Mendle et al. 2006), paternal absence (e.g., Belsky et al. 1991), stepfather presence (Ellis and Garber 2000) and the presence of stranger males in the family (Ellis et al. 2003).

The results support the LH prediction that these indicators of environmental unpredictability are either directly or indirectly related to fast LH characteristics such as early menarche (e.g., Belsky et al. 1991), early commencement of sexual activity (e.g., Byrd-Craven et al. 2007), high frequency of sexual activity (e.g., Belsky et al. 2010), teen pregnancy (e.g., Ellis et al. 2003), sexual risk taking (Belsky et al. 2010), and early age at first birth (Nettle et al. 2011). The effect of paternal absence on menarche seems to be most evident when fathers leave their daughters before the age of 7 years (Belsky et al. 1991; Ellis et al. 2003). For example, women whose parents separated before they were 6 years old were shown to mature earlier than girls whose parents did not separate (Quinlan 2003), and exposure to family conflicts assessed when the daughters were 7 years old was

shown to correlate negatively with self-reported menarcheal age (Moffitt et al. 1992). The effect also seems to be quantitatively accumulating, as indicated by several studies that have found that both the length of paternal absence and the amount of time that girls are exposed to unrelated adult males at home correlate with the timing of menarche (e.g., Moffitt et al. 1992).

Moreover, childhood experiences of both environmental harshness and unpredictability have the LH-predicted lasting effect on adult behavior. Self-reports of early childhood experiences of environmental harshness and unpredictability were shown to be related to the anxious style of attachment (Barbaro and Shackelford 2016), which, compared with the secure style of attachment, represents a fast LH strategy. A study across neighborhoods in England showed that adult women who grew up in low-SES neighborhoods gave birth to their first child much earlier than women who grew up in high-SES neighborhoods (Nettle et al. 2011). The same finding was reported in an earlier study (Wilson and Daly 1997); women who grew up in neighborhoods where life expectancies were shorter (as a result of extrinsic risks such as homicide) were shown to give birth at a younger median age than those who grew up in neighborhoods where life expectancies were longer.

In numerous studies on adult populations, experimentally induced mortality–morbidity has not been shown to have the intended main effect, but interacted with childhood harshness and unpredictability in predicting LH strategic outcomes. In such studies, participants have been asked about their childhood SES and then experimentally primed with stimuli suggesting threats of mortality–morbidity (e.g., news stories about rising homicide rates and future uncertainty). Among people reporting low-SES childhoods, induced mortality was associated with the desire to reproduce early and have more children, even at the cost of delaying one's education and career development; by contrast, these fast LH effects were shown to be absent in people who reported having grown up under favorable resource conditions (Griskevicius et al. 2011). Induced mortality

threats have also prompted participants with low-SES childhoods to opt for diversified bet-hedging by choosing different and riskier stocks over safer and less diversified options (White et al. 2013). Participants with low-SES childhoods have responded to induced environmental harshness with lowered resistance to temptation, high impulsivity, increased risk-taking, and shorter time orientation (e.g., spending more now and saving less for the future), whereas no priming effect has been observed for participants with high-SES childhoods (Griskevicius et al. 2013; Hill et al. 2014). Perceptions of personal control mitigate the psychological effects of resource scarcity threats only for people reporting high-SES childhoods (Mittal and Griskevicius 2014; Griskevicius et al. 2013). Collectively, this stream of research underscores the importance of early life experience in affecting human LH strategic changes.

Conclusion

Thus, the struggle for existence that Darwin described 150 years ago is currently understood to be powered by strategic allocations of the limited energy budget through LH trade-offs. Environmental cues keep active the contingent response between the interindividual struggle for existence and the intraindividual LH trade-offs. If there were unlimited resources and no obstacles to acquiring them, there would be no struggle for existence or need for the corresponding strategic LH trade-offs. Therefore, environmental cues relevant to LH trade-offs are all negative. They are referred to as environmental risks, which are further divided into environmental harshness and environmental unpredictability. Harshness refers to any physical or psychological strain on an individual organism. Possible contributors include resource scarcity, predatory risk, pathogens and disease, natural disasters, and interspecies violence – all of which are independent of an individual's effort for survival and cause mortality and morbidity. Among the elements of environmental harshness, probably most relevant to the survival of most nonhuman animals are levels of

resources and predation, which can also be inter-related because one individual's food may be another's predation. Because humans are the highest predators who have long had no rivals other than themselves, resources and intraspecific competition to monopolize resources – both of which are density dependent – become the major strain on survival and cause the struggle for existence. For both human and nonhuman animals, density-dependent resource limitations and intraspecific competition drive slow LH strategies by which individuals invest in growth and development and in their children's growth and development so that they become capable competitors for the limited resources. Other harshness elements causing extrinsic mortality–morbidity lead to fast LH strategies because fitness is more efficiently attained in a harsh environment by accelerating development and moving to early reproduction before extrinsic mortality or morbidity strikes.

Published studies based on human populations generally support this theorizing about the role of environmental harshness in regulating human LH trade-off strategies. However, extant human LH studies have generally not pursued a density-dependent approach (Ellis et al. 2009), nor have they examined intraspecific competition, particularly in predicting human LH strategies. The ever-increasing and complex social groups of human evolution render most selection pressures density dependent. Resource scarcity and abundance are density dependent, as are mortality and morbidity arising from such extrinsic risks as diseases, intraspecific violence, and even natural disasters; the effects of all of these factors can be converted into winning versus losing in intraspecific competition. Competition that involves garnering resources and avoiding mortality–morbidity risks therefore captures both spectra of the harshness dimension of the environment.

Humans had in some unique fashion become so ecologically dominant that they in effect became their own principal hostile force of nature [and] nothing would select more potently... than a within-species co-evolutionary arms race in which success depended on effectiveness in social competition. (Alexander 1990, pp. 4–7)

One direction for future research is to operationalize and investigate intraspecific competition at both the individual and population levels to determine how it affects LH strategies directly and mediates the relations between environmental harshness and individuals' behaviors and LH strategies.

Whereas environmental harshness refers to the absolute levels of morbidity and mortality, environmental unpredictability refers to the random or stochastic variations of morbidity and mortality. Stochastic variations rather than high frequencies of extrinsic risks are probably more relevant to human evolution because it presents a more formidable task in mastering these two hostile forces of nature. LH theory distinguishes between adult and juvenile populations that will be affected by unpredictable mortality and morbidity. When the adult population is the target of unpredictable mortality–morbidity, species adopt a fast LH strategy to allocate energy and resources for fast development and reproduction if there is adequate bioenergy, as determined by the harshness dimension of environmental risk. When juveniles are the target of mortality, species respond either with conservative bet-hedging (a type of slow LH strategy) or diversified bet-hedging (a type of fast LH strategy), depending on whether juvenile mortality and morbidity respond to parental investment. Published human LH studies do not distinguish between these two types of population mortality because they are highly correlated (Ellis et al. 2009) and because, with high parenting and child care, the child–adult mortality differential never reaches a scale such as those of many other animals (e.g., turtles) that require different LH strategies to respond to high juvenile mortality. However, it is also shown that childhood experiences of both harshness and unpredictability have a lasting effect on adult LH strategies, whereas – at least for some experimental studies – induced harshness and unpredictability of adulthood do not have the expected main effect on behavior. These findings suggest the need for further considerations when applying LH theory to humans as a species-general theoretical framework.

One consideration is the distinction between uncontrollability and unpredictability (Brumbach et al. 2009). Uncontrollability refers to the complete separation between an event's happening and an individual's effort to influence the event, whereas unpredictability includes the additional inability to anticipate and avoid the event. Because LH theory is species general, many mortality and morbidity risks that are defined as unpredictable for animals in general may be uncontrollable but predictable for humans because of the large human brain. The fact that hominin populations (e.g., *Homo erectus*) migrated from Africa as early as 2 million years ago to populate the rest of the world suggests that at least some of the uncontrollable events driving intensive human evolution in the Pleistocene must often have been predictable, because the primary reasons for migration are to purposefully seek resources and avoid risks. In fact, famine, disease, and intraspecific conflict and violence, which are all defined as unpredictable by LH theory, may be uncontrollable but predictable because ancestral humans can anticipate their coming and make adjustments to avoid them; this includes migrating from Africa multiple times during human evolution. The evolution of the large human brain, which is itself a slow LH trait, results from environmental variations (e.g., glacial and interglacial temperature variations had a greater role than the mean cooling of the ice age in effecting brain enlargement; Ash and Gallup 2007) that are certainly uncontrollable but may be predictable because they would otherwise not have led to the large human brain as a slow LH trait. It is therefore possible that many of the environmental unpredictabilities defined by LH theory are predictable to humans who respond not with fast but with slow LH trade-off strategies or with a mixture of both. An apt example of a mixture of the two strategies is the human practice of weaning offspring early and shortening interbirth intervals (fast strategies), which are accompanied by feeding offspring with prepared foods and extensive child care by kin through alloparenting and siblings helping at the nest (slow strategies). Future human LH studies can

hypothesize mixed LH strategies, especially in response to uncontrollable but predictable environmental risks.

Cross-References

- [Environmental Harshness](#)
- [Environmental Harshness/Mortality](#)
- [Environmental Unpredictability](#)
- [Environmental Unpredictability and Bet-Hedging](#)
- [Harsh Environments](#)

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Environmental Scarcity

► Environmental Harshness/Mortality

Environmental Stochasticity

► Environmental Unpredictability and Bet-Hedging

Environmental Threats and Challenges

► Environmental Risk

Environmental Unpredictability

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Synonyms

Stochastic environment; Unpredictable environment

Definition

Uncertainty about future environmental outcomes.

Introduction

Choosing to stay at a party rather than leave depends on which people might still show up. Buying a house depends on future employment prospects. In making decisions, the best course of action often depends not only on current conditions but also on predictions about the future (Frankenhuis et al. 2016b).

Environments might be predictable for two reasons. First, environmental states might be autocorrelated across time (Nettle et al. 2013). If it rains today, it is likely to rain tomorrow. Second, even without such autocorrelation, *other* current cues might predict future conditions. For example, female parasitic wasps lay more eggs on low-quality hosts if conditions indicate an approaching thunderstorm (dropping barometric pressure) than if conditions indicate a fair summer day (steady barometric pressure). Thunderstorms might kill them, so rather than saving their eggs for a higher-quality host, the wasps deposit their eggs immediately (Roitberg et al. 1993).

Adaptation to Environmental Unpredictability

Natural selection favors different adaptations, depending on the degree of environmental

predictability (Ellis et al. 2009; Frankenhuis et al. 2016a). If an environment is stable (and therefore predictable) generation after generation, natural selection might favor reliably developing phenotypes that are specialized for the prevailing conditions. If an environment is stable (and predictable) within a lifetime, but varies across lifetimes, natural selection might favor developmental plasticity – the ability to adjust development based on experience – if experience provides cues to the environmental state (Frankenhuis et al. 2013b). If an environment is variable across lifetimes and organisms cannot infer its state within lifetimes, natural selection might favor strategies that avoid extreme payoffs – either by producing generalist phenotypes, which do moderately well in all environmental conditions, or mixtures of specialists, each of which does very well in a subset of environmental conditions (Frankenhuis et al. 2016a).

Some evolutionary psychologists hypothesize that over the course of human evolution, the degree of environmental unpredictability might itself have been stable (and predictable) within a lifetime but variable across lifetimes (Ellis et al. 2009). If so, natural selection might have favored developmental plasticity for dealing with environmental unpredictability: organisms that infer the degree of environmental unpredictability during ontogeny and adapt accordingly (Frankenhuis et al. 2013a). Consistent with this idea, exposure to unpredictable childhood environments is associated with “fast” life histories, such as earlier age of first sex and first conception, higher rates of aggressive and delinquent behavior, and reduced health (Belsky et al. 2012; Brumbach et al. 2009; Nettle et al. 2011; Simpson et al. 2012). These associations remain after controlling for exposure to harshness, i.e., mean levels of morbidity and mortality.

Evolutionary developmental studies typically measure environmental unpredictability as residential changes, family disruptions, and parental job changes. An open and interesting question for future research remains whether these measures truly capture environmental unpredictability or different components of harshness (Nettle et al. 2012). A second challenge will be to empirically assess the idea that over the course of

human evolution, the degree of environmental unpredictability was itself stable (and predictable) within a lifetime but variable across lifetimes (Nettle et al. 2013). A third challenge will be to determine how individuals might infer the degree of environmental unpredictability based on their experiences (Frankenhuis et al. 2013a).

Conclusion

In *Roadhouse Blues*, Jim Morrison sings: “The future’s uncertain, and the end is always near” (The Doors, 1970). This sentence is contradictory. If the end is always near, then the future is certain: imminent death. The future is uncertain when it is not possible to predict it, that is, when current conditions are uncorrelated with future outcomes and there are no cues that predict future outcomes (Nettle et al. 2013).

Cross-References

- [Environmental Harshness](#)
- [Environmental Harshness/Mortality](#)
- [Environmental Risk](#)
- [Environmental Unpredictability and Bet-Hedging](#)
- [Harsh Environments](#)

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Environmental Unpredictability and Bet-Hedging

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Synonyms

Environmental unpredictability: [Environmental instability](#); [Environmental stochasticity](#); [Environmental variance](#); [Environmental variation](#); [Temporal or spatial fluctuation](#).

Bet-hedging: [Bistability](#); [Developmental noise](#); [Diversified or conservative bet-hedging](#); [Risk aversion](#); [Risk spread](#); [Stochastic phenotype switching](#)

Definition

Environmental unpredictability is characterized by nondeterministic and variable amounts of change within a temporal environment (Botero et al. 2015; Philippi and Seger 1989). When exposed to greater environmental unpredictability, organisms favor *bet-hedging* to maximize their fitness (Botero et al. 2015). Bet-hedging involves overall reduced variance in progeny yields, manifesting in decreased fitness in typical conditions in exchange for increased fitness in unpredictable conditions (Philippi and Seger 1989; Simons 2011; Slatkin 1974). Bet-hedging operates on the assumption that some reproductive success is better than no reproductive success in certain years (Philippi and Seger 1989).

Introduction

In unpredictable environments, organisms are unable to make reasonable predictions about future environmental occurrences. Unpredictability spurs organisms to engage in risk-management based on the duration of unpredictability and its impact on mortality-morbidity. Bet-hedging strategies are only favored when environmental unpredictability produces variance in *juvenile* survivorship (Ellis et al. 2009). By contrast, when environmental unpredictability impacts variance in *adult* morbidity-mortality rates, evolution (over time) favors accelerated reproduction and overall faster life history strategies rather than diversified bet-hedging (Ellis et al. 2009). Consequently, bet-hedging strategies are favored when unpredictable environments impact juvenile survivorship but may not be favored when unpredictable environments impact adult mortality.

Bet-Hedging as Risk Management

Different forms of bet-hedging represent distinct forms of risk management in response to varying environmental conditions; there is no single “optimal” form of bet-hedging. As a consequence, environmental unpredictability forces organisms

to evaluate different risk management strategies in order to limit their potential fitness losses (Ellis et al. 2009). Bet-hedging requires organisms to make trade-offs. Organisms are required to make sacrifices to either their number of offspring or variance in offspring quality relative to others (Starrfelt and Kokko 2012). Conservative and diversified bet-hedging are two possible strategies for managing risks in unpredictable environments.

Conservative bet-hedging (“play it safe”) occurs when organisms produce fewer, relatively higher quality offspring that are better equipped to deal with average environmental conditions (e.g., producing a clutch of eggs, all of intermediate size; Botero et al. 2015; Ellis et al. 2009; White et al. 2013). Conservative bet-hedging tends to contribute to the development of relatively slow life history strategies, as individuals delay reproduction to amass resources and invest more in their offspring’s survival (Ellis et al. 2009). *Diversified bet-hedging* (“don’t put all your eggs in one basket”) is favored when conservative bet-hedging fails (Botero et al. 2015; Ellis et al. 2009). Diversified bet-hedging leads to the production of numerous diverse offspring, equipped to deal with multiple niche environmental conditions (e.g., producing a clutch of eggs of multiple different sizes). Unlike conservative bet-hedging, diversified bet-hedging does not always favor the adoption of slow life history strategies. Given that phenotypic diversity can be achieved through a wide range of behaviors (e.g., multiple matings, intraclutch variation, accelerated reproduction), a wide range of life histories may be employed to combat unpredictability in juvenile mortality (Ellis et al. 2009; Starrfelt and Kokko 2012).

Examples of Bet-Hedging

Bet-hedging strategies manifest across all taxa, including plants, bacteria, and animals (reviewed in Simons 2011). Plant examples of bet-hedging include diversified timing of seed germination and elevated ovule numbers per flower (reviewed in Simons 2011). The bacteria *Escherichia coli* exploits phenotypic diversity to

bet-hedge against unpredictable environmental stressors (reviewed in Ellis et al. 2009). The mammalian white safika engages in conservative bet-hedging when exposed to extreme environmental unpredictability (Dewar and Richard 2007). These examples highlight the adaptation of bet-hedging across multiple taxa under unpredictable environmental conditions (Simons 2011).

Conclusion

Bet-hedging is a risk-management strategy utilized to maximize fitness in the face of environmental unpredictability and low juvenile survivorship. Bet-hedging strategies may be *conservative* (e.g., by producing offspring all of one size) or *diversified* (e.g., by producing offspring of multiple different sizes). Bet-hedging of both types have been demonstrated across taxa in response to unpredictable environmental conditions.

Cross-References

- [Adaptation](#)
- [Adaptive Plasticity](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
- [Extrinsic Mortality](#)

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Environmental Variance

- [Environmental Unpredictability and Bet-Hedging](#)

Environmental Variation

- [Environmental Unpredictability and Bet-Hedging](#)

Envy

- [Downfall of “Tall Poppies”](#)

Epigamic Display

- [Desire to Be Included Among Desirable Women](#)

Epigamic Selection

- [Female Choice and Sexual Conflict Theory](#)

Epigamic Traits

- [Secondary Sexual Characteristics](#)

Epinephrine

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Synonyms

Adrenaline

Definition

It is a sympathomimetic agent.

Introduction

The autonomic nervous system has been divided into the sympathetic arm and parasympathetic arm. The sympathetic arm delivers its action by releasing the neurochemicals – epinephrine and norepinephrine – whereas the parasympathetic arm delivers its action through release of acetylcholine. Epinephrine is a key sympathomimetic agent, commonly known as adrenaline. In the literature the terms “epinephrine” and “adrenaline” are interchangeably used. It is secreted from the adrenal medulla. It is often released in response to stress and determines the bodily responses to stress. It is also known as the “fight or flight hormone” (Goldstein 2010). Certain situations or events are recognized as threatful for the homeostasis of the body and are capable of stimulating the adrenal medulla to release epinephrine. For example, exposure to cold environment, emotional stress, severe painful conditions, and hypoglycemia induced by insulin activate the adrenal medulla to secrete epinephrine (Goldstein 2010). Certain evidences exist that demand of work is also capable of increasing the release of epinephrine among men (Pollard et al. 1996). It is possible that job pressure and perceived stress due to demands at the workplace might be responsible for release of stress hormones.

History of Epinephrine

John Abel, the scientist from the United States, prepared a crude extract from the adrenal gland and named it “epinephrine” in 1857. Then, in 1901 Jokichi Takamine prepared the pure form from the extract and patented it.

The Japanese scientist Jokichi Takamine first isolated the substance with technical help from Keizo Uenaka (Saito and Kamiyama 2011). Henry Dale, a research scientist in the United Kingdom, named it “adrenalin” as it was a different form of extract (pure form), to which John Abel used the name “epinephrine” (Aronson 2000). Epinephrine is chemically known as dihydroxyphenylmethylaminoethanol [i.e., (R)-1-(3,4-dihydroxyphenyl)-2-methylaminoethanol]. It is the name issued by the International Union of Pure and Applied Chemistry (IUPAC). Various countries adopted different generic names for epinephrine. The British approved name is “adrenaline,” whereas the internationally approved name is “epinephrine.” In Australia, France, Scandinavian countries, and many Asian and African countries, it is known by the name “adrenaline” (Aronson 2000). Epinephrine has been marked by various brand (proprietary) names in various countries (e.g., epipen in Britain).

Biochemistry and Physiology of Epinephrine

Epinephrine is a catecholamine. It has resemblance with other catecholamines like dopamine, epinephrine, and norepinephrine (Kamal and Lappin 2019). Epinephrine along with norepinephrine gets synthesized in the adrenal medulla or in the neurons of the sympathetic nervous system (Kamal and Lappin 2019). All the catecholamines including epinephrine have the same precursor amino acid (i.e., tyrosine). Tyrosine undergoes hydroxylation followed by decarboxylation in a sequential manner to form dopamine, which later undergoes hydroxylation to form norepinephrine. Norepinephrine then undergoes

methylation to form epinephrine. Dopamine, norepinephrine, and epinephrine are all active forms and together known as catecholamines (Paravati and Warrington 2019). Degradation of epinephrine occurs by several rate-limiting enzymes like monoamine oxidase (MAO) and catechol-O-methyl transferase (COMT). The end product of metabolism of epinephrine and norepinephrine is vanillylmandelic acid (VMA) (Kamal and Lappin 2019).

The release of epinephrine is regulated via the activation of hypothalamo-pituitary-adrenal axis (Goldstein 2010). The regulation of epinephrine release happens through feedback control. Hypothalamus releases adrenocorticotrophic-releasing hormone (ACTRH), which stimulates the anterior pituitary to release adrenocorticotrophic hormone (ACTH), which further acts on the adrenal medulla to cause release of epinephrine. To maintain the homeostasis in the body, through negative feedback mechanism, release of ACTH and ACTRH is controlled (Goldstein 2010).

Epinephrine, being a sympathomimetic agent, causes activation of the alpha 1 receptors in the smooth muscles of the blood vessels producing vasoconstriction, as a result of which there is increase in blood pressure (diastolic), cerebral perfusion pressure, and coronary perfusion pressure (Gough and Nolan 2018). It also produces pupillary dilatation and piloerection through its action on the alpha 1 receptor.

Epinephrine also acts on the receptors located in myocardium, skeletal muscles, and smooth muscles of the bronchial tree of the lungs. Epinephrine along with norepinephrine causes tachycardia, bronchodilation (through beta 2 receptor), increased contractility of the heart (through beta 1 receptor), and hyperglycemia (through alpha 2 receptor) (Kamal and Lappin 2019; Paravati and Warrington 2019). Epinephrine mediated glycogenolysis, and lipolysis mediated through the beta 2 and beta 3 receptors, respectively. Increase glucagon secretion and decreased insulin secretion are also mediated by epinephrine through beta 2 and alpha 2 receptors, respectively (Paravati and Warrington 2019).

Evolutionary Significance of Epinephrine

The adrenal medulla develops from the neuroectoderm. In stress-free states, the level of secretion of epinephrine almost ceases, whereas during severe stressful situation, the secretion of epinephrine reaches the peak (Pohorecky and Wurtman 1971). In the lower vertebrates, the cytoarchitecture of the adrenal is different from that of higher vertebrates. As there is progression from lower to higher vertebrates, the intimate association between the adrenal cortical cells and adrenal medullary cells (chromaffin cells) increases (Pohorecky and Wurtman 1971). Among amphibians, the adrenal tissue is present within the mesonephros (equivalent to mammalian kidney), and the chromaffin cells are present within the steroid-producing cells in a close association (Pohorecky and Wurtman 1971). The distribution of chromaffin cells in reptiles follows a unique pattern. The norepinephrine-producing chromaffin cells are present on the surface of the adrenal gland in the form of a band (extra-glandular in location), whereas predominantly epinephrine-producing chromaffin cells are present within the adrenal gland (intraglandular in location). Among birds, the chromaffin cells are randomly scattered in the adrenal gland, whereas among mammals, they are clustered in the center of adrenal gland (Pohorecky and Wurtman 1971).

Epinephrine and Health Significance

Catecholamines like epinephrine serve various physiological functions in the body. Their excess or deficit is likely to cause mental as well as physical disorders (Kamal and Lappin 2019). Tumors of the adrenal medulla (pheochromocytoma) and sympathetic ganglia (paraganglioma) may result in excessive production of catecholamines like epinephrine and norepinephrine, which is often clinically manifested as headache, hypertension, and tachycardia (Berends et al. 2019; Kamal and Lappin

2019). Increases urinary level of vanillylmandelic acid (VMA) and homovanillylmandelic acid (HMA) are sensitive biomarkers of pheochromocytoma and paraganglioma (Berends et al. 2019; Kamal and Lappin 2019).

Evidences support that stress induces the release of stress hormones, which prepare the body to readjust its needs during stress. Acute severe stress prepares the body for a flight or fight response, during which there occurs reconfiguration of the immune system. Transient decline in the immune system during acute severe stress increases the vulnerability for diseases (Adamo 2014). Stress hormones including epinephrine help in consolidation of memory that is emotionally aroused. The interaction between amygdala and hippocampus mediates the process of consolidation of memory (McIntyre and Roozendaal 2007). However, as epinephrine is incapable of crossing the blood-brain barrier, there must be some complex mechanism operating peripherally that facilitates the central processing of memory (McIntyre and Roozendaal 2007).

Lower norepinephrine to epinephrine ratio in the urine is indicator of high suicidal behavior (Ostroff et al. 1985). Epinephrine and norepinephrine are involved in the pathogenesis of mood disorders, stress-related disorders, anxiety disorders, and attention-deficit hyperkinetic disorder (Berends et al. 2019). The pharmacological agents used for treatment of these disorders alter the activity on epinephrine and norepinephrine. Certain addictive substances (stimulants) like amphetamine and cocaine act in the body by increasing the level of epinephrine. Persons using the stimulants and the sports persons, who use performance enhancers (certain kinds of stimulants and anabolic steroids), often experience adrenaline rush in the body (Davis et al. 2008).

Epinephrine (adrenaline) has been used in the anaesthetic, critical care, as well as pain management settings (Saito and Kamiyama 2011). Epinephrine has been used for cardiopulmonary resuscitation. It is a life-saving drug, though there are some evidences that it compromises the microcirculatory flow of blood to the brain (Gough and Nolan 2018). Epinephrine has been

used as a life-saving treatment modality in management of anaphylaxis (Sicherer et al. 2017). It has been reported that the cerebrospinal fluid catecholamine levels are elevated in patients with subarachnoid hemorrhage with high level of disability and who experience early mortality. Epinephrine can be considered as a sensitive marker of such outcomes associated with subarachnoid hemorrhage (Moussouttas et al. 2012). During certain surgical procedures, topical epinephrine has been used for hemostasis due to its profound vasoconstricting property (Korkmaz et al. 2015).

Conclusion

Epinephrine has a pivotal role in maintaining the homeostasis of the body. It enables the individual to combat threats and stress. It has significant implications in physical as well as mental health. It has been used as a life-saving measure in cardiorespiratory arrest and severe allergic conditions.

Cross-References

► Monoamine Oxidase and Antisocial Behavior

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Epiphenomenon

► By-Product

Episodic and Semantic Counteraction

► Scope Hypothesis, The

Episodic Memory

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Synonyms

Autobiographical memory; Declarative memory; Episodic-like memory; Explicit memory

Definition

Memory of personal past events, including the what, where, and when aspects of the event that can be explicitly accessed. In addition to these content-based aspects of a remembered experience, information about the event is integrated in a single representation and can be flexibly used to support adaptive behavior.

Introduction

When Endel Tulving distinguished episodic memory (EM from here on) from semantic memory (Tulving 1972), a crucial framework for psychological studies on EM was established. Semantic memory, or knowledge or facts about the world, is unlike EM because it does not include experiential properties or sensory information related to the occasion on which information was learned. Semantic memory, like the fact that Boston is the state capital of Massachusetts, is unlinked to the occasion on which this piece of information was learned. Such facts that are simply *known* to be true are conceptually organized rather than temporally organized in experiences like they are in EM. This distinction has propelled

studies of not only human but of nonhuman animal (nonhumans from here on) EM. We know that humans have EM because they can verbally report a memory from the past, like the memory of a last Thanksgiving holiday. Determining if nonverbal species have EM presents an obvious challenge, but comparative memory researchers are constantly developing experimental paradigms to overcome this hurdle. Though the presence of EM in nonhumans is controversial, most comparative and evolutionary psychologists contend that EM has a long evolutionary history. Cognitive and neurobiological studies that examine the presence of EM features in nonhumans are crucial in understanding the mechanisms underlying EM and in charting potential time points at which these remarkable mnemonic abilities emerged.

Human EM

Mental time travel allows humans to “go back in time” when retrieving the memory of a recent birthday: where and when the celebration took place, how good the food was, and whose company was enjoyed. EM allows a vivid picture of how the elements that comprised a personal past event unfolded over time to be painted. In addition to being contextually rich, EMs are also personally relevant. In particularly meaningful or self-defining recollections, EMs are ripe with emotion and “the feeling of being there.” This experiential ability to mentally place oneself in the past is called *autonoetic consciousness*. Human EM is similar, but should be distinguished from autobiographical memory. *Autobiographical memory* is a more involved phrase used to describe the self-memory system that combines salient EMs from one’s life with semantic memories. Together, these episodic and semantic memories feed the working self, which includes goals and images of the self.

Human introspection, recollection, and even the working self in the case of autobiographical memory have served as tools that have permitted a definition of human EM to be constructed. While

autonoetic consciousness and associated phenomenology may offer a rich lens with which humans can view their own EMs, both rely on verbal reports of subjective mental experience. For this reason most evolutionary-oriented researchers argue that phenomenological experience is not a necessary ingredient of EM. Indeed, natural selection did not select for the feelings that accompany episodic recollection, but rather the *functions* these memories served in survival and propagation of the species over time. After all, the principle of parsimony is useful because it mirrors what is found in nature. Conceptually minimalistic definitions that focus on *how* information is stored and retrieved, like the time and place of the experience, as outlined in Tulving’s original definition (Tulving 1972), offer objective functional criteria that have recently been applied to studies of EM in humans.

EM in Nonhumans

Despite the anthropocentric definition of EM that requires conscious experience and is therefore unique to humans, this view has been challenged by combining content-based approaches with paradigms that are testable in nonverbal species (for reviews, see Allen and Fortin 2013; Eichenbaum 2013; Templer and Hampton 2013b).

The first study that applied functional objective criteria for EM to nonhumans was Clayton and Dickinson’s (1998) demonstration that food-caching scrub jays could remember what types of food they stored where and when (WWW memory). To circumvent the issue that some reformulations of EM since Tulving’s original definition stress the importance of autonoetic consciousness and knowledge of the subjective self through time, this demonstration was dubbed “episodic-like memory.” Analogous WWW paradigms have been developed in several species, including magpies, black-capped chickadees, honeybees, rhesus monkeys, rats, mice, meadow voles, pigs, and humans. Studies have indicated that many of these species are capable of at least

the “what” and “where” aspects of EM and some are capable of all three, depending on the experimental paradigm (for reviews that discuss these studies, see Templer and Hampton 2013b).

Species Differences in “When”

The “when” aspect of WWW is arguably the most challenging element of EM to demonstrate. Questions of what is mentally represented when animals make apparent “when” judgments in WWW paradigms have been raised. For example, an initial concern of the Babb and Crystal (2005) study was if rats might have used time of day at testing rather than “when” or absolute (clock) time. This was controlled for in later studies by both Crystal and Roberts’ groups, but Roberts took this idea of testing for the temporal basis of EM further in an elegantly controlled design which showed that rats remember “how long ago” rather than absolute time (Roberts et al. 2008). This result is not surprising given that natural foraging decisions in rats depend on elapsed time and that the ecological relevance of a rat knowing absolute time is equivocal. In a similar vein, honeybees were shown to use circadian timing rather than “when” in a WWW memory test, likely because nectar availability follows a strict circadian pattern (Pahl et al. 2007). Species-specific ecological relevance also likely explains why monkeys failed to remember when preferred food became rotten as compared to when less preferred food remained fresh in Hampton’s adaptation of the scrub jay food-caching paradigm: monkeys do not naturally cache and keep track of decay rates of perishable and nonperishable food (Hampton et al. 2005).

To further dissociate the cognitive mechanism underlying temporal judgments in monkeys, Templer and Hampton (2013a) showed that order of events is not distinguished based on memory trace strength (familiarity), ordinal position of items, or amount of time passed, but is instead based on number of intervening items that occurred. Clearly, different species encode when, or temporal order, differently and discovery of these differences is not only interesting but crucial as they critically inform functional

characterizations of EM. Progress is made when cognitive behavioral experiments dissociate these more nuanced information processing mechanisms that underlie aspects of EM. It is also important to note that the use of one cognitive mechanism, such as when in absolute time, is not necessarily more sophisticated or evolved than a strategy that relies on “how long ago.”

Recollection Versus Familiarity

Episodic recollection of past experiences is distinguished from a sense of familiarity for stimuli previously presented. Receiver operating characteristic (ROC) is a powerful method of signal detection analysis used to quantify contributions of recollection and familiarity in a recognition memory task. Rats have been shown to have a dual processing system for recognition: their response patterns mirror humans in the indication of a familiarity process as well as a separate recollective process. It has also been shown that the hippocampus is critical in the threshold retrieval characteristic of recollection but is not necessary for familiarity judgments. Corroborating this evidence of hippocampal involvement in EM processes but not familiarity, the Eichenbaum group has also shown that the hippocampus is critical for distinguishing the order of odors of rats sampled but not for familiarity-based recognition of those odors alone (see Eichenbaum 2013 and Allen and Fortin 2013 for a review of these studies).

Neurobiological Studies Inform the Integrative Nature of EM

A requirement of EM is that it is integrative. Neurobiological studies offer a useful approach to this structural component of EM as the brain is a system that integrates sensory information into episodes. What defines an episode might be different for different species, but the neural structures, namely, the hippocampus and adjacent cortical structures in the parahippocampal regions, are highly conserved across species. Neurobiological studies in rodents and monkeys have

mapped how these streams of information about “what” and “where” are processed and integrated as item-place associations in the hippocampus. Before reaching the hippocampus, parallel processing occurs in two general streams. Item information, or “what,” is processed by the perirhinal cortex and lateral entorhinal cortex, and context, or “where,” information is processed by the postrhinal cortex (parahippocampal in primates) and medial entorhinal cortex. Neural pathways for the processing of “when” information are more challenging (Allen and Fortin 2013), but cells that keep track of time, known as “time cells,” have been identified in the hippocampus (Eichenbaum 2013). Additional evidence in human functional magnetic resonance imaging and rodent single-unit recordings and lesion studies indicate that the hippocampus is responsible for the temporal organization of mnemonic representations.

Future Directions and the Combination of Cognitive Behavioral and Neurobiological Approaches

The neurobiological studies described here are crucially informative, but researchers have importantly pointed out that memory types should not be determined solely on the basis of brain structures involved rather than cognitive mechanisms (Eichenbaum 2013; Templer and Hampton 2013b). The functional aspect of EM is ultimately behavioral. It has become increasingly apparent that the most informative studies combine innovative behavioral paradigms that identify *what* information is mentally represented with neurobiological manipulations that identify *how* information is mentally represented at the neural level. Cognitive and neurobiological methodologies have converged in several elegant studies (e.g., see Allen and Fortin 2013; Eichenbaum 2013; and Templer and Hampton 2013b for several examples). Yet, many researchers primarily operate as either neurobiologists or cognitive behaviorists, rather than cognitive neuroscientists. Application of newly developed and sophisticated behavioral techniques

to cutting-edge neurobiological investigations, including methods such as optogenetics, is integral to future success in the EM field. Such behavioral tasks that capture EM’s functional properties include its flexibility, accessibility or metacognitive properties, future-oriented and planning capabilities, and source memory components.

Conclusion

Evolutionary-based approaches have provided a wealth of knowledge about underlying information processing systems involved in encoding and retrieving an event. As such, both theoretical characterizations of EM and functional characterizations of the hippocampal system have benefited greatly. Significant progress has been made when researchers (1) move away from anthropocentric definitions of EM, (2) combine cognitive behavioral approaches with neurobiological methodologies, and (3) ask what features of EM are shared and not shared by humans and nonhumans rather than asking the unsophisticated question of “do animals have EM.”

Cross-References

- ▶ [Attention and Memory](#)
- ▶ [Declarative Knowledge](#)
- ▶ [Different Functions of Memory](#)
- ▶ [Evolution of Intelligence](#)
- ▶ [Evolution of Memory, The](#)
- ▶ [Inceptive and Derived Memory](#)
- ▶ [Long-Term Memory](#)
- ▶ [Metacognition](#)
- ▶ [Multiple Memory Systems](#)
- ▶ [Personal Memory](#)
- ▶ [Working Memory](#)

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Episodic-Like Memory

- [Episodic Memory](#)

Epistemic Reasoning

- [Emergence of Indicative Reasoning](#)

Equalitarianism

- [Blank Slate, The](#)

Equality

- [Fairness in Corvids](#)

Equity

- [Fostering Values of Fairness](#)
- [Insist on No More than Equity](#)

Erasmus Darwin

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Introduction

Charles Darwin, though he produced the most coherent and influential account of the evolution of species, was not the first Darwin to publish on the subject: That honor belongs to his paternal grandfather, Erasmus Darwin. A true polymath, Erasmus Darwin was a physician, poet, and inventor and so renowned in his time that he was offered the position of personal physician to the King, a post which he refused, preferring to continue treating the relatively poor country folk instead. Having studied at St. John's College, Cambridge, as well as in Edinburgh, he practiced as a physician first in Nottingham and then in Litchfield, where he established himself as a prominent figure in the local scientific community.

In addition to his work as a physician, he cultivated a great interest in taxonomy and botany, maintaining a large botanical garden, and building enough of a reputation that he was very close to accompanying Captain James Cook as a naturalist on one of his voyages (prefiguring in a

remarkable way the path his grandson would eventually follow), but he was prevented from doing so by conservative pressures in the scientific establishment of the time. Such pressure was applied in response to Darwin's unfortunate penchant for sharing his free-thinking, very liberal opinions quite openly and freely. He was an outspoken advocate for equality between the sexes, including education for women, as well as a vocal opponent of slavery. Additionally, he openly rejected conventional contemporary Christian views on both creation and homosexuality, refusing to pass judgment on his numerous homosexual friends as England became less tolerant of them.

Science

Although he was a Fellow of the Royal Society, Darwin was also a very active member and promoter of the Lunar Society, an early scientific society based in the English Midlands, providing a country alternative to the London-based Royal Society. The group's name derived from their custom of meeting each month on the occasion of the full moon, which provided sufficient light for the members to safely return home after the meeting in those days before the advent of streetlights. His circle of friends and associates was a truly remarkable group, including James Watt, inventor of the steam engine; Josiah Wedgwood, the famed potter; discoverer of oxygen Joseph Priestley; William Withering, the physician who introduced digitalis into medical practice; and even Benjamin Franklin, who introduced Darwin to the wonders of experimenting with electricity.

Darwin had a great fascination with machinery and was thoroughly convinced that the widespread use of machines in industry and manufacturing would be a great boon to humanity bringing about an industrial golden age that would improve life for all. He put this interest into action with a remarkable range of inventions, the best-known of which was a "speaking machine," the partially-completed prototype of which fooled some people, hearing it for the first time, into thinking they had heard a real

person speaking. The prototype's vocabulary was limited to saying "papa" or "mama," but that it worked at all is testament to Darwin's genius. He also designed one of the first mechanical copying machines, as well as a steam-powered vehicle which he called a "fiery chariot," and his design for a carriage steering system was later used in early automobiles.

Poetry

Beyond science and mechanics, Darwin's other great love was poetry, and poems were his main means of expression of his ideas, including political, historical, and scientific thoughts. His first poetic success was *The Loves of the Plants* (1789), in which he presented the current scientific understanding of plant reproduction in frankly sexual, even erotic, images. In another example of his rather radical leanings, he soon after published a revised edition incorporating new verses about the wonders of cannabis. Though the prurient portrayals of plant sexuality were the main draw, the poem also extends its metaphor to include an open, very blunt condemnation of slavery, in a series of verses noting that as newly discovered delicacies such as cashews made their way eastward across the Atlantic, a similarly valuable human cargo was shipped to the West:

E'en now, e'en now, on yonder Western shores
Weeps pale Despair, and writhing Anguish
roars:
E'en now in Afric's groves with hideous yell
Fierce SLAVERY stalks, and slips the dogs of
hell. . .

Hear him, ye Senates! Hear this truth sublime,
"HE, WHO ALLOWS OPPRESSION,
SHARES THE CRIME." (1806 edition, p. 164)

His next major work, *The Economy of Vegetation*, which together with *The Loves of the Plants* forms the larger work *The Botanic Garden*, again combines his loves of botany and poetry, in an epic that sets out to do nothing less than describe history from the dawn of creation to the start of the industrial age, illustrated lavishly by William

Blake. In its first canto, “Let There Be Light,” Darwin actually seems to be presciently describing the Big Bang theory:

Astonished Chaos heard the potent word:
 Through all his realms the kindly Ether runs,
 And the mass starts into a million suns;
 Earths round each sun with quick explosions
 burst,
 And second planets issue from the first;
 Bend, as they journey with projectile force,
 In bright ellipses bend their reluctant course;
 Orbs wheel in orbs, round centres centres roll,
 And form, self-balanced, one revolving Whole.
 (1798 edition, p. 5-6)

The other cantos go on to describe the newly discovered process of photosynthesis, along with predictions of the development of both flying vehicles and submarines. The truly controversial aspect of the poem, however, was its description of the history of the natural world without any explicit inclusion of a Creator, an idea that would be stated far more explicitly in his next book, *Zoonomia, or the Laws of Organic Life*, along with his first clear suggestion of what would become one of his grandson’s cornerstone ideas: that all life has descended, over a very long period of time, from a single ancestor. In *Zoonomia*, Darwin directly addresses evolution, posing the question, “Would it be too bold to imagine, perhaps millions of ages before the commencement of the history of mankind...that all warm-blooded animals have arisen from one living filament, which the first great cause endowed with animality, with the power of acquiring new parts, attended with new propensities...delivering down those improvements by generation to its posterity, world without end?” *Zoonomia* also takes on the adaptations of organisms to the demands of their environment, using an example that is eerily prophetic of his grandson’s work in the Galápagos:

Some birds have acquired harder beaks to crack nuts, as the parrot. Others have acquired beaks adapted to break the harder seeds, as sparrows. Others for the softer seeds of flowers, or the buds of trees, as the finches. (1809, p. 396)

This same insight, based on observations of finches, would prove vital to Charles Darwin’s argument more than 50 years later.

Erasmus Darwin’s fullest presentation of evolutionary ideas, however, comes in the posthumous publication of his epic poem, *The Temple of Nature* (1802), which presents a history of life on Earth, entirely in rhyming couplets. Many evolutionary ideas appear in the following stanzas, for example:

Organic life beneath the shoreless waves
 Was born, and nursed in Ocean’s pearly caves,
 First forms minute, unseen by spheric glass,
 Move on the mud, or pierce the watery mass;
 These, as successive generations bloom,
 New powers acquire and larger limbs assume;
 Whence countless groups of vegetation spring,
 And breathing realms of fin, and feet, and wing.

Thus the tall Oak, the giant of the wood,
 Which bears Britannia’s thunders on the flood;
 The Whale, unmeasured monster of the main;
 The lordly lion, monarch of the plain;
 The eagle, soaring in the realms of air,
 Whose eye, undazzled, drinks the solar glare;
 Imperious man, who rules the bestial crowd,
 Of language, reason, and reflection proud,
 With brow erect, who scorns this earthy sod,
 And styles himself the image of his God-
 Arose from rudiments of form and sense,
 An embryo point or microscopic ens! (Lines
 295 to 314)

In these verses, Erasmus Darwin states concisely, but poetically, that all life shares a common origin, that the common origin was a microscopic organism, and that this original life form arose in the sea and later emerged onto land.

Erasmus Darwin’s Fall from Prominence

Erasmus Darwin was very bold in his presentation of both political and scientific ideas, but his timing was rather poor, unfortunately. He and his circle had taken strong, progressive stances at a time when, facing the revolutions in America and France, a conservative backlash against these liberal intellectuals was underway. In 1791, riots erupted in Birmingham following a celebration of the fall of the Bastille, during which Joseph Priestley’s house and laboratory were set on fire and destroyed. Far from becoming widely accepted, Darwin’s evolutionary poetry was viciously mocked in 1798, in an anonymous poem (eventually attributed to George Canning)

entitled “Loves of the Triangles.” This was a parody of Darwin’s “Love of the Plants” published in the *Anti-Jacobin*, a newspaper devoted to opposing the ideals of the French Revolution. The poem is one of the most bizarre pieces in the English language, incorporating somewhat erotic verses regarding geometric forms, the story of Cinderella retold in the style of *The Economy of Vegetation*, and a description of how humanity has evolved to its present form from cabbages (this last appears in one of the many lengthy footnotes mocking Darwin’s biological ideas). This parody linked Erasmus Darwin in the public mind with both the French Revolution and sacrilegious science and was in fact very funny. This contributed directly to the neglect of Erasmus Darwin in accounts of eighteenth-century intellectual history until quite recently.

The subsequent abandonment of Erasmus Darwin by the cognoscenti in the nineteenth century is unusual in its thoroughness, especially given Darwin’s reputation prior to Canning’s parody. After *Zoonomia* appeared in 1794, for example, Darwin was for a time widely considered the most important medical writer in England and was indeed the most popular scientific writer of the Romantic era. His poetry enjoyed a similarly elevated position for a time, with Samuel Taylor Coleridge declaring in 1797 that he was the “first literary character of Europe,” a direct influence on Coleridge as well as on William Wordsworth, Percy Bysshe Shelley, and of course Darwin’s collaborator William Blake. Shelley and his colleagues spoke so much of Erasmus Darwin and his devotion to science that Mary Shelley included an anecdote she had overheard about Darwin, in which he allegedly gave life to a piece of vermicelli, in the introduction to the 1831 edition of *Frankenstein*. It is unclear what she actually overheard, as Darwin certainly had not brought pasta to life, but one possibility may lie in a *Temple of Nature* reference to *vorticellae*, or “wheel animals,” microorganisms which were in his time believed to arise in rain puddles via spontaneous generation.

Influence on Charles Darwin

Despite his prominence in literary and scientific circles in the eighteenth century, Erasmus Darwin was largely ignored by both disciplines through the nineteenth and much of the twentieth centuries. Even his most famous descendant, Charles Darwin, attempted to distance himself from his grandfather’s work, for the simple reason that he preferred that his own ideas not be seen as derivative. This was not an idle worry; in 1860, in a review of the first edition of *On the Origin of the Species*, Bishop Samuel Wilberforce noted the many similarities between the works of the grandfather and the grandson:

We do not think that, with all his matchless ingenuity, Mr. Darwin has found any instance which so well illustrates his own theory of the improved descendant under the elevating influences of natural selection exterminating the progenitor whose specialities he has exaggerated as he himself affords us in this work. For if we go back two generations we find the ingenious grandsire of the author of the ‘Origin of Species’ speculating on the same subject, and almost in the same manner with his more daring descendant. (254)

Wilberforce’s review also takes note of the philosophical attacks by Canning and the *anti-Jacobin* poetry, suggesting that the younger Darwin has effectively answered their criticisms.

Ultimately, the task of reviving the elder Darwin’s reputation was left to his grandson, who in 1879 published the definitive biography, *The Life of Erasmus Darwin*, which has long been the standard source for all others who might wish to write about the man. Curiously, all editions prior to 2002 were expurgated, missing some 16% of Charles Darwin’s original manuscript, material which had been excised by his daughter, Henrietta. Henrietta had helped Darwin with some of his previous books, and he trusted her judgment as an editor. She cut down the manuscript after criticizing it for being too long; given that in the 2002 edition, the body of the book only runs 92 pages in length, this seems unlikely. Furthermore, the excised material

included a glowing tribute to Erasmus Darwin's brilliance and prominence across a range of disciplines, suggesting an attempt to preserve Darwin's reputation as the superior, and more original, intellect in the Darwin family tree. Still, the book remains the standard reference on Erasmus Darwin and the source cited by all others.

Cross-References

- [Early Perspectives on Evolutionary Change](#)

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Erectile Disorder

- [Desire and Arousal Disorders](#)

Erectile Dysfunction

- [Desire and Arousal Disorders](#)

Eric Kandel

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Introduction

Eric Kandel is a well-known neuroscientist for his research on memory and learning for which he shared the Nobel Prize in Physiology or Medicine in 2000. His breakthrough came through his pioneering work with *Aplysia*, which provided a wealth of information regarding nonassociative learning and its forms.

Eric Kandel's Biography

Kandel was born in Vienna on the 7th of November 1929. His mother, named Charlotte Zimels, was born in 1897 in Kolomea, which was at that time part of the Austro-Hungarian Empire. Kolomea is now a part of Ukraine and has been renamed Kolomyia. She came from a well-educated Jewish middle-class family. His father, Hermann Kandel, was born in 1898 in Olesko, a small town and then part of Austro-Hungarian Empire, now part of Ukraine, and was brought up in a poor family. At the beginning of World War I, his parents moved to Vienna, Austria, where they met and married in 1923. By the time they had their first child, Lewis, his father was the owner of a toy store. Eric Kandel was born 5 years later. They lived in a middle-class neighborhood, in a small apartment, and as both of his parents were occupied with the toy business, a housekeeper was looking after the children. Approximately when Eric Kandel was 10 years of age, he moved to Brooklyn, in the United States, with his family. His parents had to work hard to bring it along and adjusting was difficult. However, Kandel speaks highly of his parents for their determination and hard work to raise him and

his brother; they were not only successful in their jobs but managed to support both of their children on their chosen paths. After their relocation, Kandel had already involved in an elementary school, of which he graduated in 1944. After he graduated from the Yeshivah of Flatbush Elementary School, he went to the Erasmus Hall High School, a local public high school in Brooklyn. By then, Kandel was already fluent in several languages, including Hebrew and Greek, and was involved in several activities including, among others, soccer, music, and writing. He then applied to Harvard College and managed to be admitted and earn a scholarship as well. He majored in European history and literature. After some interactions he had with some psychoanalysts, he became more interested in understanding the human mind and that was determinant in furthering his studies by becoming a medical doctor. During his studies, he became increasingly interested in the biological basis of the mind. By 1956, he graduated from the New York University School of Medicine. He then joined a research team in Harry Grundfest's laboratory at Columbia University where they were dealing with research on a cellular basis. Grundfest was then a pioneer on the use of oscilloscope to measure action potential conduction velocity on the axons of neurons. After the intracellular recordings of electrical activity of the cerebral cortex of vertebrates done with Grundfest's team, Kandel's interest was directed to the study of the electrophysiology of neurons of invertebrates, influenced by the work of Kuffler. The shift occurred from Kandel's belief that the mechanisms of memory storage were possibly well preserved in phylogeny and that the cellular analysis of learning in low-level animals would reveal universal mechanisms that were also found in more complex organisms. His belief was validated shortly after. The Official Website of the Nobel Prize (2018).

Around 1957, when Kandel joined the Laboratory of Neurophysiology at the US National Institutes of Health, he focused on the study of the hippocampus. William Beecher Scoville and Brenda Milner were working at that time on the hippocampus and noticed that after hippocampus

excision, a patient no longer had the ability to form new memories. Kandel was greatly intrigued yet puzzled by the findings of these researchers and begun examining the electrophysiology of hippocampal pyramidal neurons. At that time, he was working with Alden Spencer, another great neuroscientist who was also interested in the biology of learning and memory. They managed to provide electrophysiological evidence for the formation of action potential in the dendrites of hippocampal neurons, not only in the axons as it was previously suggested. These dendritic action potentials were the trigger for firing at the axon hillock. They also recorded spontaneous pacemaker-like activity in these neurons; they noticed that firing took the form of bursts of spikes. Lastly, their research outcomes indicated the presence of strong recurrent inhibitory processes in the hippocampus resulting in prolonged inhibition. Kandel began to realize that memory storage must rely on modifications in the synaptic connections between neurons and that the complexity of the connections found in the hippocampus made it an inappropriate system for the study of synapses. That's when he selected the simplest animal model for his study, *Aplysia* (sea slug). He conducted electrophysiological analyses of the synaptic changes involved in learning and memory storage and provided breakthrough information that seemed to correspond to the simplest forms of learning (habituation, sensitization). It is noteworthy to mention that during the years 1963–1965, Kandel begun his academic career as an instructor in the Department of Psychiatry. In 1965, he accepted the position of associate professor at New York University, and it was during that time period that he started working with *Aplysia*. By 1974, he became a professor, in the Department of Physiology and Psychiatry, in Columbia University, and later the director of the Center for Neurobiology and Behavior. Around 1984, he became a senior investigator at Howard Hughes Medical Institute at Columbia University. The Official Website of the Nobel Prize (2018).

On a personal level, Kandel has already met and married (1956) the French, Denise Bystryn. They had two children, Paul and Minouche, and

are currently proud parents and grandparents as well, as all family members have thrived. His wife is a professor in the Department of Psychiatry and in the School of Public Health at Columbia University and has worked extensively on the field of addictions and drug abuse in adolescents. For nearly 40 years, they have been living in Bronx, and together they enjoy a variety of hobbies and interests, visual arts, classical music, and opera, and they passionately collect art and antiques. The Official Website of the Nobel Prize (2018).

Kandel's experimental research work has been extensive and greatly influential for the scientific world. He counts numerous publications that have not only been enlightening but also determinant for the course of future research. For his excellence and achievements, he has received more than 20 awards among them the Lester N. Hofheimer Prize for Research of the American Psychiatric Association (1977), the American Association of Medical Colleges Award for Distinguished Research in the Biomedical Sciences (1985), the Gairdner International Award of Canada for Outstanding Achievement in Medical Science (1987), the Harvey Prize in Israel (1993), the Wolf Prize in Biology and Medicine (1999), and the Nobel Prize in Physiology or Medicine (2000) which he shared with two other colleagues. He has also received honorary degrees from nine universities, three of which are European. The Official Website of the Nobel Prize (2018). His awards indicate worldwide recognition of his work.

Kandel's *Aplysia*

Aplysia became known to the scientific world through the pioneer work of Kandel which provided a wealth of information regarding non-associative learning and its forms (habituation and sensitization). *Aplysia* is a species of sea snail, commonly referred to as sea hares because of their posterior tentacles that protrude like ears do in hares. Among low-level organisms, *Aplysia* has become a fitting model for studies of how neurons and neural circuits regulate behaviors.

What attracts scientists into studying them are their simplicity and the huge size of their neurons, which are easy to manipulate and work with. Also, *Aplysia* exhibits abilities on learning establishing thus its appropriateness for applying cell biological approaches to the investigation of learning and memory mechanisms Moroz (2011). Of particular interest to Kandel and colleagues was the gill and siphon-withdrawal defensive reflex of *Aplysia*. *Aplysia* has a mantle cavity on its dorsal surface that protects the gill. The gill lies beneath the mantle shelf, which terminates at the back of the cavity in a fleshy, funnel-shaped spout, the siphon, which contracts to eject water from the gill. A two-component reflex is triggered when stimulation is applied to the siphon (mantle shelf) causing both the siphon and the gill to be retracted, protecting the organism from potential threat. These two components consist of two involuntary reflexes, the so-called siphon-withdrawal reflex (SWR) and the gill-withdrawal reflex (GWR). The gill- and siphon-withdrawal reflex (GSR) is mediated by distinct neuronal pathways, enabling scientists to record activities on the synaptic and neuronal level and to directly link synaptic plasticity to behavioral plasticity. The neural circuits of these reflexes are comprised of monosynaptic connections from sensory neurons to motor neurons, as well as polysynaptic connections containing excitatory and inhibitory interneurons. Kandel and associates work on this invertebrate animal regarding the cellular mechanisms underlying habituation and sensitization observed that while light siphon stimulation would naturally cause retraction, repetitive siphon stimulation produced short-term habituation lasting for a few hours. On the other hand, long-term habituation was demonstrated by repeating multiple training sessions across several days. A single habituation training session consisting of regular trials separated with a time interval of 30 s produced typical reductions in response to the siphon-withdrawal reflex. The replication of these training sessions once per day for 4 days produced a progressive buildup of habituation within each session. Habituation preservation was tested the next day and weeks 1 and 3 after

training, and when compared to group, the experimental group exhibited greater habituation. The gill-withdrawal component of the reflex was also tested for long-term habituation with the same procedures showing that siphon training produces long-term habituation in both components of the reflex Castellucci, Pinsker, Kupfermann, Kandel (1970). Furthermore, in another series of experiments, noxious shocks at the rear produced an increase in the siphon-withdrawal reflex and in the gill-withdrawal reflex. A single shock increased the reflex for 15 min to an hour. After repeated shocks, sensitization seemed to last up to several weeks. Four brief noxious electrical shocks were applied daily for 4 consecutive days. Sensitization retaining was measured again at day 1 and weeks 1 and 3. Also greater sensitization was observed with the addition of more shocks and by spacing the training sessions (two daily shocks within 10 days) Pinsker, Hening, Carew, Kandel (1973).

Generally it was indicated that short-term and long-term habituation results from homosynaptic depression of excitatory neurotransmission, while heterosynaptic facilitation of the sensorimotor connection caused sensitization. Habituation was not brought up by changes in the activity of sensory or motor neurons. Specifically sensory neurons release less neurotransmitter because of changes in calcium channels regulating neurotransmitter release, leading to the functional inactivation of the synapse in the long term. Nevertheless habituation still occurs after direct electrical stimulation of the motor nerve, avoiding that way the sensory receptors. This is essential as it reveals that the reduction in response is not due to sensory adaptation. Furthermore, motor fatigue is also eliminated by showing that direct stimulation of the motor neurons can still provoke a normal reaction after habituation has occurred. Carew (1984) provides more detailed description of the work with *Aplysia*.

Conclusion

Eric Kandel's life story and academic path, apart from being motivational, have left the academic

society with solid grounds to work on and have provided breakthrough information adding up to the understanding of how the human mind works. His work focused on the physiological basis of learning under which he explored short- and long-term memory, neural circuits, and synaptic processes through experiments with *Aplysia*.

Cross-References

- ▶ [Aplysia](#)
- ▶ [Habituation](#)
- ▶ [Non-associative Learning](#)
- ▶ [Sensitization](#)

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Erotic Orientation

- ▶ [Exotic-Becomes-Erotic Hypothesis](#)

Erotica

- ▶ [Pornography as a Human Product and Source of Data](#)

Erotomania

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Synonyms

de Clérambault's syndrome

Definition

Delusional conviction of being loved by another person

Introduction

Erotomania (de Clérambault's syndrome) is defined as the delusional conviction of being loved by another person. It usually involves morbid infatuation and "projection" of the affected individual's own attitudes onto the perceived "love object" (Enoch and Trethowan 1991). The incidence rate is considerably higher in women than men, and the "love object" is usually a man of high social status. Anecdotal descriptions date back to ancient writings, whereas the first scientific description was published by French psychiatrist de Clérambault in the 1920s (Berrios and Kennedy 2002).

Erotomania is quite uncommon in clinical practice, though its dramatic effects on both the affected individuals and their "love object" has inspired scholars from various psychiatric "schools" to speculate about the etiology and pathogenesis of erotomania. For example, from the 1950s to the 1970s erotomania was primarily interpreted in psychodynamic terms, similar to Freud's interpretation of paranoia, while the advent of neuroimaging technology has sought to discover brain abnormalities associated with the syndrome (reviewed in Brüne 2003). In DSM-5, erotomania features among the delusional disorders (erotomantic type),

similar to previous versions of the manual, though the condition may occur in schizophrenia, schizoaffective disorder, and bipolar disorder, as well as in cases with a defined brain damage (Brüne 2003).

In any event, none of the conventional approaches has accounted for the striking sex differences in prevalence rate of erotomania, characteristics of the "love object," and the behavior associated with the condition, which typically includes harassment and sometimes severe incidents of stalking (Mullen and Pathé 1994).

Sexual Strategies Theory

While the formation of delusional beliefs may either entail cognitive biases including "jumping to conclusions" and a "bias against disconfirmatory evidence," or a deficit in information processing concerning emotionally relevant stimuli combined with aberrant belief evaluation (Bell et al. 2006; Coltheart et al. 2007), not spelled out in greater detail in this entry, the content of erotomantic delusions may best be framed in an evolutionary psychological perspective.

According to "Sexual Strategies Theory" (Buss and Schmitt 1993), throughout evolutionary history, men and women have faced divergent adaptive problems regarding parental investment in potential offspring, with direct consequences for courtship and mating behavior. That is, in mammals the minimum parental investment of females (gestation, lactation) exceeds by far the minimum investment of males (insemination). Following this logic, a female's reproductive success is constrained by the resources a potential mate is willing to provide. Thus, females would be expected to be "choosier" concerning mate selection (Darwin 1871; Trivers 1972). In contrast, males' inclusive fitness would rise with the number of partners, which is why males are intrasexually competitive for access to females. Even though cultural practices and norms may differ considerably, these principles also apply to human mating behavior. The attractiveness of human males for women therefore entails high social status and wealth,

whereas physical attractiveness and other signals of fecundity may reflect female reproductive qualities (Buss and Schmitt 1993). Such differences in “mate value” may also account for the fact that women usually prefer older men as partners, whereas men, on average, prefer younger women, because the “mate qualities” of both sexes are related to age.

Another consequence of the disparate parental investment concerns the duration of an intimate relationship. Put another way, short-term mating favors the number of potential sexual contacts and offspring, whereas long-term mating increases the likelihood of survival of offspring. Accordingly, women would be more likely to seek long-term mates due to their higher parental investment, whereas men tend to prefer short-term relationships to maximize their reproductive success (Buss and Schmitt 1993).

Erotomania Reconsidered in Light of Sexual Strategies Theory

Prima facie, the behavioral pattern associated with erotomania seems to be compatible with a long-term mating strategy, distorted and pathological as it may be expressed. Accordingly, the following predictions would arise from this hypothesis:

Erotomania is more likely to occur in adult women than men. Individuals with erotomania are likely to be unmarried, divorced, or, if married, in an ambivalent relationship. Demonstration of chastity and enhancement of attractiveness may be relevant for women with the condition.

In women with erotomania, the “love objects” are expected to be socially high-ranking (older) men, whereas male erotomaniacs tend to choose physically attractive (younger) women. When engaging in long-term mating, men are expected to activate mechanisms to detect sexual infidelity to increase likelihood of paternity (jealousy). Therefore, erotomania in men is likely associated with sexual jealousy, which may include violent harassment or stalking of their “love objects.”

Brüne (2003) has reviewed about 250 case reports of erotomania published in the scientific literature and found the predictions derived from

Sexual Strategies Theory largely confirmed. Aside from a striking similarity of the clinical picture across cultures and ethnic backgrounds, the survey revealed that more than two thirds of the case reports were about women with erotomania. Female preponderance would have been even larger, if more recent interest in forensic consequences of erotomaniac stalking (more prevalent in males) were taken into account. As predicted, erotomaniac subjects were likely to be unmarried, divorced, or, if married, in an ambivalent relationship. Moreover, in spite of limited information about attractiveness, women seemed to be more likely to enhance their outer appearance and tended to remain chaste. In female erotomania most “love objects” were socially high-ranking (older) men, whereas men with the condition tended to stalk physically attractive (younger) women.

Harassment was prevalent in both sexes, though violent stalking was much more frequent in men with erotomania (Brüne 2003).

Conclusion

Erotomania, the delusional conviction that a person is loved by another person, represents a clinical syndrome that can occur in a broad spectrum of neuropsychiatric disorders. Erotomania may be understood as a pathological variant of a long-term mating strategy that is more likely to occur in women, because of women’s higher parental investment in potential offspring. Male erotomania is more frequently associated with violent behavior which is primarily directed towards the pursued “love object,” her kin, or persons who are perceived as “rivals” (Mullen and Pathé 1994). The difference in violent behavior between men and women with erotomania may reflect the evolutionary condition of uncertain paternity, which caused the emergence of male sexual jealousy as a strategy to minimize the risk of cuckoldry, i.e., investing in another man’s offspring (Buss and Schmitt 1993; Daly et al. 1982).

Taken together, the evolutionary psychological perspective may contribute to the understanding of pathological variants of cognitions, emotions and behavior.

Cross-References

- [Darwinian Psychiatry](#)
- [Sexual Strategies Theory](#)

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Error Management Theory

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Definition

Error management theory is a middle-level evolutionary theory that explains cognitive biases.

Error management theory (EMT), proposed by Haselton and Buss (2000), explains the evolution of cognitive biases. EMT suggests that certain

psychological mechanisms, such as the ones that help form decisions, evolved because they had a reproductive advantage (Haselton and Buss 2000). One such mechanism is a proneness to make either a *false positive* (see “► [False Positives](#)” entry) or a *false negative* (see “► [False Negatives](#)” entry) in judgments when the outcome is uncertain. A false positive (also called a Type I Error) is when you identify something as true when it is false, such as perceiving a situation as dangerous when it is not, whereas a false negative (also called a Type II Error) is when you identify something as false when it is true, such as perceiving a situation as safe when it is dangerous (Haselton and Buss 2000). Adaptive biases for these errors may have been useful in ancestral situations. For example, there would be greater costs in mistaking dangerous situations as not dangerous than mistaking safe situations as not safe. We are biased toward the error that maximizes benefits while minimizing costs (Haselton and Buss 2000).

Haselton and Buss (2000) used EMT to explain women’s underestimation of men’s commitment levels (called the “► [Commitment Skepticism](#)”, see entry) and men’s overperception of women’s sexual intent (called the “Sexual Overperception Bias”, see entry). The *commitment skepticism bias* suggests women possess “intention-reading” adaptations that function to underestimate a potential mate’s commitment level, to avoid the cost of independently raising offspring, for example. Since women’s minimal obligatory parental investment is higher than that of men’s, it would be costly to believe a mating partner has a long-term commitment to the relationship when they do not (false positive) than to believe a mating partner does not have a long-term commitment to the relationship when they do (false negative). To test this hypothesis, Haselton and Buss (2000) compared cross-sex perceptions of commitment intent, with same-sex perceptions of commitment intent, and found that women’s ratings of men’s commitment avoidance was greater than men’s self-reported measures.

A second study tested the *default model hypothesis*, which suggests that men use their own sexual desire to gauge women’s sexual intent, resulting in men’s overestimation of women’s sexual intent

(Haselton and Buss 2000). Since men's minimal obligatory parental investment is lower than that of women's, it would be costly to miss possible mating opportunities. False negatives (i.e., believe a woman is not sexually interested when they are) would therefore be more costly than false positives (i.e., believe a woman is sexually interested when they are not), which is why theoretically men would be expected to overestimate women's sexual interest. Empirically, they found that men's ratings of women's sexual intent were greater than women's reports of their own sexual intent.

Haselton and Nettle (2006) broadened the applications of error management theory to explain auditory looming, food aversions, avoiding the ill, and sinister attribution error. Auditory looming refers to sounds that rise and fall in intensity. Neuhoﬀ (1998, 2001) found that sounds increasing in intensity were perceived as moving faster than sounds decreasing in intensity. Neuhoﬀ explained this effect as an evolutionary adaptation to becoming prepared for an oncoming source. When an individual hears a sound increasing in intensity, it is better to be prepared for a swiftly approaching source than to assume it is something harmless (Neuhoﬀ 2001). If the oncoming source was a predator, early preparation has no potential costs, whereas late preparation has a very high cost to reproductive success and survival. As a result, natural selection would favor psychological mechanisms that allowed a quicker response to sounds increasing in intensity (Neuhoﬀ 2001).

Error management theory can also explain food aversions. When a person becomes sick after ingesting something, they tend to associate the sickness with that food or drink. Such aversions motivate people to avoid foods that now produce an unpleasant reaction (Garcia et al. 1966; Rozin and Kalat 1971). Those with an ability to quickly learn which foods made them sick from a single trial would have had a reproductive advantage by later avoiding these sources of sickness. In ancestral environments, it would have been adaptive to avoid eating toxic foods (Haselton and Nettle 2006). Even though there is a cost of decreased calorie intake, the possibility of ingesting toxic foods has a greater cost and is a greater threat to reproductive success and survival

(Haselton and Nettle 2006). A false positive would be the least costly error to make because one would avoid the chance of possibly ingesting toxic food. A false negative has the most cost associated with it because claiming a food as nontoxic when it actually is would have resulted in sickness or even death.

EMT also applies to beliefs and actions toward sickness. Little to no proof is required to believe someone is sick, as a result, avoiding them. However, people tend to need much more evidence to prove recovery or absence of illness (Kurzban and Leary 2001; Park et al. 2003). This can be applied to individuals' fears of becoming contaminated with the illness of others. When a family member or friend is sick, people tend to maintain physical distance from them to avoid catching the sickness, even if people are aware that the risk is low just from being in the same room (Haselton and Nettle 2006). These actions can be explained as an adaptation to avoid the risk of becoming ill. The cost of not avoiding someone with an illness or disease is greater than the cost of avoiding someone who is not contagious. People therefore tend to keep their physical contact to a minimum with those who are ill. For example, even though people knew AIDS was not contagious by only being near them, it was found that participants felt uncomfortable after only 5 min of contact with the individual. It was also found that participants were uneasy about the idea of having one of their items of clothing being worn by a person with AIDS (Bishop et al. 1991; Rozin et al. 1992). Disease avoidance psychological mechanisms may reduce the chance of getting sick, but it produces more false alarms (Haselton and Nettle 2006).

The sinister attribution error has also been explained by EMT. This attribution error is when people exaggerate their perception of others' intentions based on body language and verbal communication (Haselton and Nettle 2006). In ancestral environments, when visiting an unknown group, it would be less costly to over-evaluate the possible negative intentions of their members than to be unaware of the negative social evaluations they have of you, since this could have resulted in abandonment, direct aggression, or even death (Baumeister and Leary 1995). As a result, people in new social situations become

hypervigilant of their surroundings and the actions of others around them and may misperceive simple gestures as hostile or negative (Baumeister and Leary 1995).

Error management has the potential to explain a variety of cognitive biases. In addition to the literature reviewed here, EMT has also been applied to dangerous animals, noises of uncertainty, allergies, the illusion of animacy, decoding courtship signals, and the illusions of control (Haselton and Nettle 2006). Difficulty in this line of research is measuring costs and benefits related to false positives and false negatives.

Conclusion

Error management theory explains the evolution of cognitive biases, where people are more prone to either making false positives or false negatives depending on which error maximizes benefits while minimizing costs. This approach has been used to explain cognitive biases in many domains such as avoiding the ill, taste avoidance, sound perception, and perception of others' intent.

Cross-References

- [Commitment Skepticism](#)
- [False Negatives](#)
- [False Positives](#)
- [Sexual Conflict in Mating Strategies](#)
- [Sociosexuality and Sexual Conflict in Mating Strategies](#)

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Error Management Theory: Benefit and Cost Asymmetries

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Definition

Error management theory suggests that when people make judgments of uncertain outcomes, cost and benefit asymmetries in making Type I and Type II errors result in the evolution of cognitive biases that either minimizes costs or maximizes benefits.

Decisions under uncertainty can be wrong in one of two ways: Type I errors (i.e., false positives) are a prediction of X when X is *not true* or Type II errors (i.e., false negatives) are a prediction of *Not X* when X is *true*. An example of Type I error is when a man believes there is sexual interest from a woman when there is not, whereas a Type II error would be when a man believes there is no sexual interest from a woman when there is (Haselton 2007). Error

management theory (Haselton and Buss 2000) was developed to explain proneness to making either Type I or Type II errors as a type of cognitive bias. The theory suggests that certain errors in judgments in ambiguous situations are neither irrational nor arbitrary but may be adaptive. Due to the costs and benefits of either error rarely being symmetrical, evolutionary processes would have selected a decision-making rule favoring one error over another to minimize the costs and maximize benefits.

Cost and benefit asymmetries of judgments where outcomes are uncertain can therefore be the driving force in the formation of many cognitive biases (Haselton and Buss 2000). Although a decision may both minimize a cost and maximize a benefit, there may be situations where Type I and II errors have equal benefits but unequal costs, and so we would expect a bias toward minimizing the costs. In this case, the cost asymmetry guides the decision. If, however, a scenario where Type I and II errors have equal costs but unequal benefits, we would expect a bias toward maximizing the benefits. In this case, the benefit asymmetry guides the decision.

Continuing the example of sexual interest, a Type II error (believing there is no sexual interest when there is) would have been rather costly to men. Mistaking sexual interest when none is present is not as costly as mistaking a lack of sexual interest because the latter results in a missed mating opportunity. Haselton and Buss (2000) suggest this is why men more consistently misperceive benign interactions with women as signs of sexual interest. Another commonly cited example can be seen in the potential misidentification of an object. Many people are more prone to mistaking sticks as snakes, but are not prone to mistaking snakes for sticks. There are no discernable differences in the benefits of making either mistake, but there are certainly differences in the costs.

The impact of asymmetries in the costs and benefits of Type I and Type II errors can also be seen in decisions we make when engineering products. Haselton and Buss (2000) used smoke detectors as an example. Smoke detectors are designed to have a low threshold for detecting smoke and sounding the alarm. While this low threshold may result in more “false alarms” (i.e., Type I error or false positives), they are far less costly than the

smoke detector failing to sound resulting in a false negative and people being unaware of a fire. For this reason, and to minimize the potential cost, smoke detectors are manufactured with a bias toward false positives (Haselton 2007).

Error management theory may also help us understand more complex manifestations of Type I and Type II errors because cost and benefit asymmetries of either error may be moderated by other factors. For example, the sexes may differ in the degree to which an incorrect decision is costly or beneficial, resulting in sex differences in cognitive biases. Since men can maximize fitness through increased mateships, and women can maximize fitness from a higher-quality long-term relationship, the costs and benefits of misperceiving interests from the opposite sex may also differ. When misperceiving sexual interest, it would be costly for men to assume no sexual interest when there is; however, such an error would not be as costly for women. When misperceiving relationship commitment, it would be more costly for women to assume long-term commitment when there is not, whereas such an error would not be as costly for men. Unsurprisingly, due to the tenets of EMT, women were more prone to showing commitment skepticism, and men were more prone to showing overperception of women’s sexual intent (Haselton and Buss 2000).

A difficulty in this line of research is to account for all costs and benefits given a scenario because there may be multiple costs and benefits that are asymmetrical for a particular decision. Mathematical modeling and multiple empirical tests under different cost-benefit conditions would help isolate the conditions under which cognitive biases may emerge.

Cognitive biases do not necessarily make people correct more often than they are incorrect. Some psychologists have concluded that cognitive biases are shortcoming or irrational due to this possibility of being wrong (Tversky and Kahneman 1974). EMT does not claim that the cognitive biases developed through evolutionary processes help current men and women be right more often than they are wrong. However, EMT reframes these biases and views them not as a weakness but as an adaptation, known as *adaptive errors* (Buss 2001). EMT explains the tendency

for thought processes and behaviors to be more attuned to what choice will lead to instances where survival and ultimately reproduction are the most likely outcome (Johnson et al. 2013; Haselton and Buss 2000).

Error management theory can be used to understand biases, due to asymmetrical costs and benefits in many domains. Johnson et al. (2013) provided a nice summary of topics to which error management theory has been applied, such as belief in god, antipredator actions, perceiving enemy intentions, and overconfidence, among many others. Considering humans and nonhuman animals are faced with numerous situations where a decision needs to be made about an unknown outcome, error management theory has the potential to explain a wide variety of thinking processes and behaviors.

Cross-References

► [Error Management Theory](#)

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Escorting

► [Prostitution and Women's Short-Term Mating](#)

Essential Fatty Acids

► [Docosahexaenoic Acid \(DHA\)](#)

Essentialism and Speciation

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Introduction

Speciation is the process by which a new species is propagated from an older species. The process of speciation can be driven either by natural selection or any of the other evolutionary forces, although, as Darwin argues across the first two chapters of *On the Origin of Species* (Darwin 2008), artificial selection can also be a cause of speciation.

Speciation is widely believed to refute the thesis that species can be defined by essences. This argument is one of the key reasons why essentialism – a metaphysical doctrine about how all natural kinds are to be defined – has receded in popularity.

Essentialism

Aristotle first defined an essence as the *to ti ên einai* – which translates as “the what it was to be” – of something (Cohen 2016). Roughly two millennia later, and in the course of arguing against essentialism, John Locke puts it slightly differently, “Essence may be taken for the very being of any thing, whereby it is, what it is” (Locke 1694, p. 231), or put still another way, essentialism is an answer to the question: What make some kind of things *that* kind and not some other kind? The answer is that all of the things which are members of the relevant kind must have a common set of properties and that this set properties must occur in *all* and *only* the individuals that, when collected together, form the relevant kind. Furthermore, these properties usually, but

not always, are said to be intrinsic, unchanging, or ahistorical – typically meaning that no accidental occurrence or contingent force can cause the loss of any essential properties. The relevant set of properties is the *essence* of that kind.

Essentialism has an impressive historical pedigree. Many scientists and philosophers have held the position that all natural kinds, including all species, were defined by their essences. Aristotle is probably the first Western scientist to hold that essences must be posited in order to explain the organized diversity of the biological world. The connection between the biological sciences and essentialism remained strong until Darwin, for, among many other scientists, Linnaeus notably held that essences defined species (Larson 1968).

For the purposes of this entry, essentialism has three important logical implications. Let us assume that some kind *K* is defined by the instantiation of properties *x*, *y*, and *z*, which are together the essence of *K*. The first implication is that there can be nothing else but the members of *K* which have all three of these properties: it must be *all* and *only* things that are *K*s which have *x*, *y*, and *z*. Now, suppose that something which is a *K* loses property *x*. It follows that this individual is, the moment it loses *x*, no longer a *K* – that is the second implication. Finally, the third implication is that the boundary between kinds is fixed and exact. There should be no vague or non-sharp boundaries between kinds, there should be no intermediate forms which can put just as easily placed into one kind as another, and the boundaries between kinds cannot shift over time.

Species and Essentialism

We will now review two overlapping scientific arguments for why it seems extremely doubtful that species are defined by essences.

First, it is probably the case that not a single essence has been found anywhere in the natural world. For example, what trait occurs inherently in all and only *Myocastor coypus* and no other species? *Homo sapiens*? *Sepia apama*? Although it has proven difficult to discover essential properties, there is no corresponding difficulty in, first, discovering species and, thereafter, organizing

species into any number of different taxonomic systems. There are thousands and thousands of examples from post-Darwinian biological science which show that scientists can make sense of the organized diversity of the biological world without positing essences; this history of successful taxonomy explains why systems of biological classification which presuppose essentialism have fallen out of favor (Ereshefsky 2000).

There are also compelling theoretical reasons to doubt that species can be defined in terms of essences – reasons that are independent of the question of whether or not any essential properties have been discovered. Selection, mutation, migration, and genetic drift are, among other evolutionary forces, constantly inducing changes in the genetic basis of any single species. Even if there were a set of properties common to all and only some single population of a particular species, it would be very easy for, say, a mutation to eliminate that property. An essentialist would be compelled by the logic of her view to admit that the effects of this mutation mean that a new species has come into existence – but this inference would be out of step with the contemporary scientific consensus. A large amount of both genetic and phenotypic variation within any given species must be taken for granted, as this variation itself can be a conserved adaption (West-Eberhard 2003).

It is also worth examining the problem that is created for essentialism by constant evolutionary change. Speciation is a process that produces intermediate forms of organisms, and because of this, it is difficult to impose any principled division between generations of reproducing organisms that exactly and uniquely demarcate an ancestor species from one of its offspring species. Darwin expressed the difficulty this way: “we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected” (Darwin 2008, p. 422). The boundary between the kind of an ancestor and the kind of the offspring is almost always vague and indeterminate; appearances to contrary can be by-products of a lack of access to the all of the intermediary forms produced during speciation.

This point holds even in cases of extremely rapid speciation. Consider a recent example of speciation in Galapagos finches that occurred in only two generations (Lamichhaney et al. 2018). In 1981, a single male *G. conirostris* arrived in an island where *G. conirostris* were not already present. This bird mated with two member of an endemic finch species, *G. fortis*, and the DNA of the parent birds and their offspring was collected and tracked by a team of scientists. The first generation of offspring were hybrids who were nevertheless fertile – but they were unable to mate with any of the endemic species on the island due to differences between the song of the hybrids and the songs of the endemic birds. Inbreeding among this first generation of hybrids leads to a third generation of finches with larger bodies and beaks than the other finches on the island, allowing birds in the third generation to occupy a previously empty environmental niche and subsequently establish itself as the newest species of the Galapagos finches.

It is not clear how an essentialist can offer a plausible scientific analysis of this case. The contemporary and standard view – which is a non-essentialist analysis – would hold that, in this example, there are at least three species: the original male *G. conirostris*, the endemic *G. fortis*, and the new species produced by inbreeding. But the hybrid birds are inherently hard to classify: They are either unusual *G. conirostris* or unusual *G. fortis* or some forth but very short-lived species. The most important point is that there is no principled way of solving this problem. However, recalling the implications from above and overlooking the problem of locating properties unique to all and only the hybrids, an essentialist would be forced to conclude that the hybrids were a short-lived separate species and therefore that the number of species in this example can be not less than four.

Speciation is a drawn out process that produces a large number of intermediate forms that cannot be uniquely classified on principled grounds. As Darwin noted, we often lack access to these forms and can see only the beginning and the end – or even just the end – of a process of speciation. This can give the appearance that the boundaries between species are more exact than they really

are. A nonessentialist can see the diversity of life differing in degrees and, only where the differences are large enough, differing in kinds. An essentialist, by contrast, must see all biological life as though it differs in kinds.

Nonessentialist Definitions of Species

The most common response to these and other considerations has been to abandon essentialism. This means that a new definition of what makes a set of individual organisms members of a common species must be found.

One popular alternative to essentialism is the view that species are *homeostatic-property-cluster kinds* (Boyd 1999). According to this theory, kinds are defined by sets of properties that tend to co-occur, but need not co-occur as a matter of necessary. Knowing that something has one or two properties makes it likely but does not make it certain that it also has some further properties in the relevant set. The reason these predictions typically work is that at least some of the properties in the relevant set tend to cause their co-occurrence: For example, the presence of a certain gene makes it likely but does not guarantee the presence of a certain wing geometry in organisms with that gene. A particular species concept, then, picks out whatever HPC kind – if indeed there is one – that best explains why that particular concept can play a role in fruitful scientific theorizing.

If species are defined by sets of HPC properties, then intermediary forms and both genetic and phenotypic variety cause no difficulty; since HPC kinds can have vague or indeterminate boundaries, they can share some or all of their properties with other HPC kinds, and they are not so fragile that a change in the presence of a single trait (or property) changes the kind of thing which bears the change.

Conclusion

Today, few scientists and philosophers find essentialism plausible, and while Darwin's analysis of speciation is itself not wholly responsible for the

collapse of essentialism, it plays a large role: by calling attention to the ongoing processes of speciation that are driven by, inter alia, natural selection, Darwin dramatically increased the costs of combining a commitment to essentialism with a commitment to many of the core tenets of modern evolutionary biology.

Cross-References

- ▶ [Adaptive Plasticity](#)
- ▶ [Darwin on Speciation](#)
- ▶ [History of Natural Selection](#)

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Estradiol

- ▶ [Music and Hormones](#)

Estrogen

- ▶ [Digit Ratio](#)

Estrus

- ▶ [During Ovulation](#)

Ethanol

- ▶ [Alcohol](#)

Ethical Intuition

- ▶ [Function of Morality \(Haidt\)](#)

Ethical Issues

- ▶ [Dangers of Evolutionary Ethics](#)

Ethics

- ▶ [Evolution of Morality](#)
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Ethics of Conception

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Ethnic Identity

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- [Racism and Prejudice](#)

Ethnicity

- [Birthrights and Bloodlines](#)
- [Relationship Between Culture and Race](#)

Ethnographic Fieldwork

- [Ethnography](#)

Ethnographic Literature

- [Ethnography](#)

Ethnography

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Synonyms

[Ethnographic fieldwork](#); [Ethnographic literature](#)

Definition

Ethnography is a field method used to generate firsthand knowledge of a particular human group or a behavior of interest. This term also refers to the finished written product resulting from field research (i.e., an ethnography).

Introduction

Ethnography has been a hallmark of anthropological inquiry for over a century, and its use has grown across disciplines as a means to gather both quantitative and qualitative data. This method of systematic data collection includes the use of participant observation, where a researcher lives with a host community for an extended period in order to experience and record as many aspects of daily life as possible. The goal of ethnography for many anthropologists has been to facilitate holistic cross-cultural comparisons that ultimately generate emic (insider) and/or etic (outsider) interpretations of human culture and society.

Overview

Ethnographers typically study a cohesive group of people who interact regularly (a society). Multiple ethnographies contribute to *ethnology*. Ethnography is different from ethnology in that an ethnography usually documents a single community, where ethnology is the generalized body of knowledge pieced together through multiple ethnographies. Some examples of ethnological studies might consist of understanding variation in sociopolitical organization (e.g., bands, tribes, chiefdoms, states) or variation in subsistence practices (e.g., hunting/gathering, pastoralism, horticulture, or agriculture).

In the nineteenth century, many early anthropologists/ethnologists were interested in understanding variations in kinship, social structure, and behaviors within and between human societies, but they often formed interpretations from either library research or secondhand accounts. Many anthropologists point to the emergence of modern ethnographic fieldwork in the early twentieth century with the contributions of Bronislaw Malinowski (1922), Margaret Mead (1928), and Ruth Benedict (1934). By the mid-twentieth century, anthropologists such as Victor Turner (1967) and Clifford Geertz (1973) charged anthropologists

with tailoring their ethnographic approaches toward identifying veiled cultural meanings embedded in symbolism and language. Near the end of the twentieth century, ethnography's value in providing "objective" data was questioned by those who felt that scientific objectivity was impossible and that the ethnographic method produced misrepresentations tied to the perspective of the researcher (Clifford 1986; Marcus and Fischer 1986). The debate surrounding the validity of the ethnographic method is ongoing, and what constitutes a "proper" ethnography is continually under renegotiation among anthropologists.

Conclusion

Today, the use of ethnography has proliferated to become a common method of investigation across social science, medical, and business disciplines. The primary appeal of ethnography is that it places an emphasis on behavioral observation, rather than relying on what people report about themselves via questionnaires or surveys. While the purpose of ethnography has shifted away from the goals of early researchers to document "primitive" cultures, the method continues to enjoy recognition as an effective means through which to gather firsthand experiences about people and how they live their everyday lives.

Cross-References

- [Cross-Cultural Pattern](#)
- [Franz Boas](#)

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Ethograms

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Synonyms

[Directory or catalog of behavior](#)

Definition

Catalogs of species – typical behaviors

Introduction

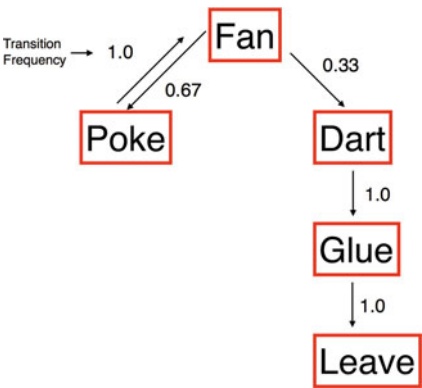
Ethograms are directories or catalogs of species-typical behaviors. These behaviors, known as action patterns, are discrete, repeatable, identifiable acts that are described in detail according to characteristics such as their form, speed, duration, strength, and/or orientation. Ethograms often contain both written descriptions and pictures or diagrams so that action patterns are described in enough detail that another observer can recognize them.

Types of Ethograms

All behaviors included in an ethogram should be mutually exclusive and objectively described (Abeelen 1964; MacNulty et al. 2007; Wilkinson et al. 2010). Ethologists typically use two types of

Ethograms, Table 1 Example ethogram of male and female threespine stickleback mating behaviors (Adapted from Tinbergen 1951)

Male		Female	
Action pattern	Description	Action pattern	Description
Zig-zag dance	Lateral darting	Courting	Show belly to male
Lead	Bring female to nest	Follow	Follow male to nest
Point	Direct toward nest entrance	Enter	Enter nest
Shiver	Shaking while fertilizing nest	Spawn	Deposit eggs
Enter	Enter nest to fertilize eggs	Leave	Exit nest



Ethograms, Fig. 1 Kinematic diagram with transition frequencies for male threespine stickleback nesting behavior. Each box represents a behavior, with the arrows indicating the order in which they were observed to occur. Transition frequencies indicate the proportion of times that one behavior follows another. For example, poking was always observed to be followed by fanning. However, fanning behavior was followed by poking in most instances and darting a smaller proportion of times

descriptions when constructing ethograms. Motor patterns objectively describe physical movements made by the animal, while descriptions by consequence are behaviors defined in relation to the animal’s environment and are concerned with why the animal moved and the outcomes of a particular movement (Hardy and Heyes 1999). Specialized ethograms are specific to a particular developmental stage and/or sex. For example, an ethogram could be developed that describes stereotypic behavior of breeding male and female threespine stickleback fish (*Gasterosteus aculeatus*; Table 1). These behaviors do not normally occur outside of the breeding season.

Analysis of Ethograms

Ethograms allow researchers to describe sequences of behavior, with the ultimate goal of producing a kinematic diagram that summarizes the likelihoods of behavioral sequences. To make a kinematic diagram, the researcher records action patterns in the order in which they occur to create a sequence of events. This sequence is then used to create a matrix that lists the number of instances in which each behavior follows another, known as the number of transitions between behaviors. Transition frequencies can then be calculated, which quantify the percentage of time that one action pattern follows another. To make the kinematic diagram, arrows are drawn between behaviors to indicate their sequence (Fig. 1).

Conclusion

Ethograms standardize species-specific behaviors so multiple observers can analyze them consistently. However, they have several limitations (Martin and Bateson 2007). They may vary tremendously in the number of categories included and the extent to which they are described in detail. They are also unavailable for many commonly studied animals. Lastly, not all members of a species behave in the same way, which creates difficulties in describing species-typical behaviors.

Cross-References

- Development
- Evolutionary Change

- [Field of Behavioral Ecology, The](#)
- [Field Research](#)

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Ethological Psychiatry

- [Darwinian Psychiatry](#)

Ethologists for the Ethical Treatment of Animals

- [Marc Bekoff](#)

Ethology

- [Cognitive Ethology](#)

Etiological Attributes

- [Causal Attributions](#)

Etiology

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Synonyms

Cause

Definition

Etiology is defined as the “cause of ill health.”

Introduction

The term “etiology” refers to the branch of science that deals with the cause of any disease. The Merriam-Webster dictionary defines “etiology” as *cause* or *origin*, which is commonly discussed in the context of ill-health (Dictionary 2006). It is derived from Greek words (*aitia* meaning cause and *logia* meaning study). The term “etiology” is used synonymously, widely in literature. Etiology is often described together with the pathogenesis (how the disease develops/evolves). The term “etiopathogenesis” is used to describe the process of development of disease with specific reference to the underlying etiology. The pathogenesis of a disease is mostly defined by its underlying etiology. For example, the pathogenesis of inflammation due to tubercular bacteria is different from that caused by herpesvirus. Etiology guides in the classification of diseases and their management.

Classification of Etiology

Etiologies can be classified in various ways. For example, etiology can be divided into infective and non-infective types. Infective etiologies result

in development of communicable diseases, and non-infective etiologies often result in non-communicable diseases. In developing and under-developed countries, infective etiologies attribute to major burden of illness. Noncommunicable diseases (NCDs) often result from lifestyle-related factors and attribute the major burden of diseases in most developed countries and several developing countries too.

Etiological factors can also be classified into biological, psychological, and environmental (sociocultural) factors (Kar and Tripathy 2019). “Biological” etiologi- cal factors are infections, deficiency of nutrients, genetic causes, traumatic causes, alterations in specific organ physiology, and metabolic causes. “Psychological” etiologi- cal factors like personality, adverse life experiences, and poor stress tolerance (increased perceived stress) might attribute to development of disorders/illnesses. “Environmental” etiologi- cal factors can be in the form of workplace/occupational hazards, pollution, exposure to ionizing radiations, climatic adversities, and epidemics.

Etiology can be understood and classified at the microscopic or gross levels. In the microscopic level, cellular (e.g., sickle cell anemia, megaloblastic anemia) and subcellular dysfunction (e.g., mitochondrial abnormality, lysosomal storage disorders) result in a disorder. At the gross level, the etiology of a disorder can be described basing on the dysfunction of a larger structure (organ). For example, hepatic failure and renal failure can cause delirium. Here, the cause of delirium is attributable to organs (liver and kidney).

The etiology of a disorder can be described on the basis of its pathogenesis, organ involve- ment, nature of the disease process, as well as clinical manifestations. For example, the etiologies of Creutzfeldt-Jakob disease (CJD) are described as infective (causative agent), neuro- degenerative (pathogenesis and organ involve- ment), as well as neurocognitive (clinical manifestations). Similarly, pediatric autoimmune neuropsychiatric disorders associated with streptococcal infections (PANDAS) describes the etiologies as autoimmune (pathogenesis) and infection by *Streptococcus pyogenes* (causative agent).

Evolutionary Significance of Etiology

Etiologies of illnesses remained unclear for centu- ries. In the ancient days, people associated various causes of illnesses merely on the basis of assump- tions and observations, backed by their sociocul- tural beliefs and traditions. People attributed the causes of diseases like tuberculosis, leprosy, and mental illnesses to supernatural powers. The exact pathophysiological mechanisms of illnesses were unknown for long. With time, scientific evidences were generated and causal (etiological) attributions were changed (Kar 2019).

Ayurveda (one of the oldest system of medicine) deduced the etiologies of illnesses to three intrinsic bodily factors (*Vata*, air; *Pitta*, bile; *Kapha*, phlegm), together known as *tridosha* (Opler 1963). Hippocrates, the father of ancient medicine, had attributed the etiology of illnesses to disequi- librium of four important body fluids (sanguine, blood; choleric, bile; melancholic, black bile; phlegmatic, phlegm), which are classically known as “four humors of Hippocrates” (Bujalkova et al. 2001; Pappas et al. 2008). During that time most of the illnesses were attributed to diet, environment (climate), and society. Hippocrates attempted to demystify the illnesses by evaluating their etiolo- gies through keen observation and by negating the prejudices (Kushner 2013).

Presently, the cause of an illness is being established by meticulous history taking clinical examination and specific investigations. Over past centuries, investigation techniques have been developed exponentially, resulting in shifting of this paradigm. Currently, diagnosis is mostly based on investigational findings rather than clinical examination. xcessive relying on investiga- tions (to establish etiology) rather than using the clinical skills is being criticized (Hofmann and Welch 2017). There should be optimal use of clinical skills and judicious use of investigations to find out the etiology of an illness.

Establishing the Etiology

Association of etiology with a disorder (illness) cannot be judged by a single case or single study.

There are many confounding variables that may falsely establish an association between the etiology and disorder (which can simply be a chance association). However, if the association is established in multiple researches, in a larger population, at different points of time, using various research designs, then the etiology can be linked with the disorder with certainty.

In clinical research, etiology of an illness can be ascertained by adopting various research methodologies (Moola et al. 2015). Broadly, three different designs (epidemiological/observational) elicit the association between cause (etiology) and effect, which are (Fig. 1):

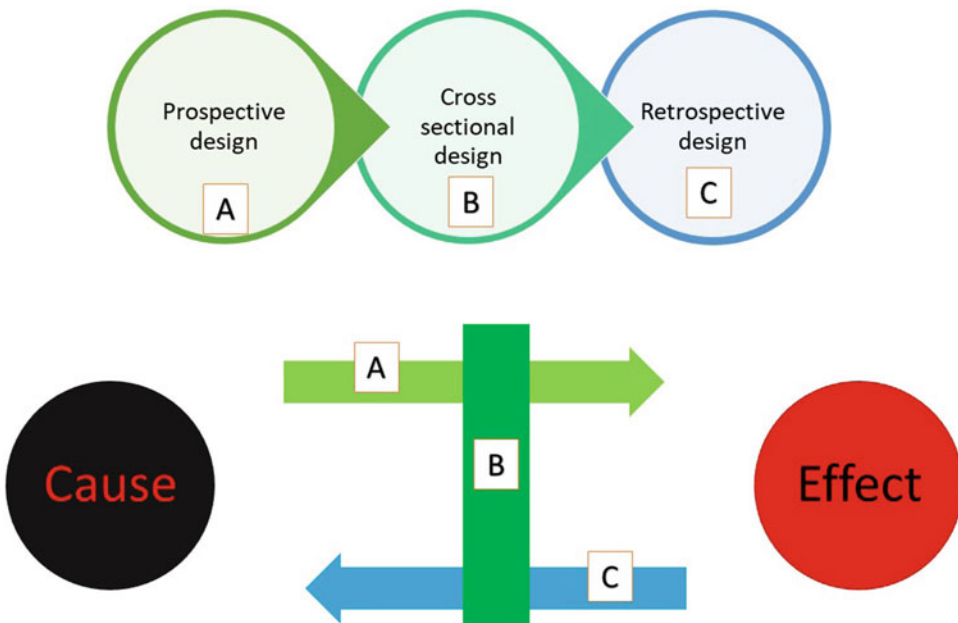
- **Prospective design:** It moves in the direction of cause (etiology) to effect. People exposed to various known etiological agents are followed over a period of time to look for disease occurrence. For example, people smoking cigarettes are followed up for occurrence of lung cancer.
- **Cross-sectional design:** Specified group of population (often diseased/ill) are evaluated at particular point or period of time for identifying the etiological agent. For example, all

patients with fever and jaundice are evaluated for hepatitis B virus infection.

- **Retrospective design:** It moves in the direction from effect to cause. People, who had already developed disease/illness, were evaluated for specific cause(s). For example, all patients with borderline personality disorder were evaluated for adverse experiences during their childhood.

Establishment of causality (etiology) can be ascertained through the strength of association, temporality of association, and specificity as well as consistency of association (Moola et al. 2015). The above research designs, applied in a larger population from time to time, generate evidences regarding association of etiological factors with illnesses.

Investigative procedures sometimes help in establishing the etiology. In clinical settings, various screening investigative procedures are used to ascertain the etiologies of specific abnormalities of health. For example, urine drug screen is used to detect the drug abused that is attributing to altered behavior in an individual, who had addiction. Similarly, toxicological screening is used for detection of poisoning; metabolic screening is used for



Etiology, Fig. 1 Various research designs for evaluating the etiological associations

detecting metabolic derangements; and HIV and hepatitis screening tests are used for detection of these infections. These screening tests can give information about specific etiologies.

The terms “sensitivity” and “specificity” are used in the context of tests or investigations used for identifying etiologies. These terms predict the accuracy with which an investigational procedure measures the association of an etiological agent and the illness (sensitivity) or non-association of an etiological agent with healthy state (specificity) (Hawkins 2005). Sensitivity measures the percentage of diseased population found to be true positive, whereas specificity measures the percentage of non-diseased population found to be true negative.

To establish the cause-effect association, causality assessment is recommended in pharmacovigilance (Ralph Edwards 2017). Drugs (medications) produce side effects. For example, steroids and antitubercular drugs (cycloserine, isoniazid) may produce psychosis. So, the drug here can be considered as the etiology of illness. Radiological (e.g., X-ray, computed tomography scan, magnetic resonance imaging) and sonological (e.g., ultrasonography, echocardiography, Doppler) investigations have been used for identification of various etiologies. For example, in Creutzfeldt-Jakob disease, there is signal alteration in the T2 images of magnetic resonance imaging at the basal ganglia. X-ray of chest may indicate about pulmonary tuberculosis. Hyperdense lesion in the computed tomography scan of brain may indicate hemorrhagic stroke. Specific modifications (e.g., use of contrast) are done in the radiological procedures to delineate specific location and nature of etiopathology. Electrophysiological investigations (e.g., electrocardiogram, electroencephalogram, and electromyogram) can be used for identification of specific disorders and sometimes their etiologies. For example, periodic complexes in electroencephalogram are seen in subacute sclerosing panencephalitis, T-wave abnormalities in electrocardiogram in lithium toxicity, and electromyogram in muscular dystrophies. Organ biopsy (e.g., liver and spleen biopsy in amyloidosis), culture of body fluids (e.g., blood culture for identification of

specific microbial organism), and hematological investigations (e.g., microcytic hypochromic blood picture in iron-deficiency anemia) are also useful in establishment of etiology. Establishment of etiology is often complex and challenging in mental illnesses. In mental illnesses, the clinician needs to do a detailed mental status examination and sometimes certain psychological assessments in addition to detailed history taking and physical examination, to establish the etiology.

Clinical Significance of Etiology

If illness is the effect, the underlying cause is referred as the “etiology.” An illness can have single etiology (one-to-one cause-effect relationship) or can have multiple etiologies (Kar 2019). Similarly, multiple etiologies can be associated with single illness. Tracing back to the etiology from the disease diagnosis helps in providing an explanatory model about the illness (i.e., why an individual develops an illness at a particular point of time). It has implications in disease prevention by health education and generating awareness. Many clinical diagnoses incorporate an etiological term in the diagnostic terminology used. For example, acute viral encephalitis diagnosis indicates that the etiology of the medical condition is “viral infection.” Similarly, metabolic encephalopathy diagnosis indicates the etiology to be “metabolic imbalance.” The diagnosis, post-traumatic stress disorder, indicates to the underlying etiology “stress-related trauma.” Certain etiological agents have been named after the clinical diagnoses (e.g., *Salmonella typhi* after the name typhoid fever; *Vibrio cholerae* after the name cholera). Understanding etiology is important from the perspective of prevention. The preventive strategies are determined by the underlying etiology. For example, prevention of HIV infection is carried out through understanding the etiopathogenesis of HIV infection/AIDS (through the knowledge of modes of transmission, course and outcome of illness, risk factors).

Understanding etiology in the context of psychiatric disorders is important and has various

clinical implications. Psychiatric disorders are the resultant of complex interaction of multiple etiological factors (Langguth et al. 2009). The causes of a particular psychiatric condition may be different in different individuals. For example, the etiology of depression may be mostly biological in an individual (who has positive family history and past history of depression) whereas predominantly psychosocial in another individual (who had a recent significant life stressor). Various models (essentialist kinds, socially constructed kinds, practical kinds, mechanistic property cluster kinds) attempted to explain psychiatric disorders, of which the mechanistic property cluster kinds explain psychiatric disorders by linking them with their potential etiologies (causal mechanisms), hence becomes the most accepted model (Kendler et al. 2011).

Conclusion

Etiology is the first stepping-stone in the journey to understand an illness. The significance of understanding the etiology is enormous as it helps in classifying illnesses, directing assessments (investigations), as well as formulating the management plan. Understanding of illness or disease remains incomplete without the knowledge of etiology.

Cross-References

► Risk Factors

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Etiology of Aggression

► Development of Aggression

Etiology of Psychopathology

► Life History Model of Psychopathology

Eugenics

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Synonyms

[Artificial selection](#); [Human improvement](#)

Definition

The term *eugenics* refers to both intellectual and political efforts at altering human heredity for the purpose of (1) decreasing the level and prevalence of perceived socially *undesirable* traits in a population (negative eugenics), especially if the rising level and prevalence of such traits are understood as effects of certain kinds of genetic change in a population (termed *dysgenics*), and/or (2) increasing the level and prevalence of perceived socially desirable traits in a population (positive eugenics).

Introduction

In 1883, *Sir Francis Galton* combined the prefix *eu*, meaning *good* or *well*, with *genic* or *genos* meaning *kin* or *stock*, to create the novel term *eugenics*. *Eugenics* thereafter became a science of particular import and a movement of deep controversy. What could be termed *folk eugenic*

thinking can however be traced back to the writings of classical philosophers, most notably Plato in his *Republic*. Charles Darwin's *On the Origin of Species* and Francis Galton's *Hereditary Genius* provided the scientific basis on which the biological theory and the applied science of eugenics were based (Hertler 2014). As an academic field, eugenics involved study of intelligence, character, and health, and indeed its pursuit early in the twentieth century spurred many significant developments in psychometrics, anthropometrics, and statistics. In its policy applications, eugenics was an attempt to replace “natural” with “artificial” forms of selection, such as selective breeding. More recent incarnations of eugenic thinking advocate for the restriction of artificial selection to prenatal interventions via the use of *reprogenetic* technologies, such as embryo and gene selection.

Review

Ideology

Applying the adjective *utopian* to eugenics might seem incongruous, but eugenics was in fact a utopian ideology. As with other ideologies, laudable ends were sometimes used to justify deplorable means (Chesterton 2000; Kevles 1998). Drawing still further parallels with other utopian, specifically *collectivist* movements, the eugenics movement advocated the top-down control of what had once been regulated by bottom-up forces. For eugenicists, the factor of interest was population quality; for communists, economy; for French revolutionaries, fraternity; for German national socialists, racial purity. Nevertheless, the utopian qualities of eugenics were idiosyncratic and limited, and so eugenics was “utopian” in a qualified sense. That is partly because eugenics as a movement was an outgrowth of eugenics as a science. Secondly, even while many a eugenicist fancied progressive visions of human enhancement, demographic anxiety was the movement's wellspring. Through the latter, eugenicists shared a deep pessimism with intersecting ideologies originating in a

nineteenth-century European culture looking downward from its zenith.

Eugenicists and *Malthusians* interfaced, as their overlapping ideologies would predict (Woodley of Menie et al. 2017). Both intellectual currents involved elites wary of the reproductive success of lower echelons of society, and both feared demographic futures characterized by degeneration and civilizational collapse. Nonetheless, eugenicists and Malthusians had different demographic concerns, the former concerned about the *quality* and the latter the *quantity* of populations, as C.V. Drysdale recognized (Klausen and Bashford 2010). In reality, it seems that both worries were often found in the same people. Consequently, at least by the 1930s, the two groups were more likely to attend the same conferences and collaborate on joint ventures than they were to argue and undermine one another (Klausen and Bashford 2010). Indeed, the interwar period resulted in the following mutual goal, detailed by Soloway (1990, p. 102): “Together [these movements] held out the promise of the intelligent control of the reproduction of the lowest classes and the promotion of more births among the ‘social units that are generally *most fit*.’”

Historicity

Soloway (1990, p. xxii) notes the following:

It is not clear to what extent the unsavory association of eugenics with Nazism, racism, and anti-socialist, pro-capitalistic class prejudices made it an unattractive subject after the war for scholarly inquiry by historians of science as well as of the social and intellectual history of modern Britain.

Consistent with Soloway’s observation, histories of eugenics are in short supply. To make matters worse, many of those that are available treat the subject with insufficient scholarly care and sophistication. This substandard academic work is frequently the fault of historians’ rush to repudiate supposed evils of the past, as Soloway’s remark above intimates.

As reviewed by Woodley of Menie et al. (2017), and also by Soloway (1990), eugenics is inaccurately viewed as an artifact of the hard right. One is made to think of libertarians, fiscal conservatives, and other elitists steeped in Social

Darwinism when reading cursory treatments of the eugenics movement. And indeed it was not unheard of for elitists and conservatives to become partisans of eugenics. On the other hand, there were extreme leftists who no less vehemently than rightists affirmed eugenic doctrines, including liberal progressives such as Sidney Webb, L.T. Hobhouse, and J.A. Hobson (Soloway 1990). In fact the communists Lenin and Trotsky both endorsed eugenic practices (Adams 1989). This may come as a surprise to modern readers but only because of the tendency to erroneously project the contemporary nexus of science and politics into the past. It was not always believed that biological explanations of social problems, e.g., crime, poverty, and inequality, ran afoul of progressives’ melioristic politics. This is partly due to the fact that what Galton called the *nature/nurture question* was a matter of some controversy among early eugenicists. Specifically, though evolution was accepted fact among eugenicists, there remained many Lamarckians among the Darwinian eugenicists; and given that Lamarckian evolutionary theory entails that hereditary stock can be altered by environmental means, progressivist meliorism was compatible with Lamarckian construals of eugenics. So a Lamarckian eugenicist could believe that the best way to improve the hereditary quality of a population is to improve the environments to which “the unfit” are exposed, rather than discourage their reproduction (though Lamarckian theory would admit of that solution too). Thus the comingling of Lamarckians and Darwinians necessitated a distinction between *natural eugenics* and *nurtural eugenics*, the former being improvement of a population’s heredity by way of breeding and the latter being such improvement by way of environmental change. It goes without saying, however, that any notion of nurtural eugenics declined along with Lamarckianism.

In addition to being bipartisan, the eugenics movement was cosmopolitan (Currell 2010). It originated in England, founded upon Galton’s work, but was thereafter imported to the United States, Italy (Cassata 2011), Spain (Cleminson 2000), Greece (Trubeta 2007), and Sweden

(Spektorowski and Mizrachi 2004). It was embraced in South America (Harris 1922), especially within interbreeding, multiethnic Brazil (Hochman et al. 2010). Eugenic science and policy thereafter diffused eastward, finding favor in Russia (Adams 1989), Japan (Otsubo and Bartholomew 1998), China (Pearson 1995), and portions of South East Asia (Amrith 2010). Within countries, not all were converts, but eugenics is described by some as having grassroots support, even while it brought social elites within its orbit, including Leonard Darwin, Winston Churchill, Alexander Graham Bell, Thomas Hunt Morgan, George Bernard Shaw, H.G. Wells, and Theodore Roosevelt (Hertler 2014). Therefore, far from being unique to Teutonic racialism or some other brand of European rightism, the eugenics movement straddled not just the right and left but also the Occident and Orient and upper and lower social strata.

Application

Eugenic policy varied in terms of private as opposed to state support and assumed different characteristics depending on its sponsoring regime and the nature of its population (Hertler 2014). Eugenic policies typically targeted procreation in efforts to prevent the existence of “the unfit,” though in rare cases eugenics could turn homicidal, aimed at destroying those who supposedly threatened to spread socially undesirable traits to future generations. But the most fundamental and critical distinction to be made with respect to eugenic policy is between *positive* and *negative* eugenics. Positive eugenics promotes the reproduction of the “fit”; negative eugenics opposes the reproduction of the “unfit.” A second distinction centers on whether eugenic policy is advocated or compelled; in other words, it matters greatly whether eugenicists merely encourage the voluntary adoption of eugenic practices or whether they seek to coercively realize eugenic aims through governmental or other means. Applications of eugenics have varied across time and space, covering the spectrum from advocacy to coercion. For instance, British eugenics programs were quite benign, e.g., they promoted early marriage for the intelligent and

capable, while German National Socialism used force in the pursuit of eugenic goals (Black 2003). The United States perhaps occupied an intermediate position, as it attempted to proselytize the uninitiated while maintaining an active sterilization program that was countenanced by the majority of states (Lombardo 2008).

Repudiation

Eugenic views found favor in various ideologies of the interwar period: socialism, communism (Adams 1989), nationalism (Quine 2010), gilded-age individualism, libertarianism, and laissez-faire economics (Hofstadter 1992) (see Woodley of Menie et al. 2017). Nevertheless, it is important to note that the last three ideological strains really exhibited *Social Darwinism* rather than straightforward eugenics as embodied in the *First-Wave Eugenics Movement*. Social Darwinism sought to achieve eugenical outcomes via *benign neglect*, i.e., the withholding of welfare and other state-based forms of social support from the lower classes with the intention of encouraging their members to live (and procreate) within their limited means. Conversely, the First-Wave Eugenics Movement, emanating most directly from the work of Francis Galton and achieving its greatest influence early in the twentieth century (prior to World War II), sought to enhance the hereditary quality of populations by directly intervening in the reproductive affairs of individuals. While both the First-Wave Eugenics Movement and Social Darwinism collapsed by the mid-twentieth century, the focus here is specifically on the former. On the matter of the First-Wave Eugenics Movement’s breakdown, a number of factors ought to be considered.

There are, first, indirect factors that undermined the First-Wave Eugenics Movement. Among these is the loss of strong national identities in the wake of globalization, a process that became especially pronounced after World War II, in that the Allied Powers sought to avoid another devastating worldwide conflict through a number of policies promoting the economic integration of nations (Westbrook 2004). To the extent that globalization superseded nationalism, the broad base of support for applications of eugenics aimed at

increasing the competitiveness of nation states in particular was sure to erode. Another, and often overlooked, indirect factor weakening the First-Wave Eugenics Movement was the definitive repudiation of *Lamarckian evolution*. Lamarckian evolution, synonymous with the *inheritance of acquired characteristics*, was, as previously mentioned, what largely enabled the embrace of eugenics on the left, which generally subscribed to environmental determinist views of human nature. Once Lamarckian evolution was discredited, it became more difficult to justify adherence to eugenics within the ideological frameworks of leftism. Although these and other indirect effects were important, direct effects likely had a greater role in undoing the First-Wave Eugenics Movement. Specifically, First-Wave eugenic policies drew fierce criticism that tarnished the movement's image.

In the early to mid-twentieth century, sterilization was a common eugenic practice (Hertler 2014). For example, nearly 8000 American citizens were sterilized in approximately 50 years of North Carolina history. Like other states, North Carolina had eugenic laws and a eugenics board. Whereas some states officially sanctioned sterilization, others tolerated its discretionary use by local physicians. California and Virginia rivaled North Carolina in the number ultimately sterilized. To these, Washington, Vermont, Utah, South Dakota, Pennsylvania, and South Carolina were added as states that sanctioned sterilization but practiced it on a smaller scale. Federally, sterilization was upheld as a constitutional practice by Supreme Court Justice Oliver Wendell Holmes. Nevertheless, such coercive negative eugenic practices invited a backlash, as it was and is thought that these involved extensive violations of human rights.

Several other factors contributed to the demise of the First-Wave Eugenics Movement. First, Soviet agronomist Trofim D. Lysenko "reimagined" heredity and evolution in line with Stalinist interpretations of dialectical materialism. In doing this, he sought to both "de-privilege" the gene as the sole vehicle of heredity and revive Lamarckian theories of the inheritance of acquired characteristics. The introduction of Lysenkoism may have given leftist academics an intellectual

basis on which to reject eugenics, which they may have been inclined to do in light of the latter's previously discussed "natural" turn. Unlike earlier Lamarckian eugenicists, Lysenkoists' interpretation of heredity was so radically at odds with standard Darwinian theory, e.g., maintaining that environment is part of heredity insofar as the former enters into "dialectical correspondence" with organisms, and so politically charged that their relation to anything derived from Darwinian thinking, such as Galtonian eugenics, was purely acrimonious. Second, a new school of anthropology, spearheaded by Franz Boas and his students, was instrumental in advancing environmentalist views of human nature to the detriment of the hereditarian doctrines on which mature First-Wave eugenics relied. Third, the eugenic research, policy-making, and theorizing of the interwar period were disrupted by World War II. Fourth, evidence was starting to accumulate that the theoretical bases of the First-Wave Eugenics Movement were seemingly false. Alarmist predictions of dysgenic decay in national intelligence, made in the interwar years, were not observed when eugenicists conducted follow-up studies comparing the performance of older and newer cohorts on intelligence tests (Cattell 1950). On the contrary, comparisons of the IQ scores of cohorts suggested that intelligence had increased over time – eugenicists were therefore among the first to accidentally find what is today called the *Flynn effect* (though the inference that dysgenic decline was not in fact occurring is likely false; see Woodley of Menie et al. 2017). Finally, New Left historical revisionism in the 1960s cast eugenics in a negative light. Rather than discuss the progressivist or even utopian cosmopolitan aspects of First-Wave eugenics, these historians argued that eugenic thought intrinsically favors programs of genocidal racial hygiene of the sort pursued by German National Socialists against Jews and other minority groups (Glad 2011).

Eugenics Behind the Natal Barrier

Active state-sponsored eugenical programs are now historical relics, commonly deplored and sincerely regretted. Chastened by the debacles and misdeeds of the past, and softened by humanistic sentiments, few would now endorse top-down

control of human breeding to prevent disadvantaged, poor, physically disabled, and/or mentally ill individuals from reproducing. Still, this does not mean that humankind is fully opposed to eugenics. It must be stressed that certain eugenic practices are in fact broadly acceptable and legally sanctioned, as long as they are voluntarily adopted by and for particular persons (or their unborn or perhaps very young children) rather than coercively imposed by others or the state.

Support for these autonomous reproductive decisions is properly recognized as the basis of the *Second-Wave Eugenics Movement*, starting around 1990 and continuing to the present. This extends beyond selective abortion and implantation to more intricate applied biotechnologies that are alternatives to rights-infringing procedures, such as forced sterilization.

Stock (2002), like Habermas (2000), relates the bioethical and broader philosophical complexities of genetic intervention. Though some are cautious and skeptical in light of the difficulty of these matters, others argue that the application of biotechnology to eugenic ends is inevitable, with the only questions being *when*, *where*, and *how* (Habermas 2000; Stock 2002; Agar 2004; Salter 2015).

The individualistic character of the Second-Wave Eugenics Movement ought to be recognized as a major deviation from the First-Wave Eugenics Movement. Woodley and Figueredo (2013) analyzed the works of major First-Wave eugenicists and found that they sought to promote traits in populations that would redound to *group-level* fitness, especially high levels of intelligence, heroism, and altruism. Therefore Woodley and Figueredo (2013) defined eugenics as efforts to increase the frequency of traits in populations that augment group-level fitness, and to decrease the frequency of traits that have the opposite effect. By contrast and as previously indicated, Second-Wave eugenicists seem mainly interested in empowering *individuals* to autonomously enhance their well-being (Agar 2004), which will largely serve to improve *individual-level* fitness, perhaps at the expense of group-level fitness. The First-Wave Eugenics Movement was largely an extension of the moral spirit of its age, which promoted concern for the survival and flourishing

of populations above such concern for individuals; this collectivist moral orientation was likely a product of the group-selection regimes to which nineteenth- and, to a lesser extent, early twentieth-century European populations were subjected as a result of the severe intergroup competition to which they were exposed (Woodley of Menie et al. 2017). The Second-Wave Eugenics Movement is, correspondingly, of a piece with the hedonistic and self-interested morality that has been ascendant in Western nations since the 1960s at the latest, which is in turn an outgrowth of the individual-level selection regimes that Western populations have experienced following the virtual disappearance of intergroup competition and hence of group selection (Woodley of Menie et al. 2017). Though the individualistic nature of Second-Wave eugenics might give it a benign appearance, the risks that attend direct manipulation of human genomes should be considered.

Consider Paul and Moore (2010), who wrote of Galton:

He stood all but alone, lacking a scientific consensus to support his biological premises. Natural selection had few adherents, and many converts to evolution, still accepting Lamarckian inheritance, doubted selection's sufficiency. Worse, Galton had little basis for applying selection to humans. He lacked data on the inheritance of mental and moral traits for any population, and his pedigree research was restricted to eminent families.

Though primarily meant to chasten Galton and Galtonian eugenicists, the lesson might well be applied to all efforts to change human heredity that carry or may carry serious risks. Some argue that should eugenic technologies become widely available for elective use, they are likely only to reduce or perhaps eliminate deleterious genetic variation (e.g., by selecting against variants that cause schizophrenia), rather than inadvertently lower levels of desirable genetic diversity (Stock 2002). However, even after genetic variants have been more reliably linked to harmful traits and conditions, the relevant scientists might still not know enough to carry out genetic interventions without serious risks. For example, pleiotropy, or the influence of one gene on more than one phenotypic trait, is an aspect of human genetic architecture that currently presents a major obstacle to the

development of some “eugenic” technologies (e.g., genome editing). This is because altering pleiotropic genes to enhance one trait could damage one or more other traits. Nevertheless, there is no reason to believe that challenges of this sort are insurmountable, especially if geneticists and related scientists are able to conduct research on these problems free from efforts to stop their work stemming from anachronistic fears about eugenics.

Conclusion

Eugenics was more than anything else an attempt at artificial, top-down control of selection processes that had previously operated from the bottom up. In the nineteenth and early twentieth centuries, elites found themselves in a world radically transformed through the industrial revolution, a process that spurred unprecedented economic development and thereby profoundly reduced levels of morbidity and mortality that in previous centuries had constrained human population growth, particularly of those carrying traits deemed to be socially undesirable. They also saw the widespread utilization of contraceptives among those high in socially desirable traits, as well as the dysgenic consequences of the aristocide and extirpation of Western monarchies that characterized World War I. The reproductive advantage that went with power, wealth, and talent in Western European premodernity for centuries was suddenly attenuated. Eugenics was first and foremost a bid to forestall the adverse consequences anticipated to result from these “dysgenic” processes.

Cross-References

► Moral Concerns

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Euler and Weitzel (1996)

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Synonyms

Grandparental care; Grandparental involvement;
Grandparental solicitude

Definition

The investment (e.g., time, emotional closeness, material resources) a grandparent allocates to a grandchild.

Introduction

The finding that parental solicitude is sex specific, with mothers investing more in their offspring than fathers (Daly and Wilson 1980), can be extended to grandparental solicitude. According to the life history theory, persons can maximize their reproductive success by parental effort, but also by their nepotistic effort (supporting persons with whom they share genes by common descent). Thus, grandparents can maximize their long-term reproductive success by allocating their grandparental effort discriminatively.

Preferential Grandparental Solicitude: Theory

Euler and Weitzel (1996) hypothesized that the amount of discriminative grandparental investment can be predicted by two sex-specific reproductive factors: (1) Because of their higher obligatory investment into each single reproduction, females could in the ancestral past best maximize their genetic replication by maximizing maternal care, whereas for human males with their high reproductive potential, the opportunity costs for parental investment were higher than for females. These costs reduced men's willingness to invest in their offspring. (2) Maternity is certain, whereas paternity may be uncertain. These two sex-specific conditions led to asymmetries which are also evident in grandparental investment into their adult children and their grandchildren. For grandparents, paternity uncertainty, here better named relationship uncertainty, may enter twice. The maternal grandmothers can be certain about her own as well as her daughter's maternity. The paternal grandfather, however, suffers paternity

uncertainty twice. He can neither be certain that his son is his biological offspring nor that the children of his son are his son's biological offspring. The other two grandparent types, the maternal grandfather and the paternal grandmother, each have one link of paternity uncertainty. Combining both sex-specific reproductive factors, a rank order of grandparental investment was predicted: Most investment can be expected by the maternal grandmother, followed by the maternal grandfather, the paternal grandmother, and the paternal grandfather.

Preferential Grandparental Solicitude: Original Data

In the Euler and Weitzel (1996) study, a convenience sample of both student and community participants (aged 16–80 years) was asked by a questionnaire how much each grandparent had cared for them (“gekümmert”) up to the age of 7 years. The German verb “kümmern” has both a behavioral and a cognitive–emotional meaning, namely, to care for, to look after, and to be emotionally and/or cognitively concerned about. From the total sample of 1,857 respondents, a subset of 603 cases were selected for analysis whose four grandparents were all still alive when the participant was 7 years old. This selection was made because due to females' higher life expectancy and the average age differences in reproductive partnerships, the maternal grandmother is the grandparent most likely to be still alive and the paternal grandfather least likely. The expected rank order of grandparent categories was obtained.

As expected, the intra-couple correlations for the grandparental solicitude ratings were high, pointing to the possibility that grandfathers comply with their spouses due to mating effort. Therefore, the order and solicitude ratings differed for grandparents living separately except for the maternal grandmother. The solicitude ratings for the grandfathers living separately from their spouse, however, dropped considerably such that

the paternal grandmothers now cared more for her grandoffspring than the paternal grandfathers, and the care showed by paternal grandfathers was extremely low. As opposed to separation, widowhood had no effect on the amount of grandparental care.

Residential distance is a strong determinant for grandparental solicitude, but the residential distances for the four grandparent types did not differ significantly. The residential distance had tendentially the least impact on care shown by the maternal grandmother.

The sex of the grandoffspring had a small effect on the reported grandparental care, with women reporting having received more care than men. Variables which did not affect grandparental solicitude were grandparental age, number of grandparents still alive, and socioeconomic status (Trivers–Willard effect).

Replications and Generalizations of Original Findings

Subsequent studies have replicated this finding (for summaries, see Coall and Hertwig 2010; Euler 2011) for a variety of indicators or proxies of investment, for example, contact measures (e.g., frequency, duration), grandparental adoptions of grandchildren, ratings of emotional closeness, mourning upon the death of a grandchild, terms of verbal address (diminutive and endearing name most often for the maternal grandmother), naming favorite grandparents, and most recently positive attitudes toward retirement during transition to grandparenthood (Wiese et al. 2016).

Sex-Chromosome Relatedness

The relatedness between grandparents and grandoffspring described at the outset applies only to autosomal genes. The sex-chromosome relatedness, however, is different because males are heterozygous (XY) with respect to the sex chromosome. The grandfather passes his

Y chromosome directly to his grandsons, whereas the X chromosome undergoes recombination. With respect to the Y chromosome, the paternal grandfather is thus 100 % related to his grandsons, but 0 % to his granddaughters. A hypothesis about preferential care of paternal grandfathers for their grandsons, however, could not be supported empirically (Chrastil et al. 2006).

Cultural Limitations

The obtained rank order of grandparents, from maternal grandmother to paternal grandfather, is not culturally universal. Most of the reported studies have been done in Western industrialized states and milieus. In traditional pastoral, expressedly patrilocal, or otherwise patrifocal societies or societal milieus, the paternal grandparent–grandchild relationships play a more important role than the maternal ones (Pashos 2000) and thus care more for grandchildren than do maternal grandparents.

Effects of Grandparental Investment on Grandchild Development

Does grandparental care, particularly the grandmaternal one, have an impact on the grandchild's development? Sear and Mace (2008) reviewed 45 studies about the presence of kin for child survival, most of them from natural fertility populations, and found that next to the mother, whose presence contributed to child survival in all studies, the maternal grandmother was the second most important kin. For industrialized Western societies, where child survival is asymptotically low, the question arises whether grandparental care makes positive contributions to the grandchild's development. Coall and Hertwig (2010) reviewed the evidence, unfortunately relatively sparse, and concluded that positive contributions by emotionally close grandparents are most likely for risk families (e.g., lack of social

support for the mother) or situations of duress, like maternal depression or drug misuse. Tanskanen and Danielsbakka (2012) reported evidence for an association between maternal, but not paternal, grandparents' involvement and fewer emotional and behavior problems in the grandchildren.

The Grandmother Hypothesis

The data about preferential grandparental care, particularly the generally prominent role of the maternal grandmother, lends support the so-called grandmother hypothesis, first stated by Williams (1957). According to this hypothesis, the relatively early menopause of human females, unequalled in other mammals, is an adaptation. Rather than to continue producing own children, a middle-aged woman gains more fitness benefits by investing her effort into helping her daughter raising the grandchildren. Whether the menopause is indeed an adaptation in its own right, however, remains a matter of debate (see Euler 2011).

Conclusion

The study by Euler and Weitzel (1996) was the first one to show that in the sample studied, grandparental solicitude as a proxy for grandparental investment differed systematically between the four different types of grandparents and that this preferential solicitude could be predicted by evolutionary theory.

Cross-References

- [Differential Parental Investment](#)
- [Father's Father Versus Mother's Mother](#)
- [Grandparental Investment and Genetic Relatedness](#)
- [Grandfather Investment Versus Grandmother Investment](#)

- [Grandparenting](#)
- [Grandparents and Grandchildren](#)
- [Kin Selection](#)
- [Life History Theory](#)
- [Maternal Grandmother Invests Most](#)
- [Nepotism](#)
- [Paternal Grandfather Invests Least](#)
- [Paternity Uncertainty](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Trivers-Willard Hypothesis](#)

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Europe

- [Western Europe](#)

Eusociality

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Synonyms

[Cooperative breeding](#); [Highly structured society](#); [Sociality](#); [Worker caste](#)

Definition

Eusociality is an elaborate form of social organization, involving a reproductive division of labor among members, overlapping generations, and cooperative care of the young.

Introduction

Eusociality is thought to have evolved as a group-living strategy where group mates were relatives and ecological conditions made it difficult to reproduce personally because of high predation risk and high rates of failure in founding new nest. It has evolved independently and separately in different taxonomic groups.

What Eusociality Is

Eusociality is an elaborate form of social behavior, where some individuals in the group (usually

called “colony”) do not reproduce for the benefit of others. Thus, a reproductive division of labor exists. Two or more overlapping generations coexist in eusocial colonies – typically, parents and their offspring – and they cooperate in caring for the young (Wilson 1971). Nonreproductive individuals – which, in some cases, are irreversibly sterile – forgo reproduction and accomplish different tasks such as foraging, colony maintenance, and defense, basically helping in raising the offspring of the breeders (Wilson 1971). Typically, there are castes in eusocial societies, that is, groups of individuals which are behaviorally specialized for a social task (in Crespi and Yanega’s (1995) view, eusociality should be limited to those social organizations where caste specialization is irreversible).

Social insects are typical examples of eusocial animals (Wilson 1971). In honeybees and ants, for example, the colony is composed of one or more egg-laying “queens” and up to thousands (even millions) sterile females (“workers”) which spend their lives helping the queen (or the queens) to raise her young. Generally, workers are queen daughters, which do not abandon the natal colony when they become adults. In some eusocial species, queens and workers differ not only physiologically and behaviorally from each other but also morphologically (i.e., phenotypic castes exist), and all individuals have irreversible roles; therefore, they cannot switch from the worker to the reproductive caste or vice versa. In some ants and higher termites, multiple, morphologically distinct, sterile castes exist, which are specialized on particular social roles within the colony, e.g., foraging or colony defense (Hölldobler and Wilson 1990). For example, in turtle ants (*Cephalotes* spp.) a soldier caste is specialized on blocking cavity entrances with their armored heads, which fit well the size and shape of nest entrances (Powell 2008). In the neotropical termite *Neocapritermes taracua*, workers have explosive “backpacks”; they burst and release a toxic sticky fluid when they are seized by enemies, such as other termites (Šobotník et al. 2012).

Eusociality is not limited to social insects. Recently, it has been reported in a few species of echinostomoid trematodes, or fluke worms. These worms are parasites and have complex life cycles involving several developmental stages occurring in different hosts. Once the founder larva infects its first intermediate host – typically, a snail – it initiates reproducing clonally, thus giving rise to a colony of genetically identical individuals living in the same host snail (Hechinger et al. 2011). Some worms develop a large size, whereas others stay relatively smaller. The large worms reproduce asexually in their turn giving rise to both large worms capable of reproducing and dispersing morphs (cercariae) which will leave the host snail and search for the next host, where they will complete their life cycle and reproduce sexually. The small worms do not reproduce at all; they spend their lives in the snail and physically fight parasites other than their clone mates when they encounter them throughout the snail body. By doing this, these worms behave as “soldiers” defending “their” snail – which is the living resource they get their living from – against competitors and thus help large worms to reproduce. In this way, they favor the spreading of copies of their genes in the next generation through the help they give to their clone mates (Garcia-Vedrenne et al. 2010; Lloyd and Poulin 2012).

Eusocial organization is not limited to invertebrates. Eusocial mole rats are small, African, sub-Saharan rodents which live in underground colonies of tens of individuals. A female (the queen) and one to three males reproduce and their offspring stay at the natal colony where they spend their lifetime digging foraging tunnels while searching for roots and tubers, maintaining the burrow and defending it against predators, such as snakes (Jarvis 1981; O’Riain and Faulkes 2008). Castes are not irreversible in this taxa: if the reproductive female dies, a female “worker” will rapidly develop a larger body size and will undertake the reproductive task. The same fate may occur to male “workers,” if one of the

reproductive males die. Because of low dispersal, individuals in the colony are usually relatives: parents and sons and daughters, cousins, aunt and uncles, etc. Eusocial mole rats typically live in arid habitats, where physical and climatic conditions are harsh: soil is hard to dig, air temperatures extreme, rain sporadic or unpredictable, and food scarce. These ecological factors may have played an important role in the evolution of mole-rat sociality, as stated by the aridity food distribution hypothesis (O’Riain and Faulkes 2008). Low success of dispersal from the natal nests (mainly limited to special morphs with large fat reserves than non-dispersers, O’Riain et al. 1996), the difficulty of digging a new burrow, and the difficulty of finding food may have favored (during evolution) individuals which stayed at the natal nests.

Eusociality: Occurrence

Eusociality is rare among animals but has evolved independently in different taxonomic groups. Besides mole rats and trematode worms, it has been reported in thrips, in sponge-dwelling shrimps, and in gall-forming aphids. In contrast, it is relatively common among hymenopteran insects (the taxon that includes ants, bees, wasps) and among termites. In order to understand the nature of eusociality, and the conditions which have favored its origin and evolution in different taxonomic groups, it is interesting to investigate which features the diverse eusocial taxa share.

Factors Favoring the Evolution of Eusociality: Genetic Factors

From an evolutionary point of view, eusociality is puzzling because it involves individuals which do not contribute their genes to the next generation through reproduction; nonetheless, helpers persist generation after generation. However, genetic relatedness between colony members offers a solution to the puzzle.

Natural selection favors those behavioral, physiological, morphological traits that increase the frequency of an individual’s genes in the next generation. Helpers are likely to increase the frequency of their own genes in the next generation if

the helpers and the breeders are likely to share identical genes by descent from a common ancestor. Typically, eusocial colonies consist of related individuals. Colonies are generally composed by a queen and their offspring or a pair of parents with their offspring; in other cases, colony members are clones (genetically identical individuals produced through asexual reproduction). For example, trematode colonies are composed of clones (genetically identical individual originated through asexual reproduction from a single “parental” individual which produces copies of itself); mole-rat colonies are sort of large families where colony members are relatives and mating between related individuals (i.e., inbreeding) is not rare (which further increases relatedness between colony members) (Reeve et al. 1990).

The observation that colonies of eusocial animals are generally composed of related members has been crucial to the understanding of the genetic background that has favored the evolution of eusociality, and the idea was originally formulated by W. D. Hamilton (1964) to account for the evolution of cooperation in social insects. In social insects, such as bees, ants, and wasps, colonies are generally composed of queens and their daughters, which help the queen to reproduce and care for their young sisters, which in turn will develop as workers and/or future queens. In Hymenoptera, genetic relatedness between sisters is especially high because these insects have a special mechanism of sex determination. Females originate from fertilized eggs (i.e., eggs fertilized by sperm), whereas males originate from unfertilized eggs. This means that males are haploid, i.e., they have a single copy of each chromosome – the only copy they received from their mother. In contrast, females have two copies of each chromosome, one inherited from their mother and the other inherited from their father. This mechanism of sex determination, which is called haplodiploidy, produces asymmetry in relatedness, simply because all sperms produced by a male contain the same copy of each chromosome – and, eventually, the same copy of each gene. This means that all sisters are genetically identical as for the genes they inherit from their father. Instead, the eggs produced by a queen (which has two copies of each chromosome and

thus two copies of each gene) contain either one or the other copy of each gene. This means that sisters have one probability out of two of inheriting the same gene from their mother. Sisters are therefore genetically identical as for their paternal genes and have one probability out of two of sharing a particular maternal gene. Therefore, haplodiploidy makes sisters genetically very close to each other (the likelihood of sharing a gene with their sisters is on average $r = 0.75$) and eventually closer to each other than to their brothers ($r = 0.25$), which may explain why sterile workers are females in social insects. In an evolutionary perspective, selection may favor either individuals that spread their genes to future generation through personal reproduction – as queens do, obtaining direct fitness benefits – or individuals which spread their genes to future generation via helping relatives to reproduce, as workers do, obtaining indirect fitness benefits. It comes from Darwin theory of evolution through natural selection (Darwin 1859) that traits which are heritable and enhance an individual reproductive success should increase their frequency across generations. The novelty of kin selection theory (or inclusive fitness theory) (Hamilton 1964) was to link the evolution of sociality in social insects with the observation that individuals can obtain a reproductive success either through personal reproduction or through reproduction of other individuals with which they share genes by common ancestry.

High relatedness between the helper and the recipient of the helping action is actually common among real eusocial insect colonies, but many exceptions exist. This is why many investigations have analyzed whether queens are monogamous (i.e., mated with only one male) or promiscuous (multiply mated). Indeed, relatedness between sisters decreases if the queen is multiply mated, which means that multiple patrilineal exist within the colony. Recently, the condition where queens mate with only one male has become one of the central focus of the analysis on the evolutionary origin of eusociality (Boomsma 2009, 2013). Monogamy is thought to be the ancestral mating system in taxa where eusociality with irreversible castes have evolved and multiple mating appears to be a trait evolved after sterile castes evolved (Hughes et al. 2008). Following Boomsma

(2013), irreversible castes have not evolved in vertebrates (such as mole rats) because vertebrates “were never monogamous enough.”

Factors Favoring the Evolution of Eusociality: Ecological Factors

Kin selection theory (Hamilton 1964) has provided a powerful explanation of cooperative parental care and worker sterility. However, ecological factors have played a crucial role in the evolution of eusociality. Generally, eusocial species live in habitats where living in group favors colony survival because it enhances the chances of finding food, defending and/or enlarging foraging territory against competitors, fighting back predators or parasites, etc. Indeed, mole rats live in extremely harsh environments, where founding new colonies is largely unsuccessful (e.g., disperser face starvation, O’Riain et al. 1996), and larger colonies are more likely to survive when conditions get even worse, such as during drought (Jarvis et al. 1988). More generally, whenever the nest is an easily defendable fortress, staying home and helping relatives to reproduce may be a valuable option to leaving and reproducing personally; similarly, if predation risk is high during foraging, group living individuals may gain a sort of life insurance because in case they were predated during foraging, their brood would be raised by their group mates (Queller and Strassmann 1998).

Are Humans Eusocial?

Recently, it has been argued that our species may fulfill the criteria for being classified as eusocial. Indeed, human societies have overlapping generations and cooperative care of the young and, in Foster and Ratnieks’ view (Foster and Ratnieks 2005), might also have a sterile caste. They reasoned that mid-age women become irreversibly sterile – menopause, a condition when they are physiologically incapable of reproducing – and usually help their close relatives. Although not occurring to young women, menopause is distinct from senescence (Hamilton 1966), and some hypotheses have been formulated to account for its evolution. One of them is the so-called grandmother-effect hypothesis that menopause in women may have been favored if aged women help their sons and daughters to

produce more grandchildren (which enhances the grandmother fitness through indirect reproduction) (Hamilton 1966). The grandmother-effect hypothesis is supported by a study documenting that the help of grandmothers significantly increased reproduction of close relatives in premodern populations (Lahdenperä et al. 2004). In this view, women in menopause may function as the sterile caste in human societies, getting fitness benefits through caring for grandchildren.

Conclusions

Ecological factors have favored group living in many species of animals, but among social animals, eusociality has rarely evolved, and it did so when high relatedness existed among group mates, at least ancestrally.

Cross-References

- [Castes](#)
- [Cooperation](#)
- [Cooperation in Social Insects](#)
- [Grandmother Hypothesis of Menopause](#)
- [Parasites](#)
- [Primate Menopause](#)

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Euthanasia

- [Assisted Suicide](#)

Evaluation

- [Social Comparison](#)

Evaluative Conversation

- [Social Consequences of Initiating Gossip](#)

Events

- [Absence of Events to Distinguish True Friends](#)

Evidence for Modularity

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Synonyms

[Mechanisms](#); [Psychological mechanisms](#);
[Specialization](#)

Definition

Modularity refers to that quality of any system wherein it consists of two or more functionally distinct mechanisms or components. In evolutionary psychology, modularity refers to this design feature in the human mind. Specifically, modularity refers to the various functionally distinct psychological mechanisms that comprise the human mind. These mechanisms are thought to serve evolutionary functions in that they address specific adaptive problems.

Introduction

Most aspects of modern design possess the quality of modularity. The cars we drive are modular in

that they have multiple mechanisms which perform distinct operations (e.g., radio, speakers, engine, carriage). Each of these modules is functionally distinct in that they each perform a distinct function. The radio receives radio waves and converts those radio waves into sonic oscillations emitted from another module: our cars' speakers. The engine (composed of several modules of its own) ignites liquid fuel, generating the kinetic force that propels the module in which we sit (i.e., the carriage) forward.

Many biological systems are also modular. Most animals' bodies are modular, in that they consist of multiple mechanisms, each of which is functionally distinct (e.g., heart, lungs, vascular system, etc.). Our hearts pump blood through our vascular system, while our lungs pull in oxygen to enrich that pumped blood.

Evolutionary psychology assumes that the human mind shares this modular design feature. Just as the modules of our bodies were shaped by evolution to solve the adaptive problems imposed by selection pressures, so too was the neural architecture of our minds shaped to solve adaptive problems.

The plethora of adaptive problems faced by our own species and our predecessors have generated a myriad of modules. These modules address adaptive problems ranging from disease avoidance to establishing and maintaining groups and communicating with those groups. In the following entry, we introduce some of the evidence for modularity. We begin, by exploring some of the more basic modules for processing kinship and indicators of disease. We then discuss models which scientists have proposed for understanding how these modules coordinate with one another.

Incest Avoidance and Kin Detection

Humans reproduce sexually. Sexual reproduction comes with many advantages. Species which reproduce sexually experience greater diversity than do species that reproduce asexually. This diversity allows sexually reproducing species to adapt to changes in their environments much quicker than can asexually reproducing species.

Further, any problematic mutations can be effectively removed from a sexually reproducing population much quicker than those same mutations could be removed from an asexually reproducing species.

However, many of these advantages of sexual reproduction are severely limited when individuals who share close genetic kinship reproduce. The genetic diversity of such a copulation is limited to that already present among the parents. Further, any mutations present in the parents would be sustained in the offspring (Lieberman et al. 2003). This creates the adaptive problem of incest aversion (Tooby and Cosmides 2005).

Building on Westermarck's (1891) proposal of an incest avoidance mechanism, Lieberman and colleagues (2003) proposed a kin detection module which would serve this incest avoidance mechanism in helping individuals solve the adaptive problem of incest aversion. Lieberman and colleagues suggested that this module would operate not only by identifying those with whom one has resided during early development (Westermarck 1891) but also by identifying those who have been cared for by one's own mother (i.e., maternal perinatal association or MPA).

Indeed, evidence confirms the operation of these modules. For instance, Lieberman and colleagues (2003) assessed how long participants reported to have lived with their siblings and the average extent of relatedness with their siblings. They then correlated these measures with how morally wrong participants found incest to be. The longer participants lived with their siblings, the more morally wrong they judged incest to be. Moreover, the more related participants felt they were to their siblings, the more morally wrong they judged incest to be.

Further, Lieberman, Tooby, and Cosmides (2007) found that participants use information about their own mother's caring for their siblings (i.e., MPA) more so than they used information about co-residence. Specifically, they found that co-residence information predicted incest aversion primarily when participants did not have information about maternal perinatal caring.

Others have replicated and extended these findings. Fessler and Navarrete (2004) found that

the longer people's history of co-residence, the greater their reactions of disgust and intolerance toward others' incest. However, this relationship was stronger in females than in males. Further, Luo (2011) replicated Lieberman and colleagues (2007) findings of MPA primacy (relying principally on MPA information when both MPA and co-residence information are available), but this primacy was greatest among men. That is, they found that women's aversion to incest with co-residing brothers was strong regardless of whether MPA information was present or absent. However, men's incest aversion only depended on co-residence when MPA information was absent (i.e., MPA primacy). Therefore, not only did Luo provide further evidences of Lieberman and colleagues' kin recognition module, but they extended it by replicating the finding revealing that females place relatively greater importance on co-residence than do men (Fessler and Navarrete 2004).

Pathogen Avoidance

Pathogens and parasites and other body invaders create a selection pressure, such that those with effective immune systems benefit, while those without effective immune systems suffer. This creates the adaptive problem of pathogen aversion. While our immune system is a clear line of defense against these invading agents of disease, Schaller (2006) has suggested that a psychological module, which he calls the behavioral immune system, developed as a first line of defense. Schaller argues that this module is sensitive to cues that indicate the presence of pathogens, parasites, and other health threats. The detection of these cues is thought to elicit cognitive (inferences of disease implying qualities) and emotional responses (disgust) that propel people away from these cues of disease.

The behavioral immune system has enjoyed a great deal of attention. This work has revealed that people react to cues of disease and illness, principally with avoidance. Those who live in pathogen-dense environments develop a suite of characteristics that motivate them to avoid new

experiences and unfamiliar people and remain close to known activities and people. For instance, those in pathogen-dense areas tend to be more collectivistic than individualistic (Fincher et al. 2008), religious, and family-focused (Fincher and Thornhill 2012) and less sexually promiscuous, less extroverted, and less open to new experiences (Schaller and Murray 2008). Further, greater feelings of disease vulnerability sensitize people to cues of disease, effectively lowering their criteria for detecting cues of disease (Miller and Maner 2012) and making them more likely to judge areas as crowded while also inclining them to avoid crowded places (Wang and Ackerman 2019).

Further, the pathogen aversion module is thought to be one of a cluster of several functionally similar modules sensitive to cues that indicate potential harm to the self. Researchers examining the behavioral immune system have found that the identification of certain threats to one's health in addition to pathogens can also trigger disgust, namely, sexual taboos and moral violations (Tybur et al. 2013). However, while cues of pathogen threat may be learned relatively early in life, the other behavior immune system modules may become sensitive to these other threats later in life (Oaten et al. 2009).

Modularity in Moral Foundations Theory

Building on our discussion of superordinate modules or clusters of modules, we now turn our attention to models which have been used as organizing frameworks for representing the coordination of multiple modules serving similar, though distinct functions. The first model we will discuss is that of moral foundations theory (Graham et al. 2013).

Moral foundations theory suggests that we rely on a set of moral intuitions (foundations) when making moral judgements (Graham et al. 2013). These moral foundations include the care/harm foundation, the fairness/cheating foundation, the loyalty/betrayal foundation, the authority/subversion foundation, and the sanctity/degradation foundation. Endorsement of these foundations

varies based on individual differences and cultural influences, but each foundation occurs cross-culturally (Graham et al. 2011). As with all modules, each foundation serves an evolutionary adaptive function.

These moral foundations can be grouped together as those serving an individuating function (operating for the benefit of individuals) or a binding function (operating for the benefit of the group; Graham et al. 2009). The individuating foundations of care/harm and fairness/cheating focus on interactions between individuals. The care/harm foundation addresses the adaptive problem imposed by the high investment necessary to rear children. Human children take an abnormal amount of nurturing before they can survive on their own. The care/harm foundation functions to promote caring and protecting children to ensure they survive to carry genes to their own offspring (Graham et al. 2013). This module may have been originally triggered by children in distress; however, the module may also generalize by reacting to signs of distress and suffering in adults, animals, and cartoons that resemble children. Reactions to these cues lead to outputs that work to ensure that people receive care until they can care for themselves. These outputs can include emotional reactions, such as compassion for the victim, anger toward perpetrators, and caring behaviors meant to relieve the distress.

The fairness/cheating module responds to the adaptive problem created by group living. Specifically, humans have had a better chance of surviving when they interact with one another, often by trading resources or services, while also avoiding free riders. The fairness/cheating foundation functions to promote the individual benefits of successfully navigating reciprocal relationships. This module may have originally been activated by either witnessing exchanges between people or hearing about an exchange from others; however, modern triggers also include inanimate objects involved in exchange, such as vending machines. Reactions to these inputs include emotion outputs thought to regulate future exchanges, such as anger and guilt in situations where an unfair exchange has occurred and gratitude when an exchange is fair.

Group living is not only transactive but also communal, creating additional adaptive problems. Being part of a cohesive group can increase chances of survival by providing access to shared resources and providing protection from other group members. The binding foundations of loyalty/betrayal, authority/subversion, and sanctity/degradation are modules focused on addressing the adaptive problems created by how people interact with one another within their groups.

Given the great advantages provided by communal group living, maintaining the cohesion of those groups becomes a selective pressure. The loyalty/betrayal module promotes formation and the maintenance of cohesive groups (Graham et al. 2013). This module responds to threat toward one's group cohesion (e.g., violating group norms). Reactions to these threats trigger behaviors meant to defend the cohesive elements of the group. These outputs include emotions such as group pride or anger toward perceived traitors.

Groups also tend to establish status hierarchies. Hierarchies provide a sense of order and organization within groups. If appropriate interactions occur between those of higher and lower status in a hierarchy, the group is more likely to work cohesively, and moving up within the hierarchy is more likely. This increases survival odds by ensuring the group is functioning efficiently to protect themselves, as well as providing those of higher status with resources. The authority/subversion module serves to promote positive interactions among members within a hierarchy (Graham et al. 2013). This module responds to violations of these status hierarchies. Modern triggers include status dismissing interactions between employees and employers, law enforcement officials and non-law enforcement officials, and among people of different military ranks. Reactions to these status violations include emotional reactions such as respect and fear for authority, which reinforces separating people of different levels within a hierarchy.

Finally, communal group living can increase the chances of exposure to health threats, triggering concern with pathogen exposure and self-

harm as discussed above. The sanctity/degradation module is largely analogous to the behavioral immune system cluster of modules and thought to help people to avoid communicable diseases (Graham et al. 2013). In addition to those triggers mentioned above, modern triggers of this module include immigration, as those coming from another country may carry diseases, and sexual deviancy, which would increase the chances of the persons involved getting a sexually transmitted infection. In general, these modules involve the reaction of disgust and lead to harsher moral judgments. For example, exposing participants to disgusting stimuli which can signal the presence of pathogens (bad smells, a messy room, or gross video) leads them to make harsher moral judgments, particularly of moral violations related to the sanctity/degradation foundation (incest, sexual deviancy, cannibalism; Schnall et al. 2008).

Each of these moral foundations acts as modules within a moral framework described in moral foundations theory. Each module/foundation functions by attending to cues of various adaptive challenges and eliciting emotional and cognitive reactions that drive behaviors that aid survival of individuals and the groups in which they live. These modules trigger reactions to issues that are experienced as moral issues. Interestingly, those groups that place greater value on group cohesion experience the issues to which the binding modules/foundations respond as moral issues more so than do those groups that place less value on group cohesion (Haidt et al. 1993).

Modularity in the Fundamental Motives Model

Moral foundations theory organizes modules related to issues experienced as moral into an organizing framework. However, the fundamental motives model is a bit more ambitious. It attempts to provide an organizing framework for modules used across most if not all functional domains. The fundamental motives model suggests that psychological modules are organized by the motive these modules serve (Kenrick et al.

2010a). It builds on Maslow's hierarchy of needs by replacing Maslow's need for self-actualization with domains inspired by evolutionary theory, pertaining directly to successful reproduction. The resulting model identifies seven functional domains in which modules may be organized: immediate physiological needs, self-protection, affiliation, esteem/status, mate acquisition, mate maintenance, and parenting.

The physiological motive and the self-protection motives and their related modules are directly related to survival. The physiological motive consists of modules that produce behaviors that satisfy physiological needs (Kenrick et al. 2010a). The modules serving this motive convert inputs such as images (e.g., appealing foods), smells, and physiological imbalances (e.g., blood sugar levels) into behaviors which can reduce or remove these cues, such as hunger, thirst, and warmth-seeking. The self-protection motive consists of modules that address threats to, and ensure, safety. Inputs to these self-protection modules (e.g., angry male faces, darkness, and others with physical abnormalities or diseases) lead to emotional outputs such as fear and apprehension (Kenrick et al. 2010b). These emotional outputs subsequently prevent one from engaging with those who could potentially pose a threat, increasing safety.

Indirectly related to survival are the affiliation motive and the esteem/status motive, which are related to interpersonal behavior. The affiliation motive consists of modules which address the cohesive/belonging aspects of group living (Kenrick et al. 2010a) such as sharing resources, knowledge, and chores to increase survival. These modules react to cues of acceptance and rejection with behaviors designed to assess, prevent, and reestablish belonging. The esteem/status motive consists of modules that address resource acquisition, alliance formation, and status striving. These modules react to cues of achievement and competition, with behaviors aimed to successfully navigate status hierarchies (e.g., aggression; Griskevicius et al. 2009).

The remaining fundamental motives involve modules that address the various challenges of successful reproduction. The mate acquisition motive involves modules which respond to cues

of sexual receptivity with behaviors that lead one to seek desired mates (estimates of romantic interest; Perilloux et al. 2012; Sundie et al. 2011) and engage in behaviors to attract a potential mate (Kenrick et al. 2010a). Mate retention motivates those modules that help people to maintain long-term alliances with their mates (Kenrick et al. 2010a). These modules respond to threats of relationship dissolution and attractive alternative mates with reactions that insulate existing relationships, such as biasing evaluations of romantic alternatives (Maner et al. 2008). The parenting fundamental motive involves those modules that address the adaptive problem of offspring survival. Caring for children often includes sharing an abundance of resources with them, even if they are unable to contribute themselves. Parents who are more alert to children in distress will have a better chance of preventing accidents that could be life-threatening for the children. These modules respond to cues of offspring needs and threats to offspring safety with mechanisms that drive parents to be caring and generous toward their children and vigilant to distress.

Conclusion

In the preceding entry, we have discussed some of the evidence of modularity in psychological mechanisms. We have discussed some of the more basic modules such as kin recognition, incest aversion, and pathogen aversion, as well as some of the more global organizational frameworks which reflect the functional similarities in the more specific modules. However, regardless of the level of specificity, these modules and the more global frameworks for organizing them reflect the basic assumption of evolutionary psychology, that is, the human mind is modular in its design just as the rest of the human organism is modular in its design.

Cross-References

- [Incest Avoidance and Dating](#)
- [Moral Foundations Theory](#)

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Evidence of Brain Modularity

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Synonyms

Brain community structure

Definition

Evidence of brain modularity is the empirical body of findings that demonstrates that the brain

is organized into semiautonomous groups of neurons and brain regions that interact with one another through relatively sparse and long-distance pathways in the brain.

Introduction

Before there were brains, there was modularity. Modularity describes the extent to which a system has components that connect to or interact with other components, each of which is independent and functionally specialized. An example of a modular system is an electric circuit board made of connected electric components. Each component of the circuit board is an autonomous module with a specific independent function, connected to other modules with similar or different functions. Biological modularity, like artificial modularity, provides the organism with robust and specialized functions. These functions can independently evolve, develop, and respond to change. From this perspective, it is unsurprising that modularity is ubiquitous across biological systems (Scholsser and Wagner 2004).

The human body comprises various modular systems such as the cardiovascular system, the respiratory system, the digestive and excretory system, the visual system, the auditory system, and the nervous system. Each system has organs that constitute system modules that work together to support the smooth functioning of the system and organism in its entirety. In the human nervous system, the visual system's main organs, the eyes, communicate with the brain to interpret light waves as images. The inner and outer ear in the auditory system communicate via the brain to help us hear sounds of varying frequencies, such as a high-pitched sound of a chalk screeching on the blackboard or a low-pitched sound of distant thunder. More generally, the nervous system is composed of the central nervous system (brain and spinal cord) and the peripheral nervous system. Within the central nervous system, the spinal cord of vertebrates is a modular system with many ganglia. The brain is the "master ganglion" in vertebrates, and within the brain, there are numerous modularized systems.

Modularity in the Brain

A new branch of neuroscience called "network neuroscience" (Bassett and Sporns 2017) uses computational approaches based in graph theory to describe the organization of anatomical and functional brain networks at different spatial and temporal resolution scales (Betzel and Bassett 2016). A brain network can be depicted mathematically as a graph $G = \{N, E\}$, where N is a set of nodes (such as neurons or brain regions) and E is a set of edges (such as dendritic or axonal connections) connecting pairs of nodes. Statistics developed in graph theory allow us to compute network properties over G to make statements about the organization and roles of nodes, edges, or indeed the entire network.

The edges (region-region relationships) in a brain network are typically defined by three types of connectivity: anatomical connectivity, functional connectivity, or effective connectivity (Park and Friston 2013). Anatomical connectivity refers to anatomical connections among regions or neurons in the brain. At a low level of organization, anatomical connectivity can be detected using labeled tracer injections (Gamanut et al. 2017). In humans, anatomical connectivity can be computed from diffusion imaging data that represents white-matter pathways among regions in the brain. In contrast, functional connectivity at a high level of organization is often computed from the pairwise relationships between nodes via signals of BOLD-fMRI or electroencephalography (EEG)/magnetoencephalography (MEG). BOLD-fMRI signal can be obtained by scanning in the MRI scanner. The EEG/MEG signals can be recorded via multichannel recording using a group of electrodes centered over distinct regions of the brain. At a high level of organization, entire functional and anatomical networks can be mapped in the human brain, forming human "connectomes" (Sporns et al. 2005).

Functional networks are assembled from estimates of statistical dependencies between neuronal or regional time series data. Specifically, functional connectivity is often defined by the correlation, coherence, mutual information, or other measures of associations between time

series across nodes. Functional connectivity does not give information about causality or directionality. In contrast, effective connectivity is estimated from the lagged relationships between nodal activity in BOLD-fMRI and EEG/MEG signals. It is sometimes interpreted to represent the potential influence one neural system exerts over another at the synaptic or cortical level. Effective connectivity can evaluate directed relationships between regions as it is estimated with models with lagged parameters (e.g., vector autoregression, Granger causality, structural equation modeling, or unified structural equation modeling) or with a model of physiological dynamics (e.g., dynamic causal modeling).

Once a graph is constructed that represents a network, statistical diagnostics can be used to describe the organization of functional or anatomical connections in the brain from local to global scales (Rubinov and Sporns 2010). “Mesoscale” diagnostics are those that describe the organization of the network in between these two scales. Modularity is a mesoscale property of a network: modularity describes the organization of nodes into groups based on their connection to one another within the brain. A network is modular when sets of nodes form densely interconnected groups with sparser connectivity between groups relative to a null expectation (Newman 2006) (Fig. 1).

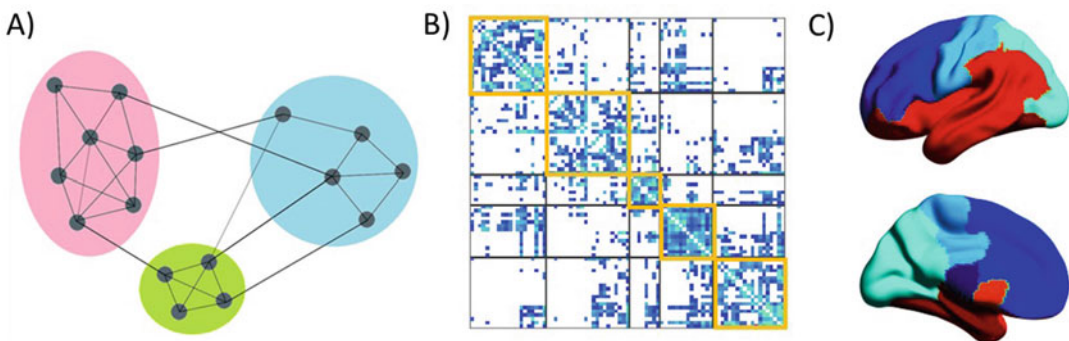
While specific definitions of modularity vary, one popular mathematical expression is defined by Newman and Girvan (2004). Consider an undirected graph with adjacency matrix A_{ij} and a partition of this graph into clusters or modules defined by $\{c_i\}$, where c_i describes which module node i belongs to; Newman and Girvan’s modularity Q is defined as:

$$Q = \frac{1}{2m} \sum_{i,j} \left(A_{ij} - \frac{k_i k_j}{2m} \right) \delta(c_i, c_j),$$

where $k_i = \sum_j A_{ij}$ is the degree of each node, $m = \frac{1}{2} \sum_i k_i = \frac{1}{2} \sum_{i,j} A_{ij}$ is the total number of edges, and $\delta(c_i, c_j)$ is defined as- $\delta(c_i, c_j) = 1$; if nodes i and j belong to the same module, $\delta(c_i, c_j) = 0$; otherwise.

Conceptually, Newman’s modularity compares the fraction of within-module edges in the graph to the expected fraction of within-module edges in a random graph with the same degree sequence as given by the configuration model. The randomization of edges is done to preserve the degree of each node for use as a null model that defines the expectation for Q under a random network of the same degree as the original network.

The value of Q is normalized such that it always lies in the interval $(-1, 1)$. The value of



Evidence of Brain Modularity, Fig. 1 What does modularity look like? (a) In principle, modularity is the extent to which nodes (gray circles) are grouped into discrete communities (nodes grouped into communities schematically represented by different colored backgrounds) based on the pattern of connections among nodes. Communities may have different sizes and configurations of within- and between-module connectivity. (b) An example connectivity matrix (“graph”) constructed from anatomical diffusion imaging data from one healthy individual. Each row and

column represents an “edge” – here, the number of estimated white-matter connections between a pair of regions. The highlighted squares along the matrix diagonal are those identified to be a module using a *community detection* algorithm. The off-diagonal rectangles are therefore the connections between modules. (c) These modules can be mapped back into a brain volume. Here, different communities are represented in different colors on a brain surface

Q depends on the partition resulting from a stochastic algorithm. Different methods for community detection have been developed to search for the partition of the graph that will maximize Q . Regardless of the specific algorithm, Q is a property of the partitioned graph and is considered a measure of modularity.

The notion of a “hub” is a key concept to understand the links within and between modules. Highly connected nodes in the brain may form links to multiple communities and are called connector hubs, which are more likely to be in the medial portions of the brain (Sporns et al. 2007). Connectors play important roles in intermodular communication. Regions that maintain relatively high connections within their own community form provincial hubs (Sporns et al. 2007; See Fig. 2). Hubs are thought to serve key roles governing organization within and between brain network modules by regulating intra- and intermodular information flow (Van den Heuvel and Sporns 2013).

Evidence of Brain Modularity (Functional and Anatomical Connections)

Evidence of brain modularity is widely observed both in anatomical and functional brain networks. Modules can allow rapid and efficient sharing of information among brain regions that tend to contribute to a common set of tasks or responses while promoting their functional specialization by creating boundaries that restrict the spread of

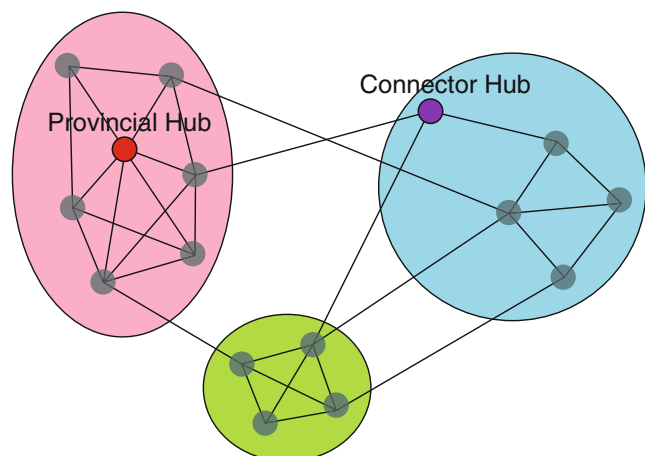
information across the entire network. Anatomical networks are more stable on shorter timescales relative to functional networks. Functional networks can be highly variable, exhibiting spontaneous dynamic changes during rest as well as characteristic modulations in different task conditions (Eickhoff et al. 2011). Some major common findings have emerged regarding anatomical and functional brain modularity.

Anatomical Brain Networks

Modular organization at the anatomical level has been studied in both animal studies and human studies. In animal studies of the cat and the macaque, whole-brain anatomical connectivity has been obtained in tracer studies (Hilgetag et al. 2000). A network partition procedure identified four subnetworks, classified as the visual, auditory, somatosensorimotor, and frontolimbic systems (Hilgetag et al. 2000). This was an early example that the general notion of modularity recovers some of the basic assumptions within functional neurology and neuroanatomy. Another study that uncovered the modularity in mouse, rat, macaque, and human connectomes showed that most communities are assortative, while others form core-periphery and disassortative structures (Betz et al. 2017). Assortative communities are those composed of nodes with similar features (e.g., numbers of connections or “degree”). Core-peripheral communities are those with a densely intra-connected set of nodes with typically fewer peripherally connected nodes. Disassortative communities are those where nodes with quite different

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Fig. 2 Schematic of hubs. A “provincial” hub (red) is a node with high connectivity with other nodes within a module. A “connector” hub (purple) is a node that connects multiple modules to one another



nodal features are associated with one another. Thus, within major networks in the brain, diverse roles in regulating information within communities can be observed, forming different putative roles in cognitive processes that are associated with variations in human performance (Betzel et al. 2017).

In human *in vivo* neuroimaging studies, modularity has been examined in anatomical networks constructed from diffusion tractography used to estimate cortical and subcortical connectivity. Examining anatomical network organization also helps us understand the functional networks commonly observed using functional neuroimaging techniques.

Modularity in anatomical brain networks can be observed early during brain development (Fan et al. 2011). The anatomical networks of early developing brains have small-world topology and nonrandom modular organization like that of adult brain networks. The so-called default-mode network is one of several major brain networks that emerges during the developmental phase from infancy and matures during brain development from adolescence to adulthood. The network activates “by default” even when a person is not involved in a task. Anatomically, the default-mode network consists of the dorsal medial subsystem and the medial temporal lobe subsystem. Like all brain networks, the default-mode network is a large-scale brain network of interacting brain regions known to have activity highly correlated with one other and distinct from other networks in the brain.

The density of connections in the brain increases from early development to adulthood, but reduces during the rest of the life-span, leading to sparsity in the module connections (Betzel et al. 2014). The brain starts developing into modules at early development, and it continues through adolescent years. As an adult, the brain is developed into modules with functional relevant roles with dense connections between modules. As we age, through the rest of the life-span, the brain experiences age-related changes leading to sparsity in the connections between the modules, potentially reducing intermodular communication and cognitive flexible performance (Song et al. 2014; Monge et al. 2017).

Modularity in anatomical networks also differs across the sexes. One study that involved a connection-wise analysis showed that male brains are structured to facilitate intra-hemispheric cortical connectivity, in the entire brain, except in the cerebellum (Ingallhalikar et al. 2014). Male brains have enhanced local, short range within-lobe connectivity. Networks in the male brain are more transitive, modular, and discrete to facilitate the within-lobe and within-hemispheric connectivity. Transitivity is characterized by the connectivity of a region to its neighbors. Male brains have higher transitivity than female brains which indicate that their brains have a greater disposition of nodes to form numerous strongly connected communities. Female brains are structured to facilitate higher interhemispheric connectivity. The connection-wise analysis was also used to examine gender differences during development. The connectivity profiles showed that adolescent and young adult males had higher intra-hemispheric connectivity and same-aged females had higher interhemispheric connectivity. This confirms that modularity in the brain networks begins from early development helping to form functionally independent modules in adult brains.

Anatomical network partitions exhibit a community structure that reproduces some functionally specialized networks, such as visual, auditory/language, somatosensorimotor, and superior parietal systems (Meunier et al. 2010). Moreover, anatomical network modularity shapes much, but not all, of the activity observed in functional modular networks (Honey et al. 2009; Hermundstad et al. 2013; Medaglia et al. 2017; Real et al. 2017; Sethi et al. 2017). However, modularity in some functional brain networks exceeds what can be interpreted from anatomy alone; thus, we need behavioral and cognitive manipulations linked to the connectivity to better understand the modularity in the brain.

Functional Brain Networks

As anatomical brain networks help us understand the stable connections in the brain that facilitate communication among regions, functional brain networks help us understand the neurophysiological dynamics of the brain. Modularity in

functional brain networks can be inferred from neural measurements such as those acquired during BOLD-fMRI imaging or from electrophysiological recording (EEG/MEG).

Functional MRI (fMRI)

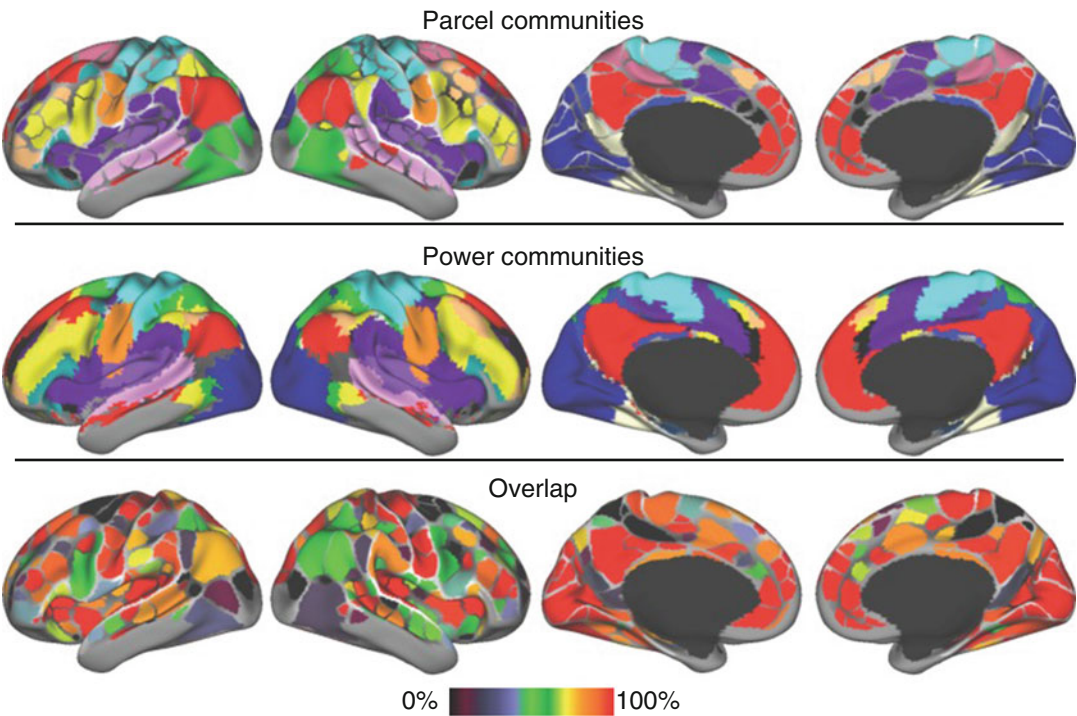
The functional modules that are observed during rest using functional MRI form identifiable resting networks that organize task-related activity. This phenomenon has been observed in a few studies (Fig. 3).

Certain brain networks such as the frontal-parietal brain network are widely recruited in a variety of cognitively demanding tasks. The dorsolateral prefrontal cortex (DLPFC) is the area in the prefrontal cortex of the brain which is involved in executive functions such as working memory, cognitive flexibility, decision-making, inhibition, and abstract reasoning. An example of the behavioral task is the combined

A-not-B/delayed response task, in which the subject finds a hidden object after a certain delay. This task requires holding information in mind, that is, using the working memory, which is one of the functions of DLPFC. Thus, the frontal-parietal brain networks are highly flexible and variably connected in the brain, which allows the frontal-parietal brain networks to use multiple networks when performing a task (Cole et al. 2013).

In another study, a region-to-region information mapping procedure was applied to real fMRI data to test its ability to infer cognitive information transfer in the human brain (Cole et al. 2016). Using a novel experimental task design meant to manipulate cognitive complexity, the brain network analysis utilized within-region vertex-level activation patterns along with vertex-to-vertex resting-state functional connectivity between regions to predict information content in each region – a measure of “flow” across the

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Evidence of Brain Modularity, Fig. 3 Module organization example from fMRI. (a) Parcel communities: Communities identified with a community detection algorithm using the boundary map-derived parcels as network nodes. (b) Network structure of the brain calculated using every

voxel as a network node. (c) Spatial overlap of the voxel-wise and parcel wise community assignments. (Figure and caption reproduced with permission from Gordon et al. 2016)

network. A region-to-region information transfer matrix was computed that represented the region-to-region information transfers at the network level. Significant region-to-region information transfers were detected in all tasks suggesting that resting-state functional connectivity is relevant to cognitive task activations due to its role in shaping task-evoked activity flow among brain regions. Thus, resting-state functional connectivity topology describes the channels of information transfer across multiple functional networks and across multiple task content domains.

Another finding by Cole et al. (2016) was that regions within the frontoparietal network collectively act as flexible hub networks to communicate task-based demands in different cognitive domains. Individual differences in intrinsic network activity flow helped explain individual differences in cognitive task activations. In addition, the reconfiguration efficiency of the functional connectivity between specific networks and the rest of the brain is significantly correlated with performance. The efficiency of some networks was related to performance on specific tasks (language task, reasoning task, and a working memory task), whereas other networks were associated with performance across multiple tasks. Efficiency in the salience network may reflect the ability to integrate and process multimodal information important for guiding behavior across a variety of task demands.

Another study showed that the cognitive control networks are global hubs, allowing for efficient information transfer across the brain. Functional and anatomical connectivity analyses illustrate that the default-mode network regions are the strongest global hubs. Using novel statistical methods with resting-state fMRI, high connectivity was demonstrated in both the cognitive control network regions and the default mode network regions. This within-module network connectivity changes can be one hallmark of cognitively relevant brain activity (Sridharan et al. 2008; Ito et al. 2017; Medaglia et al. 2018).

Brain modularity varies across people, suggesting that the amount of information segregation and integration across the entire brain

varies among people. Modular variability is related to the level of difference in the cognitive performance across individuals (Bassett et al. 2013; Yue et al. 2017). Cognitive performance is measured during cognitive processes that support sequential, goal-directed behavior.

A graph theoretic measure called the participation coefficient considers how a region's links are distributed across modules. When network links for regions are distributed across different modules (participation coefficients close to one), they help regulate intermodular communication between individual brain regions. Regions with low participation coefficients (close to zero) play a greater role in effecting communication patterns within their own module. Regions with high participation coefficients are considered parts of the default mode, salience, control, and attention networks suggesting that higher-order cognitive systems might owe parts of their functionality to the fact that their components span multiple modules and can efficiently integrate information from those sources (Betz et al. 2016).

Electrophysiological Techniques

Electrophysiological techniques are another way to measure the functional connectivity and modularity in brain networks. EEG and MEG have high temporal resolution but low spatial resolution, forming a natural complement to BOLD fMRI. Modularity in brain networks can also be observed using electrophysiological techniques. In one study, MEG electrodes were used to measure levels of synchronization in the delta to gamma frequency bands in a resting-state task in healthy individuals. Undirected unweighted graphs obtained by thresholding matrices of synchronization likelihood values showed that in the delta, theta, and gamma (>30 Hz) frequency bands, functional networks exhibited the property of "small-world networks." This showed that the brain might be organized for efficient information processing, connecting different brain areas (modules) by connections in the brain (Stam 2004). In another MEG study analyzing the connectivity structure in normal brains, brains of healthy individuals exhibited sparse connections between modules (Chavez

et al. 2010). These results suggest that modularity plays a key role in the functional organization of brain areas, maintaining relative specialization of individual modules.

EEG studies have also identified the presence of small-world networks (Micheliyannis et al. 2006). The small-world nature of the EEG networks is negatively correlated with the level of intellectual functioning. The small-world character of EEG networks is also decreased in students (aged 21–26 years) compared to children (8–12 years) in the beta and gamma bands. Thus, the “small-world” network organization is observed in this study as well from early development to adulthood (Micheliyannis et al. 2009).

Modules and the Mind

In a cognitive context, Machery suggested a “massive modularity hypothesis” (Machery 2007). The massive modularity hypothesis proposes that the human mind consists of many innate, domain-specific modules. These modules have putatively evolved due to natural selection and are functionally distinct. Many cognitive competences such as choosing one’s food habits, spatial navigation, seeing, and face recognition are supported by the modules. However, the routing and domain-integration demands in certain cognitive tasks have caused many commentators to challenge this pure modularity of the mind. For example, there are some cognitive tasks such as reading which could use many modules together or support “domain-general” and integrative processes in cognition (Carruthers 2006). Moreover, the shared variance among cognitive domains across individuals has been argued to suggest that domain-general mechanisms must exist or alternatively that the parts that compose one domain’s function contribute to multiple domains (Rabaglia et al. 2011). While these debates are ongoing, a fundamental issue remains whether and how cognitive modules map to empirically detected brain modules. However, there are several potential evolutionary advantages to brain modularity in general even if their precise cognitive relevance has not been fully clarified.

Evolutionary Origins and Selection of Brain Modularity

Brain modularity may directly or indirectly provide an organism with survival and reproductive advantages. Specifically, as described above, modularity balances specialized and integrated processing. Modular networks can engage in specialized information processing, perform focal functions, and support complex neural dynamics. In addition, modularity provides functional robustness and may in principle make the brain more naturally adaptable. Aging and disease lead to a decrease in brain modularity which reduces the ability of these systems to respond to external stress. Modular brain systems are more robust because the effect of harmful perturbations can be isolated to specific modules. In addition, if one module fails, the rest of the brain may be left relatively unaffected by having other modules perform the lost function. Thus, the brain is neuroplastic. Once a neural system evolves a basic modular architecture, it can facilitate further evolutionary adaptation. Components of modular systems can evolve semi-independently because different parts of system can be optimized separately without drastically interfering with the functioning of other parts. Moreover, different modules can be combined to create new functions. Within a modular system, information can be stored in pieces or swapped in large chunks from one module to another (Lorenz et al. 2011).

A key constraint on brain evolution concerns the energy costs and geometric constraints associated with specific brain network configurations. The wiring cost of the brain network is a fundamental trait that contributes to the brain’s modular organization (Betzel et al. 2016). The brain’s restricted energy resources form a constraint on connection lengths, which becomes skewed in favor of low-cost connections. Some features of brain modularity suggest that evolution has provided an economical wiring solution that optimizes modularity under this constraint. Brain networks favor short-range connections that densely connect nearby areas, which contribute on key aspect to the modular clustering observed

in “small-world” brain networks, facilitating local processing. However, the brain still has a small number of long-range connections which have been preserved over the course of evolution. These connections are a result of the trade-off between the formation of connections that reduce the network’s wiring cost and those that improve its functionality. Long-distance connections are extremely important for brain function, because they improve the efficacy of interregional communication and information transfer by reducing the average number of processing steps in the network, mediating communication through many hubs in the brain. This means that they are highly involved in the shortest paths across brain networks. Long-distance connections are also disproportionately observed along the brain’s longest axis, facilitating communication all the way from the anterior frontal cortex to the visual cortex. Thus, evolutionary selection has favored economical, modular brain networks that facilitate robust, flexible, and adaptive processing throughout the organism’s life-span and over evolutionary time.

Conclusion

Like many biological organisms and systems, the human brain exhibits modularity from early development to adulthood. In adulthood, the modules become refined and perform tasks under diverse demands to achieve goals. Brain modularity potentially provides evolutionary fitness by providing specialized, modifiable, and robust bases for cognitive functions. Thus, modularity in the human brain is a pervasive, dynamic, and essential phenomenon throughout the life-span.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adaptations: Product of Evolution](#)
- [Adaptive Plasticity](#)
- [All Psychology is Evolutionary Psychology](#)
- [Brain Development](#)
- [Carruthers on Massive Modularity](#)
- [Evidence for Modularity](#)

- [Modularity of Mind](#)
- [Relative Brain Size, Encephalization Quotient](#)
- [Sex Differences in Cognitive Development](#)
- [Theory of Mind and Evidence of Brain Modularity](#)

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Evidence of Intentional Killing

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Synonyms

Lethal Aggression; Lethal Conflict; Warfare; Murder

Definition

Psychological adaptations for using physical force or other lethal strategies to eliminate another individual or a group of individuals, either by oneself or as part of a coalition, with death occurring not as an accidental consequence of wounds or injuries that were meant to intimidate or subjugate.

Introduction

The question of whether or not a killing is *intentional* is problematical. In cases of nonhuman animals, we have no way of even asking whether they intended to kill another; in the case of humans, we have no way of determining objectively whether their claims of intentionality (or lack thereof) are veridical. A more objective definition of intentional killings would be restricted to those killings which appear to represent the direct adaptive function of the violent aggression that produced it, as evidence of having been shaped by selection to produce that specific outcome.

In this context, the study of lethal and nonlethal conflict and aggression aims to assess why aggressive interactions take place and who is likely to use

violence against whom, under what socio-ecological circumstances and, importantly, when killing is itself adaptive, rather than simply inflicting injuries, intimidating, and subjugating through violence. Violent behavior is usually activated to counter threats to survival and reproductive prospects. Competition and conflicts of interest over resources thus elicit aggression, potentially with lethal consequences, between rivals. Evolutionary logic is employed as a theoretical framework for investigating whether certain types of or dispositions for violent behavior are adaptive, and whether killing (not only injuring, fending off, or intimidating) serves functions or if it is a neutral or even maladaptive byproduct of such aggressive dispositions. Various different forms of and motives for lethal aggression are reviewed.

Review

From an evolutionary perspective, the capacity for engaging in violent conflict with conspecifics is understood as an adaptation and not as pathology (Lorenz 1966; Wilson 1978). Killing itself, however, has been proposed to frequently be the dysfunctional tail of a distribution of adaptive violent responses; in this view, the killing is a byproduct of the violent behavior being deployed to coerce the behavior of a conspecific, where death is not necessarily the objective of the violence (Daly and Wilson 2003; Ferguson 2011). As such, some argue that killing can be seen as too drastic a resolution for interpersonal conflicts, and not what adaptive mental mechanisms were selected to lead to in terms of outcomes. However, a specific adaptation view is supported by several lines of evidence indicating that killing does in fact facilitate gene-copying success in various circumstances, as we review below, although less extreme behavioral outputs of the same aggressive motives (e.g. competition for resources and for mates, defense of honor and reputation, etc.) may often be sufficient to promote reproductive success.

To study aggression and killing in sufficient detail, the distinction is frequently made between in-group and out-group killings (de Waal 1989).

This distinction is not only scientific (*etic*) but also culturally (*emic*) most societies discriminate between attacking and killing within the community and attacking and killing outgroup members. In many cultures (including our own), the latter form of aggression is frequently seen as positive and commendable, and thus as a service to the community, whereas within-group attacks are morally condemned and agents are seen as perpetrators, murderers, abusers, criminals, and deviants, rather than as courageous warriors and heroes fighting for a cause. The differences in attitudes and terms used to view and describe these two forms of conflict betoken a fundamental difference in the psychology of aggression. Within-group attacks may reduce cohesion, whereas between-group attacks may motivate the unity of the community and facilitate the pursuit of common goals. Thus these different forms of aggression and killing are theorized to be subjected to distinct selection pressures and to affect fitness differently, as different socioecological circumstances and adaptive problems are involved in within- and between-group conflicts.

Reasons for Conflict and Killing Within Groups

As with other manifestations of conflict, discussing the nature and possible adaptive functions of intragroup aggression remains a highly controversial topic. Descriptions of socioecological pressures that select for intimate partner violence, within-group coalitional violence, or infanticide still generate heated discussions concerning the forces that shape such phenomena phylogenetic, their status as pathological, and the phylogenetic ubiquity of these behaviors. For researchers not endorsing an adaptive view of intragroup lethal aggression, it is interpreted as either (1) the maladaptive byproduct of exacerbated individual aggression (Daly and Wilson 2003), (2) a manifestation of failed impulse control or an underlying psychopathological condition (Gottfredson and Hirschi 1990), or (3) an abnormal social behavior associated with unusual demographic pressures or a mismatch between ancestral environments of adaptive relevance and current environments (such as modern, industrialized societies in humans, or captivity in

nonhuman primates; Ferguson 2011). Furthermore, for this approach, high reported rates of fatal violence within primate species are considered an uncommon phenomenon, with researchers behind it proposing that the number of cases claimed is an overestimate based on indirect and inferential methods of tally.

Alternatively, special adaptation hypotheses of within-group killings consider the fitness benefits obtained by attackers (Buss and Duntley 2003; Hrdy 1979). Adaptationist explanations of the intragroup aggression that may lead to killing critically depends upon an assessment of the costs and benefits of life-threatening violence. These assessments must be made in comparison and contrast with any other available instrumentalities for resolving social conflicts. Furthermore, the cost-benefit tradeoffs that lead to lethal intragroup aggression may vary from individual to individual, where one individual might be more liable to incur lower costs or more likely to accrue higher benefits than another by employing interpersonal violence. These variations might be attributable to the individual costs and benefits of the aggression, but they might also be attributable to those of the alternatives to aggression. For example, if one individual is deficient in social skills or general cognitive capacity, they might be more prone to adopt a violent than a nonviolent alternative to solve challenges due to individual incompetence in solving the adaptive social problem nonviolently. These considerations lead to an examination of the sociodemographics of lethal aggression within groups.

Examples of possible fitness benefits of killing are ascending in the dominance hierarchy, achieving high status, eliminating rivals who would otherwise compete for resources or mates, decreasing the coalitional power of competitors, and gaining access to food patches. Lethal aggression within groups is not restricted to intrasexual aggression between adults. Full-grown individuals also target unweaned younglings, with attackers obtaining benefits such as restarting the ovarian cycle of females who are unreceptive during gestation or lactation, acquiring and retaining mates, and decreasing competition. Empirical support for these adaptive hypotheses

have accumulated in the scientific literature (► [“Humans: Within-Group Conflicts”](#) in the chapter by Fernandes et al., this volume; ► [“Non-human Primates: Within-Group Conflicts”](#) in the chapter by Peñaherrera-Aguirre et al., this volume).

Intragroup hostility jeopardizes the successful implementation of long-term mating strategies, continued investments among kin, and the maintenance of long-term cooperative and community efforts, thus reducing interindividual cohesion within groups in several senses (Figueredo and Jacobs 2009). However, the maintenance of social features is prioritized by individuals and groups in relatively stable, predictable environments in which cumulative and future payoffs to current investments can be prioritized. Conversely, within-group hostile and deviant behavior is expected to be a feature of individuals who have little to lose and who can have little certainty of future rewards of long-term investments in cooperation, and in familial and social cohesion. As such, higher rates of interpersonal violence are observed to be associated with risk-proneness, impulsiveness, and overall fast life history.

Reasons for competition for resources or partners which may elicit aggressive behavior exist mostly within each sex, as the two sexes differ to a considerable extent on what they aim to obtain (Buss and Shackelford 1997; Muller and Wrangham 2009). Considering the sex differences in reproductive capacity and reproductive cycles, variance in reproductive success is more variable among males than among females; mammalian males can be expected to compete more for reproductive access to females than the reverse. Males are thus more likely than females to be physically violent, be it in interindividual interactions or in warfare between groups, being equipped with anatomical, physiological, and psychological features that permit more successful violent behaviors. Females do not lack motivations for competition and aggression, and are clearly observed to engage in such interindividual interactions across primate species and human societies, due to basically the same socioecological predictors as males. Between-sex altercations, however, clearly lead to a preponderance of

injuries inflicted upon females, due to differences in strength and in the capacity to sustain damage. Intense competition among males, nevertheless, is not widespread across mammal taxa, rather being more prevalent in species with promiscuous or polygynous mating systems. Among humans, it can be expected to be more prevalent among those which prioritize short-term mating strategies and which are exposed to less stable and predictable social ecologies (Figueredo and Jacobs 2009).

Infanticide is not frequently observed in primate species and has never being observed in the wild in some taxa (e.g. orangutans; Knott et al. 2010). It is nevertheless present in diverse mammalian clades and human cultures. Infanticide is most commonly committed by unrelated males or by mothers. Proposed sources of adaptive value (Daly and Wilson 1988; Hrdy 1979) for infanticide of unrelated offspring include elimination of a competitor's genes from the population's gene pool and increased access to potentially fertile females who would otherwise be investing in the offspring rather than in reproductive activity. In contexts of infanticide of related offspring, potential sources of increased fitness include: (1) higher chances of parental survival, considering the life history tradeoff being parental and offspring health (especially in cases of poor parental health, famine, abandonment by one of the parents and absence of social support); and (2) increased chances of parental reproductive success, in cases of ill-timed, severely handicapped, or supernumerary offspring (as sacrificing an infant under such conditions would permit investing more resources in other offspring or in future reproduction). As such, infants at greater risk of infanticide are those who: (1) exhibited noticeable physical or mental problems; (2) were born too close in time to older siblings or in too large a litter, imposing demands on limited parental resources; (3) were born to a mother with little or no social support, especially if she is young and can thus prioritize investments in future reproduction, sacrificing current but unfavorable reproductive output; and (4) are more exposed to unrelated adult males, or if adulterous conception is suspected by the investing male. To reduce the likelihood of infanticide of their offspring by unrelated males, adult female primates of many taxa have been argued to evolve

reproductive strategies that couple promiscuity (thus leading possibly infanticidal males to believe that the female's offspring is theirs) with subtle morphological or behavioral cues that conceal ovulation (thus preventing male knowledge of fecundity; Knott et al. 2010).

Interactions between individuals with little relative genetic relatedness is a further risk factor for violent behavior, as indicated by higher rates of physical abuse and homicide in households in which unrelated persons live together (Daly and Wilson 1998). Nepotistic care and protection, as motivated by kin selection, can be seen as a force that reduces the likelihood of aggressive interactions among relatives compared to aggressive interactions among individuals with lower relatedness. However, within-family aggressive conflicts do occur, especially over issues of partitioning of familial resources, if conflicts of interests and direct benefits outweigh indirect benefits of favoring kin due to genetic relatedness.

It has been proposed that regulatory (i.e., leveling) social mechanisms such as public opinion, gossiping, criticism, ostracism, expulsion, and desertion diminish the risk of lethal aggression (Boehm 1999), as they may be other effective ways of eliminating or reducing the success of the competition. Examinations using cross-cultural and cross-species data have found support for this hypothesis.

Reasons for Conflict and Killing Between Groups

Competition for resources is a key feature of the evolutionary process. Scramble competition involves racing to consume resources before another individual or group can access them; contest competition involves interfering with the activities of a rival individual or group to monopolize resources, and may entail direct aggression. Contenders maximizing fitness clash with conspecifics for access to mates, cooperative partners, foraging, and resting spaces. Victorious individuals, however, may not only obtain benefits from such an endeavor, but they may also accrue several costs (e.g., risk of injury, time invested in the conflict that could be allocated to other activities, retaliation to kin or allies). This dynamic is not restricted

to animals living within one group, as intense aggression leading to clear power differentials and dominance relationships is also expected between groups (Wilson et al. 2014). Depending on the severity of the conflict, the damage inflicted on contenders can have a lethal outcome.

Early theories considered intergroup killings to be exclusive of human societies living in complex political systems such as nation-states. However, subsequent observations with subsistence societies and nonhuman primates concluded that lethal attacks across communities were not uncommon, and were in fact pervasive (Guilaine and Zammit 2008). The implications of these reports for understanding the origins of violence and intergroup aggressive conflict in human societies were met with both skepticism and opposition, as some hypothesized that the impact of modern societies on the ecologies in which studies were conducted could account for the presence of intergroup violent conflict.

As in the case of intragroup killings, cumulative nonhuman primate and mammalian data in general indicate that intergroup killings are not an outcome of human disruption of natural social ecologies (► [“Humans: Between-Group Conflicts”](#) in the chapter by Fernandes et al., this volume; ► [“Nonhuman Primates: Between-Group Conflicts”](#) in the chapter by Peñaherrera-Aguirre et al., this volume). Patterns of patrolling and lethal attacks have been found to be strategic and fitness benefits appear to be obtained through attraction of new females, induction of shorter interbirth intervals, and access to foraging patches. Rates of intergroup lethal aggression vary across mammalian taxa and are not equally affected by human presence and interference.

For decades group selection theories were largely disregarded as possible explanations for any kind of behavior, including intergroup conflict and warfare. However, more recent interest in multilevel selection models have somewhat revived the formulation of hypotheses that rely on the idea that groups can function as the unit of selection, based on the notion that phenotypes that benefit the community may be favored in spite of negative impact upon individual fitness (Choi and Bowles 2007; Woodley and Figueredo 2013). Thus several

researchers posit that ingroup altruism and intergroup warfare may have coevolved through biological and cultural group selection, with the latter being a more plausible explanation for conflicts that includes larger numbers of individuals than smaller-scale confrontations (Richerson et al. 2016). Biological and cultural group selection are not independent and separate phenomena, but are rather proposed to interact through gene-culture coevolution. The application of any form of group selection theory is however met with resistance from several fronts in evolutionary biology, anthropology, and psychology.

Warriorship (i.e., individual engagement in between-group conflicts) has also been proposed to be positively associated with individual fitness in prestate human societies (Chagnon 1988; Glowacki and Wrangham 2013). Warriors have been argued to be motivated by the opportunities for looting and capturing as a consequence of victory. Hence, by raiding, feuding or battling rival groups, warriors are thought to gain material and social benefits which can boost individual fitness. With respect to the former, some of the coveted commodities include food, weapons, tools, raw materials, livestock, ornaments, physical trophies, and territorial expansion. Similarly, captives can be taken as slaves or for execution (such as human sacrifices). Social stratification is considered as one of the cultural factors that motivate sparing the lives of the vanquished rivals. By socially integrating individuals from the defeated group, conquerors obtain economic benefits from the labor of captives, although this appears uncommon. Moreover, executions of prisoners have been considered to bolster social cohesion and legitimize the authority of leaders. It has also been hypothesized that warriors will engage in lethal violence as means for obtaining social benefits such as increasing their status in the group, accumulate wealth (not obtained during incursions), improve their marrying opportunities, obtain public recognition, and expand their network of allies. As such, different components of multilevel selection (such as individual and group selection) may interact to explain between-group aggressive conflict and killing.

Conclusion

A didactic taxonomy of aggression, lethal and nonlethal, permits examining whether certain types of violence are special adaptations, or simply byproducts of other adaptations, and at what level they are selected (e.g., with respect to individual or group-level fitness). By comparing studies of modern, industrial populations with data from prestate societies, modern or otherwise, and with nonhuman primate data, it is possible to conclude with considerable confidence that aggressive interactions among individuals and among groups are neither a feature only of civilizations, nor are they exclusive to humans, nor are they induced by a mismatch of modern or captive environments and the social ecologies to which species or populations were adapted. Killing itself may not always be functional outcome of adaptations for aggression, but neither should it be dismissed as a universally maladaptive phenomenon. The evidence strongly favors the hypothesis that intraspecific killings often have adaptive consequences for individuals and groups.

Cross-References

- ▶ [Aggression](#)
- ▶ [Conditions Required for Evolution of Warfare Adaptations](#)
- ▶ [Evolutionary Theory and the Causes of War](#)
- ▶ [Evolved Psychology of Warfare](#)
- ▶ [Homicide](#)
- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Humans: Within-Group Conflicts](#)
- ▶ [Infanticide and Parenting](#)
- ▶ [Nonhuman Primates: Between-Group Conflicts](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)
- ▶ [Variability of Aggression](#)

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Evoked Culture

► Ecology

Evolution

- Daniel Dennett: A Review of His Evolutionary Work
- Evolution of Adaptations
- Evolutionary Paradox: Adoption
- Morality
- Paternity Uncertainty and Investment in Sons and Daughters
- Psychological Determinism
- Resemblance
- Sex Differences in Emotional Communication
- Silver Fox Domestication Experiment

Evolution and Guarding Behavior

► Daughter Guarding

Evolution and Memory

► Evolution of Memory, The

Evolution and Self-Awareness

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Synonyms

Consciousness; Self-consciousness

Definition

An ability to think about one's own mental states.

Introduction

It seems clear to me that my subjective mental states are my own. Furthermore, this act of introspection shows that I have some ability to think about my mental states. I would say that I am self-aware. Furthermore, my experience indicates that most humans have such mental states of their own, including self-awareness. The question thus arises where do these subjective mental states, including self-awareness, come from? What causes or explains their presence and content? Has this human capability evolved?

From the earliest times, discussions of consciousness have been closely related to those of free will. Volition is still for many people a definitive attribute of consciousness, which in turn is a definitive attribute of humans. Both volition and consciousness, in turn, are closely allied with rational thought. Often these three capabilities are combined as the distinctive characteristics of the human soul. For many people, the attributes of these capabilities seem entirely apparent by introspection. For all of these reasons, discussions of self-awareness and volition have often become doctrinaire, for instance, in both Judeo-Christian-Islamic-Vedic morality and Brahmanic-Buddhist-Taoist-Gnostic transcendence. Human and nonhuman animals have seemed to occupy their respective rungs on a *scala*

naturae, each of which had its distinctive attributes augmenting the rung below and subsumed by the rung above. Consciousness and its concomitant volition and rationality were the attributes that separated humans from all lower forms of life.

Modern western philosophical and theological discussions began in the sixteenth and seventeenth centuries with fundamental controversies between Christian sects about divine grace and predestination and with Descartes' subsequent dictum "Je pense donc je suis." In recent centuries, contrasting positions have developed between environmentalist and nativist theories of human perception (or between sensory and mental determinants of thought). These trends have culminated in an emphasis either on culture or on intrinsic structure as the predominant determinants of consciousness and language. In all of this history, because it was assumed that the uniqueness of humans depended on consciousness and self-awareness, there was little attention to the possibility of their evolution.

Continuity Between Human and Nonhuman Animals

Darwin's revolutionary book, *The Expression of the Emotions in Man and Animals* (1872), for the first time, proposed some continuity between the minds of humans and other animals as indicated by their respective behaviors. Since then, studies of learning and instinct, as well as the ontogeny and phylogeny, of behavior have had progressively increasing influence on thinking about consciousness and awareness. Particularly relevant have been experiments that explore the limits of nonhuman intelligence. These experiments have raised difficult questions about the relationships among language and thought and learning and consciousness.

For instance, studies of a number of nonhuman animals (especially chimpanzees, other apes, parrots, and dolphins) have indicated that these organisms can respond to complex stimulation, such as encoded queries and requests, in ways that resemble our own use of language

(Savage-Rumbaugh et al. 1998). Just as we routinely attribute consciousness and will to other people by empathy based on their behavior, we are inclined to attribute these capabilities to the subjects of these experiments. These studies are unusual among biological and psychological experiments in two ways: their small samples of subjects and their intensive involvement of humans (as opposed to experiments with many comparable subjects and largely mechanical interactions with them). The small sample is justified because the interest is in the potential rather than the norm of behavior. If one individual chimpanzee can converse like a human, that alone makes the point.

The lack of replication in combination with intensive human interactions with subjects raises further issues. Each of these studies has been conducted in one laboratory and directed by one principal investigator or a small team. No team has ever carefully replicated the procedures of any other. Nevertheless, there has been an accumulation of similar results with similar protocols, so that it is becoming more difficult to exercise broad skepticism about the kinds of responses evoked.

There is an even deeper controversy about language-like responses by nonhuman animals. Interpretations of these responses often devolve into a polarity between attributing the observed responses to no more than thorough (rote) learning as opposed to the spontaneity or creativity that human language seems to show (Lutz 2009). There are twin problems here – it is difficult to distinguish complicated from random patterns of responses, and it is also hard to distinguish repeated from rote responses. Infrequent, unprecedented, and unrepeated responses, just what we look for in consciousness, cannot be easily shown statistically to differ from accidental or random responses. On the other hand, statistically significant patterns of response require replicated results, which then come to resemble thoroughly learned or rote responses.

The issue of thorough learning, as opposed to volitional thought, is a pervasive problem in comparative studies of consciousness. Consider another example of convergence in mental abilities of human and nonhuman animals – abilities to respond to oneself in a mirror and to attribute

mental states to others (and by extension therefore to oneself). Responses to mirrors are no doubt tricky. Many animals respond to mirror images (itself a remarkable capability) as if the image were another individual of its species, perhaps a rival evoking aggression. Chimpanzees in contrast behave as if they see themselves in a mirror, for instance, by touching unexpected marks on their faces that they see only in a mirror. Such responses to mirrors, which seem normal to most humans nowadays, indicate a remarkable advance in mentality. Yet this ability clearly requires learning. Humans with no experience of mirrors or photographs of themselves, as anthropologists often report, do not easily recognize their images. And anyone can try the experiment of directing movements (or even identifying oneself) in a *mirror image of a mirror image* of yourself, an experience that reveals uncomfortably that mirrors require considerable practice to master. Even recent experiments in which chimpanzees without a direct line of sight can use a mirror to sign to a human recipient, but do so only when the recipient is looking at the mirror (Lurz et al. 2018), are subject to the same questions about thorough learning. Evidently humans nowadays master some superordinate associations involving mirrors that most nonhumans have not, but humans have not mastered all the possible associations. Nor is it easy to determine whether or not some nonhuman animals have comparable mastery (De Veer and van den Bos 1999).

Actions that result from rote learning raise another question about consciousness. Humans often master well-practiced tasks to the extent that they are performed unconsciously. Conspicuous examples are actions or sequences of actions performed routinely, such as making a cup of coffee each morning. Yet on any one occasion, the awareness of having performed an action can escape us, for instance, when we are perplexed about whether we had already added the sugar. Certain actions, swallowing and walking, for instance, consist of complex muscular coordinations that we are seldom aware of, although this lack of awareness can cause serious accidents.

Furthermore, this issue of the criteria of consciousness merges with the issue of private

sensations. How can we know, other than by imputations based on coarse empathy, what another organism feels or even senses? Introspection is the source of these insights. How can it be determined that another organism, other than myself, is conscious, acting by will rather than rote, in the same way I do?

Neurophysiology of Consciousness

An obvious possibility for recognizing consciousness is to investigate neural activity during presentations of stimulation. Neurobiologists can now detect in detail the neural events that result from sensory stimulation, both those sorts that we normally are aware of, for instance most exteroceptive sensation, and those we are normally not aware of, for instance most proprioceptive sensation. This approach can extend to neural events in the brain. Physiologists now know a great deal about local areas in the brain, even particular neurons, that are specialized for analyzing sensations, controlling muscles, generating emotions, consolidating memories, comprehending or producing language, even recognizing a visual pattern as a human face. Centers in the brains of nonhuman animals have similar functions (the centers for learning and producing songs by birds are particularly well documented). Is there such a center for consciousness?

Suggestive in this case is an experiment that seems to reveal a half-second or so delay between the initiation of a spontaneous action, on one hand, and awareness of it, on the other (Libet et al. 1983). Because action precedes awareness, it appears that action triggers awareness, rather than vice versa, so that consciousness is the effect of our actions rather than their cause. Volition becomes an illusion, and consciousness seems to be a distinct operation, a candidate for localization in the brain. Some qualifications are in order, though. Subjects record their awareness of the action by remembering the exact position of a spot moving rapidly around the face of a clock. Recording this visual stimulus in memory is itself a response to the spontaneous decision to act, just as much the act itself is a response to this decision.

Such an experiment thus does not necessarily reveal that action precedes volition. Instead each of these two operations requires different neural events lasting finite, and evidently not exactly equal, amounts of time. Furthermore, the memory is encoded in language, which becomes the sole means of obtaining the datum actually recorded by the experimenter. Again we are back to questioning how we can know what another organism feels or thinks, unless that organism tells us in some way.

The inability so far to find a locus in the human brain specialized for consciousness has led to proposals that awareness results from distributed networks of neural interactions. Computer programs for learning complicated tasks often employ “neural networks,” one or more intermediate layers of “cells” that reciprocally influence each other’s activity, between an input (sensory) layer that provides initial conditions and an output (motor) layer that represents the response. Further programming defines the utility of any response and uses this evaluation to regulate the stability or variability in the properties of cells in the intermediate layers. An arrangement that produces responses with low utility is thus allowed to change (mutate) before subsequent trials; those that lead to responses of high utility are stabilized (saved), in other words, learned. Although these computer programs are called “neural networks,” it is still not clear how closely they resemble operations in a brain. Only at a superficially general level can we suppose that distributed operations in the brain share the features of computational “neural networks.” The specifics of neural processing to produce consciousness remain as elusive as ever.

Continuity Between Brains and Other Machines

The relationship between consciousness and language arises in proposals to distinguish humans from other machines – or by extension to determine whether or not any machine is conscious. Turing’s test and Searle’s modification of it are examples (Dennett 1991; Searle 1997). Each

involves a judge posing problems to unseen contestants. The issue is whether a human (conscious) contestant can be distinguished reliably from a nonhuman (unconscious) one. Searle contends that Turing's test would not distinguish between a human who understood a language and one who just followed rules by rote. It thus could not distinguish a conscious human from an unconscious machine. By extension, it is worth emphasizing, it would also not distinguish between a conscious and an unconscious machine. A fundamental question here is whether or not conscious behavior, such as language, is strictly rule-following or not. And thus whether or not humans are strictly rule-following machines or not. We might also extend this question to whether or not machines do or do not strictly follow rules.

Noise as a Determinant of Consciousness

These conundrums about the relationships of volition, consciousness, and learned and unlearned behavior all intertwine with issues of language and even communication in general. Any evidence about an organism's consciousness depends largely, in the final analysis perhaps exclusively, on what it reveals in its behavior. The evolution of consciousness thus depends in a fundamental way on the evolution of communication. It is thus remarkable that noise influences the evolution of communication in a way that provides a straightforward explanation for the evolution of subjective experience (Wiley 2015).

Noise, as Claude Shannon first emphasized in his revolutionary analysis of information, is anything that results in errors by receivers during communication (Shannon and Weaver 1963). Noise can consist of extraneous irrelevant background stimulation that mixes with signals during transmission from signaler to receiver. This is what is commonly thought of as noise. Noise, in Shannon's sense of errors by receivers, can also result from degradation and attenuation of signals during transmission. It can also result from irregularities in a signaler's nervous system which introduce irregularities in its signals; and it can consist of analogous irregularities in a receiver's

nervous system which introduce irregularities in its perceptions. As a result of any of these sources of noise, a receiver's perception only imperfectly reflects a signaler's actual situation.

To apply this approach to the evolution of consciousness, note that the dilemma confronting a receiver of signals in communication is strictly analogous to that confronting a perceiver of external objects and events in general. Noise in perception can result from mixing of sensations from irrelevant sources, from degradation and attenuation of stimulation during transmission, and from unpredictability in a perceiver's own nervous system.

At the moment of perception, a perceiver has no way to determine whether or not the perception corresponds to a particular external situation or to an erroneous illusion. All the perceiver knows at the moment is its perception. Nevertheless, memory of repeated perceptions, especially in combination with communication with other individuals, could reveal these discrepancies. In this way such an organism, capable of thought and language, could develop a sense that its own perceptions differed, in some respects and on some occasions, from those of others. Both some ability for abstract thought (a capability for generalization and discrimination) and some ability for communication of such abstractions seem crucial for this awareness. Otherwise individuals would be isolated within the shell of their own perceptions. They might well learn to avoid or to prefer certain perceptions, but it would be difficult to compare them with other individuals'.

Because of noise in perception or communication, a perceiver or receiver must make a decision every time it acts on any sensation. It must decide whether the sensation warrants a response (and also which response). In other words, it must decide whether a sensation is a signal (with some relevance for the perceiver) or noise (with no, or misleading, relevance). Noise creates the unavoidable possibility of two incompatible kinds of errors in perception, false alarm or missed detection. All perceivers, even those organisms such as sponges or bacteria with no nervous system like ours, are perforce decision-makers.

Signal detection theory (Macmillan and Creelman 1991), based on Shannon's theory of

information, and decision theory allow a formal mathematical analysis of the performance of any perceiver in the presence of noise. Because of the two conflicting sources of error, a perceiver is in a double bind. It cannot reduce one source of error without increasing the other. As a consequence, it can only optimize its decision in particular circumstances and cannot attain perfect performance. This optimization leads to a fundamental conclusion that *perceivers cannot escape from noise*; their only option is to optimize their responses in each situation.

This is what organisms actually do. All must deal with unpredictable contingencies. Evolution by natural selection provides a mechanism that can optimize, within limits, neural capabilities to make decisions that promote survival and reproduction for the organism. In a fundamental way, nervous systems are decision-making organs devoted to this task of responding efficiently to conflicting possibilities of stimulation. Every organism must confront its subjectivity with some decisions, no matter how crude the mechanism.

Awareness of subjectivity in perception, however, requires a nervous system to form higher-order associations. When these connections between subjectivity and objectivity reach awareness, we can expect consciousness. The process requires a sufficiently complex nervous system. The logical inconsistency of self-reference might indicate that no such system can ever be completely aware of all its operations, even its degree of self-awareness.

Humans clearly have achieved the highest performance so far. Yet the evolution of this capability seems likely to have emerged gradually by successively more complex mental associations. Whether or not other organisms (great apes and bottle-nosed dolphins come to mind as possibilities) have reached states of consciousness comparable (although perhaps not identical) to those of humans and whether or not some future organism or some other deterministic machine might eventually reach higher levels of self-awareness are questions for the future. Perhaps humans have reached an adaptive peak in the evolution of consciousness, so further advances might require brains evolved in a new anatomical/physiological direction.

Conclusion

The mathematical analysis of optimal behavior in noisy situations thus indicates that (1) noise is an inescapable component of communication, (2) subjective awareness of self is a higher-order association of perceptions and responses, (3) decision-making is fundamental component of all communication and perception, and (4) both processes are as unpredictable as the unavoidable noise. An advantage of this analysis of the evolution of communication in noise is the framework it provides for addressing the questions posed at the start of this essay.

To account for the source and the content of self-awareness, previous discussion has always relied either on supernatural intervention or on vague neural operations on purified sensations. Supernatural intervention of course obviates any mechanistic explanation, including evolution. Response to pure sensations, on the other hand, leaves each organism encased in its own perceptions, without a way to distinguish between subjective and objective events. The evolution of noisy communication, in contrast, shows that self-awareness (consciousness) results directly from the operations of nervous systems exposed to noisy sensations. We can expect that the neural correlates of self-awareness will depend not only on sensations of interest to an organism but also on the noise mixed with them. The resulting explanation for self-awareness requires no unnatural or unspecified components.

The principal conclusion from such an analysis is that the problems of consciousness might reduce to problems of evolution, signal detection, and neurobiology, all highly mathematical and physical, and thus mature scientific fields. Discussion of the mechanisms of consciousness might therefore migrate from philosophical to scientific discourse.

Cross-References

- [Evolution of Communication](#)
- [Evolution of Free Will](#)

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Evolution and the Theory of Games

► Evolution of Cooperation

Evolution of Adaptations

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Synonyms

Adaptations; Changes in adaptation expression; Evolution; Natural selection

Definition

Adaptations, characteristics that enhance the survival and/or the reproductive success of an organism, change their means of expression over time.

Introduction

Like organisms, adaptations evolve. Adaptations vary from physical characteristics and traits, such as gills, hair, organs, etc., to behaviors that aid the survival and reproductive success of an organism. Although an organism's physical features have been the exemplar of adaptations, behavioral and mental features as evolutionary adaptations are now under scientific scrutiny. Today, the field of *evolutionary psychology* takes initiative to shed light on human psychological adaptations despite that Charles Darwin, discoverer of biological evolution via natural selection, depicted the relationship between physical and mental adaptations back in 1859.

Evolution: Change over Time

Since evolution's inception, the term has been recklessly connoted with biological evolution via natural selection. Although biological evolution is a representative of evolution, it is not the only one. *Evolution* is a general word for *change over time*, and it is widely accepted that nothing remains uniform forever; therefore, everything changes when given the sources to. Adaptation expression is malleable.

Physical features that enable an organism to adapt to its environment are unlikely to have always been adaptive. For example, the human bellybutton and the appendix are not considered to be *adaptive*. Moreover, the appendix could even be considered maladaptive when it precipitates appendicitis. When a physical or mental feature is a *mismatch* or when it does not align with an organism's ability to adapt to its environments, it may be considered as a neutral or maladaptive trait (Geher 2014).

The expression of adaptations is subject to evolution. It is parochial to reduce the expression

of adaptations to only physical or biological properties. Actions and behaviors that practice, utilize, or enhance an organism's biological traits and abilities produce an advantage over others that do not.

Biological Adaptations

Biological adaptations are physical features that facilitate the survival and/or the reproduction of an organism. The loose and attached jawbones in some snakes, for example, permit them to devour prey larger than their bodies (Futuyma 2009). Some scientists suggest that human body height evolved for thermoregulation in hotter environments, locomotion and flexibility, and mobility (Migliano and Guillon 2012).

A more recently discovered human biological adaptation is pregnancy sickness in women, sometimes referred to as morning sickness. The healthy development of the fetus becomes at risk when exposed to toxins and pathogens within the mother. During the first trimester, pregnant women commonly experience nausea and vomiting. Regurgitation of potentially harmful foods is reckoned as a biological adaptation (McElroy and Townsend 2015).

Evidence of Psychological Adaptations as Evolved Adaptation Expressions

In *The Origin of Species* (1859), Darwin concluded that “psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation,” which was one of the first positions that mental qualities are also adaptations. *Psychological adaptations* are generally considered to be the results of biological adaptations, according to evolutionary psychologists. Every action, belief, and thought relates to the neural circuits and chemicals that constitute the mind (Cosmides and Tooby 2000).

Ants display extraordinary demonstrations of altruism, the selfless acts for others. Rather than solitarily seeking routes to travel across dangerous

obstacles, such as water, ants will cling on to each other in order to create a bridge molded of their living bodies for themselves to cross (Futuyma 2009). Instead of evolving a physical trait like wings to fly, ants acquired inherent tendencies that take advantage of their physical size to prevent water from penetrating their *living bridge*.

Numerous evolutionary scientists consider instincts to be the foundation of psychological adaptations. Distinguished emotions in humans like fear, anger, jealousy, and happiness may have been acquired due to the pressures encountered in one's evolutionary history. Leda Cosmides and John Tooby (2000) posit that each emotion is elicited by different and specific circumstances. For example, fear when crossing a bridge hundreds of feet above land is a psychological adaptation to demotivate one from being too indolent and audacious while crossing.

Other evolutionary psychologists posit that cognition skills derived from the cerebral cortex gave rise to human's cultural cornerstone, language. Linguistic skills would enable the prehistoric humans to socialize and communicate vital information. Increased efficiency in communication and socialization is believed to have contributed to the larger band size that early *Homo sapiens* or modern humans lived within (Harari 2015).

Higher cognitive function is also theorized to have given rise to *cheater-detection* and *mate selection*. Cosmides and Tooby (2000) accounted how critical it would be in a society of social humans to be weary of those who lie and act as *free riders* to obtain resources unjustly. The psychological adaptation of an enhanced memory for faces of cheaters over non-cheaters deploys pre-existing biological features in the brain for facial perception and memory.

Mate selection is considered by evolutionary psychologists to be a critical evolutionary deed. Relative to most animals in the animal kingdom, *Homo sapiens* are selective as to whom they copulate with. Selecting a partner who exhibits qualities of poor parenting could be detrimental to a helpless and premature child. Allan et al. (2012) found that heterosexual women have significantly better memory for more masculine faces of men

than less masculine ones. Masculine facial features are a proxy of testosterone, a sex hormone that is associated with immunosuppressant effects, which would signal higher genetic quality in a mate. Like cheater-detection, the biological traits in the brain that enhance memory for particular individuals serve as a new means of expression of an evolutionary adaptation.

Conclusion

Evolution strictly means *change* and that everything is subject to change. Adaptations described by evolutionary biologists ranging back to Darwin are no exception to this postulate. An organism's physical characteristics have been gradually molded into adaptive, neutral, or maladaptive traits that increase in efficacy when synchronized with instincts or behavioral traits. It is necessary for scientists to properly construe what an *adaptation* truly is and how it can be expressed in all living specimens. It is fortunate that evolutionary psychological science stands at the forefront of the investigations of psychological adaptations. After all, what it means to be human is the product of these evolved adaptations.

Cross-References

- [Environment of Evolutionary Adaptedness](#)
- [Mismatch](#)

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Evolution of Altruism

- [Helping and Genetic Relatedness](#)
- [Helping and Inclusive Fitness Benefits to Helper](#)

Evolution of Altruistic Cooperation

- [Problem of Altruism](#)

Evolution of Auditory Perception, The

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Synonyms

[Direction of sounds](#); [Mammalian ear evolution](#); [Reichert-Gaupp theory](#)

Definition

The evolution of the mammalian ear and understanding of sound.

Introduction

In order to better comprehend the evolution of ear perception, one must understand how sound is conducted until it reaches the ear. Environmental changes have imposed a need for the mammalian ear to evolve in order to enhance the survival of species. Several researchers have attempted and succeeded to unlock the evolutionary mystery and history of the mammalian auditory system and perception.

Distinguishing the Direction of Sounds

To understand the direction of sounds, we need to understand how sound is conducted. Usually, sound is created when an object is vibrated. The vibration travels through the surrounding medium, which is usually air, as pattern of changes in pressure which eventually is heard as sound (Moore 2001). Sound is called a pressure wave for the reason that when the molecules of the ear come closer, the pressure increases resulting in a process called compression; when the molecules move further apart, the pressure decreases resulting in a process called rarefaction (Oghalai and Brownell 2012). According to a theorem by Fourier, the sound could be described in sinusoids, which is an analysis of complex waveforms. A sinusoid resembles the sound produced by a tuning fork, which is often called a simple tone, or a pure tone. Each sinusoid is called a Fourier component of the sound and a magnitude plot of the components as a function of frequency is called a spectrum. The result of a Fourier analysis is to produce the spectrum of the soundwaves by splitting the waveforms into component sine waves of different frequencies (Moore 2001; Pickles 2012). There are two important variables in each sound wave, the frequency and the amplitude or intensity (loudness). Frequency is the number of waves that passes a point in a second and is measured in cycles per second, otherwise called hertz (Hz). The amplitude or intensity is related to the magnitude of the produced movements, and is measured in decibels. The traveling sound wave relies upon the

pressure of the environment which is the medium in order for the sound to be heard. This is called impedance of the medium. If the impedance is high, high pressures are needed to yield a definite velocity (see Pickles 2012, pp. 1–19).

The very first step of the hearing process is when the outer ear captures the sound waves which travel to the eardrum and cause it to vibrate. In the middle ear, the ear bones convert the air-borne vibrations of the eardrum into fluid-borne vibrations in the cochlea. The traveling wave is then converted into bioelectric signals in the auditory sense cells of the inner ear (Hoy 2012).

The sound is then analyzed in the inner ear, which is responsible for performing spectral and temporal analyses of the acoustic signal. The spectral analysis is the process of extracting and defining the various frequency components of the acoustic signal. Frequency and intensity is what is otherwise called “pitch” and “loudness.” The cochlea is responsible to tease out the frequency components of the incoming acoustic signal and determine its amplitude and the temporal aspects of it. This process is the first level of auditory processing; subsequent processing takes place in the auditory pathway to the brain (Seikel et al. 2010).

Since sound is a disturbance in the air, this causes the tympanic membrane (TM) to move. The movement, afterwards, is translated to the oval window where, based on the movement of the TM (inwards or outwards), the stapes footplate is moved accordingly. More specifically, when the stapes compresses the perilymph of the scala vestibuli, Reissner’s membrane is inflated toward the scala tympani. That is, when the fluid of the scala vestibuli is compressed, it is translated directly to the basilar membrane. In the structures of the TM-ossicle-footplate, the sound – translated into Hertz – creates a 100 Hz signal in the footplate, which in turn creates a periodic vibration to the basilar membrane where a traveling wave is initiated (Seikel et al. 2010).

The Basilar Membrane

The way the sound is distinguished depends upon the frequency of the acoustic signal. High

frequency sounds cause vibration of the basilar membrane closer to the vestibule, which is the basal end of the cochlea. Low frequency sounds result in a long traveling wave that reaches the apex, having to do more distance along the basilar membrane. Hence, the traveling wave distinguishes the frequency components of complex sounds because the higher frequency sounds are processed in basal regions, whereas lower frequency sounds are processed near the apex. The analysis and discrimination of lower to higher frequencies is credited to the basilar membrane. This was demonstrated on a series of experiments, performed by von Békésy (1948), that the elasticity of the basilar membrane is reduced towards the stapes rather than the helicotrema, consequently producing a stiffness gradient which, when the cochlea is stimulated, results in the creation of a pressure wave that travels from the base to the apex (Gelfand 2010, p. 75). Regardless of how the traveling wave is initiated, it always travels from the base of the basilar membrane towards its apex based on the certain gradient of the membrane (Seikel et al. 2010).

Binaural Hearing

In regards to sound localization, it is through the process of binaural hearing that performance is improved in auditory tasks. Specifically, an essential task for the central auditory pathways is to analyze the auditory messages sent by the two cochleae into the auditory structures of the brain. This segregation and localization of the sound messages is significant for the separation of target signals from noisy environments. For example, sound coming from a source on the right reaches the left later than the right ear – because it has to travel further – and it reaches it with a lower intensity. This is called the head shadow effect, that is, the further to the right the source is located, the larger the interaural differences (Avan et al. 2015). Binaural interaction takes place mainly and almost simultaneously at three levels of the brain: the superior olivary complex (SOC), the nuclei of the lateral lemniscus (NLL), and the inferior colliculus

(IC) (for more on the binaural pathways of the brain see Moore (1991)).

There is an evolutionary advantage of binaural processing of sounds. Information gained from this process could help detecting a predator approaching surreptitiously while the prey is engaging in a certain activity, that is, drinking water around a noisy environment. This way, the brain, by evolving and developing a refined stereophonic sound system, has contributed in the survival of species (Avan et al. 2015). Although for humans survival may not be at stake, binaural processing is helpful along noisy environments such as cocktail parties, where the listening ability depends on the type, number, and location of interfering sounds as well as the interactions of them (see Hawley et al. 2004). It is noteworthy that the increase in brain size of mammals is probably due to an increased processing ability for binaural sounds in various auditory nuclei in the brain in order to deduce the locality of sound (Manley 2010).

Reichert-Gaupp Theory

Karl Bogislaus Reichert and Ernst Gaupp created a theory regarding the origin of mammalian ossicles of the ear. To be more precise, Reichert established the relationship between the reptilian jaw bones and mammalian middle ear bones in 1837 which was later taken and perfected by Gaupp (World Heritage Encyclopedia 2017). What is hypothesized is that the malleus and incus are products of the first curves of the skeletal elements of the middle ear (Takechi and Shigeru 2010). Moreover, the stapes, incus, and malleus have been confirmed to be homologous of the reptilian columella auris, quadrate, and articular (Westoll 1944). What is notable is that this theory was established before Darwin's *Origins of Species* (Takechi and Shigeru 2010). It is, also, noteworthy that Ernst Gaupp was the first to present a synthesis of embryological and paleontological data to explain the evolution of the mammalian middle ear structures (for a historical review of the Reichert-Gaupp Theory see Maier and Ruf 2016).

Evolution of the Mammalian Ear

Regarding the evolution of the mammalian ear, Masterton et al. (1968) were set to classify historical changes in human hearing by comparing it to the hearing of the mammalian evolution. What was found is that high frequency hearing (more than 32 kHz) is a mammalian trait due to the short space between their ears, and that there is a natural selection for specific sound localization. However, sounds in the lower frequency spectrum (less than 1kHz) is mostly a characteristic of the human species.

Moreover, Manley (2017) has provided an elaborative description concerning the mammalian ear evolution. His thesis is that more than 250 million years ago (Paleozoic era) the synapsids were parted from the stem reptiles resulting in the creation of the mammalian species line. During the early stages of the Mesozoic era, the mammalian ancestors had a “temporary” middle ear that was connected to the lower jaw which was later developed to a “definite” middle ear. The organ of Corti was also formed during this period (Manley 2017).

The bone integration into the cochlea was shaped only in therian mammals and came before the cochlear coiling and the partition of Eutheria from the Metatheria. The coiling in the Cochlea resulted in the loss of the lagenar macula and, subsequently, the evolution of prestins, a motor-protein found in high concentration in the lateral cell membranes of outer hair cells that is significant for an increased sensitivity at low sound levels (for more about Prestin see Dallos 2008; Li et al. 2010; Zheng et al. 2002, 2000). The hair cells are responsible for cochlear amplification and rapid cell length changes (Franchini and Elgoyhen 2006), the transduction of mechanical activity into electrochemical activity when the stereocilia are bent (Gelfand 2010, p.76), and the compensation for the energy loss for the transmission of the traveling wave on the basilar membrane resulting in an increased sensitivity of the ear (as much as 50 dB) and an increased frequency selectivity at low intensities (Moller 2013, p. 55). According to Franchini and Elgoyhen, prestin evolved in mammals that lead to the development

of the cochlea. They also have found evidence for the positive selection in the motor-protein prestin only in the mammalian lineage.

Additionally, signatures of positive selection on the $\alpha 10$ were found, but not on the $\alpha 9$, nicotinic cholinergic receptor (nAChR) subunits (Franchini and Elgoyhen 2006). According to Franchini and Elgoyhen, the $\alpha 9\alpha 10$ -containing nicotinic cholinergic receptor plays a significant role in various physiological processes. For instance, $\alpha 9$ is required for the normal development of the efferent synapses in the inner ear, and they serve as the unique source of extracellular calcium for Ca^{2+} -activated potassium channels in mature auditory hair cells (Vazquez 2016). Franchini and Elgoyhen suggested that evolutionary changes of the $\alpha 10$ subunit most probably allowed the $\alpha 9\alpha 10$ heteromeric receptor to contribute to the function of the mammalian cochlea.

The discovery made by Montealegre-z et al. (2012) is worthy to note. The researchers postulated that there is a similarity in the hearing system between mammals and rainforest katydids. Specifically, these insects demonstrated to possess equivalent biophysical mechanisms for the processing of sounds as such of mammals, based on the three stages of collecting sound from the outer towards the inner ear. Hoy (2012) noted that these three stages are likely to have developed predominantly in insects and much later in mammals.

Conclusion

To better understand how auditory perception was evolved, one must understand how sound firstly generated. First of all, sound is generated by a pressure disturbance in the atmosphere, where sound measured in both frequency and intensity travels in wavelengths to the ears of the listener. The sound is then captured by the outer ear, and travels from the middle ear to the inner ear for processing. There have been theories of the evolution of the structures of the ear, starting from the Reichert-Gaupp Theory, who are credited with the discovery of the mammalian ossicles of the ear. Other researchers have, also, contributed to the discovery of the mammalian ear evolution.

Cross-References

- [Mammalian Ear Evolution](#)
- [Reichert-Gaupp Theory](#)
- [The Traveling Sound](#)

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Evolution of Communication

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Synonyms

[Evolution of signaling and responding](#)

Definition

Evolution of responses by a receiver to signals from a signaler.

Introduction

Understanding the evolution of communication has undergone several saltations in the past century. Nonhuman animals are now routinely recognized to have spectacular and complex forms of communication. Also, after decades of controversy, it is now clear that communication is a form of cooperation. The conditions for the evolution of cooperation have also become clear. All of these statements can no doubt still excite controversy, but beyond any contention, they raise issues for the evolution of human language, as an extreme case of complexity in communication.

This article summarizes developments in evolutionary biology relevant to communication in general and introduces some implications for the specific case of language. Another article, *Design Features of Language*, develops these implications in detail.

Comparative Study of Signaling

Study of communication by animals other than humans began in earnest with Darwin. Earlier concepts had placed organisms on an immutable *scala naturae*, with progressive elaboration of capabilities, including mental capabilities, from lower to higher, with a culmination among sublunary creatures in humans. Linnaeus' *Systema Naturae* instead formalized hierarchical classification of organisms, although humans still occupied first place with the unique attribute of wisdom.

Darwin first introduced natural selection of behavior in *On the Origin of Species* (1859), elaborated the possibilities in *The Descent of Man, and Selection in Relation to Sex* (1871), and illustrated applications to communication in *The Expression of the Emotions in Man and Animals* (1872). In subsequent decades, the study of animal behavior diverged into several paths: (1) experimental study of learning in a few convenient species, (2) experimental study of the sensory capabilities of animals, and (3) observational study of diverse organisms engaged in natural behavior. The first path quickly established unsuspected capabilities for learning in animals

and then investigated these abilities in species amenable to experimentation. The second path revealed that many animals had unsuspected sensory capabilities, including some unavailable to humans, such as complex vision, including ultraviolet and polarized light, ultrasonic sound, electric and magnetic fields, and echolocation. Mental capabilities of animals were no longer just subsets of human capabilities. The third path, close observational study of animals, was at first pursued on the fringes of academic science. It eventually established at least six points important for a comparative study of communication.

1. Many animals have sizable repertoires of actions, including vocalizations, not directly related to nutrition, survival, or procreation. Often they are relatively conspicuous, discrete, and stereotyped. The term "display" was appropriate for them.
2. These displays are usually deployed in interactions between individuals and often evoke appropriate responses. They thus fit a basic criterion for communication. Furthermore, this communication is mostly among conspecific individuals. Both displays and responses are usually species-specific.
3. The structural and behavioral traits of these displays reflect the phylogeny of species. Indeed, for a while it seemed that comparisons of these displays might reveal phylogeny better than morphology could. They appeared to have evolved in arbitrary directions, without the complications of convergent adaptations. Yet their stereotypy and elaboration (called ritualization) suggested adaptations for communication (Cullen 1966), and eventually it became clear that displays include many adaptations to their environments and their functions in communication (Wilson 1965; Wiley and Richards 1982; Endler 1992).
4. Detailed comparisons of behavior between and within species suggest that displays have often evolved by elaboration of much simpler actions, either actions for individual maintenance, incipient actions in other contexts, or actions that seemed partially inhibited or redirected in the circumstances (Tinbergen 1952, 1960).

5. Experiments show that animals often respond only to a few simple features of displays (Tinbergen 1951). These “sign stimuli” often elicit relatively stereotyped responses, a finding that provided opportunities for a comparative neurobiology of behavior.
6. The ontogenetic development of these displays and their corresponding responses often does not depend on shaping by reinforcement or encountering models. In other words, they are in many cases “innate” or relatively canalized, in the sense that they develop in a stable way despite normal variation in individuals’ experiences. In contrast, other actions and responses, equally complex and stereotyped, are learned by experience. In some cases, perhaps always, this learning is subject to constraints, predispositions such as sensitive periods, or templates. The first such case was imprinting of the following response by newly hatched precocial birds. Another was imitation of species-typical patterns of singing by songbirds. Predispositions in these cases are more canalized, within normal variation of experience, and simpler than the subsequent learned displays or responses. These examples of constrained learning have become epitomes of the interaction of genes and environment in the evolution of behavior, in particular, communicative behavior (Bateson 1981; Marler and Peters 1977; Marler 1990; Soha and Marler 2001a, b).

The discovery of such widespread and complex communicatory behavior in animals, generated by nonintuitive developmental processes and enmeshed in diverse social interactions, raised many questions about its evolution.

Evolution of Honesty

Until 50 or so years ago, the evolution of societies was explained by cooperation among individuals. Because cooperation is mutually beneficial, the action of natural selection in promoting cooperation seemed easily understood. This naïve attitude was overturned by George Williams’ *Adaptation*

and *Natural Selection* (1966) and Richard Dawkins’ *The Selfish Gene* (1976). In the first place, not all individuals in an ostensibly cooperative society benefit equally. Individuals, for instance, might reduce their exposure to predators by herding, but those near the outside of a herd have more exposure than those in the center. Williams and Dawkins emphasized that, if differences in individuals’ social behavior are associated with differences in the genes they carry, any allele (variants of genes) associated with behavior contributing to greater survival and reproduction spreads in a population, while others do not. Thus an explanation for the evolution of social behavior by natural selection requires an analysis of how each individual’s behavior in social interactions affects its reproduction and survival.

This sort of argument provokes questions about how the behavior (or any trait) of an individual is related to its alleles. This basic process of behavioral ontogeny is revealed especially clearly in the studies of constrained learning in animals. An individual’s development involves an interaction, in the statistical sense, of its genes and environment throughout the course of its life. As a result, genes do not determine anything about an individual’s development, but they influence all of it. The same is true of the individual’s environmental experiences. Natural selection results from differences in the reproduction and survival of individuals, whose traits are thus influenced more or less, in one way or another, by their alleles.

An early application of this principle was the evolution of polygynous mating systems, those in which most females mate with a few males. An argument that successful males benefit from multiple matings is insufficient without an explanation for how females benefit. The “polygyny threshold hypothesis” proposed that in habitats with high spatial variability (for instance, grasslands and marshes, where many nesting birds have polygynous mating systems), a female could compensate for reduced parental help from a polygynous mate provided that her mate’s territory provided access to more food and safer nesting sites (Orians 1969; Searcy and Yasukawa 1995). This new approach to the evolution of

social behavior set the stage for a reassessment of the evolution of communication.

Communication often involves individuals in asymmetrical roles, males enticing female mates, opponents in aggressive encounters, and competitors for food or space. Mutual advantages or cooperation in communication is less clear in cases like these, in which one individual might benefit by deceiving the other about its strength or suitability. Honesty, in contrast, would require a benefit for an individual responding to a signal as well as a benefit for the sender. Dawkins and Krebs (1978) suggested that signals are usually not honest. Instead they manipulate receivers for the signaler's advantage, despite the receiver's disadvantage. They deceive rather than inform receivers. Alternatively, Zahavi (1975, 1999) suggested that receivers avoid this problem by responding only to costly signals, because only costly signals are honest.

Zahavi's original proposal included two specific conditions for honesty: (1) costs of signals must be wanton (more than necessary); and (2) signals must have a form that impacts the attribute that is of interest to a receiver. The first of these conditions separates the costs of producing signals into a necessary component, which assures detection by a receiver, and an excessive or "wanton" component, which ensures honesty. The second condition requires that a signal interferes with its own meaning, in the sense that it must compromise the condition of the signaler that interests the receiver. For instance, a signal indicating efficiency in collecting food might partially compromise an ability to find food; or one indicating skill at avoiding predators would partially increase a signaler's vulnerability, for instance, by attracting a predator's attention or approaching and perhaps taunting predators. Such a signal would assure a receiver that the signaler was good enough at the particular task to overcome the handicap. For these reasons, Zahavi stipulated that the "wanton" costs of signals are handicaps. Handicaps thus became conditions for cooperative communication in which both signaler and receiver benefited.

This handicap principle became a central tenet of the study of animal communication, primarily

as a result of mathematical demonstrations that honesty in signaling required costs for signals. Grafen (1990a, b) and Maynard Smith (1991) used different approaches to show that (1) the cost of an honest signal must exceed 0 as a general rule but (2) the cost to the signaler or the benefit to the receiver could equal 0 when signalers were genealogically related to receivers. Maynard Smith and Harper (2004) nevertheless concluded that the costs for honesty must exceed a cost necessary to avoid ambiguity in communication. Many studies in the past three decades have demonstrated that signals are usually honest (receivers' responses have benefits in terms of survival or reproduction or have some correlated effect) and that signals have costs related to survival or reproduction (Searcy and Nowicki 2005).

The handicap principle, however, is vitiated by two problems (Wiley 2015, 2017; see also Getty 1998; Számádó 2011). (1) The mathematical analyses make no distinction between necessary and excessive costs and in fact demonstrate only that honesty requires signals with costs >0 . It is difficult, perhaps impossible, to imagine a signal that has no costs whatsoever, in terms of energy, risks, time, or lost opportunities, any of which would affect survival or reproduction. These analyses thus make no predictions about how much cost honesty requires. (2) An analysis of the optimization of communication in the presence of noise (Wiley 2015) shows that there is no distinction between costs of signals that reduce ambiguity and those that do not. During joint optimization of signalers and receivers in the presence of noise, all costs are incurred in reducing errors by receivers. Furthermore, a distinction between manipulation and information in communication is misleading, once information is more clearly defined, as proposed below.

More important, Grafen's calculations confirmed, although without much emphasis, that receivers must benefit from their responses to signals, at least on average. If receivers incur net costs for responding to a signal, then these responses do not evolve, and thus the signals do not either. The same conclusion applies to responses to signals from potential mates, although in this case, a receiver's benefits from

choosing a mate can include genes that influence survival and reproduction of the receiver's offspring (Pomiankowski 1987).

The principal conclusion of these analyses is thus not that honest signals must have costs but that both signaler and receiver must benefit from the responses. It is not necessary that every instance of a response to a signal has benefits. Instead, responses to signals must have benefits, on average, either immediate or delayed, for both signaler and receiver. Communication is indeed a form of cooperation, in which both parties do better on average by communicating than they can otherwise.

Evolution of Cooperation

Cooperation begins by one individual helping another at some cost to itself. The first step is thus an act of altruism, one that benefits another at a cost to the actor, with benefit and cost ultimately in terms of survival and reproduction. Helping, including signaling, fits this pattern. Alleles cannot spread in a population unless the individuals that carry them survive and reproduce more effectively than others. Consequently, the challenge is to determine how alleles for helping can spread when helping individuals incur net disadvantages in survival or reproduction. It turns out that altruistic *individuals*, for which helping others decreases their own reproduction or survival, can persist in a population. Nevertheless, "altruistic" *alleles*, for which association with helping decreases their frequency, inevitably disappear from a population. To reconcile altruistic individuals with selfish alleles, two possibilities are now recognized: (1) helping genealogical relatives or (2) receiving compensating benefits in the future.

The first occurs, for instance, when individuals help to raise a relative's offspring while not themselves reproducing. The example of honeybees, which had perplexed Darwin, is such a case. Somewhat similar cases have now been studied in scores of birds and mammals as well as numerous social insects (Koenig and Dickinson 2004; Bourke 2011). In many cases the helpers

(or workers) in fact reproduce to some extent either concurrently or later in life. Nevertheless, in some cases, such as honeybee workers helping queens to reproduce, the helping individuals almost never reproduce as much as the individuals they help. William Hamilton (1964, 1970) showed that alleles of individuals with lower chances of reproduction could nevertheless spread in a population provided these individuals helped close genealogical relatives. Close relatives can have a copy of any allele associated with a helper's behavior, as a result of their descent from a recent common ancestor. This "kin selection" is thus a special case of natural selection. If individuals sacrifice their lives to save the lives of more than two siblings (or more than eight cousins), any allele associated with this behavior would spread. The condition for the spread of an allele associated with helping is $C < rB$, where C is the cost in survival or reproduction for the actor, B is the benefit for the recipient, and r is the coefficient of genealogical relatedness of the actor to the recipient (one-half for a sibling, one-eighth for a cousin). Recent debate has clarified this possibility (Nowak et al. 2010; Abbot et al. 2011).

These ideas were quickly applied to mammals and especially to birds in which breeding pairs often have several helpers that feed or protect their young but do not (or are less likely to) reproduce. The evidence indicates that in most such cases, kin selection cannot provide a sufficient explanation for helping. Nevertheless, in the preponderance of cases, helpers are closely related to breeders. Kin selection in such cases contributes to the spread of alleles for helping even if it does not completely explain it. These principles apply to communication. We can expect individuals to accept uncompensated costs for signals or responses if the condition above is met.

The second case, when helpers receive later benefits, could apply to genealogical relatives and thus augment kin selection for alleles associated with helping. It might also apply to individuals without close genealogical relatedness. One possibility for later benefits is reciprocation: do unto your neighbor as you would have (or at least can expect) your neighbor to do unto you. Reciprocation though has its complications. Just because an individual helps another does not assure that the

recipient will return the favor. In addition to inevitable random contingencies, a population could plausibly include individuals with alleles associated with accepting help but never reciprocating, in other words defectors or cheaters. The possibility for cheaters in an otherwise cooperative population is pervasive. Close attention to cases of helping reveals that reciprocation is not a physical necessity, so there is always the possibility of a mutant allele that predisposes individuals to cheat by skipping reciprocation. In any instance of helping, the recipient is always possibly a cheater and the helper possibly a sucker.

In communication, the norm is honesty, but the possibility of exploitation, in other words cheating, is always present, both for signalers and receivers. On average a signaler benefits from responses by appropriate receivers, but there is always the chance of an inappropriate receiver, such as an eavesdropping rival, predator, or parasite. These inappropriate receivers exploit the signals intended for appropriate receivers. This situation is the converse of deception. In deception, an inappropriate signaler exploits the responses intended for appropriate signalers. There is always the possibility that a signaler or a receiver is a cheater in normally honest communication, and there is always the possibility that a signaler or a receiver is a sucker.

The usual recourse for analyzing the evolution of reciprocation has been game theory. In particular, the prisoner's dilemma and many related games have provided a foundation for mathematical and experimental analysis of the evolution of cooperation. An early discovery was that the behavioral strategy of iterated tit for tat permits the evolution of cooperation by reciprocation (Axelrod and Hamilton 1981; Axelrod 1984). This strategy consists of helping any new partner on the first encounter and then on subsequent encounters, either helping or not depending on whether or not the partner has reciprocated (Axelrod and Hamilton 1981; Axelrod 1984). It is a practical variant of the golden rule: do unto each partner as you expect that partner to do unto you.

Many additional possibilities for the evolution of altruistic behavior have by now surfaced. For

instance, altruistic behavior can evolve in local populations of sessile organisms, when individuals interact repeatedly with the same few partners as a result of their immobility. With the strategy win-stay-lose-shift, individuals help in their first interaction (or in random occasional interactions) and then help subsequent partners or not, regardless of whom they might be, depending on whether or not the previous partner reciprocated. In this case individuals do not keep record of their partners. Individuals might also develop a positive reputation for helping so that others would help them in the expectation that they would receive help in return. In this case, however, an individual's tendency to help would have to extend indiscriminately to other individuals. Alternatively individuals might develop a negative reputation so that others would have no expectation of reciprocation and thus refuse to help them. Finally, helpers might punish (impose extra cost on) defectors. In this case, helpers would themselves incur an additional cost for administering punishment. If the cost to each punisher was sufficiently small (perhaps shared among many helpers) and the cost to each punished non-reciprocator was sufficiently large (perhaps execution or banishment with little chance of survival or reproduction), this possibility could overturn the advantages of cheating but preserve most of the advantages of helping. Sharing the costs of punishment would, however, be another form of reciprocation, which would itself open opportunities for cheating (for instance, avoiding a fair share of taxes for policing). Sometimes cases of social approval or social disapproval are combined as contrasting examples of "social selection." All of these possibilities, when appropriate conditions are met, can explain how alleles associated with altruistic action can persist or spread in a population (Nowak 2006; for an example of punishment by monkeys, Hauser 1992).

There is one situation that does not allow such altruistic alleles to spread – badges identifying altruists. Altruistic individuals could increase the chances of reciprocation by recognizing each other by some badge associated with helping.

Richard Dawkins labeled this possibility a “green-beard effect” (on the possibility that green beards might serve for such a badge). The problem is that a shared badge just creates another opening for cheaters, individuals that sport the badge but do not reciprocate. Alleles with pleiotropic effects might work temporarily but only until a mutation broke the association between helping and development of a badge.

From decades of discussion, two conditions have emerged that always increase chances for the evolution of mutual helping: (1) genealogical relatedness between actors and recipients and (2) cognitive abilities for remembering interactions with individual opponents. Genealogical relatedness promotes the evolution of cooperation even when it does not provide a complete explanation. Memory of individual opponents is a crucial part of some options for the evolution of cooperation by reciprocity, such as tit for tat. Some options, such as tracking individuals’ reputations, require extensive memory of individuals. Nevertheless, even possibilities that require no memory of opponents, such as sessile neighborhoods or win-stay-lose shift, are even more likely to evolve reciprocity when memory of individual opponents is possible.

These possibilities for multiple contributing factors in the evolution of cooperation are often overlooked, because theoretical models have tended to take two directions, either focusing on the minimal conditions or on the maximal potential for cooperation. Those studying humans focus on the maximal possibilities for cooperation. Those studying other animals tend to focus on the minimal requirements for cooperation. Studies with humans in mind often assume complex cognitive capabilities without much comment and ignore the synergistic contribution of genealogical relatedness. They also can ignore the possibility that collaboration in a complex society, which results in unequal or uncertain advantages for individuals, generates natural selection for defection and for nothing-to-lose retaliation when disadvantaged. All these conditions for the evolution of cooperation apply to the evolution of communication.

Evolution of Individual Recognition

For the evolution of cooperation, all but the simplest possibilities rely on individuals’ abilities to remember other individuals and to associate them with particular patterns of behavior. This ability requires at least minimal object constancy for another individual, discrimination of that individual from others, and association of that individual in memory with its previous behavior. Object constancy, discrimination, and association are mental processes, perhaps each some aspect of association in general, that recur in all discrimination learning.

Abilities of this sort are now well documented for many nonhuman organisms. There are important distinctions to be made about the complexity of recognition (Wiley 2013a). First, the specificity of individual recognition can vary. An experiment might reveal that subjects respond to a neighbor or a partner (or often just to some features of such an individual) in a different way than to other individuals. Such a discrimination could result solely from habituation to repeated experience with a familiar individual. It would thus constitute recognition of a particular individual only when no other individual could have such familiarity. In some cases it is still not clear whether or not animals recognize territorial neighbors, parents, offspring, or relatives as individuals or as small sets of familiar individuals and whether or not these small sets are distinguished from others by associative learning or solely by habituation. On the other hand, experiments have shown that many territorial birds, for instance, can identify specific individuals within the small sets of their familiar neighbors.

Specificity of individual recognition is crucial for the evolution of cooperation. Only when specific individuals are recognized can interactions with possible cheaters be avoided or reduced. One report of a nonhuman animal that fits the requirements for tit for tat provides an example. A warbler in eastern North American forests can use its ability to recognize individual territorial neighbors in order to cooperate with them once mutual boundaries are settled. Experiments

with playbacks of songs show that they use tit for tat to retaliate specifically against defecting (trespassing) neighbors (Godard 1993).

The multiplicity of individual recognition can also vary, from recognition of a single other individual (for instance, a mate) to recognition of individuals in a small set (perhaps territorial neighbors, a small group, or current offspring) to recognition of potentially large numbers of individuals (as do humans). Some territorial birds are known to recognize several individual territorial neighbors, and primates (and presumably some other social birds and mammals) can recognize multiple individuals within their social groups and in nearby groups as well (Cheney and Seyfarth 1990, 2007). Associations with these individuals are probably not complicated in the case of territorial neighbors in particular locations but are possibly more complex in the case of group members encountered in diverse contexts.

Humans recognize large numbers of individuals with different degrees of specificity and different complexities of associations. There is a considerable literature on the influence of features, relationships of features, and contexts in peoples' abilities to recognize faces, but almost nothing is known about how many individuals a person can recognize nor about the cognitive complexities of how a person organizes these memories. This gap in our knowledge is surprising, because the memory, associations, categories, and relationships involved in individual recognition by humans seem to approach those needed for human language.

The hierarchical organization of many animal societies suggests possibilities for recognition that have parallels with language. The formation of a dominance hierarchy, it is important to acknowledge in the first place, might not require any individual recognition at all. Each individual can plausibly learn to recognize sets of higher- and lower-ranking opponents or even respond to one or more graded features (for instance, size, postures, or badges of dominance). On the other hand, individuals might recognize each individual opponent and respond to each in a different way. Associations with each opponent might allow inferences about the relative ranks of any two other individuals.

Especially interesting are cases in which individuals' rankings include prominent sub-groupings, and ranks across these subgroups do not follow gradations of individuals' features. In many primate groups, for instance, matrilineal groups as a whole are ranked as well as individuals within each matriline (Bergman et al. 2003). Thus a low-ranking young individual in a high-ranking matriline outranks a high-ranking older female in a low-ranking matriline. These nested hierarchies seem to arise because older relatives (mothers, aunts) shield younger ones from subordination by individuals in lower-ranking matriline. Although the pattern and the interactions are well documented, there remains the question whether this pattern is conceptualized by individual monkeys as embedded subgroups or as an overall hierarchy. Some evidence suggests that the former is possible for baboons. Playbacks of calls indicating a reversal of ranks between matriline evoke more attention than those indicating a reversal within matriline, regardless of the differences in overall rankings (Bergman et al. 2003). Baboons evidently can conceptualize a dominance hierarchy as sets of embedded individuals, although wide overlap in the ranges of responses to the two conditions raises the possibility of inconsistency in this ability.

A similar situation results from "coattail" effects in dominance hierarchies of birds (Wiley 1990; Cristal 1995). Small groups of emberizine sparrows are allowed to form dominance hierarchies in large cages in winter, when competition for food is the predominant activity. Then the top half of the hierarchy in one cage and the top half from a second cage are combined in a third neutral cage. Surprisingly, the two groups often remain coherent in the newly formed hierarchy. Each individual's rank is nested in its group's rank. The mechanism is perhaps not dissimilar to that in primate groups. The two highest-ranking individuals in a combined group interact to determine their relationship, but once this relationship is decided, the higher individual creates a coattail for its familiar subordinates. In this case, and perhaps in the primate groups also, the principal effect of the dominant individual is to let its

familiar opponents approach more closely than can others without aggression. Again the question arises: How does a relatively dominant member of a subordinate subgroup categorize opponents? First by subgroup and then by ranking within it or simply by overall rank.

Evolution of Mating Preferences by Sexual Selection

Mate choice is a well-studied example of communication. In many animals males perform conspicuous displays that increase their chances of mating. Darwin (1859, 1871) recognized that if females prefer males with certain traits, or if males with certain traits are more successful in competing with rival males, then these traits would tend to spread in a population. Even more than his theory of natural selection, this theory of sexual selection precipitated controversy among biologists. At first the primary sticking points were doubts about the cognitive abilities of females needed for preferences, but R. A. Fisher (1930) made it clear that a female's preference is no more than a neurophysiological response to a male's traits. Fisher then presented a verbal argument for accelerating evolution of male traits preferred by females. The process of sexual selection was terminated when the cost of the preferred male traits became too great.

It remained for proper mathematical analyses to verify the dynamics of this accelerating evolution (Lande 1981; Kirkpatrick 1982). Much subsequent work has confirmed predictions about mate choice in natural populations (Anderson 1994; Searcy and Yasukawa 1995). The key to the evolutionary dynamics is the genetic correlation produced when a female with a preference mates with a male with a preferred trait. Their offspring tend to inherit alleles associated with both preference and trait. The result is a genetic correlation between these alleles in the population. Within the genomes of individuals in the population, the presence of the preference allele is associated with the presence of the trait allele. This association is often called "linkage disequilibrium" by geneticists, but linkage is actually

a special case of genetic correlation, not necessarily connected with mating preferences. As generations pass, females with preferences tend to spread not only alleles for the preferred male trait but also alleles for the preference (because both males and females tend to carry both alleles). As a result of the genetic correlation of the two alleles, the preference allele spreads by "hitchhiking" with the trait allele. Another way to look at it, the preference allele spreads itself. The genetic correlation that results from preferential mating produces accelerating evolution of alleles for both of the male trait and the female preference. Sexual selection is thus a special case of natural selection, one that happens whenever individuals of one sex with a particular trait mate disproportionately with members of the other sex with the same or different trait. Preferences and other traits, to reiterate a point above, develop under the influence of alleles.

There are several points to emphasize here. First, A preference for potential mates with a particular trait is a form of communication. In the most frequent case, males produce signals to which females respond discriminately. Nevertheless, the mathematical models of sexual selection do not require direct choice of males' traits. A female might instead exert a choice indirectly. She might set conditions for mating by provoking a contest between potential mates. For instance, she might limit her matings to a particular time and place, or she might indiscriminately advertise her readiness to mate. In these cases there is no discrimination between males' traits, yet females set conditions that result in selective mating. By mating with whichever male prevails in such contests, she would indirectly choose a male whose traits allowed him to prevail against all comers. Females would, in other words, define the contest for males and then take any winner as a mate. In the case of indiscriminate advertising, a female produces a signal to which males respond by approaching. In any of these possibilities for indirect choice, genetic correlation and subsequent sexual selection would result, just as in the case of direct choice.

Second, Alleles for preferences cannot spread if females with these alleles incur net costs in terms of survival and reproduction (Pomiankowski

1987; Grafen 1990b). Responses to signals, as we saw above, must result in net advantages, on average, for receivers or their close relatives. Furthermore, sexual selection also stops when males incur net costs, when the advantages of greater possibilities for reproduction are more than offset by disadvantages for survival.

Third, Sexual selection does not spread alleles until the frequencies of the preference and trait alleles in the population exceed a threshold (or the level of genetic correlation crosses a threshold) (Lande 1981; Kirkpatrick 1982). Sexual selection does not spread mutations *ab initio*.

This hurdle applies to the initial evolution of any signal and response. No matter how advantageous communication might be, neither a response nor a signal can spread by itself. A rare mutant for a new response cannot spread without sufficiently frequent signals, and vice versa a new signal cannot spread without sufficiently frequent responses. Mutualistic signal and response must overcome a hurdle before they can spread.

Furthermore, all mutualistic interactions spread in an accelerating way once started. Responses become more advantageous as the frequency of signals increases and vice versa. It is still not clear whether R. A. Fisher (1930) had genetic correlation in mind when he proposed accelerating evolution of sexually selected traits or whether he was just thinking of the accelerating spread of any frequency-dependent mutualistic interaction (Wiley 2015). The rate of spread eventually slows down as the frequencies approach fixation, because increasing frequency of signalers results in diminishing advantages for receivers and vice versa.

Sexual selection, despite its specific application to communication during mate choice, includes parallels with the frequency-dependent evolutionary dynamics of all forms of mutualistic interaction and thus of communication in general. The evolution of mutualistic communication between individuals other than mates does not receive the extra boost from the genetical correlation that results from mating. Nevertheless it does share the initial hurdle and the subsequent acceleration that apply to all frequency-dependent mutualism.

A final point should be emphasized. The original mathematical models (Lande 1981; Kirkpatrick 1982) and subsequent derivations include the possibility that female preferences might be arbitrary. Arbitrary in this context means that mating with a preferred mate provides no benefit whatever to the female (we have already emphasized that it cannot incur a cost to the female). There are three reasons to think that such completely arbitrary preferences are unlikely to evolve. First, if alleles for two preferences exist in the same population, the one that results in a greater benefit to females spreads faster. So any preference with a benefit for females spreads to the exclusion of an arbitrary preference. Second, the same applies to the costs of male traits. Of two alleles associated with traits equally preferred by females, those with lower costs spread fastest. Finally, preferences for traits are a form of communication. Noise in communication makes the evolution of completely arbitrary signals and responses unlikely. The parameters, some ten of them, that influence the utility of a signal for a signaler (an advertising male, for instance) and the utility of a criterion of response for a receiver (a choosy female, for instance) would have to balance exactly to produce zero net utility for both signaler and receiver (Wiley 2015, 2017). Communication for mate choice, like all communication, is inescapably noisy.

Evolution of Communication in Noise

Noise requires a new approach to understanding the evolution of all forms of communication, one that is compatible in part with the preceding approaches but has advantages of defining some crucial concepts, presenting a thorough optimization of the behavior of signalers and receivers and incorporating the consequences of noise for communication. Noise opens a new perspective on the evolution of communication. Most surprising is the realization that evolution is not expected to produce noise-free communication.

Everyone is aware that noise can interfere with communication. Communication requires two parties, a signaler and a receiver. Even when

more than one signaler or receiver is active at the same time, each instance of communication is a relationship between a signaler and a receiver. A signaler produces a signal to which a receiver might respond. A signal is any pattern of energy or matter that can elicit a response from a receiver, without providing all of the power for the response. A response need not occur every time a signal is perceived, but unless a response occurs more often than at random, there is no evidence for communication.

Most previous definitions of a signal agree in stipulating that a signal must evoke a response, although it is less often emphasized that responses need to occur only more often than random. Previous definitions also require that a signal must have evolved for the purpose of communication or have a goal (or intention or function) of evoking a particular response. Often there is a complementary condition: a response must have evolved for a particular signal. These stipulations are confusing and circular: signals and responses evolve for communication which consists of signals and responses.

A signal defined as a pattern of energy that evokes a response but does not provide all the power for the response avoids this confusion. The restriction on the power of a signal excludes cases in which one individual simply overpowers another, as, for instance, in predation. A signal, on the other hand, must provide some power, enough to activate the sensory receptors of a receiver. The receiver must then provide some, often most, of the power for the response. Consequently, receivers have the final control of responses.

Signals defined in this way can originate from inanimate objects as well as living ones. Previously most definitions have excluded this possibility by insisting that signals have functions; signals without functions are instead called cues. But this measure is unnecessary. From a receiver's point of view, it makes no difference what the source of a sensation is. Signals from any source produce sensations for receivers, and receivers have final control of responses. For any receiver, including humans, information about the inanimate world has the same footing as information about the behavior of other organisms.

Nevertheless, signaling and responding by organisms can evolve. As discussed above, signals by evolving signalers are expected on average to produce net advantages in terms of survival or reproduction for signalers; responses produce such advantages for receivers. Signaling and responding by living organisms evolve jointly.

Information is another term that has caused confusion. Shannon in his pioneering papers on information theory (Shannon and Weaver 1949) described the simplest intuitive way to measure the quantity of information, but he only hinted that the quality of information ("what" rather than "how much" information) depended on the state of the signaler. A signaler's state results from its ontogeny, as described above, the accumulated influences of genes and experiences during the course of its life to present. Its state is the current condition of its body, including its nervous system and thus also its recent perceptions. The quality of information, regardless of its quantity, is the correlation between a signal and the signaler's state (Wiley 2013b). If a signal has information relevant to a receiver's survival or reproduction, alleles associated with responding appropriately to such a signal can evolve (increase or decrease in frequency in the population). If such a signal evokes a response affecting the signaler's survival or reproduction, alleles associated with producing such signals can evolve. Thus the quality as well as the quantity of information in a signal influences its evolution. Evolving signals must include some information about the signaler's state. Note once again that responses can include delayed and covert effects, such as memory or physiological changes affecting later behavior. It might include complex perceptions as well as simple reflexes.

With collateral issues resolved, a criterion for noise is possible: noise is errors by receivers. This insight by Shannon is as important as that about information. Anything that results in errors by receivers counts as noise. It can include irrelevant background energy that interferes with a receiver's detection or discrimination of signals. Background energy can include turbulence and extraneous energy impinging on the receiver's sensors. It can include signals of other species or individuals irrelevant to the receiver in question.

Noise can result from attenuation and degradation of the patterns of signals during transmission from signaler to receiver, in the atmosphere or water or even at the interface between a finger or a tongue and a receiver's skin. Noise also occurs in nervous systems. Nearly all neurons produce action potentials continuously at irregular rates, which are combined with the firing rates elicited by sensory stimulation. Little is known about how this neural noise affects perceptions of sensory sensations. Both signalers and receivers are subject to neural noise. Signalers do not always produce signals perfectly correlated with their states; receivers do not always respond appropriately to signals (Wiley 2015, 2017).

The basic insight of signal detection is that a receiver must make a decision each time it checks any of its sensory inputs (Macmillan and Creelman 1991, 2005). Because relevant signals combine with noise in a receiver's sensors, a receiver must decide whether a sensation correctly indicates the occurrence of a signal or not. Normally the combination of signal plus noise results in greater stimulation than does noise alone. Both signals and noise vary, so each produces a probability density function (PDF) of levels of excitation of a sensor. Whenever the PDF for signal plus noise and the PDF for noise alone overlap to any extent, the receiver cannot respond to appropriate signals without some error.

Another insight of signal detection is that receivers are subject to two kinds of errors, false alarms and missed detections (or errors of commission or omission or Type I and II errors in statistical comparisons). These errors result from a receiver's criterion for a decision to respond or not. The simplest criterion for response is a threshold. If the level of excitation in a sensor exceeds the threshold, then respond; otherwise, do not. More complex sensors can include filters and combinations of thresholds and filters to produce specific cognitive criteria for a response. A response, as emphasized above, can be either overt or covert, an act, a perception, or a memory. Any response might be an error.

Every time a receiver checks its input, exactly four mutually exclusive outcomes are possible. The level of excitation in its sensor might exceed

its threshold (or other criterion for response) or not; in each case, a relevant signal might have occurred or not. Excitation above threshold when a signal is present results in a *correct detection*. With no signal, only noise, the result is a *false alarm*. Excitation below threshold when only noise is present results in a *correct rejection*; with a signal present, albeit attenuated and masked with noise, the result is a *missed detection*.

A receiver in this situation can adjust its rates of error by adjusting the level of its threshold. Yet every adjustment of a threshold changes the probabilities of all four possible outcomes. For instance, by raising its threshold for a response, it would reduce its chances of a false alarm. Its chances of correct detection also decrease. On the other hand, missed detections and correct rejections increase. If a receiver lowers its threshold, its chances of a missed detection decrease, but again the probabilities of all other outcomes would also change. Most important, the two kinds of error, false alarm and missed detection, always change in contrary ways. A receiver cannot reduce one kind of error without increasing the other. Every time a receiver checks its sensors and decides to respond or not, it is in an inescapable double bind.

Signalers can influence the relationship between signals and noise for receivers. In general the more powerful or concentrated a signal, the greater its impact on the sensors of a receiver at any particular distance. Signalers thus can increase the probability of a correct detection (an appropriate response) by a receiver by increasing the exaggeration of a signal. The probability of a correct detection by an appropriate receiver in turn affects the benefit from signaling for a signaler.

The next objective is to calculate how natural selection can affect the evolution of signalers and receivers in noise. Does evolution by natural selection produce a joint solution for signaling and responding? Are there mutual advantages for signalers and receivers? Is noise eliminated by natural selection on communication? The first step is to specify net advantages and disadvantages for potential options for both receivers and signalers (Wiley 2015). For receivers, this step requires calculation of the utility of the receiver's

threshold, each time a receiver checks its sensors and decides to respond or not. This utility is a function of the signal/noise ratio (more accurately, the relationship of the PDFs for signals plus noise and for noise alone), the probability of a signal, and the level of the threshold. The threshold affects the probabilities of each of the four possible outcomes. For investigating evolution, the utility is expressed in terms of the receiver's survival $\times$ reproduction.

A similar process can specify the utility of signal exaggeration for a signaler as a function of the cost of producing a signal with a particular exaggeration and the probability of a response from an appropriate receiver. The utility of a receiver's threshold thus depends on the signal/noise ratio, which depends on the exaggeration of a signaler's signal; conversely, the utility of a signaler's exaggeration depends on the probability of a correct detection, which depends on the level of a receiver's threshold. With some calculus, it is possible to find the optimal level of a threshold for a given exaggeration of a signal or, alternatively, the optimal exaggeration of a signal for a given threshold. Further computation reveals that in most situations, thresholds and exaggeration evolve by natural selection to a joint optimum, a Nash equilibrium at which both receivers and signalers have advantages and both do as well as possible provided the other does also (Wiley 2015).

Some General Principles for the Evolution of Communication

Several important insights about communication result from these calculations. First of all, adaptation by natural selection does not escape from noise. Noise is inevitable; communication in the absence of noise is unattainable. This conclusion follows from the basic insight that both signalers and receivers face conflicting advantages and disadvantages. They also face diminishing returns: in an approach to optimal signals or thresholds, advantages increase less rapidly than disadvantages.

Second, the variables in these calculations are completely general. They apply to signalers and receivers in all cases of communication. For

instance, both exaggerations of signals and thresholds for response scale to the level of noise. Thus at close range, when background noise is minimal, optimal signals and thresholds decrease in relation to noise so that possibilities for error persist. In addition, this result applies not only to communication by nonhuman animals but also to humans and to all modes of human communication including electronic. It applies not only to communication between organisms but also to communication between and within cells. Molecular signals and receptors operate in a noisy environment, with multiple signals, multiple receptors, and chemical degradation. There is thus no reason to expect that adaptation by natural selection can eliminate noise in any form of communication. The same conclusion applies to perceptions of the external world. Optimal decisions by perceivers, based on signals from inanimate objects, cannot escape some probability of error, either false alarms or missed detections and errors of commission or omission.

Third, these calculations confirm the results of all previous calculations of the evolution of mutual interactions: neither signals nor responses can spread when both are infrequent. In the present calculations, when thresholds are too high (as when individuals have little tendency to respond to a particular stimulus) and when exaggeration of signals is too low (as when individuals have little tendency to produce them), communication collapses. Thresholds for response must not be too high, and exaggeration of signals must not be too low, for mutual communication to evolve *ab initio*.

Fourth, optimization of communication in noise opens many questions about adaptations for communication in different circumstances. Nearly every parameter in the utility functions has been measured or estimated in some case of communication (Wiley 2015), although never has there been a complete analysis of communication in noise in natural situations. There are clear predictions about the evolution of thresholds for response and for exaggeration of signals as a result of differences in signal frequency and the utilities of the four possible outcomes for receivers. A further prediction is that exaggeration of signals should not evolve in arbitrary ways but

instead specifically in ways that increase the signal/noise ratio for appropriate receivers. There is evidence that evolution of both acoustic and visual signals follows this prediction (Wiley 1991; Endler 1992; Endler and Thiéry 1996; Gomez and Théry 2004; Kemp et al. 2009). It also seems unlikely that purely arbitrary signals could ever evolve even by sexual selection. An arbitrary signal would require the multiple parameters of communication in noise to balance exactly.

Finally, although communication is never expected to reach perfection, honesty is expected to prevail. At the evolutionary optimum, both signalers and receivers benefit on average. Nevertheless, some incidence of error persists. Some errors result from random events in the environment or in signalers or receivers. Evolved adaptations by inappropriate participants also affect optimal behavior by signalers and receivers.

Deception by inappropriate signalers can reduce the utility for receivers. Eavesdropping by inappropriate receivers can reduce the utility for signalers. Communication is expected to transfer information between signaler and receiver, in other words, a corresponding perception of the actual world to their mutual advantage but always with a possibility for random errors and for manipulation by inappropriate signalers or receivers.

Investigation of communication with a hypothetical absence of errors is thus unrealistic. Noise requires study as much as signals. Nevertheless, many studies of communication, whether theoretical, observational, or experimental, take steps to reduce noise as much as possible, in order to focus on signals or responses. Study of simplified situations has its place in science, but it can also produce unrealistic results. To understand communication in any real situation, noise is as important as the signals. In other words, communication of any sort cannot be fully understood without understanding its variation in practice.

It is also clear that all communication in noise is “inferential” and “intentional.” If the “meaning” of a signal is the response it evokes in a receiver

(whether overt or covert), the meaning in the presence of noise always requires a decision by a receiver. Meaning is thus “inferential.” Furthermore, signals are often accompanied by relevant as well as noisy contexts, both of which affect the receiver’s decisions to respond or not. These decisions must often depend on the receiver’s previous interactions in a particular context and thus on the receiver’s memory of any associations with this context. They thus are “intentional.”

Signals always arrive within a context of noise. A receiver decides to respond based on its current state (including memory) and the sensations it receives. These sensations include signals (usually honest but with some noise) and relevant contexts (usually correct but with some noise). If “inferential” implies decisions by a receiver and if “intentional” implies associations for a receiver between a signal and its context, then all communication is intentional, between animals as well as humans. The decisions humans make in using language require complex criteria for responses. The distinctive features of human linguistic communication as opposed to other forms of communications lie in the specific complexities of these cognitive criteria, not in the importance of decisions or contexts in general.

Cross-References

- ▶ [Design Features of Language](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Fisherian Runaway Selection](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Game Theory](#)
- ▶ [Handicap Hypothesis](#)
- ▶ [Natural Selection](#)
- ▶ [Sexual Selection](#)

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Evolution of Cooperation

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Synonyms

Cooperation among non-kin; Cooperation to solve the prisoner's dilemma; Evolution and the theory of games; Evolution of reciprocal altruism and punishment; Strategies for successful cooperation; Theory of reciprocal altruism

Definition

A book by Robert Axelrod, published in 1984, to explain cooperative behavior in humans in light of Game Theory.

Introduction

The Evolution of Cooperation is a book by Robert Axelrod written to explain how cooperative behavior evolved and is maintained in humans in light of *Game Theory*. The book is an expansion of an earlier paper coauthored by Axelrod with William Hamilton (Axelrod and Hamilton 1981). The purpose of the research was to build on a theory of what conditions are necessary for cooperation to emerge, specifically in a scenario in which individuals can pursue their self-interest without a central source of authority (i.e., societal rules or laws) to force cooperation through future consequences.

Adaptive Cooperation

Drawing on Game Theory and using computer simulations, Axelrod investigated the power of different strategies in a sequential (i.e., multiple rounds) paradigm of the prisoner's dilemma. Axelrod invited scholars in Game Theory to submit possible strategies, and each was tested

against other strategies in a computer simulation. Through this work, the “tit-for-tat” strategy emerged as the most successful, shedding light on the nature and origins of human cooperation. The tit-for-tat strategy is where the player cooperates in the first round and then mimics the choice of the other player’s previous round in all subsequent rounds.

The prisoner’s dilemma game involves a simultaneous choice (i.e., each player must make the choice without knowing what the other will do) between two players to either cooperate or defect. In this game, defection yields a higher payoff than cooperation when paired with a cooperate choice from the other party, but if both defect, they both do worse than if both had cooperated. In addition, the cost of being defected on after cooperating is still greater (see ► [“Prisoner’s Dilemma”](#) entry for more detail).

Analysis of the data from the simulations identified four properties which accounted for the success of the tit-for-tat strategy: (1) the potential for harmony by avoiding unnecessary conflict by cooperating as long as the other player cooperates, (2) provocability in the form of retaliation for a defection by the other by defecting in the next round, (3) forgiveness after responding to a provocation with a defection by responding to instances of cooperation with cooperation after this, and (4) clarity of behavior so that the other player can adapt to the tit-for-tat strategy pattern of action.

In a single encounter, the most effective choice is to defect as this will yield the highest payoff: If the individual believes, or expects, that the other is going to cooperate, then they will gain the most points by defecting. Moreover, even if the individual believes the other will defect, it is still preferable to defect as the cost for cooperating and being defected on is greater than mutual defection. Therefore, no matter what the other player does, it is more strategic to defect. However, in a pool of other consistent defectors, this would yield the second most costly solution (with the first most costly being cooperating with a defector): The other player is naturally in the same situation, meaning, in a single encounter, both should defect, but if so the players will do

worse than if both had cooperated, leading Axelrod to conclude that individual rationality leads to a worse outcome for both than is possible (Axelrod 1984). Thus, the evolution of cooperation required that individuals have a reasonably large chance to meet again so that they have a stake in future interactions rather than just the interaction in hand. Under the conditions of potential repeat encounters, an initial disposition to cooperate (followed by reciprocation) can indeed emerge as adaptive in a world of self-interested organisms without any central authority.

From his simulations, Axelrod proves that cooperation can evolve against three potential problems. Firstly, Axelrod shows that cooperation can arise even starting from a in a world of unconditional defection. That is, cooperation can evolve from small clusters of individuals who qualify their initial predisposition to cooperation on reciprocity. Secondly, a strategy based on reciprocity can continue to thrive in a world where various other different strategies are also being attempted as it will prove superior to these alternatives in the long run. This is again due to the protection provided by retaliatory reciprocation of defection as well as the ability to recover from a vicious cycle of defection via forgiveness. Finally, once a collectively stable system is established on the basis of reciprocity, cooperation will protect itself from invasion by less cooperative strategies by outcompeting them in the long run. The only other strategy that is also collectively stable is to always defect. This strategy can never be invaded as long as alternate strategists arise one at a time. However, if tit-for-tat strategists arise as a cluster, it will thrive better and become dominant over time. That is, assuming individuals have some control as to who they interact with, a cluster of tit-for-tat strategists will interact within itself with increasing probability rather than with the always defect strategists, retaliating when they do to prevent these strategists from any further gain after the first case of defection.

Axelrod illustrates the evolution of cooperation using the real-world example of a prisoner’s dilemma: soldiers in World War I. When these soldiers were not engaged in combat, they spent most of their time in trenches near each other

without attempting to harm each other. As a volley of grenades could easily be answered with a retaliatory volley of grenades and mutual survival was more in everyone's interest than mutual destruction, cooperation (at least insofar as refraining from killing each other outside of direct battles) was maintained via tit for tat.

The Evolution of Cooperation goes further than merely providing an overview of how cooperation arose and is maintained by applying this knowledge to provide advice for individuals faced with a prisoner's dilemma style situation and suggests how to promote cooperation. When faced with circumstances demanding the selection of either cooperative or competitive strategies, outcome can be optimized by following four rules: (1) Do not be envious as envy is self-destructive. That is, rectifying a discrepancy between your own success and another's can only be achieved with defection, but defection leads to more defection and mutual punishment in an environment of reciprocity. (2) Do not be the first to defect as, in a system of reciprocity, this will likewise lead to a cascade of mutual punishment. (3) Reciprocate both cooperation and defection as a strategy of consistent defection is only suppressed by punishment via reciprocated retaliatory future defection. (4) Do not attempt to be too clever by mixing up the strategy as, assuming that the game is likely to continue for at least one more interaction, reciprocation will never allow defection to go unpunished. Building on this, when it comes to promoting cooperation, Axelrod suggests emphasizing the future ("enlarging the shadow of the future," 1984, p. 129) as mutual cooperation is only stable if the future is sufficiently important relative to the present, changing the payoffs making the long-term incentive for mutual cooperation greater than the short-term incentive for defection, teaching people to care about each other, and making the concept of reciprocity clear.

Conclusion

The Evolution of Cooperation is a book by Robert Axelrod, published in 1984, to explain cooperative behavior in humans in light of Game Theory, specifically, multiple rounds of the prisoner's dilemma

game. The "tit-for-tat" strategy (where the player cooperates in the first round and then mimics the choice of the other player's previous round in all subsequent rounds) emerged as the most successful, shedding light on the nature and origins of human cooperation. Axelrod proves that such cooperation can evolve against several potential problems and outcompete alternate strategies.

Cross-References

- ▶ [Altruism Among Nonkin](#)
- ▶ [Evolution and the Theory of Games](#)
- ▶ [Evolution of Punishment](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Game Theory](#)
- ▶ [Game Theory as a Foundation of Evolutionary Psychology](#)
- ▶ [Morality Is Cooperation](#)
- ▶ [Prisoner's Dilemma](#)
- ▶ [Prisoner's Dilemma and Cooperation](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Robert Axelrod](#)
- ▶ [Sarah Brosnan](#)
- ▶ [Social Exchange Among Non-kin](#)
- ▶ [Strategies for Successful Cooperation](#)
- ▶ [Theory of Reciprocal Altruism](#)

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Evolution of Crime, The

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Synonyms

[Criminal acts and criminal behavior](#)

Definition

Crime consists of acts which contravene the human moral code and statutory law. Evolutionary principles such as conflict and kin selection, reciprocation, sexual selection, parental investment theory, and strategies to outcompete rivals are used to explain the evolution of crime and criminality.

Introduction

The application of evolutionary principles to our understanding of crime and criminality is a recent development due to the advent of evolutionary forensic psychology. To understand the functionality of crime using an evolutionary perspective, it is important to define what crime and criminality are. A diversity of social definitions has been developed by social scientists; for our purposes here, however, we will resort to a legal approach. Despite there being cross-cultural discrepancies in how minor crimes are perceived and defined, McGuire (2004) has highlighted remarkable uniformity in how serious crimes are considered cross-culturally irrespective of the criminal justice systems employed. It is worth noting that where behavioral responses are observed to be universal, it can be taken as suggestive that they arise from ancient common origins (Brown 1991). Hence, homicide, rape, pedophilia, incest, aggravated burglary, and arson are examples of offenses that, cross-culturally, are considered as *mala in se* crimes – a legal term used to describe criminal behaviors which contravene the human moral code (Davis 2006; Taylor 2016). These types of crime are considered as very serious and induce a sense of universal repugnance.

Another cross-culturally recognized legal concept is corpus delicti. Corpus delicti encapsulates the idea of “body of crime.” Put simply, this refers to evidence and information proving that a criminal event has occurred. To ascertain corpus delicti, there has to have been a guilty act committed such as homicide (*actus reus*) and the presence of a guilty mind such as harming with intent (*mens rea*). To establish a suspect’s guilt of a specified offence, both *actus reus* and *mens rea*

are considered, and evidence is presented in a court of law. If the crime committed is of a less serious nature such as breaking the speed limit, then the perpetrator is convicted under statutory law which varies cross-culturally. This variation is socially determined, and the punishment for breaking such regulatory statutes prohibiting specified behaviors is presided using set tariffs (these are defined in *mala prohibita*). Due to their cross-cultural commonalities (and, in particular, how these criminal acts elicit very similar legal and social responses cross-culturally), evolutionary principles can best be used to explain *mala in se* crimes. Evolutionists consider that such crimes can be thought of as based around decision-making that arose to resolve recurrent ancestral challenges. In contrast, due to their cross-cultural variation, this is unlikely to be the case for *mala prohibita* crimes. Hence, here we explore adaptationist explanations that have been developed in order to understand the relationship between evolutionary principles and *mala in se* crimes. The first evolutionary explanation considered is “conflict related to status and mating opportunities.”

Conflict Related to Status and Mating Opportunities

Duntley and Shackelford (2008) reviewed the implications of interindividual conflict over status, material, and mating resources. Their basic contention is that increases in status would require an individual to develop specialized cognitive adaptations brought about by selection pressures as a means of ascending the hierarchy. Having resources such as food, territory, tools, and weapons implies an individual’s (usually male) competency and capability to survive and protect any mate and offspring from situations of jeopardy. During the ancient past, ascending the hierarchy would most likely have increased inclusive fitness. Conflict can occur both across (inter) and between (intra) the sexes. In the case of intra-sex conflict, males are more likely to take risks in order to secure mating opportunities. It is no surprise therefore that, from an evolutionary perspective, men who used violence as a risky strategy

were, in many cases, more likely to achieve their ambition of securing mating opportunities through the intimidation of their male competitors. The use of violence therefore, as argued by Daly and Wilson (1988), can be an adaptive strategy to ward off potential male competition vying for mates and resources.

Given the importance of status, material, and mate resources, males can resort to strategies of cheating, such as theft; achieving reproductive success without consent, such as rape; and attaining status and material resources through the use of violence and homicide. Theft is an antisocial behavior that deprives an individual (the victim) of their status and resources. This can potentially increase the perpetrator's social profile through having stolen status and resources ultimately used in an effort to attract a mate. Rape is a *mala in se* act because it is a sexual behavior forced upon a non-consenting female (most frequently). This is costly to the female both emotionally and physically, and additionally, she could be carrying offspring from a man who has bypassed female mate choice criteria. From the male's perspective, however, he has increased the chances of passing on his genes which might not have happened had he been subjected to female mate choice criteria.

The use of violence can also signal an individual's status as being non-exploitable and act as a buffer against violent confrontations in the future. This can also enable such an individual to obtain assets from less resilient competitors. In the case of homicide, cost-inflicting competitors are permanently removed and their resources assimilated. Buss (2005) explains violence and homicide using an evolutionary perspective. Winners of confrontations gain the reputation of being tough and can avoid having to consolidate this status through future fights. Losers of confrontations may concede their resources to the winner and gain the reputation of being exploitable. They may also become more likely to endure future fights because of their status as exploitable.

Ultimate explanations help us to understand why males were more likely to turn to violence than females in our hominin ancestry. In most present-day societies, however, levels of violent

aggression are perceived as substantially lower than during our ancestral past (Pinker 2011). This begs the questions of why this should be the case and how did it arise. Most individuals conform to the social values set within their society and develop a moral compass courtesy of a socialization process which reflects these values. Moreover behaviors considered to be appropriate are often underpinned by morals condoned by society. Antisocial behavior such as criminal acts contravenes these values. Moral behavior can be considered to be a hominin legacy which served a function in our evolutionary past. Our next evolutionary explanation relates to the importance of how morality evolved to promote prosocial behavior.

Evolution of Morality in Relation to Criminal Behavior

Social scientists generally consider that a sense of morality arises out of cultural practices. Evolutionist Denis Krebs begs to differ. Krebs (1998) considers there are three important pathways which direct the evolution of morality in all cultures: altruism via reciprocity, deference to authority, and devotion. In order to understand the importance of altruism, it is important to consider how early hominins lived and survived in a challenging environment. Fossil and artifact records suggest that ancestral groups consisted of between 20 and 200 individuals, many of whom were genetically related and others considered as fictive kin. According to Barkow (1989) cooperation between these hominin dwellers was key to their survival and relied on close bonds and reciprocation. Trivers (1972) previously referred to this as reciprocal altruism and deemed it necessary for the creation of a prosocial living environment. Under these living conditions, all individuals benefited from the results of successful foraging and hunting regardless of whether they were the ones responsible for the successful expedition. This implies that in order to survive and reproduce, all members must play by the rules of cooperation and sharing. Those who do not but still try to reap the rewards are likely to have been

considered as free riders and once detected had either to conform to the group norms or risk being ostracized. Trivers also claimed that living under these conditions helped to create emotional ties and provided selective forces for the evolution of a moral code.

Empathy and morality are important facets in the development of prosocial behavior. In a society where laws have been developed, consensus behavior becomes prosocial rather than antisocial. Nevertheless, free riders in present-day societies according to Mealey (2005) and Workman and Reader (2014) are likely to be retained in the population provided their numbers are proportionately low. Hence, cooperative societies open up opportunities for free riders. Nayef Al-Rodhan (2008) states that we act according to our emotional self-interest directed by “genetically coded survival instincts. . . .modified by the totality of our environment and expressed as neurochemically-mediated emotions and actions” (p. 16). We therefore rely on laws and rules to provide an environment of organized social order. A moral code, on balance, according to Ruse and Wilson (1985), helps increase our inclusive fitness. They draw upon the concept of epigenetic rules that are driven by our genes. Why this is important in the evolution of crime rests on how some of our laws have developed over time. One such example is the illegality of incest and why the tariff of punishment is high across many societies. Incest is a *mala in se* crime. In the case of incestuous relationships, the consequences will be an increased probability of having a karyotype littered with deleterious double recessive genes (technically known as “inbreeding depression”). According to Ruse and Wilson, these moral codes are grounded in our genotype and increase the likelihood of offspring survival. Hence, developing a law against incest is there for good reason, and such behavior is frequently punished by criminal justice systems. This is a good example of evolution and cultural development (i.e., laws) working in tandem.

With regard to the second facet of Krebs’ pathway, deference to authority, it can be seen that individuals who obey the law and behave prosocially rather than antisocially are more likely to survive. Krebs argued that a social hierarchy existed among early hominins dictated by “alpha

males.” Those who refused to show deference to such males either engaged in defiance through fighting them and winning a new founded status or fighting and losing sometimes resulting in death. This rarely happens in modern society as humans show deference to the societal infrastructure (e.g., the police force) and legal system. In the case of devotion, Krebs’ third pathway, the development of strong attachment bonds, is the glue which keeps relationships intact. It is this which helps promote the survival of any offspring. Krebs’ model is very informative in understanding the point of origin for many *mala in se* crimes. This can be seen in parental rejection and neglect of offspring, which warrants a high legal sanction. Equally, when an individual contravenes codes of appropriate behavior such as taking another person’s rights using violence or rape, then there are high legal tariffs to be served.

In addition to common cross-cultural patterns, at the individual level, scanning technology provides empirical support for an evolved neural basis of moral behavior. In some studies evolutionary psychologists have explored activity in the brain using fMRI scans while the participant is subjected to moral-oriented information. The data from studies adopting this approach reveal the existence of evolved brain mechanisms enabling us to make moral-based decisions. According to Taylor and Workman (2020), “This. . . .provides impetus to the notion of there being moral universals, which, when transgressed, can be considered to be universal crimes.” Research by Greene et al. (2001) provided evidence using fMRI scans of specific activation of localized areas in the brain when making moral decisions. Such specific areas include the medial frontal gyrus, posterior cingulate gyrus, and angular gyrus, all of which are particularly activated during moral-personal decision-making. Having evolved a neural substrate to help avoid seriously harming others (largely kin and kith) in the group would have been an effective adaptation (Taylor and Workman 2020). It is likely that the evolution of empathy allowed us to inhibit *mala in se* acts. For some individuals, however, empathy is reduced or absent. Interestingly, for many of these individuals, a diagnosis of a personality disorder helps us

understand why they are attracted to what is considered a criminal lifestyle. In recent years psychologists have identified a cluster of specific personality factors labeled the “dark triad” that increase the likelihood of criminality developing.

Crime and the “Dark Triad”

In 2002, Paulhus and Williams introduced the concept of the “dark triad.” They describe three sub-clinical personality traits: narcissism (callous and self-interest), Machiavellianism (manipulative exploitative), and psychopathy (emotionless, cold, impulsive, and risk-taking). The “dark triad” is a collection of traits clustered in individuals who have a tendency for committing crime (often *mala in se* crime). Whereas traditional psychological approaches question why the “dark triad” is maintained in the population, evolutionary psychologists believe they may have the answer. According to Jonason et al. (2009), the “dark triad” traits promote success in short-term mating and are correlated with increased intra-sexual competition. In 2017 Međedović, Petrović, Želeskov-Đorić, and Savić investigated the association between psychopathy and reproductive success by studying a Serbian male prison population. They found that some traits typifying the psychopath’s lifestyle (for instance, irresponsible and impulsive) actually correlated with fewer offspring but other (interpersonal) traits such as manipulation and dishonesty were related to having more surviving offspring. It appears that manipulation and dishonesty facilitate the psychopath’s ability to cheat (Lyons 2015). Međedović et al. conclude that different facets of psychopathy influence the number of offspring fathered. It is not only males, however, who can receive the diagnosis of the “dark triad.” Brewer et al. (2019) subjected female online participants to a series of questionnaires that measured levels of narcissism, Machiavellianism, and psychopathy. They found that high scorers on the “dark triad” engaged in sexual deception. In particular narcissism was associated with blatant lying, Machiavellianism with blatant lying and lying to escape confrontation, and psychopathy with self-serving deception and an increased

likelihood of exhibiting an avoidant relationship attachment. This latter point may be a consequence of having a callous unemotional and non-empathic disposition with a tendency for risky behavior. Over all it appears that, under certain circumstances, criminals who have the “dark triad” may be using an alternative strategy to boost their inclusive fitness.

This hypothesis is supported by McGuire and Troisi (1998) who claim that the ability to deceive and exploit others can be adaptive. Mealey (2005) adds that this adaptive strategy is more likely to be maintained among populations where reciprocity is prevalent. McGuire and Troisi state that, “In a society made up primarily of reciprocators, genes for cheaters can enter the population and remain, provided persons with such genes reproduce” (1998, p. 191).

A well-publicized account of criminal behavior by a man who clearly exhibited the “dark triad” is Mick Philpott. In 2013, UK citizen Philpott was accused of murdering his six children by deliberately starting a fire to the home using petrol while his children slept. Both he and his wife were seen on television crying and appealing to the public to provide the police with any information that could lead to the arsonist’s arrest. It was a pretense that was maintained during and post investigation. When his lifestyle choices and previous behavior were considered, it became apparent that he was a dangerous criminal psychopath. He had 17 children with different women and used violence to control the family. He had previous convictions of assault for which he was imprisoned. He later confessed to staging the fire so that he could then save the children and be seen as the hero. This typifies the egotistic grandeur of a man who has the “dark triad.”

The presence of the “dark triad” goes a long way toward explaining many *mala in se* crimes. Most serious crime, however, is committed by individuals who have not been diagnosed with a personality disorder. The majority of these serious criminals are males (Archer 2004; Campbell 1999; van Vugt 2009). But why should this be the case? Can this difference be accounted for using explanations from an evolutionary perspective? Evolutionary psychologists explain this difference

by drawing on sexual selection theory and the concept of asymmetrical parental investment.

Sexual Selection and Asymmetrical Parental Investment in Relation to Male Violence

Taylor and Workman (2020) draw upon sexual selection and parental investment theories as explanations for why more risky behavior such as aggressive and violent acts is performed by males than females. Females invest more heavily in the production of offspring than males throughout development and in particular through the processes of gestation, parturition, and lactation. It therefore makes sense for them to be more risk averse and to avoid physical aggression (Campbell 1999; Kanazawa 2009). In contrast, when males engage in aggressive acts, it is less likely to be damaging to their offspring. Archer (2004) and van Vugt (2009) argue that aggressive behavior might have provided male hominins with fitness benefits such as status, reputation, and resource gain. van Vugt labeled this the “male warrior hypothesis.” Support for the “male warrior hypothesis” comes from a study by Bourgeois and Fisher (2018) which showed an increased likelihood of males committing violent robbery than females and that a victim was more likely to incur injury when more than one male perpetrated the offence.

If we had to predict who is most likely to commit a violent crime then, rather than focusing on males in general, we should focus on young men. In fact the statistics show a preponderance of younger males committing violent crimes when compared with their older counterparts. According to Kanazawa (2009), adolescence is a period in a male’s life where he strives for status and resource attainment as an evolved strategy of attracting females. Kanazawa suggests there is a robust link between sexual selection and criminal violence among young males. Beyond the age of 30, male violence decreases as they are more likely to have reproduced and the costs of violent behavior outweigh the benefits of providing

parental care (Cartwright 2016; Kanazawa and Still 2000). There are exceptions. As we have seen, some males (such as Philpott discussed earlier) often fail to shift from aggressive behavior to a parental caring mode. The murder of children is a cross-cultural phenomenon that is a heinous crime classified under *mala in se*. Can evolutionary principles be applied to infanticide?

Infanticide: The Cinderella Syndrome

Related to the above, one of the contentions of parental investment theory is that the closer the kin, the greater the probability that parents will invest their time, effort, and resources in them. Parents will invest in their direct offspring first and then to genetically related extended family members. Conflict does arise between kin but far less frequently than observed in nonkin. Parental investment theory can help to explain this difference in conflict response through the fact that kin share genes by common descent, leading to a reduction in physical aggressive response. In a typical family of genetically related individuals, Daly and Wilson (1988) argue that the level of conflict is reduced and more likely to be replaced by altruistic behavior. In contrast, there is a preponderance of conflict in families which consist of unrelated individuals, especially when we consider homicide rates across stepparent and stepchild relationships.

Dustin and Alcock (2018) claim that, in collectivistic societies, kin often adopt the children of their genetically related extended family in situations of loss. In individualistic societies, however, reconstituted families (i.e., stepparents and stepchildren) in which there is no sharing of genes by common descent, stepchildren are often treated less favorably. This scenario is well recognized in individualistic societies. In line with the fairy-tale character Cinderella, who is treated harshly by her stepmother, this phenomenon has been labeled the “Cinderella syndrome.” Given that the offspring’s contribution to the stepparents’ inclusive fitness is generally zero, from an evolutionary perspective, we can predict the level

of parental investment will be lower for stepchildren than for biological offspring. In extreme cases this can lead to *mala in se* crimes. Daly and Wilson (1988), for example, found that infanticide was 120 times greater in a family where one stepparent was living. They also found that the probability of a 2-year-old child or younger experiencing physical abuse is seven times more likely if one of the parents was the child's stepparent than when both were biologically related (Daly and Wilson 2007). This finding was supported by Archer (2013) who uncovered evidence that in nine out of ten studies of child infanticide, the frequency and intensity of violence perpetrated by the stepparent significantly exceeded that committed by biological parents. His findings support the "Cinderella syndrome" which accounts for why some stepparents fail to cope within a reconstituted family context.

Conclusion

While social scientists and mainstream psychologists explain the existence of crime in terms of proximate situational variables, evolutionary psychologists suggest the emergence of criminal behavior can be explained by adopting adaptationist thinking. Crimes which are considered universally to be serious (*mala in se* crimes) can be seen as ways of solving ancient recurrent challenges. A number of explanations are presented for such crimes based on evolutionary principles. Such explanations include consideration of kin selection, sexual selection, parental investment theory, the maintenance of the "dark triad," and the "Cinderella syndrome." Some evolutionists consider that, by relating current criminal practices to evolved propensities, we may be better able to develop an overarching explanation for such serious antisocial behavior.

Cross-References

- [Criminology](#)
- [Criminal Personality Variables](#)

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Evolution of Desire, The

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Synonyms

Attraction; Mate preferences; Mate retention; Mate selection; Mating; Mating psychology; Mating strategies

Definition

This book provides a unified theory of human mating strategies, anchored in the best scientific evidence available on sexual psychology.

Introduction

The Evolution of Desire: Strategies of Human Mating was first published by Basic Books (Buss 1994). It took 4 years to write and represented a synthesis of a decade of research on the psychology of human mating by the author. Two chapters were added to a revised edition in 2003, although the original ten chapters remained in unmodified form. *Desire* was updated and revised thoroughly from top to bottom (Buss 2016) and represented an explosion of empirical research in the years since its original publication. *Desire* has become a citation classic (more than 2,000 scholarly citations as of 2016). It is widely used in college courses. It is used by scientists to guide mating research. And it is used by everyday readers to inform their own mating lives.

Although one previous excellent book had been written about the evolution of human sexuality – Donald Symons’s (1979) classic treatise, *The Evolution of Human Sexuality* – the goals of *The Evolution of Desire* were broader than sexuality per se. It aimed to look at human evolved

Evolution of Culture

► Human Nature and Biocultural Evolution

psychology of mating more expansively, including all the action that happens prior to, and after, sexual activity proper – strategies of mate competition, mate attraction, mate selection, mate retention, mate poaching, conflict between the sexes, mate ejection, and remating over the life span.

A key theoretical premise of *The Evolution of Desire* is that humans have a menu of mating strategies, not just a single one, and that some of these strategies show important gender differences. Humans most obviously have long-term mating (sometimes called pair-bonding, committed mating, or marriage), although this turns out to be rare among mammalian species, characterizing perhaps only 3 %. Humans also have short-term mating or casual sex, serial mating, mate poaching, and infidelity, which represents a mixed mating strategy of one long-term mateship with some sex on the side. Understanding all mating strategies requires first identifying what women and men want. It all starts with desires in a mate.

Desires in Human Mating

What people desire in a mate, selective mate preferences, captures a key component of Darwin's theory of sexual selection. Desires draw us to some potential mates. They repel us from others. Iterated over generations, the desires of one sex determine the qualities favored or shunned, producing evolution or change over time. Prior to 1989, little was known about what women and men wanted in long-term mates. David Buss's 37 culture study, involving 10,047 individuals on five continents and six islands, provided the first massive cross-cultural findings on this key topic (Buss 1989a).

The Evolution of Desire synthesized this and all scientific studies available at the time in Chapter 2 (What Women Want), Chapter 3 (What Men Want), and Chapter 4 (Casual Sex). These chapters describe sexual similarities in mate preferences, universal sex differences, and cultural variation. Universal preferences include the desire for mates who are kind, understanding, intelligent, dependable, emotionally stable, and healthy. Importantly, people worldwide want

mates with whom they are in love and who are in love with them, overturning conventional social science beliefs that love was a Western European invention and not a universal across cultures. The emotion of love exists worldwide, appears in long-term but not short-term mating, and serves as a form of psychological commitment – an idea articulated independently by the economist Robert Frank (1988) and David Buss (1988) the same year.

Desire also described universal sex differences. Women more than men desire mates who provide good economic resources, as well as the attributes linked with long-term resource acquisition such as ambition, industriousness, and social status. Men more than women prioritize physical attractiveness and relative youth – important cues to fertility. These are universal sex differences that were predicted in advance by evolutionary hypotheses; they have been robustly replicated by dozens of researchers since *Desire*; and they show no signs of diminution over time. Cultures also differed dramatically in some desires, such as the desire for virginity in a potential spouse. Swedes, for example, did not value virginity at all, whereas Chinese at the time saw virginity as virtually indispensable (Buss 1989a).

Chapter 4 delves into the deep scientific evidence for sex differences in the psychology of short-term mating (as contrasted with long-term mating). David Schmitt and David Buss were the first to systematically document gender differences in mate preferences as a function of this temporal context (Buss and Schmitt 1993). Men, for example, prioritized high sex drive, sexual experience, and physical attractiveness in short-term mating, while despising prudishness and a low sex drive. Women also increased the importance they attach to physical appearance, but ramp up their desire for immediate resource displays from a man. Chapter 4 also delves into the scientific evidence for gender differences in the desire for sexual variety. It highlights its many psychological design features of short-term mating psychology, including attraction to novel partners, letting little time elapse before seeking sex, relaxing standards for a partner, and showing a sexual over-perception bias that causes men to

over-infer women's sexual interest. It also speculated about men's attraction decrement post-intercourse – designed to motivate a hasty post-copulatory departure and minimize investment and commitment – a hypothesis that was subsequently tested and supported only for men pursuing a short-term mating strategy, as predicted (Haselton and Buss 2001).

Mate Competition: Attraction and Derogation

Several chapters in *Desire* capture what is known about intrasexual mate competition – the second key component of Darwin's theory of sexual selection. They focus on two generic strategies – *tactics of attraction* and *derogation of competitors*. According to sexual selection theory, these should focus on dimensions desired by the other sex. Stated differently, the desires of one sex establish the ground rules of same-sex mate competition. Studies bear out this key prediction. Both men and women display and deploy tactics that involve acts of kindness, intelligence, and brimming good health. Sex-differentiated tactics involve resource display, physical protection, and appearance enhancement. Women, for example, spend more than nine times as much money on beauty products. Men display status, ambition, and resources and show a willingness to commit them to one woman, at least in long-term mating.

Tactics for attracting short-term mates differ somewhat. Schmitt and Buss (1996) found that men seeking short-term mates were more likely to engage in immediate resource display, whereas women were more likely to give off cues to immediate sexual access. Because more men than women seek short-term mates, women generally have their pick on the short-term mating market, and these sexual signals are extremely effective for them. Men sometimes deceive women, feigning long-term interest for the purpose of gaining short-term sex. *Desire* goes into depth about these and other tactics of short-term and long-term mate attraction.

Derogation of competitors – the ways in which we use language to impugn the character and

desirability of our rivals – is a second strategy in the arsenal of human mate competition. And the desires of one sex again set the ground rules of the game. Men are more likely than women to impugn a rival's status, resources, and athletic prowess. Women are more likely than men to derogate their rival's physical attractiveness (e.g., “she has heavy thighs”) and sexual selectivity (e.g., “she slept with the whole football team”). Men seeking a long-term mate are hugely turned off by a woman's promiscuity, since it jeopardizes his paternity certainty. They are not averse to this quality when seeking a short-term mate. As the actress Mae West once noted, “Men like a woman with a past because they hope history will repeat itself.”

Conflict Between the Sexes

One chapter of *Desire* that garners much attention centers on sexual conflict – the ways in which men and women interfere with each other's mating strategies. Conflict between the sexes occurs on the mating market. One example stems from differing perceptions of mate value, such as when a man approaches an attractive woman he believes is within his mate value range, but she does not concur. Another source of conflict is when one person is seeking a long-term mate and the other a short-term mate, which has selected for strategies of deception. A man might feign long-term interest for short-term sexual access. A woman might present herself as costless sex and then attempt to convert the relationship into one of long-term commitment. These are all forms of “strategic interference,” whereby a member of one gender blocks or impedes a strategy pursued by the other (Buss 1989b).

Committed couples sometimes break up. The causes are well predicted by sexual strategies theory and a deep understanding of human mate preferences. Men's failure in resource provisioning, for example, violates what women want. Women's decrement in appearance or older age sometimes causes men break up. Conflict over pooled resources and over in-laws are common sources of friction. And infidelity, sexual or financial, violates desires and often leads to breakups.

Mate Retention and Mate Ejection

Tactics of mate retention and mate ejection also should follow the logic of evolved desires. Successful tactics of mate retention embody what a mate wants, such as kindness, attentiveness, love, affection, gifts, resource flow, and sexual access. *Desire* describes how men's efforts at mate retention are partly a function of women's youth and attractiveness (Buss and Shackelford 1997). Women allocate more effort to retaining mates who are higher in status and income.

Successful tactics of mate ejection are typically those that violate men's and women's initial desires. Being cruel violates the desire for kindness. Having an affair violates the desire for sexual loyalty. Withdrawing resources violates the desire for provisioning.

Mating Over the Life Span

Nothing remains static over time. Humans undergo some predictable changes, but also show enormous variation in those changes. Fertility, for example, inexorably declines with age for both sexes. Importantly, women and men show different life span fertility curves, with women showing an earlier and steeper decline than men. Access to status and resources is considerably more variable. Male status and resources rise through the 20s and 30s, along with hunting skills in traditional societies and job promotions in modern societies. Nonetheless, some experience dramatic declines with age, and others experience dramatic rises with age. In short, status and resources over the life span peak later than does fertility and show much greater variability over the life span than does fertility. These life span conditions influence important dimensions of mating – whether couples stay together or divorce – individual mate values upon reentry into the mating market and many others.

Condition-Dependent Mating Adaptations

Throughout the book, *Desire* emphasizes that human mating adaptations are contingent on key

contexts. Personal mate value, for example, is a context that affects one's ability to implement a preferred mating strategy. Sex ratio in the mating pool – the number of men relative to the number of women – influences both mate value (the rarer sex has higher on-average mate value) and also whether mating strategies shift more to short-term mating (e.g., for men, when there is a surplus of women) or long-term mating (for men, when there is a surplus of men). Our mating psychology is also contingent on many other circumstances: parasite prevalence in the local culture or ecology, the degree to which parents and kin influence and constrain an individual's mating decisions, women's access to resources, level of gender equality, and many others.

Conclusion

In 1994, *The Evolution of Desire* crystallized a new field – strategies of human mating. In the decades since its original publication, this field has mushroomed. Thousands of scientific articles have been published on the topic since 1994, and the 2016 revised and updated edition of *Desire* highlights some of the most important scientific developments. We now know the broad outlines of the strategies of human mating. But new work continues to reveal facets of our mating psychology previously undiscovered. In this sense, the scientific understanding of human mating strategies keeps expanding and deepening. Given the centrality of reproduction to evolution by selection, and of mating to reproduction, it should perhaps not be surprising that human mating psychology shows this enormous complexity of design. There still remains much mating gold to be discovered by intrepid scientific explorers.

Cross-References

- ▶ [David Buss](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Violation of Long-Term Mate Preferences](#)

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Evolution of Emotion in Social Context

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Synonyms

Evolution of social emotions; Social emotion evolution

Definition

Human emotion evolved – that is, came to be via natural selection – in an inherently social context; human emotions are therefore not separable from their social nature.

Introduction

While it is widely recognized that there is an important interplay between emotions and human social life, the social mechanisms by which emotions came to be via natural selection are not often considered. Extant theorizing on the evolution of emotions (hereafter referred to as *EvoEmo*) has traditionally focused on the modular cognitive or neural architecture that produces a small set of emotions, which are believed to serve discrete functions in the service of reproductive fitness (Cosmides and Tooby 2000; Tooby and Cosmides 2008). In these modular views, social functions are either not addressed or are just one type of function that may be important for reproductive success. Importantly, however, such modular theories are not the only perspectives that focus on the functions of emotions, nor the only theories that speak to how emotions evolved.

Two theoretical perspectives on emotion – those that adopt functionalist frameworks and those that adopt constructivist frameworks – offer important insights into *EvoEmo* that differ from classic evolutionary perspectives. Functionalist perspectives on emotion investigate a range of functions of many different emotions in modern humans and, in particular, often focus on the social functions of emotions and the social contexts in which emotions arise. Functionalist views sometimes, but not always, explicitly draw on evolutionary logic. Constructivist views of emotion, which postulate that emotions emerge from a set of more basic or fundamental ingredients rather than from modules, offer an alternative theoretical starting place for understanding *EvoEmo*. This entry presents the argument that synergy between functionalist and constructivist views provides insights into how and why

emotions evolved in social contexts and evolved to serve social functions.

The Evolution of Emotions and the Importance of Functions

The empirical study of EvoEmo is particularly challenging because emotions, like other psychological phenomena, did not leave a fossil record. Further, unlike the case of other behavioral phenomena, it is challenging, if not impossible, to make strong inferences about emotions from what is left in the fossil records. In contrast to the study of EvoEmo, for example, it is possible to study the evolution of hands by examining fossils (e.g., Almécija et al. 2015; Domínguez-Rodrigo et al. 2015). Variation observed in fossils enables theorizing about how grasping, and complex behaviors that require grasping such as throwing, clubbing, and tool making, came to be over evolutionary time via natural selection (e.g., Marzke 2013; Young 2003). No such option for linking the fossil record to emotions exists, either directly or via logical inference. As a result, scientists with interests in EvoEmo have largely focused on the study of modern humans.

In the absence of fossil record, emotion theorists interested in EvoEmo have turned to several sources of data from modern humans to support their claims. For example, classic EvoEmo theories stipulate that a small set of emotions came to be during the early period in which humans appeared – typically during the Pleistocene epoch – because they met unique evolutionary demands for reproductive fitness (Cosmides and Tooby 2000; Tooby and Cosmides 2008). This set of assumptions confers the idea that emotions are biologically hardwired and therefore present at birth in humans and universal (i.e., all humans have them). As a result, developmental data are thought to be one source of support for claims about the modular and hardwired nature of emotions, grounded in the logic that if human infants demonstrate evidence for this small set of emotions, then those emotions must be biologically endowed (for recent empirical example of infant

studies on discrete emotion perception: Cong et al. 2018; Lee et al. 2015).

Cross-cultural data are also levied to support EvoEmo claims. If a small number of emotions are perceived and expressed in all human cultures, then this is held as evidence for the idea that the small set of emotions is evolutionarily conserved because it is universal in all people (for recent examples: Cordaro et al. 2018; Fang et al. 2018; Sauter et al. 2010, 2015). Data of these sorts have been challenged robustly in recent times, calling into question the methods used, interpretation of the data, and whether the theoretical claims made based on those data are valid (a review of those challenges is far beyond the scope of this entry, but see Barrett et al. 2018; Gendron et al. 2015; Nelson and Russell 2013; Widen 2013).

Another source of data that may speak to EvoEmo is data on the function of emotions in modern humans. Classic EvoEmo views (e.g., Cosmides and Tooby 2000; Tooby and Cosmides 2008) make inherent use of functionalist data and claims based on the assumption that modular, hardwired, and evolutionarily conserved emotions in their modern form (in humans alive today) reflect emotions in their ancestral form (in the first humans) with fidelity. The functions of emotions in modern humans are therefore thought to tell us something about the functions of emotions in our ancestors, thus allowing for the development of hypotheses about how those functions promoted fitness and came to be via natural selection. For example, the emotion jealousy has been suggested to arise when a relationship is threatened in order to guide behavior to reduce or eliminate that threat or fortify the relationship in question. Jealousy is held to be particularly important in the context of sexual relationships and mate selection (both of which are thought to have a clear link to reproductive success; for a review: Buss 2018).

The problem with claims about how the functions of emotions in modern humans served fitness demands in ancestral humans is that there is no way to verify that the functions of emotions in modern humans map in a one-to-one way with functions of emotions in ancestral humans. Further, no evidence exists for the hypothesized

conserved neural and physiological modularized circuits that have been hypothesized as the biological mechanisms of emotions (for reviews: Cacioppo et al. 2000; Guillery and Bujarski 2014; Kreibitz 2010; Lench et al. 2011; Lindquist et al. 2013; Kober et al. 2008; Lindquist et al. 2012; Phan et al. 2002; Siegel et al. 2018), which itself would provide a structural constraint for emotions over evolutionary time (although note that there is evidence for conserved circuits which support discrete, reflexive behaviors that may be related to emotions or used, in some studies, to measure emotion-related processes, such as eye blinks, e.g., for a review Kim and Thompson 1997). At first blush, these claims might lead to the dismissal of functionalist data as an important source of data for understanding EvoEmo. We argue that this is not the case – and in fact, that functionalist data may provide important information regarding how and why emotions evolved. But, we argue that this is only the case if functionalist data are situated within and interpreted from an alternative theoretical perspective than those frameworks traditionally levied to understand EvoEmo.

Theories of Constructed Emotion as an Alternative Framework

Constructivist approaches to emotion are an alternative approach to classic modular views of emotion, including classic EvoEmo views (for modern references on classic modular views of emotion: Anderson and Adolphs 2014; Ekman and Cordaro 2011; Izard 2009; Panksepp 2011; Shariff and Tracy 2011; Tracy and Randles 2011). Theories of constructed emotion (TCEs) are a class of theories which postulate that emotions emerge from, or are constructed from, more basic ingredients (e.g., Barrett 2017a; Boiger and Mesquita 2012; Clore and Ortony 2013; Cunningham et al. 2013; Gendron and Barrett 2009; Lindquist 2013; Mesquita and Boiger 2014; Mesquita 2010; Russell 2003). TCEs vary, to some degree, in their specification of what those ingredients are, but all propose that one required ingredient is *affect*.

Affect is an ongoing neurophysiological state that represents an organism's relationship to the environment in terms of what is good for it and bad for it and reflects activity of processes that are required for allostasis – that is, the regulation of homeostasis (for reviews on affect, Barrett and Bliss-Moreau 2009; Russell 2003). Affect is characterized by some degree of valence (hedonics) and some degree of physiological activation (arousal). Affect can be consciously experienced (as feelings of pleasantness or unpleasantness) but need not be in order to guide behavior. Moreover, affect is thought to be transformed into an instance of emotion when it is integrated with what one knows about emotions and the context in which it is occurring (in the form of concepts and language, Barrett 2011; Lindquist 2017; Lindquist et al. 2015; Wilson-Mendenhall et al. 2011; or from a predictive encoding perspective; Barrett 2017b). While the regulation of homeostasis (the foundation of affect) can occur outside of social contexts, social contexts provide robust information about affect regulation for many animals, including humans. Further, accumulating evidence from nonhuman animals and humans suggests that healthy affective processing and its development critically hinge on social context.

Evidence from human studies demonstrates that early in development, caregivers regulate infants' homeostasis and, thus, affect. For example, infants are unable to regulate aspects of their own homeostasis such as body temperature and securing nutrients and energy (i.e., food acquisition) and must rely on caregivers to perform these functions until they develop the biological capacity themselves (Christensson et al. 1992). This core regulation process is hypothesized to generalize to affective processes. Infants are highly attuned to their mothers' affective states, detecting their mothers' affect and modifying their own behavior in response (Cohn and Tronick 1983). Furthermore, infants show physiological (e.g., cardiac; Waters et al. 2014) and behavioral (e.g., reciprocal gaze, facial expressions, verbal communication, and play; Waters and Mendes 2016) coordination with their mothers, suggesting that affective coregulation between mother and infant occurs across multiple channels known to be

critical for the experience and expression of emotions. When caregivers cannot provide adequate affective feedback to their infants, infants themselves become dysregulated, exhibiting behavioral distress, further attempts to solicit a response, and elevated heart rate (e.g., Field 1984). Chronic lack of affective feedback from caregiver to infant can have long-lasting affective consequences for infants. For example, infants of mothers with depression show distress when unable to elicit facial responsiveness from their mothers, but, after sustained inability to evoke a response, withdraw from social interactions and the environment (Field 1984; Field et al. 1988).

Evidence from the nonhuman primate literature suggests that social regulation of affect may have originated with a common ancestor and that perhaps when basic biological needs are pitted against affective and social needs, the latter dominate. Seminal work by Harlow and colleagues demonstrated that infant monkeys (*Macaca mulatta*) preferred to spend time on an inanimate surrogate that provided comfort and warmth even when that surrogate did not provide food (Harlow 1958). These cloth “mothers” did not provide sustenance in the form of nutrients, but they did provide a context for social regulation: safe bases from which the infants could explore the world and to which they could return for physical comfort (Harlow and Zimmermann 1959). While these surrogates provided some essential aspects of maternal care, they were of course unable to engage in interactive social responding, which resulted in sweeping alterations to infants’ ability to perform appropriate social, sexual, and maternal behaviors (Harlow and Harlow 1965). For example, infants reared with cloth “mothers” were less socially responsive and displayed a smaller repertoire of social and affective behaviors, as well as inappropriate sexual behavior and maternal care when they became mothers themselves.

Further, recent work suggests that the building blocks of affective coregulation – namely, responsiveness and exchange of social signals – may be similar for humans and nonhuman primates. For example, both human and monkey mothers engage

in extended periods of eye contact (gaze) with their infants, which promotes social competence (Ferrari et al. 2009). Mother-infant interactions also spark the creation of other social relationships: when an infant cannot access his or her mother, he or she seeks social engagement elsewhere and participate in infant-infant relationships that are vital to the formation of social bonds and normative behaviors (Harlow and Harlow 1965).

Studies of nonhuman primates from Harlow’s laboratory and evidence from other species including rodents and humans (Caldji et al. 1998; Harlow and Harlow 1965; Harlow and Suomi 1970; Harlow and Zimmermann 1959; Hofer 1975; Kim and Cicchetti 2010; Nelson et al. 2002; Parker and Nelson 2005; Suomi et al. 1976; Tottenham et al. 2010) provide strong evidence that providing for, and meeting, only basic homeostatic needs is not sufficient for normal affective development. Being regulated by a social other appears to be critical.

Accumulating evidence suggests that social regulation of affective processes is not only critical during development but also important for adults. For example, actual and perceived assistance from others leads individuals to perceive physical challenges, such as climbing a steep slope, as less taxing (Schnall et al. 2008) and to perceive threats (e.g., electric shock) as less unpleasant and threatening (Coan et al. 2006). Close others, particularly romantic partners, can influence physiology (e.g., cardiac: Helm et al. 2014; Levenson and Gottman 1983; cortisol: Papp et al. 2013; Saxbe and Repetti 2010) and behavior (e.g., conflict initiation and resolution: Levenson and Gottman 1983), reinforcing the social component of affect coregulation and providing the foundation for the social regulation of emotions. Indeed, people differentially regulate their overt expression of emotions based on the presence or absence of social partners (for review: Wagner and Lee 1999). Moreover, emotion perception, expression, and experience vary across cultural group and language (Gendron et al. 2014a, b; for review: Nelson and Russell 2013; Russell 1994, 2003), suggesting that social context is important not only for affect but potentially

for the emergence of emotions as well (see below for further discussion of this point).

While the presence of a social partner can provide support, the absence of social support can be deleterious. When humans' social needs are not being met, the potent experience of loneliness occurs, perhaps to provide a signal to modify behavior in order to meet social needs. Critically, loneliness has significant adverse health consequences (for review: Cacioppo et al. 2015; Capitanio et al. 2014). This has led some theorists to suggest that being social – that is, being in contexts with other people and utilizing regulatory processes that include other people as important features – is so engrained in what it is to be human that it should be considered the human baseline state (Berscheid 2003). In this view, termed “social baseline theory” (for review: Beckes and Coan 2011), evaluation of affective processes outside of social contexts reflects a deviation from the norm, rather than the norm itself. Consistent evidence across animal species – specifically that monkeys also demonstrate behavioral and biological patterns consistent with loneliness (Cacioppo et al. 2015; Capitanio et al. 2014) – suggests that nonhuman animals may also have a social baseline. Considering how social context underpins affective processes in mammals, including modern humans, is but one example of how adopting a TCE for the study of EvoEmo changes how we understand the interplay between emotions and social context.

Beyond the interplay of affect and social context, the ingredients needed to transform affect into emotions – namely, shared concepts for emotions and the words (language) used to represent them – are influenced by social environment and emerge in social contexts (i.e., those with social others, human conspecifics, present; Gendron and Barrett 2018). Further, extant research suggests that emotion words are critical for shaping a discrete emotional experiences and not epiphenomenal to those experiences (for reviews Lindquist 2017; Lindquist et al. 2015). That is all to say that some of the ingredients of emotions are *necessarily* social.

Constructivist Views Generate EvoEmo Hypotheses That Can Be Tested in Nonhuman Animals

Constructivist views not only change the unit of analysis for the study of EvoEmo from individual emotions to the ingredients of emotions (as discussed above). They also inherently shift how we understand questions related to the function of emotions and thus what evidence we levy to support evolutionary claims. TCEs do not assume that emotions themselves were conserved over evolutionary time, but do recognize that the ingredients of emotions might have been (Barrett 2013, 2017a; Bliss-Moreau 2017). As a result, studying the ingredients of emotion might provide information about evolution, but there is no reason to a priori believe that the specific functions of emotion in modern humans should be the unit of analysis for the study of EvoEmo.

Moving away from studying the functions of emotions as clues to the nature of EvoEmo necessitates another empirical approach. One such empirical approach to a constructivist EvoEmo approach is to study the ingredients of emotion in nonhuman animals, mapping their topography and emergence across phylogeny. In this way, nonhuman animals represent living fossils, allowing us to develop and test specific hypotheses about how natural selection shaped the ingredients of emotion.

One evolutionary hypothesis that is consistent with constructivist views is that affect is sufficient for survival because it provides the required cues to know what is good or bad for the organism and to modulate behavior to regulate homeostasis. Affect should, therefore, be present and quantifiable in nonhuman animals. Available evidence suggests this is the case. Even very “simple” organisms – those lacking a true nervous system – are able to respond appropriately to positive and negative cues in the environment to meet fitness goals suggesting that they have rudimentary affect. For example, bacteria engage in chemotaxis – movement that is directed toward attractants (e.g., nutrient sources) and away from repellents (e.g., poisons) – in a way that reflects

homeostatic needs and environmental conditions (Crespi 2001; Webre et al. 2003; Wolanin and Stock 2004). Nervous systems provide multimodal sensory integration, movement, and behavioral coordination, as well as complexity such as social coordination. As a result, organisms like fruit flies, ants, cockroaches, and *aplysia* all have dynamic behavioral responses to regulate homeostasis even though their nervous systems are not nearly as large and complex as primate nervous systems. Behavioral and physiological findings from species with fairly simple nervous systems (small brains or no brains at all) are consistent with the idea that homeostatic and environmental signals are being integrated into affect (e.g., Abbott and Kandel 2012; Allada and Chung 2010; Bell and Sams 1973; Comer 1985; Dankert et al. 2009; Doi and Toh 1992; Moroz 2011; Ross and Keller 1998; Spieth 1974; Walters et al. 1981).

Bigger, more complexly wired nervous systems and brains allow for greater multimodal sensory integration and behavioral flexibility. The encoding of affective value in the autonomic nervous system is likely homologous in humans and nonhuman primates (for empirical evidence: Bliss-Moreau et al. 2013) and possibly other species (for a discussion: Bliss-Moreau 2017). Moreover, activity in the autonomic nervous system is thought to be one building block of conscious affective and emotional experience (Barrett and Bliss-Moreau 2009; Craig 2009; Critchley and Nagai 2012). One hypothesis is that as brains developed across evolutionary time, so too did the neural mechanisms to support awareness of these affective responses (Craig 2011; Wise 2008). This awareness may be subserved by regions of cortex that are able to integrate sensory information from the environment (exteroceptive sensory information) with sensory information from the body (interoceptive information) (Barrett and Simmons 2015; Craig 2011; Chanes and Barrett 2016). Such integration may support conscious awareness of affective states, leading to “feelings” and “moods.” Modern evolutionary theory suggests that the evolution of consciousness occurred multiple times in different lineages, meaning that awareness of affect is likely present

in other nonhuman animals, many of whom share little evolutionary history with modern humans (e.g., octopuses; Godfrey-Smith 2016, 2017). But, awareness of affect need not be a critical for affect to confer survival and fitness advantages given that it can influence behavior outside of awareness.

If only affect is necessary for survival (and reproductive success), then the ability to experience and perceive emotions must have conferred an additional benefit beyond survival for humans. One possibility is that the ability to communicate about our internal states and the behavior of others may have been critical to early social group development (for a similar argument, see Tomasello 2014). Early communication of this nature may have been about affect (e.g., “there is food at this location”; “that animal will hurt you”), and not emotions, but at some point in our evolutionary history, emotions came to be and communicating about them may have provided some new benefit. One hypothesis is that the experience of, and communication about, emotions, above and beyond affect, allowed for the formation of very large social groups that are characteristic of humans and that typically exceed optimal group size (Bliss-Moreau 2017; for a discussion of group size dynamics, Krause and Ruxton 2002). In this view, the ability to understand group members’ experiences and predict their behavior using discrete emotion concepts rather than broad affect-related concepts conferred a substantive adaptive advantage because it meant that an individual could learn about important fitness-related features of others without direct experience with them. Emotions therefore served, and serve, inherently social functions.

Emotions Serve Social Functions

The idea that emotions inherently serve social functions is precisely the theoretical space in which theorists who identify as social functionalists sit. From a social functionalist perspective, emotions play a critical role in helping individuals achieve socially relevant goals. In the years since Keltner and Haidt’s (1999) influential article,

recent theorizing in this area has predominantly focused on dyadic and group functions of emotion (e.g., Fischer and Manstead 2008; Niedenthal and Brauer 2012; Rimé 2009; van Kleef 2010; van Kleef et al. 2016, 2017), although intrapersonal (e.g., Williams and DeSteno 2014) and cultural (e.g., Mesquita and Boiger 2014) functions of emotion have also been addressed.

A core focus of social functionalists has been to investigate the ways in which emotions that arise in the context of social interactions, often referred to as “social emotions,” guide thought and behavior. These functions are thought to impact socially relevant outcomes for the individual, dyad, group, and, or, culture. A wealth of evidence speaks to how a range of positive and negative social emotions function to promote pro-social behavior and related outcomes (e.g., embarrassment: Feinberg et al. 2012; gratitude: Bartlett and DeSteno 2006; DeSteno et al. 2010; guilt: de Hooge et al. 2007; Ketelaar and Au 2003; moral elevation: Aquino et al. 2011; Siegel et al. 2014; Van de Vyver and Abrams 2015). For example, gratitude arising from receipt of a favor from a previously unacquainted stranger promotes reciprocity (Bartlett and DeSteno 2006; Tsang and Martin 2017), trust (DeSteno et al. 2010) and relational investment (Bartlett et al. 2012) toward the benefactor (for a meta-analytic review, Ma et al. 2017). These and other findings in this tradition provide a strong empirical basis for the argument that social context is a critical component of the functionality of emotion in modern humans.

Social functionalism often has evolutionary tones insofar as social functionalists draw on logic from evolutionary psychology to derive hypotheses. This occurs despite the fact that functionalist views are not inherently evolutionary in nature (i.e., an emotion can serve functional outcomes in modern humans without necessarily being given by evolution). For example, the pro-social functions of gratitude toward benefactors “spill over” to novel interaction partners (Bartlett and DeSteno 2006; Chang et al. 2012; DeSteno et al. 2010). While such patterns have been called upon as examples of evolutionarily conferred upstream reciprocity (Nowak and Roch 2007),

an evolutionary standpoint is not required to view such effects as functional in modern societal living where incidental carry-over effects of one emotional state to another context may carry benefit.

Social Functionalism Meets Constructivism in the Study of EvoEmo

Rarely, if ever, has social functionalism been linked to constructivist views of emotion. Via this linkage, the importance of social functions of emotion sheds lights on why emotions writ large (as a class, in addition to affect) came to be, rather than why specific emotions came to be across evolutionary time. The potential utility of linking functionalism and constructivism eliminates a fundamental problem inherent when social functionalism borrows logic from classical EvoEmo approaches: tenets about functions rooted in evolutionary arguments simply cannot be tested empirically in modern humans.

The synergy of social functionalist and constructivist approaches yields novel hypotheses about the evolution of emotion. If it is the case, as discussed above, that only affect is required for survival, then emotions must have served some other functions in order to have been created via natural selection. As such, a primary evolutionary question becomes: why do humans have discrete emotions at all? As discussed above, one answer to that question is that emotions generally (as a class, rather than specific emotions) supported the ability to build, ensure, and navigate complex social relationships with many individuals. A whole host of new, specific hypotheses arise from this idea. For example, modern humans with more discrete emotions may have more complex social relationships or be better able to access social resources in situations that require them for survival. Alternatively, human infants embedded in more complex social contexts may develop their emotional repertoire faster or more efficiently, and, or, their emotions may serve more functions. Additionally, the critical points in infant development in which discrete emotion concepts come online (Widen 2013) may map to

developmental challenges in which affect alone fails to promote the ability to survive and thrive.

A secondary set of EvoEmo questions generated at the intersection of social functionalism and constructivism can be asked about how specific emotions came to be across the history of modern humans. These sorts of questions may not speak to the biological origins of discrete emotions (typically the focus of classic EvoEmo views) but instead their cultural and linguistic origins (Wierzbicka 1999; e.g., see work on how emotion word usage has changed across human history; Watt Smitt 2015), opening up a new domain for the study of cultural or social evolution of emotion.

Conclusion

Approaching the study of EvoEmo from the intersection of social functionalist and constructivist views generates the hypothesis that emotions have come into existence via natural selection *because* of the unique sociality of humans (Williams and Bliss-Moreau 2016), and thus emotions and social life must be considered together to understand either.

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Evolution of Female Resistance

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Synonyms

Female filtering; Female mating counter-adaptations; Tests of male quality

Definition

The process by which females evolved to resist male control of mate choice, allowing females control over their own mate choice decisions.

Introduction

Classic models of sexual selection by female choice invoke conflicts of interest between the sexes. While it is in a male's genetic best interests to fertilize all of the eggs of any female he encounters, that is not necessarily in the same best interests of any particular females. Thus, female traits that discriminate between males are in conflict with the reproductive interests of any particular rejected male. There are a number of models of such conflicts and how they can influence female choice. One model views males as evolving to entice females into mating and females evolving resistance to males, as opposed to attraction to them, in order to reduce the direct costs associated with mating (Gavrillets et al. 2001). Another model suggests that females might evolve resistance to males

in order to gain indirect benefits, perhaps by allowing the female to select for males based on their ability to manipulate females or their physical strength in cases where male defense of offspring and mate might be required to select for “better genes” or material resources (Cordero and Eberhard 2003; West-Eberhard 2014).

Do Females Select Via Resistance for Antagonistic Male Traits?

There are several species where forms of female resistance have been documented. In gladiator frogs (*H. rosenbergi*), it is the males who create the nests and defend the eggs. Female courtship behavior selects for aggression in males as females test male quality. Typical courtship involves a female approaching a male and “bumping” him, a behavior that simulates elements of male-male aggressive behavior (Kluge 1981). If the male retreats, the female will leave and look for a more stalwart mate. If he stands his ground, the female will begin a massaging behavior that incites him into mating. This bumping on the part of the females allows her to assess the likelihood of the male's ability to defend her clutch. She resists his sexual approach unless he has demonstrated his quality.

In several crustacean species, there have been observations of female resistance to mate guarding. Jormalainen and Merilaita (1995) tested for sexual conflict over the duration of mate guarding in three species of crustacean (*Idotea baltica*, *Asellus aquaticus*, and *Gammarus zaddachi*) by interfering with the female's ability to resist mate guarding. Experimentally decreasing female resistance to mate guarding increased the duration of mate guarding substantially in the first species, indicating that in that species female resistance generally decreases mate guarding effectiveness. It also appears to select for large size in males. However, there was no effect of experimental interference in female ability to resist mate guarding on guarding duration in the other two species, suggesting that there was no substantial difference in male and female interests in those species or that the conflict is resolved in the male's interest.

Is There Evidence for Female Resistance in Humans?

There is clear evidence in humans that females have mate preferences for physically strong men who would be able to provide protection (Barber 1995), and it may be that those preferences are exaggerated in environments where women are at risk of male aggression or domination (Marzoli et al. 2013). However, examples of female resistance, either to avoid mating costs or to filter for specific male traits, are less clear.

Some have suggested that the commitment skepticism bias in women (Haselton and Buss 2000) is a form of filter resistance that deters females from uncommitted males. This requires males to demonstrate their willingness to commit and ability to provide benefits rather than impose costs.

Research on possible anti-rape adaptations may provide some support for resistance to avoid costs. Rape interferes with women's mate choice and risks unwanted pregnancy, being blamed by third parties, reputation damage, and psychological distress. Researchers have suggested that mate preferences for physically strong and socially dominant men as well as avoiding risky activities during ovulation (Chavanne and Gallup 1998; McDonald et al. 2015) are forms of resistance to male attempts to control female mate choices.

Conclusion

It is clear that female resistance has evolved to exert female choice in settings where male and female sexual interests diverge. Whether female resistance in humans is largely designed to avoid the costs of mating or is more specifically designed to filter between males for specific benefits or qualities (e.g., good genes) is yet to be determined.

Cross-References

- ▶ Female Choice
- ▶ Rape Avoidance
- ▶ Sexual Conflict Theory
- ▶ Women's Mate Preferences

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Evolution of Fighting Assessment Abilities

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Synonyms

Contest assessment strategies

Definition

The information-gathering and decision-making processes used during agonistic encounters.

Introduction

In the natural world, intraspecific competition for access to limited resources, such as food, territories, and mates, may take the form of contests, in which animals may display and/or fight to determine the winner. Animal contests result in the unequal distribution of resources and are therefore principal drivers of natural selection (Darwin 1859). Contests also form an important component of sexual selection, via intrasexual competition for access to mates (Andersson 1994), resulting in the evolution of a fascinating array of weapons used in fights. Different species show markedly different forms of contests for resources, ranging from noncontact displays to injurious or even deadly fights (reviewed in Huntingford and Turner 1987). This variation also occurs within a species, with some contests settled by display, while others escalate to fierce fighting. It is also the case that fighting for limited resources may be costly, in terms of energy use, time, risk of injury, and increased risk of predation or death (Arnott and Elwood 2009; Camerlink et al. 2015).

Early attempts to explain animal contest behavior and answer questions regarding why animals often settle contests by display rather than all-out fighting involved group selection arguments; along the lines escalated contests would result in many animals being seriously injured, and this would potentially affect the survival of the species (e.g., Lorenz 1966). However, this argument did not explain how natural selection acting on individuals can give rise to the evolution of conventional fighting. In this regard, game theory, a branch of applied mathematics, has greatly enhanced our understanding of animal contest behavior (see ► [“Game Theory”](#)). Initially developed by economists to model human strategic decision-making, biologists were quick to spot the utility of game theory for evolutionary biology. Among them was John Maynard Smith who

was the first to apply game theory to the study of animal contests, producing the now classic “hawk/dove” game (Maynard Smith and Price 1973). Related to animal contests, game theory examines how different strategies might be used by each contestant and how the winner is determined. The approach models contests in terms of costs and benefits to individuals, illustrating how individuals try to maximize fitness in contests over resources. In this modeling approach, natural selection is expected to act in such a way that a population of animals will come to adopt an evolutionarily stable strategy (ESS), which is a strategy that if employed by most members of the population, confers a higher fitness than does any other strategy. For example, in the hawk/dove game (Maynard Smith and Price 1973), contestants only differ in their choice of initial behavior between “aggressive” hawks which use escalated injurious fighting and “nonaggressive” doves which use noninjurious displays. In this game, the ESS is a frequency-dependent mixture of hawk and dove depending on the costs and benefits of each strategy. A particular advantage of the game theoretical approach has been its suitability for modeling behavior processes and formulating testable hypotheses.

The hawk/dove model set the scene for the development of more realistic game theory models of animal contests that took into account asymmetries between contestants. For example, contestants will differ in size, development of weaponry, energetic state, general physiological state, experience or position, all of which will affect the fighting ability of the animal in a contest, and together are termed resource holding potential (RHP; Parker 1974, also see entry on ► [“Anatomical Adaptations for Fighting”](#)). The most commonly used proxy for RHP in animal contests is body size/weight, with victory tending to go to the larger or heavier contestants (reviewed in Arnott and Elwood 2009). Resource ownership is a second potential asymmetry between opponents, as occurs when one animal has occupied a territory or burrow or in cases where a male associates with one or more females prior to mating. In these cases, owners typically have a higher probability of winning the encounter than do intruders. A third asymmetry concerns the value of the

resource to each contestant (reviewed in Arnott and Elwood 2008). A key point is that selection is expected to favor contestants who gather information about asymmetries and use that information in decision-making about the behavior to be used (reviewed by Arnott and Elwood 2008, 2009). The main assessment strategies that have been modeled are outlined below, together with empirical evidence, including studies related to agonistic behavior in humans.

Assessment of Fighting Ability

Assessment refers to the gathering and use of information in making decisions. Existing game theory models can be grouped into three main types that differ in the information about RHP that contestants are presumed to gather.

1. *Pure self-assessment*: Each contestant only has information about its own abilities or state and fails to gather information about its opponent. The actions of the opponent do not inflict costs, although both opponents incur a cost from their own actions. Thus, rivals persist purely in accord with their own RHP such that weaker rivals will reach their limits first and give up. This strategy is a feature of the “war of attrition without assessment” (WOA-WA; Mesterton-Gibbons et al. 1996) and “energetic war of attrition” (E-WOA; Payne and Pagel 1996, 1997) models.
2. *Cumulative assessment*: The cumulative assessment model (CAM; Payne 1998) also presumes that both opponents only have information about their own RHP, fighting until one reaches the threshold of costs that it is prepared to pay, with no direct information gathered about the opponent. However, unlike the other self-assessment models, with CAM, costs also accrue from the opponent’s actions, and superior opponents are better at inflicting costs. Thus, in the CAM, the decision to withdraw is influenced by both an individual’s own RHP, with poor-quality individual bearing fewer costs, and also the opponent’s RHP, with higher quality individuals inflicting costs

at a higher rate. As there is no direct gathering of information about the opponent with pure self-assessment and CAM, a low and similar level of cognitive complexity has been assumed (Elwood and Arnott 2012), in contrast to the assessment strategy outlined next.

3. *Mutual assessment*: These are models which involve an assessment of relative RHP difference between opponents, generally interpreted as individuals gathering information concerning the fighting ability of the opponent and comparing this against their own ability. Mutual assessment is central to the “sequential assessment model” (SAM; Enquist and Leimar 1983; Enquist et al. 1990) and the “asymmetric war of attrition” (AWOA; Parker and Rubenstein 1981; Hammerstein and Parker 1982). This strategy is more cognitively complex since contestants assess their own abilities, gather information about the opponent, and compare the two throughout the course of a contest (Elwood and Arnott 2012). An additional feature of this strategy is that contestants start with little or no information about the opponent and that early low-cost display activities provide weak information, but that later, escalated phases of the contest provide increasingly accurate information. Thus, where there is a large difference in RHP between the contestants, the decision to abandon the contest by the weaker individual will be undertaken sooner (at lower cost and requiring less escalation) than if the difference in ability is small. Mutual assessment has the selective advantage that the contestant with the lower RHP can terminate the contest as soon as it perceives its inferiority, reducing time, energy, and risk of injury from persisting in a contest that it would inevitably lose. In this regard, pure self-assessment and CAM are clearly inferior as the contestant will always incur costs up to a threshold. Mutual assessment has intuitive appeal, and our own aptitude for this strategy (outlined below) may have led researchers to generally assume such capabilities in other species without appropriately testing for the alternative strategies (Elwood and Arnott 2012). Yet, we may be in the minority of

animal species that have evolved the cognitive capacity for mutual assessment. Empirical evidence supporting each assessment strategy is provided below.

Evidence for Assessment Strategies

The three assessment strategies do not differ in predicting contest winners but in when and how the decision to give up is made. Moreover, analyses used in earlier studies failed to use the correct approach to distinguish between them (see Arnott and Elwood 2009). With mutual assessment, if the opponents differ greatly in RHP, the loser should easily discover that it is likely to lose and give up early. In contrast, longer contests should occur when contestants are evenly matched. Thus, a negative relationship between RHP difference and contest duration was used for many years to determine whether mutual assessment occurred. However, the same relationship was shown to apply to other, less cognitively demanding models (Taylor and Elwood 2003). To discriminate between the various alternatives, it is necessary to examine the effects of individual contestant RHP (typically size or weight) on contest duration (Fig. 1). With pure self-assessment, there will be a positive relationship between loser RHP and contest duration, while the winner's RHP will be weakly positively or not related to duration (Fig. 1a, b). For CAM, there is a positive relationship between loser RHP and contest duration but, unlike for pure self-assessment, the winner's RHP is negatively related to contest duration (Fig. 1d, e). This can cause confusion because mutual assessment as modeled by the SAM also predicts the same relationships (loser positive, winner negative) as for CAM. To discriminate between these alternatives, it is necessary to examine contests in which opponents within a contest are matched for RHP, with absolute RHP varying between contest pairs. With SAM, the key factor that determines contest duration is relative ability, so when the two contestants are matched, there will be no relationship with absolute RHP and duration. By contrast, with CAM, a key determinant of duration is the absolute size of the loser,

resulting in a positive relationship between pair RHP and duration.

Evidence for Pure Self-Assessment

The amphipod *Gammarus pulex* provides a clear example consistent with theoretical predictions. In this species, single males (intruders) attempt to take over females held in precopula by other males (owners). Contests occur, whereby the intruder attempts to grab the female and tug her away from the owner's hold, and larger males have an advantage over smaller males in making and resisting takeovers. In support of pure self-assessment, Prenter et al. (2006) found a strong positive relation between loser weight (a proxy for RHP) and contest duration and a nonsignificant positive relation between winner's weight and duration.

Evidence for CAM

Male-male contests between burrow owners and intruders in the Australian fiddler crab *Uca mjoebergi* provide a clear example supporting CAM (Morrell et al. 2005). Contest duration increased with increasing size of the loser but decreased with increasing winner size. Moreover, in fights between size-matched individuals, fight duration increased with increasing mean size of the competitors, this latter finding discriminating CAM from mutual assessment. In addition, Morrell et al. (2005) simulated a computer-generated population specifically modeling the predictions of CAM. In this model, contest persistence was based on individual size-determined cost thresholds and opponents inflicted costs at a rate proportional to their size (i.e., larger rivals inflicted costs at a higher rate). Thus, the duration of contest persistence of an individual was defined as (own threshold – 1/3 × size of opponent). This simulation revealed similar results to the observed data, providing support for CAM.

Evidence for Mutual Assessment

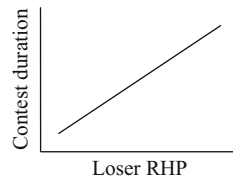
Existing research has shown a bias to assume mutual assessment even in the face of inconclusive or contradictory evidence (see Elwood and Arnott 2012). Until recently, strong evidence supporting this strategy was lacking. However,

Evolution of Fighting Assessment Abilities,

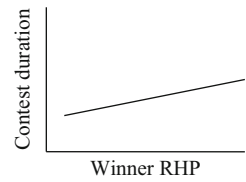
Fig. 1 Relations between resource-holding potential (RHP) and contest duration for alternative assessment hypotheses. (**a** and **b**) Pure self-assessment. (**c**) Not diagnostic of self- or mutual assessment. (**d** and **e**) Mutual assessment and cumulative assessment models (From Arnott and Elwood 2009).

Pure self assessment

a

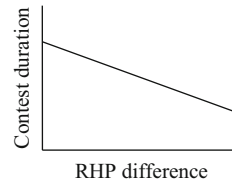


b



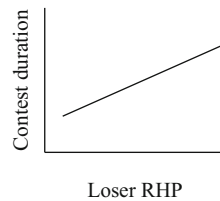
Not diagnostic of self or mutual assessment

c

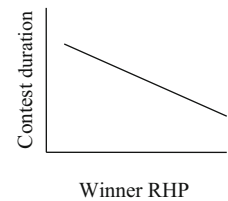


Mutual assessment and CAM

d



e



Schnell et al. (2015), using the correct approach, provide an elegant comprehensive study involving staged contests between male giant Australian cuttlefish, *Sepia apama*, with findings consistent with mutual assessment. As advocated (Arnott and Elwood 2009), they staged both RHP (size) asymmetric contests and RHP matched contests using a setup involving males displaying aggressively to each other from either side of a large tank separated by a clear partition, thus preventing any risk of injury to the animals. Regression analyses found contest duration increased with loser RHP and decreased with winner RHP, in addition to a negative relationship between RHP asymmetry and contest duration. Furthermore, in size-matched contests, there was no correlation between absolute RHP and contest duration.

An additional approach was also used to further support mutual assessment. The approach involves assessing the motivational state of an animal in a contest by using a novel stimulus that causes a contestant to temporarily cease fighting (Arnott and Elwood 2009). The time taken to resume the contest provides a measure of the individual's motivation to fight. Using this approach, with the novel stimulus being the introduction of a female cuttlefish, Schnell et al. (2015) found that the latency to resume a contest was significantly influenced by the size of the contestants. Latency was negatively associated with the size of the focal male, meaning the greater the RHP of the focal individual, the more quickly it resumed the contest, while also being positively associated with the size of the opponent male,

meaning that the greater the RHP of the opponent, the less motivated the focal was to resume fighting. Finally, in a third experiment, the researchers found males behavioral responses varied when facing either a smaller or larger rival male. Escape behavior decreased when contesting a smaller rival, while attempted physical aggression increased. Put together, these studies by Schnell et al. (2015) provide the best evidence yet supporting mutual assessment.

Assessment of Fighting Ability in Humans

A number of studies have examined aspects of human aggression within an evolutionary context (see ► [“Dominance in Humans”](#)), including an investigation of our capacity to assess fighting ability (see entries on ► [“Assessment of Fighting Ability”](#) and ► [“Male Adaptations to Assess Fighting Ability”](#)). This is an informative approach given our highly evolved cognitive abilities, together with evidence of the importance of aggression and male intrasexual selection in human evolution (Manson and Wrangham 1991; Archer 2009, also see entry on ► [“Aggression”](#)). Visual assessment of strength in humans has been clearly demonstrated (Sell et al. 2009). In this study, the strength of males was measured by their ability to lift weights (see entries on ► [“Upper Body Strength”](#) and ► [“Upper Body Strength and Fighting Ability”](#)). Subsequently, male and female subjects rated the strength and also perceived toughness of those males from photographs. Ratings of strength were correlated with those of perceived toughness, providing evidence that raters were treating physical strength as a valid measure of fighting ability, with perceived toughness also shown to correlate with the actual number of past fights that sampled males had engaged in. Intriguingly, in addition to being able to rate the strength and toughness accurately from photographs of the full person and body alone, subjects could also do this from viewing just the face. Furthermore, Sell et al. (2010) provide compelling evidence of human adaptations to assess fighting ability from the voice. Both male and female raters could accurately assess the upper-body strength, which was correlated with perceptions of fighting ability, from voices taken

from eight samples across four distinct populations and language groups, the latter illustrating that this ability was independent of familiarity with a particular language. Consistent with the greater ancestral importance of aggression in males than females, the former were assessed more accurately than the latter. Moreover, this study provided evidence of the value of using multiple cues for assessment, with findings of increased accuracy of strength assessment when both auditory and visual cues were available (see ► [“Sex Differences in Ability to Assess Fighting Ability”](#)).

Building on the above studies, Little et al. (2015) extended the approach to actual human contests by examining the perception of male faces from paired winners and losers of individual fights in mixed martial arts sporting competitions. Observers of both sex, unfamiliar with the fight outcome, performed at rates above chance in correctly predicting the fight winner. Furthermore, separate groups of observers were also asked to choose between the two male faces based on masculinity, strength, aggressiveness, and attractiveness (women raters only). This revealed winners to be perceived as more masculine, stronger, and more aggressive than losers, while women saw the winners as more attractive than the losers. Thus, these studies demonstrate that humans possess the necessary cognitive skills to assess the risks associated with aggression by assessing fighting ability in other humans and consistent with theoretical predictions from mutual assessment (Enquist and Leimar 1983).

Animal contest theory regarding assessment strategies has also been applied to gain insights into human interstate war. Briffa (2014) outlined parallels between animal contests and human warfare, including the feature that a degree of restraint is usually present, and that a game theoretical approach may aid our understanding of these scenarios. Moreover, human war has been stated to involve a degree of information exchange about relative power between the conflicting states, akin to mutual assessment. Briffa made use of publicly available datasets to source data on war duration, outcome, and national capabilities. RHP was modeled using various measures of

state power including a composite index and size of the military. These measures had a positive effect on war outcome, validating their use as indicators of RHP. However, contrary to mutual assessment predictions, there were positive relations between both loser and winner RHP and war duration, consistent with a self-assessment process and challenging some current assumptions of human warfare.

Assessment of Resource Value

Contests typically occur over fitness relevant resources (see entries on ► [“Access to Resources”](#) and ► [“Dominance and Territory”](#)) that influence the expected benefits to be gained from winning. Game theory models illustrate that selection should favor contestants that modify their behavior during fights according to resource value, with fight costs predicted to increase with the value of the resource (Arnott and Elwood 2008). Therefore resource assessment in animal contests is predicted, and experimental evidence from a range of species supports this assertion (reviewed in Arnott and Elwood 2008).

In this regard, hermit crabs have provided a useful study system to investigate resource assessment. These decapod crustaceans inhabit empty gastropod shells that protect their delicate abdomen. A key factor in the value of the shell to a hermit crab is the size of the shell relative to the size of the crab, with individuals engaging readily in shell contests. In these interactions, one crab termed the “attacker” (usually the larger crab as size correlates with RHP) approaches and grasps the shell of the defender, the latter then withdrawing into its shell. The attacker may then engage in repeated bouts of vigorous shell rapping during which it hits its shell upon that of the defender, ending with either the eviction of the defender, allowing the attacker to take the vacated shell, or alternatively the attacker may give up without evicting the defender. The resource assessment ability of hermit crabs, *Pagurus bernhardus*, in relation to the quality of their own shells has been investigated (Arnott and Elwood 2007). One group of crabs were allocated shells that had

sand glued to their inner whorls, making them much less preferred than normal shells which had been allocated to the control group. During shell fights, if crabs in the sandy shells took the role of defender, they gave up more quickly than control defenders, revealing their low motivation to defend the low-quality resource. In contrast, if they took the role of attacker, they persisted for longer in the attack than controls, revealing their higher motivation to obtain a new shell.

Does Resource Value Influence Human Aggression?

Studies on human aggression have so far not explicitly incorporated resource value theory as applied to animal contests. That said, a number allude to its importance. For example, aggressive responses from males are more likely in response to provocations involving sexual competition or challenge, such as insulting a man’s girlfriend or showing obvious interest in her (Archer and Benson 2008). Furthermore, as noted by Briffa (2014), there is scope to incorporate resource value theory into the study of human wars, examining aspects of territory value such as food, water, fuel, and mineral availability.

Conclusion

In animal contests, selection is expected to favor information gathering regarding the likely costs and benefits of persisting in the encounter. In this regard, the mutual assessment strategy is superior to self-assessment. However, evidence is now mounting across a range of species supporting self-assessment rather than mutual assessment, yet there remains a tendency to assume mutual assessment rather than correctly test for alternatives (Elwood and Arnott 2012). The aptitude of humans for mutual assessment (Sell et al. 2009, 2010; Little et al. 2015) may have led us generally to assume such capabilities in other species.

Why then may mutual assessment be less prevalent than once assumed? It could be that only a minority of species, including humans, have the cognitive mechanisms to accurately assess fighting ability. For example, mutual assessment is

typically interpreted as a three-stage process involving assessing own abilities, gathering information about the opponent, and comparing the two throughout the contest. It remains to be understood which species have the cognitive capacity for this strategy. Furthermore, in addition to a limited capacity for gathering information, there will also be trade-offs between gathering information about the opponent's ability and the value of the resource being contested. It is also possible that mutual assessment may be costly in terms of the time and energy required to process an opponent's cues and signals, detracting from a contestant's own performance in a fight. The potential costs of assessment would be even more extreme in those cases where displays are unreliable indicators of actual fighting ability. While game theory has greatly furthered our understanding of the evolution of animal contest behavior, it is clear that there are many aspects that remain to be fully understood.

Cross-References

- [Access to Resources](#)
- [Aggression](#)
- [Anatomical Adaptations for Fighting](#)
- [Assessment of Fighting Ability](#)
- [Dominance and Territory](#)
- [Dominance in Humans](#)
- [Game Theory](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Upper Body Strength and Fighting Ability](#)
- [Upper Body Strength](#)

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Evolution of Free Will

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Synonyms

Freedom; Liberty; Morality; Rationality

Definition

An ability to choose among alternatives

Introduction

It has always been accepted that free will, an ability to choose among alternative actions or beliefs, is characteristically human. It seems to

result from rational thought or perhaps is simply one aspect of rational thought. Because no non-human animal, we might presume, has the capacity for rational thought, none has free will either. As a result, possibilities for biological evolution of free will have never previously come up. Instead the focus has always been on how free will works in humans exclusively.

Descartes and subsequently Newton, in their mathematical descriptions of the universe, precipitated a crisis for any easy acceptance of human free will. Their approach suggested that the universe has a unique diachronic pattern. Philosophers often discuss this pattern as sequences of cause and effect. The mathematics however represents each event (for instance, the rate of change in the movement or location of any object) as an analytical function of its instantaneous context. In the twentieth century, the relativistic disposition of mass and energy and the probabilities of quantum transitions were refinements of these functions. At the scale of human behavior, however, the history of the world is uniquely determined with exceedingly high probability. The past included no alternatives and the future is predictable. Everything that has happened and everything that will happen can in principle be calculated from the present. Choices among alternatives do not occur.

As an apparent confirmation of this strict determinism, neurobiologists have argued in recent years that their results also exclude free will. The pertinent results are (1) failure to locate an area in the brain (a “module”) where neural activity is associated with “choice” or “consciousness” and (2) evidence that initiating an action precedes reporting awareness of the action by a few seconds or fractions of a second. Harris, for instance, concludes that freedom from determinism is therefore an illusion. Nevertheless, recognizing this illusion can make us more sympathetic toward less fortunate people. This recognition of course would also have to be deterministic (Harris 2012).

These neurobiological results, however, do not justify any strong conclusion about whether or not brains make decisions. It is true that many activities of brains are more or less narrowly localized.

Examples include primary sensory analysis, final motor control, memory, emotions, producing and understanding language (or species-specific songs in the case of some birds), and others. Yet there is no reason to think that some activities of the brain might, in contrast, be distributed widely. A capacity to make decisions might, for instance, depend on interactions of relatively few widely dispersed neurons, and, in addition, similar interactions might recur throughout large portions of the brain. Furthermore, the observation that reporting a movement follows initiating it indicates only that the act of reporting takes longer than the act of moving. When and where the pertinent decisions occur still elude us.

The invalidation of free will, which strict determinism entails, has deep ramifications for moral and legal judgments and for our sense of ourselves as individuals. Reluctant to accept these consequences of strict determinism, some philosophers such as Hume have thrown up their hands and accepted that, whatever else might be true, it is intuitively obvious that people routinely make practical choices. A similar position supposes that there are alternative worlds that a mind can choose. Others have proposed various cracks in determinism that could allow choices to seep into our behavior. In other words, somehow that choice can originate actions, *de novo*, despite causes or analytical continuity. The usual procedure is to suppose that each person includes a supernatural component, beyond rational explanation, a soul, a “ghost in the machine,” a “categorical imperative,” a “Dasein,” a self-consciousness, and a “self-forming act,” something that makes decisions. Kane has proposed that some inherently random component of rationality underlies freedom of action. Dennett and Gazzaniga propose that the source of freedom is the human “social arena” in which interactions with other humans provide and expect reasons for actions (Kane 1996; Dennett 2002; Baer et al. 2008; Gazzaniga 2011).

These recent approaches do not differ much from earlier ones, back to Descartes and Hume. Adventitious internal randomness (quantum or otherwise) might explain erratic behavior but not rational choice. On the other hand, an intrinsic imperative for rational or moral choice simply

displaces the origin of rational choice without explanation. Social arenas for human development can in many cases result in rationality and individual morality, but in other cases in rationalization and collective delusion, all strictly determined by context. To argue that humans can prejudicially accept the desirable alternatives, over the undesirable ones, assumes once again an unexplained moral imperative. Despite these shortcomings, attempts to understand freedom of choice have had the merit of emphasizing the two questions that must be addressed: (1) what is the source of *unpredictability* that provides an opportunity for choice and (2) what is the nature of *decision*.

Unpredictability and Decisions in Noise

A recent mathematical analysis of the evolution of communication by natural selection in the presence of noise reveals unexpected explanations for the unpredictability confronting an organism and for the organism's decisions. It provides an evolutionary context for investigating choice by supposing that all living animals (even plants) face these unpredictabilities and must make these decisions, each in its own way and within its own capabilities. Furthermore, it explains why the universe is deterministic but, for all organisms, the future nevertheless remains unpredictable. The crucial novelty of this approach is the inclusion of noise in an analysis of optimal performance in communication and perception. Noise here is anything that contributes to errors in reception of signals or in perceptions of sensations; errors in turn are responses disadvantageous to the receiver or perceiver in question; and a response can be overt or, in the case of a memory, covert (Wiley 2015, 2017, also see ► “[Evolution of Communication](#)”).

The first result of this analysis derives from signal detection theory. In the presence of noise, every receiver of any signal or perceiver of any sensation is in a double bind. Noise produces the possibility of errors, responses to signals or sensations that have net disadvantages. There are two possible kinds of errors in noise, false alarm and missed detection (errors of commission and omission). Regardless of the criteria for recognizing

relevant signals or veridical sensations, it is not possible to decrease the probability of one kind of error without increasing the probability of the other.

The second result of this analysis derives from decision theory. The utility (net advantage or disadvantage) of a receiver's criterion for response depends on the intensity of the signaler's signal, and the utility of a signaler's signal depends on the stringency of the receiver's criterion for a response. Consequently, signalers and receivers evolve jointly to a mutual optimum, a Nash equilibrium at which each party does the best it can provided the other party does likewise.

The result scales to the level of noise. One prevalent determinant of the level of noise, for instance, is the distance between signalers and receivers. At close range optimal communication consists of quiet signals and lenient criteria for response. At long range the optimum consists of intense signals and stringent criteria. In all cases residual noise persists. The evolution of communication cannot escape noise. It is inevitable.

This analysis makes it clear that decisions are ubiquitous for receivers and perceivers. Every time a receiver checks its sensors, it must decide whether or not a response (or which response) is justified. Nervous systems of all types must analyze sensations and coordinate movements, but between sensation and movement, nervous systems are primarily decision-making organs.

Noise in reception or perception is not completely predictable simply because nervous systems are not complex enough to compute the dynamics of the universe. The number of neurons in a human brain is vast, but not so incomprehensibly vast as the number of interacting particles in its environment. For a brain, indeed for any practical machine, the universe is under-specified. The universe is determined but, for any brain, it remains partly unpredictable. As a result, humans remain notoriously incompetent in predicting all the consequences even of their own actions.

Unpredictability of signals and sensations thus requires decisions. These decisions, like all else in the universe, are evidently determined. Each individual's brain, like all components of every living organism, is influenced by the genes it carries and by the environment in which it lives and develops

throughout its life. If a brain is complex enough to think (to use language in an internal dialogue), presumably it can weigh evidence for adopting more lenient or more stringent criteria for responses to any kind of signal or sensation. Whatever a brain thinks, as influenced by its genes and environment, is presumably determined, as are all other parts of the universe.

Nevertheless, a human brain cannot completely *predict* another comparable brain's activity. Explaining all interactions at any level of complexity would require a superordinate level of complexity. The collaboration among the brains of multiple people and workings of multiple other machines is making progress in understanding the general principles of how brains work. Who knows what superordinate complexity of thought might develop in the future. It remains unlikely, however, that a brain will ever completely understand and predict its own activity. Until that time, humans will continue to make decisions when faced with under-specified situations in the course of communication and perception in a noisy world.

An example of the interaction of predictability and decision in a deterministic universe is provided by chess. In this case the rules of the game are deterministic. They specify the possible moves and interactions of the pieces, in effect their "cause and effect" relationships. The number of possible sequences of moves in a game is unimaginably huge, but the number is finite (at least in versions excluding endless repetition of moves). Although the game has not been solved numerically, it is possible that there exists only one sequence of optimal moves. Humans nevertheless cannot predict this game from the outset – otherwise it would hardly be the challenge it is. Humans play the game by making decisions based on incomplete foresight. On the other hand, appropriately programmed computers can learn, indeed can teach themselves, to play with greater foresight than a human. Such a computer playing against itself or against another comparable (or more complex) computer would presumably often play the same sequence of moves.

A human cannot achieve this predictability because, with its more limited foresight, it cannot

predict winning moves of a computer. A human's decisions are nevertheless determined. For a computer to predict every decision by a human, it would require even greater complexity. Such a machine would have to learn the relevant parameters of a human's brain and its context. With anything short of such complexity, a machine must make decisions based on its own formidable foresight and its human opponents' unpredictability.

The under-specified complexity of human behavior that humans and machines fail to predict is the same as noise, errors in reception and perception, as discussed above. This complexity is determined by physical laws. Nevertheless, for any particular brain or machine, if the parameters of this complexity are incompletely known, then the resulting unpredictability (noise) requires decisions.

In such a noisy world, we can legitimately judge competence at chess based on the decisions a player makes. In a similar way, we can judge moral competence based on a person's decisions in other situations. These judgments are our own decisions, our own responses to perceptions of other people in a noisy context, under-specified and thus partially unpredictable. Holding a person accountable for decisions in particular situations might require an additional decision on our part. We might require, for instance, a supplementary judgment of the person's competence for rational thought. These thoughts would also be determined, as discussed above. Nevertheless, our only evidence for another person's thoughts comes from our noisy perceptions of that person's responses. For nonhuman animals, for machines, and in some situations for humans, including ourselves, we might withhold such judgments of rationality and accountability. All of these judgments, it is important to realize, are decisions in under-specified situations, in other words, in response to noisy perceptions. They are not an indefinite regression of determinism, just responses to pervasive unpredictability in a noisy world. Noise affects everything we do.

As for the evolution of free will, this analysis of communication and perception in noise opens the possibility for comparative studies of decision-

making and prediction. Indeed the fields of comparative psychology and ethology, as well as neurobiology, have made important progress. More could be done by including noise as well as signals in the comparative study of behavior or brains. The effects of noise only become apparent in the real, unpredictable world where a brain never knows as much as it would like about the source of the next sensation. It is important to investigate communication and perception in situations with multiple signals and receptors and variable sensations.

Cross-References

► [Evolution of Communication](#)

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Evolution of Genitalia, The

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Synonyms

[Genital coevolution](#); [Penile evolution](#); [Vaginal evolution](#)

Definition

Genitalia are among the most variable morphological structures in animals. In several taxa, genital variation seems to be the result of sexual selection. Human males have very wide, but contrary to popular belief, not particularly long penises. Humans have also lost the penile spines and penis bone found in most primates and apes. Some studies suggest that sexual selection may have driven enlarged penis morphology in men and that reduction of the intensity of post-copulatory sexual selection may have driven the loss of the spines and baculum. However, the potential role of other mechanisms of selection has not been explored yet.

Introduction

Male intromittent organs are very diverse, and sexual selection is generally accepted as the main mechanism responsible for genital trait variation in males (Brennan 2016). More recent work has also found that variation in female genitalia is significant, if somewhat less than that found in males (Brennan 2016). Genital coevolution can result not just from sexual selection that includes female choice, male competition, and sexual conflict, but also from natural selection to make copulation feasible, and from reinforcement (Brennan 2016). Some studies have examined the potential role of sexual selection in shaping human genitalia, but natural selection is likely to have also played an important role (Dixson 2009; Brennan 2016).

Morphology of Human Genitalia

Just like other primates, human penises have large areas of erectile tissue that become engorged with blood upon erection, and the morphology of the erect penis is quite different from the flaccid penis. Penile dimensions are highly varied. Many studies have reported variation in penis size, but these have used different methods of measurement including self-reported measurements, stretched-

flaccid measurements, as well as fully erect measurements in a clinic. Variation is high within and between studies, and there appears to be no obvious correlation with body size or ethnicity (Dixson 2009). For example, a recent study of 1661 reproductively active men in the USA reported erect penis length of 14.15 ± 2.66 cm (range = 4–26 cm) and mean erectile penile circumference of 12.2 ± 2.33 cm (range = 3–19 cm, diameter = 3.88 cm) (Herbenick et al. 2014). Relative to our body size, average penis length of humans seems to fall right on the regression line for other primates, contrary to reports that human penises are disproportionately long (Dixson 2009). However, the width of the human penis is significantly greater than in other primates (Dixson 2009).

Erection brings about a significant change of length and girth and reveals a large helmet-shaped glans, similar to that found in other primate species (Dixson 2009). Compared to our primate cousins, male genitalia lack a baculum, or penis bone, and spines on the surface of the penis (Dixson 2009).

Vaginal morphology is also variable depending on age, whether women have had children or not, and their ethnicity (Pendergrass et al. 2000). Maximum width averages 5.20 cm (3.44–5.83 cm) (Pendergrass et al. 2000). Three-dimensional castings of the vaginal lumen reveal variation in its shape and size (Pendergrass et al. 2000), but sample sizes are much smaller than investigations of penile dimensions. Compared to other primates, the length of the human vagina also appears to fall right on the regression line of body size (Dixson 2012), but unfortunately, no data are available to compare vaginal width. Finally, all walls of the vagina are densely innervated, though some regions more than others.

The Role of Sexual Selection in Shaping Human Genitalia

Several studies have investigated the potential role of pre-copulatory female choice in shaping the size of the male penis. Females seem to prefer larger penises, though only when coupled with

other attractive features of body shape like taller more muscular body types (Mautz et al. 2013). Females have also been found to have a preference for a certain penis girth, based upon choice of 3-D printed models, but their preference changes depending on whether this would be for a long-term relationship vs. a one-night stand, with females preferring thicker penises for a one-night stand (Prause et al. 2015).

This preference could relate to post-copulatory female choice for larger penises. Women rate penis width as more important than length to their sexual satisfaction, and they are more likely to have vaginal orgasms when their partner had a longer than average penis (Costa et al. 2012). Therefore anticipation of sexual satisfaction may play a role in pre-copulatory female choice for penis size.

The potential role of penile morphology in sperm competition was investigated in one study that suggested that the shape of the glans penis allows males to remove sperm from previous matings during thrusting. They used model penises and vaginas to mimic removal of an ejaculatory-like fluid and showed that the penis glans could in fact cause some backflow of fluid (reviewed in Dixon 2009). However, the sperm removal hypothesis requires that females copulate with other males in a short enough period of time, to make removing rival ejaculate an important evolutionary force (typically a matter of a few hours), and there are no data that suggest this is the case. This hypothesis also ignores the fact that several primate species have a similarly shaped helmet-like glans, and this shape bears no clear association with mating system, as would be predicted if males were trying to remove sperm from promiscuous females (Dixon 2009).

The presence of penile spines and a penis bone or baculum in mammals is associated with residual testes mass, but not mating system (monogamy vs. not), suggesting their presence is associated with intensity of sexual selection (Orr and Brennan 2016). The loss of penile spines may have resulted from the shift to increased pair bonding and parental care in ancestral humans and more monogamous mating systems (McLean et al. 2011), but without knowing the

role of penile spines in mammals, this hypothesis remains speculative. Experimental penile spine removal in primates leads to longer copulation times, likely due to reduced sensitivity, and the loss of penile spines may have resulted in longer copulation times in humans compared to chimpanzees (McLean et al. 2011). Penile spines were lost in humans as a result of the loss of one regulatory enhancer that controls expression of a localized androgen receptor (McLean et al. 2011).

The loss of the baculum remains puzzling in humans. The role of the baculum in mammals, just like spines, is unclear, and many hypotheses have been suggested to explain its presence and morphology. In Primates, intensity of sexual selection measured as residual testes mass correlates with the presence of a baculum (Orr and Brennan 2016), so perhaps just as with penile spines, the advent of pair bonding and monogamy made the baculum obsolete, but again this is mere speculation given our lack of data.

The Role of Natural Selection in Shaping Human Genitalia

One possible alternative behind the large width of the human penis is that changes in vagina morphology drove changes in penile morphology (Dixon 2009; Brennan 2016). Human babies are born with large heads, almost larger than any other primate. Such large heads require a larger birth canal, both in terms of pelvic space and vaginal opening. In order for copulation to still be successful, a wider vagina would select for a wider penis so that ejaculation is still possible because friction would be maintained during thrusting. The mechanical interaction between male and female genitalia is the closest mechanical interaction between any two structures in nature, and such close coevolution is predicted to make copulation feasible.

Conclusion

Human male genitalia are unique in that they are wider than expected for our body size, and they

lack spines and a baculum, both of which are present in our close relatives. The enlarged width of the penis may have resulted from selection on males to catch up to enlarged female vaginas that could give birth to larger babies. Males that are more closely fitting the female vagina could then provide greater stimulation during coitus leading to greater sexual satisfaction in women. Women seem to have a preference for such larger penises, but it is unlikely that female preference alone would have driven morphological changes in male genital width. The loss of the baculum and penile spines may have resulted from a shift to increased pair bonding and parental care in ancient humans, and the subsequent reduction of intensity of copulatory and post-copulatory sexual selection.

Cross-References

- [Adaptations: Product of Evolution](#)
- [Benefits of Short-Term Mating](#)
- [Competition for Resources Desired by Females](#)
- [Copulation](#)
- [Copulatory Intrasexual Competition](#)
- [Cryptic Female Choice](#)
- [Cues to Infidelity](#)
- [Evolution of Long-Term Pair-Bonding in Humans](#)
- [Female Infidelity](#)
- [Female Mate Choice \(Intersexual Selection\)](#)
- [Human Copulation](#)
- [Intrasexual Male Competition](#)
- [Mating Strategies](#)
- [Polygamy in Humans](#)
- [Reproduction](#)
- [Reproductive Strategies](#)
- [Sperm Competition Risk and Partner Abuse](#)
- [Women's Mate Preferences](#)

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Evolution of Hearing and Balance

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Synonyms

[Evolution of mammalian hearing](#); [Sound perception](#); [The traveling sound](#); [The peripheral and central auditory system](#); [Vestibular system](#)

Definition

The evolution of the human ear, the auditory system, and balance.

Introduction

To have a solid understanding of the capacity to hear and listen to sounds, there must be an education of how the sound firstly travels from its source to our brain. Therefore, there will be a brief discussion of the direction of sounds, followed by an evolutionary standpoint of the middle ear's ossicles based on Reichert-Gaupp's theory and more research on the evolution of the mammalian ear.

Next will be a brief discussion of the anatomical structures of the peripheral auditory system, namely the outer (external) ear, the middle ear, and the inner ear, along with its inner most important structures, the cochlea and the otoliths.

Important for keeping balance and movement is the role of the semicircular canals. Also, there will be a brief discussion on the deleterious effects of alcohol on the balance system of the ear, otherwise known as the vestibular system.

Lastly, the central auditory system is reviewed here, with a brief literature review on the structure and function of the primary and secondary auditory cortex, as well as the molecules responsible for transducing motion into biological reactions, known as mechanosensors.

Distinguishing the Direction of Sounds

In order to understand the direction of sounds, we need to understand how sound is conducted. Usually, sound is created when an object is vibrated. The vibration travels through the surrounding medium, which is usually air, as pattern of changes in pressure which eventually is heard as sound (Moore 2001). Sound is called a pressure wave for the reason that when the molecules of the ear come closer, the pressure increases resulting in a process called compression; when the molecules move further apart, the pressure decreases resulting in a process called rarefaction (Oghalai and Brownell 2012).

According to a theorem by Fourier, the sound could be described in sinusoids, which is an analysis of complex waveforms. A sinusoid resembles the sound produced by a tuning fork,

which it is often called a simple tone, or a pure tone. Each sinusoid is called a Fourier component of the sound and a magnitude plot of the components as a function of frequency is called a spectrum. The result of a Fourier analysis is to produce the spectrum of the soundwaves by splitting the waveforms into component sine waves of different frequencies (Moore 2001; Pickles 2012). There are two important variables in each sound wave, the frequency and the amplitude or intensity (loudness). Frequency is the number of waves that passes a point in a second and is measured in cycles per second, otherwise called hertz (Hz). The amplitude or intensity is related to the magnitude of the produced movements, and is measured in decibels. The traveling sound wave relies upon the pressure of the environment which is the medium in order for the sound to be heard. This is called impedance of the medium. If the impedance is high, high pressures are needed to yield a definite velocity (see Pickles 2012, pp. 1–19).

The very first step of the hearing process is when the outer ear captures the sound waves which travel to the eardrum and cause it to vibrate. In the middle ear, the ear bones convert the airborne vibrations of the eardrum into fluid-borne vibrations in the cochlea. The traveling wave is then converted into bioelectric signals in the auditory sense cells of the inner ear (Hoy 2012).

The sound is then analyzed in the inner ear, which is responsible for performing spectral and temporal analyses of the acoustic signal. The spectral analysis is the process of extracting and defining the various frequency components of the acoustic signal. Frequency and intensity is what is otherwise called “pitch” and “loudness.” The cochlea is responsible to tease out the frequency components of the incoming acoustic signal and determine its amplitude and the temporal aspects of it. This process is the first level of auditory processing; subsequent processing takes place in the auditory pathway to the brain (Seikel et al. 2010b).

Since sound is a disturbance in the air, this causes the tympanic membrane (TM) to move. The movement, afterwards, is translated to the oval window where, based on the movement of the TM (inwards or outwards), the stapes footplate

is moved accordingly. More specifically, when the stapes compresses the perilymph of the scala vestibuli, Reissner's membrane is inflated toward the scala tympani. That is, when the fluid of the scala vestibuli is compressed, it is translated directly to the basilar membrane. In the structures of the TM-ossicle-footplate, the sound – translated into Hertz – creates a 100 Hz signal in the footplate, which in turn creates a periodic vibration to the basilar membrane where a traveling wave is initiated (Seikel et al. 2010b).

The way the sound is distinguished depends upon the frequency of the acoustic signal. High frequency sounds cause vibration of the basilar membrane closer to the vestibule, which is the basal end of the cochlea. Low frequency sounds result in a long traveling wave that reaches the apex, having to do more distance along the basilar membrane. Hence, the traveling wave distinguishes the frequency components of complex sounds because the higher frequency sounds are processed in basal regions, whereas lower frequency sounds are processed near the apex. The analysis and discrimination of lower to higher frequencies is credited to the basilar membrane. This was demonstrated on a series of experiments, performed by von Békésy (1948), that the elasticity of the basilar membrane is reduced towards the stapes rather than the helicotrema, consequently producing a stiffness gradient which, when the cochlea is stimulated, results in the creation of a pressure wave that travels from the base to the apex (Gelfand 2010, p.75). Regardless of how the traveling wave is initiated, it always travels from the base of the basilar membrane towards its apex based on the certain gradient of the membrane (Seikel et al. 2010b).

In regards to sound localization, it is through the process of binaural hearing that performance is improved in auditory tasks. Specifically, an essential task for the central auditory pathways is to analyze the auditory messages sent by the two cochleae into the auditory structures of the brain. This segregation and localization of the sound messages is significant for the separation of target signals from noisy environments. For example, sound coming from a source on the right reaches the left later than the right ear – because it has to

travel further – and it reaches it with a lower intensity. This is called the head shadow effect, that is, the further to the right the source is located, the larger the interaural differences (Avan et al. 2015). Binaural interaction takes place mainly and almost simultaneously at three levels of the brain: the superior olivary complex (SOC), the nuclei of the lateral lemniscus (NLL), and the inferior colliculus (IC) (for more on the binaural pathways of the brain see Moore 1991).

There is an evolutionary advantage of binaural processing of sounds. Information gained from this process could help detecting a predator approaching surreptitiously while the prey is engaging in a certain activity, that is, drinking water around a noisy environment. This way, the brain, by evolving and developing a refined stereophonic sound system, has contributed in the survival of species (Avan et al. 2015). Although for humans survival may not be at stake, binaural processing is helpful along noisy environments such as cocktail parties, where the listening ability depends on the type, number, and location of interfering sounds as well as the interactions of them (see Hawley et al. 2004). It is noteworthy that the increase in brain size of mammals is probably due to an increased processing ability for binaural sounds in various auditory nuclei in the brain in order to deduce the locality of sound (Manley 2010).

Reichert-Gaupp Theory

The Reichert-Gaupp theory is a theory established by Karl Bogislaus Reichert and Ernst Gaupp. Both of them are credited with the origin of mammalian ossicles of the ear. Specifically, Reichert first established the relationship between the reptilian jaw bones and mammalian middle ear bones in 1837 which was later advanced by Gaupp (World Heritage Encyclopedia 2017). The theory postulated that the malleus and incus are derivatives of the first arches of the skeletal elements of the middle ear (Takechi and Shigeru 2010). Specifically, the stapes, incus, and malleus, besides the dermal component (the goniale of Gaupp), have been confirmed to be homologous

of the reptilian columella auris, quadrate, and articular (Westoll 1944). It is noteworthy that this theory was developed before Darwin's *Origins of Species* (Takechi and Shigeru 2010).

Despite the fact that fossil records support Reichert's theory, more detailed embryological analyses and technological advances were put forward to dispute it (Takechi and Shigeru 2010). Specifically, Otto (1984) refuted Reichert-Gaupp's theory on the bases of new embryological, teratological and morphological and functional interpretation of paleontological findings. Other theories were used to oppose Reichert's theory as well such as Hanson et al. (1962) and Jarvik (1980 as cited in Takechi and Shigeru 2010).

Nevertheless, Ernst Gaupp was the first to present a synthesis of embryological and paleontological data to explain the evolution of the mammalian middle ear structures (see Maier and Ruf 2016, for a historical review of the Reichert-Gaupp Theory).

Evolution of the Mammalian Ear

Masterton et al. (1968) have aimed to identify the significant changes in the hearing capacity of the mankind evolution by comparing it to the evolution of other mammals. The results indicated that high frequency hearing (more than 32 kHz) is a trait characteristic of mammals due to the close distance of their ears, and the result of the selective pressure for accurate and instantaneous localization of the source of brief sounds. Furthermore, low frequency sounds (less than 1 kHz) is not unique to mammals; this is mostly a characteristic of humans. The researchers stressed that the lowest threshold (or overall sensitivity) is not a general characteristic of mammals nor does it differ from birds; in other words, humans have very low frequency sensitivity in sounds.

In regards of the evolution of the eutherian mammalian ear, Manley (2017) has provided an elaborative description. Specifically, he noted that more than 250 million years ago (Paleozoic era) the synapsids were separated from the stem reptiles and formed the mammals' ancestors. During

the early stages of the Mesozoic, where most evolution of the eutherian ear took place, these ancestors had a "temporary" middle ear that was connected to the lower jaw. This was later developed to a "definite" middle ear. During this period, the mammalian ancestors adopted the organ of Corti. The bone integration into the cochlea took place only in therian mammals and came before the cochlear coiling and the split of Eutheria from the Metatheria. The coiling in the cochlea resulted in the loss of the lagenar macula and, subsequently, the evolution of prestins, a motor-protein found in high concentration in the lateral cell membranes of outer hair cells which leads to increased sensitivity at low sound levels (for more about Prestin see Dallos 2008; Li et al. 2010; Zheng et al. 2002; Zheng et al. 2000).

This protein is supposed to be a mediator between the somatic electromotility in cochlear outer hair cells. These hair cells are responsible for cochlear amplification and rapid cell length changes (Franchini and Elgoyhen 2006); the transduction of mechanical activity into electrochemical activity when the stereocilia are bent (see Gelfand 2010, p.76); and compensate for the energy loss for the transmission of the traveling wave on the basilar membrane resulting in an increased sensitivity of the ear (as much as 50 dB) and an increased frequency selectivity at low intensities (Moller 2013, p.55). Franchini and Elgoyhen noted in their study that the motor-protein prestin has specifically evolved in mammals to support the mammalian adaptation of the cochlea. They concluded that their study has found evidence for the positive selection in the motor-protein prestin only in the mammalian lineage.

Additionally, signatures of positive selection on the $\alpha 10$ were found, but not on the $\alpha 9$, nicotinic cholinergic receptor (nAChR) subunits. The $\alpha 9\alpha 10$ -containing nicotinic cholinergic receptor mediates inhibitory olivocochlear efferent effects on hair cells across vertebrates (Franchini and Elgoyhen 2006). This receptor also plays a significant role in various physiological processes. For example, $\alpha 9$ is required for the normal development of the efferent synapses in the inner ear, and they serve as the unique source of

extracellular calcium for Ca^{2+} -activated potassium channels in mature auditory hair cells (Vazquez 2016). Franchini and Elgoyhen suggested that evolution-driven modifications of the $\alpha 10$ subunit most probably allowed the $\alpha 9\alpha 10$ heteromeric receptor to serve a different function to the mammalian cochlea.

A remarkable discovery made by Montealegre-z et al. (2012) was regarding the similarity in the hearing system between mammals and rainforest katydids. Specifically, these insects demonstrated to possess equivalent biophysical mechanisms for auditory processing as such of mammals, based on the three stages of collecting sound from the outer towards the inner ear. Hoy (2012) reported that these three stages are possible to have evolved primarily in insects and much later in mammals.

Further on the mammalian ear, Radojevic et al. (2015) have found evidence of the Akt isoforms, which play significant role in the mammalian inner ear, especially in the cochlea. More specifically, the kinase Akt is a key downstream mediator of the phosphoinositide-3-kinase signaling pathway, and it is involved in a variety of cellular processes. Akt is comprised of the three isoforms, each encoded by a separate gene. On their study, they have indicated that Akt2 and Akt3 enhance hair cell resistance to ototoxicity, but Akt1 does not. The researchers have highlighted the significance of these isoforms in normal hearing.

On the same vein, Warchol (2011) has identified a regenerative ability of the sensory hair cells was lost during the mammalian evolution. Specifically, Warchol argues that the regeneration failure in the mammalian ear was the result of a trade-off between phenotypic plasticity of supporting cells and sensitive high frequency hearing.

The Auditory System

The auditory system is a sensory system that is in control for hearing. It is divided in two sub-systems, namely the peripheral auditory system (i.e., outer ear, middle ear, and inner ear) and the central auditory system, that is, the auditory

nerve, cochlear nucleus, auditory cortex, auditory ascending and descending systems, etc. (Romand and Ehret 1997; Velluti 2008).

The Outer Ear

The outer (external) ear is consisted of the pinna, which consists of other structures with specific names (see Moller 2013); the ear canal (external auditory meatus); and the ear drum (lateral portion of the tympanic membrane) (Pickles 2012; Munir and Clarke 2013).

The pinna serves mainly as a collector of sound to the area of the cochlea, which is acoustically the most important part (Seikel et al. 2010a; Moller 2013). The sound is then directed to the ear canal.

The ear canal is covered by a skin that secretes wax, otherwise called as cerumen. Cerumen has an antibacterial and antifungal function, and acts as a healing agent of any small injuries that may happen in the ear canal (Moller 2013). The skin of the external auditory meatus is filled with various nerves responsible for bodily functions such as blood circulation, heart rate, and fainting.

The ear drum creates a boundary between the outer and middle ear, and constitutes the beginning of the middle ear. Also, the eardrum is divided into three ear bones: the hammer, anvil, and stirrup (Balkany and Brown 2017).

The Middle Ear

The middle ear is a space filled with air and is located behind the tympanic membrane which contains the following ossicles (bones of hearing): malleus, incus, and stapes (Munir and Clarke 2013) or otherwise called hammer, anvil, and stirrup, respectively (Hoy 2012). This constitutes the ossicular chain, which provides the way for the acoustic energy to be transmitted to the tympanic membrane and then to the inner ear (Seikel et al. 2010a). The middle ear also consists of the Eustachian Tube which forms the air space between the nose and the throat (Balkany and Brown 2017).

There are also two tympanic muscles which are attached to the ossicles: the stapedius and the tensor tympani. The Stapedius's function is to rotate the footplate of the stapes posteriorly, thus stiffening the ossicular chain. The tensor

tympani's function is to pull the malleus anteromedially, and to reduce the movement of the tympanic membrane by assigning indirect tension on it. The tensor tympani and the stapedius reduce the strength of the acoustic signal of reaching the cochlea in order to protect the inner ear from high intensity sound (Seikel et al. 2010a).

Another part of the middle ear is the Eustachian tube, which connects the middle ear and the nasopharynx, where the cranial nerve VII passes through (Munir and Clarke 2013). Its function is to allow mucous exit the middle ear and allow oxygen to enter through and out of it. It is, also, used to balance the pressure levels of the middle ear in cases where the atmospheric pressure is different such as diving and in higher altitudes (Balkany and Brown 2017).

Reichert's (1837) hypothesis regarding the middle ear in mammals has aided the understanding of the evolutionary developments of the middle ear's ossicles. Specifically, Reichert postulated that the malleus and incus were derived from cartilages comparable to the lower and upper jaw structures of the articular and quadrate. Takechi and Shigeru (2010) have found evidence from fossil records in South Africa and Russia confirming the jaw origin of the mammalian middle ear components. Additionally, the mammalian tympanic membrane is assumed to have a small dorsal part homologous to the reptilian tympanic membrane called pars flaccida, as well as a ventral portion homologous to a mammalian middle ear feature, the pars tensa.

Manley (2010) on the contrary, suggests the tympanic membrane was developed independently and that its origin is unique. Manley further elaborated that evolution in similar groups happen independently most of the time and the results from these structures could be similar. He noted that in the development of the tympanic middle ear in therian mammals, the brain became larger and a secondary palate was developed, subsequently creating a pressure system to replace the ancestral pressure-gradient middle ear (see Manley for a comprehensive review and Maier and Ruf 2016, for a historical review of the middle ear).

The Inner Ear

The inner ear is consisted of the cochlea and the balance system, otherwise called the vestibular system. Our understanding of the structure of the inner ear is based on the work of scientists who have contributed to our understanding of the cochlea (Johnsson and Hawkins 1967). Specifically the drawings of Magnus Gustaf Retzius (Jelliffe 1920) of the cytoarchitecture of the human organ of Corti showed the membranous labyrinth and it parts on various human developmental stages (Johnsson and Hawkins 1967).

The vestibular system is made up of a vestibule, which is between the cochlea and the semicircular canals. A structure called the bony labyrinth is comprised of the cochlea, the vestibule, and the semicircular canals. The fluid inside the semicircular canals is linked with movement which affects balance (Boulpaep and Boron 2005).

The Cochlea

The cochlea is a snail-shape structure, consisted of compartments in the form of a spiral. These compartments are filled with fluids. The cochlea houses the organ of Corti which is responsible for receiving acoustic information (Chang and Khana 2013). The cochlea, together with the vestibular organ, is enclosed in the temporal bone (Moller 2013). More than 15000 hair cells in the cochlea are stimulated by the vibrations of the inner ear fluid which lead to electrical signals perceived as hearing (Balkany and Brown 2017).

The cochlea's function is to separate the sounds based on their frequency so that different sound spectra activate other auditory nerve fibers. This sensory transduction is happening in the inner hair cells. The outer hair cells help to reduce friction on the motion of the basilar membrane, increase breath vibration of the basilar membrane for the lower sound intensities, and increase the frequency selectivity of sound. Frequency selectivity is decreased when the intensity of sound is increased, a phenomenon that causes the cochlea to behave in a nonlinear way. This helps to compress sounds before the auditory nerve is stimulated. This process aids to the coding of the sounds according to their intensity (Moller 2013).

Additionally, another function of the cochlea is to produce sounds directed from the middle ear to the tympanic membrane, something that consequently helps with the production of the otoacoustic emission (OAE). In essence, this is a sensitive microphone in the ear canal that records produced sounds (Møller 2013).

Regarding the evolutionary development of the cochlea, Manley (2010) suggested that a small hair-cell epithelium for hearing (basilar papilla) existed in stem amniotes, that is, archosaurs, lepidosaurs, and mammals. Fossil evidence from the coelacanth fish *Latimeria Chalumnae* supports this, suggesting that the basilar papilla seems to be the precursor of the cochlea in mammals (Fritsch 1987), a finding that is in line with Köppl's (2011) conclusion that the basilar papilla is the mammalian organ of Corti.

The organ of Corti is covered by a gelatinous and fibrous fold known as the tectorial membrane. It consists of molecules and collagens known as tectorins (Pickles 2012). These tectorins have a significant role for the hearing process (Richardson et al. 2011). The organ of Corti also is composed of a specialized structure containing hair cells. It is located on the basilar membrane and it organizes the auditory transduction (Pickles 2012).

The features of the therian cochlea, according to Manley (2017), were developed millennia ago, a process that led to the loss of the lagenar macula. This has, as a result, the structural revolution of the cochlea's physiology (Manley 2017).

Otolith

Otoliths are small particles made of calcium carbonate. The otolithic membrane is made by these otoliths, which houses the utricle and the saccule inside the vestibule (Chang and Khana 2013; Seikel et al. 2010a).

The otolithic membrane covers the utricular macula, a sensory organ consisted of hair cells and cilia. The saccule is positioned near the scala vestibule in the vestibule and is consisted of macula and the otolithic membrane. Both the saccule and utricle are connected through the endolymphatic duct implanted in the dura mater.

Because the otoliths are dense the gravitational forces help to deflect the stereocilia when the head is dormant (Hain and Helminsky 2007). When the head is moving or tilted, the otolithic membrane and the macular surface is activated, which result in the bending of the hair cells (Oghalai and Brownell 2012), hence generating a balance in the posture and in the movement.

Balance and Motion

The balance system – or otherwise called vestibular system – is a complex system comprised of various structures in the body, namely, the bony labyrinth and the membranous labyrinth of the inner ear; the cerebellum; the eyes; the brain cortex; and the muscles and joints, which are all connected to the brainstem called the vestibular nuclei (Munir and Clarke 2013; Chang and Khana 2013).

The vestibular system has two types of sensory neuroepithelium called the macula and crista ampullaris (Chang and Khana 2013). These structures contain sensory mechanoreceptors called hair cells, and they are entrenched in a neuroepithelium membrane. The first studies that were recorded on inner hair cells were by Russell and Sellick (1978). It is presumed that the job of inner cells is to disseminate the movements of the cochlear partition to the central nervous system (Pickles 2012, p. 57; Chang and Khana 2013).

Adaptation is a significant physiological property of the macula (Chang and Khana 2013). For instance, when the head is tilted for more than a few seconds, the bent hair cells and the depolarized membrane potentials return to normal. Consequently, this process assigns to the hair cells the property of being responsive to any movement of the head (Oghalai and Brownell 2012).

Bony and Membranous Labyrinth

The bony and the membranous labyrinth is a complex balance organ in the inner ear, which is a part of the peripheral vestibular system. The bony labyrinth consists of the cochlea and the semicircular canals, and it is filled with a fluid similar to the cerebral fluid, called the perilymph (Hain and Helminsky 2007), which is used by the

perilymphatic duct into the subarachnoid space (Chang and Khana 2013).

The membranous labyrinth consists of the sensory epithelium and is embedded in the perilymph inside the bony labyrinth. Inside the membranous labyrinth there is a fluid which is called the endolymph (Chang and Khana 2013). The membranous labyrinth also consists of the utricle, the saccule, and the lateral, superior, and posterior semicircular ducts (Chang and Khana 2013). Each structure contains the macula – a sensory neuroepithelium. The macula of the utricle senses horizontal movement whereas the macula of the saccule senses vertical movement. The utricle and saccule sense the movement of the head in space and they respond to linear acceleration, forces of gravity, and the tilting of head (Chang and Khana 2013).

Semicircular Canals

The location of each semicircular canal is vertical to the other canals on the same side and belongs to the same side of the body with the opposite canals (Chandrasekhar 2013).

The three semicircular canals sense the turning motion of the head. The otolithic organs (utricle and saccule) then analyze the motion of the head and create a nerve signal to the brain to indicate movement (Munir and Clarke 2013). A structure named semicircular duct compose the kinetic labyrinth that perceives the acceleration or rotation of the head. At the end of each semicircular duct there is a structure called the ampulla, which contains the crista ampullaris, covered by a gelatinous substance contained with hair cells, called the cupula (Chang and Khana 2013). Based on the rotational motion of the endolymph, the cupula bends the hair cells which fire afferent fibers and transfer the movement information in the brain (Chang and Khana 2013).

Alcohol and Balance

Alcohol intoxication has devastating results in the organisms in many ways. Besides its negative effects in the postural sway (Woollacott 1983), alcohol intoxication also affects the oculomotor

system. Based on a study from Nieschalk et al. (1999) it is evident that the vestibule-cerebellum is, also, affected. Consistent with the research of Ikeda et al. (1980), small doses of ethanol interfere with the synaptic transmission in the lateral nucleus (LVN) monosynaptic and polysynaptic II neurons.

Additionally, Modig et al. (2012b) demonstrated in their research that postural control is significantly affected. They highlighted the fact that ethanol consumption causes destabilization in lateral motion than in anteroposterior motion and that intoxication decreases adaptation mechanisms regarding stability control.

When alcohol is taken in high amounts, the cupula in the semicircular canals is affected and becomes lighter than the endolymph leading to the buoyancy hypothesis (Fetter et al. 1999) and subsequently to a process called positional alcohol nystagmus (PAN) and rotatory vertigo. When the gravitational vestibular cues are compromised, visual information are used instead (Hafstrom et al. 2007). Essentially, alcohol intoxication causes a multifaceted deterioration of balance and movement (Modig et al. 2012a).

Evolutionary Perspective on the Vestibular System in Mammals

From an evolutionary perspective, Beisel et al. (2005) have identified a protein called osteopontin using immunocytochemistry in the otoconia (a structure inside the utricle and saccule of the ear). This protein is suggested to be a component protein of the mammalian otoconia. The researchers concluded that vestibular ear evolution appears to be linked to the enrolment of specific genes into an existing network of gene expression (Beisel et al. 2005).

Auditory Neurobiology

The physiology of the auditory nervous system was extensively reviewed more in animals than humans. It is consisted of ascending and descending systems that connect a link between the ear and the auditory cerebral cortex. Axons from the ear link to the cochlear nucleus neurons

connect to other nucleus in higher locations until they reach the cerebral cortex. Then, these neurons descend from the central structures to the nuclei of the ear distance (Moller 2013).

There are different pathways known as classical ascending pathways and nonclassical or adjunct systems. There are, also, specific nuclei between the auditory nerve and the primary auditory cerebral cortex found in the classical ascending pathway (Demanez and Demanez 2003). These are the cochlear nucleus (CN), the central nucleus of the contralateral inferior colliculus (ICC), the lateral portion of the ventral division of the contralateral medial geniculate body (MGB), and the superior olivary complex (Moller 2013). These nuclei are responsible to analyze the acoustic data through theory synaptic transmissions and their position in the brain (Moller 2013; Velluti 2008).

The function of the auditory nervous system is the so-called frequency selectivity. The frequency selectivity of the basilar membrane handles the frequency tuning of the auditory nerve cells and the cells in the ascending auditory pathways. According to the characteristic frequency, the nerve fibers of the auditory nerve, the cells of the auditory nuclei, and the cells of the auditory cerebral cortex are arranged anatomically. This is known as the tonotopic organization (Moller 2013; Polley et al. 2014).

Primary and Secondary Auditory Cortex

The auditory cortex is responsible for the processing of sound based on the many connections that handle auditory information (Moller 2013; Hackett 2015). It is noteworthy however that the complete anatomy of the auditory cortex is still to be understood and known completely. The lack of consensus between researchers regarding the exact anatomic positions of the auditory parts has contributed to the lack of the full understanding of the auditory cortex and the unfolding of a comprehensive tonotopic map (Moller 2013; Saenz and Langers 2014).

Based on studies that used MRI techniques, the location of the primary auditory cortex was found on a region on the medial two-thirds of Heschl's gyrus, linked to Brodmann's area 41 (Pickles 2012; Wasserthal et al. 2014; Moller 2013). The only

regions successfully mapped are frequency (Isaa et al. 2017; Wolak et al. 2017), modulation rate (Lithari and Weisz 2017), sensory tuning bandwidth (Saenz and Langers 2014; Wang and Eliades 2017), and sound intensity (Bilecen et al. 2002).

Regarding the secondary auditory cortex, Moller (2013) suggests that it responds to other stimuli, such as touch and vision. Several research suggest that there is a connection between the visual and the auditory cortex (Chen et al. 2013) and multimodal sensory interaction (Hosokawa et al. 2017).

Mechanosensor

Mechanosensory molecules are molecules which interact with other molecules and influenced by mechanical forces that may engage in biological reactions (Shen et al. 2017). This leads to a process known as mechanotransduction where based on mechanical stimuli there is a transduction into electrochemical signals and cellular responses (Bavi et al. 2017). They also work as molecular reporters inside the cells connecting mechanical stimuli to intracellular signaling events (Bavi et al. 2017).

Research suggests that the evolution of the mechanosensors took place independently (Delmas and Coste 2013). More insight on mechanosensors was based on the research of Kita et al. (2013) studying the birth of a mechanosensor and Kung's (2005) unifying principle for mechanosensation.

Conclusion

The most important structures of the ear have been reviewed. There was also a review of the evolution standpoint of the mammalian ear, and how it was developed to be as it is. Various structures of the inner ear work together to provide posture equilibrium. Not only the ear, but the neurobiology of the brain contributes to keep a person's balance in check.

Cross-References

- Alcohol and Balance
- Cochlea

- ▶ [Hearing](#)
- ▶ [Inner Ear](#)
- ▶ [Mechanosensor](#)
- ▶ [Middle Ear](#)
- ▶ [Otolithic Organs](#)
- ▶ [Outer Ear, The](#)
- ▶ [Primary and Secondary Auditory Cortex](#)
- ▶ [Vestibular System](#)

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not always the case, and there are numerous possible variations. For example, many animals possess the sexual organs of both genders either simultaneously or at different times of their lives. Earthworms first mature as males and then lay eggs and fertilize those after copulating with another male. Despite both animals having the male gender at the time of copulation, biologists describe such cases as hermaphroditic rather than homosexual. Clownfish start their life as males and develop into females when the group matriarch dies. In this case, biologists refer to them as sequential hermaphrodites rather than transgenders. However, nonreproductive sexual behavior has been observed between members of the same sex (homosexuality, HS) in numerous species including our own. So, is “true” HS common in nature, and why?

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Evolution of Homosexuality

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Synonyms

Biological exuberance

Definition

Study of transmission of same-sex sexual behavior across animal species and humans.

Introduction

Sexual behavior takes multiple forms across organisms, and although it has evolved for reproduction, it also serves other social purposes. The evolution of sex has also led to sexual dimorphism, meaning that there are morphologically and behaviorally distinct male and female genders. Across species, males usually have sex with females (heterosexuality); however, this is

Natural History of Homosexuality

In birds and mammals, there are numerous reports of homosexual behavior, which may or may not involve a sexual act, but can include courtship, pair-bonding, and coparenting. These have been observed in geese, flamingos, gulls, oystercatchers, warblers, dolphins, deer, zebras, giraffes, and others (Bagemihl 1999). At least 93 species of birds engage in HS (MacFarlane et al. 2010). Same-sex mounting is commonly observed in a wide variety of mammals such as gazelles, sheep, and elephants, and this has been attributed to expression of dominance or hormonal malfunction during rut (Bagemihl 1999).

Homosexual sex is particularly developed in primates. Interestingly, HS is more predominant in primate lineages more closely related to humans than in more distant taxonomic groups such as lemurs. In new-world monkeys (platyrrhines), such as squirrel monkeys, homosexual behavior seems limited to play and dominance interactions. In contrast in apes and old-world monkeys (catarrhines), homosexual sex is common and complex, involving consort bonding, reconciliation, tension regulation, and alliance formation (Vasey 1995). Among apes, pygmy chimpanzees (bonobos) are famous for the large variety of sexual acts that they perform,

including genito-genital rubbing, fellatio, and manual masturbation across all genders (De Waal and Lantin 1998). Bonobos are bisexual, and this is thought to contribute to group cohesion (De Waal and Lantin 1998). Common chimpanzees also engage in homosexual sex, for example, with about a third of mountings occurring between males (Bagemihl 1999) (Fig. 1). In mountain gorillas, which live in groups dominated by fewer males than in chimpanzees, sexual behavior between females is widespread (Grueter and Stoinski 2016). Other catarrhine examples of HS include baboons, macaques, and langurs (Bagemihl 1999). However, after bonobos, homosexual behavior is probably most common in humans and has been documented by anthropologists worldwide, across cultures and time periods (Table 1).

In all these examples, bisexuality may be the norm, as those individuals involved in HS often also take part in reproductive sex. However, there are also numerous exceptions, for example, about 15 % of male graylag geese are strictly homosexual (Kotrschal et al. 2006). There is increasing evidence that HS is common in nature; however, scientists and the public at large have only learned about it relatively recently, perhaps because the reporting of such behaviors had been previously censored due to societal and religious taboos.

Is Homosexual Behavior a Darwinian Paradox?

Homosexual behavior has often been considered a “Darwinian paradox.” This is because, intuitively, a genetically influenced focus on nonreproductive sex to the detriment of reproductive sex should reduce evolutionary fitness (i.e., reduce an individual’s number of descendants), and any such genetic variants should eventually go extinct (Kirkpatrick 2000). However, twin studies indicate that heritability of homosexuality is ca. 30 % in men and up to 60 % in women (Kirk et al. 2000). Note, however, that these values may be inflated, because twin studies generally estimate the broad-sense heritability, which includes several components of genetic variance, as opposed to the narrow-sense heritability, which only includes the statistically additive effects of genes. Nevertheless, the fact that there is some heritability of HS indicates that there is a genetic component underlying such a widespread behavior. Thus, the discrepancy between simple evolutionary expectations and the observed nature and prevalence of HS warrants explanation; but is homosexuality really an evolutionary paradox?

Among variable traits, homosexual behavior stands out, because the fitness consequences of preferring same-sex sexual partners seem obvious

Evolution

of Homosexuality,

Fig. 1 Several male chimpanzees mounting one another before intergroup encounter, Kibale forest, Uganda (Photo Aaron Sandel)



Evolution of Homosexuality, Table 1 Homosexuality across human cultures (Modified from Kirkpatrick 2000)

Continent	Society	Female or Male?	Juvenile or Adult?	Bisexual?	Frequency
Africa	Libya	M	J, A	Yes	95 %
	Sudan	F, M	J, A	Yes	Common
	Nigeria	F, M	J, A	Unknown	Common
	South Africa	M	A	Yes	Common
Europe	Classical Athens	F, M	J, A	Yes	Common
	Early Roman empire	F, M	J, A	Yes	Common
	Dinaric (Serbia)	F, M	A	Unknown	Unknown
	Florence, 15th century	M	J, A	Yes	>50 %
Americas	Lakota (USA)	M	A	Yes	Unknown
	Mohave (USA)	F, M	A	Yes	Limited
	Nambikwara (Brazil)	M	J	No	Common
	Yanomamo (Venezuela)	M	J	No	>50 %
Oceania	Precolonial Tahiti	M	J, A	Yes	Common
	Arundo (Australia)	F, M	J	No	Common
	Big Nambas (Melanesia)	F, M	J, A	Yes	100 %
	Marind-anim (Melanesia)	M	J, A	Yes	100 %
	Sambia (Melanesia)	M	J, A	Yes	100 %
Asia	China, 700–400 BC	M	A	Yes	Unknown
	China, 1865–1965	F	A	No	Limited
	Japan, 16th, 17th century	F, M	J, A	Yes	>50 %
	Putunukhtu (Pakistan)	M	J, A	Yes	Unknown

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since these pairings never result in offspring. Also, widespread cultural taboos that consider HS to be “unnatural” likely draw extra attention to it. However, there are at least two reasons why the seeming paradox of HS might be an illusion. First, the fitness consequences of HS are largely unknown and may be greatly overstated. Second, sexual preference is not a binary trait with clear homosexual and heterosexual states. Rather it is a continually variable quantitative trait, maybe involving the interactions of many genes (Bailey et al. 1993), and ranging from exclusively homosexual attraction through all degrees of bisexuality to exclusively heterosexual attraction (Sell 1997); for simplification, Kinsey scored sexual behavior from 0 (strictly heterosexual) to 6 (strictly homosexual) (Kinsey 1948). It is not unusual for continuously variable traits to have fitness costs at the phenotype extremes rather than in the middle range (Lande 1976).

HS can only be a paradox if the genetic factors that predispose individuals towards homosexual

behavior have real fitness costs. Although there are reasons to doubt whether there are actual fitness costs to homosexuality, quantifying fitness in long-lived natural populations is extraordinarily difficult (Kingsolver et al. 2001). First, in social species nonreproductive sexual behavior is common even in heterosexual pairings. This is especially true in humans, where females remain continuously sexually receptive throughout the nonfertile phases of their cycle, and even while pregnant (Gangestad and Thornhill 2008). In humans and other primates, nonreproductive sex (including homosexual sex) is thought to have important social implications (De Waal and Lantin 1998; Gangestad and Thornhill 2008; Vasey 1995). Thus, there may also be fitness costs to extreme heterosexuality due to reduced sociality, as well as fitness costs to extreme homosexuality due to lost mating opportunities. If so, some intermediate phenotype may be optimum. Second, there is some evidence that the genetic variants that predispose to HS increase fitness in

those who have the genes but not the phenotype. Support for this has been found in genetically identical twins where one is homosexual and the other heterosexual. In such twins, the heterosexual members have a greater number of opposite-sex sexual partners compared to identical twins who are both heterosexual (Zietsch et al. 2008). In this scenario, there is no evolutionary paradox so long as the lost reproductive success of homosexuals with the predisposing genes is balanced by increased reproductive success in heterosexuals with those same genes.

Furthermore, the fact that HS is not entirely heritable also points towards significant amounts of phenotypic variance being nongenetic and due to environmental variation (maybe up to 70 % in men; (Kirk et al. 2000)). Nongenetic variation needs little or no adaptive explanation even if there are fitness costs. This variance in quantitative traits is generally known to be a combination of direct effects of environment on individual phenotypes plus developmental noise, much of which may be practically unavoidable (Lande 1976).

Finally, even if there have been real fitness costs to homosexual behavior, this alone does not make the behavior unique or in particular need of biological explanation. Most traits that vary within humans are heritable and many of these will have fitness differences according to trait expression. For example, stature in humans is highly heritable (90 %) (Macgregor et al. 2006), and taller (but not extremely tall) men have greater reproductive success (Pawlowski et al. 2000). Similarly, physically attractive people have greater reproductive success than unattractive people (Jokela 2009). Yet, neither biologists nor the general public wonder why there are still short, less attractive people. It might be supposed that there is excess focus on HS compared to, say, stature, because the effects on reproductive success are more direct. However, this is not necessarily the case. For example, erectile function/dysfunction is a variable trait with clear reproductive implications. Yet, there has been almost no interest among researchers or the general public in why natural selection has not eliminated erectile dysfunction (Cellerino and Jannini 2005). The long-term maintenance of genetic and phenotypic

variation in quantitative traits despite stabilizing selection or fluctuating directional selection has long been recognized (Lande 1976; Lande 2008), and it is likely that the focus on HS as an evolutionary paradox is largely driven by cultural taboos against the behavior, rather than any real unique biological perplexity.

Biological Models of the Prevalence of Homosexual Behavior

The seeming Darwinian paradox of homosexual behavior has led to the development of several biological models to explain its prevalence. Most models fall into two broad categories: genetic and epigenetic models. Genetic models typically explain the persistence of a hypothetical “HS” gene variant (allele) through some indirect evolutionary advantage for that variant. Epigenetic models explain homosexual behavior as a result of heritable changes in gene expression patterns due to chemical modifications that occur to the DNA of developing organisms. These models each make clear predictions; however, there is only limited support for any of them.

Kin altruism selection. This model is based upon William Hamilton’s kin selection theory and suggests that homosexuals forego their own reproduction in order to altruistically aid in the rearing or reproductive efforts of relatives (Kirkpatrick 2000). Kin selection theory only predicts altruistic behavior when the reproductive benefits to the recipient are greater than the product of the cost to the altruist and the degree of relatedness. Because the costs of completely foregoing reproduction are quite high, this model predicts that only individuals of low phenotypic quality with low personal reproductive potential should adopt the strategy. It also predicts that the behavior will be more common in males because of the greater variance in male reproductive success. There is little direct support for the kin selection model. Also, it is not clear why foregoing reproduction to aid relatives would necessitate HS (Kirkpatrick 2000).

Overdominance selection. Overdominance selection proposes that men who are heterozygous for a hypothetical “HS” allele are heterosexual and have increased fitness over homozygotes for the “HS” allele (who are homosexual), as well as over homozygotes for the “non-HS” allele (who are also heterosexual). The same applies to women. In this scenario, the increased fecundity of heterozygotes maintains the “HS” allele in the population at a frequency that is determined by the relative fitness of the three genotypes. With overdominance selection, it is expected that the “HS” gene will be found on a nonsex chromosome (autosome), because it is easier to maintain overdominance polymorphisms at equilibrium on those autosomes rather than sex chromosomes (Gavrilets and Rice 2006). There is currently scant evidence for the overdominance selection hypothesis.

Sexually antagonistic selection. In sexually antagonistic selection, a hypothetical “HS” allele would result in an evolutionary cost when expressed in men (i.e., they would have fewer offspring) but would be counterbalanced by an advantage when expressed in females (i.e., more offspring), or *vice versa* (Gavrilets and Rice 2006). In this scenario, it is hypothesized that an “HS” allele would be either masculinizing or feminizing when expressed in either sex. A masculinizing “HS” allele would increase the fitness of males, but decrease the fitness of females by causing HS, and a feminizing “HS” allele would do the opposite. Under the sexual antagonistic model, it is expected that genes influencing HS would be found on the X chromosome more often because there are a wider range of relative fitness scenarios under which polymorphism can be maintained compared to the autosomes, and this is one possible way in which this model can be distinguished from overdominant selection (Gavrilets and Rice 2006). Limited evidence in support of the model comes from the finding that markers on the X-chromosome influence male homosexuality in humans (Hamer 1993).

Bisexual advantage. Another model is proposed here for the maintenance of homosexual

behavior based on the idea of stabilizing selection or fluctuating directional selection; this new model is called “bisexual advantage.” This model extends aspects of homosexual alliance formation discussed above in primates, along with a quantitative genetics approach to trait evolution. Sexuality is a continuously variable and heritable trait that ranges from exclusively homosexual attraction to exclusively heterosexual attraction. Numerous genetic loci would contribute small additive amounts to the overall heritability of this quantitative sexual trait. It is hypothesized that the optimum trait value with respect to reproductive fitness is intermediate and thus in the bisexual range (maybe between Kinsey’s 1–3 scores). Individuals with fully homosexual attraction (Kinsey’s 6 score) would fail to reproduce and be selected against, while individuals with fully heterosexual attraction (Kinsey’s 0 score) would also have fewer offspring. This may be because such individuals are poor at forming social alliances (Kirkpatrick 2000), or it may be for some yet unknown reason. Indeed, such a pattern where both phenotype extremes are disadvantaged is thought to be the most common among quantitative traits and is due to stabilizing selection or fluctuating directional selection (Lande 1976; Lande 2008). The bisexual advantage model predicts that (i) some degree of bisexual attraction is more common than exclusive homosexual or heterosexual attraction, (ii) sexual attraction is fluid and changes depending upon social context (i.e., the environmental component), (iii) many genetic loci weakly influence sexual attraction, and (iv) there are no genetic loci that strongly influence sexual attraction. The bisexual advantage model is perhaps the most conservative genetic explanation for the persistence of homosexual behavior because sexuality would then follow the pattern of the vast majority of quantitative traits where intermediate phenotypes are favored (Lande 1976). Note that this model is compatible to a degree with the sexually antagonistic model, if (i) possessing one copy of a “HS” allele contributes to some, but not

exclusive, homosexual behavior and (ii) this allele goes to fixation in the population (i.e., every individual of the population has a copy of this allele in their genome (Savolainen and Lehmann 2007)).

There is some behavioral as well as genetic support for this bisexual advantage hypothesis. First, good estimates of the frequency of bisexuality do not exist; however, the majority of human and nonhuman animals that participate in homosexual sex also participate in reproductive sex (Kirkpatrick 2000; Vasey 1995). Second, the expression of homosexual behavior is known to be condition-dependent in humans. For example, having spent time in the US Navy or in a British boarding school increases the likelihood of having had homosexual experience (Kirkpatrick 2000). Finally, genomic surveys looking for genes that influence sexual attraction have failed to find any loci that strongly predict homosexuality (Sanders et al. 2014). Instead, genome-wide scans have identified relatively few loci associated with HS, each with relatively small effect, leaving the majority of the heritability of homosexuality unexplained. This is the expected pattern if most of the heritability is contributed by loci with too small of an effect to be detected in genome-wide scans (Yang et al. 2010), suggesting that sexuality is a quantitative trait, and the majority of loci influencing sexuality are yet to be discovered.

Paternal and maternal effects. In an epigenetic model of HS, so-called epigenetic marks (changes in DNA packaging such as DNA methylation or histone tail modifications) influence sensitivity to androgen hormones by the developing genitals and brains, and therefore also influence gender preference and identity (Rice et al. 2012). In animals such as humans, male and female sex chromosomes (XY and XX, respectively) have characteristic epigenetic marks that canalize development accordingly. When discordant epigenetic marks are passed trans-generation, a child may develop a cellular mosaic whereby genital development will match the appropriate sex chromosome but brain development for sexual

preference will be canalized towards the opposite gender by the epigenetic marks. Put simply, a mother may pass onto her son discordant epigenetic marks causing the development of female sexual preference and resulting in male HS. The same logic applies to the father of a lesbian daughter. This epigenetic model of HS has advantages over genetic models: It is compatible with the relatively low concordance of HS in identical male twins (30 %; (Kirk et al. 2000)) and with the fact that genomic association studies have failed to find strong genetic markers for HS (Rice et al. 2012; Sanders et al. 2014). The model has also clear testable predictions, although the practicalities of such studies would be impaired by requirements to work with postmortem or fresh human stem cells (Rice et al. 2013). Nevertheless, those predictions include: (i) there are XX- and XY-specific epigenetic marks in the stem cells of developing heterosexuals; (ii) there are XX- and XY-discordant epigenetic marks in the stem cells of developing homosexuals; and (iii) some of these discordant epigenetic marks are trans-generationally inherited and therefore will be shared with higher frequencies by identical twins when at least one is HS, but not necessarily the other one (Rice et al. 2013).

Conclusion

Homosexual behavior is common throughout the animal world and has often been considered an evolutionary paradox. The existence of the supposed paradox is likely a confluence of the assumption that those who engage in HS fail to reproduce, coupled with cultural disapproval of homosexual behavior. Some of this confusion may also stem from the fact that most researchers have considered sexuality to be a binary trait with either homosexual or heterosexual trait states. If sexual preference is a continuous trait influenced by many different genes of small effect, or some epigenetic marks canalizing a “mosaic” development, then the persistence of homosexual behavior is not particularly surprising. In fact, it may be

the case that some degree of bisexuality is actually an evolutionary optimum phenotype in many species, including humans.

Cross-References

- ▶ [Ancient Homosexuality](#)
- ▶ [Female Homosexuality and Bisexuality](#)
- ▶ [Genetic and Prenatal Components of Homosexuality](#)
- ▶ [Homosexual Receptivity](#)
- ▶ [Homosexuality](#)
- ▶ [Homosexuality Paradox, The](#)
- ▶ [Hormonal Component of Homosexuality](#)
- ▶ [Lesser-Known Theories of Homosexuality](#)
- ▶ [Non-Western Homosexuality](#)

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Evolution of Human Male Homosexuality

► Alliance Formation Theory

Evolution of Human Sociality

► Jonathan Haidt's The Righteous Mind

Evolution of Human Sociality, The

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Synonyms

Cooperation; Human cooperation; Large-scale cooperation; Prosociality

Definition

There are different evolutionary mechanisms that explain human large-scale cooperation (which is so rare in animal kingdom) even with genetically unrelated people.

Cooperation has adaptive importance as it increases the chances of hunting success and access to resources through the establishment of coalitions in almost all primates including humans

(Tomasello 2000). Cooperative interactions are also of vital importance to the members of the group in terms of survival advantage since the resources obtained by the group are closed to those who do not contribute to the public good as a cooperative interaction. That is why cooperation can be considered as a mechanism that emerged as an evolutionarily stable strategy. Similarly, our cognitive architecture is thought to evolve in order to make cooperation possible. For instance, the emergence of a number of cognitive mechanisms such as language or sense of morality is thought to have emerged because they have a role to enhance cooperation in groups (Tomasello 2016).

If we look at the evolution of human sociality more specifically, the first cooperative interaction emerges in the interaction between mother and child as a result of the attachment relationship. In other words, caring for the offspring in terms of physical and psychological bonding occurs with the help of hormones such as oxytocin (Nelson and Panksepp 1998), and it might be considered as the origin and simplest version of human sociality. Second, this cooperation is extended to close relatives (Hamilton 1964). The rationale here is that helping relatives is actually an indirect investment in our own genes because we share certain genes with our relatives.

However, human sociality can go beyond kinship relations in contrast to other primates. Human beings interact and cooperate with genetically unrelated people and can even help by endangering their own lives. The primary evolutionary mechanism that explains the cooperation among genetically unrelated people is the principle of reciprocity (Trivers 1971). Reciprocity can take place directly or indirectly. In the case of direct reciprocity, friendship relationships are defined and the person wants to help someone else directly and to guarantee the potential provision they receive from the person in the future. In other words, if I help you, I can see the same help from you and this expectation of helping in return can explain why friendship among genetically unrelated people emerges in human animals. In indirect reciprocity, because of the reputational concerns of the person, the person helps another

person and indirectly increases the likelihood of getting help from others who witness this help. For example, helping a beggar walk down the street can be taken as an example because helping the beggar is not about expecting direct help from the beggar. On the contrary, this help gives a sign that she can be a reliable cooperation partner to other people in the vicinity, and this behavior increases her reputation and increases the likelihood that she will be helped by other members of the group when she falls on hard times in the future.

However, large-scale cooperation with genetically unrelated people without any kind of reputational concerns is not easily explained by standard evolutionary mechanisms. To solve this evolutionary puzzle, supernatural punishment hypothesis was proposed in order to understand why people help others in anonymous and one-time interactions (Johnson and Krüger 2004). According to this hypothesis, human surveillance is not enough to observe every situation that violates the norms of large-scale cooperation (such as “do not kill anyone,” or “do not steal”), and thus unable to punish every norm transgression, and thereby unable to deter future moral violations. However, belief in the existence of a supernatural entity that can observe and punish every norm transgression can sustain large-scale cooperation and deter free-riding. In other words, the idea of supernatural punishment contributes to the large-scale human sociality as a mechanism for interpersonal cooperation. This approach argues that the emergence of religions, especially of religions with big and moralizing gods, is a fundamental factor that extends human sociality and allows us to spread all over the world.

In conclusion, it is possible to say that human sociality, in part, is based on the evolutionary process. This mechanism first appears in mother–child interaction and the mother is cognitively equipped for protecting her child from potential harm. Likewise, relatives with similar genes can also help each other by protecting each other, because helping relatives is actually an investment in their own genes. People who do not have any genetic similarities help each other in regard to the mechanism we call reciprocal

altruism: if I help you, one day you can help me (direct reciprocity), or someone else in society can help me (indirect reciprocity). However, large-scale cooperation without any kind of reputational concern, which is commonly seen in human societies, still awaits a more systematic explanation. The supernatural punishment hypothesis might be a good candidate for solving this puzzle.

Cross-References

- ▶ [Coalitional Relationships](#)
- ▶ [Cooperation in Social Carnivores](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Psychology of Reciprocal Altruism](#)

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Evolution of Humor, The

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Humor can broadly be defined as verbal or non-verbal behavior which is perceived as funny and produces laughter or amusement in others (Martin

2007). Humor is integral to human interaction and is usually pleasurable to engage in (Meyer 2000), yet the explanation for why humans have evolved a sense of humor remains unresolved. Humor is complex, difficult to produce, and highly risky (Polimeni and Reiss 2006). These are qualities that might typically be associated with an adaptive trait that is integral to our survival and therefore justifies its own costly existence. However, there does not seem to be an obvious or immediate survival benefit from humor. Despite this, humor and laughter have been observed around the world suggesting a universality which is typically seen in adaptive traits. Similarly, humor and laughter appear to be innate as babies begin to laugh at the earliest stages of life (Sroufe and Wunsh 1972). Babies of 4 months of age have been observed laughing at tactile events (e.g., tickling) and by 7 months have been observed laughing at incongruities (Sroufe and Wunsh 1972). Further evidence illustrates that this is not just the product of learning social cues from parents, which strongly suggests an innateness to the sense of humor (Mireault et al. 2015). The adaptiveness, universality, and innateness of the sense of humor can most likely be explained by the social bonding function it has, which helps us to initiate and maintain friendships and relationships (Li et al. 2009). Observations that behaviors which produce laughter can be seen in other great apes provide very compelling evidence that this is the case (Provine 2017). This chapter will briefly consider what humor is before reviewing the likely origins of this behavior and the theories behind why humor has evolved. The history of the evolution of humor will first be discussed to better understand where the sense of humor may come from, which makes it clear that there are strong evolutionary origins to this complex behavior.

What Is Humor?

When it comes to determining what actually makes something funny, humor researchers largely agree that incongruity and unexpectedness are critical components (Gervais and Wilson

2005). Shultz and Horibe (1974) demonstrated this with the following joke; “Doctor, come at once! Our baby swallowed a fountain pen.” “I’ll be right over. What are you doing in the meantime?” “Using a pencil.” This example contains an incongruity between the doctor’s question and the parents’ answer, which is unexpected but can be resolved by the audience. However, unexpected and incongruous events may not always be considered humorous. For example, a woman may try to amuse her baby by wearing a red nose and behaving like a clown. For the baby, this may be very unexpected and not typical behavior of their mother and they may laugh as a consequence. However, if the woman dressed up as a clown at a funeral it would no longer seem funny even though it is unexpected and incongruous; rather, it would be inappropriate and likely offensive.

The concept of what makes something funny has more recently been extended in the Benign Violation Hypothesis proposed by Warren and McGraw (2015). This hypothesis suggests that in order for something to be funny it must contain a violation, for instance the mother with a red nose acting like a clown. But this must be combined with a benign scenario to ensure that it does not present genuine danger or a threat (as this may no longer be funny) (Warren and McGraw 2015). If an event meets these criteria, where it presents a benign violation, it may then be considered humorous. This definition offered by the Benign Violation Hypothesis means that the concept of humor may therefore extend to a wide range of behaviors; from complex verbal humor to play fighting and tickling. Indeed, tickling captures the essence of benign violation because it has the appearance of a physical threat (violation) but it is not harmful (benign) and it therefore tends to elicit laughter from the recipient (Provine 2004; Gervais and Wilson 2005; Polimeni and Reiss 2006). Gervais and Wilson (2005) suggest that the majority of research on humor tends to focus on adult humor but a behavior such as tickling may actually help us to understand the evolution of humor much more clearly.

Tickling elicits vocalizations resembling laughter in non-human species suggesting that it may have evolutionary significance (Panksepp,

2000; Provine 2004). The similarities in play behaviors which elicit laughter from both humans and other great apes provide persuasive evidence of the evolutionary origins of laughter (Weisfeld et al. 2011; Van Hooff 1972). Van Hooff (1972) observed that when non-human primates are engaging in play, they produce a specific facial expression with a relaxed open mouth along with distinctive vocal sounds. Chimpanzees, for instance, may make a guttural repetitive panting sound when they are playing (Ruch and Ekman 2001). Van Hooff (1972) suggested that these vocal sounds may be very adaptive; if two individuals are engaged in boisterous play cooperative vocal sounds will reinforce the playful nature of the situation and will make it clear that there is no real threat even when the relaxed open mouth cannot be easily seen. This play behavior may even be a signal for the play to continue and could potentially have more positive repercussions on the socialization and group relations of chimpanzees who engage in this behavior (Vettin and Todt 2005). Observational research with wild chimpanzees reveals the benefits of social play as Shimada and Sueur (2014) found that more time spent in social play for infant and juvenile chimpanzees was positively associated with having more affiliative social relationships. The adaptive significance of friendships has been shown in humans and non-human animals whereby more social connections confer important fitness benefits (House et al 1988; Seyfarth and Cheney 2012); if humor and laughter help to maintain social connections, it could potentially be argued that they could have been the product of natural selection.

This evidence is not limited to chimpanzees as acoustic analysis suggests that all great apes can “laugh” (Davila Ross et al. 2009). Davila Ross et al. (2009) performed acoustic, then phylogenetic, analyses on vocalizations made by great apes (chimpanzees, gorillas, orangutans, and bonobos) when they were being tickled. The results of this analysis suggested that the differences between human laughter and laughter sounds emitted by other great apes appear to have been shaped within existing variations along the evolutionary line. In other words, the more related humans are to each of the great apes,

the more similar their vocalizations are. Therefore, the vocalizations which occur during play for all species of great ape can indeed be referred to as laughter. This analysis of laughter is particularly important in providing biological support for Provine’s (2004) assertion that the voiced laughter of humans, and later talking, only became a possibility for humans once our ancestors became bipedal. This is an important argument in explaining why our sense of humor evolved beyond tickling and play fighting.

Provine (2004) has proposed that the quadrupedal motion of human ancestors would always have created a restraint on the vocal cords preventing vocalizations; a restraint which could potentially have been alleviated by bipedal motion. Furthermore, if the change to bipedal motion allowed for reduced energy expenditure, a species may have been able to coordinate their breathing which could lead to the development of controlled vocalizations. In turn, this adaptation may have allowed humans to develop egressive (out breath) laughter, in contrast to the ingressive laughter which other great apes demonstrate (Davila Ross et al. 2009). Interestingly, recent evidence has suggested that the laughter of babies is more ingressive and becomes more egressive as we age and start to gain more control over our vocalizations (Sauter et al. 2018), adding support to Provine’s (2004) argument. While laughing can evidently be phylogenetically traced back for 16 million years (Davila Ross et al. 2009), language is likely to be a much more recent phenomenon that may have developed around 200 KYA (Dunbar 2009), although it remains unknown when verbal humor may have begun. Dunbar (2009) has proposed that humor itself may have facilitated the evolution of language because it would have made language more enjoyable, implying that perhaps the evolution of humor may have occurred soon after the first vocalizations.

Verbal Humor

Darwin was the first to suggest that there were parallels between humans and animals in terms of

play behavior such that non-human primates may tickle each other but humans use humor to tickle each other's minds (Darwin 1872/1998). Indeed, as humans age tickling or play fighting becomes inappropriate for adults to engage in (Provine 2004) which may help us to understand the movement away from physical events toward verbal communication. Tickling may not be the only behavior which helps us to understand this process; Barrett et al. (2002) proposed that humorous conversation in humans could serve a similar function to grooming in non-human animals. Grooming is a social activity which is said to aid in bonding and maintaining close relationships (Massen and Koski 2014) in non-human animals. Humans do not groom each other but using humor to induce laughter may be an analogous behavior to grooming (Yip and Martin 2006) and may even provide further benefits as humor use can occur in larger social groups than grooming would (Dezecache and Dunbar 2012; Storey 2002). This is supported by observations carried out by Decache and Dunbar (2012) where they found that laughter tended to be shared between groups of up to four people at once in bars. As such, this may demonstrate that humor is even more useful in creating and maintaining social bonds compared to grooming, play fighting, or tickling (Decache and Dunbar 2012; Dunbar 2012).

The adaptiveness of using humor and laughter in groups is also the subject of a further theory described as the "false-alarm theory" (Ramachandran 1998). Ramachandran (1998) has proposed that laughter may have evolved as a signal to a group that there are no real threats in situations that may cause alarm. It may therefore serve as a way of easing tensions and reinforcing cooperation (Ramachandran 1998). Meyer further elaborates on this theory suggesting that humor and laughter could be used as relief from tension (Meyer 2000). This rings true in situations which could potentially be awkward, for instance when public speakers begin a speech with a joke to "break the ice" (Meyer 2000). Both theories emphasize the nature of humor and laughter as forms of social communication, which again serve to improve relations within a group. Further, acoustic analysis of different laughter types

demonstrates that affiliative, or spontaneous, laughter between friends is easily distinguished from laughter between strangers, as more affiliative laughter tended to be slightly higher pitched and more "sped up" than volitional laughter (Bryant and Aktipis 2014). Bryant et al. (2016) demonstrated that this difference is audible across 24 different societies, suggesting that the distinctive nature of laughter types could be a universal indicator of relationship quality.

This argument is critical to understanding the nature of the evolution of humor; while the sense of humor and laughter appear to be universal, this does not necessarily mean that humor will be *used* or *appreciated* universally. Rather, evidence would suggest that humor is used and appreciated in a discriminating and strategic way to affiliate with specific individuals or groups, a pattern we see throughout the lifespan and in different forms. For instance, there are patterns in humor appreciation which demonstrate cultural differences; Kazarian and Martin (2004) found that Lebanese participants used the same humor styles as Canadian and Belgian participants but significantly differed in the way they used humor, with Lebanese participants using less affiliative humor than both Belgian and Canadian participants. These findings were in-line with cultural predictions in the Lebanese sample, such that participants who identified with more a horizontal collectivistic perspective (associated with maintaining more harmony among group relations) had a stronger preference for affiliative humor whereas a more competitive outlook, vertical individualism, was associated with a stronger preference for aggressive humor (Kazarian and Martin 2004). Later, Kalliny et al. (2006) found cultural differences in humor use when they compared the preferred humor styles of American and Arab participants. These results found that Americans used relatively more self-defeating and self-enhancing humor, supporting the hypotheses made that American individualistic culture would use these humor styles more (Kalliny et al. 2006).

Interestingly, both questionnaire studies not only demonstrated cultural differences in humor use but sex differences too; particularly showing that men tended to use humor more often than

women (Kalliny et al. 2006; Kazarian and Martin 2004). This is particularly true in a mating context where men tend to produce humor and women tend to appreciate humor (Bressler and Balshine 2006; Bressler et al. 2006). Men who are funny are considered to be more attractive and have more mating success (Greengross and Miller 2011), suggesting that a good sense of humor may also be sexually selected.

Humor may also be used to select allies, as well as mates. Experimental research has demonstrated that men have a tendency to be choosy about whose jokes they find funniest, particularly demonstrating that they enjoy the humor of men who are similar to them in dominance (Cowan et al. 2016). As discussed above, creating alliances and friendships with others is highly adaptive (House et al 1988; Seyfarth and Cheney 2012) and both humans and non-human primates demonstrate a preference for creating and maintaining bonds with individuals who are similar to them, known as homophily (Massen and Koski 2014). If humor can be used as a way of finding like-minded individuals, it suggests that it may also be a form of covert signaling which could further strengthen social ties (Smaldino et al. 2018). Covert signaling refers to communicating a message that is clearly understood by some but may not be fully understood by all. Smaldino et al. (2018) suggest that humor could be one way of carrying out covert signaling that could generate cooperative relationships. This parallels the argument put forward by Li et al. (2009) suggesting that humor is used in order to indicate interest to another person, in other words; if an individual expends the cognitive effort of producing humor, it suggests a potential interest in a relationship with the recipient. If the recipient is interested in the speaker, they would typically laugh to indicate that the feeling may be mutual.

Taken together, this evidence may suggest that humor is learned behavior which would weaken the argument that it has evolved. However, it remains likely that humor is a behavior that has evolved and is innate, despite the cultural differences we might see. From birth, infants demonstrate a strong preference for laughing at humorous behaviors their mothers carry out;

MacDonald and Silverman (1978) observed that babies between 10 and 13 months old laughed relatively frequently when their mothers played “peek-a-boo” with them but tended to respond with neutral or wary expressions when strangers did the same. An alternative explanation for this effect could be that infants of this age rely on social cues from their parents to indicate when something is funny and it is therefore not innate. In an effort to test whether perception and appreciation of humorous material was derived from social cues and laughter modeled by parents, Mireault et al. (2015) tested infants’ reactions to absurd and neutral behaviors. Infants were observed while their parents either smiled or laughed at the behaviors (which were being carried out by a researcher), or remained neutral. The results demonstrated that social cues from parents laughing at the absurd events did increase laughter and smiling from the infants; however, there were still observations of laughter and smiling from the infants where their parents remained neutral in affect. Coupled with the observation that infants can smile from 5 to 8 weeks old, and can spontaneously laugh from 3 months of age (Sroufe and Wunsh 1972), the evidence seems to suggest that there exists an innate potential for a sense of humor which may then be reinforced by interaction with caregivers, and shaped by our culture.

Conclusion

It is clear that the sense of humor has previously presented something of an evolutionary conundrum. It is risky, complex, and difficult to produce humor yet it does not appear to have an immediate survival benefit, implying that it may not have been selected for. However, the research discussed above on tickling and laughter in our closet relatives provides compelling evidence that humor does have strong evolutionary foundations. Humor can be used strategically to bond with certain people; in infancy, mothers and babies bond with humor, while later in the lifespan humor can be used to indicate that we favor another person as an ally or a mate. This evidence suggests that humor performs a critical task of

helping individuals to initiate contact and bond with people who are similar to them. As such, perhaps the evolutionary conundrum can be considered somewhat solved as the sense of humor may have aided the development of useful alliances which have contributed toward our survival.

Cross-References

- [Alliances](#)
- [Bonding](#)
- [Cultural Differences](#)
- [Friendship](#)
- [Humor Production](#)
- [Mate Choice](#)
- [Sex Differences in Attractiveness of Humor](#)

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Evolution of Intelligence

► Convergent Evolution of Intelligence Between Corvids and Primates

Evolution of Intelligence, The

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Definition

Definitions of intelligence in the scientific literature center around the idea that that intelligence refers to cognitive processes that allow humans and other animals to solve novel problems in their environments. Thus, Jerison (1973, pp. 16–17) notes that “Although experts differ with regard to the nature of human intelligence, a more or less common ground is that it is a dimension of cognitive behavior – the way one knows the world and the way one uses that knowledge when adapting to changing conditions.”

Introduction

However, intelligence is not the only set of mechanisms designed to enable organisms to cope with environmental novelty. Intelligence is usually distinguished from learning which subsumes a variety of mechanisms that allow the organism to take advantage of temporary regularities in its environment – paradigmatically classical and operant conditioning (MacDonald 2013). Social learning is also usually distinguished from intelligence. Unlike classical and operant conditioning, social learning is not dependent on environmental regularities but on being able to learn by observing how the behavior of others enables the achievement of goals (MacDonald 2013). Organisms capable of social learning are then able to use this information to achieve the same or similar goals.

Intelligence, on the other hand, assumes no environmental regularities (although see discussion of Barrett and Kurzban (2006) below) – even temporary ones – nor does it refer to learning how to achieve a goal by observing others who have already solved the problem. Rather, as stated in Jerison's definition, there is the implication that the organism has a goal and is integrating its knowledge in order to solve problems.

For example, New Caledonian crows are able to quickly process causal information and use it to solve novel problems utilizing new tool types (dropping stones into water in order to gain access to buoyant food items) that are not utilized in their natural environments and have no relationship to their established behavioral repertoire (Taylor et al. 2011). These results do not appear explicable by the use of associative learning, nor is the causal rule linked to regularities utilized by the crows in their EEA. Nor is it the result of having observed other animals or humans successfully solve the problem. Rather, the behavior indicates an ability to develop and utilize an abstract causal rule in order to solve an affective goal – assuaging hunger – by novel means.

Review

Evolution of Intelligence: Theories

There are several theories for why human intelligence evolved, including climate change, the challenges of foraging, and the need to compete with and cooperate with other humans.

Climatic Selection

Vrba (1995) focuses on the finding that harsher ecological conditions (lower temperatures during the early Pleistocene period [2.5–2.8 million ybp]) resulted in higher encephalization quotient (the ratio between actual brain mass and predicted brain mass for an animal of a given size), theorized to be due to the benefits of increased cognitive ability for survival under harsher conditions. Encephalization quotient increased rapidly after this period as well, particularly in the last 500,000–1,000,000 years.

Lynn (2006) proposes that, based on contemporary worldwide IQ patterns, confronting colder, harsher climates resulted in selection for increased cognitive ability. Unlike equatorial Africa, in more northerly climates, humans had to provide means of warmth, and plant foods were only seasonally available, with the result that hunting animals and means of storing food were required. Lynn points to studies indicating an association between latitude and brain size; for example, mean winter temperatures at the present time and during the Würm glaciation are correlated with brain size (which is correlated approximately 0.24 with IQ, with northeast Asia having the lowest mean temperatures and the highest contemporary IQ).

Variability Selection

Related to the climate hypothesis is the theory that humans and other mammals were forced to adapt to inconsistent selection pressures because of rapidly changing ecological conditions – what Potts (1998) terms “variability selection.” Environmental fluctuations became increasingly extreme from the Miocene to the present. These shifts (e.g., between dense, moist forests, and cold, dry

steppe) were unpredictable and nonrepetitive rather than cyclic and included decade-scale fluctuations between glacial and warm conditions and century-long shifts between cold steppe and warm forested conditions, interspersed with periods of climatic stability. Rapid local change also resulted from volcanoes, earthquakes, and tectonic activity.

These climatic shifts are associated with increased diversity of encephalization among mammalian lineages, with some lineages – prototypically the lineage leading to humans – evolving toward larger brains and increased behavioral flexibility. There was a broad trend during the Pleistocene toward the evolution of mammalian taxa that were more flexible in eating habits, patterns of social grouping, and group size in relation to resource availability. “Hominids became less inclined to track particular habitats as change occurred and more capable of adjusting to novel conditions and the increasing range of [climatic] oscillation” (Potts 1998, p. 93).

Across mammalian species, and particularly in the line leading to humans, there are associations among brain size, mental ability, learning ability, flexibility of response, and developmental plasticity. There are also associations among these variables and the elaboration of costly parenting practices, delayed sexual maturation, and a prolonged juvenile period in which social learning is of great importance (e.g., Jerison 1973).

Associations between brain size and innovation have been found among both mammals and birds. Reader and Laland (2002) found an association between executive brain ratio (neocortex and striatum volume over brainstem) and innovation, tool use, and social learning. Their results suggested that there was selection among primates for “adaptive complex variable strategies, such as inventing new behavior, social learning, or using tools” (p. 4440). Social learning frequency was independent of group size, providing support for ecological (foraging) hypotheses for brain evolution in primates.

Harsh and varied climates dovetail with ecological models of increased hominid cranial

capacity, since ecological models posit increased ability to extract resources from the environment, posited by climate theorists to make greater demands in harsh and varied climates. Thus Kaplan et al. (2000) show that humans in traditional societies are adept at extracting resources. However, extracting resources would always be beneficial, independent of harshness of environment, so the ecological theory cannot explain the findings summarized above regarding the association between latitude and brain size and between brain size and highly variable environments.

Ecological Dominance

Several theorists have pointed to social competition among humans as a factor (Alexander 1989; Geary 2015). The essential idea is that once humans established ecological dominance, perhaps as a result of being able to maximize resource extraction as proposed by ecological and climate theories, the main source of selection was competition with other humans.

[T]he ecological dominance of evolving humans diminished the effects of ‘extrinsic’ forces of natural selection such that within-species competition became the principle ‘hostile force of nature’ guiding the long-term evolution of behavioral capacities, traits, and tendencies. (Alexander 1989, p. 458)

As populations get larger due to increased ability to extract resources, there are boom and bust cycles, such as described originally by Malthus, and different human groups come into contact with other groups. These forces create competition among humans. As Geary (2015, p. 109) notes, “the inverse relation between social status, resource control, and mortality risk creates a never-ending cycle whereby Darwin’s and Wallace’s . . . conceptualization of natural selection as a ‘struggle for existence’ becomes in addition a *struggle with other human beings for control* of the resources that support life and allow one to reproduce.” These theorists point to associations among fertility, mortality, and resource control in traditional human societies.

Finally and as elaborated below, it should be noted that confronting novel problems and

opportunities is evolutionarily ancient and that animals have developed a variety of means of solving these challenges, prototypically learning mechanisms capable of taking advantage of ephemeral regularities. Theories of climate change, efficiency at resource extraction, and social competition should be seen as forces that likely selected for greater intelligence in particular species at particular times. However, being able to solve novel problems, being able to take advantage of novel opportunities, and being able to solve ancient evolutionary challenges in a more efficient manner would always be advantageous for any organism. Intelligence would thus be beneficial in any environment. As a result, the theories of the evolution of intelligence discussed above should be seen as proposals about the forces resulting in greater selection pressures for intelligence but that the evolution of intelligence per se need not depend on climate changes, resource extraction, or social competition. As indicated below, there is evidence for a general factor of intelligence in a wide range of mammals and birds, indicating that intelligence evolved many times in many different lineages.

Slow Life History Selection

Another model of the evolution of intelligence posits that it is a consequence of selection favoring slow (high-K) life history strategies. Life history describes the ways in which species trade bioenergetic resources between different domains in order to optimize fitness given variable degrees of environmental harshness and predictability (Ellis et al. 2009). Fast or r-selected life histories are characterized by high investment into mating coupled with diminished investment into offspring care. r-selected species are typically short-lived and tend to be small in size (i.e., rabbits). Slow life history or K-selected life histories by contrast are characterized by high levels of parenting effort coupled with the production of relatively fewer offspring, which will typically attain larger body masses and will live longer (i.e., elephants). Brain mass is positively correlated with indicators of K-selection across mammalian taxa, suggesting that higher intelligence is part of a suite of high-somatic effort behavioral

adaptations in which insight, planning, and behavioral control would be favored, as in harsh, unpredictable environments, thus dovetailing with research on latitude and intelligence cited above (Rushton 2004). Within the lineage leading up to modern humans, dietary shifts, specifically increases in the efficiency with which homins were able to extract resources, may have been a major factor driving the slowing of hominin life history speed, as evidenced both by the increase in encephalization and also longevity characteristic of the more advanced hominins (Kaplan et al. 2000). Among populations of modern humans, it has been suggested that the patterns that exist among group-level variation in intelligence, brain size, longevity, fertility, impulsivity, and prosociality among other traits may have resulted from selection having favored those with slower life history traits (i.e., greater intelligence, brain size, and prosociality coupled with lower fertility and impulsivity), who were better able to anticipate and take advantage of seasonal variability (i.e., predictability) in resource availability, via stockpiling, etc. in more northerly and easterly regions of the globe (Rushton 2004).

Modular Views of Intelligence

From its origins, evolutionary psychology has taken a strong stance on how the minds of animals and humans were constructed, proposing that the minds of animals and humans consist predominantly of highly specialized mechanisms designed to solve specific problems – the massive modularity hypothesis (Tooby and Cosmides 1992). The specific problems that the human mind is designed to solve are those that repeatedly confronted our ancestors over evolutionary time. When organisms are repeatedly confronted by challenges or opportunities, the optimum response is to develop specialized methods of dealing with them. The basic logic of evolutionary psychology is that when the environment presents long-standing problems and recurrent cues relevant to solving them, the best solution is to evolve domain-specific mechanisms, or *modules*, specialized to handle specific inputs and generate particular solutions (Geary 2005).

Applied to intelligence, several theorists have attempted to develop a modular theory of

intelligence. A key issue for a modular view is to account for the available data indicating that humans and animals are able to solve novel problems. The difficulty is that modules must necessarily be activated by particular content domains for which they are specifically designed:

Advocates of evolutionary views do not deny that humans learn, reason, develop, or acquire a culture; however, they do argue that these functions are accomplished at least in part through the operation of cognitive mechanisms that are content-specialized – mechanisms that are activated by particular content domains and that are designed to process information from those domains. (Tooby and Cosmides 1992, p. 166)

Barrett and Kurzban (2006) attempt to retain a modular perspective on intelligence by interpreting domains as referring to the formatting requirements that are required by the brain in order to process the information: “Domains should be construed in terms of the formal properties of information that render it processable by some computational procedure. In this sense, even the rules of so-called content-independent logics – for example, *modus ponens* – are domain specific, in that *modus ponens* operates only on propositional representations of a particular form” (Barrett and Kurzban 2006, p. 634). Defining domains in terms of formatting requirements avoids proposing that mechanisms like working memory are restricted to particular content domains that would be used to solve specific adaptive problems, as proposed by Tooby and Cosmides (1992). Thus, for example, working memory, which is commonly viewed as a component of general intelligence, would be considered modular because the input to working memory must be encoded in a specialized manner, but there is no implication that the contents of working memory are specialized to solve particular problems encountered over evolutionary time.

Within this formulation, modules related to intelligence were thus not designed by natural selection to solve specific problems repeatedly encountered by the organism over evolutionary time. Mechanisms such as *modus ponens* and working memory are not designed to solve any particular problem; rather, they may be used to

solve a very wide and undefined range of problems – solving mathematical problems, making analogies, or figuring out the most efficient way to manufacture pianos. Such processes necessarily conform to a modular view because, while they do not require specific inputs to solve specific adaptive problems, they have specific formatting requirements for the information that they act upon.

The modular view of Barrett and Kurzban (2006) retains the concept that adaptations for intelligence must have evolved in response to environmental regularity. This reflects traditional definitions of adaptations in general. For example, Tooby and Cosmides (1992, 61–62) define adaptation as follows:

An adaptation is (1) a system of inherited and reliably developing properties that recurs among members of a species that (2) became incorporated into the species’ standard design because during the period of their incorporation, (3) they were coordinated with a set of statistically recurrent structural properties outside the adaptation (within in the environment or in other parts of the organism), (4) in such a way that the causal interaction of the two (in the context of the rest of the properties of the organism) produced functional outcomes. . . (Tooby and Cosmides 1992, pp. 61–62; emphasis added)

It is only those conditions that recur, statistically accumulating across many generations, that lead to the construction of complex adaptations . . . For this reason, a major part of adaptationist analysis involves sifting for these environmental or organismic regularities or invariances. (Tooby and Cosmides 1992, p. 69; emphasis added)

Recurrences are thus essential to the construction of adaptations, but this presents a problem for understanding how novel problems can be solved since, by definition, novel problems are not recurrent. Barrett and Kurzban (2012) attempt to analyze the adaptations underlying intelligence and ability to solve novel problems while retaining the idea that adaptations necessarily require recurrences:

Here, we think, there is a definitional issue: at a certain level, the terms “design” and “novelty” are incompatible with each other, because adaptation is impossible without *some* environmental signal, even if statistical and fuzzy, to adapt to. If “novel” means “bears no resemblance to anything in the past,” then design to deal with novelty is a priori

impossible. . . . To be clear, we don't think adaptations designed for novelty are impossible, but only if we redefine "novelty" so as to not make adaptation to it impossible. (Barrett and Kurzban 2012, p. 686; emphasis added)

Thus, according to Barrett and Kurzban (2012), adaptation to novelty would be impossible without recurrences to adapt to. They show that some adaptations may respond to novelty as a by-product of past selection. Novel tokens of types that recurred over evolutionary time are a paradigmatic example. For example, a novel food item (say genetically modified food or a novel creation of a chef) would be processed by the digestive system because it has enough similarity to the sorts of food for which the digestive system was designed. Similarly, a novel three-dimensional object will be processed in an appropriately functional manner by the visual system because the novel item does not depart substantially from the regularities that resulted in the evolution of the visual system.

There is wide agreement among both modular and domain-general theorists that there are specialized content spheres with specific formatting requirements that are component processes in intelligence. These mechanisms are conceptualized as responsive to particular types of recurrent information with specific formatting requirements. As noted, Barrett and Kurzban emphasize the formatting requirements of the inputs to working memory. The model of intelligence proposed by Case et al. (2001) includes specialized, domain-specific content areas (quantitative/relational, spatial/imaginal, verbal/propositional, qualitative/analytic, and causal/experimental) that feed into the executive processing that is central to working memory. An example would be the specialized language centers that process verbal input and produce output into conscious awareness and working memory; this output is thus accessible to executive processing. Geary (2005; see Fig. 1) proposes a variety of highly specialized, domain-specific mechanisms (spatial, verbal, visual object recognition, face recognition, auditory, olfactory, kinesthetic, and gustatory) whose highly specialized, appropriately formatted

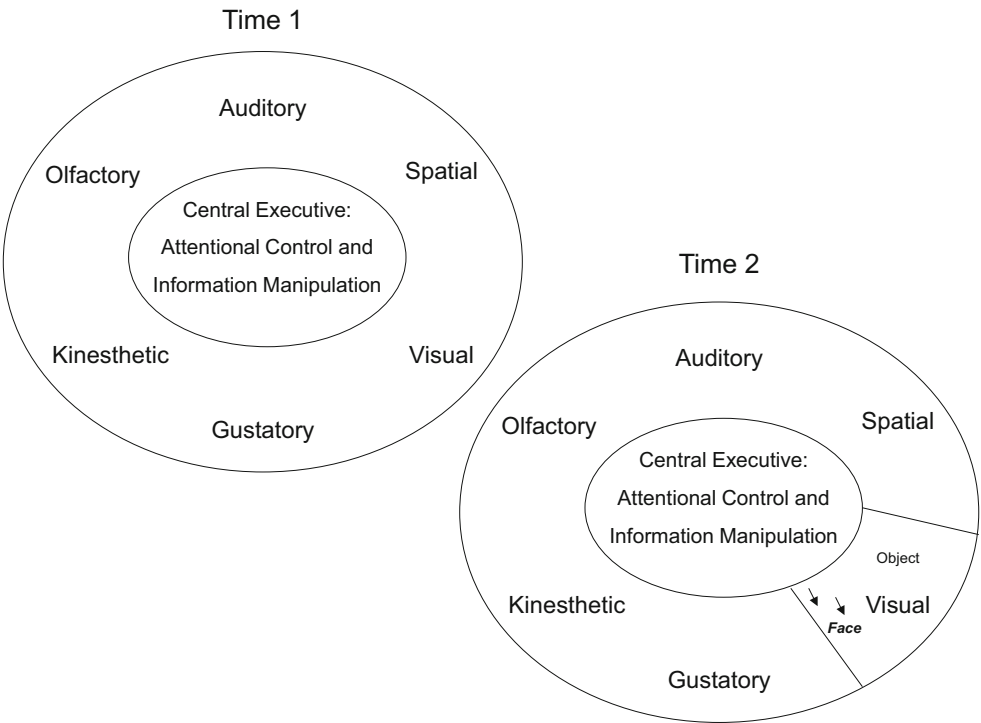
outputs feed into and may be acted on by the executive processes of working memory.

Cosmides and Tooby (2000, 2002) proposed a quite different modular theory of novel problem solving, proposing to account for the ability of humans to solve novel problems by the evolution of metarepresentational abilities. For example, they propose a "scope syntax" (Cosmides and Tooby 2002, p. 182) that marks some information as only locally true or false. This syntax includes "a set of procedures, operators, relationships, and data-handling formats that regulate the migration of information among subcomponents of the human cognitive architecture" (Cosmides and Tooby 2002, p. 183). Of particular importance are metarepresentations that allow us to decouple representations of locally true information from the rest of our knowledge base (e.g., John believes that X, where X may be true or false). This allows people to explore the properties of situations, in order to identify sequences of improvised behaviors that may lead to novel, successful outcomes.

This theory of Cosmides and Tooby implies that intelligence involves what one might term "hyper-contextualization" because it highlights local contingencies and an unspecified set of mechanisms that allow for solutions of localized problems in ways not coupled to the modular mechanisms designed to solve evolutionarily recurrent problems. As noted below, this emphasis on hyper-contextualization is quite different than data gathered by intelligence researchers showing that general intelligence facilitates solving novel problems not by emphasizing local contingency but by decontextualization and abstraction.

A Motivational Theory for the Evolution of Domain-General Mechanisms

The first question that a domain-general theory of intelligence must confront is to conceptualize how domain-general mechanisms could evolve. As noted above, a standard account of evolutionary adaptations is that they must respond to environmental conditions that were recurrent over evolutionary time and that adaptations cannot evolve in the absence of such cues. Environmental regularities effectively frame a problem to be solved and



Evolution of Intelligence, The, Fig. 1 An illustration of the proposed relationship between the central executive and a partial list of inputs: auditory, spatial, visual, gustatory, kinesthetic, and olfactory. The central executive directs attention to particular domains (e.g., spatial),

resulting in a conscious representation of the information from that domain. At Time 1 there is no specific focus of attention, but at Time 2, attention is focused on a face, resulting in conscious awareness of the face (From Fig. 7.1 of Geary 2005)

enable the evolution of mechanisms able to respond to the regularity. Regularities provide a built-in sense of relevance – a built-in sense of what the problem is, thus solving what is often termed the “frame problem” in cognitive science. Input stemming from an environmental regularity is automatically framed by the relevant modules because they are designed to be attuned to a particular environmental regularity.

An important aspect of evolution has been to solve the frame problem in a manner that does not rely on environmental regularities for the evolution of psychological adaptations (MacDonald 2013; see also Chiappe and MacDonald 2005). Humans and other animals have evolved motivational systems that solve the frame problem with systems that provide signals when their evolved goals are being met. For example, temperature regulation systems provide signals to seek means of attaining warmer or cooler environments. How

a person or animal solves this problem is unspecified and does not depend on environmental regularities over evolutionary time. However, the temperature-regulating mechanisms effectively frame the problem: They yield information regarding the nature of the problem (i.e., the feeling of being too cold or too warm), and they yield information when the problem has been solved (i.e., attaining a more comfortable temperature). This signal is not a response to an environmental regularity, but rather signals that an internal goal has or has not been met; further, achievement of this internal goal must have been linked to reproductive success in the EEA; but there is no need for reproductive success to be linked to any environmental regularity. As described in the following, such a system enables the evolution of mechanisms able to take advantage of ephemeral environmental regularities (classical and operant conditioning) or imitate successful others (social

learning). Ultimately, via the elaboration of the domain-general mechanisms of general intelligence, affectively grounded systems enable organisms to solve novel problems and (more commonly) to solve ancient evolutionary problems by novel means – means that are more efficient than any possible architecture that is linked to environmental regularities.

From this perspective, a watershed event in evolutionary history was the evolution of subjective psychological signals – positive or negative feelings – that inform the animal when its goals of survival and reproduction are being met or unmet. Imagine a primitive organism equipped only with “if p , then q ” devices, where p represents recurrent environmental events and q represents an evolved response to the event: If a certain environmental situation p occurs (e.g., presence of food), then respond with behavior q (eating). Such an organism would completely satisfy the requirements for a psychological adaptation as described above. The mind is constructed with mechanisms designed to respond adaptively to recurrent environmental events (the presence of p 's). The mechanism is entirely modular, designed to deal exclusively with a particular kind of input (domain-relevant information) by encoding the input in a manner that can be processed by the animal's nervous system; and it produces a particular kind of output (e.g., behavior such as eating p), thereby solving a very specific problem. Its disadvantage would be that there would be no way to take advantage of nonrecurring information in order to find food, for example, the information that a certain ephemerally available stimulus is a cue for food (classical conditioning), the chance discovery that a certain behavior is a good way to obtain food (operant conditioning), or observing another animal successfully obtaining food (social learning).

Examples of “if p , then q ” systems are the modular systems that figure prominently in accounts of general intelligence, such as those enumerated by Geary (2005) (spatial, verbal, visual object recognition, face recognition, auditory, olfactory, kinesthetic, and gustatory). Nevertheless, despite having specific formatting requirements, the information processed by

human modular language systems can be produced voluntarily (i.e., via executive processes) and can be coupled, via learning, to an endless variety of social functions that are not dependent on environmental recurrences. This contrasts with the fixed signaling systems of nonhuman primates and other animals in which signals occur in particular recurrent contexts (e.g., threat, danger, alarm, greeting) and are coupled to the specific circumstances surrounding their use and the functions they serve. Their meaning is therefore fixed. However, the contextual freedom characteristic of humans means that the functions of signals can change quickly over time, making them ideal for dealing with uncertain, novel situations. As in the case of social learning (MacDonald 2013), there is undoubtedly a great deal of specialized neural machinery underlying human language ability. However, like social learning, it functions as a domain-general system, with no evolutionarily fixed inputs or outputs and no fixed relationship to particular environmental regularities. Even infants 3–6 months of age are capable of many-to-many mappings between signal and function; there are a wide variety of signals, many with no social function at all.

Because of the evolution of motivational systems with an affective (reward/punishment) component, a person seeking a warmer or cooler temperature may indeed be confronted with an infinite number of behavioral choices, but the person can narrow down this infinite array by choosing behaviors likely to change the subjective feeling of warmth or coldness. The behaviors that solve the problem may include behavior resulting from ephemeral associations between a previous behavior and reward (classical or operant conditioning) and behavior learned by observing others (social learning), or it may include a mental model that is a part of the evolved machinery of intelligence (developing highly technical plans for building an air conditioner or heating system by taking advantage of knowledge of materials and thermodynamics and making a plan based on imagining possible outcomes – thus relying on mechanisms of general intelligence).

The point is that this affective motive and the fact that certain behaviors reliably result in getting

warmer or cooler give structure to the person's behavior and enable an adaptive choice from among the infinite number of possible behaviors. The resulting behavior is not random because it is motivated by the desire to attain a comfortable temperature. Motivational mechanisms can thus be thought of as a set of adaptive problems to be solved but whose solution is underspecified. Such systems enable the evolution of any cognitive mechanism, no matter how opportunistic, flexible, or domain-general, that is able to solve the problem. None of these ways of solving the problem need to have resulted in solutions that were successful in our evolutionary past.

This fits well with research showing that problem solving is opportunistic: People satisfy their goals, including evolved goals such as satisfying hunger or regulating body temperature, by using any and all available mechanisms. For example, children typically experiment with a variety of strategies and then select the ones that are effective. Children are *bricoleurs*, tinkerers who constantly experiment with a wide range of processes to find solutions to problems as they occur.

These results point to two conclusions: Given that domain generality is evolvable if the animal is equipped with reward-/punishment-type motivational systems, it is not surprising that it is evolutionarily ancient. Indeed, even primitive animals like *Aplysia* (sea slug) possessing very rudimentary nervous systems have associative mechanisms geared to produce adaptive behavior in novel ephemeral environments by pairing a stimulus with a painful unconditioned stimulus (Carew et al. 1981); the conditioned stimulus is limited only by what the nervous system of *Aplysia* can detect and need not be an evolutionarily recurrent stimulus. Secondly, given the rarity of forms of intelligence approaching the human level and even the rarity of sophisticated learning mechanisms, such as social learning, in nature, one must assume that the cost-benefit calculus for elaborating the mechanisms of intelligence and social learning is difficult to overcome. *Aplysia* is doing just fine without the elaboration of these mechanisms.

As described in section “[Evolution of Intelligence: Theories](#),” there has been considerable

debate on what evolutionary pressures resulted in human general intelligence: rapid climactic change, ecological maximization, social competition, or some combination of these. However, given the pervasiveness of domain-general mechanisms in nature and their ancient pedigree, the evolution of intelligence in a sense that would apply to the behavior of New Caledonian crows, rats, humans, and other primates would always be a theoretical possibility. That is, there is no theoretical reason why a very wide range of animals, certainly including birds and mammals, could not have evolved social learning mechanisms or the ability to infer a causal rule from their experience or to visualize and evaluate various hypothetical scenarios in order to satisfy an evolved motive such as hunger or temperature regulation. The affective basis of domain generality is evolutionarily ancient, resulting primitively in simple associative learning mechanisms (classical and operant conditioning), then elaborated greatly with social learning, and finally general intelligence as a suite of mechanisms, particularly the executive processes of working memory (see below) underlying the ability to manipulate information from a variety of sources in order to achieve goals that may or may not be linked with affective motivational systems derived from the evolutionary past.

Although intelligence is usually conceptualized in terms of the ability to solve novel problems, it should also be noted that human general intelligence is adept at finding novel, more efficient ways to solve evolutionarily ancient problems of survival and reproduction (e.g., finding better ways to extract resources from the environment or developing more effective military tactics). The novelty is quite often in the solution, not in the problem itself. Nevertheless, novel problems, as would be presented, for example, in rapidly changing novel environments, certainly pull strongly for intelligence because solutions for these novel problems are necessary for survival.

Research on Animal Intelligence

As noted above, research on New Caledonian crows has established the existence of problem-solving mechanisms able to produce novel

solutions to the ancient evolutionary problem of procuring food. Earlier research by Heinrich (2000) demonstrated the ability of ravens to solve novel problems by using long pieces of string to hang meat from a perch. For ravens, gaining access to this food was a novel problem because it did not occur in their natural environments. The solution involved repeated pulls on the string with the beak while holding and releasing the string with a foot. Though each step in the solution may be innate (e.g., grabbing objects with their beaks or with their feet), assembling these behaviors into a sequence that solves the problem was novel. Not all birds arrived at this solution, indicating individual differences in performance, as there are for general intelligence in humans. The solution did not emerge through a trial-and-error process via learning.

Importantly for conceptualizing the mechanisms underlying intelligence, Heinrich argued that the ravens formulated a goal, built mental models, and evaluated possible sequences of actions without having to endure their consequences. They took into account information from various sources in planning the solution – an obvious drawback to trial-and-error learning. Thus, the ravens did not pull up the string if the piece of meat appeared to be too large, nor did they pull up the string if it was attached to rocks rather than meat. Insightful problem solving involving goals, mental models, and evaluation of possible outcomes has also been demonstrated in apes.

Based on models of human intelligence showing the existence of a *g* factor of general intelligence, several studies have found a general intelligence factor in a wide range of animal species, including a variety of primate species (see Fernandes et al. 2014; Reader et al. 2011), rats, rodents, rabbits, cats, dogs, raccoons, ravens, and pigeons (Galsworthy et al. 2014). Further, tasks that are more *g* loaded are more heritable and are more associated with differences between species and, among humans, among different human groups (reviewed in Fernandes et al. 2014). Using principal axis factoring, Fernandes et al. found that the *g* factor explained 62% of the variance in five cognitive abilities for primates, while, utilizing a different technique, Reader et al. (2011) found a

general factor that explained 65% of the variance across diverse cognitive tasks (behavioral innovation, social learning, tool use, extractive foraging, and tactical deception) using data from 62 primate species. Better performance on these tasks was correlated with brain volume. Reader et al. conclude that their results do not support the massive modularity hypothesis and that social intelligence (e.g., tactical deception) is linked to the general factor of intelligence. Fernandes et al. and Reader et al. both found the highest interspecies variation and loadings associated with tool use, while Woodley of Menie et al. (2015) found that tool use was linked to high interspecies variation, high *g* loadings, and both additive genetic and phenotypic variance. Tool use is hypothesized to be critical for cognitive control of the environment – that is, species and individuals with higher *g* are better able to solve novel problems confronted in their environments. Woodley of Menie et al. concludes that results thus far across a wide range of species support the view that “the *g*-nexus should generalize to all taxa for which *g* is a central component of cognition, indicating profound homology” (p. 162).

A study by Crinella and Yu (1995) suggests that modular mechanisms can be meaningfully linked to a general intelligence factor in animals. They extracted a *g* factor in rats that was based on five tests and accounted for 34% of the variance, a finding that was comparable to studies of *g* in humans (Jensen 1998). Solving these problems typically involved combining information from multiple sources, including from modules specialized for processing spatial information. Spatial learning is a modular process in rats, but the frontal cortex uses the information generated by spatial modules to solve novel problems. The frontal cortex is essential to combining information from different experiences but is not essential to spatial learning per se. The ability to integrate this information with other experiences (e.g., learned associations) is part of a positive manifold linked to success in solving other novel problems and to brain size. As indicated below, models of human intelligence involve combining information from modular mechanisms, such as spatial information, into solutions to novel problems.

Intelligence and Explicit Problem Solving in Humans

The animal data fit well with research on humans, which has consistently found that more intelligent people are better at attaining goals in situations of minimal prior knowledge. Of particular importance is fluid intelligence, defined as “reasoning abilities [consisting] of strategies, heuristics, and automatized systems that must be used in dealing with ‘novel’ problems, educing relations, and solving inductive, deductive, and conjunctive reasoning tasks” (Horn and Hofer 1992, p. 88). Tests of fluid intelligence correlate strongly with *g* (e.g., Carpenter et al. 1990). Tests such as Raven’s Progressive Matrices and Cattell’s Culture Fair Test tap the capacity “to adapt one’s thinking to a new cognitive problem” (Carpenter et al. p. 404). This highlights the idea that intelligence taps conscious problem solving in situations in which past recurrences, including recurrences over evolutionary time, would be unhelpful, except perhaps by analogy or by induction, to the new situation.

Theories proposing a critical role for domain-general processes in intelligence emphasize two fundamentally different processing mechanisms, implicit and explicit processing. Implicit and explicit mechanisms may be contrasted on a number of dimensions (e.g., Geary 2005; MacDonald 2008; Stanovich 2004). Implicit processing is automatic, effortless, and relatively fast and involves parallel processing of large amounts of information. Implicit processing is characteristic of what Stanovich (2004) terms the autonomous set of systems, which respond automatically to domain-relevant information. For example, the visual systems of monkeys and humans contain

numerous areas specialized for different aspects of vision. Areas specialized for color and for motion are sensitive to different aspects of visual stimulation; processing in these different areas occurs in parallel and results in a unitary image. Other modules proposed in the cognitive literature include modules for social exchange, theory of mind, fear, folk physics, and grammar acquisition.

Although implicit processing is characteristic of evolved modules, it is not restricted to evolved modules. It occurs in a wide range of circumstances, including skills and appraisals that have become automatic with practice or repetition, perceptual interpretations of behavior (e.g., stereotypes), and priming effects. Modules, as defined here, therefore need not be domain specific; they may also result from domain-general processes of associative and implicit learning (Stanovich 2004, p. 39) (Table 1).

On the other hand, explicit processing characteristic of intelligent problem solving is conscious, controllable, effortful, and relatively slow and involves serial processing of relatively small amounts of information. Such processing is characteristic of what Stanovich (2004) terms the analytic system characterized by context-free mechanisms of logical thought, planning, and cognitive control. The analytic system is sensitive to linguistic input that allows for explicit representations of the context, including hypothetical representations of the possible consequences of actions. Explicit processing is typically experienced as an internal linguistic monologue that is associated with the experience of agency or free will. The executive processes of working memory are paradigmatic examples of explicit processing.

Evolution of Intelligence, The, Table 1 Characteristics of implicit and explicit cognitive systems

Implicit system	Explicit system
Not reflectively conscious	Conscious
Automatic	Controllable
Fast	Relatively slow
Evolved early	Evolved late
Parallel processing	Sequential processing
High capacity	Limited by attentional and working memory resources
Effortless	Effortful
Evolutionary adaptation or acquired by practice	Acquisition by culture and formal tuition

As an example of explicit processing, consider the Tower of Hanoi problem in which participants must develop a long-term plan with multiple subgoals. This problem requires one to be able to activate multiple goals and keep track of the satisfaction of each of the goals in working memory (Carpenter et al. 1990, p. 413). These goals must be consciously and explicitly held in mind while performing the task. Contrast this type of problem solving with examples of implicit processing, such as everyday perception in which, when we look around the room, our brains are automatically carrying out a large number of operations involving many different specialized modules (e.g., mechanisms for perceiving vertical contours, horizontal contours, motion, color, etc.) that allow us to see the objects in the room. The calculations are done very rapidly, and we are not conscious of making them. This latter situation would not count as an example of intelligent problem solving.

Mechanisms Underlying General Intelligence

As noted, intelligence involves explicit processing. In particular, intelligence involves central executive processes that focus attention on explicit representations of relevant information in working memory while simultaneously inhibiting information not relevant to the problem. Theories of the mechanisms underlying intelligence posit a central executive capable of explicit processing that receives input from a variety of systems, many of them modular mechanisms characterized by implicit processing, including auditory, visual, spatial, or episodic information (i.e., information from life events involving memories derived from a variety of systems) (Baddeley 2000).

Working memory capacity has been implicated as an underlying source of individual differences in fluid intelligence as indicated by moderate to strong correlations between fluid intelligence and working memory capacity (e.g., Kyllonen and Christal 1990). Thus Kyllonen and Christal found correlations from 0.80 to 0.90 between working memory capacity (assessed by tasks such as digit span and mental arithmetic) and reasoning ability (assessed by performance on

analogies and verbal reasoning). Engle et al. showed that the executive functions of working memory (assessed by tasks involving attentional control) predicted *g*, but that short-term memory capacity (assessed by tasks such as memory for sets of words) did not.

Individual differences in working memory capacity reflect differences in the capacity for controlled attention, including the ability to inhibit irrelevant information. Kane et al. (2001) found that participants with low working memory capacity were less able to inhibit the prepotent response of orienting toward a visual cue in a task that required them to look in the direction opposite the cue (looking toward a visual cue is an automatic response; looking away from a visual cue requires suppression of an automatic response; see MacDonald 2008). This supports the idea that working memory capacity plays a crucial role in controlling attention in situations in which responding does not involve automatic implicit processing – that is, in situations requiring active engagement with task goals and the inhibition of prepotent, automatic responses.

As noted above, goal management is an important feature of animal intelligence. One role of the executive functions in solving novel problems is to manage goals. This involves constructing, executing, and maintaining a mental plan of action during the solution of a novel problem (Carpenter et al. 1990). For example, the Raven's Progressive Matrices fluid intelligence test and the Tower of Hanoi problem (in which participants must develop a long-term plan with multiple subgoals) both require one to be able to activate a goal with multiple subgoals and keep track of the satisfaction of each of the subgoals (Carpenter et al. p. 413).

Executive functions underlying general intelligence are thus involved when problems call for substantial planning and keeping track of various subgoals. They are involved in dealing with situations that are highly demanding of attentional resources, as more aspects of the problem require attention. More complex tasks require more involvement of controlled processes that structure and analyze the problem, assemble a strategy of attack on it, monitor the performance process, and

adapt these strategies as performance proceeds. Keeping task-relevant information in active state is particularly challenging in conditions in which distracting information is present (Kane et al. 2001).

Is Working Memory a Domain-General Mechanism?

The executive functions of working memory and the mechanisms of activation and inhibition do not satisfy the criteria for modularity. By definition, mechanisms for solving novel problems have to be unspecialized in the domains for which they provide solutions. Although they may have access to specialized information obtained from the various modules that provide them with inputs, the problem-solving procedures would have to be general enough to allow the solution of novel problems in various domains. For example, there is a substantial correlation between performance on the Raven's Progressive Matrices and performance on the Tower of Hanoi puzzle (Carpenter et al. 1990). Both tasks require goal management, working memory, and inhibition of prepotent responses. However, the types of information used in solving these problems, the specific goals and subgoals, and the specific responses requiring suppression are unique to each task, and the tasks themselves are not problems that were recurrent in the EEA.

Moreover, measures of working memory capacity predict performance across a wide range of tasks. The only common element of these tasks is that they make high demands on attentional resources, indicating that a general capacity is involved. For example, people who did well on a mathematical processing task also tended to do well on a perceptual task requiring inhibition of prepotent responses (Kane et al. 2001). This is what one would expect if working memory "reflects an abiding, domain-free capability that is independent of any one processing task" (Kane et al. 2001, p. 169).

The executive functions are thus able to access goal-relevant information from a wide range of domains when solving a problem. Indeed, it is in being able to access representations from more

modular processes that the executive functions are able to extend cognitive competencies in ways that are unrelated to their evolutionary function. The data on general intelligence in animals is also consistent with this view. For example, Thompson et al. (1990) found that six brain regions were involved in psychometric *g* for the rat, including a visuospatial attentional mechanism, a visual discrimination mechanism, a vestibular-proprioceptive-kinesthetic discrimination mechanism, a place learning mechanism, and a nonspecific mechanism. This is consistent with models of human intelligence (Case et al. 2001).

There is much evidence that general intelligence facilitates the integration of information obtained from modules. Geary's (2005) distinction between biologically primary and biologically secondary abilities is useful in this regard. Biologically primary abilities are domain specific and include abilities such as language and simple quantitative abilities, which develop universally and spontaneously. Biologically secondary abilities, such as reading and mathematical ability, use these domain-specific modules, but in a novel manner. Rather than seeming to be spontaneous and effortless, biologically secondary abilities typically require practice and tuition, often with coercion, bribery, or exhortation. Learning these biologically secondary abilities involves explicit, conscious awareness rather than implicit awareness. Success at these biologically secondary abilities is strongly correlated with general intelligence (Geary 2005).

As a case in point, human language results from highly dedicated systems that enable children to effortlessly and unconsciously learn extraordinarily complex grammatical rules. However, skill in integrating these language systems as well as the output of visual processing mechanisms into an evolutionarily novel ability – reading – is strongly linked to general intelligence. Unlike language learning, reading is typically mastered only with a great deal of conscious effort and represents a major hurdle for many schoolchildren. The correlation between IQ and reading skills ranges from about 0.6 to 0.7, even longitudinally (e.g., Stevenson et al. 1976). IQ

correlates with reading most when decoding ability – a specialized, likely modular process – is controlled (Jensen 1998). Children at the third- or fourth-grade level are adept at decoding, and individual differences are mainly in comprehension. Reading comprehension is approximately as highly correlated with verbal as with nonverbal IQ.

Decontextualization as a Function of General Intelligence

Decontextualization enables humans to inhibit the operation of highly context-sensitive, implicit, and automatic heuristics for making inferences, judgments, and decisions (Stanovich 2004). Decontextualization enables dealing with novel and unpredictable environments because a common source of solutions to novel problems involves recognizing similarities between new problems and previously solved problems, as via analogical reasoning (Chiappe and MacDonald 2005).

As noted, logical thought, planning, and cognitive control are fundamental to intelligence, and since they operate in a context-free manner (Stanovich 2004), they are not tied to recurrent contexts but operate to find general rules, as in the example of the New Caledonian crows noted above. IQ researchers are well aware of the centrality of decontextualization for thinking about intelligence.

One of the well-known byproducts of schooling is an increased ability to decontextualize problems. In almost every subject... pupils learn to discover the general rule that applies to a highly specific situation and to apply a general rule in a wide variety of different contexts. The use of symbols to stand for things in reading (and musical notation); basic arithmetic operations; consistencies in spelling, grammar, and punctuation; regularities and generalizations in history; categorizing, serializing, enumerating, and inferring in science, and so on. Learning to do these things, which are all part of the school curriculum, instills cognitive habits that can be called decontextualization of cognitive skills. The tasks seen in many nonverbal or culture-reduced tests call for no scholastic knowledge *per se*, but do call for the ability to decontextualize novel situations by discovering rules or regularities and then using them to solve the problem. (Jensen 1998, p. 325).

Conclusion

As noted above, there is excellent evidence that general intelligence is an adaptation underlying the ability of humans to solve problems where subjects have a minimal amount of prior knowledge. Such problems are novel because they have not been previously encountered by the subject, and thus it is not surprising that more intelligent people are able to create novel solutions to ancient problems of survival and reproduction (Chiappe and MacDonald 2005). Research on human intelligence has shown that the degree to which the *g* factor loads onto cognitive ability measures positively moderates the association between these measures and a variety of biological variables, including brain size, reaction time, and inbreeding-depression effects, and also with phenotypic and genetic characteristics associated with performance on the tests, such as the magnitude of population differences in cognitive performance (Jensen 1998; Rushton and Jensen 2010). This demonstrates that it is the most domain-general measures of intelligence that have the highest validity in predicting biologically meaningful manifestations of cognition. Furthermore, the most domain-general measures of intelligence enjoy the highest criterion validity – meaning that they are better at measuring the real-world advantages that stem from high IQ (Rushton and Jensen 2010). Such individuals tend to make more money, perform better in scholastic and workplace environments, and achieve a higher social status than people on the low end of the IQ distribution. They are also more conscious of personal health and safety. On the job, the *g* factor is the best single predictor of job performance. Correlations between *g* and job performance range between 0.2 and 0.8, with greater predictive validity achieved for jobs of greater complexity. Thus, people with higher general intelligence are more adept at attaining their evolutionary goals in situations of novelty, complexity, and unpredictability – consistent with the hypothesized functions of *g* as a psychological adaptation designed by selection (Chiappe and MacDonald 2005; Geary 2005).

General intelligence is therefore at the heart of an evolutionary analysis. Although modules designed to process specific types of information are unquestionably important to an evolutionary analysis, evolutionary psychology has over-emphasized modularity and ignored the vast data indicating a prominent role for domain-general mechanisms in human and animal cognition. Indeed, research has uncovered associations between a general intelligence factor and ability to solve problems that have often been advanced as solved by domain-specific modules, such as cheater detection, social exchange, and learning (Chiappe and MacDonald 2005; Fernandes et al. 2014). Fernandes et al. also point out that very similar cognitive abilities have been found in widely divergent species (e.g., various primate species and hyenas) despite very different ecologies. The prediction from massive modularity theory – that the principal source of species differences in intelligence should be unique because each species has its own set of specialized modules that evolved to solve species-specific problems – is not supported.

Domain-general mechanisms are powerful but fallible mechanisms that are the basis for solving a fundamental problem faced by all but the simplest organisms: the problem of navigating constantly changing environments presenting new challenges that have not been recurrent problems in the EEA. Most important, the domain-general mechanisms at the heart of human cognition are responsible for the decontextualization and abstraction processes critical to the scientific and technological advances that virtually define civilization (Chiappe and MacDonald 2005).

Cross-References

- [Aurelio José Figueredo](#)
- [Bruce J. Ellis](#)
- [Conditioning and Association](#)
- [Consciousness](#)
- [Domain Specificity](#)
- [Evidence of Brain Modularity](#)
- [Intelligence Versus Natural Selection](#)
- [Rushton, J. Philippe](#)

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Evolution of Language

► Linguistic Evolution

Evolution of Live Birth in Mammals (140 MYA)

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Synonyms

Genomic imprinting; Gestation; Lactation; Viviparity

Definition

Bringing forth live young that have developed inside the maternal body, usually via the placenta.

Introduction

Mammals have extended maternal investment either through gestation or lactation, which may

explain how mammals can develop more robust brains (Tutin and Collins 1981). There are two infraclasses in mammals that are viviparous (i.e., giving birth to live young), marsupials and placentals (also known as eutherian mammals). Placental mammals diverged from marsupials roughly 140 MYA. This split resulted in a number of changes including reproductive anatomy and the length of the gestation and lactation periods. Placentals typically have an extended gestation period through which the embryo receives its nutrients through the placenta. Marsupials on the other hand usually have an extended lactation period in which the underdeveloped fetus receives the majority of its nutrients through its mother's milk.

Overview

There are two infraclasses in mammals that are viviparous (i.e., giving birth to live young), marsupials and placentals. The combination of viviparity, placentation, and lactation has made mammalian reproduction extremely successful (Renfree et al. 2013). Placental mammals diverged from marsupials roughly 140 MYA. However, there is new evidence to suggest this split may have occurred earlier (Luo et al. 2011). In both marsupial and placental mammals, females invest heavily in reproduction compared to males. Both marsupials and placentals have extended maternal investment compared to non-mammalian species either through gestation or lactation (Tutin and Collins 1981). Placentals typically have an extended gestation period through which the embryo receives its nutrients through the placenta. Marsupials on the other hand typically have an extended lactation period in which the underdeveloped fetus receives the majority of its nutrients through its mother's milk. There are a number of hypotheses that attempt at explaining the evolution of mammalian reproduction: conflict hypothesis, coadaptation hypothesis, and an explanation through life history.

The conflict hypothesis (also known as the Kinship hypothesis) is the most widely accepted and empirically supported hypothesis to date. This hypothesis assumes that the degree of

asymmetries will arise when the female breeds with multiple males (i.e., offspring may have the same mother, but different fathers; Ashbrook and Hager 2013). The conflict hypothesis also assumes the cost of gene expression is heavier for either the mother or father. The conflict hypothesis proposes that paternal genes enhance fetal growth while maternal genes suppress it.

This hypothesis is supported by the findings that several of the imprinted genes that increase growth are usually paternally expressed (e.g., *Igf2*) and the maternally expressed genes usually restrict growth (e.g., *Phlda2*; Renfree et al. 2013). Although maternal-offspring conflict is used to explain genomic imprinting, Trivers (1974) suggests this also can explain a conflict in behaviors. For example, during the weaning stage of lactation, the costs to the mother (e.g., lactation) begin to outweigh the benefits to the offspring since the offspring can find its own food. Therefore, the mother may begin to restrict the offspring's access to milk as the offspring finds its own food.

The coadaptation hypothesis assumes that the mother is the primary caregiver and the genotype of the offspring will affect interactions with the mother (Ashbrook and Hager 2013). This hypothesis also assumes that the genes that control the maternal phenotype may also effect the offspring's phenotype. The coadaptation hypothesis proposes that coadaptation between the mother and offspring is what is driving genomic imprinting. This hypothesis is supported by the findings that paternally expressed genes (e.g., *Peg3*) may also be involved in maternal care, placental nurturing, and regulation of attachment to the nipple and sucking behavior (Renfree et al. 2013).

Another explanation is that life history evolution effects placental morphology, which has been demonstrated in nonmammalian species (Fisher et al. 2001). Compared to faster life histories, slow-paced life histories are characterized by longer gestation periods, longer maximum lifespans, less offspring per female, longer generation times, older first reproduction, older onset of senescence, and slower senescence. Therefore, when there is an increase in the availability of resources and a decrease in environmentally driven mortality, a slower life history may be favored.

Reproductive Anatomy

The anatomy of the female reproductive tract differs between marsupials and placental mammals. In most marsupials, there are two vaginae, two cervixes, two uteri, and two fallopian tubes compared to most placentals which has one vagina, one cervix, one uterus, and two fallopian tubes (Tyndale-Biscoe and Renfree 1987). Marsupials have paired lateral vaginae that connect to their corresponding uteri to form the vaginal culs de sac. From the vaginal culs de sac, twin uterine cervixes open and are connected to the uterus of the same side (Taggart 1994). The uterine neck that connects the cervixes to the uteri varies in length depending on the species. During parturition, the two vaginae form a temporary median vagina (i.e., birth canal) that connects to the urogenital sinus. Since most placentals only have one vagina, one cervix, one uterus, and two fallopian tubes, the two fallopian tubes connect to the uterus. The uterus then connects to the cervix and the cervix connects to the vagina. The anatomy of the placenta will be discussed later.

Gestation Period

Gestation is a period in which a developing fetus is inside the womb and completely dependent of its mother. Compared to marsupial gestation which rarely exceeds 1 month and can be as short as 12 days, placental gestation can take much longer ranging 2 weeks to 2 years (Fisher et al. 2001; Langer 2008). This longer gestation period in placentals allows for a more mature neonatal brain compared to that of marsupials with similar brain sizes (Smith 1997). Shorter gestation in marsupials allows for the mother to jettison a pregnancy or young if conditions become extremely harsh.

Placentae

During the gestation period, the mammalian young are nourished via the placenta. The evolution of placenta has long been debated. Although it was once attempted to classify animals via the placenta, because it is one of the most varied

organ in the mammalian class, this is no longer the case. The placenta varies on invasiveness and size, but in all cases the fetus cannot survive without it.

In placental mammals, the placenta is a temporary organ that joins the mother and fetus, transferring oxygen and nutrients from the mother to the fetus and transferring waste away from the fetus. The placenta is characterized by five major features: (i) the definitive type of placental interface, (ii) fetomaternal interdigitation, (iii) placental shape, (iv) fetomaternal blood flow interrelations, and (v) neonatal/placental weight ratio (Wildman et al. 2006). The definitive type of placental interface is likely to have had at least 11 character state changes occurring since its original evolution. The placental shape is likely to have had seven character state changes since its original evolution, with primate placental shapes changing within its order (Wildman et al. 2006).

Compared to its placental counterpart, marsupials have received much less research on its yolk sac placenta, which evolution continues to be debated (Freyer et al. 2003). One of the major differences in placentals and marsupials in regards to the embryo is the lack of an inner cell mass in the blastocyst (Renfree 2010). The yolk sac contains two parts: a bilaminar, nonvascular region and a trilaminar vascular part. In addition to the yolk sac, marsupials have a permeable “shell” coat that is eventually broken down and lost.

In placental mammals, the placenta plays a role in the release of hormones that are found normally in the body (e.g., prolactin). The placenta may also augment the functions of hormones from other sources (e.g., chorionic somatomammotropin) which act as supplementary hormones to stimulate gonadal, mammary, adrenal, and thyroid functions. Although it has been understudied compared to the placental placenta, marsupial placentae also play a role in hormones. For example, in the tammar wallaby, the placenta plays a role in cortisol, growth hormones, and relaxin (Renfree 2010).

Genomic Imprinting

One of the major features of the gestation period in mammals is genomic imprinting. Imprinted

genes are genes that are expressed in a parent-of-origin-specific manner. Imprinted genes play a role in various aspects of placental and fetal development including fetal and placental growth, neonatal behavior and lethality, postnatal lethality, growth, and viability (Coan et al. 2005). This suggests that imprinting may have been vital to the evolution of the placenta. The number of genes imprinted varies between species; for example, mice have more imprinted genes than humans.

One gene in particular, *Igf2*, is imprinted in all placental and marsupial species that have been studied. This suggests that *Igf2* evolved before placentals diverged from marsupials and after milk production evolved. Therefore, one possible explanation is imprinted genes evolved due to greater maternal investment. However, there has been mixed findings with imprinting of *Igf2* in nonmammalian species.

Lactation Period

Once the mother gives birth, the lactation period begins. One of the key features that define the mammalian class is its milk production. Although nonmammalian animals produce milk (e.g., flamingos, penguins, etc.), it is not analogous to the complex nutrient transfer via a modification of the maternal physiology (Renfree et al. 2013). Milk has a variety of benefits including rich macro- and micronutrient and several health-promoting roles and is primarily composed of three parts: protein-rich whey, casein micelles, and milk fat globule (Khaldi et al. 2014; Jensen 2002).

Two antimicrobial enzymes xanthine oxidoreductase (XOR) and lysozyme may be why milk has high immunological and nutritional values (Shahani et al. 1973). It was originally hypothesized that the nutritional value of milk evolved subsequently to its immunological function (Hayssen and Blackburn 1985). New evidence supports this notion, but suggests that the immunological response may have evolved subsequently to its nutritional role (Vorbach et al. 2006). Vorbach et al. (2006) describes how

mammary glands evolved from mucus surface epithelia and muscle skin glands, which secreted only antimicrobial enzymes like the ones mentioned above. Then, muscle skin glands evolved into lactating mammary glands which had a protective (i.e., produced antimicrobial enzymes) and nutritional role (i.e., produced fat droplets, α -lactalbumin, and lactose).

Lactation in placentals can be broken up into two phases, milk-only and mixed feeding, when the mother is weaning the young off. The timing of lactation varies from species to species. As mentioned above, life history traits may affect this timing of lactation, although recent evidence suggests that this is not the case. Langer (2008) found that there was neither a relationship between life history traits and milk solids nor adult food quality in a number of mammalian orders. This may give evidence for the coadaptation hypothesis discussed above.

Although placentals and marsupials both produce milk that is protective and nutritional, marsupials have a more complex, extended lactation period (Tyndale-Biscoe and Renfree 1987). For both placentals and marsupials, the mammary gland produces milk via a positive feedback loop in response to the sucking stimulus. As mentioned above, the neonatal marsupial brain is less developed compared to a placental brain (Smith 1997). This is because the majority of marsupial maternal investment focuses on lactation. Marsupial lactation lasts up to 20 times longer than the gestation period (Fisher et al. 2001). Once the underdeveloped offspring is born, it crawls into its mothers pouch and feeds until it can transition into exclusively solid food.

Marsupials not only produce milk, but can simultaneously produce milk of different nutritional composition. For example, the tamar wallaby has four nipples and four phases of lactation. In phase 1, all four mammary glands prepare for lactation during pregnancy. In phase 2, the underdeveloped offspring climbs into the pouch and attaches to the teat of one of the mammary glands. During phase 2, the teat the offspring is attached to continues to lactate, while the other three regress. Milk during this phase has low levels of fat and protein with elevated levels of

carbohydrates. In phase 3, the offspring begins to exit the pouch to eat grass and while continuing to suck, but less often. Milk during this phase has an increase of protein and fat and a decrease of carbohydrate and overall gross milk production. At phase 4, the offspring leaves the pouch permanently, but continues to suck until fully weaned (Trott et al. 2003). Additionally, tammar wallabies can have two different-aged offspring nursing off of two different nipples that secrete milk with compositions suitable for which phase they are in (Brennan et al. 2007).

Conclusion

The combination of viviparity, placentation, and lactation has made mammalian reproduction extremely successful (Renfree et al. 2013). There are two infraclasses in mammals that are viviparous (i.e., giving birth to live young), marsupials and placentals. Placental mammals diverged from marsupials roughly 140 MYA. There are a number of hypotheses that attempt at explaining the evolution of mammalian reproduction: conflict hypothesis, coadaptation hypothesis, and an explanation through life history. In both marsupial and placental mammals, females invest heavily in reproduction compared to males. Both marsupials and placentals have extended maternal investment either through gestation or lactation (Tutin and Collins 1981). Placentals typically have an extended gestation period through which the embryo received the majority of its nutrients through the placenta. Marsupials on the other hand usually have an extended lactation period in which the underdeveloped fetus receives the majority of its nutrients through its mother's milk.

Cross-References

- [Genomic Imprinting](#)
- [Gestation](#)
- [Lactation](#)
- [Life History](#)
- [Viviparity](#)

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Evolution of Long-Term Pair-Bonding in Humans

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Synonyms

Evolution of mating systems; Human evolution; Social monogamy

Definition

Long-term pair-bonding occurs when one breeding male and one breeding female share a common territory, associating with each other for more than just one breeding season regardless of whether or not they currently have any offspring together. In humans, long-term pair-bonding can occur via monogamous or polygamous relationships.

Introduction

Humans have previously been called the “uniquely unique species” (Alexander 1990). Despite there being many different factors contributing to this uniqueness (e.g., the large brain),

one of the most important is humans having a multi-male, multi-female social organization and a long-term pair-bonding mating system (Flinn et al. 2005; Geary and Flinn 2001; Hill et al. 2011). Most species living in groups composed of multiple males and multiple females are promiscuous, while most pair-bonded species live in groups comprised of only one male and one female. There are no primates other than humans where multiple reproductive pairs live together (de Waal and Gavrilets 2013). Nuclear and extended families, as well as parental investment in offspring, are characteristics found in all human societies (Geary and Flinn 2001); such characteristics clearly set humans apart from their African ape ancestors (de Waal and Gavrilets 2013; Flinn et al. 2005). The question then is how could humans have evolved such a unique combination of social organization and mating system.

In fact, long-term pair-bonding in humans has always been considered an evolutionary mystery. Why is this practice so common in human societies around the world? How did long-term pair-bonding first evolve in humans? What were the evolutionary pressures making it beneficial to humans? Although these questions have all been asked repeatedly for decades, even centuries, there has yet to be any real consensus on their answers. Still, much progress has been made.

Monogamy and pair-bonding often get used interchangeably, but “monogamy” can mean many different things. For instance, *cultural monogamy* refers to human institutions such as marriage. *Sexual monogamy* is in reference only to sexual relations; one male and one female will mate exclusively with one another, but have no or few interactions outside of that sexual intercourse. Similarly, *genetic monogamy* is when all offspring produced by one male or female in that pair have that same mother and father. Rates of genetic monogamy can be tested in the field by looking at the genetic makeup of all offspring produced (Reichard and Boesch 2003).

Finally, there is *social monogamy* or what is more commonly called *pair-bonding*. In social monogamy, one male and one female exclusively assort with each other. This assortment is not just in terms of copulations or the genetics of their

offspring, but also in terms of with whom they live, where they sleep, and most generally where they spend their time (Reichard and Boesch 2003). In other words, under social monogamy, one breeding male and one breeding female will share a common territory, associating with each other for more than just one breeding season, regardless of whether or not they currently have any offspring together (Lukas and Clutton-Brock 2013).

It should be noted that many researchers do not restrict the word “pair-bonding” to involving *only* one male and one female. Rather, the term is often used more broadly to describe any lasting reproductive relations between particular males and females. For example, in polygyny where one male is having such lasting reproductive relations with multiple females, some would say that male is just having multiple distinct pair-bonds occurring simultaneously (Reichard and Boesch 2003). Using this terminology, humans as a whole are very much considered having long-term pair-bonds since every known human society has practiced either polygamy or monogamy (and hence long-term pair-bonding) (Chapais 2008). Considering only the raw number of human societies throughout the world (vs. also the populations of each of these societies), only about 17 % of such societies practice social monogamy. The vast majority of the rest (>80 %) practice polygyny. Even among the polygynous societies though, only a small minority of the men in each are actually polygynous; most males lack sufficient resources needed to support multiple female mates (Reichard and Boesch 2003).

True genetic monogamy is rare in humans, even in the socially monogamous cases (Reichard and Boesch 2003). However, despite the widespread prevalence of extra-pair matings, there still has yet to be a human society with sexual promiscuity as the main form of mating system (Chapais 2008). Hence, for the rest of this entry, “long-term pair-bonding” will be synonymous with “social monogamy,” thus including both monogamy and polygamy. For cases where one male and one female *do* remain exclusive with each other, this entry instead refers to these as *strict monogamy*.

In addition to all these different types of monogamy, the word “monogamy” can also

imply differences in duration. *Long-term monogamy* implies the one male and one female which form a pair will remain together across many breeding seasons. *Life-long monogamy* is then a different term used to describe when a male and female’s long-term monogamy in fact lasts for the rest of their lives. Conversely, *short-term monogamy* refers to monogamy that typically lasts for only one breeding season or year; one male and one female will be monogamous to each other, but only within that limited amount of time. Cases where pairs practice short-term monogamy throughout their lives, but in each instance of short-term monogamy have a different partner, are instead referred to as practicing *serial monogamy* (Reichard and Boesch 2003).

For example, many species of birds will be monogamous throughout each breeding season (or other period of time), but then each individual will have a different mate come next breeding season (Reichard and Boesch 2003). This means such birds are monogamous *within* breeding seasons, but not monogamous *between* breeding seasons (i.e., serial monogamy). In addition, human societies where divorce is common, as well as remarriage for both men and women following divorce, have mating systems resembling serial monogamy (Reichard and Boesch 2003).

Monogamy from a female’s perspective often makes a lot of sense. In eutherian mammal reproduction, only females must go through the costly periods of internal gestation and lactation (Opie et al. 2013). Not only are such activities quite energetically expensive for females, they make predation, death, and other injuries to the female more likely. In addition, due to relatively long gestation and lactation periods, female eutherian mammals are also much more limited than males are in the quantity of offspring they are able to have in a lifetime. While males are limited only in the number of copulations they are able to obtain with fertile females, females have their main constraint as time (Kappeler 2013).

In a monogamous mating system, having a male remain with/around a female could help the female in any number of ways, be it protection of her and/or her offspring/resources, help in securing meat or other valuable resources, and/or help

in caring for any offspring produced from the union. All of these would help loosen the female's main constraint (time) either by allowing a female's interbirth interval to be shortened (e.g., by a male helping with parental care of the older offspring), improving her health which leads to longer times of fertility (e.g., by provisioning the female with valuable foods), and/or lengthening her life and hence her fertile period (e.g., by protecting her from other males or predators) (Kappeler 2013).

On the other hand, of critical importance when considering the evolution of long-term pair-bonding is why *males* would ever play their role in a socially monogamous mating system. In eutherian mammals, males have much greater potential for producing more offspring throughout their lives than females (Kappeler 2013), due to the aforementioned female traits of internal gestation and lactation (Opie et al. 2013). This means that males mating with only one female throughout their lives are sacrificing all that "extra" reproductive potential. Thus, for long-term pair-bonding to evolve, there would have to be some fitness compensation present to make up for that loss in male reproductive potential (Kappeler 2013). The rest of this entry is primarily concerned with considering the many possible forms of such "fitness compensation."

Although certainly not prevalent, long-term pair-bonding is widespread throughout the animal kingdom. Long-term pair-bonding is most notably found in birds and mammals. Among mammals, about 3 % of species practice long-term pair-bonding (Kleiman 1977). Even the newer, upper estimate of 9 % of mammals practicing social monogamy (Lukas and Clutton-Brock 2013) pales in comparison to the 90 % of birds estimated to practice social monogamy. However, these 3–9 % of mammal species are found in many different clades of mammals, and long-term pair-bonding is believed to have evolved independently upward of *sixty* different times in mammals (Lukas and Clutton-Brock 2013).

Such pair-bonding in mammals may appear to be strictly behavioral, but neurophysiology has also been shown to play a role. Certain neuropeptide pathways (e.g., oxytocin, arginine

vasopressin, and prolactin) have been shown to have been co-opted to form pair-bonding reward pathways in several species of monogamous mammals, including primates (Lovejoy 2009). Compared to birds, social and genetic monogamy in mammals are tightly correlated, meaning mammals' rates of extra-pair copulations are relatively low (Lukas and Clutton-Brock 2013).

Rates of long-term pair-bonding of course vary significantly among mammal species. While some mammalian orders contain zero socially monogamous species, about 29 % of primate species are socially monogamous (Lukas and Clutton-Brock 2013). In addition, primates are unique among mammals in that social monogamy has evolved independently in every major primate clade, and there are relatively few transitions away from monogamy once it has evolved (Opie et al. 2013).

Among just anthropoid primates, long-term pair-bonding is believed to have evolved independently seven different times, three in Platyrrhini (New World monkeys) and four in Catarrhini (apes and Old World monkeys). Indeed, socially monogamous species among anthropoid primates today include species as varied as New World monkeys (e.g., marmosets, tamarins), Old World monkeys (e.g., De Brazza's monkeys, Sumatran surilis), and apes (e.g., gibbons, humans) (Sillen-Tullberg and Moller 1993). Despite social monogamy not being ubiquitous among primates, its widespread prevalence indicates there must be some significant benefit to species practicing social monogamy. Although this entry focuses on humans, many of the hypotheses and ideas presented below could similarly apply to many of these other primate species as well.

It is the aim here to first discuss the transition *to* long-term pair-bonding: what were human societies like prior to long-term pair-bonding becoming the norm? Second, the many hypotheses which have been given to explain the evolution of long-term pair-bonding in humans will be discussed. Then, both empirical and theoretical work will be looked at as they pertain to each of these hypotheses. Finally, other work which takes a broader look at the question of long-term pair-bonding in humans will be discussed.

Pathways for the Transition to Monogamy in Groups

Part of the debate surrounding the evolution of long-term pair-bonding in humans is over the ancestral social organization and mating system of genus *Homo*. Were human ancestors monogamous? Or promiscuous? Did they live solitary? In one-male groups? Or in multi-male, multi-female groups? These ancestral-state questions are still very much debated, with many researchers having wildly different, and often directly contradicting, views (Duda and Zrzavy 2013).

Humans, and many other primate species, are group living. Such groups of individuals come in various sizes, but all with their associated benefits and costs (Hill et al. 2011). For instance, groups afford members protection against both predators and other groups. Such protection could come from group members' alarm calling, alerting other group members of some impending danger, or in the form of an alliance against a predator or invading group. Groups can also facilitate resource sharing, whether it be with meat, other valuable foods, or other resources. Individuals in groups are better guaranteed a steady supply of nourishment, with food sharing in groups especially helping with food/resource scarcity in the event of a drought or other severe ecological conditions. In the case of species with alloparenting, group living can help with child-rearing and allowing females to have more offspring than they would be able to otherwise. Finally, group living may also help with acquiring mates. By living in groups with at least one male and one female, potential mates are always nearby and mating attempts likely easier to facilitate (Flinn et al. 2005).

On the other hand, group living can also come with potential costs to all group members, primarily from ecological competition (for resources, mates, etc.) (Hill et al. 2011). Living in groups can result in conflict between group members. Such conflict can be energetically costly to those group members, even resulting in injury or death if fighting is the outcome. Living in close proximity to others can increase theft of resources, food, mates, etc., making group members expend

more energy and time guarding such resources and again potentially fighting over them. Finally, visibility by a predator, disease, and other parasites becomes more prevalent when living in the higher population densities that come with groups. Such risk would be absorbed by all group members, not only potentially resulting in increased susceptibility to predation, lasting disability, and death but also potentially in loss of resources and other vulnerabilities (Flinn et al. 2005).

Humans' closest living relative, the chimpanzee, is certainly a group-living species. Chimpanzees live in highly promiscuous multi-male, multi-female societies. Most evidence does not point to monogamy being the ancestral state of the chimpanzee-human last common ancestor. Rather, their ancestral state was likely some type of promiscuity, with monogamy in humans being a derived trait. However, this broad framework still leaves much room for debate in terms of what that ancestral human social organization, and resulting mating system, specifically looked like (Chapais 2013). The following are the four main pathways which have been proposed for such an ancestral state.

Promiscuity

First, the *Pan*-human last common ancestor could have been very much like *Pan* (chimpanzees and bonobos). In this case, the ancestral state for *Homo* would be individuals living in fully promiscuous (i.e., with no stable mating bonds) multi-male, multi-female groups. From this backdrop, humans would have retained this multi-male, multi-female social organization, but then evolved to a socially monogamous mating system from the promiscuous *Pan*-like one (Chapais 2013).

Harems

An often-favored alternative to the above is if the *Pan*-human last common ancestor had a harem-style mating system, similar to that of gorillas. In this case, the social organization would have consisted of groups made up of one male with many females (his "harem") and then lone roaming males outside of any group. The one

male in the harem would mate with all of the females in the harem and also provide protection/guard them, while the roaming males got few, if any, copulation opportunities. From this backdrop, humans would have reorganized into a social organization consisting of multiple males and multiple females making up any one group while still keeping their long-term pair-bonding structure (Chapais 2013). Evidence for this pathway includes humans' *australopithecine* ancestors having large body size sexual dimorphism (larger than either chimpanzees, modern-day humans, or later human ancestors), which is indicative of fierce one-on-one male competition, as seen in gorillas (Geary and Flinn 2001). In addition, one mathematical modeling approach found this pathway to be the most likely one leading to humans (Nakahashi and Horiuchi 2012).

Multilevel Societies

A third alternative discussed is the idea of multilevel societies. Here, the chimpanzee-human last common ancestor would have lived with a social organization and mating system similar to hamadryas baboons. Under this framework, males still have harems (i.e., groups made up of one male and multiple females, all of whom that one male mates with and protects), but then multiple harems live together in larger groups, often referred to as "clans." Under this backdrop, these larger groups would already be practicing long-term pair-bonding. However, from this humans could have even evolved strict (one-male, one-female) monogamy, since "clans" could contain "harems" of one male and precisely one female. If the size of the male harem was reduced to only female per male, strict monogamy would be the effective result (Chapais 2013).

Strict Monogamy

Finally, although considered unlikely by many, it is also possible that strict monogamy was the ancestral mating system for humans. Similar to gibbons and other primates with such monogamy, monogamous pairs would have been spaced out geographically and not had any kind of group social organization. What evolved from this backdrop would then be the group social organization:

monogamous pairs moving closer to each other, ultimately forming multi-male, multi-female groups while still retaining their monogamous mating system. Again, although this pathway is certainly a logical transition, there is little evidence supporting the chimpanzee-human last common ancestor being strictly monogamous (Chapais 2013; Sillen-Tullberg and Moller 1993).

Hypotheses for the Evolution of Social Monogamy

Regardless of from where exactly it came, there is no doubt that long-term pair-bonding evolved at some point in humans' past. Similar to the debate over the ancestral state of *Homo*, there is also much debate over how long-term pair-bonding first evolved in humans. Again, there have been many different hypotheses proposed, some directly contradicting each other, and relatively little headway made in finding concrete answers as to which hypothesis is the most likely. Despite no consensus after decades of research, progress has still been made. Note some hypotheses presented below are unique to humans, while others are more widely applicable to many primates or even mammals in general. Some hypotheses are also highly dependent on one or more of the pathways discussed above, while other hypotheses could still be possible regardless of the specific pathway from which early humans evolved. Also note that some hypotheses below only work with regard to strict monogamy (these will be noted), while most do not specify the type of long-term pair-bonding needed.

In general, all the hypotheses discussed below can be grouped into four main categories. The first is ecological. This hypothesis has gained much support for the evolution of social monogamy among nonhuman mammals, but is widely discredited as being a factor in the evolution of social monogamy in humans. The second group of hypotheses include those having to do with protection, of either the offspring, the mate, or one's self. The third group of hypotheses relates to food: provisioning of the mate, the offspring, or in cooperation. Finally, the fourth group of

hypotheses involves conflict, either strictly between males fighting over mates, group-related, or among siblings produced by the same male. It should be noted that most of these hypotheses are not mutually exclusive, but rather two or more could have simultaneously contributed selection pressure to the evolution of long-term pair-bonding in humans.

Ecological Hypothesis

The first hypothesis discussed here is the “ecological” hypothesis (Komers and Brotherton 1997). Females are assumed to be solitary and relatively spaced out geographically (due to ecological competition), while males are roaming, looking for mates. However, because of the females’ geographic spacing, it may become increasingly lucrative for a male to stick to just one female’s range. Doing so will save males’ energy resources expended in searching for females and also better guarantee males a mate. If they instead wandered, males would have to travel long distances between females with no guarantee of, first, even finding another female, and, second, her desiring to mate with said male once found (Komers and Brotherton 1997).

A recent study found the most likely ancestral state for all nonhuman mammals is solitary females and roaming males with overlapping ranges (Lukas and Clutton-Brock 2013). They then found social monogamy to have evolved in nonhuman mammals under conditions involving intense female-female competition, low female density, and where breeding females were intolerant of sharing their ranges. Under these conditions, males would likely be unable to defend access to more than one female. Among all nonhuman mammals, socially monogamous species today do in fact live at significantly lower densities than solitary species, even after controlling for body size differences and despite the fact that both socially monogamous and solitary species share similar home-range sizes (Lukas and Clutton-Brock 2013).

Although considered by many to be a favored hypothesis for the evolution of social monogamy in nonhuman mammals, this hypothesis is much less accepted with regard to human evolution since

humans did not likely come from solitary ancestors. Each of the three pathways which assume humans had non-strictly monogamous ancestors (i.e., three of the four discussed above) all centers on early humans living in groups of more than two individuals (Kappeler 2013). However, it is certainly possible that changes in early human dietary patterns (even within groups) lowered female densities, making it much harder for one male to guard multiple females. In this way, a transition from polygyny to strict monogamy could still have been facilitated in humans under the ecological hypothesis (Lukas and Clutton-Brock 2013).

Protection Hypotheses

The following three hypotheses all deal with protection as the main selection pressure on early humans for the evolution of long-term pair-bonding.

The first hypothesis under this category deals with protection of one’s offspring, namely, protecting them against the risk of infanticide. Infanticide, the practice of killing an infant not one’s own prior to it being weaned, has been widely documented across primates (van Schaik and Dunbar 1990). In most instances, infanticide is committed by a new alpha male who has just taken over a group. By killing any infants not his in the group prior to their weaning, he is forcing their mothers to return to fertility sooner, increasing the probability of him having offspring with one or more of those ex-mothers and hence increasing his overall fitness. Such evolutionary benefit for males has already been well-established (van Schaik and Dunbar 1990).

Having an offspring killed in its first year of life is clearly very costly; the biological mother and father would each get zero fitness benefit from the said offspring, despite the mother (and possibly the father as well) investing much time and energy into the pregnancy and early life of the offspring. As such, it may behoove the father to stick around that offspring up until the point it gets weaned in order to protect it from any infanticidal attacks by other males. In doing so, such a male has effectively formed the groundwork for having a pair-bond with the mother of his offspring (van Schaik and Dunbar 1990).

Infanticide is quite common among primates, in large part due to altriciality (and in turn long durations of lactation), which makes the infants more susceptible to having infanticide committed against them (Opie et al. 2013). These facts would hold for humans as well. In addition, Opie et al. found that in primate phylogeny, infanticide by males typically precedes social monogamy (Opie et al. 2013). They concluded that not only is social monogamy in primates much more likely to evolve in the presence of high male infanticide, once social monogamy *does* evolve, it is more likely for there to be a subsequent decline in the amount of male infanticide than an increase in the level of polygyny (Opie et al. 2013).

There is still much debate over the role of infanticide in the evolution of long-term pair-bonding in nonhuman mammals. Contrary to the Opie et al. work discussed above, other prominent researchers (Lukas and Clutton-Brock 2013) found “the available evidence suggests that male infanticide is unlikely to be the principal mechanism for the evolution of social monogamy in mammals.” Despite finding rates of male infanticide among socially monogamous species (9 %) to be lower than rates among solitary species (27 %), they concluded from their analysis that this difference was most likely due to “an independent evolution of the two traits” (Lukas and Clutton-Brock 2013).

One key factor considered there was that in most socially monogamous mammals, the duration of female lactation does not typically exceed her gestation period. However, it is in cases where such lactation duration *does* exceed gestation length that a benefit would be expected for males killing other males’ offspring (Lukas and Clutton-Brock 2013). This is because female mammals will not typically have two unweaned offspring concurrently. Hence, if lactation duration exceeds gestation length, there is benefit to the male in killing one offspring, so the next (his) can be born sooner and the female will still only have one unweaned offspring at any given time (Opie et al. 2013).

For example, in modern-day humans, one study found 50 % of nursing women to return to normal estrous cycling within 10 months of

giving birth and 100 % of the women by 20 months, while the cross-cultural average age of weaning in humans is 30 months (Quinlan 2008). In chimpanzees, offspring are typically weaned around 4 years of age, while females on average only have one offspring every 5 years, meaning female chimpanzees will also only have one offspring to care for at a time (Pillsworth and Haselton 2006).

The second hypothesis under the category of protection deals with mate guarding or a male protecting his mate. In most formulations, this hypothesis centers on the idea of paternity certainty. After mating with a female, males can either stay around that one female (“guarding” her) or leave her in search of new mates. By guarding her, a male can prevent other males from mating with that female (which can increase his fitness by reducing or eliminating completely any sperm competition), as well as offer protection to her physical well-being (discussed later). Roaming males attempting to copulate with a guarded female normally face a high cost-to-benefit ratio in any fight with a male guard, and the guards typically win these fights (Reichard and Boesch 2003).

In general, a male must choose between acquiring *more* mates and increasing his paternity certainty with *one* mate. If conditions make the latter more important to a male’s fitness than the former, one could expect pair-bonding to evolve, as the male constantly remains near his one mate to help ensure paternity certainty, which would increase his fitness (Hawkes 2004). However, note that mathematical models of this hypothesis have not supported mate guarding as a strong enough selection pressure for long-term pair-bonding to evolve (e.g., see Gavrillets (2012)).

Among socially monogamous species, levels of mate guarding vary drastically. Kokko and Morrell (2005) constructed a theoretical model and found that males will evolve to guard little if females are either very faithful or very unfaithful. The intuition behind this finding is again that in gaining paternity, males face a trade-off between having more mates and increasing paternity certainty in their one mate. Hence, if a female is highly faithful, her mate would be able to gain

more mates by guarding little, with little risk to the paternity certainty of his mate's offspring. Similarly if a female is highly unfaithful, her mate would likely have little to lose by trying to gain more mates by guarding little since even if he spent his time/energy instead guarding her, she would likely still sneak copulations outside this mating bond. In addition, Kokko and Morrell found that attractive males are predicted to guard less, with the intuition being they are more likely to find *more* mates, and hence paternity certainty becomes less crucial in the trade-off (Kokko and Morrell 2005).

A related hypothesis to mate guarding, involving the direct physical protection of one's mate mentioned earlier, is the bodyguard hypothesis (Chapais 2008). Rather than paternity certainty being the driving selection force behind the evolution of long-term pair-bonding, it could instead be physical protection of the female. If a group is such that a female must be constantly worried about harassment/violence from other males, her (and her future offspring's) fitness would be increased by having the male stick around her. However, in doing so he would also be increasing his paternity certainty, especially if the harassment she was receiving was sexual in nature, meaning the mate guarding and bodyguard hypotheses are largely indistinguishable (Chapais 2008).

The last hypothesis in this category deals with protection of one's self, namely, against the threat of sexually transmitted diseases (STDs) (Kokko et al. 2002). This hypothesis hinges on the fact that STDs were increasingly problematic among early humans, as group size and population density increased (i.e., as humans became increasingly ecologically dominant). As these STDs became more widespread and lethal, the costs of having sexual relations with multiple partners greatly increased. If such costs increased sufficiently enough, it could have been better in terms of a male's fitness to have *fewer* mates rather than more. If that was the case, individuals would have switched to a strategy favoring remaining faithful to one or two mates rather than promiscuity, and hence long-term pair-bonding could have evolved (Kokko et al. 2002).

In addition, using the same reasoning, STDs could influence female choice. A female may view a dominant male, or a male who has mated with many females, as too risky to mate with due to the threat of getting an STD from him. Hence, females may actively begin rejecting mating with such males. Mathematical models have supported this hypothesis as a way for mating systems to change and long-term pair-bonding to become more prevalent (Kokko et al. 2002).

Provisioning Hypotheses

These next three hypotheses all fall under the category of food or other provisionings as the key selection pressure on the evolution of long-term pair-bonding in early humans.

The first hypothesis under this category, food-for-sex, deals with males provisioning their mates or, in particular, males provisioning females in exchange for copulations. As hunting became more important in early human history, and also the nutrients obtained from meat more valuable, females could increase their fitnesses by mating with males in order to obtain more high-benefit foods or other valuable resources. Females were able to increase their fitnesses through such beneficial provisionings, while males increased their fitnesses by increasing their likelihoods of obtaining mates. Provided such benefits were strong enough, and these exchanges consistently occurring between the same male and female, long-term pair-bonding could ultimately be selected for (Reichard and Boesch 2003).

Such exchanges of important foods for copulations are routinely seen in the genus *Pan* (chimpanzees and bonobos). "Important foods" include meats and fruits high in fats and/or proteins, as well as foods requiring increased search time (Lovejoy 2009). Looking at primates, there is an association between the evolution of social monogamy and a reliance on relatively scarce foods (Lukas and Clutton-Brock 2013). Fruit, compared to foods like gum, bark, and fungi, offers much higher nutritional value while also being a more limited resource. Indeed, fruit constitutes a main part of the diet in about 90 % of socially monogamous primate species and only 28 % of solitary primate species. Conversely,

foods like gum, bark, and fungi constitute the main part of the diet in about 40 % of socially monogamous primate species and 78 % of solitary primate species (Lukas and Clutton-Brock 2013).

In addition, a hypothesis related to both the above and the ecological hypothesis, the resource defense hypothesis, posits that social monogamy could have evolved from a male defending a highly valued (e.g., due to food resources) territory, able to keep all intruders out. In this case, a female may want to remain in that territory permanently, not so much because of the male himself, but because of the valuable territory he is able to control (Reichard and Boesch 2003).

The next hypothesis in this group, paternal care, looks at a different type of male provisioning, this time to his offspring (Benshoof and Thornhill 1979). Parental investment is any expenditure benefiting an individual's offspring at some cost to that individual (even if just an inability to invest that energy into other fitness components) (Quinlan 2008). Offspring fitness is increased when a male is around to help provision the said offspring. Provided this helping male is indeed the offspring's biological father, the male will be helping his own fitness as well (Wittenberger and Tilson 1980). 59 % of socially monogamous mammal species have been found to have regular carrying or provisioning of offspring by males, whereas only *three* non-monogamous mammal species have such carrying or provisioning (Lukas and Clutton-Brock 2013). Mammals in particular may require the extra help from offspring provisioning because of that special energy-intensive (i.e., 670 kcal/day in humans) lactation period in a female mammal's life (Quinlan 2008).

In addition, some researchers believe that as the human brain got bigger and human infants became increasingly dependent on others (altricial) during the early years of their lives, mothers were no longer able to care for their offspring alone (Benshoof and Thornhill 1979). For instance, children cross-culturally consume more calories than they produce until at least age fifteen; contrast this with chimpanzees who typically produce more calories than they consume by age five (Conroy-Beam et al. 2015). Over the past

4 million years, human ancestors underwent a doubling of the length of their developmental period (Geary and Flinn 2001). Among modern-day hunter-gatherers, females on average have one child every 3–4 years, meaning most women will have multiple dependent offspring to care for at the same time, unlike in chimpanzees and other primates (Pillsworth and Haselton 2006). In addition, parental investment in offspring does not just stop; rather, it often continues all the way through to become “grandparental investment” (i.e., alloparenting) (Conroy-Beam et al. 2015).

If more than one adult was needed to care for an offspring, fitness-wise it made sense that that “other adult” would be the offspring's biological father, since no other adult (besides the mother) would have as much genetic material invested in the offspring. As hunting became more important in the early human diet, males (the hunters) were increasingly needed as meat providers. Hence it could have been some combination of increasingly altricial offspring, the importance of hunting, and bipedality (meaning humans were more easily able to carry offspring and/or the provisionings) that could have helped long-term pair-bonding to evolve, provided paternity certainty was sufficiently high (Benshoof and Thornhill 1979). However, two separate phylogenetic analyses suggest that paternal care is more likely to be a secondary adaptation occurring either with or after the evolution of long-term pair-bonding, rather than a main driver of this evolution (Lukas and Clutton-Brock 2013; Opie et al. 2013).

The next hypothesis under this category, related to both parental investment and food-for-sex, is that of economic interdependence (Conroy-Beam et al. 2015). Much research has gone into the evolution of a division of labor among early humans, namely, why, how, and when did men and women become solely responsible for specific and different tasks or chores. The economic interdependence hypothesis hinges on the fact that, on average, men have more strength/endurance needed for hunting large game than women do. In addition, during pregnancy and lactation, women are already expending more energy in their daily lives than men and would likely encounter increased risk during large-game hunts

(Conroy-Beam et al. 2015). For example, a pregnant female requires 8–10 % more in caloric intake than a nonpregnant female and a lactating female about 26 % more (Pillsworth and Haselton 2006).

Under this hypothesis, males and females would then engage in economic partnerships, whereby each sex would focus on that resource acquisition they could accomplish most efficiently. Hence, males would provide meat for a female and her offspring, and the female would share with him the foods she had produced or gathered. Not only does this give females easier access to valuable meat, it also provides males with protection in the event that he is unsuccessful in hunts (Conroy-Beam et al. 2015).

A related idea to this involves the idea of cooking (Wrangham et al. 1999). Cooking food is beneficial in terms of (1) calorie intake, (2) protection from disease or other sickness due to food poisoning, and (3) increasing the edible range of plant foods through digestibility. While men went out to hunt, women were left at the camp and hence became in charge of cooking. While males relied on women then for the cooked food each night they came back to camp, women in turn also relied on the men to help protect these valuable cooked foods as well as any foods which had already been gathered but yet to be cooked. It is in this way that such a relationship benefited both the male and female and could have fostered the formation of long-term pair-bonds (Wrangham et al. 1999).

Once producing one's own food became prevalent among early human societies, there were two main strategies each individual could adopt, producing vs. scrounging. An individual following the producing strategy would be focused on producing his/her own food and then storing such food for later consumption. On the other hand, an individual following the scrounging strategy would instead not be focused on producing his/her own food, but rather finding already-produced food elsewhere. Since females were naturally less mobile (due to the demands and restrictions of pregnancy, lactation, and parental care) and males naturally stronger, a logical division of labor resulted where females followed the producing strategy and males the scrounging strategy.

However, this means males were often stealing already-produced foods from females, making it in females' best interests to "buy protection" in any way they could. Since one such form of payment could be the female giving one male her exclusive reproductive rights, long-term pair-bonds could have evolved under this selection pressure (Wrangham et al. 1999).

Conflict Hypotheses

Finally, this last category of hypotheses all deals with conflict as the main selection pressure for the evolution of long-term pair-bonding in early humans.

The first hypothesis in this category, one specifically relating to humans, has to do with the idea of leveling (Chapais 2013). As tool and weapon use became increasingly common across early humans, male size/strength dimorphism became less important in fights. Just because an alpha male is bigger and stronger than a lower-ranked male does not necessarily give that alpha male an advantage in a physical confrontation if the lower-ranked male has more and/or better tools/weapons available to him than the alpha male (Chapais 2013). This meant that any fights between two now-evenly-matched males were much more costly to both males involved and also more likely to end without a winner despite the larger cost involved. Hence, it was harder and more costly for an alpha male to protect any "harem" of females, making pairs of one male and only one female increasingly common until only strict monogamy was left (Chapais 2008).

Males fighting over mates can be very costly to a group as a whole. If males' time and energy are being spent in intragroup conflict, there will be less time and energy available to devote to intergroup conflict. As such, this second hypothesis under the category of conflict predicts that groups with more monogamous pairs will be more successful in the long term than promiscuous groups which routinely have intragroup fighting over mates. This hypothesis posits that since cooperation is key to early human survival and long-term pair-bonding supports such cooperation, long-term pair-bonding could have been able to evolve (Chapais 2013).

There is little doubt that cooperation is in fact key to early human survival. Humans are a cooperative group-living species, and coalitions are often formed in human social competition (Geary and Flinn 2001). Among contemporary hunter-gatherers, cooperation is shown in ways far exceeding that of other primate species. Such examples include sharing food across all members in the group, groups having high levels of alloparental offspring care, cooperative hunting or other food acquisition strategies, construction and maintenance of living spaces, transportation of children or resources, contribution to public goods, etc. (Hill et al. 2011).

There is some evidence for this hypothesis from the palaeontological record (Lovejoy 2009), albeit rather controversial. Fossils 4.4 million years old of *Ardipithecus ramidus*, a species occurring relatively soon after the hominin/chimpanzee split, indicate reduced sexual size dimorphism and reduced upper canine teeth size, both of which are indicative of a decline in male-male conflict (Lovejoy 2009). *Homo erectus* appeared about 1.5–2 million years ago with males about 20 % heavier than females (similar to the sexual dimorphism seen in today's humans). Contrast this with the 60 % heavier males found in the *Australopithecine* species from up to 5 million years ago (Geary and Flinn 2001). If reduction in intragroup conflict was a driving force behind early human evolution, it would be expected that related characteristics like sexual dimorphism would evolve quickly in humans' ancestral line. The above fossil record provides support for this idea.

One intriguing alternative related to this hypothesis is if long-term pair-bonding evolved via cultural evolution (i.e., as an institution via marriage) instead (Henrich et al. 2012). This means that instead of relying on the evolution of *gene(s)* relating to long-term pair-bonding, it is instead *cultural* traits (norms) that are important in this evolution. Humans and their ancestors are still sexually dimorphic in size (as discussed above), an indication that the species should perhaps not be considered genetically monogamous and that it is culture playing the crucial role instead (de Waal and Gavrillets 2013). However, note these cultural

hypotheses would be operating on a much shorter time scale than the genetic hypotheses (i.e., tens of thousands vs. hundreds of thousands of years) (Fortunato and Archetti 2010).

Henrich et al. question how one-male, one-female (strict) monogamy came to be when approximately 85 % of societies (meaning raw number, not considering each society's population size) in the anthropological record allow for polygyny. They reason that strict monogamy was favored by cultural evolution because of how much it benefits groups (i.e., cultural group selection). Similar to the above *gene* evolution, because of those benefits, groups with strict monogamy would do better in the long term than their counterpart groups with polygamy (Henrich et al. 2012).

So where do such benefits come from? As already discussed, monogamy can lower male-male competition within a group; it can also reduce the number of unmated males within the group. This is true regardless of the mating system of the comparative group (i.e., promiscuous vs. polygynous). Having fewer unmated males within a group can reduce crime rates (for murder, rape, assault, robbery, etc.) and other personal abuses which are harmful to groups. Males low enough in rank/status that they get no mating opportunities will have essentially zero fitness and thus, evolutionarily, nothing to lose. This creates males who are more willing to take risks in order to get copulations and hence creates conflicts within their groups (Henrich et al. 2012). Again, groups who impose long-term pair-bonding as the social order will do better than those that do not. Under this hypothesis, even if selection on the actual genes is not strong enough to produce long-term pair-bonding, such evolution is still possible, just considering instead evolution on the related cultural traits.

Finally, the last hypothesis considered here deals with conflict between a male's various offspring, especially if produced by different females (Fortunato and Archetti 2010). As it became the norm for humans for property and/or other resources to be passed on to the next generation, more clearly defined familial lines became increasingly beneficial. A father's fitness can be decreased by having to split his wealth (resources)

among the more offspring he would have by having more mates. Strict monogamy would allow male/female mating bonds to be stable over time and hence all the male's resources to be given to his offspring, all full siblings. In this way, strict monogamy could simply be a strategic behavior on behalf of males and females in allocating their resources to the next generation (Fortunato and Archetti 2010).

In particular, Fortunato and Archetti (2010) constructed a mathematical model and found two conditions which would make strict monogamy (or "monogamous marriage" in their words) the most beneficial cultural mating system. First is when there is unigeniture, meaning only one offspring inheriting all of a parent's wealth, and second is when women are more faithful in a monogamous bond than a polygynous one. If the latter is the case, while men would still have that fitness loss from not mating with more than one woman, they *would* get a benefit from that one woman being more faithful than otherwise (i.e., increased paternity certainty). Note the female of this long-term pair-bond would also benefit, in that her male mate would be investing his resources exclusively in her children for the next generation (Fortunato and Archetti 2010).

This hypothesis could help explain why monogamous marriage is so common in societies with intensive agriculture (e.g., plow or irrigation agriculture of much of Europe and Asia, as opposed to hoe agriculture or pastoralism of much of sub-Saharan Africa). In intensive agriculture, land is often the limiting resource, so splitting land among multiple heirs can only go so far. Hence, this hypothesis would be predicted to have much greater selective pressure under intensive agriculture than other forms of agriculture (Fortunato and Archetti 2010).

Comparative Work

Most of the research discussed above focuses on only one of these hypotheses. There is relatively little comparative work done pitting such hypotheses against each other. One exception to this is Gavrilets (2012). In this paper, Gavrilets constructed models for several of the above

hypotheses in order to look at how long-term pair-bonding could have evolved in early humans' past. In particular, he found that long-term pair-bonding was rarely predicted to evolve in (1) the baseline scenario ("communal care"; males allocate some amount of effort toward helping *all* offspring in their group), (2) with mate guarding, (3) with food-for-sex, and (4) with "mate provisioning" (equivalent to the food-for-sex hypothesis except males are only able to provision one female and females to be provisioned by one male) (Gavrilets 2012).

However, long-term pair-bonding *was* able to evolve provided two things were present: (1) inequalities between males in their fighting abilities (i.e., rank among males in a group) and (2) differences in females in both "faithfulness" (how faithful any given female will be to her mate) and choosiness (for a male who will provision her more). These results imply that it is likely that more than just mate guarding or food-for-sex is needed in order for long-term pair-bonding to evolve. Not only is male rank important (since lower-ranked males may initially be the only ones who do better pursuing a pair-bonding mating strategy), but females' ability to choose mates (namely, those who provision more and/or provide more care) is also important in allowing long-term pair-bonding to evolve (Gavrilets 2012).

The above study looked at individual fitnesses, meaning how different mating systems could have evolved by benefiting the individuals within such a system (Gavrilets 2012). Another theoretical study instead took a group selection approach, looking at how different mating systems could have evolved by benefiting *groups* as a whole (Nakahashi and Horiuchi 2012). These authors constructed a mathematical model looking at the evolution of the alpha male strategy, as well as female mating and grouping strategies. In particular, they found that a human-type mating system (i.e., one in which groups consist of multiple females and multiple males, male-male competition is weak, and there is no female promiscuity) can evolve when having a larger group is beneficial (e.g., in defense against other groups) and when the cost of female promiscuity is large (e.g., due to the many types of human venereal diseases) (Nakahashi and Horiuchi 2012).

Conclusion

Despite all the research and curiosity surrounding the evolution of long-term pair-bonding in humans, few concrete answers have yet to be obtained. In particular, there is still debate over the ancestral mating system in early humans, as well as the main selection pressure(s) resulting in humans switching their mating system to one of long-term pair-bonding. Indeed, researchers still contradict each other over whether the chimpanzee-human last common ancestor had a promiscuous mating system (like chimpanzees), a harem-style polygynous mating system (like gorillas), or multilevel societies (like hamadryas baboons). Many of the hypotheses for the evolution of long-term pair-bonding in humans have more support under only one of these mating system ancestral states, making this a related, and equally important, research question.

In terms of how long-term pair-bonding evolved and whether strict monogamy was a culturally and/or genetically evolved trait in humans, these are both still very much unanswered research questions. Many different researchers have contributed much to this ever-growing body of literature spanning over a century, but few agreed-upon answers have yet been obtained. Some hypotheses have certainly gained more support throughout the years than others, but there are still so many being actively considered. The time is ripe for researching human origins, and progress will likely be made in this upcoming decade. Being human, it is only natural to ask the question of from where did this species come and to investigate those traits that make humans the “uniquely unique species” (Alexander 1990). The human universal of forming long-term pair-bonds is just one such trait.

Cross-References

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Evolution of Mammalian Hearing

► Evolution of Hearing and Balance

Evolution of Mammalian Vision, The

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Synonyms

Evolution of sight in mammals

Definition

The history of heritable modifications that improved and limited the visual systems of mammals, and their associated sense of sight, over the course of successive generations.

Introduction

Light contains a wealth of sensory information that is critical to many animals' daily lives; from the color of a ripening fruit to gauging the distance to a nearby shelter or spotting the movement of an incoming predator, visual cues play a

foundational role in these organisms' survival. While the eyes of all vertebrates are derived from a common ancestor, they have been adapted to a myriad of different ecological niches. Mammalian visual systems in particular have undergone considerable flux throughout their evolution.

Pre-mammalian Eyes

While there are many different shapes and sizes of eyes across the animal kingdom, vertebrate eyes are typically single-chambered structures described as being "camera-like" with an open aperture in the front directing incoming light onto the photosensitive retina which, in the camera analogy, acts somewhat like the camera's film. When it comes to what sets mammalian vision apart from other vertebrates, however, the shape of the eye is less divergent than the organization and development of the retina and photoreceptors, known as rods and cones. Rods are highly sensitive to light and are responsible for scotopic, or nocturnal, vision. They contain a high concentration of photosensitive pigments, improving each cell's ability to detect individual photons, and the resulting signals are amplified as multiple rods synapse with each ganglion cell (Hauzman et al. 2018). This signal convergence drastically improves sensitivity, at the cost of overall acuity. Cone photoreceptors amplify visual acuity for photopic, or diurnal, vision. Cones are less sensitive to light and are activated in high luminosity conditions; however they allow for the discrimination of different colors, mediated by comparing the outputs of different cone subtypes that each express photopigments tuned to respond maximally to specific wavelengths of light.

Reptiles and birds have evolved four cone opsin types, sensitive to long, medium, short, and ultraviolet wavelengths of light. These opsins can be expressed within one of the two morphologically distinct cone subtypes; single cones, which can produce one opsin type each, or double cones that typically express either the long-wavelength opsin or both the long and medium opsins in tandem (Bowmaker 2008; Enright et al. 2015). Inside these cones is a particularly interesting adaptation: small globules of colored oil

that act as tiny micro-lenses and light filters to help improve color discrimination (Toomey and Corbo 2017). In mammal lineages, however, these vision-enhancing adaptations have largely been lost. Most mammals have only two cone opsin classes (Jacobs 2009), and while some marsupials have retained both the oil droplets and double cones with the long-wavelength opsin (Ahnelt et al. 1995), the loss is complete in Eutherian (placental) mammals, as illustrated in Fig. 1. Instead most mammals have an eye design more optimized for low-light conditions, with higher sensitivity at the cost of lower acuity (Heesy and Hall 2010). It has been proposed that this difference hints towards a period of strong selection towards a nocturnal lifestyle early in the evolution of mammals.

The Nocturnal Bottleneck

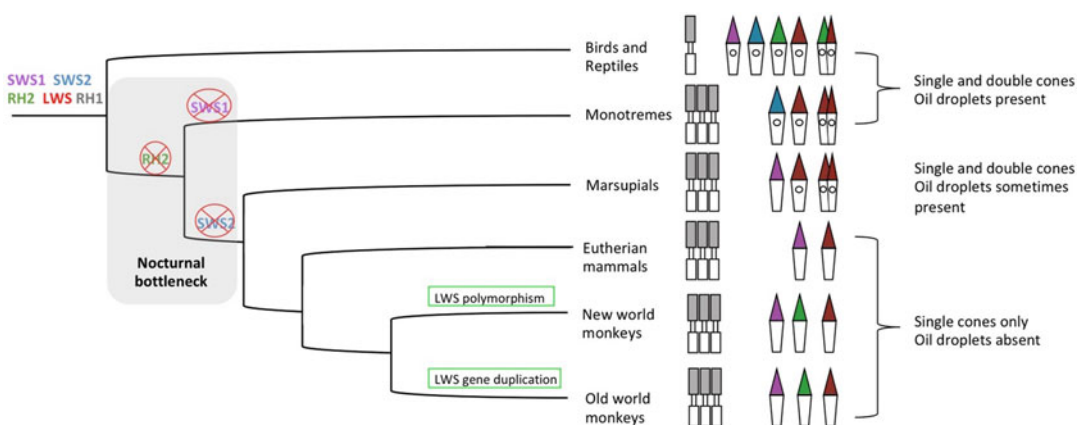
During the Mesozoic era, 250 million years ago, reptilian dinosaurs were a dominant force in the world. Ancestral mammals at the time presumably developed strategies for surviving against such formidable predators. A prominent hypothesis is that in order to avoid the large reptiles, who were likely ectothermic and active mostly during the day, most early mammals adopted a nocturnal lifestyle (Walls 1942). This shift in their behavioral niche would have required them to adapt to seeing in low-light conditions, involving significant restructuring of their visual systems. Even after the extinction of the dinosaurs, and the release of the strong pressure to remain nocturnal, mammals have retained many features that hint at their nocturnal ancestry to this day. The overall shape of mammalian eyes tends to favor larger corneal diameters relative to axial length, a feature common in nocturnal birds and lizards (Hall et al. 2012). This eye design allows for more light to enter the eye at once, an adaptation that maximizes sensitivity in low-light conditions at the cost of visual acuity. The ratio of photoreceptors in the retina has also been skewed heavily in favor of the highly sensitive rods (Gerkema et al. 2013; Kim et al. 2016). The source of rod photoreceptors during eye development appears to have expanded in mammals compared to fish,

such that cells that would otherwise produce cones evolved to produce rods, perhaps to accommodate or empower the nocturnal shift in habits of early mammals (Kim et al. 2016).

This trend towards visual sensitivity at all costs is reflected not only in the structural changes to the visual system but also in the mammalian genome. The photopigments that allow for color discrimination are produced by a series of opsin genes. Vertebrates produce one rod opsin (RH1) and four classes of cone opsin genes: two for short-wavelength opsins (SWS1 and SWS2), a long-wavelength opsin (LWS), and a rod-like cone opsin (Rh2) that is tuned to medium wavelengths (Jacobs 2013). While the full complement of cone opsin classes can be found in other vertebrates, no mammal expresses more than two. Mammals managed to preserve the long-wavelength-sensitive opsin, but the short-wavelength opsins were repeatedly lost as various groups diverged (Fig. 1). SWS1 was lost in the monotremes, while marsupials and eutherians lost SWS2 instead. The Rh2 opsin is completely absent in all mammals, implying that it was lost sometime before the divergence of the mammalian ancestor (Jacobs 2013). Mammals have even lost the *opn4x* gene, which expresses photopigments in non-retinal tissues in other vertebrates, as well as several structures related

to melatonin production involved in the regulation of the circadian rhythm (Heesy and Hall 2010).

It has been suggested however that the long-wavelength cones may play some critical role, a nonvisual function, such as the circadian rhythm, considering its consistent retention in all mammals (Schwab 2012). The short-wavelength cones may therefore have few, if any, ancillary functions and would be far more sensitive to genetic drift in a changing sensory ecology. For example, despite their nocturnal niche, most bats have retained long-wavelength-sensitive opsins, but across species, short-wavelength opsins show considerable differential conservation (Simoes et al. 2019). Some species relying almost entirely on echolocation have lost the SWS1 genes completely, while others have retained some SWS1 function to augment their navigation with a small amount of short-wavelength vision (Zhao et al. 2009). Possibly lending credence to this argument is the apparent lack of abundance of short-wavelength-sensitive cones in most mammalian retinas. As many as 10% of all mammalian species have lost the SWS1-expressing cone subtype entirely, with the trend that these species have all currently inhabit, or have an ancestral history of inhabiting, nocturnal niches (Jacobs 2013).



Evolution of Mammalian Vision, The, Fig. 1 A simplified Cladogram showing the gradual loss of cone opsin classes across mammalian groups and the re-acquisition of trichromatism in new and old world monkeys. The

nocturnal bottleneck, represented by the grey box, marks a period of loss of cone opsin classes and subsequent increase in rod production

Seeing in Color

After the nocturnal bottleneck, following extinction of the dinosaurs, ancestral mammals were free to once again reclaim a diurnal lifestyle but were left with visual systems already adapted to their nocturnal niche. The loss of cone opsin genes had reduced the range of color discrimination from four color channels (tetrachromatic) down to only two (dichromatic). This loss was not immediate or entirely complete, as there is some evidence of progressive degeneration of opsin genes in more basal-branching mammals. For example, there is evidence of trichromacy in marsupials, though most are dichromats (Arrese et al. 2002). While extant species of monotremes are dichromats, a third nonfunctional opsin gene remains identifiable in their genome (Jacobs 2009). Such remnants of the ancestral state may reflect an intermediate stage of color vision loss. Among mammals, only the primates have acquired a true, consistent trichromatic vision. Some early-branching primates, like the lemurs of Madagascar and other “prosimians,” have maintained a nocturnal lifestyle and the dichromatism that came with it (Schwab 2012); however most extant primates have acquired a third cone opsin and regained trichromatic vision, though they’ve done so in markedly different manners.

In new-world monkeys, the callitrichids and the cebids, the X-linked LWS gene has developed several different alleles. This polymorphism allows for the production of an additional opsin with a slightly different spectral sensitivity in heterozygous females (Bowmaker 1998). Old-world monkeys, like the great apes and humans, derived trichromacy through a gene duplication event that resulted in two separate long-wavelength-sensitive opsins (in “red-sensitive cones”), one of which was free to mutate into a stable novel gene with a shifted spectral sensitivity (producing “green-sensitive cones”), allowing for trichromatism in both males and females (Bowmaker 1998).

The Value of Vision

The prevalence of dichromatism among mammals suggests that despite the restricted range of color

vision, it may not be entirely detrimental and could possibly even prove beneficial in certain circumstances. For example, it has been demonstrated that dichromatism is more likely to subvert color-based camouflage (Morgan et al. 1992), making it adaptive for finding well-camouflaged prey like insects among dense underbrush. However, to be considered adaptive, such advantages would need to outweigh those of trichromacy, such as locating brightly colored foods like fruits and leaves (Dominy and Lucas 2001), standing out to attract a suitable mate (Ryan and Keddy-Hector 1992), or detecting certain predators (Pessoa et al. 2014).

The organization of an organism’s visual systems may also be indicative of their lifestyles. Diurnal species tend to have cone-dominated retinas, though the distribution of these cones is far from uniform and is highly correlated to their ecological needs. Many species produce a circular area of the retina with an increased density of cones than the surrounding areas called an *area centralis* (Hauzman et al. 2018). This retinal configuration is often seen in species living in forests, where wide open lines of sight are less common and more focus is needed on the immediate surroundings. In the *area centralis* of birds, reptiles, and primates an area of even higher cone density sometimes forms a pit in the retina called a fovea. By displacing the surrounding supporting neural retinal cells, an increased surface area of the cone dense patch is more directly exposed to light (Bowmaker 2012). It is suggested that forming this pit magnifies the image-forming surface to improve visual acuity despite primates’ relatively low abundance of cones. This focused retinal surface, combined with large brains and complex neurological systems to integrate binocular signals, gives primates excellent depth perception (Barton 2004) – adaptations that could prove useful for climbing through the trees as well as for holding and manipulating nearby objects.

Many species do not possess an *area centralis*, but rather an elongated zone of increased ganglion cell and cone cell density that spans the horizontal or vertical axis of the retina (Bowmaker 2012). Rather than providing a single clear image, these “visual streaks” sample a panoramic view of the

surrounding environment without the need for much eye movement (Hauzman et al. 2018). The orientation of the visual field is strongly correlated with an organism's environmental niche. Vertical visual streaks are quite rare, found mostly in species with vertically oriented behaviors, such as certain fish migrating through the water column or sloths climbing along branches. Horizontal visual streaks are typically seen in species, e.g., rabbits, that inhabit open terrain such as fields. This arrangement allows consistent scanning of the horizon and responds strongly to fast-moving objects, rather than focus on any one location in particular (Levick 1967; Collin 2008), a critically important ability for detecting approaching predators.

Conclusion

The history of mammalian vision runs parallel with the history of mammals themselves. The vertebrate ancestor likely possessed four classes of cone opsin, spread between two single cone types and a double cone. However, shifting to a nocturnal lifestyle reduced the evolutionary pressure to maintain strong color vision, instead provoking a shift towards large eyes with rod-dominated retinas that resulted in a loss of several cone subtypes. Although they are now released from the nocturnal bottleneck, the evolution of mammalian visual systems has been shaped by the limitations imposed by an ancestral state that heavily favored visual sensitivity at the cost of acuity. Only the old-world primates, humans included, have managed to re-acquire stably heritable trichromatic vision, and all the benefits that come with it.

Cross-References

- Eye, The
- Retina, The
- Vision

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Evolution of Mating Systems

► Evolution of Long-Term Pair-Bonding in Humans

Evolution of Memory, The

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Synonyms

Adaptive memory; Evolution and memory; Memory and survival

Definition

The adaptive function of memory and its role in the survival and fitness of the humankind. Memory is the process of acquiring, storing,

and recalling/retrieving information either verbal, nonverbal, sensory, or emotional.

HM

HM at the age of 27 lost his ability to memorize new information. A neurosurgical operation succeeded to reduce his intractable epileptic seizures but left him with a dense memory loss, amnesia. In the 1950s we did not know the important functioning of the hippocampi, the structures removed in HM's surgery to reduce his epileptic activity. HM's global amnesia developed immediately, given that the bilateral surgical removal of his hippocampi caused him to lose the ability to form new memories. Later of course this finding about the functioning of the hippocampi was cross-validated with more case studies and animal studies. Of course, neurosurgeons from then on took extra care not to damage or remove hippocampi bilaterally as it was shown that this small structure, in the center of our brain, holds the secret of memory formation, in other words, the encoding of new information. What was even more remarkable in HM's case was that after the removal of the hippocampi, the newly learned explicit factual and verbal information, as well as memory about events, disappeared from his mind within minutes. However, he was still able to learn and remember newly learned motor movements and perceptual info, and he retained most information that he learned before his surgery (retrogradely; he lost memories made up to 11 years before his surgery, so he had memories up to the point he was 16 years old). HM's studies and all similar future research revealed to us areas of the brain related to memory and how learning, encoding of new information, and memory systems function.

What was evident from HM was that a person cannot survive all alone with bilateral damage in the hippocampi; in other words, a person without the ability to record new memories and learn new information is doomed not to survive, if not for the help of their family or community. If HM was born thousands or hundreds of years ago, his survival would have been really difficult, if not impossible.

Areas of the Brain Related to Memory

The amygdala is the center for memories involving emotions, while the hippocampus is the center of declarative (explicit), episodic, and semantic memories. Declarative memories refer to the store and recollection of factual conscious information, while episodic memories, a subdivision of declarative memories, refer to the store and recollection of our own personal factual information. Semantic memories, the second subdivision of explicit memories, refer to the store and recollection of general knowledge, which is not personal (autobiographical) in nature. Both the amygdala and hippocampus belong to a greater brain system called the limbic system.

Given the aforementioned information, extensive damage to the amygdala (bilaterally) generates lower levels or absence of emotions (such as fear), while memories related to emotions are impaired. Extensive damage to the hippocampus, bilaterally, leads to impaired encoding (registration of new information) and anterograde amnesia, the inability or impaired ability to store (and consequently recall) new information. Our amygdala and hippocampi are also responsible for consolidating our factual and emotional memories and moving them from short-term to long-term storage; therefore their damage impairs the consolidation of various memories and their conversion from short-term to long-term memories.

Another area of the brain, much larger than the ones already discussed, the cerebellum is the center for procedural and motor memories. For example, learning and remembering the procedure required to ride a bike would fall in this category or memories. Learning new motor and procedural skills, fine-tuning them over time via practice, and storing these procedures are functions related to the cerebellum.

The basal ganglia, a group of brain nuclei, are also involved in motor memories. Learning, storing, and recalling such information are functions relating to basal ganglia. The basal ganglia, however, are also involved in implicit memory, the creation and store of information that we might not be readily aware, and some scientists refer to these memories as subconscious memories.

Our frontal lobe, the largest lobe of the brain, is responsible for coordinating all of the aforementioned memory functions and is also responsible for our concentration (required to learn new information) and planning and organization, functions which are also important in learning and memorizing. Without our frontal lobes, it would not be easy to select the appropriate piece of information, at any given time, among all of our memories and stored information, in order to control our behavior in the best way possible and, therefore, search for memories and information crucial to our survival in some instances.

The frontal lobe is also responsible for controlling our working memory, our ability to retain some information for short periods of times and behave accordingly. For example, the short retainment of a math problem, which is read by a teacher, until it is solved and the answer is given, requires a good working memory. Finally, our frontal lobes, as they are the planning center of the brain, are responsible for our prospective memory, remembering what is needed to be done in the near or distant future, which is also crucial for our species success and survival.

The temporal lobe is the lobe that controls our ability to recognize pieces of information that we encountered in the past, a process plainly called “recognition,” which is not part of our aforementioned memory systems. For example, it is difficult to actively remember and recall the name of a historical person, who was mentioned 2 years ago in a documentary. However, it is much easier to recognize that name when somebody else mentions it or if you are asked to recognize it among multiple choices. This is what makes multiple choice questions generally easier, in school tests, than recalling information verbatim in written answers to essay test questions. The temporal lobe also mediates our memory and recognition of faces and mediates our learning, store, decay, and recall of verbal information. It is therefore obvious that recognition of information and recall of verbal of information could be also very important in our species sustainability. For example, when re-encountering a dangerous person or a dangerous animal that you could not recall their name or face/shape readily, you would quickly

recognize them, and you could quickly escape to save yourself.

The parietal lobe has a role, as well, in memory. It mediates our memories related to our sensations and perceptions. For example, memories related to physical pain and touch could be mediated by the parietal lobe.

Finally, the occipital lobe, the lobe that lies to the far posterior area of our brain, is the visual center; it mediates visual memories and is associated with learning visual symbols, such as letters and numbers.

Memory, Learning, and Evolution

Drosophila, a fruit fly, showed us that, through generations of the species, changes in the genotype are responsible for nervous system alterations, which could critically affect learning, retaining, and recall (Sherry and Schacter 1987). Evolutionary scientists are collecting evidence and hypothesize that similar changes, favoring our survival and reproductive success, developed our memory systems, related to specific brain loci, that will be discussed below.

The brains of reptiles and birds, and even mammals, are similar in that they are organized in some similar divisions and subdivisions (Kaas 2013). The two main divisions, namely, the cortex and subcortex (subcortical nuclear structures), have several subdivisions, as Kaas (2013) states, which are the lateral/side regions with olfactory control, dorsal areas with control of other sensations, and medial deeper areas that are in control of learning, memory, and recall. In primates, apes, and humans, the dorsal cortex evolved into a thicker structure, with humans having a very thick cortex (or neocortex) as compared to other mammals and primates. The neocortex, lobes of which we discussed above, take up the higher order processing of information, complex thoughts, sensations, and responses. Our medial structures continue, however, to be responsible for learning, memory, and recall of information; the aforementioned hippocampus is a very important memory medial structure. Through the years, our cortex became organized in layers and columns,

and our memory centers started communicating with these higher cortical areas that little by little gave rise to memory systems, which are the products of simultaneous synchronous functioning of cortical and subcortical areas.

“Human Memory is an evolved trait, fine-tuned over generations by the process of natural selection” (Nairne and Pandeirada 2016). All of our traits that are deemed favorable for our reproduction and survival are adopted; memory functioning and memory systems therefore have been evolving to suit our living, survival, and mating. Nairne and Pandeirada (2016) hypothesize that memory could have evolved from a simple perceptual processing into a complex function. They also conclude that recalling and memory decay creates an “adaptive behavior” selected to improve our fitness and chances of reproducing and surviving.

Recalling has apparent benefits for human beings, as learning and memorizing would not be useful without being able to recall information when needed. The decay of memories and learned information is also adaptive for human beings. This is evident in a rather cliché example, that of a woman, who gives birth might not attempt in the future to reproduce if the difficulties and pains of pregnancy remain vividly active in her mind long after giving birth. Similarly, a couple tends to remember mostly the happy times of raising a newborn, toddler, child, and teenager, otherwise vivid memories of the “bad times,” and often anguish related to raising difficult children or children with impairments, might be a deterrent for having more children.

All categories of information that we acquire, retain, and recall or forget are due to our memory, which allows us to learn and survive. Like history for humanity, memory is what allows us to remember past experiences, past hurtful situations, past positive livings, and adapt to our environments by taking advantage of what we already know. We solve the same, similar, or even brand-new problems based on our previous experiences and learned information, and we survive by remembering what is lethal, unwanted, or beneficial for ourselves.

It is not only our memory that is being perfected over generations but also all of our

cognitive systems such as sensations and cognitive perceptions (visual, auditory, tactual, etc.), our executive functions (such as planning, organizing, attending, and fluency), our language (comprehension and production), and every other aspect of our cognition that evolved in along and in an interplay with our memory. Of course, as we saw above, memory is often in a mutual exchange of information between other cognitive systems. For example, language comprehension and production depend on past learning but also the retrieval of words, idioms, and meanings in order to be effective.

Some of the first studies of learning were the biological research of Spalding on animal imprinting (Spalding 1873), which is a learning process through which animals during a critical age period (phase-sensitive period of learning) learn very fast a behavior, which is not contingent to consequences, as in operant conditioning. For example, in some birds it is the strong attachment association of a young chick with its caregiver or even the first moving object they see after their birth, most often their mother. Later Thorndike stipulated the relationship between a stimulus (S) and its response (R) and how this S-R learning is established by either the frequent or intense pairing of a stimulus and its response (Thorndike 1913, 1932). For example, the connections made by Thorndike’s cat between a lever (S) with escaping (R); a pairing which developed and strengthened the learning that the pressing of a lever leads to escaping from a confined space. Similarly, a child wanting a cookie throws tantrums and exhibits bad behavior having learned in the past (via S-R learning) that this behavior sooner or later will force the parents to give into her requests. Later, behaviorists recognized that the learning is not only based on S-R pairings but also on an organism’s individual internal processes which affect the learning process. This new behavioral notion became known as S-O-R (stimulus, organism, response). For example, an adult with better attention will learn faster or better a taught process at work than other colleagues with poorer attention or concentration difficulties. In Pavlovian classical conditioning (Moore 2004), the difference is that here learning involves not

only a stimulus (plus an organism) and response but also a pairing of an unrelated stimulus (conditioned stimulus) with the response. For example, the child in the previous experiment learns after several pairings of eating a cookie while watching cartoons, to associate a previously neutral stimulus (watching cartoons) with the need of having a cookie. Animals and humans also learn through operant conditioning where reinforcers and punishers increase or decrease the likelihood of a behavior occurring. For example, an animal that receives a treat every time it sits at command learns through operant conditioning. Finally, animals and humans alike learn via observation (modeling or social learning), and a cat that sees another cat hunting to eat could learn better hunting techniques itself or how to hunt altogether. All in all, the type of learning is imperative in our encoding (learning), memorizing, and remembering/recalling how to behave in certain environments, instances, and ultimately to our survival.

A very recent approach to understanding mental health in humans studied language and its evolution in humans. The most distinctive characteristic that we developed as humans is exactly that, language (Sherwood et al. 2008). Arguably, and according to acceptance and commitment therapy (ACT), humans make verbal associations continuously, and these verbal associations may lead to connections of words, circumstances, and places with happiness (e.g., a friend's name that could instigate happy feelings), sadness (e.g., passing by a road that brings about terror and thoughts of doom because it was associated with an accident), or any other feeling. These verbal associations of course happen always in a context. Relational frame theorists (RFT), who stipulate this theory, said that "...the core of human language and cognition is learning to relate events mutually and in combination not simply on the basis of their formal properties (e.g., size, shape) but also on the basis of arbitrary cues" (Hays et al. 2013). Therefore, the development of language in humans not only helped us in communication but also in recalling (consciously or subconsciously) associated feelings with objects, people, animals, circumstances,

etc. that could be vital to our survival. For example, verbally associating a viper snake and its habitat with feelings of doom and danger after watching another person being bitten and later dying will most definitely help us actively avoid such encounters. Often we overgeneralize through mental verbal associations that lead to non-adaptive learning. Following the previous example with the snake, such associations/learning may not be ultimately adaptive as our newly learned associations may lead us to avoid all snakes (beneficial or not) and entire fertile areas (which could lead to better crops) that we verbally associated in our mind with danger (the viper). This association and learning could have happened because of one and only specific experience, meeting a dangerous viper.

The understanding of memory systems and memorization, learning, and recalling became even more robust in the past few decades as neuropsychology started adopting memory tests from primate experiments for humans and also developed new memory tests (Murray et al. 2017). Neuropsychology developed rapidly following the two world wars when wounded soldiers with traumatic brain injuries were returning home in the thousands with cognitive impairments, which were not fully studied up to that point. Neuropsychology, the study of brain behavior associations, evolved itself into clinical neuropsychology (American Psychological Association 2010) that determines, through thorough cognitive assessment, the cognitive impairments caused by transient (e.g., medication or a mental disorder) or permanent (e.g., chronic adrenal disorder or diabetes) environmental and organic reasons or by direct brain lesions and damage following a traumatic brain injury or surgery. What is evident in clinical neuropsychology is that brain lesions, brain damage, and transient or permanent environmental factors affect most often memorization, recalling, attention, and concentration and less often other faculties and brain functions. The hippocampus, in particular, is a very sensitive structure in the brain that is among the first to be negatively affected by environmental or organic causes of brain abnormalities (Anand and Dhikav 2012).

Memory Systems

Memory is not just one unified system or faculty, as previously discussed, but multiple systems, and each one of them controls or mediates a memory function (Poldrack and Packard 2003). However, these systems do not exist in isolation, even though they can work independently (Sherry and Schacter 1987). They also interact with each other in order for us to encode, learn, move information to short- and long-term memory, and recall that information. At the same time, there are times when memory systems compete with each other; in a simplistic example, trying to memorize a particular location while driving could be negatively impacted by the encoding of emotional stimuli (e.g., fear, panic, etc.) which could lead to the encoding of other types of information that suddenly appeared during the process of memorization of a location. Memory in human beings has been evolving into different memory systems and different structures in the brain (as mentioned above) assumed, through evolution, the control or organization of these different memory systems. Memory systems are defined as “. . .an interaction among acquisition, retention, and retrieval mechanisms that is characterized by certain rules of operation. . .” (Sherry and Schacter 1987).

According to Murray et al. (2017), the development of neuroscience and neuroimaging (e.g., fMRI, MRI, CT scans, spectroscopy, etc.) allowed neuropsychologists and neuroscientists to make clinical correlations between damaged brain areas and their neighboring surviving brain areas with memory systems. In addition, Murray et al. (2017) present in a table the neuroscientifically accepted memory systems along with the brain areas associated with them. Specifically, the memory system that involves our personally learned habits' system is associated with the basal ganglia, whereas our explicit memory system is associated with the temporal lobe (medial structures). In addition, according to Murray et al. (2017) our emotional memory system is associated with the amygdala and our motor memory system is associated with the cerebellum. Finally, our priming of behavior's system is associated with the sensory cortex.

Apart from the memory systems, and the brain loci associated with each one of them, which were described by neuroscientists, evolutionary cognitive scientists recognize seven memory systems, according to Murray et al. (2017). These systems developed through evolution to aid our survival. These are:

1. Reinforcement memory system, which describes memories made via contingencies (stimuli, responses, and outcomes) and solidified with reinforcers
2. Navigation memory, which refers to our memories that help us find our way through our environment
3. Biased-competition memory, which is formed via competitive stimuli and representations and allows us to differentiate among already existing representations engraved in our memory and new ones
4. Manual-foraging memory, which developed following the locomotion in two legs that freed the arms and hands for feeding and action, while vision helps find and select what the individuals deems as valuable
5. Feature memory, which categorizes stimuli and information into their individual characteristics of color, shape, weight, surface, etc.
6. Goal memory, which helps us remember objects, places, etc. and associate them with actions, targets, and behaviors for achieving goals and plans
7. Social subjective memory, which are stores of representations of ourselves and representations of other individuals that help us in our socialization and self-awareness

In a more classical cognitive psychology view of memory and learning, different types of memory, as assessed in cognitive and neuropsychological assessments, are also viewed as different memory systems, as well (Squire 2004). In this article, declarative memory, defined at the beginning, is one memory system divided into semantic and episodic memories. A second memory system named nondeclarative memory involves our procedural memories (skills and habits), classical conditioning, nonassociative learning (reflexes),

and priming and perceptual learning (Levy et al. 2004). Priming and perceptual reasoning were not previously defined and refer to learning that is aided by previous experiences associated with new learning material. For example, a student memorizes and remembers better the word “needle” if it follows the word “vaccination” in a word list that needs to be memorized through rote memorization (memorization through repetitive exposure to stimulus).

Conclusion

The evolution of our memory (visual, auditory, olfactory, and tactile memories) and memory systems are definitively crucial to our survival as species. Our memory and memory systems will keep evolving and most probably, at some point, they will include more memory systems and functions that adapt to the great technological advances that humanity has been experiencing, since the industrial revolution, along with the vast digital advancements that we are experiencing nowadays.

Cross-References

- [Different Functions of Memory](#)
- [Inceptive and Derived Memory](#)
- [Multiple Memory Systems](#)
- [Personal Memory](#)

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Evolution of Morality

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Synonyms

[Ethics](#); [Morals](#); [Right and wrongs](#); [Righteousness](#); [Virtue](#)

Definition

The Evolution of Morality is the development and transformation of moral behavior or thoughts across the course of human evolution.

Introduction

Morality is a crucial component to humanity and society (Haidt 2012). In particular, morality provides individuals with a set of rules that allow them to live together in relative harmony. Despite the awareness of morality's significance, one of the most frequent questions in moral psychology is where does morality come from? Consequently, the purpose of this entry is to provide a brief overview regarding the origin and various foundations of morality. Lastly, this entry will conclude with recent advances in moral psychology by focusing on Moral Foundations Theory as well as suggestions for future research.

Morality

Morality can be defined as a system of “interlocking sets of values, virtues, norms, practices, identities, institutions, technologies, and evolved psychological mechanisms that work together to suppress or regulate selfishness and make social life possible” (Haidt and Kesebir 2010, p. 800). Morality is also an evolutionary adaptation that can be thought of as a form of social behavior (Allchin 2009; Haidt 2012). For example, the most intricate animal societies develop morality in order to promote and maintain group cohesion, decrease the likelihood of harm, and increase the likelihood of group success. Taken together, morality is a highly social process because many of the motives, behaviors, and values that are associated with morality concern social benefits (e.g., mating, nesting, protecting one's territory; Allchin 2009).

The Sources of Morality

Individuals often argue that morality has its origins in either nature or nurture (Haidt 2012). A *nativist* is an individual who believes that morality is innate and comes from nature. For example, nativists may argue that morality was implemented by a higher power (e.g., God) or perhaps evolved intuitively or emotionally. In contrast, an *empiricist* believes that the mind is a

blank slate at birth and that morality emerges during the socialization process. An empiricist may argue, for example, that morality develops as children learn the differences between right and wrong from adults in their social environment.

There is also a third possibility regarding how morality develops which is often referred to as *rationalism*. Rationalism refers to the belief that morality is neither innate nor learned from adults but is self-constructed from experiences (Haidt 2012). More specifically, a child learns to be moral through experiences of harm and fairness, which allow the child to solve complex moral problems as he or she develops (Piaget 1932). In sum, rationalists believe that the final stage of moral development is when an individual is able to engage in socially acceptable moral reasoning (Haidt 2012).

However, many of these answers have been rejected due to recent research. In particular, morality cannot be entirely innate because it has been found to vary by culture (Haidt 2012). For example, in some cultures the aspect of purity has been found to be a significant part of the moral compass used in some cultures but a relatively weak aspect of morality in other cultures (Haidt 2012). Furthermore, individuals have been found to experience gut feelings (i.e., intuitions) when faced with moral dilemmas which suggest that morality may not be based entirely on socialization (Haidt 2001).

Dual Process Model of Morality

Recent advancements in morality research suggest that morality develops from a set of evolved intuitions that are innate, but there is a strong socialization component because children learn how to apply these intuitions within their particular culture (Haidt 2012). More specifically, nature provides the first draft of morality, but this initial version of morality is malleable which allows it to be shaped by the socialization process (Marcus 2004). Haidt (2001) proposed the *social intuitionist model of morality*, which is an approach that rejects one of the former views regarding the development of morality (i.e., the rationalist view) – the model combines the importance of

evolved intuitions as well as the significance of social and cultural forces. For example, when an individual is presented with a moral dilemma, he or she will first experience an immediate gut feeling (i.e., a moral intuition) which may then elicit a moral judgment (i.e., good or bad evaluations; Haidt 2001). However, when an individual's moral judgment has been challenged he or she may engage in moral reasoning (Haidt 2001). For instance, if an individual is asked to explain his or her moral decision, then he or she will often develop something akin to an "inner lawyer" that will attempt to provide an explanation for the relatively intuitive moral judgment (Haidt 2001). Lastly, this moral decision-making process can be modified depending on one's social environment (e.g., peer influence) and culture (i.e., some cultures emphasize different moral intuitions; Haidt 2001).

This model of morality can also be thought of as a dual process model (Haidt 2012). More specifically, moral intuition – which reflects an automatic process – comes first and may be followed by moral reasoning – which is a controlled process – if this sort of cognitive action is required (Haidt 2012). Moral intuitions are fast, effortless, and linked to motivation, which can strongly influence one's behavior (Haidt 2012). In contrast, moral reasoning is a more recently evolved ability that relies on cognition and language-based reasoning (Haidt 2012). Many theorists have argued that one of the main reasons for the evolution of language was to keep track of the behavior of other individuals (Dunbar 1998) and to improve reasoning (Haidt 2012). However, the controlled process is slow and effortful which may contribute to the automatic process serving as the default process (e.g., Haidt 2001, 2012). Consequently, in order for an individual to change his or her moral judgments, he or she must develop new moral intuitions (e.g., Haidt 2001, 2012).

The Five Moral Intuitions

The Moral Foundations Theory specifies that humans have been equipped by the evolutionary process with a set of automatic moral intuitions, but these moral intuitions are malleable and can be altered by social and cultural influences (Haidt

2012). Haidt and Graham (2007) argued that there are five basic moral foundations: Harm/Care, Fairness/Reciprocity, Ingroup/Loyalty, Authority/Respect, and Purity/Sanctity. The Harm/Care foundation concerns the suffering of others and evolved in order to elicit a caring and sensitive response to help those in need (Haidt 2012). The Fairness/Reciprocity foundation evolved in response to the adaptive threat of being exploited by cheaters and increasing one's chances of receiving benefits of cooperation (Haidt 2012). The Ingroup/Loyalty foundation evolved in order to maintain group cohesion by making an individual aware of others that want to hurt or ostracize members of the group (Haidt 2012). The Authority/Respect foundation evolved in response to maintaining and respecting social hierarchies – this foundation makes us aware of any potential threats to one's status or rank (Haidt 2012). Lastly, the Purity/Sanctity foundation evolved in response to the danger of pathogens and parasites – this foundation includes the behavioral immune system, which makes individuals aware of any potential threats to symbolic objects or values (Haidt 2012).

These five moral foundations can be separated into two higher-order factors that are referred to as *individualizing* (i.e., Harm/Care and Fairness/Reciprocity foundations) and *binding* values (i.e., Ingroup/Loyalty, Authority/Respect, and Purity/Sanctity foundations). Past research has shown that political ideology is associated with certain moral values that people adopt (Haidt and Graham 2007). For example, liberals have been found to be more concerned with individualizing foundations, whereas conservatives are more likely to adopt binding foundations. In addition, pathological personality features (e.g., antagonism) have been found to be negatively associated with specific moral values (e.g., individualizing values; Noser et al. 2015). Taken together, there are important individual differences that may further explain moral intuition and reasoning.

Conclusion

Morality plays a vital role in the social lives of individuals and is crucial for the functioning of

society. Morality has its origins in innate beliefs but the moral system is complex and it can be cultivated depending on social and cultural contexts. Moral Foundations Theory provides a framework for considering evolved moral intuitions, but future research may benefit from considering the possibility that other moral foundations exist. In addition, more research is needed that goes beyond self-report to capture actual behaviors in situations that involve moral judgments.

Cross-References

- ▶ [Evolved Moral Foundations](#)
- ▶ [Function of Morality \(Haidt\)](#)
- ▶ [Jonathan Haidt's The Righteous Mind](#)
- ▶ [Mismatch Between Evolved Morality and Modern World](#)
- ▶ [Moral Concerns](#)
- ▶ [Moral Development](#)
- ▶ [Moral Emotions](#)
- ▶ [Moral Instincts](#)
- ▶ [Moral Instincts and Morality](#)
- ▶ [Moral Language Regulation](#)
- ▶ [Morality](#)
- ▶ [Morality is Cooperation](#)
- ▶ [Philosophical Foundations for a Modern Morality](#)
- ▶ [Relevance of Evolved Interests to Modern Morality](#)
- ▶ [Robert Kurzban on Group Processes](#)
- ▶ [Science and Morality](#)
- ▶ [Theory of Moral Development](#)

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Evolution of Music

- ▶ [Evolutionary Musicology](#)

Evolution of Play

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Synonyms

[Adaptive play behavior](#); [Phylogeny of play behavior](#); [Play as adaptation](#)

Definition

Play behavior can be studied as an adaptation evolved to develop motor and problem-solving skills, assess one's own capabilities in relation to one's environment, and learn how to interact and perhaps cooperate with social partners; play can also be considered phylogenetically as a trait that has evolved divergently, convergently, and in parallel.

Introduction

Play behavior can be observed across much of the animal kingdom, especially in the mammalian lineages. The prevalence of play suggests that play behavior could be a behavior that has evolved to be adaptive, but developing and testing hypotheses to explain its origins has proved challenging. Understanding play behavior from an evolutionary perspective requires that play be clearly defined, that we have clear hypotheses explaining the relative costs and benefits of play, and that these adaptive hypotheses can be tested through direct or indirect observation. This entry explores how ethologists have observed and defined play in a variety of animal species (including humans) and how play has been explained from an evolutionary perspective. The evolution of play has been investigated through the methods of ethology and phylogenetics, both of which will be reviewed here. As the most playful species on the planet, humans have much to learn from studying both human and nonhuman play from an evolutionary perspective.

Why Play?

Why did play behavior evolve? It is tempting to assume that play emerged because it immediately provided benefits. But play is most likely to have emerged as a by-product of other adaptive behavioral processes, a by-product that would eventually be co-opted to serve new functions (Pellis et al. 2015). That play probably evolved via circuitous evolutionary routes makes it all the more difficult to ascertain whether our questions should be about how play emerged (What were the original processes that led to the appearance of play behavior?) or why play persisted (What functional value might allow a by-product to evolve into a benefit?).

Although it is possible that some of the play behaviors we observe today are still a by-product of other adaptive behaviors, many forms of play may persist because they are adaptive. By definition, a behavior is an adaptation if it increases an individual's chances of surviving and reproducing

relative to alternative behavioral options. Playing sometimes seems like a waste of time, or inordinately risky, because play behaviors don't always provide immediate benefits: play is frivolous, a luxury. How might play increase the overall prospects for survival and reproduction? What benefits offset the costs of play, and when/how do these benefits appear? How have organisms evolved to respond to particular environmental conditions by playing? How is play related to development and the attainment of reproductive maturity? Why are some species prolific players, while others do not play at all? Understanding play from a Darwinian perspective requires that we address these questions.

Costs of play: Play is a behavior with clear potential costs. There could be an opportunity cost associated with play behavior, as it sometimes produces no immediate benefits: time spent playing could be spent resting, searching for a mate, or finding resources. Many forms of play are physically demanding and therefore come with an energetic cost. Because play is immersive and often occurs in open spaces, it can leave individuals more exposed to predators. Many forms of play involve risk-taking, making injury a potential cost as well. The fact that there are so many measurable risks of play behavior makes it all the more important to establish what benefits might have driven the evolution of play.

Play as an evolutionary paradox: Play is an apparent paradox because sometimes it appears, on first assessment, to be a wasteful behavior. Why would an animal expend energy, exclude itself from more immediately productive activities, and expose itself to increased risk if playing provides no direct or immediate benefits? So long as the benefits of play remain unquantified, play appears to be an evolutionary paradox. This paradox can be resolved if play behaviors lead to indirect or delayed benefits that are large enough to offset the immediate costs of playing. Since many forms of play have little immediate function, it is important that potential benefits be measured after play has occurred; how long it takes for these benefits to be manifested depends on the life history of the animal as well as the kind of play that that animal engages in.

Benefits of play: Numerous benefits of play have been suggested, but most fit into one of seven broad categories. Play can be used to:

1. Contend with negative cognitive processes
2. Develop motor skills
3. Train for the unexpected
4. Assess one's own physical and cognitive capabilities
5. Assess the reliability and capabilities of potential social partners
6. Learn social norms
7. Foster social cohesion

Play may simply be a way for animals to reduce anxiety or to escape boredom, suggesting that during lower-stress intervals play may help animals contend with evolved cognitive processes that are more geared to the most rigorous elements of their environment. Some animal species maintain plastic neurological systems that allow for the development of motor skills through the practice that play can provide; such developmental employment of play is particularly common in juveniles. Whereas developing motor skills involves training for normal or expected behavioral responses; it is also possible that the spontaneous and uncontrolled nature of play may train animals to respond to unexpected environmental conditions. Play may be a means by which animals can assess their own capabilities in relation to prey, competitors, or predators; such assessment may enable animals to manage the behavioral balance between risk and reward in varying environments. Play may also be a means of assessing the capabilities of potential social partners; such assessment is crucial for animals which choose to work cooperatively with particular members of their social group. For species whose survival depends on social interactions, play can be a means by which young animals learn the norms that govern those interactions. And in species where social cooperation is important, play can be a means by which individuals form the bonds that create a cohesive social group.

While each of these potential benefits is distinct from the others, particular forms of play can provide more than just one of these benefits. An

animal batting around an inanimate object may be both developing better predatory motor skills and gaining an understanding of what sorts of prey it is capable of actually catching. Play-fighting may develop motor skills (for example, to escape predators) but in addition may allow individuals to assess the capabilities of their social partners and create the social cohesion necessary to foster social cooperation.

It is relatively easy to observe play behavior and hypothesize various benefits it might provide, but testing these hypotheses by observing the increases in fitness they predict is more challenging (Burghardt 2005). Studies of horses (Cameron et al. 2008) and bears (Fagen and Fagen 2004) have demonstrated that the degree to which animals play as juveniles positively correlates with their prospects for survival to adulthood. Juvenile Belding's ground squirrels that played more often scored higher on tests of motor skills (Nunes et al. 2004). Playing as juveniles increased the resiliency of elephant calves and increased their probability of surviving as adults (Lee and Moss 2014). A study of captive mink showed that increased rough-and-tumble play correlated with optimal adult sexual behaviors in both males and females (Dallaire and Mason 2017). Perhaps the most extensive studies of the benefits of play behavior have been carried out in rats, where play deprivation has been shown to be associated with social impairments, cognitive deficits, and increased anxiety-like behaviors (Vanderschuren and Trezza 2014). Further study is required to causally link play behavior to one or more of the benefits outlined above and ultimately to increased probabilities of survival and reproduction. When they are rigorously assessed, play benefits are often found to be lacking where they were hypothetically imagined, further reinforcing the need to empirically test adaptive hypotheses.

When play should evolve: Evolutionary theory suggests that play behavior should persist when the benefits of that behavior exceed its costs, with both costs and benefits measured as changes in the probability of surviving and reproducing. The benefits and costs of play may vary in different environments. In particular, resources may play a role in modulating costs

and/or benefits: in a resource-rich environment, the opportunity costs of playing may be reduced, while the potential benefits of playing may increase. For this reason, animal parents may invest in their offspring in ways that optimize the cost-benefit ratio of play (Cameron et al. 2008), allowing play to evolve as a critical component of normal physical and social development.

Hypotheses explaining why play evolves: The potential functional benefits of play imply hypotheses about why play has evolved in various species; nonfunctional hypotheses are also potentially important, especially if play behaviors represent a by-product of other adaptive traits. Spinka et al. (2001) considered their own hypothesis (*training for the unexpected*) alongside three other functional explanations (*motor training*, *self-assessment*, and *surplus energy*) and one by-product explanation (*surplus resources*). They then created a framework for comparing the relative support for each hypothesis by delineating 24 predictions that created strong contrasts between each hypothesis. Interestingly, their framework of comparison did not explicitly address some of the hypothesized social benefits of play (although if conceived broadly, “training for the unexpected” can produce benefits that relate to social norms and cohesion).

Testing the predictions made by different hypotheses: Understanding how play evolved requires that alternative hypotheses make clear predictions and that these predictions be testable. Hypotheses explaining the evolution of play can be applied to specific play behaviors in particular species or to play behavior across the animal kingdom (e.g., Spinka et al. 2001), although the diverse nature of play makes it unlikely that a single hypothesis will explain all instances of play behavior (Burghardt 2014). Even within a particular species, more than one hypothesis may be required to explain the full breadth of play behavior; for example, Sommerville et al. (2017) reviewed the literature on play behavior in domesticated dogs and discovered strong support for the predictions of both the *motor skills development* and *social cohesion* hypotheses. In considering why adult dogs play, Bradshaw et al. (2015) reached a similar conclusion and suggested that

different forms of dog play behavior may actually have independent evolutionary origins.

The prospect of studying play from an adaptive perspective is exciting, as doing so could resolve the apparently paradoxical nature of play. Play can have an ultimate function, even if it seems frivolous at the time. But in order to study play behavior scientifically, we need a clear definition of what kinds of behaviors constitute play. We can roughly identify play by its characteristics: it is fun, it is done for its own sake, and it is done in times and places that feel safe. But actually distinguishing play from non-play behaviors is not so simple and has presented a challenge to scientists who study play.

Defining Play (Is Not So Easy)

What is play? As an extremely playful species, humans ought to be able to identify play when we see it. But play turns out to be very difficult to precisely define. One reason that play can be difficult to identify is that it takes many forms and can serve many functions, making it a “heterogeneous” behavior requiring a fairly broad definition. Play behavior itself is often separated temporally and spatially from the benefits it can provide, making it more difficult to determine whether an observed behavior should be called “play.” Play behaviors are often defined by an affective state (“having fun”) which itself is difficult to define (or directly observe). That humans are as a species so playful also complicates our ability to determine what defines play; our tendency to anthropomorphize the behavior of other animals may produce definitions of play that are too inclusive, whereas our tendency to take a very anthropocentric view of our own behaviors can produce definitions of play that are too exclusive. For play to be studied scientifically, a clear definition is required.

Many (conflicting) definitions: Play has been a subject of serious study for well over a century, but researchers examining play have failed to come to consensus on a definition of what constitutes play (Burghardt 2005). There is disagreement over whether play is productive or a waste

of time, whether it is pro-social or antisocial, and whether it is safe or dangerous. Some researchers argue that play is not definable and therefore beyond scientific study, whereas others seek to define play as a behavior that can be studied from a Darwinian perspective.

Some of the conflict over how (and whether) to define play emerges from the different approaches of the ethological and psychological sciences. Whereas ethologists rely on clear behavioral distinctions that do not require knowledge of the internal state of the animal performing that behavior, psychological definitions may emphasize the private experience that underlies behavior (Brown 2009).

Burghardt's five criteria: To mitigate some of the confusion over what constitutes play and to advance the study of play from an evolutionary perspective, Burghardt (2005) advanced five criteria to define play behavior. These criteria are briefly summarized as:

1. Limited immediate function
2. Endogenous component
3. Structural or temporal difference
4. Repeated performance
5. Relaxed field

That play behaviors have *limited immediate function* hinges on the idea that the evolved benefits of play are indirect or delayed; although not all behaviors that fail to produce immediate benefits should be considered play, the absence of clear immediate benefits sets up the possibility that a behavior could produce delayed benefits. Behaviors with an *endogenous component* are performed in a manner that is not simply a response to external stimuli; Burghardt defines these behaviors as "spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic." To display *structural or temporal difference*, a play behavior must differ in some manner from other behaviors that serve a more direct functional purpose; many play behaviors are performed partially, in an exaggerated form, or in different times and places than analogous non-play behaviors. *Repeated performance* implies that during some point in the development of an animal, a particular behavior is practiced, often in

a progressively varying manner. Finally, play behaviors are performed in a *relaxed field*, which is to say that animals only play when they are healthy, their basic needs are met, and they are free from intense stress or competing motivational processes. A key aspect of Burghardt's five criteria is that they are interactive: while no single criterion sufficiently filters play from non-play behaviors, applying all five criteria can produce a relatively clear distinction.

Categories of play: Ethologists who study play have conceptualized three main categories of play behavior. *Locomotor-rotational play* includes various forms of body movements performed independently by individual animals. *Object play* involves the manipulation of objects found in the environment. *Social play* occurs when two or more animals interact as part of the play behavior.

These categories of play are not mutually exclusive: in fact, it is possible to imagine all three co-occurring in particular contexts. For example, wild bottlenose dolphins have been observed numerous times surfing waves into the shore, usually independent of feeding or any other behavior with direct function (Paulos et al. 2010). Surfing by dolphins is definitely a form of locomotor-rotational play because it requires that dolphins practice body movements that produce the ability to ride the wave. It could also be a form of object play where the wave itself is the object that is played with. And if dolphins surf together, having to maintain safe distance to avoid collisions with groupmates, then surfing could also be a form of social play.

Many forms of human play also simultaneously encompass all three forms of play. Consider a group of people at the park throwing around a flying plastic disc. This play is most obviously object play, as the players must learn how to throw and catch the disc. But learning how to play with the flying disc also involves locomotor-rotational play, especially in catching errant throws from less experienced players. And as with any game of "catch," playing with a flying disc is an inherently social activity that requires players to empathize with and anticipate the needs of their playmates.

Levels of play: A number of play researchers have suggested that play should be considered along a continuum of hierarchical levels. These include Robert Fagen's five levels of play, which emphasize the complexity of social interaction involved in play, and Robert Mitchell's four levels, which emphasize the degree of simulation and intent involved in a particular form of play (Burghardt 2005). Both of these classification schemes recognize that solitary play differs from play that is done in parallel or direct interaction with other individuals and consider social play to be more sophisticated than solitary play.

Particularly human extensions of animal play: The diversity of human play presents particular challenges to any categorization scheme. In addition to engaging in play behaviors that can be classified as locomotor-rotational, object, or social, humans also engage in forms of play that involve creative exploration, mental simulation, and complex roles. Some of these behaviors differ from other animals in extent, but others appear to differ in kind. It has been argued that many animals maintain rules of play (Bekoff and Pierce 2009), but no other animals play employing the complex rule sets of organized sports or strategy games. While it may be impossible to fully ascertain the degree to which other animals perform mental simulations and pretend, the unique complexity human language and – more recently – audio and visual technologies creates the potential for unrivaled levels of play that emerges predominantly within our brains. Play is a major source of innovation (Bateson 2014), and it is innovation that drives the human species' unique form of cumulative culture. To more fully encompass the diversity of human play forms, many researchers employ additional categories such as “free,” “creative,” “narrative,” and “reenactment” (Dallaire et al. 2017).

Differentiating play from other functional and dysfunctional behaviors: A number of common animal behaviors should not be considered play despite sharing some of the characteristics that typify play. Humans often associate being playful with exploration and pursuits that satisfy our curiosity. While exploratory behaviors motivated by curiosity can be forms of play, it is

important to recognize that many forms of exploration more closely resemble stalking or vigilance behaviors (Burghardt 2005). An animal may intensely examine a new enclosure or novel environment, but such an examination could simply provide valuable information about where to find resources or where to avoid exposure to aggression or predation. For exploration to constitute play, it must be repeated in some manner and occur in a low-stress environment.

Animals sometimes display behaviors that are maladaptive rather than adaptive and therefore do not constitute play. For this reason, stereotypies such as continual pacing and excessive grooming should not be considered a form of play. That such dysfunctional behaviors have almost exclusively been observed in the radically different environments created by captivity suggests that perhaps stereotypies could result from a mismatch between evolved play responses and the unnatural environments created for other animals by humans.

Four perspectives on play behavior: As with all forms of animal behavior, it can be useful to consider play behavior from Tinbergen's four perspectives. The first perspective considers the *proximal cause of the behavior* and requires that we examine both the role of external stimuli and internal neural states in prompting play behavior. Internal proximal causes of play such as “having fun” are assumed to be the product of evolution and imply that play is an adaptive behavior, but simply looking at the proximal cause of a behavior cannot illuminate how or why it may have evolved. The second perspective considers the life history of play (development of behavior throughout an individual's lifespan) and can be highly relevant to considerations of how juvenile play can produce adult benefits. The third perspective is perhaps the most crucial to adaptive studies of play, as it seeks to understand the function of behavior. That play behaviors produce benefits that are indirect or delayed makes accurately assessing their function more difficult but also crucial to differentiating play from non-functional or dysfunctional behaviors. The fourth and final perspective addresses how a particular form of play evolved and can range from

considering play as an exaptation of ancestral behaviors to putting particular forms of play in a phylogenetic context.

Evolution of Play in Nonhuman Animals

Although animals that play are relatively rare in all but a few taxonomic groups (such as primates, canids, cetaceans, parrots, and corvids), a diversity of play behavior has been observed across an intriguingly broad spectrum of animals. All three of the major forms of play (locomotor-rotational, object, and social) are prevalent among those species that display play behavior; what is less clear is the degree to which nonhuman animals engage in various forms of play that require mental simulation (e.g., pretending, imagining, creative planning). Considering the diversity of play in animals can shed light on both the functional origins of play and the evolutionary processes that yielded species that play.

Examples of animal play: The sheer number of different kinds of play behavior that have been observed in animals highlights both the importance and heterogeneous nature of play. Although relatively few invertebrates play, a few notable exceptions are worth mentioning. Spiders of the species *Anelosimus studiosus* engage in non-conceptive “sexual play” that enhances the fitness of both male and female players (Pruitt et al. 2012). Among invertebrates, octopuses are the champion players, the subject of many anecdotal accounts of playful behavior in the wild. Captive studies have shown that when provided with objects constructed from Lego toys, most octopuses of the species *Octopus vulgaris* will play with the objects (Kuba et al. 2006). Many ethologists have been skeptical that invertebrates can display play behavior, but in both of these cases, the observed behavior met all five of Burghardt’s play criteria, showing the value of employing objective play criteria to separate our anthropomorphic biases from our interpretation of behavioral observations.

Although birds and mammals are the most prolific animal players, other vertebrate lineages also display play behaviors. Cichlid fish have been observed to push around weighted

thermometers in aquarium environments (Burghardt 2014). Many species of fish repeatedly leap over each other and also will bat around floating balls left in their enclosures (Burghardt 2005). Fagen (2017) has suggested that particular forms of salmon jumping should be considered play. Poison dart frogs engage in rough-and-tumble play, and tadpoles have been observed to ride the bubbles produced by aquarium aerators.

Play has also been observed in reptiles. Dinets (2015) reports that crocodilian species engage in locomotor play (mostly associated with riding currents or waves), object play (involving streams of water or floating objects), and even social play (giving each other rides, rough-and-tumble play with other species). Komodo dragons engage in object play that is reminiscent of domesticated dogs (Burghardt 2005). Some species of aquatic turtles will play in captivity with floating objects and engage in tug-of-war bouts with their keepers (Burghardt 2005).

Many bird species engage in either locomotor, object, or social play with some orders (woodpeckers, parrots, songbirds, and raptors/pelicans) displaying all three kinds of play (Burghardt 2005). Many predatory birds engage in the playful dropping and recatching of objects in midair. Aerial play is also common in birds, which will ride currents of air and perform acrobatics independent of any attempt to catch prey, avoid predators, or defend territory. Many birds play with various useless objects, which may aid in the development of later functional tool use and/or caching behavior. Social play is less common among birds, but two taxa – the parrots and the corvids – play together. Parrot species, which live in groups, initiate play-chases and play-fights (Diamond and Bond 2003). Ravens engage in social object play in which two individuals will play tug-of-war over a stick (Heinrich and Smolker in Bekoff and Byers 1998). Corvids and parrots possess a highly encephalized brain in comparison to other bird orders, suggesting a parallel with the most playful mammal species (Osvath et al. 2014). The playful nature of these species may also explain their exceptional ability to solve problems in both natural and laboratory settings (Bateson 2014).

Mammalian play is diverse, commonplace, and relatively well-studied. Marsupials play with locomotor and social play being more common than object play. Kangaroos and wallabies engage in all three forms of play, including play-fighting, manipulation of found objects, and rapid-motion locomotor play (Watson in Bekoff and Byers 1998).

Play is even more common among the placental mammals. Pronghorn males join sparring matches that simulate actual fighting but mitigate the risks of real aggression (Miller and Byers in Bekoff and Byers 1998). Both wild and domesticated horses play as juveniles, running alone or in groups and sparring with others in their band (Cameron et al. 2008). Elephants play as juveniles and adults, both alone (manipulating objects, mud, dust, or water with tusks, trunk, mouth, or feet or running/spinning/rocking/kicking) and socially (wrestling, sparring) (Lee and Moss 2014). Bears will wrestle and chase each other, manipulate objects, and play through locomotion and body rotation (Fagen and Fagen 2004). Mustelids are highly playful, primarily engaging in juvenile rough-and-tumble play that is crucial to the development of normal social behavior (Dallaire and Mason 2017).

As a marine mammal taxon, cetaceans demonstrate the great potential for play in aquatic environments (Paulos et al. 2010). Whale and dolphin locomotor-rotational play includes erratic swimming, aerial leaps/breaches/flips, intentional self-stranding, and surfing on waves. Object play is also common in both the wild and in captivity: bowhead whales play with floating logs, various dolphins play with bubbles they create a variety of cetaceans play with both natural and human-made found objects, and orcas and a few other dolphin species have been observed playing with prey items. Cetacean social play in the water resembles social play in terrestrial mammals: young whales and dolphins are especially fond of chasing and bumping each other and performing aerial behaviors in synchrony. Another fascinating aspect of dolphin play is how often it includes other species, including birds, sea turtles, other cetaceans, and sea lions (Kuczaj and Eskelinen 2014).

The prominent role of play behavior in the development of primates has been appreciated

for longer than in any other taxonomic group. This appreciation likely emerges from both how playful primates are and a certain degree of anthropomorphic interpretation of play behavior in other species. Every species of primate whose behavior has been marginally observed displays at least one type of play behavior (Burghardt 2005). The play of chimps and bonobos – our closest primate relatives – is of particular interest. Both chimps and bonobos engage in locomotor-rotational and object play, but social play is the most commonly observed form of play. Juvenile social play is similar in both species, but there is a marked difference in frequency and type of adult play: bonobo adults play more, perhaps because their social structures require more of the kind of social grooming and bonding that regular play can provide (Palagi 2006). Some forms of bonobo play involve remarkable forms of risk and trust. Bonobos play the “ball game,” a form of chase in which a male “leader” trusts his play partner to gently grasp his testicles while both circle around a tree or bush. Bonobos also play trust games such as the “hang game,” in which one individual swings another by the arm from an elevated tree branch.

Rodents also play, although the distribution of rodent play is quite heterogeneous. Those rodents who do play tend to be social, and social play is the most commonly observed form of rodent play. Prairie dog adults facilitate social play with juveniles, and beavers “dance” together in their aquatic environment (Burghardt 2005). Rough-and-tumble social play is prominent in rat development, as juvenile rats attempt to gently bite their play partner on the neck, while that partner employs a variety of defensive tactics (Pellis and Iwaniuk 1999).

All canid species also play. Domesticated dogs are well-studied and represent an interesting case because they maintain strong social bonds with other dogs and with humans (Bekoff and Pierce 2009). The coevolution of humans and dogs may explain why domesticated dogs play more than their wild relatives: humans appear to have selected for neotenuous traits that may extend juvenile behaviors into adulthood (Bradshaw et al. 2015). Dogs will run, jump, and manipulate

objects in solitary play but are more likely to engage in a diversity of social play. Dogs play together through games of chase, play-fights, and mock sexual mounting (often in sex-reversed configurations). Dogs also enjoy social object play: “fetch” and “tug-of-war” are commonly played with humans, and dogs show increased interest in objects that other dogs or humans are manipulating (Bradshaw et al. 2015). The dog’s enthusiasm for social object play has been exploited by breeders to create “sporting dogs” that will retrieve the quarry of human hunters (Sommerville et al. 2017).

Rules of the game: Social play is common among mammals, but there is some debate as to whether there are any universal features of mammalian social play. Animals playing socially may employ “play signals” that help their partners to differentiate between play and aggression. Bekoff and Pierce (2009) have suggested that these signals are part of a larger system of social rules that represent a definable animal morality. For example, individuals from various canid species appear to observe the following rules:

1. Signal that you want to play
2. Employ real skills, but keep them in check
3. Reverse roles
4. Self-handicap
5. Apologize if you break the rules
6. Forgive rare transgressions

Individuals who consistently break these rules are more likely to be socially ostracized, suggesting that canid play exists at least in part as a means of assessing potential social partners. Bekoff and Pierce (2009) emphasize that the rules of what’s allowed in play may vary from species to species but that these general rules for playing are shared among many species that play socially.

Who plays, and when?: Although there is increased appreciation and understanding of play behavior that occurs in adulthood, the vast majority of animal play occurs in juveniles (Burghardt 2014), a fact that strengthens the connection between development and play. Although there

are no universal rules governing which sex plays or how, numerous studies have shown that sex matters in how individuals play; some studies have even demonstrated the different benefits that each sex realizes from playing (e.g., Dallaire and Mason 2017). In general, larger-brained mammal species tend to display more complex play behavior, although this correlation is stronger at higher taxonomic levels of comparison and may not distinguish more playful from less playful species within a clade (Iwaniuk et al. 2001).

Divergent, parallel, and convergent evolution of play: There are a great number of play behaviors across the animal kingdom that resembles each other in form, often sharing a common discernable function. How did evolutionary processes produce these similar behaviors? One possibility is that a common ancestor evolved a particular play behavior, passing this behavior along to the many species that have since evolved. While this divergent explanation for animal play may apply to the very recent evolution of particular play behaviors in fine-scale taxonomic groups; it is clear that divergent evolution cannot explain the heterogeneous distribution of play behaviors across the tree of life. That the most prolific animal players are corvids, parrots, great apes, and dolphins demonstrates that some combination of convergent and parallel evolution must be responsible for the diversity of play we can observe (Osvath et al. 2014).

Distinguishing parallel from convergent evolution is difficult in general and may be particularly difficult for the various forms of play behavior. Parallel evolution suggests that evolved characteristics in a common ancestor served as a precursor trait that was subsequently similarly modified to produce similar play behaviors. Sociability may serve as such a precursor in many species, with social play evolving independently in related lineages but based upon shared foundational social interactions. The alternative is that play evolved convergently, with play behaviors evolving completely independent of each other, presumably due to similar environmental demands. Because play behaviors do not fossilize, it is very difficult to find evidence to untangle the

subtle differences in pattern produced by convergent and parallel evolution (Burghardt 2005).

Phylogenies of play: One way to determine how play has evolved is to place different kinds of play behaviors on the tree of life, looking for patterns that would be indicative of convergent, parallel, or divergent evolution. Where play is less common, the power of convergent evolution to independently produce play behavior in disparate lineages is clear. If spiders and octopuses are the only invertebrates yet known to play, it is highly unlikely that these behaviors were inherited from a common ancestor (divergent evolution) or even emerged from the independent modification of traits inherited from a common ancestor (parallel evolution). Interestingly, in birds it also appears that the two major taxa that are the most prolific social players – corvids and parrots – are most likely to have independently evolved their similar forms of social play, as both have many closer relatives that do not play socially (Diamond and Bond 2003).

While octopuses, corvids, and parrots may have each evolved play independently *as lineages*, play is common among species within each of these clades, suggesting that divergent evolution may explain the distribution of play at lower taxonomic levels. The most compelling case for divergent evolution of play occurs in particular mammal lineages. All primate species and all canid species play, suggesting that the common ancestor of each of these clades displayed some form of play behavior. Play is also sufficiently common among placental mammals (Burghardt 2005) that it is reasonable to surmise that the common ancestor of all mammals may have displayed play behavior, although the finding that brain size correlates more strongly with play between rather than within clades suggests a role for parallel evolution of mammalian play (Iwaniuk et al. 2001). A study of play among the muroid rodents revealed that neither divergent nor convergent evolution provided a satisfactory explanation of the heterogeneous level of play among species in the clade, suggesting a role for parallel evolution of play or loss of play by some species in the clade (Pellis and Iwaniuk 1999).

Evolution of Play in Humans

Our interest in the play of other animals likely stems from our desire to understand our own very playful nature. Human play has many products that can be readily observed in both small-scale and large-scale societies. Musical play and dance is a nearly ubiquitous feature of human societies. Every culture has its own kinds of games and sports. Word play, jokes, and other creative uses of language suggest that words aren't just for functional communication. While art may be a very serious business in particular segments of many human societies, our drive to playfully create appears to be as ancient as the cave paintings of Chauvet or Maros.

Play in human juveniles: Children are prolific players. The incredible diversity of what constitutes a “toy” (and the broad range of target ages for toy designs) underscores the importance of object play to young humans, but kids are also highly adept at turning all manner of found items into play objects. Locomotor-rotational play emerges within the first year of life and is a whole-body experience: infants move their limbs, use their hands to grasp, and explore with their mouths. Playground equipment is designed to meet the play demands of older children for climbing, sliding, swinging by their arms, and moving rhythmically. Children also demonstrate from an early age the importance of mental play to humans, eventually becoming immersed in a world of imaginative play that can be – from their perspective – indistinguishable from experienced reality.

What makes locomotor-rotational, object, and imaginative play in human children all the more fascinating is how often these forms of play are also social. Children love to play games with both adults and other children that involve chasing and mimicking movement. All manner of objects are used to play with others. And imaginative play frequently involves the creation of fantasy worlds and detailed role-play with other children.

Another form of social play in human juveniles is rough-and-tumble play. As with forms of rough-and-tumble play displayed by other

animals, children will initiate bouts of vigorous but also restrained hitting, pushing, and wrestling, with larger children self-handicapping to maintain a playful interaction. Many studies have demonstrated the gendered nature of this sort of play: boys are far more likely than girls to engage in rough-and-tumble play. While many have suggested that these differences emerge from sex differences in hormonal expression, it is very difficult to separate out the effects of cultural expectations on the relative prevalence of rough-and-tumble play in girls and boys. Future work is needed to assess how gender expectations and biological sex interact developmentally to produce rough-and-tumble play.

All of the forms of juvenile play outlined above can be performed voluntarily and spontaneously; that is to say children are avid devotees of “free play.” But adults also create “structured play” opportunities for juveniles in the form of sports, games (including those hosted on digital devices), and educational activities. Understanding how self- and other-directed forms play differ in their pattern, purpose, and product would further illuminate the role of play in child development, an especially important area of research for societies in which structured play is rapidly displacing opportunities for free play.

Developmental role of play: Play is an essential component of normal human development. Children are playful from an early age; some have suggested that the rolling, punching, and kicking that occur in utero are the first forms of play to emerge (Brown 2009). A few months following birth, human infants begin a process called attunement, an interactive form of play that both strengthens the parent-offspring bond and builds cognitive skills. In their first year, infants also engage in a wide variety of locomotor-rotational play, allowing them to develop the physical coordination, strength, and balance required to begin walking upright. Objects also play an important role in early childhood, as manipulating various components of the encountered environment fosters understanding of physical properties.

A major transition from infancy into early and middle childhood occurs when children move

from playing strictly with adults or older children to playing socially with their peers. While locomotor play and object play still allow for development of physical aptitudes and understanding, childhood shifts dramatically toward fostering an understanding of how to interact with other individuals. Children’s social play can be seen as a way of building two fundamental understandings, a general awareness of how other humans respond emotionally to various kinds of interactions and a more specific awareness of the cultural rules that govern their particular society. The cultures in which children develop vary dramatically, but the role of social play in familiarizing children with the norms of those cultures is invariant.

Adolescence is a period of development with radically different meaning in different human societies. In some societies – particularly smaller-scale subsistence societies – adolescence may be a time in which children assume adult roles (this is especially true of girls). In large-scale societies that require huge amounts of learning in order to attain sociocultural maturity, functional adolescence may extend well beyond the attainment of physical and reproductive maturity. While adolescence varies in timing and duration, it does have some common features across cultures. There are shifts in social play from modes that emphasize group dynamics (such as friendship alliances) to modes that emphasize courting and mating behaviors. It could be argued that where “dating” behavior occurs, adolescents are essentially playing at mate selection and pair bonding in preparation for adulthood. Another key aspect of play in adolescent development relates to experimentation with ideas outside of the family: adolescents become open to new and foreign experiences that have the potential to dramatically broaden their cultural repertoire.

Humans maintain juvenile characteristics for a very large fraction of our overall lifetime. Long periods of childhood and adolescence allow for the advanced development of a variety of physical skills (such as throwing, chasing, running, and fighting) that may have been crucial to the survival of our ancestors. This extended maturation process also increases our ability to learn culturally and may account for our success not only

relative to other primates but also relative to other (now-extinct) hominin species (Nowell 2016). Play is a very effective means by which the long developmental period of human juveniles can be leveraged to maximize behavioral plasticity in relation to a variable environment (Pellegrini 2009).

Play in human adults: The degree to which human adults play is a matter of some debate, as many forms of adult play behavior are intertwined with rigid rules, competition, and social/sexual signaling. Still, some have argued that adult play is a key expression of personality (Brown 2009). Humans are a species capable of lifelong learning, which means that some forms of play could continue to serve the same developmental roles that dominate childhood and adolescence. The role of play in adult tinkering, experimenting, and discovery is well-studied (Bateson 2014), but other play-like behaviors displayed by adults merit further investigation aimed at determining if adults frequently use play in ways that are analogous to the play of children and adolescents.

Many functional roles of human play: Play behavior serves many functional roles in humans. Some of these functions are directly analogous to the functional roles of play in other animals. A young child climbing on a playground structure is developing locomotor skills and potentially training for the unexpected. Humans playing around with tools to make things or trying out various sports are assessing their physical and cognitive capabilities. Forms of social play ranging from dancing to board games to competitive sports all open up the opportunity to assess the reliability and capabilities of potential social partners. A child playing by the rules of a recess kickball game is learning both social norms for fair play and how to cooperate with classmates.

Clearly there is a continuum between the play of other animals and human play, but the functional role of play in humans appears to be different in both extent and kind. Self-assessment provides one example of an “extended function” of human play. Whereas other animals may use self-assessment to determine what prey are profitable to pursue or to what degree they stand a chance in direct forms of sexual competition,

humans actually use play to self-assess and decide what skills to work on for a lifetime. This decision may not be conscious: we find playing at things that bring us success to be more rewarding, which means that we are more likely to pursue and practice those activities which we experience as “fun.” Studies have demonstrated the level of mastery that can emerge from this kind of autotelic play behavior. For example, rugby players are dramatically better at distinguishing between deceptive and honest body movement signals.

The extent of human social play also exceeds that of other animals. This extension of social play could be a reflection of the degree to which humans rely on cooperation with nonrelatives. Other animals may use play to choose allies from within a small social group, but human play forms such as joking, dancing, game playing, sports, and playful conversation are used to create an extensive network of friends that engage in mutual aid. Play’s potential to foster social cohesion may have reached its apex in humans.

Another clear extension of human play relates to when humans play throughout their life histories. While juveniles may play differently than adults, humans tend to play in multiple ways throughout their lives. Play can be used to develop new skills at any age, and humans stay motivated to play throughout adulthood and even as they senesce. While physical forms of play may decrease in frequency as humans age, other forms of play – such as language play or creative play – may be maintained or become more frequent. While most play by adults in other animals is directed at juveniles (and thus may be related to “parenting for play”), human adults also engage in extensive play with other adults.

In nonhuman animals and in smaller-scale human societies, play is generally not needed in order to “keep in shape”: the day-to-day activities required to meet basic needs maintain physical fitness. Humans have clearly evolved a “use it or lose it” physiology that adjusts both musculature and cardiopulmonary capacity to whatever level of physical activity has been recently undertaken. In large-scale industrialized societies, meeting basic needs through various economic exchanges often does not require much physical exertion. In

these societies, play has taken on a new role as a means of maintaining physical fitness. While not all forms of human exercise is playful – for most people, running on a treadmill is work! – many forms of play have assumed a role in producing optimal health outcomes.

Perhaps the most distinctive function of play in humans is our use of mental play (Burghardt 2005). Humans have a strong ability to play entirely in our own minds. One such form of play involves simulation of fantasy worlds via mental rehearsal or reenactment, which allows us to both process past events (Dallaire et al. 2017) and to plan and prepare for future events. In this sense, fantasy play is a kind of time travel, allowing us to learn from things that have already happened and to anticipate events that haven't yet happened. Mental play can also be used to come up with new cultural ideas. In humans, imagination and improvisation are closely related to problem-solving and innovation; our creativity relies in large part on our playfulness (Bateson 2014). We like to play with ideas that we have learned from others, tweaking and modifying existing culture in a way that allows for collective innovation through cumulative culture. It is hard to know if other animals engage in mental play, and there are a few other species (such as ravens) that appear to come up with novel solutions to problems via playful behavior. But a consideration of the abundant cultural products of human mental play makes it clear that if we are not the only mental players, we certainly rely on mental play to an unprecedented extent.

One interesting aspect of human play behaviors is that many lead to what would be best categorized as performance. In animals, the difference between play and performance is generally pretty clear: playing at mock-mating happens at a different developmental stage and in a different context than real mating, and there is a distinct behavioral difference between play-fighting and agonistic fighting. But many human behaviors that relate to play blur the line between play behaviors with immediate and delayed functions. A musician may be “playing” music (and certainly a lot of music-making is initially purposeless), but this playing could be a display with the

potential to attract a mate. Is the cultural importance of music the result of selection for playful experimentation or for play as a product of sexual selection? The fluidity of human play makes answering such a question difficult. An athlete may be playing a particular team sport, but this playing could be a display with the potential to cement cooperative relationships with other players once they leave the field of play. The manner in which play is integrated into everyday human life (and not just among children) makes it difficult to distinguish when the potential benefits of human play are manifested.

The Playful Mind: Implications for Human Well-Being

That play could be an adaptive behavior has important implications for human health and well-being. If play is a human adaptation that empowers complex learning, mental preparation, physical fitness, social bonding and cooperation, and discovery and creation, then maintaining access to beneficial opportunities to play is a serious health issue.

Play as a cause and correlate of mental health: There has been a long debate in the animal behavior and psychology literature about whether or not play can be used as either indicative of welfare or as a means to achieving optimal welfare. Many studies have shown that play can improve the welfare of both animals (e.g., Held and Špinka 2011; Bateson 2014) and humans (Landreth 2002). A more subtle question is whether the presence or absence of play behavior can be used to assess welfare. While there is compelling evidence that depression of play activity can be used as an indicator of poor welfare, the opposite is not true: an abundance of play does not necessarily indicate positive mental or physical health (Dallaire et al. 2017). This is particularly true in humans, who may use forms of solitary play, such as reenactment, to deal with trauma. An exciting possibility is that shifts in the mode of play – such as from social to solitary – might be used to diagnose the affective state and overall welfare of human patients.

Zone of proximal development and productive forms of play: Russian psychiatrist and researcher Lev S. Vygotsky was the first to conceptualize the idea of a *zone of proximal development* (ZPD). The ZPD was based on the idea that in order to gain new understandings, a learner must be challenged beyond their current level of competency but not be overwhelmed by a challenge far beyond their capabilities. Play often appears to occur in environments that seem to create a ZPD: we don't enjoy playing in environments that present too few challenges because they are boring, but we also don't enjoy playing in environments that are overly challenging because they are unduly stressful. Vygotsky saw play as the ideal means by which children productively enter the ZPD and orchestrate their own learning. The kind of play that Vygotsky's research demonstrated was key to learning is observed less in children today than those of past generations, suggesting a unique challenge to modern-day educators: how do we restore play as an optimal means for enabling learners to enter their ZPD (Bodrova and Leong 2015)?

Changes in the role of play in large-scale societies: Large-scale, industrialized societies have dramatically changed what we play, how we play, and how much we play at different points in our life histories. If a "relaxed field" is required to stimulate play behavior, industrialized societies certainly increase the abundance of such environments: compared to our ancestors, a much larger fraction of people are free from daily concerns about food availability or personal safety. An overall increase in leisure time also enables many people more time in which to play in this relaxed field. In addition to creating an environment that is conducive to play, large-scale societies tend to require more extensive cultural learning; this requirement for extended and sometimes lifelong learning can functionally extend adolescence (a time of intense play) and make play important throughout adulthood.

Ironically, despite the unprecedented resource availability and safety of our time, certain forms of play appear to be in decline, at least in large-scale/industrial societies. For example, in the latter half of the twentieth century, the time children

spend playing – in particular outdoor play not directed by adults – has dramatically declined. This decline in play is associated with increased levels of anxiety, depression, and narcissism in adolescents and young adults, leading some to suggest that this shift in the abundance and pattern of childhood play is a major mental health issue (Gray 2011). Despite evidence to the contrary, parental perception of dangers external to the home seem to be a major driver of this change in play behavior, marking a major shift in the culture of childhood play.

Other forms of cultural evolution have also dramatically changed how we play. The Internet creates the potential for social interaction that differs from our ancestral social environments in both extent and kind, opening up unprecedented opportunities for social play. Virtual online worlds become not just additional spaces in which to play: they create entirely new play environments. Industrialized societies produce novel objects that foster totally new forms of play (e.g., skateboards, mountain bikes, skis, sailboats, and all manner of balls). Play has also been highly commercialized, opening up the possibility that forms of play behavior may be influenced not just by our evolved propensities to play but also by marketing.

Play has also infiltrated the world of design, where creative industries have strived to harness the power of play to create novel ideas and motivate extraordinary human effort. Companies provide their employees with break spaces that encourage play and try to incorporate play into the way that they address business challenges (Brown 2009). Although an understanding of our playful nature has impacted some workplaces, it would be mistaken to overestimate the extent of this impact: work environments that embrace play represent a tiny fraction of the overall global workplace and tend to exist in the sector of industries that rely on the creation of new products or other forms of novel design.

Play as a privilege: Although many people have been enabled to play more frequently and further into adulthood, this condition is far from universal. Inequities within and between societies create a dynamic in which some people live under

ideal conditions for play and others are deprived of the opportunity to play. This deprivation applies to children as well as adults: kids who are undernourished or have to work are less likely to spend their time playing (Bateson 2014). Acknowledging that play is currently a privilege but is also an evolved developmental need, the United Nations issued a proclamation establishing play and a “universal and inalienable right of childhood” (Landreth 2002).

Mismatch theory and modern play: Human play behaviors evolved in a very different environment than the one that most people experience today. Our play emerged in smaller social groups of hunter-gatherers who interacted with far fewer individuals and far fewer objects (especially human-made cultural objects) during a human lifetime. Thanks to the prolific cultural evolution produced by modern industrialized societies, we now have access to far more objects to play with, environments to navigate, and people with whom to interact. The cultural evolution that creates these new environments dramatically outpaces human genetic evolution, setting up the potential for play behaviors that are “mismatched” to our current environment.

One potential outcome of this mismatch is various forms of play-related addictions. Perhaps the most obvious play addictions are to electronic games, particularly those which combine vivid forms of fantasy play with real-time social interactions with a limitless supply of play partners (Brown 2009). Such addictions may emerge because opportunities for free play are being supplanted by more structured forms of play. Many forms of gambling may also exploit playful human curiosity, leading some people to become compulsive gamblers. Such addictions can, ironically, pull people away from healthy forms of play that are key to maintaining physical and mental health.

Another potential outcome of this mismatch is play that is excessively risky. Again, it is the use of new cultural technologies that may shift normal play behavior into maladaptive territory. Online dating apps may turn normal sexual play into a compulsion. Access to various kinds of motor vehicles produces new and dangerous forms of

locomotor play that can be a major source of mortality among young adults. Certain forms of “new play” enabled by both novel material culture and novel cultural ideas (such as free solo rock climbing, big wave surfing, and BASE wingsuit jumping) attract some people to play under extraordinarily risky conditions.

Understanding how and why humans evolved to play can enable us to better design modern societies – and forms of play within those societies – that create fewer of these pathologies and extreme risks.

Conclusion

Play is a rare but remarkable animal behavior that in some cases is an adaptation to the challenges of a dynamic social and ecological environment. The role of play is most prevalent in juveniles, with many of the benefits of play being manifested through developmental processes, but play can also serve a function in adulthood. While the most complex forms of play are found in the mammalian lineage, the prevalence of play in other animal groups suggests both its broad adaptive utility and the role of play in the success of many lineages of the animal kingdom.

The delayed nature of play benefits, combined with the difficulties of comprehensively observing any complex animal behavior in a natural setting, makes studying play from an evolutionary perspective a challenge. There is still much scientific work to be done to unravel the functions of play in both humans and nonhuman animals and to illuminate how play evolved, but substantial progress has been made over the last two decades. A major innovation in the field has been the positing of clear, distinct hypotheses that make contrasting predictions about what we should observe in animals that display play behavior.

Humans are a particularly playful species, with play behavior enabling much of the learning that occurs during humans’ extended developmental period. The persistence of play well into adulthood suggests that human neurological development continues well past attainment of sexual maturity and that in some ways humans may be

continually developing. Understanding humans as a species that evolved to develop via play can enable us to design better educational systems, improve workplace creativity, and foster better mental and physical health outcomes.

Cross-References

- [Combat Sport](#)
- [Development of Adaptations](#)
- [Dominance in Humans](#)
- [Duration of Childhood](#)
- [Empathy in Rats](#)
- [Evolution of Fighting Assessment Abilities](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Learning Versus Imitation](#)
- [Marc Bekoff](#)
- [Newborn Behavior](#)
- [Peer Socialization](#)
- [Play and Social Learning](#)
- [Play and Tool Use](#)
- [Play Fighting in Boys](#)
- [Proto-tool](#)
- [Sensorimotor Play](#)
- [Social Play](#)
- [Social Withdrawal in Childhood](#)
- [Tool Play](#)

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Evolution of Punishment

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Synonyms

Castigation; Chastisement; Correction; Discipline

Definition

The infliction of a penalty in retribution for an offence.

Introduction

Punishment is a human universal, and it is also found among many social animals. It applies to all social relationships but may take on different forms and fulfill different functions depending on whether it is applied to children, inferiors, or peers, for example. Here, we consider the adaptive value of punishment, and why specific kinds of punishment may have evolved.

Competing theories attempt to explain the cross-cultural propensity to punish. Punishment may confer reduced fitness, such as when the punishment reduces the social status, or the somatic health of the recipient, such that it negatively affects the recipient's number of offspring. In general, punishment is imposed because the recipient will not cooperate; he behaves in a manner that is costly to the punisher but beneficial, at least in the short term, to the recipient. The question is then how reducing the fitness of some members of a group can elevate the fitness of the group, such that a propensity to punish remains.

Evolution of Psychological Faculties

► Alfred Russel Wallace (1858)

Theories of the Evolution of Punishment

One school of thought holds that the key purpose of punishment is to prevent the

repetition of the punished form of behavior. For example, more experienced individuals can share their knowledge by punishing less experienced individuals (such as children) for performing behaviors that are dangerous to themselves or to the group. Punished behaviors would thus include playing near a cliff or a water-front, so that a moment's loss of control leads to injury or drowning, or it could be chattering and shouting in the vicinity of competing bands, exposing one's own group to ambush. However, this does not account for the propensity, found in many societies, to punish overly-severely, unfairly, or with no obvious benefit for the recipient. Another school holds that punishment generally involves a reaction to some form of cheating or non-cooperation. Severe punishment can be explained by the way in which it deters free-riders and cheats who undermine the cohesion and adaptive operation of the group to which they belong (see Nakao and Machery 2012). Specifically, punishment behaviors would be naturally selected for to the extent that the fitness elevation they entail outweighs the fitness reduction which they cause. To this elevation must be counted long-term adaptive effects of cooperation and rule-following, behaviors that tend to be adaptive both in individuals and among groups when in conflict with other groups (see Dutton and Woodley of Menie 2018). Capital punishment is an extreme example in that there is no possible benefit to the recipient, so it must thus be compensated for by a substantial benefit for the group. Benefit would accrue, for example, when an individual's destructive behavior is due to genetic influence, which is thereby decreased in the gene pool through his execution. Examples include psychopathy, mental instability, and other anti-social behavioral tendencies that entail betrayal, violence, and internal conflict (Dutton and Madison 2018).

In these situations, behavior modification of the recipient is of no direct benefit to either party, in which case it has been argued that punishment may have evolved, in part, because of the benefits accrued by the one who punishes. If the punishment consists of the withdrawal

of some form of aid (this being a self-imposed cost) that constitutes a benefit to the punisher, especially if it means that the recipient becomes less able to harm him. More generally, depending on the severity of the punishment, it means that the punisher may end up with more descendants than the recipient (Nakao and Machery 2012). When including this macro-perspective of punishment, behavior modification is merely one aspect of its evolution. Nevertheless, many forms of punishment, such as the spanking of children by parents, likely aim to elevate the genetic fitness of the recipient. Indeed, a parent has conceivably no interest in reducing the fitness of its offspring other than in extreme circumstances, such when a young woman in a very difficult labor has to choose between her own life and that of her baby. Should she survive she would be able to have many more children. Accordingly, there may be several strands in that a propensity to punish has evolved because those who punish are more likely to survive, those who have been punished for key violations are more likely to survive and so pass on the inclination to punish, and groups who punish are also more likely to survive.

The Evolution of Spanking

Some particular characteristics of punishment practises may be informative with regard to punishment's evolution and adaptive function. The dominant forms of punishment vary between cultures. In many tribal societies, those who are physically punished are beaten up until they plead for mercy (e.g., Freeman 1983). However, the propensity to beat the buttocks, a.k.a. spanking, appears to have developed independently in both Europe and Northeast Asia, testified to by evidence of the ancientness of the practice in both contexts. Children were beaten on the bare buttocks in ancient Pompeii as well as in Early Modern England, where it was applied to wives, children, errant servants, and certain kinds of criminals (McCoy and Keen 2013). Spanking has developed independently in quite unrelated developed cultures, such as those of the Far East,

in which flogging men and boys to the point of bleeding on the bare buttocks is documented from sixteenth century China (McCoy and Keen 2013).

Due to the similarity in procedure in two independent cultures, spanking is unlikely to be a “fluke” development, and it has thus been suggested that it may be a result of evolutionary processes. Importantly, spanking is associated with positive life outcomes for the recipient when this violence is ritualistic, structured, controlled, not overly severe, and administered by a parent or guardian who is predictable and otherwise loving, controlling for factors such as socioeconomic status (Larzelere 2000). Indeed, when the children in studies were from groups which tend to have poor impulse control and low agreeableness then the outcome was positive even if the corporal punishment was extremely severe, as long as it was structured and predictable (Lansford et al. 2009). When imposing genetic controls, corporal punishment only led to poor life outcomes if comprised of random violence, such as punching and kicking (Lynch et al. 2006). Morris (1969) suggests that spanking may have a common evolutionary root in a submissive social behavior observed in chimpanzees. If a subordinate male gets into a situation of conflict with a dominant chimp, he will instinctively present his posterior to the dominant chimp. The dominant chimp will then briefly mount him, which defuses the situation. These kinds of behaviors seem to increase the fitness of the lower-status individual. Many mammals – with dogs offering their necks or being mounted by same-sex superiors as the prime example – perform acts of submissiveness, humiliation, and ritualized violence in substitution for real violence. Likewise, mimicking femininity may function to pre-empt violence by changing the role of the adversary from a male to be competed with into a female to be mated with if one wishes. Both dominating and submissive behaviors are likely reinforced by regulation of serotonin, for example, extending them in time. In effect, inflicting serious injury is avoided while the teacher, parent, or other authoritative agent can still maintain a trusting

relationship. In addition, undergoing a ritual which involves submissiveness, degradation, and pain, but also control and predictability, may foster the recipient’s character to deal with a milieu that is harsh and yet highly predictable. This would, therefore, be of particular benefit in the ecologies of Europe and Northeast Asia that have historically been particularly “harsh yet predictable” (Dutton and Woodley of Menie 2018).

Evolution of Less Violent Punishment

There are many ways in which people can be punished, ranging from slighting, verbal abuse, and threatening, to shouting, slapping, and varying degrees of physical violence, including execution (Clark 2007). It has accordingly been suggested that punishment has tended to take a violent form because of evolutionary reasons. For example, Frost and Harpending (2015) have shown that the widespread execution of criminals in Medieval and Early Modern Europe had the effect of removing from the gene pool those with particularly low Conscientiousness and Agreeableness, leading to a more cooperative society, better adapted to triumph over rival societies and over the elements. Dutton and Madison (2018) extended this argument to intelligence and religiousness, both of which they show to be associated with in-group cooperation. From the Early Modern Period onward, when Western societies were nevertheless still under preindustrial conditions of Darwinian selection, punishments became decreasingly violent and bloodthirsty (Clark 2007). In terms of the evolution of punishment, this may be because intelligence was increasing every generation up until the Industrial Revolution, due to the association between intelligence and wealth and the concomitant positive association between wealth and fertility, as shown using proxies from Clark’s research (Dutton and Woodley of Menie 2018). Clark’s research shows, for example, that the richer 50% of English testators in the seventeenth century had almost double the number of surviving

children than the poorer 50%. Dutton and Woodley of Menie aver that as intelligence is associated with empathy, punishments began to become less violent as people became more empathetic, although a period of particular environmental harshness would have lessened this supposed evolutionary trend. They accordingly conclude that rising intelligence, combined with decreasing environmental harshness and decreasing stress, helps to explain a decreased propensity towards violent punishment. As such, punishment has been indirectly affected by selection for a certain trait – intelligence – in humans.

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Evolution of Reciprocal Altruism

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Synonyms

Behavioral game theory; Cooperation; Evolutionary psychology; Reciprocity; Theory of mind

Definition

Evolution of reciprocal altruism studies the evolutionary basis of cooperation within evolutionary agents (here special focus on *Homo sapiens*)

Introduction

Humans (*Homo sapiens*) are arguably the most cooperative primates (Smith 2003). We display unique characteristics such as cooperating on tasks with non-kin members in large groups across cultures (Tomasello et al. 2005). Human cooperation studies have gathered wide interest from psychologists, evolutionary anthropologists, behavioral ecologists, economists, etc. Humans, therefore, make an interesting case study for reciprocal altruism. In the face of theoretical puzzles around reciprocal altruism, the scale of human cooperative societies seems particularly defiant.

Cooperation in Humans

One common explanation for this seemingly abnormal scale of cooperation was the existence of social norms and the ability to understand others' intentions (Fehr and Fischbacher 2004; Tomasello et al. 2005). Norm-based cooperative theories suggested that players who were aware of social normative expectations would act cooperatively in order to fulfil social norms. This was

corroborated by several studies in behavioral game theory showing that human players routinely violated selfish rational expectations and chose to consistently cooperate (across demographics) even at a cost to themselves (Camerer 2003). This norm-based reasoning seemingly presented a cross-cultural advantage to humans in building large successful societies.

However, a large cross-cultural study by Henrich et al. (2001) revealed that when studied in behavioral game theoretic experiments, human players from different cultures exhibited peculiar but remarkably variant patterns. This finding forced a reexamination of the social norm-based explanation for human cooperative systems. If players in culture A consistently shared 50 % of their endowment with other players in an ultimatum game, why did players from culture B share close to zero? This would seem to violate the assumption of common social norms shared across human societies, which contribute to the widespread cooperation. The apparent violation of social norms deserves some attention.

Tomasello et al. (2005) argue for the existence of particular and exceptional abilities such as theory of mind and “shared intentionality” is likely to be a reason humans are remarkable cooperators and altruists. If true, these abilities could function to inform the other player’s expectations and reactions, which in turn would allow their opponents to make a variety of decisions in behavioral games. For instance, a player in culture A could be aware that their opponent who is from their own culture would think it is normal for a proposer to split the endowment unevenly, whereas in a different culture, 50 % sharing could be the norm. The combination of insights from Tomasello’s and Henrich’s work reveals that rather than being a standard “fairness” based social structure, player reasoning could operate by anticipating other person’s perception of their actions.

Conclusion

The inclusion of theory of mind and shared intentionality measurements in cross-cultural studies is likely to be able to test this concern and provide

additional theoretical power to behavioral game theoretic studies.

Cross-References

- [Adaptations for Reciprocal Altruism](#)
- [Cooperation and Social Cognition](#)
- [Theory of Mind](#)

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Evolution of Reciprocal Altruism and Punishment

- [Evolution of Cooperation](#)

Evolution of Religion

- [Evolutionary Perspectives on Religion](#)

Evolution of Secondary Sexual Characters

- [Charles Darwin: Theory of Sexual Selection](#)

Evolution of Self

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Synonyms

Consciousness; Metacognition; Self-awareness; Self-consciousness; Self-reflection; Self-thought

Definition

The term “the self” is broad. It can encompass: (1) knowledge that one is separate and distinct from others, (2) knowledge about the degree to which one is consistent over time, (3) knowledge about how one is a causal agent in the world, (4) information about the attributes (e.g., appearance, personality traits, habits) that one possesses, (5) information about one’s goals or motives as well as plans to execute them, (6) knowledge about one’s significant roles and relationships, (7) the result of judgments made about oneself, and (8) feelings or emotions that one experiences in response to self-thought.

Introduction

People experience “a sense of self.” This may include ideas about how they look, who they are now, how they were in the past, and what they have done in the past. They have the experience that *they* (not an outside agency) do things, and that *they* (and not an outside agency) are the source of their own thoughts. Scholars have long been captivated by the study of the origins, functions, and functioning of this sense of self, and the long and intensive study of this topic has generated a voluminous empirical and theoretical literature (for a sampling, see Leary and Tangney 2012). Indeed, self-awareness has been called

“arguably the most fundamental issue in psychology . . .” (Rochat 2003).

One proposition in the self literature is that the mental experiences linked to the self have emerged via evolution (Sedikides et al. 2006). This evolutionary perspective reflects the following assumptions: (1) some organism’s psychological characteristics are rooted in genetics; (2) these genetically influenced psychological characteristics will spontaneously vary across organisms in a population; (3) some characteristics are a better fit to an organism’s environment than are others; (4) those individuals who possess the advantageous psychological characteristics will be especially effective in the organism’s environment, which will contribute to the organism being particularly successful in reproductive activities; (5) reproductive success will lead to a subsequent species increase in the extent to which the advantageous characteristics occur in the population; and (6) this shift in characteristics will be accompanied by continuing variability among individuals in the population (such variability is a precondition for evolution).

These assumptions have several implications for the patterns of data that one should observe when searching for evidence related to the self. One implication is that the human experiences of self are linked to physical elements of the body (e.g., genetics, brain structure, brain function). A second implication is that the current human experience of the self may not match the experience of the self in early species members (or in earlier hominid species), but may have changed over time. A third implication of an evolutionary approach to the emergence of the human self is that at least some self-like capabilities may be shared with nonhuman species. A fourth implication is that the self should be adaptively functional. This chapter briefly elaborates on these implications and presents evidence.

None of the relevant sources of evidence is conclusive on its own. For example, although high current trait functionality is consistent with an evolutionary perspective, it does not constitute sufficient evidence for it. A trait can be functional in a given environment, but can still be solely derived from experience (e.g., pathogen

exposure). Moreover, even when rooted in natural selection, trait functionality can shift across the evolutionary timescale. A trait may have initially evolved in response to a given set of environmental selection pressures, but, as time progresses, selection of the trait might be governed by a set of environmental pressures that are entirely different from the ones that were originally responsible for its selection.

Another potential concern is that traits exhibited by a species are simply side effects that emerge from the process of selection, but they are not themselves a focus of those selection pressures. For example, evolution may have worked to promote the production of neurons that are densely interconnected with other neurons. If one collects enough neurons, if the neurons are of the correct type, and if the neurons are interconnected in the right way, then the sense of self may spontaneously emerge from the resulting system. Moreover, this sense of self may be functional. Thus, even if humans can be shown to have a biologically influenced sense of self that enhances functioning, it may not be true that evolution specifically selected individuals who have a sense of self.

However, although each source of evidence pertaining to the evolutionary origins of the human self may not be definitive on its own, it is also the case that the available evidentiary sources strongly converge, favoring the evolutionary hypothesis. We illustrate this point by highlighting some of the converging evidence.

Getting a Grasp on the Self

Exactly what is this “self” that has been the object of so much theoretical speculation and empirical attention? One answer comes from a developmental perspective, which posits that the self develops gradually through a succession of behaviors. The ability to monitor and reflect on these behaviors, otherwise known as metacognition, is thought to be an indicator that an individual possesses a self-concept. For example, using reactions to a commonly used test for the self-concept, the

“mirror test” (e.g., how one responds to one’s own reflection in a mirror), Rochat (2003) proposed five levels of self-awareness. These are as follows:

Level 0: Confusion. At this level, there is no self-awareness. The person is unaware of any mirror reflection or the mirror itself. They seem to perceive the mirror as an extension of their environment.

Level 1: Differentiation. The individual realizes the mirror is able to reflect things. They understand that what is in the mirror is different from what is surrounding them. They differentiate between their own movement in the mirror and the movement of the surrounding environment.

Level 2: Situation. The individual can link the movements in the mirror to their body perceptions. This is the beginning of the realization that what is visualized in the mirror is special to the self.

Level 3: Identification. The individual can now see that what’s in the mirror is not another person but actually him/herself. Thus, at this stage, instead of referring to the mirror while referring to him/herself, the individual refers to him/herself while looking in the mirror.

Level 4: Permanence. Once the individual reaches this level, they can identify the self beyond the present mirror imagery. The individual now experiences a “permanent self,” and this is accompanied by the ability to identify the self in previous pictures as looking different or younger.

Level 5: Self-consciousness or “meta” self-awareness. Here, thinking is accompanied by the realization that the image in the mirror can be seen from a third person’s view, and not just the first person perspective. The individual begins to understand that they can be “in the mind of others.” For example, the individual may understand how they are seen by others.

However, such conceptions may focus unduly on metacognitions and self-reflection. The more researchers consider the activities and functions that are linked to the self, the more complex they

find the answer to the question “what is the self” to be. For example, Klein and Lax (2010) noted seven types of self-knowledge.

1. Episodic memories of one’s life events.
2. Semantic summary representations of one’s personality traits.
3. Semantic knowledge of facts about one’s life.
4. An experience of continuity through time: The “I” experienced now is connected to the “I” experienced at previous time points.
5. A sense of personal agency and ownership: The belief or experience that “I” (agency) am the cause of “my own” (ownership) thoughts and actions.
6. The ability to self-reflect: Forming meta-representations where the agent is the self and where the agent makes inferences on the basis of those representations.
7. The physical self: Represent and recognizing (e.g., in mirrors, photographs) one’s body.

Some theorists have attempted to find an underlying organization to these different facets of self-knowledge. For example, one conception (Fingelkurts et al. 2016) suggests that the experiences of self incorporate three main contributors. One provides the first-person perspective and the sense of agency (the witnessing observer); the second provides the experience of self as a localized embodied entity, emotion-related thoughts, and autobiographical memories (representational-emotional agency); the third provides the experience of thinking about oneself, including momentary narrative thoughts (reflective agency). The theoretical conception has the additional advantage of grounding each of these contributors in brain structure and function. The conception suggests that selfhood involves the activation of a default mode network (DMN) that links neural activity in frontal-left, posterior-right, and posterior-left areas of the cerebral cortex. More specifically, the DMN is commonly viewed to include the left and right middle frontal gyri, bilateral frontal medial areas, left and right middle temporal and occipital gyri, and left and right precuneus. These are thought to be active and functionally synchronized during

self-related tasks and when participants engage in self-generated thoughts.

On the Adaptive Functionality of the Self

The study of self-related brain functioning is only one source for the converging evidence pointing to the evolutionary origins of the self. One other clue to the natural selection of a characteristic lies in the characteristic’s functionality. That, if the self is an adaptive trait for a species, a researcher ought to be able to document the ways in which the self is functional to the species. Parker (1997) has made exactly this evolutionarily driven self-functionality argument not only for humans but also for nonhumans, as well. We will consider the nonhuman angle of the self later. For now, we focus on the functionality of the self for humans.

As would be expected from an evolutionary standpoint, there is variability among individuals in terms of their ability to experience a self. Clearly, when considering this variability, some forms of self-related thought are not adaptive for humans. Excessive focus on the self can produce maladaptive thinking and can impair task performance (Pinel and Bosson 2013). Moreover, an excess of “selfness,” manifested in the form of narcissism, can similarly produce negative consequences (Sedikides and Campbell 2017).

However, when viewed from a broad perspective, the evidence also suggest that humans who have a well-formed self do better than those who do not. For example, the ability to experience a self may be diminished in persons with schizophrenic disorder (Molnar-Szakacs and Uddin 2016) and persons with autistic spectrum disorder (Lind 2010; Lyons and Fitzgerald 2013). Similarly, a person who experiences damage to, or an impairment of functioning in, their right hemisphere will sometimes suffer from depersonalization disorder, manifesting an altered, detached, or estranged sense of self (Kober et al. 2005). Moreover, while sometimes able to function adequately, those whose self-related memory (and thus, their sense of self) is diminished because of disease-induced or accident-induced brain damage exhibit impaired functioning in real-world

contexts, including the social and/or occupational functions of daily life.

Theorists argue that this functionality is especially evident in the human social world (e.g., Humphrey 1986). Indeed, it may be the case that only species capable of self-reflection are able to use introspectively based social strategies and to experience socially grounded emotions, such as evaluative embarrassment, pride, shame, and guilt. Thus, reflecting on and understanding one's own behavior allows one to engage in sophisticated and nuanced social behavior. This is especially true when species members have a high degree of interdependence, as do humans. Both cooperation with, and competition against, other species members can be enhanced when one has the ability to reflect on the self and to anticipate one's own behavior as it relates to the behavior of others in various social contexts. Moreover, mental simulations that involve the self may be especially important for optimal selection of long-term goals and a reduction in the likelihood of failure.

Behavioral Evidence and Cognitive Evidence from Nonhuman Species Linking Evolution to the Self

Cross-species comparisons of behavioral characteristics and cognitive characteristics can also provide converging evidence pertaining to the thesis that the self is a product of evolution (Sedikides and Skowronski 1997). Evolution does not create something from nothing – it merely selects from what is already available. Thus, any given biologically based characteristic ought to be present in other species, though perhaps only in rudimentary form.

One such characteristic is self-recognition. It has long been known that chimpanzees are capable of recognizing as “self” their own image in a mirror. Subsequent investigations showed that this capacity is shared among other great apes (bonobos, gorillas, orangutans), and perhaps even among primates such as rhesus monkeys who are not as similar to humans as are the great apes. However, even some nonprimate animals

seem to exhibit this capacity. The list includes dolphins, orcas, and the Eurasian magpie (for a cross-species overview, see Mitchell 2012).

This list may lengthen substantially in the near future. Recent thinking indicates that additional evidence of the presence of the self in nonhuman animals can be obtained by “tuning” self-tests to the species being tested. That is, many studies looking for evidence of animal self-concepts have used “the mirror test.” This test seeks evidence that an animal somehow recognizes an image in a mirror as “them.” The test, however, may not be diagnostic of the presence of a self-concept in animals that rely on nonvisual sensory systems. For example, studies conducted with dogs using olfactory cues instead of visual cues tentatively suggest that dogs may possess a self-concept.

Such cross-species diversity might have emerged because evolution often solves similar environmental problems in similar ways. Thus, if a nonhuman species occupies an environmental niche similar to the niche occupied by the species in the evolutionary line that led to the human species, then nonhuman species might be expected to exhibit characteristics similar to the human species. For example, the hominid line has included relatively large-brained individuals whose food sources were widely dispersed in time and space. Similar descriptions can be applied to elephants and dolphins. Thus, the emergence of “the self” in all these species may not be coincidental but instead may reflect evolutionary convergence.

An additional indication of self-producing evolutionary convergence comes from the observation that many of the species that exhibit self-recognition also tend to be highly social. This observation suggests that self-recognition capacities may enhance individual functionality in a social context. This converges with the view that primate brains are “built to be social.” Via evolution of the capacity for self, nature may have found a way to tune big-brained social organisms so that they be well suited to survival in environments that present difficulties in food procurement.

Pursuing a related line of thought, Hills and Butterfill (2015) proposed behavioral and

biological commonalities between external foraging in space and internal foraging over environments specified by cognitive representations, and they explored the implications of these commonalities for understanding the origins of the self (for similar ideas, see Sedikides and Skowronski 1997). Hills and Butterfill suggest that one of these components is auto-noetic consciousness, a term that refers to the ability to mentally place the self in the past, in the future, or in counterfactual situations. This capability allows one to examine one's own thoughts, a kind of self-consciousness that likely is a contributor to the self-multiplex.

Exploration of whether nonhuman species have auto-noetic consciousness has concentrated on the seeming ability of nonhuman species to experience episodic memories. Episodic memories involve subjective event re-experiencing (including images, sights, smells, and feelings), as well as the knowledge that these events occurred in an earlier time. Lou et al. (2004) reasoned that auto-noetic consciousness emerges via retrieval of episodic memories and that such retrieval affects conscious self-representation. This episodic memory capability would seem to be functional to the self. In the absence of the ability to recall experiences and reflect on them, humans would be stuck in a state of constant awakening, without a past and therefore unable to prepare for the future.

Accumulating evidence suggests that episodic memory (and, by extension, auto-noetic consciousness) may not be unique to humans (but see Klein 2014). For example, research results show that animals can act as if they remember time. This tendency can be seen in species that are, in evolutionary terms, close to humans, including chimpanzees and bonobos, baboons, and rhesus monkeys. For example, in one study (Martin-Ordas et al. 2010), preferred perishable food (frozen juice) and less preferred but non-perishable food (grape) were hidden from primate subjects. The subjects could choose one of the foods either after 5 min or 1 h. The frozen juice was still available after 5 min, but melted after 1 h, becoming unobtainable. The primate subjects chose the frozen juice to a significantly greater extent after 5 min and the grape after 1 h,

suggesting that they could remember how the passage of time affected the results of their foraging episodes. Similar findings have been reported for nonprimate species, including nonprimate mammals (rats, meadow voles, Yucatan minipigs, dogs) and birds (pigeons, black-capped chickadees, magpies).

Given these findings, that animal behavior can be sensitive to time is not in much doubt. At issue is whether an animal's ability to use time reflects the presence of an episodic memory system and/or auto-noetic consciousness. Attempts to resolve this conundrum may come from neuroimaging and neuroanatomy studies. Results from such studies indicate that episodic memories in humans depend on the integrity of the hippocampus and related structures. This also seems to be the case for nonhuman species. For example, after encountering a sequence of five odors, the behavior of rats with hippocampal lesions was inconsistent with the idea that they could recall odor order. This insensitivity to order occurred despite the rats acting as if each odor was familiar (Eichenbaum 2013). Additional support comes from studies of monkeys with fornix lesions. Such lesions disrupt the hippocampal system: lesioned monkeys were unable to make accurate recency judgments (Charles et al. 2004). In all, the probable presence of a time-sensitive episodic memory-like system in nonhuman species, as well as in humans, fits with the general thesis that the human self was formed as a result of evolutionary pressures.

One other indicator of the self is a sense of agency over one's actions: the subjective awareness that one is initiating, executing, and controlling one's volitional actions. This sense of agency is sometimes impaired in humans who have a disrupted self, such as those with schizophrenic disorder or autistic disorder (Molnar-Szakacs and Uddin 2016).

Do nonhuman species share this sense of agency? The answer seems to be "yes" (Moore 2016). For example, in one study (Kaneko and Tomonaga 2011), chimpanzees were presented with two cursors on a computer display. One cursor was manipulated by a chimpanzee using a trackball, whereas the other cursor displayed

motion that had been produced previously by the same chimpanzee. Chimpanzees successfully identified that cursor they were able to control. Additional studies showed that at least one chimpanzee could monitor the movement that was theirs in both the temporal dimension and the spatial dimension. Such understanding of agency may also extend beyond the primate line (e.g., to dolphins).

We speculate that this sense of agency may (at least partially) be rooted in the mirror neuron system. Although this system has been implicated in one's ability to mimic others, it also seems to be involved in the monitoring of self-movements, which may contribute to the sense of agency (Maeda et al. 2015). Interestingly, the mirror neuron system may, in evolutionary terms, be relatively old, given that it is shared with other species, such as birds (Prather and Mooney 2015). This may represent another example of how evolution co-opts existing traits. The mirror neuron system, which likely evolved to facilitate social learning, may have been shaped by evolutionary pressure to be a contributor to an individual's sense of self.

For How Long Has the Human Species Possessed a Self?

The possibility that the self (or at least components of the self) can be shared across species suggests that "selfness" (or at least some components of the self) ought to be present in early humans, or even in the hominid species that may have predated humans. Evidence relevant to this point can be examined by looking at the things that the human species have left behind over time.

Using such evidence, early views of the self's emergence in humans noted that evidence of human "selfness" was in place for humans who lived as early as 50,000 years ago (Leary and Buttermore 2003). The evidence for such a date was relatively ample and included the presence of artistic figurines, bow-and-arrow technology, and personal ornamentation. The evidence also indicated that humans were performing ritualized burials. However, recent

artifacts (Hublin et al. 2017) have pushed this "selfness" date back substantially, even to as long as 300,000 years ago. For example, recovered beads, likely used for personal adornment, dated to about 100,000 years ago. Other finds indicate that ochre, a color often associated with bodily adornment, was used by hominid species about 164,000 years ago. Some evidence even suggests that the capacity for self predates the human species: A carving of the head and torso of a woman attributed to *Homo heidelbergensis* has been dated to at least 250,000 years ago.

Evidence Linking Brains, Genes, and the Self

A substantial corpus of research has explored whether self-related thought is linked to specific areas of the brain. Reviews of the work that explores self-related thought (Northoff 2013) lead to clear results. A set of brain regions collectively referred to as the cortical midline structures (CMS) show a special significance in self-related thought. Studies looking at neural activity levels demonstrate that stimuli that are personally relevant (vs. not) to individuals induce higher neural activity in several CMS regions. Such patterns emerged across stimuli, including faces, trait adjectives, movements/actions, memories, and social communication. The implicated CMS regions include the perigenual anterior cingulate cortex (PACC), the ventromedial and dorsomedial prefrontal cortex (VMPFC, DMPFC), the supragenual anterior cingulate cortex (SACC), the posterior cingulate cortex (PCC), and the precuneus.

Interestingly, some of these areas also may be implicated when thinking about others. Such areas include the midline regions, the dorsomedial prefrontal cortex, and the posterior cingulate cortex. This result points to an intrinsically social dimension in the human neural activity, which may be essential for any subsequent consciousness of both one's own self and other selves.

However, this focus on self-referential thought may not capture all kinds of self-related thought. As noted earlier, there may be different facets of "selfness," and these facets may be related to

distinct brain areas. One approach to this multifaceted self (Fingelkurts et al. 2016) links the experience of selfhood to the activation of a default mode network (DMN). This network interconnects neural activity in frontal-left, posterior-right, and posterior-left areas of the cerebral cortex. Specific areas implicated are the left and right middle frontal gyri, bilateral frontal medial areas, left and right middle temporal and occipital gyri, and left and right precuneus. These are active and functionally synchronized during self-related tasks and when participants engage self-generated thoughts. The frontal-left structures are linked to the first-person perspective and the sense of agency (the witnessing observer). The posterior-right areas are linked to the experience of self as a localized embodied entity, emotion-related thoughts, and autobiographical memories (representational-emotional agency). The posterior-left areas are linked to the experience of thinking about oneself, including momentary narrative thoughts (reflective agency).

Research in anthropology and comparative biology indicates that the self is associated not with physical elements of the brain, but also with elements of the human genome. These lines of research culminate to the conclusion that the modern human mind is a mosaic of traits inherited from a common ancestry with close relatives (Sherwood et al. 2008). Indeed, the human brain is generally organized in a fashion similar to that of other primate species, and the greater the relation of those nonhuman species to humans, the more similar the organization. For example, the planum temporale, a surface feature of the cerebral cortex in the region of Wernicke's area, displays left hemisphere dominance in humans, bonobos, chimpanzees, gorillas, and orangutans.

However, human brains also have been enhanced via evolutionary specializations within particular domains. These include cognitive adaptations and linguistic adaptations that are correlated with enlargement of the neocortex and related structures. Several anatomical and molecular changes have occurred that seemingly reflect the modern human brain's high metabolic demand and enhanced synaptic plasticity. Illustrating this point, in humans higher-order unimodal and

multimodal cortical areas have grown disproportionately relative to primary cortical areas. Moreover, in comparisons of the brains of higher-order primate and the brains of humans, only humans have multiregion lateralized networks, which provide frontoparietal connectivity. Sherwood et al. (2008) maintain that this pattern of within-hemisphere connectivity distinguishes human brains from the brains of nonhuman primates.

Hominid DNA evidence leads to similar conclusions. Researchers have recently reproduced a complete genomic sequence of a Neanderthal woman (Prüfer et al. 2015). Only a small list of simple DNA sequence differences distinguished these Neanderthals from modern humans. A good deal of these differences implicated the biology of the neocortex, a finding that is consistent with the idea that evolution prompted the emergence of the modern human self.

A similar conclusion can be derived from studies that examine the brain structure alterations linked to various psychopathologies in which symptoms include alterations in the sense of self (Northoff 2014). Four of the most studied disorders involve self-distortions are schizophrenia, autism spectrum disorder, major depression, and borderline personality disorder. The relevant evidence indicates that distortions of the sense of self in these psychological disorders are associated with alterations in the brain's cortical midline system (including the perigenual anterior cingulate, inferior frontal gyrus, and insula), mirror neuron system (including the frontoparietal region [precentral gyrus, precuneus, supramarginal gyrus, inferior parietal lobule] and limbic system [anterior insula and anterior mesial frontal cortex]).

Additional findings link dysfunctions of the self to genetics. For example, Won et al. (2016) explored activity in regulatory regions of genes on the human genome that may be related to schizophrenia. These regions work like rheostats, increasing or decreasing a target gene's activities. Such rheostat-like loci regulate the activity of genes that are known to be crucial to brain development and that are very active early in brain development. It follows that disorders such as schizophrenia – and, by extension, the self-distortions that are

symptomatic of schizophrenia – may have a similar basis in the genetics that control brain development.

Researchers also have compared the genetics of nonhuman primate species to the human genome in order to gain insight into brain alterations that may have occurred during evolution. Relevant studies have examined corticogenesis (the process in which the cortex of the brain is created during neurodevelopment), and again have focused on those gene regions that regulate the expression of genes. Consistent with an evolutionary perspective, Reilly et al. (2015) concluded that many human lineage changes reflect alterations in gene regulation. That is, these alterations operate within older regulatory mechanisms and evolutionary processes essential for building the mammalian cortex, but they appear in modified form in humans. Saphire-Bernstein et al. (2011) forged a link among elements of the self, the brain, and genetics. They reported that varying genetic forms of the oxytocin receptor are associated with varying levels of self-esteem and depression.

There is a long way to go when trying to understand how evolution may have produced physical alterations in the brain and the human genome that link to the human experience of self. Nevertheless, the steady stream of results has taken substantial steps toward establishing the anatomical and genetic underpinnings of the self.

Conclusion

Psychologists have long had a fascination with the concept of “the self.” One thread of research into this topic has explored the possibility that any or all of the various facets of self-related thought have been promoted in humans by natural selection. Evidence favoring this idea comes from disparate sources. These include studies of archeology, cross-species studies of biology, psychology, and behavior, studies of anatomy and genetics, and studies of brain action and neural function. Individually, none of these sources is sufficient to establish unambiguously that the human self has emerged as a product of natural selection. However, the evidentiary converge provides strong support for this thesis.

Cross-References

- Brain Development
- Brain Imaging
- Brain Lesion Studies
- Brain Size Growth in Humans and Nonhuman Primates
- Burials
- By-Products of Adaptations
- Cognitive Development in Non-Human Primates
- Convergent Evolution of Intelligence
- Development of Adaptations
- Environmental Unpredictability and Bet-Hedging
- Episodic Memory
- Evolution and Self-Awareness
- Evolution of Adaptations
- Evolution of Memory, The
- Evolution of The Brain, The
- Evolutionary Perspective, The
- Frans de Waal’s (1982), *Chimpanzee Politics*
- Mindblindness
- Narcissism
- Naturalistic Fallacy, The
- Selection for Cooperative Relationships
- Self-Assessment of Fighting Ability
- Self-Concept
- Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?
- Self-Esteem as a Status-Tracking Mechanism
- Self-Esteem Reflects Assessments of Valuation
- Self-Esteem Tracks Social Evaluation and Relational Value
- Self-Observation
- Theory of Mind
- Theory of Reciprocal Altruism

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Evolution of Selfishness and Altruism

- [Selfish Gene, The](#)

Evolution of Sight in Mammals

- [Evolution of Mammalian Vision, The](#)

Evolution of Signaling and Responding

- [Evolution of Communication](#)

Evolution of Social Emotions

- [Evolution of Emotion in Social Context](#)

Evolution of Teaching

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Synonyms

[Adaptation](#); [Behavioral engagement](#); [Civilized norms](#); [Cultural development](#); [Knowledge enrichment](#); [Progressive learning](#)

Definition

Teaching is a procedure in which a donor conveys information to a receiver and aims to enrich his/her knowledge, a cooperative behavior in that one engages in an activity that benefits another, at some cost, or with no immediate benefit to itself.

Introduction

The values that describe human societies managed to create a culture that renders humans as the only species to be separated qualitatively from other animals. It is argued that the tendency of early humans to be curious in their nature fostered the learning of useful strategies that selectively became genetic capabilities and which rendered the ongoing development of culture as a remarkable achievement. Human species evolved over generations, and communication became more complex. Arbitrary cultural meanings are found to be assigned to animate and inanimate objects in the environment, allowing for a vivid indication that early culture initiations were occurring. As communication is a vital component in the realm of enculturation, language appeared to develop in parallel with human cultural values. Throughout a continuous, systematic progress, there is evidence of memory expansion and brain size increase that

facilitated and possibly co-interacted with the development of enculturation and the entry of humans in social norms. The ongoing evolution and the development of hierarchical structures within cultures rendered the role of educators vital for functional authority frameworks and the growth of civilized nations.

Teaching and Cumulative Culture

Knowledge is widely thought to underlie the success of humanity by allowing high-fidelity transmission of information and skills between individuals, facilitating both cumulative knowledge gain and normative culture. Teaching indicates signs of evolution, whose costs are eliminated by the inclusive benefits that result from the individual adapting and constantly seeking to acquire valuable information (Csibra and Gergely 2006). This leads to a narrow range of traits for which teaching would be efficacious and justifies the rarity of teaching in nature, its unusual distribution, and its highly specific nature. Further models that allow for cumulative cultural knowledge gain suggest that teaching evolved in humans because cumulative culture renders otherwise difficult-to-acquire valuable information available to teach. Interpretively, it resolves the mystery of why teaching should be widespread in human societies but extremely rare in other animals (Kirby et al. 2007). Compared to animal teaching, human teaching is a very general capability, reliant on high-fidelity mechanisms such as speech, instruction, and direct shaping, and it allows the transmission of complex information that could not be devised by a single individual (Hoppitt et al. 2008). Humans have undergone cumulative cultural evolution, which has in essence reduced reliance on information acquired asocially (Rapaport and Brown 2008) and allowed the transfer of knowledge and skills that would be difficult to learn without direct guidance and instruction. For instance, valuable information, concerning industrial practices or technological manufacture, has become available to teach through the accumulated efforts of many individuals. Potentially, teaching and cumulative culture

might have coevolved, extending the possibility to allow for cumulative knowledge gain by allowing individuals that have acquired the information to gather further knowledge that improves it (Taylor et al. 2007), simultaneously, making the information more fitness enhancing but more difficult to learn.

Key Characteristics of Teaching

Importance of Relatedness

From an evolutionary perspective, teachers do not gain any benefits unless the pupils learn, while the delayed benefits of teaching depend on both the teacher's efficacy and the pupil's aptitude. It is argued that high relatedness may favor the evolution of cooperation and, hence, teaching may be most common between closely related individuals (Hamilton 1964). Interpretively, teaching might be especially common as a form of parental care since the noticeable discrepancy in knowledge between adults and infants implies that parents can raise their offspring's potential fitness by assisting them to learn critical skills (Thornton 2007).

Behavioral Coordination

One of the most critical characteristics of teaching is the behavioral coordination of individuals because it serves to distinguish it from other forms of social learning and may allow for insight into its evolutionary history (Kirby et al. 2008). In standard social learning, naïve animals attend to knowledgeable individuals. Studies have shown that even the presence of an anesthetized conspecific is sufficient to cause naïve individuals to approach a food patch and acquire information (Laland and Plotkin 1991; Galef and Giraldeau 2001). On the other end of the spectrum, teaching is characterized by the interaction of a donor and a receiver of information that attend to each other and engage in different but coordinated behaviors. In other words, it is necessary for educators to modify their behaviors to foster learning in students; however, if students are unresponsive, learning will not occur. Efficient behavioral coordination is the product of the coevolution of

teacher and student strategies (Feldman and Zhivotovsky 1992). The coevolution would potentially result in mechanisms whereby each party responds to cues from the other. Behavioral coordination and feedback between individuals do have important implications for the debate over sensitivity and evaluation in teaching. It is vital that teachers respond sensitively to their audience's changing competence and underline noticeable signs of growth in students (Pearson 1989). This involves attributing knowledge to students and responding flexibly to changes in students' performance (Pearson 1989; Premack and Premack 1996). This can be achieved through showing sensitivity by adjusting the behavior in response to cues representing students' age and competence level. Teachers may demonstrate greater ability to track improvements in the abilities of individual students when there are fewer students to monitor and when the costs of a failure to learn are greater.

Adaptive Behaviors in Response to Learning

Teaching is designed by natural selection to fulfill the goal of promoting learning; an individual modifies their behavior accordingly to facilitate learning (Thornton and Raihani 2008). Some authors support that any human behavior involved in the transfer of declarative information is a form of communication in that senders influence the behavior of receivers. Functionally referential alarm calls are characterized for their immediate function, which rather disregards additional positive selection that would help individuals to learn. The immediate response instantly adopts alerting conspecifics to the presence of a particular type of predator so that it may provide appropriate reaction. Learning in this case is an incidental by-product, although infants may learn associations between given call types and predators simply by hearing calls in context (Seyfarth et al. 1980). Evolutionarily, it is shown that teaching may be the most parsimonious explanation for behavior. Widespread reports demonstrate that mothers in various species gradually allow their offspring opportunities to handle live prey (Caro and Hauser 1992; Kitchener 1999).

Studies on Learning in Other Species

Costly changes in maternal provisioning behavior in cheetahs and domestic cats were documented, as cubs grew older. Animals that were consistently exposed to live prey in the presence of their mother showed improved hunting skills compared to those who were merely exposed to prey alone (Rendell et al. 2010). Combined results are highly suggestive of teaching, and they support that selection would eliminate seemingly wasteful behavior such as giving young live prey that might escape unless it serves a function (Grafen 1984). The results derived out from studies of this nature suggest that adults give their young opportunities to handle live prey and facilitate their learning, fact that constitutes a parsimonious explanation for the striking changes in provisioning behavior (Cavalli-Sforza and Feldman 1981).

Procedural and Declarative Knowledge

Once procedural knowledge is gained, it tends to become implicit. Information that belongs in the realm of procedural knowledge lies outside of human awareness. It is argued that it can be also named as the "muscle memory" since the human body proceeds to operate physical tasks effortlessly after mastery is accomplished.

Categories of declarative knowledge are facts, world or personal history, and rules for mathematics operations. A key feature of declarative knowledge is that it is easy to express it in the form of words or symbols. Declarative procedures function explicitly and are expressed through the human consciousness. Individuals are consciously aware of their declarative understanding.

Controversy

The distinction between procedural and declarative knowledge is a controversial issue. This controversy of meaning-as-action versus meaning-as-context parallels the earlier psychological issue of behaviorism versus Gestaltism. However, the current debate reflects a more advanced understanding, being essentially mentalistic and having reference to internal states. The questions are refined intrinsic versus extrinsic computation,

intentional versus extensional contexts, the modularity/efficiency trade-off, and heuristic power versus logical consistency. What is most important is that the programmer possesses the ability to put knowledge anywhere in the system that can be used and that facts are conceptualized in the form of advice regarding their use. Research on procedural evolution is necessarily concerned with the nature of expertise. The representation of domain-dependent knowledge should be accessible by situational goals (Tehrani and Riede 2008); the problem of recognition; the trade-off with structural problem-solving techniques; and physical and mechanical analogies. Most important in studying children's programming is the role of learning. The emphasis is on learning how versus learning that and the importance of a carefully organized sequence of problems, solutions, and near misses to solutions. Compared to animal teaching, human teaching is a very general capability, reliant on high-fidelity mechanisms such as speech, instruction, and direct shaping, and it allows the transmission of complex information that could not be devised by a single individual (Hoppitt et al. 2008).

Conclusion

Teaching will evolve only where the costs to teachers facilitating learning in others are outweighed by the long-term fitness benefits they accrue once students have learned. Nevertheless, it needs to be taken into consideration that cases of individuals who tend to acquire information easily without assistance will render teaching as unlikely to be favored by selection. Hence, behavioral coordination should be facilitated from both the donor and the receiver in an attempt to maintain social structure, hierarchy, and cultivation of values within the frame of civilized communities. Signs of learning and teaching effectiveness in species other than humans indicate cohesive evolution of teaching, whereas the controversial debates concerning procedural and declarative knowledge allow for implications of knowledge complexity and constant evolution of human perspective, physically and mentally.

Cross-References

- [Declarative Knowledge](#)
- [Human Enculturation](#)

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Evolution of the Brain, The

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Synonyms

Brain evolution; Comparative neuroanatomy; Paleoneurology

Definition

Evolutionary neuroscience is an interdisciplinary field of study which seeks to understand the evolution of the brain and nervous system and provides a

framework for interpreting evolutionary changes in the brain and brain component size or shape.

Introduction

The field of evolutionary neuroscience has provided us with an enormous amount of comparative data and relevant theoretical principles to support our current understanding of the evolution of the nervous system. Evolutionary neuroscientists are interested in understanding how the brain evolves and in reconstructing the natural history of the nervous system from a structural and functional perspective. Evidence of brain evolution can be documented through the lens of various biological fields, including biological anthropology, ethology, paleontology, comparative psychology, comparative neuroanatomy, cognitive science, and molecular biology and genetics. The brain, like other organs of the body, is a result of evolutionary processes which have shaped its structure and function. Some of these evolutionary forces have uniquely adapted each nervous system to the environment in which that species lives, while others (either due to shared environmental pressures or common developmental/phylogenetic/architectural plans) have generated remarkable similarities across species.

Comparative Studies

Often when studying the evolution of the nervous system, investigators will choose to perform a comparative study of extant (living) species that are united by a particular characteristic (i.e., feature or trait) and share a common evolutionary history. These characteristics are said to be homologous in nature, that is, they evolved only once and through a common ancestor, rather than through separate/independent evolution. Such studies are phylogenetic in nature and differ from other comparative studies in that the choice of species under investigation is guided by how closely related they are to one another (Butler and Hodos 2005). These studies help us learn more about the historical development of a lineage and are important as they help us identify evolutionary novelties in brain structure, when these novelties emerged within the lineage and how a particular

feature varies in closely related species. This allows the investigator to see if there are any common trends that unite the characteristics of the nervous system in the studied species (Butler and Hodos 2005) and may also help identify features which are unique to particular species (e.g., Krubitzer et al. 2011; Healy and Krebs 1996).

As an alternative to the phylogenetic approach, comparative studies may also focus their comparisons on species that show marked differences in a specific characteristic (e.g., behavioral differences such as sociality, aggression, or structural differences such as in the size of a particular brain structure) irrespective of their phylogenetic relatedness. These types of studies are primarily focused on examining the form and function of the nervous system in an adaptive context (e.g., Barton and Harvey 2000; Harvey and Krebs 1990) and providing insight into how environmental pressures uniquely shape the nervous system so it is adapted to challenges in a particular environment. Both adaptation and phylogenetic comparative studies are important as together they help paint a more complete picture of the evolutionary trajectory of the nervous system.

Brain Size

One of the most striking features when comparing brains across species is the notable difference in brain size. The brain, like all other parts of the body, undergoes a proportional increase/decrease with body size. Allometry is defined as changes in the size of an object (e.g., body or brain) which result in predictable changes in the size of its components (Striedter 2007). Using this mathematical approach allows evolutionary neuroscientists to undertake cross-species comparisons of the relative size of the brain (or its subcomponents) by removing the influence of body size and helping us identify which species have brains (or brain parts) that are smaller or larger (encephalized) than expected for their body size. In contrast, isometry implies that the size of the brain (or brain part) is as one would expect for an organism of its given body size (i.e., there has been no proportional change relative to body size).

When brain mass is plotted against body mass data for all mammalian species, it is apparent that brain size scales in an allometric fashion with body size. Most body parts are known to scale

allometrically with body size (Schmidt-Nielsen 1984), and comparative studies have demonstrated that relative brain size has shifted several times either up or down during the course of vertebrate evolution. While there is a certain amount of overlap in the data, these types of analyses have demonstrated that the major vertebrate groups (i.e., mammals, birds, reptiles, amphibians, and fish) differ quite markedly from one another in terms of relative brain size (Jerison 1973). When relative brain size is compared between these groups, mammals are shown to have the largest relative brain sizes of all vertebrate groups. The majority of mammals have relative brain sizes larger than birds, while birds in turn have larger relative brain sizes than reptiles and amphibians. Similarly, the cartilaginous fish (i.e., sharks, skates, and rays) are shown to have larger relative brain sizes than all other fish. Using this approach, comparative studies have identified that the human brain is markedly larger than one would expect for a mammal of its given body size (i.e., humans have relative brain sizes which far exceed that of all animals) (Manger et al. 2012, 2013). When we look at an overview of relative brain size within the various taxonomic groups, it becomes clear that relative brain size has increased independently in several different lineages (Northcutt 1981) dispelling the notion of a linear increase toward the human condition as supposed by early evolutionists. As pointed out by Striedter (2005), these increases in relative brain size within each lineage coincide with major radiations within the taxonomic groups; in other words, species diversity increased in groups soon after they underwent an increase in relative brain size (e.g., birds and mammals), and similarly species diversity decreased in groups that underwent a decrease in relative brain size (e.g., salamanders and newts). This suggests that there is a particular selective value associated with increases in relative brain size, with more encephalized species likely able to occupy new niches as well as better buffer themselves against environmental changes (Striedter 2005).

Brain Component Size

Brain size (both absolute and relative) is not the only element acting on species behavior, but may

be viewed as the sum of the individual components that make up the brain (i.e., brain parts, connections, and cellular and overlying neurochemical components) and collectively determine its function. An alternative application of the allometric approach has been to look for structural and functional correlations between the individual components of the brain. The resulting data has led to an interesting ongoing debate within the field of evolutionary neuroscience with two major camps emerging: those who argue that most changes in the brain are due to evolutionary constraints and those who argue that most changes in the brain occur as a result of mosaic evolution (adaptations). Under the influence of constraints, one would expect evidence that the underlying components of the brain change in a concerted manner (i.e., individual brain parts scale up or down in a proportional way), whereas in mosaic evolution, one would expect that individual brain parts would be free to vary in size as selective pressures favor particular functions/behaviors over others. Evidence for both concerted (Finlay and Darlington 1995) and mosaic (Barton and Harvey 2000) evolutionary changes in brain component size have been presented. Overall, the majority of changes in brain component size appear to follow a concerted evolutionary process which generally hold true across most mammals, but mosaic evolution has also played a significant role, albeit occurring more infrequently.

Functional Significance of Changes in the Brain or Brain Component Size

While studies on the functional consequence of changes in relative brain size are numerous, it is important to note that conclusions derived from these studies are dependent on the techniques used for comparison as well as the species and level of organization under study, so extrapolating these findings to other groups should be done with caution. That being said, there are several lines of evidence for behavioral correlates with relative brain size. For example, correlations have been uncovered between altricial behavior (i.e., hatchlings born in an underdeveloped state) and encephalization in birds. Hatchlings that are underdeveloped tend to have larger relative brain sizes

than their less feeble counterparts (Iwanuk and Nelson 2003). Others have argued for correlations between relative brain size and life span in primates (Allman et al. 1993), relative brain size and diet in bats (Hutcheon et al. 2002) and in primates (Clutton-Brock and Harvey 1980), as well as relative brain size and foraging strategy in birds (Bennet and Harvey 1985; Clayton et al. 2001) to mention a few. Several studies have also argued in favor of correlations between relative brain size and aspects of sociality (e.g., Dunbar 1998). All these observations and accompanying hypotheses point to the fact that explaining the biological significance of changes in relative brain size is a rather complicated task often filled with controversies and that it is rather simplistic to expect that a measure as broad as brain size should be the result of a single selective pressure or likewise constrained by a single mechanism (Striedter 2005).

Evidence for the functional significance of changes in brain component size have largely come from physiological studies and have added support to the idea that brain evolution proceeds in a mosaic fashion. These physiological mapping studies have demonstrated that species with highly developed sensory or motor abilities also tend to have larger corresponding motor and sensory areas within the neocortex. A classic example is the enlarged representation of the paw/forelimb in the raccoon motor and somatosensory cortex, a feature which matches the behavioral observations of remarkable dexterity demonstrated by the raccoon paw, in comparison to other carnivores (Welker and Campos 1963). Similarly, otter species that use their forepaws more extensively also have larger representations of the forepaw in their somatosensory cortex (Radinsky 1968), and sensitive appendages like the pig's snout (Finger 2000) or the platypus bill (Pettigrew et al. 1998) used for exploring the environment also have relatively enlarged representations in the sensory cortex.

However, comparative studies have not only indicated that brain components can increase (or decrease) in size, but there also appears to be evidence that new components may be added, thus theoretically increasingly the complexity of the system. For example, it is well known that the

cerebral cortex (i.e., the outer surface of the brain) may be partitioned into different cortical regions each with their own unique cellular anatomy and functional correlates. This outline of the cortical surface into a brain map was initially described through the pioneering work of Korbinian Brodmann who went on to describe some 52 cortical brain regions. Brodmann's map has been modified over the years with the addition of physiological and connectional studies, but his approach of mapping the cortical surface has been used successfully in mapping the brains of various species and providing comparative data to evaluate potential evolutionary changes in cortical regions. These studies have confirmed what Brodmann observed which is that the number of cortical areas differs between species. For example, the visual system of the macaque monkey has been shown to consist of around 30 distinct cortical areas (van Essen et al. 1992), while comparative studies on smaller brained mammals (e.g., mole or hedgehog) indicate that these species have far fewer cortical areas (Catania et al. 1999; Northcutt and Kaas 1995). These studies suggest that the number of cortical areas has increased with the evolution of large brains. Collectively, comparative studies at the level of the cortical area, as well as similar studies on smaller subunits of the nervous system (e.g., Bianchi et al. 2011; Spocter et al. 2015), emphasize that changes in size are not the sole factor to consider when looking at the evolution of the brain.

Conclusion

The field of evolutionary neuroscience has contributed significantly toward our understanding of the processes that have shaped the nervous system and that permit variation in the form and function of the brain. From a historical perspective, the field of evolutionary neuroscience is still emerging in many ways, coopting many of its ideas from that of general evolutionary biology (Striedter 2007). The relevance of evolutionary neuroscience in unraveling the mysteries of the human brain as well as the mechanisms that unite the function of all nervous systems remains a crucial contribution.

Cross-References

- [Costs and Benefits of a Large Brain](#)
- [Relative Brain Size, Encephalization Quotient](#)

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Evolution of the Human Brain

► Neurons in the Cerebral Cortex

Evolution of Tool Use

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Synonyms

Archeology; Lithic technology

Definition

The emergence of stone tools represents a significant milestone in hominin evolution culminating in the uniquely flexible abilities of humans to use and make tools. Studies on the evolution of tool use are aimed at reconstructing the evolutionary history of this adaptation. Although this area of inquiry has historically been the interest of archeologists, the integration of modern brain imaging techniques and the accumulation of comparative behavioral data in other animals have continued to widen its scope of study.

Introduction

The archeological record has revealed that humans and human ancestors have had a long reliance on stone tools (Larsen 2008). Since the early Pliocene (approximately three million years ago), the frequency and complexity of stone tools, as uncovered from archeological sites, gradually increased with a major expansion in tool technology occurring within the last 12,000 years (Boyd and Silk 2009), suggesting that tool use likely

conferred our ancestors with an adaptive advantage. This long co-occurrence/coevolution of tool usage and humans created a “biocultural feedback system” (Washburn 1960), whereby our evolved abilities not only allowed us to shape these tools but our interactions with them (and the act of shaping tools), resulting in changes to our underlying biology (e.g., changes in the hand and brain). Given the immense reliance and flexibility of humans at shaping and using tools, one would be forgiven for thinking that tool usage is a uniquely human feature. However, evidence garnered from the hominin fossil record (Asfaw et al. 1999; Semaw et al. 1997; Semaw 2006) and observations of tool usage in extant species (e.g., Rutz et al. 2016; Krützen et al. 2005; Whiten et al. 1999) challenge this assertion.

Comparative Tool Use in Other Species

One of the challenges with comparative behavioral research is being mindful of the pitfalls of anthropomorphism or indirectly setting up a *scala naturae* in our interpretations (Hodos and Campbell 1969). Therefore, it is important to clearly define the phenomena under investigation and to outline the associated criteria that make this comparable between species. When it comes to comparing data on tool use in different species, it is foremost important to define what a “tool” is and what are the criteria for usage. In this regard, a tool is usually defined as an object (which is not part of or produced by the animal’s body) that is used to attain a particular goal (Shumaker et al. 2011). Examples of this include the use of objects such as twigs to gather a food source as observed in birds (Rutz et al. 2016). Perhaps the most elegant of these observations are those seen in the New Caledonian crow appearing to even safeguard their preferred tools between tasks (e.g., Hunt and Uomini 2016; Uomini and Hunt 2017). A wide range of animals are known to use tools with a recent compendium indicating the observation of nonhuman tool use in nine classes of animals (sea urchins, insects, spiders, crabs, snails, octopi, fish, birds, and mammals) spanning four phyla (Shumaker et al. 2011). When examined across this wide range of species, the pattern of tool use behavior aligns poorly with our

understanding of brain size and neurological complexity (Shumaker et al. 2011; Sanz et al. 2013; Lemert and Spocter 2018a, b), suggesting that a further criterion separates the tool use behavior of humans from that of other species. Shumaker et al. (2011) assert that the real challenge is not only in the making of tools but in flexibly altering the sequence of actions during toolmaking especially when faced with novel challenges. As highlighted by Gunturken (2014), only some primate (Fragaszy et al. 2013), parrot and corvid species (Auersperg et al. 2011) have met this criterion, suggesting a much narrower band of animals for comparison. Toth and Schick (2013) suggest tool use in non-primates is driven by instinct whereas primates (including humans and other great apes) exhibit a gradual acquisition of tool use abilities (e.g., Shumaker et al. 2011) likely mediated through social learning and mimicry. Among the nonhuman primates, these abilities are most accentuated in that of our closest living relatives, the chimpanzees. Like humans, tool use behavior in chimpanzees is learned through the observation of other conspecifics and through trial and error (McGrew 1992, 2004). These behaviors include a number of complex behaviors including observations of chimpanzees deliberately shaping twigs for use in termite fishing (Whiten et al. 1999), evidence of geographic differences in tool culture between groups (Toth and Schick 2009; Whiten et al. 2009), and the ability of bonobo chimpanzees in learning to craft simple (Oldowan like) stone tools remarkably similar to that found in the hominin fossil record (Schick et al. 1999; Toth et al. 2006). Collectively, these observations suggest that humans share some components of our neural framework important for tool use with chimpanzees and that this framework likely helped support the emergence and subsequent evolution of tool use in fossil hominins.

The Hominin Fossil Record and Tool Use

Based on the fossil record, fossil hominins emerged on the continent of Africa some 7–8 million years ago and diversified into a numerous hominin forms (Larsen 2008). One can group these hominins into three main groups: (1) the

pre-australopithecines, which included more ape-like hominins dated between 7 and 4 million years ago; (2) the australopithecines dated between 3 and 2.5 million years; and (3) fossils belonging to the group *Homo*, dated from around 2–2.8 million years ago (Larsen 2008). In addition to these three major groups, there also evolved a group of later australopithecines (*Paranthropus robustus*, *Paranthropus boisei*) which, although sympatric with *Homo* (up until one million years ago), is believed to be an evolutionary dead end due to their rather specialized cranio-dental morphology (Grine 1988).

The Australopithecines

The early australopithecines are believed to be ancestral to *Homo* (Johanson 2004; Tattersall 2008) from which our species *Homo sapiens* emerged at around 160,000 years before the present (Larsen 2008). These early australopithecines were small-brained hominins, well adapted to bipedalism. Comparative endocast morphology suggests that early australopithecines (belonging to the species *Australopithecus africanus* and *Australopithecus afarensis*) had undergone slight brain expansion and restructuring in the neocortex, with a relative increase in the posterior parietal association cortex, along with a concomitant reduction in the size of primary visual cortex (Holloway 1981; Holloway and Kimbel 1986). Interestingly, the posterior parietal cortex coincides with the location of the temporoparietal area (Tpt), a key language area in humans, which is smaller in size in chimpanzees (Spocter et al. 2010). Among these early australopithecines, a hominin known as *Australopithecus garhi* (Asfaw et al. 1999) is considered one of the earliest candidate toolmakers. Remains from this species were found in the same region and in fossiliferous deposits of similar age (between 2.6 and 2.5 mya) to stone tools recovered from Ethiopia (Semaw et al. 1997; Semaw 2000, 2006). Stone tools from these sites mark the beginning of what is called the Paleolithic.

Early *Homo*

With the emergence of *Homo* (at around two million years), we see evidence for marked

hominin brain expansion (Klein 2009). The earliest stone tools are referred to as “Oldowan” stone tools and are named after the site Olduvai Gorge (Hovers and Braun 2009). By approximately 2.3 million years ago, Oldowan sites became numerous and widespread on the African continent and are attributed to the toolmaking abilities of *Homo habilis* and *Homo rudolfensis* (Schick and Toth 2006; Toth and Schick 2010). Oldowan tools are simple tools made by deliberately hitting one rock against one another and striking off stone flakes (Toth 1985). The emergence of these tools was a significant step in hominin evolution, and it is perhaps no coincidence that there is an alignment between the appearance of stone tools in the fossil record and the marked expansion in brain size in *Homo* (Holloway et al. 2004; Toth and Schick 2010). Some of the most striking evidence emerging from the study of Oldowan tools is the observations that hominins were clearly sourcing these materials from different localities and taking them to different sites (Leakey 1971; Schick and Toth 1993, 2006).

By around 1.8 million years ago, the larger brained *Homo ergaster*/*Homo erectus* appears in Africa and Asia (Lordkipanidze et al. 2013; Manger et al. 2012). It was during this time that some of the most striking evidence of stone tool evolution occurred. In particular, we see the development of new stone tools, called Acheulean, which were markedly different from the simple Oldowan form (Klein 2009, 2013; Lepre et al. 2011). This new stone tool industry was characterized by the shaping of handaxes, cleavers, and picks but still used the flaking approach of the Oldowan. Toth and Schick (2009) have demonstrated experimentally that the manufacture of Acheulean tools require a larger number of cognitive decisions and procedures than those required for making Oldowan tools and that these tools could be used efficiently in animal butchery (Schick and Toth 1993; Toth and Schick 2009). This tool industry became more sophisticated with time, and there is a suggestion that this refinement in the technology might even indicate an appreciation of aesthetics (Schick and Toth 1993).

Later *Homo*

Given the observation that stone tool sites continued to proliferate along with the rapid expansion of the genus *Homo*, it is parsimonious to assume that species from this genus are responsible for the majority of early stone tools uncovered. In both Africa and Europe, later *Homo* belonging to the taxonomic group “archaic *Homo sapiens*” include the species *Homo heidelbergensis* and *Homo neanderthalensis* (Klein 2009). It is during this time that a transition in stone tool industries occurs from later Acheulean to the Middle Paleolithic. Stone tools from the Middle Paleolithic are characterized by flaked tools (e.g., scrapers and points) which were often made by carefully shaping the external surface through striking off flakes, likely requiring higher cognitive skills. In addition, during this time period, there is increasing evidence of fire use at habitation sites (Mellars 1996; Roebroeks and Villa 2011) which would have conferred additional advantages to hominins from this time period.

Modern Humans

By around 160,000 years ago, fossils found in parts of Africa and the Near East are considered to belong to early *H. sapiens* and are associated with Middle Paleolithic which then progressed to Upper Paleolithic as humans became more widespread (Klein 2009). During the Upper Paleolithic, modern hunter–gatherers had tools consisting of long, thin blade technologies which served as efficient cutting tools (Pettitt 2013). Tools during this period continued to be refined becoming increasingly smaller and forming part of composite tools (e.g., used as points or knives) (Klein 2009). The appearance of composite tools was a major achievement in tool use, requiring arguably a higher level of planning and forethought than previous tools (Ambrose 2010). Composite tools were made of two or more materials that were prepared separately before being combined into a single tool (Ambrose 2010). During this time period we also see the use of other materials such as bone and ivory in the making of tools (Klein 2009; Pettitt 2013) as well as the development of mats and textiles (Adovasio

et al. 1996), symbolic expression through the development of ornamentation and figurines (White 2003; Cook 2013), and the evidence of engraving and painting (Clottes and Arnaud 2003; White 2003; Cook 2013).

Tool Use and Reorganization of the Brain

As shown through observations from the fossil record, the gradual increase in tool complexity and associated expansion in hominin brain size suggest that tool usage must have been adaptive and resulted in some degree of brain reorganization (Teschke et al. 2013). While this is still an emerging area of research, comparative neuroimaging data has provided some interesting evidence to support this claim. In particular, evidence for reorganization in the brain following tool use has been shown in both monkeys and humans (Iriki et al. 2001; Maravita et al. 2002). Exposure to a tool using task resulted in an adjustment in body perception, with both species perceiving the tools as extensions of their individual bodies (Iriki et al. 2001; Maravita et al. 2002). Similarly, there are species-specific differences in the somatotopic representation of the hand and foot in humans and monkeys (Hashimoto et al. 2013). In particular, while both humans and monkeys have separate somatotopic units for the fingers, the human foot representation has undergone reorganization away from the fused map of all five toes (as found in monkeys) toward a dedicated somatotopic unit for the big toe markedly separate from the other toes (Hashimoto et al. 2013). This unique organizational feature is hypothesized to be indicative of the shift toward bipedalism. Furthermore, there is also evidence to suggest that tool use in non-primates might also be associated with reorganization in the brain. In particular, a recent study of the tool-making New Caledonian crows has indicated that this species has evolved enlarged brain areas involved in associative and motor learning, suggesting an independent evolution of cognitive skills supporting tool making in both corvids and primates (Mehlhorn et al. 2010). One more area that has made significant contributions to the question of tool use and which promises much in expanding our understanding of the evolution of tool use has been the comparative study of hand

morphology in primates (Stout 2002; Marzke et al. 1998; Marzke's 2013).

Conclusion

The evolution of stone tools was a significant step in hominin evolution, undoubtedly serving as an important input for the development of other biocultural features. Ongoing inquiry in this field has helped to advance our understanding of own tool abilities to use tools and the evolutionary history of our species. This area of inquiry has also helped gain much needed insight into species differences in tool use and how human tool use differs from that of other species.

Cross-References

- [Brain Evolution](#)
- [Evolution](#)
- [Hominin Evolution](#)
- [Stone Hammers](#)

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Evolution of Virulence

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Synonyms

[Differences in viral infection](#)

Introduction

Within nature, there exist a variety of parasites that can cause a wide range of problems to the infected host. Some parasites are relatively benign, while others can cause serious medical complications. The simplified answer is that certain levels of virulence were naturally selected to be beneficial to the parasite over others.

Virulence and Trade-offs

The term virulence can have several different definitions depending on the context of the

discussion. According to Cressler et al., “The most general definition of virulence is the reduction in host fitness caused by infection. In mathematical models, virulence is quantified as an infection-induced increase in host mortality rate or reduction in host reproductive rate. In experimental or observational data, virulence is often quantified by measures of ‘harm’ done by the parasite, such as host anemia, weight loss, or morbidity, assuming that this harm is correlated with negative impacts on host fitness” (Cressler et al. 2015). For the purpose of this excerpt, virulence will refer to the mortality rate that is caused by the infection. According to the Centers for Disease Control (CDC), some of the most notably virulent diseases include those with very high rates of infection, such as Ebola, HIV/AIDS, tuberculosis, and pneumonia.

When it comes to understanding the evolution of virulence, there are several important factors to take into consideration. Firstly, the variation of virulence between different parasites can best be explained by what is known as “evolutionary trade-offs.” Trade-offs are best defined as “A situation that occurs when a change in one trait increases fitness, but a simultaneous change in another trait reduces fitness, thus preventing the organism from optimizing both changes” (Oxford References 2010). For example, there are two different levels that influenced differences regarding virulence. The first level is the population of the host. The greater the number of potential hosts, the greater the opportunity the parasite has to infect them. However, the parasite is only as successful as its ability to survive within the host without being immediately destroyed by the immune system, antibiotics, or other measures. Hence, the success regarding the host population is also inherently related to the success regarding the interactions within a host (Van Baalen and Sabelis 1995).

The second level that influenced differences within virulence is within the host’s population. For example, this means that the success of the parasite is also dependent on factors such as on-going infections, different parasites already present, and many other factors. Cressler states that “These interactions may be antagonistic,

when parasites compete for resources or provoke a cross-reactive immune response, or they may be facilitative, when closely related strains cooperate or cotransmit” (Cressler et al. 2015). It is important to note that the parasite must be successful regarding both of these levels; therefore, this model can help explain differences regarding virulence. Mideo et al. report that “Because parasites must ultimately be successful at both the within-and between-host scales, virulence is expected to evolve to balance these potentially conflicting selection pressures” (Mideo et al. 2008).

Conclusion

The information provided within this expert is a cursory exploration into the evolution of virulence. There are numerous different theoretical and empirical literature that make the case for different approaches to this topic. It is important to note that the biological processes that take place cannot be overlooked, as they play a key role in understanding the fundamentals regarding the evolution of virulence.

Cross-References

- [Parasites](#)
- [Virus](#)

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Evolution Theory

- [Jean-Baptiste Chevalier de Lamarck](#)

Evolution's Empress: Darwinian Perspectives on the Nature of Women

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Definition

An edited book that focusses on women as active agents within the evolutionary process.

Introduction

Evolution's Empress: Darwinian Perspectives on the Nature of Women was published by Oxford University Press in 2013 and co-edited by Maryanne Fisher, Justin Garcia, and Rosemarie Sokol-Chang. It contains 22 chapters, plus an additional foreword by Sarah Blaffer Hrdy, and an Introduction. The chapters span a range of topics such as health and reproduction, competition and cooperation, parenting, and mating and communication. The goal of the editors was to integrate evolutionary and feminist perspectives, showing that they can work together to provide novel insights into behavior.

Integrating Evolutionary and Feminist Perspectives

In the Introduction, the editors of *Evolution's Empress* propose that there can be a meaningful reconciliation between the feminist scholarship and that based on an evolutionary framework. They acknowledge that both of these broad areas are

grounded in different histories and consequently often arrive at disparate conclusions. Those studying behavior using an evolutionary perspective rely on the scientific method, espousing objectivity, and believe they are building programs of research based on past, objective research. Feminist scholars often rely on qualitative methods, question the existence of objectivity, and propose that research does carry real-world social and political consequences. The editors review a growing dissatisfaction within the field of evolutionary psychology with respect to how women have been viewed as passive, or the neglect of topics that are critical for women, such as mothering, female alliances, and female physiology. Thus, one aim of the editors was to show that women have a leading rather than backseat role in human evolution.

Sex Roles, Aggression, Competition, and Cooperation

Evolution's Empress is divided into five sections. Section one, "Sex Roles, Aggression, Competition, and Cooperation," starts with an examination of female social relationships and contains four chapters. The section begins with Maryanne Fisher's overview of the topic of women's intrasexual competition for mates. It moves onto a chapter by Laurette Liesen, who analyses female aggression, alliance development, and how women view status. Liza Moscovice examines female alliances within the bonobo, a great ape that is closely aligned genetically with humans. This section ends with a chapter by Patricia Gowaty who presents the development of theoretical (and mathematical) predictions pertaining to sex differentiated behavior and the study of individual differences.

Mothering and Parenting

Section two contains five chapters. It begins with Kathryn Coe and Craig Palmer discussing the role of women in transmitting traditions regarding cooking and storytelling. Nicole Cameron and Justin Garcia then review the extraordinary and

distinct biological contributions that maternal effects have on adaptive offspring development. In their chapter on flexible parenting strategies, Lesley Newson and Peter Richerson investigate diverse parenting behavior and show that one commonality is female cooperation in the raising of children. Rosemarie Sokol-Chang suggests that listeners are responsive to vocalizations from attachment partners, proposing that these vocalizations have led women to solicit help in child rearing. Laura Betzig authors the last chapter in this section and reviews historical evidence on conflict between fathers and sons, showing that sons win conflicts when they have strong mothers.

Health and Reproduction

Section three contains four chapters. To start, Chris Reiber demonstrates how limited knowledge exists for women's reproductive physiology and the important contributing role that an evolutionary feminist perspective may play in furthering this area. In her chapter, Bobbi Low uses a life history/behavioral ecology approach to explore human fertility, as it relates to social, cultural, and ecological factors. One theme in Low's chapter, the trade-off between present and future reproduction, is the focus of the chapter by Johannes Johow, Eckart Voland, and Kai Willführ. They examine grandmothers, in particular, and contend that grandmothering is based on relevant conditions, including whether they are a grandmother based on their son's or daughter's reproduction. This theme of present or future considerations carries into the last chapter in this section by Michelle Escasa-Dorne, Sharon Young, and Peter Gray who explore woman's life history decisions in terms of childcare and views of romantic relationships, as influenced by life course development.

Mating and Communication

In the first of four chapters in this section, Linda Fedigan and Katharine Jack discuss, as an example species, female white-faced capuchins' active

rather than passive role in male mating strategies and throughout the full reproductive process. David Frederick, Tania Reynolds, and Maryanne Fisher present how women's choice of mates across diverse circumstances reflects flexibility in mating strategy. One trait, humor, is the focus of a chapter by Christopher Wilbur and Lorne Campbell. They discuss how women's choice of men with humor has actively shaped men's evolutionary history. In the last chapter in this section, Elisabeth Oberzaucher reviews sex differences in communication styles as a possible explanation for global inequality.

New Disciplinary Frontiers

The last section contains five chapters, spanning a considerable range of topics that collectively demonstrate how evolutionary and feminist perspectives may be integrated, leading to novel research developments. Tami Meredith presents how previously documented sex differences are better understood when one includes examination of motivations. She concludes that many of the sex differences are not absolute, but instead rely on different motivations, or occur at different frequencies. Nancy Easterlin continues with this theme, suggesting that sex differences do not necessarily imply differences in value. She uses the example of Brontë's novel *Jane Eyre* to show that evolved differences do not determine social outcomes but instead allow one to explore male control of female's strategies related to reproductive fitness and personal autonomy within pair-bonds. Julie Seaman reviews the necessity for a merger between feminist legal scholars and evolutionary psychologists, which would lead to insights of the latter group to be incorporated and thereby enable a deeper understanding of the human behavior that the law seeks to shape and regulate. Michele Pridmore-Brown combines queer theory with research on cooperative breeding to explore the "queering" of nature and the biologization of culture. Leslie Heywood, in the final chapter of the book, applies the extended synthesis of evolutionary biology as a way to resolve conflict and facilitate a conversation between evolutionary

psychology and feminist theory. She clarifies with several precise examples how the extended synthesis may serve to mediate the central tenets of feminist theory and those within evolutionary psychology.

Conclusion

The aim of the editors of *Evolution's Empress: Darwinian Perspectives on the Nature of Women* was to collect chapters that represent the range of research on women's active role in evolution. These chapters show, to varying extents, the ways in which evolutionary perspectives of human behavior and the feminist scholarship may be integrated, yielding novel directions for research. They contend that prior research that overlooks the inclusion of women and their viewpoints leads to the default and often erroneous conclusion that women are like men. They further posit that research on sex differences is of high importance but must consider women in a way that reflects their active role in human evolution. This book represents the contemporary shift from seeing women as passive to active agents within disciplines that rely on an evolutionary framework.

Cross-References

► [Maryanne Fisher](#)

Evolutionary Aesthetics

► [Landscape Preferences](#)

Evolutionary Aggression

► [Strategic Aggression](#)

Evolutionary Altruism

► Problem of Altruism

Evolutionary Arms Race

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Synonyms

Coevolution of the sexes; Intrasexual selection

Definition

The positive feedback loop created as genes, traits, sexes, or species complete and develop adaptations and counteradaptations to each other in order to optimize their fitness. In this case, it is in reference to the human sexes.

Introduction

A recurring feature of street slang is the phrase “size matters.” Growing evidence suggests that when it comes to human reproductive competition and genital morphology, size does matter.

The Evolutionary Arms Race and Genitalia

Gallup et al. (2003) devised a way to simulate sexual encounters under laboratory conditions to test what has come to be known as the semen displacement hypothesis. According to this hypothesis, sperm competition among human

males not only has led to larger ejaculates that contained more sperm but the human penis may also have evolved as mechanical means of competing with rival male semen in the female reproductive tract. The unique configuration of the human penis with its enlarged, bulbous glans at the head of the penis accompanied by the coronal ridge, which encircles the glans at the interface between the glans and the shaft of the penis, evolved to cope and compete with the presence of semen left by other males in the female’s reproductive tract by scooping and displacing the left-over semen from her prior suitors back away from the cervix to enable the male to substitute his semen for those of his rivals.

To test this hypothesis, Gallup et al. (2003) simulated sexual encounters under laboratory conditions using an array of artificial human genitals. The human penises consisted of latex dildos of different shapes and sizes, and the vaginas consisted of commercially available latex devices engineered to fit over the penis in such a way that males could use the latex vagina to masturbate. Gallup et al. (2003) also concocted different recipes for producing simulated semen which could be introduced into the artificial vaginas. Semen displacement trials involved inserting different artificial penises into the vaginas that had been loaded with simulated semen so that they could measure/quantify resulting variation in the magnitude of semen displacement.

Gallup et al. (2003) discovered that artificial penises that approximated human penis morphology displaced significantly more semen than did those of other shapes. They also discovered that the magnitude of semen displacement was directly proportional to the depth of insertion of the penis into the vagina. Follow-up questionnaire data included in the same paper showed that both men and women in committed relationships reported that following periods of either separation or allegations of female infidelity (as proxies for insemination by rival males), males engaged in significantly deeper and more vigorous penile thrusting during intercourse which would function to affect more complete displacement of rival male semen from the female’s vagina.

Conclusion

These findings bear directly on the possibility of a genital evolutionary arms race during human evolutionary history. With the emergence of semen displacement as another sperm competition strategy there may have been selective pressure operating on males to deposit semen in the deepest and most remote parts of the female vagina to minimize semen displacement by other males. This in turn could have put a premium on the development of bigger and longer penises that could more effectively access and displace semen left by other males from the most remote areas of the vagina. That in turn could have led to an evolutionary arms race which gave rise to the fact that among the other great apes which are our closest living relatives, the human penis is the largest, longest, and most peculiarly configured with an enlarged glans and coronal ridge.

To return to the question does size matter, the evidence suggests that as a consequence of sperm competition and the emergence of semen displacement during human evolutionary history, size did and may continue to matter when it comes to intrasexual competition for paternity among human males.

Cross-References

- [Genital Evolution](#)
- [Sperm Competition](#)

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Evolutionary Behavioral Psychology

- [Selectionist Models: Implications for Behavior](#)

Evolutionary Biologist

- [David Haig](#)
- [Peter Kropotkin](#)

Evolutionary Biology and Feminism

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Synonyms

[Feminism](#), [Evolutionary Psychology](#)

Definition

There has been an ongoing uneasy relationship between evolutionary biology and feminism(s) due to highly differing perspectives about objectivity in science, issues of sex differences, and the role of biology versus social and cultural construction.

Introduction

The tension between evolutionary biology and feminism(s) is palpable when it comes to understanding and explaining human behavior. At times, there seems to be no space for integrating the two perspectives: for example, Birke (2017) discusses how biological sex (i.e., anatomically female or male) and more generally the “ghost of biology” still remains problematic for feminist thought. Typically, feminists often view evolutionary based research as anti-feminist, reductionist, and neglecting the inclusion of social and cultural influences. This tension has been

documented for at least four decades by a range of scholars (Fausto-Sterling 1997; Fedigan 1986; Fisher et al. *in press*, 2013; Gowaty 1997; Hager 1997; Heywood 2013; Hrdy 1981; Kelly 2014; Nier and Campbell 2013).

One important consideration is that there is no unitary, integrated theory that can be accurately called feminism, as there exist many different variants and perspectives. Thus, there is no central, general theory that holds feminist views together (Eagly and Wood 2011); even the terms “feminist” and “theory” are debated within the feminist community (see Radtke 2017, for a review). The very heart of third-wave feminism is the reliance on multiple perspectives/multivocality and an intersectional approach leading to inclusivity and nonjudgment, rather than synthesis with theoretical justification that leads to “differences” (Snyder 2008). This issue aside, gender construction, sex, and human-focused research are considered to be comfort zones for exploring feminist issues (Åsberg and Birke 2010).

Those using an evolutionary perspective tend to ground their work in the scientific method and evolutionary theory. They form inquiries using past research that they perceive as inherently objective (i.e., value free), rather than subjective. In contrast, those working in feminist areas question this very objectivity (see Hankinson Nelson 2017) and have indicated the numerous ways bias enters the scientific method, as well as the fact that research has real-world social and political effects (Fisher et al. 2013). One example is simply the language used in biology and medical texts to explain human fertilization: the ovum is described as passive while the sperm is described as active (for this and other examples, see Hankinson Nelson 2017). Fisher et al. (*in press*) document that the key arguments used by feminists pertain to the analysis of evolutionary scholars when biological, social, cultural influences collide to shape human sexuality and how the latter generalize their findings.

One particular source of disagreement rests on evolutionary scholars’ reliance on parental investment theory. Parental investment theory (Trivers 1972) leads to conclusions of sexual inequalities,

such as women’s obligatory investment in pregnancy and children, women’s proportionately lower reproductive variance than men’s reproductive variance, and women’s higher choosiness in mate selection as compared to men. Such conclusions are not necessarily accurate or as applicable to primates as they are to other animals (see Gowaty 2013; Heywood 2013; Hrdy 1986). Feminists argue that this approach to human sexuality reinforces sexual double standards, while simultaneously neglecting any action or thinking that would reduce or remove social inequalities and injustices, especially directed at women and minority populations. Further, feminist scholars often see research on sex differences enforcing heteronormativity/heterosexuality, propagating and supporting stereotypical and ethnocentric beauty standards for women, and rationalizing or normalizing harmful behaviors of men towards women (e.g., speculation about the adaptive function of rape [Thornhill and Palmer 2001], family conflict [Daly and Wilson 1999], or domestic violence [Wilson and Daly 1998]).

The role of social constructionism in feminist scholarship also prohibits a strong integration with evolutionary viewpoints and is the cornerstone of much feminist writing (e.g., Heywood 2013). Social constructionism generally refers to “the belief that rather than our living in a readily knowable ‘out there’ reality, we dwell in a world that is socially constructed, constructed by our experiences with others, and validated consensually and communally” (Barkow 2006, p. 24). According to typical feminist scholars, evolutionary theorizing rests on a foundation of biological essentialism and biological determinism and rejects social and cultural factors (e.g., Eagly and Wood 2011). This divide may be artificial, given as Barkow (2006) reviews: we are a culture-bearing species, meaning we rely on socially transmitted information for our survival and reproduction. Any argument in favor of social construction demands that humans are able to socially transmit and receive information, and evolutionary perspectives show that this capacity has itself evolved. The human brain has changed over time to adapt to increasingly complex social environments, and we need to be able

to acquire and then use information about our local environmental (i.e., geographic, social, familial, cultural) conditions. This information leads to successful responses within these environments, which means that humans possess evolved mechanisms that permit – and even rely on – social construction. Social construction is not *against* biological explanations of behavior but instead is synergistic; both are constrained by our evolved brains and bodies. Indeed, our only option is to agree with the assertion by Janicki and Krebs (1998, p. 202): “purely biological models will not be able to supply a full account of human behavior without reference to cultural process.”

There have been numerous attempts to integrate evolutionary perspectives with feminist scholarship. These attempts generally are aimed at arriving to a more holistic comprehension of humans, particularly in terms of sex and gender. Relatively recent developments in evolutionary theory, from the modern synthesis to the extended synthesis of evolutionary biology, show noteworthy potential for integrating feminist and evolutionary approaches to the study of gender, sex, and sexuality in behavioral sciences (see Garcia and Heywood 2016). These types of developments showcase social environments are as significant a consideration as material biology and highlight how they are co-constitutive such that one responds to the other, typically in heritable ways. Similar frameworks in behavioral ecology, cultural evolution, and gene-culture co-evolution have been created and view biological species in a social environmental context. We note that, like Campbell (2006), acknowledging the importance of culture in shaping human factors such as gender/sex is not asserting that there is an absence of biological influences to consider.

There have been decades worth of biologists who are feminists (e.g., Haraway 1978), as well as those working within feminist evolutionary biology (e.g., Fausto-Sterling et al. 1997; Smuts 1995). There is notable interest in the area, as seen by the formation of the Feminist Evolutionary Perspectives Society in 2009 (Sokol-Chang and Fisher 2013). There are now special issues of peer-reviewed journals have been devoted to the topic, as well as entire books and edited

volumes, including several feminist rebuttals (see Fisher et al. [in press](#), for a review).

Conclusion

In summary, evolutionary theory has existed for well over a century, and feminist responses to it emerged shortly after. Additionally, feminisms have long studied the effect of culture, which in turn is created by evolved minds. However, both disciplines have historically failed to see where integration was obvious, necessary, or beneficial. While strides have been made, we argue that there remains much work to be done. This work needs to come from both fields. We previously noted that incorporating feminist views within evolutionary perspectives has made inroads, but there is resistance for the reverse transaction. These impediments must be identified, reviewed, and eliminated.

Cross-References

- [Evolutionary Psychology](#)
- [Evolutionary Psychology, The Handbook of](#)
- [Feminism](#)

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Evolutionary By-Products

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Synonyms

[Aptation](#); [Co-opted adaptation](#); [Co-opted spandrel](#); [Exaptation](#); [Non-aptation](#); [Secondary adaptation](#); [Spandrel](#)

Yet living organisms are historical structures: literally creations of history. They represent, not a perfect product of engineering, but a patchwork of odd sets pieced together when and where opportunities arose. (François Jacob 1977 – *Evolution and Tinkering*, p. 1166)

Definition

In broad evolutionary terms, a by-product is a characteristic of an organism that evolved simply because it happened to be structurally

and inextricably associated with an adaptation via historical constraints. As opposed to adaptations, evolutionary by-products are not the primary targets of natural selection. They have no functional design: they did not originate as solutions to adaptive problems. They only come about through the correlated selection of adaptations, and not because they were, themselves, *originally* selectively advantageous (i.e., during the period of evolution of the phenotypic trait under study). I will further define three types of evolutionary by-products, namely, spandrels (i.e., fitness-neutral by-products of adaptations), fitness-enhancing co-opted adaptations (i.e., exaptations Type 1), and fitness-enhancing co-opted spandrels (i.e., exaptations Type 2).

Introduction

A primary goal in evolutionary science is to determine whether a given phenotypic trait is an adaptation, a by-product of naturally selected features (i.e., spandrel, exaptation Type 1, or exaptation Type 2), or a residue of noise – or the result of a sequential combination of these products over evolutionary time. Among all these products of evolutionary processes, the first one has received the most attention, whereas the evolutionary significance of the others tends to be misunderstood and underestimated. After defining each of these concepts, I will highlight some common terminological confusions associated with the claims that a trait belongs to one of these categories. I will discuss the reliability and validity of such claims, particularly for behavioral and psychological characteristics that do not leave systematic traces in the fossil record. I will review some of the conceptual and methodological tools that allow researchers to distinguish among different evolutionary products and to test “evolutionary by-product” hypotheses. Moving away from a purely adaptationist stance, I will use examples from various research disciplines (e.g., evolutionary biology, evolutionary psychology, evolutionary linguistics) to rehabilitate evolutionary by-products as truly representative of the historical essence of the process of evolution, rather than “best-of-a-bad-job,”

and often underrated, explanations one resorts to when functionalist hypotheses have failed to be supported by the data at hand.

A Few Evolutionary Processes and a Range of Constraints on the Evolution of Adaptations

Five Main Evolutionary Processes

Biological evolution is defined as a change in allele frequencies and thus in the phenotypic distribution, within a population of individuals from a given species, across generations and over geological time. In the scientific community, there is a consensus on the various evolutionary processes or forces, which can cause such changes. These include (1) mutations, defined as random errors occurring during DNA replication and generating new genetic variants; (2) genetic recombination, defined as the rearrangement/reshuffling of DNA sequences during meiosis by a series of breakage; rejoining and copying of chromosome segments; (3) gene flow, defined as the transfer of alleles from one population to another through the migration of individuals that carry those gene versions; (4) genetic drift, defined as the variation in the relative frequency of different genotypes because of the random sampling of individuals from one generation to the next due to chance events, whose effects are stronger in smaller populations; and (5) natural selection, defined as the differential reproductive success of individuals contributing to the gradual and generally directional shaping of phenotypic traits, due to heritable phenotypic variation (Ridley 2004). It is noteworthy that sexual selection is considered a mode of natural selection in which assortative/disassortative (i.e., nonrandom) mating is defined as the tendency for individuals to select mates that are more similar/dissimilar to themselves in terms of phenotypic characteristics than would be expected by chance. To some extent, all these evolutionary processes create changes in the biologically inherited traits (i.e., genotype) of a population of individuals over successive generations. It is also widely acknowledged that natural selection is the primary driver of evolutionary change of organisms in response

to the external pressures of the ecological environment and the only evolutionary process that can produce adaptations (i.e., integrated features designed to solve particular fitness-related problems in the ancestral past; Williams 1966).

Yet, beyond these broadly accepted notions, the literature on evolutionary theory has long been the battlefield of heated debates, including clashes about the relative power of natural selection and the relative ubiquity of adaptations (e.g., Gould and Lewontin 1979; Sterelny 2001). Indeed, all evolutionary scholars agree that Darwinian evolution cannot be reduced to the following sequence of events: a series of random genetic mutations bringing about a large pool of phenotypic variants, gradually winnowed away by the exclusive action of external selective pressures, and necessarily leading to adaptations. Such a simplistic and deterministic view would correspond to a null model assuming that organisms evolve only in response to ecological factors, independently of internal factors (i.e., in the absence of constraints). We know this model is not tenable. Even Darwin and scientists who may be characterized as early ultra-Darwinists (e.g., Thomas Henry Huxley) or neo-Darwinian hardliners (e.g., Daniel Dennett, Richard Dawkins, and Steven Pinker) have never denied the importance of multiple constraints that limit the range of phenotypic outcomes of selection (but see Olson 2019a, for a false dichotomy between adaptation and constraint; see also Antonovics and van Tienderen 1991, for the claim that most studies of constraints are limited by the lack of a clear null hypothesis).

Constraints

In evolutionary parlance, a constraint is a causal mechanism – originating from the internal organization of the system under study – that reduces the range of possible phenotypes available for sorting by the selection process based on external pressures (Raff 1996). In other words, constraints usually refer to the limited ability of natural selection to break or modify the structural correlations among an individual's constitutive characters. A constraint prevents directional selection from continuously changing any phenotypic trait and

always creating more optimally designed adaptations (i.e., the highest fitness-enhancing phenotype cannot be reached). By setting boundaries to phenotypic variability, a constraint produces stabilizing selection, lessens the evolutionary response of phenotypic traits to external selective factors, limits the adaptation of the system to its ecological environment, and holds powerful reins over possible evolutionary pathways (Schwenk and Wagner 2004).

There are many types of constraints (e.g., time-lag effect, available genetic variation, costs involved in the construction of adaptations; Dawkins 1982), and the most relevant type to account for evolutionary by-products is referred to as historical constraints. Indeed, living organisms are not blank slates on which natural selection would optimally design new traits but historical structures with highly integrated body plans; their building blocks are not independent entities but interrelated packages of features that emerged from historically contingent events associated with the tinkering process of natural selection (Jacob 1977). Therefore, the evolutionary history of a lineage is deeply entrenched into the structure of its constituent taxonomic units, channeling their respective phyletic heritages, delimiting their pathways of development, and restricting modes of changes in their general architecture. This is why historical constraints on the evolution of organisms often include phylogenetic and developmental constraints but also structural, architectural, anatomical, morphological, geometric, allometric, pleiotropic, and epigenetic constraints (Antonovics and van Tienderen 1991). Historical constraints are found at different levels of internal organization of a biological system, including the genomic, organismic, or social levels (Thierry 2013).

From this perspective, organisms and their suites of phenotypic traits are not puppets with infinite potential for change because there are tight historical constraints on their optimal designs. Sometimes, there is simply no way to get there from here. According to Buss et al. (1998, p. 539), “[a]daptations are not optimally designed mechanisms. They are better described as jerry-rigged, meliorative solutions to adaptive problems

constructed out of the available materials at hand, constrained in their quality and design by a variety of historical and current forces.” In short, natural selection is not the only and all-powerful force of evolution, and adaptation is an onerous concept, just one among other evolutionary products (Williams 1966).

Five Main Products of Evolutionary Processes and Constraints: The Key Role of Causal History

There are five main products of the aforementioned evolutionary processes and constraints, namely, adaptations, co-opted adaptations (i.e., exaptations Type 1), spandrels, co-opted spandrels (i.e., exaptations Type 2), and residues of noise (please see Table 1 for general definitions and characteristics of these concepts; see also Linde-Medina 2017, for an extended “taxonomy of non-fitness”).

Adaptation

The term “adaptation” refers to both the *process* by which natural selection modifies a trait that facilitates the propagation of a (set of) gene(s) and the *end product* (i.e., the trait itself) that has been designed by this process. Strictly speaking, an adaptation (*sensu product*) is a trait that owes its existence to its causal history (i.e., because it was favored in the past by natural selection), regardless of its current usage or role. According to Sober (2000, p. 85): “Characteristic *c* is an adaptation for doing task *t* in a population if and only if members of the population now have *c* because, ancestrally, there was selection for having *c* and *c* conferred a fitness advantage because it performed task *t*.”

The primary usage that caused the adaptation to evolve is called a “function.” The function of an adaptation was the fitness benefit that led to the adaptation being favored by natural selection. Therefore, inferring the function of a trait consists in making a claim about why this trait came into existence during its period of evolution, and not what this trait performed later or currently does. This is why evolutionists and philosophers insist

on the terminological distinction between an “adaptation” and an “adaptive” trait (Burian 1983). They argue that these two concepts answer two questions that refer to two different temporal stages in the evolution of a trait, namely, what was the trait’s primary usage (i.e., its function) that favored its selection when it *originally* emerged in the ancestral past (i.e., the trait as an adaptation) and what was (*later*) or is (*currently*) the trait’s fitness-enhancing contribution (i.e., the trait as being adaptive).

Even though many traits are both adaptations and adaptive, the two terms are not interchangeable. A trait may be adaptive without being an adaptation. Indeed, a trait could, at any point in time, (have) become useful in performing task *t* and as a result (have) increase(d) the fitness of its bearers, even though the trait in question was not originally selected for this usage; for example, it might have arisen through one (or the combined effect) of the aforementioned nonselective evolutionary process(es), such mutation, genetic recombination, gene flow, or genetic drift. Conversely, a trait may be an adaptation without being adaptive. Indeed, a trait that was originally favored by natural selection to serve a particular function could, at any point in time, and if the environmental conditions change, lose its positive correlation with the survival rate or reproductive success of its bearers. Therefore, adaptation and adaptiveness are not synonymous because the definition of the former is history-laden, whereas the latter term does not speak about the evolutionary history of the trait. Historical causes and constraints are also at the core of the three main evolutionary by-products of naturally selected traits, namely, spandrels, exaptations Type 1, and exaptations Type 2.

Spandrel

Spandrels are fitness-neutral by-products of adaptations. Therefore, spandrels are *selected* (i.e., they arise through natural selection), but not *selected for* by-products of *selected for* phenotypic traits. Like other evolutionary by-products, spandrels have no functional design: these traits did not originate as fitness-enhancing solutions to ancestral adaptive problems *during* their period of

Evolutionary By-Products, Table 1 Definitions and characteristics of five products of evolutionary processes.

Name of evolutionary product	Adaptation	Evolutionary by-products			Residue of noise
		Exaptation Type 1 (aka: Co-opted adaptation)	Exaptation Type 2 (aka: Co-opted spandrel)	Spandrel	
Definition	Inherited and reliably developing trait that came into existence through natural selection because it helped to solve a specific problem of survival or reproduction better than alternative designs existing in the population during the period of their evolution	Trait arising from a preexisting adaptation whose original structure is subsequently co-opted for a new fitness-enhancing usage (i.e., effect) but without being modified by natural selection for this effect	Trait arising from a preexisting spandrel whose original structure acquires a fitness-enhancing usage (i.e., effect) without being modified by natural selection for this effect	Unselected(-for) and fitness-neutral by-product of an adaptation resulting from historical constraints, and arising as a necessary and functionless side effect of an adaptive design	Trait shaped by random effects resulting from forces such as chance genetic events during the development, or sudden and drastic environmental changes
Evolutionary process(es) causing the trait to evolve	Natural selection	Natural selection operating on preexisting adaptation	Natural selection operating on preexisting spandrel	Natural selection operating on original adaptation that is coupled with spandrel	Genetic mutations, genetic recombination, gene flow, genetic drift
Fitness-enhancing <i>during</i> the period of evolution of the trait?	Yes	No	No	No	No
Fitness-enhancing <i>after</i> the period of evolution of the trait?	Possibly (but not necessarily)	Yes (aptation)	Yes (aptation)	No (non-aptation)	No
Characteristic of the usage causing the trait to evolve	Primary	Secondary	Secondary	Not applicable	Not applicable
Name of the usage causing the trait to evolve	Function (in the historical sense)	Effect (i.e., later/current utility)	Effect (i.e., later/current utility)	Not applicable	Not applicable

evolution. Unlike other evolutionary by-products, spandrels did not acquire any fitness-enhancing role at any point *after* their period of evolution: these traits have never been, and are still not, adaptive. Spandrels have no, and never had any,

function and effect. Even though a spandrel was not, itself, selected, it evolved through a process of natural selection operating on the original adaptation that was structurally and necessarily coupled with the spandrel via historical

constraints. The inextricable structural connections between adaptations and spandrels can be explained by a number of biological mechanisms, including pleiotropy (i.e., genetic effect of a single gene on multiple and seemingly unrelated phenotypic traits in an organism) and linkage disequilibrium (i.e., nonrandom association between allelic variants at different loci within a population due to the history of recombination, mutation, and selection in a genomic region).

In a seminal paper aiming to combat pan-adaptationism – and its “just-so stories,” overestimating the number of adaptations in any organisms and erroneously attributing functions to any traits – paleontologist Stephen Jay Gould and geneticist Richard Lewontin introduced the term *spandrel* into the evolutionary literature (Gould and Lewontin 1979). In architectural terminology, a spandrel (or a pendentive) refers to the two-dimensional (or three-dimensional) and roughly triangular space that unavoidably appears between the tops of two adjacent round arches and the ceiling of a building (or the domed roof of a church). The arches are adaptive features that were designed to serve the function of supporting the ceiling/dome. However, spandrels are not adaptive features; they are the results of structural constraints and come about as inevitable and functionless side effects of the design of the building. “Spandrels [...] are necessary architectural by-products of mounting a dome on rounded arches” (Gould and Lewontin 1979, p. 581). Spandrels would not exist without arches (i.e., their adaptive counterparts). Even though the use of the term “spandrel” in evolutionary biology/psychology is relatively recent, the concept might go back to Darwin’s (1859/1964, p. 5) notion of “correlation of growth” (Gould 1997). It is beyond the scope of this review to further venture into terminological and conceptual debates. However, it is noteworthy that Gould and Lewontin’s (1979) influential critique of the adaptationist program has been itself heavily criticized by evolutionists, architects, and philosophers for (1) overstating the role of constraints in evolution (Rose and Lauder 1996); (2) mistaking spandrels for pendentives, which might not be the only structural solution possible

to mount a dome on top of arches (Houston 1997); and (3) discounting the argument that pendentives could be adaptive if they were “chosen from a set of equipossible alternatives largely for aesthetic reasons” (Dennett 1995, p. 274).

Despite the initial appeal and the potentially revolutionary implications of the spandrel metaphor, it is clear that the adaptationist program has not been shaken to the core over the past 40 years. Why not? According to Olson (2019b), the answer is simple: Current evidence of true biological/psychological spandrels is (at best) rare, anecdotal, limited to a few species, refractory to empirical testing, and even the handful tractable cases remain controversial. Let me examine these issues one by one.

First, Gould (1991) promised “spandrels by the thousands” (p. 58): “The number and complexity of these spandrels should increase with the intricacy of the organism under consideration. In some region within a spectrum of rising complexity, the number and importance of usable and significant spandrels will probably exceed the evolutionary import of the primary adaptation” (Gould 1997, p. 10754). However, a thorough literature review yields only a few examples of undisputed spandrels, most of them being morphological phenotypic traits: (1) the human chin originated as an unselected but necessary structural side effect of the selection for reduced mandibles in modern humans; (2) male nipples are functionless developmental by-products of the strong selective pressure on females to have functional nipples, and both sexes inherit these anatomical traits because of shared developmental pathways; (3) likewise, human female orgasm is largely considered a nonadaptive developmental collateral to the selection on male orgasm; (4) the extremely masculinized genitalia (often referred to as “pseudo-penis”) of female spotted hyenas are regarded as a nonselected but inevitable by-product of the selection for androgen-mediated aggressiveness that gives adult females a competitive advantage in the specific social system of this carnivore species; and (5) the umbilicus, defined as the axially aligned and hollow cone-shaped space within the whorls of a coiled mollusk shell, is a necessary and generally nonadaptive

structural side effect of winding a tube around an axis (Frank 1997; Gould 1997; reviewed in Olson 2019b).

Second, even much-cited examples of spandrels have not been empirically studied in detail in the primary literature; instead, they tend to be found in the secondary literature and are based on the authors' intuition (Olson 2019b; but see Frank 1997; Raia et al. 2010, for two notable exceptions). Third, spandrels appear to be idiosyncratic and sporadic in their phylogenetic distribution, making these traits non-amenable to cross-species comparative study – which is one of the most powerful methodological tools to explore the origins and evolution of biological features. Fourth, many spandrels are intractable to the hypothetico-deductive model and empirical methods. Buss et al. (1998) claimed that “Without specifying the origin of the adaptation that produced the by-product [...], the hypothesis that something is a spandrel generally cannot be tested” (p. 542). According to Olson (2019b), this failure is due to the persistent problem of “trait delimitation”: Spandrels do not represent “traits” or “parts” that could respond quasi-independently (i.e., as an almost atomized/discrete organismal unit) to natural selection. In Olson's (2019b) terms: “True spandrels are not things but simply spaces left over between things” (p. 63). Fifth, on closer examination, some often-cited examples of so-called spandrels turn out to be initially unselected traits capable of being subsequently put to use (i.e., simply misapplied synonyms for a particular type of exaptation).

Two Main Types of Exaptation

In 1982, paleontologists Gould and Vrba addressed a question that was not properly answered by most evolutionists: “What is to be done with useful structures not built by natural selection for their current role?” (p. 6). To avoid conflating a trait's current usage with its historical origin, they coined a new term that was apparently missing in the evolutionary science of organismal design, including its intricate fit between form and function: “Exaptation.” The term “aptation” comes from the Latin *aptus*, which means “fit,” and designates any trait that currently enhances

the fitness of its bearer, regardless of its evolutionary genesis. If the trait was originally designed and selected for this current usage (i.e., *ad-* in Latin, which means “toward”), it is an “adaptation.” If the trait was not originally designed and selected for this current usage, but owes its fitness-enhancing capacity to features present for other reasons, and is therefore *aptus* “by reason of” or “as a consequence of” (i.e., *ex-* in Latin) its form, it is an “exaptation.” The prefix *ex-* indicates that the trait's quality of being *aptus* is posterior to its origin. Therefore, an exaptation is one of the aforementioned examples of traits that are currently adaptive without being adaptations.

Exaptations capture four essential notions inherent to biological, psychological, and cultural evolution. First, a preexisting trait, including one that has evolved via natural/cultural selection, can be put to (a new) usage through a process called “co-option” or “co-optation” (i.e., functional recycling of ancestral structures), based on historical contingency (i.e., changing selective pressures and structural constraints). Second, because usage does not always precede form, the current usage of a structure cannot be used as a default explanation of the past origin and evolutionary history of that structure. Third, a multitude of fitness-enhancing phenotypic traits were not originally built by natural selection for their later or current usages. Fourth, because the current (or recent) capacity of an exaptation to enhance fitness did not contribute to the original selection of this trait, the fitness benefit the trait is “exapted to” cannot qualify as a function. Just as the primary usage causing an adaptation to evolve is called a “function” (i.e., its original usage), the (secondary) usage causing an exaptation to evolve is called an “effect” (i.e., its later/current usage; Gould and Vrba 1982).

Exaptations occur in two main forms (but see Pievani's (2003) four meanings of the word). An exaptation Type 1 is a trait arising from a pre-existing adaptation whose original structure is subsequently co-opted for a new fitness-enhancing usage (i.e., effect) but without being modified by natural selection for this effect. If any further adaptive benefits are gained by the co-opted adaptation through structural

modifications of the original design via natural selection, then the trait becomes a “secondary adaptation” (Gould and Vrba 1982). Most complex phenotypic traits have probably undergone a long and tinkering-like process of primary adaptation (toward a fit for an original/first function), followed by a primary exaptation (in which the structure is recruited for an effect but to which it may not be perfectly suited), followed by a secondary adaptation (improving the performance of the exaptation for this new usage/second function), etc. A typical example of this chain of consecutive adjustments is the evolution of feathers. This morphological trait may have first arisen as a primary adaptation for thermoregulation in ground-dwelling/nonflying ancestral birds, then been co-opted as imperfect flight-producing structures (i.e., first exaptation Type 1), then structurally modified by natural selection to hone their flight-related properties (i.e., secondary adaptation), and then co-opted again but without structural modification, for use as water-shedders by extant long-legged wading birds stretching their wings out while foraging for fish (i.e., second exaptation Type 1). Other examples of hypothesized sequential co-options in other phenotypical categories include ritualized behavior patterns in various animal species, as well as the evolution of religious beliefs and linguistic components in humans. In addition to solving the problematic conflation of a trait’s current usage with its historical origin, Gould and Vrba’s (1982) new term (i.e., exaptation – Type 1) aimed to address the misleading and teleological flavor of a previous label which embarrassingly connoted foresight: “preadaptation.”

An exaptation Type 2 is a trait arising from a preexisting spandrel whose original structure acquires a fitness-enhancing usage (i.e., effect) without being modified by natural selection for this effect. In the architectural domain, a textbook example of co-opted spandrel is the display of Christian iconography that was secondarily added to the tapered spaces (i.e., spandrels) created between the archways and the domed roof of the basilica of San Marco in Venice (Gould and Lewontin 1979). In the biological domain, the aforementioned umbilicus is used by some

species of snails as a protective egg-brooding chamber (Gould 1997). The fontanelles (i.e., soft membranous gaps between cranial bones) and skull sutures caused by delayed cranial closure during embryogenesis probably first arose as spandrels of adaptive processes shaping the skeleton of various vertebrate taxa, including reptile and bird species that reproduce by oviparity, but may have been exapted by placental mammals to facilitate the parturition of large-headed neonates that need to pass through a narrow birth canal (Gould and Vrba 1982). As exemplified above, “exaptation is not incompatible with natural selection, but with an oversimplified representation of it” (Pievani and Serrelli 2011, p. 12). The concept of exaptation (Type 1 and Type 2) emphasizes the importance to consider the range of adaptive processes and products, beyond adaptation.

Residue of Noise

A residue of evolutionary noise is defined as a trait shaped by random effects resulting from forces such as chance genetic events during the development or sudden and drastic environmental changes. The evolutionary processes causing these traits to evolve include genetic mutations, genetic recombination, gene flow, and genetic drift, but not natural selection. To illustrate this type of traits and other evolutionary products reviewed in this paper, let us consider two examples, a naturally occurring one (the belly button) and a humanly designed artifact (the lightbulb).

First, the belly button is a morphological spandrel in placental mammals: it is a necessary and fitness-neutral by-product of a specific adaptation (i.e., the umbilical cord, naturally designed to provide food and oxygen to the developing embryo and fetus). The particular shape of an individual’s belly button can be considered a residue of noise. Hypothetically, one could imagine a cultural scenario in which a pierced belly button would give its human bearer a survival/reproductive advantage in certain ethnic groups, making this modified evolutionary by-product a co-opted spandrel (or an exaptation Type 2). Second, the incandescent lightbulb is an adaptive design comprised of features (i.e., the tungsten filament

surrounded by a high-vacuum atmosphere contained within an all-glass envelope) that were originally selected/engineered to serve the function of light production. However, lightbulbs also generate heat as a by-product of light. In most cases, heat is a useless side effect of light production (i.e., a spandrel). In some cases, the heat generated by the lightbulb can be co-opted and serve as a heating system (i.e., an exaptation Type 2). Finally, the minor imperfections in the smoothness of the glass envelope resulting from insignificant imprecisions during the manufacturing process, but that have no bearing on the functioning of the lightbulb, can be considered residues of noise.

Testing the Hypotheses That a Trait Is an Adaptation or an Evolutionary By-Product

The traditional approach to testing “functionalist” and “non-functionalist” hypotheses is based on Williams’ (1966) argument that demonstrating adaptation carries an onerous burden of proof. In other words, a trait can be confidently identified as an adaptation on two mandatory conditions: (1) it met the strict evidentiary requirements of a special design, and (2) a set of alternative hypotheses (i.e., exaptation Type 1, exaptation Type 2, spandrel, residue of noise) have been systematically considered, have been rigorously tested, and have unequivocally failed. To achieve these goals, the conceptual and methodological toolkit of evolutionists include a number of evidence-based criteria grouped into different categories, namely, (1) *phylogenetic*, broaden cross-species comparisons and further the cladistic information pertaining to the phenotypic trait under study to reconstruct evolutionary scenarios about step-by-step changes over time; (2) *physiological*, acquire a deep and integrated view of the ontogenetic, allometric, genetic, and epigenetic underpinnings of this trait to provide an “evo-devo” perspective to the problem; (3) *intraspecific structural variability*, compare, across individuals of the same species, the structural variability within a pair of phenotypic traits that are

developmentally and evolutionarily linked but vary in their functional constraints – the prediction being that the adaptation should be less structurally variable than the corresponding spandrel/exaptation, because there was no direct selective pressure on the latter; (4) *structure-usage correspondence*, explore the multiple usages of a given structure, as some may be original functions and others may be subsequent effects, and the multiple structural options for a given usage to test the strength of the structure-function correspondence necessary for a strictly adaptationist hypothesis; (5) *(reverse) engineering* or *optimal design*, conduct biomechanical experiments and formal mathematical simulations to evaluate the supposed fitness-enhancing values of more or less altered/constrained phenotypic structures; and (6) *fitness/utility maximization*, test the actual correspondence between structure and function/effect/benefit in living and fossil species in their respective current and reconstructed ancestral environments (Andrews et al. 2002; Pievani and Serrelli 2011).

However, testing hypotheses about “adaptations” versus “evolutionary by-products” is a daunting task, for a number of interrelated reasons (Buss et al. 1998). First, these hypotheses should lead to the formulation of clear, specific, and testable/falsifiable predictions. Second, in principle, the five aforementioned evolutionary products are compatible and not mutually exclusive. They can even all play a role in explaining the evolution of a given phenotype. Evolutionists must demonstrate empirically the respective roles and causal sequence of action of different products in the evolutionary history of a trait. Third, investigating the emergence, diffusion, or maintenance of an adaptation, an exaptation Type 1, an exaptation Type 2, or a spandrel, consists in asking different questions, based on different assumptions (e.g., gradualist versus saltationist views on the speed of evolutionary changes), involving different schools of thought (e.g., weak versus strong adaptationism) and requiring different research techniques. Fourth, some traits (e.g., behavioral and psychological characteristics) are not readily amenable to phylogenetic inquiry

because they are (1) poorly represented in the fossil record, (2) variable across individuals, and (3) plastic within individuals, now and (presumably) in the past. Fifth, due to historically contingent, and thus unpredictable, structural constraints, an adaptation could show suboptimality and fail fitness maximization tests (i.e., a “false-negative” case). Sixth, there are no general rules that could be applied across phenotypic traits, species, and environmental conditions; testing “evolutionary by-product” hypotheses must be done on a case-by-case basis. Seventh, this line of research is still crippled by pervasive cognitive biases: some scientists remain vulnerable to teleological stories, and too many functionalists believe that finding a by-product explanation for the evolution of a trait devalues this trait, as if finding an adaptation was more scientifically appealing than finding an evolutionary by-product.

Conclusion

For decades, Williams (1966), Gould (1997), and their evolutionist and developmentalist followers have championed Darwinian pluralism by highlighting the variety and significance of evolutionary by-products and advocating for an extended taxonomy of fitness (Pievani 2003; Stump 2010) and non-fitness (Pigliucci and Kaplan 2006; Linde-Medina 2017), including aptations (i.e., fitness-enhancing traits, such as adaptations, secondary adaptations, and exaptations), non-aptations (i.e., fitness-neutral traits, such as bonuses, postaptations, and spandrels), and malaptations (i.e., fitness-reducing traits, such as maladaptations, malexaptations, and maladaptive spandrels). With their transcendent “spandrel” metaphor (Gould and Lewontin 1979) and their concept of “exaptation” as a modern and stronger rendition of Darwin’s notion of preadaptation (Gould and Vrba 1982), a few insightful structuralists (e.g., paleobiologists and geneticists) have sought to challenge the fields of evolutionary biology/psychology by encouraging their functionalist counterparts to take evolutionary by-products

seriously, consider non-adaptationist hypotheses diligently, focus on the problem of trait delimitation, and clarify the internalist/externalist dichotomy.

As a result of their heuristic approach, research on organismal form and function has been profoundly transformed. Gould’s pluralistic perspective on evolutionary theory, grounded in the interwoven concepts of constraints, spandrels, and exaptations, is now part and parcel of “textbook” evolutionary biology/psychology (Andrews et al. 2002; Ridley 2004). In their seminal paper about exaptations, Gould and Vrba (1982) reminded us about the very nature of our quest: “As evolutionists, we are charged, almost by definition, to regard historical pathways as the essence of our subject” (p. 7). The concepts addressed here, namely, adaptations and three main types of evolutionary by-products (i.e., exaptations Type 1, exaptations Type 2, and spandrels), as well as their fitness-enhancing or fitness-neutral contribution (i.e., functions, effects, or lack thereof), are *historical* in nature and were treated as such.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adaptationist Program, The](#)
- [Adaptations: Product of Evolution](#)
- [By-Product](#)
- [By-Products of Adaptations](#)
- [Evolution of Adaptations](#)
- [Frugivory By-Product Hypothesis](#)
- [Identifying Adaptive Functions](#)
- [Maladaptive By-Product Hypothesis](#)
- [Richard Dawkins on Constraints on Natural Selection](#)

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Evolutionary Change

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Synonyms

[Descent with modification](#)

Definition

Evolutionary change is the heritable change in populations and species over time, due to mechanisms such as natural selection, random genetic drift, and sexual selection.

Introduction

Evolution is heritable change over time, through which species change, diverge, and sometimes create new lineages. “Evolution” and “natural selection” are often used interchangeably, but the two are distinct: evolution is the pattern, and natural selection is one of many mechanisms that *cause* evolution. Under natural selection, organisms which are better adapted to their environment have more (or healthier) offspring, so their traits are more often passed on to future generations. In this manner, natural selection drives evolution. However, other mechanisms can also drive evolution, such as random genetic “drift,” or random changes in genes and traits over time, artificial selection by humans for human-desired traits in other organisms, and sexual selection for traits that increase an individual’s chance of mating. All of these mechanisms operate by impacting heritable variation to drive evolution.

Evolutionary change requires that individuals vary in ways that are passed on (in whole or in part) to their offspring. Although the observation of heritability in nature (“like begets like”) is sufficient for some evolutionary inquiry, scientists now have a rich understanding of the primary mechanism of heritability: genetics. All life on earth is based on genetic code that is carried within cells and translated into observable traits. Humans, sea horses, mushrooms, the common cold virus, and more all reproduce by passing genetic material in the form of deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) on to their descendants. Every organism is the sum of interactions of their genes (functional stretches of DNA or RNA) with their environment, resulting in their phenotype, i.e., the set of all traits that are expressed in a given environment and are seen by other individuals. In addition to genetics, “epigenetic” modifications (changes to the ways genes are expressed, such as conditional switches that turn genes “on” or “off”) can also be heritable and thus can play a role in evolution.

Mutation generates variation in the genetic code due to (i) random errors in our cellular machinery or (ii) environmental influences (induced errors). Genetic mutation can translate

into heritable differences in an organism’s observable traits, or phenotype, with neutral, positive, or negative effect on the organism’s fitness. While mutation, and thus differences between organisms’ genetic code, is the basis of variation, several higher-level factors contribute to variation. Gene flow between separated populations of the same species can also induce variation, and recombination during sexual reproduction reshuffles genes and their associated traits.

Scientists research evolutionary change by examining the fossil record, interpreting genetic evidence in the present, inferring genetic pathways over time, modeling change, and performing real-time evolutionary experiments with model organisms such as flies, yeast, and mice. This wealth of approaches has contributed greatly to a scientific understanding of the causes and persistence of variable life on earth.

Evolution is popularly conceived as a stairway of progress – from simple to complex, from bad to good, and from animals to man. This is completely untrue. Rather, it is more like a tangled bush with connections, splits, divergences, and interlocking parts. Humans are merely a tiny tip at the end of a tiny branch on the gigantic “Bush of Life.”

Heritability

Genetics

Genes control heritable traits and are the units of heredity. “Genotype” refers to the genetic material in an organism, while “phenotype” refers to observable characteristics whether inherited or not. Phenotypes result from genes, from environment/behavior, or from the interaction of genes with the environment (often popularly written as “nature plus nurture”). Selection generally acts on phenotypes, but phenotypes are not directly transmitted from parents to offspring – genes are. A single human’s overall phenotype could include tall height, brown hair, brown eyes, interest in and success at computer science, preference for neutral-toned clothing, no memory for details, and great storytelling ability. As this example suggests, not all phenotypic characteristics are

heritable! Eye color is fully heritable from known genetic variants, but interest in computer science is determined in part by inherited talent but also in large part by one's environment growing up. This is one complication of evolutionary inquiry: there is not a one-to-one correspondence between traits we can observe and measure (phenotypes) and heritable units (genes) coded in DNA.

DNA, deoxyribonucleic acid, is a long thin molecule that contains the "code" which is translated into proteins, the building blocks of cells, tissues, organs, and ultimately our bodies (some viruses use RNA, rather than DNA, as their unit of heredity; it is debated whether viruses are truly alive). DNA has an iconic "double helix" structure, with chemical bases in the center surrounded by phosphate-sugar chains. The chemical bases are of four kinds, represented by the four letters A, T, C, and G (which refer to adenine, thymine, cytosine, and guanine, respectively). DNA is shaped roughly like a spiral ladder, and these four bases pair up with one another (A with T, C with G) to form the rungs while the outer bars are formed by phosphate and sugar. DNA is "transcribed," i.e., copied by the enzyme RNA polymerase into messenger RNA, a molecule similar to DNA, which is then "translated" into protein. DNA base pairs are grouped into sequences of three called "codons" which correspond to specific amino acids (or in some cases, "stop" codons signal a stop in translation). The third position of a codon is called the "wobble" position because base pairs in that slot do not always obey the pairing rules described above (A with T, G with C); further investigation of this important phenomenon is outside the scope of this article.

Genes are stretches of DNA, ranging between less than one hundred base pairs to over two million, that in essence code for a specific string of amino acids which in turn folds into a specific protein. Almost all human DNA is the same in every individual human (over 99%); thus, only a very small proportion of the genome comprises individual variation.

Genes sit in a specific place on "chromosomes," which are the dense threadlike packages of genetic information that cluster inside the nuclei of our cells. However it is worth noting that our nuclear

DNA – the DNA on chromosomes in the nucleus – is not the only DNA we have in our bodies. Most notably, mitochondria have their own DNA that is inherited from mother to child (since mothers' ova contain the cell organelles). Mitochondria have DNA because they were independent organisms which our ancestors "domesticated" and put to work inside our cells. Chromosomes consist of DNA coiled around "histones," a special type of protein that allows the supercoiled structure of DNA. Humans have 23 pairs of chromosomes (since we inherit 23 from our mother and 23 from our father). Twenty-two pairs are "autosomal" chromosomes, which conventionally are numbered from 1 to 22 from largest to smallest, while the 23rd pair consists of our sex chromosomes. These are the X and Y chromosomes that determine our biological sex (Other animals have different mechanisms of sex determination, such as temperature-dependent sex determination in some reptiles (Warner and Shine 2008).). Female humans have XX sex chromosomes, while males have XY chromosomes. Some autosomes may be familiar to you; for example, if an individual inherits three copies of chromosome 21 instead of the usual two copies, this is referred to as "trisomy 21" or "Down syndrome."

The place of a certain gene on a chromosome is called its locus. Genes can have multiple slightly varying forms known as alleles; these allelic differences code for many of the differences that separate humans from one another. For most genes, we inherit two copies (one from each parent); if you have two copies of the same allele, you are *homozygous* for that allele. If you have two different alleles, you are *heterozygous*. The ways in which the two different alleles interact determine your phenotype. Different alleles can be codominant, where both are expressed to some extent; they can be in a dominant-recessive relationship where only one copy of an allele is necessary for expression; or different alleles can be related in more nuanced interactions. For an artificial, simplified example, imagine that eye color is a trait coded by a single eye color gene. Assume that you can inherit either a blue or brown allele from your parents and that brown is dominant to blue. If you have two blue alleles, you have blue eyes; similarly, two brown alleles produce brown

eyes. But if you have blue and brown alleles, since brown is dominant to blue in this imaginary simplified scenario, you will have brown eyes. However, you could have a child with blue eyes, as long as (i) you pass your blue allele on to the child and (ii) that child inherits a blue allele from their other parent as well! This is an important principle: traits that are not expressed in a parent can nonetheless be genetically hidden only to be expressed in later generations (Most traits, including eye color, are much more complex than described here).

Crucially, DNA can replicate itself. This is the basis of life. When our cells divide, DNA is copied so that each cell contains a complete copy of our genetic code. During cell division, which is essential for growth, maintenance, and reproduction, DNA is “unzipped” and copied by molecules and enzymes dedicated to these tasks. Sometimes during this process of copying, our copying mechanisms make errors. A stretch of DNA that read AATC might get accidentally copied as AATG. If this mistake is not noticed and corrected by our cellular mechanisms, it will be preserved in that cell’s genetic code as a mutation. If that cell is a reproductive cell, the mistake could replicate to offspring. There are many kinds of mutations, which we will turn to below; this is one source of the variation that can drive evolution.

Note that in many cases, genetic mechanisms and inheritance are more complicated than described above. The full complexity of genetics is beyond the scope of this entry, but it is important to note several caveats. “Selfish” genes act as self-interested agents that seek to further their *own* reproduction (Dawkins 2016). Indeed, sometimes the conflicting “agendas” of genes result in ingenious mechanisms for violating traditional modes of inheritance (Burt and Trivers 2006). Genes can be “sex-linked,” expressed only in the phenotypes of one sex, or “incompletely penetrant,” whereby, for example, a gene is not activated unless certain environmental conditions are met. Further, the connection between complex traits and genes is an ongoing mystery that geneticists are solving on a case-by-case basis with large data sets and statistical inference.

Epigenetics

We used to think that the DNA code that is passed from parents to child is the only mechanism of heritability. However, we now realize that this is not the whole story. “Epigenetics” describes changes to our gene *expression*, prompted by life experience. Remarkably, some of these changes are heritable. Consider the following landmark study on the inheritance of learned fear (Dias and Ressler 2014). Mice were trained to associate a certain specific cherry-like scent – acetophenone – with fear. Every time the scientists flooded the mice’s cage with the scent, they delivered small mild shocks to the mice. When the mice reproduced, the babies knew to fear the scent of acetophenone *without ever having undergone training*. Somehow, the learned experience – fearing acetophenone – was passed on to the mice’s offspring. This was not associated with *genetic* changes. While the specific mechanism in this case is still a mystery, we know it must be due to epigenetic inheritance.

So what exactly is epigenetics? While scientists define this term in many different ways, epigenetics broadly refers to modifications that control how genes are *expressed*. A very large part of our genome is not genes but rather is specific stretches of DNA that regulate expression of genes. Recall that genes are expressed by coding for proteins which perform a variety of functions; “silenced” genes are no longer expressed as proteins, while “upregulated” genes are expressed at higher levels than usual (and “downregulated” genes do the opposite). In many cases, protein-coding genes are regulated by associated stretches of regulatory DNA or regulatory regions in the genome usually (but not always) near a particular gene. In other cases, stretches of DNA pick up “tags” or reconfigure their shape in ways that silence, upregulate, or otherwise affect expression. Epigenetics refers to external influences (e.g., environment or behavior) that modify expression of genes, leading, for example, to turning genes on or off or affecting the timing and levels of expression of genes.

For our purposes, we are most interested in heritable epigenetic changes. Two of the most

important such mechanisms are DNA methylation and histone modification.

DNA methylation silences genes through chemical binding. Specifically, methyl groups are added to the chemical structure of DNA; where methyl groups bind, genes tend to be *less expressed* or turned off. Methylation is very important in genetic imprinting, which is the way in which genes are “tagged” as coming from one’s mother or father (and have corresponding expression modifications). A notable example of imprinting in humans is seen in Prader-Willi and Angelman syndromes – clinically distinct disorders associated with multiple anomalies and mental dysfunction, both usually due to deletions in part of chromosome 15. Whether an individual has Prader-Willi versus Angelman syndrome depends on which parent transmitted the faulty chromosome 15 to the child.

Histone modification affects DNA packaging, which determines which regions are “exposed” to the cellular machinery of gene expression. Recall that DNA is wrapped around histone proteins – it is packaged in a particular way that, with the help of these proteins, influences transcription and translation (the steps of gene activation). The shape of the histone proteins and the way in which DNA interacts with and wraps around histones can change based upon environmental influences and can be inherited.

Scientists do not yet fully understand how histone modifications are heritable; however, several studies have begun to unpack the ways in which methylation patterns are preserved from parent to child. For example, methylation patterns reveal whether a chromosome originated from the mother or father. On a maternally derived chromosome, genes that represent paternal interests are methylated and thus silenced. This is an intriguing and tricky concept and a famous category of “genetic conflict”; in short, in many mammalian species, mothers and fathers have different evolutionary interests, which are expressed through epigenetic “imprints” on their child’s genome. Genomic imprintings, as it is called, is known to occur in fungi, plants, and animals—including humans. For example, in humans, mothers bear the child and thus have an

evolutionary interest in keeping the baby’s body at a reasonable size. Fathers, however, have an evolutionary interest in making babies as large and well-nourished as possible, thus extracting maximum resources from the mother’s body. In our genomes, we see many patterns of methylation around genes related to infant growth and maternal provisioning that clearly demonstrate these opposing genetic interests a parental tug-of-war (Moore and Haig 1991, Haig 1993).

Thus, epigenetic inheritance is an additional component of heritability. It is counterintuitive to people familiar with strict genetic heritability, but there is no doubt that epigenetic inheritance plays a role in fitness, variability, and reproduction; therefore, it is important to consider as part of evolutionary change.

Variation

For evolution to occur, organisms must have heritable variation. That is, individuals must differ from others in ways that can be passed on to their offspring. Variation in genes and thus in individuals comes about through three primary mechanisms: mutation, recombination, and gene flow. In all of these cases, differences in the genetic code are the basic level at which variation occurs; these differences can be encountered and arise through mutation in an existing population, sexual recombination, described below, or gene flow (the movement of individuals and genes between populations that have been genetically diverging).

Mutation

Mutations are changes in the genetic code of an organism. Mutations can be categorized in many ways, but the most important categories for our purposes are “germline” versus “somatic” mutations, because these categories determine whether or not a mutation is passed on to offspring. In order for mutations to be passed on to offspring, they must be present in the germline, such as a mother’s ova or father’s sperm in humans. Mutations in somatic cells, or cells of the body that do not pass on to offspring, therefore do not affect an offspring’s fitness.

Alleles are different *versions* of one gene. For example, ABO blood type is determined, very simply, by which alleles you have of the “ABO blood type” gene. You get one copy of the gene from your mother and one copy from your father. The possible alleles you could have are A, B, and O. If you have the “A” allele and the “B” allele, you are blood type AB. Alleles A and A or A and O produce blood type A and likewise for B. Finally, if you have alleles O and O, you are blood type O. These alleles vary among individuals, just as do all other alleles. Species tend to have allelic variation; that, in combination with environmental variation, is why we do not all look and behave the same! Identical twins have very little allelic variation, because they inherited the exact same copies of the same alleles from their biological parents. Thus, in general, differences between identical twins are driven by the environment and the ways in which the environment impacts gene expression. Studies of identical twins (Boomsma et al. 2002) have found a variety of intriguing and peculiar findings about which traits are inherited and which are primarily driven by environmental variation.

Different alleles are generated by mutation, which occurs for two reasons: first, as DNA undergoes the process of replication, it can make a mistake. Each time a cell divides, there is a chance for the DNA to be copied incorrectly – this difference is a mutation. Second, environmental factors can directly cause mutation. Chemicals, or certain types of radiation, can break down DNA to such an extent that our DNA repair processes cannot adequately fix the damage.

Mutations can be “silent,” “deleterious,” “beneficial,” or “lethal.” Silent mutations in the genetic code, such as redundant base pair substitutions, have no effect on the gene’s function. Proteins are built from amino acids, and DNA codes for amino acids – however, each type of amino acid can be generated by multiple DNA templates. A mutation can also be silent if it occurs in a stretch of DNA with no function (But have caution! For many years, we thought long stretches of DNA that were known as “junk” DNA did nothing. Really, they served important, if complicated, regulatory purposes.). Mutations without strong

effects, and ideally without any effects at all, can be used to calibrate “molecular clocks” (Ayala 1986); that is, when we are trying to understand how long ago a species diverged from another species, we can compare how many mutations each species has in nonfunctional regions (Ho and Larson 2006). This is better than looking at functional mutations, since selection can act on those and interfere with our perception of how much time must have passed. A fundamental assumption, required to use the idea of molecular clocks, is that DNA not under selection accumulates mutations at a constant rate.

Of all functional mutations, the majority are deleterious, or harmful to the fitness of the organism in which they occur. Studies of the model fly species *Drosophila melanogaster* indicate that about 70% of functional mutations – that is, mutations that change the protein coding of a gene – are deleterious (Sawyer et al. 2007).

Beneficial mutations confer some fitness advantage to their host organism. Sometimes, of course, we might not understand their benefit in today’s world! Once we are removed from the evolutionary context in which a mutation was selected for, it can begin to have negative consequences.

Many beneficial mutations come about when a stretch of genome is duplicated and passed on to offspring (but see Lynch and Conery 2000). In this case, there is genetic “redundancy” that gives a buffer for mutation. If something changes over the generations in one copy of the gene, it is less likely to cause trouble since the individual has another copy. A famous example of this is the evolution of trichromatic color vision in humans. Our ancestors used to have only two types of cones – long wavelength (red) and short wavelength (blue). There was a duplication in the gene coding for long-wavelength opsins, or light-sensitive proteins. Over time, the duplication allowed one set of long-wavelength opsins to diverge slightly and differentiate enough such that one set became specifically sensitive to green light and one to red light. Thus, we and two other primate groups independently evolved trichromatic color vision with our familiar sensitivity to red, green, and blue light through gene duplications (Dulai et al. 1999).

Indeed, *de novo* (new) gene duplications account for the largest family of genetic differences between humans and chimpanzees (Cheng et al. 2005). They are not always good – some are associated with human-specific diseases!

Finally, lethal mutations are simple and aptly named. They kill you.

Gene Flow/Migration

Mutations can arise in an existing population. However, another source of variation can come from interaction between populations. When individuals move from one population to another, they carry their genes with them. Thus, spatial migration is accompanied by genetic flow. Plants sending pollen far and wide, animals leaving their native ranges due to human pressures, and people migrating from place to place are all mechanisms of gene flow.

A related phenomenon is that of a “genetic bottleneck.” In this scenario, a population of a single species encounters a “squeezing” effect on their genetic diversity, as if they are flooding from a wide bottle into a narrow bottleneck, typically due to a very small population size. This can be caused by environmental disasters, such as an asteroid strike, flood, fire, disease that sweeps through most but not all of a population, or geographic separation (due to a small group populating, say, an island). If a small subset of a population becomes reproductively isolated and “founds” a new population, biologists call the resulting lack of genetic diversity the “founder effect.” Indeed, it is well understood that modern humans evolved in Africa and then spread to the rest of the world, encountering a genetic bottleneck on their way out of the continent. This is one reason why populations in (or descended from those in) Africa are far more genetically diverse than the rest of humanity.

Human impacts have had catastrophic effects on many species by decreasing their population size; overfishing, overhunting, and environmental destruction have led to mass extinctions and severe drops in genetic diversity.

Sexual Recombination

Children may look like a blend of their biological parents, but sexual reproduction does not actually

blend traits. Instead, genes “reshuffle” during the process of sexual reproduction. You are not a copy of either of your parents, nor are you perfectly in between. You wind up with combinations of traits that are not found together in either of your parents.

In sexually reproducing organisms (which are most animals, including humans), each parent passes on 50% of their genes to their child. In humans, for example, each individual sperm and each individual egg have been produced through a process that splits the parent’s genome in two. Most of our cells have 23 pairs of chromosomes – two chromosome 1s, two chromosome 14s, etc. and either two X chromosomes or one X and one Y chromosome. This process of creating eggs and sperm – which is known as meiosis – involves stages whereby these pairs of chromosomes pair up, exchange genetic material through “crossing over,” and then separate to be sequestered into eggs or sperm. Each sperm and each egg have 23 individual chromosomes, and these individual chromosomes are “reshuffled” versions of their parent’s chromosome pairs. Fascinatingly, some loci in a genome can manipulate meiosis to enhance their own transmission, such that they are found in more than 50% of germ cells. This is known as meiotic drive, and it is not yet known to what extent meiotic drive has influenced our evolutionary history.

Mechanisms That Drive Evolution

Natural Selection

Natural selection is the most commonly discussed mechanism of evolution, although it acts in concert with the other mechanisms described below to drive evolution. In short, natural selection requires variation, differential reproduction, and heritability. Organisms compete for resources and to reproduce; individuals vary in a population and pass on much of this variation to offspring; and individuals that are better adapted to local conditions pass on more copies of their genes to future generations. This is popularly termed “survival of the fittest.”

The building blocks of natural selection are variation within a population, differential reproductive success, and heritability. We have already seen that DNA makes up genes which are passed from parents to offspring; clearly, heredity is present. Further, variation is present in natural populations; this is clear from simple inspection, and the many studies linking genes to observable traits have demonstrated that variation is in large part heritable. Finally, “differential reproduction” refers to the fact that different individuals leave behind more or less offspring depending on how “fit” they are. Fitness is variably defined, but can be summarized as “an organism’s ability to survive and reproduce”. If populations were unlimited and every individual had equal chance to mate and leave behind equally fit offspring, the criteria of “differential reproduction” would not be met.

Artificial selection, or selection conducted by humans, is closely related to natural selection. Animal and plant breeding over the generations produces evolutionary change along metrics that humans care about – larger plants we want to eat, purebred dogs with arbitrarily preferable traits, and docile fat cattle for the slaughterhouse. It is the same exact mechanism as natural selection, except humans choose who gets to reproduce, rather than a harsh environment selecting for reproductive fitness.

Sexual selection is a special case of natural selection whereby individuals evolve traits that increase their chances of copulating with the opposite sex. This will be discussed in greater detail in the subsequent section “sexual selection.”

Since life has heritable variation and differential reproduction, natural selection is in effect. We see overwhelming direct evidence of natural selection in real time, in the fossil record, and in our genes.

Convergent Evolution: Strong Evidence of Natural Selection

The most powerful evidence for evolution by natural selection is the remarkable “convergence” of distantly related species who face similar selective pressures. That is, many species independently evolve similar traits because they are

useful and confer a fitness benefit within a specific environment. Sharks and dolphins share a similar body form even though one is an elasmobranch fish and one is a mammal the pressures of aquatic life led to selection for a torpedo-like body shape with fins. Vertebrates evolved wings for flight at least three times in birds, bats, and pterosaurs; further, mammals have evolved “gliding” body forms, with flaps of skin stretched between legs, in both the flying squirrels and the distantly related marsupial sugar gliders. While these examples are common, they barely scratched the near-unbelievable surface of convergent evolution over time and space.

Consider, for example, the phenomenon of “mammalian woodpeckers” (Cartmill 1974). In some areas of the world, there are no naturally occurring woodpeckers, and instead, mammal species evolved to fill the woodpecker “niche.” (“Niche” is a catch-all term describing an organism’s or species’ ecological role in the environment: e.g., what they eat and how they eat it). Today, there are two living mammal species who evolved to fill the woodpecker niche: the striped possum in Australia (*Dactylopsila trivirgata*) and the aye-aye from Madagascar (*Daubentonia madagascariensis*). These mammals are distantly related, and evolved completely independently on their respective islands. However, both have massive protruding incisors that they use to bore through and tear at wood, finely tuned ears that listen for grubs squirming within the wood, extremely elongate single fingers to reach into the wood and pull out grubs, and a uniquely reinforced skull to deal with the pressures of wood-boring (Cartmill 1974; McCoy and Norris 2012)! There are two additional proposed “mammalian woodpeckers” from the fossil record: *Hegetotherium mirabile*, an enigmatic notoungulate from South America, and *Yalkaparidon*, a marsupial from Australia. All of these species are only distantly related and yet evolved remarkably similar morphological adaptations to the specific niche of wood-boring; in other words, these animals evolved similar traits long after the split from their common ancestor. This is extremely strong evidence for the mechanism of natural selection (although the aye-aye

and striped possum are extremely similar, I am sorry to say that the aye-aye looks like a frightening demon while the striped possum looks like an adorable pet).

Selection at What Level?

The history of evolutionary biology is filled with arguments about the level at which selection operates (Okasha 2006). Does it operate on cells, genes, individuals, and species? An overview of this debate is beyond the scope of this entry. To briefly summarize, life is composed of many replicating “selfish” elements, perhaps most notably genes (Dawkins 2016) and individuals. Selection acts on phenotypes, and genes are the unit of heritability that are passed from parent to offspring. The correlation between gene and phenotype is not perfect, since the environment exerts an influence as well. Individuals who share a high proportion of their genes may be evolutionarily motivated to “help” each other; this is known as “kin selection theory” or “inclusive fitness” (Hamilton 1964). Over geologic time, paleontologists often talk about species-level selection, by which species diverge and emerge in response to fluctuating niches (Gould 2002). Some biologists will hear nothing of selection at a level higher than the gene.

To all levels of selection, there is some truth (Okasha 2006).

Genetic Drift

Genetic drift, unlike natural selection, is completely random and not determined by fitness. In any population, whether of people or parakeets, some individuals will be more successful by chance. They will leave behind more offspring – not because they are measurably “fitter” due to selected adaptations but because that’s the way the cookie crumbled. Without selective pressure on certain alleles, alleles drift in a random walk until one allele becomes “fixed” in the population – that is, until one allele is present in every individual in a population. If a population is small, such as in the case where a small subset gets cut off from the main population, or where a few members of a species populate an island, there is a higher chance that a certain allele will drift to fixation despite having a neutral or even negative effect.

There is much debate about whether selection or drift exerts stronger influence on evolution in a population. Are most traits there by chance or because they were selected for? Proponents of the “neutral theory” of evolution argue that much of evolution is caused by genetic drift and the random fixation of alleles. It is difficult to quantify the relative contributions of random drift and natural selection (for reasons such as “genetic draft,” see below), but both have demonstrably played a role in evolutionary change over time.

Genetic Hitchhiking (“Genetic Draft”)

Genetic “draft” is closely related to the phenomena of drift and selection. It is also called genetic “hitchhiking,” because it can be conceptualized as certain neutral or even deleterious alleles “hitching a ride” with beneficial alleles.

Genes recombine during sexual reproduction; however, the rate of recombination between genes varies depending on the distance between them. Further, the position of genes on a chromosome influences the likelihood that they will recombine and be separated from each other. If genes are close to each other, they are said to be “linked.” The nonrandom association of alleles at different loci is known as their “linkage disequilibrium.”

When two genes are linked, specific combinations of their alleles are almost always passed on and inherited together – as a unit. A few implications are obvious. First, if two genes are functionally related and become linked by chance, then there will be strong pressure for them to remain linked; for example, what if the gene for purple hair gets linked to a gene for preferring purple hair?

Second, a highly useful gene variant can be linked to a neutral or even deleterious gene. If they happen to be close together on the chromosome, that neutral or negative allele might sweep to high frequencies in the population just by “hitchhiking” along in the “selective advantage bus” driven by its neighbor gene. So when looking at genes in a population, it is not always safe to assume that a very common gene variant has a selective advantage. It may have “drifted” to high frequencies or been “drafted” by a neighbor.

Interpreting Evolutionary Evidence: Notes of Caution

Evolutionary “Spandrels” and Exaptations

In two landmark papers, Stephen J Gould, Elisabeth Vrba, and Richard Lewontin provided a fundamental note of caution when interpreting evolutionary evidence. It is tempting to look at a current organism with its suite of traits and think about why each trait is evolutionarily beneficial. However, scientists must be aware of “exaptations” or evolutionary “spandrels,” traits that either (1) evolved for a past purpose before being co-opted or (2) are just incidental by-products of adaptive traits.

Vrba and Gould coined the word “exaptation” to describe the following evolutionary truth: the current function of a trait does not always correspond with its historical function and origin (Gould and Vrba 1982). For example, we see that birds fly using feathered wings and think “Aha! Feathers evolved so that birds could fly.” However, a wealth of paleontological evidence calls this into serious doubt. Feathers evolved in dinosaurs long before flight evolved; they almost certainly aided in insulation and may have played a role in display, waterproofing, or defense (Prum 1999). Only later were feathers *co-opted* for the purpose of flight.

Related to “exaptations” are Gould and Lewontin’s evolutionary “spandrels,” a term inspired by architectural phenomena at the San Marco Cathedral in Venice (Gould and Lewontin 1979). This cathedral has a beautiful dome resting upon arches, and “spandrels” are the triangular windows between the intersecting arches. Usually spandrels are decorated ingeniously, as is the case at San Marco. If one just looks at the spandrels, they might be tempted to conclude that the spandrels were carefully and intentionally shaped and designed, and perhaps even that the rest of the building exists only to frame them. But in reality, spandrels are a necessary result of mounting a sphere on a dome; they are only an incidental by-product of the grander architectural scheme.

Similarly, it is tempting to look at an evolved creature, focus on a certain trait, and try to come up with its evolutionary purpose. But sometimes,

that trait is just a “spandrel” – an insignificant by-product of a trait that was truly evolutionarily significant. Indeed, Gould and Lewontin give as a primary example of spandrels the many peculiar processes in the human brain that we cannot fully understand (Gould and Lewontin 1979).

An Incomplete, Mysterious Fossil Record

Often in evolutionary history, we have incomplete evidence. Fossils give us clues about the past, and we can only see current life as a mere snapshot of the continuously changing spectrum of life and diversity.

The vast majority of life on earth is available to us only through fossil evidence. Some fossils are remarkably well-preserved, which allowed us to see, for example, the imprint of soft tissue, the outlines of dinosaur feathers, and more. Other fossils are frustratingly incomplete.

But even when scientists have a wealth of evidence, it is common to initially misinterpret fossils. For example, one of the most famous fossils of all time, the Tully monster (*Tullimonstrum gregarium*), was thought to be a mollusk or worm until it was recently found to be a vertebrate (McCoy et al. 2016).

This example illustrates the difficulty of correctly interpreting fossil evidence, even in the case of the relatively abundant Tully Monster. The history of human evolutionary biology is replete with sparse fossil finds, angry feuds, and misinterpretation. Many species of our hominin relatives were initially thought to be “deformed” examples of normal *Homo sapiens*, including Neanderthals and *Homo floresiensis*. Further, many of our hominin relatives are known by only extremely tiny scraps of bone and fossil. As Gould once wrote, “an old paleontological joke proclaims that mammalian evolution is a tale told by teeth mating to produce slightly altered descendant teeth.”

Evolutionary Change over Life’s History

The complete history of life ranges over four billion years, through alien worlds of sulfurous oceans beneath asphyxiating air, past iron-breathing bacteria and microscopic chimera, to arrive at last at our

familiar world of oxygen and ozone, forested valleys, and animals that swim, walk, and fly. Scheherezade could hardly have invented a more engaging tale. – Andy Knoll, *Life on a Young Planet*

A History of Life, Skewed Toward Vertebrates

The origins of life are uncertain, but scientists have generated some likely conditions and circumstances (Knoll 2015).

Life began in the ocean about 4 billion years ago, and it stayed there for some time. The last universal common ancestor (LUCA), the most recent type of organism from which all living things commonly evolved, was likely a thermophilic, anaerobic microbe (Weiss et al. 2016).

Life requires replicating molecules. The earliest such molecules were probably RNA, which is a nucleic acid similar to DNA that is capable of self-replicating. In short, certain RNA molecules can act as a polymerase which can replicate template RNA molecules by joining together individual RNA monomers, much like the current protein RNA polymerase. This process, self-replication, is crucial for life.

From the initial, murky moment that self-replication first came to be, three major branches of life evolved. The three domains of life are Bacteria, Archaea, and Eukarya. The first two, Bacteria and Archaea, lack a nuclear membrane; some members of Archaea are known to thrive in the most extreme environments, such as in volcanoes or at the bottom of the ocean. Eukarya are most familiar to us: we belong to Eukarya, as do fungi, plants, all animals, and some single-celled organisms such as amoeba. We eukaryotes are united by our possession of a nucleus within our cells – a tightly packed center of genetic code.

Millions of years ago, ancestral eukaryotes domesticated other single-celled organisms by enveloping them; these became our mitochondria. Mitochondria take care of certain respiratory functions of our cells. This phenomenon is known as endosymbiosis and has played many important roles in large evolutionary transitions. For example, endosymbiosis involving photosynthetic cyanobacteria and other organisms allowed photosynthesis to spread across the globe.

About 600 million years ago, the first animal species evolved. These mysterious early species are called the Ediacaran biota and are poorly understood. Some look like jellyfish, others look like worms, and some look distinctly different from anything living today; much of what we know about the enigmatic Ediacarans comes from fossil molds of the original bodies, so we have very little information about their ecology and evolutionary relationships. During the so-called Cambrian explosion, which actually lasted many years, most of the modern phyla of animals came to be (Briggs et al. 1992). The most famous fossil record of these species is the Burgess Shale, a rich deposit in Canada.

Four hundred million years ago, plants evolved from “green algae” (which had already domesticated cyanobacteria to enable photosynthesis). Then, 380 million years ago, vertebrates clawed their way onto land (in the form of amphibious critters). Arthropods were the first terrestrial animals by many millions of years, but we do not know exactly when they first crawled ashore.

Two hundred and fifty million years ago, the earth saw the most catastrophic extinction event in its history: the Permian Extinction, also known as the “Great Dying.” Somewhere between 81% and 96% of all life went extinct during this period; it took 30 million years for Earth to recover a comparable diversity of life. Both catastrophic and gradual processes led to the Great Dying, including volcanic eruptions, methane release from the sea floor, and increased anoxia and aridity worldwide (Sahney and Benton 2008).

Around 200 million years ago, in the wake of the Permian Extinction, sauropsids, archosaurs, and dinosaurs came to dominate land vertebrates. At this time, mammals were mostly small and insectivorous- but not for long.

Sixty-six million years ago, the Cretaceous period ended with a comparably minor mass extinction: the extinction of the dinosaurs (and many other animal groups). An asteroid collided with the earth which, in combination with other factors, wreaked havoc on the reptilian population. However, their descendants and relatives, birds, still cover the earth today. Indeed, from a formal phylogenetic perspective, birds are

dinosaurs. The extinction of the nonavian dinosaurs paved the way for mammals to stride forth from their nocturnal, small-bodied forms. Humans have recently become a particularly notorious ape.

Now, human actions are causing a global mass extinction greater and swifter than any before on record.

Human Evolution: Early Fossils, Close Relatives, and Genetic Traces

Four out of five animals on Earth are nematode worms – if all solid materials except nematode worms were to be eliminated, you could still see the ghostly outline of [the continents]. . . in nematode worms. – E. O. Wilson

And yet, here is a section dedicated to the evolution of man.

Humans evolved from apes. From fossils, we know that primates came to be about 55 million years ago, while genetic evidence (using molecular clocks) indicates that they first evolved 85 million years ago. Many, many species of *Homo* and relative genera flourished in Africa while our direct ancestors were evolving. Just a few of them emerged from Africa before our own migration out: *Homo floresiensis* (the hobbits), *Homo neanderthalensis* (the Neanderthals), and *Homo sapiens denisova* (the “Denisovans,” status as species or subspecies currently debated).

East Africa is rich with fossils of early hominins, particularly in the regions of Olduvai Gorge and Lake Turkana. Many of these fossils were found by the famous Kamoya Kimeu as well as Leakey family: Mary and her husband Louis, as well as their son Richard and daughter-in-law Meave. They were assisted by extremely capable fossil hunters and paleontologists.

Three of the most famous and important early fossils in this region are Lucy, Ardi, and the Nariokotome Boy. They are important because they are relatively complete, early relatives of ours who have human-like traits in combination with apelike traits.

Donald Johansen discovered “Lucy” (so named for the Beatles song “Lucy in the Sky With Diamonds”), the most famous hominid fossil of all time: Lucy lived about 3.2 million years

ago as a member of the small-brained, bipedal species *Australopithecus afarensis*. Lucy is also known as Dinkinesh, a translation of “you are marvelous” in the Amharic language. Lucy is famous for being a biped from so long ago and for indicating that bipedalism apparently preceded brain enlargement.

“Ardi” that is a hominid fossil more complete and older than Lucy was found first by a college student named Yohannes Haile-Selassie and uncovered and examined fully by Tim D. White. This was Ardi, a female individual of the species *Ardipithecus ramidus*, featuring opposable thumbs and *opposable big toes*, as well as an apparently bipedal gait. The species name comes from the words Ardi (“ground floor”) and the word ramid (“root”) in the Afar language – the point being that Ardi lived on the ground and lies at the root of all humanity.

Kamoya Kimeu, found the Nariokotome Boy: this fossil, formerly known as the Turkana Boy, is a young *Homo erectus* dating to 1.5–1.6 million years ago. It is the most complete early human skeleton known and had an extremely large brain and tall stature.

The East African fossils are incredible, but a recent, remarkable find brought Southern Africa back onto the map: *Homo naledi* was found in South Africa in the “Cradle of Humankind,” where 15 individuals were found in an extraordinary cave deposit, seemingly placed there intentionally. These fossils have not been dated due to the unique circumstance of their deposition, but the morphological characteristics make them strange chimera of near-modern features and highly “primitive” apelike features: human feet but apelike shoulders, human-like hands with apelike curved fingers, and a tiny brain. The full significance of this fossil find will be unraveled in years to come.

Our direct ancestors, archaic *Homo sapiens*, evolved sometime between 400,000 and 250,000 years ago. The “out of Africa” model describes how humans evolved to our modern form about 200,000 years ago, then left Africa, and displaced, interbred with, and perhaps outcompeted the other species of *Homo* already spread across the globe. It is certainly possible that

Homo sapiens left Africa multiple times. There may have even been a coastal dispersal of humans from the horn of Africa, leading to populations in Oceania and Southeast Asia.

Our closest living relative is the chimpanzee. We share between 95% and 99% of our genomes with chimps. However, we see genetic persistence of Neanderthal and Denisovan DNA in many populations of *Homo sapiens* today. This is because our ancestors interbred with these related subspecies of human; most human lineages of non-African origin have 1–3% Neanderthal DNA in their genomes (while a jawbone from an early modern human from Romania had 6–9% Neanderthal DNA (Fu et al. 2015)); many modern humans also have Denisovan DNA (Reich et al. 2010). For example, genes conferring resistance to high altitudes in Tibetans were derived from gene flow with Denisovans (Huerta-Sánchez et al. 2014).

Interestingly, human culture has driven genetic evolution (This gene-culture coevolution was recently demonstrated to exist in orcas as well, the first nonhuman species for which this has been conclusively demonstrated Foote et al. 2016). For example, a turn toward cultivating cattle for milk in Europe led to the evolution of human lactase persistence genes, genes that facilitate lactose digestion and allow adults to drink milk without adverse digestive upsets (Beja-Pereira et al. 2003).

The Evolution of Psychological Traits

When you light a candle, you also cast a shadow. –
Ursula K. Le Guin

All we ever see of stars are their old photographs. –
Alan Moore, Watchmen

Much of evolutionary inference comes from looking at shadows. This is true perhaps most of all for cognitive and behavioral traits, which tend to disappear in the fossil record (except for leaving “traces” such as footprints and stone tools) (In Chauvet Cave in Southern France, the footprints of a boy from 20 to 30,000 years ago appear alongside the footprints of a wolf with an apparently shortened middle digit, a characteristic of dogs (Garcia 1999). Was the

wolf domesticated? Did the boy and the wolf explore the cave together? Or are the footprint sets merely aligned by chance, separated by hundreds or thousands of years in real time?). Luckily for evolutionary psychologists, certain psychological phenomena have evident molecular, morphological, and genetic correlates which can be tracked by the fossil record and our own genomes.

Sensory perception is the tunnel between our brain and the world, and a wealth of evolutionary, molecular, and genetic evidence has unwound the perplexing spools of sight, smell, touch, and hearing (If we were so lucky to be pit vipers or vampire bats, we could also sense infrared; likewise for many other animals and their ability to sense electromagnetic fields). For example, we know about when our ancestors switched toward a primarily visual mode of life, because we see evidence that vision improved while our sense of smell got worse. Scientists have noted genetic signatures of color-sensitive cell evolution paired with the degeneration of olfactory ability. Similarly, we can interpret certain sensory and cognitive biases by better understanding how the visual system works; phenomena such as “color correction” (by which a red apple looks red whether it is in the bright sunlight or dark blueish light) are highly conserved across many vertebrate lineages.

Sensory perception is not the only evolutionary avenue to the brain: for example, certain genes have been tightly linked to higher cognitive functions. The defining human trait of syntactical language depends at least in part on a mysterious gene called *FOXP2*, which is necessary for proper speech and language. Scientists can trace the evolutionary history of *FOXP2* in the genomes of humans around the world, our close ancestors, and our extinct human relatives. Neanderthals, for example, shared our variant of *FOXP2* (Krause et al. 2007). We have discovered this gene’s function through characteristic language deficiencies in a family with many members who had an impaired copy of the gene; we have further expanded upon this knowledge with model organism experiments (Vargha-Khadem et al. 2005). Only two amino acid changes separate our human version of *FOXP2* from that of chimpanzees, our nearest living relative; despite this tiny

difference, chimpanzees do not have any communication system that we would call language.

The fossil record can even tell us information about the cognitive capacity of our ancestors and sister groups. Fossil endocasts of human brains – that is, the inside of preserved skulls of our human relatives – give us information about how large their brains were and sometimes even whether or not they had enlargement of certain regions associated with language processing, such as Wernicke’s Area and Broca’s Area (Jerison 2012). Braincases are fragile and are rare to discover in the fossil record, but they can reveal the brain volume of an extinct human and help us understand its relative cognitive abilities.

Finally, indirect correlates in the paleontological and archeological record provide clues to the nature of human cognition. For example, cave art and artistic engravings are associated with increasing creativity and complex psychology. Even more simply, tool use is associated with intelligence. Of course, humans are not the only toolmakers and users. For example, New Caledonian Crows (who live on a peculiar South Pacific island) are sophisticated toolmakers (With New Caledonia’s relative isolation, rich metal deposits, and friendly climate, one cannot help but wonder: is there an alternate world where intelligent crows dominate the globe?). But the existence of hominin-made tools in the fossil record tells us a bit about cognitive development and technological advances over time. When these tools are found in close company with actual hominin fossils, we can learn even more. The fossil record is filled with stone tools from our ancestors and our hominin sister taxa, including stone axes, stone choppers, stone flakes for cutting, and hammerstones. The oldest stone tools were long thought to be made 2.6 million years ago, in eastern Africa, by the aptly named *Homo habilis*. However, a wealth of tools found at Lake Turkana in Kenya date back even farther to 3.3 million years (which is prior to the evolution of the genus *Homo*). Thus, scientists think that these early tools may even have been *Australopithecus afarensis* or *Kenyanthropus platyops* (Harmand et al. 2015).

Finally, evolutionary psychology can draw upon behavioral and cognitive studies of extant

nonhuman animals. Most useful for these purposes are (i) our relatives, most notably great apes and other primates, and (ii) distantly related species who convergently evolved similarly enlarged brains, complex social behaviors, and sophisticated cognition. From our primate relatives, we have learned much about the evolutionary roots of primate social structure, behavior, cognition, and perception. For example, a study of monkeys who were introduced to a system of currency suggests that the roots of “loss aversion” (our exaggerated “dislike” for losses that exceeds the corresponding “like” for an equivalent gain) run deep in our evolutionary history (Chen et al. 2006). Cetaceans, elephants, corvids, and other large-brained animals have given us further information about *in what circumstances* and *along what pathways* complex cognition has arisen in evolutionary history. For example, with the notable exception of the short-lived, asocial, intelligent octopus, most animals who have convergently evolved large brains and complex cognition are social and long-lived.

Through fossil evidence (such as brain endocasts), archeological and paleontological records (such as cave paintings and tools), genetic history of genes such as the famous *FOXP2*, genetic and molecular studies of sensory perception, and comparative cognition studies of living organisms, we can begin to understand the evolution of our large, unusual brains.

Conclusion

Over time, species change and diverge under the influence of natural selection, genetic drift, and population effects such as bottlenecks. Scientists can learn much about the evolutionary history of extant organisms, and their relatedness to each other, by examining the fossil record and genetic evidence. Natural selection is a powerful force that has shaped our own evolution, and that of all living things. Natural selection does not select “good” traits; rather, it selects traits that allow organisms to survive and reproduce. Evolution is not a staircase describing the ascent of man;

rather, it is a complicated bush with myriad organisms adapted to myriad environments. Interpreting evidence to make evolutionary conclusions is difficult, particularly when scientists seek to understand complicated traits such as human intelligence, which have a spotty fossil record and complex genetic and environmental underpinnings. Nonetheless, no trait can be completely understood outside of an evolutionary framework. Understanding evolution can help explain where we humans came from, where we are going, and why the way we are. As Theodosius Dobzhansky famously wrote, “nothing in biology makes sense except in the light of evolution”.

Cross-References

► Adaptations

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Evolutionary Clinical Psychology

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Synonyms

Darwinian psychiatry; Evolutionary medicine; Evolutionary psychiatry; Evolutionary psychopathology

Definition

Evolutionary clinical psychology, or evolutionary psychopathology, is the study of mental disorder from an evolutionary perspective. Evolutionary psychology, in general, studies primarily how the mind works, in its normal and universal state. Different evolutionary approaches consider both the conditions that mainstream mental health care and research have defined as abnormal or pathology, or offer evolutionary perspectives to how these conditions may be considered adaptive, or even how one may fundamentally understand what psychopathology is.

Introduction

Evolutionary clinical psychology is the study of mental disorder from an evolutionary perspective. This enterprise involves discussions of how to understand the human capacity for mental

disorder (Gilbert 1998; Nesse 2011), definitions of mental disorder (Wakefield 1992, 1999), and even adaptationist approaches to symptoms and disorders (Andrews and Thomson 2009). Evolutionary approaches to mental disorders have existed ever since Freud explained the Oedipus complex with a phylogenetic explanation. This early attempt was obviously incorrect, as the castrated young boy hardly could pass on his anxiety or his genes to later generations. Later functional approaches to anxiety, and a basic evolutionary understanding of attachment between mother and infant (Ainsworth and Bowlby 1991), became influential within mental health care. Throughout the years, there have been several attempts at providing mental health research with evolutionary underpinnings (Kennair 2003; McGuire et al. 1992). Alas, few of these have been successful in collecting the field or creating consensus for a shared metatheory (Kennair 2011). To some degree, there is also some tension in the field between evolutionary oriented clinicians and clinically interested academics, which most clearly comes to a head in discussions of the possible adaptive function of major depressive disorder (Kennair et al. 2017). The current chapter will address a few of the most relevant contributions and controversies of this field.

Defining Psychopathology: The Harmful Dysfunction Analysis

It is hard to clearly define the boundary between nondisorder and disorder, especially within psychopathology. An important reason for this is that mental disorders have both biological foundations and are at the same time value-based perceptions of what is considered “normal” and “abnormal.” From an evolutionary perspective, it is obvious that neither how many suffer, subjective experience of suffering, or physical sequela, provide good enough grounds for defining pathology. Disease can be common, and some evolved traits can be rare. In the Harmful Dysfunction analysis of mental disorders, Wakefield (1992) combines both the biological and the value-based aspect of mental disorders.

“Harmful” refers to social norms on what is considered good or bad for the well-being of people or societies. While “dysfunction” refers to an evolved function that fails to perform the function for which evolution designed it. Wakefield’s definition of psychopathology is one of the most influential contributions to mainstream psychiatric and clinical psychological theory. The problem, though, is obvious: It is possible in a specific culture at a specific time to agree on what is harmful, given social norms. However, that brings with it the problem that different conditions and morphs may be redefined as normal or pathology due to social changes. Further, we currently do not have a full catalog of evolved mental mechanisms and their normal functions. There might, therefore, be reason to argue for greater integration of evolutionary psychopathology with evolutionary normal psychology, also as a research paradigm (Kennair 2011). We need to know the normal functions of the mechanisms of the mind, in other words a comprehensive evolutionary psychology, to be able to define psychopathology as harmful dysfunction.

Life History Approach to Taxonomy

Recently, Marco Del Giudice (2014) made a thorough contribution to the conceptualization and taxonomy of psychopathology from an evolutionary psychology perspective. Based on his analysis on fast and slow life history, Del Giudice attempts to synthesize and integrate the underlying processes of psychopathology. The many different responses to his target paper reveal both support and skepticism – not least to the somewhat simplifying fast-slow dichotomy, but also to Del Giudice’s conceptualization of some of the specific disorders such as subtypes of OCD that involve fast lifestyle impulsivity (Kennair 2014). However, criticism of an explicitly formulated theory demands that one generates empirical tests. For example, Del Giudice’s taxonomy suggests that measures of life history strategies should predict depressive symptoms, and slow life history should predict more depressive symptoms than fast life history, at least for some subcategories of depression (Del Giudice 2014). Yet, again, this is testable, and will produce data. Ultimately, this

is, therefore, a major positive development of the field of evolutionary psychopathology.

Evolutionary Medicine: Why Does Psychopathology Exist?

Evolutionary perspectives are useful within medicine and clinical psychology because it helps us to think clearly about what symptoms are. Sometimes symptoms are defenses against disease, rather than a manifestation of disease itself (e.g., coughs, fever, and diarrhea). Nesse and colleagues (Nesse 2011; Nesse and Williams 1996) have been very clear about the aim of an evolutionary medicine approach to psychopathology: the aim of an evolutionary approach is to describe how evolved human nature and the human mind make us vulnerable to developing mental disorder. This is also Paul Gilbert's (1998) approach: the mind has constraints and is not perfect, and mental disorder may arise as a result.

A fundamental insight from evolutionary medicine and psychopathology is that natural selection does not care about our well-being. Whatever works for effective gene replication is what is selected for. That is not to say that selection does not construct brains capable of pleasure, but rather that evolution does not select for happiness as a goal in itself. The smoke-detector principle is a good illustration of this (Randolph M Nesse and Williams 1996). If you want to avoid fire in your home, its better to have sensitive alarms that sometimes go off inappropriately, but always go off when there is a fire. In the same way, evolution does not select for fear and anxiety mechanisms that protect individuals from worrying too much because anxiety feels bad. False alarms cost a few calories, but not reacting to a life-threatening situation is an evolutionary catastrophe.

The causal power of natural and sexual selection to design vastly complex machinery such as the human brain is awe-inspiring. Nevertheless, it would be terribly naive to claim that all symptoms of mental disorders (e.g., psychosis, autism, and major depression) always are the products of underlying evolved adaptations. Despite the power of selection, disruption of evolved design

happens for environmental reasons, such as modern humans sleeping too little, eating too much sugar, and doing too little exercise. And dysfunctions also happen for genetic reasons, such as deleterious mutations constantly eroding evolved design. We will look at these factors in the problems section below.

The opposing view to the Darwinian Medicine or vulnerability approach is the most radical version of clinical evolutionary psychology. The approach that considers that disorders or symptoms of disorders are adaptive, examples range from Andrews and Thompson (2009) who consider major depressive disorder and rumination adaptive (but see also Kennair et al. 2017), to researchers who consider psychosis to be adaptive from a group of selectionist perspective (Polimeni and Reiss 2002). It must be said that also within seemingly maladaptive states, such as psychopathology and even suicidal behavior (de Catanzaro 1995), the idea that the trait is adaptive is both original and testable, hallmarks of good scientific theorizing. Despite being skeptical of this approach, it is worth noting that even this panadaptationist approach provides grounds for basic empirical testing, which the field of evolutionary clinical psychology sorely needs.

Problems Within Evolutionary Clinical Psychology

Looking at clinical psychology from an evolutionary perspective is useful for the same reason that it is so useful in psychology generally: It provides a unifying framework for generating hypotheses about human nature. However, there are many unsolved problems within evolutionary clinical psychology.

The Problem of Explaining Diseases as Evolved Traits

Evolutionary psychopathology is a young field and pitfalls and dead-ends are expected (and often useful) in a young science. Nesse (2011) has provided 10 useful questions to ask when doing evolutionary studies of disease vulnerability, the first of which is:

“Is the object of explanation a uniform trait in the species, or is the goal to explain variations in a trait among groups or individuals?” Many adaptive hypotheses of psychopathology typically fail to be clear on that first question, or ignores it altogether.

Questions such as “why did schizophrenia evolve?” can be misleading because it suggests that we need to find hidden evolutionary advantages that the disease may have. A more useful evolutionary question is to ask why humans are vulnerable to developing diseases such as schizophrenia, anxiety, and depression (Nesse 2011). In practice, this entails to have an adaptive approach to species-typical design, for example, for understanding mood systems involved in fear and sadness, in what situations they are activated, and the selection pressures that caused their design, and then disentangle how that design leads humans vulnerable to dysfunctions in those systems.

The Problem of Genetic Variation

Successful genetic variants will spread throughout the population. Therefore, selection reduces genetic variance over time. For this reason, evolutionary psychologists often assume that the heritability of evolved adaptations should be very low. If there is no genetic variation, genes cannot explain differences among people. Evolutionary psychologists are interested in evolved psychological adaptations, and have therefore assumed that genetic variation between people is largely fitness-irrelevant noise or exist entirely for creating biochemical differences that are useful for defending against pathogens (Tooby and Cosmides 1990). However, humans differ dramatically on psychological traits, and it has become increasingly clear that a substantial proportion of this variance is due to genes (Polderman et al. 2015; Turkheimer 2000).

It is an important evolutionary question *why* these genetic differences exist (Zietsch et al. 2015). There are three main evolutionary forces that can account for the maintenance of genetic variation (Arslan and Penke 2015). The first is mutation-selection balancing. Here, the genetic variance is constantly a balance between new

deleterious mutations and their eventual removal by selection. The second is neutral mutation drift, which means that genetic variance is maintained because these variants are neutral to selection, and hence their introduction and removal are due to chance. The third is balancing selection, which is a group of evolutionary processes that actively maintains genetic variance because their relative frequency is adaptive in particular genetic and environmental contexts.

Evolutionary theories of psychopathology, for example of depression (see ► [Depression](#) chapter, this volume), typically only considers neutrality or balancing selection as potential forces that can explain genetic variance underlying psychopathology. In all likelihood, Darwinian psychiatry and psychopathology has concerned itself primarily with balancing selection because it keeps natural selection at the causal forefront. However, to explain heritable genetic variation, other types of evolutionary tools than pure adaptation are required. Explaining genetic variation is simply different than explaining species-typical traits (Keller and Miller 2006).

If mental disorders were maintained by balancing selection (for example, negative frequency-dependent selection), we would expect that just a few genes maintain the prevalence of the disorder in the population. In recent years, though, it has become clear that most human traits, including psychopathology, are extremely polygenic. That is, genetic variation is caused by thousands of genes that individually have very low effect sizes (Chabris et al. 2015). Further, inbreeding increases the risk for serious psychopathology (Rudan et al. 2003). These facts are more consistent with severe psychopathology being caused by the constant influx of new mutations into the human genome (Keller 2008). The brain, after all, is so complex that it has a large “mutational target size,” meaning that most mutations affect the development of the human nervous system. Further, because people of similar genetic quality mate with each other (assortative mating), genetic variance increases and is maintained. Hence, mutation-balancing selection is the most likely candidate for explaining the

maintenance of genetic variation underlying serious psychopathology, not balancing selection.

The Problem of Evolutionary Mismatch

A popular idea within evolutionary approaches is that modern living conditions result in pathological development or do not stimulate mental mechanisms adequately within their expected bandwidth for normal development or output (Kennair 2003) “Diseases of civilization” such as diabetes, obesity, and heart disease increased in western or modern societies after the agricultural and industrial revolution. However, when traits are expressed due to mismatches (depression caused by lack of exercise), that trait is not in itself an adaptation, but rather a manifestation of a vulnerability arising from evolved design. This perspective is often not considered fully in adaptationist hypotheses of mental disorders. It might be worth noting, though, that modernity has been blamed for malaise since the seventeenth century. Some ideas such as breakup of extended family care influencing especially young female depression, or reduced fatty acids in food, reduced physical activity, have all been suggested as explanations for mental disorder. Sandseter and Kennair (2011) suggested that reduced natural risky play among children, and less exposure for emotionally activating setting, might, in general, increase phobias and emotion regulation in the population.

Specific Disorders

There have been formulated a large number of specific evolutionary theories for each of the specific disorders. These have, in general, generated little empirical evidence and had limited influence on mainstream mental health research or care. The exception is evolutionary approaches to fear and phobias. Some approaches are adaptationist, some focus on mismatch, others invoke life history theory, some balancing or frequency-dependent selection, and there are even a few group selectionist approaches. This lack of integration is one of the field’s great limitations. Establishing a few criteria, such as a focus on evolved mental mechanisms and

a Harmful Dysfunction analysis of pathology, might be beneficial for future integration and a more comprehensive research program (Kennair 2011). Most importantly, the field needs to be able to communicate better with mainstream mental health care, and also generate more data to improve the unfortunate theory:data ratio. The following section will address some of the evolutionary theories and speculations for some central-specific mental disorders.

Anxiety

One of the best understood areas of mental disorders is the anxiety disorders. Due to an evolutionary and functional approach being considered fundamental by most anxiety researchers and therapists, we consider normal fear to be adaptive and functional because it elicits species-specific defense responses and potentially lifesaving avoidance (Kennair 2007; Marks and Nesse 1994). Consequently, we understand that contextually exaggerated fear responses, anxiety, will result in nonfunctional safety behaviors and maladaptive avoidance. This lays the ground for treatment in general, as we may learn what is and what is not dangerous, threatening, or painful: systematic exposure and prevention or discontinuation of maladaptive or unhelpful safety behaviors. Some of the safety behaviors consist of cognitive processing, others external behavior. The different anxiety disorders are thus defined by what the patient has exaggerated fear of and what maladaptive safety behaviors maintain this fear.

Along the way, there has been a shift from treating anxiety disorders in general from a behavioral perspective (Marks and Nesse 1994), which mirrors the historical shift in evolutionary research on human behavior, namely from behavioral sociobiology to the cognitive science of evolutionary psychology. Specific disorders are treated with largely specific treatments. While specific phobias are effectively treated with one-session exposure, other anxiety disorders are treated with more cognitive and metacognitive approaches (Kennair 2007). There is probably too little attention on new effective clinical treatments within evolutionary psychopathology.

Generalized Anxiety Disorder

The identifying feature of GAD is worry. Worry is largely based on verbal processing of negative, often catastrophic anticipation of future events. There are therefore few relevant animal models. It is further unclear whether worry at subclinical levels is adaptive; it might be a form of the classical cheater detection mechanism that breaks our confirmation bias and makes us reconsider our risky course of action. Young men seem to have increased mortality compared to middle-aged men and women (Kruger and Nesse 2004), most likely due to hypophobia, while women are more worried and develop generalized anxiety disorder more than men. The evolutionary underpinnings of generalized anxiety disorder need further work based on an integrative evolutionary approach to worry (Kennair et al. in prep).

Obsessive Compulsive Disorder

Obsessive Compulsive Disorder (OCD) is probably one of the more wrongly conceptualized disorders: sometimes compulsions are compared to repetitive behavior and perseveration, which is wrong. It is not as much a neuropsychological condition as a neurotic disorder. Del Giudice's (2014) suggestion that there is an impulsive and dangerous subgroup, is probably not correct (we would treat people with OCD who were afraid of what they might do with knives by exposing them to knives) (Kennair 2014). Boyer and Liénard (2007) precaution system approach is neither fully precise, as their description might be more correct for the danger monitoring and anticipation of generalized anxiety disorder. Finally, the idea that OCD should be a result of brain sequela, due to childhood throat infection, is unlikely. How a few sessions of exposure and response behavior should be able to change neurological dysfunction or sequela is hard to conceptualize. OCD is to a large degree a disorder of neurotically (or magically) attempting to control the uncontrollable – and especially the compulsion is about neutralizing the obsession. From a normal disgust and hygiene perspective, it may come across as hyperactivation of disgust systems, but it is worth noting that it is the anxiety

or disgust the patient is attempting to remove with excessive washing, rather than really attempting to become clean. From a behavioral therapy perspective, compulsions are pretty simple to treat: exposure and prevention of the safety behaviors (Solem et al. 2009). From a metacognitive perspective, it is a disorder of beliefs about effects of thoughts (the power of the obsessions). Obsessive thoughts may be thought to govern the patient's behavior against the patient's own will (thought-action fusion), to change future events (thought-event fusion), or thought-object fusion, where essential qualities of objects may contaminate the patient (like curses or talismans). Alas, there are no current evolutionary perspectives on obsessions from a metacognitive approach.

Panic Disorder and Agoraphobia

Panic, as flight, has been considered the adaptive foundation of panic disorder. It is unlikely, though. While untethered escape expending all resources probably is a good way of escaping some external threats; panic disorder rarely involves escape or caloric expenditure during attacks. Rather the four things people fear is based on misinterpretations of bodily symptoms of activation – in other words a catastrophic misinterpretation of anxiety symptoms: fainting, having a heart attack, choking, and going mad. The safety behavior that patients engage in reflects this. Typically lying down is more typical than running away, in fear of fainting and heart attacks. One of the recurrent problems with evolutionary approaches is that they have not considered the functional psychotherapy interventions that reduce the maladaptive safety behavior that the patient is engaged in and that maintains the anxiety. Especially, there is a lag as cognitive and metacognitive methods have proven to be efficient (Kennair 2007). There probably ought to be more feedback from the functionalist therapeutic methods to evolutionary approaches.

In the case of panic disorder, any misinterpretation of bodily symptoms causing anxiety is possible. There is therefore reason to believe that there are few relevant animal models. The evolutionary roots will probably lie in the mental mechanisms involved in interpreting signals of danger,

but given that cultural explanations are invoked (heart attacks in Western contexts or djinns in Muslim cultural contexts), it is also relevant to consider the cultural transmission of dangers. Among many therapists, there is a fear that the patient may faint; but this is not the case. The important question, therefore, must be: why do we have the capacity to scare ourselves into panic attacks, with unfounded beliefs about imminent and catastrophic danger?

Social Anxiety Disorder

Social anxiety is characterized by an intense fear of possible negative evaluations by others. Hence, the patients with this condition avoid social situations that are perceived as threatening.

It is likely that social mammals like human beings evolve motivations, affects, and behaviors that increase the chances of managing the fitness-relevant resources that groups contain. Social fears can adaptively work as inhibitors of murder, mate-poaching, stealing, and so on (see the ► [Social Anxiety](#) chapter in this volume and Buss 1990). Öhman (1986) has argued that humans fear dominant and aggressive others because it is useful for avoiding tissue damage. Other evolutionary theories of social anxiety propose similar functions, namely to protect oneself from physical aggression and to avoid exclusion from social groups (Trower and Gilbert 1989). Another theory is that social fear exists in order to regulate and enhance self-representation and relational value (Leary et al. 2014).

Social exclusion is very harmful to humans, and adaptations have evolved to make it painful (Baumeister and Leary 1995). Humans avoid it at all costs. However, are the symptoms of social anxiety disorder in themselves evolved adaptations? There is no evidence to suggest that people without social anxiety disorder experience any damage to their physical safety, social status, or reputation. It therefore seems most likely that social anxiety disorder is a dysregulated activation of otherwise adaptive features of the human mind.

Specific Phobias

Beyond the function of fear and general understanding of fight-flight-freeze and species-specific

defense responses, the most obvious contribution of evolutionary perspectives to the anxiety disorders is the understanding of preparedness in phobias (Öhman and Mineka 2001). There are many phenomena in the world that may be dangerous to us, but that we do not fear, despite many health and safety campaigns by the authorities. In many cases, this is due to mismatch. On the other hand, we fear spiders, snakes, heights, the dark, and strangers much more than what is reasonable. Specific phobias are defined as exaggerated fear of these specific phenomena (combined with maladaptive avoidance or safety behaviors). There is continuous evolutionary inspired research on prepared and specific mechanisms involved in phobias based on this tradition (see chapter on ► [Fears and Phobias](#)).

For many decades, we have known that one-session systematic exposure (with response prevention) is an effective treatment. The effective behavioral approach to treatment resulted in a widespread belief that these phobias were conditioned. In recent years, longitudinal studies suggest that phobias appear due to natural maturation (known as nonassociative pathways) and then disappear due to developmental processes (Poulton and Menzies 2002). Sandseter and Kennair (2011) suggested that children's natural tendency to engage in risky play motivates them to naturally expose themselves to situations that previously were dangerous to them, but that they actually can cope with as they develop.

Blood Injection Injury Phobia is a special case. Rather than causing increased activation and escape (fight and flight), this is the only anxiety disorder where the patient actually faints (unlike panic disorder, where the patient fears fainting, but does not). From an evolutionary perspective, this may be adaptive, as increased physical activation and adrenalin might be deleterious and dramatically reduced blood pressure might be beneficial if there is risk of severe blood loss (Kennair 2007).

Depression

It is estimated by World Health Organization that unipolar depression will become the second leading cause for disability in the world by 2020

(WHO 2001). Given the overwhelming social and economic consequences of the condition, an effort to understand why it exists at all should be a major concern for the academic society. Although an evolutionary understanding has shown to be useful for guiding clinicians in the treatment of various anxiety disorders, this is not the case with depression. In fact, with the present state of the field one can get very different recommendation for treatment practice dependent on which evolutionary theory that is endorsed (Kennair et al. 2017). Perhaps because of the lack of consensus in evolutionary understanding, mainstream research on clinical depression is seldom guided by predictions drawn from evolutionary theories of depression. Clinical practice is even less so.

An evolutionary analysis will have to address the fact that depression is common, but at the same time having obvious fitness reducing consequences, like reduced interest in reproduction. How is it that a phenomenon evolves to be both debilitating and common? Most clinician's unfamiliar to evolutionary thinking assume that depression is a harmful dysfunction, meaning that they think of depression as a malfunction of the emotional system. Contemporary clinicians thus look for environmental, developmental, or neurobiological abnormalities that could explain the syndrome (Beck and Alford 2009). Nettle (2004) has made the argument that depression is a harmful dysfunction based on an evolutionary analysis. However, an evolutionary approach also must consider that depression can be an adaptive response to fitness relevant triggers that is part of the common architecture of the human mind.

There are two broad categories of adaptive evolutionary theories of depression; the involuntary behavior inhibition category and the social bargaining or social problem-solving category. In the involuntary behavior inhibition theories, depression is viewed as beneficial because it retracts the individual from investing or taking risk when there exists information that such behavior is unlikely to be rewarded with fitness relevant gains (e.g. Price et al. 1994). So the function is to downregulate the normal workings of other psychological mechanisms. Depression is thus a "negative" adaptation, in the sense that it

downregulates other adaptations in contexts where those other adaptations are detrimental to fitness.

Both the bargaining theory and the social problem-solving theory view depression as a "positive" adaptation, in the sense that the syndrome of depression solves unique adaptive problems that the psychological architecture of the human mind would not otherwise be designed to solve. In bargaining theory, depression is viewed as honest signals about the inability of the individual to contribute to a shared fitness relevant investment. This would again force the significant others to invest more or lose all. Hagen (1999) uses the case of post-partum depression as an example of such. If the mother (or father) receives information that their partner is contributing less than necessary, this could trigger a depressive episode that would force the partner to contribute more or lose the baby. Andrews and Thomson (2009) suggest that depression is designed to enhance social problem-solving. They postulate that the symptoms associated with major depression help individuals think repetitively about what caused, and how to deal with, complex social problems. They assume that repetitive analysis will lead the depressed patient to solutions that ultimately solve the problem of navigating the social environment.

The clinical consequences of these evolutionary approaches to depression are very different. Proponents from the involuntary behavior branch typically view major depression as being a result of excessive downregulating of normal psychological mechanisms, meaning that the adaptive function of normal depression is lost when depression has become severe. However, proponents from those who endorse the view that depression is a "positive" adaptation typically do not view major depression as dysfunctional. In the social problem-solving approach, the severity of depression is thought to vary with the complexity of the social problem. Clinicians informed by this theory would help their patients increase their rumination to solve the underlying social problem. Clinicians informed by an involuntary behavior inhibition approach would assume that a patient with major depression need techniques that either helps them

upregulate the workings of the psychological mechanisms downregulated by the depression, or techniques that alleviate the downregulation from the depression.

Bipolar Disorder

Bipolar disorder is estimated to affect at least 1% of the population worldwide (Alonso et al. 2011). When considering subthreshold bipolar disorder and cyclothymic disorder, the combined prevalence rises to 2–4% making the suffering associated with the bipolar spectrum significantly detrimental to mental health (Grande et al. 2016).

Compared to unipolar depression, there are few adaptationist theories about why bipolar spectrum disorders exist. There are two main views in the literature on the evolutionary origin of bipolar disorder. One line of argument focuses on the assumption that constituent traits associated with bipolar disorder are adaptations, but that the disorder itself is not. Those constituent traits are thought to increase the mate value of the individual through increased performance in artistic activities, better leadership, or social skills, depending on the affective temperament in question (Akiskal and Akiskal 2005). Although experiencing maladaptive consequences, such as psychotic episodes during mania, individuals with bipolar disorder might benefit from those characteristics. In addition, even if the disorder is causing severe maladaptation in some individuals, the “good genes” might get a more benign expression in the phenotype of the children of the sufferers. This would mean that there is a balancing selection between lack of reproductive success in one generation versus success in the next.

The other main view about the evolutionary origin of bipolar disorder argues that the syndrome of bipolar disease, as a whole, is an adaptation, including the manic episodes in bipolar I. In the perhaps most provocative version of that proposition, Sherman (2012) theorizes that the phenotype that is seen in the circular (alternating between manic and depressive episodes) version of bipolar I is an adaptation to severe northern climate during the Pleistocene. This is a hybridization of theories derived from earlier findings about the association between the bipolar

spectrum and (1) biological clocks and seasonal alternations in mood, and (2) pyknic (compact, cold adapted) physical characteristics. Bipolar disorder is thought of as a human equivalent of hibernation and involves an optimization of resource allocation during winter and summer where risky behaviors are postponed, through depression, to the more agreeable season. However, if the conditions become bad enough so that a risk averse strategy would not work (i.e., the food storage runs out), the gambling strategy would be the only way out of certain death. Sherman (2012) thus proposes that the capacity for mania could be an adaption to the problem of emergency. She argues that the syndrome first evolved among the Neanderthals because they experienced extreme selection pressure toward solving the adaptive problem of cold climate without advanced technology such as clothing and shelter construction. The genes associated with cold resistance eventually ventured to the human genome through interbreeding between Neanderthals and those of the *Homo sapiens* that left Africa before the Neanderthals went extinct.

New research has concluded that part of the human genome derives from Neanderthals (Green et al. 2010). Even so, the hypothesis that bipolar disorder derives from this population remains controversial. It would mean that those who are decedents from ancestors that never left Africa would not have the capacity for developing bipolar disorder, at least not the manic episode (Sherman 2012).

Eating Disorders

There are several disorders related to eating behavior such as binge eating, obesity, anorexia, and bulimia. While obesity is a multifaceted issue with many proximate causes, humans possess some key universal adaptive mechanisms that are instrumental for an evolutionary understanding of this disease: First, humans find high calorie and sugary foods delicious, and will often crave such foods. Second, any excess calories they consume will be stored in their bodies as fat and glycogen. These energy reserves were likely critical for survival in an EEA where food was scarce. These adaptations are as powerful

today as they have ever been, even for those of us who now live in an environment with endless access to calorically dense food, and almost no need for exhaustive activity. This is because this type of environment has probably been almost nonexistent in our evolutionary history; hence, there has not been a significant selection pressure against eating too much, or storing too much fat in our energy reserves. An understanding of this mismatch between the EEA and the post-industrialization environment is crucial for understanding obesity and other lifestyle diseases.

Another major eating disorder is Anorexia. Anorexia is a disorder where patients (mostly adolescent girls) are obsessed with weight, and will starve themselves to get rid of imagined excess fat. Life history theory has been a useful analytical framework for understanding this disorder, with key findings suggesting that anorexia is associated with a fast life history. There is a mismatch between adaptive female intrasexual competition and the modern world where there is an intense focus on the attractiveness of thin female bodies, results in disordered eating patterns. These ideas are in opposition to early psychoanalytical theories of anorexia, which propose that sexually repressed girls seek to delay adulthood by starving their bodies. Some evolutionary theorists have also speculated in the adaptive function of delaying reproduction, although anorexia may be a maladaptive approach to doing this.

Personality Disorders

Personality disorders involve enduring problems in interpersonal functioning due to maladaptive and inflexible behavior, cognition, and emotions. However, this general mental health definition to personality disorders does not consider that sometimes personal feelings or social desirability of a phenomenon says nothing of whether an evolved mechanism is working or not. Further, while personality disorders are generally conceptualized as disrupted development or extremes of normal personality, an evolutionary approach might consider how different personality disorders may be expressions of normal variation or different evolved morphs.

An example of this is the evolutionary analyses of psychopathy in which we both find mental mechanism failure approaches (true Harmful Dysfunction psychopathology), normal variation in black triad traits, and the suggestion that there are two types of psychopathy: the frequency selected approach to exploiting others and a developmental ecologically elicited adaptive response to circumstances (Mealey 1995). Especially, the frequency-selected approach is of interest. If everyone was antisocial and exploitive, there would be no socially generated surplus to exploit, but if the majority is prosocial and cooperative there will be a possible surplus for to parasitize. Lack of empathy might therefore be beneficial to many in some situations or to a small minority across social contexts. In that case, despite diagnosing lack of empathy, this might not be due to mental mechanism dysfunction – the lack of empathy might be a sign of evolved function.

Borderline personality disorder is another disorder that has received attention from an evolutionary perspective. Typically, patients with this disorder have unstable relationships, unstable mood, and a sense of chronic emptiness. Brüne and colleagues focus on how facets of borderline personality disorder including unstable relationships, impulsivity, and sexual risk behavior may be understood from an evolutionary life history perspective (see also Del Giudice et al. 2014). As such, some of the traits of borderline personality disorder may be considered extreme versions of adaptive traits in contexts of low long-term investment. It is worth noting that this research is in line with other correlational research where shared parent-offspring genetics might both predict unstable childhood experiences and impulsivity and unstable relationships as an adult. In general, all such research needs to control for genetic influences. Also, other personality disorders may be due to extremes or maladaptive combinations of adaptive traits. Nettle and Clegg have shown how facets of personality disorders may be beneficial to mating success, as in the case of schizotypy. While the personality disorder in itself may be problematic, some of the symptoms may be linked to fitness enhancing traits.

Schizophrenia

The prevalence of schizophrenia is roughly 1% across all human cultures. This universality suggests that schizophrenia has been a part of the human condition at least since humans first migrated from Africa. In addition, findings from twin and adoption studies show that schizophrenia is highly heritable. If we also consider the fact that schizophrenia is a dramatically debilitating disorder, an important question emerges: Why are the genes responsible still in our gene-pool? This has been called the schizophrenia paradox, and has attracted much attention from evolutionary psychopathologists. Evolutionary models of schizophrenia include group selectionist explanations, viral explanations, explanations from social hierarchy theory, as well as nutritional explanations – proposing increased prevalence of schizophrenia due to decreased intake of fatty acids. However, Crespi and colleagues have found that genes associated with schizophrenia show signs of selection. While their results does not indicate why these genes are selected, they do support a by-product theory of schizophrenia fronted by Timothy Crow: This model proposes that the genetic evolution underlying our language capabilities and hemispheric lateralization, the very mutations that made us human, also made us vulnerable to schizophrenia (Crow 1995).

It has also been suggested that schizophrenia is at the extreme unattractive end of human fitness indicators (Shaner et al. 2004, 2008). Fitness indicators such as language and other courtship abilities evolve to attract mates and are associated with reproductive success. All evolved fitness indicators (“good genes” indicators) will have an unattractive low-end to them, hence it is possible that the heterogeneous schizophrenia symptoms are simply manifestation of failed sexually selected fitness indicators, not adaptations in themselves.

Sexual Dysfunctions

Sexual dysfunctions in men need to be explained from an evolutionary perspective, although a large number of these may be explained by current medical conditions or other mental health disorders (Apostolou 2015). There would have been

very strong selection against any condition that reduced reproductive ability. In explaining why three different male sex dysfunctions – premature ejaculation, erectile dysfunction, and male hypoactive sexual desire disorder – exist today, Apostolou bases his analyses to a large degree on very limited female choice in the EEA and the resulting mismatch or ancestral neutrality. There was therefore, according to Apostolou, no need to extend sexual intercourse beyond 1 min, no reason to have performance anxiety (a major factor in erectile dysfunction in younger males), or need for long-term oriented males to mate continuously. There is therefore no true dysfunction involved, rather a new context with greater female choice that changes the evaluation of harmfulness (or undesirability) of the behavior – but from a Harmful Dysfunction analysis sexual dysfunctions are not considered psychopathology by Apostolou.

The same is the case for female sexual dysfunction. Considering the typical female sexual dysfunction of low sexual desire, Apostolou (2016) suggests that in the ancestral context there was balancing selection of morphs with low and high sexual desire where both are favored. In addition, though, there were less negative consequences of low sexual interest due to less conflict with parents about premarital sex, and less choice in relation to partners about when to have sex. This is thus partly a mismatch approach, suggesting that what may be deemed dysfunctional in modern society was not fitness reducing in the EEA. This is, as in the case of male sexual dysfunction, based on the premise that there was little or no female choice. These first analyses of sexual dysfunctions are based on specific premises that may be considered controversial. The predictions need to be tested empirically.

Recently in an investigation of sex differences in type and degree of Negative Postcoital Emotions, the different feelings associated with the wish to detach in males and bond in women after short-term sex, show signs of adaptation (Fernandes et al. 2016). This despite most mental health research into the topic has suggested that this may be pathology.

Substance Abuse and Dependency

Substance abuse and dependency is a very costly set of mental disorders, both in terms of economic concerns and human well-being. There is no brief way to account for the etiology of these disorders, and any satisfactory explanation would need to address many proximate factors from several fields, such as biochemistry, genetics, history, social science, etc. Notable among recent contributors from an evolutionary perspective is Hagen et al., who proposes that the EEA was substance rich, and that substance seeking may protect against parasites, which may suggest adaptive reasons for recreational drug use. This is contrary to the “conventional” evolutionary perspective, which assumes a substance-free EEA, and substance abuse being a result of a mismatch after the introduction of substances of abuse into our environment. Other evolutionary approaches, such as life history theory, have also been fruitful, bringing with it biopsychosocial integration, and testable hypotheses and original ideas.

Evolutionary Informed Psychological Treatments

To date, there are few therapies that are more than merely metaphorically informed of evolutionary theory; despite both Freudian psychoanalysis being influenced by phylogenetic musings and Bowlby's attachment theory being specifically based on evolutionary understanding. Further, even fewer of these have been empirically tested. On the other hand, most who treat anxiety will consider the functional aspects of safety behaviors and specific albeit exaggerated fear, and will accept at least functional but most often explicit evolutionary underpinnings. In addition, they will probably involve at least some functional/evolutionary reasoning in psychoeducational interventions to explain both the normalcy of fear and the function and psychophysiology of anxiety.

Among actual evolutionary based interventions, there have been some attempts at targeting supposed environmental mismatch with the EEA that might cause depressive symptoms and also adding an adaptiveness approach to CFT. The problem is

peer reviewed clinical trials. A treatment that has at least one randomized controlled trial with a clinical sample is Gilbert's Compassion Focused Therapy. Obviously, there is a need for more studies, although few evolutionary psychopathologists seem to have aspirations beyond providing psychoeducation based on insights from evolutionary theory and knowledge about the EEA.

Conclusion

Ever since Freud, evolutionary perspective has informed discussions of both normal human nature and psychopathology. For most of these years, evolutionary approaches to mental disorder have mainly been a theoretical enterprise. Despite many different theories and book length expositions of the field of mental health care from various evolutionary perspectives, few of these efforts resulted in any empirical testing. This may be changing. The controversy surrounding the adaptive nature of rumination, for example, has resulted in different groups considering the benefits of specific types of rumination, and this is expected to result in future development and data collection. Further, Del Giudice's taxonomy of mental disorders based on Life History Theory also opens for empirical testing. There is reason to believe that in the near future, the theory to data ratio, that has been troubling high for development and relevance of the field will improve, and data-driven discussions will develop our knowledge of how symptoms may or may not be adaptive and why some evolved vulnerabilities result in harmful dysfunctions.

Cross-References

► [Fears and Phobias](#)

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Evolutionary Cognitive Psychology

► Neurons in the Cerebral Cortex

Evolutionary Contradiction

► Evolutionary Paradox: Women Choosing Not to Have Children

Evolutionary Criminology

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Synonyms

Evolutionary forensic

Definition

The study of the psychological mechanisms, naturally selected throughout human evolutionary history, underlying violence, and crime.

Introduction

Criminology, since the nineteenth century, has proposed to examine the transgression of formal law, chasing scientific explanations for a vast plethora of human behavior that could be classified as crimes. As an interdisciplinary field, it tries to articulate different sources of knowledge, e.g., psychology, sociology, biology, or political science, rather than restraining itself in only one aspect when evaluating criminal matter (Durrant and Ward 2012). Despite acknowledging this potential contribution of many disciplines for the understanding of crime, many criminologists point out that, in reality, the field has been dominated, in most part, by the sociological perspective (Barnes et al. 2015).

Although criminology has actually begun with biologically oriented studies, before the emergence of the sociological perspective (see Lombroso 2006), in recent years, research concerning organic and biological aspects has gained importance. Due to this, once *nothing in biology makes sense except in the light of evolution* (Dobzhansky 1964), the variables that are taken into consideration when studying crime and similar topics should not be examined without

the proper comprehension of the evolutionary context that leads to the endurance of some anti-social behaviors.

Basic Principles

Evolutionary psychologists have been analyzing different aspects of human evolutionary history that could have been responsible for the emergency of violent and antisocial behaviors, its selection throughout history, and its maintenance in present days (Barnes et al. 2015). In other words, the main proposition of evolutionary criminology is that the kind of behavior that modern societies classify as crimes was naturally selected over a millions of years' period. Nonetheless, these researchers recognize that not all acts of violence are driven by specific selected mechanisms. Otherwise, some are by-products of those (for more details, see Goetz 2010).

Violence appears as natural mechanism that evolved along with other prosocial behavior and is intrinsic to humans and other species. Despite those acts being harmful to the group as a whole, evolution can mold conducts that are not considered to be ethical or moral, once these can be successful to the individual in a given context. This means that they serve the purpose of solving an adaptive problem, like increasing fitness or facilitating reproduction. This aspect brings up an important characteristic about interpersonal violence among humans: it is not random. Rather, it is context-sensitive evolutionary trait that serves specific purposes that favor survival and/or mating success (Goetz 2010). They rely on specific contexts with stimuli that could indicate a high probability of reward. For example, the necessity of feeding will only be safely satisfied if the individual, in the presence of a predator, could restrain itself. In another delicate circumstance, a mate pursuit, for instance, depends on the absence of a dominant male and the presence of sexually available females. The capacity of self-control in these scenarios represents an evolutionary adaptive mechanism, preventing lethal conflicts (Durrant and Ward 2012). Therefore, it is logical that

classical criminological theories, e.g., general theory of crime (Gottfredson and Hirschi 1990), use the self-control as a central mechanism to understand criminal conduct.

These comprehensions help to address old issues on the criminological field. Yet, evolutionary criminology does not sign this kind of behavior as inevitable or mechanically determined, but rather, they study the environmental triggers that promote these types of responses, in order to reduce their occurrence.

Classic Criminology Issues and Evolutionary Propositions

One of the most recurrent problems that emerge from classic criminological research is the gender gap in crime rates, by which men are consistently more involved in criminal activities than women. For this matter, evolutionary psychologists comprehend this disparity in the context of mating competition and parental investment (Buss 2015). To achieve reproductive success, both men and women often have to compete with same-sex individuals to be able to pass along their genes to the offspring and guarantee its survival. Nonetheless, those substantial differences on the parental investment provided by males and females to offspring survival are what could explain this gap. Since human males present less parental investment, they are unable to face more severe selective pressures. Once they do not have to concern as much with the offspring as female, considering they don't go through gestation and nursing, they are more inclined to adopt risky behavior, such as violence. Moreover, in human history, females, more commonly, had the power to choose their partners. Thus, men usually had to compete with each other to be able to mate. This dispute, more often than not, involved displays of might through aggressive behavior (e.g., gang fight) or, less frequently, violence encounters that eventually led to injury or death. This is the handicap principle, which approaches the perspective that when the male succeeds after facing a great risk, such as a struggle, he can prove his quality as a strong and powerful mate to the female (Zahavi 1975). Women, otherwise,

have an extensive expense during the process of choosing partners, mating, gestating, and nursing the offspring. Consequently, as a trade-off, once women do not have the selective pressure to prove her quality by engaging herself in such violent behaviors, the energy can be allocated to ensure the survival of both herself and the offspring.

Other issues that are rarely addressed by classical criminologist and are given plausible explanations by evolutionary criminologists are the crimes of infanticide and parricide. In a few mammals, the majority of offspring of a certain group would come, mostly, from when a dominant male mates with several females of the group, achieving a monopoly of the reproductive chances. Due to this, for a given period of time, these females would not be reproductively available, given the period of nursing of the children (Lukas and Huchard 2014). So, to achieve the possibility to reintroduce the women in the reproductive process by shortening the postpartum infertility, males would kill the offspring of rival males, eliminating the genes of their rivals in future generation and also being capable of mating with the females again. In other contexts, mainly in resource-scarce environments, parents would kill their own children. In these cases, individuals would not be driven by mate competition, but rather by the need to ensure one's own survival (Liddle et al. 2012; Lukas and Huchard 2014).

As for parricide, it can be defined as the act of killing a parent, a crime in modern society. Despite being considered a criminal behavior, from an evolutionary perspective, the killing of a parent does not genetically represent any disadvantage to the gene perpetuation. That's because gene natural selection occurs by genetic heritage, so the real value of the species perpetuation is contained in the offspring (Ridley 2009). Nevertheless, this behavior could be interpreted as a status manifesto, a dominance achievement on the group hierarchy, and a conflict of interests. This is due to the value of an individual in a group, once children are extremely valuable for their parents, because they represent a vehicle of their parents' genes. Yet, they are only 50% genetically related. Therefore, in human evolutionary history, an individual loses his value to their children as

they grow old, facing a great risk of being killed by their own offspring, once they become less valuable with time (Buss 2015). For that reason, young individuals, who have not yet achieved mating success, are even more inclined to displays of power that can escalate to violent behavior (Liddle et al. 2012).

Conclusion

Evolutionary criminology recognizes that, like in many other species, violence is a natural behavior which occurred persistently in given contexts throughout the evolutionary human history. The contextual aspect of this conduct leads to the fact that humans, despite using violence as a form of achieving higher statuses, gaining or maintaining resource, or having mating success, are not necessarily violent by nature. Otherwise, violence and psychological mechanisms underlying it have emerged as a viable way of the enduring evolutionary pressures. Negating the influence of naturally selected psychological mechanisms on the emission of acts that lead to crimes diminishes the possibility of the comprehension of modern antisocial behaviors, as well as complicates the prevention of such acts. Once these are not mechanically determined, the understanding of this mechanisms and the triggers that activate them could possibly contribute to reduction of their frequency, avoiding the contexts that produce them.

Cross-References

- Aggression
- Most Perpetrators are Men
- Physical Aggression
- Same-Sex Homicide
- Siblicide

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Evolutionary Cultural Psychology

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Synonyms

Cultural evolution and cultural psychology;
Evolutionary psychology and culture

Definition

Cultural evolutionary psychology is an approach to study the evolution of culture applying the evolutionary psychology perspective based on the concepts and knowledge of Darwinian evolutionary process.

Introduction

Culture: Definition and Concepts

Humans depend on cultural learning for all aspects of lives like managing resources, protecting family, wooing a mate, enhancing status, or forming political alliances. This shows that humans are cultural species. Our cultural experiences shape our ideas, values, feelings, and strategies. Psychological processes in humans like self-concept, social orientation, cognitive reasoning, aggression, and moral reasoning have been found to be influenced by cultural variations (Nisbett et al. 2001; Heine and Buchtel 2009). Various definitions of culture have been given. Richerson and Boyd (2005) have defined culture as “information capable of affecting individuals’ phenotypes, which they acquire from other conspecifics by teaching or imitation.” Another definition given by Laland and Hoppitt (2003) says culture is a “group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.” These definitions show that social learning is majorly the way in which information is acquired from one member of one species to another member. Cultural learning is not just confined to humans. Many other species like pigeons (Lefebvre and Giraldeau 1994) and rats (Galef 1988) also engage in cultural learning. In chimpanzees cultural learning is quite substantial (Whiten et al. 1999). Though cultural learning is not just restricted to humans, the learning from conspecific in humans is unique (Herrmann et al. 2007). It is unique in humans in two ways: firstly they have linguistic abilities which allow better communication, and secondly they have a well-developed theory of mind which helps them to understand the intentions of the fellow humans. Thus humans are able to do imitative learning in the true sense as they are better able to understand the intentions of their comrades. Some other species like chimpanzees also engage in social learning, but it is not fully imitative because they are not able to understand the intentions of their conspecifics.

Cultural Evolution

Concept and Relevance

Cultural evolution uses the Darwinian evolutionary process to understand the cultural change in humans and other species with the help of concepts, tools, and methods used by biologists to study biological evolution (Mesoudi 2011). Cultural evolution researchers try to explain the complexity of culture and changes in cultural phenomena just like how the evolutionary biologists try to explain the diversity of life and living organisms. In recent times the cultural evolution research has been on the rise. Works of evolution are seen even before Darwin published *The Origin of Species* in the historical descent of languages. The descent of language is based on the similar principle of Darwin in the sense that there are no genes for languages like English or Hindi and it is transmitted socially (van Wyhe 2005). It evolves over time, and language once extinct never reappears. Certain new words come over time, and preservation of certain words is based on natural selection.

The theory of evolution as given by Darwin is based on three principles (Lewontin 1970):

- (i) Principle of variation – which says that entities differ in their characteristics.
- (ii) Principle of differential fitness – which says that entities have different rate of survival and reproduction.
- (iii) Principle of inheritance – there is a correlation between parent and offspring entities in those characteristics that contribute to differential fitness.

Similarly the theory of cultural evolution is based on the theory of evolution in the sense that there is variation in cultural traits (words, ideas, etc.), the rate of survival is different for different traits, and social learning in the form of imitation is the method for transmission of traits from person to person.

Lieberman et al. (2007) have used vast database of English verb usage over time to quantify

this principle. He found that over 1200 years the usage of verb has evolved over time. They varied in past tense form (principle of variation), and those verbs that were not used much got replaced with the words that were regularly used (principle of differential fitness). It was also found that the verbs were transmitted in different generations through social learning (principle of inheritance).

It is also believed that cultural evolution is not completely identical to genetic evolution. Both are different in certain aspects as well. For example, cultural evolution does not require any unit which is required for genetic evolution. Cultural evolution is also guided by intention of humans; it is not completely blind which is the case in genetic evolution (Mesoudi 2011). Another difference is that cultural evolution can happen even when traits are transmitted from genetically unrelated human beings, while genetic evolution believes that half the genes are transmitted from the biological parents.

Culture Variation

People in different cultures tend to vary in their belief systems, behavior, and practices. Culture variation exists almost everywhere. From food sharing and child-rearing activities to religious belief systems, body decoration variations exist. A thorough understanding of culture variation may explain variation between and within cultures.

Growing cross-culture researches have potential to expand the horizons of cultural diversity, resulting in theories of human behavior gaining greater credibility and generality. Evolutionary psychologists postulate that living beings adapt behavior in response to their environmental conditions. However, adaptive adjustments cannot take place by a single evolved process; rather it requires organisms to behave in a certain way to be responsive to the environment. In short, it means that the possibility of specialized, problem-specific adaptations within group or between groups is what is termed as “culture.”

Another view states that social learning biases and transmission pathways explain how cultural variation is transmitted from one generation to another. The question arises from where cultural variation has originated. Historical evidences suggest that these psychological differences such as individualism–collectivism and analytic–holistic cognition have their origins in the ancient philosophical modes of thought of ancient China and ancient Greece (Nisbett et al. 2001). Assuming that these traits are not genetic forms the basis of long-term cultural macroevolution, just like long-term use of language or tools.

Several hypotheses have tried to explain the origins of psychological differences. One by Chang et al. (2011) has been truly inspired by cultural evolutionary theory. He explained that East–West differences in psychological dimensions as in collectivism–individualism and interdependence–independence are a result of different weightings given by society to social and individual learning. Theoretical models have stated that both social and individual learning are effective means of adaptation and thus there should be a mixture of both (Boyd and Richerson 1995). However, this blend depends on various factors, one of them being environmental change. Stable environment favors social learning, as other knowledge may remain relevant overtime, while unstable environment favors individual learning as other knowledge may become irrelevant with time (Aoki and Feldman 2014).

These insights of Eastern and Western psychological differences were used by Chang et al. (2011). They said the primary means of cultural adaptation in the East (mainly China) was influenced by social learning. It comprises strong social ties and social interdependence, respect for elders and conformity of social norm, less innovation and more rote learning, etc. The primary means of cultural adaptation in the West (Western Europe) was individual learning. It has weaker social ties, less rigid rules for following elders, or existing norms; more focus on science and technology; there is encouragement for creativity and independent thinking; etc. They also postulated that these differences in learning patterns are

related to environmental differences, as there is greater instability and fluctuations in Western Europe than in China in terms of migration, climate, agriculture, governance, etc.

Pathways of Culture Variation

Culture as mentioned is studied as amalgamation of belief systems, practices, values, and attitudes that characterize a group of people. There are basically two naturalistic pathways by which culture variation emerges: evocation and transmission (Tooby and Cosmides 1992).

Evoked Culture

Culture that is evoked from environmental triggers, e.g., war, drought, abundance, etc., is termed as evoked culture. Such conditions “evoke” different behavioral forms resulting in different culture formation. Tooby and Cosmides explain how the same activity like that of food sharing can have different cultural norms. Egalitarian norm of food sharing suggests hoardings are strong where there is variability in success of hunting across time in comparison to where the supply of food is stable. They even put evoked culture at the center of evolution framework.

Food Sharing and Food Variance

Different classes of food have variation in their distribution. Foods of high variance differ greatly in their availability. For example, in Ache tribe of Paraguay, getting meat from hunting is a high-variance resource; it means that some hunters will be successful in a day, whereas others will come back empty handed. Here, food sharing plays an important part, and the benefits of cooperative food sharing increase in such conditions. However, gathered food on the other hand is a lower-variance food resource. Here, surplus from food gathered is dependent more on skill and effort.

Cashden (1980), in the Kalahari Desert, found that San groups are more egalitarian than others. This egalitarianism is highly correlated with the

variance in food supply. In !Kung San's, food supply is highly variable, and having an egalitarian belief system, they therefore share food. Being called a “stinge” (stingy) is one of the worst insults in the group. The group levies strong social sanctions for stinginess and high regard for food sharing. On the other hand, in Gana San food variance is low, and it has great economic inequality. Therefore, they hoard their food and hardly share food outside their extended families.

Therefore, it could be said that environmental conditions can evoke some behaviors, such as sharing and cooperation. Everyone does have the capacity of sharing and cooperation, but environmental differences play a part in the extent of sharing and cooperation in different cultures.

Pathogen Load and Attractiveness

Pathogens always pose threats to the health of any long-lived organism. The host therefore should evolve defenses against these pathogens. However, any solution to the threat of pathogens is never final because pathogens again evolve to overcome these defenses. Pathogens are major killers of humans, especially in the early life period. Therefore, nearly 30–50% of the population in the ancestral human group used to die because of diseases, even before reaching reproductive age (Hill and Hurtado 1996).

Finding healthy mates was thus considered crucial in the human hunter–gatherer groups. Healthy mates are considered to survive for mating and less likely to pass pathogens to the chosen mate and result in more disease-resistant offspring (Hamilton and Zuk 1982).

Overt unhealthy signs, e.g., oozing pustules, open sores, and lesions, are generally disfavored by both sexes. There are also subtle healthy signs. Symons (1979) postulated that “physical attractiveness” function as “health certificates.” Gangestad and Buss (1993) explained that mate preferences shift when a person has high level of parasites. In such situations, physical attractiveness becomes a certificate of current health or an indicator of pathogen-resistant genes. Parasite prevalence is indeed positively correlated with mate preference for both sexes (Buss 1989). These differences were reflecting in evoked

culture as these patterns were due to evolved responses, in mating psychology. The ecological factors were responsible for association between characteristics and mate value (Gangestad and Buss 1993).

Transmitted or Epidemiological Culture

Cultural transmission as the term suggests is the transferring process of cultural information from one generation to another, or from one group to the next. Cultural transmission is a universal process. Cultural evolution takes place through the process of passing off traits (Mesoudi 2011). There are vast differences among cultural traits like belief systems, moral values, and attitudes across the globe. Some of these traits persevere (e.g., some belief systems continue to be relevant over the years and these traits are passed to other persons through social learning). It can be in the form of teaching, imitation, language, etc. (Tomasello et al. 1993).

Cultural macroevolution takes place over large scale and over long period of time and also over large geographical areas. Phylogenetic methods, which use the current distribution of species to study the evolutionary history of those species, are used by biologists to study biological macroevolution. This information helps generate lineage of similar kind of species. Cultural evolution researchers have used the same techniques to construct history of cultural traits by high fidelity cultural transmission, e.g., languages (Bouckaert et al. 2012), folklore (Tehrani 2013), prehistoric tools (O'Brien et al. 2014), and sociopolitical systems (Currie et al. 2010).

However, the process of passing of traits is different from that of genetic mutation. Cultural evolution researchers have studied experimentally on how cultural evolution functions among individuals, genesis of cultural variation, changes over time, and its transmission from person to person. These form the basis of cultural “microevolution” (Mesoudi 2011, 2016; Richerson and Boyd 2005; Richerson and Christiansen 2013). The term “cultural” may be applied to those traits that are transmitted by any process of non-genetic

transmission. Researchers have studied when and why people copy their parents as compared to non-parents. However, learning takes place from non-parents as well, and that is termed as “social learning strategies” or “biases” (Laland 2004). It explains the process of learning. It includes:

1. Conformity – it is described as disproportionately copying the most common trait from the group (Morgan and Laland 2012).
2. Prestige bias – copying from preferentially high-status individuals (Cheng et al. 2013; Henrich and Gil-White 2001).
3. Content biases – it is where specific ideas are preferably transmitted, mainly those that raise social interaction (Mesoudi et al. 2006; Stubbersfield et al. 2014) or disgust (Eriksson and Coultas 2014).

Cultural Transmission Pathways

Cultural psychologists have studied variations among societies in their psychological process. But this variation is maintained over time even with migration happening. What maintains this variation? This can be understood in terms of transmission pathways.

Cultural evolution researches (Cavalli Sforza et al. 1982; McElreath and Strimling 2008) have proposed three channels or directions of cultural transmission in terms of:

1. Vertical cultural transmission – it is learning from one biological parent to the offspring. It includes transmission of personality traits, cognitive development, occupational status, education level, conception of sex role, attitudes toward feminism, sexual activity, political beliefs, religious beliefs, phobias, self-esteem, language, and linguistic usage.
2. Oblique cultural transmission – it is learning from unrelated elders, e.g., teachers/mentors.
3. Horizontal cultural transmission – it is learning from the same generation like peers.

Both oblique and horizontal transmitted traits comprise of aspirations, career and social

mobility, adolescent behavior, aggressive behavior, altruistic behavior, social values, moral values, language and dialect, clothing innovation, conformity, language and dialect, games, and rituals.

It can be noted that some traits are transmitted either way, while others follow a dual inheritance model, and also that vertical transmission is slower change than oblique transmission, which is slower than horizontal transmission. Studies by Hewlett and Cavalli-Sforza (1986) state that parents are majorly a source of knowledge during early childhood, while transmission from knowledgeable elders and peers is more important mainly during late childhood, adolescence, and early adulthood.

Mechanism of Transmission

The process of transmission is a two-stage process. The first stage is of awareness of the information that is to be transmitted, while the next stage is of acceptance of the information. These two stages can be only distinguished when there is a choice to accept or reject and is based on the drive to teach or impart knowledge. Externalization attempts on transmitter side and internalization attempt on receiver side form the basis of transmission process which is influenced by teaching and learning (Kuczynski et al. 1997).

Human beings use their cognitive abilities for acquiring knowledge without any reinforcements, and it is also not restricted to specific learning domain which is not the case with other species. Flexibility and spontaneity are other characteristics present in humans in terms of transmission.

Another view is that all the transmission requires presence of specialized inference mechanisms in the receiver's mind to recreate representations. This mechanism is important because information originating from any individual in a social group is limitless; infinite range of ideas compete for the attention of humans. Evolved psychological mechanism thus must be present in the receiver's mind to gauge the barrage of ideas, selecting only a subset for reconstruction.

Therefore, for transmission of culture, evolved psychological mechanism is required. The mechanism must have the properties such as *selective attention* for attending to some ideas and ignoring others; *selective encoding* for encoding ideas in memory and forgetting others; and *selective transmission* for transmitting some ideas to others while failing to transmit to others. This could best be understood from the example of human's tendency to imitate the clothing styles of high-standard members of their society. The evolved psychological mechanisms caused people to attend to high-status people more than low-status people, encode their clothing style in memory, and access the memory while shopping for clothes (Buss 2007).

Memes

With reference to culture, memes are ideas, behaviors, and even styles that are spread from one person to another within a culture. Its main objective is to convey a particular phenomenon represented in a meme. It acts as a unit of carrying cultural ideas, practices, etc. that are transmitted from one mind to another in the form of writing, gestures, speech, and rituals with a mimicked theme (Gordon 2002).

The traditional view has tried to explain evolution of psychological mechanisms through social learning, but evolutionary psychologists are of a different view saying that learning is not an explanation to psychology but rather it is also a phenomenon like other mechanisms.

Evolutionary Psychology

Emerging Discipline

Evolutionary psychology tries to understand the human mind and how it is designed. The theories and principles of evolutionary biology are applied in evolutionary psychology to better understand the structure of human mind. The approaches by evolutionary psychology are changing the traditional viewpoints in the way that it believes mind to be an information processing machine which was designed to

solve problems arising over time by natural selection.

Charles Darwin in his seminal work on evolution theory had predicted a new foundation for psychology to understand the human mind in the evolutionary perspective. Later on William James in his works on experimental psychology described “instincts” referring it to be specialized neural circuits common to every member of a species and scribed it to be product of that species’ evolutionary history. Collection of circuits of instincts is collectively referred to as “human nature.” Earlier conventional thinking thought that other animals are ruled by instinct, whereas humans have gradually lost their instincts and are ruled by “reason” and that’s why humans are considered much more flexibly intelligent than other animals. William James proposed the opposite view and argued that humans have more instinct than animals, but we tend to be blind of the existence of these instincts because they process information effortlessly and automatically and structure our thought so powerfully so that we take normal behavior for granted. This “instinct blindness” which he referred to as making the “natural seem strange” makes the study of psychology difficult. As a result psychologists have neglected to study some of the most interesting machinery in the human mind.

The Standard Social Science Model

Both before and after Darwin, there is a consensus view among scientists and philosophers that the human mind resembles a blank slate, virtually free of content until written on by the hand of experience (James 1890).

This concept that mind is a blank slate has changed over time from blank slate to switchboard to general purpose computer. It is considered that the architecture of the mind that has evolved consists of small number of general purpose mechanisms that are content independent, namely, learning intelligence, imitation, rationality, and culture, while the remaining human mind derives from the environment and social learning. Thus it states that there are the same mechanisms for learning language or recognizing emotional expressions or how one thinks about incest. It

also believes that all that we feel or believe is derived from social learning or environment. As per this model, the architecture of the mind has no role to play; it is only the external world that plays a role.

With improved research and progress in cognitive psychology, evolutionary biology, and neuroscience, it has shown that this concept is not correct stating that human mind is not a blank slate. The alternative view given by evolutionary psychologists states that over time the human mind develops regulatory circuits which are specialized in function and these functions are domain specific. The way we interpret experiences and add meaning to the intentions and actions of others is based on these circuits. It is also believed that all humans share certain views and assumptions about the nature of the world and human action by virtue of these human universal reasoning circuits.

Basic Principles of Evolutionary Psychology

Evolutionary psychologists believe that psychology is a branch of biology that tries to study the brain, how information is processed in the brain, and how behavior is generated by information processing programs in the brain. As psychology is a branch of biology, then the theories, principles, and observations of biology can be applied to understand the human brain. The five principles of biology can be applied to understand the human mind which helps to see connections between vision, reasoning, and sexuality. The five principles as given by Cosmides and Tooby (1997) are described below:

Principle 1. The brain is a physical system. It functions as a computer. Its circuits are designed to generate behavior that is appropriate to your environmental circumstances.

The first principle says that brain is just like a computer, and its functions are governed by similar laws of chemistry and physics just like computer. The difference is that the brain is made of organic compounds, while the computer is made of silicon chips. This means that chemical reactions in the brain produce thoughts, hopes, dreams, and feelings. The

information in the brain is transmitted through neurons which are known as electrochemical reactions. Just like the computer, the brain also has circuits in the form of different neurons which are connected in an organized way and determine how the information is processed in the brain. The behavior is generated by these circuits of the brain in response to the information from the environment.

Principle 2. Our neural circuits were designed by natural selection to solve problems that our ancestors faced during our species' evolutionary history.

Computers are designed by human engineers, so they can program a certain function which is suitable for solving a particular problem, but with brains, it is not designed by any engineer. The programming of the brain is designed by evolutionary process. The process that is most applicable here is natural selection. It means that those behaviors that resulted in better solving the problems which our ancestors faced were programmed. These circuits helped in the survival of our ancestors. The computational system of the brain is developed naturally, and it consists of all the circuits whose function is to solve adaptive information processing problems.

These circuits are designed to solve adaptive problems only which have occurred again and again in the history of evolution and their solutions have affected the number of offspring produced. Any circuit which reduces the reproductive rate of an organism will gradually disappear. Only those circuits which result in solving adaptive problem get designed by natural selection.

Principle 3. Consciousness is just the tip of the iceberg; most of what goes on in your mind is hidden from you. As a result, your conscious experience can mislead you into thinking that our circuitry is simpler than it really is. Most problems that you experience as easy to solve are very difficult to solve – they require very complicated neural circuitry.

The superficial simplicity of any bodily function can deceive us as it could be the response of many different stimuli which are

working together in the hind side which are not controlled by us consciously. The experience of seeing something is in itself so complex and involves so many different parts of the body that is hard to imagine that it could be so complex. The eyes capture rays which are printed on the retina in 2D form which is further converted in a 3D image with the help of specified neural network dedicated for the function of seeing any object in its physical form not as a piece of 2D drawing. Therefore it is with our concise experience we are able to evaluate only cream of conclusions rather than the thousands of specifically dedicated mechanism involved in gathering, analyzing, and evaluating information along with counterchecking for mistakes, filling any missing information, and making final conclusion.

Principle 4. Different neural circuits are specialized for solving different adaptive problems.

A solution to one problem need not be the answer to the second problem; the same can be said about the function of the human brain. The neural network dedicated for one task may not be able to solve the problem aroused in some other field, for example, the network dedicated for seeing an object cannot hear what sound that object is producing or even smell it. In order to hear, see, or smell, different neural networks are involved which can be visualized as a minicomputer dedicated to solve a specific problem. However, the evolutionary perspective suggests that most of the biological systems are calibrated to a specific environment, for example, the grass will always appear green no matter what the spectral timing of the sun is. Most of the rational algorithm for response is content independent as Bayes' rule does not have domain explicit knowledge, therefore it cannot be applied to inference of two different selection. Different problems require different solutions as the solution applicable for a living thing may not be applicable to a nonliving thing.

Principle 5. Our modern skulls house a Stone Age mind.

To survive in an environment requires a specified brain design which was governed by

natural selection; it takes a very long time to develop a neural network that is suited for a known environment. The neural network development process is so slow that we can say our modern skulls house a Stone Age mind, as the neural networks are not designed to solve modern day-to-day problems. The Stone Age neural network works better at some problems such as fear of snake in comparison to fear of electric shock. Despite being a Stone Age neural network, our mind can be compared to a highly sophisticated problem in which a network is designed to face problem faced by our ancestors on a daily basis.

Scope

Evolutionary Psychology Provides the Needed Causal and Explanatory Bridge from Evolutionary Theory to Manifest Behavior

Tooby and Cosmides (1989) provide the missing link between evolutionary theory and manifest behavior. It has further reinforced the importance of innate psychological mechanisms which are shaped or influenced by the evolutionary processes and are transmitted from one generation to the next. Structures of these innate psychological mechanisms influence the manifest behavior within a generation. It emphasizes that innate psychological mechanisms are the focal point of any evolutionary analysis of behavior. Adaptationist logic leads to characterization of modern behavior as either adaptive or maladaptive based on the principle of fitness maximization model, whereas evolutionary psychology focuses on knowledge of the innate psychological mechanisms that actually predict behavior more closely and it provides a unified core of models which assimilates the phenomena drawn from social science, psychology, anthropology, etc. According to Tooby and Cosmides, evolutionary psychology allows a new validating model to analyze the modern behavior. By including economic, cultural, and social factors into evolutionary algorithms, the modern behavior can be better explained not merely as an adaptive or maladaptive phenomenon but as an outcome of

development of the human mind and external conditions that are acting as an input for the architecture of the mind.

The Method of Evolutionary Psychology

As per the principles mentioned above, some guidelines in terms of to carry out research in the area of evolutionary psychology were proposed by Tooby and Cosmides (1989), which can be briefly described as the following:

1. In order to cultivate any model considering adaptive problem in which psyche of a person is involved, the starting point of model development should be an evolutionary theory.
2. Any adaptive problem manifested is directly related to close environment such as social, ecological, genetics, and physical situation, and it should be specified in details as this information contains information related to solve the problem. The building of a cognitive program should be such as it will guide behavior as per the adaptive path based only on the information provided to it in Pleistocene condition.
3. The adaptive model problem should be integrated to existing information of the relevant Pleistocene conditions, in order to derive any valid and useful inferences from current set of constraints. The specific information processing problem should be chronologically sequenced, which must be solved in order to achieve adaptive function. The computational theory will be further used to generate hypotheses related to cognitive programing structure needed to solve the adaptive problems in the question.
4. The computational theory will be used to determine whether there is any design feature in cognitive program for solving adaptive problem and also creating and improving candidate models of cognitive programs that might have been evolved in humans to solve a particular adaptive problem. It must be made sure that the model should be powerful enough in principle to realize the computational theory.

5. The alternative candidate models should be eliminated based on experiments and field observation, as the extensive methods developed by cognitive psychologists to track complex information should be taken full advantage. In the end a validated model for a cognitive program in question along with model environmental information is available for further studies.
6. Lastly a comparison should be drawn between models against behaviors that are produced by modern condition. Input from modern environment should produce behavior by the cognitive model already developed.

Cultural Universals

Cultural universals are traits or complex present in all individuals, all societies, all cultures, or all languages – provided that the trait is not too anatomical or physiological or too remote from the higher mental functions (Brown 1991). For example, myths, legends, rules, daily routines in the cultural realm; all languages consists of phonemes, morphemes, syntax, antonyms; and gestures, aggression, facial expressions in the behavioral realm. Many of the universals do not exclusively exist in one realm, e.g., the kinship terminologies in English like father, mother, brother, sister, etc. fall in the social, cultural, and linguistic realm. Another universal revenge is both behavioral and social.

Universals can be distinguished as either *emic* or *etic*. They are derived from the English words – phonemic and phonetic. The *etic* approach assumes that the features studied in one culture have significance in all cultures, while the *emic* culture assumes that cultural norms are specific to one culture only. For example, grammar is an *etic* fact, i.e., all individuals or cultures have grammar as part of language, but not all peoples have an overt cultural representation of the idea of grammar.

Some of the features of universals are as follows: a universal can be further subdivided like facial expression being universal. Further its

variations like smile and other expressions are also universal. Universals are simple as well as complex. Some universals are complex rather than being referred to as individual, for example, all cultures have music and dance, but not all individuals know dance or music. Universals can also be present only in one sex or in all individuals of particular age ranges.

There are some universals which are features of the human mind like the language acquisition device (as described by the linguist Noam Chomsky), emotions, classification, and psychological defense mechanisms. We are better able to understand the psychological mechanisms with psychobiology and evolutionary psychology. Psychology has been said to be majorly influenced by biology; thus the theories of evolution can also be applied to psychology presupposing universality of psychological mechanisms. Cognitive science considers the human mind to be like a computer which again believes that the psychological processes are universal. Thus it can be said that the psychological mechanisms are universal indicating psychic unity of mankind.

Conclusion

Humans are cultural species, and therefore psychological processes in humans have been found to be influenced by cultural variations. Cultural evolution incorporates evolutionary principles for understanding the cultural variations and transmissions in humans and other species. Traditional anthropology and social science theories view cultural evolution and transmission from the perspective of adaptational theory facilitated by the unitary principle of learning. Culture is generated through the rich and intricate human psychological mechanism which includes learning mechanisms that govern the cultural dynamics. In order to understand cultural processes, the processes and properties of complex and specialized innate psychological mechanisms acquire the center stage. Evolutionary psychology gives a new and promising approach for research on the structure of human mind incorporating the

knowledge and principles from evolutionary biology. By the pioneer work of Leda Cosmides and John Tooby, the basic principle and guidelines for conducting research in this area have been proposed. Though evolutionary psychology is in its infancy stage, it is expected that the advancements/growth in this field will provide us a more comprehensive model of the innate mechanisms of human psyche.

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Evolutionary Forensic Psychology

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Synonyms

[Criminal behavior and evolution](#); [Evolutionary psychology of crime](#)

Definition

Evolutionary forensic psychology is the study of the evolved psychological mechanisms that give rise to thoughts, emotions, and behaviors underlying crime and forensic-related issues.

Introduction

This entry explores some of the insights and research that an evolutionary psychological perspective has generated around forensic-related issues. Emerging from theory and research in this area is an evolutionary forensic psychology literature that provides a unique and powerful understanding of the frequency of crimes, who is likely to commit crimes, and environmental and social factors that increase the likelihood of crime (Duntley and Shackelford 2008). A particularly influential aspect of evolutionary forensic psychology is that it provides a foundation rooted in the principles of the life sciences to understand forensic-related issues, allowing it to address ultimate as well as proximate causes of criminal behavior. The former refers to long-term historical and/or evolutionary explanations of why criminal behavior occurs, while the latter refer to short-term developmental and/or social explanations

Evolutionary Forensic

► Evolutionary Criminology

of how criminal behavior is caused (Tooby and Cosmides 1992). Thus, one of the strengths in using an evolutionary forensic psychology perspective is that it allows for answering questions about *why* we even have forensic issues. Why is crime and criminal behavior the way it is and not some other way (Pinker 2012)? An evolutionary view of crime allows us to question the very assumptions about what constitutes crime and our responses to it.

In this entry, we briefly outline how evolution informs us that the very notions of “crime” and “law” reflect our moral impulses as a species. We will then offer a preliminary exploration of the interface between nature and nurture before examining how a focus on individual differences (i.e., personality) reveals their interaction. Regarding personality, we will cover broader personality traits before turning toward a look at the specific personality type that is most strongly associated with criminality: psychopathy. Finally, we turn from these person-based views toward studying two examples of a more behaviorally oriented view that focuses on two salient and consequential categories of criminal behavior: homicide and sexual crimes. We will pay particular attention to why these crimes are prevalent in specific contexts that an evolutionary perspective frames for us.

“Law” and “Crime” as Reflecting Moral Impulses

Where does our society’s notion of what constitutes a “crime” come from? Why do we have a “law” that most people want to uphold? These are questions rarely asked outside of an evolutionary forensic context, but they formulate the very basis for understanding and even having a criminal justice system (Walsh 2000). It might seem obvious and even odd to point out, but notions of crime and the law are mental constructs that are rooted in our moral impulses of what is right and wrong, fair and unfair, and just and unjust (Haidt 2001). They exist and have their origins in our minds, and yet they structure society, regulating and governing behavior both implicitly and explicitly.

What we deem as criminal behavior is thus a complex interface between evolved and/or historical predispositions along with more recent societal norms and values (Pinker 2012).

In the context of this interface, moral impulses describe thoughts and feelings that underlie our sense of right and wrong, fairness, and justice (Haidt 2001; Krebs 2008). What happens to your mind and body when you observe a child being harmed? How does this change if it is an adult stranger harming a child compared to if another child is the one doing the harm? The thoughts and feelings that emerge upon viewing the harmed child and the context that surrounds the harming *are* the moral impulses in action. The point made from an evolutionary forensic psychology perspective is that the “law” itself and its “crimes” are often a result of these moral impulses being activated, thought-about, and written down in response to actions that elicit them (Daly and Wilson 1988; Duntley and Shackelford 2008).

These types of actions that activate our moral impulses have fitness consequences (Krebs 2008; Walsh 2000). This is the main evolutionary argument for why we experience negative affective reactions toward criminal behavior, because the costs they instill are so large (Daly and Wilson 1988). When thinking about cheaters anywhere from tax evaders to thieves, the benefits accrue for individuals at the expense of the common good and social order (Joyce 2007; Krebs 2008). Thus, in these instances where the law creates crimes that are unlawful, we see moral impulses framing our attention in their direction, and the attention is being drawn there by the forces of evolution over previous human (and prehuman) generations. On the other hand, the cultural evolution of justice systems, state punishment, and common moral values has also had an important influence on the execution of moral impulses in modern society (Pinker 2012).

Adaptive Criminal Calibration

This interaction of nature and nurture reflects a persistent question regarding behavior: Which is more important, biological predispositions or

environmental influences (Ellis et al. 2012)? The answer is neither. Much like one needs both chocolate and an oven to make chocolate cake, behavior is a product of the interaction between environments and biological predispositions (Ellis et al. 2012; Kim-Cohen et al. 2006). In this light, an individual who displays antisocial tendencies may not be expressing a maladaptive or “broken” pattern of development (Ellis et al. 2012). Rather, they may be displaying a specific adaptation toward environmental circumstances that better guide their development toward behavior that will be adaptive under those environmental conditions (Lalumière et al. 2005). For example, exposure to violence has been shown to associate with an improved memory for some details (e.g., dominance) that might represent important evolutionary outcomes (Frankenhuis et al. 2019). Individuals raised in an environment that values aggression and fearlessness may well reward violent behavior under the right circumstances (Chagnon 2013; Mealey 1995).

Fortunately, as mentioned above, we can alter the environment so as to change the costs and benefits of criminal behavior in ways that make it less appealing and prevalent (Barr and Quinsey 2004; Pinker 2012). We strongly emphasize that any biological predispositions for criminal behavior should not be viewed as biologically predetermined, unresponsive to environmental factors, or morally sanctioned by evolutionary principles. Indeed, there may be instances where the commission of criminal behavior represents the maladaptive expression of a more modest adaptation. For instance, circumstances could lead an incidence of bullying (a generally adaptive aggressive behavior; Volk et al. 2012) to escalate into an unintended homicide, which would be labelled a maladaptive by-product of bullying (Daly and Wilson 1988; see section “[Is Homicide an Instance of Adaptation?](#)”). Thus, an evolutionary view of forensic psychology is not deterministic, or offering moral value to “natural” behavior, but instead examines the role of evolved predispositions as one of many interactive factors causing criminal behavior. Instead, the knowledge of any such predispositions affords information about how to best alter, reduce, and/or prevent

the expression of those predispositions. To best make effective alterations (e.g., interventions, social policies, and laws), we should therefore understand the underlying preferences and predispositions that could encourage the development and expression of criminal behavior (Ellis et al. 2012). We will bear forth this interactive view as we examine two of the more common individual factors that may influence criminal behavior: general personality (i.e., the HEXACO) and specific antisocial personality (i.e., psychopathy).

Personality and Crime: A Focus on Individual Differences

With a focus on individual differences, personality has a fundamental role to play in the evolution of antisocial and criminal behavior. Trait-based personality items have the potential to represent heritable individual differences that can differentially relate to adaptive outcomes in different environments (Buss and Hawley 2010). While there are numerous specific personality types associated with forensic psychology (e.g., psychopathy, narcissism, borderline personality, Machiavellianism, sadism, etc.), the origins of these varying types of personality quickly present a large number of requisite unique adaptations required to explain their existence. What may be more plausible – and both useful and parsimonious to know – is that a smaller range of personality traits may have evolved that can be tweaked given environmental input to produce varying adaptive outcomes. Some have suggested that the Dark Triad of psychopathy, narcissism, and Machiavellianism represents just such a more unified cluster of adaptive personality traits with the idea being that all three types of personality share a common core of antisocial personality (Paulhus and Williams 2002). Intriguingly, the core of these variables may be the personality trait Honesty-Humility, from the HEXACO model of general personality, with its negative pole showing an almost perfect match to the core of the Dark Triad ($r = -0.95$; Hodson et al. 2018). Honesty-Humility represents a general tendency to exploit

others for one's own benefit (Ashton and Lee 2007) that may well underlie the general tendency for individuals to invest and act in their own self-interest, producing much of the crime in society.

The advantage of having a general model of personality like the HEXACO as the foundation of forensic personality psychology is that it not only connects forensic applications of personality with more general applications of personality, but it also does not require the creation of adaptive evolutionary scenarios for each type of forensic personality. Instead, one simply has to dial up or down various combinations of the six factors of the HEXACO to obtain varying forensic personality types (Ashton and Lee 2007). For example, Machiavellian personality may be associated with lower Honesty-Humility and lower Agreeableness (i.e., lower patience and forgivingness). Psychopathic personality may have similar negative correlations, but with the addition of negative correlations with Emotionality (i.e., lower sentimentality and anxiety) and Conscientiousness (i.e., lower impulse control and planning). This makes the HEXACO much more plausible evolutionarily and developmentally, as it requires genetic ties to only six traits that are presumably present in virtually all normally developing humans. The cross-cultural validity of the HEXACO further enhances this plausibility (Ashton and Lee 2007), as does the fact that the HEXACO cleanly lines up with a unique genetic factor for each factor (Lewis and Bates 2014). Thus, the HEXACO offers the potential for parsimoniously explaining not just general personality from an adaptive, evolutionary perspective, but it may also serve as a useful tool for studying the evolution of forensic personality types. Indeed, in surveys of male convicts, the HEXACO accounted for almost half of the variance in self-reported antisocial behavior, making it a valuable tool for use with forensic populations (Mededović 2017).

In summary, personality traits, and the HEXACO model in particular, may present a useful and parsimonious way of understanding person-level risk factors in engaging in antisocial and criminal behavior. These personality traits

should be conceptualized not as inborn tendencies, but rather inherited predispositions being shaped through life experience to produce personality orientations that attempt to optimize survival and reproductive gains.

Psychopathy: A Forensic-Revealed Adaptation?

While the HEXACO represents a broad measure with similarly broad validity, there may be more specific measures of antisociality that account for even more variance with respect to criminal behavior (Harris et al. 2015; Mededović 2017). Psychopathy is a set of personality and behavioral traits that are related to a number of socially undesirable and adverse outcomes, foremost being involvement with crime (e.g., Hare 2003). Traits fall broadly into two categories labelled as Factor 1 and Factor 2. Factor 1 is comprised of interpersonal and affective characteristics, including manipulativeness, superficial charm, and a profound lack of empathy and remorse. Factor 2, on the other hand, contains more behavioral features, including a tendency for impulsivity, irresponsibility, and having poor behavioral controls and aggression.

Individuals with psychopathic traits are more likely to engage in criminal behaviors and are much more likely to reoffend after release. In fact, psychopathy is the single best predictor of violent recidivism (Harris et al. 2015). Research consistently finds heritability around 50% (for a full review, see Glenn et al. 2011), and multiple researchers have suggested that psychopathy, rather than being a "disorder," may be an evolutionary adaptation designed to exploit others (e.g., Barr and Quinsey 2004; Mealey 1995).

For a trait or constellation of traits to be considered an adaptation, it must have conferred relative benefits in facilitating survival and/or reproductive success (Andrews et al. 2002). Importantly, psychopathy is not associated with "neurodevelopmental perturbations" that would normally accompany a disorder, including fluctuating asymmetry, obstetric complications, and comorbidity with mental disorders (Lalumière

et al. 2005). In terms of being related to reproductive success, psychopathy has been found to be related to the tendency to engage in a fast life history strategy (one emphasizing short-term mating effort, increased risk taking, and selfish exploitation) (Barr and Quinsey 2004). For example, people with psychopathic traits have earlier sexual experiences and are more promiscuous and engage in more short-term marital relationships, which also constitute two items on the Psychopathy Checklist-Revised (Hare 2003). Further, research finds that those higher in psychopathy have as many (or more) children compared to those lower in psychopathy (Mealey 1995). Interestingly, offenders manifesting more psychopathic traits appear less likely to victimize kin in their crimes, which supports psychopathy being selected based on the principles of inclusive fitness (Krupp et al. 2012).

Many of the researchers who take an adaptationist perspective focus on the exploitative nature of psychopathy. These researchers have suggested that psychopathy may be an adaptation for social predation/exploitation (e.g., Mealey 1995), and early descriptions of psychopaths highlight their exploitative nature (e.g., Cleckley 1976). Empirical research supports the assertion that psychopaths do tend to exploit and manipulate others and use deception across numerous social contexts (Jonason and Webster 2012). As well as being deceptive and manipulative, psychopaths are impulsive and aggressive (Hare 2003), using such strategies to get what they want from others. The combination of exploitativeness and aggression as a strategy has been coined the “Cheater-Hawk Hypothesis” (Book et al. 2015).

Frank (1988) suggested that a successful opportunist should be able to judge vulnerability in others and also to avoid detection. Early anecdotal descriptions of psychopaths suggest that they are able to judge vulnerability in others (Cleckley 1976), and empirical research suggests that people with psychopathic traits are able to judge victim-related traits, such as assertiveness and vulnerability, from body language (Book et al. 2013). As well, Jones (2014) suggested that psychopaths engage in short-term strategies

involving social mimicry to acquire resources and that this represents how they avoid detection. We know from previous research (discussed above) that psychopaths use deception and manipulation across many contexts. Another important part of social mimicry involves feigned emotional states, and there is some empirical support for the idea that psychopathic individuals are able to feign basic emotions such as fear and social emotions including remorse (Book et al. 2015).

To summarize so far, there is some evidence and support for the idea that psychopathy is an adaptation for social predation and exploitation of some kind, but the nature of that adaptation is yet unclear. Commonalities across most adaptation hypotheses of psychopathy suggest sex (i.e., being male) was important in selecting for psychopathy as was a short-term exploitative strategy that may have ensured reproductive success (Mealey 1995). While less research has focused specifically on the “special design” features of psychopathy (Krupp et al. 2012; cf. Brazil and Forth 2019), two broader-level evolutionary models have been proposed that support psychopathy fitting an evolved reproductive strategy (Glenn et al. 2011).

The first model is known as *balancing selection*, which suggests that psychopathy would have been shaped for its fitness advantage in the ancestral environment as an alternative reproductive strategy (Glenn et al. 2011). One potential balancing selection model to explain psychopathy is *frequency-dependent selection* (e.g., Barr and Quinsey 2004; Mealey 1995). In this model, psychopathy is maintained at a consistently low ratio in the population, an expectation that is supported by the low prevalence of psychopathy (at or around 1% of the general population; Hare 2003). This model is supported by computer simulations showing that “cheating” is only an evolutionarily stable strategy when it exists at low frequencies (Dawkins 1976). Presumably, when the frequency of cheating is too high, there is heightened risk of interacting with other cheaters which would obviously reduce the effectiveness of the cheating strategy. This low frequency needs to

be accounted for in models describing the evolution of psychopathy.

While balancing selection does account for the low prevalence of psychopathic traits in the population, there are environmental conditions that differ over both time and place in effecting the expression of psychopathy. Another model that attempts to deal with these conditions in explaining psychopathy as an adaptation is contingent shifts. In *contingent shifts* “psychopathic traits are an adaptive response to specific environmental conditions” (Glenn et al. 2011, p. 371). In this model, the level of psychopathic traits expressed in a population would differ depending on the environmental context and its tendency to provide benefits that outweigh the costs of manifesting the traits. In other words, there may be certain environments that encourage the expression (and, alternatively, discourage the expression) of psychopathic traits; costs and benefits are weighed according to this model, and sometimes the benefits are high for psychopathic traits that gives them a fitness payoff. A good example would be the effect of parenting style and attachment on the expression of psychopathic traits. In children who have the capacity to develop these traits, abuse or neglect may “unlock” them during development, making them respond flexibly and adaptively to the conditions to ensure chances of survival and reproduction.

Importantly, balancing selection and contingent shifts models are not mutually exclusive. This means that psychopathy may have been selected and maintained in the population over human history based on a combination of these models. Uncovering and testing the “special design” features of psychopathy and continual research into its potential as a forensic-revealed adaptation will provide more information about these models in explaining psychopathy from an evolutionary perspective. With this coverage of individual differences in light of forensic-related issues, we now focus on criminal behaviors of homicide and sexual crimes that an evolutionary forensic psychology perspective emphasizes, further illustrating the interface between nature and nurture in producing crime.

Homicide

Just over half a million homicides occur every year around the globe (Krug et al. 2002), which is likely an underestimate due to misreported and undocumented homicides. Homicide is one action that can inflict the ultimate fitness cost on the victim, making it a plausible strategy for eliminating fitness competitors and a clear behavior that evolutionary researchers need to contend with (Duntley and Buss 2011), and it has been argued that an evolutionary lens can enhance our ability to understand the underpinnings of homicide (Liddle et al. 2012). We should note that not every homicide need be adaptive, and some have argued that some cases of homicides may be the by-product of more modest adaptive predispositions (e.g., an adaptive tendency toward mate guarding could escalate into a maladaptive case of homicide; Daly and Wilson 1988). While differentiating between adaptive and by-product behaviors is beyond the scope of the current manuscript (e.g., Durrant and Haig 2001; Sosis 2009; Tooby and Cosmides 1992), we offer the opinion that the difference between the two can at some level be semantic as many of the underlying evolutionary pressures are similar. In either case, evolutionary theories generate hypotheses that can test between these two levels of explanations. For that reason, we will focus primarily on adaptive explanations of criminal behavior.

We can also appreciate why certain types of homicides are likely to be committed by men and women differently, at different times during one's lifetime, and differently depending on one's life circumstances. An evolutionary forensic psychology perspective enables an explanation of why certain patterns of homicide occur and what conditions enhance the likelihood of homicide. Martin Daly and Margo Wilson's book *Homicide* (1988) influenced evolutionary forensic psychology and provided one of the first comprehensive studies of behavior and psychology using the lens of evolution. They demonstrated how homicide committed by men and women should differ due to differing adaptive problems faced by the sexes over evolutionary time and that different types of homicides should expectedly emerge in

different social contexts that may reflect solutions to adaptive problems.

Homicide Committed by Men

At first blush, homicide may seem to be an entirely male endeavor. This is far from being true, and we will also describe some of the instances when women kill, but it is not an overstatement to claim that men are disproportionately involved in homicides – as both perpetrators and victims (Daly and Wilson 1988; Krug et al. 2002). In a study of Detroit homicides, it was shown that just over 82% of homicides were committed by male perpetrators. Of these homicides committed by men, just over 82% had a male victim (Daly and Wilson 1988). This means males were disproportionately responsible for killing others, and they were disproportionately killing other men. Krug et al. (2002) also found that around the globe, 78% of homicides were committed by men. (These findings may suggest homicide falls under a “four-fifths effect,” whereby men are killing and being killed by other men in four-fifths of all homicides.) Another factor is that the vast majority of those both killing and being killed were young men, with the risk of being involved in homicide decreasing as one aged. This led to the proposition that the competitive and risk-taking traits underlying violence and homicide might be called a “young male syndrome” (Daly and Wilson 1988).

Not all young men, however, are involved in committing such fatal violence. Two additional risk factors increased the chances of a young man being involved in such violent altercations: (1) being unemployed and (2) being unmarried (Daly and Wilson 1988; Krug et al. 2002). From an evolutionary perspective, these two factors are expected to increase a male’s propensity to engage in competitive violence since they touch on the variance in male reproductive success and on having access to resources (Geary 2010). Unemployment indicates lacking resources and having low prospects for the future, while being unmarried may indicate that the man is without a long-term partner and thus unlikely to reproduce. Being unmarried certainly does not preclude having other sexual relationships (and potentially

children), but it may signal to the young man that they are not desirable as a long-term partner, and this may have a strong influence on the evolved psychological mechanisms in orchestrating the competitive behavior of these young men.

An evolutionary approach to studying violence in general and homicide more specifically requires examining context in order to ascertain the “specific inputs that are likely to activate the psychological mechanisms that generate violent behaviors” (Liddle et al. 2012, p. 33). Evolutionary theory has led to the collection of strong empirical evidence that as economic inequality increases, so too do male-male violence and homicide (Daly 2016). This pattern of findings appears consistent across a number of countries for which data are available, suggesting that economic inequality may, or should, be thought of as a potential *cause* of male-male violence and homicide (Daly 2016). That male reproductive success is more highly variable compared to females suggests this inequality may have differing adaptive consequences across the sexes (Daly and Wilson 1988; Duntley and Buss 2008). A competitive arena where some males have (reproductive) success and many lose out may breed competition among men, often escalating to violence and homicide in men’s attempts to garner resources and status (Betzig 1982). This perspective allows for making predictions about what social and economic circumstances should give rise to male-male violence and homicide. More egalitarian and equitably distributed societies should be expected to engage in less male-male violence, a contention that has some support from anthropological research (e.g., Friedl 1978).

In conclusion, when it comes to understanding an evolutionary perspective of homicide regarding men specifically, one should consider the degree to which boys and young men are growing up in an environment that fosters and is structured by competition that has differential outcomes for its participants (Daly 2016). The greater the difference in experiencing either reward or loss and thus being a big winner or big loser, the greater seems to be the likelihood of men engaging in violence that can progress to fatalities (Betzig 1982). This seemingly simple observation is

borne out by evidence from around the globe that was facilitated by using an evolutionary forensic psychology perspective of the problem of homicide and points to the usefulness in using such a perspective when trying to understand complex social problems.

Homicide Committed by Women

Women's involvement with homicide differs starkly from men's involvement facilitated by competitive environments. There are primarily two instances where women are occasionally engaging in homicide: (1) killing newborn children and (2) killing their spouses (Daly and Wilson 1988). Even though women are not showing up in police records in high numbers for these crimes, these two instances represent evolutionarily expected instances of women deciding to engage in violent fatalities. They may represent extreme measures taken at an instance in time in the woman's life where a threat to her survival is evident. In the instance of killing spouses, women are often killing their male partners when the male partner is threatening her life or in an instance of infidelity. When killing her child, a woman may be making such a decision not as a remorseless psychopath but instead based on difficult and particular life circumstances that suggest she is engaging in adaptive decision-making influenced by harsh realities (Hrdy 1999). This is not to excuse such actions, but it does help in understanding why women decide to kill their offspring, and it gives researchers a means by which to promote alternative circumstances to what women at risk tend to experience. The presence of two such circumstances, young age and not having a committed partner, influences whether a woman may be at risk of infanticide, both historically and in modern contexts (Daly and Wilson 1988; Hrdy 1999).

Because women are disproportionately responsible (physiologically, psychologically, and socially) for the upbringing of children, investment decisions can be a high-stakes matter. If current circumstances and prospects appear grim for a woman to raise healthy offspring, she may begin to consider fatal alternatives that will not compromise her future chances of reproductive

success (Hrdy 1999). Because younger women have higher reproductive potential (ability to bear more future offspring), there may be less of a cost to infanticide since future reproductive potential would be higher for them. This helps make sense of why women committing infanticide in these early years are not necessarily at risk to do so later in life (Daly and Wilson 1988). The young mother may also currently be in less of a position to provide the appropriate investment care in her offspring to guarantee their survival. In societies where state-supported child care is absent and a child's survival depends mostly on the mother, the decision to kill offspring becomes less morally intertwining and more based on harsh realities (Hrdy 1999).

The emphasis on biparental care in humans may explain why lacking a long-term partnership may be a risk factor for infanticide (Daly and Wilson 1988). Even if not direct biparental care, human mothers often depend on raising offspring with at least the indirect help of fathers in the form of security or material resources (e.g., Hewlett and Macfarlan 2010). In the absence of any extra social support from a male partner, new mothers appear at an increased risk of infanticide. Again, this appears to be a decision that is made by women surveying their environment when making investment decisions in their offspring's development. In the occasions where a partner is absent (and especially if other social support including extended family is also absent; Hrdy 1999), her risk of killing her child may increase due to the investment payoff lessening. Though the emotionally evocative nature of infanticide can be overwhelming, it is not surprising when taking an evolutionary forensic psychology perspective why women engage in this behavior.

Types of Homicide

There are a number of homicide typologies that have emerged over the years (e.g., Daly and Wilson 1988). These typologies attempt to cluster together similar types of homicides in seeking to understand and potentially prevent similar homicides from occurring in the future. Most existing typologies, however, do not consider an evolutionary framework to classify homicides making

them relatively more subject to author/researcher bias in terms of how they get clustered together. An example of this is the category “intimates” whereby spouses, family members, and close friends are considered together in one group or another where “family” consists of both spouses, biological kin, and non-related kin or step relations (Daly and Wilson 1988). An evolutionary forensic typology of homicide, however, would be sensitive to whether victim-offender relationships have genetic relatedness as in the case of biological children and siblings compared to step relations such as stepparents or stepchildren. Homicide records should show less closely related victim-offender observations because of the evolutionary principles of genetic relatedness and inclusive fitness (Hamilton 1964). Across multiple cultures, this appears to be the case, with the vast majority of homicides involving “family” and “intimates” actually showing that the victim or offender are non-related kin or spouses rather than biologically related kin (Duntley and Buss 2008). This also happens to be the case for killing infants and young children, where there is approximately a 100-fold increased risk of a child being abused or killed when there is at least one stepparent in the household (Daly and Wilson 1988).

Another typology that has become clarified and comprehensible with the inclusion of an evolutionary forensic psychology perspective is male-male violence that escalates to homicide. In the past, these forms of homicide have been described as “trivial” altercations between men, no doubt with the assumption that these men lacked rationality and emotion regulation skills to keep their passions in check. While this may be true, this is merely descriptive and not explanatory. Why men from cultures around the world should engage in escalating violence due to “trivial” matters is made comprehensible by an evolutionary perspective that focuses on how social competition has reproductive consequences (Betzig 1982; Daly and Wilson 1988).

“Social conflict homicides” is an atheoretical accumulation of homicides involving business, jealousy, family, and friends. What may be surprising from this atheoretical perspective,

however, is that more than half of social conflict homicides involve “trivial altercations” between men (Daly and Wilson 1988, p. 63). An evolutionary forensic psychology perspective sees these altercations as evolutionarily consequential and thus allows us to understand them as instances of “saving face” or generating respect in one’s social group. This is not to excuse the actions involved in these social conflicts, but it does help us understand why men can become psychologically convinced that responding to the escalating social conflict with fatal violence is the only option available to them and why these are the most common of the social conflict homicides.

While many male-male homicides seem to fall into the typology of “trivial altercations,” other social conflict homicides involving male-male altercations including sexual jealousy homicides and revenge homicides may share similar motives (Duntley and Buss 2011). These motives revolve around acquiring and maintaining group respect within a status hierarchy, attracting opposite-sex mates, and ensuring paternity certainty. Intriguingly, but expectedly from an evolutionary view, these motives share in common ensuring the reproductive success of men within a social group. Men fight about status, and they fight about women, often with fatal consequences. There is little doubt that the *degree* to which this occurs depends on culture (e.g., Daly and Wilson 1988) but that it occurs across cultures around the world is of little doubt (e.g., Duntley and Buss 2008). From gangs in the United States to the Yanomamö tribes of what is now Brazil and Venezuela, men are ostensibly fighting and killing over status and women. These social conflicts have documented fitness consequences as well, whereby men who have killed in both US gangs (Duntley and Buss 2008) and the Yanomamö tribes (Chagnon 2013) each see their status and reproductive success increase afterward. These unusual findings of violence “paying off” are made clear when we have an evolutionary forensic psychology perspective directed at them. Indeed, in order to fully understand fatal violence and its motives, an evolutionary explanation seems necessary; otherwise, motives and behaviors get arbitrarily described as “trivial,” thus

giving the impression of being random and difficult to understand.

Is Homicide an Instance of Adaptation?

While there appear to be reproductive benefits to engaging in lethal violence as described above, does this entail there being underlying psychological mechanisms that have been shaped to execute homicidal thoughts and behaviors? Some researchers have argued that this is indeed the case (e.g., Duntley and Buss 2008, 2011), whereas others also see the possibility that homicide may be a by-product of escalating violence (e.g., Daly and Wilson 1988). We do not offer any attempt at a definitive answer here but instead focus on what it means to have adaptations for homicide. Further, we stress the need to consider context as environmental cues are clearly important for activating any psychological mechanisms that may generate violence (Liddle et al. 2012).

Having adaptations for homicide would indicate that humans have psychological mechanisms that produce phenotypic effects (thought patterns, emotions, behaviors) that have explicitly been shaped into our available heritable traits that provided relative fitness benefits (Duntley and Buss 2011). These should be thought of not as a single adaptation or module for homicide, but rather many possible modules that may have similarities but are differentially activated depending on contextual factors. For instance, a young mother that recently had her partner leave her and has dismal familial social support may have an infanticidal thoughts and behaviors mental module become more active, whereas a man who sees his partner with another man will have a sexual jealousy mental module activated. This perspective takes the contextual nature of homicides to its extreme and proposes that thoughts and behaviors related to killing are context-specific and should not occur outside of those contexts (Duntley and Buss 2011). That many of the homicides reported throughout this entry are context-specific is in line with this perspective (Liddle et al. 2012), but the scope and veracity of the idea of homicide adaptations are still in its infancy.

Sexual Crimes

What we are calling sexual crimes are behaviors between the sexes that the law defines as illegal and constitute some of the most cognitively and emotionally disturbing realities in society. These crimes include sexual harassment, rape, and intimate partner violence and are far more often committed against women by men (Daly and Wilson 1988). Additionally, we will describe the crime of prostitution, which in some jurisdictions is not considered a crime (Salmon 2008). Sexual crimes are some of the most easily understood crimes when using an evolutionary perspective, given their importance and consequences regarding reproductive success (Duntley and Shackelford 2008).

Sexual Harassment

There are broadly two types of sexual harassment. First, quid pro quo forms of sexual harassment involve acquiring benefits or avoiding costs contingent on performing sexual acts (Browne 2008). This is the classic case where usually male supervisors offer to promote a female subordinate on the condition that she engages in sexual activity with him or threatens to fire her if she does not. The second form of harassment is hostile environment harassment where the working environment is claimed to be overlaid with sexual insults, intimidation, and discrimination. This form of harassment is less directed at any particular individual but has the capacity to discriminate, intimidate, and unfairly influence certain individuals' experiences at work, especially young and attractive women (Browne 2008).

Why do men mostly engage in sexual harassment, whereas women are often, but not always, the targets? One common perception in non-evolutionarily informed social science research is that men use sexual harassment as a tool to reinforce and demonstrate their social positions of power (Browne 2008). An evolutionary perspective, however, enables us to move away from this unidirectional perspective and also see that men use their power to obtain sex. Referring back to Geary's (2010) suggestion that men's reproductive success is constrained by the number of

females they mate with allows us to understand the logic of selection pressures acting on men's minds to increase their number of mating partners when given the chance (i.e., when having the status and resources to do so). Across instances in history, men with an inordinate amount of power such as Genghis Khan and other despots have regularly used that power to acquire many sexual partners (Betzig 1982; Daly 2016), often leading to enormous reproductive success (e.g., Zerjal et al. 2003). Indeed, history seems to suggest that unyielding power in the hands of men reliably leads to their optimizing that power and influence for sexual gain. This has implications for policy such that an evolutionary view supports the notion that absolute power in the hands of few individuals – particularly men – is not a practice that workplaces should promote (Browne 2008).

Equally as important for understanding the evolutionary logic of sexual harassment is why women do not engage more in it. Again, referring to the idea that women are less likely to gain reproductively from acquiring additional sexual partners and that parental investment tends to be skewed toward females makes their involvement in sexual harassment less beneficial reproductively and thus less likely to occur (Geary 2010). This does not mean women cannot become tyrannical sexual harassers in the workplace, but it does indicate that women are far less likely to use their power and influence *for* sex. Instead, women may use sexual harassment strategically for career advancement or influencing their position in society, whereas men are likely to use sexual harassment *for* sex (Browne 2008).

Rape

Sexual coercion, or rape, is a difficult topic to discuss because of the emotional toll it causes victims and the morality surrounding such coercive actions. Nevertheless, a disturbingly high proportion of women (with some estimates as high as 13% in some US states) report experiencing rape at some point in their lives, with an especially high-risk during young adulthood when reproductive potential is highest (McKibbin et al. 2008). Additionally, sexual

coercion extends deep into our history as a species and across the globe (Lalumière et al. 2005). Rape victims are not exclusively female as many males experience sexual coercion as well, but the reality is most victims tend to be women and girls, while perpetrators tend to be men and sometimes boys. Corroborating that rape is committed mostly by men, some unsettling research show that many men report having coercive sexual fantasies and at least one-third say they could see themselves committing rape under specific conditions (Huppín and Malamuth 2016). Clearly, understanding the contexts under which men may become rapists and why this is the case is crucial for researchers and social policy.

What an evolutionary perspective adds to forensic research into rape is framing *why* some men come to commit such coercive actions and even why there is a cost, psychologically and reproductively, to women of such actions. An evolutionary perspective allows us to appreciate, beyond moral and emotional reactions to sexual coercion, the reasons why such actions are costly to women (McKibbin et al. 2008). However, it also frames an understanding of the potential benefits men may accrue from sexual coercion, hence why they may commit such actions. It should be noted that there is debate about whether rape should be considered an adaptation on its own or whether it is a by-product of the tendency to engage in sexual coercion, more generally (Thornhill and Palmer 2000).

For women, and from an evolutionary perspective, costs of rape are subversion of mate choice in whom she has offspring with, creating the possibility of becoming impregnated by a male that she otherwise would not want to have a child with (McKibbin et al. 2008). Women also face the evolutionary cost of being perceived as less desirable by some men if they have been raped by another man, which can limit her mate choice and future reproductive success (Huppín and Malamuth 2016). Lastly, and especially in foraging ancestral environments (e.g., Tooby and Cosmides 1992), rape may force women to experience the cost of investment in unwanted pregnancy that takes physiological and social

resources that are valuable and not unlimited away from other offspring investment (either in the future or her current children), potentially compromising her current and future reproductive success. For men, and from an evolutionary perspective, the benefits of rape are to potentially sire offspring without having to invest in courtship behaviors. Because males may benefit reproductively from accessing multiple females, one plausible way of acquiring extra mates may have been through coercion (Lalumière et al. 2005). Additionally, if reproductive success is skewed for males in a population, rape may become one method for attempting to reproduce. Thus, from an evolutionary perspective, rape provides a “solution” to the problem of overcoming the variance in male reproductive success, and this may be unique to specific kinds of men within their social hierarchies (e.g., Betzig 1982; Lalumière et al. 2005; McKibbin et al. 2008; Zerjal et al. 2003).

It is important to point out here that rape may not have had as much reproductive benefit for male ancestors as might be gleaned upon reading the paragraphs above. Counter-selection pressures (e.g., women’s fear of strange men, women’s protective bonds with others) and other selection pressures within males (e.g., for social emotions, bonding, paternal care) likely created ancestral environments where rape may not have reliably added to a male’s reproductive success. Instead, it may have occurred mostly as a response to particular conditions – wartime, societies with high male reproductive variance, and unstable male coalitions – whereby men perceived particularly opportunistic, anonymous, or dismal future conditions for themselves, making rape a “last resort” at reproduction (Lalumière et al. 2005). This suggests that halting the commission of rape in cultures around the world may require an appreciation for and understanding of the social and economic conditions that facilitate men’s propensity to engage in this behavior.

Intimate Partner Violence

Once in a relationship, it may seem that intersexual violence is likely to decline. While this is the case for many relationships, many others

experience domestic or intimate partner violence (Goetz et al. 2008). Intimate partner violence including verbal, emotional, and physical abuse of one’s partner occurs at a high rate in countries around the world. In the Yanomamö, men regularly hit their wives for the slightest of indiscretions, which often involve perceived flirtation on the part of the wife with another man in the group (Chagnon 2013). In Western countries, both sexes engage in intimate partner violence, but men tend to facilitate the abuse, and they tend to exact more severe abuse on their partners than do women (Daly and Wilson 1988; Goetz et al. 2008).

An evolutionary reading of intimate partner violence, particularly actions committed by men toward women, involves acknowledging the differences in the certainty of having a relationship to one’s offspring. Specifically, for men, there is always a component of uncertainty of his paternity regarding his children that a mother does not contend with. This has likely created an anxiety that selection has influenced in men’s phenotypes, making them more likely to experience sexual jealousy, be preoccupied with a partner’s (in)fidelity, and have feelings of sexual proprietariness toward their partner (Daly and Wilson 1988; Goetz et al. 2008). In other words, men’s minds have likely been shaped to more easily see women as property that needs to be guarded, and they are more likely to ruminate about their partner’s sexual intentions and actions (Duntley and Buss 2008). One possible consequence or shaping feature that selection may have instilled in the minds of men as a result of this paternity uncertainty is the behaviors they execute if they believe their partner has been unfaithful (Goetz et al. 2008). For instance, men may rape their wives if they believe they have been with another man, which, if they had been, may potentially displace the other man’s sperm. Another possible response is cordoning off his partner from friends and family to ensure she cannot be unfaithful again. Either way, these behaviors motivated by sexual jealousy and proprietariness that have an evolutionary logic cause substantial psychological and emotional abuse of women, making understanding them that much more important.

Prostitution

Often described as the world's oldest profession, prostitution constitutes an interesting example from both an evolutionary and legal perspective. From a legal perspective, some countries, and even within some states in the United States (e.g., Nevada), prostitution is not considered a criminal offense (Salmon 2008). In many other countries including Canada, it is not illegal to sell sexual services (i.e., to offer sex for money). In Canada though, prostitution legislation gets complicated because it is actually illegal to purchase these sexual services and it is illegal to advertise such services. These laws emerge from a long history of attempting (but failing) to curb the exchange of sex for resources and protect sex workers (who are mostly women) from abuse and criminal prosecution. That societies have laws and manifest such a stake in the sex lives of individuals reflects again the moral impulses that govern the laws and determine what constitutes a crime (Walsh 2000). Because of its connection to reproductive success, sexual activity of all kinds would have been highly regulated and monitored in ancestral environments, with modern environments being a predecessor of such conditions. Prostitution laws, being rooted in deeply moralistic reasoning, reflect this inheritance.

Who tends to purchase sex for money? Overwhelmingly, men are the clients, and they are often, but not exclusively, purchasing the sexual services of women, some of whom are street sex workers, but most (~75%) of whom are in-call or out-call sex workers (Salmon 2008). Why are men tending to be the purchasers and women the sellers? An evolutionary perspective suggests that because men have had a stronger history of selection toward sexual variety and obtaining multiple partners (e.g., Geary 2010), they should experience a stronger desire for sexual experiences that offer these potential reproductive benefits. With prostitution, facilitated by anonymity and economic exchange, men are able to simply offer resources (i.e., money) to obtain "just sex" (Salmon 2008). This allows men also (similar to the case of rape) to bypass the courtship often involved in relationship acquisition before being "allowed" sexual access to a woman.

Interestingly, women sex workers do not engage in prostitution for the same reasons men do (i.e., for "just sex"). Instead, they are largely engaged in prostitution for the economic and material rewards (i.e., the money). This is also predicted from an evolutionary perspective, whereby women show a deep resourcefulness for finding ways to obtain and secure economic and social resources for her and her children's well-being (Hrdy 1999).

Conclusion

Evolutionary forensic psychology provides an interdisciplinary theoretical explanation for many of the forensic-related issues facing society. From homicide to sexual harassment and from rape to infanticide, using an evolutionary perspective allows for rooting these deeply troubling social issues into a framework that explains why they exist and the specific contextual factors that may elicit their expression. Using the principles of evolution, evolutionary forensic psychology is primed to understand and explain why sex and age continue to be significant and reliable predictors of the commission of crime across the globe. Criminal activity is certainly socially disruptive and emotionally devastating, but its enactment does not only produce costs for the individuals committing these actions; they are also permeated with benefits, many of which are connected to the evolutionary expectation of enhancing reproductive success through resource acquisition, status accumulation, and mating. Understanding these benefits and the costs of criminal behavior may better allow us to tailor interventions toward reducing the prevalence and impact of criminal behavior on individuals and society as a whole.

Cross-References

- ▶ [Criminal Personality Variables](#)
- ▶ [Criminals are Made Not Born](#)
- ▶ [Criminology](#)
- ▶ [Evolutionary Personality Psychology](#)

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Evolutionary Foundations of the Attachment System and Its Functions

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Definition

The attachment system, as defined by John Bowlby, is a behavioral control system that continuously monitors proximity to caregivers. Bowlby argued that the attachment system has been retained as proximity to caregivers has been associated with increased chances of survival, and ultimately reproduction, in humans’ ancestral environments.

Introduction

Universally, human infants form strong bonds – attachments – to their caregivers. That is, children who have formed attachments seek to maintain proximity to their caregivers and protest separations by means of positive (e.g., smiling,

vocalizing) and aversive (e.g., crying, screaming) signaling behaviors and active behaviors such as approaching and following. Children's striving for proximity is particularly evident in situations that signal potential danger, in which children typically signal to and/or approach and cling to their caregivers. However, children also monitor their caregiver's whereabouts in absence of threat signals, using the caregiver(s) as a reference point, a "secure base," for exploration of the environment. John Bowlby, a psychoanalyst and child psychiatrist, sought to understand the phenomenon of attachment, which at the time was deemed secondary to other processes, such as psychical energies and the caregiver's ability to provide nourishment. Bowlby termed these theories, which he thought were unscientifically formulated, "secondary-drive theories" (see psychodynamic foundations).

Bowlby performed some initial research that pointed toward negative effects on children's development from prolonged separations from caregivers (Bowlby 1944) and conducted a report for the World Health Organization regarding the effects of separation (Bowlby 1951; see John Bowlby: Pioneer of Attachment Theory). To develop a scientifically based understanding of the nature of children's ties to their caregivers, Bowlby started a seminar group with participants from various scientific disciplines. This seminar group became important for Bowlby who came to draw on and integrate knowledge from evolutionary theory and ethology, cybernetics, and cognitive research. Bowlby became heavily influenced by evolutionary theory and ethology through the pioneering control theory ethologist Robert Hinde (e.g., Hinde 1970), who also became a close friend. Hinde was at the time shifting his own research interest toward mother-infant interactions in rhesus monkeys, and Bowlby noted that infant rhesus monkeys showed a pattern of behaviors in relation to their mothers that was highly similar to that shown by human infants (van der Horst et al. 2007). Bowlby realized the potential of explaining human attachment behaviors using evolutionary and ethological theory. Not only was ethology concerned with the development of close social bonds between animal offspring and their

parents, but it was also firmly anchored in the usage of empirically grounded methods such as naturalistic observations which appealed to Bowlby's scientific ideals. The evolutionary foundation of the attachment system and its function, as outlined by Bowlby, is discussed below.

Evolutionary and Ethological Foundations of Attachment Theory

Development of Behavioral Systems

Ultimately, Bowlby's starting point became evolutionary theory, following Darwin (1859) and the theory of natural selection. Indeed, Bowlby argued that attachment theory is "a direct descendant of the theory outlined by Darwin in *The Origins of Species*" (Bowlby 1997/1982, p. 172). Moreover, Bowlby felt that ethology was the best application of Darwin's theories to behavioral systems in animals and argued that humans, like all other species, should have become endowed with behavioral systems that once evolved have been retained because they have served an adaptive function in our ancestral species-typical environments. More specifically, individuals who became endowed with certain behavior systems had increased rates of survival and ultimately reproduction (see infant survival). Thus, the genes of these individuals must have been differentially passed on to future generations by these individuals having more progeny, and such behavioral systems therefore eventually became stable characteristics of a species. As argued by Bowlby, "...once gene survival is recognized as the true criterion in terms of which the function of instinctive behavior is measured; some old-standing problems evaporate" (Bowlby 1997/1982, p. 133).

Bowlby explicitly argued against teleological explanations, such that behavioral systems were caused by their outcomes so as to serve a specific purpose. For example, saying that birds are building nests to have somewhere to rear their young, and implying that this particular "need" causes the nest building, would be an example of a teleological statement according to Bowlby. As argued by Bowlby; "...because such a theory entails

supposing that the future determines the present through some form of ‘finalistic’ causation, it lies outside the realm of science” (Bowlby 1997/1982, p. 125). Bowlby therefore drew a strict line between cause and function. According to Bowlby, causes are those circumstances that activate and terminate a behavior system, whereas its function is related to the consequences that typically arise from the way the system is structured (cf. predictable outcome; see below). Needs, such as having somewhere to rear offspring, do not cause behavior systems per se; they constitute the selection pressure under which behavioral systems have evolved and have thus determined the functions they serve. Function, therefore, can only be ascribed afterwards, as an explanation for why a characteristic has become more common in a species. Some behavioral systems and their respective behaviors have just happened to be differentially functional as regards increasing rates of survival and have therefore been retained through the process of natural selection.

Predictable Outcomes and Functional Consequences of Behavioral Systems

Bowlby used the term predictable outcome to denote the species-typical functional consequence of the activation of a behavior system. As regards attachment Bowlby argued that proximity to caregivers is the predictable outcome of activation and protection from dangers its functional consequence. Indeed, the signaling behavior and active approach behavior that children show when the attachment system is triggered by internal (e.g., pain, illness) and external signals of threat (e.g., threatening external stimuli, separation from the caregiver) tend to result in proximity to caregivers (and thereby protection). Bowlby was however careful to differentiate between predictable outcome and functional consequence. In any given individual, the functional consequence (i.e., the species-typical predictable outcome) may only sometimes, or never, follow from the activation of a behavioral system. As argued by Bowlby, in any given individual, a behavioral system becomes active, reaches a more or less typical predictable outcome, and then becomes inactive, all without reference to the system’s function.

Bowlby exemplified this with infants’ sucking of dummies, which does not result in nutrition. As regards the attachment system, some children’s proximity-seeking behavior is met with rebuff/rejection (see “individual variations in attachment”) or even potentially harmful responses (see “disorganized attachment and reactive attachment disorder”). Bowlby therefore argued that understanding of any system’s function is impossible from studying any single individual; it necessitates studying a population of individuals. Whereas predictable outcome refer to the working of a system in a particular individual, functional consequence refers to a property in a population of individuals. However, for a population to survive, and hence for a behavior system to be retained, it is important that the predictable outcome is consonant with its functional consequence in a sufficient number of individuals. In the case of attachment, the predictable outcome of proximity to caregivers must have resulted in its functional consequence of protection in a sufficient number of individuals.

The Environment of Evolutionary Adaptedness and Development of Behavioral Systems

In tracing the function of behavioral systems, and the attachment system in particular, Bowlby argued that functions must be sought in the environment(s) in which humans have historically evolved, which have provided the pertinent selection pressures. With the words of Bowlby, “Just as Darwin found it impossible to understand the structure of an orchid flower until he knew what insects flourished and visited it. . . , so, it is held, it is impossible to understand man’s instinctive behavior until we know something of the environment in which it evolved” (Bowlby 1997/1982, p. 61). Bowlby termed this environment the “environment of evolutionary adaptedness” (EEA). This assumption and terminology was later picked up as an important guiding principle in evolutionary psychology (see Laland and Brown 2011; Tooby and Cosmides 1990). Bowlby argued that in our primeval environment, humans were living as nomads in small hunter-gatherer societies, in an environment comparable to that of other large

ground-living species of higher primates. A key characteristic of our ancestral environment, according to Bowlby, was a risk of falling prey to predators and other natural dangers. Thus, a behavioral system that helped increase and maintain proximity to caregiver(s) should have served an important function that increased the chances of survival. Human children are indeed born very vulnerable and thus dependent on their caregiver's support for a proportional amount of time largely unparalleled in other species. With the words of Bowlby, "Because immature organisms are usually very vulnerable they are commonly endowed with behavioral equipment that produces behaviors specifically likely to minimize risk, e.g. behavior that maintains proximity to a parent" (Bowlby 1997/1982, p. 143). Thus, Bowlby argued that proximity to caregivers is the predictable outcome of activation of the attachment system, as proximity to caregivers reduces the risk of falling victim to predators and other natural dangers. Hence, Bowlby argued for a narrow definition of the functional consequence of proximity, as opposed to alternative suggestions that proximity to caregivers may have increased chances of learning skills important for survival from caregivers (see infant survival).

Bowlby noted that human infants typically display a specific sequence of reactions following separations from their caregivers: protest, despair, and detachment. Protest, shown by aversive signaling behaviors, draws the attention of the caregivers and may prevent separation (i.e., maintain proximity). Evolutionarily, it can be argued that children left unattended in our ancestral EEA were more susceptible to predators and other dangers. During despair, which follows if a separation is prolonged, children's motor activity typically declines and they become more silent. Evolutionarily, this may have been an adaptive secondary strategy as excess movements and loud protests, when not in the proximity of the caregiver, may have increased the risk of injuries or drawn the attention of predators. During the final stage, detachment, which follows if the separation is not ended, infants gradually resume normal behavior and become more receptive toward other individuals. Bowlby argued that this may

have facilitated the formation of new attachment bonds (i.e., maintaining proximity to a new attachment figure). From an evolutionary perspective, this may be adaptive as new caregivers may be willing to provide the resources necessary for survival (Simpson and Belsky 2008). The various patterns of attachment that children develop, which primarily depend on the caregiver's pattern of responding to the child's signals (see individual variations in attachment), have also been described as different strategies to obtain as much proximity to the caregiver as possible (Main 1981; Main and Solomon 1986).

Bird Imprinting and Attachment Behavior in Other Primates

Bowlby drew heavily from all ethological research existing at the time. Indeed, it has been said that Bowlby was a psychoanalyst by trade but an ethologist at heart (Suomi 1995). Accordingly, Bowlby argued that insights into behavioral systems in humans may be gained from knowledge about the behavioral systems of other species and that our behavioral systems, although they may seem unique to us, should be seen as modifications of prototypes found in other species. With the words of Bowlby: "...we share anatomical and physiological features with lower species, and it would be odd were we not to share none of the behavioral features that go with them" (Bowlby 1997/1982, p. 7). Bowlby was particularly influenced by Konrad Lorenz (1963), Niko Tinbergen (1951/1963), and Harry Harlow (1958).

Bowlby regarded Lorenz's (1963) research regarding birds' imprinting as the first findings to seriously question the secondary-drive hypothesis. Bird offspring, who themselves had the ability to find food and thus were not reliant on their parents for nutrition, nonetheless formed strong bonds to and followed the parent wherever it went. Hence, Bowlby reasoned that proximity to the parent must have evolved due to it serving a function other than nourishment. Lorenz had originally argued that imprinting was unique to birds, that there was a critical phase early in development where imprinting had to occur, that imprinting was irreversible whence formed, and that

imprinting was fundamentally distinguished from other types of learning. However, research that followed subsequently revised these claims, for example, showing that imprinting is reversible and that sensitive periods are a more appropriate characterization than critical periods. Perhaps most importantly for Bowlby, the features of imprinting also seemed applicable to mammals to some degree. Indeed, the phenomenon of imprinting was descriptively similar to the two main characteristics of attachment: maintaining proximity to another animal and a specificity of the other animal (i.e., the caregiver[s]). Bowlby therefore accepted the phenomenon of imprinting in a generic sense, implying the development of a clear preference, which develops rather quickly and during a limited phase of life and that once formed remains relatively fixed. However, as acknowledged by Bowlby, drawing conclusions about behavior systems in humans from behavior systems in birds is problematic, since the phylogenetic lines of birds and mammals parted early in evolution.

Harlow's studies on rhesus monkeys (e.g., Harlow 1958) therefore became important for bridging the gap. Indeed, it has been argued that Bowlby tailored attachment theory to not only account for the behaviors shown by virtually all human infants but also those shown by our closest evolutionary relatives (Suomi 2008). Harlow performed multiple experiments with rhesus monkey infants and inanimate surrogate mothers, for example, comparing the importance of the surrogate mothers' ability to provide nourishment or closeness and warmth. In one of the experiments, Harlow used a steel-clad surrogate mother that was able to provide nourishment and one soft wool-clad surrogate mother that could not provide nourishment but that could provide closeness and warmth. Contrary to the secondary-drive theories, the young rhesus monkeys preferred the soft surrogate mother and only clung to the steel mother that could feed them when hungry. With the words of Bowlby, "All these experiments showed that 'contact comfort' led to attachment behavior whereas food did not" (Bowlby 1997/1982, p. 213). Interestingly, further experiments also

revealed that the infant rhesus monkeys preferred the soft wool-clad surrogate mother even when it hurt and frightened the infant monkeys (e.g., using a buzzer that blasted compressed air through the nostrils). In fact, the rhesus monkey infants even clung harder to the surrogate mother then. Although this latter finding may seem counter-intuitive, Bowlby argued that it was logical from an attachment perspective. If the function of the attachment behavioral system is seeking and maintaining proximity to caregiver(s), particularly in situations signaling potential danger, and they were attached to the surrogate mother, they would "instinctually" seek proximity when frightened.

In this vein, Bowlby referred to attachment behaviors as "instinctual" in a descriptive sense, pertaining to behaviors that show great regularities within a species (following a similar and predictable pattern in almost all members), that is not just a simple response to a stimulus but a sequence of behaviors that have usual outcomes that are of survival value and that typically develop even when most opportunities for learning are absent. In the case of attachment, Bowlby noted that "attachment of young to parents are found in almost all members of the human race and seem best considered as expressions of some common plan and, since they are of obvious survival value, as instances of instinctive behavior" (Bowlby 1997/1982, p. 39). Bowlby argued that the similarities between humans and other animals were likely due to convergent evolution since many species have shared the same evolutionary environment, containing a risk of falling prey to predators.

Bowlby reviewed a number of observations of human infants indicating that attachment behavior in humans resembles those of other mammals; "...the development of attachment behavior in human infants, though much slower, is of a piece with that seen in non-human mammals. Much evidence supports that conclusion and none contradicts it" (Bowlby 1997/1982, p. 222). For example, once attached, infants prefer the attachment figure to other persons, typically persisting even in the face of separations. As for other mammals, human infants are also born with the

capacity to cling. Human infants also show a narrowing of responsivity to objects, which over development (though with a slower pace) becomes more directed toward a few objects (i.e., caregivers). Human infants also show a marked bias toward responding to particular stimuli (such as human faces), and the more experience with a particular person, the stronger the preference. Bowlby also argued that the early development of attachment in human infants, which typically forms during the first year, could be taken as an indication that there may also be a sensitive period for attachment in humans.

Interestingly, attachment theory, as outlined by Bowlby, has subsequently been successfully applied to ethological research on rhesus monkeys. As reviewed by Suomi (2008), infant rhesus monkeys show some patterns of relationships with their mothers that parallel the attachment patterns found in human infants, which as for humans depend on the caregiver's pattern of responding. Bowlby's and Ainsworth's "secure base" phenomenon has also been shown to be applicable to infant rhesus monkeys, and as for humans, an inability to use the parent as a secure base from which to explore is related to maladaptive development in rhesus monkeys (see "effects of attachment quality and organization").

Nature vs. Nurture and Behavioral Systems

Bowlby sought to avoid getting into a debate about whether the attachment behavioral system was innate or learned. Drawing on Hinde (1959), he thought of behavioral systems on a continuum of more or less "environmentally stable or instable," with environmental effects and learning most pertinent to more instable systems. Bowlby also argued that what is inherited is not an instinct per se but a potential to develop certain sorts of behavioral systems and that "the forms . . . differ in some measure according to the particular environment in which development takes place" (Bowlby 1997/1982, p. 46). Bowlby argued that the human attachment system is a moderately stable system, which may stem from the fact that behavior typically described as instinctual tends to be stable as long as the environment remains in the range of

that in which a species typically lives. Importantly, in the case of attachment, the species-typical environment generally includes caregivers responding to children's signals, thus rendering the phenomenon of attachment a relatively stable characteristic (but see "disorganized attachment and reactive attachment disorder" for detrimental effects following severe social deprivation). Indeed, Bowlby argued that the attachment system is complemented by a caregiving system in adults, which makes caregivers responsive to their children's signals. Following inclusive fitness theory, Bowlby argued that the caregiving system has developed as the adult's genes are only passed on to future generations to the extent that their offspring survives to reproduce. Thus, child attachment develops through a collaborative and synchronized process, with children socially biased and prepared to bond with their caregivers by drawing their attention through signaling behaviors and caregivers biased to respond to children's signals (Simpson and Belsky 2008). The development of attachment seen in almost all children has been termed the universality principle of attachment theory (van IJzendoorn and Sagi 1999).

Although stable in one sense, the attachment system is also moderately labile. Although labile systems typically have a disadvantage of taking time to mature and become functional, Bowlby argued that the advantage of such systems, which are open to learning, is that they permit modifications to suit the environment at hand. However, no systems can be suited to work in all environments, and if a system gets programmed for a particular environment, it may not work well in different environments. Openness to learning is, for example, seen in the relation between quality of caregiving (e.g., sensitivity) that children receive and the different organization of attachment behaviors (i.e., quality of attachment) that they develop (see "individual variations in attachment"). Thus, a consequence of the instability of the system is also that atypical environments can make the attachment system programmed in such a way that a child becomes at risk for problems in other environments (see "effects of attachment quality and organization").

A Control Systems Approach to Behavior Systems

Inspired by Hinde, who applied control theory in ethology, Bowlby also drew from control systems theory for understanding the basic structure of the attachment behavioral system. As outlined by Bowlby, any system serves a particular function (i.e., has an instruction/plan), a goal that it is preprogrammed to achieve. Bowlby argued that these instructions have reached us through natural selection and termed these the “set goals” of the systems, which he argued can be either for time-limited events or ongoing conditions. Bowlby argued that the set goal of the attachment system is continuous, as the task of the attachment behavioral system pertains to “control” of an ongoing relationship (i.e., continuous maintenance of spatial relations in relation to certain objects over time).

Apart from having a set goal, feedback is another important part of complex behavioral control systems. By feedback, and using machines (e.g., thermostats, missiles) as a metaphor, Bowlby referred to processes “... whereby the actual effects of performance are continuously reported back to a central regulating apparatus whereby they are compared with whatever instruction the machine was given; the machine’s further action is then determined by the result of this comparison and the effects of its performance are thus brought ever closer to the initial instruction” (Bowlby 1997/1982, p. 42). The degree of activation of the attachment system therefore varies depending on sensory input from internal or external sources, with activating signals (internal/external), those that signal possible danger, and terminating signals, those signals (internal/external) indicating that there is no more cause for alarm.

Bowlby argued that behavioral systems can be more or less complex, depending on whether they are organized to take feedback regarding ongoing performance into account in order to achieve their predetermined outcome (i.e., their evolved function). Fixed action patterns, which whence they are triggered by a stimulus tend to reflexively run their course with little account of ongoing feedback, exemplify simple behavioral systems. Such

patterns are often organized like chains of behaviors with actions of certain behavior systems in a specific order. The effect produced by one behavior system terminates the actions of that system and triggers the actions of the next system. Bowlby exemplified this notion with the collection of honey by bees, wherein bees first react to a certain color of a flower that triggers approach behavior, when getting closer to the flower reacting to the smell of the flower, etc. These behaviors are triggered in a certain order, and no step can be skipped. Although such systems can be intricate and important, their performance fails if the action of one link miscarries, as in the saying that no chain is stronger than its weakest link (Bowlby 1997/1982).

Bowlby used the term “goal corrected” for more complex systems, such as the attachment system, which are structured by means of feedback. That is, goal-corrected systems continuously monitor deviations between the set goal and current performance. However, Bowlby argued that the special characteristic of goal-corrected systems is the process by which they reach their set goal. Goal-corrected systems are typically not stereotyped and organized in chains, but rather by means of plans in plan hierarchies (cf. executive functions). Here Bowlby drew from Tinbergen (1951) and Miller et al. (1960) to denote that complex goal-corrected systems can make use of varying behaviors depending on the situational constraints and perform behaviors in different orders. Following activation of the attachment system, a child can, for example, cry in one situation and approach and cling to the caregiver in another. The advantage of such systems is thus that the predictable outcome can be achieved even though circumstances vary substantially. Bowlby argued that many behavioral systems of humans, as compared to other species, are complex and goal corrected, although we are endowed with a mix between simple and complex systems.

Bowlby further argued for a maturational developmental perspective on goal-corrected behavioral control systems such as the attachment system. The attachment behavioral control system, he argued, is not a functional goal-corrected

system at birth but develops into one with maturation. The reason for this is that the operation of goal-directed systems is mediated by various other systems and thus dependent on their development. Therefore, behavioral control systems tend to be organized as simple chains in infancy and become more goal corrected over time as more simple behavior systems become integrated under higher-order systems. For example, the reliance on sensory feedback makes the attachment system dependent on the development of the sensory organs. Behaviors also need to be oriented, and effector equipment such as locomotor ability is therefore important for goal-corrected behavior. Indeed, a child who has acquired the ability to crawl and walk is much more able to independently regulate proximity to the caregiver in a goal-directed manner.

Organisms also need to be able to organize sensory input into representations of the world, and goal-corrected attachment behavior therefore depends also on cognitive development. Bowlby used the term “internal working models” (IWMs), adapted from early artificial intelligence theorizing by Young (1964), to denote such cognitive representations of the environment: “The use to which a model in the brain is put is to transmit, store and manipulate information that helps in making predictions as to how what is here termed set-goals can be achieved” (Bowlby 1997/1982, p. 80). Bowlby thus argued, as do many current-day cognitive psychologists, that the brain is a prediction apparatus. Part of our immense adaptability and complexity is that we can make small-scale experiments based on our IWMs, to guide our behavior in various future situations that are, to varying degrees, similar to ones already encountered. Bowlby argued that we necessarily construct one organismic model (a model of ourselves and our abilities) and one environmental model (a model of others, including what to expect from others). These models, which are often referred to as models of self and others in attachment theory, are thought to be complementary. In order to function adaptively and not become too rigid, these models must be open to learning so that they can be continuously updated. Drawing from Piaget (1955), Bowlby argued that

we typically make small corrections to our models, and the IWMs become stable due to information being assimilated into the current models. However, given sufficiently strong new input, substantial change occurs through a process of accommodation.

Attachment Theory and Current Evolutionary Perspectives

Inclusive fitness theory may be regarded as the current superordinate theory of evolution (Simpson and Belsky 2008), encompassing Darwin’s notion of fitness according to one’s own reproduction and Hamilton’s (1964) notion of kin selection (i.e., that reproductive fitness also includes reproduction by biological relatives). Theories addressing specific adaptive problems that humans have faced are placed one level below and called “middle-level theories.” Attachment theory is today generally seen as one such middle-level theory. The principles put forth by middle-level theories are in turn regarded as one further level down, in the case of attachment theory pertaining to principles regarding species-typical development (development of an attachment bond) and development of predictable patterns of individual differences. Attachment is conceivably one of the first theories to acknowledge the need to describe both normative (or species-typical) development and individual variations.

It has however been argued that Bowlby focused too much on the survival function of attachment behaviors and not sufficiently addressed its possible role for differential reproduction (Simpson and Belsky 2008). For reproductive fitness, it is argued that not only must one survive into reproductive age, one must also leave progeny which in turn reaches reproductive age and leaves progeny (and so on). Thus, some attachment researchers are now exploring if childhood variations in attachment are related to different reproductive strategies in adulthood (e.g., Belsky 2007; see also “attachment in adulthood”). Relatedly, attachment research has been critiqued for advocating a notion of one

solitary human EEA, with the secure attachment pattern advocated as a “species-typical”/primary pattern and the insecure patterns as deviations/secondary strategies. In contrast, it has been argued that there were multiple EEAs and that the different childhood and adult attachment patterns all represent different adaptive tactics designed for improving reproductive fitness in their respective EEAs. Moreover, it has been argued that Bowlby’s attachment theory “equates” the interests of parents and offspring and does not acknowledge differences in reproductive interests between parents and children, as, for example, captured in Triver’s (1974) -parent-offspring conflict theory (see also Bowlby 1997/1982). According to parent-offspring conflict theory, parental investment in a particular child should depend on both benefits and costs of the investment. Theories following this line of reasoning argue that variations in parental investment and sensitivity, and subsequently variations in attachment, should partly stem from cost-benefit trade-offs due to, for example, attributes of the parent and the child, the family (e.g., presence of siblings), and the local environment. Lastly, attachment theory has been critiqued for putting too much emphasis on mothers as the principal attachment figures. For example, cooperative breeding theory (Hrdy 2005) emphasizes that cooperative parenting, involving other adults and older siblings (alloparents), has likely been the norm throughout our ancestral history.

Conclusion

In formulating attachment theory, Bowlby drew on Darwin’s theory of natural selection and ethological theory and research, including imprinting and control systems theory as applied in ethology. The human attachment system, similarly to other animals, is argued to constitute a behavioral control system that has been retained because it served an adaptive function in our ancestral environments. Specifically, Bowlby argued that the set goal of the attachment system is maintaining a certain degree of proximity to

caregivers and that the predictable outcome of activation of the attachment system is increased proximity to caregivers, which has served an evolutionary function of protection against predators and other natural dangers. Lastly, it has been argued that the attachment system develops into a complex, goal-corrected system that continuously uses feedback to monitor deviations between its set goal and its performance and that this system is moderately labile and open to learning.

Cross-References

- ▶ [Attachment in Adulthood](#)
- ▶ [Charles Darwin: Theory of Natural Selection](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Disorganized Attachment and Reactive Attachment Disorder](#)
- ▶ [Effects of Attachment Quality and Organization](#)
- ▶ [Individual Variations in Attachment](#)
- ▶ [Infant Survival](#)
- ▶ [John Bowlby: Pioneer of Attachment Theory](#)
- ▶ [Parent-Offspring Conflict \(Trivers\)](#)
- ▶ [Psychodynamic Foundations](#)
- ▶ [Robert Hinde](#)
- ▶ [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Evolutionary Game Theory

- [Game Theory as a Foundation of Evolutionary Psychology](#)
- [Prisoner's Dilemma and Cooperation](#)

Evolutionary Hierarchy of Needs

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Synonyms

[Fundamental motives](#); [Fundamental social motives](#)

Definition

A framework of universal human needs that have been naturally selected because they promote relatively higher reproductive fitness.

Introduction

Abraham Maslow's (1943) hierarchy of human needs continues to enjoy fame in the popular consciousness. Briefly, Maslow posited that humans have a universal suite of basic needs that appear in sequence as each need is met. According to this framework, fulfilling immediate physical needs frees attention to fulfill security needs,

which leads to pursuing social needs for love and belonging, followed by ego needs for power and prestige, and finally the need to self-actualize by pursuing one's highest potential. Recent work taking an evolutionary approach to motivation "renovated" Maslow's pyramid (Kenrick et al. 2010a; see Fig. 1). Current evolutionary theory suggests that, inasmuch as these needs are universal, they ultimately serve to promote reproductive fitness. Viewed this way, self-actualization is still a lofty goal, but the ultimate function of it or any other motivated pursuit is to satisfy evolved needs. Furthermore, evolutionary theory suggests that needs would not emerge in discrete stages but would come online throughout the life span, interplaying with life stage and environment.

Evolved Needs

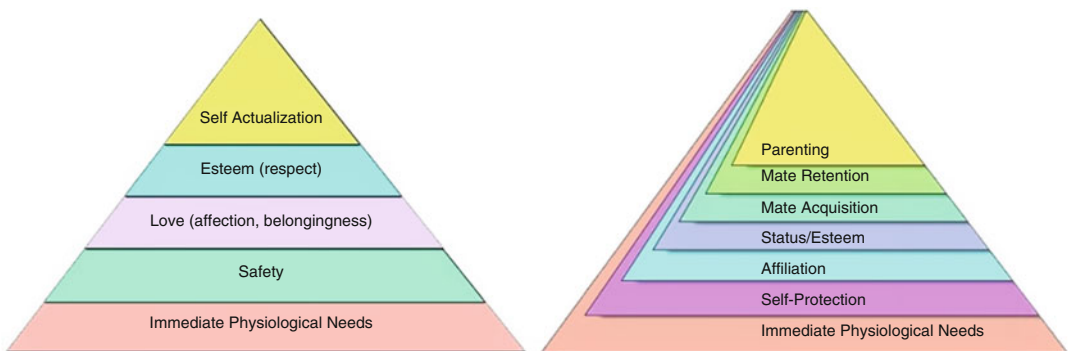
Humans are believed to possess evolved psychological mechanisms that solve recurrent challenges to reproductive fitness. The renovated pyramid of fundamental motives is comprised of those universal drives, which, when satisfied, can help humans increase their fitness (Kenrick et al. 2010a; see Fig. 1; Kenrick et al. 2010b; Schaller et al. 2017) (Kenrick et al. 2010a, b; Schaller et al. 2017). According to the fundamental social motives model, the drives to protect oneself from danger, avoid diseases, build a social network,

acquire social status, find a mate, keep that mate, and care for kin all help to promote fitness. For example, a drive to avoid diseases might help to promote fitness by motivating individuals to steer clear of visibly infected others.

The Sequence of Needs Within the Hierarchy

Unlike Maslow's model, individual fundamental motives are not part of a strict gatekeeping order by which one graduates to a new level of motivation and forgets the previous one. Instead, lower goals make way for higher goals but also remain online in the service of reproductive fitness. For example, we are just as repulsed by rotten foods after having children as we were before. Lower motives do not necessarily atrophy when higher motives are satisfied. Also note here, however, that some higher goals cannot be met without first achieving lower ones (e.g., mating and caring for offspring).

Thus, different goals can become salient in different situations (Morse et al. 2015). Any number of fitness-relevant stimuli can activate a fundamental motive to selectively focus attention and energy toward mitigating a current threat or taking advantage of a current opportunity (Kenrick and Krebs 2018). For example, when a self-protection motive is activated, memory for potentially threatening male faces improves even



Evolutionary Hierarchy of Needs, Fig. 1 Maslow's (1943) pyramid of needs (left) and Kenrick et al.'s (2010a) revised pyramid of needs (right)

though no additional attention is observably paid (Becker et al. 2010).

Individual Differences and Changes in Focus over the Lifespan

The Fundamental Social Motives Inventory (FSMI; Neel et al. 2016) is a reliable measure of evolved needs which confirms that individual differences in each of these social domains predict unique variance in cognition and behavior. For example, individuals higher in the self-protection motive are more likely to believe the world is a dangerous place and to have taken steps toward increased safety in the past year (e.g., improved home security, self-defense classes).

An evolved hierarchy of needs likely promotes individual fitness in different ways depending on life history variables and ecological conditions, meaning that individuals vary in which motives are chronically salient. For example, we might expect that status motives are more salient for men – and especially single men – because women prefer high-status males (Buss 1989). When ecological conditions include resource scarcity and concomitant violence, self-protection motives are more likely to be chronically active. Recent evidence suggests that evolved motives do vary in response to life history variables. Mate-seeking motivation is higher among men and decreases with age, whereas kin care motivation is higher among parents and especially those with young children (Neel et al. 2016).

What to Do with Self-Actualization?

Self-actualization is a state wherein an individual has all basic needs met and is pursuing his or her highest potential (Maslow 1943). Individuals who have reached their fullest potential are said to be self-actualized. Unlike Maslow's pyramid of needs, an evolutionary hierarchy of needs does not count self-actualization as the apex of human motivation but instead as a vehicle for promoting reproductive fitness. For example, one might self-actualize by becoming an excellent violinist, but there is no

reason to expect that evolution has programmed humans to master musical instruments. Rather, evolution has programmed humans to seek optimal reproductive fitness through a variety of available means. An evolutionary hierarchy of needs posits that any self-actualizing activity is undertaken ultimately to promote reproductive fitness.

Humans pursue fitness-relevant goals, as doing so may have reliably increased reproductive fitness (Symons 1992; Tooby and Cosmides 1992). Likewise, activities that make us feel good are thought to do so because they signal progress toward some fitness-relevant goal(s). To the extent that self-actualization is a universal need and/or feels good, this suggests that it may signal progress toward adaptive ends. Indeed, research suggests that creative pursuits (self-actualizing behaviors) are one avenue toward gaining social status and attracting mates (Griskevicius, Cialdini, & Kenrick 2006; Miller 2000), suggesting that self-actualizing activities may be associated with fitness-relevant goals. Krems et al. (2017) found that participants strongly associated their own self-actualizing activities (e.g., “working on my PhD in biology”) with pursuing status (and affiliation). Recent experimental work (Scott and Cohen 2019) further supports such theorizing that well-being tracks progress toward fundamental social goals (Krems et al. 2017; Kenrick and Krems 2018): Participants randomly assigned to write about fully accomplishing their kin care and mating goals felt increased purpose in life, as did those writing about status achievements. Taken together, the evidence suggests that self-actualization is associated with – and may ultimately serve to promote – reproductive fitness.

Conclusion

From an evolutionary perspective, any universal hierarchy of needs must be associated with reproductive success.

Cross-References

► [Fundamental Social Motives](#)

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Evolutionary Medicine

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Synonyms

Darwinian medicine

Definition

Evolutionary medicine is a transdisciplinary field of study aimed at applying evolutionary concepts and thinking to our understanding of medicine.

Introduction

Unlike the traditional approach to medicine which is aimed at identifying and treating the proximate causes (i.e., symptoms) of disease, an evolutionary medicine approach is focused on identifying the evolutionary origins (ultimate cause) of a disease and to use this to help inform medical

practice (Williams and Nesse 1991; Trevathan 2010; Ruhli and Henneberg 2013). Evidence in support of evolutionary medicine is provided by observers working in various fields, including cognitive science, anthropology, demography, biochemistry and molecular biology, and genetics. Evolutionary medicine thus offers a broader and more holistic perspective to medicine. The significance of using an evolutionary approach to medicine is highlighted by the tremendous insight gained from our understanding of antibiotic resistance (Davies and Davies 2010) and the rise in recent viral or bacterial outbreaks (e.g., Ebola, Measles, COVID-19). Interest in evolutionary medicine has grown exponentially (Alcock 2012) with this field contributing significantly toward our understanding of important topics in human health including immune function (Cooper and Herrin 2010; Litman and Cooper 2007), aging (Stearns et al. 2000; Stearns 1989), infectious disease (Ewald 1994; Schmid Hempel 2011), reproductive health (Trevathan 2011), behavioral and mental disorders (Keller and Nesse 2006; Nesse 1999), inflammation (Straub 2012), diet (Chakravarthy and Booth 2004), and cancer (Merlo et al. 2006).

History

Neese and Williams (Williams and Nesse 1991) are credited with bringing about a resurgence of interest in the field of evolutionary medicine through their now classic articulation of the key concepts covered by a “Darwinian” approach. However, the field of evolutionary medicine has a much longer and often forgotten history dating back to some of the earliest champions of the comparative approach (Trevathan et al. 2008). Aside from the seminal work of Charles Darwin, to whom we owe the foundations of our current understanding of evolution, one of the earliest proponents of evolutionary medicine was in fact Charles’s grandfather, Erasmus Darwin. Erasmus was one of the first physicians to think about the impact of nature on humans and published a taxonomic catalog of known diseases of his day, along with their causes and treatments (Darwin 1794–1796). In 1926, physician Dudley J. Morton expounded on Darwin’s views and stated that

diseases should be viewed through the lens of human variation and adaptation and that clinicians should aim to understand the evolutionary basis of adaptation to disease (Morton 1926). While these early calls to action linking evolution to medicine were somewhat forgotten in the early part of the twentieth century, what emerged from them was a growing interest in understanding human adaptations to particular environments and its impact on the underlying anatomy and physiology. By the middle of the twentieth century, this emerging research area was further enhanced by studies of sickle cell disease in various populations, demonstrating that variation in human hemoglobin structure was associated with immunity to the malaria parasite (Allison 1953, 1954; Barnicot, Ikin, and Mourant 1954). Furthermore, the impact of humans on the environment and our role in disease propagation was highlighted by further studies emerging from this field, highlighting the influence of human agriculture on the breeding behavior and distribution of the malarial parasite (Livingston 1958). In the later part of the twentieth century, questions in evolutionary medicine have extended upon these earlier themes to identify diseases of modernity (e.g., type 2 diabetes, hypertension, addiction) and their evolutionary origins as well as the role of human activities and industrialization in shaping disease progression (Trevathan 2010). Some of these topics include the appearance of novel metabolic processes such as lactose tolerance (Matthews et al. 2005), the genetic variations in the abilities of humans to process alcohol (Jornvall 1994), changes in the human skeleton (Schwidetsky 1962; Ruff 2002), changes in human body weight and height (Katmarzky and Leonard 1998), and changes in the size and number of human teeth (Brace et al. 1987). These and other microevolutionary changes to the human body likely resulted from environmental changes resulting from modern living (Ruhli and Henneberg 2013).

Fundamentals of Evolutionary Medicine

Before outlining some of the core principles of evolutionary medicine, it is important to remember the basic assumptions of Darwinian evolution and one of the auxiliary theories often used in

evolutionary medicine. In order for a feature to be considered Darwinian in nature, (1) the feature must exhibit variability in phenotype, (2) this variability must be heritable (i.e., transmitted from parents to offspring), and (3) the feature must exhibit selective fitness (i.e., impact species reproduction and/or survival to reproductive age) (Boyd and Silk 2009). The auxiliary theory often used in evolutionary medicine is that of life history theory which recognizes that the growth, maintenance, and reproduction of the organism is determined by the differential allocation of energy budgets which are themselves influenced by Darwinian processes (Stearns 1989). While the scope of evolutionary medicine covers all known areas of human disease, Neese and Williams (Williams and Nesse 1991) originally described five major categories of evolutionary explanation to which “Darwinian medicine” could be applied. Recently, using an expert consensus approach, the components of evolutionary medicine have been expanded to include a more extensive list of core principles, aimed not only at focusing the teaching of evolutionary medicine but also at guiding ongoing research in this field (Grunspan et al. 2018). Below, we briefly outline some of these core principles agreed upon by experts in the field.

Proximate vs Ultimate Causes and Host Defenses vs Pathogen Offences

One of the core principles of evolutionary medicine is distinguishing between the mechanistic (proximate) and evolutionary (ultimate) explanations for a disease (Grunspan et al. 2018). The difference between these two explanations is often conveyed as the dichotomy between the questions “what is the disease” or “how does it form” versus the question of “why the disease exists in the first place” (Spoceter and Strkalj 2007). Both mechanistic and evolutionary explanations are important to completing our understanding of the human body and disease vulnerability (Williams and Nesse 1991).

Building from this approach, it is also important to recognize that many signs and symptoms of disease may in fact form part of the body’s natural defense mechanism (Ewald 1980). From this perspective the protective nature of host

defenses, which include among other signs nausea, vomiting, pain, fatigue, and diarrhea, are distinguished from that of pathogen offenses (Williams and Nesse 1991). The challenge for the clinician is thus knowing when to interfere with these inherent host defenses as the cost of intervention while alleviating discomfort for the patient may result in the promotion of pathogen transmission and offenses. For example, studies of Shigellosis infection have demonstrated that diarrhea in these cases is in fact a host defense mechanism used by the body to reduce the contact time between the pathogen and the intestinal lining (DuPont and Hornick 1973). Thus, treatments which decrease the frequency and number of bowel movements (e.g., Lomotil therapy) are contraindicated in Shigellosis infection as they result in extended illness in the patient and are likely to contribute to the patient becoming a carrier of this infection (DuPont and Hornick 1973).

To think of it another way, one can consider this example as highlighting the importance of distinguishing between the immediate impact of a disease which is driven by the host defense response and its later impact which forms part of the pathogen offense. For example, a clinician might consider a fever as a (proximate) cause of an infection and in most cases would seek to treat this fever with fever-reducing drugs to spare the patient the immediate discomfort associated with the disease. However, several studies have shown that fever is a host defense mechanism and benefits the organism by decreasing viral replication rates in many pathogens while increasing the speed of immune reactions (Kluger 1979; Kluger et al. 1996). Thus, from an evolutionary medicine perspective, the reflex like tendency to administer fever-reducing drugs in most mild cases of fever is counterproductive as it diminishes the body’s natural ability to combat infection (Kluger and Rothenburg 1979). It is, however, important to note that an evolutionary medicine perspective does not advocate that fever-reducing drugs should not be used at all as there are particular cases as in a high fever where the impacts on the patient might exceed the limits of the immune response and thus intervention is necessary

(Trevathan et al. 2008). This is certainly the case for certain pathogens which are known to increase their reproductive fitness in response to fever (Ewald 1994). Another example of a host defense is the acute phase response, which results in a series of complex innate reactions shortly after tissue injury. As part of this defense mechanisms, there is the release of inflammatory cytokines (such as interleukin 6, tumor necrosis factor alpha, and interleukin 1 beta) which mediate the upregulation of acute phase protein, an important component of this systemic defense response, as well as several clinical signs which include fever, listlessness, and loss of appetite (Smith et al. 2013). The fact that these cytokines are found across vertebrate species suggests that the acute phase response is a universal defense mechanism shared by this group (Spocter and Strkalj 2007) and that the associated subcomponents to the response are likely to confer added defense to the organism (Weinberg 1984; Kluger and Rothenburg 1979; Hart 1985).

Sexual Selection and Reproductive Fitness

The scope of evolutionary medicine has grown to include the consideration of several important evolutionary processes. Among this wide range of processes, most experts in the field agree that this includes the classic Darwinian process of natural selection but also the consideration of genetic drift, mutation, migration, and non-random mating, all of which are important for our understanding of disease (Grunspan et al. 2018). In addition, the influence of sexual selection and reproductive success are also considered important concepts in understanding the origins of disease. For instance, the reproductive fitness of the organism could be favored by natural selection at the expense of health and longevity or could similarly decrease in response to other factors as argued for humans (e.g., Westendorp and Kirkwood 1998). In addition, the influence of sexual selection might also differentially impact health risks and outcomes in males and females (e.g., Janicke et al. 2016). Sexual selection is known to have a significant impact on the epidemiology of sexually transmitted diseases (STDs) (Janicke and Morrow 2019). Stronger

sexual selection in males results in males investing relatively more resources into mate acquisition at the expense of their own health and contributing toward riskier behavior in males (Zuk 2009).

Constraints, Trade-Offs, and Life History Theory

Several constraints might also prevent or inhibit the ability of natural selection to optimally shape human health and thus serve as an additional mechanism by which human susceptibility to disease might have evolved. These limits on natural selection include developmental, architectural, metabolic, or phylogenetic constraints (Spocter 2009) as well as trade-offs resulting from pleiotropy and mutations (Williams and Nesse 1991). For instance, one example of an architectural constraint known to have several clinical implications is the constraining influence of evolving bipedalism (Trevathan 2011). Humans are the only habitual mammalian biped, and those adaptations which make us uniquely suited to this form of locomotion have also made us susceptible to the occurrence of a range of clinical conditions including lower back pain and complications arising during childbirth (Spocter and Strkalj 2007). Furthermore, the evolution of bipedalism has also imposed constraints which have an impact on prenatal brain growth within the skull as the adult female is challenged with passing a relatively large head of a child through the relatively narrow pelvic outlet (Trevathan 2011).

Trade-offs in evolutionary medicine refer to the existence of linked changes between traits such that an evolutionary change increasing the fitness of one trait results in a decrease in fitness to another trait (Trevathan et al. 2008). In Neese and William (1991) articulation of Darwinian medicine, trade-offs were considered central to explaining disease vulnerability in evolutionary medicine and are intimately related to life history theory (Stearns 1989). Life history traits are shaped by natural selection and include traits such as the age of menarche and rate of senescence both of which have implications for human health and disease (Stearns 1989). In brief, one may understand the organizing principles of life

history theory as stressing that there is only a finite amount of energy available for an organism's growth, maintenance, and reproduction (Stearns 1989). Thus, the allocation of energy budgets to either corresponding life stages (e.g., gestation, weaning, lifespan) or growth within body components (e.g., body growth versus brain growth) requires trade-offs between components. For instance, energy spent on child rearing to maturity comes at a cost to energy that could have been used for reproduction, and in a similar way, energy spent on evolving a large brain (a metabolically expensive tissue) comes at the cost to free energy that might have been used for other organ systems such as the gut Aiello and Wheeler 1995).

Multiple Levels of Selection

Human vulnerability to disease may also result from the conflicting/opposing force of selection acting at different (or multiple) levels of organization (e.g., at the level of the molecule, gene, cell, organism, kin, or population) (Williams and Nesse 1991). Prime examples of this include genetic conflicts and somatic selection in cancer. For example, the differential interests of competing genes (or gene networks) in the human immune response could result in a myriad of genetic conflicts as the organism mounts a defense against an invading pathogen (Levin and Bull 1994). This conflict is a result of the complex and tiered arrangement of the host's defenses (Spocker and Strakalj 2007). Thus, understanding these complex interactions requires considering the differential impacts of selection at each level. Some postulate that sexual reproduction exists primarily to increase variability through rapid genetic change in response to the competing influence of pathogens (Hamilton et al. 1990). Similarly, it is argued that a genetic conflict between male and female gametes is responsible for the vast amount of sperm required for fertilization and the complexity of the female reproductive tract (Wedekind 1994).

Coevolution

Evolutionary medicine is also concerned with the influence of coevolution in driving health and

disease. Some examples include the establishment of an evolutionary arms race between a host and a pathogen (Ewald 1980), the establishment of symbiotic relationships such as those seen in the human gut microbiome (Williams and Nesse 1991), and the coevolutionary competition between bacteria resulting in antibiotic production (Davies and Davies 2010).

The effect of pathogens on the human body and their differing patterns of virulence (i.e., severity) have been the subject of much discussion in evolutionary medicine (e.g., Ewald 1980, 1988, and 1994). Society has become increasingly aware of differences in virulence between recent pathogenic threats (e.g., SARS-CoV2 versus Influenza A virus) and the importance of vaccination efforts and personal hygiene practices to ward off epidemic or pandemic spread (Ehret 2003). Some have argued quite cogently that the development of vaccines is an area in modern medicine which could benefit most strikingly if an evolutionary perspective is adopted (Read et al. 1999). Earlier arguments looking at the virulence of pathogens had supported the view that pathogens will naturally evolve toward less virulent states, a so-called equilibrium state, striking a balance between host survivability, transmission, and virulence (Levin and Svanborg-Eden 1990). Subsequent studies have shown that the concept of an equilibrium state falls short of describing all potential pathogen-host interactions and a richer view of virulence dynamics has emerged (Levin and Pimentel 1981; Frank 1996; Ebert 1999; Ebert and Bull 2003). Ewald (1980) has shown that the influence of "selfish gene" mutations in benign pathogens may still result in an increase in virulence provided that the rate of pathogen replication and transmission is increased. From an evolutionary perspective, transmission and replication of the pathogens genetic material is the most important consideration, not the state of its host, and thus host maintenance only becomes a consideration in cases where transmission is slow (Ewald 1980).

A further consideration in the evolution of virulence has been observation that some pathogens are able to effect host behavior to enhance transmission and that these pathogens tend to

progress toward greater states of virulence (Ewald 1988, 1994). While there are several striking examples of dramatic behavioral changes in hosts favoring pathogen transmission, such as the increased aggression and diminished fearlessness observed in hosts infected with rabies (Jackson 2016) or *Toxoplasma* (Berdy et al. 2000) and parasitic flukes (Wickler 1976), it is important to keep in mind that other more subtle changes in behavior may also help facilitate pathogen transmission. For example, while speculative, one might postulate that the relatively late onset of symptoms and the differential mortality in younger individuals as observed in the recent SARS-CoV2 pandemic might serve to enhance pathogen transmission, suggesting that this virus might continue to evolve toward increased virulence, impacting decisions on vaccine development. Mathematical modelling looking at the evolution of pathogen virulence has shown that vaccines that prevent infection may limit the virulence of the pathogen. However, those vaccines that only limit antitoxin immunity lead to increased prevalence and virulence (Gandon et al. 2001). In this regard, Read and colleagues (1991) have argued that rather than pursue the development of vaccines aimed at eliminating all forms/strains of a given virus, a more prudent and evolutionary informed approach would be to develop vaccines only against the most virulent strains of a virus, thus using mild forms of the virus as a means of conferring immunity. This approach is akin to that used in young children, where the child is infected with a mild strain of the virus through vaccination and from which subsequent immunity for all strains (including the more virulent ones) usually develops (Trevathan et al. 2008). Some argue that maintaining a coexistence with mild pathogenic strains is a more sustainable approach to vaccination, as a complete lack of exposure to a virus may leave a large sector of the population at risk to more virulent forms of a virus (Trevathan et al. 2008). It goes without saying that an awareness of host-pathogen interactions as viewed through the lens of evolutionary medicine is also critical to the way we address current or future healthcare crises both at the frontline as medical practitioners and biomedical

scientists but also as a global community, mindful of how our actions (or inaction) could promote pathogen transmission.

Evolutionary Mismatch/Adaptations to Novel Environments

For practitioners of evolutionary medicine, one particularly important source of disease is that which one might call “diseases of modernity.” These ailments, described as maladaptations, include diseases such as obesity, hypertension, type 2 diabetes, and back pain. It is hypothesized that these ailments arose as a result of a mismatch between the environments in which the human body evolved and that of our modern lifestyles to which our bodies have adapted to (Eaton et al. 1988; Eaton and Eaton 1991). Central to this hypothesis is the idea of an environment of evolutionary adaptiveness (i.e., an environment to which our bodies are most optimally adapted) (Irons 1998). Subsequent scientific discourse has seen the expansion of this idea away from the incorrect assumption that humans are optimally adapted to a single environment (e.g., a Paleolithic environment as initially proposed by Williams and Nesse 1991) and the acknowledgment that this mismatch may also result from migration between stable environments (Grunspan et al. 2018; Gluckman et al. 2016). The underlying principle is that there is a dichotomy between “past” and “present” such that our bodies (and minds) have not had enough time to adapt to our modern environments (Sharma 1998). For instance, one might consider obesity and its accompanying sequelae of hypertension and atherosclerosis as one example of a disease resulting from such an environmental mismatch. In comparison to Paleolithic communities, modern humans consume large amounts of sugars, salts, and fats (Eaton and Eaton 1991; Eaton et al. 1996; Nesse and Williams 1999), all of which were scarce and highly prized in Paleolithic communities but are relatively abundant in modern environments. Our brains, however, still perceive and process these stimuli as if we are in the Paleolithic, driving us toward acquiring larger quantities of these components to the detriment of our own health and exasperated by the reduction in

human activity levels. Another example of this type of maladaptation is that of human drug dependency (Lende 2008), with comparative genomic studies indicating an interesting overlap in genes involved in addiction propensity and human self-domestication (Calvey 2019). In addition, human sleep disorders may also result from our modern environments. In primate evolution, we observe a transition from that of arboreal sleep to the building of nests that would secure a more efficient and longer sleeping time to humans sleeping on the ground, enhanced by the discovery and control of fire conferring security to our hominin ancestors (Nunn et al. 2016). The advent of electricity and industrialization made a significant impact on human sleep pattern, and one may argue that the speed of technological evolution and impact on human societal behavior has outpaced the speed of human biological adaption, explaining some of the myriad of sleep disorders (Deboer 2020) and, more commonly, insufficient sleep time, with all the associated health consequences.

Plasticity and Cultural Practices

The impact of plasticity and cultural practices on human disease are two more recent additions to the field of evolutionary medicine. All organisms possess a general capacity for plasticity, for example, the phenotype of an organism may shift in the course of development as genes interact with varying environments (Lea et al. 2017). In evolutionary medicine, there is the acknowledgment that environmental factors may have an impact on human development resulting in changes to health and that plasticity itself is an adaptive mechanism under the influence of evolutionary processes (Lea et al. 2017; Grunspan et al. 2018). Especially important for evolutionary medicine are mechanisms that influence development in response to environmental cues detected during critical developmental periods (Lea et al. 2017). Cultural practices are also acknowledged to have a significant impact on human health and disease vulnerability. These cultural practices may influence evolution (e.g., of humans, pathogens, or other species within our environment) or influence medical practice (e.g., antibiotic, chemotherapy, or caesarean

section frequency within a given population) (Grunspan et al. 2018). In terms of evolutionary medicine, cultural practices are considered an important non-Darwinian (i.e., non-genetic) trait and along with other epigenetic factors (e.g., Handel and Ramagopalan 2010) influence human health and disease in a Lamarckian manner.

Conclusion

The field of evolutionary medicine has contributed significantly toward our understanding of disease etiology and the evolutionary origins of human susceptibility to disease. While this perspective continues to gain interest among specialists, especially biomedical scientists, it is hoped that a growing set of clinicians might use the insight gained from evolutionary medicine to better address the healthcare needs of the communities they serve.

Cross-References

- [Darwinian Medicine](#)
- [Darwinian Medicine and Survival Problems](#)
- [Evolution](#)
- [Evolutionary Clinical Psychology](#)
- [Life History Theory](#)
- [Trade-offs](#)

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Evolutionary Mismatch

- [Boredom as an Adaptation](#)
- [Darwinian Medicine](#)
- [Evolutionary Psychiatry](#)
- [Maladaptive By-Product Hypothesis](#)

- [Mismatch Between Evolved Morality and Modern World](#)
- [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- [Social Media](#)

Evolutionary Musicology

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Synonyms

[Biomusicology](#); [Evolution of music](#); [Music evolution](#)

Definition

Evolutionary musicology is a subdiscipline of biomusicology, the study of music from a biological perspective, which embeds the psychological and physiological mechanisms of human music perception and production in the theory of biological evolution. Evolutionary musicology studies the origin and evolution of music in the human species, encompassing vocal communication and musical behaviors in non-human animal species; behavioral, cognitive, and neurological development of musical processing and skill; cross-cultural human universals in musical capacity and cognitive processing; and archeological evidence to develop hypotheses concerning the evolution of human musical appreciation and music-making.

Introduction

Music is a pervasive, universal, and foundational feature of human social life. Although humans appear to be more attuned to the creation and appreciation of this phenomenon than any other

species, the social and biological function of human music has not been fully investigated (McDermott and Hauser 2005). Several scholars have suggested that musical appreciation is a by-product or side effect of properties of the auditory system that evolved for language, general hearing capacity, or other purposes unrelated to music (e.g., Pinker 1997). This view is known as the *byproduct hypothesis*. However, other scholars contend that music-making evolved for the function of social bonding, as human communities increased in size over the course of human evolution (Dunbar 2012; Fitch 2010; Oesch 2019). This view is known as the *social bonding hypothesis*. Although arguments have been made for both perspectives, there is considerable recent evidence in favor of the latter hypothesis. This work falls into three main areas of related research: (1) music and social bonding in non-human primates, (2) music and social bonding in human child development, and (3) music and social bonding in human social interactions.

On the Origins of Evolutionary Musicology

The origins of the field can be traced back as early to Charles Darwin, who first wrote in the *Descent of Man*:

We shall see that primeval man, or rather some early progenitor of man, probably first used his voice in producing true musical cadences, that is in singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes — would have expressed various emotions, such as love, jealousy, triumph — and would have served as a challenge to rivals. It is, therefore, probable that the imitation of musical cries by articulate sounds may have given rise to words expressive of various complex emotions. (Darwin 1871)

Curiously, this hypothesis of a “musilanguage,” sometimes referred to as a “musical protolanguage,” has been revived and re-discovered repeatedly, often without attribution to Darwin (Brown 2000; Geissmann 2002; Marler 2000). Musilanguage is a hypothetical form of

communication, possibly present in early human cultures, prior to the evolution of modern music and language (Brown 2000; Darwin 1871). The term *musilanguage* suggests a blurring of the distinction between modern human music and language; indeed, most hypotheses suggest that music and language probably co-evolved more or less simultaneously (Brown 2000; Morley 2013; Oesch 2019).

That said, there are challenges inherent in testing this hypothesis directly, as songs and other complex vocalizations do not fossilize or leave behind an archeological record. However, at least one plausible evolutionary trajectory (phylogeny) has been argued, based on modern primate communication systems. Several theorists speculate that the earliest phylogenetic step may have involved nonreferential emotional or mechanical primate signals (e.g., Watts 2016), which was followed by a rough *musilanguage* stage, possibly resembling extant gibbon calls (Brown 2000). Then, hominin song likely came next, developing into music made by primitive instruments and finally resulting in modern language (Dunbar 2012). A more informed view, however, suggests that a spectrum has always existed between music and language, contingent on the species and the ecological context, as the two phenomena coevolved (Morley 2013; Oesch 2019).

Current Competing Hypotheses for the Adaptive Significance of Musilanguage

While it is not fully understood how or why humans developed music or language, an influential proposal known as the *social bonding hypothesis* postulates that both served as adaptations for promoting social cohesion in groups of increasing size and social complexity over the course of human evolution (Dunbar 2012; Freeberg et al. 2012; Oesch 2019). Although other *musilanguage* proposals have been offered, most alternative explanations are at present rather speculative, with arguably less evidence in their favor than the social bonding hypothesis (for a review, see Oesch 2019). For instance, the *investment in*

learning hypothesis argues that individual differences in musical ability allowed for the socio-cultural assessment of biological fitness, as expressed in musical performance (Kirby 2012). More specifically, musical performance could reflect important underlying traits, such as superior cognitive and motor skills, as well as superior economic, temporal, and other resources, thereby providing a unique selective advantage in terms of increased reproductive opportunities. In other words, this hypothesis argues that music-making evolved to be a universal feature of human nature, as evidence of musical prowess was consistently attractive to prospective mates. However, there is currently little evidence for this proposal (Mosing et al. 2015), but see Madison et al. (2018), for a recent exception. An alternative explanation, often referred to as the *kin communication hypothesis*, claims that selection for language came from the benefit of the transmission of information between adults and their offspring (Fitch 2004). However, this proposal is also problematic, not least of which is the fact that both music-making and language are typically used or displayed between non-relatives. A third potential explanation, known as the *coalitional display hypothesis*, argues that human music evolved from animal territorial signals, which eventually became modified into a method of signaling a group's social cohesion to other groups, for the purposes of making beneficial multi-group alliances (Hagen and Bryant 2003). However, this explanation arguably puts the cart before the horse, as it fails to account for how cohesive groups became bonded in the first place, if not through music, language, laughter, and other factors which appear to promote social bonding. Moreover, this explanation also fails to account for why it was music that was critical for such displays, when grooming and spatial proximity appear to signal this information adequately in non-human primates (Keverne et al. 1989). In summary, all three of these proposals suffer from a number of important theoretical and empirical limitations and, at least in their present formulation, appear to be incomplete explanations for the evolution of music and language (Fitch 2013; Kirby 2012; Zawidzki 2006). That said, in the interest of an empirical

analysis based in comparative animal behavior, we now turn our focus to the presence of “musilanguage” in various extant species, as well as why we might be led to expect a common evolutionary origin and history for both music and language.

Music and Social Bonding in Non-human Primates

First, it is important to consider the development of music over evolutionary history. In non-human primate societies, social bonding is achieved through dyadic grooming, facilitated by endorphin-reward activation, as the physiological mechanism that motivates this behavior (Keverne et al. 1989). However, an emergent view suggests that many non-human primates may further supplement social grooming through song or other music-like behaviors, and the same may be true of humans, both in terms of music and endorphins (Oesch 2018, 2019). For instance, Dunbar (2012) has argued that once hominin group sizes became too large to be socially bonded using non-human primate strategies of social grooming alone, music emerged as a mechanism for facilitating social bonding.

Duetting, the most common method of group vocalizations in other animals, is typically described as coordinated song with overlapped phrasing, generally within a mated pair (Haimoff 1986). Duetting has only been documented in a few non-human primate species, particularly Old World primates including gibbons, spectral tarsiers, indri lemurs, and Mentawai langurs. Interestingly, nearly all known cases of duetting are found in the roughly 10% of primate species that are characterized by monogamous mated pairs (Haimoff 1986). In most species of gibbons, for instance, male-female pairs alternate their “songs” while duetting, albeit with significant synchronized phrasing, which appears to facilitate social bonding (Geissmann 2002). Pairs who produce the most highly synchronized duets typically allocate more grooming time, prioritize the same activities, and spend more time in proximity. As lesser apes, gibbons vary from the great apes –

including chimps, orangutans, bonobos, gorillas, and humans – by their monogamous behavior, owed in part to the protracted decade long period critical for child-rearing. Interestingly, the coordinated vocalizations of Mentawai langurs, Madagascan indri lemurs, and spectral tarsiers show a similar pattern, in the relationship between duetting and pair bonding. These primate behaviors are particularly relevant to the evolution of human music and language, given the human tendency toward serial social monogamy and biparental care and our proclivity for forming close non-familial bonds, necessary for bonding the largest societies of any living primate (Oesch 2018, 2019).

In addition, even among polygamous chimpanzees, the presence of pant-hoot chorusing (a form of synchronized sound-making) is generally indicative of the intention for short- and long-term social bonding that is typical of fission-fusion chimpanzee groupings. As in human music-making and conversation, gibbons, chimpanzees, and indris can adjust the pitch, unit duration, timing, and interval duration of their social vocalizations. The presence of chorusing, duetting, and similar calls in these species suggests a case of convergent primate evolution: adaptations to similar social organizations and ecological niches requiring group cohesion (Haimoff 1986). Additionally, duetting in other animals including dolphins, bats, elephants, whales, and naked mole-rats provides further support for music-making as a mechanism of social cohesion. For example, duetting is strikingly common in socially monogamous mated bird pairs; in fact, more than 90% of birds are socially monogamous, and roughly 40% or over 400 species exhibit duetting. Moreover, though original estimates implied an absence of vocal learning in non-human primates, more recent investigations appear to indicate the presence of limited and sometimes complete vocal learning in many non-human primates, suggesting further parallels to human speech and singing. In summary, a wealth of recent studies from comparative animal behavior suggests the origins and evolution of music may be explained in terms of social bonding (for a review, see Oesch 2019).

Music and Social Bonding in Human Child Development

Second, it is important to note the role of music in child development. For example, several developmental studies have shown that infants prefer consonant over dissonant melodies; in some cases, from as early as 2 months old, indicating the human preference for consonant melodies may be innate (e.g., Trainor et al. 2002). Several recent studies have further shown that synchronized action (i.e., behaviors of two or more people occurring at exactly the same time), including synchronized actions set to music, leads to directed helpfulness and cues of group membership. For example, in a study of 4-year-old children, subjects who swung together in synchrony in a swing seat were more altruistic toward their peers, compared to a baseline control condition (Rabinowitch and Meltzoff 2017). Similar results have also been found in infants who bounce in synchrony while held by an adult participant (Cirelli 2018). With respect to musical activities, previous studies have also revealed that singing to infants increases parent-to-infant bonding (Fancourt and Perkins 2018), while other studies have shown that synchronized singing and dancing increases prosocial behavior in 4-year-old children (Kirschner and Tomasello 2010).

Music and Social Bonding in Human Social Interactions

Third, it is important to consider the use of music in human social interactions. Previous research has shown that synchronized musical activities, such as communal singing (Pearce et al. 2015), dancing (Tarr et al. 2016), and drumming (Dunbar et al. 2012), promote social bonding and endorphin activation. Recent theoretical work further suggests this effect may also extend to coordinated action (i.e., behaviors of two or more people occurring in coordination with one another to produce something greater than the sum of the individual parts) music-making (Oesch 2019). In general, coordinated music-making is often standard for most forms of music-making in social

interactions; thus, this is an important area for further inquiry.

Moreover, these effects do not seem to be limited to active, interpersonal musical participation, as merely listening to music from a specific culture can often evoke implicit affiliation toward members of that culture more generally (Vuoskoski et al. 2017), showing that music can be an important part of personal identity formation (Hargreaves et al. 2002). In fact, just hearing music activates several motor areas in the brain (Grahn 2012), pointing to an important biological connection between music and movement, perhaps further suggesting an evolutionary link between music and dance. At present, however, it is poorly understood whether alternative forms of instrumental music-making also facilitate social cohesion, possibly due to the release of endorphins during these activities. An important aim of current research is to uncover whether other music-making tasks facilitate social cohesion, how such tasks compare to equally engaging non-musical social activities, and which aspects are most central for aiding this process, such as synchrony, coordination, rhythm, physical exertion, a steady beat, and endogenous opioids (Tarr et al. 2014).

Direct and Derived Functions of Human Music

Despite much suggestive evidence supporting the social bonding hypothesis, social cohesion is not necessarily the sole function of complex vocalizations, song, or music in humans or other animals. Most evolutionary biologists acknowledge a division between *ancestral* and *derived* traits or functions, also commonly called *direct* and *derived functions* in evolutionary musicology and linguistics parlance (Origg and Sperber 2000). The *direct function* refers to the ancestral adaptive purpose for which a trait has evolved in a particular species, while a *derived function* indicates the trait's co-option for any secondary purpose(s). In the case of music and language, several functions have been suggested, including sexual advertisement (Madison et al. 2018;

Oesch 2017), deception (Oesch 2016), and, of course, social bonding (Oesch 2018, 2019). All of these functions have some degree of empirical support, suggesting they may not be mutually exclusive. However, in comparison to other proposals, there appears to be the frequent and pervasive occurrence of musical and non-musical vocalizations, across a wide variety of taxa, for the function of social bonding. Therefore, it seems more plausible to posit an ancestral rather than derived social bonding function for many of these same vocalizations.

Conclusion

In summary, based on steadily increasing evidence, social cohesion may be the direct function for which music and language evolved. Cultural learning, signaling, sexual display, territorial advertisement and defense, and others are possibly derived functions, expressed in unique ways, contingent on the ecological circumstances.

Cross-References

- [Biomusicology](#)
- [Evolution of Music](#)
- [Music Evolution](#)
- [Musical Protolanguage](#)

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Evolutionary Neuroandrogenic Theory

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Definition

Theory that contends that men exhibit more deviancy and criminal behavior than women because of women’s preference for mates that either are able to or appear to provide resources.

Introduction

The evolutionary neuroandrogenic (ENA) theory provides fundamental explanation of the differences between genders in respect to cognition and behavior. This theory has two components; the genetic evolutionary factor which explains the why, and neurology and endocrinology factors which explain the how component. It describes how each sex contributes to the reproductive process and also examines the physiology of sexual differentiation. The theory states that gender differences in cognition and behavior stem from reproductive needs in response to natural selection (Ellis 2011).

Over the years, females have evolved the proclivity to form lasting sociosexual relations with males who are inclined to provide optimal resources. In this theory, it is assumed that females will reproduce more often in following generations if a mate is able to sustain and provide the resources that are needed (Ellis 2011). This does not imply that females who are self-sufficient will

not be able to reproduce successfully, but they will be unable to reproduce as prolifically as those who are able to depend on their mates for resources. Ellis (2011) also stated that populations of females with predisposed genetic biases for males with significant provisioning abilities will be favored by natural selection. The neuroandrogenic theory assumes that these biases may have resulted in the evolution of a broad array of cognitive and behavioral inclinations in males that differ significantly from those of females.

Although these hypotheses lack sufficient supporting evidence, two empirical studies supported the assumption that mate preference is genetically influenced. They additionally supported the premise that females have a higher preference than males do for mates with reliable financial prospects and a desire to make a living, in all cultures studied (Ellis 2011). On the other hand, it is said that males have reproductive options that stem further than adhering with female preferences for loyalty and resource procuring competence. These preferences derive from the evidence that commitment of energy along with the time consumption it takes to reproduce is less crucial for males than it is for females (Johnstone et al. 1996). No correlation between a male's wealth or procuring capabilities and his mate's fertility has been made evident due to the differences between genders.

It is to be noted that several factors will be needed in order to reproduction to be successful. For instance, when it comes to males, fertility can be boosted by having multiple sexual relations. This rarely influences the reproductive success of both sexes. Researchers have also argued that women should evaluate their options "long-term sociosexual alliances" when it comes to solely depending on males provisioning against the likelihood of abandonment after she has provided offspring. Females would be most likely well off with a mate who can moderately provide resources but will be loyal rather than one who is not (Ellis 2011).

The evolutionary neuroandrogenic theory also assumes that there has been an evolution of genetic variants in males, which has led them to respond to female biases toward males who can

proficiently provide resources. It is said that some males have alleles that persuade them to adhere to these biases while other males are genetically predisposed to respond in a deceptive way. ENA theory proposes that there are two functional differences responsible for most differences between genders. One being suboptimal arousal, and the other a right shift in neocortical functioning (Ellis 2011).

Suboptimal arousal determines how quickly people grow weary of stable environmental surroundings. It is hypothesized that when a person is exposed to high levels of androgens the brain satiates on stable conditions more rapidly, a mental state which is referred to as suboptimal arousal. Due to this, those with high androgenized brains seek fewer familiar surroundings, although it may in turn result in discomfort or punishment (Ellis 2011). The function of arousal is regulated by the reticular formation which interacts with both the limbic and prefrontal brain structures.

Rightward shift in neocortical functioning is the hypothesized change in the brain which results from high exposure to androgens, which are male hormones. According to research, it is known that for most individuals, the left hemisphere is more dominant than the right. When males were compared to females, males showed less of a left-dominant tendency than do females (Ellis 2011). It is said that in males, the two hemispheres tend to operate more individually and independently on tasks than females. These minor but significant gender differences in neocortical functioning compose what is known as rightward shift.

This theory also predicts that males will tend to engage in more sexual activity than females. This supports the evolutionary theory that males have the ability to reproduce faster than females by simply having multiple partners. Because of this, males have a greater desire for sexual relations since it will provide a variety of sexual experiences. It is said that gender differences in cognition and behavior between sexes will be small, and due to social learning, attenuation can occur many of these differences (Ellis 2011). The theory predicts that differences between genders derive from reproductive needs that females prefer mates who will provide adequate resources and loyalty.

Several researchers have also discovered that in broad variations of social circumstances, smiling occurs more frequently in females rather than males (Ellis 2006). Articles found offer theoretical reasoning for these differences based on the argument that testosterone as well as other sex hormones have evolved the habit to change brain functioning in a way that hinder males from smiling. This inhibition is seen during phases in their lives in which they are most reproductively active. The theory also assumes that females have been naturally selected to favor males who offer the ability to aid in long-term child bearing when choosing a mate. The focus of this is primarily being able to provide resources. It is also stated that males partly accommodate to this preference by battling with competing males who are also vying for resources, which they will use to attract females. In addition, male smiling is stated to hinder their ability to effectively intimidate their rivals in such situations.

If this theory is equitable, this would mean that genes are involved in promoting the propensity to compete for resources. The Y-chromosome is said to be the location responsible for this (Ellis 2006). As stated previously, these genes are said to operate in part by constraining social signals of fear and submissiveness.

The ENA theory also argues that testosterone alters brain function in a way that shifts the neocortex further from the left hemisphere, which is responsible for prosocial behaviors and friendliness. Due to this shift, the right hemisphere supersedes control, resulting in less social behaviors. Testosterone also seems to affect the dopaminergic and serotonergic system. This type of activity has demonstrated the enhancement of a person's willingness to engage in risky behaviors and also tolerate pain while doing so. This means, dopamine activity is more likely to promote criminality and any other forms of competitiveness in order to obtain resources. Serotonin is also said to be involved with criminality, because low levels of serotonin seem to be correlated with increased criminality due to impaction symptoms of mental illness, for instance, depression (Hoskin and Ellis 2014).

Another theory stemming from ENA theory is the theory of criminal and antisocial behavior and

the effects that androgens have on brain changes, specifically in the subcortical and neocortical regions of the brain (Ellis 2005). Due to females evolving preferences for mates who are or show to be more adequate to provide resources, males have evolved to accommodate this preference by producing higher levels of androgens to enhance this competitiveness (Ellis and Hoskin 2015). The theory claims that since androgens have evolved, these changes evoke in the brain and increases the probability of criminal behavior. This is said to be especially true in those who have been violent in the past or have victimizing types of offenses. ENA theory states that androgen-influenced bodily traits along with muscularity are correlated with criminality specifically offenses that are from a victimizing or violent nature. If this theory was proven to be true, it would mean that higher crime rates will be seen in males as opposed to females.

This theory was tested with a large sample of college students in North America. In the study, as hypothesized, males were seen more involved in crimes than were females. Within both genders, many minor but significant positive correlations were discovered between self-reported criminality and androgen-promoted physiological characteristics. It was noted that self-reported criminality was positively correlated with sex drive, physical strength, body appearance, and masculine mannerisms. There was also a positive correlation with low-deep voice, upper body and lower body strength, and amount of body hair. The regression in males showed that it is possible to statistically eradicate the sex differences in violent crime by including the androgen-promoted physiological traits in the prediction equation (Ellis et al. 2008).

This theory ties into the idea that males have been selected for distinctly competing behaviors and victimization of others because generally speaking doing so would assist them in acquiring the resources needed to ultimately attract mates. It is asserted that criminality is an unrefined form for competitive behavior in order to provide resources, assert status, and gain mating opportunities (Ellis and Hoskin 2015). The neuroandrogenic theory claims that exposure to testosterone along with other androgens is an

important contributor for victimizing behavior. This could be in either the shape of simple business competition or criminality. For instance, this can be seen in everyday business exchanges of services or goods. Criminality would be examples of robbery or assaults which would lead the male to obtain resources (Hoskin and Ellis 2014). From a physiological perspective, the ENA theory states that males are more likely than females to victimize others due to the exposure in their brains to increased levels of testosterone and other androgens (Ellis et al. 2007).

Family factors can also influence one's participation in criminality. The entire nature and extent of the actual influences are uncertain. During the last couple of years, testosterone has been determined a strong contributor to offending in those within their adolescent years. One study conducted by Ellis, sought out to resolve whether two imperative familiar factors are in fact, interacting with testosterone. The two factors that were researched discussed the relationship between amicable parent-child relationships and parental socioeconomic status. These factors are thought to interact with testosterone and perhaps other androgens to influence the likelihood of delinquency (Ellis and Das 2012). Another study looked at self-reported instances of involvement in eight different categories of delinquency in college students in North America. It also looked at the various androgen-related traits such as muscularity and low-deep voice. It took into account the nature of parent-child relationships and parents' social status. Within both sexes, the relationship between androgens and parent-child relations were significantly associated with delinquency. It is important to note that parent social status was not a significant variable. According to the findings, the nature of the parent-child relationship had an effect on delinquency rates (Ellis and Das 2012).

Conclusion

Overall, the neuroandrogenic theory proposes almost all individuals have evolved the propensity to openly compete while searching for resources

and opportunities to mate. This is mostly seen in males due to them being greatly motivated in this regard (Hoskin and Ellis 2014). Females have been stated to have evolved the proclivity to choose males who will be able to provide resources successfully and have the ability to remain loyal, which in turn may reinforce males for displays of control and power that may include deviancy.

Cross-References

- [Female Mate Choice](#)
- [Intrasexual Rivalry Among Men](#)
- [Sexual Selection](#)
- [Survival and Reproduction](#)

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Evolutionary Paradox: Adoption

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Synonyms

Adoption; Altruism; Evolution; Parenting benefits; Parenting costs; Parenting

Definition

Adoption is generally described as permanently caring for biologically unrelated offspring.

Introduction

Studying adoption practices across cultures and species provides important information regarding general parenting behaviors as adoptive parents, unlike biological parents, do not receive the same evolutionary benefits of parenting as biological parents. Parental investment theory suggests that the high physical, somatic, and social costs of investing in an offspring may be compensated by investing in a genetically related offspring, who can increase parents' genetic fitness (Trivers 1972). Based on this theory, adoptive parents are inevitably missing out on an important evolutionary benefit of parenting, which is maximizing their genetic fitness, while still incurring the high evolutionary costs of parenting. Yet, adoptive behaviors have been found in over 120 species of mammals and birds (Riedman 1982). In fact, there is evidence that parents from one species sometimes adopt offspring from genetically unrelated species (Hrdy 1999). In humans, adoption has been recorded throughout history (e.g., Moses was adopted by Pharaoh's daughter in the bible, and Augustus was adopted by Julius Caesar in Roman history) (Burguiere et al. 1996) and is still prevalent today as approximately 2–2.5% of

children are adopted in the USA each year (Tan et al. 2015). If parenting theories suggest that adoptive parents cannot increase their genetic fitness by investing in adopted children, why are adoptive behaviors still prevalent across cultures and species?

Evolutionary theories provide an explanation by suggesting that adoption may be a form of altruistic behavior. However, this explanation has faced some criticism as some researchers have associated altruistic behaviors with genetic relatedness. For example, Hamilton's (1964) theory of kin selection highlights the importance of genetic relatedness in influencing altruistic behaviors due to the benefit of increasing the frequency of shared genetics in a given gene pool. According to this theory, altruistic behaviors may not have evolved without genetic relatedness. However, Trivers (1971) argued that altruism cannot exist between genetically related organisms and that the cooperative behavior seen between genetically related organisms are rather mechanisms to increase genetic fitness, rather than altruism. Therefore, Trivers defined altruism as cooperative behavior that benefits a genetically unrelated recipient while being costly for the organism performing the behavior. This is adaptive because it benefits the organism performing the behavior in the long run as the recipient of the behavior may return the altruistic act at a later time, known as reciprocal altruism. However, other researchers have suggested that reciprocal altruism may be applied to closely related organisms as there is evidence that even close kin expect reciprocity (Terrell and Modell 1994).

In order for a behavior to be considered a form of altruism, it may be required to meet the following criteria. One of the criteria is that the cost of the altruistic behavior for the organism performing the behavior is relatively small compared to the benefit for the recipient (Trivers 1971). Another criterion is that the cost for the benefactor should still be generally high, so that the altruistic act will have a higher chance of being reciprocated (Tesser et al. 1968). Finally, fundamental evolutionary theories suggest that certain behaviors will

become adaptive if the benefits of those behaviors outweigh the costs based on the organism's life-history features, demographic, and ecological conditions. Therefore, in order to understand adoption practices, it is important to outline the evolutionary motivations behind this behavior by investigating whether or not adoptive behaviors may be driven by altruism according to Trivers' definition.

Before delving into further discussion of adoption, it is important to highlight the difference between adoption and other forms of (non-biological) parental caregiving, such as fosterage and alloparenting. Adoption is generally defined as providing permanent care for genetically unrelated offspring (Terrell and Modell 1994). However, as outlined in the following sections, this definition may not be as stringent across cultures. Fosterage differs from adoption in that it is providing temporary care for genetically unrelated offspring (Volk 2011) although it may be viewed as adoption in some cultures (see below). Finally, alloparenting is when individuals other than the biological parents provide care for the offspring, usually in conjunction with the biological parents (Hrdy 1999). Throughout this chapter, the term adoption is intended as the abovementioned operational definition and will be specified if used otherwise.

In order to understand the motivations of adoptive behaviors and investigate their connection to altruism, the following sections outline some of the key costs and benefits of adoption for the main people involved in this process: adoptive parents, biological parents, and adopted children.

Benefits of Adoption

Benefits for Adoptive Parents: Even though adoptive parents are unable to maximize their genetic fitness, they may acquire other benefits which may explain the prevalence of adoption practices today. First, adoptive parents may be benefiting from filling the void of providing care for biological offspring (Hamilton et al. 2007). Evolutionary theories suggest that some human behaviors may

be adaptive, not due to the behavior itself but rather because they are derivatives of other important behaviors (Hamilton et al. 2007). Thus, the caregiving behaviors seen in adoptive parents toward adopted children may be one such derivative. As ancestral humans frequently lived in close-knit groups where they provided care for genetically unrelated children, adoptive parents today (who usually adopt children due to an inability to produce biological offspring; Riedman 1982) may be predisposed with this "baby lust" (Hrdy 1999), which describes the desire to show parenting behaviors even toward genetically unrelated children. Consequently, adoptive parents may be receiving psychological benefits of love and happiness from raising a child (Volk 2011).

A second benefit for some adoptive parents may be increasing their genetic fitness by adopting children within the kin as form of kin selection (Hamilton 1964). Adoptive parents in most modern western countries are shown to adopt kin more often than non-kin in cases where the biological parents are deceased, have a lack of resources to provide for the child, or are neglectful toward the child (Volk 2011). In addition, when biological parents decide to give up their child for adoption, they are shown to prefer kin, rather than non-kin, to adopt their child with the notion that genetic relatives will provide better care for the child. This is seen in various cultures including the Kiribati of the Gilbert Island, West Africa, Brazil, and Peru (Volk 2011). In addition, transgendered uncles in Samoa, known as *fa'afafin*, are shown to provide alloparental care to kin (VanderLaan et al. 2015). Although this is not strictly adoption by definition, the predisposed motivation behind this behavior is noteworthy. VanderLaan and colleagues suggest one explanation for the increased caregiving behavior toward niece and nephews seen by the *fa'afafin* is adaptive as it may be the only opportunity for the *fa'afafin* to maximize their genetic fitness.

However, there are many instances where parents with biological children choose to adopt additional children. For example, adoption in Inuit societies frequently occurs when biological parents want to abandon or kill their infants (usually

due to less resources), but do not do so due to other members of the community who volunteer to adopt the child, even if they have their own biological children (Terrell and Modell 1994). In addition, in African-American communities, families usually have a biological and a social father, where the social father is sometimes seen as more important to the child compared to the biological father (Furstenberg 1995). In these cases, it may be other benefits that are driving caregiving behaviors in adoptive families, such as of gaining economic resources and social networking.

Therefore, a third benefit for adoptive parents may be increased economic resources through the adopted children. This is theorized to be the most common reason for adoption in ancestral humans (Volk 2011). Adoptive parents can receive direct economic resources from the adopted children when the adopted children serve as future providers and/or workers for the family. For example, adopted children among the Baatombu of West Africa (Silk 1987) and in Wogeo (Volk 2011) serve as extra manpower for cheap labor and kin support. Also, among the Yupka of South America and the Yap in Micronesia, parents most often adopt children in order to provide care and support to the elderly (Volk 2011). Similarly, children on the Mandok Island of Papua New Guinea are adopted with the purpose of providing economic resources for the adoptive parents when they are older (Terrell and Modell 1994). Adoptive parents can also increase their economic resources indirectly by forming alliances with the biological parents of the adopted child. For example, adopting children among wealthy families in Britain and Ireland has been shown to be a method of securing political links (Volk 2011). Similarly, among the Yap, adoption is used to trade or access land. In addition, adoption may also be used to transfer familial dynasty in the absence of biological children in various cultures (Volk 2011).

A fourth benefit for adoptive parents may be the opportunity for social networking by forming and strengthening social bonds with the biological parents of the adopted child (Volk 2011). In Oceanic societies, such as Hawaii, adoption is relatively more common in comparison to Western societies and is a method to adjust for the large

family sizes and low economic resources (Silk 1980). Adopting a child from another family in these cultures establishes friendships and creates social networks. However, unlike most Western adoptions, the adopted children in Oceanic societies continue to maintain emotional bonds with their biological parents, possibly so that the biological parents can ensure that their children and receiving adequate care as adopted children may not always be treated well by the adoptive parents (Silk 1980). Adoptive parents may also benefit from social networking by using adoption to resolve conflicts. For example, Roman kings adopted princes from other countries in order to resolve conflicts and form political alliances with other countries. Similarly, parents in the Wogeo adopt children as a form of settlement with the notion that an individual is less likely to attack you if you are caring for his biological child. Adoption can also increase social networking by securing brides for the biological sons. For example, one of the most common reasons couples in China adopted a girl was so that their infant or future sons could marry her (Johnson 2004). In addition, older men among the Yupka adopt girls in order to marry them once they reach puberty (Volk 2011).

Fifth, adoption practices may help with the transmission of social learning. This may not be directly adaptive for the adoptive parent. However, it may benefit the parents' genetic fitness. In most mammals and birds, parents are shown to transfer decision-making strategies related to mate preference, predator avoidance, and food preferences to their offspring (Avital et al. 1998). This is especially adaptive for the genetic relatives if the parent has a socially transmittable trait that is unique from the general population as parents can transmit these socially transmittable traits to other members of their close-knit community and consequently increase the kin's survival rates, along with the parents' genetic fitness. The transmission of these traits can be amplified by transferring them to biological offspring, as well as adopted offspring (Avital et al. 1998). This behavior is seen in the communal caregiving observed in cats and mice, where when the biological parent is killed or injured, an adoptive parent replaces the

biological parent in order to increase chances of the litter's survival. The young in the litter consequently learn this behavior and transfer it to their future adopted and biological young. Although, there is less research on how this theory may be applicable to humans, the practice of adoption itself has been theorized to be spread through the transmission of such social learning practices (Avital et al. 1998).

Benefits for Adopted Children: In addition to benefits for the adoptive parents, adoption may also have benefits for adopted children. The most important benefit for adoptive children may be increasing their chance of survival in the absence of care from their biological parents (Avital et al. 1998). This is especially important when the children are young and require adult care to reduce risks for mortality (Volk and Atkinson 2013). Moreover, adopted children usually have better chances of growth, development, and survival in the care of adopted parents compared to their biological parents as adoptive parents in typical Western societies are relatively young (30–40 years), educated, and wealthy (Volk 2011), while biological parents that give up their children for adoption usually have less resources to provide for the offspring (Brannan and Gillet 2005). In fact, it is suggested that adopted children may seek out adoptive parents who have relatively more resources compared to their birth parents (van Ijzendoorn and Juffer, 2006). For example, children in adoption agencies have shown to influence the choices of potential adoptive parents by acting more friendly with those they wanted to be adopted by and more violently toward those they did not want to be adopted by.

Benefits for Biological Parents: Adoption would not exist if biological parents did not give up their children for adoption (with the exception of cases where the biological parent dies or children are stolen from biological parents; Hrdy 1999). However, why would parents give up the opportunity to maximize their genetic fitness by abandoning their offspring? One explanation is because biological parents benefit from receiving free care for their offspring while increasing their own genetic fitness (Volk 2011). For example, majority of children who are given up for adoption

are shown to be from unmarried mothers with less social and economic resources (Brannan and Gillet 2005). In addition, poor families in Huan Warle, Jamaica, and Claudia Fonseca in Brazil give up their children for adoption due to the inability to provide for them (Reidman 1982). Further, adoptive parents may sometimes provide financial compensation to the biological parents in exchanged for their child (Volk 2011).

Another benefit for biological parents may be freeing up time, energy, and resources to produce and invest in another offspring (Volk 2011). This is an evolutionarily better alternative compared to killing the infant due to the inability to provide for the infant and the infants' perceived low chance of survival (Brannan and Gillet 2005). By having the adoptive parents care for the offspring, biological parents are increasing their genetic fitness by ensuring the survival of two or more offspring while only investing in one. This theory is supported by traditional cultures in the Western Caroline Islands who are shown to give up their biological children to be raised by others in order to have increased availability of resources to invest in their remaining biological children (Volk 2011).

Adoption also comes with the following costs for the adoptive parents, biological parents, and adopted children.

Costs of Adoption

Costs for Adoptive Parents: An evolutionary cost for adoptive parents is investing time, energy, and resources in a genetically unrelated offspring without increasing their genetic fitness (Trivers 1972). From an evolutionary perspective, this is the most substantial cost for an organism. Another cost for adoptive parents is making an increased effort of creating a parent-child relationship due to the lack of genetic relationship, which may deplete energy, time, and resources that can be conserved for other vital functions. Further, adoptive parents also face the possibility of the adopted child seeking to connect with his/her biological parents and eventually deserting the adoptive parents (Volk 2011). In this situation, adoptive

parents lose any social benefits that they could have acquired from the adopted child. As a result, the abandonment of the adopted child may cause emotional grief for the adoptive parents. Possibly for this reason, many adoption agencies follow closed adoption practices (Volk 2011).

Costs for Biological Parents: The evolutionary costs for biological parents may be risking improper care of their offspring by the adoptive parents. In nonhuman animals, a biological mother may immediately take back her offspring if they are inadequately cared for by the adoptive parent (Hrdy 1999). Due to this risk, biological mothers among the Massai in Kenya, who are sometimes required to give up their biological baby to an infertile woman within the kin, are shown to strongly protest against this practice (Volk 2011). In addition, Brazilian mothers who unknowingly gave up their infants for adoption are shown to still experience grief and sadness due to the inability to retrieve their children. Therefore, the separation from biological offspring may have emotional costs for parents as it may create feelings of loss and void, which can sometimes lead to long-term depression (Brodzinsky 1990).

Costs for Adopted Children: A social cost for adopted children is being cut off from the biological parents, which may elicit perceptions of lost identity (Brodzinsky 1990). Adopted children in international and transracial adoptions may also lose touch with their cultural roots when adopted by parents with different cultural backgrounds (Terrell and Modell 1994). In addition, in families that consist of both biological and adopted children, the adopted child may feel secondary to the biological child (Silk 1980). For example, studies have found that sibling comparisons between the adopted and biological children may result in feelings of jealousy and/or envy for the adopted child (Brodzinsky 1990).

Is Adoption a Form of Altruism?

Based on this brief list of the costs and benefits for adoptive parents, biological parents, and adoptive children, it can be argued that adoption is indeed a form of altruism. First, it can be suggested that

adoption is a form of altruism because the cost for the adoptive parents (inability to maximize genetic fitness, depletion of resources in creating a parent-child relationship, and potential abandonment by the adopted child) is relatively minor compared to the collective benefits for the adoptive child (maximizing the child's survival and genetic fitness) and his/her biological parents (maximizing genetic fitness). In addition, the altruistic behavior by the adoptive parents may also have a high chance of being reciprocated by the adopted child as the costs for the adoptive parents are generally high. Finally, based on adoptive parents' greater ability to provide for the adopted child (relatively more resources and maturity compared to the biological parents), the benefits of the adoption may outweigh the costs for adoptive parents.

However, while the evidence above suggests that adoption may be a form of altruism, there is also evidence which suggests otherwise. Most parenting behaviors are shown to be instinctive across species (Hrdy 1999). For example, first-time mother mice that do not have any previous parental experience are shown to instinctively clean the embryonic fluid, eat the placenta, and lick the pups (which helps to facilitate the pups' healthy development) after giving birth. This instinctive behavior is theorized to be associated with increased levels of oxytocin in the mother mice right after giving birth. Similarly, in humans, high levels of oxytocin, along with other pregnancy-related hormones, are found in new parents, which is theorized to increase caregiving behaviors (Champagne 2008). However, adoptive parents do not have such pregnancy-related hormones to trigger caregiving behavior. So how are adoptive parents able to show good parenting behaviors? One explanation is that since adoptive parents face much stigma (see below), they may be compensating for it by trying to prove that they are good parents (Volk 2011). Another reason could be due to the long administrative process of completing the adoption process, which may psychologically commit adoptive parents to create a long-lasting family (Volk 2011). While these social factors may be influencing the positive caregiving in adoptive parents, another possibility

is that adoptive parents are influenced by forced perceptions of genetic relatedness.

Forced Perceptions of Genetic Relatedness

Forced perceptions of genetic relatedness seen in the adoption process may be one argument against adoption being a form of altruism. There is evidence that various mechanisms may simulate genetic relatedness between adoptive parents and adopted children. One mechanism may be kinning (see chapter ► [“Paternity Uncertainty and Investment in Sons and Daughters”](#)), in which adoptive parents make an increased effort, more than biological parents, to explicitly and frequently expose the adopted child to members of the immediate and extended family in order to increase emotional bonding and perceptions of relatedness. This increased exposure may also influence stronger perceptions of resemblance and kinship (Volk and Atkinson 2013). If adoption is unrelated to altruism, this behavior may be risky as adopted children could face mistreatment and abuse from adoptive parents due to the lack of genetic relationship (Daly and Wilson 1996). In fact, it is theorized that this risk may be increased when a child does not resemble his/her adoptive parents (Terrell and Modell 1994). Therefore, facial resemblance between the adoptive parents and the adopted child may be another mechanism that simulates perceptions of genetic relatedness and consequently influences motivation for caregiving behaviors (see chapter ► [“Resemblance”](#)). For example, studies have found that hypothetical adoption ratings are correlated with high levels of facial resemblance between the adult and child, especially for men (Volk and Quinsey 2002). In addition, practical studies on parenting have found that fathers invest more in children with high levels of facial resemblance (see chapter ► [“Paternity Uncertainty and Investment in Sons and Daughters”](#)). Further, adoption agencies are found to match the adopted children with adoptive parents based on the degree of facial resemblance between the adopted child and adoptive parents (see chapter ► [“Paternity Uncertainty and Investment in Sons and Daughters”](#)).

Other facial cues in children may also be influential in parents' adoption decisions, such as age and health. With regards to age, adults are shown to have a general preference to adopt younger children. Indeed, studies show that approximately 84% of unrelated adopted children are under 11 months old (Brannan and Gillet 2005). Hrdy (1999) suggests this to be the result of vulnerability seen in the infantile facial cues in young children which influences adults to be attracted to and care for young children. Additionally, social perspectives suggest that preference for younger adopted children may also be associated with younger children being easier to assimilate into the family as older children may come with previous life experiences which may be challenging to form parent-child attachments (Brodzinsky et al. 1995).

However, infants have higher changes of mortality compared to older children (Volk and Atkinson 2013). Therefore, the predisposition to invest in the youngest children may be overpowered by cues of good health. Studies show that adoptive parents frequently review the adopted child's medical history, especially during international adoptions (Volk 2011). Moreover, a photograph of the child is sometimes analyzed by medical professionals to assess the adopted child's health (Volk 2011). Assessing children's health through facial cues is also shown to be used during hypothetical adoption decisions (Volk and Quinsey 2002). In these studies, children with normal body weight are shown to receive higher hypothetical adoption ratings compared to children with lower and/or higher than average body weight. Possible explanations for this could be that children born with extremely low body weight may be associated with health problems such as difficulty gaining adequate weight when older. Similarly, children who are above average in weight are also at risk for health problems such as gallstones and hepatitis (Whitlock et al. 2005). In addition to body weight, abnormal facial features are also shown to negatively influence hypothetical adoption ratings (Waller et al. 2004) and possible explanations for infant abandonment. This may be because abnormal facial features may be a proxy for low genetic fitness.

Conclusion

The goal of this chapter was to determine whether or not adoption may be a form of altruism according to Trivers' (1971) definition of altruism. Although some evidence suggests that adoption maybe a form of altruism, there is also evidence to the support the argument that adoption may not be a form of altruism and may rather be driven by forced perceptions of genetic relatedness. Although inconclusive with regard to the relationship between adoption and altruism, the evidence presented in this chapter suggests that adoption may be a multiply determined construct, as is general parenting, and thus may be motivated by various (altruistic and non-altruistic) factors (Bjorklund and Pellegrini 2000). This chapter also depicts that even though there is much evidence that adoptive parents are just as capable of providing care for adopted children as biological parents are, adoption is still viewed in a negative light.

Even though the percentage of adoption rates continues to increase (Tan et al. 2015), there is a general negative stigma associated with adoption, such as perceptions of adoption being second best to biological families (Terrell and Modell 1994). One reason may be that because parents usually adopt children due to an inability to produce biological children (Volk 2011), adoption may be associated with infertility, which is looked down upon in various cultures. For example, in India, adoption is shown to be a last resort and may only be acceptable when fertile couples adopt children in addition to their biological children (Bharadwaj 2003). In addition, some parts of Egypt have strict prohibition laws against any form of adoption (Inhorn 1996). Another reason may be that these negative perceptions may be stemming from historical stigmatizations of mothers who had children out of wedlock (Volk 2011).

The negative stigma associated with adoption is also reflected in the terminology around adoption, such as real parents vs. adoptive parents (Hamilton et al. 2007). In addition, adoptive parents are perceived to be inadequate parents and consequently have lower levels of self-esteem regarding in their parenting skills. Further, it is assumed that adopted children have less healthy

hereditary genes compared to biological children. Finally, even most researchers studying adopted children most often take a negative view of adoption such as studying the mental health problems of adoptees and risks for adopted children (Hamilton et al. 2007).

This negative stigma associated with adoption may be due to the relatively less research on this adoption in comparison to alternate forms of family structures (Hamilton et al. 2007). Therefore, in order to further understand adoption and help reduce the stigma associated with this form of parenting, more studies need to focus on the positive aspects of adoption. For example, future studies should explore adoption practices across in more cultures in order to gain a deeper understanding of adoption and general parenting motivations. In addition, future studies should investigate the relevance of certain adoption theories, such as transmission of social learning, in humans by investigating if adopted children are more likely to be adoptive parents themselves and the forms of social traits that may be transmitted through adoption in humans. Finally, more studies should study adoption from an evolutionary perspective as evolutionary theories help understand the adaptive responses of adoptive practices (Bjorklund and Pellegrini 2000).

Cross-References

- [Adoption Preferences](#)
- [Consolidating Familial Power](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)
- [Resemblance](#)

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Evolutionary Paradox: Women Choosing Not to Have Children

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Synonyms

Childless women; Evolutionary contradiction;
Reproductive fitness

Definition

The catalyst for evolution is the propagation of one's genes. In modern times, women are choosing to have less or no offspring, which is seemingly an evolutionary paradox.

Introduction

Females are the choosier sex in almost every species. In modern times, the argument could be made that as a result of more women obtaining college degrees and high-paying jobs, less high mate value males exist (Buss 2016). As a result, human females are having to choose whether to copulate with lower mate value men or whether to take themselves out of the mating game entirely. With mortality rates at an all-time low and economic stress at high, parents may also be choosing to invest more resources in fewer offspring. Additionally, with the advent of modern birth control, women can have sex without the consequence of pregnancy. While the drive for sex still exists, the consequences are more variable, giving women a choice they have never had before.

Reproductive Fitness

When it comes to choosing a mate, women are often much choosier than are men. This is a result of women's greater initial investment in reproduction (Trivers 1972). This difference begins at the basic level of sex cell size. Women's sex cells are larger and packed with nutrients and are in fixed and non-replenishable supply. Men's sex cells are much smaller and replenish at about a rate of 12 million per hour. Additionally, women's greater investment continues with 9 months of gestation, followed by lactation, and several years of caring for their offspring which may close off any possibility of other mating options. Men's investment, however, can end with fertilization, opening them up to other mating opportunities immediately. As a result of this great disparity in initial parental investment, women are valuable and will not allocate their reproductive resources indiscriminately (Buss 2016; Trivers 1972).

Female reproductive opportunities are also limited as it takes 9 months to have at least one child, and a woman can only have a limited number of children as she has a limited number of eggs. In contrast, males' reproductive opportunities can be fruitful and are dependent on

available and willing fertile females. Ancestral women who were indiscriminate about mates would have experienced lower reproductive success and therefore would have had less children survive to reproduce. As a result of the sex discrepancy in human parental investment, evolution favored women who were more selective about their mates because women in the evolutionary past risked enormous investment by having sex. Men, on the other hand, lose only a few minutes or hours of time and can move on to a new coupling. While gender equality and modern birth control methods have drastically changed these costs and benefits, sexual and mate preferences evolved over millions of years, and thus, modern humans still possess this underlying sexual psychology despite environmental changes (Buss 2016).

Evolution has also favored women who prefer men who possess certain adaptively valuable characteristics and who are likely to confer the most benefits, while they dislike men who possess poor attributes that confer costs (Buss 2016). A woman choosing a mate will likely begin by analyzing her own individualized needs. She will then identify and evaluate the potential mate's qualities followed by integrating her knowledge about each potential mate to determine the best candidate (Buss 2016). Several characteristics women look for in a potential mate include resource potential, commitment, social status, men who are older than they are, ambitiousness and industriousness, dependability and stability, intelligence, compatibility, size, strength, V-shaped torsos, symmetry, masculinity, love, and kindness (Buss 1989; Langhorne and Secord 1955). In short, women who preferred men who were reliable and willing to commit to a longer-term relationship were more likely to have children who survived and thrived.

Even in the more gender equal modern environment, women favor men who have professional degrees, are financially successful, have high social status, have greater intelligence, and are tall, independent, and self-confident. This is especially true for women who are highly educated and financially successful themselves. Again, this is accounted for by the fact that sexual

selection takes millions of years to develop and is not easily changed by the modern environment. One of the most important characteristics to women is commitment as conceiving a child when support is unavailable would be detrimental to reproductive fitness for the female. Committed males also bring with them resources that they are willing to provide to their chosen mates and her children (Buss 2016).

Operational Sex Ratio

One reason why women may be choosing not to reproduce is the current operational sex ratio. The operational sex ratio is the ratio of sexually active males relative to the number of fertile females at a given time (Buss 2016). This sex ratio is said to affect the ways in which females compete with other females and males compete with other males for mates. For example, whether men and women choose to utilize short-term or long-term mating strategies is in part related to the operational sex ratio. If there are more sexually active males in the population than there are fertile females, females can afford to be more choosy, male intrasexual competition will increase, and long-term sexual strategies will be the norm. If there are more fertile females than there are sexually active males in the population, women cannot afford to be as choosy and will have to compete with each other for the small number of most desirable men, and short-term sexual strategies will be the norm (Buss 2016).

Many factors affect the operational sex ratio. Some examples include wars in which more males than females are killed, risky behaviors such as fighting which occur more frequently with men, homicide which affects more men than women (both in being perpetrators and victims), and differential marriage rates by age in which women remarry less and less often than men with increasing age. In scenarios in which there are many available men in relation to fertile women, many men will be excluded from mating (Buss 2016). The men who can attract women in these conditions will jealously guard their mates against potential rival mates. This ties into an

evolutionary theory about rape which suggests that some men will turn to rape and sexual aggression to gain what they cannot with their current mate value. In situations in which available fertile women are in short supply, long-term sexual strategies become the norm because males have no choice but to appease the available females by committing and providing.

The change in the ratio of men to women throughout life can cause a shift in mating strategies. Younger men have less access to available (young, attractive, fertile) women because these women prefer men with higher status and more resources, something that older men tend to have. As a result, it seems that younger men engage in risky competition behaviors such as committing violent crimes of sexual coercion, robbery, battery, and murder. As men age, the ratio between the sexes tilts into their favor. If they have managed to survive the risks associated with intrasexual competition and have upped their mate value through increased status and resource attainment, they will have a larger pool of potential mates to choose from (Buss 2016).

The possibility that short-term mating is on the rise can be explained by a theory that states that the unbalanced sex ratio among college-educated individuals suggests a lack of eligible men and a rise of eligible women. In this scenario, men are able to shift to short-term sexual strategies because the sex ratio is in their favor and they are able to “implement their desire for variety” (Buss 2016, p. 125). Women in this scenario do not have much choice but to shift to a short-term strategy as well because there is shortage of men who are willing to invest or commit. Similarly, in populations or contexts in which there is little benefit for women to commit to one mate, the females will shift to a short-term strategy. Some examples include if a woman’s kin provide her with more resources than could a potential mate and if pursuing multiple short-term sexual relationships will provide her with resources from multiple men, or cultures in which food or other resources are shared communally (Buss 2016).

The college sex ratio imbalance, therefore, leads to a scenario in which many women

compete for the limited amount of high mate value men and thereby many are left to settle for short-term or casual sexual relationships. Additionally, because there are fewer men than women on college campuses, men don't have to commit to one woman or provide for her at all. They are freer to pursue multiple mateships because women cannot afford to lose out on the opportunity of mating with the only high mate value males in the population. This puts women at a great disadvantage if they do choose to reproduce because there is no guarantee of commitment (Buss 2016).

Childcare Conditions

Lack of commitment and paternal investment, particularly financial, is one reason cited by women who have had abortions (Hill and Low 1992). Furthermore, because women's sexual strategies have developed over millions of years with the idea that some men, because of a lack of resources, social status, etc., are not worth copulating with, there may be some evolutionarily derived psychological mechanism that is stopping women from choosing to have children in this current sex ratio. In other words, females have evolved to be choosy when selecting a mate to reproduce with, such that they want to make sure the men they choose are committed, have many resources, and are willing to give women and their children those resources. In the modern age in which more women are educated and therefore may be more financially independent than women of the past, they are having a much more difficult time finding high-quality mates (Buss 2016). These evolved mechanisms also make it less likely that women will want to raise children on their own.

Even though women have taken on new economic responsibility and have become increasingly more educated than women of past generations, women are still primarily responsible for childcare (Hill and Hill 1990). As a result, women must sometimes choose between staying home to rear their children, thus losing out on learning important work-related skills, or taking a job with flexible hours and does not require

travel, which likely does not pay well (Hill and Hill 1990). A third option is to opt out of childbearing entirely, whether deliberately, to concentrate more time to other activities such as work, or because there is no time to have and care for children. Mothers who work tend to face scheduling conflicts, dealing with family issues while at work, and missing days (Hill and Hill 1990). For men, only single fathers face these same issues at a comparable rate (Hinde 1971). Hill and Hill (1990) suggest that in order for women to participate in the job market equally, either economic activities must be carried out concurrently with childcare or the extent to which mothers bear the primary responsibility for childcare must be reduced. It can be theorized that since neither of these suggestions has become a reality, many women are choosing to opt out of childbearing altogether.

Other Reasons

Older women are forced to compromise their mating strategies by lowering their standards, becoming more competitive by enhancing their appearance, securing resources on their own, or opting out of the mating market altogether (Buss 2016). Choosing to opt out of mating rather than meeting these demands can also help explain the increase in childless women. With women obtaining more professional degrees than men, women are getting married or seeking long-term relationships at older ages. As a result, they may have difficulty attaining a high value mate due to being less fertile, less physically attractive, and less young looking. Rather than becoming more competitive to attain a mate, they may just choose to fill their lives with other meaningful things.

Another reason why women may be choosing not to reproduce is the advent of birth control. Until recently, sex and reproduction were inextricably linked. Modern birth control methods have changed the outcomes of having sex, but not the mechanisms behind why humans decide to engage in it to begin with. Sex is perceived as being pleasurable because it enhances reproduction (Low 2015). This is known as a proximate

cause which tends to drive the system, while sexual selection acts as a passive filter (Low 2015). Evolution has selected individuals who enjoy sex because those individuals had children who also had interest in sexual activity. While people are likely still interested in sex, birth control gives women a choice of whether they'd like to be mothers. It creates a possibility in which men and women could be on equal footing in which sex does not equate to parental consequences (Low 2015). In other words, selection pressures are unable to exert the outcomes of pregnancy on women who want or enjoy sex mainly because we operate on proximate causes as selection pressures are lost to our subconscious (Low 2015). The link between sexual pleasure and parenthood has not been broken.

Abortion is another option that potentially overrides selection (Low 2015). While women may be engaging in sexual activity at the same rate or even at a higher rate than they historically have, the outcome of sex no longer must be pregnancy, and pregnancy no longer must result in a child. Additionally, it may be that women do not develop a desire to nurture and be a parent until after their child is born and the release of oxytocin, the hormone that is related to bonding (Elgar 2015). Therefore, women are still fulfilling the demands of their evolved psychological mechanisms to copulate, but due to modern advances, they are not actually reproducing. Women now have the room to make personal choices about whether or not they want to be mothers, something that is not true in evolutionary history and has not been accounted for in the literature (Elgar 2015).

In addition to individual women choosing not to have children, the birth rate as a whole has also decreased (Low 2015). Some proximate causes of the low birth rate include factors affecting exposure to copulation, factors that deliberately control fertility such as birth control, and natural fertility factors that exclude birth control and abortion (Bongaarts 1978). In terms of exposure to copulation, women who are not in sexual relationships for most of their reproductive years and who have children at later ages will have less children (Low 2015). In terms of deliberate control of fertility,

there are temporary means of birth control such as condoms or the pill, as well as more permanent means such as vasectomy and tubal ligation (Gray and Anderson 2010). Elective abortion is another method of birth control. It is seen in a U-shaped distribution with young women in their teens who are not ready to have a family and have not secured male commitment and women in their 40s who have already achieved their desired family size and risk complications in their pregnancies being at either end (Hill and Low 1992). In the middle are women in their 20s and 30s. Natural fertility factors include factors such as erectile dysfunction, low coital frequency, and sterility (Gray and Anderson 2010). These combined factors have led the average fertility of many nations to fall below the replacement level or having two children in order to replace both the mother and the father (Gray and Anderson 2010).

An anthropological theory introduced by Bobbi Low proposes that since mortality has decreased, individuals tend to invest more in a lower number of children since they are likely to make it to reproductive age (Low 2015). As a result, birth rate has decreased. In addition to this, economically, it is more difficult for men to accrue the abundant number of resources needed to care for a child in modern times. With the cost of living and education having increased, parents are more likely to have less children and put all their resources in these few offspring. However, a caveat is that men with more resources are always more fertile than men without (Low 2015).

Low (2015) suggests that hunter-gatherer societies (as illustrated by current societies of this nature) likely experienced both high fertility and high child mortality. Industrialized society has brought about a "demographic transition" which can be characterized as having low fertility as well as low mortality (Low 2015). In these modern times, both marital status and a number of existing children play a role in individuals' deliberate fertility decisions (Low 2015). Other factors that have an effect include whether the government offers tax breaks or taxes fertility. As stated, working to increase one's wealth has harsher trade-offs for women than it does for men (Low 2015).

Demographic transitions are often a result of factors such as education and wealth (Gray and Anderson 2010). This seems to be supported by the numbers which point to more educated countries having lower fertility than less educated countries (Gray and Anderson 2010). The number of offspring an individual has is no longer a good predictor of reproductive success as each of these offspring will be so costly (Low 2015). However, less educated and poorer women have more children than their more educated, richer counterparts (Low 2015). Likely, this is because children of lower-income less educated women face higher mortality rates which brings about a quantity over quality strategy, whereas higher-income more educated women take a quality over quantity strategy and tend to invest heavily in only a few children (Low 2015). This does not mean that those with incredible wealth can reproduce boundlessly, as fertility is bound to decline as per capita investment in children continues to rise (Smith et al. 2010).

Other theories such as one by Caldwell (1976) posit that children may be a form of retirement insurance in countries or areas in which social security does not exist. Theories such as this suggest that one benefit of having children years ago was that they could participate in labor and that they could be helpful to parents when they became too old to work (Gray and Anderson 2010). It would therefore be less fruitful to have many children today as children spend many years in school before they can be economically beneficial to the family (Gray and Anderson 2010). In conjunction with this theory, evolutionary theory would suggest that a strategy in which parents funnel their resources into their children until they become too old and then those children funnel their resources into their parents is one that natural selection would likely have favored (Kaplan 1996).

Conclusion

The objective of human evolution is the propagation of one's genes. However, in the modern world, the birth rate has continued to decrease in

industrial societies. One factor affecting the low birth rate may be women's choice not to reproduce. This begs the question of why women would not want to have children. Thus far, research suggests that due to an increase in low mate value men and a decrease in high mate value men, women are having more short-term relationships which are not conducive to raising children. In addition, with mortality rates decreasing and economic stress increasing, women may choose to reproduce less in order to invest more resources into less children. Lastly, with the rise of modern birth control, women are no longer as restricted in having sex because pregnancy is not the mandatory outcome. Future research should continue to investigate these factors.

Cross-References

- [Effect of Birth Control on Women's Preferences](#)
- [Operational Sex Ratio](#)
- [Parental Investment and Sexual Selection](#)

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Evolutionary Personality Psychology

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Synonyms

Individual differences; Life history theory; Personality models; Personality traits; Reproductive strategies

Definition

A field of study that merges personality and evolutionary psychology research with an emphasis on understanding both the universality of personality traits and its variation across individuals

Introduction

One of the most significant questions that psychologists across multiple fields attempt to answer is, “why are there no two persons who are the same?” Why are some people more dominant and assertive while others are more shy and withdrawn? Why are some people more agreeable and friendly while others are more hot-tempered and aggressive? Approaching these questions about personality through an evolutionary lens may help researchers, professionals, and lay people alike to better understand *why* individual differences exist across people and cultures, and differ within populations, by focusing on the ultimate functional causes of this variability. In taking an evolutionary perspective, personality and individual differences can be situated and comprehended as beneficial for the survival and reproduction of ancestral humans, illustrating the nonarbitrary instances of how selection has shaped us. Furthermore, by focusing on the adaptive qualities of conventionally “maladaptive traits,” an evolutionary perspective seeks to understand why such traits are advantageous, rational, and useful strategies under certain environmental contexts.

The profound consequences of these differences between individuals are not limited to our ancestors. Even among contemporary humans, differences in personality may predict how long an individual will live, what kinds of relationships that person has with others, how long these relationships will last, how many children a person will have, and what kind of parent a person may be. Furthermore, personality characteristics are also associated with how humans situate themselves in relation to the world. For example, personality differences may influence how individuals believe society should be organized (i.e., political affiliations) or the relationship they perceive between themselves and a higher power (i.e., religiosity; see Buss 2009 for review). In this regard, personality is often seen from an evolutionary personality psychological perspective as a series of adaptive options that organisms may have from which to choose in calibrating themselves to their environments. This is not unique to

personality traits, nor is it unique to humans; the process of adaptive calibration that occurs through development adapting an organism to their environment is a theme observed throughout nature (e.g., Nettle 2010; Stearns 1992).

Personality as an Instance of Developmental Adaptation

On average, any given personality trait has heritability estimates of about 50% (Bouchard and Loehlin 2001). However, much of the observable variation in personality traits appears to come about through salient early-life experiences that may induce long-term and stable changes by interacting with the organism's biological predispositions (discussed further in section "Genes and Personality"). Responsiveness to early environmental cues may therefore be adaptive when the cues that are present to an organism during development are able to represent future conditions moderately well (Stearns 1992). For example, consider a species of freshwater snails, *Physella virgata*, that are prey for both fish and crayfish. Each of these predators leaves its own distinct chemical signature in the snails' environment. This chemical signature is thought to trigger a cascade of developmental events that optimizes the snails' defenses against the predators that they are likely to encounter. Consequently, snails who encounter fish will benefit from developing rotund shells that are difficult to bite and the ability to leave the water. Similarly, snails who encounter crayfish will benefit from growing narrow shells that are difficult to enter, and faster shell maturation to defend against vulnerability (DeWitt et al. 2000). The differing development of the same species of snails under different conditions suggests that certain phenotypes may be packaged together *strategically* by natural selection to give the organism adaptive advantages. These clusters of traits, or *behavioral syndromes*, are observed across the animal kingdom (Nettle 2010). Similarly, human personality traits appear to cluster together to solve adaptive problems. The leading theory that conceptualizes and explains personality

and individual differences in humans using developmental adaptation is life history theory.

Life History Theory

Life history theory (LHT) is an evolutionary-biological metatheory that describes individual differences as reflective of a series of coordinated adaptive trade-offs that organisms must make to maximize their allocation of the limited resources that are available to them in their environment. The ability to pursue the "optimal" life history strategy for one's environment is associated with increasing one's evolutionary fitness (e.g., Stearns 1992). LHT is generally concerned with resource trade-offs in two categories: (1) somatic effort (i.e., having to do with growth and maintenance) and (2) reproductive effort. Within reproductive effort, there are two subcategories: (1) mating effort (i.e., seeking out a mate, establishing pair bonds) and (2) parental effort (i.e., gestation, childbirth, breastfeeding, provisioning of resources toward kin) (Stearns 1992). Due to the finite nature of such resources, organisms are often forced to make trade-offs to allocate their resources in the most "optimal" way in their current environment, leading to suites of coadapted traits.

Classical conceptualization of life history strategies predicts that organisms will fall generally into one of two categories: *fast* and *slow* life history strategies (e.g., Stearns 1992). Organisms that pursue a fast life history strategy will typically come to reproductive age earlier, have a shorter life span, and emphasize bearing many offspring with limited parental investment. Slow life history strategies entail the opposite – that is, coming to reproductive age more slowly, having a longer life span, and having greater parental investment in fewer offspring. In sum, LHT predicts that organisms pursuing a fast life history strategy will favor resource allocation toward reproductive efforts, while organisms that pursue a slow life history strategy will favor resource allocation toward continued growth and maintenance; both are seen as viable strategies that

ultimately facilitate survival till reproduction. Through the lens of LHT, suites of coevolved personality traits can be understood as adaptive strategies to increase reproductive success (and consequently evolutionary fitness) under the organism's current environmental context. Traits that are related to life history domains tend to vary together, and these may organize generally into the fast and slow life history strategies, with the goal of calibrating organisms to best fit their environments.

Different types of environments favor the adoption of different life history strategies. In unpredictable environments with high mortality rates, the environment may favor organisms that are less inclined toward future planning. While future planning may be adaptive in stable and predictable environments, this strategy may lead to costs such as missing out on mating opportunities. Along these lines, LHT predicts that fast life history strategies will be related to personality structures that are associated with less prosocial motivations and behaviors since reliance on social rules and connections is most often a long-term investment strategy (Frank 1988).

Traits that cluster together to resemble a slow life history strategy, such as positive relationship attributes and attachment, are negatively correlated with traits that cluster together to resemble a fast life history strategy, such as Machiavellianism and risk-taking (see Gladden et al. 2009 for review). Similarly, Figueredo and colleagues (2007) found empirical support for the relationship between life history strategies and personality structure. Multiple traits that were related to life history domains, such as future planning, quality of parent's relationship, social support, attachment to romantic partners, and prosocial behavior, clustered together. These traits are related to a slow life history strategy because they emphasize investing resources in the future, rather than in short-term gains. Although this fast-slow dichotomy is useful in conceptualizing these distinct strategies, it should be noted that it may be more realistically viewed as a fast-slow continuum. Regardless, the clustering of specific individual differences across this fast-slow continuum

tends to give rise to particular personality traits (see Table 2). The following section discusses how these personality clusters were revealed to researchers, and how personality models have since been constructed and utilized.

Psychometrics of Personality Measures

Most personality measures are created using one of two approaches. The first involves the creation and administration of questions or items to a large sample to determine the validity of the measure (i.e., is the measure actually measuring what it is believed to measure?) (Myers et al. 1985). The second and more prominent method is the lexical approach (e.g., Lee and Ashton 2004). Researchers who utilize this method compile various personality-related adjectives. These adjectives are then rated by a large number of people responding about themselves (self-report) or others (observer-report). These ratings are then statistically analyzed using factor analysis to generate clusters of personality adjectives (e.g., shyness and lower talkativeness may be grouped together in a factor analysis). These clusters are finally named as various personality traits (e.g., introversion). Many prominent personality measures, including the Big Five Model (Costa and McCrae 1992) and the HEXACO Personality Inventory (Lee and Ashton 2004), were created using this method.

The Big Five Model

Within the Big Five Model (also called the five-factor model; Costa and McCrae 1992), each of the five personality factors (i.e., Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism) has distinct motivational and behavioral tendencies. From the perspective of evolutionary personality psychology, the "optimal" level of each trait is dependent on the environmental context.

Individuals who are high in the Big Five factor Openness to Experience are inventive and curious

and demonstrate an appreciation for artistic and intellectual endeavors (Costa and McCrae 1992). High levels of Openness to Experience have been associated with both positive (i.e., artistic creativity and intelligence) and negative (i.e., proneness to supernatural beliefs, schizotypal personality disorder, and psychosis) outcomes. As such, depending on the environment, high levels of Openness to Experience may be beneficial or detrimental (Nettle 2010).

Individuals who are high in the Big Five factor Conscientiousness are organized, dutiful, and disciplined, and make long-term plans and goals (Costa and McCrae 1992). As such, high levels of conscientiousness are particularly advantageous in a modern environment that emphasizes productivity. High levels of Conscientiousness are also related to rigidity and inflexibility. Thus, in an unpredictable environment, high levels of this trait may be costly if it limits an individual's capacity to react appropriately on short notice (Nettle 2010).

Individuals who are high in the Big Five factor Extraversion are outgoing, energetic, social, and stimulation-seeking (Costa and McCrae 1992). Such individuals typically have more sexual partners and more social status and are more physically active. The fitness benefits of such traits are obvious, as they take advantage of the highly social nature of human beings. Indeed, these characteristics are most adaptive in novel environments with fluid group structures, as individuals high in Extraversion will successfully influence the group and attain multiple mates. However, in environments where the dominance hierarchy is very stable, being gregarious and charismatic may be a costly strategy (Nettle 2010).

Individuals who are high in the Big Five factor Agreeableness are friendly, compassionate, trusting, and helpful (Costa and McCrae 1992). Such individuals are highly cooperative and will seek out joint connections and interpersonal relationships. Like Extraversion, high levels of Agreeableness also take advantage of the social nature of humans. However, low levels of Agreeableness may be beneficial if an individual exists in a population that is high in Agreeableness, as it provides the opportunity to exploit other individuals (Buss and Duntley 2008).

Finally, individuals who are high in the Big Five factor Neuroticism are less resilient to stress, are at a higher risk of mental illness, have difficulties in interpersonal relationships, and may experience significant negative affect (Costa and McCrae 1992). However, negative emotional states such as these are useful in environments where high sensitivity to threat is necessary for survival. For example, women are generally higher in this trait than men, and it is thought to reflect the adaptive nature of high threat detection when reproductive success is so costly (i.e., costs associated with carrying, delivering, and rearing offspring; Nettle 2010).

The HEXACO Model

The HEXACO model is a contemporary model that provides advantages such as strong cross-cultural validity and an explicit evolutionarily informed theoretical foundation (Lee and Ashton 2004). The HEXACO model includes six personality factors, each of which can be further broken down into four facets. The HEXACO model arose from a lexical database that included data from individuals in multiple cultural contexts, such as Korea, Italy, Poland, and a French-speaking part of Canada (Ashton and Lee 2007). By expanding their lexical data to include different cultures, they were able to identify a sixth trait called Honesty-Humility. Additionally, the HEXACO factors Emotionality and Agreeableness differ substantially from the analogous and respective Big Five factors Neuroticism and Agreeableness. A major difference in these constructs is the HEXACO's emphasis on capturing evolutionarily relevant kin-altruistic tendencies in crafting Emotionality and Agreeableness (as well as Honesty-Humility), whereas the Big Five Neuroticism and Agreeableness did not have this same objective. Furthermore, while the HEXACO facets Extraversion, Conscientiousness, and Openness to Experience share a name with factors in the five-factor model, they have notable differences in their definitions (see Table 1 for factor descriptions).

The traits in the HEXACO model can be interpreted as related to one of two adaptive

Evolutionary Personality Psychology, Table 1 Descriptions of the HEXACO personality factors

Function	Factor name	Facets	Description
Engagement and endeavor	Extraversion	Social self-esteem	High levels of Extraversion indicate self-confidence, enjoyment of social gatherings, feelings of enthusiasm, and energy. Low levels indicate feelings of awkwardness in social settings, indifference to social activities, and less optimism and liveliness
		Social boldness	
		Sociability	
		Liveliness	
	Conscientiousness	Organization	High levels of Conscientiousness indicate orderliness, attention to detail, dutifulness, and long-term planning and goal setting. Low levels indicate disorderliness, disorganization, and limited self-regulation
		Diligence	
		Perfectionism	
		Prudence	
	Openness to Experience	Aesthetic appreciation	High levels of Openness to Experience indicate aesthetic appreciation, interest in radical ideas, imaginativeness, and inquisitiveness. Low levels indicated limited curiosity and creativity and limited interest in art and novel ideas
		Inquisitiveness	
		Creativity	
		Unconventionality	
Altruism vs. antagonism	Honesty-Humility	Sincerity	High levels of Honesty-Humility indicate little interest in social status, avoidance of manipulation and exploitation, and modesty in terms of wealth. Low levels indicate willingness to exploit others for personal gain, an inclination to break rules, motivation from material wealth, and a sense of self-importance
		Fairness	
		Greed avoidance	
		Modesty	
	Emotionality	Fearfulness	High levels of Emotionality indicate fearfulness and anxiety, need for emotional support, empathy, and sentimentality. Low levels indicate limited concern of physical harm or stressful situations and emotional detachment from others
		Anxiety	
		Dependence	
		Sentimentality	
	Agreeableness	Forgivingness	High levels of Agreeableness indicate willingness to forgive others, leniency in judgments, willingness to cooperate with others, and limited anger. Low levels indicate a proneness to holding grudges, a propensity to be critical others, stubbornness, and higher levels of anger
		Gentleness	
		Flexibility	
		Patience	

Note: Information in this table from Ashton and Lee (2007). Visit www.hexaco.org for more information

functions: (1) endeavor and engagement-related functions or (2) altruism versus antagonism-related functions (Ashton and Lee 2007). Extraversion, Conscientiousness, and Openness to Experience describe one’s propensity to engage in, and allocate time and effort toward, social activities, task-related activities, and idea-related activities, respectively (Ashton and Lee 2007). An individual who is high in these three factors will be engaged, active, and invigorated, whereas an individual who is low in these three factors will be inert and passive (Ashton and Lee 2007). Depending on the environmental context, these traits may be beneficial or costly.

An individual who was high in the HEXACO factor Openness to Experience more interested in learning about one’s world may have had the advantage of possessing knowledge related to garnering resources which may aid in attracting mates. However, high levels of Openness to Experience may be costly. For example, the desire to explore new areas may impose some risks to physical health. Similarly, individuals who were high in Conscientiousness would have had energetic costs due to the propensity to engage in more tasks, some of which would have involved physical labor, but also the energetic costs of self-regulation and inhibiting one’s impulses. Conversely, in more modern environments, the

foresight and productivity associated with high levels of Conscientiousness may be adaptive. Individuals with high levels of Extraversion would have had similar energetic costs due to being lively and sociable. However, higher levels of Extraversion may have also afforded an individual a larger social network, and the advantage of having more options for allies and mates (Ashton and Lee 2007).

More specifically, the HEXACO factors Honesty-Humility, Emotionality, and Agreeableness each represent an individual's tendency to be altruistic or antagonistic. Honesty-Humility and Agreeableness are thought to be indices of an individual's orientation toward reciprocal altruism. While Honesty-Humility is a marker of an individual's willingness to exploit others (or avoid exploiting others) for personal gain, Agreeableness measures an individual's willingness to forgive or be exploited by others (Ashton and Lee 2007). High levels of this trait offer the important benefit of receiving reciprocal cooperation from others through the demonstration of mutual respect and trust. However, the cost of being high in Honesty-Humility is missed opportunities for personal gain that individuals who are low in Honesty-Humility will readily seize. Individuals who are high in Agreeableness may incur the cost of being taken advantage of by individuals who are low in Honesty-Humility, as they tend to be more lenient in their judgments of others and are prone to being cooperative. However, this cooperativeness also grants adaptive benefits as individuals with high Agreeableness will benefit from continued and reciprocal cooperation from others. Emotionality is hypothesized to be uniquely related to an individual's orientation toward kin altruism and self-preservation (Ashton and Lee 2007). Individuals who are high in Emotionality will avoid physical danger and the related costs, thus negating much of the harm that may fall on themselves or their kin. High Emotionality is also associated with the development of separation anxiety disorder and phobias, due to the high degree of dependence, sentimentality, fearfulness, and anxiety that characterize high levels of this trait (Ashton and Lee 2007).

Despite the differences in these personality models, certain clusters of personality traits seem to emerge that may represent "optimal" responses to specific environmental cues as per LHT. Key to an evolutionary view is seeking an understanding between the observable characteristics of an organism (its phenotype) and its genetic code (its genotype). Thus, an evolutionary personality psychology view requires a consideration of the putative genetics underlying the phenotypic and observed personality clusters of these dominant models of personality (Table 2).

Genes and Personality

Personality, like other complex traits, is polygenic. That is, personality traits are influenced by a combination of genes (Plomin et al. 1994). As such, there are multiple factors at the genetic level that may influence the variation in genes that may consequently influence personality traits. The genetic influences of personality traits are typically evaluated by comparing the traits that are similar across individuals that share both genetic material and their environment, such as identical versus fraternal twins. These studies suggest that almost all aspects of personality traits are, at least in part, heritable (Plomin et al. 1994). More specifically, various adoption, twin, and family studies have demonstrated significant similarities in personality traits between close genetic relatives and fewer similarities between more distant genetic relatives. For example, one study showed that the average correlation between monozygotic twins was 0.55, compared to -0.07 for dizygotic twins (Plomin et al. 1994).

Additionally, environmental influences are also equally powerful in shaping one's personality traits (Van Gestel and Van Broeckhoven 2003). For example, antisocial personality and its associated behavior is, in part, influenced by the interaction between childhood maltreatment and the monoamine oxidase A gene (Caspi et al. 2002). Similarly, researchers have demonstrated that aggressive and competitive environments have

Evolutionary Personality Psychology, Table 2 Life history strategies and associated personality traits

Life history strategy	Observed personality traits	Survival and reproductive value
Slow life history strategies	Big Five:	Outgoing and adventurous to meet and attract mates Open to new ideas and experiences with others
	Extraversion	
	Openness	
	Conscientiousness	
	Agreeableness	
	Low Neuroticism	
	HEXACO:	Uphold the rules of the group Cooperate with others
	Honesty-Humility	
	Extraversion	
	Agreeableness	
	Conscientiousness	
Fast life history strategies	Big Five:	Cooperate as long as it takes to get the resources needed to survive/reproduce
	Low Agreeableness	
	HEXACO:	
	Low Honesty-Humility	More mating compared to parenting effort Bully others to get resources
	Dark Triad:	
	Narcissism	
	Psychopathy	
	Machiavellianism	

Note: Information in this table from Ashton and Lee (2007), Figueredo et al. (2007), Gladden et al. (2009), and Manson (2016). Visit hexaco.org for more information

significant effects in changing an individual’s testosterone levels and consequently their aggressive behaviors (Archer 1991). These examples support the importance of calibration of an organisms’ genetic composition/predisposition as well as environmental pressures in shaping personality traits and associated behaviors. More specifically, both the genetic predispositions and environmental contexts may be important correlates that help us to understand the link between personality and various behaviors. The genetic profile within everyone prepares individuals to respond to their environment with either or both prosocial strategies and antisocial strategies in the service of survival and reproduction.

Personality and Prosocial Behavior

Prosocial behavior is defined as overt, voluntary action intended to benefit others (Batson 1998).

Prosocial behavior may have proven especially beneficial in early human environments characterized by unpredictable climate, food supply, and the threat of competing tribes (Simpson and Beckes 2010). Considering the division of labor among early humans, which involved different members taking responsibility for such important tasks as hunting, gathering, child care, and security, it would have been beneficial to the group’s survival to work cooperatively to collectively reap the benefits.

More specifically, prosocial behavior that helps propagate one’s genes through acts directed toward genetic relatives may be the most obvious illustration of its adaptive quality. Indeed, humans demonstrate extensive prosocial networks among genetically unrelated individuals in addition to their kin. One theoretical explanation, the Cooperative Breeding Hypothesis, describes a social system characterized by alloparental care, in which individuals take on caregiving roles toward non-descendants. Cooperative breeding therefore

facilitates the formation of family units, systems in which prosocial acts are even more beneficial to the actor. In other words, prosociality toward kin benefits the survival of genes in related organisms (Hrdy 2007).

According to the HEXACO model, prosociality is most closely linked with the trait Honesty-Humility. This is illustrated, for example, by individuals who are high in Honesty-Humility demonstrating an increased tendency to actively cooperate and engage in pro-environmental behavior (Ashton and Lee 2007). While the research emphasizes Honesty-Humility as an important trait in relation to prosocial personality, there are other personality traits that may account for specific prosocial tendencies. This is illustrated within the HEXACO model by the interstitial scale of Altruism versus Antagonism, a representation of a blend between Honesty-Humility, Agreeableness, and Emotionality. High scorers on these domains tend to be sympathetic toward others and react with generosity to those in need of help, indicating that being high on these facets may be related to increased prosociality (Ashton et al. 2014). A specific example may be in the context of relationships in which individuals score highly on the sentimentality facet of Emotionality, associated with the development and maintenance of strong emotional bonds, as they may be more inclined to behave prosocially (Ashton et al. 2014). This may unfold in the context of familial relationships, such as the parent-child or within extrafamilial contexts, and between members of the same in-group. These findings generally suggest that prosocial tendencies may have clearer links with living a slow life history strategy as opposed to a fast one since inherent in this orientation is reciprocity, a forward-thinking behavior that relies on continual interactions between individuals.

There is little doubt that as an obligate social species with cooperativeness as one of its hallmark traits, humans have been selected to manifest prosocial traits and behaviors. However, within any social system lies the possibility for the emergence of exploitation and cheaters. Hence, we must also consider the potential adaptive benefit of non-prosocial individuals.

Personality and Antisocial Behavior

Descriptions of personality traits tend to revolve around thinking, feeling, and behaving in social situations, but not all encounters have positive social intentions. This points to the existence of personality traits and styles geared toward deception, self-enhancement, aggression, and callousness toward others, suggesting the presence of attributes with more negative social intentions. These types of personality traits have been described as *dark personalities*. The most prevalent model of dark personalities is the Dark Triad model developed by Paulhus and Williams (2002), which includes the personality dimensions narcissism, Machiavellianism, and psychopathy.

Narcissism is a personality construct that emerged from the clinical conceptualization of individuals preoccupied with their own self-image, social status, and personal dominance (Furnham et al. 2013). It owes its name to the ancient Greek story of Narcissus, a hunter that fell in love with his own reflection upon seeing it in the water, thereafter being unsatisfied with the love and connection felt with others. Machiavellianism describes a personality that has interpersonal manipulation at the core of its manifestation, along with characteristics of distrust of social rules and morals and a cynical and pessimistic attitude about life (Furnham et al. 2013). The construct owes its name to the political thinker Niccolò Machiavelli, who lived in sixteenth-century Florence, Italy. His book *The Prince* was written as a guide to attaining political and economic power using unprincipled methods of deception and manipulation. Lastly, psychopathy is a personality construct that also came from clinical observations of chronically difficult and enigmatic patients who exhibited marked and reduced emotional affect, interpersonal charm and grandiosity, and disinhibited and sensation-seeking attitudes (Furnham et al. 2013). These individuals often come in contact with the law or engage in behavior that would constitute versatile illegal or criminal conduct such as fraud, assault, and sexual coercion (Hare 2003).

What makes these personalities “dark” and others not? One proposed idea has been that

these traits each have a callousness at their core in how they deal with other people (Paulhus and Williams 2002). From this perspective, the motivations and behaviors of individuals who are unbothered by committing callous, harsh, and aggressive acts against others constitute darkness of personality. This has led some researchers to consider the personality construct of everyday sadism to also be considered a dark personality, creating four constructs that make up the Dark Tetrad. A second idea comes from empirical observations that these personalities all covary with lower levels of the Big Five factor Agreeableness (Furnham et al. 2013). The aspects of lower Agreeableness on the Big Five factor suggest that Dark Triad personalities are immodest, non-compliant, untrusting, less altruistic, not straightforward, and lacking tender-mindedness. A third idea uses the HEXACO model of personality, particularly the Honesty-Humility factor of this model (Hodson et al. 2018). From this perspective, what makes dark personalities “dark” is their covariance with Honesty-Humility, which captures sincerity, modesty, fairness, and greed avoidance (Lee and Ashton 2004).

From an evolutionary personality psychology view, these three attempts to understand dark personalities and its associated antisociality all represent attempts to locate where in personality antisocial tendencies comes from. Focusing on antisocial behavior instead of dark personalities, lower Honesty-Humility appears to be associated with aggression and bullying (e.g., Book et al. 2012). Moreover, individuals who are lower in the HEXACO factor Agreeableness may also be more likely to engage in aggressive or uncivil behavior, as these individuals have a propensity to be uncooperative with others and are more likely to respond to negative situations with anger. Dinić and Wertag (2018) found that while lower Agreeableness was the strongest predictor of aggressive behavior, lower Honesty-Humility and lower Emotionality (in females) were also significant predictors of aggressive behavior, emphasizing the importance of studying these complex personality profiles. Further, from an adaptive perspective, it is important to consider that there are not only various costs and benefits to

higher and lower levels of each trait but also costs and benefits to engaging in different types of antisocial behavior.

How might we view dark personalities when considering a more ultimate, less proximate, view of human behavior and personality in using the tools afforded by an evolutionary perspective? Most perspectives have emphasized a life history framework for understanding dark personalities, placing them in the category of fast life history strategies that are geared toward mating and away from parenting (Furnham et al. 2013). The pattern of men consistently scoring higher on all three dark personality traits compared to women (Muris et al. 2017) provides some evidence for this claim, since males are more likely to be faced with the adaptive problem of access to mates, making their reproductive success more skewed than females, and subsequently selecting for more mating-focused personality styles (see section “Sex Differences in Personality”). Another evolutionary-informed view of the dark personalities takes into consideration their unprincipled lack of social orientation. This can be described as investing time and energy in agency and the self at the expense of community and others, or in manipulation and deception at the expense of commitment and transparency.

Acknowledgment of humans as an obligate social species does not necessitate that all humans engage in prosocial acts. Quite conversely, the fundamental dependence humans have placed on each other in creating a social realm guarantees the existence of social rules and expectations that themselves can be relied upon for exploitation and self-gain (Buss and Duntley 2008). Dark personalities may be one example of social rules and expectations among human groups having selected for exploitative and self-oriented individuals, if those strategies indeed had some reproductive payoff. For example, Honesty-Humility (and Agreeableness from the Big Five) tends to be normally distributed in populations. This suggests that human history may have been colored by both prosocial and exploitative personalities. An evolutionary personality perspective can conceptualize dark personalities in a nonarbitrary way (Buss 2009), potentially connecting their very origin

and emergence to the origin of human social groups. This view challenges non-evolutionary perspectives of “darker” personality styles as pathological (i.e., narcissism and psychopathy, including other personality constructs such as Borderline Personality Disorder and Histrionic Personality Disorder). Instead of viewing these as somehow pathological, an evolutionary personality perspective forces consideration of how these personality styles reflect traits and behaviors that underlie a response of organisms to specific environmental pressures to ensure their survival and reproduction.

Sex Differences in Personality

A benefit in using an evolutionary perspective of personality is that it affords a nonarbitrary formulation and appreciation of the connection between organism and its environment (Buss 2009). In other words, organisms manifest specific traits that help “match” them to a particular environment, ensuring survival and reproduction. Since reproduction is funneled and constrained by the fusion of gametes (i.e., sperm in males and eggs, or ova, in females), a fundamental part of this decision would be identifying one’s biological sex and planning a strategy accordingly. According to traditional notions of the evolution of traits and the sexes, females incur more of the costs of reproductive investment (both gestating and parenting), which includes having to wait a necessary period before having more offspring (e.g., at least 9 months for humans), and thus have been selected as the choosier sex. Males, on the other hand, are not limited in their reproductive capacity since the amount of reproductive effort can be as short as a few seconds (i.e., insemination). Thus, males may have faced more selection pressures to exhibit a more mating-focused strategy compared to a more parenting-focused strategy of females. This is not to say that females cannot be mating-focused or that males are not parenting-focused; it is simply to acknowledge that selection pressures can act on each of these reproductively constrained sexes to create different viable strategies for having one’s genes

propagated into the next generation. Individuals of each sex diverging too far from the “optimal” level of thinking and behaving as a member of that sex would be subsequently selected against (Geary 2010). The resultant distributions of female-like and male-like personalities would represent the varying viable strategies for acquiring mates, reproducing, and raising healthy offspring that themselves can reproduce.

Based on this evolutionary logic, it is expected that both personality similarities and differences should exist among the sexes (Geary 2010). Similarities between the sexes should be strongly rooted in the existence and maintenance of a cohesive and functioning social group (see section “[Personality and Prosocial Behavior](#)”). Both sexes share an interest in the well-being of the members of their social group, especially closely related kin. As a social-dependent species, humans require the guarantee of social cooperation, mutual dependence, and partitioning of labor into distinct tasks and groups. It is no wonder, then, that normative personality traits have included socially relevant characteristics including communion, emotion-related traits (e.g., Neuroticism, Emotionality), trust-related traits (e.g., Agreeableness), honesty-related traits (e.g., Honesty-Humility), and work-related traits (e.g., Conscientiousness). The existence of these personality traits reflects selection pressures acting on a social species, and both sexes should exhibit minimum threshold and possibly equal levels of these traits (Geary 2010).

However, some differences are expected between the sexes as well, which may represent the specialization of two major sex-biased pathways that have emerged and contribute to the social welfare of the group: those of warriors and worriers (Benenson 2014). These differences characterize boys and men as warriors, and girls and women as worriers based on defined sex-specific adaptive problems of surviving and reproducing. As warriors, tasks of developing individual skills and ensuring group security foster a need for emotional strength and resilience as well as a preoccupation with specializing in a particular niche to contribute to the group. As worriers, the prime task of caring for and raising the young of the group fosters a dependence on

keen social navigation skills, emotional understanding, and acceptance that can ensure survival of offspring through extended care and support from the social group. Interspersed within this framework exists the selection pressures of sexual selection, including both intrasexual competition and intersexual mate choice (Geary 2010). Intrasexual competition, especially among males due to the higher variance in reproductive success, can create environments where competition for access to mates may select for more disagreeable, hostile, and cheating personality traits in an effort to oust the mate competition. Intersexual mate choice, on the other hand, can select for particular personality traits (e.g., risk-taking) in the opposite sex that may not be as desirable to the other sex. Either way, these selection pressures can create sex differences in the personality and individual differences we see in humans.

Sex differences in personality traits can be confounded by variables such as age, culture, and historical context. Still, empirical research regarding sex-based personality differences often produces complex and controversial results. Research that utilizes the HEXACO model has suggested that females report a higher mean level of Emotionality-related traits than males (Ashton and Lee 2007). For the Dark Triad traits, meta-analyses suggest that males score significantly higher than females on all three traits, most notably on psychopathy (Muris et al. 2017). That these traits may capture more of a mating-focused personality (e.g., Furnham et al. 2013) is in line with their male-biased manifestation. While there are significant and well-documented differences between the sexes in terms of personality traits, there appears to be some commonality in the ways that these traits change as individuals mature and grow older.

Personality Throughout the Life Span

Although personality traits are often believed to be stable, there is evidence that personality changes in specific ways throughout the life span, particularly from adolescence into adulthood (e.g., McCrae 2010). Cross-cultural data

that utilizes the Big Five model has demonstrated a tendency to decline in the traits of Openness, Extraversion, and Neuroticism and increase in Agreeableness and Conscientiousness over this period of development (e.g., McCrae 2010). It appears that as people mature, they tend to be able to forgive more easily, are more willing to cooperate with others, and generally become more organized and focused on their goals. Increases in these traits may be indicative of individuals learning from their previous experiences in a way that modifies their traits through their life experience and changing environmental context. This highlights the modest plasticity of personality over the life span due to environmental influence and further demonstrates the developmental adaptability of personality. Therefore, the change in these traits may be an adaptive strategy for individuals to cooperate more with others as they move to adulthood and become more independent members of society, as well as to attain their goals.

Moreover, longitudinal research examining personality traits across the life span suggests that trait stability increases as individuals age (e.g., Roberts and DelVecchio 2000). That is, individual personality traits are more likely to change earlier on in development and change less as individuals get older, which is supported by LHT predictions that early-life calibration sets the stage for one's traits and behaviors, with plasticity becoming rarer as individuals age and developmental windows close.

Conclusion

In this entry, we have sought to demonstrate broadly the usefulness that an evolutionary personality psychology perspective provides for understanding some of the individual differences in behavior (e.g., prosocial, antisocial) and personality that we see in humans. Its primary strength is in providing a nonarbitrary conceptualizing of individual differences and showing how personality and other individual difference traits may represent gene-environment calibrations that have emerged within humans through many generations of selection.

Cross-References

- [Daniel Nettle](#)
- [Development of Sex Differences](#)
- [Life History Strategies](#)
- [Personality](#)
- [Personality Development](#)

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Evolutionary Perspective, The

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Synonyms

All psychology is evolutionary psychology; The breadth of general evolutionary theory

Definition

The evolutionary perspective is a contemporary approach originating from Darwin's theory of natural selection and endorsing the interactionist paradigm by considering the roles of genes and the environment as the sources of behavior.

Introduction

All modern evolutionary approaches are based on Charles Darwin's theory of natural selection (Buss 2012). According to this view in evolutionary biology, biological properties often have adaptive functions (i.e., adaptation), while they may also emerge as a by-product of some other adaptation. It could also be that a random product came out completely by chance. For example, the umbilical cord is adaptive because it provides the exchange of nutrients between the placenta and the embryo. The belly button is the by-product of this adaptation. The shape of the belly button varies from person to person, so it is a random product.

The evolutionary approach in behavioral sciences (i.e., evolutionary psychology) derives from the assumption that higher cognitive functions such as intelligence, analytical thinking, language, or empathy are either adaptations or by-products of other adaptations (Confer et al. 2010). In other words, evolutionary psychology claims that, like biological organs, certain mental traits are transmitted to the next generations as a result of natural selection, because many of these psychological mechanisms are adaptations that have emerged as long-term solutions to problems related to survival or reproduction. Having emerged in psychology, this perspective can be applied more generally: to all subfields of psychology and to many nearby disciplines (i.e., political sciences, economics) and to many ancient philosophical debates such as the origins of morality and religious belief, language, and intelligence. For example, there are approaches arguing that belief in God is an adaptation on its own (Johnson 2015) or a by-product of a higher-level adaptation (i.e., the theory of mind, Boyer 2001). There are also theoretical approaches proposing that our moral sense emerged due to having adaptive features (i.e., Haidt 2012).

However, the main problem of evolutionary approaches is the lack of consensus about what to categorize as an adaptation. Particularly in the field of evolutionary psychology, this ambiguity is extreme, because having a genetic basis is often seen to be a condition for labeling a trait as an adaptation. But this condition by itself is not sufficient since, for example, adaptations (other than gender-specific) must be prevalent across the species. Adaptations do not have to be innate, but they must at least occur during the development process. The most important feature of the adaptations is that it should solve a problem in the past environment in an efficient and economical way. For example, there is some evidence suggesting that moral sensitivity in general, religious belief in particular, serves functions in terms of promoting large-scale cooperation among humans.

In addition, there are two different levels of explanation in the evolutionary approach. The first is the ultimate explanation that reveals the

evolutionary origins of behavior (explaining why and how it came about) and revealing its brain foundations. For example, it is a kind of ultimate explanation to say that the evolutionary function of the human language is to promote large-scale cooperation commonly seen in human societies. The other is the proximate explanation and is concerned with the psychological meaning of behavior. For example, stating that the reason why we help our relatives more than others is due to feeling emotional closeness to them is a kind of proximate explanation.

Evolutionary psychology relies on an interactionist paradigm. In other words, behavior and underlying mental processes cannot be explained completely either by genetics or by environmental factors. The emergence of behavior depends on a combination of these two. For example, there are approaches arguing that people have a biological potential to acquire language (Hauser et al. 2002). Even though the capacity for language is a genetically acquired evolutionary trait, when this biological potential does not interact with environmental stimuli (i.e., speech of others), one will not develop advanced language skills. Therefore, the evolutionary approach endorses the interactionist paradigm by considering the roles of genes and the environment when explaining behavior.

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Evolutionary Perspectives on Rape

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Synonyms

[Sexual assault](#)

Definition

The use of force or threat of force to achieve penile-vaginal penetration of a woman without her consent (Kilpatrick et al. 1992; Thornhill and Palmer 2000).

Introduction

When sociologists and clinical psychologists look at rape, they look at certain variables and outcomes, such as how victims are affected, what kind of psychological impact does the victim experience, and what factors could have been changed that may have affected the outcome. Evolutionary psychologists have attempted to explain why perpetrators engage in rape. This entry will outline major evolutionary psychological theories and perspectives regarding why rape occurs. Because the majority of rapes are perpetrated by men (Black et al. 2011), this entry will focus on evolutionary psychological research focusing on male perpetrators.

The Five Types of Rapists

As proposed by McKibbin et al. (2008), male rapists can be divided into five categories. These five types of rapists are (1) the specialized rapist, (2) the disadvantaged male, (3) the opportunistic rapist, (4) partner rapists, and (5) the high-mating-effort rapist. Using an evolutionary perspective,

we will also examine the mechanisms that motivate these males to engage in rape.

The Specialized Rapist

Perpetrators of this category often fit a certain criterion in which they are sexually aroused by violent stimuli (McKibbin et al. 2008).

Since this particular perpetrator is the most common that people think about, we can now look at the topic of insemination. Thornhill and Palmer (2000) hypothesized that these specialized rapists have a developed or evolved mechanism that makes them more likely to rape a highly fertile woman versus a woman who is less fertile. With that being said, it is still unclear if this is truly a mechanism specific to rapists or if this is a trait that is shared by all men as a mating strategy. Another adaptive outlook proposed that what these rapists may have is the ability to produce large amounts of semen which, when ejaculated into a woman during rape, would increase the chance of inseminating that woman. This would support the claim that rapists perform this act in the effort to pass on their genes.

The Disadvantaged Male

Perpetrators of this category normally feel disadvantaged some way that what they feel make them unworthy or unable to find a long-term mate. These disadvantages can range and vary widely, but some examples would include being impotent, some sort of physical disfigurement, social awkwardness, etc. Evolutionary perspectives on the perceived non-attractiveness these males feel, or experience, deal with poor facial symmetry, which is perceived as less desirable by potential mates (Gangestad and Thornhill 1999). When these males feel as though they will never find a mate, they turn to other measures, such as rape, in order to pass along their genes and produce offspring (see above).

The Opportunistic Rapist

Opportunistic rapists are men who use rape or sexual coercion in instances when the backlash (associated costs) that is normally associated with rape is low. This includes retaliation by victims and the victims' families or societal prosecution

and/or persecution (McKibbin et al. 2008). Gottschall (2004) explains that instances of rape actually increase during times of war, and this is attributed to the opportunistic rapist because men at war are subject to little or no backlash from crime.

Partner Rapists

Perpetrators of this category engage in what is known as partner rape. These perpetrators already have a long-term mate but feel the need to force themselves upon their mate against his/her wishes. This is believed to be a response to stimuli which are triggered when the male believes his partner has engaged in unfaithfulness. This often leads him to establish dominance. A mechanism associated with this is what's known as kamikaze sperm (Baker and Bellis 1988). These are sperm that are specifically tasked with locating competitive sperm inside the vaginal canal and then destroying the rival sperm. Another mechanism viewed is that when the mate suspects unfaithfulness, the male will produce excess amounts of sperm in order to flush out any competitor sperm (Thornhill and Palmer 2000).

The High-Mating-Effort Rapist

Males within this category are not socially awkward, and they are not disadvantaged; they are, in fact, more sexually active and more attractive than almost all other rapist subsets. Lalumière et al. (2005) hypothesized that males of this category are often aggressive and dominant and have a high amount of self-esteem, concluding that these rapists display many psychopathic traits. Lalumière et al. (2005) also noted that these males primarily use typical mating strategies to produce a high number of mates but then will turn to rape and sexual assault when conventional means fail them.

Effects on Females

Defense Mechanisms

Davis and Gallup (2006) noted in their research that women may have defense mechanisms that would protect them from the costs that would come with being raped. They proposed that

preeclampsia, miscarriages, and spontaneous abortion are adaptive responses by the female body to terminate pregnancies that are not in the women's best interests, whether that be health or reproductive related. This adaptation is being associated with rape because there is a higher rate of those occurring with victims of rape. Smuts (1992) proposed that women make more alliances with groups of men to protect themselves from rapists. Wilson and Mesnick (1997) call this *The Bodyguard Effect* which says that women's mating preferences lean more toward physically and socially dominating males in order to deter possible dangers like abuse, assault, and rape.

Emotional and Societal Effects

Perilloux et al. (2012) point out that when women become victims of rape, they retain feelings of rage, fear, humiliation, and shame. This often leads to the development of various clinical issues such as depression, anxiety, sexual dysfunction, and PTSD. An evolutionary perspective on the effects of rape could be beneficial to research because a key feature of women's mating strategies is their evolved perceptions of viable romantic and sexual partners. Rape impedes those evolved mechanisms and could possibly lead women to lose out on potential long-term mates due to the psychological costs of rape.

Perilloux et al. (2012) conducted an experiment in which they looked at two groups, "victims of completed sexual assault" and "victims of attempted sexual assault." Researchers measured a host of variables which consisted of health, self-esteem, self-perceived attractiveness, self-perceived value as a romantic partner, family relationships, work life, social life, social reputation, desire to have sex, frequency of sex, enjoyment of sex, and long-term committed relationships. What was discovered was that 11 of the 13 domains analyzed showed a statistically significant impact on "victims of completed sexual assault" livelihood. The largest effect size was seen in self-esteem, self-perceived value as a romantic partner, and sexual reputation. The two domains that did not differ between groups was work life and enjoyment of sex. Based on results of the experiment, researchers see a strengthened argument, in

an evolutionary psychological and fitness point-of-view, on how rape and/or sexual assault is so costly and how rape plays a key role in victims' mating strategies and mating outcomes.

Conclusion

Looking back on the evidence that has been pulled together by researchers around the world in various fields of psychology, there are a couple of statements that show a lot of proof and are represented by the research. Firstly, we can break the term rapist into different subsets of the term depending on hunting strategies, preference, and thought processes. Evolutionary speaking, these subsets of rapists could lead us to further research in which we identify evolutionary or adaptive mechanisms that would explain formations of the cognitive processes that would form and lead to the blooming of a rapist.

Secondly, there is research out there that suggests that women have certain mechanisms cognitively that would allow them to protect themselves from would-be rapists and/or unwanted offspring that would come about from being raped. Evolutionarily speaking, these mechanisms would protect oneself from harm as well as keep the woman from harm, both mentally and physically.

Lastly, victims of rape can be affected in a variety of ways. Oftentimes, however, the repercussions and costs that are experienced by victims of sexual assault differ from the costs and repercussions that a victim of attempted sexual assault would experience. These repercussions affect all sorts of domains such as how enjoyable sex is to self-perceived value as a romantic partner. These costs could lead to a decline in a woman having offspring, which in turn prevents genes from being passed on, ultimately falling into the "survival of the fittest" category that do not survive.

Further research is required to really delve more into all these proposals. There are plenty of avenues that researchers can take in order to test more on the evolutionary perspectives of rape, and these hypotheses can have an impact on other areas of psychology as well.

Cross-References

- ▶ [Alcohol and Rape on College Campuses](#)
- ▶ [Drugs and Rape on College Campuses](#)
- ▶ [Ecological Factors and Rape](#)
- ▶ [Female Counter-Adaptations to Rape](#)
- ▶ [Life History Theory and Rape](#)
- ▶ [Partner Rape](#)
- ▶ [Rape](#)
- ▶ [Rape and Dating](#)
- ▶ [Rape Avoidance](#)
- ▶ [Rape in Warfare](#)
- ▶ [Sexual Coercion and Rape](#)

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Evolutionary Perspectives on Religion

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Synonyms

[Evolution of religion](#)

Definition

How and *why* are the two different questions to examine the evolution of religions. The first question requires taking a sociohistorical (and perhaps also a phylogenetic) perspective on religion and giving an exposition of the historical development of the phenomena collectively known as religion. The second requires taking a functional/adaptive perspective on religion and answering the thorny question of whether religion evolved as an adaptation or a by-product.

How Did Religion Evolve?

There is no consensus among scholars on the definition of religion. Some even argue that the concept of religion does not apply to all cultures and historical periods. For the present purposes, however, we will adopt Durkheim’s (1912) classic definition of religion as a set of beliefs and practices that unite groups into a moral community around a sense of the sacred. The “sacred” often, but not always, involves a supernatural realm with supernatural agents. Beliefs are mostly about the supernatural, whereas practices include rituals that aim to appease supernatural agents or to invoke their intervention in worldly affairs.

No nonhuman animal species display behavior that conforms to this definition of religion. We can

thus assume that full-blown religion is uniquely human. On the other hand, ritual-like behavior of elephants around the dead and mourning for the dead in several species have been observed. There is also suggestive evidence regarding Neanderthal burials, which might indicate belief in an afterlife. However, there is no conclusive evidence that religion existed before the advent of behavioral modernity.

The evolutionary history of religion in *Homo sapiens* has been most thoroughly described by the sociologist of religion Robert Bellah in his magisterial work *Religion in Human Evolution: From the Paleolithic to the Axial Age*. This section will follow his exposition.

Bellah (2011) describes three stages in the historical evolution of religion based on the evolution of representational abilities. The first is tribal religion which existed throughout the Paleolithic age. Following the psychologist Donald Merlin's (1991) classification, Bellah states that mimetic culture and enactive representations characterize this stage. The main form of religious practice is ritual, for which child play is the evolutionary precursor. Rituals enact social relationships, relationships to ancestors and to spirits and thus maintain the social order. Ritual burials with grave goods are first evidence of religious behavior which suggest belief in an afterlife. We still see tribal religion in modern hunter-gatherer societies.

In the next stage, we encounter archaic religion. This is the religious form of large agricultural societies. Mythic culture and symbolic representations (images and icons) characterize this stage. Religious concepts are communicated through visual art and oral narratives. Simple emotions are transformed into more specialized emotions and attitudes through symbolic representation: awe, equanimity, self-transcendence, etc. We first see the examples of this type of religion in ancient Mesopotamia, ancient Egypt, and Zhou China. The society is hierarchically organized and the god-king is the mediator between the national gods and the people.

In the final stage, we encounter Axial religion. Axial age is the name first given by Karl Jaspers (1949) to the period between 800 and 200 BC

(sometimes extended to cover the whole first millennium BC). This is the time when great religious traditions that still exist came into being almost simultaneously and with little contact among each other: Confucianism and Taoism in China; the Upanishads and Buddhism in India; teachings of the reformist prophets Isaiah and Jeremiah in ancient Israel; and those of Socrates and Plato in ancient Greece. What characterized this period was a quest for human meaning in the universe and the rise of an elite class of religious leaders and thinkers.

Theoretical culture and conceptual (standpoint free) representations characterize the Axial age. Religions develop a theology for the first time and they make a claim to be universal rather than just nationalist. Religion does not just serve to maintain status quo but criticizes and transforms it. Culture depends on writing and external storage of memory. The deity becomes transcendent and an ontological divide is introduced between God and humans.

Bellah maintains that, through this process of cultural evolution, new stages do not merely replace old ones but build upon them. Thus, theoretic culture is added to the already existing mimetic and mythic cultures. Interestingly, Bellah does not touch upon the two largest world religions today: Christianity and Islam. He thinks they are extensions of the classic Axial age religions and do not represent a new stage in the evolutionary history of religions.

Why Did Religion Evolve?

According to modern evolutionary theory, a trait that comes about as a result of the process of evolution has to be one of three things: an adaptation (the direct product of natural selection), a by-product (the nonadaptive vestige of another adaptation), or a random effect (not produced directly or indirectly by natural selection but the product of historical accidents; see Buss et al. 1998). Since religion is a highly complex and functional (in the nontechnical sense) phenomenon, we can rule out the possibility that it is an

accidental or random product of evolution. Thus, it either evolved because it somehow provided survival or reproductive advantage to ancient humans, or else it evolved as a side effect of other traits that did provide such an advantage. Accordingly, we can distinguish between religion as adaptation theories and religion as by-product theories.

Religion as an Adaptation

Adaptationist theories of religion generally emphasize the cooperative nature of religion: Religion promotes cooperation within a society. Large-scale cooperation between genetically unrelated individuals is usually seen as what makes humans unique among animals and what enables human civilization and is clearly adaptive. Since it is assumed that large-scale cooperation is unlikely to be brought about by standard evolutionary mechanisms (e.g., kin selection, direct or indirect reciprocity), religion is offered as the mechanism to do the job. If religion indeed promotes large-scale cooperation, it can be seen as an adaptation. Religion might play this role in several different but complementary ways.

One prominent aspect of many religions is the extravagant displays they employ: circumcision, fasting, snake handling, etc. One has to engage in these displays to be accepted and to remain in the religious group. One reason religion has defied an adaptationist analysis is that these displays are so costly, time consuming, and downright dangerous that they clearly decrease one's chances of survival. However,

The performance of these costly behaviors signals commitment and loyalty to the group and the beliefs of its members. Thus, trust is enhanced among group members, which enables them to minimize costly monitoring mechanisms that are otherwise necessary to overcome the free-rider problems that typically plague collective pursuits. (Sosis and Alcorta 2003, p. 267)

Thus, costly rituals engender trust among group members precisely because they are hard to fake by others who do not share the moral outlook of the group and only want to join the group to reap the benefits of group living without contributing anything. Trust, on the other hand, is

what enables cooperation among individuals who do not know each other personally (see also Bulbulia 2004; Henrich 2009).

Another way religion can promote cooperation and harmony in large groups is by invoking supernatural agents (traditionally referred to as gods) who are watchful, morally concerned and powerful. Noncooperators and other norm violators need to be monitored and deterred if intragroup cooperation is to be maintained. This becomes increasingly difficult to do on a personal basis as group size increases. If, on the other hand, everyone in the group believes in the existence of supernatural agents who watch and know about everyone, who are concerned with morally relevant behavior of group members, and who are powerful enough to punish norm violations wherever and whenever they occur, then norm violations can be effectively prevented. The so-called supernatural punishment hypothesis has been used to explain how religions with big moralizing gods can foster cooperation and vice versa: As religions expand at the expense of less successful forms of religion, their networks of cooperation also expand, and an ever-expanding large-scale cooperation is enabled (see Norenzayan 2013). The fact that participants who are reminded of a punishing God behave more altruistically to anonymous partners in an economic game (or hypothetically) is one type experimental support for the theory (Shariff and Norenzayan 2007; Yilmaz and Bahcekapili 2016). In addition, it has been observed that there is a negative correlation between belief in hell and national crime rates, whereas a positive correlation between belief in heaven and crime rate, again supporting the supernatural punishment hypothesis (Shariff and Rhemtulla 2012).

Religion as a By-product

Cognitive scientists of religion generally argue that religious thought is nothing special; general cognitive mechanisms that subserve belief formation produce religious beliefs under certain circumstances as well. Thus, religious thought is a by-product of ordinary thought, which has itself evolved as an adaptation.

Some of those general cognitive mechanisms include agency detection, theory of mind, and precautionary reasoning. Agency detection is the ability and tendency to detect the presence of agents that might cause harm to the individual. Theory of mind is the ability and tendency to attribute beliefs and desires to an agent and thus to predict the likely behavior of the agent. If these tendencies are extended to natural events without obvious explanations, one can deduce the existence of supernatural beings behind thunder, earthquakes, and the normal cycles of life, and thus take precautions to prevent or appease such beings. Religious belief and ritual can therefore be explained as a by-product without reference to a separate religious mental module or an adaptive function subserved by religion (see Boyer 2001).

If religious belief is a natural extension of ordinary cognitive processes, why do some individuals altogether lack such beliefs? An evolutionary psychology of religion should also be able to explain the evolution of irreligion. A recent attempt to do so argues that the same cognitive and cultural processes that lead to religiosity can also create a tendency toward atheism (Norenzayan and Gervais 2013). If theory-of-mind (or mentalizing) abilities create a disposition toward religious belief, individuals with weak mentalizing skills should be disposed toward religious disbelief. In fact, the autistic spectrum is associated with lower levels of belief in a personal God. Second, if religious belief is intuitive, individuals who routinely suppress intuitive thinking tendencies in order to think analytically should be disposed toward religious disbelief. In fact, scientists generally show much lower levels of religious belief compared to the general population. Third, if religious belief needs cultural support to be maintained, lack of public displays of religiosity should lead to irreligion. In fact, religious belief is especially low in secular societies where religious education and symbols have left the public sphere. Finally, if religious belief is a solution to existential needs such as security and control, individuals might be indifferent to religion if such needs are met by other means. In fact, religious belief is especially low in Scandinavian societies where social security systems are especially powerful.

Cross-References

- [Evolution of Cooperation](#)
- [Religion](#)
- [Religious Beliefs](#)

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Evolutionary Political Psychology

- [Social Dominance Orientation \(SDO\)](#)

Evolutionary Precursor to Language and Music

► Musical Protolanguage

Evolutionary Pressure on Meat Eating

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Synonyms

Carnivorous, Flesh eating, Predacious,
Omniphagous

Definition

Factors influencing abandonment of herbivorous diet and favoring the inclusion of meat in a more omnivorous eating pattern.

Introduction

As far as we can tell the first primate appeared 65 million years ago, just about at the time that the dinosaurs had gone extinct together with over half of the world's other animal species. *Purgatorius* was a small animal who was an accomplished tree climber and looked much like a cross between a mouse and a squirrel. *Purgatorius* was also a vegan who took advantage of the fruits, flowers, and leaves which were now more abundant since the large herbivorous reptiles had disappeared from the planet. For millions of years, the descendants of *Purgatorius*, who were now evolving into monkeys and apes, diversified their diet somewhat, adding seeds and nuts to their diets along with occasional worms and insects (that may have been eaten more by accident than intent). Ultimately, however, that mostly vegan diet would prove not to be adaptive.

The First Meat Eating Primates

It was around 6 million years ago that the first *hominid* (or protohuman) entered the scene in Africa. *Sahelanthropus tchadensis* was a short, flat faced, small brained creature that represented a split from our closest relatives, the chimpanzees and apes. There is some convincing evidence that *Sahelanthropus*'s successors, such as *Australopithecus* did eat meat, at least occasionally. The meat which they obtained probably came through scavenging rather than through hunting (Blumenshine and Cavallo 1992). Eating raw meat, however, almost certainly comprised only a small percentage of the *australopith*'s diet since his gut (namely his stomach and intestines) was set up to process fruits and leaves. This means that he had a big cecum, which is a pouch at the beginning of the large intestine that contains lots of bacteria to help process fibrous materials. If an *australopith* gorged himself on a large quantity of raw meat, this could result in a twisting of the colon that would produce stomach pains and bloating and this might even result in death.

Successive versions of *hominids* had to deal with climate changes which affected the amount of rainfall that in turn affected the amount of grassy plants with seeds (like wheat and barley) and the availability of nuts. Both of these food sources are rich in fats but poor in fiber. Such a diet encourages the growth of the small intestine where the digestion of lipids occurs, and the shrinking of the cecum, where the digestion of fibers occurs. As the climate continued its steady change, much of the rain forest would have turned into sparsely wooded grasslands which, although providing fewer high-quality plants to eat, would be populated with more grazing animals which could now serve as a source of meat.

Later Hominids

By the time that *Homo erectus* appeared on the scene, significant changes had occurred in the gut which allowed meat to be eaten. Scavenging could still play a large part in the way in which meat was obtained. Recent research has shown that typically 95% of bones that are abandoned

by large predators still have some flesh remaining on them and over 50% have significant amounts of meat left (Pobiner 2015). It appears that early hominids often carried large bones and skulls back to their campsites. Using stone tools they could crack the skulls to get at the nutrient rich brains (which were very difficult for the hunting carnivores of the time to take advantage of). In addition, by using stone tools, they could crack the large bones to get at the fatty and calorie rich bone marrow inside.

The Expensive Organ Hypothesis

Homo erectus and his successors eventually began to actively hunt for meat. This new behavior required increased intelligence to outsmart the prey animals (after all fruits and vegetables don't try to run away) and to also support communication necessary for cooperative hunting. Hunting requires weapons, while stripping and processing flesh from the animals that are killed requires tools. Thus the major activities associated with hunting, and weapon and tool use, required a larger brain size.

The evolutionary problem is that brains are expensive. Modern human brains take up only around 2% of our body weight as adults yet they use about 20% of our energy. It is possible to offset some of the energy requirements for a large brain by reducing the size of the liver and gastrointestinal tract, since these, like the brain, are metabolically expensive tissues. But reducing the size of the gut is related to diet. Smaller guts require a diet that contains high-quality food that is easy to digest. The evolutionary solution was to take advantage of the nutritionally dense muscle mass of other animals. Some scientists have argued that without the abundance of calories afforded by meat eating, the human brain simply could not have evolved to its current form (Aiello and Wheeler 1995).

Culture and Cooking

Meanwhile, cultural and technological changes were also causing revolutions in our dietary

history. One of the principal events was the development of cooking. Cooked food is physically easier to chew and chemically easier to digest. This allows the extraction of more energy from the same amount of food. Cooking can also release more of certain nutrients than can be obtained from eating that same food raw. It can also render certain poisonous plants palatable. Cooking also saves energy that can be diverted to the brain (Wrangham 2009). One study looked at how Paleolithic food processing affected chewing force production and efficiency in humans consuming meat. It found that if meat comprised one-third of the diet, the number of chewing cycles per year would have declined by nearly 2 million (a 13% reduction) and also required 15% less bite force. Thus cooking combined with the availability of meat greatly increases the amount of energy available for that larger evolving brain (Zink and Lieberman 2016).

The Effects on Fertility

While increased meat eating was supporting the growth of the brain and intelligence, it appears that this change in diet also effectively increased human fertility. Recent research has shown that there is a strong connection between meat eating and the duration of breast-feeding. Data shows that all carnivorous species have relatively short periods of breast-feeding and early weaning compared to primate species whose diet is composed only of plant matter. This means that by shifting the diet of humans toward the consumption of more meat reduces the time between births. This increased fertility had an impact on human evolution and allowed the global spread of humans to accelerate (Psouni et al. 2012).

A History of Continuous Change

It appears that humans have bodies that are continually changing to cope with the availability of new foods. The case of organized

agriculture is the most clear. With agriculture, some human populations evolved extra copies of amylase genes, which allow them to be better able to deal with starchy foods. In response to animal husbandry and the keeping of animals that provide milk, several human populations independently evolved gene variants that coded for the production of lactase which breaks down lactose, a substance that comprises 2–8% of milk by weight. In some human groups, adults do not produce lactase and for them the eating or drinking of milk-based food results in lactose intolerance which has symptoms including abdominal pain, bloating, diarrhea, gas, and nausea.

Not all of these changes in the ability to utilize certain food sources are due to genetics. If we consider the digestive system of a typical mammal, we find a stomach that breaks down the protein, a small intestine that absorbs sugars and a large intestine that ferments and digests whatever plant material is left over. The length of the intestines is important. In humans, the large intestines are shorter than those of living apes relative to the overall size of our gut (more like 25% of the whole, compared to 46% of the whole in chimps). This shortness appears to make humans less able to obtain nutrients from the cellulose in plant material than are other primates. However, each stage of digestion requires the assistance of many gut bacteria. These make up the *microbiome* which has become an active area of study recently. The gut microbes can vary among different human populations, making some foods more or less digestible. Thus humans in Japan have a kind of bacteria in their guts which appears to have stolen genes for breaking down seaweed, a foodstuff that became popular along with rise of an agricultural Japanese diet. One current presumption is that our Stone Age ancestors, by eating a little bit more meat tended to cultivate more of the bacteria that help break down meat during digestion. These microbes were then passed on to successive generations during pregnancy and birth, thus giving their descendants a head start on the ability to process meat (Lambert 1998).

Drifting Away from Carnivory

One must not suggest that the natural course of evolution must inevitably be toward the eating of more meat. Remember, that we mentioned that during the agricultural revolution human beings began to pick up extra copies of the amylase gene, which allows them to process carbohydrates. An interesting case of a species evolving away from an intensively carnivorous, meat eating diet can be found in the comparison between wolves and dogs. Most of the genetic evidence says that the animals that we recognize as dogs emerged in the Neolithic period. That would be just about the time when humans were beginning to transition from a hunter-gatherer lifestyle to one involving agriculture and fixed settlements. Since dogs were domesticated around this time, it appears to have some implications for how dogs have diverged genetically from wolves and which resulted in dogs turning away from a purely meat-based diet.

To understand this, you must consider the scavenger hypothesis about how dogs were domesticated. This is the hypothesis which says that wild canines began to hang around human settlements to eat the scraps of food that humans tossed into their garbage heaps. Since this was the dawn of organized agriculture more grain-based starches and carbohydrates were beginning to make their way into the human diet. Through natural selection, the wild canines that could best process and survive on such a starch-based diet would obviously thrive the best and produce the most offspring. Over generations, natural selection would cause a set of genetic differences to evolve, eventually leading to our domesticated dog having an ability to process such foods more easily. In such a way, dogs would drift away from a purely carnivorous diet to one that could also utilize plant-based carbohydrates.

Recent research has shown that genetic differences have evolved between dogs and wolves. The strongest example is one alpha-amylase gene that is involved in the processing of starch in the pancreas. While the wolf genome carries 2 copies of this gene, dogs carry anywhere from 4 to 30 copies. Furthermore, chemicals associated with the digestion

of carbohydrates that are influenced by this gene are 28 times higher in the pancreas of dogs and nearly 5 times higher in their blood. Thus while the wolf remains a nearly obligatory carnivore, dogs can happily survive on a diet that is not solely based upon meat eating (Axelsson et al. 2013).

Conclusion

Thus the conclusion is that meat eating in humans and other species depends upon a number of factors. The availability of meat versus specific plant materials and the presence of a brain with high metabolic needs seem to be the forces most prominently driving the evolution of this behavior (Zaraska 2016).

Cross-References

- [Australopithecus Group](#)
- [Brain Evolution Resulting from Cooking](#)
- [Brain Size and Intelligence](#)
- [Canines](#)
- [Ecological Influences](#)
- [Evolution of Intelligence](#)
- [Evolution of the Brain, The](#)
- [Gut Microbiome](#)
- [Increased Energy/Reduced Digestion](#)
- [Reproductive Frequency](#)

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Evolutionary Psychiatry

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Synonyms

[Darwinian medicine](#); [Evolutionary mismatch](#);
[Vulnerability to mental disorders](#)

Definition

Evolutionary psychiatry applies the principles of evolutionary theory in psychiatric research and clinical practice. It utilizes and synthesizes similar theoretical models and research as Darwinian medicine, but focuses more on specific disciplines including psychology, psychiatry, and behavioral genetics. The evolutionary view of mental complaints highlights the role of functional capacities and biological adaptations in defining psychiatric disorders. This Darwinian approach provides an integrated biopsychosocial model for mental health and a theoretical framework for understanding human vulnerability to mental problems.

Introduction

Similar to Darwinian medicine, evolutionary models of psychiatric disorders contribute to a more comprehensive understanding of human

mental health and disorders (Brüne 2015). In order to describe the reasons why humans are vulnerable to mental problems, evolutionary psychiatry uses the same principles and explanations as Darwinian medicine (Nesse 2015). It emphasizes that selection processes formed human characteristics in order to serve our survival and/or reproduction and not to maintain our health. Evolutionary models of mental disorders also highlight the influence of the environments in which humans used to live and the effect of the rapid and excessive change of circumstances transforming *adaptive capacities* into risk for illness (Brüne 2015; Nesse 2015).

Functional Capacities and Mental Health

The criteria used to determine psychiatric disorders are based on the level, the extent, and temporal course of impairment (Troisi and McGuire 1998, 2002). However, to separate normal functioning from abnormal in terms of mental processes requires the evaluation of the appropriateness of a reaction or behavior to the situation (Nesse 2015). An integrated analysis of mental health including evolutionary models can help to separate normal and abnormal reactions or functions based on two key principles: (1) the *capacity to achieve biological goals* and (2) to *consider environmental factors* in which individuals live (Troisi and McGuire 1998, 2002).

Selection mechanisms favor psychological and behavioral traits that benefit the effective adaptation of the individual to certain environmental factors. Behavioral strategies enhancing individual evolutionary success include traits that enable the person to accomplish biological goals. A trait can be considered as adaptive if it can enhance the inclusive fitness of the individual. Nevertheless, different traits represent divergent forms of adaptations and they can be beneficial only in certain environments. Therefore, adaptations or functional traits are “case sensitive”; no trait is adaptive in every environment. Adaptations can enhance inclusive fitness in specific environments and if the circumstances change, they may no longer be functional or beneficial (Troisi and McGuire 1998, 2002).

Evolutionary psychiatry argues that the capability to achieve short-term biological goals is a valid indicator for adaptations, and functional capacities are predictive for future accomplishment of these goals. Correspondingly, focusing on functional capacities and biological benefits would allow clinicians to build up a more comprehensive assessment of the patients and the impairments linked to their disorders. Moreover, it contributes to the distinction of normal and abnormal behavior or characteristics and provides an integrated framework for psychiatric evaluation and diagnostics.

Individual Differences

Gene-environment interaction plays an important role in explaining individual vulnerability, that is, why some individuals get ill while others in the same environment do not. Correspondingly, the interplay between genes and environmental factors is acknowledged as a dominant causal factor creating individual differences in proneness to develop mental disorders. However, to understand and explain how genotype interacts with environmental factors is highly difficult. Moreover, other factors can also affect variations among individuals: differences can be caused by differences in genes, environmental factors, or by the interactions of these two key factors (Brüne 2015).

As pointed out earlier, models of evolutionary psychiatry share the vast majority of explanation and principles of Darwinian medicine. Accordingly, individual vulnerability to psychiatric disorders can be influenced by mechanisms, which can be also accounted for influence individual risk of physiological or somatic illness. Effects of trauma, toxins, or other harmful conditions, or cultural and interpersonal experiences guiding the development of social competences can also increase or decrease the vulnerability of the individual. Several random factors (e.g., neural development) or contrariwise, nonrandom factors, such as *assortative mating* (homogamy), finding a partner with highly similar characteristics and probably with similar genotype can also impact the development of individual differences (Nesse 2015).

Conclusion

Evolutionary psychiatry is based on two key points: First, Darwinian models of mental health are outcome-centered, thus, conditions considered as pathological have harmful consequences for the individual. Consequences of the environmental factors, which can be detrimental in case of insufficient adaptation, are primarily emphasized as casual factors and not the circumstances per se. Second, environmental factors determine the efficiency of functional capacities. Optimal conditions can moderate or even overrule inadequate functions, whereas more disadvantageous environments might compromise the adaptability of these capacities. Consequently, functional impairment and biological adaptation are the fundaments of evolutionary psychiatry.

Cross-References

- ▶ [Anxiety \(Randolph Nesse\)](#)
- ▶ [Darwinian Psychiatry](#)
- ▶ [Evolutionary Clinical Psychology](#)
- ▶ [Evolutionary Medicine](#)
- ▶ [Evolutionary Mismatch](#)
- ▶ [Simon Baron-Cohen \(Darwinian Psychiatry\)](#)
- ▶ [Stress Reduction and Mental Health](#)
- ▶ [Psychiatry of Nonhuman Apes](#)

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Evolutionary Psychologist

- ▶ [Douglas Kenrick](#)

Evolutionary Psychology

- ▶ [Adapted Mind, The](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Evolutionary Biology and Feminism](#)
- ▶ [Evolutionary Psychology, The Handbook of](#)
- ▶ [Genuine Altruism](#)
- ▶ [Jay Belsky](#)
- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)
- ▶ [Morality](#)
- ▶ [Repeated or Iterated Prisoner's Dilemma](#)

Evolutionary Psychology and Culture

- ▶ [Evolutionary Cultural Psychology](#)

Evolutionary Psychology and Intimate Partner Violence

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Synonyms

[Domestic violence](#); [Infidelity](#); [Partner-directed violence](#); [Sexual conflict theory](#); [Sexual jealousy](#)

Definition

Intimate partner violence (IPV) refers to when an individual attempts to harm or control their

current/former romantic partner, in a manner that is against that partner's will (Chester and DeWall 2018). Broadly, IPV includes physical, psychological/emotional, and/or sexual forms of abuse (Arnocky et al. 2015; Caldwell et al. 2012). Intimate partner stalking has also been conceptualized as a form of IPV (Norris et al. 2011).

Introduction

Worldwide, IPV prevalence estimates are high, with World Health Organization statistics indicating that almost one third of women almost one third of women report having experienced some form of physical and/or sexual violence by their intimate partner in their lifetime (World Health Organisation 2017). Although women, particularly younger women, are more likely to experience IPV (Sugg 2015), it should be noted that women also perpetrate violence toward partners, and as such a comprehensive overview of IPV should also include consideration of women-initiated violence (see Buss and Duntley 2011). Both men and women engage in vigilant and violent behaviors in an attempt to protect and defend mating relationships (Buss and Shackelford 1997).

A range of theoretical perspectives have been applied in an attempt to understand and examine IPV, including considerations of cultural and societal conditions (e.g., Brownmiller 1975) and psychological perspectives, such as evolutionary psychology. These approaches are not considered mutually exclusive; Chester and DeWall (2018) highlight that IPV likely results from a combination of multiple processes.

In this entry, evolutionary psychology perspectives of IPV are presented and discussed. Specifically, this entry will consider the evolved mechanisms that are considered to motivate and perpetuate IPV. The following sections will be discussed: (1) sexual conflict theory, (2) jealousy and sexual control, and (3) other adaptive problems and IPV. Finally, additional considerations and a conclusion will be provided.

Sexual Conflict Theory

To begin understanding the occurrence of IPV, Buss and Duntley (2011) recommend consideration of sexual conflict theory, a broad framework for understanding sexual conflict that occurs between males and females. Sexual conflict occurs when there are contrasting reproductive strategies for the sexes (Bonduriansky et al. 2008); specifically, the reproductive success for one sex potentially harms the reproductive potential for the other sex (see Promislow 2003). For example, the tendency for females to be the "choosier" sex (a strategy to promote their own potential reproductive success) potentially conflicts with the male tendency to acquire many sexual mates (a strategy to promote their own potential reproductive success). Such sexual conflict can occur across all stages of the relationship: before mating has taken place, during the relationship, and relationship termination/aftermath (Buss and Duntley 2011). In sum sexual conflict theory provides an appreciation for understanding that conflict in mating relationships is expected and common (Buss and Duntley 2011). However, although such theory provides a framework for understanding why conflict may occur, this does not condone or excuse violent and aggressive behavioral tactics employed in relationships (Buss and Duntley 2011).

Jealousy and Sexual Control

According to evolutionary perspectives, IPV may have evolved as it facilitated survival and reproductive goals; further, reproductive benefits gained from IPV ensured continued perpetuation of this behavior (Chester and DeWall 2018). In this section, I discuss reproductive benefits that may be facilitated by IPV.

Such violent behaviors enacted by men and women may be fuelled by jealousy (Shackelford and Duntley 2008). Jealousy, an emotion experienced when a relationship is threatened by a real or imaginary rival, primarily functions as a mechanism to maintain relationships (Goetz 2010). Although both men and women

experience jealousy as a reaction to threatened relationships, a sex difference is often seen in the type of jealousy experienced (Goetz 2010). Specifically, women are more likely to experience emotional jealousy and men are more likely to experience sexual jealousy; this sex difference is directly attributable to adaptive costs associated with the sexes (Goetz et al. 2008b). Men's emotional infidelity could threaten women's reproductive potential to secure a mate who will provide the necessary resources to ensure offspring survival, whereas women's sexual infidelity could threaten men's reproductive potential of paternity certainty, thus resulting in cuckoldry (Goetz 2010). Research has also shown men and women to be particularly jealous of rivals that might increase a mate's reproductive potential; for example, women are more upset by a physically attractive rival, whereas men are more upset by a rival with high status and resources (Brase et al. 2004).

This sex difference in jealousy has been replicated in a range of studies, ranging from self-report (Sagarin et al. 2003), experimental studies (Thomson et al. 2007), and physiological evidence (Buss et al. 1992). Regarding IPV, men's sexual jealousy is one of the most frequently cited causes (Buss as cited in Goetz et al. 2008b). The reproductive costs of mate infidelity and cuckoldry are considered so great for men that they have evolved to be particularly sensitive to sexual infidelity (Kaighobadi et al. 2009a); and IPV is a behavioral output of this sexual jealousy. Jealousy is viewed as an extremely important factor in men's violence against women (Puente and Cohen 2003).

Due to internal female fertilization processes and ovulation, men's genetic relatedness and paternity of offspring can remain relatively uncertain (Arnocky et al. 2015). As such, a man's ability to anticipate and prevent mate sexual infidelity has particular strong reproductive benefits (Starratt et al. 2007). Men may have evolved psychological mechanisms that motivate behaviors designed to prevent their partners from performing costly reproductive behaviors, such as being sexually unfaithful or terminating the relationship (Miner et al. 2009b; Starratt

and Shackelford 2012). According to initial researchers in this field, to prevent and overcome paternity uncertainty, males exert control over females' sexuality – referred to as “male sexual proprietariness” (Wilson and Daly 1996). As such, IPV is a tactic used to restrict and ultimately control a female mate's sexual behavior (Daly et al. 1982; Wilson and Daly 1993). IPV is not about controlling females, but controlling their sexuality (Wilson and Daly 1993).

If male-perpetrated IPV is an evolved mechanism to control females' sexuality and deter infidelity and relationship termination, then according to this hypothesis, IPV should vary with women's reproductive potential – assessable by age (see Wilson and Daly 1993). In 2002, Peters, Shackelford, and Buss tested the hypothesis that IPV rates would vary with women's reproductive value; specifically, IPV would decrease as female age increased. Data was collected from the United States-based police incident reports concerning nonlethal domestic disturbance; these reports are provided to the Domestic Violence Prevention Project (DVPP) of Safe Horizon, whom then provided the researchers with the data. In total, there were 3,969 cases involving 1 female victim and 1 male perpetrator. The average age of victims was 32.7 years ($SD = 9.3$), and the average age of perpetrators was 35.1 years ($SD = 9.6$). Data showed women in the youngest age category (aged 15–24 years) were at greatest risk of experiencing IPV (twice as high as the next age category [aged 25–34 years]), and these rates declined with age. Further, data also showed that although IPV was most often perpetrated by younger men, women were most likely to experience IPV when mated to a man two age categories older. As such, the authors concluded that the risk women experiencing IPV cannot be attributed to mating with younger, violent men. Peters et al. (2002) concluded that the findings based on the data were consistent with the hypothesis that IPV functions to control women's sexual behavior during her reproductive years. This pattern of results has also been demonstrated outside of research testing evolutionary hypotheses (age-IPV curve; Johnson et al. 2015).

A significant amount of research has supported the relationship between infidelity suspicion and prevention and IPV (Wilson and Daly 1998, provide a review). Different forms of violence may be enacted for different purposes; for example, physical aggression might punish a partner for infidelity or discourage the partner from future indiscretions (Arnocky et al. 2015), whereas psychological aggression might serve to reduce a mate's self-esteem, thus exercising further control (Buss 1994/2003/2016). Further substantiating the importance of the importance of infidelity suspicion when enacting IPV, research has shown the relationship between personality traits (e.g., emotional stability, agreeableness, and conscientiousness) and partner-directed violence to be dependent on risk perceptions of partner infidelity (Kaighobadi et al. 2009b).

It is important to note that suspicion of partner infidelity may not initially escalate to violence, and a temporal hierarchy may exist between nonviolent and violent mate retention behaviors. Kaighobadi et al. (2008) tested the hypothesis that accusations of female infidelity would predict men's partner-directed violence across two studies (men's self-reports and women's partner reports). Results indicated that female sexual infidelity was positively related to IPV; further, nonviolent mate-guarding behaviors mediated the relationship between accusations of infidelity and female-directed IPV. To explain this mediation, the authors speculated a temporal hierarchy between nonviolent and violent mate retention behaviors. Specifically, men may initially enact less costly nonviolent behaviors before ending in acts of violence.

A final consideration here regards the interesting relationship humans have with jealousy. Specifically, humans tend to interpret acts of jealousy as acts of love, an interesting trend given the relationship between sexual jealousy, infidelity suspicion, and IPV. Over three studies, Puente and Cohen (2003) explored observer interpretations of acts as jealousy. Participants were presented with a jealous man who abused his wife and a jealous man who did not abuse his wife. Results indicated that participants believed jealousy to be a sign of love and did not believe

jealousy-related violence indicated a lack of love. Participants viewed the jealous man who abused his wife and the jealous husband who did not abuse his wife as similarly loving. Importantly (and concerning), participants viewed the abusive, jealous man as significantly more loving than the nonviolent, non-jealous man.

Sexual coercion and IPV. A particular type of IPV – sexual coercion – is also hypothesized to manifest from suspicions of sexual infidelity (Goetz et al. 2008a) and male sexual jealousy (Kaighobadi et al. 2009b). Sexual coercion refers to “the use of force, intimidation, lying, or psychoactive substances to receive or perform sexual acts” (Gladden et al. 2008, p. 319). Here, I refer to sexual coercion within relationships. Physical abuse in a relationship has been shown to be a reliable predictor of sexual coercion (Shackelford and Goetz 2004), and men's suspicion of partner infidelity has also been linked to increased sexual coercion (Goetz and Shackelford 2009). Sexual coercion in relationships has been attributed to men's motivation to achieve dominance over and control his partner (see Goetz and Shackelford 2009, for a full discussion) and evolutionary perspectives. Specifically, sexual coercion may have evolved in response to infidelity and cuckoldry and may function to introduce the male's sperm into the female to be in direct competition with any rival male's sperm (Goetz et al. 2008b; Starratt and Shackelford 2008). Given the high reproductive costs of female infidelity and cuckoldry, sexual coercion, and in turn sexual violence, in relationships may have evolved as an “anti-cuckoldry” strategy (Starratt and Shackelford 2008).

In sum, research has shown sexual coercion to be predicted by both partner infidelity suspicions and male control (Goetz and Shackelford 2009); as such, both of these predictors provide adequate interpretation for perpetrating sexual IPV.

Other Adaptive Problems and IPV

Mate value. Although the evolved violent behavior enacted to avoid sexual infidelity and relationship termination is often cited as a key

explanatory perspective of IPV, there are other adaptive problems men and women might face in which IPV could be employed. One of these adaptive problems concerns an imbalance in mate value.

Assortative mating refers to a nonrandom mating pattern where mates express more similar phenotypes than would be expected by random mating (Buss and Duntley 2011). Mate value, one of the strongest domains of assortative mating, is defined as the genetic quality of oneself as a sexual partner, displayed through observable characteristics (Kirsner et al. 2003). Despite this initial definition, Fisher et al. (2008) argue that mate value need not exclusively depend on reproductive characteristics and suggest mate value is defined as “the total sum of characteristics an individual possesses at a given moment and within a particular context that impacts on their ability to successfully find, attract, and retain a mate” (p. 157).

An imbalance in mate value arises when the value of one mate may exceed, or be considered inadequate, to the value of the other mate. For example, status and resources are considered, cross-culturally, to be important determinants of a man’s mate value, whereas physical attractiveness is considered, cross-culturally, to be important determinants of a woman’s mate value (Buss et al. 1990). A mate value imbalance could exist when one mate possesses a high level of the characteristics desired by the opposite sex. Alternatively, a man might consider himself to be at a competitive disadvantage with other competitors if he has less of the characteristics (i.e., status and resources) desired by the opposite sex (thus lower mate value; Figueredo et al. 2012).

Buss and Duntley (2011) discussed how mate value discrepancies can trigger a causal chain of behavior, leading to IPV. Specifically, higher mate value (particularly of women) increases the likeliness of infidelity. Higher mate value also increases the likeliness of relationship termination. Finally, men’s lower mate value is usually associated with lower status and resources, characteristics women desire in a mate. Due to this lower mate value and inability to provide desired resources, this increases the likelihood of

a woman committing infidelity or terminating the relationship. This causal chain therefore increases the likelihood of IPV, particularly male-directed violence.

Although somewhat limited, there is evidence that mate value discrepancy in a relationship predicts IPV behaviors; the mate lower in mate value is more likely to express controlling and aggressive behavior toward their mate. An imbalance in mate value in a relationship has even been shown to predict nonviolent relationship behavior. In a sample of 158 women, Miner et al. (2009a) asked participants to provide information about their own mate value, their partner’s mate value, and their partner’s verbal insults. Male mate value, compared to female mate value, was found to be a better predictor of men’s verbal insults directed at the partner. Further, when the man had lower mate value than the woman, the verbal insults were more frequent. It should be noted though that low mate value may be inexplicitly linked to sexual jealousy (Figueredo et al. 2012). As such, low mate value may therefore be a better explanation for experiencing sexual jealousy, which in turn predicts perpetration of IPV.

Sex ratio. An evolutionary psychology perspective also posits that a high sex ratio (i.e., more of one sex than another) will induce intersex competition. For example, when there are more men than women in the population, this increases competition between men for access to women. Specifically, as the proportion of men to women in a population increases, men may become increasingly concerned about infidelity; this in turn fuels sexual jealousy which, as discussed above, perpetuates IPV (see Wilson and Daly 1998). This produces a rather simple hypothesis; in a population where there are more men than women, there should be an increase IPV. Not all research has shown this relationship, with South and Messner (1987) finding no relationship between sex ratio and homicide data drawn from Supplemental Homicide Reports. However, given the relative infrequency of intimate partner homicide, such indices may not be a reliable assessment of the occurrence of IPV; indeed, South and Messner (1987) indicated that future research

should explore the relationship between sex ratio and female victimization in non-homicidal violence. To explore this relationship, D'Alessio and Stolzenberg (2010) assessed data from the Federal Bureau of Investigation's National Incident-Based Reporting System (NIBRS) and the US Census for reports of male-on-female intimate partner violence. Results showed that after controlling for a variety of factors (e.g., income, race), a high sex ratio is a significant predictor of increased male-on-female IPV. D'Alessio and Stolzenberg (2010) posit that their data supports an evolutionary perspective; the disparate sex ratio increases intersex competition, and as such men use IPV as a mechanism to control their mate's sexual behavior. The link between sex ratio and IPV has been replicated in other research; for example, La Mattina (2013) found that in post-genocide Rwanda where there was a significant decrease in the number of men (thus significant disparate sex ratio between men and women), there was a significant increase in occurrence of IPV.

Resource infidelity and scarcity. Buss and Duntley (2011) discuss resource infidelity and scarcity are two circumstances that could possibly eventuate in mate-directed violence. Resource infidelity is described as diverting resources away from the mate and offspring and directing these resources toward extra-pair mating (Buss and Duntley 2011). Such resource infidelity can occur for men and women; however, given the importance women place on status and resources in a relationship (see Buss et al. 1990), resource infidelity might provoke a stronger jealous response in women. Although research has not yet specifically explored resource infidelity as a precursor to IPV, Buss and Duntley (2011) suggest that this is a predictable form of couple conflict which could result in aggression and violence.

Like resource infidelity, resource scarcity might also be perpetuate conflict in a relationship, which could result in IPV. Resource scarcity refers to the insufficient supply of provision of resources in the relationship. This resource deficit might have been present from the onset of the relationship, such that the mate is of lower

mate value in comparison to competitors. Alternatively, the resource scarcity might have eventuated during the course of the relationship, owing to financial hardship, job termination, etc. In either circumstance, these men experiencing resource scarcity might use cost-inflicting tactics as a way to maintain the relationship, preventing infidelity and relationship desertion (Wilson and Daly 1993). Research supports this premise, with links documented between economic hardship and increased IPV (see Flynn and Graham 2010). In sum, the failure for men to provide the resources women necessitate in mateship could trigger couple conflict, which in turn could perpetuate IPV.

Relationship termination. IPV may also function to prevent the mate from leaving the relationship or to encourage relationship reacquisition. Further, IPV may also act as an encouragement for the mate to reenter the relationship after termination. After one mate has defected from the relationship, the other might employ violent strategies in an attempt to convince the mate to return (e.g., stalking). Wilson and Daly (1998) suggest that mate-directed violence could be employed as a "final" effort to salvage a relationship, threatening the mate that intends to leave. Although this might not always work (and may even hasten the relationship termination), in some cases this act of violence might deter the mate from leaving, thus reinforcing the use of violence in the future. As Perilloux and Buss (2008) discuss, if a man can force a woman to remain in a relationship, then he has overcome her ability to choose a mate, one of the most crucial components of a female mating strategy.

Other contributing factors. Primarily, an evolutionary psychology perspective of IPV focuses on controlling a mate's sexuality and deterring infidelity or possible relationship termination. However, there are other notable factors that may contribute to perpetuating IPV, such as the quality of sex in the relationship, economic resources (Figueredo and McCloskey 1993), and a lack of female kin protection (Smuts 1992). Other contributing factors include childhood socialization and control of anger

(Wilson and Daly 1993) and anxiety (Arnocky et al. 2015).

Recently, researchers found anxiety to have a particularly important role in the perpetration of IPV. In a sample of 66 participants, Arnocky et al. (2015) found that anxiety mediated relationships between anticipated partner infidelity and aggression (physical, psychological, and sexual). Anxiety is an emotion that has evolved as an adaptive response to threats; as such, it is reasonable to expect that the relationship between the possible threat and behavior (i.e., infidelity and violence) is dependent on responding to the threat (i.e., anxiety).

Finally, a consideration of neurobiology (see Wilson and Daly 1993) provides interesting future directions for evolutionary psychology perspectives of IPV. In a double-blind, placebo-controlled, between-subjects experiment, DeWall et al. (2014) found that oxytocin (a nonapeptide) increased IPV inclinations, as assessed by the probability participants would engage in various partner-directed aggressive behaviors (e.g., slapping, throwing an object that could hurt). However, this effect was limited to individuals with higher levels of trait physical aggression. These results provide the first evidence of a biological basis of IPV and provide a possible framework for future researchers examining IPV through an evolutionary psychology lens.

Conclusion

Exploring IPV through the lens of evolutionary psychology attributes the behavior to evolved mechanisms designed to overcome reproductive threats and limitations. Understanding the etiology of IPV provides a framework for intervention and prevention of the occurrence of violence in a relationship (Peters et al. 2002). This entry has provided an evolutionary perspective to explain and understand IPV; however, it should be noted that while this perspective provides an adequate explanation, there are many other factors and perspectives that have not been discussed. Despite this, an evolutionary psychology perspective

can guide research on exploring the mechanisms that have evolved to motivate IPV (Kaighobadi et al. 2009a).

Cross-References

- ▶ [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- ▶ [Coercive Control](#)
- ▶ [Cues to Infidelity](#)
- ▶ [Frequency of Infidelity](#)
- ▶ [Infidelity](#)
- ▶ [Jealousy and Infidelity](#)
- ▶ [Prevention of Infidelity](#)
- ▶ [Sex Differences in Jealousy](#)
- ▶ [Sexual Coercion and Violence](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)

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Evolutionary Psychology of Crime

► Evolutionary Forensic Psychology

Evolutionary Psychology Research

► Paul Vasey

Evolutionary Psychology, The Handbook of

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Synonyms

Evolutionary psychology; Handbook

Definition

A compilation of 52 chapters and essays, written by evolutionary scientists, summarizing theories and research in major branches of evolutionary psychology.

Introduction

Charles Darwin was the first evolutionary psychologist. He described his vision for the future of psychology at the end of his classic 1859 treatise *On the Origin*: “In the distant future I see open fields for more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation.” Close to a century and a half later, his prophecy began to come to fruition. *The Handbook of Evolutionary Psychology*, first published in 2005, logged in at more than 1,000 printed pages with some 35 chapters (Buss 2005). The second *Handbook of Evolutionary Psychology*, published in 2016 with more than 52 chapters and essays, highlights how dramatically the field has expanded. Darwin turned out to be right (Buss 2016).

What the Handbook Showcases

The *Handbook* showcases “the best and the brightest” in the field, although space limitations required excluding many major players. It reveals several important developments in the actualization of Darwin’s vision. First, evolutionary psychology serves as a “metatheory” for the entire field of psychology (Buss 1995; Tooby and Cosmides 1992). It is not a subbranch of psychology, but rather a metatheoretical framework within which all psychology becomes organized and integrated. Stated differently, there is no such “non-evolutionary psychology” in the sense that no other causal processes, other than evolutionary ones, are responsible for whatever psychological machinery humans possess. The evolutionary metatheory currently organizes biology and all of the life sciences, and there is no reason why psychology should be magically exempt.

Second, evolutionary psychology has penetrated every single branch of the traditionally delineated branches of psychology – sensation, perception, cognitive, social, personality, developmental, clinical, and neuroscience. Individual chapters on these topics showcase the utility of evolutionary perspectives in discovering phenomena previously missed by approaches lacking an evolutionary lens. Examples include the vertical descent illusion in vision,

cross-sex mind-reading biases in social cognition, the predictable developmental emergence of phenomena such as stranger anxiety, important psychological sex differences where previous psychologists assumed monomorphism, and many others.

Third, the *Handbook* showcases the many emerging interdisciplinary enterprises, such as evolutionary endocrinology, evolutionary political science, evolutionary genetics, and cultural evolution. A strong case can be made syllogistically: All human behavior rests on a foundation of evolved psychological mechanisms; all such complex mechanisms owe their existence to evolution by selection; therefore, all fields that involve human behavior must have evolutionary psychology as a foundational explanatory framework. The expansion of evolutionary psychology into disciplines such as political science, sociology, economics, and even literature and the formation of new hybrid disciplines with evolutionary theory as their organizing core are hallmarks of the future and herald a consilience of the sort envisioned by E. O. Wilson (1999).

Fourth, the *Handbook* highlights that massive and rapidly expanding empirical foundation of the new science of the mind. Early in its inception, evolutionary psychology was viewed as a highly speculative enterprise. Some derided it as “just-so stories,” with the implication that it more resembled cocktail party musings rather than serious, testable, and falsifiable empirical science. The *Handbook* shows that, although evolutionary psychological hypotheses do span the spectrum of precise and testable to looser and less amenable to empirical rigor, there is no doubt that evolutionary psychology consists largely of sound empirical science. Every year, the empirical edifice grows. New discoveries are made using the theoretical lenses of the field. And knowledge about the science of the mind accumulates within EP’s cogent metatheoretical framework, each new discovery building on the others in a way that makes the growth of scientific knowledge truly satisfying.

Another development showcased by the *Handbook* is the fact that competing evolutionary psychological hypotheses are increasingly being advanced and pitted against each other in empirical test. Outsiders sometimes ask what “the” evolutionary hypothesis is about a particular phenomenon. As shown in cases such as the

female orgasm, menstrual cycle shifts in women's mate preferences, and adaptationists versus by-product hypotheses about homicide, competing evolutionary hypotheses act as fulcrums, catapulting the field forward.

Finally, the *Handbook* reveals that evolutionary psychology has become a sufficiently mature science to generate practical applications or to become "translational" in the current jargon of the field. The *Handbook* provides a sampling of these – evolutionary consumer behavior, organizational leadership, and the law. These developments auger well for future translational applications of the new science of the mind.

Conclusion

The *Handbook of Evolutionary Psychology* should be a core reference manual on the shelf or computer of every scientist who deals with human behavior. Evolutionary psychology is no longer an optional exercise. It guides researchers to important domains of inquiry. It reveals facets of human psychology previously undiscovered. It provides a metatheory that provides a justification for why all the different branches of psychology belong within the covers of the same book. And it provides the foundation from which all disciplines that deal with human behavior can be enlightened. Darwin prophesied that psychology would someday be based on a new foundation. That day has come. The foundation is now firmly in place. Future researchers can now use that foundation to construct the larger edifice – the mature science of the human mind that Darwin envisioned.

Cross-References

► [Evolutionary Psychology](#)

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Evolutionary Psychology's Role in Behavioral Science

► [How Evolutionary Psychology Can Still Explain Behavior](#)

Evolutionary Psychopathology

► [Darwinian Psychiatry](#)
 ► [Evolutionary Clinical Psychology](#)

Evolutionary Puzzle of Homosexuality

► [Homosexuality Paradox, The](#)

Evolutionary Social Psychology

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Synonyms

[Adaptationist perspective](#); [Social psychology](#)

Definition

Evolutionary social psychology is the study of the adaptive psychological mechanisms through

which real or imagined others affect individuals' cognition, emotions, and behaviors. This definition is a slight modification of one classically used to define social psychology that reflects the modular approach to human behavior typical of evolutionary psychology.

Introduction

Social psychology is arguably the second oldest of the modern fields of psychology. The first social psychology textbook (McDougall 1908) was published not long after the first psychology textbook was published (James 1890). Even in those earliest days of social psychology, the field had an appreciation of the role of evolution in human social behavior. The typical approach to social behavior, whose origin is often attributed to Kurt Lewin, emphasizes the interaction between trait-like individual differences and dynamic situational factors. This approach is not unlike that approach adopted in evolutionary psychology. Evolutionary psychology assumes that evolution has shaped the mind into a modular network of psychological mechanisms, each designed to address specific recurrent adaptive problems (Tooby and Cosmides 2005). Researchers assume that mechanisms are sensitive to various inputs from the environment, which then elicit a subset of reactions (cognitive, affective, and behavioral) that address the problem people face. This is roughly analogous to the person by situation interaction approach assumed in traditional psychology. Perhaps it is for these reasons that social psychology was among the first to reincorporate an evolutionary framework.

Examining human social behavior from the perspective of evolutionary biology has been very fruitful. Almost every major area of social psychology has benefited from utilizing an adaptationist approach (Tybur et al. 2009). Approaching human social behavior from the perspective of evolutionary biology, by identifying the adaptive problems faced by in human social life and attempting to identify the adaptive modules shaped by selection (natural and sexual) to resolve those problems, has provided direction previously unavailable. It has

done so, not only by suggesting novel research questions but also by providing a potential organizing framework to a field that, traditionally, has been highly splintered.

In the following review, we will explore some of the advances that the evolutionary approach has provided. First, we will review ideas that have been employed repeatedly in our understanding of human social behavior. We will then turn to how these ideas have shaped our understanding of how people think about others. It should be noted that this review is not meant to be exhaustive, and the reader is encouraged to explore the wealth of ideas and research that has been generated by this evolutionary approach to social psychology. First, we will review some recurring concepts.

Recurrent Concepts

Social psychology has benefited from many ideas that follow from evolutionary biology. While, we would direct the reader to the relevant entries within this volume for more in-depth coverage of these concepts, we address some of the major factors that have proven useful in delineating the psychological mechanisms that have emerged due to the selective pressures of social living. These concepts include the costs of false positives and false negatives and sexual selection. First, we will briefly revisit the concept of a psychological mechanism.

Psychological Mechanisms. A psychological mechanism is any module of the mind, which processes specific, adaptively relevant information, and generates output in the form of thoughts, emotions, or behavioral inclinations (Tooby and Cosmides 2005). A psychological mechanism is a module shaped by selection pressures in the same way that the eye is a sensory module, or the heart is a cardiovascular module. They develop as a solution to an adaptive problem persistently faced across evolutionary history. The eye is an old biological module originally thought to have developed for the regulation of the circadian rhythm and other biological processes and later modified to facilitate navigation. The heart is a still older biological module designed to address

the adaptive problem of pushing vital fluids, proteins, and nutrients throughout an organism's body. In the same way, psychological mechanisms arise as the result of neurobiological modules designed to address recurrent and persistent adaptive problems created by human social life, some of which, like the eye, may have been modified to facilitate new functions.

It takes time for environmental contingencies to shape genotypes. For example, if a genotype produces a phenotype that successfully helps its possessor overcome an environmental or social challenge with greater frequency than are other members of the same species able to, then that individual *may* reproduce more successfully. However, even if this individual has many offspring, and each of those offspring have many offspring of their own, and on and on, it takes many generations for that genotype to become common for the entire species; and this process is slowed by the extent to which offspring do not share the advantageous quality.

It is for this reason that many modern advances and changes cannot have had an enduring change on the psychological mechanisms that comprise current human social nature. Social media, the Internet, or even modern cultural advances and the new selection pressures they may introduce have not had the time to shape the typical genotype of the species. For this reason, evolutionary social psychology emphasizes the selection pressures created by social life that have endured across many thousands of years, well into our approximate 200,000-year history as a species and beyond.

Living in groups creates numerous and diverse selection pressures. These challenges include problems such as avoiding pathogens that one might encounter when interacting with others (Schaller 2006), correctly identifying the intentions of other social agents (e.g., do they want to harm me, do they want to mate with me), identifying the best possible mates, and successfully navigating group life. We will now turn to some of the common evolutionary processes and factors involved in solving these selection pressures. We will then explore what these factors' application has revealed about human behavior.

False Positives and False Negatives

We get a lot of information from our environment. Some of this information is useful, in that it can help us make decisions that help others or us. However, not all of this information is useful. Some of this information is entirely irrelevant to the decisions we make. In signal detection terms, useful information can be thought of as a signal, while useless information can be thought of as noise. Signals are usually embedded among noise. Take for instance when trying to write an encyclopedia entry in your office and hearing what you think might have been the buzz of your silenced phone indicating that you have received a message. The signal in this scenario is the buzz from the silenced phone. Colleagues talking in the hallway, electronic devices of various types humming, and wind from outside the office window all create signal irrelevant noise. We signal detectors must determine whether signals (the message notification on our phones) are present among the noise.

If we correctly identify a signal when it is present, then in terms of signal detection, we have a hit. If we correctly identify that a signal is absent, then we have a correct rejection. However, sometimes the noise can so obscure the signal that our ability to detect the signal can falter. If we incorrectly identify a signal as being present when it is not, then we have a false positive. If we incorrectly identify a signal as being absent when it is present, then we have a false negative or a miss.

All animals must detect useful signals that indicate the presence of adaptive problems in their environments, and, as social animals, we humans must detect signals in our social environments. Sometimes, incorrectly identifying the presence of a cue is non-consequential. However, this is not always the case. When false positives and false negatives are consequential and these consequences persist across time, evolutionary logic holds that we will develop signal detection biases that result in the least harmful consequence (Haselton and Buss 2000). That is, if it is safer or more advantageous to guess that a signal is present when it is not, then we will adopt a liberal

response bias and err toward guessing that signals are present when we are less than certain. On the other hand, if it is safer or more advantageous to guess that a signal is absent when it is present, then we will adopt a conservative response bias and err toward guessing that signals are absent when we are less than certain.

Sexual Selection

As pervasive a process as natural selection is, adaptations also develop within sexual species by way of sexual selection. Because sexual species, like humans, reproduce with other members of the same species and produce offspring with genotypes that reflect a combination of both parents, the needs of each sex create selection pressures for the opposite sex (Buss and Schmitt 1993). That is, those who meet the needs of the opposite sex have greater chances of reproducing successfully than do those who do not meet those needs. As males and females have shared the lion's share of adaptive problems, males and females are largely more similar than they are dissimilar. However, in the context of reproduction and bearing offspring, the adaptive problems faced by each sex have diverged.

Prior to the advent of modern methods of determining paternity, males had no way of being certain of their paternity. This created selection pressures on males that females did not experience, given that females were always completely certain of their paternity. On the other hand, females have faced a different adaptive problem. Specifically, females are more invested in the bearing of offspring. This is the case even if they relinquish responsibility for rearing their offspring. Human offspring gestate in females for approximately 32 weeks. During that time, mothers are responsible for providing for their gestating offspring's every need. As many mothers might attest, this responsibility can be temporally, calorically, and mentally demanding. Further, males can share these tasks only to a very limited extent. Beyond birth, provided mothers choose to continue tending to their children,

females are one of principle providers for their infant's nutritional needs (i.e., breastfeeding). This is also something that males can share to a very limited extent. Beyond these differences, which are largely a product of the physical machinery involved in gestation and lactation, males and females' investments in offspring can largely, if not entirely, converge. However, these differences create powerful selection pressures for human females in the vast majority of mammalian species.

Trivers (1972) proposed that this adaptive problem of parental investment has led to sex differences in certain aspects of mating behaviors. Specifically, as females are more invested in bearing and rearing offspring, copulating with all males is not equally beneficial. In fact, copulating with some males might be harmful as they may impose certain genotypic burdens, health burdens, and social burdens. Therefore, Trivers argued that females would be more discriminating in their mate choices, while males, on the other hand, would be more likely to compete with one another for access to mates more heavily than would females. Indeed, this increased competition is thought to be one of the reasons for the sex differences in size across species. Typically, the least invested sex, and therefore, the sex that competes the most for mates, is larger than their more invested, less competitive counterparts. We see this sexual dimorphism in those species in which females are more invested in the bearing and rearing of offspring, including humans. Indeed, some anecdotal examples from history suggest that this increased competition may be at least partially responsible for some of the warmongering in our species history (Daly and Wilson 1988). Take, for instance, the following quote attributed to Genghis Khan.

The greatest happiness is to vanquish your enemies, to chase them before you, to rob them of their wealth, to see those dear to them bathed in tears, to clasp to your bosom their wives and daughters.

Interestingly, when this investment asymmetry is reversed, we see a reversal of these general patterns of sexual dimorphism. That is, in species in which males invest more in the bearing and

rearing of offspring, the females compete more heavily and are often physically larger. Examples of this reversal can be found in phalarope birds, Mormon crickets, and seahorses.

Shaping Human Social Nature

We will now turn our attention to how these forces (and others) have advanced the study of social psychology. Evolutionary researchers have fruitfully applied the principles of evolutionary biology to many, if not most, of the fields in social psychology. It is far beyond the scope of this entry to review this work in its entirety. However, we will discuss how evolutionary reasoning has advanced the study of person perception.

Person Perception

Person perception is a subarea of social psychology in which researchers focus on the processes involved in the detection, categorization, and interpretation of others' behaviors. Person perception researchers often explore how we make inferences about others' intentions (e.g., is this person a friend, foe, or romantic flame). Work in evolutionary psychology has illuminated how certain selection pressures have shaped the inferences people form of others' intentions.

Two fundamental dimensions on which people tend to form impressions include the extent to which others want to harm or help us (i.e., warmth) and the extent to which they are capable of doing what they set out to do (i.e., competence, Cuddy et al. 2008). People often want to know whether someone wants to hurt them before caring whether they can. Therefore, here we will explore what an adaptationist approach to the study of impression formation reveals about the impressions we form of others' warmth.

First Impressions

Research examining first impressions reveals that people make judgments about others' internal qualities in as little as a tenth of a second (Willis

and Todorov 2006). Because we make these judgments so quickly, they utilize a very thin slice of information (Ambady and Rosenthal 1993) about other people in order to make these judgments. That is, people often form judgments of others based on superficial, observable features. Interestingly, research examining the first impressions that people form based on these superficial features have revealed that we extract information relevant to some of the adaptive problems that social living has presented us with and form our impressions based on this information.

When meeting new people, we must determine whether we should interact or not. Therefore, interacting with strangers creates a selection pressure. Interacting with any new person could create a survival relevant contingency for a number of reasons. One reason is that other people may want to hurt us. A second reason is that those new people may carry diseases, which might infect us, harming us unintentionally. Work has revealed that our first impressions glean information relevant to these concerns.

Mechanisms for Avoiding Harm in Person Perception

Our assumptions concerning whether strangers want to hurt us depend on our quickly made impressions of others' interpersonal warmth. Several pieces of information available at first glance inform these impressions concerning others' warmth. These include the presence of baby-faced features, similarity, sex, and outgroup membership.

Humans have a prolonged developmental period. As infants, we, therefore, require the aid of older individuals to survive. Researchers have proposed a suite of psychological mechanisms that might address this adaptive problem. One of which, thought to facilitate caring for infants appears to influence the impressions we form of others' warmth. Specifically, this mechanism responds to cues of infancy with a cute response. The cute response involves reactions of protectiveness and careful behavior (Sherman et al. 2009) to infantile cues. People can retain infantile features into adulthood, giving them baby-faced features. These features include qualities such as

relatively large eyes, small chins, and large foreheads (Zebrowitz and Montepare 2006). The overgeneralization hypothesis holds that the psychological mechanism for infant care may overgeneralize and influence the impressions we form of adults with these baby-faced features in such a way as to facilitate interacting with these baby-faced individuals (Zebrowitz and Montepare 2006). Indeed, people do tend to think that those with infantile facial features are more trustworthy and interpersonally warm (Zebrowitz and Montepare 1992).

Additionally, although our current culture espouses the laudable value of treating all individuals equally, doing so in ancestral environments would have been risky. Indeed, mistakenly guessing that a person wants to harm us would have been far less detrimental to our survival (i.e., resulting in a potential missed opportunity, false positive) than would have mistakenly guessing that a person *does not* want to harm us (resulting in potential death, false negative; Schaller 2006). This may have created a selection pressure whereby people who did not successfully differentiate those who meant them ill from those who did not would have been more likely to encounter malicious actors. Therefore, mechanisms for differentiating between friends and foes would have been advantageous.

Evidence suggest that one such mechanism responds to cues of similarity. We lived in small, genetically related groups for the majority of our evolution (Tooby and Cosmides 2005; Kenrick 2011). Therefore, most of those likely to help us would have looked similar to us. A mechanism, which responded to cues of similarity with reactions that facilitate interaction, would have been beneficial. Indeed, work shows that people assume that similar-looking individuals are more trustworthy than are less similar-looking others (DeBruine 2005). For example, using photo-editing software, DeBruine modified images of participants' faces by creating composite images composed of those images of participants' faces and composite images composed of other, opposite-sex participants' faces, which DeBruine had collected in prior research. DeBruine then asked participants to make a series of forced

choices between pairs of composite images. Those self-similar images were randomly dispersed among the pairs of images between which participants had to decide. For each pair of images, DeBruine asked participants to choose the most trustworthy-looking face, the face that appears the most attractive for a long-term relationship, and the most attractive for a short-term relationship.

When asked to select the most trustworthy face, DeBruine found that participants were more likely to select the composites that included their own faces (i.e., similar to themselves) more often than they were to select the composites that did not include their own face. Interestingly, though, they did not choose the self-resembling image the most when selecting the face that they thought was most attractive as a long-term mate and were less likely to choose the self-resembling image when selecting the face they thought to be most attractive for a short-term mate.

In addition to identifying friends, additional mechanisms for identifying those that might wish us ill would have been advantageous. One such mechanism is thought to respond to cues of maleness with avoidance. For various reasons (see Daly and Wilson 1988), males have historically been more physically aggressive than women have been. For this reason, being leery of men would have yielded a net benefit. Again, being overly cautious with others might lead us to miss opportunities, but being overly gregarious with others, in a world without protections, might have resulted in our deaths. Therefore, given the wide sex difference in physical aggression, it would seem a safer bet to be cautious with unknown men. Indeed, work suggests that we have mechanisms that lead us to be leery in the presence of men. For instance, neutral male faces are interpreted as angry (an emotion often associate with aggression) more so than are neutral female faces (Becker et al. 2007), and, interestingly, androgynous angry faces are more often interpreted as being men than are androgynous happy faces (Kenrick 2011).

Outgroup members may have been another potential source of threat. Outgroups may not

always be hostile, but given the aforementioned costs of a false negatives (thinking someone intends no harm with they do; Schaller 2006), mechanisms for responding to cues of outgroup membership with caution and vigilance would have been advantageous. Indeed, we do appear to have mechanisms that respond in this way. We are more apt to misinterpret the neutral facial expressions of members of outgroups as angry, than we are to misinterpret the neutral facial expressions of in-group members (Becker et al. 2010). We also pay more attention to angry and threatening outgroup's faces (Ackerman et al. 2006).

Mechanisms for Avoiding Disease in Person Perception

Not all harm is intentional. We carry a host of biological passengers with us, and sometimes these passengers can be harmful to strangers. For example, many Native Americans became sick, and many died from exposure to the unseen biological passengers that Europeans brought with them. Pathogens have been an ever-present aspect of ancestral environments, and social living created one more avenue by which pathogens might find their way to us. For these reasons, a series of pathogen aversion mechanisms have been thought to respond to cues of pathogen exposure with a host of reactions designed to minimize our exposure to pathogen-carrying individuals.

Some evidence suggests that a series of pathogen avoidance mechanisms, collectively referred to as the behavioral immune system, reacts to cues of the potential presence of pathogens in others with aversion. For example, people report being less willing to get physically close (i.e., shaking hands and sitting closely) to those with visible signs of illness (Van Leeuwen and Petersen 2018). Other superficial features of poor health or signs of disease can also trigger these pathogen avoidance mechanisms. For example, the stigma against obese individuals and the elderly have been attributed to the pathogen avoidance mechanisms. Additionally, facial symmetry, a core feature of attractive faces, has been thought to be an indicator of one's ability to fight off infection

(Grammer and Thornhill 1994). Indeed, exposure to cues of potential pathogens leads people to prefer symmetrical faces to asymmetrical faces (Young et al. 2011).

Cues of pathogen presence also trigger the pathogen aversion mechanism leading us to avoid those from other groups. Disgust, an emotion thought to be elicited by cues of noxious stimuli in order to motivate avoiding exposure (Tybur et al. 2013), motivates people to avoid *unfamiliar* others. For example, those who are more apt to react to stimuli with disgust (i.e., greater disgust sensitivity) are more inclined to avoid unfamiliar outgroups (Aarøe et al. 2017). Therefore, when motivated to avoid disease, superficial features, such as cues of illness, poor health, poor resistance to health, or outgroup membership, can influence how people form negative impressions of *strangers*.

Perceptions of Romantic Intentions

In addition to identifying whether a stranger is a friend or foe, deciding whether a stranger might be a potential mate was an adaptive challenge faced by both males and females. Useful inferences people can make when identifying mates includes whether someone returns our interest and what type of mating arrangement they are pursuing. However, differences in the adaptive problems males and females have faced shaped different patterns of inference.

Given that men face the problem of parental certainty, missing a potential mating opportunity would be more detrimental (i.e., false negative) than mistaking disinterest for interest (i.e., false positive). When a potential mate does not reciprocate our interest, then no mating opportunity exists. Therefore, approaching an uninterested mate yields little change in one's current state, beyond the possible self-denigration that might ensue. No mating opportunity existed when a male approaches an uninterested mate, and no mating opportunity exists after the uninterested mate rejects the male. However, when a potential mate is interested, then a mating opportunity does exist. Therefore, failing to approach an interested mate does change one's current state. A mating opportunity did exist, but this opportunity may

evaporate when the male leaves without approaching the potential mate.

For these reasons, error management theory (Haselton and Buss 2000) suggests that male' mechanisms for identifying potential mates may be overly sensitive to cues of sexual interest. In terms of signal detection, they may have a liberal bias when searching for cues of sexual interest. Indeed, Haselton and Buss (2000) found this pattern. Specifically, when they asked men to estimate the extent to which a woman is sexually interested when they perform certain innocuous behaviors, they found that men overestimated how interested women were. That is, males formed impressions of female's romantic interest based on limited, superficial aspects of their behavior, and the nature of these impressions appear to have been shaped by the consequences of missing mating opportunities.

However, for the reasons discussed above, women have faced the problems of parental investment. Therefore, females face a different set of consequences than men do. Namely, misestimating a male's commitment could have left that female alone with the responsibility of rearing their child. For this reason, inferring commitment when it does not exist (false positive) would have been more detrimental than inferring no commitment when it does exist (false negative).

For these reasons, error management theory (Haselton and Buss 2000) suggests that female' mechanisms for identifying potential mates may be less sensitive to cues of commitment. That is, in terms of signal detection, they may have a conservative bias when searching for cues of commitment. Illustrating this pattern, Haselton and Buss gave women descriptions of the same innocuous behaviors they had shown men but attributed these behaviors to a man. They then asked women to judge the extent to which these innocuous behaviors indicated commitment. Haselton and Buss found that women underestimated men's commitment. That is, females formed impressions of males' romantic interest based on limited, superficial aspects of their behavior, and the nature of these impressions appear to have been shaped by the consequences of choosing uncommitted mates.

In the preceding discussion, we have reviewed how evolutionary reasoning has advanced our understanding of the way people interpret strangers' behavior. While evolutionary reasoning has shaped our understanding of other subjects studied in social psychology, we will refer the reader to some useful sources, such as the numerous chapters that have been written about evolutionary social psychology (Kenrick et al. 2015; Neuberg et al. 2010) and the textbooks and monographs written to review this work (Kenrick 2011; Schaller et al. 2014). However, before closing, we will turn to an important cautionary consideration for those interested in approaching the study of human social behavior with an evolutionary approach.

Important Considerations

Evolutionary reasoning has advanced our understanding of how selection pressures have shaped human social nature; however, evolutionary social psychology stands in a tenuous position given the nature of its subject matter and several common biases. Social psychologists study topics that are of great interest to the public and are often the topic of pundits, twitter users, bloggers, and other social commentators. Many of these social justice and civil liberty issues can be polarizing, even for social psychologists. Indeed, the field of social psychology is in the midst of some soul searching concerning these biases, as researchers have documented a bias within social psychology concerning these issues (Inbar and Lammers 2012). Although, our commitment, as scientists, to objectivity should overcome these biases, such that we would set aside our opinions and beliefs when conducting our research, evidence suggests that this has not happened (Conway et al. 2018).

Evolutionary social psychology has not escaped the consequences of this bias (Von Hippel and Buss 2017). The typical bias of traditional social psychology has led some of its participants to characterize the work of *evolutionary* social psychologists as having a bias that contradicts that of the rest of the field (Kenrick 2011). Indeed, certain anecdotal reports seem to suggest that

reviewers sometimes recommend rejecting manuscripts, which report evolutionary social psychology research that contradicts the prevailing bias of the field.

These biases may rely on at least two fundamental misunderstandings: the misunderstanding of the way nature and nurture operate together and the endorsement of the naturalistic fallacy. Researchers in the biological-based psychological fields now dismiss the nature-nurture dichotomy as being false. Instead, these researchers have come to the realization that biology and environment interact with one another, rather than contributing to behavior in an additive fashion. Therefore, the question of the extents to which behavior is a product of biology or environment is fallacious.

Further, beliefs driven by mistaken questions, such as these, are made even more problematic when accompanied by the naturalistic fallacy. The naturalistic fallacy is the misbelief that biologically based behaviors are good. That is, this assumption holds that that which is natural is good. This misbelief can lead to misunderstandings and misuse of evolutionary reasoning. Believing that biologically derived behaviors, or those that they mistakenly believe are the product of nature alone, are good may encourage people to identify biological bases for any behavior they support. On the other hand, the opposite may be true for behaviors, which people do not support. For these behaviors, people falling prey to the naturalistic fallacy may think of accepting evidence of any biological contribution as tantamount to justifying harmful or immoral behaviors. Though this is not the case, they may try to argue against and dismiss any evidence that suggests that those behaviors, which they do not support, have any biological contribution and thus resist any evidence they feel reveals such a contribution.

These same misunderstandings may lead scientists to misapply evolutionary reasoning. In their zeal to identify those behaviors they approve of as good and dismiss those behaviors which they do not approve of as bad, they may erroneously turn to evolutionary-like reasoning. Again, thinking that biologically based behaviors are good and

that, therefore, bad behaviors cannot be biological may lead people to seek ad hoc biological rationalizations for those behaviors they approve of. This type of reasoning is antithetical to the proper application of evolutionary reasoning. Evolutionary psychology begins by attempting to identify certain selection pressures that humans would have encountered across their evolutionary history by exploring the nature of human life in distantly ancestral times. Next, evolutionary psychologists attempt to identify what psychological algorithms (e.g., decision-making rules) might have helped early humans to overcome these selection pressures. Starting with a behavior and then looking for a selection pressure is the exact opposite approach. Therefore, while it may be tempting to look for reasons why those behaviors a person approves of might be “natural,” doing so is an exercise in poor science. Researchers interested in utilizing the evolutionary approach must necessarily keep these considerations in mind.

Conclusion

Evolutionary reasoning has yielded a number of theoretical advances in social psychology. Here we have focused on some of the major theoretical considerations employed when using an evolutionary approach, some of the contributions of these theoretical considerations to the study of person perception and important considerations for those new to the field to keep in mind. However, the contribution of evolutionary reasoning to the field goes far beyond that discussed here. When researchers can overcome the allure of the naturalistic fallacy and the misunderstanding of how nature and nurture interact, employing an evolutionary approach can bear a bounty of theoretical direction and insight.

Cross-References

- ▶ [Disgust](#)
- ▶ [Error Management Theory](#)
- ▶ [Pathogen Avoidance](#)
- ▶ [Sexual Selection](#)

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Evolutionary Sociology

► Crisis in Sociology

Evolutionary Stable Strategies

► Mating Strategy Equilibria

Evolutionary Standards of Female Attractiveness

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Synonyms

Universals in beauty

Definition

Aspects of female appearance that are linked to perceived attractiveness and/or biologically relevant information.

Introduction

Homo sapiens is the product of an evolutionary process. Evolutionary constraints shaped our bodies, perception, cognition, preferences, and behavior. The thus evolved characteristics are still present today. From a biological viewpoint, the ability to promote the own genetic information is central. This is why cues that are linked to reproductive potential are perceived as attractive.

Preferences for attractive features can be observed from early stages in life: Babies aged 2–6 months look longer at attractive faces. This “attractivism” continues to affect our lives

favoring attractive people in various contexts. Attractive pupils get better evaluations than their less attractive peers; the same holds true for students at University. In professional life, attractive people are more likely to be offered a job and higher wages. This clearly unfair treatment of people according to their physical attractiveness can be explained by our general preference for beautiful things that affects our actions on a sub-conscious level (Hamermesh 2011).

Given the major impact attractiveness has on our everyday lives, it is not surprising that a substantial number of research studies have attempted to identify and quantify characteristics linked to attractiveness. In general, those characteristics are not so much specific features but describe more general construction concepts.

The elements that have been identified as contributors to attractiveness allow for predictions about the biological fitness of the carrier and thus about the potential for successful reproduction. The face plays a prominent role in communication among humans and does so also for the assessment of attractiveness. So far, eight elements have been identified as the foundation of attractiveness.

Neoteny or Youthfulness

Neotenus features are described in Konrad Lorenz' Kindchenschema: The relative proportions of a large head, large round eyes, small stubby nose, and a large upper and small lower face are shared by young members of all mammal species. A small lower face and large eyes are perceived as attractive (Cunningham 1986). This as well as the preference for neotenus characteristics like lack of body hair, hair coloration, and skin texture point towards the role of youthfulness as attractiveness marker. Younger women have, on average, higher reproductive prospects. Therefore the preference for youth can be attributed to a tendency to maximize the reproductive outcome. Women, on the other hand, try to maintain a youthful appearance to improve their mate choice prospects (Jones et al. 1995).

Symmetry or the Lack of Fluctuating Asymmetries

Bilateral organisms usually deviate to some degree from perfect symmetry. There are two main types of asymmetries: (a) Directional asymmetry is common in all organisms and constitutes the phenomenon that one half is slightly smaller than the other. This directed asymmetry does not affect attractiveness but increases the memorability of stimuli – a small degree of directional asymmetry makes stimuli easier to recall than perfectly symmetric ones. (b) Fluctuating asymmetries are manifested through deviations from this main direction. The degree of fluctuating asymmetry is linked to developmental instabilities. An organism exposed to parasites, nutritional deficits, or environmental stressors will develop such fluctuating asymmetries. Thus, a lack of fluctuating asymmetries is an indicator of developmental stability, which could be due to favorable environmental conditions or an immune system that could handle the developmental challenges well. Indeed, a lack of fluctuating asymmetries increases the mate value in many species and is perceived as more attractive in humans (Thornhill and Gangestad 1993).

Averageness

Contrary to popular belief, averageness seems to increase attractiveness (Thornhill and Gangestad 1993). Composite faces generated by computer algorithms are perceived as more attractive than the faces used to generate this composite, on average. This avoidance of extremes holds true only for female attractiveness. In male faces, composites are less attractive than the original faces, which is likely due to less pronounced hormone markers, which leads to a less masculine appearance.

Skin Texture and Coloration

A homogenous skin texture without blotches and pimples is perceived as attractive, as irregularities

in skin texture indicate compromised health. Evenly distributed red coloration indicates peripheral blood circulation and is perceived as more attractive. During ovulation, peripheral blood is increased (Oberzaucher et al. 2012).

Hormone Markers

Hormone Markers are sex-specific characteristics that develop under the influence of sex hormones. Typically male hormone markers require high levels of testosterone during ontogeny, i.e., protruding eyebrow ridges and a robust and longer lower face. Estrogen leads to pronounced cheekbones and a generally more fragile facial structure. Besides enhancing sex-typicality these features boost attractiveness. The communicative function that is named most often is that high levels of sex hormones pose a developmental handicap. High levels of testosterone suppress immune response. Therefore the generation of hormone markers requires a delicate balance between testosterone levels on one hand and keeping the immune system functional on the other, in order to keep fluctuating asymmetries low.

Body Proportions

The body plays a more important role for female attractiveness than for male attractiveness. Some features seem to be strongly affected by cultural variation, such as the body mass index (BMI). These cultural differences could be due to differences in the socioecological conditions, i.e., in an environment with limited access to high-energy food, a higher BMI would be an indicator of sufficient energy availability and thus considered attractive. In most Western cultures, calories are abundant, and therefore a preference for lower BMI has manifested. The preference for a waist to hip ratio (WHR) around 0.7 seems to be culturally invariant. A lower WHR is linked to youthfulness and fertility. During menopause, the waist moves upward and the WHR approaches the value 1 (Singh and Young 1995).

The preference for long legs in female bodies is likely linked to accelerated longitudinal growth of extremities under favorable conditions.

Contrary to popular belief, breast size is not relevant for attribution of attractiveness. Breast size is – other than breast asymmetry – not linked to the ability to lactate.

Olfaction

Body odor plays an important role in mate selection: It informs about the immune system, nutritional, and health status. In women, the attractiveness of faces and body odor correlates (Rikowski and Grammer 1999).

Motion and Voice

Usually we do not perceive faces and bodies in static postures but in motion. Motion quality depends on the construction of the moving body. Physiological parameters affect the motion quality, modifying movement patterns over the female cycle.

Multiple Cues or Redundant Signaling?

The large number of cues that affect attractiveness could be due to two alternative communicative functions. The redundant signaling hypothesis postulates that the attractiveness of different body parts correlates highly (an attractive face is associated with an attractive voice, body, and body odor) – thus making these different cues merely parts of a redundant signaling system (Grammer et al. 2001).

Each cue could be responsible for communicating one specific aspect of biological fitness. If that were true, the computational effort required to assess the biological parameters would be rather high. This idea is supported by the association of different characteristics with different biologically relevant factors: Hormones, developmental stability, and life history affect organisms in specific ways that modulate different indicators of attractiveness.

Conclusion

In nonhuman animals, cues of attractiveness usually are indicators of reproductive potential. This seems to hold true for humans, too. Pflüger et al. (2012) showed that female attractiveness is indeed linked to a larger number of offspring. The facial shape corresponding to a larger number of children is characterized by a more gracile lower face, fuller lips, and larger eyes. A similar facial shape combined with enhanced redness of the skin corresponds to the form of ovulation (Oberzaucher et al. 2012). These facial features correspond closely to attractiveness ratings. This is the basis for the new hypothesis that facial attractiveness could have similar roots as the sexual swellings in apes, and as in apes, the biological function of sexual attraction is achieved through a proximate mechanism that boosts female attractiveness.

Cross-References

- [Body Attractiveness](#)
- [Concealed Ovulation](#)
- [Conception](#)
- [Cues of Female Estrous](#)
- [During Ovulation](#)
- [Facial Attractiveness](#)
- [Fertility](#)
- [Fluctuating Asymmetry](#)
- [Mate Value](#)
- [Ovulation](#)
- [Physical Health](#)
- [Randy Thornhill](#)
- [Reproduction](#)
- [Reproductive Value](#)
- [Waist-to-Hip Ratio](#)
- [Women's Mate Value](#)
- [Youth and Fertility](#)

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Evolutionary Theory

► [Dangers of Evolutionary Ethics](#)

Evolutionary Theory and the Causes of War

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Synonyms

[Evolved functions of warfare](#); [Intergroup conflict](#); [The causes of war](#); [Theory of war](#)

Definition

The causes of war remain a strangely obscure subject. While people have a good idea of the aims that may motivate states to go to war, an attempt at a strict definition of them is widely regarded as futile. This entry seeks to show how the various causes of violence and war all come together and are explained within an integrated human motivational complex, shaped by evolution and natural selection.

Introduction

The age-old philosophical and psychological inquiry into the nature of the basic human system of motivation is fundamental to the question of why people fight. Numerous lists of basic needs and desires have been put together over the centuries. The most recent ones show little if any marked progress over the older, such as Hobbes's insightful propositions in *Leviathan*, chapter 6. Such lists have always had something arbitrary and often trivial about them. They lacked a unifying regulatory rationale that would suggest why the various needs and desires came into being or how they related to one another. Thus, while Sigmund Freud claimed that the basic human drive was sexuality, Alfred Adler argued that it was in fact the striving for superiority, and Karl Jung emphasized the quest for creativity and whole being. There was no way of deciding, other than faith within what indeed became semi-religious sects, why it was this drive rather than the other that was the “truly” basic one or why in fact there should be a unitary basic drive at all.

Arguing that the human motivational system as a whole should be approached from the evolutionary perspective, we begin with an examination of the “human evolutionary state of nature,” the roughly 150,000 years, or more than 95% of *Homo sapiens*' evolutionary history, in which humans lived as hunter-gatherers. During this long stretch of time human natural predispositions were shaped. Once people developed agriculture some 10,000 years ago, which led to the growth of the first states about 5000 years ago, they set in

motion a continuous chain of developments that have taken us far away from our evolutionary natural way of life. However, cultural evolution has not operated on a clean slate nor has it been capable of producing simply anything. Its multifarious and diverse forms have been built on a clearly recognizable deep core of innate human propensities. Biologically, we are very much the same people as our Stone Age forefathers and are endowed with the same predispositions.

In contrast to long-held Rousseauian beliefs that reached their zenith in the 1960s, widespread deadly violence within species has been found to be the norm in nature, including among pre-agricultural hunter-gatherers (Keeley 1996; LeBlanc 2003; Gat 2006, 2015). The evidence from a whole range of hunter-gatherer societies reveals a staggering rate of violent fatalities: on average perhaps 15% of the adult population, 25% of the men, and all the surviving men were covered with scars. This rate is five to ten times higher than that of historical state societies.

At the same time and contrary to other fashionable 1960s notions, traced back to Freud's later-day theorizing, violence is not a primary, "irresistible" drive that requires release, like hunger or sex. The Swedes and Swiss, for example, have not fought for two centuries, yet they show no special signs of deprivation on this account. But try to deny them food or sex and their reaction would be quite predictable. On the other hand, the fact that violence is not a primary drive does not mean that we are not hardwired for it. People often make the mistake of assuming that violence must be either a primary drive or entirely learned, whereas in fact its potential is deeply ingrained in us as a tool ever ready to be employed. People can cooperate, peacefully compete, or use violence in order to achieve desired objects, depending on what they believe can serve them best in any given circumstances. They are biologically well equipped for pursuing each of these social strategies, with conflict being only one tool, albeit a major one – the hammer – in our behavioral toolkit.

Although we shall now go through the reasons for fighting one by one, it is not the intention here to provide yet another "laundry list" of separate

causes. Instead, the following seeks to show how the various "causes" come together in an integrated motivational complex, shaped by the logic of evolution and natural selection and its calculus of survival and reproduction.

Subsistence Resources

Subsistence resources are a prime cause of aggression and deadly violence in nature. The reason for this is that food, water, and, to a lesser degree, shelter against the elements are tremendous selection forces. As Darwin, following Malthus, explained, living organisms, including humans, tend to propagate rapidly. Their numbers are constrained and checked only by the limited resources of their particular ecological habitats and by all sort of competitors. Contrary to the Rousseauian imagination, humans, and animals, did not live in a state of primordial plenty. The specter of hunger and starvation was ever present. Affecting both mortality and reproduction, they constantly trimmed down population numbers. Thus, struggle over resources was very often evolutionarily cost-effective. Hunting and fishing territories were the main cause of conflict between human groups, as meat's nutritious value is the highest. Rich concentrations of fruit, roots, and seeds were also the object of competition and fighting. And in arid environments, water holes, critical for survival, were often a primary cause of conflict.

The benefits of fighting had to be matched against possible alternatives (other than starvation). One of them was to move elsewhere. This, of course, sometimes happened, especially if one's enemy was much stronger, but this strategy had clear limitations. By and large, there were no empty spaces for people to move to. In the first place, space is not even, and the best, most productive habitats were normally already taken. One could be forced out to less hospitable environments, which may also be already populated by other less fortunate people. Furthermore, a move meant leaving a habitat with whose resources and dangers the group's members were intimately familiar and travelling into uncharted environments. Such a change could involve heavy penalties. Finally, giving in to pressure from outside

might establish a pattern of victimization. Encouraged by its success, the alien group might repeat and even increase its pressure. Conflict is about deterrence; no less than it is about actual fighting.

Having discussed fighting's possible benefits and alternatives, deterrence brings us to its cost side. Conflict becomes an evolutionarily more attractive strategy for those who resort to it, the lower their risk of serious bodily harm and death. Consequently, displays of strength and threats of aggressive behavior are the most widely used weapons in conflict, both among animals and humans. Furthermore, when humans, and animals, resorted to deadly violence, they mostly did so under conditions in which the odds were greatly tilted in their favor. It is not the open battle but the raid and ambush – asymmetrical fighting – that constituted the principal and by far the most lethal form of “primitive warfare.”

The advent of agriculture, followed by state civilizations, changed human motivations that lead to fighting less than one may assume. Territories for cultivation (and for pasture) replaced hunting and foraging territories as an object for competition. But the real novelty brought about by cultivation was the exploitation of human labor. With cultivation, it became possible to live off of other people's work. Accumulated foodstuffs and livestock could be appropriated by looting. Furthermore, not only products but also the producers themselves could be captured and carried back home as slaves, to labor under direct control. Finally, looting could be further upgraded into tribute extraction, a more systematic and more efficient appropriation of labor and resources through political subjugation.

Sex and Reproduction

Together with subsistence resources, reproductive opportunities are the other major cause of fighting in nature. The anthropological evidence across the range of hunter-gatherer peoples tells the same story. Within the tribal groupings, women-related quarrels, violence, so-called blood feuds, and homicide were rife, often constituting the principal category of violence. Between groups, the picture was almost equally uniform. Warfare regularly involved the stealing of women, who were

then repeatedly raped by groups of men or taken for marriage, or both.

Both somatic and reproductive elements are intimately interconnected, for people must feed, find shelter, and protect themselves in order to reproduce successfully. Thus, conflict over resources was at least partly conflict over the ability to acquire and support women and children and to demonstrate that ability in advance, in order to rank worthy of the extra wives. Anthropological studies show that successful men in hunter-gatherer societies had several wives, in rare cases as many as a dozen, with a record of two dozen in the most productive environments. Many wives naturally meant a large number of children for a man, sometimes scores, who often comprised a large part of the next generation in the tribe (Chagnon 1979; Symons 1979; Keen 1982; Daly and Wilson 1983). Again, women are such a prominent motive for competition and conflict because reproductive opportunities are a very strong selective force indeed. This does not mean that people always consciously want to maximize their number of children. It is mainly the desire for sex – Malthus's “passion” – which functions in nature as the powerful biological mechanism for maximizing reproduction. As humans, and other living creatures, normally engage in sex throughout their fertile lives, they have a vast reproductive potential, which, before the introduction of effective contraception, mainly depended on resource availability for its realization.

Because of the asymmetry in their reproductive potential, men tend to be more polygamous than women and more competitive on that account. It has been shown that in all societies – from hunter-gatherer communities and tribal societies to medieval and modern nation-states – over 90% of all homicides are carried out by men, irrespective of the society's actual murder rate, which may vary greatly (Daly and Wilson 1988). Furthermore, the murder rate perpetrated by males peaks in both London and Detroit (although 40 times higher in the latter) at the age of 25 (Jones 1993). More mature males, already in possession of women and children, are “programmed” to adopt more conservative, safer, behavioral strategies.

The reproductive logic of human fighting remained in force also in state societies. Students of war scarcely think of sexuality as a motive for fighting. Nonetheless, throughout history, widespread rape by soldiers went hand in hand with looting as an inseparable part of military operations. Like looting, the prospect of sexual adventure was one of the main attractions of warlike operations that motivated people to join in. While in heroic sagas of semi-barbaric societies, such as the *Iliad*, the sexual value of that prize was barely veiled, the practice was no less in force – openly or more discretely – in the armed forces of more civilized societies (Thornhill and Palmer 2000; also Goldstein 2001). In modern imperial Japan, the troops still indulged in state-tolerated mass rape while serving abroad, some of it in the form of state-organized forced prostitution. At least two million women are estimated to have been raped by Soviet soldiers in conquered eastern Germany in 1945. Mass rape has been a major feature of the recent ethnic wars in Bosnia, Rwanda, Darfur, and West Africa. In the armies of the Western democracies, although rape is severely punished, American and other Allied troops widely availed themselves of an abundant supply of low-cost prostitution in ruined Western Europe after World War II and, later, in desperately poor Vietnam. In the opposite direction, the impact of sexuality on war has been demonstrated by the effects of the sexual revolution since the 1960s. By lessening the attraction of foreign adventure for recruits and far increasing the attraction of staying at home, it may have contributed to advanced societies' growing aversion to war. "Make love, not war," was the anti-war youth movement's slogan.

Fighting advanced reproductive success not only directly, as women were raped and kidnapped, but also indirectly, as the resources and status won by fighting advanced one in the intra-social competition for the acquisition and upkeep of women domestically. Where polygyny was permitted, the rich and powerful acquired a greater number of wives and enjoyed a marked advantage in choosing young, beautiful, and otherwise worthy ones. In addition to wives, many societies sanctioned official concubines, and there were, of course, unofficial concubines or

mistresses. Finally, there was the sex trade per se, where again the most consummate and graceful exponents of the trade could be highly expensive.

The manner in which power, wealth, and sexual opportunity were linked is most strikingly demonstrated at the apex the hierarchic pyramids. Rulers possessed large harems. According to the Greek authors, Alexander the Great captured 329 of King Darius III's concubines after the Battle of Issus (333 BC). According to the state records of China, the imperial harem of the Early Han (second and first centuries BC) comprised some 2000–3000 women, whereas that of the Later Han (first and second centuries AD) reached 5000–6000. The records of the Ottoman Privy Purse indicate that at its zenith, during the first half of the seventeenth century, the sultan's harem comprised some 400 women, with another 400 kept on a "retired list."

A remarkable study conducted on the Y (male) chromosome in Central and Eastern Asia demonstrates the great reproductive advantage gained by rulers (Zerjal et al. 2003). It reveals that some 8% of the population in the region (0.5% of the world's population) carry the same Y chromosome, which can only mean that they are the descendants of a single man. Furthermore, the biochemical patterns indicate that this man lived in Mongolia about a 1000 years ago. It was not difficult to identify the only likely candidate, Chinggis Khan, an identification confirmed by an examination of the Y chromosome of his known surviving descendants. This, of course, does not mean that Chinggis Khan alone sired so many children from a huge number of women, an obvious impossibility even if he had ceased his military conquests altogether. The tremendous spread of his Y chromosome is due to the fact that his sons succeeded him at the head of ruling houses throughout Central and East Asia for centuries, all enjoying staggering sexual opportunities.

Chinggis Khan was among the greatest warlords ever and his dynasty probably the most successful. Countless unsuccessful bidders for power, whose lines ceased because of their failures, have to be figured into the other side of the equation. Ruling was a high-stake – high-risk-

high-gain – affair, with force as its mainstay. The historical records of dynasties around the world show that the majority of rulers died violently. All the same, the apex of the social pyramid held such a powerful attraction for people because it was there that evolution-shaped human desires could be set loose and indulged on a gigantic scale. On a more modest scale, the same considerations held true further down the social hierarchy.

Status, Honor, and Prestige

From the interconnected competition over resources and reproduction, other causes and mechanisms arise. First, there is status in the group. Among all social animals, possessing higher rank in the group promises one a greater share in the communal resources, such as hunting spoils, and better access to females. For this reason, rank in the group is hotly contested. It is the strong, fierce, and – among our sophisticated cousins, the chimpanzees – also the “politically” astute that win status by the actual and implied use of force. Rivalry for rank and domination in nature is, then, a proximate means in the competition over resources and reproduction. For this reason, people jealously guard their honor. In traditional societies in particular, people were predisposed to go to great lengths in defense of their honor. The slightest offense could provoke violence.

Competition over rank and esteem could lead to violent conflict indirectly as well as directly. For instance, even in the simplest societies, people desired ornamental, ostentatious, and prestigious goods. Although these goods are sometimes lumped together with subsistence goods, their social function and significance are entirely different. Body and clothes ornamentation are designed to enhance physically desirable features that function everywhere in nature as cues for health, vigor, youth, and fertility. It is precisely these products of the “illusion industry” – cosmetics, fashion, and jewelry – that people everywhere spend so much money. Furthermore, where some ornaments are scarce and therefore precious, the very fact that one is able to afford them indicates wealth and success. Hence the source of what economist Thorstein Veblen called “conspicuous consumption,” in reference to the early

twentieth-century American society. In Stone Age societies as well, luxury goods, as well as the ostentatious consumption of ordinary ones, became in themselves objects of desire as symbols of social status. For this reason, people may fight for them. Indeed, while the consumption capacity of simple, subsistence products is inherently limited, that of more refined, lucrative ones is practically open-ended. One can simply move up the market.

Again, the potential for the fulfillment of the quest for honor and prestige increased exponentially in large-scale societies. The stelae on which autocrats celebrated their achievements in superhuman images are interpreted by scholars as instruments of royal propaganda, but, equally, they express the quest for the ultimate fulfillment of the craving for boundless glory and absolute domination, which could now be extended to the “four corners of the world” and “everything under the sun,” as the mightiest of imperial rulers boasted.

The same applied not only to rulers but also to political communities at large. Community members bathed in their collective glory and were willing to pay for its advancement and protection. Individuals and political communities jealously guarded their honor and responded forcefully even to slight infringements, not because of the trifle matters involved but because of the much more serious ones that might follow if they demonstrated weakness. To paraphrase Winston Churchill: choosing shame rather than war might very likely beget shame and then war.

Revenge

Revenge is one of the major causes of fighting cited in anthropological accounts of prestate societies. Violence was activated to avenge injuries to honor, property, women, and kin. If life was taken, revenge reached its peak, often leading to a vicious circle of death and counter-death. How is this risky and bloody behavior pattern to be explained? From the evolutionary perspective, revenge is retaliation that is intended either to destroy an enemy or to foster deterrence against him, as well as against other potential rivals. If one does not pay back an injury, one may signal

weakness and expose oneself to further injuries. A process of victimization might be created. This rationale applies wherever there is no higher authority that can be relied upon for protection, that is, in so-called anarchic systems. Thus, the instinctive desire to strike back is a basic emotional response which evolved precisely because individuals and groups who struck back were generally more successful in protecting their own. This is remarkably supported by the famous computerized game that found tit for tat the most effective strategy a player can adopt (Hamilton and Axelrod 1984).

However, tit for tat poses a problem. One's offender cannot always be eliminated. Furthermore, the offender has kin who will avenge him, and it is even more difficult to eliminate them as well. In many cases, tit for tat becomes a negative loop of retaliation and counterretaliation from which it is very hard to exit. One original offense may produce a pattern of prolonged hostility. Retaliation might produce escalation rather than annihilation or deterrence. Fighting seems to feed on, and perpetuate, itself, bearing a wholly disproportional relation to its "original" cause. People become locked into conflict against their wishes and best interests. It is this factor that has always given warfare an irrational appearance that seems to defy a purely utilitarian explanation. A prisoner's dilemma situation is created, producing vicious cycles of retribution and deadly violence. In the absence of an authority that can enforce mutually beneficial cooperation on people, or at least minimize their damages, the cycle of retaliation is often their only rational option, though, exposing them to very heavy costs; it is not their best option.

The prisoner's dilemma is of great relevance when explaining the war complex as a whole and not only that of revenge and retribution. Still, it ought to be emphasized that not all violent conflicts or acts of revenge fall under the special terms of the prisoner's dilemma. In the context of a fundamental resource scarcity, if one is able to eliminate, decisively weaken, or subdue the enemy and consequently reap most of the benefits, then this strategy is better for one's interests than a compromise.

Power and the Security Dilemma

The basic condition of competition and potential conflict, which gives rise to endemic suspicion and insecurity, invites not only reactive but also preemptive response, which further magnifies mutual suspicion and insecurity. Potential conflict can thus breed conflict. When the "other" must be regarded as a potential enemy, his very existence poses a threat, for he might suddenly attack 1 day. For this reason, one must take precautions and increase one's strength as much as possible. The other side faces a similar security problem and takes similar precautions. Thus, measures that one takes to increase one's security in an insecure world often decrease the other's security and vice versa.

What are the consequences of this "security dilemma"? In the first place, it tends to escalate arms races. Arms races between competitors take place throughout nature. Through natural selection, they produce faster cheetahs and gazelles, deer with longer antlers to fight one another, more devious parasites and viruses, and more immune "hosts." Many of these arms races involve very heavy costs to the organisms, which would not have been necessary if it were not for the competition. This, for example, is the reason why trees have trunks. Trees incur the enormous cost involved in growing trunks only because of their life-and-death struggle to outgrow other trees in order to get sunlight. As with humans, competition is most intense in environments of plenty, where more competitors can play and more resources be accumulated. This is why trees grow highest in the dense forests of the water-rich tropical and temperate climates.

Arms races often have paradoxical results. In many cases, every step on one side is matched by a counterstep on the other. Consequently, even though each side invests increasing resources in the conflict, neither gains an advantage. This is called, after one of Alice's puzzles in Lewis Carroll's *Through the Looking Glass*, the "Red Queen effect": both sides run faster and faster only to find themselves remaining in place. Arms races may thus become a prisoner's dilemma.

The special characteristic of the security dilemma is that its basic motivation on both

sides is defensive. Since suspicion is difficult to overcome, the sides may choose to actively preempt, that is, take not only defensive precautions but attack in order to eliminate or severely weaken the other side. Indeed, this option in itself makes the other side even more insecure, making the security dilemma more acute. Warfare can thus become a self-fulfilling prophecy. Since full security is difficult to achieve, history demonstrates that constant warfare can be waged, conquest carried afar, and power accumulated, all truly motivated by security concerns, “for defense.” Of course, in reality, motives are often mixed, with the security motive coexisting with a quest for gain.

With resource accumulation and hierarchic organization that became the norm in historical state societies, both resources and power could be accumulated and expanded on a hitherto unimaginable scale. Thus, power, like money, grew into a universal currency by which most objects of desire could be secured. For this reason, the quest for power seemingly acquired a life of its own and was also pursued for its own sake. At the minimum, the security dilemma in itself drove people and political communities to expand their power as a defensive measure.

Ideas and Identities

What about the world of culture? After all, it is our most distinctive mark as humans. Do not people kill and get killed for ideas and ideals? In the first place, people exhibit a marked, evolution-shaped predisposition to favor close kin, or those they perceive as close kin, over more remote kin, or “strangers,” that is, to favor those with whom they share more genes. As culture, particularly among hunter-gatherers, was local and thus closely correlated with kinship, cultural identity became a strong predictor of kinship. Moreover, culture sharing – most notably language, but also shared symbols, values, and customs – is also crucial for social cooperation, hence the phenomena of tribalism, ethnocentrism, and nationalism. Whether or not national communities are genetically related (and most of them are), they feel and function *as if* they were (Gat 2013). Independence from foreign domination has been perceived as

crucial to a people’s prosperity as a community of kinship and culture, often evoking most desperate expressions of communal devotion in its defense.

Furthermore, from the Stone Age on, the spiritual life of human communities was imbued with cultures that supported supernatural beliefs, sacred cults and rituals, and the practice of magic. The all-familiar glory of the gods, let alone missionary quests, never appear as reasons for hunter-gatherers’ warfare. The most regular supernatural reason cited by anthropologists for fighting among hunter-gatherers is fear and accusations of sorcery. It should be noted, however, that these did not appear randomly but were directed against people whom the victim of the alleged sorcery felt had reasons to want to harm him. This, of course, does not necessarily mean that they really did. What it does mean is that competition, potential conflict, animosity, and suspicion were conducive to fears and accusations of sorcery. To a greater degree than with the security dilemma, the paranoia here reflects the running amok of real, or potentially real, fears and insecurity, thus further exacerbating and escalating the war complex.

Finally, people everywhere kill and get killed over ideas – religious and secular ideologies – irrespective of kinship and across nations. How is this lofty sphere, often the most abstract of metaphysical ideas (all too often seemingly absurd notions), connected to the practicalities of life? The evolutionary status of religion is beyond our scope here. From Emile Durkheim (1965), functionalist theorists have argued that religion’s main role was in fostering social cohesion, inter alia in war. This idea has now been expressed in evolutionary terms (e.g., Wilson 2002). It means that in those groups in which common ritual and cult ceremonies were more intensive, social cooperation became more habitual and more strongly legitimized, which probably translated into an advantage in warfare.

Throughout history, religious and, later, secular ideologies have been interwoven with the other, more mundane, causes of war. Humans have a strong propensity for interpreting its surroundings as deep and as far as the mind can probe, so as to decipher their secrets and form a

mental map that would best help to cope with their hazards and opportunities. We have an innate, omnipresent, evolution-shaped predisposition for ordering the world, which inter alia extends to form the foundation of mythology, metaphysics, and science. We are compulsive meaning-seekers. Thus, the array of ideas regarding the fundamental structure and working of the cosmos and the means and practices required for securing its benevolent functioning have been largely perceived as *practical* questions of the utmost significance, evoking powerful emotions and motivation for action – including violence (e.g., Boyer 2001).

Conclusion

Conflict and fighting among humans, as in nature in general, is fundamentally caused by competition over scarce resources that are vital for survival and reproduction. While violence is evoked, and suppressed, by powerful emotional stimuli, it is not a primary, “irresistible” drive; it is a highly tuned, both innate and optional, evolution-shaped tactic or tool, turned on and off in response to changes in the calculus of survival and reproduction. Wars have been fought for the attainment of the same objects of desire that underlie the human motivational system in general – only by violent means, through the use of force.

Modernity, most notably its liberal path, has sharply reduced the prevalence of war (Gat 2006, 2017; Pinker 2011). The reason for this change is that the violent option for fulfilling human desires has become much less promising than the peaceful option of competitive cooperation. Furthermore, the more affluent and satiated the society and the more lavishly are people’s most pressing needs met, the lesser their incentives to take risks that might involve the loss of life and limb. People continue to compete vigorously over scarce objects of desire. However, the violent option, the “hammer,” in the human behavioral tool kit seems to have declined in utility for attaining desired aims, most notably within the world’s affluent and democratic areas, where war has all but disappeared.

Cross-References

- ▶ [Coalition Leaders](#)
- ▶ [Conditions Required for Evolution of Warfare Adaptations](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Rape in Warfare](#)
- ▶ [Sexual Access as Benefit of Victory in War](#)

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Evolutionary Theory of Aging

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Evolved Infant Feeding Behaviors in Humans

- [Duration of Breast Feeding in Ancestral Environments](#)

Evolved Moral Foundations

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Synonyms

[Evolved moral intuitionism](#); [Intuitive morality](#); [Moral domains](#); [Moral foundations theory](#)

Definition

There is a set of five values from which moral rules are derived: care/harm, fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation. These values arise from a set of criteria laid out in the *Moral Foundations Theory*, which outlines theorized evolved foundations of moral behavior.

Introduction

For much of the history of psychology, beliefs around moral development were dominated by

the work of Kohlberg and Piaget (Donleavy 2008). They believed that morality was the result of a rational process and that as children developed they progressed across multiple stages of moral development. As children matured, it was argued that their morality became centered on ideas of justice and that these beliefs were the result of an internal dialogue processing facts logically. Unsatisfied with this explanation, Haidt (2001) proposed a counter model to moral beliefs, which he termed the *social intuitionist approach to morality*. This approach argues that instead of moral reactions being the product of logical thought, they are actually the result of emotional intuitions, later justified by gathering supporting data and ignoring conflicting information. Further research into this topic led Haidt and Joseph (2004) to refine the social intuitionist approach, producing a *model of evolved moral foundations*.

Haidt and Joseph (2004) proposed that humans possess multiple intuitive ethics, each of which evolved to navigate social situations. Through collaboration and cross-cultural work, Graham et al. (2013) proposed the current model used to explain moral foundations. *Moral Foundations Theory* rests on four claims: nativism, cultural learning, intuitionism, and pluralism. Once all of these claims are accepted, Graham et al. (2013) propose five moral foundations on which all moral development should rest: care/harm, fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation.

Moral Foundations Theory

Within Moral Foundations Theory, *nativism* refers to the theory that the mind is developed before birth with prerecorded information (Graham et al. 2013). This means that the mind is organized before it can experience anything. To be clear, this does not mean that humans are immune to environmental influence but that nature provides a “first draft” of the mind. Moral Foundations Theory proposes that this first draft includes mechanisms designed to identify and record information relating to values, norms, and behaviors relevant to recurrent adaptive social problems. As these

problems are not equally important in every society, it is proposed that the types of information preferentially attended to should be based on cultural expectations.

Cultural learning refers to the process of editing the first draft of the mind. Depending on the requirements of a culture, the base modules included in the first draft of the mind will preferentially encode information relevant to that child’s culture, and this will be demonstrated through drastic differences later in life (Graham et al. 2013). For example, a woman in a highly conservative religious country will learn from an early age which scenarios allow for which specific behaviors, and in which scenarios those behaviors are prohibited. Developing this culturally specific knowledge may lead to her automatically initiating the proper behavior to show strong deference to authority. On the other side, most Western women will have vastly different experiences in childhood, and although they started with the same modules, their behavior later in life will be altered due to the cultural learning process. To further illustrate this point, Graham et al. (2013) use an analogy related to buildings; all humans start with the same moral foundation modules and they are shaped by cultural learning. This means that a culture can impact which of the moral foundations are built up, but it cannot create new moral foundations.

The third claim, *intuitionism*, states that intuitions about a situation arise first and the reasoning behind them come second. This was first applied to moral psychology in Haidt’s (2001) *Social Intuitionist Model*, which argues that moral judgments occur as the result of moral intuitions and that supporting evidence is found after a moral evaluation is made. This is most clearly seen in cases of moral dumbfounding. A common example of this is the following scenario:

A brother and sister want to feel closer together and decide to have sex. They tell no one what they have done, they use protection, and no harm was caused to anyone. After the fact both siblings feel closer to each other and are happy with their decision.

When presented this scenario, most participant will say what they did was morally wrong (intuition), but because the scenario is designed

in such a way that there is no logical justification for why what they did is wrong, participants will frequently come up with nonsensical answers (Haidt 2001).

The final claim of the moral foundations theory is *pluralism*. Pluralism states that throughout our evolved history, humans faced many recurrent social problems and that many social problems would require a moral foundation to overcome it. Graham et al. (2013) lay out five major adaptive problems our ancestors would have faced (i.e., care/harm, fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation) and how these problems could have been solved through specific moral foundations. They then lay out how each of these foundations would have functioned compared to how they function today.

Moral Foundations

The care/harm foundation developed to promote the care of vulnerable offspring for extended periods of time. As human children are dependent for such an extended period of time compared to other mammals, and because they frequently require parenting from both parents, humans would have developed a mechanism to promote this care. The care/harm foundation developed to originally be triggered by visual and auditory signals of distress, neediness, or suffering by one's offspring. However, these triggers can be set off by other conceptually similar things, such as other children, animals, or cartoons, that share the proportions of children. The responses to these signals are frequently compassion for a victim and anger at a perpetrator (Graham et al. 2013).

The fairness/cheating foundation developed as a way to navigate cooperative social interactions. This foundation was originally triggered through observation or cooperation by a social partner or through gossip. However, current triggers can include inanimate objects, such as a vending machine, failing to produce a product when given money. The fairness/cheating foundation would have evolved such that those individuals who had a built-in module to detect cheating

would be less likely to be exploited compared to those who had to learn through trial and error. Responses to these signals are frequently anger at an exploiter, gratitude at a cooperator, and guilt for being an exploiter (Graham et al. 2013).

The loyalty/betrayal foundation developed as a way to facilitate coalitions. This foundation would have become especially important once intergroup competition between humans developed, as those tribes with stronger group cohesion would be more likely to succeed compared to less organized groups. Original triggers for this foundation would include large obstacles that an individual could not overcome or a joint enemy such as a rival tribe. Currently this foundation is frequently triggered by sports fandom and brand loyalty. Responses to these triggers include group pride and rage at traitors (Graham et al. 2013).

The authority/subversion foundation developed as a way to organize dominance hierarchies. As long as there were benefits associated with being able to scale the hierarchy, those individuals predisposed to understand how hierarchies operate would be more successful than those who had to learn as they went. Original triggers of this foundation are the presence of a social hierarchy in a social group. Recent triggers include the presence of governmental agencies, work place hierarchies, and familial hierarchies. Responses such as obedience, deference, and praise are associated with interacting with high authority figures, whereas failure to behave this way can cause outrage from both the authority figure and other subordinates (Graham et al. 2013).

The sanctity/degradation foundation developed as a way to minimize pathogen and parasite loads. Individuals who had to learn through trial and error that eating spoiled meat would lead to sickness would not survive as well as those with built-in disgust reactions. This foundation is frequently referred to as the behavioral immune system (Schaller and Park 2011). As this foundation operates as a pathogen avoidance system, there are few current triggers that were not potentially present in our ancestral environment. Such potential triggers include sexual deviance (sexually transmitted diseases), spoiled food (pathogen ingestion), and foreign groups (introduction of

new pathogens). The most frequent response to these triggers includes disgust and fear (Graham et al. 2013).

Although these are the current five major moral foundations, there are many more proposed foundations that do not meet the required criteria. To be classified as a moral foundation, the foundation must meet five criteria: concern in third-party judgments, automatic affective evaluations, culturally widespread, innately prepared, and adaptive advantage. For a review of other proposed foundations, see Graham et al.'s (2013) original article.

Moral Foundations Criteria

The first criterion of a moral foundation is that humans share a common concern in third-party normative judgments regarding the foundation. This is frequently referred to as a shared intentionality, or the ability for multiple people to hold a shared mental representation of what they are trying to do (e.g., Tomasello and Carpenter 2007). These shared representations exist because the idea is frequently transmitted between individuals through gossip. By frequently sharing gossip, individuals demonstrate a preoccupation with third-party violations and a concern that others will judge them based on these criteria. Therefore, if a potential moral foundation is rarely discussed in the same situations where other moral foundations are discussed, it likely does not warrant as a moral domain.

The second criterion of a moral foundation is the presence of automatic affective evaluations. As the moral foundations theory is an intuitionist theory, any moral foundations which are not the product of automatic process or are not emotionally charged do not meet criteria. This means if a moral response cannot be elicited easily or if a violation of a proposed moral foundation is not met with outrage, then it does not meet criteria.

The third criterion of a moral foundation is that it is culturally widespread. This simply means that if the moral foundation cannot be found in some basic form in most human cultures, then it does

not meet criteria. As moral foundations are evolved modules, their presence in human cultures should be near ubiquitous.

The fourth criterion of a moral foundation is the evidence of innate preparedness. As it is impossible to prove that a moral foundation is present in a culture due to an evolved mechanism versus the result of nondomain-specific intelligence, a moral foundation must demonstrate that it is present in either close relatives to humans, such as chimpanzees, or in children too young to have been subjected to learn the proposed foundation.

The final criterion of a moral foundation is that the moral foundation being proposed can demonstrate a clear adaptive advantage for humans who would have possessed such a trait compared to those who did not. In every moral foundation listed above, a clear adaptive benefit is presented to explain the presence of the moral foundation. If a moral foundation has no clear adaptive benefit, it is unlikely that it is an innate foundation as there would have been no selection pressure for it.

Conclusion

Relative to previous work on moral development, Graham et al. (2013) and others have demonstrated evolved moral foundations as the most likely explanation for the evolution and development of moral domains. This work has solidified five major moral foundations: care/harm, fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation. However, there may be many more moral foundations yet to be discovered, and thus they lay out five criteria for the inclusion of additional moral foundations. This work helps explain previous research through an evolutionary perspective while opening up the possibility of future expansion of this theory.

Cross-References

- [Mismatch Between Evolved Morality and Modern World](#)

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Evolved Moral Intuitionism

► Evolved Moral Foundations

Evolved Navigation Theory

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Definition

Evolved navigation theory, or ENT, identifies how natural selection, acting on genetic variation related to navigational behaviors, shaped cognitive and locomotor mechanisms over evolutionary time.

Introduction

I proposed evolved navigation theory as a means to understand navigational behavior over evolutionary time (Jackson 2005; Jackson and Cormack 2007). This theory identifies that the

costs and risks of navigation to humans and other species pose strong sources of selection. Further, it outlines how cognitive and locomotor adaptations reflect this selection across a variety of behaviors. Evolved navigation theory investigations have discovered some of the largest scale phenomena in areas such as distance perception, motivation, and visual illusions. Understanding these themes is essential in order to understand how evolution shaped broad dimensions of behavior because navigation is prerequisite to most behaviors.

Natural selection acting on navigation takes many forms, as outlined by ENT. Energetic expense, exposure to predation, opportunity loss, and other environmental risks all select for specific navigational behaviors. Currently, the most well-explored source of such selection is the risk of falling.

Navigation and Cognitive Adaption Example: Falling

An often unrecognized source of natural selection in terrestrial navigation is the risk of falling. In modern contexts, falling is often the primary accidental source of injury and fatality in humans. Falling can be severe, but it is also visually predictable because it results from navigating vertical or sloped surfaces. ENT proposes a means for avoiding falls via a visual mechanism that already weights navigational decisions by costs: distance estimation. Humans, and likely most species, tend to pursue nearer navigational goals and avoid overestimated routes (Jackson 2013).

The above points predict that humans should overestimate the length of surfaces that are vertical in the environment. Although this idea directly contradicts mainstream theories of distance perception, it predicted exactly how we perceive such surfaces. People overestimate surfaces that are vertical in the environment, regardless of the surface's orientation on the retinae (Jackson and Cormack 2008; Jackson et al. 2013b). The average magnitude of this *environmental vertical illusion* is roughly equivalent to a person accurately

estimating the length of a school bus when such a distance is horizontal but estimating the height of a five-story building when that same distance is vertical.

From ENT, I also predicted that observers should estimate a surface differently if it poses different levels of risk. In fact, humans fall more often and to greater injury during descent than ascent. Thus, humans should overestimate the vertical extent of the same surface more while standing on top of it than while standing at its bottom. As predicted, human observers perceive greater vertical distance from the top than the bottom of the same vertical surface (Jackson 2005; Jackson and Cormack 2007). On average, people perceive a five-story building to be the equivalent of nine stories tall while standing on top of it. Compared to the method of calculating most distance illusions (5–15%), this previously unknown *descent illusion* is apparently the largest demonstrated in any species (nearly 90%). Whereas most illusions do not replicate across environment or culture, colleagues and I have found that the *descent illusion* replicates at identical magnitudes across groups that include isolated indigenous people of the Americas (Jackson and Gómez de García 2017; Jackson and Kizer 2017).

If falling risk over evolutionary time truly generated these illusions, then adding or subtracting evolutionarily relevant falling risks should induce or remove these illusions. Indeed, these illusions disappear when we remove such falling risks (Jackson and Cormack 2010) and appear when we add falling risks to surfaces otherwise perceived accurately (Jackson and Willey 2011, 2013). This work redefines acrophobia as a condition of altered spatial perception that produces a normal fear response, rather than its clinical definition as an abnormal fear of stimuli perceived normally (Jackson 2009). ENT research has investigated how these mechanisms are influenced by learning (Jackson et al. 2013b), navigational ability (Amiton et al. 2010, Willey and Jackson 2014), and exposure (Jackson et al. 2013a). These investigations also led to the discovery of one of the most powerful navigational algorithms, which can also quantify selection and behavioral motivation across species (Jackson 2013).

Conclusion

ENT illusions are not small effects occurring only in contrived environments; they are among the largest magnitude phenomena in their respective areas and they occur ubiquitously in everyday vision. Participants in these studies are unaware that their estimates are wildly inaccurate or that they are being tested for falling risk, even when asked explicitly. These illusions are robust across environment, method, and culture and have been replicated in competing labs. Prior to this research, these mechanisms were unknown and yet they are a primary predictor of a broad source of mortality – both in the environments in which we evolved and in the modern world.

Cross-References

- [Depth Perception](#)
- [Descent Illusion, The](#)
- [Visual Illusions](#)

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Evolved Physiological Reactions

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Synonyms

Fight-or-flight; Physiology; Systems; Threat responses

Definition

Species-specific physiological reactions have evolved in response to evolutionarily stable opportunities and challenges. Many of these responses are conserved across species and can be studied in humans as sets of interrelated, and coordinated, physiological reactions to stimuli with intrinsic and/or learned values.

Introduction

The survival of a species relies on multiple motivational factors: appetitive, defensive, and reproductive. In mammals, each of these factors are characterized by specific patterns of physiological reactions designed to cope with challenges and opportunities in the environment. Research has described physiological profiles of a variety of motivational states, ranging from basic avoidance of predators and defense against threatening conspecifics (Blanchard and Blanchard 1990) to complex social states, such as deception (de Waal 1992) and empathy (Zaki 2014). Avoiding threats and, at the same time, maintaining opportunities for foraging and mating constitute strong environmental constraints that have favored the selection of physiological reactions that facilitate the detection of, responding to, and learning about, salient cues in the environment. The particular set of activated physiological reactions to, for example, threat and reward cues vary across species as a function of the evolutionary constraints operating on the species habitat. In addition to ecology-dependent variation between species, individuals within each taxon vary considerably in their physiological response profile. In humans, extreme physiological reactions to threat and reward cues constitute the bases for common psychiatric disorders.

In humans, the autonomic part of the nervous system coordinates a host of physiological responses that have evolved to cope with opportunities and challenges in the environment. In this entry, we focus on a series of physiological reactions to threat that have been extensively studied and described: endocrine, cardiovascular, pupillary, electrodermal, and respiratory. In the following, each of these evolved reactions will be briefly described together with their known key brain correlates.

Physiological Reactions to Stress and Reward

Physiological responses of an organism aid in survival, optimizing the trade-off between possible rewards and threats present in the surrounding.

Mammals react to the presence of a threat, such as a predator, by reduced heart rate and immobilization (Mobbs et al. 2015). Other immediate reactions, among them enhanced orienting and arousal (Öhman 1986), increase the chances of survival by facilitating information processing and preparation for action. At any given moment, an animal must strike a balance between exploring possible resources and avoiding being attacked. The choice between passive and active coping strategies in the face of threat is regulated by its proximity (Mobbs et al. 2015). If escape is possible or fight is an option, the prey prepares for active coping. The fight-or-flight response has evolved to aid escaping and fighting the aggressor, and is therefore characterized by specific physiological changes to support this, such as an increasing blood flow, which supplies the muscles with energy. In turn, and as a part of the ongoing arms race between prey and predators, predator physiology is designed to maximize its chances of catching the prey by increasing mobility and readiness for action. The behavioral principles governing these decision processes across species have been discussed extensively in behavioral ecology (Stephens and Krebs 1986). Freezing, on the other hand, is a passive coping strategy and is used when escape is not possible or in immediate proximity to the predator. This state allows the animal to both avoid detection and assess defense strategies. For example, flight behavior can be initiated while freezing.

In the laboratory, researchers have predominantly used Pavlovian fear conditioning procedures to study reactions to threat (LeDoux 2012). During Pavlovian conditioning, an emotionally neutral stimulus (CS) is repeatedly paired with a naturally aversive unconditioned stimulus (US), such as an electrical shock. As a result of this pairing, the CS elicits an enhanced orienting toward the stimulus, and a slew of defensive responses, such as freezing and autonomic arousal (Lang and Davis 2006). In many social species, threat information is transmitted efficiently between individuals, offering a more safe learning strategy as compared to individual trial and error learning (Laland 2004). Social learning about threats is supported by partly the same

physiological responses as Pavlovian fear conditioning (Olsson and Phelps 2007).

The emotional value of threats and rewards can be described along two key dimensions: (1) valence and (2) arousal, each one linked to partially different physiological response profile. Valence varies from negative to positive, whereas arousal ranges from low to high. In humans, the arousal component is commonly measured through autonomic activity, which can be quantified by, for example, changes in electrodermal activity (sweat production on the surface of the skin). Valence is commonly measured through the potentiation of the basic, brain-stem mediated, startle reflex, to sudden sensory stimuli (Lang and Davis 2006). This response can be measured across species and is therefore relatively well described in terms of its neural bases. Human research often uses electromyography (EMG) to record the amplitude of the eye-blink startle reflex in response to external stimuli. In comparison to a neutral baseline, aversive stimuli potentiate, and rewarding stimuli augment, the startle reflex.

Not only must the individual respond immediately to threats and opportunities. The value of past experiences should also be used to predict future encounters. Physiological responses have therefore evolved to facilitate the encoding of, for example, threats, thereby optimizing behavioral responses. Indeed, emotional arousal improves memory (McGaugh 2002), constituting an adaptive physiological function that has been preserved across many species. Human and animal studies have highlighted the hippocampus as the key region for declarative memory formation in the brain (Kim et al. 2015). The amygdala, which is located in close proximity to the hippocampus, is thought to facilitate plasticity in hippocampal regions, thereby promoting learning of emotionally salient information for future use. The amygdala promotes learning indirectly through modulating memory formation in different regions of the brain, such as the hippocampus (McGaugh 2002), and directly, through acquiring, storing, and expressing learned threat responses (LeDoux 2012).

Two parts of the peripheral nervous system orchestrate human physiological reactions: the

somatic and the autonomic. The somatic nervous system consists of motor nerves, responsible for voluntary muscle control from the central nervous system (CNS) to the body and sensory nerves that are responsible for perception of external stimuli from the sensory organs and the environment to the CNS. The autonomic nervous system (ANS) coordinates the physiological reactions. These bodily responses are to a large extent not under voluntarily control and are unleashed before a behavior is performed to prepare for its execution.

The ANS controls human physiology through its two parts: the sympathetic nervous system (SNS) and the parasympathetic nervous system. Generally, these two systems work in opposition to each other. For example, the parasympathetic nervous system activity antagonizes the SNS and the body enters into relaxation (e.g., heart rate and digestion reduces) and restoration. The detection of, and learning about, threats are regulated by a combination of different physiological pathways in many different organs and tissues: the endocrine, the cardiovascular, the pupillary, the electrodermal, and the respiratory. Each of these subsystems will be briefly described below in relationship to their evolved functions and associated key brain structures that are involved in creating these responses.

The Endocrine System

The endocrine system consists of the glands distributed in an organism that secrete hormones in order to regulate physiology and behavior. Hormones are secreted into the circulatory system, allowing different organs to communicate with each other. Apart from maintaining homeostasis, hormones are responsible for creating responses to internal and external stimuli.

The hypothalamus links the nervous system, from which information about external stimuli is acquired, to the endocrine system through the pituitary gland. Together, hypothalamus and the pituitary glands are part of a larger complex called the hypothalamic-pituitary-adrenal (HPA) axis, which controls a range of states from sleep to stress. The main hormones that are secreted by

the glands of the HPA-axis are glucocorticoids (“cortisol” in humans), the so-called stress hormone, through adrenal glands. Stress can be defined as a state, which systems adopt when facing a threat to the homeostatic balance. This threat can be a direct threat to the physical integrity of the individual, such as the presence of a predator, or of psychological kind, such as the perceived harmfulness of getting bankrupt. Glucocorticoids influence behavior through regulating neural pathways that facilitate or hinder certain behavior, depending on when they are released: before, during, or after encountering the stressor.

The onset of the stress response depends on the environmental conditions and the learning history of the organism. As mentioned earlier, the state of arousal resulting from the presence of threat augment learning, and a key structure is the hippocampus. The hippocampus is densely populated by glucocorticoid receptors (Kim et al. 2015). Mild stress has a transient effect and leads to changes in memory, yet strong and chronic levels can lead to permanent morphological changes (Conrad 2008). While it is important to remember sources of threat for survival, severe, and long-term stress leading to such permanent changes can create to unwanted outcomes, such as in the case of posttraumatic stress disorder (PTSD) (Kim et al. 2015).

The activation of the SNS is faster than the secretion of cortisol in response to threat, mediating the immediate responses. Noradrenaline (NA or norepinephrine) is secreted by the adrenal medulla and reaches the blood stream as a hormone during fight-or-flight and freezing responses and mediates metabolic effects such as an increase in glucose and free fatty acids in blood. NA is also activated in the brain as a neurotransmitter and facilitates Pavlovian fear learning through long-term potentiation (LTP) in the amygdala (Weinberger et al. 1984). SNS activation also lead to the activation of the HPA, which results in an increase in cortisol levels, highlighting the interplay of fast nervous system and slow hormonal responses in the face of threat. NA has both central and peripheral effects, on the sensory organs NA acts as a neurotransmitter that leads to a plethora of events such as pupil dilation,

increased heart rate, and increased blood flow to large muscles (Fig. 1).

The Cardiovascular System

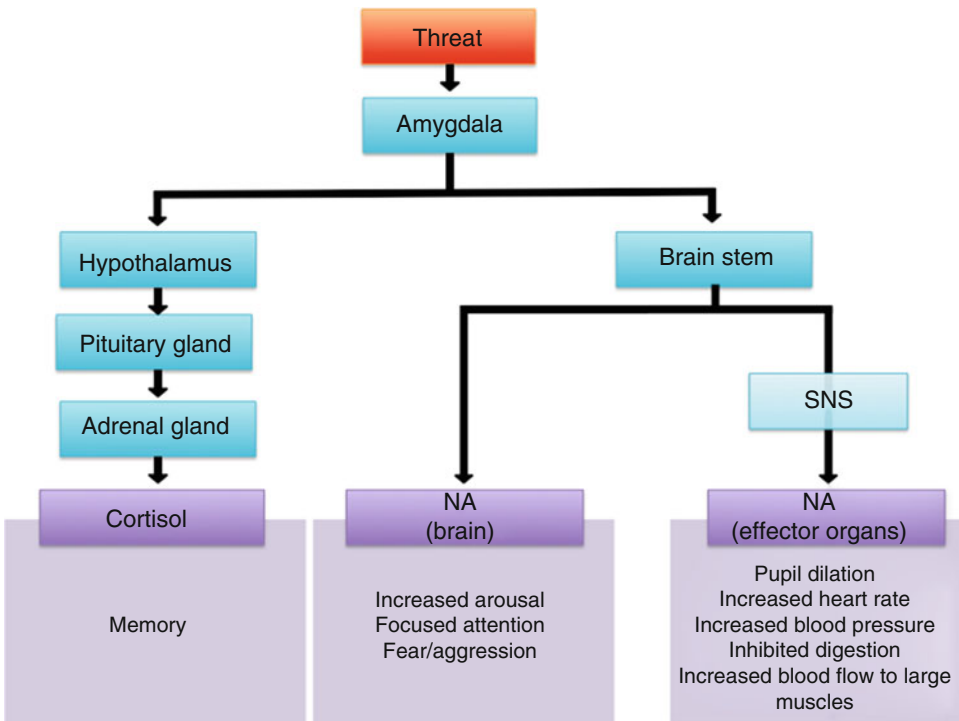
The cardiovascular system is responsible for distributing oxygen and energy throughout the body. Blood flow is regulated by the demand for oxygen in active tissues, and the rate of delivery is the product of heart rate and blood pressure. Heart rate and blood flow are controlled by many factors, such as hormones and the autonomic nervous system. In times of stress, for example during fight-or-flight responses, cardiac output, respiration, and blood flow increase in response to the NA released from the SNS. During this active strategy, the amygdala mediates the changes in cardiac and respiratory outputs (Cacioppo et al. 2007). Increase in heart rate and blood flow to

large muscles aids in survival by meeting the metabolic needs of the animal when flight is the best behavioral strategy.

In the case of a passive coping strategy, heart rate slows down. Decrease of heart-rate, *fear bradycardia*, has been associated with freezing in animal studies, including humans (Lang and Davis 2006). Immobilizing decreases the chances of being detected by the predator, increasing the chances of survival. Humans vary to the extent with which their heart rates are changed in response to fear conditioning; low heart rate variability is commonly believed to be a precursor for higher responses in fear-potentiated startle (Hamm and Weike 2005).

The Pupillary System

The diameter of the pupil regulates how much light enters the eye and is controlled by two



Evolved Physiological Reactions, Fig. 1 When exposed to a threat, the amygdala starts a signaling cascade. This results in engaging the HPA-axis, which results in cortisol release, and sensory nervous system (SNS) innervation, leading to the secretion of noradrenaline (NA).

Cortisol has memory enhancing effects. NA can act either in the brain as a neurotransmitter, and upon secretion causes a plethora of physiological reactions (*middle box*) or on sensory organs causing behavioral reactions (*right box*) in the latter

muscles: sphincter and dilator pupillae, which are under the control of ANS. Pupil dilation does not only occur in low light conditions, but has been found to reflect cognitive and emotional processes. Pupils dilate more to emotional words (Siegle et al. 2003), auditory stimuli (Partala and Surakka 2003), and pictures (Bradley et al. 2008) than to neutral ones. The evolutionary advantage of dilated pupils is still debated, but one prominent idea is that increased light allows better vision in dark environments.

The dependence on other individuals and the group has been an important factor during primate evolution. This dependence is likely to have selected for various abilities to detect and respond to conspecifics' intentions, emotions, and trustworthiness. Pupil size, along with characteristics such as facial expressions, is a social cue used to predict others' behaviors by ascribing intentions and emotions to them. For example, exposure to large vs. small pupils activates the amygdala (Harrison et al. 2006), which regulates the arousal system, and helps preparing for defensive responses (see above). More complex social behaviors, such as in-group trust, have been linked to mimicry of the pupil. For example, partners with dilated pupils are generally more trusted than those with constricted pupils (Kret et al. 2015).

The Electrodermal System

One of the most widely used psychophysiological reactions used in human research on basic affective and survival responses is electrodermal activity (EDA). ANS regulates sweating through sweat glands: the eccrine sweat glands cover most of the body and are more concentrated on the palms and soles of the feet; and the apocrine sweat glands are located in the armpits and the genital areas.

Most researchers study the skin conductance property of the EDA, which measures the skin resistance or conductance. Tonic level of skin conductance is referred to as skin conductance level (SCL), whereas phasic changes overlapping with the tonic response is referred to as skin conductance response (SCR). In a laboratory setting, changes in EDA can be the signal of different

level of activation of the SNS: sensory input, expectation/preparedness, increased attention, and arousal (Boucsein 1992). Along with interindividual variability in ANS responses, variations in SCR between individuals are related to differences in personality (e.g., introversion/extraversion) and psychopathology (e.g., anxiety disorders) (Boucsein 1992).

Many studies investigating threat responses report an increase in SCR and SCL in response to stimuli associated with threatening, compared to "safe," stimuli. Pavlovian fear learning paradigms have shed light on mechanisms of threat learning and extinction learning (the updating of threat value when the CS is no longer dangerous (e.g., Phelps et al. 2004). Learning each and every threat source is inefficient for the organism, thus generalizing the threat information to an extent would be optimal for survival. SCR to stimuli from the same category as the CS+ do not need to be specifically conditioned in humans, generalization occurs most readily between typical members of categories and less between atypical ones (Dymond et al. 2015). Overgeneralization, however, is a characteristic of certain psychopathologies (i.e., PTSD, panic disorders and specific phobias) (Dunsmoor and Murphy 2015). Just as in the case of enhancement of memory upon stress (see above), this highlights how an adaptive physiological mechanism can become dysfunctional in its extreme cases.

The Respiratory System

The respiratory system provides the oxygen for the organism that is needed to carry out metabolic processes that create energy in cells. The respiratory system is closely linked to the cardiovascular system: variance in depth or rate of breathing affects heart rate. As heart rate in turn controls blood flow, thus the rate at which oxygen travels to required tissues is controlled by both respiratory and cardiovascular systems. Rate of respiration is controlled by the ANS and has therefore been used in research to investigate ANS activation, complementary to other physiological measures mentioned above (e.g.,

heart rate, SCR). When faced with threat, cardiac acceleration is accompanied by faster breathing, dilation of the airways (bronchioles), decrease in respiratory volume, and thus a decrease in blood CO₂ levels (Kreibig et al. 2007) as the body gets ready for defense. Metabolic needs of the organism are met in the face of threat, allowing a successful flight or fight. Relief from threat decreases the respiratory activity and increases sigh frequency (Blechert et al. 2006).

The Motor System

When the threat is perceived and an appropriate response is initiated, it is the skelomotor system's responsibility to enact any of the three basic behavioral responses; freezing, fleeing, or fighting. The startle response is defined as a series of rapid muscle movements throughout the whole body, in the face of an abrupt sensory input. In many animals, this facilitates escape (e.g., the whole body startle in mice), but it might also function to protect the organs. For instance, the eye-blink startle reflex causes a blink, which serves to protect the eye from damage. Mammals under threat elicit stronger startle reflexes, due to the state of arousal, which is also reflected in greater amygdala activation (Lang and Davis 2006).

A great part of nonverbal communication in humans and other primates involves facial expressions. Correctly interpreting, and responding to, others' facial expressions is crucial for both successful social interactions and survival. In humans, six basic facial expressions have been identified to represent emotional states and assumed to have a universal meaning: happy, sad, fear, anger, surprise, and disgust (Ekman et al. 1983). Based on lacking support of neural activities corresponding to discrete emotional labels, recent researchers have emphasized the dimensional approach to emotions (Lindquist et al. 2012). The response of the ANS to perceiving facial emotional expressions is sensitive to the valence of the emotion and can distinguish among negative emotions (i.e., between anger, fear, disgust, and sadness).

Conclusion

Many physiological reactions have clear evolutionary advantages in the face of environmental opportunities or challenges. Internal physiological and environmental cues support the individual's choice between different survival and foraging strategies, allowing the organism to behave adaptively and thus increasing its chances of survival. To this aim, different systems work in concert under the control of the nervous system. In this entry, we have described a selection of integrated physiological reactions, their survival functions, and associated key neurobiological bases.

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Evolved Psychology

► Evolved Psychology of Warfare

Evolved Psychology of Warfare

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Synonyms

Evolved psychology; Predictors of violent intergroup conflict; Theories

Definition

Psychological processes involved in aggressive collective actions of groups toward other groups, typically characterized by high levels of destruction and mortality.

Introduction

Intergroup violence and warfare can have different forms. In raids, attackers significantly outnumber their opponents, whereas battles involve roughly equal numbers of combatants on both sides. Among traditional small-scale societies, battles occur less often than raids and are often ritualized, nonlethal encounters. In modern societies' war history, however, there are countless examples of lethal large-scale intergroup encounters, like the Battle of Stalingrad, which caused more than two million military and civilian casualties. This battle was part of the deadliest war of human history, World War II from 1939 to 1945, with more than 60 million deaths overall. Violence between groups remains omnipresent today, causing about 180 thousand deaths in 2014, let alone massive destructions of infrastructure and the ecosystem, as well as large-scale emigration from warzones.

It has repeatedly been argued that violent intergroup conflict may have played a major role in our ancestral past and that the selective pressure it exerted may even have been so intense to actually have shaped our cognitive mechanisms (Bowles 2009; Choi and Bowles 2007). In fact, today many archeologists and evolutionary anthropologists agree that warfare has steadily accompanied human prehistory and that deadly fighting between groups was far more common than within groups (e.g., Keeley 1997).

Although the absolute numbers of casualties of modern wars certainly exceed those of intergroup conflicts within and between more traditional societies by a great margin, relative to population size, current wars can be argued to be relatively petty (Pinker 2011). The available data on war casualties in traditional societies, though, suggests

that war was a much more important source of adult mortality in our ancestral past. For societies in which war was present, estimates of (male) adult mortality due to intergroup violence range from around 10 % to more than 50 % (Bowles 2009; Keeley 1997). Consequently, several theories of an adaptive psychology of warfare have been proposed.

Theoretical Perspectives on Warfare

War requires collective action. The potential benefits of victorious intergroup conflicts are often shared quite equally among members of the winning group, whereas individual fighters incur the costs and hazards of participation in combat like injury and death. Accordingly, warfare has been argued to constitute a within-group social dilemma, in which conflict participation is a cooperative action toward the own group. Theories of parochial altruism use group selection models to explain human warfare (Bowles 2009; Choi and Bowles 2007). Their basic assumption is that the willingness to aggress against other groups at personal cost is an act of true altruism toward the own group. Computer simulations based on rather specific assumptions about population structure, group interactions, and the costs and benefits of war support the hypothesis that altruism toward members of the own group and parochialism, i.e., disregard or even aggressiveness toward members of other groups, may have coevolved and eventually spread in the meta-population (for a detailed review, see Rusch 2014). Furthermore, warfare requires sophisticated cognition in order to correctly determine group memberships but also to detect and sanction noncooperators within the own group.

Other scholars reject population genetic explanations of warfare (for an overview, see van der Dennen 2002). They propose that war is a cultural phenomenon. One of its functions, for instance, may be the regulation of population size (man/land ratio). Cultural group selection models represent an integration of these opposing perspectives (for an overview, see Richerson

et al. 2016). According to this view, genetic group selection may not be sufficient to explain intergroup violence when group sizes exceed a few dozen individuals and migration between groups becomes larger. Instead, these authors propose that genes and culturally transmitted traits interact in forming our psychology of war. More specifically, they claim that while our readiness to learn and to obey social norms likely is genetically hardwired, this only leads to violent intergroup conflict where social norms promote such aggression. Eventually, these social norms may then have spread, because they gave aggressive cultures an advantage over more peaceful groups.

Empirical Evidence

Complementary to theoretical accounts of human warfare, there is plenty of empirical evidence collected by various disciplines on the different forms of and motivations for participation in violent intergroup conflict. Evidence is accumulating, for example, that collective action to the benefit of the own group in the presence of competing other groups is greater than in single-group social dilemmas (for an overview, see Benard and Doan 2011). This supports the notion that within-group cooperation is linked to intergroup competition.

However, when individuals can choose between peaceful within-group cooperation and aggressive between-group conflict, the available evidence is less conclusive. Therefore, several moderating factors have been suggested. For instance, theoretical and empirical research has shown that the motivation to participate in aggressive intergroup interactions is larger if individuals perceive their own group in a defensive rather than offensive position (e.g., Böhm et al. 2016). Moreover, there is theoretical and empirical evidence that increased reproductive access to women is an important driver of male participation in conflicts. Hence, men may be more likely to participate in warfare in order to obtain additional

reproductive access to out-group females and increased attention of in-group women (McDonald et al. 2012).

Conclusion

Warfare is a frequent phenomenon among humans. Explanations for its occurrence based on natural selection, cultural evolution, and combinations of both exist in the literature. Empirical evidence suggests that there are important structural factors and individual differences affecting the motivation to participate in warfare, including offensive versus defensive conflict objectives and gender.

Cross-References

- ▶ [Conditions Required for Evolution of Warfare Adaptations](#)
- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Defense Against Attack](#)
- ▶ [Group Selection](#)
- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Lethal Violence](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Male Warrior Hypothesis](#)
- ▶ [Men but Not Women Will Have Adaptations for War](#)
- ▶ [Rape in Warfare](#)
- ▶ [Self-Defense](#)
- ▶ [War](#)
- ▶ [War More Likely with Higher Likelihood of Success](#)

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Evolving Environments

► Climate and Habitat Diversity

Examples of Group Selection

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Synonyms

Multilevel selection theory

Definition

Cases of behavioral traits among groups of animals that were naturally selected at the group level instead of the individual or genetic level.

Introduction

Group selectionists argue that specific traits may have been positively selected because they aid in the survival of groups as opposed to enhancing the survival of the individual or gene. In other words, individuals within the group may incur a cost that eliminates their survival and/or reproduction, but the group as a whole continues to survive and reproduce. Although group selection is a controversial theory in evolutionary biology, supporters of this theory have presented many examples as corroborating evidence. This entry discusses some of these examples that group selectionists have discovered.

Group Selection

Although natural selection at the level of the individual may favor selfish behaviors, some argue that natural selection at the level of the group may favor cooperative behaviors (Nowak 2006; Nowak et al. 2010; Seeley 1997). Groups of cooperators will survive and reproduce more successfully than groups of selfish individuals (Nowak 2006). Group selection has been applied to explain a myriad of behaviors across many species and biological levels. For instance, some have argued that group selection may account for the development of cooperative behaviors within multicellular organisms (an individual cell inside a person's body does not act selfishly but acts cooperatively to help sustain the overall body) (Nowak 2006).

Many other examples of group selection stem from eusocial insect societies, such as ants and honeybees. Eusociality refers to very organized cooperative behaviors among individuals in a group, often in which an individual will forego his/her own reproductive opportunities for the sake of the group (see Nowak et al. 2010, for a review). For example, researchers have recently found that army ants will connect their bodies with each other to form bridges, which allow the other ants in the colony to cross gaps and areas of water (Reid et al. 2015). This is a useful tactic that allows the rest of the group to find a food source or

escape a predator. This coordinated action often results in the death of some of the ants that form the bridge, but the rest of the colony is able to survive and eventually reproduce.

Seeley (1997) proposed, and empirically tested, a mathematical model that supported the group selection of honeybee colonies. In particular, the bees that forage for nectar will engage in a particular dance – a waggle dance – that communicates to the hive to activate more nectar foragers, but this dance is only utilized when the entire hive's rate of nectar collection is low. Engaging in this dance does not grant the bee any direct benefit but increases the nectar collection of the hive as a whole – allowing for the enhanced survival of the entire colony.

There has been considerable debate over whether group selection theory accounts for certain mammalian behavioral traits – such as alarm calls in ground squirrels and meerkat sentinels – in which one individual will emit a loud sound to alert the others within the group that a predator is near (Clutton-Brock et al. 1999). These individuals incur a potential cost (e.g., an increased probability of being noticed, chased, and eaten by the predator) for the rest of the group to benefit. It is important to note that alternative explanations regarding nepotism and reciprocity may also account for these cooperative behaviors.

Although examples of group selection are often applied to eusocial insects and nonhuman mammals, some psychologists have argued that group selection may apply, on a cultural level, to humans as well. Humans in large-scale groups benefit because of the cooperation that occurs for the acquisition of public goods. Public goods refer to resources that are accrued at a cost to each individual, but benefit the overall group, such as paying taxes, contributing to charities, and conserving/defending natural resources. In order to maintain this cooperation for public goods, altruistic punishment toward those who do not contribute to the public good is utilized. Altruistic punishment refers to having a third party enact a negative consequence upon an individual who has violated a social norm (e.g., committed a crime, did not contribute to the overall

public good, or engaged in a behavior that is deemed negative).

Altruistic punishment is a cultural phenomenon that is argued to be best explained by group selection (Boyd et al. 2003; Rebers and Koopmans 2012). Imagine an individual evades paying his/her taxes and is then prosecuted for this crime. No individual citizen within the group gains any benefit from the tax evader's punishment, but the punishment promotes the successful survival of the group (or society) by obtaining the public goods (e.g., taxes) and enhancing the cooperative behaviors of the other individuals in the group by illustrating a deterrent. Empirical data suggests that groups who engage in altruistic punishment also possess higher levels of cooperation (Fehr and Fischbacher 2003).

Conclusion

Group selectionists view these examples of cooperative behaviors within different groups and species as evidence that natural selection does not necessarily have to occur at only the individual or genetic level. It is possible that, in some cases, natural selection may influence the survival and reproduction of groups as a whole, rather than influencing the survival and reproduction of each individual within the group. However, it is important to note that critics of group selection posit many alternative explanations – such as inclusive fitness theory (Hamilton 1964) and reciprocal altruism theory (Trivers 1971) – with supportive empirical evidence that may also account for these cooperative behaviors within groups. The debate over whether group selection adequately accounts for cooperative group behaviors will continue when examples such as these are discovered.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Cooperation](#)
- ▶ [Cultural Evolution](#)

- [Eusociality](#)
- [Group Selection](#)
- [Multilevel Selection Theory](#)
- [Problems with Group Selection](#)

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Exaptation

- [By-Products of Adaptations](#)
- [Evolutionary By-Products](#)

Exclusive Pair Mating

- [Monogamy](#)

Exclusivity and Pair-Bonding Among Non-humans

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Definition

Pair bonding is a term used in biology to indicate a strong interindividual relationship within breeding pairs most often consisting of a male and a female. The term is closely related to social monogamy, a mating system based on long-lasting relationships between sexual partners. Social monogamy differs from sexual monogamy in that it does not imply sexual exclusivity.

Introduction

Males and females from sexually monogamous species pair to mate and procreate exclusively with each other, whereas socially monogamous (pair-bonded) males and females share a territory, mate and take care of the offspring together, but also engage in extra-pair copulations on occasion. Strict sexual monogamy is rare in nature. Social monogamy is however more common, and the prevalence of this mating system differs remarkably across different groups of the animal kingdom. For example, monogamy is rare in fish, amphibians, and reptiles with a few exemptions such as shinglebacks, the red back salamander and the Caribbean cleaner goby. In contrast, up to 90 % of all bird species display some degree of monogamy and species from several genera of birds including geese, swans, and eagles form

lifelong pair bonds. A large phylogenetic study comprising 2,545 mammalian species showed that 9 % of mammals are socially monogamous, a number previously thought to be slightly lower (3–5 %) (Lukas and Clutton-Brock 2013).

Evolutionary Explanations of Pair Bonding

The large disparity in monogamy occurrence between different classes of animals has been explained by factors related to parental investment. In mammals, for example, following birth, offspring get their nutriment exclusively from the lactating mother and therefore only in rare cases do female mammals rely on paternal investment. In birds however, both parents can contribute equally to feeding the offspring and the evolutionary benefit of bi-parental care, and consequently pair bonding, is more prominent and therefore common.

Ultimate explanations for mammalian monogamy have been a topic for debate in evolutionary biology. There are two prevailing explanations for its existence. One suggests social monogamy evolved because of the fitness benefits this mating strategy gives offspring and to some extent mothers, such as male resource provisioning and protection against predation and aggression from competing males, including infanticide. The alternative hypothesis proposes that monogamy may represent a mate guarding strategy and could have evolved in situations where males were unable to defend access to more than one female. Based on phylogenetic evidence, the evolution of social monogamy in mammals does not appear to have been driven by high risk of male infanticide and paternal care seems to be a consequence rather than a cause of social monogamy (Lukas and Clutton-Brock 2013). Instead, monogamy in this class seems to have evolved where females are intolerant of each other and the population density is low, and thus represents a male mating tactic that has developed where males are not able to defend access to multiple females. Spatial properties of the social environment males live in, as

well as how individuals can navigate this environment, have therefore played an important role in the evolution of pair-bonding in mammals.

Proximate Causes of Pair Bonding

Regarding neural mechanisms of pair-bonding behavior, most of our knowledge today comes from studies in a particular group of rodents, voles. In the socially monogamous prairie vole (*Microtus ochrogaster*), males and females form long-lasting pair-bonds and both sexes take care of offspring. Research using this rodent as a model organism has provided remarkable insights into the neurobiology of social attachments and diversity in social behavior. In both male and female prairie voles, mating facilitates the development of an enduring pair bond, which can be assessed in the laboratory using a partner preference test (Johnson and Young 2015). Bonded animals prefer to spend time in close contact with their partner compared to a novel stimulus animal. Pair-bonding behavior in prairie voles is regulated by multiple neural mechanisms involving several brain regions and is speculated to be the result of linking the neural encoding of the social stimuli of the partner with the reward system, increasing the reinforcing value of partner stimuli relative to other social stimuli. Of these neural systems, neuropeptide dependent circuitry is particularly well studied and important for pair bonding. The peptides arginine vasopressin (AVP) and oxytocin (OT) have been shown to play important roles in the neurobiology of social behavior in animals (Johnson and Young 2015). Both are neuropeptides and are mainly synthesized by neurons of the paraventricular nucleus of the hypothalamus. They structurally differ only by two amino acids and share the same evolutionary origin. OT is implicated in a wide range of social behaviors including parental care, social motivation, and cognition (Ross and Young 2009). AVP regulates several male-typical behaviors, including territorial behavior, intrasexual aggression, and paternal care (Young and Wang 2004). Both OT and AVP are important for the formation and

expression of social memory including mate recognition, and these peptides have central roles in the regulation of pair-bonding behavior in prairie voles. Dopamine, which is involved in reinforcement learning in nonsocial context, and the opiate system also play important roles in the formation and maintenance of the pair bond.

Vasopressin and Pair Bonding in Voles

In laboratory experiments, pair-bonding behavior in male prairie voles has been shown to be facilitated by brain AVP and prevented by central injections of a vasopressin 1a receptor (V1aR) antagonist (Young and Wang 2004). The neuro-anatomical distribution of V1aR differs considerably between vole species. For example, prairie voles display relatively high density of V1aR in the ventral pallidum, a component of the mesolimbic dopamine system, compared to the non-monogamous meadow vole (*Microtus pennsylvanicus*). Remarkably, increasing the density of V1aR in ventral pallidum of meadow voles, using viral vector mediated gene transfer, makes these voles more social and display prairie vole like pair-bonding behavior (Young and Wang 2004). These findings suggest that AVP, acting on V1aR, played an essential role in the evolution of monogamy in voles.

Studies in voles have also provided intriguing insights into the genetic regulation of pair-bonding behavior. While the coding region of the gene coding for V1aR (*avpr1a*) is 99 % homologous between prairie and meadow voles, there is an approximately 400 base pair long repeat sequence (microsatellite) in the prairie vole promotor region not found in meadow voles. This particular part of the gene has in laboratory experiments been shown to associate with levels of V1aR binding in some brain areas in prairie voles as well as both intra- and interspecies variation in pair-bonding behavior (Young and Wang 2004).

In addition to laboratory experiments, the influence of variation in the vasopressin 1a receptor gene on pair-bonding behavior has been studied in more ecologically relevant settings (Phelps 2010). In the wild, male prairie voles can display

two distinct mating tactics. The “resident” strategy involves males pairing with a female and staying within constricted home-ranges allowing them to effectively guard their mate and protect offspring. In contrast, “wanderers” display a more opportunistic strategy. These unpaired males have large home-ranges overlapping several conspecifics’ territories and will mate with unpaired females as well as with paired females willing to engage in extra-pair copulations. Variable lengths of the *avpr1a* promoter microsatellite predict V1aR density in the retrosplenial cortex, a brain region important for spatial memory, and in the wild abundance of V1aR is associated with space use, sexual monogamy, and mate guarding ability. In particular, “wanderers” with relatively low levels of V1aR in the brain had higher reproductive fitness than those with high densities of this receptor, possibly driven by spatial ability.

In addition to microsatellite variation, single nucleotide polymorphisms (SNPs) in the prairie vole *avpr1a* have been shown to strongly predict V1aR density in the retrosplenial cortex and associate with sexual fidelity in male prairie voles (Okhovat et al. 2015). Interestingly, the variation in this gene important for both receptor density and behavior seems to be maintained through balancing selection. Prairie voles exhibit wide fluctuations in population density and future studies will investigate if density dependent selection promote variation in *avpr1a* and related behaviors. Taken together, these findings indicate that brain systems involving AVP play an important role in the evolution of pair-bonding behavior and are in line with the phylogenetic data suggesting that spatial navigation contributed to the evolution of social monogamy in mammals.

Oxytocin and Pair Bonding in Voles

The neuropeptide oxytocin plays a similar role as vasopressin in regulating pair-bonding behavior in the prairie voles. While previous work has suggested that the effects of vasopressin and oxytocin are highly sexually dimorphic, it is becoming increasingly clear that this picture is an oversimplification. In particular, recent research has shown the OT system to be important for

both male and female pair-bonding behavior (Johnson et al. 2016). Central OT infusion facilitates partner preference formation, and central infusion of an OT receptor antagonist (OTA) prevents mating-induced partner preference, in both males and females. Oxytocin acts within the mesolimbic dopamine reward pathway, including the nucleus accumbens and prefrontal cortex, to facilitate partner preferences in prairie voles, although a contribution of other brain regions cannot be excluded. The prefrontal cortex and nucleus accumbens of the prairie vole have high densities of OT receptors, and site-specific infusion of an OTA in either region prevents mating-induced partner preference formation in female prairie voles. Interestingly, nonmonogamous vole species, such as meadow voles, do not express OT receptors in the nucleus accumbens.

The density of OT receptors in the nucleus accumbens is under strong genetic control in prairie voles demonstrated by work showing that SNPs in the oxytocin receptor gene explain more than 70 % of the individual variance in oxytocin receptor levels (King et al. 2015). This finding supports the evolutionarily pertinent possibility that relatively small changes in the genetic code can have a large impact on the brain phenotypes and could help explain both the neuroanatomical and behavioral differences between closely related vole species.

Less is known about the influence of the OT system on pair-bonding behavior in the wild, but studies have shown that the levels of OT receptors in the nucleus accumbens is higher in the more monogamous resident male prairie voles compared to wanderers. Future evolutionarily informed studies will investigate the relationship between variation in the OT receptor gene, brain phenotypes, behavior, and reproductive success in prairie voles.

While prairie voles have been most intensively studied with regard to neural mechanisms, there is evidence that the OT/AVP system also plays a role in pair-bonding behavior in primates (French et al. 2016) and song birds (Klatt and Goodson 2013).

Conclusion

The occurrence of pair-bonding behavior varies to a large extent between different groups of the animal kingdom, and these differences can be explained evolutionarily by factors related to parental investment. Among mammals it seems pair-bonding has primarily evolved as a male mating tactic developed in situations where mate guarding of multiple females has been associated with low fitness. Studies in voles have shown pair-bonding behavior to be regulated by neural systems involving the neuropeptides oxytocin and vasopressin.

Cross-References

- Biparental Care
- Monogamy
- Parental Effort Versus Mating Effort
- Parental Investment Theory
- Social Monogamy

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Executive Attention

► Selective Attending

Executive Control

► Executive Functioning

Executive Functioning

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Synonyms

Cognitive control; Executive control

Definition

Executive functions (EFs) refer to a broad class of complex cognitive processes that guide the allocation and use of lower-order cognitive processes and behaviors (e.g., motor responses,

perception (Snyder et al. 2015)). Examples of EFs include planning and organizing thoughts and behavior, maintaining and manipulating information in short-term memory, inhibiting undesired responses, maintaining focus on a selected task, and flexibility in the application of sets of mental rules in accordance with environmental contingencies.

Introduction

Differences in individual EF abilities are linked to a host of important outcomes, including academic achievement, interpersonal effectiveness, occupational functioning, and general mental health (Snyder et al. 2015). There is considerable variability in EF measurement and the specific constructs that are subsumed under the umbrella EF term. Indeed, there is no general consensus on the best conceptualization of EF (Snyder et al. 2015), which has led to the examination of various neurocognitive processes as possible EFs. For example, findings from Miyake et al. (2000) provide evidence for a three-factor model of EF in young adults, with factors reified as shifting, updating, and inhibition. These factors represent separable, albeit highly correlated, neurocognitive processes. In contrast, findings from developmental literature suggest that EF may be best represented by a more unitary, domain-general structure, particularly at the preschool age (Wiebe et al. 2011). Working memory, planning, set-shifting, inhibitory control, and self-monitoring reflect the most commonly examined EFs and are detailed below.

Organizational EFs

Working Memory

Working memory (WM) is a limited capacity neurocognitive system responsible for the temporary storage and mental manipulation of phonological and visuospatial information. Several theoretical models present opposing hypotheses regarding the structure of the WM system. For example, Baddeley's (2000) multicomponent model of WM proposes two independent phonological

and visuospatial storage/rehearsal slave systems, a domain general central executive, and an episodic buffer responsible for the storage of bound, multimodal stimuli. Alternatively, Cowan (1999) proposes the embedded processes model, suggesting that WM is defined as a limited capacity focus of attention on information activated from long-term memory. Overall, equivocal findings from experimental and factor analytic studies provide support for various theoretical models of WM, which leads to conflicting hypotheses regarding the true definition and/or structure of WM.

There also exists an abundance of heterogeneity across methodological approaches used to measure WM. For example, standardized intelligence tests classify tasks that place high demands on short-term storage/rehearsal processes (e.g., digit span forward and backward) as WM tasks, while numerous experimental studies utilize tasks that explicitly require mental manipulation and/or updating of information. Nevertheless, given the well-established relationship between WM and other vital cognitive processes (e.g., attention), the reliance of numerous complex cognitive activities for adequate WM functioning, and the positive relationship between strong WM and positive life outcomes, the WM system is likely the single most influential EF within the realm of human cognition.

Planning

Planning is the process of deliberating possible options, steps, and/or outcomes necessary to successfully attain a goal. Effective planning requires the use of several upstream cognitive processes that allow an individual to compare and contrast choice-options, reflect on outcomes of previous decisions, and use forethought to determine the consequences of carrying out particular actions. Consequently, it is difficult to examine planning as a discrete EF, given many planning tasks indirectly place demands on additional neurocognitive processes (e.g., WM). Nonetheless, paradigms such as the Tower of London, Tower of Hanoi, and Porteus Maze tasks are commonly used to measure planning. Metrics from these tasks most often include the

amount of time spent deliberating, number of errors made, and frequency of successful task completion.

Set-Shifting

Set-shifting, sometimes referred to as *task-shifting* or *cognitive flexibility*, is an EF that allows for the disengagement of attention toward a prepotent response or problem solving strategy, and subsequent reengagement in a novel response or strategy. This EF is critical with regard to one's ability to efficiently adapt to novel situations, think flexibly, and alter behavioral or cognitive perseverative response styles. Set-shifting is often referred to as a "higher order" EF, given its reliance on the adequate functioning of more basic cognitive processes (e.g., attention, WM). The Wisconsin Card Sorting Task and Change Task are commonly used to examine set-shifting abilities, as both tasks intermittently require individuals to alter prepotent response strategies for successful completion.

Regulatory EFs

Inhibitory Control

Inhibitory control is a broad term that is applied to both cognitive and behavioral processes. *Behavioral inhibition* refers to the discontinuation and/or withholding of prepotent responses and is frequently measured using tasks such as the Go/No-go and Stop Signal paradigms. These tasks require examinees to withhold responding to prepotent stimuli when stop-stimuli are presented. *Cognitive inhibition*, in contrast, refers to the filtering of task-irrelevant information from entering the WM system, in turn allowing for improved accuracy and/or efficiency of cognitive processing. This interference control results in more efficient processing of relevant information and consequently greater likelihood of successful encoding and/or retrieval. The Stroop task is the prototypical task utilized to examine cognitive inhibition.

Self-Monitoring

Self-monitoring refers to the internal regulation of actions responsible for gauging the quality,

accuracy, and acceptability of a particular cognition or behavior. While self-monitoring appears to rely on other EFs, such as inhibitory control and WM, the evaluative component of this EF differentiates it from other processes. That is, self-monitoring allows for live introspection and provides salient information regarding one's trajectory toward accomplishing a particular goal. Self-monitoring is challenging to objectively measure given the inherent difficulty associated with examining internalized self-talk; however, tasks that allow for the examination of perseveration and/or self-correction of errors (e.g., Tower of Hanoi task) provide estimates of an individual's ability to monitor their behavior.

EF and Neural Correlates

Findings from neuroscience studies demonstrate that frontal and parietal structures (e.g., dorsolateral prefrontal cortex, anterior cingulate cortex) are more active during the completion of EF tasks, relative to non-EF tasks (Niendam et al. 2012). Localizing these complex cognitive processes to singular neural regions or structures is overly simplistic. Consequently, most contemporary research indicates that EF performance is dependent on a complex interaction between larger neural networks that span across frontal and parietal lobes, rather than discrete neural structures.

EF and Psychopathology

Deficits of EF are associated with a number of mental health disorders including schizophrenia, internalizing disorders, and externalizing disorders. For example, large-magnitude deficits of shifting, inhibition, updating, and WM have been revealed in studies of schizophrenia. Deficits in those same EFs are also associated with depression, although the magnitude of deficits is smaller (small to medium effect sizes), while medium sized deficits in shifting, inhibition, and WM are associated with bipolar disorders (Snyder et al. 2015). EF has received relatively less attention in anxiety research, with the notable exception

being studies of threat-related attentional biases. Specifically, meta-analytic research has indicated a consistent attentional bias in which anxious individuals are more likely to attend to threat-related information (Bar-Haim et al. 2007).

EF problems are strongly related to externalizing disorders, such as attention-deficit/hyperactivity disorder (ADHD), oppositional defiant disorder (ODD), and conduct disorder (CD), and recent models suggest ADHD-related executive dysfunction is the core feature of the disorder (Alderson et al. 2010). That is, moderate- to large-magnitude deficits in WM, inhibition, and set-shifting are consistently found in children and adults with ADHD (Willcutt et al. 2005). While findings from studies of ODD and CD have been relatively mixed with respect to WM functioning, findings of inhibitory deficits have been relatively consistent.

EF Training

EF training has been hypothesized as a fruitful intervention for remediating EF deficits associated with mental health and general cognitive functioning. These brain training programs involve cognitive exercises, usually completed via computer, that are purported to improve EF strength, in a process akin to increasing muscle strength by lifting weights. Multiple EFs, such as inhibition, WM, and emotion regulation, have served as targets of these interventions (Rapport et al. 2013).

While early findings appeared promising, recent meta-analytic research indicates that these EF training interventions have limited utility in terms of the long-term gains and transfer effects (Rapport et al. 2013). Specifically, although studies of EF training have demonstrated increased performance on tasks that are similar to the task on which the individual was trained, there has been less support for performance gains on tasks dissimilar to the trained task (e.g., academic achievement).

Conclusion

EFs are a broad class of cognitive abilities that play a fundamental role in navigating one's

environment by maintaining relevant information in mind, suppressing undesired or inappropriate responses, and following-through with tasks. They also help individuals organize their thoughts, plan behavior, and change their course of action as needed based on environmental demands. There is no consensus on what exactly constitutes EF, but WM, inhibition, updating, and shifting are among the most-often studied EFs. Moreover, while EFs are frequently thought of as “frontal lobe functions,” neuroimaging/functioning studies have indicated that EFs rely upon a diffuse neural network. Nevertheless, given the indispensable role of EFs in everyday life, it is not surprising that deficits in these neurocognitive processes are incorporated into etiological models of several mental health disorders.

Cross-References

- [Attention](#)
- [Attention and Memory](#)
- [Brain Development](#)
- [Cognitive Development](#)
- [Different Functions of Memory](#)
- [Discounting of Future Returns](#)
- [Frontal Cortex](#)
- [Inhibition](#)
- [Intelligence](#)
- [Judgment and Decision-Making](#)
- [Working Memory](#)

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Exercise

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Synonyms

[Physical activity](#); [Training](#); [Workout](#)

Definition

Activity that requires physical effort, frequently associated to the maintenance or improvement of health and fitness

Introduction

Demanding physically activities have always been part of hominid life. In a hunter-gatherer context, frequent physical activity was required for survival (Lieberman 2015b). The ability to run long distances escaping from predators or hunting preys, caring food or occasionally babies, for example, could be considered a crucial form of physical activity for humans. Hence, adaptations such as bipedalism and efficient heat exchange mechanisms were essential for human evolution.

Adaptations to Exercise: Heat Exchange and Bipedalism

Physical activity generates heat, and excessive heat may represent a risk to the organism's health and survival. Adaptations that enable efficient heat release and exchange, such as sweating, nasal and brain cooling, and bipedal posture, were essential to human survival (Lieberman 2015a).

The ability of cooling the body through evaporative heat loss is a very efficient form of fast heat exchange, especially in warm environments. Although it is metabolically costly, the secretion of vaporized water through the skin is the main responsible for most of the heat exchange in humans. Another mechanism of heat exchange is through the respiratory system, fresh inhaled air cools the internal organs, and the heat is released in the warm exhaled air. Anatomical adaptations of humans (e.g., high density of eccrine glands in the scalp) also facilitate the cooling of essential body parts, such as the brain.

Finally, an important adaptation in human evolutionary history is our atypical way of locomotion: bipedalism. Despite the costs of loss of speed and stability compared to alternative ways of locomotion (e.g., knuckle-walking), bipedalism provided strong fitness benefits, such as a more efficient long distance locomotion, food acquisition, ability to observe possible predators, and reduction of the body area exposed to solar radiation (Lieberman 2015b). In addition, bipedalism is energetically more efficient than alternative

forms of locomotion, such as knuckle-walking (Lieberman 2015a).

Besides their direct effect on survival, these adaptations (e.g., heat exchange and bipedalism) have allowed humans to endure frequent and intense physical activities. For example, the ability to exercise influenced many aspects of human life, including mate choice and disease prevention.

Physical Appearance and Mating

Physical traits related to attractiveness that can be modified through exercise, such as strength, athletic prowess, and a heavily muscled body, are often correlated with health and may be used as indicators of good genes (Zahavi 1975; Nedelec and Beaver 2014; Lu et al. 2015; Buss 2015; Buss and Schmitt 2016). Because physical features related to an increased immunocompetency are perceived as attractive (Buss 2015), highly attractive partners (vs. unattractive partners) are likely to generate healthier offspring, more likely to survive. Thus, they would have a selective advantage over less attractive/healthy individuals. Because developing and maintaining attractive physical attributes is costly – for example, a skin is more likely to develop scars in environments with high parasite load (Buss 2015) – highly attractive physical attributes can be honest signals of the survival capacity of an individual (Zahavi 1975). Consequently, the body shape, weight, and muscle structure of an individual who is unable to endure intense exercise (e.g., due to unhealthy joints) would be very different from that of a healthy individual, who is able to work out. Hence, healthy individuals with the ability to engage in physical activity would be more easily identified as attractive, better mates, good providers, and a good stock of genes (Lu et al. 2015; Buss 2015; Nedelec and Beaver 2014).

Exercise in Modern Society

Modern environmental conditions allow humans to be constantly physically inactive. The combination of a sedentary routine and a high-caloric

diet lead to an increase in the prevalence of metabolic diseases that were relatively infrequent in the past (e.g., cardiovascular diseases). Although the ability to exercise was not directly selected for its therapeutic benefits, exercising became an alternative to avoid illness such as obesity, diabetes, coronary diseases, and comorbidities (Lieberman 2015b; Penedo and Dahn 2005).

Conclusion

In sum, due the environmental conditions that humans were submitted in their evolutionary history, physical activity was a constant in the hunter-gatherer routine. Such dynamic lifestyle may have selected for some unique adaptations like bipedalism and efficient mechanisms of heat exchange.

Physical activity was a constant necessity in early human life, and exercise was not a choice but a necessity for survival. Nevertheless, the selective pressures humans had to face were fundamental to modulate what is known as exercise in modern society, from home workouts to Olympic training.

Cross-References

- [Body Attractiveness](#)
- [Body Posture](#)
- [Hunter-Gatherer Societies](#)
- [Physical Attractiveness](#)
- [Regulation of Body Temperature](#)
- [Upper Body Strength and Fighting Ability](#)

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Exotic-Becomes-Erotic Hypothesis

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Synonyms

[Erotic orientation](#); [Sexual orientation](#)

Definition

An individual's predominant sexual orientation toward men and/or women.

Introduction

There is evidence that biological factors, including genes, are correlated with an individual's sexual orientation. (For a recent review, see Bailey et al. 2016). The Exotic-Becomes-Erotic (EBE) hypothesis proposes that biological factors do not, however, directly influence an individual's sexual

orientation but act indirectly by influencing the child's preferences for sex-typical or sex-atypical activities. Children who prefer sex-typical activities and who play primarily with same-sex playmates are called *gender conforming*; children who prefer sex-atypical activities and who play primarily with opposite-sex playmates are called *gender nonconforming*. These preferences lead children to feel different from either opposite- or same-sex peers – to perceive them as dissimilar or exotic: Gender-conforming children will experience opposite-sex children as different from themselves and gender-nonconforming children will experience same-sex children as different from themselves. This feeling of difference produces heightened emotional arousal to members of the dissimilar sex that subsequently becomes transformed into an erotic attraction to them (Bem 1996).

Evidence that Genes Are Correlated with Sexual Orientation

To determine whether a physical feature or personality trait is correlated with genetic factors, researchers look to see whether individuals are more similar to close relatives on that trait than they are to more distant relatives. For example, individuals' heights are more closely related to the heights of their parents than to the heights of their aunts and uncles. This implies that the physical trait of height has a significant genetic component or is *heritable*. Because they control for age, sex, and the home environment, the best studies are those that compare identical twin pairs (called *monozygotic* twins) with a matched sample of same-sex fraternal twin pairs (*dizygotic* twins). Monozygotic twin pairs share all of their heritable genes with one another whereas dizygotic twin pairs share only about half of their heritable genes with one another. So if monozygotic twin pairs are more alike on a trait than are same-sex dizygotic twin pairs, we can infer that the trait is partially heritable.

Studies have now established the heritability of sexual orientation for both men and women.

In a study of gay men who had twin brothers, 52 % of monozygotic twin brothers were also gay compared with only 22 % of dizygotic twin brothers. Some men also had adopted brothers in their families, men who did not share any heritable genes with their gay brothers: Only 11 % of those adopted brothers were also gay (Bailey and Pillard 1991). A parallel study of lesbians showed the same pattern: 48 % of monozygotic twin sisters were also lesbian compared with only 16 % of dizygotic twin sisters and 6 % of the lesbians' adopted sisters (Bailey et al. 1993). A subsequent study of nearly 5,000 twins who had been drawn from a twin registry confirmed the heritability of sexual orientation for men (Bailey et al. 2000).

Gender Conformity/Nonconformity Is Also Correlated with Sexual Orientation

There have now been many retrospective and prospective studies that confirm a correlation between childhood gender conformity/nonconformity and an adult sexual orientation (Bailey and Zucker 1995). The largest of these compared nearly 1,000 gay men and lesbians with 500 heterosexual men and women on many aspects of their childhoods, including family relationships and early sexual experiences with both sexes. None of these correlated with their later sexual orientations. In fact, there was only one childhood variable that correlated with adult sexual orientation for both men and women: gender conformity/nonconformity (Bell et al. 1981).

For example, many more gay men than heterosexual men reported that as children, they had not enjoyed typical boy activities (such as sports), had enjoyed typical girl activities, and had had more childhood friends who were girls. Similarly, more lesbians than heterosexual women reported they had not enjoyed typical girl activities, had enjoyed typical boy activities (especially sports), and had had more childhood friends who were boys.

Gender Conformity/Nonconformity and Feeling Different

The Exotic-Becomes-Erotic hypothesis (EBE) proposes that gender-conforming children will feel different from opposite-sex children, and gender-nonconforming children will feel different from same-sex children. The large study, cited above, found that 71 % of the gay men and 70 % of the lesbians in the sample had felt different from their same-sex peers during childhood. When asked in what ways they had felt different, they overwhelmingly cited gender-related reasons. Gay men were most likely to reply that they had not liked sports; lesbians were most likely to reply that they had liked sports more and had been more masculine than other girls. In contrast, fewer than 8 % of heterosexual men and women said that they had felt different from same-sex childhood peers. Those who did tended to cite nongender-related reasons such as having been poorer, more intelligent, or more introverted than other children.

How Does Exotic Become Erotic?

In his first-century Roman handbook, *The Art of Love*, Ovid advised any man who was interested in sexual seduction to take the woman in whom he was interested to a gladiatorial tournament because she would there be more easily aroused to passion. A contemporary version of Ovid's claim can be understood to be a special case of what psychologists call the two-factor theory of emotion. It states that the physiological arousal of our nervous system can provide cues that we feel emotional but that the more subtle judgment of *which* emotion we are feeling often depends on our interpretation of the surrounding circumstances. The experience of erotic arousal thus arises from the conjunction of physiological arousal and circumstances that permit it to be interpreted as erotic arousal.

There is now experimental evidence that an individual who has been emotionally aroused – whether that arousal is neutral, pleasant, or

unpleasant – will show heightened sexual responsiveness to an appropriate target person. In one study, male participants were physiologically aroused by running in place, by hearing an audio-tape of a comedy routine, or by hearing an audio-tape of a grisly killing. No matter how they had been aroused, these men reported greater erotic interest in a physically attractive woman than did a control group of men who had not been aroused (White et al. 1981).

This effect has also been observed physiologically. Men and women were shown an erotic video while their physiological sexual arousal was monitored (penile erection in men and vaginal blood flow in women). But before seeing the erotic video, half the participants first saw a disturbing video of a grisly automobile accident; the remaining participants saw a video of peaceful landscapes. Participants who had seen the disturbing video subsequently showed more sexual arousal to the erotic video than did those who had seen the peaceful video (White et al. 1981).

The Exotic-Becomes-Erotic hypothesis thus proposes that an individual's experience of feeling different from same- or opposite-sex peers in childhood produces a physiological arousal that gets eroticized when the maturational, cognitive, and situational factors coalesce to provide the defining moment when it can be interpreted as sexual arousal. The timing of this moment, however, is influenced by several factors, including actual sexual experience with opposite- and same-sex peers and the norms of the surrounding culture. The heightened visibility of gay men and lesbians in our society in recent years is leading individuals who experience same-sex arousal to recognize it, label it, and act on it at earlier ages than previously.

An Empirical Test of the Exotic-Becomes-Erotic Hypothesis

The discovery that genes are correlated with sexual orientation has led some people to believe that there must be a “gay” gene or set of genes that directly influence sexual orientation. In contrast,

the Exotic-Becomes-Erotic hypothesis proposes that the link between genes and sexual orientation is only indirect: The genes influence early personality traits that socially define a child as gender-conforming or gender-nonconforming, and it is that gender conformity or nonconformity that provides the important intervening link between the genes and sexual orientation. Because the large study of twins, cited above, assessed both sexual orientation and gender conformity/nonconformity, those data enable a test for both the direct and the indirect paths from genes to sexual orientation (Bem 2000).

First, the data confirmed the first link proposed by the Exotic-Becomes-Erotic hypothesis: Monozygotic twins were significantly more alike on gender conformity/nonconformity than were same-sex dizygotic twins. This was equally true for both men and women. Second, the data confirmed the second link proposed by the hypothesis: Childhood gender conformity/nonconformity was significantly correlated with sexual orientation. When the direct and Exotic-Becomes-Erotic paths were statistically compared, it was found that the indirect path accounted significantly for the correlation between genes and sexual orientation but the direct path did not (Bem 2000).

This one test of the Exotic-Becomes-Erotic hypothesis does not, of course, establish the validity of the entire theory, which proposes several other links and processes (e.g., the link between feeling different in childhood and later erotic attractions). But it does demonstrate that the correlation between the genes and sexual orientation should not be interpreted as a direct causal link.

Conclusion

It is now considered a truism that most human traits and behaviors are influenced by both biological and environmental/developmental variables and their interactions. But because sexual attraction and behavior appear to be so obviously grounded in our evolutionary history, people have been quick to assume that there must be a “sexual-orientation” gene. But there is also a correlation

between genes and getting divorced: If a monozygotic twin is divorced, his or her twin is also more likely to be divorced than if they are dizygotic twins (McGue and Lykken 1992). And yet nobody has proposed that there must be a “divorce” gene. This is because it is obvious that there must be intervening heritable personality traits (e.g., irritability, clinical depression) that account for the link between genes and divorce. The Exotic-Becomes-Erotic hypothesis is an example of this same reasoning applied to sexual orientation.

Cross-References

- [Female Homosexuality and Bisexuality](#)
- [Human Sexuality](#)
- [Sexual Orientation and Human Sexuality](#)

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Expanding Circle, The

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Introduction

As it is the basic concept which is taught at school level to everyone that, “Man is a social animal.” Without socialization one cannot develop his personality. Many other important phases of life cannot be achieved without socialization. A mother initiates this process from very early stage of childhood and teaches their child to explore himself and to maintain contact to the person who cuddles him/her, loves him/her, care him/her, and concern about the child. These things continue in more compact form when child enters as a student and institutionalization occurs. His/her teachers teach him moral values along with academic curriculum like sharing of tiffin with other classmates, friends, and many more such activities. Basically all these activities just expand the circle of socialization of the child and helps in the development of personality too.

The idea of the “expanding circle” was first penned by the Irish historian WEH Lackey in his 1869 book, “A History of European Morals.” Lackey wrote that we expand the number of people who deserve our moral consideration like a circle. At one time, he explained, “philanthropic affection only embraces the family, soon in the expansion of the circle first a class, then a nation, then a coalition of nations, then all humanity, and finally, feel its effects is done.” (Warner 2014).

Definitions

The relationship between reason and ethics is truly defined as “*The Expanding Circle*.”¹ Relationship between morality and biological capacity of altruism is explained by Singer. As per him, altruism is well defined for wider circles and then it is considered as moral and limited to family, community, tribe, or a country.

This is due to human capacity, which “normalizes or universalizes” our philanthropic tendencies beyond the groups we are biologically reflected upon. As such, reason is not contrary to feelings and instincts but is formed on the basis of it (Browning 1982). The expansion cycle is therefore a product of both ethics and sociology. The process by which a human-being begin at infancy acquires the habits, beliefs, and accumulated knowledge of society through education and training for adult status is the expanding circle.

Peter Singer’s critique of sociology as applied to ethics comes from the It’s-OK-But-It-Presumes- school of thought. Rather than dismiss Wilson’s perceptions of altruism, Singer spent much time restoring and defending notions of kin selection, interpersonal altruism, and, to a lesser extent, the genetic basis for group selection. With homage to Dawkins, we hear again about the strategies of the prisoner’s dilemma and other situations in which mutual altruism is superior to pure selfishness. Only in the second half does Singer offer his particular view, which is that moral behavior reflects the human capacity for reasoning. As individuals and cultures mature, the reason allows the expansion of the moral code, sometimes to a growing population.

We should start designing our culture so that it encourages widespread concerns without the disappointment of important and relatively permanent human desires. Certainly not the last word of ethics in sociology but in a way unrelated and similarly inadequate as the Singer Defense of Reason (Kirkus 1980).

Moral extension and moral concern and refers to the breadth of entities considered worthy of treatment. A morally less expensive person restricts concern for entities that are considered “close” (e.g., their family). A more moral extender extends moral care and consideration beyond these boundaries to “distant” institutions (e.g., animals or plants). Therefore, moral elaboration captures the desire to increase moral concern for others (the “breadth” of an individual’s moral world). Moral foundation theory (MFT; Haidt and Joseph 2004) focuses on the basic foundations that people rely on to make ethical decisions, such as the notion of care/loss or sanctity/

degradation, rather than moral consideration that is an appropriate entity. Moral elaboration also differs from moral identity; self-conception is organized around the degree to which a set of desirable moral traits (e.g., caring, compassionate, honest) is individually valued (Aquino and Reed 2002; Crimston et al. 2016; Caplan 1983; Patience 1984).

Meaning

The process of expanding the circle begins during childhood by which individuals acquire the values, habits, and attitudes of a society. Exposure of a young domestic animal (such as a kitten or puppy) to a variety of people, animals, and situations to minimize fear and aggression and promote friendliness also expands the circle. Some adult dogs, because of a lack of socialization combined with genetic tendencies, can never transfer certain individuals from the “unfamiliar” to the “familiar” category (Steven 2011).

Theories Related to Expanding Circle

Sigmund Freud’s Psychoanalytic Theory

According to Freud, human behavior, experience, and cognition in childhood are largely determined by unconscious drives and events. First, human behavior, experience, and cognition are largely determined by irrational drive. Those drives are largely unconscious. Attempts to bring those drives to awareness, as a defense mechanism, meet psychological resistance. Apart from the inherited constitution of personality, one’s development is determined by events occurring in childhood. Conflict between a conscious approach to reality and unconscious (repressed) content can result in mental disturbances, such as neurosis, neurotic symptoms, anxiety, depression, etc. Freedom from the effects of subliminal material is achieved through bringing this material into consciousness.

Jean Piaget’s Cognitive Development Theory

While studying the field of education, Piaget identified two processes: accommodation and

assimilation. Assimilation describes how humans experience and adapt to new information. It is the process of taking an environment and new information and fitting it into an already existing cognitive schema. Housing, unlike assimilation, is the process of taking one’s environment and new information and changing an already existing schema to fit new information.

Daniel J. Levinson’s Theory of Positive Adult Development

As a theory, positive adult development claims that development continues after adolescence, long into adulthood. In positive adult development research, scientists question not only whether development stops after adolescence but also the notion that it is popular by many gerontologists that it declines after late adolescence. Positive adult developmental processes are divided into at least six areas of study: hierarchical complexity, knowledge, experience, expertise, knowledge, and spirituality.

Implications to Expand the Social Circle

Connect With Connectors

A great way to expand your social circle is to connect with someone through whom you will meet many other people. Those “connectors” are the type of people who have friends on Facebook by the thousands, host parties, and always hook up with a large group of people. Often, these are very open people and are easier to connect with than you think. They may not have time to invest in a deep friendship with you, but they like to know more interesting people to add to their circle (Warner 2014).

Meet New People Constantly

A great habit is always meeting people whom you can add to your circles. In reality, all the people you meet will not become your friends and all your current friends will not last forever. This is why I always say that if you are not making new friends, then you are actually making less. I suggest that you go to places where it is easy and appropriate for someone to walk and

introduce you. Ideally, you need to visit places where others are open to meeting new people as well. Common places to meet with new people might be trade shows, opening nights, galas, cultural or charitable events, seminars, and talks (Dunstan 1984).

Establish Yourself as a Giver of Value

When meeting a lot of people, you have to “hook.” Nothing hooks better than having a donor attitude. First, imagine what they say and imagine if you were theirs; see the world through their eyes. Second, be prepared to share stories, contacts, or quick advice to those who are talking to them.

When you meet new people, there are some psychological theories that determine whether they want to meet you again. It works on a subliminal level. One of the most important principles is the giver/taker attitude. If they think you only care about yourself, the connection is not going to happen.

You can illustrate the giver’s attitude in two ways. The first is really about hearing about what they say, imagining the world through their eyes, and giving them their opinions on their stories and situations. The other way is to prove that you are ready to share the same type of stories they are talking about or introduce them to someone who can help them (Denman 1983).

Commit to a Local Community

One of the fastest ways to promote your social life is to join a community that has the type of people you want as a friend. This community should be in your local area and social gathering once a month, or longer.

You get what you do, which you probably find on Meetup.com, and help those who run it. They most likely accept it, even if they don’t need that help; they will only be what you are interested in. It works great because it gets you from everyone, and because it establishes you as a giver of value (Dent 1984).

Reach Out to People on a Regular Basis

If you want to keep your social circle alive, it is important to stay in touch. You need to follow-up

with people you just met and catch up with existing friends. The challenge here is that we get distracted and forget about it, and later regret it.

To solve this problem, you can create a weekly ritual, where you spend only one hour calling, texting, and messaging people. Just put a specific day and time on your calendar, and do it every week. A great time to do this is Tuesday or Wednesday, as it gives you the opportunity to plan for the weekend with people (Clark 1985).

Know the Kind of Friends You Want in Advance

Do a little planning before you start spending more time on making friends. Try to know what kind of people you want to hang out with. List some qualities, character traits, or interests, and don’t hesitate to be a little more ambitious than usual. This is important because it allows your mind to quickly tell if the person you meet can be a great fit for you.

Here are some qualities you can start: giver, interesting, fun, ambitious, honest, loyal, curious, and reliable. If you want, you can add others, and you can also make a list of activities you want to do with your future friends. These lists will not be definite, but the clarity they bring will save you a lot of time and frustration. I also recommend that you take a little time to learn about friendship and how it works.

Expanding circle can provide many benefits to your physical and mental health. Longevity, better physical and mental health, and reduced risk of other organic mental disorders are also benefits of expanded circle.

Conclusion

Socialization is important because it helps to maintain societies and cultures; it is also an important part of personal development. We are influenced by both nature (our genetic and hormonal makeup) and nutrition (the social environment in which we are raised). Sociology is most concerned with how the way society influences

our behavior patterns makes it clear that behavior varies across class and gender.

Our direct interactions with social groups, like families and peers, teach us how others expect us to behave. Similarly, formal and informal institutions of a society socialize their population. Schools, workplaces, and media communicate and reinforce cultural norms and values. Socialization is a lifelong process, as we enter new stages of life, such as adulthood or senior age. Resocialization is a process that removes the socialization that has developed over time and replaces it with newly learned rules and roles. Because it incorporates old habits that have been created, resocialization can be a stressful and difficult process. So expanding circle incorporates personal development, personality development, and also the development of different phases of life. This allows for the maximum of effective.

In fact, the socialization gives us the tools to fill our evolutionary roles. They are our building blocks.
Warren Farrell

Cross-References

- [Friendship](#)
- [Socialization](#)

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Expanding Lifespan

- [Increasing Longevity](#)

Experiment

- [Little Albert](#)

Experimental Analysis of Behavior

- [Methods and Enduring Impact of Behaviorism](#)

Experimental Economics

- [Game Theory as a Foundation of Evolutionary Psychology](#)

Explicit Memory

- [Episodic Memory](#)

Exploitation of Psychological Mechanisms

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Synonyms

Misuse/misapplication of psychological mechanisms

Definition

The process by which our psychological mechanisms are exploited by evolutionary mismatch, or the effect by which our rate of technological advancements far outweighs the speed of evolution, leading to a “mismatch effect.”

Introduction

As discussed in the previous chapter, evolutionary mismatch is a phenomenon by which our minds are still essentially Stone Age minds meant for hunter-gatherer lives. The rate of technological advancement has been far too fast for our bodies to catch up, leading to various situations by which we are “mismatched” with our bodies to our current environment. Many businesses have taken advantage of this mismatch effect and sell their product through the knowledge of what will appeal to consumers based on what we psychologically desire.

Food and Other Products

Food is a classic example of something that is taken advantage of to appeal to consumers.

Turning on any TV station will inevitably result in watching commercials that appeal to a certain demographic. Often times, food is depicted on these commercials, and made to look extremely appealing to the eye, and often increases consumption of these foods, especially in front of the television (Anschutz et al. 2011). Many times, the food is coated in inedible artifacts such as gloss or shine that superficially make the food more appealing to the eye, an example of a *supernormal stimulus* taking advantage of the mismatch effect. This effect is common across all ages and occurs even in those as young as preschool age (Borzekowski and Robinson 2001). Given that our bodies desired foods heavy in calorie and fat ancestrally, businesses use this practice to appeal to something all humans desire as a result of our ancestral past, or, more specifically, the evolutionary mismatch effect.

Why Sex Sells

Another common example on how our psychological mechanisms are exploited is in the media and the idea that “sex sells.” When it comes to finding mates, males tend to look for physically attractive women who possess indicators that they have good genes and will most likely survive childbirth and be able to produce more than one offspring. Such cues include a small waist-to-hip ratio, good skin, facial and body symmetry, and so on. Most men tend to look for women with these characteristics, yet there is a huge difference between what men (or women!) want and what they get. Although most men would probably like a mate that looks like a model, most men do not end with such a woman for myriad reasons; these attractive women will go for the most attractive males that can offer her the most resources, not to mention that not all women look like perfect models.

The problem arises when we are constantly bombarded by images of attractive females, who not only dedicate their lives to keeping those bodies but who also get photoshopped, thus making their bodies unattainable for the most part. Despite knowing these bodies are unrealistic, they still play on male’s psychological

mechanisms. Kenrick (2011) describes all the negative effects that being exposed to these images lead to. For starters, males who were exposed to several attractive females first and then saw an average-looking female rated this average target as less attractive than males who had first been exposed to several unattractive females. This contrast effect may sound innocuous, yet a later study found that men who were presented with playboy centerpieces reported less commitment and romantic feelings toward their partners than men who had been presented with abstract paintings. Females also fall prey to similar stimuli, albeit in a different way. When it came to physical attractiveness, there were no differences among women who had seen playgirl centerpieces or abstract paintings. However, when the study was replicated using successful, powerful males rather than physically attractive ones, women did report lower commitment and romantic feelings toward their partners after seeing males with resources as opposed to abstract stimuli.

The implications of these studies are enormous because we live surrounded by media that constantly shows us attractive, sensual females and successful, high status males. We are naturally interested in individuals with these characteristics because our ancestors evolved to pursue them because of their high mate value.

Conclusion

Our minds can be easily fooled, and our psychological mechanisms can be tricked. The world in which we live today is plagued by stimuli that mess with our evolved mechanisms in ways we are not consciously aware of. Understanding these mechanisms paves the way to knowing how to activate and manipulate them, a strategy that several companies have mastered in order to better sell their products.

Cross-References

- [Evolutionary Mismatch](#)
- [Mismatch](#)
- [Supernormal Stimulus](#)

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Exploitative

- [Defection](#)

Exploratory Play

- [Object Play](#)

Exponential Growth

- [Malthus on Population](#)

Expression of Altruism

- [Observation of Altruism](#)

Expressions of Emotions Theory

- [Pooh-Pooh](#)

Expressive Theory

- [Pooh-Pooh](#)

Extended Family

► Kinship and Emotional Closeness

Extended Family Relations

► Grandparents and Grandchildren

Extended Kin Role

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Synonyms

Complete family unit; Joint family

Definition

The family that extends past the nuclear family of parents could include aunts, uncles, grandparents, and cousins all living nearby or in the same household.

Introduction

Typically when one thinks of extended kin, it includes the grandparents, aunts, and uncles, and in some cases these people could be living in the same household and the nuclear family. The extended kin's role can provide a huge amount of stability in one's life, even if these family members are not seen on a daily basis; the very fact that they are family is enough to keep the relationships in one's life.

Evolution of Extended Kin Role

Since humans typically lived in tribal communities, extended kin facilitated one of the most

crucial aspects of survival, sharing. For example, the male in the family could be hunting without catching anything to eat, whereas the women, children, and extended family members were still able to forage berries and fruit, therefore without sharing, the family unit would go hungry. Extended kin such as grandparents living within the nuclear family was also common as they aided in the gathering of food to feed the family and helped to take care of the grandchildren. Research has suggested that earlier societies were typically very simplistic, usually organized largely by kinship as genetic commonalities (Purzycki 2004). The only real exception for this was in terms of an individual possessing activities such as a shaman or crafting weapons. There has been a link over the decades as researchers see a correlation between extended kin and large brain sizes (Noone and Paper 2015). Research discussed how large extended families has provided for more extensive caretaking during the critical stages of brain development for children. Remarkably, the social environment from larger and more developed clans of humans provided children with more stimuli which, in turn, lead to more advanced mental abilities.

Some believe that there is a "family decline" hypothesis, whereas families are getting smaller, mainly consisting of one mother, one father, and a biological child. Yet, more research is hypothesizing since humans are now living longer than we ever have and the rate of extended kin is becoming more common than it was 100 years ago (Bengtson 2001). For example, culturally, grandparents will move into their children's homes when they are unable to maintain their own and then share in the family responsibilities and functions such as helping to take care of their grandchildren.

Conclusion

Extended kin roles have been important from early human existence with a focus on the survival needs of the community and how sharing impacted that. Extended kin was predominately made up of biological aspects since reproduction was necessary to a tribe survival and "outsiders"

were not commonly welcomed. As we have evolved and are living longer lives, extended kin is still very important to the family unit today. It can almost be viewed as a win-win circumstance where the parents are getting help from the grandparents in terms of the care of their children, and the grandparents continue to feel needed and able to remain social connections as a result.

Cross-References

- Familial Violence
- Life Expectancy In Hunter-Gatherers
- Parental Investment and Parenting

References

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Extended Phenotype, The

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Definition

The Extended Phenotype by Richard Dawkins is a book widely seen to have made a major contribution towards developing and popularizing the gene-centered view of evolution.

Introduction

In *The Extended Phenotype*, Richard Dawkins supports and motivates two major claims: first, that genes are the proper units of selection and, second, that genes code for phenotypes that extend beyond an organism's skin and into its environment. This entry sketches Dawkins's gene's eye view of evolution, lays out his view of the extended phenotype, and briefly notes some major criticisms of these views.

The Gene's Eye View of Evolution

Dawkins develops the gene's eye view of evolution by drawing a distinction between two kinds of evolutionary entities: replicators and vehicles. According to Dawkins, a replicator is “anything in the universe of which copies are made,” and a replicator is “active” so long as its “nature has some influence over its probability of being copied” (Dawkins 1982, p. 83). Dawkins argues further that genes are the quintessential active replicators: genes are copied across generations, and they also exert influence on their probability of being copied. In particular, through the process of protein synthesis, genes are transcribed into RNA and then translated into proteins (which make up the tissues that determine the organism's phenotype), which, in turn, affects the extent to which they are copied (Dawkins 1982, p. 83).

For Dawkins, though, genes are not the only active replicators: “memes” make up another set of replicators. Memes are units of information that take on physical manifestations (Dawkins 1982, p. 109). If, for example, a given person finds a particular song on the radio appealing, then that person is likely to share this song with a friend, who is then likely to share the song with their friend, and so on. The idea of the song, it might be said, has been copied across individuals and now resides as a unit of physical information in various people's brains. Furthermore, memes influence their probability of being copied; catchier songs, for example, are more likely to be shared (Dawkins 1982, p. 110). However, Dawkins also notes that treating memes as units

of selection may prove to be of secondary importance to evolutionary biology, as it is unclear whether the process of meme replication bears a sufficiently close resemblance to the process of gene replication (Dawkins 1982, pp. 110–112).

Apart from replicators, the other key evolutionary biological entity for Dawkins is “vehicles.” Vehicles are the biological entities in virtue of which genes (or other active replicators) propagate themselves (Dawkins 1982, p. 82). To illustrate this, note that the many phenotypic features of an organism – such as a dove’s wing or a Peregrine falcon’s talons – make it possible for the organism to escape from predators, attack prey, locate potential mates, reproduce, and provide for its offspring; however, these features are replicated only in so far as the genes underlying them are replicated. For this reason, Dawkins does not see these features as replicators in their own right. Still, they are very important, in that they *enable* the relevant replicators to be inherited across generations. Put differently, the replicators reside “inside” these vehicles, and their copying success is determined (at least to a large extent) by the nature of the vehicles they reside in.

With the replicator/vehicle distinction in hand, Dawkins then argues that, by and large, understanding the way biological evolution occurs is best done in terms of genes. The only other option is vehicles. However, when considering the two main types of vehicles in existence – organisms and groups of organisms – it becomes clear that neither of these has the necessary stability to qualify as the basic unit of an evolutionary process. Individual organisms (particular hawks or doves) do not survive for more than a few years (Dawkins 1982, p. 97), and groups of organisms “are constantly blending with other populations and so losing their identity” (Dawkins 1982, p. 100). In this way, Dawkins argues that genes should be made the major focus of evolutionary biological analysis (Dawkins 1982, p. 178).

Dawkins further develops this gene-focused view of evolution by arguing against conceptions of natural selection that make appeal to inclusive fitness, and by showing why apparently Lamarckian phenomena are only Lamarckian on the surface. In short, Dawkins argues that we should see

genes at the center of evolutionary biological analysis, as genes are the only (or at least the major) replicator – and it is replicators that should be the focus of this analysis.

The Extended Phenotype

The second major contribution of Dawkins’s *The Extended Phenotype* consists in the thesis that gives the book its name. Given the above remarks, this thesis can be relatively easily stated.

Recall that, according to Dawkins, genes are active replicators that generate phenotypes (vehicles) to promote their reproduction and survival. Dove genes code for dove wings to promote the survival and reproduction of dove genes. Hawk genes code for hawk beaks to promote the survival and reproduction of hawk genes. Importantly, though, Dawkins thinks there is no reason to see phenotypes as restricted to features on or within the skin of an organism. Indeed, Dawkins thinks that many external features of the environment – such as the nests of the bowerbird – may be regarded as tools “by which that gene could potentially lever itself into the next generation” (Dawkins 1982, p. 199) just like dove wings and hawk beaks. Dawkins calls such traits extended phenotypes, as, unlike dove wings and hawk beaks, these phenotypes extend beyond the organism’s skin into the environment, but like dove wings and hawk beaks, these phenotypes promote the survival and reproduction of genes. Nests, for instance, provide the bowerbird with protection from predators as well as a means for displaying their mate quality, thereby promoting the successful reproduction of the bowerbird’s genes. It is in this regard that nests, then, perform the same function as the bowerbird’s wings and beak. Wings, beaks, and nests may all be regarded as phenotypic tools “by which that gene could potentially lever itself into the next generation” (Dawkins 1982, p. 199).

Dawkins goes so far as to see genes as coding for the behaviors of *other* organisms. Consider parasites, for instance. Nematomorph larvae dwell in host organisms (i.e., bees) and manipulate their bodies to promote their reproduction and

survival. The larvae do this by manipulating bees to dive into water, where the larvae live and develop as worms and the host organism dies (Dawkins 1982, p. 216). In these cases, genes manipulate other organisms to promote their survival and reproduction in much the same way that genes manipulate phenotypic traits to promote their survival. In short, Dawkins thinks that it will frequently make it a lot easier to understand why certain genes are selected for if we see these genes as coding for features that go beyond to skin of the organism (Dawkins 1982, p. 214).

Criticisms

Dawkins' arguments in *The Extended Phenotype* have not been left untouched by critical analysis. To bring out the breadth of the discussion raised by the book, it is now useful to sketch three criticisms that have been of especially great importance in the literature. These criticisms all center on the worry that Dawkins brushes aside non-gene-focused views of evolution too quickly.

The first of these criticisms notes that it appears that Dawkins downplays the importance of vehicles (quite generally) in evolution. It may be true that phenotypes can only be inherited through the genes coding for these phenotypes – however, it is also true that these genes are only “visible” to selection through their phenotypes. Put differently, perhaps *vehicles* should be seen to be at the heart of evolutionary biological analysis, not replicators: what natural selection targets are vehicles – while genes can be used to “keep the books” of the evolutionary process, they are not integral elements of the causal processes making up biological evolution (for more on this criticism, see, e.g., Sterelny and Griffiths 1999).

The second criticism notes that Dawkins appears too rash in presuming that groups of organisms, specifically, are too unstable to be units of selection. Recent work in evolutionary biology has emphasized that the conditions needed for groups to persist long enough to evolve themselves appear more easily satisfied than what Dawkins appears to presume (for more on this

criticism, see, e.g., Sober and Wilson 1998; Okasha 2006; Aktipis 2004).

The third and final criticism worth mentioning here argues that Dawkins has not externalized traditional evolutionary biological analysis enough. To see this, consider the idea of niche construction. Niche construction occurs when organisms construct a niche to promote their reproduction and survival. Put differently, beavers do not just inherit genes for building beaver dams – they inherit the dams, too! Thus, we might criticize Dawkins's view for being too limited in his extensions of traditional evolutionary biological analysis: it is not just that genes should be recognized to have effects that extend into the environment – organisms (and their genes) should be seen as partially responsible for generating that environment in the first place (for more on this criticism, see Odling-Smee et al. 2003).

There is much more that can be said concerning these criticisms – indeed, Dawkins himself has responded to many of them throughout his career (see, e.g., Dawkins 2004). However, all that matters here is noting that, at the very least, there can be no doubt that Dawkins's *The Extended Phenotype* has raised important issues that have furthered the discussion concerning the nature of biological evolution.

Conclusion

Dawkins's *The Extended Phenotype* presents, develops, and extends a gene-based view of evolution. In particular, Dawkins argues that genes, as the key replicators (other than possibly memes), should be seen to be at the heart of the evolutionary process. He further argues that genes should frequently be seen to have phenotypic effects that go beyond the skin of the environment. While his arguments have been criticized – e.g., for not appreciating the importance of vehicles (whether organismic or group-based) in evolution and for not appreciating sufficiently that organisms are often actively involved in generating their environment – there is no doubt that they have made for a significant

advance in the scientific and public understanding of the evolutionary process.

Cross-References

- [Richard Dawkins on Constraints on Natural Selection](#)
- [Selfish Gene, The](#)

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Extended Phenotypic Effect

- [Helping and Genetic Relatedness](#)

Extended Postmenopausal Lifespan

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Synonyms

[Postmenopausal Somatic Maintenance](#) [Post-Reproductive Longevity](#)

Definition

It has been proposed that human menopause exists because lifespans have expanded beyond the point of natural reproductive senescence. As a feature of the grandmother hypothesis, this account describes how human females have gained the ability to provide enhanced care to kin.

Introduction

The grandmother hypothesis proposes that the function of postmenopausal (i.e., post-reproductive) life in females is to provide enhanced care to kin. One interpretation of this hypothesis is that postmenopausal life is the consequence of extended human lifespans, living beyond the physiological degradation of reproductive functioning. This interpretation is in contrast with the description of menopause, or the cessation of ovulation, as an adaptation designed to make grandparental care more efficient.

Evidence

Research into the grandmother hypothesis has primarily supported the notion that postmenopausal life is the result of adaptations in somatic maintenance (keeping the body alive), rather than the result of a controlled process of dismantling reproductive capacity in middle age. First, primate reproductive biology suggests that female reproduction is constrained by the number of oocytes, or immature egg (ova) cells, that can develop in the embryonic female. Our closest primate relatives show similar menopausal timing or, at least, begin to show early signs of menopause just prior to their death of old age (Alvarez 2000). This suggests that human evolution has included the extension of life into postmenopause. Second, looking at the human “mortality profile” and modern data on the lifespans and infant mortality of hunter-gatherers, humans have a species-typical age of somatic decline, around 70 years, well beyond oocyte depletion (Gurven and Kaplan 2007). While hunter-gatherers (and, presumably, ancestral

humans) have 30 times the infant mortality of industrial society (driving down their average lifespans), survivorship after the age of 15 is only about a decade short of the healthiest cultures on Earth (72 vs. 85 in Japan). This suggests that longevity is not a consequence of modern lifestyles but a human trait. Third, human life histories are distinct among the primates with later age of maturity, higher annual birthrate, and shorter weaning times (Alvarez 2000). These life history features are predicted by a tradeoff between early developmental speed and longevity, favoring longevity and compensating for the loss of developmental speed by creating a class of grandmother caretakers. The amount of extra lifespan available to humans also appears to coincide with the time needed for a grandchild to reach developmental maturity.

Following menopause, female humans show enhanced investment into kin. There is limited evidence that this investment improves outcomes for children in industrialized societies (Coall and Hertwig 2010; Hawkes 2004) and stronger evidence that child life expectancy in non-industrialized societies is improved by the presence of a maternal grandmother (Strassmann and Garrard 2011). Cross-cultural research demonstrates that maternal grandmothers tend to invest the most, followed by maternal grandfathers, followed by paternal grandmothers, and finally paternal grandfathers (Bishop et al. 2009). This investment tends to flow most strongly towards offspring who show the highest likelihood of surviving and reproducing (i.e., more attractive, healthier, and higher status children; Leek and Smith 1991) and are most assuredly related to the grandmother (are the offspring of daughters or sisters, rather than sons or brothers).

Conclusion

When interpreting the grandmother hypothesis, modern researchers more often adopt the stance that human longevity provided a selective advantage by creating a class of experienced, elderly caretakers, rather than proposing that the cessation of ovulation provided a selective advantage by limiting reproductive options and hazards for the elderly, thus making them better caretakers.

Cross-References

- [Adaptation](#)
- [Alloparenting](#)
- [Grandmother Hypothesis](#)
- [Kin Selection](#)
- [Menopause](#)
- [Senescence](#)

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Extending the Length of Life

- [Increasing Longevity](#)

External

- [Factors That Influence Bullying](#)

External Ear

- [Outer Ear, The](#)

Externalities

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Synonyms

Neighborhood effects; Spillover effects; Spillovers

Definition

Externalities are the “[b]enefits or costs of an individual’s activity that the individual does not receive or bear” (Ekelund et al. 2006, p. 415). They arise whenever the actions of one person affect the welfare of another. There are positive (when others receive a benefit) and negative (when others are burdened with costs) externalities that may arise from production and consumption decisions. When the production or consumption of a good carries externalities, the effects spill over outside of the market and consequently are not fully reflected in the good’s price. Widespread consumption of schooling leads to a reduction in the crime rate, a positive externality (Lochner and Moretti 2004). Steel production generates air pollution, a negative externality. You receive a benefit living among educated citizens and you pay a cost living downwind of a steel plant, but neither is likely to influence the market price of schooling or steel without some coordination or intervention (for reasons discussed below). The production or consumption of a good can result in multiple, potentially opposite externalities with varying effects across a population. Air pollution from steel production will harm those with respiratory illnesses more than their healthy neighbors and may even benefit air-filtration salespersons. One can frame most negative externalities as positive externalities, or vice versa, by flipping the spillover’s reference

point. For example, air pollution is a net-negative externality from steel production, and cleaner air is a *positive* externality of *reduced* steel production.

Introduction

While the concept of externalities is not controversial, their consequences for market efficiency, and resultant recommendations for policy interventions, have spurred a wealth of research and considerable disagreement among academics and laypersons alike.

Failing Markets and Policy Responses

Market Failure

Pareto efficiency, or so-called social welfare maximizing outcomes, wherein no individual can be made better off without someone else being made worse off, is a common goal for welfare economists (though it is not necessarily sufficient for a normatively appealing distribution of resources) [A]. Provided a host of conditions are met, competitive markets arrive at such outcomes. One of these conditions is that the costs or benefits from producing/consuming a good accrue only to the decision-maker – that is, there are no externalities. In the presence of externalities, the market “fails” to maximize social welfare as individuals are driven to underproduce/consume goods with positive externalities and overproduce/consume goods with negative externalities. Although Pareto efficient outcomes are still possible, the market *by itself* will not arrive at that distribution of resources.

To see why this happens, consider that individuals strive to maximize their welfare, broadly conceived [B]. They do this by engaging in a desired action until its *private marginal benefit* equals its *private marginal cost*. At that point, net benefit is zero, and additional production/consumption is undesirable as most actions have increasing marginal costs and decreasing marginal benefits [C]. Absent externalities, an action’s *social* marginal costs and benefits – its private marginal costs and benefits summed across all affected individuals – are the same as its private

marginal costs and benefits because the decision-maker is the sole beneficiary of her action. Not so in the presence of externalities when private actions help or hurt outsiders, too. With positive externalities, an action's social marginal benefit is greater than its private marginal benefit. If individuals do not consider the public ramifications of their decisions, markets will promote *underproduction/consumption* of the good or service in question (e.g., too few vaccinations) because the decision-maker *bears all the costs* of her actions but *shares their benefits*. With negative externalities, an action's social marginal cost is greater than its private marginal cost, and the market will promote its *overproduction/consumption* (e.g., too many people texting while driving) because the decision-maker *reaps all the benefits* of her actions but *shares their costs* across society. In both instances, the market has failed to deliver the (economically defined) optimal outcome.

Government Responses to Externalities

To increase social welfare, public policymakers seek to correct externality-caused market failures with a variety of instruments, each with their own (dis)advantages, enthusiastic champions, and vehement opponents [D]. Among the most politically heated, governments can counteract the under-/over-provision of positive/negative externalities through "command-and-control" tools, mandating a specific level or method of the good's production/consumption for each actor and levying fines if standards are not met. In the United States, the Affordable Care Act (ACA, aka Obamacare) was such an attempt, aimed at enrolling in health insurance – with its positive social spillovers – citizens who were either unable or unwilling to purchase it. The ACA's "individual mandate" requires individuals to purchase health insurance or face a fine. When policymakers deem externalities sufficiently large, government agencies may take over production to fully regulate the spillovers, as is the case with single-payer healthcare in countries such as Canada, the UK, and France. Although command-and-control approaches inspire strong ideological- and efficiency-based criticisms, there are instances when these tools provide the most (cost-) effective solutions (Cole and Grossman

1999). As such, the question is not whether to employ command-and-control but under what circumstances.

Policymakers can also rely on market forces to improve social welfare by (i) artificially aligning private and public marginal costs and benefits via a per-unit tax or subsidy on the externality or (ii) capping an externality at the socially optimal level and then allowing producers/consumers to trade rights to produce/consume the externality among themselves. These "market-based" instruments rely on government agencies to set the price or the quantity of the externality but let the market reduce compliance costs [E]. For example, a Pigouvian tax forces steel mills to internalize the social cost of their production externality by taxing each ton of air pollution they generate. The value of that tax will equal the difference between (i) the marginal cost of one ton of pollution to *society*, which is relatively high, and (ii) the marginal cost of one ton of pollution to *the mill*, which is relatively low. Making the mills cover the full cost of their actions yields efficient production decisions (Pigou 1920). Similarly, cap and trade systems mandate the amount of an externality that an industry may produce but then allow producers within that industry to efficiently distribute externality production among themselves through a market. For example, in the 1990s, the Environmental Protection Agency (EPA) capped the amount of sulfur dioxide the US energy industry could emit. It then distributed emission permits to the individual energy providers, who could trade those permits, meaning providers who found it cheapest to reduce emissions could sell their permits to higher-cost emitters. This approach resulted in more cost-effective emission reductions than would have occurred via command-and-control (Keohane 2007).

In general, market-based interventions are more cost-effective than strict command and control because the most efficient actors will be the ones to achieve the abatement in negative externalities or the provision of positive externalities. The distribution of regulatory burden is different from that of command-and-control approaches, which mandate individual targets (Baumol and Oates 1988). In addition, market-based

instruments encourage *innovation* as there is now an incentive to lower the cost of reducing/producing a negative/positive externality. However, for a number of reasons, market approaches have not always received the widespread application that these benefits might warrant [F].

Market-based interventions are attractive, but humans systematically deviate from the rational actor models that undergird them (Kahneman 2011). Policymakers can leverage these deviations from rational behavior by restructuring the decision-making environment (without limiting options available to the decision-maker) so that it nudges people into making choices that improve their and society's welfare (Thaler and Sunstein 2008). For example, individuals often struggle to align their immediate preferences and behaviors with their long-term goals. Consequently, relatively few individuals join employer-offered retirement saving programs despite their long-term advantages, and many who do participate do not save enough for the kind of retirement they want. The cognitive and disciplinary demands of forgoing present consumption for greater future consumption are challenging even for people who care about their retirement. But what if the decision were reversed? Policymakers can make saving, rather than deciding on whether and how much to save, the default so that individuals have to opt out rather than opt in. Automatically enrolling employees in such programs and periodically increasing the minimum contribution rate substantially increase retirement savings (Benartzi and Thaler 2013). This carries benefits for savers because their lifetime consumption is now more even across time, and it benefits their compatriots by reducing the costs of communal elderly care. Policies of this sort, which rest on the growing cognitive and behavioral science literatures, highlight the importance of nuanced institutional design to individual and social welfare (Ostrom 2009), thus expanding the debate beyond state versus market and market instruments versus command-and-control [G].

Coasean Bargaining

Because government is not subject to the same profit-based efficiency motivation as industry, and

because calculating private and social marginal costs and benefits can be difficult, some academics argue that government intervention may be worse than the market failures it tries to correct. In situations where enforceable property rights exist and there are few barriers (i.e., "transaction costs") to individuals bargaining, parties affected by externalities may resolve market failures themselves, without recourse to the interventions discussed earlier (Coase 1960). To illustrate this approach, consider if our steel mill was located upstream from a fishery. In the absence of regulation, the steel mill imposes a negative externality on the fishery in the form of water pollution. If, however, the fishery possesses property rights over clean water, its owners can demand compensation from the steel mill for the damages to their fish stock. The steel mill is thus forced to include in their production decisions the marginal cost that their behavior imposes on the fishery, thereby aligning private and social marginal costs and benefits and ensuring an efficient market outcome [H]. Here, government's role may be limited to establishing and maintaining the conditions under which the market can overcome potential failures. Among these conditions are well-defined property rights, rule of law, and so forth. There exist, however, many situations where property rights are difficult to enforce, or where transactions costs are high due to numerous parties involved in negotiations, such that efficient outcomes may require more extensive intervention.

Externalities and Cooperation

Externalities are essential to understanding cooperation (or lack thereof) on matters of social import. Free riding on others' efforts or investments is often a winning strategy when externalities are present, making cooperation difficult. To illustrate, let us return to the Coasean bargaining example, but with a twist: the steel mill, now with rights to pollute the river, finds itself upstream of *numerous* fisheries all equally affected by its pollution. No fishery alone can compensate the steel mill for its reduced production; they must cooperate to raise sufficient funds. All of the fishery owners want a

cleaner river, but each knows she will enjoy its benefits *whether or not* she contributes toward the mill's compensatory sum, so long as that sum is reached. The environmental improvement is a positive externality and its benefits non-excludable. Its costs, however, can be shared and shirked. The fisheries benefit most overall if all fisheries pay to compensate the steel mill to reduce pollution as much as possible, but each fishery owner has an incentive to *free ride* – withhold her funds and hope that the other owners will make up for her lost contribution [I]. Because all the fishery owners have the same incentive to free ride, there is a real possibility that the fisheries will not raise enough funds to stop the mill's polluting, making everyone worse off than if all or even a few fisheries had shouldered the financial burden. Game theory predicts that there is little chance of cooperation in social situations centered around such externalities – discouraging given the number of situations that display this general incentive structure (e.g., charitable giving, open-access computer code, environmental resource management, student group projects, etc.) [J].

Remarkably, the externality-borne incentives at the heart of the market failures discussed earlier are the same as those leading to the cooperative breakdowns just laid out. (Technically, defecting in a prisoner's dilemma constitutes a market failure and full cooperation the Pareto optimum.) When studying cooperation, however, researchers focus less on externally imposed market corrections (such as command-and-control tools or market-based instruments) in favor of studying the conditions under which cooperative success might be achieved endogenously (i.e., from within the system as it already exists), often via group-imposed incentives. For instance, behavioral economists and psychologists research the conditions under which individuals are willing to cooperate in creating/reducing goods with positive/negative externalities (e.g., see Chaudhuri 2011), finding that individuals vary widely in (i) their proclivities to cooperate (e.g., Fischbacher and Gächter 2010) and/or (ii) in their expectations of how others might respond to cooperation on their part. For example, some display ostensibly altruistic behavior (i.e., cooperating regardless of what others are doing)

or conditionally cooperative behavior (i.e., cooperating if others are too), suggesting that cooperative success is not impossible [K]. Even when group composition is not favorable to cooperation (e.g., when few altruists are present), institutional settings (e.g., how much oversight there is, whether punishment is possible, how benefits are distributed, etc.) can discourage free riding on others' efforts to produce/reduce goods with externalities (Ostrom et al. 1994). These institutions then mirror, in part, the exogenous market corrections implemented by government officials, albeit with more reliance on self-governance.

Conclusion

While the theory on externalities is well established, the real-world implications are, unsurprisingly, controversial. Externalities are prevalent in society – few decisions do not impact those around us. But society often struggles over whether and how to address externalities. Strict economic efficiency analyses, probably the most common approach to evaluate how to tackle externalities, may not be sufficient to make policy decisions – in part because analyses on the cost-effectiveness of solutions to problems that arise out of externalities often disregard costs and constraints that go beyond economic considerations, such as political realities and societal preferences (Richards 1999). There are a variety of reasons why society might often prefer one approach over a more efficient one.

Further, there is often disagreement over whether something constitutes an externality in the first place. People will disagree over how “public” a problem is. The recent debate regarding gay marriage demonstrates this well. Some advocates argue that no one but the consenting individuals marrying are affected by the ability to lawfully wed, while opponents argue that such relationships spill over to them, undermining their own heterosexual coupling. Moreover, some people may view gay marriage as a right (constitutional, human, or otherwise). In this case, these individuals will argue that economic efficiency criteria are irrelevant – the debate over whether externalities exist ceases to be of importance. Additional philosophical issues arise in the debate over whether animal welfare in, say, food

production or product testing constitutes a negative externality even though humans are not directly affected. If so, does it warrant increased regulation with potential impacts on the cost of food and welfare implications for food producers?

Externalities exist, and economic theory gives us many of the tools to assess and regulate their efficient distribution. However, the realities of designing effective policies are complicated, in part because of the difficulty of grappling with the underlying questions about how to conceive of goods and how far afield we are willing to look for their impacts.

Connections and Extensions

[A] Well-functioning markets arrive at a Pareto efficient resource distribution, of which there may be many, but there is no guarantee that the specific distribution of resources is politically or morally palatable. In addition, the “liberal paradox” shows the impossibility of achieving Pareto efficiencies while respecting individual liberties.

[B] The classic rational choice model of human decision-making allows individuals to receive (dis) utility from numerous and often nonpecuniary sources such as social standing, kudos from others, the warm fuzzy feeling you get from sharing/voting/volunteering, etc. and is thus broad in its view of what motivates individuals to act. However, it does posit (at times unrealistically) that actors have the time, desire, and cognitive capacity to calculate the costs and benefits associated with available actions, allowing them to choose the course that results in maximum net utility. Consequently, researchers have identified instances when individuals violate the classic model’s assumptions and behavioral predictions (Kahneman 2011), and subsequent extensions to the rational choice approach have incorporated general and context-specific bounds on human cognition. Still, given the model’s intuitive appeal, its mathematical tractability, and its ability to provide clear and, in some cases, accurate predictions, the classic rational choice model remains at the core of public policy analysis.

[C] “Marginal” means consuming or creating a single unit of a good or service on top of what already exists. For example, building an additional

floor in a skyscraper costs more than the last because it requires reinforcing the foundation and lower levels (increasing marginal cost), and eating an additional scoop of ice cream yields less joy than its predecessor (decreasing marginal benefit). [D] Market failure stemming from externalities and their subsequent violations of the Pareto conditions is one of the main motivations for public policy intervention in the economy, along with lowering transaction costs and changing resource allocations on moral grounds (Weimer and Vining 2017). However, there are several requirements for Pareto efficiency beyond those related to externalities, and they also frequently go unmet. Thus, almost all markets exhibit market failure to varying degrees, and economists and policymakers spend much time and effort determining *which* market failures government should try to correct.

[E] Compliance costs refer to the resources (e.g., time and money) spent by industry (or individual consumers) to comply with a given regulation.

[F] Among the reasons for the relative lack of market-based instruments are industry opposition to regulation generally, regulator experience with command-and-control over market-based instruments, and legislators—who are often trained lawyers—preferring policy rooted in law rather than economics (Stavins 1998).

[G] It is important to distinguish between the state versus market debate and the market instruments versus command and control debate. The first contests whether government should intervene at all. Contrast this with the second debate, where the issue is not intervention per se, but what form the intervention should take. Market-based instruments are still government interventions, but do not mandate individual behavior as command-and-control would.

[H] Efficient market outcomes are not contingent upon which party holds property rights (Coase 1960). If the steel mill has property rights over the water, then the fishery pays it to reduce its pollution, but the final level of pollution will be the same as when the fishery holds the rights.

[I] This assumes constant marginal costs and benefits of pollution reduction.

[J] Scenarios like these, where community welfare is at odds with individual incentives, are called

“social dilemmas.” To study behavior in these settings, researchers often abstract these scenarios as n-player prisoner’s dilemmas and public goods games.

[K] Evolutionary game theory provides justification for why these preferences may exist despite these preferences often leading to less desirable outcomes for the individual. In repeated games, cooperating when others cooperate can lead to mutually beneficial outcomes over mutual defection, thus suggesting that evolving cooperative strategies and preferences may provide an advantage (Axelrod 1984).

Cross-References

- [Game Theory](#)
- [Indirect Reciprocity](#)
- [Prisoner’s Dilemma](#)

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Extinction

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Synonyms

[Behavior elimination](#); [Behavior that became extinct](#); [Extinguished response](#)

Definition

Extinction is a functional process through which a behavioral response is loosened and ultimately becomes extinguished due to the absence of conditioned and/or operant reinforcement.

Introduction

Ivan Petrovich Pavlov was the first who theoretically and operationally designated and described

the behavioral process that is widely known as extinction through his work on conditioned reflexes (Ramnero and Torneke 2011), specifically, in a well-known experimental procedure that I. P. Pavlov had conducted, where dogs were classically conditioned to secrete saliva and digestive fluid in response to the sound of a bell which had consistently proceeded their usual food (i.e., meat powder). When the dogs acquired the classically conditioned association between a meat powder (i.e., unconditioned stimulus) and the sound of a bell (i.e., conditioned stimulus), the sound of the bell was consistently presented to them in the absence of the meat powder, leading the conditioned response of saliva and digestive fluid secretion to be loosened and ultimately to become extinct (Shanks 1995).

Contemporary Definition of the Term Extinction

In the contemporary literature related to learning, the term extinction is used to designate and define the progressive weakening of behavioral responses as well as the experimental techniques which set the ground for this functional process (McSweeney and Murphy 2014). The behavioral process of extinction has come to be one of the most well-examined behavioral mechanisms in the fields of both responded and operant conditioning (Staddon 2014). This tremendous interest for the process of extinction is to some extent due to its clinical significance. Specifically, it has been consistently cited that the functional principles that governed the process of extinction constitute the underlying foundation of therapeutic interventions that are widely applied to treat anxiety disorders, substance abuse disorders, and other behavioral abnormalities (McSweeney and Murphy 2014).

Functional Qualities of the Extinction as a Behavioral Process

Extinction is a multifaceted behavioral mechanism that has been recently found not to remove the initial leaning experience (Schmajuk 2010). For instance, I. P. Pavlov indicated through his

work on conditioned reflexes that the reaction that became extinct has the capacity to be reactivated in a future time, a phenomenon that is termed as “spontaneous recovery” (Schachtman 2011). Subsequently, the functional phenomenon of “spontaneous recovery” has been experimentally verified in the fields of both respondent and operant conditioning (McSweeney and Murphy 2014). However, the phenomenon of spontaneous recovery does not always appear and when it does appear it is usually for a short period of time. In addition, when the phenomenon of spontaneous recovery takes place the conditioned and/or operant behavioral response is of lower intensity than it used to be before it became extinct (Staddon 2014).

As already mentioned the behavioral process of extinction reflects the elimination of formerly received unconditioned stimuli and/or reinforcers, yet it also reflects the lack of a contingency between a reaction and a reinforcer and/or between a conditioned and an unconditioned stimulus (Spence 1978). Declarations such as extinction comprised of eight appearances of the conditioned stimuli in the absence of the unconditioned stimuli and/or extinction took place due to reinforcers’ elimination depicts this utilization of the term extinction (Klein and Mowrer 1989).

At an operational level, the process of extinction designates the reduction of reactions from higher intensity as detected previously to extinction, to lower intensity after the application of one of the aforesaid processes (Schachtman 2011). Declarations such as the conditioned response became extinct, and responding by the 8th trial depicts this utilization of the term extinction. Despite the fact that this procedural result is widely demonstrated, it is subject to specific qualifications (Schachtman 2011). Firstly, the amount of time and the operational degree of reactions’ elimination relies to a high extent on the way that the procedural conditions of extinction changed from the ones formed prior to extinction, that is, while the reaction was first acquired and maintained. Secondly, even though, a reaction that has become extinct has the potential to be fully eliminated, there are various environmental conditions that could set the ground in such a manner that its reactivation at least to some extent is fairly possible. In addition, when it comes to

outcomes, simultaneously with decreasing the learned reaction which constitutes the aim of the extinction, the process of extinction might also trigger the activation of additional reactions (McSweeney and Murphy 2014). Yet, if the additional reactions that have been triggered by the extinction process do not receive either operant and/or conditioned reinforcement they would be a temporary result, and eventually vanish.

A Theoretical Conceptualization of the Term “Behavioral Extinction”

Theoretically, the term extinction designates and describes a behavioral process of functional nature. Declarations such as extinction’s operational mechanisms of inhibitory nature did not remove the initial learning outcome, which depicts this utilization of the term extinction (McSweeney and Murphy 2014). In addition, similarities among behavioral effects indicate associated underlying mechanism between classical and instrumental extinction. Moreover, some theoretical perspectives related to extinction directed mostly their attention on either external processes or on internal processes (Schachtman 2011). Specifically, on the one hand behavior-analytic theoretical perspectives of instrumental extinction directed mostly their attention on external processes, that is, the ones that could be observed and measured. On the other hand, the associative theoretical perspectives of classical and instrumental extinction directed mostly their attention on internal processes, that is, the ones that could be inferred (Shanks 1995).

The Role of Prediction Error in the Behavioral Process of Extinction

Most of the current theoretical perspectives related to learning propose that the behavioral process of extinction is governed by the error correction process, a conceptualization that became widely known through the classical conditioning model of Rescorla-Wagner (McSweeney and Murphy 2014). This model

claims that learning takes place when an unconditioned stimulus is surprising enough for an organism. In addition, this model proposes that the presentation of the conditioned stimulus in the absence of the unconditioned stimulus during the extinction process is surprising too. In addition, in order for the prediction error to be fixed, the classically conditioned association of the conditioned–unconditioned stimulus presentation is loosening till the conditioned stimulus precisely foresees the no unconditioned stimulus result. Given an adequate quantity of extinction, this model presumes that the force of an association could be fully extinguished (Schachtman 2011).

Conclusion

The term extinction is used to designate and define the progressive weakening of behavioral responses as well as the experimental techniques which set the ground for this functional process. In the last two decades, the functional processes and qualities of the extinction have been extensively researched (McSweeney and Murphy 2014). Contemporary research related to extinction has consistently proposed that extinction does not remove the initial learning outcome. Specifically, there is high level of consensus in that the behavioral process of extinction depends to a high extent on a new form of learning which is either interfering and challenging or inhibiting the initial learning outcome (Schachtman 2011). Additionally, the context in which the process of extinction operated constitutes a significant variable when it comes to the formation and preservation of the extinction outcome (Staddon 2014). Extinction constitutes a functional procedure and a behavioral mechanism which is highly important in order to empirically and theoretically examine learning outcomes and their actual implementation. In-depth knowledge of the way that the behavioral dynamics alters over the course of the process of extinction is crucial as it sheds light on various phenomena of classical and instrumental conditioning related to the acquisition and preservation of associations (McSweeney and Murphy 2014).

Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Death](#)
- [John Watson](#)

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Extinction of Neanderthals

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Synonyms

[Death](#); [Elimination](#)

Definition

The process of coming to an end or dying out, annihilation, being extinguished.

Introduction

Between 60 and 40 thousand years ago (kya), during a time period known as Marine Isotope

Stage 3 (MIS-3), the species *Homo neanderthalensis*, or, Neanderthals, disappeared. There is still debate around what caused their disappearance. The two hypotheses that have garnered the most research and attention are climate change and competition with modern humans. The first uses changes in the environment as the cause of Neanderthal extinction, especially considering how many there were, and how drastic they were during the period (Finlayson and Carrion 2007; Jimenez-Espejo et al. 2006). The second argues that a more likely explanation of Neanderthal extinction comes from either direct or indirect competition with modern humans (Banks et al. 2008). Naturally of course there is also the argument that both of these factors influenced Neanderthal extinction in their own ways.

In general, the time period that is focused on in research about Neanderthal extinction spans between 20,000 and 60,000 years ago (Gilligan 2007; Stewart 2007). However, it is suspected that Neanderthals will have disappeared from different areas at different times. It is likely that the forces that influenced their eventual extinction (not simply local extinction) will have been due to some combination of the factors listed above (Smith 2013). The following entry elaborates on the morphology of Neanderthals, and the environment they lived in, in addition to describing the main theories that surround this mysterious extinction.

Neanderthal Morphology

It is crucial to understand that Neanderthals were built differently than the modern humans we see today. Their bodies were much thicker, their limbs shorter, and their faces protruded more around the nose and jaw area. Various hypotheses surround what selective pressures caused them to adapt this way. The main theory describes the cold temperatures that they lived in and suggests that their morphology was suited for surviving very cold temperatures (Smith 2013; Gilligan 2007; Stewart 2007). While the climate did oscillate during the Neanderthal habitation of Western Europe, the past 80,000 years of their inhabitation would have been much colder than previous eras (Smith 2013).

Their thick bodies were presumably to preserve heat, broad noses were meant to allow for expanded oxygen intake, and shorter limbs helped to preserve circulation (Smith 2013; Gilligan 2007; Stewart 2007). These adaptations also made Neanderthals very powerfully built, with strong bones and large amounts of muscle across the body. While other modern humans were also built for power, the morphology of Neanderthals remains unique partly due to the extent to which they were so powerfully built but also because they were so well adapted to cold, much more so than anything we see in modern humans (Smith 2013).

The large size and cold adaptiveness suggests that a Neanderthal lifestyle would have necessitated a high-protein diet, especially because of the frigid temperatures (Smith 2013). A high-protein diet requires a large amount of hunting, an activity that could have easily taken up most of an individual's day. Another theory surrounding the morphology of Neanderthals concerns their hunting environment.

Neanderthals lived in climates that were more closed off, unlike the warmer and more open climates associated with modern humans (Stewart 2005). This closed habitat would not have necessitated long-distance running, meaning that longer limbs would not have been selected for. Together, the colder climate and the closed nature of the environment would likely have selected for shorter distal limbs. Their thick bodies may have also served to aid Neanderthals with carrying large amounts of hunted material, as well as simply surviving the rigorous activity that was hunting in itself (Stewart 2005). These hypotheses are certainly plausible compared with the theories on thermoregulation; it is important to remember that while an adaptation may have been selected for a given reason, it can still serve to aid the animal in a variety of ways beyond that reason.

Climate Change

If Neanderthals were so well-adapted to the cold weather of Western Europe, how could colder temperatures have caused them to go extinct. An important detail, according to Stewart (2005), is that each climactic era, and the transition between

them, is different, and just because the Neanderthals had survived previous eras, does not necessitate that they would be equipped to survive all of them.

Climate change can have a drastic impact on a variety of species that live in a particular habitat, even in ways that are not simply due to the changes in temperature. Issues from drastically changing habitats, to causing decreases in pollinator species, or increasing populations of pathogens, can all be caused by climate change. A review of climate change and its impact on species can help illuminate just how it can have such drastic effects on different populations, leading to the eventual extinction of some (Cahill et al. 2013).

MIS-3 was an era of drastic climactic variation and overall cooling of the environment, as the world approached the Last Glacial Maximum (LGM) which would have caused severe temperature drops as well (Smith 2013; Stewart 2007, 2005). Naturally one important and somewhat obvious problem caused by climate change is the potential for new temperatures to be outside of the survivable range for a particular species (Cahill et al. 2013). Neanderthals were typically cold-adapted; however, if temperatures managed to get much colder at the beginning of the LGM, it may have posed a challenge for them. Not only was the air cold, but increases in wind and wind bursts around this time could have also made a difference in temperature and climate. The increase in wind likely also increases dust and thus makes the climate more arid and less livable (Gilligan 2007).

These changes would have severely limited their ability to move around outside shelter to do things like hunt for food. Gilligan (2007) notes that there is very little evidence of Neanderthal clothing, and it is assumed that because their bodies were already adapted to cooler climates, they would not have a need for large amounts of external clothing. He points out that this would have been precisely the problem, if the temperature dropped quickly enough to prevent them from finding adequate covering, lack of clothing could have made the harsh climate potentially lethal.

Neanderthals may not have been the only mammals that suffered due to these drastic climatic changes, especially since it is clear that climate change can have an effect on several species (Cahill et al. 2013). In a comparative analysis of other large fauna that were extant during MIS-3, Stewart (2007) provides evidence to suggest that Neanderthals were not the only large, cold-adapted mammals to go extinct during this time. This suggests that this transition into the LGM and the resulting changes in temperature and environmental conditions would have been difficult to survive for many different creatures, making it more likely that it could have precipitated or encouraged the extinction of the Neanderthals as well. Some of these other species to go extinct included the wild cat, the Iberian lynx, leopard, hyena, and antelope (Stewart 2007).

It appears as though one of the most compelling reasons for climate changes causing extinction is related to the loss of potential prey and food as species go extinct, potentially causing other species to go extinct as well. This seems to be the most common cause of species extinction (Cahill et al. 2013). As these other mammals went extinct, Neanderthals may have suffered from a lack of food resources, which would have encouraged their move toward extinction (Cahill et al. 2013).

There is evidence that suggests that Neanderthals were able to adapt to some climate changes; however, abandonment of sites as well as local small-scale extinctions was not uncommon in their history as certain areas became potentially uninhabitable. We do know that they survived for quite a while during a period of varying climate, which suggests a degree of adaptiveness, but in the end there may have been other factors, or it simply was not enough (Jimenez-Espejo et al. 2006).

In general the area around the Iberian Peninsula would have produced an environment huge in biodiversity, but also high in levels of climatic variations, especially with the presence of Heinrich Events and Dansgaard-Oeschger Events (Jimenez-Espejo et al. 2006). Archeological evidence indicates that caves in Southern Iberia may have been the last remaining habitat for extant

Neanderthals until about 28,000 (Jennings et al. 2011). This area featured a climate with high variability in rainfall and temperature, which created several different environments that would have been suitable for Neanderthal populations. Based on the numbers of archeological sites in these areas, it appears that Neanderthals tended to prefer climates that were either warm/wet or cool/wet, with large amounts of rainfall. The last few Neanderthals lived in areas that typically received between 400 and 600 mm of rain each year, but as the climate changed, their habitats became broken up as rainfall decreased. It is possible that the increase in isolation between these groups as rainfall decreased could have promoted their eventual extinction (Jennings et al. 2011). This would have been around the time when anatomically modern humans were migrating into the area, as the climate of the area was shifting, which of course brings about the hypothesis that modern human migration impacted the extinction of the Neanderthals.

Competition with Modern Humans

It is currently believed that Anatomically Modern Humans (AMH) evolved in Africa and then migrated outward at some point well after 80,000 years ago (Smith 2013). One group of researchers suggests that as AMH populations migrated into the Iberian Peninsula, they began to push the Neanderthal populations living there further south down the peninsula. This would have been just before Heinrich event 4, which was a period during which icebergs collapsing into the North Atlantic caused decreases in North and Mid-Atlantic sea temperatures, cooling the environment (Banks et al. 2008; NOAA 2008).

Climate research that has focused on some of the last climatic events Neanderthals would have seen before going extinct indicates that the areas to the North of the Iberian Peninsula, where they were settled primarily at that time, would have been of mild climate, indicating that had the Neanderthals wished to expand Northward, they could have done so without climate being an issue. Overall, this contradicts the idea that climate would have been the main or only driving force

behind Neanderthal extinction, since they may have had an option that kept them out of the cold. The encroaching AMH population into the Iberian Peninsula can then be the only suitable explanation for Neanderthal Extinction, per Banks et al. (2008).

This study illustrates, not the reasons why competition may have led to extinction, other than the assumption that if AMH and Neanderthals were living in the same areas, AMH would win; however, it is saying that climate alone would not have been the force that drove the Neanderthals to their eventual end.

However, Gilligan (2007) points out that there is little evidence to date that supports the idea that tool use in humans made them objectively superior in terms of food procurement, meaning that it was unlikely that they out-competed the Neanderthals. Assumedly, the Neanderthals in the region would have been plenty successful at hunting and gathering, and there is no reason that modern human success would necessarily disadvantage them (Gilligan 2007). In addition, Villa and Roebroeks (2014) found no archeological evidence to convincingly suggest that the modern humans living near or around the Neanderthals were superior enough to have caused their extinction.

To a certain degree, every environment will have different species' who are competing for resources (Faria 2007) and the MIS-3 environment with AMH and Neanderthals would have been no different. The question is whether or not their competition for resources was intense enough to lead to the extinction of the Neanderthals, in the absence of other challenges.

It is also suggested that while AMH and Neanderthals may not have been in direct competition with each other, the stronger genes, higher fertility, and greater intelligence may have simply allowed the modern humans to be more adaptive to changing environments, leading to the replacement of the Neanderthals (Faria 2007). This theory suggests an extinction pattern that merely coincided with AMH migration into the area, and less an active annihilation by the modern humans. It is possible that the addition of culture to a human population

made surviving the cold easier for AMH and could have caused them to outcompete the Neanderthal's biological adaptations of being robustly built. Additionally, if the Neanderthals needed to spend more energy keeping warm as the environment became colder, they had less energy for hunting or other important survival activities, including reproduction (Smith 2013).

In a model created by Faria (2007) it is illustrated that none of the hypotheses, competition, replacement, war, or disease, could have been sufficient for the extinction of Neanderthals, either when taken alone or when analyzed together. This clearly indicates that there must have been other forces at work to drive the Neanderthals out completely.

Assimilation

A hypothesis that falls under this umbrella of theories surrounding Neanderthal extinction at the hands of modern humans is the assimilation hypothesis, which essentially states that Neanderthals and modern humans interbred enough that as the "pure bred" Neanderthals died out, all that was left was modern humans with trace amounts of Neanderthal DNA, evidence for which we still see today (Smith 2013). Shea (2008) notes that any time you have populations intermingling there is bound to be reproduction between the two, which suggests a certain degree of cooperation as well.

There is evidence to suggest that there is a fraction of the modern human genome, especially for those with ancestry in Western Europe, that is Neanderthal in origin (Smith 2013). This provides provocative evidence that when modern humans migrated into Western Europe, they did not simply replace or wipe out the Neanderthals, there must have been some interaction between the two in other forms for our genome to turn out this way.

In general modern human populations at a given site were larger than Neanderthal populations at another site. So overall, modern humans had several advantages over Neanderthals, those included living in larger groups and having fitted clothing to protect from the cold.

Smith (2013) proposes that while modern humans likely came into the area, interbred with a small portion of Neanderthals that were left, and the Neanderthal DNA became slowly incorporated and soon diluted by the vast number of modern human DNA that it was competing with.

It is possible that after interbreeding with *Homo sapiens*, their genes became dominant and led to them outliving Neanderthals (Faria 2007). Various ideas have been proposed that capture Neanderthal extinction within the whole picture of human evolution. It is possible that modern humans migrated and replaced the Neanderthals or that they lived together and cooperated for many years (Stringer 1990; Wolpoff 1989). Other ideas are a mixture of these two, suggesting that neither is a complete picture of what may have really happened (Faria 2007).

Conclusion

Overall the main cause of Neanderthal extinction would have likely been lack of resources, and it is unlikely that one and only one source contributed to this. The above theories discuss different means by which either climate change or interference by AMH populations could have helped to create this lack of resources. One example being that as the climate became colder and other mammals began to die out, Neanderthals no longer had a viable food source, which caused increased mortality and decreased fertility (Gilligan 2007).

In a comprehensive review of climate change and its effect on animal populations, it is pointed out that it does not make any sense to regard climate change as the sole cause of extinction. As climactic patterns fluctuate, creating changes in the environment, animal behaviors change as resources change in availability, which will absolutely have an effect on all of the fauna in a particular habitat (Cahill et al. 2013).

The migration of the modern humans may not have directly killed off the Neanderthals, especially since there is strong genetic evidence that they interbred with each other (Smith 2013). However, the modern human cultural adaptations like tools and, most importantly, fitted clothing may have

contributed to their increased ability to survive. In addition, as they began to interbreed with Neanderthals, it is possible that slowly the last few “pure-bred” Neanderthals began to die out (especially if their prey was also dying out) leaving the only remaining pieces of Neanderthals as fractions of our modern human genome (Smith 2013; Faria 2007).

Alas, while we do not have Neanderthals wandering the earth the way they would have done thousands of years ago, for many, there is a small part of the Neanderthal genome that is still alive and with us today.

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food sources (susceptible to extraction from a matrix or a case).

Introduction

The Extractive Foraging Hypothesis (EFH) is one of three interrelated hypotheses, first proposed by Parker and Gibson in 1977, about object manipulation and tool use in nonhuman animals. It states that *intelligent tool use* arose as an adaptation for *extractive foraging*, i.e., exploiting a variety of seasonally limited, local, high-energy, embedded food sources. The hypothesis further states that increased brain size of great apes and hominids arose as part of this adaptation.

Extinguished Response

► Extinction

Extra Pair Copulation

► Infidelity Risk

Extractive Foraging Hypothesis, The (Parker and Gibson 1997, 2015)

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Synonyms

Scavenge hunting

Definition

Intelligent tool use arose as an adaptation for *extractive foraging*, i.e., feeding on embedded

A Taxonomy of Object Manipulation and Tool Use

Parker and Gibson (1977, 1979) proposed three distinct hypotheses about object manipulation and tool use in nonhuman animals. First, they suggested a taxonomy of object manipulation (including simple prehension, simple object manipulation, object-substrate manipulation, complex object manipulation, and social-object manipulation), and on the basis of this taxonomy they distinguished between *intelligent* and *context-specific* tool use. Both taxonomies, of object manipulation and of tool use, have been derived from Piaget's (1952) theory of sensorimotor stages in human infants.

The second hypothesis addresses the *evolutionary origin* and *functional significance* of intelligent tool use in the nonhuman animals. The authors claimed that *intelligent* tool use arose as an adaptation for *extractive foraging* and feeding on a variety of seasonally and locally variable encased foods. In contrast, *stereotyped* tool use is associated with *context-specific* foraging on a single nonseasonal food source. The latter form of tool use also correlates with extractive foraging but on nonseasonal embedded foods and a specialized diet.

The third hypothesis consists of a phylogenetic localization of intelligent tool use in the animal

kingdom. After analyzing the so far reported cases of tool use, based on the characterization of the required forms of object manipulation, the authors suggested the emergence of intelligent tool use in the common ancestor of cebus monkeys and independently in the common ancestor of great apes and hominids.

Object Manipulation

Despite a number of caveats and critics, Piaget's theory has many strengths to address the origin, nature, ontogeny, and function of animal as well as human knowledge. According to Piaget, the sensorimotor development is characterized by three sequentially developed circular reactions. While the *primary circular reactions* are characterized by repeated actions on the self or on environmental objects that can be assimilated to simple schemes, the *secondary circular reactions* depend on voluntary prehension and involve repeated actions that aim at re-creating contingent effects on the environment. When schemes become mobile and freely combinatory, the differentiation between actions that serve as means – like setting aside an obstacle – and the final actions – like grasping the object – emerges. The transition to the *tertiary circular reactions* occurs when the subject begins to explore new objects through serial application of its familiar schemes, thereby getting interested in the outcome of actions rather than in the actions themselves. These actions do not focus on relations between one's own action and an object but rather towards the relations among objects.

Feeding Ecology

In its essence, the original version of the EFH (but see Parker 2015) proposes an *ecological* account for the emergence of intelligent tool use. Times of low-resource availability forced species to exploit novel food items and prompted various behavioral innovations, such as extractive tool use. In general, behaviors involved in locating, extracting, preparing, distributing, storing, and eating food

items may be considered as adaptations to the temporal and spatial distribution of food sources in a given habitat.

In behavioral ecology, a major distinction is between generalists and specialists, which may be better viewed as ends on a continuum. Dietary generalists, such as cebus monkeys, great apes, and hominids, feed on a variety of seasonally available foods. Such a feeding strategy may involve the extraction from a matrix or a case through intelligent complex object manipulation and means for discovering and remembering their spatial and temporal location. In contrast, dietary specialists, including context-specific tool users, like Galapagos finches or New Caledonian crows, may have evolved sophisticated forms of production and use of tools (e.g., hooked-tool manufacture) in order to gain access to high-quality food sources (e.g., larvae) during most of the time, making up a large portion of their natural diet.

Tool Use

It is not the *fact* that animals use tools that is interesting or significant in itself, but the *manner* in which the tool is employed. In order for tool use to qualify as being “intelligent,” it needs to be flexibly and creatively adjustable to novel situations.

In general, two sets of factors might explain the difference in tool use between two or more species under investigation. Extrinsic factors (i.e., in response to external stimuli) are ecological and social factors, which alone or together can shape the emergence and maintenance of tool use in the wild. Species may also differ intrinsically, in terms of their cognitive ability, their predisposition, or intrinsic motivation for tool use.

A recent collection of reviews (Biro et al. 2013) has shown that in many prominent cases of tool use empirical evidence for extrinsic factors is weak. For instance, a close examination of the habitats and behaviors of bonobos and chimpanzees revealed that the difference in their tool use may be better explained by predispositions rather than social or ecological

opportunities. It is also possible that tool use evolved as a by-product of generalized intelligence evolved in another context.

Taxonomic Distribution

The most recent comprehensive attempt to define and categorize tool use has proposed that associative (or intelligent) tool behavior includes five types of tool use: tool sets, sequential tool use, tool composite, multifunction tools, and secondary tools (Shumaker et al. 2011). Chimpanzees show all five, and capuchin monkeys at least three, possibly also all five, types of associative tool use. This latest survey would support Parker and Gibson's proposal. However, experiments are under way – in the field as well as in the laboratory – to examine carefully what types of associative tool use other nonhuman animals, especially the prime candidates among mammals and birds, show.

Brain Evolution

Reader et al. (2011) have explored the idea of general intelligence with a principal components analysis. It included extractive foraging plus tactical deception, innovation, tool use, and social learning, as well as three lifestyle or socio-ecological measures (diet breadth, percent frugivory, and group size). All five cognitive variables clustered together on the first component, while the three lifestyle measures clustered on a second, independent, component. This suggests that some form of general intelligence (abbreviated as *g* in the literature) might underlie the evolution of the different cognitive measures, supporting a battery of hypotheses regarding the factors driving brain evolution.

Reevaluating the Extractive Foraging Hypothesis

In 2015, Parker reexamined the extractive foraging hypothesis in light of recent behavioral and brain data, new methodologies for quantifying extractive

foraging, and a new phylogeny of primate intelligence. In this paper, Parker questioned the dichotomy between extractive foraging and social intelligence as mutually exclusive hypotheses for the evolution of primate cognition and brain size. Part of the argument is that cognitive abilities in great apes arose not only as an adaptation for extractive foraging through intelligent tool use but also its social transmission. With this extension, the extractive foraging hypothesis became a socio-ecological, rather than a strictly ecological model.

Nevertheless, some challenges and critical issues to the EFH remain:

- It has been criticized that applying the Piagetian framework, which aimed at describing the cognitive development of human infants, may not be appropriate for animals with very different morphologies, ecologies, and life-history traits.
- Not all tool users are extractive foragers, as tools may also be used for different means (e.g., agonistic interactions, physical maintenance, mate attraction). Especially in primates the focus on tool use employed to extract food overlooks the fact that tools are applied in several different contexts as well.
- One of the best opportunities to examine whether feeding ecology can explain differences in the presence of intelligent tool use is the bonobo–chimpanzee comparison. However, recent studies of tool use in the genus *Pan* have not supported the hypothesis that it is a response to resource scarcity.
- Defining intelligent tool use as being associated with extractive foraging and extractive foraging as foraging aided by intelligent tool use is a somewhat circular argument.
- The distinction between *context-specific* and *intelligent* tool use is too rough, as it blurs the distinction between tool sets, sequential tool use, tool composite, multifunction tools, and secondary tools.
- The breath of the EFH is too narrow, having a strong focus upon primate tool use (chimpanzees, in particular). There is complete overlap between the Aves and Mammalia orders in terms of the tool use context, arguing against any special abilities of mammals or primates (Smith and Bentley-Condit 2010).

Even within primates, high levels of intelligence have independently evolved at least four times, with convergent evolution not only in cebus monkeys and great apes but also in baboons and macaques.

- The EFH argues that capuchin monkeys evolved only limited tool use abilities. This statement overlooks a huge body of recent research on capuchins (e.g., Visalberghi et al. 2015) that shows striking similarities in percussive tool use of capuchin monkeys and chimpanzees.
- It is possible that the seemingly qualitative difference of tool use, between primate tool users and all other tool using species, simply reflects differences in length and intensity of observations.

Conclusion

There is a strong correlation between extractive foraging, tool use, and social learning. While this is consistent with the later extension to the EFH, the correlations indicate a general primate intelligence trait (g), supporting many hypotheses regarding the factors driving brain evolution. Neither social nor ecological intelligence seem to be the sole cause of brain evolution but rather may be intrinsically linked in group-living animals.

Parker and Gibson (1977, 1979) have suggested that intelligent tool use has emerged twice in evolution, both in the primate lineage. However, recent work on tool use – together with innovation and insightful object manipulation– in corvids and parrots suggests that we have much to learn from thinking about hominin intelligence in terms of convergent, multiple independent evolutionary events (Lefebvre 2013). To understand the intelligence of *Homo*, the most invasive and opportunistic primate genus, an invasive and opportunistic avian genus like *Corvus* might be as useful as the currently dwindling and geographically limited populations of our closest sister taxa, the great apes.

Cross-References

- [Object Manipulation](#)
- [Tool Use](#)

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Extra-Dyadic Interaction

- [Sex Differences for Pursuing](#)

Extradynamic Involvement

- [Infidelity Risk](#)
- [Jealousy and Infidelity](#)

Extra-Dyadic Relationships

- [Cues to Infidelity](#)

Extradynamic Sex

- ▶ [Infidelity Risk](#)

Extra-Dynamic Sex

- ▶ [Sex Differences for Pursuing](#)

Extramartial Affair

- ▶ [Personality and Mate Poaching](#)

Extramartial Sex

- ▶ [Frequency of Infidelity](#)

Extrapair Copulation

- ▶ [Frequency of Infidelity](#)

Extra-Pair Copulations

- ▶ [Cues to Infidelity](#)

Extra-Pair Copulations (EPCs)

- ▶ [Multiple Matings](#)
- ▶ [Seeking Extra-Pair Partners](#)

Extra-Pair Sex

- ▶ [Sex Differences for Pursuing](#)

Extrastriate Visual Cortex

- ▶ [Visual Association Cortex](#)

Extraversion

- ▶ [Five-Factor Model](#)

Extreme Environments

- ▶ [Harsh Environments](#)

Extrinsic Environmental Hazards

- ▶ [Extrinsic Mortality](#)

Extrinsic Morbidity-Mortality

- ▶ [Extrinsic Mortality](#)

Extrinsic Mortality

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Synonyms

Environmental harshness; Extrinsic, age-independent environmental mortality; Extrinsic environmental hazards; Extrinsic morbidity-mortality;

Extrinsic risk; Mortality risk; Nonsenescent-related mortality; Perceived social threat.

Definition

Extrinsic mortality is the age-specific risk of death caused by external forces that is equally shared by all members of a population (Quinlan 2007). Extrinsic mortality is determined by nonintrinsic environmental stressors that are not under individual control (e.g., war, nonlethal injuries, violence, and disease; Machluf and Bjorklund 2015). Organisms experiencing high extrinsic mortality are unable to reduce their mortality risk through increasing resource allocation to somatic maintenance, growth, or defense (Ellis et al. 2009; Placek and Quinlan 2012).

Introduction

Extrinsic mortality is commonly conflated with *environmental harshness* – environments producing greater possibility of death or disability (Ellis et al. 2012). Although harsh environments generate greater mortality risks, these risks include both intrinsic mortality – mortality rates influenced by changes in resource allocation – and extrinsic mortality risks (Ellis et al. 2009; Stearns 1992). Extrinsic mortality cannot be controlled by individuals. Intrinsic mortality, by contrast, is controllable through within-individual shifts in resource allocation. Increasing resource allocation for somatic maintenance, growth, or defense, may reduce an organisms' susceptibility to intrinsic mortality (Stearns 1992). High extrinsic mortality, however, tends to more uniformly favor more accelerated life history strategies (Placek and Quinlan 2012; Wells et al. 2017). Since harsh environments also promote the adoption of fast life history strategies (Del Giudice et al. 2015), extrinsic mortality and environmental harshness are often not differentiated (e.g., Ellis et al. 2009, 2012; Machluf and Bjorklund). Lack of differentiation between concepts may also occur because of practical difficulty in distinguishing between intrinsic and extrinsic sources of mortality (Stearns 1992).

Extrinsic Mortality and Life History Strategies

Life history theory postulates that greater sources of death and disability (i.e., high morbidity-mortality) promote accelerated life history strategies that favor immediate survival reproduction over somatic investment and long-term health (Ellis et al. 2009). Specifically, when extrinsic mortality is high, organisms tend to increase energy investments in rapid growth and earlier reproduction and reduce investments in somatic maintenance and defense (Wells et al. 2017). These allocations lead to accelerated aging and shorter lifespans, rapid growth and early maturation, and increased risk-taking (Wells et al. 2017). By contrast, low-extrinsic mortality favors increased somatic investment and delayed reproduction, leading to slower senescence, more gradual growth, delayed maturation, and longer lifespans (Placek and Quinlan 2012; Wells et al. 2017).

Exemplars of extrinsic mortality are evident in animal and human behaviors. For example, when controlling for intrinsic mortality, Chen and Maklakov (2012) found that nematodes (*Caenorhabditis remanei*) adapted to high extrinsic mortality by adopting an accelerated aging and reproduction schedule. Nematodes that experienced high intrinsic mortality lived 20% longer (Chen and Maklakov 2012). Similar effects have been observed in humans, although it appears that humans appear to be sensitive to more than just external mortality. According to Ellis et al. (2009), human reproductive efforts are not only influenced by extrinsic mortality, but also by extrinsic morbidity. Contemporary life history theory more generally refers to *extrinsic morbidity-mortality*, accounting for effects of various sources of death or disability on resource allocations and reproductive efforts (Ellis et al. 2009). In humans, high extrinsic morbidity-mortality is associated with reductions in parental investment, given that in such environments, parental investment is less consequential for offspring survival (Quinlan 2007). For example, increased exposure to famine and warfare are associated with decreased human maternal care, and high levels of pathogen stress decrease both maternal and paternal investment (Quinlan 2007).

Conclusion

Extrinsic mortality – external sources of morbidity and mortality – favors the development of accelerated life histories. Extrinsic mortality tends to be higher in environments characterized by harshness or unpredictability (Ellis et al. 2009). Given that harsh and unpredictable environments often contribute to both extrinsic and intrinsic mortality, it is often difficult to practically distinguish the two types of mortality. Nonetheless, clear sources of extrinsic morbidity-mortality have been observed in both humans and animals, with resultant behavioral consequences (Chen and Maklakov 2012; Quinlan 2007).

Cross-References

- [Adaptation](#)
- [Adaptive Plasticity](#)
- [Environmental Harshness](#)
- [Environmental Harshness/Mortality](#)
- [Environmental Risk](#)
- [Harsh Environments](#)
- [Life History Strategies](#)
- [Life History Theory](#)

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Extrinsic Risk

- [Extrinsic Mortality](#)

Extrinsic, Age-Independent Environmental Mortality

- [Extrinsic Mortality](#)

Eye Contact with Adults Versus Babies

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Synonyms

[Bonding](#); [Connection](#); [Gaze](#); [Social communication](#)

Definition

The act of looking into another's eyes as a form of nonverbal communication.

Introduction

Various pieces have investigated the importance in eye contact with babies versus that of adults most likely because it is one of the most universally understood forms of communication. The importance of eye contact between adults and children will be discussed and how they differ from each other and then how this impacts humans on an evolutionary scale and what purpose it serves.

Eye Contact in Babies

One of the most impactful connections begins from the moment the mother first makes eye contact with her infant in which there is a biochemical change in the mother's brain and ends with a bond or as some developers call "attunement" (Cogen 2000). This attunement is what creates trust, and the baby is more likely to form a relationship with a mother/caregiver to respond to their needs on a visual level. Eye contact is what mediates a nonverbal transition in humans, it allows them to feel safe and protected but is not a skill that can be learned, it has to be experienced. The best way to understand eye contact with babies is that there is a connection between the two brains, one of the infant and the other of the adult, and the eyes are what provide that link. Evolutionarily speaking, there is an importance with eye contact since the same is true for the infant when they make eye contact with their parent. For example, when the parent smiles, this creates chemicals in the child's brain to heighten alertness which can calm, protect, or reassure them (Klaus et al. 1970). Think of an example of if you have ever watched a child before and they begin crawling by a table and start reaching for something to knock down. Prior to doing this, they will tend to look back at the parent or caregiver as a "check-in" almost to see if what they are doing is permitted or not. Since humans have been reproducing this unspoken form of communication is what helps create bonds and protects the child.

Eye Contact in Adults

Whereas eye contact in babies can be more thought of as a form of bonding, connection, and security as we age, eye contact in adults is a crucial role in communication as an almost synchronizing signal to understanding one another. Eye contact is also a form of feedback which is why people tend to look up at one another to confirm if what they just said is accurate and if the other person agrees with them (Farroni et al. 2002). There is a purpose for eye contact with adults; we are trying to hand the "conversation baton" as it were to initiate the next person to speaking which could explain why eye contact and autism is such a researched subject. Eye contact also is a way of initiating individuals into something as a form of acceptance. This can be seen daily in a classroom when a teacher poses a question to the class and the students who don't know the answer refrain from eye contact as to not be called on.

Conclusion

It is clear that when we are younger, eye contact is much more important as a means of bonding and survival for the infant, whereas, in the adult stage, it is a form of nonverbal communication exhibiting feelings of understanding and acceptance. Eye contact is one of the most understood nonverbal reciprocal forms of communication that we as humans have. This allows for both giving and receiving information so that we can allocate in mutually understood message with other and do so successfully.

Cross-References

- ▶ [Familial Violence](#)
- ▶ [Maternal Bonding](#)
- ▶ [Maternal Role](#)
- ▶ [Pair-Bonding](#)

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Eye, The

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Synonyms

[Eyeball](#); [Ocellus](#)

Definition

The primary organ by which animals receive light information and the only structure by which image-forming vision is possible.

Introduction

The glint of a predator’s gaze, plumage of a potential mate, or the ominous dark cloud announcing the approach of a violent storm all represent visual signals imperative to an organism’s survival, and all necessitate the use of vision. Across the animal kingdom, the use of eyes to receive light information has undoubtedly contributed to the massive

radiation and diversification, seen in fossilized and extant members of the animal kingdom.

Sight was one of the major sensory innovations to arise during the “Cambrian Explosion” and provided animals with the means to interpret and react to light information, a driving force in the growing divergence of life strategy and corresponding body plan (Plotnick et al. 2010; Parker 1998; Conway-Morris 2003). The evolution of novel eyes coincides with the first observed examples of complicated behavioral strategies such as predation, demonstrating the value of vision as a tool by which early animals’ thrived (Parker 1998; Conway Morris 2000).

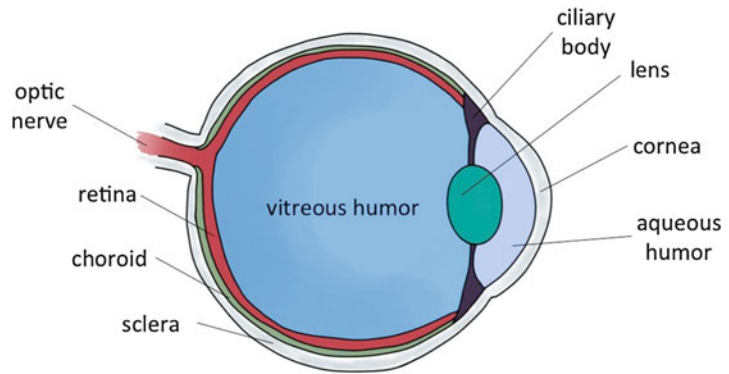
Light information is multifaceted and can be interpreted based on intensity, wavelength, or polarization either alone or in combination. As such, there are multitudes of different ways by which animals receive and use this information, leading naturally to a great diversity of light receiving strategies. Herein is described the basics of eyes found throughout the animal kingdom, with a focus on vertebrates (Fig. 1). The text will briefly explore the immense diversity in structure, function, and development of vertebrate eyes as well as the seemingly contradictory deep conservation and similarity. Such captivating mysteries of multiplicity are expected to instill an appreciation of the intricacy and beauty of eyes that induced researchers since the time of Charles Darwin to wonder how it was all possible.

What is An Eye?

The basis of sight is built on the foundation of a capacity for detection of photons by specialized sensory cells: photoreceptors. These cells are chiefly responsible for the transduction of light energy into cellular signals through the action of a group of light sensitive photopigments – the opsins. In order to efficiently capture photons, photoreceptors require membranes with high surface area in which a multitude of opsins are housed. When photons interact with a photoreceptor’s associated opsins, a chain of signals is induced which culminate in electrochemical signals sent to the brain (Wald 1968).

Eye, The**Fig. 1 Anatomy of a vertebrate eye.**

A simplified illustration of the conserved morphological features found in vertebrate eyes



E

Photoreceptors have been recruited to a variety of structures and organs including some that are nonvisual, such as the pineal-complex which is involved in the entrainment of circadian rhythms in vertebrates (Ekstrom and Meissl 2003). Though photoreceptors are most famously associated with eyes, additional photoreceptive structures exist that are not considered eyes such as the “frontal eye” of the cephalochordate, amphioxus (Vopalensky et al. 2012; Lamb et al. 2007). These structures, while able to detect light intensity, are unable to collect sufficient light information to form images, and by our definition are not true eyes. An image is an integration of light information received by the eye from multiple directions into a signal which, when carried to the central nervous system, is interpreted as a dimensional representation of the environment. An eye is an organ capable of producing such an image.

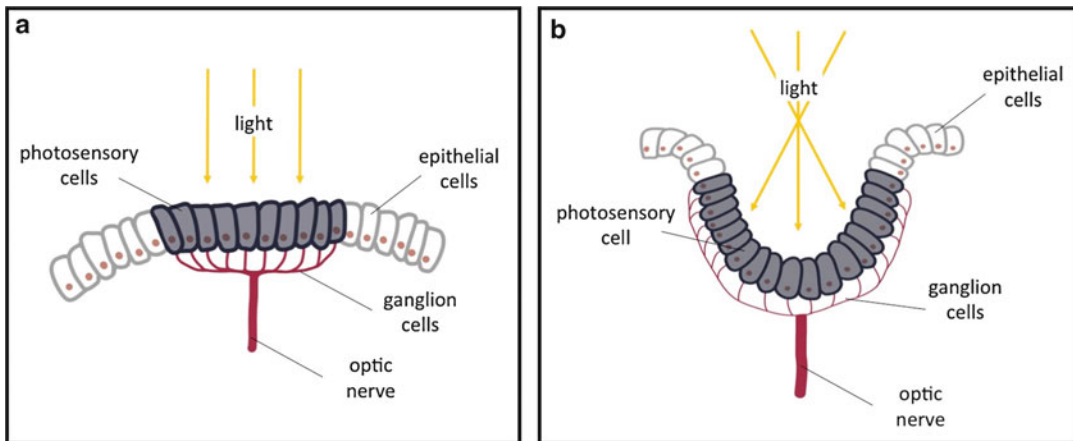
Image formation requires more than a singular photoreceptive cell, it requires a group, and this grouping must be arranged in such a way that directionality can be perceived. By arranging photoreceptors in a cup shape, the amount of light that can be captured is drastically improved (Fig. 2) In being able to capture directional information, detection of such things as texture, shape, and trajectory of movement is possible. The evolution of an eye with these capabilities allowed for animals to pursue higher energy food, provided another means of species recognition, and most importantly allowed for immediate reactions to potential threats (Lamb et al. 2007).

The Diversity of Eyes

Image forming eyes appear in a diverse number of animal phyla including: molluscs, chordates, annelids, and arthropods. We recognize that the eye of a great horned owl is vastly different than that of a house fly – and yet, both are recognized as eyes. Beneath the umbrella of “image forming” visual organs we find a great number of eyes that have evolved in distinct lineages and elaborated in vastly different ways. In order to better understand the forms that exist, eyes are generally categorized by a few major criteria: (1) if the eye is compound or simple and (2) the type of photoreceptors that comprise the light detecting tissue.

The basic components of any eye involve an opening through which light enters, and a photosensory retina which transduces the light energy into an electrochemical signal. Compound eyes differ from simple eyes in that they combine multiple individual units of light collection. The canonical examples of compound eyes can be found in insects in which many single units of photoreception (ommatidia) group into a large mosaic eye. With the exception of some larval stages, all insect eyes are compound. In contrast, a simple eye [or chambered eye, or ‘camera-style’ eye] relies on the action of a single lens which focuses light through a single opening onto a photosensory tissue, known as the retina. Simple eyes with image forming capabilities are found in molluscs, arthropods, and chordates.

Photoreceptors can be separated into one of two major groups based on their morphology



Eye, The, Fig. 2 An eye cup offers the advantage of detecting directionality of light. Over the course of evolution, early photoreceptor structures like the light sensitive eye patch (a) developed first. Relatively simple in organization, the eye-patch is comprised of pigmented photosensory cells which synapse onto ganglion nerve

fibers for the transport of light information to the brain. As discussed, the presence of visual pigments are necessary for the proper photoreceptive function of the photosensory cells. An eye cup (b) improves visual acuity by better allowing the perception of direction (Eakin 1982)

and mechanism of cellular signaling (Eakin 1965). An important feature of photoreceptors is their capacity to hold opsins within their membranes. In ciliary photoreceptors, opsin levels are increased by a corresponding expansion of the membrane surface by the specialization of cilia. Rhabdomic photoreceptors increase membrane surface area by forming microvilli on the cell surface (Eakin 1982, 1965). This dichotomy of ciliary and rhabdomic photoreceptor cell types is defined not only by morphology, but also by intracellular signaling in response to the conformational change to the opsin upon absorbing light. In ciliary photoreceptors intracellular signaling via phosphodiesterase is utilized to hyperpolarize the cell, whereas in rhabdomic photoreceptors depolarization is initiated by phospholipase C (Arendt 2003; Fernald 2000). A large scale appraisal reveals a general pattern, in which invertebrates have typically retained the rhabdomic style, while vertebrates use ciliary photoreceptors, though ciliary and rhabdomic types do co-occur in some instances (Arendt 2003).

The Vertebrate Eye

Vertebrates represent a wide array of body plans, adapted to suit aquatic, terrestrial, nocturnal,

diurnal life histories, among others. Yet, despite this divergence, vertebrate eyes are strikingly similar. All vertebrate eyes follow the same pattern: camera-style simple eyes containing a cornea, lens, and three-layered neural retina and performing vision via ciliary photoreceptors (Fig. 1).

Each eye begins in the same way: as a lateral bulging-out of the anterior portion of the neural tube, an embryonic structure of neural ectoderm origins that will give rise to the central nervous system. These out pockets (optic vesicles) come into contact with epithelial ectodermal tissue overlying the neural tube, which induces invagination of the neural tube to form an optic cup, and the epithelial ectoderm to form the lens placode. From here, the optic cup develops the major sensory tissue of the eye (the retina), while contact with the ectodermal tissue induces the formation of the lens from the lens placode. In this sense, the eye can be considered a direct extension of the brain.

The resulting eye is organized into several layers. Most exterior are the sclera and cornea, involved in providing structural support and protection for the eye, and focusing light onto the retina, respectively. Next is the choroid, which contains a network of vasculature responsible for supplying all other layers with blood, and the

ciliary body, which includes the intraocular muscles as well as the ciliary epithelium which produces the fluid of the aqueous humor, the liquid that fills the space between the cornea and ciliary body. The innermost layer is the three-layered retina comprised of photoreceptors, interneurons (such as bipolar, amacrine, and horizontal cells), and the retinal ganglion cells which together form the optic nerve and are responsible for transferring information to visual processing regions of the brain.

In simple terms, the eye can be imagined as a photoreceptive layer which has, over the course of evolutionary time, elaborated its own structure and organization as well as adopted accessory structures to improve vision. The lens, cornea, and other nonsensory components of the eye all work to improve acuity, efficiency, and longevity of the eyes function. Together, these tissues have become one of the most relied upon sensory structures dictating animal behavior and ultimately success.

Vertebrate Eyes: A Case Study in Evolutionary Innovation

Vertebrate eyes are an incredible example of evolutionary conservation. While invertebrate taxa with image forming eyes such as molluscs have drastically diverse eyes ranging from compound to camera-style, all vertebrates share the same basic eye structure. This high degree of shared similarity provides a unique perspective from which to study eye development as a whole. Since the same eye we see in mammals is seen in even the most basal vertebrate group – lamprey – we know that the vertebrate eye has remained relatively unchanged since its first recorded appearance around 500 million years ago (Dickson and Collard 1979; Morshedien and Fain 2015). This leads to the conclusion that the last common ancestor of lamprey and jawed vertebrates must have possessed some version of the camera-style eye that we see in extant vertebrates. Remarkably, then, the vertebrate eye as we typically consider it arose in evolution prior to the appearance of jaws or paired limbs.

Naturally, curiosity has led to the study of living members of lineages that evolved earlier than vertebrates for clues as to how the vertebrate eye evolved. An obvious candidate for study is hagfish. Like lamprey, hagfish is a jawless fish, but due to the incongruence between molecular and morphological data they have not been included with lamprey as a vertebrate (Lamb et al. 2007). In hagfish, the eyes are comparatively small and lack many of the characters found in vertebrates such as a lens, cornea, or intraocular and extraocular musculature (Lockett and Jorgensen 1998). The eyecup is relatively simple and masked by semitransparent or nontransparent overlying epidermis and a bilayered retina that appears to lack interneurons (Lockett and Jorgenson 1998; Holmberg 1970). This final piece of evidence, the lack of retinal layering like that seen in vertebrates, in addition to projecting the optic nerve to the region of the brain associated with circadian rhythm rather than image processing, is what has led many to categorize the hagfish eye as more pineal-like than eye-like (Lamb 2013). Due to its apparent “primitive” structure in combination with the hagfish’s basal phylogenetic position, it is an attractive idea to hypothesize that the hagfish eye might represent the basal condition of the vertebrate eye before it evolved into the highly conserved structure across extant vertebrates. However, the contentious relationships within cyclostomes remain unresolved which complicates any interpretations we can make from this (Lamb et al. 2007).

The ammocoete (larval stage of the lamprey) provides yet another unique perspective on the history of vertebrate eye evolution. As the ammocoete reaches maturation, it will undergo a drastic metamorphosis in order to reach adulthood. During the larval stage, the eyes of the lamprey are much less developed than that of their adult counterparts. Similar to adult hagfish, the eyes of the ammocoete are relatively small and found beneath a layer of epidermis with a retina that lacks defined layering of the adults (Rubinson 1990). Over the 5 years of maturation that takes place, the cellular differentiation of the retina that occurs follows a nearly identical sequence we see in jawed vertebrate eye during development (Rubinson 1990; Rubinson and Cain 1989).

The crossover between the features of the hagfish and larval lamprey has either been interpreted as lamprey evolving from some ancestral state shared with hagfish, or that possibly hagfish evolved from a lamprey-like state but retained its larval features into adulthood. However, there still remain too many unanswered question for conclusions to be made as the hagfish's position in relation to lamprey is still contested. This underlines the importance of more fully understanding the hagfish in order to better tell the story of how the vertebrate eye evolved.

Conclusion

In vertebrate and invertebrate groups alike, eyes have evolved in a colorful array. The distinct and numerous image forming eyes that exist speak to the great importance that light has played as an invaluable environmental signal in the evolution of animals. The eye has undeniably served as a fundamental driving force in the success and rapid radiation of animal phyla. In vertebrates, the benefit of the eye is most markedly observed in its conservation across the entire subphylum – evolved in some early ancestor and left nearly unchanged through such evolutionary novelties as the jaw and tetrapod limb. As we gain a greater knowledge of living examples of eyes, we can begin to draw more decisive conclusions and better understand the events in the evolutionary history of the eye. In doing so, we draw ever closer to better knowing the eye that developed 500 million years ago and has been serving us nearly unchanged since then.

Cross-References

► [Retina, The](#)

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Eyeball

► [Eye, The](#)

Eyespots

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Synonyms

[Ocelli](#); [Ocellus](#)

Definition

Animal color patterns consisting of roughly concentric rings of contrasting colors.

Introduction

Eyespots are animal color patterns consisting of (roughly) circular, often concentric rings of contrasting colors. Eyespots have received their name because (at least to humans) they often resemble the vertebrate eye. Eyespots are common in many terrestrial (land-living) animals such as insects (particularly in larval and adult moths and butterflies), birds and reptiles, but they are also widespread in many aquatic animals such as mollusks, flatworms and fishes (Poulton 1890). Eyespots are highly variable in appearance and occur in a variety of sizes, number and

color combinations. Laboratory studies on butterflies have shown that the processes that explain the development of eyespot patterns are relatively simple and that it requires only one or at least very few changes in the regulatory genes to change the position, color and number of eyespots (Brakefield et al. 1996). This suggests in turn that the evolution of eyespots can occur relatively fast.

Because of their appearance and widespread occurrence in the animal kingdom, the function of eyespots has intrigued naturalists and biologists for more than a century (e.g., Poulton 1890). In some animals, eyespots may play a role in intra-specific (within species) communication or reproductive signaling (Robertson and Monteiro 2005). For example, eyespots of the butterfly *Bicyclus anynana* have proven to be an important signal in mate selection, as females of this species prefer males with larger UV-reflective spots (the center of their eyespots) (Robertson and Monteiro 2005). Another, classic example is the Indian peafowl (*Pavo cristatus*), where the females are attracted to males with more eye spots on the tail. Although these examples show that the eyespots in some species are important in mate choice, eyespots are most well known for their protective function against predators. There are two hypotheses that have been put forward to explain how eyespots in prey protect against predators: (1) *the diversion hypothesis* (also called the *deflection hypothesis*) and (2) *the intimidation hypothesis*.

The Divertive (Deflective) Effect of Eyespots

The common occurrence of (generally small) eyespots found on the wing margins of many moths and butterflies, as well as eyespots located on the caudal area in some species of fishes, has been explained by the divertive function of such eyespots (Poulton 1890; Blest 1957). According to the diversion hypothesis, eyespots serve to direct the strikes of attacking predators toward less vital or defended parts of the prey's body, or toward a direction that would facilitate prey escape (Blest 1957; Kjærnsmo and Merilaita 2013). For example, in a study using yellow buntings (*Emberiza citrinella*) as predators and mealworms (*Tenebrio*

molitor) with a simple spot painted onto them as prey, Blest (1957) argued that the birds directed their attacks toward the eyespots, although firm conclusions could not be drawn as his study was not scientifically sound. However, some empirical evidence for the divertive effect of eyespots has been revealed recently in study systems using passerine birds as predators and butterflies that have marginal eyespots as prey (Olofsson et al. 2010). Olofsson and others showed that the marginal eyespots of the woodland brown butterfly (*Lopinga achine*) drew the attacks of blue tits (*Cyanistes caeruleus*) toward the eyespots, but only under specific light conditions where the UV-intensity of the light was high and the intensity of longer light wavelengths were low (Olofsson et al. 2010). Many species of fish have eyespots located near the area of their caudal fins, and these spots have been shown to misdirect attacks from predatory fish (Kjernsmo and Merilaita 2013; Kjernsmo et al. 2016). The mechanisms behind the divertive effect, at least in the case of fish, may be because the specific shape of eyespots resemble the real eye (eye-mimicry) and confuses the predator (Kjernsmo et al. 2016).

The Intimidating Effect of Eyespots

Another possible antipredator function of eyespots that has been invoked to explain their existence in some prey is predator intimidation (Poulton 1890, Blest 1957). According to the intimidation hypothesis, generally large eyespots (for example, those found in many species of butterflies and moths) could serve to intimidate potential predators, subsequently thwart, delay, or otherwise prevent an attack from being successful. Recent studies have provided support for the intimidating effect of eyespots against passerine birds (Vallin et al. 2005; Stevens et al. 2007; Olofsson et al. 2012; De Bona et al. 2015). However, the question why some eyespots intimidate predators has so far been unresolved and debated. Two main hypotheses for the intimidating nature of eyespots have been proposed. The first is that eyespots resemble the eyes of the predator's own enemy (Poulton 1890; Blest 1957) and hence suggest the presence of a potential threat. The other is that the high conspicuousness of eyespots

is a property that intimidates (Blest 1957; Stevens et al. 2007). Some studies have provided indirect evidence for the idea that predators might associate eyespots with the threat posed by their own enemies. For example, in a study using the domestic fowl as predator and the peacock butterfly (*Aglais io*) as prey showed that when the birds were exposed to butterflies with intact eyespots, they were more vigilant and elicited more alarm calls than those that were exposed to butterflies that had their eyespots painted over (Olofsson et al. 2012).

Conclusion

Even though eyespots in some species are involved in mate choice signaling and intraspecific communication, the existence of eyespots in many prey species can be explained through their protective function against predators. Some, indirect evidence suggests that eye mimicry (the similarity between the eyespot to real eyes) may be an important factor contributing to the extraordinarily wide occurrence of the eyespot pattern.

Cross-References

► [Altruism and Watching Eyes](#)

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Fa'afafine

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Definition

Samoan feminine/transgender, same-sex attracted males who are recognized as a “third” gender.

Introduction

In the Samoan language, *fa'afafine* means: “in the manner of a woman.” Like Samoan men, *fa'afafine* are biological males. However, *fa'afafine* do not identify as men nor do the members of their society recognize them as such. Consequently, they have been described as a type of “third” gender that is distinct from both “men” and “women.” In addition, *fa'afafine* differ from Samoan men in that they behave in a feminine manner. From a Western perspective, many *fa'afafine* would be considered effeminate males or transgender. The majority are not transsexual,

however, because they do not experience dysphoria with respect to their genitals. Although it is not unusual for *fa'afafine* to hold certain occupations (e.g., florist) more than others (e.g., mechanic), they have no institutionalized role in Samoa.

Fa'afafine Gender, Sexuality & Social Acceptance

Individuals are recognized in childhood as *fa'afafine* based on their tendencies to engage in female-typical activities (e.g., playing with girls) and their aversion toward male-typical activities (e.g., rough-and-tumble play). This process of recognition does not mean that Samoans make male children into *fa'afafine*. Rather, in Samoan culture, boyhood femininity is interpreted to mean that such individuals simply are *fa'afafine* and it is understood that they will not grow up to be “men.” Some families react negatively to the presence of a *fa'afafine* child with corporal punishment, but the majority have a more laissez-faire attitude, and some even facilitate the child's feminine behavior (Bartlett and Vasey 2006; Vasey and Bartlett 2007).

In adulthood, *fa'afafine* are, almost without exception, exclusively androphilic (i.e., sexually attracted to adult males), and consequently they do not have children (Vasey et al. 2014). *Fa'afafine* do not, however, engage in sexual activity with each other and express disgust at the thought. Instead, they engage in sexual

activity with masculine men. Research indicates that the masculine male sexual partners of *fa'afafine* exhibit bisexual patterns of sexual attraction. Not surprisingly, the majority of these men engage in sexual activity with women, as well as *fa'afafine*.

In Samoa, *fa'afafine* enjoy a high level of social acceptance that, while not absolute, stands in stark contrast to the situation experienced by Western transgender male androphiles. Indeed, *fa'afafine* are highly visible and active members of Samoa society. They occupy all manner of positions from stay-at-home caregivers to Assistant Chief Executive Officers in the government. The Prime Minister of Samoa is the Patron of the National *Fa'afafine* Association and has spoken publically on many occasions about the value of *fa'afafine* for Samoan society.

Conclusion

Owing to their status as feminine/transgender androphilic males, *fa'afafine* exemplify the evolutionarily ancestral form of male androphilia (VanderLaan et al. 2013).

Cross-References

- [Personality, Gender, and Culture](#)
- [Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Kin Selection](#)
- [Kin Selection Hypothesis](#)
- [Non-Western Homosexuality](#)
- [Paul Vasey](#)
- [Same-Sex Relationships](#)
- [Sexual Orientation](#)
- [Sexual Orientation and Human Sexuality](#)

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Face

- [Culture of Honor](#)

Face and Object Recognition

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Synonyms

[Face perception](#); [Face processing](#); [Object perception](#); [Visual recognition](#)

Definition

Recognition is the ability to perceive the physical characteristics of objects (including faces and non-face objects) and categorize these characteristics into classes (e.g., size, shape, color), in order to apply a semantic label to the object (e.g., “coffee cup”) or identify the face (e.g., “Jim from the office”).

Introduction

Human vision evolved to support two distinct mechanisms: recognition of objects and visual guidance of movement. As such, visual processing is instantiated in the brain by way of two

distinct visual pathways that both originate in primary visual cortex (V1) and project to the temporal (ventral stream) or parietal (dorsal stream) cortex (Kravitz et al. 2013). The distinction between these two pathways has been demonstrated in case studies, showing that patients with lesions in the ventral stream nevertheless demonstrate the ability to appropriately reach and grasp objects, despite being completely blind (Goodale et al. 1991). These functionally dissociable neural pathways afford the possibility of using visual information in two fundamentally different ways: the ventral stream for identifying objects and the dorsal stream for guiding action (Kravitz et al. 2013).

Visual recognition is accomplished by integrating both physical properties and spatial information about things in the environment (DiCarlo et al. 2012). That is, objects are generally identified and discriminated based on their size, shape, and color. However, in order to interact with objects, spatial information such as location and position is imperative for visually guided motor actions (e.g., reaching for an object). Humans rely largely on the visual system to perceive and interact with the environment. As humans experience the world, visual information is constantly received by the photoreceptors in the retina of the eye, which is further converted into neural signal and processed through the visual system. The computational burden of this automatic task lies in the fact that while humans may interact with a single object frequently (e.g., coffee cup), the retinal image for that object is *never* the same.

The visual system is comprised of a series of complex mechanisms that have evolved to support survival and reproduction of the species. For example, a highly evolved visual system facilitates such behaviors as navigation or locomotion (Gibson 1966), the ability to quickly detect threat in the environment (e.g., for review, see Green and Phillips 2004), as well as the pursuit and acquisition of resources and mating (e.g., for review, see Motta-Mena and Puts 2017). In the service of rapid valuation and appraisal of the environment, visual perception and attention tend to be adaptively tuned in humans – selectively focusing on the features of the environment that are most important for accomplishing specific goals to

meet the demands placed on the organism (Gibson 1979). In what follows, this entry will review face and object recognition in humans and discuss the contexts in which the perceptual system likely evolved to facilitate survival of the species through rapid detection and valuation of threats and opportunities in the environment.

The Visual Processing System

Anatomically, the ventral visual stream in the brain (colloquially described as the “What” pathway) is a neural pathway comprised of a series of feedforward neural circuits that receive visual input at the retina and innervate through the inferior temporal cortex to facilitate object identification and recognition (DiCarlo et al. 2012; Kravitz et al. 2013). Additionally, the dorsal visual stream in the brain (colloquially described as the “Where” pathway), which projects to the parietal cortex, facilitates the localization of objects in space relative to the perceiver (Kravitz et al. 2013). Together, these functionally specialized and anatomically segregated pathways provide the neural foundation for humans to identify objects in the visual field and provide visual guidance for interaction or motor action (i.e., grasping). The need to identify, recognize, localize, and avoid dangerous objects and predators has likely contributed to the specialization of these highly efficient neural mechanisms found in modern humans (Yovel and Freiwald 2013).

Additionally, there is a network of brain regions in the ventral visual stream that is highly sensitive to biologically relevant information (e.g., faces; Haxby et al. 2000). Humans and nonhuman primates have developed highly sensitive, face-selective cortex to identify and recognize faces vs. nonfaces, arguably due to the critical role that faces play in conveying threat or sociability in the service of species survival (e.g., Green and Phillips 2004).

As one example, the fusiform face area (FFA) is a well-studied brain region that consistently demonstrates pronounced neural selectivity to faces compared to any other type of object (McGugin et al. 2018). Although numerous studies have focused on evaluating the FFA in

humans, the most widely cited model now posits that the neural basis of face processing exists in a *distributed* network of regions in the cortex, including the occipital face area (OFA), superior temporal sulcus (STS), and anterior temporal lobe, all of which serve different, but overlapping, functions (Haxby et al. 2000). For instance, the FFA is sensitive to processing the identity of a face, whereas the OFA and STS are sensitive to facial features and emotion expression, respectively (Tsao and Livingstone 2008). The functional specificity of these brain regions provide context for understanding how environmental demands shaped the evolution and sensitivity of the human visual system to objects and faces.

The Computational Challenge

Objects. The ability to visually detect and recognize objects has clear advantages for survival, as it affords an organism the ability to respond adaptively to different sources of visual information. Survival mechanisms such as avoiding obstacles, detecting dangers and food, and manipulating objects (i.e., tool-making) have afforded modern humans the ability to detect and classify thousands of different types of objects with relative ease and speed (Biederman 1987). However, it is critical to note the computational complexity and biological demand of this seemingly automatic task. The ability to detect, identify, and categorize an individual object that can produce an unlimited amount of different retinal images under varying conditions is at the core of the computational challenge for the visual system. This “invariance challenge” reflects the fact that the visual system must recognize individual objects and faces from various degrees of object positions, scale, illumination, and visual clutter (DiCarlo et al. 2012). For example, visual information for the same object can be ambiguous in different scenarios or contexts (e.g., when an object’s resolution is unclear or partially occluded). This ambiguity must be resolved in order for an organism to respond to, or interact with, the object effectively. Thus, the ability to integrate information beyond the direct visual input at the retina alone was likely adaptive for detecting and identifying threats (e.g., predators), as well as opportunities (e.g.,

food sources), in situations of low acuity or spatial resolution.

The visual system is robust to various perceptual differences in viewpoint, spatial orientation, luminance, occlusion, and acuity of objects in the visual field, something that computer vision has struggled to emulate. It should be noted that from an evolutionary perspective, object recognition in humans may reflect a common mechanism that evolved across various species to solve the problem of visually interfacing with the environment, particularly in the service of navigation. Therefore, despite some differences in gross neuroanatomical organization, many visually oriented animals such as nonhuman primates and pigeons exhibit analogous behavior (e.g., error-driven learning) and neural structures (e.g., basal ganglia) that support visual object recognition in a similarly adaptive way (Soto and Wasserman 2014).

Faces. As in object recognition, face recognition involves a unique set of computational challenges in which an individual must identify and individuate faces under dynamic, varying conditions of illumination, angles, occlusion, and cosmetic changes (e.g., makeup, aging). Additionally, unlike objects, which can provide very heterogenous visual information, all human faces have highly homogenous components such that all human faces look very similar. Therefore, invariant face recognition reflects an even more computationally demanding task than object recognition because the visual system must be highly tuned and sensitive to subtle variations among human faces. Critically, in order to draw accurate and complete social inferences, social behavior fundamentally depends on the ability to form invariant representations of individuals through visual perception in the context of this dynamic, invariant information.

Invariant identification and recognition of faces has been shaped by environmental demands. For example, the organization of social groups into tribes led to unique social demands placed on humans that required accurate identification and recognition of friendly and nonfriendly faces (Parr 2011). As well, in social interactions, the visual system must extract information from the

face in order to determine if a stranger is a friend or enemy in order to engage in the appropriate reciprocal interaction. Humans that were more accurate in categorizing threats from nonthreats (especially when solely based on visual information from a distance) may have been more likely to survive and reproduce. As such, the human visual system has evolved invariant identification and recognition face systems that are robust to variations in luminance, spatial orientation, and cosmetic characteristics such as makeup.

Object Recognition

Historically, faces have been studied the most extensively among all object classes, largely due to their social relevance. However, understanding how recognition for non-face objects is achieved is critical for elucidating the mechanisms supporting visual recognition more broadly. Although the nature of object recognition and how these representations are instantiated in the brain remains hotly debated in the literature, it is unquestionable that humans are highly adept at distinguishing object categories (e.g., cars, places, scenes; Scherf et al. 2007). On the one hand, some researchers contend that object recognition is a unique ability, independent from face recognition (Shakeshaft and Plomin 2015). On the other hand, results from several studies measuring individual differences in perception of non-face objects and faces suggest that recognition for faces overlaps highly with certain non-face objects, such as cars (e.g., Gauthier et al. 2014). While it is yet unclear whether object recognition evolved as a uniquely separate mechanism from face recognition, both processes are highly specialized for supporting survival of the species.

Goal-Directed Behavior Shapes Visual Object Recognition

In Gibson's ecological approach to perception (1979), visual perception is intimately linked with the action systems guiding an organism's behavior. Gibson argued that perception is guided by the possibilities – or *affordances* – that an object provides, such that an object may be

perceived and utilized in different ways given an organism's different goals (Gibson 1979). For instance, a tree branch may be used as a crutch for the injured or as a weapon for self-defense. Importantly, the organism's *perception* of the object physically does not change but rather that the possibilities to act on an object change as a function of the goal of the organism (Gibson 1979). Further, Gibson described the relationship between perception and action as direct, with no sensory processing and without consideration for the organisms' past experiences, present emotional state, or overall social cognition. Gibson's ecological approach to perception is highly functional in nature and provides an understanding of how an organism employs visual perception to interact with its environment.

Applying such theoretical principles to social cognition involves extending the theory to include other intangible aspects of the organism, including mental and emotional states, functionally relevant individual differences, and overall social cognition (McArthur and Baron 1983), in order to understand how such perceiver characteristics may influence visual perception.

Face Recognition

Human faces are pervasive within the visual environment. From birth, humans spend more time looking at other human faces than any other classes of objects. But is this attentional bias uniquely human? The phylogenetic distribution of face recognition shows evidence of convergent evolution for some species that are organized in social groups and that primarily rely on visual information for survival. For example, the ability to recognize the faces of individual conspecifics is evinced in nonhuman primates (for review, Parr 2011) and even paper wasps (Tibbetts et al. 2019). This indicates that some species (including humans) evolved a highly sensitive face processing system for detecting and recognizing conspecific faces to meet selection demands. For primates, sociality was likely driven by the need to minimize predation risk and acquire resources (Gintis 2000). As such, natural selection favored

those primates who were better able to recognize conspecifics in their group. Consequently, increased sociability generated novel fitness demands due to local competition for scarce resources including food and potential mates. Therefore, the face processing system likely evolved to meet two environmental demands: (1) The ability to recognize members of the species to reduce predation risk and (2) recognize individual members within the group for peer and threat identification. This ability to recognize individual faces as friend or enemy presents a unique set of visual demands since most faces have the same or similar configuration. As such, it is through the use of configural information and holistic processing that the human visual system makes faces dissociable and recognizable.

Configural Information

All primate faces have a first-order configuration represented by the canonical inverted triangle shape formed by the spatial arrangement of the eyes, nose, and mouth (Diamond and Carey 1986). As such, modern humans are perceptually attuned to this specific orientation, and this perceptual attunement supports the detection of faces vs. nonfaces. Faces are also categorized based on second-order configural information, which represents the relative spatial arrangement among these facial features including position and spacing (Diamond and Carey 1986). To individuate faces of conspecifics, it is necessary to discriminate and recognize subtle variations in second-order information as all humans have the same basic first-order configural information. Outlined by Bruce and Young (1986), humans first encode the visual perceptual properties or the “structure” of the face to recognize it as another person. Secondly, humans map individual traits to that particular face as a distinct entity. It is through the sensitivity of this configural information that humans are capable of recognizing individuals. By extracting this information from the face, humans are able to recognize friends versus enemies, kin vs. non-kin, and potential mates by making sex-based judgements using sexually dimorphic facial features (Boyer and Bergstrom 2011). In short, humans are

perceptually attuned to perceive faces displaying a highly specific configural orientation.

One of the most common ways to evaluate the use of configural information for face processing is by instructing individuals to detect and remember a face that is rotated 180 degrees (upside down). In humans, inverted faces are detected more slowly and are harder to remember compared to upright faces (Yin 1969). This indicates that humans have likely evolved a specialized neural system to rapidly process a specific type of stimuli: upright faces. If sociability drove the evolution of primate vision, recognition of conspecifics as sources of opportunity or threat almost certainly was unique to upright faces. As such, disrupting the natural configuration of a face disrupts the face-selective neural mechanism for processing the inverted face as a face. Instead, inverted faces are processed like objects using local (or featural) information instead of configural information (Tanaka and Simonyi 2015). Objects tend to be processed on the basis of their individual parts, while faces are processed by the sum of their parts, or holistically (Tanaka and Simonyi 2015), thereby reflecting a core difference in the underlying mechanisms subserving face and non-face object recognition.

Holistic Processing

Unlike objects, it is widely accepted that faces are processed holistically by way of integrating all parts of the face into a unified perceptual whole (for review, see Tanaka and Simonyi 2015). This has been demonstrated in an experimental paradigm referred to as the “part/whole” task, in which participants view images of faces and then must recognize facial features in isolation or in the context of the whole face. Generally, people show a superior recognition advantage for parts when they are presented with the whole face (Tanaka and Simonyi 2015).

Another common method for evaluating holistic processing is by using a composite task in which face stimuli are created by joining two complementary halves of two different faces (Richler and Gauthier 2014). When presented, participants must identify one half of a single composite face while ignoring the other. When

aligned, the composite halves are processed holistically making it slower and harder to identify a single half (usually the top). However, when the halves are misaligned, the holistic representation (among both halves) is disrupted, and the halves can be more easily and quickly identified (Richler and Gauthier 2014). This demonstrates that humans have evolved a holistic processing strategy for perceiving faces, which likely facilitates the use of all face information for individual face recognition. It is evident that humans use configural information and holistic processing to discriminate numerous face identities, generally with high precision. Importantly, however, this ability is developmentally sensitive and is refined over time with age, experience, and other factors.

Development of Visual Recognition

Object Recognition

The building blocks for object recognition are evident early in infancy. Within the first few months after birth, infants can make use of object features such as texture, line junctions, edges, shape, and size to categorize and recognize three-dimensional objects. Additionally, once familiarized, infants can recognize the individual parts of simple compound objects but struggle with recognizing more complex objects such as bicycles or chairs (Jüttner et al. 2006). Increasing evidence shows that, through experience with complex objects and functional brain development of the ventral stream, object recognition reaches adult-like levels in late childhood (Jüttner et al. 2013). As well, complementary evidence from developmental neuroimaging studies also demonstrates that the magnitude of object-selective cortex activation in the ventral stream is comparable across childhood and adults (Scherf et al. 2007). Importantly, however, development of one of the most widely studied objects classes, faces, is protracted and continues well into adulthood.

Face Recognition

The literature on the development of face recognition has primarily addressed two key questions:

(1) What is the initial state of face recognition at birth? and (2) When does the face-processing system mature or reach adult-like levels? Within this framework, some authors have proposed that humans evolved an intrinsic predisposition to process face information (Morton and Johnson 1991) whereas others have suggested that face expertise develops in response to experiencing faces, the most frequently viewed category of stimuli in humans (Nelson 2001).

Morton and Johnson (1991) proposed the CONSPEC/CONLERN theory, which has been one of the most influential developmental theories of face processing. The first aspect, CONSPEC, is a set of subcortical sensory systems that directs infants' attention to face-like information to facilitate the detection of faces. Numerous studies have demonstrated that newborns show natural preferences to face-like compared to non-face stimuli (Morton and Johnson 1991). However, others have shown that newborns also preferentially attend to face-shaped stimuli that have more components in the top half compared to the bottom half (Macchi et al. 2004). Furthermore, evidence from neuroimaging shows that these "top-heavy" visual stimuli activate the FFA in adults (Caldara et al. 2006). In short, there is still much debate about whether early visual preferences for faces is face-specific or reflect general visual preferences. Regardless, these early visual biases to face-like information likely stem from the vital importance for newborns to detect their caregiver or kin through the use of visual information.

The second component, CONLERN, is a face-specific cortical system that develops with exposure to faces and affords infants the ability to individuate faces, allowing face recognition abilities to develop. By 2–3 months of age, infants show increasing preference to the inner configural features of faces, even when compared to "top-heavy" face-like stimuli (Turati et al. 2005). Importantly, these specific face-processing skills, like the use of configural information, are refined with experience and lay the building blocks for adult-level face recognition in adulthood. For example, evidence from neuroimaging studies demonstrate that face-selective areas of cortex

become increasingly specialized as children age (Scherf et al. 2007).

As demands on the visual system continuously change throughout childhood and adulthood, so does the ability to successfully and accurately recognize faces. Specifically, face recognition improves well into adulthood (Hills and Lewis 2018), and the functional development of face-selective cortex have similarly protracted developmental trajectories into adulthood (Scherf et al. 2007). This indicates that while face processing abilities such as the use of configural information and holistic processing develops rapidly in children, the computational demands of face recognition, which reflect the most computationally demanding form of visual recognition, may require more time to develop. In sum, infants have some level of expertise in face-processing including the use of configural information and holistic processing, but these abilities are not adult-like yet, and face recognition abilities continue developing through adolescence and into adulthood.

Conclusion

To conclude, the human visual system is a highly specialized and computationally complex neural system that has evolved to support visual recognition of objects and faces in the service of facilitating survival of the species. Faces and non-face objects provide a wealth of information that must be rapidly processed by the visual system for rapid categorization and processing of the stimulus (including a face's age, sex, and race, or an object's color, shape, and size). Despite the vast computational challenge this presents for humans, these abilities are supported by neural architecture that underlie the rapid integration of both physical properties and spatial information about a stimulus (DiCarlo et al. 2012). For faces, this rapid integration of information is instantiated through the use of configural information and holistic processing allowing rapid and accurate discrimination of individual people, which is present in infancy. However, these abilities develop through childhood and adolescence, and in the case of face recognition, into adulthood. Ultimately, the ability

to identify and recognize numerous objects and faces is a highly evolved ability that is arguably refined with experience. While object and face recognition in typically developing humans is well studied, future research would benefit from evaluating populations with neurological disorders and/or impairments in visual processing. As an example, some of the most compelling evidence in favor or against certain theoretical models of face processing have been informed by patients with lesions to the ventral visual stream, or prosopagnosia (i.e., face "blindness"). As well, neurodevelopmental disorders such as autism, which is characterized by deficits in face but not object recognition, can provide insight into the distinctiveness and plasticity of these neural systems and theoretical models.

Cross-References

- Ability to Recognize Individuals
- Eye, The
- Object Permanence
- Ventral Stream, The
- Vision

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Face Blindness

- [Prosopagnosia \(Face Recognition\)](#)

Face Memory

- [Face Recall](#)

Face Perception

- [Face and Object Recognition](#)

Face Preferences

- [Facial Attractiveness](#)

Face Processing

- [Face and Object Recognition](#)

Face Recall

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Synonyms

[Face memory](#); [Face recognition](#)

Definition

Face recall is the cognitive ability to retrieve previously stored face information without visual input of the stimulus.

Introduction

The visual system in modern humans is marked by a number of cognitive specializations that have been shaped by evolution. One such specialization is the ability to rapidly extract, store, and retrieve visual information from the face. For example, humans can store and freely recall up to 1000 face identities without explicit training or effort (Jenkins et al. 2018). Furthermore, humans can recognize nearly four times the number of face identities that they can recall (Jenkins et al. 2018). These two abilities – *face recall* and *face recognition* – are distinct cognitive processes that involve different levels of perceptual input, engage unique but overlapping neural mechanisms, and were likely shaped by different environmental demands. This entry will focus specifically on what makes face recall a particularly unique cognitive ability among the various mechanisms supporting face processing behavior.

Recall Versus Recognition

Face recognition is the ability to discriminate faces from nonfaces and recognize familiar and unfamiliar conspecifics (and heterospecifics) based on information retrieved from visually perceiving a face. In contrast, *face recall* is the cognitive ability to retrieve previously stored face information *without* a need for visual input of the stimulus. This means that to recall a face (relative to recognizing a face), the brain must actively generate the neural representation of the intended face and determine if it is the “correct” one (Yonelinas 2002). To illustrate, the dual-process theory would suggest that face recall begins by “replaying” the pattern of neural activity that was originally generated when the face was perceived and encoded (Yonelinas 2002). The

reason this is a challenging task is because the brain must first reconstruct the information by engaging the pattern of neuronal activation involved in the memory and then determine if the generated memory is the correct one (e.g., for review, see Yonelinas 2002). This subtle difference in perceptual input (e.g., whether a face is visually present) is what makes face recall distinct from face recognition; recall requires the active generation and retrieval of a face identity, whereas recognition requires a familiarity judgment of the face that is currently viewed.

In modern psychology, face recall is commonly evaluated through the use of memory paradigms utilizing famous faces as the stimuli of interest (Russell et al. 2009). These paradigms involve participants viewing images of famous faces and subsequently recalling the faces they saw without the images or contextual cues presented. The reason famous or familiar faces are used is that there is a tightly linked semantic label that participants can verbally associate with the image (e.g., Lady Gaga, Brad Pitt) and subsequently recall when prompted. Without this semantic association, it becomes difficult to quantify the ability to recall faces as participants would simply describe various features of the faces that they remember without a clearly associated verbal label or identity for the face. Behaviorally, humans can only recall 25% as many faces as they can recognize (Jenkins et al. 2018). This asymmetry suggests that face recall and recognition are distinct processes with different levels of cognitive demand.

Face and Memory Neural Systems

Episodic memories are personally relevant experiences or episodes, like viewing a face, that are stored in long-term memory (Renoult et al. 2016). Therefore, the ability to retrieve face identities from long-term memory fundamentally depends on the core neural substrates of episodic memory, which include the medial temporal lobe (MTL; Aggleton and Brown 1999). In particular, the role of the hippocampus in episodic memory formation and retrieval is nearly ubiquitous for not only

faces but nearly every type of stimulus (Bird 2017). Given the strong role of the hippocampus in recalling past experiences, there has been extensive debate as to whether recognition memory is also hippocampal-dependent or if recognition is accomplished through familiarity processing in the ventral visual stream and extra-hippocampal areas (e.g., Montaldi and Mayes 2010). However, when considering face stimuli, there is overwhelming evidence of intact visual recognition in hippocampal-lesioned nonhuman primates and humans who sustained hippocampal damage (see Bird 2017). This indicates that the hippocampus may be required for face recall, but not necessarily recognition.

Face recall and face recognition are at least partially instantiated in the brain as distinct mechanisms. On one hand, face recognition is primarily supported by the core face processing network (Gobbini and Haxby 2007). On the other hand, face recall is supported by the “core” face processing network *and* the episodic memory system, which are instantiated in the ventral visual stream and the medial temporal lobe (MTL) of the brain, respectively (Gobbini and Haxby 2007; Squire et al. 2004). These neural systems are anatomically and functionally distinct, but converging neuroanatomical evidence suggests that the ventral visual stream has substantial anatomical projections directly to the MTL, including perirhinal cortex, entorhinal cortex, and the hippocampus (Suzuki and Amaral 1994). Importantly, these neural regions, especially the hippocampus, support long-term memory storage and retrieval, highlighting the fact that the face processing network has direct neural connections with the core nuclei for episodic memory, and reflecting the importance of encoding visual information into long-term memory. As a consequence, the ability for humans to recall as many as 1000 faces fundamentally depends on the neural structures that support memory.

Face Recall Facilitates Group Cohesion

The visual system in modern humans facilitates species survival through a variety of mechanisms,

including rapid detection and valuation of threats, and opportunities in the environment (e.g., Griffin and Motta-Mena 2019). In particular, the ability to identify and respond to *facial* information would have been evolutionarily adaptive for such behaviors as threat detection, resource acquisition, and development of social networks. In fact, humans have developed complex cognitive face processing mechanisms to recognize faces but also support the storage and retrieval of hundreds of face identities (Gobbini and Haxby 2007). In what follows, we describe the potential adaptive value of face recall and how it may have differed from face recognition.

Face recognition is a crucial adaptation that facilitates immediate detection of threatening and non-threatening conspecifics and heterospecifics in social species. This is evinced phylogenetically in a number of species including nonhuman primates, paper wasps, canines, and sheep (Calder et al. 2011). Consequently, the extent to which face recognition is a shared evolutionary ability across primates has been extensively reviewed (Griffin 2019; Parr 2011). In contrast, the degree to which face recall is a cognitive and behavioral adaptation that emerged through evolutionary pressures may be rooted in sociality of the primate species. Humans maintain social networks of around 100–200 individuals, and 60% of communication is related to gossip or past experiences (Dunbar 1993). Relatedly, storytelling is universal in humans, and its adaptive value is demonstrated in coordinating group behavior, facilitating social cooperation, and establishing social norms of the group (Smith et al. 2017). For example, sharing experiences or stories about previous conflicts promotes cooperation among group members since it teaches group members about the payoffs of cooperation and sets expectations for how the group will behave (Smith et al. 2017). The social communication and transmission of these expectations and social norms from generation to generation are the cornerstone of cultural knowledge and information preservation across generations. Importantly, face recall supports the ability to share experiences and stories about other *people* because individuals are most rapidly individuated by their

face. Therefore, throughout evolutionary history, face recall likely facilitated increased sociality among individuals, which is related to larger group sizes, reduced predation, and access to resources (Chapman and Teichroeb 2012).

Conclusion

Face recall and face recognition differ in the amount of visual input, neural processing, and evolutionary adaptiveness. For example, face recognition is the ability to recognize a currently viewed face as familiar or not, whereas face recall is the ability to recall the face identity without currently viewing the face. Although both abilities are supported by neural structures serving the face processing system, face recall is additionally dependent on the episodic memory system, especially the hippocampus. Face recall may have adaptive value in the sharing of past experiences with other group members, which increases social cohesion, whereas face recognition serves to rapidly evaluate immediate threats in the environment based on visual input. Face recall may be a recent evolutionary adaptation that strengthened social networks, increased group size, and ultimately, survival and evolution of modern human cognitive abilities.

Cross-References

- [Evolution of Memory, The](#)
- [Face and Object Recognition](#)

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Face Recognition

- [Ability to Recognize Individuals](#)
 - [Face Recall](#)
-

Face-Blindness

- [Prosopagnosia](#)
-

Facial Aesthetics

- [Facial Attractiveness](#)
-

Facial Apperception

- [Prosopagnosia](#)
-

Facial Attractiveness

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Synonyms

[Face preferences](#); [Facial aesthetics](#); [Facial beauty](#)

Definition

Attractive faces are faces that are liked and preferred over less attractive faces. Attractiveness is often measured using rating scales in which faces are rated on a scale of attractiveness (e.g., 1 = low attractiveness and 7 = high attractiveness) or using two alternative forced choice decisions (e.g., which face is more attractive face A or face B?). Facial attractiveness concerns the traits

that make individual faces more or less attractive as well as the mechanisms via which facial attractiveness is appraised.

Introduction

Our physical appearance is the first thing that people can observe about us and the human face is one of our most prominent physical features. People are very interested in the faces of other people and consequently faces dominate our art and media. The reason for this interest is that our faces play an especially important role in our social lives. Faces are the focus of our attention because of the information we glean from them: we can see a person's sex and age, tell what they are attending to, and guess their feelings and emotions from their face. It is then unsurprising that humans have extraordinarily well-developed abilities to process, recognize, and draw information from others' faces. Humans also appreciate attractive faces, and evolutionary approaches have shed light both on what features make a face beautiful and the reasons behind why we might find such traits attractive.

If you were to describe a beautiful face you might find that the qualities that make it attractive over other faces are difficult to articulate. Despite this difficulty in accessing the causes of our preferences, we assess facial beauty quickly and there appears to be agreement within a particular culture and also between individuals from different cultures (see Langlois et al. 2000 for a meta-analytic review). This agreement on which faces are attractive and which faces are not attractive suggests that people are all using the same, or at least similar, criteria in their judgments. Even infants at 3–6 months prefer to look at faces which are rated more highly for attractiveness by adults than at faces rated lower (Samuels et al. 1994). It therefore appears that before any substantial exposure to cultural standards of attractiveness infants demonstrated a preference for attractive faces that are in agreement with adult judgments. Both early developmental and cross-cultural agreement on attractiveness are evidence that suggest that attractiveness ideals are not slowly absorbed by

those growing up within a particular culture and that there is something universal about attractive faces (and unattractive faces) that is recognized both across individuals and cultures, in adults and in infancy.

An Evolutionary Approach

So, why are some faces preferred over others? Evolutionary theory may cast light on what features are attractive and why attractiveness is important to us. An evolutionary view suggests that preferences should serve an adaptive function: preferences drive us to acquire high quality mates and the traits that we find attractive in individuals may be directly linked to their value as mates (Symons 1987). High quality/value mates are those who can best enhance the reproductive success of the judge. Women and men should both be sensitive to cues that indicate higher mate value because individuals who were attentive to cues of high mate value, and based mate-choice decisions on them, left behind more offspring, which would be healthier and more fecund, than those who failed to attend to these cues.

There are two main types of benefit that may be associated with mate quality that involve benefits to the chooser. These are indirect benefits, usually genetic benefits that are passed onto offspring such as genes associated with strong immune function, and direct benefits, reflecting a wide range of factors that directly benefit the chooser such as access to resources and territory, high quality parental care, and lower chances of contagion from healthy individuals. While the distinction may be important, it is difficult to disentangle the two benefits. For example, choosing a healthy partner may lead to offspring inheriting genes resistant to disease but avoiding a parasitized mate also has obvious direct advantages whether parasite resistance is heritable or not.

In support of this evolutionary view, there is evidence of potential benefits associated with mating and reproducing with an attractive partner. Individuals who partner with attractive faced

people may then produce more children and have a long-lived partner to provide parental care for their offspring. If these traits are heritable, then those who select attractive faced partners may also produce offspring who are attractive, long-lived, and who will themselves produce more children.

Attractive Face Traits

As noted already, describing the traits associated with attractiveness is difficult. Faces vary in many different ways and many of these variations impact on the judgment of attractiveness. Research has highlighted a large number of facial traits that impact on attractiveness and a comprehensive review is beyond the scope of this entry. In terms of what people on average find attractive, younger appearing faces are more attractive than older faces, healthy appearing faces are more attractive than unhealthy faces, average faces are more attractive than less average/more distinctive faces, and symmetric faces are more attractive than asymmetric faces (see Little et al. 2011 for review). There are potential benefits associated with choosing individuals based on each of these traits and so directional preferences can be predicted. For example, youth is associated with a longer period of potential parental investment and, at least in women, youth is strongly associated with the ability to produce offspring over time. Choosing a healthy partner has obvious adaptive benefits both in terms of direct and indirect benefits, and the traits of averageness and symmetry have both been linked to health: average faces may be attractive because the owners of average faces possess a diverse set of genes which may lead to better resistance to common pathogens while symmetry may be a marker for developmental stability (see Little et al. 2011 for review).

Masculinity, Femininity, and Attractiveness

The relative masculinity and femininity of a face has also been linked to attraction in many

studies. Larger jawbones, more prominent cheekbones, and thinner cheeks are all features of male faces that differentiate them from female faces. There is considerable evidence that feminine female faces are considered attractive. Studies measuring facial features from photographs of women (Grammer and Thornhill 1994) and studies manipulating facial composites (Perrett et al. 1998) all indicate that feminine features increase the attractiveness of female faces across different cultures. The link between sexual dimorphism and attractiveness in male faces is less clear. Studies using facial measurements have found that females preferred large jaws in males, but several studies have also shown that feminine characteristics and faces of low dominance are of increased attractiveness (see Little et al. 2011 for review). Studies manipulating masculinity and femininity in faces also produce mixed results: several studies have documented preferences for femininity but similar computer graphic studies have also reported preferences for masculinity (see Little et al. 2011 for review).

One explanation for the variety in findings to do with masculine versus feminine preferences for male faces may lie in the personality traits masculine and feminine faced males are assumed to possess. Increasing the masculinity of face shape increased perceptions of dominance, masculinity, and age but decreased perceptions of warmth, emotionality, honesty, cooperativeness, and quality as a parent (Perrett et al. 1998). It appears that socially valued traits such as honesty, warmth, cooperation, and skill as a parent are associated with feminized versions of male faces, while traits such as dominance are associated with masculinized face shapes. Feminization of male face shape may increase attractiveness because it “softens” particular features that are perceived to be associated with negative personality traits. Female face preferences may thus represent a trade-off between the desire for good-genes, or other benefits, and the desire for a cooperative partner. This trade-off means that masculinity in male faces may be more or less attractive under certain contexts and to certain individuals generating variation.

Variation in Perceived Attractiveness

Despite broad agreement on attractiveness, there are many other factors that may influence an individual in determining who they find attractive. In fact, in a truly adaptive view of preferences we might expect that individuals would vary in their preferences according to their personal circumstances and environment. Again, a comprehensive review is beyond the scope of this entry, but research has highlighted a number of factors related to variation in preferences. There are potential within-person differences. For example, women judging men for short-term relationships prefer more masculinity in faces than those judging for long-term relationships (Little et al. 2002). While masculine faces are seen as dominant, feminine faces are seen as making good fathers (Perrett et al. 1998), which means the difference in long-term versus short-term preferences is consistent with the hypothesis that while masculinity may be an important trait for short-term choice, for long-term relationships where investment is an issue, women may change their priorities and look for cues to long-term investment that are not necessarily consistent with traits that indicate high genetic quality or dominance. There are also potential cross-cultural differences. For example, in an environment with high pathogen-risk, the risk of contagion is higher and the probability of offspring survival and eventual reproduction decreases and so individuals under such conditions may favor traits associated with healthy partner. There is some evidence to support this view, with stronger preferences for male masculinity in Jamaicans than in the UK and Japan (Penton-Voak et al. 2004), stronger preferences for facial symmetry in a tribe of African hunter gathers than in the UK (Little et al. 2007), and in a larger cross-cultural sample of 30 countries, stronger preferences for male masculinity in countries with poorer health, such as higher mortality and incidence of disease (DeBruine et al. 2010).

Conclusion

In conclusion, attraction and mate choice are critical components of evolutionary selection, which

can help us understand the importance of facial beauty. There are many face traits that are associated with facial attractiveness in humans, and each may indicate direct and/or indirect benefits to individuals who act on these preferences. If some traits are reliably associated with some benefit to the perceiver, then we can expect directional preferences for particular traits and, on average, there will be preferences for those traits. People tend to agree that traits such as age, health, symmetry, and averageness are attractive in faces. While some traits will be attractive across individuals this does not preclude interesting variation both across individuals and across cultures. Overall, the determinants of facial attractiveness are complex, and an evolutionary approach can help us explain both why we agree on the attractiveness of some faces and also why beauty is, at least partly, in the eye of the beholder.

Cross-References

- [Body Attractiveness](#)
- [Face and Object Recognition](#)
- [Long-Term Mating](#)
- [Male Mate Choice](#)
- [Male Qualities and Likelihood of Orgasm](#)
- [Opposite-Sex Relationships](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Prospective Mates](#)
- [Sexual Selection in Evolutionary Psychology](#)
- [Social Cognition](#)
- [Vocal Attractiveness](#)

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Facial Beauty

- [Facial Attractiveness](#)

Facial Behavior

- [Facial Expressions](#)

Facial Cues

- [Adoption Preferences](#)
- [Resemblance](#)

Facial Disfigurement

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Synonyms

[Attraction](#); [Avoidance](#); [Disease avoidance](#); [Stigma](#)

Definition

A distortion or a perceived abnormality, as a result of a medical condition or accident that has taken place during the individual's life.

Introduction

Facial disfigurements such as psoriasis, cleft lip, or asymmetry due to congenital or acquired causes are subject to a wide range of stigmatization. Individuals with facial disfigurement have reported being avoided by others when forming and maintaining interpersonal relationships (Clarke 1999) and receive discriminatory treatment in a wide range of settings, such as in education, employment, and healthcare (Lanigan and Cotterill 1989). Such strong avoidance of individuals with facial disfigurement can be attributed to the fact that the face plays an important role in social interaction and is particularly salient for inferring a rapid number of evaluations when making initial contact with someone. Two of the most important evaluations are based on whether they should be approached (i.e., do they appear to be in good health) and whether they appear to be attractive and could make a good partner. These two evaluations correspond with the two most important aspects of evolution, survival and reproductive fitness, respectively. Because of this, the rest of this article will discuss the role of disease avoidance and facial disfigurement as well as the role of attractiveness and facial disfigurement from an evolutionary perspective.

Facial Disfigurement and Disease Avoidance

Disgust is an emotion that is designed to keep us away from disease threats. It is a key component of the disease avoidance system that is designed to detect and avoid disease threat before it makes contact (e.g., the Behavioural Immune System; for a review, see Murray and Schaller 2016). Activation of disease avoidance includes trigger-specific negative emotions such as disgust and anxiety, cognitions such as negative attitudes, and behavioral avoidance. As the majority of pathogens and parasites that cause disease are difficult or impossible to see, animals, including humans, have evolved mechanisms that respond to perceptual cues that infer disease threat. As perceptual cues do not always mean that a disease threat is present, this can lead to inference errors. In simple terms, this means that there is the possibility that a disease threat may be present and could be missed (false negative error) or that a disease threat is not present and avoidance strategies are activated (false positive error). Given the potential high costs associated with missing disease threat and becoming ill, the disease avoidance system has evolved to be overly inclusive and avoid those people who have a cue that could be associated with disease threat where no disease threat is present (Park et al. 2003) and motivates stigmatization (Kurzban and Leary 2001). Furthermore, activation of disease avoidance mechanisms is functionally flexible, meaning that levels of activation are context-specific (e.g., heightened activation if an individual believes themselves to be particularly vulnerable to disease).

As well as disfigurements causing the activation of an overinclusive disease avoidance system, the face itself has been historically associated with providing cues for a wide range of diseases. Sixteen of the 25 diseases that have been found to currently and historically produce the highest rates of mortality and morbidity show signs of visible facial lesions (Wolfe et al. 2007). Despite the link between facial lesions and some of the most harmful diseases, there are many facial lesions that are not associated with infectious disease. For example, a birthmark or a disfigurement

such as a cleft palate would not be considered as a source of disease threat or have the potential to contaminate others. Despite this obvious inference, evidence has demonstrated that these non-disease salient facial disfigurements have the propensity to activate disease avoidant strategies.

Ryan et al. (2012) conducted a study to see whether avoidance behaviors could be associated to seeing facial disfigurements that are not considered as contagious. Participants watched one of three clips that showed actors interacting with objects. One actor appeared healthy, one had a port wine stain birthmark, and one had influenza-like symptoms. Participants were observed interacting with the props in the video and their behaviors recorded. Participants in the birthmark condition showed the same avoidant behaviors (e.g., disgusted expressions, wiping the prop) as were observed in the influenza-like condition. Despite these similar behaviors for the two conditions, participants reported that influenza was far more contagious and lethal than a birthmark. These results show that despite participants being aware that birthmarks are not contagious, disease avoidant behaviors were still activated. Furthermore, it demonstrates how behaviors are not always rooted in rational and conscious motivations. Instead, these disease avoidant behaviors are based on an evolved mechanism that is activated when we are unaware of it and tasked with the sole responsibility of maximizing survival.

Facial Disfigurement and Attraction

Attractiveness serves as the feature that can lead to motivating romantic relationships and ultimately mating. The evolutionary perspective suggests that those features that are considered as attractive are markers that provide indications of health. If an individual does appear healthy, it can be inferred that they will have healthy genes and these will increase the chances of healthy offspring and their subsequent survival.

Fink and Penton-Voak (2002) proposed three features that were associated with the evolutionary perspectives of facial attractiveness. These are

symmetry, averageness, and nonaverage dimorphic features. Symmetry refers to how symmetrical the face would suggest a high quality of development and therefore a high quality of genetic health. The averageness of some facial features could be associated with heritable traits and are therefore preferred. Indeed, computer-generated averaged faces are almost always preferred when compared to the individual faces that were used to make up the averaged ones (Fink and Penton-Voak 2002). Sexual dimorphic traits are associated with masculine features that come from higher levels of testosterone production to encourage mating and competing for mates. When considering individuals with facial disfigurement, they are likely to fail in two out of the three categories that have been described. Any form of disfigurement will have an effect on the overall symmetry of the face and may cue concerns towards the genetic health of the individual. Those with facial disfigurement are also likely to have facial features that are not normally observed in the general population. Again, this may cue a lack of genetic health.

Despite the suggestion that facial disfigurement would be associated with decreased levels of attractiveness and genetic fitness, there is evidence that demonstrates the opposite. A study by Burriss et al. (2009) found that women preferred men with facial scars for short-term relationships, but the same effect was not found for men. For long-term relationships, both men and women showed equal preference for people with or without scarring. Those males with scarring could be preferred for short-term relationships as they appear both masculine and like heroic risk takers. This explanation supports the importance of sexual dimorphism and may be a cue for mate quality (Fink and Penton-Voak 2002). This is further supported by the fact that the preference was only found with females. A further explanation could be that scars demonstrate that the individual has been through a trauma and has survived it. This would suggest that they are a “tried and tested” person with good genetic fitness, instead of someone who can only be predicted as having good genetic fitness.

Conclusion

Due to the historical prevalence of facial cues inferring disease threat and an overinclusive disease avoidance system, this does provide an explanation for why people with disfigurements receive discriminatory treatment and are stigmatized in a wide range of settings. The relationship between attractiveness and facial disfigurement show how features can be used as cues for the genetic health of an individual. However, the picture is far from clear. On the one hand, facial disfigurements can show decreased attractiveness, whereas facial scars on men can actually increase attractiveness by being associated with masculinity. It is possible that rather than an overinclusive response to facial disfigurement and attractiveness, the finer details, such as the inferences, play an important role.

It is important to remember that many of the mechanisms described come from innate mechanisms that are activated at an unconscious level. However, as sentient beings, we have the ability to accept or reject these aversive attitudes or behaviors at a conscious level and we are ultimately still responsible for our own actions.

Cross-References

- [Disease Avoidance](#)
- [Long-Term Mating](#)
- [Pathogen Disgust and Perceptions of Attractiveness](#)
- [Reproductive Potential](#)
- [Sex Differences in Short-Term Mating Preferences](#)

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Facial Expressions

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Synonyms

Configurations; Displays; Facial behavior;
Signals; Signs

Definition

Psychologists' interest in facial expressions arose from the long-standing belief that, just as our

dreams were Freud's royal road to the unconscious, our smiles, frowns, pouts, grimaces, and other faces are the royal road to our emotions. The phrase "facial expression" is a presupposition that some event inside, typically an emotion, is pushed outside for public consumption. To avoid any such presupposition, *facial behavior* is used here to describe the movements and positioning of the facial muscles. Likewise, *emitter* and *observer* are used to avoid implying that any "content" is necessarily transferred by the face.

Introduction

Human facial behavior results from a set of roughly 20 muscles. Except for the masseter, which clenches the jaw, these muscles originate on the bones of the face but insert in the skin, where they act as tractors, dilators, or sphincters that modify the orifices formed by the eyes, nose, and mouth. Although the nature of "facial expressions" was discussed for centuries, Darwin's noncommunicative formulation remains foundational.

A Brief History

Historical accounts of research on facial behavior usually begin with Charles Darwin's (1872) *The Expression of the Emotions in Man and Animals*, but his work on *Expression* was a reaction to writings a half-century earlier by physician-artist Charles Bell. Bell had written and illustrated a volume on facial behavior in which he endorsed the prevailing natural theology and regarded the human facial musculature as divinely gifted solely to humans to express emotions.

Bell's depictions themselves drew upon prescientific theorists like Aristotle, who declared that certain faces expressed the "passions and their contraries." Descartes elaborated upon Aristotle's system and listed six primary passions – wonder, love, hatred, desire, joy, and sadness. The Cartesian passions were adopted by Charles Le Brun, court painter to Louis XIV, who prescribed exactly how each should be "expressed" on the face in paintings, drawings, and sculptures. The

French neurologist Duchenne, best known for his “faradism” (electrical stimulation of muscles and nerves), argued from faradic studies that 60 different emotions could appear on the face.

Darwin (1872), intent on discrediting special creation, sought to overturn Bell’s creationist account. As he confided in an 1867 letter to Alfred Russel Wallace, “I want, anyhow, to upset Sir C. Bell’s view . . . that certain muscles have been given to man solely that he may reveal to other men his feelings” (Fridlund 1992). In *Expression*, Darwin rebutted Bell’s twin claims of human uniqueness and special communicative function, first noting how human “expressive” behaviors resembled those of other species and then highlighting numerous noncommunicative features of those behaviors. To that end, Darwin explained most “expressions” using his *Principle of Serviceable Associated Habits*, by which he meant “habits associated with actions once serviceable ancestrally” but which survived only in degenerate form, like webbed feet on land birds, male breasts, and the human appendix. Darwin’s contention that much of our “expressive” behavior is similarly vestigial was decisive for biological evolution: functional movements or structures could be either God’s handiwork or evolution’s, but nonfunctional vestiges could not. Thus, our ancestors might have bared their teeth before kill-biting an interloper, but now we merely bare our teeth without progression to biting. This rudimentary habit no longer accomplishes anything; any signal value is incidental.

Basic Emotion Theories

In the first half of the twentieth century, psychological research found no clear mapping of faces to emotions but instead suggested that (1) observers used contextual information (e.g., what led to making the face) to attribute emotion to the face, (2) facial behavior was better interpreted in terms of broad dimensions (e.g., pleasantness and intensity) rather than discrete emotions, and (3) the interpretations of faces varied somewhat with culture.

Much of this information was eclipsed in the 1960s with the advent of *Basic Emotion Theories*, a set of related frameworks which began with the

writings of personality theorist Silvan Tomkins (for history and critique, see Leys 2017). Tomkins took the received wisdom from Descartes and Le Brun that much of our facial behavior was eruptive and nonintentional, consistent with Darwin’s view, but he also argued *contra* Darwin that these movements arose via natural selection. Faces revealed precisely nine specific, biological “primary affects”: interest, enjoyment, surprise, distress, anger, fear, shame, disgust, and contempt. These affects were categorical, and the faces they produced were iconic. Tomkins’ theory gained traction with the 1960s–1970s research of two proteges, Carroll Izard and Paul Ekman.

Most prominent was Ekman’s *neurocultural theory* with its clear enunciation of the *universality thesis*, which contended that (1) certain “facial expressions of emotion” revealed a small number of categorical “basic emotions;” (2) each expression resulted from a modular emotion “program” in the brain which was triggered by a constrained set of elicitors; (3) these expressions were phylogenetic and, as such, would be produced uniformly, recognized by humans panculturally, and found early in child development and among nonhuman primates; and (4) deviations from uniformity were due to supervention by cultural *display rules* reflecting learned conventions or modes of dissimulation (Ekman, in Fernández-Dols and Russell 2017).

One clear accomplishment of the basic emotion approach was the late 1970s dissemination of an anatomically based system for scoring facial movements (updated by Ekman et al. 2002) developed originally by the Swedish anatomist Carl-Herman Hjortsjö (1969). The basic emotion approach continues to develop conceptually and methodologically and is the basis for much “emotion recognition” software (Keltner and Cordaro, in Fernández-Dols and Russell 2017).

Contrary Evidence

Ekman’s “neurocultural theory” achieved fame with a series of cross-cultural matching (“recognition”) studies, some also conducted by Izard. In these studies, individuals in diverse cultures –

including some small-scale societies in Papua New Guinea and Borneo reputed to have been minimally Westernized – were able to match photos of posed Caucasian faces to indigenous emotion terms at rates greater than chance. The simplicity of forced-choice matching procedures led to their widespread adoption (reviewed by Gendron and Crivelli, in Fernández-Dols and Russell 2017).

The cross-cultural studies were controversial from the beginning especially among field anthropologists who argued that the (1) posed photos were ecologically dubious caricatures, (2) designated categorical “emotion” terms did not capture the diversity of emotion concepts across cultures, (3) investigators underestimated the participants’ degree of contact with the West, (4) matching procedure did not capture participants’ spontaneous interpretations of the faces, and (5) translators may have helped the participants choose the expected responses in cultures that emphasized cooperation (Russell, in Fernández-Dols and Russell 2017).

Subsequent research ratified these doubts. Findings from the first half of the twentieth century on contextual influence, dimensionality, and cultural diversity were all replicated. Agnostic, bottom-up psychophysical methods showed that European and Chinese students differed in their mental representations of faces for specific emotions (Jack and Schyns 2017). Observers matched faces to predicted emotion labels better when the posers were from the same culture. Evidence from African and Melanesian societies, using more sophisticated and diverse research designs, did not replicate the Ekman studies (reviewed by Gendron and Crivelli, in Fernández-Dols and Russell 2017). Trobrianders in Papua New Guinea understood the putative “fear expression” as an agonistic display instead (Crivelli et al. 2016). When the Himba group in Namibia sorted into piles a series of posed faces, they did not recreate the classic “expressions of basic emotions” when the sorting was unconstrained but did so only when emotion concept words anchored the piles at the outset (Gendron et al. 2014).

The matching studies were attempts to test how people understood facial “expressions,” but not

what produced them. Even if people everywhere see happiness in a smile, much as they hear it in birdsong, the question remains whether happiness actually produces the smile (or the song). Contrary to basic emotion predictions, smiling was found to depend more on the presence of an audience than on the emitter’s emotions. In such studies of *audience effects*, people smiled (1) during films only when with friends or believed they were; (2) when bowling strikes, mainly after pivoting to see their fellow bowlers; and (3) after winning Olympic gold medals but only when looking at the audience. One study of the putative “surprise expression” had participants enter a laboratory by a corridor, then leave by the same door only to find a room with posters, bold green walls, and a red office chair. Participants reported great surprise and believed that their faces showed it, but only 3 of 60 made the “surprise expression” expected by basic emotion theorists (Schützwohl and Reisenzein 2012). Overall, production studies like these have shown weak relations between emotion and the predicted facial behavior (Duran et al., in Fernández-Dols and Russell 2017), with one exception: reports of feeling amused correlate strongly with smiling and laughing.

Theoretical critiques of basic emotion theory also emerged: (1) the claim that certain emotions were “basic” lacked foundation (Ortony and Turner 1990), partly because of difficulties with the emotion concept itself, and (2) greater knowledge of biology-culture interactions proved inconsistent with its dual presumptions that “universality” implied phylogenesis, whereas diversity signified cultural learning (Crivelli and Fridlund 2018). To the contrary, diversity may equally arise from phylogenesis (Darwin’s *adaptive radiation*) and commonalities from cultural learning (*convergent cultural evolution*). Buss (2014) questioned using universality among humans and presence among nonhuman primates, as criteria for determining the “basicness” of emotions, when (1) “jealousy” was not on any basic emotion list and (2) traits that were unquestionably phylogenetic often span very few species (e.g., ultrasonic echolocation, documented only among microchiropteran bats).

Contemporary Research Agenda

The most important advance in psychology's study of facial behavior may lie in the sophistication of its inquiry. Questions loaded with presuppositions (Does this society "recognize" the "basic emotions" from these posed faces?) are being replaced with more neutral questions, such as (1) What facial behavior occurs? (2) In what context does it occur? (3) How does that behavior influence an observer? (4) What about the observer and context leads him or her to react in that way? Of course, faces of emitters and observers quickly form a reciprocal interaction loop.

Childhood development. What facial behavior is seen in early development? One researcher made diaries and video records of her daughter's facial behavior over 8 weeks and found notable departures from basic emotion theory's predictions. For example, similar stimuli frequently elicited wholly different facial behaviors, and "distress-pain" faces occurred during bathing with no obvious distress (the body of research supporting this conclusion is summarized by Camras et al.; in Fernández-Dols and Russell 2017).

Studies of infants concluded that even neonates respond to facial behavior, and habituation studies showed that infants can even discriminate among different facial configurations. Still, two more specific issues remain unresolved. The first concerns whether neonates can imitate facial behavior, and one question hinges on whether certain neonatal facial behaviors that were considered frank imitation instead signify mere arousal produced by the model's behavior (see Meltzoff et al. 2017; and Oostenbroke et al. 2016, for opposing views). The second issue concerns when children learn to apply their culture's emotion concepts to faces. It appears that young children begin by making valence-based (good vs. bad) attributions and use more differentiated emotion labels increasingly over the preteen years (Widen, in Fernández-Dols and Russell 2017).

The bivalent way that young children react to facial behavior is readily seen in infant social referencing, in which infants as early as

6 months who confront conflict or ambiguity (e.g., in traversing a visual cliff) use the facial behavior of a caretaker to guide how they respond. Caretaker smiles are cues to engage or proceed, while frowns promote disengagement or retreat (Feinman 1992). Maturation brings sharper discernment of others' facial behavior. Joint attention, or following another's gaze, may predict where the emitter goes or what he or she talks about next. Others' facial actions may suggest people's intentions, dispositions, or what they will say when asked, "How are you feeling?"

Signaling. Ethologists long stressed the signaling role of behavior in animal communication. Might our facial behaviors have evolved as *signals*, rather than having "devolved" (degenerated) to mere residues of once functional acts as Darwin proposed? That was the conclusion from early twentieth-century avian observations by Heinroth and Huxley, who suggested that behaviors used as signals evolved to be more conspicuous by prior selection for their predictive value. These *displays* tended to be ones that preceded overt acts (e.g., baring teeth before biting) and foreshadowed the acts themselves. Teeth baring, through natural selection, would become more dramatized and conspicuous and increasingly independent of its origins in biting. Such *intention movements* (Heinroth) were thus said to become displays by *ritualization* and *emancipation* (Huxley). An analogous process – *conventionalization* – results from cultural rather than natural selection (Smith 1977).

These ritualized actions are potentially beneficial for both emitter and observer: conspicuous tooth baring alerts an interloper that I may pounce and bite, so that the interloper flees and neither of us draws blood. Krebs and Dawkins (1984) characterized the coevolution of displays and vigilance as a signaling ecology which, like many social strategies, is probabilistic; it will be leveraged by deceivers who may force the evolution of more "honest" (i.e., predictive) displays, but the signaling ecology nonetheless carries overall reproductive benefits.

Might human facial behavior be conceived similarly? Noting that ethology had jettisoned the earlier view that animal signals were

stereotyped and “released” and now considered them contextual and strategic, Fridlund (1994) suggested that human facial displays might work identically. He proposed the *Behavioral Ecology View* of facial behaviors, reconceiving them as “social tools” which serve as cues of contingent action in social negotiation. This view suggested a functionalist, externalist approach to research in which constructs like “emotion” were unnecessary detours.

The approach has seen wide application. One contemporary effort is in artificial intelligence (AI), where the task is to understand everyday interactive facial behavior and then simulate it using embodied computerized agents. Although most software efforts have been benchmarked on “recognition” of iconic “expressions of emotion,” doubts about the usefulness of this approach have arisen, and AI alternatives based on the functionalist behavioral ecology view have been proposed (Crivelli and Fridlund 2018).

Miming and deception. Like stage actors, people in everyday impression management adjust their facial behavior with their social role transitions, e.g., from partner to parent to employee. As Goffman (1959) noted, it is often difficult to separate non-acting from this “miming” or frank pretense. Indeed, the facial muscles are sometimes termed the *mimetic* muscles.

One unexpected instance of miming may be “showing empathy.” Bavelas et al. (1986) analyzed dyadic conversations and found that listeners produced facial movements like those of speakers, not by reproducing the speakers’ sentiments but to convey understanding of those sentiments; thus, empathic facial behavior needs not be “feeling as you do” but “showing you how you feel.”

It’s a thin line between pretending and deceiving, and detecting deception via the face has been a consistent theme in facial behavior research. Despite several claims, research has failed to substantiate any reliable facial signs of deception or inauthenticity (Vrij et al. 2011).

Signs. Much of our facial behavior (1) aids in regulating respiration, lacrimation, olfaction, vision and light adaptation, food ingestion or

expulsion, and speech articulation; (2) is recruited in protective reflexes like coughing, sneezing, blinking, and nose wrinkling; and (3) is involved in homeostatic adjustments like yawning, burping, and vomiting. Some so-called “expressive” facial behavior may simply be “given off” in the process (e.g., widening the eyes takes in more light, and flaring the nostrils takes in more scent; Lee and Anderson, in Fernández-Dols and Russell 2017; Susskind et al. 2008). In this way, research is returning us to Darwin’s non-communicative view of facial behavior.

Appraisals. Some theories posit that facial behavior results from information processing beyond mere registration of the situation. Several *appraisal theories* assume the basic emotion theory’s “emotion program” but contend it is triggered by prior appraisal. Other such theories treat “emotion” as a folk concept rather than a scientific one, and for these theories, an “emotion episode” results from a series of appraisals of one’s situation which leads to reactions that include facial behavior. Such constituent appraisals may be (1) bottom-up (stimulus-driven) or top-down (based on preconceptions from one’s interaction history), and (2) fast and automatic or slow and integrated with other cognition.

Appraisals, these theories hold, are made along dimensions such as novelty, valence, goal relevance, goal congruence, certainty, coping potential, and agency. Each appraisal dimension has separate and independent effects on facial behavior: novelty results in eye widening, positive valence in smiling, and so on. The large number of possible appraisal patterns implies commensurately numerous patterns of facial behavior, from which observers may make inferences about the emitter (Scherer et al., in Fernández-Dols and Russell 2017).

Conclusion

Scientific work on human facial behavior has advanced by the slow, painful abrogation of long-standing presuppositions, both explicit and implicit. This research has brought home the fact

that approaches to facial behavior based on received wisdom, assumed subpersonal events, posed faces, and categorical emotions will be insufficient to understand how that behavior arises and functions in social interaction and how to simulate it in our future android interactants. These questions and others dovetail with new interdisciplinary efforts that combine psychologists with specialists in fields that include anthropology, biology, biomedical engineering, communications, computer science, the history of science, and the neurosciences. The result is the emergence of fundamentally different conceptions about human facial behavior and the ways to study it.

Cross-References

- [Adaptation and Natural Selection](#)
- [Charles Darwin](#)
- [Cross-Cultural Studies](#)
- [Evolution of Communication](#)
- [Neonatal Imitation](#)
- [Social Cognition and Communication in Chimpanzees and Bonobos](#)
- [Social Development](#)

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Facial Resemblance

► [Promoting Paternity \(You Look Like Your Father Phenomenon\)](#)

Facial Resemblance and Kinship Detection by Strangers

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Synonyms

[Phenotypic similarity](#); [Physical self-similarity](#); [Visual similarity](#)

Definitions

Facial resemblance

- Amount of physical similarity between individuals' facial features.

Kinship detection

- Assessment of the degree of relatedness or genetic similarity among individuals.

Introduction

Human sociality is characterized by cooperation within large social groups. These groups often contain a large fraction of people not personally known to a given individual. It has been proposed that, in the absence of any knowledge about a prospective social partner, the detection of morphological similarity potentially underlies social assortment among strangers. The objective of the following is to provide a brief overview on recent findings on the role of facial resemblance in guiding human social preferences.

Humans Prefer Similar Others

Humans have evolved to form and live within large and complex social systems. They are exceptional in the extent to which they engage in cooperative exchange, even with strangers. This human-specific feature has been viewed as a challenge for evolutionary explanations of cooperative behavior – that it must be established through benefiting both the individual and the inclusive fitness of the cooperator, e.g., by cooperating with an individual's offspring. In order to maintain complex societies, cooperative actions and prosociality need to be directed toward likely cooperators, i.e., individuals that will likely reciprocate the behavior toward a common, group-benefiting goal. Cooperative actions need to be directed away from likely defectors, i.e., individuals who benefit from altruistic acts without reciprocating. Defining oneself not only as an individual but also as a member of a cooperative group seems a key feature of human psychology. However, in order to maintain cooperation and prosocial behavior, the individual needs to be able to recognize likely cooperative interaction partners.

During human evolution, social networks increased to a size where individuals were more likely to encounter unfamiliar than familiar others. Faced with large numbers of strangers, which cues guide individuals to select and deselect others and to focus discriminatory attention on certain others? One such cue that can influence social assortment is the perceived level of similarity. It has been argued that choosing to cooperate with more similar strangers maximized the chance of successful cooperative interactions as because similar individuals were more likely to share relevant behavioral tendencies (McElreath et al. 2003).

In various experimental settings, it was shown that adults trust and prefer others more that resemble themselves with regard to facial similarity, a tendency that has been interpreted as a consequence of an adapted kinship detection mechanism (DeBruine 2002; Bressan and Kramer 2015). These findings suggest that the detection of morphological similarities potentially underlies social assortment among strangers.

Perception and Use of Facial Similarity in Others

The closer related two persons are, the more genes they share, and the more similar they will look. Because craniofacial morphology is highly heritable (Djordjevic et al. 2016), genetic similarity between individuals tends to be expressed as phenotypic similarity. From early in life, humans are able to categorize their conspecifics by facial resemblance (especially those of the same sex, age, or ethnicity) and to discriminate among kinship relationships via facial phenotype. Thus, facial morphology appears to be a prominent cue for ascribing familiarity and relatedness among individuals, and facial resemblance is most likely the most commonly used physical cue of kinship (DeBruine et al. 2007).

Various experimental studies have shown that adults can detect kinship among strangers from facial portraits. For example, in simple matching tasks, participants are able to correctly associate siblings with one another (Maloney and Dal Martello 2006). Likewise in third-party judgments of pictured stranger faces, humans can reliably assess the relatedness of close (i.e., parent/child) and distant kin (i.e., grandparents/grandchildren, aunt/uncle and nephew, as well as cousins) (Alvergne et al. 2010; Kaminski et al. 2009).

A few experiments have further directly studied the effects of facial self-resemblance on social behavior in adults and demonstrated that people have more positive evaluations of faces that subtly resemble themselves and familiar others. Usually set up within economic game contexts, the participants were provided with pictures of their ostensible partners while unaware that these pictures had been manipulated to look like themselves. Typically, in such experimental manipulations, image transformation software had been used. Using the tool of “morphing,” these programs allow for digitally altering portrait pictures. Specifically, by blending in the facial features (shape, color, and texture information) of two or more facial pictures, a novel composite face is created that resembles its input faces to a certain degree. To ensure that participants are unaware of that manipulation, the morphed faces usually consist

of 40% or less of their own face, a threshold at which subjects generally do not detect their own facial features in the composite morph. Such subtle cues of experimentally manipulated self-resemblance increase perceived trustworthiness in strangers (DeBruine 2002; Verosky and Todorov 2013) and decrease perceived attractiveness of opposite-sex stranger faces (DeBruine et al. 2007). It was also shown that people are more likely to vote for unknown political candidates whose faces have been manipulated to subtly resemble their own faces (Bailenson et al. 2009). Further, the presence of slightly self-similar faces in a group of strangers promotes cooperation for the public good in an experimental setting where participants can choose how much to invest (Krupp et al. 2008). Interestingly, humans are sensitive to negative relatedness cues as well. Krupp et al. (2012) have shown that faces that deviate from the average in a direction opposite to one's own face are judged less attractive and less trustworthy.

However, all these works exclusively used adult participants to explore effects of facial resemblance. In order to argue for this preference to be an evolutionary adapted behavior, one needs a better understanding of its ontogenetic emergence and functional mechanism. Face processing matures fully during early childhood and children constantly interact with unknown others, so it is likely that already at a young age, they sensitive to morphological self-similarity in unfamiliar peers.

A study by Kaminski et al. (2013) investigated a slightly different skill in 5- to 11-year-old children, namely, their ability to detect mother-offspring resemblance in faces of unknown others. Their findings show that by the age of 9, but not younger, children could efficiently match a newborn's face with that of his/her birth mother. Thus, the ability to discriminate kinship in unknown others via perceptually salient facial features does not fully develop until middle school age.

Yet surprisingly, preschoolers at the age of 5 years already use facial self-resemblance when they make social judgments about unknown others (Richter et al. 2016). In the absence of any additional knowledge about prospective peers, children preferred those who look subtly like themselves over complete strangers. However, the correspondence

between detection of self-similarity and social preferences is not perfect – the 5-year-olds in that study reliably detected resemblance to their own face, but they did not always use this information in their social preferences (Richter et al. 2016). It thus remains an interesting challenge for future studies to further investigate the specific cognitive mechanisms underlying the effects of facial self-resemblance preferences.

Summary

Various studies have shown that morphological similarities trigger social preferences. Even slight facial self-resemblance, a subtle cue of kinship, is a salient cue that promotes prosociality and trust toward unknown others. As has been shown recently, such responsiveness to self-similarity seems to be present already early in life. For example, preschoolers at the age of 5 years use facial resemblance when making social judgments about unknown others. Thus, the tendency to select social partners based on facial similarity begins well before adulthood, and facial similarity is a strong guide to social assortment, especially when any other useful information about the potential interaction partner is missing.

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Facial Width to Height Ratio and Dominance

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Synonyms

Aggressiveness; FWHR; Prestige; Social status

Definition

The facial width-to-hip ratio (FWHR) is an anthropometric measure of facial shape. It is calculated by taking the distance from one zygion to the other and dividing it by facial height. Dominance refers to an individual's position within a social hierarchy, while dominant behavior describes a number of traits including, but not restricted to, inflexibility, drive for achievement or power, and controlling the behavior of others.

Introduction

Natural selection has shaped the evolution of human visual systems to be highly attuned to extracting socially relevant information, such as age, ethnicity, gender, and emotions from the face (Little et al. 2011). While interpreting facial expressions and displays of emotion are of critical importance during human interpersonal interactions, static facial cues also provide meaningful information relating to sexual maturity and a healthy endocrine system that influence interpersonal interactions (Little et al. 2011). Sexual selection may also have shaped the evolution of face perceptions to extract relevant information from same-sex rivals or in the opposite sex for mate selection purposes. This chapter briefly summarizes some recent research detailing the role of craniofacial morphology in determining dominance and intra-sexual competition.

Sexual Dimorphism in Craniofacial Shape and FHWR

Men and women differ in a number of craniofacial and cutaneous facial characteristics, owing largely to the effects of sex hormones during development (Dixon et al. 2016). Male typical facial shape, or facial masculinity, includes a larger brow ridge, thicker jawline, narrower eyes, and a more robust midface than is typical in women (Whitehouse et al. 2015). Facial masculinity may develop due to organizational effects of androgens during fetal development that are most likely

activated during pubertal androgenic surges (Whitehouse et al. 2015).

One component of facial masculinity is the facial width-to-height ratio (FHWR), which is calculated by taking the distance from one zygion to the other and dividing it by facial height (Geniole et al. 2015). Interestingly, FWHR in adulthood is not associated with fetal androgens (Whitehouse et al. 2015), variation in androgens during adolescence (Hodges-Simeon et al. 2016), or current levels of testosterone in adulthood (Whitehouse et al. 2015; Bird et al. 2016). Analyses of 4,740 female and 6,133 male FWHRs revealed that the FWHR is sexually dimorphic, being larger in men than women, although the size of this effect was small ($d = 0.11$; Geniole et al. 2015). However, recent meta-analyses suggest no sex differences in FWHR (Kramer 2016). The following sections will review the role of male FWHR in communicating attractiveness to opposite sex and formidability to members of the same sex in order to place its importance in the context of human evolution via sexual selection.

Sexual Selection and FWHR as an Intra-sexual Cue of Dominance

Sexual selection is a form of natural selection that occurs when individuals are in competition for mates (Kokko et al. 2006). One of the consequences of sexual selection is the evolution of sexually dimorphic morphological features that function in mate attraction or mate competition (Kokko et al. 2006). Sexually selected traits can be ornamental, serving to attract members of the opposite sex via intersexual selection, or be badges of status or weaponry employed during same-sex or intra-sexual displays of dominance and aggressiveness (Dixon et al. 2005).

Men's FWHRs may be marginally larger, on average, than women's (Geniole et al. 2016; but see Kramer 2016), and larger FWHRs are judged as more masculine than smaller FWHRs in male but not female faces (Geniole et al. 2015). Interestingly, while some studies have reported that male FWHRs are positively associated with reproductive success, men's FWHR is negatively

associated with women's judgments of male facial attractiveness (Geniole et al. 2015), suggesting that female choice may not have shaped the evolution of men's FWHRs.

Sexual dimorphism in body size is often attributed to effects of sexual selection via intra-sexual competition among anthropoid primates (Dixon et al. 2005). Facial and bodily attributes may provide information relating to body size and function in concert during behavioral displays. FWHR in both women and men is indeed positively associated with BMI (Geniole et al. 2015), suggesting a role of FWHR in intra-sexual displays of dominance and in direct agonistic contests. Ratings of dominance and threat are positively associated with male and female FWHR (Geniole et al. 2015) and are likely independent of beardedness (Geniole and McCormick 2015), which is a strong determinant of perceived male dominance and aggressiveness (Dixon and Vasey 2012). It is important to note that the positive associations between male FWHR and ratings of masculinity, dominance, and aggressiveness are stronger when derived from natural faces than when using composites, avatars, and other artificially generated faces that manipulated FWHR (Geniole et al. 2015). Nonetheless, threat and dominance were still positively influenced by FWHR in studies using artificially manipulated stimuli (Geniole et al. 2015).

Evidence from Behavioral Studies that FWHR Is an Intra-sexual Cue of Dominance

If FWHR is of importance to understanding intra-sexual competition, then it should be a predictor of outcomes in dominance-related and agonistic interactions between men. There is some evidence that men with more robust midfaces have greater muscularity (Holzleitner and Perrett 2016) and FWHR is positively associated with BMI (Geniole et al. 2015). In studies of mixed martial arts fights, larger FWHRs were positively associated with fighting performance (Geniole et al. 2015; Haselhuhn et al. 2015). Similarly, in professional ice hockey, more aggressive males who spent longer in the penalty box following foul plays had larger

FWHRs (Geniole et al. 2015; Haselhuhn et al. 2015). Finally, in a study spanning 32 nations competing in the 2010 soccer world cup, aggressiveness was positively associated with FWHR in midfield and forward players (Geniole et al. 2015). Although some studies have not replicated the association between male aggressiveness and FWHR, meta-analyses have found that when taking the literature as a whole, men with larger FWHRs are more aggressive in sporting contests (Geniole et al. 2015; Haselhuhn et al. 2015).

In addition to aggressiveness in sporting contests, men with larger FWHRs behave in more socially dominant ways in business negotiations (Geniole et al. 2015). For example, a CEO's ability to achieve returns on assets, a seller's ability to achieve high sales prices, and an individual's ability to negotiate a salary bonus were all more likely to be higher among men with larger FWRs (Geniole et al. 2015). Men with larger FWHRs are also significantly more selfish and pejorative than men with smaller FWHRs (Geniole et al. 2015). These findings, coupled with evidence that men with larger FWHRs also have higher self-ratings of social dominance and are judged as looking for socially dominant by naïve raters than men with smaller FWHRs, suggest this metric of facial shape to be associated with dimensions of social dominance and threat (Geniole et al. 2015; Haselhuhn et al. 2015).

Conclusion

One criticism of using ratios in studies linking morphology to biological, behavioral, and social outcomes is that these measures are derived from complex multivariate phenotypes. For example, while a large literature has focused on how the waist-to-hip ratio (WHR) determines bodily attractiveness, multivariate analyses have shown that effects of WHR are likely due to selection acting on multiple components of shape rather than a discrete ratio (Brooks et al. 2015). Associations between FWHR and dominance may occur as a consequence of trait interactions, as it reflects a discrete measure that forms part of a multivariate measure of facial masculinity. However, there is

some evidence that male FWHR is a stronger predictor of dominance than a measure of facial masculinity (Lefevre et al. 2014; but see Dixon et al. 2016 for mixed results). Further studies placing the FWHR within a multivariate context would be valuable. Finally, it remains to be determined whether any of the findings relating FWHR to male dominance and formidability extend to small-scale societies wherein behavior manifests in ecological settings that are closer to those of human ancestry than modern multilevel and often industrialized cultures. For the present, the FWHR appears to be larger in men who are more behaviorally dominant and are judged as looking more dominant, but not more physically attractive, suggesting a role of intra-sexual selection shaping masculine facial robustness.

Cross-References

- [Dominance in Humans](#)
- [Height and Dominance](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Size and Dominance](#)
- [Vocal Indicators of Dominance](#)

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Factors Associated with Suicide

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Synonyms

Gestures of despair; Self-destruction; Self-sacrifice

Definition

The act of taking one's life.

Introduction

On the surface, suicide seems to pose a problem for the idea that humans seek to maximize their own fitness (i.e., pass on their own genes). In fact, it could be argued that suicide serves the exact opposite purpose—to maximally reduce fitness by completely eliminating any future chance of passing on one's genes directly. However, an evolutionary perspective on suicide might suggest otherwise. The elimination of one's life does not necessarily preclude the propagation of one's genes, as individuals with shared genes may be able to still successfully reproduce. Therefore, there may be an important trade-off between the reproductive costs and benefits that accompany a suicidal act.

Humans evolved in largely social contexts that required a high degree of cooperation. In such environments, there would be certain behavioral alternatives that could change the cost-benefit ratio of actions to favor those most beneficial for a group, rather than for a single individual. An inclusive fitness perspective on suicide incorporates this idea by identifying factors that go beyond self-survival and instead emphasizes the idea that suicide may actually help genetic transmission if it can increase the likelihood that other individuals with shared genetic makeup can pass on their genes. More specifically, this phenomenon can be explained by kin selection—the idea that fitness loss by an individual may be valuable if it is followed by a compensatory increase in fitness for close relatives. Some of the most common factors associated with understanding suicide from this, and other evolutionary views, are outlined below.

Reduced Ability to Contribute to One's Fitness, and Perceived Burdensomeness to Kin

In a series of seminal literature pieces spearheaded by Dr. Denys deCatanaro (e.g., deCatanaro 1986, 1995), it was argued that suicide is most

probable for individuals that have a significantly reduced ability to contribute to their own fitness. In this case, the reduced ability for fitness contribution is thought to relate to many factors, including current poor health or expectations of future poor health (e.g., older individuals), low prospects for reproduction with opposite sex partners (e.g., individuals who are single, widowed, divorced, low in mate value, or reporting low romantic relationship satisfaction), and, perhaps most notably, perceived burdensomeness to kin. Indeed, results of empirical studies show support for the idea that suicidal ideation—thought of as a proxy for suicidal behavior, given that suicide is often preceded by ideation—is, for example, positively correlated with perceived burdensomeness, and negatively correlated with recent or lifetime heterosexual sex, success and stability in heterosexual relations, and number of children. deCatanaro's research also demonstrates that concerns about health burdens receive increased importance in older individuals, and that this perceived burden is also associated with suicidal ideation. Many other empirical investigations, including clinical studies and direct tests of this model, have also provided support for deCatanaro's idea by showing that perceived burdensomeness is a stronger predictor of suicide than emotional pain (e.g., van Order et al. 2006).

Parent-Offspring Conflict

Suicidal behavior, at least among adolescents, has been proposed to act as a negotiating tactic to promote greater parental investment to particular offspring. In this case, the goal of the behavior is not death, but rather the signal of "need" to parental figures. Although this explanatory factor has received less attention than the inclusive fitness model, there is some evidence to support it. Andrews and colleagues (2006) tested this idea using a sample of over 1600 adolescents. Findings revealed that adolescent dissatisfaction with the mother predicted suicide attempts 1–2 years later. However, there was also evidence that middle-born adolescents made fewer attempts than offspring in different birth orders, yet those attempts made by the middle-born offspring were more severe than the other siblings. This finding was interpreted as

potentially supporting other research showing that middle-born children are in a disfavored position (e.g., mother feels least close to them, child feels least close to mother, less quality parental time spent with the middle child), therefore requiring the middle-born child to take more severe risks. The more severe attempts (yet seemingly paradoxical lower number of attempts) by these middle-born offspring might suggest that the value of increased parental investment is weighed carefully against the risks of death. Thus, suicidal ideation may be a tactic to assess parental sensitivity to risk, the feedback from which can then be used to determine the relative cost in the risk of dying, and finally to create a plan where “the risk matches the threshold needed to compel parental capitulation” (Andrews 2006, p. 206).

Suicide as a By-Product of Bargaining

Suicidal gestures (e.g., self-harm, attempts not ending in death) may also be used as a cry for help in situations requiring the attention of other members of a social group. At first glance, a suicidal gesture seems unnecessary, as there are less costly ways to signal need to another individual (e.g., verbal expressions, acts of crying). However, if relations between social partners are not strong, the less costly methods may be insufficient to garner attention and may therefore require more drastic actions to convince seemingly distant social partners that the need is in fact genuine (Hagen et al. 2008). By the suicidal individual making their requirements explicitly known, others may recognize these unmet needs and be put in a position where they are forced to act. While the need to act might be unnecessary in some cases in the modern environment, the environment in which our species evolved would have involved tightly knit social groups, with largely family-based organizations. Thus, *not* acting on such behavior would have likely had greater consequences.

It is important to note that the suicidal gesture in this case can impose costs on the receivers (i.e., social partners) in the sense that the receivers may rely on the contribution and productivity of the individual to the group as a whole. Therefore, the

motivation to help an individual in need (i.e., the one making suicidal gestures) may be to strengthen the productivity of the group as a whole, which may include helping and attending to the needs of the suicidal individual. These types of personal interactions are often thought to be bargaining strategies in that suicidal gestures threaten the benefits to other members (especially in the case where the suicidal individual has a monopoly on benefits provided to the group), therefore compelling members of the group to negotiate with the individual; the ultimate goal, here, is to have a mutually beneficial arrangement (i.e., the bargaining model). That is, suicidal gestures function to give the suicidal individual help and support from members of the social group, while the social group receives the benefit and cooperation from someone who is no longer incapacitated by despair. In short, individuals may make suicidal gestures when they suffer higher costs that can be relieved by others in the group; with the threat of social losses, the benefits for members of the social group to help the suffering individual may outweigh the costs of not helping them.

So how does bargaining with suicidal gestures serve as a factor related to actual suicide? Evidence indicates that suicidal gestures significantly predict actual suicide attempts and completed suicide later on (e.g., Prinstein et al. 2008; for additional evidence, see a brief review by Syme et al. 2015). Therefore, it is possible that acts of suicide completion are simply an accidental byproduct of dangerous forms of self-harm, and especially following repeated acts of self-harm (e.g., Zahl and Hawton 2004). In contrast to models subscribing to inclusive fitness, this model suggests that completed suicide is simply an accidental by-product of suicidal bargaining gestures, rather than an act resulting in death whereby fitness benefits are promoted through surviving kin.

Comparing Theories of Factors Leading to Suicide

Some recent research has explicitly tested the inclusive fitness and bargaining models against

one another to help understand what evolutionary factors might be most associated with suicide. Using data collected from 53 cultures, Syme and colleagues (2015) undertook an impressive analysis of nearly 475 accounts of suicide from ethnographic material spanning multiple centuries. Results from this work revealed some evidence for the inclusive fitness model in finding that after controlling for the lethality of a suicide attempt, 13.9 % of records fit this explanation. Furthermore, 30.2 % of the cultures showed evidence that at least some of the victims were perceived to be a burden on others. Perhaps more convincingly, however, was evidence for the bargaining model, in which 80.6 % of records showed at least one variable that included evidence from this model.

Suicide Terrorism

Liddle and colleagues (2011) have provided an evolutionary framework for a specific form of suicide called suicide terrorism. In the same way that suicide may be a way of helping genetically related kin, suicide terrorism may simply be the malfunction of a mechanism that was designed to help kin, and instead is used as a means to help one's genetically unrelated group (e.g., religious group, although this is nonetheless a close group—sometimes considered “fictive kin”). As with other forms of suicide, for such a behavior to be advantageous in some way, the benefits to “kin” (i.e., group members) must outweigh the costs. Liddle and colleagues suggest that religious beliefs may play a partial role in facilitating these acts, because without the belief that life continues after death, the costs of such an act (e.g., death) may outweigh the benefits. In this and other ways, religious beliefs may be a factor associated with acts of suicide terrorism. However, it should be noted that religious belief on its own is not inherently related to suicide terrorism, but rather, it may be a catalyst to such an act in some cases.

Conclusion

A number of evolutionary models have been proposed to explain factors associated with suicide—a

seemingly paradoxical act for a species where individuals seek to maximize their fitness. It is possible that suicidal behavior may not have been entirely maladaptive in the ancestral past, given that individuals with shared genetic makeup could still pass on their genes via genetically related kin. Further, suicidal gestures may have been useful as a bargaining tool for increasing parental investment, or increasing attention from social partners, but may have sometimes resulted in death as a by-product of such behavior. Despite some compelling findings over the past few decades for each of these models, future research will be needed to shed further light on the theorized factors associated with suicide, as well as other potential interactions between specific factors identified by such theories (e.g., interactions between perceived burdensomeness and reproductive potential; for recent evidence, see Brown et al. 2009) and how other specific forms of suicide (e.g., suicide terrorism) are related to evolved mechanisms, or the malfunctioning of such mechanisms.

Cross-References

- ▶ [Birth order](#)
- ▶ [Denis Decatanzaro](#)
- ▶ [Edward Hagen](#)
- ▶ [Environment of Evolutionary Adaptedness](#)
- ▶ [Ethnography](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Mate Value](#)
- ▶ [Parental Investment](#)
- ▶ [Parent-Offspring Conflict](#)
- ▶ [Religion and Religious Beliefs](#)
- ▶ [Reproductive Benefits must Outweigh Costs](#)
- ▶ [Suicide](#)
- ▶ [Suicide Terrorism](#)

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Factors That Influence Bullying

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Synonyms

Contexts; Ecology; Environmental; External; Individual; Internal

Definitions

Bullying includes behaviors influenced by various internal and external factors to intentionally harm

weaker individuals and adaptively obtain resources (Volk et al. 2014).

Introduction: Bullying and Ecological Systems

Bullying is a behavior that can be adaptive under various ecological systems. Under these conditions, bullying may be used to obtain material, social, and reproductive resources (Volk et al. 2014). In the microsystem, or most proximal factors, an individual's characteristics and direct relations with parents and peers can influence bullying (Bronfenbrenner 1979). Beyond the microsystem, factors in the mesosystem or interactions between social relationships can affect competitive climates that facilitate bullying. Such climates can be embedded into the exosystem, or system of more distal community environments, and the macrosystem, which includes cultural norms. Finally, major life events in the widest chronosystem may influence bullying.

Age

At the innermost microsystem, the sociodemographic characteristics of an individual may influence bullying. During childhood, direct physical and verbal bullying behaviors are most common (Volk et al. 2016). As individuals transition into adolescence, there is increasing social and sexual competition that coincides with the start of puberty and high school. Consequently, the benefits of establishing dominance through maximizing victim harm may increase the prevalence of bullying, with approximately 30–40% of adolescents involved (Volk et al. 2016). Moreover, cognitive advancements with age allows for an increase in strategic, complex covert bullying, such as social exclusion or gossiping, that minimize perpetrator identification and victim retaliation (Volk et al. 2016). The strategic use of various forms of bullying is also evident in sex differences.

Sex

Sex is another important individual characteristic in the microsystem that reflects the differential

selection pressures consistent with the sexual selection and parental investment theories (Trivers 1972). In particular, males often bully out-group members to strengthen in-group cohesiveness (Volk et al. 2014, 2016). A solid in-group allows males to engage in riskier, direct physical and verbal behaviors. Demonstrating such strength can deter out-group members from challenging the male alliance (Volk et al. 2014, 2016). Also, the tough status may signal the ability to protect prospective opposite-sex mates and offspring. Thus, direct forms of bullying may provide adolescent and adult males with important social and reproductive goals. Contrarily, given that females may encounter reproductively costly risks when using direct bullying, they may prefer indirect behaviors as a means to strategically enhance their own status while targeting a rival female's promiscuity (Volk et al. 2016). Through indirect behaviors, females can create exclusive popular in-groups comprising of high status males, from which they can pick the best suitor (Volk et al. 2016). Males and females with certain personality traits may also strategically use bullying.

Personality

Personality is a third important intrinsic factor in the microsystem and is associated with genetic predispositions that may facilitate bullying (Book et al. 2012). Individuals with particular traits may find bullying is more adaptive and use it more frequently. For instance, studies on temperament found children higher in callousness and lower in empathy were more likely to bully than children lower and higher in these two traits, respectively (Book et al. 2012). Likewise, studies on the Big Five personality found children less agreeable, more emotional, and less conscientious also bullied more. Recently, studies used the HEXACO personality model to investigate adolescent bullying and found those lower in Honesty-Humility, which encompasses strategic exploitation of others, had higher perpetration of global (e.g., Book et al. 2012) and verbal, social, and racial forms of bullying (Farrell et al. 2014).

Individuals who have a predisposition to selectively exploit may be more likely to use bullying, a behavior characterized by adaptively harming others. Beyond an individual's sociodemographic and personality characteristics, external social relationships in the micro- and mesosystems can also influence bullying.

Parenting

Children often form their first social relationship with parents, and therefore, parents can set the basis for acceptable behaviors in future relationships. Thus, parenting can be a direct relationship influencing children in the microsystem, but also interact with wider relationships including peers, teachers, and schools to comprise a factor in the mesosystem. Authoritarian parenting styles characterized by low warmth and responsiveness often predict child aggressive behaviors including bullying (e.g., Baldry and Farrington 2000). Such parenting styles may directly model aggressive behaviors, but also indirectly model a lack of concern for others, which can facilitate behaviors that inflict harm on victims without remorse (Volk et al. 2016). Directly and indirectly facilitating bullying via parenting behaviors is consistent with the evolutionary notion that parents demonstrate behaviors that can lead to resource acquisition for survival. This acquisition serves to directly benefit children, but also indirectly benefit parents through offspring survival and securing genetic proliferation (Trivers 1972). Thus, children and adolescents may adaptively use bullying behaviors with peers during times of heightened competition for resources.

Peers

As children age, peers play a primary role in socialization within the microsystem, while parents begin to play a secondary role. Similar to parenting, peers can be a direct influence in the microsystem, but interact with parents, teachers, and schools to influence within the mesosystem. The start of high school is a heightened time of

competition for limited dominant roles in a newly forming peer network (Volk et al. 2016). Peer group dynamics beyond a single bully and victim can influence bullying. For instance, when popular adolescents used bullying to achieve status, peers viewed bullying as a productive strategy to obtain a desired goal (Dijkstra et al. 2008). Consequently, individuals in the peer network may then encourage the use of similar bullying behaviors as a method to obtain valued goals. This may be one reason why the wider peer network often view bullying as a negative behavior, but still play direct roles as bullies or indirect roles as assistants, bystanders, and reinforcers. Moreover, the moderating role of popularity may explain why on average adolescents who use aggressive behaviors are rejected, but when the same behaviors are used strategically by popular adolescents are associated with high social status (Dijkstra et al. 2008). Thus, status goals can be achieved through bullying behaviors, but in combination with peer-valued characteristics. Bullying in the absence of these valued characteristics may result in peer rejection. In sum, it appears that a few, key popular individuals can set bullying norms within a peer group (Dijkstra et al. 2008). However, these peer norms may be only one important factor embedded in the broader school climate.

School

The school is a wider factor in the mesosystem that incorporates interactions between the individual and their immediate relationships within the microsystem, including peers. Since adolescents spend the majority of their time in school with peers, several aspects of the school atmosphere may facilitate bullying. For instance, teacher anti-bullying attitudes may influence classroom bullying (Volk et al. 2016). Teachers who are perceived as effective at decreasing bullying by their students had classes with lower peer-reported bullying (Volk et al. 2016). Accordingly, teachers can model antibullying attitudes and behaviors, which can enhance prosocial behavior and also decrease bullying. Teacher and student attitudes can also

affect wider climates of school competition, which can influence bullying.

In a highly competitive school environment, bullying can be used to establish social and/or tangible resources (Volk et al. 2016). Schools with a highly competitive atmosphere may facilitate dominance hierarchies based on social status through popularity or academic status through grades or scholarships (Volk et al. 2014). These hierarchies may encourage students to assess their social and/or academic abilities relative to one another (Volk et al. 2014, 2016). Adolescents with higher abilities may then adaptively exploit this evaluation by bullying individuals with lower abilities to maintain higher rank. In fact, classes with a few, key popular adolescent bullies often had higher levels of classroom bullying, with poorer quality of peer relationships (Dijkstra et al. 2008). Bullying to compete for limited school resources mimics the advantages of bullying for survival evident in competitive historic hunter-gather societies with scarce food resources (Volk et al. 2014). Although to a lesser degree, bullying in competitive schools reflects the evolutionary advantages of bullying for limited resources. Competition can also extend to the distal exo- and macrosystems, which can directly and indirectly influence bullying.

Community

Similar to a school, including relationships from the microsystem, the community is an even wider ecological factor that incorporates the previous micro- and mesosystems. The community can be considered a part of the exosystem since an individual plays an active role but does not directly influence it. Additionally, the community can be considered a part of the macrosystem since it encompasses broader cultural norms (Hong and Espelage 2012). In particular, community inequality may influence bullying at both the exo- and macrosystems.

Several studies on income inequality found higher inequality within a community and/or school was associated with higher levels bullying (Elgar et al. 2013). The actual degree of inequality

reflects the exosystem, while the underlying power imbalances and competitive cultural norms reflect the macrosystem. Consequently, at both systems, bullying may be influenced by the prospective financial and material gains in communities with high inequality. This is again similar to the adaptive, survival-based benefits of bullying in historic societies with scarce resources (Volk et al. 2014, 2016). Moreover, researchers suggest that some cultures and political regions that promote competition and oppression of particular ethnicities, disabilities, sexual orientations, genders, and socioeconomic backgrounds may have higher bullying perpetration, since it is a culturally accepted method to reinforce hierarchies (Hong and Espelage 2012). Thus, bullies may learn to exploit their ethnic, cultural, or economic advantage from their parents at home, and peers and adults at school, who may also share and use these advantages. On the contrary, individuals may have little to gain from bullying in communities where residents have relatively equal access to resources. Instead, bullies in these equal communities may experience greater costs, including disapproval or punishments from community members. Taken together, distal community factors are interconnected with proximal factors that can influence bullying at both an economic and cultural level.

Life Changes

At the broadest level, the chronosystem includes major life changes (Bronfenbrenner 1979; Hong and Espelage 2012). These changes can be normative, such as starting high school, and also nonnormative, such as a family death (Bronfenbrenner 1979). The chronosystem also incorporates previous ecological systems. At the narrowest level, this system accounts for an individual's age and cohort effects with respect to event timing. The changes can also occur within relationships from the microsystem (e.g., changes in family) or at the macrosystem (e.g., changes in political structure; Bronfenbrenner 1979). For example, evidence suggests that major family restructuring such as parental divorce has been linked to lower self-regulation (i.e., personality

changes) and higher aggression in children (Hong and Espelage 2012). These changes may signal to children instability, and consequently more prospective gains of bullying. Thus, major changes in life events may influence bullying directly but also indirectly by influencing other ecological factors.

Conclusions

Overall, the multiple factors in the micro-, meso-, exo-, macro-, and chronosystems can all influence bullying independently and also interdependently. Under certain ecological conditions, an individual may find harming weaker individuals may lead to more material, social, and reproductive advantages than under other ecological conditions. Accordingly, bullying behaviors are not limited to one specific demographic or environment. Instead, by exploring bullying from a holistic, evolutionary ecological framework, it is evident that bullying can be a facultative adaptation, providing numerous avenues for more effective anti-bullying efforts.

Cross-References

- [Boys Bully More Than Girls](#)
- [Boys Physical Bullying](#)
- [Bullying](#)
- [Girls Psychological Bullying](#)
- [Same-Sex School Bullying](#)
- [School Bullying](#)

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Factual Information

► Declarative Knowledge

Fairness

- Sarah Brosnan
- Science and Morality
- Wild Justice

Fairness in Corvids

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Synonyms

Birds; Crows; Equality; Justice

Definition

Understanding or being attentive to states of inequality, either in degree of effort towards a goal or in distribution of rewards or payoffs.

Introduction

A sense of fairness is a key component of morality and is a motivator of moral behavior (Allchin 2009). If other animals behave in a way to suggest they understand fairness, it suggests that they have some components of morality.

Evidence For Fairness

There is some evidence that two corvid species (crows and ravens) have a sense of fairness. This is displayed by the fact that they show “inequity aversion” – that is, when rewards are unequal, ravens and crows will refuse to take rewards or participate in tasks, despite the fact that this behavior minimizes their total rewards. Both ravens and crows will decrease participation in a task (such as exchanging a token for a food reward with a human experimenter) if they see another raven or crow receiving that reward for free or receiving a higher quality food item for the same task (Wascher and Bugnyar 2013). This shows sensitivity to equality of food rewards, but also of working effort; they expect a certain reward for a certain level of effort (Wascher and Bugnyar 2013).

On a cooperative problem-solving task where two strings had to be pulled simultaneously to bring food rewards into reach, ravens showed attentiveness to “cheaters” (Massen et al. 2015). When one raven monopolized both food rewards, the “cheated” raven was less likely to continue participation. This example, unlike the previous one, may be due to simple associative learning (i.e., when a raven does not get a reward for participation, it forms a negative association with cooperating, decreasing the likelihood of cooperating in the future; Massen et al. 2015). These appear to be the only examples of attention to fairness in any corvid species, but this is an area

of research that is still relatively new. Thus, more examples may emerge in the near future.

Conclusion

A sense of fairness is limited in corvids; the only evidence appears in two studies with ravens and crows. However, relatively little research has investigated fairness among corvids, and therefore more information of fairness and morality among different corvid species may be forthcoming.

Cross-References

► [Corvids](#)

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Fairness in Nonhuman Primates

► [Fairness in Primates](#)

Fairness in Primates

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Synonyms

[Fairness in nonhuman primates](#); [Inequity aversion in primates](#)

Definition

Fairness is the preference for equality and resistance to an inequitable distribution of resources. This entry covers research on fairness in primates.

Introduction

It has been proposed that inequity aversion (or a sense of fairness) may have coevolved with cooperation (Brosnan and de Waal 2003). During cooperative efforts, it would be crucial from an adaptive standpoint, for individuals to be able to compare and measure their labors and rewards with the other members of their cooperative groups and react negatively to an unequal division of labor and rewards. As human beings are not the only species that display cooperation, it seems likely that those nonhuman animals that exhibit cooperation may also exhibit inequity aversion.

Evidence for Fairness

Brosnan and de Waal (2003) demonstrated that capuchin monkeys (*Cebus apella*), a cooperative species of primate, reacted negatively toward unequal distribution of food rewards. In their study, capuchin monkeys were trained in a task in which they exchanged a token with an experimenter for food. The monkeys were then placed in adjacent cages in which they could observe the interactions of a partner with the experimenter. There were two conditions: In the equality condition, both monkeys exchanged the token and were each rewarded with cucumber. In the inequality condition, one monkey was rewarded with cucumber (a less preferred food item), while the other was rewarded with grapes (a highly preferred food item) for completing the same task. They found that monkeys receiving cucumbers in the inequality condition were significantly less likely to complete the token exchange task. Incomplete exchanges were defined as the monkey failing to hand back the token for the offered reward item or failing to accept or consume the reward after handing back the token. In a follow-up experiment, Brosnan and de Waal (2003) then

introduced two additional conditions: the “effort control” condition in which one monkey continued to exchange the token for cucumber while their partner was given grapes without completing the task (no effort) and a “food control” condition in which there was no partner monkey (i.e., there was an empty cage into which grapes were placed). They found that the effects of the inequality condition were magnified in the “effort control” condition with the monkeys reacting even more negatively to the unequal distribution of rewards when their partner had put in no effort at all. They also found that the mere presence of grapes (in the “food control” condition) did not have an effect of rates of refusal (whether refusing to exchange the token or accept the reward). Brosnan and de Waal suggest that the rejection of a reward, which under most other circumstances is readily consumed, may indicate a violation of expectations – in this case an expectation of grapes.

Van Wolkenten et al. (2007) modified the methodology in the previous study in order to rule out the *greed hypothesis* (i.e., that the negative reaction of the monkeys was merely due to the visibility of the preferred food item) and the *frustration hypothesis* (i.e., that the negative reaction was due to the monkeys having received the preferred items in the immediate past). To rule out the *greed hypothesis*, preferred items were shown to the monkeys before each exchange. They found that displaying the grapes before each trial did not change the results (i.e., the monkeys still reacted negatively to inequality). To rule out the *frustration hypothesis*, they compared rates of refusal for trials which immediately followed trials rewarded with cucumber or trials rewarded with grapes, and they found no difference in responding. Further supporting the findings of Brosnan and de Waal (2003), Van Wolkenten et al. (2007) also found that the greater the effort of the subject, the more negative their response to the inequity of rewards.

Research has also investigated whether our closest relative, the chimpanzee (*Pan troglodytes*), has a sense of fairness using the same paradigm described above. Brosnan et al. (2010) found that chimpanzees also respond to inequity, but only in the context of performing a task. When a preferred reward was given to the partner

(without requiring a token exchange), the subject was less likely to respond negatively than when both had performed the exchange task. This may be due to the fact that the chimpanzees frequently receive food directly from keepers and so are not averse to some amount of inequality in the distribution of their daily diets. These researchers also found that the dominance hierarchy (rank) and sex also affected refusal rates in response to inequity, such that low-ranking or female chimpanzees were less likely to respond negatively to inequality than higher-ranking or male chimpanzees.

Conclusion

Similar to humans, it appears that both capuchin monkeys and chimpanzees judge fairness based off of the range of possible outcomes and how the rewards are then distributed. While the described research cannot explicitly determine the underlying motivations of the behaviors observed, the data do suggest that nonhuman primates may share some of the same underlying psychological mechanisms which would promote inequity aversion. One possible mechanism, social emotions (also known as “passions” by economists), is known to influence human responses to the distribution of resources and may play a role in non-human primates as well (Brosnan and de Waal 2003).

Cross-References

- [Cooperation Among Nonchimpanzee, Nonhuman Primates](#)
- [Fairness in Corvids](#)
- [Sarah Brosnan](#)

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Fair-Weather Friends Versus True Friends

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Synonyms

Fair-weather friends: Free-riders

Definition

Fair-weather friends are exploiters of true friendship who are interested in unilaterally receiving support. True friends (or close friends) not only receive support, they are also willing to provide support to each other in times of need.

Introduction

Friendship is a mutual support system between two non-kin individuals. Importantly, it is characterized by the provisioning of need-based support (Hruschka 2010; Silk 2003). Whereas a true friend is concerned about your welfare, happily helping you in times of need, a fair-weather friend is concerned only about his or her own welfare and thereby fails to help you when you need it most (Tooby and Cosmides 1996). Fair-weather friends are thus *free-riders* in the sense that they exploit the demands implicit within the friendship

contract. Many solutions have been proposed to this so-called free-rider problem, but the primary context in which they have been studied, namely, the iterated prisoner's dilemma (Axelrod 1984; Axelrod and Hamilton 1981), produces a solution (i.e., tit-for-tat reciprocity) which may not readily apply to the evolution of friendship. In this entry, we first summarize how fair-weather friends pose at least three different puzzles to the evolution of friendship and then introduce potential solutions to these puzzles.

Three Puzzles of Friendship

The evolution of friendship is associated with a set of difficult problems because need-based support appears vulnerable to exploitation by fair-weather friends. Friendship of this sort seems like an evolutionarily unstable strategy because need-based support not only requires people to ignore their partner's past behavior, it also necessitates that they disregard the prospect of future reciprocation – two important factors that enable reciprocal altruism to evolve. Moreover, even when a pair of friends mutually commit to a friendship, subtle suspicion might arise because it is not always clear that a current partner is indeed a true friend. As a result, such suspicion could lead to degradation or dissolution of the friendship.

Friends Turn a Blind Eye to Past Inequity

Friendship is generally considered as an instance of dyadic cooperation that is more or less unique to humans. Although the standard evolutionary model of dyadic cooperation is *reciprocal altruism* maintained by the *tit-for-tat* strategy (TFT) in the iterated prisoner's dilemma game (Axelrod 1984; Axelrod and Hamilton 1981; Trivers 1971), need-based support is incompatible with this strategy. Let us consider each of the qualities that characterize TFT: niceness, revengefulness, and forgivingness (Axelrod 1984). TFT is nice in the sense that it starts dyadic interactions by cooperating (an altruistic choice) and keeps cooperating as long as its partner behaves in kind. TFT is revengeful in the sense that it immediately

stops cooperating when its partner defects. Yet TFT is forgiving in the sense that it reverts to cooperating (i.e., ceases to defect) as soon as its partner reinitiates cooperation. Due to the last two characteristics (i.e., revengefulness and forgivingness), TFT can be conceived as an account-keeping strategy – it makes the balance between giving (its own cooperation) and receiving (its partner's cooperation) as even as possible.

Account-keeping (or tit-for-tat reciprocity) and need-based support appear to be two distinct forms of dyadic cooperation (e.g., Aktipis et al. 2011, 2016; Silk 2003). Before the existence of modern insurance systems, friendship was an essential source of support in the face of predicaments such as illness, injury, and failure to forage. Because these sorts of predicaments arise haphazardly, however, strict account-keeping is not amenable to these risks. If one individual (A), for example, suffers two or more successive instances of misfortune, while another individual (B) remains safe for a substantially long period of time, an imbalance between giving and receiving is a likely consequence: A would receive more from B than he/she would be able to provide in return. If B were to follow a strict account-keeping strategy, B would cut off assistance to A until he/she somehow reconciled the imbalance. This is a highly inefficient insurance system given the random nature of misfortune. In fact, agent-based simulations have revealed that need-based support, modeled after an extant form of friendship (*osotua*) among Maasai cow herders, is a more efficient risk-pooling strategy than strict account-keeping (Aktipis et al. 2011, 2016).

Furthermore, experimental evidence shows that friends are less concerned about the details of their partner's previous behavior than that of strangers or acquaintances (see Silk 2003, for a review). In other words, the real-world friendship appears to be much closer to a need-based system rather than an account-keeping system. However, due to a lack of contingencies for past behaviors (e.g., leniency regarding inequity), the need-based support system appears to be vulnerable to invasion from exploitative individuals, such as fair-weather friends. Therefore, the first puzzle of friendship is that true friendship appears to be

evolutionarily unstable in the presence of fair-weather friends.

Friends Cooperate Even When the Probability of Future Interaction Is Low

In their pioneering work on the evolution of friendship, Tooby and Cosmides (1996) proposed the notion of the *banker's paradox* to illuminate the puzzle of friendship. Because bankers must be selective in deciding in whom to invest their limited resources, “just when individuals need money most desperately, they are also the poorest credit risks and, therefore, the least likely to be selected to receive a loan” (Tooby and Cosmides 1996, p. 131). In a similar vein, although you would benefit most from having a true friend when you are in dire need (e.g., when you suffer serious illness, are on the verge of bankruptcy), “selection would seem to favour decision rules that caused others to desert you exactly when your need for help was greatest” (Tooby and Cosmides 1996, p. 132).

The banker's paradox is distinct from the account-keeping problem. Even when a partner has helped you before, you are better off withholding help from that partner when he or she might not survive the current predicament. In the repeated prisoner's dilemma game, if the number of interactions is a known quantity, any rational (i.e., benefit maximizing) player should defect on the very last round. However, when information about the last round is not available, it appears that a “shadow of the future” (or anticipated benefit from long-term cooperation) is the rationale for why players tend to cooperate in the iterated prisoner's dilemma. Indeed, formal evolutionary game analyses have revealed that the presence of sufficiently long-lasting interactions within the same dyad is the key ingredient for the evolution of dyadic cooperation (Nowak 2006). Therefore, if friendship is just a form of tit-for-tat reciprocity, it is expected that friends should be sensitive to the prospect of future interactions.

Nevertheless, people direct altruistic behavior toward their close friends even when reciprocation of a costly favor cannot be expected. For example, in an experimental game study, people

were more likely to help their close friends than non-close friends in an anonymous situation where no reciprocity was possible (Leider et al. 2009). Thus, the second puzzle is that friends appear to help each other even when the prospect of future interactions is conspicuously absent.

People have Difficulty Distinguishing True Friends from Fair-Weather Friends

Positive affect, manifested as feelings of warmth, intimacy, and closeness, is one of the universal characteristics of friendship (Hruschka 2010). In other words, friendship appears to be maintained by subjective mutual commitment (Nesse 2001). Notice that this observation basically paraphrases the idea that friendship is associated with the two abovementioned puzzles. If you subjectively commit to a relationship with a particular friend, you tend to help him/her regardless of his/her past behavior or prospects of his/her reciprocation. In addition, subjective commitment is associated with another, distinct puzzle. That is, it seems difficult to accurately assay your friend's commitment to you.

Suppose that one individual, A, subjectively commits to the relationship with B. However, this does not guarantee that B commits in a commensurate manner. When there is this sort of asymmetry in levels of commitment, the less committed partner can be considered a fair-weather friend. Imagine A helped B even though doing so was extremely costly. If there is no immediate subsequent opportunity for B to reciprocate, A might begin to doubt whether B really is a true friend. The presence of this suspicion of B's commitment would then lead to degradation of the committed relationship. To avoid this, both parties need to be able to accurately assay each other's commitment to the relationship. Nonetheless, the most accurate assessment is only possible in times of dire need. If your partner helps, he/she is a true friend; if not, he/she is a fair-weather friend. Therefore, the third puzzle is that friendship based on subjective commitment requires an accurate assessment of commitment levels, but this is not easily knowable until you, in fact, come to need your partner's help.

Possible Solutions to the Puzzles of Friendship

Researchers have proposed several solutions to the puzzles of friendship. Because the three puzzles are interrelated to each other, the proposed solutions are not necessarily mapped on to each of the three puzzles separately. The first solution, which applies to the first and second puzzles, is to make yourself *irreplaceable* to your friend (Tooby and Cosmides 1996). If you are irreplaceable, your friend would be compelled to commit to the relationship with you. In other words, irreplaceability ensures partner commitment. Accordingly, mutual irreplaceability can be a basis of true friendship. The second solution to the first two puzzles is to transform the incentive structure of staying in the current relationship. For example, introducing some *start-up cost* (Bergstrom et al. 2008) and increasing the benefits of staying in the current relationship (Roberts and Sherratt 1998) are two possible transformations of incentive structure. The solution to the third puzzle (i.e., how to accurately assess a partner's level of commitment) is to use honest signals of commitment (e.g., Yamagishi et al. 2005; Yamaguchi et al. 2015). If you can convince your partner of your true commitment to the relationship, degradation of the relationship due to suspicion can be avoided. Another solution to the third puzzle is to actively test your partner's commitment by imposing some stress on your partner; whether or not your partner can bare this stress tells you whether or not your partner is a true friend (e.g., Kelley 1983; Zahavi 1977).

Irreplaceability

Tooby and Cosmides (1996) proposed that making oneself irreplaceable to one's partner is a solution to the banker's paradox. Suppose that you can provide a service or material good that your partner cannot obtain from anyone else and that your partner depends on you alone for the good/service. Now imagine you suffer a serious injury, such as a snake bite, which puts your survival at risk. Although the prospect of future interactions is small, if your partner does not want to lose the good/service, he/she has no

option but to help you. This seemingly solves the banker's paradox because the partner's helping behavior is motivated by his/her own self-interest (i.e., maintaining the source of the otherwise unavailable good/service) rather than by the expectation of future reciprocation.

However, it is noteworthy that an irreplaceable individual, who can provide a useful good/service that no one else can provide, should be highly valued by everyone in the community. Suppose that a highly skilled hunter, who can hunt extremely large prey animals that no one else in the community can hunt, is valued by everyone in the community. If the hunter becomes sick, every member in the community will be incentivized to help him/her. This does not fit with a central archetype of friendship, that is, a dyadic mutual support system. Therefore, the sheer presence of some highly valued (i.e., irreplaceable) community members does not explain friendship.

Tooby and Cosmides further argue that some individual differences might cause the initial impetus of a runaway-like process of dyadic commitment formation. If you value a particular community member only slightly more than other members, you might be slightly more concerned about that member's welfare. Importantly, he/she might recognize that you are more willing to help him/her than others. This increases his/her concern about your welfare. Accordingly, he/she becomes more willing to help you when you are in dire need. This gives you another reason to value him/her. As this process continues, like the Fisherian runaway sexual selection process, mutual commitment becomes far stronger than expected from the initial subtle concern for each other's welfare. Once this process has sufficiently strengthened feelings of mutual irreplaceability, the banker's paradox is solved. You help a particular friend even when he/she is at risk of his/her life (and thus future reciprocation is less likely to be expected) because his/her survival influences your fitness.

This runaway friendship provides one solution to the banker's paradox. It assumes that even slight individual differences in interest in the welfare of particular others can initiate this dynamic process. However, it requires that each

individual is able to assess partner interest in his/her welfare. Remember that this is the third puzzle of friendship.

Start-up Costs and the Raise-the-Stakes

Friendship is generally assumed to develop gradually. Although in some cases people make a decision to form a friendship quickly at an early point in their acquaintance, the breadth and depth of interactions nevertheless progresses and increases over time (Hays 1988). If some significant period of time is necessary to develop a fully functioning, dependable friendship, deserting a current friend and attempting to make a new one can be costly. Deserters will at least temporarily lose access to the safety net that was provided by the previous friendship. Even if they easily find a new potential friend, it will take time to deepen their bonds. Thus, a "courtship" period serves as a start-up cost to friendship. Because of this start-up cost, the incentive to stay in a cooperative relationship with one's current partner increases (Bergstrom et al. 2008). Therefore, the incentive to behave as a fair-weather friend is substantially curtailed by start-up costs.

The apparent "courtship" period of friendship might serve another important purpose. A classic theory of relationship development, the social penetration theory (Altman and Taylor 1973), assumes that as social relationships develop, initial shallow social exchanges transition to deeper, more full-fledged social exchanges. This theory can be formalized using Roberts and Sherratt's (1998) *raise-the-stakes strategy*. In their evolutionary game analysis, players can choose not only their own behavior (i.e., cooperate or not) but also the level of cooperation, in the case that they have chosen cooperation. Suppose that each player is endowed with 10 units of a resource. Each player can choose how much of the 10 units he/she will transfer to his/her partner. The transferred resource will then be doubled and given to the partner. The raise-the-stakes strategy starts at a low level of cooperation (e.g., giving only 1 unit) and increases its level of cooperation if the partner's level of cooperation matches its own. By initiating the social exchange with a relatively trivial amount of a resource, each individual can avoid large exploitations by the partner at

early stages of relationship development. By the time both parties can exchange relatively large resources, the partner becomes irreplaceable (because replacing the current partner means that they incur the start-up cost inherent to a new relationship). Experimental studies have revealed that people in fact gradually increase the stakes of social exchanges over the course of relationship development (Roberts and Renwick 2003; Yamagishi et al. 2005).

Applying the raise-the-stakes logic to the context of random predicaments, Hruschka (2010) revealed that the following rule of thumb can be adaptive: “Always help [your friend], unless there is some reason to believe he is not a friend” (p. 239). This rule of thumb is adaptive when erroneously deserting true friendship is more costly than erroneously committing to a fair-weather friend. In particular, if you have helped your partner on successive occasions but your friend has not reciprocated due to lack of opportunities, this rule of thumb tells you to stay in the relationship because you do not yet have convincing evidence that the partner is a fair-weather friend. In other words, Hruschka analytically showed that relative indifference to precise equity is adaptive in the context of mutual support provisioning.

Commitment Signals

Runaway friendship formation and the raise-the-stakes strategy explain how the capacity for subjective commitment can be adaptive. As both parties progressively commit to a particular friendship, the incentive to desert the current friend decreases. Recall that for this runaway-like process to progress, each individual must be able to recognize his/her partner’s subtle commitment to the relationship. Nevertheless, a partner’s level of subjective commitment is not necessarily transparent, and uncertainty about partner commitment undermines dynamic increases in mutual commitment. Moreover, the conditional part of Hruschka’s (2010) rule of thumb (i.e., “unless there is some reason to believe he is not a friend”) also requires some cue to distinguish fair-weather friends from true friends.

Yamagishi et al. (2005) devised a game setting where each player cannot only raise the stakes but also signal one’s commitment to the relationship. In their model, each player chooses a level of dependence on the partner. If A chooses a high-stakes game rather than a low-stakes game, A benefits more from B’s cooperation, but also loses more from B’s exploitation. Therefore, A can move to the high-stakes game when and only when he/she trusts B. Because A’s choice of the high-stakes game is potentially costly (i.e., A becomes more vulnerable to B’s exploitation), A’s choice serves as an honest signal of A’s trust in B. If B knows that A trusts him/her, B immediately recognizes that A is his/her valuable exchange partner. This may provide a reason for B to (at least slightly) prefer A as an interaction partner because B knows that A values him/her but does not know whether others value him/her as much as A does. Therefore, A’s signal of trust can serve as an initial impetus to start runaway-like friendship formation between A and B.

Making oneself vulnerable (i.e., performing a costly behavior to demonstrate sincere trust) is not the only way to communicate commitment to a relationship (Yamaguchi et al. 2015). Friends occasionally make some small sacrifices for their partner (e.g., missing a favorite TV show to go out with friends). Friends regularly exchange small, and thus less costly, gifts (Hruschka 2010). Friends pay attention to how each other are doing (Ohtsubo et al. 2014). These commitment signals might not appear sufficiently costly to convince the signal recipient that the signaler is indeed a true friend. However, people can only send such signals to a limited number of partners. Time and social attention are both finite resources, and the resource allocation problem forces signal senders to limit the number of recipients (Ohtsubo et al. 2014; Sutcliffe et al. 2012). Accordingly, these relatively less costly signals may be sufficient to dispel suspicions that the signaler is not a friend. This is the information that Hruschka’s (2010) rule of thumb requires, and it is possibly sufficient to start the runaway-like friendship formation process that leads friends to be mutually irreplaceable.

Testing the Strength of a Bond

If both partners do not spontaneously send any commitment signals, can either party know the partner's level of commitment? In fact, friends might actively test their partner's commitment by imposing some stresses on each other (Kelley 1983; Zahavi 1977). This is called a *bond testing*. Although your friend may fail to make a spontaneous sacrifice for you, he/she may be willing to do so if you explicitly ask. Basically, bond testing involves soliciting some costly commitment signal from partners. If your partner tolerates the stressful situation you impose upon them, this means that your friend is committed to the relationship with you.

Although bond testing has not yet been well-studied in humans, some primatologists use this notion to explain otherwise unexplainable primate behaviors. For example, Perry (2011) observed that pairs of white-faced capuchin monkeys (*Cebus capucinus*) mutually insert their partner's finger into their own eye sockets. This is an extremely dangerous behavior in that it might lead to damage to the eye or even a loss of vision. Therefore, one might not engage in such a dangerous behavior with someone whom he/she cannot fully trust. In other words, the joint engagement in such a dangerous behavior reveals strong mutual commitment. Accordingly, Perry interprets this dangerous behavior as a bond-testing ritual. Human instances of bond testing in the context of friendship seem to merit further research.

Conclusion

Friendship is characterized by need-based support provisioning. Unlike account-keeping reciprocity, friendship is especially vulnerable to the presence of free-riders (i.e., fair-weather friends). We pointed out three interrelated puzzles that pertain to the evolution of friendship. First, without strict account-keeping (i.e., behaving in a manner contingent with a partner's previous behavior), friendship is vulnerable to invasion by fair-weather friends. Second, without concern for the shadow of the future, one might misplace one's investment in a partner who is unlikely to

reciprocate (i.e., the banker's paradox). Third, even when friends have a capacity for subjective commitment, without a way of confirming this commitment, mutually committed relationships may be susceptible to doubt and deteriorating trust. We presented two possible solutions to the former two problems: making oneself irreplaceable to one's partner and using the raise-the-stakes strategy. These two solutions can make friendship adaptive to the extent that individuals have some ability to keep track of a partner's current level of commitment to the relationship (but perfect precision is not needed). This problem may be solvable by commitment signals. For example, if someone commits to a particular relationship, that person may regularly give small gifts or simply pay attention to his/her partner's needs. Although these behaviors are relatively low cost compared to the tangible support required in the times of real need, they may still serve as sufficient signals of friendship. Alternatively, friends may occasionally engage in active tests of their partner's commitment. These behavioral tendencies (to signal one's commitment or test a partner's commitment) are necessary to maintain the "nearly" unconditional altruism that is characteristic of friendship.

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Fair-Weather Friends: Free-Riders

► Fair-Weather Friends Versus True Friends

Faith

► Religion

Faking Orgasm

► Women Pretending Orgasm

Fall of “Tall Poppies”

► Schadenfreude

False Beliefs

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Synonyms

Counterfactual mental states; False perceptions; Mentalizing; Mindreading; Pretense; Psychological reasoning; Reality-incongruent beliefs; Representational mental states; Theory of mind

Definition

False-belief understanding requires understanding (at least implicitly) that the mind is representational in nature and, as such, can hold beliefs that are inaccurate or that deviate from reality in some way.

Introduction

Adults make sense of others' actions by inferring the mental states that underlie these actions; this ability is variously referred to as psychological reasoning, mind reading, mentalizing, or exhibiting a theory of mind. Over the past two decades, numerous reports have presented evidence that psychological reasoning emerges early in life: When infants observe an agent act in a simple scene, they infer the agent's motivational (e.g., goal, attitude) and epistemic (e.g., knowledge, ignorance) states, and they use these mental states to predict and interpret the agent's subsequent actions and to guide their own responses to the agent (for a review, see Baillargeon et al. 2016). Such early competencies naturally give rise to the following questions: How similar is infants' psychological reasoning to that of older children and adults? Is there substantial continuity across development, or do fundamental changes take place in the types of mental states that can be attributed to agents?

When Does False-Belief Understanding Emerge?

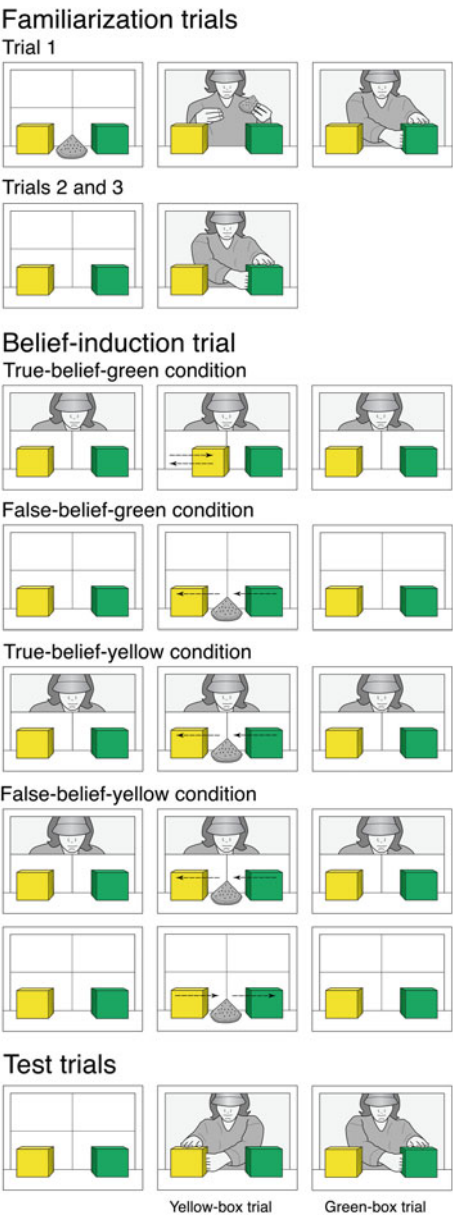
For many years, it was generally assumed that a major shift does take place around 4 or 5 years of age in the development of psychological reasoning: Children become capable of understanding false beliefs and other counterfactual mental states (Wellman et al. 2001; Wimmer and Perner 1983). This conclusion was based mainly on evidence from *elicited-prediction* tasks in which children must answer a test question about the likely behavior of an agent who holds a false belief about a scene. In the classic Sally-Anne task

(Baron-Cohen et al. 1985), for example, children listen to a story enacted with props: Sally hides a marble in one of two containers and then leaves; in her absence, Anne moves the marble to the other container; Sally then returns, and children are asked the test question, "Where will Sally look for her marble?" Beginning at age 4 or 5, children answer correctly and point to the marble's original location; in contrast, younger children point to the marble's current location, as though they are unable to understand that Sally holds a false belief about the marble's location. This developmental pattern – from below-chance to above-chance performance – was consistently observed in different elicited-prediction tasks and in different cultures around the world (Wellman et al. 2001). Based on these results, many researchers came to regard false-belief understanding as a hallmark of advanced or full-fledged psychological reasoning. In essence, success at elicited-prediction tasks was taken to demonstrate that children finally grasp the representational nature of the mind: They realize that beliefs are mental representations and, as such, can deviate from reality.

In recent years, however, the conclusion that false-belief understanding is not attained until the preschool years has been called into question, as evidence has steadily accumulated that toddlers (age 2–3) and infants (under age 2) succeed at simpler false-belief tasks (for reviews, see Baillargeon et al. 2016; Carruthers 2013). To date, converging demonstrations of early false-belief understanding have been obtained in *spontaneous-response* and *elicited-intervention* tasks; key findings with each type of task are summarized in the next sections.

Spontaneous-Response Tasks

In a spontaneous-response false-belief task, children watch a scene in which an agent comes to hold a false belief, and their spontaneous responses to the unfolding scene are measured. The first spontaneous-response task administered to infants (Onishi and Baillargeon 2005) used the *violation-of-expectation* method, which takes advantage of infants' natural tendency to look



False Beliefs, Fig. 1 In the task of Onishi and Baillargeon (2005), 15-month-olds first received familiarization trials in which an agent hid a toy in a green box (trial 1) and then reached into the box as though to grasp her toy (trials 2 and 3). In the belief-induction trial, infants saw one of four events: While the agent watched, the yellow box moved toward the green box and then returned to its starting position (true-belief-green condition); in the agent's absence, the toy moved from the green to the

yellow box (false-belief-green condition); the toy moved to the yellow box in the agent's presence (true-belief-yellow condition); the toy again moved to the yellow box in the agent's presence but then returned to the green box after she left (false-belief-yellow condition). In the test trials, the agent reached into either the yellow box (yellow-box trial) or the green box (green-box trial) and then paused

longer at events that violate, as opposed to confirm, their expectations (Fig. 1). In the task, 15-month-olds first received familiarization trials

in which an agent hid a toy in a green as opposed to a yellow box. Next, infants received one of four different belief-induction trials that resulted in the

agent believing, truly or falsely, that the toy was in the green or the yellow box: In the true-belief-green condition, the agent watched as the yellow box moved a short distance and then returned to its original position; in the false-belief-green condition, the agent was absent when the toy moved from the green box into the yellow box; in the true-belief-yellow condition, the agent saw the toy move into the yellow box; finally, in the false-belief-yellow condition, the agent watched as the toy moved into the yellow box, but was absent when it returned to the green box. In the test trial, the agent reached into either the green or the yellow box and then paused. In each condition, infants expected the agent to act on the information available to her, whether it was true or false. Thus, infants in the true-belief-green and false-belief-green conditions expected the agent to reach into the green box, whereas infants in the true-belief-yellow and false-belief-yellow conditions expected her to reach into the yellow box; in each case, infants detected a violation (as indexed by longer looking times) when the agent searched the other box.

These results suggested that infants can already attribute false beliefs to agents. Subsequent investigations extended these results in many different directions.

Different Spontaneous Responses

Evidence of early false-belief understanding has been obtained not only in violation-of-expectation tasks such as that of Onishi and Baillargeon (2005) but also in other types of spontaneous-response tasks. In *anticipatory-looking* tasks, 17- to 25-month-olds visually anticipated that an agent who falsely believed an object was in location-A (when it was in fact in location-B or had been removed from the scene) would search location-A for the object (Southgate et al. 2007; Surian and Geraci 2012). In *anticipatory-pointing* tasks, 18-month-olds spontaneously pointed to inform an agent who falsely believed an object was in location-A that the object had been moved to a new location (Knudsen and Liszkowski 2012). In *preferential-looking* tasks, 2.5-year-old toddlers who were told a false-belief story accompanied by pictures looked preferentially at the final picture that correctly, as opposed to

incorrectly, completed the story (Scott et al. 2012). In *affective-response* tasks, 2.5-year-olds expressed more tension in their facial expressions when an agent who was approaching a container was mistaken, as opposed to ignorant, about some aspect of its contents (Moll et al. 2017).

Researchers have also obtained evidence of early false-belief understanding in spontaneous-response tasks tapping neural (as opposed to behavioral) responses. In a *neural-prediction* task, 6-month-olds showed an increase in sensorimotor alpha-band suppression (an EEG correlate of action prediction) when an agent falsely believed a box contained a ball, but they showed no such increase when she falsely believed the box was empty. Infants thus anticipated that the agent would search for the ball when she falsely believed it was present, but not when she falsely believed it was absent (Southgate and Vernetti 2014). Finally, in a *neural-occlusion* task, 8-month-olds showed an increase in temporal gamma-band activation (an EEG correlate of sustained object representation during occlusion) when an agent falsely believed an object was behind an occluder (unbeknownst to the agent, the object disintegrated once occluded); infants showed no such increase when the agent witnessed the object's disintegration (Kampis et al. 2015).

Different False Beliefs

Infants and toddlers in spontaneous-response tasks have been found to represent false beliefs about the *location* (Onishi and Baillargeon 2005), *presence* (Southgate and Vernetti 2014), *identity* (Scott and Baillargeon 2009), and *nonobvious properties* (Scott et al. 2010) of objects. In a task on identity (Scott and Baillargeon 2009), for example, 18-month-olds first received familiarization trials in which an agent faced a one-piece penguin that did not come apart and a disassembled two-piece penguin (Fig. 2). In each trial, the agent hid a small key in the bottom piece of the two-piece penguin and then assembled it; once assembled, the two-piece penguin was identical to the one-piece penguin. In the test trials, while the agent was absent, an experimenter assembled the two-piece penguin, placed it under a transparent cover, and then placed the

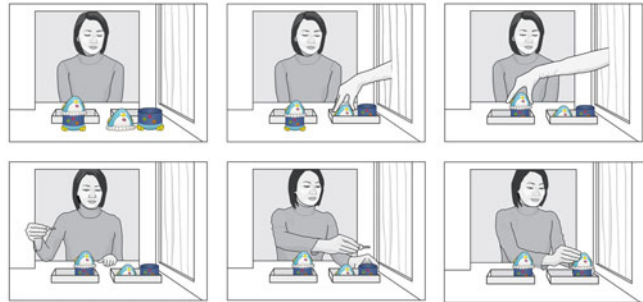
False Beliefs, Fig. 2 In the task of Scott and Baillargeon (2009), 18-month-olds first received familiarization trials involving two toy penguins that were identical except that one could come apart (two-piece penguin) and one could not (one-piece penguin). In each trial, as an agent watched, an experimenter's gloved hand placed the disassembled two-piece penguin and the one-piece penguin on platforms (trials 1 and 2) or in shallow boxes (trials 3 and 4); next, the agent hid a small key in the bottom piece of the two-piece penguin and then assembled it. During the test trials, while the agent was absent, the gloved hand assembled the two-piece penguin, covered it with a transparent cover, and then covered the one-piece penguin with an opaque cover. The agent then returned, reached for either the transparent cover (transparent-cover trial) or the opaque cover (opaque-cover trial), and then paused

Familiarization trials

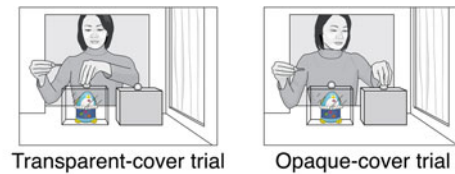
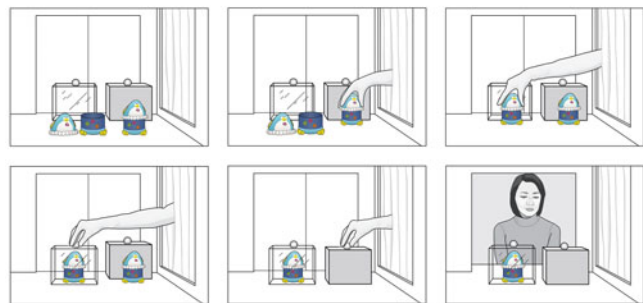
Trials 1 and 2



Trials 3 and 4



Test trials



one-piece penguin under an opaque cover. The agent then returned with her key, reached for either the transparent or the opaque cover, and then paused. Infants expected the agent to reach for the opaque cover and looked longer when she reached for the transparent cover instead (this looking pattern reversed if the agent witnessed the experimenter's actions). These results indicated that infants attributed to the agent two

interlocking false beliefs: They expected her (a) to mistake the penguin visible under the transparent cover for the one-piece penguin (because the two-piece penguin had always been disassembled at the start of the familiarization trials) and hence (b) to falsely conclude that the disassembled two-piece penguin was hidden under the opaque cover (because both penguins were always present in the familiarization trials).

Additional findings confirmed that infants could distinguish between false belief and ignorance: When both covers were opaque, infants held no particular expectation about which cover the agent would reach for.

Implanting False Beliefs

Infants and toddlers in spontaneous-response tasks have been shown to reason correctly not only about the actions of agents who *hold* false beliefs (e.g., where they will search for a hidden object or which object they will select to produce a desired effect) but also about the actions of deceptive agents who seek to *implant* false beliefs in others. In a task with 17-month-olds (Scott et al. 2015), a thief attempted to secretly steal a desirable rattling toy during its owner's absence by substituting a less desirable silent toy (Fig. 3). Infants first watched a series of rattling-toy and silent-toy familiarization trials. In each rattling-toy trial, the owner entered with a toy on a tray; she shook the toy, which rattled, placed it back on the tray, and then left. In her absence, the thief picked up the toy, shook it, and then replaced it on the tray. When the owner returned, she stored the rattling toy in a treasure box. The silent-toy trials were similar except that the toy was silent, the thief did not play with it, and the owner discarded it in a trash can when she returned. In the test trial, the owner brought in a rattling test toy that was visually identical to a silent toy she had previously discarded in the trash can. As before, she shook the toy and then left. In her absence, the thief picked up the rattling toy, peered into the trash can, and selected either the matching silent toy (matching trial) or a nonmatching silent toy (nonmatching trial). The thief placed the silent toy on the owner's tray, hid the rattling test toy in a pocket, and then paused. Infants looked significantly longer if they received the nonmatching as opposed to the matching trial, suggesting that they realized that (a) the thief sought to steal the rattling test toy without the owner's knowledge by substituting a discarded silent toy the owner could mistake for the rattling test toy, and (b) the thief could achieve this deceptive goal only by substituting the matching silent toy. In a control experiment, the owner always shook her toy again

when she returned in the familiarization trials, before storing or discarding it. Infants now looked equally during the matching and nonmatching trials, suggesting that they realized that the owner could not be deceived by the substitution of either the nonmatching silent toy (she would detect the substitution as soon as she saw the toy) or the matching silent toy (she would detect the substitution as soon as she shook the toy).

Different Linguistic Demands

Toddlers have been shown to succeed at spontaneous-response tasks with no linguistic demands (Southgate et al. 2007) as well as spontaneous-response tasks with high linguistic demands comparable to those of elicited-prediction tasks (Barrett et al. 2013; Scott et al. 2012). In a preferential-looking task (Scott et al. 2012), for example, 2.5-year-olds listened to a false-belief story, accompanied by a picture book, about a character named Emily and her apple. In the final double page of the book, one picture showed Emily searching for her apple where she falsely believed it to be (original-location picture), and the other picture showed Emily searching for her apple in its current location (current-location picture). Upon hearing the final line of the story, which stated that Emily was looking for her apple, children looked preferentially at the original-location picture, suggesting that they represented Emily's false belief and understood how it would guide her actions. Similar results were obtained in three traditional non-Western societies: a Salar community in China, a Shuar community in Ecuador, and a Yasawan community in Fiji (Barrett et al. 2013). These results make clear that the reason why young children fail at elicited-prediction tasks but succeed at spontaneous-response tasks cannot be that the former are highly verbal whereas the latter are not: Young children can succeed at highly verbal spontaneous-response tasks.

Elicited-Intervention Tasks

In an elicited-intervention task, children watch a scene in which an agent comes to hold a false

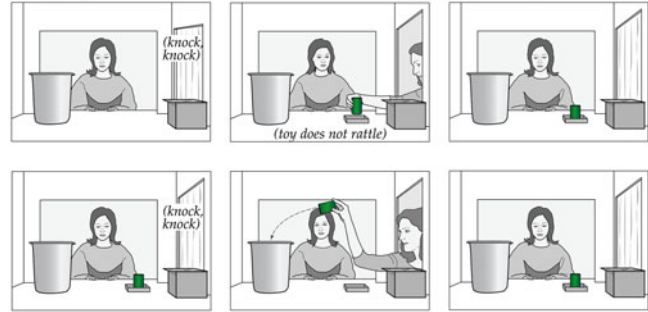
False Beliefs, Fig. 3 In the task of Scott et al. (2015), 17-month-olds saw three rattling-toy and three silent-toy familiarization trials; a different toy was used in each trial, and the six toys differed in color and pattern. In the rattling-toy trials, the owner entered with a toy on a tray; she shook the toy, which rattled, returned it to the tray, and then left (the toy rattled only when briskly shaken). In her absence, the thief shook the toy and then replaced it on the tray. When the owner returned, she stored the toy in a treasure box. In the silent-toy trials, the toy was silent, the thief did not shake it, and the owner discarded it in a trash can. In both test trials, the owner first brought in a rattling test toy that was visually identical to a silent toy she had previously discarded in the trash can; as before, she shook the toy and left. The thief then picked up the rattling test toy, looked into the trash can, and selected either the matching silent toy (matching trial) or a nonmatching silent toy (nonmatching trial). The thief placed the silent toy on the owner's tray, hid the rattling test toy in a pocket, and then paused

Familiarization trials

Rattling-toy trials

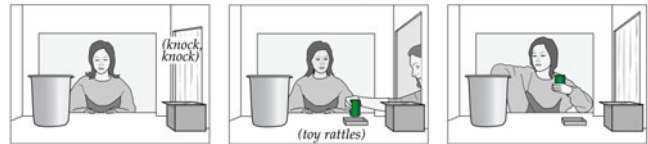


Silent-toy trials

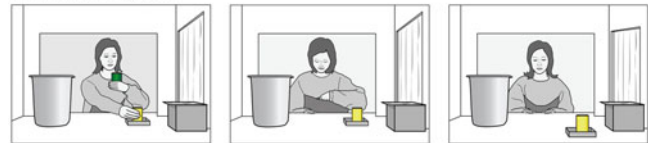


Test trials

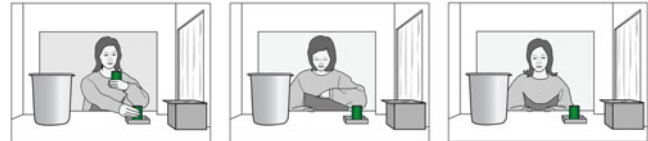
The two test trials began the same way and then continued as shown.



Non-matching trial



Matching trial



belief, and then they are prompted to perform some action for the agent; for children to succeed, their actions must be guided by an understanding of the agent's false belief. Positive results have been obtained with infants and toddlers using a variety of prompts, including helping the agent retrieve an object and selecting one of two objects

for the agent (Buttelmann et al. 2009, 2015; Southgate et al. 2010).

In the helping task of Buttelmann et al. (2009), for example, an experimenter first showed 18-month-olds how to lock and unlock two lidded boxes; the boxes were left unlocked. Next, a male agent entered the room, hid a toy in one of the

boxes, and then left. While he was gone, the experimenter moved the toy to the other box and locked both boxes. When the agent returned, he tried vainly to open the box where he had hidden his toy. When prompted to help him (“Go on, help him!”), most infants approached the box the agent had not acted on, suggesting that they understood he wanted his toy and falsely believed it was still in its original location (when the agent witnessed the toy’s transfer, infants inferred that he wanted to open the empty box, and they approached that box instead). Southgate et al. (2010) tested 17-month-olds with a similar task. An agent hid two distinct objects in two lidded boxes and then left; in her absence, an experimenter switched the objects. When the agent returned, she pointed to one of the boxes, said she wanted to play with the object in it, and asked the infants, “Can you get it for me?” Most infants approached the box the agent had not pointed to, suggesting that they understood she held a false belief about which object was in which box.

In addition to false beliefs about location, elicited-intervention tasks have been used to examine infants’ understanding of false beliefs about contents and identity. In a task on identity (Buttelmann et al. 2015), for example, 18-month-olds and an agent encountered a deceptive object, such as an object that appeared to be a toy duck, in each of four trials. The agent then left the room, and in her absence, infants learned the object’s true identity (e.g., the duck was in fact a brush). The deceptive object was then placed on a high shelf. When the agent returned and reached vainly for the deceptive object, infants were shown two test objects, one that matched the deceptive object’s appearance (e.g., a toy duck) and one that matched its true identity (e.g., a brush), and they were asked to give the agent what she wanted. Infants tended to choose the test object that matched the deceptive object’s appearance rather than the test object that matched its identity (this pattern reversed if the agent was present when the object’s true identity was revealed). Buttelmann et al. concluded that infants understood that the agent held a false belief about the identity of the deceptive object (e.g., she thought it was a toy duck) and used this belief to decide which test object to select for her.

Elicited-Prediction Tasks Revisited

How can we explain the discrepancy between the negative findings of elicited-prediction tasks and the positive findings of spontaneous-response and elicited-intervention tasks? At present, there are two main views on this question.

Two-system view

According to some researchers, two different psychological-reasoning systems underlie performance in elicited-prediction tasks, on the one hand, and in spontaneous-response and elicited-intervention tasks, on the other (Butterfill and Apperly 2013; Low and Watts 2013). In the two-system account of Butterfill and Apperly (2013), for example, the (conscious, non-automatic, slow, flexible) *late-developing* system emerges around 4 years of age as a result of linguistic, executive-function, and meta-representational advances; this advanced system is capable of representing false beliefs and other counterfactual states, and it makes possible correct responses in elicited-prediction tasks. The (unconscious, automatic, fast, inflexible) *early-developing* system is already present in infancy; although it cannot represent false beliefs per se, it can track simpler, belief-like “registrations” that are sufficient to allow success at spontaneous-response and elicited-intervention tasks. Upon encountering an object, an agent registers its location and properties; by tracking this registration – even if it becomes outdated in the agent’s absence – the early-developing system can predict the agent’s actions (e.g., an agent will search for her toy where she last registered it).

However, there are reasons to doubt that two systems with distinct neurological substrates and computational capacities underlie false-belief understanding in different tasks. First, neuroscientific investigations with adults indicate that elicited-prediction and spontaneous-response tasks engage anatomically similar regions within the temporal-parietal junction (Bardi et al. [in press](#)). Second, claims about the early-developing system’s signature limits (e.g., an inability to track false beliefs about identity or complex interactions among mental states) have been overturned

(Buttelmann et al. 2015; Scott and Baillargeon 2009; Scott et al. 2015). More generally, the sophistication of the false-belief understanding that has been revealed in many spontaneous-response and elicited-intervention tasks casts doubt on the view that infants and toddlers are capable of only a minimal form of false-belief understanding (for discussion, see Carruthers 2016; Scott et al. 2015).

One-system view

According to other researchers, a single psychological-reasoning system underlies performance in elicited-prediction, spontaneous-response, and elicited-intervention tasks (Baillargeon et al. 2016; Carruthers 2013; Leslie et al. 2004). In this view, young children's difficulties with elicited-prediction tasks stem from their heavy processing demands. Among these, two separate lines of research have highlighted the importance of executive-function and more specifically *inhibitory-control* demands. First, in their computational model of elicited-prediction tasks, Leslie and his colleagues proposed that an inhibitory process plays a key role in allowing children to express their false-belief understanding (Leslie et al. 2004). When children are asked the test question "Where will Sally look for her marble?", an inappropriate prepotent response focused on the marble's actual location is triggered (exactly why this is so is currently widely debated among developmental researchers). This prepotent response must then be inhibited for children to select an alternative response consistent with their representation of Sally's false belief. Because young children's inhibitory control is immature, however, they cannot effectively suppress this prepotent response and thus mistakenly point to the marble's current location.

Second, many correlational studies with 3- to 6-year-olds have reported a significant association between performance in elicited-prediction tasks and performance in tasks that tap inhibitory control and especially conflict inhibition, the ability to suppress a prepotent response while activating a conflicting response (e.g., saying "day" when shown a picture of the moon and saying "night" when shown a picture of the sun; Carlson and

Moses 2001; for a meta-analysis, see Devine and Hughes 2014). This association typically persists even when potentially confounding factors such as age and verbal ability are statistically controlled. These correlational findings are often taken to indicate that inhibitory-control advances are necessary for the *emergence* of false-belief understanding (Carlson and Moses 2001). In light of the positive results of spontaneous-response and elicited-intervention tasks, however, it seems likely that inhibitory-control advances contribute more to the *expression* of this understanding, as suggested by Leslie et al. (2004).

Predictions of the One-System View

If processing demands are the cause of early difficulties with elicited-prediction tasks, as the one-system view claims, then reducing these demands should enable young children to succeed at these tasks. In line with this prediction, many researchers found that when inhibitory-control demands were reduced by various means, 3.5- to 4-year-olds now succeeded at the tasks. However, children age 3 and younger performed only at chance. In an experiment by Setoh et al. (2016), for example, 2.5-year-old toddlers heard a low-inhibition story accompanied by a picture book: Emma found an apple in one of two containers, moved it to the other container, and then went outside to play with her ball; in her absence, her brother Ethan found the apple and took it away. Emma then returned to look for her apple. In the test trial, children were shown pictures of the two containers and were asked the test question, "Where will Emma look for her apple?" Because toddlers did not know the apple's actual location, the prepotent response triggered by the test question should have been weaker and hence easier to suppress. Nevertheless, toddlers performed only at chance.

The negative findings obtained with young children in low-inhibition elicited-prediction tasks were generally taken to constitute an important challenge for the one-system view (Devine and Hughes 2014; Wellman et al. 2001). Why was a reduction in inhibitory-control demands not sufficient to lead young children to express their false-belief understanding and perform above chance levels? Proponents of the two-system

view suggested that perhaps such a reduction could help only transitional children who were nearly 4 years of age and whose late-developing system was already beginning to emerge.

To address this challenge to the one-system view, Setoh et al. (2016) hypothesized that toddlers might have performed at chance in the low-inhibition Emma task described above because the *total amount of concurrent processing demands* in the tasks exceeded their limited information-processing resources, leading to random or confused responding. The task involved at least three processes: (a) *false-belief representation* (as the story unfolded, toddlers had to build and maintain a representation of Emma's false belief), (b) *response generation* (when asked the test question, children had to interpret it, hold it in mind, and generate a response), and (c) *inhibitory control* (toddlers had to inhibit the weak incorrect prepotent response triggered by the test question in order to tap their representation of Emma's false belief and generate the correct response). If toddlers failed because they were overwhelmed by the total amount of processing demands in the task, then they might succeed if this amount were lowered by *also* reducing response-generation demands via practice trials.

To test this prediction, Setoh et al. (2016) interspersed two practice trials among the story trials in the Emma task (Fig. 4). In one practice trial, children saw an apple and a banana and were asked, "Where is Emma's apple?"; in the other, they saw a ball and a Frisbee and were asked, "Where is Emma's ball?" In each case, toddlers were required to point to the matching picture. Note that these practice trials were not intended to support the false-belief-representation process: Pointing to the pictures of Emma's apple and ball was unlikely to help toddlers understand Emma's false belief about the apple's location. Rather, the practice trials were intended to support the response-generation process: They gave children practice interpreting a "where" question and producing a response by pointing to one of two pictures.

As predicted, toddlers now performed above chance in the test trial, pointing to the container

Emma falsely believed held her apple. In additional experiments, toddlers responded at chance when they received fewer than two practice trials or when they received two practice trials that did not match the test trial as closely (e.g., only one picture was shown in each practice trial), rendering them less effective at reducing response-generation demands. Finally, toddlers performed below chance when the practice trials were embedded in a high-inhibition false-belief story, thereby increasing inhibitory-control demands.

Based on these results, Setoh et al. (2016) concluded that there are at least two reasons why young children may fail at an elicited-prediction task. On the one hand, they may lack sufficient skill at one of the processes involved in the task; for example, they may lack sufficient inhibitory-control skill to suppress their own knowledge or resist "the pull of the real." On the other hand, they may be able to execute each process separately but lack sufficient information-processing resources to handle the total processing demands of the task.

Together, the results reported in this section thus provide strong support for the one-system view and for the claim that early failures at elicited-prediction tasks stem from limitations in young children's ability to cope with these tasks' processing demands, rather than limitations in their ability to understand false beliefs.

Conclusion

The results reviewed in this article suggest two broad conclusions. First, false-belief understanding emerges early in life, as evidenced by the converging demonstrations from spontaneous-response tasks, elicited-intervention tasks, and elicited-prediction tasks with reduced processing demands. Second, it is only by considering the full range of processing demands associated with each false-belief task that researchers can make sense of divergent findings within and across types of tasks.

These conclusions do not support the long-standing view of false-belief understanding as a major milestone in the development of

Story trial-1		“This is a story about a girl named Emma. Look! There’s Emma!”
Story trial-2		“Emma finds an apple in a bowl. in a bowl.”
First practice trial		<i>“Where is Emma’s apple?”</i>
Story trial-3		“Emma puts her apple in a box for later.”
Story trial-4		“Then she goes outside to play with a ball.”
Second practice trial		<i>“Where is Emma’s ball?”</i>
Story trial-5		“When Emma is gone, her brother Ethan finds the apple and takes it away.”
Story trial-6		“Emma is hungry. She comes in to look for her apple.”
Test trial		<i>“Where will Emma look for her apple?”</i>

False Beliefs, Fig. 4 In the task of Setoh et al. (2016), 2.5-year-olds faced a large picture book and heard a low-inhibition false-belief story. The story introduced Emma (trial 1), who found an apple in one of two containers on a table: a bowl covered with a towel and a lidded box (trial 2). Emma moved her apple to the other container (trial 3), and then she went outside to play with her ball (trial 4). In her absence, her brother Ethan found the apple

and took it away (trial 5). Emma then returned to look for her apple (trial 6). In the test trial, children saw pictures of the bowl and box and were asked, “Where will Emma look for her apple?” To reduce response-generation demands, two practice trials were interspersed among the story trials. In each practice trial, children saw two pictures and were asked a question that required them to point to one of them (i.e., “Where is Emma’s apple/ball?”)

psychological reasoning, which is not attained until the preschool years. Nevertheless, it may still be the case that humans' capacity for reasoning about false beliefs and other counterfactual mental states plays an important role in everyday social cognition. Many years ago, Leslie (1987) argued that pretend beliefs and false beliefs are fundamentally similar and that as infants have no difficulty understanding the former (e.g., in pretend play activities), performance factors must limit their ability to understand the latter. Building on the notion that pretense and false-belief understanding are closely related, Baillargeon et al. (2013) suggested that one critical function of counterfactual-state reasoning in daily life may be that it allows humans to understand and produce *social acting*, the well-intentioned social pretense that helps maintain positivity within social groups. Of course, counterfactual-state reasoning also makes possible strategic deception in competitive interactions, which infants also understand (Scott et al. 2015). According to the social-acting hypothesis, however, it is in the routine, everyday practice of social acting in cooperative interactions that humans make the most use of their capacity for holding in mind distinct representations of reality. White lies, tactful omissions, feigned interest, shows of loyalty where individuals publicly endorse opinions that diverge from their own – all of these require individuals to decouple what they privately think or feel from what they choose to communicate to others. As investigations of early social cognition are now expanding to include sociomoral reasoning, future research will be able to shed light more broadly on the various ways in which infants' abstract and early-emerging capacity for understanding false beliefs and other counterfactual states contributes to their social world.

Cross-References

- ▶ [Does the Chimpanzee Have Theory of Mind?](#)
- ▶ [False-Belief Test, The](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)
- ▶ [Theory of Mind and Nonhuman Intelligence](#)

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False Negatives

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Error management theory was proposed to explain the evolution of cognitive biases, particularly errors in judgment (Haselton and Buss 2000). One type of error is known as a false negative (also referred to as a type II error), which is when a person believes “not X,” when X is true, or is cognitively unable to perceive an effect where one exists. A commonly cited example of a false-negative error is thinking an object is something other than a snake, when it is a snake. People are not prone to making this type of mistake because it would have been costly relative to the other type of mistake of thinking an object is a snake when it is not. This latter error, referred to as a false positive or a type I error, is not as costly, and so according to error management theory, we have evolved a tendency to make this error.

False negatives are not always more costly than false positives. For example, in ancestral environments, abandonment from an intimate partner may impose costs toward their offspring, due to lack of resources and protection, and so women's careful attention to selecting a mate who is committed and resourceful is important. It would therefore be adaptive for women to under-perceive a prospective mate's potential commitment (type II error or false negative – believe a person is not committed when they are), since this error would have been less costly than believing the person will be a committed partner when he is not (type I error or false positive). Erring toward false negatives would allow women to be more judicious in choosing a mate by selecting a mate with the strongest potential for long-term commitment. There is still a cost to such decisions, which is ruling out potential mates who were genuinely interested in commitment. Still, for women, erring on caution is theoretically less costly than under-inferring commitment interest. Empirical evidence supports the hypothesis that women are more prone to showing false negatives when

predicting partner commitment (Haselton and Buss 2000; Henningsen and Henningsen 2010).

Generally, according to error management theory, people may have evolved a proneness to making false negatives if making such an error minimized costs and maximized benefits relative to false positives (Johnson et al. 2013).

Cross-References

- [Error Management Theory](#)
- [False Positives](#)

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False Perceptions

- [False Beliefs](#)

False Positives

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Error management theory is a middle-level evolutionary theory that was proposed to explain cognitive biases, particularly systematic errors

in judgment (see Haselton and Buss 2000; ► [“Error Management Theory”](#) entry). One type of error people can make when the outcome is uncertain is a false positive (or type I error), which is when there is a belief in X when X is not true. People may be biased toward making this type of error if it is not as costly as the alternative error, known as a false negative (or type II error), which is when there is a belief in “not X” when X is true (Haselton and Nettle 2006).

A commonly cited example of a false positive is the male sexual overperception bias (see [“Male Sexual Overperception Bias”](#) entry). When determining a possible mate’s sexual interest, a false-positive error would be made if one were to perceive a potential partner as sexually interested when they are not sexually interested. Alternatively, a false negative would be perceiving a potential partner as not sexually interested when they are (Haselton and Buss 2000). Among men, due to having lower minimal obligatory parental investment, there is a greater cost to making a false negative (thinking there is sexual disinterest when there is), so Haselton and Buss hypothesized that men’s proneness to assume sexual interest, even if it leads to more false positives, is adaptive. That is, it would be more beneficial for a male to make the false-positive error than it would for him to make the false-negative error since the costs of losing face or being rejected are lower than the costs of losing the potential mate. Empirically, data support the notion that men are more prone to making this type of false positive (Haselton and Buss 2000), and researchers are now studying factors that may moderate these effects (Perilloux et al. 2012).

The logic from error management theory applies to how we engineer some products. For example, fire alarms are designed to be more prone to making false alarms (detecting a fire when there is no fire), because it would be very costly to make the other type of error (not detecting a fire when there is one). Even though there may be some costs to making a false-positive error, such as inconvenience or lost time, this cost is minimal compared to the costs of a false negative, which includes injury or even death.

Generally, according to error management theory, people may have evolved a proneness to making false positives if making such an error minimized costs and maximized benefits relative to false negatives (Johnson et al. 2013).

Cross-References

- [Error Management Theory](#)
- [False Negatives](#)

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False-Belief Test, The

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Synonyms

[The Sally-Anne test](#)

Definition

An influential experimental paradigm designed to assess whether an individual possesses a theory of mind, based on his or her ability (or lack thereof) to attribute false beliefs to others.

Introduction

Since the late 1970s and early 1980s, the false-belief test has played pivotal roles in both developmental psychology and comparative psychology. In both fields, it has long functioned as a litmus test for assessing the presence and development of a theory of mind in human infants and great apes.

In developmental psychology, the standard method for conducting this test is widely referred to as the Sally-Anne test. Experimental data has been largely consistent insofar as the majority of children under the age of four – along with most autistic children (Baron-Cohen et al. 1985) – fail this test, while children between the ages of four and five reliably pass it (Gopnik and Astington 1988). As a result, it has long been the opinion of psychologists that normally developing children undergo a fundamental change in their cognitive abilities between the ages of four and five (Baillargeon et al. 2010). This shift is widely attributed to the emergence of a *theory of mind*, namely, the ability to attribute mental states such as beliefs, knowledge, and intentions to oneself and to others. In the twenty-first century, the value of the false-belief test to assess mind reading abilities has been widely challenged.

In comparative psychology, variations on the false-belief test have been conducted on great apes (see Krachun et al. (2010) for a review). Despite a wealth of evidence from other experimental paradigms suggesting that chimpanzees possess a theory of mind (see Call and Tomasello (2008) for a review), chimpanzees consistently fail false-belief tests. As in developmental psychology, many twenty-first-century scholars of animal cognition have questioned the value of these findings (e.g., Andrews 2015).

The Sally-Anne Test

In the standard Sally-Anne test, children are first introduced to two dolls named Sally and Anne. They are then told a simple story involving these

characters as it is simultaneously being acted out with the puppets. In this story, Sally hides a toy or treat in a box while both dolls are present and then leaves the stage. When Sally is gone, Anne then moves the desirable object from its original location to another box. Sally then returns to the scene and the infant test subject is asked, “Where will Sally look for the treat?” When the children being tested are 4–5 years old, they answer the question correctly: Sally will look in the original box. These children will also provide explanations for why Sally will *not* look in the box to which the treat has been moved. However, when children under the age of four – as well as autistic children more generally – are asked the same question, they nearly always answer incorrectly: they say that Sally will look in the new location where the treat actually is.

The common explanation for these findings is that sometime around the age of four, normally developing children begin to demonstrate an understanding of the concept of *belief* as well as the ability to apply this concept to the minds of others in order to predict their behavior. In other words, by demonstrating the ability to attribute mental states to others, children around this age are thought to have developed a theory of mind that is lacking in younger children.

The False-Belief Test in Comparative Psychology

Since the publication of Premack and Woodruff’s (1978) seminal paper, “Does the Chimpanzee Have a Theory of Mind?” the false-belief test has played an important role in the philosophy and science of animal cognition. Through a series of ingenious experiments, Premack and Woodruff concluded that an adult chimpanzee did, in fact, possess the ability to attribute mental states to others. The critical commentary for this paper proved to be extensive and highly productive for the future of work in comparative psychology. Among the most influential responses suggested that since complementary non-mind reading explanations

were possible to explain the chimpanzee’s behavior, an alternative false-belief experiment would be a far more convincing indication of theory of mind in a nonhuman species (e.g., Harman 1978).

Over the past several decades, there have been various attempts to modify the Sally-Anne test to accommodate the ecological differences between humans and chimpanzees; chimpanzees have repeated failed competitive and cooperative variations on this test (see Krachun et al. (2010) for a review). Some have taken these findings as evidence that while chimpanzees may possess a “minimal theory of mind” in the sense of attributing goals and intentions to others, humans alone possess the ability to attribute mental states such as beliefs and knowledge (Call and Tomasello 2008).

Contemporary Resistance to the False-Belief Test

In the twenty-first century, various criticisms of the false-belief test emerged that have challenged its capacity – particularly in its standard “Sally-Anne” form – to effectively test for theory of mind abilities. In an influential paper, Paul Bloom and Tim German present two reasons for why the ability to pass a false-belief test is neither necessary nor sufficient to demonstrate the capacity to attribute mental states to others (Bloom and German 2000). First, they argue that there is no reason for why one cannot at the same time possess a theory of mind in the sense of attributing beliefs to others, while likewise failing to explicitly reason about *false* beliefs. It may well be the case, they claimed, that children are attuned to the mental states of others well before being able to pass a Sally-Anne test. On this view, false-belief tests merely demonstrate that children ages four and above are able to express *in language* that which they understand much earlier in their socio-cognitive development.

This conjecture leads to the second of Bloom and German’s criticisms: that the standard Sally-Anne test actually evaluates the presence of various *non-mind* reading capacities, such as

linguistic proficiency, response inhibition, and improved memory for understanding narratives, rather than those necessarily tied to theory of mind. To this point, Kristine Onishi and Renée Baillargeon (2005) published a powerful argument suggesting that the false-belief tests place unfair cognitive demands on infants younger than 4 years old. In their *nonlinguistic* variation on the test, which relied on anticipatory looking and violation-of-expectation paradigms, Onishi and Baillargeon produced results suggesting an intuitive understanding of false beliefs in children as young as 15 months old.

With respect to the value of the false-belief test in contemporary autism research, a growing number of psychologists have likewise become skeptical of the extent of its importance (e.g., Tager-Flusberg 2007). One reason for this is that in most false-belief tests conducted on autistic children, several of these individuals *do* pass the test. One potential reason for this disparity could be, as noted above, that issues related to language development may function as confounding variables when conducting Sally-Anne-style tests on autistic children.

In terms of animal cognition research, Kristin Andrews (2015: 144) has likewise argued that since “there are possible non-mentalistic heuristics that could be applied in order to pass the test,” contemporary primatologists and philosophers should not place so much emphasis on the value of false-belief tests in comparing the cognitive abilities of apes and human infants.

Conclusion

The false-belief test has played a pivotal role in theory of mind research in both developmental and comparative psychology over the past 30 years. Although the standard false-belief test has been challenged from various angles in both fields, and while nonlinguistic false-belief tests have become increasingly popular, debates continue with respect to the most scientifically responsible interpretations of their results.

Cross-References

- [Autism](#)
- [Does the Chimpanzee Have Theory of Mind?](#)
- [Theory of Mind](#)

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Falsifiability

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Synonyms

[Empirical](#); [Scientific](#); [Testable](#)

Definition

Definition of falsifiable: a property of a theory such that one can conduct an empirical study that will show the theory is false if it is actually false.

Scientific theories are models for making predictions about the world. These models can be evaluated based on how accurately they predict the aspects of the world they model: models that make accurate predictions gain credibility and models that make inaccurate predictions are discredited (or “falsified”). A theory is *falsifiable* if it is possible to specify the particular conditions under which that theory would be shown to be false. If an idea is *unfalsifiable*, it makes no specific predictions, and it is impossible to test such an idea. Falsifiability is, therefore, a necessary feature of scientific theories.

Evolutionary theories are sometimes accused of being unfalsifiable and, therefore, unscientific. Often, this concern is rooted in the assumption that evolutionary theories are proposals about historical events (i.e., whether something in the past happened or not), a proposal which makes no predictions that can be tested in the here and now. However, this is a misunderstanding of the nature of evolutionary theories and the ways they can be tested. Using the adaptationist program (see listing in this volume), theories generally propose that a feature of human nature is an adaptation to solve a particular adaptive problem or a by-product of an adaptation. Each of these alternatives makes direct predictions about characteristics the feature should have – either design features to solve the adaptive problem if it is an adaption or a lack of design features to solve the by-product function and better fit to the alternative adaptation if it is a by-product.

Consider, for example, the studies showing that people automatically encode the racial identity of others (e.g., Hewstone et al. 1991). Kurzban et al. (2001) note that the ability to travel long distances is evolutionarily recent, and so our hominid ancestors were exceedingly unlikely to ever encounter someone from a different race. Thus, there should be no expectation of cognitive machinery specially designed to encode race.

Keeping track of group membership, however, would have been very informative for predicting behavior and, therefore, highly fitness relevant for our hominid ancestors. Kurzban et al. proposed that encoding race is actually a by-product of adaptations for diagnosing and tracking coalition membership in a world where patterns of cooperation and competition frequently segregate along racial lines. This theory predicts that racial encoding should decrease or disappear when race is shown to be unrelated to patterns of cooperation and competition, and this was what these authors found. So, while this theory is premised on a pattern of natural selection that happened in the ancestral past, it is directly testable by investigating the design of human psychology in the here and now and is therefore a *falsifiable* scientific theory.

Conclusion

Like all scientific theories, evolutionary theories are generative of predictions that can be falsified (in principle) by empirical data. If a theory is not falsifiable, it is not a scientific theory.

Cross-References

- Adaptation
- Adaptationist Program, The
- By-product
- Empirical
- Evolutionary Theory

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Familial Disease

► Genetic Abnormalities

Familial Violence

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Synonyms

Child abuse; Domestic violence; Sibling violence

Definition

Physical, psychological, or sexual violence between parents, offspring, siblings, and partners within a kinship structure.

Introduction

Just as *Hamilton's rule* can be used to describe the weighing of evolutionary costs and benefits as applied to determining the likelihood of altruistic behavior among kin, it can similarly predict the likelihood of aggression between close relatives (Buss 1999). This violence is predicted through the variables of degrees of shared kinship and reproductive value (RV). These, in addition to the availability of resources necessary to survival, explain many present patterns of within-kin relationships.

Parent-Offspring Violence

Step-Parents

Research has supported the hypothesis that stepchildren are at a higher risk of abuse and homicide, a phenomenon coined the “Cinderella effect” (Daly and Wilson 1985). Further illustrating this pattern, among parents who have both

biologically related and unrelated children, stepchildren were significantly more likely to be victims of violence (Lightcap et al. 1982). For instance, Daly and Wilson (1985) compared 841 households with children ranging from 17 or younger and 99 abused children from a children's aid society in Hamilton, Ontario, Canada. Children living with just one biological or natural parent were approximately 40 times more likely to be physically abused, as compared to children living with both of their biological parents.

Biologically Related Parents

The parent-offspring conflict model (Trivers 1974) suggests that some conflicts between parents and their genetic offspring are a result of the child seeking more resources than the parent is willing or able to offer. The reproductive value of both the child and the parent are proposed as indicators of when this conflict may result in violence. The RV of a child is lowest in early life and increases with maturity. Other variables of a child's RV include quality of offspring and the resources held by parent, where a lack of either results in a lower overall value. For example, children are at a higher risk of abuse by parent when they exhibit illness or handicap in infancy and in the presence of a single parent with access to fewer resources (Lightcap et al. 1982; Daly and Wilson 1988). The decrease of parental RV with age suggests that a child would become more valuable to them as the parent becomes older, and this is reflective in the decrease of child abuse as the mother's age at childbirth increases (Daly and Wilson 1988).

Sibling Violence

Violence between stepsiblings, who share less genetic relatedness, occurs at rates significantly higher than between full siblings (Daly and Wilson 2000). When violence between siblings does occur, it can often be explained in terms of resource conflict, with potential benefits outweighing the cost of kin violence. This has been supported with, for instance, analyses of sibling conflicts over inheritance, money, and

land; the most often cited cause of serious sibling conflict (Daly and Wilson 1988).

Families facing economic challenges are also more likely to have higher rates of sibling violence. This goes back to the idea of resource conflict mentioned above (Daly and Wilson 1988). For example, Hardy (2001) found that “financial and business stresses, and any work transitions in the family, increase the likelihood of sibling violence” (p. 499). These stressors can increase the social isolation of the family, which fosters an environment where sibling violence is more likely to occur. Having boundaries between the family and outsiders (i.e., religious affiliations, etc.) is also responsible for contributing to higher rates of sibling violence.

Partner Violence

Much of violence against a partner can be explained by noting implications from the principal of male paternal uncertainty. Paternity uncertainty is the possibility that a putative father is not actually the biological father of a child. Through acts of mate guarding, the fertilization by a particular male can be better protected, a countermeasure against the risk of providing parental investment to a child fathered by a different individual (Wilson and Daly 1993). These tactics to limit partner autonomy and secure paternity have been associated with men’s violence against romantic partners. (Buss et al. 2008). Consistent with this pattern, women of reproductive age are much more likely than older women to be victims of domestic abuse (Peters et al. 2002). These findings support an interpretation that sexual jealousy-fueled violence is not itself an adaption but instead is often the byproduct of mating strategies.

Conclusion

Instances of violence can occur between individuals that are genetically related, non-genetically related and involved in domestic relationships. These types of violence incidents are usually the result of many different aspects influencing

whether individuals are more likely to be altruistic or aggressive toward one another. For example, individuals that are genetically related are more likely to be altruistic to one another, while non-genetically related individuals are more likely to experience higher rates of abuse. Another important factor is the availability of resources and how that influences the pattern within the different types of relationships. In conclusion, there are many different factors that influence the nature of relationships and potential acts of violence within them.

Cross-References

- ▶ [Cinderella Effect, The](#)
- ▶ [Martin Daly and Margo Wilson \(Founders of Evolutionary Psychology\)](#)

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Familiarity-Based Kin Recognition

► [Helping and Genetic Relatedness](#)

Familiarization

► [Habituation](#)

Familicide

► [Filicide](#)

Family

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Synonyms

[Kin](#); [Kinship](#); [Relatives](#)

Definition

People who are related by descent (including adoption) and marriage.

Introduction

In every human society, people identify certain others as family. These social relationships are an important part of people's lives, with family (or descent) groups being the main unit of social organization in many societies. While kinship is a human universal, norms about who is

considered family, and the expectations and obligations of family members vary cross-culturally. Family tends to include those related by descent and marriage. Kin are typically categorized as *consanguineal*, meaning related by descent, or *affinal*, meaning related by marriage. Given that humans are a social species, family relationships influence many aspects of people's lives.

Evolutionary Perspectives

When examining family from an evolutionary perspective, researchers tend to focus on those individuals who are biologically related. This is because help to kin, and its amount, can be predicted from the inclusive fitness benefits of helping behavior. In other words, an individual can propagate one's genes not solely through direct reproduction but through helping individuals who share the same genes. Hamilton's rule states mathematically when we expect biological kin to help. It specifies that kin should help one another when the benefit to the recipient (B), devalued by the probability that the individuals share a gene by common descent (r) is greater than the cost (C) to the individual providing the benefit ($B \cdot r > C$) (Hamilton 1964). Costs and benefits should be conceptualized as reproductive success gained or lost, but such measures are nearly impossible to calculate in humans. There is substantial evidence showing that kin provide help to one another and that individuals are more likely to help closely related kin than distantly related kin, both in humans and in other species.

Evolutionary theory has a harder time explaining help among family members that are not biologically related, although this helping behavior clearly occurs. One of the main avenues for creating such kin ties among unrelated individuals in humans is marriage. There is some evidence that people's helping behavior towards affines follows similar patterns as those for genetically related individuals (Burton-Chellaw and Dunbar 2011), even though other mechanisms must be at work. Helping which cannot produce inclusive fitness benefits has been explained via other mechanisms such as reciprocal altruism,

indirect reciprocity, norm enforcement, or increased reputation through “showing off.” One of the most impressive forms of nonbiological kin helping is that of adoption, where individuals provide extensive parental investment to unrelated offspring (and offspring are unlikely to ever “repay” their adoptive parents). This type of behavior cannot be explained via reciprocal altruism or other mechanisms and may be purely altruistic. Evolutionary explanations for adoption include reducing social stigma associated with not reproducing (where, in some societies, social status is mainly achieved through one’s reproduction) or the adaptive desire to parent being co-opted for care of nonbiologically related individuals. Empirical studies have compared parental investment of adopted versus biological children and found mixed results. Evidence from an American sample showed adopted children receive *more* investment than biological children counter to predictions by kin selection theory (Gibson 2009). This may be partially explained by the more negative outcomes experienced by adopted children and suggests a greater need for investment by adopted children than biological ones. In contrast, data from Oceania suggests that adopted children (who tend to be related but less so than offspring) tend to receive less land inheritance than biological offspring (Silk 1980). There may be inherent differences between investment patterns of parents who seek out and invest significant time and money to adopt versus those who do not.

Humans as Cooperative Breeders

Given that human females *need* help from others to raise multiple dependent offspring, Hrdy has proposed that humans are cooperative breeders (2005). In most nonhuman ape species, females raise offspring without help from others and those offspring are independent food producers once they are weaned. This is in a sharp contrast to human children, who at the age of weaning still have many years of food dependence. Estimates suggest that children may not produce as much food as they consume until

15–20 years of age (Kaplan 1994; Lee and Kramer 2002). Given the unique human life history of short birth intervals and a long period of dependence, individuals other than the mother, including fathers, grandparents, older siblings, other kin, and even unrelated individuals help to raise children. While the help received allows women to have faster reproductive rates, it is necessarily balanced by more time in non-reproductive stages allowing both juveniles and post-reproductive women to help raise reproductive-aged women’s offspring.

Kin Conflict

While there is a wealth of evidence documenting the cooperation that exists between kin, there is also significant conflict. We expect conflict to occur since individuals (other than identical twins) are more related to themselves than to their kin. This can result in conflicts between mothers and offspring, siblings, pair-bonded parents (who may not be related at all, but have a common interest in their joint offspring), among others. Intergenerational conflict models have also been developed to potentially explain human life history characteristics like menopause and age at first birth. These models assume reproductive conflict – where limited resources result in competition among kin to reproduce. By examining how much each individual has to lose (genetically) by not reproducing, these models argue that the individual with *more to lose* reproductively will be likely to win these conflicts. For example, Cant and Johnstone (2008) show that under conditions of reproductive conflict and patrilocal post-marital residence, models predict that daughters-in-law have “more to lose” genetically and will therefore reproduce, while their mothers-in-law will opt to stop reproducing, possibly leading to menopause. There may also be kin conflict that occurs at the community level, where individuals who do not migrate (given sex-biased dispersal patterns) are less likely to compete since their local competitors will be kin. These models have been developed to explain behavior in both human and nonhuman species.

Role of Family Structure on Pubertal Timing

Extensive research has examined how early life events and family structure may influence a person's transition to adulthood (indicated by age at puberty), reproductive timing, and reproductive rate. These studies conceptualize reproductive outcomes as markers of an individual's reproductive strategy. Empirical results show (particularly in high-income societies) that girls who grow up without their biological father in the household (typically the result of parental divorce) tend to have earlier age at menarche (Webster et al. 2014). These empirical findings may be the result of individuals using cues of their environmental harshness and uncertainty to accelerate their reproductive careers to maximize reproductive success, given a high-risk environment (Ellis et al. 2009), focusing their reproductive careers to a time when they can expect to have the most help from their main alloparent – their mothers (Geronimus 2003), or an outcome of intergenerational kin conflict. Under conditions of reproductive conflict between mothers and daughters, if daughters expect their mothers to produce full-siblings (because their biological parents remain pairbonded), daughters may opt to delay reproduction and instead act as an alloparent to a full-sibling (since an individual is equally related to an offspring as a full-sibling). Based on the model, daughters should be less willing to delay reproduction if their mothers will produce half-siblings, since these siblings will be related by only half as much (Moya and Sear 2014). Future research should attempt to test these different theoretical underpinnings of the empirical finding that family structure in high-wealth countries influences menarcheal timing.

Conclusion

Family is considered important in all human societies. While evolutionary researchers tend to focus on biological relatedness, human kinship also includes individuals who are not biologically

related. Empirical research has demonstrated the role of biological relatedness in predicting helping behavior, but less is known about patterns of help among nonbiological family members. Some research has examined differences in investment among biological and nonbiological offspring, showing that in some contexts, nonbiological offspring receive at least as much (or more) investment than biological offspring, counter to evolutionary predictions. While kin cooperation is evident, it is also important to recognize and understand kin conflict that can occur at dyadic, family, and community-levels. Finally, understanding the different theoretical frameworks by which kinship influences human behavior and life history allows for different predictions to explain similar empirical phenomenon.

Cross-References

- Adoption Preferences
- Consolidating Familial Power
- Father Absence
- Forms of Adoption
- Function of Adoption
- Hamilton's Rule
- Inclusive Fitness
- Kin Elders Encourage Youth to Cooperate
- Kin Selection
- Kinship
- Kinship and Emotional Closeness
- Life History Strategies
- Life History Theory
- Parent-Offspring Conflict
- Sexual Conflict Theory

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Family Constellation

- [Birth Order](#)

Family Literacy

- [Language Acquisition in the Home](#)

Family of Orientation

- [Kinship and Emotional Closeness](#)

Family Order

- [Birth Order](#)
- [Frank Sulloway \(1996\) On Birth Order](#)

Family Order Effects

- [Birth Order and Parental Investment](#)

Family Planning

- [Contraception](#)

Family Relations

- [Kinship and Cortisol in Caribbean Village \(Flinn et al., 2005\)](#)

Family Relationships

- [Birth Order and Sibling Relationships](#)

Family Roles

- [Women's Personal Resources](#)

Family Size

- [Birth Order and Sibling Relationships](#)

Family Violence

- [Methods of Filicide](#)

Fantasy

- [Fiction](#)

Fantasy Aggression

- [Aggressive Fantasies](#)

Fantasy Violence

- [Aggressive Fantasies](#)

Fare

- [Diet](#)

Fast and Slow Strategies

- [Life History Strategies](#)

Fast Life-History Strategy

- [Psychopathy](#)

Fast Versus Slow Strategies

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Synonyms

[Life history strategies](#); [r/K-selection strategies](#)

Definition

Fast and slow life history strategies are predictable patterns in energy allocation that fall on a life history “continuum” of how organisms allocate their limited energetic resources between the competing demands of somatic development and reproduction so as to maximize fitness in their local ecology. Strategies with a bias in effort made towards somatic development are called *slow* life history strategies, while strategies with a bias in effort made towards reproduction are called *fast* life history strategies.

Introduction

Life history theory states that energy is inherently limited and that tradeoffs must be made in how energy is spent because organisms cannot simultaneously invest energy into multiple competing needs. Thus, organisms should make tradeoffs in allocations that best help to enhance fitness in their local ecology (Roff 1992). The predictable patterns of tradeoffs made across organisms’ lifespans can be thought of as falling on a spectrum, ranging from “fast” to “slow.” Strategies towards the fast end of the spectrum favor *quantity* of reproductive opportunities over quality, whereas slower strategies favor reproductive *quality* at the cost of quantity. There is variation in the type of life history strategy adopted (faster or slower), both between species but also within species. For example, while humans as a species err on the slower side of the life history strategy

Fast Versus Slow Strategies, Table 1 Contrasts between fast and slow life history strategies in humans

	<i>Fast strategy</i>	<i>Slow strategy</i>
Development and decision-making		
<i>Juvenile period</i>	Shorter	Prolonged
<i>Pubertal timing</i>	Earlier	Later
<i>Physiological aging</i>	Faster	Slower
<i>Reward orientation</i>	Riskier, more immediate rewards	Risk averse, delayed rewards
<i>Cooperation</i>	Low trust, low investment	High trust, high investment
Mating and parenting		
<i>Sexual debut</i>	Earlier	Later
<i>Age of first reproduction</i>	Earlier	Later
<i>Partner number</i>	Greater	Later
<i>Offspring number</i>	Greater	Fewer
<i>Romantic relationships</i>	Short-term orientation	Long-term orientation
<i>Offspring investment</i>	Lower	Higher

spectrum (e.g., a bias towards somatic effort), there is considerable variation within humans in life history strategy.

Two factors in the local ecology that calibrate organisms’ life history strategies are *harshness* and unpredictability. Environments that are harsh and unpredictable in nature tend to promote the adoption of faster life history strategies, where effort is made towards reproducing before succumbing to morbidity or mortality. Environments that are benign and predictable tend to favor the development of slower life history strategies, where effort is allocated towards growth and maintenance so as to maximize resource acquisition and offspring competitiveness (Ellis et al. 2009). Below, this article will summarize some of the empirically supported differences in fast versus slow strategists’ physiology and psychology (see Table 1 for a summary).

Development

Because organisms falling on the “faster” end of the life history continuum invest a great deal of effort in mating, they tend to experience shorter juvenile periods and earlier puberty than those pursuing a slower life history strategy. Faster life history strategies tend to favor investing less time in a juvenile period (e.g., childhood) by speeding up development to reach sexual maturity sooner because earlier

maturity enables organisms to begin reproducing earlier and more often than organisms that do not mature as quickly (Ellis 2004). Such shifts in development increase the chance that one will be able to successfully reproduce (and do so often enough to produce surviving offspring) before succumbing to morbidity or death in harsher environments (Roff 1992).

Mating

In addition to earlier pubertal timing, people (and organisms) that pursue a faster life history strategy tend to sexually debut earlier than individuals following slower life history strategies (Belsky et al. 1991). Further, faster strategists tend to have an earlier age of first reproduction and a greater number of lifetime sexual partners than slower strategists (Wilson and Daly 1997). Relatedly, research has found that slower strategists, who form longer-term pair bonds with fewer partners, are more selective when choosing prospective mates, with slower strategists (a) being more likely to engage in positive assortative mating and (b) being choosier about mating opportunities than faster strategists. Some research indicates that these looser pair bonds may be related to differences in attachment styles, with insecure attachment styles being represented at higher rates among people from harsh and unpredictable environments (Chisholm et al. 2005). It is

hypothesized that for faster strategists adopting such mating choices (e.g., looser pair bonds, less selectivity in mate choice, greater desire for variety) would favor having greater numbers of children with genetically diverse partners – an adaptation that would help to ensure some offspring will survive to reproductive age in a harsh and unpredictable environment (Ellis et al. 2009; Roff 1992).

Parenting

Life history theory predicts that individuals in harsh and unpredictable environments will favor having more offspring sooner because such *fast* strategies would favor the chance that (a) one will reproduce successfully before dying and (b) at least some of one's offspring will possess the genotypic or phenotypic qualities needed to survive in an uncertain future (Chisholm et al. 2005; Ellis et al. 2009). Having more offspring at an earlier age comes at the cost of being able to invest less in each individual offspring. However, in environments where future survival is more certain, it is more beneficial to reproduce later and in fewer numbers while investing more in the upbringing of each individual offspring (Roff 1992). People following faster life history strategies (e.g., those reared in more impoverished, dangerous regions) tend to have more children at an earlier age and have looser attachments to these children than people who have adapted slower strategies (Belsky et al. 1991; Wilson and Daly 1997). Faster strategists may be more prone to engaging in harsher (e.g., authoritarian), less consistent and sometimes “dysfunctional” child-rearing behaviors, which increase the chances that their children will also develop faster life history strategies (Belsky et al. 1991). Conversely, slower strategies are more likely to demonstrate affection for offspring, encourage achievement, and invest resources more heavily in their children. Finally, faster strategists may be more vulnerable to environmental stressors in adulthood, and thus are more likely to shift resources towards hastening reproduction in response to cues of harshness and uncertainty in adulthood than are

individuals from more benign environments (Griskevicius et al. 2011a).

Psychological Differences

Another way that differences between fast versus slow life history strategies may be conceptualized is by envisioning strategies as investments in present versus future mating effort. Faster strategists are more likely to adapt psychology and behaviors that favor more immediate reproduction, while slower strategists adapt those that favor later reproduction (Ellis et al. 2009). Future survival and reproduction are often uncertain for those pursuing faster strategies; thus, fast strategists tend to place a greater emphasis on the present, preferring more immediate rewards to holding out for rewards they might not live to reap. Research consistent with this hypothesis reveals that faster strategists tend to engage in more risky, gain-seeking behaviors, exhibit greater impulsivity, and are more likely to discount the future when evaluating rewards (Griskevicius et al. 2011b). Slower strategists, who hail from more certain environments, tend to be more risk averse and more forward thinking when evaluating both time horizon and reward options, which manifests in lowered risk taking and heightened ability to delay gratification. Such divergences are most pronounced in response to cues of harshness and uncertainty in adulthood and may be mediated by differences in perceived control.

In a related vein, the investment in immediate versus delayed reproduction may also manifest in the cooperative strategies that people pursue. For example, people pursuing faster life history strategies are more likely to engage in behaviors that are impulsive, rebellious, or deceitful in nature than slower strategists – behaviors that would favor immediate gains in resources for oneself but not the long-term preservation of coalitions with other people. On the other hand, slower strategists tended to place higher investment in close relationships, trusting individuals more and forgiving transgressions more often than those pursuing a faster strategy.

Health

Although earlier puberty offers an earlier chance for reproduction, research indicates that the shortened developmental period associated with faster life history strategies comes at the cost of building a more robust body for adulthood (Rickard et al. 2014). For example, the experience of psychosocial and physical stressors in early childhood (e.g., lower socioeconomic status, poor nutrition, abuse) have been linked to HPA axis dysregulation, a “pro-inflammatory” phenotype, and consequently higher risk of contracting heart disease, diabetes, and certain cancers, even in those who attain improved circumstances in adulthood (Miller et al. 2011). In short, although pursuing a fast life history strategy may lead to reproductive benefits in the short term, it may also be linked to chronic diseases and inflammation later in life.

Conclusion

The type of life history strategy that an individual adopts can have profound implications for one’s physiology, psychology, and reproductive outcomes. As such, life history theory represents a powerful predictive framework that can be used to predict individual differences in a wide range of traits and behaviors. Although both fast and slow strategies can both lead to long-term reproductive success in harsher versus more benign ecologies (Roff 1992), further investigation into the trade-offs that come with the pursuit of each strategy and their longer-term consequences for health and well-being represents an important area of future research. As such, greater application of life history theory with existing research paradigms in the fields of psychology, neuroscience, and medicine are integral.

Cross-References

- Fundamental Tradeoffs
- Life History Strategies
- Life History Theory

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Fat

- Body Reserves and Food Storage

Fat Man, The

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Synonyms

Footbridge; Man with backpack

Definition

The fat man is a variation of a choice in the moral dilemma called, “the trolley problem” where a fat, large, or man with a backpack can be pushed or dropped onto tracks to stop a trolley.

Introduction

The trolley problem is a moral dilemma used first by philosophers starting in 1967 and then adopted by psychologists to examine moral thinking in humans (Cathcart 2013). The original problem was made by Philippa Foot in a philosophical paper about abortion. The original problem was simply many variations of a scenario where someone had to make a choice of killing one to save five, one of which was switching a tram to a different track (1967). The current fat man variation is generally stated as such:

You are standing near a trolley track, there is a trolley heading down the track toward five workers who are unaware of the trolley and whom will die if nothing is done. There is a fat man next to you, large enough to stop the trolley if pushed onto the tracks; this will kill the fat man. Do you stop the trolley by pushing the fat man onto the tracks or let the trolley hit the five workers on the track (Cathcart 2013)?

The Fat Man

This moral dilemma has many variations including the fat man being a man with a large backpack instead, the man being on a separate track that the

trolley can be turned onto, the fat man and participant being above the track on a footbridge instead of next to the track, or that the fat man can be dropped through a trap door on the footbridge onto the track by pulling a lever (Cathcart 2013; Greene 2013).

From an evolutionary perspective, the fat man variation is good for analysis of moral and spatial thinking. For instance, people will rarely choose to push the fat man onto the tracks, but more people are willing to pull a lever to open a trap door dropping the fat man, and many more are willing to switch the trolley onto a different track killing only one instead of five (although this is still only 20 % of people; Greene 2013).

Joshua Greene, April Bleske-Rechek, and Peter Singer are examples of psychologists and philosophers whom have used an evolutionary perspective in their analysis of the dilemma regarding the fat man variation.

In Joshua Greene’s *Moral Tribes* (2013), Greene takes an in-depth evolutionary approach to the trolley problem and its many variations, with a large focus on the fat man variation, or in his synonymous version of the problem, “man with backpack.” Green explains that only 20 % of people are willing to push the man onto the tracks to save the five workmen. Pushing the man with a backpack or the fat man saves the most lives, but people have a negative emotional reaction to this. This negative reaction is reduced when the man is described as being on a separate track. When given this scenario involving a second track, known as the loop variant, 53 % (Bleske-Rechek et al. 2010) to 86 % (Greene 2013) of participants sacrificed the man – single man to save the five.

Both Greene (2013) and Singer (2005) argue that the reason for the variance in negative emotional reactions sacrificed the single man to save the fat man is based on innate moral responses or empathy, which is further affected by our spatial reasoning. Pushing the man onto the track is a personally direct action, whereas pulling a lever is an indirect and distant action. This empathy response makes pushing the fat man difficult, but pulling the lever an easier choice since the five and one share distance. Greene (2013) provided

support for this hypothesis when he gave the trolley problem to psychopaths/sociopaths, finding that they nearly all answered to push the man to save the five regardless of the personal distance involved.

Conclusion

The fat man variation of the trolley problem is used to understand moral thinking in humans. The fat man variant is the general situation in the trolley problem that involves dropping or pushing a man onto the tracks to stop the trolley as opposed to redirecting the trolley. The emotional response to not push the fat man is stronger when the man is younger, more related, or a potential mate, suggesting that moral reasoning varies according to context and the traits of the potential victim (Bleske-Rechek et al. 2010).

Cross-References

- [Loop Variant, The](#)
- [Morality](#)
- [Trolley Problem](#)
- [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)
- [Utilitarianism](#)

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Fatality

- [Death](#)

Father Absence

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Definition

The term “father absence” is generally taken to indicate that an individual has spent some or all of their childhood with a nonresident biological father. While this can be due to paternal death, the majority of research concentrates on cases of non-resident fathers who are separated from (or were never pair bonded with) the individual’s mother.

Introduction

Evolutionary research into the impacts of father absence on offspring has largely fallen into two camps, which one might roughly characterize as developmental psychology versus behavioral ecologically, respectively, and investigated two sets of outcomes: offspring reproductive outcomes and offspring condition.

Reproductive Development of Offspring

A considerable body of work has amassed investigating the reproductive outcomes of children (mainly daughters) of father-absent households in the West. Although interest in the links between father absence and girls’ sexual behavior dates back to developmental psychologist Marion Hetherington’s 1970 observation that daughters of divorced, but not widowed, mothers displayed elevated sexual behavior as teenagers, the more recent contribution of evolutionary research was,

at its core, to propose that early father absence (potentially among other stressors) may accelerate pubertal development and the onset of sexual behavior in daughters as a response to environments which were unstable and/or unlikely to support viable pair-bonds (Belsky et al. 1991; Draper and Harpending 1982). As such, maximizing reproductive success might best be achieved, for girls, by starting reproduction earlier.

Studies of the association between father absence and puberty in girls typically report father-absent girls experiencing first menses around 6–12 months earlier than their father-present counterparts. Webster et al. (2014) published a meta-analysis of this literature and reported a significant mean weighted association of $r = 0.14$ between father absence and earlier menarche. This suggests that approximately 5.6 % of variance in age of menarche may be explained by the presence or absence of the biological father from the home in early childhood. Alongside earlier menarche, father absence in Western samples is also typically associated with earlier sexual activity and earlier reproduction in women (e.g., Ellis et al. 2003; Boothroyd et al. 2013). The dominant current explanation for these phenomena focuses on the influence of stress on the maturation of the endocrine system (see, e.g., Ellis 2013). It is particularly in the context of this latter potential mechanism that father absence is posited as one among many potential stressors, and adaptive hypotheses center around the fitness benefits of either successfully predicting the harshness of the environment in which reproduction will take place (standard psychosocial acceleration models) or of responding appropriately to the effects of the current environment on one's own condition (internal prediction models: Rickard et al. 2014). The key factor from either perspective is that father absence may trigger earlier menarche and earlier reproduction as a means of maximizing reproductive success when faced, in some form, with harsh environments.

There has been less attention to the sequelae of father absence in boys. Although father-absent boys are more likely to go on to be absent fathers themselves (see, e.g., Jaffee et al. 2001), and to reproduce earlier in the West, the literature regarding timing of puberty in boys is sparse and the

results decidedly mixed, with some authors even finding father absence to predict later puberty in boys (e.g., Sheppard et al. 2015). Several authors have argued that a sex difference in responses to father absence is consistent with sex differences in predictors of reproductive success, with males perhaps benefiting most from building competitive advantage rather than accelerating reproduction in harsh and/or low-paternal-investment environments (see Draper and Harpending 1982; James et al. 2012).

Behavioral Ecology Approaches to Reproductive Development in Offspring

Behavioral ecology approaches to father absence have tended to concentrate on offspring outcomes in terms of survival and fertility, often with the primary goal of understanding drivers of parenting behavior, rather than drivers of child development. The remarkable feature of this particular literature is the extent to which father absence (or presence) often makes very little difference to offspring at all. In a wide-ranging systematic review, Sear and Coall (2011) found that, while among low-fertility samples (i.e., “WEIRD,” Western, educated, industrial, rich, democratic (Henrich et al. 2010)) the presence of fathers appeared to have an inhibitory effect on fertility (indexed by less teenage pregnancy, later first birth) as discussed above, fathers in high-fertility samples had a facilitatory or no effect on offspring fertility. Where there were significant associations, present/living fathers were typically associated with earlier first birth and a greater number of children born, the former of which is directly at odds with the data from Western samples. Perhaps the most likely explanation for these results is that in small-scale and high-fertility populations, the most critical contribution of secondary caregivers (as fathers tend to be) is to supplement the child's nutritional or social status in a manner which makes a much greater contribution to maturation and/or marriageability than any variation induced by psychosocial stressors. Indeed the simple fact that girls in WEIRD samples display considerably

earlier menarche than in small-scale societies suggests that considerable nutritional constraints on menarche have been lifted in the West and, as such, raises the question of how much these WEIRD samples can tell us about ancestral selection pressures on reproductive development.

Mortality and Morbidity Outcomes in Offspring

One factor which unites both the behavioral ecology and evolutionary developmental psychology approaches to father absence is an interest in how paternal care may influence offspring viability and condition. Indeed, as discussed above, one strand of developmental interest in father absence argues that earlier menarche in father-absent daughters is an adaptive response to the effects of adversity on the well-being of offspring. There are a number of large epidemiological studies in the West which find an association between parental divorce (usually synonymous with father absence in these data) and poorer adult health, shorter adult height, and shorter life expectancy in offspring (e.g., Maier and Lachman 2000; Schwartz et al. 1995; Sheppard et al. 2015). In some samples, the associations between family structure and later offspring outcomes were mediated by stressors inherent in, or other sequelae of, the separation (e.g., Maier and Lachman 2000), which is consistent with other evidence suggesting relational stress in childhood may be associated with health outcomes in later years.

Unlike the data regarding reproductive development, these associations are not limited to WEIRD samples. For instance, Flinn and England (1997) assessed the living conditions of children and adolescents living in a village in Dominica and took regular saliva samples (several times a day for multiple days) to assess their levels of cortisol (a stress-related hormone) and monitored children's health. The population they studied was matrilocal and the parenting conditions were very varied; half of children (approx. 54 %, averaging across 4 study seasons) were living with their mother and their biological or stepfather, while a further 12 % lived alone with a single parent. The

remainder of the children lived with mother and kin, grandparents, distant kin, or nonrelatives. Flinn and England found that children living without their biological father experienced significantly more days of illness and had significantly higher cortisol levels than those living with both parents (even if their father was often absent from the home, e.g., for work or after rows). They also found a moderate positive correlation (0.35) between levels of cortisol and self-reported days of illness, again supporting the suggestion that any impacts of father absence on offspring health are mediated by stress.

The impacts of father absence on *mortality* in preindustrial populations, however, are rather more ambiguous. While there are notable examples of father absence or death of father being associated with slightly higher offspring mortality in both anthropological and historical records, Sear and Coall (2011) found that in more than half of small-scale societies for which data were published, father loss (by death or absence) had no significant link with offspring survival.

Conclusion

Overall, these data suggest that father absence may sometimes be detrimental to offspring survival (and ergo adaptive benefits of long-term pair-bonds may certainly include greater reproductive success in some ecologies), but is perhaps more likely to impact on offspring condition. This may be mediated by stress, and while in WEIRD samples, daughters may be able to offset any loss of condition via accelerated reproductive development, there is no evidence that sons or non-WEIRD daughters do the same. The primary challenge facing the literature at the current time may be to comprehensively unite these diverse results in a single explanatory framework.

Cross-References

- [Absence Prior to Puberty](#)
- [Children Without Paternal Investment](#)
- [Ecology of Paternal Investment](#)

- Ecology of Pair-Bond Stability
- Father-Absence and Stepfather Presence
- Jay Belsky
- Life History Strategies
- Puberty
- Stress Reactivity

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Father Absence and Stress Reactivity

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Synonyms

Fatherlessness; Stress response system

Definition

The absence of a father during the formative childhood years.

The functioning of the stress response system in response to stressors.

Introduction

According to the Adaptive Calibration Model (ACM), an evolutionary theory of human development, early childhood environments shape an individual's stress responsivity in a functional manner in preparation for the anticipated social

and physical adult environment (Del Giudice et al. 2012). Although there are many factors that affect the relative stressfulness of childhood environments, one significant aspect is father absence. Unlike many mammals, humans generally engage in bi-parental rearing of children, with both the mother and father investing heavily in the development and survival of the offspring (Lovejoy 1981). Lack of paternal investment inherently engenders a stressful rearing environment marked by access to fewer resources, increased financial hardship, and less parental care for offspring. Indeed, children growing up in father absent homes are found to experience higher levels of anxiety, stress, and depression (Draper and Harpending 1982; Weinraub and Wolf 1983), as well as increased impulsivity, lower problem-solving abilities, poorer psychological adjustment, increased risks of incarceration and substance abuse, and for girls, a host of precocious sexual outcomes.

The Effect of Father Absence on the Stress Response System

The stress arising from father absence during childhood triggers calibration of the stress response system, known as the hypothalamic-pituitary-adrenal (HPA) axis. Stressful events activate the HPA axis, which leads to release of the hormone cortisol into the bloodstream. Chronic activation of the HPA axis, and hence high levels of cortisol, has a wide range of negative health effects, including downregulation of the immune system, increases in heart rate and blood pressure, reduction in metabolic processes, a reduction in growth, and a reduction in somatic resources to invest in reproduction (Segerstrom and Miller 2004). Children who grow up in father absent households or those characterized by unstable parental pair bonds exhibit highly abnormal cortisol levels, which has profound negative impacts on health (Flinn and England 1997). Although both boys and girls show increased stress reactivity in response to father absence, some research suggests that the male neuroendocrine response (compared to that of females) may be more

pronounced by paternal absence, with males exhibiting more abnormality in cortisol levels during childhood, adolescence, and continuing into adulthood (Flinn et al. 1996). While the neuroendocrine response to father absence is more marked in sons, there is much evidence indicating that father absence has a discernable impact on the life history of daughters as well.

The Effect of Father Absence on Reproductive Outcomes

According to paternal investment theory, paternal disengagement, especially in the early years of life, serves as a signal to daughters that the local mating ecology is one in which male investment is unreliable and unnecessary. For daughters of absent fathers, a robust body of evidence finds that father absence predicts earlier pubertal timing, earlier sexual debut, and earlier age at first reproduction (Ellis 2004; James et al. 2012). Consequently they also tend to have a higher number of sexual partners and lower expectations of investment in offspring by mates (Draper and Harpending 1982). Research indicates that father absence in females increases subsequent sexual risk taking, leading to risky promiscuous mating behavior, and also negatively influences the later family environment in which their offspring are reared (Quinlan and Flinn 2003). This mating behavior contributes to an intergenerational cycle of early calibration of father-absence-related stress reactivity and fast sexual strategies in single-mothers and their children.

Conclusion

In sum, father absence causes increased stress experienced during childhood, leading to heightened stress reactivity and precocious sexual behavior amongst daughters. It is important to note that calibration of the stress response system is adaptive for preparing the child for the ostensibly stressful adult environments to come. Because paternal presence and investment is vitally important during development, father absence during

childhood provides a cue that the environment is harsh and unstable. Therefore, it may be adaptive for individuals that experience father absence to develop a stress response system that would promote survival in such an environment and for women, encourage early reproduction of offspring.

Cross-References

- [Bruce J. Ellis](#)
- [Paternal Investment](#)
- [Stress Reactivity](#)

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Father of American Anthropology

- [Franz Boas](#)

Father Presence

- [Two-Parent Families](#)

Father Responsibility

- [Paternal Role](#)

Father's Father Versus Mother's Mother

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Synonyms

[Genetic relatedness](#); [Grandparental investment](#); [Investment in more certain kin](#); [Paternal grandfather versus maternal grandmother](#); [Paternity uncertainty](#); [Pattern of biased grandparental investment](#); [Relationship certainty](#)

Definition

Although all grandparents share an average of 25% of their genes with their grandchildren, they are not in an equal position relative to their

grandchildren. Due to paternity uncertainty, sex-specific reproductive strategies, and age, the unequal positions of the grandparents are most evident between a father's father and a mother's mother. A mother's mother is typically the most involved with her grandchild's life and a father's father is the least involved.

Introduction

Hamilton's rule predicts that individuals invest more in their close kin than in distant kin or nonkin when all else is equal (Hamilton 1964). Grandparents share approximately 25% of their genes with their grandchildren. Therefore, one may assume that different grandparent types (i.e., mother's mother, mother's father, father's mother, and father's father) invest nearly equally in their grandchildren. However, due to paternity uncertainty (or relationship certainty), all grandparents are not in an equal position relative to their grandchildren. In the case of grandparents, paternity uncertainty means that no uncertain links exist between a grandchild and the mother's mother. A mother's father and a father's mother have one kinship link with paternity uncertainty and a father's father is in the most uncertain position because he cannot be totally sure that he is related to his son and his son cannot be sure that he is related to his child. Therefore, fathers' fathers have two uncertain links of paternity and paternity uncertainty creates the most bias between a mother's mother and a father's father. Evolutionary theory predicts that because of paternity uncertainty, a mother's mother should invest the most in grandchildren and a father's father should invest the least.

Paternity uncertainty is closely related to sex-specific reproductive strategies. Sex-specific reproductive strategies derive from the fact that due to pregnancy and lactation, for example, a single offspring is more costly for women than for men, meaning that maternal investment is more obligatory than paternal investment, which can be facultative (Trivers 1972). Similarly, with paternity uncertainty, sex-specific reproductive strategies predict biases in grandparental

investment between grandmothers and grandfathers and between maternal lineage and paternal lineage.

Due to differences between men and women in the mean age at marriage and the mean age at first birth, maternal grandparents are usually younger than paternal grandparents and the age difference is the greatest between the mother's mother, who is likely to be the youngest of the grandparents, and the father's father who is likely to be the oldest (Strassmann and Garrard 2011). Therefore, in addition to paternity uncertainty and sex-specific reproductive strategies, grandparental age may also create biases between a mother's mother and a father's father. Grandchildren typically have the most shared years of life with their mother's mother and the least, if any, with their father's father.

Empirical Evidence

One of the most common findings in grandparent studies is that the mother's mother typically invests the most, followed by the mother's father and the father's mother, but the father's father usually invests the least (see Coall and Hertwig 2010 for review). This is consistent with the assumption predicted by paternity uncertainty. The pattern of biased grandparental investment tends to hold even in countries with no explicit preference for matri- or patrilineal family relations and when several potentially confounding variables are controlled for (Danielsbacka et al. 2011). Although age differences are evident between grandparents, especially between a mother's mother and a father's father, prior studies have shown that mothers' mothers invest the most in their grandchildren and fathers' father invest the least, even after the grandparental age is controlled for (Euler 2011). In addition, the pattern of biased grandparental investment is not limited only on grandparents' reports. Grandchildren and parents (i.e., the middle generation) typically assess the investment from the maternal grandmother to be the largest and from the paternal grandfather the smallest (Danielsbacka and Tanskanen 2012; Danielsbacka et al. 2015).

In addition, divorce and re-marriage in parental and in grandparental generations may further increase the bias between a mother's mother and a father's father because the negative effect of divorce on family relationships is usually stronger on fathers than on mothers (Euler 2011). Divorce can also occur in the grandparental generation and divorced grandfathers tend to have less contact with their grandchildren than married grandfathers, but divorce did not matter in grandmothers regarding their contact with their grandchildren (Danielsbacka and Tanskanen 2016).

Conclusion

The pattern of biased grandparental investment is widely studied in contemporary western societies. The most evident finding is the bias between a father's father and a mother's mother, which is realized in grandparental investment; a mother's mother typically invests the most and a father's father the least. In evolutionary psychology, the pattern and especially the difference between a mother's mother and a father's father is usually explained by paternity uncertainty and sex-specific reproductive strategies. In addition to the sex, lineage, and the degree of relationship certainty, the age difference between a mother's mother and a father's father typically favors the mother's mother, who is usually the youngest grandparent while the father's father is the oldest.

Cross-References

- [Grandparents and Grandchildren](#)
- [Maternal Grandmother Invests Most](#)
- [Paternal Grandfather Invests Least](#)

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Father-Absence and Stepfather Presence

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Synonyms

[Boar effect](#); [Novel male effect](#); [Socioendocrinology](#)

Definition

The term “Father-Absence and Stepfather Presence” refers to a familial situation in which an individual is reared in a household before puberty without the biological father present and with the presence of a genetically unrelated male adult.

Introduction

Life history theory suggests that organisms possess phenotypic plasticity for various life history traits as a function of ecological conditions. To enhance fitness, “decisions” must be made concerning the trade-off between present and future reproduction, between quantity and quality of offspring, and between mating and parenting effort (Kaplan and Gangestad 2005). Subsumed within life history theory are theories that posit that familial relations and parental investment (e.g., Draper and Harpending 1982) or a broader range of familial stressors including family composition (e.g., Belsky et al. 1991) prime certain female reproductive strategies such as the timing of puberty or menarche. More specifically, it has been proposed that early psychosocial stressors in the family environment characterized by conflict, divorce, insecure attachments, lack of supportive and positive relationships, and unpredictable resources lead to an accelerated developmental trajectory that results in an earlier pubertal maturation and initiation of sexual behavior. More stable and supportive family environments code for later puberty and sexual behavior (Belsky et al. 1991).

Father Absence

The most consistent socioendocrinological finding in the literature is the correlation between biological father absent (FA) and early menarche in girls (Ellis 2004; Moffitt et al. 1992; Romans et al. 2003; Surbey 1990), also verified in a recent meta-analysis (Webster et al. 2014). This effect has been found in both prospective longitudinal studies (Campbell and Udry 1995; Ellis and Garber 2000) and in large sample retrospective studies (Matchock and Susman 2006; Quinlan 2003; Surbey 1990), although a few studies have found no effect for father absence on age of menarche (Anderson 2015). Moreover, some studies have found that the longer the father has been absent from the home, the earlier the menarche (Moffitt et al. 1992; Surbey 1990).

Etiological explanations to explain the link between father absence and age of menarche include the psychosocial acceleration theory of Belsky et al. (1991), girls learn that the family environment is unstable and untrustworthy and accelerate puberty; parental investment theory, father investment is reduced in FA families, so girls mature early (Ellis 2004); genetic explanations, early maturing mothers possess genes that contribute to both early menarche and an earlier more unrestricted sociosexuality (or an X-linked androgen receptor gene in the father; see Comings et al. 2002); pheromonal explanations, Matchock and Susman (2006) and Ellis (2004) proposed that delaying menarche when reared next to biological fathers may be an anti-inbreeding strategy, perhaps mediated by inhibitory olfactory cues from the father.

Father Absence and Stepfather Presence

The effect of both FA and stepfather presence (SFP) on menarcheal age has not systematically examined in enough detail to provide a clear picture of this relationship. Many studies do not differentiate between FA and FA-SFP families, and sample sizes tend to be prohibitively small when FA girls are divided into FA and FA-SFP groups. There is also not a consensus on the evolutionary underpinnings for an effect of SFP on menarche. Ellis (2004) suggested that the presence of a stepfather in the household would be indicative of unstable parental relations and unreliable resources, thus directing girls toward an accelerated reproductive strategy. A natural extension of this logic would be to compare households in which the mother has a single stable long-term male pair-bond to households in which the mother has a series of short-term pair-bonds (many stepfathers), with presumably one stable stepfather delaying menarche and a series of stepfathers accelerating menarche (Ellis 2004). As yet, this has not been thoroughly examined in the literature. At the core of psychosocial acceleration and parental investment theories is the idea the SFP is stressful (e.g., because of increased conflict or reduced parental investment).

Glucocorticoid levels have been reported to be elevated in children with stepfathers (Flinn and England 1997), and cortisol levels increase near puberty as well (Barra et al. 2015). This is paradoxical, though, as stress is generally viewed as inhibitory on the hypothalamic-pituitary gonadal (HPG) axis because glucocorticoids (stress) disrupt the pulsatile release of GnRH (Whirledge and Cidlowski 2013), unless the relation between stress and the timing of pubertal development is curvilinear as suggested by Ellis (2004).

Another evolutionary approach is to view any putative effect of a stepfather on menarcheal age as being consistent with the “novel male effect” or the “boar effect” (Kirkwood and Hughes 1981; Izard 1983). Essentially, in a wide variety of mammalian species, introduction of a novel male to a social group of female conspecifics can induce an earlier puberty through the stimulatory effect of male pheromones (Colmenares and Gomendio 1988; Izard 1983). In addition to the direct benefits of mating with the new male, it has been suggested that early menarche or displayed signs of estrous in primates may convey a social advantage which would be to obtain the new leader’s support and ascend the social hierarchy. This new alliance would confer an advantage in female-female competition and thus change their social status, ultimately increasing total reproductive output (Colmenares and Gomendio 1988). In addition, maintenance in the natal group of genetically related conspecifics can delay puberty, presumably through pheromonal cues with the evolutionary advantage of preventing inbreeding (French et al. 1984). It has been hypothesized that FA (prevention of inbreeding) and FA-SFP (enhancement of breeding) could both be mediated by pheromonal cues to increase reproductive fitness (Ellis 2004; Matchock and Susman 2006).

In a longitudinal study of 87 FA girls, Ellis and Garber (2000) found that both familial/dyadic stress and stepfather presence (more so than biological father absence) each separately and significantly accounted for earlier pubertal maturation. Moreover, the younger the daughter at the time of the stepfather’s arrival, the earlier the menarche, but only when the mother-stepfather relationship was perceived as stressful by girls. This dose-

response relationship between duration of stepfather exposure and puberty is consistent with greater boar exposure in gilts leading to early puberty (Hughes and Siswadi 1997). In a retrospective study of over 10,000 participants, Quinlan (2003) also found that living with a stepfather was associated with reproductive development, but the duration of the stepfather exposure had no effect. Another longitudinal study of 71 girls also found that stepfather present in the household was a better predictor of earlier puberty than FA alone (Mekos et al. 1992).

Surbey (1990) in her sample of over 1200 girls found that girls with stepfathers present in the home experienced menarche almost two months earlier than FA girls without stepfathers, although this difference was not significant. Alvergne et al. (2008) asked 1200 women to report family composition during age ranges from 0–5, 5–10, and 10–15 years. The FA-SFP-father group had an earlier first sexual intercourse than the FA only group, but only for the 10–15-year time period; age of menarche was not significantly earlier for the FA-SFP group than the FA only group. Sheppard et al. (2014) used a very large, but older, sample of 16,207 participants from the Kinsey survey from 1938 to 1963. FA only and FA-SFP groups were associated with more accelerated life history outcomes than mother-absence households. FA and FA-SFP groups did not differ though. Adopted girls (Proos et al. 1991; Surbey 1990), girls who experience frequent residential relocations (Clutterbuck et al. 2015), and sexually abused girls (Mendle et al. 2016) also tend to have an earlier puberty, both of which are situations associated with putative exposure to unrelated adult males. Finally, the fact that mother-absence girls usually do not experience early puberty (Surbey 1990) would seem to argue against psychosocial and parental investment theories.

However, other studies with relatively large (Bogaert 2005; Matchock and Susman 2006) and small (Hoier 2003) sample sizes have found that having a stepfather in the household did not predict early menarche, independent of father absence alone. Moreover, Mendle et al. (2006) used a genetic “children-of-twins approach” to decouple genetic factors from environmental

factors such as FA and stepfathers. That is, rather than comparing children with stepfathers to an unrelated group of children without stepfathers, the offspring of twin parents discordant for having a stepfather for their children were analyzed. Results indicated that girls raised with stepfathers had menarche approximately 6 months earlier than girls raised without stepfathers. However, when genetic controls were implemented, this effect was significantly attenuated, as the presence of a step-uncle was just as predictive of early menarche as the presence of a stepfather. The offspring of female twins discordant for having a stepfather in the home were equally at risk for early menarche. These data suggest a genetic causal mechanism or perhaps a shared environment confound (e.g., frequent visits by the step-uncle).

Conclusion

Taken together, research suggests that living without a biological father and with a stepfather may be a risk factor for early menarche. The specific biological mechanisms that mediate this relationship have not been fully elucidated yet, nor is there a well-accepted explanatory evolutionary theory. More well-designed studies are needed comparing FA to FA-SFP girls that examine the duration of the stepfather exposure and stepfather-daughter dynamics, including studies that disentangle genetic and environmental factors.

Cross-References

- [Father Absence](#)
- [Life History Strategies](#)
- [Puberty](#)

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Fatherhood

► Paternal Investment

Fatherlessness

► Father Absence and Stress Reactivity

FBO

► Fraternal Birth Order, The

Fear

► Anxiety Disorders

► Correlates of Fear

Fear Affords Protection

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Definition

“Fear affords protection” refers to the evolutionary function of fear as an emotion, which is at root a form of protection or an early warning system

against potentially serious threats. Fear itself has been defined as the “usually unpleasant feeling that arises as a normal response to realistic danger” (Marks 1987, 5). As was explained as early as 1704: “Fear . . . is a disturbance of mind proceeding from an apprehension of an approaching evil, threatening destruction or very great trouble either to us or ours” (Dennis 2000 [1704], 101). In its safe, narrative-generated form (e.g., in terror fiction such as horror novels or films), fear – and the adrenaline rush often associated with it – can become addictive (McCarty 1994, viii). This is because “beside lust and anger . . . [fear is] one of the three most exciting emotions of which our nature is susceptible” (James 1891, 2: 415).

As a very strong emotion, fear serves to alert an animal to any potential dangers, such as from a variety of attacking predators or any looming environmental dangers (e.g., cliff edges or jagged rocks), so as to effectively prepare for rapid action and/or to undertake the required behavior in order to have a better chance of remaining safe (Barrett 2005; Scalise Sugiyama 2006). For example, fear enables various animal response behaviors such as: quickly escaping by the safest route, defense upon imminent attack, freezing if this might assist in predator avoidance, or submitting to an attacker if this may yield a better chance of survival, for example, in intraspecies conflicts (Buss 2004, 91). The protective response of humans freezing in response to the fear generated by an individual suddenly glimpsing “the merciless teeth of Wolves” was noted as far back as the seventeenth century (Brown 1672, 134).

Fear also produces specific physiological and chemical responses, such as epinephrine being released, the heart rate speeding up or slowing down, and increased blood flow to the muscles, all of which assist in the fighting or fleeing behaviors that may be needed in order to survive the approaching danger. As an emotion, fear topped a recent psychologists’ chart of the top ten basic emotions (Parkinson 1994, 488).

Darwin on Fear

Pioneering scientific work on understanding the nature of fear as an emotion, and some associated predatory behaviors, was undertaken by Charles

Darwin. For example, he was particularly interested in “monstrous” or carnivorous plants and conducted his own experiments on how these carnivorous plants absorbed different types of animal flesh as forms of captured prey (Darwin 1875). He also took a stuffed snake to a monkey house in order to test the fear responses of different types of monkey (Darwin 1874 [1871], 72). Darwin was interested in fear as an emotion as part of his wider evolutionary approach to understanding animal behavior.

In *The Descent of Man*, he explained that terror as an emotion caused “the muscles to tremble, the heart to palpitate, the sphincters to be relaxed, and the hair to stand on end” (Darwin 1874 [1871], 69). Although such associations are now sometimes seen as literary clichés, this does not mean that they are entirely inaccurate from a physiological perspective. The physiological changes that are now known to be affected by fear include: blood leaving the digestive tract and rushing to the periphery of the body; the adrenalin level spikes; the heart rate changes, either upwards for fleeing or downwards for freezing; and instruction to various parts of the musculature are sent (Tooby and Cosmides 2005, 54).

In *The Expression of the Emotions in Animals and Man*, Darwin provided a more detailed account: horror was accompanied by the body turning away, or the arms being violently protruded, or the raising of the shoulders, and a shudder and a deep expiration or inspiration (Darwin 1999 [1872], 308). He accounted for the biological function of the physiological reflexes associated with fear and horror as follows:

Some of the signs may be accounted for through the principles of habit, association, and inheritance – such as the wide opening of the mouth and eyes, with upraised eyebrows, so as to see as quickly as possible all around us, and to hear distinctly whatever sound may reach our ears. For we have thus habitually prepared ourselves to discover and encounter any danger . . . Men, during numberless generations, have endeavoured to escape from their enemies or danger by headlong flight, or by violently struggling with them; and such great exertions will have caused the heart to beat rapidly, the breathing to be hurried, the chest to heave . . . And now, whenever the emotion of fear is strongly felt, though it may not lead to any exertion, the same results tend to reappear (Ibid., 308–309).

The underlying principle that was expressed in this paragraph is still valid: the emotions of terror and horror have evolved in direct response to the threats to human life that were represented by animal predators and other human competitors.

Sometime later, in “A Biographical Sketch of an Infant,” he reported that: “*Fear*. – This feeling probably is one of the earliest which is experienced by infants,” as was demonstrated by young children exhibiting startled reactions to any sudden sounds from a very early age, from when they were only a few weeks old (Darwin 1977 [1877], 194). For Darwin, this clearly demonstrated that the fears of young children were independent of learning/experience, and instead were actually instinctual responses to common dangers encountered during the environment of evolutionary adaptedness, or what he called “ancient savage times” (Ibid., 195).

Darwin’s approach to defining the emotions of fear was rather sophisticated, distinguishing between horror and terror/extreme fear by arguing that although horror included terror and was almost synonymous with it, there was an anticipatory and sympathetic element involved with horror that was not present in terror. Terror was thus his term for a fearful emotion that was experienced directly by an individual, whereas horror was the appropriate term for when such terror was either anticipated for oneself, or sympathized with in the case of others (Darwin 1999 [1872], 306).

Darwin’s work on fear was part of his much larger project to understand the evolution of animal instincts, the development of which in its current manifestation is contemporary evolutionary psychology. A much more sophisticated account of the evolutionary basis of fear is consequently now available in the literature on this topic.

Fear as an Evolved Emotional System

Fear has been identified by contemporary neuroscientists as one of the four core premammalian emotional systems, as it is present in all vertebrates (Panksepp 2007, 146). As has been

explained, the fear system in animals is “designed to detect danger and produce responses that maximize the probability of surviving” such danger (Campbell 2007, 368). This fear module has various different behavioral, physiological and verbal-cognitive components, and different animals react to the activation of their own specific fear system differently. For example:

Faced by a dog, a cat will bristle its fur. Because it is frightened, it becomes frightening. A butterfly of the Brazilian forests, the *caligo* defends itself by changing itself into the shape of a head of a bird of prey. It arches its body into the shape of a beak, and opens its wings which bear the image of an eye . . . and thus manages to give such a perfect imitation of an owl . . . (Volta 1965, 73).

Horses often respond to fear by bolting (Romanes 1898 [1878], 329). Fear programming and the fear response in animals thus varies by species and also by individual predator.

Moreover, the fear module is “organized around the amygdala, a limbic structure in the medial anterior temporal lobe . . . Its sharing among mammals and its subcortical location suggest that it has an ancient evolutionary origin” (Ohman and Mineka 2001, 486). To be more precise, it is the central nucleus of the amygdala that is primarily involved in the fear response (Carlson 2011, 278). As has been explained in this regard:

The location of the amygdala gives us a clue to the precise nature of its role in processing fear. It has connections to the autonomic nervous system . . . as well as to other brain regions that process sensory input. It’s like a neurological crossroads, the hub of a network of pathways in the brain, a special “rapid response unit,” if you like, primed to act quickly when presented with danger (Winston 2002, 49).

The fact that the amygdala acts so quickly when the fear module is activated indicates clearly that fear is an instinctual response, not a conscious or controllable one. Confirmation that the amygdala is involved in evaluating potential dangers, such as whether to trust unknown individuals or not, is available from people with damage to this region of the brain, who exhibited (on average) greater attribution of trustworthiness to strangers than a control group with no such brain injury (Patel et al. 2007, 50).

As has been outlined, the fear system has four basic characteristic features: (1) it is stimulus-specific, being activated by particular animals or situations, e.g., snakes or the danger of falling debris; (2) it is automatically and immediately stimulated by the relevant situations; (3) as already indicated, it is not under conscious control; (4) it has specific neural circuitry associated with it (Ohman and Mineka 2001).

Regarding the first characteristic, two key factors assist in tailoring fear reactions to specific stimuli. Prepotency is the fact that certain stimuli take the attention and cause more significant reactions in individuals than others, e.g., snakes and spiders cause much stronger fearful reactions in human beings than flies or birds. Preparedness is the fact that specific responses are tailored to specific stimuli, e.g., human beings exhibit a fearful reaction to snakes but a nauseated reaction to rotting food (Rossano 2003, 170–172).

The fact that this type of fear reaction is instinctive and generated by psychological mechanisms that have evolved in relation to the most common dangers found in the environment of evolutionary adaptedness is indicated by the fact that most human beings still exhibit a fear of snakes and spiders, which are in many contemporary urban environments only a very small danger, but exhibit no fear whatsoever of cigarettes and alcohol, two of the biggest killers of contemporary human beings across the globe.

Not only are specific fears tailored to specific stimuli, the developmental appearance of different fears in the human child progresses according to a well-designed pattern:

The emergence of certain fears, such as fear of strangers (stranger anxiety), fear of separation from a caregiver (separation anxiety), fear of heights, and fear of collision, all show consistent patterns based on the physical maturation of the infant . . . For example, the first evidence of stranger anxiety can be found in 4–5-month-olds in the form of a delayed negative reaction to the prolonged presence of a strange face (Rossano 2003, 173).

In addition, there is also an important place for environmental interaction/influence in the developmental appearance of fear, or what is termed social referencing, with infants responding to their

own unique environmental experiences by showing modified expressions of particular fears, as is appropriate to their own particular environments.

Finally, it has been observed that not only do prey experience intense fear when they are under direct attack from predators, but some predators also experience some degree of fear when attempting to capture some types of prey. For example, when very powerful prey animals are being attacked, which usually occurs only in exceptional circumstances, the attacking predator animal also experiences fear, as they themselves are in some degree of danger too (Curio 1976, 123). As William James noted, “*Fear* is a reaction aroused by the same objects that arouse ferocity . . . We both fear, and wish to kill, anything that may kill us” (James 1891, 2: 415).

Sex Differences in Fear Behavior

There is a general consensus in the literature that there is a degree of difference in how males and females behave with respect to fear, with women (on average over large numbers of individuals) generally experiencing fear somewhat more intensely, more frequently, and for longer durations than men (Campbell 2007, 368), although this is true in relative terms only. Men can still experience very intense fear, given the right circumstances of danger, just as women can. It is probably accurate to state that men and women can experience the same overall range of fear, but that the fear system in men appears to be (on average) set at a little less sensitively than the fear system in women.

This sex difference in fear response is partly confirmed by the fact that, physiologically, it has been reported that women exhibit higher rises in skin conductance and a heightened startle reflex in reaction to scenes of danger compared to men, and that women tend to exhibit greater degrees of phobic fear (Campbell 2007, 369). It has been suggested that this sex difference in fear sensitivity is linked to the fact that males tend to take more risks in general terms than females, for example, in relation to engaging in physical altercations with other members of the same sex. Males also

tend to take more risks (on average) compared to females in relation to their degree of involvement in other physically risky activities, e.g., extreme sports participation and vehicular driving styles.

Malfunctions of The Fear System

The fear system in human beings, however, has some significant in-built flaws that can have important consequences for understanding aspects of contemporary human behavior. For example:

Because self-protection is imperative from an evolutionary perspective, the mind is designed to be hyper-sensitive to threats, even if such threats are ambiguous or hypothetical, similar to how a sensitive smoke detector detects and acts upon the tiniest bit of evidence indicating potential danger at the cost of occasional false alarms (Griskevicius et al. 2012, 315).

The logic at work here is that it is better to set the activation of the protective fear system threat level very low, even with the potential for many false alarms, rather than to fix it at too high a setting, the latter enabling the potential for some genuine threats to go unnoticed.

However, this may mean that some human beings are potentially liable to certain afflictions/malfunctions of the fear system, such as anxiety attacks, vertigo, and various different phobias (e.g., arachnophobia, agoraphobia, claustrophobia), which, instead of assisting the individual to function well, may actually hinder their normal operation in certain very specific circumstances (Marks and Nesse 1994). From an evolutionary perspective, potential malfunctions of the fear system are unavoidable costs that have to be borne, given the overall positive benefit that this system generates for human survival prospects in assorted dangerous environments.

Fear and Intergroup Prejudice

It has been suggested that certain types of intergroup prejudice can be traced to the existence of coalitional psychology as it evolved in relation

to the tribal prehistory of human beings, to associated intertribal conflicts, and to the evolution of in-group out-group fears that were based on the existence of various outsider threats (Park 2012, 188; Kurzban and Neuberg 2005, 667). The related concepts of inclusive fitness and ethnic kinship further suggest that ethnic-nepotism was, in evolutionary times, sometimes a form of adaptive behavior, as it served a useful protective function (Salter 2007, 541).

Tribal conflicts and intergroup hostilities were, therefore, an unavoidable part of human prehistory, and it seems likely that specific psychological mechanisms evolved to deal with these realities. These hypotheses lead to the conclusion that fear, as an evolved emotional system of protection against outsider threats, might be at the root of at least some of the contemporary manifestations of intergroup prejudice. Correctly recognizing the evolutionary roots of this type of fear, therefore, has the potential for better understanding the nature of intergroup prejudice and, in turn, devising better/more effective methods of dealing with it.

Critics of evolutionary psychology may argue that, by positing the existence of this evolutionary basis for in-group out-group prejudice and also for ethnic nepotism, the results can be the justification of such prejudice. These critics need to understand that, if the framework of evolutionary psychology is correct, then ignoring or denying the reality of evolved human nature will not assist in overcoming prejudice. It is much more effective to work alongside human nature in order to solve contemporary problems rather than to work against it or to deny that human nature exists at all.

Fear in Art and Literature

Although of very ancient animal origin, fear is still very much a contemporary emotional reality, one indication of this being the ongoing popularity of the horror *genre* in film and literature across the world (Barnett 2018). If fictive fears in the horror *genre* experienced indirectly – through art and literature – are seen to reflect the

terrors of dangerous splits in the social realm, then real-life fears experienced directly can be seen to reflect the terrors of dangerous splits in the natural world, primarily that between predator and prey (Moretti 2005 [1978], 83; Scalise Sugiyama 2006). These two worlds of art and nature sometimes overlap, providing a further enabling of the protective function of fear.

Consider the example of the werewolf, the mythology of which is “anciently and universally diffused” across Europe and elsewhere, going back at least as far as the thirteenth century (Summers 1934, 20). For Darwin, the transformative power of wolves was not an entirely fictitious quality; he noted reports that a few wolves varied the color-shading on their fur in order to match seasonal changes in the environment (Darwin 1874 [1871], 542). Some human tribes even wore wolf-skins as a symbolic attempt to harness their animalistic powers, and this practice of making hunting disguises from animal skins has been cited as the origin of the werewolf mythology (Langford 1997, 1006; Stewart 1909, 260).

The historian of occult mythology Montague Summers, known for his belief in the reality of supernatural creatures like vampires and werewolves, unknowingly described very clearly how natural predators like wolves readily assumed a larger-than-life quality in the ancestral human consciousness:

Throughout the ages, even in the prehistoric world, whilst his howling athwart the stillness of nature and night struck fear into the heart of primaeval man . . . further down the centuries when he was known as the savage plunderer and swift pitiless marauder of the shepherd’s grazing flocks, not sparing to attack child and maid or even the solitary wayfarer by the wood . . . all down the vistas of dateless centuries the wolf has ever been the inevitable, remorseless enemy of man . . . [part of] the experience and dearly purchased knowledge of our forefathers . . . (Summers 1934, 64–65).

Summers’ error was in taking the mythologized version of the wolf too literally, when what should have been taken literally, was the folk-narratives that have been used to warn of the real dangers of wolf attacks: “as the flesh-and-blood wolf continues to haunt the Transylvanian forests, so long will his spectre brother survive” (Gerard 1888, 187).

The link between superstitions expressed in nightmares and the “sudden transformation of one person into another or into some animal; the occurrence of phantastic and impossible animal forms” has previously been highlighted (Jones 1931, 238). This fearful link makes concrete the connection between primitive animal dangers and modern horror narratives that allude to the animal side of human nature and related transformative themes, which in reality are simply mediated embellishments on much older predator fears.

Conclusion

Beginning with Darwin’s pioneering work on understanding fear, evolutionary psychologists have more recently given the protective function of fear their full investigative attention, as it is a powerful and an important emotion that affects many different aspects of human behavior, most importantly, assisting the survival instincts. Consequently, instead of the false promise of the anemic adage “nothing to fear but fear itself,” the much more realistic maxim that animals live by is “nothing to fear but the many thousands of predators spread across the globe.” From a Darwinian perspective, fear is not a “mind killer” that has no real rational foundations, as has been argued elsewhere (Plamper and Lazier 2012), but instead is an essential “mind saver” that all animal life constantly relies upon for its ongoing survival.

However, various malfunctions of the fear system are also important to understand as they may be at the root of the prevalence of various contemporary panic and anxiety disorders. In addition, only by understanding the evolutionary origins of fear as an emotion, will any potentially negative side effects of it that are still being manifest today, such as intergroup prejudice, be able to be effectively mitigated. Finally, it should be stressed that human beings should not be frightened of expressions of fear but instead should celebrate and revel in them, as such frightful and terrific expressions of emotion have undoubtedly contributed to saving countless human and animal lives across the vast evolutionary past.

Cross-References

- [Art](#)
- [Michelle Scalise Sugiyama](#)
- [Prejudice as an Expression of Tribalism](#)
- [Supernormal Stimuli](#)

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Fear of Cuckoldry

- [Threats of Sperm Competition](#)

Fear of Strangers

- [Stranger Anxiety](#)

Fear of Weight Gain

- [Anorexia Nervosa](#)
- [Eating Disorders](#)

Fears

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Synonyms

[Frights](#); [Horrors](#); [Scares](#); [Terrors](#)

Definition

Real or imagined objects or situations that elicit psychological, physiological, biomedical, and behavioral responses to protect an organism against perceived danger or threat.

Introduction

In Isaac Marks' [1987](#) book *Fears, Phobias, and Rituals: Panic, Anxiety, and Their Disorders*, he described fear as an emotion produced following the perception of present or impending danger that leads an organism to avoid threat, has obvious survival value, and is normal in appropriate situations (Marks [1987](#)). Fear reactions exist in

humans and across animal species to protect or defend against present or anticipated threats in the environment. Fear is characterized by a number of psychological and physiological reactions and biomedical changes, occurring simultaneously or sequentially. These include visible behavioral expressions, such as freezing or fleeing, and accompanying psychological and physiological changes, such as feelings of terror, crying, a pounding heart, nausea, and an urge to run and hide. Finally, biomedical changes associated with fear include the secretion of both adrenalin and noradrenalin at the peripheral nerve ending of the autonomic nervous system. Marks suggested that some aspects of what we fear and how we express it are biologically determined, while others are affected by our individual and group experiences. Examining the development and acquisition of fears has been the focus of extensive research, as researchers have struggled to explain individual differences regarding if, when, and how both evolutionarily relevant and nonrelevant fears are formed.

Conditioning Theory of Fear Acquisition

Fears are assumed to be acquired and the process of acquisition is a form of conditioning. Fear conditioning is similar to classic conditioning pioneered by Pavlov ([1927](#)), but pairs the conditioned stimulus with an intrinsically noxious or harmful unconditioned stimulus to elicit species-typical fear responses. Proposed by Eysenck and Rachman ([1965](#)), the conditioning theory of fear acquisition assumes that any stimulus can be transformed into a fear signal. This theory suggests that given similar frequency and intensity of exposure, all stimuli should have nearly an equal chance of being transformed into fear signals. It also states that the strength of the fear is determined by intensity of the experience in addition to the number of repetitions of the association between the painful or frightening experience and the stimuli. Finally, the theory suggests that the likelihood of fear developing is increased by factors such as exposure to high-intensity pain and/or fear experiences and by frequent repetition

of the novel association between the stimulus and the pain or fear. One of the most famous studies of fear conditioning was conducted by Watson and Rayner (1920), who conditioned fear of a white laboratory rat in a young infant referred to as “Albert” by pairing the presentation of the rat with a loud and frightening noise. They also observed that Albert’s conditioned fear generalized to similar furry stimuli, such as a rabbit and furry dog, consistent with the conditioning theory’s claim that stimuli resembling the fear-evoking ones also acquire fearful properties. However, Rachman (1977) noted that researchers had mixed results when testing Watson and Rayner’s finding and presented several arguments against the conditioning theory of fear acquisition. These included the failure of people to acquire fears in fear-evoking situations, difficulties producing conditioned fear reactions in humans, and evidence against the premise that any two stimuli can be associated with each other with equal ease. Therefore, Rachman proposed a three-pathway model of fear acquisition.

The Three-Pathway Model

While Rachman (1977) acknowledged that direct conditioning remained an important fear-induction process, he proposed that at least two other pathways could be identified, distinguished by being indirect processes of acquisition, and integrated into a single model. The first is the vicarious acquisition of fears, where humans and animals can acquire fear of a stimulus (animal, object, or situation) by witnessing another individual’s fear of it. Based on observational learning, Rachman suggested that fears could be acquired directly or vicariously and that neutral stimuli would likely acquire fearful qualities if they were directly or vicariously associated with painful or frightening experiences. The ability to appropriately detect and respond to signs of fear and pain in a member from the same species likely conferred an important selective advantage during evolution. In addition to alerting the receiver about potential imminent danger, they also assign a threat value to the

context or cue associated with the threat (Olsson and Phelps 2007). A recent review of cross species research on vicarious fear learning, also referred to as social fear learning, by Askew and Field (2008) supports the claim that this pathway plays an important role in the development of many fears. However, researchers also agree that vicarious learning is likely a form of conditioning and that experiencing an aversive episode vicariously may not in itself be sufficient to predict fear acquisition.

The second pathway proposed by Rachman was fear acquisition by the transmission of information and/or instruction. He remarked that information giving is an inherent part of raising a child, carried out continuously by parents and peers during the child’s earliest years, and is likely the basis for the most commonly encountered fears of everyday life. However, fears acquired in this way are more likely to be mild rather than severe. Rachman proposed that an advantage of these two additional pathways was that unlike conditioning, they could account for the fact that people display fears of situations and objects which they have never encountered. He suggested that accepting that fears can be acquired by informational processes allows us to explain some, but not all, of the failures to acquire fear in situations where it might have been expected to occur based on the conditioning theory. That is because information and instruction also help humans and animals to learn to distinguish those situations and objects which are not dangerous and therefore need not be feared.

The Nonassociative Pathway

Decades later, Poulton and Menzies (2002b) proposed a fourth pathway to account for fears that are not acquired by conditioning or other learning processes, for which the three-pathway model struggles to explain. They suggested that the addition of a nonassociative pathway contributes to the understanding of the nonrandom distribution of fears, failures to recall conditioning events in fear onset, and the seemingly paradoxical finding that people with high levels of fear report less

direct traumatic events than those without such fear. Poulton and Menzies claim that a non-associative model of fear acquisition asserts that members of a species, given normal maturational processes and background experiences, will show fear to a set of biologically and evolutionary-relevant stimuli. Evolutionary-relevant fears (e.g., fears of spiders, heights, water, darkness) acquired in this way would have the following features: the feared stimulus must represent a longstanding danger to the species, fear and avoidance of the stimulus must have increased reproductive opportunities in our ancestors, and the fear and avoidance of this stimulus is partly under genetic control. Therefore, this pathway enables researchers to account for fears with an evolutionary background appearing without any relevant direct or indirect associative learning experiences. Evidence for the nonassociative model has largely come from the findings of retrospective and longitudinal cohort studies, which suggest that relevant associative learning experiences had not occurred based on recall by phobic individuals. Critics of this model highlighted methodological problems with these studies, such as the unreliability of retrospective recall, especially when it is generally many years after the alleged experience took place (Mineka and Öhman 2002). However, Poulton and Menzies (2002a) maintained that an expanded four-pathway model offers the most inclusive, comprehensive, and parsimonious theoretical account of fear acquisition that integrates diverse findings from multiple disciplines.

Conclusion

Fears are crucial to the survival and well-being of humans and animals, allowing organisms to avoid threat, react to danger, and enhance performance. Fear is a package of reactions, occurring simultaneously or sequentially, resulting in psychological, physiological, biomedical, and behavioral changes. Theoretical models of how fears are acquired have changed, starting with a direct conditioning theory of fear acquisition, to a three-pathway model that includes indirect acquisition

pathways, and finally to a four-pathway model to incorporate a nonassociative pathway of fear acquisition. This comprehensive model of how fears are acquired is crucial in order to understand the development and treatment of maladaptive fear such as anxiety and phobias.

Cross-References

- [Correlates of Fear](#)
- [Fear Affords Protection](#)
- [Phobias](#)
- [Universal Human Fears](#)

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Fears and Phobias

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Synonyms

Anxiety; Blood injection injury phobia; Simple
phobias; Specific phobias

Definition

Fear is a normal emotional response to actual danger; it motivates individuals to either avoid the danger or to elicit adaptive species-specific defense behaviors, which reduces threat to life or general harm or loss. Phobias are exaggerated fear responses to specific stimuli that are not really as hazardous as the response suggests, and the avoidance and safety behaviors patients engaged in are maladaptive or unnecessary and often the maintaining feature of the disorder.

Introduction

Every living thing intuitively responds to threat. Fear, a quick and normal emotional response to danger, motivates species-specific defense behaviors, such as the fight-or-flight response. Fears are considered rational, appropriate when such defense or avoidance behaviors are elicited in response to a definite danger; as such, the function of fear is to avoid harm or death. Anxiety is an inappropriate or irrational fear response triggered in the absence of actual danger. Exaggerated, irrational, and extreme manifestations of fear or disgust and avoidance of specific stimuli in the absence of proportional danger are considered specific phobias.

Anxiety disorders are highly prevalent in the population, afflicting approximately 18% of the U.S. adult population in any given year. For females, lifetime and past-year rates of anxiety disorders are 1.5–2 times higher than in males, a trend that is mirrored in the domain of specific phobias.

Few areas of mental disorders have been as clearly influenced by functional and evolutionary thinking as anxiety. Almost all anxiety researchers and clinicians accept the idea that normal, adaptive fear functions as a signal that triggers appropriate defensive response. Because anxiety constitutes an exaggerated, maladaptive response despite there being no objective, present danger, and because persistent attempts to remove such nonexistent threat contribute to its maintenance, it is generally considered maladaptive. Even if a stimulus involved mild discomfort or pain (e.g., wasps and injections), the fear or disgust response may be considered exaggerated compared to actual pain or danger. This includes the avoidance that may reduce general function, well-being, or health benefits.

Evolutionary Accounts

Considering the phenomena people in general are most phobic of quickly reveals a list of possibly evolutionary relevant phenomena: heights, dark, strangers, small and large animals (and especially snakes and spiders), and open and closed spaces. Since none of these ancestral hazards are specifically dangerous today, evolutionary accounts of preparedness therefore ring true for most clinicians (Kennair 2007; Marks and Nesse 1994; Öhman and Mineka 2001). Further, governmental health and safety campaigns often attempt to instill fear toward specific stimuli, yet they commonly fail to do so. This is due to the hedonic valence of the stimuli, making our approach behavior to harmful stimuli (e.g., fat, sugar, speeding, drugs including nicotine and alcohol, unprotected sex, and speeding) problematic. Our desire to enjoy these things so much overrides their fear-inducing potential, to an extent that they through their availability present a challenge

to our health in a modern, evolutionary mismatched ecology – even if they were not dangers in the EEA.

Acquisition of Phobias

For many decades, phobias were considered a result of conditioning. According to Mowrer's behaviorist theory (Mowrer 1947), two types of conditioning were involved: first, classical conditioning, i.e., being stung by wasp, and, second, operant avoidance, e.g., avoiding a room with a wasp in it. However, many stimuli do not provide a basis for classical conditioning, and one often finds that those who have been stung are less phobic than those who avoid wasps due to their phobia. Model learning has also been offered as an explanation, but this only moves the explanation of phobia acquisition back a generation or more. The limitations of associative pathways were recognized early by anxiety researchers (Rachman 1977), and experimental research has challenged the generalizability learning or equipotentiality of stimuli (Seligman 1970; Öhman et al. 1976). Work by Öhman and Mineka (2001) considered how humans are prepared to fear specific stimuli. The recent years have seen an increased focus on non-associative pathways, championed by the longitudinal work of Poulton, Menzies, and colleagues (Poulton and Menzies 2002a, b). Recently, Sandseter and Kennair (2011) suggested that childrens' tendency to engage in risky play might constitute a mechanism that reduces naturally maturing and occurring fears of ecologically relevant threats coinciding with the development of psychophysical and motor skills, thereby promoting approach and reducing safety behaviors. The mode of acquisition of phobias continues to be addressed from an evolutionary perspective (Hoehl and Pauen 2017).

Recent Evolutionary Developments

Recent evolutionary research is still inspired by the pioneering work of, e.g., Öhman and

colleagues. Certain fears and phobias occur naturally during different stages of human development (e.g., separation anxiety and fear of heights) that follow a complex, yet stable, pattern (Boyer and Bergstrom 2011). Employing visual detection paradigms, recent developmental work has demonstrated that visual attention in infants and young children is prioritized for potentially dangerous stimuli resembling ancestral hazards, well before they acquire any threat-relevant fears. Others show that infants readily associate snakes with fear (DeLoache and LoBue 2009) and are quicker to detect the presence of spiders than various categories of biological distracter stimuli (LoBue 2010). Using a preferential looking and habituation paradigm, Rakison and Derringer (2008) demonstrated a perceptual template for spiders that generalizes to real-world images of spiders, but not for other nonthreatening biological stimuli in infants as young as 5 months old. These findings are in line with studies that show that other arthropods (e.g., bees/wasps) are not perceived as threatening as spiders (Gerdes et al. 2009; New and German 2015).

Other studies show that these threat-detection mechanisms are maintained in adults. Jackson and Calvillo (2013), for instance, demonstrated that participants completing a visual search task located evolutionarily relevant and animate objects fastest and with the least impact of high perceptual load, compared to evolutionarily novel and inanimate objects. Further evidence stems from research on an unusual but common phobia, trypophobia, in which images of holes instill fear. Conducting a spectral analysis on a variety of images that induce trypophobia, Cole and Wilkins (2013) found that fear-inducing stimuli had a spectral composition typically associated with a range of potentially dangerous animals. Kazanas and Altarriba (2017) demonstrated memory advantages for unknown (supernatural) predators. Overall, these findings echo evidence that animate objects are mirrored more closely than inanimate objects, independent of considerations about which pose more serious threats in modern environments.

In an original approach to the evolution of phobia, Miloyan et al. (2016) suggest that for

humans, specific phobias demand a capacity for mental time travel. This may account for the chronicity of this disorder, as actual dangers in the EEA would need to be avoided consistently and over long periods of time, including mechanisms of planned avoidance.

The Special Case of Blood Injury Injection Phobia

The special case of blood injury injection phobia, the only anxiety disorder that leads to fainting of those affected, illustrates the adaptationist evolutionary approach to danger – an actual danger is countered by a relevant adaptive response. Rather than increasing adrenalin and activation, there is a fall of blood pressure, which might be the most adaptive response to severe blood loss (Kennair 2007; Marks 1988).

Treatment

Despite the fact that phobias are not necessarily acquired through associative pathways such as conditioning, behavioral therapy – exposure therapy including response prevention – constitutes the most efficient treatment of phobias. In general, it seems that reducing avoidance and discontinuing safety behaviors lead to a decrease in anxiety levels. The idea that evolved mechanisms are malleable and that learning is an evolved function, which better makes us better adapted to our environment, is not at odds with an evolutionary perspective.

Conclusion

Generally, evolutionary clinical psychology has had little influence on mainstream mental health care. Most anxiety therapists will use evolutionary perspectives in psychoeducation, to explain the patients' exaggerated responses and, in so doing, normalize these. The obvious exception is treatment of anxiety in general and phobias

specifically. Beyond the understanding of the function of fear and safety behaviors, evolutionary perspectives have informed our understanding of predispositions to fear specific stimuli and how phobias and anxiety may mature through non-associative pathways. Recent work continues a tradition of considering specific evolutionary relevant stimuli and the evolved mental mechanisms designed to perceive these.

Cross-References

- [Anxiety](#)
- [Anxiety Disorders](#)
- [Anxiety \(Randolph Nesse\)](#)
- [Evolutionary Clinical Psychology](#)
- [Fear](#)
- [Social Anxiety](#)
- [Stranger Anxiety](#)

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Febrile

- [Fever](#)

Fecundity

- [Fertility](#)

Federal Public Archives

- [Public Records](#)

Federal Public Documents

- [Public Records](#)

Federal Records

- [Public Records](#)

Feeding

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Synonyms

[Consumption](#); [Eating](#); [Provisioning](#)

Definition

Consumption of edible resources in order to sustain an organism’s energetic and nutritional demands.

Introduction

All heterotrophic organisms feed on other life; therefore, feeding is fundamentally an interaction between consumer and the consumed, and its relationships to surrounding contexts can be informative. Feeding is ecological, where agents like predator and prey interact within physical, biotic, and perhaps social contexts and exchange energy inside ecosystems. For humans, feeding intersects with our social worlds, and our foodways – the cultures surrounding food – are enmeshed in biocultural feedback loops.

Feeding is essential to offspring development, particularly in humans where parental investment sustains young individuals as they develop and grow, and values and social norms are enculturated via foodways.

This entry discusses evidence from the human fossil record, archaeological traces of feeding, and behavioral ecological data from extant nonhuman primates and humans practicing diverse subsistence strategies to investigate how the evolutionary history of human feeding and dietary ecology may underlie adaptations that define humanity, notably our cognitive abilities, long childhoods, reliance on technology, and our extreme sociality.

Bento Boxes: A Contemporary Example of Enculturation Through Food

In Japan, bento or lunch boxes full of creatively prepared and neatly organized food items prepared by mothers accompany young children as they begin nursery school, leaving the comfort of home and beginning an important journey of cultural development. Allison's (2013) ethnographic account shows bento's role as ideological state apparatus. In other words, the lunch box itself, but also the contexts surrounding its preparation and its consumption at school, functions to reinforce cultural values. In this case, mothers' food preparation reifies gendered social roles, and other cultural values like discipline and obedience to authority are reflected in the social pressures that guide mothers' bento preparation. Proper bento should attract children with interesting and cute shapes, prompting them to quickly eat their lunch.

This behavior is reinforced by teachers who monitor the classroom and encourage proper eating behavior to instill the discipline necessary for the child's future schooling – where success is crucial for their adult employment.

A Biocultural View of Feeding and Human Life History

The previous example shows how western, industrialized ideology is delivered through food and how the biological necessity to eat is enmeshed in a cultural context. The diversity of human foodways is vast, and examining the interaction of feeding culture and biology provides an interesting analytical perspective to address important questions in human life history like why, compared to other mammals and primates, we have long childhoods and live a long time, including a long post-reproductive period (Crittenden et al. 2013). Further, males and females face different energetic trade-offs related to gestation, and parental investment via nursing and other provisioning, and address these needs with the help of complex cultural mechanisms. Although diversity in human mating systems is wide-ranging, pair-bonding (sometimes serial in nature) and allo-parenting along with other means of offsetting costs of childrearing through kin networks are unusual in the primates, but common in many human groups.

Additionally, maternal and paternal investment differ; parents provision their offspring indirectly during gestation and during their juvenile phase while nursing and, as they wean, introduce children to adult foods and teach them to support themselves. Here it is informative to examine trends in human groups across a variety of cultures that engage different subsistence strategies (i.e., foraging, horticulture, industrial agro-capitalism, etc.). A study of nursing behavior and parental investment in 58 cultural groups found that on average humans wean their infants at 2.5 years, which is earlier than expected for primates given dental developmental markers and life history variables like adult size. This suggests weaning age "may be at an adaptive minimum; hence in many

environments the challenge is not to find ways to reduce lactation, but rather to extend it” (Quinlan and Quinlan 2008, p. 89). After considering a host of variables, they find that alloparenting and divorce prevalence most strongly predict early weaning, suggesting that conjugal stability is related to delayed weaning cross-culturally, but social networks surrounding nursing mothers also impact the length of nursing. Further, because lactation may suppress reproductive cycling and limit reproductive success, a shorter nursing period may reflect selection for a shorter inter-birth interval that improves individual reproductive success and may underlie human population growth (Kennedy 2005).

Like chimps and some other tool-using animals, juvenile humans learn technologies to feed themselves through social interaction, not only from elders but by playing with kin and age mates (Horner et al. 2006). For children living in the contemporary industrial world, food is mediated by parents or caretakers with access to capital, but foraging juveniles are provisioned as they are weaning and quickly begin to accumulate a large portion of their daily caloric needs on their own, often targeting resources appropriate for their size (Lew-Levy et al. 2017).

Evidence from the Fossil Record

The fossil record of human evolution provides evidence to address the intersection of life history and feeding in earlier human taxa, but these data are typically rare and often incomplete. However, with careful interpretation, conclusions about human prehistory serve as important signposts that document humanity’s evolving physical, behavioral, and cultural adaptations at points in time and space.

Tool-assisted feeding is not restricted to humans. Chimps modify objects to create tools for extractive foraging, but human tool use is complex and involves greater movement of material across landscapes compared to other animals. Controversial marks on fossil bone at Dikika, Ethiopia (3.4 million years ago) may reveal evidence of the earliest known butchery of animals with unmodified stone to access marrow and other

within-bone nutrients. Once the archaeological record begins to offer clear evidence of tool-assisted carnivory, abundant evidence shows that early genus *Homo* is flaking stone and using it to butcher a variety of animals from monkeys to hippos (Ferraro et al. 2013). The introduction of animal foods (and aquatic foods) may have played an important role in dietary changes which underlie evolution of increasing brain size, but this conclusion should be considered alongside the facts that plant foods and other dietary items are less visible in the fossil record and many paleoecological inferences about ancient feeding behavior cannot be addressed because of the resolution of the archaeological record. Therefore, a more robust conclusion from the fossil record recognizes that the human diet has evolved to its current state through technological and social adaptations. The increasingly complex technological innovation that characterizes human evolution often focused on feeding adaptations, from the use of tools to butcher animals, to projectile hunting technology, and plant and animal domestication, and throughout, these changes in subsistence involved social transmission of knowledge.

Despite the fact that much of prehistory people learned about their foodways and associated technology socially, evidence of social transmission of technological knowledge between individuals is hard to find. For example, the archaeological record is often too coarse to discern children’s tool-making (Shea 2006). However, fossil skeletal material provides evidence to assess certain aspects of diet across the lifespan and therefore understand more about how feeding and life history were interwoven in prehistory. In particular, enamel hypoplasia, or disruptions in enamel formation during tooth crown formation caused by metabolic stresses or dietary changes, provides a useful tool for understanding how feeding and life history intersect in an individual (Smith 2013).

Interpreting growth in fossil taxa is possible by identifying the neonatal line and counting daily enamel deposits, providing a high-resolution age estimate. However, age estimates lose resolution after dental growth ceases because age-related skeletal degeneration and tooth wear provide much less precise reconstructions of the later phases of hominin

life history. Further, comparing patterns of growth in fossil humans suggests that the prolonged childhood and exaggerated life history that characterize *Homo sapiens* may have occurred to a lesser degree in relatively recent taxa like *H. heidelbergensis* and the Neanderthals.

Austin et al. (2013) developed a new method for measuring the barium distribution across developing teeth that captures evidence of dietary changes during early life history. Using a living macaque experimental model and data from human infants, they trace changes in barium levels in the womb where it is blocked by the placenta, through birth and the onset of nursing where barium is enriched, and the subsequent drops in barium that occur when nursing is supplemented with solid food and when it ceases entirely. Applying this method to a juvenile Neanderthal tooth from Scladina, Belgium, dated to 80–127,000 years ago, indicated that as expected the 8-year-old child grew relatively quicker than *Homo sapiens*. Prenatal enamel formation lasted 13 days before barium increased with the exclusive consumption of milk for around 7.5 months. Afterward, intermediate levels suggest supplemental provisioning with solid food until about 1.2 years when barium levels dropped significantly with the abrupt cessation of nursing. Although the life history of this Neanderthal child appeared quicker than modern humans, meaning it achieved dental developmental markers at a relatively earlier age, its weaning age fits inside with the normal range that surrounds the human average of 1–4 years. Continuing dental development showed that this child lived beyond tooth formation, but we have no evidence to reconstruct its diet or how it changed later in life. We don't know whether weaning was initiated by a younger sibling's appearance, the mother's disappearance, the beginning of adult-like foraging behavior, or some other reason.

Typically, diet is reconstructed in human fossils by analyzing carbon and nitrogen isotopes in teeth but this only offers a blurred glimpse at the trophic position (i.e., relative animal versus plant foods) and the overall consumption of woody or grassy plant foods. Further, these methods only record dietary preferences during tooth formation, which occurs early in life. In contrast, dental

microwear analysis, which can discriminate certain food items mainly by their texture and hardness, offers a snapshot of which foods were consumed during adult life, but only for the final 2 weeks before death when tooth wear is not overprinted. Unfortunately, these methods provide sophisticated ways to address feeding ecology in fossil human taxa, but do not provide a longitudinal view of diet throughout the complete life course, and often stand as the only sample of dietary ecology for an entire fossil species or period of time.

Still, single specimens provide intriguing evidence of the prehistory of another prevalent human social behavior – care for the sick or elderly. The Iraqi Neanderthal skeleton Shanidar 1 (35–45 thousand years old) was likely blind and deaf and carried a healed, amputated arm. Because foraging in this condition would be difficult, this specimen arguably represents an early prehistoric instance of care of sick or incapacitated group members. The deep roots of care for elderly individuals may go back even further if the edentulous *Homo erectus* cranium from Dmanisi, Georgia (1.8 million years ago), is correctly interpreted as a long-lived individual who may have been provisioned by other group members.

Conclusion

Feeding behavior is complex in living people. We are omnivorous, social, and technological, and these flexible adaptations contribute to significant diversity in human foodways. Even if the dietary items or specific foraging behaviors cannot be precisely reconstructed throughout most of the human evolutionary record, individuals not only feed themselves but also provision offspring and may be fed by others as they age, highlighting the biocultural nature of our diet and its intersection with life history stages. Selection pressures that favored a slower human life history and lengthened childhood in *Homo sapiens*, providing a time where individuals socially acquire skills and are enculturated with the tools necessary to live, including how to feed themselves. This life history trend appears in earlier members of our

genus and has co-evolved with the other unique human traits like increased brain size, cultural complexity, and technological sophistication.

Cross-References

- [Body Reserves and Food Storage](#)
- [Brain Evolution Resulting from Cooking](#)
- [Convergent Evolution of Hyena and Primate Social Systems](#)
- [Homo Rudolfensis](#)

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Feeding Offspring

- [Gathering Returns When Nursing Infants](#)

Feeling Sick

- [Nausea](#)

Feelings of Excitement and Brotherhood

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Synonyms

[Agonistic support](#); [Male-male competition](#); [Male-male cooperation](#); [Non-human primates](#); [Polyadic aggression](#)

Definition

A coalition is defined as an aggressive attack of two or more individuals against one or more targets. Most frequently coalitions involve two individuals aggressing against a common target. Coalitions are prevalent throughout the animal kingdom and their frequency between males is surprising as males are most frequently the

dispersing sex and thus there should be no kin-related benefits of cooperation. The formation of a coalition can be opportunistic whereby one individual joins one of two individuals during a dyadic aggression. Coalitions can be very basic and involve no communication between the coalition partners and an individual purely intervenes in an on-going aggression. Alternatively, coalitions can be coordinated attacks with individuals aggressing against a common target with similar forms of aggression and movement. These aggressions can involve recruitment of specific individuals from a population or social group. Individuals can use specific behaviors and vocalizations to recruit their partner and the aggression often appears to occur spontaneously between the coalition partners.

Introduction

In the animal kingdom coalitions have been observed among many taxa from birds to cetaceans to social carnivores and ancestral human species. Coalitions are most frequently observed in nonhuman primate species and occur under a variety of circumstances and constellations described below (reviewed in; Smith et al. 2010).

Many different functions can be provided by coalitions including defense of or access to resources, rise in rank position for one or both partners, defense against aggression from a more dominant individual or defense against group take-overs from rivals (reviewed in Harcourt and de Waal 1992; Olson and Blumstein 2009; Smith et al. 2010). Nepotism and kin-related benefits of cooperating and supporting relatives are considered to be the main drivers behind coalitions between group-living females (Isbell 1991; Sterck et al. 1997; van Schaik 1989; Wrangham 1980). In the majority of primate species, males are the dispersing sex, and therefore move from their natal group at maturity. They are without kin or may not recognize kin in their new group but coalition formation is still often seen. Coalitions can either be between individuals within the same group (within-group coalitions) or individuals of one social group join together to fight against

another group of individuals of another social group (between-group coalitions).

Within-Group Coalitions

Gregarious male primates compete for access to mates within their social groups, and in many primate species males can use within-group coalitions to gain access to females. This form of cooperation is intriguing as under such circumstances males are competing for access to a non-divisible resource (access to females) and so cooperation should be unlikely. Recently a mathematical model has been developed to explain the evolution of different male-male coalition types within groups (Pandit and van Schaik 2003; van Schaik et al. 2004, 2006; also see Young et al. 2014b; for a review of alternative coalitionary models see Bissonnette et al. 2015). These models predict when certain coalition constellations and types are likely to occur within social groups. The model assesses the profitability (the coalition must provide fitness benefits for the partners) and feasibility (the coalition partners must be able to defeat the target) of certain coalitions occurring at different levels of contest competition within groups. Contest competition is based on the level with which the alpha male can monopolize mating access to females. Coalitions can be classified into three constellations based on the ranks of the allies (coalition partners) and target in the coalition: (1) *all-up*, where both allies are lower ranking than the target, (2) *all-down*, where both allies are higher ranking than the target, and (3) *bridging*, where the target is ranked between the allies. These coalition constellations were further categorized into types by their function, being either “*rank-changing*” when they affect participants’ rank position, or “*levelling*,” when they reduce the inequality in the distribution of matings/paternities across ranks. Rank-changing coalitions are also known as “political” or “revolutionary” coalitions. One of the main assumptions of the model is that payoffs for the coalition partners are mediated by dominance rank rather than male fighting abilities.

Contest potential within groups' ranges from very high (where the alpha male has complete monopoly of mating access) to very low (where all males can mate with females and scramble competition occurs). In species with very high contest potential, coalitions are not expected between males as mating access is highly skewed to the alpha male. There are often few subordinate males and the high contest leads to large power differentials between males, hence, coalitions become unfeasible. Conversely, if contest potential is extremely low, then scramble competition is likely to develop and all males in the group can gain access to females and thus cooperation provides costs but no benefits to the allies. The mathematical models, therefore, predict that male-male coalition formation should occur from high to medium levels of contest potential but not at the extremes. The models further predict the coalition constellations which will occur at differing contest potential, these are outlined below.

Levelling coalitions become feasible as contest competition begins to decrease to a mid-high level as males can gain benefits from cooperation, which were not possible at extremely high contest. Here males can cooperate opportunistically to gain access to receptive females, by breaking up a consortship between a male and female dyad: as has been observed in savannah baboons, *Papio cynicephalus* (Bercovitch 1988; Noë and Sluijter 1990, 1995; Packer 1979) and Barbary macaques, *Macaca sylvanus* (Bissonnette et al. 2011). By combining their extrinsic fighting abilities, males are able to reduce mating opportunities of higher ranked rivals, effectively creating a level mating skew for subordinate males. When recruiting a partner, males must weigh-up the available allies and the target to recruit a partner who will provide enough combined intrinsic fighting ability to defeat the target. The undecided nature of the payoff outcome can make the opportunistic coalitions attractive for both partners (Noë 1990) as the highest ranked partner does not always gain access to the female. Both benefit by breaking up the consortship and simultaneously reducing the future mating opportunities of the consorting male and increasing the probability of future mating opportunities for the coalition partners.

Levelling coalitions provide a short-term, opportunistic alternative mating strategy to gain direct benefits in the form of access to consorted females.

Coalition formation is not only beneficial in terms of gaining temporal access to females, and the payoffs to individuals are not only related to immediate benefits of access to the female. Male dominance rank position is highly correlated to reproductive success, thus, attaining high rank position can increase a male's reproductive success. As contest potential decreases further, males can cooperate through rank-changing coalitions to increase the rank position of one or both partners. Rank changes through coalition formation can be achieved with one interaction but may require repeated coalitions afterwards to defend the new rank position and thus partners may need to interact over longer periods than with levelling coalitions. Rank-changing coalitions carry high immediate costs to the participants as higher ranked targets can show counter-aggression, and sexual selection has equipped males with extensive weaponry (e.g., large canines and body size). Recruitment of a coalitionary partner should therefore consider the reliability of the partner previously because if they were to defect (i.e., leave the fight as it is on-going) then their partner would be left in a vulnerable position possibly leading to serious injury during the fight (Ostner and Schülke 2014; Young et al. 2014b). As the rank change occurs with the cooperation of another individual, the intrinsic fighting abilities of those involved remain the same and as a result the partners should continue to form coalitions to defend and cement the newly acquired higher rank position (Ostner and Schülke 2014; van Schaik et al. 2006; Young et al. 2014b).

Regular coalitionary partners can provide further benefits as they can act to increase a males extrinsic power even in the absence of the partner and function to intimidate opponents and reduce the probability of aggression from higher rank individuals (Berghänel et al. 2011). Under such circumstances, male-male social relationships might be the key as the formation of social bonds between group members can help to facilitate this cooperation between individuals.

Repeated affiliation between individuals through social behaviors such as grooming, being in close proximity without aggression or triadic male-infant-male buffering may show a willingness to cooperate and develop strong social bonds between individuals (Ostner and Schülke 2014). A correlation between grooming given and support received has been shown in both male and female primates (Schino and Aureli 2008). This is highlighted in Assamese macaques (*Macaca assamensis*) where male future rank position could be predicted by the frequency with which they formed coalitions and those forming coalitions more often rising in rank in the future (Schülke et al. 2010). Additionally, those males without strong bonds, formed coalitions less frequently and fell in rank. Furthermore, male coalitionary partner choice is related to social bond strength. In Barbary macaques, males recruited the partner with the greatest social bond strength more frequently from the pool of available bystanders when a dyadic aggression occurred. Males were also more likely to fail to recruit a partner if their opponent had a stronger social relationship or was of higher rank to the bystander than between the bystander and the recruiter (Young et al. 2014a). Only a small number of primate species show male-male affiliation, but where affiliation is frequent and social bonds are formed and differentiated, these factors are expected to play a major role in coalitionary partner choice. Although strong social bonds are important for the selection of a reliable partner, rank-changing coalitions have also been observed where male-male affiliation is infrequent or absent. In general, rank-changing coalitions can be considered a more long-term strategy to increase an individuals' position in the dominance hierarchy and lead to long-term reproductive benefits of higher status.

Besides rank-changing and levelling coalitions, the third constellation is bridging coalitions. These coalitions involve a high ranked individual and a subordinate against a target ranked between them. These coalitions are predicted to occur between kins as only by assisting a relative can they remain profitable for the high ranked partner. But they are also observed in species where

individuals show strong male-male social bonding and where individuals have a regular socially bonded partner. For example, if a rank-changing coalition has occurred involving two bonded partners, it may be one partner remains low ranked and the two continue to form coalition's post-rank change to cement the higher individuals' new rank position. As a result these coalitions would then be bridging. A subordinate may support a high-ranked partner against a mid-ranked challenger in order to gain future favor and support. Thus, where males form social bonds and recruit their bonded partner, bridging coalitions are more likely to occur.

Between-Group Coalitions

Besides within-group coalitions, males can form coalitions with members of their own social group against members of another social group (known as between-group coalitions). These usually occur in defense of resources such as feeding sites or females against single males, multiple males, or other groups. These between-group coalitions are common as males cooperate against a common enemy and success leads to a common benefit for those involved defending the resource in question. Currently, a mathematical model predicting their feasibility, constellation, and occurrence is lacking. Additionally, future costs of cooperation can be lower as the target(s) of the aggression will not be in their social group at a later date when possible retaliation could occur. These coalitions are often very large in size compared to within-group coalitions. Males can also use coalitions to takeover a group; for example, an influx of bachelor males can usurp the current alpha male and even other resident males to assume control of the group (Borries 2000). In some instances, male coalitions against neighboring groups and within their own social group can be lethal and either directly or due to the injuries sustained in the aggression lead to the death of the target. In chimpanzees (*Pan troglodytes*), in particular, this behavior has been witnessed many times and has been likened to human warfare. Lethal coalitionary aggression is seen more frequently

in species with fission-fusion dynamics where one party can have a large numerical advantage over their rival. These lethal aggressions can benefit the victors by increasing their territory, hence, food resources and reduce the number of future competitors or rivals who can form coalitions against them (Watts et al. 2006; Wrangham and Peterson 1996). The exact motivation behind lethal aggressions is still debated as death can merely be the unintentional result of fierce aggression and large injuries sustained to one of the competitors. Lethal coalitionary aggression has also been observed in ancestral human societies. For example, the Yanomamö tribal society of Amazonia where individuals who show stronger alliances are more likely to fight together and this can often be in the form of lethal aggression (Macfarlan et al. 2014). Although it is worth noting these coalitions often differ from those of chimpanzees and other non-human primates as the coalitionary partners can be from neighboring communities against a common enemy (Macfarlan et al. 2014). Hunter-gatherer societies also used levelling coalitions mainly involving males, and these were of larger size than seen in nonhuman primate species (Bowles 2006; Pandit and van Schaik 2003). It is thought that these coalitions carry lower costs due to the use of language allowing greater coordination and the greater number of participants reduces the costs for the aggressors (Pandit and van Schaik 2003). Historically, in human societies males are generally more closely related than females and as a result coalitions are thought to have evolved between related individuals within groups against a common out-group enemy similar to that of nonhuman primates.

Conclusion

Coalitions can occur both within and between groups in nonhuman primates. The level of contest within a group can determine the probability and feasibility of the occurrence of within-group coalitions. At too high or too low contest coalitions, within-groups are not expected. At mid-high contest levelling, coalitions are feasible as males fight over access to females and either male

could gain access to the female once a coalition has broken-up a consorting pair. At lower contest, rank-changing coalitions are more likely and may require several aggressive bouts to allow one or both partners to rise in rank. Thus these coalitions should require a reliable partner. In species where male affiliation is common, those males with stronger social bonds may be more likely to form coalitions. Individuals in the same group may also form a coalition against members of another social group. For these, the individuals involved share a common goal of defeating a common enemy, making such coalitions more feasible. In some species, these contests can be intense and lead to physical injury or even death. Such lethal coalitionary aggression has been described as similar to that of human warfare.

Cross-References

- [Alliance Formation Theory](#)
- [Alliances](#)
- [Alpha, Beta, and Gamma Males](#)
- [Coalitional Relationships](#)
- [Male Adaptations that Facilitate Success in War](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Mechanisms to Prefer Traits in Coalition Members](#)
- [Self-Assessment of Fighting Ability](#)
- [Sexual Access as Benefit of Victory in War](#)

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Fellatio

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Synonyms

[Blow job](#); [Oral sex](#)

Definition

The oral stimulation of the penis, especially to orgasm.

Introduction

“Fellatio” is defined as the oral stimulation of the penis, especially to orgasm. The word derives from the Latin “*fellatus*,” meaning “to suck.” Fellatio is a common form of foreplay in sexual relationships as well as a sexual end in itself. The practice has been documented in animals, in ancient societies, and in contemporary primitive societies, strongly implying that it has some form of evolutionary benefit.

Flying foxes and fruit bats have been documented to engage in fellatio, with sex lasting longer between fruit bats if the male is first fellated

(Tan et al. 2009). The Indian *Kama Sutra*, written in the first century AD, explores the subject of fellatio in considerable detail. The author believed that it was commonly practiced by promiscuous women, that it was a ritually unclean practice, and that those who were known to engage it in were often shunned by civilized society. Homosexual fellatio is depicted on the Greek Attic red figure kylix, which has been dated to around 510 BC. Anthropologists have recorded fellatio among assorted tribal groups. The initiation rite of passage of the Sambia, of Papua New Guinea, involves prepubescent boys, aged between 7 and 10, daily fellating older males and swallowing their semen (Soble 1997, p. 124).

Fellatio and Evolution

There is much debate on how the practice of fellatio may have evolved. A number of studies have indicated direct benefits in terms of fertility and health. The first benefit is that oral sex, as foreplay, makes fertilization more likely. Tan et al. (2009) suggest that fellatio-related foreplay increases the degree to which the penis is lubricated, increases the size of the erection, and increases the length of intercourse, heightening the level of secretion from the pituitary gland. All of these factors, they argue, increase the likelihood of successful fertilization. Secondly, the same researchers suggest that saliva may reduce the risk of passing on certain sexually transmitted diseases, ensuring a healthier partner and offspring.

Thirdly, research has shown that when a woman regularly swallows her partner's semen, her immune system becomes used to it to, making it more likely that the mother's immune system will accept the proteins in the father's semen. It has been found that many miscarriages, or preterm births, occur because the mother's immune system treats these proteins, in the fetus, as foreign bodies. It has been found that 82% of women without preeclampsia (a condition marked by high blood pressure during pregnancy which can lead to miscarriages and preterm births) regularly practiced fellatio on their partner, but only 44% of

those with preeclampsia did (Koelman et al. 2000). Accordingly, fellatio aids the birth of offspring who are more likely to survive.

Thus, fellatio appears to have evolved, in part, because it is associated with fertility and health. However, parallel dimensions of its evolution have been suggested. Pham and Shackelford (2013) proposed that infidelity detection may be one reason why women may wish to fellate their partners. In a context of relatively poor cleanliness, it is possible that cues of infidelity could be unconsciously picked up through tasting the penis. Pham et al. (2015) found that both men and women reported being more satisfied with their relationships the more oral sex they had and length of relationship was moderately inversely correlated with frequency of and length of oral sex. Thus, part of the purpose of oral sex would appear to be simply bonding. Indeed, giving oral sex within a relationship has been shown to be positively associated with Agreeableness (Pham et al. 2015), which is itself associated with the capacity to foster strong bonds.

Fellatio and Religion

This bonding dimension would be consistent with the practice of fellatio by children in Papua New Guinea on older males. The practice is likely to create a bond between the two males, inducing the older male to assist the younger one in times of need. In this sense, it can be seen to elevate in-group cooperation, and it has been found that internally cooperative groups, all else being equal, tend to triumph over less internally cooperative groups (see Sela et al. 2015). In addition, among the Manchu people of China, a mother may show affection to her son, under the age of 2 years, by kissing his penis or putting his penis in her mouth (e.g., Renteln 2004, p. 243, footnote 49).

Moreover, it has been argued that, to a great extent, religion should be understood as an evolutionary strategy which renders individuals and groups more likely to survive under conditions of natural selection (e.g., Sela et al. 2015).

Consistent with this, many forms of behavior which religious groups promote as divinely mandated have been shown to ultimately promote selection (Sela et al. 2015). Homosexual fellatio in New Guinea tribes – among heterosexual males – reflects a central part of the tribes' belief system. They believe that young boys do not yet have semen and so they must acquire it from other men via fellatio and acquire as much of it as possible.

Fellatio, Group Differences, and Life History Strategy

A number of studies have found group differences in the extent to which fellatio is performed. If a significant dimension to fellatio is bonding, then this is to be expected. Rushton (2000) has argued that different racial groups vary in their life history speed, in a model known as Differential *K*. Fast life history (LH) strategists, evolved to a plentiful but unstable ecology, tend to invest more resources simply in reproduction. As life is unpredictable, they are evolved to seek out and copulate with as many fertile and healthy people as they can, investing little energy in their partners and hoping some offspring survive. Slow LH strategists, in a harsh yet predictable ecology, reach the carrying capacity for their group and start competing to a greater extent with each other. This selects for quality over quantity. Accordingly, they invest more energy in the nurture of their (smaller number of) offspring and more energy in their (smaller number of) sexual partners, to ensure their offspring's survival. They create strongly bonded units. Accordingly, to the extent that fellatio is a matter of bonding, there should be group differences in its extent.

Rushton argues that sub-Saharan Africans are, on numerous measures, faster life history strategists than are Caucasians. Pham et al. (2015) have shown that Agreeableness (an aspect of a slow LH) positively predicts performing oral sex. The available studies on group differences in fellatio

are consistent with this. They all find that African Americans, compared to Whites, are markedly more likely to have never been fellated or to have never fellated and they are more likely to have experienced or performed fellatio in a relationship only after the performance of penetrative sex, with this ordering being reversed in Whites (e.g., D'Souza et al. 2014). Unfortunately, studies comparing White and East Asian people are confounded by the fact that relatively young samples are employed (e.g., Meston et al. 1996) and East Asians appear to become sexually active later than White people (Rushton 2000).

Consistent with the idea that fellatio is associated with a slow LH, some research has found evidence that lower SES people are less likely to engage in fellatio than higher SES people (e.g., Schofield 1965). Black people in the USA, on average, have lower socioeconomic status than White people, so this may be the mediating factor. Lower SES people, on average, follow a faster LH strategy than higher SES people (Rushton 2000).

Future Research

In terms of future research, it would be of great interest to establish in more depth the extent to which the practice of fellatio varies between different groups and thus the degree to which it may be a reflection of life history strategy. Related to this, it would be interesting to understand the origins of different attitudes to fellatio in different religions, as it may be that fellatio is more or less adaptive in different ecologies. Exploration of the Manchurian practice of briefly fellating babies and toddlers would also be interesting. In Western countries, young children are sometimes patted on the buttocks by adults, supposedly as a form of affection, or at least they have been historically. It is possible that there may be some evolutionary reason behind what some would regard as the unacceptable sexual touching of young children, though precisely what is a matter for future research to address.

Cross-References

- [Cunnilingus](#)
- [Masturbation](#)

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Fellowships

- [Same-Sex Relationships](#)

Female Age as a Predictor of Men's Aggression Against Women

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Synonyms

[Homicide](#); [Intimate partner violence](#); [Mate retention behavior](#); [Physical aggression](#); [Rape](#); [Sexual aggression](#); [Stalking](#)

Definition

Men use various forms of physical (homicide and intimate partner abuse) and sexual (rape and sexual coercion) aggression against women to control female sexuality and circumvent female sexual choice. Female age predicts physical and sexual forms of men's violence. Young, fertile women, as compared to older women, are reproductive commodities and, thus, are the primary targets of men's aggression.

Introduction

Men have evolved a sexual preference for youthful, reproductive-age women. Men's sexual preference for younger women is one feature of human male sexual strategy (Kenrick and Keefe 1992; Thornhill and Palmer 2000). Youthfulness is a reliable indicator of fertility. Ancestral men who were primarily attracted to fertile women thereby increased their reproductive success. Additionally, young women are more valuable to men as mates. Men report that youth is one of the most important characteristics in a partner, across 37 cultures (Buss 1989). Buss (1989) found that men in all 37 cultures rate youthfulness as a

highly desirable trait in a marriage partner. On average, and across cultures, men prefer a mate that is roughly 24 years old, an age near women's peak reproductive value, or expected future reproduction. Youthfulness is an important trait among men's preference not only for long-term mates but also for short-term mates. Across five cultures, younger female escorts advertise a higher fee for their services, compared to older escorts (Dunn 2018). Given an evolved desire for youth, men are willing to pay younger escorts more money than older escorts. Younger escorts present more observable signs of fertility and reproductive value than do older escorts and therefore can charge and are paid more.

Men use sexual and physical aggression against women to deter rivals, secure sexual access, circumvent female sexual choice, and minimize investment for sexual access. Men may use physical aggression, such as partner violence, to dissuade a woman from desertion or infidelity. Sometimes, however, men kill their partners to thwart abandonment or cuckoldry. Men use sexual aggression, such as rape, to secure sexual access without providing investment or resources. Men's use of aggression is an aspect of a sexual strategy designed to control women's sexual behavior to thereby secure exclusive sexual access to her. Given men's preference for youth and fertility, men primarily use aggression against younger women.

Men with younger, reproductive-age partners are more likely to inflict violence on them to control their sexual behavior (Smuts 1992). Young women are more fertile and are more likely to reproduce than are older women. Whereas women can be certain that an offspring is their genetic kin, men can be deceived into providing resources and investment to an offspring that is not their genetic kin. Younger women pose greater risk than do older women to men's reproductive success: the costs of a reproductive-age women's sexual infidelity or desertion are more devastating to men, as compared to an older partner's deceptions. Older women can no longer reproduce and cannot cuckold or trick a man into investing resources into a child that is not his genetic kin. Thus, the prospects of sexual infidelity and

paternity uncertainty/cuckoldry motivate men's aggression against *younger* women more frequently than against older women. To avoid being deceived into raising genetically unrelated offspring, men deter women with violence. Ancestral men who successfully used aggression against younger women, thereby convincing a woman to stay in a relationship or to deny a potential mate poacher, were likely to achieve greater reproductive success. In sum, younger women are greater assets to men than older women, given younger women's greater fertility and reproductive value; thus, sexual infidelity, abandonment, and lost sexual opportunities are distressing events for men, resulting in men's use of aggression – especially directed against younger women.

Intimate Partner Violence and Homicide

The age of a woman predicts the likelihood she will be the target of intimate partner violence or homicide. Young women aged 16–24 years report the highest levels of nonlethal intimate partner violence (Rennison and Welchans 2000). Intimate partner violence may take multiple forms, including physical violence and emotional or psychological aggression (e.g., threats of physical violence or defection). Buss and Duntley (2011) suggest that intimate partner violence may reflect a mate retention strategy in which men attempt to deny a partner's relationship defection or infidelity. Intimate partner violence functions to control a woman's sexuality and to thwart rival sexual access. Male sexual jealousy is the most common cause of intimate partner violence and homicide (Daly and Wilson 1988). To combat the threat of cuckoldry, male sexual jealousy may have evolved as a mechanism of infidelity prevention or detection and as a motivator of subsequent, sometimes violent, behavior (Buss 2000). Given men's evolved interest in securing young, fertile women with high reproductive value as mates, male sexual jealousy should be especially sensitive in the context of mateship to younger women. Because younger women are more desirable to male rivals, male sexual jealousy may motivate

men to use aggression against their partner to stop them from defecting. In sum, men may benefit by restricting a younger mate's, as compared to an older, nonfertile mate's, sexuality through physical aggression because this aggression ancestrally increased male reproductive success by lowering the risk of cuckoldry and abandonment.

Intimate partner violence occasionally escalates to homicide, particularly targeting young women. Young women are more likely to be killed by their partner than are older women (Shackelford et al. 2000). Specifically, women aged 15–24 years, within the peak reproductive years, are most likely to be killed by their partner (Daly and Wilson 1988). The greatest risk of uxoricide (wife-killing by husband) in Canada fell on the youngest registered wives (Wilson et al. 1993). These women were also in the 15–24-year age range, aligning with an evolutionary perspective on men's use of strategic aggression against younger women. Another study found that the risk of uxoricide decreases with a woman's age (Shackelford 2001). Men's partner-killing may be produced by an evolved psychology designed to produce death in these circumstances (Buss 2006). Specifically, ancestral men may have increased their relative reproductive success by permanently dissuading their partner from defecting or committing sexual infidelity – and thereby eliminating entirely any risk of cuckoldry or defection. Researchers have investigated whether younger women are killed more often than older women because younger women are mated to younger men, who commit the majority of violent crimes. The results of this research found that younger women are more likely to be killed across *all* male partner age groups (Shackelford et al. 2000). Because young, fertile women have the highest reproductive value, it follows that men should primarily commit physical aggression against younger mates, which research supports.

Stalking

Buss (2006) proposed that stalking is a feature of men's reproductive strategy. Stalking is an extreme form of mate guarding and refers to a range of persistent psychological and physically

abusive activities, often in the form of spying, surveillance, or threats (Buss 2000). Stalking may function as a mate retention strategy to deter rivals/mate poachers, to acquire new mates or ex-mates, or as a sexual predation or exploitation tactic (Duntley and Buss 2012). Duntley and Buss (2012) suggest that psychological adaptations may facilitate and motivate stalking. The psychology of stalking may have evolved because it increases the likelihood of mate reconciliation and dissuades rivals, which thereby increased the ancestral stalker's reproductive success.

Similar to intimate partner violence and homicide, women within the peak reproductive-age bracket are most likely to be the victims of stalking. A majority (56%) of college-aged (18–24 years) women report having been stalked (Buss 2000). Additionally, Buss (2000) reported that 80% of women who have been stalked in their lifetime indicated that they were younger than 40 years at the time of the stalking. Most of those women were between 18 and 29 years, with an average age of 28 years. Given that fertility peaks in the mid-20s (Thornhill and Palmer 2000), most stalking victims were within the peak reproductive period, suggesting that stalking may be produced by an evolved psychology. Most women report that the men who stalked them did so to keep them from leaving the relationship (Buss 2000). Women's perceptions of stalking align with an evolutionary explanation of stalking. Stalking also sometimes functions as a tactic to sexually coerce women. When successful, it may deter rivals from gaining sexual access, thereby interfering with female sexual choice. Some (but not all) women who are stalked eventually date the man who stalked them (Duntley and Buss 2012). Because young women are the primary targets of stalking, the men who successfully stalk them and gain sexual opportunities, while fending off rivals, may have been ancestrally more reproductively successful.

Rape

If rape is produced by an adaptation that increased ancestral male reproductive success, one might

expect that rapists would target fertile, reproductive-age women, as opposed to older, nonfertile women. Similar to men's physical aggression and stalking behaviors against women, rapists target youthful, reproductive-age women (Thornhill and Thornhill 1983). It is possible that a victim-preference mechanism, such as a desire to copulate with younger, more attractive women, may have increased the ancestral reproductive benefits of rape. Ancestral men who successfully raped reproductive-age women may have thereby increased their reproductive success, without providing resources or investment to the woman and subsequent offspring, thereby circumventing female sexual choice. In an analysis of over 34,000 robberies, the highest risk of being sexually assaulted or raped during a robbery fell on women aged 15–29 years (Felson and Cundiff 2012). Male perpetrators of *all* age groups that committed sexually aggressive acts during robbery targeted women in this reproductive-age bracket. However, there was no difference between instances of rape and of sexual assault during robbery. The adaptation hypothesis suggests that rape is a reproductive strategy with which ancestral rapists increased their reproductive success by circumventing female sexual choice (Thornhill and Palmer 2000); sexual assault alone would not have increased ancestral reproductive success. Thus, the adaptation hypothesis of rape is not fully supported; however, those who exclusively committed sexual assault primarily targeted younger women, so sexual aggression as an adaptation cannot be dismissed. Additionally, women may have evolved mechanisms to prevent being raped (Buss 2006). Given the costs of rape (e.g., caring for a child without paternal investment), young women are especially fearful of situations that put them in sexual or physical danger (Scott 2003). Scott (2003) reported that as a woman's age increases, her fear of being a victim of various forms of victimization, including sexual aggression, decreases. Research indicating that younger women rate dangerous sexual situations as more distressing than older women provides evidence for evolved anti-rape mechanisms in women. Anti-rape mechanisms may have coevolved in response to evolved sexual aggression

mechanisms in men. However, the tendency for men to rape younger women, as compared to older women, does not convey whether men have specialized rape adaptations or if rape occurs as a by-product of other evolved mechanisms (e.g., attraction to youthfulness).

In uniquely violent cases, young women (20–24 years) are the special targets of rape-homicide (Shackelford 2002a). Although it has been hypothesized that younger women may be special targets of men's aggression because they are more frequently associated socially with younger men, who commit most violent crimes, including homicide, rape, and rape-homicide (Daly and Wilson 1988; Thornhill and Palmer 2000), Shackelford (2002a) provides evidence to the contrary. Young women were *not* overrepresented in cases of theft-murder, only in rape-homicide cases, suggesting that association with younger, violent males is not the cause of younger women's greater risk of rape-homicide. Instead, women's age is the primary predictor of men's perpetuation of rape-homicide. Shackelford (2002b) also found that younger women are more likely to be the victims of rape-homicide involving two or more male offenders, further indicating that rape-homicide is not an outcome of young women being more frequently socially associated with younger men. However, most men who rape do not subsequently kill the victim, perhaps because rape may have increased ancestral reproductive success only when the victim lives to produce a child (Buss 2006). Shackelford (2002a, b) suggests that men who commit rape-homicide kill because the costs of detection may outweigh the benefits of reproduction or because the perpetrators have especially low impulse control or other psychopathic characteristics.

Conclusion

Younger women, as compared to older women, tend to be the target of men's aggression. Younger women are the primary victims of men's aggression because fertile, reproductive-age women ancestrally afforded men the greatest reproductive success and social status. If controlling a younger women's sexuality, as compared to an older,

nonfertile woman's sexuality, conferred reproductive benefits on ancestral men, mechanisms may have been selected that motivate male sexual proprietariness. Intimate partner violence and homicide are male tactics used to inhibit young women from committing sexual infidelity or deserting the relationship. Stalking may be used by men as a fear-inducing mate retention strategy, particularly targeting younger, reproductive-age women. Men may rape younger women to increase their own reproductive success without investment, thereby denying the woman sexual choice and freedom. In sum, men of all ages may increase their own reproductive success by using physical and sexual aggression primarily against young, fertile women.

Cross-References

- [Conflict Between the Sexes](#)
- [Contexts for Men's Aggression Against Women](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Homicide Adaptation Theory](#)
- [Male Sexual Jealousy to Deter Partner Infidelity](#)
- [Partner Abuse and Homicide](#)
- [Sexual Coercion and Violence](#)

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Female Choice

- [Female Reproductive Variance](#)

Female Choice and Sexual Conflict Theory

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Synonyms

[Epigamic selection](#); [Female mate choice](#)

Definition

When females are the choosy sex and retain primary control over which males they will mate with. Thus, members of the lower investment sex, usually males, compete for features that are attractive to members of the high investing sex, usually females. In this sense, females choose on the basis of male displays or traits.

Introduction

The outcome of sexual selection is the evolution of secondary sexual characteristics that are designed to attract and compete over mates. Traits that evolve via sexual selection do so as a result of competition for mates (intrasexual competition) or mate attraction (epigamic selection). Intrasexual competition is competition between members of the low investment sex (usually males) for copulations with the high investment sex (usually females). Since males are usually the low investment sex, they are the most intrasexually selected. This results in traits beneficial for competing with other males such as organs of threat (antlers, large size, aggressiveness, etc.). In some cases, these traits will be used in direct physical combat with other male; in other cases, they may be used to establish dominance hierarchies where the males at the top monopolize mating opportunities. An example of intrasexual selection for size is found in elephant seals where males are substantially larger than females, spend much of their time competing for females, and the most dominant males father the majority of pups in any given season.

Epigamic selection is competition between members of the low investment sex for features that are attractive to the high investment sex. As with intrasexual selection, the sex that invests less per offspring is usually the male. Thus, this type of selection is often referred to as female choice; the females choose on the basis of male displays or attributes. The result of female choice is the elaboration of displays, coloration, and courtship rituals as the males try to “impress” the females by competing with other males via

display mechanisms. Under female choice, highly elaborated traits can evolve, such as the peacock’s tail (Petrie 1994). Such traits exist because of the female preference for them. Males with those traits, or the most impressive examples of such, were the most successful at reproducing and passed those traits on to their offspring. However, this raises the question of what benefit those traits are to the reproductive success of females? Why do they choose them?

Runaway Selection or the Sexy Sons Hypothesis

The effects of female choice can lead to what Fisher (1915, 1930) referred to as runaway selection. In this process, females are initially predisposed to favor a particular male trait (reason unspecified) and those males possessing the favored trait attract females and experience greater reproductive success, which in turn passes on the male trait as well as the female preference for that trait. The joint selection for that trait creates a positive feedback loop that continuously favors both these traits (the trait in males and preference for it in females). The result can be “runaway” selection of the male trait, leading to the evolution of more elaborate or extreme versions of the original trait. This has been used to explain the evolution of elaborate male ornamentation or other secondary sexual traits that would seem to reduce the survival of those who possess them, though presumably the runaway process would cease when the survival costs outweigh the benefits of attracting mates (Pomiankowski and Iwasa 1993). Where does the original preference for the trait on the part of females come from? The trait might have had some adaptive value, as a health indicator, for example, bright coloration revealing the male to be free of parasitic infection. Or the trait could have been preferred by females for purely arbitrary reasons unrelated to fitness. For example, a bird could have a color preference or sensory bias due to a food item of that color being a major component of their diet. As a consequence, anything with that color, including a male of their species, may be

perceived as attractive. It has been suggested that such sensory bias has influenced female choice in guppies. Rodd et al. (2002) suggested that male color patterns are the result of female choice of males with orange spots due to the attraction of both sexes to inanimate orange objects. Guppies frequently eat orange food items; thus, the suggestion is that selection for easy detection of orange food items results in selection for preferences for orange males. However, Houde (1997) and Kennedy et al. (1987) suggest that female choice for males with orange spots is adaptive because males must ingest carotenoids to produce these colors and thus the bright color could be an honest indicator of male quality.

Related to runaway selection is the sexy sons hypothesis which states that females choose males with attractive traits, such as large size or bright colors, because these traits will be passed onto their sons who will also be able to attract many mates. From this perspective, females that choose a male whose genes will give her sexy sons will have a good chance of having their own genes passed on by her sexy sons. Evidence in support of the sexy sons hypothesis of female choice has been found in several bird species including European starlings (Gwinner and Schwabl 2005) and beetles (Pai and Yan 2002) though others suggest that good genes are what females are choosing for as will be discussed next.

The Handicap Principle and Honest Advertisements

Why do males evolve extravagant costly traits like peacock tails or nest displays like satin bowerbirds? While these traits help them attract mates, they also attract predators, can make it difficult to escape from them, and are metabolically costly.

Zahavi and Zahavi (1997) suggested that a trait would be selected for if it provides a cost to its carrier that indicates something about the quality of the carrier. The peacock is often highlighted as an example of Zahavi's handicap principle with the male tail serving as a costly signal. Peahens select from a pool of possible mates. Assuming that genes are all that the males

provide and that males vary in genetic quality, peahens should aim for the male with the best quality genes available.

As genetic quality cannot be directly assessed, peahens attend to cues that males provide. Peacocks advertise genetic quality via large, colorful, symmetric tails. Such an ornament is a handicap in that it is energetically costly to build and difficult to hide from predators. A poor quality male would not be able to produce an impressive tail as his energies are required just for basic somatic maintenance as well as predator avoidance. A high quality healthy male, however, can afford the cost of such an advertisement. Since only high quality males can afford impressive tails, peahens prefer males with large, bright, symmetrical tails to mate with as they serve as honest indicators of male quality (Loyau et al. 2005; Petrie 1994). Studies have documented similar impacts of female choice on advertisements in long-tailed widowbirds (Andersson 1994), the vocalizations of male American Bison (Wyman et al. 2008). Studies in humans have also suggested a role for honest advertisements in the mating arena including face shape preferences, such as male face shape as an indicator of immunocompetence (Scott et al. 2014), and humor on the part of males as an indicator of intelligence and good genes (Miller 2000; Greengross and Miller 2011).

Is Female Resistance a Form of Female Choice?

Female resistance is defined as the process by which females evolved to resist male control of mate choice, allowing females control over their own mate choice decisions. Thus, female resistance can be seen as a form of sexual conflict through which females use resistance to select mates and perhaps shape the evolution of male structures and behaviors. Female resistance to males might be designed to gain indirect fitness benefits by allowing the female to select for males based on their ability to manipulate females or their physical strength in cases where male defense of offspring and mate might be required, and to select for "better genes" or material

resources (Cordero and Eberhard 2003; West-Eberhard 2014).

Female selection of antagonistic traits in males via resistance has been documented in gladiator frogs (Kluge 1981). However, the evidence with regard to the role of female resistance in female choice in other species is rather limited. In the case of human females, it has been suggested that the commitment skepticism bias in Haselton and Buss (2000) is a form of filter resistance that deters females from being deceived about the costs of mating that a male may impose due to a lack of commitment. Such a bias on the part of females requires males to clearly demonstrate their willingness to commit and ability to provide benefits rather than impose costs.

Conclusion

While mate choice was once viewed as something males engaged in, males mainly competing for access to females, it is clear that females also engage in mate selection and their choices influence the evolution of male traits. Females may exert choice through inciting male display of honest advertisements of quality in addition to antagonistic displays, including female resistance. Females may also shape male traits via selection for the production of sexy sons.

Cross-References

- [Evolution of Female Resistance](#)
- [Intrasexual Competition](#)
- [Sexual Conflict Theory](#)
- [Women's Mate Preferences](#)

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Female Choice for Men High in SDO

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Synonyms

[Dominance](#)

Definition

Female choice for men with high SDO describes preferences for men who are competitive, formidable, anti-egalitarian, and prefer short-term mating.

Introduction

In mate choice, females often face a trade-off in choosing the best possible mate where genetic quality and parental investment are prioritized. Males who exhibit good genes may also be men who are socially dominant and competitive, and therefore, more likely to be interested in short-term sexual encounters. Females seeking dominant males may be attempting to secure the benefits bestowed by them, such as access to material resources, protection from threats, and producing strong and healthy children (Kruger and Fitzgerald 2011). However, preferences for dominant males may be modulated by factors associated with fertility, relationship context, and masculinity. Recent research has found evidence on the link between social dominance orientation and political conservatism, thus, it is worth mentioning if female mate choice for socially dominant males also carries over to preferences in political attitudes associated with social dominance.

Female Choice for Men High in Social Dominance

Why do females choose males who are high in social dominance orientation as mates? Socially dominant males, as measured by the SDO, are males who are callous and manipulative, desire power, oppose income redistribution, are formidable, and tend to pursue short-term mating strategies (Sinn and Hayes 2018). Although these characteristics are also associated with low paternal investment, females who pursue dominant males are benefitting from the advantageous of males who are competitive, can obtain access to material resources, and have increased genetic quality. Access to these types of mates may be dependent on the type of relationship context that females are pursuing, such as prioritizing a short-term partner over a long-term partner. In searching for dominant males, females pursuing short-term mating may benefit from healthy offspring, immediate resources acquisition, and protection from threats. However, females searching for long-term relationships with dominant males run the risk of an intersexually competitive male who may not be willing to invest heavily in one female. Dominant males have been found to be associated with preferring short-term mating, aggressive behaviors, and having highly masculine appearances and behaviors. This contrasts with males who are considered high in prestige, who are associated with preferring long-term relationships but achieve social status through noncoercive means (Kruger and Fitzgerald 2011).

Preferences for dominant males can be modulated by fertility status. If females are to gain from choosing dominant males, then it should occur during a time period that corresponds with peak fertility, where reproductive advantageous (i.e., genetic quality) are most likely to occur. Research investigating fertility status and preferences for dominant traits in men have found that the point of the menstrual cycle that corresponds to peak fertility, as measured by hormonal fluctuations, influences dominant trait preferences. Women have been shown to prefer dominant traits

when luteinizing and follicular stimulating hormones are highest, which are hormones that are associated with the fertile window. Interestingly, as aforementioned, these preferences were for short-term partners, which suggests that women may upregulate interest in cues to genetic quality during the fertile window and downregulate interest in these cues during infertile times of the menstrual cycle (Lukaszewski and Roney 2009). It is important to mention that recent studies investigating the role of hormones in preferences for dominant men have failed to find an effect for fertility status (Garza and Byrd-Craven 2019; Jones et al. 2019), suggesting that hormonal detection in dominant men is more complex than previously thought.

Although it is known that women pursuing short-term mating relationships have preferred men high in social dominance, are salient physical traits able to account for those preferences? Men who display dominant and masculine physical characteristics are considered sexually attractive (Swami and Tovee 2005), and it can be argued that these physical characteristics can account for the advantageous gained from traits associated with social dominance, such as resource acquisition, and offspring and mate protection. Men with V-shaped bodies are considered physically dominant and masculine (Buunk and Dijkstra 2005), and these traits can explain the reason why females are attracted to men who are socially dominant because they have the physical capability to carry out socially dominant behaviors. Women have been known to be attentive to physical characteristics associated with dominance, such as preferring taller men, symmetrical men, and body types that resemble the android pattern, where fat distribution is deposited on the upper region of men's bodies. Research investigating determinants of romantic partner desirability has shown that dominance and a lower waist to shoulder ratio is a reliable predictor in desirability for a one-time sexual encounter; however, dominance did not mediate the relationship between WSR and desirability for a sexual encounter (Braun and Bryan 2006). Simply put, the physical

characteristics associated with dominance (i.e., low WSR) were considered desirable by women.

Do preferences for social dominance relate to preferences for sociopolitical attitudes, such as egalitarianism? Social dominant characteristics, like formidability, provide men with the tendency to be more competitive and benefit from successes in inequalities in status and resource distribution (Price et al. 2017). Just as some physical characteristics are associated with dominance, research linking social dominance with sociopolitical attitudes has shown that body formidability, as measured by a composite of upper body strength, is negatively related to sociopolitical egalitarianism and support for redistribution. In addition, body formidability has been shown to be positively related to social dominance orientation, which may suggest that men with certain types of physical characteristics indirectly display psychological attributes associated with dominant behaviors. Studies with larger samples have also demonstrated that formidable characteristics are positively related to anti-egalitarianism (Petersen and Laustsen 2018). Similarly, men with higher bicep circumferences (i.e., formidability) have been shown to be more supportive of military action, and this effect has been larger in men than women (Sell et al. 2017).

Given the relationship between formidability and sociopolitical attitudes, and women's preferences to dominant men, what if any is the relationship between female mate choice to men with political ideologies associated with dominance, such as conservatism? Most research has focused on women's mate preferences to men that display dominant characteristics, and most research on social dominance has focused primarily on same-sex attributions of formidability and egalitarianism. Literature on political behavior has identified patterns in political ideology identification, where attractive individuals are likely to claim Republican or conservative parties (Peterson and Palmer 2017). However, it is unclear whether female mate choice for socially dominant men also reflect preferences for political ideologies that overlap with social dominance. In addition, research should begin

investigating females' own level of dominance and political ideology and their preferences for males with similar characteristics. With this approach, testable predictions can be formulated regarding women's mate preferences to socially dominant men, such as women's level of social dominance and/or egalitarianism and its association with men's physical characteristics that reflect social dominant traits (i.e., formidability, strength).

Conclusion

In conclusion, preferences for socially dominance men (SDO) can provide many direct benefits to women, such as resource acquisition, status transmission, and protection against threats to offspring. However, preferences for dominance is mitigated by many factors that can enhance those direct benefits, such as relationship preferences and fertility status. An important thing to note is that women's preferences for physical characteristics associated with dominance has shown strong empirical support, yet female preferences for SDO and physical characteristics has not been explored. Lastly, given the relationship between SDO and sociopolitical egalitarianism, future research could begin investigating if female preferences for SDO men also overlap with their own political ideologies in addition to the political ideologies of potential mates.

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Female Choice Polygyny

► Polygyny Threshold, The

Female Coalitions

► Female-Female Alliances

Female Copulatory Orgasm

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Synonyms

[Orgasm triggered by sexual intercourse](#)

Definition

Emerging evidence suggests that orgasm elicited by sexual intercourse evolved to give women feedback about mate choice and to induce changes that increase the likelihood of impregnation.

Introduction

Orgasm in men is nearly universal. However female orgasm is much more variable in frequency. Many theories have been advanced to explain the advantage that orgasm might confer in women. This entry examines recent evolutionary-based interpretations of female orgasm.

One of the leading interpretations of female orgasm is that because orgasm produces vaginal and intrauterine contraction it enhances sperm transport and retention, and it enables a woman who mates with multiple partners to selectively experience orgasm with the man with the best genes, thereby increasing the likelihood of conception and the corollary fitness of her offspring. This interpretation is supported by a study with undergraduate college students where female orgasm frequency and intensity were positively correlated with partner attractiveness (Gallup et al. [2014](#)). Frequency of female orgasm was also correlated with partner family income level, suggesting a mechanism for identifying mate-provisioning ability. Additional support for this

interpretation comes from a study where it was discovered that a woman's likelihood of orgasm was positively correlated with how attractive the woman thought her partner was to other women (Sela et al. [2015](#)).

Sperm Retention

There are other reasons to believe that orgasm increases the chance of impregnation. One study found that the experience of female orgasm increased the level of sperm retention after copulation for up to 8 days (Baker and Bellis [1993](#)). Although this effect gradually declined with time, any orgasm which occurs afterward (including noncopulatory) served to reinstate and promote sperm retention. Additionally the amount of sperm retained from the first copulation was negatively correlated with the amount retained during a second copulation. It has been shown that oxytocin triggered by orgasm produces a dramatic increase in uterine peristaltic movements, which selectively propel sperm into the fallopian tubes (Wildt et al. [1998](#)). Coupled with research which links levels of oxytocin with intensity of orgasm (Berlow [2004](#)), it is reasonable to suppose that as orgasm intensity increases so should sperm transport and the likelihood of impregnation.

Multiple Orgasms

One of the biggest differences between male and female orgasm is the latter's ability to experience multiple orgasms in a single encounter. The likelihood of experiencing multiple orgasms is positively correlated with female orgasm frequency and intensity, and the age of her partner (Gallup et al. [2014](#)). Since the frequency and intensity of female orgasm is correlated with partner attractiveness and family income, this suggests that the experience of multiple orgasms functions as a signal that the woman has found a mate of significant fitness and provisioning potential. In addition, multiple orgasms may result in an even greater production of oxytocin thereby furthering the chances of conception.

Sedative Properties of Orgasm

Other adaptive features of female orgasm are its sedative properties. Females that experience sedative effects of orgasm are more likely to remain in a prone position for an extended period of time following insemination, and would benefit from reduced “flow-back” leading to increased sperm retention. The release of both oxytocin and dopamine in the brain during orgasm fall sharply afterward. This sudden surge and withdrawal of neurochemicals creates a feeling of being drained of energy; meanwhile as dopamine and oxytocin levels fall, prolactin levels rise which lead to feelings of satiation (Berlow 2004). Additionally prolactin increase following orgasm in females is four times greater after intercourse than masturbation (Brody and Kruger 2006). The sedative effect of orgasm is further implicated by a survey where 32 % of women reported the use of masturbation as an aide to help them fall asleep (Ellison 2000). The sedative effects of orgasm may play a role in mate choice by ensuring retention of the male’s sperm, prevention of further insemination by potentially lesser-quality males, and promotion of pair-bonding between the female and the high-quality male.

Extra-Pair Copulations

The role of orgasm during extra-pair copulations (EPC) may also serve to increase the likelihood of conception by the extra-pair (EP) male. Previous work has found that women are more likely to experience an orgasm and report orgasms of greater intensity during an EPC (Gallup et al. 2006); some research has even found that women are more likely to have multiple orgasms during EPCs. Baker and Bellis (1993) report that women who engaged in EPCs were more likely to retain the sperm of their EP mates and less likely to retain sperm from their committed partner (CP). This was due to the fact that orgasms were much more likely during an EPC, and that the number of noncoital orgasms increased after the EPC. The greater likelihood of orgasm during an EPC served to retain more sperm and the increase in

noncoital orgasm frequency (largely as a consequence of masturbation) between the encounters serves to further promote retention of the EP sperm and block the CP sperm.

Lastly for a woman with a large number of children sired by her CP, each additional child becomes an increasingly redundant sample of the father’s genes. The reason for this is that the proportion of her partner’s genes not previously sampled is reduced by 50 % with each successive child. As a result, by the time a woman has three children sired by the same man she will have sampled on average 87.5 % of his genes. As a consequence conception as a result of an EPC/change in paternity would function to dramatically increase the range of genetic variance among her existing children, and genetic variation may be a hedge against an uncertain future.

Conclusion

Emerging evidence suggests that female orgasm functions to promote the movement of sperm up through the female reproductive tract and increase the likelihood of impregnation as a consequence. Research also suggests that female orgasms promote greater retention of sperm, and coupled with the sedative properties of orgasm women are more likely to remain in a prone position for an extended period of time following coitus which diminishes the loss of semen. There is also evidence that orgasms give women feedback about mate choice; i.e., females in committed relationships with an intelligent, healthy, high quality man are more likely to experience orgasm and their orgasms are also experienced as being more intense.

Cross-References

- ▶ [Cryptic Female Choice](#)
- ▶ [Female Orgasm](#)
- ▶ [In-Pair Copulation](#)
- ▶ [Male Qualities and Likelihood of Orgasm](#)
- ▶ [Orgasm](#)
- ▶ [Robin Baker and Mark Bellis](#)

- Sexual Behavior
- Sperm Competition

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Female Counter-Adaptations to Rape

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Synonyms

Coercion; Crime; Rape avoidance; Sexual assault

Definition

Rape is defined as “penetration, no matter how slight, of the vagina or anus with any body part or object, or oral penetration by a sex organ of another person, without the consent of the victim” (The United States Department of Justice 2012). Rape counter-adaptations entail specialized mechanisms that reduce women's risk of male sexual coercion.

Introduction

In the USA, an estimated one in six women will be raped in their lifetime, with 29% of victims being between the ages of 18–24 years (Tjaden and Thoennes 2006). However, it is likely these figures only represent a small number of rape victims, as rape is seldom reported to the police. Approximately 15% of victims are estimated to report sexual violence to the police (Office for National Statistics 2013). Low reporting may stem from societal misconceptions surrounding rape, including victim blaming. What is more, rape often has serious psychological consequences for victims. For instance, victims often sustain posttraumatic stress disorder (PTSD) following rape.

This chapter reviews the literature on evolutionary explanations of rape. In particular, it will discuss research that has investigated whether women have rape counter-adaptations. The discussion will be necessarily restricted to rape perpetrated on women by men. Although women can perpetrate rape and men can be the victims of rape, most rapes are perpetrated by men against women (Office for National Statistics 2013). Accordingly, evolutionary explanations of rape have been concerned with accounting for male-perpetrated rapes against females.

Costs of Rape

The evolutionary framework assumes that animals strive to attain two fundamental goals: survive and reproduce offspring. In women,

successful reproduction is considered to be passing on the strongest genes and resources that will increase the chances of survival of the species. During peak fertility, women aim to attract the highest quality mate to achieve this. Successful reproduction for males involves the quantity of their offspring, with less importance being placed on their quality (Trivers 1972). In order to survive, some psychologists propose that humans weigh up the costs and benefits of putting themselves in certain situations, which could prove fruitful, in terms of achieving resources to benefit fitness, such as meeting mates, but could also pose risks in terms of encountering aggressive mates, for example. For the purposes of this chapter, benefits refer to outcomes of a positive sexual encounter (e.g., increased chances of successful reproduction), while costs refer to the consequences of a negative sexual encounter (e.g., decreased chances of successful reproduction). Rape, therefore, is a high cost due to the reduced chances of a successful and wanted reproduction.

Perhaps one of the most obvious costs of rape is the psychological pain felt by the victim. With regards to reproductive fitness specifically, however, pregnancy arising from rape is considered to be one of the highest costs of rape. Pregnancy reduces a woman's reproductive fitness significantly because she must carry and raise offspring with a mate not of her choosing, thereby limiting her reproductive resources. For many female animals, mate choice is of high importance. However, rape circumvents female mate choice, and so, according to the evolutionary framework, it is particularly costly with regard to unwanted conception.

Evolutionary models emphasize the differential investment that women and men make in reproduction. Relative to men, women have fewer sex cells and they generally provide more time and energy to raising offspring following conception. Therefore, it is detrimental to a woman's reproductive fitness if pregnancy occurs with an undesirable mate and under conditions in which valuable resources to support the offspring are unavailable. Parental investment theory (Trivers 1972) proposes that investing in offspring increases the offspring's chance of survival while

limiting other reproductive opportunities. One hypothesis that can be derived from this is that women must take care to choose a mate who will invest time and provide valuable resources with respect to offspring. Supporting this hypothesis, women are more fearful of stranger rape despite it being much less common than acquaintance rape (Thornhill and Thornhill 1990b, as cited in Thornhill and Palmer 2000). It has been argued that fear is lower in acquaintance rape because, arguably, relative to a stranger, an acquaintance is more likely to provide resources to an offspring of rape, which reduces the cost for a woman. Furthermore, research has shown that psychological pain varies across victims, with women who are married reporting more psychological pain than victims who are single (Thornhill and Palmer 2000). It has been posited that married women suffer more pain because of the potential for abandonment and a loss of resources from their spouse if they are perceived as adulterous. Furthermore, it has also been found that women of a reproductive age who would face greater costs to their future reproductive fitness report more psychological pain (Thornhill and Thornhill 1990a, as cited in Thornhill and Palmer 2000). Women of reproductive age are more fearful of being assaulted and raped, than older women, who in turn are more fearful of a burglary. Fear seems to contribute to the experience of psychological pain, which might account for some of the variation in psychological pain in response to rape. Thus, although pregnancy is one of the most widely researched costs of rape, it is important to recognize it is not the only cost for victims.

Due to the high cost of rape, it has been theorized that women have evolved counter-adaptions in order to reduce the likelihood of rape occurrence (e.g., Thornhill and Palmer 2000). Adaptations are evolutionary solutions to environmental challenges faced by our ancestors (Ridley 1987, cited in Thornhill and Palmer 2000). Adaptive traits are selected through natural and sexual selection. That is, traits that increase "fitness," through successful reproduction and survival, are reproduced in future generations. Thus, adaptations work to increase the chance of reproduction and/or survival. Psychological pain, in particular,

has been theorized to serve an evolutionary function in regards to the adaptation of behaviors and cognitions in order to overcome problems. Thornhill and Thornhill proposed that in regards to rape, psychological pain has an adaptive benefit, focusing a woman's attention on circumstances that may have led to the rape occurring. This would then allow women to avoid a similar situation in the future, with this mechanism being passed on to future generations to allow offspring to avoid rape without ever directly experiencing the psychological and physical pain of rape.

In view of the high costs of rape, it has been proposed that women evolved adaptations to counter rape. These are referred to as counter-adaptations, because, quite controversially, some evolutionary psychologists have hypothesized that rape by a male onto a female has evolved as an adaptive reproductive tactic to spread their genetic make up to a high degree (see Thornhill and Palmer 2000). Thus, a rape avoidance adaptation in women has evolved to counter to this male adaptation. The theory and some of the evidence behind the hypothesis that rape is an adaptive male behavior will now be reviewed briefly. However, the focus of this chapter will be on reviewing the theory and evidence behind the hypothesis that women have evolved counter-adaptations to rape.

Is Rape Evolutionary?

It has generally been thought that rape by a male of a female evolved as a tactic to allow males to spread their genetic make up to a high degree (see Thornhill and Palmer 2000). However, it is important to consider that rape may be a by-product of other evolved male traits, such as a greater desire for sexual variety, a higher sex drive, or aggressiveness.

Although rape may be a byproduct of other evolutionary traits, it is also hypothesized that rape has evolved to increase the chances of successful genetic reproduction in males who cannot receive legitimate consensual intercourse from desirable female partners (see Thornhill and Palmer 2000). It is argued that males who do not have access to desirable attributes for both females and potential offspring are more likely

to rape than those who do. This concept has been shown in male scorpion flies, whereby males who lack the resources (i.e., nuptial gifts) to be selected as mates have been shown to attempt forced copulation (Thornhill 1980). In humans, criminal statistics suggest that men from low socioeconomic areas are more likely to rape, as discussed by Thornhill and Thornhill (1983). High status men are deemed less likely to rape as they are considered to have access to potential partners who would freely give sexual consent, whereas "low status" men may not have this (e.g., see Thornhill and Thornhill 1983). Alternatively, Thornhill and Thornhill (1983) argue that it may be in certain societies, such as in the United States, wealthier men are less likely to be caught or are in a better position to gain legal help to either have a case over turned or to settle out of court. It may also be the case that men who are considered to be "upstanding citizens" or are of a higher class will not be tried as harshly alongside having access to the best legal assistance. Therefore, it may not be the case that men from low socioeconomic backgrounds are more likely to rape than their higher socioeconomic counterparts, but rather, that they are overrepresented in prison statistics because they have inadequate access to legal assistance. It is, therefore, difficult to fully know whether there is a relationship between socioeconomic level and the propensity to rape, as the representation of low status males in rape data is likely to be inflated.

Analysis of pregnancy rates after rape has suggested that the per-incident rate of conception after rape is higher than consensual pregnancy rates after controlling for birth control use, suggesting that rape has evolved to allow males to spread their genetics (Gottschall and Gottschall 2003). In this study, data were collected from the National Violence Against Women survey, involving a random-digit dialing sample of households in the United States. Participants were considered to be rape victims if they answered yes to the question "Regardless of how long ago it happened, has a man or boy ever made you have sex by using force or threatening to harm you or someone close to you? Just so there is no mistake, by sex we mean putting a penis in your vagina." In

order to help estimate whether pregnancy was a result of a specific rape encounter, women aged 12–45, who had been sexually assaulted one time only, were included in the analysis. Among the 405 women who were eligible for inclusion in the study, 26 reported a pregnancy post rape. When accounting for likely use of hormonal contraceptives, it was estimated that the overall per-incident rape-pregnancy would be 7.98%, which is higher than consensual per-incident pregnancy rates, of around 2–4%. This study suggests that per-incident rape-pregnancy rates are more likely than consensual pregnancies, suggesting rape may give an evolutionary advantage to males who desire to spread their genetic makeup.

Animal Adaptations to Rape

Humans are not the only species in which rape occurs. It is believed that rape occurs in animal species, including bottlenose dolphins and wild-fowl species, for the same reasons as it does in humans, where it is a reproductive tactic to allow males to have a higher chance of successful reproduction. There is evidence to suggest that drake ducks have evolved to allow them to engage in forced copulation (e.g., Brennan et al. 2007). Drake penises have evolved to extend in an anticlockwise motion up to 20 cm in less than half a second and have backward pointing spikes that enable them to stay attached to a female. They also have soft “dusters” which allow the removal of other drake’s sperm.

Therefore, there is evidence that may suggest that rape has evolved as a reproductive tactic in humans, as well as in some animal species. However, regardless of the reasons for rape, rape is undoubtedly costly. Rape can be argued to be particularly costly to females due to the chance of conception with an undesired mate. As sexual assault is highly detrimental on a number of levels, women may have evolved counter adaptations to rape that are inherited in later generations.

For example, despite the apparent adaptation in drakes, which may help to increase the rate of reproduction, only 3% of these forced copulations results in fertilization (Burns et al. 1980). It is

therefore possible that female ducks have evolved their own counter-adaptations to reduce the risk of pregnancy from unwanted copulation. One such counter-adaptation comes from the clockwise direction in which a duck’s vagina spirals. Brennan et al. (2007) found that a drake could project its penis into a straight test tube or one that spirals anticlockwise with ease. However, it was much more difficult to insert into a tube that spiraled clockwise, in the same way that a duck’s vagina does. This creates great difficulty for forced copulation for the drake and suggests that rape as an evolutionary tactic and counter-adaptations to rape go across species. There is also evidence suggestive of female counter-adaptations to rape in water striders (Rowe et al. 1994) and scorpion flies (e.g., Thornhill 1980). However, extrapolation from research on animals to suggest the evolution of a rape adaptation in humans is questionable. As such, to be able to suggest the evolution of a female counter-adaptation to rape, it is also necessary to look at research on humans.

Counter-Adaption Rape Behavior

As well as evidence of female counter-adaptations to rape in animal species, there is evidence to suggest that women may have evolved mechanisms to reduce the likelihood of rape. It is important to note that considering evolutionary perspectives of rape and women’s avoidance of rape in no way justifies this terrible crime and certainly does not shift the blame to victims. Rather, the purpose of this chapter is to provide an overview of the evidence that has been put forward as support for the hypothesis that women may have evolved a counter-adaptation to rape that allows them to maintain their reproductive success and overall fitness. For example, it has been suggested that women appear to behave in certain ways that may reduce their risk of rape. The Rape Avoidance Inventory (RAI; McKibbin et al. 2009) details behaviors women report they would perform to avoid rape. These behaviors fell into 4 broad categories: avoid strange men, avoid appearing sexually receptive, avoid being alone, and be aware of surroundings/

defensive preparedness. Therefore, there appears to be common behaviors that women engage in to potentially reduce the risk of rape.

The Bodyguard Hypothesis (Wilson and Mesnick 1997)

As well as adopting certain behaviors, which may contribute to the avoidance of situations that could result in a rape, it has also been suggested that women have evolved preferences for mates and male friends who can protect them, known as the bodyguard hypothesis (Wilson and Mesnick 1997). This hypothesis proposes that women choose to surround themselves with mates and male friends who are likely to be able to offer protection, through being physically formidable and strong, particularly in high risk places (e.g., in a nightclub or walking at night). Women may choose to surround themselves with strong or intimidating looking males to either intimidate or act as protectors towards potential attackers. However, it is also possible that women may surround themselves with formidable mates and friends because, on average, they are physically weaker compared to men and thus want physical protection in general, rather than specifically as a counter-adaptation to rape. Indeed, women's fear of crime in general is associated with preferences for physically formidable and dominant mates (e.g., Ryder et al. 2016), which may suggest desire for protection is associated with vulnerability more generally, rather than as a mechanism to prevent rape specifically.

Hormonal Influences on Female Counter-Adaptations to Rape

There appear to be hormonal influences on women's counter-adaptations to rape. Although rape is always traumatizing and carries a high cost, there are some situations in which counter-adaptive rape behaviors are also costly to a female as they limit the chances of finding a suitable mate. In order to balance this, it may be that counter-adaptations to rape are particularly active when the costs of rape are considered to be higher,

such as when rape is most likely to result in an unwanted pregnancy. Chance of conception is highest during ovulation and lowest during the early follicular phases. Therefore, although the costs of rape are always high, rape that has a high chance of unwanted conception can be argued to be relatively more harmful to a female's fitness. It may, therefore, be the case that rape avoidance mechanisms are particularly active during ovulation, the phase of the menstrual cycle during which conception is most possible.

Female mate choice is argued to be of primary importance, particularly during the phase of peak fertility, known as the cycle shift hypothesis. A woman's choice of mate is closely related to increasing the chance of reproduction with a male who has strong genetics. In order to increase the chances of reproducing with a male with quality genetics, women find masculine features attractive when they are ovulating compared to the rest of their cycle. For example, while ovulating, females are particularly attracted to males with traits that signal high masculinity, such as masculine symmetric faces (e.g., Penton-Voak et al. 1999). In contrast, women appear to have stable preferences for traits that indicate that a man will likely be a long-term partner who will provide for offspring (e.g., Gangestad et al. 2004). Rape takes away this choice from women and so is particularly costly, especially in regards to unwanted conception.

In brief, the average menstrual cycle lasts from 28 to 35 days. The follicular phase begins on day 1 of menstruation (which on average will last around 5 days) and ends on either day 14 or 15 when ovulation begins. At this point, fertility is highest for women. After this, the luteal phase begins and will usually last until day 28, or until menstruation begins again. Therefore, in summary, conception risk fluctuates over the menstrual cycle and is highest during the ovulatory phase. Although rape is always traumatizing and costly, regardless of menstrual cycle phase, there may be trade-offs associated with rape avoidance behaviors. That is, it could be costly to consistently behave in a way to avoid rape. For example, avoidance of situations of increased risk of rape, such as not going out late at night, could hinder mate-seeking opportunities and chances of

attracting a potential mate. Therefore, mechanisms that may be associated with a female counter adaptation to rape may be particularly prominent when the benefits of these provisions outweigh any costs. Evidence will now be reviewed in support of this theory.

Risk Avoidance Over the Menstrual Cycle

In order to decrease the likelihood of rape during ovulation, it is thought that women will avoid “high risk” situations that increase their risk of rape during the fertile phase of the menstrual cycle. These situations generally include ones in which a woman is alone and vulnerable to an attack by a predatory male.

Research investigating female counter-adaptations to rape across the menstrual cycle was first conducted by Chavanne and Gallup (1998). They tested whether women who were in the ovulatory phase compared to other phases of the menstrual cycle would report having engaged in fewer behaviors that would increase their risk of rape (e.g., letting a stranger into their home, walking in dimly lit areas, going to church). They presented women with a checklist of activities and asked them to indicate the activities that they had participated in during the past 24 h. Participants’ current menstrual cycle phase was measured using the forward count method, which entails estimating the ovulatory window based on the date of a woman’s last menstrual period. Further, each activity had an associated numerical “risk” score, as determined by ratings of rape risk that had been given by a separate group of participants. The activities, thus, could be grouped into high, medium, and low rape risk categories. It was found that naturally cycling women reported having engaged in fewer high risk behaviors if they were in the fertile phase compared to the non-fertile phase of their menstrual cycle. Additionally, women who were using hormone-based contraception had no significant fluctuation across their cycle with respect to risk taking behavior. These results suggest that avoidance of rape-specific risk behaviors may be specific to ovulation when perceived costs of rape may be at their

highest and overshadow the benefits of situations where a suitable mate may be found.

However, Chavanne and Gallup’s (1998) methodology has been critiqued. For example, the validity of the rape risk measurement has been called into question. For instance, women who had engaged in several low risk activities (e.g., staying home to watch a film) could still have an overall risk taking score similar to women who had engaged in a few highly risky activities (e.g., walking home at night down a poorly lit street). In addition, the forward counting method of determining cycle phase is generally considered to be unreliable and inaccurate, particularly when relying on retrospective memories of participants (Bröder and Hohmann 2003). A backward counting approach is preferable; here, participants contact the experimenter on the date when their period begins, and the experimenter can count backwards from that date to determine the ovulatory window. Another limitation is that changes in risk taking behavior as a function of menstrual cycle phase were examined between rather than within subjects. For reasons that have nothing to do with fertility, it is possible that ovulating women as a group were on average more risk-averse compared to their nonfertile counterparts. This made it difficult to understand whether overall, risk taking behaviors truly fluctuated, and thus, in view of these limitations, replication was warranted.

Bröder and Hohmann (2003) sought to replicate Chavanne and Gallup (1998), refining the risk-taking measure. A group of participants rated the riskiness of a range of activities. The 20 highest rated activities were considered risky (e.g., walking alone in a park) and the lowest were considered nonrisky (e.g., speaking on the phone to a friend). In a new sample, women’s menstrual cycle phase was measured within-subjects, and they reported their risk taking during different points of their menstrual cycle. The researchers estimated the stage of menstrual cycle through using both the forward and backward cycling method. They replicated Chavanne and Gallup’s (1998) findings. Risky behaviors were found to decrease during ovulation, while the frequency of engaging in non-risky behaviors remained constant across the cycle.

Thus, the reduction risky behavior cannot be accounted for by a general reduction in activity. However, both Bröder and Hohmann's (2003) and Chavanne and Gallup's (1998) research studies were based solely on self-report. Self-reports of behaviors may also be inaccurate due to retrospective remembering of activities and responding in a socially desirable way. Women may be hesitant to report instances wherein they went out alone, or on a date, for example. Furthermore, risk behaviors in the checklists were limited to instances of stranger rape, without consideration of acquaintance rape, despite being more common (Office for National Statistics 2013).

Both studies are widely reported when discussing adaptations to rape, as they support the bold claim that women avoid situations that heighten their risk of rape, particularly during peak fertility. However, risk behaviors, such as going out alone late at night, could potentially increase one's risk of rape, but at the same time, they also could potentially increase one's chances of meeting a desirable mate. Therefore, perhaps there are mechanisms that allow women to establish when to engage in high risk behavior. Further, perhaps there are other behaviors and cognitions that vary across the menstrual cycle to allow women to control their risk of rape, which will now be reviewed.

Increased Strength

Theoretically, increased physical strength is one possible way in which women may counter their risk of rape. In unwanted sexual scenarios, this would be advantageous as it would allow them to potentially fend off an attacker and avoid rape. Thus, given the high evolutionary cost of rape, increased strength during ovulation may have evolved as a counter-adaptation to rape in women.

To test this hypothesis, Petralia and Gallup (2002) tested whether fertility status influenced strength by gauging women's reactions to sexual assault in relation to their menstrual cycle phase. Women of reproductive age completed a handgrip test to obtain a baseline strength level. After this, they completed a questionnaire regarding the regularity of their menstrual cycle. Participants were

then exposed to one of two brief scenarios. The control scenario described a woman walking to her car in broad daylight in the presence of other people. The sexual assault scenario described a woman walking to her car late at night through a forest while being followed by an unknown man. The scenario ends with the woman beginning to unlock her car door and feeling the unknown man's hand on her shoulder. Participants then carried out two further handgrip and reaction time tasks while being asked to consider the scenario that they had read. Finally, the participants used a urine-based test to estimate menstrual cycle phase.

It was found that there was no difference in baseline handgrip strength as a function of menstrual cycle phase. However, participants who were ovulating and had been exposed to the sexual assault scenario had stronger posttreatment handgrip strength when compared to ovulating women who were exposed to the control scenario. All other groups (i.e., women during phases of lower conception risk or who were using hormonal contraceptives) exhibited a decrease in handgrip strength following the scenario, regardless of the scenario to which they were exposed. Taken together, these results suggest that women's counter-adaptations to rape can be captured in physiology and appear to be most active during ovulation, when the reproductive costs of rape are highest.

Petralia and Gallup (2002) hypothesized that as women in their ovulatory phase are less likely to be raped, there may be a connection between increased strength and rape avoidance. However, other research has suggested that rape is not less frequent during ovulation (Fessler 2003). While Petralia and Gallup (2002) suggested that this finding is representative of the increased ability to thwart off a sexual attack when it would have the most reproductive costs, it is not entirely clear what increased handgrip strength in response to the likelihood of sexual assault occurring was operationalizing. Moreover, while their sexual assault scenario was suggestive of rape, participants may have alternatively thought that the scenario would end in a physical assault or robbery. It may be the case that women increase their risk aversion more generally during ovulation to maximize reproductive success.

Avoidance of Potentially Threatening Males

Other behavioral evidence that women's counter-adaptation to rape may be particularly active during the phase of peak fertility is that of Guéguen (2012), who examined women's avoidance of "strange looking" men. Participants were led to believe they would be participating in a lexical decision task and were asked to take a seat in a waiting room. Participants placed a labial band strip on their tongue, which they believed was to measure cortisol levels. Unbeknownst to the participants, the labial band measured levels of luteinizing hormone to determine menstrual cycle phase. A male confederate, who had been manipulated to appear "shady looking," was also in the waiting room. The investigators were actually interested in determining the location in which women sat while they were waiting. It was found that ovulating women sat significantly further away from the "suspicious looking male" than women who were not ovulating. The investigators concluded that women are more avoidant of "dangerous looking" men around ovulation. This may be indicative of a counter-adaptation to rape. However, there was no control condition wherein a male confederate who did not appear "shady" looking was present in the waiting room. Therefore, it cannot be concluded that fertile women were avoiding the man specifically because of his appearance.

Evaluation of Potential for Coercion

Other researchers have also shown evidence that women may perceive men differently according to their fertility status. One particular counter-adaptation to rape that would be advantageous would be an increased ability to detect the potential for sexual coercion early in an encounter with a man. By so doing, women may be more accurate at detecting a man's actual desires and therefore, will be better able to avoid men who may pose a threat to their fitness. To test this hypothesis, Garver-Apgar et al. (2007) conducted an experiment to test women's perceptions of different

types of men as a function of ovulatory status, which was measured within subjects. They found that women were much more accurate in detecting sexual coercion while ovulating. Furthermore, when participants believed a man to be suspicious, they were likely to overestimate the level of danger he posed to them. Women reported that this strategy enabled them to maximize their ability to avoid dangerous men. Garver-Apgar et al. (2007) suggest that a cognitive error management bias may be the cause of these overestimations. It is less costly to overestimate the likelihood of coercion than to underestimate it.

Garver-Apgar et al. (2007) suggested that it is possible that rather than relating to a counter adaptation to rape specifically, their results may reflect a general increase in fear mid-cycle. However, they contend that fear and anxiety appear to be greater during the luteal phase rather than during ovulation. Previous research does, however, show enhanced sensitivity to fear during ovulation (Pearson and Lewis 2005). Therefore, these findings may reflect an increase in risk perception or fear more generally during ovulation, rather than the counter adaptation to rape being particularly active during ovulation.

Outgroup Evaluation

Women may also differentially avoid outgroup members depending on fertility status. Navarrete and colleagues (Navarrete et al. 2009; McDonald et al. 2011) studied bias towards outgroup members over the menstrual cycle. Outgroup members may have been considered threatening in evolutionary history (Daly and Wilson 1988, as cited in Navarrete et al. 2009), possibly due to the lack of social controls that may be inherent in in-group members. Navarrete et al. (2009) examined attitudes and ratings of attractiveness and "scariness" of outgroup members (as defined by being of a different race) across the menstrual cycle. Women showed higher racial bias, as measured by higher fear and decreased attraction of outgroup members during the phase of peak fertility. McDonald et al. (2011) showed the bias towards outgroup members during ovulation extended beyond race

using an implicit associated test. These findings therefore suggest that women may have a psychological mechanism that increase bias towards men who may be considered threatening with regards to conforming to social norms and thus may be associated with an increased risk of sexual assault, with the bias being emphasized during peak fertility when the costs of rape are arguably the highest. This could be considered as evidence for a counter-adaptation to rape in females, with the mechanism being influenced by hormones.

However, some researchers have suggested that women may be more attracted to outgroup members during peak fertility as a way to increase genetic heterogeneity in offspring (e.g., Marlowe 2004, as cited by Navarrete et al. 2009), which appears contradictory to the findings of Navarrete et al. (2009). Navarrete et al. (2009) suggest further research is necessary to understand the coercion-avoidance versus heterogeneity-attraction processes.

Directions for Future Research

Evidence appears to suggest that women, and some female animals, may have evolved counter-adaptations to rape. Moreover, mechanisms associated with a counter-adaptation to rape in women appear to be particularly active during the phase of peak fertility, which may be due to the relatively higher costs of rape when conception is most possible. For example, women behave in a way that may help to decrease their risk of encountering a sexually aggressive man. However, some research regarding women's behavior over the menstrual cycle may appear contradictory to a female counter-adaptation to rape, and women may behave in ways that could put themselves at greater risk of encountering a sexually aggressive male during ovulation. It is important to note that exploration of the association between menstrual cycle phase and risk of sexual assault in no way justifies violence against women, and it does not shift the blame to the victims.

Ovulating women have been shown to have an increased desire to attend social events where they are more likely to meet men (e.g., a singles mixer, Haselton and Gangestad 2006). Additionally,

research has shown that in order to increase the likelihood of attracting a mate, ovulating women are more likely to dress in a provocative manner (Durante et al. 2008). During ovulation, partnered women become more partial to having sex with unfamiliar men (Gangestad et al. 2005) and were significantly more likely to dance with a male confederate in a nightclub, despite having never met him before (Guéguen 2009). Such situations could increase the chance of encountering a sexual aggressive male and seem to contradict the suggestion that women have evolved a mechanism that works to decrease the risk of rape. Future research should aim to test the relationship between adaptations designed to seek good quality mates at peak fertility while balancing the costs of rape.

Counter-adaptations to rape need to involve assessing the type of male to which they are interacting with, and thus involve complex, but sophisticated mechanisms. In humans, a cognitive error bias may offer a reason as to why women may feel comfortable with strange men in some situations (e.g., Guéguen 2009) and not others (e.g., Guéguen 2012). For example, a nightclub (e.g., Guéguen 2009) is a social place with bouncers who are there to ensure all event goers are safe throughout the night. Women in this context may, therefore, be more accepting towards a strange man who approaches her and will more accurately judge their sexual coercion. However, a woman could meet the same man down a long dark alley, and overestimate the danger posed by the man, and may consider him to be suspicious due to an environment which may feel less safe. Alternatively, the reason may be due to the appearance of the man. In Guéguen (2012), the male confederate was manipulated to appear "shady" and therefore the further distance that ovulating women sat may be avoidance of a potentially threatening male in line with a female counter-adaptation to rape. On the other hand, the male confederates to which ovulating women responded favorably to a romantic gesture from in Guéguen's earlier research (Guéguen 2009) were chosen for their attractiveness. Similarly, while ovulating women showed a desire to dress more provocatively, this was in response to being told they would meet single, attractive males at the

event. Furthermore, while Flowe et al. (2012) found women to show increased engagement with a male during their ovulatory phase, this was only true if the male appeared masculine. In contrast, engagement in nonverbal behavior was relatively lower in ovulating women when the male appeared “shady” (Guéguen 2012). This may represent the fact that women’s behavior has the highest reproductive consequences at peak fertility; they must balance the goals of behaving in a way to both benefit reproductive fitness (e.g., seeking a quality mate) with preventing costs to reproductive fitness (e.g., rape). Future research examining the relationship between attraction versus avoidance of certain males during peak fertility should consider the appearance of the man and setting. For example, having a control condition in Guéguen’s (2012) study wherein there was a male who was manipulated to appear attractive, or neutral, in addition to the condition with the “shady looking” male, may have allowed an understanding of women’s avoidance behaviors over the menstrual cycle.

Are Avoidance Behaviors Specific to Rape, or Risk More Generally?

Women’s avoidance of situations of increased risk of rape may simply reflect danger avoidance more generally rather than a female counter-adaptation to rape specifically. That is, it is not known from previous research whether women are avoiding rape specifically, or are avoidant of all danger and risk in a more general sense, particularly at peak fertility. It is possible that females may be more receptive to any type of danger during ovulation in order to protect their fertility in general. For example, in Petralia and Gallup’s (2002) study on female strength and ovulation in response to risk of sexual assault, the sexual assault scenario did not specifically state that a sexual assault was about to occur and instead left it to the imagination of the female participant. Some participants may, therefore, have thought the scenario was suggesting that a robbery, carjacking, or a physical assault was going to occur. Additionally, the questionnaires used by both

Bröder and Hohmann, and Chavanne and Gallup did not specifically refer to behaviors specific to sexual assault. Although behaviors that are commonly linked to sexual assault appeared on the questionnaires (e.g., walking in dimly lit areas), these behaviors are also closely related to other crime and danger more generally. Therefore, it is unclear whether a risk-averse response from female participants is directly linked to rape-avoidance, or avoidance of danger.

Garver-Apgar et al. (2007) examined domain specificity in women’s perception of male traits over the menstrual cycle and reported that women were more attuned to sexual coercion when ovulating in comparison to other male traits outside of fluctuations in risk avoidance. However, the factors that were assessed as a measure of “sexual coercion” (e.g., creepiness) may also correspond to dangerous males in general. Moreover, bias towards outgroup members (e.g., Navarrete et al. 2009) suggests wariness of potentially threatening men, rather than males who are likely to rape specifically.

In support of the mechanism being domain general over domain specific, there is evidence suggesting that females engage in risk avoidance behaviors during ovulation in situations that are not sexual. Kaighobadi and Stevens (2013) studied the effects of ovulation and risk taking behaviors in women who were gambling. It was found that ovulating women would engage in less impulsive behavior when shown pictures of attractive men while gambling. However, impulsivity did not change when shown a picture of attractive landscapes, or in nonfertile females. Women have also been shown to take less risks in an investment task when ovulating and working with strangers (Ball et al. 2013). Furthermore, females may have an increased response to threatening images in general and have been found to have enhanced detection of faces showing fear (Pearson and Lewis 2005). Similarly, there is neural evidence to suggest that the way in which women process risk may differ depending on their phase of the menstrual cycle. When fertile, women showed increased activation in brain areas associated with risk evaluation when being shown images of typically masculine males, which may

be considered a threat compared to nonfertile women (Rupp et al. 2009). Finally, Šukolová and Sarmány-Schuller (2011) also found that women perceive risk differently according to their fertility status, regardless of what the risk was. It may therefore be that women are more perceptive to risk in general during ovulation, rather than it being an evolutionary adaptation which is specific to rape avoidance.

Taken together, there is evidence to suggest that risky behaviors may be lessened during ovulation in a more general sense, rather than specifically in response to rape. Therefore, evidence suggestive that there is a counter-adaptation to rape, may not apply specifically to women's rape avoidance, but rather their avoidance of risk more generally. Future research should focus on testing for domain specificity through assessing women's responses to the physical versus sexual costs of rape, for example, or through assessing risk aversion over the menstrual cycle more generally. However, researchers should consider the assumptions of the shadow of sexual assault hypothesis (Ferraro 1996) when designing research into female counter adaptations to rape. This hypothesis proposes that women's disproportionate fear of crime in relation to men's and their risk of victimization is due to the assumption that any crime could potentially escalate into a sexual crime. That is, that due to the higher costs (e.g., risk of unwanted conception), women's fear of sexual assault will "shadow" their fear of encountering other types of crime (e.g., robbery). Therefore, it could be difficult to distinguish whether responses are specific to risk of rape, or danger more generally. One suggestion for future research is to assess women's responses to risk and how they vary over the menstrual cycle, in response to danger while controlling for the risk of rape, such as by assessing responses to female-perpetrated crimes. To be able to conclude that ovulatory declines in risky behavior represent an evolved rape-avoidance adaptation to prevent pregnancy resulting from rape, evidence showing "special design" for performing a specific function which cannot be explained with other accounts is necessary.

Conclusion

In summary, women appear to behave in ways that could be suggestive of a female counter-adaptation to rape. For example, female animals have specialized physiology that may prevent forced copulation from males (e.g., Brennan et al. 2007; Rowe et al. 1994; Thornhill 1980). Women also appear to have mechanisms that may be indicative of evolved adaptive traits that could help to reduce the risk of rape, such as avoidance of situations of increased risk of rape (McKibbin et al. 2009) and a preference for mates and male friends who may be able to offer protection (Wilson and Mesnick 1997). What is more, mechanisms that may help to prevent rape appear most active during the phase of peak fertility, when rape arguably poses the highest costs to fitness. For example, during ovulation, women are more avoidant of situations of increased risk of rape (e.g., Chavanne and Gallup 1998; Bröder and Hohmann 2003), show increased strength in response to a scenario suggestive of sexual assault (Petralia and Gallup 2002), overestimate male's sexual coercion (Garver-Apgar et al. 2007), show bias towards outgroup members (Navarette et al. 2009; McDonald et al. 2011), and keep further distance from a male manipulated to appear "shady" (Guéguen 2012). Taken together, these findings appear to support a female counter-adaptation to rape, which is particularly active when conception risk would be highest. However, much of this research is based on self-reports of behavior, which may be inaccurate due to retrospective reporting and errors in remembering, and socially desirable responding on surveys. Moreover, research also suggests that women behave in ways that could potentially increase their chances of encountering a sexually aggressive male (e.g., Guéguen 2009; Durante et al. 2008; Gangestad et al. 2005). Therefore, future research should focus on refining the relationship between balancing mechanisms designed to seek good quality mates at peak fertility and avoiding situations that could potentially be associated with increased risk of rape, with a preferential focus on behavioral, as opposed to self-report methods. Secondly, future

research should consider assessing whether the mechanisms as reviewed above are specific to a female counter-adaptation to rape, or work to protect women from all harm more generally by assessing women's responses to the risk more generally over the menstrual cycle.

Cross-References

- Adaptations
- Defending Against Attack
- Error Management Theory
- Female Choice
- Fertility
- Forced Copulation
- Hormone Effects on Human Fetal Development
- Luteinizing Hormone
- Menstrual Cycle
- Ovulation
- Parental Investment Theory
- Rape
- Rape Avoidance
- Risk of Conception
- Risky Behavior
- Sexual Coercion

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Female Deception

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Men and women likely evolved different strategies for sexual selection based on the relative time they invested in their offspring (Buss and Schmitt 1993). Male preferences for choosing a mate are primarily based on a female's fertility and reproductive value (Thornhill and Grammer 1999). Men will try to choose a partner whose characteristics signal that she is likely to conceive and who appears to have overall good health (Buss and Schmitt 1993), resulting in women being typically younger in a marriage across societies (Kenrick and Keefe 1992). The signaling that takes place among women is typically done during intersexual competition. Women signal men through verbal and non-verbal means to let men know they are interested in interacting with them (Grammer et al. 2000; Renninger et al. 2004; Wade and Slep 2013; Wade and Feldman 2016), and to get an opportunity to find out about the men's personalities (Grammer et al. 2000).

In order for women to compete intersexually as well as intrasexually, it was adaptive for women to deceive both their rivals and men in order to match the male preferences and obtain an optimal mate (Haselton et al. 2005). Consistent with this reasoning, research has found that women may employ deceptive tactics in order to align with a male's mate preferences.

Previous research discovered that deception typically involved women altering their physical appearance (Tooke and Camire 1991), altering the appearance of their body through behaviors such as wearing facial makeup and exaggerating their hip movements while walking (Tooke and Camire 1991), and withholding their age when writing a personal advertisement for a mate (Pawlowski and Dunbar 1991). Women most frequently report

using intersexual competition tactics that involve altering their physical appearance to exhibit “more” of their physical assets in the hope that such action would elevate a potential male partner’s perception of their physical assets. The women who decide to withhold their age are typically in the 35- to 50-year-old range since older women such as this have lowered fertility and reproductive value. It is adaptive for this group of women to withhold their age in order to obtain a more optimal mate. Also, this type of age withholding deception may be viewed as more passive than active (Pawlowski and Dunbar 1999). Women were found to most frequently report intersexual competition tactics that serve as a strategy for a female to present “more” of her assets in order to alter a potential male partner’s perception of her physical attributes. This alteration of physical appearance is motivated by males’ general preferences for attractive and youthful female partners.

Women may also deceive men about their sexual experiences. In some cases, this is dependent on the current mating strategy (Buss and Schmitt 1993) the women is motivated by. For example, women may downplay their sexual experience because personality traits that signal promiscuity are not desirable for a long-term mate (Buss and Schmitt 1993). Additionally, women may also deceive a male partner about their commission of sexual infidelity. If a woman was to successfully deceive a male by engaging in an extra-pair copulation (EPC), she could increase her fitness since this EPC partner choice diversifies the genetic material of resultant offspring and can lead to the receipt of more paternal investment (Smith 1984). If the woman does not deceive the male partner about her commission of sexual infidelity, she could suffer harm from her male partner, a lower parental investment from him, and mate expulsion as a consequence since he is being cuckolded. Thus, a woman would have to deceive her partner about the commission of any EPCs in order to maintain her current long-term partnership.

So, clearly, deception on the part of a woman is a tactic that includes multiple behavioral strategies that may be used by females to facilitate the chances of finding an optimal mate and keeping an optimal mate.

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Female Extra-Pair Copulation

► Female Infidelity

Female Filtering

► Evolution of Female Resistance

Female Gangs

► Anne Campbell

Female Homosexuality and Bisexuality

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Synonyms

Female sexual orientation; Lesbianism; Same-sex sexuality; Sexual fluidity

Definition

Female homosexuality and bisexuality are broad terms that are used to refer to the phenomenon by which women experience sexual attractions and/or pursue sexual behavior with other women. Lesbianism denotes a pattern of exclusive same-sex attractions and behavior, whereas bisexuality refers to a pattern of mixed same-sex and other-sex attractions and behavior.

Introduction

Sexual orientation is generally conceptualized as a stable, trait-like predisposition to experience sexual attractions for the same sex (homosexuality), the other sex (heterosexuality), or both sexes (bisexuality). In the past, the phenomenon of sexual orientation was thought to operate equivalently for men and women, such that female and male homosexuality and bisexuality had similar causes, developmental trajectories, and adult manifestations. Yet scholars no longer think this to be the case. This entry will review some of the most distinctive aspects of female homosexuality and bisexuality and will discuss some of the potential causes for differences between male and female sexual orientation.

Female homosexuality and bisexuality show different patterns of development and expression than male homosexuality and bisexuality. Perhaps most notably, women are more likely to show bisexual patterns of attraction and behavior than

exclusively same-sex patterns of attraction and behavior. One recent review examined the prevalence of exclusive same-sex attractions versus bisexual patterns of attraction in 16 studies published between 2000 and 2016, each of which used a representative probability sample of adults, with sample sizes ranging from several thousand to several million participants (Diamond 2016). These studies consistently found that women were more likely to report bisexual attractions than exclusive same-sex attractions, whereas men were typically more likely to report exclusive same-sex attractions than bisexual attractions. The reasons for this difference between female and male expressions of same-sex and other-sex attractions are not definitively known. This difference might result from a basic sex difference in the phenomenon of sexual desire and arousal, such that women have a stronger fundamental capacity for bisexual sexual desire and arousal than do men. A series of studies examining sex differences in genital responses to sexual stimuli has found support for this view (Chivers et al. 2004, 2007). Specifically, self-identified lesbians and self-identified heterosexuals show similar levels of genital arousal to their preferred sexual stimuli (same sex for lesbians and other sex for heterosexuals) and their non-preferred sexual stimuli (other sex for lesbians and same sex for lesbians). Yet gay-identified and heterosexual-identified men show substantially stronger genital arousal to their preferred sexual stimuli than to their non-preferred sexual stimuli. In essence, these findings suggest that even women who generally experience their sexual attractions as exclusively same sex or exclusively other sex possess a *capacity* for bisexual genital arousal and that this capacity is greater among women than men. Importantly, genital arousal does not always correspond to the subjective psychological experience of sexual desire, and women generally show less correspondence between patterns of genital and psychological arousal than do men (Suschinsky et al. 2009). Hence, women who are capable of becoming genitally aroused to their “non-preferred” gender would not necessarily describe themselves as possessing bisexual attractions or seeking sexual partners of both genders. An additional complication in interpreting women’s patterns of same-sex

and other-sex arousal and desire is the fact that women tend to show more “category-specific” forms of genital arousal (such that lesbian-identified women become specifically aroused to same-sex stimuli and heterosexually identified women become specifically aroused to other-sex stimuli) when they are shown static photos of male or female genitalia, as opposed to videos depicting individuals engaged in sexual activity (Spape et al. 2014). Such findings underscore the difficulty in operationalizing and measuring sexual orientation (Bailey 2009; Chivers and Bailey 2007; Rieger et al. 2005; Savin-Williams 2006). Specifically, is it best conceived as a pattern of sexual arousal (to what specific types of stimuli), a pattern of sexual attraction (to what types of partners and how consistently), or a pattern of sexual behavior (how frequently and under what circumstances)? How should researchers interpret cases in which these patterns conflict with one another? Scholars have not reached consensus on these questions, which makes it particularly difficult to interpret gender differences in such phenomena. For example, if women are more likely to report bisexual patterns of attraction than do men, does this reflect a gender difference in the nature of sexual orientation, a gender difference in social opportunities to express bisexual versus exclusive patterns of same-sex attraction, or a gender difference in the social costs associated with same-sex sexuality? It is likely that all of these factors play some role.

Another distinctive characteristic of female homosexuality and bisexuality concerns the capacity for change over time in sexual attractions and behavior. Although sexual orientation is typically conceptualized as a stable trait, numerous longitudinal studies have found that the specific distribution of an individual’s attractions may shift over time, between exclusive homo-/heterosexuality and bisexuality and vice versa (but rarely between exclusive homosexuality and exclusive heterosexuality). Some studies find that these changes are more common in women than in men, although other studies find similar rates of change in both genders (reviewed in Diamond and Rosky 2016). It is important to note that these changes occur on their own and should not be confused with effortful changes that are sought

in the context of “reparative therapy,” which typically seeks to eliminate same-sex attractions altogether and which has found to be ineffective and psychologically harmful (APA Task Force on Appropriate Therapeutic Responses to Sexual Orientation 2009).

The large-scale longitudinal studies which have documented changes in sexual attractions (usually over the time span of 2–10 years) do not provide any meaningful information about the underlying reasons for these changes. Some interview-based studies of women suggest that entering or exiting certain intimate relationships can facilitate changes in women’s attractions (Diamond 2008), and some scholars have suggested that female sexuality might be intrinsically more “plastic” than men’s (Baumeister 2000). Another possibility is that the phenomenon of sexual “plasticity” or “fluidity” is simply a by-product of women’s propensity for bisexuality. Changes over time between periods of exclusive homo- or heterosexuality and bisexuality are arguably more likely to occur for bisexual individuals, who may sometimes find themselves in environments that foster one “side” of their attractions more than the other (Weinberg et al. 1994). Hence, sexual “fluidity” or “plasticity” may be viewed as a specific form of bisexuality.

In addition to considering the existence of a basic sex difference in the expression of female versus male sexual orientation, it is important to consider the role of social and environmental factors. Extensive research has shown that around the world, women’s sexual behavior and expression has been subject to more social, cultural, familial, and political control than male sexuality (Baumeister and Twenge 2002; Fine 1988). In particular, women have been more seriously penalized than men for deviating from culturally traditional roles as wives and mothers (Faderman 1981; Rich 1980). As a result, women with same-sex attractions may show more variability than men in same-sex attractions and behaviors over the life course, sometimes expressing and sometimes suppressing same-sex desires depending on the characteristics of their local environments (such as opportunities for same-sex relationships and stigmatization of same-sex sexuality) which

may bear on their social and economic livelihood. These factors have also historically operated for men, but arguably with less intensity, given men's greater social power, especially in domains of family and sexuality.

If social and environmental factors have the power to change women's and men's expressions of homosexuality and bisexuality at different points of time and in different social contexts, then one might expect that large-scale historical shifts in the social acceptance of same-sex sexuality should correspond to large-scale historical shifts in the population prevalence of homosexuality and bisexuality. In fact, this appears to be the case and more so for women than for men. Gartrell and colleagues (2012) compared rates of same-sex contact as reported by 17-year-olds in the 2002 and 2011 administrations of the National Survey of Family Growth and found that although the percentage of 17-year-old boys reporting same-sex contact was lower in 2011 (1.4 %) than in 2002 (6.6 %), the percentage of girls reporting same-sex contact was twice as high in 2011 (10 %) as in 2002 (5 %). Twenge and colleagues (2016) examined reports of same-sex behavior across multiple consecutive administrations of the US General Social Survey from 1973 to 2014. They found that the percentage of US adults reporting that they engaged in post-adolescent same-sex sexual contact doubled between 1990 and 2010 (from 4.5 % to 8.2 % among men and from 3.6 % to 8.7 % among women), and these changes were partially – but not exclusively – accounted for by concurrent increases in the social acceptance of same-sex sexuality (Twenge et al. 2015).

Similar findings have emerged from studies conducted in other countries. Mercer and colleagues (2013) examined the prevalence of same-sex attractions in British men and women in three separate administrations of a national probability study. At each administration, over 15,000 men and women were surveyed. Among men, rates of self-reported same-sex attractions were relatively stable across the 30-year period, ranging around 7 % of the population. Yet among women, rates of same-sex attractions increased

from 3.7 % in 1990 to 9.7 % in 1999 and 16 % in 2010). Data collected from the Netherlands shows a similar pattern: Kuyper and colleagues (2009) found that the number of Danish men reporting same-sex attractions from 1989 to 2005 increased from 6 % to 13 % and the number of Danish women reporting same-sex attractions over this period increased even more, from 3 % to 18 %.

The fact that historical changes in the prevalence of same-sex sexuality appear larger among women than among men is consistent with the notion that women's sexuality is more fluid and situation dependent than men's sexuality.

Conclusion

Of all of the presumptions about sexual orientation which researchers have come to question and revise over the years, one of the most important is the presumption that female and male sexual orientation are parallel phenomena, with the same origins and manifestations. Although much work remains to be done in understanding the extent and cause of differences between male and female expressions of same-sex sexuality, scientists now have at their disposal an increasingly reliable body of data charting such differences (reviewed in Diamond 2016). At the present time, the most reliable gender differences concern the prevalence of bisexual versus exclusive patterns of attraction and the propensity for change over time in sexual attractions. Our task now is to determine the bases and reliability of these differences and to understand their implications for models of female and male sexual orientation as well as human sexuality more generally.

Cross-References

- ▶ [Genetic and Prenatal Components of Homosexuality](#)
- ▶ [Homosexuality Paradox, The](#)
- ▶ [Hormonal Component of Homosexuality](#)
- ▶ [Lesser-Known Theories of Homosexuality](#)
- ▶ [Non-Western Homosexuality](#)

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Female Hypergamy

► Women Marry Up

Female Infidelity

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Synonyms

Female extra-pair copulation

Definition

Female who is intimate with someone other than her partner.

Human mating is socially monogamous, where males and females create long-term pair bonds that share space, resources, and responsibilities for raising offspring. Not all such relationships are sexually monogamous, however, because significant proportions of males and females engage in extra-pair copulations. Extra-pair copulations are observed across various fish, bird, mammal, and insect species (Birkhead 2000). In humans, data from the most recent General Social Survey showed that 20% of men and 13% of women report having sex with someone who is not their partner (Wang 2018). Prevalence rates vary across location, sampling, and measurement methods, with some studies reporting female infidelity rates up to 25% (Whisman and Snyder 2007).

Theoretical explanations for the relatively high prevalence rates of female infidelity address its possible functions. Unlike men, women cannot increase offspring number through increasing mate number, but extra-pair copulations may increase female fitness by mating with males with better genes, gaining additional resources, confusing paternity to improve offspring safety, enhancing status, diversifying genes, increasing social networks for employment, or replacing a low-quality mate (reviewed in Mulder and Rauch 2009; Wilson and Daly 1992).

There are two potential factors that increase the risk of female infidelity: female mate value and the amount of time the couple spends apart (Stieglitz et al. 2012). A female's mate value is typically determined by age and her ability to reproduce successfully. Younger females are more likely than older females to be reproductively successful and have higher reproductive value, which makes the potential loss of a younger wife more costly to males. Consistent with this view, Stieglitz et al. (2012) found that women reported their partner experienced more jealousy under these conditions.

Female infidelity may also be costly because of the risks associated with partner jealousy,

including relationship conflict, intimate partner violence, and in some cases, homicide (see ► [“Partner Abuse and Homicide”](#) entry). It appears as though men are more jealous in response to sexual infidelity (i.e., when a partner engages in an extra-pair copulation) than emotional infidelity (i.e., when a partner spends time and resources with someone outside their relationship), since sexual infidelity may result in cuckoldry, which incurs a cost to men. Various sexually coercive behaviors, such as intimate partner sexual and physical violence, may have evolved to prevent or minimize the risk of cuckoldry (Camilleri and Quinsey 2012; Goetz and Shackelford 2006; see ► [“Sperm Competition Risk and Partner Abuse”](#) entry). Considering infidelity is risky and even dangerous, females put great effort in attempt to evade their partner during extra-pair copulation.

Men appear to respond to both direct cues to cuckoldry risk (i.e., by partner's actions that are indicative of infidelity) and indirect cues to cuckoldry risk (i.e., proportion of time spent away from a partner since last having intercourse), where more salient and recent cues are associated with either a greater propensity to engage in either sexual coaxing or sexual coercion (Camilleri and Quinsey 2009).

Cross-References

- [Partner Abuse and Homicide](#)
- [Sexual Conflict Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)
- [Sperm Competition](#)

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Female Intrasexual Aggression

- [Contexts for Women's Aggression Against Women](#)

Female Intrasexual Competition

- [Contexts for Women's Aggression Against Women](#)

Female Intra-sexual Competition for Resources and Mates

- [Competition for Resources Desired by Females](#)

Female Jealousy

- [Sexual Jealousy Among Women](#)

Female Manipulation of Men

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Introduction

Errors in judgment can either be a false positive (incorrect judgment that something is present) or a false negative (incorrect judgment that something is not present). Error management theory suggests that these overestimation or underestimation errors in judgments or choices may be adaptive (Haselton and Buss 2000) and are sometimes referred to as adaptive biases. In the context of mating, it is possible that females may manipulate particular male biases.

One bias that may be manipulated is men's overperception of female sexual interest (see "Male Sexual Overperception Bias" entry). According to error management theory (see ► "Error Management Theory" entry), it would have been adaptive for men to err on assuming women are sexually interested when they are not, because it would be costly to err on assuming women are not sexually interested when they are. Men, for example, are prone to misperceiving women's friendliness as sexual interest (Abbey 1982). Men, also, will often make advances and may provide some sort of "gift" or attention in order to maintain or enhance her interest (e.g., buying her a drink, dinner, etc.) (Haselton 2003). It is therefore possible that some women may take advantage of men's misperception by accepting resources offered by these men. By using men's own tendency toward making false-positive errors, women can manipulate the way in which men perceive their interest in order to acquire resources (Haselton 2003). For example, women may flirt with and entertain men at a bar even though they have no interest in forming a relationship with

them, sexual or otherwise, because there is a chance he will pay for her expenses.

Women may also use their attractiveness or sexual suggestiveness to manipulate men's mating effort to acquire resources. That is, showing sexual interest manipulates men's interest in indiscriminate sex, motivating men to make some investment to pursue a potential mating opportunity. Although manipulative tactics are generally not sustainable because they incur a cost, tactics that manipulate adaptive errors could be persistent when the benefits of those errors outweigh the costs of being manipulated (Haselton 2003). Also, counteradaptations may evolve in response to manipulative tactics to "exploit the exploiters" (Buss and Duntley 2008). Although the emphasis here is on women's manipulation of men, men may also manipulate women's biases.

Conclusion

Women may manipulate men's overperception of female sexual interest or men's mating effort to gain resources.

Cross-References

► [Error Management Theory](#)

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Female Mate Choice

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Synonyms

[Females' mating strategies](#); [Women's sexual preferences](#)

Definition

A complex system of conscious and unconscious mechanisms leading to an expression of a preference toward a certain individual or a certain feature.

Introduction

Sex differences in mate choice arise from differences in minimal investment in children between men and women (**minimal parental investment**). For men, basic investment is energy spent for sperm production and then fertilization. For women, not only is the energetic expense for ovum much higher than men's investment in sperm cells, but minimal cost also includes pregnancy and then usually breast-feeding. Due to these primary differences, men and women differ greatly in what they seek in a partner and what choices they make.

Women's mate choice is not fixed throughout their lifetime and depends on a multitude of conditions. Those conditions can be defined as more "internal" (such as hormones or sexual openness) or "external" (e.g., living conditions, family structure, or past sexual experiences). Also due to minimal parental investment inequality, men and women differ in what they want to receive from a partner (putative parent of their future children).

Sex Hormones and Preferences

Women's sex hormones' levels (mostly estradiol and progesterone) vary greatly, both during their lifetime (being highest during fertile years and lower before puberty and after menopause) and monthly (over the menstrual cycle). It is suggested that change in levels of sex hormones influences what women want in a given time of life or month (Anthony C. Little et al. 2010; Penton-Voak et al. 1999). It has also been suggested that women express **dual sexuality** – their preferences and behaviors vary between fertile and non-fertile phases; however, there is an ongoing debate about how strong such menstrual cycle shifts are (for meta-analyses leading to contradictory results on this topic, see Gildersleeve et al. 2013 and Wood et al. 2014).

Mating Context and Relationship Status

Depending on whether women are judging putative partners for a long-term or short-term relationship, they can favor different characteristics. In a long-term relation, parental skills or emotional stability are more sought after. For more of short-term liaison, women direct their attention toward attractiveness (Li and Kenrick 2006) or masculinity and health, manifested through symmetry (Anthony C. Little and Jones 2012). Mating context can change, however, depending on the relationship status of a woman (exerting preference for good genes from a one-time encounter with a masculine man “pays-off” only if a woman is already in a long-term relationship (A. C. Little et al. 2002)).

Sexual Openness

Women's past sexual experience and how easily she enters into physical relationships with emotional engagement play an important role in what she looks for, for example, women who are more sexually open have a stronger preference for masculinity (Sacco et al. 2012) than their more reserved peers.

Living Conditions and Country Characteristics

Mating choices of women also vary depending on the living conditions of their surroundings. Women in countries with worse living conditions show a higher preference toward more masculine men (Brooks et al. 2011; DeBruine et al. 2010), most probably as such men can provide better genes for future children.

Conclusion

Due to differences in minimal investment in children, women are the choosier sex – meaning their preferences will be more complex and expectations will be more stringent than men's when it comes to pairing. Women's characteristics and their life history play an important role in how her mate choices are shaped.

Cross-References

- Differential Parental Investment
- Female Choice and Sexual Conflict Theory
- Male Qualities and Likelihood of Orgasm
- Ovulation
- Ovulatory Shifts in Psychology
- Reproductive Strategies

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Female Mate Choice (Intersexual Selection)

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Synonyms

Women romantic partner choice; Women sexual partner selection

Definition

Romantic or sexual partner selection by women; characteristics that guide female choice of their romantic or sexual partners.

Introduction

Parental investment theory (Trivers 1972) states that male and female have different court behaviors because of the amount each sex invests in offspring. In general, females invest more energy and time in them. This investment becomes even clearer in mammals since gestation and breastfeeding are mandatory for descendants' survival. Because of the energy spent by females, they are limited to a certain number of children they can have and raise. This number depends on several factors such as length of gestation, necessity of taking care of children after birth, and available resources. Thus, females are considered the limiting sex, investing more in parenting effort, while males are known as the competitor sex. For men, greater access to females means a higher probability of increasing their reproductive success, while females' access to resources is a limiting factor for their reproductive success.

Sexual Strategies Theory

Buss and Schmitt (1993) noticed that men and women have a different pattern of choosing their romantic partners. Natural selection has acted on both sexes behavior and modulated their mate preferences in order to maximize individuals' reproductive success.

Women have 9 months of gestation, at least 6 months of breastfeeding and the primary care with children. Due to this high investment in offspring, a mate who helps her with protection against predators and rivals and provides resources to her and their offspring increases the possibility of survival and tends to be considered more attractive (Buss 1989; Buss and Schmitt 1993).

Long-Term Relationship Preferences

According to the evolutionary perspective, women who chose a partner that could provide protection and resources to them and their offspring had greater reproductive success. Due to females' high investment in children, they tend to be more selective than males when looking for their romantic partners and to prioritize long-term relationships. In order to help her to raise children, a man needs to establish a commitment with her. Because of that, they also look for a partner who is willing to invest in them and in their offspring, which may be observed through traits like faithfulness and commitment (Buss 2003). Besides being committed, being faithful assures women that her partner invests in her and their offspring, decreasing the risk of having to share his resources and time with another woman and her family.

Environmental Influence on Females' Mate Choice

In general, women tend to invest more in long-term relationships and choose their partners accordingly, as aforementioned. Such strategy and preferences may change, however, depending on the environment.

Gangestad and Simpson (2000) claimed that women change their strategies according to environmental features, such as pathogens' level and amount of resources available. In general, women prefer a partner with high socioeconomic status, as predicted by the sexual strategies theory. Nevertheless, it occurs in an environment where pathogens' levels are not too high or when biparental care is important for children survival. In high pathogens' levels environment, women face another problem: assurance of good genes, a good immunological system in order to survive. For this matter, they no longer use a long-term strategy. Instead, they tend to choose a partner who is physically attractive. Physical attractiveness is related to the good capacity to protecting the human body against pathogens. Body and facial symmetries, for example, gives men and

women clues about their pathogens' history. A symmetrical person indicates that she or he had enough energy in the childhood to develop their body symmetrically at the same time their immunological system was fighting against external and internal agents (Pawlowski 2000; Thornhill and Gangestad 1993). A woman who chooses a more attractive partner, in a harsh environment, tend to have children both more physically attractive and with better pathogens resistance, increasing their capacity of survival and procreate, and consequently, higher probability of increasing women's reproductive success (Gangestad and Simpson 2000).

Menstrual Cycle

Besides environmental conditions, women's mate choice can suffer influence of other factors, such as menstrual cycle. Women who do not take contraceptive pills tend to rather more masculine men when they are in the most fertile phase, while women who were in other phases (luteal phase, for example) found more attractive as a romantic partner men that have more feminine traits (Jones et al. 2008). Men with more masculine faces, bodies, and voices, in general, have higher testosterone levels and are considered also as more aggressive, unfaithful, prone to engage in more risky behaviors, having a higher number of sexual partners, and less prone to engage in a long-term relationship. These men, at the same time that signal good genes, signal less probability of invest in them and in their children. However, men with more masculine characteristics are good partners to have a short-term relationship with, increasing the change of successful pregnancy, and to provide good genes to their children when women are most fertile (Jones et al. 2008).

Conclusion

Due to the high investment (energetic, physiological, and in time) women make in children, they tend to choose a partner who can help them with their offspring, investing with resources and being

committed to them. However, the environment also modulates females' mate choice. In harsh conditions, they may change her mate preferences in order to maximize their reproductive success, investing more in short-term relationships and preferring characteristics that indicate good immunologic system quality, such as physical attractiveness, instead of resources.

Cross-References

- [Intersexual Selection](#)
- [Limited Reproductive Potential](#)
- [Male Mate Choice](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Reproductive Strategies](#)
- [Sexual Strategies Theory](#)

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Female Mate Interests

- [Women's Mate Preferences](#)

Female Mating Counter-adaptations

- [Evolution of Female Resistance](#)

Female Mating Strategies

- [Luring Hypothesis](#)

Female Mimics

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Synonyms

[Reproductive parasite](#); [She-male](#); [Sneaker](#)

Definition

Female mimics are males of otherwise sexually dimorphic species that resemble females in appearance and behavior.

Introduction

In sexually dimorphic species, some males will look more like females than males when it comes to size, coloration, pheromone signaling, and behavior. Such female mimics are widespread across the animal kingdom; they have been described in beetles, ants, mollusks, crustaceans, and every vertebrate class, among others (Oliveira

et al. 2008). Taking up the female appearance can be permanent or temporary. In the majority of cases it is a form of deceit to gain competitive advantages, for example, female mimicry is used as an alternative mating strategy by smaller males who otherwise would not be able to mate. In their disguise, the sneaker male can approach females and avoid agonistic interactions by the larger males and frequently manages to steal copulations.

Alternative Mating Strategies

In species with strong sexual selection, matings are often monopolized by very few dominant males. To become dominant, a male typically needs to be large and aggressive. Under these circumstances smaller males hardly ever have the chance to mate. Female mimicry is an alternative mating strategy that enables some males to gain reproductive success. Disguised as a female these males are often not detected by their dominant rivals and can hence avoid aggressive confrontations and eviction from the territory and stay in close proximity of receptive females that have been attracted to the dominant male. Whether females choose to mate with the sneaker male or cannot avoid the sneaky copulation when attempting to mate with the dominant male is unclear, although the current evidence points towards a preference for the dominant males and female avoidance of sneakers where possible (Oliveira et al. 2008).

The sneaker male will mimic females in many morphological and physiological traits, coloration, and behavior. Pretending to be a female is not restricted to visual effects. In the tropical ant *Cardiocondyla obscurior* the sneaker male mimics the queen's chemical bouquet to avoid fights with aggressive males that otherwise often lead to death (Cremer et al. 2002). This chemical mimicry is effective in competition for matings with virgin queens in the nest, which otherwise would be monopolized by the aggressive males. Sneaking behavior and female mimics also have hormonal adaptations; for instance the mimics often have lower levels of testosterone, which is

associated with aggressive behavior, than the ordinary males (Cardwell and Liley 1991; Sinervo et al. 2000; Küpper et al. 2016). Female mimics do not express typical male ornaments, nevertheless he always possesses male gonads. The testes of sneaker males are occasionally larger than those of dominant males and may increase its chances of siring offspring during sperm competition (Küpper et al. 2016).

Female mimics have two principal behavioral tactics. They may either try to avoid the attention of the dominant male or stealthily sneak copulation when the dominant male is engaged otherwise. Alternatively, they may actively distract the dominant male from copulations by posing as a receptive female and drawing attention away from the female to themselves. This deceit is very effective and the mimic is frequently mounted by the male who will then waste time, sperm, and energy on the female impersonator.

As other alternative mating strategies, female mimicry is often under negative frequency dependent selection since the deceit is most effective when mimics are rare within a population. By enabling more males to participate in reproduction it reduces the reproductive skew within a population.

Permanent Versus Temporary Female Impersonation

Female mimicry can be expressed permanently or temporary by males. Permanent mimicry is known to have a genetic basis in birds and crustaceans. In the Ruff *Philomachus pugnax*, the genes responsible for the female mimicry are located within a chromosomal inversion (Küpper et al. 2016). A genetic basis, however, does not necessarily mean that female mimicry is expressed life-long. In the common Side-blotched Lizard *Uta stansburiana*, female mimics can develop into monogamous territorial males that have higher fitness when the frequency of the sneaker male is high (Sinervo et al. 2000). Temporary female mimics occur in some fish. In the Stoplight Parrotfish *Sparisoma viride*, individuals change their sex from female to male throughout

their lifetime. Large size is required for males to successfully defend a territory and therefore fish start off as a female and become males only once they have grown to the appropriate size. Some male parrotfish maintain the female phenotype despite having already developed male gonads. These males then live temporarily as sneakers on the territories of dominant males until they have grown enough to become a competitive territorial male (Cardwell and Liley 1991). In Pied Flycatchers *Ficedula hypoleuca*, second year males often retain the juvenile/female plumage since in this disguise they are tolerated by older males and not recognized as competitors, which provides them with advantages in conflicts over resources (Sætre and Slagsvold 1996). Sneaker males of the Giant Cuttlefish *Sepia apama* can actively change between male and female appearance and behavior within seconds (Hanlon et al. 2005). An example for extreme flexibility is provided by the Mourning Cuttlefish *Sepia plangon*, where some males have been observed to take up female coloration and patterning only for the parts of his body that is exposed to a male competitor while simultaneously displaying as a male to a female with the other side of its body (Brown et al. 2012).

Other Contexts

Female mimicry also occurs in nonbreeding context. Male garter snakes that recently woke up from hibernation in spring produce female pheromones to attract other males. Within the resulting male aggregation the mimics can avoid predation better and increase their own body temperature and hence become mobile quicker (Shine et al. 2001).

Conclusion

Female mimicry is an effective deceit strategy of males that is often found in populations with high sexual selection and strong reproductive skew. It increases the fitness of males that otherwise would not be able to mate but is most effective when rare. Female mimics usually don't display to females and can be seen as reproductive parasites of

territorial males that dominate male-male competition. Through morphological, physiological, and behavioral adaptations mimicry increases phenotypic variation.

Cross-References

- [Sexual Selection](#)
- [Sneak Copulation as an Alternative Mating Strategy](#)

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Female Orgasm

- [Robin Baker and Mark Bellis](#)

Female Orgasm and In-Pair Copulation

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Introduction

Evolutionary analyses of human behavior characterize modern phenotypes as potential products of natural and sexual selection. Within evolutionary psychology, the human female orgasm generates debate as to an adaptive function because, compared to male orgasm and ejaculation, it is not required for fertilization (e.g., Lloyd 2009 and Puts and Dawood 2006). Evolutionary researchers have proposed two main theories offering adaptive explanations for the female orgasm (Puts et al. 2012a). These Mate-Choice Hypotheses argue that female orgasm increases the probability of producing offspring, thereby falling within the purview of natural selection. Of these adaptive hypotheses, the Pair-Bond Hypothesis would increase survival of offspring through women's selection of long-term mates, while the Sire Choice Hypothesis focuses on orgasm's potential to increase genetic quality of offspring through women's selection of high-quality mates. We describe these models to frame current research on the relations among human female orgasm and in-pair copulation.

Female Orgasm and Conception

Several authors have described in detail the physiological mechanisms that could increase correspondence between women's orgasm and fertilization (e.g., Welling 2014). Briefly, female

orgasm increases the probability of conception via oxytocin release and subsequent uterine contractions that favor fertilization (Puts et al. 2012a). Furthermore, women are more likely to experience orgasm when fertile (Udry and Morris 1968), and the mechanical process of orgasm increases sperm retention in the vaginal canal (Baker and Bellis 1993; cf. Lloyd 2009). Interestingly, when oxytocin stimulates uterine contractions during the fertile phase of the menstrual cycle, fluid transport is directed to the fallopian tube of the dominant follicle which increases the probability of pregnancy (Wildt et al. 1998; Zervomanolakis et al. 2007). In comparison, during non-fertile phases, fluid is transported to both fallopian tubes.

Pair-Bonding

The Pair-Bond Hypothesis states that the survival of our large-brained offspring was dependent on investment from the male; one female alone would not have been able to provide all the necessary care to a helpless, immobile infant (Fisher 2004). Purportedly, a woman who could procure investment from a male would be more likely to survive, as would her offspring. The Pair-Bond Hypothesis stipulates that were a female to forge an affectionate and monogamous bond with her mate – and, critically, signal paternity certainty that he might otherwise lack – she would be able to receive long-term investment and cooperative parenting (Ellsworth and Bailey 2013; Fletcher et al. 2015; Wheatley and Puts 2015). Her orgasm frequency might encourage her to remain with one partner who could provide repeated pleasure, and feelings of calm and trust (Acevedo 2015; Zak et al. 2004). Each time a female orgasms, a multitude of feel-good chemicals – oxytocin, dopamine, and serotonin – are released in the body, solidifying the bond and promoting feelings of love and reward-seeking behavior (Fisher 2004; Thornhill and Gangestad 1996). This, of course, supposes that her male partner has prosocial qualities, such as empathy, with a vested interest in his partner's pleasure (Kennedy and Pavlicev 2018). His altruistic interest in her pleasure could serve as a means to prevent infidelity (Kennedy and Pavlicev 2018; Welling 2014; Wheatley and Puts 2015).

Penile-vaginal orgasm occurrence in relationships is associated with intimacy, satisfaction, and passion (Costa and Brody 2007), supporting the idea that orgasm occurs in the presence of an intimate bond. Relationship length and happiness also correlate positively with orgasm frequency (Eschler 2004; Gebhard 1966), and women have been reported to seek out long-term sexual relationships, rather than short ones, unlike their male counterparts (Clark and Hatfield 1989; however, see also Hald and Høgh-Olesen 2010). Eschler (2004) surveyed 202 women about their sexual behaviors and discovered that women are motivated to remain in relationships in which they achieve orgasm. Over three-quarters reported that reaching orgasm with their sexual partner was “very” or “somewhat” important, while only 1% stated it was “very unimportant.” The women also reported that their level of enjoyment during sex was heavily influenced by whether or not they had an orgasm. In a later replication of this work, two-thirds of female respondents ($n = 274$) were extremely satisfied in their relationships, whether short or long term, when they experienced orgasm, while only 6% were satisfied in relationships in which they never had an orgasm (Patch et al. [In preparation](#)). On the other hand, some studies have indicated that individuals in monogamous relationships report lower levels of satisfaction and have sex less frequently than those in nonmonogamous relationships (Conley et al. 2018). The authors suggested relative sexual satisfaction in monogamous versus nonmonogamous couples may reflect differences in the amount of effort or time placed upon cultivating an exciting sex life (Conley et al. 2018).

Partnered males who are more satisfied in their relationships report greater interest in their partner’s ability to achieve copulatory orgasm (Welling 2014). If orgasm is important to forming and sustaining bonds, individuals might be tempted to fake an orgasm. Although both men and women report having pretended orgasm, sex differences exist in their reasons for doing so. Among women, feigning orgasms is more likely when they perceive higher risk of partner

infidelity and as part of a larger mate retention strategy (Kaighobadi et al. 2012). Feigning orgasm in these contexts would generally support relationship maintenance and are consistent data showing women report higher interest and persistence in ensuring partner orgasm than men (Barnett et al. 2018). In contrast, Ellsworth and Bailey (2013) reported that females who were more likely to fake an orgasm were also more likely to engage in extra-pair copulations and, additionally, that a male’s perception of their partner’s fidelity was not predicted by orgasm occurrence. These two pieces together weaken support for the pair-bonding hypothesis, which places importance on a male’s accurate detection of their partner’s orgasm.

If female orgasm evolved to support pair-bonding, we might expect differences in orgasm frequency in females who are less likely to form attachments. Females with avoidant attachment style are more likely to report less enjoyment from sex and low satisfaction in intimate relationships, which might reduce orgasm frequency (Cohen and Belsky 2008). Women with avoidant attachment styles were less likely to achieve orgasm and were also less likely to be in a relationship, while anxious attachment was not significantly correlated with orgasm frequency (Cohen and Belsky 2008; Patch et al. [In preparation](#)).

Sire Choice

The Sire Choice Hypothesis predicts higher rates of orgasm with high-quality mates whose phenotypic quality correlates with genotypic quality. This perspective explains the variation in women’s coital orgasm experience as reflecting greater choosiness in mates. Specifically, researchers employing an evolutionary lens propose that lower frequency and greater complexity involved for women to achieve orgasm reflect selective mate choice, presumably in favor of mates with higher-quality characteristics (Wheatley and Puts 2015). This perspective is supported by research reporting lower frequencies of orgasm among women and data indicating that orgasm frequency increases with high-quality mates. For example, Lloyd (2009) reports that just 25% report always

experiencing coital orgasm and about 60% reporting orgasm most of the time.

With regard to orgasm with high-quality mates, prior research has demonstrated associations of coital orgasm with mates who were physically attractive (Gallup et al. 2014; Puts et al. 2012b; Shackelford et al. 2000), symmetrical (Thornhill et al. 1995), and more masculine (Puts et al. 2012a) and had relatively dissimilar genes in the major histocompatibility complex (MHC) region of the genome (Garver-Apgar et al. 2006; see also Black and Cabeza de Baca 2018). One study found that women reported more orgasms with wealthy partners (Pollet and Nettle 2009), but follow-up research found these results were confounded by differences in women who partner with higher-income partners. Specifically, women with high-income partners were younger, healthier, happier, and better educated than women with lower-income partners (Herberich et al. 2010; Pollet and Nettle 2010). Still, more recent research found that women's orgasm frequency was positively associated with the partner's family income (Gallup et al. 2014). Furthermore, several studies have shown increased preference for these traits near ovulation (e.g., Gangestad et al. 2004; Little et al. 2011; Puts 2006). Taken together, these findings support sex-specific adaptation of the female orgasm.

Although these data are strongly suggestive of a gene capture strategy, other studies show that women's orgasms are more frequent within long-term relationships (Armstrong et al. 2012; Eschler 2004; Patch et al. *In preparation*). Inferences about Mate-Choice Hypotheses in this case are challenging, as analyses involving both high-quality mate characteristics and relationship duration show mixed findings. For example, Shackelford et al. (2000) found that only partner attractiveness predicted orgasm in regression models that included duration of relationship. Puts et al. (2012a) found relationship duration predicted women's orgasm during or after men's orgasm, but not before men's orgasm. Prior research indicates that vaginal contractions associated with women's orgasm may accelerate male ejaculation (Meston et al. 2004). Furthermore, when women's orgasm occurs within 1 minute

prior to (and up to 45 min after) male ejaculation, sperm retention increases (Baker and Bellis 1993). In light of these findings, women's increased orgasm prior to men's orgasm, which is associated with male masculinity and dominance (but not relationship duration), may be less likely to result in conception. In contrast, both the man's attractiveness and couple relationship duration predicted women's orgasm during and after men's orgasm, which more closely maps on to the period in which increased conception is likely.

Further challenges to the Sire Choice Hypothesis include data from Sherlock et al. (2016) which found support for partner attractiveness increasing orgasm, but not masculinity, dominance, or fitness as found in previous studies. Gallup et al. (2018) offer alternative explanations for absent but expected effects according to Sire Choice, suggesting that the methodology used may have limited partner fitness in the sample, since women were asked to report on their current partner and one with which they had the most orgasms. Still, it is fairly common for existing research on women's orgasm to ask women to reflect on a current or past partner, so similar criticisms could be lodged against those studies as well.

Another study examined whether women's partner characteristics predicted orgasm by distinguishing "surface" and "deep" orgasms, which roughly mapped on to clitoral and vaginal orgasms, respectively (King and Belsky 2012). Deep orgasm, they argued, is more likely to produce physiological changes to increase the probability of conception compared to surface orgasm. Their results showed deep orgasm was associated with higher attractiveness of partner's smell, dominance, and considerateness, but not partner's masculinity, muscularity, or aggressiveness. However, further research confirming their proposed physiological differences between these two types of orgasm is necessary to fully interpret their findings within an adaptive framework.

High mate value males may be less likely to invest in partners (Gangestad and Simpson 2000), so this gene capture strategy may manifest in shorter-term sexual relationships or extra-pair relationships (Gangestad and Thornhill 1997).

However, studies have documented that, compared to men, women experience fewer orgasms during one-night stands (Eschler 2004) and first-time hookups (Armstrong et al. 2009). Some have proposed that the orgasm disparity may partially be explained by gender role socialization that promotes male sexual pleasure while criticizing women's sexuality (e.g., Armstrong et al. 2009). Others have highlighted individual differences, such as sociosexuality. Women with unrestricted perspectives of casual sex report having had orgasms with their last short-term sex partner (Armstrong et al. 2012). Among women who have engaged in extra-pair copulation, more frequent coital orgasms occur with extra-pair mates compared to in-pair mates (Baker and Bellis 1993; Gallup et al. 2006). Their extra-pair partners have low fluctuating asymmetry (Gangestad and Thornhill 1997).

Critiques of Adaptive Perspectives

By-product Hypothesis

The By-product Hypothesis suggests that female orgasm results from shared ontogeny with men and serves no adaptive function. Male nipples represent other human phenotypic traits that are thought to be products of shared developmental processes (Symons 1979). When traits are strongly selected in one sex, then, the opposite sex may retain similar but diminished versions of these phenotypic features. However, it should be noted that traits initially produced as by-products at one point may develop an adaptive function under different circumstances when they become correlated with reproductive success.

Puts et al. (2012a) note that the female orgasm does not appear to be diminished relative to male orgasm, contradicting the By-product Hypothesis. Rather, female orgasm may be more psychologically intense, and women are more likely to report experiencing multiple orgasms compared to men. Zietsch and Santtila (2011) tested the By-product Hypothesis, arguing that if true, male and female relatives should show similar patterns in orgasmic sensitivity. Analyzing data from monozygotic and dizygotic twins and non-twin siblings, Zietsch

and Santtila compared ease of achieving orgasm and showed no positive associations among opposite-sex sibling pairs. Although these data fail to support the By-product Hypothesis, they do not rule out the possibility that selection pressures favoring male orgasm have produced species-wide genotypes that influence orgasm.

While early arguments for the By-product Hypothesis suggest that female orgasm is too inconsistent to be associated with an adaptive function (Symons 1979), proponents of evolutionary models argue that women's selectiveness about mates (Trivers 1972) also applies to female orgasm (Puts and Dawood 2006; Puts et al. 2012a). In summary, while this hypothesis provides sound evidence in some respects, there have been and continue to be critiques of the By-product Hypothesis.

Limitations of Evolutionary Evidence

Studies testing evolutionary hypotheses about female orgasm often operate under assumptions that the female orgasm is easily identifiable by sexual partners, the female orgasm is derived from and similar to male orgasms, and sexual intercourse evokes the same response in both males and females (Lloyd 2009). While it is reasonable to test specific hypotheses, it should be noted that evolutionary assumptions restrict the focus of hypotheses, data collected, and conclusions drawn. For instance, evolutionary hypotheses focus on sexual encounters as they relate to reproduction; however, human sexuality is a multifaceted phenomenon not always manifested under circumstances that could produce offspring.

Second, the literature shows conflicting evidence on several of the key relationships identified by evolutionary researchers. As an example, one study examined women's orgasm characteristics (frequency, method, and behaviors) and characteristics of male partners with which orgasm occurred (Sherlock et al. 2016). Only some traits predicted by evolutionary hypotheses were significantly associated with women's orgasm. Specifically, creativity, attractiveness, humor, emotional warmth, faithfulness, and body odor pleasantness were greater in high-orgasm partners (Sherlock et al. 2016).

Additionally, high-orgasm partners scored highly on behaviors such as communication, use of sex toys, oral sex, foreplay duration, and clitoral stimulation (Sherlock et al. 2016). While these results are consistent with some previous studies, the results fail to show differences between high- and low-orgasm partners on the basis of relationship length and traits such as intelligence, dominance, athleticism, muscularity, fitness, earning potential, and height and weight – each of which is predicted or demonstrated in prior evolutionary research.

How Women Achieve Orgasm

Gebhard and colleagues found 84% of female orgasms achieved through masturbation were derived through the stimulation of the clitoris and the labia, and less than one-fifth of women orgasm by penetration of the vagina, but the majority of those women who do, also accompany penetration with clitoral stimulation (Gebhard et al. 1970, p.15; Lloyd 2009, p. 111). Studies on the female orgasm offer data which provide that the number of females who orgasm by penetrative intercourse unassisted by clitoral stimulation is fairly low – less than 35% (Eschler 2004; Lloyd 2009; Wallen 2006; Welling 2014). If the female orgasm served strictly a reproductive function, one would expect women to orgasm more through coitus, rather than the commonly reported higher frequency of orgasm through stimulation of the vulva and clitoris.

Metascientific Critiques

Perhaps one of the most increasingly argued critiques of evolutionary models of female orgasm involves the androcentric point of view which has largely generated and interpreted the data to date. Several evolutionary biologists have discussed how female orgasm and sexual experiences are framed within the literature, such as orienting women's orgasm around men's sexual experiences (e.g., Hrdy 1979; McClintock 1981). Wasser and Waterhouse (1983) compiled a list of claims regarding female phenomena, including the following regarding female orgasm: “the female orgasm evolved to make women quiescent following copulations so as to prevent the male's sperm

from leaking out of the vagina (Morris 1967); the female orgasm evolved as a ‘byproduct’ of selection for male orgasm” (Symons 1979).

In our review of literature on women's sexuality and orgasm experiences, we noted similar sentiments. Wheatley and Puts (2015) argue that clitoral and vaginal orgasms are produced through stimulation of the same underlying structures, partly due to the expanding structure of the clitoris, which includes the bulbs, corpora, and crura, and attachments among these structures by connective tissues in the mons pubis, labia, urethra, and vagina. They conclude that, in contrast with several studies that show women distinguish between vaginal and clitoral orgasms (Brody and Weiss 2010; King and Belsky 2012; King et al. 2011), “women may be unable to reliably differentiate clitorally- and vaginally-induced orgasms” (p. 126) on the basis of one study with 38 participants and a second study that which in actually showed women were able to distinguish between clitoral and vaginal orgasms (Clifford 1978; Prause 2011). While we agree with Wheatley and Puts (2015) that physiological measures of these different experiences would contribute to the field, we disagree with the notion that extant research is “insufficient” evidence for distinct kinds of orgasm.

Another involves research investigating the female G-spot, stating, “Why then do some women have difficulties achieving vaginal orgasm if every woman supposedly had the equivalent of a penis?”, referencing the clitoral complex (p. 1223, Foldes and Buisson 2009). It is difficult to find a place to start offering clarification to these authors, but this quote is illustrative of numerous papers on women's sexuality citing women's reports on their sexual experiences, but nevertheless with the subtext, “What do women want?”

This is perhaps not surprising, as “most researchers have historically been males, or at least trained in the ‘male tradition,’ [which] has resulted in a disproportionately large amount of behavioral research on vertebrates that is focused predominantly on males” (p. 19, Wasser and Waterhouse 1983). Thus, we echo the sentiments of Wasser and Waterhouse (1983) who acknowledge that “our poor understanding of female

behavior, and hence needs has already detrimentally affected health care...education... and economic quality among women, as well as caused us to sidestep the importance of a number of female psychological...and physiological processes.” And, while we too do not intend to critique previous researchers themselves, we think it is worth noting in our review, 26 years after the publication of *Social Behavior of Female Vertebrates* (Wasser 1983), we found that, still, most of the researchers publishing on female orgasm, who often couch the phenomenon only with reference to its role in heterosexual intercourse, do so in an androcentric way.

Conclusion

We described and presented evidence offering explanations for women’s orgasm experiences in the context of in-pair copulation, using By-product, Pair-Bond, and Sire Choice Hypotheses as frameworks. The By-product Hypothesis is unlike evolutionary theories of the female orgasm because it does not suggest that the human female orgasm is purposeful for reproductive success. In contrast, Mate-Choice Hypotheses, which include Pair-Bonding and Sire Choice, are well-known evolutionary theories of the female orgasm which propose functionality or support for reproductive success. This review finds that several studies fail to support the By-product Hypothesis (see Puts et al. 2012a for a summary). While the Pair-Bond and Sire Choice Hypotheses have been presented as alternative explanations for women’s orgasm in relationships, it is possible that coital female orgasms reflect allocation of resources toward both obtaining mates’ long-term investment and high-quality genes (Wheatley and Puts 2015).

Furthermore, the focus on in-pair copulations neglects findings from a variety of studies focusing on individual differences that contribute to women’s orgasm experiences. These include genetic influences (Dawood et al. 2005; Zietsch and Santilla 2011), life history strategies (Gallup et al. 2014; Patch et al. *In preparation*; however, cf. Zietsch et al. 2011), attachment (Costa and Brody 2011); psychological maturity (Brody

et al. 2011), and personality (Harris et al. 2008). It is also beyond the scope of this entry to discuss at any meaningful length women’s orgasms during nonreproductive activities such as masturbation, in nonheterosexual relationships or in nonmonogamous relationships. Nor can we provide adequate discussion of the impact of gender role socialization and sexual double standards that contribute to the orgasm disparity among men and women. Thus, although we have described research applying evolutionary perspectives, it should be noted that a thorough analysis of female orgasm would benefit from a broader lens.

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Female Orgasmic Disorder

► Orgasmic Disorders

Female Partner Preferences

► Women's Mate Preferences

Female Reproductive Variance

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Synonyms

Female choice; Parental investment theory; Reproductive variance; Sexual selection

Definition

The degree to which sexual selection pressures female members of a species. Female reproductive

variance is tied to the fertility of the individual and less to their ability to mate and reproduce. Hence, female reproductive variance is quite low relative to male reproductive variance.

Introduction

Research has found a pattern of reproductive variance for many species in which females have far less variability in their reproductive output than males. Three factors contribute to the pattern of mating behaviors that are typical for females: most females successfully reproduce, the amount of copulations shows a weak relationship with the number of offspring for females, and for many species, females have a greater minimum obligate investment to produce viable offspring.

Female Reproductive Variance

Angus Bateman is among the first to formally study reproductive variance. In 1948, Bateman tracked the reproductive output of male and female fruit flies (*Drosophila melanogaster*) (Bateman 1948). Bateman made two important observations regarding sex differences. First, very few females failed to successfully mate (about 4%), while a much larger proportion of males failed to reproduce. Second, the reproductive output of females showed a much weaker relationship with the number of copulations than for males. Based on these observations, Angus Bateman articulated what would be known as Bateman's principle: reproductive variance is greater for males than for females.

This relationship has been found consistently across a wide range of species. Among humans, the majority of women who are able to produce offspring will be able to, assuming they have the desire to do so. Additionally, the maximum amount of offspring a woman can birth in her lifespan is highly limited, practically not much more than 12 (Buss 2014).

According to Robert Trivers' parental investment theory, females, among most vertebrate species, have a greater minimum obligate investment

in the production of offspring (Trivers 1972). This is largely accounted for by the anisogamy of male and female gametes as well as the burden of internal gestation. Due to this higher minimum investment in offspring, Trivers proposed that females adopt a mating strategy based on being highly selective and "choosy" when assessing potential partners and mating opportunities. Put another way, because reproductive output is much more constrained for females, a more viable strategy is to focus on quality of mating opportunities rather than quantity.

It is important to note that there are species that do not conform to this pattern of behavior, however. The phalarope is a genus consisting of three species of shore birds known for having sex-reversed roles (Colwell 1986). These species engage in polyandry in which females are larger with more coloration and compete for mates, while males incubate and provide primary care for the offspring. These exceptions to the rule can be explained by factors such as operational sex ratio (Colwell and Oring 1988).

Conclusion

There is a pattern across many species where the females will adopt a mating strategy of being highly selective of mates. Although this strategy is not found among all species, the prevalence of this strategy can be largely attributed to the lower reproductive variance that often characterizes the females of a species as well as the greater minimum obligate investment that females of most species must endure in order to produce viable offspring.

Cross-References

- [Male Reproductive Variance](#)
- [Reproductive Variance](#)

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Female Same-Sex Alliances

► Female-Female Alliances

Female Same-Sex Friendships

► Female-Female Alliances

Female Sexual Interest/Arousal Disorder

► Desire and Arousal Disorders

Female Sexual Orientation

► Female Homosexuality and Bisexuality

Female Sneak Copulation

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Synonyms

Sneaky mating; Undetected extra-pair copulation

Definition

Undetected copulation with the partner of another female or in defiance of the dominant female; often punished if detected.

Introduction

A female sits with her partner, or with a dominant male. She is able to reproduce and benefits due to her partner's parental care and protection. Another female – of low rank, in a female-driven dominance hierarchy – has failed to find a partner and has yet to mate. In each case, the female can increase her reproductive fitness by mating with an additional male, with additional males, or by mating for the first time. But in order to do so, she must overcome various forms of resistance. In the first case, the partner of the female, or the dominant male, will not want her to “cheat” on him. Likewise, the partners of her additional mates will not want “their” males to cheat on them. Finally, in the case of the low-rank female, a dominant female will not want her to win over reproductive access, because this could lead to a dilution of the benefits that she receives both in terms of parental care and protection.

Here then is the basis for two broad forms of female sneak copulation (FSC). One is based on a partnered female's attempt to “have her cake and eat it”, in which she tries to obtain the benefits of additional mates – such as additional parental care or genetically diverse offspring – while also attempting to avoid the costs of discovery, which are likely to result in lower parental investment by her partner or even physical punishment. Another arises when a female attempts to break rank, to the same end but with different risks. Yet cut across these two forms is another division. In the case of the partnered female, the punishment (i.e., fitness loss) is meted out not only by the male partner but also by the *female* partners of her additional mates. In the case of the low-rank female, the punishment is administered by the dominant *female*. The rest of this section focuses on these female-female interactions linked to female sneak copulation (FSC), where a female tries to ensure additional, secretive reproduction, in defiance of other females.

The Lay of the Land

Many aspects of the female-female contest for copulation are understudied, and the same is true of FSC (Neff and Svensson 2013). Indeed, there is practically no direct evidence on this topic at all. Nonetheless, it is plausible that FSC could be common. And if so, it could well have been important in the evolution of animal behavior, cognition, and psychology, and maybe in particular in humans. Given the dearth of direct evidence, the approach taken here is to first provide an overview of the evolutionary requirements of FSC. This is followed by a brief review of the direct and indirect evidence in favor of each form of FSC: in relation to the partners of other males, and in defiance of dominant females. A discussion of the behavioral mechanisms that could facilitate the operation of FSC in nature is then provided, along with a discussion of the relevance of FSC to human evolution. A conclusion is then provided that looks to the future, at the questions that remain to be addressed.

Female Multiple Mating (FMM)

FSC requires that there are benefits to female multiple mating. In males, multiple mating is expected to arise due to the linear relation between the number of matings that a male secures and a male's total paternity. Just such a relationship was found in Bateman's classic study on the fruit fly, *Drosophila melanogaster* (Bateman 1948). In contrast, females have often been viewed as the limited sex, with fitness being determined by reproductive output rather than mating rate. Yet even in 1948, Bateman was able to find evidence that females increased their reproductive success with the addition of extra mates. Moreover, females have been observed to mate multiple times with multiple partners in multiple species across multiple taxa. Ascribing this all to male activity with the implication that the female is just a passive vehicle now seems absurd (Trivers 1972), and recent work has rightly rejected this simplistic dichotomy. Multiple mating is as much a female mating strategy arising from female

action as it is a male mating strategy based on male action.

But why do females mate multiple times? The act of copulation is associated with a number of costs (Jennions and Petrie 2000; Forstmeier et al. 2014). Copulation itself can be associated with direct damage to the female reproductive tract, for example, in species where the male penis carries spines, or it may simply use up a crucial resource – time. Likewise, precopulatory behavior can injure females. Postcopula, there are further risks resulting from the transmission of sexual diseases by multiple mating, while female longevity has been shown to decline due to the transfer of male-derived ejaculate products that raise a male's paternity at a cost to female survival. Mixed ejaculates are also associated with increased risk of embryo mortality via polyspermy. And there may be additional dangers if predation risk is increased in copula (or if a female suffers costs due to attacks by her partner or by other females). Given this, there must be clear benefits to FMM.

The most obvious direct benefits arise when the female herself benefits from mating, because the male provides a nuptial gift, such that more mating results in greater resource acquisition. Another example is the increased parental care that a female can obtain if she mates with more males, as a larger number of males will have a stake in her brood. Mating may also cause a reduction in male harassment or a decrease in the risk of male-driven infanticide. A final – special – example is that of fertility assurance. Females may become sperm limited in situations where some males have reduced fertility, where males invest few sperm per copulation (due to the partitioning of their resources across multiple females), or where there are limits to the length of time that sperm remain viable. All of these benefits provide reasons for females to mate multiple times: to accrue benefits to themselves in terms of resources or to ensure all of their eggs are fertilized (Jennions and Petrie 2000).

In addition to these direct benefits to the female, females can also obtain indirect genetic benefits to their offspring via multiple mating. A female can mate with a more ornamented male to obtain “attractiveness genes” (in so far as the

male ornament is preferred by other females) or “viability genes” (where ornament size correlates with male genetic quality). A female can thus trade up genetically by multiple mating if she mated first with a low attractiveness or low genetic quality male. In other cases “compatible genes” will be more important. Here, multiple mating can open up postcopulatory mechanisms that can select for compatibility (based on relatedness, MHC complexes, selfish element suppressors; Forstmeier et al. 2014). Alternately, multiple mating can be a simple bet-hedging strategy to increase the genetic diversity of a female’s offspring. In this case, multiple mating can either compensate for nonperfect female mate choice or increase the chances that some offspring fit their environment (Fox and Rauter 2003). As a final indirect genetic benefit, it is notable that, postcopula, “cryptic female choice” and “male sperm competition” are enabled by multiple mating and may simply select for sons that are good at fertilization – as such sons will inherit their father’s more competitive sperm.

Extra-Pair Copulation and FSC

As seen above, there are various benefits to multiple mating that are necessary for FSC. However, FSC also requires that multiple mating takes place in a social context. It is not possible to “sneak” in isolation. A simple social context is the monogamous pair bond. Here, a female is joined in a social pair with a male, and they jointly raise their offspring. However, the benefits of female multiple mating remain, even in this monogamous context. This can lead to selection for female alternate mating strategies, such as extra-pair copulation (EPC) or FSC (which is in this context a subclass of EPC).

EPC arises when a male or female mates with an individual other than their partner. It can be driven by males or females. Males can force females to mate with them in the face of true female resistance (forced copulation, coercion) or females may solicit males to mate with them (Griffith 2007; active female solicitation). Usually the interaction between the sexes reveals that

males search and display to females and that the females passively accept such advances, or put up a threshold of resistance (Westneat et al. 1990). The females’ behavior is presumably a reflection of the costs and benefits associated with extra-pair paternity. It is in this context that FSC subclasses of EPC might evolve.

A classic example of this FSC-EPC was provided by Kempenaers et al. (1992), who combined behavioral and genetic data to show that female-driven EPC was common in monogamous pairs of the blue tit, *Parus caeruleus*. In the wild population studied, 31 % of clutches included extra-pair paternity. Further, of the 7 EPCs (out of 90 copulations) observed, more than 70 % were classified as female driven. In these cases, females moved onto the territory of neighbors and were either chased off by the resident female or – if undetected – were sometimes able to solicit and take part in an EPC. The observation that resident females showed aggression toward intruders highlights the extra costs to this form of EPC, which must nonetheless be outweighed by the benefits, and provides evidence of a selective pressure that could promote the evolution of costly female sneak behaviors leading to copulation.

Primate Tactical Deception and FSC

Another class of species in which FSC-EPC could be important is the primates. Exclusive pair bonds are rare in most mammals (around 3 %). But they are relatively common in primates, with 14–18 % of species forming monogamous sexual bonds (Drea 2005), while the percentage is even higher if nonexclusive “pair” bonds nested within hierarchies are included (such as when a male has exclusive access to several females, see “[Hierarchies and Defiant FSC](#)” below). Female-driven EPC has been observed in several primate species, and male mate guarding behavior is known to be common (Drea 2005). Females are also known to take part in competitive interactions with other females, as well as to use various forms of physical and social punishments (Stockley and Campbell 2013). Hence, the FSC forms of EPC could be common in primates.

An advantage to recent studies on EPC in primates is that a number have started to provide insight into the psychological processes and cognitive mechanisms that underlie EPC. For instance, Overduin-de Vries et al. (2015) found evidence of EPC based on tactical deception in captive populations of the macaque species *Macaca mulatta* and *Macaca fascicularis*. They observed that females appear to deliberately create distance between themselves and other females before EPC events – a more complex level of cognitive processing than chance exploitation of a peripheral location but less complex than taking the perspective of other females into account (e.g., by deliberately hiding out of view behind screens). Similar tactical concealment was also observed in a wild Ethiopian population of the gelada monkeys, *Theropithecus gelada*, in a recent study by le Roux et al. (2013). As tactical deception is known to occur in relation to food and other nonsexual contexts in fish, corvids, apes, and monkeys (Overduin-de Vries et al. 2015), this behavior could also be widespread in FSC contexts of EPC. But at present there is little direct evidence for FSC-EPC in primates or of the role of tactical deception in this. This is due mostly to a lack of studies. Hence, such mechanisms *could* often be utilized in an FSC-EPC context, and there remains a need for further studies on this issue to determine if this is the case.

Hierarchies and Defiant FSC

Another social context in which FSC might appear is that based on the rank and social hierarchy seen in a variety of species, including cetaceans, elephants, corvids, and primates (Overduin-de Vries et al. 2015). A diverse array of such hierarchical systems exists. But the most relevant in terms of the evolution of human psychological processes are the primates. Here, hierarchies are based on both male and female rank (Drea 2005). Higher-ranked females often have higher reproductive success. And such females are also known to suppress the reproduction of lower-ranked females (Drea 2005). Hence, another type of FSC that could be important is

that of “defiant FSC” – where a lower-ranked female mates with a male, in defiance of a higher-ranked female. As in the case of tactical deception, there is little direct evidence about defiant FSC. Nonetheless, a number of studies have provided indirect evidence that this could be common. For instance, both Overduin-de Vries et al. (2015) in macaques and le Roux et al. (2013) in gelada monkeys found evidence of male rank-related audience effects on EPC – females and lower-rank males were less likely to copulate when a male of higher rank was nearby and were often punished by these males if sighted. Female rank-related audience effects were not observed in either case. However, these are the first studies of their kind and highlight the potential for such defiant FSC to arise in nature.

FSC in Humans: “Woman Beware Woman”

It has also been suggested that FSC is likely to be common and important in humans. Like other primates, humans have complex social structures and form close pair bonds. Females (women) have flatter “hierarchies” than males (men) (Sidanius et al. 1994) but are known to enforce these via subtle social as well as physical means (Campbell 2013; Stockley and Campbell 2013). Women are also known to “cheat” on men and to punish this behavior in other women, especially if the target of the FSC-EPC was “their” man. In street “gangs” such punishment can even lead to the death of another woman (Campbell 2013). Hence FSC is likely to be important in humans and could well involve – or have been involved in the evolution of – the complex psychological processes and cognitive systems that define humans. But once again there is very little solid observational or experimental work that would establish human FSC beyond anecdotal reports; so more studies are needed.

Conclusion

Female sneak copulation (FSC) is likely to be common in nature. However, all female-female

sexual competitive interactions remain relatively poorly investigated, and FSC is no exception. Nevertheless, the field is starting to move forward, and it is likely that within the next 5–10 years the mechanisms of FSC, its prevalence in nature, and its importance in human evolutionary psychology will be better known. The results are awaited with anticipation!

Cross-References

- [Female Deception](#)
- [Female-Perpetrated Violence](#)
- [Inclusive Fitness](#)
- [Intrasexual Competition](#)
- [Male Dominance Hierarchies](#)
- [Multiple Mating](#)
- [Reproductive Strategies](#)
- [Sneak Copulation](#)

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Female Strategies

- [Women's Prosocial Dominant Acts](#)

Female's Mate Retention Tactics

- [Women's Long-Term Strategies](#)

Female's Romantic Partner Maintenance

- [Women's Long-Term Strategies](#)

Female-Biased Postcopulatory Sexual Selection

- [Cryptic Female Choice](#)

Female-Female

- ▶ [Cost of Same-Sex Friendships](#)
- ▶ [Same-Sex Friend](#)

Female–Female Aggression

- ▶ [Contexts for Women’s Aggression Against Women](#)

Female-Female Alliances

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Synonyms

[Female coalitions](#); [Female-female friendships](#);
[Female same-sex alliances](#); [Female same-sex friendships](#)

Definition

Relationships between two or more females that are based on mutual benefit.

Introduction

When females have abundant resources, they birth more offspring and have more offspring survival than females who have limited resources (Mulder [1987](#)). Allies who share a common goal are likely to share resources, so individuals who form alliances have a greater likelihood of survival and reproduction than individuals who do not form alliances (Chapais [1995](#)). Female-female alliances are often formed for food competition,

particularly among nonhuman primates, but alliances afford females a variety of advantages including physical protection, emotional support, and child care.

Benefits of Female-Female Alliances

Alliances increase reproductive fitness, or one’s ability to pass genes to subsequent generations, by enhancing one’s ability to secure and maintain resources. Food and status are common resources obtained through alliances (Chapais [1995](#)). Another valuable resource, particularly among human mothers, is child care (Hrdy [2009](#)). Human infants are born altricial – they require extensive care for survival. Allomothers, or caregivers other than the mother or genetic father, are highly valuable to a mother. If a mother does not have kin nearby, a female-female alliance that results in child care increases her children’s likelihood of survival.

Female-female alliances are also associated with mental health advantages. Women’s friendships are characterized by high levels of social support and self-disclosure, which are thought to positively impact mental health (Uchino et al. [1999](#)). The more female friends co-ruminate, or discuss negative feeling and experiences, the closer they feel to their friend (Rose [2002](#)). Another benefit of female-female alliances is support during competition with rivals. Women’s intrasexual competition typically occurs by indirect actions such as gossip and rumor spreading aimed to promote equality (Campbell [1992](#)).

Costs of Female-Female Alliances

Although some aspects of women’s same-sex friendships promote mental health, other aspects may negatively impact health. Co-rumination among girls and adolescents predicts increased anxiety and depression over time (Rose [2002](#)), and co-rumination among women is associated with increased levels of physiological stress (Byrd-Craven et al. [2011](#)).

Women's same-sex friendships are also fragile relative to men's same-sex friendships (Benenson and Christakos 2003). Competition for resources, such as attention from a mate or status, can dissolve an alliance. If women portray themselves as superior to their allies, exclusion from the group is a likely consequence (Campbell 1992).

With Whom Do Females Form Alliances

Genetic relatedness, similar social status, and similar age are variables that increase the likelihood that females will form an alliance (Chapais 1995). Indeed, maternal kinship bonds are one of the primary sources of social status and alliance formation among many nonhuman primates. Alliances form among females who share similar goals such as guarding food and mates (Rucas, Gurven, Winking, and Kaplan, 2012). Familiarity is also a factor in alliance formations. Females are more likely to be allies the more often they interact socially (Dunbar 1980).

High-status females tend to form alliances with other high-status females, and befriending a high-status female can increase one's own social status (Chapais 1995). Females sometimes betray kin and close friends if a prospective ally can help them improve or maintain their own rank (Benenson 2013). Moving up the social rank by forming an alliance with a high-status female is rare because there is little advantage to a high-status female to forming an alliance with a low-status female. Although alliances typically form between individuals of similar social status, there are exceptions. In bridging alliances, one ally is ranked below a target, and the other ally is ranked above the target (Chapais 1995). The alliance results in the lower ranked ally moving up in rank above the target. In a revolutionary alliance, both allies initially rank below the target but both move up in rank above the target after the alliance.

Conclusion

Female-female alliances are relationships between two or more females that are based on

mutual benefit. Alliances enhance an individual's ability to secure and maintain resources, which ultimately increase one's reproductive fitness. Some of the resources that females secure through alliances are food, territory, status, mates, and child care. Female same-sex friendships can provide social support, but they can also increase physiological stress. Alliances between women are based on equality, and they are quick to dissolve if an individual is perceived as acting superior to the group.

Cross-References

- ▶ [Alliances](#)
- ▶ [Cooperative Alliances](#)
- ▶ [Same-Sex Friendships](#)
- ▶ [Special Case of Bonobos and Female Counter-Adaptations to Rape](#)

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Female-Female Competition

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Synonyms

Intrasexual competition; Rivalry; Women

Definition

Competition that females of a given species engage in against each other in order to access limited resources, including mates, that impact on their survival and reproductive success.

Introduction

Females of many species compete with each other to gain access to limited resources that directly impinge upon their survival and reproductive success. Competition is usually highest among members of the same sex, given they most often compete for the same resources, including mates (see Stockley and Campbell 2013, for a review). Within-sex (i.e., intrasexual competition) is therefore a significant evolutionary pressure. During the last decade or so, there has been noteworthy research that indicates females can be as aggressive, or even more so, in competitive interactions than males (see Stockley and Campbell 2013, for a review).

Originally, much of the literature pertained to male intrasexual competition, but the focus has turned within recent decades to females (see, for example, Stockley and Campbell 2013; Fisher 2017). Perhaps this former neglect is because female competition is typically characterized as being subtle and covert (Hrdy 1999). It rarely involves escalating contests or exaggerated secondary sexual characteristics (Clutton-Brock and Huchard 2013), and in humans, women suppress it when men are present in order to avoid seeming undesirable (Cashdan 1999).

Female Aggression

Researchers have proposed a link between aggression and competition, such that aggression is necessary for competition to occur (e.g., Schuster 1983). While men are often found to engage more frequently in direct physical aggression than women, the latter engage more frequently in indirect aggression. Indirect aggression occurs when a perpetrator attempts to cause harm but simultaneously tries to make it appear as though there is no harmful intention (Björkqvist et al. 1992). Girls and women use indirect aggression when they engage in behaviors such as breaking confidences, criticizing others' appearances, excluding others from the group, or spreading gossip (Björkqvist 1994; Owens et al. 2000). Social networks are often used, which further obscures intentions to cause harm and thereby reduces the possibility of retaliation and counter-aggression (Björkqvist et al. 1992).

Campbell (1999; but see Liesen 2013) suggests that women's lack of direct physical aggression is a successful female adaptation that results in reproductive benefit. She argues that when women become mothers, they become the primary caregivers and protectors of their children. Hence, it is important for mothers to remain alive, leading to the use of indirect, low-risk, strategies to resolve disputes. She posits girls and women avoid competing for status and instead focus on competition for resources, using indirect means (see Liesen 2013 for a review). There are alternative views; for example, Liesen (2013) proposes

girls and women use direct and indirect strategies, pursuing dominance and status to gain access to material resources (e.g., food, space, mates) but also to reduce female harassment and establish alliances. She argues that for girls and women, the goal is not to be at the top of a hierarchy but rather the center of attention where the maximal social, material, and reproductive benefits are located.

Competition for Mates

Women compete in many arenas, just like females of many species. Females compete for access to desired mates (see Fisher 2013 for a review), as well as for resources that may influence their reproductive fitness outcomes, such as food, nest-sites, protection, territories, and by interfering with the reproduction of other females (Stockley and Bro-Jørgensen 2011).

Women are obligated to significantly invest in their children, at least in terms of gestation and lactation, which leads to a decreased reproductive potential relative to men who have a far smaller obligatory investment. Females of many species compete when there are high levels of maternal investment, when paternal investment is beneficial, and where there are large aggregates of individuals living together which increases competition for proximal resources (Apicella and Dreber 2015). Humans show all of these features. In addition to maternal investment, men, compared with males of other species, tend to provide high levels of paternal care for children (Clutton-Brock 1991). Humans also live in social groups with plentiful opportunities to be in close proximity to other mothers with children, leading to competition for scarce resources that effect the survival of themselves and their children, as well as further reproduction.

It is undeniable that women compete for mates. Universally, women intrasexually compete to gain access to high quality mates who possess phenotypic characteristics that indicate high genetic quality, an interest in (and ability to provide) paternal care (Gray and Anderson 2015), and an ability to accrue resources (see Fisher 2013 for a

review). Women use a variety of information sources to make decisions about how and when to effectively compete. For example, women rely on information about rivals in their local environment to determine their own and potential rivals' mate value, alongside the value of potential mates (Fisher and Fernández 2017). As another example, factors such as a scarcity of quality mates leads to increased intensity in competition (Dillon et al. 2017). The bulk of research findings apply only to single, young women from Western cultures and has, for example, neglected women who are married, above the age of the average college student, or mothers (Fisher 2017). Further, the vast majority of past work has focused on the hormonal underpinnings of women's mating competition, or women's use of beautification or physical alterations to outcompete mating rivals.

Competition Between Mothers

The overwhelming neglect of competition among mothers is particularly curious, given that such competition has direct outcomes on individual fitness. Mothers have found and potentially secured a mate, but they still need to ensure that mate provides care, time, and resources to herself and any resulting children. Also, once a woman becomes a mother, she does not necessarily stop reproducing, and indeed, she may engage in behaviors to remove the current child to increase her chances of reproduction or in securing a better mate (Hrdy 1999). Consequently, locating, obtaining access to, and retaining a quality mate are highly critical to a women's reproductive success, in that it will lead to healthy children who ideally will survive and reproduce.

However, there are other domains outside of mating that impact on a mother and her child(ren), such as relational status, social dominance, and obtaining sufficient resources (Fisher and Moule 2013). These necessary resources improve child longevity and include clean drinking water and medicines, given that the most common cause of mortality for children under 5 years of age is infectious disease (68%; Black et al. 2010). Women, like all mammals, invest substantially,

from the gamete stage, throughout pregnancy, lactation, and childcare. To benefit from this investment, they must ensure their children survive, which dictates that they compete for limited resources in support of themselves and their children (Stockley and Bro-Jørgensen 2011). The importance of this competition must be emphasized; Clutton-Brock (2009) suggests that females in many species may compete more intensely for reproductive resources than access to mating opportunities.

Cooperation and Competition

One of the most important issues for understanding female intrasexual competition is the delicate balance between cooperation and competition with same-sex others. The most likely allies are those who are around the same age, with similar personality characteristics, values, and mate value (see Fisher and Fernández 2017, for a review). However, these are also the most probable rivals for mates, status, or access to resources in support of children. The quandary of competing with potential allies poses a problem. Women may gain particular benefits through intrasexual competition (e.g., status, power, dominance, resources, potential mates), but at the cost of their friendships or alliances with other women. Maintaining a cooperative relationship is critical; women engage in intense cooperation because male partners can be absent, noncommittal, unable to help, or abusive. Without the assistance of other women, women and their children are in serious danger (see Sokol-Chang et al. 2017 for a review). In fact, circles of supportive women are at times called “survival networks” (Dominguez and Watkins 2003; Högnas 2010). Therefore, the issue becomes: how do women compete against same-sex friends yet remain in strong sharing, dyadic relationships with these individuals? One solution is to use indirect aggression, as outlined. Women may attack their victim circuitously, prohibiting the likelihood of being correctly identified (Björkqvist 1994). Alternatively, one may use an indirectly aggressive act under the ruse of self-improvement. A strategy women (and men) rely

on is self-promotion, whereby one attempts to make herself look better than a rival. However, it is possible that she could say that she was not involved in a competition but merely engaging in self improvement, thus hiding any intention to compete (which may explain why self-promotion is the most often used strategy for intrasexual competition for access to, and retention of, mates; Fisher et al. 2009). In this way, competitiveness is hidden and enables women to remain allies with those they are competing directly against. As women proceed through their lifespan and change (e.g., have children, experience increases or decreases in their mate value and reproductive potential), they encounter situations where they must make new decisions about whether to cooperate or compete (see Fisher et al. 2017). Each of these situations has limitations and exceptions, as women may cooperate as a strategy to obtain mates, and mothers may forgo cooperation in favor of competing for limited resources for themselves and their children, for example. Herein lies the interesting dichotomy in women’s relationships with other women, as they must decide between providing cooperative support or being competitors with the goal of maximizing their own reproductive success.

Conclusion

Female intrasexual competition is observed in many species. The outcome of intrasexual competition influences access to limited resources that directly affect one’s survival and reproductive success. Consequently, female intrasexual competition is a significant evolutionary pressure. Here we specifically review women, and the link between their use of aggression and competitive behaviors. Women intrasexually compete to gain access to quality mates and also for resources, status, and other considerations that impinge upon themselves and their children. Women are faced with a difficult decision of whether to cooperate or compete with same-sex others; given the benefits resulting from cooperation, competition is likely to occur in a way that disguises either the perpetrator or the actual competitive act itself.

Cross-References

- [Boys Bully More Than Girls](#)
- [Competition for Resources Desired by Females](#)
- [Derogation of Promiscuity](#)
- [Intrasexual Competition Between Females](#)
- [Meta-analysis of Sex Differences in Aggression](#)
- [Verbal Derogation](#)
- [Women and Competition, The Oxford Handbook of](#)

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Female–Female Competition

- [Contexts for Women's Aggression Against Women](#)

Female-Female Friendships

► Female-Female Alliances

Female-Female Strategies

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Synonyms

Reproductive competition; Women's intrasexual competition

Definition

Behaviors or actions that females engage in against same-sex others for the purposes of maximizing reproductive fitness.

Introduction

Female intrasexual competition has gained considerable momentum as a topic of study (see Fisher 2013). The majority of this work, as it applies to humans, is focused on mating competition. However, there has been a surge of recent interest in human competition outside of this context. Thus, competition over limited resources important for reproductive fitness is first reviewed and then issues pertaining to mating competition. Given the strategies involved in women's intrasexual competition are typically subtle and indirect, research on relational and indirect aggression is presented. After this discussion, the four types of strategies that women use within mating competition are reviewed, followed by a section on future work.

Human females, like females of many mammalian species, are group living and reap the benefits associated with sociality. Among

mammals, these benefits may include decreased predation and increased access to resources. However, individuals within groups also face costs, such as the transfer of pathogens, increased probability of infanticide, and competition for limited resources and mates (for a review of the costs and benefits of mammalian sociality, see Ebensperger et al. 2012). The outcome of competition for resources and mates is critical, as it confers reproductive benefits that directly influence reproductive success.

Competition for Limited Resources and Mates

These limited resources are ones that vary in quality and may include food, territories, and protection (see Stockley and Bro-Jørgensen 2011), all of which impact on the well-being of the female and her offspring. Gestation, and in particular, lactation, places high energetic demands on females, such that the ability to locate and acquire food may constrain reproduction. Indeed, the distribution of food is thought to be one of the major determinants of within group competition (Isbell 1991). For example, due to limited food resources, there may be clearly defined female dominance hierarchies resulting from aggression, increased home range size in conjunction with increased group size in order to acquire additional resources, and longer distances traveled each day in response to increased group size (Isbell 1991).

Therefore, females should compete for access to food, in order to sustain reproduction. This competition has many repercussions. For example, Stockley and Bro-Jørgensen (2011) review how dominance is important for some species, given that dominant females may have improved access to better food, drinking sites, nest sites, territories, and better protection (e.g., be in the central, safer position of a pack during an attack). However, while dominant females seem to have higher reproductive success in many mammalian species, especially in free-ranging species where resources are limited, it is not ubiquitous (see Stockley and Bro-Jørgensen 2011).

As a side note, that females intrasexually compete outside of a mating context has led some scholars to question Darwin's view of sexual selection and argue that it is overly narrow (e.g., Clutton-Brock 2009). Thus, there has been debate as to whether there should be a distinction for within-species dynamics to be divided between sexual selection (i.e., competition for access to, or retention of, mates) and social selection (i.e., access to, and retention of, resources that impinge upon reproductive success but are outside of a mating context).

With respect to competition for mates, it must first be noted that females and males of many species energetically invest to differing degrees in offspring (for a review, see Trivers 1972). In mammals females substantially invest energetically in offspring, so they must compete to guarantee the highest rate of return on this investment (i.e., that their offspring survive and reproduce). Males, by contrast, do not need to invest much, and indeed, in approximately 95 % of mammalian species, there is a pattern of intense male intrasexual competition for access to mates and minimal parental investment, coupled with discriminative female choice (Clutton-Brock 1989).

However, in humans, many men do provide some investment, by provisioning, childcare, and/or protection, and hence, women intrasexually compete for men high in these attributes. Men differ in their abilities to protect offspring and in their abilities to provide resources. Protection and provisioning by men very often increase the survival rate of offspring, and as a result, are important resources for women. Subsequently, good protectors and providers are in greatest demand and are relatively rare. Moreover, men with superior phenotypes (which may indicate superior genotypes) are also in demand. Women attend to cues that may signal sterility or impotence (Campbell 1995) and hence, notice physical indicators of youth, strength, and libido when selecting mates. Note that some of women's mate preferences for men's physical characteristics such as facial masculinity may vary according to their ovulatory cycle status, but this has recently been debated (see Marcinkowska et al. 2016).

Inherent in Darwin's (1871) theory of sexual selection is the idea that characteristics evolve to enable individuals to gain advantage over same-sex competitors thereby securing successful matings. Moreover, both elements have evolved in unison, so traits that are most preferred by the opposite sex are the traits that are of most benefit in same-sex competition. While there are some similarities, the sexes differ in their mate preferences in conjunction with the constraints of reproductive success (e.g., Buss 1989; Trivers 1972). That is, although both sexes consistently show a desire for mates who are kind, intelligent, and loving, there are some notable sex differences. Universally, men typically express a strong preference for attractive women as potential mates (e.g., Buss 1989), and thus, women compete in terms of attractiveness. Likewise, women tend to have a strong preference for men with financial security and access to resources (e.g., Buss 1989), so men compete to appear wealthy. Indeed, women compete via their attractiveness, whether it be through self-promotion of their own appearance, or derogating rivals' appearance (Fisher and Cox 2011). Men compete via displays of their wealth (e.g., self-promoting or derogating the resources of other men; Fisher and Cox 2011).

Last, the anticipated duration of the relationship influences mate preferences. For example, women seeking short-term relationships place a higher premium on appearance (i.e., potential phenotypic cues of gene quality) and decreased importance of personality traits or traits related to accruing resources. Men seeking short-term relationships generally seek ease of sexual access and decrease preferences overall, but emphasize physical attractiveness and youth (i.e., potential proxies for fecundity) in long-term mates (see Schmitt 2014). Thus, individuals should adjust the form of intrasexual competition in relation to the intended duration of the relationship, given there are shifts in mate preferences. Findings indicate partial support, as reviewed later (Schmitt and Buss 1996).

Unlike competition for resources, there has been considerable research into competition for mates. Therefore, the remainder of this entry will focus on the latter topic.

Types of Aggression Used by Women in Competition

The primary way that women compete with each other is through the use of relational and indirect aggression. The sexes do not differ significantly with respect to the frequency of aggressive behavior in general (e.g., Bettencourt and Miller 1996). However, the form of the aggression is sexually differentiated, as women are thought to engage in more relational and indirect aggression than men. If the aggression involves the manipulation of peers via their relations and reputation, and/or interference with friendships and group inclusion, it is relational aggression; the only criterion is that relationships are the central consideration. Another form of aggression is indirect aggression, where a perpetrator tries to inflict harm while simultaneously attempting to make it appear as though there was no harmful intention (Björkqvist 1994), presumably to decrease the likelihood of retaliation. Often indirect aggression is used within the context of relationships and social networks, directed at someone's reputation, or for the purposes of group exclusion, for example, and hence, it often falls within the realm of relational aggression.

Benenson et al. (2013) argue that one form of relational aggression, social exclusion, is of particular importance to girls and women. Social exclusion may reduce the number of competitors for resources that relate to reproductive fitness, and thus, be an effective strategy to aggress against other women. They further posit that women's friendships may be less instrumental than men's friendships, and thus, the cost of ostracism to the perpetrator is low. Indeed, compared to men, it does appear to be an effective and often used strategy among women, as they face relational aggression via ostracism more often, are typically more affected by it, and react more strongly (Benenson et al. 2013). One reason for its effectiveness and frequency of use may be that women tend to prefer interactions that are one-on-one, whereas men tend to engage in larger groups; the probability of social ostracism is greater in the former than in the latter (see Benenson et al. 2013 for a review).

Indirect aggression is more often used by women than by men, and women less frequently engage in direct physical confrontation (e.g., Campbell 1999). However, it should be noted that women sometimes do engage in direct aggression; for example, Burbank (1987) found 61 % of the 137 cultures she studied documented women's physical aggression, typically in the form of women fighting other women over men in an effort to protect their relationships and resources for their children. Moreover, Campbell (2004) found that women's physical aggression most often occurs among lower socioeconomic classes, which may indicate that competition increases when resources are more limited. However, even in contexts where variables that influence the severity of competition are observed, such as sex ratios that are biased against women, age of oneself and potential rivals, or high variance in men's resources, women's use of direct aggression is still less, as compared to men (Campbell 2013).

There are various proposals as to why women rely on indirect aggression. First, because women generally possess less physical strength than men, they evolved alternative methods to aggress, and consequently, rely on different competitive strategies (Björkqvist 1994). Second, Campbell (1999) contends women are typically the primary caregivers and protectors of their children and engage in indirect, low-risk strategies to resolve disputes, which helps ensure they (and their children) remain alive. Third, Hess (*in press*) points out that the high costs of direct aggression are the same for all female mammals, yet nonhuman mammals routinely engage in physical aggression. Therefore, she argues that women engage in indirect aggression because it is particularly effective for competing against women, not because it is safer to the perpetrator.

How Women Compete for Mates

There appears to be four primary behavioral strategies that capture women's intrasexual competition for mates. The first is self-promotion, which is the enhancement of one's positive qualities,

relative to those possessed by members of the same sex. This strategy was first documented by Buss (1988), who surveyed people's use of self-promotion for the purpose of mate attraction. He found that among other characteristics, women self-promoted by manipulating their appearance and men by displaying and bragging about their resources. Walters and Crawford (1994) extended Buss' work, widening the focus to be an investigation of self-promotion for the purpose of intrasexual competition rather than solely mate attraction. They largely replicated his results.

The second strategy that has been well explored is competitor derogation. This strategy refers to any act used to decrease a rivals' mate value relative to oneself. Using surveys, Buss and Dedden (1990) found that women self-report a tendency to derogate rivals' appearance, while men self-report they derogate rivals' physical abilities and resources.

Researchers have examined self-promotion and competitor derogation together, in order to determine their use according to sex, relationship status, and context. For example, in a study by Schmitt and Buss (1996), both sexes were found to self-promote and derogate potential competitors when pursuing a relationship, but that the length of the expected relationship influenced strategy use. With respect to self-promotion, men expecting a short-term relationship said they would emphasize immediately available resources, whereas those seeking a longer-term relationship focused on future resource potential. Women in the short-term scenario reported they would emphasize their sexuality and attractiveness, whereas those pursuing a long-term relationship promoted their faithfulness and sexual restrictiveness. The pattern for competitor derogation was somewhat similar, in that women pursuing a short-term relationship would describe potential rivals as "ugly," "frigid," and "unhygienic," and emphasize a rival's promiscuity in the long-term condition. Regardless of duration, men reported that they would say potential rivals were "promiscuous," "dangerous," and "unhygienic."

In a meta-analysis, Schmitt (2002) found women were far more effective at using physical

appearance for the purposes of self-promotion than men, but that this sex difference was dramatically reduced when it was within the context of competitor derogation. Generally, both sexes were perceived to be less effective when using physical appearance-related tactics for competitor derogation, as compared to self-promotion. In contrast, when using tactics related to resources, the sex difference was large, such that it was judged more effective when used by men than by women for self-promotion, and this difference increased when used for competitor derogation.

To make a more direction comparison of the two strategies, Fisher et al. (2009) asked students in a forced choice survey whether they would be more likely to self-promote or competitor derogate for particular contexts (e.g., regarding physical appearance). They showed that self-promotion was selected significantly more often, regardless of context, sex, or relationship status, than competitor derogation. They then asked members of the community to complete continuous measures and found that women, more than men, reported using self-promotion, while men reported more use of competitor derogation than women. Romantic relationship status mattered; dating and single individuals used both strategies more than those in common-law or married relationships.

Aside from the strategies of self-promotion and competitor derogation, there is also mate manipulation and competitor manipulation. Fisher and Cox (2011) asked students to list the ways in which they compete for mating attention, which replicated the existence of the former two strategies, and lead to the discovery of the latter two strategies. Mate manipulation is when an individual removes the target of the competition so that no competition is necessary, such as by sequestering the mate or displacing attention from a potential rival. The other is competitor manipulation, wherein an individual tries to convince a rival that the potential mate is not worth the costs of competition. They also found that most tactics were classified as self-promotion, followed by mate manipulation, competitor derogation, and competitor manipulation. There were significant sex differences as well; women were more likely to

report self-promoting their physical appearance, and men were more likely to list direct actions such as bullying or derogating a rival's material possessions.

The discovery of mate manipulation as a strategy was particularly interesting, as it highlights that intrasexual competition does not end at mate acquisition. After an individual has selected a suitable mate and gained access, she must still engage in competition to retain him and prevent him from leaving the relationship. The use of the four strategies may thus change, depending on one's romantic relationship status, but also according to the intended duration of the relationship, one's level of commitment towards it, perceived mate value of oneself and mate, and the existence of potential rivals who may infiltrate the relationship. These potential influences need to be explored by future researchers.

Issues to Address in Future Work

One area that warrants further investigation is how to include a multigenerational approach into studies of female competition. As Stockley and Bro-Jørgensen (2011) indicate, females use strategies that influence the quantity of offspring but also the quality of offspring in terms of survival and reproductive success. Thus, the key is not looking at the immediate offspring, but rather to take a long time perspective and document the outcomes in a multigenerational view.

Further, as mentioned, there has been significant research into women's intrasexual competition for mates, but less work into resource competition. One avenue to gain insights into what resources are at the heart of women's competition may be to look at cooperative versus competitive mothering and see how women strategize to maximize their reproductive fitness overall, even if it means sacrificing equal shares in gained benefit. For example, one inroad may be to join the ongoing debate involving cooperation for childcare and allomothering. Communal breeding is generally understood to result from competition over resources relevant to reproduction (Mace 2013). Among humans, for example,

there may be competition for limited household resources, whereby inclusive fitness may be improved by sharing goods (even if the portions are unequal) rather than potentially harming relatives. While some scholars focus on cooperation among allomothers who provide childcare for related or unrelated individuals (e.g., Hrdy 2009), others focus on how this model is not readily applied to all human populations. For example, Strassmann (2011) reports that among the Dogon of Mali, mothers are critical for child's survival and cannot be replaced by any other individual. She argues that cooperative breeding is a facultative response to a given environment, and as such, it is not species typical. The extent to which cooperative breeding is an appropriate model for humans thus remains to be determined. However, some researchers suggest that cooperation and competition go hand-in-hand and that it is reproductive competition between and within families that has led to fertility patterns such as menopause, and cultural norms such as marriage patterns, inheritance of goods, and location of residence (Mace 2013).

Research into cooperation and competition also illuminates a second issue: what causes a woman to decide that a potential member of the group represents an ally versus a rival? The literature on indirect aggression suggests prosociality may be the key. Aggressive individuals may be able to remain central to the group, obtaining personal gains with minimal personal cost. While group living leads to inevitable costs and competition among group members, it also leads to the acquisition of resources that may not be achievable by individuals working alone (Hawley 2003). Thus, Hawley (2003) proposes that in order to effectively compete, some individuals within the group are prosocial (i.e., indirect and cooperative), while others are coercive (i.e., direct and assertive). To maximize advantages, one should be high on both the dimensions of prosociality and coercion. These bi-strategic individuals possess high social competence, as they may act in a highly aggressive manner and still retain their status in a peer group. Within the context of competition for resources necessary for survival of oneself and one's children, being

able to sustain power and yet maintain social alliances would be highly advantageous.

- [Women's Mate Value](#)
- [Women's Long-Term Strategies](#)

Conclusion

Women deploy a variety of strategies when engaging in intrasexual competition, with the theme that they tend to favor indirect and relational aggression. Human strategies for mating competition, such as self-promotion, competitor derogation, mate manipulation, and competitor manipulation show the nuances of directing one's actions and behaviors towards different audiences to reap the best competitive advantage. The overwhelming majority of literature pertains to women's competition for mates, yet there has been recent interest in competition outside of this realm. Indeed, given that women heavily invest in children, one might argue that they should compete more for access to resources that improve their children's survival than for mates, but this possibility needs to be explored. In general, the research on competition for resources shines light onto areas that need to be further investigated, including the actual resources that women compete over that enhance their reproductive fitness, and the strategies they use.

Cross-References

- [Aggression for Sexual Access](#)
- [Contexts for Women's Aggression Against Women](#)
- [Derogation of Attractiveness](#)
- [Evolution of Human Sociality, The](#)
- [Female Choice](#)
- [Female Mate Choice](#)
- [Female-Female Competition](#)
- [Indirect Aggression](#)
- [Intrasexual Competition](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Sex Differences](#)
- [Variance in Female Reproductive Success](#)
- [Women's Long-Term Strategies](#)
- [Women's Mate Preferences](#)

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Femaleness

- [Masculinity and Femininity](#)

Female-Perpetrated Violence

- [Defense Against Attack](#)

Females as the Spoils of War

- [Sexual Access as Benefit of Victory in War](#)

Females Remain with Natal Group

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Synonyms

[Philopatry](#)

Definition

In most mammalian (social) species, one or both sexes disperse, either to avoid inbreeding or as a result of increased competition for limited resources. The sex that remains in their natal group is considered **philopatric**, remaining and breeding in their natal range or group (Clutton-Brock and Lukas 2012). The sex that migrates or disperses to another group to find mating partners exhibits **natal dispersal** – a permanent movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it survives (Greenwood 1980). If there is migration subsequent to reproduction,

we call this **breeding dispersal** – movement of individuals that have reproduced, between successive breeding sites. Due to the costs of dispersing (see below), typically, individuals only disperse a single time in their lifetime. However, if an animal disperses more than once, they are considered **secondary dispersers** – permanent or semipermanent movement of breeding adults that have already left their natal group or range (Clutton-Brock and Lukas 2012).

Introduction

In any social species, one or both sexes typically disperse, while the other remains in their natal group. There has been contentious debate over the causes of dispersal, but primarily animals disperse either to reduce mate and food competition or else to avoid inbreeding. There are numerous benefits to being the philopatric sex or the sex that remains in their own natal group. These center around building and maintaining a detailed spatiotemporal map of food and water resources, threats (predators), and escape routes. Additionally, there are social advantages, namely, gaining support from kin, especially helpful when ascending dominance hierarchies within the group and fending off attacks from rivals (Clutton-Brock and Lukas 2012).

The Costs of Dispersal and Benefits of Philopatry

It is generally accepted that the sex that is most dependent on resources for reproduction (usually females among the mammals) should be philopatric, while the other sex disperses. For example, natal philopatry – at times accompanied by resource sharing from parent to offspring – predicts a kin-structured population and has been argued to represent a precursor for the evolution of sociality. Most social mammals, primates particularly, are characterized by this female philopatry, although examples abound of female transfer (Clutton-Brock 1989; Moore 1984). Some have argued that the direction of

sex-biased philopatry is a direct result of the mating system of the species in question (reviewed in Greenwood 1980).

In primates, scientists have historically attempted to decouple philopatry from bondedness (van Schaik 1983) and describe philopatry as an evolved, social response to within and between group competition dynamics, as well as infanticidal avoidance (Sterck et al. 1997). The decision to disperse, however, may be a far more active process. Williams and Rabenold (2005) suggested that in some male corvids, forays into neighboring territories were actually reconnaissance missions to evaluate potential mating opportunities for later dispersal. Accordingly, dispersing carries with it risks, especially for social animals. Resident individuals are often resistant to immigrants or even xenophobic, aggressing at new arrivees; immigrants must also compete with other dispersers, resulting in secondary and even tertiary dispersal attempts (Cheney and Seyfarth 1983). In some species where females disperse (e.g., African lions, meerkats, howler monkeys, prairie dogs), unless immigrating females usurp resident females, dispersers are faced with either founding their own social groups or dying.

Conclusion

In Jim Moore's (1984) 57-page manifesto on the topic of female transfer, he contextualized the historical significance of our attempts to understand animal (specifically, primate) sociality, beginning with Hamilton's (1964) work on inclusive fitness and continuing into the early work into matrilineal relatedness in macaques (*Macaca* sp.) and baboons (*Papio* sp.). The prevailing view, as Moore noted, was one of stable mammalian groups based on female kin, with exceptions noted throughout the Class (see above). He concluded by saying that "...while kin selection may be a very powerful force among close relatives... for many species it may be relatively weak or even negligible between more distant ones," and thus the numerous "exceptions" to female philopatry may actually support an earlier description of

primate groups as “loosely bound aggregations of individuals which may have little long-term core of kin” (Jolly et al. 1982). That interpretation notwithstanding, we can say that in the vast majority of social mammalian species, and primates specifically, females remain within their natal group, using strong kinship relationships to learn about and exploit their physical and social environment.

Cross-References

- ▶ [Alarm Callers Are Females with Greatest Genetic Representation](#)
- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)

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Females' Mate Maintenance Tactics

- ▶ [Women's Long-Term Strategies](#)

Females' Mating Strategies

- ▶ [Female Mate Choice](#)

Femicide

- ▶ [Partner Homicide](#)

Femininity

- ▶ [Biology of Human Gender, The](#)

Feminism

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Synonyms

[Women's liberation](#); [Women's movement](#);
[Women's rights](#)

Definition

“Advocacy of women’s rights on the grounds of the equality of the sexes” (*English Oxford Living Dictionaries*).

Introduction

Feminism's history is both a compilation of women's experiences and a record of the different strategic interventions employed to argue women's cause (Joan Wallach Scott, *The Fantasy of Feminist History*).

Arguably one of the most maligned and misunderstood of terms, "feminism" has a long, complex, and dynamic history. Prejudices and politics aside, far from being a monolithic ideology, feminism is more aptly characterized as "feminisms" owing to the various theoretical approaches associated with it, such as liberal feminism, Marxist feminism, socialist feminism, radical feminism, intersectional feminism, transfeminism, anarchist feminism, and transnational feminism. Depending on both its national and cultural context, feminism may also stress different aspects of, and remedies to women's social and political oppression. Whereas Western feminism might focus more on individual rights, such as equal pay and opportunities for employment advancement, Eastern European or Latin American feminism might emphasize collective concerns such as labor rights. However, all feminisms necessarily subscribe to the denotative meaning identified in the Oxford English Living Dictionary (cited above) and are committed to women's advancement. How sex inequality is manifested and how best to address it has been a matter of debate, hence the term feminisms. "Central to feminism is the view that women's" secondary status in patriarchal societies "is socially constructed, and therefore open to change" (Hannam 2007). On the basis of this shared fundamental meaning, the singular "feminism" may be accurately used. Moreover, as feminist scholar Lorna Finlayson argues, feminism is best understood as a combination of "theory" and "praxis" (2016); that is, the activism associated with the various theoretical approaches.

Women's Oppression

Just as feminism is dynamic and responsive to cultural conditions, the longstanding patriarchal

system that it challenges is neither static nor universal. Historian Estelle B. Freedman explains: "Prehistoric artifacts suggest that men and women have at times shared spiritual prestige" (2002), which is a key source and justification for a dominant governing system, and prehistory offers ample examples "in ancient Egypt and among Bedouins in pre-Islamic Arabia" of powerful female leaders (Freedman 2002). Given evidence of more egalitarian societies in pre-history, historians such as Gerda Lerner and Karl Marx have speculated about patriarchy's origins (Freedman 2002). Some feminists have theorized "the subordination of women and found their explanation for it in the male 'need' to dominate the female" (Scott 1999), while Estelle Freedman explains how "a shift from subsistence agriculture to trade fostered . . . more highly stratified societies" (2002). Colonialism in Asia and the Americas also exacerbated unequal gender relations in the developing world: "Colonialism transported many ideas about gender that both reinforced existing inequalities and introduced new ones" (Freedman 2002). Whatever its origin, or origins, the institutionalization of the gendered hierarchy privileging men over women gave rise to feminism, and it coincided with the shift to a land-based economy driven by trade and private property ownership, wherein the female was regarded as the property of her father or husband. Traditional values and social expectations around women's childbearing and mothering have also played a major role in women's oppression. Moreover, against the backdrop of both nationality and ethnicity, it is difficult to disentangle the interlocking systems of capitalism and patriarchy, since the one fuels and reinforces the other.

Origin of "Feminism"

The term feminism, which originated with the French word "feminisme," entered the English language in the late nineteenth century (*New World Encyclopedia*). Both the term and the political movement associated with it arose in western society in the eighteenth century as a response to patriarchy's reliance on the political and social oppression of women as a class. Challenges to the status quo and women's oppression, however,

date back at least to the middle ages in France, with Cristina de Pisan's bold call for women's separate education in *The Book of the City for Ladies*, circa 1405. "Arguably the first woman in Europe to earn a living as an author" according to the World Digital Library, de Pisan "is widely regarded as an early feminist who spoke out for the rights of women and espoused female achievement". Inklings of "feminism" of a sort may also be found in the life and writings of the Greek poet Sappho, the German ascetic and composer Hildegard of Bingen, and the English anchoress Julian of Norwich from the early medieval period. In England, the seeds of modern feminism date back to the late sixteenth century (Finlayson 2016). British pamphleteer Jane Anger, whose name is a possible pseudonym, mounted an angry and vigorous challenge to the artificial constraints by which women were denied access to education, prevented from developing their intellect, and then unfairly condemned for their ignorance (Finlayson 2016). Similarly, in *Essay to Revive the Ancient Education of Gentlewomen in Religion, Manners, Arts and Tongues*, Royal governess Bathsua Makin "insisted . . . on the importance of women receiving an education" (Walters 2005). A rash of feminist proposals and polemics followed in America as well as Great Britain. In her seminal feminist work, *A Vindication of the Rights of Women: with Strictures on Political and Moral Subjects* (1792), Mary Wollstonecraft advances the views of de Pisan, Anger, Makin, and others, with her rigorous philosophical analysis of the conditions and deleterious effects of women's secondary status (Finlayson 2016). Wollstonecraft argues that providing women with an education would counteract women's oppression, specifically the sexual double standard. It would also correct the shallowness of "feminine" socialization that made women vain and prepared them for a life of domesticity and little else. She situates her argument within the framework of liberalism, and the late eighteenth century's emphasis on reason and the French "Rights of Man" that countered blind faith in the monarchy and church and culminated in political revolutions in France, Great Britain, and America. Wollstonecraft contends that allowing women to

cultivate their intellect would necessarily make them better wives and more moral and fit mothers of the new Republic's future citizens. In Germany, "Helene Lange and Bertha Pappenheim pressed for equal education and careers for women" while "political liberalism in Scandinavia encouraged women's societies in support of education and the Swedish Society for Married Women's Property Rights" (Freedman 2002).

Although these early advocates for women's rights were forward thinking and radical for their eras, they do not go so far as to lay claim to full civil and political equality with men in their respective discourses. That demand would be more clearly articulated in the 1848 "Declaration of Sentiments," modeled on America's Declaration of Independence and presented at the Seneca Halls Women's Rights Convention in Albany New York, calling for women's "equal treatment under the law, equal right to education, and the equal right to vote" ("Rights for Women: The Suffrage Movement and Its Leaders").

Major Traditions of Feminism: Liberal Feminism, Marxist Feminism, Radical Feminism

Liberal feminism stems from the natural rights doctrine that emerged during the Enlightenment period, and the notion "that all men are created equal, that they are endowed by their Creator with certain unalienable rights, that among these are life, liberty and the pursuit of happiness . . ." (*Declaration of Independence*). Women were not included in this doctrine because of the widely held, albeit mistaken belief that women were biologically, morally, and intellectually inferior to men and lacked the capacity to reason, an essential ingredient for citizenship (Hannam 2012). Finlayson explains that liberal feminism's defining features emphasize: "*Individualism*" (that is, "'autonomy,' 'freedom,' and 'rights'"); '*Distribution*,' "or the equitable distribution of "wealth" as well as "costs"; '*Abstraction*,' wherein "the liberal theorist may begin from a reflection on the *concept* of 'equality' or 'justice'" in order "to produce normative principles"; '*Positivity*,' and the emphasis on what could/should be done; and '*Capitalism*,' by which liberal feminism is

“committed to a capitalist economic framework of one kind or another” (2016). In sum, liberal feminism is tied to a political ideology born of the Enlightenment period, as well as to any of its associated shortcomings. In contrast to Liberal Feminism and its cozy relationship with a capitalist economic structure, Marxist Feminism involves “a commitment to . . . social change; an emphasis on social class and social struggle” while advocating “the revolutionary replacement of capitalist relations of production with communist ones” (Finlayson 2016).

Marxist feminism sees women’s largely uncompensated labor and oppression as the result of class, or economic oppression. Accordingly, this condition may be remedied by replacing capitalism with some form of socialism to regulate production and distribution more equitably, through communism (Cuba, China), or social democracy (Canada, Norway) as examples. From a Marxist perspective, liberal (or mainstream) feminism disregards socioeconomic class differences and focuses too narrowly “on the concerns of (white) middle-class women . . . preoccupied with formal rights and freedoms like suffrage, and neglecting the issue of the material deprivation suffered disproportionately by women” (Finlayson 2016).

Radical feminism: While liberal feminism emphasizes equality and individual rights, radical feminism speaks in terms of “‘oppression,’ ‘domination,’ ‘exploitation,’ ‘violence,’ and ‘subordination,’” and “concrete relations of power” (Finlayson 2016). In particular, radical feminism is concerned with violence against women in its myriad forms (prostitution, pornography, rape, etc.). Both radical feminism and Marxist feminism challenge fundamental sociopolitical and economic structures within which liberal feminists try to work; whereas liberal feminists work to change laws and policies, radical and Marxist feminists see the patriarchal and capitalist systems as fundamentally unjust and incorrigible.

The Waves of Feminism

Scholars have long used the “wave” metaphor to describe modern feminism’s major advances, although the concept can be misleading. For

instance, Laura Finlayson observes how its usage tends to obscure ongoing feminist activity that occurs between the major cultural developments in the waves (2016). Given this caveat, however, the wave metaphor can be a useful way to describe the surge of social and political energy that occurred during watershed moments, resulting in significant gains for women. Feminist history “identifies two key periods of political activism – ‘first-wave’ feminism, c. 1860s to 1920 and ‘second wave’ feminism in the 1960s and 70s” (Hannan 2007). Less politically but more complicated and culturally significant third- and fourth-wave feminisms have their own idiosyncratic features. Although there have been positive outcomes associated with each wave of feminism, oversights and limitations have caused contention. Additionally, to some extent each wave, intending to rectify errors or oversights of the previous waves of feminism, inevitably make their own.

First-Wave Feminism: Suffrage

Although agitation for women’s rights had been simmering for centuries, the Seneca Falls Convention served as a key rallying point and catalyst to modern feminism’s first major wave. June Hannan notes that by this time “women in Europe, America, New Zealand, and Australia” had started organizing “to achieve changes and improvements in the social, political and economic lives of women” (2007). According to Hannan, agitation for suffrage was not an isolated social movement but “part of a much broader campaign – to free slaves, to introduce representative government, to advance the rights of workers and to achieve property reforms” (2007). In America, many activists were also involved with the temperance crusade. Notably, Quakers in America and Great Britain were pioneers in both the feminist and abolitionist movements.

Organizers in the first-wave rallied around the call for suffrage which “held a central place in histories of feminism, especially in Britain and the United States” (Hannan 2007). While necessarily concerned with key issues such as property rights, access to education and employment

opportunities, many American and British activists viewed suffrage as the key to unlocking women's prison of oppression. By contrast, French feminism, which was tied to Republicanism, was slower to unfold and focused on educational and legal reform (Hannan 2007). It cannot be overstated how unconventional, and at times dangerous it was for women activists to venture out of the home and trespass onto public (male-dominated) spaces as these early feminists assuredly did in order to speak out against slavery and on behalf of women's rights. Although lower class women worked in factories, and later in retail, and female slaves worked in the plantation fields, women's socially sanctioned place was in the domestic sphere, and only disreputable women ventured in public alone. Nevertheless, activist women defied social convention, and their methods of activism varied from country to country. Generally, in addition to lobbying political leaders, activists met in small groups, circulated petitions, and wrote and distributed pamphlets and leaflets (Hannan 2007). Under the leadership of Emmeline Pankhurst, founder of the Women's Social and Political Union, and her daughters Christabel and Sylvia, British women resorted to minor acts of violence after years of campaigning with more politic approaches failed to win them the vote. Following Britain's entrance into the war, however, women activists turned their energies to the war effort, and by 1918 Parliament conceded and women (over the age of 30, initially) were granted the right to vote.

A small cadre of activists, in particular Lucy Stone, Elizabeth Cady Stanton, and Susan B. Anthony, organized the Seneca Falls Women's Convention and laid the groundwork for the American feminist movement. Stanton and Anthony headed up NAWSA (National Woman's Suffrage Association) for the express purpose of getting individual states to ratify Suffrage and strengthen their hand for a federal amendment. By design, the American movement for Suffrage did not involve violent methods, although college-educated leaders, in particular Quaker Alice Paul along with Lucy Burns, participated in the British women's movement and were inspired by their zealous sisters' hunger strikes,

and other radical actions that often sent them to prison. Marking the difference in methods, British activists were called Suffragettes, while American activists went by the name Suffragists. Together with Carrie Chapman Catt, British born Anna Howard Shaw, inheritor of Susan B. Anthony's moral mantle (*American National Biography Online*), took over NAWSA and its tedious state-by-state campaign for suffrage. The group splintered, with Paul and Stone working within the CU (Congressional Union) and the newly founded NWP (National Women's Party), to campaign more militantly if not violently for the Susan B. Anthony federal suffrage amendment to the Constitution given the sluggish pace of NAWSA's state by state strategy. Members of the NWP and CU organized a publicity-garnering Washington, D.C. parade for suffrage the day before Democrat Woodrow Wilson's election in March of 1913. Suffragists also brazenly picketed the Whitehouse for months beginning in 1917 and in spite of the US entrance into World War I. Holding banners quoting the Constitution, they exposed the hypocrisy in Wilson's speeches about democracy and the rights of free people being trampled upon while ignoring women's appeal for suffrage. In doing so these "unladylike" Victorian women highlighted their disenfranchisement, drawing both admiration and ire from the public. The "Woman Question" was taking a prominent place in public discourse, given an ethos in which the woman was viewed as the "angel of the house" who had no business engaging in politics in the corrupt, male-dominated public sphere. After hundreds of Whitehouse protestors were arrested and shipped to Occuquam Prison on the bogus charge of obstructing traffic, the battle heated up. The tipping point came with public outrage when the Virginia workhouse's unsanitary conditions and brutal treatment of its prisoners were publicized, in particular, the force-feeding of the women-activists who had gone on a hunger strike to dispute their political arrest. By 1919, the suffrage amendment was on the floor with Wilson's backing, and after heavy campaigning throughout the states it was ratified in 1920. Enfranchisement spread across North America and Europe and was the signature

achievement of first-wave feminism; and similar “campaigns gathered momentum in the inter-war years in Latin America and parts of the Caribbean” as well (Hannan 2007). According to “Key Dates in International Women’s History”: in 1918, women in Russia went on strike for “bread and peace”, an occasion that would later be dubbed International Women’s Day, Women won voting rights in Brazil and Thailand in 1934, in Japan in 1948, and in South Korea and Israel in 1949.

While winning a political voice signified a major leap forward for women, it failed to eliminate the dense layers of cultural and legal barriers to women’s parity with men. For instance, the Comstock Law of 1873, which made contraceptives (along with pornography) illegal in the USA, was not overturned until 1962 in Griswold vs. Connecticut, and then it only applied to married couples. Unmarried individuals would have to wait another 10 years or so for legal access to birth control. Alice Paul and the NWP crusaded for the ERA (equal rights amendment) to redress such persistent legal, social, and economic impediments to women’s freedom and independence in the USA. Their efforts failed. When the ERA was taken up again during feminism’s second wave, it fell three states shy of ratification and remains unratified to this day, a clear indicator of why the work of feminism continues.

Second-Wave Feminism: Sisterhood and the Personal Is Political

The United Nations inaugurated the Commission on the Status of Women in 1947, and in a formal acknowledgement of women’s rights “issued a Declaration of Human Rights” in 1949 (Walters 2005). Several international conferences followed, attesting to the legitimacy and viability of feminist activity that continued churning between the waves. Feminism’s second major wave, or the “women’s liberation” movement, came in the wake of the civil rights movement in the USA, and it both dovetailed and at times, clashed with the gay rights and anti-Vietnam war movements in the late twentieth century. Influential texts of the second wave include Simone deBeauvoir’s rigorous philosophical analysis of

the manufactured nature of women’s secondary status, in which she argues that in spite of the appearance of being natural, “a woman is not born, but made” (*The Second Sex*, 1949); Kate Millett’s *Sexual Politics* (1970), in which she critiques the institution of patriarchy; Germaine Greer’s *The Female Eunich* (1970) that challenges the patriarchal constructs of femininity and womanhood; and Betty Friedan’s *The Feminine Mystique* (1963). Friedan, a founding member of Now (National Organization of Women) identifies “the problem with no name” plaguing American middle-class women in the post-World War II years. Having been actively engaged and gainfully employed in the war effort on numerous fronts, American women were unceremoniously sent back to home and hearth upon their soldier-husbands’ return from the war. As Friedan explains, instead of finding domestic bliss as suburban housewives, many women found themselves depressed and frustrated, since they came to view the private sphere as oppressive, and proof of their secondary status.

When increasing numbers of women did enter the workforce, “they continued to be viewed as women first, workers second” (Freedman 2002). Consigned to low-paying “pink-collar” jobs, as nurses, teachers, clerks, and secretaries, women did not have access to higher paying “male-identified” jobs and professions. They also met obstacles when pursuing advanced education in male-identified fields, such as science and engineering, and had no recourse when they were underpaid or overlooked for promotions or payraises. Women’s desire for better employment and equal educational and financial opportunities was but one major prong of the women’s movement’s second wave. Throughout the western world women also sought sexual freedom, akin to what men enjoyed, and reproductive rights, specifically protection against pregnancy. As well, they sought legal and social protections from sexual harassment, and more crucially, from the domestic and sexual violence that had long been tolerated and gone unaddressed inside as well as outside the home. Given the high number of women’s deaths caused by “back-alley” abortions, access to safe, legal abortion was also high on the feminist

agenda. These issues were identified by women in Great Britain and America who formed “consciousness-raising” groups as a mechanism for identifying “common experiences” of oppression (Walters 2005).

“Sisterhood,” according to Margaret Walters, “was one of the most popular feminist slogans in the 1960s and 70s” (2005), and marches, sit-ins, and social protests became commonplace. In 1968, activists protested the sexual objectification of women at the Miss America Pageant in Atlantic City by throwing girdles and bras into a trash bin, and “300 French women signed . . . ‘The Whore’s Manifesto’ to declare that they had had an illegal abortion . . . followed by a similar public declaration in West Germany”; while women “in Britain, West Germany, and Italy” marched to “‘Reclaim the Night’ . . . to assert their right to be in public spaces in safety after dark” (Hannan 2007). A major outcome of second-wave feminism is the “Take Back the Night” vigils and marches that continue to be held annually in cities and on college campuses throughout the world. The “personal is political” mantra, the title of an article written by journalist Carol Hanisch (1970), aptly captures the era’s spirit, since feminists made the argument that women’s experiences of oppression are not a private issue to be ignored but a political issue requiring widespread cultural changes and significant legal remedy. Liberation was the clarion call in grass-roots campaigns throughout western countries, as Hannan explains: “emancipation implied freedom from constraints and . . . social policies to enable women to achieve their potential” (2007). As a result, a woman’s ‘natural’ role in the home as wife and mother became a hotly contested site that pitted feminists against those who held to traditional womanhood, ultimately contributing to a backlash against feminism. Another area of contention that drew the ire of religious and anti-feminist leaders, and continues to be a chief bugaboo of feminism, was the campaign for legal abortion.

Like feminism’s first-wave, second-wave feminism was largely spearheaded by educated white women, whose cause would ultimately be soundly critiqued for its racial, ethnic, and sexual-identity blindness. Second-wave feminists incorrectly

assumed that the experiences of first-world white women were universal and applied equally to all women. For instance, Margaret Walters notes how “women in the ‘Third World’ have had to confront . . . more intractable problems” having to tackle “sexism in the form of deep-rooted local beliefs and practices, to do with class, caste, religion, and ethnic biases” and often in the context of nondemocratic societies (2005). Additionally, women’s rights in Muslim and African countries have lagged far behind those of western women, especially in theocratic countries, and women of color and lower socioeconomic class in all societies must contend with different priorities largely ignored in feminism’s first two waves. In Mexico, the women’s movement “concentrated on the need for legal abortion, increased sentencing for rapists, and help for battered women” (Walters 2005). Throughout Latin America, feminists “were interested in equal rights and economic redistribution”, and key concerns were with “female illiteracy, and . . . the miserable circumstances of . . . women living in shanty towns and slums” and dying from “botched abortions” (Walters 2005). In failing to consider layered forms of oppression and differences among women, in terms of ethnicity, class, religion, and sexual identity, both first- and second-wave feminism fell short of its equality aims.

In spite of its cultural blindness, however, feminism in western countries made significant inroads on behalf of many women, and on virtually all the aforementioned fronts of women’s liberation. They won landmark legislation, amassed social, political, and economic resources for their cause and weakened the wall between the public and private spheres that served to separate the sexes and fortify the patriarchal sex/gender hierarchy. In the USA, this meant the availability of oral contraceptives in the 1960s, and the inclusion of sexual harassment in Title VII of the 1964 Civil Rights Act. Title IX (1972) guaranteed girls’ and women’s equal access to resources from educational institutions receiving federal aid, enabling them to be involved in competitive sports and earn athletic scholarships. The landmark *Roe v. Wade* (1973) amendment gave American women the right to a legal and medically safe

abortion within limits, while abortion laws throughout Europe were loosened. In addition, contraceptive advice became more widely available, and rape hotlines and crisis centers were established, as were shelters for victims of domestic violence. Finally, Women's History and Women's Studies became legitimate areas of study in the academy. Academic and social programs, as well as social science research proliferated, as did textbooks that acknowledged women's previously unacknowledged contributions to literature, history, and the sciences.

Third-Wave Feminism: Popular Culture and Personal Choice

In spite of three U.N. sponsored international conferences uniting women from around the world during the "Decade for Women, 1976–85", second-wave feminists "in Europe and North America could see that their movement was losing momentum and had become . . . fragmented" (Hannan 2012). In part, this was due to the glaring differences among women that were becoming more evident and contentious, thus challenging the second-wave concept of universal "sisterhood." Feminism's erosion beginning in the 1980s was also exacerbated by the post-structuralist challenge to the universalist notion of "woman" as having one fixed and stable meaning, especially when one's sex is complicated by other aspects of identity (and levels of oppression), such as race or sexual orientation (Hannan 2012). "Queering" or Queer theory in popular culture and the academy emerged from this ethos, destabilizing the heteronormative and fixed categories of gender, sex, and sexual orientation, complicating the feminist cause. Additionally, feminism in the USA found itself in an increasingly hostile political and social climate, partly as a result of its significant gains in the traditionally male workplace and on the reproductive-rights-front. The feminist challenge and changes to the status quo, together with disparaging media hype, such as the women-burning-bras-myth extending from the Atlantic City protest, gave feminism a black eye, and backlash ensued. "Postfeminism" was one response, a view which holds that, contrary to ongoing evidence of sex oppression,

women have achieved equality and so feminism is no longer viable, as expressed in the 1998 'Is Feminism Dead?' *Time* cover story. Fractured and wounded, feminism was hardly dead and the work of women's rights continued on multiple fronts. Nevertheless, feminism found itself in a heightened defensive posture, and an increasing number of women shied away from the feminist label as a result. Because of this, as Hannan explains, the language of activism shifted away from focusing on 'women' to emphasizing the "health and well-being of families", such as "in Latin America where political parties took up feminist demands around employment and social welfare, but were reluctant to pursue reproductive rights, sexuality and sexual violence" (2007). In this fractured milieu, a cultural form of feminism labeled the third-wave flourished.

Beginning in the mid-late 1980s in the USA and Great Britain, the Guerilla Girls, operating anonymously and wearing gorilla masks, engaged in a creative form of guerilla warfare that took on the sexism and racism dominating the art world. They made public appearances, disseminated information, and produced art that appeared on billboards and posters. One classic example is the infamous: "Do women have to get naked to be in the Met Museum?" billboard (and poster) of a supine naked woman wearing a gorilla mask, underscoring the paltry number of art works by women artists in museums relative to art work by male artists, much of which featured naked women. In the early 1990s, the "Riott Grrrls" engaged in a similar form of activism on the punk-rock music front, signifying the birth of the "Girl Power" movement. Reclaiming "girl" from its traditionally demeaning usage, by which men might refer to mature women, and calling forth the more intact self-esteem of pre-puberty girls, these musician-activists tackled the intractable sexism in the male-defined rock music industry head-on. The more mainstream and commercially successful *Spice Girls* in Great Britain came both to epitomize and popularize the "girl power" movement that would, over time, become a template for similar groups such as *Destiny's Child*. Originally, a call to feminist arms, "girl power" has also been co-opted and made into a marketing slogan.

Blogs and zines, or online magazines, including *Bust* and *Bitch*, proliferated during the third-wave period and into the new millennium. Zines became a virtual gathering place for young women to express their anger at the sexist world and talk frankly about “taboo topics, such as rape, incest, and eating disorders”, according to Karen Schilt in “The History of Riot Grrls in Music”. Third-wave feminism was powered by Generation X-ers, who dis-identified from their foremothers’ emphasis on sisterhood, and political action in organizations such as NOW (National Organization of Women) and the feminist publication *Ms.* Whereas second-wave feminists rallied in opposition to the sexual objectification of women and saw “femininity” within patriarchy as male-defined and a cause of their ongoing oppressed status, third-wave feminists claimed both their sexuality and femininity as sources of their power. They also co-opted previously derogative terms intended to keep women in their place, including “girl,” “bitch,” and “chick.” Moreover, unlike second-wavers who critiqued the traditional role of wife/mother as a key site of women’s secondary status, third-wavers instead privileged personal choice, and in this context motherhood might well be a “feminist” choice. More focused on personal empowerment than public policy and collective activism, third-wave feminism found expression in popular culture, and its principles are articulated in such texts as Jennifer Baumgartner and Amy Richards’ *Manifesta*. Within this brand of sex-positive feminism, superstars Madonna, Beyonce, and Lady Gaga could dictate the terms of their hypersexualized musical personas, offsetting charges of their sexual objectification. At the same time, an explosion of T.V. shows and films featuring women as heroes and warriors hit small and big screens: Buffy in *Buffy, the Vampire Slayer*; Ripley in the *Alien* film series, and the crime-fighting “angels” in three film adaptations of the 1970s T.V. show, *Charlie’s Angels*, to name a few. Such pop culture texts, examined through the lens of feminism, also became legitimate areas of feminist intervention and academic scholarship. As with the shortcomings of previous waves, third-wave feminism’s emphasis on individual choice

and expedient connection to pop culture has morphed into a more superficial consumer and celebrity brand of feminism that privileges women of financial means, masking or diluting key feminist principles and aims in the process (Finlayson 2016).

However, the third wave did see increased awareness of and attention to previously overlooked issues of race, ethnicity, religion, sexual orientation, and gender identity, and the ways in which these interact with sex and gender identity and add to women’s experience of oppression.

Fourth-Wave Feminism: Intersectionality and Social Media

With closer attention to the intersection of identities, including race, ethnicity, religion, gender, and sexual orientation, what some are calling feminism’s fourth wave of the new millennium has seen both a re-evaluation of feminism and a resurgence of feminist activity, largely on social media and powered by the internet. According to Ealsaid Munro: “In an effort to draw attention to these axes of difference, contemporary feminists advocate several tactics, including the much-maligned practice of ‘privilege-checking’. As a tactic, privilege-checking is about reminding someone that they cannot and should not speak for others (“Feminism: A Fourth Wave?”). Intersectional feminism reflects this heightened consciousness, and it was perhaps most remarkably displayed in the 21 January 2017 Women’s March on Washington, and in cities around the world, numbering in the millions in protest of the inauguration of Donald Trump, and his perceived anti-feminist and anti-immigrant platform. The march originated with a Facebook posting and was broadcast via social media, and its organizers, speakers, and protestors represented all age groups, as well as a range of ethnic, religious, sexual and gender identities, a glaring contrast to many of the protests and marches in previous waves of feminism. Still being defined, fourth-wave feminism is testimony to the fact that feminism continues to adapt and evolve in response to systematic and pervasive discrimination on the basis of sex and gender, and an increasing number

of men as well as women identify as feminists. In her 2013 TEDx talk, Nigerian writer Chimimanda Ngozi Adichie proudly proclaimed, “We Should All Be Feminists”, following it with an elegantly argued book-length essay in 2014 of the same title, signaling a championing of the once-scorned label. Celebrity feminists have abetted this reclaiming, evidenced in British actor Emma Watson’s work on behalf of the United Nation’s “HeForShe” campaign, and in superstar Beyoncé’s unique, if controversial, blend of black womanhood and third-wave feminism, as declared in the 2014 MTV Awards-show and expressed in her recent music and performances.

Conclusion

Although the feminist label remains controversial, especially among those invested in traditional femininity and traditional roles of men and women, the story of feminism continues. While it is convenient to separate feminism’s waves, it is less that they begin and end, and more that they fold into one another to create energy anew. The feminist work of providing opportunities and advancing equality on behalf of women and girls is ongoing throughout the developed and developing world and is responsive to significant contemporary issues, as well as longstanding ones, such as sex trafficking, rape and genocide as weapons of war, child marriage, and female genital mutilation.

Cross-References

- [Evolutionary Biology and Feminism](#)
- [Patriarchy](#)
- [Sex Differences in Same-Sex Aggression](#)

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Feminist Waves

- [Patriarchy and Feminist Perspectives](#)

Fermentation

- [Frugivory By-Product Hypothesis](#)

Fertile Window

- [During Ovulation](#)

Fertility

Vikas Kaushal
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Synonyms

[Fecundity](#); [Generativeness](#); [Prolificacy](#); [Puberty](#); [Virility](#)

Definition

The state and quality of being fertile and fruitful or an ability of an individual or couple to reproduce healthy offspring in abundance and of the earth to bear fruit through normal sexual activity.

Introduction

The term “fertility” is taken to indicate biological fertility, the capacity to conceive given unprotected intercourse, in contrast to demographic fertility, the actual number of children. It can be looked at from a functional perspective, by the use of biomarkers, or from a mechanistic viewpoint. Functional fertility refers to how easy or difficult a couple find it to conceive, given that they are having unprotected intercourse, and tends to be assessed by looking at how long this takes, since more fertile couples tend to conceive more quickly (Jofee [2010](#)).

Basic Fertility Concepts

Biological conditions that affect fecundity are obviously important in understanding fertility, and since vast majority of people are biologically able to reproduce, and technology affects fertility only if it is used. Basic measures and rates are essential tools for describing what has happened and is happening to fertility. Fertility rates are especially useful because they are, by definition, the number of births per unit of the population;

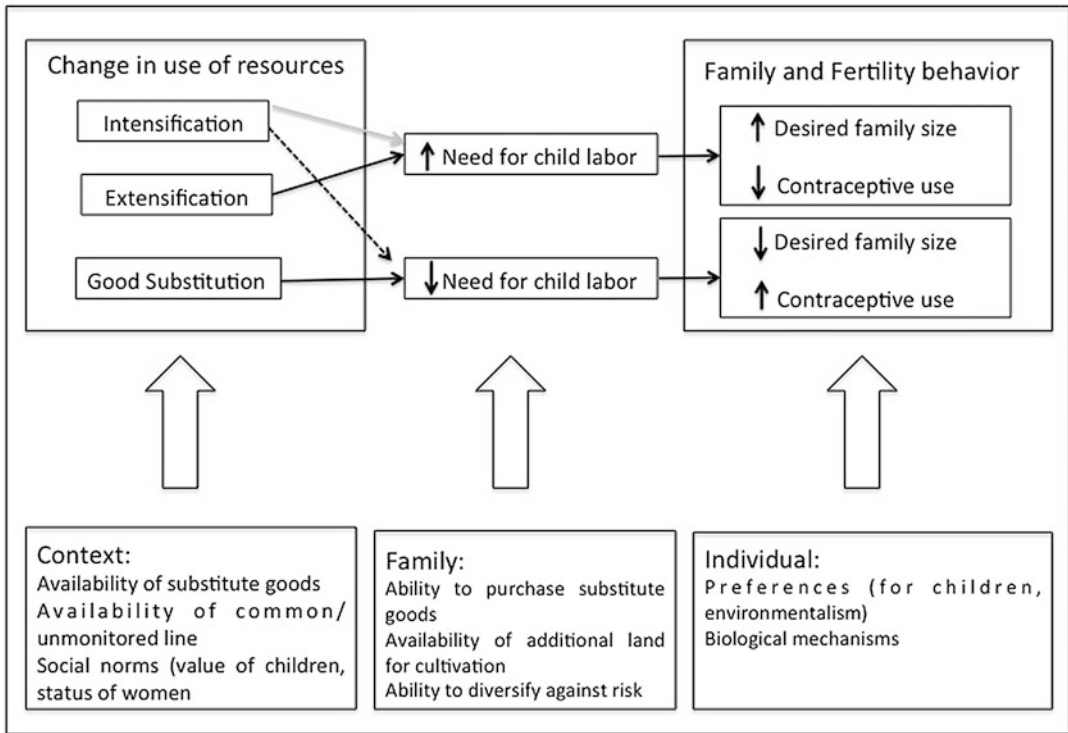
rates make it possible to compare countries with different population bases and time periods during which the population has changed. Crude birth rate which is the number of live births per 1,000 population in a given year is a rough or crude measure of fertility because the number of births is related to everyone in the population. General fertility rate is the number of births per 1,000 women of childbearing ages, usually considered 15–44 or 15–49. A related but even more precise measure is the age-specific fertility rate, which is the number of births per 1,000 women in a particular childbearing age group. Age-specific fertility rates are usually given in 5-year intervals, from 15–19 through 45–49. Another common measure of fertility is the total fertility rate. The completed fertility rate can be calculated only after women have finished having children. It is the number of births that did occur per 1,000 women during their reproductive years of life (Miller [1987](#)).

Fertility and Economics

Fertility in most of the world has undergone a sustained and seemingly irreversible transition. Today, a low fertility regime is the norm in the developed world, with some regions (particularly in Europe) experiencing sub-replacement fertility. This demographic transition enabled the productivity advances of the Industrial Revolution to be transformed into higher living standards and sustained economic growth. Understanding the revolution in fertility behavior between the Malthusian and the modern eras has therefore been a central research question (Cummins [2011](#)).

Linking the Environment to Fertility

A theoretical framework for understanding how environmental quality is related to fertility behavior (Brauner-otto [2014](#)). (Fig. 1) A vast body of sociological research has provided evidence that community, or context, matters for family and fertility behaviors. Some research has considered how the physical environment or land use patterns are related to fertility. The natural environment is



Fertility, Fig. 1 Heuristic representation of theoretical framework for the effect of poor environmental quality on family and fertility behaviors. Pathways are not

mutually exclusive and diversification involves simultaneous pathways operating. Dashed lines signify conflicting theoretical possibilities

one more dimension of social context likely to influence fertility (Leopold 1986). The economic theory suggests that future changes in climate may substantially influence fertility patterns via the process of structural transformation, among other possible avenues. Noneconomic factors, especially cultural norms, have important consequences for fertility decisions. Economic theories of fertility focus on the desire for a specific level of fertility. Fertility also depends on access to birth control. It is thus possible for climate change to impact fertility through availability of contraception (Casey et al. 2019).

- [Ovulation](#)
- [Sexual Signaling During Ovulation](#)
- [Women's Preferences During Ovulation](#)

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Cross-References

- [Age of Parent](#)
- [Concealed Ovulation and Pregnancy](#)
- [Fitness Benefits of Costly Signalling](#)
- [Male Counter Strategies to Cyclic Shifts](#)

Fetal

- [Early Stage of Brain Development at Birth](#)

Fetal Alcohol Syndrome

- [Teratogenic Effects of Alcohol Exposure on the Fetus](#)

Fetal Malformation

- [Teratogenic Effects of Alcohol Exposure on the Fetus](#)

Fetal Programming

- [Prenatal Environment, The](#)

Fetus Development

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Synonyms

[Developing infant](#); [Early life](#); [Embryo](#); [Ontogeny](#); [Prenatal development](#)

Definition

The continuous growth and development of an embryo and fetus during pregnancy or gestation that begins with fertilization and ends with the birth of an infant.

Introduction

Viviparous animals carry fertilized, developing eggs to term within their bodies and give birth rather than laying eggs (Roberts et al. 2016). The fertilized egg is called an embryo from conception through to 9 weeks of development, when it is then termed a fetus. Gestation is approximately 40 weeks in length, similar to other primate species; however, human infants are not born with the ability to survive on their own and require the care of their parents, defined as an altricial species. Humans often produce a single offspring during a gestational period, trading superfecundity, for variation, heritability, and diversity. The evolutionary pressure to drive the ontogeny of human infants and the stages of development are variable and are widely discussed in literature.

Pre-embryonic Development

A complete gestational period is 280 days, or approximately 40 weeks, beginning with the start of the last menstruation through until birth. The first week of development is called pre-embryonic and goes through six stages of events until the beginning of the second week, where embryonic development continues for 2 months.

The first stage of pre-embryonic development is ovulation, whereby an oocyte, or egg, is released from a female's ovaries by the follicle bursting. If the egg is fertilized, the follicle develops into a corpus luteum, which is important in the hormonal regulation and maintenance of the pregnancy through progesterone production. The second stage is fertilization, which typically occurs in the fallopian tubes, when the head of a sperm fuses with the egg nucleus to form a zygote. After this event, cleavage (cell division), growth, morphogenesis, and differentiation occur throughout the rest of development.

The third stage, cleavage, involves exponential, mitotic cell division that leads into the morula stage – a multicellular ball that becomes an early blastocyst. The blastocyst will become the chorion, a vital component for survival of the fetus. The chorion is one of a few membranes that also

develops alongside of the embryo. The names of the membranes are given based on shelled animal functions but are functionally different in humans. The chorion is the fetal portion of the placenta. The allantois leads away from the embryo, and its blood vessels become the umbilical cord vessels, used to transport blood to and from the fetus. The first membrane to actually appear is the yolk sac and is the first site of blood cell formation. The amnion develops and continues to grow in size with the embryo/fetus and contains fluid to insulate against heat and cold and absorbs shock from maternal movements.

The final stage of pre-embryonic development is implantation. The new embryo implants into the uterine wall through secretion of enzymes by the chorion to digest the uterine endometrium (Norwitz et al. 2001). It also begins to secrete the human chorionic gonadotropin hormone (HCG), which stimulates the corpus luteum in the ovary to produce progesterone, preventing the next menstrual cycle (Staun-Ram and Shalev 2005).

Embryonic Development

During the beginning of embryogenesis, gastrulation starts, where cells begin to change morphological shape and migrate to become three separate layers. These layers, according to evolutionary data, are homologous with other vertebrates and non-vertebrates that also develop into more complex creatures by progressive cellular division and morphological changes (Hall 1998; Nakanishi et al. 2014). The outermost layer is the ectoderm, which will continue to develop into skin, oral, and rectal epithelium, as well as the nervous system. The middle layer is the mesoderm, and it develops into the skeletal, cardiovascular, urinary, reproductive, digestive, and respiratory systems, as well as dermal skin layers. The inner layer, the endoderm, becomes epithelial lining of the digestive, urinary, and respiratory tracts.

By 6 weeks of gestation, these morphological changes are visibly apparent, and the embryo can be recognized as human. The nervous system has

developed significantly and reflexes, such as startle, are present (Schoenwolf and Smith 2000; Solnica-Krezel and Sepich 2012). At the end of the second month, the embryo has undergone massive development and changes and is now considered a fetus.

The Placenta

Among other eutherian mammals, humans produce placental organs to provide an exchange site of numerous nutrients and functions (Burton and Jauniaux 2015). The first lineage of cells from the embryo is destined to become the placenta and is called the trophoblast or trophoctoderm, where troph means nourishment and blast means embryo. Placental organs are pertinent for resource exchanges between the developing offspring and the mother and are present across multiple species, a product of convergent evolution. The placenta is an organ that is grown and shed during the pregnancy and the birth process. It is responsible for nutrient and gas mobility and immune function and acts as a barrier between the mother and fetus. Placentas have evolved independently across multiple animal groups, the consequence of maintaining an egg in the reproductive tract, rather than laying eggs and having the yolk sac and shell provide required nourishment for development and maturation. The mother's new requirement to provide nourishment for herself leads to competition for survival between the mother and the fetus.

Fetal Development

The fetus develops to a limit; human offspring are altricial, especially compared to other primate species, and continue to develop motor skills and neuronal connections after birth. This promotes substantial interactions with caregivers, leading to social learning and variation in behavioral phenotypes. Immaturity at birth allows infants to process specific stimuli, but not at capacity of an adult, hypothesized to permit growth and plasticity of cognitive and behavioral development.

During the third and fourth months of fetal development, cartilage begins to be replaced by bone, increasing the strength and rigidity of structures that will require support or protection when walking, falling, and exploring typical activities. The skin of the fetus is initially covered by lanugo, a soft, furry layer. The lanugo, in turn, is covered by the vernix caseosa, a greasy substance that is produced by fetal sebaceous glands, hypothesized to protect the delicate fetal skin from the amniotic fluid.

The vernix caseosa is uniquely a human developmental feature; however, other animals have different structures with similar functions. The components of the structure, and experimental evidence, indicate osmoregulation is a key function (Hoath et al. 2006). Other hypothesized functions, since the vernix caseosa is hydrophobic, is to protect the infant from detrimental heat loss when in contact with water, while also containing significant water content to moisturize the developing skin (Youssef et al. 2001). Due to its antimicrobial and vitamin components, it has also anti-infective and antioxidant properties and acts as a bacterial barrier with potential wound-healing properties. Evolution of this fetal structure indicates it is adaptive to protect the fetus during gestational environmental exposures, while its innate and adaptive immune responses are underdeveloped.

During the later months of fetal development, 8 and 9 months, the fetus accumulate a lot of fat, which is related to maternal nutrition (Herring et al. 2018). Well-nourished infants store a lot of subcutaneous fat compared to adults due to the consumption rates while growing and learning. Healthy, full-term infants with a good body weight have higher chances of survival (Kessel et al. 1985). Extensive research has been conducted on maternal nutritional deficiency and the outcomes on the infant. Notably, the thrifty phenotype hypothesis was coined by Hales and Barker in 1992, stating stressors acting on the fetal environment are linked to silenced and activated genes that are involved in physiological and behavioral phenotypical profiles. Through permanent and inheritable changes of the fetus' transcription factors, known as fetal programming,

the fetus' physiological and metabolic phenotype becomes adapted to a nutrient-deficient environment. When the fetus is born, if it is raised in a nutrient-dense environment, contrary to the fetal state, the adaptive response becomes aversive – predisposing the infant to obesity, hypertension, and diabetes (Nguyen et al. 2015). This phenotype has been shown to occur in the offspring of multiple species.

Other stressors that can influence genetic phenotype and variability of offspring include maternal illness, psychological insult such as abuse or loss of a family member, injury, or exposure to toxic elements. Each stressor increases maternal endogenous glucocorticoids, which can overwhelm the placental enzymatic barrier and then bind to fetal DNA binding sites, such as CPG islands, modifying genetic activity.

During fetal growth, maternal hormones are also key to the development and survivability of the fetus. Increased levels of progesterone act to decrease uterine motility, smooth muscle contractions, as well as the maternal immune response against the fetus (Druckmann and Druckmann 2005; Di Renzo et al. 2016). Estrogen output increases blood flow to the uterus and lowers arterial expansion, which lowers blood pressure (Mata et al. 2015). Estrogen also stimulates the renin-angiotensin-aldosterone activity that increases water and salt retention, increasing total blood volume.

Birth

The fetus is considered full-term and ready for birth at approximately 40 weeks of gestation. Due to the evolution of bipedalism and larger, complex brains, fetuses have relatively large heads. Fetal heads have developed near the size of the birth canal, which has been preserved in fossil records. The fetal skull has six membranous “soft spots” or fontanelles that permit the skull flexibility to reshape during birth. Unfortunately, some fetuses still outgrow the size of its mother's birth canal and require cesarean sections to ensure the safety of both the fetus and the mother; prior to the development of the

emergent surgery, both the fetus and mother historically died during such a birth.

Conclusion

Different adaptive pressures occur at different points in ontogeny, for example, disruption during organ development versus neural development may lead to lower birth weights and predispositions for adulthood disease versus behavioral changes. The embryonic development is critical to survival and proper organogenesis, whereas the fetal environment can predispose offspring child and adulthood diseases that are adaptive reactions to adverse in utero environments. The fetus does not develop into a completely self-sufficient individual, but to a point that allows live birth considering the female anatomy and the large fetal head. Variability in behavior and physiology and intelligence have evolved to benefit the species in contrast to superfecundity.

Cross-References

- [Brain Development](#)
- [Implications for Pregnancy](#)
- [Maternal Malnourishment](#)
- [Maternal-Fetal Conflict](#)
- [Prenatal Environment, The](#)

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Feuding

- [Humans: Between-Group Conflicts](#)

Fever

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Synonyms

Febrile; Pyrexia

Definition

A controlled increase of body temperature, commonly as part of an inflammatory response to pathogens.

Introduction

Fever represents one of a selection of “sickness behaviors” that occur in response to pathogens that have infiltrated the body (Harden et al. 2015). It was itself originally considered a disease, though now has long been recognized as a defense mechanism and an aspect of the immune system. However, the degree to which fever is beneficial or detrimental to the host is still widely disputed (Hasday et al. 2000). Accordingly, the treatment of fever is just as controversial, even after being practiced for thousands of years (Earn et al. 2014).

Matthew Kluger presented some of the early evidence for the benefits of fever in fighting disease. Kluger et al. (1975) gave evidence that lizards injected with *Aeromonas hydrophila* (a bacterium) were more likely to survive when their body temperature was elevated. As such, the increase in heat caused by fever is argued to aid the survival of the host by heightening the immune system and by reducing the growth of pathogens. Recent research, however, suggests that the effect of fever is more complicated than initially considered, as are the consequences for treating it (Harden et al. 2015).

Adaptive Value

Fever has remained a part of the immunological response of both vertebrates and invertebrates (Kluger 1986) for millennia (Evans et al. 2015). Its presence in such a variety of animals is indicative that a febrile response has been present throughout much of evolutionary history, with some estimates suggesting its existence for over 360 million years (Hasday et al. 2000). This extended presence suggests that fever provides an adaptive advantage to the host, as without this survival benefit, it is unlikely that it would be so prevalent today (Kluger 1986).

Further evidence suggesting an adaptive advantage conferred by fever is that the activation and maintenance of a febrile response are energetically costly. For each 1 °C increase in temperature, the body has to increase metabolic rates by 10 % (Kluger 1986). As fever generally increases body temperature by between 1 °C and 4 °C (Evans et al. 2015), this would confer a significant disadvantage to the host if there were no benefits for the energy expenditure.

Though fever appears to benefit human survival in the vast majority of instances, there are situations where a high fever can be dangerous to the host. Such examples include individuals with heart anomalies and pregnant women, the latter being linked to increased rates of birth defects (Kluger 1986). However, these cases are in the minority in comparison to the overall population, and as such fever still provides an evolutionary advantage in enhancing the chances of survival of the host.

Antipyretics

As fever has been present throughout much of our evolutionary history, questions have been raised about whether treating fever is beneficial or harmful to the host's survival. Antipyretics are treatments for fever, most commonly pharmacological within contemporary society, with examples including paracetamol (Harden et al. 2015). These medications aim to artificially reduce fevers and to ease the discomfort in the patient (Zitelli

1991). However, fever has remained a part of the immunological response in a wide variety of species, implying it provides an adaptive advantage. As such, there is potential for antipyretics to negatively impact the immune response of the body by removing the advantages provided by the fever.

Unfortunately, the degree to which the treatment of fever benefits or detracts the host's defense mechanisms is still uncertain, with little definitive evidence to support either conclusion (Harden et al. 2015). The consensus within contemporary research appears to be that, in the majority of instances of fever caused by influenza, there is little evidence to suggest that the use of antipyretics is beneficial (Harden et al. 2015). Conversely, there is also little evidence that the treatment of influenza-caused fever is detrimental other than the potential for altering the inflammatory process (Harden et al. 2015).

There is, however, evidence of a detrimental effect of antipyretic use during the treatment of metastatic melanoma (advanced-stage skin cancer). This is the result of fever enhancing the production of natural killer and T cells during fevers, a benefit which is removed following the use of antipyretics (Køstner et al. 2015). The benefit of a high fever in this example is associated with improved survival rates due to the improved immunological response (Køstner et al. 2015).

Conclusion

Many species have evolved a pyretic response to invading pathogens over a course of millennia. Though fever has a high-energy cost to the host, the immunological enhancement it affords provides an adaptive advantage for survival. However, the overarching benefits and drawbacks of treating fever have received little empirical study. In treatment of conditions such as influenza-based fever, however, the current consensus suggests that there is little benefit gained from treating the fever. There are conditions where fever has been evidenced as boosting the immune response of the host, for example, melanoma and for critically ill patients.

Cross-References

► Adaptation

References

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Fiction

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Synonyms

Drama; Fantasy; Imagination; Myth; Storytelling; Untruth

Introduction

There is no doubt fiction makes a better job of the truth by Doris Lessing Fiction is the dream or imagination of the writer consisting of people, events, or places which is not based on facts or history (Abrams 2017). It is literature in the form of prose. In its most narrow usage, fiction refers to novels, but it may also denote any “literary narrative” (Abrams 2017) including novels, novellas, and short stories. More broadly, fiction has come to encompass storytelling with imaginary elements in any format, including writings, audio recordings, live theatrical performances, comics, animated or live-action films, television programs, games (most notably, role-playing and video games), and so on (Oxford Learner’s Dictionaries 2015). Fiction, literature created from the imagination, is not presented as the fact, though it may be based on a true story or situation (Predelli 1997).

Definition of Fiction

According to Oxford dictionary	Fiction is the type of book or story that is written about imaginary characters and events and not based on real people and facts.
According to Merriam-Webster	Something invented by the imagination or feigned.
According to Literary Devices	Fiction is a type of literature that describes imaginary people and events, not real ones.

Concept of Fiction

Etymologically, the word fiction has been derived from Latin word “fictus,” which means “to form.” It consists of stories, novels, and dramas and their construction is based on imagination and fabricated stories and characters (Oxford Learner’s Dictionaries 2015). Fiction contains certain symbolic and thematic features. In other words, fiction narrates a story, which aims at something bigger than merely a story. Fiction may be based on

stories of actual historical events. Although fictitious characters are presented in a fictitious setting in stories and novels, they may have some resemblance to real life events and characters. Writers alter their characters very skillfully when they take them from actual life (Literary Devices Editors 2014).

Function of Fiction

The function of fiction is to entertain, educate, and inspire the readers and the audience. Literature in general and fiction in particular is capable enough to sweep our emotions (Beardsley 1981). Therefore, fiction gives the audience an experience beyond their daily lives. It provides them an insight into the life of the characters, their manners, vicissitudes, and events related to them (Predelli 1997). It also is used to point out the flaws and drawbacks of a society, race, and nation in a manner that it does not touch the boundary of stricture or criticism. Rather, fiction points out drawbacks and then suggests solutions for the individuals and the nations alike. To sum up, fiction can also provide a vent to our pent-up emotions such as hatred, anger, and dislike but in a very light manner without pointing out specific individuals or groups (Literary Devices Editors 2014).

Elements of Fiction

Plot, Setting, Character, Conflict, Symbol, and Point of View, etc., are the main elements which fiction writers use to develop a story and its Theme.

Because literature is an art and not a science, it is impossible to specifically quantify any of these elements within any story or to guarantee that each will be present in any given story (School Work Helper 2010).

1. Plot

Plot is the most important element of a good story. Plot is the order in which things move and happen in a story. It was the carrot on the

string that pulled us through a story as we wanted to see what would happen next.

With that understanding, let's examine the elements ("Reedsyblog" 2018).

- **Exposition:** The de-facto introduction that brings out the story's cast of characters and plants the seeds of conflict.
- **Rising Action:** In which a series of events (usually triggered by an inciting incident) escalates and sets the rest of the story in motion.
- **Climax:** The moment of peak tension in a story – in other words, what everything else builds up to.
- **Falling Action:** The Bridge between the climax and the resolution in which subplots and mini-conflicts are resolved.
- **Denouement:** The wrapping up of the whole story.

2. Setting

The time and place in which the action occurs.

3. Theme

Theme is the main idea that weaves the story together. It is the meaning of the whole story. The term also indicates a message or moral implicit in any work of art.

4. Character

A person, an animal, or an imaginary creature that takes the part in the action of the story.

Character types:

Protagonist – Main character of the story that is most central to the action of the story.

Antagonist – The person or thing working against the protagonist, or hero, in the story.

5. Point of View

The vantage point from which a narrative is told. A narrative is typically told from a first-person or third-person point of view. In a narrative told from a first-person perspective, the author tells the story through a character who refers to himself or herself as "I." Third, person narratives come in two types: omniscient and limited. An author taking an omniscient point of view assumes the vantage point of an all-knowing narrator able not only to recount the action thoroughly and reliably but also to enter the mind of any character in

the work or any time in order to reveal his or her thoughts, feelings, and beliefs directly to the reader (Beardsley 1981). An author using the limited point of view recounts the story through the eyes of a single character (or occasionally more than one, but not all or the narrator would be an omniscient narrator) (Mosley 2019).

6. Style

The author's type of diction (choice of words), syntax (arrangement of words), and other linguistic features of a work.

7. Conflict

Conflict is the struggle between two entities. In story writing the main character, also known as the protagonist, encounters a conflict with the antagonist, which is an adversary. The conflict may be one of six kinds (School Work Helper 2010):

- Character vs. character
- Character vs. nature or natural forces
- Character vs. society or culture
- Character vs. machine or technology
- Character vs. God
- Character vs. himself or herself

8. Symbolism

A person, object, image, word, or event that evokes a range of additional meaning beyond and usually more abstract than its literal significance.

Types of Symbols

Conventional symbols have meanings that are widely recognized by a society or culture. Writers use conventional symbols for reinforcing meanings.

A literary or contextual symbol can be a setting, character, action, object, name or anything else in a work that maintains its literal significance while suggesting other meanings. Such symbols go beyond conventional symbols; they gain their symbolic meaning within the context of a specific story.

9. Tone

Tone is the author's implicit attitude toward the reader, subject, and/or the people, places, and events in a work as revealed by the elements of the author's style.

Genres of Fiction

Genres of fiction are typically defined by their tone and subject matter. The term “genre fiction” generally encompasses popular types of fiction situated within a specific genre outside of standard literary fiction.

1. **Commercial fiction:** It attracts a broad audience and may also fall into any subgenre, like mystery, romance, legal thriller, western, science fiction, etc. Commercial fiction is generally plot driven, and read for entertainment rather than its art (Malatesta 2018). The commercial fiction writer’s challenge is to find creativity within the bounds of genre, while meeting the expectations of a particular audience.
2. **Literary fiction:** It tends to appeal to a smaller, more intellectually adventurous audience. It often focuses on artistry, with the story being driven by character and internal motivations. It presents a broader canvas to writers with endless possibilities for exploring character, theme, setting, and style (Valken 1998).

Other Types of Fiction

1. **Historical fiction:** Historical fiction has characters based on real people and often bases its plots on real-life events. Generally, many elements of plot or dialogue are fabricated by the author, although it is up to the writer how much to invent. For example, *Pink and Say* by Patricia Polacco. Writing historical fiction requires a balance of research and creativity, and while it often includes real people and events, the genre offers a fiction writer many opportunities to tell a wholly unique story (MasterClass 2019).
2. **Literary fiction:** Literary fiction describes mainstream highbrow fiction. Literary fiction encompasses most books taught in high school English courses and most books that are up for major annual prizes like the Pulitzer Prize or Man Booker Prize. Literary fiction

often depicts nuanced themes and incorporates literary devices.

3. **Mystery fiction:** Mystery novels are plot driven thrillers based around a crime or other form of mystery. The story provides clues throughout the story, but the mystery is not typically solved until the end of the story. For example, *I Want My Hat Back* by Jon Klassen.
4. **Science fiction:** Science fiction, abbreviation SF or sci-fi, a form of fiction that deals principally with the impact of actual or imagined science upon society or individuals. Science fiction is a genre of fiction that often depicts stories set against the backdrop of futuristic technology and dystopian societies and it relies heavily on scientific facts, theories (Sterling 2019). Science fiction writers often seek out new scientific and technical developments in order to prognosticate freely the techno-social changes that will shock the readers’ sense of cultural propriety and expand their consciousness (Science fiction 2015). In science fiction stories describe how humans interact with computers, nanotechnology, bioengineering, virtual reality, artificial intelligences, or other parts of technologically driven society. These stories often question the concept of what it means to be human. For example, Movies like *Avengers endgames*, *interstellar*, *Gravity*, *Arrival*, etc.
5. **Children’s fiction:** Children’s literature is a genre of fiction that can range from books for toddlers to full length young adult novels.
6. **Fan fiction:** Fan fiction is a genre of fiction in which fans take source material from existing franchises and then spin them off into separate narratives of their own. The author uses copyrighted characters, settings, or other intellectual properties from an original creator as a basis for their writing. Common bases for fan fiction include novels, movies, and video games. For example, A web series *Fifty Shades of Grey* by E. L. James.
7. **Fantasy Fiction:** Fantasy fiction typically involves a fiction, or untrue, story. The story could not happen in real life and it involves

magic or supernatural powers and most of the time takes place in another world or has make believe characters, such as wizards or dragons in *Game of thrones*.

8. **Realistic Fiction:** It has a story that has believable events and characteristics that could actually happen in real life. It can take place in a real setting; it is not based on history or science. The character seems like real people with real issues solved in a realistic ways. For example, *The Fault in our stars* by John Green.
9. **Romance fiction:** The word “romance” also refers to romantic love. Romance, as pointed out, is a type of fiction, comprising idealized love, chivalry, obsessive association with somebody or some idea, and mysterious adventures. However, Romanticism is a specific movement and period in English literature during which poems, stories, and novels related to Romantic ideas were created. William Wordsworth, P. B. Shelly, Lord Byron, and John Keats are some of the most famous poets and writers of the Romantic period.

For example, *Pride and Prejudice* by Jane Austen, *The Count of Monte Cristo* by Alexander Dumas, etc. (“Roamance Fiction” 2014).

10. **Horror Fiction:** Horror is a genre of fiction which is intended to, or has the capacity to frighten, scare, disgust, or startle its readers or viewers by inducing feelings of horror and terror. For example, Novels like *At the mountain of Madness* by H. P. Lovecraft, *The Bad Seed* by William March, etc.

Formats of Fiction

Traditionally, fiction includes novels, short stories, fables, legends, myths, fairy tales, epic, and narrative poetry plays (including operas, musicals, dramas, puppet plays, and various kinds of theatrical dances and play). However, fiction may also encompass comic books, and many animated cartoons, motion pictures, anime, manga, films, video games, radio programs, T.V. programs (comedies and dramas), etc., digital libraries such as Project Gutenberg,

OPEN LIBRARY, Google-ebook store, Amazon free kindle books make public domain texts more readily available. The combination of inexpensive home computers, the Internet, and the creativity of its users has also led to new forms of fiction, such as interactive computer games, for example, Choice of Deathless or computer-generated comics, for example, Shatter. Countless forums for fan fiction can be found online, where loyal followers of specific fictional realms create and distribute derivative stories. The Internet is also used for the development of blog fiction, where a story is delivered through a blog either as flash fiction or serial blog, and collaborative fiction, where a story is written sequentially by different authors, or the entire text can be revised by anyone using a wiki (“Wikipedia” 2020).

Novel: Novel is a genre of fiction and it is an invented prose narrative of considerable length and a certain complexity that deals imaginatively with human experience, usually through a connected sequence of events involving a group of persons in a specific setting. Within its broad framework, the genre of the novel has encompassed an extensive range of types and styles: picaresque, epistolary, Gothic, romantic, realist, historical. Some of the famous Novels are *Pride and prejudice* by Jane Austen, *The History of Tom Jones, Foundling* by Henry Fielding, *War and peace* by Tolstoy.

Short Story: Short story is a brief fictional prose narrative that is shorter than a novel and that usually deals with only a few characters. A brief story usually 5–20 pages long only has 1–2 main characters and one main setting. There are five key elements that go into every great short story: character, setting, conflict, plot, and theme. For example, *A Haunted House* by Virginia Woolf, *Shooting an Elephant* by George Orwell, *A Sound of Thunder* by Ray Bradbury, etc.

Fable: A fable is a very brief story in prose or in verse that teaches a moral or a practical lesson about how to succeed in life. A fable is a very brief story in prose or in verse that teaches a moral or a practical lesson about how to

succeed in life. For example, *Animal Farm* by George Orwell, Panchtantra stories, etc.

Folk tale: A folk tale is a story with no known author. Folk tales are passed down from one generation to another by word of mouth. They teach lessons and teach you about the consequences of certain kinds of behaviors or attitudes. For example, Cinderella, Sleeping Beauty, Snow White, Rapunzel, etc.

Legend: A legend is a semi-true story, which has been passed on from person-to-person and has important meaning or symbolism for the culture in which it originates. A legend usually includes an element of truth, or is based on historic facts, but with “mythical qualities.” Legends usually involve heroic characters or fantastic places and often encompass the spiritual beliefs of the culture in which they originate. For example, *Ali Baba*, *Fountain of Youth*, etc.

Novella story: A novella is a work of narrative prose fiction, longer than a short story but shorter than a novel. Between 20 and 100 pages, can also be a collection of short stories. For example, Joseph Conrad’s *Heart of Darkness* (1899), *Animal Farm* by George Orwell, etc.

Myth: A myth is a story passed down from generations trying to explain how our world works or how we should treat each other. Myth is a legendary or a traditional story that usually concerns an event or a hero, with or without using factual or real explanations. These particularly concern demigods or deities and describe some rites, practices, and natural phenomenon. Typically, a myth involves historical events and supernatural beings. There are many types of myths, such as classic myths, religious myths, and modern myths. For example, *Romeo and Juliet* by William Shakespeare, *No Second Troy* by William Butler Yeats, *Paradise Lost* by John Milton.

Fairy tale: Fairy tale is an imaginative story or piece of literature told in a variety of media. Stories which are based on magic and fantastical settings, plots, and characters and happy endings. Such stories typically feature entities such as dwarfs, dragons, elves, fairies, giants,

gnomes, goblins, griffins, mermaids, talking animals, trolls, unicorns, or witches, and usually magic or enchantments. For example, Cinderella, *Elves and the Shoemaker*, *Emperor’s New Clothes*, etc.

Epic: Epic refers to genre of poetry. Stories and songs emerged as an oral means of communication and preserving the past: tales of heroic battles or struggles, myths, or religious beliefs. In a time before mass communication, the oral tradition enabled people to pass down stories, most often in the form of rhyming poems. For example, *Buddha*, *Krishna*, *Odysseus*, *Dionysus*, *Zoroaster*, and *Zarathustra* (Literary Devices Editors 2014).

There are many genres of epic like epic fantasy and it describes works of fantasy, such as in J. R. R. Tolkien’s *Lord of the Rings*. Epic fantasy has been described as containing three elements: it must be a trilogy or longer, its time-span must encompass years or more, and it must contain a large back-story or universe setting in which the story takes place. Epic fantasy is not limited to the Western tradition, for example, Arabic epic literature includes *One Thousand and One Nights* and Indian epic poetry includes *Ramayana* and *Mahabharata* (“Wikipedia” 2020).

Difference Between Imagination and Fantasy

Imagination is the experience that one has when they deal with reality, or how they deal with reality, while fiction or fantasy is an unrealistic by product of that imagination.

Imagination is defined by the Dictionary of Psychology as, “the reorganization of data derived from past experiences, with new relations, into present ideational experience.” This means that imagination is often based on real life experiences or a person’s experience with their own reality of life. It is safe to say that imagination is how one views the world. For some it could be a half glass full, while for others it can be a half glass empty. It is often a recreation of the world (Literary Devices Editors 2014).

Fantasy is defined by the Merriam Webster Dictionary as, “something that is produced by the imagination: an idea about doing something that is far removed from normal reality.” So, imagination is what leads one to create a fantasy. Fantasy can also be defined as a branch of fiction that deals with the supernatural such as magic, legends, myth, superpowers, etc. (Menadue and Cheer 2017).

A simple way to distinguish between the two is imagination is the experience that one has when they deal with reality, or how they deal with reality, while fantasy is an unrealistic byproduct of that imagination.

Impact of Fiction on Society

Literature inevitably makes us better human beings. Reading fiction improves our ability to access the mental states of other people, but that is a morally neutral skill, one that can be put to the service of manipulation just as easily as it can be put to the service of philanthropy.

1. **Empathy: Imagining creates understanding**

Reading fiction makes us nicer a more empathetic. An exposure to book really improves our emotional intelligence (Bal and Veltkamp 2013).

2. **Disengagement**

Reading fiction is the best way to relax and get rid of by stress and tension than listening to music, sipping tea, or going for a walk (Mar and Oatley 2008).

3. **Sleep**

Regular readers sleep better. Reading books at night help to relax, increased focus, and improve our sleep pattern.

4. **Improved relationships: Books are a “reality simulator”**

People who read for pleasure have better social skills, better parent child communication, lower rates of depression, dementia, and overall emotional health and relationship.

5. **Readers have less cognitive decline in later life**

When we read a book we use many parts of our brain. We use vivid imagery as well as

memory to follow a plot, or main idea. Reading can be like a mental Gymnastic. Readers experience slower memory declined later in life compared to nonreaders. In particular, later-in-life readers have a 32% lower rate of mental decline compared to their peers (Tamir et al. 2016).

6. **Inclusivity: Stories open your mind**

Reading stories makes us inclusive, tolerant, and open-minded (Bergland 2014).

7. **Vocabulary: Fiction readers build more language**

A 2013 Emory University compared the brains of people after they read fiction (specifically, Robert Harris’ *Pompeii* over nine nights) to the brains of people who did not read. The brains of the readers showed more activity in certain areas than those who did not read – especially the left temporal cortex, the part of the brain typically associated with understanding language.

8. **Creativity: Fictions allows for uncertainty**

Reading boosts creativity via developing imagination and explores our mind. A study published in *Creativity Research Journal* asked students to read either a short fictional story or a nonfiction essay and then measured their emotional need for certainty and stability. Researchers discovered that the fiction readers had less need for “cognitive closure” than those who read nonfiction, and added:

9. **Pleasure: Reading makes you happier**

Survey of 1500 adult readers in the UK found that 76% of them said reading improves their life and helps to make them feel good.

Other findings of the survey are that those who read books regularly are on average more satisfied with life, happier, and more likely to feel that the things they do in life are worthwhile.

Impact of Fiction on Science

Yuval Noah Harari, author of the best-selling book *Sapiens and Homo Deus*, says “Today science fiction is the most important artistic genre. It shapes the understanding of the public on things like artificial intelligence and advance

biotechnology, which are likely to change our lives and society more than anything else in the coming decades” (Wired 2018).

Science fiction occupies a vital role in our society. It makes concrete ideas, hopes, and fears about our relationship to technology, progress, and even to the human body. Science fiction is important for at least three reasons. Firstly, by considering worlds that are logically possible, science fiction can be used to explore our place in the universe and consider fundamental philosophical questions about the nature of reality and the mind. Books that explore these issues include *Flatland* by Edwin Abbott Abbott, *Ubik* by Philip K. Dick, and *2001: A Space Odyssey* by Arthur C. Clarke.

Secondly, science fiction can inspire and motivate number of people to become scientists. Edwin Hubble, who provided strong evidence for the *big bang theory* and was the first person to prove that galaxies exist outside of the Milky Way, was inspired to become a scientist after reading Jules Verne novels (Kupperberg 2004). Astronomer and science fiction author Carl Sagan was influenced by Robert A. Heinlein (Sagan 1979), and theoretical physicist Michio Kaku enjoyed the television show *Flash Gordon* as a child.

Thirdly, and perhaps most importantly, science fiction is the only genre that depicts how society could function differently. This is the first step towards progress as it allows us to imagine the future we want, and consider ways to work towards it. It also makes us aware of futures we wish to avoid and helps us prevent them.

Perhaps the most famous example of the positive effect of science fiction comes from the inclusion of a multiracial cast on the original *Star Trek* television series. When Nichelle Nichols, who played Lieutenant Uhura, was considering leaving the series, civil rights leader Martin Luther King Jr. convinced her to stay (NASA News 2012). King argued that her inclusion on *Star Trek* was important because, as a black woman, she helped represent a future people could aspire to, one where people were judged solely on the content of their character (Kilgore 2010).

Shortly after, Nichols publicly criticized NASA for only selecting white male astronauts, she was invited to NASA headquarters and asked to assist in convincing former applicants to reapply [7b]. This led to the selection of Sally Ride and Guion Bluford, who became NASA’s first female and first black American astronauts, respectively. NASA’s first female black American astronaut, Mae Jemison, directly cited *Star Trek* as an influence [8], and later appeared on *Star Trek: The Next Generation* (NASA News 2012).

As well as considering the effects of current and developing technologies, science fiction can help address long-term problems, such as global warming. It can help with the development of space exploration and prepare us for problems we may not anticipate. One day, time travel, teleportation, or the genetic engineering of humans may happen, we might communicate with aliens, invent simulated realities, or build intelligent robots, and we will be better prepared to deal with these, and other potential dilemmas, if we have already thought about them.

The Windup Girl by Paolo Bacigalupi, *Neuromancer* by William Gibson, *Stranger in a Strange Land* by Robert A. Heinlein, *The Time Machine* by H. G. Wells, *Stranger in a Strange Land* by Robert A. Heinlein.

Related Genres

Utopian Literature: The word utopia resembles both the Greek words “no place,” “outopos,” and “good place,” “eutopos.” A vision of an ideal society. *Utopia* has come to mean a place that we can only dream about, a true paradise. For example, Samuel Johnson’s *The History of Rasselas, Prince of Abissinia* and Samuel Butler’s *Erewhon*.

Dystopian Literature: Dystopia is defined as a society characterized by a focus on mass poverty, squalor, suffering, or oppression. Most authors of dystopian fiction explore at least one reason why things are that way, often as an analogy for similar issues in the real world. Examples of fictional dystopias include Aldous Huxley’s *Brave New World* (1932).

Ecotopian Literature: Where the author posits either a utopian or dystopian world revolving around environmental conservation or destruction. Ecotopian fiction contains visions of a negative, dystopian future that connects with a range of environmental issues. For example, Margaret Atwood's *MaddAddam Trilogy* examines human environmental manipulation and world-wide disaster (Pressley 2015).

Themes of Science Fiction

- Space travel to and from other planets, for example, Stars Wars, Star Trek
- Time travel to the past and future, for example, Back to the future
- Psychological/biological change to man brought about scientific changes, for example, The incredible hulk
- Supernormal Power/talents, for example, Superman, Spider man and Batman
- Science applied to human relations for constructive or destructive purpose
- Battle with Alien life forms, for example, Signs
- Alternate universe, for example, Star War

Best Sci-Fi Movies

- A Clock Orange (1971)
- A Andromeda Strain (1971)
- Solaris (1972)
- 2001: A Space Odyssey
- District 9 (2009)
- The Prestige (2006)
- 12 Monkeys (1995)
- Alien (1979)
- Children of Men (2006)
- Interstellar (2014)
- Arrival
- Her (2013)

Prominent Authors of Fiction

Here is the list of famous fiction writers:

- William Shakespeare (Othello, Romeo and Juliet, Hamlet)

- Agatha Christie (The A.B..C. Murders, The Murder of Roger Ackroyd, A Pocket Full of Rye)
- Barbara Cartland (Love in the Ruins, As Eagles Fly, Messenger of Love)
- Harold Robbins (The Dream Merchants, The Carpetbaggers, Stiletto)
- Georges Simenon (La Premiere Enquete de Maigret, La Marie Du Port, La Veuve Couderc)
- Sidney Sheldon (Bloodline, Rage of Angels, The Naked Face)
- Enid Blyton (Fifth Formers of St. Clare's, Third Year at Malory Towers, The Rockingdown Mystery)
- Danielle Steel (The Long Road Home, Mirror Image, Honor Thyself)
- Dr. Seuss (The Cat in the Hat, Green Eggs and Ham, Oh)
- Gilbert Patten (Frank Merriwell at Yale, Frank Merriwell, Junior's)
- J. K. Rowling (Harry Potter and the Philosopher's Stone, Harry Potter and the Sorcerer's Stone, Harry Potter and the Deathly Hallows)
- Leo Tolstoy (War and Peace, Anna Karenina, Resurrection) (Ranker 2018)

Conclusion

Fiction contributes to a person's moral psychological development and their ability to have empathy or understanding. It enhances our ability to connect with each other. Science fiction can be used to explore our place in the universe and consider fundamental philosophical questions about the nature of reality and the mind.

Cross-References

► [Narrative](#)

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Fictive Kin

- Manipulative Use of Kin Terminology

Fictive Kinship

- Kinship Psychology Manipulations

Fidelity

- Benefits of Commitment and Marriage

Field of Behavioral Ecology, The

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Definition

The study of the ecological and evolutionary basis of animal behavior.

Introduction

Behavioral ecology has its origins in field studies that examined associations among behavior, inter-individual interactions, and the environment (Martin and Bateson 2007). The primary focus is on the study of the ecological and evolutionary basis of animal behavior, specifically the functions of behaviors and their adaptive advantages. Adaptive behaviors allow an individual to increase or maximize its reproductive success, or fitness. Behavioral differences with an underlying genetic basis are subject to natural selection or the differential survival and reproduction of organisms that differ in heritable ways.

Under selection, behaviors best adapted to the local environment increase in frequency over generations relative to less well-adapted behaviors. The behavior that maximizes fitness will depend both on interactions with other individuals as well as the ecological context (environment). Since natural selection can only operate on genetic differences among individuals, for a behavior to evolve, there must be heritable variation in a population and some behaviors must result in greater reproductive success (increased fitness) than others (Krebs and Davies 1993).

However, behaviors do not always vary in ways that are adaptive. Traits may have evolved because they were beneficial in the past, but no longer confer a selective advantage. Traits may also evolve due to neutral processes, such as genetic drift or gene flow. Genetic drift refers to variation in the frequency of genotypes in a small population due to the disappearance of particular alleles, or gene variants, as individuals die or fail to reproduce. Gene flow refers to a substantial change in allele frequencies, typically due to migration.

Proximate Versus Ultimate Causation

Behavioral ecologists distinguish between proximate versus ultimate causation (Mayr 1961). Proximate causes describe how the behavior is performed and provide explanations for it based on immediate causes. Examples include

understanding how a behavior develops, determining what stimuli elicit the behavior, and identifying the genetic and phenotypic factors that underlie behavior. Behavioral ecologists focus primarily on ultimate causes, which take an evolutionary approach to understand why a behavior is performed, proximate mechanisms occur, and organisms respond the way they do. Examples include understanding the adaptive value of a behavior, whether a behavior maximizes fitness, and how behaviors differ among species.

Key Individuals

In 1973, the Nobel Prize in Physiology or Medicine was awarded to Nikolaas (Niko) Tinbergen, Karl von Frisch, and Konrad Lorenz for their research on individual and social behaviors. One of Tinbergen's major contributions to ethology, the study of animal behavior, was to organize the types of questions biologists can ask about behavior into categories: (1) cause, (2) development, (3) function, and (4) evolutionary history (Tinbergen 1963). In one of Tinbergen's studies of survival values, or how an animal's behavior allows it to increase its own or its offspring's survival, he determined that parental gulls remove eggshells from their nests after their offspring have hatched because crows use the white interior of a broken eggshell to find and prey upon unhatched eggs (Tinbergen et al. 1962). Karl von Frisch's major contribution to ethology was in describing the honeybee's (*Apis mellifera*) waggle dance (von Frisch 1967), which is used to relay directions to a patch of flowers to the colony. Konrad Lorenz investigated imprinting behavior, the process by which some birds bond instinctively with the first moving object they see shortly after hatching (Lorenz 1935).

J.H. Crook and David Lack developed a comparative approach in which they associated the behavior of birds with environmental variation. Crook (1964) focused on comparing species of weaver birds in evergreen forests and savannahs. He found that Birds living in forests foraged primarily on insects, were monogamous, and defended large territories, in contrast to the birds

in the savannah, which were granivorous, nested in large colonies, and were typically polygynous. Since food supply in the forest is scattered and unpredictable, reproductive success is limited by the ability of parents to provide food for their offspring. Monogamy is therefore the preferred mating strategy because biparental care is essential for obtaining food. In contrast, in the savannah, food supplies are unstable, but locally plentiful. The polygynist mating strategy used here is likely linked to risk of predation, with the number of mates males acquire dependent upon the number of nest sites they are able to defend. David Lack associated differences in bill morphology and foraging behavior in Darwin's finches in the Galapagos to adaptations to specific food resources (Lack 1947). Their comparative approach highlighted the importance of ecological factors in shaping behavior and the difficulty in distinguishing between correlations and causations in associations between behavior and the environment.

John Maynard Smith coined the term evolutionary stable strategies to describe, using mathematical tools and game theory, how natural selection maintains a balance between opposing characteristics within a species. Game theory analyzes situations in which the best option for one individual depends on the decisions of another (von Neumann 1928). Smith used game theory to demonstrate that natural selection may favor both aggressive and nonaggressive behaviors in a context-dependent manner using a comparison of hawk versus dove strategies. In this example, hawks will always battle over resources, whereas doves will never behave aggressively. A population entirely comprised of doves would be unstable because it would be destroyed by the introduction of a hawk. However, in a hawks-only population, an introduced dove would have a long-term advantage because the hawks' consistently aggressive behavior would lead to frequent injury among hawks, while the dove would avoid harm. Smith demonstrated that a certain ratio of hawks to doves forms an evolutionary stable strategy and that balancing selection is able to maintain both characteristics within a population (Maynard Smith 1976).

Adaptive Behaviors

Behavioral ecologists study the effects of behaviors on foraging, territoriality, mating success, parental care, communication, and likelihood of predation, and how different behavioral strategies contribute to fitness.

Foraging Behavior. Natural selection acts on behaviors that increase feeding efficiency. Foraging includes not only eating, but also searching for, identifying, and capturing food, and involves a trade-off between a food's energy content and the cost of obtaining it. Foragers need to make decisions about what types of food to consume as well as where and how long to search for it. Large food items may contain more energy, but are often more difficult to capture and less readily available than smaller items. Efficient foraging may mean that individuals consistently or periodically maximize energy intake or minimize variation in intake.

Optimal foraging theory states that natural selection will favor individuals whose foraging behavior is as energetically efficient as possible. This theory proposes that animals tend to consume prey that maximizes their net energy intake per unit of foraging time. Shore crabs (*Carcinus maenas*), for example, preferentially feed on intermediate-sized mussels, which provide the greatest energetic gains. While larger mussels provide more energy, they also require considerably more energy to open (Elner and Hughes 1978).

One assumption of optimal foraging theory is that natural selection will only favor behavior that maximizes energetic gains if increased energy is associated with increased reproductive success. For example, direct relationships have been found between net energy intake and reproductive success in captive zebra finches (*Taeniopygia guttata*; Lemon and Barth 1992).

Optimal foraging theory also assumes that foraging behavior is subject to natural selection. In the fruit fly (*Drosophila melanogaster*), variation in a gene called *forager* (*for*) underlies the foraging behavior of larvae. Larvae with the *for^R* ("Rover") allele travel nearly twice the distance while feeding as larvae with the *for^S* ("Sitter")

allele. Experimental studies confirmed that this locus is under selection by demonstrating that individuals maintained at low numbers foraged a shorter distance than those maintained at high numbers. In the low-density group, the *for^S* allele increased in frequency, while the *for^R* allele increased in the high-density group. At low population densities, short foraging trips yield sufficient food, while in high density groups, individuals may have to travel long distances as nearby resources become depleted (Sokolowski et al. 1997).

Optimal foraging theory also has limitations. Animals have needs besides energy acquisition that can conflict with foraging, such as watching for predators, searching for mates, and defending territories or nest sites (Milinski and Heller 1978). Another limitation is that individual differences in foraging success are often due to development, rather than natural selection (Wunderle 1991). Ontological differences in habitat or patch use may be due to dominant adults displacing juveniles, the inability of juveniles to adequately choose patches, diet differences, and/or changing nutritional needs throughout development.

Territoriality. Territoriality refers to the behavior that an individual displays to maintain exclusive rights to an area that contains a limited resource, such as food, nesting sites, or mates. Individuals must make decisions about whether to be territorial and what size territory to defend. Territorial displays and aggressive behaviors are costly because they require energy, can harm the individual, and may alert a predator to an individual's location.

Despite these potential costs, there are benefits to territoriality, including increased access to resources or protection from predators. Since territorial behavior requires time and energy, a territory must provide net benefits greater than those available to an individual that is using the space non-territorially (Brown 1974). For hummingbirds and songbirds, the benefits of territory defense depend upon the amount of nectar in flowers and the birds' ability to efficiently harvest it. If flowers are scarce or nectar levels low, the bird may not get enough energy to offset the cost of territoriality. Alternatively, if flowers are

abundant, then the bird may be able to meet its energy requirements without having to defend a flower patch. Therefore, territoriality is only advantageous at intermediate levels of flower availability and high levels of nectar production (Gill and Wolf 1975).

Territory size may be correlated with food availability, body size, and number of competitors. Territory sizes tend to be smaller when food is more plentiful or nutritious and are often positively correlated with body weight (Schoener 1968). More competitors are attracted to resource-rich areas, making them more costly to defend.

Reproductive Behavior. Reproductive success is determined by an individual's lifespan, mating success, and number of offspring produced per mating. Reproductive behavior is influenced by natural selection and involves searching for a nesting site, finding a mate, and rearing offspring. Reproductive strategies are sets of behaviors that have evolved to maximize reproductive success.

Many species exhibit mate choice, or an evaluation and selection of a potential mate or mates. Since each reproductive event is relatively inexpensive for males, they are able to maximize their fitness by mating with as many females as possible. In contrast, reproductive events are much costlier for females, as they are limited by the number of eggs that they can produce. Females, therefore, have an incentive to be selective in choosing the mate that can provide the best benefit to future offspring (Darwin 1871). Mate choice by both males and females may be found in species with parental care in which both parents contribute equally to the cost of rearing offspring. In some instances, males invest more in reproduction than females. For example, male Mormon crickets (*Anabrus simplex*) transfer a spermatophore to a female during mating that is nearly one-third of the male's body weight (Gwynne 1981).

Competition for mates is termed sexual selection and operates through variance in reproductive success. Selection usually acts more strongly on males because they experience greater variance in success than females (Trivers 1972). Sexual selection leads to the evolution of two types of male secondary characteristics. Intrasexual (male-male) selection influences traits involved in

fighting other males, while intersexual (male-female) selection influences traits important in attracting mates (Darwin 1871). For example, aggressive defense of females can lead to increased male strength and size. In many territorial species, males are considerably larger than females because the largest males have greater mating success. These physical differences between the sexes are called sexual dimorphisms.

Another example of sexual dimorphism includes the horns, antlers, and tusks of males, which may serve as weapons against predators or other males and/or indicators of strength, fighting ability, vigor, and quality. For example, male caribou (*Rangifer tarandus*) with smaller antlers tend to withdraw from sparring matches with caribou that have larger antlers (Barrette and Vandal 1990). In forked fungus beetles (*Bolitotherus cornutus*), males with the longest horns have increased access to females (Brown and Bartalon 1985).

Individuals may select mates based on a variety of criteria. In some species, mates with high fecundity or fertility are preferentially chosen. For example, male Mormon crickets prefer larger females because they carry more eggs than smaller females (Gwynne 1981). Mates may also be chosen based on ability to provide nuptial gifts, typically in the form of food (Vahed 1998). In the hangingfly (*Hylobittacus apicalis*), females tend to only accept males that provide insect prey above a certain size. Because mating occurs while the female is eating, presentation of a larger insect allows for longer copulations and increased likelihood of fertilization. The males who are able to capture larger prey may also be of higher quality (Thornhill 1976).

Mates may also be chosen based on parenting ability. Female threespine stickleback fish (*Gasterosteus aculeatus*) are more likely to lay eggs in nests that already contain eggs (Ridley and Rechten 1981). Having more eggs in the nest reduces the chance that any particular egg will be preyed upon and males who already have eggs in their nests expend more energy defending them than males who are engaging in courtship. In fifteen-spined stickleback (*Spinachia spinachia*), females are more likely to choose males that shake

their bodies frequently during courtship because this behavior is associated with increased fanning of fertilized eggs, which increases rates of successful hatching (Ostlund and Ahnesjö 1998).

Sexually selected traits should be correlated with aspects of fitness such as growth rate, predator avoidance, disease and parasite resistance, and competitive ability (Kodric-Brown and Brown 1984). For example, in zebra finches, carotenoids are associated with increased immune responses (McGraw and Ardia 2003). Females have been found to prefer experimentally carotenoid-enhanced males over controls. Female canaries (*Serinus canaria domestica*) select mates based on their singing ability, which is an honest signal of health (Suthers 1990).

Preference for a specific trait may develop and be maintained if it is correlated with male quality or made males easier to find. If the phenotype has a genetic basis, this advantage will be passed on to future sons and the genes that cause females to prefer the trait will also be favored. This positive feedback is termed runaway selection. A classic example of this is in widowbirds (*Euplectes prognus*; Andersson 1982), in which females select males with long tails. Mating success decreases for males with experimentally shortened tails and increases for those with elongated tails.

However, conspicuous male traits may represent a handicap if they reduce survival (Zahavi 1975). Strong, healthy individuals will produce larger ornaments because they can take on greater handicaps at a lower cost. Handicap size therefore serves as a reliable indicator of quality.

Mates may also be chosen based on access to resources. In green frogs (*Rana clamitans*), females choose males with territories in dense vegetation that is favorable for laying eggs (Wells 1977). In choosing a mate with high status, mating success may be increased because copulation is likely to occur without interruption by other males. In cockroaches (*Nauphoeta cinerea*), for example, dominant males mate more often than subordinates (Breed et al. 1980). Progeny may benefit from their father's status by receiving increased parental care and protection and/or inheriting traits that will enable them to achieve high status as well.

Species use various mating systems to maximize their fitness. In polygynous species, one male mates with multiple females, which increases the variance in male reproductive rates, resulting in heightened selection for increased size and strength (Alexander et al. 1979). Polygyny may be favored if males hold territories that have enough resources for multiple females or in precocious species, in which offspring require little parental care. Polygyny is more common than polyandry, in which females mate with multiple males. One example of polyandry is in spotted sandpipers (*Actitis macularius*), in which males incubate the eggs and care for young, while females mate with multiple males. Monogamy may be favored in altricial species, such as birds, that require two parents to care for young.

Some species of fish (including salmonids and sticklebacks) have two genetically distinct groups of males. One is large and defends territories to acquire mates, while the other, called jacks or sneaker males, is small and remains at the edge of large male territories rather than defending their own. When the territorial male is fertilizing eggs, the smaller jack will dart in and release his own sperm, thus fertilizing part of the clutch.

Parental Care. There is a trade-off between rate of population increase and parental care. R-selected species maximize r , which is the rate of population increase, and minimize parental care, while K-selected species maximize survival and reproduction only when population size is at or near K , which is the carrying capacity, and exhibit greater parental care. Parents typically care for young that face harsh environments, increased predation, and/or intense competition. Females are typically the primary care-giving sex because the costs of producing eggs exceed that of sperm (Trivers 1972). In mammals, females are also responsible for gestation and lactation, which are energetically expensive.

At some point, it becomes more profitable for parents to stop caring for their current offspring and instead devote energy to producing additional offspring, which often results in inter- and intrabrood conflicts (Trivers 1974). Since parental investment is fixed, nestlings may try to

manipulate parents and outcompete siblings to gain a greater investment. For example, in American robin (*Turdus migratorius*) nestlings, begging is positively associated with likelihood of being fed and nestlings respond to increased begging of a sibling by increasing the intensity of their own begging (Smith and Montgomerie 1991).

Social Behavior. There are both costs and benefits to living in groups. Living in groups may help individuals forage more efficiently than they would if they were on their own. Foraging groups may increase the rate at which patches of food are found because individuals learn what or where to eat by observing others. In Great tits (*Parus major*), foraging success is greater in flocks than when birds forage alone (Krebs et al. 1972). Foraging groups can also reduce variation in feeding rate (Baker et al. 1981) if individuals share information about the location of food patches (Krebs 1974). For example, naïve red-billed Quelea (*Quelea quelea*; DeGroot 1980) are able to find resources more often when in the presence of trained birds. Individuals in groups may be able to capture larger prey and have increased success when competing against other species for access to food resources.

Group living may also confer increased protection from predators. Individuals in groups may shelter themselves by placing other group members between themselves and a predator and increased group sizes will decrease the likelihood of any one individual being preyed upon. Group members may be able to detect predators more efficiently than solitary individuals. When individuals pay attention to other group members' behavior, the entire group is alerted if one individual detects a threat. Certain individuals or species (in interspecific groups) in a group may serve as lookouts. For example, in the Amazon, white-winged shrike-tanagers (*Lanio versicolor*) act as sentinels in canopy flocks, while bluish-slate antshrikes (*Thamnomanes schistogynus*) serve as sentinels in understory flocks (Munn 1986). These species are typically the first to alarm when predators approach, alerting other species of imminent threat. Group members may also cooperate to drive predators away. Nesting bluegill sunfish

(*Lepomis macrochirus*) work together to keep bullhead catfish from preying on their eggs (Gross and McMillan 1981).

There can also be drawbacks to living in a group. Group members may have to expend energy to maintain high status positions (Taborsky and Grantner 1998), experience reduced fitness (Hotker 2000), compete with each other for access to food (Scheel and Packer 1991), and be more vulnerable to infection (Alexander 1974). If groups get too large, individuals may become more vulnerable to predators. For example, wolves (*Canis lupis*) can capture caribou in large herds more easily than those in small herds, implying that individuals in large groups may not be able to detect approaching predators (Crisler 1956).

The optimal group size will vary among habitats and species and the group size that is optimal for one individual (a dominant one or an adult) may not be the same for another individual (a subordinate or a juvenile). Individuals should choose group sizes and habitats that maximize fitness (Fretwell 1972). The optimal group size is determined by comparing the fitness of the lowest-ranking group member to the fitness that the individual would have if they were solitary and in a poorer habitat.

Dispersal. Species may exhibit two types of dispersal. Natal dispersal refers to movement from the birth site to location of reproduction, and breeding dispersal is the movement of adults between breeding attempts. Dispersal is energetically costly and may expose the individual to predators. However, it can be beneficial for a variety of reasons. Innate dispersal refers to a genetic predisposition to disperse and is common in animals such as the spruce grouse (*Falcipennis canadensis*), in which the young disperse without receiving cues from their parents (Keppie and Towers 1992). Dispersal also has a genetic basis in fire ant (*Solenopsis*) queens, in which individuals carrying one genotype pursue new nesting sites, while individuals with the alternative genotype are more likely to return to their natal nesting place (DeHeer et al. 1999). Proximate causes for dispersal include responses to environmental factors, such as the absence of or competition for

suitable resources. Ultimate causes of dispersal include inbreeding avoidance and competition for mates or resources.

In birds and mammals, dispersal is sex-biased. Dispersal may be costly to female mammals because their reproductive success is limited by nutritional constraints, while males are limited by the number of females with whom they can successfully mate. Female mammals may benefit more from philopatry, remaining in or returning to their birthplace to breed, because they would be more familiar with resources, whereas males may benefit from increased dispersal because they would have greater access to mates. Female Belding's ground squirrels (*Uroditellus beldingi*) remain in close proximity to their birthplace because they need a territory in which to rear their young and their mothers are able to help them defend their territories (Holekamp 1984). Similarly, female lions (*Panthera leo*) remain near their birthplaces so they can benefit from access to familiar hunting grounds and safe places to rear offspring (Pusey and Packer 1987), while dispersing male lions are able to mate with non-relatives (Hanby and Bygott 1987). In birds, males may be more successful at establishing territories in their natal area, whereas females may benefit from the opportunity to disperse to choose different mates.

Cooperation. Cooperative behavior evolves to provide a benefit to another individual and increases the fitness of both the giver and the recipient. Rodents, mammalian carnivores, and birds with young that require a high degree of parental care may engage in cooperative breeding, in which non-breeding adults contribute physically, but not genetically, to rearing young. Helpers may increase offspring survival by providing additional protection from predators and more food. Helpers' fitness may increase if individuals are able to learn parenting behaviors or inherit a territory.

Cooperation may also be inter-specific. Aphids (*Aphidoidea*) secrete a liquid that ants (*Formicidae*) like to eat. In exchange, the ants protect aphids against predators and will sometimes raise their eggs and larvae inside their colony (Dawkins 1977). Some fishes, such as the

goby (*Gobiidae*), will feed on ectoparasites of other fish.

Communication. Communication describes an action of one organism that changes the behavior of another organism. Communication can increase fitness if a stimulus or signal provides an advantage to either the signaler or its group.

Information may be communicated using visual, chemical, tactile, and/or auditory cues. The type of communication used by an individual is dependent upon their life history characteristics and environment. Both nocturnal and diurnal species use auditory cues to communicate. However, nocturnal animals are more likely to use olfactory signals that can be detected in the dark, while diurnal animals rely more heavily upon visual cues.

Individuals communicate to attract mates, scare off predators, and locate food. For example, male Mallorcan midwife toad (*Alytes muletensis*) calls stimulate the reproductive physiology of females (Lea et al. 2001). To alert gravid females that they are ready to reproduce, male threespine stickleback fish engage in elaborate courtship rituals that entice females to deposit eggs in their nests. Honeybees will engage in waggle dances to direct colony members to the location of food (von Frisch 1967). Signals also help individuals conserve their energy. For example, roaring in male lions and erection of spines in stickleback are less energetically expensive behaviors than attacking invaders.

Conclusion

Behavioral ecology has a rich history of study dating back to Darwin's observations in the 1800s. Researchers focus on the purposes of behaviors and their adaptive advantages. Adaptive behaviors with a heritable basis increase individuals' reproductive success and are under positive natural selection. The field focuses on ultimate causes of animal behavior, such as whether they maximize fitness and how behaviors vary among species. Foraging efficiency, territoriality, mating strategies, parental care, and communication are all types of behaviors that influence survival and reproductive success across species.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Adaptations: Product of Evolution](#)
- [Competition for Resources Desired by Females](#)
- [Competition for Parental Investment](#)
- [Charles Darwin](#)
- [Differential Parental Investment](#)
- [Differential Reproductive Success](#)
- [Ecology](#)
- [Ecology of Paternal Investment](#)
- [Evolution of Adaptations](#)
- [Evolutionary Change](#)
- [Game Theory](#)
- [Heritability](#)
- [Kin Recognition](#)
- [Male Ornamentation](#)
- [Monogamy](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Parental Investment](#)
- [Parent-Offspring Conflict](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Prey Choice](#)
- [Reproductive Strategies](#)
- [Secondary Sexual Characteristics](#)
- [Sex Differences](#)
- [Sexual Selection](#)

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Field of Comparative Psychology, The

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Synonyms

[Animal behavior](#); [Integrative biology](#)

Definition

A multidisciplinary field that examines the similarities and differences in the behavior of organisms with special emphases on the development and evolution of the behaviors.

Introduction

Modern comparative psychology, one of the interdisciplinary fields in psychology, developed from the convergence of a number of separate disciplines including ethology, behavioral ecology, psychology, systematics, and genetics (Gariépy 1998). Examining questions of functional adaptiveness, development, and evolution of behavior, comparative psychology incorporates all aspects of a living being: anatomy and physiology, genetics, affect, cognition, and sociality. This diverse field explores questions of behavior, behavioral development, cognition, communication, emotion, learning, mating, memory, motivation, perception, social relationships, spatial navigation and orientation, parental behavior, and many other specific topics. Comparative psychology incorporates a specific method of investigation in which multiple species are compared systematically to address various questions about evolution and shared phylogeny.

History

References in which the history of comparative psychology is described generally point to the publication of Charles Darwin's (1809–1882) two most influential books, *On the Origin of Species* (1859) and *The Expression of the Emotions in Man and Animals* (1872), as the pivotal moments in which animal behavior was brought into mainstream science (e.g., Greenburg and Haraway 1998; Siiter 1999; Slater 1999). Focused on the importance of the similarities in physical, behavioral, and emotional attributes of individuals of common descent, Darwin's ideas impacted the fields of biology and psychology.

This fledgling field of animal behavior was expanded by George John Romanes (1848–1894), a British naturalist and staunch admirer of Charles Darwin and his ideas. Romanes applied Darwin's idea of evolution and its mechanism of natural selection to mental processes, including higher-order thinking (e.g., planning, comparing, and contrasting), proposing that intelligence ranged in complexity from the least complex

animals to the most complex animals (i.e., humans) (Gariépy 1998; McInnis 1998; Siiter 1999). This gradient approach to the spectrum of mental abilities across species influenced the fields of learning, comparative cognition, and developmental psychology. A proponent of the anecdotal method, Romanes developed his hypotheses from individual pieces of evidence obtained from firsthand experiences, secondhand stories, or descriptions of interesting and clever behavior across many species of animals. Unfortunately, this data collection method is subject to inherent biases as humans often attribute human characteristics to animals (i.e., anthropomorphism), endowing animals with characteristics that may be more than necessary.

C. Lloyd Morgan (1852–1936), a British psychologist, close friend, and critic of Romanes, emphasized the importance of objectivity and empiricism when interpreting animal behavior. While agreeing with the possibility that mental processes also evolved, Morgan reminded early and future comparative psychologists to avoid explaining behavior using higher mental processes when lower-level psychological processes could account for the behavior (Gariépy 1998; Greenberg and Haraway 2002; McInnis 1998; Siiter 1999). This rule is known as Morgan's Canon as Morgan was the first to apply this idea of parsimony to animal behavior (Siiter 1999).

Following this early venture into comparative psychology and the importance of comparing different animal species using objective, empirical methods, the psychology-based field of behaviorism advanced comparative psychology. Focused on uncovering the general principles of learning and motivation, behaviorists such as Ivan Pavlov (1849–1936), Edward Thorndike (1874–1949), and John B. Watson (1878–1958) continued to utilize characteristics of comparative psychology by emphasizing the specific mechanisms and the development of behavior (Greenberg and Haraway 2002; Siiter 1999). Although the era of behaviorism examined learning and motivation in several species (e.g., rats, *Rattus norvegicus*; dogs, *Canis lupus familiaris*; cats, *Felis catus*), the behaviorists were heavily criticized for their lack of diversity in topics and species (reviewed by Gariépy 1998; Greenberg and Haraway 2002).

While comparative psychology was growing in America, the field of ethology was emerging from biology, led by Konrad Lorenz (1903–1989), Nikolaas “Niko” Tinbergen (1907–1988), and Karl von Frisch (1886–1982), among others. Emphasizing the importance of instinct or innate behaviors, biological explanations, and naturalistic field studies, ethologists focused on the adaptiveness of particular behaviors and the evolution of those behaviors (Greenberg and Haraway 2002; Siiter 1999).

Key Concepts

Anthropomorphism Anthropomorphism is the attribution of human qualities to nonhuman animals. Early studies in comparative literature relied heavily on anecdotal evidence of humanlike behavior in animals. Scholars such as Romanes and Buchner focused on three main areas: complex reasoning, social behavior, and social emotions (such as sympathy, shame, jealousy, and humor). Lloyd Morgan's Canon (1894) emphasized parsimony, urging scientists to limit their conclusions to the psychologically simplest process consistent with the data. With Morgan's Canon, anthropomorphic explanations were viewed with more skepticism but still held a place in the field. It was during the 1920s, with the rise of behaviorism and the biological perspectives of ethology, that anthropomorphism started to be viewed as unscientific and even a fallacy of reasoning. Animal behavior research and ethology focused on objectivity and qualitative data. Research on animal emotions, especially social emotions, and complex reasoning was rejected as inherently flawed by anthropomorphic assumptions. Curiously, zoomorphism, the application of animal motivations to explain human behavior, held some popularity from the 1960s to the 1970s.

As behaviorism receded in psychology, comparative research on cognition, problem-solving, and emotions in animals resumed. While anthropomorphism is still widely considered by many to be invalid scientific reasoning, a minority perspective on the values of anthropomorphism is

gaining strength. As a well-regarded primatologist, Frans de Waal, PhD writes in his 1997 article, *Are We in Anthropodenial?*, “As soon as we admit that animals are far more like our relatives than like machines, then anthropodenial becomes impossible and anthropomorphism becomes inevitable – and scientifically acceptable” (de Waal 1997). However, not all anthropomorphism is useful, as also noted by de Waal. Through hours of observation, a primatologist knows that a seemingly grinning chimpanzee may be aggressive, just as many pet dog owners can differentiate a snarl from human smiling. “A careful observer may thus arrive at an informed anthropomorphism that is at odds with extrapolations from human behavior.”

Anthropocentrism Anthropocentrism is the tendency to interpret the behaviors, emotions, or cognition of other animals using humans as a reference point. Anthropocentric, meaning human centered, perspectives take on four major forms in comparative psychology. First, studies can directly compare animal cognition, emotion, and behavior to humans. Often humanlike outcomes are considered the standard for success. Traditional anthropocentric ideas used the phylogenetic scale to legitimize their perspective. The phylogenetic scale, or *scala naturae*, is the notion of a linear ladder of evolution from low-level worms, fish, and reptiles to more complex birds, mammals, and primates. Humans were viewed as the pinnacle of evolution. While terminologies like “higher” and “lower” animals remain, modern conceptualizations of phylogeny see evolution along distinct branches, rather than a linear progression.

Second, researchers can latently interpret behavior as more sophisticated or desirable, when it is merely more humanlike. Ecological and adaptation approaches offer alternatives to these aspects of anthropocentrism. For example, early research on memory examined if animals formed abstract categories, similar to humans. Ecological approaches ask different questions, examining how animals use their memory for tasks such as foraging, traveling long distances, or managing complex social hierarchies.

Third, research designs and research questions can neglect to consider the different sensory experience of animals. Jakob von Uexküll (1957) proposed the idea of “*umwelt*,” taken from the German word for “environment” or “surrounding world,” to remind researchers to consider the “subjective experiences” of all species and individuals within a species even when they are living in the same environment. When the sensory abilities and perceptions of species other than humans are ignored, the behavioral and social repertoires remain incomplete. For example, many insects perceive ultraviolet waves that emanate from potential food sources or from conspecifics. These abilities were untapped initially because researchers limited their measures to the human visual perception range, forgetting that some species have extrasensory abilities. Infrasonic communication between elephants over long distances (Payne et al. 1986) and ultrasonic communication for some dolphins and whales (e.g., Samarra et al. 2010) were only discovered once equipment with the appropriate measuring range was utilized.

Finally, research in comparative psychology can be considered anthropocentric if its expressed goal is to further the understanding of human psychology. Advocates of comparative psychology suggest that animals should be studied for their own sake rather than to advance the understanding of humans.

Ethology and Tinbergen’s Four

Questions The Dutch ethologist and zoologist Nikolaas Tinbergen was one of the most influential figures in the ethological branch of comparative psychology. He believed that an organism’s behavior can be assessed through complementary perspectives expressed as four questions that he proposed to guide ethological research, two assessing the *ultimate* causes of behavior (e.g., What is the evolutionary function of this behavior?) and two assessing *proximate* causes of behavior (e.g., What environment or motivation triggers this behavior?) (Tinbergen 1963).

Questions about ultimate causes of behavior center around the evolution across phylogenetic backgrounds and the adaptive function of a behavior. A researcher who is interested in the

phylogeny of a targeted behavior may direct the attention toward the understanding of the patterns of that behavior and may be interested in conducting a cross-species comparison to determine whether the behavior of interest is shared and among which animal species it is shared. A researcher who is interested in the *adaptive function* of a targeted behavior may want to examine how a targeted behavior is adopted by the animal to efficiently use its external environment, to establish social relationships with its conspecifics, and to successfully reproduce. Phylogeny and adaptive function are the two levels that constituted Tinbergen's theory of *ultimate* causes of behavior.

Questions about proximate causes encompass biological *causal mechanisms* and the development of a specific behavior (*ontogeny*) (Bateson 2014; Papini 2010). Answers to questions that address phylogeny and adaptation of behaviors do not provide information about the emergence of behavioral skills that are necessary to perform a specific behavior. A researcher who is interested in the *mechanism* that regulates a behavior may investigate the integration of sensory and motor information, the various functions of the brain and the influence of those functions on behavior, and the external factors that determine the occurrence of a behavior. A researcher who is interested in the *development* of a particular behavior may explore the influence of age, experience, presence of social partners, type of interaction, observational learning, and other factors that could contribute to changes over time of the behavior under study.

Phylogeny Versus Ecology To the extent that comparative psychology is facilitated by the comparison of psycho-behavioral phenomena across species, the issue of choosing a comparison species or comparable behaviors remains central dilemmas. Traditional comparative psychology seeks to determine how the mechanisms that guide behavior evolved and how it is distributed across the animal kingdom, Tinbergen's question of *phylogeny*. In studying behavior across related species, researchers aim to reconstruct the origin of the behavioral mechanisms and perceptual responses in evolutionary history. Behaviors are

considered homologous if they share a similar origin or a common ancestry.

The social ethology (sometimes called socio-ecology) perspective shifts the focus from historical ancestry to the modern ecology of species. Social ethologists see shared environmental pressures as more important to understanding behavior and social structure than evolutionary history. Comparisons based on phylogeny as well as shared ecology are prevalent in modern comparative psychology.

Evolutionary-Developmental Framework:

Nature Versus Nurture Comparative psychology searches for the genesis of behavior, evolutionarily as well as through the developmental lifespan of individuals. Particular emphasis has been placed on early development in an effort to discern innate from learned behavior. Scholars of instincts focus on innate behavioral responses present at infancy, such as imprinting in birds. Ethologists emphasized the role of "nature," meaning innate instinctual responses. Behaviorists focused on "nurture," studying infancy and early development as a "blank slate" for learning. During this time, the diversity of species studied by comparative psychologists diminished in favor of a model species approach. Learning was theorized as a universal process following general rules that was relatively invariant across species.

Modern comparative psychologists study both the innate and learned influences of behavior, as well as the complex interplay between the two influences. Comparative psychology studies an ever-increasing number of diverse species and behaviors. Rather than focusing on classifying a behavior dichotomously as innate or learned, comparative psychologists use the onset of a behavior during the developmental process to explain behavioral patterns.

Methodology

Comparative Approach Sharing its name with the discipline, this approach incorporates the comparison of behavior and traits between individuals

that share a common ancestry or traits that emerged due to convergent evolution (Hailman 1998). A current example is represented by the work of Elisabetta Palagi and colleagues on the presence and nature of play across a number of mammals (Palagi et al. 2015). Their work has indicated that, in primates, egalitarian species display more social play and tolerance along with a greater use of play signals often expressed in facial expressions (e.g., Ciani et al. 2012; Scopa and Palagi 2016). The comparative approach is also used to examine the behavior and traits of extant species to make generalizations about extinct species (Hailman 1998). Using fossils and contextual clues, paleontologists can draw inferences about prey-predator relationships, physical movement, parental care, foraging habits, or degree of sociality of extinct species. When combined with behavioral and physiological information from currently living descendants, scientists can model various processes by which a particular lineage evolved. The comparative approach addresses questions regarding the relationship between genetics and environment, the pressures that led to changes in ancestral species to the current descendants, and evolved differences in sociality and adaptability to different environments. Comparing across species was the primary method used during the infancy of comparative psychology. However, when the behaviorist approach gained momentum, the comparative method was reduced to a narrow set of species that were easily managed and experimentally manipulated in laboratories (Gariépy 1998). The emergence of ethology encouraged scientists to resurrect the comparative method using more naturalistic contexts and methods (Gariépy 1998).

Experimental Approach One of psychology's traditions is to conduct experimental-based research in which an independent variable is manipulated under controlled circumstances to assess the resulting effects on a dependent variable. While this method allows for causal conclusions, it also limits the generalizability of the findings due to the artificial setting created during experimental conditions. The experimental

approach was especially popular during the height of the behaviorists when most of our current knowledge of motivation, classical conditioning, operant conditioning, memory, and other learning phenomena was derived from laboratory-based experiments using a narrow range of species, such as albino rats (*Rattus* sp.; e.g., Watson, Thorndike), zebrafish (*Danio rerio*; e.g., Bitterman), and pigeons (*Columba* sp.; e.g., Skinner, Wasserman). Considered a major limitation by more traditional comparative psychologists and ethologists, the experimental approach was criticized for its narrow scope and limited ability to approximate naturalistic conditions especially with semi-domesticated or laboratory-bred species (reviewed by Beach 1960; Gariépy 1998; Haraway and Maples 1998). Despite these limitations, experimental studies were and remain critical in understanding the causal mechanisms of behavior. For example, research conducted on the mating preferences of male and female lizards has tested experimentally a number of mechanism and phylogenetic hypotheses by experimentally manipulating different physical attributes for males and females and testing mate preference (e.g., Keren-Rotem et al. 2016; Sacchi et al. 2015; Swierk et al. 2013). These tests have been conducted both in the field and in the laboratory with wild-caught and bred lizards using both natural variation in live animals and experimentally manipulated models.

Ethological Approach In response to the artificial contexts of experimental research, ethologists emphasized the importance of examining behavior within naturalistic settings, arguing that the laboratory setting constrained the production of natural behavior (reviewed by Gariépy 1998; Haraway and Maples 1998). Focused on questions about the function, the development, and the evolution of a given trait or behavior, ethologists approached these questions using closely related species in their natural habitats (Gariépy 1998; Haraway and Maples 1998). Early ethologists primarily used observational techniques to study animals in their natural habitat. Looking for similarities between individuals of a species, ethologists mapped species-typical behavior

using very detailed observation notes and behavioral checklists called ethograms in completely uncontrolled environments. Jane Goodall's work with the chimpanzees of Gombe (Goodall and Pusey 2016) and Dian Fossey's work with the mountain gorillas of Africa (Fossey 1970) are prime examples of the importance of conducting observational research over long periods of time. A consistent presence in the field allowed the animals to acclimate to their presence and provided both researchers with opportunities to experience and observe behaviors that were unparalleled in laboratory or zoological settings (e.g., holding infants, alliance formation, homosexual behavior). Contemporary ethologists incorporate both observational (paper and electronic behavioral ethograms) and experimental techniques (e.g., playbacks, model simulations, cross-fostering) into studies today to investigate traditional topics of species-typical behavior like courtship, parenting, foraging, and locomotion as well as more psychologically oriented topics, such as empathy, problem-solving, memory, play, and cooperation (e.g., de Waal 2008; Osvath et al. 2014; Plotnik and de Waal 2014).

Extensions of comparative psychology and ethology included E.O. Wilson's (1929–current) sociobiology, which emphasized the biological basis and evolution of social behavior and ultimately developed into behavioral ecology (e.g., Krebs and Davies 1978) and evolutionary psychology (e.g., Cosmides and Tooby 1987). Behavioral ecology is the scientific study of behaviors that evolved due to ecological pressures (Krebs and Davies 1978) while evolutionary psychology focuses on the adaptiveness of psychological and mental processes displayed by humans and our ancestors as influenced by evolution (e.g., Cosmides and Tooby 1987).

Today, all of these disciplines are actively investigating a diverse set of questions with each discipline focused on a particular aspect of behavior, whether it is problem-solving, cooperation, migration, foraging habits, learning, parenting, aggression, communication, sociality, or mating. Comparative psychology exists in many forms, including behavioral neuroscience, animal science, zoology, behavioral ecology, and ethology

to name a few. Each field emphasizes different methodologies including laboratory-based experiments, field-based observations, and naturalistic-based experiments. Some fields focus on specific animal models, while others incorporate more diverse species that systematically vary across phylogenetic background. And, within each field, researchers may focus on proximate questions of ontogeny and mechanism or on ultimate questions of phylogenetic evolution and functional adaptation.

Conclusion: The Future of Comparative Psychology

As discussed here, a clear definition of comparative psychology has been challenging to determine, partly due to the fact that this branch of psychology is one of the oldest fields within the study of psychology (Papini 2010). Since the controversies of the mid 1900s between psychologists and biologists interested in the study of animal behaviors, Tinbergen's approach (1963) has been the most closely related method used to conduct comparative research. Questions that address how the causes of specific behaviors relate to the phylogeny and adaptive significance of behavior, whereas questions that address how individuals come to adopt different behaviors dependent upon the situation relate to the mechanism and the development of behavior (Tinbergen 1963). Comparative psychology is the discipline which integrates these aspects of behaviors and examines the related questions utilizing the knowledge of psychological theories and the understanding of behavioral neuroscience, developmental biology, behavioral ecology, and evolutionary principles (Papini 2010). The interdisciplinary nature and integrative perspective that distinguish this branch of psychology may be the fundamental reason for recent concerns about the future of comparative psychology as addressed by Abramson (2015). The majority of undergraduate psychology programs in the United States do not include comparative psychology in their academic core classes, and very few of these programs offer

an academic course identified as *comparative psychology* (Abramson 2015). Within the field of psychology, the comparative method has been adopted by the majority of the subfields, such as developmental psychology, cognition, social psychology, and psychology of learning. For both human and nonhuman animal studies, comparative psychology is utilized to compare behaviors across various stages of development, to investigate interspecies differences and commonalities in cognitive abilities, to examine the influence of culture and social environment on an individual's behaviors, to study behavioral variations dependent upon different life experience. This research approach has extended to various biological sciences, including developmental biology, comparative physiology, comparative anatomy, neuroscience, comparative neurobiology, and animal science, which use the comparative method to approach their questions. Despite the concerns exposed by Abramson (2015), the majority of comparative psychologists, who responded to Abramson's commentary, agreed that comparative psychology, today, must be seen as a perspective rather than a discipline on its own (Chiandetti and Gerbino 2015; McMillan and Sturdy 2015; Osvath and Persson 2015; Vasconcelos and Pandeirada 2015). It is an interdisciplinary approach that teaches critical thinking skills through cross-discipline training. It is the bridge that brings biological and social sciences together with the goal of providing a more complete knowledge of principles that govern behaviors and developing novel ideas that advance apparently distant research fields.

Cross-References

- Corvids
- David Wasserman
- Development
- Field of Behavioral Ecology, The
- Primates
- Play and Social Learning
- Social Development in Nonhuman Primates

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Suggestions for Additional Reading

- Comparative Psychology: Evolution and Development of Behavior, 2nd Edition. By Mauricio R. Papini.
- Comparative Psychology: A Handbook. By Gary Greenberg, Maury M. Haraway.
- Cognition, Evolution, and Behavior. By Sara J. Shettleworth.

Field of Linguistics, The

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Synonyms

None.

Definition

The scientific study of human language(s) and/or the human language faculty.

Introduction

“Asking a linguist how many languages they speak is like asking a biologist how many pets they have.”
–Unknown

Comparing biologists with linguists illustrates one of the more common misunderstandings about linguistics: although language is the *object* of study in linguistics (like living things are the object of study in biology), the relationship between linguists and language is most often one of observation rather than ownership or fluency. Using a language and being able to describe how a language works are two very different things: for example, if you're reading this, you are presumably fluent in English. But, unless you've studied linguistics before, it's unlikely that you can say whether the 'p' at the end of the word *stop* is aspirated or not. (For interested readers, in the case of the word *stop*, the p is not aspirated; say

pin and *stop* with your hand directly in front of your mouth. When you say *pin*, there will be a puff of air – this is aspiration, which is absent in *stop*.)

This highlights another major misconception about linguists and linguistics: the vast majority of linguists are concerned with observation and description, not with policing and correction. Linguists want to know why languages work the way they do, revealing why language in general works how it does, and illuminating new facts about the human mind in the process. Grammatical ‘errors’ (like stranding a preposition at the end of a sentence) are the sorts of phenomena that linguists are especially fond of. The types of errors we make in speaking or writing can be revelatory about how we process language in the brain (Harley 2013) and can even indicate shifts in the way a particular language works. Speakers of Middle English would find our Modern English “ungrammatical” to say the least – it might even be incomprehensible in some cases. However, this doesn’t mean modern English is *wrong*, only that it has changed over time (and space, e.g., British vs. American English). As a culturally transmitted phenomenon, languages are constantly changing and evolving at a rapid rate.

The main focus of this entry will be *descriptive linguistics*, wherein linguists are concerned with understanding and describing how language *is*, a feat traditionally accomplished by field work, wherein linguists make a specific effort to document a language *in situ* in the culture where it is spoken. This can be contrasted with *prescriptive linguistics*, which proscribes how particular parts of a specific language *should* be. Having prescriptive rules in a language is necessary particularly for teaching and writing contexts, and very often, descriptive work on a particular language will eventually inform prescriptive rules that are taught to learners or writers.

However, the vast majority of linguists engage in descriptive work of some kind, and it is particularly this type of work that is usually more revelatory about human evolution and evolutionary psychology. If linguists approach the study of language with a prescriptive slant, they risk overlooking important and potentially revealing phenomena. This means that while we consider a

language to be a cohesive unit, at least conceptually, linguists not only acknowledge but are particularly interested in linguistic *variation* both within and across speakers.

This entry will start with an operational definition of what language *is*. Although humans use it almost constantly – and there is a sense that language is somehow different from other animal communication systems – there is a specific set of features which set language apart. After defining the object of study in more detail, the entry will delve into a more technical breakdown of how linguistics is studied.

Like other sciences such as biology, psychology, and physics, linguistics is fundamentally diverse and includes several subfields which illuminate different aspects of human language and cognition. After an introduction to the different facets of linguistics, the entry will conclude with a brief overview of the major ongoing debates and divisions in the field, many of which mirror larger issues being grappled with in other areas of cognitive and social science. Understanding these broad divisions the field is crucial to understanding how it interleaves and interacts with evolutionary psychology and cognitive science more generally.

What Is Language?

Human language is a complex phenomenon, a fact often lost given how easily children learn languages, and how effortlessly we use language day to day both for communication and thought. Although the question “what is language?” may seem at first glance to be a trivial one (it’s what you’re reading right now, it’s what we speak every day, etc.), a formal definition of language is more difficult than it seems. There are currently estimated to be between six and seven thousand different languages spoken on the planet, and they exhibit considerable variation (Dryer and Haspelmath 2011). In many respects, there is still debate about what language is, what language isn’t, and what it is for. This section will give an overview of a well-accepted operational definition of language and provide more detail about how language is organized and studied.

Design Features of Language

In 1960, the linguist Charles Hockett identified 13 design features of language. Originally, the first feature was that languages occur in the vocal-auditory channel; at the time, there was a paltry understanding of the richness of sign languages which use a gestural-visual channel, as well as little acknowledgment of the role of the gestural channel even in spoken languages (McNeill 2000; Tomasello 2009). Given this updated understanding, this feature is now often omitted. To be concise, this entry will generally refer to speech and hearing, but unless otherwise noted, anything that applies to a speech signal being sent/uttered or heard/received in a spoken language context also applies to a linguistic gesture being signed/uttered or seen/received in a sign language context. The remaining 12 features identified by Hockett (1960) have stood the test of time and provide a useful operational definition of language by delineating what language is (and is not) in terms of what it can do and how it does it.

Language has (i) *broadcast transmission with directional reception*, meaning that while a speech signal can be heard by anyone within auditory range, the speaker (i.e., the direction from which the utterance came) is readily identifiable. Language is also (ii) *rapid fading*, meaning that speech sounds can only be perceived as they are made and are by definition impermanent (a feature shared by many other animal communication systems).

Writing systems naturally change this dynamic by providing a visual analogue of spoken language which lasts much longer, potentially thousands of years. However, particularly in an evolutionary context, writing systems tend not to be a central focus, since they are young relative to spoken language. While the oldest writing systems are estimated to be perhaps 5–6,000 years old, human language itself is much older, with estimates ranging from at least 100,000 years old to millions of years. Nonetheless, written language interacts with spoken language where there is a written form (this will be further discussed in detail in the “[Tools and Methodologies](#)” section).

Language is also fundamentally (iii) *interchangeable* – that is, speakers and hearers can uniformly use the language in the same way.

This is a property not shared by many animal communication systems, which may exhibit cross-species communication where sender and receiver cannot articulate the same signals, or where conspecifics exhibit marked sex differences (e.g., in many bird species, males have complex songs, while females do not). Another feature of language is (iv) *feedback*, that is, a speaker can hear themselves and control and modify their own signal as they produce it. Linguistic signals are also (v) *intentional*, that is, they are intended consciously by the speaker to be communicative, unlike, for example, how a limp in a prey animal would unintentionally communicate weakness to a predator.

Language is simultaneously (vi) *semantic* and (vii) *arbitrary*. Language conveys specific meaning or *semanticity*, but the form of a linguistic signal has an arbitrary relationship with its meaning. In other words, while English speakers share a convention that the word *rose* represents a specific type of flower, there is nothing about the sounds in the word *rose* that point to that meaning beyond this shared convention – in other words, a rose, by any other name, would still smell as sweet. Although some words in language are non-arbitrary – for example, in an onomatopoeic word like *hiss* the sound of the word is similar to and representative of the sound a snake makes – the vast majority of linguistic symbols are arbitrary.

Language also exhibits (viii) *discreteness* and (ix) *duality of patterning* – language is discrete in that it is made up of distinct units which combine and recombine in rule governed ways. Duality of patterning means that these discrete units occur at two levels: individual sounds – which are themselves meaningless – form together to make meaningful units, which can in turn combine again to make meaningful utterances.

These properties contribute to another feature, (x) *productivity*. Productivity refers to the fact that the rule-governed recombination of meaningless and meaningful units gives rise to the ability for speakers to create and interpret novel utterances (this feature is sometimes also known as *generativity*). Duality of patterning – and thus, the level of productivity present in human language – is arguably unique to human language and has not been definitively shown in any other

animal communication system. However, relatively little is known about dolphin communication, and the possibility remains that it (or other understudied animal communication systems) exhibits one or both of these features to some extent.

Language also enables *displacement*, or the ability to talk about and refer to things that are not necessarily present, concrete, or even true. While other animal communication systems might have both arbitrariness and semanticity (e.g., macaque warning calls to signal the presence of different predators), which should in theory allow for displacement, in practice, this type of displaced reference is thought to be unique to human language. Although instances of deception have been documented in other primates, these are relatively rare (Whiten and Byrne 1900). Using language, we can talk about language itself (a property known as (xi) *reflexiveness*), and unlike many other forms of animal communication, language is not constrained to honesty: although one could easily exaggerate their personal athleticism using words, the signal an animal would use to display physical fitness is often the physical fitness itself, and so exaggeration is virtually impossible (see Zahavi and Zahavi 1990).

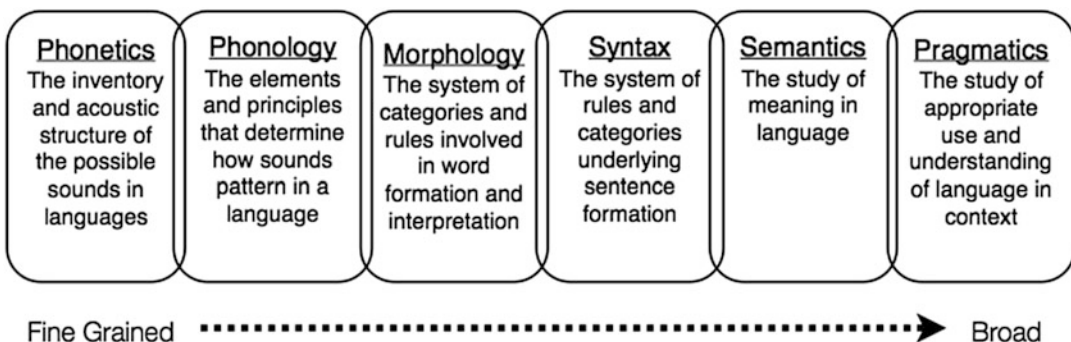
Finally, language is crucially (xii) *learnable* and (xiii) *culturally transmitted*. In order to persist over generations, language has to be both learnable and usable – for example, although binary code can be used to convey complex messages, and the use of only two minimal units

(1 and 0) is arguably highly efficient, children would have a very difficult time learning a rich expressive system in binary, and so language structure takes a very different form. It is also crucial that language learners acquire their language from other speakers, and other learners will in turn acquire from their production. Many researchers argue that many of the properties we observe in language are the result of biases in learners which are amplified by cultural transmission (Chater and Christiansen 2008).

Given these design features, it is generally accepted that no other known natural communication system can do what language does. While many animal communication systems may share some features with human language, no known system combines all of these features in the way that human language does.

Levels of Language

The current understanding of language generally divides its structure into six interacting areas (1): *phonetics*, *phonology*, *morphology*, *syntax*, *semantics*, and *pragmatics*. This section will aim to give a very brief overview of these areas and how they interact with one another. Starting with phonetics and moving up through semantics and pragmatics, these areas become increasingly broad: phonetics focuses on the fine-grained acoustics of language, while pragmatics focuses on whole linguistic interactions, including not just speech sounds, but inference, implication, and common ground (Fig. 1).



Field of Linguistics, The, Fig. 1 The levels of language, forming interacting areas of linguistic study. Areas become more broad from left to right: with phonetics involving

acoustic description well below the word level and pragmatics encompassing entire interactions (Definitions adapted from O’Grady et al. 1996)

Phonetics and Phonology

Phonetics and phonology both involve the sounds of language, but the distinction between the two areas is important. While phonetics studies speech sounds that humans can produce in language generally, phonology deals with the rule-governed, patterned organization of speech sounds in a particular language. Phonetics deals with the acoustic properties of human speech, while phonology deals with sound patterns in specific languages. As an illustration, while aspiration is a phonetic property which occurs in many languages, the phonology of aspiration is different in different languages (e.g., in English, *p* is aspirated depending on where it is in a word, whereas in Thai, *p* is aspirated depending on what the word means).

A description of a language's phonology will include an inventory of its *phonemes*, defined as the sounds in a language that are contrastive with respect to meaning. Although sign languages have no acoustic component, they do have what are considered to be phonologies, only the "phonemes" are visual features such as hand shape, position, and facial expression (Brentari 2011). Although the human vocal tract can make hundreds of distinctive sounds (and human hands can make hundreds of distinct gestures), individual languages use these available units as phonemes to varying extents – the language with the most phonemes is !Xũ (spoken in southern Africa, with 141 phonemes), while the language with the least is Rotokas (spoken in Papua New Guinea, with only 11 phonemes; Crystal 2010).

A language can make use of a particular sound, or *phone*, without it necessarily being classed as a phoneme. To return to the aspirated version, while both *p* and *p^h* occur in both English and Thai, these are only two separate phonemes in Thai, where the presence or absence of aspiration can change the meaning. On the other hand, one could aspirate the *p* in the English word *stop*, and it might sound strange or emphasized, but it wouldn't be a different word. This means that in English, *p* and *p^h* are *allophones*, defined as variants of a phoneme which change slightly depending on context.

In order to describe phonology with maximum accuracy, linguists employ the International

Phonetic Alphabet (IPA), which uses hundreds of symbols to describe the sounds found across human languages. This tool is crucial for an accurate description of a language's phonology – for example, the Roman alphabet has only 26 letters, but English itself has about 44 phonemes (slightly more or less depending on the variety of English being described). Beyond this, the IPA allows researchers to describe and compare the phonologies of disparate languages in a systematic way, such that direct comparisons can be made between genetically distant languages with different writing systems like English and Thai.

What sounds are relevant in a language is equally as important as how those sounds combine. The rules that govern sound combinations in a language are known as *phonotactics*. While a language might include, for example, 30 phonemes, these sounds are not generally combined in unrestricted ways. For example, while the sound *-ng* (the sound at the end of the word *interesting*, represented in the IPA as ŋ) occurs frequently in English, it never occurs at the beginnings of words. This may seem like a physical constraint to a native English speaker (i.e., they have difficulty pronouncing ŋ without a vowel before it), but this sound does occur word-initially in many of the world's languages, so this is simply a phonotactic quirk of English.

Morphology

While in phonology phonemes provide *contrasts* in meaning, by definition they do not *encode* meaning. That is, although *pat* and *bat* mean different things, and differ only in the sounds *p* and *b*, the sounds in and of themselves mean nothing. This changes at the level of *morphology*, where a *morpheme* is defined as the smallest unit of meaning in language. Phonology and morphology interact considerably: first, morphemes are necessarily governed by a language's phonological and phonotactic rules. Second, phonemes are the minimal units which comprise language and recombine to form the minimal *meaningful* units represented by morphemes – this property is often known as *combinatoriality*, which forms one of the two parts of the crucial duality of patterning identified by Hockett (1960).

Morphemes are often entire words, like *pat* and *bat*, known as *free morphemes*. Morphemes can also be bound, meaning that they contain semantic information, but only occur bound to other morphemes. For example, the morpheme *un-* contains meaning in that it can negate an adjective (e.g., *unbearable*, *uninviting*), but it cannot stand on its own as a word-unit – it must be attached to what is known as a *root* (in the previous example, *bearable* and *inviting*) via *affixation*.

Bound morphemes also come in two general types: *inflectional* and *derivational*. Inflectional morphemes alter meaning (un-like) but cannot change the category of a word (i.e., *bearable* and *unbearable* are both adjectives). Derivational morphemes, on the other hand, do alter category – for example, the bound morpheme *-able* transforms the verb *bear* into the adjective *bearable*, and can be similarly productively applied to make adjectival forms of other verbs (e.g., *share* → *shareable*).

While these examples all come from English for ease of understanding, these morphemic categories can be used to describe any language, although different languages use different morphological processes to different degrees. Languages can be classified according to their predominant morphological strategies along two main continua: the synthetic-analytic continuum and the fusional-agglutinative continuum. In *analytic* languages, most words are a single morpheme (i.e., bound morphemes are rare, and words tend to be uninflected). On the other hand, highly *synthetic* languages have single words which may contain many morphemes. Among languages with some degree of synthesis, inflection can be either predominantly *fusional* or *agglutinative*. In fusional languages, bound morphemes are indistinguishable from the roots to which they attach and may involve subtle changes in stress or tone. In agglutinative languages, bound morphemes are well delineated and readily identifiable and are generally attached to roots via affixation.

Syntax

Morphology interfaces to a large extent with *syntax*, roughly defined as the rules governing word

order in language. This interface is comprehensive enough that some research focuses specifically on the intersection between morphology and syntax, known as *morphosyntax*. The morphological properties exhibited by a language often give hints as to some syntactic properties of the language. For example, languages which are highly synthetic are more likely to have some flexibility in syntactic rules. Since in a synthetic language properties of a word's component parts provide grammatical information, word order is often varied or may be used to convey nongrammatical information. For example, in Italian, verb affixation encodes the subject (e.g., *io cammino* [I walk] vs. *tu cammini* [you walk]), such that speakers can simply say *cammino* and drop the subject all together, or invert the order (*cammino io*) to emphasize the subject. In English, on the other hand, subject drop is impossible. Without the subject pronoun, substantial semantic information is lost – the obligatory subject inclusion and fixed subject-verb order has too heavy of a functional load to be optional.

Beyond its interaction with morphology, syntax is a large independent field within linguistics. Although the roots of linguistics generally grow out of anthropology, the field underwent a formative shift in the late 1950s. This shift was spearheaded by the publication of Noam Chomsky's book *Syntactic Structures* (1957, 2002), which drew more heavily on mathematical formalisms than traditional descriptive field work. Chomsky's work focused on creating a *generative grammar* of a language given some minimal sample of it. In other words, he sought to formalize a minimal set of rules from which all valid utterances of a language could be generated.

This influential work had the effect of making an understanding of syntax central to an understanding of language, and thus, central to modern linguistics. Syntax is sometimes identified as the feature of language which makes it unique to humans (Hauser et al. 2002), and, coupled with morphosyntax, as the primary driver of linguistic productivity – the other half of duality of patterning (meaningful subparts coming together to form larger meaningful wholes). The syntactic structure

of language means that a finite set of rules can generate an infinite set of valid utterances, and generally underlies a form of hierarchical structure which makes language particularly productive: *recursion*.

Recursion is the process by which a particular type of phrase can include an instance of itself, meaning that it can build upon itself indefinitely. As a visual example, think of two mirrors facing each other, resulting in an image of mirrors inside of mirrors inside of mirrors, ad infinitum. In broad terms, recursion means that you can have sentences inside other sentences. This means that in theory, a single sentence could have infinite length (e.g., *John knows that [Mary knows that [I know that [David knows...]]]]*), although in practice memory and processing limitations generally place constraints on this. Some research has even tied this recursive ability to the ability to recursively represent the mental states of others (also known as *theory of mind*) (Corballis 2014), a cognitive ability that is relatively rare in the animal kingdom (Hauser et al. 2002). While there is considerable syntactic variation among the world's languages, most all languages make use of recursion, and where this hasn't been definitively shown (most notably in Pirahã; Everett 2013), all humans seem to have the *capacity* for recursion, a feature not definitively demonstrated even in unusually sophisticated language trained apes (Hess 2008).

Semantics

Although syntax is productive, and makes language well suited to conveying complex ideas and relations, language is also fundamentally defined by the fact that it can reference meaning (i.e., the semanticity identified by Hockett). Syntax is to some extent divorced from meaning, known in linguistics as *semantics*, and there are two main pieces of evidence for this.

First, there are animals whose communication systems exhibit many features of syntax, but the systems do not engage in referential meaning. For example, both birdsong and whale song have been found to have repeating elements and features of hierarchical structure (Cate and Okanoya 2012), but the meaning

these carry is broad and unchanging (something along the lines of, “mate with me”). Meaning in human language, however, is incredibly nuanced, expressive, and constantly changing, to the point where it can express entirely new ideas with ease. Although some rudimentary form of structure seems to exist in some animal communication without rich semantic reference, semantic productivity is fundamentally tied to syntactic and morphological processes. For example, morphological processes mean that in the space of a couple of decades speakers can go from barely having a shared concept of [SEARCH ENGINE], to having nouns (*google*), verbs (*to google*), and adjectives (*googleable*) growing out of this concept.

The second piece of evidence for a divide between syntax and semantics comes from human language itself. First, sentences can be syntactically well formed but semantically vacuous or nonsensical. Chomsky's famous example was the sentence “Colorless green ideas sleep furiously” (Chomsky 2002). In terms of a grammar, this sentence is perfectly well formed, but semantically, the sentence is at best nonsense and at worst downright confusing. Second, brain damage as a result of stroke or injury can selectively effect syntactic or semantic processing. Language disorders known as *aphasias* (from the Greek *a-* “without” and *phasis* “speech”) can be divided into Broca's aphasia, which seems to predominantly effect sequential processing (resulting in halted speech), and Wernicke's aphasia, wherein patients display speech often syntactically fluid but deficient in terms of content words (e.g., nouns, verbs) (Harley 2013).

As with the other levels of language, languages vary semantically, although this is generally less straightforward to quantify than phonological, morphological, or syntactic variation. Researchers can take text from a language and make very good inferences about its general syntactic structure with little semantic information, but gathering detailed semantic information requires considerable effort and, ideally, access to native speakers. Broadly, semantics is studied in from a variety of perspectives, with approaches ranging from formal logic with a

root in philosophy to approaches from psychology which consider meaning from a more cognitive perspective. Prior to Chomsky's syntactic revolution, two prominent figures in linguistics, Edward Sapir and Benjamin Whorf, went so far as to suggest that linguistic meaning could in fact shape cognition itself, arguing that the language one speaks can constrain thought. For example, while a language like English makes a distinction between the concepts of *on* and *in*, a language like Korean does not (using a single word to express both). Sapir and Whorf argued that this kind of difference could have meaningful consequences in terms of cognition. Although a strong version of this hypothesis (known as *linguistic determinism*) is now generally rejected, there is some evidence for an interplay between concepts in language and concepts in cognition (Everett 2013).

Pragmatics

Semantics deals with meaning which is encoded within linguistic signals themselves; roughly, how we know that the sequence of sounds in *rose* generally means a particular type of flower. Pragmatics, on the other hand, deals with meaning that is not necessarily conventionally encoded in the linguistic signal itself, but arises from communicative context and common ground. Communicative context is roughly defined as the context in which an utterance is made, for example, while the (spoken) utterance "that's my rose" is a perfectly well formed sentence both syntactically and semantically, what it actually means is highly *ambiguous* out of context. What "that" refers to and what is intended by ROSE (an actual flower, a ceiling rose, a person named Rose, etc.) is impossible to resolve without access to the communicative context. *Common ground* is a specific kind of context that comes from having a history of interactions (e.g., between close friends) or shared group status: for example, if a hearer was already aware that the speaker knew someone named Rose, it would resolve much of the ambiguity in the utterance "that's my rose".

Pragmatics can be challenging to study, since it is in essence the study of how we say things

without ever actually *saying* them – for example, it is trivial for someone to understand the declaration "I'm cold" to actually *mean* "close the window," even though the speaker never said anything about windows or closing. Studies in pragmatics aim to illuminate how context resolves ambiguities and potentially even imbues meaning barely hinted at in the linguistic signal itself, how common ground is built, and the rules that govern linguistic *interactions* (as opposed to linguistic *signals*). Pragmatic rules vary greatly from culture to culture, as well as between subcultures and contexts. For example, in the context of press conferences surrounding North Korean nuclear negotiations, American officials were more likely to offer outright refusals to answer a question, while Chinese officials were more likely to avoid a question or provide a circumspect answer (Jiang 2006). Outside this context, avoidance might be interpreted as a genuine lack of knowledge, but contextualized in a culture where this strategy is commonplace, avoidance pragmatically communicates a desire not to answer the question, without being aggressive or threatening to the questioner.

Pragmatics necessarily interfaces with sociology, anthropology, and psychology in specific ways while also interacting heavily with all other levels of language. Theory of mind and mind reading are central to pragmatics: without the ability to hypothesize about the internal states of others, it becomes difficult to imagine how we would draw meaning from context or common ground, particularly where *most* of the meaning is drawn from these factors (e.g., as with using "I'm cold" to actually mean "close the window"). In terms of other levels of language, pragmatic considerations can govern variation at the phonological, morphological, and syntactic level. For example, a phonetic phenomenon known as "g-dropping," wherein a speaker says "goin" or "drawin" (in lieu of "going" or "drawing") is often conditioned by context, such that it is more likely in informal contexts (Labov 2001). Likewise, word choice (e.g., "died" vs. "passed away") or sentence structure is often pragmatically conditioned, even within a single speaker.

Tools, Methodologies, and Subfields

Tools and Methodologies

Language is most usually studied at least partially through the lens of the areas of linguistics identified above, but how this study is approached can vary greatly. Methodologically, approaches to the study of language usually fall into one of three categories: naturalistic data, experiments, and computational models.

A linguistic corpus (plural *corpora* from the Latin for “body”) is a body of text which can be used as data to study language. Corpora can be used to study phenomena at almost every level of language – there are even pragmatically annotated corpora – and they have become increasingly essential in linguistic research in the last few decades. While text sources have long provided a useful source of data for linguists, until relatively recently, their reach was necessarily limited. Corpora were generally small and not randomly sampled – for example, a collection of published fiction can reveal a lot about style in fiction and popular themes, but it does not provide a good representative sample of a language.

In the advent of the Internet age, corpora have become much more widely available as well as more comprehensive – the freely available Google Books corpus covers over 150 billion word tokens in English and also has (usually slightly smaller) corpora in several other written languages (Linell 2004). This means that linguists have been able to gain new insights into many properties of language, such as linguistic change occurring over hundreds of years (Cuskley et al. 2014) and language varieties diverging as they disperse across the globe (Michel et al. 2011). Likewise, other fields such as complex systems science and physics have begun to overlap and interact with linguistics due to the ready availability of a great deal of linguistic data which can shed light on dynamic social and cultural dynamics more generally.

While there are available corpora of spoken natural language, such as the CHILDES Corpus of child language (MacWhinney 2000) and the Switchboard Corpus (Godfrey and Holliman 1993), available language corpora are

overwhelmingly drawn from written language. Due to its permanence, written language provides a rich source of data for linguists to study, but caution is required when it comes to general conclusions drawn from most corpora. First, while written language is a mirror of its spoken counterpart to some extent, some results gleaned entirely from written corpora might only apply to written language.

More problematically, many general conclusions drawn about language are heavily skewed towards languages which have a written form, meaning interesting features which may occur in languages which are exclusively spoken are overlooked or difficult to even discover in the first place. This forms part of a general bias towards making assumptions and conclusions about human language generally from a relatively confined and homogenous set of European languages (Linell 2004). Even where spoken corpora are used, these are overwhelmingly drawn from languages which have a written form. Thus, there is still a very important place in linguistics for traditional fieldwork, particularly to gain knowledge about languages spoken by smaller populations which may not have written forms.

Experimental approaches in linguistics are relatively new to the field – before the latter half of the twentieth century approaches were predominantly anthropological or theoretical. The experimental methodologies used in linguistics are often borrowed from experimental psychology. Common experiments with high relevance for linguistics are Artificial Language Learning (ALL) experiments, lexical decision experiments, and grammaticality judgments.

In ALL experiments, participants learn miniature artificial languages. How quickly and accurately they learn these languages, and what kinds of errors they make in learning, are often revealing about how we process language. Lexical decision tasks involve participants making split-second decisions about words, often about their meaning in a categorical sense (e.g., is the word “spaghetti” a noun or a verb). These experiments can reveal a lot about how the levels of language interact in processing, for example, semantic information might interfere with making syntactic category

judgments (such that “destruction” would be more difficult to identify as a noun than “spaghetti”). Grammaticality judgments involve asking participants to rate the acceptability of different sentences, in order to allow for a comprehensive description of the generative rules which govern a language. Aggregate grammaticality judgments over many participants allow researchers to describe in greater detail the rules that underlie, for example, why *the girl rode the bike* is acceptable, but **the girl looked the bike* is not.

Various other experimental methods are employed in linguistics, and many of them are combined with other experimental approaches, such as having a participant complete a lexical decision task inside an fMRI machine to better understand how language processing works in the brain. However, as with corpus linguistics, some caution is warranted given the fact that participants in studies are not only overwhelmingly Western, literate, and often specifically European but, like in psychology generally, tend to be a specific subset of this already confined sample (often university undergraduates; Henrich et al. 2010).

Computational models are also an invaluable resource in linguistics. Although there is a necessary level of abstraction in computational modeling, the approach also allows for considerable control, and in many cases a view of language processing and/or transmission which is not language specific. At the individual level, computational modeling allows for insights into how we process language. For example, by trying to teach a simple network to accurately learn the English past-tense given minimal input data, we can gain insights into how our own brains might solve this problem (Pinker and Ullman 2002). Computational models also offer the opportunity to examine large-scale population level phenomena by using populations of artificial agents. This allows for crucial insights into how language is used across large groups and transmitted between learners, providing a valuable complementary resource to the smaller-scale data provided by experimental approaches.

Computational approaches are essential for more practical applications in linguistics, such as machine translation and advances in artificial

intelligence. However, despite considerable progress in both of these areas in recent decades, artificial intelligence is far from having comprehensive linguistic competence. In terms of machine translation, while there is unprecedented accuracy at the level of individual words, the error rate in automatic translation of longer texts is considerable, and this is to say nothing of machines interpreting much noisier natural speech. While the ability to do this has improved considerably in recent decades, there is still a noticeable level of error particularly with different language varieties (e.g., many speech recognition systems do not handle non-standard accents well). The area where a failure of AI to meet human performance is most noticeable is arguably in pragmatics. Although an AI might be able to interpret and answer a single question (e.g., like Apple’s Siri © or Amazon’s Alexa ©), and produce fairly realistic-sounding speech, realistic sustained conversation is an open problem. While there is clearly room for improvement in all of these areas, more advances have been made in the last decade than in the previous century.

While naturalistic data, experiments, and computational approaches arguably form the methodological core of linguistics, other approaches provide valuable contributions to the field, which, like any other field, is constantly changing and growing. Comparative approaches which aim to describe the communication systems of other species can provide valuable insights into human language, especially attempts to teach language-like systems to nonhuman animals. Formal mathematical approaches have been revolutionary in syntax, and information theory and complex systems science have made promising inroads into formalizing broad properties of language.

Conclusions

The previous sections provided a concrete operational definition of what language is, identified the different levels at which it is structured, and briefly outlined how the study of language is approached methodologically. While basic facts about language are broadly agreed upon in the

field, there are of course divisions within the field and open questions. Researchers in the Chomskian tradition are proponents of *Universal Grammar* (UG), which proposes that some minimal aspects of language are innately (or even genetically) encoded. However, many functional or cognitive linguists argue that learning plays a crucial role not just in the individual development of language but in shaping the structure of language itself over time (Chater and Christiansen 2008). Very broadly, this debate mirrors the “nature-nurture” question at the heart of many problems in cognitive science.

A related open question concerns the *domain specificity* of language. Proponents of UG lean towards the notion that the processes involved in language are specific to language and specifically evolved for language. On the other hand, cognitive or functional linguists argue that more *domain general* constraints – such as memory or a general preference for simplicity over unnecessary complexity – govern and shape language.

Nonetheless, researchers broadly agree that language is defined by some essential features, the particular combination of which makes language unique among other communication systems. Particularly, the discreteness, duality of patterning, arbitrariness, and productivity of language allow it to engage in displacement. This means that unlike many other communication systems, language is theoretically an infinite system (particularly due to recursion) and can be readily used to engage in communicating things that are neither present nor true. Language is formally divided into minimal meaningful units (phonemes), which combine to create minimally meaningful units (morphemes), which in turn recombine in syntactically rule-governed ways to create an endless array of meaningful utterances. The areas of phonology, morphology, and syntax study these properties in different languages, while the areas of semantics and pragmatics concern how meaning is encoded both within linguistic signals and in linguistic interactions. There are many ways to approach the study of language, but most often any given approach can be categorized as either leveraging naturalistic (often corpus-based) data, using controlled experiments, or targeted computational modeling.

Cross-References

- Arbitrary
- Broca’s and Wernicke’s Areas
- Communication, Cues, and Signals
- Displaced Reference
- False Beliefs
- Gestural Theory
- Human Deception
- Language Modularity
- Linguistic Evolution
- Meaning (Philosophy)
- Nativism
- Phonemes and Symbols
- Pidgins and Creoles
- Semiotic Constraints
- Sign Language
- Symbolic Culture

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Field Research

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Synonyms

Fieldwork

Definition

Gathering information by observing individuals in their natural setting.

Introduction

Field research (“fieldwork”) refers to information gathered by observing individuals in their natural setting. Field research can be both qualitative and quantitative in nature. Qualitative research emphasizes the importance of observing variables and their interactions. Quantitative research attempts to objectively gather data to make associations, comparisons, and predictions among variables. Field studies that sought to associate behavior with inter-individual interactions and/or the environment formed the foundation for the field of behavioral ecology (Martin and Bateson 2007).

Field research involves observations of free-living wild animals in their natural habitats while minimizing perturbations or disturbances to their environment or behavior. Field excursions may require some or all of the following (Lagler 1956): funding for travel, salary, supplies, and lodging; field assistants to help with data collection; information about the area; planning and coordination; and a schedule of tasks to be completed. Fieldwork may involve the observation, capture, and measurement of animals and collection of environmental data. Documenting the environment of the population under study is an interdisciplinary effort that may require knowledge of surveying, geology, chemistry, and botany.

Field studies can provide insight into the causes and complexities of animal behavior. Animals regularly interact with their environment through activities associated with breeding, eating, and movement. More accurate information may be obtained about these behaviors if they are studied in wild versus captive animals because captive individuals are often too constrained by artificial environments to behave naturally. Furthermore, evidence that a variable can influence behavior under laboratory conditions does not

mean that it influences behavior of wild animals. Field studies, therefore, are invaluable for observing the full range of an animal's behavior and understanding its ecological context. Observers are able to note the circumstances in which behaviors do and do not occur, which allow them to infer their function and proximate causes (Martin and Bateson 2007).

Exploratory data obtained from field observations can form the basis for follow-up experimental studies in artificial settings that can experimentally test for causality. Field studies aid understanding of how a behavior is adapted to a particular environment. Habitat can influence behavior, so it may be important to choose study sites that are in different environments to be able to generalize a species' typical behavior (Martin and Bateson 2007). Scientists can conduct controlled field experiments, in which certain aspects of the environment are manipulated to test a hypothesis. For example, to test weaverbirds' abilities to differentiate between their own eggs and those of other parents, researchers planted nests with the eggs of other parents (Lahti and Lahti 2002). By experimentally

manipulating gull eggshells, Tinbergen (1962) learned that parents remove broken eggshells to reduce predation by crows.

Goals of Field Sampling

Field studies can help scientists understand how individuals or species interact within populations or ecosystems, anthropogenic effects on individuals or populations, and a population's life history characteristics. Knowing the natural history and ecological context of organisms is also helpful in conservation efforts. Studies can focus on the distributions of populations/species, the presence/absence of a species in a given area (particularly a species that is threatened or invasive), determination of environmental limitations or advantages for a population, or obtaining specimens for further study in the lab.

Four main aspects of behavioral ecology can be addressed in field studies: action patterns, abundance, survivorship, and resource allocation (Bart et al. 1998; Table 1). When sampling

Field Research, Table 1 Types of field observations, goals, sampling methods, and potential difficulties (Bart et al. 1998)

Type of observation	Goal	Methods	Difficulties
Behavior	Estimate time spent engaged in different behaviors	1. Scan sampling 2. Focal sampling	1. Observer influences behavior 2. Animals disappear out of sight
Abundance	Estimate trends in population size in time or space	Surveys	1. Changes in survey efficiency can influence estimates 2. Defining the trend in population size 3. Missing data 4. Variation in observer skill 5. Pseudoreplication
Survivorship	Estimate the number of individuals that survive in a given time period	1. Telemetry 2. Nesting success 3. Capture–recapture	1. Finding and following all nesting attempts 2. Monitoring efforts unevenly distributed over time
Resource selection	Determine why animals use some areas or consume some food items while not using or consuming others	1. Surveys of habitat use 2. Behavior sampling	Modeling complexity

behavior in the field, the first step is to define the behavior(s) of interest and then estimate how often they occur. Activity budgets can be quantified by recording the proportion of time spent engaging in a behavior, its frequency, or average duration. The definitions of behaviors of interest, often outlined in ethograms, need to be specific enough for different observers to be able to interpret them in the same way. Depending on the behavior, activities may be divided into bouts, or periods in which a behavior is engaged in frequently.

When monitoring abundance, observers can estimate population size through time and/or space, often with regard to an ecological variable of interest. Population sizes may be estimated through the use of long-term surveys or telemetry. Field surveys can also lend insight into a population's resource selection, the process by which animals use a specific area or consume certain food items, while not using or consuming others. Additional characteristics of a focal individual may also be recorded (Table 2).

Field notes typically contain detailed descriptions of the physical environment and individuals under study, including their behavior and communication with others. Methodological notes describe how data are acquired as well as justification of techniques used and may incorporate ideas for future studies.

Sampling Methods

An observer might engage in either focal individual or scan sampling (Lehner 1996). Focal sampling follows only one or a few individuals, while scan sampling involves periodic observations of all or a subset of individuals in a group. Observers may sample either continuously or intermittently. In continuous sampling, the start and end times or occurrences of behaviors are recorded during finite time intervals. Intermittent sampling provides snapshots of an animal's behavior by recording their activity at regular intervals. Continuous sampling is best when

Field Research, Table 2 A description of an individual in the wild may include any or all of the following characteristics (Lagler 1956)

Category	Characteristics
Taxonomy	Genus and species
Range	Where is the organism found? How do the current and original ranges vary? What ecological factors influence the size of the range?
Distribution	What ecological factors influence distribution?
Physical description	Morphology Color Sexual dimorphisms
Foraging strategies	How do they change throughout development? How selective is the individual in choosing food? Does diet vary seasonally? What are the daily food requirements? How often does the organism eat? How do they eat? What factors influence what food is eaten and when?
Growth rate	What is the organism's age, length, and weight? Does the organism exhibit allometric growth? What factors influence growth?
Reproduction	When is sexual maturity? What is the sex ratio? Are there courtship rituals? When and how do individuals breed? How fertile are individuals? Do they exhibit parental care? What is the offspring's survival rate? Are the breeders oviparous or semelparous? What factors influence reproductive success?
Early development	What are critical environmental windows? When does hatching occur? How long is larval development? What factors influence development?
Behavior	What movements are observed? Does the species migrate? Do individuals school? Are they territorial? Do you observe individuals learning? Are individuals engaging in social behaviors? What factors influence behavior?

Field Research, Table 3 When reporting the results of field studies, the following characteristics should be included as appropriate (Lagler 1956)

Basic background	Location
	Nearby geographical features
	Map, including source and cardinal directions
	Coordinates
	Natural history
	Extent of development
Physical characteristics	Size of field site
Geological characteristics	Soil type
	Ground cover
	Vegetation type
	Presence of dispersal corridors
Chemical characteristics	Temperature
	Oxygen availability
	Salinity
	pH
	Extent of pollution
Biological characteristics	Food sources
	Predators
	Competitors

only a few easily recognized behaviors are recorded that either occur infrequently or last a long time while. Intermittent sampling is preferred for recording fine-scale behaviors that may change rapidly. Decisions about the use of one technique over the other requires an evaluation of the pros and cons of obtaining a lot of data on a few focal individuals or limited data on a larger number (Cochran 1977). Intermittent and continuous observations are commonly combined with general observations of group dynamics (Bart et al. 1998). Basic information about the individual or population’s environment should also be reported (Table 3).

One or a combination of sampling techniques may be employed (Bart et al. 1998). Simple random sampling refers to a situation in which all possible samples from the population are equally likely to be selected. Random sampling is not always feasible in natural settings, so nonrandom sampling may instead be used, particularly with regard to selection of focal animals. Researchers may choose to focus on individuals at a particular

developmental stage or focal individuals distributed evenly across a population.

Sources of Error

Both observer influences on behavior and measurement bias are potential sources of error in field studies (Bart et al. 1998). It is not uncommon for animals to change their behavior in the presence of an observer, and the extent to which animals are affected may depend on species and/or life stage (Martin and Bateson 2007). Therefore, an acclimation or acceptance period may be required if the animal appears to react to the researcher. Acclimation periods are typically short but vary depending upon the species being studied. The presence of an observer can also influence the behavior of the focal species’ predators or prey. As a result, it is important for the observer to minimize disturbances and wait until after the acclimation period to collect data.

Hides or blinds may reduce disruption, but can restrict the observer’s ability to monitor individuals. An animal moving out of sight can result in selection bias, when data are not recorded at the scheduled time, or measurement bias, if the individual is hidden for only part of the scheduled observation time. While the use of a hide or blind reduces the ability of animals to see the observer, it does not prevent the animals from detecting the observer’s sounds or smells. To further minimize the likelihood of disrupting normal behavior, remote video cameras may be used. While they may not be able to observe all of the behaviors of the individuals under study, resulting in selection and/or measurement bias, they create a permanent record of the behavior that can be replayed and may also help detect behaviors that occur so rapidly that they are difficult to record accurately in real time (Martin and Bateson 2007). An additional benefit of having a permanent record of behavior is that follow-up studies may be conducted without having to return to the field site. Recorded behaviors may also be used as educational tools

or deposited into open-access databases that are used by the research community.

Prominent Field Researchers

In the mid-1800s, Charles Darwin developed his theory of evolution by natural selection after conducting field observations of a variety of species while voyaging on his ship, the *Beagle*, and studying the plants and animals that were local to his home in England (Darwin 1859). In the 1920s–1930s, Margaret Morse Nice captured and marked sparrows in her yard and studied them throughout their development (Nice 1937). In the 1930s–1950s, Konrad Lorenz, Karl Frisch, and Nikolas Tinbergen developed the field of ethology, or the science of animal behavior. Their studies of numerous animal taxa, including birds, fish, and insects, helped researchers to better understand the causes of behavior, its evolution, and how it relates to fitness (Dewsbury 2003). At about this same time, J.H. Crook and David Lack used their studies of birds to develop a comparative approach to behavioral ecology in which they associated behaviors with the birds' environments (Lack 1947; Crook 1964). Jane Goodall began working with chimpanzees in Tanzania in the 1960s (Goodall 1990). Through her decades of field observations, she greatly increased our understanding of primate behavior and documented behaviors that were previously thought to be unique to humans, including tool use and warfare. Her work has helped protect wild primates and has publicized issues of animal conservation.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Adaptations: Product of Evolution](#)
- [Field of Behavioral Ecology, The](#)
- [Competition for Parental Investment](#)
- [Competition for Resources Desired by Females](#)
- [Charles Darwin](#)
- [Differential Parental Investment](#)

- [Differential Reproductive Success](#)
- [Ecology](#)
- [Ecology of Paternal Investment](#)
- [Ethograms](#)
- [Evolution of Adaptations](#)
- [Evolutionary Change](#)
- [Kin Recognition](#)
- [Male Oramentation](#)
- [Monogamy](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Parental Investment](#)
- [Parent-Offspring Conflict](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Prey Choice](#)
- [Reproductive Strategies](#)
- [Secondary Sexual Characteristics](#)
- [Sex Differences](#)

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Fieldwork

- [Field Research](#)

Fighting

- [Defending Against Attack](#)

Fighting Ability

- [Nonverbal Indicators of Dominance](#)
- [Self-Assessment of Fighting Ability](#)

Fighting Ability Assessment

- [Fighting Assessment](#)

Fighting Assessment

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Synonyms

[Fighting ability assessment](#); [Formidability perception](#)

Definition

Neuro-cognitive processes involved in estimating others' and one's own ability to inflict harm and

other fitness-related costs in physical confrontation based on available cues related to the likelihood of success in physical conflict.

Introduction

When organisms are competing for the same resource there are multiple strategies that each individual might take. They might cooperate, they might try to scramble to outcompete, they might leave and seek alternative sources, or they might aggressively compete (Duntley 2005). This last choice is a decision to inflict costs on the other and is likely made where at least one of the other strategies are available. It is therefore an interesting question to analyse when and how organisms decide to aggressively compete.

While a number of factors will be at play in the wider context, such as the value of the resource and how divisible it is, for our purposes here we focus on the relative fighting abilities of the prospective combatants in a human context or as Parker (1974) describes it the decision whether to fight or not may be based upon an assessment of “relative resource holding potential.”

It is possible that assessment of the other prospective candidate may be unnecessary. Arnott and Elwood (2009) report that in a variety of species, there is evidence for a pure self-assessment where the prospective combatant pays attention to its own resources and health and will only deescalate from a fight if these resources drop below some trigger point. This strategy avoids the costly effort of evaluating others. There is some evidence for use of this reduced cost strategy in humans. Taller men (Watkins et al. 2010a) or merely individuals that feel powerful in the moment (Watkins and Jones 2012; Watkins et al. 2010b) have a reduced ability to discriminate differences in male facial dominance. This suggests that their self-assessment is sufficient to at least ignore rival characteristics although not precisely evidence that self-assessment would be enough to escalate to a fight.

What is more likely, however, is that human competitors mutually assess rivals before

considering escalating to physical aggression. Various models exist to describe this but all involves initial low-cost sampling of the rival abilities before escalating (Arnott and Elwood 2009).

In many species, agonistic conflicts with conspecifics are key determinants of access to fitness contributors like resources, territory, and mating opportunities or promotion in social hierarchy (Ellis 1995). Species that engage frequently in physical confrontations with conspecifics calibrate their behavior according to their relative fighting ability. Many such species assess fighting ability from visual, auditory, or olfactory cues. Moreover, individuals remember these assessments over time, use them to determine relative fighting ability, calibrate their assessments based on previous victories or losses in fights, and engage in ritualized behavior involving displays and mutual assessments of formidability, and these contests are frequently resolved when one of the antagonists surrenders, which prevents actual costly fights (Sell et al. 2012).

Any individual that can reliably assess the chance to win a conflict in advance and that can make more sensible decisions about whether to initiate, escalate, or retreat from a potential fight is likely to obtain selective advantage. Thus, it seems likely that natural selection would have favored the evolution of cognitive and behavioral mechanisms that would facilitate assessment of fighting ability and that promote the most appropriate decisions and responses to decrease costs and increase benefits from potential confrontations.

Perception of numerous socially relevant characteristics that are important in social contexts (e.g., confrontations and negotiations) are frequently determined by physical traits like conspecifics' morphology. In many species, direct visual inspection of others' physical size is well documented (Arnott and Elwood 2009) as primary determinant of social dominance and formidability (see Třebický and Havlíček 2017). Individuals across various taxa can recognize the relative dominance, including fighting ability, of their conspecific upon first encounter depending on displays of body size or presence and size of

armaments, ranging from paper wasps (Tibbetts and Lindsay 2008), hermit crabs (Neil 1985), monitor lizards (Frýdlová et al. 2017), numerous avian species (Fretwell 1969; Senar and Camerino 1998), domestic pigs (Rushen 1987) to non-human primates (Bergman et al. 2009; Ghazanfar and Santos 2004).

Recalibrational Theory of Anger

Fighting ability could be described as an ability to efficiently use physical strengths (among other means), against a conspecific antagonist. Greater fighting ability of the given individual should increase the costs the individual is able to inflict upon the opponent. The willingness to use ones' fighting ability against competitors is commonly mediated via anger. Individuals are deemed to use anger to convince others to treat them better, and the more power they had to harm others, the more convincing they would have been (Price et al. 2012).

The recalibrational theory of anger (Sell 2011) is a computational evolutionary model which proposes that the function of anger is to recalibrate individuals who place insufficient weight on the welfare of the angry individual when making fight-or-flight decisions. According to this theory, (i) individuals differ in terms of their anger thresholds and selective usage of negotiation tactics, (ii) they need to estimate others' traits relevant to the ability to inflict any costs (e.g., fighting ability) and provide any benefits (e.g., mate value or resource gathering potential), (iii) and use these estimates to calibrate their welfare trade-off ratios (Tooby et al. 2008). More weight is placed on the welfare of individuals who have higher Resource Holding Power – the abilities and willingness to inflict higher costs or appropriate benefits from others (Parker 1974; Sell 2011). Individuals with higher resource holding power easily win conflicts, attain preferential access to mates, and benefit themselves at the expense of others in other ways (Sell 2017). Individuals are expected to have evolved to calibrate their welfare trade-off ratios to maximize their own welfare. Such recalibration strategy confers important selective advantage over fighting without prior assessment.

Due to the significant role of mate selection in evolutionary theorizing, the vast majority of investigations in current behavioral sciences emphasize that intersexual selection (i.e., processes underlying mate choice) is responsible for men's phenotype (but see Sell et al. 2017; for review Třebický et al. 2012). However, recent studies suggest that a variety of masculine traits appears to be primarily designed for intra-sexual competition rather than for attraction of potential mates (Hill et al. 2013; Puts 2010; Sell et al. 2017).

Human inclinations towards antagonistic interactions have been displayed throughout our evolutionary history. Forensic evidence suggests that antagonistic interactions among our ancestors – especially among men – have been rather common and significant selection force in our ancestral environment (Manson et al. 1991; Walker 1997, 2001). Facial skeletal trauma supposedly caused by fist fighting exists in the fossil record of *Australopithecus* (Roper 1969) and early *Homo* (Wu et al. 2011) and many other samples of historic skeletal remains (Walker 1997). Historical records and ethnography literature contain numerous examples that acts of physical encounters are not exceptional in many human cultures across the globe (Archer 2009; Horns et al. 2015; Walker 2001) and ritualized combats in the form of folk wrestling and martial arts are also common and have a long history (Green 2010). As in many other vertebrate species, men show higher levels of physical aggression, engage in physical contests and homicides to members of the same sex more frequently than women, and since practically all wars were fought prevailingly by men, this potential seems to be much higher among men than women in virtually all societies worldwide (Archer 2004, 2009). These patterns suggest a relatively high level of male intrasexual physical competition in human evolutionary history. This may account for some typical features of the human male physique, especially for the upper body shape and a greater amount of muscle mass and strength compared to the female body (Lassek and Gaulin 2009). Evolutionary-informed scholars therefore argue that physical encounters have probably

generated powerful selection pressures in humans as well that have contributed to the establishment of various neurocognitive and behavioral complexes, whose function is to perceive, assess, and specifically act in antagonist situations or even prior to actual encounters (Carré et al. 2013; Puts 2010; Sell et al. 2009a).

Physical Armaments

Physical competition often favors evolution of anatomical armaments (structures used as weapons or armors). Unlike some other animals, humans are not equipped with dangerous weaponries such as sharp canines, claws, or poisonous glands. Before humans started using and fabricating objects as weapons, physical combat had depended on hits executed by hands and striking with fists appears to be universally employed in many cultures across the globe as dominant striking technique used in modern combatant arts and “street fights” as well (Horns et al. 2015; Morgan and Carrier 2013; Scoggin et al. 2010). Ancestrally, a man's upper body strength was therefore a major component of his ability to inflict costs on others. Upper-body strength is considered as critical for physical encounters, particularly for wrestling, punching, or choking, which were the most common types of combats in ancestral populations according to analyses of skeletal remains (Walker 1997). Hence, greater strength should set the individual's formidability higher.

Interestingly, hand morphology which is similar to modern humans was present in basal hominins (Horns et al. 2015) and although, proportions of the hand may improve manual dexterity, at the same time they make it possible for the hand to clench into fist and be used as a club against opponents. According to the protective buttressing hypothesis, bones of the human hand are proportioned in a way so that they provide a supportive buttress while clenched into fist which protects the hand from injuries and also that the human fist functions effectively to strengthen and stabilize the hand during punches, which allows competing males to strike with higher force while substantively reducing the risk of hand injury (Horns et al. 2015; Morgan and Carrier 2013). Nevertheless, the frequency of

hand bone fractures resulting from fighting (Jeanmonod et al. 2011) has been used to argue that the hand is too fragile as a weapon (King 2013). Importantly, in fist fights the primary target is the face (Brink et al. 1998), and bones of our faces break much more frequently than do bones of the hands during fights, indicating that the fist is a sufficiently effective weapon (Carrier and Morgan 2014).

Facial Morphology

Studies focusing on the locations of injuries that result from assaults and interpersonal violence found that the face was the most common site (Brink et al. 1998; Shepherd et al. 1990) and fractures most frequently occurred in the mandibles, nasal complex, zygoma arches, maxillae, and supraorbital arches. Interestingly, the bone structures that suffer from the highest fracture rates are the parts of the skull that exhibit the greatest increase in robusticity during the evolution of genus *Homo* (Carrier and Morgan 2014) and are the most sexually dimorphic parts of the human skull (Enlow et al. 1996). Overall facial shape, expansion, and bunodont form of post canine teeth, increased robusticity of the orbits, excessively stronger masticatory system are the traits that tentatively represent functional features of protective buttressing of the face against injury during fighting (Carrier and Morgan 2014). It is also likely that masculine features of the face convey direct information about the degree to which the face is vulnerable to injury. A robust facial skeleton may make an individual stronger opponent simply because he is less susceptible to knockouts and serious injury.

Understanding others can help one to forecast others' future behavior and adjust oneself accordingly. Being able to assess mating interests, trustworthiness, willingness to cooperate, or formidability of conspecifics is of high importance for individuals' fitness, therefore to have neuro-cognitive mechanisms that work for perceiving and responding to these characteristics and intentions would be very effective. Such mechanisms should swiftly recognize adequate cues in others relying minimally on direct interaction and should be sensitive to cues that are related to fighting

ability in this instance. This is carried out by first impressions – impressions that can be formed very quickly, based on whatever information is available. Such first impressions are often formed by using, among other features, the visual appearance of physical features of one's face. A substantial body of evidence shows that people attribute various characteristics to others based on their facial appearances like physical strength (Holzleitner and Perrett 2016; Sell et al. 2009a) and aggressive behavior (Carré et al. 2009), among others.

Converging lines of evidence show that people infer various psychological traits based on static facial features. For instance, people judged as more powerful were reported being higher in assertiveness, aggressiveness, and power (Berry 1991), those who were judged as stronger and better fighters were physically stronger (Sell et al. 2009b), fighting success was congruently assessed (Little et al. 2015; Třebický et al. 2013, 2015), and even criminals who were judged as more violent were more likely to have been confined for violent crimes (Stillman et al. 2010). Majority of research on cues of threat potential in humans has investigated the relationships between measures of men's threat potential such as body size, upper-body strength, or actual fighting ability and assessments of their facial traits (Arnott 2017; Sell 2017; Sell et al. 2012; Třebický et al. 2013). Several studies have reported positive correlations between measures of men's upper-body strength and ratings of their facial dominance, strength, and ascribed fighting ability (Fink et al. 2007; Holzleitner and Perrett 2016; Windhager et al. 2011). Other studies found that faces of taller men are perceived as more dominant (Burton and Rule 2013; Re et al. 2013a; Watkins et al. 2010a). Ratings from distinct cultures including hunter-horticulturalists, people from industrialized regions, and pastoralists show that cues of physical strength and aggression are present in the face and that these cues can be extracted and assessed rapidly and accurately (Sell et al. 2010; Short et al. 2012; Třebický et al. 2015; Zilioli et al. 2014). A recent study by Han et al. (2017) showed that men's perceived "facial threat potential"

(a composite measure derived from dominance, strength, and weight ratings based on their faces) was positively related to their scores on the “actual threat potential” (constructed from men’s handgrip strength, weight, and height). Man’s handgrip strength (a proxy measure of upper body strength) is positively correlated with women’s ratings of their facial dominance (controlling for age and body weight) (Fink et al. 2007). Also, perceived strength from faces is correlated with actual muscle performance (Holzleitner and Perrett 2016; Hugill et al. 2009) and peer ratings of each other’s fighting ability are tracked by rating of dominance from facial images by strangers (Doll et al. 2014).

Threat Potential May Not Directly Relate to Formidability

It should be stressed, however, that previous studies concerning assessment and measures of formidability (Han et al. 2017; Sell et al. 2009b) rely on body strength or body size as a proxy for fighting ability. While physical strength is undoubtedly an important component of fighting ability, there are many additional sources of variation in the ability to fight. These studies are rather studying a threat potential; however, even high threat potential does not need to translate into actual fighting ability. Several researchers (Dixson et al. 2017; Kraus and Chen 2013; Little et al. 2015; Palmer-Hague et al. 2015; Pollet et al. 2013; Třebický et al. 2013) have overcome this issue by using available data on fighting ability from databases of mixed martial arts contests. Nevertheless, the generalization from these data might be limited as the sample consists of elite athletes highly skilled in hand-to-hand combat and individual bouts are fought only within restricted weight classes.

In most cases of hand-to-hand confrontation in general public, little-to-no experience or formal training can be expected, and therefore other factors like overall body size that influence the outcome of a physical fight must be at play. The fighting ability is undoubtedly a complex skill affected by various characteristics (i.e., ability to concentrate in stress, hand-to-eye coordination, overall stamina, or experiences) and our

knowledge in this area is far from definite and contribution of other characteristics may vary according to the form of the fight.

A growing body of research aims to identify exact facial (and bodily) morphological traits and whether people use them as visual cues to estimate those characteristics from the face and body and subsequently test how accurately perceived characteristics relate to relevant morphological structures. For example, in the case of body size, taller people generally have more elongated faces than shorter ones (Windhager et al. 2011) and heavier men have wider and squarer lower facial regions (Coetzee et al. 2010). Available evidence also indicates that people use the abovementioned or related facial cues to assess others’ body weight and height, and they are fairly accurate in their judgments (Re et al. 2013b). It was found that low brows, large chins, wide noses, and narrow mouths are morphological traits related to perceived dominance and strength in both natural and computer-generated faces (Toscano et al. 2014), and that physical strength is associated with rounder faces with wider eyebrows and more prominent jaws (Windhager et al. 2011). While these studies demonstrate that there are specific facial morphological features associated with formidability-related traits and that people pay attention to these traits, they do not demonstrate whether these particular features are indeed present in more formidable individuals. Using the geometric morphometric methods, Třebický et al. (2013) showed systematic differences in structural configurations of facial features, perceived aggressiveness, and actual fighting success in sample of professional fighters (although, the association between facial configuration and fighting success was restricted to heavyweight fighters). Shape regressions revealed that aggressive-looking faces are generally wider and have broader chins, more prominent eyebrows, and larger noses than less aggressive-looking faces.

Facial Width-to-Height Ratio (fWHR)

Currently, the most frequently investigated facial measure is the facial width-to-height ratio (fWHR or relative facial width) (Weston et al. 2007).

Previous studies found that fWHR is related to several behavioral and personality characteristics including aggressive behavior and perceived aggressiveness (Geniole and McCormick 2015; Haselhuhn et al. 2015), even in cross-cultural context (Short et al. 2012). Stirrat et al. (2012) found that narrow-faced men were more likely than wider-faced men to die by contact violence compared to other causes of death or homicide. In a sample of professional MMA fighters, the variation in fWHR is associated with actual fighting performance, perception of aggressiveness, fighting ability, body weight (but not height) (Třebický et al. 2015), and higher numbers and proportions of wins and longer fighting careers (Zilioli et al. 2014).

Future Directions

One, currently rather neglected aspect of formidability related research, is cohesiveness of coalitions that seems to influence the outcome of conflicts. Most of the studies conducted so far are aimed on only one specific scenario of physical confrontations, where only two opponents confront. Though, physical encounters among men are not limited solely to the two individual opponents and may frequently involve other, the allies. Of high adaptive importance would be the ability to assess the prowess of a potential opponent as that of a potential ally, in terms of deciding whether to enter the fight and pursue relevant joined activities. Assessments of formidability are therefore not relevant solely in the context of a potential opponent but also in the context of selection of allies. Some species, particularly social primates, assess alliances and cooperative value and show deference toward individuals with more allies or with the ability to deny benefits (Smuts et al. 1987). Men with higher fWHR also show some evidence of increased sensitivity to coalitional alliance (Stirrat and Perrett 2012).

Many factors were suggested to affect assessments of formidability; nevertheless, it is not yet fully understood how these assessments work in real-life situations. We propose a model of multi-

level assessments of formidability that tries to cover processes responsible for the fight-or-flight decision when faced with a potential antagonist. In terms of decision-making models, this would correspond to “The fast and frugal tree” model where an individual follows a decision-tree with an exit option after each attribute (Martignon et al. 2003). We suggest that assessment of potential opponents acts on multiple levels. Based on the knowledge of one’s own formidability, a resource holding power (Parker 1974) of each competitor is evaluated regarding the potential costs he can inflict and benefits he can gain from confrontation, so that the welfare trade-off ratios (Tooby et al. 2008) which help to recalibrate appropriate level of anger of rivals could be calculated (Sell 2011). In general, judgments of fighting ability seem to focus on overall probability of winning a fight. The first step, in such a multilevel fight-or-flight decision-making process, might depend predominantly on the overall size of the opponent, as suggested by the ratings of fighting ability in our previous study (Třebický et al. 2015). If one of the competitors is substantially larger (e.g., taller, more muscular, or bulkier), the smaller one surrenders and withdraws from the conflict. When the rivals have roughly equal sizes, a further level of assessment takes place – which might be related to the perception of bargaining potential such as the assessment of aggressiveness from facial features (Třebický et al. 2013). If both competitors feel equally formidable, the confrontation may get escalated.

Conclusion

Antagonistic conflicts with conspecifics are a fundamental factor influencing fitness in many social species, including humans. Fighting ability had profound implications in our evolutionary past and, in some communities, continues to have significant implications in contemporary societies. Evolution of adaptations that facilitate decision-making in potentially agonistic interactions is therefore expected, as the individual must determine whether it is best to fight, flee, or appease the prospective foe. According to the

recalibration theory of anger (Sell 2011), benefits of minimizing the costs of engaging in violent conflict are thought to have shaped adaptations for the assessment of others' capacity to cause physical harm.

The main aim of this chapter was to review evidence whether morphological features served as reliable cues to the actual formidability and whether our visual perception is sensitive towards such cues. Current body of evidence support this notion and show that morphological features predicts which of two opponents are likely to withdraw from an aggressive encounter and based upon converging results of current studies investigating competition in men, we can conclude that our morphological features are valid predictive cues of actual performance in physical fights and that raters are sensitive toward these cues. These studies demonstrate that there are specific morphological features associated with formidability-related traits and that people pay attention to these traits. Raters are able to distinguish the winner of consequent fights with accuracy higher than chance (Little et al. 2015); the winners are rated as better fighters, as stronger, more dominant and attractive, compared to losers (Little et al. 2015). Holistic facial shape analyses and simple facial features ratios showed systematic differences in structural configurations of facial morphology in successful competitors, compared to unsuccessful ones and between individuals perceived as more aggressive compared to less-aggressive ones (Třebický et al. 2013, 2015).

At first glance, it seems obvious that winning and losing in a physical fight is determined by physical strength and body size. Height and bulk are two physical characteristics that are easily observable traits that can be used to provide a relatively crude, albeit somewhat accurate, appraisal of fighting ability among adolescent males (Beaver et al. 2015). Although assortment of other factors like health, skill, hand–eye coordination, proper technique, and armaments may come at play.

Currently, the research mainly focused on thin slices of information provided by a single cue rated on a single behavioral/personality characteristic. However, our perception is not limited to gathering information through just one

perceptual modality, e.g., just with our sight and we do ascribe many characteristics based on a single slice of information. Utilizing multiple cues assessment and/or multiple characteristics rating, testing the agreement between modalities and scales, and their subsequent interplay remains a challenge for future studies.

We propose that the assessment of potential opponents acts on multiple levels, then simply based on first impressions. In this multilevel “fight or flight” decision-making model, individuals assess their potential competitors following a decision-tree with an exit option after each attribute. At the first level, the decision-making process might depend predominantly on the overall size comparisons.

Although, competition in humans becomes widely investigated area in behavioral sciences, we are still at realms of rather skin-deep understanding to how the assessments of potential opponents take place. Abovementioned evidence is an important contribution to emerging body of research concerning evolution of neurocognitive and behavioral processes fine-tuned toward perception and adequate behavioral responses toward potential opponents.

Cross-References

- ▶ [Aggression](#)
- ▶ [Anatomical Adaptations for Fighting](#)
- ▶ [Assessment of Fighting Ability](#)
- ▶ [Costs of Aggression](#)
- ▶ [Evolution of Fighting Assessment Abilities](#)
- ▶ [Male Adaptations to Assess Fighting Ability](#)
- ▶ [Nonverbal Indicators of Dominance](#)
- ▶ [Physical Aggression](#)
- ▶ [Recalibration Theory of Anger](#)
- ▶ [Sex Differences in Ability to Assess Fighting Ability](#)
- ▶ [Strength and Anger-Proneness](#)
- ▶ [Upper Body Strength and Fighting Ability](#)

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Fighting Sport

► [Combat Sport](#)

Fight-or-Flight

► [Evolved Physiological Reactions](#)

Filial Imprinting

► [Imprinting](#)

Filial Infanticide in Humans and Other Primates

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Synonyms

[Filicide](#); [Parental filicide](#); [Parental infanticide](#)

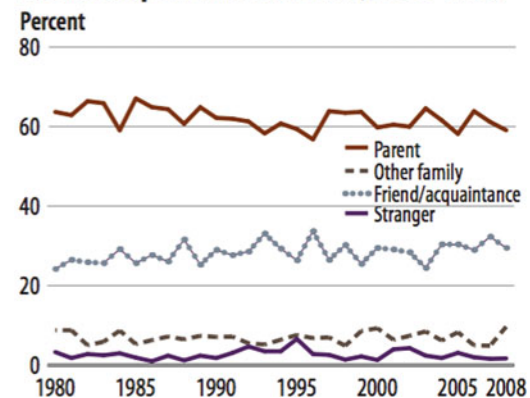
Definition

Filial infanticide is the deliberate killing of one's own child, usually during the first year of its life

Introduction

Filial infanticide is the practice by which a parent terminates its own offspring. According to the US Department of Justice, homicides of children under the age of 5 are most often perpetrated by a parent (Fig. 1). Though there are a variety of motives leading parents to commit filicide, the practice has been prevalent in both humans and animals throughout history and has held steady in the United States in recent decades, despite a precipitous drop in all other forms of homicide during that same period (Cooper and Smith 2011). At first glance, the killing of one's own child seems tremendously paradoxical, in terms of achieving reproductive success, due to the immediate reduction of fitness following the loss of offspring. Conversely, there may be an underlying evolutionary drive toward filicide in certain instances through the advancement of inclusive fitness. Certain filicide cases may actually facilitate a net gain of reproductive success despite the initial fitness loss resulting from the killing. As such, filial infanticide may act as a form of natural

Homicides of children under age 5, by relationship with the offender, 1980–2008



Filial Infanticide in Humans and Other Primates, Fig. 1 Infanticide cases of children under the age of 5 are most likely to be perpetrated by a parent. (Retrieved from: Cooper and Smith 2011)

selection, advancing the success of the perpetrator through inclusive fitness.

Inclusive Fitness

The theory of inclusive fitness was first developed by W. D Hamilton, one of the leading evolutionary theorists of the twentieth century. He defined inclusive fitness as the support of successful offspring, and possibly grand-offspring, thus maximizing the success of favorable genes those offspring inherit (Hamilton 1964a). Personal fitness, or direct fitness, is a subset of inclusive fitness and is defined by the number of successful offspring that one produces. Inclusive fitness begins with personal fitness but extends to other strategies for long-term reproductive success. Inclusive fitness is also comprised of indirect fitness, measured by reproduction of an individual's relatives (Hamilton 1964b). Organisms may engage in kin selection, which helps to explain altruistic behaviors that further the reproductive success of close relatives despite personal cost, and still acquire fitness gains for the shared genes (Smith 1964). Interestingly, considering fitness at a level larger than the individual lends direct support to the gene-centric, rather than the individual-centric view of evolution (Dawkins 1976; Burt and Trivers 2006). The gene-centric view of evolution is currently the unifying theory of sociobiology. Recognizing the comprehensive nature of inclusive fitness is crucial to understanding the motivating forces of complex social behaviors.

In order to analyze the proximate motives of filicide, the nature of the relationship between parent and child must be explored. Of course, parents are motivated to care for their young in order to maximize overall survival rates and achieve reproductive success. Due to the inclusive fitness benefits gained by investing in successful offspring, parents provide care for their offspring with little to no reciprocity. However, parental care is a finite resource, and friction arises when offspring require a greater degree of care than a parent is prepared to offer. This results in a phenomenon called parent-offspring conflict by Robert Trivers, one of the founding theorists of sociobiology (Trivers 1974). Within this conflict, offspring must vie for parental investment against other competing factors,

including and especially their siblings. If an infant were to display early signs of deficiency, thereby requiring a higher degree of parental investment, a parent may choose to neglect the weakling in order to further invest in healthy individuals with a greater chance at ultimate survival. Therefore, evolutionary conflict leads to unequal allocation of parental investment favoring stronger offspring over vulnerable ones.

Filial Infanticide

In 1979, Sarah Blaffer Hrdy first classified potential motives of infanticide. Most were described as providing evolutionary benefit to the perpetrator. The first category is the exploitation of the infant as a resource, often through cannibalistic practices. Second is the elimination of resource competition. When the death of an infant will increase resource availability for the rest of the population, the perpetrators are almost never parents of the victim, who have little incentive to divert resources from their own inclusive fitness to that of others. Non-parents, however, may experience fitness gains by killing another's offspring in order to divert limited resources toward their own offspring. The third potential motive is sexual selection, wherein a male perpetrator terminates offspring that are not his own in order to reduce reproductive success of competitors and potentially gain access to fertile females. This form of infanticide serves to assert dominance in a group, maintain control over sexual partners, and increase reproductive success. These first three categories rarely apply to infanticide perpetrated by parents (Hrdy 1979).

Hrdy outlines the fourth potential motive for infanticide as parental manipulation: the elimination of an ill-timed, handicapped, or unhealthy infant in order to spare resources for offspring more likely to achieve success. This form of infanticide is always perpetrated by the parent of the infant and may even be driven by empathy, as discussed below. Rather than invest in an offspring that has little chance at ultimate survival, it may be favorable to end the infant's suffering early, for both the benefit of the child enduring the

pain and the parent investing resources attending to an infant that is unlikely to be reproductively successful. Parental manipulation appears to be the most common motive for filial infanticide because of its focus on maintaining reproductive fitness and terminating weak offspring in order to invest in healthy ones (Hrdy 1979). Filial infanticide may act as a potential solution, ensuring net reproductive success via direct and indirect fitness gains.

Inopportune Birth of Offspring

Lack of Childcare/Presence of Other Offspring

One instance in which infanticide leads to a potential advancement of inclusive fitness is through the termination of a mistimed infant. The moustached tamarin (*Saguinus mystax*) is a species of New World monkey in which the common social structure is that of very small groups with multiple adult males and communal alloparenting. A recent case study of these tamarins details how the lack of childcare and presence of other offspring at the time of birth may lead to infanticide (Culot et al. 2011). In this study, researchers observed a wild female tamarin kill her own infant when another female was pregnant and there were only 2–3 male helpers in the group. The perpetrator had given birth to numerous successful offspring in the past, when there had been 4–5 capable helpers present. Researchers suggested that this infant may have been terminated due to the low availability of male helpers at the time of birth. According to these researchers, “the possible maternal infanticide reported fits the parental manipulation hypothesis and can occur in a group with a poor capacity to raise offspring with multiple breeding females, with birth intervals shorter than 3 months, combined with an estimated low infant survival probability.” Indeed, the number of helpers (and their ratio to the number of infants) in a group directly correlates with infant survival rates (Culot et al. 2011).

Humans face comparable challenges relating to the lack of childcare and presence of other offspring, acting as a contributing factor in cases of infanticide (Bourget et al. 2007; Daly and

Wilson 1988, p.51). The Ayoreo peoples are nomadic hunter-gatherers indigenous to the central plains of South America, some tribes of which remain uncontacted or minimally so. A striking degree of filial infanticide has been reported in this population and follows a consistent pattern. Bugos and McCarthy studied filicide within the Ayoreo Indian population and found that infants born to women with limited resources and male protection are commonly terminated immediately following birth. Survival of a healthy newborn in the Ayoreo community is highly dependent upon a mother’s physical and social support, or lack thereof, at the time of birth (Bugos and McCarthy 1984). In Canada, perpetrators of maternal infanticide tend to be younger and unwed, with single mothers committing over half of the maternal infanticide cases reported to police (Daly and Wilson 1987, 1988). Interestingly, a cross-cultural study showed a dramatic reduction of infanticide cases in societies in which social relief was offered to lighten maternal burden, supporting the view that infanticide is linked to ecological factors (Granzberg 1973).

An infant born at an inopportune time, when the parent faces economic stress with limited childcare options, carries a greater than normal burden to parents (Smithey 1997). This is especially true when prior offspring are still dependent on parental care, whose survival is placed at greater risk when subsequent children are born (Hrdy 1979). Therefore, inopportune birth timing may be a contributing motive for filial infanticide. Termination of the infant could result in an increase of inclusive fitness by allowing the perpetrator to distribute proper investment in other current or future offspring.

Economic/Resource Stress

Another potential factor in filicide is economic stress. In 2002, cases of maternal infanticide in the Federal Bureau of Investigation’s Supplemental Homicide Reports were cross-referenced with the US Census information to reveal those in which financial instability may have played a role. The combined data indeed exhibits a correlation between economic stress and infanticide (Gauthier et al. 2003). This corroborates an earlier

study in which researchers analyzed interviews of infanticide perpetrators in Texas and found that unstable economic conditions along with a lack of interpersonal support was a common theme specific to the filicide cases (Smithey 1997).

An ethnographic study of the Yānomamō tribal peoples also recorded circumstances of infanticide in which a newborn is at risk of termination if born in close proximity to an older sibling, causing resource competition between the two for milk (Chagnon 1968). Similarly, Ayoreo women are more likely to commit infanticide when a child is born too soon following the birth of a previous one (Bugos and McCarthy 1984). Resource scarcity lends itself to competition between siblings (Trivers 1974), potentially leading to parental intervention in the form of infanticide to ensure survival of older children, for whom more investment has already been expended.

These reports suggest that, both in humans and tamarins, if a mother suffers from economic/resource instability or a lack of childcare support, she is more susceptible to perpetrating infanticide (Gauthier et al. 2003; Smithey 1997). When resources become limited, siblings are placed in competition against one another (Trivers 1974). Therefore, the termination of an infant could advance inclusive fitness in certain instances if it allows the perpetrator to invest limited resources in other current and/or future offspring and increase their chance of survival.

Parental Perception of Fitness

In 1998, in a band of wild saddle-back tamarins (*Saguinus fuscicollis*), researchers watched as a newborn was killed and partially consumed by its mother after having fallen from its carrier numerous times (Herrera et al. 2000). The researchers inferred that the motive behind the filicide was parental manipulation, likely due to the perceived damage that the several falls had inflicted. Though the newborn had actually sustained minimal visible damage (Herrera et al. 2000), its mother may have chosen to remove investment in the child early on because she

perceived the falls themselves as an early sign of weakness.

Researchers concluded that the mother's motive behind the infanticide was most likely in line with Hrdy's parental manipulation hypothesis (Hrdy 1979). Meat exploitation was ruled out because only the head and brain of the infant were consumed, ignoring the rest of the body. Additionally, the tamarin's bite was inconsistent with its usual killing bite used with prey. The categories relating to sexual selection and resource competition were also ruled out, given that this was a case of filial infanticide in which the mother killed her own child (Herrera et al. 2000).

Similarly, in 1985, it was reported that Brazilian shantytown mothers tend to entirely remove parental investment when they perceive a child to have a physical or developmental disability, purposefully withholding care and food (Scheper-Hughes 1985). Early on, mothers tend to prefer babies with characteristics of a "fighter" and "survivor," and passive babies are deemed as "good for nothing" (Scheper-Hughes 1985). Though the infants are not typically terminated by direct infanticide, the removal of parental investment leads to the same fate (Daly and Wilson 1987). Similar attitudes toward weak or deficient infants have been recorded in history and pseudo-historical folklore. For example, the Spartans of Ancient Greece were said to have eliminated weak children from their population in order to perfect the army (Melillo 2017). More recently, Ayoreo Indian mothers have been reported to terminate newborns displaying signs of illness or deformity due to perceived weakness and limited survivability (Bugos and McCarthy 1984). Like behavior has also been found in the Aymara community in Andes of Bolivia, where biological defects were viewed as justification for infanticide (de Hilari et al. 2009). Indeed, a cross-cultural analysis by Martin Daly and Margo Wilson noted 21 societies in which the rejection of a newborn of poor health could be categorized as an adaptive parental response (Daly and Wilson 1984).

These studies unify Trivers' parental investment theory and Hrdy's parental manipulation hypothesis. Therefore, at least in extreme

conditions of limited resources or alloparental care, parental perception of offspring's health and vigor is vital to infant survival, given that a mother's investment is directly related to her perception of the child's fitness early on. In both humans and tamarins, the infanticide of offspring with a seemingly slim chance of ultimate survival may advance the parent's inclusive fitness.

Empathy and Altruism

Altruistically motivated homicide, known colloquially as euthanasia, may be the most common mode of filial infanticide (Resnick 1969). An altruistic act is one performed out of selfless concern for the well-being of another despite cost incurred, however small, to the actor. Perpetrators of altruistic filicide are thus driven to spare their child physical or mental suffering (Bourget et al. 2007; Friedman et al. 2005; Resnick 1969), and empathy is the proximate cause of the act. Of note, some cases of altruistic infanticide are based on a deluded belief of the child's suffering (Bourget et al. 2007; Friedman et al. 2005). Hrdy calls this "social pathology" (Hrdy 1979) because these acts are likely maladaptive. However, true altruistically motivated filicide, in which the suffering of the child is real, may indeed be regarded as adaptive through inclusive fitness gains in some cases.

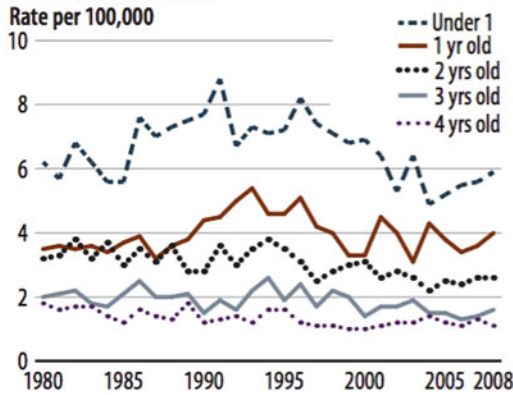
In Australia, researchers found that altruism plays a primary role in the termination of infants by their mothers (Eriksson et al. 2016). In one instance, an infant was suffering from a chronic disability, and his mother sought an end to his struggles and pain. Another infant was terminated due to recent episodes leading to an unstable home environment and the mother's fear that the child would be irreversibly traumatized. In both cases, the homicides were driven by empathy with the aim of alleviating their child's suffering. Additional studies have documented altruistically motivated filicide as a worldwide phenomenon (Gowda et al. 2018; Razali et al. 2015). Though empathy may be the proximate drive of these filicides, gains in fitness may still underpin the ultimate mechanisms by allowing the parent to invest in future healthy offspring.

Discussion

When considering the evolutionary roots of behavior, it is necessary to differentiate between proximate cause and ultimate cause. According to Ernst Mayr, "proximate causes govern the responses of the individual (and his organs) to immediate factors of the environment whereas ultimate causes are responsible for the evolution of the particular DNA code of information with which every individual of every species is endowed" (Mayr 1961). A proximate cause is an immediate and mechanistic response driving an action. On the other hand, an ultimate cause serves as the greater evolutionary reason for the act to persist, focused on the natural selective forces at play and the resulting fitness gains of the act. Individuals may understand the proximate drive of their actions, but ultimate mechanisms are almost always hidden from their awareness.

Though filial infanticide may bring an immediate cost to the parent's fitness, given the resulting loss of offspring, the act may still advance overall inclusive fitness in the long run. Factors predicting such cases are inconvenient timing (with relation to finances, childcare options, and the presence of siblings), the presence of weakness and/or physical defects, and empathy for a suffering child. Because infanticide lessens economic burdens and removes stressors prohibiting the parent from caring for other offspring (whether they be future or current), a gain in inclusive fitness is possible. Infanticide of offspring perceived to be weak or deficient, whether the act is motivated by empathy or not, may also advance inclusive fitness for similar reasons. The foreseeable advancement of a parent's inclusive fitness may be the ultimate mechanism underpinning infanticide. In the case of altruistic filicide, in which the perpetrator is acting out of a selfless concern for its child, empathy may be of proximate cause, driving the act itself. However, inclusive fitness is still likely to be the ultimate cause. Altruistic filicide allows a parent to give rise to future healthy offspring with only minimal investment given to a weak one, while simultaneously alleviating the suffering of the infant in question.

Homicides of children under age 5, by age of victim, 1980–2008



Filial Infanticide in Humans and Other Primates, Fig. 2 Infanticide risk increases with age, with the highest number of victims aged less than 1 year. (Retrieved from: Cooper and Smith 2011)

The demographic data on filial infanticide in humans support this theory. The overwhelming majority of infanticide victims are less than 1 year of age upon termination and the risk of infanticide decreases with age (Fig. 2; Cooper and Smith 2011; Fox and Zawitz 1999). This can be interpreted through the lens of Trivers' parental investment theory: the earlier the termination occurs, the more resources are preserved. It is also relevant to note here that parental cost is heavily front-loaded in mammals and steadily declines with the age and developmental independence of the offspring.

In most cases, the fitness of current and/or future siblings is favorably impacted by infanticide through the resulting boost in parental investment. The elimination of a competitor, their sibling, ultimately furthers their likelihood of survival (Trivers 1974). According to Hrdy and Hausfater, "The death of an infant and termination of parental investment will sometimes improve the chances for survival of either the mother or her older offspring [possibly both] or will otherwise lead to the greater net reproductive fitness for the mother of the infant, the father, or both" (Hausfater and Hrdy 1984). The filicide of an infant instantly lowers the number of offspring vying for care, increasing the amount of parental

investment and resources available to the remaining siblings.

Conclusion

Further research into the behavioral ecology of filicide is needed. There is a dearth of recent empirical studies documenting the impact that infanticide has on current siblings. Such studies would provide powerful evidence in support or refutation of the parental investment-based theories of filial infanticide. Further, with greater confidence in the ultimate mechanism of filial infanticide, we can bolster support for policies that reduce its prevalence in humans. For example, guaranteed socialized support for the childcare, healthcare, and education of children, especially infants, may reduce the degree of perceived parental investment necessary for the thriving of a newborn, especially those with special needs. This, in turn, could reduce the perception that children compete with each other for limited time, attention, and resources from parents. The reduced perception of competition could undercut the evolutionary psychological triggers that drive filial infanticide and, potentially, save lives.

Cross-References

- [Filicide](#)
- [Infanticide](#)
- [Infanticide and Parenting](#)
- [Infanticide in Nonhumans](#)
- [Marital Status and Infanticide](#)
- [Methods of Filicide](#)
- [Sex Differences in Death by Filicide](#)
- [Predictors of Infanticide](#)

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Filicide

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Synonyms

Child homicide; Familicide; Infanticide; Neonaticide

Definition

Filicide is the killing of an underage victim by a caretaker (i.e., genetic parent or stepparent). Filicides are conventionally categorized as infanticide if the victim is <1 year of age and neonaticide when the victim is killed <24 h after being born.

Introduction

Evolutionary psychologists Martin Daly and Margo Wilson (1988) proposed the hypothesis that homicides, including filicide, occur in the context of reproductive conflicts. A reproductive conflict occurs when the fitness interests (i.e., interests pertaining to the potential number of offspring sired) one individual has come at a cost to the fitness interests of another individual. It may at first seem contradictory that there could occur reproductive conflicts between offspring and their caretakers, as they share the evolutionary significant interest in the offspring's eventual reproduction. However, as the scholarly works of evolutionary theorists such as Richard Alexander (1979), William D. Hamilton (1964), and Robert Trivers (1972, 1974) collectively inform on, there are circumstances in which a caretaker's investment of resources in a given offspring may not necessarily reward the caretaker with an equivalence of fitness return. In such circumstances there arises a reproductive conflict with regard to the level of investment the caretaker makes in the offspring. The works of these evolutionary theorists further inform on the fact that caretakers who identify circumstances in which the potential fitness returns of their investment may not be rewarding, and adjust their level of investment accordingly, may ultimately leave more offspring than those caretakers who lavishly invest in all offspring in their care regardless of the potential fitness return. This will, in turn, inevitably lead to the evolution of the ability to perform discriminant parental investment in the species in question.

Daly and Wilson (1988) noted that there is no theoretically sound reason to expect that humans

have been immune to the selection processes favoring individuals with the ability to perform discriminant parental investment. Fostering children to reproductive maturity in our species is dependent on relatively high levels of investment over a prolonged period of time. And in our ancestral past, these resources would be limited and finite for each individual caretaker. In conditions where the caretaker's investment would not guarantee a fitness return (e.g., the survival of offspring to reproductive maturity), investing these resources indiscriminately would, in evolutionary terms, be an irrevocable waste. Drawing on this knowledge, Daly and Wilson proposed that filicide may occur as a rare and extreme result of discriminant parental investment, where the parent's solicitude towards the child is accidentally lowered to lethal levels.

Although homicide is a behavioral action, Daly and Wilson (1988) argued that adaptation must be sought at a psychological rather than behavioral level when studying its perpetration. They proposed that there are psychological mechanisms that are triggered when individual caretakers assess whether and how much to invest in a given child in their care. These mechanisms may elicit a range of behavioral responses, including violence and neglect at both lethal and nonlethal levels. According to Daly and Wilson, it is these psychological mechanisms that are the products of evolutionary selection forces and not the range of behavioral responses that may be performed. Thus they proposed that filicide is an epiphenomenon, a by-product of evolved psychological mechanisms that have the adaptive function of enabling the individual to perform discriminant parental investment.

Later, evolutionary psychologists Joshua Duntley and David Buss (2008, 2011) proposed that there are psychological mechanisms which have been selected for the specific function of eliciting homicide perpetration – including filicide. They argued that psychological mechanisms that specifically elicit filicide perpetration would be favored by evolutionary selection processes because killing a child would ensure a more abrupt and lasting prevention of any potential

waste of finite resources than a mere nonlethal reduction in parental investment would.

Disaggregating Filicide to Identify Patterns in Characteristic Traits

Considering under what circumstances a conflict over parental investment might arise in our species' ancestral past, Daly and Wilson (1988) disaggregated filicide into subcategories depending on the perpetrators sex, genetic relationship to the victim, and psychopathology. In doing so, they uncovered a unique pattern of characteristic traits for each subcategory.

Disaggregating Genetic Parents and Stepparents as Perpetrators

As genes are the unit for evolutionary selection, the reproductive value of an offspring to a caretaker is, at least in part, conditional on their genetic relatedness. The greatest potential for a reproductive conflict may therefore be in the absence of relatedness (Alexander 1979; Hamilton 1964). It is therefore expected that caretakers will experience a greater reluctance towards investing in stepchildren than in their genetically related children (Daly and Wilson 1988, 1994, 2001; Duntley and Buss 2008, 2011). And it is therefore expected that filicides perpetrated by genetic parents and stepparents will differ in their characteristic trait. Firstly, it is predicted children living in stepparental households will be at an increased risk for victimization compared with households with two genetic parents. Secondly, it is predicted that stepparental perpetrated filicides will be characterized by the caretaker's hostility towards the victim and lapses in parental solicitude. Specifically, it is predicted that stepparents will typically perpetrate fatal abuse. In contrast, genetic parents are predicted to more often have altruistic motives for their filicides and thus be more likely to perpetrate their homicides by methods that limit their victims' suffering.

Studies that disaggregate filicides perpetrated by stepparents and genetic parents lend

empirically support the above predictions. For instance, Daly and Wilson (1994) found in a Canadian national sample, 1974–1990, that victims were 60 times more likely to be killed by a stepparent than a genetic parent and further that stepparental perpetrators were 120 times more likely to beat their victims to death than genetic parents were. In contrast, genetic parents were more likely to shoot or asphyxiate their victims. Similar findings are confirmed in other samples from Canada (Daly and Wilson 1988; Harris et al. 2007; Wilson et al. 1995), the USA (Daly and Wilson 1988; Weekes-Shackelford and Shackelford 2004), Australia (Alder and Polk 2001), the UK (Flynn et al. 2013; Daly and Wilson 1994; Wilson et al. 1995), the Netherlands (Liem and Koenraadt 2008a), Finland (Vanamo et al. 2001), and Sweden (Daly and Wilson 2001; Nordlund and Temrin 2007; Somander and Rammer 1991; Temrin et al. 2004, 2011).

The listed studies have explored the characteristics of filicides perpetrated by stepfathers. One may however expect that living with a stepmother may pose an equal, if not greater, risk for filicide (Harris et al. 2007). As mothers make greater parental investment in children than fathers, in terms of direct physical resources and therefore also time, the reproductive cost of investing in a genetically unrelated child may be greater for women than for men. The potential for reproductive conflict over parental investment may thus be greater when the caretaker is a stepmother than a stepfather.

Two studies on filicide that included stepmaternal perpetrators have been performed on a Canadian national sample, 1997–2003 (Harris et al. 2007), and a US national sample, 1976–1994 (Weekes-Shackelford and Shackelford 2004). Both studies found an overrepresentation of both stepmaternal and steppaternal perpetrators compared to genetic parents. Further, in the Canadian study, Harris et al. (2007) had access to data that revealed that children victimized by their stepmothers had experienced harsher treatment leading up to the homicide compared to children victimized by stepfathers or genetic parents of either sex.

Disaggregating Maternal and Paternal Perpetrators

When a species has two sexes that contribute different levels of parental investment and face different challenges in securing reproductive success, heritable sex-differentiated traits may evolve (Trivers 1972). Taking into account the unique challenges that faced ancestral women and men, respectively, Daly and Wilson (1988) proposed sex-differentiated psychological mechanism underpinning filicide perpetration and predicted that the characteristics of such homicides would differ with maternal and paternal perpetrators, respectively.

To secure the highest potential reproductive success across a life span, individuals calculate how much parental investment to allocate in present versus future offspring. Such calculations may be conscious, but they may also be performed on a level the individual is not conscious of and influenced by processes the individual is not aware. Daly and Wilson (1988) noted that as the individual's residual reproductive potential (fecundity) decreases with age, the potential for having or replacing an offspring also decreases. From this biological fact, they proposed that genetic parents would be less discriminant in their investment in children with age. Specifically, they predicted that a caretaker's young age would be associated with an increase in the risk for filicide. Because reproductive fecundity declines at an earlier age for women than for men, they further predicted that maternal perpetrators would be younger than paternal perpetrators.

There is empirical support for their predictions cross-culturally. For instance, in a Fijian national sample, 1993–1996, the mean age of maternal filicide perpetrators was 25 years, whereas the mean age of paternal perpetrators was 30.3 years (Adinkrah 2000, 2001, 2003). Similar findings have been confirmed in samples from the USA (Friedman et al. 2005), the Netherlands (Liem and Koenraadt 2008a), and Finland (Kauppi et al. 2010; Vanamo et al. 2001).

As women gestate and nurse, they make more direct and heavy investments in the youngest children. It is therefore predicted from EP perspectives that the youngest children would be at an

increased risk of victimization by their mothers (Daly and Wilson 1988; Duntley and Buss 2011). There is empirical support for this prediction cross-culturally. For instance, in a Finnish national sample, 1970–1994, mothers perpetrated 90% of the filicides where the victim was killed during their first year of life (Kauppi et al. 2010). Similar findings have been confirmed in another Finnish samples (Vanamo et al. 2001), and in samples from the USA (Overpeck et al. 1998), Canada (Harris et al. 2007), the UK (Flynn et al. 2007, 2013), Fiji, (Adinkrah 2000, 2001, 2003), the Netherlands (Liem and Koenraadt 2008a), Denmark (Laurssen et al. 2011), and Sweden (Nordlund and Temrin 2007; Somander and Rammer 1991).

Considering the amount of resources required to foster a child to reproductive maturity, one may expect that it would have more often than not required two parents in our ancestral past. Further, having a child from a previous union may have been an impediment for future relationships, as potential new partners could perceive a stepchild as a reproductive burden. It has therefore been proposed that single parenthood may increase the risk for a reproductive conflict between a caretaker and child (Daly and Wilson 1988; Duntley and Buss 2011) and further predicted that children will be at an increased risk for victimization in households with a single caretaker compared to households with two genetic parents. Theoretically, single parenthood may be an important cue for discriminative parental investment for women and men equally. And in a Swedish national sample, 1965–1999, where maternal and paternal perpetrators were not disaggregated, 32.2% of the victims lived with a single parent, yet only 12.6% of the children in the general population lived with a single parent (Temrin et al. 2004). However, the rates of single mothers in the general population are greater than the rates of single fathers. And there is cross-cultural empirical support for that single parenthood is characteristic of maternal perpetrators. For instance, in a British national sample of infanticides, 1996–2001, less than half the mothers were either married or cohabiting with a partner at the time of perpetration (Flynn et al.

2007). Similar findings have been confirmed in the USA (Friedman et al. 2005; Overpeck et al. 1998; Stone et al. 2005), Canada (Daly and Wilson 1988; Harris et al. 2007), Australia (Alder and Polk 2001), Fiji (Adinkrah 2000, 2001), and Italy (Camperio Ciani and Fontanesi 2012).

A reproductive challenge that has been singular to ancestral men is the potential uncertainty as to whether or not a child in their care is their genetic offspring. It has therefore been argued that evolutionary selection would favor psychological mechanisms among men that would protect against being cuckolded. Such mechanisms may include a heightened sensitivity to cues of and concern with a partner's sexual infidelity and proprietary feelings towards their partner. It has further been proposed that there will be sex-differentiated motives for partner homicide. Specifically, it has been predicted that there will be an increased risk for male-perpetrated partner homicide when the woman has left or intends to leave the relationship (Daly and Wilson 1988; Duntley and Buss 2008; 2011).

There is empirical support for this prediction, as sexual jealousy and female-initiated relationship dissolution are the context in which intimate partner homicides most frequently occur (e.g., Daly and Wilson 1988; Shackelford et al. 2003).

From the same reasoning, it has further been predicted that familicide (i.e., homicides where a current or former intimate partner and one or more children are killed) will predominantly be perpetrated by men and occur in the context of the woman actually or potentially leaving the relationship (Harris et al. 2007; Wilson et al. 1995). There is empirical support for these predictions cross-culturally. For instance, 93% of familicides in Canada, 1974–1990, and 96% of familicides in the UK, 1977–1990, had male perpetrators (Wilson et al. 1995). Further, the children were rarely the objects of conflict that elicited the familicide. Rather, the familicide was elicited by a relationship dissolution initiated by the woman. Similar findings have been confirmed in other Canadian and UK samples (Daly and Wilson 1988, 1994; Harris et al. 2007) and in samples from the USA (Friedman et al. 2005), Australia (Alder and Polk 2001), Fiji (Adinkrah 2001,

2003), the Netherlands (Liem and Koenraadt 2008b), Finland (Kauppi et al. 2010;), and Sweden.

It has further been predicted that men may perpetrate filicide as part of their attempt to control and punish their current or former partner at a higher rate than women (Harris et al. 2007; Wilson et al. 1995). There is empirical support for this prediction cross-culturally. For instance, in a Swedish national sample, 1965–1999, 72% of the cases that occurred during interpersonal conflict where the motives appeared to be jealousy or revenge on a current or former partner had a male perpetrator (Nordlund and Temrin 2007). Similar findings have been confirmed in other Swedish samples (Somander and Rammer 1991; Temrin et al. 2000) and in samples from Canada (Harris et al. 2007), Australia (Alder and Polk 2001), the Netherlands (Liem and Koenraadt 2008b), and Finland (Kauppi et al. 2010).

From an EP perspective, it has further been proposed that the proprietary feelings men may have towards their partners and children could be associated with their ancestral role as the main providers for the family (Harris et al. 2007; Wilson et al. 1995). It has therefore been predicted that men will be more likely than women to perpetrate filicide and familicide in association with a threat to their role as a provider. There is cross-cultural empirical support for this prediction. In the abovementioned Swedish study, all but one of the filicides that appeared to be motivated economic hardship had a male perpetrator (Nordlund and Temrin 2007). In four of the seven incidents, the male perpetrator killed the whole family. Similar findings have been confirmed in other Swedish samples (Somander and Rammer 1991) and samples from Canada (Daly and Wilson 1988), the USA (Friedman et al. 2005), and Fiji (Adinkrah 2001, 2003).

Disaggregating Perpetrators with Psychopathology

From an EP perspective, psychopathology may be understood as mental states in which the individual no longer perceives or acts in accordance with his or her reproductive interest (Daly and Wilson 1988; Wilson et al. 1995). From this perspective

one may infer the hypothesis that filicides that contradict adaptive logic will be associated with perpetrator psychopathology (e.g., psychosis or suicidal ideation) at a higher rate than those filicides that do not contradict this form for logic (Daly and Wilson 1988; Duntley and Buss 2008; Stone et al. 2005). A series of predictions concerning the characteristics of filicides associated with perpetrator psychopathology follow from this hypothesis.

As the potential reproductive value of a child partly depends on the genetic relationship to the caretaker, one may predict that there will be a higher rate of psychopathology among genetic parents than among stepparents who perpetrate filicide. There is empirical support for this prediction cross-culturally. For instance, in a Swedish national sample, 1971–1980, half of the genetic parents committed suicide in conjunction with the homicide (29 of 58), whereas only a quarter of stepparents did so (one of four) (Somander and Rammer 1991). Similar findings have been confirmed in other Swedish samples (Nordlund and Temrin 2007) and in samples from the USA (Shackelford et al. 2008), Canada (Daly and Wilson 1988, 1994; Harris et al. 2007; Wilson et al. 1995), the UK (Daly and Wilson 1994; Flynn et al. 2013; Wilson et al. 1995), and Finland (Kauppi et al. 2010). However, in a study of filicides in Chicago, 1965–1994, there was no significant difference between stepparents and genetic parents in their suicide rates (Shackelford et al. 2005). According to Shackelford and colleagues, this is the only known study where there is no significant difference between the suicide rates of the two perpetrator categories. Shackelford and colleagues attributed their finding to the small percentage of genetic parents that commit suicide in their sample.

Because the potential reproductive value of an offspring to its caretaker increases as it reaches reproductive maturity, killing an older child is potentially a greater compromise to a caretaker's reproductive success than killing a younger child. It is therefore predicted that there will be a higher rate of psychopathology among perpetrators with older victims than younger victims (Stone et al.

2005). There is empirical support for this prediction cross-culturally. For instance, whereas the rate of lifetime history of mental disorder found among perpetrators of infanticide in England and Wales, 1996–2001, was similar to that of the general population, there was a correlation between an increased risk for suicide and an increase in the victims' age (Flynn et al. 2007, 2013). Similar associations between perpetrators' psychopathology and victims' age are confirmed in other samples from the UK (d'Orban 1979) and from the USA (Friedman et al. 2005; Shackelford et al. 2005, 2008; Stone et al. 2005), Canada (Daly and Wilson 1988b; Harris et al. 2007), Australia (Alder and Polk 2001), Fiji (Adinkrah 2000, 2001, 2003), Italy (Camperio Ciani and Fontanesi 2012), and Finland (Haapasalo and Petäjä 1999; Kauppi et al. 2010).

As an individual's residual reproductive potential is reduced with age, it is predicted that an increase in the perpetrators' age will be associated with an increased probability for perpetrator psychopathology (Stone et al. 2005). There is empirical support for this prediction cross-culturally. For instance, in a Chicago sample, 1965–1994, Shackelford et al. (2005) found that, among genetic parents, there was a greater percentage of perpetrators who were 26 years or older who commit suicide in conjunction with the filicide than perpetrators who were younger (10.8% and 1.5% of the two age groups, respectively). Similar findings have been confirmed in other US samples (Friedman et al. 2005; Shackelford et al. 2008; Stone et al. 2005) and in samples from Canada (Daly and Wilson 1988; Harris et al. 2007), Australia (Alder and Polk 2001), the UK (d'Orban 1979; Flynn et al. 2007, 2013), Italy (Camperio Ciani and Fontanesi 2012), and Finland (Kauppi et al. 2010).

A final prediction concerning filicides associated with psychopathology is that they are more likely to have multiple victims than filicides without such an association. There is empirical support also for this prediction cross-culturally. For instance, in Canadian national sample, 1974–1990, Wilson et al. (1995) found that familicidal perpetrators commit suicide more often than single-victim perpetrators (50.9% and

25.3%, respectively). Similar findings have been confirmed in other Canadian samples (Daly and Wilson 1988) and in samples from the USA (Freidman et al. 2005; Shackelford et al. 2005, 2008; Stone et al. 2005), Australia (Alder and Polk 2001), the UK (d'Orban 1979; Flynn et al. 2013; Wilson et al. 1995), Finland (Kauppi et al. 2010), Denmark (Laursen et al. 2010), and Sweden (Nordlund and Temrin 2007; Somander and Rammer 1991).

Criticism against Evolutionary Psychological Perspectives on Filicide

Criticism against evolutionary psychological perspectives on filicide has mostly focused on whether the cross-culturally confirmed overrepresentation of stepparental perpetrators reflects objective realities or, if so, what alternative explanations than current evolutionary psychological perspectives might there be for this overrepresentation. One of the more prominent critics of evolutionary psychology, the philosopher David Buller (2005), has argued that the overrepresentation may be due to a systematic bias, whereby stepfathers are more likely to be detected and reported than genetic fathers. However, as noted, Buller's conclusion is highly unrealistic considering the number of undetected filicides it implies. With "estimated rates of fatal batterings of Canadian children under 5 years of age in 1974–1990 at 2.6 deaths per million child-years at risk for those residing with and killed by their (presumed) genetic fathers (based on 74 deaths in 28.3 million child-years at risk) versus 321.6 per million child-years at risk for those residing with and killed by stepfathers (55 in 0.17 million child-years at risk). The latter rate is more than 120 times higher than the former. To give Buller's argument its best chance, suppose for the moment that stepfathers were always caught whereas genetic fathers often got away with murder; even so, for the "true" rate of fatal batterings by genetic fathers to equal that for stepfathers, there would have to have been more than 500 undiscovered paternal murders each year in addition to the annual average of 4 that were detected."

Buller's unlikely conclusion might have been due to a lack of calculation of the extent the potential detection bias against stepparent would have to be to annul their overrepresentation in official records. Other critics have based their conclusion of a lack of overrepresentation of stepparental perpetrators on calculation errors. This was the case for Temrin et al. (2000) who concluded that stepparents were not overrepresented as perpetrators in Sweden, 1975–1995. Daly and Wilson (2001) corrected this error and found that stepparents were in fact overrepresented, albeit to a lesser extent than that found in previous studies in other types of societies. Daly and Wilson (2001) further criticized Temrin and colleagues for not presenting their finding, assuming it had been correct, as a local exemption, but rather as disproving the hypothesis of discriminant parental investment depending on genetic relatedness and thus ignoring the overwhelming support the hypothesis has received cross-culturally (see also Temrin et al. 2011 for similar conclusion). A local exemption for the level of risk for stepparental perpetrated filicide in a modern welfare society, such as Sweden, would be more theoretically sound than that an evolved human parental psychology would not be discriminant depending on genetic relationship.

Conclusion concerning a lack of significance of genetic relationship for parental investment may have been due to a theoretical misconception of evolutionary psychology as advocating determinism. It is crucial to note that the proposal of evolved psychological mechanisms is not a proposal of determinism. With its theoretical foundation firmly placed in modern evolutionary biology, evolutionary psychology stresses the importance of the individual's environment for eliciting a manifestation of evolved psychological mechanisms. In other words, the expression of evolved psychological mechanisms is context specific – triggered and manifested only under evolutionary salient cues in the environment. From an evolutionary psychological perspective, filicide rates are not expected to be invariant between societies, nor are the rates of different perpetrator categories expected to be invariant between societies. Rather, cross-national

variations in the magnitude of risk are expected, as the psychological mechanisms that may lead to filicide are activated by circumstances that are salient cues to reproductive conflicts. For instance, it is expected that the risk stepparents will pose for filicide in a given society will be closely associated with cues for extreme discriminative parental investment (e.g., if it is a social or economic burden caring for stepchildren) (Daly and Wilson 2001). It is therefore not a threat to the validity of the evolutionary psychological perspectives that different societies do show different rates for the risk for filicide in general or for different perpetrator categories. It is actually to be expected that, for example, whereas the risk for victimization by a stepfather was 100 times higher than the risk for victimization by a genetic father in the USA in 1972 and 70 times higher in Canada, 1974–1983 (Daly and Wilson 1988), the risk was reduced in Sweden, 1965–2009, to a rate where perpetrators per million parents per year was 1.9 for genetic parents and 3.2 for stepparents ($p = 0.008$) (Temrin et al. 2011).

Daly and Wilson (2001) argued that a possible explanation for why stepparents were not over-represented as filicide perpetrators to the same extent in current day Sweden as in other types of societies is the alleviation of pseudoparental obligation of stepparents in modern, well-developed welfare societies. As parental investment required from stepparents is reduced in such societies, this will in turn alleviate potential reproductive conflicts in step-relationships, thus decreasing the risk for filicide. Daly and Wilson (2001) further argued that as fatal abuse is less likely to occur in societies where corporal punishment of children is illegal, such as in current-day Sweden, filicide perpetration by fatal abuse might be an inappropriate assay for measuring discriminant parental investment in such societies.

A second example of a possible theoretical misunderstanding concerning determinism by critics of evolutionary psychology is seen in homicide researchers Alder and Polk's (2001) suggestion that the fact that not all stepparents perpetrate filicide somehow undermines EP perspectives on stepparental perpetrators. However, as in most psychological research and research on

the patterns in characteristic traits of homicide, evolutionary psychological perspectives search for tendencies on group levels. The proposed predictions concerning the patterns in characteristic traits for filicide are therefore not expected to be absolute – one does not expect every single family who shares the listed characteristic traits to be associated with an increased risk for filicide to be determined for filicide. Just as explanations at a proximate level of analysis for the overrepresentation of stepparental perpetrators, such as jealousy or lack of attachment to a stepchild, do not imply that filicide is determined to occur at the hands of stepparents or in the context of such emotions, merely statements of what contexts might increase the risk for filicide perpetration.

However, a truly comprehensive theory for understanding filicide should however account for the apparent individual differences caretakers have in their risk for perpetration. Only a small fraction of caretakers who find themselves in circumstances associated with an increased risk actually perpetrate filicide, and current evolutionary psychological perspectives lack an explicit account of why individuals would differ in this way in similar circumstances.

Conclusion

Drawing on theoretical and empirical knowledge from the fields of evolutionary theory and biology of how discriminant parental behavior inevitably evolves, evolutionary psychologists have derived the hypothesis that filicide occurs in the context of reproductive conflicts and as an extreme outcome of discriminative parental investment. This hypothesis has in turn catered a comprehensive theoretical foundation for disaggregating filicide into meaningful subcategories, depending on the perpetrators' sex, genetic relationship to the victim, and psychopathology. The hypothesis has further enabled the successful prediction of the characteristic traits of the respective subcategories. As the predictions derived from the hypothesis have gained cross-cultural, empirical support, the validity of the hypothesis has become strengthened.

Cross-References

- David Buss
- Filial Infanticide in Humans and Other Primates
- Frugivory By-Product Hypothesis
- Marital Status and Infanticide
- Martin Daly and Margo Wilson (Founders of Evolutionary Psychology)
- Homicide Fantasies and Evolved Homicide Module Theory
- Parental Investment Theory
- Parent-offspring Conflict
- Partner Homicide
- Predictors of Infanticide
- Risk Variation with Parent Age
- Sex Differences in Death by Filicide

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Financial and Hierarchy Maintenance

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Definition

The need to maintain social hierarchy social status will lead individuals to make matrimonial decisions based on social connections and financial status. As such, individuals may restrict potential marriage partners through set marriage patterns

such as endogamous marriage, marrying within a specific group, or isogamous marriage, marrying someone of equal status. In rare cases, hypergynous marriages may also occur where an individual will marry into a higher social class or social status. This need to preserve social rank and financial status will also extend into inheritance patterns with specific offspring being selected as the preferred heir. Historically this most often took the form of primogeniture with the eldest son being the preferred inheritor (Hrdy 1992, 1993).

Introduction

Among societies with heritable wealth, a scarce resource, specific inheritance patterns will develop which are designed to guarantee the financial and hierarchical status within families and/or social classes. This pattern can be seen clearly in historic aristocratic families who arranged and secured marriages and alliances, which were designed to best preserve the social status and wealth of ruling families.

Heritable Wealth

Heritable wealth can take multiple forms: land, livestock, money, titles, or other forms of wealth. Social status can also be part of the transmission of wealth from one generation to the next. The transmission of wealth can take several forms including primogeniture (eldest child, often the eldest son), ultimogeniture (youngest child, often the youngest daughter), passage to a favored heir (usually a son), distribution among all sons or all daughters, or an even distribution among all heirs. In agricultural societies, land becomes the method of wealth transmission, while in stratified societies, inheritance will include titles, social status, and substantial wealth.

Heritable wealth, whether land, titles, or other forms will lead to specific inheritance patterns which are designed to secure the passage of wealth from one generation to the next. Inheritance laws will favor certain heirs over others creating inheritance patterns such as primogeniture, which was prevalent in Medieval Europe. In

historic European cultures, primogeniture secured the passage of titles, especially the throne, to the eldest male heir.

The transmission of heritable wealth fosters strict marriage patterns. Among stratified societies with large amounts of heritable wealth, individuals were required to make endogamous and/or isogamous marriages. By marrying within their own social group, it maintained the wealth or status of the group/family. Ultimately the desire to secure the transmission of wealth will lead to the creation of a closed social group and may ultimately lead to intermarriage among close relatives (e.g., uncle-niece marriage among the Spanish royal house in the fifteenth, sixteenth, and seventeenth centuries).

Boone (1986, 1988) found that high nobility sought endogamous and/or isogamous marriages for their firstborn sons, while lower status nobility often arranged endogamous hypergynous marriages for their daughters. By marrying their daughters up, possibly to the sons of the high nobility, they were able to bring additional power, prestige, and social connections to the family. Such marriages were made through political alliances and secured by substantial dowries.

Dickemann (1979) found that among the aristocracy of medieval Europe, eldest sons inherited their father's land, titles, wealth, and social status through primogeniture. This inheritance pattern also dictated that only sons were eligible to receive the greatest inheritance, the throne.

Primogeniture first appeared as an inheritance pattern during the reign of the Capetian (French) kings in the tenth century (Duby 1978). Prior to the tenth century, inheritance was often passed to a favored male heir who may or may not have been the firstborn. There were three types of potential heirs, children born into a marriage, adopted children, and illegitimate children born outside marriage. Children born to a marriage were the first to inherit followed by adopted children. Illegitimate children were not allowed to inherit family estates or principle titles, although they could inherit less important titles or wealth.

To secure the inheritance, and prevent in-fighting, only the eldest sons of the medieval French aristocracy were allowed to marry. Only in the event that an elder brother died without

marrying or leaving an heir would a younger son be allowed to marry. A slightly different pattern would develop in medieval England where all sons were allowed to marry, but only the eldest son was eligible to inherit the familial estate.

Conclusion

When resources are scarce, such as heritable wealth, distinct patterns for marriage and inheritance will develop, which are designed to maintain the financial standing and hierarchy within a family or social group.

Cross-References

- [Birth Order](#)
- [Differential Parental Investment](#)
- [Kin Selection](#)
- [Nepotism](#)
- [Parental Investment Theory](#)
- [Social Status](#)

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Financial Distress

- ▶ [Economic Hardship](#)

Financial Pressure

- ▶ [Economic Hardship](#)

Financial Prospects

- ▶ [Social Status and Economic Resources](#)

Finger Length

- ▶ [Digit Ratio](#)
- ▶ [John Manning](#)

First “Period”

- ▶ [Menarche](#)

First Coitus

- ▶ [Sexual Debut](#)

First Intercourse

- ▶ [Predictors of Sexual Debut](#)

First Intercourse Experience

- ▶ [Sexual Debut](#)

First Language Acquisition

- ▶ [Language Acquisition](#)

First Menstruation

- ▶ [Menarche](#)

First Order Relational Reasoning

- ▶ [Same-Different Categorization](#)

First Sexual Behavior

- ▶ [Sexual Debut](#)

Fish, Amphibian, and Reptile Tool Use

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Synonyms

[Aquatic](#); [Cognition](#); [Ectothermic animals](#); [Tool use](#)

Definition

A general definition of tool use describes the active manipulation of an external object to attain a goal.

Introduction

Fish, amphibians, and reptiles are frequently excluded from reviews of tool use (e.g., Bentley-Condit and Smith 2010) for a number of reasons including, first, the fact that there is a low expectation among cognitive scientists and comparative psychologists that these animals are clever enough to use tools and, second, that they are seldom observed with the same level of scrutiny afforded to primates and birds. Careful observations have, however, shown that there are examples of fish and reptiles using tools in the literature, though as yet there are no clearly documented examples for amphibians.

A Historical Perspective

Jane Goodall shocked the world when she first described tool use in primates in 1960 (Van Lawick-Goodall 1968). The idea that tools were solely the domain of *Homo sapiens* was firmly entrenched in both the philosophy and science of the day, beliefs that still color popular assumptions today (Ambrose 2001). Louis Leakey, anthropologist, famously responded to the news by saying “Now we must redefine tool, redefine man, or accept chimpanzees as human” (Peterson 2008). However, observations of tool use in fish had already been published 3 years prior to Goodall’s revelation, described without fanfare in a manual on the care of the brown hoplo catfish, *Hoplosternum thoracatum* (Bshary et al. 2002; Patton and Victoria 2015).

A number of factors lead to the decidedly differential response to tool use between the two species. At the time, it was astonishing enough that primates might use tools, let alone any other animal, so it is not surprising that observations of tool use in fish were overlooked. Still today, the

image of a cold-blooded, witless fish having little capacity for higher-order cognition is pervasive. Despite the fact that cognition is notably absent from any definition of tool use, the assumption that a measure of intelligence is required for the behavior has persisted. Nevertheless, examples of tool use in animals lie in the full spectrum of cognitive underpinnings, from deterministic patterns of response to stimuli through novel, flexible problem-solving (Patton and Victoria 2015; Brown 2011). Rather than decreasing the value of tool use as a method of understanding animal cognition and behavior, however, the breadth of this spectrum serves to create a valuable and complex arena in which to understand the process of problem-solving in animals in the context of their environment (Patton and Victoria 2015).

Early assumptions that tool use might only occur in a small group of primate or primate-like species resulted in an unintentional problem of definitions. The most widely adapted definition required that a tool be disassociated from the surrounding environment and held in some way by the user (Beck 1980). This causes the paradox that using a rock to crack a shell would be categorized as tool use, but cracking a shell against a rock would not. Beck later adapted the definition to include any circumstance where the user controlled the tool, though this amendment in turn inspired debate about what precisely “control” meant (Shumaker et al. 2011). These standard definitions are problematic for any species lacking grasping appendages. Additionally, the physics of mechanically operating objects in an aquatic environment is fundamentally different from the parameters in air (Brown 2011; Pasko 2010). In the viscous environment of water, especially areas prone to strong flow or current, it may be more appropriate to maintain primary “control” over the object of interest. As any scuba diver has experienced, a dropped object immediately runs the risk of floating away (Pasko 2010). Therefore, we turn to Goodall’s original definition – the use of an external object in the attainment of an immediate goal – as the most appropriate definition inclusive of variety in both physiology and habitat type (Brown 2011; Patton and Victoria 2015).

Today, we know that tool use is not only present but also remarkably widespread throughout the animal kingdom (Brown 2011; Shumaker et al. 2011). In addition to primates and fish, there is evidence of tool use in elephants (Hart et al. 2008), bears (Deecke 2012), sea otters, dolphins (Krützen et al. 2005), crows (Hunt and Gray 2003), mongooses (Müller 2009), octopuses (Finn et al. 2009), ants (Möglich and Alpert 1979), and wasps (Brockmann 1985), among other species (Patton and Victoria 2015).

Tool Use in Fish

Considering the logistical difficulties in conducting long, unobtrusive hours observing fish behavior due to the restricted overlap in our natural habitats, there is a surprisingly large and increasing volume of literature providing evidence of the varied nature of tool use in fish.

To return to the brown hoplo catfish that provides our first known example in fish, the tool in question was a leaf on which the catfish would glue its eggs. Then, if threatened for any reason, they grasp part of the leaf in their mouth and carry it in the manner of a tray to move the eggs to the safety. It is noteworthy that this behavior fits the strictest definition of control, as the tool is carried directly by the fish. Similarly, both male and female South American cichlids will pick up and “test” several leaves before one is selected. As with the hoplo catfish, they lay their eggs on the leaf and then pick up it up and move it to a more protected location when threatened (Keenleyside and Prince 1976).

Rock anvils are common tools utilized by a number of fish species in order to smash open sea urchins, clams, and other well-protected food items. In 1971, two species of wrasse (*Cheilinus trilobatus* and *Coris angulata*) were found to use rock anvils to smash open sea urchins. They would repeatedly return to a particular stone located inside their territory, indicating a preference in their choice of tool (Fricke 1971). The yellowhead wrasse (*Halichoeres garnoti*) has also been observed breaking scallops on a rock anvil (Coyer 1995). As underwater cameras

became more ubiquitous, compelling photographs and video evidence have grown, including photographs of a blackspot tuskfish (*Choerodon schoenleinii*) (Jones et al. 2011) and video footage of an orange-dotted tuskfish (*Choerodon anchorago*) (Bernardi 2011) using an underwater anvil in the wild. In captivity, the sixbar wrasse (*Thalassoma hardwicke*) kept in communal aquaria and fed with pellets too big to be ingested also used an anvil to smash food into more manageable pieces (Pasko 2010), indicating that this behavior is not limited to native habitats.

Dead coral has also been seen being used as an anvil. In 2016, an adult blue tuskfish (*Choerodon cyanodus*) was videoed dragging a juvenile green turtle (*Chelonia mydas*) with its mouth. Tuskfish are known to be a primary predator of turtles, but until this footage there had been no observations to indicate the method of predation. In this case, the tuskfish first used a rock as an anvil against which to hit the turtle, before shifting to a larger dead coral head for its anvil and successfully stunning the turtle (Harborne and Tholan 2016).

These anvil-using species fall under the family Labridae, which may suggest that anvil use is a deeply conserved ancestral behavior in this group (Harborne and Tholan 2016). However, Labridae also include species of cleaner fish known for complex cognitive capacity, so a measure of cognitive flexibility in this evolutionary branch of fish may have helped tool use to develop.

A particularly unique example of innovative tool use has been observed in farmed Atlantic cod (*Gadus morhua*) (Millot et al. 2013). These fish were provided with self-feeders that allowed the release of food pellets into the tanks by means of a pulley. Activating the pulley required the fish to bite the string and swim forward and then release it and swim to the area the food was released. In these tanks, individual cod were identified by means of a beaded tag located by the dorsal fin. In two separate tanks, fish accidentally entangled then disentangled their bead with the pulley mechanism, in the process triggering the feeder to release pellets. After these initial accidental interactions, three fish spread across the two tanks learned to hook their bead in the trigger mechanism to activate the feeder. Analysis of the

movement shows that the series of actions were both coordinated and fine-tuned over more than 100 repetitions of the behavior across each fish. Using the tag to trigger the device was advantageous because the fish was able to rapidly catch the pulley, swing around, and end immediately by the food outlet instead of having to mouth the pulley, let it go, and then turn and swim back to the food. The speed at which the fish was able to return to the outlet when using the tag to trigger the device allowed them to beat their competitors to the food source (Millot et al. 2013).

It cannot be overlooked that water itself can be used as a tool, even in an aquatic environment. A further method of overcoming the defenses of sea urchins (clearly a common problem among many fishes) is displayed by the rippled triggerfish (*Balistes fuscus*). By blowing a stream of water directly under sea urchins to dislodge them from the rock, they expose the less-spiny underside of the urchin. The fish can then bite the oral disc, the weakest and least defended part of an urchin. In an experimental setting, it also was determined that the fish would only select smaller urchins, as the larger, heavier specimens were generally unmoved by the strategy. A different approach is employed by the orange-lined triggerfish (*Balistapus undulatus*); here, the fish breaks off the sea urchin spines one by one until the urchin can be grasped and lifted into the water column. After swimming upward a certain distance, the fish then drops the urchin. As it drifts downward, the triggerfish swims under the urchin and bites it from the undefended angles (Fricke 1971).

Water is used ballistically by fish as well. Archerfish (*Toxotes* sp.) are opportunistic hunters that use a specialized groove in their mouth to precisely shoot jets of water at aerial prey (Schuster 2007). Almost all aspects of the archerfish's hunting skills are learned (Schuster et al. 2004; Schuster 2007, 2010; Schlegel et al. 2006), and young archerfish will learn both by practice and by observing the action of more skilled archers. In aiming, the fish cope with refraction at the air–water interface (Schuster et al. 2004), discern camouflaged targets against complex backgrounds (Schuster 2007), and estimate both distances and speed of targets to

successfully knock down prey with their shot (Schuster et al. 2006; Schuster 2010).

It is becoming increasingly clear that, despite the early assumptions in the field, it is not at all uncommon for fish to manipulate external materials available to them in order to accomplish a task. Though the underlying cognitive capacity may vary from basic to complex, there is good evidence that indicate that higher-order cognitive processing can be involved.

Tool Use in Reptiles

Use of objects as hunting lures is rare among animals, with examples found in capuchin monkeys, a few bird species, and one insect (Shumaker et al. 2011). Dinets and collaborators (2015), however, recently reported the use of small twigs and sticks as bird lures by two species of crocodilians (*Crocodylus palustris* and *Alligator mississippiensis*). Both species live in ponds where some birds species, and particularly egrets (*Egretta garzetta*), nest in trees. The crocodilians appear to deliver protection against tree-climbing nest predators such as snakes, monkeys, and raccoons; however, the birds pay a direct cost for this protection when chicks that accidentally fall into the water are snatched up and consumed by waiting crocodilians (Dinets et al. 2015). On the whole, the protection seems to be worth the cost, and many crocodile farms and alligator parks are often found alongside egret rookeries when appropriate egret-nesting trees are in the area.

In 2007, while studying the behavior of mugger crocodiles (*C. palustris*) in large ponds where the rookery trees were growing, Dinets and colleagues repeatedly observed large muggers lying in the shallow water along the edge of the pond with small sticks and twigs positioned across their snouts. The crocodilians remained perfectly still for hours, and if they did move to change position, they did so in such a way that the sticks remained balanced on their snouts. The behavior potentially fooled nest-building birds wading in the water for sticks, and when birds approached and stretched their necks toward the stick, the crocodilians lunged at the bird.

To see if the stick was intentionally positioned on the snout, Dinets and his colleagues performed systematic observations of alligators for 1 year at four sites in Louisiana, including two rookery and two non-rookery sites. The researchers observed a significant increase in alligators displaying sticks on their snouts from March to May, the time when birds build nests for breeding. Specifically, the reptiles in rookeries were observed with sticks on their snouts during and after the nest-building season. At non-rookery sites, the reptiles used lures during the nest-building season. The research by Dinets and colleagues is the first report of tool use by any reptiles and also the first known case of predators timing the use of lures to a seasonal behavior of the prey.

It is unknown what factors stimulate stick-displaying behavior at particular locations and at a particular time of year. The predators might be reacting to different environmental cues such as the presence of large numbers of wading birds flying over the water or the sounds made by the courting birds. It is also unknown to what extent stick displaying by crocodilians is produced by individual insights, cultural transmission, and/or previously evolved instinct.

Regardless of what underlies these observations, however, the historic view of crocodilians as lethargic, slow, and boring is challenged by the fact that these animals exhibit flexible, multi-modal signaling, advanced parental care, and highly coordinated group hunting tactics (Doody et al. 2013). These discoveries are particularly interesting because they could suggest that tool use behavior will be more widespread within the reptilian group.

Tool Use in Amphibians

Currently, there is no record of tool use in amphibians (Shumaker et al. 2011). The fact that there is no publication on this topic does not mean that amphibians are not able to use tools; it seems more likely that it simply has not been expected and so has not been explicitly searched for. However, given observations of tool use in both fish and reptiles, it is reasonable to conclude that there

may be examples of amphibians using tools eventually reported.

Conclusion

A small change in the common definition of tool use – the requirement a tool must be held to be employed – allows the enormous variety in both physiology and environment that animals possess to be taken appropriately into account. This has released fish from an obvious anatomical constraint and allowed a remarkable number of examples of tool use in fish to be correctly categorized. As both technique and technology allow our capacity to conduct long-term studies of in situ fish behavior to dramatically expand, we expect there will be more examples of unique behavior to be recorded. In reptiles there is just one recent report of tool use, and examples are still lacking for amphibians. The paucity of literature for these latter taxonomic groups is most likely due to the difficulties of making behavioral observations in their natural environment and may also be because amphibians and reptiles are often considered to have limited cognitive capacities that may not support innovation and tool use. Nonetheless, reports of tool use in both fish and crocodilians are significant because they suggest tool use has a much longer evolutionary history than has been previously recognized.

Cross-References

- [Cephalopod Tool Use](#)
- [Confounding Use of Tools on Physical Tasks](#)
- [Innate and Learned Tool Use](#)
- [Role of Experience in Tool Use](#)
- [What Makes a Tool](#)

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Fisher Process

- Fisherian Runaway Selection
- Sexy Son Hypothesis

Fisher's Reproductive Value

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Definition

The expected contribution of genes made by an individual or class to generations in the distant future.

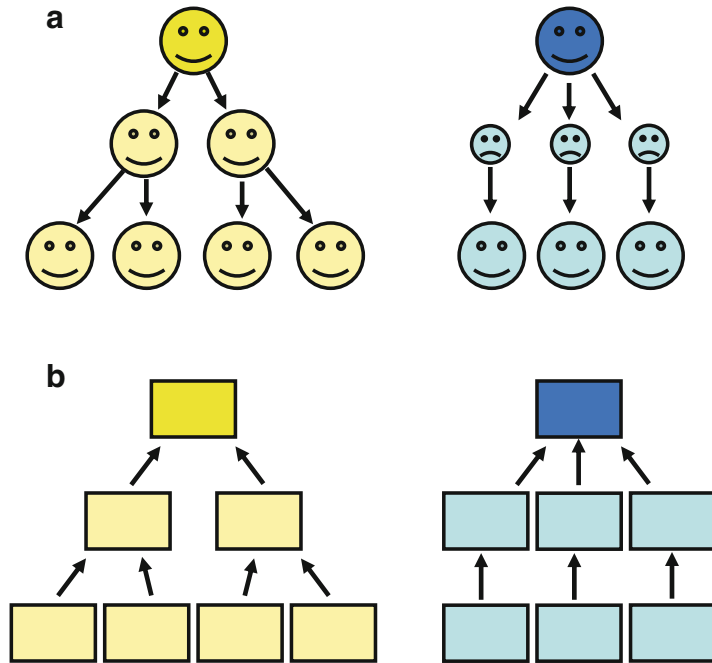
Natural selection is driven by differences in individual reproductive success, but a simple count of the number of children that individuals produce is often insufficient to describe their Darwinian fitness. For example, in a well-mixed population with a female-biased sex ratio, a mother who produces only sons will tend to have more grandchildren than will a mother who instead produces an equal number of daughters. And simply counting the number of grandchildren may also be insufficient, as these too may differ in their quality in terms of how many children they will have. R. A. Fisher's theory of reproductive value resolves this conundrum by defining the fitness of individuals – or whole classes of individuals – in terms of their expected contribution of genes to generations in the distant future. This concept has broad application within Darwinian evolution and is particularly crucial for the understanding of social evolution.

An individual's reproductive value can be defined recursively, in terms of her share (typically one half, in a diploid population) of her children's aggregate reproductive value, with each child's reproductive value being their own share of their own children's aggregate reproductive value, and so on. Although this might appear to lead to an unresolvable infinite regress, reproductive value can be readily calculating using elementary linear algebra. Indeed, the mathematics of reproductive value directly mirrors that of Google's hugely successful *PageRank* algorithm, which quantifies the importance of a webpage on the Internet according to the aggregate importance of all the webpages that link to it (Fig. 1). Whereas

PageRank is the relative probability that an Internet surfer who clicks on links entirely at random will, after some large amount of time, find themselves browsing a particular webpage, reproductive value is the relative probability that a gene chosen at random from the distant future will trace its ancestry to a particular individual or class in the present generation.

Fisher first introduced the concept of reproductive value in relation to age-structured populations, in the prelude to his derivation of the "fundamental theorem of natural selection" (Fisher 1930). The problem here is that while Fisher defined natural selection in terms of systematic change in the genetic constitution of a population, there are systematic changes associated with other factors, such as age. For instance, a neutral allele that is found only in post-reproductive individuals will inexorably decline in its per capita frequency until it is lost from the population, not through the action of natural selection but rather on account of that age class leaving no descendants. Accordingly, Fisher corrected for such class effects by defining the population frequency of an allele as a weighted sum of its frequencies within each of the age classes, with the class reproductive values providing the weights. This recovered Darwin's (1859) stipulation that natural selection increases the frequency of beneficial variants, decreases the frequency of deleterious variants, and does not alter the frequency of neutral variants.

In the context of his treatment of age structure, Fisher (1930) made some cryptic remarks as to the potential for natural selection to have molded the relationship between age and incidence of natural death, on account of it having greater power to improve survival at those ages at which reproductive value is greater. Fisher appears to have mistakenly focused on the reproductive value of the individual, rather than the whole age class, but this was rectified by Peter Medawar (1952), who developed the idea into a fuller evolutionary theory of senescence. Medawar's account emphasized the tension between natural selection and recurrent deleterious mutation, with the decline of class reproductive value with age weakening natural selection's ability to purge the population



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Fisher's Reproductive Value, Fig. 1 Fisher's reproductive value and Google's *PageRank*. (a) Offspring number is not a good measure of Darwinian fitness, because offspring can vary in quality. Reproductive value provides a better measure, because it also describes the success of these offspring, the success of their offspring, and so on down the generations. The yellow individual has only two offspring, but these are of high quality, each leaving two offspring of their own. The blue individual has three offspring, but these are of low quality, leaving one offspring each. Calculation of reproductive value requires that we know how successful these grandoffspring will be but, all else being equal, the yellow individual has the highest reproductive value, as she leaves the most descendants. (b) The number of links pointing to a webpage is not a good measure of that webpage's

importance, because linking webpages can vary in their own importance. Google's *PageRank* – so-called because it was developed by Larry Page, rather than because it ranks webpages per se – provides a better measure of importance, because it also describes how many links point to these linking webpages and so on through the whole of the Internet. The yellow webpage is only linked twice, but these are from important webpages that are also linked twice. The blue webpage is linked three times, but these are from unimportant webpages, each linked only once. Calculation of *PageRank* requires that we know how the whole Internet is linked together (see Page et al. 1999 for details) but, all else being equal, the yellow webpage has the highest *PageRank*, as it is altogether more linked to by the rest of the Internet

of mutations contributing to death in older age. Medawar also suggested that genes responsible for senescence might actually be favored by natural selection, on account of possible pleiotropic increases in fertility manifesting earlier in life, with the decrease in class reproductive value with age making the fertility of the young relatively more evolutionarily important than the survival of the old.

Fisher (1930) next used the notion of reproductive value to great effect in explaining why there is usually equal investment of parental resources into sons and daughters, building and improving

upon arguments put forward by Charles Darwin and Carl Düsing (West 2009). On account of the total reproductive value of all newborn females being equal to that of all newborn males then, in the event of any population imbalance in the investment into females versus males, a unit of parental investment into the underinvested sex will on average yield a higher return of reproductive value. Accordingly, Fisher argued that natural selection favors those parents who act to correct any imbalance in the population's sex allocation and will thereby restore the equal investment into sons versus daughters. This "rarer-sex effect" lies

at the heart of a very large body of theoretical and empirical work on sex allocation (West 2009).

The application of reproductive value to sex allocation illustrates how it provides not only a measure of how different individuals are differently valued by natural selection but also how they are differently valued by each other. On account of reproductive value considerations, a mother is favored to invest more heavily into sons than daughters when males are the rarer sex. Another factor that influences the valuation that one individual places on another is their degree of genetic relatedness, which is central to the theory of kin selection. Hamilton (1972) first incorporated the mathematics of reproductive value into kin selection theory to illuminate the biology of social insects, whose colonies exhibit age, sex, caste, and ploidy forms of class structure, and the modern theory of kin selection puts relatedness and reproductive value on equal conceptual footing, recognizing both as fundamental measures of value (Frank 1998). This development has been essential in moving the explanatory domain of formal kin selection theory beyond simple interactions between generic, interchangeable individuals and enabling its application to real-world biological systems in all their complexity.

The other major approach to social evolution is the group selection or multilevel selection approach. In contrast to what has been done in relation to kin selection, there has been very little interest in reproductive value in the context of multilevel selection. Yet the concept of reproductive value resolves several of the conundrums that plague that literature (Gardner 2015). For example, a long-standing dispute concerns whether it is better to conceive of a group's fitness being equal to the number of daughter individuals it produces (the "collective fitness 1" approach) versus the number of daughter groups it produces (the "collective fitness 2" approach), with this decision leading to different fitness estimates when daughter groups can contain different numbers of daughter individuals, and hence ambiguity as to how group selection is supposed to operate and what phenotypes it actually favors (Okasha 2006). The theory of reproductive value provides a resolution, by recasting the fitness of the group as its

expected genetic contribution to the distant future – which can be alternatively viewed as its share of the aggregate of the reproductive values of its daughter individuals or daughter groups, with both aggregates yielding the same total reproductive value (Gardner 2015).

Conclusion

Fisher's notion of reproductive value is a fundamental concept in the study of Darwinian adaptation and is of particular importance to the study of social evolution in which fitness consequences of social behaviors for multiple parties must be rendered in the same universal currency if they are to be properly understood.

Cross-References

- [Adaptation](#)
- [Group Selection](#)
- [Hamilton's Rule](#)
- [Inclusive Fitness](#)
- [Kin Selection](#)
- [Multilevel Selection Theory](#)
- [Ronald Aylmer Fisher](#)
- [Selection Pressures as a Function of Age](#)
- [Senescence](#)
- [Sex Ratio](#)

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Fisherian Process

► [Sexy Son Hypothesis](#)

Fisherian Runaway

► [Fisherian Runaway Selection](#)

Fisherian Runaway Process

► [Sexy Son Hypothesis](#)

Fisherian Runaway Selection

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Synonyms

[Fisher process](#); [Fisherian runaway](#); [Runaway selection](#); [Runaway sexual selection](#); [Self-reinforcing choice](#)

Definition

Fisherian runaway selection refers to the theory first proposed by R.A. Fisher (1930) that the exaggerated secondary sexual characteristics of animals could evolve by means of a runaway evolutionary process in which an initial small adaptive dimorphism was then further developed into a much more heightened trait by an ongoing

interactive combination of female selective choice and increased male advantage.

Darwin on Sexual Selection

Charles Darwin had first posited the existence of two distinct principles involved in sexual selection (Darwin 1874 [1871]). The first was the “law of battle,” or males combating each other for access to females (intrasexual selection), and the second was female choice (intersexual selection), or females selecting which of the surviving males they elected to mate with (Fisher 1930, p. 131). Across the first few decades of work on evolution after Darwin, it was generally the case that the “law of battle” principle was accepted much more than the principle of female choice.

Darwin had certainly attributed the ability to discern beauty to females, both animal and human, explaining that:

When we behold a male bird elaborately displaying his graceful plumes or splendid colours before the females ... it is impossible to doubt that she admires the beauty of her male partner. As women everywhere deck themselves with these plumes, the beauty of such ornaments cannot be disputed. (Darwin 1874 [1871], p. 92)

By implication, Darwin was asserting that female birds and female human beings share a common aesthetic judgment, at least in relation to evaluating bird plumage. However, opposition to the idea of female choice was asserted by A.R. Wallace, the co-originator of the idea of evolution by natural selection, who asserted that it was “almost inconceivable that female preference could have been effective in the way suggested” by Darwin (Wallace 1889, p. 295). Wallace’s opposition to female choice was important in that many later contributors to the theory of evolution took their impetus on this topic from Wallace rather than Darwin.

Fisher on Runaway Selection

One of the few early twentieth-century contributors who took their impetus on sexual selection directly from Darwin was Ronald Fisher. He

developed Darwin's theory by proposing that male selective advantage, and the associated female choice for this advantage could, in certain instances, mutually reinforce each other in a runaway process, or a positive feedback loop (Prum 2017, p. 37), that served to develop the male trait and its correlated desirability in females to an exaggerated degree. As Fisher explained:

In such cases the modification . . . proceeds under two selective influences (i) an initial advantage not due to sexual preference . . . and (ii) an additional advantage conferred by female preference . . . The importance of this situation lies in the fact that the further development of the . . . character will still proceed, by reason of the advantage gained in sexual selection, even after it has passed the point in development at which its advantage in Natural Selection has ceased . . . There is thus in any bionomic situation, in which sexual selection is capable for conferring a great reproductive advantage, the potentiality of a runaway process, which, however small the beginnings from which it arose, must, unless checked, produce great effects, and in the later stages with great rapidity. (Fisher 1930, pp. 136–137)

This runaway selection process, after being first initiated, would eventually encounter some natural checks that would end it. For example, if the disadvantage to the males of their exaggerated sexual ornaments so diminished the number of survivors in the breeding season that counterselection occurred in favor of less ornamented males, then the runaway process would end.

Fisher hypothesized that runaway selection most likely occurred in sudden spurts of change that were brought to a swift halt by such counterselection tendencies. Examples that he discussed were *Homo* traits for heroism, valor, and public spiritedness, which he implied had been subject to sexual selection pressure as exerted by tribal opinion (Fisher 1930, p. 247). One more general innovation pointed out by Fisher was that an organism's reproductive success was measured not simply by the number of its own offspring, but also the likely success of these offspring in having offspring themselves (Fisher 1930, p. 143). Another key aspect of Fisher's account was that it was clearly specified that animal traits could evolve that diminished survival

advantage, but heightened the capacity of females to discriminate aesthetic qualities (Milam 2010, p. 46).

Fisher's book was first published in 1930, when there were still some significant doubts being expressed about the idea of female choice, as was initiated by Wallace, even though a few others had supported it, so Fisherian runaway selection was not immediately taken up and lauded as the more sophisticated theory that it was.

Runaway Selection After Fisher

It was not until the early 1970s, and the publication of a volume devoted to the topic (Campbell 1972), that sexual selection was fully reinstated as a key component of the theory of evolution as Darwin had intended it to be. This volume briefly considered Fisher's runaway idea that "controlling female preference and advantageous male characters should evolve with extreme rapidity" (Selander 1972, p. 219). New impetus to Fisher's work on runaway selection then occurred in the contributions of Peter O'Donald (1980), Russell Lande (1980), and Mark Kirkpatrick (1982), each of whom developed a more sophisticated version of Fisher's initial idea.

O'Donald added the idea that "females will respond to the more extreme males as to a 'supernormal stimulus' and prefer them to the others" (O'Donald 1980, p. x), as a means of explaining why females would select for the more extreme versions of particular traits. Kirkpatrick concluded that "the initial selective advantages for the female preference . . . are not necessary for either the origin or subsequent elaboration of mating preferences for traits associated with reduced survivorship" (Kirkpatrick 1982, p. 1), as the advantage of having sexually attractive offspring by itself was sufficient: Fisher's sexy son hypothesis. Two approaches to the female choice component of runaway selection have subsequently emerged, relative and absolute preference. In the latter, females have an innate preference for a specific degree of dimorphism, whereas in the former, they have only a relative preference for

bigger/brighter is better (Gould and Gould 1997, p. 183).

In order to better understand the interaction between natural selection and sexual selection processes in generating trait evolution, both Lande and Kirkpatrick designed mathematical models of the coevolutionary dynamics between display trait development and mate choice criteria. Together they showed that:

... natural and sexual selection on display traits will establish a balance between the two opposing forces. At this equilibrium, the male may still be quite far from the natural selection optimum, but that's the cost of doing business with sexually autonomous, choosy females ... this balance between natural and sexual selection is not restricted to a single point. Rather, there exists a line of equilibrium – literally, an infinite number of possible stable points of balance between natural and sexual selection on a given display trait ... the further away a display trait is from the natural selection optimum, the stronger the sexual advantage must be for it to evolve. (Prum 2017, pp. 42–43)

In addition, it was pointed out that elaborate physical ornaments are subject to random mutation, but that these mutations are more likely to make the ornament less elaborate rather than more elaborate. This mutational bias toward lesser ornamentation showed that it was definitely worthwhile for females to select the most ornamented males (Ridley 1994, p. 140).

More recently, it has been suggested that mate preferences may in certain instances evolve cyclically, or through successive runaway periods, instead of toward a stable long-run equilibrium. If small differences in risk factors exist between different populations, cyclic evolution among species can lead to divergence and to sexual isolation (Pomiankowski and Iwasa 1998). This is part of the larger topic of the role of sexual selection in sympatric speciation.

In addition, the recent tendency in the developed world for parents to favor super-high levels of investment in a very small number of children has been analyzed as a form of runaway parental investment (Mace 2007, p. 393). Also, it has been suggested that runaway selection can occur even in the absence of a correlation between male traits and female preferences, as social influences on

mate evaluation can facilitate its initiation (Bailey and Moore 2012). And in opposition to runaway selection, the related process of chase-away sexual selection has been outlined. This involves antagonistic coevolution where the female develops an aversion to the evolving male trait, which in turn causes the trait to become more pronounced as a means of overcoming the female aversion (Holland and Rice 1998).

Finally, in economics the concept of runaway capitalism has been proposed as a way of understanding the problematic evolution of some companies. Single-measure company success criteria often begin as being valid but over-reliance on them can lead to a runaway process in which the single measure becomes both more significant, but also increasingly out-of-touch with overall company performance (Meyer and Kirby 2012, p. 68; Giddens 2002; Miller 2007).

Sexual Selection and Evolutionary Psychology

It is worth briefly considering Fisherian runaway in relation to the psychological mechanisms that have been proposed in evolutionary psychology. As has rightly been explained, “Sexual selection ... is concerned not merely with the evolution of the physical characters of the body, but also, and no less, with the psychological attributes thereof” (Pycraft 1913, p. 18). Therefore, by extension, some of the psychological attributes of animals have been subject to runaway sexual selection pressures, just as some of the physical attributes have been, perhaps producing exaggerated *Homo* traits such as high intelligence and the runaway brain. Runaway brain evolution has progressed so far in human beings that most brain size growth now occurs after birth, an unusual phenomenon (Wills 1995, p. 6).

Moreover, if in the literature on evolutionary psychology it is accepted that there are sex differences in cognition (see Puts et al. 2007), then one component part of these sex differences must be sex differences in aesthetic cognition (or aesthetic dimorphism), i.e., sex differences in conceptions of beauty. This would not necessarily mean that

aesthetic cognition was in all respects different in males and females, only that some aspects of it would vary between the sexes. This aesthetic dimorphism is related to (but is not identical with) sex differences in evaluating the various different features of mate value.

It can further be hypothesized in this respect that, as the degree of sexual dimorphism exhibited in a given species increases, the associated sex differences in aesthetic cognition might also increase. This aesthetic dimorphism will most likely be contained as sexual dimorphism in the psychological mechanisms that are associated with artistic evaluations. For example, on average over large numbers of individuals, men prefer women shorter than themselves whereas women prefer men taller than themselves, despite the fact that tall women have a reproductive advantage: larger pelvises facilitate less problematic births (Touraille 2015, p. 515). Consequently, aesthetic categories may well be in operation in promoting such sexual selection judgments.

Returning to Fisher's work, he outlined a speculative theory as to the origin of all aesthetic criteria as follows: "there can, I think, be little doubt that it [the aesthetic category of evaluation] arose as an intellectual synthesis of the innumerable points, each a factor of sexual preference, which an enlarging intelligence would learn to harmonise" (Fisher 1915, p. 188). Thus, the ultimate foundation of all aesthetic judgment was a synthesis of the evolved psychological mechanisms of sexual attraction.

Conclusion

The contentious status of sexual selection as part of the wider theory of evolution has waxed and waned ever since Darwin first developed the idea (1874 [1871]); similarly, the status of Fisherian runaway selection – and associated female aesthetic capacity – has also varied over time. Its main recent competitors have been, first, the Zahavi handicap principle (1975), which asserts that female choice criteria are linked to fitness-exhibiting traits ("good genes"), or the ability of males to function successfully while carrying

physical incapacities (or handicaps), rather than the purely aesthetic criteria of beauty, and, second, truth in advertising or that costly handicaps directly assist survival (Kodric-Brown and Brown 1984). Opponents of runaway selection also posit that the costs associated with the time-consuming process of mate choice mean that there must be some fitness benefits to ornaments.

Some recent research has suggested that, in fact, both runaway selection/aesthetic capacity and the handicap principle may apply, but to different types of animals. Animals with only a single main ornamental feature obey the fitness-indicating handicap principle, whereas animals with multiple different ornaments employ purely arbitrary aesthetic criteria (Ridley 1994, p. 148). In addition, it is possible that the initial form of an ornament may evolve for fitness-enhancing reasons, then runaway selection may assume control, but as the exaggerated trait becomes ever more costly to maintain, only the strongest and healthiest individuals will be able to cope, thereby ultimately producing an honest signal of overall fitness.

It is also necessary to point out that "mate choice" is often a complex process with many different factors being involved, such as individuals attempting to interfere in mating behaviors, being subject to predator dangers, employing multiple substitutable attraction criteria, evoking prior experiences, being embedded in nested levels of competition, being subject to the effects of mating hotspots, and attempted association with dominant "hotshot" males (Gibson 2002, p. 614).

Finally, it is worth noting that Fisher's first article on the topic of sexual selection began by making the assertion that, of all the branches of biological science, "few, if any, are as attractive as the subject of Sexual Selection" (Fisher 1915, p. 184), implying that Fisher had selected this topic to investigate because of its intrinsic beauty, further reinforcing the importance of attraction criteria to varied forms of animal behavior (Miller 2002).

Cross-References

- [Female Choice](#)
- [Female Mate Choice](#)

- [Sexual Dimorphism and Sex-Biased Gene Expression](#)
- [Sexual Selection](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Fitness

- [Decreased Reproductive Success](#)
- [Maternal and Offspring Condition](#)
- [Reproductive Value and the Evolution of Aggression](#)
- [Sexual and Reproductive Development](#)

Fitness Benefits of Costly Signalling

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Synonyms

Cues; Fertility; Genetic quality; Reproduction+;
Reproductive value

Definition

Signals convey information between living organisms. Sexual signals advertise genetic quality and may serve to enhance the reproductive fitness of the signaller. The high costs associated with such signals serve to maintain their integrity.

Introduction

Signalling theory is an area of evolutionary biology concerned, in part, with communication between individual living organisms. This field of research has received considerable attention, and signals may broadly be considered in two categories (Nur and Hasson 1984). The “Additive Model” concerns signals aiming to deter an opponent, such as that from prey to predator. During a chase, gazelles (*Gazella* sp.) may communicate fitness and speed by “slotting” or vertically jumping, when fleeing a predator. On first appearance, this may seem energetically wasteful, because the energy involved in jumping could be otherwise directed toward escaping. However, the communicated message of speed and agility may discourage the predator from the pursuit, thereby facilitating the gazelle’s escape. In addition to deterring an opponent, signalling is also used to promote sexual fitness. The second category, the “Multiplicative Model,” considers signalling of a sexual nature, which endeavors to communicate value as a prospective mate. Investment in such signals may enhance mating success by communicating underlying genetic and reproductive quality, which might otherwise be unobservable. It is this form of signalling in humans that will be the focus of this entry. The mechanisms acting to maintain signal integrity will also be discussed.

Maintaining Signal Integrity

This system of communicative signalling between individuals can only operate effectively if signal integrity is assured. However, individuals would benefit from the ability to deceive others through dishonest signalling, which would allow for a

false portrayal of their genetic and reproductive quality. Such dishonest signalling may serve to deter a predator or to attract a potential mate. Although natural occurring dishonest signalling is difficult to demonstrate, recent observations of claw size in male fiddler crabs (*Uca annulipes*) suggest that cheating may be common and undetectable (Backwell et al. 2000).

The handicap hypothesis (Zahavi 1975) was proposed to explain how evolution might lead to reliable signalling between individuals, despite the powerful motivation for duplicitous communication. The handicap hypothesis suggests that for a signal of quality to be reliable and honest, it must be costly to the signaller.

This principle is exemplified by sexual signalling in male deer (Cervidae), who grow new antlers each year. While antlers enhance fighting ability and therefore boost mating success, they require massive energetic investment in growth and impede the deer when escaping predators. Antlers therefore enhance reproductive success while concurrently decreasing fitness in other ways. Only male deer with high levels of fitness to begin with are able to afford to reduce their fitness and still survive by growing large antlers. An individual of lower genetic quality would therefore be unable to mimic the signal, ensuring that the integrity of the signal is maintained (Sugiyama 2015). The inherent principle is that any costly signal will serve as a reliable indicator of reproductive quality and be attractive to the opposite sex (Graffen 1990; Zahavi 1975).

Signalling in Humans

The cues which attract men to women and vice versa have been the subject of much research interest. The evolutionary importance of sexual signals stems from individual variability in heritable fitness, with the result that those who reproduce with an individual of high heritable fitness will gain a fitness benefit relative to those who do not. As underlying genetic quality cannot be observed directly, the ability to both signal and perceive cues of genetic quality evolved through intersexual selection.

Although there are similarities between the sexes with respect to which traits are deemed desirable in a partner, there are also well-documented differences. The psychological mechanisms underpinning judgements of attractiveness in the opposite sex are considered to be evolutionary adaptations serving to promote one's own genetic survival through successful reproduction (Thornhill and Gangestad 1999). This section will go on to discuss the underlying qualities sought in a mate by both men and women and provide examples of how such characteristics may be signalled.

Female Signalling

Female cues of beauty are thought to signal general health, reproductive potential (a measure of future reproductive potential, strongly linked to youth), and current fertility (i.e., hormonal profile) (Sugiyama 2015). Such cues positively correlate; women with attractive faces also have attractive figures, body odors, and voices (Feinberg et al. 2005). The ability to communicate underlying reproductive quality is evolutionarily important as fertility may vary considerably between women. General health is valuable in a female partner because it not only predicts fertility but also demonstrates ability to provide quality care for offspring and to pass on healthy genes. Consequently, as age and health are major indicators of reproductive potential, attractiveness is also often linked to visual cues communicating youthfulness and vigor.

Hair is a putative signal of youth (and therefore reproductive potential) and health. Age is communicated through color (although this can now be manipulated), and hair may signal health through a shiny and strong appearance. In contrast, illness may damage hair, and full-term pregnancy may cause coarseness or brittleness, potentially allowing women who have borne children to be distinguishable from those who have not (see Hinsz et al. 2001).

Pitch of voice and facial femininity may also be indicative of mate quality. The two cues positively correlate, and males find the faces of

women with high-pitched voices more attractive than those of women with low-pitched voices (Feinberg et al. 2005). This male preference for feminine faces and voice may be adaptive, as both associate positively with reproductive development and health via elevated estrogen and decreased testosterone. Both signals may thus be communicating the same underlying qualities of hormonal status and reproductive health. Furthermore, the attractiveness of female faces (Roberts et al. 2004), voices (Pipitone and Gallup 2008), and body scent (Gildersleeve et al. 2012) varies across the menstrual cycle, increasing during the fertile phase. This may lead to reproductive benefits for females by being better able to attract mates at a time when conception is most likely (see Welling and Puts 2014).

Populations do not exist in isolation of their environment; the dynamic nature of energy availability influences signals of mate quality. The significant energetic burden of pregnancy and lactation makes a reproducing female vulnerable to food insecurity. Due to the historical (and, to a lesser extent, contemporary) prominence of this challenge, female reproductive robusticity may be enhanced, and signalled, by fat storage. The anatomical distribution of fat stores is linked to the onset of pubertal endocrinological activity and has implications for reproductive potential. The most significant, and observable, distribution pattern is the relative adiposity of the waist and the hip (the waist to hip ratio, WHR). Low ratios (i.e., large hips in relation to waist) are linked with greater current fertility and are deemed more attractive as a reproductive partner. In addition to being linked to fertility, WHR is a predictor of health and therefore of potential to provide parental care and contribute healthy genes to the next generation. As with facial attractiveness, WHR varies by menstrual cycle stage, reaching a low point during ovulation. In this way, WHR may act as a signal of when a woman has reached peak fertility (see Confer et al. 2010; Welling and Puts 2014).

The female face and the body may convey different cues concerning health and fertility. Faces are thought to reflect youth and health and hence provide information about reproductive

potential. In contrast, women's bodies reflect current fertility. Men may exhibit a condition-dependent adaptive propensity to prioritize bodily cues of attractiveness when assessing a potential short-term partner and facial cues for potential long-term partners. This is thought to be because current fertility is more pertinent than future reproductive potential in a short-term mate (Confer et al. 2010). Although individual males naturally differ in the extent to which they may pursue one mating strategy over another, situational factors such as an increase in relative status or mate value following sporting competition may cause a shift toward a short-term approach in order to capitalize on reproductive opportunities (Longman et al. 2018).

Male Signalling

Human males may signal mate value by demonstrating ability to provide ongoing care and resources, as well as through physiological cues pertaining to genetic quality. The high value placed by females on male ability to acquire resources has been well documented (Buss 1989). This is evident in pre-industrial human societies, where males exhibit a positive relationship between status and number of surviving offspring. Prior to agriculture, hunting may have represented an important means by which male resourcefulness could be demonstrated. Food is inexorably linked to status in many cultures around the world, and there is evidence that superior hunters enjoy not only social prestige within the community (Altman and Peterson 1988) but also enhanced reproductive success (Hill and Kaplan 1993; Kaplan and Hill 1985). Hunting may therefore be motivated by male-male competition (Hawkes et al. 2001). Recent research suggests that hunting ability might act as a reliable signal of male fitness by demonstrating ability to acquire resources, in addition to its function of calorie acquisition (see Longman et al. 2015).

The same may be true of contemporary Western society. Both anthropologists and historians have argued that an integral characteristic of human societies is that men seek to acquire wealth

and status, with the aim of converting such gains into reproductive success (see Nettle and Pollet 2008). Today, increasing male income has been shown to have a significant effect on male reproductive success and desirability as a marriage partner (Hopcroft 2006). This appears to be consistent across a range of cultures, suggesting that selection for male wealth will exist wherever there are accumulable resources. It is worth noting that various studies have failed to observe positive relationships between male socioeconomic status and reproductive success but that it has been argued that these studies have inherent methodological and conceptual problems (see Nettle and Pollet 2008).

Thorstein Veblen, a Norwegian-American economist and sociologist, coined the term "conspicuous consumption" to describe the act of spending money on acquiring expensive goods and services in order to publically communicate wealth or status (Veblen 1899). Although such spending may be perceived as being wasteful, the observation that it seems to be a consistent feature spanning history and culture suggests an evolved explanation, one aimed at signalling wealth and converting this into reproductive advantages. Such spending may be concerned not only with displaying economic resources, but rather it signals a specific, short-term mating strategy, and women perceive this as such (see Sundie et al. 2011).

Male physical cues, in addition to the behavioral cues previously discussed, may also play an important role in communicating desirability as a sexual partner. As previously stated, a man's value as a mate depends on both his ability and willingness to provide paternal care and support, as well as his heritable fitness (Gangestad and Simpson 2000). While both aspects of mate value are important when selecting a long-term partner, a man's value as a short-term mate depends heavily on his heritable fitness. A range of studies have demonstrated that women's mate preference depends upon whether a short-term or a long-term partner is desired (see Gangestad et al. 2007) and is influenced by menstrual cycle phase. The role of male masculinity in mediating these preferences is an active area of research interest.

Male masculinity is considered an honest signal of genetic quality. As previously discussed, in order for a signal to be honest and reliable, it must be costly to the signaller. Masculinity is indicative of androgenization, which comes with a fitness cost due to the immunosuppressive effects of testosterone (the “Immunocompetence handicap hypothesis,” Folstad and Karter 1992). High levels of testosterone are also linked to increased incidence of prostate cancer, oxygen radical production, reduced tissue and organ maintenance, injury associated with aggressive confrontational behavior, and suppression of innate immune function (Lassek and Gaulin 2009; Muehlenbein 2006). Masculinity may be conferred through facial structure, as well as through muscularity. In addition to the aforementioned costs of androgenization, muscularity imposes a significant metabolic burden due to the high energy demands of muscle tissue (Elias 1992). While both traits have been proposed to be a positive cue of genetic and therefore heritable quality, both may also serve as negative cues of paternal investment.

Women’s preference for masculine traits is understood to vary with probability of conception. During the follicular (fertile) phase of the menstrual cycle, women may be more attracted to more masculine facial features, muscularity, and scent (a correlate of bilateral symmetry and hence developmental stability). These shifts in preference occur only when ovulating women are considering a man as a short-term partner. As masculine traits infer genetic quality, the timing of such preference changes may be adaptive in that they promote the acquisition of high-quality genetic material at a time when conception is most likely to occur (see Frederick and Haselton 2007; Gildersleeve et al. 2014; Jones et al. 2008).

Summary

Signalling is used to communicate underlying characteristics that may otherwise be unobservable. The integrity of such signals is maintained due to the high cost of the signal itself. Adaptive mechanisms have evolved to both

confer and perceive traits that may enhance one’s own fitness.

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Fitness Benefits of Mate Guarding for Males

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Definitions

Evolutionarily stable strategy: An evolutionary game theory that helps create a framework of the differential success of cooperating and defecting strategies, culminating in an equal payoff for players the majority of the time (Ray-Mukherjee 2016).

Mate guarding: Is the act of males spending time with females pre- or post-copulation, longer than is required for fertilization, in order to reduce sperm competition (Chaudhary and Geethanjali Mishra 2017).

Free-riding competitors: A competitor who chooses to not cooperate in collective action situations, thereby not incurring costs but receiving benefits from others' action. Also known as the prisoner's dilemma (Molander 1992).

Introduction

Many biologists and anthropologists study mating strategies to better understand different methods of passing on genetic material. Across species, males and females exhibit differing

bonds (pair-bonds, extra-pair copulations, promiscuity), different ratios of resources devoted to mate competition (aggressive displays, physical competition, mate guarding), and differing levels of care for offspring (female-only caregiving or male and female sharing caregiving responsibilities).

Fitness Benefits

To model offspring production, Hawkes et al. (1995) reduces the complexity of parental strategies by focusing on three main male strategies of optimizing paternity. The studied male strategies consist of contending for mating opportunities, guarding his current mate from other males, and caring for his offspring. This means models ignore the powerful effects of female choice, these models are also simplified by setting competition, guarding, and care as mutually exclusive, and ignoring temporal restraints.

A robust outcome is that males focus their energies on competition and guarding, rather than caregiving. In several computer simulations under a wide range of conditions, allocation to caregiving is very low, even when the potential effect of care is large. This is partially explained because the payoffs from mating competition are frequency dependent (as care is not) and pay so well it's not evolutionarily stable for competition to remain rare. Additionally, males face a "Social dilemma: shifting efforts to care rather than mate acquisition/guarding should give an advantage to free-riding competitors" (Gavrilets 2012). Males must allocate resources to production, but if no resources go toward preventing theft (by competing for and guarding mates), anyone can lose paternity to theft. So, males also dedicate resources to mate guarding to prevent theft by cuckoldry.

Hawkes et al. (1995) models this dilemma in terms of evolutionary game theory and finds the equilibrium strategy shifts in favor of conflict and equal incomes for competitors. As the number of contestants increases or as individual production increases, there are more opportunities to steal or there is more paternity to steal, and participants allocate greater resources toward mate guarding

(competition). The stable strategy again allocates few resources to caregiving.

The computer simulations used all assume a population of 100, with each group containing five males. Populations are modeled when males are less efficient at child care than females and when males are as efficient at care as females. With both parameters, males devote their time to mate guarding rather than offspring care. Hawkes then attempts to reconcile the models with observations of male care. In the past male care was explained by an increase in survival of young, or as an effect of pair-bonding. However even when mates are pair-bonded, more recent research has suggested male care is not essential for the success of offspring. Strong mating competition, rather than payoffs for care, enforces monogamy (Davies 1992).

Conclusion

Under a variety of conditions, it appears to be more evolutionarily stable for males to devote their resources toward mate guarding or mate acquisition. Evolutionary stable strategies for males generally reinforce devoting little care for their offspring, because of low pay-off rates.

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Fitness Effect

► Biological Function

Fitness-Related Goals

► Self-Beneficial Political Attitudes

Fitness-Relevant

- Predators as Attention-Grabbing
 - Selective Attunement to Adaptive Problems
-

Five-Factor Model

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Synonyms

Agreeableness; Conscientiousness; Extraversion;
Neuroticism; Openness to experience; Personality
dimensions; Personality traits; The Big Five

Definition

A model of the overarching dimensions of behavioral, cognitive, and emotional tendencies that account for a large proportion of the variability in these regards across individuals in a population.

Introduction

People differ in their characteristic patterns of thinking, emotions, and behavioral tendencies, which is known as personality. Each individual is typically rather stable in these patterns across

different situations and across the course of life, which means that a person's previous patterns are predictive for their future patterns. To utilize such information on the group level, (1) it must be reduced to a manageable number of dimensions, (2) these dimensions have to account for a substantial proportion of the variability across individuals, and (3) they have to be reliably measured. This is what personality models attempt to do. The first point can be approached top-down, through deductive reasoning based on theoretical assumptions, biological, social, evolutionary, or neurological knowledge, or some combination thereof. Once this is done, instruments can be devised to measure the proposed dimensions, which will show how much of the variability can be accounted for. Instead, the five-factor model (FFM), or its closely related Big Five model, applies a bottom-up approach to determine the dimensions, based on the covariance structure of an exhaustive set of personality indicators. These indicators could be peer ratings or observations of behaviors, but are almost exclusively self-ratings of initially thousands of words that could describe personality traits. Factor analysis is then used to indicate how many dimensions are optimal for explaining as much as possible of the variance while still rendering each dimension interpretable in terms of a consistent meaning of the words that aggregate in each factor. Seminal work along these lines was done by Gordon Allport in the 1930s (John and Robins 1993), J. P. Guilford in the 1940s and 1950s, and Raymond Cattell, who developed the influential 16PF model (Cattell et al. 1988).

The Big Five Factors and Specific Traits for the Most Common Models

The Big Five are often referred to as their acronym OCEAN:

Openness to experience. Those who score high on this are creative, imaginative, aesthetic, artistic, and open to new ideas, in contrast to those who are practical, conventional, and fixed in their ways.

Conscientiousness. Those high in C tend to be organized, directed, hardworking, persistent, and controlling, in contrast to being spontaneous, careless, sloppy, and prone to addiction.

Extraversion. The extraverted are outgoing, enthusiastic, and active, seek novelty and excitement, and experience positive emotions strongly, while those who score low on E are aloof, quiet, independent, cautious, introverted, and enjoy being alone.

Agreeableness. Trusting, cooperative, altruistic, and slow to anger, as opposed to being stingy, uncooperative, and hostile.

Neuroticism. Prone to stress, worry, and negative emotions and who require order. The opposite is emotionally stable and tolerable to risks and uncertainty.

Thus, each factor is conceived of as a spectrum along which every individual can be positioned, and that is named after one extreme on that spectrum. Most of the personality models that have been proposed within academic psychology have eventually been abandoned and forgotten, and many have effectively been subsumed by the FFM. The main exceptions include Cattell's 16PF, the HEXACO model, and John Holland's RIASEC model of interests for vocational choice. Cattell's 16 factors are Warmth, Reasoning, Emotional stability, Dominance, Liveliness, Rule-consciousness, Social boldness, Sensitivity, Vigilance, Abstractedness, Privateness, Apprehension, Openness to change, Self-reliance, Perfectionism, and Tension. The two latter have six factors each. RIASEC stands for Realistic, Investigative, Artistic, Social, Enterprising, and Conventional (Holland 1997). Although these are apparently quite different from the Big Five, there is a large overlap (McKay and Tokar 2012). The HEXACO model adds a factor called Honesty-Humility and replaces Neuroticism with Emotionality, but the interpretations of the remaining factors also differ somewhat from the FFM (Lee and Ashton 2012).

There are several well-known and often used instruments to measure the Big Five. One of the most comprehensive is the NEO-PI-R, which has 240 items, 8 for each of the 30 facets, which are

then aggregated 6 and 6 to obtain the 5 factors according to the following structure: Openness to experience (O1 Fantasy, O2 Aesthetics, O3 Feelings, O4 Actions, O5 Ideas, O6 Values); Conscientiousness (C1 Competence, C2 Order, C3 Dutifulness, C4 Achievement Striving, C5 Self-Discipline, C6 Deliberation); Extraversion (E1 Warmth, E2 Gregariousness, E3 Assertiveness, E4 Activity, E5 Excitement Seeking, E6 Positive Emotion); Agreeableness (A1 Trust, A2 Straightforwardness, A3 Altruism, A4 Compliance, A5 Modesty, A6 Tendermindedness); and Neuroticism (N1 Anxiety, N2 Hostility, N3 Depression, N4 Self-Consciousness, N5 Impulsiveness, N6 Vulnerability to Stress) (Costa and McCrae 2008).

The NEO-PI-R is proprietary, but there is a family of open-access instruments called International Personality Item Pool (IPIP), with 300-, 120-, and 60-item versions. It takes around 20–30 minutes to fill out the 240 NEO-PI-R items, but if one is not specifically interested in the facets, there are abridged versions that only yield the five factors, the most common being the Big Five Inventory (BFI-44) with 44 items (John et al. 1991) and the Ten-Item Personality Inventory (TIPI) with 10 items (Rammstedt and John 2007).

Which Model Is Best?

For the purpose of most research that considers personality traits, we may not have to choose between bottom-up and top-down or even among specific models. Although they might have different numbers of traits with different names, they tend to share some level of aggregation at which they essentially account for the same main dimensions. For example, the most fine-grained level has 10 traits in Guilford's model, 16 in Cattell's 16PF, and 30 in Costa and McCrae's NEO-PI-R instrument (Costa and McCrae 1992, 2008). However, all these traits can be aggregated so that they largely conform to the five-factor model (For comparisons of many personality models, see, e.g., <http://wbphillipskhs.pbworks.com/w/file/fetch/106978269/big-five-personality.pdf>

and <http://www.psychologycharts.com/big-five-personality-traits.html>.). At this level of aggregation, twin studies therefore indicate a heritability of traits in the region of 50% regardless of model (Nettle 2007; Bouchard and McGue 2018). Any model can be further aggregated into super-factors like Alpha and Beta (Digman 1997), Stability and Plasticity (DeYoung et al. 2002), the Giant Three (P-E-N, see Eysenck et al. 1992), and the General Factor of Personality (van der Linden et al. 2010) (GFP). If the research question considers more narrow or specific traits than the Big Five, one needs to choose the model that encompasses those. For example, a ten-factor solution that is intermediate to the Big Five and the 30 NEO facets seems to be quite useful (DeYoung et al. 2007).

Conclusion

The five-factor model has become widely accepted and is currently the most commonly used in behavioral research. It measures individual differences in personality traits with documented validity. Group differences is of particular interest and importance within evolutionary psychology, and reliable national-level differences have been reported (McCrae 2002; McCrae et al. 2005; Allik et al. 2017). However, national differences should be interpreted with caution, as their validity may be compromised by the self-report method. If a group is very high in conscientiousness, for example, a member of that group will rate herself in relation to her peers and thus underestimate her conscientiousness. Consequently, the group mean will be similar to, or even below that of, groups with lower conscientiousness (Heine et al. 2008). To what extent this applies to groups within the same society remains an open question. For example, sex differences tend to be large (Verweij et al. 2016; Del Giudice et al. 2012) and consistent across nations (Feingold 1994; Lipka 2010).

Although there are many competing conceptualizations of personality, which have more or less, and to some extent different traits, the five-factor model encompasses most of these. Its popularity

probably stems from its ability to integrate most conceptions of personality and stimulate research, and the availability of public domain instruments with documented psychometric properties. For many research applications, it is simply “good enough.”

Cross-References

- Adaptations: Product of Evolution
- Altruism
- Anxiety
- Criminal Personality Variables
- Cross-Cultural Pattern
- Cross-Cultural Similarities
- Daniel Nettle
- Evolutionary Personality Psychology
- Male-Male Competition or Male Provisioning?
- Sex Differences in Same-Sex Aggression
- Within-Species Comparisons

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Fixed Action Patterns

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Synonyms

[Fixed behavior patterns](#); [Modal action patterns](#)

Definition

Inherent behaviors that occur invariantly in succession and almost always execute to completion regardless of any changes in the initial sign stimulus.

Introduction

Behaviors are unique to each species. Every species has a common goal – to be fit and live long enough to reproduce; to replicate their genes. Each generation of a species has the potential to adapt to the ever-changing environment and increase their fitness, which is often done in utilizing the most efficient behaviors. Fixed action patterns (FAP), or fixed behavior patterns, are an innate sequence of behaviors that have been “hard-wired” into an individual through the evolutionary history of its species. These patterns tend to be triggered by specific stimuli and almost always run to completion – the cascade of behaviors happen without the organism even consciously reacting, they simply just occur and fully execute to completion due to a natural response (Baum 2017).

Fixed action patterns in nesting gray geese

The idea that fixed behaviors occur due to a specific stimulus came about at the beginning of the twentieth century during the start of the field of ethology. A fixed action pattern is not learned and cannot be altered. This specialized sequence of behaviors toward stimuli must be shown to be acted out by the entire species and may be accidentally initiated by a different stimulus. Lorenz and Tinbergen demonstrated this phenomenon with a graylag goose while nesting. The female goose would reach beyond an egg that rolled out of the nest, always using the underside of her bill to roll the egg back toward the nest. In experimental conditions, even if the real egg is replaced with a plastic egg, the female goose will continue to roll the egg back to the nest in the same fashion (Goodenough et al. 2010). This emphasized Lorenz's points concerning fixed action patterns – they are innate, unlearned behaviors that the entire population exhibits and they may sometimes be utilized in inappropriate situations but will ultimately always run to completion. There were some that had their doubts about the entirely “fixed” nature of these behaviors, which will be discussed below with modal action patterns.

Variance Versus Invariance: Arguments Against FAP/MAP

A. Mather 1986

One of the main arguments with FAP was with the overall rigidity of the concept – there was no room for any type of variance with Lorenz's original explanation. The behaviors being examined were entirely too formal with hardly any room for discrepancies, which many ethologists felt simply was not true. There were some in the field that believed that these “fixed” patterns of behavior could show variance when influenced by cognitive or environmental factors (Gadbois et al. 2015). The sequence of behaviors may be genetically ingrained in the species to be performed in certain ways, but only when given a specific, innately recognized stimulus. Other cognitive

functions or changes to the common environment could cause behavior to vary slightly, showing adjustment to the current situation. This is where modal action patterns came into theory – modal allowed statistical variability within the observed patterns, arguing that not all patterns were concrete and indefinitely similar in every circumstance as “fixed” previously described. George Barlow also theorized that the only “fixed” part of these sequences of behavior was their statistical inference, otherwise these behaviors could be very flexible (Pellis et al. 2009). The common argument usually does fall among both theories – stating that technically both are true to some extent. While these behaviors are basically entirely innate and do follow through as a “pattern” that is stereotypical to that species, many also consider that there are influences from the current environment. Mather (1986) examined sand digging techniques compared across seven different *Sepia officinalis*, a cephalopodic mollusk, when conditioned were changed. A. Mather found that by changing the sand grain size, the behaviors that were once common across all seven mollusks (blow forward, blow backward, wiggle) now varied based on the size of the grains of sand. This showed that while basic behavior may be genetically hardwired, it can also be influenced by (in this case) peripheral feedback.

Conclusion

Fixed action patterns were first theorized to be programmed sequences of behavior that could be found in every member of a species – consistent behaviors that acted the same toward a given sign stimulus that would run to completion regardless of any other factors. Beginning ethologists believed that certain sequences of behavior could be operational; these patterns would be seen throughout the entire species, regardless of any other influence on the individual from internal factors or the environment, with absolutely no evidence of variance. Later ethologists theorized that this could not be the case, and began to explore the idea of modal action patterns – the

possibility that there may be evidence of variance among these common behavioral patterns within the same species. The debate is still open today, but many believe that like with most things in this world, nothing is perfect, not even a genetically programmed behavior pattern. This would mean that these sequences of behavior are open to individual interpretation, regardless of the innate behaviors of the entire species, and they may be influenced by external environmental factors.

Cross-References

- [Adaptation](#)
- [Biological Function](#)
- [By-Products of Adaptations](#)
- [Heritability](#)
- [Inhibition](#)
- [Physiological Responses](#)

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Fixed Behavior Patterns

- [Fixed Action Patterns](#)

Fixed-Interval Schedule

- [Reinforcement Schedule](#)

Fixed-Ratio Schedule

- [Reinforcement Schedule](#)

F

Flashy Consumption

- [Conspicuous Consumption \(Marketing and Economics\)](#)

Flesh Eating

- [Evolutionary Pressure on Meat Eating](#)

Flexibility

- [Adaptive Plasticity](#)

Flintknapping

- [Human Tool Making](#)

Flirting

- [Perceiving Sexual Intent](#)

Flocking

- [Non-human Leadership](#)

Fluctuating Asymmetry

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Synonyms

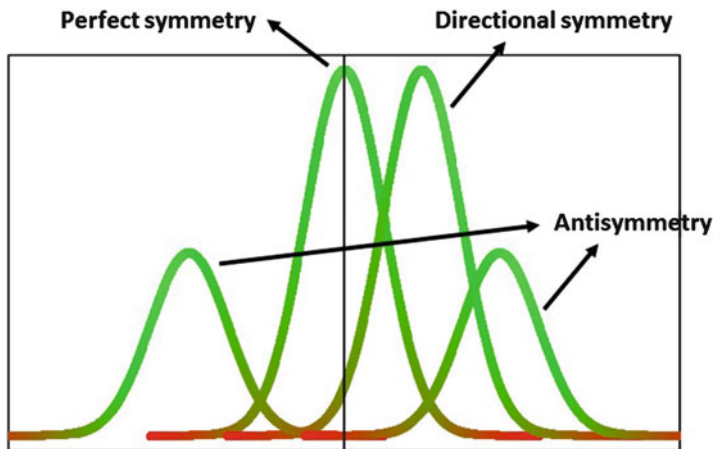
Directionally random morphological asymmetries; Left-right differences

Definition

Developmental instability (DI) is the inability of an organism to buffer its development adequately against random perturbations – has been put forward as a biological signal of (genetic) quality. As increased DI increases morphological asymmetries (fluctuating asymmetry), it has been predicted that women should have a preference for more symmetric phenotypes. While several studies point in this direction, the adaptive value of this preference is not fully understood. This chapter highlights the current state of knowledge and important caveats that require further study.

Introduction

Asymmetry as a measure of stress and quality: The adaptive value of mate preferences for specific traits requires that these features signal “individual quality” in terms of direct or indirect benefits. A specific trait of interest in evolutionary biology and behavioral ecology which potentially signals “quality” is morphological symmetry. In bilaterally symmetric organisms, perfect symmetry is often the norm, in the sense that on the average, the differences between the trait values (e.g., length of a bone) on left and right equals zero. However, most individuals in such populations are not perfectly symmetric. This variation in asymmetry is assumed to result from the accumulation of developmental perturbation, i.e., small mistakes that occur during growth/development. Consequently, individuals which are less able to correct for these developmental mistakes, a process termed developmental instability (DI), will develop a less symmetric phenotype. As the direction in which the asymmetry develops is not relevant, this type of asymmetry is termed fluctuating asymmetry (FA) (Fig. 1). When at the population level, the average asymmetry deviates from zero, directional asymmetry (DA) is



Fluctuating Asymmetry, Fig. 1 Distribution of three types of asymmetry. In the case of fluctuating asymmetry, all variation between *left* and *right* are assumed to reflect the accumulation of developmental perturbations. Higher asymmetries, i.e., in the tails of the distribution indicated in

more *orange-red* color, correspond to higher developmental instability. In the case of directional asymmetry and antisymmetry, the average population asymmetry is assumed not to be related to developmental instability, but variation around it does

observed. As a third type of asymmetry, anti-symmetry is distinguished, where the distribution of asymmetry follows a bimodal pattern (Palmer and Strobeck 1986) (Fig. 1).

The term fluctuating asymmetry was first coined by Ludwig in 1932 (Palmer and Strobeck 1986). After some time, FA research started to bloom during the mid of the twentieth century, focusing on associations between FA and different types of stress (pollution, pesticides, genetic variation). Until the early 1990s, studies mainly focused on population level FA, after which we witnessed a shift towards the use of FA as a measure of individual (genetic) quality, mostly through observations of FA-fitness associations and the study of the genetic basis of FA and DI. In spite of being a very appealing paradigm – where complex biological features like fitness and individual (genetic) quality could be measured easily by measuring traits on the left and right hand side of an organism – it became clear that observed patterns were often not highly repeatable or consistent, leading to quite intensive debates in the scientific literature. Nevertheless, this variation of patterns among studies deserves further research in order to understand the biological causes of heterogeneity among studies (e.g., Van Dongen and Gangestad 2011). At present, one can safely conclude that at least in some cases, FA increases with decreasing individual “quality” and increases with levels of stress experienced during development. In addition, it seems fair to conclude that FA cannot be considered as a consistent signal of stress and quality, but this is probably true for any other measure.

Fluctuating asymmetry in humans: The study of fluctuating asymmetry in humans already started about 40 years ago. To my knowledge, one of the first studies to report associations between FA and developmental perturbations is the work by Woolf and Gianas in 1976 (see Van Dongen and Gangestad 2011 for reference), showing an association between congenital cleft lip and FA. Over several decades, a large amount of human FA literature has accumulated. Patterns correspond to those in other taxonomic groups, in the sense that overall there was a robust and highly statistically significant association between

FA and the various “quality” measures, but additionally, the strength of association varied substantially among studies (Van Dongen and Gangestad 2011). The reasons for this heterogeneity remain largely unknown. In addition, there were indications that the literature showed publication bias where null results are less likely to be published. While there is little reason to doubt that morphological asymmetries do signal health or quality in some cases, the generality of these associations is highly questionable. Indeed, a large recent study found no association between health and facial FA (Pound et al. 2014). In human fetuses, developmental perturbations need to be very far-reaching (often-lethal birth defects that emerge during early organogenesis and extreme genetic abnormalities) in order to increase limb FA (Bots et al. 2014). Clearly, it remains very difficult to predict if and when FA increases with decreasing health or quality. Therefore, the adaptive value of preferences for symmetry remains speculative.

Asymmetry and male attractiveness: Along with studies investigating associations between FA and attractiveness in many species, research into these patterns were also initiated in humans in the early 1990s. Experiments follow two approaches, either by manipulating symmetry of pictures generating stimuli for evaluation by opposite sex raters or by studying the association between natural asymmetry levels by presenting natural pictures for evaluation of attractiveness. Both approaches have their pros and cons. Manipulating symmetry has the advantage that pictures can be presented in combination with the natural versions to identify the most attractive one. This is a statistically powerful approach, indeed leading to stronger effects, but can also lead to counterintuitive results where symmetrized faces were judged to be less attractive. A potential drawback of manipulating asymmetry in pictures is the possible breakup of associations between asymmetry and other candidate markers of attractiveness and quality, and potentially leading to an unnatural presentation of morphological asymmetries. In addition, the signal of such studies is likely to be related to the degree of manipulation of levels of FA (Van Dongen 2011). Studies investigating

associations between FA in natural pictures and their attractiveness from opposite sex raters do not suffer from these disadvantages, but likely require relative high sample sizes because many other aspects of attractiveness may blur associations with FA. In a review of this literature Van Dongen (2011) pointed out that: (i) overall sample sizes of studies of associations between FA and attractiveness were relatively small; (ii) the literature showed signatures of publication bias; (iii) there is likely to be a direct role of the observable asymmetry in determining physical attractiveness, weakening the importance of developmental instability and thus compromising the adaptive basis of preferences for symmetry; and (iv) there was stronger evidence for an association between FA and other forms of attractiveness, like scent, dance, and voice. The latter was, however, based on relatively few studies. More recently, it has been emphasized that the overall weak – if any – associations between FA and physical attractiveness may be due to the fact that FA is often summarized as a combination of FA in several linear measurements, while multivariate shape analyses may be more powerful. However, recent studies did not find associations between facial attractiveness and 2D or 3D shaped FA (e.g., Farrera et al. 2015).

Overall, women's preferences for physical symmetry seem to be supported mainly when symmetry of pictures are manipulated, yet less convincingly so when evaluating natural levels of asymmetry. It is important to note though that women's choosiness depends on several factors, including own perceived attractiveness, use of hormonal anticonceptions, timing in menstrual cycle, context of choice (long- vs. short-term relationship), and the presence of signals of disease prevalence (Windhager et al. 2011). The most common explanation is that women's preference for particular traits, including FA, is adaptive in a good genes context, where potential fathers are selected to provide genetic characteristics like high immunity. This is why some have argued that both sexual dimorphism and FA are both signals of good genes, but a review of this literature did not find strong support for this claim (Van Dongen and Gangestad 2011). This is also in line

with the recent very large study concluding that women's preferences for symmetry – if adaptive – most likely evolved “to motivate avoidance of markers of substantial developmental disturbance and significant pathology” (Pound et al. 2014). This conclusion is also supported by studies in human fetuses where FA is only increased when development is severely disrupted (Bots et al. 2014). Nevertheless, it is also important to note that most of the FA research in humans has been conducted in a relatively wealthy and well-nourished environment in which effects of ill health on development are perhaps likely to be minimal (Van Dongen 2011; Pound et al. 2014).

Conclusion

When the concept of FA gained widespread notice in human evolutionary biology, expectations were high, probably unrealistically high (Van Dongen and Gangestad 2011). Over the last two decades, these expectations were toned down. At the same time, by no means does DI offer a simple, complete explanation of maladaptation, good genes, attractiveness, and so on. Despite the considerable amount of work that has been done to date, a variety of important questions remain unanswered, and more work is needed to provide a full understanding. In general, important caveats have been reported elsewhere, and priority should be given to the link between FA and different aspects of health and quality. Research in sub-optimal non-Western societies may be most relevant here (Van Dongen 2011; Van Dongen and Gangestad 2011; Pound et al. 2014). More specifically in the context of women's preferences for symmetry three important aspects remain crucial. Firstly, there is a need to increase our understanding as to why there is such a discrepancy in strength of effects between studies in which pictures are manipulated and those studying natural variation in FA. Second, many traits, including human face and body, show DA. While this source of variation is often ignored, this may not be correct because: (i) preferences for faces may be related to traits not showing DA only (Simmons et al. 2004), (ii) stress may also

increase DA (Klingenberg et al. 2013), and (iii) DA also affects attractiveness ratings (Meyer-Marcotti et al. 2011). Finally, (facial) FA is often expressed as a composite average across different traits. However, asymmetries of different areas in the face differ in their impact on visual attractiveness, calling for a thorough 3D shape analysis (Meyer-Marcotti et al. 2011). Clearly, with the growing possibilities of high-density surface scans of faces and bodies very powerful and detailed analyses are now easily accessible and can be expected to increase our understanding of the adaptive relevance of asymmetries in determining opposite sex attractiveness.

Cross-References

- [Effect of Birth Control on Women's Preferences](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Robert Trivers](#)
- [Women's Preferences During Ovulation](#)

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Fluent Aphasia

- [Broca's and Wernicke's Aphasia](#)

Fluid Carrying Tools

- [Fluid Transportation](#)

Fluid Transportation

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Synonyms

[Fluid carrying tools](#)

Definition

Locomoting while transporting a tool that holds or has a fluid into or on top.

Introduction

There are three types of tools used by primates to obtain fluids: containers, absorbents (or sponges), and probes (dipping tools). Primates have been observed to use all three types of tools both in the wild and in captivity. However, while there are reports of primates in captivity using tools to transport fluids, this has not been reported for primates in the wild.

Evidence from the Wild

Wild primates use and make tools to obtain water, honey, sap, and other fluids (reviewed in Shumaker et al. 2011; Wynn et al. 2011).

Chimpanzees use (1) folded leaves as simple containers to drink water; (2) leaves, plant fibers, stems, fruits, and moss as sponges to absorb water, plant fluids, and occasionally fluids from inside a prey's skull or a fruit shell and even palm wine from containers left by humans in forest trees; and (3) twigs, branches, vines, and sticks as probes to dip for honey or water. *Bonobos* use moss as sponges to drink water. *Orangutans* use (1) leaves as containers to scoop water from ground puddles, (2) crumpled leaves as sponges to drink water, and (3) branches as probes to extract honey and leafy branches to dip for water from tree holes. *Capuchins* use (1) leaves as containers to drink water from tree cavities, (2) sticks, vines, and branches as probes to access honey and water, and (3) once they used a crumpled leaf as a sponge to absorb water from a tree hole.

However, no transport of fluids using tools has been reported for wild primates.

Evidence from Captivity

Captive primates have been observed to use and make tools to obtain water and other fluids (reviewed in Shumaker et al. 2011) and to transport such fluids using these tools.

Great Apes

Chimpanzees, *bonobos*, *orangutans*, and *gorillas* use a wide variety of materials as containers,

sponges, and probes to obtain fluids spontaneously, during experiments, or from artificial feeders (e.g. termite mounds). They use natural materials from plants (leaves, sticks, twigs, branches, fruit shells, bark, straw, grass, fibers) or animals (eggshells) and human-made materials (tableware, textiles, paper, toys, cans, bottles, hats, buckets) to get a variety of fluids such as water, juice, honey, syrup, or yogurt.

There are reports of all great ape species carrying fluids using tools. For example, *chimpanzees* used an empty coconut shell to collect water and transported it to a different place to drink (McGrew 1992) and plastic bottles to obtain water from a moat also carrying them elsewhere to drink (see Fig. 1). A *bonobo* filled a plastic bottle with water from a lake and carried it to a fence in her enclosure where she seemed to be pretending to drink from it (Gruber et al. 2010). *Orangutans* contained fluids in vessels and carried them within their enclosures (Shumaker et al. 2011). *Gorillas* used buckets to collect water and transported them around their exhibit (Margulis et al. 2012).

Rehabilitant and pet great apes, or those who have been part of language experiments, easily utilize human-made containers and use them to carry fluids.

White-handed gibbons were observed to use pieces of cloth as sponges to absorb water and a leaf as a container and later as a sponge to obtain water from a pool, but they were not reported to transport these fluid-containing tools.

Monkeys

Capuchin monkeys spontaneously and during experiments use tools provided by humans or made from natural materials as containers, sponges, and probes to get water and fluid foods. They have also been observed carrying these tools. For example, scoops containing water and sponges soaked with juice were both transported to different parts of their cage (Westergaard and Frigaszy 1987).

Yellow baboons used twigs and leaves as probes to extract sweet syrup from a container with a narrow opening in one experiment and paper towels to absorb juice from a container in a second experiment; they transported the soaked paper towels to consume the juice away from the



Fluid Transportation, Fig. 1 A chimpanzee at the Kristiansand Zoo in Norway fills up an empty plastic bottle with water from a moat (a) and transports it several meters (b) before drinking. Courtesy of Tanya C. Minchin

container (Westergaard 1992). *Rhesus monkeys* used different human-made objects to scoop and transport drinking water (Parks and Novak 1993). *Squirrel monkeys* spontaneously used cups to contain water and often transported them to the back part of their cage for consumption (Buckmaster et al. 2015).

There are reports of other monkey species in captivity using tools to obtain fluids during experiments or spontaneously. A chacma baboon used a blade of grass as a probe to extract the oils from a pipe to eat them. Lion-tailed macaques used sticks to extract fluid food from holes and tubes. Finally, a *Sulawesi macaque* used sticks and branches to dip for fluid food from a tube. However, no transport of fluids with tools was reported for these species.

Conclusion

Wild chimpanzees, orangutans, and capuchin monkeys use three tool types (container, sponge, and probe) and bonobos one type (sponge) to acquire

fluids. However, despite the extensive evidence of such tool use, there are no reported observations of wild primates using tools to carry fluids.

There are numerous reports of captive chimpanzees, orangutans, gorillas, bonobos, and capuchin monkeys employing a variety of objects as tools to obtain fluids, but only a few studies have described the transport of fluids using these tools. It cannot be discarded, however, that some instances of tool transportation after having obtained and while still holding the fluid have simply not been reported in captivity.

Why wild primates lack tools to transport fluids? In captivity, a benefit of using tools for transporting a fluid seems to be to avoid competition with conspecifics for access to that fluid (Westergaard and Frigaszy 1987; Westergaard 1992; Buckmaster et al. 2015). Thus, the use of tools to carry fluids could offer an advantage to wild primates during competition for fluid resources (e.g., honey). However, in contrast to most tools used by captive primates to transport fluids, the tools utilized by wild primates hold

only minimal amounts of fluid and are not efficient for transport. Plant raw materials to make efficient, long-distance containers are available to wild primates, but without bipedal locomotion or a home base containers cannot be carried efficiently or stored and thus may not be necessary tools for primates in the wild (McGrew 2004).

Cross-References

- [Evolution of Tool Use](#)
- [Primate Tool Use](#)
- [Stick Tools for Foraging](#)
- [Tool Manufacturing](#)
- [Tool Use](#)

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Fluidity in Self Perception and Expression

- [Self-Concept](#)

Flying

- [Nonhuman Primates: Species Typical Movement](#)

fMRI

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Synonyms

[BOLD-MRI](#); [Functional brain imaging](#); [Functional MRI](#)

Definitions

fMRI is an advanced magnetic resonance imaging application for functional brain imaging.

Introduction

Functional magnetic resonance imaging (fMRI) uses the different magnetic properties of oxygenated and deoxygenated hemoglobin to look for blood flow patterns in different areas of the brain in relation to different sensory stimuli and motor activities. The subjects are presented with visual, auditory, and sensory stimuli or asked to perform some simple motor tasks while within the MRI scanner. fMRI can reveal brain areas activated with these processes. Due to absence of radiation, high spatial resolution, and moderately high

temporal resolution, fMRI is replacing PET for functional brain imaging.

Principles of fMRI

fMRI is based on the concept of Blood Oxygen Level Dependent (BOLD) imaging. BOLD fMRI uses the different magnetic properties of oxygenated and deoxygenated hemoglobin to identify regional blood flow changes in brain, in response to a specific task. Oxygenated hemoglobin (oxyhemoglobin) is a diamagnetic substance which means it is repelled by externally applied magnetic field. In contrast, deoxygenated hemoglobin (deoxyhemoglobin) is a paramagnetic substance which means it is weakly attracted by an externally applied magnetic field. So during an MRI scan when external magnetic field is applied, deoxyhemoglobin increases local field inhomogeneity (Kornienko and Pronin 2009).

When a patient is asked to perform a particular activity (e.g., speaking, singing, finger thumb apposition), this results in increased neuronal activity. So there is increased blood flow to the activated area to meet the increased oxygen requirement which is much more above the resting state of brain. Increased oxygen delivery results in increased concentration of oxyhemoglobin with corresponding decrease in deoxyhemoglobin. Any area of signal change that correlates with neurological task is identified and compared with corresponding high resolution anatomical image. So what we measure in fMRI is not the neuronal activity but the local hemodynamic response to such activity. It may be noted that PET scan which is another modality of functional brain imaging, measures neuronal glucose metabolism (Adam et al. 2014).

Advantages of fMRI

- High spatial resolution (1–4 mm thin sections) provide excellent anatomical image.
- Moderately high temporal resolution (0.1–1 s).
- No use of radiocontrast isotope. So there is no health hazard and it is absolutely safe.

- It is a noninvasive procedure.
- Both functional and anatomical images can be obtained in one session.
- It is cost effective and doesn't cost much extra than a conventional MRI.

Limitations of fMRI

- It can't be quantified. It is a qualitative measure of brain function.
This technique is very sensitive to movements. So, all tests should be done without head movement. For example, speaking and hand apposition.
- Artifacts are more common in areas adjacent to air (sinuses). So interpreting brain areas close to paranasal sinus (orbitofrontal cortex and medial temporal cortex; the emotional brain areas) is difficult.

fMRI Examination: Task Protocol

In fMRI, patient or a subject is given a task and the region of brain activated are assessed. The following types of tasks are often employed.

1. Motor: For example, finger tapping, apposition of thumb with index finger, it localizes the hand representation in primary motor cortex (Brodmann's area 4).
2. Language and cognitive: visual and auditory commands for language examination.
3. Passive paradigm: tactile, auditory, visual stimuli. For example, light flashing activates visual area (Brodmann's area 17,18,19) in occipital cortex. Auditory area (Brodmann's area 41,42) in posterior part of superior temporal gyrus can be activated by sound tones.

Clinical Applications of fMRI

(Atlas 2016; Logothetis 2008; Detre and Floyd 2001)

1. *Understanding functional brain areas:* As previously described, fMRI helps in localizing

functional brain areas by performing specific tasks for that area.

2. *Understanding psychiatric diseases:* fMRI has been used since its first uses to study neuronal basis of mental illness. The major psychiatric disorders like schizophrenia and depression were previously considered because of disordered neurological circuitry widely distributed throughout the brain. But recent fMRI studies have shown that there are certain areas of brain that shows altered activation pattern in certain psychiatric diseases. For example, major depression is associated with hyperactivity in anterior cingulate gyrus. And effective pharmacological treatment for depression results in normalization of this activity. Similarly schizophrenia is associated with decreased activity in anterior cingulate gyrus
3. *Dementia:* fMRI at present is not performed routinely in evaluation of patients of dementia, but it offers promise in future for earliest detection of prodromal dementia. fMRI studies till date shows altered activation pattern in memory specific brain regions like medial temporal lobe, hippocampus in patients of early stage dementia
4. *Determination of hemispheric dominance for language:* In general population about 95% are right handed. Left hemisphere is dominant in about 99% of right handers, in about 60% of lefties. Among the rest 40% of left handers, 20% have right hemispheric dominance and rest 20% have mixed dominance. (Campbell Jr and DeJong 2013). Determination of hemispheric dominance is very much important, particularly in presurgical evaluation and planning of patients to be considered for epilepsy surgery or surgery for any intracranial tumor.
5. *Neurosurgical planning:* fMRI delineates the functional areas of brain preoperatively, so helping the neurosurgeon predicting the surgical approach and postsurgical disability. One of major application of fMRI is in epilepsy and most importantly temporal lobe epilepsy syndromes. Here task correlated localization of language and memory areas and localization of ictal and paroxysmal phenomena helps in

predicting postsurgical risk and success of surgery. fMRI is also a useful tool in patients of primary brain tumor. Presurgically, these patients are imaged for anatomical margin of tumor and nearby functional areas. A distance of 1 cm or more between the functional cortex as localized by fMRI and tumor margin is found to be associated with significantly less risk of postoperative loss of function.

Conclusion

Due to absence of radiation, high spatial resolution, and moderately high temporal resolution, fMRI is replacing PET for functional brain imaging. fMRI finds utility in management of brain diseases and in neuroscience research. Major clinical applications of fMRI include surgical planning of patients planned for epilepsy surgery and brain tumor surgery. Its role in neurological and psychological disorders has been well recognized and new applications are emerging day by day.

Cross-References

► Brain Imaging

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Focus

► [Attention](#)

Foetal Death

► [Abortion](#)

Folk Psychology

► [Theory of Mind](#)
 ► [Theory of Mind and Evidence of Brain Modularity](#)

Food

► [Resources](#)

Food Aversions and Cravings

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Synonyms

[Dietary preferences](#); [Dietary shifts](#)

Introduction

The sudden shift in dietary preferences, such as the onset of food aversions and unusual cravings, is considered a hallmark of pregnancy. Aversions and cravings can be understood as strong urges to avoid or consume certain foods and nonfood substances regardless of the cultural norms or other

perceived health indicators that aim to regulate avoidance or consumption. Several influential evolutionary theories have been put forth to explain these shifts, and accumulating evidence suggests that environmental, biological, and cultural factors all play a role in shaping women's dietary preferences.

Dietary Aversions

Dietary aversions in pregnancy are characterized by distaste or disgust toward a specific food item, typically beginning during the first trimester, and coincide with nausea and vomiting ("morning sickness"; Flaxman and Sherman 2000). The leading hypotheses to explain dietary aversions include *maternal-fetal protection* and *resource scarcity*.

From an evolutionary perspective, the longest-standing hypothesis, the *maternal-fetal protection hypothesis*, states that food aversions protect mothers from ingesting substances that could pose a threat to themselves and the developing fetus and focuses on immunological changes women experience during pregnancy (Hook 1976; Fessler 2002; Flaxman and Sherman 2000; Profet 1988). In the first trimester, the maternal adaptive immune system shifts to support growth and development of the placenta and fetus. As a result, both mothers and fetuses are particularly vulnerable to the harmful effects of certain pathogens (e.g., malaria and listeria) and toxins (e.g., nicotine). Hook (1976) and Profet (1988) initially emphasized that certain plant teratogens, which cause birth defects or miscarriage, should lead women to experience aversions to bitter-tasting, pungent, plant-based items. A cross-cultural test of this hypothesis found, however, that although dietary shifts and morning sickness co-occurred in the first trimester, women's food aversions targeted meat products and not plant-based items (Flaxman and Sherman 2000). Fessler (2002) therefore concluded that feeling averse to meat is adaptive since animal products are particularly susceptible to pathogens that can pose a threat to pregnancy.

Although the maternal-fetal protection hypothesis has generated several lines of evidence, food aversions do not always target items that are considered evolutionarily harmful; instead, in some cases, women report aversions to innocuous staple foods (Demissie et al. 1998; Placek et al. 2017). In these studies, researchers highlight the role of resource scarcity and cultural factors in shaping the timing and expression of pregnancy food aversions. In Southern Ethiopia, for example, women were averse to staple cereals and reported cravings for meat and other animal products since these items were scarce (Demissie et al. 1998).

Dietary Cravings

Dietary cravings in pregnancy can be defined as the compulsive desire and ingestion of food or nonfood substances. Pregnant women are known for craving calorically and nutrient-dense foods, such as sweets and fruits, along with odd combinations such as “pickles and ice cream,” or pica substances, such as clay and chalk (Flaxman and Sherman 2000; Placek and Hagen 2013; Young 2010). Several hypotheses have been proposed for pregnancy cravings: *maternal-fetal protection*, *nutrient-seeking*, *resource scarcity*, and *social bargaining*.

Similar to aversions, one evolutionary explanation for dietary cravings is that they provide defense against toxins and pathogens during the first trimester when women are particularly vulnerable (the *maternal-fetal protection hypothesis*; Fessler 2002). Women’s vulnerability is further intensified by metabolic shifts associated with placental development, which impact bioavailability of dietary antioxidants (King 2000). Accordingly, women should report cravings for substances rich in defensive compounds, such as antioxidants. In support of this hypothesis, cross-cultural studies of food cravings have shown that women typically report cravings for fruit, fruit juices, and unripe fruits (Flaxman and Sherman 2000; Placek 2017). Cravings and subsequent consumption of unripe fruits, which are high in vitamin C, can reduce teratogenic effects of

environmental toxins (Fessler 2002). Furthermore, unripe fruits tend to contain tannins, which can aid in the treatment of ulcerated or inflamed tissues and also provide a stable source of antioxidants. The craving for culturally defined nonfood items, “pica,” is also common during pregnancy (Young 2010). Support for the maternal-fetal protection hypothesis of pica stems from the evidence that certain pica substances have the capacity to detoxify specific ingested chemicals, such as tannins (Young 2010), and consumption is often linked to external cues of pathogen exposure (Placek and Hagen 2013).

The *nutrient-seeking hypothesis* of cravings proposes that cravings target foods dense in calories and nutrients after the tenth week of pregnancy when women need to store excess fat to support fetal growth and development (King 2000). Evidence for this hypothesis is illustrated in a study conducted in Tanzania which found that pregnant women in the second trimester craved a diversity of nutrient-rich foods (Nyaruhucha, 2009). Accumulating evidence for pica cravings paints a similar picture: women often consume nonfood substances during periods when they are deficient in certain micronutrients, such as iron, zinc, and calcium, suggesting that they might not be meeting nutritional demands from regular food sources (Young 2010). The nutrient-seeking hypothesis is similar to the *resource scarcity* hypothesis, but not mutually exclusive. The *resource scarcity* hypothesis proposes that cravings for certain foods and nonfoods are heightened in resource-scarce environments. This perspective differs from the nutrient-seeking hypothesis in that women might experience cravings for substances that provide no nutritional benefits. Pregnant women in South Ethiopia, for example, craved meat and vegetables, two items implicated in the maternal-fetal protection hypothesis that were otherwise unavailable due to a lack of resources (Demissie et al. 1998). Furthermore, pica substances, such as soil, have been used to quell hunger at different points of time, and consumption has been associated with physical indicators of resource scarcity (Placek and Hagen 2013; Young 2010). The resource scarcity hypothesis, however, is not typically

accepted as the overarching explanation for consumption of pica substances, primarily due to observations that substances are frequently craved between meals and consumed in such small quantities that consumers would be unlikely to feel satiated (Young 2010).

The *social bargaining* hypothesis for cravings in pregnancy proposes that women who perceive an uncertain future for their offspring crave items that are either locally viewed as dangerous or dangerous in light of evolutionary theory (e.g., toxic plant compounds or pathogenic animal products), in order to garner resources in the form of monetary and social support (Placek 2017). A study conducted among South Indian women lent support for this hypothesis by demonstrating that self-reported cravings for pathogenic and toxic foods were associated with a combination of factors that signaled a lack of resources in the form of social support and adequate access to food (Placek 2017).

Conclusion

The current leading hypotheses for both pregnancy aversions and cravings include maternal-fetal protection and resource scarcity. In addition to these, pregnancy cravings are explained by nutrient-seeking and social bargaining. Evidence of pregnancy dietary aversions and cravings suggest that in some circumstances, women target foods that provide protection and support during heightened periods of vulnerability, whereas in contexts of resource scarcity (in the form of either material or social), targeted foods might signal a need to diversify intake or garner additional support. Additional research is needed that simultaneously tests these hypotheses to tease out how environmental variability, cultural norms of diet, and trimester of pregnancy shapes women's preferences.

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Food Dunking

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Synonyms

Food washing

Definition

The placement, dipping, or emersion of a food item in and out of water either before or during the consumption process.

Introduction

Food dunking is a relatively rare form of “borderline” or “proto”-tool use found among a few animal classes. It is primarily limited to Passeriformes within Aves and Primates within Mammalia, with a few exceptions among other birds and mammals. It is generally classified as “borderline” tool use (Bentley-Condit and Smith 2010) or proto-tool use (Morand-Ferron and Lefebvre 2007) rather than “true” tool use as a true tool is manipulated by the user while a borderline tool remains part of the substrate from which it originates (Bentley-Condit and Smith 2010). Thus, in dipping a food object into a water source, the food dunker does not control or manipulate the water even though the water is “used” to alter the food. In most cases, food dunking appears to be a food preparation technique. It is used primarily to either soften foods or to remove dirt or other substances such as toxins from a food item. Food dunking differs from bait fishing in that, in the latter, an item (sometimes food) is placed in the water specifically to attract a desired prey by the “fisher,” whereas in the former, it is the item placed in the water that is consumed. Some of the controversy surrounding food dunking lies not in the behavior itself but in what it means, i.e., whether it indicates animal “culture.” Food dunking has been observed under both wild and captive conditions for animals ranging from birds to great apes to suids.

The frequency and conditions under which food dunking occurs varies for both species and individuals and may involve a cost/benefit analysis. Food dunking may shorten the time it subsequently takes an animal to consume a food item, for example, when a dry object is softened, thus providing a benefit. However, the act of food dunking may be costly in that the animal may

need to transport the food item to a water source and devote more time to the item’s preparation or that, in doing so, the food item may be more likely to be stolen (Morand-Ferron and Lefebvre 2007).

Food Dunking by Birds

Morand-Ferron et al. (2004) report that food dunking by birds has been observed in the wild in more than 25 species. In most cases, the birds appear to be removing dirt or toxins, softening a hard item, or occasionally smoothing the fur or feathers of a prey item to make it easier to swallow. Birds will dunk food items including, but not limited to, frogs, eggs, hard bread, and insects. Dunking may also be a method to provide water to nestlings in areas where water is in short supply (Koenig 1985). More rarely, dunking is used to actually drown prey. However, in these latter cases, it is debatable as to whether or not this actually represents “dunking” as opposed to “predation.” What we see most consistently is the softening, cleaning, or facilitating swallowing functions of the behavior among birds. As well, the majority of the reports of food dunking among birds are anecdotal. However, Morand-Ferron et al. (2004) and Morand-Ferron and Lefebvre (2007) have conducted numerous field-based experiments to investigate these behaviors in the Carib grackles of Barbados.

Food Dunking by Primates

One of the most well-known examples of food dunking among primates is the “sweet-potato washing” practiced by Japanese macaques (*Macaca fuscata*) on Koshima Island in Japan (Hirata et al. 2001). The washing initially spread among playmates (the first one to perform this food dunking was a juvenile female named Imo) and then from younger to older individuals between 1953 and 1959. After 1959, it spread primarily from mother to offspring as it had become established in almost 80% of the younger adult monkeys. Since those early observations, the Koshima Island monkeys have continued to

dunk and wash sweet potatoes across the generations (Hirata et al. 2001).

Food dunking, or washing, has also been reported among captive capuchin monkeys (*Cebus apella*), crab-eating macaques (aka, long-tailed macaques; *Macaca fascicularis*), and great apes (Allritz et al. 2013; Visalberghi and Frigaszy 1990) and by free-ranging Japanese macaques at Katsuyama, Japan (Nakamichi et al. 1998). Items dunked/washed ranged from apples to grass roots. More recently, the long-tailed macaques of Nom Sao Island, Thailand, have been observed to wash the fruits of prickly pear cactus as part of the spine-removal process (Tan et al. 2016).

Food Dunking by Other Mammals

Food dunking by mammals other than primates is much more rare. It has traditionally been reported for raccoons (*Procyon lotor*), but, in reality, raccoon food washing appears to be an artifact of both captivity and the fact that raccoons forage in water and handle their food as part of the evaluation and identification process (Lyll-Watson 1963). Thus, they are not technically dunking food items in order to clean or soften them. However, captive North American river otters (*Lontra canadensis*) wash their food in order to remove dirt and debris (Neunteufel 2007), and recent data regarding captive Sulawesi babirusa suids (*Babryrousa celebensis*) and European wild boar (*Sus scrofa*) indicate that they do as well (Sommer et al. 2016; Ito et al. 2017).

Conclusion

In conclusion, food dunking is a relatively rare form of proto-tool use found primarily among Primates and Passeriformes in which a food item is submersed as part of the food preparation process. The behavior has sometimes been referred to as “pre-culture.” It is this aspect of food dunking that has been controversial, e.g., whether its existence is an indication of culture in other animals. While it appears to often represent the social transmission of a behavior – and sometimes

transgenerational continuity – whether that constitutes culture depends largely on how that term is defined and to what criteria we hold other animals. Whether or not it indicates culture, food dunking appears to be widespread within those populations/species that practice it.

Cross-References

- ▶ [Bait Fishing](#)
- ▶ [Bird Tool Use](#)
- ▶ [Cephalopod Tool Use](#)
- ▶ [Fish, Amphibian, and Reptile Tool Use](#)
- ▶ [Fluid Transportation](#)
- ▶ [Nonhuman Tool Use](#)
- ▶ [Primate Tool Use](#)
- ▶ [What Makes a Tool](#)

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consume a wide range of foods, which is evident in the great variability of diets worldwide. While omnivores or food generalists are not programmed for any specific diet, humans display universal tendencies such as an innate aversion to bitter tastes or fear of new foods – these preferences protect the organism from ingesting possibly dangerous items. Challenging this tendency for caution is the need to explore new edibles in order to vary the diet and prevent nutrient deficiencies. This conflict between an interest in novel foods and a fear of them is a dilemma with which omnivores must deal.

Food Ingestion

► Energy Consumption

Food Preferences

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Synonyms

Human dietary predispositions

Definition

An overview of human dietary preferences, including innate predispositions to favor and avoid certain tastes as well as the role of culture and environment in shaping food preferences.

Introduction

Humans occupy a multitude of habitats on earth – a success possible due to our dietary flexibility, among other things. As omnivores – animals that eat both plants and other animals – we are able to

Omnivores and their Dilemma

For omnivorous species, taste is a crucially important sense: with a wide range of potential foods, one could face both nutritional benefits and dangers of toxin ingestion. The proper dietary strategy of our ancestors, Paleolithic foragers, would have been to consume small amounts of different foods to decrease impacts of toxins, pathogens, and poisons (Rozin and Rozin 1981). The need for dietary variety is hard-wired biologically (Rolls et al. 1982), and its goal is a balanced diet with an adequate range of micronutrients, as well as limited toxin ingestion (Remick et al. 2009).

The drive to explore novel foods leads to a conflict between neophilia (interest in and liking the unfamiliar) and neophobia (fearing and avoiding it), called the “omnivore’s dilemma” (Rozin 1976; Rozin and Rozin 1981). Neophobia is adaptive as it can protect against illness or death from poisonous foods, but it limits dietary variety, possibly causing deficiencies. Learning through experience, though, can override the fearful response to the new – a food first rejected can become a preference (alternatively, a negative experience can lead to rejection of the previously liked food item). Cuisine – a cultural system that defines edible foods and how to eat them – is another way to deal with neophobia, making every meal familiar and thus nonthreatening (Rozin and Barker 1982). Variety is additionally ensured with palate fatigue, a sensor-specific satiety that prevents one from fixating

on a food item and limiting the diet (Rollo and Marota 1999).

Innate Preferences Through Taste

Being able to taste is so important to an omnivorous eater that the taste system is the most durable of all sensory systems – the taste bud and gustatory epithelium (the taste organ) are one of the very few human organs capable of total regeneration (Fausto et al. 2012). An inability to sense flavors can lead to ingestion of rotten or poisonous foods with a potentially lethal outcome to the organism. There are five tastes detected by most mammals: sweet, salty, sour, bitter, and savory (or umami). While other nutrient taste qualities have been suggested, such as receptors for fatty acids, there is little agreement on whether they can be described as unique tastes yet.

The tastes of sweetness and its opposite, bitterness, display universal preferences with humans being quite fond of sweet tastes, while avoiding bitter ones. The preference for sweet foods is seen with both newborns and adults, who have an attraction to moderately strong sweet sensations. These preferences make sense as, in nature, most sweet foods are fruits and are thus easily digestible sources of calories. Over millions of years, these food sources of sweetness were rather limited, making the modern abundance of refined sugar a very recent and unusual event.

Moderately bitter tastes are rejected by newborns with an innate aversion. The human ability to taste, dislike, and avoid bitterness is considered adaptive, since many toxic compounds are experienced as bitter. Most naturally occurring bitter compounds are toxins at certain higher concentrations, and for stronger bitter tastes the body responds as if a toxin were about to be ingested (e.g., with vomiting). For weak bitter tastes, such a response is not present since normal foraging behavior would require some habitual intake of moderate bitter tastes. With a varied diet, various toxins contained in plants should not become problematic, as we would not ingest enough of them to cause harm. Besides, bitter plant compounds are often beneficial and have medicinal

properties (e.g., antioxidants). Bitterness is also experienced with free fatty acids in foods as they are involved in food deterioration – the ability to detect these may reflect an adaptation against eating spoiled foods containing oxidized fats (Drewnowski and Almiron-Roig 2009).

The ability to sense bitterness is a variable trait in humans, as there is genetic variation between populations in how sensitive they are to bitter taste. Specifically, people have been found to differ in their response to PTC – a bitter chemical phenylthiocarbamide. Half of the population is estimated to be tasters (able to taste PTC), 25 % are considered supertasters or those very sensitive to the chemical, and the remaining 25 % are classified as nontasters (Bartoshuk 2000). The receptors involved in this variation respond to plant secondary compounds (those made by the plant to be poisonous or unpalatable to predators), and supertasters with their high sensitivity tend to dislike vegetables containing such bitter compounds. These foods include many cruciferous vegetables like broccoli, whose secondary compounds can be beneficial for health.

Having moderate sensitivity to bitterness would seem like the best solution – one would avoid strong bitter-tasting foods yet still include health-promoting plants with low levels of natural toxins. However, being a nontaster could also be advantageous under certain conditions. Having such low sensitivity has been hypothesized to be protective for individuals living in endemic malaria regions of Africa, as some secondary plant compounds in the area have antimalaria effects. The protection from eating such bitter plants would outweigh the danger of poisoning (Soranzo et al. 2005). Nontasters are also less sensitive to strong spices, which could present another benefit – protection from microbial food contamination. Sherman and Hash (2001) analyze spice use in relation to ecology and show a pattern of increased spice use in hotter climates. This pattern is only true for spices that inhibit bacterial growth and only in dishes made with meat. Thus, cultural preference for spicy food appears to have risen due to their antimicrobial properties.

Lastly, our preferred tastes include salt and savory. Humans begin showing a preference for

a salty taste around 4 months of age, and moderate salt concentrations in food are highly attractive to us (Breslin et al. 1995). As humans lose salt through sweat, they prefer a higher intake of salt than other omnivores. The savory (or umami) taste is another important preference and is found in many cooked and fermented foods. Cooking and fermenting increase availability of glutamate, an amino acid for which humans have developed an affinity. The savory taste of glutamate could be a marker of protein content, though fresh raw protein foods are not in fact savory without the transformation of either heat or fermentation. Thus, fondness of this taste could suggest a preference toward easily digested proteins in cooked or slightly aged meats (Breslin 2013).

Food Palatability

The Maillard reaction – a chemical reaction responsible for browning and flavor production in foods when cooked – increases palatability of many foods (Maillard 1916). Cooked foods in general appear to be preferred to raw ones by humans, and every human culture cooks. We are not the only ones attracted to cooked flavors – great apes also inherently prefer cooked meat and starchy foods when a raw version is present (Wobber et al. 2008). Products of the Maillard reaction have both negative (e.g., carcinogenic, prooxidant) and positive (antiallergenic, antioxidants) impacts on health (Tamanna and Mahmood 2015), but we might have developed defenses against the dangerous byproducts. For example, acrylamide is toxic in mice and rats but appears less dangerous in humans.

Cooking does not simply increase palatability of various foods – it also would have provided omnivores with the most varied dietary choices, allowing us to diversify our diets to items that are toxic or indigestible when raw, in turn expanding the environmental range for human habitation. Because of universal reliance on cooking by all human cultures, Furness et al. (2015) even propose that humans should be classified not as omnivores but *cucinivores* – species with the dietary

specialization of eating cooked or otherwise prepared foods.

The fat content of foods also contributes to its enjoyment and palatability (Drewnowski and Almiron-Roig 2009). Palatability has a direct relationship to nutritional value with high-energy foods receiving higher preference, and fat – the most concentrated source of edible calories – is the reason palatability is so closely related to energy density (Drewnowski 1997). Children learn to prefer flavors associated with high-energy foods rather quickly and begin selecting fatty foods early in life (Birch 1992), as high-fat food items induce the least neophobia (Rankin and Mattes 1996).

Developing Preferences: Genes and Environment

Food processing through cooking, fermenting, and other techniques is an important element of human culture, and several examples illustrate the significance of these behaviors in the evolution of food preferences. Differences in the ability to digest starches are a prominent example of coevolution between genes and culture. The enzyme necessary to digest starchy foods – amylase – is produced in the pancreas by all mammals, but certain few mammals additionally produce it in the salivary glands, which predigests starches in the oral cavity. Humans are unique among these few mammals as we have a higher number of copies of the salivary amylase gene (AMY1). Agricultural advances over the past 10,000 years have increased reliance on starchy grains as staples, which appears to have resulted in increased AMY1 copies for societies with traditionally high-starch diets (Furness and Bravo 2015). AMY1 is not effective on digesting raw starches, however, so it has been proposed that cooking and increased AMY1 copies evolved simultaneously (Hardy et al. 2015), allowing starches to become important reliable sources of extra energy in the diet.

Another example of gene-culture coevolution affecting food preferences is lactase persistence into adulthood. For mammals in general and the

majority of humans, the enzyme lactase (necessary to digest lactose, a major sugar in milk) disappears after weaning. However, populations with a legacy of dairying have evolved the ability to digest lactose in adulthood – a trait that has evolved independently both in Europe and Africa in only about 7000 years (Tishkoff et al. 2007; Ranciaro et al. 2014). Development of dairy farming and consumption of milk products into adulthood correlates with the selection for genes that code for the persistence of lactase expression (Perry et al. 2015). Not surprisingly, lactase persistence is a common phenomenon in populations that have a long history of milk production: adult lactase expression is present in 75% of northern Europeans, yet only 5% of populations that hunt and gather in the same regions have it (Malmström et al. 2010). Ability to ingest dairy, as an energy-rich food high in nutrients and water (which would be important in arid climates), could have provided an evolutionary advantage.

Modern Food Environment: The Mismatch

Innate preferences for sweet and salty, as well as rejection of bitter tastes, do not predispose humans to pursue a diet currently recommended by many governments and health agencies – rich in plants yet low in sugars and sodium. The industrial revolution led to an abundance of highly processed and palatable foods. Such items feature not only high sugar, sodium, and fat profiles – a combination highly attractive to humans – but they also bypass sensory fatigue by presenting many flavor variations despite poor breadth of ingredients. One hundred years of rapid dietary changes would not have been enough for humans to adapt adequately in only a few generations (Carrigan et al. 2015). Modern health problems related to these novel processed diets – such as obesity and diabetes – also would not be selected against, since the dietary conditions that facilitate them are so recent in evolutionary history. The dramatic recent rise of these noncommunicable conditions may be due to the evolutionary

advantage of having thrifty genes, which increase efficiency of fat storage yet predispose one to chronic disease. According to the “thrifty genotype” hypothesis (Neel 1962), having a large appetite and rapid energy uptake was advantageous in the past, as these traits would have been selected for to deal with feast and famine periods. Such thriftiness would however become harmful in a time of plenty with easy access to unlimited, cheap calories. This hypothesis, however, has received criticism and alternative ones have been proposed, e.g., Speakman (2008) suggests that the obese phenotype is due to genetic drift, not the positive selection of “thrifty” genes.

While human innate preferences appear problematic in the times of plentiful, inexpensive calories, they can be changed and reversed through learning. In addition to the genetic predisposition for certain tastes, humans also possess the predisposition to develop new preferences based on experience with foods – associating foods with context and consequences shapes and modifies preferences. We surely learn to enjoy tastes of some bitter foods like dark chocolate, coffee, and wine; we can also develop an aversion to a previously preferred food, such as after a food poisoning episode. In other words, flavors and tastes that become associated with energy and nutrients become preferred, while illness and poisoning cause associated flavors to be aversive – a process that is not necessarily conscious (Breslin 2013).

Conclusions

An omnivore’s eating strategy must account for two needs: to avoid poisoning and death and to ensure a balanced diet without nutrient deficiencies. The taste system plays a major role in ensuring the survival of an omnivore that faces limitless eating decisions. Our innate taste preferences guide this process by disliking and avoiding bitter foods – often containing toxins in nature – and preferring sweet, savory, and salty tastes that signal high caloric values. Sweetness is an indication of easily digested sugars, while savory tastes could indicate protein sources that have been cooked, thus being more digestible and safe

from foodborne bacteria. Differences in bitterness sensitivity might reflect important adaptations, such as lower sensitivity in malaria areas leading to higher ingestion of bitter protective plants. Lastly, the coevolution of culture and genes has resulted in the importance of dairy and starches in human diets, as the evolving ability to digest them would have provided an advantage to those who could make these energy-rich food sources a reliable part of their diet. These human food preferences appear maladaptive in the current environment, characterized by access to highly palatable and energy-rich foods, yet they can be modified with learning in order to prevent health conditions associated with overnutrition.

Cross-References

► Neophobia

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eat itself, to another individual. It includes active donation of food but also tolerated theft.

Introduction

Feeding on food that it has foraged is of great importance to ensure the fitness of an animal. Giving up this food for a conspecific is thus one of the most prominent examples of altruism.

Although it may bear immediate costs for the donor, sharing food may however be beneficial on the long term. There are various examples of food sharing in the animal kingdom, most of which can be explained by mechanisms such as kin selection or reciprocity (Stevens and Gilby 2004).

F

Food Restriction

- ▶ [Anorexia Nervosa](#)
- ▶ [Eating Disorders](#)

Food Selection

- ▶ [Diet](#)

Food Sharing

- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)

Food Sharing and Nonhuman Reciprocal Altruism

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Definition

Food sharing is a form of altruism, during which an animal gives up food, which it could otherwise

Mechanisms and Examples of Food Sharing

Food sharing has been extensively studied in various species. In social carnivores, for example, active food sharing is rare, but passive sharing i.e., allowing conspecifics to feed from the same carcass at the same time, is common (reviewed in Feistner and McGrew 1989). Some carnivores such as African wild dogs (*Lycaon pictus*) and wolves (*Canis lupus*) regurgitate food for pups. This type of active food sharing is mostly driven by kin selection, as members of the family predominantly show this behavior, such as older siblings for the younger ones (Malcolm and Marten 1982). Through kin selection, an individual gains fitness by helping a conspecific sharing proportions of the same genes and thus promote the representation of these genes in the gene pool of the next generation (Hamilton 1964).

However, African wild dogs unlike other carnivores also regurgitate food for adult pack members, both related and unrelated. Thus, where kin selection can not explain why an individual may give up food for a conspecific, Stevens and Gilby (2004) suggest other mechanism to maintain such altruistic behavior in a population. Young ravens (*Corvus corax*) for example may inform other individuals about the location of food through recruitment calls (Heinrich 1988). In groups,

they are able to overwhelm otherwise dominant adult territory holders and thereby gain access to carcasses they could not get on their own. Thus, by sharing food, they gain immediate benefits through increased foraging success. Other immediate benefits occur when food is provisioned to mates (nuptial feeding), as in many arthropods (Gwynne 2008), or by reducing aggressive behavior of an opponent, such as in primates (Stevens 2004).

In other cases, there are no obvious immediate benefits for the donor. One of the most prominent examples of nonprimate food sharing is the one by common vampire bats (*Desmodus rotundus*; Wilkinson 1988). Vampire bats feed on blood of large vertebrates and heavily depend on successful foraging trips, as an otherwise starving individual would die within a few days. As most other bats, vampires live in large colonies of both related and unrelated individuals. Successfully foraging vampires have been observed to regurgitate blood for unsuccessful conspecifics and thus save them from starving, a behavior which is reciprocated, mostly in dyads (direct reciprocity). While food sharing in this case does not have large negative consequences for the donor, it is of tremendous value for the receiver, and thus there is a net benefit for food sharing dyads. Besides food-for-food, vampire bats also seem to share food for grooming (Wilkinson 1988). Thus, as other altruistic services, food may be traded against other commodities, which is frequently the case in primates (Jaeggi and Gurven 2013), where food is exchanged for grooming, support during conflicts, and access to mates. Furthermore, sharing food with conspecifics can enhance the overall status of an individual within a group or lead to overall benefits for the group such as increasing group size and thus survival of group members (Stevens and Gilby 2004).

While food sharing in nonhuman animals is frequently enforced by harassment, much human sharing is voluntary and proactive (Jaeggi and Gurven 2013). It is widely observed across populations and attributed to various functions: By sharing high quality food, men could enhance their status as good hunter in a group, and thus increase reproductive success. However, women

also frequently share food, for example, as part of a sexual division of labor which increases foraging efficiency and thus family provisioning. Food sharing among nonrelatives overall increases social status in humans and recruit support for times in need. Furthermore, investing in social capital through contributing to public goods may buffer the risk of unpredictable foraging success in the future. As in other species, reciprocity may play an important role in human food sharing among nonkin, as giving and receiving food seems to be highly correlated across human populations.

Conclusion

Food sharing is one of the most common forms of altruism. Although it is costly in the first place, it may as well have short- and long-term benefits for the donor. As during other altruistic acts, food may be exchanged for other commodities, such as social support or mating opportunities, and thus be part of a complex social behavior network.

Cross-References

- ▶ [Adaptation and Natural Selection](#)
- ▶ [Adaptation](#)
- ▶ [Adaptations for Reciprocal Altruism](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism and Watching Eyes](#)
- ▶ [Altruism in Kin Selection](#)
- ▶ [Altruism Norms](#)
- ▶ [Altruism](#)
- ▶ [Cooperation Among Fishes](#)
- ▶ [Cooperation Among Nonchimpanzee, Nonhuman Primates](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Cooperation in Social Carnivores](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Cooperation](#)
- ▶ [Cooperative Alliances](#)
- ▶ [Cooperative Foraging](#)
- ▶ [Cooperative Hunting](#)
- ▶ [Corvids](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Discounting of Future Returns](#)

- Empathy in Rats
- Evolution of Cooperation
- Evolution of Reciprocal Altruism
- Field of Behavioral Ecology, The
- Game Theory
- Gratitude, Sympathy, and Empathy
- Group Hunting
- High-Cost Altruistic Helping
- Ingredients of Reciprocal Altruism
- Iterated Prisoner's Dilemma Model
- Kin Selection
- Living in Groups
- Nonhuman Primates
- Nonhuman Reciprocal Altruism
- Nuptial Gift
- Peer Competition and Cooperation
- Primate Cooperation
- Primates
- Prisoner's Dilemma, The
- Problem of Altruism
- Psychology of Reciprocal Altruism
- Puzzle of Altruism, The
- Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- Reciprocal Altruism and Cooperation for Mutual Benefit
- Reciprocal Altruism and Group Living
- Reciprocal Altruism
- Reputation and Altruism
- Robert Axelrod's (1984) *The Evolution of Cooperation*
- Robert Trivers
- Strategies for Successful Cooperation
- Theory of Reciprocal Altruism

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Food Sharing Hypothesis

- Male-Provisioning Hypothesis

Food Sharing in Vampire Bats

- Blood Sharing by Vampire Bats

Food Washing

- Food Dunking

Footbridge

- Fat Man, The

Foragers

- Hunter-Gatherer Societies

Foraging Ability

- Social Status and Economic Resources

Foraging Decision

► Prey Choice

Force

► Violence

Forced Copulation

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Synonyms

Forced mating; Rape; Resisted mating

Definition

Aggressive tactics that are used to overcome mating resistance.

Forced Copulation

Forced copulation, also referred to as *forced mating*, is when aggressive tactics are used, typically by males, to overcome mating resistance. This term is typically used to describe unwanted copulation in nonhuman species, whereas the term *rape* is reserved for humans. *Resisted mating* describes unwanted copulation in species where female resistance and male use of force is the most common form of mating. In these species, resistance may function by indirectly or directly “choosing” a dominant male (Lalumière et al. 2005). Forced copulation is different from resisted mating because it occurs in species where aggressive tactics are only sometimes used to circumvent female choice for preferred mates. Females in these species are receptive to preferred males

and unreceptive to non-preferred males or are unreceptive during non-preferred times. Males who use force to copulate are non-preferred or pursue copulation during a non-preferred time.

Unlike other forms of sexual coercion, such as harassment (i.e., persistent sexual pursuit until the female capitulates or flees) or sequestration (i.e., aggressive removal of a female from her social group), forced copulation describes direct, aggressive attempts to mate. Female resistance to male sexual advances includes fleeing, resisting, avoiding genital contact, and forceful attempts to heave or fling a mounted male. Actions by the aggressors include pursuing, surprising, grasping, restraining, and biting, many times resulting in injury. In some species, there are physical or physiological traits that appear to assist with forced copulation, such as the notal organ in *Panorpa* scorpionflies, which is used to grasp females (Thornhill 1980).

Forced copulation may have evolved as a sexually dimorphic adaptation, functioning either as a facultative or obligate trait. Forced copulation is facultative when coercive mating depends on certain environmental circumstances (e.g., in American black ducks *Anas rupribes*, males force copulate in response to cuckoldry risk) and can either be flexible (propensity to engage in forced copulation is flexible across the lifespan) or fixed (propensity to engage in forced copulation is generally fixed after a certain point in development). Forced copulation is obligate when sexually coercive males are genetically different from males who are not sexually coercive (e.g., in pygmy swordtail *Xiphophorus nigrensis*, males who engage in sneaky copulation are genetically different from males who do not engage in sneaky copulation). For more examples and details, see Camilleri and Stiver 2014; and Lalumière et al. 2005. Forced copulation is studied as a form of sexual conflict, where an adaptation in one sex (forced copulation and/or mating resistance) comes at a cost to the other sex (see ► “Sexual Conflict”).

Lalumière and colleagues (2005) identified five conditions under which forced copulation has been observed: (1) the *circumstantial opportunist* – species that do not form pair bonds and

males force copulate when faced with an unreceptive female; (2) the *opportunistic spouse* – species that form pair-bonds and males sometimes pursue extra-pair copulation through forced mating; (3) the *cuckold* – species that form pair-bonds but males sometimes force copulate one's mating partner, typically in response to cuckoldry risk; (4) the *competitively disadvantaged* – species where males resort to forced copulation when they are not preferred by females due to having poor health, few resources, or lower dominance; and (5) the *morph* – species where males who pursue forced or sneaky copulations are genetically different from males who do not pursue such tactics. Some forms of forced copulation may not be adaptive but may result as a byproduct of other adaptations (e.g., Davian behavior) or as a disordered adaptation (e.g., paraphilias).

Forced copulation is observed across many insects, fish, reptiles, and mammals. Recommended in-depth reviews of forced copulation, and sexual coercion more generally, among nonhuman animals can be found in Camilleri and Stiver (2014), Clutton-Brock and Parker (1995), Lalumière et al. (2005), Muller and Wrangham (2009), Smuts and Smuts (1993), and Thornhill and Palmer (2001).

Cross-References

- [Forced Mating](#)
- [Rape](#)
- [Rape and Dating](#)
- [Resisted Mating](#)
- [Sexual Conflict](#)
- [Types of Sexual Coercion](#)

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Forced In-Pair Copulation

- [Partner Rape](#)

Forced In-Pair Copulation (FIPC)

- [Men's Suspicions of Partner Infidelity and Women's Defection](#)

Forced Mating

- [Forced Copulation](#)

Forced Matings

- [Prevalence of Forced Copulation in Orangutans](#)

Forced Sexual Intercourse

- [Rape](#)

Forecasting

- [Predicting Events and Behavior](#)

Forgiveness

- [Be Forgiving](#)

Formidability

- [Individuals that Impose Costs](#)
- [Nonverbal Indicators of Dominance](#)
- [Reputation as a Context for Men's Aggression Against Men](#)
- [Vocal Indicators of Dominance](#)

Formidability Assessment

- [Assessment of Fighting Ability](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Upper Body Strength and Fighting Ability](#)
- [Upper Body Strength from Photo](#)

Formidability Perception

- [Fighting Assessment](#)

Forms of Adoption

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Synonyms

[Adaptation](#); [Alloparenting](#); [Family](#); [Fostering](#);
[Nepotism](#)

Definition

What are the different ways of caring for children who are not one's biological children?

Introduction

On the surface, adoption is something of a paradox from an evolutionary perspective as it appears to run counter to the evolutionary principle of passing on copies of one's own genes as one instead invests time and resources into other people's offspring (Hamilton 1963). However, adoption is nearly ubiquitous across known cultures, suggesting that it might have some evolved component (Silk 1990; Volk 2011). What is noteworthy about adoption is the variety of forms it can take. These forms are tied closely to cultural norms and the functional outcomes of adoption preference. There are two main forms of adoption, based on whether one is adopting an unrelated child or a related child.

Adopting Related Children

Evolutionary theory suggests that parents should invest in related children so long as the cost to themselves (i.e., their own genes) is offset by the benefit to the shared genes in the related children (Hamilton 1963). So from a crude evolutionary point of view, it is worth sacrificing one-fifth of one's time and energy to raise a niece or nephew who shares one-fourth of one's genes. Thus the degree of support provided to adopted children in this context likely depends on how closely they are related (e.g., a niece versus a second cousin) and how costly the investment will be to the adopting parent(s) (e.g., if they don't have any children of their own, then the costs will be lower and the benefits greater; Rawson 2003). Even in modern contexts where the primary motive is altruistic parental substitution, the success of an adoption is based on kinship networks of support (Johnston 2012), highlighting the role of kin in any adoption process. The critical role of human non-parents as alloparents who support the upbringing of most children (Hrdy 2009) makes it

a very small leap from many adults providing some alloparental care to some alloparents providing all of the parental care (i.e., adoption or fosterage).

The most likely circumstances for this form of adoption are when one or both of the parents die (Halbmeyer 2004), a not uncommon event in the evolutionary past (Volk and Atkinson 2008). Particularly in an evolutionary context, children without their parents (and especially without their mother) face greatly increased levels of mortality (Sear and Mace 2008). Under these circumstances, the related adopting parent functions enable the survival of the related child (a large benefit) for a relatively modest cost (a smaller cost than birthing and raising one's own child – particularly if the child is older). This is likely a relatively ancient pattern of behavior (Hrdy 2009) as chimpanzees have been observed to adopt younger siblings if they are maternally related (Hobaiter et al. 2014).

Further, in humans, this function of adoption is not limited to orphaned children as it may also apply to children whose biological parents lack the mental, emotional, and/or economic means of caring for them (Volk 2011). This pattern is commonly observed in fosterage systems (caring for the child of a living parent) where children are placed in the care of a related individual (Scelza and Silk 2014). In North America, just under half of all adoptions are by kin who are supporting children with a living parent (Stolley 1993), while 31 % of fostered children are raised by kin (Testa 2004). These numbers might as well be higher as many families rely on informal systems of adoption and fosterage to support ill-equipped biological parents. This too is a relatively ancient practice, as it is fairly widely practiced among hunter-gatherers and agriculturalists (Alber et al. 2010; Silk 1990; Volk 2011). It was also extensively practiced in the seventeenth-century Europe when poor parents gave up their children to wealthier relatives with the hopes of eventually being able to reclaim them under better economic conditions (Cunningham 2005). Similar practices were common in Brazil until recent times, leading to tragic modern scenarios where some mothers give up their children for others to raise only to find that when their economic circumstances have

improved, the government no longer allows them to reclaim their children (Fonesca 2004). Overall, these patterns of kin adoption or fosterage allow broader family networks to adaptively pool their resources in order to optimize their investment in the next generation.

Perhaps the most dramatic example of kin support fosterage comes from the Baatombu of Northern Benin. Traditionally, almost all Baatombu children were raised by relatives other than their biological parents (Alber 2003; Alber et al. 2010). Boys were raised by male relatives and girls with female relatives, with the father's side of the family getting the firstborn, the mother the second, etc. (Alber 2003). Interactions between the birth parents and their children were strongly discouraged in order to maintain the adopted kin structure. The Baatombu believed that this served two important purposes. First, it promoted child survival by ensuring that only adults with sufficient resources were entrusted with raising a child. Second, it promoted within-family solidarity by reinforcing the kin network by sharing its most precious resources – their children. So a process of kin selection is reinforced not only by increased child survival and thus shared genetic transmission but also by using adoption to build stronger familial social networking.

Adopting Unrelated Children

From an evolutionary perspective, the adoption of unrelated children is not immediately adaptive as one is not invested in the transmission of shared genes to future generations (Hamilton 1963). To get around this evolutionary issue, parents who adopt unrelated children have relied on a variety of motives. Some are adaptive, while others may be the unintended by-products of adaptive behaviors and motivations.

Altruistically Motivated Adoption

The most widely familiar modern function of adoption is as an altruistic substitution for biological children, typically due to infertility or

child mortality (Volk 2011). Under these circumstances, parents are strongly motivated by a (potentially innate) desire to raise children but do not have any biological children of their own to whom they can apply this motivation. In modern society, such parents are typically of Western descent and are wealthy, educated, older (late 30s to early 40s), and highly motivated to care for a child (Hamilton et al. 2007). The adaptive function of this behavior is questionable as it typically does not translate into the transmission of one's genes. Indeed, adoption is often a very costly affair for the adopting parents (Cunningham 2005; Howell 2006). Instead, it may represent a mismatch between an adaptive, evolved desire to have a biological child and the inability to do so. Humans appear to be one of, if not the most, parental care-oriented primates (Hrdy 2009), so it is not terribly surprising that the motive to care for children leads some adults to engage in maladaptive behaviors. The strength of this motivation is such that it may even result in caring for offspring of other species (Riedman 1982; Vining 2003). Thus, the selfish desire to invest in one's own genes can be overcome, in some cases, by the evolved desire to care for younger members of one's own, or of even a different, species (Volk et al. 2007). In other cases of adopting non-kin, the payoffs are more concrete.

Socially Motivated Adoption

Among some societies, childlessness is viewed as immoral, leading wealthy infertile women to choose to adopt an unrelated child to maintain the social structure of motherhood (Talle 2004). Failure to do so would result in social ostracism that could potentially impact an individual's survival. The urgency of this form of adoption is illustrated by the reality that sometimes this adoption occurs despite the protests of the biological mother, whose husband forces the exchange of their child for material gains (e.g., a cow; Talle 2004). This form of parental substitution may or may not be altruistically motivated given the social pressures associated with the decision. But

it does result in a more concrete benefit than does purely altruistically motivated parenting.

Another socially motivated form of adoption was the creation or maintenance of social alliances (Volk 2011). The general idea in this context is that if an individual raises another person's child, then the biological parent has a vested interest in the success and well-being of the adoptive parent as they are responsible for raising their biological child. Many native North and South American groups used adoption as a means of ending blood feuds as well as integrating captive children into their new groups (Volk 2011). Similar practices were observed among other violent hunter-gatherer groups that practice blood feuds (e.g., New Guinea highlanders). The practice was also quite common in historical cultures ranging from ancient Rome to medieval Europe to late Imperial China (Cunningham 2005; Hsiung 2005; Rawson 2003; Volk 2011). In all of these cases, kin selection was used as a tool for both reducing tensions and violence between groups and promoting new social networks by offering one's children as a guarantee for one's social cooperation and against one's use of violence. Ancient Romans also used it as a means of spreading their cultural values. By raising the son of a conquered chief, that adopted son could then be used as a cultural liaison with their former tribe once they were adults to promote the interests and values of Rome (Rawson 2003).

A final form of socially motivated adoption is its use as a means of fostering marriage arrangements (Volk 2011). This can either be through exchanging children who are to be later married or by adopting a child who is meant to serve as a future wife when they are older (Halbmayer 2004).

Economically Motivated Adoption

This form of adoption is generally not present in modern Western cultures, but it is relatively common in other cultures and earlier in Western history. It involves the adoption of unrelated children in order to gain economic resources or labor. Historically, child abandonment was the basis

for a form of economic adoption whereby either wealthy individuals could adopt found children as slaves (Rawson 2003) or institutions could be set up to receive money for raising orphans (i.e., founding institutions; Cunningham 2005). The economic benefits to the participating adults are clear in either case, but both typically represented very costly forms of care for children who suffered from much higher levels of mortality (up to 90% in some cases) at the hands of economically motivated strangers (Cunningham 2005).

Evolutionarily speaking, a more common form of economically motivated adoption was for known individuals (e.g., members of a village) to exchange children in return for economic benefits. In the case of resources, children are valued primarily for their current and/or future capacity for labor. A typical example would be for economically poor biological parents to exchange their child for resources with wealthy and/or elderly fostering parents (Kirkpatrick and Broder 1976). The benefit to the latter would be the free labor provided by the adopted child. While this is to a degree, a form of childhood servitude, most cultures enforce rules on how adopted children are to be cared for and treated (Talle 2004; Testa 2004). If the adopting parents violate these rules, then the biological parents can cancel the contract and reclaim their child. Thus, it is typically a reciprocal agreement whereby poor biological parents get much needed resources and are relieved of the costs of raising a child, while wealthy/elderly adopting parents are able to translate material resources into labor outside of a free-market economy.

However, there are some potential variations to this theme. For example, among the Ifaluk of the Western Caroline Islands, wealthy individuals give away their biological children to poorer adopting parents (Betzing 1988). This does not appear to be a form of reciprocal altruism. Rather, it appears to be an effort by elites to translate their economic and social power into parasitic brooding. That is, the biological parents force less powerful adopting parents to bear all of the costs of raising the adopted child without offering any benefit in return. While perhaps morally dubious, this does offer powerful individuals a means

of increasing their potential reproductive success by dramatically passing off the costs of raising their biological offspring to unrelated individuals.

Conclusion

Adoption is a flexible tool that can serve one or both functions within or outside of family networks. From an evolutionary perspective, there appears to be a gradient of parental care from raising one's own children to investing in related kin (alloparenting), to raising kin (adoption), and to raising unrelated children in exchange for altruistic, social, and/or economic benefits. The sheer versatility of the functions adoption and fosterage suggests it is an ancient and fairly ubiquitous means of promoting individual and familial evolutionary fitness. It is ironic that the most familiar form of adoption in modern Western society is perhaps the least evolutionarily motivated and viable function of adoption (altruistic parental substitution). Yet it is perhaps the most socially altruistic expression of the evolved human desire to protect, care for, and spend enormous time and emerging raising biologically unrelated relatively helpless infants and children. Nevertheless, it is important to recognize that adoption is a highly varied behavior whose form and function can vary widely between individuals, cultures, and time periods.

Cross-References

- [Adoption Preferences](#)
- [Consolidating Familial Power](#)
- [Evolutionary Paradox: Adoption](#)
- [Function of Adoption](#)
- [Resemblance](#)

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Formula Feeding

► Bottle Feeding

Fornication

► Penile-Vaginal Sex

Fostering

► Forms of Adoption

Fostering Values of Fairness

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Synonyms

Equity; Justice

Definition

The processes by which evolution can design cognitive mechanisms equipped with certain assumptions about what counts as fair.

Introduction

Because natural selection designs phenotypes that favor the replication of the genes that built them, contemporary evolutionary theory predicts that organisms should be strongly biased toward their and their kin's own interest. However, in some species, including humans, the complexity of social life has led to the emergence of values that are not exclusively aligned with self-interest.

It is widely agreed that among these values is a concern for fairness. But what counts as fairness to the human mind? Depending on circumstances, it can refer to a number of different things. As an example, what is a fair division of the spoils of a hunt among the members of the hunting party? Several criteria are possible, some of which might conflict with each other: one is equal division between the members, another is a division proportional to each party's contribution to the hunt, yet another is a division that is proportional to their need. "Fairness" has also been used to describe the impartiality of a procedure (regardless of its eventual outcome) or even a general concern for others.

Norms of fairness and their influence on human behavior have been extensively studied by psychologists and economists. Because of their diversity, they raise several issues that evolutionary theorists have recently focused on.

Explaining Deviations from Selfishness

Human behavior in a number of economic games deviates from the standard economic model, which sees agents as rational and self-interested. For instance, in a task called the dictator game, players are given a sum of money and may choose to share part of it with another player; their decision is anonymous. In contrast to the self-interested model, a substantial portion of players choose to share some of the money. This and other "anomalous" results have been taken to show that humans are averse to inequality (Fehr and Schmidt 1999). Furthermore, developmental work suggests that humans develop a sensitivity to distributive justice from an early

age: as an example, Geraci and Surian (2011) have shown that 16-month-old infants prefer looking at events in which resources are divided equally between recipients. A concern with equality raises the question of why people do not care solely about their own interests instead.

One explanation of these moral concerns is that humans are not in fact designed to look for their own interest. In models of cultural group selection, coevolution between genes and culture give rise to institutions that promote behavior for the good of the group and curtail selfishness: groups in which such institutions are prevalent outcompete other groups, causing the propagation of the institutions (Henrich et al. 2010). Although group selection models can explain generosity, they have trouble explaining why individuals would be opposed to inequality, a concern that sometimes leads to nonoptimal allocation, or even destruction, of resources and hence runs against the greater good (Shaw 2013).

Hence, most evolutionary theories explain instances of human selflessness by showing that they ultimately lead to individual benefit in the long run. These attempts focus on mutualism: in some situations, it is beneficial for both parties to interact with each other. For instance, parties in a trade benefit from the interaction, because otherwise they wouldn't take part in the exchange. In such cases, it is in the interest of an individual A to manipulate a current or potential interaction partner B so that B takes part in the interaction; often the best way to do this is to ensure that the interaction is beneficial to B. In Trivers (1971) model of reciprocal altruism, individuals are ready to suffer a cost to help another organism, if by doing so they increase the likelihood that the latter will help them in return, in a logic that can informally be described as "scratch my back and I'll scratch yours."

Recent work has extended this framework to take into account the possibility of partner choice, where people compete with each other to attract interaction partners. In the ultimatum game, a proposer offers to divide an amount of money between a responder and himself. If the responder agrees to the division, it is paid out, but if he refuses, both players get nothing. While

standard game theory predicts that the proposer offers the minimal possible nonzero amount to the responder and the latter accepts, André and Baumard (2011) show that the outcome is different when players are allowed to choose who they want to play with. In versions of their model in which it is easy to choose one's partner, evolution favors proposers who divide the resource almost equally between the responder and themselves, because by doing so they attract other players and get to take part in a greater number of beneficial interactions. When partner choice is harder, proposers can afford to make lower offers. Under this framework, what constitutes a "fair" offer is thus determined by the parties' relative bargaining power. Related game-theoretic considerations suggest that evolution should favor individuals who distribute a resource in proportion to each individual's contribution to its production, because productive individuals are more valuable partners and have better outside options. Indeed children as young as 3 years old display a tendency to distribute goods according to individual contributions (Baumard et al. 2012).

As noted above, an everyday-life example of mutually beneficial interaction is economic exchange. Behavioral economists have collected ample evidence that people have strong concerns for fairness in this domain. Kahneman et al. (1986) have shown that people object to increases in prices if they are not motivated by similar increases in production costs: it is unfair for a store owner to increase the price of snow shovels to take advantage of the increased demand caused by a snowstorm. In line with the idea that fairness norms are shaped by the parties' relative bargaining power, Friedman (2004) has proposed that this phenomenon is caused by a fundamental asymmetry of information in the relationship between buyers and sellers: while the buyer knows his reservation price (the maximum price he is willing to pay for the good), it can only be guessed by the seller. Therefore, the buyer can pretend that the current price of a good is very close to his reservation price and credibly threaten that he will not buy in case of a price

increase. Because trade of goods or favors was common in man's ancestral environment (e.g., food vs. help in intragroup conflict), such commitment strategies might have evolved in this context.

The Puzzle of Impartiality

Mutualistic accounts explain why people hold values that go beyond their own self-interest, but they do not explain why fairness is often characterized by impartiality. If people preferentially care about the welfare of individuals they can have beneficial interactions with, then they should exhibit favoritism toward them. By contrast, Shaw (2013) reviews data showing that strong impartiality is an important part of human values. People sometimes value impartial individuals over individuals who treat them preferentially: for instance, children preferred a distributor who distributed four erasers equally between the subject and another child over a distributor who gave all four items to the subject. Accordingly, people strive to be impartial, even if achieving that goal means discarding resources: people imagining themselves in the role of an employer refused to give a pay raise to an employee if it was not accompanied by a raise to his equally hardworking colleague. Shaw conjectures that selection pressures related to coalitional dynamics gave rise to this concern for impartiality. In a social species, the existence of alliances might have a negative impact on outsiders, giving the latter incentives to curtail the formation of new coalitions. Punishing partiality is one way to achieve this goal, and the potential for such punishment might then encourage people to appear impartial. That people are motivated to appear impartial, rather than intrinsically valuing impartiality, is supported by experiments showing that they are less concerned with fairness when their behavior is not made public (Shaw 2013).

More generally, in an interaction between two individuals, A and B, A's interaction with another

individual C matters to B, because it contains useful information. In the example of an economic transaction, in which B buys a good from A, B does not have full information about A's reservation price, but observing A selling the same good at a lower price to C gives her information about A's reservation price (namely, that it is lower than what A currently charges B), allowing her to bargain for a better deal. Indeed, people react with outrage when they learn that someone else pays a lower price for the same good or service (Kahneman et al. 1986). Therefore, impartiality can be a means of concealing strategic information. This has broad consequences, because such strategic information can also be exploited by third parties (agents exterior to the transaction), who might be motivated to punish an ungenerous individual in order to signal that they expect better treatment from him if they happen to interact in the future, or to avoid him altogether (Krasnow et al. 2012).

Conclusion

Empirical data shows that humans hold certain early-developing, complexly patterned moral values, which point to the existence of a biological sense of fairness. There is no clear consensus yet about the exact way by which natural selection has implemented these values in us, but an emerging body of theoretical work has tackled the challenge. Fairness cannot simply be equated with generosity, and the complexity of human intuitions about what constitutes fair behavior provides a fascinating benchmark against which to compare evolutionary models.

As theories of natural selection acting at the individual level suggest (e.g., Trivers 1971), moral values might not have evolved for the good of the group. Although a concern for fairness can mitigate the negative impacts of self-interested behavior on the greater good, it also has the potential of canceling some its positive impact: for instance, by disrupting the normal operation of supply and demand, it can cause markets to fail to clear,

resulting in a nonoptimal distribution of resources (Kahneman et al. 1986). Whether and how we as a society choose to foster the taste for fairness that nature has endowed us with depend on what we ultimately consider to be desirable, and careful considerations of the consequences of our intuitive preferences.

Cross-References

- [Evolution of Cooperation](#)
- [Fairness in Primates](#)
- [Game Theory](#)

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Founder of Four-Field Anthropology

► [Franz Boas](#)

Founders of Evolutionary Psychology

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Synonyms

[David Buss](#); [John Tooby](#); [Leda Cosmides](#); [Margo Wilson](#); [Martin Daly](#)

Definition

Evolutionary psychology is a psychological science where hypotheses are informed by evolutionary theory (especially middle-level theories, such as Trivers' parental investment theory or life history theory, see Buss 1995), as well as a consideration of known features of the species' relevant evolutionary past, i.e., relevant selection forces. In addition, there is a specific model of mind, where one considers the mind made up of a mosaic of mental mechanisms. This form of modularity follows Pinker's (1997) definition where modules are only partially informationally compartmentalized, not Jerry Fodor's more informationally encapsulated definition, as the modules are partly interacting and partly informationally encapsulated. These mechanisms are designed through natural, social, or sexual selection. They are context-dependent and process information according to specific rules as selected for. This may by many be called the Santa Barbara school of evolutionary psychology, but that specific approach has been somewhat broadened by a greater interest in sex differences and individual

differences during the last decades. Founders are those who contributed to the formation of the psychological evolutionary research program as it may be recognized today, especially as opposed to other evolutionary research programs within human behavioral science such as human behavioral ecology or gene-culture coevolution. Founders presented in the following include John Tooby and Leda Cosmides, Margo Wilson and Martin Daly, and David Buss. These were historically the five scholars who worked on the very first "Foundations of Evolutionary Psychology" at Palo Alto.

Introduction

Evolutionary psychology was founded in the 1980s, developed into a comprehensive and burgeoning field during the 1990s, and slowly became an integrated part of psychology in general the last 20 years. Considering the foundations of evolutionary psychology therefore warrants a look at papers written during the 1980s and the early 1990s, as well as work that has influenced the field the last 30 years.

There are three major research labs/groups that may be recognized as foundational and will be considered in greater detail in this chapter, although they all met at Harvard: John Tooby and Leda Cosmides, founding directors of the Center of Evolutionary Psychology at the University of California at Santa Barbara; Margo Wilson and Martin Daly, McMaster University, Canada; and David Buss, at Harvard, University of Michigan, and the University of Texas at Austin in charge of the evolutionary psychology and individual differences graduate program.

The current chapter will provide a brief introduction to some of the most influential contributors to the formulation and foundation of mainstream evolutionary psychology (EP). This research program was developed through more or less formal meetings over several years, but was most clearly formulated by John Tooby and Leda Cosmides as what is sometimes referred to as the Santa Barbara school. Parallel to Tooby and Cosmides' empirical work, Margo Wilson and

Martin Daly published large studies based on basic EP principles. The major communicator of EP within academia is probably David Buss, who in addition to large empirical studies also added a focus on sex differences to the mainstream EP research program, as well as personality and individual differences. While many more researchers – both independent and collaborators of the aforementioned – have also contributed to mainstream modern EP, this chapter will be restricted to the basic contributions of these five founders.

Evolutionary Psychology Is Not Sociobiology

Historically, evolutionary psychology is obviously not the first evolutionary approach to behavior, psychology, or human nature. In *Origin* Darwin is often quoted as pointing out that he believes that “In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation.”

This is an interesting quote, but from a historical perspective, it is important to note how early this was in the development of any scientific psychology. Certainly Darwin’s work on human emotions is one of the first works on human psychological features from an evolutionary perspective, and he is also one of the first developmental psychologists with his observational study of his own child published in *Mind*. Pioneers such as William James and Sigmund Freud also were famously interested in phylogenetic musings and speculation. Prominent mainstream theorists such as John Bowlby and Mary Ainsworth were explicitly evolutionary, despite many current attachment scientists downplaying the evolutionary foundations of their classical theoretical work. Within anxiety theory, mainstream clinical work has always been based on an appreciation of the evolved functional underpinnings (Kennair 2007; Marks and Nesse 1994). However, none of these previous evolutionary approaches to behavior or psychology were part of an organized theoretical framework or research program. The most influential approach to human evolved behavior prior to the advent of evolutionary psychology was human sociobiology, strongly

influenced by E.O. Wilson’s popular work on sociobiology, heralding the use of recent theoretical developments in evolutionary biology to investigate behavior in animals, including humans.

It is important to note at this point the difference in considering manifest behavior versus considering the underlying evolved mental mechanisms. Dennett suggested that EP is merely the marriage of sociobiology with cognitive science. This might not fully appreciate the complexity of focusing on the adaptation as a cognitive structure (Kennair 2002). Once one accepts mental mechanisms as the relevant object of study, something behaviorists such as Wilson was hesitant to do, this affects both methods and how one implements theory in generating hypotheses. First, one stops primarily counting babies; that is, one stops to primarily consider current selection or adaptiveness. Don Symons was dismissive of evolutionary oriented scholars who sought a psychologically agnostic science, where humans are fitness maximizers. Cosmides and Tooby (1987) provide the link between manifest behavior and evolutionary science: the evolved psychological adaptation.

It takes time to construct human mental mechanisms through selection. Human universals, and thereby the cognitive underpinnings of our human nature, have to have been in place before humans migrated out of Africa. It is therefore not necessarily our current environment we are adapted to, but rather the relevant selection forces that were stable enough across deep time to design the mental mechanisms that make up universal human nature. Environments change faster than selection can form adaptations, especially when species migrate as far as humans have. Such mismatch makes it less relevant to consider current adaptiveness, but predictable output from hypothesized mental adaptations may be studied, and design features may be discerned based on such output.

While sociobiology considered current adaptiveness and built upon a behaviorist psychological model that studied behavior in current environments, evolutionary psychology predicts that mental mechanisms have been formed over

evolutionary time due to middle-level evolutionary theory and available knowledge about the relevant selection forces (EEA). Evolutionary psychology thus focuses on adaptations and is inherently founded on a mainstream social-cognitive psychology model of mind. This shift made evolutionary psychology more relevant for mainstream psychological science. In summary, where sociobiology was founded on the psychological theory of behaviorism, which studied observed behavior and considered whether this was currently adaptive, evolutionary psychology was founded on mainstream cognitive theory, which studies the results of mental processing and considers the underlying evolved mental adaptations.

Basic Evolutionary Underpinnings

Dawkins has had a great influence on EP through his synthesis of how selectionist reasoning and the new (in the 1970s) theories of behavioral and social evolution by Hamilton (1964a, b) and Trivers (1972, 1974) might be implemented in research. George Williams also provided fundamental insight, through the focus on formal criteria of the adaptation. It is important to note that the field also in general clearly identifies with Williams' refutation of group selection and his focus on the adaptation. From an evolutionary psychology perspective, group selectionist models are moot. Thus evolutionary psychologists in general take a Darwinian, gene level selectionist approach, focusing on inclusive fitness and middle-level theories (i.e., Trivers 1972) or specific versions of these (i.e., sexual strategy theory, Buss and Schmitt 1993) that may generate testable hypotheses and predictions (Buss 1995; Ketelaar and Ellis 2000).

In addition to focusing on identifying mental adaptations and using middle-level theories, an evolutionary psychology approach builds on what is known about the species' relevant evolutionary past: the relevant selection forces or the environment of evolutionary adaptedness (EEA). Knowledge about selection forces may suggest how specific traits could be shaped today. The combination of these two aspects provides the evolutionary basis of evolutionary psychology hypothesis and prediction generation.

At this point it may also be important to note the following: Evolutionary psychology is not a comparative approach, like sociobiology often was. Other species have had species-specific selection that has formed the adaptations that define those species; the same is true for human evolution. Considering what model species to choose when attempting to consider either warfare or sexual behavior is hard enough; chimpanzees and bonobos are both related to humans to an equal degree, but differ dramatically in those two specific areas. Furthermore, many of the most interesting human psychological phenomena are species-specific and demand a consideration of specifically hominin evolution. That said, it is the same underlying middle-level theories that describe the selection mechanisms in all species.

A Short Introduction to Evolutionary Psychology

Evolutionary psychology is really indistinguishable from mainstream psychology if one considers research methods, statistics, or even to a large degree the journals evolutionary psychologists publish in. And despite what some critics argued, there probably are no differences in politics either (Tybur et al. 2007). More than traditional social psychologists, and despite changes in the last decade, evolutionary psychologists share a natural science epistemology and an acceptance of biological underpinnings to social cognition. That is not surprising given the fact that the most basic tenet of evolutionary psychology is that many relevant human psychological abilities, traits, or phenomena are the results of directional natural, social, or sexual selection.

One of Cosmides and Tooby's foundational contributions is the formulation of how the mind is best conceived within evolutionary psychology. While many other psychological theories either have no precise formulation of how the mind may be understood, evolutionary psychologists suggest that the mind is best understood as a mosaic of mental mechanisms. This is what is referred to as the modular mind. These modules are not fully informationally encapsulated; they are partially interconnected and communicate with each other, but particular parts are not

connected to all other parts, and they all process information differently. These modules are, as stated above, considered to be mental adaptations, results of selection. They are therefore behavior-generating mental organs evolved to solve specific tasks relevant to reproduction and survival. They are therefore also context dependent to some degree, with a certain expectation of specific forms of input. These mechanisms contributed to increasing fitness due to processing information according to certain rules and generating fitness-enhancing behavior in evolutionary relevant ecologies in our species' past. The sum of these mental adaptations and their output make up human universal nature.

Methodologically, as mentioned above, the aim is to apply knowledge about the past environment and evolutionary middle-level theories to generate original, testable hypotheses and predictions (Buss 1995; Tooby and Cosmides 1990b). These predictions are often concerned with specifying the functionally specified mental mechanisms, and specific predictions will suggest how these will process relevant information. This functional cognitive approach to hypothesis generation is at the heart of what makes evolutionary psychology stand out among psychological research programs. While most psychologists probably agree with evolutionary theory being the only explanation of how life has diversified and adapted to local ecological demands, psychologists in general seldom consider how evolutionary middle-level theories can help specify the information-processing mechanisms they study. Also, evolutionary theory is generally considered explanatory, not hypotheses generating. Further, while in the recent years most psychologists, even within social psychology, will accept a biological underpinning of mental activity, continued resistance to considering human behavior as a result of natural and sexual selection still exists.

A Meeting During an Earthquake

Ground shifting science rarely happens while the ground actually shakes. It did for evolutionary psychology. In the years 1989–1990 (during which the Loma Prieta earthquake occurred), David Buss collected five major names within

evolutionary psychology at the Center for Advanced Study in the Behavioral Sciences in Palo Alto for a special center project entitled “Foundations of Evolutionary Psychology.” Although no great manifest was published, there is little doubt that this was an important meeting given the theoretical and empirical output over the next few years from all involved. The five were, of course, Margo Wilson, Leda Cosmides, John Tooby, Martin Daly, and David Buss. These are therefore the founders whose work and contributions will be considered in further detail below.

Wilson and Daly: Young Male Syndrome and Homicide

Margo Wilson and Martin Daly are two of the most important pioneers of empirical research into human behavior from a psychological and evolutionary perspective. Science only grows and matures through data collection and hypothesis testing. While theoretical contributions are necessary to formulate a research program and develop the hypotheses to be tested, without empirical research, there will be little development.

Beyond their own scientific contributions, it is probably a safe claim that they influenced the field immensely with their editorship of the Human Behavior and Evolution Society flagship journal. This journal changed its name from *Ethology and Sociobiology* to *Evolution and Human Behavior*, marking both theoretical development and its increased scientific impact.

Young Male Syndrome

Sex differences are still a source of controversy within the social sciences and even to some degree within psychology. Many differences are quite small, and generally evolutionary psychology is not as interested in such differences: Relevant differences must have been due to stable evolutionary selection forces over evolutionary time and differences predicted by evolutionary middle-level theories.

Who will take the most risk? Based on sexual selection theory and analyses of age and sex, Wilson and Daly (1985) point out that those who have had the greatest reproductive competition

and are at greatest danger of not reproducing are young men. They consider how many violent crimes may be the result of status competition, however petty the situations that can lead to violence among men might seem (e.g., bar fights). These male-male violence and status competitions are driven ultimately by increased reproductive success among young men who can acquire status, as risk-taking behavior including crime and violence has historically been one possible avenue to greater status for disenfranchised young men. They report how specifically young males but not young females show a surge of violent crime after puberty. Without the *young male syndrome*, many crimes might not be committed. War might not even be possible without this effect. One needs a certain hypophobia concerning one's own mortality, as pointed out by Tooby and Cosmides in their analysis of the necessary psychological foundations of human warfare. The paper also considers general risky behavior among young men, including gambling.

Risky lifestyle choices, including risk-taking behavior, lead to increased mortality. Kruger and Nesse's studies on male to female mortality ratios have continued this line of work. Being born male is the greatest epidemiological risk factor for early mortality in Western countries. Research on risk versus worry highlights how both women in general might worry more, but men – especially young men – may be in danger due to being hypophobic, a concept used by Marks and Nesse to describe less than normal levels of anxious activation. The concept of the young male syndrome therefore sets the stage for a different appreciation of relevant health psychology and safety and risk phenomena based on an understanding of the function of reduced anxiety and greater risk-taking behavior in a specific subset of the population.

Homicide

Who kills who? And when and why do people kill each other? Daly and Wilson's (1988) classical book *Homicide* was groundbreaking as it was explicitly based on an evolutionary approach to behavior. Most importantly, and despite a background in comparative psychology, it focused on

specific human behavior, and it left mere theoretical speculation behind: It backed up several of the theoretical a priori predictions with evidence from official registers. This was novel. As such, it mapped an epidemiology of violence and abuse from an evolutionary psychology perspective, actually stating this explicitly and using the concept of evolutionary psychology in the foreword. From violent crimes to killing of kinfolk, Daly and Wilson chronicled different aspects of the history of homicide, human life history, evolved sex differences, and the killing of family members.

One of the most discussed and challenged results of this evolutionary approach to murder and abuse was the *Cinderella effect*, the increased likelihood of stepparents killing their partner's child, compared with biological parents killing their own children. This finding has been challenged both on the basis of findings from different countries and on the basis of bias in the registration of murder and abuse of children. In both cases, correcting the sample statistics suggests that there might be differential rates of murder across nations as well as a bias for registration of stepparents as perpetrators, but in general the Cinderella effect is supported and robust, and no other explanation has outcompeted the original evolutionary perspective. As a side note, even if one resorts to attachment theory for a competing explanation, it is surprising that critics are not aware that in their eagerness to refute one evolutionary perspective, they are actually invoking another. Finally, it is important to make clear how the Cinderella effect works: Many believe that Daly and Wilson are suggesting that humans, like lions taking over another male's pride, kill children that are not theirs to increase their own fitness. This is explicitly not what Daly and Wilson claim; they refute this position in *Homicide*. Their position is that for stepparents the bond that prevents parents in general from hurting their children is weaker, and therefore, some stop mechanisms have reduced function. They are therefore not arguing that biological parents cannot kill their offspring or that stepparents in general will hurt their stepchildren. At the population level, the Cinderella effect is still a statistically documented phenomenon.

Cosmides and Tooby: Human Universals and Interpersonal Competition

John Tooby and Leda Cosmides were recently awarded the lifetime achievement award by the HBES. They may be considered the most influential theoreticians within EP and probably the founders of the basic theory through their theoretical papers in the 1980s and early 1990s. While some of the theoretical claims such as the non-adaptiveness of personality differences might not be accepted by the entire field, their work on human universals sets the stage for a social-cognitive evolutionary psychology situated safely within normal psychological science methodology. At the same time, their attacks on the Standard Social Science Model (SSSM) created a certain distance to social psychology and social science, but highlighted the necessity of functional analysis, which they rightly claimed given their own fruitful methodology is not an explanatory luxury; it is a tool which when properly applied provides novel insights into how cognitive mechanisms function.

Culture, Learning, and Evolved Human Universals

In one of the most provocative and misunderstood essays, Tooby and Cosmides (1992) identify and criticize the Standard Social Science Model (SSST). They suggest that explanations of behavior that rely merely on invoking the general concepts of culture or learning as explanations in themselves – without actually explaining the mechanism of transference in detail – are not scientific. This criticism caused reactions, including a misplaced conclusion that evolutionary psychology is adverse to learning in general. The biophobic social scientist was also, according to detractors of Tooby and Cosmides position, a strawperson. Many researchers claimed that there was more attention given to the biological underpinnings of culture and learning than Tooby and Cosmides acknowledged. On the other hand, the lip service to such biological factors with no place for any specific theory, no methodology that accounted for the relevance of such factors, and a general reflexive dismissal of all attempts to add functional approaches to scientific explanation was

exactly what Tooby and Cosmides were targeting. Most evolutionary psychologists have met these alleged straw men among both editors and reviewers, as well as colleagues. Actually, to some degree, some evolutionary psychologists share SSST features in their thinking about development, with regard to behavioral genetic findings.

There was no dismissal of learning nor culture, as relevant and important phenomena in this essay. Only a very clear caveat that learning is not an explanation without further specification of what exactly it is that one means. It is very unlikely that Skinner would have disagreed with their critique of the simple incantation of general learning by general mechanisms without further evidence and description of the mechanism, including the possible evolutionary history of the learning mechanism. This essay largely functioned as a call to arms for evolutionary psychologists, laying the foundation for a more stringent science of both learning and culture from an evolutionary perspective. As such, one might note that it was considered more convincing in the long run by psychologists than by anthropologists.

Solving the Wason Selection Task

The Wason selection task is a logical problem in which people are shown four cards. They have a numeral printed on one side and a letter on the other side. They are placed on the table in front of the participant. Two of these cards are dealt with the numeral facing up; the other two show the letters, for example, [7][H][3][D]. The participant is then given a rule for the cards and asked which card(s) to turn to test the rule. In this case the rule is behind every [D], there is a [7]. The question then is: Which cards would you turn? Typically, people are governed by their confirmation bias. They therefore flip over [7] and [D], in both cases to confirm the rule rather than attempting to falsify it. This phenomenon occurs irrespective of intelligence and education. Furthermore, when people have learnt the solution of by heart, they will in some cases still provide erroneous explanations, yet again reverting to their confirmation bias – which illustrates how strong this tendency is. The correct answer, which is not typically the human response,

is to flip over [3] to find a [D], and the most difficult, to flip over [D] to *not find a* [7].

It may seem strange, given how much more attention sexual research gets, that an abstract cognitive bias test was probably the single empirical research finding that paved most of the way for EP as a specific scientific research program. While Tooby and Cosmides have continued their research into coalitional, innate, and evolved psychology (including topics from war to incest avoidance), it all started with a groundbreaking finding: that human limitations in solving logical problems, documented in a multitude of studies, vanished once they were made ecologically relevant for detecting social contract rule breaking (Cosmides 1989).

It is not particularly important what social contract rule one tests; it can be made up or a familiar social rule in participants' culture. If the rule to be tested is a social contract rule and there are potential cheaters to be detected, people solve the Wason selection task much more frequently. Note that from a logical perspective, the problem and solution are the same.

Consider this example: Four cards representing four people in a seedy bar. The rule is that only those who are older than 18 may drink beer. The cards display the age (either above or below 18) on one side and what the person is drinking (either soda or beer) on the other. The four cards show [Soda] [Beer] [Above 18] [Below 18]. Who do you want to check, to test the rule? While most people want to check and confirm [D] and [7] above, that solution is no longer interesting. Now most people want to find cheaters. Most people want to see whether the person below 18 is drinking beer (falsification not confirmation) and how old the beer drinker is (yet again and contrary to what one does in the non-social cheating context, in order to check whether the person is too young).

In other words, we become natural Popperian falsifiers and ditch our normal human confirmation bias problems if someone might be breaking a social contract. This applies to the majority of people, and it is not dependent upon familiarity or cultural context. Finally and most importantly, it was not predicted by any other theory. Perhaps

most surprisingly, there is probably dedicated neural circuitry involved in cheater detection (Stone et al. 2002) – which in turn provided support for the modular approach.

Why should we be good at discovering cheaters? We are hyper-social intelligent animals, both dependent upon and in active competition with other humans. We are able to make social rules and break these same rules. Being naïve about rule breakers is not a viable evolutionary strategy. The finding that a module for solving a specific, adaptively relevant problem could make us better at solving generally unsolvable logical problems was groundbreaking. The immense creativity of these founders, and their ability to succinctly formulate the basic theoretical logic underlying many psychological problems, has resulted not only in fundamental theoretical papers: research into other social, coalitional cognitive processes, such as welfare-benefit ratios and race perception followed from the same interest in the underlying evolved adaptations and provided our science with findings and explanatory principles that were both original and counterintuitive.

Strategic Modeling

Together with Irvin DeVore, John Tooby wrote a classic on why human evolutionary psychology must take into account specific human evolution. While many earlier approaches to human evolutionary behavioral science were to a large degree comparative, Tooby and DeVore (1987) point out that in order to study the species-specific adaptations of humans, such an approach will be severely limited. Evolutionary psychology is therefore to a much lesser degree comparative in its general approach than sociobiology was or to the degree that more biological approaches to human psychology often are. While homologous structures exist, when considering human nature, it is primarily relevant and even imperative to consider specific hominin evolution and selection, especially those traits that are unique to humans. This gem is not as often cited as it ought to be but provides insights into how early evolutionary psychology theorizing differed from other evolutionary approaches to both animal and human

behavior. While many academics believe that humans are freed from the animal shackles of evolution, Tooby and DeVore suggest that the complexities of proximate mechanisms hide the fact that the ultimate function has not changed. Strategic modeling of complex proximate mechanisms is therefore a tool to reduce such complexity, which reveals how they are “adaptively patterned.” Note that while this chapter is primarily a contribution to paleontological modeling of hominin species, the principle strategic modeling they suggest is most relevant as a metatheory of evolutionary and behavioral analyses of function and specific human evolution.

Buss: Individual Differences and Mate Preferences

Mate choice is a fundamental aspect of evolution, and mates vary. There are individual differences among potential mates, and we choose among these potential sexual partners either to mate romantically for life or for the sexual thrill of the moment. If someone were to steal our romantic partner, it would hurt us, both emotionally and through possible fitness costs. All of these areas that might seem very familiar to anyone with an interest in evolutionary psychology have been pioneered by David Buss. And beyond important theories such as sexual strategy theory, with David Schmitt, and error management theory with Martie Haselton maybe Buss is the researcher that has provided the field with the broadest and deepest empirical basis. This has also aided the communication of evolutionary psychology to the rest of academic psychology. For the field, his textbook and *The Handbook of Evolutionary Psychology* have become landmarks, improving the teaching and uniting the field.

Cross-Cultural Mate Preferences

Cross-cultural research has not been typical in social sciences in general or psychology specifically. While critics of merely considering Western, Educated, Industrialized, Rich, and Democratic (WEIRD) populations have made important corrections to the generalizability of psychological research, it is worth noting that from early on evolutionary psychology has been

oriented toward cross-cultural studies and more so than many other areas of psychological research. One of the most groundbreaking of these evolutionary cross-cultural studies was David Buss’ mammoth collaborative study of mate choice in 37 cultures.

Building on his early work on mate choice (Buss 1985), and inspired by Don Symons’ (1979) work on human sexuality and human universals, Buss started collecting one of the largest international data sets at the time. While some have criticized the cultural variance and national sample sizes, this is a landmark study, with few studies in psychology, and especially cross-cultural studies, coming close in influence and citations.

Buss (1989) reported several cross-culturally robust similarities between the sexes. For example, both men and women are interested in intelligence and agreeableness traits, especially in long-term relationships. On the other hand, stable male-older findings, where both sexes seem to agree that he should be older than her, greater male interest in female physical attractiveness, and greater female interest in male financial prospects suggested evolutionarily predictable sex differences in partner preferences. These original findings have been reproduced repeatedly and have proven to be stable across cultures as well as within cultures across time. Age preferences have also received attention in the last few years. While many critics of evolutionary psychology have attempted to challenge these findings on human universal mate preferences, they appear to be among social psychology’s most replicated conclusions.

Evolutionary Personality Psychology

There are two major approaches to the science of psychology reflected in many areas of research. In some disciplines and theories, one considers human universal nature, and the theories and findings are considered relevant for all humans. Such areas include learning psychology and to a large degree social psychology in general. Personality psychology, on the other hand, considers individual differences. This is one of the interesting areas of open disagreement among the founders of

EP. The basic formulation of EP by Tooby and Cosmides (1990a) focuses explicitly on human universals and does not even consider sex differences in their study of evolved mental mechanisms. As mentioned above, EP is in its original formulation by Tooby and Cosmides, largely a theory of the minds of both men and women, equally. Tooby and Cosmides (1990a) were quite explicit about personality and other individual differences not being key areas of study from an EP or adaptationist perspective. There is therefore a certain shift in focus in different directions even within mainstream EP. On the other hand, they suggested mechanisms that could explain adaptive individual differences, including frequency-dependent selection and their concept of reactive heritability (where, e.g., some traits are more efficient in specific bodies or in concert with other traits and thus may become more expressed under the right and adaptive circumstances).

A full understanding of human nature demands that we also understand the evolution of stable differences in fitness-relevant behaviors, as defined by traits. Also, trait psychologists have suggested that evolutionary psychology has to address the question of how the five major personality traits of openness, conscientiousness, extroversion, agreeableness, and neuroticism have evolved (Nettle 2011). David Buss pioneered the area of evolutionary personality psychology, which has been slow to gain momentum in empirical data collection, but in recent years' has increased with interest in life history approaches. Future empirical testing is still much needed for evolutionary personality psychology data collection to catch up with theory generation. At the moment, we have different approaches within EP that consider either how individual differences in life histories may provide testable predictions about behavior, but also theories of how the five major personality traits are a result of specific evolutionary processes, including selective neutrality, frequency-dependent selection, and mutation-selection balance. We need more work testing different hypotheses. At the same time, from an evolutionary personality psychology perspective, it would be odd if these value-laden descriptions of others that make up

the basis of traits had not been relevant for selection. Noise or adaptive? We still do not know. This area still needs more evidence.

Sexual Strategy Theory

Formulated with David Schmitt, sexual strategy theory (SST) is one of the most influential approaches to the understanding of human sexual behavior (Buss and Schmitt 1993). SST starts with the general principles of Trivers' (1972) parental investment theory, but specifies the theory for human women and men and our species-typical adaptive sexual problems. An important contribution of the theory is the attention given to mating context as well as sex: Men and women have different preferences and behavior in short-term and long-term mating contexts. This lays the foundation for several predictions about how men and women in short-term and long-term mating situations will act or display preferences.

Women and men have engaged in both long-term and short-term sexual relations throughout evolutionary history and been selected for these kinds of behavior if the benefits outweigh the average cost. But each context presents different adaptive problems for the two sexes. Due to differences in minimal parental investment and possibilities to benefit from multiple matings, men will have greater interest in short-term sex than will women. This exemplifies one adaptive problem difference, but there will be predictable similarities and differences between men and women in all four combinations of sex and context. Buss and Schmitt (1993) list the following four adaptive problems for men for either a long-term relationship or short-term sexual encounters:

Long-term relationships: (1) discerning reproductive value, (2) ensuring paternal certainty, (3) identifying good mothers, and (4) identifying willingness to commit

Short-term sexual encounters: (1) acquiring a large number of partners, (2) discerning who is sexually accessible, (3) discerning fertility, and (4) minimizing any investment and commitment

Note that reproductive value is very important for long-term relationships, while current fertility is relevant for short-term relationships. Similarly, minimizing investment is not as relevant for a monogamous long-term relationship. The ability and willingness to commit in long-term relationships will not differ between the sexes and should rank high among partner preferences for both sexes.

Women's reproductive success has not been constrained by access to sex, but rather access to resources and maybe genes of the men that are interested in investing in them and their offspring, both here and now and on a long-term basis. The following five adaptive problems need to be solved by women in the adaptive problem of acquiring the best possible long-term relationship (Buss and Schmitt 1993): discerning men who are (1) able and (2) willing to invest resources in her and her children on a long-term basis, (3) identifying men who will be good fathers, (4) identifying men who are willing and able to commit, and (5) identifying men who will be both able (formidable) and willing (aggressive) to defend them against other men.

The evolutionary perspective suggested that men and women have been selected so that they on average will solve the adaptive problems effectively when engaging in short-term sex or long-term relationships. While the word strategy might be confusing, the strategy is the evolved, effective solution to the adaptive problems, the mental adaptations solving context specific adaptive problems, with no conscious goal being assumed. Beyond being a very influential theoretical paper, it also provided data that tested direct predictions about, for example, male interest in both long-term and short-term relationships and interest in sexual variety.

SST met with criticism from mainstream social psychology. One claim was that our sexual psychology is inherently monomorphic, but cultural structures will cause differentiation. Therefore, detractors of SST believed one would not find similar results as in the American sample in other more gender egalitarian nations. Such criticism must be testable in order to be scientific; one cannot make such claims and not accept findings

from the world's most gender egalitarian nations as not relevant. Since 1993, hypotheses from SST have been tested internationally; in some cases, there are differences – with both smaller and larger sex differences being reported from more gender egalitarian nations than the USA. In general, though, these results have supported SST as the best theory for generating hypotheses about modern human sexual behavior and sex and context differences in preferences. For example, direct tests suggest that one finds almost exactly the same results for the original SST findings in a more gender egalitarian Norwegian sample.

Jealousy

It is simple: Imagine that there is no parental investment, no long-term relationships, and full knowledge of who both parents are. In this scenario there is no jealousy. Now, change a few things: Add father investment with no or low paternal certainty. Is it then possible that male sexual jealousy would not evolve? Men are among 5 % of mammals in which fathers invest in assumed offspring. Concealed conception results in less than complete paternity certainty, despite different cultural inventions that attempt to control female sexuality. What would happen to the more protective and skeptical or jealous men compared to the men who are naïve and uncaring about their partner's sexual escapades? The same is the case for women: What would happen to women who were uninterested in their partner's interest in investing in their joint children? Rather than attempt to prove how sex differences in jealousy evolved, one might turn that around: How could these specific types of interest in fatherhood or future resource investment *not* evolve? And what feedback mechanism could help us learn the effects? Men would never get to know the negative effect. If women did see the effect, it would certainly be too late.

Prior to Buss' original work on jealousy, psychologists were not aware of sex differences in jealousy: men being more distressed by sexual infidelity than emotional infidelity than women are (Buss et al. 1992). It is worth noting that it is the interaction that is relevant by testing whether men, relative to women, find sexual infidelity

more distressing than emotional infidelity. While the logic of the evolutionary theory seems convincing, there have been several challenges to the theory. First, that one sort of infidelity (either emotional or sexual) would elicit the conclusion that the other form had occurred, so that there was not really a sex difference. This was called the double-shot theory. It is simple to test: One changes the question from “what is most distressing, sexual or emotional infidelity?” to “if both sexual and emotional infidelity have occurred, which type is most distressing?” In this double-shot scenario, sex differences persist. Another challenge is that the stable sex difference is not detectable with continuous measures, maybe due to ceiling effects. At the same time, continuous measures are considered more meaningful by some critics, and some suggest the sex difference is merely a methodological artifact. Recent work found that when randomly distributing either continuous or forced choice questionnaires in the same population, there was no difference between the two methodologies (Bendixen et al. 2015). This study also found that, rather than there being smaller sex differences in jealousy in more gender egalitarian nations, the effect sizes are larger, probably driven by greater expected male investment as proposed by Buss et al. (1992). Another criticism is that sex differences in jealousy might only hold for young, heterosexual participants. However, finding that postmenopausal female partners elicit less jealousy is congruent with evolutionary theory.

Considering Future Developments

Evolutionary psychology has developed during the almost 35 years since the first formulations of the evolutionary psychology basic theory, not just in general acceptance among academics and inclusion in mainstream psychology textbooks but also as a theory. In the beginning, the focus was largely on human universals, but there has been a clear shift toward considering individual differences in both normal personality (Buss and Penke 2015) as well as psychopathology (Del Giudice 2014; Kennair 2011) and the effects of cultural differences, highlighted by the work of David Schmitt. In the last few years, greater

emphasis has been placed on life history theory (Del Giudice et al. 2015), primarily as an explanation of individual differences, but also psychopathology. Furthermore, there is a continued interest in evolutionary developmental science. All of these areas need empirical and theoretical developments to be tempered with knowledge from the field of behavioral genetics in order to fully come to fruition. While many researchers are now considering how unstable childhood environments predict instability in personality traits or behavior of young adults, it is worth noting that behavioral genetics research suggests that parent-offspring similarities in general are due more to genetics rather than environmental influences.

The many students of the founders have also started making large contributions in their own right, both empirically and theoretically, and many of these may be considered part of the foundations of EP. Two select examples: Martie Haselton and David Buss's (2000) *error management theory*, is generating both supportive and critical research within EP. Also, research on race perception, originally developed by Kurzban et al. (2001), is providing an evolutionary base for conceiving of race as merely one of many arbitrary and therefore inherently malleable out-group cues.

Conclusions

These five founders of EP as a specific research program have established an evolutionary-based approach to psychological research, which over the last three decades has become part of mainstream psychological science after initially being considered both politically and scientifically suspect. At the same time, there have obviously been many other influential figures in the field who have inspired the development of both evolutionary psychology research and theory, both by challenging and developing the original formulations. As such, the area of study has been influenced by critics, students, and colleagues working around the globe in collaboration and competition.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adaptationist Program, The](#)
- [Adapted Mind, The](#)
- [Anxiety](#)
- [Cinderella Effect, The](#)
- [Cheater Detection](#)
- [Controversies in Evolutionary Psychology](#)
- [David Buss](#)
- [Environment of Evolutionary Adaptedness](#)
- [Evolutionary Clinical Psychology](#)
- [Evolutionary Personality Psychology](#)
- [Evolutionary Psychology, The Handbook of](#)
- [Extended Phenotype, The](#)
- [George Williams](#)
- [Homicide](#)
- [Jealousy](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)
- [Life History Theory](#)
- [Martin Daly and Margo Wilson \(Founders of Evolutionary Psychology\)](#)
- [Mate Preferences](#)
- [Modularity of Mind](#)
- [Reliability, Efficiency, and Economy](#)
- [Richard Dawkins on Constraints on Natural Selection](#)
- [Robert Trivers](#)
- [Selfish Gene, The](#)
- [Sexual Strategies Theory](#)
- [Standard Social Science Model](#)
- [Young Male Syndrome](#)

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Four-Stage Model of the Sexual Response

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Synonyms

[Human sexual response](#); [Sexual response pattern](#); [The sexual response cycle](#)

Definition

The four-stage model of the sexual response is a descriptive model of the physiological changes which correspond with human sexual arousal and sexual behavior. In the four-stage model of the sexual response, the typical markers of arousal are organized into a temporal framework. This model was proposed by Dr. William Masters and Virginia Johnson (1966) and made possible by their groundbreaking research, including the systematic physiological recordings of individuals and couples engaging in sexual contact in the laboratory. The four stages of the human sexual response cycle, as defined by Masters and Johnson (1966), are (1) excitement, (2) plateau, (3) orgasm, and (4) resolution.

Introduction

This entry will detail the four-stage model of the sexual response and will explain the physiological changes associated with human sexual arousal, particularly emphasizing the 1966 work of Masters and Johnson, *Human Sexual Response*. While

other works had – prior to the publication of *Human Sexual Response* – explicated physiological markers of the human sexual response (see Ellis (1928) *Studies in the Psychology of Sex* which particularly emphasized the destigmatization of sex and the need for sexual physiology and function to be taught in schools), Masters and Johnson uniquely relied upon physiological data and novel empirical methods to construct their four stage descriptive model of the sexual response cycle. This four-stage model of the sexual response *still* characterizes the understanding of the physiological substrates of human sexual arousal and behavior in the many domains of psychology (e.g., biological, social, evolutionary) which apply their own theoretical perspectives and methodologies to the study of human sexuality.

Four-Stage Model of the Sexual Response

The four-stage model of the sexual response was (1) based upon direct observations and recordings of human sexual activity (partnered and solitary) in the laboratory and (2) used a body of existing scientific knowledge to construct a framework that would provide order to the tremendous individual differences in sexual responses and broad array of physiological changes that correspond with the experience of sexual and physiological arousal. According to Gray and Garcia (2013):

(Masters and Johnson's) model was built on cutting edge physiological studies of individuals and couples in a laboratory setting. They recorded responses as varied as male heart rate and female uterine contractions. Through these measures, they were able to document the most intimate physiological details in unprecedented, real-time, ways. For its time, their work was controversial. (p. 200)

This discussion will be organized into the (chronologically sequenced) stages of the human sexual response proposed by this model: (1) excitement, (2) plateau, (3) orgasm, and (4) resolution.

(1) Excitement

The four-stage model of the sexual response begins with the (1) excitement phase. This phase

is generally characterized by the initiation of physiological arousal. During the first phase, Masters and Johnson (1966) describe a response in the presence of “any source of somatogenic or psychogenic stimulation” (p. 5) wherein physiological arousal begins to build. While this stage does characterize the beginning of the sexual response cycle for solitary sexual practices (i.e., masturbation), colloquially the excitement phase is referred to as “foreplay.” During this initial stage, somatogenic or psychogenic stimulation produces an increase in heart rate, respiratory rate, blood pressure, and a dilation of the pupils – all general markers of physiological arousal (Pinel 2014). Also, the skin of the male and the female – particularly the chest, breasts, and back – becomes slightly reddened or “flushed,” called the “sex flush” by Masters and Johnson (1966). This reddening is particularly likely to occur in females, where the skin of the chest will become red and resemble a rash. Additionally, the female excitement phase is characterized by the labia majora thinning, parting, and beginning to “flatten against the perineum” (Masters and Johnson 1966, p. 38); the labia minora begins to lubricate the vulva and enlarge (Gray and Garcia 2013).

In males, a similar swelling of the external genitalia occurs during the excitement phase – the dilation of arteries (i.e., internal pudendal arteries) promotes the movement of the blood to the penis and scrotum, causing the penis to become erect and the testes to swell and lift closer to the pelvic floor (Masters and Johnson 1966). During the excitement phase, in females – and more variably in males – the nipples become erect. Masters and Johnson (1966) go on to characterize the excitement phase in males and females as being characterized by (a) increasing sensitivity to sexual stimulation (especially in areas such as the nipples, external genitalia, and anus), (b) increasing muscle tension, and (c) long duration (compared to the rest of the phases of the sexual response cycle). In fact, many therapists recommend long durations of foreplay to promote the achievement of sufficient arousal and stimulation to reach orgasm, particularly for females (Gray and Garcia 2013).

(2) Plateau

According to Masters and Johnson (1966), a transition to the second phase of the response cycle is characterized by an increase in intensity of physiological arousal (due to continued stimulation) during the excitement phase. The second phase, the plateau phase, is described via this increased intensity of arousal and characterizes the physiological changes that facilitate the transition between initial arousal/excitement and the experience of orgasm. For females, the physiological changes which characterize this second phase of the sexual response cycle are a continuation of the lubrication (facilitated by the activity of Bartholin's glands) and swelling of the labia minora; according to Masters and Johnson (1966), "... the labia minora increase at least two, occasionally three, times in diameter" (p. 41). Further, "vivid color changes develop in the engorged minor labia during the plateau phase of the sexual response cycle" (p. 41), termed "sex skin" by Masters and Johnson. Interestingly, the reddening of skin has – in the evolutionary history of primates – served as a signal to nearby potential mates. A reddening and swelling of the vulva is common in many species of (female) primates and is hypothesized to function as a signal of sexual receptivity (i.e., peak fertility) rather than a mere correlate of the experience of sexual arousal (Dixon 2012). Females also experience the continuation of the parting, thinning, and elevation of the labia majora during this phase. Additionally, the clitoris typically retracts during the plateau phase – but is hypothesized to do so in response to physical stimulation, rather than as an involuntary physiological precursor to orgasm (Masters and Johnson 1966). The vaginal walls continue to display signs of vasocongestion, and the vagina increases (only *very* slightly) in width and depth.

Males also continue to experience vasocongestion of the external genitalia – the scrotum continues to enlarge, the testes continue to elevate, while penis size changes very little during the plateau phase as full erection is typically achieved during the excitement phase (Masters and Johnson 1966). While the male

experience is much more variable (e.g., this can occur during some sexual encounters and not others and is not observed in the majority of men), males may also experience a reddening of the external genitalia, namely, the glans of the penis. Males may also experience increased sensitivity to physical stimulation during this phase and pre-ejaculatory secretions (Gray and Garcia 2013). In a general sense, the physiological changes which characterize the plateau phase are a continuation and intensification of physiological changes which have been initiated during the excitement phase, for both the male and the female.

(3) Orgasm

Continued "adequate" (Masters and Johnson 1966, p. 6) stimulation during the plateau is required for the individual to achieve the third phase, orgasm. In fact, Masters and Johnson (1966) indicate that certain specific physiological changes during the plateau phase (e.g., the reddening of the labia minora) *always* cue the imminent experience of orgasm. In other words, experience of sufficient continued somatogenic and/or psychogenic stimulation to produce many of the physiological changes that characterize the plateau phase would *inevitably* produce orgasm. While the excitement and resolution phases of Masters and Johnson's four-stage model of the sexual response are the longest in duration, orgasm is the shortest.

The female experience of orgasm is characterized an experience of peak intensity of many of the physiological markers of the excitement and plateau phases, such as the "sex flush" of the skin, hyperventilation, and increased heart rate. Involuntary muscular spasms of the muscles in the neck, arms, abdomen, buttocks, legs, and face are experienced during orgasm. Vaginal and uterine contractions also occur (the uterus lifts away from the pelvic floor), wherein greater frequency and intensity of these contractions are associated with a stronger subjective experience of orgasm – over time these contractions rapidly decrease in frequency and intensity. Importantly, Masters and Johnson (1966) performed empirical work regarding the physiological correlates of female orgasm

which contradicted a popular perspective regarding the function of orgasm at the time – the “upsuck theory.” According to this perspective, “during orgasm the uterus develops some form of pressure and sucks the seminal fluid through the external cervical os into the cervical canal” (p. 122). Masters and Johnson used a “reasonable facsimile of seminal fluid” with a radioactive tracer to determine the extent to which uterine contractions associated with orgasm facilitated the movement of seminal fluid into the endometrial cavity. Masters and Johnson concluded that “in none of the six individuals was there evidence of the slightest sucking effect on the media in the artificial seminal pool” (p. 123).

The male experience of orgasm is similarly described as an experience of peak intensity of many of the physiological markers of the excitement and plateau phases, such as the “sex flush” of the skin, hyperventilation, and increased heart rate – as well as the occurrence of “total body” muscular spasms. Characteristic of the male experience of orgasm, and unique to the male experience of orgasm, is the expulsion of seminal fluid through the urethral meatus (Masters and Johnson 1966). Furthermore, males experience rapid contractions of muscles in the pelvic floor and surrounding the external genitalia (e.g., the deep perineal, sphincter urethrae, and the transverse superficial perineal muscles).

Consistent with evolutionary explanations of the experience and function of female orgasm, which suggest that the complexity and variability of females’ orgasmic experience serve as an opportunity to evaluate the commitment and investment of their sexual partner (Puts et al. 2012), Masters and Johnson (1966) explain: “There is great variation in both the intensity and the duration of female orgasmic experience, while the male tends to follow standard patterns of ejaculatory reaction with less individual variation” (p. 6).

(4) Resolution

The final phase of the sexual response cycle, resolution, is generally characterized as a disappearance of the physiological markers of excitement

and orgasm. That is, the slowing of respiration, constricting of the pupils, lowering of blood pressure, and slowing of heart rate. For females, the “sex flush” and reddening of the areolae and labia minora quickly disappear, while the swelling of the breasts (due to vasocongestion) decreases much more slowly. The clitoris returns to its homeostatic, unretracted state as the shaft of the clitoris relaxes (notably, quite similar to the relaxation of the shaft of the penis following ejaculation (Masters and Johnson 1966). The vagina decreases in diameter, the uterus lowers toward the pelvic floor, and lubrication of the labia minora and vaginal walls ceases. Interestingly, Masters and Johnson (1966) note that continued lubrication and vasoconstriction observed in the vulva during the resolution phase provide a cue to a female’s propensity to quickly return to the orgasmic phase.

In males, the experience of resolution is typically characterized by a rapid loss of penile erection; however, erection may be maintained after the experience of orgasm of physical stimulation of the penis persists (Masters and Johnson 1966). During this phase the “sex flush” on the chest, neck, and back and reddening of the glans of the penis disappear, the scrotum lowers, testicular size decreases, and the testes descend lower into the (now relaxed) scrotum. Masters and Johnson also describe the significant variability in males’ ability to achieve multiple orgasms in a short period of time – while some of their participants were able to achieve as many as three orgasms in 10 min, the time needed between the experience of the resolution phase and the reinstatement of physiological markers of excitement depended greatly on age. Older males typically required longer durations of time to pass between the experience of resolution and the reinstatement of excitement and plateau (Masters and Johnson 1966).

Conclusion

Masters and Johnson’s (1966) the four-stage model of the sexual response was, importantly,

based upon direct observations and recordings of human sexual activity in the laboratory and thus provided clinicians and researchers with a deeper understanding of both the physiological and the psychological correlates of the human sexual response cycle. Their work revolutionized the treatment of sexual dysfunction and disorder, increased understanding of sexual activity in aged populations and the female capacity to experience multiple (rapid) orgasms (both topics surrounded by much stigma and misunderstanding), and constructed a framework that would provide order to the broad array of physiological changes that correspond with the experience of sexual and physiological arousal.

Cross-References

- [Female Orgasm and In-Pair Copulation](#)
- [Long-Term Mating](#)
- [Masters and Johnson](#)
- [Physiological Mechanisms](#)
- [Sexual Intercourse](#)

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Francis T. McAndrew

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Definition

Teacher, scholar, and essayist in evolutionary psychology.

Introduction

Francis “Frank” T. McAndrew is the Cornelia H. Dudley Professor of Psychology at Knox College, a small private liberal arts college located in Galesburg, Illinois. In academic circles, McAndrew is probably best known for his popular 1990s textbook *Environmental Psychology* (McAndrew 1993) and for his more recent research exploring the psychology of gossip (McAndrew et al. 2007; McAndrew 2014, 2016, 2017). In the public arena, he may be best known for his numerous print, radio, and television interviews discussing the evolution of social behavior and for his *Psychology Today Magazine* blog “Out of the Ooze: Navigating the 21st Century with a Stone-Age Mind” (www.psychologytoday.com/blog/out-the-ooze).

McAndrew was born in Augsburg, Germany, in 1953 where his father was stationed with the US Army; the family moved back to The USA before his first birthday. Along with two brothers and two sisters, young Frank would spend his childhood in Northeastern Pennsylvania; the first 6 years in Scranton and the remainder in the small borough of Dallas. McAndrew writes, “from kindergarten through college I survived 17 years of Catholic education, and my only noteworthy achievement during my school days was being a two-time place winner in my high school state wrestling tournament. Except for that, I mostly just hung around a lot” (<http://faculty.knox.edu/fmcandre/biography.html>). Wrestling turned out to be a lifelong love of Frank’s – he was a member of the wrestling

Foxes

- [Canines](#)

team during his undergraduate years at Kings College in Wilkes-Barre, Pennsylvania, and was a member of the wrestling coaching staff at Knox College for 27 years, including 12 seasons as Head Coach.

During his senior year at Kings College, McAndrew found another lifelong love in sophomore Maryjo McCarthy. Although he graduated in 1974 and moved to Orono to pursue his doctorate at the University of Maine, the bond between Frank and Maryjo continued to grow and they were married in 1978. They have now been married for nearly 40 years, have two grown children and a granddaughter.

In 1981, McAndrew received his Ph.D. in General-Experimental Psychology from the University of Maine. His research at the time related to social aspects of nonverbal behavior and human territoriality. It is unlikely that he would have classified himself as an evolutionary psychologist at the time, but during the 1970s both areas of study were heavily influenced by research in ethology and comparative psychology. McAndrew, who also did graduate work in zoology at Maine, was undoubtedly drawn to the connections between biology and psychology.

In 1979, a year after his marriage and 2 years before defending his dissertation, McAndrew took a job as an instructor of psychology at Knox College. This job would transition to assistant, associate, full, and ultimately endowed professor positions. Working as faculty at a small liberal arts college has undoubtedly had a profound impact on McAndrew's teaching and scholarship. At the time he started at Knox, and many years after that, he was one of three faculty members in the Department of Psychology (current staffing is at seven). Such a small teaching staff requires faculty to be generalists rather than specialists. During his time at Knox, McAndrew developed 17 different courses on diverse topics including animal, cognitive, environmental, evolutionary, history and systems, industrial/organizational, introductory, quantitative, and social psychology. In addition to these classes, and on top of the variety of committee work expected of faculty,

McAndrew was also instrumental in founding Knox's Environmental Studies Program, directed this program for 7 years, and chaired his department for 9 years. This breadth of courses and responsibilities did not diminish the quality of McAndrew's teaching; among the honors he has earned are the college's top award for distinguished teaching both in 1983 and 2000; top award for faculty achievement in 1999, 2009, and 2013; and the Cornelia H. Dudley Endowed Chair in Psychology (1998 to present).

McAndrew's program of research has also been influenced by his position at Knox College. In line with the school's emphasis on undergraduate education and experiential learning, every psychology major is expected to design and carry out a two-term research project (three-term for honors students). From a faculty perspective, this means that scholarship typically involves collaboration with undergraduate researchers and each project requires a new set of negotiations to find topics of mutual interest between students and mentor. The outcome of this process is often a larger number of smaller publications (i.e., that can be completed in an academic year) that are thematically eclectic (i.e., reflecting diverse student interests). A review of McAndrew's vita reveals studies in environmental psychology, nonverbal behavior, gender and stereotyping, adoption and namesaking children, aggression, altruism, and more recently on gossip and attributions of "creepiness." Almost two to two thirds of McAndrew's peer-reviewed journal articles have undergraduate coauthors, many of whom have gone on to graduate school.

Despite the diversity of topics in McAndrew's publications, there is also conceptual continuity in his program of research; McAndrew writes, "To the extent that there is a common theme tying my research together, it is that I study human social behavior from an evolutionary perspective" (<https://www.knox.edu/academics/majors-and-minors/psychology/faculty/mcandrew-frank>). One of these recurring themes over the past two decades has been the evolutionary psychology of gossip. At the time of this writing, McAndrew has nine academic and five

popular press publications on this topic, as well as a book in the works, several conference presentations, and over 20 invited talks. The idea that gossip might serve an adaptive function in the species has also caught the public's attention, as evidenced by numerous interviews with McAndrew, and references to his research, in documentary film and popular television, radio, Web, and print media (well over 100 to date).

Perhaps because of the popular interest in his research on gossip, McAndrew has recently branched out as an essayist and blogger, sharing his passion for evolutionary psychology with the public at large. In his *Psychology Today Magazine* blog "Out of the Ooze: Navigating the 21st Century with a Stone-Age Mind," McAndrew has presented an evolutionary perspective on such topics as masculinity and gun violence, social media and identity, "creepiness" in people and places, the fleeting nature of positive emotions, religious experience, and, of course, gossip. In all his posts, McAndrew's knowledge of the field, remarkable talent as an educator, and wry sense of humor shine through.

Conclusion

For nearly 40 years, Frank McAndrew has been studying, promoting, and contributing to the field of evolutionary psychology in the classroom, through his research, and through his popular publications. No doubt his ongoing efforts to "study human social behavior from an evolutionary perspective" will continue to intrigue and inform his students, the discipline, and the public at large.

Cross-References

- ▶ [Gossip and Grooming Hypothesis](#)
- ▶ [Gossip and Indirect Reciprocity](#)
- ▶ [Gossip, Rumors, and Social Exclusion](#)
- ▶ [Heroic Rescue in Humans](#)
- ▶ [Mail-Order Brides](#)
- ▶ [Sex Differences, Initiating Gossip](#)
- ▶ [Social Consequences of Initiating Gossip](#)

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Frank Sulloway (1996) On Birth Order

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Synonyms

[Family order](#); [Ordinal position](#); [Sibling position](#)

Definition

The sequence in which children are born into the family.

Introduction

In 1996, Frank Sulloway's book *Born to Rebel: Birth Order, Family Dynamics, and Creative Lives* was published. In it, he outlined his adaptationist approach to birth order focusing on differential parental investment and sibling competition. The book documents personality differences by birth order and how they play out in terms of revolutions in science, religion, and politics. It has also spawned a new generation of research into birth order effects, not just

concentrating on effects on personality but also examining the impact of birth order on behavior.

Role of Parental Investment in Creating Birth Order Effects

Parental investment is any investment that a parent makes that increases the likelihood of an offspring's survival and reproduction at the cost of that parent's ability to invest in other current or future offspring (Trivers 1972). This can be anything from providing food and shelter to attention, education, and other financial support. As Sulloway articulated, the importance of birth order to parental investment is related to both the age of offspring and age of the mother. An offspring's expected contribution to parental fitness rests mainly in their reproductive value which increases with age until puberty, making older immature offspring more valuable from a parental fitness perspective than younger ones, as discussed in full in Daly and Wilson's work (1988) on the psychology of discriminative parental solicitude. It is this assurance of parental favoritism (and the lack of early competitors) that makes firstborn children defenders of parental values and the status quo while laterborns are more frequently rebellious. However, lastborns may also get some special benefit from being the last one born, the last opportunity to invest, and from being born to older mothers, all else being equal. Which likely accounts for the curvilinear birth order effects that are sometimes found with regard to aspects of parental investment such as money provided by parents for college (Kennedy 1989; Salmon and Schumann 2011). It is also possible that even when parents intend to allocate resources equally among their children, the cumulative result is inequity due to parental resource variability over the lifespan (Hertwig et al. 2002).

Sibling Niche Theory

Sulloway has suggested that children adopt different roles or niches within the family due to sibling competition over limited parental resources.

Specialization of roles within the family, like specialization of species in the wild (such as Darwin's finches), reduces levels of sibling competition. Specialization also makes children more unique. Eldest siblings often occupy the role of surrogate parent with its responsibilities and adherence to rules. For laterborn children, there is no advantage to trying to duplicate the same role, they need to find their own niche and their openness to experience with less adherence to rules and authority facilitates this. Healey and Ellis (2007) provide supportive evidence for Sulloway's niche theory with regard to differences between firstborns and secondborns. This tendency for siblings to diversify makes adjacent siblings more different than those farther apart in age and with other siblings in between. It has also been suggested that while parental influence may tend to create linear birth order effects, sibling competition and diversification in search of a family niche will tend to create quadratic effects. Pollet and Nettle's (2007) study of face to face contact with siblings reports that firstborns are more likely to take on the role of family contact, taking on the responsibility of keeping track of and informing siblings of family news. An excellent study by Paulhus, Trapnell, and Chen (1999) also tested Sulloway's Darwinian model of birth order effects on personality using the preferred method of within-family data and having respondents compare themselves and their siblings on a number of personality dimensions with results supportive of the achieving/conscientious firstborn and the rebellious/liberal/agreeable laterborns. In a similar vein, Sulloway and Zweigenhaft (2010) tested the risk-taking lastborn niche by examining participation in risky athletics and major league baseball in particular, reporting on 700 major league brothers, demonstrating that laterborn brothers engage in risky strategies (such as base stealing) more frequently and more successfully than firstborns.

Functional Birth Order and Adaptive Strategies

Sulloway also emphasized the importance of attending to what he referred to as functional birth order. There is a difference between

biological order of birth and functional birth order which focuses on the environment one is born into with particular attention on the family niche one ends up in. Typically, biological and functional birth order may be the same. However, there are factors that can shift the functional birth order of a specific sibling. For example, if the eldest sibling dies at a relatively young age, the next born child may end up taking on the firstborn role in the family. Other factors that can cause shifts in the functional birth order of siblings include disability, significant age gaps, adoption, and remarriage. This highlights the environmental nature of birth order as a variable influencing various traits and behaviors.

In addition, Sulloway drew attention to the adaptive strategy perspective on personality. Birth order differences in personality reflect the different strategies siblings adopt in their attempts to acquire the resources they need, whether the main source is from family or friends. Sulloway focused on the Big Five model of personality which includes the following five basic dimensions: conscientiousness, agreeableness, extraversion, openness to experiences, and neuroticism. In general, Sulloway demonstrated that firstborns score higher on conscientiousness than laterborn siblings as they often adopt the surrogate parent role as well as being supporters of the parental status quo as it befits their often privileged status as first child. Agreeableness and openness to experience are traits that laterborns score more highly on than firstborns. This facilitates strategies of negotiation and cooperation, rather than firstborn power strategies, which are likely to be more successful for smaller, less heavily parentally favored laterborns. In addition, openness to experience facilitates a willingness to embrace novelty which enables laterborns to explore novel family and social niches to find their unique roles. Its role in innovating thinking will be discussed in the following section. Extraversion is an interesting dimension in that it contains traits such as dominance and assertiveness that firstborns, secure in their authority, score high in. But it also includes sociability which laterborns score higher on as they are more inclined to find pleasure in the developing of close social ties, a strategy that

serves them well in seeking social support outside their immediate family.

Evidence Presented in *Born to Rebel*: Birth Order and Scientific Revolutions

There is a massive amount of data in support of birth order effects presented in *Born to Rebel*, but one of the most interesting aspects is the historical evidence on birth order and support for innovative change in scientific and political thought. Sulloway documents support for innovations in science, such as Darwin's theory of natural selection, from extreme opposition to extreme support. Based on historical accounts, laterborns were 9.7 times more likely than firstborns to endorse evolution by natural selection before the *Origin of Species* was published (Sulloway 1996). Other evidence of the laterborn willingness to support controversial or radical scientific ideas includes laterborns being 5.4 times more likely to support the Copernican revolution prior to 1609, 3.1 times more likely to endorse Newtonian mechanics, 3.8 times more likely to endorse Freudian psychoanalysis, and 9.0 times more likely to endorse phrenology (Sulloway 1996). The relationships between birth order and social movements of a nonscientific nature are also documented in the latter half of Sulloway's book. For example, during the Protestant Reformation, greater support came from laterborns in comparison to firstborns. And when one examines militancy in the pursuit of radical reform, such as the black rights movement in the United States, a curvilinear relationship is seen in which the most militant reformers tend to be firstborns and lastborns while those advocating nonviolence have been middle children, such as Martin Luther King Jr.

Conclusion

Sulloway's *Born to Rebel* revived interest in examining the impact of birth order on a variety of traits and behaviors, and it did so partly by providing a solid adaptationist approach to family dynamics, personality traits, and the factors that

shape individual differences in attitudes towards scientific and political thought. It also provided an abundance of evidence from studies conducted by the author and others that demonstrated impacts on personality as seen in psychological studies in combination with historical and biographical evidence on the real world implications of birth order for supporting, or failing to support, various revolutions in scientific and ideological thought. Sulloway's book emphasized that it is not only genes that make siblings different from each other; it is also nonshared environment. In particular, he illustrated that their nonshared family niches and the adaptive strategies that are associated with them shape many sibling differences.

Cross-References

- [Birth Order](#)
- [Parental Investment Theory](#)
- [Sibling Conflict](#)

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Frans de Waal

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Definition

Frans de Waal is a Dutch biologist whose research demonstrates that nonhuman primates show aspects of behaviors previously considered to be exclusively in the domain of humans, such as empathy, reconciliation, and fairness, emphasizing the continuity between humans and other species.

Introduction

Frans B. M. de Waal has studied animals all of his life. As a child, he observed (or collected and then observed) any animal he could near his home in the Netherlands, developing a fascination with the behavior of all species. This ultimately led to a career studying a variety of different topics that, as a whole, demonstrate the substantial cognitive and emotional continuity between humans and other animals. In particular, he has focused on the many ways that animals negotiate with one another to avoid, minimize, ameliorate and, if all else fails, reconcile conflict to maintain their beneficial social relationships. Although his research focuses on nonhuman primates, his work is key

to understanding social behavior and cognition across the animal kingdom.

A Life Studying Primates

Shortly after receiving his PhD from the University of Utrecht in 1977, where he studied the social behavior of the chimpanzees at the Royal Burgers' Zoo in Arnhem, the Netherlands under the direction of Jan van Hooff, de Waal rose to prominence with the publication of *Chimpanzee Politics*, which followed the social relationships among the adult males of the Burgers' zoo chimpanzee colony over a 4-year period. This book, which highlighted the ways in which these apes use conflict resolution to maintain their social order, brought primates' social strategizing to the forefront, over the then dominant view that aggression controlled behavior. Moreover, foreshadowing a career that integrated ideas from other disciplines into his scientific thinking, in this book de Waal explicitly compared the chimpanzees' political behavior to the ideas introduced by Machiavelli in his book *The Prince*. While at Burgers' Zoo, de Waal was the first person to recognize consolation and reconciliation in nonhuman primates and established the methodology for their study (postconflict/matched-control; de Waal and van Roosmalen 1979). In later years, with Filippo Aureli, he further documented that while reconciliation appears to be widespread across the animal kingdom, consolation is more rarely seen, possibly indicating that it requires more advanced cognition.

In 1982, de Waal emigrated to the USA, working first as a research scientist at the University of Wisconsin, Madison, and then, 10 years later, moving to Emory University in Atlanta, Georgia, where he remains the C. H. Candler Professor of Primate Behavior in the Psychology Department and the founder and Director of the Living Links Center of the Yerkes National Primate Research Center. In the USA, de Waal's research became more experimental, with the goal of elucidating underlying behavioral mechanisms for the behaviors he had observed earlier in his career. While exploring the mechanisms underpinning the

primates' behavior, however, he maintained his focus on the animals' natural behaviors, and never forgot the importance of the observational approach. Combining experiment and observation has led to important insights. For example, continuing his exploration of mechanisms that animals use to avoid and ameliorate conflict, he and Jessica Flack demonstrated that high ranking individuals in rhesus monkey groups play a control role that helps to maintain stability in the social group (Flack et al. 2006).

De Waal was one of the early researchers to recognize the benefits of studying capuchin monkeys, a large brained neotropical species of primate sometimes referred to as the "New World chimpanzee." This species is highly cooperative in the wild, and in his earliest work with capuchins, he delved into cooperation and related behaviors. He first demonstrated that capuchin monkeys not only shared food reciprocally, but that they understood their partner's role in tasks that required joint action to obtain a reward and adjusted their decisions based upon their partner's behavior (de Waal and Berger 2000). Extending this, he and Josh Plotnick later showed that elephants, too, understood their partner's role in a cooperative task (Plotnik et al. 2011). He and Sarah Brosnan found that both capuchin monkeys and chimpanzees responded negatively to receiving a less preferred reward than a social partner (Brosnan and de Waal 2003). This was the basis for their hypothesis that the evolution of fairness is linked to the need for social partners to be able to evaluate their contribution to a cooperative endeavor relative to their partner's, in order to judge whether or not to maintain the relationship.

Social animals that can recognize themselves and their social partners should have an advantage over those who cannot, and de Waal has also explored the ways in which individuals show this recognition. He and Lisa Parr demonstrated that chimpanzees could recognize familial relationships simply by looking at photographs of unknown chimpanzees (Parr and de Waal 1999). Later, he and Jennifer Pokorny showed that chimpanzees could also recognize females by their swellings (sexual skin in the ano-genital region that becomes bright pink and swollen during the

females' estrous phase), but only for known individuals, suggesting whole body knowledge for other individuals in their social group. This work garnered them an Ig Nobel prize in 2012. Finally, he and Pokorný showed that capuchin monkeys recognize other members of their social group and, with Marietta Dindo, de Waal demonstrated that while capuchins do not recognize themselves in the mirror, they do not treat the mirror as a stranger, indicating that a more nuanced approach is needed for our discussions of self-recognition.

One advantage to living in a social group is that individuals can pass information among other members of the group. In order to better understand how these animals decide who and what to copy, with Kristin Bonnie, Victoria Horner, and Andy Whiten, he studied cultural transmission in primates (Bonnie et al. 2006). They demonstrated that, as with humans, subjects chose who to copy based on both the prestige of the demonstrator and what the other members of the group were doing, called conformity. In particular, he argues in his book *The Ape and the Sushi Master* that much social learning occurs as a result of young members of the group absorbing the behavior of older ones, much like the sushi apprentice learns from the master. Of course, animals can also explicitly share information through communication, and he and Amy Pollick explored the role of gesture in the evolution of language, studying the flexibility of both gestural and vocal signals in bonobos and chimpanzees (Pollick and de Waal 2007).

Finally, de Waal was one of the first scientists to consider whether social behavior in primates is underpinned by empathy, and he and Stephanie Preston developed an influential hypothesis to explain the origins and evolution of empathy (the Perception-Action Model; Preston and de Waal 2002). De Waal has since demonstrated that both capuchins and chimpanzees will give prosocially to other members of their group and that these effects are mediated by factors such as the inequity of the outcome, the degree of relatedness of the partners, and the behavior of the potential recipient. Most recently, he has returned to his roots studying consolation behavior, this time in rodents; he and collaborators Larry Young and James Burkett demonstrated that the consolation

behavior in prairie voles is most likely underpinned by empathy.

De Waal has accomplished much; to date, he has been on the editorial board or editorial staff of 15 journals, is currently a Review editor for *Science* and the Editor-in-Chief of *Behaviour*, and has published more than 150 peer-reviewed papers, 100 chapters, and 75 commentaries in multiple languages. He is a member of the US National Academy of Sciences and the Royal Dutch Academy of Sciences, a Fellow of the American Academy of Arts and Sciences and the Japan Society for the Promotion of the Sciences, and the recipient of two *Doctor Honoris Causa* degrees and the American Society of Primatologist's Distinguished Primatologist Award. In 2013 he was appointed as Distinguished Professor at the University of Utrecht.

Aside from his research, in what he describes as a "second career" (de Waal 2009), de Waal has done much to promote scientific interest and literacy in the public. He had written 13 books on primate behavior and edited an additional 10, with the goal of bringing the science of primate social behavior to the public. His most recent book, *Are we smart enough to know how smart animals are?* is representative, challenging people to reconsider what we consider to be "intelligence" in other species by dropping our anthropocentric assumptions and taking into account the environment in which the animal evolved (that is, what sort of intelligence the animal needs in order to survive and thrive). Aside from his books and lectures, his TED talk on the evolutionary roots of morality has become an Internet sensation (http://www.ted.com/talks/frans_de_waal_do_animals_have_morals.html). Outreach such as this has led to him being recognized as one of *Discover* magazine's "47 All-time Great Minds in Science" and *Time* magazine's "100 Most Influential People."

Conclusion

Frans de Waal has done more than perhaps any other primatologist to demonstrate the continuity between humans and other species. He was one of the first scientists to seriously argue for the

presence of empathy in other species, and his research in that area has been ground breaking. De Waal has also shared his passion for nonhuman species with the public, writing more than a dozen best-selling science books about primates and other animals and giving innumerable talks and presentations, including a very successful TED talk. As a result, he is one of those rare scientists whose work has influenced both scientists and nonscientists alike.

Cross-References

- Cooperation
- Cooperation Among Nonchimpanzee, Nonhuman Primates
- Empathy
- Evolution of Cooperation
- Fairness in Primates
- Food Sharing
- Food Sharing and Nonhuman Reciprocal Altruism
- Frans de Waal's (1982), *Chimpanzee Politics*
- Great Apes
- Non-Human Primates
- Primate Cooperation
- Prosocial Behavior
- Reconciliation
- Sarah Brosnan
- Social Cognition
- Social Learning

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Frans de Waal's (1982), *Chimpanzee Politics*

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Definition

This 1982 book by Frans de Waal follows the 4-year power struggle among a group of chimpanzee males, documenting the complexity of their social lives and offering up a lesson on the importance of understanding other species' behavior to understand the evolution of human behavior.

Introduction

If Shakespeare had focused his political plays on chimpanzees rather than British royalty, *Chimpanzee Politics* would likely have been a plot he relished. The interactions among the chimpanzees, masterfully conveyed by de Waal, include overthrows, shifting alliances, and the murder of the former ruler. This fascinating book follows several years in the lives of a group of

chimpanzees housed at the Royal Burger's zoo in Arnhem, the Netherlands, documenting their social lives and, in particular, the power struggle among the group's males. Through his approach, readers are not only drawn into the saga, but come away understanding how to study behavior in other species and why it is so critically important for understanding the evolution of human behavior.

Power and Dominance in Chimpanzee Society

One of the most notable things about *Chimpanzee Politics* (de Waal 1982) is the approachable way in which it was written. Rather than diving immediately into a dry account of the interactions between the animals, de Waal carefully sets the stage, allowing the reader to fully understand the ensuing story. He first introduces the characters, then considers their behavior. Throughout it all, de Waal is careful to separate the observations of each event from his interpretation of those events, which allows readers to understand where his assertions come from and then draw their own conclusions based on the observations. No less important is the inclusion of hundreds of photographs of the chimpanzees and behaviors that de Waal is discussing, most by de Waal himself; there is barely a page without at least one photograph. This is highly unusual in scientific books, but the impact is profound. The pictures allow the reader to create that essential mental image of the situation that enables them to not just read about, but mentally see, the narrative as it plays out.

After the stage is set, de Waal describes a 4-year period during which the reigning alpha male, Yeroen, is dethroned by the upstart Luit and then forms a 3-year alliance with the now second-ranking male, Nikki, that allows the two of them to dominate the more powerful Luit. Nikki benefits by being the king, and Yeroen benefits by maintaining substantial power despite his lower dominance – in fact, a key point throughout the book is that in politics, rank and power are not synonymous, a point as relevant to human society as it was to Yeroen, Nikki, and Luit. Yeroen maintains many of the benefits of

rank, including relatively more free mating privileges than would be expected of an otherwise third-ranked male. It all falls apart 3 years later, quite literally overnight, when, for reasons unknown, but likely relating to Nikki's increasing intolerance of Yeroen, the alliance disintegrates. With the ruling males' sudden break, Luit immediately regains his position as the unchallenged alpha male. Although the original book ends here, the twenty-fifth anniversary edition adds an Epilogue that completes the story; ten short weeks after Luit became the alpha male, Yeroen and Nikki reunite for a single battle that kills him. They remove fingers, toes, and testicles, leaving him dead of blood loss. Shortly thereafter, young Dandy, who had previously been excluded from the males' intrigues, joins the dominant male triangle as the alliances shift again.

The story itself is captivating, but its scientific importance lies in its value as a record of this social group's dynamics. De Waal was able to acquire an astonishing amount of detail over an extended period of time (more than 4 years). This is due in part to his exceptional skills as an observer and in part to the fact that he was able to observe the group so intensively for such a long time frame. Although other longer-running studies exist, particularly in the wild, de Waal was able to get this level of detail because this is a captive group (albeit in a very large space), so he could see most of the animals most of the time, allowing for a level of completeness that is unprecedented. As a result, he knew who groomed whom, who mated with whom, who deferred to whom, and how the relative levels of these activities varied across the different manifestations of the dominance hierarchy during these 4+ years. Although correlations drawn from observations can never indicate causation, the degree of documentation is sufficient that the full picture emerges, allowing speculation about not only the animals' actions but also their motivations. Moreover, because this is such a large population, including multiple adult males (a rarity in most captive populations), the dynamic is more complex than can typically be obtained in a captive population.

Prior to the writing of this book, almost all scientists studying animal behavior based their analyses and interpretations on tallies of events

and behaviors that had occurred in the group. De Waal does the same – throughout the book, he discusses frequencies of grooming or aggression and displays charts of how these various behaviors altered depending on who was currently dominant – but he subsidizes this approach with historiography. In this, his goal is to understand the details of what happened in the group during these periods of social instability. To do so, he also relies more heavily than most on anecdotes. There is a saying in science, used to disparage one-off observations, that “the plural of anecdote is not data,” but de Waal takes issue with this when it comes to key events that are not replicated because there is no way for them to be replicated. For example, there has only been one American president to leave office under threat of impeachment (Richard Nixon, who resigned before he could be impeached for the Watergate scandal), but just because it has only happened once makes it no less important to understanding what causes the downfall of a key political official. In particular, to understand why among US presidents brought up for impeachment, only Nixon fell from power, it is instructive to compare his story to those of the only other two attempted impeachments of US presidents, which were not successful (Andrew Johnson, in 1868, for violating the Tenure of Office act following the suspension of Secretary of War Stanton and Bill Clinton, in 1998, for perjury and obstruction of justice following his statements regarding his relationship with Monica Lewinsky). The power of anecdotes for understanding rare events is no less true with chimpanzees; the fact that the Yeroen–Nikki coalition was unique does not make it any less important for understanding what happens in chimpanzee male social interactions.

Although the book is written at a level to be enjoyed by a general audience, this was also the first book to widely introduce several of de Waal's scientific ideas. For instance, it is here that he first brings the idea of the minimally winning coalition to studies of chimpanzees and emphasizes its role in understanding power dynamics. He also provides the data to support a disambiguation of dominance and power. As he shows, the individuals who are at the top of the dominance hierarchy, as evidenced by the direction of formal

subordination signals (i.e., the pant grunt in chimpanzees) are not always the ones who have the power in the group, as evidenced by who is allowed to mate, who intervenes in fights, and who has the support of the other key chimpanzees (i.e., the alpha female). Finally, in this book, de Waal makes a claim that verges on shocking in today's society, which is that the dominance hierarchy is not always a bad thing. As he shows, the worst fights and the highest levels of stress occur when the dominance hierarchy is unstable. When rank is clear, there is nothing to fight over; each individual knows their place, and days can go by without a fight, even in the presence of otherwise conflict-inducing events, such as an estrous female. However distasteful this may be in our society that strives for egalitarianism, this insight provides insight into the causes of conflict and instability among humans.

Throughout, de Waal repeatedly emphasizes the links between chimpanzee and human behavior. This likely causes strong reactions in almost everyone, ranging from those who find these links obvious to those who are horrified, either at the audacity of his attempt to level the playing field between humans and chimpanzees or his willingness to imbue these nonhuman creatures with motives, planning, thought, and other hallmarks of higher-order cognition. No matter what the reaction, it is in this way that the book is perhaps its most important, by reminding readers that humans are also products of their biology and their evolutionary history. Whether it causes the reader to reevaluate his or her position in the state of nature or work harder to understand the antecedents of human-specific cognition and behavior, this understanding is critical for fully understanding human behavior.

Conclusion

De Waal has written an astonishingly large number of very well-received books for any author, much less one who has simultaneously led a productive research career. What is it about *Chimpanzee Politics* that causes it to stand out? It has never been out of print and is now in the twenty-fifth anniversary edition. Not only is it routinely cited by

academics, but it is well known in the nonacademic world; then-US Speaker of the House Newt Gingrich reportedly put it on his recommended reading list for freshman representatives. Part of it is likely the story itself. This is not a dry textbook about animal behavior; this is, at heart, a narrative about Yeroen, Nikki, Luit, Mama, Gorilla, and the other chimpanzees. The aforementioned inclusion of photographs throughout the book reinforces this by giving the reader faces to put with names and a mental image of the various behaviors that de Waal discusses. Part of it is the balance between data and narrative; de Waal conveys the story, but never loses sight of the data that underpin it. The rest is the obvious connection between these apes and humans. The narrative rises above a discussion of chimpanzee politics and allows the readers to see human behavior, as reflected in the lives of these chimpanzees.

Cross-References

- [Dominance](#)
- [Frans de Waal](#)
- [Hierarchy](#)
- [Power](#)

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Franz Boas

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Glossary of Terms

Anthropology The study of humans and their societies in the past and present.

Anthropometry	The study of measurements and proportions of the human body.
Apperception	The perception of a new experience in relation to a past experience.
Archaeology	The study of past human activity and populations through material remains.
Cross-sectional data	Data collected by observing many subjects at the same point in time for a single observation per subject.
Diffusion	The spread of an idea or item from one culture to another through interaction.
Ethnocentrism	The belief that one’s own culture is more valuable or superior to another.
Ethnography	The study of a single group through direct contact with the culture.
Ethnology	A branch of anthropology that compares and analyzes the characteristics (e.g., origins, languages, customs, traditions) of different groups and the relationships between them.
Folklore	Traditional art, literature, knowledge, and practices that are passed on largely through oral communication and example.
Habilitation	A postdoctoral qualification that requires a thesis written at a professorial level based on completely independent research.
Independent innovation	When a culture forms an idea without any influence from another culture.
Linguistics	The scientific study of language: form, meaning, and context of languages.
Longitudinal study	A research design that involves repeated observations of the same variables in the same subjects over long periods of time.

Migration	The movement of people from one place to another with the intention of settling in the new location might be temporary or permanent.
Mythology	The collection of stories that a group of people tell to explain nature, history, and customs.
Phonemes	Units of sound in a language.
Phonetics	The study of the sounds of human speech, their physiological production, acoustic properties, auditory perception, and neurophysical status.
Physical anthropology	The branch of anthropology concerned with the biological and behavioral aspects of humans, their living relatives, and their extinct ancestors.
Psychophysics	A field that examines how organisms perceive their environment through their senses.
Salvage ethnography	The recording of practices and folklore of cultures threatened with extinction as a result of modernization, assimilation, or acculturation.
Stratigraphy	A branch of geology that studies rock layers (strata) and layering in order to lend context and place artifacts in sequence.
Teleology	Implies a purpose, directive principle, or goal; in this case, all stages are moving toward the goal of civilization.

Synonyms

[Father of American Anthropology](#); [Founder of four-field anthropology](#)

Definition

Franz Boas (1858) is widely known as the Father of American Anthropology and pioneer of the

four-field approach to anthropological research. His highly influential research career spanned each of the four subfields of anthropology, uniting them under one common goal – the holistic study of man. Modern methods in subjects as varied as human growth studies and folklore studies were introduced or reinvigorated by his adherence to scientific rigor and his innovative approach to cultural studies using his concepts of historical particularism and cultural relativism. The Boasian tradition lives on in the modern anthropological research and his later-in-life devotion to the education and professional development of students.

Introduction

Franz Boas (1858–1942) was a German-born American anthropologist and widely considered the “Father of American Anthropology.” An innovative and productive researcher, Boas is credited with a critical restructuring of anthropology that introduced culture as a central concept in anthropological research, emphasized more rigorous scientific methods, and advocated for academic and professional development. He was one of the most influential anthropologists of his time, espousing a holistic approach to the study of man that unified four subfields (physical anthropology, cultural anthropology, linguistics, and archaeology) under one overarching goal – to define the human species in totality. His four-field model of anthropology and his pioneering research in each subfield had a significant impact on modern anthropology.

Boas challenged traditional views of racial categories and cultural evolution with the introduction of cultural relativism and historical particularism to anthropological research. He made innovative strides in methodology for the study of linguistics, ethnology, human growth, migration, folklore, mythology, and environmental plasticity. However, his research contributions only comprised a portion of Boas’s influence, as his most lasting legacy was his efforts in educating students that would go on to become prominent anthropologists that carried on his Boasian tradition.

Early Life and Education in Germany

Franz Uri Boas was born on July 9, 1858, in Minden, Westphalia, Germany. As a young boy, Boas developed an interest in nature and exploration, with a specific fascination with zoological and geographical topics (Cole and Boas 1999). Boas attended the University of Heidelberg and the University of Bonn to study mathematics, physics, and geography. At the University of Kiel, Boas graduated with a PhD in physics with a minor in geography in 1881. His dissertation, “Contributions to the Understanding of the Color of Water,” was in the field of psychophysics. After graduating, Boas entered the military for a mandatory year (Cole and Boas 1999).

After his military service finished, he began planning an Arctic expedition that would redirect his career path toward anthropology and shape his academic research and interest in the First Nations of the Pacific Northwest. To prepare, Boas studied Danish, English, and Eskimo (Inuit) languages, cartography, astronomy, and anthropometry (Cole and Boas 1999). The focus of the expedition was the unexplored Baffin Island in Canada that was inhabited by the Inuit (Knötsch 1993).

In 1883, Boas set off to Canada to investigate the relationship between Inuit migrations and the physical geography of their region (Knötsch 1993). Boas’s time with the Inuit was eye-opening. Though geographic articles were funding his expedition, his ethnological articles surpassed the geographic articles in number. Boas collected extensive ethnographic research that would later become a monograph, “The Central Eskimo” in 1888 (Chapman and Routledge 2005). Boas recognized a great urgency to study indigenous people in Canada before the European assimilation and the projected loss of languages and customs (Cole and Boas 1999).

Ethnology began to take the forefront when Boas returned to Germany. At the University of Berlin, Boas pursued habilitation with the thesis Baffin-Land in 1885 (Cole and Boas 1999). He also worked as an assistant in the Royal Ethnological Museum. He associated with several anthropologists and met two Bella Coola Indians

from British Columbia. Their dance and language fascinated him, and by 1885, Boas had committed to anthropology as his primary field of study. He began planning an expedition to British Columbia that would be the first of many throughout his career and establish a lifelong relationship with the Native Americans of the Pacific Northwest (Chapman and Routledge 2005; Cole and Boas 1999).

Boas in the United States

Boas traveled to British Columbia for the first time in 1886, and on a return trip through New York, he was offered an assistant editor position at *Science* magazine. For personal and political reasons, Boas had been looking for an opportunity to move to the United States so he accepted the offer and soon after, married his fiancée, Marie Krackowizer (Cole and Boas 1999). They would go on to have six children, one of whom died in infancy.

In 1888, the British Association for the Advancement of Science (BAAS) asked Boas to go on an ethnological expedition to British Columbia that turned out to be the first of many BAAS-funded expeditions to the Pacific Northwest (Strazny 2013). Around the same time, Boas started teaching at Clark University where he would create the first department of anthropology in America, head the department in 1889, and graduate the first American PhD in anthropology, A. F. Chamberlain. He ended his tenure at Clark University in 1892 (Cole and Boas 1999).

After a few productive BAAS-funded expeditions, particularly focused on linguistics and the Kwakiutl, Boas became involved with the Chicago World’s Fair. From 1892 to 1894, he was hired as chief assistant of anthropology at the World’s Columbian Exposition under Frederic Putnam, the director and curator of the Peabody Museum at Harvard University. Boas used Kwakiutl to represent the Pacific Northwest in the exhibition, and after the World’s Fair ended, he was hired to organize the material into a museum that would later be called the Field Museum of Chicago (Cole and Boas 1999).

Boas would follow his experiences in Chicago with the most intensive ethnographic fieldwork of his career, a 3-week stay among the Kwakiutl of British Columbia. In 1896, upon his return from the field, Boas joined Putnam in New York as an assistant curator of ethnology at the American Museum of Natural History (AMNH) and also joined Columbia University as a lecturer in physical anthropology. By 1899, Boas had become a professor of anthropology at Columbia University, and in 1901, he transitioned to a curator position at AMNH (Chapman and Routledge 2005; Cole and Boas 1999).

At AMNH, he convinced Morris Jesup, the president of AMNH, to support an ambitious 5-year major research investigation of the people of the Pacific coasts of America and Asia before the populations disappeared. The scope of the Jesup North Pacific Expedition was international and involved the collaboration of professional and reliable researchers. The project required considerable organization by Boas as it ran from 1897 to 1902 (Cole and Boas 1999; Lewis 2001). As the project came to a close, Boas was starting a new phase of his life – the pursuit of education and overhauling of anthropological theories, concepts, and methodologies starting at Columbia University.

Boas resigned from AMNH in 1905 and turned his focus to promoting the academic and professional development of anthropology. He established anthropology at Clark University and would go on to establish the first PhD program in anthropology at Columbia University in 1908 (Moore 2000). He was active in multiple scientific organizations, including the American Anthropological Association, the *International Journal of American Linguistics*, the American Ethnological Society, and the American Folklore Society, and he led the founding of a new national anthropological society – the American Anthropological Association and an *American Anthropologist* journal attached to it (Strazny 2013).

Boas established Columbia University as the center of the new century's professional anthropologists, and soon Columbia and Boas were changing the face of the American anthropology.

Boas influenced some of the most prominent figures in the American anthropology, including Margaret Mead, Alfred Kroeber, Ruth Benedict, Robert Lowie, Edward Sapir, and F. G. Speck (Moore 2000). Throughout these processes, Boas maintained a rigorous schedule of his own scientific work and continued publishing in many areas of anthropology even after his retirement, and an emeritus status was given in 1938 in Columbia.

Four-Field Anthropology

Boas is perhaps best known for his four-field model of anthropology, where anthropology is composed of four subfields: cultural anthropology (ethnology), linguistics, physical anthropology, and archaeology. This concept differed from the European tradition in which linguistics and social anthropology were separate fields of study. The four-field tradition was launched by Boas at Columbia University, and his students would establish four-field anthropology in universities across the United States (Jacknis 2002).

In 1904, Boas introduced the four-field model as an approach that would produce a holistic understanding of what it meant to be human by uniting different anthropological research (Boas 1904). The realm of anthropological knowledge was defined as “the biological history of mankind in all its varieties; linguistics applied to people without written languages; the ethnology of people without historic records; and prehistoric archaeology” (Boas 1904). Each subfield contributed knowledge to the holistic study of man, and Boas stressed the integration of multiple perspectives: cultural history, material culture, anatomy, social organization, customs, folklore, grammar, language use, and population history.

Boas contributed to all four branches of anthropology in wide-ranging and diverse projects. His contributions bore the hallmarks of the Boasian tradition: rigorous scientific methods, an emphasis on empiricism, and an understanding of how perception can affect the object of study. Alfred Kroeber, Boas's first student, outlined the three empirical principles of the Boasian

anthropology – that science must begin with questions, not answers; that science must be dispassionate and unbiased in the search for truth; and that sweeping generalizations are out of place in a natural world ruled by variation (Kroeber 1949). Boas put the search for truth above all else and trained anthropologists to follow rigorous scientific standards and only formulate conclusions after thorough and extensive data collection (Jakobson and Boas 1944; Lewis 2001).

Cultural Anthropology (Ethnology)

Ethnology was a main pillar of Boas's fieldwork in the Pacific Northwest, and he would spend over 50 years of his life devoted to understanding the cultures of the Native American groups, particularly the Kwakiutl, in order to provide a comprehensive archive of these rapidly dwindling cultures (Chapman and Routledge 2005; Cole and Boas 1999; Lewis 2001). His efforts to develop fieldwork techniques, train natives to act as informants and investigators, record native texts, and gather all relevant views from the natives themselves would lay the foundation for the American ethnology. Boas believed that ethnology would be a vital aspect in the critical analysis of unique cultures in anthropological research (Boas 1940).

Boas was motivated by a sense of urgency in the efforts to capture Native American cultures and languages before they vanished. Today, this approach is known as "salvage ethnography," and the premise is that documentation will preserve a dwindling culture's rituals, beliefs, and customs in perpetuity (Erickson and Murphy 2008). Boas embodied this mentality and spent years returning to British Columbia and gathering and recording extensive information on Native American cultures that were threatened by expanding Euro-American influence (Chapman and Routledge 2005).

Boas introduced culture as the primary concept for describing differences in behavior and thought between human groups and gave it a place of prominence as a central analytical device in anthropological research (Moore 2000). Culture,

to Boas, was composed of thousands of activities and modes of thought that constitute a group's daily lives. These thoughts and behaviors were largely unconscious, learned from birth, and caused an individual to act in conformity within the group (Boas 1911b). Culture remained unconscious unless confronted by a different way of life or inhibited from expression (Boas 1940; Stocking 1966).

In the Pacific Northwest, Boas was interested in evaluating diffusion versus independent innovation of cultural ideas. Boas provided an example of agriculture, which developed at the same time in the Americas and Asia, but without transoceanic communication, it is considered independent innovation (Boas 1940). Boas was interested in tracking the diffusion of customs and rituals through neighboring tribes down from the Bering Strait, but with the base assumption of independent innovation. Empirical proof of diffusion required systematic and extensive data collection of every element of culture (Boas 1940).

Boas introduced two critical concepts to ethnological research: historical particularism and cultural relativism. Historical particularism is the idea that each society has a unique history that informs its cultural development. Boas rejected the prevailing idea of a deterministic and unilineal evolutionary path, where all societies evolve teleologically through the same universal stages, from primitive to civilized (Boas 1940). The use of generalities and universal laws masked the truth of a culture, so Boas argued that cultural traits needed to be explained within their own specific cultural contexts because each culture had a unique and different history (Moore 2000).

Cultural relativism is the idea that a person's activities or beliefs should be understood in the terms and values of their own culture, not the observer's culture (Boas 1911b, 1940). Boas opposed the ethnocentrism of the European anthropology and argued that biased perceptions based on the ethnographer's own culturally acquired norms skew the true understanding of a culture. Cultural relativism required an insider's perspective through data collection, integration

and interaction with members of the culture, and analysis of the unique cultural history. Boas moved away from the singular “culture,” as something humans possess to varying degrees or stages, toward the plural “cultures” with different but equal potentials (Stocking 1966).

In Boas’s seminal work, *The Mind of Primitive Man* (1911b), his thesis argued that assertions of the mental superiority of Europeans over Native Americans could be traced to differences in culture – the unconscious traditions and customs that govern all individuals’ thoughts, actions, and choices since birth (Stocking 1966) – and the flawed and biased perceptions of the anthropologists observing these mental differences. Boas showed that Native Americans exhibited the same mental powers of abstraction, inhibition, and choice as civilized Euro-Americans and that the daily behaviors and thoughts that constitute culture are as numerous in Native American culture as they are in the European culture (Boas 1911b; Stocking 1968). Boas’s principles of systematic and unprejudiced evaluations of culture within their specific context and valuing fieldwork and cultural history recordings would shape ethnographic practices across America.

Folklore and Mythology

In his ethnological fieldwork, Boas developed a passion for collecting folklore, mythology, and art from the Pacific Northwest (Boas and Tate 1916). Boas recognized the central and important functions of folklore and mythology in rationalizing traditional cultural behaviors and expressing native values and thoughts (Boas and Tate 1916; Stocking 1966). He worked to professionalize the study through scientific methods and championed the use of extensive research, fieldwork, and strict guidelines for scholarship. His continued scholarship promoted the complexity, diversity, and functionality of folklore, mythology, and art within a culture, opposing the prevailing views that dismissed these forms as simplistic or non-functional through the lens of ethnocentrism (Boas 1940; Chapman and Routledge 2005).

Linguistics

Linguistics took an early and prominent place in Boas’s fieldwork as much because of the urgency of documenting the disappearing Native American cultures as his sincere fascination with the languages of British Columbia (Jakobson and Boas 1944). Boas sought to understand and preserve these indigenous languages, and he brought his characteristic scientific rigor to linguistic description. He believed that languages were an important tool for ethnographic fieldwork and produced an extensive body of valuable linguistic descriptions of numerous indigenous languages, including Tsimshian, Chinook, Tlingit, and Kwakiutl (Chapman and Routledge 2005; Strazny 2013).

His first major contribution to linguistics was “On Alternating Sounds” (1889). The paper addressed the phenomenon of “alternating sounds,” or speech sounds that were vague, that linguists thought signaled the linguistic inferiority and lower evolutionary stage of Native Americans (Strazny 2013). Boas argued that this was not an issue of language, but with linguists recording languages with radically different phonetic systems than their own native language. The linguists were apperceiving the sounds of the indigenous languages and the different speech sounds translated into a misunderstanding of the sounds (Boas 1889).

In 1911, Boas wrote an introduction to the *Handbook of American Indian Languages* (1911a) where he laid out an approach that sought to eliminate every linguistic prejudice that had thus far limited the systematic and thorough discovery of indigenous linguistic phenomena. Boas’s empiricism meant describing and analyzing languages from an insider’s perspective, not through the figurative “blindness” of a linguist’s native language. Each new language should be approached without preconception or rigid attachment to a familiar grammatical and phonemic structure. Applying ethnological concepts, Boas also argued that each language was a unique representation of the speakers’ culture and there was no inherent superiority of languages (Boas 1911a; Jakobson and Boas 1944).

Boas endeavored to find the “inner form” of a language that would capture unconscious categories that could then be used to analyze that particular language. Each language chose different ways to express concepts (e.g., by simple terms or combinations of terms, by related or unrelated terms), and Boas presented the system of phonemes and grammatical devices as a necessary base for linguistic analysis (Jakobson and Boas 1944). Boas uncovered universal elements among diverse linguistic structures that suggested they were necessary elements in every language’s grammar and phonemics (Jakobson and Boas 1944; Strazny 2013).

In order to study diffusion, Boas introduced a comparative aspect to his linguistic studies and noted that unrelated but contiguous languages manifested common grammatical and phonemic characteristics (Jakobson and Boas 1944). He found evidence of borrowing of linguistic elements and language mixture between groups and that languages could develop as convergence from diverse sources or divergence from a common origin (Strazny 2013). These revolutionary findings and his two seminal works had a major impact on linguistics, causing a fundamental shift in how linguists approach new languages and analyze the organization and production of sounds.

Physical Anthropology

Boas pioneered many efforts within the field of physical anthropology as a result of his interest in understanding human variation and its connection to the environment, race, migration, and genetics. His contributions debunked the idea of racial fixity, established a design for migration research, introduced the concept of environmental influence on human biology, and uncovered significant discoveries about human growth (Little 2010). Physical anthropology continues to draw on the series of innovations in statistics and research design that are a lasting legacy from Boas.

Boas drew on his knowledge of statistics, anthropometry, and natural sciences as he began exploring factors influencing human biological

variation (Little 2010). In 1888, Boas made his first overture in the study of human growth using previously collected data (Tanner 1959). He discovered that variation in height during adolescence could be explained by individual variation in growth rates, or as he called it “tempo of growth” (Little 2010; Tanner 1959). The finding of “tempo of growth” led Boas to question the statistical validity of cross-sectional designs of growth studies (Boas 1892; Little 2010).

Boas spearheaded the first American longitudinal growth study, which represented a significant breakthrough in the field of human growth studies (Tanner 1959). In 1891, he conducted a longitudinal survey of local children and showed that variability at adolescence was reduced when chronological age was replaced by “time of peak velocity,” which was the beginning of the concept of physiological or developmental age as distinct from chronological age (Boas 1930).

Boas would publish numerous papers on the topic of growth studies and introduce biostatistics to physical anthropology. Five of his most important contributions to the field of human growth studies were (1) the production of the first National Growth Standards, (2) the introduction of the concept of physiological or developmental age, (3) the evidence of the impact of social and environmental conditions on growth, (4) the establishment of a link between “age of peak velocity” and measures of physical size during adolescence, and (5) the discovery of a secular trend in growth (Boas 1892, 1930; Little 2010; Tanner 1959).

In 1908, Boas initiated a migration study to examine the impact of migration on human biological characteristics and to address the idea of fixed races, a prevailing idea in mainstream anthropology that humans could be divided into a fixed number of pure races and that these rigid groupings corresponded to biological differences in personality, intelligence, and capacity for culture (Little and Kennedy 2010). He began with a pilot study in New York and expanded it to more than 18,000 subjects from different ethnic groups (Boas 1911b, 1912a; Tanner 1959). Boas employed a simple study design that compared parent-child measurements in cases of children

born before immigration and cases of children born after immigration to the United States (Little and Kennedy 2010; Tanner 1959).

One of the main traits that Boas investigated was the cephalic index, a measure of head form that is the ratio of skull breadth to width. The cephalic index was considered a stable, hereditary trait that linked fixed races with intelligence differences. Boas found significant differences between the children born pre- and post-immigration in the cephalic index, suggesting significant variation in cephalic index within groups or “races” (Boas 1911b, 1912a; Little 2010). He additionally found that the use of statistical averages could not be used to distinguish fixed races empirically and that the averages of different races showed little difference compared to the large range of variation that existed within races (Boas 1911b; Little 2010).

This was not Boas’s first attack on the fixed race concept. One early example was *The Half-Blood Indian* (1894), in which Boas challenged the current assertions that a “hybrid” race would exhibit decreased fertility, increased mortality rate, and likely physical and mental deficits (Boas 1894). He examined 16,000 Native Americans and demonstrated that the fertility and stature of children born of different races actually surpassed that of either parental population (Lewis 2001).

In *The Mind of Primitive Man*, Boas argued that these results proved that human variation was complex and unrecognized by traditional fixed race categories, invalidating race as a biological concept that could be used to classify the intelligence or superiority of a group of individuals in comparison to another group (Boas 1911b; Little 2010). Boas moved the focus from the “fixed races” as an explanation for human variation to the role of the environment in shaping physical characteristics and the plasticity of human biology in response to environmental factors (Little 2010; Mascie-Taylor and Little 2004).

The findings of his migration study were confirmed with later work that used Boas’s migrant research design and found similar changes among Japanese migrants to Hawaii, Mexican-American migrants, and Chinese migrants to America (Little 2010; Mascie-Taylor and Little 2004). Boas’s

study would become a model for future migration studies and investigations into the impact of environment, migration, and environmental plasticity, and human growth studies continue to use Boas’s longitudinal research design and statistical methods of analysis.

Archaeology

Boas’s contribution to archaeology was limited compared to his contributions to the other subfields, but no less important. At the turn of the century, Boas was increasingly concerned with the state of the American archaeology which was dominated by amateurs, lacked rigorous methodology, and was largely a descriptive and classificatory discipline. An opportunity in Mexico gave Boas the chance to leave a lasting impression on Central American archaeology (Godoy 1977).

From 1910 to 1912, Boas took a sabbatical to Mexico to collaborate on the establishment of the International School of American Archaeology and Ethnology (Godoy 1977). The endeavor had several objectives: (1) to expand fieldwork of Native American cultures beyond the southern border to continue the investigation of the diffusion of culture (Boas 1912b), (2) to increase the quality of archaeological and ethnological investigation, (3) to create a professional institution dedicated to scientific research that was economically independent (Stocking 1968), and (4) to educate Mexican archaeologists to carry on research after Boas’s departure (Godoy 1977).

The most significant project undertaken was the establishment of a chronological sequence for the large diversity and number of pottery fragments found in the Valley of Mexico. Under Boas’s direction, stratigraphic techniques were used to systematically investigate the geological sequences of strata for the first time in the American archaeology. Concurrently, in the Boasian tradition, anthropologists were analyzing grammar, structure, and distribution of Mexican languages and the impact of European colonization on language and culture (Godoy 1977). This would lay the foundation for modern Central American archaeology.

Social and Political Activism

As an established leader of the American anthropology, Boas was an outspoken activist in social and political issues surrounding human rights, equal opportunities, defeat of prejudice, and war (Lewis 2001). His engagement with the political sphere was motivated by a series of person core values that bridged the gap from his anthropological research to the public sphere: (1) the use of science to pursue “truth” and improve the human condition (Bunzel 1962), (2) equal rights and opportunities for everyone (Boas 1911b), and (3) rejection of the prevailing assumption that one culture was superior to others (Boas 1911b).

At the turn of the century, Boas became more directly involved in the “race problem” in America. He was drawn to the plight of African American intellectuals, like W. E. B. Du Bois, and he argued that “Negro” performance was inferior because of the conditions of slavery, but they were just as capable of culture as Europeans. Boas would become involved with the NAACP (National Association for the Advancement of Colored People) and regularly speak out against racism and encourage the study of African and American Negro culture (Hyatt 1990; Lewis 2001).

Boas’s book, *The Mind of Primitive Man* (1911b), where he laid out his arguments against the inherent superiority of civilized man over primitive man, was widely read and influential (Bunzel 1962; Lewis 2001). It would lend support and ammunition for activists fighting against Jim Crow laws, racially based on immigration restrictions and inequalities in rights and opportunities (Lewis 2001).

During World War I, Boas vocally opposed the American involvement in war and disapproved of the increasing xenophobia against Germans and the German culture as a result of the war (Lewis 2001). In 1919, he was involved in a scandal in which he published a letter titled “Scientists as Spies” that decried anthropologists that went into the field as spies under the cover of science. This move would negatively impact his positions in the AAA and the National Research Council (Hyatt 1990; Stocking 1968).

Postwar, Boas continued to speak out against racism, imperialism, and colonialism, particularly

as the Great Depression and the rise of Nazism in Europe grew more concerning. He combatted Nazism and all it stood for early on, fighting their racial ideas until his death (Lewis 2001). On December 22, 1942, Boas held a luncheon in honor of his colleague, and after concluding a speech against all forms of racial prejudice, he fell back into his chair and died. His last words were that “racism is a monstrous error or an impudent lie” (Lewis 2001).

Conclusion

Boas has had an enduring influence on anthropology. By the end of his life, he had written six books and more than 700 monographs and articles. He held many honorary degrees and honorary memberships from dozens of institutions and academic associations and served as president to some of the largest anthropological associations in America. Many of Boas’s original discoveries and methodological contributions hold up to modern scrutiny. Today, nearly all anthropologists accept the necessity of Boasian empiricism and the use of methodological cultural relativism in anthropological research.

Boas’s work with Native Americans in the Pacific Northwest inspired generations of anthropologists to study and record vanishing cultures with a firm commitment to field research that involved living among the group, learning the local language, and developing relations with native informants. Outside of academia, Boas spoke out continually against racism and racial prejudice, playing an important role as a scientist bridging the divide between academic and public spheres to communicate his research findings and affect social change. In the words of Boas’s student, Alexander Lesser, “his scientific legacy is the modern science of anthropology; his greater legacy the manner in which he changed our conception of man.”

Cross-References

- [Archaeological Records](#)
- [Cross-Cultural Expression](#)

- [Cross-Cultural Differences](#)
- [Cross-Cultural Studies](#)
- [Cross-Cultural Variation](#)
- [Cultural and Moral Relativism](#)
- [Cultural Differences](#)
- [Cultural Evolution](#)
- [Cultural Transmission](#)
- [Cultural Variation](#)
- [Ethnography](#)
- [Field of Behavioral Ecology, The](#)
- [Field of Linguistics, The](#)
- [Language](#)
- [Phonemes and Symbols](#)
- [Public Records](#)
- [Racism](#)
- [Racism and Prejudice](#)

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Fraternal Birth Order, The

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Synonyms

FBO

Definition

Fraternal birth order (FBO) refers to the birth order of sons within a family – whether, for example, a boy is the oldest, youngest, or middle child among his brothers. The number of sisters is irrelevant to fraternal birth order. The fraternal birth order (FBO) *effect* refers to a consistent finding in men's sexual orientation, such that gay men have a greater number of older brothers compared to heterosexual men.

Introduction

In the search for clues about the development of sexual orientation, psychologists Ray Blanchard and Anthony Bogaert published a seminal paper in 1996 on the association between birth order and sexual orientation in men. They found that in a sample of 302 gay men, matched on year of birth with 302 heterosexual men, number of older brothers was associated with being gay. Older sisters, younger brothers, younger sisters, and age of parent at time of birth of the men were not related to sexual orientation. Also, each additional older brother increased the odds of being gay by 33 %.

The Fraternal Birth Order Effect and Its Origins

Blanchard and Bogaert's (1996) finding came to be known as the fraternal birth order (FBO) effect because of the specificity of the effect to older brothers and to men's (and not women's) sexual orientation (e.g., Bogaert 1997). In later research, it was further estimated that about 28 % of gay men owe their sexual orientation to the FBO effect explanation (vs. other explanatory factors in men's sexual orientation development; Blanchard and Bogaert 2004). Moreover, the reliability of the FBO effect was confirmed in a recent meta-analysis (Blanchard and VanderLaan 2015; see also Blanchard 2004 for a review).

In addition to year of birth and parental age, the FBO effect has been found to be independent of other potential confounds: age, socioeconomic

status, and sibship size (e.g., VanderLaan and Vasey 2011). Also, the original FBO effect (Blanchard and Bogaert 1996) has been replicated numerous times, including by independent researchers (see Blanchard 2004; Bogaert and Skorska 2011 for reviews) and in diverse samples, such as in boys with gender dysphoria (Blanchard et al. 2002), although there have also been some failures to replicate the FBO effect (see Bogaert and Skorska 2011 for a review; see Blanchard and VanderLaan 2015 for a commentary on failures to replicate the FBO effect). Thus, the FBO effect seems to be a very robust and reliable finding related to men's sexual orientation.

To explain the FBO effect, an immunological explanation, also known as the maternal immune hypothesis, has been put forward (e.g., Blanchard and Bogaert 1996; Blanchard and Klassen 1997; Bogaert and Skorska 2011). According to this hypothesis, a mother's immune system is exposed and immunized to male-specific proteins that are associated with the Y-chromosome with each successive male fetus. A mother may become immunologically reactive to these proteins because her body does not possess a Y chromosome and thus does not produce such male-specific proteins. The antibodies a mother develops after each male fetus cross the blood–brain barrier of the fetus to affect specific areas in the brain associated with the development of sexual orientation. These affected brain areas would, in turn, influence the sexual orientation of the man as an adult.

Several lines of research provide evidence that the maternal immune hypothesis is plausible: transfer of material occurs from the fetus to its mother, male-specific substances cause immune responses in women, the relevant male-specific substances play a role in sexual differentiation of the brain (independent of prenatal hormones), and a maternal immune response to male-specific substances affects fetal brain development (see Bogaert and Skorska 2011 for a review of these lines of research).

Currently there is no direct empirical support for the maternal immune hypothesis. However, there have been some studies that provide indirect evidence that a prenatal mechanism is responsible for the FBO effect. First, some researchers have

found that handedness, which has been shown to be determined prenatally, interacts with FBO in predicting sexual orientation in men. Specifically, right-handed men who had older brothers were more likely to be gay, whereas left-handed or ambidextrous men were unaffected by older brothers in their likelihood to be gay. Further, the interaction with right-handedness might apply only to moderately right-handed men and not to extremely right-handed men (see Bogaert and Skorska 2011 for a review). Second, in a key study related to the origins of the FBO effect, Bogaert (2006) found that biological older brothers were associated with a same-sex orientation in men, but nonbiological siblings (e.g., adopted or step-brothers) were not associated with sexual orientation. Moreover, the biological older brothers predicting men's same-sex orientation were often raised in a different environment (e.g., a different household) than the participant, thus providing additional support for the prenatal (and not postnatal) nature of the FBO effect.

Conclusion

Thus, one of the most reliable findings in the sexual orientation field is that men who have a greater number of older brothers (i.e., a later fraternal birth order) are more likely to be gay. An immunological explanation (the maternal immune hypothesis) has been proposed as an explanation for the fraternal birth order effect. Several lines of research support the plausibility of the maternal immune hypothesis, and there is indirect support for the biological and prenatal basis of the FBO effect. Future research will likely illuminate the origins of the FBO effect, including testing of the maternal immune hypothesis.

Cross-References

- Genetic and Prenatal Components of Homosexuality
- Hormonal Component of Homosexuality
- Non-Western Homosexuality
- Sexual Orientation and Human Sexuality

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Fraternal Relationality

- Male Friendship

Fraternity

- Male Friendship

Fratricide

- [Siblicide](#)

Free Rider

- [Emotional Solutions to Free Riding](#)

Free Riding

- [Defection](#)

Free Will

- [Psychological Determinism](#)

Free Will (Philosophy)

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Synonyms

[Metaphysical freedom](#)

Definition

In the contemporary free will debate, free will is often defined as a kind of control over action in virtue of which individuals can be held morally responsible for their actions just given that individuals perform those actions with understanding of the latter's moral quality (Pereboom 2016).

Introduction

Understandings of free will vary widely among philosophers and other thinkers who have studied the subject. Some have thought that free will is merely the power of an agent to do what it wills, which could be (and has been) alternatively framed as an agent's freedom from impediments to do what it wills. Others have suggested that free will is the ability through which an agent can be the ultimate source of its actions, as opposed to those actions stemming in the end from anything outside an agent's control. Since there is no clear consensus on what free will is, this entry will focus on just one conception of free will and the *contemporary* debate that surrounds it. That conception is defined in terms of *moral responsibility* (McKenna and Pereboom 2016, p. 6). Specifically, free will is said to be the causal power in virtue of which an agent can be held morally responsible for its actions "just because [it] has performed [those actions on condition that it understood their moral quality]" (Pereboom 2016, p. 2) (Pereboom [2016] refers to this as the "basic desert" sense of moral responsibility: "The desert at issue here is basic in the sense that the agent would deserve to be blamed or praised just because she has performed the action. . . and not. . . merely by virtue of consequentialist or contractualist considerations" [p. 2].) The following considers a major threat to belief in free will of this kind and responses to that threat.

The Problem of Causal Determinism

The thesis of causal determinism holds that every event, condition, or state of affairs in the universe is the necessary consequent of some antecedent event(s), condition(s), and/or state(s) of affairs, together with the laws of nature. Phrased differently, it is the view that everything in the universe inevitably or unavoidably occurs or obtains, given what has previously occurred or obtained and the laws of nature. Causal determinism is often associated with a broadly "scientific" worldview, when such a worldview is taken to posit invariant causal laws that, at least in principle, predictably

govern the behavior of all physical objects in a non-probabilistic way. (As Horst [2011] argues, it may be false that the laws of nature are all non-probabilistic. It is widely believed that phenomena at the quantum “level” of reality are genuinely indeterministic, though this does not seem to be necessarily incompatible with causal determinism at “higher” orders of reality [Caruso 2013].) An apparent corollary of this posit is that two separate physical systems with precisely identical initial conditions and characteristics will be indistinguishable with respect to all activity that they exhibit, assuming that nothing is externally introduced to one system but not the other.

Perhaps *the* central concern of the contemporary free will debate is whether causal determinism is compatible with free will. If the thesis of causal determinism is true, it follows that every action performed by every person was ineluctable from the moment the universe came to be. A number of philosophers have believed that this is at least *prima facie* a threat to free will in a number of senses, including free will as the power enabling moral responsibility in the “basic desert” sense. Those philosophers who think that free will and causal determinism are incompatible are called *incompatibilists*. Incompatibilists come in two salient kinds: libertarians and hard determinists. The former believe that free will and causal determinism are incompatible and that free will exists and the thesis of causal determinism is false. (To be sure, libertarians need not hold that causal determinism never applies to physical objects. They can maintain that humans have special causal powers, over which they have control, that at least sometimes can be the ultimate source of humans’ actions, rather than anything outside of their control being that ultimate source.) The latter believe that free will and causal determinism are incompatible and that the thesis of causal determinism is true and hence that free will does not exist. It is worth noting that the idea that the nature of causality in the universe threatens free will need not only apply if the universe is deterministic. Pereboom (2016) points out that indeterminism may undermine free will as much as determinism, in that if agents’ actions are

brought about indeterministically but emerge randomly or probabilistically, then their actions do not appear to be under the sort of agential control required for moral responsibility. Alongside incompatibilism, the other major sort of response to the apparent tension between free will and causal determinism is *compatibilism*. As the name suggests, compatibilists maintain that free will and causal determinism are in fact compatible. The term “soft determinists” is sometimes used to refer to compatibilists who believe that the thesis of causal determinism is true.

The Manipulation Argument and Compatibilism

In much of the contemporary free will debate, it would appear that compatibilists and incompatibilists have been talking past each other, insofar as they have not had the same thing in mind when they have addressed the matter of whether “free will” exists. The philosopher Daniel Dennett, for instance, although a vociferous compatibilist, was recently happy to publicly concede that free will of the sort required for “basic desert” moral responsibility does not exist (Moscow Center for Consciousness Studies 2014). That is because the sort of free will in which Dennett, and many other compatibilists, is interested is not the one needed for “basic desert” moral responsibility but just that which he thinks will allow justification of important human practices (e.g., punishment; Dennett 2015). But a number of compatibilists, such as Sartorio (2016) and Mele (2006), do assert that free will in the “basic desert” sense is compatible with causal determinism, allowing them to have real argumentative engagement with incompatibilists, who seem to hold this conception of free will much more frequently than compatibilists.

At this point what is likely the most prominent contemporary argument for hard determinism, or, more broadly, free will skepticism, can be considered, along with a compatibilist reply (the argument is not meant to address libertarians since it assumes the truth of determinism). This

argument, called the manipulation argument, is presented in its most sophisticated form by Pereboom (2016). It is a thought experiment that has one consider four cases consecutively in which an agent is causally determined to kill another agent by factors outside of the former agent's control. In the first case, neuroscientists remotely manipulate the agent's brain ("neural states") such that he is causally determined to kill the other agent; in the second case, neuroscientists program the agent's brain from birth so that he is causally determined to kill the other agent; in the third case, aspects of the agent's community have effects on his development that causally determine him to kill the other agent; in the fourth case, the agent's circumstances are unremarkable, but he is simply causally determined to develop a nature that will lead him to kill the other agent (Pereboom 2016, pp. 76–79). Importantly, a number of conditions for free will that are popularly specified by compatibilists are posited in this thought experiment – for instance, consistency of first-order desires (desires for something) and second-order desires (desires to desire something) on the part of the murderous agent. Another such condition that it is assumed the murderous agent satisfies is responsiveness to reason; in other words the agent is amenable to changing his behavior in light of rational reflection about his reasons for action. These are the sorts of conditions that some compatibilists argue are all that must be realized to hold agents morally responsible for their actions. Nonetheless, Pereboom (2016) claims that he cannot see a "principled" distinction between any of the four cases, and therefore the ordinarily causally determined agent in case 4 is no more morally responsible for the murder in the "basic desert" sense than is the manipulated agent in case 1, who certainly seems non-responsible. This implies that normal causal determination leaves agents no more morally responsible for their actions than causally manipulated agents.

One ambitious reply to the manipulation argument has been offered by the philosopher Michael McKenna, who has endeavored to exploit the fact that the manipulation argument turns on *intuitions* about whether the murderous agent in the cases is

morally responsible for the acts of killing. McKenna argues that we can just as easily see the manipulation argument backwards, proceeding from case 4 to case 1, and alleges that in doing so the compatibilist conditions of free will, such as the consistency of first- and second-order desires, will figure more prominently in one's mind than the acts of manipulation, and thus one may at least come to reasonably doubt that the agent in case 1 is not morally responsible for the murder (McKenna and Pereboom 2016, pp. 167–168). But one may think it does too much violence to the concept of moral responsibility even to doubt that the agent in case 1 is not responsible for the murder since, after all, the murder flows so directly from the activities of other agents. One might hope that compatibilists could draw a more robust distinction between, on the one hand, cases 1 and 2 and, on the other, cases 3 and 4 that could not be answered by mere revision of the manipulation argument (on the matter of avoiding rebuttal by way of such revision, which McKenna's response explained above aims to do, see McKenna and Pereboom 2016, p. 164).

Libertarianism

Libertarianism about free will comes in three varieties: event-causal, agent-causal, and non-causal – but only the first of the three will be considered here given limitations of space. Event-causal libertarianism is the view that free agents' actions are indeterministically generated in such a way that the actions are "truly up to" (Strawson 1986) the agents but are nonetheless brought about by other actions (or mental "events") of the agent. In the experience of the current author, libertarians less often marshal reasons to believe that libertarianism is true than they merely try to show that libertarianism is possible or coherent. Some libertarians have argued that the phenomenological experience of free will is *prima facie* evidence for the existence of free will, and that in light of this evidence we are justified in believing in free will until we have reasons sufficiently strong to engender doubt or skepticism about the accuracy of this

phenomenology (which free will skeptics would of course claim we *do* have). Event-causal libertarianism specifically faces the problem of plausibly explaining how actions can be indeterministically generated but still within the agent's control, such that performing the actions is really "up to" the agent. It is hard to see how the mental events of agents cause their actions but do not fully determine those actions, in a way that is ultimately outside of the agents' control, or randomly or probabilistically generate them.

Conclusion

The contemporary free will debate most saliently involves diverse responses to the threat of causal determinism. Since all aspects of the debate are characterized by strong, even inveterate, disagreement, there is no consensus on whether or not free will exists.

Cross-References

- ▶ [Genetic Determinism](#)
- ▶ [Psychological Determinism](#)

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Freedom

- ▶ [Daniel Dennett on Free Will](#)
- ▶ [Evolution of Free Will](#)

Free-Rider

- ▶ [Problem of Cheating](#)

French Kissing

- ▶ [Kissing](#)

Frequency of Infidelity

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Synonyms

[Adultery](#); [Extramarital sex](#); [Extrapair copulation](#); [Unfaithfulness](#)

Definition

Infidelity In the context of marriage, sexual activity with a person other than the marriage partner

Introduction

This entry will discuss the frequency of infidelity in the context of marriage, defined as "a socio-sexual and socially recognized bond of some duration" which is typically, but not always, established between a man and a woman

(Weisfeld et al. 2018, p. 5). Typically, marriage has the purpose of raising children in common; this nearly universal arrangement usually brings with it a commitment to sexual exclusivity with regard to one's spouse. In this context, infidelity is then a violation of that commitment to sexual exclusivity by one spouse or the other, by means of sexual involvement with another person outside the marriage. The entry here will not deal with polygamy (the publicly recognized arrangement whereby one may have multiple spouses), or polyamory, defined as the practice of having more than one sexual relationship at the same time, with the full knowledge and consent of all partners involved.

First, a brief review of problems in conducting research will be discussed, followed by some statistics on infidelity. Then a discussion of evolutionary and cultural pressures to increase or decrease infidelity will be presented, followed by results from research on five different cultural groups (Nowak et al. 2014).

Research on Infidelity

It is difficult to conduct research on marital infidelity, for several reasons; furthermore, these challenges make it difficult to compare results from different studies. First, there is the issue of timing of the act(s) of infidelity; one tends to get lower percentages of people answering affirmatively if the question is "Are you currently sexually involved with someone outside your marriage?" as opposed to "Over the course of your marriage, have you ever been sexually involved with someone besides your spouse?" Also, young couples may not have experienced non-marital sex yet but may later on. Second, the meaning of infidelity may not be the same for all respondents; some may see engaging in heavy petting or oral sex with a non-marital partner as being unfaithful, while others insist that only sexual intercourse with a non-marital partner would qualify as sexual activity amounting to infidelity. Thirdly, there are methodological issues; for example, Whisman and Snyder (2007) found that when married women were asked face-to-face

about infidelity, 1.08% answered affirmatively but when asked via online questionnaire, 6.13% of women reported being unfaithful to their spouses. Lastly, there is the issue of cultural taboos regarding infidelity itself and also research on infidelity. For example, in the research in China reported below, there was great resistance to asking the question about infidelity; eventually, a compromise was reached with the Chinese collaborators whereby the question in the survey was written in such a way that respondents could be referring to real or imagined infidelity (Nowak et al. 2014).

Frequency of Infidelity

The first major sex survey in the USA was Alfred Kinsey's research described in his two best-selling but heavily criticized (due to nonrandom sampling) volumes. In the first volume, the research team reported that 50% of men had had sexual relations outside their marriage at least once; in the second volume, they reported that 26% of women had been sexually unfaithful at least once while married. Subsequent research efforts have reported lower numbers. For example, Hunt (1974) reported an incidence of 41% for US men and 18% for women. The National Health and Social Life Survey (NHSLS) conducted interviews with 3432 participants selected randomly from noninstitutionalized US citizens; this research reported that 25% of married men reported ever being unfaithful to their wives, while 10% of women reported ever being unfaithful to their husbands (Laumann et al. 1994). These last numbers are also in line with Greeley's 1994 article, in which he reported 21% of husbands and 11% of wives describing having been unfaithful at some point in the course of their marriage.

Cross-culturally, more societies report that infidelity is moderately common than societies report that it occurs at a very low rate. Broude and Greene (1976) reviewed data on 56 societies and found that virtually all men engaged in extra-marital affairs in 13% of tribal societies, a moderate number in 56%, and relatively few in 31%. Only 23% of 116 societies prohibited male

infidelity, compared with 89% for female infidelity, a testament to the ubiquity of the double standard. Rates of infidelity can also be indirectly estimated by studies investigating non-consanguinity rates for father-child dyads. These rates can be as high as 20% (Geary 2005). Russell and Wells (1987) estimated non-paternity on the basis of relatives' feelings of closeness to various children and concluded that the rate was somewhat higher than the 4% found in an earlier British study. Another indirect indication of the evolutionary prevalence of infidelity is the existence of adaptations in men for sperm competition and for selection of semen from different men in women.

Evolutionary Pressures

Evolutionary pressures have been cited as influences working to increase marital infidelity and to decrease it; the same can be said about cultural inputs. A consistent finding is that men's rates of extramarital sex exceed women's. This is consistent with sexual selection theory. In most species including all mammals, the female makes the greater total parental investment, so a male can gain by securing sexual opportunities that may eventuate in his passing on his genes even with minimal parental effort on his part. Therefore men may increase their fitness through sex outside of marriage at little cost to themselves. Female mammals will inevitably have to invest appreciably in their offspring, and so an ill-considered mate choice is hazardous. In species with paternal investment such as humans, the female will gain greatly by securing some paternal investment, so extra-pair sex whereby such support is uncertain is seldom a viable option.

An unfaithful wife risks incurring the wrath of her husband. However, in theory a wife might increase her fitness by being fertilized by a high-quality male (one with good genes or abundant resources), as long as she does not seriously enrage her husband or he remains ignorant of the affair. Wives sometimes engage in extramarital affairs in the process of moving toward divorce and remarriage. Wives are more likely to be

unfaithful when ovulating, which is when they find masculine men especially attractive, thus supporting the good genes hypothesis. At mid-cycle, men engage in more mate guarding.

Cultural Influences

Cultural forces can vary these considerations. For example, in matrilineal cultures, the mother's brother tends to invest in her children more than her husband does (the avunculate). Marriages tend to have high rates of promiscuity because the wife is less dependent on her husband for assistance and so may choose to risk offending him by being unfaithful.

In cultures in which the wife has her own economic resources and is less dependent on her husband, she may be willing to be unfaithful and risk his deserting her. In cultures and social classes in which husbands contribute relatively little in parental investment, enforcement of norms of female infidelity is more lax.

Cultures in which the father invests substantially in his children may effectively enforce the wife's sexual fidelity by practices such as her sequestration, chaperoning, veiling (to prevent other men from forming amorous attachments to her), and sex segregation.

Some cultures strongly discourage divorce even in cases of infidelity if valuable economic or political alliances are built up between the families of the wife and husband.

Extramarital sex may also take the form of rape, which is more common where there are many unmarried males, as in polygynous cultures. Rape is common in warfare when women are unguarded. Another form of extramarital sex is prostitution, resorted to almost exclusively by husbands rather than wives.

Findings from the MARQ Studies of Five Cultures

The Marriage and Relationship Questionnaire (MARQ) was developed in England as a multi-purpose survey instrument appropriate in various

cultures (Russell and Wells 1993). The MARQ has undergone rigorous invariance testing (Lucas et al. 2008), and its major scales have demonstrated both cultural and gender invariance, thus making the MARQ a reliable instrument for examining predictors of marital satisfaction and dissatisfaction across cultures (Weisfeld et al. 2018).

Nowak et al. (2014) reported on the percentages of husbands and wives who responded affirmatively to the question, “Do you find sexual fulfillment outside your marriage?” Responses were counted as negative if the respondent marked “Not at all” or “Not really.” Affirmative responses were those marked “Some” or “Quite a lot” or “Very much.” (Note that the question asks about the current time, rather than whether an incident of infidelity ever happened over the course of marriage – the latter question would generate higher percentages.) In every country, husbands were one-and-one-half-to-two times as likely to report being unfaithful as compared to wives; each sex difference is statistically significant. Percentages of husbands reporting infidelity were 29.2 (Chinese), 25.2 (Russian), 12.9 (Turkish), 9.3 (American), and 6 (British). Percentages of wives reporting infidelity were 19.8 (Chinese), 14.3 (Russian), 6 (American), 5.9 (Turkish), and 4.3 (British). A quarter of the Turkish marriages were arranged, as opposed to being self-selected, and the frequency of sexual fulfillment outside the marriage was not significantly different in those two groups. These cultural groups were combined to examine predictors of infidelity via regression analyses, and those results are reported in the 2014 paper (Nowak et al.). Also, as the paper points out, with regard to the American sample, “The infidelity sex ratio of the comparable Laumann cohort (1963–1974), 1.58, was very similar to that of our own US sample, 1.56.”

The MARQ data require qualification regarding cultural differences in frequency of marital infidelity. The infidelity rates in China were high partly because so many couples lived in different cities and also because of the discreet wording of the questionnaire item, mentioned above. The Russian rates were high in part because of

the difficulty for estranged couples to find housing in order to divorce and live apart.

Conclusion

In general, infidelity is more likely if love and sexual satisfaction within marriage are low and if the spouse is unfaithful. Less attractive spouses guard their mates more than do more attractive ones. More attractive spouses are guarded more closely than less attractive ones.

Cross-References

- ▶ [Cuckoldry Risk](#)
- ▶ [Extrapair Copulation](#)
- ▶ [Human Mate Poaching](#)
- ▶ [Infidelity](#)
- ▶ [Infidelity Risk](#)
- ▶ [Marriage](#)
- ▶ [Mate Guarding](#)
- ▶ [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Sperm Competition](#)

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Frequency-Dependent Selection

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Synonyms

Negative frequency-dependent selection; Positive frequency-dependent selection

Definition

Frequency-dependent selection occurs when the fitness of a phenotype, genotype, or allele varies with its relative abundance in the population.

Introduction

Frequency-dependent selection occurs when the differential survival and reproduction of organisms in a population depends on the trait (allelic, genotypic, or phenotypic) frequencies of other conspecifics in the same population. It is common in nature and perhaps even the norm for most biological systems (Dieckmann and Ferriere

2004). Traits that affect mating success, resource competition, and predation, for example, often generate situations where the relative fitness of a trait variant depends on its frequency in the population. Despite its ubiquity, frequency-dependent selection is too often neglected when reasoning about selective processes.

Types of Frequency-Dependent Selection

There are two basic varieties of frequency-dependent selection: *negative* frequency-dependent selection and *positive* frequency-dependent selection.

Negative frequency-dependent selection has clearly garnered the lion's share of attention in evolutionary population biology. It occurs whenever the fitness of a trait decreases as its frequency relative to competing trait variants in a population becomes greater. Put simply, becoming more common makes a trait, along with the organisms that bear it, less fit.

Undoubtedly, the most celebrated example of negative frequency-dependent selection comes from the work of Carl Düsing and subsequent articulation by Ronald A. Fisher, after whom it has come to be called “Fisher's Principle” (Fisher 1930; Edwards 1998). It has been shown that, for any out-breeding sexual species, the probability of an individual being able to breed depends on the frequency of its own sex in relation to the opposite sex. The explanation of equal sex ratio begins by assuming that the reproductive cost of producing a female is equal to that of producing a male and, then, stipulating a biologically realistic scenario in which excess females are born to the parents (P) of first-generation offspring. In such circumstances, any first-generation offspring (F1) of the male sex would have better mating prospects on average than any first-generation offspring of the female sex. Consequently, a first-generation (F1) male tends to contribute more offspring on average to the subsequent second-generation (F2) than its female counterpart. Now, from the perspective of the original parental generation (P), any genetic disposition to produce more male offspring will

have been favored by natural selection as it yields more average grandoffspring (F₂). Genes for producing male offspring are accordingly expected to spread in the population until the sex ratio reaches 1:1 (50% male, 50% female). At that point, however, the selective advantage which accrued to genes for producing male offspring ceases since males no longer have better mating prospects than females of the same generation. The sexes then have equal relative fitness. Furthermore, capacities that produce females will be at a selective advantage whenever there are excess numbers of male offspring. Whereas the male phenotype and any genetic mechanisms which bias gamete formation in its direction were favored in circumstances of excess female production, exactly the opposite holds true when there are excess numbers of male offspring. There is thus a pendulum-like frequency change in evolutionary dynamics which stabilizes around the equilibrium sex ratio of 1:1 and ultimately explains why a sex-determination mechanism yields equal proportions.

Examples of negative frequency-dependent selection abound. Within biological game theory, which focuses exclusively on phenotypic traits (or strategies) and the optimal outcomes (or payoff states) of episodic natural selection, an organism playing an aggressive or confrontational strategy known as “hawk” will flourish in a population comprised primarily of passive players known as “doves.” However, a dove will tend to do better in a population composed mainly of hawks (Maynard Smith 1982). It has recently been shown (Kokko et al. 2014) that the head-color polymorphism of red and black Gouldian finches (*Erythrura gouldiae*) strongly supports the game-theoretical model for limited aggression in an animal population. The aggressive red morph is behaviorally dominant and successfully invades black populations, but when red “hawks” become too common, their fitness is severely compromised via decreased parental ability. Other studies indicate negative frequency-dependent selection for self-sterility alleles in plants, handedness in the feeding morphology for scale-eating cichlid fish, and male reproductive strategies in a marine isopod (Stevens 2011).

For a human example, we need to look no farther than studies of host-pathogen coevolution. The African sleeping sickness parasite (*Trypanosoma brucei*) sequentially changes surface antigens as hosts develop antibodies. Host antibodies tend to target the most common antigens, and negative frequency-dependent selection preserves genetic diversity of parasite antigens as well as genetic diversity of the antibodies in their hosts (Stevens 2011). Overdominance or heterozygote advantage presents yet another interesting example in this area. Overdominance occurs when the heterozygous genotype is selected over either of the homozygous genotypes. The classic case involves sickle-cell disorder in malaria-ridden regions. There is a frequency-dependent component in this case because rare (deleterious recessive) alleles are disproportionately found in heterozygous genotypes, whereas common alleles are disproportionately found in homozygous genotypes. So rare alleles always appear to have an advantage.

Positive frequency-dependent selection often goes unmentioned alongside its more oft-cited counterpart. It is, nevertheless, no less important to evolutionary dynamics. Positive frequency dependence occurs when the fitness of a trait variant increases as its frequency relative to competing trait variants in a population becomes greater. In other words, becoming more common makes a trait type, along with the organisms that bear it, more fit.

Perhaps, the most uncontentious example of positive frequency dependence is that of Müllerian mimicry (Müller 1879). Consider, for example, viceroy and monarch butterflies. Both species share an honest color indication of their unprofitability (noxious taste) to predators in the form of bright orange wing coloration and pattern. It is likely the case that predators (e.g., birds) must kill a certain number of individual butterflies with a certain signal before they learn to avoid it. When predators must learn to avoid only one signal instead of two or more distinct signals, it decreases any individual butterfly's risk of being killed. By sharing an honest warning signal, then co-mimic species can benefit from the shared mortality costs of educating the predators to

avoid that signal. An increase in the number of any of the co-mimics should benefit all, as the more individuals there are that share the honest signal, the lower the per capita predation risk. Consequently, rare signal variants that are not genuinely distasteful or simply much less distasteful to predators should be at a disadvantage (Ihalainen et al. 2008).

The Importance of Positive and Negative Frequency-Dependent Selection

Frequency-dependent selection is apparently widespread in many natural populations. While the extent of its scope is a somewhat recent discovery, the phenomenon of frequency-dependent selection has been entertained since the work of Charles Darwin. Why, then, is so much current research focused on elucidating frequency-dependent selection?

Answering this question requires briefly revisiting the general features of natural selection. As resources are limited, there will be heightened intraspecific competition among individuals within a population who bear distinctive heritable trait variants. Insofar as these trait variants differentially affect the average probability of survival and reproduction for the individuals that bear them, the frequency of such traits will systematically change across generations. Trait variants that increase relative fitness tend to become more common or even go to fixation, while less fit variants correspondingly decrease or possibly disappear. This is the (oversimplified) microevolutionary basis for adaptation and ultimately the macroevolutionary phenomenon of speciation. Note that the role of natural selection is primarily one of culling existing variation and, thereby, continually adapting populations to deal with local environmental challenges to survival. The explanatory problem is that most populations exhibit abundant genotypic and phenotypic variation which cannot alone be explained by observed rates of mutation or migration.

It is precisely at this point where the appeal of negative frequency-dependent selection becomes clear. Because becoming more common reduces

the fitness of a trait variant, rare trait variants can be maintained. Here is an explicit way to maintain genetic and phenotypic variation in a population that does not rely on reference to a spatially or temporally variable environmental. Negative frequency-dependent selection is thus typically considered a form of “balancing selection” in that it explains the preservation of variation and extends the possibility of evolutionary rescue.

Positive frequency-dependent selection, in contrast, amplifies the effects of directional selection. Other things being equal, directional selection in finite populations will increase the relative frequency of the fittest trait variants and eventually drive them to fixation if unencumbered. Positive frequency dependence simply accelerates this process since it increases the relative fitness of a common trait variant as its relative frequency increases. There will correspondingly be ever stronger selection against rare variants as they become scarcer. This can obviously have dramatic consequences regarding the rates of adaptive evolutionary change.

Conclusion: The Conceptual Challenge of Frequency-Dependent Selection

Frequency-dependent selection makes fitness values depend on a constantly evolving trait distribution in a population. As such, an individual cannot reliably transmit its fitness to its offspring even when it has the capacity to transmit its traits with perfect fidelity. But if fitness is not stable across generations because of frequency dependence, then mean fitness in a population will not necessarily increase. Gene frequencies might just cycle indefinitely without ever attaining equilibrium (Rice 2004, p. 14). This is a bleak outcome, for it threatens to sever the intuitive explanatory link between natural selection and adaptation.

Responses to this rather dire possibility have fallen largely into two camps. In order to preserve the causal and explanatory connections between natural selection and adaptation, some contend that individual fitness can be maximized despite the apparent problem posed by frequency dependence. Notable among those who are so inclined is

the theoretician Alan Grafen, who has dubbed his approach the “Formal Darwinism Project” (Grafen 2009). An altogether different response can be found in a research program that is based on the mathematical framework known as “adaptive dynamics” or “evolutionary invasion analysis” (Geritz et al. 1998). This approach arose in the early 1990s largely in response to the conceptual difficulties posed by frequency-dependent selection. It extends evolutionary game theory to account for more realistic ecological dynamics, and it can incorporate both frequency- and density-dependent selection. Only time will tell whether either of these responses suffices to meet the challenges posed by frequency-dependent selection.

Cross-References

- [Adaptation](#)
- [Müllerian Mimicry](#)

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Freud and Gender

- [Freud on Sex](#)

Freud and Human Sexuality

- [Freud on Sex](#)

Freud and Psychosexual Development

- [Freud on Sex](#)

Freud on Sex

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Synonyms

[Freud and human sexuality](#); [Freud and gender](#); [Freud and psychosexual development](#)

Definition

Freud's emphasis on sexuality in his explanations of human psychology.

Introduction

In the popular imagination, even among those who are otherwise almost entirely unfamiliar with his work, most people who have heard of Freud at all surely associate him with the notion that sex motivates all human activity. Though a bit of a cliché, this belief is in fact quite accurate, to a degree that even many of the professors who talk about his work (mostly in history of psychology classes, these days) may fail to fully appreciate.

Sex as the Foundation of All Neurosis

Freud always saw himself, throughout his career, as a biological scientist with firm scientific roots, and most of his theory is built on a foundation of inherited, evolved instincts and drives that are required to insure survival. What made him unique among late-nineteenth and early-twentieth century thinkers was simply that he placed greater emphasis on the sex drive than on such things as hunger and thirst and did so in a remarkably transparent manner.

In 1909, 10 years after the publication of *The Interpretation of Dreams*, his most successful book, the then-53-year-old Freud was invited to deliver a series of lectures and receive an honorary degree as part of the twentieth anniversary celebration of Clark University in Worcester, MA. On what would turn out to be the only visit he ever made to the United States, Freud took the opportunity to introduce his core ideas to the American audience in a very straightforward series of lectures, published the following year in the flagship journal of the American Psychological Association. These lectures are a vital source of information on Freud's attitudes in middle age toward his own ideas, and he devotes a considerable portion of the fourth lecture both to the role of sexuality in his theory and to how that has been received by other psychologists:

Even those investigators who gladly follow my psychological labors, are inclined to think that I overestimate the etiological share of the sexual moments. They ask me why other mental excitations should not lead to the phenomena of repression and surrogate-creation which I have described. I can give them this answer; that I do not know why they should not do this. . .but experience shows that they do not possess such a significance, and that they merely support the effect of the sexual moments, without being able to supplant them. (Freud 1910, p. 206)

To the objection that other doctors do not find that their patients report experiences that support Freud's ideas, he responds in the same lecture:

Men are not candid in sexual matters. They do not show their sexuality freely, but they wear a thick overcoat—a fabric of lies—to conceal it, as though it were bad weather in the world of sex. And they are not wrong; sun and wind are not favorable in our civilized society to any demonstration of sex life. . . . But when your patients see that in your treatment they may disregard the conventional restraints, they lay aside this veil of lies, and then only you are in a position to formulate a judgment on the question in dispute. (Freud 1910, p. 206–207)

The most scandalous thing about Freud's perspective, ultimately, was not his emphasis on sexuality, but rather his insistence that it was a fundamental drive for all humans, regardless of age or apparent innocence:

Is there an infantile sexuality? you will ask. Is childhood not rather that period of life which is distinguished by the lack of the sexual impulse? No, gentlemen, it is not at all true that the sexual impulse enters into the child at puberty, as the devils in the gospel entered into the swine. *The child has his sexual impulses and activities from the beginning, he brings them with him into the world* [italics mine], and from these the so-called normal sexuality of adults emerges by a significant development through manifold stages. (Freud 1910, p. 207).

Based on this understanding of sexuality as a fundamental, inborn element of human nature, Freud made those stages the centerpiece of his description of development from infancy to adulthood.

Infantile Sexuality

Freud described the fundamental sexual drive as a quest for sensual pleasure and described his stages of psychosexual development as a progression

through different ways of satisfying that search. During the first stage, the *oral* stage, lasting from birth to around age 2, the child derives pleasure primarily from the mouth, beginning with the acquisition of nourishment from the mother's breast, and thus explores all unfamiliar objects by placing them there first. For approximately the next 2 years, which coincide with the child's acquisition of bowel control and the onset of toilet training, the child is in the *anal* stage, in which the child derives pleasure from controlling the actions of the anus.

The third stage, the *phallic* stage, is perhaps the best known, as it is so intimately connected with two of Freud's most familiar, and most controversial, ideas. During this stage, the focus of sensual pleasure, at least for boys, becomes the penis, which little boys often spend a lot of time touching. Freud's explanation for what girls are focused on during this time also concerns the penis, specifically the girl's realization that she doesn't have one and the resentment this brings. While boys are experiencing sensual pleasure, girls are experiencing *penis envy*.

The really big idea contained in Freud's phallic stage, however, is the *Oedipus complex*, named after the Greek protagonist Oedipus, who inadvertently kills his father and marries his mother. During the phallic stage, boys go through a period in which they bond strongly with their mothers and show less interest in their fathers. According to Freud, on an unconscious level, the boys fantasize about growing up and marrying their mothers. Recognizing his powerlessness against his father, *who might take away the penis if he finds out*, the boy resolves this conflict by identifying strongly with the father instead of competing with him for mother's affection. The same mechanism occurs in reverse for little girls, who fantasize similarly about marrying their fathers and resolve the conflict by identifying with their mothers. Freud saw incomplete resolution of the Oedipus complex as central to all subsequent mental illness, saying that it "represents the *nuclear complex* of every neurosis (Freud 1910, p. 212)" and that mental life cannot be understood without it.

The phallic stage, with all its implications for later mental health, is followed by the *latency* stage, a period, from roughly 6 to 12 years of

age, where the child concentrates on schoolwork and sexual impulses seemingly lie dormant. This dormancy ends with the onset of puberty and the start of the *genital* stage, in which sexual pleasure is sought in the company of others, a stage which carries the child into adulthood and beyond.

Conclusion

In a world in which men's descriptions of their own sexuality wore a thick overcoat of lies, Freud's emphasis on sexuality as the primary source of our unconscious motivations, even in early childhood, was so startling that it remains controversial over a century later. Although scientific research has tended not to support his ideas, and modern scientific psychology has largely distanced itself from his influence, his ideas undeniably remain quite well known, and quite influential, in our new century.

Cross-References

- ▶ [Freud's Psychoanalytic Theory](#)
- ▶ [Infancy](#)
- ▶ [Psychodynamic Foundations](#)
- ▶ [Sexuality](#)

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Freud's Psychoanalytic Theory

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Synonyms

[Freudian theory](#); [Psychodynamic theory](#)

Definition

Sigmund Freud's (1856–1939) revolutionary, unique approach to understanding the human mind and personality, emphasizing the role of unconscious conflicts and motivations in determining human behavior.

Introduction

While its scientific utility (or indeed, its status as a scientific theory) remains a subject of much controversy, there can be no doubt that Sigmund Freud's (1856–1939) psychoanalytic theory has had as great an impact, both within psychology and in the larger world of medicine and popular culture, as the work of any other thinker before or since. Where Kepler changed humanity's view of itself by taking away our location at the center of the universe, and Darwin changed it again by taking away our unique status as the obvious pinnacle of biological development, separate from and above the animals, Freud changed our self-regard once more by removing much of our self-awareness, arguing that much of what motivates us internally is unconscious and inaccessible to direct observation.

In Freud's model of the human personality, there are three essential components that determine, via their interactions with each other, how people think and behave: id, ego, and superego. The id and the superego belong entirely to the realm of the unconscious mind, whereas the ego represents the conscious part of the psyche, the part of the self of which we are aware and which we willingly show to others. Of these three elements, only the id is already present at birth. The ego begins to develop during infancy and early childhood, and the superego appears some time later. To illustrate the importance of the unconscious components in determining behavior, Freud favored the metaphor of an iceberg to describe the structure of the human mind: when an iceberg is floating in the sea, only about 10% of it is visible above the water's surface, with the remaining 90% unseen beneath the surface. So it is with the

psyche: the vast majority of it is hidden from view, even to its possessor.

The Id

The only component of the personality that is present at birth, the id comprises, in Freud's own words, "... everything that is inherited, that is present at birth, that is laid down in the constitution: above all, the instincts" (Freud 1938/1973, p. 2). The infant, without reason or restraint, is filled with inborn, instinctive needs demanding fulfillment. According to Freud, these unfulfilled needs cause libidinal energy within the id to build up, creating a pressure that demands release, a release that is experienced by the infant as pleasure. Conversely, the postponement or prevention of release is experienced as pain. The infant, possessing no ability to delay release, demands immediate gratification. The id is driven solely by the goal of experiencing as much enjoyment and avoiding as much pain as possible and is therefore said to operate according to the *pleasure principle*.

The id completely controls the newborn, demanding immediate gratification of its needs for food, drink, sensual pleasure, and affection. The infant has neither learned nor experienced adult rules or social conventions; thus the id is quite irrational, demanding that its needs be met without regard for present circumstances. This is obvious to anyone who has ever handled a hungry infant but been unable to feed him or her right away: there can be no reasoning with the newborn, no making of excuses. Delays in gratification are met only with increased anger and agitation. According to Freud, the baby's awareness is, at first, limited to two things: discomfort, created by unfulfilled needs that demand attention, and pleasure and relief when those needs are satisfied. As the child has not yet developed any sense of differentiation or boundaries between self and other, his/her own needs form the whole of the universe.

Over time, the infant begins to develop an increasing awareness of its surroundings, along with a slowly growing sense of the distinction

between those surroundings and the self. Whenever an infant feels hungry and cries, somebody will eventually feed the infant, thus reducing the tension of hunger and producing the feeling of pleasure. Over many iterations of this cycle, the baby's memory will eventually store a representation of both the food and the feeder, via their taste, smell, sight, sound, and feel. Non-psychoanalytic psychologists would describe the process differently, but all would recognize the result: the baby can now bring to mind the objects that will provide a particular kind of satisfaction (in the present case, food), in response to a particular way of releasing libidinal energy (in the present case, crying).

It is important to note that the id's lack of reason is inevitably accompanied by complete amorality. With no internalized notion of social conventions regarding right and wrong (this will develop later), the id is purely hedonistic. What brings pain and discomfort is always wrong, and what gives pleasure is unequivocally right. If the psyche were to simply stop developing with the id, a person would clearly not get far in life. Fortunately, another component will soon develop that functions, at least in part, to keep us alive and out of jail. This second component, *the ego*, recognizes the limits and requirements of the environment, while also being aware of the demands of the id, and is tasked with finding morally acceptable ways of relieving the pressure of libido, or instinctual energy.

The Ego

Of the three major components of the personality, it is the ego that actually interacts consciously with the world. Its task is to help the id to delay gratification until its needs can be met in ways that do not violate the rules and conventions of society, rules of which the id remains unaware. The ego, according to Freud, develops directly out of the id and is actually a part of the id that has been modified by external influences, thanks to its conscious awareness of that outside world. The id, meanwhile, remains unconscious and unaware and as irrational and hedonistic as ever.

One way of conceiving of the ego's function is as a referee, or mediator, constantly negotiating the conflicts that inevitably arise between the id's (often unreasonable) demands and the reality of the requirements of the social and physical environments. This is difficult, as it requires delaying gratification for an entity that exists entirely below the threshold of consciousness and lacks any awareness of the real world. Unlike the id, however, the ego is conscious and quite aware of the restrictions of the environment. The ego is therefore responsible for providing the child with an initial recognition of the rules and customs of his or her society, as well as an understanding of the penalties that may accompany violations of those regulations.

Whereas the id, which knows only the pursuit of pleasure and the avoidance of pain, operates according to the *pleasure principle*, the ego, with its awareness of the real social and physical environments, operates according to the *reality principle*. Unlike the id, the ego is able to recognize that simply satisfying the drives, especially the sexual and aggressive drives, in ways that are socially inappropriate, is ultimately detrimental to one's chances of survival, whereas observing society's rules and releasing that energy in more acceptable ways will ultimately result in greater satisfaction and less pain.

The Superego

In Freudian theory, there are no innate, inborn moral principles; there is no natural moral law. Morality is a social construction, which must somehow be learned by infants who, as previously noted, are amoral pleasure-seekers, with no sense of right or wrong at all. Newborns do, however, possess the capacity to gradually internalize the values they are exposed to, and which are imposed on them, both by their environment and by the people in it. Infants also arrive equipped with emotional reactions that can be evoked by violating the rules as well as by following them. Acting in a way consistent with our values results in feelings of pride and contentment, whereas acting in opposition to our values results in guilt, shame,

and fear of punishment. These internalized values become the superego, which emerges from the ego just as the ego develops out of the id.

The superego's job is to internalize the monitoring that has previously been performed by adults in the external world: it observes the ego, gives it orders, judges it, and threatens it with punishments, exactly like the parents and others whose place it has taken. Contrary to a frequent popular presentation of Freudian theory, it is not entirely correct to equate the superego with the conscience, which is actually one of its two components: the conscience and the *ego ideal*. The conscience is an internal listing of the prohibitions of the child's society, the actions that will result in punishment (the should *nots*). By contrast, the ego ideal represents positive moral values (the *shoulds*). Very young children, controlled by the id, must be consistently punished for violations and rewarded for good behavior, whereas older children and adolescents often do not require outside consequences, either positive or negative. As they have internalized values as their own, both punishment and approval now also emerge from within. When they violate the rules, they feel remorse and shame, courtesy of the conscience. When they adhere to their values, doing what is right and good, the ego ideal provides praise, pride, and general good feelings.

With all three components in place, the psychoanalytic structure of personality is now complete, and the ego's job has just become harder. In older children, adolescents, and adults, the choice of how to behave now requires the ego to act as a sort of referee among three conflicting sets of demands. The id, irrational as ever, continues to demand immediate gratification, while the ego must also contend with present circumstances in the environment, which often determine the conditions under which wishes can actually be satisfied and which are often beyond the individual's control. While dealing with those demands, the ego must also satisfy the superego, which is frankly just as irrational in its demands as the id. Just as the id demands gratification with no regard for practical or moral considerations, so the superego demands inflexible adherence to the rules, with no allowances made for present

circumstances or the strength of the id's requirements. Imagine, for example, a situation in which a person is on the verge of starvation, and the only way to access food requires stealing it. The id, of course, insists, with no regard for the law, that the food be taken immediately! The superego, with equally small regard for practical considerations such as imminent starvation, vehemently insists that stealing is always wrong, without exceptions! The ego's job is to take both sets of demands into consideration, along with the circumstances of the actual situation, and choose a course of action. There is no course of action that will serve to satisfy both the id and the superego, however, and so whatever action is taken, the result will inevitably include some internal conflict, much of which, like the id and superego themselves, will remain unconscious.

Defense Mechanisms

It is inevitable that circumstances will arise in which resolving the inner conflict in ways that produce no guilt, shame, or other inner trouble will simply not be possible, resulting in anxiety. For these situations, the ego has a specialized set of tools intended to minimize the anxiety resulting from internal conflict.

Freud called these techniques ego defense mechanisms, often shortened simply to defense mechanisms. These are strategies taken to reduce anxiety when more rational approaches to resolving a problem have failed. What all defense mechanisms have in common is that they occur automatically and unconsciously, and when not used to excess, their implementation is normal and even psychologically healthy.

The core idea of psychoanalytic theory is that failure to resolve inner conflicts effectively is the source of psychological problems in general, so it is important that the ego has tools available to prevent anxiety from getting out of hand. Here are some of the better-known defense mechanisms:

Repression: Freud described repression as "deliberate forgetting." In repression, thoughts and feelings that arouse anxiety are simply

banished from consciousness. Freud once drew an analogy to a disruptive audience member in an otherwise polite lecture audience. As such a person would make it impossible to continue the lecture, he would be forcibly removed from the lecture hall and the door locked behind him. He is therefore repressed, but he may make an even greater fuss once he's outside, yelling and banging on the door. Freud's point is that anxiety-provoking thoughts and memories are never completely repressed, and they can only be made to stop disrupting the ego by being allowed back in (during psychoanalysis), thus stripping them of their disruptive power. Repression is a basic mechanism underlying the other defense mechanisms, as they all serve the purpose of protecting the mind from unwelcome thoughts and impulses. The idea of repression has had a great, and often negative, influence in more recent times as the source of Western society's widespread belief in buried memories of trauma, despite an absence of evidence for the existence of such repressed memories.

Regression: A person handles anxiety or conflict by retreating to an earlier, more infantile state of development, as when a child reverts to thumb-sucking during the first few days of school. Freud explained regression as a retreat from unsatisfying reality into an earlier phase of sexual development in which satisfaction was more easily obtained, as well as a return to more primitive forms of self-expression, as when an adult reacts to overwhelming stress by throwing a childlike tantrum.

Reaction formation: The ego (unconsciously) makes uncomfortable or unacceptable impulse look like their opposites. The classic example is seen on school playgrounds, where information that one is liked by another child, especially a child of the opposite sex, is often greeted by exaggerated revulsion. More formally, since instincts and drives can be arranged as pairs of opposing tendencies (life/death, dominance/submission, love/hate, etc.), the ego may handle anxiety-arousing emotions and impulses by facilitating the expression of their opposites.

Reaction formation is in danger of becoming a sort of all-purpose explanatory mechanism, which has been used to explain everything from

homophobia (as a reaction to internal, hidden homosexual tendencies) to Stockholm syndrome (fear of captors is so overwhelming that hostages come to love them instead). The danger of relying too heavily on reaction formation as an explanation of behavior, of course, is that any behavior at all can be represented as actually revealing its opposite: a very kind person is actually hiding sadistic tendencies, the charity worker is actually a misanthrope, and so forth.

Projection: The individual sees his or her fault very clearly in someone else. More formally, threatening, anxiety-provoking impulses are disguised from the self by being attributed to others, as in the case where the married man deals with his own adulterous impulses by becoming convinced that his wife is cheating. Projection especially appears to be a key mechanism in racism, in which impulses or wishes the individual finds completely unacceptable, shameful, or dangerous are attributed to members of another group to which he or she does not belong, where they can then be identified and condemned. Freud, who had many encounters with anti-Semitism as a Jewish scientist in Austria, saw projection as central to that sentiment and as a central reason why the racist so often sees criminality and sexual immorality in other races but not in his own.

Rationalization: Rationalizations are self-justifying explanations for decisions, actions, or beliefs, generated to replace and conceal the actual path by which the person arrived there. Like all defense mechanisms, this process occurs unconsciously to protect the ego from the real reasons for its actions, as when the habitual heavy drinker says that he or she drinks just to be sociable. Rationalization is frequently accompanied by denial, allowing a person to ignore evidence that a particular impulse or habit is harmful by focusing on other information instead, as when a daily cigar smoker insists that his habit is actually healthy, because George Burns smoked them daily and lived to the age of 100.

Denial: When a person is faced with information that is too shameful, uncomfortable, or unpleasant to accept, one way of handling the tension is to simply reject it outright, sometimes despite overwhelming evidence. Denial is almost

certainly the most widely referenced defense mechanism in American popular culture, partly because of its preeminence in discussions of addiction: the first step in 12-step programs frequently consists of admitting that the problem exists. Elisabeth Kübler-Ross also spread the idea widely, making denial the first of her five steps in the confrontation of one's own impending death. Overuse of denial as an explanatory mechanism can lead to unfalsifiable (and therefore useless) hypotheses about other people: anything the subject of the hypothesis says or does that seems to disprove the hypothesis can be interpreted as the subject being in denial, rather than the hypothesis being wrong.

Displacement: Aggressive impulses toward a person who is an unacceptable target for those feelings, due to unequal status or power, are diverted onto a safer target. A man who is humiliated by his boss cannot express his rage directly, as it would get him fired, so he goes home and yells at his wife instead, for example. The wronged spouse may then yell at a child (and may perhaps, via rationalization, believe she is legitimately punishing the child), who then is rude to a younger sibling, and so on.

Sublimation: The process by which a socially forbidden, shameful, or otherwise unacceptable impulse finds a useful, socially acceptable means of expression, rather than continuing to be repressed. Freud primarily gave examples involving artistic expression, as in his attempt to explain the artistic genius of Leonardo da Vinci as the sublimation of his unacceptable homosexual urges. Sublimation also helps people with powerful aggressive drives, however, who may find expression for those drives in competitive sports such as mixed martial arts and American football.

Stages of Psychosexual Development in Childhood

Possibly the most controversial portion of Freud's theory is his view of personality development in childhood, which he described as proceeding through an orderly, invariant set of five stages, each named for the primary focus of the id's

quest for sensual pleasure during that time. Freud believed that if conflicts that arise in each stage are not resolved in a satisfactory manner, it is possible to become fixated on the particular stage, resulting in an abnormal preoccupation with that stage's source of pleasure later in life. A heavy smoker or gumchewer, for example, might be regarded as fixated at the oral stage, during which the primary focus of sensual pleasure is the mouth. The stages are as follows:

Oral Stage: The first stage comprises approximately the first 2 years of life, during which non-psychoanalytic observers would certainly agree that children do indeed use their mouths to explore new objects and enjoy putting things in their mouths. Freud explained that this occurs in part because the child's first contact with the mother in feeding is via the mouth and argued that the child's bond with the mother is therefore inextricably linked with oral contact. Failure to successfully navigate this stage and begin to forge a separate identity from the mother would result in oral fixation. In terms of the mother's contribution to this, Freud argued that oral fixation might be a result of either insufficient time *or* too much time spent nursing, depending on the individual case.

Anal Stage: According to Freud, during this stage the focus of sensual pleasure shifts to the anus, and subsequent personality development will be directly impacted by how parents handle the task of toilet training. Between ages 2 and 4, the child gains control over his or her bowels, making the act of defecation one of the very few things the child can control in an environment that is almost entirely determined by the whims and preferences of adults. If toilet training is started too soon, this will intensify the child-caretaker conflict. Increased conflict can also arise as a result of delaying the start of training for too long, however. If toilet training is experienced as too frustrating *or* as excessively gratifying, this can also increase conflict, along with the possibility of fixation at the anal stage. Parents who are too strict, are too punitive, or lack sufficient patience may produce a problem, but parents whose approach to toilet training is too lax and permissive may cause trouble as well. The result of such conflict may be that the child learns to

control his or her environment through excessive retention or expulsiveness. The anal-retentive person learned as a child to exercise control and get what he wants by refusing to excrete; as an adult he is excessively concerned with neatness and organization, controlling his environment by keeping everything in its place. The anal-expulsive type may have instead controlled his parents by excreting freely and liberally and as an adult may attempt to control others through sloppiness.

The powerful influence of Freud's description of childhood is well-illustrated by the widespread use for much of the twentieth century of the term anal-retentive personality, or simply anal character, to refer to a subclinical form of what is today known as obsessive-compulsive disorder. The anal-retentive character does not come up often in conversation among psychologists and psychiatrists these days, but the idea has certainly penetrated deep into American popular culture. References to such a personality are still readily found, though often the term is shortened and people are simply referred to as "anal."

Phallic Stage: As the stage name suggests, this is the period, roughly from 4 to 6 years old, during which a boy's id shifts the focus of pleasure to the penis. As with the oral stage, the evidence that boys go through something like this is easily obtained; getting little boys to understand that they mustn't sit with their hands in their pants is a major concern in preschools and day-care centers or on outings to public places in general. Given this remarkably male-centric description, Freud would point out that girls are also concerned with penises during this stage, specifically with the question of why they *don't* have one. Observing that boys have penises and girls do not, a little girl may wish that she did and suspect deep down that she had one at one time and that it was removed. Freud called this *penis envy*. During this stage, some boys also fear that they may lose theirs as a punishment; Freud called this *castration anxiety*.

This is also the stage in which Freud suggested the existence of the Oedipal conflict or complex, named after the Greek protagonist Oedipus, who inadvertently kills his father and marries his

mother. During the phallic stage, boys go through a period in which they bond strongly with their mothers and show less interest in their fathers. According to Freud, this occurs partly because on an unconscious level, the boys fantasize about growing up and marrying their mothers. Only one thing stands in the way: dad, who is large and frightening. Recognizing his powerlessness against his father, *who might take away the penis if he finds out*, the boy resolves this conflict by identifying strongly with the father instead of competing with him for mother's affection. When the same essential conflict occurs in girls (substitute father for mother in the preceding text), psychoanalysts call it the Electra complex.

Freud, like much of the psychiatric community until the early 1970s, regarded homosexuality as a disorder to be diagnosed and treated, and he saw its etiology as a failure to properly resolve the Oedipal conflict. Freud argued that boys who failed to successfully navigate and resolve this conflict would remain too strongly attached to their mothers, trying to emulate them rather than their fathers, and would thus grow up homosexual. A similar pattern occurs for girls; psychoanalysis viewed lesbians as women who identified too strongly with the male role model rather than bonding properly with their mothers.

Freud saw the Oedipus complex as the most important event in all of childhood, describing it as "the nuclear complex of all neurosis." In other words, he saw all psychological difficulties, anxiety, and maladjustment in general as originating in this brief period of childhood. All subsequent difficulties have their origin in how the ego handles this unconscious struggle over forbidden sexual desires and the irrational fears that arise from this struggle.

Latency Period: This period follows the phallic stage with several years of concentration on schoolwork until sensual concerns blossom again with the coming of adolescence. It is as though the id has temporarily halted the search for physical pleasure.

Genital Stage: This period begins with the onset of puberty, when the id turns its attention outward in the direction of contact with others, usually of the opposite sex. The genital stage, as

the final stage in the sequence, also describes adulthood.

The Most Direct Path to the Unconscious Mind: Dreams

As the various desires, wishes, and conflicts roiling the unconscious mind are, by definition, hidden from conscious awareness, Freud needed to find a way to access this content in psychoanalytic therapy. Much of psychoanalytic practice consists of *free association*, in which the patient/client simply expresses everything that crosses his or her mind, but this cannot reveal the things which are *not* crossing that conscious mind. For this kind of access, Freud turned to dreams, which he considered the only direct link, the “royal road,” to the unconscious.

Freud's own self-analysis focused heavily on dreams, and before long he decided to write a book about the role of dreams in resolving unconscious conflicts. First printed in 1899.

The Interpretation of Dreams is widely regarded as Sigmund Freud's most important work, and it remains his most widely read book today. The central argument of the book is that the primary function of all dreams is wish fulfillment, including fulfillment of the secret desires which we cannot admit even to ourselves on a conscious level. He further argues that the source of the superficial content of the dream can often be located in the events of the day preceding the dream, which he called the “day residue.” This can appear rather obvious in very young children, because they have very straightforward dreams of the fulfillment of wishes that they were thinking about the previous day. In adults, however, the process of tracking down the source of a dream is rather more complicated, since their dreams, unlike those of the children, have become distorted in order to conceal the underlying wishes. Just as the mind itself has both a conscious and an unconscious component in Freud's model, so every dream functions on two levels, one obvious and one deeply concealed. The surface content, or *manifest content*, is a heavily disguised version of unconscious wishes and desires, which

he called the *latent content*. Understanding the contents of the subject's unconscious mind, which is a primary goal of psychoanalysis, therefore requires correct interpretation of the symbolic meaning of that individual's dreams.

The latent content appears in our dreams because, in Freud's view, many of our unconscious motivations are so unacceptable to us that they create a great deal of intrapsychic conflict between the ego and the unconscious parts of the mind. The only way to alleviate the tension and anxiety resulting from that conflict is to allow the forbidden content to surface, though heavily disguised, in dreams. The disguise is necessary because even in dreams, the individual's resistance to these unacceptable impulses remains too strong to acknowledge them directly. The dream's real significance is completely concealed from the dreamer, and dreamers are unable to grasp the actual meaning of their dreams without the help and guidance of the psychoanalyst. The latent dream content has been transformed by the work of the ego's defenses, operating even while the dreamer sleeps, under the direction of the superego. To Freud, every dream represents some degree of compromise, allowing the disguised fulfillment of repressed wishes while preventing sleep from being interrupted by an impulse so disturbing that it awakens the dreamer.

Based at first on his analysis of his own dreams and later on those of others, Freud believed that certain elements in the manifest content of dreams tend to correspond consistently with certain latent content. Phalluses, for example, are symbolically replaced in manifest content by a wide range of objects that are similar to them in their form, including most long or tall things that jut out in some way; thus a penis can be suggested by mountains, trees, poles, sticks, umbrellas, spires, monoliths, etc. Phallic symbols also encompass virtually anything that has the purpose of penetrating the body and doing harm, including most weapons, such as swords, lances, spears, and guns of all sorts. Freud's list of phallic representations also includes most objects and geographic formations from which water runs or sprays, including pipes, fountains, geysers, crashing waves, garden hoses, and even watering cans. Objects that can be

lengthened can also represent the phallus, including balloons, antennas, springs, and even snakes. The number three is also symbolic of the male genitalia, as well as any dream thoughts that consist of three parts; thus even the appearance of the Trinity in a Christian's dreams may represent the phallus!

Most criticism of Freud's dream symbols tends to focus on the omnipresent phallic symbols, but it is not only male genitalia which are artfully concealed in dreams. In Freud's dream analyses, female genitalia are represented by virtually any hollow object that can contain other objects, including but not limited to bottles, dishes, boxes, bottles, mineshafts, caves, tunnels, pockets, tins, closets, churches, houses, forts, purses, and even landscapes. The phallic snake has female analogues as well: among animals, snails, mussels, clams, scallops, oysters, and the like also represent female genitalia. Meanwhile, fruits such as apples, peaches, pears, and coconuts generally stand in for breasts. Dreams in which playing occurs, whether it be the playing of outdoor games or the playing of musical instruments, are symbolic of masturbation, as are sliding, slipping, or even the breaking of branches. Conversely, a dream that includes a visit to the dentist, or extraction of teeth, is symbolic of *punishment* for masturbation. Many other activities and elements stand in for sexual intercourse itself, including climbing or descending ladders or stairs, traveling on a train, dancing, riding horses, raising a weapon, or running into a house.

Later theorists who embraced the idea of dream interpretation, most notably Carl Jung, tended to place much less emphasis on repressed sexual wishes than Freud did. Though Freud certainly saw other types of anxiety and conflict buried in the latent content of dreams, his focus for the bulk of *The Interpretation of Dreams*, and numerous case studies published in later years, remained primarily on sexual wish fulfillment. Given the fundamental underpinnings of psychoanalysis, this is unsurprising. As noted earlier, he built much of his theory upon the foundational idea that all psychological difficulties originate in the degree to which the individual overcomes, or fails to overcome, the Oedipal conflict in childhood.

Conclusion

While much of Freud's theory has long since dropped out of favor in the scientific psychological community, the fundamental notion that we are frequently not consciously aware of our own motivations, and that those motivations are often sexual, or perhaps repressed memories of long-forgotten trauma, continues to broadly impact popular culture into the twenty-first century. Although his ideas are now seen as pseudoscientific speculation, at best, by most of the scientific community, it is important to note that Freud always saw himself as a biological scientist and that all of the more bizarre elements of his theory grow out of his focus on the role of inherited drives and instincts, as expressed by the id.

Cross-References

- [Anxiety](#)
- [Breast Feeding](#)
- [Freud on Sex](#)
- [Psychology](#)
- [Sexuality](#)

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Freudian Theory

- [Freud's Psychoanalytic Theory](#)

Friends

- [Absence of Events to Distinguish True Friends](#)

Friends with Benefits

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Synonyms

[Booty call](#); [Casual sex](#); [Hooking up](#)

Definition

The term “friends with benefits” generally refers to a casual arrangement in which two people have both a friendship and sexual relationship at the same time. Though not romantic in nature, it is possible for romantic interest to precede the arrangement or develop as it unfolds. Friends with benefits have the potential to take various forms depending on the amount of emphasis placed on the friendship versus sexual component of the relationship as well as the motives, goals, and expectations that each partner brings.

Introduction

It has become increasingly common for Americans to report having had sex with someone they consider to be a friend. For instance, General Social Survey data indicates that among college students surveyed in the late 1980s, 56% had engaged in sex with a friend; among students surveyed in 2012, the proportion had increased to 71% (Monto and Carey 2014). The phenomenon of friends who have sex with one another is often referred to in the popular media and scientific literature alike as “friends with benefits” (FWBs).

Research suggests that FWBs can take various forms and that different people define this term in different ways. For example, in a survey of 177 heterosexual college undergraduates who were asked to define “friends with benefits” in

their own words, seven distinct types of FWBs emerged (Mongeau et al. 2013). FWBs appear to vary in terms of the partners’ prior relationship status (e.g., friends, acquaintances, lovers) as well as the motivations and expectations brought to the relationship (e.g., opportunistic sex, romantic interest). That said, the modal FWB appears to be one in which two persons with a preexisting friendship add a sexual component to their relationship. Most FWBs are not sexually exclusive and, though romantic interest is sometimes present at the beginning or develops over time, commitment to these relationships tends to be modest at best (VanderDrift et al. 2012).

Though popular among college students, FWBs are not limited to young adults, nor are they limited to persons of a particular sex or sexual orientation. Research suggests that those who participate in FWB relationships are diverse in terms of their demographic backgrounds (Lehmiller et al. 2011).

Sex Differences in Approaching Friends with Benefits

Heterosexual men and women appear to differ when it comes to their motivations for beginning FWB relationships, as well as their expectations for how these relationships will evolve over time. Lehmiller et al. (2011) surveyed 411 adults who reported current involvement in an FWB relationship and found that men were significantly more likely than women to indicate that sexual gratification was their primary motivation (72% vs. 56%, respectively). By contrast, women were significantly more likely than men to indicate that emotional connection was their primary reason for starting the relationship (37% vs. 25%, respectively). With respect to their plans for the future, most men (60%) reported a desire for the relationship to stay the same, whereas most women (63%) indicated a desire for the relationship to transition into a romance or revert back to a friendship.

One potential way to explain these sex differences is through the lens of evolutionary psychology. Though casual sex can be seen as having adaptive value for men and women alike, men

on average usually stand to gain more than women from casual encounters due to differences in parental investment (Buss and Schmitt 1993). In the context of FWBs, which tend to be sexually nonexclusive (VanderDrift et al. 2012), there is a reproductive advantage offered to men in that these relationships allow them the ability to obtain low-investment sex with more than one partner at a time. From this perspective, it makes sense that men would be more inclined to cite sexual motives for pursuing an FWB and would desire to maintain these open-ended opportunities for casual sex for as long as possible. For women, however, maintaining low-investment, casual relationships with multiple men is riskier because, should they become pregnant, they may lack dedicated resources from the father to support their offspring. Therefore, it makes evolutionary sense that women would be more likely to view FWB opportunities as time-limited or as vehicles for beginning longer-term, higher-investment relationships.

Alternatively, men's and women's reported differences in motivations and expectations for their FWB relationships may be a product of the *sexual double standard*, which refers to the finding that women tend to be judged more harshly than men for engaging in sexually permissive behavior. Given that women are not evaluated as negatively for engaging in casual sex when they are seen as emotionally involved with their partners, it is possible that social pressure may lead women to underreport sexual motives for beginning an FWB and instead emphasize emotional connection.

Outcomes of Friends with Benefits

Given that men and women tend to approach FWBs quite differently and diverge in their expectations for the future, it should come as no surprise that opposite-sex FWBs do not always end well. Further complicating matters is the fact that both sexual and nonsexual communication are lacking in FWBs compared to romantic relationships. Research indicates that most people with FWBs fail to establish ground rules for their relationships

(Bisson and Levine 2009) and that they are less likely than those in romantic relationships to discuss their sexual desires and talk about safer-sex practices (Lehmiller et al. 2014). Part of the reason for these communication deficits may stem from the frequently reported finding that many FWBs only get together when they have been consuming alcohol.

With respect to the outcomes of FWBs, a study of college students who reported FWB experience and who were asked about their relationship status found that 28.3% still had an ongoing FWB relationship, 35.8% were still friends but not having sex, 9.8% had become romantic partners, and 25.9% had no relationship of any kind with their former FWB (Bisson and Levine 2009).

Similar numbers were obtained in a one-year longitudinal study of FWBs, which also revealed that communication was one of the strongest predictors of relationship outcomes (Ioerger et al. 2014). Those who set up ground rules for their relationship at the beginning were more likely to maintain at least some type of relationship with their partner over time. In addition, certain relationship goals were more likely to be achieved than others. Specifically, those whose goal was to maintain a friendship tended to be more successful at doing so than those whose goal was to transition into a romance.

Friends with Benefits and Personality

Research indicates that people with certain personality traits may be more inclined to enter FWB relationships than others. For example, compared to persons in other types of heterosexual relationships, those in cross-sex FWBs tend to have higher levels of attachment avoidance as well as a more unrestricted sociosexual orientation (Greszta et al. 2016). In other words, persons in FWBs are more likely to be uncomfortable with intimacy and have an easier time separating sex from emotion.

Personality is also linked to relationship satisfaction among FWBs (Lehmiller et al. 2016). Specifically, both attachment anxiety (i.e., fear of abandonment) and neuroticism (i.e., emotional

instability) are linked to lower satisfaction. By contrast, erotophilia (i.e., responding positively to sexual cues), sexual sensation seeking (i.e., a desire for thrilling and risky sexual encounters), and an unrestricted sociosexual orientation were related to higher levels of satisfaction.

Conclusions

Casual sex relationships can take many forms, with FWBs being one particularly common – and increasing – variant. Though FWBs are frequently viewed as a monolithic group, research suggests that these relationships vary substantially depending upon the individuals involved and their motivations. This, combined with low levels of communication and differences in men's and women's relationship goals, means that FWBs are often quite complex to navigate and have the potential to result in a range of relationship outcomes.

Cross-References

- [Casual Sex](#)
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Friendship

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Friendship and Modern Life

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Definition

Friendships are interpersonal relationships that are voluntary, personal, affective, mutual, and equal.

“Modern life” refers to the set of technologies and means of social interaction that has developed around and with the rise of the Internet. Friendship and modern life is then the set of interpersonal interactions and consequences thereof, which have the features noted above and arise out of relationships between agents as mediated by modern technology and society.

Introduction

The starting point for most modern analyses of friendship is Aristotle. In the *Nicomachean Ethics*, Aristotle describes three kinds of friendship, of which two, the friendships of utility and of pleasure, are imperfect, and the final one, the friendship of virtue, is perfect. In a friendship of virtue, claims Aristotle, each participant wishes well for the other for their own sake, rather than as a means to either the utility or pleasure of the lesser friendships (Ross 1998). According to Aristotle, this perfect friendship is uncommon but has the most capacity to generate the strong positive outcomes that friendships are claimed to produce. This division of friendships remains useful to modern researchers, as the notion of friendships of virtue helps to explain the intuitive dissatisfaction reported by many research participants when it is suggested that friendship between humans can be fully explained by notions such as reciprocal altruism (Tooby and Cosmides 1996).

The distinction between imperfect and perfect friendships in Aristotle is matched by a distinction between “fair-weather friends” and “true friends” in Buss (2016). True friends, on this account, are those who one can trust even when things are bad, and friends of this kind are comparatively rare. This desire for true friends presents us with an adaptive problem, namely, “how to differentiate true friends, who are deeply engaged in your welfare, from fair-weather friends, who will disappear at your hour of greatest need” (Tooby and Cosmides 1996). This problem is compounded by the fact that modern life, as Buss points out, suffers from a relative scarcity of critical events that would allow us to accurately assess those who are

deeply engaged in our welfare and discriminate them from our fair-weather friends (Buss 2016).

As human activity has collectively moved online, the means by which friendships are developed have changed. Until recently, the possibility of developing strong friendships online or in virtual spaces was itself contentious, and at the time of writing this entry, the claim that online friendships differ in kind from offline friendships is a commonplace. Many authors have claimed that true friendships, or friendships of virtue (depending on the academic background of the proponents of the claim), either cannot be established in virtual spaces or online environments or that their development in these domains is significantly more difficult than in more traditional environments. By contrast, it is widely accepted that lesser or imperfect friendships can and do develop in online environments (Cocking and Matthews 2000). This entry examines how modern friendships are created, developed, and maintained and the various issues arising from these methods.

Standard Accounts of Friendship

The five characteristics of friendship outlined by Rawlins that friendships are voluntary, personal, affective, mutual, and equal encompass the core of the notion of friendship (Rawlins 2016). They incorporate notions philosophers have appealed to as being important components of friendship, such as affection and well-wishing (Cocking and Kennett 1998), as well as those of mutual caring, intimacy, and shared activity (Helm 2010). These characteristics are also common in psychological accounts of the type and strength of friendship, which rely on notions of friendship as dyadic and co-constructed, containing elements such as reciprocity, closeness, and intimacy (Amichai-Hamburger et al. 2013). Taken together, these characteristics generate a conception of friendship wherein each friend cares for the other and does so for the sake of the other, not themselves; where the relationship is not one of mere collegiality or acquaintance but is deeper; and where the friends do things together both because they each enjoy

the thing in question and because they enjoy doing this thing in the company of friends (Helm 2010).

The process by which bonds such as those described above develop must however be examined. Friendships do not come into existence containing all these characteristics, and the strength of any of them within a particular friendship can vary dramatically. So, features such as closeness, intimacy, and mutual caring must be developed, and this development requires specific kinds of engagement between friends. Many modes of interaction, including those commonly shared with workmates or casual acquaintances, do not provide meaningful opportunities for shared activity, and participants therefore lack the opportunity to develop these features in those contexts. As Aristotle says, “friendship requires time and familiarity,” and people cannot “admit each other to friendship or be friends till each has been found lovable and been trusted by each” (Ross 1998).

Deep or higher-order friendships provide a range of benefits to those who have them. The development of friendships of this kind enhances the self-knowledge that is necessary for virtue. It provides moral role models for the friends in question, enhances their moral sensibilities, and provides them with objective views of one another (Cocking et al. 2012). If online friendships cannot become deep friendships, and if they replace offline friendships, then the opportunity for these benefits is lost. However, both of these considerations are empirical matters, and there is a growing body of research into how online friendships (and mixed/hybrid friendships) in fact operate. This research is encouraging for those who think that online and hybrid friendships are non-problematic.

Friendship and Modern Life

The modern world has drastically altered how friendships form and develop, and these alterations impact in a range of important ways on how friendships should now be treated. Some of the developments have been gradual, as with the expansion of the ease of travel for the average citizen of a developed nation. From bicycles

through steam travel to cars and cheap international flights, as people’s horizons have expanded, so too have the range of people they can meet and, correspondingly, friends they can make. At the same time, the likelihood that any person will remain in one place has diminished, and so the length and closeness of friendships have been undermined. This combination, of having more potential friends and a lower likelihood of remaining physically close to those friends, puts the status of any particular friendship at more risk than it would have been previously. Framed in Aristotelian terms, the already difficult to establish and build upon friendships of virtue have been getting progressively more difficult. The less valuable, although easier, friendships of pleasure and utility are correspondingly more widespread.

In psychological terms, the worry is that deep friendships offer benefits that shallow (“fair-weather”) friendships do not and that we are increasingly developing shallow friendships at the expense of deep ones, often without realizing that we have done so. Whether this concern is realized depends on the nature of our interactions in online spaces, and the science is not settled on this. Opinion remains deeply divided on whether recent technological developments are helping or hindering the development of friendships. On the one hand, retaining contact with those who one no longer lives near to is made possible by the connected nature of an Internet-enriched world. But on the other hand, the kinds of interactions one has online may not, many claim, be relevantly similar to those we have in the physical world. They may lack something crucial to (or merely helpful for) the development of friendships. Fröding and Peterson, for example, claim that online friendships are of the kind Aristotle would have described as lower order or less valuable (Fröding and Peterson 2012). McFall similarly claims that higher-order Aristotelian friendships cannot occur entirely online (McFall 2012). In these and similar objections, the presumption is that offline friendships are distinct from and superior to online friendships. This claim arises both from the Aristotelian friendship tradition and from psychological research into the strength of different types of

friendship (online, offline, and mixed). There are two features of the research that should be examined. Firstly, there is a worry about the mischaracterization of online friendships, in that friendships within particular online domains are often compared to friendships developed offline. This comparison is biased in favor of offline friendships in ways that diminish the value of online ones, as will be discussed below. Secondly, much of the research focuses on deep or higher-order friendships, at the expense of consideration of the more common kinds of friendship. This focus obscures the value of lower-order friendships, whether online or offline. Before analyzing the concerns shaping each of these approaches, the conceptual space within which the different kinds of friendship operate should be considered. Firstly, there are offline friends. These are friendships developed in the traditional manner, through interaction in the physical world. Secondly, there are online friendships, those developed in virtual spaces and online worlds. Finally, there are mixed-mode friendships, those in which the virtual and the physical world both play roles. Within this last category, the extent to which the offline and online modes of interaction occur varies dramatically.

Three Kinds of Modern Friendship

Until recently, there have been few options other than to establish friendships through the medium of the offline world. Communication with those not physically co-located was slow, expensive, or both when the available options were letter writing, telegrams, or even telephones. However, the advancement of technology and the development of the Internet have removed many of the barriers to communication between distant persons. As such, there are now three clearly distinguishable ways in which friendships can be developed. It remains possible to develop friendships offline, in the physical world. Friendships can be developed online, eschewing physical interaction. Finally, a combination of online and offline interactions can be utilized to develop “mixed-mode” friendships (Antheunis et al. 2012).

It is worth noting that friendship solely mediated in the physical world is rapidly becoming less common, as the reach of online communication tools expands, both in terms of availability and uptake. More and more frequently, friendships that begin purely offline expand into online domains, simply because virtual worlds are becoming ubiquitous. Indeed, it is increasingly uncommon for a friendship not to include online components, as a key part of the development of a friendship is, now, to connect with the friend’s online presence.

Consider a paradigmatic tale of the development of friendships for an individual. The earliest of our friends are those whom we meet and interact with when we are very young. They will be, for example, the children of our parent’s friends, if similar in age to ourselves. Otherwise, they will be our classmates from preschool or the early years of school. As people age and move from school to university, or into the workforce, they will both develop newer friendships and discard some of the old ones. Sometimes this will be intentional, as one party or the other discovers that they lack shared interests with some of their earliest friends or as their interests diverge. At other times, circumstances will separate people from these friends, as when families move away. These friendships, as described, arise solely in the offline world, and they share a common feature, that is, they are discerning. This means simply that individuals do not automatically develop friendships with all those they meet, regardless of the domain in which they meet them. One can have classmates and work colleagues who are not friends. Rather, similarity is important, as similarity enables a deeper and more meaningful connection with others. Further, both parties to a friendship need to enjoy each other’s company for a friendship to prosper. This is a mutuality requirement. Whether this is the case is discovered via engagement in shared activity. By engaging repeatedly in shared activities over time, people develop the bonds of intimacy and mutual caring which characterize deep friendships.

This description relies solely on offline interactions. Yet it is easy to see how online interactions could supplement this story, thereby leading

to an origin story for a mixed-mode friendship. It is perhaps not as easy but still relatively simple to replace the initial offline points of contact with online points of contact and from there to describe the development of a friendship that is purely online. To the extent that our behaviors in the online worlds we inhabit in our modern lives parallel those behaviors we exhibit in the offline world, the case for friendship remains the same. However, there is some reason to believe that a twofold disruption of this similarity is occurring. Firstly, geography and contact have been separated – it is now possible to maintain close connections with those who are not geographically co-located, in ways that were impossible even a generation ago. Secondly, the pace of change is now rapid, such that any status quo regarding friendship formation and maintenance behaviors is unstable. These two factors are a concern for all three kinds of friendship in modern life.

Friendships are valuable things. They influence our moral behaviors, insofar as friendships generate motivations to act toward friends that are not present toward strangers. They enhance our knowledge, in that exposure through the medium of friendship to the lives and experiences of those different from ourselves provides us with insights into these other worlds that we either do not get or do not fully understand, when we are exposed to them in other ways. So, both issues of geography and issues of technological change could seriously impact on our well-being, if these changes disrupt our modes of friendship formation, causing us to have fewer or less beneficial friendships than we previously had. However, the widespread pessimism regarding online interactions seems ill founded. There is a tendency to assume that as online interactions increasingly replace offline ones, important components of socialization are lost. After all, young people are no longer doing the sorts of things their parents did. They eschew offline social gatherings (at least to some degree) in favor of online interactions. But there is value in these online interactions, and at least some of this value is unique to the online space. In spending their social time online, people who develop true friendships in online spaces are making friendship connections with a broader and

different range of persons than are generally available to them through physical world social networks. This is more important than is sometimes recognized, as for those engaging in online activities, there are a significant number of potential friends, from a divergent range of backgrounds, societies, and situations, who would not be available as potential friends absent the online environments which enable contact with them (Munn 2012).

The above considerations are general advantages potentially accruing to those who engage in online social interactions. It is however also very important to note that there are significant advantages to the possibility of developing friendships either purely online or in mixed modes, which accrue to certain people within society. Those who for whatever reason do not conform to societal norms and expectations of behavior are offered greatly expanded opportunities for friendship in online domains. Consider the wheelchair-bound teenager, who will never be able to physically play football with others. An online community allows them to develop friendships with others based on a shared enjoyment of football, and to play football, albeit in digital form, with these others. This is not merely a means of connecting with those who the teenager could have met otherwise – those in the same offline area. It also connects them with people for whom the fact of the particular physical disability is irrelevant. If one has a reasonable expectation that they will never physically meet someone, then a physical restriction such as being wheelchair bound not only does not matter as much but also may be purely irrelevant to the development of the friendship.

It is possible to usefully divide the possible advantages offered by online friendship formation into three kinds: frequency, variety, and opportunity cost. The frequency advantage offered by online friendship formation is simply that we can have many more online friends than offline friends, as interactions with them are able to be faster, more flexible, and easier to accommodate around competing schedules. This results in more opportunities for development of these friendships. The advantage in variety arises from the availability of potential friends online. We have

a wider potential friend base online. There are no geographical constraints, as asynchronous communication renders time zones irrelevant, and the online medium eliminates the need for propinquity (Amichai-Hamburger et al. 2013). This does not mean that physical co-location ceases to play a role in friendship development. Rather, online communication serves an important role in strongly mixed friendships, with social networks being used in large part as a supplementary means of communication between people who are in roughly the same physical location, either within the same state or within the same city (Mazur and Richards 2011).

There is, importantly, a reduced emphasis online on common signals of differential social status, such as age, race, and social class, as well as a reduced emphasis on behavioral cues such as physical attributes and perceived similarity (Chan and Cheng 2004). These things are not as relevant to online friendships (or to mixed-mode friendships, although they retain more relevance in that context). As such, online friendships are distinctly valuable because they provide the opportunity for those that have them to interact with and gain knowledge of people in social settings distinct from their own, more easily than is the case without online friendship. This knowledge could be gained in other ways (as, e.g., when one befriends new arrivals from abroad), but the possibility of real friendship formation online makes such friendships more feasible for more people, more often.

Finally, the nature of online friendships is such that the opportunity cost of developing them is less than is the opportunity cost of developing offline friendships. Buote et al. note this in claiming that online friendships are perceived as less risky and easier to initiate, and that it is easier, in online environments, to present oneself as one wishes to be perceived. The asynchronous nature of communication means that those less confident in expression, or quick of thought, have the time to ensure they say what they mean, in ways that are unavailable in offline interactions (Buote et al. 2009).

Much the same expansion of opportunity has arisen across many domains of human behavior

and in ways that the offline world could not provide. Whether an individual is shy or socially awkward, or has a set of beliefs or values that is not common in their physical community, or any of a variety of other considerations, the online world provides hitherto unfathomable opportunity to discover like-minded individuals and to form relationships with them. These relationships, even if they begin online, will with some frequency become offline friendships as well. Even as far back as 2007, Cole and Griffiths found that it was very common for people to meet online friends in offline environments, with 55% of females and 38% of males reporting having met online friends in “real life” (Cole and Griffiths 2007). This is suggestive of the increasing importance of mixed-mode friendships, those mediated both through offline and online interactions, as not only are offline friendships moving into online spaces as a supplementary means of engagement, but the reverse is true. This is a component of the stimulation hypothesis, which sees the role of online communication as being to enhance existing friendships, thereby developing stronger bonds which improve the friendships (Valkenburg and Peter 2011).

It is at this point that the distinction between fair-weather friends and true friends, or between imperfect and perfect friendships, again becomes relevant. While we clearly can and do develop friendships of some kind online, it is still open to the defender of traditional (offline) friendships to claim that these online friendships are only of the lesser kind; that they are not deep or true friendships, they are imperfect. If this claim holds, then there is reason to be skeptical of online friendships, as there is a value in true friendships that is not present in fair-weather friendships, and something important would be lost if we lost this. However, it is already the case that in order for the claim to be true, it must be that many users of a broad range of online services are themselves mistaken, as they do not think that the quality of friendships offered by the online world is inferior to that offered by the offline world (Amichai-Hamburger et al. 2013).

The Capacity to Develop (True) Friendships

Recall that modern friendship is divisible into three distinct kinds: offline, online, and mixed friendships. Arguments about the capacity to develop these friendships focus on online and mixed friendships, as it is uncontroversial that we are capable of developing friendships in the physical world. We do develop them; therefore, we can develop them. The question for proponents of the possibility of developing either online or mixed-mode friendships is then the following: is there anything to distinguish between purely offline interactions on the one hand and purely online or mixed-mode interactions on the other, when it comes to developing the kinds of bonds that lead to friendships? The currently available evidence suggests that there is not, and that as such, online and mixed-mode friendships can be all that offline friendships are. Indeed, there are particular advantages that online and mixed-mode friendships appear to have over offline friendships, such that they may be in some ways superior. For instance, there is evidence to suggest that whether a particular friendship is same sex or cross sex matters less in online spaces, as sex matters less. Chan and Cheng argue that this is because the structural and normative constraints present offline have not, or not wholly, established themselves online and so are less effective in impeding the development of cross-sex offline friendships (Chan and Cheng 2004). While one can hold to the possibility of a friendship becoming sexual, the triggers for such behavior are diminished online, and the strength of the possibility is diminished also. Chan and Cheng found, for example, that under their methodology, online cross-sex friendships were stronger, or of higher quality, than were online same-sex friendships, while for offline friendships, the reverse was true (Chan and Cheng 2004). This could be because the triggers for certain breakdowns in friendship (such as the attempt on the part of one friend to change the nature of a relationship from companionable to sexual) are less available in online spaces. The Internet is, to some degree

at least, a safe environment for the development of cross-sex friendships, in ways that the offline world is not (Chan and Cheng 2004).

A distinction commonly appealed to in defense of the claim that there is a meaningful difference between offline and online interactions is that, while the offline world enables us to interact with each other and learn about characteristics such as our character and desires with some degree of accuracy, the online world does not. As such, it is claimed that we are able to trust and to make judgments on the validity of claims to friendship in the offline world, but not in the online world. The key feature of this type of argument is a reliance on shared activity: friends do things together, and it is this engagement that lets them develop the strong bonds of friendship. However, shared activity is increasingly possible in online spaces, and it is unclear there is anything special left for the offline domain. Buote, Wood, and Pratt found that online friendships provided equal levels of quality, intimacy, and self-disclosure as did offline friendships and concluded that this was evidence that online friendships were a positive and beneficial alternative to traditional friendships (Buote et al. 2009). Winning a game in your casual football league does not matter any less if the league is virtual than if it is physical (although one's intuitions may be triggered more by the reversed claim that winning a game in your casual football league does not matter anymore if the game is physical rather than virtual). That example is of a paradigmatically physical activity, but there are many shared activities for which historical expedience seems to be the only compelling reason to engage in them offline in preference to online. For example, gossiping about the activities of a mutual acquaintance is a shared activity, of the kind that builds the relevant bonds of friendship. It is not at all clear that there is any particular advantage to doing this offline rather than online, and indeed, the stereotypical precedent for this kind of activity is that of the teenage child tying up the phone line for hours on end talking with their friends, a precursor to the modern forms of interaction now under consideration.

The proponent of offline friendships may nevertheless appeal to a further characteristic of

offline interaction, namely, that it provides fewer opportunities for deception, or, conversely, it offers more opportunities for us to recognize deception when it is practiced and so to curtail the development of a friendship (upon recognition that one party to it lacks the appropriate motivations for the development of the friendship). To continue with the example of the football game, it is easy to be sure that your opponent is who they say they are when you can see them and less easy when you can only see their avatar. However, the online football game will now commonly feature both voice and video of one's opponent, such that this too is similar between the domains. That is not to claim that worries about deception are misguided. When entering into a friendship, one must be wary of deception. After all, not every person who claims to want to be your friend means it. These issues of trust and motivation are ones that we have developed an array of techniques to overcome. We rely on an array of indicators such as body language, tone, and inflection in speech in order to determine the veracity of the claims people make to us, and the usefulness of these techniques does not translate smoothly from offline to online interaction. It is much harder, in an online environment, to determine whether those we are speaking with are being truthful, whether about their desires, their motivation, or their descriptions of themselves. There is evidence that as many as a third of people deceive others when making claims online and that people believe that the frequency of online deception is higher than that (Caspi and Gorsky 2006).

Rather than denying that these issues are problematic, the defender of online and mixed-mode friendships can instead appeal to a lack of uniqueness in the problem. That is, while online interactions are vulnerable to deceptions in these ways, the vulnerabilities are, increasingly, the same vulnerabilities that offline interactions have. As the available modes of online interaction expand, and as technology improves, we are becoming better able to rely on offline cues in online spaces. Voice technology and video technology give us access to relevant information on tone, inflection, and body language. Further, what we do online has changed. We can and

commonly do engage in shared activities online, in ways that were not possible, or were not common, in the relatively recent past. Shared activity is an important tool for determining the veracity of the claims someone makes about themselves, as it is hard to sustain a deception (harder still, the more complex the deception) while under pressure to engage with others. So, in online as in offline interactions, it is difficult for participants to present the "carefully constructed self" that Cocking and Matthews claimed prevents friendship formation online (Cocking and Matthews 2000). While people develop closeness or intimacy in online settings in different ways to those they utilize offline, it does not seem to be any less fulfilling once established. It appears that, at the least, people take their online relationships to be as real, close, and important as their offline ones (McKenna et al. 2002).

So, there is a problem with discerning between true and fair-weather friendships. It used to be the case that it was significantly easier to make the relevant judgments in an offline environment than an online environment, due to certain contingent features of available online environments which rendered them inferior at providing opportunities to judge things like motivation and character. However, these contingent features have been removed or diminished by the development of new technologies and by increases in the volume and kind of information that online media transmit. So, even if for any given online friendship, the chance of it turning, with appropriate time and effort, into a genuine friendship, is less than the chance for any offline friendship, this is insufficient reason to prevent us from engaging in the attempt. There are more opportunities online, and with a wider range of people, such that at least some of the necessary preconditions of genuine friendship are more likely to be fulfilled by those one meets online than those one meets offline.

It may still be that the difficulties are greater in online than in offline friendships, but the difficulties are now recognizably of a kind with those we have historically faced when developing friendships, and they are appropriately responded to in

the same way – we factor the considerations into our behavior; we build up a body of evidence, over time and in a variety of circumstances regarding how our friends behave; and we constantly revise our conclusions regarding how strong our friendship is in light of this evidence. The capacity to develop true friendships exists both in the offline and the online world, and whether that capacity is achieved is a matter, not of the mode of interaction but of the friendships in question and the participants therein.

Maintaining Friendships

Friendships do not simply exist. Rather, they must be maintained by all parties if they are to remain robust. This requires a range of behaviors on the part of friends to continue and to develop the relationship they have, and these behaviors will be both routine and strategic (Oswald et al. 2004). The modern world has characteristics that both aid and impede this friendship maintenance. For example, it is comparatively common now to move between cities, states, or nations during the course of one's life. Each such move leaves behind the friends one has made in a particular place. Historically, such drastic upheavals with their resultant changes to friendship relations were uncommon. So we might think that modern life makes the maintenance of these life-long friendships more difficult. However, the rise of technology-mediated communication allows for the maintenance of friendships in virtual rather than physical space, in ways that were difficult or impossible in the recent past. This allows individuals to maintain friendships that would previously have had to be abandoned.

Analyses of the value of online friendships frequently fail to consider virtual worlds holistically. Rather, they examine particular subdomains of virtual space, such as Facebook, e-mail, or Twitter, and conclude that as stand-alone systems, these lack the features which enable the development of strong friendships (see Condella 2010; Vallor 2012). But these interfaces are not stand-alone systems. They are interrelated, such that one's online friendship tracks over a variety of domains

and builds upon them. The correct comparison is not "Facebook versus the physical world" but "offline versus online" or "Facebook versus the local pub." The comparison of particular online subdomains to the physical world at large is a rigged one, unfair in its choice of starting points. Facebook, for example, is an aspect of an online friendship, just as your social football team is an aspect of an offline friendship. Neither is complete in isolation. We should, in this context, consider virtual spaces to be "third places" which provide an environment of "informal sociability" in which friendships can be maintained and developed (Steinkuehler and Williams 2006). They are, in other words, serving the function that pubs and coffee shops serve, but doing so online.

This characterization of online spaces points to a key benefit of online interaction. Online interactions enable the maintenance of friendships in the absence of continued physical interaction. Whereas previously an old college friend who moved abroad to study or teach at a different institution would have fallen out of touch with you (or at the very least have had significantly fewer opportunities to maintain contact and had these opportunities only in a very limited set of ways), they are now able to maintain a broad and frequent range of interactions. While you may now go years without being physically co-located, you have a preexisting friendship relationship and an understanding, dependent on the quality of your friendship, of the friend's character, motivations, and goals. A sudden flurry of Facebook activity might mean that your friend is compensating for something that has occurred to them in real life, perhaps homesickness, and you can address your enquiries to this end. Without the knowledge formed through the offline relationship, this option would not be available, but without the online medium, you would no longer be in a position to know that your friend has these concerns. By maintaining offline relationships in online environments, that is, by turning these friendships into hybrid or mixed-mode friendships, you are able to keep in closer contact with your friends through social media and other online communication than was previously possible.

Conclusion

The rapid pace of technological change in modern life has introduced many significant difficulties for conceptions of friendship. The standard means of the development of friendships, namely, through interaction with potential friends in the offline world, have been supplemented by a hybrid interaction involving both offline and online interactions, and by a set of purely online interactions, entirely divorced from the offline world. Thus, we now have three means to friendship, rather than one. This expansion has been contested, in the first instance, by those who claimed that there was something unique about the offline world such that friendships could develop therein but not develop in the online world and in the second instance by those who claimed that there was something superior in a friendship developed offline. The best available candidate for uniqueness in offline friendships arises from a distinction between kinds of friendship, which is found across the range of academic disciplines in which friendship is discussed, beginning with Aristotle, who distinguished between higher-order friendships of virtue and lower-order friendships of utility and pleasure, and present through to modern psychology, where David Buss distinguishes between fair-weather friendships and deep/true friendships. The idea is that offline friendships offer opportunities to develop the strong kinds of friendship, which are absent in online friendships. However, even this claim to uniqueness is undermined by the evidence of friendship development in hybrid and purely online environments. At best, it seems as though it may be somewhat easier to develop true friendships in the offline world than it is via online interactions alone. In such a situation, hybrid friendships appear superior to either offline or online friendships, in the sense that they offer a higher chance of developing into true/deep friendships.

The standard view overstates the value of offline friendships, as most do not result in these strong friendships that are so desirable. It is as yet unclear whether the optimal approach to friendships involves concentrating on success rate or total number of successes, where success equals

the development of a higher-order friendship. It may well be that the success rate of offline friendships is higher than that of online friendships, even significantly so. However, online friendships are sustainable in much greater numbers, and it may be that mixed-mode friendships offer both a higher chance of development into deep friendships, and are available in larger numbers, than are offline friendships (although these would still be available in smaller numbers than are purely online friendships).

There is also a tendency in the literature to worry about the extent to which online friendships are replacing offline friendships. This concern appears misguided; as for most people, friendships are maintained in large part online but are formed offline; thus, they are mixed-mode friendships. In supplementing offline friendships with online components, and in meeting online friends in the offline world, mixed friendships are replacing both. Further, as online interactions become ubiquitous, the argument threatens to resolve itself, simply by transforming all our interactions into technologically mediated ones. As people age in the presence of online environments, relationships formed or maintained in them will become more common, less surprising, and more accepted.

Cross-References

- [Absence of Events to Distinguish True Friends](#)
- [Altruism Defined by Benefits Conferred](#)
- [Fair-Weather Friends Versus True Friends](#)
- [Friendship](#)

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Friendship Groups

► Peer Groups

Friendships

- Absence of Events to Distinguish True Friends
- Peer Relationships in Childhood
- Same-Sex Friendships
- Same-Sex Relationships

Frights

► Fears

Frontal Cortex

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Synonyms

Anterior cerebral cortex; Frontal lobe; Pallium; Pre-frontal cortex

Definition

The frontal cortex is the anterior portion of the neocortex, and select structural and functional

differences exist across species. The frontal cortex serves many complex cognitive, social, and language functions, such as complex sequence learning and self-control.

Introduction

Given the complexity, sophistication, and relative dominance of humans compared to other primates and mammals, a common question has been: *What gave humans the evolutionary advantage?* The answers are clearly not superior strength, speed, endurance, or physical size. The answer is commonly assumed to be that human intelligence and exceptional communication skills underlie human dominance. Thus, comparative studies have focused on differences in brain sizes, structures, and functions as probable explanations for human dominance.

The frontal cortex, in particular, is thought to underpin these comparative differences. In humans, the frontal cortex is the largest lobe of the neocortex and is commonly assigned primary responsibility for many complex cognitive functions (e.g., complex problem-solving, and thinking about thinking) and language functions (e.g., symbolic representations of abstract concepts and future scenarios and subtle social messaging; Badre 2008; de la Vega et al. 2016). From an evolutionary or phylogenetic perspective, the frontal cortex is considered the most recently developed brain region (Teffer and Semendeferi 2012). Similarly, from a developmental or ontogenetic perspective, the frontal cortex is one of the last brain regions to reach full maturity (Johnson et al. 2009). This combination of features suggests that the frontal cortex, in particular the prefrontal cortex, is one of the most important brain structures that separates humans from other primates (Teffer and Semendeferi 2012) and may, in large part, account for the human evolutionary advantage.

Frontal Cortex Anatomy

In the human cerebrum, the frontal lobe lies anterior to the central sulcus, superior (on the lateral

surface) to the Sylvian fissure, and superior (medially) to the eyes and nasal cavity. Major sections of the frontal cortex include the inferior, middle, and superior (lateral) gyri and the orbitofrontal (medial) gyri. The frontal cortex also can be subdivided according to its cytoarchitectural organization (i.e., cellular tissue).

German anatomist Korbinian Brodmann developed a cytoarchitectural brain map with 52 topographical subdivisions of the human neocortex identified with numerical Brodmann Area (BA) labels (Verkhatsky 2006). The frontal cortex includes several major cytoarchitectural regions. The precentral gyrus or primary motor cortex (BA 4) is anterior to the central sulcus. The adjacent, anterior section includes the supplementary motor cortex (superior and medial, BA 6), the premotor cortex (lateral middle BA 6), and Broca's language production area (BA 44; Caplan 2006). Anterior to these latter regions is the prefrontal cortex (PFC) which represents a cytoarchitecturally diverse set of subregions (Murray et al. 2016; Petrides et al. 2012) including the dorsolateral PFC (BA 9 and 46), medial PFC (BA 25 and 32), and orbitofrontal cortex (BA 11, 12, 13, and 14). The anterior tip of the frontal cortex is the frontopolar cortex (BA 10).

Note, the frontal cortex does not function in isolation. It is structurally interconnected into functional networks with other brain regions. These networks support several adaptive functions (Jung et al. 2017; Medaglia et al. 2015; Racz et al. 2018; Smith et al. 2013).

Evolutionary Structural Comparisons

Comparing brain structures across species (or phylogenetic classes, orders, families, or genera) is not a simple matter. One common method is to compare overall (or region-specific) brain size relative to body size within the same clade (or genetic lineage; Sherwood and Smaers 2013). Certainly, the human brain is substantially larger than that of other primates, and human heteromodal association areas (which assess and integrate multiple forms of sensory or motor information), such as the frontal cortex, account for

much of this proportionately larger size (Sherwood and Smaers 2013; Verendeev and Sherwood 2017). Some researchers argue that the frontal cortex has expanded disproportionately more than other cortical regions (Sherwood and Smaers 2013; Passingham and Smaers 2014); others disagree (Barton and Venditti 2013; Gabi et al. 2016). Evidence suggests that select areas of the frontal cortex (e.g., frontopolar cortex, BA 10) are larger in humans than other primates, while other areas (e.g., primary motor cortex, BA 4) are not (Sherwood et al. 2012). Thus, humans likely show phylogenetically based volumetric differences in specific frontal cortex regions.

Phylogenetic differences also are evident in the distribution and density of brain-cell types. Research reveals that the frontal cortex of humans has a lower neuron cell-body (gray matter) density and higher dendrite, axon, and synapse density than that of the great apes (Sherwood et al. 2006). Humans also have the highest ratio of glial-to-neuron cells in the dorsolateral cortex (BA 9) relative to the 17 other primate species in their homologous (structurally equivalent) brain regions (Sherwood et al. 2006). In the human brain, glial cells (white matter) are as numerous as neuron cells (Azevedo et al. 2009), and emerging evidence indicates that glial cells serve higher cognitive functions not merely neuron-support functions (Han et al. 2013). These differences in cellular structures are hypothesized to reflect greater intracortical connectivity in humans compared to other primates (Verendeev and Sherwood 2017).

Evolutionary Functional Comparisons

Investigating functional differences across diverse species is quite challenging (Wilson et al. 2017). The investigations require measures which can be performed by creatures with very different physical capabilities and perceptual systems (e.g., birds, rodents, dogs, elephants, and primates), while representing comparable underlying information processing demands. Below we identify two measurement designs and core functions

which reveal phylogenetic differences in frontal cortex functioning (MacLean et al. 2014; Wilson et al. 2017).

The first measurement design represents sequence learning or the recognition of patterns (e.g., expected sequences of sounds, images, or multimodal experiences; Wilson et al. 2017). Once a species has recognized and learned a sequence, they respond in a predictable manner. If new events violate the learned pattern, adaptive and observable behavioral and neural changes are expected. If a species does not show a change to pattern violations, this lack-of-change implies that the creature did not detect (i.e., learn) the pattern.

A systematic evaluation of sequence learning across primate families and subfamilies shows distinct phylogenetic differences in select regions of the frontal cortex (Wilson et al. 2017). For example, various primate families show comparable sequence learning and comparable frontal operculum activation during certain sequences (e.g., temporally adjacent events). This comparability has been interpreted as an evolutionarily conserved function across primates including humans. In contrast, more complex sequence learning (e.g., temporally separated but associated events) is not evolutionarily conserved. Humans show unique complex sequence learning and dorsal PFC (ventrolateral - BA 44 & 45 and dorsolateral - BA 46 & 9) responses not shown in other primates. Wilson et al. (2017) highlight the link between human language processing and the complex learning sequences. They suggest that the dorsal PFC responses support the unique human capacity for advanced language function compared to our primate ancestors.

The second measurement design, which supports across-species comparisons and links to frontal cortex function, represents self-control (Herculano-Houzel 2017; MacLean et al. 2014). This design requires each species first to demonstrate a reward-action response (e.g., observing and retrieving hidden food). Next, for the test trial, the reward is moved to a new location, and the species must avoid searching in the previously rewarded location (e.g., an A-not-B task; MacLean et al.

2014). Thus, the test trial demands self-control and the inhibition of the previously learned (prepotent) response. The number of neurons in the cerebral cortex (or pallium in birds) has predicted across-species, task-performance differences (Herculano-Houzel 2017). For example, great apes with the largest number of cortical neurons performed the best on this self-control task. These results support an evolutionary model of phylogenetically advanced frontal cortex development.

Other Potential Evolutionary Frontal Cortex Functions

Above we presented strong comparative evidence for the evolution of the frontal cortex and select functions. Noncomparative human studies suggest the frontal cortex supports several other evolutionarily relevant functions. For example, a recent study reported that the PFC was activated significantly in response to moral violations between genetically related sisters unlike adoptive, non-genetic sisters (Bacha-Trams et al. 2017), which is consistent with evolutionary models suggesting greater resource allocation among genetic relatives (kin).

The PFC also is associated with risk-taking (Ernst et al. 2006). Risk-taking supports evolutionary functions such as exploration and competition for resources and sexual mates, but excessive risk-taking will undermine survival and reproduction. A recent study illustrated the link between PFC function and sexual risk-taking behavior (Goldenberg et al. 2013) revealing that adolescents reporting risky sexual behavior (i.e., reduced contraception use) showed reduced PFC engagement during a response inhibition task (Goldenberg et al. 2013).

The PFC also plays an important role in determining the motivations and intentions of others (i.e., mentalizing or “mind reading”) as part of a larger network of brain regions (Van Overwalle 2011). The ability to mentalize supports improved prediction of others’ actions which has individual survival and reproduction implications.

Furthermore, Hare (2017) presented comparative evidence that mentalizing underlies inter-individual cooperation and collaboration, which enhances group-level survival and reproduction.

Future Directions

The comparative studies above focus on between-species response differences, while the human studies focus on within-species diversity. Evolutionary insight will be enhanced by incorporating both forms of diversity in future investigations. Given that more neurally complex species likely exhibit greater within-species response diversity than less neurally complex species, we suggest that phylogenetic differences in the structure and function of the frontal cortex will prove relevant to future comparative studies of within-species response diversity.

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Brain Development](#)
- ▶ [Cognitive Science](#)
- ▶ [Evidence of Brain Modularity](#)
- ▶ [Evolution of the Brain, The](#)
- ▶ [Human Brain Evolution](#)
- ▶ [Implications of Object Permanence](#)
- ▶ [Inhibition](#)
- ▶ [Learning](#)
- ▶ [Neurons in the Cerebral Cortex](#)
- ▶ [Object Permanence](#)
- ▶ [Psychology](#)
- ▶ [Relative Brain Size, Encephalization Quotient](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)

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Frontal Lobe

► Frontal Cortex

Frugivory By-Product Hypothesis

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Synonyms

Alcohol; Fermentation; Taste preferences

Definition

As ethanol provides cues to fruit ripeness, the human penchant for consuming alcohol may be a by-product of adaptive fondness for ripe fruit.

Introduction

Alcohol pervades most, if not all, human cultures, and its consumption is regarded as a desired accompaniment to a wide variety of activities. From serving as a social lubricant to playing a role in addiction, many researchers have taken an interest in studying how alcohol is consumed and the consequences of that consumption, resulting in an impressive literature on alcohol. More elusive, however, are explanations for why humans as a species consume alcohol at all despite its significant toxicity (Brooks 1997). The current entry describes the hypothesis put forth by Dudley (2000) that alcohol (ethanol) tolerance and consumption may have emerged as a by-product of our ancestors' adaptive penchant for ripe fruit.

The Evolution of Frugivory Diets

According to fossil records, hominoids have historically survived on a diet consisting

mainly of fruits and plants (Andrews 1981). As descendants of the hominoid line, all modern apes, including humans, are similarly adapted for frugivorous diets. Primates such as the lowland gorillas, orangutans, and chimpanzees have all been observed to consume a wide range of fruits in copious amounts (Rodman 1977; Tutin et al. 1991).

Fruits offer the highest dietary benefits when they are ripe. When fruits ripen, a variety of changes occur. Starch is converted to sugar, resulting in a hike in sugar concentration levels and an increase in sweetness. Frugivores are adapted to find the sweet taste of sugar palatable, which then motivates them to seek and consume fruits particularly when those fruits are in a ripened state where caloric and nutritional content is highest. Other biochemical processes that occur during ripening, such as changes in acidity, color, aroma, and texture (Dudley 2004), also entice frugivores' consumption of ripe fruits. In return, frugivores aid fruits and plants in seed dispersion through a mutually beneficial coevolutionary process. Indeed, fruits that are unripe and carry seeds that have yet to mature have chemical and physical safeguards to prevent untimely consumption by frugivorous seed dispersers (Benner et al. 2002).

Ripened fruits, however, are not always accessible or available, especially in tropical forests where harsh or sporadic weather patterns can hinder fruit development (Leigh 1999). Coupled with intense competition between species of frugivores for scarce ripe fruit, frugivores evolved to be extremely competent foragers. It has been argued that the advanced cognitive and visual capabilities of frugivorous primates are attributable to the selection pressures brought on by the desire for ripe fruit (Milton 2006).

Alcohol Consumption as a Byproduct of Frugivory Diets

Noting the adaptive challenge of acquiring and consuming ripe fruit, Dudley (2000) surmised that frugivores likely evolved to exploit cues

that could facilitate the acquisition and intake of optimally ripe fruit. Fermentation occurs during fruit ripening, which is a complex biochemical process whereby yeast feeds on sugar and produces ethanol. Through fermentation, the odorous plumes of volatile ethanol that emanate from ripe fruit may serve as far-ranging olfactory signals for frugivores. Moreover, ethanol has a distinct taste, which can serve as an additional indicator of ripeness alongside the fruit's sweetness. Thus, utilizing the smell and taste of ethanol enables frugivores to predict a fruit's caloric value (Singh 1985), and frugivores that could detect the odor of fermenting fruit from afar also had a better chance of acquiring the nutrition and calories needed for survival.

Furthermore, as fruits that are optimally ripe are likely to be seized and consumed quickly, many frugivores have to settle for leftover over-ripe fruits that contain substantial amounts of ethanol (Dudley 2004). When metabolized, the caloric content of ethanol is estimated to be 7.1 kcal/g, which is actually higher than that of carbohydrates. As some ethanol consumption may have been unavoidable and ethanol can also provide a source of nutritional supplement, frugivores possibly evolved to be somewhat tolerant of ethanol's toxicity. As descendants of early hominoids who may have evolved to be amenable to ethanol as a by-product of pursuing frugivorous diets, humans may likewise be adapted to not only tolerate the toxicity of ethanol but also have a taste for it.

Conclusion

The frugivory by-product hypothesis suggests that alcohol consumption in humans and our subsequent fondness for the substance may originate from our frugivorous ancestral heritage. Through selection pressures borne from the need to acquire nutritious food sources, frugivores may have evolved to respond favorably to ethanol in order to find and consume ripe fruit. Patterns of alcohol use by humans in contemporary environments may therefore reflect a co-option of ancestral nutritional strategies,

specifically the adaptive sensory biases that lead frugivores to associate ethanol with nutritional reward.

Cross-References

- [By-Products of Adaptations](#)
- [Food Preferences](#)

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Fuck Buddies

- [Casual Sex](#)

Full Sibling

► Siblings

Full Siblings Versus Half Siblings

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Synonyms

Genetic relatedness; Sibling relationships

Definition

Full siblings share the same biological mother and father, maternal half-siblings share the same mother only, and paternal half-siblings share the same father only. Therefore, full siblings share, on average, 50% of their genes with one another and half siblings share approximately 25%. Because individuals share more genes with their full siblings than their half siblings on average, full siblings are predicted to invest more in each other compared to half siblings. By investing in full rather than half siblings, individuals can more effectively increase their own inclusive fitness.

Introduction

Individuals tend to invest time and resources in their kin. Evolutionary researchers have explained this by inclusive fitness theory (Hamilton 1964), which assumes that the degree of genetic relatedness is associated with the investment directed

towards relatives. Individuals share approximately 50% of their genes with full siblings and 25% of their genes with half siblings. Therefore, according to inclusive fitness theory, individuals should invest more in their full siblings than in their half siblings.

Sibling relationships do not, however, include only altruistic support but also competition and conflict (Tanskanen et al. 2017). Sibling conflicts may reflect competition over parental resources and are most common during childhood and adolescence when parental investment matters the most (Salmon and Hehman 2014). Conflicts may especially occur when siblings are the same gender and the age difference between the siblings is moderate (Pollet and Hoben 2011). Although conflicts between siblings can also occur in adulthood, adult siblings typically provide resources and emotional help to one another, meaning that adult siblings often form social support systems (Pollet and Hoben 2011). In this entry, we consider relationships between full siblings and half siblings from an evolutionary perspective and take the ambivalent nature of this social tie into account.

Cooperation Between Full and Half Siblings

An increasing number of studies show evidence for the inclusive fitness theory prediction that the degree of genetic relatedness will influence the investment that individuals direct towards their kin among humans and nonhuman species (Salmon and Shackelford 2011). Moreover, studies have shown that the degree of genetic relatedness may play an important role in sibling relationships in different populations (Pollet and Hoben 2011). Full siblings can be favored also in situations where cultural values are against preferring full siblings at the expense of half siblings exist in the population (Jankowiak and Diderich 2000).

In terms of half sibling relationships, an important difference exists between maternal and paternal half siblings. In modern Western societies, children tend to stay with their mothers if the parents separate, meaning that maternal half

siblings are more likely to be raised together than paternal half siblings. Since maternal half siblings often spend their childhood in the same household with each other, they may have more shared life experiences than paternal half siblings who have often spent their childhood in different households. Evolutionary psychologists have identified two human kin detection mechanisms in the case of human siblings that may both typically exist in the case of maternal half siblings, but not in the case of paternal half siblings. These are maternal perinatal association (e.g., seeing one's own mother nurse another child), which is a cue that can only be used by older siblings, and childhood co-residence duration (Lieberman et al. 2007). Therefore, one may assume that maternal half siblings have better relationship quality than paternal half siblings.

Consistent with this assumption, studies have found that maternal half siblings tend to be closer to each other than paternal half siblings (Pollet 2007; Tanskanen and Danielsbacka 2014). Moreover, unequal parental treatment as perceived by the children could mediate the sibling relationship quality between maternal half siblings and full siblings (Danielsbacka and Tanskanen 2015).

The relationship quality between full and half siblings can also be extended to siblings' children. Individuals share an average of 25% of their genes with full siblings' children and 12.5% of their genes with half siblings' children. The inclusive fitness theory predicts that more investment should be directed towards nieces and nephews via full siblings than nieces and nephews via half siblings. Consistent with this prediction, a previous study found that individuals have more contact with their nieces and nephews via full siblings than via half siblings (Tanskanen and Danielsbacka 2014).

Qualitative differences in full and half sibling relationships have also been found among non-human species. Holmes and Sherman (1982) investigated Belding's ground squirrels where the female offspring tend to live in the same nest with both their full and half-sisters. In this species, female full siblings have been found to be more cooperative and less antagonistic towards one another compared to female half siblings.

Conflicts Between Full and Half Siblings

Evolutionary researchers have explained conflicts between siblings by the sibling conflict hypothesis, which is an extension of the classic parent-offspring conflict theory by Trivers (1974). Based on this theory, parents are expected to invest as many resources as necessary to guarantee their offspring's survival. In terms of parents' fitness benefits, the optimal level of parental investment in any particular offspring is related to the parents' ability to provide investment in either this offspring or others. From a parental perspective, investing all resources in only one offspring may not be the most evolutionary beneficial strategy. At the same time, offspring are "programmed" to acquire as much parental investment as possible, even at the expense of the resources that his or her siblings receive. This is because the child is 100% related to himself or herself but only 50% related to his or her full siblings (if the child does not have a monozygotic twin).

According to the parent-offspring conflict theory (Trivers 1974), siblings are predicted to compete with each other over parental investment, creating conflicts between siblings. Sibling competition ranges from small disagreements to aggressive interactions including fights and even siblicide. Siblicide is more common in birds (Mock and Parker 1997) but rare in most mammals, including humans (Hudson and Trillmich 2008). In contemporary human populations, less than 2% of all homicides are found to be siblicides and siblings are more likely to kill a third party together than each other (Daly and Wilson 1988). However, milder conflicts and disputes between siblings can be defined as a natural part of sibling relationships across human populations (Pollet and Hoben 2011).

The degree of genetic relatedness is assumed to be associated with conflict occurrence in that the degree of relatedness increases the probability for decreased conflicts (Salmon and Hehman 2014). This means that half siblings should have more conflict than full siblings. Consistent with this prediction, toddlers who are living in the same household with their full siblings only have been found to have a lower likelihood of injuries

compared to toddlers living with both full and maternal half siblings (Tanskanen et al. 2015). However, a set of previous studies has shown that contrary to this prediction, full siblings tend to have more conflict with each other than half siblings (Salmon and Hehman 2015; Tanskanen et al. 2016; Tanskanen et al. 2017). These findings have been explained by the diluted competition model (Tanskanen et al. 2017). Full siblings compete over the investments of the same two parents, but half siblings have another parent who may invest resources in him or her. This means that the investment received from the nonresident parent may dilute the sibling competition among half siblings.

Conclusions

Relationships between siblings can last for a lifetime, making sibling ties the longest-lasting social bonds in the course of human life (Cicirelli 1995). However, although siblings form important social ties and support systems, conflicts are also a built-in aspect of sibling relationships. In this entry, we have considered sibling cooperation and conflict while taking genetic relatedness into account.

According to previous evidence, important differences are apparent in full and half sibling relationships. Full siblings tend to have more contact and tend to be emotionally closer with each other compared to half siblings. These findings are consistent with the inclusive fitness theory, which assumes that when the degree of genetic relatedness between individuals increases, so does the relationship quality between them. Full siblings are also found to have more conflicts with one another compared to half siblings. This finding can be related to diluted competition. Based on the fact that half siblings can often receive investment from a nonresident parent, full siblings typically compete for the investments of the same two parents.

Studies have also shown qualitative differences between maternal and paternal half siblings. Maternal half siblings are found to have closer relationships to each other compared to paternal half siblings. In contemporary societies, children

usually stay with their mothers if the parents divorce, meaning that maternal half siblings typically spend their childhood in the same household. In contrast, paternal half siblings are more likely to live in different households. Therefore, the differences in maternal and paternal half sibling relationships could be related to human kin detection mechanisms that are based on childhood co-residence duration and maternal perinatal associations.

To conclude, studies have shown that genetic relatedness tends to shape sibling relationships. However, longitudinal studies are needed to investigate how relationships between full and half siblings change over time and if any differences emerge in these changes based on genetic relatedness.

Cross-References

- ▶ [Half-Siblings in Human Evolutionary History](#)
- ▶ [Presence of Siblings](#)
- ▶ [Sibling Conflict](#)
- ▶ [Sibling Studies](#)
- ▶ [Siblings](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)

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Function of Adoption

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Synonyms

Adaptation; Alloparenting; Family; Nepotism

Definition

What is the purpose of caring for children who are not one's biological children?

Introduction

On the surface, adoption is something of a paradox from an evolutionary perspective as it appears to run counter to the evolutionary principle of passing on copies of one's own genes as one instead invests time and resources into other people's offspring (Hamilton 1963). However, adoption is nearly ubiquitous across known cultures, suggesting that it might have some evolved component (Silk 1990; Volk 2011). Indeed, adoption appears to serve multiple functions that can be adaptive or maladaptive, depending on the contextual point of view. In particular, it can serve as an altruistic parental substitution, a form of kin support, or as a form of social networking.

Altruistic Parental Substitution

The most widely familiar modern function of adoption is as an altruistic substitution for biological children, typically due to infertility or child mortality (Volk 2011). Under these circumstances, parents are strongly motivated by a (potentially innate) desire to raise children, but do not have any biological children of their own to whom they can apply this motivation. In modern society, such parents are typically of Western descent and are wealthy, educated, older (late 30s to early 40s), and highly motivated to care for a child (Hamilton et al. 2007). Thus, this form of adoption is an attempt to replace biological parenting with a socially equivalent parenting of a typically unrelated child. The adaptive function of this behavior is questionable as it typically does not translate into the transmission of one's genes. Instead, it may represent a mismatch between an adaptive, evolved desire to have a biological child and the inability to do so.

Interestingly, parents who adopt unrelated children are often keenly motivated to create the

social and psychological impressions of relatedness and incorporation into their kinship circle (Howell 2003, 2006). This further reinforces the hypothesis that the function of this kind of adoption is to replace biological children with distantly related or unrelated children (Silk 1990). Indeed, among some societies, childlessness is viewed as immoral, leading wealthy infertile women to choose to adopt a child to maintain the social structure of motherhood (Talle 2004). Sometimes this adoption occurs despite the protests of the biological mother, whose husband forces the exchange of their child for material gains (e.g., a cow; Talle 2004). This form of parental substitution may not be as altruistically motivated given the social pressures associated with the decision.

Traditionally, adoption of unrelated children in modern societies has been viewed as a mix of risk factors. While adopting parents are often well equipped mentally and economically to adopt a child, adopted children typically have a higher risk of preexisting developmental issues (Palacios and Brodzinsky 2010). The latter can potentially lead to more negative outcomes. Interestingly though, in Western societies, the drive to provide optimum care for all children can actually lead parents to provide more resources to their adopted versus their biological children (Gibson 2009). While this appears to be maladaptive behavior from an evolutionary point of view, it is likely motivated by the same mechanisms associated with parental solicitude that initially resulted in the desire to adopt and that respond more vigorously to the typically greater needs and poorer outcomes of adopted children in Western countries (Gibson 2009). In contrast, in non-Western countries where parental resources are scarcer, adopted children typically receive fewer resources than biological offspring (Silk 1990).

Kin Support

Another function of adoption is kin selection, or the support of individuals who share related genes. Evolutionary theory suggests that parents should invest in related children so long as the cost to themselves (i.e., their own genes) is offset

by the benefit to the shared genes in the related children (Hamilton 1963). So from a crude evolutionary point of view, it is worth sacrificing 1/5th of one's time and energy to raise a niece or nephew who shares 1/4th of one's genes. Thus the degree of support provided to adopted children in this context likely depends on how closely they are related (e.g., a niece vs. a second cousin) and how costly the investment will be to the adopting parent(s) (e.g., if they don't have any children of their own, then the costs will be lower and the benefits greater; Rawson 2003). Even in modern contexts where the primary motive is altruistic parental substitution, the success of an adoption is based on kinship networks of support (Johnston 2012), highlighting the role of kin in any adoption process. The critical role of human nonparents as alloparents who support the upbringing of most children (Hrdy 2009) makes it a very small leap from many adults providing some alloparental care to some alloparents providing all of the parental care (i.e., adoption or fosterage).

The most likely circumstances for this form of adoption are when one or both of the parents die (Halbmayer 2004), a not uncommon event in the evolutionary past (Volk and Atkinson 2008). Particularly in an evolutionary context, children without their parents (and especially without their mother) face greatly increased levels of mortality (Sear and Mace 2008). Under these circumstances, the related adopting parent enables the survival of the related child (a large benefit) for a relatively modest cost (a smaller cost than birthing and raising one's own child – particularly if the child is older). This is likely a relatively ancient pattern of behavior (Hrdy 2009) as chimpanzees have been observed to adopt younger siblings if they are maternally related (Hobaiter et al. 2014).

Further, in humans, this function of adoption is not limited to orphaned children as it may also apply to children whose biological parents lack the mental, emotional, and/or economic means of caring for them (Volk 2011). This pattern is commonly observed in fosterage systems (caring for the child of a living parent) where children are placed in the care of a related individual (Scelza and Silk 2014). In North America, just under half

of all adoptions are by kin who are supporting children with a living parent (Stolley 1993) while 31% of fostered children are raised by kin (Testa 2004). These numbers might well be higher as many families rely on informal systems of adoption and fosterage to support ill-equipped biological parents. This too is a relatively ancient practice, as it is fairly widely practiced among hunter-gatherers and agriculturalists (Alber et al. 2010; Silk 1990; Volk 2011). It was also extensively practiced in seventeenth-century Europe when poor parents gave up their children to wealthier relatives with the hopes of eventually being able to reclaim them under better economic conditions (Cunningham 2005). Similar practices were common in Brazil until recent times, leading to tragic modern scenarios where some mothers give up their children for others to raise only to find that when their economic circumstances have improved, the government no longer allows them to reclaim their children (Fonesca 2004). Overall, these patterns of kin adoption or fosterage allow broader family networks to adaptively pool their resources in order to optimize their investment in the next generation.

Perhaps the most dramatic example of kin support fosterage comes from the Baatombu of Northern Benin. Traditionally, almost all Baatombu children were raised by relatives other than their biological parents (Alber 2003; Alber et al. 2010). Boys were raised by male relatives and girls with female relatives, with the father's side of the family getting the firstborn, the mother the second, etc. (Alber 2003). Interactions between the birth parents and their children were strongly discouraged in order to maintain the adopted kin structure. The Baatombu believed that this served two important purposes. First, it promoted child survival by ensuring that only adults with sufficient resources were entrusted with raising a child. Second, it promoted within-family solidarity by reinforcing the kin network by sharing its most precious resources – their children. So a process of kin selection is reinforced not only by increased child survival and thus shared genetic transmission, but also by using adoption to build stronger familial social networking.

Social Networking

This kind of social networking represents the third potential form of adoption and is the most prevalent function of nonkin adoption among many traditional cultures. Typically, it serves to reinforce social bonds and/to provide additional resources to the adopting family.

In the case of resources, children are valued primarily for their current and/or future capacity for labor. A typical example would be for economically poor biological parents to exchange their child for resources with wealthy and/or elderly fostering parents (Kirkpatrick and Broder 1976). The benefit to the latter would be the free labor provided by the adopted child. While this is to a degree a form of childhood servitude, most cultures enforce rules on how adopted children are to be cared for and treated (Talle 2004; Testa 2004). If the adopting parents violate these rules, then the biological parents can cancel the contract and reclaim their child. Thus, it is typically a reciprocal agreement whereby poor biological parents get much-needed resources and are relieved of the costs of raising a child while wealthy/elderly adopting parents are able to translate material resources into labor outside of a free-market economy.

However, there are some potential variations to this theme. For example, among the Ifaluk of the Western Caroline Islands, wealthy individuals give away their biological children to poorer adopting parents (Betzing 1988). This does not appear to be a form of reciprocal altruism. Rather, it appears to be an effort by elites to translate their economic and social power into parasitic brooding. That is, the biological parents force less powerful adopting parents to bear all of the costs of raising the adopted child without offering any benefit in return. While perhaps morally dubious, this does offer powerful individuals a means of increasing their potential reproductive success by dramatically passing off the costs of raising their biological offspring to unrelated individuals.

The final form of social networking that was common among nonkin was adoption as a form of alliance creation or maintenance (Volk 2011). The general idea in this context is that if an individual

raises another person's child, then the biological parent has a vested interest in the success and well-being of the adoptive parent as they are responsible for raising their biological child. Many native North and South American groups used adoption as a means of ending blood feuds as well as integrating captive children into their new groups (Volk 2011). Similar practices were observed among other violent hunter-gatherer groups that practice blood feuds (e.g., New Guinea Highlanders). The practice was also quite common in historical cultures ranging from ancient Rome to medieval Europe to late Imperial China (Cunningham 2005; Hsiung 2005; Rawson 2003; Volk 2011). In all of these cases, kin selection was used as a tool for both reducing tensions and violence between groups and promoting new social networks by offering one's children as a guarantee for one's social cooperation and against one's use of violence. It has also been used by some cultures as a means of fostering marriage arrangements (Volk 2011). This can either be through exchanging children who are to be later married or by adopting a child who is meant to serve as a future wife when they are older (Halbmayer 2004).

Conclusion

Adoption is a complex behavior that has roots in both reciprocal altruism and in kin selection. It is a flexible tool that can serve one or both functions within or outside of family networks. From an evolutionary perspective, it is a small leap from a general propensity for alloparenting to a more intensive investment in adopted or fostered children. The sheer versatility of the functions of adoption and fosterage suggests it is an ancient and fairly ubiquitous means of promoting individual and familial evolutionary fitness. It is ironic that the most familiar form of adoption in modern Western society is perhaps the least evolutionarily motivated and viable function of adoption (altruistic parental substitution). Yet it is perhaps the most socially altruistic expression of the evolved human desire to protect, care for, and spend enormous time and emerging raising biologically unrelated relatively helpless infants and

children. Overall, the adaptive and maladaptive functions of adoption clearly reinforce Hrdy's assertion (2009) that humans really are the most social and alloparental ape.

Cross-References

- [Adoption Preferences](#)
- [Consolidating Familial Power](#)
- [Evolutionary Paradox: Adoption](#)
- [Forms of Adoption](#)
- [Resemblance](#)

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Function of Dominance

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Synonyms

Power; Prestige; Social status; Status

Definition

Dominance describes a method for obtaining status, involving priority access to limited resources through the use of fear and coercion.

Introduction

Dominance reflects a strategy in which intimidation and force are used to achieve high status within a group. Leadership, in this case, is attained through fear and maintained through deference that is coerced, rather than freely conferred (Case et al. 2018). An alternative strategy for achieving status is prestige, in which deference is freely granted toward an individual who displays competence and knowledge in valued domains (Henrich and Gil-White 2001). Positions of prestigious leadership are maintained through contributions toward the well-being of the group, personal sacrifice, and maintenance of positive social relationships with subordinates. The fact that both routes are successful for achieving status implies that there should be contextual determinants of the effectiveness of each strategy. Particularly in cases in which assertive, forceful action can lead to the greater accumulation of scarce resources or neutralizing threats posed by a competing group, dominance-based strategies should be more functional than prestige-based strategies.

Characteristics of the Hierarchy

The time course over which social influence within a group emerges has important implications for the relative function of dominant traits in attaining status. Within a specific competence domain of critical importance to a social group – for example, hunting skills in a subsistence economy – high status may emanate from demonstrably superior skills and success. However, in newly formed or less cohesive groups, where casual or shorter-term interactions are the norm, there is much less opportunity for group members to evaluate individual variation in competence in critical

domains. In such cases, motivated individuals can achieve influence through the expression of dominance behaviors because, in the absence of evidence to the contrary, their assertive and forceful nature is assumed to derive from actual superiority—despite the lack of evidence for actual competence (Anderson and Kilduff 2009). Once the group becomes more established or cohesive, however, influence may shift toward individuals who are more skilled in that particular domain.

The distribution of resources within a hierarchy may provide another avenue for dominant individuals to attain influence. Unequal access to resources, in which benefits accumulate at the top of the hierarchy, creates competition for leadership roles. Hierarchies characterized by high levels of inequality, therefore, should favor individuals expressing dominance behaviors because such strategies facilitate the monopolization of resources, leading to downstream fitness benefits such as increased reproduction (Ronay et al. 2018). These strategies are evident in baboon colonies in which food sources are relatively dispersed and female reproductive fertility is both brief and easily recognizable. In such ecological conditions, scarce nutritional and reproductive resources are easily monopolized by the largest and most aggressive males. A similar pattern can be seen in certain small-scale human societies, such as the Yanomamö hunter-horticulturists located in the Amazon basin. The sedentary Yanomamö rely on limited access to rivers as a source of protein to supplement their diet. Restricted access to the rivers allows for the monopolization of these resources through violence, and, as a result, power is concentrated with dominant individuals who are capable of obtaining these resources for themselves and their tribes. Reproductive success is also linked to dominance within the Yanomamö, as the number of wives a man has is directly proportional to the number of people he has killed. Dominance, therefore, provides an adaptive advantage in situational contexts characterized by high levels of inequality because it facilitates the acquisition of limited resources.

Group Success

Group members can gain an adaptive advantage by subordinating to successful leaders, provided that the leader's actions coincide with the best interests of the group. Dominant leaders, however, often prioritize the preservation of their power over ensuring group success when their position is uncertain (Mead and Maner 2012). For example, protecting a position of threatened power typically leads a dominant leader to treat group members as threats rather than allies. Leaders may closely supervise skilled group members who have the potential to become competitors for the leadership position. In this way, leaders can monitor and downregulate the threat posed by the skilled individual, thereby protecting their position of power within the group.

Given the propensity for dominant leaders to protect their positions, even at the expense of group success, prestigious leadership is often preferred because their motivation to be respected and appreciated may make them more inclined to behave in ways that benefit the group. The primary route to prestigious leadership involves gaining social approval and support from members of a group. Therefore, prestige-oriented individuals should be highly motivated to achieve and maintain acceptance, and may be highly concerned with how they are perceived (Case et al. 2018). When group success and social approval are aligned, achieving prestige is relatively straightforward. However, sometimes making decisions for the benefit of the group conflicts with the opinions of the group members. In such situations, when forced to make decisions in which the group's collective success is at odds with social opinion, prestigious leaders' decisions depended upon the transparency of the situation (Case et al. 2018). When given the choice of performing one of two tasks, prestige-oriented leaders were more likely to choose the task they believed the group would be most successful at (despite the group members voting for the second task), but only if their decision was kept anonymous from the group. When their decisions were made public, however, prestigious leaders were more likely to ignore their own judgments and pander to the wishes of the group in order

to maintain social approval. Thus, when social approval is at stake, prestigious leaders may make decisions that undermine their group's success. Consequently, endorsing a prestigious leader does not always lead to the best outcome for the group, and, under certain circumstances, a dominant leader may be more advantageous.

In line with this, the presence of a rival group seems to galvanize dominant leaders toward beneficial decisions for the group and away from self-serving ends. For example, during an intergroup competition, dominant leaders no longer closely supervise skilled group members and instead increase their autonomy and allow them to contribute to group success (Mead and Maner 2012). Additionally, in competitive intergroup interactions, dominant individuals are more likely to be elected as a group representative than prestigious individuals (Halvey et al. 2012). In a social dilemma game, benefitting in-group members was associated with perceptions of prestige, but maximizing in-group advantage by either directly harming or reducing shared resources toward an out-group was associated with perceptions of dominance. Furthermore, individuals willing to benefit in-group members at the expense of out-group members were more likely to be elected as a group representative in a subsequent competitive interaction. Therefore, the presence of an external threat makes dominant leaders more attractive, perhaps because they become more concerned with group success and benefitting in-group members at the expense of out-group members.

Methods and Mechanisms for Obtaining Status Through Dominance

Dominance can be used to obtain status via multifarious means, including both behavioral expressions (e.g., aggression) and morphological features thought to reflect cues of dominance (e.g., facial width to height ratio, muscularity, vocal pitch), each of which has been shaped by natural and sexual selection pressures. A full review is beyond the scope of this entry, but a small selection of methods and mechanisms for obtaining status through dominance is provided.

Aggression. Consistent with the notion that dominance is a forceful, fear-based strategy, aggression represents one behavioral mechanism by which dominance can increase individual status within a social hierarchy. Among the Yanomamö, for example, men who have survived multiple ritualized club fights are subsequently admired and feared, resulting in greater status and power (Changnon 1983). Various other studies show a positive relationship between trait dominance and aggression, hinting at aggression's potential utility in gaining status.

Testosterone. Research efforts have also been dedicated to identifying biological mechanisms linking dominance, aggression, and status. One candidate of particular interest is the steroid hormone testosterone. While some work has shown positive correlations between trait dominance and basal levels of testosterone, and between basal levels of testosterone and aggression, others have failed to replicate such findings. Such inconsistencies have been attributed to differences in methodology (e.g., self-report aggression vs. behavioral aggression), and testosterone's dynamic nature, with levels flexibly rising or falling in the face of evolutionarily relevant contexts and cues (e.g., status threats). Indeed, more consistent seems to be that changes in testosterone, rather than basal levels, predict future behavior aimed at gaining or maintaining social status. For example, a rise in testosterone following competition has been found to predict a suite of motivational and behavioral displays, including subsequent competitive motivation and performance, as well as aggression (see Zilioli and Bird 2017). This pattern is consistent with theoretical suggestions that a competition-induced rise in testosterone serves to promote behavior aimed at maintaining social status, while a drop promotes submissive behavior aimed at preventing further loss of status (i.e., The Biosocial Model of Status, reviewed in Zilioli and Bird 2017). Recent work has also examined the causal relationship between testosterone and aggression by using exogenous administration, and findings show that the effects of testosterone on aggression are dependent on certain personality traits. For instance, Carré et al. (2017) found that testosterone increases aggression but only among men with

personalities characterized by high trait dominance and high impulsivity. The extent to which contextual variables (e.g., competition win or loss) interact with the effects of hormone administration and personality characteristics to predict dominant behavior remains to be determined, but there are likely complex interactions between situational, motivational, and physiological variables.

Pride. Certain emotions have also been identified as important to dominance- or prestige-based strategies, with pride in particular being especially relevant to status-seeking efforts. Two distinct forms of pride have been identified, including hubristic pride—characterized by arrogance and self-admiration—and authentic pride, reflecting feelings of confidence and success. Notably, research has found that these two facets of pride differentially relate to status strategies: individuals high in trait hubristic pride self-report and receive higher peer ratings of dominance, whereas individuals high in trait authentic pride self-report and receive higher peer ratings of prestige (Cheng et al. 2010). This work also found that dominant individuals were characterized by a combination of traits such as aggression, narcissism, disagreeableness, and extraversion, whereas prestigious individuals were characterized by traits such as conscientiousness, prosociality, and high genuine self-esteem. Such findings provide evidence to suggest multifaceted contributors (e.g., emotions, personality) to different status-based strategies.

Conclusion

Certain contextual moderators make dominance-based strategies for achieving high status more functional than prestige-based strategies. Specifically, in situations in which the distribution of resources is unequal or the group is newly formed, dominance is advantageous because it signals competence and facilitates the accumulation of resources through force and intimidation. Group members may also reap the benefits of dominant leadership under certain circumstances, such as during intergroup competition. The presence of an external threat alters the focus of dominant

leaders from prioritizing individual status toward group needs and thus may be more functional in terms of facilitating group success compared to prestige-based leaders.

There are a range of behavioral, biological, and personality-based characteristics underpinning dominance behaviors that may facilitate status achievement in these particular contexts. For example, changes in testosterone levels following competition may promote behaviors such as aggression, which are aimed at maintaining social status. Additionally, hubristic pride promotes dominance-related tendencies such as arrogance and narcissism that promote status. These characteristics are particularly functional in achieving status in contexts in which forceful, agentic behavior is likely to result in success, such as during intergroup competition or the accumulation of limited resources.

Cross-References

- [Dominance and Testosterone](#)
- [Dominance in Humans](#)
- [Facial Width to Height Ratio and Dominance](#)
- [Higher Status in Group](#)
- [Humans: Between-Group Conflicts](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Reputation as a Context for Men's Aggression Against Men](#)
- [Social Hierarchies](#)
- [Status and Dominance Hierarchies](#)
- [Testosterone](#)
- [Voice Pitch](#)

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Function of Morality (Haidt)

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Synonyms

Ethical intuition; Moral; Moral foundations; Right and wrong

Definition

The functions of morality are understood as the solutions of adaptive challenges in the ingroup-outgroup dynamics.

Introduction

Morality plays a role among humans in functions that are crucial to the evolutionary process of humans as social beings. Group valorization is of great importance for the survival of the species and morality acts in this field. The purpose of this chapter is to provide an overview of the functions exercised by morals in the process of human evolutionary development.

Foundations and Functions of Morality

According to Graham et al. (2013), the idea of human morality is derived from multiple innate mental systems shaped by different evolutionary process. The Moral Foundation Theory (MFT) proposes that morality is intuitive, nonrational, innate, and highly dependent on environmental influences, being a pluralistic theory as a bridge to evolutionary and anthropological approaches to moral judgment. Thus, morality is organized into five main domains or foundations. Each foundation was evolved to solve adaptive challenges or problems and has a specific function in the human behavioral repertoire (Gould and Lewontin 1979). Some of these problems are social and the human mind developed mechanisms to solve them guided by an ethical intuition as the groups and society began to expand (Richerson and Boyd 2005; Tomasello et al. 2005).

According to Haidt (2008), the moral system is an “interlocking sets of values, practices, institutions, and evolved psychological mechanisms that work together to suppress or regulate selfishness and make social life possible” (p. 70). The evolution of morality contributes to enable human life. As a pluralist theory, because there were many recurrent social challenges, so there are many moral foundations (Graham et al. 2013). The five foundations are: care/harm; fairness/cheating; loyalty/betrayal; authority/subversion; sanctity/degradation.

Each one of these foundations has evolved to accomplish specific functions in the evolution process of the human being. The foundation of care/harm has possibly evolved to solve the

challenge of caring for the vulnerable offspring for an extended period of time (Graham et al. 2013). The main function of this foundation is to lead to the disapproval of individuals that cause pain and suffering and to approve those who prevent or alleviate harm. Disapproval of harmful behaviors might be driven by an overarching concern with a vulnerable group; on the other hand, care for vulnerable members also avoids suffering, distress, or neediness and provides protection (Graham et al. 2013; Koleva et al. 2012).

Fairness/cheating or fairness/reciprocity possibly has been triggered by acts of cheating or cooperation by one's own direct interaction partners and might have the function of reap benefits of two-way partnerships (Graham et al. 2013). This foundation can also be understood as widespread intuitions about ingroup-outgroup dynamics and make the individuals sensitive to issues of equality and justice and leads us to frown upon people that violate these principles (Koleva et al. 2012; Haidt 2007). It has evolved in response to the adaptive threat of being exploited by cheaters and increasing one's chances of receiving benefits of cooperation (Haidt 2012).

The third foundation is loyalty/betrayal, which became decisive for survival because its function is to form cohesive coalitions as the humans developed intergroup competitions (Graham et al. 2013). Another function is based on the attachment to groups (e.g., our family, church, or country) that leads to approve those who contribute to the group's well-being and cohesion (Koleva et al. 2012). According to Haidt (2012), this foundation evolved in order to maintain group cohesion by making an individual aware of others that want to hurt or ostracize members of the group.

The authority/subversion foundation forges beneficial relationships within hierarchies (Graham et al. 2013). This foundation is based on the tendency to create hierarchically structured societies of dominance and subordination and had evolved with the function of maintenance of and respect for the social hierarchies, which make the group aware of potential threats to one's status or rank (Koleva et al. 2012, Haidt 2012). This foundation includes approval of individuals who fulfill the duties associated with their position on the

social ladder, for example, by showing good leadership, or obedience (Koleva et al. 2012).

Finally, the sanctity/degradation foundation has the function of avoiding communicable diseases and is the only one for which the original adaptive challenge was not social – it was mainly nutritive challenges (Graham et al. 2013; Haidt and Joseph 2007). This foundation has evolved in response to the danger of pathogens and parasites but also to various social contaminants like spiritual corruption, or the inability to control one's base impulses (Haidt and Joseph 2007; Koleva et al. 2012). Therefore, it makes individuals aware of any potential threats to health and symbolic objects or values (Haidt 2012).

Conclusion

The moral foundations, as innate mental structures, are likely to be the most effective responses to adaptive challenges that humans have faced during the evolution process in the social world (Graham et al. 2013). The most common functions of moralities were developed to solve ingroup-outgroup dynamics and challenges; as Haidt and Joseph (2006) indicated: rearing children and helping kin; selectively cooperating with non-kin while remaining vigilant for cheaters; forming strong ingroups for the purpose of cross-group competition; organizing themselves hierarchically; and attending to each other's physical states and altering interactions and contacts accordingly.

Thus, morality is understood as the result of adaptive processes with the main function of survival and group cohesion. This is a functionalist vision and contributes to understand human behavior and the development of morality based on natural selection and cultural influences.

Cross-References

- [Evolution of Morality](#)
- [Morality](#)
- [Morality is Cooperation](#)
- [Philosophical Foundations for a Modern Morality](#)

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Function of Pathogen Prevalence (Thornhill and Fincher)

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Synonyms

Behavioral immune system; Parasite adversity;
Parasite-stress theory

Definition

Function of pathogen prevalence refers to the effects of pathogen risk and disease stress on regional variations in mental, social, and personality traits such as intelligence, conservatism, ethnocentrism, religiosity, cultural diversity, and others.

Introduction

Pathogens are organisms that live in (or on) a host organism, at the nutritional and health expense of the host. They can cause the host to suffer a quick and lethal damage or be present for longer (in which case they are often referred to as *parasites*). The function of pathogen prevalence is very well described by Thornhill's and Fincher's parasite-stress theory of values and sociality. All text refers to Thornhill and Fincher (2014a) unless stated otherwise.

Local Pathogens and Local Immunity

Human immune system can vary greatly across regions due to different levels of pathogen prevalence. A good example of this is caste-specific immunity to diseases in India (Pitchappan 2002) or – on an even more local level – village-specific immunity to diseases in Sudan (Miller et al. 2007). History provides even more examples of the drastic consequences for members of isolated groups when they encounter (via trade or conquest) novel groups from other regions. Recently, bacteria thought to kill the majority of Aztecs were traced back to European strain of *Salmonella* (Callaway 2017).

Pathogens are the main drive of evolutionary change in modern humans, being responsible for more evolutionary changes in the genome than any other environmental factor, including climate and geographical and dietary factors. Immunity-related genes are more diverse across regions than are genes related to any other environmental factor (Fumagalli et al. 2011). Moreover, infectious disease was the

largest mortality factor among children and youth in three different ethnographic samples, representative of human evolution steps (Volk and Atkinson 2013).

Regional Variation in Pathogen Prevalence

The Earth differs greatly with regard to pathogen prevalence: low latitudes are areas of higher parasite stress than high latitudes. When living in a pathogen-rich environment, only members of one's own group (ingroup) used to be disease-safe, while members of other groups (outgroups) posed a serious disease threat. Benefits and costs of interactions with outgroups change across regions related to how prevalent pathogens in these regions are. When the pathogen risk is low, the potential disease costs of an interaction with other groups decrease and are outweighed by the benefits (e.g., trade, marriage). Under high parasite stress, societies often take a form of an assortative society: one where individuals mate based on similarity of traits and do so more often than a random mating pattern would predict. What follows as a consequence of pathogen prevalence is also the occurrence of social attitudes such as xenophobia, ethnocentrism, and philopatry, which are components of an assertive society. These attitudes and related practices limit contacts with outgroups, who pose threat from novel pathogens and are more common when parasite stress is high. Local food and hygienic practices often serve to manage local diseases and help preserving the ingroup immunity. Thus, preferring traditional ways of thinking and avoiding foreign ideas can be perceived as defenses against novel parasites brought by outgroups (Kurzban and Leary 2001) and is closely linked to the behavioral immune system. Behavioral immune system is adaptive and comprises psychological and behavioral processes involved in pathogen avoidance (Schaller and Park 2011).

There is a quantitative relationship between the components of assortative society and parasite stress across the world regions. In consequence, high parasite stress areas have more ethnic groups

than low parasite stress areas, as groups tend to merge and dilute more when the risk of catching a disease is lower (Thornhill and Fincher 2014b). While in humans this is related to language and cultural diversity, in other animals, high parasite prevalence is also related to high number of species in a given region.

Functions of Pathogen Prevalence

The mechanisms described in the previous section have multiple consequences for human behavior. Differences in parasite stress have been linked to societal values, such as those mentioned before (xenophobia, ethnocentrism) and many others. To begin with, pathogen prevalence is related to sexual behavior. It influences mate choice preferences: under high pathogen threat, attractiveness of the mate is of special importance as it signals genetic quality; local mating is more popular as well. Parasite stress is also important for sexual restrictiveness. Specifically, high parasite stress is related to more conservative sexual behavior. Second, there are more religions under high parasite stress conditions. Many cultural aspects are thought to rise as a function of pathogen prevalence: (a) collectivism is associated with high parasite stress and individualism with low, (b) high pathogen prevalence regions are more culturally diversified, and (c) more conformity is present when pathogen risk is high. Last but not least, nonhuman interactions can also be influenced by pathogen prevalence, for example, in terms of attitudes to and presence of pets (e.g., dogs). In high parasite stress regions, where these animals can be hosts to more pathogens, human contact with them is less frequent, and keeping them at home is less popular.

Personality and mental traits are also influenced by pathogen prevalence. Prevalence of infectious diseases is related to IQ, which is a measure of intelligence. Countries and regions with higher prevalence have lower average IQ. Certain personality traits, for example, introversion and openness to new experience are more common under low parasite stress, while the opposite (extraversion, skepticism toward new

experiences) prevail under high parasite stress. In fact, much of the uniqueness humans show in terms of mental and social abilities may arise from the ecological dominance they established by a combination of strong selection of traits that protect against parasites and condition-dependent social values, which relate to local parasite adversity. The condition-dependent social values are simply shifts in social values caused by temporal changes in local parasite stress.

Conclusion

Regional and temporal variations in pathogen prevalence have a great impact on humans and human societies. Degree of parasite stress has been linked to aspects of social life such as democratization, conservatism/liberalism, gender equality, sexual restrictiveness, propriety rights, personality family values, and religiosity. In general, higher risk of disease leads to more closed societies, which prefer local contacts and mating and cherish conservative and traditional values. Low risk of disease promotes interaction with other groups and spreading and is linked to more liberal values and higher within-group variety.

Cross-References

- [Disease Avoidance](#)
- [Disease Avoidance Hypothesis](#)
- [Environmental Risk](#)
- [Neophobia](#)
- [Parasites](#)
- [Pathogen Disgust and Perceptions of Attractiveness](#)
- [Pathogen Risk](#)
- [Prejudice](#)
- [Randy Thornhill](#)

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Function of Reproductive Strategy (Kurzban)

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Synonyms

Breeding; Duplication; Procreation; Producing young; Replication

Definition

Reproduction (or procreation or breeding) is the biological process by which new individual organisms – “offspring” – are produced from their “parents”.

Introduction

The most important strategy in the life of any mammal is to beget offspring and thereby perpetuate the species. Although there is considerable variety of reproductive patterns in nonmammalian vertebrates (Weir and Rowlands 1973), reproductive strategies for the human species have basically remained unaltered. Since *Homo sapiens* first appeared, probably in the valleys of Africa, males have always attempted to pass their genes to the largest feasible number of females. Males select those females capable of providing the best quality of oocytes; females invariably have sought a male capable of providing the best means of survival for herself and her offspring. That means the human sexuality has been essentially reproductive in nature, although over the period of time it began to lose fundamental purpose in the cultural evolution of the species. There have been certain major revolutions in the twentieth century. First, with the availability of contraception, sex without the intension of reproduction became a reality; then, with the advancement in assisted reproduction technology, humans have reproduced without intercourse; finally, very recently, women have begun to reproduce beyond the reproductive age. Additional strategies will, no doubt, soon be available, although we cannot as yet clearly see whether, or when, reproduction without sex and gametes, or in vitro gestations, will become available. (Benagiano 2012).

Studies have shown a variety of patterns in sexual desires. Evolutionary psychologists argue that ancestral men who possessed a desire for multiple short-term sex partners, to the extent that they were capable of attracting them, would have left more descendants than men without such a desire. However ancestral women, unlike men, have maximized reproductive success by mating with as many partners as possible, but they preferred to mate with those men who were most able and willing to invest themselves in their offspring. However they have evolved to show sexuality in a bid to compete to get resources from potential men.

One classic study by Clark and Hatfield (1989) found that when college students were interviewed on campus and asked if they wanted to “go to bed” with the opposite sex partner, 75% of the men said yes while 0% percent of the women said yes. There is also an evidence which indicates that across cultures men report a greater willingness to casual sex (Schmitt 2005). A larger desired number of sexual partners (Schmitt (2005) and a greater desire to have sex sooner in a relationship (Schmitt 2005). These sex differences have been shown to be reliable across various studies and methodologies (Baumeister et al. 2001; Oliver and Hyde 1993). However, there is some controversy as to the scope and interpretation of these sex differences (Conley et al. 2011; Schmitt et al. 2012).

There is also evidence that men have a strong desire for casual sex, unlike women. Men are often considered as wanting many opposite sexual partners to increase reproductive success (Flanagan 2012). Evolutionary mechanisms for short-term mating, as well as mate-guarding behaviors and sexual jealousy are evident today. Sexual relations with multiple partners became a recurrent adaptive problem (Buss and Shackelford 1997). The willingness of modern-day men to have sex with an attractive opposite sex partner (Clark and Hatfield 1989) and the prevalence of extramarital affairs in similar cross-cultural are evidence of an ancestral sexual behavior in which polygamous mating strategies were adopted (Buss 1994). However, there is an argument that monogamy has been used to control human female sexual behavior and human female sex drive is not lower than the human male (Smith, Emily Esfahani 2013).

Some of the predictions by evolutionary psychologists stated that when compared to women, men place a greater value on youth and physical attractiveness. The sexual behaviors of youth are associated with reproductive value, features, and physical attractiveness that men usually find in women. These features are thought to signal health and fertility (Buss and Schmitt 1993). In comparison, men who mated with women who are healthy, fertile, and reproductively valuable have

left more descendants than other men who did not, which is being the reason for decline in the reproductive values in women than men with the age since they could not exhibit as strong of a preference for youth in a mate. It is also speculated that women are more attracted to ambition and social status in men, as they associate these characteristics with men's access to resources. Women who mated with men who are capable of having greater access to resources have left more descendants than women who did not mate preferably. These predictions have been tested by evolutionary psychologists across the cultures. Some sex differences in mate preferences may be attenuated by national levels of gender equity and gender empowerment (Eagly and Wood 1999). The specific role that culture plays in modulating sex differences in mate preferences is subject to debate (Gangestad et al. 2006; Schmitt 2011). It is interesting to know that there have been cultural variations in mate preference. Finding a mate with resources becomes less of a priority, and a mate with domestic skills is more important. This is due to women's access to resources varies between cultures, so does mate preference. (Gangestad et al. 2006).

Conclusion

Though human sexual intentions are fundamentally reproductive in nature, due to cultural evolution there have been tremendous changes happening. The reproductive strategies have become multifactorial. Sexual desires and preferences have shown a diversified pattern across cultures. Men and women have been following variety of reproductive strategies based on the resources available to nurture their young ones.

Cross-References

- [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- [Sexual Conflict Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)

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Function Versus Capability

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Synonyms

Biological function; By-products; Identifying adaptive functions; Random effects

Definition

Function	what a biological organization or physical object was designed to do
Capability	all that a biological organization or physical object is able to do, including its designed functions as well as by-products

Introduction

In the memory studies, the capacity of memory has a long history. Until the introduction of modern evolutionary biology into psychology, researchers began to emphasize the origins and nature of memory systems, that is, what the memory system was designed to do (Klein et al. 2002). Knowing the functional design of memory systems helps in figuring out its components and explaining why they exist.

The Capabilities of Memory Systems

The capabilities of memory systems have been studied for almost a century (Klein et al. 2002).

For example, the working memory integrates and infers information to solve current problems (Baddeley 1992), whereas long-term memory helps in planning for the future (Altgassen et al. 2015), making decision (Lynch 1991), acquiring language, and developing relationships with others and personal identity (Klein et al. 2002; Tulving 1985). There are few flaws in memory systems, such as false memory and forgetting. It indicates various capabilities of memory systems are not equally weighted. Finding what is the priority of all these capabilities of a system may give researchers an insight into the designed function of memory.

The Functions of Memory Systems

A biological organization can serve various purposes, but many of them are by-products (Gould and Lewontin 1979; Williams 1966). As most memory systems deal with a great variety of problems, it is a challenge for scientists to identify their designed function. George C. Williams (1966) in his book *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* summarized, “An effect should not be called a function unless it is clearly produced by design and not by chance.” To discriminate the functions of a biological organization from its by-products, Klein and his colleagues (2002) set criterion of whether this capability is well designed to solve adaptive problems.

However, any functionalist claim in psychology cannot be grounded without an evolutionary perspective. It is very difficult to make the distinction between functions and their by-products in a functional organization. It is important to note that multiple memory systems have been shaped and constructed by the prior natural selection in the evolutionary process (Klein et al. 2002; Sherry and Schacter 1987). Besides the products of natural selection, the stochastic process of evolution also introduced noise into functional designs (Klein et al. 2002). In the late twentieth century, researchers attempted to distinguish the original design of memory systems and the functional product of evolved adaptations by investigating

what adaptive problems a memory system was designed to solve (Klein et al. 2002; Nadel 1994; Sherry and Schacter 1987).

Generally, researchers argue that memory systems are designed to take advantage of previous information to solve adaptive problems posed by the environment, such as offspring, the locations of food, and environmental threat (Klein et al. 2002). For example, memory systems allow birds to recognize and keep potential predators away from their nest and young, remember the winners and losers of a previous contest to reduce the cost of competition, exploit efficiently the available food resources, and associate flavor or appearance of food with illness (Sherry and Schacter 1987). Moreover, multiple memory systems have distinct functions. In 1987, Sherry and Schacter highlighted that the evolution causes the functional specialization of multiple memory systems. A memory system is designed and evolved to solve the demands posed by a new environmental problem, which the other system cannot handle. Thus, memory research needs to identify the functions of each memory system, the components of these functional organizations, as well as the causal relationship between the functions and their structures. Besides, knowing the functions of memory systems can help to find the other nonfunctional capacities.

Conclusion

Any system designed to solve a problem has its well-designed organization and structure to achieve a particular goal. Memory systems use acquired information to facilitate present and future behaviors. A conceptual distinction between functions and capabilities plays a vital role in advancing our understanding of the functional design and structure of memory systems.

Cross-References

- [Biological Function](#)
- [Evolution of Adaptations](#)
- [Identifying Adaptive Functions](#)
- [Random Effects](#)

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Functional Behaviorism

- [Selectionist Models: Implications for Behavior](#)

Functional Benefits of Punishment

- [Motivates Punishment](#)

Functional Brain Imaging

- [fMRI](#)

Functional Fixity

- [Content Specificity](#)

immediate physiological needs, self-protection, affiliation, status/esteem, mate acquisition, mate retention, and parenting, respectively (Kenrick et al. 2010a).

Functional MRI

- [fMRI](#)

Functional Play

- [Sensorimotor Play](#)

Functional Specialization

- [Language Modularity](#)
- [Specialized Cognitive Skills](#)

Introduction

In the last decade, some researchers have begun reconceptualizing Abraham Maslow's classic 1943 hierarchical model of human motivations to reflect recent insights from the fields of psychology, anthropology, and evolutionary biology (e.g., Kenrick et al. 2010a). Since that reconceptualization, this line of research has followed three trends: (1) activating different motives to explore their effects, (2) examining individual differences in the fundamental motives, and (3) looking at how fundamental motives apply cross-nationally.

Conceptualizing the Fundamental Motives Framework

The fundamental motives were conceptualized as an update to Maslow's classic hierarchical models of human needs, which included separate needs related to one's physiology, safety, esteem, and self-actualization, respectively (Maslow 1943). From this classic work, the fundamental motives framework retains the idea that motives are discrete (i.e., reflect different drives) and hierarchical (i.e., that they reflect the order of cognitive priorities if particular needs are deprived as well as the order of development across the life span). In addition, the new framework retains the idea that motives can be activated without conscious awareness (Kenrick et al. 2010a).

The fundamental motives framework also leverages insights from evolutionary theory to somewhat retool which motives are contained in its hierarchy. First, it incorporates the idea of *inclusive fitness*, namely, the insight that over time, particular traits have been selected in part because they have consistently been successful at helping organisms pass on their genes either via successful reproduction or the care of

Fundamental Motives

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Synonyms

[Fundamental motives framework](#); [Fundamental social motives](#)

Definition

The fundamental motives refer to a hierarchical set of discrete human motivations, separated in terms of their evolutionary function and organized in a pyramid based on the order in which they develop across the life span and the order in which they are prioritized when triggered. Specifically, the fundamental motives include

kin with shared genes. By this logic, human motivations are likely to account for persistent selection pressures that may have affected humans' ability to successfully pass on their genes. Importantly, successful mating and kin care in humans require that several additional goals be accomplished: they must successfully gather resources as well as create and maintain the social networks and status required to successfully recruit and retain mates. Accordingly, the fundamental motives framework incorporates such goals in its pyramid of human motives, which include, in order of cognitive and developmental priority, *immediate physiological needs*, such as warmth and sustenance, *self-protection*, *affiliation*, *status/esteem*, *mate acquisition*, *mate retention*, and *parenting* (Kenrick et al. 2010a; Schaller et al. 2017). Notably, and as alluded to above, people do not have to be consciously aware of that they are pursuing a given motive—indeed, some recent work suggests that the things people do when they are feeling most self-actualized are typically linked to status-seeking motives (Krems et al. 2017).

A second evolutionary insight that the fundamental motives framework incorporates is *life history theory*. Specifically, it emphasizes the notion that organisms experience a fundamental tradeoff in the time and resources they invest in one of three things: their bodies (i.e., somatic effort), mating, and parenting. So too do these trade-offs manifest differently across the life span; whereas young children concern themselves with meeting their physical needs, people later begin to prioritize reproductive, mate-retentive, and kin care goals. Later goals sometimes build on successful completion of earlier goals; for example, to successfully recruit a mate, one needs to be able to socially affiliate in order to attain the status needed to recruit a mate. Thus, in terms of life history, the motives lower in the hierarchy are more aligned with somatic efforts, and the motives higher in the hierarchy are aligned with mating and parenting efforts (Schaller et al. 2017). Notably, people don't "grow out of" lower levels of motives, they simply add on more of them; if a stimulus triggers a lower motivation, people are still equipped to

respond to it (Kenrick et al. 2010a; Schaller et al. 2017).

There are several lines of research associated with the fundamental motives framework. These involve (1) activating different motives to explore their effects, (2) examining individual differences in the fundamental motives, and (3) looking at how fundamental motives apply cross-nationally.

Activating Fundamental Motives to Explore their Effects

One line of work in the fundamental motives tradition has focused on examining the effects of activating different fundamental motives on various aspects of social cognition and decision-making. Studies in this line of research temporarily prime, or activate, different motives, often by using film clips (e.g., Maner et al. 2005) or evocative vignettes (e.g., Griskevicius et al. 2006, 2009, 2010) to examine their effects. For example, whereas, a story about a late-night break-in might be used to elicit a self-protection motive, a story about a vacation where someone meets a romantic interest might be used to elicit a mating motive (Griskevicius et al. 2006), and a story about a competitive job environment might be used to activate a status desire motive (Griskevicius et al. 2009, 2010).

Work in the fundamental motives priming tradition has suggested that different motives have different downstream consequences. For example, when a self-protection motivation is activated, people tend to conform more (Griskevicius et al. 2006) and perceive more anger on outgroup (but not ingroup) faces (Maner et al. 2005; Kenrick et al. 2010b). By contrast, other work has suggested that when a status desire motive is activated, people are more likely to select expensive versus inexpensive green products (Griskevicius et al. 2010).

Some work in this tradition has also suggested both person and situation-level moderators of the downstream consequences of specific fundamental motives. For example, sex has often been identified as a moderator of the effects of mating and status motive primes. Mating motive primes lead men, but not women, to perceive sexual arousal in attractive opposite sex faces (Maner

et al. 2005). And, whereas status desire motives have been found to make women more indirectly aggressive and men more directly aggressive, this finding only holds for men under a mating motive prime when they are in the presence of other men (Griskevicius et al. 2009).

Examining Individual Differences in the Fundamental Motives

Another approach has moved from examining state-level differences in fundamental motives to exploring trait-level differences in these motives. This work has resulted in the creation and validation of a 66-item inventory which covers individual differences in fundamental motives across the domains of self-protection, disease avoidance, affiliation, status, mate seeking, mate retention, and kin care (Neel et al. 2016). This work has suggested that some of these motives break down into further subcomponents when considered at the trait level. Specifically, affiliation motivations consist of three distinct subcomponents, group affiliation, exclusion concern, and independence; mate retention consists of two subcomponents, general mate retention and concerns over breaking up; and kin care also consists of two subcomponents, care for one's family more generally and care for one's offspring in particular.

This work has also begun to explore the personality and behavioral correlates of individual differences in the fundamental motives. For instance, Neel and colleagues examined some of the relations between the fundamental social motives and other individual difference measures, such as belief in a dangerous world and the Big Five Personality Inventory. They found that whereas motives for self-protection and disease avoidance were related to constructs such as belief in a dangerous world, motives for affiliation group and kin care family were strongly related to agreeableness from the Big Five. Participants high on different fundamental motives also reported different kinds of behaviors. For example, people higher on a self-protection motive were more likely to have reported having taken a self-defense class in the last year, whereas people higher on a kin care family motive were

more likely to have taken care of a young relative in the last year (Neel et al. 2016).

Looking at how Fundamental Motives Apply Cross-Nationally

Although prior research on individual differences across the fundamental motives has primarily been conducted using American samples (Neel et al. 2016), recently, researchers have become interested in how individual differences in the fundamental motives apply in cross-national contexts, as well. For example, in one study utilizing data from 27 different countries, people consistently viewed familial goals, such as kin care and mate retention, as among the most important motives, and mate-seeking goals as among the least important motives (Ko et al. *in press*). Moreover, the familial goals were linked with higher levels of well-being, whereas mate-seeking goals were linked with increased depression and anxiety (Ko et al. *in press*). This kind of cross-cultural work, and work which focuses on mate retention and kin care motives in particular, reflects an active area of study.

Conclusion

The fundamental motives framework updates more classic, hierarchical models of human motivations to include insights from evolutionary theory. More specifically, the fundamental motives constitute a hierarchical set of discrete needs which are organized both in terms of their developmental and cognitive priority; however, these motives do not fully replace one another across the life span. The motives consist of *immediate physiological needs*, such as sustenance and warmth, *self-protection*, *affiliation*, *status/esteem*, *mate acquisition*, *mate retention*, and *parenting* (Kenrick et al. 2010a; Schaller et al. 2017). Typically, experimental work has examined how activating different motives at the state level can have differential consequences for outcomes like cognition (e.g., Kenrick et al. 2010b) and behavior (e.g., Griskevicius et al. 2010). More recent work has also expanded into considering more trait-level individual differences in

the fundamental motives, both in US (Neel et al. 2016) and cross-national (Ko et al. *in press*) samples, and reflects an area of relatively active research.

Cross-References

- [Evolutionary Hierarchy of Needs](#)
- [Inclusive Fitness](#)
- [Life History Theory](#)
- [Self-Beneficial Political Attitudes](#)

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Fundamental Motives Framework

- [Fundamental Motives](#)

Fundamental Social Motives

- [Evolutionary Hierarchy of Needs](#)
- [Fundamental Motives](#)

Fundamental Tradeoffs

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Definition

Trade-off: Allocation of a finite energetic budget toward two or more competing phenotypic traits
Life history theory: A mid-level evolutionary theory that investigates between and within species variation in size at birth, age at weaning, age at

sexual maturity, age at first reproduction, adult size, senescence, and intergenerational birth interval and number of offspring produced.

Introduction

Life history theory is a branch of evolutionary biology that combines information about mortality, reproduction, growth, and development (Chisholm et al. 1993; Stearns 1992) with the intent to understand variation in size at birth, growth rate, age and size at sexual maturity, parity, the number of offspring produced, life span, and mortality rates across species (Stearns 1992, 2000). For example, some species grow slowly, reach a very large adult size, reproduce late and few times during their life, produce few offspring that they care for a long period, and have longer lifespans. Other species are characterized by exactly the opposite, a small adult size, early reproduction, large litter size, and short life span. Evolutionary biologists interpret these correlations across species as an indication that these traits are distributed on a slow to fast life history continuum and use different theoretical models such as *r/K* selection (MacArthur and Wilson 1976; Pianka 1970) and bet-hedging (Promislow and Harvey 1990) to investigate them. From these models and the empirical studies that followed from them, it is apparent that organisms make strategic reproductive decisions depending on the ecological factors they experience, which are linked to mortality rates, and that these decisions have costs that can influence the organism future reproduction and risk of mortality. Obviously these decisions are not the result of conscious thought but instead they are the result of a complex combination of genetic variation and phenotypic plasticity resulting from environmental conditions (Ellis et al. 2009).

One of the most important tenets of life history theory is that time and energy are limited factors that must be optimally allocated toward competing life functions, such as growth, survival, and reproduction. Everything else being equal, organisms should have been selected to maximize their

metabolic and the intake of material resources per units of time (Pianka 1970) or, in other words, organisms did not evolve to acquire an infinite amount of energy at no costs. Because of this limitation, the energy that an organism directs toward a specific life function, let's say growth, cannot be allocated to reproduction. Likewise, the energy allocated toward reproduction cannot be used also to improve survivability, for example, by investing it toward strengthening the immune system. In fact, one of the most intriguing proposals of life history theory is that a hormonal biomarker of reproductive status such as testosterone could negatively influence the effectiveness of the immune system in fighting infections (Roney 2016).

Biologists consider that individual organisms engage in two types of efforts during their lifetime: somatic and reproductive efforts. Somatic effort is represented by the time and energy allocated to systems important for growth and survival. Reproductive effort is represented by the time and energy allocated to mating and parenting effort (Alexander 1987). The decisions that organisms face when allocating energy between these different efforts are defined as life history trade-offs and these trade-offs shape intra-individual and intergenerational life history variables such as when to reproduce, how frequently, how many offspring, how much investment should go toward each of them and lifespan. There are three fundamental trade-offs in life history theory: current versus future reproduction, quantity versus quality of offspring, and mating versus parenting effort (Kaplan and Gangestad 2005; Del Giudice et al. 2015).

Fundamental Trade-Offs in Life History Theory

Current versus future reproduction. This is probably the most important life history trade-off (Ellis et al. 2009). If current conditions are not optimal for successfully growing new offspring, investing in reproduction would certainly be a waste of resources with intergenerational and individual

costs. Intergenerational costs are represented by the likelihood that offspring will not survive to reproduce, thus decreasing inclusive fitness. Individual costs are represented by the impossibility of reallocating the invested resources toward future reproduction, with the extreme case in which current costs are so high that the mother will not survive to the next reproductive season. For example, breastfeeding is energetically expensive and resources allocated in lactation cannot be allocated in fat storage. A nursing red deer may face higher risk of mortality following weaning of her calves if winter conditions are harsh (Clutton-Brock et al. 1982). In such circumstance, natural selection should favor organisms that give up current reproduction while investing in somatic effort. However, if the prospective for future reproduction is very small, for example, because of high mortality risk from environmental factors, it may pay to invest everything in current reproduction. The current versus future reproduction trade-off is very important in shaping the relationship between somatic and reproductive effort and is strongly linked to life-expectancy, quality versus quantity of offspring, and mating versus parenting effort (Caudell and Quinlan 2012; Ellis et al. 2009).

For a developing organism, the most fundamental decision is when to begin to reproduce, that is, at what age should be reproductively mature. Everything else being equal, a further investment in growth and survivability will postpone the age of sexual maturity. The benefits of this type of strategy is that resources can be allocated toward growth of traits that are advantageous for intra- and intersexual selection: larger size, more elaborated phenotypes that are important for courtship, and, especially for humans, an increase in embodied capital (Kaplan et al. 2003) that allows the learning of sociocultural rules and the exploitation of ecological resources in ways that provide intrasexual competitive advantages. However, a serious cost of this strategy is the risk of dying before reaching sexual maturity or to reach sexual maturity when there is not much time left to be reproductively successful. On the contrary, reproducing at an earlier age can increase life-long fertility, but it is unlikely that

this strategy will translate in higher fitness per number of offspring produced (Gillespie et al. 2008).

Hence, life expectancy plays an important role in shaping the trade-off between current and future reproduction and the resulting life history traits. Life expectancy depends partially on mortality risk originating from extrinsic factors, that is, from unpredictable events that are ecology dependent such as the levels of predation, violence, and morbidity (Ellis et al. 2009). When mortality risk is low, we observe that species tend to shift toward the slow end of the slow to fast life history continuum. The contrary is expected when mortality rates caused by extrinsic factors are high. Several scholars of life history theory (Chisholm et al. 1993; Del Giudice 2009; Ellis et al. 2009; Quinlan 2007) hypothesized that children can use the level of parental support experienced during the first 5–7 years of life (Belsky et al. 1991) to gather information about the harshness (levels of morbidity and mortality) of the future adult environment and, accordingly, adjust their reproductive strategies.

This model has been used by many developmental evolutionary psychologist and evolutionary anthropologists to explain, for example, variance in girls' pubertal development and age at first reproduction across different socioeconomic statuses and ecologies. For example, Sheppard and collaborators (Sheppard et al. 2016) reported that in a high socioeconomic status (SES) historical population from the United Kingdom girls from lower SES and with crowded housing tended to give birth at an earlier age and had an overall higher fertility. Similar results have been reported for other industrial populations (Nettle 2010). Likewise, less supportive parenting during early childhood predicts earlier adrenarche and sexual maturity in girls (Ellis and Essex 2007).

Plasticity in age at sexual maturity depends on different types of environmental cues which, at first sight, may look contradictory. For example, chronic stress from lack of nutritional status during early childhood results in postponed pubertal development while, as previously described, early stress resulting from lower parental support

results in an earlier reproductive development (Ellis 2004). Hence, different types of stressors may have different effects on life history trajectories and Ellis and collaborators proposed a model in which, in harsh environments, parenting sensitivity and provisioning plays the most important role in determining life history reproductive strategies (Ellis et al. 2009).

Quantity versus quality of offspring. Since parents have limited resources that can be invested in reproduction, for every additional offspring produced the amount of resources that can be allocated to each decreases. Put it simply, the larger is the investment in number of offspring, the smallest is the investment per offspring. Evolutionary biologists found that this is a very successful reproductive strategy when ecological conditions are unpredictable and there is a high adult mortality rate (Stearns 1976). In these conditions, from a parent's fitness perspective, it pays to produce many small size offspring (size is generally a proxy for smaller parental investment) where at least one of them may successfully reproduce as an adult. On the contrary, when the ecology is stable, juvenile mortality is comparatively higher than adult mortality, and the adult socioecology requires highly competitive adults, as it pays to increase parental effort, that is, to invest in less offspring but of higher quality. In this way, parental investment increases the chances of survival of the few offspring through the juvenile period, and it increases their competitive advantage once they reach adulthood (Del Giudice et al. 2015; Ellis et al. 2009).

As a species, humans stand in the slow end of the fast-slow continuum of life history strategies, with mothers that give birth to one child and rarely to twins or triplets. However, the trade-off between quantity and quality of offspring in relation to ecological uncertainty can still be observed. For example, in a population from rural Ghana which experiences high mortality rates, fertility was very high, and for each additional child in a family there was more than a 2% decrease in offspring survival (Meij et al. 2009). A similar result was reported by Gillespie and collaborators (Gillespie et al. 2008)

who used historical census records representative of a pre-industrial population of Northern Europe. In their study, Gillespie and collaborators reported that women from lower SES had higher fertility but lower fitness compared to women of higher SES since a smaller proportion of their children lived long enough to reproduce. Yet, given their socioeconomic status, from a purely evolutionary biological perspective, they made the best out of a bad situation.

Mating versus parenting effort. The trade-off between mating and parenting effort is closely related to both current versus future reproduction and offspring quantity versus quality trade-offs. For species that reproduce sexually mate searching and copulation have substantial risk, time, and energy costs (Del Giudice et al. 2015; Kaplan and Gangestad 2005). For a parent the investment in current offspring reduces the time and energy required to produce and/or invest in other offspring (it decreases fertility), while investing in further fertility reduces the investment in current offspring. This trade-off results in reproductive conflict of interest between parents which, in the majority of vertebrate species and for reasons explained by sexual selection theory, resolve with females tending to invest more in parenting effort and males in mating effort.

Life history theory predicts that sex specific and individual differences in the preference for mating versus parenting efforts depend on the levels of mortality risk and morbidity. Generally speaking, the sex that experiences the highest mortality is the one that invests the most in phenotypes and behaviors that increase mating competition (Del Giudice et al. 2015). Compared to other mammals, human males provide high paternal investment (Geary 2000) and, as for other biparental species, women mate choice can select for males that provide support for their offspring, a strategy that would increase female fertility and offspring survival.

Life history theory provided an important model for the study of variation in the proportion of maternal and paternal efforts across different human populations. For example, Quinlan

(2007) showed that in harsh environments characterized by famine, warfare, and high pathogen loads, maternal and paternal investment are lower, with mother terminating breastfeeding at earlier ages. When ecological conditions are harsh, the lower level of parental investment appears to be a consequence of the limited benefits that the parent would gain by investing further energy and time toward children with poor survival expectations. In turn, children can use the levels of their parent's investment to develop behavioral and psychological reproductive strategies that are functional for dealing with that specific ecology (Ellis et al. 2009). The prediction of life history theory is that if the future environment is harsh and little parental support is received then, through the development of specific attachment styles, children will tend to follow a mating effort strategy which is characteristic of a fast life history (Chisholm et al. 1993; Del Giudice 2009; Ellis et al. 2009). Behaviorally this strategy is characterized by unrestricted sociosexuality, a decreased ability to delay gratification, higher risk taking, aggressive, and competitive behaviors.

In this regard, life history theory has been used by psychologists and evolutionary anthropologists to explain the relationship between life expectancy and risky behaviors that place youth at higher risk of mortality and morbidity (Wilson and Daly 1997; Ellis et al. 2012). For example, several studies looked at behavioral and psychological correlates of mating effort, family structure, and socioeconomic status and showed that children growing up in a family with a single mother or a stepfather have an earlier sexual debut, abuse illicit substances, and report higher rates of violence (Copping et al. 2013; Sheppard et al. 2014) and colleagues (Kruger et al., 2008) showed that in a population of youth from a blue collar city of the United States, kids from poorer and harsher neighborhoods scored higher in aggression and illegal resources acquisition and that the relationship between ecology and risky behaviors is mediated by a present oriented time preference. Another study showed that subjects from lower SES prompted

with cues of a shorter life expectancy have preference for behaviors indicative of high mating effort (Griskevicius et al. 2011). Likewise, being exposed to a stressful environment at an early age influences youth's preferences for unrestricted sociosexuality, aggression, and delinquency (Simpson et al. 2012).

Conclusion

Life history theory is a mid-level analysis theory that historically has been used by evolutionary biologists to understand differences in functions and structures between species and individuals. The idea of trade-offs between competing traits and the costs that these tradeoffs have for the organism's fitness represent the core of life history theory. There are three types of fundamental trade-offs, each concerned with how an organism should, from an evolutionary point of view, optimally invest its limited metabolic budget: (1) when and how much to invest in current or future reproduction; (2) Investing in more offspring of lower quality or in few of higher quality; and (3) when and how much to invest in mating effort or parenting effort.

In recent years, the use of life history trade-offs by evolutionary psychologists and anthropologists has been successful in modeling variation in human parenting styles, pubertal development, trends in fertility, and also more psychological variables such as time perspective, sociosexuality, and risky behaviors. All of these factors have broad health and economic impacts on modern societies, and very likely, the use of more sophisticated approaches that aim at identify more subtle subtypes of life history trade-offs (Del Giudice et al. 2015; Nettle et al. 2013) will provide a powerful tool that makes very exciting the future study of psychopathology, biomedicine, and demographics.

Cross-References

► [Cost-Benefit Analysis](#)

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Funereal Rites

- [Burials](#)

Funniness

- [Neurology of Humor](#)

Funny

- [Humor Production](#)
-

Future Reproductive Capacity

- [Children Have Greater Reproductive Value than Sibs](#)

FWHR

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G

G. C. Williams

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Gait

- ▶ [Humans Crawl: Species Atypical Movement](#)

Game Theory

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Synonyms

[Probability theory](#); [Theory of games](#); [The science of strategy](#)

Definition

The science of strategy studied using mathematical, interdependent, logic choice games between two or more players.

Introduction

In essence, *game theory* is the science of strategy. Research in this field aims to determine the action or set of actions that players should logically take to secure the best outcomes for themselves. The set of conditions and rules dictating players' choice of actions, and consequences of those actions are referred to as games. There are numerous specific games, but they all share the common qualities of *interdependence*, in that the outcome for each player depends on the chosen actions of other players, and *conflict*, in that there is the potential for different gains or losses between players. Thus, decisions in games are different from decisions made in a "neutral" context without other players (such as with inanimate objects), and as in a neutral context, there is no dependence linked to the chosen actions.

"Games" in Game Theory

There are three broad categories of games in relation to outcome: (1) zero-sum games, (2) positive-sum games, and (3) negative-sum games. *Zero-sum* games are where one player's gain always causes another player's loss meaning that the interests of the players conflict totally. A classic example of a zero-sum game is *Rock, Paper, Scissors*. *Positive-sum* games are where there is the option for mutual gain, and conflict arises between the division of gain or sometimes options

alongside mutual gain or loss for the other player. Lastly, *negative-sum* games are where there is similarly the potential for mutual loss as well as some conflict on the degree of loss.

Game theory was first coined by mathematician John von Neumann (who was one of the conceptual inventors of the stored-program digital computer and who was involved in the Manhattan Project). Neumann originally focused on zero-sum games (games of total conflict); if there was cooperation, it was typically “yoked” (i.e., players were supposed to choose actions together). Most recent research typically focuses on games that are neither pure conflict nor purely cooperative. In other words, researchers now use games where the players choose actions separately, but they include consequences for others, yielding both a competitive and cooperative component.

A player in a game must recognize that they are interacting with other players. At the core of these games is the interaction and interdependence of the player’s strategies. There are two general types of interdependence: sequential and simultaneous. In sequential interdependence games, the players make choices and act in sequence, aware of the other player’s (or players’) previous actions, whereas in simultaneous games, players act at the same time, aware of the other player’s (or players’) actions. Note that simultaneous games can be played in sequence (i.e., multiple rounds), making the overall game a hybrid of the two. In a sequential game, players need to consider how the other players will respond to each choice, and how they will respond to other player’s choices. That is, a player needs to anticipate what consequences choices will lead to in relation to how it will influence the other player (s) and use this information to decide on the best option. Therefore, games require mind perception and person perception (Epley and Waytz 2010).

Some examples of common games in game theory are (1) the *Bargaining Game*; (2) the *Ultimatum Game*; (4) the *Public Goods Game*; and (5) the *Hawk-Dove game*. The *Bargaining Game* is a simple two-player interaction used to model bargaining scenarios. Two players demand a portion of some good (e.g., an amount of money) and both players get their request if the total amount

requested by the players is less than the total amount available, but, if not, neither player gets their request. Similarly, the *Ultimatum Game* is a simple two-player interaction where each player takes a different role; the “proposer” player determines how to split a set amount of some good (e.g., an amount of money) between the players, and then the “responder” player decides whether to accept or reject the offer. If the offer is rejected, neither player receives any of the good. In the *Public Goods Game*, participants are given an amount of some goods (e.g., tokens) and covertly choose how much of this good to put into a public pot and how much to keep. After each player has done so, the public goods are multiplied by some factor and evenly divided among players. The *Prisoner’s Dilemma* game involves a simultaneous choice (i.e., each player must make the choice without knowing what the other will do) between two players to either cooperate or defect. In this game, defection yields a higher payoff than cooperation when paired with a cooperate choice from the other party, but, if both defect, both do worse than if both had cooperated. In addition, the cost of being defected on after cooperating is still greater (see Prisoner’s Dilemma entry for more detail). The *Hawk-Dove game* is a simple two-player interaction used to model conflict vs. sharing of a resource. It is similar to the Prisoner’s Dilemma except the cost of both players choosing conflict (equivalent to defecting in the Prisoner’s Dilemma) is significantly greater.

In solving these games, if one player’s best choice is the same no matter what the other player(s) do, it is called a “dominant strategy,” and if a player’s strategy uniformly yields a bad outcome, it is called a “dominated strategy.” Through active research or simulations, game theorists are typically concerned with identifying dominant strategies and eliminating dominated ones. Often, the dominant strategy is dependent on whether the game is one-shot (only played once per game partner) or round based (played multiple times between the same players in sequence). For example, in a one-shot ultimatum game, the responder should choose to accept the absolute minimum amount from the split as anything is better than nothing. However, in multiple

rounds, this strategy can be exploited by the proposer to repeatedly give the receiver the bare minimum share. Therefore, it can be more advantageous for the responder to “stick to their guns” at a more even split (or even a split in their favor) over multiple games, forcing the proposer to be more fair (or even concede the larger portion) to the responder to avoid having offers thwarted, and thus receiving no share. Also see “The Evolution of Cooperation” entry, for the dominant strategy in multiple Prisoner’s Dilemma games, or Axelrod (Axelrod and Hamilton 1981; 1984).

Conclusion

Game theory is the science of strategy studied using mathematical, interdependent, logic choice games between two or more players. The set of conditions and rules dictating players’ choice of actions, and consequences of those actions are referred to as games. The various specific games all share the common qualities of interdependence, in that the outcome for each player depends on the chosen actions of other player(s), and conflict, in that there is the potential for different gains or losses between players.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Cheater Detection Adaptations](#)
- ▶ [Evolution and the Theory of Games](#)
- ▶ [Evolution of Punishment](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Game Theory as a Foundation of Evolutionary Psychology](#)
- ▶ [Morality Is Cooperation](#)
- ▶ [Prisoner’s Dilemma](#)
- ▶ [Robert Axelrod](#)
- ▶ [Robert Axelrod’s \(1984\) *The Evolution of Cooperation*](#)
- ▶ [Social Exchange Among Non-Kin](#)
- ▶ [Strategies for Successful Cooperation](#)
- ▶ [Theory of Reciprocal Altruism](#)

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Game Theory as a Foundation of Evolutionary Psychology

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Synonyms

[Behavioral game theory](#); [Decision theory](#); [Evolutionary game theory](#); [Experimental economics](#); [Mathematical biology](#)

Definition

Game theory is the mathematical analysis of interdependent systems composed of fitness- or utility-maximizing “actors” (e.g., humans, animals, genes, or viruses) whose success depends on the strategies of others.

Introduction

Game theory is a useful tool for understanding interdependent systems. It is a mathematical description of how individuals should behave in contexts in which the outcomes of their actions depend on the behavior of other individuals. Game theory has been applied to topics as varied as climate change negotiations (Helm et al. 2012), the evolution of cooperation (Nowak 2006b), and viral population dynamics (Turner and Chao 1999). Game theory makes sense of different “strategies” and “payoffs” by using the

mathematical logic of each individual agent's perspective. Game theory was first used to model rational, conscious actions by humans in strategic settings; however, its usefulness now extends well beyond the realm of decision-making. The interaction between "strategies" could involve individuals making choices on a playing field, phenotypic traits occurring at different frequencies within a population, or genes within a body fighting to be passed on. In all of these cases, a successful "strategy" – choice, trait, or gene – depends on what others are doing (Maynard Smith 1982). Traits of interest to evolutionary psychologists are highly suitable to game theoretic approaches, because they so often depend on interactions between individuals.

Game theory is of fundamental importance to evolutionary psychology in four domains. First, traditional game theory played a role in the historical transition of psychology away from behaviorism and Freudian thought and toward experimentalism, microeconomic methodology, and evolutionary psychology (Gintis 2009). Second, game theory provides a rigorous methodology for documenting human decision-making and understanding the evolutionary basis of seemingly "irrational" human behavior. Third, evolutionary game theory yields new insights into the development and maintenance of complicated and seemingly paradoxical traits such as cooperation, long-term partnership, and altruism. Finally, many small, self-interested agents compete ("play games!") within our bodies – selfish genes, microbes, viruses, and more – with demonstrable impacts on our psychology and behavior. Because of its contributions in these four areas, game theory is a valuable tool in our effort to model and understand our evolved brains.

Game Theory

"The world" is something like a great chess game being played by the Gods, and we are observers of the game. . . . If you play chess you must know that it is easy to learn all the rules, and yet it is often very hard to select the best move or to understand why a player moves as he does. So it is in nature, only much more so – Richard Feynman.

Historical Background

Game theory, like probability theory, arose from literal games. Probability can model and interpret dice rolls and games of chance, but game theory models poker and chess – games that depend at least in part on uncertainty about other players' decisions (Sigmund 1993). John von Neumann and Oskar Morgenstern are the true fathers of game theory, but their brilliant twentieth century contributions did not occur in a vacuum; more than 200 years before their work, the first game-theoretic (i.e., mathematical) analysis of strategy was proposed. In 1713, Francis Waldegrave described a mathematical "mixed strategy" solution to the two-person card game *Le Her* in a letter to probabilist Pierre-Remond de Montmort. Montmort, in turn, passed the solution on to the mathematician Nicolaus Bernoulli. (This ongoing web of correspondence is most famous for its analysis of the St. Petersburg Paradox, a game with mathematically infinite "expected value" but paradoxically low subjective value to humans. This paradox is an early example of our growing awareness that humans are not perfectly rational actors in a classical, economic sense.) Waldegrave analyzed which strategy would give a player the best odds of winning, taking into account card distributions as well as the opponent's strategy. A more detailed discussion of *Le Her* and Waldegrave's work is beyond the scope of this entry; it is sufficient to note that this was apparently the first instance of a mathematical treatment of human strategy.

Games such as Chess, *le Her*, and Go inspired much verbal and some brief mathematical treatment of strategy for several centuries. But game theory in its true, mathematical form is the invention of John von Neumann and Oskar Morgenstern, with significant fundamental contributions from John Nash (among others). (John von Neumann was a genius who made significant and fundamental contributions to multiple fields, from pure mathematics to physics, computer science, and statistics. His impact beyond the invention of game theory is not always fully appreciated; Nash was admitted to Princeton as a PhD student with a three-sentence letter of

reference concluding “He is a mathematical genius.” He went on to receive the Nobel Prize for a single-page paper.)

In 1928, von Neumann wrote a seminal paper which founded the modern form of game theory (von Neumann 1928). In the 1940s, von Neumann and Morgenstern wrote a definitive treatise on game theory, entitled *The Theory of Games and Economic Behaviour* (von Neumann and Morgenstern 1944). They described games in formal mathematical detail and proposed rigorous methods of assessing behavior. In the preface to the first edition, von Neumann and Morgenstern outline their aims as follows: to provide a rigorous analysis of games, as well as sociological and economic problems, that involve “questions of parallel or opposite interest, perfect or imperfect information, free rational decision or chance influences.” (von Neumann and Morgenstern 1944). The pair’s greatest contribution was a formal mathematical treatment of topics characterized by opposing or colluding interests, chance, and varying levels of information availability.

In the middle of the twentieth century, John Nash came onto the scene with fundamental contributions that led to game theory as it is today. He furthered our understanding of what is now known as a Nash equilibrium a “stable state” of a game in which no single participant can gain from unilaterally changing strategy while all other participants’ strategies remain the same. Over the course of game theory’s development, much attention has been given to developing robust “solution concepts,” or predictions about how a game should be played to maximize payoff, against a variety of new introduced complications (such as repeated games, and errors of judgment).

Since the work of these early pioneers, game theory has been employed and expanded upon by economists, political scientists, philosophers, biologists, and mathematicians; it has been the subject matter of many Nobel Prizes and has made significant contributions to multiple fields. In particular, game theory has played an important role in the transformation of psychology over the last 70 years from a field defined by Freudian thought, behaviorism, conditioning, and proximate cause to its current formulation as an

experimental, biological, and mathematically rigorous evolutionary discipline (Gintis 2009). Game theory’s influence began to be felt as early as the 1950s and 1960s, when psychologists began to uncover paradoxes in supposedly rational human thought through experimentation (e.g., Allais 1953); these results – and the emerging widespread interest in game theory (perhaps most notably exemplified by Martin Gardner’s famous “Mathematical Games” column in *Scientific American* from 1957 through 1986.) – soon led psychologists to analyze decision-making via game theoretical experiments. The theories that emerged – e.g., regret theory, hyperbolic discounting, risk aversion, and other modes of discovered “irrationality” – owe a clear intellectual debt to the methodologies and principles of game theory (Gintis 2009).

While psychology was undergoing this experimental revolution, leading biologists and ethologists such as Konrad Lorenz and Niko Tinbergen began to investigate seeming paradoxes between self-interested evolution and cooperative animal behaviors. E. O. Wilson applied interpretations of animal behavior to human behavior in his landmark 1975 book (Wilson 1975), while John Maynard Smith (no relation to John Maynard Keynes, founder of macroeconomics) formalized and described evolutionary game theory as a fundamental new tool of biological analysis (Maynard Smith 1982). In short, game theory has helped provide mathematical rigor and experimentation to the field of psychology and has thus paved the way (with biology) to the development of evolutionary psychology.

Traditional Game Theory

Overview

In its original and simplest form, game theory is an economic tool to model human strategic behavior. It is often used in behavioral economics, experimental economics, decision theory, psychology, economic psychology, and more. When will individuals be selfish? When does it pay to be aggressive, and when does it pay to cooperate? What circumstances give rise to altruism? As

we will see below, many experimental “games” answer these questions in a lab setting, such as the commonly-described games Prisoner’s Dilemma, Hawk-Dove, and more.

A “game” is an interplay of actors, each of whom rationally seeks to maximize her own preferred results (formally defined as her utility). These actors can adopt a number of “strategies,” or methods of engaging with other actors, and, as time goes forward, good strategies are rewarded and bad strategies are punished.

Each person does not know what strategy the others will employ. Eventually the game may result in a stable “solution” – a solution where one best strategy rises to dominance among all the actors, or where the proportion of actors with certain strategies remains constant over time. As we will see later, such stable strategies are not always achievable – consider a game where strategy A beats strategy B, strategy B beats strategy C, and strategy C beats strategy A. Furthermore, there can be “high” and “low” peaks of stability; imagine two adjacent mountain ranges with a valley in between. Human actors seeking to climb as high as possible can only tell whether they are headed up or down; as a result, they may well continue on a path toward a “good” outcome (the lower of the two peaks) without ever catching sight of the “best” outcome. We will discuss evolutionary game theory in detail in section “[Evolutionary Game Theory](#)” below, but for now simply note that evolutionary game theory deals with “actors” that can be individual organisms, single species, or genes and with “strategies” that are quite broadly defined to include not only behaviors but also a wide range of other variables such as phenotypes and proportions of genes in a population.

Types of Strategies and Strategy Sets

Actors can adopt pure or mixed strategies from a strategy set that is continuous or discrete. Pure strategies are individual and consistent for a given actor. In traditional game theory, pure strategies are a single actor’s commitment to act in a single way all the time. A prisoner could always defect (not cooperate), or always cooperate. As we will see in more detail in section “[Evolutionary](#)

[Game Theory](#)” below, single-locus-determined genetic traits, such as hair color (determined by a single gene), are “pure” strategies (in the evolutionary sense).

Mixed strategies involve assigning a probability (sampled from a continuous distribution) to each element of a finite, discrete set of strategies. For example, when choosing from the strategy set “cooperate” or “defect,” an individual could consistently cooperate with others at a 60% rate and defect at a 40% rate. This does *not* require that she knows what others will be doing; it simply means that 60% of the time she encounters another person in a game, she will cooperate, and 40% of the time she will defect.

In game theory, continuous strategy sets can be distinguished from discrete strategy sets. One example of a continuous strategy set would be an investor deciding *when* to sell a stock, because time is continuous. (Since we can only measure time at discrete moments, it is only an approximation to say time is continuous.) She could select any time within brackets, with a probability distribution over the range of times. Many evolutionary “strategies,” or “traits,” are continuous, such as height, weight, brightness of color, or neuron density.

In contrast, discrete strategy sets offer well-defined, nonoverlapping options – such as the potential behaviors “cooperate” or “defect,” or a gene coding for blue eyes versus brown eyes.

Types of Games

Games can be symmetric or asymmetric. The former involves players with access to the same set of strategies: for example, in a symmetric hawk-dove game, each individual can choose to act as a hawk or a dove. Hawks in this game are aggressive: they attack whomever they encounter in order to try to claim the whole food resource. Hawks receive a bonanza if they encounter a pushover Dove, but self-destruct through fighting if they encounter another Hawk. Doves are docile; they either accept defeat (and a small payoff) if they encounter a Hawk or split the reward if they encounter another Dove. In typical formulations of the game, each actor will adopt a consistent strategy to be either a Hawk (H) or a Dove (D) for

all of that actor's encounters (in most formulations of the game, actors do not know which strategy their opponents will choose). The optimal strategy ultimately depends on the relative payoffs of the four possible types of encounter (H-H, H-D, D-H, and D-D), where encounters are usually treated as being "commutative" – i.e., H-D has the same result for the Hawk and the Dove as D-H; there is no importance to the ordering of the participants in an encounter. There are circumstances where order does matter, even in symmetric games. For example, where the actor initiating an encounter has an advantage. One can imagine a scenario where in a D-H encounter the Dove and Hawk both survive and go their separate ways unscathed (because the Dove sees the Hawk and flees) while in H-D the Hawk catches the Dove by surprise and takes its bounty.

The second kind of game is asymmetric – the actors do not have access to the same strategy sets, or have unequal knowledge about opponent strategies or the environment. This is often more realistic for evolutionary games; games could play out between two sexes, two ages, two sizes, or territory owners and territory invaders (Maynard Smith 1982). Imagine again the hawk-dove game, but give an extra bonus to one of the two players – whichever player "owns" the territory on which the fight occurs (and such "ownership" is not a variable – the actors have no opportunity to choose whether they are owners or invaders – but instead are assigned one role or the other as a parameter of the game). This is asymmetric, because the players do not have equal access to strategies and knowledge.

Games can also be "zero-sum" or "non-zero-sum." In zero-sum games, the total benefit to all players sums to zero. In other words, a player can only benefit at the expense of other(s). Non-zero-sum games do not have this restriction. Poker zero-sum game, while many games are non-zero-sum, since some outcomes result in net benefit or net loss.

Solution Concepts

You've got to know when to hold 'em, know when to fold 'em, Know when to walk away,

know when to run. The Gambler, by Don Schlitz, sung most notably by Kenny Rogers.

Solution concepts are formally described predictions of how a game should be played to maximize a player's payoff. For example, in most classic formulations of the Prisoner's Dilemma (described in detail in a later section), the rational solution concept is "always defect." For a Hawk-Dove game, a solution concept could be "choose to act like a Dove 40% of the time and like a Hawk 60% of the time," or, equivalently, "40% of the population are pure Hawks and 60% are pure Doves." (This equivalence is explained below in section "[Evolutionary Game Theory](#)"). These percentages depend on relative payoffs. There are many variations of solution concepts in traditional game theory, depending on the motivations of the actors, whether a game is "iterated" (i.e., repeated over time between two actors or in a group of actors), whether a game is symmetric or asymmetric, and more. Any description of a solution to a game is technically a solution concept, whether or not the behavior is deemed normatively good.

Two important categories of solution concept are "Pareto-optimal solutions" and "Nash equilibria." Pareto-optimal solutions feature a distribution of strategies such that no one actor's lot can be improved without hurting the lot of another (Pareto 1896). On the other hand, Nash equilibrium is reached when no single player can improve her own lot by *unilaterally* changing her strategy (Nash 1951). In fact, Nash equilibria are not always Pareto-optimal. Consider the classic prisoner's dilemma game: two prisoners accused of having jointly committed a crime are brought into a divided room; they cannot communicate with each other, but both are told the rules of the game. Each prisoner can either cooperate (with the other prisoner, not with the police!) by staying silent about the crime or "defect" by confessing and trying to gain freedom – figuratively throwing the other prisoner under the bus. If both cooperate, and neither confesses, they each get only 1 year in prison. If both "defect" by confessing, they each get 2 years in prison. And if one defects but not the other, the first goes free

and the second gets 3 years in prison. Nash equilibrium is reached when both players defect; in this case, both players get 2 years of prison, and neither player can improve her own outcome by unilaterally changing her strategy to “cooperate.” If she did, she would receive 3 years in prison while her partner would go free. However, this solution is not Pareto-optimal. The Pareto is reached if both players cooperate and do not confess: here, both players get 1 year, which is collectively better than both players getting 2 years. Obviously, though, this Pareto optimum is not a Nash equilibrium, since if one player defects and confesses, they go free while the other player gets 3 years in prison. In sum, this classic prisoner’s dilemma game illustrates that solutions which are Pareto-optimal are not always examples of Nash equilibria and vice versa. Indeed, if Nash equilibria were always Pareto optimal, game theory would be a good deal less interesting than it is.

Examples and Notation

Let us take a very simple example as illustration. The “Hawk-Dove” game discussed above has also been called the “Snowdrift” game and the game of “Chicken,” names that reflect the diverse research fields which have happened upon mathematically identical games. The games vary slightly by conventional assignment of symmetry versus asymmetry and cost-benefit ratios. Although the names are lighthearted, the “Snowdrift/Hawk-Dove/Chicken” game describes the fundamental underpinnings of mutually assured destruction by nuclear war. Bertrand Russell describes the game of “Chicken” in an extended allegory (Russell 1992) (Fortunately, at least so far, Russell’s fears have proven to be unfounded, possibly displaying some of the limits of game theory, or alternatively of Russell’s employment of it in this context.):

Since the nuclear stalemate became apparent, the Governments of East and West have adopted the policy which Mr. Dulles calls ‘brinkmanship’. This is a policy adapted from a sport which, I am told, is practiced by some youthful degenerates. This sport is called ‘Chicken!’. It is played by choosing a long straight road with a white line down the middle and starting two very fast cars towards each other from opposite ends. Each car is expected to keep the wheels on one side of the white line. As they

approach each other, mutual destruction becomes more and more imminent. If one of them swerves from the white line before the other, the other, as he passes, shouts ‘Chicken!’, and the one who has swerved becomes an object of contempt. . . . The game may be played without misfortune a few times, but sooner or later it will come to be felt that loss of face is more dreadful than nuclear annihilation. The moment will come when neither side can face the derisive cry of ‘Chicken!’ from the other side. When that moment is come, the statesmen of both sides will plunge the world into destruction. (Russell 1992)

Let us imagine a game of Chicken played by two teenagers named Marty and Tory. They drive cars toward each other at high speed, and can choose at the last second to maintain course or to swerve. If both maintain course (strategy “maintain”), they collide and both cars are destroyed. Let us assume that the people inside survive unscathed, because they were wearing seatbelts and had properly functioning airbags, but the financial loss is devastating. If one swerves (strategy “swerve”), she makes it out, car undamaged – but with the label “chicken” and its associated social cost, while her opponent is the brave victor. If both swerve, they both save face. These strategies and payoffs can be represented with a simple payoff matrix:

		Tory	
		Swerve	Maintain
Marty	Swerve	<i>Tie, tie</i>	<i>Coward, Hero</i>
	Maintain	<i>Hero, coward</i>	<i>Crash, crash</i>

In italics within each box, Marty’s choice is represented on the left and Tory’s on the right. In the top left box, both choose to swerve and they tie. In the top right box, Tory maintains course while Marty swerves – so Tory is a hero and Marty is a chicken. We can assign numerical values to these outcomes as follows, assuming catastrophic losses if they collide and minor gains/losses if one swerves:

		Tory	
		Swerve	Maintain
Marty	Swerve	0,0	–1, +1
	Maintain	+1, –1	–10, –10

To simplify matters, let us adjust our notation by writing the payoff matrix only for Marty's expected payoffs:

		Tory	
		Swerve	Maintain
Marty	Swerve	0	-1
	Maintain	+1	-10

Brief inspection of this matrix reveals that the potential loss of swerving (at most -1) is insignificant compared with the risk of staying on course (-10). However, suppose that Tory thinks this through and realizes that Marty will probably arrive at that same conclusion. Might it not be better for Tory to assume that Marty will act reasonably, so Tory can choose to maintain and thus collect the +1 value of being a hero? Formally, this symmetric game has one Nash Equilibrium that is a mixed strategy: swerve with probability P and maintain with probability $(1-P)$. This probability P depends on the payoff matrix; in this case, without writing out the math, $P = 1/10$; each player should swerve 9 out of 10 times and maintain course 1 out of 10 times. On the other hand, if one driver is gifted with the knowledge of what the other driver will do – that is, if we convert this into an asymmetric game – the Nash equilibrium is to “do the opposite of your opponent.”

The “Snowdrift” formulation of the game is somewhere different. Two drivers, Tom and Sam, both get their cars caught in a snowdrift. They each can choose to cooperate by getting out of the car and shoveling in the bitter cold, or defect by relaxing in their cars listening to The Beatles. The benefit b is getting home, while the cost c is shoveling in the cold. If they both cooperate, they can split the work so the cost is $c/2$ while the benefit of getting home remains b .

Here is the payoff matrix, written from Sam's perspective:

		Tom	
		Cooperate	Defect
Sam	Cooperate	$b - c/2$	$b - c$
	Defect	b	0

Clearly, Sam would most like to do no work but nonetheless get home safely – the case whereby she defects and Tom cooperates. Indeed, if $b > c$, the best strategy is to do the opposite of your opponent assuming you have special ability to see their choice (defect if they cooperate, cooperate if they defect). But what if $b < c$ – if the costs of doing the work alone outweigh the benefits of getting home? In that situation, both players are better off defecting.

Indeed, this unorthodox formulation of the snowdrift game wherein solo costs outweigh benefits is mathematically equivalent to the Prisoner's Dilemma. Consider such a case, where the cost of shoveling alone is 6 and the benefit of getting home is 3.

		Tom	
		Cooperate	Defect
Sam	Cooperate	0	-3
	Defect	3	0

Whether Tom defects or cooperates, Sam is better off defecting. If Tom cooperates, Sam could earn 0 or 3 by cooperating or defecting, respectively; if Tom defects, Sam could earn -3 or 0 by cooperating or defecting, respectively. Since $3 > 0$ and $0 > -3$, Sam should always defect. Since Tom will make the same realization, Tom will always defect as well – and we have arrived at equilibrium, sitting inside two cars in a snowdrift listening to The Beatles. (Of course, games where cooperating is the best move for both parties also exist! They just aren't very compelling.)

Conventionally, the name of a game reflects the ranking of payoffs, such that, for example, a “prisoner's dilemma” must have “defect” as the optimal strategy.

These are the building blocks of traditional game theory, which models rational actions and strategies for individuals seeking to maximize their own utility. But the astute reader may notice a flaw: humans are not rational, and utility is not easily quantified. We will discuss this and other drawbacks of game theory in section “Limitations of Game Theory.”

Evolutionary Game Theory

Overview

Evolutionary game theory was founded and developed by John Maynard Smith (Maynard Smith 1982) as well as Karl Sigmund and many others. It was first introduced formally to biologists in 1973 in a *Nature* paper entitled “the Logic of Animal Conflict” (Maynard Smith and Price 1973) and has been used extensively since then. However, prior to the pioneering work of John Maynard Smith, the ideas of game theory were used in evolutionary biology in R. A. Fisher’s work on sex ratio theory (what sex ratio should a female give birth to, given the current sex ratio of the population?), Bill Hamilton’s subsequent work on sex ratio and his introduction of an “unbeatable strategy” (which would give rise to evolutionarily stable strategies), and Lewontin’s work on populations “playing against nature” (Fisher 1958; Hamilton 1967; Sigmund 1993).

Classic game theory models conscious actions and resulting outcomes by individual players; it relies on a premise of rationality and an end goal of utility maximization. How can this method be applied to evolution, to populations of individuals with static traits? Evolutionary game theory plays with Darwinian fitness (instead of rationality) and natural selection (instead of utility maximization). Evolutionary game theory does not require rationality or even conscious thought at all. However, classical game theory does not technically require conscious thought either. The fundamental requirement for game theory is that the success of strategies depends on what others are doing; equivalently, a strategy interacts with the strategy of other actors to determine outcomes. This is perfectly suited to evolutionary systems. Strategies are just traits – phenotypes, in a population – whether the trait is physical, behavioral, or otherwise. Of course, evolutionary game theory does not presume the absence of conscious decision-making; it is equally useful when modeling traits such as cooperation and defection as it is when modeling hair color or genetic conflict.

Evolutionary game theory extends the domain of “games” to include the competition for survival among “agents” – in this case, organisms and

genes. The driving force underlying classical game theory is rational utility maximization, but the driving force in evolutionary game theory is natural selection – in other words, reproductive fitness replaces utility. Finally, “strategies” in evolutionary game theory are biological traits, or phenotypes, that can arise from the interaction between the individual’s genotype (i.e., genetic makeup) and the environment. For example, traits can include brain size, neuronal density, hair color, altruistic decision-making, mate choice preferences, viral deadliness, and aggression in mate competition. Evolutionary game theory models the changes in relative frequency of these traits over time (and over generations) in a population. Its crucial contribution to biological modeling is the ability to interpret situations where an individual’s fitness depends on the proportions of phenotypes in a population and interactions between phenotypes (Nowak 2006a), often exemplified by the value of being a “rare” type in biological systems. For example, if a common virus sweeps through a human population, generally most humans develop an immune response; a new, rare, variant of that virus is far more successful than its precursor. In other words, evolutionary game theory helps us understand frequency-dependent fitness, and phenotypic interaction, both of which are ubiquitous in biological systems (Vincent and Brown 2005).

Like traditional game theory, evolutionary game theory has a solution concept, labeled evolutionarily stable strategies (ESS), which is closely related to the concept of a Nash equilibrium, although those who first described ESS were unaware of Nash equilibria at the time. The defining characteristic of an ESS is that it is “uninvadable” by alternative strategies: when the population is at or near an ESS, that ESS is robust against other strategies. For example, “cooperation” is only a pure evolutionarily stable strategy if the invasion of cheating at low levels would not be favored; indeed, social punishment of cheaters is often seen to be a mechanism by which cooperation remains a stable strategy. In other words, the incremental introduction of alternative strategies cannot successfully invade a population at ESS.

The definition of “pure” versus “mixed” strategies, and their involvement in solution concepts, in evolutionary game theory requires additional explanation. A gene coding for a particular phenotypic trait regardless of environmental involvement is a “pure” strategy for an individual. Imagine a gene in frogs that determines whether a male frog “sings” or “keeps quiet” in its quest to attract a mate. That gene might control with 100% accuracy whether or not a frog sings; in this case, we can describe a solution concept as being a population of “pure strategy” frogs where 30% always sings and 70% always keep quiet. That would be the exact proportion that successfully represents the proportional tradeoff between attracting unwanted attention of predators and attracting the desired attention of potential mates. It is mathematically equivalent to a different scenario: a scenario whereby each individual frog adopts a “mixed strategy” of “sing 30% of the time and keep quiet 70% of the time.” That solution is mathematically identical to a population split between two types of pure strategist frogs.

Biology: Game Theory at Many Levels

Any modern organism is a Russian doll of actually or potentially reproducing units. – Leo Buss (1999)

Selection can act at many levels, and self-interested agents compete for their own purposes in many biological arenas. For this reason, evolutionary game theory has applications in many levels of biological organization, from proteins to populations.

Previously, evolutionary game theory has been conceptualized as two interlocking games: the inner game and the outer game (Vincent and Brown 2005). In the inner game, players interact with one another using “strategies” (phenotypes) and receive payoffs. In the outer game, evolution itself takes place: successful phenotypes (“strategies”) are more frequently passed on, and population phenotypic frequencies alter in response (the inner game and outer game correspond, respectively, to Hutchinson’s ecological theater and evolutionary play (Hutchinson 1965)). In the eyes of evolutionary game theory, a player can be

at one of many levels: a human in a prison; a hyena in a group; a species in a community; an ant colony; cancerous cells within our body; or genes that exist at different frequencies in a population. In classical game theory, players consciously choose strategies from an available array; in evolutionary game theory, players inherit strategies as phenotypes. Further, evolutionary games can have many actors who are strategically identical: same strategies; same payoffs (this can be true of classical game theory as well). In sum, a classic conception of evolutionary game theory maximizes fitness of “agents” by looking at heritable phenotypic “strategies.” In the inner game, mice compete against other mice to gather nutrients and do their best to avoid predators of other species; in the outer game, successful mice pass on their genes which vary in frequency within a population over time.

However, there is a third arena for biological games: within each individual mouse, “strategic genes” (Haig 2012) are playing chess too. As Austin Burt and Robert Trivers write in their landmark book on genetic conflict, “the genes in an organism sometimes ‘disagree’ over what should happen” (Burt and Trivers 2006). For example, whether a particular allele in an individual comes from its mother or father influences its evolutionary “priorities” and subsequent expression, as modulated through a process known as “genomic imprinting” (Haig 2002). (The intriguing phenomenon is too complicated to discuss further here, but refer to ► “Imprinting” in this volume.) Further, genes have many clever strategies to enhance their own transmission, or to change their host’s behavior toward related individuals. Some genes kill off opposing genes and “drive” themselves toward high frequency levels; some genes “overreplicate” to achieve an unfair advantage (Burt and Trivers 2006). Genes interests do not always align with the interests of the organism in which they reside; sometimes they are neutral, and sometimes they even hurt an organism’s fitness. Game theory, in combination with other approaches, can effectively model games between and among genes (Traulsen and Reed 2012). Genetic conflict is a third arena in which competitive or cooperative games play out,

and it is one that clearly influences evolutionary psychology (as we will see below).

Genetic conflict is not the final arena. Just as our own native genes fight with one another, other self-interested players inhabit our body: gut microbes; brain microbes; foreign human cells; viruses; and more are engaged in an ongoing game with our body and each other. These dynamics are perfectly suited to game-theoretical modeling (Nowak 2006a), and these organisms demonstrably impact our psychology and behavior (Kramer and Bressan 2015). The rabbit hole goes deeper still; even proteins folding and enzymes acting in catalytic pathways can be better understood via game theoretical methods (Bohl et al. 2014). But let us not get lost too far in wonderland. Suffice it to note that game theoretical “individuals” in an arena are sometimes arenas themselves.

These interesting, and interlocking, games also complicate a more traditional approach to evolutionary game theory, where “individuals” are coherent beings with unified fitness of all of their parts, instead of arenas where genes and viruses compete for their own selfish interests. We return to this topic below, in “[Frontiers of Game Theory in Evolutionary Psychology](#).”

The Influence of Game Theory on Evolutionary Psychology

Lord, what fools these mortals be! – Robin Goodfellow, *A Midsummer Night's Dream*, William Shakespeare.

Game theory has been helpful in unraveling some of the greatest mysteries in evolutionary psychology. The first and most well-known such contribution involved a series of behavioral experiments in the mid-late twentieth century revealing that our brain has been shaped by evolutionary pressures to think in ways which do not line up with intuitive predictions that our decisions would be guided by rational analysis. These experiments showed that humans are not rational thinkers in a classical sense: we greatly discount the future; are unduly influenced by striking events; exhibit loss aversion, and more. These results opened the door

to questions – which are still the subject of active research – about *what* our brains work to maximize, *how* we process information, and *in what contexts* we depart from pure rationality.

Most subsequent incorporations of game theory into biology concern biological problems which are of interest to evolutionary psychologists, such as sex ratio, parent-offspring conflict (here, we refer to genetic conflict, as described in a previous section), the evolution of language, and the evolution of cooperation (Nowak 2006a). Game theory has helped to model and explain seemingly suboptimal life strategies, such as long-term pairing and cooperation between unrelated humans. It facilitates insights into the maintenance of human psychological variation, and analyses of genetic conflict and subcellular games provide insight into inefficiencies of human behavior and our own social attitudes. Any psychological trait which depends on similar traits in other humans is a good candidate for game theoretical analyses. Below are just a few examples of the wide breadth of research in the field.

Classic Applications: Humans Are Not “Rational”

Game theory's direct influence on evolutionary psychology first arose in the mid-twentieth century, when researchers brought game theory to bear on psychological experiments. This body of work, from the mid-twentieth century to today, is often known as behavioral game theory. A major contribution of behavioral game theory was the observation that human behavior does not line up with what would be expected of a rational, utility-maximizing actor. One of the earliest conducted experiments in behavioral game theory uncovered the Allais Paradox. This describes a phenomenon by which humans given a choice of different lottery conditions make seemingly inconsistent choices with what the expected payoff would be (Allais 1953). The experiment can be written simply as two choices: Test 1 = $[A + X \text{ versus } B + X]$, and Test 2 = $[A + Z \text{ versus } B + Z]$, where each letter represents a payoff and a probability. Since in Test 1, X is consistent between the choices, and in Test 2, Z is consistent between the choices, the rational expectation would be for people to

consistently prefer the first option in both test cases or the second option in both test cases. This, however, is not what experiments demonstrate! Instead, the type of addition contributed by X or Z can make humans, seemingly illogically, choose the first option in Test 1 but the second option in Test 2.

Another classic experiment, which has been repeated with twists for many years, is the “dictator” game, whereby a single player (the “dictator”) can split a cash reward between herself and an assigned receiver (Bolton et al. 1998). She could be given \$10 and decide to split it \$5–\$5, \$7–\$3, \$10–\$0, or anywhere in between. The receiver has no power to reject the split. While it would be “rational” for a dictator to assign all of the money to herself, in reality dictators usually allocate some proportion of money to their receivers. Clearly, humans are not acting solely out of self-interest!

The wealth of behavioral game theoretical studies demonstrates the ways in which humans diverge from purely “rational” behavior. We regret loss more than we appreciate an equivalent gain, we discount the future, we are concerned with building a good reputation, and we change our behavior to benefit others. We are very different than the hypothetical utility-maximizing *Homo economicus*.

Altruism, Cooperation, and Monogamy

Purity is obscurity – Ogden Nash, Reflections on a Wicked World.

Why do humans engage in long-term, formally monogamous pairings? And what can explain our extreme levels of cooperation and altruism? It would seem that such pure actions would be costly to individuals compared with alternatives. However, game theoretical analyses can begin to unravel these mysteries.

We are one of a tiny minority of mammals who exhibit long-term mate pairings. Long-term matings seem to have many fitness costs: for example, committing to one mate means one must forego many other opportunities, and paternity uncertainty means that males risk investing years in someone else’s offspring. In short, it is hard to

explain why individuals with the *opportunity* to mate with many others would not do so. However, when researchers conceptualize long-term relationships as public goods and generate an appropriate game-theoretical model, the payoffs make such an investment worth it (Conroy-Beam et al. 2015). In short, long-term relationships can provide at least three types of payoff: first, mutual investment leads to fewer conflicts of interest than would arise in short-term relationships; second, two-parent investment synergistically combines for a larger resource pool overall; and third, long-term partnership allows for consistent division of labor that leads to specialization and increased efficiency (Conroy-Beam et al. 2015). Further, long-term partnership provides a mechanism to punish “romantic free-riders” who try to drink from the “mutual pool” without investing in it.

Another analysis of monogamy versus polygamy, explained in the book *The Red Queen: Sex and the Evolution of Human Nature* (Ridley 1994) and examined in detail by John Maynard Smith (Maynard Smith and Price 1973), conceives of sex as a game. Imagine a population of polygamous birds, where a new type of “monogamous male” emerges who ends up partnering with one female and raising her offspring, thus increasing the fitness of that baby. Monogamous males are selected over polygamous males. In this manner, monogamy can “invade” a population of polygamy. A more formal mathematical treatment is necessary to demonstrate conditions under which monogamy can resist an invasion by polygamous males.

Robert Trivers, Martin Nowak, Karl Sigmund, and many others have also examined the question of why humans are so cooperative from a game theoretical perspective. (The field is characterized by an ongoing debate between proponents of “inclusive fitness theory,” or kin selection, and its opponents. Interested readers should investigate the primary literature for a more complete account.) Nowak evaluates five mechanisms by which cooperation might evolve, and uses game theory to generate simple rules that must hold true in order for each mechanism to be effective (Nowak 2006b). For example, one of Nowak’s proposed mechanisms for the evolution of cooperation is “direct reciprocity,” whereby you help someone else and

they help you (as if life were a series of repeated Prisoner's Dilemma games). Although it would pay to defect in a one-off Prisoner's Dilemma, things are different in a real-life version of this game, where the dilemma can occur multiple times: over time the strategy of cooperation through direct reciprocity can emerge if the probability of encountering the same individual again exceeds the ratio between costs and benefits of a cooperative act (Nowak 2006b). Similar trade-off equations can be written down for the other four proposed mechanisms: indirect reciprocity, where cooperation buys one a good reputation that moves via gossip among a population, bringing future benefits; kin selection, whereby one's selfish genes are benefited by cooperating with a related individual; network cooperation, where spatial organization plays a role; and group selection, where groups which evolve a cooperative strategy succeed more than anti-cooperative groups (Nowak 2006b).

The evolution of cooperation has been, perhaps, the most exciting and contentious area of game theory (Maynard Smith 1982; Nowak 2006a; Sigmund 1993). It will be examined in greater detail in subsequent sections.

The Persistence of Human Psychological Variation: Rock, Paper, Scissors, Sandpiper

Consider the classic game, "rock-paper-scissors." Rock beats scissors by smashing them; scissors beat paper by cutting it; and paper beats rock by wrapping around it. (Countless children worldwide have shaken their fists at the sky wondering how paper could *possibly* beat rock.) In other words, A beats B, B beats C, and C beats A. Intuitively, we can see that no one strategy is best; the evolutionarily stable equilibrium would be characterized by cycling or by the persistence of stable proportions of different strategies in the population. This may seem to be purely theoretical, but we have now observed many examples of multiple, coexisting strategies in nature. Here is one striking example.

The Ruff, a type of shorebird known as a sandpiper, is so-named for the male's beautiful feather ornamentation reminiscent of Elizabethan collars. However, not all males look the same –

and they do not exist on a continuum, but instead fall into one of three distinct reproductive "morphs:" independent; satellite; and "faeder" (Küpper et al. 2015). Independent males have an elaborate, colored ruff, and display to females in large groups where each male defends a small territory. Satellite males have a white ruff, and mooch off of the independent males' display by lurking around the edges and attracting females when the moment allows. Finally, faeder males are indistinguishable from females; they sneak in and try for quick copulations when females indicate their approval for displaying independent or satellite males. None of these mating strategies is uniformly the best strategy, and the success of one often depends on the persistence of others; indeed, the highest rates of mating overall occur on display grounds which are prominently occupied both by independent and satellite males. Ruffs are Nature's rock-paper-scissors. Intriguingly, these distinct reproductive and behavioral morphs are encoded by a "supergene," a group of genes that are inherited together as a block (Küpper et al. 2015). This unusual genetic mechanism ensures that variation will be maintained in the population, because animals carrying two copies of this inversion cannot survive. In other words, homozygosity is lethal. This is an important genetic feature which drives persistence of multiple phenotypes, and must be taken into account – in addition to the frequency-dependent effects of behavior – in any complete model of sandpipers.

Just as evolutionary game theory helps to explain why the ruff has three consistently present male morphs, it can explain the maintenance of human psychological and cultural variation (Dall et al. 2004; Nettle 2006; Wilson 1998). Stable populations can have multiple strategies, and individual personality traits interact with different tradeoffs of costs and benefits. It is not the case that a single "best" suite of personality traits exists, and formal game theory helps researchers explain why multiple personalities persist in a population.

Here game theory was able to illuminate a truth that was lurking in the shadows, waiting to be noticed.

Frontiers of Game Theory in Evolutionary Psychology

Game theory has already made powerful contributions to evolutionary psychology, as described above. However, there are several frontiers (yet to be explored!) where game theoretical methods will undoubtedly help explain further phenomena. The two most exciting of these are: (i) game theoretical conflicts between “selfish” genes, and their impact on our psyche, and (ii) game theoretical conflicts between non-human inhabitants of our bodies, such as viruses.

The Imprint of Genetic Conflict on our Psyche

I'm afraid that some times / you'll play lonely games too. Games you can't win / 'cause you'll play against you – Dr. Seuss, Oh, The Places You'll Go!

Genes within an organism can have different goals; conflicts within a body between self-interested genes are fertile grounds for game theoretical examination (Burt and Trivers 2006; Haig 2002). Further, this is particularly relevant to evolutionary psychology because genetic conflict is specifically and tightly connected to human behavior and psychology (Haig 2011). “Imprinted” genes, which are a representative hallmark of genetic conflict between maternal and paternal interests, are “highly prevalent” in the brain, with functions ranging from cognition and sociality to synaptic plasticity (Perez et al. 2016). Relationships between mother and child; our attitudes toward close and distant relatives; our respect affinity for and behavior towards maternal versus paternal kin; the timing and nature of sexual maturation; and other traits are all to be likely impacted by the genetic conflict present between genes of maternal and paternal origin (Haig 2011). Indeed, experimental, anthropological, and epidemiological evidence all support the connection between genetic conflict and evolutionary psychology (Haig 2011). For example, certain “imprinting” diseases, which reveal the hidden battle within our genomes, predictably affect behavior and

psychology (see ► “Imprinting”). Beneath these psychological and behavioral patterns lie game theoretical conflicts at the level of the genome.

We can take our inference one step further back: when genes within an organism are fighting, rather than purely cooperating, they will likely lead to suboptimal functioning. War expends resources! Could competition games between genes explain “inefficiencies of mental function” and the “high frequency of pathology in human social interactions” (Haig 2011)? Imprinted genes are particularly enriched in the brain (Perez et al. 2016), and human social interaction is a major determinant of individuals’ fitness. Therefore, mathematical analysis of the relative “strategies” of genes and alleles in opposition could provide fruitful inquiry into human psychological inefficiency and pathology.

Humans: Camper Vans for Competing Microorganisms

Curiouser and curiouser! – Lewis Carroll, Alice in Wonderland.

Humans are not coherent individuals that single-mindedly seek to improve fitness. Instead, our body plays host to a vast array of gut microbes, brain microbes, viruses, and invading human cells that compete to exert influence within the body. Further, these agents – and their game theoretical competition – impact our everyday psychology and behavior, both by accident and by design (Kramer and Bressan 2015). Anxiety, depression, schizophrenia, and more all have demonstrable connections to the small, selfish agents hitching a ride in our bodies.

Influencing the mind is like influencing the president of the USA – the mind can powerfully influence fitness, since it provides executive control (conscious and unconscious) over so many other bodily functions. For these reasons, small, selfish agents have strong motivation to hijack our brains.

A most unsettling example comes from *Toxoplasma gondii*, a unicellular protozoan parasite which passes between the brains of mice and rats and the muscles of cats (and, as it turns out, the

brains of humans). *Toxoplasma*'s life cycle requires that it develops as an egg inside cat intestine; therefore, the mature organism has an incentive to manipulate rats and mice to be eaten by cats. Indeed, in rats, *Toxoplasma* demonstrably makes the rat *less afraid of cats*, slower to react to stimuli, and, in some cases, sexually attracted to cat urine (Webster et al. 2013). Though humans are not intended hosts of *Toxoplasma* (the parasite cannot complete its life cycle after entering a human host because human brains are rarely eaten by cats), *Toxoplasma* can take up residence in a human brain. Recent evidence shows that *Toxoplasma* infection is tightly connected to a wide variety of mental deficiencies, from slow reaction times to schizophrenia and depression (Kramer and Bressan 2015; Webster et al. 2013). Some evidence strongly indicates that it is causal of, not merely correlated with, mental disease (Kramer and Bressan 2015).

The evolutionary dynamics of viruses and other small, selfish agents have recently been unpacked effectively with evolutionary game theoretical methods (Nowak 2006a). Common wisdom holds that a small, selfish invader cannot be too deadly, or it will exhaust its supply of hosts and not be able to be successfully transmitted. This makes sense. But there are many virulent diseases that appear to violate this principle! What dynamics lead to the evolution of virulence? What is the "health" outcome of many small selfish agents competing within a single host? In what context can virulence paradoxically be maintained over time (as in the case of human malaria)? High virulence can be a successful strategy if the population of hosts is large or sub-divided enough that the parasite is not at risk of depleting it. Mathematical analysis indicates that evolution maintains stable proportions of viruses with different levels of virulence over time, and that linkage between ability to infect a host and virulence maintains virulence beyond what would seem to be ideal levels for the parasite (Nowak 2006a). But virulence well in excess of the transmission-viability equilibrium can be selected for as well when different parasites compete within the same "superinfected" host. When a single host is invaded by many

microparasites, they compete; this competition leads to (i) coexistence of parasites with a range of virulences, (ii) higher average virulence to the host than single infection would generate, and (iii) complicated dynamics with the potential for surges in virulence (Nowak 2006a).

The connection between mental health and our microbiome is a trending topic in medicine (Foster and Neufeld 2013). Fecal transplants and oral ingestion of gut bacteria to cure gastrointestinal ills are all the rage, and gut microflora clearly affect mental state (Foster and Neufeld 2013). But in order to properly treat mental illness in connection with our microbiome, we must properly understand the evolutionary dynamics. Competing individual agents interact in complex webs within our body, with the potential for catastrophic spikes (Nowak 2006a). Some of these agents share our interests in bodily health, and some do not. Lest we interfere in the wrong manner, we must employ game theory to understand the connections between and among microorganisms in our body – and their demonstrated effect on our psychology.

V. Limitations of Game Theory

Traditional Game Theory: Poor Assumptions about Humanity?

Man is many things, but he is not rational – Oscar Wilde, *The Picture of Dorian Gray*.

Many real-world phenomena interfere with our predictions about human behavior and reasonable solution concepts for a given game. Humans are not always rational in an economic sense; myriad factors can interact to influence the outcome of a game (including, for example, intangibles such as social pressure). It is possible that humans are rational, but that we cannot conceive of all perceived costs and benefits, nor quantify them. Behavior which may seem irrational, because it comes at a cost to the individual while helping a stranger, might actually serve a "hard to quantify" purpose, such as building reputation or providing a "warm glow" of good feeling to the helper. Thus, classical game theory cannot always

estimate the sum of people's true utility. It has also faced some methodological criticism: for example, laboratory experiments cannot be a perfect proxy for reality (Gintis 2009). People are aware that they are in an experiment and behave in unusual ways.

Further, a "trembling hand" or "fuzzy mind" is used as shorthand for the prevalence of mistakes, behavioral or phenotypic, that might lead someone to mistakenly play the "wrong" strategy or misremember what their opponent has done so far. In more detailed examinations of game theory, theorists and experimentalists test proposed solution conceptions against "trembling hands," or occasional errors. Since the real world is filled with errors, a solution strategy must be robust against a "trembling hand" (rather than irrevocably altered by one). It is said that "close" only matters in horseshoes and hand grenades; we now know that "close" should also matter for successful game theory solution concepts!

Complications of Heritability and Individuality: A Crisis for Evolutionary Game Theory?

In physics, every crisis is an opportunity – Richard T. McCoy, *Physics of Time* (The Princeton Time Project).

The aforementioned complications about genetic conflict, and the multiple hierarchies of players within a single body, raise two major criticisms of evolutionary game theory at high levels. Generally, in evolutionary game theory, we deal with "individuals" who pursue high "fitness" for themselves. Both "individual" and "fitness" encode hidden assumptions.

The maximizing principle of "fitness" assumes that selection operates on observable, heritable phenotypes in a direct and effective manner. For example, the trait of "cooperation" in a population is often modeled as a simple, consistent, and perfectly heritable trait, although in fact it can be (i) influenced by the joint action of many unlinked genes, (ii) variable in different environments and across contexts, and (iii) underpinned by complex gene-on-gene battles. In fact, a fascinating result

from a type of colonial marine invertebrate, ascidians, demonstrates that apparent superficial cooperation – the fusing of two colonies – is in fact a brutal example of parasitism, where one colony becomes disproportionately represented in the germline (Buss 1999). Although the colonies seem to be fusing and sharing resources, one wins the Darwinian game and one loses. If we were to model this as a game without full knowledge, it would seem that both players benefit from the arrangement – and this is clearly not the case. This is an illustration of a now well-known theory: that the history of life is a history of "conflicts between units of selection" (Buss 1999). Characteristic features of life's organization – such as mitochondria within a cell, microbes within a body, ants within a colony, and so forth – evolve to suppress parasitism at lower levels. Is all apparent cooperation underpinned by conflict? Games are not always as they seem.

Second, "individuals" are really complicated battlegrounds for bacteria, viruses, warring genes, "chimeric" cells from distinct genetic individuals, and more. A marmoset, for example, is born as one of a nonidentical twin pair that freely swaps cells in the womb (Haig 1999). That is, an "individual" marmoset is actually a composite of two genetic individuals – a mosaic of cells with two distinct genomes, one being "itself" and the other its twin. In an evolutionary game, is an individual marmoset pursuing fitness for itself, its body? Or for a genetic individual? *Which* genetic individual? These are not simple questions. Further, humans often conflate evolutionary fitness with lifetime happiness; however, often the brain works in ways that seem counter to our day-to-day happiness but have understandable evolutionary underpinnings.

Does our richer understanding of heritability and the dynamics between levels of selection render high-level game theory useless?

In a word: no; high-level game theory is still fruitful. (Otherwise, this could have been a much shorter chapter.) Unless we have reason to suspect particularly unusual mechanisms of inheritance, the fact of heritability, rather than the details thereof, is often sufficient for game theoretical purposes (Vincent and Brown 2005). Darwin did

not even know what the unit of heritability might be – he merely postulated that like begets like, organisms struggle to exist, and heritable traits influence the struggle. The mechanisms of inheritance are useful for many purposes, but they are not *particularly* essential to studies of broad evolutionary dynamics.

Nonetheless, it is worth being aware of complications of heritability, particularly those arising from genetic conflict. Indeed, these complications are more “opportunity” than “crisis:” they provide fertile ground to employ game theoretical methods at many levels, from proteins to populations.

In *A Brief History of Time*, Stephen Hawking relays the following anecdote: “A well-known scientist (some say it was Bertrand Russell) once gave a public lecture on astronomy. He described how the earth orbits around the sun and how the sun, in turn, orbits around the center of a vast collection of stars called our galaxy. At the end of the lecture, a little old lady at the back of the room got up and said: “What you have told us is rubbish. The world is really a flat plate supported on the back of a giant tortoise.” The scientist gave a superior smile before replying, “What is the tortoise standing on?” “You’re very clever, young man, very clever,” said the old lady. “But it’s turtles all the way down!””. Countries compete on Earth, political parties compete within countries, humans compete within political parties, and viruses compete within humans: it’s game theory all the way down!

Conclusion

Game theory, and its cousin Evolutionary Game Theory, have set the stage for evolutionary psychology on multiple levels. Game theory provided mathematical tools for interpreting systems where individual success depends on the strategies of others – i.e., all human interactions. It also revealed truths about the human brain- that we are not rational according to economic definitions, and that interesting features of the mind lurk in areas where we deviate from predicted rationality. Evolutionarily game theory placed these methods and topics into a biological context, which allows

us to interpret complicated phenomena such as the evolution of altruism and monogamy. Games are played in many arenas ranging from the internal wiring of our brain to complicated displays aimed at attracting a life partner to international politics. Perhaps one day games will be played among the stars. In all of these domains, the game theory will illuminate many secrets waiting to be discovered.

Cross-References

► [John Maynard Smith](#)

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Gamete Dimorphism

► Production of Eggs and Sperm

Gamete Size

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Synonyms

Reproductive cell size; Sex cell size

Definition

The sizes of reproductive cells in sexual reproduction.

Introduction

Female gametes are larger than male gametes. This is not an empirical observation, but a definition: in a system with two markedly different gamete sizes, we define females to be the sex that produces the larger gametes and vice-versa for males (Parker et al. 1972), and the same definition applies to the female and male functions in hermaphrodites. Although asymmetry in gamete size rather than number is usually used as the defining characteristic, size dimorphism has the almost inevitable consequence that females produce fewer gametes than males due to a simple physical trade-off – larger things can be produced in smaller numbers, given a limited amount of resources. Therefore, in practice females differ from males in terms of both gamete size and numbers. This definition of the two sexes is a very simple one, yet it leads to some intricate, surprisingly difficult, and even controversial questions concerning both the origin and consequences of gamete size dimorphism. Given that these questions relate directly to the origin of the two sexes, this is a topic that captures the attention of scientists and the public alike.

Isogamy and Anisogamy

Anisogamy refers to gametic systems where gametes are dimorphic in size: one gamete type is larger (e.g. ova) than the other (e.g. spermatozoa), and gametic fusion occurs only between the larger and the smaller gametes, while *isogamy* implies that all gametes are of similar size (Lehtonen and Parker 2014). Therefore, only anisogamous species can be said to have male and female gametes, and in this sense the origin of anisogamy is synonymous with the origin of the two sexes. Both isogamous and anisogamous species exist today, with a fascinating range of organisms from isogamy all the way to highly dimorphic anisogamy, and our ancestors were almost certainly isogamous (Lessells et al. 2009). Given that our ancestors had a gamete size ratio of 1:1, why is it that a ratio of 10^6 :1 is now not uncommon in nature?

Evolution of Gamete Size

Theoretical work over several decades has focused on understanding the selective pressures that result in disruptive selection on gamete size. An early model (Kalmus 1932) showed that if a fixed amount of total provisioning from gametes is required for zygote development, then under some conditions the highest population-wide rate of successful fertilizations is achieved if gametes are highly dimorphic. However, this argument relied on outdated group selection thinking, and the first argument fully grounded in individual level selection was based on competition between gametes for fertilizations (Parker et al. 1972): while ‘proto-females’ (parents producing large gametes) can produce zygotes with high survival, ‘proto-males’ (producing many small gametes) gain a large fraction of fertilizations with these large gametes, benefitting from their zygote provisioning in an almost parasitic way. There are therefore incentives to increase gamete size on one hand (higher offspring survival), and increase gamete numbers on the other (larger proportion of total fertilizations via primordial sperm competition). Here selection is not assumed to benefit the group or species, but is driven largely by individual level benefits in competition for fertilizations. These two approaches have often been called ‘gamete limitation’ and ‘gamete competition’ theories for anisogamy evolution, and the gamete competition theory (Parker et al. 1972) has been widely accepted as a likely evolutionary explanation for anisogamy. However, it has since been shown that these theories are not mutually exclusive, and can in fact act in the same direction and reinforce each other (for a review of gamete limitation and gamete competition theories, see Lehtonen and Parker 2014). There is also an alternative suite of theories that are based on so-called intracellular conflicts: evolutionary conflicts of interest between cytoplasmic and nuclear genes carried by gametes. These theories originate with Cosmides and Tooby (1981), and are reviewed in Lessells et al. (2009). However, current evidence suggests that intracellular conflicts are unlikely to be the main driver of the

evolution of anisogamy (Lessells et al. 2009). Although models of anisogamy evolution generally predict a unidirectional divergence in gamete sizes, it is also possible for sexual selection to drive a secondary increase in sperm size, such as in some *Drosophila* species (Lüpold et al. 2016). Although sperm size can secondarily approach egg size in these cases, this is not an evolutionary reversal per se, as the two gamete types remain clearly morphologically distinct.

Evolutionary Consequences of Gamete Size Dimorphism

Given that we have an understanding of evolutionary pressures that select for gamete dimorphism, the next obvious question is whether an asymmetry at the gamete level selects for further asymmetries at the organism level. Is there a logical, causal link from gamete size to morphological or behavioural traits that are observed in males and females in nature? Should we expect one sex to be more competitive over fertilization opportunities than the other? Should we expect one sex to more commonly care for offspring than the other? These are not new questions. In 1871 Charles Darwin already wrote *‘We are naturally led to enquire why the male, in so many and such distinct classes, has become more eager than the female, so that he searches for her, and plays the more active part in courtship. It would be no advantage and some loss of power if each sex searched for the other; but why should the male almost always be the seeker?’* (Darwin 1871). Bateman (1948) later provided a famous empirical justification for why males should be more strongly selected to compete for matings: his experiments showed that male fertility in *Drosophila* is more dependent on frequency of insemination than female fertility. Bateman’s result is still very influential, but there is nevertheless lingering controversy over whether differences in gamete size really drive sex-specific selection patterns. A recent theoretical argument demonstrates how such a link can come about using simple principles of resource trade-offs and fertilization probability (Lehtonen et al.

2016): As a thought experiment, imagine an ancestral organism where males and females are initially absolutely identical apart from differences in gamete size. Next, decompose fitness w into two multiplicative components, gamete number n and probability of fertilization of each gamete p , so that $w = np$. Assume there is a trade-off between resource investment into gamete number n and into a sexually competitive trait that increases p . This trait could be anything that affects fertilization probability, either at the organism level or gamete level, such as male-male combat or faster swimming sperm. Now, because male gametes outnumber female gametes (often by a very large margin), it is possible that $p = 1$ for females, but not for males, and in most cases, p is inevitably much lower than 1 for males. Therefore, as long as fertilization probability of female gametes is high (p close to its maximum value 1), it is clear that males are more strongly selected to divert resources to sexually competitive traits that increase p . The asymmetry in gamete numbers therefore creates a simple asymmetry in gamete-level fertilization probabilities, which creates asymmetrical, male-biased selection to increase this fertilization probability. This asymmetry can be shown to persist even when female fertilization is incomplete ($p < 1$ for females as well as males), although the asymmetry does diminish with increasing sperm limitation (Lehtonen et al. 2016). Recent theory (Fromhage and Jennions 2016) also confirms that individuals benefit less from caring for their offspring when they face stronger sexual selection and/or lower certainty of parentage, both of which are often expected to be associated with smaller and more numerous gametes. The latter is clearest under internal fertilization, where a female who receives gametes from males can be sure that she is the mother of the offspring that she carries, even if she and her male partners have had multiple mating partners. A male, on the other hand, can only be certain of paternity if he is certain that his mating partner has not mated with anyone else. Therefore males run a risk of caring for offspring that have been fathered by others, creating an asymmetry in the benefits of parental care.

Conclusion

Gamete size is the defining feature of the male and female sexes. Our ancestors were isogamous, meaning that they produced gametes of just one size, and hence had no separation into male and female gametes or male and female sexes. The evolutionary origin of the two sexes is therefore intimately tied to the evolutionary divergence of gamete sizes, which in turn is likely linked to the trade-off between provisioning zygotes with large gametes, and producing a larger number of smaller gametes. Although some controversy has surrounded the connection between gamete size and the subsequent evolution of sex-specific behavioural traits that we observe in nature, evolutionary theory now also demonstrates clear logical connections between gamete size, sexually competitive traits, and parental care.

Cross-References

- [Parental Investment and Sexual Selection](#)
- [Paternity Uncertainty](#)
- [Sexual Selection](#)
- [Sexual Selection via Direct Male-Male Interactions](#)

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Gametes

- [Production of Eggs and Sperm](#)

Gang Affiliation

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Synonyms

- [Coalition alliance](#); [Gang membership](#)

Definition

Membership in a group wherein its members have a high degree of interaction, similarity, as well as mutual interests and goals that are often achieved via criminal means.

Introduction

Membership in gangs is associated with increased involvement in violent crime (Bjerregaard and Smith 1993; Esbensen and Huizinga 1993). This presents obvious risks, including the potential to be physically harmed during violent altercations and to be prosecuted for crimes committed. Given these risks, there are likely benefits of gang affiliation that offset these costs. Here we describe the structure of gangs and what benefits might accrue to members of gangs.

Entitativity of Groups

Groups vary in the extent to which they are perceived as a coherent entity; this entitativity or “groupiness” (Dasgupta et al. 1999) is determined by a number of factors. In particular, entitative groups exhibit a high degree of interaction, rate membership in the group as important, have shared goals, mutually dependent outcomes, a high degree of similarity across members, low permeability, smaller size, and a long duration (Lickel et al. 2000). Gangs exhibit many of these characteristics. Indeed, when participants were asked to rate the entitativity of forty different groups, gangs were rated in the top five of the most entitative groups (Lickel et al. 2000).

Entitative Characteristics of Gangs

Over many years researchers have developed a variety of definitions that attempt to paint a picture of the essence of gangs. Thrasher (1963) defined gangs on the basis of six characteristics: cooperation as a result of external hostility, direct relations, organization, spontaneous origin, common tradition, and partiality for a particular geographic area. Many of the characteristics described by Thrasher (1963), as well as others discussed below, map on to attributes of entitativity. First, there is a high degree of interaction, particularly considering their preference to occupy a particular territory or geographic area. Indeed, proximity to a gang, and therefore an increased likelihood of

interaction with gang members, is a major risk factor for joining a gang (Decker and Curry 2000).

Individuals’ motivation to join gangs reflects their shared goals and high degree of interaction. Decker and Curry (2000) examined factors that influenced individuals to join gangs. These factors include status obtained through interactions within and outside of one’s specific gang, respect among peers, family affiliations within gangs, protection from external dangers, and access to mating opportunities. Miller’s (1980) definition of gangs also exemplifies the shared goals and outcomes among gang members: “A youth gang is a self-formed association of peers, bound together by mutual interest, with identifiable leadership, well-developed lines of authority, and other organizational features, who act in concert to achieve a specific purpose or purposes” (1980, p. 121). Based on Miller’s definitions the basic structure of gangs may not be all that different from other groups; however, the shared goals of members (e.g., acquisition of power and resources) tend to be manifested in the form of criminal activity.

Although gang membership is not isolated to any particular demographic, research suggests that males, Hispanics, and Blacks are more likely to be involved in gangs than females or other races (Hill et al. 1999). Moreover, there appears to be a high degree of similarity within gangs on the basis of socioeconomic status, ethnicity, race, and religion. For example, gangs present in other nations have a strong degree of religious homogeneity (Covey 2003). Homogeneity of gang membership on the basis of race, sex, and ethnicity, within gangs, has been documented in the United States, as well as Canada (reviewed in Martin 2005) and the United Kingdom (Covey 2003). Gangs also express their similarity through their shared identification under a particular group name (Klein 1971).

Average size of gangs, as well as the duration and permeability of membership is difficult to determine because there are varying degrees of gang involvement. Membership may consist of peripheral followers that only socialize with the gang, solidified but short-term membership, and extremely loyal and committed, long-term members. Thus, on the whole gangs may be large and

permeable (some of the largest gangs in the United States have 8,000–10,000 members; Swecker 2005), but the core group of veteran members is likely to be small, difficult to penetrate as a new member, and of long duration. Moreover, this highly structured, hierarchical nature of gang membership likely also contributes to the perception of entitativity.

Overall, this information is helpful in describing gangs, yet does not provide an explanation for why gangs exist, for that it is useful to turn to an evolutionary perspective.

An Evolutionary Perspective on Groups

Throughout human evolutionary history living among other people afforded humans many advantages, including the ability to: acquire and protect resources and territory necessary for survival, practice specialized labor, select long-term mates, and be protected from predators and conspecific threats. Given the many advantages to group living afforded to our evolutionary ancestors, it is not surprising that modern humans express a strong motivation to “belong” to groups (Baumeister and Leary 1995). Even more telling is the psychological distress experienced by individuals who are excluded from a group, even when that group is novel and relatively unimportant for one’s social identity (Williams 2009). These features of human psychology are indicative of psychological mechanisms that function to increase reproductive fitness by promoting the formation and maintenance of group bonds.

Among humans’ hunter-gatherer ancestors, groups existed at multiple levels, ranging from small kinship-based bands (25–100 individuals) to tribes of multiple kin groups, and large societies that encompassed many individuals sharing the same cultural system or language in a particular region (a few hundred or thousand individuals) (Wrangham and Glowacki 2012). Reviewing the anthropological evidence, Gat (2015) has suggested that conflict occurred between groups at all of these levels. This shifting of coalitional alliances suggests that humans are likely equipped

with flexible cognitive machinery for adopting novel coalitional memberships, and quickly detecting the relevant coalitions in a given environment.

Indeed, research supports both claims. Research on “minimal groups” has demonstrated that individuals who are assigned to a novel group on the basis of largely arbitrary criteria, such as a coin flip, painting preferences, or the tendency to over- or underestimate dots, display a preference for their minimal ingroup members over the outgroup (e.g., Tajfel and Turner 1986). Moreover, research by Kurzban et al. (2001) has demonstrated that individuals encode novel coalitional memberships on the basis of cues of verbal allegiance and visual similarity (i.e., shared style of dress), even when they are not told to do so. Overall, these findings suggest that humans may be quite tribal, able to quickly adopt group identities that may serve their interests, and to quickly identify the coalitional alliances of others in the local environment.

The Function of Gangs

Gangs appear to serve a similar function as coalitional groups did for our evolutionary ancestors. Members are often connected by kinship, they work together to protect their territory, and to acquire and defend their group’s resources. Moreover, they engage in aggressive behavior against other groups to increase their access to resources. That gangs tend to achieve these goals through illegal activity is likely a result of the low socioeconomic status of the members, and the lack of opportunities to ascend a status hierarchy using legal means. Strong loyalty to one’s gang likely facilitates greater ability to protect one’s resources in a highly volatile environment where intergang conflict is common. Gang signs, symbols, and names serve as indicators of membership and further perpetuate the strong divisions that exist between rival gangs.

The tendency for gangs to be largely male dominated (Jaggers et al. 2013) is also consistent with evolutionary theorizing. The theories of

parental investment and sexual selection are necessary for understanding why this is the case. Parental investment theory (Trivers 1972) argues that differences in the reproductive physiology of males and females incentivize different reproductive strategies. In particular, males and females differ in the minimum level of investment that is required of each sex to produce viable offspring (Trivers 1972). The obligatory investment for males ends after fertilization, but females bear the costs of gestation, birthing, and lactation. Men and women also differ in the length of their reproductive lifespan, with men capable of producing offspring for far longer than women. As a result, over a lifetime men can produce many more offspring than women.

As the lower investing sex with a longer reproductive lifespan, males benefit to a greater extent than females from engaging in competition with other males for access to mating opportunities. Through the process of intrasexual selection, this male-male competition exerts selection pressure for traits that increase success in competition. These traits include physical features, such as greater muscle mass and upper body strength (reviewed in Sell et al. 2012), as well as psychological characteristics, such as a greater inclination to use aggression and a stronger desire to achieve high status, compared to women (Archer 2009).

Competition among males for access to reproductive resources may be direct, such as physical contests for sexual access to mates, and indirect in the form of competition for resources that can be leveraged to increase one's appeal to females, including status. Importantly, this competition for increased resources can occur within a group, but also between groups, where one group of men attack another group to take their resources (McDonald et al. 2012). Overall, this perspective suggests that the greater tendency of males to engage in violence and aggression is due to the reproductive benefits awarded to males who succeed in male-male competition.

In contrast, there are comparatively low pay-offs available to women who invest heavily in competition with other women. Females' large investment in offspring makes their presence

particularly important in the survival of offspring. Indeed, the death of the mother is more likely to lead to the death of the child than the death of the father, an effect which is particularly dramatic in the first year of life (Campbell 2005). Thus, the costs of aggression for women are extremely high, and likely created selection pressure to inhibit aggressive behavior.

Given these sex differences in reproductive strategies and intrasexual competition, it is not surprising that gangs are largely comprised of men. There are greater reproductive incentives for them to protect and defend a territory that provides them with resources, particularly given that doing so often requires violent competition. Evidence for this comes from research demonstrating that male gang members, particularly those in high-status positions, have higher mating success than non-gang members (Palmer and Tilley 1995). That this behavior is relatively rare in females is consistent with the fact that engaging in violent competition for access to reproductive resources is less able to be converted to reproductive resources in women, and is potentially very costly if it leaves a woman unable to care for her offspring (Campbell 2005).

Conclusion

Gangs represent a highly cohesive group, displaying many features of entitativity. Membership in gangs appears to serve many of the same benefits as were afforded to our evolutionary ancestors living in groups, namely acquisition and protection of resources and territory, increased mating opportunities, and protection from conspecific threats. Thus, although entrance into a gang comes with great costs, the benefits of membership appear to outweigh its risks, particularly for men.

Cross-References

- [Access to Resources](#)
- [Group Living](#)

- [Male Coalitions for Hunting](#)
- [Social Dominance and Sexual Access](#)

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Gang Attacks

- [Chimpanzee Raiding](#)

Gang Membership

- [Gang Affiliation](#)

Gaps in Darwin's Initial Theory

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Synonyms

[Criticisms of Darwin's work on natural selection;](#)
[Shortcomings in the *Origin of Species* related to](#)
[Darwin's/Wallace's theory of natural selection](#)

Definition

Shortcomings in and criticisms of the theory *Origin of Species* related to Darwin's/Wallace's theory of natural selection and how those gaps were filled.

Introduction

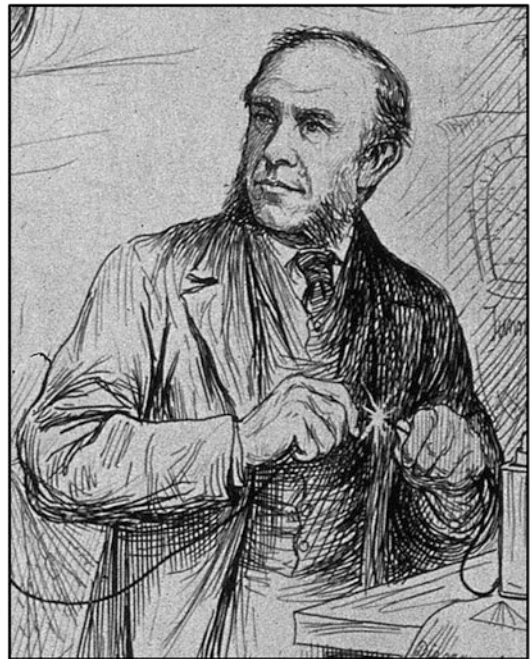
This entry focuses on gaps in the initial theory of Charles Darwin in his 1859 book *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* and its six subsequent revisions. This work can be summarized as two major arguments (Bowler 1989): First, it argued that species evolved via a process of “descent with modification.” Second, it argued that this process was driven by natural selection, an evolutionary mechanism co-discovered with Alfred Russel Wallace that required a struggle for existence, variation with fitness consequences, and inheritance of that variation. This work remains standing as a centerpiece of current evolutionary thought. Despite this, acceptance of Darwin's work was never smooth sailing, as it faced a mix of criticism and praise from scientific and societal communities. Some bona fide gaps in the original theory were exposed by these critiques. Darwin was clearly moved by some of the criticism, as is

evidenced in the book's revisions and in his correspondence with intellectual contemporaries. Other gaps existed but it is unclear whether Darwin recognized them.

By necessity, the coverage of gaps in this entry is somewhat selective but includes (a) arguably the most important gap in the lack of a proper understanding of genetics; (b) gaps of immediate relevance to researchers interested in the evolution of human behavior, including evolutionary psychology, in the theory's inability to explain seemingly maladaptive traits; and (c) gaps in the macroevolutionary claims in Darwin's early work which are of relevance for understanding the early theory's relevance for human evolution.

Fleeming Jenkin's Critique

In 1867, Scottish engineering professor, Fleeming Jenkin (Fig. 1), published a review of *Origin of*



Gaps in Darwin's Initial Theory, Fig. 1 Fleeming Jenkin, a Scottish engineer, published a three-part critique of Darwin's initial theory. Darwin conceded to Jenkin with regard to the inheritance of variation but was unmoved by his criticism that the earth was insufficiently old. (Henry Charles Fleeming Jenkin. Etching by W. Holl, 1884. Credit: Wellcome Collection. CC BY)

Species wherein he advanced a three-part critique of Darwin's ideas (Gayon 1998). The critique exposed two gaps in the initial theory and another that rested on reasonable-for-the-time theory that was later disproved.

The most famous of his criticisms centered on the inadequacy of blending inheritance, the mechanism favored by Darwin and his contemporaries, for sustaining natural selection (Charlesworth and Charlesworth 2009). Even when a trait confers a selective advantage, offspring fail to inherit it due to the “swamping effect” of blending. Rather, they will inherit a phenotype intermediate between their mother’s and father’s. Despite Jenkin’s belief that this was problematic for the inheritance of small changes, but not large ones (referred to as “sports”), Darwin’s theory rested on the accumulation of small changes. Darwin conceded to Jenkin in subsequent editions of *Origin of Species* and in a letter to Wallace. Jenkin’s criticism lost its bite with the eventual acceptance of Mendel’s principles, which were published 2 years prior to the publication of Jenkin’s review, but did not receive wide circulation until the turn of the twentieth century (Bowler 1989; Charlesworth and Charlesworth 2009; Gayon 1998). This paved the way for the “Modern Synthesis” – a new understanding of evolutionary processes and their consequences based on a tying together of Mendel’s and Darwin’s (and Wallace’s) ideas.

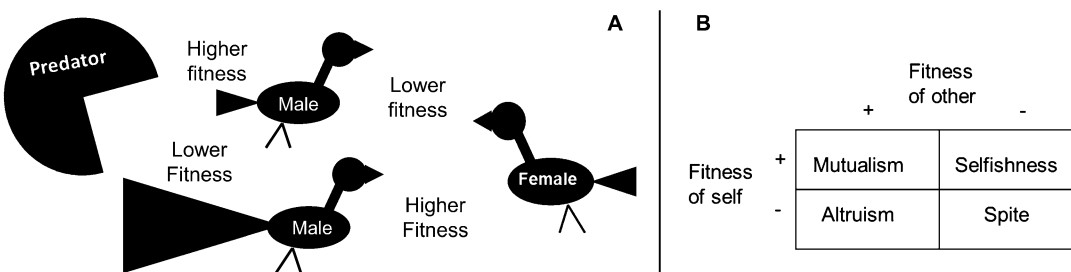
Jenkin offered two additional points of criticism (Gayon 1998). The second was that variability within a species was bounded and that natural

selection, thus, was insufficient to drive speciation. This is discussed in further detail below. The third criticism was that the earth was insufficiently old to have supported the evolution of its diverse life forms. This was a direct refutation of geologist Charles Lyell’s findings, on which Darwin’s theory was propped, that the earth was sufficiently old to have allowed “virtually unlimited amounts of time” (p.206) for evolution to have occurred (Bowler 1989). Jenkin’s point here was based on a critique of Lyell’s work by Lord Kelvin. Darwin was unconvinced by this part of Jenkin’s criticism, which was for the best as Kelvin was proved wrong by advances in early twentieth century physics (Bowler 1989).

Explaining Seemingly Nonadaptive Traits

Darwin (1859) viewed his theory as providing a mechanism that would favor individually beneficial traits, never those that were “injurious to itself as natural selection acts solely by and for the good of each” (p.201). Explaining the existence, and thus evolution, of seemingly nonadaptive traits – such as aesthetic displays and altruism – was a gap in Darwin’s initial theory (Fig. 2).

Darwin felt that his initial theory could not explain the evolution of exaggerated or purely ornamental features on the basis that they appeared nonadaptive (Bowler 1989; Cronin 1991; Jones and Ratterman 2009). In a letter written in 1860 to his friend, American botanist Asa Gray, he opined that “the sight of a feather in a peacock’s tail, whenever I gaze at it, makes me



Gaps in Darwin's Initial Theory, Fig. 2 Nonadaptive traits posed a problem for Darwin's initial theory: (a) extravagant displays, such as the peacock's train, were viewed as nonadaptive in the context of regular natural selection; as shown on the left, they might attract the attention of or slow the escape from predators. Darwin later elaborated the theory of sexual selection which can

favor these traits when they provide a mating benefit (as shown on the right). (b) Altruism, defined as behavior that benefits others at a cost to individual fitness, was a problem for Darwin's original theory that took a century to solve. There is a debate over whether Darwin himself recognized it as a problem

sick!” Darwin presaged his eventual solution to the problem in *Origin of Species*, but it was in his second major work, *The Descent of Man, and Selection in Relation to Sex* (Darwin 1871), that he detailed the theory of sexual selection. In essence, he argued that it worked via two mechanisms: female choice (intersexual selection) and direct male-male competition (intrasexual selection). Darwin and Wallace disagreed about both mechanisms. Wallace argued that female choice could not have driven evolution and that traits that may have arisen via male-male competition, such as an elk’s antlers, would evolve via regular natural selection for utilitarian purposes. Although Darwin was correct in essence, and there were some advances in the interim, sexual selection did not become part of the canon of evolutionary theory until the second half of the twentieth century (Cronin 1991).

Another problem with Darwin’s initial theory was its inability to explain the evolution of altruism – those behaviors that provide a fitness benefit to others while incurring a cost to the actor (Cronin 1991; Dugatkin 2007; Ratnieks et al. 2011). Altruism includes, of course, traits such as alarm calling and providing care to young by parents and others. Darwin singled out the evolution of sterile workers in honeybees, something that today is viewed through the lens of altruism, as posing a “special problem” for his theory (Darwin 1859, p.236). While some see this as evidence that he puzzled over the evolution of altruism (e.g., Dugatkin 2007), others argue that he never recognized the problem as such (Cronin 1991; Ratnieks et al. 2011). Regardless, it was a gap in the initial theory, and a satisfactory solution, despite being presaged by Darwin and others following him (Dugatkin 2007), was only offered with the formulation of inclusive fitness theory in the later half of the twentieth century. The delay in resolution, though certainly attributable to a multitude of factors, may have been caused to some degree by the debate over individual versus group selection (Domondon 2013; Ratnieks et al. 2011).

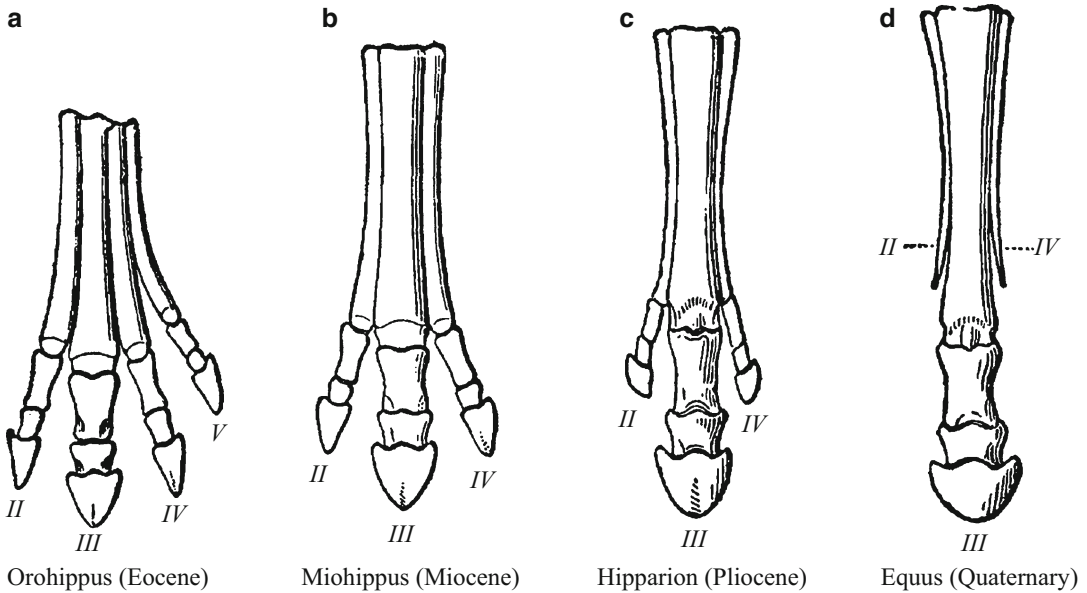
The Origin of Species and Transitional Forms

The lack of evidence for the second of Darwin’s main claims, and the element of the theory from which derived the name of his most famous

work – that natural selection would lead to the origin of new species – was an important problem for his theory. Huxley, for instance, who was otherwise one of Darwin’s most vociferous allies (his “bulldog”), argued that the most conclusive evidence for selection would come when it can be shown to “produce a new species” (as quoted in Bowler 1989, p. 195). Darwin’s erroneous ideas about what constituted a species have been pointed out as another weakness (Mallett 2008). Nonetheless, Darwin’s ideas about the mechanisms that would drive speciation – geographic isolation – mirror modern ideas on allopatric speciation but downplay the ability of speciation to occur without it, which is today referred to as sympatric speciation.

Another related gap in the initial theory was the lack of “transitional forms” (Bowler 1989). Darwin claimed in *Origin of Species* that fossils supported his theory but understood that there were weaknesses in the evidence. For instance, he argued at length that the gap-like nature of the record inevitably leads to the sudden appearance of species and the lack of transitional forms (Bowler 1989). Given this, he posed a strikingly indifferent stance on the appearance of clearly transitional forms found shortly after the first publication of *Origin of Species*. For instance, despite his close ally’s gradual support for *Archaeopteryx* as transitional between reptiles and birds, Darwin included only one timidly phrased sentence about it in later revised editions. Gawne (2015) argues this may have been due to Darwin’s position on species and his desire for more complete sequences (i.e., successions) rather than “missing links” such as those discovered later for early horses (Fig. 3), which Darwin called the “best support for the theory” (p.1082).

Finally, Darwin notably steered clear of applying his theory to human evolution in *Origin of Species* (Darwin 1859) but covered it in depth in his later writings, particularly *Descent of Man, and Selection in Relation to Sex* (Darwin 1871). Part of the explanation was Darwin’s worry that his ideas would be condemned on religious or moral grounds, but it was probably also due to the lack of the sorts of evidence for human evolution that we have today (Tattersall 2009). Neanderthals had been discovered a year before the



Gaps in Darwin's Initial Theory, Fig. 3 The lack of transitional forms was a gap in the evidence to support Darwin's initial theory. Later work, such as Othniel Marsh's fossil horses which showed a progressive

evolution toward a single toe, pictured here, was viewed as important evidence (Gawne 2015, p.1082). (Image: public domain)

publication of *Origin of Species*, and Darwin mentioned them in his later work. The more transitional, ape-like *Australopithecus* was not discovered until the first half of the twentieth century.

Conclusion

This entry focused on gaps in Darwin's initial theory – a theory he co-discovered with Wallace and then elaborated in his 1859 book. Rather than providing an exhaustive account of the perceived and real problems with the work that originated from the scientific community and from society at large, the entry has focused on a sample of gaps chosen for their relevance to evolutionary psychologists and others interested in the evolution of human behavior. In doing so, it should be clear that, although Darwin was fallible and not right about everything, he was a careful and thoughtful scholar, and the criticisms led to a refinement of his ideas where that was possible and necessary. This is in large part, along with its sheer simplistic elegance, why Darwin's early theory remains standing as a centerpiece of current evolutionary biological thought.

Cross-References

- ▶ Alfred Russel Wallace and Charles Darwin
- ▶ Charles Darwin
- ▶ Charles Darwin: Theory of Sexual Selection
- ▶ History of Inheritance
- ▶ Impact of Early Theory on Charles Darwin
- ▶ Puzzle of Altruism, The

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Garment

► To Afford Protection Against Climate and Weather

Gathering Returns When Nursing Infants

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Synonyms

Feeding offspring; Lactation; Nursing

Definition

Benefits of nursing

Introduction

Nursing is a crucial aspect of maternal care as it helps with the important evolutionary benefit of infant survival and growth. As such, mammals may have evolved to nurse their infants quiet intuitively, albeit bearing some costs (Noonan and Rippeyoung 2011). These costs mainly stem from the fact that mothers require adequate energy to meet both maternal and offspring needs. For instance, some mothers of species that are relatively smaller in size may face higher energy demands due to the large correlation between maternal size and milk output (Ofstedal 1984). Lactation for these mothers may sometimes require energy demands that may be greater than any other time in life (Prentice and Prentice 1988). This may also be the case for species that produce large litters as these mothers would need to have enough physical resources to meet the requirements of the large litter of infants as well as for the mother herself (Rogowitz 1996). However, there may be evolutionary mechanisms that help attenuate these costs and increase the benefits associated with nursing.

However, the costs associated with nursing are sometimes overemphasized. This is suggested to likely stem from implicit misconceptions associated with the parent-child conflict theory (Roulin 2002). Parent-child conflict depicts that parents and offspring may have opposing interests with regard to how much parents should invest in their offspring. However, this may be perceived as if investment in offspring will always come at the cost of parents' somatic energy (Trivers 1974). However, this may not always be the case. For example, in the case of nursing parent-child conflict theory suggests that it may be in the best interest for the lactating mother to wean the offspring sooner while it may be in offspring's best interest to resist weaning for as long as possible. However, nursing the offspring does not typically appear to bear great costs on the mothers' own health especially in typical environments with adequate resources (Roulin 2002).

Calibration of Nursing Based on Environment

Given that newborns across many species require to be nursed when they are born suggests that there may be mechanisms in place to help optimally allocate mothers' energy resources between the energy demands for herself and her offspring. For example, in one study, Rogowitz (1996) showed that the growth rate differences in cotton rat pups of small and large litters were significantly different. These differences were not due to differences in the maternal size of both rat mothers as both mothers were similar in size but rather due to the different energy levels of milk flow from mothers to offspring during lactation. Mothers with the smaller litter had higher levels of energy flow compared to the mothers with the larger litter. What's more, despite the different levels of energy flow, both mothers were found to have adequate levels of energy for their own sustenance. In a similar vein, studies have shown that even the quality of milk changes as a result of the environment, such as the growth rate of the infant (Hinde et al. 2009). These results suggest that the quality of milk flow may be calibrated based on various contextual factors while accounting for mothers' energy requirements. This may be one important factor that allows for the benefits of nursing to outweigh the costs.

Evolutionary Benefits of Breastfeeding

Nursing appears to have broad evolutionary benefits across species. Nursing may help to increase the duration of birth intervals through lactation amenorrhea (not menstruating after giving birth). This is beneficial for helping mothers to focus their investments on the current offspring at least until weaning. Nursing also helps to keep the offspring dependent on the mother as well as proximally close to the mother so that the mother can ensure the infant's nourishment despite any environmental scarcity. This also allows the mother to protect the infant from predators and harm (Sellen 2007). Additionally, nursing is suggested to increase mothers' oxytocin levels

and consequently help facilitate mother-infant bonding.

Allonursing and Benefits of Nursing

The evolutionary benefits of nursing are especially exhibited when examining the literature on allonursing. Allonursing is when female mammals nurse offspring that are not their own and is observed to occur in over 60 species including humans (Roulin 2002). This behavior helps support the theory that the benefits of nursing may greatly outweigh the costs because, if nursing does impose high costs on females, they would not choose to nurse infants that are not their own. Evidence suggests that allonursing helps with inclusive fitness as mothers may typically prefer to nurse an offspring that is not her own, but nevertheless, still choose to nurse a genetic relative compared to a nongenetic relative. This would help the nursing female to propagate her genes. Females may also nurse offspring that are not their own in order to evacuate surplus milk that is not consumed by their own offspring. This may help to reduce pain associated with the pressure in the breast due to excess milk as well as teat infections which can ultimately allow the female to focus the energy on other important somatic functions.

Conclusion

The prevalence and intuitive nature of nursing is an indicator that this behavior is associated with important benefits for the mother and infant. Moreover, the calibration of energy demands for the mother and infant when nursing provides important insights into the underpinnings of maternal investment and behavior. That is, evolutionary mechanisms may be in place so that maternal investment in offspring does not typically come at the cost of maternal health. Mothers who are unable to breastfeed specifically due to deficits in their environment should therefore be provided with the necessary support to help make optimal parenting decisions for themselves and for their infants.

Cross-References

- ▶ [Alloparenting](#)
- ▶ [Breast Feeding](#)
- ▶ [Breast Milk Composition](#)
- ▶ [Duration of Breast Feeding in Ancestral Environments](#)
- ▶ [Maternal-Fetal Conflict](#)
- ▶ [Parental Investment](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Parent-Offspring Conflict](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)

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Gaze

- ▶ [Eye Contact with Adults Versus Babies](#)

Gender

- ▶ [Masculinity and Femininity](#)
- ▶ [Peer Rejection, Gender Differences in Response to](#)

Gender and Sexual Minorities (GSM)

- ▶ [Sexual Identity](#)

Gender Categorization

- ▶ [Categorization by Sex](#)

Gender Development

- ▶ [Biology of Human Gender, The](#)

Gender Differences

- ▶ [Relationship Between Sexuality and Gender](#)
- ▶ [Sex Differences in Death by Filicide](#)
- ▶ [Sex Differences in Intimate Partner Violence](#)
- ▶ [Sex Differences in Participation](#)
- ▶ [Sexual Dimorphism](#)

Gender Differences in Disgust

- ▶ [Sex-Differences in Disease Avoidance](#)

Gender Differences in Lachrymation

- ▶ [Sex Differences in Crying](#)

Gender Differences in Lacrimation

- ▶ [Sex Differences in Crying](#)

Gender Differences in SDO

► Sex Differences in SDO

Gender Differences in Sobbing

► Sex Differences in Crying

Gender Differences in Weeping

► Sex Differences in Crying

Gender Distinction

► Kinship Distinctions According to Sex

Gender Dysphoria

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Synonyms

Gender identity disorder; Gender incongruence; Transsexualism

Definition

Gender dysphoria refers to a person's discontent and distress with regard to the gender that they were assigned to at birth.

Introduction

As a diagnostic term, gender dysphoria was introduced in the fifth edition of the *Diagnostic and Statistical Manual of Mental Disorders* (American Psychiatric Association 2013). It replaced prior diagnostic labels, such as gender identity disorder and transsexualism.

As a diagnosis, the symptoms must be accompanied by clinically significant distress and/or impairment. It is a more narrow construct than terms such as "transgender," "gender variance," or "gender nonconformity."

Phenomenology

Gender dysphoria can have either an early onset (in childhood) or a late onset (in adolescence or adulthood). In the early-onset form, children exhibit a range of stereotypical gender-typed behaviors associated with the other sex (e.g., in peer preferences, toys and activity interests, roles in fantasy play, clothing preferences, etc.), co-occurring with the verbalized desired to be of the other (which is conceptually the most important parameter of the clinical presentation). The sex-typed behaviors associated with gender dysphoria occur in concert, not in isolation, and, therefore, a thorough diagnostic assessment is needed to identify whether a significant pattern of cross-gender behavior is present. For some children, there is an insistence that they are of the other gender. In the late-onset form, the strong desire to be of the other gender is expressed for the first time at some point after puberty, accompanied by significant anatomic dysphoria. For adolescents with gender dysphoria, the DSM-5 criteria do not include concrete behavioral indicators. Instead, the criteria emphasize more abstract phenomenology (e.g., Criterion A6 reads as "A strong conviction that one has the typical feelings and reactions of the other gender. . .or some alternative gender different from one's assigned gender"). Adolescents with late-onset type of gender dysphoria, particularly males, typically do not present with a pervasive pattern of childhood cross-gender behavior or identification and are

often described by parents as stereotypically masculine as children. Sexual orientation (to whom one is attracted to romantically and sexually) is reliably associated with the early- and late-onset forms of gender dysphoria. In males with gender dysphoria, those with an early onset are almost always attracted sexually to biological males (“androphilia”), whereas those with a late onset are primarily attracted to biological females (“gynephilia”), or they are sexually aroused at the thought or image of oneself as a woman (“autogynephilia”) (Lawrence 2010). In females with gender dysphoria, those with an early onset are almost always attracted to biological females (gynephilia), whereas those with a late onset are more variable: many, but not all, are sexually attracted to biological males (androphilia).

Epidemiology

In adults, the prevalence of gender dysphoria has been estimated to occur in 1:14,705 adult males and in 1:38,461 adult females (Arcelus et al. 2015). In children and adolescents, the prevalence is unknown. Using self-identification as transgender, which is a broader term, one study found that 1.2% of high school students in New Zealand answered “yes” to the question “Do you think you are a transgender?” In the United States, a study of adults found that 0.5% considered themselves to be “transgender.” Over many decades, gender dysphoria has been considered more common in males than in females across the life-span, based on referral rates to specialized gender identity clinics. More recently, there has been a shift favoring females, but only among adolescents (for review, see Zucker 2017).

Associated Psychopathology

Many studies have found that gender dysphoria is associated with a range of mental health problems. These problems become increasingly common starting in middle to late childhood. Common problems include depression and anxiety, substance misuse, and suicidality (Zucker et al.

2014, 2016). Some recent studies suggest that gender dysphoria can be associated with an autism spectrum disorder (van der Miesen et al. 2016). Explanations for the presence of mental health problems include an underlying biological vulnerability, the inherent distress that is associated with gender dysphoria, and “minority stress,” i.e., stigma and discrimination.

Developmental Course of Gender Dysphoria

Follow-up of children, adolescents, and adults with gender dysphoria have identified different long-term trajectories. Clinically, this information is of high importance to parents, who will often ask whether their child will pursue a gender transition or whether their child’s gender dysphoria will go away (i.e., desist). Studies of adolescents and adults who have been diagnosed with gender dysphoria suggest that persistence is very common unless it is treated by specific methods (see below). In contrast, follow-up studies of children suggest that persistence is less common, even without any type of treatment. In boys, persistence rates have ranged from 0% to 20% (Singh 2012); in girls, persistence rates have ranged from 12% to 50% (Ristori and Steensma 2016). In comparing the long-term outcome of children with gender dysphoria obtained in prospective studies to retrospective studies of adolescents and adults with gender dysphoria, a notable disjunction with regard to gender identity outcome is observed. While adolescent and adult males with gender dysphoria, particularly those who are androphilic (sexually attracted to biological males), recall a pattern of childhood cross-gender behavior that is consistent with the phenomenology of gender dysphoria, most children with gender dysphoria do not continue to have gender dysphoria in adulthood. How might this disjunction be understood? Children with gender dysphoria have different developmental trajectories, and this leads to diverse outcomes in adolescence and adulthood. Perhaps there is malleability or plasticity in gender identity differentiation early on in development; however, it becomes more fixed as

development progresses into adolescence and adulthood (Singh 2012). Clinical observation and empirical evidence support this idea – persistence of gender dysphoria, including the desire for sex change, is higher among patients assessed for the first time during adolescence and then followed up than among patients first assessed in childhood and then followed prospectively (Singh 2012). In Cohen-Kettenis and van Goozen's (1997) follow-up study of Dutch adolescents with gender dysphoria, the rate of persistent gender dysphoria was 66.6%. This is similar to the percentage of adolescents recommended for puberty-blocking hormonal treatment at the Toronto clinic (Zucker et al. 2011). If we assume liberally that the adolescents recommended for puberty blockers would persist in their gender dysphoria, the persistence rates obtained by Cohen-Kettenis and van Goozen and Zucker et al. in their adolescent samples are substantially higher than that obtained in the follow-up studies of boys with gender dysphoria first referred in childhood.

Follow-up studies of children with gender dysphoria have identified severity or intensity of childhood cross-gender behavior (Singh 2012) and an early social transition (Steensma et al. 2013) as predictive of persistence among biological males with childhood-onset gender dysphoria.

Casual (Etiological) Explanations

Both biological and psychosocial factors have been proposed to explain the origins of gender dysphoria. Biological explanations include genetic factors, alterations in the prenatal hormonal milieu, and, in males, a late fraternal birth order. Concordance for gender dysphoria is more common in monozygotic twins than in dizygotic twins. Structural magnetic resonance imaging studies have examined variations in sex-dimorphic neural structures in both adolescents and adults with gender dysphoria when compared to unaffected males and females. Guillamon et al. (2016) reviewed this literature and found that there was some evidence to suggest that certain

“regions of interest” were altered in people with gender dysphoria. When differences were detected, they were either intermediate between that of unaffected males and females or closer to the “other” biological sex. However, such differences are not always detected: in these instances, the region of interest was no different than that of controls of the same biological sex. Blanchard (2017) reported that adult males with gender dysphoria (restricted to those who sexual orientation was androphilic, i.e., sexual attraction to biological males) were more likely to have older brothers than unaffected males. The explanation for this is that, with each successive pregnancy of a male fetus, there is an antigenic maternal immune response that impacts male-typical psychosexual differentiation.

Psychosocial factors include gender dysphoria thinking about gender identity, an early identification with the opposite sex parent, reinforcement of gender-variant behaviors in early childhood, and traumatic experiences (e.g., sexual abuse) that cause one to feel unsafe vis-a-vis one's birth-assigned gender. In early childhood, it is common for children to have fairly gender dysphoria notions about gender. For children who express gender-variant behavior, this “black and white” thinking might lead some children to believe that because they have interests that are similar to the other gender, then perhaps that means that they should be that gender or that they actually “are” that gender. Because “black and white” thinking is very characteristic of children with an autism spectrum disorder, this has been given as one possible explanation for the co-occurrence with gender dysphoria (Strang et al. 2016). Because most children have their first attachment to their mother, it has been argued that this is one reason that gender dysphoria is more common among boys than girls because they have greater difficulty in shifting their gender-related identification to their fathers or a father figure. In girls, this is less of a problem because initial attachment to the mother makes a same-gender identification less complicated. Early studies of parental response to marked gender-variant behavior in boys indicated that it was common for parents to either view the

behavior as “only a phase” and that the behavior was either tolerated or reinforced (Green 1987).

Therapeutics

Over many decades, a general consensus emerged that psychological or psychiatric treatment of gender dysphoria in adults was not particularly effective, even when the patient desired it. This led to the search for alternative methods to reduce the gender dysphoria. Thus, common treatments nowadays include a social transition to living as the desired gender; hormonal treatment to alter, where possible, the phenotypic markers of the desired gender; and gender-affirming surgery. It is now recognized that in carefully evaluated adults, these treatments lead to a reduction in the gender dysphoria (Coleman et al. 2011).

In adolescents, it is also believed that, in the majority of patients, psychological or psychiatric treatment is also ineffective, again even if the patient desires it. As a result, contemporary treatments include a social transition to living as the desired gender, the use of puberty-blocking hormonal treatment to suppress somatic masculinization (in males) or feminization (in females), subsequent implementation of contra-sex hormonal treatment, and, in adulthood, gender-affirming surgery when it is desired. In carefully evaluated adolescents, this treatment protocol appears to be successful in reducing the gender dysphoria (de Vries et al. 2014).

In children, best-practice treatment is more controversial and less definitive. Some clinicians argue that some form of psychologic intervention can be successful in reducing the gender dysphoria (Zucker et al. 2012), noting, for example, the high rate of desistance, even in the absence of formal treatment (Singh 2012). Others argue for a “watchful waiting” approach (de Vries and Cohen-Kettenis 2012), and some clinicians argue that children should be supported, if not encouraged, to socially transition to the desired gender (Ehrensaft 2012). The differences among these treatment approaches are related to differences in theoretical and philosophical conceptualizations of the origins of gender dysphoria, and,

nowadays, it has become more apparent that parents of children with gender dysphoria differ in which treatment approach they desire for their children. Unfortunately, there is little in the way of systematic studies comparing these treatment approaches, and so various clinical guideline documents recommend a case-by-case decision-making practice in which parents are given as much information as possible in order to make an informed decision about treatment options (Drescher and Byne 2012).

Conclusion

In summary, considerable clinical and research advances have been made over the past several decades in understanding various aspects of gender dysphoria: phenomenology, epidemiology, associated mental health problems, developmental course, causal mechanisms, and best-practice therapeutics. However, much remains unknown. For instance, we still do not understand the process through which gender dysphoria desists or have a thorough understanding of the various factors that interact to influence long-term outcome. The role of therapeutics on long-term outcome also remains unclear. Over the past few years, there has been a substantive increase in professional interest in the well-being and health disparities among children, adolescents, and adults with a minority gender identity. This will, undoubtedly, lead to further accumulation of knowledge with translational benefits for clinical care of patients experiencing gender dysphoria.

Cross-References

► [Biology of Human Gender, The](#)

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Gender Equality

► Women's Personal Resources

Gender Identity Disorder

► Gender Dysphoria

Gender Incongruence

► Gender Dysphoria

Gender Inequality

► Sexism

Gender of Friend

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Synonyms

Biological sex of friend; Same-sex friend; Cross-sex friend; Opposite-sex friend; Friendship

Definition

The evolutionary origins of why and how friendship differs as a function of the biological sex of friends.

Introduction

Friendship is a relationship between two people based on mutual liking in which partners provide support to one another in times of need. Because it does not require a familial or formal tie, friendship is typically regarded a nonobligatory relationship of choice. Although individuals often choose to enter into and remain in a friendship, friends are expected to have genuine positive regard and concern and provide emotional and instrumental support to each other (Hall 2012; La Gaipa 1977). Characteristics of friendship are very similar across cultures (Hruschka 2010; Terrell 2015). One of the unique qualities of friendship is that it does not follow tit-for-tat exchange. Rather, friends provide aid and support to one another based on need. This challenges evolutionary explanations for its emergence (Hruschka 2010; Silk 2003).

The expression and expectations of friendship have shown some sex differences (Hall 2011; Reis 1998). This chapter will review two prominent evolutionary accounts of sex differences in friendship (e.g., Geary et al. 2003; Taylor et al. 2000) and examine several evolutionary explanations for the function of cross-sex friendships (Bleske and Buss 2000; Bleske-Rechek et al. 2012; Lewis

et al. 2015). In general, research on friendship from an evolutionary perspective is still in early stages of development, and evolutionary explanations of sex differences in friendships constitute only a small subset of this body of research.

Levels of Friendship

A relationship is “a tie between two or more individuals that is stable over time and across contexts” (Brown and Brown 2006, p. 4). Relationships require mutual and specific acknowledgement, or individuation from a group, and some degree of mutual influence (Hall and Davis 2017). These three defining characteristics of a relationship (i.e., stability, individuation, interdependence) allow humans to effectively and efficiently regulate social, emotional, and material investments in another person in relation to future returns. It is notable that friendship-like bonds among nonhuman primates and other social animals (e.g., dolphins, elephants) share these three definitional properties (Seyfarth and Cheney 2012). Considering the evolutionary origins of friendship, Seyfarth and Cheney (2012) contend that a *relationship* is constituted by the “cumulative memories and emotions created by many previous interactions,” and other group members can recognize its existence (p. 166). The ability to form enduring associations with preferred others and the ability to recognize that bond between others preceded the rise of *Homo sapiens*. Therefore, a relationship, at its most minimal form, is not a uniquely human trait.

Humans can differentiate between various types of relationships. There is a minimum standard for calling someone a friend, but once identified as such, friends are not equal or interchangeable; some are much more valuable than others (Silk 2003; Tooby and Cosmides 1996). Classic research on the friendships of children (La Gaipa 1977) and adults (Weiss and Lowenthal 1975) demonstrates that friendships vary by emotional closeness, expectations and rules of conduct, and nomenclature. Dunbar (1996) has offered an evolutionary-inspired theory of friendship taxonomy and has proffered four categories of friendship: support

clique, sympathy group, friends, and clansmen. The first group (1–5 individuals) may include non-kin best friends but mainly includes immediate kin (Mollenhorst et al. 2014). The sympathy group, which subsumes the support clique, is three times larger (10–15) and may include several good friends or best friends (La Gaipa 1977). The next two groups grow in size by a factor of three (40–50 friends; 120–150 clansmen) (Dunbar 1996). Acquaintances are not friends: adults and children show little difficulty in differentiating a casual friend from an acquaintance (La Gaipa 1977; Weiss and Lowenthal 1975).

One important qualification of contemporary research on the evolutionary origins of friendship is that distinctions between types of friends are rarely so fine-tuned. Many of the unique properties of friendship, especially in terms of positive regard and treatment, are only noticeable at high levels of closeness (Hruschka 2010). Some theories of sex differences in same-sex friendship make explicit distinctions between close friends and group members (e.g., Geary et al. 2003). However, it is more typical that when the concept of *friendship* is referenced, best, close, or very good friends are the object of study.

The Evolutionary Roots of Friendship

Although the particular evolutionary mechanism(s) (e.g., direct fitness, inclusive fitness) enabling the formation of friendships, particularly with non-kin, is a matter of debate (Seyfarth and Cheney 2012; Terrell 2015; Tooby and Cosmides 2008), there is strong evidence that establishing and maintaining friendships offer an array of survival and reproductive benefits, including resource sharing, cooperation, protection, and reproductive opportunity. Due to a high degree of tribal interdependence and the increased likelihood of death following social isolation, the investment of resources in others may have been essential for early human survival (Brown and Brown 2006; Tooby and Cosmides 2008). Heritable traits motivating and regulating the formation and maintenance of social bonds would have been selected for, while traits maladaptive for the individual's bonding

and inclusion would have been selected against (Hruschka 2010; Tooby and Cosmides 2008).

A friendship, therefore, is an adaptive mechanism, enabling the recognition of a uniquely valuable other and streamlining decisions about the type and amount of investment of resources to be made in and to be expected from another, especially among non-kin (Hall and Davis 2017; Seyfarth and Cheney 2012). Although this mechanism enables the development and maintenance of friendships, differentiation among potential friends based upon desirable qualities is another necessary ability. Friends are selected based upon the potential for emotional support and social bonding (Ainsworth 1989; Hruschka 2010) and other valued and observable characteristics (Hall 2012; Tooby and Cosmides 1996). Just as individuals have varying reproductive values as mates, they also have varying association values as friends (Kendrick et al. 2005). This ability to differentiate among others likely had other functions independent of friendship. The ability to estimate the value of particular qualities or behaviors in another person is an important adaptation for the comprehension of social exchange and altruism (Tooby and Cosmides 1996). The ability to differentiate among potential friends based on their association value, the ability to regulate social exchange not based upon tit-for-tat rules, and the ability to recognize and form relationships are all components necessary for the evolution of human friendship.

Sex Differences in Friendship

Two distinct approaches offer mechanisms for interpreting sex differences in the expression of friendships. Drawing from Hartup and Stevens' (1997) recognition of the importance of deep structures of friendship, Hall (2011) argued that ideal friendship expectations define the meaning or essence of friendship. These expectations are the standard upon which new and ongoing friendships are judged (Fehr 1996). This approach embraces the concept that friends differ by association value, and ideal friends possess qualities that yield the greatest benefits. The particular

qualities sought in an ideal friend should differ depending upon the needs of the individual. Biological sex may influence which qualities in ideal friends are most needed. Specifically, sex differences in expectations are more likely to have evolved in circumstances where females and males differ in outcomes needed or desired from friends (Hall 2011). For example, when one type of friendship characteristic offers benefits to or serves the needs of females more than males, females should more highly value these behaviors or qualities in an ideal friend.

Another mechanism that could influence the emergence of sex differences is niche construction (Bahns et al. 2017; Terrell 2015). The preference for friends who are similar based on attitudes, personality traits, and values is a well-established tendency (La Gaipa 1977; Hall 2012; Newcomb and Bagwell 1995). Rather than passively awaiting friendships to form with proximal others, humans seek out and put effort into forming and maintaining friendships with preferred others. The niche construction perspective suggests that humans shape their physical and social environment to be more suitable, agreeable, and adaptive (Bahns et al. 2017; Terrell 2015). Similarity between friends increases time spent in mutually enjoyable activities (Fehr 1996), creates coherence and consistency in friends' interpretation of external events and people (Terrell 2015), and plays a critical role in friendship selection (Bahns et al. 2017). Niche construction is a self-protective and self-gratifying process that is beneficial inasmuch as it facilitates social acceptance and harmony, speeds information transmission, and increases the chances of joint activity accomplishment. Below, both approaches will be considered in conjunction with perspectives of sex differences in same-sex friendships.

Same-Sex Friendships Among Women

In proposing a model for understanding sex differences in stress response, Taylor et al.'s (2000) tend-and-befriend hypothesis also provides an evolutionary explanation for sex differences in friendship generally. Taylor et al. (2000) suggest

the tendency toward a tend-and-befriend response to stress evolved in females due to asymmetric investment in offspring and a need to form and maintain protective female coalitions. The befriending response is marked by the development of affiliation with group members who provide resources and protection for females and their offspring in times of need (Taylor et al. 2000). That is, friends, particularly close friends, offer protection from predators and other humans. These risks were more likely for women due to the likelihood of assault from men and because fleeing responses were constrained by greater responsibility for the survival of offspring (Taylor et al. 2000). Among nonhuman primates and social animals, strong friendship-like bonds between females are much more common than between males. Matrilineal kinship, particularly between mothers and daughters, is "the single most important factor affecting the development of long-term bonds among animals" (Seyfarth and Cheney 2012, p. 160). Furthermore, stronger and more permanent bonds are more frequently found among non-kin female primates than among non-kin male primates (Seyfarth and Cheney 2012). Taylor et al. (2000) suggest that because caring, supportive, and protective friends would be more valuable for females compared to males, sex differences favoring females in emotional support and intimacy should exist. Such evidence is abundant. Females, compared to males, are more likely to cope with stress by seeking emotional support, expect more intimacy and understanding from their same-sex friends, have more emotionally close friendships, and have a few intimate friendships rather than many weak ties.

Evidence supporting females' greater tendency toward using emotional support to reduce stress has shown marked sex differences (Tamres et al. 2002), wherein females seek out, receive, and are more satisfied with social support. The strongest sex differences in coping strategies involved seeking emotional support, particularly for stresses originating from emotional causes (Tamres et al. 2002). Investigating sex differences in ideal expectations of intimacy, emotional support, and empathic understanding from close friends (i.e., communion expectations), Hall (2011) found

a medium-sized difference ($d = 0.388$), which was not moderated by culture. This is consistent with past meta-analysis that demonstrates females' greater behavioral intimacy in friendship (Reis 1998), even as children (La Gaipa 1977). Part of this difference may be due to different types of relationship engagement. The tendency for boys to play in groups and girls to interact in dyads is "perhaps one of the most well-established findings in the children's friendship literature" (Fehr 1996, p. 117). Taken together, as children females prefer same-sex friendships based on dyadic interaction, which likely shapes ideal expectations of communion from same-sex friends and matures into greater intimacy and emotional support for same-sex adult female friends. Compared to men, women experience more intimate and higher-quality same-sex friendships for close friends and less close friends alike (Fehr 1996).

Same-Sex Friendships Among Men

Geary and colleagues (Geary and Flinn 2002; Geary et al. 2003) focus on other factors that may have shaped same-sex friendships among men, many of which are complimentary to the arguments of Taylor et al. (2000). Geary and Flinn (2002) focus on the role of philopatry, which is tendency for females to migrate to another group (e.g., through marriage), compared to males who are more likely to stay in their birth group. Noting that two-thirds of groups are composed of male kin and female non-kin, Geary and Flinn (2002) suggest females were more likely to be among unrelated others compared to males. Therefore, females would be more likely to develop mechanisms of obtaining mutual and reciprocal benefits from unrelated others (Geary et al. 2003). By contrast, male coalitions were more likely to be marked by competition and predominantly nonreciprocal relationships due to associating with hierarchically differentiated male kin. Under these conditions, reciprocity between friends would be a critical component of female-female friendships but less so for male-male friendships.

One implication of Geary and colleagues' argument is that males should seek out

characteristics in friends that might offer benefits within the group and during inter- or intragroup competition or aggression. Within males' social network, friendships reflect a balance of cooperative and competitive behaviors. Because group unity and cooperation is necessary for achieving group-level goals, the stabilizing bonds of friendship were also necessary. In the social environments of men and boys, competition, once resolved, results in a more stable social structure for the entire coalition. Within the group, men and boys might wish to develop friendships with men who are well positioned, well connected, or well resourced. Through the reciprocal bonds of friendship, males can gain access to resources and protection (Geary et al. 2003; Kendrick et al. 2005). In this sense, the ideal male friend would have accessible and valuable resources.

In his meta-analysis, Hall (2011) tested Geary and colleagues' argument: compared to women and girls, men and boys should be more likely to favor resources, prowess, and status from same-sex friends. Identifying these characteristics as *agency* expectations, Hall (2011) found that males are more likely than females to describe ideal same-sex friends as well resourced (e.g., financial resources, physical fitness, social connections) ($d = -0.337$). This difference was not moderated by age or culture. Additionally, Geary and Flinn (2002) suggest that sex differences in intimacy, exclusivity, and emotional support favoring females may have also been influenced by philopatry. If men were more likely to be among male kin, they could count on them to come to their aid with or without friendship. In maintaining larger groups of weak ties, men would not be able to invest sufficiently to each relationship to create expectations of intimacy or emotional support.

Similarities Shaping Differences Between the Sexes

Four characteristics of same-sex friends do not differ by sex and are similar across culture and age: propinquity, homophily, inclusion, and preference for same-sex friends. Propinquity, or physical proximity, and homophily (i.e., similarity

between friends) are identified as the fundamental building blocks of friendship. The lack of sex differences or cultural variation in expectations of homophily (Hall 2011) suggests that niche construction through similarity selection may be a fundamental friendship process that does not vary by sex. Furthermore, inclusion, or the desire to be in the company of and invited by friends, is similar between the sexes (Hall 2011). Among children, friends spend more time together than non-friends primarily because of similar play behaviors and shared activities (Newcomb and Bagwell 1995). Furthermore, there are no sex differences in time spent with friends at various ages (Fehr 1996). Finally, children and adults tend to choose best friends of the same sex across cultures (Borner et al. 2015; Hruschka 2010).

Considered in conjunction with niche construction processes, these four characteristics may play an important proximal role in creating sex differences. Hall (2011) pointed out that inclusion by, time spent with, and preference for same-sex peers is a crucial proximal mechanism for the emergence of sex differences from both an evolved and a developmental perspective. Group-level dynamics are a factor in the evolution of sex difference precisely because of preference for same-sex relationships, socialization, and coalition formation (Kendrick et al. 2005). From a niche construction perspective, cross-cultural and cross generational tendency toward a preference for same-sex friends might arise from a desire to find similar others based on friendship expectations, play and activity preferences, and a shared perspective. A combination of similarity in preference for same-sex friends and a lack of sex difference in the importance of inclusion by friends suggests that sex may be one selection criteria that influences the construction of friendship niches. That is, from a niche construction perspective, preference for similarity in sex of friends and inclusion by friends would likely produce overlapping niches of similarity for sex-linked traits, preferences, and behaviors. These would likely reify sex differences through behavioral reinforcement, as conforming to friendship expectations plays a crucial role in making and keeping friends (Fehr 1996; La Gaipa 1977). That sex differences

in communion expectations grow as the age of the sample increases supports this conclusion (Hall 2011).

Finally, it is notable that the most essential and important characteristics of friendships, such as trust, genuine regard, and loyalty (Fehr 1996; Hartup and Stevens 1997), do not show substantial sex differences (Hall 2011). There appears to be a great deal of cross-cultural similarity in these aspects of friendship and among adults (Hruschka 2010) and children (Borner et al. 2015). Hall (2011) concludes that because less than 3% of the variance in these essential characteristics can be explained by sex, differences are unlikely to be the result of evolved mechanisms. As Hartup and Stevens (1997) argue, there should be few sex differences in the most essential friendship expectations because both sexes seek out, maintain, and find considerable value in trust, commitment, and genuineness in friends.

Cross-Sex Friendships: Sexual Strategies Theory, Risks, and Benefits

Friendships between heterosexual men and women (i.e., cross-sex friendships) are most commonly considered in relation to reproductive risks and benefits rather than stress amelioration or navigation of kin hierarchies. In this section, the risks of cross-sex friendships for individuals in committed romantic partnerships will be considered first, and then the risks and benefits of cross-sex friendships among noncommitted adults will be considered.

For individuals in an existing romantic relationship, especially those with children, cross-sex friends are threatening for two primary reasons: mate poaching or resource sharing (Bleske and Buss 2000; Bleske-Rechek et al. 2012; Lewis et al. 2015). For both men and women, a partner's cross-sex friendship could undermine the existing relationship through sexual infidelity or mate poaching. This threat is warranted by research reporting that one-third of those who had had sex with a cross-sex friend were dating someone else at the time (Afifi and Faulkner 2000). According to sexual strategies theory (SST)

(Buss and Schmitt 2016), one primary risk for men in committed long-term relationships is that paternity probability is not fully knowable. SST would predict that men would feel threatened by their partners' cross-sex friend because it poses a risk of sexual infidelity and would experience jealousy and engage in mate guarding to prevent infidelity. A cross-sex friendship could develop into a romantic relationship, putting men and women at risk of losing their long-term partner (i.e., mate poaching). This also poses risks to the well-being of offspring from the initial relationship, especially if children from the first pair bond are raised by stepparents. According to SST, one of the distinct risks women face when their male partners have cross-sex friendships is resource sharing, especially if the cross-sex friendship develops into a reproductive relationship. Additional partners and/or children diminish the resources available in the initial pair bond and can potentially result in a long-term split of the man's resources between two women and, potentially, two sets of offspring. Although both men and women might maintain a cross-sex friendship as a backup mate, SST would predict that women may be more inclined to seek out a backup mate as a form of insurance if the initial partner is unfaithful or unreliable (Buss and Schmitt 2016). Unsurprisingly, Hruschka (2010) cites widespread cross-cultural evidence of suspicion of cross-sex friendships, typically due to concern for their impropriety and threat to romantic relationships.

The benefits of a cross-sex friendship have also been explored from the perspective of SST (Lewis et al. 2011). Aside from the benefits of friendship in general (e.g., support, trust, genuine positive regard), cross-sex friendships offer valuable insight into the mind of the opposite sex, and, as such, cross-sex friends can become trusted informants and confidants (Bleske-Recek et al. 2012; Sapadin 1988). From the perspective of SST (Buss and Schmitt 2016), this insight might translate to greater access and success in mating, especially if cross-sex friends help each other find partners through friendly introductions or helpful approach strategies (Lewis et al. 2015). Furthermore, men often identify cross-sex friends as

valuable sources of emotional support, intimacy, and self-disclosure, and women often identify cross-sex friends as sources of instrumental support, fun, and enjoyment (Fehr 1996; Sapadin 1988). SST suggests that characteristics valued in a cross-sex friend are similar to characteristics desired in long-term partners. Lewis et al. (2011) demonstrate that cross-sex preferences for friends were similar to cross-sex preference for mates: men preferred female friends who were physically attractive with unrestricted SOI, and women preferred men with more physical prowess and resources.

SST has implications for same-sex friendships as well. Taylor et al. (2000) and Geary et al. (2003) argue that having high status, attractive, and athletic friends has clear implications for mating opportunities for males in hierarchically arranged group. Men might prefer agency characteristics (e.g., status, athleticism) in their male friends, not just for the status it confers within the group but also as those characteristics might increase mating opportunities (Bleske and Buss 2000; Lewis et al. 2015). It stands to reason that through intimacy and emotional support shown with same-sex friends, women are demonstrating characteristics of good parents and committed partners, both of which are attractive traits to men seeking a long-term relationship.

Even among single adults, the challenges of romantic potential and sexual desire complicate cross-sex friendships. Although the taboo of spending time with cross-sex friends has diminished greatly in Western cultures and 92% of young adults can name at least one close cross-sex friend (Halatsis and Christakis 2009), nearly 52% of respondents report being openly or secretly attracted to a cross-sex friend (Reeder 2000). Indeed, cross-sex friendships are a common pathway to romance: two-thirds of men and nearly half of women agreed that friendship could become a path toward romantic or sexual intimacy (Sapadin 1988). Thus, it is very likely that at least one side of a cross-sex friendship has considered the possibility of a romantic or sexual relationship. This attraction is based in reality: friends are accurate when estimating how much cross-sex friends are interested (Koenig et al. 2007), and

attraction in cross-sex friendships is more often mutual than not (Bleske-Rechek et al. 2012). Although romantic attraction seems to be experienced at similar rates by men and women (Koenig et al. 2007), men are much more likely to be sexually attracted to their cross-sex friends, and women are more likely to experience unwanted sexual pursuit (Lewis et al. 2015). Thus, women are more likely to underestimate, and men are more likely to overestimate sexual attraction from their cross-sex friend (Koenig et al. 2007). These findings are consistent with SST in that men are more likely to seek sexual access through cross-sex friendships, and women are more likely to seek backup mates, especially with men with greater long-term mating potential.

Caveats to Cross-Sex Claims

There are two caveats to characterization of cross-sex friendships based on SST: a narrow focus on types of friendships and types of affection in friendship. Sex differences in reported sexual interest, desirable qualities in cross-sex friends, and the virtues of cross-sex friendships are all supportive of SST (Buss and Schmitt 2016). These findings are likely most applicable to young, single adults in Western cultures that allow cross-sex friendships. Like most studies on friendship, these findings focus on primarily emotionally close friendships to the exclusion of many cross-sex friendships that are neither particularly close nor likely to develop closeness in the future. Indeed, some stated benefits of a cross-sex friend, such as self-disclosure or instrumental support or protection, are neither likely nor appropriate in weak-tie friendships, whether same- or cross-sex. Although experiencing jealousy from an emotionally intimate cross-sex partner appears to be normative, being jealous of every cross-sex casual friend is likely rare. Furthermore, close cross-sex friends are relatively rare in adult samples, compared to college-aged samples, especially between friends of the same age. As such, threats from cross-sex friends are likely infrequent among adult as they have few cross-sex friends generally. Finally, cross generational, familial,

and ceremonial friendships exist commonly across the world, albeit much less so in Western countries (Hruschka 2010; Terrell 2015). Cross generational, inherited or ceremonial, familial friendships connect friends' offspring in an inter-generational web of relationships that approximate kin (Hruschka 2010; Terrell 2015). In the United States, such friends take on familial names, such as aunts, uncles, or cousins. Many such friendships are cross-sex but are unlikely to be explainable from the predictions of SST. Lewis et al. (2015) concur that the adaptive challenges and benefits of cross-sex friendships likely change over the life course. Human friendship psychology may be sensitive to such changes, yet the research on these types of friendships is scarce.

Considering cross-sex friendships from the perspective of sexual access and opportunity may overstate the role of sexual desire in cross-sex friendships. Many cross-sex friendships do not report sexual tensions or interest, and friends make active efforts taken to avoid perceptions of sexual or romantic interest. In intimate cross-sex friendships, the social attraction and genuine regard are often so valuable to friends; they actively avoid even the appearance of sexual interest. Furthermore, A Western cultural lens might confound of friendship and sexual interest to a degree not shared cross-culturally. In Hruschka's (2010) review of friendship across cultures, he posits that Western cultures have only recently strongly linked companionate love (i.e., affection as close friends) with sexual desire and long-term union. He persuasively argues that the feeling of bonding, connection, and closeness can develop independently from public, ritualized unions producing children and from sexual relationships. Hruschka (2010) cautions against sexualizing the expression of affection between friends in Western and non-Western cultures alike. Applying his argument to cross-sex friends, companionate love between cross-sex friends may be reduced sexual desire or romance due to a narrow, Western understanding of both marriage and friendship. If companionate love between friends were more acceptable culturally and marriage was not a primary source of friendship for adults, then cross-sex friends might be regarded with more

acceptance and less suspicion. Hruschka (2010) concludes that cross-sex friendships are not clearly understood from an evolutionary perspective.

Conclusion

The role that sex of friend plays in friendship from an evolutionary perspective has been informed by several prominent theories. More research is needed to test these theories and to better understand variation between cultures, ages, and levels of emotional intimacy in the expression and development of friendship.

Cross-References

- [Friendship](#)
- [Kinship](#)
- [Reciprocal altruism](#)
- [Sexual strategies theory](#)

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Gender Role Inventory

- [Sex-Role Inventory, The](#)

Gender Schema

- [Sex Differences in Participation](#)

Gender Schema Theory

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Synonyms

[Cognitive schemas](#); [Organizers](#)

Definition

Gender schemas are cognitive structures that organize information about gender.

Introduction

Scientists have long sought to explain gender differences in a number of phenomena – for instance, in relationships, interests, activity level, and communication styles. Cognitive approaches, including gender schema theory, have been proposed to address the development of such gender differences by explaining the cognitive processes underlying gender typing.

As discussed here, gender consists of the individual identification with and societal roles assigned to male and female groups, which differs from sex, the biological components of humans such as reproductive systems and secondary sex characteristics. Thus, gender typing (i.e., matching a gendered prototype) is the process by which individuals become differentiated by

gender in their behaviors, preferences, and cognitions. Although biological predispositions and consistent socialization influence this process, a cognitive approach suggests that cognitive structures like schemas also contribute as important mechanisms of gender typing. Gender schemas, then, are cognitive organizers of information related to gender (e.g., traits, behaviors, appearance) that motivate future information processing and behaviors. Thus, gender schema theories address how schemas are used in processes that create gender differences.

Early Theory Development

Although the cognitive revolution in psychology influenced the development of gender schema approaches, cognitive approaches to understanding stereotyping have been evident in the literature for many years. During the 1970s and 1980s, interest in social schemas emerged in psychology, and cognitive approaches, including gender schema theory (GST), were informed by these more general social psychological studies. Interestingly, three gender schema theories were proposed within 1 year, and other researchers were also exploring their use even before these theories were published (for review, see Martin 1991). These theories (here all considered GST) share the ideas that (a) individuals form gender schemas and there are variations in these schemas, (b) individuals actively process information using their gender schemas, and (c) these schemas have specific effects on memory and behavior. However, the variations of GST differ in emphasis. Here we discuss the two most well-developed and researched approaches: the Bem (1981) version of the theory that emphasized variations in the salience of gender schemas in adults and the Martin and Halverson (1981) version of the theory that focused on developmental issues, functions of schemas, and resulting biases associated with using schemas.

Features of Bem's Gender Schema Theory

Sandra Bem approached the issue of variations in gender typing in adults and from her research

proposed a theory based on the idea of gender schemas (Bem 1981) and then later extended this to children (Bem 1983). Bem proposed that, because much of global society organizes based on gender, individuals develop a specific schema to facilitate the processing of gender-related information. For example, individuals learn commonly stereotypic things like what personality traits, activities, appearance, and behaviors are considered appropriate for each gender (e.g., women are expressive, men are dominant). Bem suggests that an individual's self-concept (i.e., how one perceives the self) becomes assimilated into the gender schema, which means that the information categorized as relevant to their gender group is information relevant to themselves.

Bem wrote that processing information in this way is associated with a number of outcomes, including using gender schematic information as a guide for what to learn and how to behave, such as developing skills and engaging in activities only appropriate for their gender. Gender schemas are prescriptive: individuals can evaluate themselves (and their adequacy as a person) in terms of how they match their gender's characteristics (as stored in their gender schema). Thus, a gender schema becomes an internal motivating factor to conform to gender norms, which can contribute to a readiness to develop in gender-typed ways.

Furthermore, the focus of the theory is not on the content of the schemas but instead on the availability of gender schemas and how this varies across individuals. The frequent use of the gender schema contributes to a tendency for information to be processed in a gendered way or to see the world through a gendered lens (Bem 1993). Bem described the tendency of having highly accessible schemas as schematicity or the degree to which one uses gender schemas in their reasoning. That is, gender is highly salient for some people and not as much for others (i.e., aschematic). Aschematic individuals are less bound by the proscriptions of their gender schemas and embody traits associated with members of each gender group (not just their own, as would highly schematic individuals). Bem called this androgyny, meaning that they have both positive masculine and feminine characteristics,

which was considered advantageous for healthy development (Bem 1974).

Features of Martin and Halverson's Gender Schema Theory

Martin and Halverson (1981) also proposed a gender schema theory, which was published in the same year as Bem's and complemented her work. Both theories sought to provide cognitive explanations for the development of gender differences; thus, both highlighted the role of schemas in the processing of gendered information. They also both posit that gender schemas serve to not only organize information but also to motivate an individual to conform to schematic norms associated with their own gender group.

The Martin and Halverson gender schema theory, however, has a few key differences from Bem's. First, there is a developmental focus to this theory such that as individuals' gender identity develops, gender schematic processing becomes more salient; after learning to identify with a gender category, gender typing emerges more strongly. In addition, Martin and Halverson proposed a slightly different mechanism for developing an own-gender schema. Rather than assimilating the self-concept into the gender schema, Martin and Halverson proposed that there are multiple schemas including a superordinate schema that contains information about what traits and activities are appropriate for each gender and an own-gender schema that contains detailed plans of action for carrying out own-gender appropriate activities. Children then self-socialize; that is, they seek information appropriate for their own gender while discounting other-gender information. That is, the own-gender schema guides their behavior and knowledge of the other-gender suggests what is not appropriate. This also highlights the intergroup focus of this theory, such that information processing is divided along social group lines (in-group and out-group) – in this case, gender lines.

A central theme in this version of GST is that children develop gender schemas and then these schemas are influential as they guide their behavior and thinking to be consistent with their schemas (Martin et al. 2002). The superordinate

schema promotes memory for stereotypic consistent information and directs behavior toward stereotypic consistency vs. inconsistency. For instance, individuals tend to better remember information consistent with these schemas (male firefighter) than inconsistent information (female firefighter). The own-gender schema promotes memory for in-depth information and facilitates complex behaviors aligned with one's gender.

Experimental studies confirm that children are more likely to interact with, attend to, and remember information consistent with their own gender. These studies involve using novel, unfamiliar, and nongender-typed toys, giving them labels suggesting a gender preference (e.g., "this is a toy that boys really like"), and observing children's behavior and assessing their memory for the toys and their labels. The same toy labeled as a toy boys like was played with more by boys and remembered better than a toy labeled as a toy girls like; when labels were reversed for other children, boys avoided that toy. Also, in other studies, a novel toy liked by a boy can be made less appealing by saying that it is a toy girls like to play with. A number of studies have demonstrated these patterns (for review, see Martin et al. 1995).

Gender schemas also influence the social judgments individuals make about others. One line of research assessed the judgments that children made about peers. Although there are developmental patterns in these findings, generally children use information about gender (and if they are older, about children's gender-based interests) to make inferences about how much they would like these children, and they use gender schemas to make predictions about how gender-typical these children's interests are. Younger and older children tend to believe they will like other children of the same gender better than children of the other gender.

Gender schema theory also holds that individuals will develop broader "gender theories" that they apply when they lack information. For instance, they are likely to infer that someone the same gender as themselves will share similar interests, values, and beliefs, and that they will likely follow gender stereotypes. Research studies illustrate the way gender theories lead to

differentiated behaviors and expectations: a girl who says she would really like a particular novel toy also thinks other girls will like it but boys probably will not. These theories may help explain the strong tendency of individuals to show same-gender preferences and to thus gender segregate.

Holding gender schemas also leads to a number of distortions and biases. The Martin and Halverson version of GST gave a detailed description of these biases. One bias is memory distortions that change information toward the direction of the schema. For instance, a child seeing a picture of a woman police officer may later remember that information differently, more stereotypically, by remembering that the police officer was a man. These kinds of distortions make changing schemas a challenge and may explain why programs designed to reduce gender stereotyping are often ineffective (Martin and Halverson 1983).

Newer research on this version of gender schema theory has focused on variations in gender schemas to better understand within gender differences. Tomboys, girls who identify as girls but enjoy counter-stereotypic activities and interests, do not appear to hold to traditional gender schemas. However, assessments of their schemas show that they hold somewhat more broad schemas, more inclusive ones (that acknowledge more exceptions), but that they still hold their behavior to be consistent with these schemas (Martin and Dinella 2012). Even more recent, researchers are in the process of exploring the schemas of socially transitioning children – children who feel they are a different gender than the one they were born – and these children conform to the schemas they hold (Olson et al. 2015). In some ways, these studies provide the strongest evidence of the power of individual's self-socializing since they often experience socialization pressures to conform to their natal gender assignment.

Summary

Both versions of GST were developed to better explain questions of interest to gender researchers: why do individuals stereotype others,

why do individuals engage in gender-typical behaviors and relationships, and what accounts for variations in these behaviors? The cognitive approach adopted by GST assumes that individuals are actively involved in processing, attending to, remembering, and interpreting information about gender from their social worlds, and for individuals with salient gender schemas, they are actively searching for information about gender.

Although these two versions of gender schema theory have slightly different focuses, they integrate well to explain the phenomenon of gender typing. They both emphasize the cognitive structures present in processing gendered information; they also highlight the active role of the individual in shaping their learning through differential attention and motivation associated with own-gender-appropriate information. Although gender schema theory focuses on the cognitive structures and processes behind gender typing, its tenets are compatible with other theoretical explanations like social learning and biologically driven perspectives.

Applications to Evolutionary Psychology

The principles of gender schema theories complement work by evolutionary psychologists in many ways. Given the infinite amount of information available to be processed, humans have evolved to create cognitive systems to narrow and simplify cognitive processing through directed attention, encoding, and memory, thereby reducing cognitive load. For example, we form schemas to make information storage and retrieval more efficient and guide future information processing. This includes developing schemas to categorize individuals and characteristics into social groups – by age, by race, or by gender. Also, as we have evolved to attend to and encode cues relating to gender, gender schemas are efficient methods for storing this information.

The categories into which information is sorted (and thus the “titles” of the schemas) and the information contained in these schemas are dependent on what is adaptive to learn in a specific context. This information is often related to

the affordances posed by individuals in certain social groups. Because social groups, like gender, have many affordance implications, it is adaptive to have easily accessible information about the groups that are functionally relevant within a culture. For example, in a culture that strongly emphasizes gender group differences, knowing what interests, preferences, or characteristics to associate with someone of a certain gender helps an individual know what to expect from interacting with them. In addition, although this varies by history and culture, knowing how to fill the prototypical role of one's own gender can be adaptive for many reasons, such as ensuring continued parental care and support, gaining necessary social skills from positive peer interactions, and attracting a desirable mate.

Conclusion

Several gender schema theories were independently developed, and they share a number of similar features including the focus on people being actively involved in processing information about gender. Gender schema theory also elucidates the cognitive processes behind gender typing; individuals organize information by gender and focus especially on learning things considered to be appropriate for their own gender. Cognitively organizing information by gender and selectively encoding own-gender information has implications for individuals' skill development, academic achievement, and even career choice. Important future directions for applying this theory include understanding gender schematic processing of gender nonconformity and similarities in gender schemas for cisgender and transgender individuals. Cognitive approaches do not dismiss the social, biological, or evolutionary contributions to gendered patterns but instead offer a complementary perspective.

Cross-References

► [Gender Schema](#)

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Gender Segregation

► [Sex Segregation](#)

Gender Self-Stereotyping

► [Self-Stereotyping](#)

Gene Disease

► [Genetic Abnormalities](#)

Gene-Centered Theory of Evolution by Natural Selection

► [Selfish Gene, The](#)

Gene-Culture Coevolution

► [Dual Inheritance Theory](#)

General Intelligence Factor *G* (Reader, Hager, and Laland, 2011)

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Definition

The General Intelligence Factor (*G*) describes the covariance that exists among species-level aggregates of cognitive performance, first described by Reader et al. (2011). The upper-case *G* has been employed in subsequent publications to differentiate this construct from that which exists in the correlations among individual differences in performance on cognitive ability measures (the

lower-case *g*-factor). There exists debate about whether *G* and *g* are one and the same constructs, the resolution of which has considerable implications for evolutionary models of general intelligence.

Introduction

Reader et al. (2011) were the first to identify a *G* factor in the associations among various primate species aggregates of indicators of cognitive performance. Since this publication, subsequent work has elaborated the empirical (Fernandes et al. 2014) and theoretical (Burkart et al. 2016) underpinnings of the construct.

Review

Presented here is a review of Reader et al. (2011) and three subsequent publications, which build on this work. These papers have advanced both the theoretical and empirical foundations of the *G* construct.

Reader, Hager, and Laland (2011)

A common view in the animal cognition literature is that different taxa exhibit unique, specific cognitive abilities tailored to their niche, and thus their intelligences cannot be compared on a common metric. According to this line of thought, differences in cognition between species are mainly of kind, not degree. An alternative view is that, even though species-specific adaptive problems may lead to the existence of some modular abilities, some overarching domains may also exist (e.g., social intelligence; Whiten and Byrne 1988) each involving many specific abilities. Going a step further, a general processing mechanism adapted to deal with evolutionarily novel problems may be a locus of difference in performance among taxa, with different tasks being expressions of the same latent general intelligence.

Experimental, laboratory studies comparing several mammal and bird species, reviewed by Reader et al. (2011), support the existence of

such a common factor, with taxa exhibiting high performance in certain tasks tending to do well across others. However, relying only on experimental data to test the existence of the *G* factor is a limited approach, as laboratory tests can be species biased (i.e., unfair to particular species), may not reflect natural conditions (i.e., being ecologically invalid), and are available for few species. As a much-needed alternative to this approach, Reader et al. (2011) collated counts of cognitive flexibility-related behaviors in the wild from the primatological literature to examine the existence of *G* in the primate order. In this *tour de force*, the authors compiled extensive data for 62 primate species for five categories: tool use, extractive foraging, innovation, social learning, and tactical deception.

Factor analyses involving these five measures confirmed the extraction of a *G* factor, explaining up to 65% of their variance. The importance of this effect is compounded by two observations: (1) this estimate is higher than most found for the extremely replicable general intelligence (*g*) factor among human individuals (50%); and (2) the *G* factor appears extremely robust to controls for many potential confounds (e.g., phylogenetic or geographic inertia, group and population size, brain and body size, exclusion of data from captive specimens). Apes, on average, exhibited the highest scores in *G* and prosimians the lowest, but high *G* scores evolved independently in capuchins, baboons, and macaques. As expected, neuroanatomical size measures appeared to underlie the species differences in cognitive ability. Moreover, as social learning was found to be an integral part of the *G* complex, it is likely that this domain-general capacity permitted the evolution of cultural transmission and complexity.

Fernandes, Woodley, and te Nijuenhuis (2014)

Fernandes et al. (2014) conducted further analyses of the cross-species dataset of primate cognitive abilities compiled by Reader et al. (2011). The results of this study indicated that *G* (the term first having been introduced in this study) has had a more important role in primate cognitive evolution than previously thought. This is suggested by the observations that (1) the size of

species differences in cognitive abilities was found to be larger for abilities that are more central to the *G* factor (i.e., cognitive functions that share more variance with others); (2) less *G*-loaded abilities are more phylogenetically conserved (i.e., have undergone less recent evolution); and (3) they have evolved at lower average speeds. It thus appears that cognitive flexibility-related behaviors have been more salient to positive selection pressures if not modularized in primate phylogenetic history. This was especially the case in the evolution of tool use proficiency, a capacity that may have permitted inceptive niche construction.

Burkart, Schubiger, and van Schaik (2016)

Psychometric studies of human intelligence have distinguished between *G*, a single factor extracted from population-level cognitive ability indicators, and *g*, an intelligence factor calculated based on individual-level scores. Evidence for *g* in non-human species has been found in multiple examinations of cognitive abilities in various avian and mammalian taxa (Galsworthy et al. 2014). In some of these studies, *g* explained 40% of the performance variance, was positively associated with neuroanatomical volume indicators (e.g., overall brain size), and was heritable. A similar pattern was found in nonhuman primates, with *g* explaining 48% of performance variance in a sample of rhesus macaques (Herndon et al. 1997). More recent analysis with chimpanzees has found a single heritable intelligence factor (Hopkins et al. 2014; Woodley of Menie et al. 2015).

Despite the evidence supporting the underlying existence of *g* and *G* in nonhuman species, studies extracting a single intelligence factor across species based on individual-level scores (i.e., mixed studies), have not been that successful. For example, comparisons across primate taxa, including studies contrasting the scores of 23 individuals from four great-ape species were unable to extract *g* (Hermann and Call 2012). Similarly, another (Amici et al. 2012) study examining the scores of 99 individuals (seven different primate species) did not locate either *g* or *G*. According to Burkart and colleagues (2016), one of the issues of mixed

studies is that the effective sample is not the total number of subjects, but rather g is calculated based on the number of individuals within species, and G is estimated based on the number of species. Consequently, this statistical inconsistency increases the amount of noise in the analyses. Furthermore, Burkart et al. argue that mixed studies do not take into consideration domain-specific adaptations across species; these differences are predicted to modify the mean score for some tests but not others, weakening the correlations across test performance.

Woodley of Menie, Fernandes, te Nijenhuis, Peñaherrera Aguirre, and Figueredo (2016)

Similar to Burkart et al. (2016), Woodley of Menie et al. (2016) acknowledge that the mixed design does not take into account difference in factorial characteristics between species. Thus, the absence of measurement invariance hinders the adequate estimation of g in pooled samples of individuals from different species. Floor and ceiling effects are also proposed as factors affecting measurement invariance. Thus, tasks relatively simple for one species may be unsolvable for another. The presence of ceiling and floor effects is usually examined according to the statistical distribution in performance. Moreover, specialized abilities are considered to be particular to each species and are predicted to have weaker loading in a single factor.

Woodley of Menie and colleagues proposed that mixed designs could estimate g , if the differences across species are larger on tests with a higher proportion of shared variance, but not in cases where the variation in species performance is uniform. To test these predictions, the authors used a combined dataset of chimpanzee and human children performance on various tasks used to measure intelligence. As hypothesized, children outperformed chimpanzees on more g -loaded tests. However, by sequentially removing from the analyses tests with the smallest coefficients of variation, and correlating the vector of task g -loading with the difference in performance between species (d), the correlation between g and d increased inversely to the number of tasks retained. These findings indicate that differences

across species are indeed concentrated on g and that this is likely therefore the principal source of G . However, this is only apparent when examining tasks that allow enough within-species variation for both species being compared.

Conclusion

The G factor of primate cross-species differences, first identified by Reader et al. (2011), has yielded much in the way of subsequent theoretical and empirical investigation. Many of the insights gleaned from research into the construct could be applied to the task of identifying similar G factors from other groups of taxa where individual differences g factors have been identified within species, such as birds and the nonprimate mammals.

Cross-References

- [Brain Size and Intelligence](#)
- [Convergent Evolution of Intelligence](#)
- [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- [Evolution of Intelligence, The](#)
- [Intelligence Versus Natural Selection](#)
- [Nonhuman Intelligence](#)
- [Relative Brain Size, Encephalization Quotient](#)

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Generativeness

► Fertility

Genes and Culture Interaction

► Human Nature and Biocultural Evolution

Genetic Abnormalities

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Synonyms

Familial disease; Gene disease; Genetic disorder;
Genetic mutation; Inherited disease

Definition

A missing, extra, or irregular component of the genome that can be inherited, can occur spontaneously, or can be caused by the environment.

Introduction

Genetics, just as every other aspect of science, has seen significant advances in recent years. The understanding we have obtained from these genetic advances has enabled genetic mapping and the early discovery of genetic abnormalities. With this new understanding comes a plethora of questions. These advances have also yielded a necessity for the psychological and social aspects of behavior to be incorporated into the realm of human biology. To understand the evolution of psychology, as it relates to genetic abnormalities, we will discuss the history of genetics, the basics of genetics and genetic abnormalities, and the involvement of psychology and its benefits for those with genetic abnormalities.

The History of Genetics

The genetics that is discussed, observed, manipulated, and studied today has its origins in the teachings of Aristotle and his ideologies regarding the creation of life. His teachings explained that we are each a mixture of our parents' traits with the father supplying the life force and the mother supplying the building blocks (Schwartz and Sharpe 2006). For many centuries his theory remained unquestioned, until the research and memoir of Gregor Mendel in 1866. While his research was published, it did not make an imprint on genetics or heredity until its rediscovery in the 1900s. Several researchers, such as De Vries, Bateson, Johannsen, Morgan, Watson, and Crick, helped rocket Mendel's laws to the forefront of biology. It was Mendel's laws that taught the world about heredity and how inheritance follows particular patterns; his work with pea plants led to the understanding of traits and genetics that we have today (Gayon 2016; Durmaz et al. 2015).

Genetics

To fully understand genetic abnormalities, we must first understand the basics of genetics.

Genetics is the term used to describe the study of genes and heredity among organisms. Genes are the microscopic nucleotides of deoxyribonucleic acid (DNA) that make up the 23 chromosomes. A zygote inherits a gamete cell from each parent; these gametes each contain only one set of chromosomes which is combined to make 23 pairs. On each pair of chromosomes exists two copies of each gene, one inherited from each parent. Genes are the determinants of traits; there are three different types of traits, polygenic, pleiotropic, and Mendelian. Polygenic traits are traits that involve many genes; pleiotropic traits are multiple traits that are affected by one gene; and Mendelian traits are traits that are solely attributed to one gene. An allele is either dominant or recessive and can impact the way a particular trait is presented in an individual. Each individual's genetic makeup is unique, and the combination of genes and chromosomes determines both their genotype and phenotype (Gayon 2016; Durmaz et al. 2015).

Evolution and Psychology

As previously discussed, Gregor Mendel provided the foundations for genetics and how traits come to be. The ideas of evolution, natural selection, and mate selection come from the research and discoveries of Charles Darwin. Darwin's work created the foundations for evolutionary psychology. Darwin and Mendel were not privy to each other's discoveries; but, the ideologies of the two come together for us to fully understand the evolution of genetic traits and how they are passed on to offspring (Buss 2009; Dewsbury 2009).

By merging the discoveries of Mendel and Darwin, we can now study how genetics change within a population. Population genetics is the study of how populations of species change genetically over time, leading to their evolution. The principles of population genetics attempt to explain how genetics and evolution influence each other. Allele frequency, one of the elements that most strongly impacts population genetics, describes how often alleles appear in the genetic sequences of a certain population. Alleles, more

frequent in the population, are more likely to be passed on to offspring, whereas less frequent alleles can be left behind in the process of evolution. There are five factors that can impact the frequency of alleles (Clark 2001; Lowe and Allendorf 2010):

1. **Natural Selection:** This factor is based on Darwin's idea of natural selection, survival of the fittest. Within natural selection, the alleles that are the strongest, or most adaptive, become more frequent in the population (Clark 2001; Lowe and Allendorf 2010).
2. **Sexual Selection:** This factor again comes from Darwin's idea of nonrandom mating. Certain individuals are more sexually attractive to mates than others because of specific traits they possess. Therefore, alleles of most successful maters will have a higher frequency. Similar to sexual selection is the idea of artificial selection. New scientific advances now allow individuals to decide which alleles they want passed on to their offspring, leading to the presence of more attractive alleles within the population (Clark 2001; Lowe and Allendorf 2010).
3. **Genetic Drift:** This factor is attributed to random chance and has no attribution to the adaptivity of a particular allele. In certain instances (e.g., natural disasters), a sample of a population may be lost or isolated, leading to a difference within the alleles of the population (Clark 2001; Lowe and Allendorf 2010).
4. **Gene Flow or Migration:** This factor describes how migration changes allele frequency by introducing individuals with different alleles into a genetically different population (Clark 2001; Lowe and Allendorf 2010).
5. **Mutation:** This factor has to do with the mistakes that happen in the copying process of DNA. Some errors can be favorable and are passed on through mating, leading to the presence of favorable alleles to become more prevalent in the population's gene pool. Other errors can lead to deformation or disease or have other negative consequences. These unfavorable alleles are often less prominent (Clark 2001; Lowe and Allendorf 2010).

For the purpose of this article, the factor that we are most interested in is mutation. These mutations are what we call genetic abnormalities.

Genetic Abnormalities

The research of genetic mutation, by Herman Muller, and genetic analysis, by Tjio and Levan, made it possible to identify abnormalities within the genetic structure of chromosomes that are attributed to congenital defects. These abnormalities within the genetic structure can be caused by deletions, duplications, repetitions, modifications, translocations, and the absence of genes on any one of the chromosomes. The genetic location of the abnormality will determine the effect it will have on the individual (Gayon 2016; Durmaz et al. 2015).

Thousands of genetic abnormalities have been discovered by researchers; some are considered harmless, and others can be debilitating or life-threatening. There are four classifications of genetic abnormalities; single-gene disorders, multifactorial disorders, chromosomal disorders, and mitochondrial disorders (Funk and Wagnalls Corporation 2018). Single-gene disorders are classified as such because it is the mutation of one gene that results in the presence of this particular class of disorders (Bates 2005; Psychological and Social Implications 2010). Multifactorial disorders are characterized by the variety of factors that lead to their development; multiple errors in gene mutation and environmental factors contribute to these disorders. The genetic makeup of these disorders can often be described as a predisposition for a multifactorial genetic disorder (Bertella et al. 2007; O'Neill and Kennedy 1998). Chromosomal genetic disorders are classified by genetic variations of partial or entire chromosomes. Lastly, mitochondrial disorders are the rarest form of genetic abnormality. Mitochondrial disorders are caused by a genetic mutation of the mitochondria that inhibits its production of energy (Cao et al. 2018).

How are specific genetic abnormalities selected through evolution? As previously mentioned when discussing allele frequency, the most frequent alleles are often the most prominent in a

population. Genetic abnormalities, while not always adaptive, can also become present in a population and passed on or selected for a particular reason or environmental factor (Gall 2011; Abrams 2009).

Psychological Aspect of Genetic Abnormalities

Evolution as we know is the process of change over a period of time; and just as humans have evolved, the brain has evolved along with it. The brain was no longer used simply for survival but also for learning, intellect, and conscious awareness. However, the brain itself is not immune to being impacted by the genetic mutations and abnormalities that occur during the evolutionary process. However, the genetic abnormalities within the brain can have characteristics that do not necessarily present themselves physically, but behaviorally. It is through these behavioral impacts that genetic abnormalities can attribute to psychological deficits. These deficits are largely due to the complexity of the human brain (Buonomano 2011; Solso 2003).

In his book, *Brain Bugs* (2003), Dean Buonomano described the evolution of the brain as “new structures were placed on top of older functional structures, leading to redundancy, waste of resources, unnecessary complexity, and sometimes competing solutions to the same problem” (pp. 12). As complexity increases so does the capacity for error, in this case, genetic abnormalities occur that lead to changes within the cognitive processes of the human brain. These errors lead to deficits that impact cognitive function such as Down syndrome, Alzheimer’s disease, developmental delays, learning disabilities, mental retardation, and many more (Genetic Disorders 2018; Buonomano 2011; Psychological and Social Implications 2010).

Another bridge between psychology and genetics is through the diathesis-stress model. The diathesis-stress model states that individuals have predisposing factors within their genes. However, the way that an individual interacts with their environmental stressors determines if and when they will meet criteria for a specific

diagnosis. Diagnoses such as schizophrenia, major depressive disorder, and bipolar disorder have strong genetic components; but, without the “right” stressor, an individual with a genetic predisposition can live their entire life without experiencing the psychological effects of these disorders (Anderson and Nickerson 2005).

Other Psychological Effects

The evolutionary aspect of treating genetic abnormalities turns to psychological treatment as a means of improving quality of life for individuals that suffer from them. In previous years, due to the lack of understanding of these disorders, patients with genetic abnormalities were not faced with the opportunity to improve behavioral, interpersonal, cognitive, or other nonmedical aspects of their lives. However, relatively recent advances in genetics allow for the treatment of the individual from a psychosocial standpoint, which considers their mental health as well as psychical well-being (McDaniel 2005).

Additionally, a new dilemma of genetic testing comes into play with the newest genetic advances and the capacity of genetic mapping. Genetic testing yields answers to previously unknown aspects of our lives. There are obvious benefits and disadvantages to genetic testing that may leave individuals in a panic and wondering if knowing the definitive truth about their genetics is really better than embracing the unknown. The answers provided by genetic testing may lead individuals to experience negative self-esteem, anxiety, or depression or have negative impacts in their interpersonal relationships (McDaniel 2005).

Benefits of Psychological Treatment

Psychological treatment when dealing with psychosocial effects of genetic abnormalities may be beneficial. Genetic testing, while controversial, can benefit the people around the individual with the disorder to effectively understand a support them. Psychoeducation may be beneficial when provided for both the individual and the family,

allowing them to ask questions and know what to expect regarding the disorder. Behavioral limitations of the individual may be addressed along with proper decisions about their well-being and overall quality of life. Additionally, intellectual, behavioral, and cognitive function may be improved through psychotherapy, yielding an effective style of coping, allowing the processing of emotional responses, developing an open avenue for family communication, and stimulating a positive environment and a greater quality of life for the individual (Otter et al. 2018; McDaniel 2005; Jiménez et al. 2018).

Conclusion

In conclusion, genetic abnormalities can originate through a variety of different methods: natural selection, sexual selection, genetic drift, gene flow, or mutation. Regardless of how abnormalities arise their impact on the individual is apparent. These abnormalities can not only physically affect the individual but also cognitively, impacting the overall fitness of the individual. Additionally, the proper support and psychological intervention may help with the psychosocial effects of the genetic abnormalities that may come our way and aid in the positive interpretation of information that may be hard to handle. Future research can be done to determine the most effective forms of psychotherapeutic treatment.

Cross-References

- ▶ Genetic Influences of Puberty
- ▶ Human Genome Project, The
- ▶ Problem of Genetic Inheritance, The
- ▶ Recessive Genes

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Genetic Alterations

► Mutation

Genetic and Prenatal Components of Homosexuality

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Synonyms

Biology of homosexuality

Definition

The biological mechanisms that determine, at least in part, same sex versus opposite sex attraction.

Introduction

Homosexuality, the sexual attraction to members of the same sex (as opposed to heterosexuality) is commonly assumed be controlled by social interactions (constructivism), early learning (ethology/

behaviorism), or blockade of sociosexual development (Freudism). Recent research in genetics or endocrinology has shown that genes and hormones, acting pre- or immediately postnatally, contribute to a large extent, if they do not completely determine, the sexual orientation of a subject.

Homosexuality can be viewed as a sex reversal of sexual preferences since homosexual males are sexually attracted by the sex that is normally the target of women's attention and vice versa. Substantial evidence suggests that the mechanisms that control the development of sexually differentiated characteristics also participate to the determination of sexual orientation.

Hormonal Influences

In mammals, sex chromosomes (XX in females and XY in males) determine in early life the sex of the gonads (ovaries or testes), and subsequently, testosterone produced by the embryonic testes determine the development of primary sexual characteristics (penis vs. clitoris, sperm ducts vs. vagina and uterus). The work of Young and colleagues (Phoenix et al. 1959) and hundreds of studies that followed extended this principle of sexual differentiation of morphology to behavior. Independent of the chromosomal sex, embryonic exposure to high male-typical concentrations of testosterone, or its metabolite estradiol, leads to the development of a subject with a "male brain" who will in adulthood be able to display male-typical sexual behavior in response to testosterone but will be unable to display female-typical behaviors in response to estradiol plus progesterone. Conversely the absence of exposure to these high testosterone concentrations during early life will produce female subjects unable to display male typical behaviors in response to testosterone but producing female behaviors in response to estradiol and progesterone. These organizational effects of testosterone take place during a critical period of development and are afterwards irreversible.

Multiple experiments in several species of mammals (mostly rodents) suggest that sexual

partner preference develops under similar hormonal influences somewhat independently of a direct action of the genetic sex. Subjects exposed during early life to high concentrations of testosterone (or estradiol) will display male-typical partner preferences and be sexually attracted to and try to have sexual interactions with females, whereas subjects developing in the absence of testosterone will be sexually attracted to males, a female characteristics.

Two types of arguments indicate that this type of early hormonal mechanism is implicated, to some degree at least, in the control of sexual orientation (see Balthazart 2011; LeVay 2011 for reviews). Firstly, human pathologies that are associated with substantial modifications of the embryonic endocrine environment are associated with increased incidences of homosexuality. For example, girls affected by congenital adrenal hyperplasia, a condition that exposes them to high concentrations of androgens before birth, display a significantly increased incidence of homosexuality even if their endocrine status is pharmacologically corrected after birth. This is also the case of girls born from mothers who had been treated during their pregnancy with the synthetic estrogen diethylstilbestrol in the hope of preventing spontaneous abortions. Note also that conversely, XY embryos who were exposed to male-typical concentrations of testosterone before birth will generally display in adulthood a male-typical sexual identity and orientation even if they were raised as girls from birth for different reasons such as malformation or accidental destruction of the penis leading to sex reassignment and surgical correction of genital structures during the first postnatal weeks.

Secondly, numerous studies have compared the expression of sexually differentiated traits that are known to be controlled, at least in part, by embryonic testosterone in homosexual and heterosexual populations and found that these traits are on average feminized in homosexual men and/or masculinized in homosexual women. These traits include morphological characteristics such as the relative length of the second and fourth finger, the relative length of long bones in the legs, arms, and hands, or the volume of several brain

structures such as the suprachiasmatic nucleus, the anterior commissure, or the interstitial nucleus of the anterior hypothalamus number 3. Several physiological characteristics that are affected by prenatal testosterone also show similar differences between homosexual and heterosexual populations including aspects of the inner ear physiology (otoacoustic emissions), the estrogen feedback on the secretion of luteinizing hormone, and the brain activation by male or female odors as detected by positron emission tomography or magnetic resonance imaging.

Together these data point to a role of pre- or perinatal endocrine influences on the development of sexual orientation. It is clear however that the research does not suggest at this point that sexual orientation is completely determined by hormonal factors since correlations between sexually differentiated traits and homosexuality only explain a limited part of the variance and no endocrine pathology results in a complete reversal of sexual orientation in all subjects.

Genes

Even if embryonic steroids were fully determining sexual orientation, this would only move the quest for the mechanisms one step further; the next question would then be why is steroid action atypical in some subjects resulting in a homosexual orientation? External events such as an enduring exposure to stress are known to inhibit fetal testosterone secretion in rodents, and based on epidemiologic studies on boys born in Berlin during World War II, it has been claimed that chronic embryonic stress could cause male homosexuality. No other study has however been able to confirm this finding.

Exposure to endocrine disruptors that are now widely present in the environment is also of great concern, but this theoretical idea has not received any experimental support so far, and such evidence will obviously be difficult to obtain due mainly to the long latency between exposure and expression of sexual orientation.

Many studies have demonstrated that male and female homosexuality are partly heritable

therefore suggesting the existence of genetic influences (Ngun et al. 2011). These influences can in theory be relatively direct (presence of genes affecting sexual orientation) or mediated by hormonal mechanisms (changes in the synthesis or catabolism of embryonic sex steroids, alteration of steroid receptors, etc.). Within a family, if a son is gay, 20–25% of his brothers will share this orientation, compared to 4–6% in the whole population. Similarly, lesbians have a greater probability than heterosexual women of having a homosexual sister. This increased incidence could obviously reflect communality of educational or social factors, but the comparison of true (monozygotic) and false (dizygotic) twins allows to a large extent to reject this interpretation: concordance of sexual orientation is systematically higher in true than in false twins who had to a large extent the same postnatal experiences. Based on multiple studies analyzing this concordance, it seems that in social conditions typical of Western societies, approximately 50% of the variance in human sexual orientation would be explained by genetic factors.

However, the quest for the genes that are influencing sexual orientation has met with limited success so far. Studies of the incidence of male homosexuality in family lineages indicated that this homosexuality is largely transmitted through the maternal lineage: a gay man has a higher than average probability of having gay relatives in his maternal uncles and cousins than on the paternal side. This finding that was replicated several times was suggesting that genetic influences on male homosexuality were transmitted via the X chromosome (the only one systematically inherited from the mother), and a highly publicized study by Dean Hamer and colleagues identified in 1993 a linkage of male homosexuality with the telomeric region of the X chromosome called Xq28 (Hamer et al. 1993). This linkage has been replicated in three more studies including a very recent one published in 2015 that was based on a large sample of several hundred subjects (Sanders et al. 2015). The specific gene(s) located in Xq28 that seem(s) to affect sexual orientation has(ve) however not been identified, but it is intriguing to note that the gene coding for

the androgen receptor coregulator MAGE-11 is located in this chromosomal domain and thus potentially controls sex steroid action at the receptor level. This gene could provide the link between hormonal and genetic mechanisms.

The putative genetic controls of sexual orientation are however quite complex: linkages with other chromosomal loci have more recently been identified (Ngun et al. 2011), and evidence is progressively accumulating indicating that epigenetic mechanisms differentially affect gene expression in homosexual and heterosexual subjects (Rice et al. 2012; Ngun and Vilain 2014).

It is also interesting to note that the relative incidence of homosexuality in a family increases by approximately 33% for each older brother born to the same mother. This effect has been established and replicated several times based on the study of thousands of gay men, and thanks to this huge sample size, it has been possible to demonstrate by partial regression techniques that the increased incidence of homosexuality does not relate to the age of the mother or father, nor to the number of older sisters or younger brothers, nor to the total number of boys present in the family (Bogaert and Skorska 2011). The only possible interpretation of this effect is based on the progressive development in mothers bearing a male fetus of antibodies that would interfere with the normal development of the male brain.

Conclusion and Societal Impact

It is at this point impossible to ignore that various biological factors including sex steroid hormones, genes, and epigenetic mechanisms affect in a prominent manner sexual orientation. It is also clear that none of these factors is able to explain by itself all cases of homosexual orientation. There are possibly different forms of homosexuality that are controlled by different factors (differential controls in gays and lesbians, in more or less masculine/feminine men and women), or alternatively different hormonal and genetic factors must interact to result in a homosexual attraction, or finally these biological factors do not, by themselves, determine sexual

orientation but rather modulate the probability of acquiring a homo- versus heterosexual orientation, and this orientation will then develop in interaction with unidentified influences of the postnatal environment. Recent studies from the laboratory of Melissa Hines in Cambridge, UK, have shown in this context that, contrary to control girls, girls who were exposed to abnormally high concentrations of androgens in utero due to congenital adrenal hyperplasia do not copy the use or preference for toys that were declared or shown to be typical for their gender (Hines et al. 2016). One can speculate that sexual partner preference could develop under similar interactions of pre- and postnatal influences.

Even if multiple questions still remain unanswered, it appears obvious that sexual orientation is heavily influenced by a variety of biological factors. It is a complex behavioral trait that can be voluntarily accepted and publicly assumed, but it is not only a matter of free choice. Therefore ostracism and persecution have no rational foundation and should be altogether abandoned.

Cross-References

- [Sexual Attraction](#)
- [Sexual Differentiation](#)

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Genetic Codes

- [Good Genes](#)

Genetic Codification of Behavior

- [Study of Instinct, The](#)

Genetic Conflict

- [Paternity Uncertainty and Father-Offspring Conflict](#)

Genetic Conflict Between the Sexes

- [Intralocus Sexual Conflict](#)
- [Intralocus Sexual Conflict Across the Genome](#)

Genetic Deterioration

- [Dysgenic Concerns](#)

Genetic Determinism

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Synonyms

[Biological determinism](#)

Definition

There are at least two views of genetic determinism, one of which no scientist or intellectual of any significance has ever believed to be true, but which is nonetheless widely known, and another which is novel and is proposed and defended in this entry. The first, received, conception maintains that genetic factors alone are causally responsible for the behavioral traits/outcomes of human beings. The second, novel, conception maintains that *variation* in at least some socially salient human behavioral traits/outcomes is caused primarily by individual and social genetic, rather than nongenetic environmental, factors (at least in adults).

Introduction

Genetic determinism is usually construed as the idea that “an organism’s phenotype is determined by genotype alone” (Sesardic 2005, p. 14). Though genetic determinism in this sense could apply to any life-form, the substantial controversy surrounding the notion predominantly or

exclusively concerns its application to humans. Moreover, the supposed claim that human *behavioral* rather than physical traits/outcomes are genetically determined has engendered virtually all of the cultural and academic rancor associated with the concept of genetic determinism, with one behavioral trait in particular, intelligence (whether presented in terms of IQ or general intelligence [g]), having proved especially incendiary in this context (see, e.g., Glad 2008).

The trouble is that no serious scientist or intellectual has ever endorsed genetic determinism as just defined, and thus it is *prima facie* mysterious how the concept has garnered so much attention. In considering the history of the idea of genetic determinism, this entry aims to explain the likely drivers of the controversy that has attended the concept. But the central goal of this entry is found elsewhere. Specifically, it attempts to define and defend a tenable genetic determinist view in light of the best relevant scientific evidence currently available. As it happens, the expectation or hope that nongenetic environmental factors, particularly those that are at least to some extent under human control, chiefly or entirely determine (variation in) key human behavioral traits/outcomes is almost certainly false. There may be political and moral reasons for wanting this environmental determinist thesis to be true. But those do not change what the germane empirical data indicate, even if they do inspire resistance to the implications of those data.

History

It is probably impossible to find any noteworthy scholar or scientist who thought or has thought that genetic factors alone determine phenotypic traits. Neven Sesardic goes further, averring that “there is literally *no one* who ever subscribed to genetic determinism” (2005, p. 14; emphasis added). When one attempts to study the history of the thesis of genetic determinism, only two things are typically found: (1) social scientists and humanists – hostile to biological modes of explanation of human behavioral phenomena – employing “genetic determinism” and cognate terms to

smear and misrepresent those who have attempted to study the genetic (and sometimes other biological) bases of human behavior (hereafter, the latter individuals are referred to as “hereditarians”); and (2) hereditarians explicitly distancing themselves from the idea of genetic determinism, hoping to avoid attacks from their “biophobic” peers. In most academic discourse that includes it, “genetic determinism” is thus nothing other than a term of abuse.

John Glad (2008) makes a similar point, maintaining that “unalloyed genetic determinism is . . . partly an invention of egalitarian environmentalists, who attribute [the view] to their opponents in an effort to discredit them” (p. 62). Helmuth Nyborg (2003) copiously documents the “demonization” (p. 443) of modern and contemporary scientists who have reported substantial genetic influences on behavioral traits/outcomes in humans, and also suggests that “fear that genetic determinism is morally wrong” significantly motivates support for competing environmental determinist models (p. 480; it is worth noting that Nyborg also highlights the tendency of critics of hereditarianism to pit it only against “an extreme version of the environmental paradigm,” rather than “admit to even a moderate form of genetic determinism” [p. 480]). Sesardic (2005) argues at length against the many distortions and caricatures of hereditarian research that a number of philosophers of biology, and some scientists, have advanced, most prominently Philip Kitcher and Daniel Dennett (to his credit, Kitcher [1985] at least shows awareness that hereditarian researchers deny that they are genetic determinists [p. 8]). In the course of his critical assessment of these anti-hereditarians, Sesardic makes clear that they have inveighed against their targets for moral and political, not just scientific, reasons, at least at times (see also Cofnas 2016). Kitcher (1985), for example, assails the psychological research of Cyril Burt for its supposed role in creating the allegedly harmful British 11-plus exam (Sesardic 2005, pp. 42–44), lamenting the purported fact that this exam, and the “misguided science” (which is to say biobehavioral science applied to humans) underpinning it, wrongfully “mangled” the “aspirations” of children (p. 11), perhaps especially “working-class and lower-middle-class” ones (p. 1). (These claims of

Kitcher's are either false or misleading [see Sesardic 2005, pp. 42–44], and it should be noted that he is in a long line of academics who have unjustifiably maligned the work of Cyril Burt [see Tredoux 2015 for a defense of Burt].) He also condemns “sociobiology” as “potentially damaging to the cause of social justice” (Kitcher, 1985, p. 7).

In view of the foregoing, one has the impression that critiques of hereditarianism, including bad faith efforts to connect it with the “ludicrous” (Sesardic 2005, p. 14) idea of genetic determinism, have more to do with concerns about adverse *consequences* that may emanate from hereditarian scientific inquiry than anything else. To be more precise, it is the fear that hereditarianism might justify or engender social and/or political evils that signally motivates anti-hereditarianism. This fear seems to have originated from fairly recent historical events. Feltham (2017) observes that “[t]wenty-first century collective Western consciousness remains haunted by Nazism and the Holocaust”: “the Holocaust exerts a massive moral and symbolic pull towards the concept of human rights and their enshrinement in international law ... [Contemporary leftist causes] unconsciously gain moral traction from implied associations [of perceived enemies] with Nazi persecution, eugenics and threatened extermination” (p. 17). In other words, horror at the prospect of another Holocaust or a similar moral catastrophe has compelled militant opposition to anything that can be associated, however tenuously, with the worldview of German National Socialism, including virtually all of rightist thought and politics. Since National Socialists saw the characteristics of human groups and individuals as determined to some extent by heredity, and because this belief was part of National Socialists' basis for practicing eugenics, some understand any attempt to relate genetics to important existential outcomes, for groups or individuals, as tending intrinsically to genocidal politics. Some anti-hereditarians have indeed associated their critical targets with National Socialism and related ideologies, typically without any basis for doing so (see Nyborg 2003).

But the notion that hereditarian beliefs have had an exceptional role in mass political killing

is not congruent with the record of history. It is a plain fact that people understood hereditary factors to be causally associated with interindividual behavioral variation and social inequality for many centuries before the emergence of National Socialism; Plato, for example, considered intelligence to be substantially heritable, a belief that partly motivated his support for eugenic practices (Ruse 1985, p. 135). Many or most of the historical societies in which such basically hereditarian beliefs predominated were, to be sure, violent and cruel, largely due to challenging existential conditions typical of preindustrial life (Woodley of Menie et al. 2017a) and to related genetic factors (Frost and Harpending 2015), but they did not all participate in the mass murder of innocents. Moreover, the totalitarian Marxists of the Soviet Union alone, not to mention other genocidal and democidal Communist regimes, e.g., of China, Cambodia, Vietnam, and North Korea, killed many more civilians, indeed millions more, than the National Socialists, despite strong commitment to environmental determinism (see Courtois et al. 2001; Pinker 2003). (It is worth asking why few contemporary Western intellectuals think that Lysenkoism and other environmental determinist models of the bases of human behavior promote genocide while almost all of the same people believe that hereditarian thought does so. It should be recognized that the ideas about human behavior of many prominent figures [living and dead] in Western academia, for example, Stephen Jay Gould [see Sesardic 2005, p. 191], are about as environmentalistic as those of the murderous Soviets. The hypocrisy of such people in accusing hereditarians of inciting genocide and the like, simply by virtue of their hereditarianism, is therefore striking.) These facts are almost never mentioned in discussions of the supposed potential to instigate violence latent in hereditarian thinking. But even more seldom broached is the fact that the largely liberal Allied powers were potentially responsible for the violent deaths of around two-and-a-half million “ordinary Germans” in the wake of World War II (MacDonogh 2009). It would appear, then, that other elements of National Socialist society must be invoked to explain its genocidal activities, for the mere fact that it

maintained a hereditarian ideology seems neither necessary nor sufficient.

Moralistic protest against hereditarianism thus should be seen for what it is: a rationalized effort to deform and control science in accord with prejudice against biobehavioral ideas. Interestingly, many involved in this effort are quite unvarnished about their moral and political biases against hereditarian (and sometimes more broadly biological) perspectives on human behavior. An example comes in the form of a paper from a team of sociologists, which investigates attitudes in the American population about the “importance of genes for understanding individual differences in a series of broad domains: physical illness, serious mental illness, intelligence, personality, and success in life” (Shostak et al. 2009). The piece fails to mention the fact that variation in outcomes in *all* of the “domains” considered is under substantial genetic control (e.g., Bouchard 2004; Clark 2014; Kujala 2011; Panizzon et al. 2014; Riemann and Kandler 2010). Indeed, the article shows no meaningful interest in whether genetic factors *are* important determinants of variability in these outcomes, but instead expresses much anxiety, through a survey of the works of other sociologists, about the potential for hereditarian explanatory paradigms to “justify existing inequalities” and “promote ‘essentialism’” (Shostak et al. 2009, p. 78). This concern about the possible deleterious ramifications of hereditarian ideas strangely begs the question against hereditarianism – for it seemingly assumes that social and ideological factors (e.g., hereditarian beliefs) can greatly contribute to the generation and sustainment of certain unwanted social outcomes (e.g., inequality), but that genetic factors cannot. Hereditarianism is evidently assumed to be wrong out of hand. In asking why this is done, one may find an answer from the authors, who are helpfully forthright in acknowledging the source of this rather nonscientific, politicized orientation to the subject of hereditary influences on human behavior: “Some analysts have argued that beliefs in genetic causation are likely to resonate most strongly with the world views [*sic*] of people who occupy socially privileged positions or who have conservative political orientations . . . social scientists who favor progressive social change may

[therefore worry about the implications of genetics research]” (p. 78). The claim that those on the academic left are generally wary of and hostile to hereditarian thought fits, as has already been shown, with the history of opposition to the idea of genetic determinism. And it is also supported by empirical work on the relationship between political outlook and views about the relative importance of environmental and genetic factors to behavioral outcomes, which has found that academics and (more so) leftist academics, especially those in disciplines such as sociology that are dominated by leftists (Carl 2015), are inclined to genetic denialism or skepticism of various sorts (Geher and Gambacotra 2010; Horowitz et al. 2014).

Hereditarianism and Existential Ideals

A further ideological basis for resistance to hereditarianism is not so much moral or political as it is existential. In Western societies especially, a common aspiration is to direct the course of one’s life free, to the extent possible, from the constraints and influence of unchosen circumstances (Rubin 2015). The metaphysical thesis of causal determinism, well known in the free will debate, has been interpreted as a threat to such hopes for self-formation (Kane 1996), insofar as it posits that everything that occurs in the universe inevitably results from prior states of the universe coupled with the laws of nature, leaving apparently no room for ultimate human agency. But crucially, the thesis of causal determinism is compatible with, say, the possibility that human nature and each individual person’s life are open to radical change: it holds simply that whatever change in fact occurs ineluctably occurs, given prior states of the universe and natural laws. Hereditarianism, particularly strong forms of it that posit that differences in key human life outcomes are largely under genetic control, is actually far more threatening than mere causal determinism to the aforementioned hopes for autonomy, for it indicates that such life outcomes are typically stable, perhaps bordering on immutable, at least in relation to the outcomes of others. To take an example, if social status is settled mostly by genetic factors (and

evidence suggests that it is; see Clark 2014), and if, because genetic, these factors are not open to relevant change for any given individual, then ordinary Western expectations to rise in one's social hierarchy may be largely irrational. One is left most rationally expecting "more of the same," which is perhaps disturbing to those seeking to improve their lot in life. Kitcher (1985) appears to fear precisely this possibility, insofar as he warns about the potential of hereditarian ideas to "mangle" people's "aspirations" (as noted above).

But it should be asked how good *unrealistic* expectations are (see Sesardic 2005, p. 180). Surely hereditarianism is potentially beneficial if it frees people of unreasonable hope and helps them to adopt more sensible goals given their abilities and dispositions. Those who have internalized a culture that values social mobility and self-formation may be inclined to uncritically accept Kitcher's portrayal of hereditarianism as dangerous. Yet this inclination might be little more than an artifact of moral blindness issuing from that same culture, an inability to appreciate the harms that may come of refusal to accept human biological limitations, and thus is no reason to drop the hereditarian paradigm. (Nevertheless, if variation in cultural values is under strong genetic control, which is highly likely, efforts to change such values by way of argument may often be futile.)

The Case for (Revised) Genetic Determinism

In setting out to defend a more reasonable conception of genetic determinism, it is first necessary to be clear about what that conception posits. Revised genetic determinism is qualified with respect to both the traits/outcomes and individuals to which it applies and the causal power that it ascribes to genetic factors. Moreover, it does not make claims about the degree to which traits/outcomes are "caused by" genetic factors, but rather about the degree to which trait/outcome variation is under genetic control, and does not claim that variation in all traits/outcomes is mostly under genetic control. It would be absurd to argue that heredity is the primary determinant of differences

in *all* human behavioral traits/outcomes, since some of these, e.g., short-term memory, exhibit almost no heritability, i.e., interindividual trait/outcome variation due to interindividual genetic variation (Woodley of Menie and Fernandes 2015). Further, revised genetic determinism applies only to *adult* humans, given that the heritability of at least some behavioral (and other) traits/outcomes rises into adulthood. Thus revised genetic determinism maintains only that variation among adults in certain significant behavioral traits/outcomes is primarily genetically determined, those being general intelligence, executive functions (i.e., cognitive controls of behavior), life history speed, and social status. (This is not to imply that there are no other important behavioral traits/outcomes variation in which is substantially genetically determined; rather, it is simply taken to be part of the definition of revised genetic determinism that it only concerns the four traits/outcomes just listed, a choice explained in the following.)

The focus is on these traits/outcomes because they are so widely believed to be extremely important for the quality of human lives, which is why research on them has generated so much controversy in the behavioral sciences (the case of general intelligence, mentioned above, is illustrative here). Whether and to what degree, say, differences in individual preferences for ice cream flavor are genetically determined is not an issue on which anything meaningful seems to hang. But it is of obviously profound importance whether and to what degree variation in general intelligence is genetically determined, since this trait substantially influences a number of critical life outcomes (Strenze 2015), e.g., educational attainment, and because the extent to which differences in it are malleable carries a number of major implications for social policy. Therefore, the fact that the ambit of revised genetic determinism is quite narrowly circumscribed barely reduces the importance of its claims relative to original genetic determinism.

With preceding sections of this entry in mind, it should be apparent that revised genetic determinism does not hold that genetic factors are the exclusive determinants of variation in any

human behavioral trait/outcome (there is not sufficient evidence to support the belief that individual differences in any such trait/outcome are fully genetically determined at this point in time, at least). When writing about the greater relative contribution of genetic as opposed to (nongenetic) environmental influences to differences in behavioral phenotypes and outcomes, terms such as “primarily,” rather than “entirely” or “completely,” are therefore used.

A point that merits emphasis and elaboration is that revised genetic determinism is concerned with the degree to which trait/outcome variation is genetically determined, not the degree to which traits/outcomes are “caused by” genetic factors. It is unclear whether the latter issue will ever be elucidated. In discussions of the relative effects of genes and environmental factors on phenotypic development, it is often remarked that without “environmental input,” a genome would only make a “damp spot on the carpet” (quoted in Sesardic 2005, p. 14). This statement suggests the obvious point that neither genes nor environmental factors are in isolation sufficient to produce a phenotype. Indeed, given their interdependency, it is no clearer whether genes or environments contribute more to the development of some phenotype than it is whether kerosene or sparks contribute more to a fire resulting from their interaction, a matter that quickly leads to probably irresolvable philosophical debates about the nature of causation itself. Moreover, it is apparent that what is at issue in controversies surrounding “genetic determinism” has nothing to do with the overall degree to which a trait/outcome is “caused by” genetic or environmental factors. It does not seem likely that many people would take umbrage at the idea that the ontogenetic development of intelligence is overwhelmingly “genetically determined,” *if* this were paired with the claim that all *variation* in intelligence among persons is environmental in origin. The (mostly leftist) critics of hereditarianism clearly have been concerned with the determinants of trait/outcome variation, given that their primary moral-political goal is typically the reduction or elimination of inequality among humans, not the causal bases of trait/outcome development *per se*,

despite their frequent (mis)use of the “genetic determinism” smear. Nevertheless, such critics *are* wont to observe that certain traits that are clearly under strong genetic control exhibit no variation in healthy human populations and thus would exhibit no heritability in standard behavior genetic studies (e.g., the number of chambers of the heart). This is sometimes presented as if it were a devastating critique of the usefulness of behavior genetic research in uncovering the role of genes in trait/outcome development; but since behavior genetic studies never have been intended to measure the “overall” genetic determination of traits/outcomes, but instead the relative contributions of genetic and environmental variation to trait/outcome variation, this line of attack is simply confused (see Sesardic 2005, pp. 28-33 for a more detailed treatment of this issue).

Crucially, difficulties for any effort to establish the “overall” degree of “genetic determination” of phenotypes do not apply when analyzing the causes of phenotypic *variation*. Since phenotypic, heritable, and environmental variation are quantifiable, statistical analyses can reveal how these variables associate in the case of any particular trait/outcome; one can establish, for example, how much phenotypic variation remains after environmental variation has been controlled statistically or via study design, and thus how much phenotypic variation may be due to variation in heritable factors (such controls will be imperfect, but will nonetheless offer insight into the relative contributions to phenotypic variation of heritable and environmental variation). (That is to say that holding other putatively causally relevant variables constant allows assessment of the potential causal effect of an uncontrolled variable on another variable; in hypothetical studies of the “overall” genetic determination of traits/outcomes, this is seemingly impossible, as genetic and environmental factors contribute to phenotypic development in all cases, and so neither class of factor can be completely controlled statistically or via study design so as to assess the isolated effect of the other.) In light of such analyses, one can determine, for example, the percentage of phenotypic variation for which heritable variation accounts. Such findings then

can be evaluated alongside competing hypotheses and relevant bodies of evidence to determine which causal claims about the respective roles of heritable and environmental variation in producing phenotypic variation are best supported.

But it must be understood that what is classified as trait/outcome variation due to heritable variation in traditional behavior genetic studies does not necessarily indicate the effects of genetic variation alone. Traditional (quantitative) behavior genetic studies do not involve measurement of the effects of individual genetic variants on phenotypic variation (molecular behavior genetic studies aim to do this, however). Instead, they attempt to determine how the phenotypic similarity of individuals associates with environmental variation and genetic relatedness. For instance, a behavior genetic study may examine the phenotypic similarity of monozygotic (or “identical”) twins, who are (usually) genotypically identical, raised in distinct environments. If such genotypically identical individuals tend to exhibit high levels of phenotypic similarity across sufficiently variable environments, then there is apparent evidence that genetic factors have greater control over phenotypic variation than environmental ones. In this standard behavior genetic study design, however, anything that contributes to similarity in the phenotype under investigation of monozygotic twins raised apart should register as a “heritable” source of phenotypic variation. Conversely, any factor that contributes to dissimilarity of the phenotype under investigation of monozygotic twins raised apart should register as an “environmental” rather than a heritable source of phenotypic variation. It is known that in some cases, monozygotic twins are not in fact genotypically identical – one twin may carry mutations that the other lacks (Liu et al. 2018). Mutations are of course a potential genetic source of variation in a phenotype of interest, but if they are not common between monozygotic twins, they will not contribute to the “heritable” component of phenotypic variation in standard behavior genetic studies. By the same token, monozygotic twins raised apart may have environmental factors in common that raise their phenotypic similarity, but these would register as “heritable” sources of

phenotypic variation unless they were accounted for in an appropriate way. While one should be aware of these caveats, it must be stressed that there is little reason to doubt that the heritability coefficients of traditional behavior genetic studies, which, again, indicate the percentage of phenotypic variation due to heritable variation in some population, overwhelmingly reflect the degree of genetic determination of phenotypic variation, and thus “heritable” and “genetic” are often used interchangeably in behavior genetic research. As this entry will discuss at greater length shortly, efforts to find environmental contributions to phenotypic variation that “mimic” heritable variation have not been generally successful (see, e.g., Woodley of Menie et al. 2018).

Given all of this, what can be said in favor of revised genetic determinism? The point of departure here is the substantial behavior genetics literature finding that, among individuals, variation in heritable factors (likely genes) primarily accounts for variation among adults in the four central traits/outcomes listed above. IQ, for instance, is consistently found to be 70–80% heritable by adulthood (Plomin and Deary 2015), with general intelligence, or *g*, having an even higher heritability of 86% (Panizzon et al. 2014; corrected for measurement reliability, Panizzon et al.’s data indicate that *g* is 91% heritable [Woodley of Menie, te Nijenhuis and Murphy 2014]). The factor underlying executive functions may be as much as 99% heritable (Friedman et al. 2008). Life history speed, reflected in the Super-*K* factor – which is superordinate to personality and (mental and physical) health, as well as various other behavioral traits/outcomes such as relationship stability, communitarian attitudes, and insight, planning, and control – is 68% heritable (Figueredo et al. 2006; note that life history speed subsumes executive functions, but the latter cluster of behavioral phenomena nevertheless has been listed as if it were a separate trait, given its unique importance in shaping human life outcomes, even among life history traits – for example, executive functions underlie the critical behavioral factor of self-control). And social status, over the course of centuries and in multiple societies, appears to be about 50–80% heritable

(Clark 2014; it should be noted that in the foregoing work, Clark does not employ standard behavior genetic methods to reach his estimates, but he nonetheless provides ample evidence for the high heritability of social status; however, Clark and Cummins (2018) present further and even higher quality evidence that variation in social status is under strong genetic control).

These findings alone might appear to vindicate the revised genetic determinist view. But efforts have been made to explain such findings away, to show, in other words, that behavior genetic studies of the kind cited above have not ruled out environmental determinism (i.e., the view that environmental factors primarily or exclusively determine variation in critical human behavioral traits/outcomes). One common argument to that effect stresses that behavior genetic studies are only informative about the degree to which genetic and environmental factors explain variation in some trait/outcome *within* whatever population is studied. Indeed, to say that intelligence is 80% heritable is allegedly to simply assert that 80% of the variation in intelligence in a *particular* population is due to variation in genetic factors in that same population. Therefore, it is supposed to be difficult or even senseless to extrapolate from behavior genetic studies to broader claims about the extent to which any particular trait/outcome “in general” varies among people due to genetic variation. Further complicating the “generalizability” of behavior genetic findings is the possibility that heritability estimates at the population level are not informative about heritability at the individual level (the latter would “capture the degree to which a given trait is reliably transmitted across generations” [Woodley of Menie et al., 2015, p. 6]). Finally, and consistent with earlier discussion, critics of hereditarianism sometimes stress the fact that traditional behavior genetic studies merely report *correlations* between *apparent* sources of phenotypic variation and measured phenotypic variation. Given this, these critics are quick to observe that *apparent* heritable sources of phenotypic variation could in fact have no direct causal connection to phenotypic variation (see, e.g., Turkheimer 2016); to reiterate, standard behavior genetic studies do not isolate probable causal

effects of individual genes, but rather estimate the degree of phenotypic variation due to variation in environmental and heritable (widely thought to be genetic) factors generally (though efforts may be made to ascertain the relative importance of additive and non-additive genetic effects and of “shared” and “non-shared” environmental effects – this entry will return to the latter topic). For example, the seemingly high heritability of IQ could reflect the mere fact that people who are highly genetically similar or even identical (identical twins) will tend to have very similar appearances. If appearance substantially influences treatment by others, and if treatment by others substantially affects IQ, then the apparent high heritability of IQ may reflect hidden gene-environment correlations (associations between genetic factors and environmental exposures) that, once properly understood, would indicate that IQ variation is under stronger environmental than genetic control.

These objections to revised genetic determinist conclusions drawn from behavior genetic research are either misleading or just incorrect, however. First, the claim that the individual-level heritabilities of traits/outcomes cannot be estimated is simply false. Woodley of Menie et al. (2015) developed a novel method by which such heritabilities can be estimated and found that, at least for the Super-K factor and related traits and factor structures, these heritabilities are broadly consistent with population-level heritability estimates in standard behavior genetic studies and are roughly the same in the USA and Sweden. Thus there is respectable evidence that population-level heritability estimates correspond to the degree to which traits/outcomes are “reliably transmitted across generations” (Woodley of Menie et al. 2015, p. 6). Second, there are good reasons to be skeptical about the insistence that the heritability of a trait/outcome “in general” cannot be derived from relevant available evidence. For it to be true that we could not make this derivation, the heritability of whatever trait(s)/outcome(s) is at issue would have to vary non-negligibly across populations or subpopulations in different environments, thereby indicating that, perhaps by way of environmental effects on gene expression, environmental factors can appreciably

modify trait/outcome heritability (or at least it would have to be shown that there is no compelling evidence suggesting that environmental factors *do not* have this effect). But the preponderance of germane data gives no reason to believe that environmental effects are so potent, or at least no reason to believe that these effects are *typically* so potent. The facts that IQ is almost always found to be highly heritable by adulthood and that this has been observed in many different populations the world over suggest that intelligence exhibits *developmental homeostasis*, i.e., the tendency of the development of a phenotype to be largely insensitive to environmental and even some genetic variation (Sesardic 2005, pp. 75–80, makes the same essential point). Consistent with these findings, studies have generally found that variation in socioeconomic status is unrelated to the heritability of IQ, and that there are no known environmental interventions by which to reliably and lastingly raise IQ or (especially) *g* in healthy individuals (Protzko 2015; Woodley of Menie et al. 2018). Further to this point, variance in intelligence has not meaningfully changed over long periods of time in which enormous improvements in material quality of life and concomitant reductions in health and material wellbeing inequality (Rindermann 2018) have occurred (Rowe and Rodgers 2002). This is inconsistent with the idea that variation in IQ is to a substantial degree a result of inequality in health and material wellbeing, which environmental determinists seem to often believe.

Social status, or rather the heritable dispositions and behaviors that interact with social environments and have the effect of producing individual differences in social status, seems to be developmentally homeostatic as well. Clark's (2014; see also Clark and Cummins 2018) research offers excellent evidence for this view, insofar as it indicates not only that the heritability of social status is roughly the same in a number of different societies with substantially different cultures and standards of living – e.g., China, Chile, Japan, Sweden, and the USA and UK – but also that the heritability of social status has hardly changed over time. In fact, the heritability of social status was, if anything, slightly *lower* (at times) in preindustrial England than in modern

Sweden, even though the latter is widely extolled for its progressive political and economic culture. England experienced almost no change in the heritability of social status from approximately AD 1300–2000, despite “the Industrial Revolution of the late eighteenth century ... the political reforms of the nineteenth century ... [and] the rise of the welfare state in the twentieth century,” among many other highly significant social, cultural, technological, and economic developments (Clark 2014, p. 87). It is striking that social status, which is seemingly not biological in the way that, e.g., height is, but rather depends on complex interactions between individuals and their sociocultural environment, saw no meaningful change in its heritability over seven centuries in England during which massive and supposedly relevant environmental changes took place. Critics of behavior genetic studies, who expect that environment strongly modifies the heritability of important traits/outcomes, would predict substantial alterations in the heritability of social status from such profound environmental shifts. The relative constancy of the heritability of social status *despite* these changes is therefore quite devastating to the environmental determinist view. Perhaps environmental factors do more to alter the heritability of intelligence, social status, and/or other important traits/outcomes where material circumstances are much poorer than those that have been canvassed in the studies cited above. These environments must be quite rare, however, since late medieval England was extremely poor by modern standards. There is thus robust evidence that, certainly in the modern world, individual differences in important behavioral traits/outcomes are probably mostly a result of genetic rather than (nongenetic) environmental influences.

It is easy for critics of hereditarian science to posit that the heritability coefficients from standard behavior genetic studies *may* not track the causal effects of genetic variation on trait/outcome variation, *may* be contaminated with unmeasured environmental effects that mimic heritable variation, *may* be substantially variable across environments due to environmental effects on gene expression, and so on. Some of these possibilities are likely not favorable to

environmental determinists and are probably compatible with revised genetic determinism. For example, gene-environment correlations involving environmental effects that partially produce phenotypic variation may be largely generated by genetic effects on human behavior (e.g., genetic factors leading individuals to sort into certain environments). Moreover, it is far from obvious that attempts to disrupt apparently spontaneously emerging gene-environment correlations for the sake of engendering behavioral equality would be successful (indeed, it is well known that Soviet social engineering effectively along these lines was an utter failure with morally abhorrent consequences [MacDonald 2010]).

That notwithstanding, such objections from environmental determinists are unconvincing without supporting evidence. (And, in any event, environmental determinists who are unsatisfied with hereditarian explanations that offer anything less than fully elaborated causal pathways linking genetic variation to differential behavioral traits/outcomes would do well to recognize that proposed environmental explanations of phenotypic variability are, at best, no less often and no less seriously incomplete.) Take for example the previously noted claim that the high heritability of IQ may simply reflect the tendency of people who look alike to be treated alike. As it happens, this idea has not withstood empirical scrutiny, since the correlation between physical attractiveness and IQ is near zero (Lee 2010; as Lee notes, environmental determinists could respond with the claim that some other aspect of appearance may be causally relevant – but, again, without supportive evidence, this is mere hand waving; crucially, Segal, Hernandez, Graham and Ettinger's 2018 study of genetically unrelated "look-alikes" offers strong evidence that "[t]he criticism that [monozygotic] twins are alike in personality because their matched looks invite similar treatment by others" is false (p. 402)). This entry has already detailed the failure of efforts to find environmental effects that non-negligibly modify the heritability of IQ or social status, or to find any environmental intervention that can reliably and permanently raise IQ in

healthy individuals (see also Haier 2017). Indeed, attempts to find evidence for extravagant claims about the power of environmental effects to modify behavioral trait/outcome heritability have had minimal success at best (Duncan 2014). For example, despite early findings indicating that the heritability of IQ may vary dramatically as a function of socioeconomic status (e.g. Turkheimer et al. 2003), subsequent research on this effect has determined that it is, if real at all, of very small size (see, e.g., Woodley of Menie, Pallesen and Sarraf 2018). These results align with straightforward theoretical interpretations of high heritability coefficients, i.e., that differences in traits/outcomes with such coefficients are mostly genetically determined. Moreover, it should be recognized that environmental determinists exhibit a questionable selectivity with respect to the heritability estimates about which they are skeptical. Human height is consistently found to be highly heritable, yet no one, or at least very few people, seems motivated to argue that this finding is spurious and may be due, for example, to unmeasured environmental factors that mimic heritable variation. Only in the case of politically sensitive traits/outcomes, such as intelligence, do such objections seem to be offered with any significant frequency.

General critiques of twin studies and related behavior genetic research designs abound in the academic world (e.g., Joseph 2014; Richardson 2017); but all substantive elements of these critiques have been repeatedly addressed (Barnes et al. 2014; Felson 2014; Liu et al. 2018) and have not inspired doubt regarding the soundness of these methods among the relevant scientists – the results of twin studies are still recognized as basically accurate estimates of trait/outcome heritability and "environmentality" (see Polderman et al. 2015; see also Bouchard, Jr. 1987, 2009 on the "pseudoanalytical" nature of sweeping critiques of behavior genetics and hereditarianism). (For example, Liu et al. 2018 show that misestimation of twins' genetic and epigenetic relatedness tends to *downwardly* bias heritability estimates [but only to a small extent, and primarily for high- as opposed to low-heritability

phenotypes], whereas Richardson 2017 wrongly insinuates that the failure of quantitative genetic studies to accurately measure twin epigenetic relatedness generally *upwardly* biases heritability estimates.) Furthermore, the high heritability estimates found for a number of traits/outcomes via twin studies have been replicated using different study designs (for an example, see Schwabe, Janss and van den Berg 2017). Some argue that the “problem of missing heritability” in molecular genetic studies of complex quantitative behavioral traits – i.e. the likely causal genetic variants identified account for far less of the variation in these traits than expected in the light of traditional behavior genetic estimates – casts doubt on the validity of twin studies. However these findings are not surprising (given that molecular genetic approaches to estimating trait/outcome heritability are still in their infancy, and thus have serious limitations), and it is unlikely that phenomena that would create deep problems for standard behavior genetic estimates of trait/outcome heritability are at play, even if trait/outcome heritability is (currently) difficult to totally account for at the molecular genetic level of analysis (see Kendler et al. 2016; Kendler et al., as with Schwabe et al. 2017, offer highly compelling evidence that twin studies *do not* overestimate the heritability of traits, and thus that biases in twin studies likely *do not* contribute appreciably to the problem of missing heritability).

Though the facts thus far presented already leave the environmental determinist position very much in doubt, there are further considerations that render it clearly untenable. First, it must be recognized that environmental determinists expect or assert that environmental factors that are under human control are primarily responsible for behavioral trait/outcome variation. Intellectuals such as Kitcher (mentioned above), for example, hope that the facts about differential human behavioral traits/outcomes will be friendly to ordinary “aspirations” for, e.g., social mobility. It would hardly help their case if behavioral differences among humans were matters not of genetics but of some other biological and/or environmental factors that are outside of relevant

human control (Sesardic 2005, pp. 178–182 raises the same point), such as aspects of the uterine environment or “random developmental noise” (Jensen 1980). But as it happens, understanding of whatever truly environmental effects on trait/outcome variation that behavior genetic studies may detect is quite poor – by adulthood, these influences appear to be completely independent, or nearly so, of “shared” experiences of, e.g., families and schools (shared environmental effects increase the similarity of persons living in the same household, net of the effects of genetic relatedness). They are perhaps environmental experiences that are unique to individuals, which does not inspire confidence about possible efforts to control them such as to, say, raise individuals’ IQ. And to some extent, what registers in behavior genetic studies as “non-shared” environmental effects is measurement error, and perhaps poorly understood chance events and idiosyncratic and random developmental processes. Burt, Klahr and Klump (2015) note that non-shared environmental effects are generally not stable over time prior to adulthood, which is consistent with the impression that these apparent effects are mostly “noise”; the authors do note other research showing that the effects of non-shared environment become more temporally stable in adulthood, but even then, the research that they cite suggests that only a minority of such effects are stable among adults.

The inclusion of measurement error in estimates of non-shared environmental influence probably explains the tendency for higher-precision measurements of whatever phenotype is under investigation to produce larger heritability and smaller “non-shared environmentality” coefficients. A possible example of this effect is found in Rindermann’s (2007) analysis of international differences in academic and cognitive test performance, which found that a single psychometric factor – analogous to the highly heritable *g* at the individual-differences level – accounted for 94–95% of the variance. This suggests the possibility that the nongenetic variance in intelligence within groups (which is typically estimated at around 20% of the variance among adults)

is largely measurement error and other random factors that may be broadly the same across groups, such that genetic differences may account for almost all of the variance at higher levels of aggregation, where such evenly distributed “noise” is canceled out. The possibility that intelligence exhibits such minimal true “environmentality” is yet another piece of information that fits with the consistent failure to find any environmental variable the manipulation of which can reliably and permanently raise the IQ of healthy individuals (Protzko 2015; Woodley of Menie et al. 2018), which is to say that not only behavior genetic studies suggest the relative importance of (*controllable*) environmental factors in determining variability in adult human behavioral traits/outcomes.

Additionally, Riemann and Kandler (2010) found that personality traits exhibit very high heritabilities (some around 85-90% heritable) and low “non-shared environmentalities” when multiple methods of trait/outcome measurement are used, an approach expected to reduce measurement error. By contrast, studies of the heritability of personality traits that use less sophisticated measurement techniques typically find heritabilities of 50% or less. This again indicates that a substantial portion of non-shared environmental variation found in behavior genetic studies is due to measurement error.

Studies of life history speed in humans also suggest that “controllable” environmental factors widely thought to substantially affect human behavioral variation may in fact be highly unimportant. Sociologists have long maintained that discrimination and other forms of “socially constructed” (i.e., in principle changeable through nongenetic processes) disadvantage are central to explaining correlations among mental and physical health, relationship quality, sexual behavior, subjective well-being, personality, and other domains subsumed under life history speed. Specifically, sociologists believe that discrimination on the basis of and other disadvantages associated with differences of race, sex, and class explain a great deal of human behavioral variation. But it turns out that the latter sociological variables, even when all pooled together (and with

educational attainment added), explain *at best* less than 10% of the variance among life history traits, whereas the highly heritable Super-K factor explains nearly all (91%) of the variance (Figueredo et al. 2007). The failure of these variables, which are so central to mainstream sociological theory and analysis, to meaningfully explain the interrelations of such critical human traits/outcomes is remarkable.

Finally, it must be noted that to the extent that environment matters for important human behavioral traits/outcomes, some of the relevant environmental factors are likely genetic. There is a substantial literature on social epistasis, i.e., inter-organismal genomic transactions whereby the genotype of one organism affects the gene expression and phenotypic development of another organism (see Woodley of Menie et al. 2017b). Revised genetic determinism therefore extends in a surprising way to the environment as well.

Furthermore, though much has been made in some quarters about the power of environmental factors to epigenetically modify organisms, those offering such claims frequently miss the fact that epigenetic effects operate by way of preexisting genetic potentials and do not undo the significance of (likely) genetic variation captured in standard heritability coefficients (Figueredo et al. [in preparation](#)).

Critics of hereditarian science should recognize that attempts to trivialize the role of genes in determining individual differences easily fall into opposition to basic principles of modern evolutionary theory. Evolution via selection simply is differential reproductive success as a function of heritable phenotypic variation and environmental circumstances (with heritable factors subject to mutation). If traits cannot be reliably transmitted across generations, because they are open to such radical environmental/epigenetic alteration that genetic variation should not be expected to yield at least fairly reliable patterns of trait/outcome variation, then it would seem that the very idea of evolution by selection is in trouble. This implication suggests that the efforts of anti-hereditarians to attenuate or even sever the connection between inter-individual genetic and trait/outcome variation are without much sense.

Conclusion

Genetic determinism, though indefensible in its traditional but entirely fictitious form, is eminently defensible as revised and presented here, given the best pertinent scientific evidence to date. There are various possible moral, political, and existential reasons that individuals resist the latter thesis, but these of course do not count as reasons to reject it as false.

Cross-References

- [Controversies in Evolutionary Psychology](#)
- [Eugenics](#)
- [Free Will](#)

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Genetic Disorder

► Genetic Abnormalities

Genetic Diversity Hypothesis

► Offspring Diversity Hypothesis

Genetic Hypotheses of Homophobia

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Synonyms

Homonegativity; Sexual prejudice

Definition

An umbrella term for a negative (attitudinal, affective, or behavioral) response towards homosexuality and homosexuals

Introduction

The impact of the genetic makeup on homophobia and its interplay with environmental factors have been neglected for a long time, because social factors were conceived as purely environmental

(e.g., parental socialization) and thought to be the key contributors to the development of attitudes, prejudices, and discriminatory behavior towards homosexuals. The shifts in the scientific paradigms and the subsequent (re-)emergence of biological and genetic hypotheses have led to studies demonstrating genetic influences.

Evidence for a genetic contribution to homophobia comes from behavior genetic studies. For example, a study on 4,688 Australian twins, who completed a questionnaire concerning sexual behavior and attitudes towards homosexuals, found 36 % of individual differences in homophobic attitudes to be attributable to genetic differences (Verweij et al. 2008). The remaining variance in attitudes toward homosexuality was primarily due to environmental factors not shared by twins reared together. Thus, the contribution of objectively shared environmental influences to individual differences in homophobia, such as norms and values taught by parents as socialized aspects in forming positive or negative attitudes toward homosexuals, was negligible.

The findings of substantial genetic influences on homophobia are primarily based on studies of twins and self-reports on attitudes toward homosexuality. However, classical twin study designs cannot take gene-environment interplay into account, and self-reports, in particular in case of social attitudes, may be biased to some degree by socially desirable responding, which itself may be heritable to some degree. Thus, we actually do not know whether estimates of genetic variance reflect substantial genetic influences, gene-environment interplay, or artifact. Despite these limitations, we can speculate on cogent explanations and scientifically sound hypotheses on the genetic basis of individual differences in homophobia.

Genetically Driven Threat Perception and Management

Past research showed that evolved neurophysiological threat management systems help navigate the individual through unfamiliar and, thus, potentially threatening situations by triggering

specific cognitive, affective, and behavioral responses to avoid threat to one's own physical, mental, and social integrity. Those fitness-relevant threats range from endangerment of the physical health through contagion and contamination, through aggression of conspecifics, to threat to one's own status in the social group (Boyer and Bergstrom 2011). Indeed, the association between negative attitudes towards strangers or unfamiliar behaviors and a diversity of expected (rational and irrational) threats has been repeatedly demonstrated (e.g., Riek et al. 2006).

Similarly, for heterosexual men, negative cognitive responses (i.e., prejudice; e.g., Kite and Whitley 1996), negative affective responses (i.e., disgust, anger, and fear; e.g., Inbar et al. 2009; Zeichner and Reidy 2009), and negative behavioral responses (i.e., aggression against homosexual men; e.g., Parrott and Zeichner 2008) towards (particularly male) homosexuals have been observed, suggesting homosexuality to be an unfamiliar, fitness-threatening stimulus. Consequently, the genetic basis of homophobic reactions may reflect phylogenetically developed autonomic threat-avoidance mechanisms. Moreover, genetic differences in the sensitivity to potential threat, manifested in individually differing thresholds for the categorization of unfamiliar stimuli, such as homosexuality, may result in genetic variance in homophobia (hypothesis 1).

However, these threat management mechanisms cannot explain profound genetic variance, because selection processes would act to decrease genetic variance in threat management systems due to the fact that individuals with the best (i.e., most sensitive) threat management systems would be the fittest in this regard. Considering that homosexuals do not pose a realistic threat to one's own fitness, threat management systems are equally sensitive and responsive to cues of threat that are subjective, imagined, or irrational. Hence, the functionality of threat management systems may also play a vital role. This functionality may depend on other heritable characteristics, such as intelligence or personality traits. For example, lower cognitive abilities predict greater anti-homosexual prejudice (e.g., Hodson and Busseri 2012). This association was partially

mediated by right-wing authoritarianism (RWA). RWA is a substantially heritable personality characteristic which has been discussed to be closely associated with avoidance of societal and cultural threat (e.g., Onraet et al. 2013), hinting at the importance of threat experience in the development of outgroup attitudes. This is positively correlated with homophobia (see ► [“Social Hypotheses of Homophobia”](#)). Thus, genetic variance in homophobia might also be due to genetic differences in the functionality of threat perception and processing (hypothesis 2).

Mutation-Selection Balance and Assortative Mating

Apart from genetic differences in threat perception and management, the genetic variance in homophobia might be influenced by occasional spontaneous gene mutations, which counteract selective processes. Especially since complex human traits and attitudes are thought to be polygenic (i.e., influenced by a number of genes), and the probability of spontaneous gene mutations is exponentially heightened for polygenic characteristics, the genetic variance of homophobia within a population may be due to a mutation-selection balance (hypothesis 3).

Another plausible explanation is positive assortative mating, which has been found for diverse attitudes and negativity toward others (e.g., Kandler et al. 2015). Positive assortative mating – that is, the choice of partner regarding characteristic similarity that is normally substantial for attitudes (e.g., shared prejudice towards homosexuality) – has two implications: It acts to increase genetic similarity among relatives and increases the polarization of genetic differences in polygenic phenotypes in a population. Taking positive assortative mating of the twins' parents into account, Verweij and colleagues (2008) estimated a total of 51 % of variance in homophobia to be due to genetic factors. Consequently, assortative mating reflects a possible mechanism that acts to maintain genetic variance in homophobia (hypothesis 4).

Sex Differences in Homophobia

Negative cognitive, affective, and behavioral responses towards homosexuals have been found to be less likely for women (e.g., Kite and Whitley 1996). This indicates that homosexuals and homosexuality might constitute a threatening stimulus exclusively for male heterosexuals. Several accounts might explain this sex difference.

Masculinity has been linked to homophobia (see ► [“Social Hypotheses of Homophobia”](#)), which may be amplified under threat (—ened masculinity). From a phylogenetic point of view, displaying masculinity might not only be advantageous for the reproductive fitness of a male but also for the fitness of all ingroup members insofar as the permanent expression of one’s or the group’s strength and physical superiority over others and outgroup members might avoid intergroup threat. Whereas heterosexual men might not see homosexual men as rivals within the group, they may have a genetically driven tendency to perceive homosexual male group members as too weak and too feminine to defend the ingroup against threat due to intergroup rivalry (hypothesis 5).

In addition, it has been shown that women are more socially oriented and seek more contact and intimacy with others, which is in accordance with their respective ancestral roles (e.g., care for the offspring and elder group members as opposed to exploration and joint defense of the territory). This might allude to the fact that familial socialization might be more important for individual differences in homophobic responses in women. In line with this differentiation, Verweij and colleagues (2008) reported that 55 % of the variance in homophobic attitudes in men was due to genetic differences, whereas genetic factors could account for only 20 % of individual differences in homophobic tendencies in women. Consequently, genetic factors may play a larger role in individual differences in homophobia for men (hypothesis 6).

develop differently depending upon their genetic sensitivity to environmental influences. Humans are self-determined individuals who make their own choices and environments based upon their heritable characteristics. The genetic control of the construction of experiences and the exposure to certain environments can act as propulsive mechanism of reinforcing initial tendencies. For example, (primarily male) heterosexual homophobes tend to avoid confrontation with homosexuals if possible, which – in terms of the contact hypothesis (see below) – reduces the probability of change in homophobic tendencies (Hodson and Busseri 2012). To the contrary, this genetically driven avoidance of environments is an example of a so-called active gene-environment correlation which reinforces homophobic tendencies (hypothesis 7).

While the aforementioned hypotheses can explain recurring and persistent homophobia in a society and underlying genetic variance in individual homophobic tendencies, they cannot explain the average decline in prejudice towards homosexuals in Western societies (e.g., Herek 2015). Changes in the individual’s environment, whether actively initiated (e.g., leaving a former, more conservative and joining a new, more open-minded neighborhood and community due to relocation) or by chance (e.g., having homosexual colleagues or neighbors), can alter the perception of threat and attitudes towards homosexuals. Similarly, positive contact with homosexuals can diminish homophobia (see ► [“Social Hypotheses of Homophobia”](#)). Such environmental factors might be enforced through societal developments and changes, which establish an atmosphere of “de-stigmatization,” acceptance, and inclusion of sexual minorities like homosexuals. In contrast, the societal exclusion of homosexuals (e.g., in Russia or Saudi Arabia) may enhance the genetic diathesis. In other words, the genetic influence on homophobia may depend on the sociocultural context (hypothesis 8).

Gene-Environment Interplay

Environments provide the range and variety of developmental opportunities in which people

Conclusion

In sum, several theories and findings suggest a substantial contribution of genetic factors and

gene-environment interplay to homophobia. In order to confirm these hypotheses, large-scale genetically informative studies are required, such as longitudinal extended-twin-family studies with measured environments, ideally separately for men and women. Furthermore, future research should use comprehensive measures of homophobic attitudes and behavior beyond self-reports (e.g., implicit measures or reports from well-informed peers) to disentangle substance from measurement artifact. Finally, neurogenomic research can provide important insights into the molecular genetic basis and neuronal mediators of cognitive (i.e., prejudice), affective (e.g., disgust), and behavioral components (i.e., discrimination) of homophobia.

Cross-References

► Social Hypotheses of Homophobia

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Genetic Influences of Puberty

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Synonyms

Adolescence; Pubescence; Sexual maturity

Definition

Puberty is defined as the physical transition from sexual immaturity to being sexually mature.

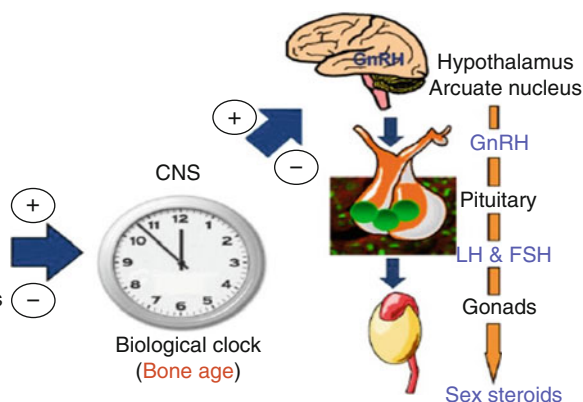
Introduction

Adolescence is sometimes considered a synonymous term but implies more of a psychosocial

Genetic Influences of Puberty, Fig. 1

Multiple factors implicated in pubertal onset. *CNS* central nervous system, *GnRH* gonadotropin-releasing hormone, *LH* leutinizing hormone, *FSH* follicle-stimulating hormone. (Martos-Moreno et al. 2010)

- Age (bone age)
- Sex
- Race
- Inheritance
- Timing
- Nutrition
- Stress
- Body mass
- Body fat
- Geographical factors
- Sex steroids
- Adrenarche
- Cerebral lesions



maturation that comes with puberty. The mean age for the onset of first signs of puberty among girls is around 10.5 years of age (range: 8–12 years), while among boys, it is around 11.5 years (range: 9–13 years) (Susman et al. 2010). Some variability occurs between individuals with regard to the timing and sequence of pubertal maturation. However, most of boys and girls follow a predictable course through pubertal maturation.

Pubertal onset in both girls and boys appear to be occurring earlier all over the world as compared to that reported in the literature previously (Sørensen et al. 2010). Several factors like increased BMI and fat mass have been implicated in causing this earlier pubertal onset, but substantial evidence is still lacking in this regard. Also, pubertal timing varies significantly between different ethnic groups. Genetics seem to play an important role in causing these racial/ethnic differences (Gajdos et al. 2010).

Gonadotropin-releasing hormone (GnRH) is the master hormone of the reproductive endocrine system, largely controlling the secretion of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from pituitary gonadotrope cells. An increase in the pulsatile secretion of GnRH from the hypothalamus is considered to be a critical hormonal event in puberty. FSH and LH then evoke steroidogenesis and gametogenesis from the gonads, culminating in secondary sexual features development and fertility. There are multiple other factors involved in the initiation of puberty as well, and the complex interactions between genetic and environmental factors controlling

this process are just beginning to be understood (Fig. 1).

Regulation of Puberty

Puberty is a mysterious phenomenon and not all is known to answer the various complicated steps occurring in this process. Several mechanisms have been implicated in the onset of puberty. The process seems to undergo neuropeptide, genetic, metabolic, and environmental regulation.

Neuropeptide Regulation of Puberty

A sustained increase in pulsatile release of gonadotrophin-releasing hormone (GnRH) from the hypothalamus is an essential, final event that defines the initiation of puberty. This depends on coordinated changes in transsynaptic and glial–neuronal communication, consisting of activating neuronal and glial excitatory inputs to the GnRH neuronal network and the loss of transsynaptic inhibitory tone.

The prevalent excitatory systems stimulating GnRH secretion involve a neuronal component and a glial component. The neuronal component consists of excitatory amino acids such as glutamate and peptides such as kisspeptin and neurokinin B. The glial component uses growth factors such as TGF- β , EGF, IGF-1, and bFGF and small molecules for cell–cell signaling such as SynCAM1 and RPTP β .

KiSS1 located on chromosome 1q32.1 encodes the peptide kisspeptin, which acts via its receptor, encoded by the gene KISS1R (also known as GPR54) located on 19p13.3. It is

thought that KISS1 signaling through KISS1R in the hypothalamus at the end of the juvenile phase of development may contribute to the pubertal resurgence of pulsatile GnRH release. The three key features of the kisspeptin–Gpr54–GnRH neuron axis leading up to puberty are (i) the expression of adult-like levels of Gpr54 mRNA in GnRH neurons well in advance of puberty, (ii) a modest increase in the electrical response of GnRH neurons to Gpr54 activation across post-natal development, and (iii) the “sudden” appearance of kisspeptin fibers surrounding GnRH neuron cell bodies/proximal dendrites just prior to puberty onset. Another important pathway in the initiation of puberty may be TAC3 signaling. TAC3 is located on chromosome 12q13.3, and the gene that encodes its receptor TACR3 on chromosome 4q24, and loss of function mutation in these genes have been associated with hypogonadotropic hypogonadism (Topaloglu et al. 2009).

GABAergic and opiateergic neurons provide transsynaptic inhibitory control to the system, but GABA neurons also exert direct excitatory effects on GnRH neurons. New evidence suggests that additional peptides inhibit GnRH neuronal activity. The discovery of such gonadotropin-inhibitory hormones, examples of which include the RF amide peptides, RFRP1 and RFRP3 (encoded by the QFRP gene on chromosome 9q34.12), have further clarified the role of genes that inhibit the GnRH axis until the appropriate signals to initiate puberty come in to play (Jiang et al. 2003).

Other pathways, especially in the appetite control center of the hypothalamus, have also been shown to influence pubertal onset. Neuropeptide Y (NPY) and Agouti-related Peptide (AgRP) are orexigenic peptides that have been found to influence the production of proopiomelanocortin (POMC), another neuropeptide which affects normal pubertal onset (Martos-Moreno et al. 2010).

Genetic Factors Regulating Puberty

Genetic factors have been established to account for 50–75% of the variability in timing of normal pubertal onset. Several genetic loci have been identified which are associated with age of

pubertal onset. The genetic mechanisms that provide encompassing coordination to this cellular network are not clearly known. The timing of puberty varies greatly among healthy individuals in the general population and is influenced by both genetic and environmental factors (Gajdos et al. 2010). The high correlation of the onset of puberty seen within racial/ethnic groups, within families, and between monozygotic compared to dizygotic twins all provides evidence for genetic regulation of pubertal timing. These data suggest that 50–80% of the variation in pubertal timing is determined by genetic factors. Environmental and physiologic effects also influence the timing of puberty, and there is evidence supporting secular trends in the timing of puberty. It is possible that gene by environment interactions play an important role in regulating the timing of puberty.

It is tempting to consider that a single gene may be responsible for the initiation of puberty, since mutations in genes such as GNRHR, GPR54, TAC3, TACR3, and KISS1 result in pubertal failure. Functional studies have failed to demonstrate that any one of these single genes plays a commanding role in synchronizing the neuronal and glial networks involved in the initiation of puberty. This has led to the current concept of genetic networks regulating the neuroendocrine control of puberty initiation (Ojeda et al. 2010). This network is envisioned to be a host of functionally related genes hierarchically arranged. The highest level of control in this network is likely provided by transcriptional regulators that, by directing expression of key subordinate genes, impose an integrative level of coordination to the neuronal and glial subsets involved in initiating the pubertal process.

The use of new techniques of genetic analysis coupled to systems biology strategies should provide not only the experimental bases supporting this concept but also unveil the existence of crucial components of network control not yet identified. The question of whether the first step in the initiation of puberty is a loss of central restraint or the activation of stimulatory inputs to GNRH neurons still remains unanswered. It may very well be that transcriptional repression and activation of key genes occurs simultaneously to

orchestrate this complex process. One recent advance in this direction is the identification of the polymorphisms with age at menarche in the leptin and leptin receptor genes in humans (Riestra et al. 2011). In addition, we are learning more about various transcription factors such as thyroid transcription factor 1 (TTF1) and a transcription factor encoded by the gene C14ORF4 located on chromosome 14q24.3 which modulate gonadotropin-releasing hormone (GnRH) expression (Cukier et al. 2013) (Figs. 2 and 3, Table 1).

Metabolic Control of Puberty

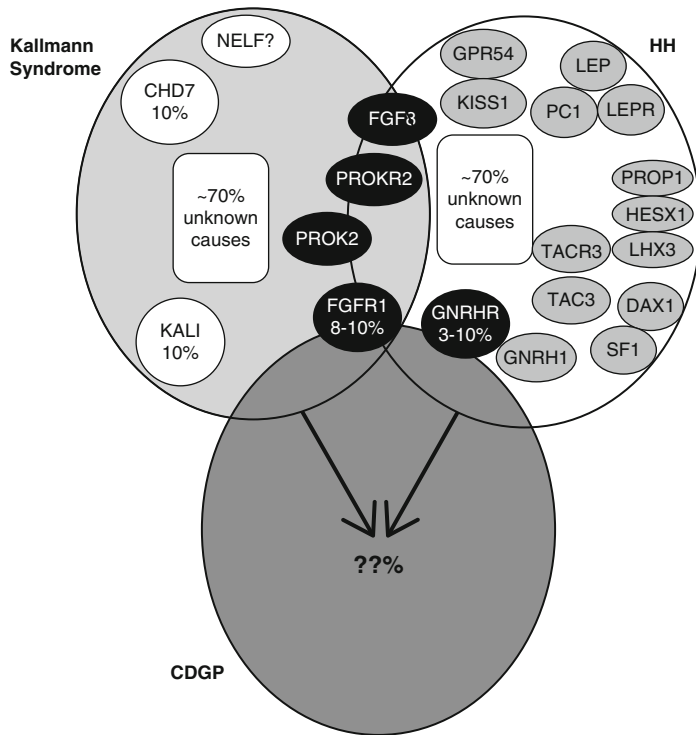
Both growth and reproduction consume high levels of energy, requiring suitable energy stores to face these physiological functions. The state of body energy reserves is a key determinant for the onset of puberty. During the last two decades, our knowledge concerning how peptides produced in the digestive tract (in charge of energy intake) and in adipose tissue (in charge of energy storage) provide information regarding metabolic status to the CNS has increased dramatically. Moreover,

these peptides have been shown to play an important role in modulating the gonadotropic axis with their absence or an imbalance in their secretion being able to disturb pubertal onset or progression (Martos-Moreno et al. 2010).

Leptin is an adipocyte-derived hormone and its synthesis is directly related to the amount of body fat. Thus it is involved in the control of energy homeostasis and modulates several neuroendocrine systems, including the HPG axis. Animal knockout models have shown that infertility is characteristic of leptin-deficient mice (ob/ob) and that this can be overcome by leptin treatment. Humans that are leptin deficient due to homozygous gene mutations present with hypogonadotropic hypogonadism, with long-term recombinant leptin treatment being able to achieve pulsatile nocturnal gonadotropin secretion in these patients. Humans with leptin receptor deficiency present with different degrees of hypogonadotropic hypogonadism.

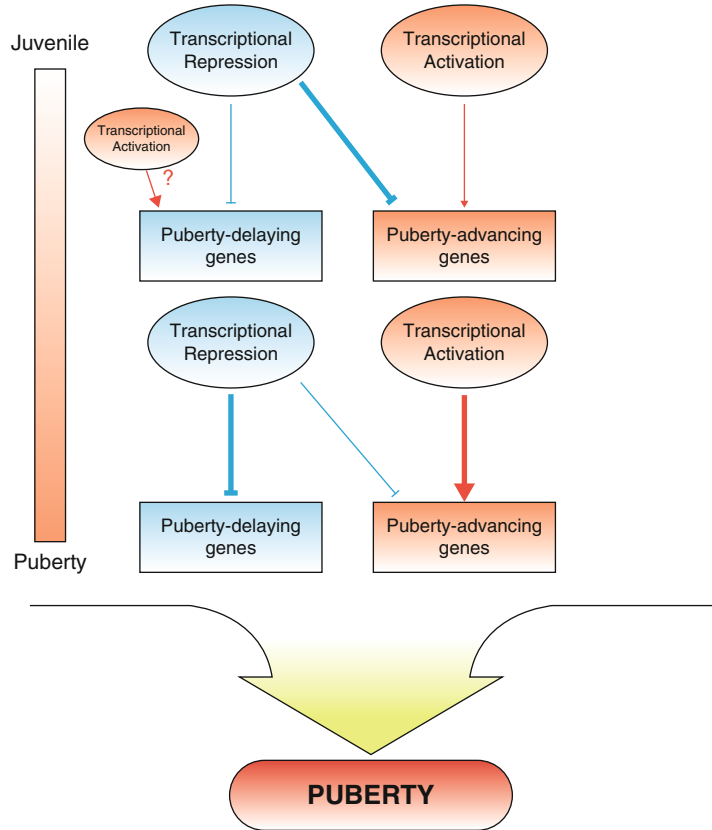
Leptin is considered to be the main peripheral signal providing information about the body's energy stores to the hypothalamic circuits in

Genetic Influences of Puberty, Fig. 2 Different genes involved in disorders of delayed puberty. *HH* hypogonadotropic hypogonadism, *CDGP* constitutional delay of growth and development. (Gajdos et al. 2010)



Genetic Influences of Puberty,

Fig. 3 Transcriptional regulation of the initiation of puberty. (Ojeda et al. 2010)



charge of controlling energy homeostasis, thus communicating this information to the HPG axis by means of mechanisms that are far from being fully understood. Leptin appears to play a permissive role in the initiation of puberty and in the maintenance of the reproductive function. The earlier initiation of puberty seen in obese children may also be partly explained by higher leptin levels. The role of other adipokines such as adiponectin and resistin on the HPG axis is currently poorly understood.

Growing evidence suggests that insulin and leptin interact to downregulate arcuate nucleus (ARC) production of orexigenic peptides such as NPY and AgRP and, in collaboration with serotonin, enhance POMC production and release. Thus insulin could be another peripheral metabolic signal involved in HPG axis functioning.

Ghrelin is a gut-derived hormone, whose function as a growth hormone secretagogue is well described. More recently, it has been shown that

ghrelin modulates energy homeostasis by stimulating the expression of the genes encoding NPY and AgRP in the arcuate nucleus of the hypothalamus and by binding to presynaptic terminals of arcuate NPY and POMC neurons, respectively stimulating and inhibiting their activity and peptide release. This results in a net orexigenic effect, functionally opposite to that produced by leptin. Thus it is currently thought that ghrelin plays a role in reporting information regarding the fuel availability in the body to the CNS, and that there is an inverse relationship between activation of the HPG axis and ghrelin levels. The role of other gut-derived factors such as peptide YY (PYY) is currently being explored.

Environmental Influences on Puberty

Since genetic background explains 50–80% of variability in the timing of puberty, it is not surprising that the observed environmental effects are rather modest when individual exposures are

Genetic Influences of Puberty, Table 1 Genes implicated in the disorders of delayed puberty. *GnRH* gonadotropin-releasing hormone, *NHH* normosmic hypogonadotropic hypogonadism, *HH* hypogonadotropic hypogonadism, *KS* Kallman syndrome, *POMC* pro-opiomelanocortin

Gene	Protein	Function	Disease
<i>KISS1</i>	Kisspeptin	GnRH secretion	NHH
<i>GPR54</i> (<i>KISS1R</i>)	Kisspeptin receptor	GnRH secretion stimulation	NHH
<i>GNRH1</i>	Gonadotropin-releasing hormone	GnRH synthesis	NHH
<i>GNRHR</i>	GnRH receptor	GnRH signaling	NHH
<i>TAC3</i>	Neurokinin B	Unknown	NHH
<i>TACR3</i>	Neurokinin B receptor	Unknown	NHH
<i>FGF8</i>	Fibroblast growth factor 8	Migration of GnRH neurons	KS/NHH
<i>FGFR1</i>	Receptor for FGF8 protein	Migration of GnRH neurons	KS/NHH
<i>PROK2</i>	Prokinectin	Migration of GnRH neurons	KS/NHH
<i>PROKR2</i>	Prokinectin receptor	Migration of GnRH neurons	KS/NHH
<i>CHD7</i>	Chromodomain helicase DNA-binding protein 7	Development of GnRH neurons	CHARGE syndrome, KS/NHH
<i>NELF</i>	Nasal embryonic LHRH factor	Migration of GnRH neurons	KS
<i>KALI</i>	Anosmin 1	Migration of GnRH neurons	KS
<i>LEP</i>	Leptin	? GnRH secretion	Obesity and HH
<i>LEPR</i>	Leptin receptor	? GnRH secretion	Obesity and HH
<i>PC1</i>	Prohormone convertase	Cleavage of POMC	Obesity and HH
<i>HESX1</i>	Pituitary transcription factor	Pituitary development	Hypopituitarism
<i>LHX3</i>	Pituitary transcription factor	Pituitary development	Hypopituitarism
<i>PROPI</i>	Pituitary transcription factor	Pituitary development	Hypopituitarism

assessed. The fact that the age of onset of puberty has been declining in the USA since the mid-1990s, with similar trends are being seen more recently in Europe, points towards such rapid changes having environmental rather than genetic causes (Toppari and Juul 2010).

Endocrine disrupting chemicals have thus been implicated as being such environmental factors affecting pubertal onset. Endocrine disrupters can cause pubertal disorders by several mechanisms. They can act as hormone agonists or antagonists or both depending on the dose and background hormone levels, i.e., the same compound can be an agonist when the level of endogenous hormone is very low (childhood), whereas it can be an antagonist when the real hormone is available (adulthood). Multiple chemical exposures have been considered, but definitive studies are lacking. Examples of such chemicals include polychlorinated and polybrominated biphenyls (PCBs and PBBs), phthalates, dioxins, DDT, and

lead. Apart from the association of lead and delayed puberty, the evidence is unclear.

Conclusion

It is now clear that initiation of puberty involves complex neurohormonal stimuli that are regulated by various genetic and environmental factors. Advances in genetic technologies and a systems biology approach will help with diagnosis and treatment of disorders of pubertal development and help us understand environmental influences that perturb the balance of pubertal development.

Cross-References

- [Absence Prior to Puberty](#)
- [Puberty in Boys](#)
- [Puberty in Girls](#)

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Genetic Inheritance

► Heritability

Genetic Load

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Definition

Genetic load describes the fitness burden resulting (principally) from deleterious mutations that accumulate within an organism's genome and is estimated relative to a hypothetical mutation-free or fitness-optimized genome. Individual differences in mutation load, especially with respect to pleiotropic mutations, may be a major source of individual differences in both the variance and covariance among fitness indicating traits in humans and other sexually reproducing taxa.

Introduction

This entry will first review the conceptual basics of genetic load and will present a mathematical overview of the phenomenon. It will then consider the phenomenon in relation to its applicability to evolutionary psychology.

Review

Genetic Load

Genetic load is a term coined by Muller (1950) to describe a phenomenon first noted by Haldane (1937), namely the fitness loss that accrues principally from the accumulation of deleterious mutations (this being *mutation load*) in addition to the effects of *segregation/migration load* (the fitness costs associated with breaking up coadapted allelic complexes) and *substitutional load* (the fitness costs associated with limits on trait evolvability imposed the low probability of desirable alleles being found in combination with one another), estimated relative to a hypothetical mutation-free or fitness-optimized genome.

In sexually reproducing organisms, mutations (the principal contributor to genetic load) can arise spontaneously, i.e., where the mutation occurs in the germ cells of a parent and is then passed on to the diploid genome of the offspring or where the mutation gets passed on to the offspring from the parents as a *legacy mutation*. Mutations are more likely to contribute to mutation load via accumulation under conditions of relaxed purifying selection, i.e., when the fitness cost of the mutations are mitigated by changes in selection pressures, or in instances where the mutations have only very mild effects on fitness, such as where they are harbored by recessive alleles. Mutation load also increases rapidly in instances where populations become more inbred and homozygous, typically in response to decreased population size. Where purifying selection is insufficient to remove mutations at a rate proportional to the rate at which they drift to fixation, *mutational meltdown* occurs, whereby the population collapses rapidly under the fitness burden of runaway mutation accumulation.

The equations used in estimating genetic load (L) in their most basic form consider single locus systems comprised of alleles $A_1 \dots A_n$, which have a fitness distribution of $w_1 \dots w_n$ and frequencies $p_1 \dots p_n$, thus L can be calculated as follows:

$$L = \frac{w_{\max} - \bar{w}}{w_{\max}} \quad (1)$$

Here, $w_{\max}$ corresponds to the hypothetical (i.e., load-free) fitness for the given distribution of fitnesses and $\bar{w}$ corresponds to the mean of the fitnesses weighted by the frequencies of their given alleles. If $w_{\max} = 1$ then Eq. 1 simplifies to:

$$L = 1 - \bar{w} \quad (2)$$

This equation necessarily makes certain simplifying assumptions, such as the assumption that the population is at equilibrium (i.e., no frequency dependent selection on the alleles). The assumption of a fitness optimized, load-free genome is also problematic in as much as estimates of mutation load and the fitness costs of subsequent

mutation accumulation have led to a *mutation load paradox* when applied to human reproduction, where based on the addition of around 100 de novo mutations to the average diploid genome every generation, very high fitness loss should be observed (i.e., 88 % of individuals should fail to reproduce and reproducing females should engage in very high compensatory reproduction in order to maintain population viability) (Kondrashov and Crow 1993). The paradox stems specifically from the observation that reproductive failure and compensatory reproduction on this scale is simply not observed in modern, industrialized populations. Solutions to the mutation load paradox have emphasized the role of relative fitness differentials between individuals of differing mutation loads as a source of soft purifying selection in modern populations (Lesecque et al. 2012). It has also been observed that very high reproductive failure and compensatory reproduction was characteristic of historical Western populations and is still characteristic of compensatory hunter-gatherer populations (Volk and Atkinson 2008), hence the hypothetical mutation-free genome may actually have been closer to the reproductive optimum historically and that modern industrialized populations by comparison might therefore be in the process of undergoing gradual mutational meltdown by virtue of relaxed purifying selection and mutation accumulation (e.g., Lynch 2016).

The Significance of the Concept to Evolutionary Psychology

A critical application of the concept of genetic and mutation load in particular to evolutionary psychology has been in the development of *fitness indicators theory* (Houle 2000; Miller 2000), which provides an evolutionary framework within which the adaptive function of human individual differences can be understood.

Fitness indicators theory is premised on the assumption that among sexually reproducing organisms such as humans, deleterious germ-line mutations can influence fitness outcomes in ways related to their pleiotropic effects on traits, meaning that they can influence the development of multiple traits simultaneously. This has led to the

prediction that there exists a latent *fitness factor* (typically abbreviated to *F*) among traits believed to signal the sensitivity of development to perturbation stemming from the presence of deleterious mutations (Houle 2000; Miller 2000). Thus in sexually reproducing taxa, there should exist genetic correlations among seemingly quite distinct traits, encompassing aspects of physical condition, behavior, health, and reproductive viability, high-levels of which are *unconditionally favored* by *sexual selection* across different environments (Penke et al. 2007).

Under conditions where purifying selection occurs in proportion to the fitness costs of spontaneously occurring germ-line mutations, individual differences in and genetic correlations among fitness salient traits will be maintained within a population, as spontaneously arising deleterious mutations conferring few fitness disadvantages to their carriers (by virtue of recessiveness) can persist as part of genetic load for many generations, with the addition of each new mutation cumulatively reducing the fitness of the lineage relative to others that are burdened with fewer such mutations. This mechanism by which variance is maintained with respect to fitness salient traits in a population is known as *mutation-selection balance* (Fisher 1930) and is the principal mechanism through which population variance in *F* is believed to be maintained (Penke et al. 2007).

Conclusion

Genetic load is an old concept in population and evolutionary genetics. It is a concept with clear utility to evolutionary psychology also, especially as it pertains to reconciling the massive modularity approach, with its emphasis on human universal and domain-specific cognitive adaptations, with the existence of both apparent individual differences in and also covariance among the functioning of not only these mechanisms but also other physiological sources of individual differences pertaining to physical condition (Miller 2000). The relevance of the genetic load concept to the issue of future micro-evolutionary trends in fitness stemming from relaxed purifying selection

and mutation accumulation in industrialized populations is also significant.

Cross-References

- [Dysgenic Concerns](#)
- [Fertility](#)
- [Individual Differences](#)
- [Mate Value](#)
- [Mutation Accumulation Theory](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Reproduction](#)
- [Reproductive Value](#)

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Genetic Mutation

- [Genetic Abnormalities](#)

Genetic Polygamy

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Definition

Genetic Polygamy refers to patterns of inheritance that indicate different male and female effective population sizes through genetic analysis. It is different than “social polygamy,” in that it is a measure of the actual genetic parentage that allows researchers to trace paternity, rather than the apparent or culturally institutionalized mating patterns that are witnessed.

Introduction

Evidence of polygamous mating patterns is generally identified by the apparent pair-bonding behaviors of individuals within a group. In humans this may be displayed through the institutionalized mating practices within cultures. However, these apparent behavioral patterns are only a proximate measure of a species, or groups, actual mating pattern. Other ways to determine such patterns are by examining the dimorphic physical or behavioral traits that males and females display. Sex differences in traits such as body size, ornamentation, and behavior give some evidence of a species evolutionary mating history, where larger dimorphisms relate to larger disparities in male and female effective population sizes (i.e., polygamous mating). The differences in the amount of variation between male and female genetic markers offer another line of evidence. This question may be explored in a variety of ways, with the two most common being examining the ratio of variation in the X-chromosome versus autosomal DNA and the amount of distinct genetic lineages in the nonrecombining portions of DNA (e.g., mitochondrial and the non-recombining portion of the Y-chromosome).

Basic Methods for Examining Genetic Variation

The first approach is to compare the amount of neutral genetic variation on the X-chromosome (X) to that of the autosomes. Because the X-chromosome is only passed through matrilineal descent and the autosomes are passed by both matrilineal and patrilineal inheritance, the expectation is that in a monogamous species with an approximately 1:1 sex ratio at reproduction, we should see ratio of diversity of 0.75 between X and the autosomes (Hammer et al. 2008). This ratio is due to a 25 % reduction of X due to males only carrying one copy. In species that are polygamous we should see deviations from this ratio.

The second method focuses on measuring the amount of genetic variation in the mitochondrial DNA (mtDNA) and nonrecombining portion of the Y-chromosome (NRY). These genetic markers are uniparentally inherited, with MtDNA passed down the matrilineal line and NRY passed down the patrilineal line. Here, researchers group together alleles into haplogroups (historically referred to as clades). These haplogroups (named alphabetically A, B, C, etc.) are combinations of alleles that are genetically linked and therefore passed down from parent to offspring in an unbroken line of descent. Over evolutionary time, mutations cause slight changes in the structure of these genetic markers, leading to a nested (or hierarchical) structure where an individual belongs to a haplogroup at the top of the structure down through a haplotype and subclade. By counting the number of mutations (in relation to a standard mutational clock, which varies by location on the particular allele) researchers can identify the approximate date when a particular haplogroup coalesced.

Human Genetic Patterns of Mating

Whether referring to X-chromosome versus autosome, mtDNA, or NRY variation, the genetic diversity between matrilineal and patrilineal lines would be an indication of the amount of reproductive variance in a population (i.e., the

number of males relative to females that reproduced). In species that have an approximately 1:1 sex ratio at reproductive age, different genetic patterns would be expected based on their evolutionary mating patterns. With a monogamous pattern, where there is low reproductive variance, we would expect a similar number of mtDNA and NRY haplogroups and approximately a 0.75 ratio of X to autosomal DNA variation (Hammer et al. 2008). In a polygynous system, with high reproductive variance, we would expect to see more variance in the number of mtDNA versus NRY lineages, as well as more variation in X. In polyandrous species, where one female is maintaining exclusive mating privileges with multiple males, we would expect more NRY lineages and less X variation, because only a few females would be reproducing. This last expectation, however, may be attenuated where there are patterns of *kin-based* polyandry (i.e., a single female mating with related males).

To date, genetic evidence aimed at identifying the species-typical mating pattern in humans has been difficult to interpret, with single-study evidence of lower, equal, and higher effective population sizes in males. For example, a study by Segurel et al. (2008) found differences in variation between X and autosomes in a direction indicating a larger effective population size for females (i.e., polygyny) in Central Asian populations. Whereas a study by Ramachandran et al. (2004) showed no differences in effective population size (i.e., monogamy) in a population of genetic markers extending across Africa, America, Asia, Europe, the Middle East, and Oceania. However, much of this discrepancy may be due to methodological difference between studies (i.e., sample size, number of genetic markers uses, genetic assay techniques). A recent review by Heyer et al. (2012) has summarized these findings by comparing the methodological strengths and limitations of each study. Their conclusion was that across the majority of studies genetic evidence has identified higher levels of X variation than expected in monogamous systems.

Studies examining mtDNA and NRY haplogroups have offered a similar answer. To date, the number of mtDNA versus NRY

haplogroups is higher, suggesting a history of a smaller effective population size in males. Research by Lippold et al. (2014) came to a similar conclusion. By examining the X and NRY genetic markers in males from 51 different populations, Lippold et al. identified a pattern of X versus NRY variation suggesting polygyny and potentially sex-specific migration over human history. As a further indication, researchers have compared the coalescence dates of particular haplotypes to known historical events. One noteworthy example comes from NRY haplotype C-M217. This genetic marker is spread throughout 16 distinct cultural populations in Central Asia, is shared by approximately 8 % of Asian men, and shows a coalescence date in Mongolia approximately one-thousand years ago (Zerjal et al. 2003). Due to these factors and that it exists in known descendants of Genghis Khan, researchers have suggested that this genetic marker belongs to Ghengis Khan himself, the Borjigin Clan from which he came, or one of his descendants.

Conclusion

An evolutionary history of sex-biased processes in human mating is evident through a variety of methods ranging from comparison of phenotypic traits to genetic markers. While current social mating trends may be toward more apparently monogamous social bonds (more accurately, serially monogamous), the amount of genetic variation between X and autosomes, and X and NRY at both regional (e.g., Segural et al. 2008) and global (e.g., Lippold et al. 2014) levels suggests an evolutionary history of higher effective population sizes for females versus males. Taken as a whole, we may conclude that humans have been *at least* mildly polygynous over evolutionary history.

Cross-References

- [Mating Systems](#)
- [Operational Sex Ratio](#)
- [Polygyny Threshold, The](#)

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Epigenetic	Changes in gene activity that is influenced by factors other than DNA sequence alterations, such as environmental exposures
Genetic diversity	The total number of characteristics in the genetic makeup of a species
Genetic variation	The tendency of genetic characteristics to vary within and among populations
Genotype (v)	The process of determining which genetic variants an individual possesses
Heritability	A statistical determination of how much variation of a trait is attributable to genetics
Missing heritability	The observation that the total known genetic variations attributed to a trait cannot account for all of the trait’s estimated heritability
Monogenic inheritance	When a single gene determines a genetic trait
Penetrance	The proportion of individuals carrying a variant (allele) of a gene that also express the trait associated with that variant
Phenotype	An observable physical or biochemical trait
Polygenic inheritance	When two or more genes determine a genetic trait



Genetic Predispositions

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Synonyms

Alteration; Characteristic; Mutation; Phenotype; Predisposition; Risk; Susceptibility; Trait; Variant

Definitions

Allele A variant form of a gene which may or may not result in a different observable trait

Introduction

Genetic diversity ensures species’ survival though enabling evolutionary adaptations in response to environmental changes. The genetic variation which allows for this diversity is mostly due to de novo mutations which create new gene variants (alleles), random mating, and the shuffling between maternally and paternally inherited chromosomes during meiosis (homologous recombination). While most genetic variations are neutral, meaning they do not alter any observable trait, some do affect gene function and may lead to improved or decreased fitness. The forces of natural selection over time increase the frequency of advantageous alleles while selecting against those

that put the carrier at a reproductive disadvantage. Thus, particularly devastating genetic diseases are rare, and more common disease-associated genetic variants tend to occur late in life after reproduction, such as cancer and dementia. While there exist many traits and diseases that are caused by a single gene alone (monogenic), most are polygenic in nature, meaning that two or more genes contribute to the phenotype. Often a large number of genes are involved, each with a small effect and may interact with each other and/or the environment. Examples of polygenic traits are height, weight, and skin pigmentation. Therefore, in isolation, most functional genetic alterations predispose rather than predetermine. Genetic predisposition is the increased likelihood of developing a particular trait or disease as influenced by one's own genetic makeup. While many polygenic traits seem to have an obvious genetic component, it is difficult to associate any specific genetic variant as it is unusual that a single gene's effect would be sufficient. This is especially true for behavioral traits and psychological disorders where the environment plays an undoubtable role as well. Even so, there are ways to determine whether a trait or disease has a high genetic component without knowing the underlying genetic causes.

Estimating the Heritability of a Trait

For complex traits such as depression, intelligence, or susceptibility to various diseases, it's wise to first establish an estimate of how much of the phenotypic variance is due to inheritance before attempting to implicate any genetic variants. One classic means of determining the heritability of a trait is through twin studies which measure the similarity of a trait between monozygotic twins as compared to dizygotic twins. Monozygotic twins are derived from a single fertilized egg and thus share the same genetic material, while dizygotic twins, formed from separate eggs, share about half of their genes. Because both sets of twins share the same environment, at least in childhood, this approach controls for much of the environmental contribution. If monozygotic twins

resemble each other more than dizygotic twins for a particular trait, then the heritability of that trait is estimated as twice the observed difference. For example, monozygotic twins generally have a correlation of about 40% for depression (meaning that if one experiences depression, the other twin will also in about 40% of cases), while dizygotic twins have a correlation of 20%. The difference in the correlation between both sets of twins (40–20) doubled is 40%. Therefore, the genetic contribution (heritability) to depression is estimated at ~40%. Twin studies have suggested high heritability for anxiety, intelligence, and numerous behavioral traits (Boomsma et al. 2002).

Implicating Genetic Variants

When a trait or disease is suspected to be inherited, there are various approaches that can be employed to identify the genes and variants responsible. One approach is through linkage analysis, a hypothesis-neutral means to find segments of DNA which all affected persons of a family share but the healthy relatives do not have. This is possible because genetic variants that are close in proximity tend to be inherited together. The analysis begins with genotyping genetic "markers" (highly variable regions of the DNA) on each chromosome for both affected and unaffected individuals of a family. Once a region is identified as shared between and unique to those affected, additional markers are added to further narrow the search within this region until a specific gene and genetic mutation is implicated. This method is most appropriate when attempting to map monogenic disease mutations and is responsible for discovering the gene for cystic fibrosis (Bowcock et al. 1986).

For complex traits and disease predisposition, a better approach to implicating genetic variants is through association, such as a *genome-wide association study* (GWAS). As the name implies, these studies look for genomic variants that are statistically more prevalent in cases versus controls by genotyping across the entire genomes of hundreds or thousands of individuals both with and without

the trait/disease of interest. GWA studies have identified predisposition variants in traits such as anxiety (Otowa et al. 2016), longevity (Zeng et al. 2016), and even intelligence (Davies et al. 2011). However, they lack the statistical power necessary to detect rare variants (which are more likely to have a high effect) and instead tend to implicate common variants with low effect. Even so, these low-effect variants are informative as they may highlight biological mechanisms underlying a disease. For example, an interesting relationship has been established between susceptibility to schizophrenia and certain variants located in genes responsible for the major histocompatibility complex, a key component in immunity. However, the biology underlying schizophrenia and the immune system is not entirely clear (Sekar et al. 2016). Similarly, GWA studies often identify disease-associated variants in areas of the genome with no known function. Because there exist various reasons that a spurious association could occur, replicating findings through additional association studies is encouraged, and associated variants should be functionally validated through experimentation in cellular or animal models.

Population Genetics and Environmental Influences

Population genetics is a subfield focused on genetic variation within and among different human populations. Specifically, population geneticists study phenomena such as adaptation, speciation, and migration through examining the fluctuation of allele frequencies with time across various populations, making it an indispensable tool for understanding evolutionary biology. Allele frequency refers to the incidence of a particular variant in a population at a given time in history. The frequency of an allele is not stable as it is subject to four main evolutionary forces: natural selection, new mutations, gene flow (the transfer of alleles between populations), and genetic drift (variation due to chance). Selection for or against a particular allele can be inferred through the age of the mutation and its frequency in the population. For example, if a mutation has

occurred recently but is observed at a high frequency in a population, this is evidence for positive selection. Estimating the age of genetic variants is possible since DNA is shuffled during meiosis and therefore is inherited in segments called “haploblocks.” A haploblock refers to a stretch of DNA that related individuals share due to recent ancestry. With each generation, additional chromosomal shuffling occurs, resulting in haploblock decay, meaning the shared stretch of DNA between ancestors lessens with each generation. Therefore, one can estimate the age of a genetic variant by examining the haploblock size of as many individuals as possible with this same variant, to see how much of their surrounding DNA sequence is also shared. A longer haploblock signifies a young variant as chromosomal shuffling had not had enough time to break up that shared surrounding segment. Vice versa, an allele on a very small haploblock indicates that the allele is a lot older as many generations and meiosis has likely occurred.

Environmental factors exert a heavy influence on selection, and therefore whether a mutation is advantageous or not often depends to the environment of the carrier. Relatively recently, it was discovered that the environment can lead to phenotypic variation via “epigenetic” alterations. Epigenetics refers to changes in gene activity not caused by any alteration in the DNA sequence. Instead, the change in activity is often due to chromosome structural alterations which inhibit or promote gene accessibility thus inhibiting or promoting the ability for cellular machinery to transcribe and translate the gene’s message into its respective protein product. These chromosomal changes are influenced by one’s environment. For example, various studies have confirmed a correlation between fetal malnutrition due during pregnancy and predisposition to obesity in adulthood. This phenomenon is hypothesized to be due to a “*thrifty phenotype*,” whereby epigenetic alterations to metabolic pathways occur to prepare the fetus for survival in famine. If there is no famine, then the metabolism of the child is maladapted to the actual environment and may be prone to metabolic diseases and obesity (Rourke 2015). There is still a lot unknown about

epigenetic mechanisms, but they are believed to have the ability to be passed on to the next generation.

Genetic Testing

In terms of health care, genetic testing was once mostly limited to confirming a suspected diagnosis. However, due to the ever-decreasing cost of genome sequencing, testing is now being offered to assess an individual's risk of developing disease in the future and even to predict response to certain therapeutic drugs. The field of oncology has really been a pioneer for genetic testing in this aspect. Much research has gone into discovering mutations that lead to an increased lifetime risk of developing certain cancers, especially those known to have a relatively high heritable component. For example, current estimates suggest that approximately 25% of ovarian cancer cases arise due to an inherited risk mutation (Walsh et al. 2011). Therefore, individuals with a suspicious family history are encouraged to seek genetic testing as risk reducing surgeries and therapies are available to those who have inherited a predisposing mutation. However, as with many multifactorial diseases, there is a gap in our knowledge of the genetics underlying the predisposition. Often, the known genetic variations attributed to a disease do not account for its total estimated heritability. This is referred to as *the missing heritability issue*. A recent study focused on ovarian cancer risk has suggested that a portion of the missing heritability is likely due to genes that have not yet been implicated in predisposition and rare mutations in established disease genes whose effect on protein function is not yet described and that high risk may be incurred through the inheritance of multiple low-risk variants (Stafford et al. 2017). For certain diseases, this unexplained heritability often limits how informative genetic testing can be. However, even when the total genetic cause of a disease is known, there may be no preventative measures to avoid disease onset and no treatment.

Conclusion

The field of genetics has experienced vast growth since completing the sequencing of the human genome in 2003. This monumental achievement is responsible for many scientific advancements in health care; however the genetics of disease predisposition have proven to be highly complex and often dependent other genetic and nongenetic factors. Sex differences, environmental stimuli, genetic penetrance, and epigenetics all play a crucial role in predisposition, and each trait or disease is unique in these aspects. As technologies advance, so does our understanding of genetics and therefore our ability to apply this knowledge where applicable.

Cross-References

► [Problem of Genetic Inheritance, The](#)

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Genetic Quality

► Fitness Benefits of Costly Signalling

Genetic Relatedness

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Synonyms

Coefficient of relatedness; Coefficient of relationship; Relatedness coefficient; Relatedness parameter

Definition

The probability that an allele in one individual is also found in another individual.

Introduction

Relatedness is an important parameter in kin selection or more generally inclusive fitness theory. One significant puzzle in the history of evolutionary theorizing is the evolution of altruism. Kin selection, with the use of the relatedness parameter, often denoted by r , permits to solve this puzzle.

The Puzzle of Altruism

A classical approach to natural selection tells us that only traits which confer a heritable fitness (reproductive) advantage to their bearer will evolve by natural selection. For instance, suppose a population of organisms which vary in height and in which the taller an organism is the higher its reproductive output. We could imagine that the organisms are giraffes and that giraffes which are taller have access to leaves on the top of trees while smaller giraffes do not. Because of this access to more resources, taller giraffes can produce more offspring than smaller ones. If taller giraffes produce taller offspring, everything else being equal, so that height is heritable, then tallness will evolve by natural selection. Under this picture of evolution by natural selection, following the three conditions of variation, difference in fitness, and heritability (Lewontin 1970), only traits that are beneficial to the individual bearer of these traits can evolve by natural selection.

Following this Darwinian scheme, we should thus expect to see only traits that confer a fitness advantage to their bearer in nature, since every time a mutation conferring a disadvantage emerges in the population it should be eliminated by natural selection (assuming what is known as genetic drift can be ignored). Thus, in our example, we should not expect giraffes to get smaller over time on average, because small giraffes have a lower probability to reproduce than tall giraffes. Although this Darwinian scheme seems impeccable, it is contradicted by empirical evidence: everywhere one looks, one finds traits costly to the individual. Think about the ultimate sacrifice of a worker in an ant colony. The worker defends

the colony, takes care of the offspring produced by the queen, or gathers food, and yet it never has the chance to reproduce; only the queen does. Ants and termites, for which the reproductive activity of the colony is typically carried by a single female, have been estimated to represent only 2% of the total number of species of insects. Yet, their biomass is estimated to represent more than a quarter of the total animal biomass (Wilson 1990). Eusocial insects are evolutionary very successful despite contradicting the classical scheme for Darwinian evolution.

Solving the Puzzle

As described by Dawkins (1976), one solution to the problem of altruism proposed by some biologists has been to say that, although a costly trait does not provide any advantage to the individual that bears it, it nevertheless provides an advantage to its group or species. In fact, if workers suddenly stopped defending the hive, taking care of the larvae, or bringing food, the colony would soon disappear. But this explanation faces the problem that any worker unwilling to pay the reproductive cost paid by other workers would get an evolutionary advantage over individuals paying the cost. In fact, following this logic, a worker deciding to reproduce instead of paying the cost of gathering food, taking care of the larvae or defending the nest, would soon produce workers like it with the same properties, all of which would have a (short term) evolutionary advantage over sterile workers. Thus, the “good of the group” proposal cannot be the whole story, for, following its rationale, groups would irremediably be subverted by selfish individuals.

William Hamilton (1936–2000) was the first one to give a formal solution to the problem of altruism without relying on a form of the good of the group argument (Hamilton 1963, 1964a, b). His solution is reductionist in that it requires taking the perspective of a gene borne by an individual, also known as the “gene’s eye view,” which was made famous by George Williams’s *Natural Selection and Adaptation* (1966) and even more so by Richard Dawkins’ *The Selfish Gene* (1976).

Before Hamilton, some evolutionists, including J. S. B. Haldane and Darwin himself, seem to have gestured to the same solution to the puzzle of altruism, but not as rigorously as Hamilton did.

Hamilton’s solution to the problem of altruism is that an allele incurring a fitness cost to its bearer can be compensated for if another individual with the same allele receives a benefit from the first individual which is equal or superior to the cost that it incurred. For instance, suppose an individual “actor” with an allele **A** helps another individual “recipient” with the same allele by providing the recipient with some resources. In doing so the actor pays a cost in terms of offspring it can produce. It is altruistic. We could imagine that without helping the recipient, the actor would produce three offspring while if it helps the recipient it can only produce two offspring. We could further suppose that the recipient, without any help from the actor, would be unable to produce any offspring, but produce two offspring when it receives some help. In this setting, if we compare the number of **A** alleles present in the offspring population when the actor helps the recipient to the situation in which it does not, the outcome will be four offspring (each with a single copy of the **A** allele) rather than three, respectively. Even though the actor produces fewer offspring when it helps the recipient, it is evolutionarily advantageous from the point of view of allele **A** that the actor helps the recipient. Helping the recipient will, after all, permit an increase in the number of copies of **A** when compared to the situation in which no help is provided. More formally, because the benefit obtained by the recipient “*b*” is higher than the cost “*c*” incurred by the actor – so that $b - c > 0$ – the altruistic behavior, if it is heritable, can evolve (i.e., successfully “invade” the population).

Although this reasoning provides a solution to the problem of altruism, there is a complication. We assumed in the example that the recipient has allele **A** with certainty. Yet, from the point of view of the actor, there is typically no guarantee that the recipient has allele **A**. Suppose that the actor helps the recipient, yet the recipient does not have allele **A**. In such a case, being altruistic is evolutionary disadvantageous since the *guaranteed* number of

copies of **A** in the offspring generation is, then, two rather than three.

The coefficient of relatedness r measures the probability from the point of view of the actor with a given allele (say **A**) that the recipient also has this allele. The more technical definition of r is slightly different since it takes into account the average probability of sharing an allele in the population, but this need not concern us here (for details see Bourke 2011, p. 31). The reason r stands for “relatedness” is that one common cause of having a copy of the same allele is being related by descent, as in actors and recipients belonging to the same family. But the modern understanding of r is more general than that as we will see below.

Using r in Hamilton’s Rule

For a population in which social interaction is dictated by family structure, it can be evolutionarily advantageous to be an altruist. Whether it is evolutionarily advantageous from the point of a view of an allele not only depends on the cost of the actor and benefit of the recipient, as we saw earlier, but also on the probability that the recipient receiving the benefit bears the same allele as the actor which is measured by r . Modifying the rule for the evolution of altruism given earlier ($b - c > 0$) by considering relatedness, we obtain $rb - c > 0$, which is known as “Hamilton’s rule.”

If we take our going example and assume that the actor and the recipient are full siblings, then because the benefit obtained by the recipient is two offspring and the relatedness is 0.5, it is not more advantageous, from the point of view of allele **A**, for the actor to help the recipient. In fact, in both cases, on average, the number of copies of **A** at the offspring generation will be 3. We have $rb - c = 0$ since $0.5 \times 2 - 1 = 0$. In a different situation in which the cost of one offspring paid by the actor would lead to a benefit of three offspring for the recipient (a full sibling), the altruistic behavior could evolve. In fact, we have $rb - c > 0$ since $0.5 \times 3 - 1 = 0.5$. With the actor and the recipient being first cousins, altruism is however disadvantageous. In fact, assuming the previous cost of one

offspring for the actor but a benefit of three offspring for the recipient, because r is now 0.125 instead of 0.5, we have $rb - c < 0$ ($0.125 \times 3 - 1 = -0.625$).

Although a classical context in which relatedness plays a role is family, this is not the only one. It has been imagined that individuals with the same allele could recognize one another even without being related. This is known as the “green-beard effect” (Dawkins 1976; Gardner and West 2010). Even though empirically, “greenbeards” seem to be limited to a small number of cases and mostly not relevant for human evolution (Gardner and West 2010), their possibility shows that relatedness, following its most general definition, does not solely measure the extent to which individuals socially interacting are related by descent. It is much more general than that. Note also that it does not require recognition between individuals. Individuals might be altruistic towards one another because they live in the same place rather than because they know they are siblings. All these subtleties mean that despite the simplicity of Hamilton’s rule, relatedness is a concept one should manipulate with care.

Conclusion

Relatedness is an important concept in evolutionary theory. Embedded within inclusive fitness theory, it extends a solution to one of the most important puzzles in evolutionary theory, namely, the evolution of altruism. Together with reciprocal altruism proposed by Trivers (1971), inclusive fitness theory is one of several evolutionary mechanisms for explaining the formidable level of cooperation in humans.

Cross-References

- ▶ [Adaptive Problem of Detecting Kinship](#)
- ▶ [Children and Sibs Share Same Proportion of Genes](#)
- ▶ [Father’s Father Versus Mother’s Mother](#)
- ▶ [Full Siblings Versus Half Siblings](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Detection by Odor](#)

- [Kin Recognition](#)
- [Kin Selection](#)
- [Maternal Grandmother Invests Most](#)
- [Paternal Grandfather Invests Least](#)
- [Theory of Reciprocal Altruism](#)

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Genetic Relatedness Affects Aid to Kin

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Synonyms

[Inclusive fitness](#); [Kin selection](#)

Definition

Any two same-sex humans share about 99.9 % of their genes. Family members also share significant portions of the remaining 0.1 %. This shared portion is referred to as genetic relatedness. In

reference to a target individual, siblings or parents have a genetic relatedness of $r = 0.50$; nephews, nieces, aunts, or uncles $r = 0.25$; and cousins $r = 0.125$. The level of genetic relatedness is assumed to affect the amount of aid reciprocated by two individuals, everything else being equal.

Introduction

Why do we help our relatives? One could claim that a gene that promotes helping kin should not have been selected for, since it involves a price to the helper. For many years this dilemma was indeed a problem in evolutionary theory. The breakthrough arrived when Hamilton (1964) suggested that in some instances a helper can gain an evolutionary advantage by assisting his or her relatives. Hamilton's (1964) Kin-selection theory claims that an individual can gain inclusive fitness through the promotion of reproduction of genetically related kin. According to Hamilton (1964, p. 17), "a gene may receive positive selection even though disadvantageous to its bearers if it causes them to confer sufficiently large advantages on relatives". Specifically, Hamilton posited that altruistic acts can be selected for when $b \cdot r > c$, where b is the benefit to the recipient, r is the level of genetic relatedness between the altruist and the recipient, and c is the cost to the altruist. Hamilton's law does not necessitate assisting kin in all animals and under all conditions. It simply indicates the conditions under which kin assistance can be selected for (Park 2007).

Animal Studies

Following Hamilton's law a debate arose as to whether it could empirically explain animal behavior. Do helpers actually prefer their close kin over their distant ones? Some of the studies showed that individuals provide greater help to closer kin, but others did not (Griffin and West 2003). Using meta-analytic tools Griffin and West (2003) summed up the results from 18 cooperatively breeding vertebrate species and found that,

overall, relatedness correlated with helping behavior ($r = .33$). Next, they attempted to explain the variability in the results and demonstrated that in species where the help was less beneficial to the target, effect sizes were smaller. This is congruent with Hamilton's law that claimed that altruism is constrained by the benefit that it provides.

Self-Report Measures

What about humans? Do we follow Hamilton's law? In an early series of studies, Japanese and American students were asked to choose one of two people to assist (Burnstein et al. 1994). The assistance was needed for a life-or-death condition (saving from a burning house) or for everyday assistance (running an errand). In each choice the recipients differed in their genetic relatedness to the student: acquaintance or acquaintance's child ($r = 0$); cousin ($r = 0.125$); nephew, niece, aunt, or uncle ($r = 0.25$); and sibling or parent ($r = 0.50$). Each of the choices included additional variables such as the age, health, gender, or wealth of the recipient. In all studies there was a consistently large effect for relatedness, with assistance increasing with relatedness. This was true for both life-or-death instances and for everyday help. Later studies confirmed the link between genetic relatedness and the reported willingness to assist a person in need (e.g., Korchmaros and Kenny 2006). Similar results were also obtained when participants were asked about their past behaviors. For example, in a large-scale Dutch survey, participants were asked to report how much concern they gave or received from a specific sibling (Pollet 2007). The results showed that half-siblings reported less concern for each other in comparison to full siblings. This difference held true for maternal half-siblings as well, although they grew up together.

Observational Measures

Are these results limited to self-report or are there observational data establishing that humans assist

their close kin more than their distant kin? This question has been evaluated in Western society in two major life events: marriage and death. In Israel it is customary for newlyweds to record the monetary gifts they receive from each wedding guest. An analysis of such records revealed that kin offered more money than non-kin, and highly related kin ($r = 0.50$ and 0.25) offered more money than more distant kin ($r = 0.125$ and 0.625). However, no significant differences were found between the two highly related kin groups nor between the two distant kin groups (Tifferet et al. 2012). At the end of life, an analysis of British Columbian wills found that the genetic relatedness with the beneficiaries predicted the generosity of the benefactor (Webster et al. 2008). The mean estate percentage granted to relatives of $r = 0.125$, 0.25 , and 0.50 were 1.9 %, 9.7 %, and 38.7 %, respectively. This demonstrated that close kin were granted more than distant kin. Observations of traditional societies also show that relatedness is associated with helping. Among the Ache of Paraguay, for example, nuclear families share food with others. Observations showed that close kin ($r = 0.50$) were more likely to receive food than were distant kin ($r = 0.125$ – 0.25), but there did not seem to be a difference between distant kin and unrelated families (Gurven et al. 2000). The results, however, were difficult to interpret since relatedness was highly correlated with geographical proximity, so it is not clear whether the increased food share resulted from proximity or relatedness.

Proximate Mechanisms

It appears that in general, individuals help their close kin more than they do their distant ones. What would drive them to do so? Korchmaros and Kenny (2006) identified a number of mechanisms. First, genetic relatedness arouses a feeling of obligation that drives a person to help. Second, it arouses emotional closeness that also drives a person to help. This emotional closeness is further enhanced due to past cohabitation, perceived similarity, and frequent interactions, all hallmarks of genetic relatedness. Note that past cohabitation,

perceived similarity, and frequent interactions may serve as cues by which we recognize our kin and identify their level of relatedness. As such, they could be the basis of evolved mechanisms for kin preference.

Conclusion

Preferential altruism toward close kin has been documented in humans and other animal species. These acts are congruent with Hamilton's (1964) law, claiming that altruism may be selected for when targeted toward kin. The link between actual genetic relatedness and altruism may be mediated by proximate cues of genetic relatedness. More studies are required that assess actual behaviors in natural settings.

Cross-References

- ▶ Alarm Callers Are Females with Greatest Genetic Representation
- ▶ Altruism
- ▶ $C < R_b$
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Emotional Closeness Predicted by Relatedness
- ▶ Full Siblings Versus Half Siblings
- ▶ Genetic Relatedness
- ▶ Helping and Genetic Relatedness
- ▶ Helping More Likely with Close Kin Than More Distant Kin

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Genetic Relatedness and Child Abuse

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Synonyms

Childhood maltreatment; Emotional; Neglect; Physical

Definition

Physical or emotional abuse or neglect to an individual 18 years of age or younger by a parent or parent substitute.

Introduction

Child abuse can be represented in a number of ways: physical abuse, physical neglect, emotional abuse, emotional neglect, or threats of maltreatment. According to the National Incidence Study (1996) by Sedlak and Broadhurst, physical abuse is anyone 18 years and younger who experienced injury or is/was at the risk of injury by a parent or parent substitute. This involves being hit with a hand or object or being kicked, shaken, thrown, burned, stabbed, or choked. Physical neglect is the harm or endangerment as an effect of inadequate nutrition, clothing, hygiene, and/or supervision. In addition, child abuse can also be emotional abuse, the use of nonphysical punishment or threats of maltreatment or emotional neglect, absence of affection and/or emotional support, or the exposure to domestic abuse.

Kin Selection

Child abuse can occur at any age up to 18 years and by either a biological parent or parent substitute. Based on an evolutionary perspective, parental love and care is established on the fitness value that the child shares (Temrin et al. 2011). Stepparents attempt to feel the kindness of that of a biological parent but often do not result in the lack of connectedness and satisfying relationships with children. Thus, parent substitutes (stepparents) are going to show less attentiveness based on lack of genetic relatedness and has been proven to explicate higher data for child abuse and homicide found within stepfamilies. Additionally, natural selection has focused on the intensity of parental care in our ancestry, and therefore these favored genotypes and phenotypes that triumph in parenting to develop individuals successful for reproduction have become the ones to flourish (Daly and Wilson 1986). With this, Daley and Wilson (n.d.), predicated that step relationships have a higher rate than genetic-related parent relationships with the controlling factor of socioeconomic status for child maltreatment and now referred to as the “Cinderella effect.” Based on the

stepfather effect on child abuse, results from Hilton et al. (2015) study on genetic relatedness found that among 144 men having at least one stepchild, 18% assaulted their stepchild, and among 361 men with at least one genetically related child, 8% assaulted their related child. Among ten households consisting of both genetic-related and stepchildren, only the stepchildren were abused within nine of the homes and one stepchild and one genetic-related child were both abused, and there were no scenarios where a genetic-related child was abused and a stepchild was spared (Daly and Wilson n.d.). Within households the paternal involvement in a child’s life is evident in the influence of abuse; paternal involvement in child caregiving is a leading protective mechanism (Lee et al. 2009). Conclusively, Hilton et al. (2015) propose that among men with both genetic-related children and stepchildren, the odds of assaulting a stepchild is twice as likely of assaulting a genetic-related child.

On the other hand, although studies have shown that stepparents abuse and sometimes kill their children at a higher rate than genetic-related parents, this does not implicate stepparents being the main factor but rather an underlying correlation with parental characteristics (Daly and Wilson n.d.).

Parental Characteristics

In addition to genetic relatedness, it has been found that fathers with pre-existing dysfunction characteristics are more probable to enter stepparent roles and have an increased risk of presenting childhood maltreatment. These abusers often have previous convictions; have personality traits of anxiety, depression, irritability, and antisociality; or have entered parenthood at a young age and face economic hardship. However, according to Temrin et al. (2011), “even if there are other differences between stepfamilies and families with two genetic parents than the non-genetic relatedness between stepparents and stepchild, these differences cannot

explain the Cinderella-effect, since the violence in families that include both stepchildren and genetic children is discriminatively targeted towards the stepchildren.” Hilton et al. (2015) found that step-parents with antisocial personality assaulted their stepchildren by 6% more than related children supporting their hypothesis of discriminative parental solicitude. Although Hilton et al. (2015) discovered that antisociality within men is correlated with a greater risk to assault stepchildren and, in some cases, display more assaultive behaviors, this personality trait cannot entirely be accounted for in the stepfather effect in child abuse. Moreover, the history of convictions and criminal behaviors lies within families of stepparents more so than families with two genetic parents and can be a confounding factor in the explanation of child homicide and abuse in stepfamilies. Temrin et al. (2011) concluded that there is a higher rate of crime-prone individuals within stepfamilies, and offenders of child homicide are significantly higher within parents of previous crimes.

Another confounding characteristic to have a significant impact on the outcomes of child abuse is socioeconomic status. Socioeconomic status puts stress on one’s family, and this stress of poverty can highly influence the likelihood of parents to abuse and/or kill their children. Correspondingly, the stress of poverty is a high factor in divorce and remarriage, therefore leading to stepparent relationships a related correlate of abuse (Daly and Wilson n.d.). Within well-established stepfamilies that are of middle class, it was reported that 53% of stepfathers and 25% of stepmothers were able to say that they had parental feelings for their stepchildren (Daly and Wilson n.d.) leading back to the evolutionary prospective of fitness value and therefore stepparents spending less time and attention to stepchildren (emotional neglect). Having a positive involvement within a child’s life is noticeably associated with a lower level of risk for childhood maltreatment and physical abuse (Lee et al. 2009). These indications of characteristics on stepparents increase the risk for child abuse and maltreatment.

Conclusion

All in all, children from stepfamilies are at a significantly higher risk for child abuse and maltreatment than children of families with two genetic parents based on a Darwinian natural selection and family characteristics. This conclusion has been scientifically proven through the process known as the kin selection theory or the “Cinderella effect” (Temrin et al. 2011). Families with both genetic parents are significantly more likely to have households consisting of love and attentiveness, less criminal activity, higher socioeconomic status, and therefore less child abuse and maltreatment.

Cross-References

- ▶ [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- ▶ [Cinderella Effect, The](#)
- ▶ [Child Abuse](#)
- ▶ [Child Abuse and Bullying](#)
- ▶ [Familial Violence](#)
- ▶ [History of Abuse](#)
- ▶ [Partner Homicide](#)
- ▶ [Paternal Role](#)
- ▶ [Sexual Assault and Intimate Partner Violence](#)
- ▶ [Two-Parent Families](#)
- ▶ [Victims of Violence](#)

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Geneticist

► [David Haig](#)

Genital Arousal

► [Sexual Arousal](#)

Genital Coevolution

► [Evolution of Genitalia, The](#)

Genital Cutting

► [Genital Mutilation](#)

Genital Evolution

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Synonyms

[Penile evolution](#); [Co-evolution of the sexes](#);
[Sexual selection](#)

Definition

The shift in the morphology and other features of genitalia over the evolution of a given species.

Introduction

Among sexually reproducing species, the penis evolved to serve as an internal fertilization device. But across different species, penises come in a bewildering array of shapes and sizes (see Eberhard 1985). Penile morphology varies greatly across the animal kingdom. Length, girth, and major morphology differ greatly, but penises also differ in specific features: some have spines, barbs, spicules, huge coronal ridges, or none at all. For example, just in terms of length, penises range from 10 ft long (the blue whale) and 6 ft long (the elephant) to less than 1/100th of an inch (e.g., the mosquito). Many ungulates have a pronounced glans (zebra, horse, rhinoceros), and many primates have a tapered shaft (bonobo, short-tailed macaque). Other primate species, such as langurs, have a pronounced coronal ridge. Among the great apes, humans have the longest penis, average length 5.1 in., followed by chimpanzees at 3.1 in. Orangutans and gorillas have much shorter penises at 1.6 in. and 1.2 in., respectively.

Male and Female Genitalia

The vaginas of females of a given species also contain analogs or complements to penile morphology (long twisted oviducts, enforced walls, etc.) This is not to assume that female genitalia reflects male genitalia, but just the opposite. As female genitalia shifted to optimize female control over fertilizations, male genitalia evolved to match.

The human penis does not possess spicules or barbs, like many feline species, but it does have distinctive characteristics. In humans, the distinctive characteristics of the penis, relative to other primates, are its length, circumference, glans, and

coronal ridge. The typical erect human penis ranges from 127 to 178 mm in length (Masters and Johnson 1966), with an average circumference of 24.5 mm (Wessells et al. 1996). In contrast with our closest living relative, the human penis is roughly twice as long and wide as that of the common chimpanzee (Short 1981). The glans and coronal ridge of the human penis are also uniquely configured (Izor et al. 1981). The posterior portion of the human glans is larger in diameter than the penis shaft. At the junction between the shaft of the penis and the head is a protrusion which encircles the base of the glans called the coronal ridge. At the interface between the glans and the shaft, the coronal ridge is positioned perpendicular to the shaft. Common chimpanzees have no clearly differentiated glans or coronal ridge.

It has been suggested that species differences in genital morphology can be used as an indicator of sexual competition/selection (Dixson 1987; Eberhard 1996). Another example of genital difference that has obvious implications for reproduction and competition is testes size. Among the great apes, chimpanzees greatly outnumber the other species with 600 million sperm per ejaculate and 120 g testicles. Humans are a distant second with 250 million sperm per ejaculate and testicles that range from 25 to 50 g. Orangutans and gorillas possess considerably lower sperm counts (70 million and 50 million) and smaller testicles (35 and 30 g, respectively). Testes size and sperm counts directly reflect levels of sperm competition in these species: The larger the testes, the higher the sperm count, the greater the advantage in a highly competitive mating context. Chimpanzees have the highest levels of sperm competition, while gorillas have the lowest.

Sperm competition and mating competition do not only affect testicle size; they also affect other facets of mating and genitalia. Likewise, intrasexual competition is not the only factor in mating; intersexual competition also plays a large role. This can be seen above, with penile morphology shifting to match vaginal morphology. In humans, ovulation is not accompanied by salient external signals and fertilization occurs internally. As a consequence, females have a considerable

reproductive advantage over males. Whereas maternity is always certain, males have to contend with uncertain paternity, i.e., the possibility of their partners producing offspring sired by other males. Because of internal fertilization, human males have been selected to utilize paternal assurance tactics. First, male can increase the probability that the children he is caring for are carrying his genetic material by monitoring and/or sequestering the female partner during the period that she is fertile to minimize being cuckolded.

Secondly, should the female succeed in an extra-pair copulation (or at the very least be out of the man's sight for a period of time), the male can physiologically increase the probability of paternity through sperm competition. For example, Baker and Bellis (1989) have shown that sperm counts fluctuate according to how much time the male spends with his female partner. The less often the male sees his female partner over a 3-day period, the higher his sperm count upon resuming sexual intercourse with her. In the event of a double mating (having intercourse with more than one man within 5 days, according to Baker and Bellis), the man who increases his sperm count would have a greater chance of impregnating the female.

As evidence that the length of the human penis has been shaped by the recurrent adaptive problem of sperm competition, consider the following. During ejaculation, thrusting diminishes and vaginal penetration reaches its maximum point (Masters and Johnson 1966). Not only does this serve to release semen in close proximity to the cervical opening, but data on ejaculatory pressure shows that the first several ejaculatory contractions project seminal fluid with such force that it can be expelled at a distance of 30–60 cm if not contained in a vagina (Masters and Johnson 1966). Thus, there appear to have been a series of adaptations that serve to confine or focus the release of semen to the uppermost portion of the vaginal tract as a means of making it less vulnerable to displacement.

There has been some speculation that the human penis evolved not only as an internal fertilization device but also as a mechanism for displacing semen left by rival males in the female

reproductive tract (e.g., Baker and Bellis 1995). The human penis, with a larger glans and pronounced coronal ridge, could function to displace seminal fluid from other males in the vagina by forcing it back over/under the glans. The effect of repeated thrusting, according to this analysis, would be to draw/displace semen left by other males back away from the cervix. If a female copulated with more than one male within a short period of time, this would allow males to “scoop out” semen deposited by others before ejaculating (Baker and Bellis 1995). The coronal ridge acts to scoop semen left by other males away from the cervix and enables the male to replace rival semen with his own.

In support of this interpretation, Gallup et al. (2003) simulated sexual encounters using artificial models and found that phalluses approximating the human penis did displace artificial semen. In a series of studies designed to simulate sexual intercourse under laboratory conditions using artificial genitals, Gallup et al. found that when latex vaginas were loaded with simulated semen, phalluses that approximated the configuration of the human penis displaced 80 % or more of the semen by drawing it away from the cervical end of the vagina (Gallup et al. 2003). Through a series of experimental manipulations, it was determined that the coronal ridge may be an important feature of the penis in mediating semen displacement. Thus, as a mechanical means of affecting sperm competition, the human penis may enable successive males to displace foreign semen from the female reproductive tract and substitute their semen for those of their rivals. The displacement of artificial semen was robust across different prosthetic phalluses, different artificial vaginas, different semen recipes, and different semen viscosities.

In a survey of over 600 college students, reported in the same paper, Gallup et al. (2003) found that following periods of separation or allegations of female infidelity, both males and females report that penile thrusting is noticeably deeper and more vigorous. Therefore, how men unwittingly use their penis also may be related to its semen displacement properties, and the parameters of penile thrusting appear to vary as a

function of the likelihood that there may be semen from other males in the female reproductive tract.

Under conditions that raise the possibility of females engaging in extra-pair copulations (e.g., periods of separation, allegations of female infidelity by a regular male partner), Gallup et al. (2003) also found that males appear to modify the use of their penis in ways that are consistent with the displacement hypothesis.

Conclusion

There is ample evidence to support the hypothesis that genitalia have evolved not only for reproduction but to be successful at reproductive competition, both intrasexual and intersexual. In addition, data suggest that human genitalia was selected for both size and shape in order to ensure conception and paternity, and human behavior has also been selected to shift in ways to assist these strategies.

Cross-References

- ▶ [Evolutionary Arms Race](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Last Male Advantage](#)
- ▶ [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- ▶ [Threats of Sperm Competition](#)

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Genital Evolution and Sexual Selection

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Definition

The effects of intrasexual competition and cryptic female choice on the evolution of genitalia.

Introduction

The genitalia of internally fertilizing animals are one of the most diverse characteristics within and across taxonomic groups. In many organisms, male genitalia exhibit extravagant spines, papilla, domes, hooks, and flaps and spines. The latter are generally made of keratin and can be found in a diverse array of animals including snakes and waterfowl; in domestic cats, penile spines scrape the female reproductive tract during copulation, which stimulates oviposition or egg-laying. Females too exhibit huge variation in genitalia; in the spotted hyena *Crocuta crocuta* females display a pseudo-penis that closely resembles a male penis, but is formed by the clitoris and fused

labia. In many organisms, particularly insects, male genitalia have other uses aside from reproduction, such as rubbing, grasping and stroking the female organs and sensory structures such as hairs and sensillae.

Extreme variation in genitalia is observed even amid some of the most similar looking species, making it one of the reliable traits to decipher between closely related animals. Both male and female genitalia exhibit extremely rapid evolution, and this is particularly evident in species that exhibit more promiscuous mating patterns. Genitalia evolve faster than practically any other morphological trait, and the explanation for this has been the subject of debate for decades (Langerhans et al. 2016). Researchers still argue that the evolution of genitalia remains relatively poorly understood.

Numerous theories have been proposed as to what forms of selection produce such distinct patterns in genital evolution. The three most popular theories are: (1) lock-and-key hypothesis, (2) pleiotropy hypothesis, and (3) sexual selection hypothesis, although these are not mutually exclusive.

Lock and Key

Originally proposed in 1844 by Léon Dufour (Dufour 1844), the lock-and-key theory is deeply ingrained among many biologists as a functional explanation for divergent genital evolution (Arnqvist 1997). The lock-and-key hypothesis suggests that male genitalia evolve in order to mechanically fit to their own species' female genitalia. Therefore, male genitalia evolve to be unique in order to be species-specific. Hence, the male genitalia are the “key” that mechanically corresponds perfectly with the “lock,” female genitalia.

Under this hypothesis, genitalia evolve to be highly specialised, in order to reduce the likelihood of hybridization with other species. Hybrids provide little evolutionary benefit, as generally most hybrids are not viable and will not form, and if hybrids do form, they are usually infertile. Thus, selection favors a pre-mating mechanical incompatibility between different species, in order to prevent mating occurring between them. Under

the lock and key hypothesis, any changes in male genitalia should be closely followed by changes in female genitalia resulting in male female coevolution (Simmons 2014). It has been suggested that selection driven by the lock-and-key mechanism should be stronger in monandrous species where females rarely re-mate, compared to polyandrous species where females mate with multiple males (Arnqvist 1997). It is expected that monandry would drive selection for reproductive isolation more intensely as the cost of mating with an individual of a different species is higher when re-mating is rare.

There are some criticisms of the lock-and-key hypothesis. It predicts that genital morphology between males and females should be complementary and it has been argued that female genitalia should be capable of physically excluding the male genitalia of other closely related species. However, studies have shown that female morphology is often uniform across species, without this ability to mechanically exclude similar species. Additionally, under this hypothesis alone some argue that genitalia are limited to stabilizing selection, which favors intermediate variants rather than extreme and diverse phenotypes, leading to relatively low amounts of phenotypic variation in genital morphology. As genitals are highly diverse, this does not conform to a fundamental assumption of the hypothesis (Eberhard 1985).

Pleiotropy

Mayr (1963) suggested that the vast differences observed in genitalia have a minor role, if any, in pre-mating mechanical isolation. Instead, Mayr suggested that pleiotropic effects acting on genes that code for both general morphological characters and genital traits were responsible for the strong variation we observe among genitalia. Evolutionary speaking, the morphological features that selection is working on are linked to genital characters, meaning any change in the selected features also affects the linked traits, almost as a side effect. Genitalia that have evolved through this hypothesis are proposed to exhibit high genetic and phenotypic variation and variation in genital morphology under the pleiotropy

hypothesis is assumed to be great but also largely nonfunctional (Arnqvist 1997). This results in no or very few instances of assortative meeting, in which males and females of similar phenotypes mate with one another more frequently. Under this assumption, preferential mating between male and female organisms for distantly different genital forms is not expected.

The pleiotropy hypothesis has come into question as it is unclear why genital organs should be disproportionately targeted by pleiotropy compared to other morphological traits (Hosken and Stockley 2004). Furthermore, male genitalia continuously exhibit high amounts of species-specificity, to such extent that it is a key trait to distinguish between closely related species as noted above (Langerhans et al. 2016). As under pleiotropism, selection is neutral but variation is high, species-specificity would not be a direct target of selection. This would make genital specificity difficult. Eberhard (1985) rejected the pleiotropy hypothesis based on observations that in many species in which males possess secondary sexual structures, also involved during copulation, it is these structures that exhibit the greatest amount of diversity in comparison to the primary genitalia.

Sexual Selection

Eberhard (1985) suggested that sexual selection could be responsible for the rapid diversification and evolution of genitalia. Sexual selection is driven by a preference for behavioral and morphological characteristics in the opposite sex, and competition within the same sex for access to members of the opposite sex (reviewed in Andersson 1994). Usually females choose between males, and males compete among themselves, as reproduction is generally more costly for females. As genitalia are well understood to be involved in sexual reproduction, to many, the idea that sexual selection is responsible for the evolution of genitalia seems indisputable (Arnqvist 1997).

The evidence for sexual selection driving genital diversity is based on observations of male genitalia increasing male fertilization success (reviewed in Simmons 2001). Sperm competition, postcopulatory male-male competition, occurs

when sperm from two or more males compete to fertilize the female's eggs within her reproductive tract. Sperm competition has been shown to operate in a number of ways, and one way is that males increase their fertilization success by removing sperm from rival males. For example, the genitalia of male damselflies *Calopteryx maculate* are spoon shaped and are used to scrape rival male sperm from the female reproductive tract. Variation in male genital morphology has also been observed to influence paternity success in the millipede *Antichiropus variabilis* while in the earwig *Euborellia brunneri* a longer and more exaggerated male genitalia results in greater sperm competitiveness. Therefore, sperm competition may be the leading force acting on genitals.

In addition to sperm competition, there are three other sexual selection-related mechanisms that have been suggested to explain rapid genital evolution; sexy sons (Runaway or Fisherian selection), good genes, and sexual conflict (Simmons 2001). The "sexy sons" hypothesis is associated with the inherited mate-attracting potential of the sons of a female. The "good genes" hypothesis is similar, but the benefits also include increased offspring viability (Hosken and Stockley 2004). Under both the "sexy sons" and the "good genes" hypotheses, the evolution of genital diversity is proposed to be driven by female choice for male genitals that best stimulate them when mating (Hosken and Stockley 2004). For example, in 2013, Yoshitaka Kamimura showed that in earwigs (*Euborellia brunneri*) longer genitalia is proposed to result from cryptic female choice for elongated genitalia, which in turn results in the production of larger sons; the mechanisms underlying this effect is not currently known.

Sexual conflict is the evolutionary arms race taking place between males and females in order for them to maximize their respective reproductive interests (Hosken and Stockley 2004). Essentially, unless reproductive interests are completely aligned, which they rarely are, sexual conflict favors traits that increase the fitness of one sex but comes at a cost to the other. For example, male ducks will often attempt to force copulation on females; however, the complex genitalia of female ducks make it mechanically difficult for sperm

from such matings to fertilize her eggs, as shown by Patricia Brennan's 2010 research. Male bed bugs (Heteroptera; Cimicidae) fertilize females by piercing her abdominal wall with the penis and injecting the sperm into her body cavity. This results in visible scars and leaves the female vulnerable to infection (Carayon 1966). Arguably, this traumatic insemination reduces female re-mating with competing males, and increases their investment in the current offspring if they perceive damage as a threat to survival. Females have evolved a counter adaption in the form of a specialized organ known as the spermalege; this tough fibrous organ is where the males pierce the female, and it reduces the physical and immunological costs imposed by this form of copulation. Thus, the coevolutionary arms race between males and females can potentially drive genital evolution.

Conclusion

Ongoing research currently favors sexual selection as the most likely mechanism responsible for the rapid diversification of genitalia, although it is less clear which mechanism of sexual selection is likely to be more important. However, the lock-and-key mechanism has not been disregarded as a possible mechanism in the evolution of genitalia. Sexual selection alone may not fully explain the specificity of genitalia that we observe between similar organisms. The lock-and-key mechanism may enforce species isolation, whereas sexual selection keeps genitalia evolving at a fast pace.

The focus of the majority of prior studies was previously centered on the divergence of genitalia in males, which resulted in the long-standing dominance of male-genitalia research. It was proposed that male genitalia appeared more elaborate and varied implying a greater diversity than the less-observable female genitalia (Arnqvist 1997). These assumptions have led to a lack of scientific attention on female genitalia (Langerhans et al. 2016). However, recent studies show that female genitalia also demonstrate a vast amount of variation. Although, in the past little was known about the rate of female genital evolution, a growing

volume of studies and literature suggests they have also rapidly evolved along with male genitalia. Ongoing research and novel methods are bringing forth new theories of selection responsible for the genital divergence in females, as well as possible patterns of coevolution of male-female genital evolution. To fully investigate both the causes and consequences of genital evolution we must consider the functions of both sexes and their interactions.

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Genital Mutilation

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Synonyms

Circumcision; Genital cutting; Genital operations; Genital surgeries

Definition

Genital mutilation involves permanent, physical modifications of varying invasiveness made to human sex organs that are performed for religious, cultural, social, or other reasons.

Introduction

Genital mutilation procedures are practiced on human males and females in different cultures across the world (Wilson 2008; World Health Organization [WHO], 2016). Both female genital mutilation (FGM) and male genital mutilation (MGM) encompass a diversity of surgical operations made to genitalia that vary in severity and could therefore involve the complete or partial surgical removal or modification of external genitalia (Wilson 2008; WHO 2010). Debates about FGM have often been framed using two well-intentioned positions that are typically at odds in principle: *cultural relativism*, and the similar doctrine of *ethical/moral relativism*, versus universal human rights (which according to the Universal Declaration of Human Rights include the right to life, liberty, the security of personhood, health, and education; Danial 2013). The philosophy of *cultural relativism* holds that moral values are valid to individuals of different societies, traditions, and groups and that we should show tolerance and respect for their customs (see Danial 2013). While debates about MGM (i.e., *circumcision*) also address human rights but less frequently involve the invocation of relativism, some scholars have argued that cultural bias is responsible for the normalization of ritual infant circumcision (e.g., Darby 2015; Solomon and Noll 2007). Consequently, different terminology is used to refer to genital mutilation for both males and females, often respective to the ethical position being advanced. Central to these debates is whether genital mutilation offers any benefits to the recipient – whether those benefits be social, cultural, physical, etc. – and whether they outweigh the risks of the procedure in question (e.g., see Danial 2013; Darby 2015). Although there is controversial, preliminary evidence suggesting that male circumcision may be

associated with a slight decrease in risk of acquiring the human immunodeficiency virus (HIV; e.g., Auvert et al. 2005), overall, no FGM procedures have been found to offer any medical benefits to its recipients (WHO 2016). Below, the practices of MGM and FGM are discussed in more detail, along with the nature of the controversies surrounding each.

Female Genital Mutilation

According to the WHO (2016), female genital mutilation refers to procedures that are deliberately carried out in order to alter or injure external female genitalia for nontherapeutic purposes. It is estimated that over three million girls are subjected to these procedures every year, with the girls between infancy and adolescence comprising the majority of the recipients (WHO 2016). These procedures take place most frequently in countries in Africa, the Middle East, and parts of Asia (WHO 2016). FGM also occurs in localities where it did not originate, such as North America, Australia, New Zealand, and Europe, due to emigration from countries where FGM is still commonly practiced (WHO 2010). Different surgical variations of FGM are performed that vary in severity and detrimental health consequences and are classified into four types: clitoridectomy (i.e., partial or total removal of the clitoris and/or the prepuce), excision (i.e., partial or total removal of the clitoris and the labia minora), infibulation, and other harmful procedures to the female genitalia for nonmedical purposes (e.g., piercing, scraping, cauterization; WHO 2010). The most dangerous form of FGM is infibulation, which involves surgically narrowing the vaginal orifice by slicing and sealing the labia minora and/or the labia majora together, and may or may not include the removal of the clitoris (WHO 2010). Numerous studies have documented both short-term and long-term health complications for recipients of FGM. FGM compromises women and girls' physical health, by creating immediate complications such as infection, extreme pain, hemorrhaging, and urine retention, as well as long-term problems, including cysts, infertility, difficulties with

childbirth, and recurrent infections, and can even result in death (WHO 2016).

There are several reasons for the practice of FGM in different cultures; however, many of them share the belief that such procedures signify femininity, purity, cleanliness, and chastity (Danial 2013; WHO 2016). FGM is often considered a rite of passage for women entering into adulthood, society, and marriage (Danial 2013; WHO 2016). In many of the cultures where FGM takes place, a woman's social status, viability for romantic relationships, economic security, and overall value are gravely diminished if she has not undergone these procedures, in large part because they are generally believed to establish that she is a virgin (Danial 2013). Thus, FGM is a socially upheld behavioral norm that is not intended to be harmful to the recipient, but nevertheless has serious consequences (WHO 2010).

Critics of FGM argue that these practices should be abolished for several reasons. Chief among them is the condemnation of FGM by opponents who maintain that none of the various procedures offer any direct benefits to those who undergo them and that, instead, they pose recipients undue psychological harm and health risks (WHO 2010, 2016). FGM is recognized by international organizations (e.g., the United Nations Children's Fund, the United Nations Populations Fund, the International Council of Nurses) to constitute an act of violence that causes extensive physical and psychosexual harm to women and girls (WHO 2010). Another charge by critics of FGM is that it violates the basic human rights of women and girls, including their right to health, life, information, freedom from violence, and physical integrity (WHO 2010). Some defenders of FGM invoke *ethical/moral relativism* (or the similar doctrine of *cultural relativism*) to justify the practices, although many do not necessarily condone FGM but hold an impartial position on the issue (see Danial 2013). Because the philosophy of *ethical/moral relativism* holds that there are no unbiased criteria for establishing what beliefs and practices are morally valid, and genital mutilation is practiced in a variety of forms, for diverse reasons, and in several different cultures, it is argued that these procedures reflect cultural

and religious norms (e.g., Shweder 2000). A common accusation made by critics of the anti-FGM movement is that they promote a Western imperialist narrative (e.g., Nnaemeka 2005; Shweder 2000). Indeed, *cultural relativism* arose in opposition to the historical tendency of prosperous Western nations to impose their ethical and cultural perspectives on less well-developed nations (Danial 2013). However well intentioned those who advance relativistic positions may be, there could be consequences resulting from the popularity of this perspective. For example, some health providers who do not themselves approve of FGM may agree to perform genital surgeries out of respect for sociocultural differences (WHO 2010). In opposition to the relativistic position on FGM, several global health organizations (e.g., Joint United Nations Programme on HIV/AIDS, UNICEF, WHO, International Federation of Gynecology and Obstetrics) contend that, while the freedom to practice religion and cultural traditions are secured by international law, individuals' fundamental rights trump their freedom to engage in surgical genital procedures on women and girls (WHO 2010).

Male Genital Mutilation

MGM is thought to occur in 25 % of societies worldwide, and as with FGM, it encompasses several surgical procedures that differ in severity and often represent a societal rite through which boys are granted social benefits (Wilson 2008). For example, the most pervasive MGM procedure, *circumcision*, refers to the removal of the penile foreskin (prepuce), whereas the most extreme, but less common, MGM procedure of *testicular ablation* is the practice of destroying or crushing one testis (Wilson 2008). Because infant circumcision is the most widespread form of MGM and elicits considerable controversy, it will be specifically discussed, below.

Routine male infant circumcision is a common procedure that the majority of newborn boys undergo in the United States, although it is not standard procedure in other industrial nations (Frisch et al. 2013). In the United States,

circumcision is an elective procedure that is performed at the behest of the infant's parents, who frequently cite religious, cultural, ethnic, or cosmetic reasons for deciding whether to circumcise their sons (Solomon and Noll 2007). Three recent studies found that circumcision may reduce the transmission of HIV in heterosexual men in geographic regions with outstanding HIV prevalence (e.g., Auvert et al. 2005), leading American medical associations, including the American Academy of Pediatrics and the Centers for Disease Control and Prevention, to endorse routine infant circumcision (Frisch et al. 2013). Critics have raised issues with medicalizing the procedure based on these findings, which they hold do not generalize to male infants, or homosexual men – who are at greatest risk for contracting HIV – since these studies used adult, heterosexual participants (e.g., Frisch et al. 2013). Instead, they argue that HIV is easily preventable by behavioral choices such as consistent condom use.

Critics of circumcision also contend that the alleged benefits of circumcision, if there are indeed any, do not outweigh the risks and/or potential risks resulting from the procedure (e.g., Darby 2015; Frisch et al. 2013; Solomon and Noll 2007). For example, circumcision may lead to complications ranging from minor problems, such as bleeding and meatal stenosis, to partial penile amputation (see Frisch et al. 2013). Although the extent of risks arising from circumcision is unknown, some work has shown that it may lead to reduced penile sensation and psychological and sexual issues (see Darby 2015; Frisch et al. 2013). Another criticism of ritual male infant circumcision comes from opponents who maintain that the procedure violates principles of bioethics, human rights, and the right to body integrity of minors who are affected (see Darby 2015).

Conclusion

Both FGM and MGM are procedures associated with alterations made to male and female genitalia that are most commonly performed on male infants (i.e., circumcision) and young girls

between infancy and adolescence (Solomon and Noll 2007; WHO 2016). Because children and infants are not generally considered to be capable of providing consent, genital surgeries performed on these vulnerable populations are deemed morally problematic by critics (see Darby 2015) and are argued to represent human rights violations (Frisch et al. 2013; WHO 2010). Some critics of circumcision have suggested that there is a double standard whereby male circumcision constitutes a harmful act that should be considered as legally and ethically objectionable as FGM (e.g., Darby 2015; Solomon and Noll 2007). Opponents of circumcision observe that MGM and FGM both involve risky and invasive operations made to normal, healthy genitalia in the absence of medical necessity and carry potential health and psychosexual consequences (e.g., infection, hemorrhaging, future sexual problems, regret of genital condition post-surgery; Frisch et al. 2013; Darby 2015).

Defenders of FGM frequently invoke *cultural relativism* and/or *moral/ethical relativism* to justify the surgical procedures. However, some advocates for male infant circumcision seem to appeal to culture, as well, to preserve its routine practice. These critics note that, while Western law views FGM as always impermissible (Solomon and Noll 2007), FGM in the form of a small incision may be less invasive than male circumcision, thus arguing that the United States are culturally biased in promoting male circumcision (Frisch et al. 2013; Solomon and Noll 2007). In this way, it is argued that MGM represents a normalized cultural tradition in the United States rather than a justifiable, medically necessary procedure, since scholars observe evidence for its medical benefits are scarce, inconclusive, and potentially absent (see Frisch et al. 2013; Solomon and Noll 2007).

Cross-References

- ▶ Cultural and Moral Relativism
- ▶ Cultural Differences in Sexual Socialization
- ▶ Modern Moral Relativism
- ▶ Moral Concerns
- ▶ Victims of Violence

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Genital Operations

- ▶ Genital Mutilation

Genital Surgeries

- ▶ Genital Mutilation

Genomic Imprinting

- [Evolution of Live Birth in Mammals \(140 MYA\)](#)
- [Maternal-Fetal Conflict](#)
- [Robert Trivers](#)

Genotype

- [Reaction Norms and Tokens](#)

Genuine Altruism

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Synonyms

[Evolutionary psychology](#); [Pro-social behavior](#)

Definition

According to the evolutionist perspective, altruism refers to behaviors that increase gains in fitness for the beneficiary (i.e., it favors the reproductive success and the maintenance of the species) at a certain cost to the benefactor. However, to better understand this psychological phenomenon, it makes sense to consider both proximal and distal causes. According to De Waal (2008), proximate causes refer to situations that promote psychological, neural, and physiological mechanisms of the organism, as well as behavior. Distal causes refer to the selective processes that maintain behaviors throughout the evolution of the species due to their consequences for fitness. In this sense, the author considers that to better understand the evolutionary causes of altruism,

one should focus on distal causes, particularly the effects of altruistic behaviors

Introduction

It is intriguing to contemplate how individuals of the human species, as well as others, can act so differently in the face of their fellow man in need, such that, at times, they ignore even desperate requests for help, while, at other times, they engage in actions that may endanger their own life, to try to help the other individual. Among a list of behaviors that are directed to benefit third parties, and considering their potentially high costs to the benefactor, altruistic actions are discussed in this entry.

The French philosopher Auguste Comte was the first to use the word altruism as a concept to oppose selfishness. The term refers to a notion that has become one of the most controversial themes in social and behavioral sciences, for it involves a discussion as to whether this psychological phenomenon is developed for selfish/extrinsic or genuine/intrinsic reasons. One might think that it would be a difficult term to define, since, on one hand, the literature recognizes altruism as an act aimed at benefiting another organism, yet on the other, there are conflicting views in discussion as to what factors would be involved in its costs and benefits. This is highlighted in the question of whether altruism is performed for intrinsic or extrinsic reasons (Bykov 2017), such as (respectively) satisfaction with life or gains derived from the action. However, considering the complexity and relevance of this construct, it is important to discuss the conception of altruism, with the desire to seek a better understanding and contribute to the discussion within this field of study. In view of this, we have presented at the beginning of the entry (definition session) what has been found in the literature with respect to genuine altruism.

In the literature, we find differing theoretical currents such as kinship selection or even reciprocal altruism directed toward understanding altruism. The perspective of altruism as arising from kin selection, in accordance with Lopreato

(1981), was developed by William D. Hamilton, in which altruistic actions develop taking into account genetic proximity to the beneficiary of the action. This approach thus argues that the probability of occurrence of altruism increases when the coefficient of relations between distributor and recipient increases and when the gains achieved by the beneficiary are greater than the costs to the benefactor. From the perspective of reciprocal altruism, elaborated by Robert L. Trivers, also as discussed by Lopreato, reciprocal altruism is developed in view of a high possibility of future repayment.

Considerable debates have been waged concerning kinship and reciprocal altruism. However, certain behaviors (such as those addressed to strangers in recognized need) have for some time been calling the attention of scholars. Such actions are often called pure, ascetic, or genuine altruism, the latter being the designation that will be adopted in this entry.

Genuine altruism is normally attributed to group selection (Lopreato 1981). In this sense, Boorman and Levitt (1980) argue that if certain genotypes multiply, reducing the possibility of extinction of a certain group, then phenotypes are likely to evolve, even if harmful to the individual. In accordance with this conception, groups possessing more altruistic individuals may well prevail over groups formed mostly by selfish subjects.

It seems that altruism may have been selected because of inclusive fitness. Particularly, in the case of the human species, people sometimes consider others within their social group as honorary relatives (Allen-Hermanson 2017), which ends up bringing advantages not only to the group but also to the individuals, since each of the individuals in the group enjoys an increased fitness as well. It should be mentioned that the concept of inclusive fitness was introduced by William D. Hamilton when discussing elevation of reproductive success probability, (a traditional conception of fitness developed by Darwin) as being alone insufficient to explain the plurality of behaviors that occur in nature in many species.

Altruism can be found in various species of the animal kingdom, such as insects, ants, and bees and even in human and nonhuman primates. Accordingly, research developed by De Waal

(2008) has confirmed that if newborn simians are rejected during weaning, their lives may be spared from possible consequences of the neglect if another member of the group takes over for their care, avoiding premature death.

With specific regard to human primates, Warneken and Tomasello (2009) argue that this would be a genuinely altruistic species, since aptitude for altruism arises at the beginning of ontogenesis, before socialization is able to exert an even greater influence on the baby's development. Consistent with this perspective, Warneken (2010) points out that the emergence of altruistic behaviors so early in ontogenesis suggests that social and moral norms are not the principal source of altruism. By contra-arguing that children grasp cultural patterns quickly and parents might be stimulating altruistic behaviors, the authors argue that if this was really the case, such altruistic manifestations would not be found in chimpanzees. Based on this set of ideas, in addition to environmental influences, it is proposed that altruism in the human species arises from a biological tendency, not predetermined as specific behavior, yet enabling a varied (and comforting) performance toward the subject who is in trouble (Warneken and Tomasello 2009).

The notion of genuine altruism involves three characteristics: (I) the helping act consists as an end in itself, not aiming at gains for oneself; (II) is practiced voluntarily; (III) is aimed at benefiting other individuals (Leeds 1963). From this logic, as truly altruistic behaviors/actions, we cite anonymous donations to charities, donation of food and clothing for victims of public calamities or natural disasters, or even donating hair for people with cancer. Certain considerations concerning genuine altruism have already been noted. However, for a better understanding of perspectives adopted toward this phenomenon, we believe that it is fundamental to address aspects questioning genuine altruism

Genuine Altruism: Points and Counterpoints

There are those who argue that altruism is developed in the light of future gains that such

actions might bring about, and it is then attributed to selfishness, albeit indirect. Nevertheless, Andreoni et al. (2017) have shown that even after suppressing incentives, in a considerable number of situations, research participants choose options that involve equal benefits for all involved and as well that avoid selfishness. Similarly, Forsythe et al. (1994) tested the hypothesis of justice, using dictator and ultimatum games in which the players receive an amount to divide between them. Contrary to expectations, the results, to a significant extent, indicated that players decided to donate to their opponent an amount equal to or greater than their own reward. This choice cannot be explained solely by some yearning for justice. The findings, at least in part, can be attributed to altruism.

The following question might be raised, “what would lead one individual to act for the other at the cost of his own fitness?” In order to try to understand this question, studies developed by one of the most notable theorists Daniel C. Batson discussing the dilemma of whether or not altruism can be purely attributed to selfish reasons become useful. Taking this paradox into account, and using as a starting point a defense of the conception of genuine altruism, he argues that altruism would be motivated by empathy, which culminated in the formulation of the empathy-altruism hypothesis. Additionally, this author in addition has developed experiments using selfish motivations in different situations, thus putting to the test the hypothesis and confirming it, as can be verified in Batson et al. (1981). From this perspective, empathy would be a proximal cause of altruism (De Waal 2008).

The conception that altruism may be motivated by empathy was not introduced recently, but it was proposed by Adam Smith and David Hume back in the eighteenth century. However, it was Batson who first formulated the *hypothesis of empathy-altruism*, which defends the idea that empathic emotional states foster the development of altruistic motivations and behaviors (see Batson et al. 1981).

In accordance with this hypothesis, an individual, upon verifying that someone is in need, experiences an empathic concern generated by observation, which, in turn, would lead to

behavior in response to the situation. And in this sense, the empathic concern presents itself as a propeller of the altruistic act directed toward the other, with the purpose of diminishing their suffering.

To illustrate this idea, the study by Batson et al. (1981) examined degrees of difficulty in escaping such situation without giving assistance (high or low) and of levels of empathy (high or low). University students were asked to observe a supposed student receiving electric shocks and had the option of assisting the person by receiving the shocks instead. The results demonstrated that high levels of empathy are accompanied by aiding activity, regardless of the cost (high or low) that such aid might require.

Along the same lines of thought, and in response to the conception that altruistic behaviors are based on potential rewards, Batson et al. (1983) argue that, if this were so, increases in pro-social actions would only occur in contexts in which people might think they are being evaluated, that is, in cases where their empathy is being measured before the development of pro-social acts. However, the literature indicates that participants perform acts of helping/altruism even before they realize that their levels of empathy are being evaluated.

Conclusion

Altruism is a controversial subject. Some scholars believe that behaviors aimed at benefiting another organism are developed for selfish reasons, such as a future reward. Others defend the idea that altruism is intended solely to assist another individual in a situation of recognized need. Given the existence of different perspectives on the origin of altruism, this entry purposes not to solve the theoretical conflicts but simply to briefly discuss genuine altruism.

This entry presents arguments that endorse altruism as motivated by intrinsic reasons, such as empathy. Thus, the studies of Batson, a recognized scholar involved in empirical studies and theoretical formulations regarding altruism, are emphasized. Although it is known that there is a hegemonic theoretical perspective that argues

that actions for the benefit of others are due to personal or species gains, more and more studies are being developed to understand genuine altruism. Indeed, the literature has been recognized that this psychological phenomenon has biological as well as environmental roots, enabling a behavioral repertoire as extensive as comforting for the individual in need (Warneken and Tomasello 2009).

Evolutionary psychology brings important contributions to understanding the roots of genuine altruism. However, any attempt to understand altruism on a solely phylogenetic basis, without taking into account factors such as ontogenesis, culture, and context, may be (given all of its complexity) too simplistic for human nature.

Cross-References

- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism And Costs To Altruist](#)
- ▶ [High-Cost Altruistic Helping](#)
- ▶ [Puzzle of Altruism, The](#)

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Geoffrey Miller

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Synonyms

[The mating mind](#)

Definition

Using sexual selection to explain human psychology.

Introduction

The publication in 2000 of Geoffrey Miller's book *The Mating Mind: How Sexual Selection Shaped the Evolution of Human Nature* heralded the first in-depth and wide reaching exploration of how sexual, rather than natural, selection could explain human behavior and psychology (Miller 2000). A central premise of this book is that as human *encephalization* (brain growth) has been very rapid, lacks any obvious survival benefits, and is unique to one species, it cannot be adequately explained by theories drawn from natural selection. Instead, Miller (2000) believes that our mental traits can best be explained as being the result

of runaway sexual selection in order to signal desirable traits in mate choice.

The Mind as a Fitness Indicator?

Subsequently, Miller (2000) views the mind as a fitness indicator as it is an extremely effective way for an individual to signal their genetic quality. This is because as the complexity of traits increase, so too does the genetic input needed to allow the trait to develop. Similar to the peacock's tail, therefore, variability in the human brain will signal the *mutational load* (the number of genetic mutations present) of an individual, which can provide potential mates with a great deal of information about their genetic fitness.

Creativity

Based on the handicap principle, whereby an individual can advertize their true fitness only through signals that are costly to produce, Miller explores specific mental abilities. For example, he points to human creativity as an effective means of signaling mental fitness, and he uses human artistic output (such as art, music, and poetry) as examples of traits that have little or no role in survival but do in terms of reproductive success. Evidence of this can be seen in the higher number of sexual partners that professional and/or serious artists have compared to individuals who had no artistic output (Nettle and Clegg 2006). Furthermore, as signals of genetic fitness are expected to be greater in men due to asymmetry in parental investment, it has also been shown that men also become more creative when they have been romantically primed (Griskevicius et al. 2006) and creative men are preferred over richer men by fertile women (Haselton and Miller 2006).

Language Use and Vocabulary

Similarly Miller (2000) also examines language use through the lens of sexually selected signaling. Miller points out that although language use

overall has clear survival benefits, our vast vocabulary does not. Therefore he suggests that it is valuable in mate choice, as elaborate language use acts as an honest signal of genetic quality. Evidence of this can be seen in how high verbal proficiency increases attractiveness (Lange et al. 2014) and the finding that men use lower frequency (i.e., rarer) words following an encounter with a potential partner (Rosenberg and Tunney 2008).

Altruism as a Courtship Display

Miller (2000) also explores how altruism can be explained as being sexually selected. He agrees with other researchers who believe that altruistic behaviors can act as costly signals of quality and states it can be an important signal in human courtship. Building on this, Miller (2007) argues that, more widely, moral virtues (such as agreeableness, kindness, and heroism) can be sexually attractive and act as reliable signals of an individual's genetic and parenting/partner qualities. Subsequently a large body of research has provided evidence that such behaviors are indeed important signals in mate choice (e.g., Barclay 2010; Farrelly 2011).

Modern Day Consumerism as a Costly Signal

Finally, Miller (2009) extends his view of the importance of sexual signaling in human nature to modern-day consumerism. He argues that human instinct to display costly signals of quality combined with social norms has led to twenty-first century capitalism, include our fascination with expensive brands and modern technology (Miller 2009). Here he further suggests that our personality and general intelligence are also signaled through our choice of products and services, from brand of car to university degrees. As these traits can be appealing in mate choice at different levels (e.g., high agreeableness may be desirable for long-term relationships, whereas low agreeableness may be desirable for short-term), Miller

(2009) suggests that the vast range of things we can consume are the result of our motivation to signal to others our individual qualities.

Conclusion

Geoffrey Miller's contribution can be considered as pivotal in switching the emphasis in human sexual selection research from physical signals to mental and psychological ones. *The Mating Mind* (Miller 2000) offered a broad approach to this, but it was not without criticism. This includes a lack of supporting research at the time and issues with regards to whether female or mutual mate choice could be the driving force behind such adaptations. However, by viewing much of our nature as potentially the results of sexual selection, its influence extends to many of the key areas of research in evolutionary psychological science, such as altruism and language use.

Cross-References

- ▶ [Brain Size and Intelligence](#)
- ▶ [Costly Signaling and Altruism](#)
- ▶ [Geoffrey Miller on Conspicuous Consumption](#)
- ▶ [Linguistic Evolution](#)

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Geoffrey Miller on Conspicuous Consumption

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Synonyms

[Conspicuous consumption](#); [Conspicuous leisure](#);
[Conspicuous reputation](#); [Conspicuous waste](#)

Definition

Conspicuous consumption, a term first made popular by the American institutionalist economist Thorstein Veblen in his well-known book *The Theory of the Leisure Class* (1899), is the phenomena of the ostentatious display of high levels of wealth through the purchase and display of very expensive items (e.g., designer watches, fine wine, and sports cars) that usually offer few practical benefits above their basic equivalents but are exclusive to the very wealthy simply because of their very expensive price tags.

By this type of consumption of exclusive consumer products, the wealthy act to publicly display their accumulated wealth, and by this means they connote to their peers (and to others) that they have achieved very notable success in their working lives. Various additional meanings of conspicuous consumption have also been outlined, over and above the simple display function. Conspicuous consumption may also facilitate the

following: acting in conformity with conventional symbols; compensating for lack of sufficient symbols; compensating for lack of satisfaction; enjoying or instrumentally using goods; and making oneself more attractive to others (Wicklund and Vanderkerckhove 1999, pp. 106–110).

Introduction

This entry will first consider the origins of the conspicuous consumption concept in Thorstein Veblen's work, before proceeding to consider the more recent development of this concept by the evolutionary psychologist Geoffrey Miller. The first economist to use a variant of the term conspicuous consumption was actually John Rae in 1834, who wrote that: "Articles of which consumption is conspicuous, are incapable of gratifying the passion" (quoted in Stankovic 2008, p. 119). Therefore the concept of the public display of wealth was certainly discussed by economists and others before Veblen, although there was no precise term that was consistently applied to the phenomenon across all of the literature until Veblen coined the phrase "conspicuous consumption."

Veblen on Conspicuous Consumption

The economist who first made the concept of conspicuous consumption an important cornerstone of institutional economics, and thereby more widely known to the general public, was Thorstein Veblen in his book *The Theory of the Leisure Class*. It should be noted that there is an entire chapter devoted to conspicuous consumption in Veblen's book (Ch. IV), so only a brief account of some aspects of it can be discussed here. Here is Veblen on conspicuous consumption from 1899:

The quasi-peaceable gentleman of leisure, then, not only consumes of the staff of life beyond the minimum required for subsistence and physical efficiency, but his consumption also undergoes a specialisation as regards the quality of the goods consumed. He consumes freely and of the best, in

food, drink, narcotics, shelter, services, ornaments, apparel, weapons and accoutrements . . . Since the consumption of these more excellent goods is an evidence of wealth, it becomes honorific . . . Conspicuous consumption of valuable goods is a means of reputability to the gentleman of leisure (Veblen 1925 [1899], pp. 73–75).

Veblen explained further that as wealth accumulated significantly over time, the leisure class and its habits of conspicuous consumption differentiated into an elaborate system of hierarchical ranks and grades, including vicarious conspicuous consumption by wives and other dependents bearing the insignias of their wealthy masters. The larger the number of vicarious dependents that an individual was able to support, the greater was the connoted indication of their wealth.

Another important aspect of conspicuous consumption highlighted by Veblen was that: "Throughout the entire evolution of conspicuous consumption . . . runs the obvious implication that in order to effectually mend the consumer's good frame it must be an expenditure of superfluities" (Veblen 1925 [1899], p. 96). In other words, in order to be reputable expenditure, it must also be wasteful expenditure, or as Veblen termed it, conspicuous waste. However, he was at pains to clarify that a good "may be useful and wasteful both" and that even apparently purely ostentatious goods can also have some useful purposes as well (Ibid., p. 100). Conspicuous consumption eventually became Veblen's most well-known and widely employed concept and it quickly developed a productive life of its own outside the pages of *The Theory of the Leisure Class*.

Miller on Conspicuous Consumption

In his book *Spent: Sex, Evolution, and Consumer Behavior* (2009), Geoffrey Miller further developed and extended the conspicuous consumption concept in line with recent developments in evolutionary psychology and biology, and also behavior economics (Griskevicius et al. 2007). According to Miller:

People have radically diverse responses to the very idea of conspicuous consumption. Some folks

consider it blindingly obvious that most human economic behavior is driven by status seeking, social signalling, and sexual solicitation ... Other folks consider this an outrageously cynical view, and argue that most consumption is for individual pleasure ("utility") and family prosperity ("security") ... (Miller 2009, p. 106)

Miller supported the first hypothesis, although this does not mean that the second was entirely false, as both could be accurate to a degree.

In his work developing the conspicuous consumption concept, Miller employed costly signalling theory as developed by the biologists Zahavi and Zahavi (1997). Costly signaling theory states that only very fit and healthy animals have the ability to "waste" a lot of time, effort, and resources on developing costly signals, or handicaps, such as the peacock's tail, or in human beings the highly developed muscles of the body-builder (Miller 2009, p. 91). Miller further explained that:

... inspired by costly signalling theory my colleagues ... ran a series of four experiments whose goal was to see how people's consumption decisions might shift as the potential mating benefits of costly signalling became more or less salient ... [it was shown that] conspicuous consumption (for men) and conspicuous charity (for women) can be increased by thinking about mating opportunities, and so can function strategically as a form of mating display (Miller 2009, p. 107)

These experiments demonstrated that, on average, men in what was called a mating condition, where they were actively thinking about finding a sexual partner, spent more on conspicuous luxuries than men not in a mating condition, and thereby not actively thinking about mating or seeking a sexual partner. Another experiment conducted elsewhere demonstrated that men's testosterone levels responded directly to conspicuous consumption, as testosterone levels increased when expensive sports cars were driven by men in public settings (Saad 2011, p. 72).

Miller explicitly linked costly signalling theory in biology with Veblen's original monetary conception of conspicuous consumption, explaining in this respect that:

Signal costs can certainly include costs in terms of an animal's general energy budget (food calories

eaten) or ecological resources (such as mating territories acquired by threats and fights), which are similar in some ways to money. When such moneylike costs are paramount, costly signalling theory most resembles Thorstein Veblen's theory of conspicuous consumption. In *The Theory of the Leisure Class*, Veblen argued that luxury goods and services are acquired by the rich mainly to display their wealth, not to increase their happiness ... Costly signaling theory simply generalizes Veblen's insight to the biological world. (Miller 2009, p. 114).

As Miller explained, buying expensive products in order to display status is a means of suggesting by the display of wealth that a particular individual's physical and mental traits are superior to most others, as these traits have produced the ability to obtain the great wealth that is on display through the status-indicating luxury product (Ibid., p. 73).

Miller also outlined that one important way that conspicuous consumption now operated was through the development of brand names and associated brand equity, or the psychological value of a particular brand's name recognition to consumers (Ibid., p. 125; Miller 2007; Barnett and Weedon 2014). This value can be quantified using data such as the percentage of people that recognize a specific brand name and the percentage of the market for a given good that is captured by a particular brand.

Conspicuous Consumption of Fine Wine

Finally, this entry will briefly apply the conspicuous consumption logic to a particular luxury commodity: fine wine. Thorstein Veblen explicitly listed connoisseurship of expensive beverages as something that the gentleman of leisure should be seen to cultivate, with a \$20,000-per-bottle burgundy (e.g., Domaine de la Romanée-Conti, DRC) now constituting the epitome of an expensive beverage (Veblen 1925 [1899], p. 74). Geoffrey Miller listed rare burgundy as a luxury drink employed in order to publicly demonstrate an individual's consumer narcissism (Miller 2009, p. 58).

DRC's Romanée-Conti wine is produced in very small quantities, with only around

500 cases each vintage being available for the entire world market (\$240,000 per case), meaning that, at most, only the wealthiest 500 people in the world get to buy it on its initial release. All the wines of DRC are examples of a Veblen good, for which demand increases as the price increases.

The serious fine wine collector has various different opportunities to engage in conspicuous consumption as a form of honorific display. They usually have a dedicated wine cellar to house their fine wine collection, with prestigiously labelled bottles on display that connote to any invited visitors the precise degree of wealth of the collector (Spurrier 1986). In addition, they have the opportunity to serve select examples of their fine wines to guests at various social functions such as dinner parties and yearly celebrations.

The fine wine collector also has the opportunity to buy and sell fine wine at public auctions and to buy fine wine in the public futures market. Finally, there are now numerous fine wine tastings organized at which both old and new fine wines can be publicly sampled and evaluated, and also the possibility of visits to famous French Chateaus (e.g., Chateau Mouton-Rothschild or Chateau Margaux in Bordeaux) undertaken as a form of secular worship at the elaborate cathedrals of fine wine. As it can be argued that fine wine is consumed both for status and pleasure in equal measure, it might be suggested that the exhibition of status can also be a form of pleasure.

Conclusion

It can be highlighted that conspicuous consumption is not only a feature of individual behavior but of some types of group behavior as well. For example, organizations such as private companies may employ conspicuous consumption (e.g., the ownership of expensive large office buildings in very desirable locations) in order to advertise their company's business success. These buildings may also be used as part of an overall branding strategy.

Perhaps the most famous example of this company branding strategy is that of the former *The*

Apprentice host Donald Trump, with his brash Trump Tower and his extensive portfolio of other properties found at various prestigious locations around the world. The Trump Presidency can, from this perspective, be seen as the ultimate global branding opportunity – the White House as a new Trump Tower located at 1600 Pennsylvania Avenue, Washington, D.C. – serving as the crown exhibit of the entire Trump brand.

It is also worth pointing out that in more recent times, there has been a rise in the prevalence of inconspicuous consumption and/or ordinary consumption, as the very wealthy may sometimes prefer to remain to some degree anonymous, rather than to advertise their wealth to everyone and anyone (Gronow and Warde 2001). Too much conspicuous consumption may serve to attract thieves and loafers wanting to obtain their own personal slice of the wealthy lifestyle through illegitimate means.

Cross-References

- Behavioral Economics
- Economists and Evolutionary Psychology

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George C. Williams

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Synonyms

[George C. Williams \(Founder of Darwinian Medicine\)](#); [George Williams](#); [George Williams on Group Selection](#)

Definition

George Williams was a highly influential evolutionary biologist best known for criticizing group-level selection and advocating in its place a focus on individual-level selection and adaptation.

Introduction

George Christopher Williams (1926–2010) was a highly influential evolutionary biologist best known for his contributions to understanding the evolution of senescence, to criticizing group-level selection and advocating individual-level selection and adaptation, and along with Randolph Nesse to establishing the field of evolutionary medicine. Williams was a professor in the Department of Ecology and Evolution in the State University of New York at Stony Brook.

Theory of Senescence

In 1957, Williams published *Pleiotropy, Natural Selection, and the Evolution of Senescence* – perhaps the most influential paper on the evolution of aging ever published. In it Williams made the argument that natural selection should result in aging because the force of selection is stronger earlier in life than later, and therefore selection would favor genes that have beneficial effects early in life even if they have detrimental effects later in life. His theory was thus based on pleiotropy – when single genes have multiple effects. His theory is often called the *antagonistic pleiotropy theory of senescence*. Peter B. Medawar had briefly mentioned the possibility of such pleiotropic genes resulting in aging in 1952, but Williams substantially developed the idea into a coherent explanation. In addition to antagonistic pleiotropy, the other core idea of Williams's theory was that natural selection tends to be stronger earlier in life than later in life. That the force of selection depends on age had first been recognized by one of the founders of modern evolutionary theory, Ronald A. Fisher, in 1930. Its underlying mathematics were elucidated by William D. Hamilton in 1966 in a paper whose focus was further elaborating Williams's argument that aging should result from age-dependent forces of natural selection. Subsequent research has largely supported Williams's theory, and to this day it is the leading explanation for the evolution of aging (another complementary and generally accepted theory, proposed by Medawar in 1952, is that harmful mutations expressed late in life should build up in a population because natural selection is weak or nonexistent at sufficiently advanced ages).

Group-Level Versus Individual-Level Selection and Adaptation

In 1966, evolutionary biologists often used group-level selection as their explanation of observed phenomena. In that year, Williams

published his most influential work, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. The book intended to “purge biology of . . . unnecessary distractions” (p. 4) and it soundly criticized using group-level and species-level selection as biological explanations, going so far as to say that “There is no respectable evidence of mechanisms” for such selection (p. viii). Many pages of this book summarize examples of biological phenomenon that were explained by others as due to group-level selection – for which Williams provides more parsimonious explanations using individual-level selection. This book was an early example of the shift in biological thinking in which evolution is seen from the gene level (an idea more fully developed by Richard Dawkins in his 1976 book, *The Selfish Gene*). Williams also clarified how biologists should use the idea of *adaptation*. For example, he argued that “Adaptation is a special and onerous concept that should not be used unnecessarily,” that “adaptation should be attributed to no higher a level of organization than is demanded by the evidence,” and that “Natural selection is the only acceptable explanation for the genesis and maintenance of adaptation” (p. vii). The emphasis that Williams placed on adaptations and the clarifications he made regarding them were influential in the historical development of what has been called the adaptationist perspective – a focus on adaptations as the key product of natural selection. The adaptationist perspective is arguably the foundational principle of evolutionary psychology (see, e.g., Barkow et al. 1992).

Notably, in 1992 Williams published a book in which he argued that although individual-level selection is the proper explanation for adaptations, it is insufficient as an explanation for which species exist on earth at any time – its biota. The explanation for the evolution of the biota, Williams argued, included that species and populations differ regarding their fitness as a group and so when considering macroevolution – the evolution of species and populations – group-level selection and multilevel selection can be important (along with chance events such as catastrophes).

Evolutionary Medicine

Williams, along with Randolph Nesse, published a paper (Williams and Nesse 1991) and then a book, *Why We Get Sick: The New Science of Darwinian Medicine* (Nesse and Williams 1994), that brought substantial prominence and recognition to the incipient field of evolutionary medicine (also known as Darwinian medicine). In their work, Williams and Nesse argue that medicine focuses on proximal causes of symptoms and so address what they see as a lack of awareness of the importance to understanding medical issues of the evolutionary (ultimate) perspective. Among six evolutionary explanations for diseases, they showed, for example, how some symptoms of illness – such as fever and iron deficiency – that are often thought harmful are instead part of the evolved human defense against pathogens. In addition to defenses, they addressed other aspects of medicine for which evolutionary theory would be expected to provide insights. Toxins damage tissue and cause birth defects, so pregnancy sickness suffered by human women today can be explained as a result of an adaptation for avoiding toxins in ancestral times. Some genetic diseases are likely the result of evolutionary selection for other effects of the same genes that are beneficial – especially early in life. Humans evolved in a stone-age world but live in a modern environment, and so mismatches of the modern world with our evolved biology and psychology might result in disease, as exemplified by excessive consumption of salt, fat, and other nutrients that were previously scarce. Williams and Nesse proposed that medical doctors should receive training in evolutionary approaches to the body and diseases, such approaches should be integrated into medical textbooks, and that evolutionary medicine be instantiated in departments, programs, and research institutes.

Conclusion

George Williams was a deep-thinking and far-sighted scholar who helped reign in unwarranted group-level explanations of

adaptations, refocused the attention of biologists and psychologists on the importance of adaptations and of selection at the individual and gene levels, and paved the way for a coherent approach to understanding medical issues from an evolutionary perspective.

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Cross-References

- [Adaptation](#)
- [Adaptationist Program, The](#)
- [Adaptations: Product of Evolution](#)
- [Darwinian Medicine](#)
- [Darwinian Medicine and Survival Problems](#)
- [Evolutionary Medicine](#)
- [Evolutionary Mismatch](#)
- [Fever](#)
- [George C. Williams \(Founder of Darwinian Medicine\)](#)
- [George Williams](#)
- [George Williams on Group Selection](#)
- [Group Selection](#)
- [Identifying Adaptive Functions](#)
- [Problems with Group Selection](#)
- [Senescence](#)
- [Theory of Senescence](#)

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George C. Williams (Founder of Darwinian Medicine)

- [George C. Williams](#)

George Williams

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Synonyms

[G. C. Williams](#)

Definition

George C. Williams was an evolutionary biologist with a specialty in ichthyology, best known for his book, *Adaptation and Natural Selection*, published in 1966, in which he asserted that the concept of evolutionary adaptation should be restricted to cases in which the demographic and population genetic evidence clearly supports the idea that a trait is the result of differential reproductive success. He also provided a strong argument against the concept of group selection and in favor of the classical Darwinian concept of individual selection. He also proposed that William D. Hamilton's newly proposed concept of kin selection could provide a testable explanation for the phenomena formerly explained by group selection.

Introduction

In 1962, V. C. Wynne-Edwards' book, *Animal Dispersion in Relation to Social Behavior*, was published in England by Oliver and Boyd (Wynne-Edwards 1962). It contained the most comprehensive analysis of animal social behavior published up to that time. Wynne-Edwards was an ornithologist, with a special focus on seabirds, which he cited as many examples in his *magnum opus*. Wynne-Edwards argued that many (perhaps most) social behaviors – everything from communication to socially induced mortality to territoriality – could be explained as evolutionary adaptations, the underlying effect of which would be the reduction of individual reproductive success within social groups. Such a reduction would have the effect of reducing ecological disruption to the environment of such social groups, thereby resulting in the increased survival of such groups relative to groups in which individuals maximize their reproductive success.

Main Idea

By 1962, George Williams had already published a landmark paper in evolutionary biology, "Pleiotropy, natural selection, and the evolution of senescence," (Williams 1957). In it he argued that a gene with pleiotropic effects – that is, a gene affecting more than one phenotypic trait – could produce antagonistic effects. One of the effects might result in increased reproductive success, while another effect of the same gene could result in decreased reproductive success. Williams proposed that any gene that resulted in early reproductive success would be selected for, even if it resulted in early senescence following reproduction. Such a gene would essentially result in individuals that "lived fast, loved hard, and left more offspring," and then died at a relatively young age as the result of degenerative conditions brought about by their "fast" early lives.

This idea – that adaptation is ultimately the result of differential reproductive success best attributed to natural selection at the level of genes – was central to Williams' most influential

work, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, published in 1966 (Williams 1966). Williams wrote it at least partly in response to Wynne-Edwards' earlier work. In it, Williams presented three interrelated arguments:

1. That the concept of evolutionary adaptation should be restricted to cases in which the demographic and population genetic evidence clearly supports the idea that a trait is the result of differential reproductive success
2. That the concept of group selection as proposed by Wynne-Edwards and others was unstable, as groups of individuals who reduced their reproductive success by whatever means could always be invaded and out-competed by individuals who maximized their reproductive success
3. That William D. Hamilton's newly proposed theory of kin selection (i.e., selection at the level of genes, rather than individuals or groups) could best explain the evolution of social behaviors, especially those that appeared to be altruistic

Williams first pointed out that far too many evolutionary biologists assumed that many (or even most) of the characteristics of animals qualify as evolutionary adaptations. He pointed out that the common assumption that a characteristic is an adaptation simply by virtue of its existence is a fallacy. Citing Darwin, Williams asserted that the concept of adaptation should be considered to be "... a special and onerous concept that should only be used where it is really necessary" (Williams 1966). He argued that only when a characteristic (i.e., a "trait") could be empirically shown to be the result of differential survival and reproduction and that this could be tied directly to a gene or genes producing that characteristic, should it be considered to be an evolutionary adaptation.

Williams' emphasis on natural selection being best analyzed at the level of genes is squarely in the tradition of the "modern evolutionary synthesis," as formulated by R. A. Fisher, J. B. S. Haldane, and Sewall Wright and

elaborated by Theodosius Dobzhansky and Ernst Mayr. The “modern synthesis” had its roots in the Hardy-Weinberg equilibrium law, first proposed in 1908 by British mathematician G. H. Hardy and German physician Wilhelm Weinberg. According to the Hardy-Weinberg law, there will be no change in allele frequencies in a population if four conditions are met: (1) no net mutation, (2) no net gene flow, (3) an effectively infinite population, and (4) random survival and reproduction. This law was based on the assumption that natural selection ultimately operates at the level of genes (i.e., alleles, alternate versions of genes), which produce the characteristics of organisms that result in their relative survival and reproductive success.

This idea – that evolution by natural selection ultimately happens at the level of genes – was central to the “modern evolutionary synthesis.” W. D. Hamilton’s (Hamilton, 1964) concept of kin selection was based on this same underlying idea that social behaviors, and especially altruism, could be explained by differential survival and reproduction of genes, with individual animals serving simply as their vehicles. This idea of the “selfish gene,” usually attributed to Richard Dawkins, has its roots in George Williams’ critique of Wynne-Edwards’ concept of group selection. Williams argued that virtually any group of individuals who collectively reduced their reproductive output could be invaded and ultimately replaced by individuals who maximized their reproductive output.

Consider a population of social animals – say birds in a forest. There are only enough resources available in the forest to support a limited number of birds. According to Wynne-Edwards’ theory of group selection, a group in which all of the individuals limit their reproductive output by whatever means (courtship and dominance displays, territoriality, etc.) would be more likely to survive than a group composed of individuals that maximized their reproductive output because the self-limiting group would be less likely to exceed the carrying capacity of their environment.

However, what would happen if individuals that did not limit their reproductive output entered such a group, either by immigration or mutation

(i.e., of a gene or genes that regulated their reproductive behavior)? In a fairly short time, such “selfish” individuals would outnumber their “altruistic” cohorts and would eventually replace them. In essence, altruistic individuals that restrict their reproductive output should always eventually be replaced by individuals that maximize their reproductive output. The only conditions under which this would not happen would be in highly circumscribed, very limited ecosystems in which the individuals are relatively genetically homogeneous, conditions rarely if ever met in nature.

This argument is similar to Garret Hardin’s concept of the “lifeboat ethics.” Imagine a lifeboat adrift in cold water following the sinking of a ship (e.g., the *Titanic*). There are two “types” of people in the lifeboat and in the surrounding water. One type are “altruists,” who will give up their places in the lifeboat to anyone in the surrounding water. The other type are “selfish” individuals who will either not give up their places in the lifeboat or will climb into the lifeboat from the water. The result of the interactions between these two types of individuals will inevitably be a lifeboat full of “selfish” individuals and the surrounding water full of “altruists,” who will eventually die of hypothermia (Hardin 1974).

In *Adaptation and Natural Selection*, George Williams argued for an alternative explanation for the evolution of social behavior and altruism: the theory of kin selection, proposed by British population geneticist and evolutionary biologist William D. Hamilton. According to Hamilton’s rule, behaviors that benefit others at some cost to the individual performing the behavior can evolve (i.e., be selected for) if the individual (s) receiving the benefit is closely genetically related to the individual performing the behavior. Algebraically, Hamilton’s rule is

$$C < r \times B$$

where C = the cost to the individual performing the behavior, r = the coefficient of relationship between the individual performing the behavior and the individual receiving the benefit, and B = the benefit to the individual receiving the benefit. This means that the more closely related two individuals are, the greater the benefit

to the altruist's genes that are shared with the recipient of their altruism.

Again, this idea is squarely in line with the underlying basis of the "modern evolutionary synthesis," that natural selection happens at the level of genes, not individuals or (especially) groups. What ultimately matters is not whether the individual performing any particular social behavior survives or reproduces, but rather whether the genes carried by that individual increase or decrease in frequency in the population as the result of the behavior. If the answer is yes, then the tendency to perform such behaviors can increase in frequency even if the individuals performing them survive and/or reproduce less often than the recipients of their altruism.

Williams' arguments in *Adaptation and Natural Selection* were extraordinarily influential among evolutionary biologists, especially in the United States and the United Kingdom. The concept of group selection was considered to have been thoroughly debunked and theories explaining the evolution of social behaviors based on kin selection were accepted in their place. In the years following its publication, and the publication of Hamilton's papers on kin selection, field and laboratory research testing these new theories accelerated dramatically. There were many successes, as empirical research supported the new paradigm and suggested further applications of the theories and their underlying concepts.

Another landmark in the development of evolutionary theory following Williams' publication of *Adaptation and Natural Selection* was Robert Trivers' publication of "The evolution of reciprocal altruism" in 1971 (Trivers, 1971). Trivers pointed out that not all cases of apparently altruistic behavior could be explained by kin selection. In particular, close social cooperation between completely unrelated individuals, such as cleaner fish and their hosts and warning calls in mixed species flocks of birds, occurs between individuals of different species. Trivers presented a theory based on reciprocal altruism: individuals will cooperate with other individuals if the cost they incur by doing so is offset by a related benefit they receive as the result of reciprocation of that

behavior. According to Trivers' theory, six conditions must be met for reciprocal altruism to evolve:

1. Interactions between potential reciprocal altruists must be repeated multiple times.
2. The cost to the individual performing a single altruistic act must be relatively small, especially at first.
3. The recipient of an altruistic act must eventually reciprocate the altruistic act to the individual that performed it for them.
4. Individuals participating in reciprocal altruism must be able to recognize specific individuals and remember the outcome of their previous interaction(s).
5. Individuals must be able to recognize non-reciprocators (i.e., "cheaters") and retaliate.
6. There should be no definite end point to the interactions between individuals.

If these conditions are met, cooperation between reciprocating individuals can evolve and increase indefinitely.

Triver's theory of reciprocal altruism was extended by W. D. Hamilton and Robert Axelrod in 1981, with the publication of *The Evolution of Cooperation* (Axelrod and Hamilton 1981). Axelrod and Hamilton organized a computer tournament in which mathematical game theorists could submit programs that would compete to see which behavioral strategy had the highest "fitness" (defined as obtaining the largest relative quantity of benefits from an altruist). The default strategy was pure selfishness, which was pitted against all of the submitted programs by Axelrod and Hamilton. The program that won was submitted by game theorist Anatol Rapaport. Called "tit for tat," this program was simple: cooperate during the first interaction and then do exactly what one's opponent/partner does in response. If the other player "defected" (i.e., was "selfish"), then the first player would be selfish until the other player cooperated (if ever). "Tit for tat" not only won, it was able to invade and eventually replace a population of purely selfish individuals, as long as there was at least one other altruist in the group.

The rapid development of the application of evolutionary theory to social behavior following Williams' publication of *Adaptation and Natural Selection* led to the founding of a new field of evolutionary biology. In 1975, Harvard evolutionary biologist E. O. Wilson published *Sociobiology: The New Synthesis* (Wilson, 1975). In it he drew together all of the various threads of theoretical evolutionary biology, natural history, anthropology, and psychology in a comprehensive analysis of the evolution of social behavior through the animal kingdom. Wilson divided *sociobiology* into four main sections: a historical outline of the development of the field, a presentation of the major theoretical components of the discipline, a phylogenetic review of the various social species of animals (organized into four subsections: the colonial invertebrates, the social insects, the social vertebrates, and primates), followed by an extended analysis of human social behavior.

Like most of the work upon which it was based, Wilson's sociobiology was ultimately grounded in the concepts of evolution by natural selection at the level of genes. Wilson, like Williams, argued that ultimately all evolutionary adaptations could be explained by differential survival and reproduction of particular genes, which in turn produce the phenotypic characteristics that allow the carriers of those genes to survive and reproduce. For most evolutionary biologists, this extension was not controversial, as the idea that evolution by natural selection ultimately happened at the level of genes was a founding concept of the "modern evolutionary synthesis."

However, these ideas were very controversial in the social sciences. Wilson was accused by some social scientists of reviving a kind of "scientific social Darwinism." Wilson was attacked, both in the press and in person, and the concepts of sociobiology were vilified, even when applied to nonhumans. So intense and prolonged was this controversy that eventually the term "sociobiology" became a negative epithet, and evolutionary biologists who pursued it were vilified and their work attacked.

In time, this resulted in the coining of a new term for the application of evolutionary theory to

the understanding of human behavior. This new field, evolutionary psychology, is one of the fastest growing and controversial disciplines within evolutionary biology and psychology. However, unlike sociobiology, evolutionary psychology does not necessarily reject natural selection at the level of individuals nor even at the level of groups.

This is most noticeable among those evolutionary psychologists who base at least some of their ideas on the theoretical work of George R. Price, an American mathematician, physical chemist, and population geneticist. Price did virtually all of his work alone, outside of established academic circles. Largely self-taught, Price re-derived Hamilton's theory of kin selection using a mathematical model that has become known as the Price equation (Price, 1970). Based on a mathematical process called covariance, the Price equation provides a theoretical mechanism by which a group can increase in fitness relative to another group because of the presence of altruistic individuals within the group. According to the Price equation, groups that include altruists can increase in fitness relative to groups without altruists, even if the relative proportion of altruists within such groups decreases over time. Under such conditions, the absolute number of altruists in the successful group can be larger than the absolute number of individuals in a competing group lacking altruists. Therefore, altruists have higher fitness when compared with non-altruists in competing groups, even though they have lower fitness within their groups.

Once again, the Price equation is ultimately founded on the theoretical basis of the "modern evolutionary synthesis," that evolution by natural selection happens at the level of genes. This idea also conforms to George Williams' caveat about the restricted applicability of the concept of adaptation. Applying the Price equation to real populations fulfills Williams' requirement that calling a phenomenon an adaptation be grounded in measuring fitness by measuring survival and reproduction, albeit at the level of genes rather than individuals.

George Williams counselled evolutionary biologists to avoid explanations based on group

selection. However, one of the paradoxes of modern evolutionary theory is that by applying Williams' strictures to actual populations – that is, by requiring that any analysis of fitness be grounded in differential survival and reproduction – it is now possible to derive a mechanism of natural selection that can be shown to happen at the level of groups, in addition to the level of individuals and the level of genes. This idea, called multi-level selection, has been most vigorously promoted by David Sloan Wilson of Binghamton University. Wilson has used group selection theory based on the Price equation to explain group social behavior in such disparate groups of animals as chickens and humans. In *Unto Others: The Evolution and Psychology of Unselfish Behavior* (co-edited with Elliot Sober) (Wilson & Sober, 1998), Wilson and Sober explored how human social behavior can evolve via group selection as well as individual selection. They concluded that altruism – defined as behavior that benefits other individuals without benefiting one's shared genes or requiring reciprocation – can evolve by natural selection.

Conclusion

George C. Williams' influence on evolutionary biology has been and continues to be profound and long-lasting. His debunking of Wynne-Edwards non-quantitative idea of group selection and its replacement with Hamilton's quantitative theory of kin selection ultimately led to the founding of sociobiology, a new field within evolutionary biology. Sociobiology, in turn, gave rise to the new and rapidly growing field of evolutionary psychology. Paradoxically, this has resulted in the quantitative reformulation of group selection theory and its application to human social behavior.

Williams' exhortations to evolutionary biologists to use the term "adaptation" parsimoniously have also resulted in an increased emphasis on three qualities in evolutionary research: reliability, efficiency, and economy. Evolutionary explanations that are grounded in quantitative analysis are ultimately more reliable than qualitative

explanations. Quantitative explanations can be empirically tested and either validated or falsified. This has resulted in greatly increased efficiency in field and laboratory research in evolutionary biology, as investigators can much more easily decide which explanations are more likely to reflect biological reality. Finally, Williams' emphasis on quantitative explanations accords with one of the foundational principles of all of the natural sciences: the concept of parsimony, often referred to as Occam's razor. Evolutionary explanations based on quantitative analyses are more parsimonious – they require fewer assumptions and produce much more straightforward and unambiguous results and interpretations than more qualitative explanations. As such, the theories of evolutionary biology that have themselves evolved from George Williams' exhortations have resulted in a body of knowledge that is simultaneously more economical and more comprehensive. The field of evolutionary psychology owes a great debt to his work and can continue to benefit from following his advice.

Cross-References

- [E. O. Wilson](#)
- [Evolution of Cooperation](#)
- [Evolutionary Psychology](#)
- [George C. Williams](#)
- [Group Selection](#)
- [Hamilton's Rule](#)
- [Individual Selection](#)
- [Kin Selection](#)
- [Reciprocal Altruism](#)
- [Robert Axelrod](#)
- [Robert Trivers](#)
- [Selfish Gene, The](#)

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George Williams on Group Selection

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Synonyms

[G. C. Williams](#)

Definition

In the study of adaptation, George Williams makes clear that group selection is not a valid explanation for traits developed by individual organisms. In his book *Adaptation and Natural Selection* (1966), he outlines some previous claims concerning the validity of group selection and discusses how they are frequently inadequate to explain the adaptation and evolution of species. There are several theories to which he gives some merit, but only in special cases that are not common in nature.

Introduction

Group selection, to George Williams, is frequently not a plausible explanation for the way that

individual organisms develop adaptations that enable them to survive in their respective environments. While he concedes that there are a select few group selection theories that have merit, he largely considers the approach to be misguided. While it often might seem that a population has evolved, Williams (1966) argues that in actuality the survival of the population is due to adaptations in the individuals that comprise it. The population itself has not involved per se but is comprised of adapted individuals.

A point Williams (1966) makes early in his book, *Adaptation and Natural Selection*, to support his claims is that the difference between phenotype and genotype expression is key to understanding how group adaptations can appear to occur. Whereas it is possible for an individual's environment to affect the way that a genotype is expressed through a phenotype, that environment does not truly alter the genotype. The phenotypic expression of a gene can differ between individuals, but the underlying genotype remains the same. Thus, while environmental pressures can alter phenotypic expression, they do not affect an actual genetic change within members of the population.

Probable Cases of Group Selection

Williams gives some consideration to Wright's (1945) theory that group selection functions in populations that are divided into several smaller populations. Wright argued that in a population divided into smaller populations, group selection would be most effective, as movement of individuals between the populations would alter the group genes and correct adverse selection and create a stronger species overall. In order for this type of population to exist and evolve in such a way, however, the populations would have to be of a very specific size and with a very specific immigration rate, which would both be difficult to occur by chance in nature.

The only theory of group selection that Williams truly admits has merit is that of Lewontin (1962) and Lewontin and Dunn (1960). In his studies of a species of house mice, he found what Williams considers to be one of the only

plausible cases of group selection. In the species, there exists a gene that produces a segregation distortion in sperm that creates a strong selective advantage for a certain gene. When studying wild populations, however, this gene, though it should be selected for, appears at a much lower frequency than would be expected in a deterministic model of selection. It was thus concluded by Lewontin and accepted by Williams that in this specific case, group selection within small populations and familial groups might be what causes the discrepancy in gene frequencies. This type of population, however, where lethality and sterility are to blame for the segregation distortion, is very rare, and Williams therefore would not generalize the type of group selection observed within the house mice to other species.

Conclusion

Overall, Williams maintains that group selection is very rarely the process that is driving the adaptation of organisms. The point of advantageous adaptations, he argues, is to keep the individual alive and able to reproduce; there is no mechanism that drives adaptations that favor the survival of the group. This is not to say that the group will not benefit from the adaptation of individuals – in many cases, a group of adapted individuals will experience increased fitness – but this benefit is only a fortunate side effect of individual adaptation.

Cross-References

- [Adaptation and Natural Selection](#)
- [George C. Williams](#)
- [George Williams](#)

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Germes

- [Pathogen Risk](#)

Gestalt Perception

- [Gestalt Theory](#)

Gestalt Psychology

- [Gestalt Theory](#)

Gestalt Theory

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Synonyms

[Composition](#); [Gestalt perception](#); [Gestalt psychology](#); [Structure](#)

Definitions

Gestalt is a German word that roughly translates to shape or form. Gestalt Theory attempts to define the fundamental rules of how individuals perceive stimuli in the environment as a complete form, rather than a group of smaller disconnected parts. A Gestalt is a complete percept that arises from the integration of small individual parts of a whole. This “whole” is not simply a sum of its parts, but becomes something more (Wagemans

et al. 2012a). The whole becomes something else entirely; something that has a greater significance (Koffka 1935).

Introduction

Gestalt theory is a theoretical standpoint in perceptual psychology that emerged from the work of Max Wertheimer's 1912 paper on the phi phenomenon, or apparent motion (Wertheimer 2014). Apparent motion is the illusion that results when researchers present two stationary visual stimuli successively and create the percept that one object has moved through space. In other words, the whole becomes completely different than any sum of its parts; it becomes a Gestalt. This discovery led to a cascade of scientific experiments examining the laws that govern how the brain stitches the world together. Most researchers consider Max Wertheimer to be the father of Gestalt theory, which took a fundamentally different approach to the mind than the Structuralist point of view. However, Wertheimer was by no means the only researcher examining the science of perception. Wolfgang Kohler and Kurt Koffka are both prominent researchers that helped to expand and disseminate the core ideas that would become the organizational principles of perceptual psychology (Wertheimer 2000).

Gestalt Organization

Gestalt organization refers to the ways in which the perceptual system organizes the world into meaningful wholes. There are several distinct categories of Gestalt organization. First, there are Gestalt grouping principles, which are the most well-known of the organizational laws. Gestalt grouping principles refer to the way that the brain interprets percepts as together or apart. Gestalt organization also includes figure-ground organization. Figure-ground organization refers to the ways in which the perceptual systems organize objects into a three-dimensional world based on their properties. Finally, contour integration also falls under the label of organizational principles.

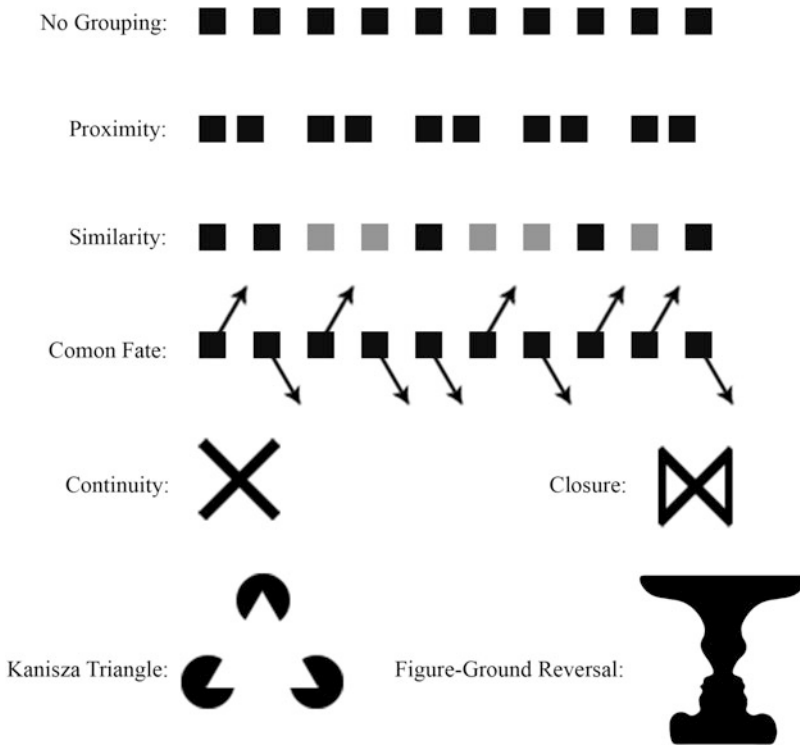
Contour integration refers to the diverse ways that contours affect how we perceive different aspects of the environment (Wagemans et al. 2012b).

Gestalt Grouping Principles

Gestalt grouping principles examine the relational qualities of percepts and how those qualities lead to specific groupings (see Fig. 1). Some of the most common Gestalt grouping principles are the principles of proximity, similarity, common fate, symmetry, parallelism, continuity, closure, common region, and connectedness (Wagemans et al. 2012b). Some of these principles are easier to illustrate using simple geometric shapes, while others can be more difficult.

The principles of proximity, similarity, and common fate are some of the easier principle to illustrate. The principle of proximity was the first of Wertheimer's principles of grouping and referred to the ways that objects group together. Specifically, objects, like dots, group together based on their relative distance from one another. When the dots are equidistant from one another, the perceptual system does not see them as being part of the same group. However, when the space decreases between every other dot, the brain perceives each pair of dots as an individual group, separate from the rest. Another primary principle of Gestalt grouping is the principle of similarity. The principle of similarity states that the perceptual system groups together objects that are similar. Similarity can refer to the color, size, shape, and about any other set of characteristics one could think of. A third major principle of Gestalt grouping is the principle of common fate. The principle of common fate states that the perceptual system groups items that move in the same way. More recently, research by Sekuler and Bennett (2001) has illustrated that the principle of common fate can apply to more widespread characteristics than just movement, like luminance changes.

Other principles of Gestalt grouping apply less to general objects, like dots, than to qualities and features, like lines and areas. For example, the principles of symmetry and parallelism tend to



Gestalt Theory, Fig. 1 Principles of Gestalt grouping. *No Grouping*: how objects appear when there are no grouping principles at work. *Proximity*: objects group together when they are closer together. *Similarity*: similar items group together. Both the *black* and *gray squares* form their own groups. *Common Fate*: items that are moving in similar directions group together (the *arrows* represent vectors of motion). *Continuity*: two lines that cross over each other in the middle of each line will result in observing two lines passing through one another, rather than two

opposing angles. *Closure*: items that form closed objects will group together. *The Kanisza triangle*: illusory contours can create a recognizable image (e.g., triangle), despite having no actual contours. *Figure-Ground Reversal*: the figure and ground of an image can shift based on the observers focus. If the observer looks at this figure with the *black* area as the image, a chalice will appear. However, if the observer focuses on the *white* area as the image, two faces appear looking towards one another

form groups with items that are either symmetrical or parallel. The principle of continuity states that two lines that intersect in the middle of each length will appear as lines that continue to go through one another, rather than forming two opposing angles. In other words, the perceptual system parses an “X” as two lines passing through one other rather than two obtuse angles meeting at their vertices. The principle of closure states that the perceptual system will group items together when they create a closed object. The principle of closure is a powerful grouping principle that it tends to overwhelm that of continuity (Wageman 2012b).

An additional area of Gestalt grouping are principles that relate to global spatial relationships. These are the principles of common region and connectedness. The principle of common region states that the perceptual system interprets objects confined to a common spatial area as being a part of the same group. For example, when looking at a face, one understands that the eyes and nose belong to the same face. Connectedness refers to the fact that the perceptual systems describe connected items as part of the same group. That is not to say that the principle of connectedness is the same as the principle of proximity, as proximity does not account for

objects behaving together (Palmer and Rock 1994).

Figure-Ground Organization

Figure-ground organization refers to the way that percepts in the environment separate from one another in three-dimensional space, some objects becoming figures and others becoming the ground. Specifically, how the perceptual system organizes figure-grounds relies upon several parameters, like motion and previous experience.

The major figure-ground organizational phenomena are convexity and symmetry, but there are many others. Convexity refers to the way in which convex items appear as figure items about 90% of the time (Wageman 2012b). Symmetry refers to the organizational principle that symmetrical items are more often seen as being figures, while asymmetrical areas tend to be the ground or background. Other forms of figure-ground segregation also exist in the form of top-bottom polarity, edge-region grouping, and motion. Top-bottom polarity refers to the way objects that have a wider base and a thinner top appear as if they are the figure in an image. Edge-region grouping refers to the way Gestalt grouping principles effect the perception of where figures belong in a three-dimensional space. Motion can be a major cue to figure-ground separation as well. The visual system interprets the motion of borders that appear to grow as the figure overtaking the ground. Also, when contours change dynamically, observers tend to assign the concave surface to the figure rather than the ground (Barenholtz and Feldman 2006). Some figures can have figure-ground reversals, such as the face-chalice image (see Fig. 1).

Illusory Contours

Contour integration and perception also make use of Gestalt grouping principles. Principles like continuity, closure, proximity, and similarity all work together to help with the perception of contours. These grouping principles can even create

illusory contours where none exist, like in the Kanisza triangle (see Fig. 1). Though no contours are present, the observer perceives the presences of a triangle due to the powerful grouping principles of closure and continuity.

Conclusions

The brain faces the complex task of making sense of an ever-changing world every second of every day. The sheer amount of detail that exists even in a small fragment of time is beyond even the capability of the attentional system of the brain to understand. Yet, each of those fragments of time consists of moments filled with recognizable and describable items that the brain interprets. The brain interprets these items as “whole” objects, not as lines and edges undefined in space. Gestalt theory describes the laws that create the “whole.” In essence, Gestalt theory is the study of how we experience the world.

Cross-References

- Camouflage
- Cognitive Science
- Evolution of Mammalian Vision, The
- Eye, The
- Face and Object Recognition
- Occlusion
- Psychological Mechanisms
- Spatial Mapping
- Vision
- Visual Illusions

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Gestation

- [Adaptation for Single Births](#)
- [Evolution of Live Birth in Mammals \(140 MYA\)](#)
- [Preterm Birth](#)

Gestation Period

- [Implications for Pregnancy](#)

Gestational Diabetes and Maternal-Fetal Conflict

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Synonyms

[Gestational diabetes mellitus \(GDM\)](#); [Pregnancy-induced diabetes](#); [Type III diabetes](#)

Definition

A condition in which previously nondiabetic women develop insulin resistance and high blood glucose levels during pregnancy. Typically occurs late in pregnancy (third trimester) and usually resolves shortly after delivery.

Introduction

Evolutionary conflict occurs when natural selection acts in opposing directions on different genes involved in an interaction (Burt and Trivers 2008). The conflict can be found at all levels of organization, from conflict between species, to conflict between individuals within a species, to conflict within an individual itself. Most of these forms of conflicts revolve around competition for resources and differences in optimal resource allocation among individuals. Between genetic relatives, what is beneficial to one relative may not be beneficial, and may even be detrimental, to another. This situation occurs when there is an unequal probability that genes from one individual will be shared with another. For example, if a mother invests abundant resources in one fetus, it benefits both that fetus and, due to shared genes, the mother herself; however it will detract from the mother's ability to invest in other offspring. From the maternal perspective, she shares half her genes with each of her children, so she benefits optimally from maximizing her reproductive output. However, from the perspective of any one child, there is a lower probability that a gene found in that child's genome will be present in other siblings (although there is a 50 % probability that a maternal gene found in one sibling will be found in the other, the sibs may not be paternally related, thereby reducing their probability of genetic similarity) (Trivers 1974). Therefore there is an unequal benefit for the child relative to the mother when she allocates resources to any one child versus conserving resources for other potential offspring. These situations produce what is known as maternal-offspring conflict.

Just as siblings bicker over who gets the biggest piece of cake, so too there is competition over

metabolic resources in the womb. While mom wants healthy offspring, it is in her best interest to limit the resources given to each child, so that she will be able to conserve her resources for future reproductive outputs. However, the paternally inherited genes found in the baby benefit from extracting as many resources from the mom as possible, with less concern for her future reproductive success. One way in which this materializes is over regulation of maternal blood glucose.

What is Gestational Diabetes?

Pregnancy results in a variety of metabolic changes, including increased blood glucose and decreased insulin activation. These are necessary to accommodate high and rising fetal energy demands. However, gestational diabetes (GD) refers to a condition wherein maternal blood glucose levels are abnormally high, usually during the second or third trimester (Di Cianni et al. 2003). This can result from inadequate insulin levels or increased insulin resistance, whereby the glucose is not being absorbed by cells in response to increased insulin concentration. Evolutionary theory can help us understand why GD is so common, affecting approximately 9.2 % of American mothers in 2010 (DeSisto et al. 2014) and up to 20 % of pregnancies in other cultures (Brown et al. 2013).

While fasting blood sugar levels fall early in gestation, they appear to stabilize at a lower baseline from the 12th week of pregnancy until delivery. By contrast, maternal insulin levels remain quite stable until the last trimester, at which time they increase to meet the rising metabolic demands of the growing fetus (Haig 1993). However, during this time maternal responsiveness to insulin's effects is decreasing. While this may seem odd, these phenomena can be explained through the lens of genetic conflict. Evolutionary predictions are as follows: (1) fetal glucose demands will be larger than the maternal optimum; (2) maternal countermeasures should

be in place to limit fetal access (Haig 1993). There is indeed evidence for both of these hypotheses.

Prediction 1: Fetal Glucose Demand

To address the first prediction, compare the rate of glucose consumption by the placenta relative to glucose concentrations in maternal blood. The placental glucose transport system has excess capacity, meaning that the placenta can continue to transport glucose to the fetus at a rate proportional to the glucose available in maternal blood, even when that is well above the normal physiologic range (Desoye et al. 2011; Hauguel et al. 1986; Ingermann 1987). In fact, the placenta is able to store excess glucose in the form of glycogen for later fetal transport (Desoye et al. 2011). In the case of GD, where the maternal blood glucose levels are extremely high, this often results in fetal complications, including macrosomia (high birth weight for gestational age) (Di Cianni et al. 2003). Furthermore, placental hormones block the ability of the maternal body to utilize insulin (conferring insulin resistance), and the placenta contains enzymes for rapid insulin degradation (Haig 1993). In fact, late in pregnancy maternal insulin action is 50–70 % lower than in nonpregnant controls (Butte 2000). This demonstrates a reduced efficacy of insulin in reducing glucose in the maternal blood stream, thereby increasing the amount of time glucose is available to the developing fetus.

Prediction 2: Maternal Countermeasures

To examine the second prediction, look into maternal insulin production. Early in pregnancy, when fetal glucose demands are still quite low, maternal fasting blood glucose levels fall and appear to restabilize at a lower level (Haig 1993). This has been interpreted as a “resetting” of maternal homeostasis in preparation for increased fetal demands (Haig 1993). By contrast, maternal insulin levels remain low early in

pregnancy but increase as fetal glucose demands rise. However, while more maternal insulin is being produced, it becomes less and less effective at reducing maternal blood sugar levels; the increase in maternal insulin production appears to be a competitive compensatory response to its decreased efficacy (Haig 1993). Furthermore, there is evidence that maternal insulin production spikes by about 120 % immediately after glucose intake, while the longer-term effects (5–60 min after intake) remain the same as in nonpregnant controls (Butte 2000). The longer the mom takes to reduce her available blood sugars, the more the fetus is able to extract. These results are consistent with the hypothesis of maternally evolved countermeasures to reduce placental glucose availability, as they demonstrate a timely maternal response.

Conclusion

While these fetal/maternal coadaptations work to produce healthy offspring in the majority of pregnancies, the modifications to the maternal glucose and insulin systems during pregnancy can trigger GD in some mothers. In a study of nondiabetic pregnancies, women whose blood glucose levels were higher within two hours after eating tended to give birth to heavier babies (Lorenzo et al. 1986); this indicates a direct benefit to the fetus at a cost to the mother, as women who show increased insulin resistance during pregnancy are more likely to develop diabetes later in life (DeSisto et al. 2014). Maternal response through decreased baseline blood sugar levels and increased insulin production later in pregnancy appears to be evolved countermeasures in response to increased fetal demands.

Cross-References

- Maternal-Fetal Conflict
- Parent-Offspring Conflict

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Gestational Diabetes Mellitus (GDM)

- Gestational Diabetes and Maternal-Fetal Conflict

Gestural Communication

► [Understanding Human Points](#)

Gestural Glottogonic Theory

► [Gestural Theory](#)

Gestural Origin Theory

► [Gestural Theory](#)

Gestural Theory

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Synonyms

[Gestural glottogonic theory](#); [Gestural origin theory](#)

Definitions

The gestural theory of language evolution states that the languages that humans speak today arose from an earlier form of communication that was expressed primarily through arm and hand gestures.

Introduction

According to the gestural theory of language evolution, our ancestors were able to communicate intentionally through gestures but could not control their vocalizations. Therefore, they primarily

used gestures to communicate purposefully; spoken language only began to emerge from this primarily gestural form of communication as our ancestors' ability to control their vocalizations increased.

Different gestural theories of language evolution have been proposed (e.g., Arbib et al. 2008; Corballis 2002; Hewes et al. 1973). Gestural theories of language evolution contrast with an opposing set of theories that assert that it is more parsimonious to assume that language evolved from simpler forms of primate *vocal* communication, such as song, because human language is now communicated primarily through vocalizations (e.g., Livingstone 1973). Current evidence suggests that gestural *and* vocal theories of language evolution are not incompatible. In fact, both may be more accurate when combined into a multimodal theory of language evolution, wherein human language evolved from, and continues to utilize, mutually informative gestures and vocalizations (e.g., Armstrong 2002; Masataka 2008).

The History of the Gestural Theory of Language Evolution

In 1973, Hewes published a paper wherein he synthesized then recent research about nonhuman primate communication to provide support for a gestural theory of language evolution. According to Hewes (1973) version of the gestural theory of language evolution, our ancestors communicated primarily through a language composed of arm and hand gestures; spoken speech only later replaced gestures as the dominant mode of human linguistic communication. Although his theory provided little detail about the process by which gestures came to be replaced by vocal speech, he speculated that our ancestors could have learned to speak by imitating animal noises as they began to hunt more frequently. Hewes emphasized that vocal communication in no way completely replaced gestures in modern languages as people still use gestures to add nuance and emphasis to their speech. He also stated that different aspects of modern culture are rooted in

gesture (e.g., painting) and vocal communication (e.g., poetry) respectively.

Hewes began his paper by providing a list of distinguished authors, beginning with Condillac in 1746, all of whom he believed had also promoted the idea that “man’s first language was primarily gestural” (Hewes et al. 1973, p. 65). He stated that the descriptions of the gestural theory of language evolution provided by earlier scholars were limited by their lack of access to then recent discoveries about primate communication. Key findings that Hewes used to support a gestural theory of language evolution included: (1) evidence that nonhuman primates (e.g., chimpanzees), who even after years of teaching cannot learn to express more than a few words through speech, can be taught to communicate effectively through sign language (e.g., Gardner and Gardner 1969), (2) anecdotal evidence that chimpanzees commonly communicate through gestures (e.g., Van Lawick-Goodall 1968), (3) evidence that nonhuman primates’ calls are involuntary emotional reactions that are emitted regardless of whether others are around to hear them (e.g., Bates 1970), (4) evidence that our ancestors could not produce certain sounds that are essential for modern human speech (i.e., the vowels [a], [i], and [u]) derived by reconstructing the vocal apparatus of ancient nonhuman apes from fossils (Lieberman et al. 1972), and (5) evidence that skilled motor movements, such as those required to use tools, and language are both primarily controlled by the left side of the brain (Lenneberg 1967a as cited by Hewes et al. 1973).

A number of subsequent researchers have extended upon Hewes’ work to provide further evidence for and alternative conceptualizations of a gestural theory of language (e.g., Arbib et al. 2008; Armstrong 2002; Bonvillian et al. 1997; Corballis 2009; Pollick and De Waal 2007; Skoyles 2000). For example, Bonvillian et al. (1997) described a study conducted over 400 years ago by Akbar, the then emperor of Hindustan, that revealed that infants reared by mute nurses never learned to speak and only communicated with gestures; they asserted that this study provided evidence for a gestural theory of language evolution.

Subsequent research has provided support for a number of the pieces of evidence that Hewes’ used to support his version of the gestural theory of language. For example, subsequent research has demonstrated that other apes (besides the chimpanzees who learned sign language with the Gardners), including orangutans and gorillas, also learned to communicate effectively through sign language but not through spoken language (e.g., Miles 1990; Patterson 1978). Subsequent research has also provided extensive support for his claim that nonhuman apes commonly communicate through gesture (e.g., Pollick and De Waal 2007; Roberts and Roberts 2016). In addition, striking commonalities between nonhuman and human primates have been observed in the types of gestures they use and the process by which their gestures often develop (i.e., during meaningful interactive routines; Bard et al. 2014; Gillespie-Lynch et al. 2014).

Subsequent studies have also supported Hewes’ assertion that the gestural communication of nonhuman primates is far *more* flexible than their vocal communication (e.g., Pollick and De Waal 2007). However, more recent research has *not* supported his assertion that apes are not able to control their vocalizations at all. Instead, research demonstrates that nonhuman primates adapt their vocalizations *and* their gestures to shifting social situations. For example, chimpanzees modify their vocalizations based on whether dominant individuals are present (Laporte and Zuberbühler 2010) and more often use gestures that make a noise which can be heard at a distance, like drumming, when they have a larger number of other apes who they are close with to stay in touch with (Roberts and Roberts 2016).

Subsequent research has also challenged Hewes’ assertion that our ancestors were incapable of producing human-like speech sounds by critiquing Lieberman and colleagues’ reconstruction of the vocal apparatus of a Neanderthal. For example, Falk (1975) asserted that the reconstruction was inaccurate because a key bone (the hyoid bone) was positioned too high in the larynx (the voice box) in the process of reconstruction; not only would an animal with such a high hyoid bone

not have been able to communicate through articulate speech, it also would not have been able to swallow. Indeed, a subsequent study utilizing the fossil of an ancestral ape with a complete hyoid bone revealed that the structure of the hyoid bone was remarkably similar to that of a modern human, which the researchers interpreted as evidence that ancestral apes were capable of producing modern speech sounds after all (Arensburg et al. 1990).

Subsequent researchers have extended upon Hewes' assertion that skilled motor movements and language are typically both supported by the left side of the brain by focusing on specific regions of the brain that support both language and skilled motor movements (e.g., the mirror neuron system) to develop their own adaptations of a gestural theory of language evolution. The mirror neuron system consists of neurons in different regions of the brain that respond when primates see others make a movement or when they do the same movement themselves. This system is believed to help primates understand one another's intentions and learn from one another.

Arbib et al. (2008) and Corballis (2009) both indicated that the presence of mirror neurons within a portion of Broca's area (an area in the prefrontal lobe of human brains that supports the production of both language and skilled movements) and its homologue (an area with a similar position and structure) in nonhuman primates provides evidence for their respective adaptations of a gestural theory of language evolution. Mirror neurons are distributed in many regions throughout the brain including a network of regions that support language (Fogassi and Ferrari 2007). Both Arbib and Corballis stated that mirror neurons could provide language learners, including our ancestors who were developing language, with the insights about the intentions and perspectives of those they were communicating with needed to produce and understand shared communication. Both researchers attempted to address a key gap in Hewes (1973) paper, specifically his lack of clarity about how gesture was eventually supplanted by vocal communication. However, they did so in different ways.

Arbib et al. (2008) asserted that the ability to imitate others that mirror neurons provide allowed our ancestors to learn to pantomime one another and that these early pantomimes developed into "protosign" or conventionalized gestures. He believed that "protosign" served as the foundation for "protospeech" or conventionalized vocalizations and that "protosign" and "protospeech" evolved together to become "protolanguage" (an early form of language which he believed to be multimodal). Although Arbib believed that language grew to be multimodal with time, he stated that gesture played the initial role in allowing our ancestors to develop language.

Corballis (2009) also focused his adaptation of the gestural theory of language evolution on the mirror neuron system. He also emphasized the support that recent evidence demonstrating that signed languages are as grammatically complex as spoken language provides for a gestural theory of language (Armstrong 2002). Unlike Arbib, Corballis did not believe that language *ever* transitioned from gesture into either a vocal or an explicitly multimodal mode of communication. Instead, he stated that modern "language, whether spoken or signed, can be viewed as a gestural system, evolving from the so-called mirror system in the primate brain" (p. 19). He supported his assertion that vocal language is a type of gesture by referring to the motor theory of speech perception. This theory states that our understanding of language is derived from how words are produced rather than the specific sounds produced (Liberman et al. 1967). Corballis stated that a gradual transition from manual gestures to increasing use of gestures of the face and mouth could have co-occurred with the increasing involvement of the hands in tool manufacture and use.

Further support for a gestural theory of language evolution has arisen from the field of developmental psychology. Infants typically learn to express concepts first through gestures (e.g., by pointing at a cat) before later expressing them through spoken speech (e.g., by saying the word "cat"; Capirci et al. 2005). A recent study evaluated if gesture supports the symbolic development of both human and nonhuman primates by

examining the gestural and symbolic development of language-enculturated (e.g., reared in language-enriched environments) primates possessing a common immediate ancestor (Gillespie-Lynch et al. 2014). Communicative behaviors observed among multiple species sharing a common ancestor are likely to have been present in the common ancestor. A chimpanzee, a bonobo, and a human child were reared in language-enriched environments and evaluated at comparable stages of communicative development. Similarities in the form and function of many gestures produced by the chimpanzee, bonobo, and human child suggest that gestural skills may indeed have contributed to linguistic development for our common ancestor. Indeed, a developmental transition from greater reliance on gesture to increased reliance on linguistic symbols was present for all three species though it was more pronounced for the child than the apes. However, multimodal expressions of communicative intent (e.g., pairing vocalization with eye-contact) were typical for the child, but far less common for the apes. This direct comparison of the development of members of three species of apes when raised in similar environments provided support for the gestural theory of language development but also suggested that increasing multimodal communication (or pairing of gestures and vocalization) supported the emergence of language among the ancestors of humans.

Conclusions

Although some of the evidence put forth in support of different adaptations of the gestural theory of language evolution has turned out to be less accurate than other evidence over time, a substantial body of evidence from multiple domains of research has been put forth to support gestural theories of language evolution. This body of evidence has grown increasingly more robust over time. Therefore, available evidence strongly suggests that gestures played an important role in the evolution of language and supports a version of the gestural theory of language.

However, evidence that gestures preceded rather than co-occurred with vocalizations in supporting the evolution of language remains very limited. Given that many researchers believe that language is currently multimodal (e.g., Arbib et al. 2008; McNeill 1985), gestural theories of language evolution may be more parsimonious if adapted into a multimodal theory of language evolution, wherein human language evolved from, and continues to utilize, mutually informative gestures and vocalizations (Armstrong 2002; Masataka 2008). Indeed, Hewes cited Condillac as one of the earlier scholars to put forth a gestural theory of language. However, Condillac and Aarsleff's (2001/1746) description of the process by which language evolved is more consistent with a multimodal than a gestural theory of the evolution of language. Condillac stated that spoken language developed from a "language of action" which consisted of a combination of gestures and vocalizations wherein our ancestors connected their "cries with some movement, gesture or action that made the expression more striking." (Condillac and Aarsleff 2001/1746, p. 114).

Cross-References

- [Language and Handedness](#)
- [Language Modularity](#)
- [Linguistic Evolution](#)
- [Neurobiology of Language](#)
- [Primate Gesture](#)
- [Sign Language](#)

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Gesture

► Communication and Developmental Milestones

Gestures

► Social Cognition and Communication in Chimpanzees and Bonobos

Gestures of Despair

► Factors Associated with Suicide

Gifts

► Charity

Girls Psychological Bullying

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Synonyms

Direct bullying; Emotional distress; Indirect bullying; Intrasexual competition; Relational; Aggression; Verbal bullying; Victimization

Definition

Bullying is a strategic, goal-oriented, and malicious behavior that harms individuals who have less power (Volk et al. 2014).

Introduction

Although girls' psychological bullying is a broad term that could apply to one's reaction of being physically assaulted, we define it as a behavior centered on spreading rumors, manipulating, criticizing, socially excluding, or assassinating the character of victims (SooHoo 2009). Indirect targeting behaviors that stem from relational bullying (e.g., rumor spreading) often occur with, but prior to, direct bullying behavior (e.g., rejecting the victim in front of a group) (Besag 2006; Letendre and Smith 2011). Regardless of the mode of aggression employed by bullies, the harm caused to victims of psychological bullying can be significant (Besag 2006). Whether girls are receiving benefits from using psychological bullying, as well as what their motivations may be, will be considered.

Evolutionary Motives Behind Girls' Psychological Bullying

Bullying appears to offer the same benefits to girls as it does for boys, namely increasing resources,

reproduction, and reputation/dominance (Volk et al. 2014). Specific to girl versus girl bullying, the potential motives behind this often psychological bullying may be related to the evolutionary concept of intrasexual competition and the desire to protect one's kin. Psychological bullying protects bullies' self-esteem and increases their marketability (Besag 2006). In an effort to appear as an eligible candidate to prospective mates, girls may use verbal and relational aggression to psychologically and socially devalue their competitors' worth and/or promote their own value as potential mates (Volk et al. 2012). The increased probability of achieving adaptive goals is a compelling incentive that negatively reinforces bullying behavior (Volk et al. 2012). Attractiveness conveys the message that a female is fertile and has high genetic quality, which is critical for reproductive investment (Hrdy 1979). Researchers have found that according to their peers, girls who bully are not only viewed as more attractive and popular but they also have greater access to reproductive opportunities and dating partners (Volk et al. 2014, 2015). On the other hand, girls who are more attractive and/or who date frequently are often targeted as victims by other girls, presumably as a form of intrasexual competition (Volk et al. 2012). This intrasexual female victimization has been linked to the development of eating disorders as well as to internalizing problems such as depression, anxiety, and suicidal ideation (Duarte et al. 2015). Thus, it appears to be an effective, if antisocial, solution to dealing with potential competitors.

Females' quest for reproductive status cannot be separated from their ambition to keep themselves and their offspring alive (Hrdy 1999). Women's reproductive output/success is likely to be equally, if not more so, influenced by parental care as it is by mating opportunities (Hrdy 1999). Achieving a dominant position within the context of a power imbalance allows girls to psychologically bully or exploit others who have visible signs of weakness (e.g., not having many friends) (Besag 2006). This may allow improved access to resources for the bully and their offspring as the victim is unable to mount an effective counter-response to the bully's psychological aggression

(Volk et al. 2012). Emanating social dominance is also valuable for preventing victimization and future threats to kin (Letendre and Smith 2011). For instance, great apes that are heavier than non-pregnant rival females can protect their newborn kin from infanticide, whereas the infants of subordinate great apes are considerably at risk of being killed by rival females (Hrdy 1979). Also, dominant rhesus macaques and squirrel monkeys can prevent subordinate mothers from retrieving their own infants (Hrdy 1999). It is likely that amongst humans, dominant women's children are less likely to be harmed or hindered.

However, there are limits to female bullying. Mothers are the most important feature of an infant's environment with regards to increasing an infant's chances of survival, followed by maternal grandmothers and elder sisters (Sear and Mace 2008). A substantial study examining the effects of kin on children's survival found that loss of a father did not affect the mortality of children, whereas loss of a mother increased children's odds of death by 99 % (Sear and Mace 2008). As the higher investing parent, it is crucial for mothers to maintain a high level of maternal care that is not adversely affect but too much overt aggression. Girls therefore avoid physical injury by adopting less risky psychological, as opposed to physical, forms of aggression that are nevertheless potentially effective at securing status, protection, and the ability to produce high quality offspring (Besag 2006; Hrdy 1999). For these reasons, boys are much more likely than girls to engage in physical aggression, while the sexes are roughly equal in their usage of verbal and social psychological aggression (Volk et al. 2014).

Conclusion

Psychological bullies use aggression within the context of intrasexual competition to achieve psychological benefits to themselves while at the same time imposing psychological harm/costs on their competitors (Besag 2006; Volk et al. 2014). For teachers, parents, and authority figures, efforts to address psychological bullying can be especially time consuming and laborious in comparison to overt physical bullying (Besag 2006).

Societal expectations depict bullying as normal and offer poor suggestions for how girls should overcome victimization (e.g., talking it out with the bullies, generating compassion) that do not coincide with evolutionary theory (SooHoo 2009).

Since bullying is considered an adaptive behavior, researchers suggest encouraging bullies to replace their behavior with socially just and effective alternatives, rather than trying to stop their harmful behavior or elicit empathy for victims (SooHoo 2009; Volk et al. 2012). Other effective methods for decreasing girls' bullying include increasing the rewards for compliance, the presence of visible and supportive peer mentors, and providing girls with the opportunity to learn valuable life strategies such as listening, compromising, and dealing with conflict (Letendre and Smith 2011). In order to successfully intervene, we must be more sensitive to the costs and benefits associated with girls' psychological bullying.

Cross-References

- [Boys Bully More Than Girls](#)
- [Boys Physical Bullying](#)
- [Same-Sex School Bullying](#)

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Girls' Interest in Familial Care

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Introduction to Girls' Interest in Familial Care

Girls demonstrate a greater interest in familial care than boys, and this bias emerges early in development. Girls seek out childcare opportunities more often than boys and are more responsive to infants (Maestripieri and Pelka 2002). Compared to males and multiparous females, young nulliparous women show greater visual attention toward infant faces (Cardenas et al. 2013; Maestripieri and Pelka 2002), as do nulliparous female rhesus monkeys (Waite et al. 2007). It has been suggested that this attentional bias toward infant faces may reflect a developmental mechanism directed at preparing nulliparous females for motherhood by increasing the likelihood that they will gain the experience and parenting skills needed to raise their own offspring. Waning attraction to infants in older multiparous females is consistent with idea that the function of juvenile interest in infants is to facilitate the acquisition of parenting skills.

Play Parenting

Girls' interest in familial care is especially reflected in play parenting, which girls engage in more often than boys. The sex difference in play

parenting emerges in preschool and becomes more pronounced throughout development (Byrd-Craven and Geary 2007). Play parenting generally takes the form of handling or playing with an infant or infant substitute (e.g., dolls) and has been documented in both Western and traditional societies. It has been proposed that play parenting evolved to provide practice and experiences that improve later parenting skills (Pryce 1993; Byrd-Craven and Geary 2007).

In support of this idea, early play parenting experiences significantly improve the survival rate of firstborn offspring in many primate species (Pryce 1993). While primate studies suggest that juvenile play parenting experience is not necessary for the expression of maternal behavior, it does serve to improve parenting skills to some degree (Pellis and Pellis 2006). Females reared in socially impoverished environments with few opportunities to interact with infants show deficiencies in maternal behavior (Maestripieri and Roney 2006). Early experience with play parenting appears to improve mothering skills primarily by reducing the fear elicited by an unfamiliar infant. Adult female rhesus monkeys without play parenting experience spend less time in close proximity to their infant and exhibit more fear-related behavior toward the infant (Pellis and Pellis 2006). Human and animal studies have indicated that the amygdala plays a role in the development of appropriate responsiveness to infants, and young female rhesus monkeys with lesions of the amygdala fail to exhibit the species-typical interest in infants and infant handling (Toscano et al. 2009), suggesting that the amygdala may provide the neural basis for juvenile play parenting behavior.

Biological Basis of Play Parenting in Humans

While it has been argued that human sex differences in play parenting are due to differential socialization pressures, several studies have shown that sex differences in play parenting are related to prenatal androgen exposure. Girls affected by CAH show reduced interest in infant care (e.g., babysitting), and play with dolls less

frequently (Byrd-Craven and Geary 2007). Fetal testosterone in normally developing children has also been linked to sex-typical play behavior (Auyeung et al. 2009), as has testosterone measured in infancy (Lamminmäki et al. 2012). Evidence from twin studies suggests that genetics may play a role in sex-typed play behavior, including parental play (Byrd-Craven and Geary 2007). These studies suggest that sex differences in children's interest in play parenting cannot be explained entirely by the effects of gender socialization.

Conclusion

Sex differences in parental play and juvenile interest in infant care reflect sex differences in parental investment and plausibly evolved to allow for the practice of the skills and/or competencies needed for later reproductive success. Women have a greater interest in babies and engage in more play parenting as children. Studies attempting to demonstrate the role of parental and societal influences on the development of this sex difference have largely failed to do so (Maestripieri and Roney 2006), and evidence suggests that genetic factors and prenatal exposure to gonadal hormones play a role in the development of sex-typical interest in infants. Early female interest in familial care and engagement in parental play likely reflects a developmental adaptation that allows individuals to develop appropriate emotional responses toward infants, thereby improving parenting skills and increasing offspring survival.

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Giving Up

► Learned Helplessness from an Evolutionary Mismatch Perspective

Global Homicide Trends

► Cross-Cultural Pattern

Global Warming

- [Climate Fluctuations in the Last 200 Ky](#)

Gluteal–Femoral Region

- [Waist-to-Hip Ratio](#)

Goal Detection

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Synonyms

[Intention](#); [Teleology](#)

Definition

The ability to make inferences about the causes of human behavior.

Introduction

A hallmark of human cognition is the capacity to read beneath the surface appearance of behaviors. Being able to see beyond the physical properties of an action and interpret it in terms of underlying intentions is integral to successful social functioning. Driving safely, negotiating job offers, playing a tennis match, and engaging in a conversation all require on-line, moment-to-moment predictions about other people's actions. When observing another person perform an action, adults and children typically fixate the goal of the action before it is completed (Flanagan and Johansson 2003).

Goal Detection is Precocious

Given that we live in a world of perceived intentional agents, an important question is, at what age are the actions of others perceived as guided by intentions? Over the past 20 years, researchers have developed sophisticated techniques (such as habituation) to address this question in preverbal infants. The findings from this research have shown that infants, like adults, can attribute goals to others (Robson and Kuhlmeier 2016). During the first year of life, infants appreciate the goal directedness of successful intentional actions. In one body of work, researchers showed that 6-month-old infants visually anticipate other people's actions that they were familiar with, and are later able to visually anticipate others' unfamiliar, more complex actions by 12 months of age (Gredebäck and Daum 2015). For example, infants who view feeding actions anticipate the arrival of the spoon at the mouth and, like adults, quickly disengage from the hand and fixate on the goal of the ongoing action (the mouth) just before the hand reaches this location. Although these findings suggest that infants can predict actions from early in life, it is unclear whether they anticipated the goal *per se* because the goal and motion path are confounded. In other words, after observing a spoon repeatedly moving to the mouth, a gaze shift to the goal is also a gaze shift to the endpoint of a familiar trajectory. A more conservative test would require that infants' predictions be tested when the context has changed, so that the same goal is reached with a different movement.

In an influential study, Woodward (1998) addressed this issue. In a procedure that has since become widely utilized, 6- and 9-month-old infants first watched as a hand moved out onto a table containing two objects. The hand would approach and grasp one object from the pair and would remain in this position until the end of the trial. This action was repeated upon the same object until the infants habituated (i.e., their looking time to the event decreased significantly). At this point, the locations of the objects were switched, and the hand reached either toward the same object in a new location or the previously

untouched object in the familiar location. Infants dishabituated (increased looking behavior) to the latter, indicating that they encoded the original reach as directed to a particular object. Interestingly, in a control condition where a claw replaced the human agent, the infants looked randomly, unless a person controlled the claw. The same procedure, with the switch of the target object location, showed that infants as young as 11 months made their first look from the hand to the goal object, now in a new location but looked first at the familiar location when a claw is the agent. Other studies have replicated these findings by changing the motion of the arm toward a single object. After infants were habituated to an actor reaching over a barrier with an arcing motion to retrieve a ball, the barrier was removed and infants saw the actor reach directly for the ball (i.e., same goal, a new path) or indirectly (i.e., old goal, same path). Infants looked longer at the indirect than at the direct test event, even when computer-generated agents were the actors (Phillips and Wellman 2005). Finally, it is worth mentioning that evidence of goal detection does not come exclusively from visual habituation experiments, but comes from overt social behaviors as well. For example, 7-month-olds will select the toy that an actor has grasped over another one that she simply touched with the back of her hand.

Can Infants Detect Failed Goals?

A critical test for understanding the depth of goal detection is one that requires reasoning about the goal of a *failed* action. The attribution of a goal when it is unfulfilled requires to reason more deeply than about the visual appearance of the action because the goal is opaque in the outcome or actor's action. The first demonstration of this ability came from a study by Meltzoff (1995) who showed 18-month-old infants an actor who tried, but failed, to perform several actions on objects. When given the opportunity to imitate the model, infants performed the action the experimenter intended to do (but never actually did) as often as those who had seen a demonstration in which the actor achieved his goal. This experiment has

been replicated and extended to younger infants and there appears to be a developmental progression in infants' ability to infer a goal from surface behavior between 12 and 18 months of age. There is also a developmental continuity between successful goal detection measured through a looking time measure at 10 months and failed goal detection measured through an active imitation task at 14 months (Olineck and Poulin-Dubois 2009).

The findings of recent studies suggest that infants' understanding of failed actions might even develop during the first year of life when a simple, familiar action (e.g., reaching) is tested with looking time procedures or in a toy sharing situation. By 9 months of age, infants show more patience when someone tries but fails to give them a toy than when she appears to intentionally prevent the infants from getting the object (i.e., teasing). When the test of goal detection with an arm successfully reaching over a barrier is modified to include a failed-action condition, infants as young as 10 months also look longer at the indirect than at the direct test event.

Is Goal-Detection Species-Specific?

What is the evolutionary origin of the precocious human ability to understand and predict the behavior of others? Do other animal species, especially our nearest relatives the chimpanzees, also understand the intentional actions of others? Recent studies have yielded results similar to those reported previously for human infants. For example, chimpanzees spontaneously (without training) behave differently depending on whether a human was unwilling or unable to give them food. They produce more behaviors and leave the testing station earlier with an unwilling compared to an unable (but willing) experimenter. Goal-based action predictions have recently been tested in great apes, including bonobos, chimpanzees, and orangutans, with the eye-tracking technology (Myowa-Yamakoshi et al. 2012). In the first attempt to adapt eye-tracking technology to chimpanzees, Myowa-Yamakoshi and colleagues reported that when chimpanzees observed actions such as pouring juice, they anticipated an action

goal in the same way as human adults. On the other hand, 8-month-old infants showed no evidence of goal anticipation. 12-month-old infants showed mixed evidence in that strong goal anticipation was not observed, but these infants did show weak predictive tendencies that were comparable to those of human adults and chimpanzees. Interestingly, infants scan goal-directed actions differently such that they spend more time looking at the face.

Another piece of important evidence comes from a study conducted by Kano and Call (2014). The researchers tested bonobos, chimpanzees, and orangutans that were familiarized to movie clips of a human hand reaching to grasp one of two objects. Then, as in the standard goal attribution task, the objects' locations were swapped, and in the test event, the hand made an incomplete reach between the objects. A mechanical claw performed the same actions in a control condition. The results were similar to those reported previously for human infants, and predictive looking did not differ among the three species of great apes. In a study including three preferential looking-time experiments on macaques, modeled on previous work on human infants (Rochat et al. 2008) tested whether macaque monkeys are sensitive to the functional efficacy of familiar goal-related hand motor acts performed by an experimenter. Like human infants, macaques gazed longer at less efficient actions (e.g., arching gesture in the absence of a barrier).

What about goal attribution in nonprimate species? To our knowledge, only one study has been conducted to address this issue. Adopting the same task as used in human infants, researchers presented dogs with either an inanimate agent (a black box) or an unfamiliar individual interacting repeatedly with one of two distinct objects (a globe vs. a watering-can). Once the dogs were habituated to the scene (habituation phase), the position of the objects was switched (test phase). The dogs were then exposed to three trials, in which they saw the agent (animate or inanimate) interact with the usual object (in the new location). This was followed by three subsequent trials in which the agent interacted with the

new object (in the familiar location). The dogs showed a similar response pattern relative to infants, in that they looked longer during the new goal than old goal trials. No such difference emerged with the inanimate agent (the black box) (Marshall-Pescini et al. 2014).

Conclusion

The rich literature on goal detection and attribution across species reviewed in this entry brings up the issue of the underlying mechanisms driving the perception of human actions as goal-directed. Is this type of behavior based on mentalistic processes or on simple learned associations? Some research has shown that performance on a goal-encoding task at 6 and 7 months of age is linked to implicit and explicit false belief reasoning years later. Such developmental continuity suggests that goal detection could be a precursor to later intention reasoning. A number of authors have suggested that an understanding of goal-directed actions, even in human infants, does not necessarily imply an understanding of mental states. Alternatively, other authors dismiss the looking time studies arguing that such data only provides evidence for infants' abilities to form statistical associations during the course of an experiment. Finally, the role of mirror neurons in goal detection has received much attention. Mirror neurons are visuomotor neurons that discharge both when a person performs an action and when that person observes someone performing a similar action (Rizzolatti and Craighero 2004). Whether mirror neurons are an innate evolutionary endowment or are gradually activated in response to learned actions is currently a topic of debate.

Goal attribution is a complex process and there is a wealth of information available to the viewer when watching someone who is performing a goal-directed action. In conclusion, the literature on goal detection suggests that human and non-human primates do not simply perceive the behaviors of others, they also interpret it. In human infants, researchers have documented a developmental trajectory in which the early intentional understanding of actions appears later than the

more precocious action- and object-based understanding. An important question in contemporary research on the developmental origins of goal detection is whether infants' understanding of intentionality is dependent on experience with human actions or more abstract, that is, detected in the actions of nonhuman entities.

Cross-references

- [False Beliefs](#)
- [Great Apes](#)
- [Imitation](#)
- [Mirror Neurons](#)

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Goals

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Synonyms

[Adolescents](#); [Contraceptive use](#); [Control education](#); [Health education](#); [Sex education](#); [Sexuality and birth](#)

Definition

The goal of sex education is to reduce sexually transmitted infections (STI's), HIV/AIDS, and unintended pregnancy among young people.

Introduction

The goal is to review research conducted on sex education in schools and to evaluate the goals of such programs from an evolutionary psychological perspective. This review aims to examine the effectiveness of sex education through a discussion of the environmental factors that influence adolescents' sexual life trajectories. Furthermore, the review discusses implications of these trajectories and works to determine how best to align each strategy with individual adolescent behaviors.

The primary goal of sex education is to reduce STI's, HIV/AIDS, and unintended pregnancies

among young people. Sex education, in school, is divided by various approaches to prevent negative health outcomes for adolescents. Sex education programs are typically either abstinence-only, or they are comprehensive approach. Abstinence-only approaches teach adolescents to avoid sex outside of marriage, and typically do not address birth control or safe sex methods. A comprehensive sex education approach focuses on a sequential program that focuses on multiple dimensions (e.g., physical and emotional) of sexuality and helps to inform decision-making. This approach equips adolescents with the necessary education on contraception use to reduce the spreading of HIV/AIDS, STI's, and unintended pregnancies. This review will examine the research done on the effectiveness of both approach type programs in light of adolescent's environment.

Life History Strategies and Risky Adolescent Behavior

Life history theory highlights that all people face a fundamental trade-off between investing into longevity and growth (i.e., building physical and mental capital through knowledge and skills) or reproductive efforts that involve sex and reproduction. Those that invest largely in reproductive effort at the expense of growth, maintenance, and longevity can be categorized as following a faster strategy, whereas those that invest heavily in longevity and growth and delay reproduction can be categorized as following a slower strategy (for a review, see Griskevicius et al. 2011).

Children who experience a significant amount of stress in their environment during childhood (e.g., insecure attachment, stressful family interactions, poverty) are prone to carry out strategies consistent with the fast life history trajectory in their adolescent years (for a review, see Kenrick et al. 1996). Rates of adolescent birth, pregnancy, and STD infection are higher among racial and ethnic minority groups, and these differences are often attributed to poverty, which is more common among these groups. Contraceptive use at first intercourse is also associated with poverty

status and race/ethnicity (for a review, see Santelli et al. 2000).

In a study examining life expectancy, neighborhoods with the highest life expectancy had mothers giving birth at a median age of 27.3 years, whereas in the neighborhoods with lowest life expectancy it was 22.6 years. The same pattern emerged in a study examining the relationship between violent crime rates and age of reproduction across 373 counties in the USA that represent over 146 million people. Higher violent crime rates were associated with earlier ages of reproduction, even when controlling for socioeconomic status (SES) (for a review, see Santelli et al. 2000).

Rational for Sex Education in Schools

In the USA there are 19.7 million new STI's diagnosed among adolescents each year. In addition, there is an estimated 614,400 pregnancies among girls aged 15–19, over 80% are unintended (for a review, see Finer and Philbin 2013). While there have been fewer pregnancies over the years, there is still great disparity in sexual health outcomes among adolescents living in low socioeconomic status communities (Centers for Disease Control and Prevention (CDC) 2013; Kost and Henshaw 2014). The high rates of STI's and unintended pregnancies in disadvantaged communities can be connected to behaviors and patterns among adolescents raised in high stress environments. While 95% of young people in the USA report some sort of formal sex education, in a school or community setting by the age of 18 (for a review, see Finer and Philbin 2013).

What Is Sex Education and What Are the Current Goals?

Sex education programs are typically an abstinence-only or comprehensive approach (also referred to as abstinence-plus). The abstinence-only approach focuses on teaching abstinence, from all sexual activity, as the only

acceptable behavior for unmarried adolescents (Visser and van Bilsen 1994). The comprehensive approach equips students with knowledge on the usage of contraceptives to reduce the risk of unintended pregnancies and sexually transmitted diseases. Research shows that such programs have helped decrease behavior that puts young people at risk of STI's, HIV, AIDS, and unintended pregnancies (for a review, see Finer and Philbin 2013). Rather, than influencing teens to engage in earlier sexual activity, comprehensive knowledge and access to contraception will equip older teens who already engage in sexual activity with the proper resources (Boonstra 2011).

Implications for Intervention

By better understanding how unhealthy sexual practices have evolved as an adaptive outcome for disadvantaged groups, sex education will be better able to guide adolescents in healthier and more desirable directions. Abstinence-only approach may have little impact on young people growing up in stressful environments and who see limited value in preparing for their future (for a review, see Frankenhuis and Del Giudice 2012). With this in mind, it would be more effective to teach adolescents to think about delaying immediate benefits like early childbearing, due to the potential costs (i.e., possible job and educational losses) (for a review, see Frankenhuis and Del Giudice 2012).

Conclusion

Intervention goals which address strategies that are aligned with adolescent's evolutionary motivated behavior will be most effective in the primary goal of promoting positive health outcomes among adolescents. If the goal of school-based sex education is to increase positive health outcomes for youth, comprehensive (or "abstinence-plus") sex education has far more research to support it as an effective method of sex education. Abstinence-only programs run the serious risk of

leaving young people, especially those who are at elevated risk, uninformed, and at-risk for poorer life outcomes (for a review, see Ellis et al. 2012).

Cross-References

► [Sex Education in Schools](#)

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Gonadarche

► [Puberty in Boys](#)

Good Genes

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Synonyms

Better genetic material; Genetic codes; Heredity; Mating selection; Sexual selection

Definition

A set of genes that carries the best adaptive characteristics and genetic traits that promote the selection of evolutionary tools, such as adaptability, health, or genetic variability.

Introduction

Sexual selection is a complex process and involves many variables still not completely clear to researchers. Among these variables, there is one called “good genes,” an indirect benefit that cannot be observed directly but has hypothetical indicators of masculinity, symmetry, health, and physical attractiveness.

The Role of Good Genes for Sexual Selection

Selecting the ideal partner involves the analysis of several factors. The best option for a long-term relationship not always seems to be the same for a short-term relationship. This is because, according to the sexual strategies adopted or the period of the sexual cycle (as in ovulation), the valued characteristics change, mainly for females (Penton-Voak and Perrett 2000).

As sexual evolution adjusts to evolutionary pressures, it is quite feasible to favor or prefer genetic benefits (good genes), even if implicitly. Research has shown that female, when looking for partners for short-term relationships, for reproduction, or when they are in the fertile period, usually values the so-called good genes more. Producing offspring with better genetic characteristics would be the most urgent goal, ensuring reproductive success and improved adaptive characteristics (Gangestad 2000; Roberts and Little 2008). However, assessing which individuals have good genes is not a direct task, since only the phenotype is accessible externally. This does not pose a problem, since subjects look for traits that may indicate the partners’ genetic qualities or complementary genes. Studies show that visual, olfactory, and auditory characteristics are used to select good genes, especially among females (Roberts and Little 2008).

These characteristics would be read as indicators of some adaptive advantages: a muscular body would indicate physical strength, an important characteristic of survival and protection, even more if associated with torsos with a form of “inverted triangle”; the shape of the body would indicate physical strength; height would indicate reproductive success; symmetry would indicate precision in development; and virility and skin health would indicate general health. In addition to these indicators, extreme traits of dimorphism, height, and muscles are usually avoided because the indicators could indicate developmental and/or environmental maladjustments. The exaggeration of these characteristics, which in the right measure would be good indicators, in excess would be unattractive (Buss and Shackelford 2008; Gangestad 2000; Roberts and Little 2008; Swami et al. 2007).

In addition, high levels of sex hormones would be related to a better immune system. For example, the immunocompetence handicap hypothesis suggests that testosterone-based male ornaments are honest signals of immune function, because testosterone suppresses immune function, so the ability to have high testosterone and yet still have a good immune system is an indicator of good genetic quality, while estrogen influences

the immune profile females adopt by suppressing cell-mediated immune function and enhancing humoral-mediated immune function (Foo et al. 2017). A better immune system is an indicator of good genetic quality. Besides that both estrogen and testosterone modulate facial features, such characteristics could be an indicator of good genes. An efficient immune system would be one of the best indications of good partner genetic material. This adds to findings on skin health and masculinity as indicators of good health (Sefcek et al. 2007; Thornhill and Gangestad 1996).

The theory of “good genes” is reinforced by some particularities found in studies of birds and mammals. Among the latter, males mostly do not offer parental care, and therefore it is the indicators of good genes that are decisive for the females’ sexual choice. In most species, such as in primates, a combination of underlying genetic characteristics and indicators of parental care and resource provision is likely to occur (Gangestad 2000). In turn, women appear to have evolved to mixed-breeding strategies (Buss and Shackelford 2008).

Extra-pair copulation, which seems to be a search for good genes, emerges in this context. Some bird species privilege paternal care for their choice of partner but have a high rate of extra-pair cases with individuals presenting indicators of good genes, such as symmetry. An increased number of extra-pair cases increases the genetic diversity of the population. Other evidence would be that these relations occur more in the fertile period, as well as the fact that males who are more symmetric have more partners and are more often chosen for this type of relation. Women in fertile periods prefer the smell of symmetrical men; another characteristic is the preference for more masculine faces for short-term relationships (Gangestad 2000).

Women’s physical attractiveness is taken as the main indication used by men to select good genes. On the other hand, women consider a greater number of variables (especially attraction-related ones, which have high market value), categorized into good genes, investment indicators, and indicators

of good parenting and good partnership: virility, physical attractiveness, sexual attractiveness, physical fitness and beauty, as well as other social benefits (Buss and Shackelford 2008).

Conclusion

Thus, the search for good genes seems to encourage competitiveness in the selection of sexual partners. As genetic traits are not easily observed, other traits and behaviors provide indicators of what would be good genes to be transmitted to the offspring, such as physical attractiveness, symmetry, and strength. In this process, gene variability acts on the development of strategies for partner retention and the adaptive skills and abilities necessary for the survival and perpetuation of genes.

Cross-References

- [Facial Attractiveness](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Sexual Dimorphism and Sex-Biased Gene Expression](#)
- [Sexual Selection in Evolutionary Psychology](#)

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Good Genes Theory

► [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)

Good Health and Stable Future

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Synonyms

[Complete health](#); [Healthy state](#); [Steady future](#)

Definition

Good health refers to a harmonious state of mind, body, and soul, in the absence of any illness, disability, or deformity.

The future that is consistent, steady, sustainable, productive, and promising is considered as stable future.

Introduction

Health is an important determinant of survival or sustainability of an individual. Since ancient times, the human focus mostly remained on maintaining a healthy state. The basic needs of life (food, shelter and sex) intend at restoration of health and survival. The theory of evolution of Charles Darwin emphasizes about survival of the fittest in the evolutionary race. The survivors are the fittest. To become fittest, an individual need to be healthy enough to overcome natural adversities. Since times immemorial, health gained importance as human beings tried to overcome sufferings (sorrow, trauma, pain, disability, poverty) by various means. There is always an intense human desire to remain in a healthy state; probably this need has given birth to the science known as *medicine*. An individual will have a future, only if he or she survives. Survival needs a healthy state of the individual in a healthy environment with adequate resources for survival. Thus, it is amply clear that there cannot be stable future without good health.

Evolving Concept of Health

Researchers and philosophers earlier attempted to define health, which are still acceptable in the modern medicine. Greek philosopher Plato emphasized the relevance of harmony between the individual and its environment for having good health as the Greeks believe good health as “*a healthy mind in a healthy body*” (Svalastog et al. 2017). Similarly, Pinder in fifth century defined health as a state of “harmonious functioning of organs” (Svalastog et al. 2017).

World Health Organization (WHO) defines health as “a state of complete physical, mental and social well-being and not merely the absence, of disease or infirmity” (World Health Organization 2014; Svalastog et al. 2017). This definition was adopted in 1948; however, over past 70 years, significant changes have occurred in the determinants of health and health care needs. Many researchers argue that the existing definition of health given by WHO fails to address

all the domains and determinants of health; hence, there is need to redefine health. It is proposed to incorporate “spirituality,” “adaptation,” and “equilibrium between human and nature” in the universal definition of health (Charlier et al. 2017; Nobile 2014). For e.g., peace cannot be defined as mere absence of war, it is much more than that. Similarly, instead of classical biomedical definition of health, we need to move to socioecological concept of health which is known as “New Public Health” (Fien 2010). This concept of New Public Health has evolved gradually over last 20 or so years. The fundamental conditions and resources for health under this concept have been enumerated in Table 1.

Good health refers to a positive state of health. For achieving good health, there should be a

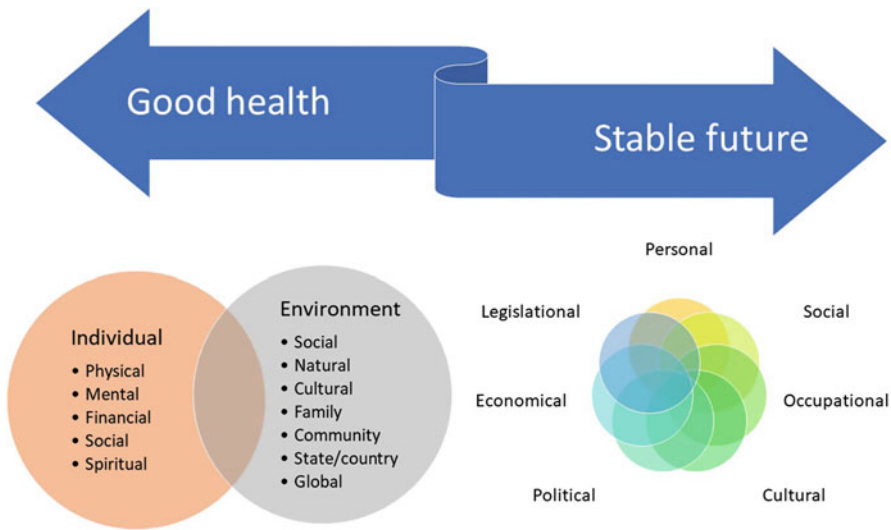
Good Health and Stable Future, Table 1 Fundamental conditions and resources for health

Peace
Shelter
Education
Food
Income
Stable ecosystem
Sustainable resources
Social equity and justice

balance between the internal environment and external environment of the individual. The internal environment of an individual consists of mind, body, and soul, which refers to the mental health, physical health, and spiritual health, respectively (Cumbie 2001). The external environment refers to family and community in a narrower sense to the national and global scene in a broader sense. The holistic view of health as conceptualized under “New Public Health” has laid strong emphasis on the fact that health of people, health of communities, and the health of natural environment are closely interlinked, at local, national, and global levels (Fig. 1).

Determinants of Good Health

The determinants of health are broadly of two types, viz., personal and environmental (Brown and Closser 2016). The personal determinants are the individual specific characteristics and the environmental determinants are specific environmental factors that significantly influence health. For having good health (a healthy state of mind, body, and soul), there should be optimal functioning of all the organs of the body along with sound and harmonious state of mind. These should be supplemented with fulfillment of spiritual needs, financial needs, sociocultural stability, and availability of adequate resources and support. An



Good Health and Stable Future, Fig. 1 Integration of good health with stable future

equilibrium needs to be maintained between the individual and its environment to make the individual adaptable to its environment.

Evidences suggest inequality of income stands as an obstacle of health and social cohesion, as a result of which health is adversely affected (Kawachi and Kennedy 1997). Nutritional inequality also adversely affects the health. Individuals from low socioeconomic status suffer more from nutritional deprivation and have compromised health (James et al. 1997). There are many other factors that directly or indirectly affect health in an adverse manner. These factors are – poor education leading to unawareness, racial discrimination, lack of legislations and policies related to health, funding for health, availability of health infrastructure, and political commitment (Braveman et al. 2011). Countries having strong health policy have better health infrastructure, adequate health care resources, and better health care delivery facilities at the primary care level in a reasonable cost, which has strong impact on the health of countryman (Starfield and Shi 2002).

Determinants of Stable Future

Probably, the best way to conceptualize stable future is to understand the sustainable development goals (SDGs) laid down by United Nations Development Programme (Table 2) (Fien 2010).

While framing these goals, it has been tried to inculcate all the possible factors that shall lead to achieve a state that is steady, stable, consistent, sustainable, productive, and promising. It is noteworthy that stable and sustainable future incorporates development and security of individual, community, and environment separately as well as collectively. It is also possible to summarize the essence of 17 SDGs into four dimensions viz. social, economic, ecological, and political. Achievement of stable future depends on simultaneous and balanced progress in all these four dimensions which are again totally interdependent (Fig. 1).

Integrating Health with Future

From the above discussion, it is amply clear that health and future are closely interlinked and there is no way one could be separated from the other.

Good Health and Stable Future, Table 2 United Nations’ sustainable development goals

No poverty
Zero hunger
Good health and well-being
Quality education
Gender equality
Clean water and sanitation
Affordable and clean energy
Decent work and economic growth
Industry, innovation and infrastructure
Reduced inequality
Sustainable cities and communities
Responsible consumption and production
Climate action
Life below water
Life on land
Peace and justice strong institutions
Partnerships to achieve the goal

Among the 17 SDGs listed in Table 2, three are directly related to health and the rest are actually working towards achieving these. There can neither be good health nor stable future if people are experiencing social, economical, or political instability, or if the environment is ignored in race of development.

If health is analyzed across the lifespan of an individual, successful completion of the life stages is important for meeting the future needs. Evidences suggest that early life adversities (e.g., abuse and neglect during childhood) are likely to affect the future of the individual. Health care needs of different stages of life are different. Hence, understanding the health care needs of different stages of life continuously and meeting them adequately will help in maintaining good health and may give a stable future.

Conclusion

As good health is a major determinant of stable future, health promotion is likely to brighten the stable future. Attainment of good health is possible not merely focusing on the physical health, rather equally focusing on all the dimensions of



health and maintaining a harmony between them. An individual with stable future is often considered to be having good health and individuals with good health shall have stable future.

Cross-References

- [Complete Health](#)
- [Steady Future](#)

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Good Parenting Qualities

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Synonyms

[Parental investment](#), [Positive parenting](#)

Definition

Parental behavior that facilitates child development

Introduction

Good parenting qualities are commonly defined as parental behavior that increases a child's chances of good health, happiness, and success. Such parental behaviors can include everything from the provision of fundamental resources, such as nutrition and shelter, to modeling good relationship skills and encouraging a healthy lifestyle. Depending on cultural context and values, parental behaviors can also include different forms of education, spiritual guidance, and informing children about expectations and norms that will help them navigate society later in life. Understandably, what is seen as being good parenting is often determined by the effects parental behavior have on the child's personal development – the evaluation of which is, at least partly, defined by cultural norms and subject to variation over time.

Evolutionarily, parental behavior has been selected so as to optimize the parent's total reproductive output by balancing investment across both current and future children. Contrariwise, children's behavior has been selected to demand more investment from their parents than their parents are prepared to give (Trivers 1972). This means that although natural selection has promoted behaviors that increase the genetic fitness of parents and children, natural selection has not

necessarily promoted parental behavior that is commonly considered “good.” Neither has natural selection promoted unlimited investment in each individual child, as this would come at a cost to the parent’s total reproductive output. Thus, there may be situations in which there is a conflict between what is considered good parenting and the psychological adaptations of parents.

Parenting Behavior and Genetic Confounding

A litany of studies has aimed to investigate parental behaviors that have desired or undesired effects on children’s development. For example, meta-analytical reviews suggest that positive involvement, parental support, and positive affect are associated with desired child outcomes such as decreased relational aggression and higher academic achievement (e.g., Fan and Chen 2001; Kawabata et al. 2011). On the contrary, controlling behavior, negative affect, abuse, and parental neglect are associated with undesired child outcomes such as higher relational aggression, increased risk of delinquency, anxiety, and depression (e.g., Kawabata et al. 2011; McLeod et al. 2007). The strength of the observed associations is, however, usually only weak to moderate. In most cases, interpreting the findings of such studies as parental behavior having causal effects on child outcomes is complicated by the fact that a possible genetic confound has not been controlled for. In fact, a central precept of Darwinism is the genetic inheritance of traits from parents to children. This means that any gene that promotes behavior X (e.g., aggression) in the parent might be inherited to the child and promote behavior X (or even behavior Y [e.g., delinquency], if behaviors X and Y share genetic background) also in the child. For example, the observation that children with socially distant mothers display poor attachment, and that this predicts social dysfunctions in adulthood could be the result of genetic material being shared between the mother and the child. That is, a potentially correct observation of an association between a parental behavior and child outcomes might incorrectly

be considered causal, as sufficient evidence for actual causality is lacking (Barbaro et al. 2017). This lack of proper evidence for causal effects of parental behavior on child outcomes, and the fact that most associations between these two are weak, has been thoroughly discussed by Harris (2009), who additionally points out that many of the behaviors that parents attempt to influence in their children are also shaped by their peer groups. Interestingly, this suggests that parents might be able to influence child outcomes by trying to influence the social environment of their children.

Mothers and Significant Others

The extent of maternal investment that is necessary to produce and raise a child clearly outweighs the necessary investment of fathers. In comparison to most mammals, actual paternal investment in humans is nevertheless relatively extensive. The amount of paternal investment varies considerably between different cultures, and, because fathers are quite capricious caregivers, and human children demand large amounts of investment, it has been suggested that children historically depended greatly on investment from other maternal relatives and female kin (Hrdy 2009).

The selective forces behind the evolution of costly investment in children are contingent on the probability of shared genetic material. Inclusive-fitness theory (Hamilton 1964) postulates that the ratio between costs to self and benefits to other of a particular investment, weighted by the degree of relatedness (i.e., the probability of sharing gene copies due to common descent), dictates the selection pressure behind investing in close kin. Because there is a 0.5 probability that a copy of a particular gene in a parent is present in their own biological child and only a 0.25 (or smaller) probability for nieces or nephews, costly investment is expected to be larger in own compared to other’s children. Indeed, studies generally support this hypothesis. Both women and men invest more in own children compared to their nieces and nephews (e.g., Antfolk et al. 2017), and behaviors that negatively

affect a child (e.g., sexual abuse) are less likely to be directed towards own children compared to nieces and nephews (e.g., Kresanov et al. 2018). Although the lack of biological relatedness is reflected in relatively decreased positive investment and increased risk of abuse, investment in stepchildren, adoptive children, and foster children – who in the majority of cases are not biologically related to their caregiver – is in most cases considerably higher than investment in unrelated children outside the family (e.g., Antfolk et al. 2017). In this context, it is important to note that regardless of whether a child is the biological descendant of the parent or not, a particular parental behavior is likely to have similar effects on the well-being of the child in question.

Conclusion

A variety of parenting qualities has been associated with positive child outcomes. These include, for example, positive involvement, support, positive affect, and acceptance. However, associations tend to be weak to moderate, and proper evidence of a causal effect of parenting behaviors and child well-being has rarely been established. Although biological parents tend to display a greater willingness to invest in their children, many non-biological parents invest equally much, and the possible effects of parental behaviors are unlikely to depend on the degree of biological relatedness per se.

Cross-References

- [Obligatory Parental Investment](#)
- [Offspring–Parent Attachment](#)
- [Parental Investment](#)
- [Parent–Offspring Conflict](#)
- [Step-Parenting](#)

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Good Standing

- [Gossip and Indirect Reciprocity](#)

Good-Sperm Models

- [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)

Gordon Orians

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Introduction

Gordon Howard Orians (born July 10, 1932) is Professor Emeritus at the University of Washington and a noted ornithologist and ecologist. He completed his PhD in Zoology in 1960 at the University of California at Berkeley and has been at the University of Washington ever since. His doctoral dissertation on social systems of marsh-nesting blackbirds was instrumental in establishing the emerging discipline of behavioral ecology. An investigator in the fields of ecology, evolutionary biology, and animal behavior, he is the author of numerous scientific journal articles and books and the recipient of many national and international awards.

American Blackbirds

As a vertebrate zoologist at the University of Washington, he focused his attention on American blackbirds of the family Icteridae due to his interest in the various types of avian social organization – territorial, colonial, polygamous, and brood parasitism. His work in this area produced theoretical papers as well as tests using experimental manipulations and comparative analyses of interspecific patterns. Many students will recognize Orians as the coauthor of a widely used introductory biology text (Purves et al. 1992). His scientific books include monographs on blackbirds and an edited volume on biodiversity in tropical forests.

Community Ecology

It is well-known but still surprising that in most environments herbivores consume a relatively

small proportion of the biomass of green plants. Orians pointed to the possible role of chemical defenses of plants against grazing as an explanation for this intriguing pattern in community ecology. He conducted research on the types of defensive chemicals synthesized by different kinds of plants, how their production may be stimulated by herbivore attacks, and how herbivores neutralize toxic chemicals produced by plants. Plant-defensive chemistry, he concluded, is part of the explanation for why the world is so green.

Savanna Hypothesis

According to the savanna hypothesis, our current habitat preferences were shaped by selection pressures in our ancestral past (Orians 1980, 1986). In a broad sense, the savanna hypothesis addresses the issue of how we select places to live and why we find some landscapes more beautiful than others. The theory argues that selection favored preferences, motivations, and decision rules that attract us to resource rich environments while avoiding environments populated with survival threats and lacking resources. The African savanna, widely believed to be the site in which humans originated, fulfills these requirements.

The details of the savanna hypothesis include three stages of habitat selection: *selection*, *information gathering*, and *exploitation* (Orians and Heerwagen 1992). The primary decision faced in stage 1 is whether to canvass or flee a landscape upon initial encounter. Assuming the experience in first stage is decent, individuals begin exploring the environment for resources and possible hazards. Stage 2, *information gathering*, involves mentally mapping the area for hidden places to harbor oneself, family, and allies. The decision of whether to stay or leave is at the heart of stage 3, *exploitation*. This final stage involves elaborate mental calculations that help to determine if one should stay long enough to enjoy the full bounty of resources available in the habitat.

Snakes, Sunrises, and Shakespeare: How Evolution Shapes Our Loves and Fears

In his book, *Snakes, Sunrises, and Shakespeare: How Evolution Shapes Our Loves and Fears*, Gordon Orians explores the role of evolution in human responses to the environment, arguing that many of our aesthetic preferences – from landscape beauty to food and entertainment – are the lingering result of natural selection.

Orians reveals how our lives today are shaped by decisions our ancestors made generations ago on African savannas. During this time humans selected places to live, sought food and safety, and socialized in small hunter-gatherer groups. Through this process specific likes and dislikes became wired in our brains, as the appropriate responses to the environment meant the difference between survival and death. He explains in rich detail why we prefer parks and gardens with tropical savanna elements, why we have developed discerning palates for wine, and why we find some odors unbearable.

Awards and Service to the Profession

In addition to his research in behavioral ecology, he devoted great effort to the interface between science and public policy. From the beginning of his career, Orians has taken an active interest in environmental problems, often taking positions within organizations that aid in the preservation of biodiversity. He was the director of the University of Washington's Institute for Environmental Studies for 11 years, served two terms on the board of directors of the World Wildlife Fund-US, and was the president of the Organization for Tropical Studies for 8 years. Orians has served his profession as a member of the US National Academy of Sciences and the American Academy of Arts and Sciences and is the past chairman of the Board on Environmental Studies and Toxicology of the National Research Council. In 1999, the Cooper Ornithological Society presented him with the Loye and Alden Miller Research Award for lifetime achievement in ornithological research.

Conclusions

For more than five decades, Gordon Orians has been an influential figure in the field of biology – especially on the topics of territoriality, habitat selection, mating systems, and population studies. Modern behavioral ecology owes a debt to his pioneering research.

Cross-References

- [Ancestral Threats Versus Modern Threats](#)
- [Landscape Preferences: Climate and Weather](#)
- [Natural Versus Artificial Environments](#)
- [Savanna Hypothesis and Landscape Preferences, The](#)

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Gossip

- [Sex Differences, Initiating Gossip](#)
- [Verbal Derogation](#)
- [Verbal Derogation Among Women](#)

Gossip and Grooming Hypothesis

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Synonyms

[Machiavellian intelligence](#); [Social brain hypothesis](#)

Definition

Posits that language evolved as a means of forming and maintaining alliances when group size became too large for relationships to be managed solely through grooming

Introduction

The gossip and grooming hypothesis is an attempt to explain the steady and pronounced increase in hominid brain size over the last four million years. Developed by Robin Dunbar (1996), it begins from the premise that brain expansion was driven by the computational demands of monitoring, predicting, and manipulating the behavior of conspecifics. It sees language as one of the adaptations that evolved in response to these tasks. Specifically, it posits that language evolved as a means of forming and maintaining alliances when group size became too large for relationships to be managed solely through grooming.

Our primate ancestors lived in the tropical forests of Africa, but when these forests began to shrink around ten million years ago due to climate change, competition for food intensified. In response, some individuals began venturing onto the expanding savannas to make their living. This exposed them to greater predation risk, because open grasslands provide few avenues of escape. One way organisms cope with predation risk is by living in larger groups: the larger the group, the

more eyes and ears there are to detect predators and the lower the odds of becoming one of their victims. However, living in larger groups exacerbates competition over food, mates, and safe sleeping sites. Under these circumstances, stronger individuals can advance their interests by bullying weaker ones. In response to this problem, many primates have evolved the ability to form alliances with other group members in order to provide mutual support against harassment. In nonhuman primates and – presumably – early hominids, these alliances are formed and maintained by grooming. Geleda baboons are a case in point: There is a positive correlation between the frequency with which females are groomed and the frequency with which they are supported in agonistic interactions. Tellingly, primate species that form cooperative alliances – such as chimpanzees, baboons, macaques, and vervet monkeys – tend to live in comparatively large groups.

Although grooming is an effective bonding tactic, it is also very time-consuming. Thus, once group size expands beyond a critical threshold, grooming loses its effectiveness: As group size increases, individuals have to maintain increasingly larger grooming circles; this leaves less and less time for foraging until, eventually, groomers face starvation. Language solves this problem by enabling individuals to groom their alliance partners verbally: Instead of removing parasites, verbal groomers provide their partners with valuable information. Whereas physical grooming limits individuals to interacting with one partner at a time, language enables individuals to service several partners at once. Thus, by circumventing the time constraints of physical grooming, information sharing enables individuals to maintain a larger number of alliances. Dunbar argues that language evolution was driven not only by the need to manage alliances more efficiently but by the benefits of sharing information that is instrumental to alliance formation and maintenance – information about the interests, goals, relationships, and character of the occupants of one's social universe, including oneself. Others argue that language evolution was driven, at least in part, by the benefits of transmitting

ecological knowledge. This debate is part of a larger question about the selective forces that drove hominid brain expansion. Key to resolving this question is an understanding of the ecological niche to which humans are adapted and its implications for human cognitive design.

Hominid Brain Expansion and Colonization of the Foraging Niche

The gossip and grooming hypothesis is an offshoot of the social brain hypothesis, which is one of two main branches of thought regarding hominid brain expansion. The chief bone of contention between them is whether this process was driven by the demands of ecological or social information processing (Byrne and Whiten 1988). The ecological hypothesis posits that hominid brain expansion was driven by the demands of complex resource extraction and associated tasks such as wayfinding. In contrast, the social brain hypothesis posits that brain expansion in humans was driven by the computational demands of cooperation and social competition. The hypothesis originated in the 1960s and 1970s with Alison Jolly, Ralph Holloway, and Nicholas Humphrey but remained untested until the early 1990s (Dunbar 1996). A third framework (Tooby and DeVore 1987; Kaplan et al. 2000) synthesizes the ecological and social models.

Hominid brain expansion is a biological puzzle. The human brain has more than tripled in size since the emergence of the Australopithecines roughly 4 ma, from approximately 400–500 cc to 1400 cc (Dunbar 1996). Most of this expansion took place after the emergence of our genus, *Homo*, 2.8 ma. Large brains are unlikely to evolve due to the high metabolic costs of growing and maintaining them: Although the human brain comprises only 2 % of adult body weight, it consumes 20 % of total energy intake (Dunbar 1996). Thus, the high energetic costs of a large brain must be offset by commensurate benefits. This presents two questions: How can the high costs of a large brain be supported, and what are the benefits of investing in brain expansion?

An answer to the first question was proposed in the expensive tissue hypothesis (Aiello and Wheeler 1995), which argues that, since the liver and gastrointestinal tract are as metabolically expensive as brain tissue, the costs of encephalization can be offset by a reduction in gut size. This, in turn, can be achieved through diet. Digestion of large quantities of low-quality foods requires a large gut, while digestion of small quantities of nutrient-dense foods can be accomplished by a much smaller gastrointestinal system. Aiello and Wheeler (1995) found a pronounced negative correlation between relative brain and gut mass in primates: Species with relatively large brains have relatively small guts. The relationship between diet quality and brain expansion is supported by evidence that, in primates, large brains and neocortices are associated with omnivorous feeding strategies, which require complex extraction strategies (Byrne and Whiten 1988; Dunbar 1996). Further support comes from the finding that frugivores have larger brains than foliovores and that the former have larger home ranges, which may require more computational power due to the greater demands that frugivory makes on spatial reasoning (Dunbar 1996).

Much research on human brain expansion has thus focused on diet. Several lines of evidence indicate that the Australopithecine-*Homo* transition was characterized by increased consumption of energy- and nutrient-dense foods such as meat, nuts, and tubers. Tooth enamel analysis indicates that at least some Australopithecine species were omnivorous and that early *Homo* moved in the direction of increased dependence on animal foods (Balter et al. 2012). This finding is consistent with the pronounced reduction in posterior dentition and mandibular robusticity seen in early *Homo* (Leonard et al. 2007). Brain expansion almost certainly would have required an increase in the proportion of meat in the diet. This is because in mammals docosahexaenoic acid (DHA) and arachidonic acid (AA) are essential to brain growth (Leonard et al. 2007) and, on the African savanna, only wild ruminants provide moderate to high amounts of these nutrients (Leonard et al. 2007). Other good sources of DHA and AA are freshwater fish and shellfish,

but there is little evidence of their regular exploitation until much later in human evolution (Leonard et al. 2007). Cooking is another means of increasing dietary quality, but there is scant evidence for the control of fire before 1.5 ma (Leonard et al. 2007). A modest proportion (10–20 %) of meat in the diet would have been sufficient to support initial brain expansion (Leonard et al. 2007); however, modern forager diets indicate that a higher proportion of 45–65 % was needed to support expansion to *H. sapiens* levels (Cordain et al. 2000).

The social brain hypothesis argues that the dietary shift removed an energetic constraint on brain expansion, but was not a causal factor (Dunbar 1996; Leonard et al. 2007). While conceding that ecological selection pressures may have contributed somewhat to this process, Dunbar (1996) argues that the cognitive demands of the human feeding niche are not significantly greater than those of other primates. In a test of three versions of the ecological hypothesis, he found that neither the percentage of fruit in the diet, size of home range/length of day journey, nor degree of extractiveness in the diet predicted neocortex size in nonhuman primates. In contrast, neocortex size was positively correlated with social complexity, operationalized as group size. Using human neocortex volume to extrapolate a value for human group size from the primate equation, Dunbar predicted an average group size of 150, operationalized as a set of people who know everyone in the group as individuals. A survey of traditional forager and small-scale horticultural societies found that group size reliably hovers around 150. The same pattern is evident in the earliest farming villages in the fertile crescent, in twentieth-century Hutterite farm communities, and in modern horticulturalist villages in southeast Asia and South America (Dunbar 1996). In Western industrialized societies, many cooperative networks and units, such as church congregations and military companies, average around 150 members (Dunbar 1996). Further evidence that hominid brain expansion was driven by the demands of monitoring and managing the social environment comes from research on ability to track multiple-order intentionality. Tests

show that, beyond 4th-order intentionality, error rates increase significantly (Dunbar 1996), suggesting that processing multiple-order intentionality is computationally taxing.

The social brain hypothesis has been criticized on the grounds that it underestimates the cognitive software demanded by human foraging methods, a claim supported by research indicating that human extractive efficiency is nearly double that of nonhuman primates (Gaulin and Konner 1977). On this point, treating degree of diet extractiveness and social complexity as discrete phenomena obscures a key feature of the human ecological niche: the extraction of resources using complex techniques *and* cooperation. Use of these strategies enables humans to bypass their anatomical limitations and acquire resources that would otherwise be prohibitively costly or dangerous to access (Tooby and DeVore 1987; Kaplan et al. 2000). The use of these techniques is scaffolded by an extensive range of skill and knowledge sets: Human foragers depend so heavily on the acquisition, generation, transmission, and application of information that the foraging niche has been characterized as a “subsistence economics of information and knowledge use” (Barrett et al. 2007, p. 242). The quantity of information demanded by complex extraction exceeds an individual’s ability to acquire it by the onset of sexual maturity through first-hand experience alone (Boyd et al. 2011). The solution that evolved in response to this problem is social learning: Studies of cultural transmission in forager groups indicate that the bulk of subsistence-related skill and knowledge sets are acquired from conspecifics (Hewlett and Cavalli-Sforza 1986). Social learning greatly reduces the time and energy costs as well as the dangers of acquiring information through feedback learning.

Research in developmental and cognitive psychology indicates that a considerable proportion of human cognitive architecture is dedicated to the task of information extraction and transmission (Barrett et al. 2007). For example, the ability to reason counterfactually enables humans to generate new knowledge through experimentation and invention (Barrett et al. 2007). This capacity

enables the generation of mental models (Tooby and DeVore 1987), including representations of past, future, and possible scenarios (see entry on Narrative). These models reduce extractive risk and increase extractive efficiency by making it possible to simulate possible problems and test the effectiveness of alternative responses (Tooby and DeVore 1987). The ability to reason counterfactually emerges at around 15 months (see entry on Narrative), which is what we would expect if occupation of the foraging niche were dependent on the production and deployment of complex extraction techniques. Similarly, the ability to share attention emerges near the end of the first year of life (Baron-Cohen 2005), which is what we would expect if the foraging niche required a long learning period supported by information transmission. Social learning also requires shared intentionality or the ability to attain a goal by inferring the goal and copying the relevant actions of a conspecific (Tomasello et al. 2005). This in turn depends on the ability to make inferences about the mental states of conspecifics, or theory of mind. Theory of mind is integral to the acquisition of language, which greatly increases the efficiency of information transmission (Barrett et al. 2007), thereby facilitating teaching or *ostensive communication* – the demonstration of knowledge by experts and the recognition of this behavior by novices (Csibra and Gergely 2009). More broadly, theory of mind enables the strategic deployment of information to manipulate the beliefs, affective states, and behavior of conspecifics (Humphrey 1976; Byrne and Whiten 1988), which is useful for the transmission of precautionary information to children (Scalise Sugiyama 2011) but can also be used for darker purposes, such as tactical deception. And finally, social learning is subserved by an elaborate suite of mechanisms dedicated to social exchange (Cosmides and Tooby 2005). Although they most likely evolved in the context of food transfers, these mechanisms enable the exchange of resources of all types, including information. Additionally, the ability to cooperate in groups exponentially increases the productive capacity of human labor (Barrett et al. 2007), thereby

enabling social groups to accumulate and maintain vast stores of knowledge (Scalise Sugiyama 2011).

The interdependence of complex extraction and cooperation is illustrated by a fundamental problem posed by tool manufacture: The processes involved in making and/or utilizing complex extraction techniques cannot be inferred from the technology itself. This has led some researchers to hypothesize that language evolution was driven, at least in part, by the benefits of increased accuracy and efficiency in the transmission of tool technology (Csibra and Gergely 2009, p. 148). Experimental evidence supports this claim. Morgan et al. (2015) measured rates of transmission for Oldowan tool manufacture using five different learning techniques: reverse engineering, imitation/emulation, basic teaching, gestural teaching, and verbal teaching. The volume and quality of tools produced, and the rate at which they were generated, were highest in the verbal instruction condition. Conversely, little learning occurred in the reverse-engineering and imitation conditions. This finding attests to both, the complexity of human extractive methods and their pronounced dependence on cooperation.

The composition of the human forager diet points to the extractive challenges ancestral humans faced. Compared to other primates, humans are much more dependent on resources that require extensive knowledge to acquire. Kaplan et al. (2000) compared the chimpanzee and human forager diet on the basis of types of foods exploited: collected resources (foods that can be obtained and eaten simply by gathering them from the environment), extracted resources (nonmobile resources that must be separated from a protective context), and hunted resources (mobile resources that must be extracted and processed before consumption). While collected foods make up 95 % of the chimpanzee diet, they only account for 8 % of the forager diet. In contrast, the forager diet consists of 32 % extracted and 60 % hunted foods. Thus, 92 % of the human forager diet consists of extracted and hunted resources, compared to 5 % for chimpanzees. Additionally, compared to other animals,

humans exploit a greater diversity of prey species. A study of game taken between 1980–1996 found that Ache foragers utilized at least 78 different mammal species, 21 different species of reptiles and amphibians, probably more than 150 species of birds (more than the researchers were able to identify), and over 14 species of fish (Kaplan et al. 2000, p. 171). Humans also use a wider range of strategies and techniques to capture prey than other animals (Kaplan et al. 2000). Similarly, efficient exploitation of plant resources requires the ability to identify, locate, and process dozens of plant species, and to predict availability and abundance based on weather and growing conditions, while the use of food storage requires knowledge of preservation techniques such as drying and smoking (Scalise Sugiyama 2011).

Another measure of extractive complexity is children's ability to forage for themselves. Although, in some habitats and/or seasons, children are able to acquire considerable quantities of collected resources, data indicate that children cannot easily acquire extracted or hunted resources, or cannot acquire them in sufficient quantities to be self-supporting (Scalise Sugiyama 2011). In a comparison of three forager populations, Kaplan et al. (2000) found that difficulty of acquisition predicts the age profile of food production: High return rates for extracted and hunted resources are not reached until early-to-mid adulthood. In a range of biomes, peak foraging efficiency is not reached before the age of sexual maturity (Scalise Sugiyama 2011), and juvenile consumption exceeds production until the late teens or beyond (Kaplan and Robson 2002). If human extractive techniques were cognitively undemanding, we would expect children to become self-supporting much earlier in the lifespan.

Moreover, studies indicate that children's foraging ability is sharply limited by ecological constraints (Scalise Sugiyama 2011). High juvenile return rates tend to be associated with safe, easy-to-navigate environments or with foraging while accompanied by adults, which relieves children of the tasks of predator evasion, avoidance of environmental hazards, and wayfinding (Scalise

Sugiyama 2011). Research on children's foraging suggests that, in at least some habitats, skills auxiliary to foraging are not mastered until mid-to-late adolescence (Scalise Sugiyama 2011). Additionally, as Kaplan et al. (2000) note, humans exploit much larger territories (200 km² or more) than chimpanzees (10 km²), which may compound the cognitive demands of spatial reasoning. Evidence also points to qualitative differences between chimpanzee and human foraging cognition: Chimpanzees are capable of memorizing the location of potential food sources and using mental maps to locate them later; however, they appear to be incapable of finding food patches without prior knowledge of their existence (Wrangham 1977). Humans, in contrast, can predict probable locations of food resources based on the properties of known locations (Mithen 1996).

The foraging niche poses social challenges as well: Forager subsistence practices are dependent on the use of complex cooperative strategies. Food sharing is a case in point. Human life history is characterized by both inter- and intragenerational food transfers (Kaplan et al. 2000). The prolonged juvenile period, for example, is made possible by extensive male provisioning of females and offspring (Kaplan et al. 2000). In many forager societies, foraging risk is managed by the sharing of subsistence information: For instance, hunters add to their store of knowledge by observing other males and listening to them recount their hunting experiences (Scalise Sugiyama 2011). Similarly, subsistence stress is mitigated by within- and between-group exchange networks that mandate resource sharing among members, including territory (e.g., Minc 1986) and information regarding resource availability and location (Heffley 1981). Additionally, cooperative hunting is widely used to increase the chances of acquiring game or to acquire game in larger quantities (e.g., game drives; Anell 1969). And across forager societies, oral tradition is used to inculcate social norms prescribing generosity and industriousness, and proscribing selfishness and sloth (Scalise Sugiyama 2011). Food sharing is also used to manage the risk of starvation during periods of illness or

injury (Gurven et al. 2000; Sugiyama and Chacon 2000). To effect these strategies, humans must acquire, process, integrate, store, and retrieve large quantities of social information. This task is compounded by the fact that social relationships are in constant flux, which means that individuals must continually update their mental map of the social environment.

However, the physical environment is in continual flux as well: Animals move, hide, and migrate; plants grow, ripen, and die; and weather and topography change with the seasons, cataclysmic events, and long-term fluctuations. Thus, occupation of the foraging niche depends on access to both ecological and social information. This makes it difficult to dismiss the ecological hypothesis out of hand. Dunbar suggests that one way to disentangle these selection pressures is to examine the content of conversation. If language evolved in response to the demands of cultivating and maintaining alliances, he reasons, we would expect conversation to be devoted primarily to the exchange of social information.

Studies in modern industrialized societies indicate that this may be the case: Roughly two thirds of conversation time is dedicated to the transmission of social information (Dunbar 1996). The majority (65 %) of this information consists of social experiences, half of which concern the speaker or his/her audience and half of which concern individuals who are not present (Dunbar 1996, p. 176). Wiessner (2014) found a similar proportion of social information in the daytime conversations of !Kung foragers: 31 % of conversation addressed economic matters (e.g., foraging plans, resource availability, hunting strategies, technology), while the remainder focused on complaints and criticisms of behavior (34 %), joking (16 %), land rights (9 %), stories (6 %), and interethnic relations (4 %). Interestingly, nighttime conversation was heavily biased toward storytelling (81 %). Although Wiessner claims that these stories did not contain much environmental information, Biesele notes that “much subsidiary information about the behavior of animals, the habitats of plants, and the customs of humans regarding them is tucked within” !Kung stories,

and “appears to be utilized later as part of a general fund of knowledge” (1993, p. 45). Tellingly, the stories in Wiessner’s study “almost always described what people were eating at the time of the event” (2014, p. 14029). The blending of social and economic information in forager storytelling suggests that conversational accounts of “social experiences” might encode ecological information, and that using content analysis to disentangle the selection pressures involved in language evolution is not a straightforward matter. Moreover, given the substantive proportion of forager conversation devoted to economic topics, the higher proportion of social information does not rule out the possibility that language evolved in part to meet the demands of complex extraction. The widespread use of storytelling by foragers to transmit ecological information (Scalise Sugiyama 2011) supports this claim, as does the use of vocalizations by nonhuman primates to communicate both social and ecological information. For example, vervets use different calls depending on whether they are approaching a dominant animal or a subordinate one, yet also use calls specialized for the ecological threat of predation: One type is used for terrestrial predators such as leopards, another type is used for aerial predators such as eagles, and yet another type is used for snakes (Dunbar 1996).

Conclusion

The functionally heterogeneous nature of the human mind (Barrett et al. 2007) argues against a monolithic explanation for brain expansion. As with the rest of the body, the brain was subject to different selection pressures at different times over the course of hominid evolution. Similarly, the use of complex extraction techniques that include cooperation argues against a content-centered model of language evolution. The use of language to transmit both ecological and social information suggests that there was selection not for the communication of a specific type of content, but for the communication of mental representations (Tooby and DeVore 1987; Barrett

et al. 2007). This view is in keeping with evidence that the mind has evolved intuitive ontological categories: domain-specific learning rules and inference systems for reasoning about different types of entities in the world, such as artifacts, natural kinds, and agents (Boyer and Barrett 2005). The existence of such mechanisms attests to the evolutionary importance of the information domains they serve. If it is beneficial to store information from all of these domains, it stands to reason that it is beneficial to share information from all of these domains.

Two time-tested models that take a holistic approach to hominid brain expansion are the cognitive niche hypothesis and the embodied capital hypothesis. The former focuses on mapping the design of the mind, arguing that the cognitive abilities that appear to be unique to (or more highly developed in) humans are largely dedicated to the generation, extraction, storage, organization, integration, and exchange of information (Tooby and DeVore 1987; Barrett et al. 2007). The latter focuses on mapping human life history evolution, arguing that the increase in information-processing capacities coevolved with long lifespan, prolonged juvenility, and inter- and intragenerational resource transfers as hominids moved into a skill- and knowledge-intensive feeding niche (Kaplan et al. 2000). For over thirty years, these cross-disciplinary models have provided a structurally sound foundation for the generation and testing of hypotheses regarding the ecological and social selection pressures posed by ancestral human environments, suggesting that an integrated approach to hominid brain expansion and language evolution is the surest path forward.

Cross-References

- Cultural Transmission
- Language
- Life History Theory
- Narrative
- Relative Brain Size, Encephalization Quotient
- Social Intelligence Hypothesis, The
- Social Learning

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Gossip and Indirect Reciprocity

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Synonyms

Cooperation; Good standing; Reciprocal altruism; Trust

Definition

Gossip is a way of communicating our thoughts about other people: thoughts which can be negative or positive. Indirect reciprocity is helping someone, with the belief the favor will be later returned by a third party. Gossip and indirect reciprocity are linked together through cooperation, trust, and reputation.

Introduction

Evolutionary perspectives have had trouble pinpointing why cooperation among strangers with an uncertain future of meeting again still occurred. Richard Alexander coined the term “indirect reciprocity” to explain why these instances kept happening among individuals (Nowak and Sigmund 1998). Indirect reciprocity is when a person helps someone with the expectation of the favor being returned later from a third person. Alexander (1987) asserted indirect reciprocity involves reputation and status, the underlying theme being people care about what others have to say about them. Since indirect reciprocity takes place among multiple people, gossip, cooperation, and trust are all valued.

Individuals gain such things as reputation, status, and trust through gossip. Gossip is what

people say about others when they are not present. We tend to think of gossip in a negative manner, but positive outcomes can result from gossip and indirect reciprocity. For example, avoiding negative gossip and its consequences can foster cooperation and other prosocial behaviors (Feinberg et al. 2014). When people gossip in a positive way (i.e., describing a positive attribute), they can build trust among peers, which can result in cooperation, reciprocity, and reputation (Sommerfeld et al. 2008). When someone gossips in a negative way, they tend to be ostracized, and later, they will be compelled to cooperate more with the group (Feinberg et al. 2014). Very simply, people like those who do good and say good. Those who cooperate and do good acts will later receive indirect benefits from third parties (Wu et al. 2016). Thus, people gain indirect reciprocity through reputation. Since indirect reciprocity is based on reputation, people need to gain trust and reputation through cooperation and gossip (Nowak and Sigmund 2005).

Nowak and Sigmund (2005) presented a model of indirect reciprocity based on image scoring. During indirect reciprocity games, participants were given “scores,” and other members would view their scores. This perspective helps study the role of observers assessing the reputation of donating players (Mohtashemi and Mui 2003). It was later argued that Nowak and Sigmund’s model did not fully explain indirect reciprocity. Leimar and Hammerstein (2001) argued their model failed to represent the true strategy interest of an individual. They proposed individuals could be interested in a “good standing” strategy. People want to be good, and they also want to show others they are good.

Other indirect reciprocity games like the prisoner’s dilemma and public good games provide a better understanding of indirect reciprocity. Nowak and Sigmund (2005) summarize players are willing to contribute to public goods but eventually stop their willingness after a few rounds. This is changed when participants understand their reputation will be communicated among other players. Again, gossip takes place in an indirect reciprocity game, and this is important to participants because if they are not cooperating,

their reputation could be at stake. The result could be ostracism from the group.

Conclusion

Gossip and indirect reciprocity are beneficial to people who are willing to cooperate with others. If not, people will be ostracized from their group, but it has been explained that individuals who are ostracized will be more compelled to cooperate as a result (Feinberg et al. 2014). Different models have explained why people are willing to cooperate to gain indirect reciprocity, trust, and reputation. People who gossip in a positive way and are willing to cooperate and show trust can gain reputation and later be benefited from indirect reciprocity. In the end, if you do good for someone, eventually, that good will come full circle.

Cross-References

- [Adaptations to Avoid Ostracism](#)
- [Altruism Advertises Cooperativeness](#)
- [Altruism Advertises Generosity](#)
- [Altruism Defined by Benefits Conferred](#)
- [Altruism Norms](#)
- [Cooperation](#)
- [Evolution of Cooperation](#)
- [Evolution of Reciprocal Altruism](#)
- [Gossip, Rumors, and Social Exclusion](#)
- [Indirect Benefits of Altruism](#)
- [Indirect Reciprocity](#)
- [Ingredients of Reciprocal Altruism](#)
- [Nonhuman Reciprocal Altruism](#)
- [Prosocial Behavior](#)
- [Reciprocal Altruism](#)
- [Reputation](#)
- [Reputation and Altruism](#)

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Gossip, Rumors, and Social Exclusion

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Synonyms

[Disguised aggression](#); [Indirect aggression](#)

Definition

Forms of social and verbal aggression

Introduction

Folk wisdom suggests that women engage in gossip and spreading of rumors more than men do. The evidence however is unclear, with adolescence being the only stage of life when females seem most likely to engage in gossip and spreading of rumors more than males (Archer 2004). However, the extreme consequence of gossip and spreading of rumors is social exclusion. Theory and evidence suggest that girls and women

may employ social exclusion of unrelated same-sex peers more than boys and men do (Benenson 2013).

The Functions of Gossip and Rumors

Gossip and spreading of rumors constitute an aggressive strategy that allows the perpetrator to manipulate the reputation, status, and relationships of a target. Because innuendo is frequently utilized, gossip and spreading of rumors constitute a powerful form of aggression unconstrained by objective evidence. Further, because the target typically is not present, harm is inflicted on a target with no opportunity for self-defense. A target's reputation therefore can be destroyed by dissemination of accurate or false information. Because the target has no possibility of providing a differing perspective, situating actions with a broader context, or recruiting the support of allies, the perpetrator is free to shape the impression of the target without any verification of facts. The requisite absence of the target means that by definition, the target has been excluded, at least temporarily.

In addition to harming the reputation of the target, gossip and spreading of rumors can also damage or sever the bonds between the target and his or her allies. By persuading listeners to believe the validity of defamatory information, the perpetrator can indirectly or directly suggest that social connections to the target be weakened or dissolved. If the perpetrator's claims appear serious enough, then the listeners jointly can decide to exclude the target from the social milieu permanently. Once a target's reputation has been maligned severely enough, listeners typically do not contradict the perpetrator, so as to avoid tarnishing their own reputations thereby risking their own social ties.

Theoretical Advantages of Social Exclusion to Females

Social exclusion likely is utilized most frequently when the perpetrators derive no benefit from

cooperating with the target and may even benefit from the target's absence. This requires an ecology in which individuals are not cooperating to obtain resources or more generally engaging in joint enterprises or in which specific individuals do not appear capable of contributing to the common goal. Societal institutions which require cooperation cannot afford to exclude valuable allies, especially energetic, reliable, skilled, and social individuals.

Because cross-culturally men typically have cooperated with unrelated same-sex peers during lethal inter-group aggression as well as in numerous community institutions, including governments, religious organizations, and other societal institutions (Baumeister 2010; Wrangham and Peterson 1996), social exclusion of unrelated same-sex peers may be particularly damaging to men's interests. Inter-group contests typically are won through strength in numbers, so exclusion can be beneficial only when extra individuals cannot make any contribution to the common good.

Women, in contrast, cooperate more with kin spouses, and affines who provide critical assistance with child care. These individuals share genetic investment in a woman's children, so benefit from investing in ensuring their well-being. Women then would be expected to preserve relationships with individuals who provide assistance with child care and who share genetic investment in her children. Unlike unrelated men who jointly defend and aggress against external groups, the presence of unrelated women does not provide the same benefit. Rather, unrelated women often deplete social and material resources for a woman and her children.

A classic example is when adolescent girls and women compete for long-term mates. In monogamous and polygynous communities, a woman must best other women to form a long-term pair bond. A husband who invests in her and their children will greatly increase a woman's probabilities of survival and reproductive success (Rucas et al. 2012) and of her children's thriving in modern societies (Amato and Gilbreth 1999). Maintenance of the pair bond further requires repelling additional

women. In polygynous communities, unrelated women compete continuously for material resources and emotional investment of their common husband (Jankowiak et al. 2005). Regardless of type of pair bond, a woman and her children benefit from reducing the presence of other women. Females' preference for interaction with one other individual at a time begins in early childhood where they interact in more exclusive one-on-one same-sex friendships compared to males who prefer larger, more interconnected groups of same-sex friends (Fabes et al. 2003).

Gossip and rumors that result in social exclusion constitute a valuable aggressive strategy for females for an additional reason: Social exclusion is an unusually safe form of aggression. Because females' continued investment in children exerts a greater effect on future reproductive success compared to males' investment, females must take greater care to protect their well-being (Campbell 1999). Responsibility for protection of children from proximate threats also typically falls to mothers. Reducing risk therefore is more critical for females than males. By requiring allies and outnumbering a lone target, social exclusion diminishes the probabilities of both immediate physical injury and future retaliation. Social exclusion thereby provides a means of eliminating rivals without endangering a woman or her children.

Because social exclusion often may be carried out by unrelated females, girls and women do benefit from maintaining a close bond with one or two same-sex friends whom they trust. Together, females may select a target and employ gossip and rumors, and perhaps social exclusion, to expel a rival. At the same time, a girl or woman is protected from social exclusion simply by the presence of a close, loyal friend. In order to reduce the probability of retaliation, social exclusion typically is directed against lone targets. Thus, same-sex friendship is extremely important to females in middle childhood and early adolescence before they form a pair bond (Benenson 2013). In the presence of kin husbands, or affines, however, the role of a close female friend is diminished.

Conclusion

In conclusion, gossip and rumors likely are employed as aggressive strategies by both sexes but may be utilized by females more than males in adolescence when human females typically form pair bonds. Social exclusion may result when gossip and rumors lead to severe damage to an individual's reputation and hence promote the severing of ties to the target. Females benefit more than males from social exclusion of unrelated same-sex peers because an exclusive pair bond provides critical social and material resources to a woman and her children, and social exclusion can be safely executed without fear of physical harm.

Cross-References

- [Cost of Same-Sex Friendships](#)
- [Derogation of Rivals](#)
- [Female-Female Competition](#)
- [Pair-Bonding](#)
- [Paternal Investment Relative to Maternal Investment](#)
- [Reputation](#)
- [Same-Sex Coalitions That Exclude Women](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Verbal Derogation among Women](#)
- [Women's Use of Direct Versus Disguised Social Aggression](#)

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Governmental Public Archives

- [Public Records](#)

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Gradually Deprive of Mother's Milk

- [Weaning](#)

Grammar

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Synonyms

[Sentence structure](#); [Syntagmatic relations](#)

Definition

Grammar is a combinatorial computational procedure that can generate an infinite number of novel expressions from a finite set of building blocks.

Introduction

Acquiring a language involves learning its grammatical rules that combine the words to create new utterances. The discussions surrounding the acquisition of grammar have so far mainly focused on the relative contributions of children's innate endowment and the environmental input they receive to their success at the language-learning task. It is clear that the cognitive underpinnings of the *ability* to acquire language must be encoded in the human genome, as this ability is unique to humans. Considering that humans acquire different languages depending on their experience, it follows trivially that environmental stimuli also play a role in shaping language development. The real challenge, however, is to figure out which aspects of the grammar – if any – require postulating an innate Universal Grammar that pre-specifies the structural principles of language and which aspects can be constructed in a piecemeal fashion by processing the regularities in the environmental input via domain-general mechanisms, without needing innate language-specific constraints. In what follows, the arguments that have been advanced in favor of both nativist and emergentist/constructivist viewpoints will be introduced.

Innate Principles: Argument from the Poverty of the Stimulus (PoS)

In linguistics, nativists have long advocated that humans' knowledge of the grammar of their language surpasses what they could have reasonably learned by listening to the linguistic input they were exposed to. The ensuing argument, called *argument from the poverty of the stimulus (PoS)*, was that the knowledge of any grammatical principle that lacked evidence in the input had to be

innate. A classical example cited in this context is the *principle of structure-dependency*. Chomsky (1971) has argued that, upon encountering the sentences “The dog in the corner is hungry” and “Is the dog in the corner hungry?,” a speaker could posit two rules to explain how the interrogative sentence was derived from the declarative. First, she could hypothesize that the *leftmost auxiliary* in the declarative sentence was moved to the sentence-initial position to form a question. This would be a *structure-independent* rule, as it relies on linear order. This rule, however, fails to generate the correct interrogative if the declarative is a complex sentence with a relative clause, such as “The dog that is in the corner is hungry.” To derive the correct question in this case, the speaker must hypothesize a rule that relies on the hierarchical structure of the sentence and not on the linear order of the constituents (i.e., a *structure-dependent rule*), such as “move the auxiliary of the main clause to the sentence-initial position.” It was claimed that even 3–5-year-old children never made any errors that would indicate that they were following a structure-independent rule for forming the interrogatives of such sentences, even though they may not have encountered these forms in the speech directed to them. This was thought to show that children possessed the innate knowledge that grammar is structure-dependent (Crain and Nakayama 1987). But it should be noted that a later study by Ambridge et al. (2008) has shown that children do produce interrogative sentences that violate structure-dependency, albeit rarely. These authors contended that the absence of these errors in Crain and Nakayama's study might be related to the near-exclusive use of the auxiliary *is* in their test sentences, with which children are particularly proficient.

Other assumptions that the PoS argument relies on, too, have been called into question in subsequent research. For example, by presenting a simple recurrent network (SRN) with incremental language input, Lewis and Elman (2002) trained it to predict the syntactic category of the next word to come in the sentence. Crucially, the training set did not contain questions with subjects modified by a relative clause (e.g., *Is the boy who is smoking crazy?*), because these were precisely

the structures that might serve as evidence for structure-dependency, which were argued to be missing in the input. Lewis and Elman (2002) demonstrated, however, that the SRN predicted an auxiliary (e.g., *is*) and not a participle (e.g., *smoking*) after “seeing” the relativizer *who*, even in the absence of this direct evidence. As the strings predicted by the SRN conformed to a structure-dependent grammar, it was argued that a structure-dependent grammar could simply be learned by utilizing the stochastic regularities in the input. Later, a study by Real and Christiansen (2005) has shown that simple statistical models that exploit bigram and trigram frequencies (i.e., the co-occurrence statistics for two-word and three-word sequences) that were trained on a set of utterances extracted from a corpus of child-directed speech could also successfully choose structure-dependent interrogatives over ungrammatical interrogatives, because the bigram and trigram frequencies revealed the former to be much more probable. Furthermore, Perfors et al. (2011) have contested the nativist claim that linear grammars were simpler and that children would therefore hypothesize a linear grammar and commit structure-dependency errors if they did not have an innate bias for favoring hierarchical structures. These authors have pointed out that hierarchical grammars sacrifice simplicity in return for “goodness-of-fit” to the data and unlike linear grammars, a hierarchical phrase-structure grammar can also generalize beyond the input (e.g., extrapolating the transformational rules for forming complex interrogatives from simpler structures) – the crucial ability that lies at the heart of the PoS problem. These points run counter to the prediction that a linear grammar would be the first hypothesis for a naive learner to entertain. As a matter of fact, Perfors et al. (2011) showed that a rational Bayesian learner will prefer a hierarchical grammar over a linear one when confronted with actual language input. Similarly, a child learner may also never entertain a linear grammar to begin with, as the input strongly favors a hierarchical grammar. These findings suggest that environmental stimuli may not be too impoverished to support conclusions about structure-dependency, after all.

While this does not preclude the possibility of there being an innate constraint of structure-dependency, it should be remarked that learning accounts are superior to accounts that postulate innate constraints, *ceteris paribus*, as they are more parsimonious. Also, even if humans have an innate bias for adhering to structure-dependency, this bias may not be language-specific. For example, there is evidence that humans perceive and process hierarchical structures in music as well (Koelsch et al. 2013). So, it should be kept in mind that processing structural dependencies may well be a domain-general capacity.

Parameters: Explaining Language Variation

While the universal properties of languages have been designated as *principles* in the generativist tradition, language variation has been dealt with via *parameters*. One example would be the pro-drop or null-subject parameter, which specifies whether a language allows phonologically unrealized subjects. For instance, English is a non-pro-drop language, hence the sentence *John eats an apple* is grammatical, while the string **eats an apple* would be ungrammatical. The Italian counterpart of this string (i.e., *mangia una mela*), however, is grammatical, since Italian allows omitting subject arguments; because the rich inflectional system of Italian can represent the subject via person agreement markers on the verb.

As children have the capacity to acquire any language, they cannot have the correct parameter setting for the language of their community pre-specified at the outset. Rather, children will have to *set* their parameter to the correct value upon encountering relevant evidence in the input, the argument goes. Thus, for an English child who makes subject-omission errors, one example of a “triggering” input that is needed to learn that her language is non-pro-drop may be the presence of semantically vacuous subjects in sentences such as “It rains.” The expletive subject *it* has no purpose other than fulfilling a syntactic requirement, and indeed, in Italian where lexical subjects are

syntactically not required, statements about weather lack a subject, e.g., *piove*, “*rains.” Hyams (1986) has observed that English-speaking children cease to make subject-omission errors at around the same time they start using expletive subjects and concluded that the co-occurrence of these events showed that English-speaking children set their parameter to non-pro-drop on the basis of exposure to this triggering input.

One problem that needs to be tackled, however, is whether “parameter-setting” constitutes an instantaneous and discrete change in a child’s grammar as it tends to be represented in some traditional accounts, or whether it is a continuous and rather unsteady process. As a matter of fact, there is some evidence that young English-speaking children’s argument-omission errors might stem from a sensitivity to the discourse status of arguments. In a sentence-repetition study conducted with 3–4-year-old English-speaking children, Graf et al. (2015) found that children never dropped a subject (or any other constituent, for that matter) when it was used contrastively, e.g., the subjects in the coordinated structure “the pig throws the pillow and the ladybird throws the pillow” were not omitted, but the objects occasionally were. This shows that the relative informativeness of arguments guides children’s syntactic decisions, even though the result may be ungrammatical in the adult language. While children eventually need to overcome this pragmatic bias to attain the adult grammar, this is much more likely to be a gradual process than a rapid and abrupt one.

The same reasoning presumably applies to the acquisition of the canonical word order in one’s language. For example, in head-initial languages such as English, the verb (i.e., the head of a verb phrase) precedes its object (i.e., its complement), while in head-final languages such as Japanese this ordering is reversed. According to a strong interpretation of the parameter-setting account, English-speaking children should converge on the SVO word order of their language at an early age. Objecting to this proposal, Akhtar (1999) has demonstrated that English-speaking children below the age of 4 were willing to use made-up

verbs in sentences with SOV and VSO orders if these verbs had first been introduced in these syntactic frames by the experimenter; though they were more likely to “correct” the word order used by the experimenter, if the verb was familiar. But 4-year-olds predominantly used the SVO structure, with novel and familiar verbs alike. This shows that, while children may have formed an abstract syntactic generalization about the word order of their language by age 4, younger children’s “syntactic” knowledge may still be lexically specific and unproductive; and this conclusion is not compatible with a strong version of a parameter-setting account where a rapid and discrete change happens in the child’s grammar by exposure to input. Thus, as both the non-nativist learning accounts and the parameter-setting account concede, many aspects of language will be learned from the input; but the two lines of thought crucially differ in the quantity of data that will be required for learning, as well as the developmental trajectory in grammar acquisition.

While the principles and parameters account provides an insightful and convenient shorthand for describing the diversity and the putative underlying uniformity of the world’s languages, it is important to note that the linguistic variation that is observed cannot be easily characterized by a handful of binary parameters. In fact, according to the latest estimates, the total number of parameters may amount to thousands; and linguists can hardly agree on what to include in their list of parameters (see Dąbrowska 2015). As far as language acquisition is concerned, it is clear that children revise their hypotheses about the grammar of their language as they encounter new data that may be unexplained by their current hypotheses, yet given the uncertainty surrounding the concept of parameters, it may be best to remain agnostic as to whether this revision process is the same as what nativists have in mind when they refer to parameter-setting.

Conclusion

Knowing the grammar of a language entails knowing its rules. Two central questions in the

field of grammar acquisition are (1) whether any grammatical rules are unlearnable from the input and must therefore be innate and (2) how a child can extract grammatical rules from the input. Current evidence for innate grammatical principles is sparse, and recent research suggests that, even if there arises a need for postulating some innate constraints for learning grammar, it is probable that these constraints will be domain-general rather than language-specific. There is also accumulating evidence that children may draw upon both their cognitive capacity to statistically analyze the language input and their sensitivity to discourse-pragmatic constraints in figuring out the grammatical rules of their language.

Cross-References

- [Cognitive Development](#)
- [Field of Linguistics, The](#)
- [Language Acquisition](#)
- [Language Development](#)

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Grammaticalization

- [Spontaneous Language](#)

Grammaticalization Theory

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Synonyms

[Grammaticization](#); [Grammatization](#).

Definition

Grammaticalization is the gradual historical process through which grammatical items are created.

Introduction

Grammaticalization is the continuous, gradual, historical process through which languages generate grammatical material like affixes, articles, pronouns, and prepositions. The emergence of grammatical items is not arbitrary or sudden: they are not invented, as terms for new objects and activities often can be, but instead develop from already existing lexical items which are gradually modified to express increasingly

grammatical meanings. This entry describes (1) the specific mechanisms of historical language change which underpin grammaticalization, (2) the major competing explanatory accounts of grammaticalization, (3) the pathways of change along which grammaticalization takes place, and (4) current issues and recent developments in grammaticalization research.

Grammaticalization

Grammatical items have a largely functional role in language, such as marking tense and agreement (e.g. past tense marker *-ed*, plural marker *-s*), identifying participants in the discourse (e.g. *she*, *this*) and indicating the connections and structural relationships between them (e.g. *and*, *with*, *behind*). They can be usefully distinguished from lexical items, which by contrast carry meaningful semantic content (e.g. *tortoise*, *move*, *slow*), and typically describe things, events, and qualities. Lexical items make up the vast majority of the words in every language and are primarily phonologically and syntactically independent; grammatical items, by contrast, are typically syntactically dependent on other items and often phonetically reduced (e.g. the future tense marker *'ll*, the negative particle *n't*). Grammaticalization therefore describes specific changes in the properties of linguistic items from those characteristic of lexical items to those characteristic of grammatical items; through this process, the items themselves become increasingly grammatical (Heine and Kuteva 2002). Importantly, grammaticalization does not happen to single words in isolation, however, but rather to sequences of words or linguistic constructions in specific repeated discourse contexts where they become automated, processed as single chunks of language, and gradually lose their independence of use.

Mechanisms

Grammaticalization has been described as the interaction of four independent but interconnected mechanisms of linguistic change, namely context extension, semantic bleaching, decategorialization, and phonetic erosion (Heine and Kuteva 2002),

which are seen as “different components of the one and same general process [of grammaticalization]” (Heine 2003, p. 579). The canonical example of grammaticalization in the literature is probably the development of the English future construction *be going to* (Heine et al. 1991; Hopper and Traugott 2003; Hoefler and Smith 2009). Historically, this construction had a transparent contentful meaning of MOTION combined with PURPOSE, but it has over time developed additional meanings, firstly of INTENTION and then of PREDICTION, and is, in today’s modern English, most frequently used as a purely grammatical marker of the future tense. Examples of its usage with these three indicative meanings are shown in Ex. (1a–c), which also serve to illustrate the historical progress of the construction from earliest to latest.

- (1) a) I am going to see the bishop.
PURPOSEFUL MOTION
b) I am going to stay here.
INTENTION
c) It is going to rain.
PREDICTION (FUTURE)

Several relevant parallel developments which are characteristic of grammaticalization can be observed in the changing properties of the *be going to* construction shown above. During grammaticalization, meanings frequently change from more specific to more abstract; the loss of semantic content in the construction is often called *desemanticization* or *semantic bleaching* (Heine and Kuteva 2002). The earliest usage in (1a), for instance, has multiple possible interpretations, depending on the context in which it is uttered. In addition to its original meaning of ‘I am moving with the purpose of seeing the bishop’, it can also be interpreted with either of the newer meanings ‘I intend to see the bishop’ and ‘I will see the bishop’. The middle usage in (1b), however, can be interpreted either as ‘I intend to stay here’ or ‘I will stay here’, but not as PURPOSEFUL MOTION, while the most recent construction in (1c), by contrast, can *only* be interpreted with the future meaning ‘it will rain’. In general, earlier constructions will allow newer interpretations, but newer constructions will not allow the older

interpretations. Moreover, the newer, more abstract meanings only gradually supplant the older meanings, which can therefore coexist alongside each other in the appropriate contexts for considerable periods of time, an effect known as *layering* (Hopper and Traugott 2003) or *overlapping* (Heine et al. 1991).

Closely connected to the gradual development of increasingly generic meanings is the phenomenon of *extension*, which describes how the construction is used in increasingly more contexts, becoming more schematic and less syntactically restricted in the process. With the meaning of PURPOSEFUL MOTION, for instance, the original *be going to* construction had two key restrictions: it could be used only with certain main verbs, and only with animate subjects. These restrictions were a direct result of its meaning: it only makes sense to talk about people ‘going to do things’ if they can move independently and with purpose. As the secondary meaning of INTENTION became more prominent, however, it became possible to use the construction also with main verbs like *stay*, when the original interpretation with PURPOSEFUL MOTION would have been impossible, because of the explicit contradiction between the meanings of *go* and *stay*. In fact, it is only when a construction is used in a context where an older meaning is not interpretable that such an extension can be definitively detected, and the change is then said to have been actualized. In modern English, *be going to* has of course been dramatically further extended, as its function has developed into a marker of the future tense, so that there are now no longer any restrictions either on its main verb or its subject: in Ex. (1c), indeed, the meaningless dummy subject *it* is now perfectly acceptable.

Characteristic of the later stages of grammaticalization is *phonetic erosion*, where the construction’s pronunciation is considerably reduced in prominence, and much of its internal phonetic substance can even be lost altogether. Phonetic erosion comes primarily from the construction being processed not as a sequence of individual words, but rather as a single linguistic unit; sequences which are pronounced within a single intonation unit are particularly susceptible to such

so-called chunking (Croft 1995). Chunking inevitably stimulates a loss of salience for the individual words in the construction, and their amalgamation into a single form with its own stress pattern, which is then frequently phonetically reduced as a simple consequence of being used frequently. In modern English, for instance, the future tense “I’m going to” is not usually pronounced as three individual words, but instead as “I’m gonna,” or even as “amna,” with its original form becoming increasingly obscured.

When words become fixed into a construction which is undergoing grammaticalization, semantic bleaching and phonetic erosion are often accompanied by *decategorialization*, where the individual words begin to lose some of the morphosyntactic properties which (used to) mark them as a member of their lexical category, perhaps even losing their status as independent words. The conjunction *while*, for instance, was originally a noun meaning a specific length of time (cf. “we played outside for quite a long while”), but it no longer has the characteristic properties of a noun when it is used as a conjunction introducing a subordinate clause (e.g. “we went out while they were playing”), and so cannot be accompanied by articles, quantifiers, or adjectives in this grammaticalized function.

Most of these interconnected mechanisms of grammaticalization are usually framed in terms of feature loss (e.g. of meaning content, of morphosyntactic properties, and of phonetic substance), but it is important to note that they can also be seen in terms of gaining new functions and meanings in ‘compensation’ for the loss. *While*, for instance, has gained the ability to be used to indicate a temporal relationship between two clauses, and *be going to* can be used in many more contexts as a future tense marker than as a verb signifying PURPOSEFUL MOTION. The development of these additional abstract meanings, and the extension of the contexts in which the constructions can be used, are, of course, some of the main features of grammaticalization.

Explanations

Two competing schools of thought offer different explanations for the fundamental origin of

grammaticalization: one identifies the cognitive process of metaphorical extension as the key mechanism (Heine et al. 1991), the other focuses on the reanalysis of existing linguistic items in appropriate pragmatic contexts (Hopper and Traugott 2003; Traugott and Dasher 2005).

Metaphorical language uses occurs in a situation where an existing linguistic form is used to express a novel meaning which is similar, but not identical, to its conventional, ‘literal’ meaning (Kövecses 2002). Extending the range of a word through metaphor requires creative conceptualization, or the ability to conceptualize one cognitive domain in term of another, to draw analogies between them based on their perceived similarity, and thereby to use a word associated with one meaning to express another meaning. Such creative expression of novel meanings is an extremely powerful linguistic tool, though it is far from exceptional, and indeed metaphorical deviations from conventional meanings are almost ubiquitous in everyday discourse (Deutscher 2005). The human body, for instance, provides an expedient template of reference points which have been used metaphorically in many languages, both to refer to spatially derived parts of a whole, and then, through grammaticalization, to yield spatial prepositions and adverbs, as shown by Ex. (2), which illustrates the development of the Swahili word **-bele* ‘breast’ into a noun ‘front part’ and then adverb ‘in front, ahead.’

(2) Swahili (Heine et al. 1991: 131)

a) *mbele* *ya* *gari* *lake* *ni* *nyeusi*
front of car his is black
‘The front part of his car is black’

b) *gari* *liko* *mbele*
car is front
‘The car is in front/ahead’

Through frequent repetition and memorization, metaphors become gradually entrenched in linguistic knowledge, until they can eventually be used without invoking the analogies needed for their original creation (Langacker 1987). Metaphor does not always lead to grammaticalization, of course, but when it is used to express an abstract domain in terms of a more concrete domain, it naturally results in the layering of

more generic meanings, context expansion, and thus the gradual development of grammatical material.

The second account of grammaticalization places its explanatory emphasis on context-induced reanalyses of linguistic material, which subsequently allow the gradual extension of contexts in which the construction is used (Traugott and Dasher 2005). The *analysis* of a linguistic form is a description of how the form is linked to its meaning; reanalysis occurs when these associative connections change in some way. Reanalysis can affect many different levels of language, from how the parts of the form are mapped to the parts of its meaning (e.g. the word *hamburger* used to be analyzed as “from Hamburg,” i.e. *Hamburg* + *er*, but was later reanalyzed as *ham* + *burger*, yielding novel words such as *cheeseburger* and *beefburger* by analogy), to whether parts of the meaning are better inferred from the context or are explicitly encoded in particular forms. In practice, the complexity of the mappings between individual forms and meanings, and of how a situational context might be conceptualized, means that any two analyses of any two situations will be almost inevitably different, so reanalysis, too, is effectively communicatively ubiquitous (Hoefler and Smith 2009).

On this latter account of grammaticalization, the future meaning of *be going to*, for instance, may have been originally inferred pragmatically from the fact that any purposeful movement to do something automatically implies that the activity will actually take place at some point in the future, meaning that both the (originally encoded) meaning of movement and the (naturally invited) inference of futurity would always be possible interpretations of the construction. After sufficiently frequent similar context-induced reinterpretations, the originally invited inference of futurity can become generalized and eventually turn into the conventional encoded meaning in its own right. Such interpretations, repeatedly inferred and routinely associated with certain expressions, thus yield grammaticalization through conventionalization and context absorption (Traugott and Dasher 2005; Nicolle 2011).

Both these accounts rely on innovative changes in form-meaning mappings, and both provide plausible and persuasive analyses of how these changes can be propagated within linguistic communities. Hoefler and Smith (2009), however, have shown that they can in fact be unified under a single analysis based on the fundamental cognitive mechanisms which underpin ostensive-inferential communication (Sperber and Wilson 1995). In such a model, communication is conceptualized not as the transfer of a coded signal, but rather in terms of a speaker providing evidence for what they are trying to communicate, and a hearer using that evidence to infer the speaker's communicative intentions (Scott-Phillips 2015). Successful communication depends on the specific conversational context, and on the interlocutors' beliefs about what their counterpart understands, or their common ground (Clark 1996). This allows them to determine each other's communicative goals, what information is relevant to those goals in the current context, and thus what the most plausible and relevant interpretation of the communicative episode should be. Both the metaphor and reanalysis accounts of grammaticalization fall naturally out of an ostensive-inferential model; the crucial difference between the accounts lies simply in the intentions of the speaker. Metaphor starts with a deliberate speaker-driven innovation which is then subsequently understood and later adopted by the hearer, while reanalysis comes from a (perhaps unintentional) mismatch between the interlocutors, leading to the hearer's inference of a novel meaning (Hoefler and Smith 2009). In both cases, however, grammaticalization is an inevitable by-product of the imprecise, uncertain, and approximate nature of ostensive-inferential communication, which provides both motivation and means for the use of concrete, accessible forms to express and be interpreted as more abstract, more grammatical meanings.

Pathways

In modern English, *be going to* is increasingly frequently used to express the future tense, and may be on the way to usurping *will* as the main marker of this grammatical function. Such a

replacement would, if fully realized, potentially mark the final chapter in the grammaticalization of *will* itself in English, from its origins in a normal verb meaning DESIRE. Bybee (2015) describes how, in Old English, the verb *willan* could already be used in several different constructions with different meanings, as in Ex. (3). It was used with a direct object to mean WANT SOMETHING (3a), and with the infinitive of another verb to mean INTEND TO DO SOMETHING (3b).

- 3) a) *Ne drincð nan man eald win,*
not drinks no man old wine,
& wylle sona þæt niwe.
and will at-once the new
'No man drinks old wine and immediately
wants some new (wine).'

(1000 WS Gospels: Luke)

- b) *Ic wille mid flōde folc ācwellan.*
I will with flood people to.kill
'I intend to kill the people with a flood.' (1296
Genesis)

(after Bybee 2015, p.118)

Throughout Middle English, the construction with the infinitive in (3b) became much more frequently used than the direct object construction, and by Shakespeare's time the meaning of *will* had expanded to include first INTENTION, then later WILLINGNESS and PREDICTION. When expressing the future tense, the construction then began to be represented in writing by contracted spellings (e.g. I'll, he'll), indicating both its amalgamation into a single linguistic unit, and its subsequent phonetic reduction (see subsection ► "Mechanisms"). English therefore currently has two different grammaticalized markers for the future tense, one which originated in a verb of volition and one in a verb of movement.

A third common source of future tense markers is exemplified in Western Romance languages like French and Spanish, where the basic future tense developed from an original Latin construction made up of a form of *habēre* "to have, hold" following an infinitive. This construction's meaning changed from its original OBLIGATION through INTENTION and then PREDICTION, and the forms of the verb *habēre* were correspondingly reduced over time, via the now familiar processes of

context extension and phonetic reduction, eventually becoming suffixes bound to the main verb in the synthetic future tenses like French *chanter-ai* and Spanish *cantar-é* (both meaning “I will sing”).

Importantly, these three sources of future tense markers are neither exceptional nor restricted geographically to Western Europe, rather they recur in multiple languages all over the world: for instance, those deriving from movement verbs are found in languages as diverse as Bari, Sotho, Margi, Klao, Tzotzil, and Tamil; those deriving from verbs of volition in Modern Greek, Chinese, Swahili, and Inuit languages; and those deriving from obligation in Basque and Danish as well as the Romance languages mentioned above (Heine and Kuteva 2002; Bybee 2015). From these different original sources, the constructions all extend their meanings in intriguingly similar ways, first encompassing INTENTION and then PREDICTION, so that a general grammaticalization pathway of semantic change can be abstracted as follows:

- (4) VOLITION/OBLIGATION/MOUMENT TOWARDS >
INTENTION > PREDICTION (FUTURE)
(after Bybee 2015, p.123)

The formal morphosyntactic properties of constructions undergoing grammaticalization have also been frequently visualized as a similar continuum, or *cline*, of linguistic material, with independent lexical items at one end and bound grammatical affixes at the other, as in Ex. (5). The process of grammaticalization can then be considered as any movement of a linguistic item from left to right along the cline.

- (5) content item > grammatical word > clitic >
inflectional affix (> zero)
(Hopper and Traugott 2003, p.7)

Large-scale cross-linguistic analysis of many attested examples of grammaticalization (Heine and Kuteva 2002) have shown a surprisingly large degree of consistency in the pathways from which grammatical material tends to be derived. The grammatical expression of tense and aspect,

for instance, develops in similar ways in unconnected and unrelated languages. Ex. (4) has already illustrated the main sources of future tense markers, while Ex. (6) shows common examples of the development of past tense markers, which tend to derive from a different, but still restricted, set of sources:

- (6) RESULTATIVE/MOUMENT FROM/FINISH >
ANTERIOR > PERFECTIVE > PAST
(after Bybee 2015, p.143)

Similar pathways have been discovered and catalogued for a large number of grammatical distinctions found in languages across the world (Heine and Kuteva 2002). As mentioned above, the human body is one particularly pervasive source of cross-linguistic grammaticalization, with its salient parts being repeatedly employed to express spatial relationships by analogy with the usual vertical posture of a human being standing upright: *head* can refer to the space ABOVE something, *foot* to BELOW, *face* or *breast* to FRONT, *back* or *buttocks* to BEHIND, *belly* to INSIDE. Interestingly, a cultural aspect to the sources likely to be used in grammaticalization can be seen in an alternative model of space based on the body of a four-legged animal, which is found predominantly in societies focused on nomadism and pastoralism in East Africa. In languages spoken in these communities, for instance, words meaning *back* and *head* are the source of spatial markers meaning ON and FRONT respectively (Heine et al. 1991). Already grammaticalized items like these spatial markers can become even more grammaticalized through the same processes described in ► “Mechanisms”, developing into strongly grammaticalized material like case markers denoting the roles played by particular nouns in a sentence, or definite articles and relative clause markers indicating wider structural relationships within texts (Heine et al. 1991).

The many common documented pathways of grammaticalization (Heine and Kuteva 2002) have also been used to develop a proposed evolutionary network of grammatical change, linking clusters of commonly recognized grammatical categories into evolutionary layers (Heine and

Kuteva 2007), and suggesting that all major morphosyntactic categories can be ultimately derived from prototype nouns and verbs. Evolutionary linguists have therefore proposed that the earliest human language, often called *protolanguage*, probably contained only basic noun-like and verb-like units (Hurford 2012), and that its gradual complexification into modern language took place through the very same processes and mechanisms of metaphor, reanalysis, entrenchment, and conventionalization which underpin grammaticalization today (Smith 2011).

Issues

Perhaps the most important and persistent criticism of grammaticalization is that it is not necessarily a specific linguistic phenomenon in its own right, but simply a cluster of different mechanisms which appear independently in other kinds of historical language change, and which is therefore undeservedly privileged over other potential clusters (Campbell 2001; Janda 2001). The fundamental aim of grammaticalization theory, however, is to provide explanations of the origins of grammatical material, and it is beyond doubt that the mechanisms described above ► “Mechanisms” are the basis of such explanations. More importantly, these mechanisms are not simply independent processes which fortuitously happen to be clustered together, but they are rather interwoven processes, reliant on each other and connected causally (desemanticization, for instance, leads directly to decategorialization and phonetic erosion), which together yield grammaticalization.

One of the pillars of grammaticalization theory has been that movement along the clines is not only gradual but also unidirectional, i.e. from left to right in Ex. (5). This principle has also been the subject of much robust critical debate (Newmeyer 1998), due largely to the presence of apparent counter-examples such as the *degrammaticalization* of derivational affixes like ‘isms’ and ‘ologies’ or function words such as ‘ups and downs’ into lexical items. In her comprehensive treatment of degrammaticalization, Norde (2009) concludes that although unidirectionality is clearly not sustainable as an exceptionless principle, the restricted nature of the very few exceptions which do occur, in comparison to the massive weight of

evidence showing the development of grammatical material from lexical items, actually lends support to a slightly weakened form of unidirectionality as a strong tendency rather than an inviolable principle.

Other important theoretical issues in research into grammaticalization center around disentangling the extent to which grammaticalization should be differentiated from, or should be considered to include, related linguistic processes such as: (1) *lexicalization*, the creation of semantically contentful words or constructions whose meanings are not (or no longer) predictable from their constituents, such as a “black market” which is neither black nor a market, or “mermaid” which is derived from the Old English words *mere* “sea” and *mægd* “maiden” (Brinton and Traugott 2005); and (2) *pragmaticalization*, the development of new discourse markers and particles like “you know”, which are differentiated from other grammatical material in terms of their purely pragmatic function (Diewald 2011). To a considerable extent, the importance of making and maintaining such distinctions depends on the particularities and assumptions of the linguistic framework in which the explorations are being carried out.

One particularly fruitful framework for the investigation of grammaticalization is that of construction grammar (Langacker 1987; Croft and Cruse 2004), which is singularly compatible with grammaticalization due to its foundation on the twin assumptions of the symbolic and usage-based theses. The symbolic thesis assumes that the fundamental linguistic unit is an association between form and meaning, that all linguistic material, no matter how schematic, is inherently meaningful, and that linguistic knowledge can therefore be modeled as a structured taxonomic network with default attribute inheritance. The usage-based thesis, meanwhile, holds that linguistic knowledge, learning, and change all originate through straightforward inductive abstractions of form-meaning associations from their use in language. Construction grammar therefore allows linguistic innovation to be modeled in terms of an extension from a prototype which overrides its default inheritance, and grammaticalization as a gradual increase in schematicity and productivity

of existing constructions, corresponding to unidirectional movement along a continuum (Gisborne and Patten 2011; Smith and Hoefler 2017).

Over recent years, as the field has continued to mature, the focus of grammaticalization research has broadened considerably, both encompassing different linguistic frameworks, including generative approaches, and expanding in a number of new directions to embrace a wide range of fascinating phenomena (Narrog and Heine 2011; Smith et al. 2015). Prominent among these recent developments is the growing interest in the grammaticalization of co-speech gestures in sign languages (Pfau 2015).

Conclusion

Grammar emerges gradually through a complex and subtle interplay of connected mechanisms of historical language change, in which linguistic constructions in specific contexts are repeatedly interpreted with more abstract, functional meanings, fusing their constituent parts together into integrated chunks of language and thereby losing their independence of use. These mechanisms are based in universal fundamental properties of human ostensive-inferential communication, and their repeated application leads to the emergence of consistent pathways of language change, which have shed light not only on where the grammatical material in modern languages comes from but also on the ultimate origins and evolution of human language itself.

Cross-References

- [Linguistic Evolution](#)
- [Metaphor and Analogy](#)
- [Modeling Language Transmission](#)

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Grammaticization

► Grammaticalization Theory

Grammatization

► Grammaticalization Theory

Grandfather Investment Versus Grandmother Investment

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Synonyms

Alloparenting; Biased grandparental investment; Grandparental involvement; Sex effect

Definition

The investment of grandfathers and grandmothers includes different types of support and resources grandparents can target toward their grandchildren. Grandparental investments can include different types of actions, for instance, financial transfers, emotional support, and care. Grandparents can invest in their grandchildren either directly or indirectly via a third party (e.g., via the grandchildren's parents). Typically, grandfathers tend to invest less in their grandchildren than grandmothers, except when comparing paternal grandmother's and maternal grandfather's investment.

Introduction

Grandparents share, on average, 25% of the same genes with their grandchildren, and thus, they can increase their inclusive fitness by investing time and resources in their descendants. Nonetheless, all grandparent types tend not to be in the same position with each other in their relations with grandchildren (Tanskanen and Danielsbacka 2018). Only maternal grandmothers can be 100% certain of their relatedness to grandchildren, while maternal grandfathers (via themselves and their daughters) and paternal grandmothers (via their sons and their children) have one link of uncertain paternity, and paternal grandfathers have two (via themselves and sons and via sons and sons' children). Hence, within the kin lineages, grandmothers are more likely to be genetically related to their descendants compared to grandfathers, meaning that maternal grandmothers are expected to invest more than maternal grandfathers and paternal grandmothers more than paternal grandfathers. This entry considers the role of grandfather investment compared to grandmother investment.

Grandfather and Grandmother Investment

Although the role of grandfathers could have been relatively minor in traditional and historical

populations (Sear and Mace 2008), in contemporary nations, grandfathers are often highly involved in their grandchildren's lives. Indeed, in some circumstances, the investment of grandfathers can approach that of grandmothers. For instance, based on cross-national evidence from Europe, 58% of grandmothers and 49% of grandfathers look after their grandchildren at least occasionally (Hank and Buber 2009). Moreover, in current societies, the investment of both grandmothers and grandfathers is observed to be associated with improved child well-being (Sear and Coall 2011), although it is unclear whether there is a causal association between grandparental investment and child outcomes (Tanskanen and Danielsbacka 2017).

In addition to sex-based differences (i.e., sex effect), grandparental investment varies by lineage, meaning that maternal grandmothers usually invest the most, followed by maternal grandfathers, then paternal grandmothers, and, finally, paternal grandfathers (Coall and Hertwig 2010; Euler 2011). Among evolutionary scientists, the most important explanation for this biased grandparental investment pattern is based on paternity uncertainty. However, paternity uncertainty cannot directly explain why maternal grandfathers often invest more than paternal grandmothers.

With regard to preferential investment in more certain kin theory, the amount of grandparental investment changes according to the availability of other "investment options" (Laham et al. 2005). If grandmothers and grandfathers have grandchildren via both daughters and sons, they are expected to invest more in their daughter's children compared to their son's children. If grandchildren via daughters do not exist, grandparents are expected to invest more in grandchildren via sons. Often, maternal grandfathers may invest more than paternal grandmothers because the latter typically have more certain investment options (i.e., grandchildren via daughters). If more certain investment options are unavailable, maternal grandfather and paternal grandmother should invest equally in their grandchildren. A previous study including over 22,000 European grandparents provided evidence

in support of the preferential investment theory (Danielsbacka et al. 2011).

Conclusions

In recent decades, there has been increasing academic interest in the grandparental role in human families. However, an obvious limitation in many of these studies is that older men have often been ignored and, in practice, "grandparents" have been used as a synonym for "grandmothers" (Coall et al. 2016). Although grandmothers are known to invest more time and resources in grandchildren than grandfathers, the role of grandfathers is far from negligible. Thus, when one considers grandparental investment, it is important to consider also the role of grandfathers.

Cross-References

- [Grandparental Investment](#)
- [Level of Grandparental Investment](#)
- [Maternal Grandmother Invests Most](#)
- [Paternal Grandfather Invests Least](#)
- [Paternal Investment Relative to Maternal Investment](#)

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Grandiose Self-Esteem

► Narcissism

Grandmother Hypothesis

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Synonyms

Postmenopausal altruism

Definition

The grandmother hypothesis is a proposed solution to the evolutionary puzzle of midlife menopause and postmenopausal longevity in several mammal species, whereby postmenopausal females confer greater alloparental care to their kin than would be possible if they continued ovulating or died following menopause.

Introduction

The grandmother hypothesis proposes that the function of postmenopausal (i.e.,

postreproductive) life in females is to provide alloparental care to kin. The hypothesis is invoked to explain not only why senescence and menopause occur and why much of female life is spent in an infertile state but also why post-reproductive females provide especially high amounts of investment to the members of their kin group.

Senescence and Menopause

The grandmother hypothesis was developed as a solution to the apparent puzzle of menopause as observed in humans and other species. Menopause is best defined as the permanent, non-pathologic, age-related cessation of ovulation that occurs long before death (Walker and Hurdon 2008), in other words, when the female ceases to produce egg cells or ova. Nonhuman species that are believed to experience menopause include chimpanzees, macaques, baboons, killer whales, dolphins, and pilot whales. Females in several other species, including dogs, elephants, and laboratory rats and mice, experience rapid declines in ovulatory consistency in the years leading up to their death, reducing their fertility but not eliminating it. It remains controversial as to whether the captive lifestyle contributes to the appearance of menopause and allows animals to reach ages that would be unrealistic in the wild. In general, the challenges of observing wild populations and collecting data on fertility severely limit our understanding of menopause in nonhumans. For each of the primates mentioned, late-life (post “menopausal”) childbirths have been recorded, suggesting that a definite cessation of ovulation is uniquely human. The marine mammals mentioned, however, show consistent and distinct signs of menopause. What constitutes true, humanlike menopause remains controversial.

Senescence is the process of deterioration and dysfunction that occurs as animals age. Theories regarding the evolution of senescence are helpful in describing the potential function of menopause. First, the wear and tear hypothesis suggests that bodies simply degrade over continued use, and the systems that regenerate damaged tissues become less efficient over time and eventually fail after a predictable interval. All female mammals are born

with a fixed number of oocytes (immature ova), usually many thousands more than they will ever need to use in their life (humans enter puberty with 400,000), but these cells deteriorate at a rapid pace across the life span until around age 50 when the last of the oocytes are depleted (Wise et al. 1996). This degradation has been linked with a reduced efficiency at repairing damaged ovarian cells over the life span (Titus et al. 2013). A second possibility is that in ancestral human environments, females did not live long enough to experience menopause, and so the genetics that contribute to menopause have never been exposed to negative selection. Deleterious genetic expressions that would arise in late age could have no history of selection because human life has never consistently extended into late age. This is described by the mutation accumulation hypothesis and antagonistic pleiotropy (Hamilton 1966). Life after menopause could thus be the novel consequence of human environmental conditions and cultures that facilitate unprecedented longevity. A third possibility is that senescence is caused by programmed cellular deaths that accelerate in late age. Telomeres represent a genetic clock, and when they are exhausted apoptosis occurs, a controlled death cycle. Cellular death is known to contribute to aging, and it has been theorized that aging and death serve the function of removing organisms that have already reproduced and accumulated mutations and toxins, while making room for new copies of those organisms. Whether the late-life depletion of oocytes is a controlled process, a process that has never experienced selection, or a consequence of natural wear and tear, the question remains as to why the female body maintains itself and remains healthy for the years following menopause, particularly among humans who can survive well beyond menopause.

Grandmothers and Alloparenting

Alloparenting refers to any behaviors that contribute to the survival and reproduction of offspring who are not your own. Supportive behaviors can include resource provisioning, defense, status enhancement, instruction, etc. The grandmother hypothesis is not limited to the care that older

females can provide to their grandchildren, it also includes care directed toward children, cousins, nieces, nephews, and any local kin that could benefit from the aid of a postmenopausal female. On average, postmenopausal females will benefit more from caring for kin of greater genetic similarity and caring for kin whose genetic relatedness is more assured. More accurately, the genes that promote postmenopausal alloparenting are more likely to reside within more closely related individuals, meaning that the relative success of those genes depends on a preference for providing care to the kin who are most likely to contain them (i.e., assuredly close kin). Confirming these predictions, in late age, female great apes, including humans, show enhanced alloparental care to kin, primarily toward kin who are more directly related and those related through female relatives (Coall and Hertwig 2010). The reason that a female will favor kin who is related to them through a female relative (e.g., a daughter's son rather than a son's son or a sister's son rather than a brother's son) is that she can be certain that the individual is indeed her kin. In the case of a son's child, for example, the grandmother cannot be certain that the child is the product of her son's sexual efforts, just as he cannot be certain that he is the father in the way that the mother can be certain that she is the mother (for the father, this is referred to as paternity uncertainty and is a natural consequence of internal fertilization). Cross-cultural research demonstrates that maternal grandmothers tend to invest the most, followed by maternal grandfathers, followed by paternal grandmothers, and finally paternal grandfathers (Bishop et al. 2009). This investment tends to flow most strongly toward offspring who show the highest likelihood of surviving and reproducing, i.e., more attractive, healthier, and higher status children (Leek and Smith 1991). In general, evolutionary theory predicts that investments made into offspring who can best capitalize on investments will be favored. Thus, depending on the context, grandparents can be expected to invest more heavily into male or female kin, as well.

Following menopause, female humans show enhanced investment into kin. There is limited evidence that this investment improves outcomes for children in industrialized societies (Coall and

Hertwig 2010; Hawkes 2004), and stronger evidence that child life expectancy in non-industrialized societies is improved by the presence of a maternal grandmother (Strassmann and Garrard 2011). While it is clear that human life spans have expanded considerably in the last 10,000 years, with the arrival of agriculture and medicine, research on existing hunter-gatherer tribes suggests that postmenopausal life has been a feature of human life long before the rise of civilization (Gurven and Kaplan 2007). Looking at the human “mortality profile” and modern data on the life spans and infant mortality of hunter-gatherers, Gurven and Kaplan found that humans have a species-typical age of somatic decline, around 70 years. They also show that while hunter-gatherers (and, presumably, ancestral humans) have 30 times the infant mortality of industrial society (driving down their average life spans), survivorship after the age of 15 is only about a decade short of the healthiest cultures on Earth (72 vs. 85 in Japan). If menopause is a product of modern medicine facilitating old age, one would expect to see that the human typical somatic decline occurred at about age 50 and that the modal life span of women in hunter-gatherer societies hovered around 50. These data cast some doubt on the argument that postmenopausal life has not existed long enough to experience selection for enhanced kin alloparenting.

As mentioned, the most important way that grandmothers in hunter-gatherer societies assist their kin is by reducing child mortality, suggesting an interesting relationship between late-life survival and early-life survival. Humans are a remarkably altricial species; we are born in a very vulnerable state, requiring nearly constant attention and resource provisioning (in large part because we are grossly encephalized). Humans are usually considered cooperative breeders, recruiting the aid of local kin and friends to assist with child-rearing, often in a reciprocal manner. It could be suggested that postmenopausal longevity and altriciality coevolved, as having another kin member to provide assistance allows for the evolution of larger, more complex cortex (that requires greater investment). The arguable nonexistence of postmenopausal life among wild populations of primates is weak evidence against

the possibility that more recent human evolution has benefitted from adaptations for increased survivorship and grandparental care beyond oocyte depletion.

Evolutionary Timeline

There are two main ways to interpret the evolutionary timeline of the grandmother hypothesis. The first, original interpretation is that menopause evolved as an adaptation to reduce the risk of late-life pregnancy in women who have (i) accumulated more germ-line mutations, (ii) become less likely to survive childbirth or produce a live child, and (iii) could better benefit from investing in large numbers of kin. In this account, the cessation of ovulation occurs in mid-life to facilitate a new familial role as a grandparent. The second, more recent interpretation is that female life spans expanded beyond the point of natural oocyte depletion and reproductive senescence that would normally coincide with death. In other words, selection favored longer life among women but did not or could not favor later reproductive capacity in women. In this account, the adaptation for grandmothering is the extension of somatic maintenance into late age, regardless of reproductive maintenance. Of course, these explanations are not entirely incompatible (both processes may have contributed), but the debate rests on whether menopause or longevity shows more distinct signs of being designed as adaptations or better resemble by-products or physiological constraints. For example, one could argue that there is a natural constraint on the number of oocytes that can be produced in the embryonic human, leading to a necessary depletion following 50 years of ovulatory cycling, rather than an artificial cap on oocyte production or a controlled process of oocyte destruction. Likewise, one can argue that longevity is a byproduct of the conditions of human life following the invention of tools and cooperation, rather than the accomplishment of adaptations for somatic maintenance. Support for the latter timeline is mounting. First, comparative researchers suggest that our nearest primate relatives show similar menopausal timing, or, at least, begin to show early signs of menopause just prior

to their death of old age (Alvarez 2000). Second, oocyte depletion does not show the characteristics of a controlled process, whereby oocytes are actively limited or destroyed. To the contrary, female reproductive biology appears to strive valiantly to maintain oocyte health. That said, characteristic menopausal shifts in hormone levels do suggest adaptive physiological and psychological adjustments, once oocytes are depleted.

Conclusion

The grandmother hypothesis presents a compelling evolutionary explanation for life after menopause, particularly in human females. As it stands, there is good evidence for the hypothesis that human life spans expanded beyond the limitations of oocyte production and maintenance in order to better facilitate cooperative breeding with kin. Human longevity beyond reproductive senescence does not appear to be a novel feature of human culture (i.e., from the past 10–20,000 years), but it is a novel feature among our closest primate relatives (i.e., from the past 5–10 million years). Interpretations of the grandmother hypothesis differ, and too little is known about nonhuman menopause to make strong claims of human uniqueness, homoplasy, or homology. However, research into marine mammal reproductive cycles may shed light on the life history, social, and physiological characteristics that select for longevity beyond menopause.

Cross-References

- [Alloparenting](#)
- [Apoptosis](#)
- [Cooperative Breeding](#)
- [Encephalization](#)
- [Extended Postmenopausal Lifespan](#)
- [Hunter-Gatherer Societies](#)
- [Kin Selection](#)
- [Menopause](#)
- [Menopause Affords Grandparental Investment](#)
- [Mutation Accumulation Theory](#)
- [Paternity Uncertainty](#)
- [Senescence](#)

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Grandmother Hypothesis of Menopause

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Synonyms

Altriciality lifespan hypothesis; Stopping early hypothesis

Definition

Grandmother hypothesis of menopause claims that human females stop reproducing early in relation to their long lifespan because they can gain more fitness benefits by investing in their children or grandchildren rather than by reproducing themselves. Grandmother hypothesis tries not to explain the evolution of menopause *per se* but rather the evolution of long non-reproductive lifespan of human females.

Introduction

Long nonreproductive lifespan of human females presents an evolutionary puzzle. Evolutionary theory predicts that individuals are programmed to maximize their number of descendants in future generations, meaning that they should reproduce until death. Thus, there should be selection against living well beyond one's fertile years. In contrast to some earlier views, based on current knowledge, menopause is not a feature of humans only, but exists also in some non-primate species, namely dolphins, whales, and perhaps elephants (Euler 2011). However, the long nonreproductive lifespan of human females that can last decades could be a unique feature of human species. This non-reproductive lifespan gives human grandmothers a great opportunity to increase their inclusive fitness by investing resources in their offspring (Lahdenperä et al. 2004). In addition to this "positive" selection pressure, a "negative" selection pressure might also play a role in the evolution of menopause. Negative selection pressure means that reproducing simultaneously with own descendants may cause an intergenerational reproductive conflict that in turn may reduce the survival of both generations' offspring (Lahdenperä et al. 2012). The reproductive conflict can in theory occur between a daughter and a mother or between a daughter-in-law and a mother-in-law.

Empirical Evidence

During the recent decades, the predictions of the grandmother hypothesis have been tested in

several studies. These studies have investigated whether the presence of a grandmother is associated with increased female fertility and improved child survival rates. Studies testing the predictions of grandmother hypothesis have mostly used data from natural fertility and natural mortality populations, including demographic records from historical populations, data from hunter-gatherer populations, and data from modern populations that are living traditionally (Sear and Mace 2008). The empirical studies testing the assumptions of grandmother hypothesis have, however, produced mixed results. While some studies have found support for the grandmother hypothesis, others have not (Coall and Hertwig 2010). Thus, it is not self-evident that the menopause has evolved because it provides inclusive fitness benefits (or prevents negative fitness outcomes) for grandmothers themselves.

The opponents of the grandmother hypothesis have argued that the caring grandmotherhood is a by-product of long infecundity of human lifespan (Coall and Hertwig 2010). This view points out that the long post-reproductive lifespan of human females could have evolved first and caring grandmotherhood only after that. Based on this argument, it could be that during their non-reproductive years grandmothers, who cannot have children of their own, invest resources in their children and grandchildren, because supporting their offspring is better than nothing at all.

Conclusion

The debate continues whether the menopause is an adaptation, by-product of long human age, or something else. Whatever is the truth the grandmothers have often been in the right place at the right time improving parental fertility, grandchild survival, and thus their own inclusive fitness.

Cross-References

- ▶ [Grandparents and Grandchildren](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Importance of Grandparental Investment](#)

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Grandmother Hypothesis, The

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Synonyms

[Altriciality life span hypothesis](#); [Mother hypothesis](#); [Stopping-early hypothesis](#)

Definition

The grandmother hypothesis states that the long post-reproductive life span in human females would have evolved because women were able to gain more fitness by investing in their adult offspring and grand-offspring rather than by reproducing until old age. Because of this fitness benefit, selection would have favored a longer

post-reproductive life span during human evolution.

Introduction

In most animals, reproductive and somatic senescence occurs at the same time as a part of the gradual decline in overall physical condition with age. In few species, however, the reproductive functions show an abrupt deterioration well before other body functions, leading to a total loss of fertility during middle age and subsequent post-reproductive life span of several decades. So far, the most convincing evidence from menopause and long post-reproductive life span comes from a few whale species, namely, killer whales and short-finned pilot whales, and human females whose post-reproductive life span contributes to a significant proportion of their total life span (Ellis et al. 2018).

The paradox of long post-reproductive life span has puzzled evolutionary biologists because it runs against the central presumption of traditional evolutionary theory of individuals trying to maximize their evolutionary fitness during their life span, which usually comes from individuals reproducing until death. In humans, it has been suggested that the long female post-reproductive life span evolved through kin selection and the inclusive fitness benefits gained after menopause by investing in their adult children and grand-offspring (Hawkes et al. 1998).

Hypothesis and Background

The grandmother hypothesis is based on the kin selection theory by William Hamilton (1964) and ideas proposed by George Williams (1957). The kin selection theory explains helping behavior in social species. According to this theory, an individual should help relatives as long as the benefits from helping are greater than the costs, to increase the individual's inclusive fitness and pass their genes to future generations. With kin selection theory, evolutionary biologists have been able to explain many puzzling altruistic behaviors in animals, for instance, the existence of sterile workers

in social insects. Williams (1957) was the first to suggest that menopause was adaptive and beneficial for human females because there are costs involved in continuing to reproduce until old age, and women who cease to reproduce earlier would be able to devote their remaining energy to the care of the living children (often referred to as the “mother hypothesis” or “stopping-early hypothesis”). The costs in old age would be realized as elevated risk of stillbirth or fetal loss for women and higher risk of birth defects for offspring (e.g., chromosomal abnormality). The late born children would also have a greater risk of mother loss, and late births would risk not only the latest child but also previous dependent children, as there is increased risk of mortality associated with late-life pregnancy (Penn and Smith 2007). Therefore, rather than facing the risk of late births and the high cost of rearing infants, it would be more beneficial for women to devote their remaining reproductive effort toward increasing the survival and reproductive success of their own young juvenile and adolescent offspring.

The grandmother hypothesis was first proposed in its current form by anthropologist Kristen Hawkes and her colleagues in the 1990s, who studied Hadza hunter-gatherers of Tanzania. They noticed that postmenopausal grandmothers were important caregivers to their grandchildren, and variation in children’s weight was positively correlated with their grandmother’s foraging time (Hawkes et al. 1997). Hawkes and colleagues formulated the hypothesis to specifically explain the selection for longer life span after menopause while not explaining the evolution of menopause per se (Hawkes et al. 1998; Hawkes 2003). They also suggested that the grandmother hypothesis would explain other traits specific to humans: our late maturity, small size at weaning, and high fertility based on Charnov’s dimensionless assembly rules for mammalian life histories (Hawkes et al. 1998). This hypothesis was proposed to mainly concern daughters having helping mothers because mothers and daughters face similar trade-offs, whereas sons must invest in mating competition (Hawkes et al. 1995). Additionally, the genetic relatedness to the grandmother is uncertain when it is a question of the son’s child, and the benefits to the grandmother’s fitness with regard

to helping her son and daughter-in-law reproduce are much more uncertain than in the case of the grandmother’s own daughter (Hawkes et al. 1998).

The grandmother hypothesis was originally associated especially to mother-child food sharing. According to Hawkes et al. (1998), older women could provide for their daughter’s weaned offspring, thereby enhancing the children’s survivorship and allowing their daughters to produce more children sooner. Also, the helping grandmother may lower her daughter’s age at which she begins to reproduce, the inter-birth intervals might become shorter, and hence the daughter could produce more children with increased survival. Consequently, the daughter’s fitness increases, as well as the grandmother’s own inclusive fitness. However, food sharing is not the only contribution of postmenopausal women to their daughter’s reproductive success. Grandmothers are often providers of childcare and shelter in addition to contributors toward food gathering and processing (Coall and Hertwig 2010). Any economic or social support provided by grandmothers could increase their daughter’s lifetime reproductive success as well (Volland and Beise 2002).

Evidence

The grandmother hypothesis has gained support from many populations worldwide; however, some studies have shown controversial results. The hypothesis has been tested, for the most part, among populations with natural fertility and mortality, such as historical or hunter-gatherer human populations, but there are also studies in modern human populations living in traditional settings or in modern Western populations. In natural fertility populations, grandmother help is often associated with increased survival of the grandchildren, enhancing their growth or increasing the offspring’s reproductive success (Hawkes et al. 1997; Lahdenperä et al. 2004; Sear and Mace 2008; Volland et al. 2005). In modern populations, grandmothers may have improved their grandchildren’s well-being, which is measured by cognitive skills, health, educational

achievements, or socio-emotional measures (Sear and Coall 2011; Tanskanen and Danielsbacka 2017, 2018). Several studies have indicated that the maternal grandmother could be more beneficial to grandchildren than the paternal grandmother (Sear and Mace 2008). Additionally, grandmothers are often most beneficial during the most sensitive periods during child development, for example, during weaning (Lahdenperä et al. 2004; Sear and Mace 2008). However, in contrast to these studies on helpful grandmothers, some studies have not found evidence for the prediction that grandmothers benefit their children or even have adverse effects on their grandchildren (Voland et al. 2005). Similarly, as some fitness calculations have found, the grandmaternal helping effects appear to be enough to select for longer post-reproductive life span in human females; some have found the grandmaternal helping effects to be too weak alone to select for longer life span after menopause (Kim et al. 2012; Lahdenperä et al. 2012).

Recently, it has been suggested that other animals should be studied in different taxa with or without menopause and long post-reproductive life span to compare with humans and enhance our understanding of the evolution and selection pressures on post-reproductive life span and long life in general (Croft et al. 2015). Indeed, several species without menopause also show evidence of grandmaternal help but the potential fitness benefit of this behavior remains unclear. In few animals, the grandmothers have had measurable fitness benefits from helping. For instance, the presence of grandmothers was associated with increased survival of grand-offspring in vervet monkeys, Japanese macaques, and Asian elephants (Fairbanks and McGuire 1986; Pavelka et al. 2002; Lahdenperä et al. 2016).

Other Hypotheses for Human Menopause, Post-Reproductive Life Span, and Longevity

Several other hypotheses have been formulated to explain the occurrence of menopause and post-menopausal life span in women. Some researchers have proposed that these traits result from a

physiological trade-off favoring efficient reproduction early in the fertile part of life (Wood et al. 2000, “by-product hypothesis” or “antagonistic pleiotropy hypothesis”), whereas others have suggested that menopause and postmenopausal life span in humans are by-products of recent increases in life span or life expectancies due to improved nourishment, medicine, and hygiene and, thus, are not evolutionarily meaningful (“modern artifact hypothesis”). Such suggestions are, however, not upheld by the current knowledge that prolonged longevity in humans had already evolved in the late Pleistocene epoch (Caspari and Lee 2004) and is, therefore, not a recent phenomenon.

It has also been suggested that female menopause or longevity is a by-product of selection for greater male longevity (Tuljapurkar et al. 2007) or due to a mating preference of older males for younger females (Morton et al. 2013). Consistent with these hypotheses, Kaplan et al. (2000) argued that the high nutritional provisioning of older males to reproductively active women and children could increase male mating success in old age and would have, hence, indirectly resulted in increased longevity in females (“embodied capital hypothesis”). These explanations are, however, unlikely, as selection in one sex would be unlikely to give rise to a greater response in the other sex, given that female life span is on average slightly longer than male’s in nearly all populations worldwide (Møller et al. 2009).

Recently, “reproductive conflict hypothesis” concerning the evolution of menopause (and not the long post-reproductive life span per se) suggested that menopause and the minimal reproductive overlap between generations in humans might be the outcome of reproductive competition between generations (Cant and Johnston 2008). The onset of menopause coincides with the age at which a female can become a grandparent and face reproductive competition from the younger generation. In these circumstances, it would be more beneficial for women to stop reproducing and, instead, help their adult offspring to reproduce. This hypothesis has gained support from some empirical studies in humans and in killer whales (Lahdenperä et al. 2012; Croft et al. 2016). In the preindustrial human population,

grandmothers and daughters-in-law faced high costs when reproducing simultaneously (Lahdenperä et al. 2012). According to some inclusive fitness models, these intergenerational costs together with beneficial grandmother effects could have led to menopause and long subsequent post-reproductive life span in human females (Lahdenperä et al. 2012; Croft et al. 2016).

Conclusion

There is substantial evidence that grandmothers provide significant survival and reproductive benefits to their children and grandchildren in humans and in some other animals. There remains considerable debate in the literature regarding which hypothesis explains the evolution of long post-reproductive life span in females. Potentially, a combination of different hypotheses considering both the cooperation and competition between generations would be the most fruitful approach for explaining the evolution of menopause and prolonged post-reproductive longevity in females.

Cross-References

- Grandmother Hypothesis
- Grandmother Hypothesis of Menopause
- Menopause Affords Grandparental Investment

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Grandparent Investment

► Level of Grandparental Investment

Grandparental Care

- Euler and Weitzel (1996)
- Importance of Grandparental Investment
- Predictors of Grandparental Investment

Grandparental Investment

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Synonym

Grandparental solicitude

Definition

Grandparental investment refers to the various types of care (like solicitude, looking after grandchildren, getting in contact, investing time, and tangible resources) grandparents may provide for their grandoffspring.

Introduction

Evolutionary psychologists assume that grandparenthood is not only a social role (Kahana and

Kahana 1971) but has profound implications for reproductive success (Volland et al. 2005). From birth on, children are highly dependable on their parents and require a great amount of parental investment (Trivers 1972). According to the cooperative breeding hypothesis, substantial child care is provided by helpers other than the biological parents (alloparents; Hrdy 1999). In the EEA (environment of evolutionary adaptedness), two parents would not have been enough to rear highly dependent human children for many years until they have reached adulthood. Humans are therefore characterized by a network of family helpers. Today, however, modern demographic changes affect family relationships considerably. In Western societies, birth rates and conjugal stability decreased and life expectancy increased. State welfare provisions substitute for some kin support in raising children, while female participation in the labor force increases the need for child support (Euler 2011). In this entry, however, we argue that grandparents are still a valuable source for child support.

From an evolutionary point of view, it is important to distinguish between consanguine (genetically related) and non-consanguine grandparents (step-grandparents). First, we focus on consanguine grandparents and explore why they invest at all in their grandchildren. Evolutionary psychologists distinguished the sex of the grandparents, the laterality (maternal or paternal), and the sex of the grandchildren in their analyses and found biased grandparental investment in their grandchildren. We refer to different ultimate (grandmother hypothesis, paternity certainty hypothesis, sex-specific reproductive strategies, preferential investment hypothesis, asymmetric genetic relatedness and sex of grandchild), as well as proximate, explanations (sociostructural explanations, aunt and uncle investment, family ties) to explain differences between the investment of the four grandparents. Finally, we review the empirical evidence with regard to non-consanguine, step-grandparental investment.

Definition and Measurement of Grandparental Investment

Generally defined, investment in offspring increases the offspring's fitness at some fitness opportunity costs to the investor (e.g., Clutton-Brock 1991). Evolutionary theories of animal behavior group investments into three types: calories, risk acceptance, and time (Daly and Wilson 1983). Feeding children is still of prime importance in premodern societies but less important in industrialized societies. Risk acceptance, for example, the question of eating or avoid being eaten, is not the primary survival task for humans. Time, however, probably was (and still is) a limited resource throughout human evolution. The time devoted to a particular grandchild, in terms of contact frequency and duration, is one of the main and direct grandparental investment measures and is easily assessed by paper-and-pencil ratings (Euler and Weitzel 1996). Money spent or gifts for the grandchildren are also often used as direct indicators of grandparental investment (Euler and Michalski 2007).

The disposition to invest in kin is expected to be mediated through emotions, especially through feelings of closeness and nurturance toward children and grandchildren (Smith 1991). One of the most frequently used measures for assessing the emotional closeness between grandparents and grandchildren is a direct rating of the emotional closeness or relationship closeness. This variable also seems to be least influenced by situational factors like residential proximity or individual indicators like the age of the grandchild (Euler 2011). Consequently, studies include ratings of emotional closeness, naming favorite grandparents, or grandparental mourning after a grandchild's death as indirect measures of grandparental investment (Euler and Michalski 2007). Indeed, measures of investment and emotional closeness are found to be highly correlated (Pashos and McBurney 2008).

After defining grandparental investment, the next important question is who to ask in order to measure the extent of grandparental investment.

Adult grandchildren are preferred over grandparents as study participants for the following reasons: (1) Every person has had grandparents, but not everybody is a grandparent; (2) older study participants are more difficult to recruit than younger ones; and (3) if the rating questions imply preferring one grandchildren above the other, norms of impartiality may prevent grandparents from expressing favoritism (Euler 2011).

Different measures of more or less successful grandparental investment have used, including child mortality, birth weight, breastfeeding, infanticide, homicide, abuse, inheritance, and educational investment (Coall and Hertwig 2010).

The evolutionary literature distinguishes grandparents along the lineage (maternal or paternal) and the sex of the grandparent (grandmother or grandfather). One of the most intensively studied questions from an evolutionary perspective is the question which of the four grandparents (maternal grandmother, maternal grandfather, paternal grandmother, and paternal grandfather) invests most in their grandchildren (biased grandparental investment).

Thinking about biased grandparental investment from an evolutionary perspective requires the differentiation between consanguine (genetically related) and non-consanguine (step-) grandparents, because different mechanisms are supposed to be responsible for biased grandparental investment for these two categories of grandparents.

Consanguine Grandparental Investment

Genetic relatedness. The coefficient of relatedness between a consanguine grandparent and a grandchild is estimated as $r = 0.25$ on average. Thus, kin selection theory (Hamilton 1964; Maynard Smith 1964) predicts that grandparents invest in their grandchildren in order to increase their own inclusive fitness. The empirical evidence supports this claim. For example, relationships with step-grandparents are less close than those with biological grandparents (Aldous 1995).

Grandmother hypothesis. Other relatives are also related to oneself by $r = 0.25$, for example, half siblings or aunts/uncles, and are also expected to show some mutual interest in related individuals. What is the special social position of grandparents, as compared to these other relatives, and why do we observe such an early and irreversible cessation of fertility followed by a relatively long postmenopausal life expectancy in humans? Williams (1957) considered the human menopause as an adaptation because the benefit of care for existing children outweighs the cost of further reproduction for mothers. This is also called the prudent mother hypothesis. Hamilton (1966) extended this idea to grandmothers, but he was uncertain whether the menopause was an adaptation in its own right. When considering other species, it turns out that in animal kingdom, menopause is not unique to humans. Evolutionary anthropologist Kristin Hawkes thus argued that not menopause but rather life span after menopause has evolved in women (Hawkes et al. 1998). In this view, grandparenthood has evolved together with human longevity because grandmothers, namely, the maternal grandmothers, were needed as important mothers' family helpers. Hawkes' version of the grandmother hypothesis has become the most popular. There are, however, also evolutionary anthropologists who believe that the grandmother's role as family helper is overestimated in the theory, compared to the importance of male family helpers (Hill and Hurtado 2009). The debate continues in biological anthropology whether menopause is an adaptation, a by-product, or a modern artifact (Voland et al. 2005). Nonetheless, the grandmother hypothesis is currently the most influential theory to explain female longevity beyond menopause, and it raised particular attention to the maternal grandmother's investment in grandchildren. Sear and Mace (2008), for example, investigated the effects of the presence of various kin on child survival in 45 (mostly) natural fertility populations. They found that next to the mother, the maternal grandmother is often, but not always, found to contribute more to a child's survival. In

their study, the presence of the other three grandparents including the paternal grandmother was often found less beneficial for the survival of a grandchild.

Paternity certainty hypothesis. How can the difference between maternal and paternal grandparents be explained? Genetic relatedness predicts, all else equal, the same amount of grandparental investment from all four grandparents. The reproductive lifespan of grandfathers, however, is less restricted than the reproductive lifespan of grandmothers. As men grow older, men can still increase their direct fitness, but menopause restricts the reproductive capacity of women. Thus, the grandmother hypothesis predicts more grandparental investment from grandmothers compared to grandfathers. However, what might be an evolutionary explanation for a greater importance of maternal grandparents compared to paternal? The paternity uncertainty hypothesis claims to explain this difference. Grandparents, as well as parents, are not equal in their maternal and paternal certainty of their descents. The famous old Roman principle “*Mater semper certa est, pater semper incertus est*” (“the mother is always certain, the father is always uncertain”) illustrates this sex difference. If, due to internal gestation, mothers can be 100% certain about their biological relatedness to the child, but fathers not, then this differential certainty applies to grandparents as well. Maternal grandparents should be more certain about their relatedness to their grandchild than paternal grandparents.

However, the same differential uncertainty of grandparents also refers to their children (parents of their grandchildren) as well. Thus, the maternal grandmother (mother’s mother) should have the highest certainty about their grandchild. She is certain about her own child, and due to the maternal certainty, her daughter (the mother of the grandchild) is also certain about her child. The most uncertain grandparent is the paternal grandfather (the father’s father). The paternal grandfather can neither be certain about the genetic relatedness of his son (the father of the grandchild) to his son (grandchild) nor can he be certain about his relatedness to his son. Maternal

grandfathers and paternal grandmothers both share certainty on one link.

Smith (1988, 1991) was the first to investigate biased grandparental investment. He found that grandmothers invest more in their grandchildren than grandfathers and that grandparents invest more in daughters’ children (the maternal lineage) than in sons’ children (the paternal lineage). Thus, the predicted rank order of grandparental investment is maternal grandmother (highest investment), maternal grandfather and paternal grandmother (both moderate investment), and the paternal grandfather (showing the lowest investment).

The paternity uncertainty hypothesis states that only mothers, but not fathers, can be 100% sure about their genetic relatedness to their child. Early studies estimating paternity uncertainty in Western societies showed a level of around 10% paternity uncertainty (Macintyre and Sooman 1991), which would fit very well to the effect sizes of biased grandparental investment found empirically. Newer studies, however, estimated the level of paternity uncertainty to only 1–3%, which is too low as sole explanation of the biased investment (Euler, this volume; Voracek et al. 2008; Wolf et al. 2012). At least three different implications regarding the relationship between paternity certainty and grandparental investment are possible. First, the asymmetric caregiving pattern reflects paternity uncertainty in the environment of evolutionary adaptedness (EEA) rather than the actual, genetically verifiable paternity certainty (Euler and Michalski 2007; McBurney et al. 2002). Second, psychological processes do not necessarily operate with base rate probabilities. Applying signal detection theory (Green and Swets 1966) to the paternity certainty problem, two errors are possible. The father may wrongly assume his child to be his biological child or he may wrongly doubt his paternity. According to error management theory (Haselton and Nettle 2006), whenever the costs of the errors are asymmetric, it is assumed that selection fashions adaptations which are biased toward making the least costly error. In this case it could be very costly to devote all time, energy, and resources to a non-related child. This could

also explain why paternal grandfathers invest the least of all four grandparents although the objective paternity uncertainty rates are relatively low. Third, even if paternity uncertainty is a popular explanation for biased grandparental investment, it may not be sufficient alone.

Sex-specific reproductive strategies. Other authors incorporated sex-specific reproductive strategies into their models of grandparental investment, in order to explain the strong matrilineal bias of kin investment (Euler and Michalski 2007; Euler and Weitzel 1996). In mammals the production of eggs and the internal gestation require higher minimal parental investment in females compared to males (Trivers 1972). In order to maximize genetic replication, females ought to maximize maternal investment and reduce further mating efforts. Males, however, due to their reproductive success through mating with multiple females, ought to reserve resources for further mating effort and not expend all resources on paternal effort.

As a consequence, individuals ought to direct their kin support to where it is needed most, that is, sex – specifically to female kin. Thus, maternal grandparents ought to invest more in their daughters and their daughters' children than paternal grandparents invest in their sons and their sons' children (Euler and Weitzel 1996).

The paternity uncertainty explanation predicts the same amount of investment of the maternal grandfather and the paternal grandmother, as both have one link of paternity uncertainty. The assumption of sex-specific strategies, however, further predicts differences in grandparental investment between the maternal grandfather and the paternal grandmother. Following this reasoning, maternal grandfathers, as they invest in their daughter's children, should invest more than paternal grandmothers, who invest in their sons' children (Euler and Weitzel 1996).

The combined effect of paternity uncertainty and sex-specific reproductive strategies thus predicts the often found pattern of grandparental investment, where the maternal grandmother invests most, followed by the maternal grandfather, the paternal grandmother, and the paternal grandfather (Coall and Hertwig 2010). This

asymmetric pattern of biased grandparental investment cannot be explained away by confounding factors like the age of the grandparents (the maternal grandmother is, on average, the youngest and the paternal grandfather the oldest) or residential distance (Euler and Weitzel 1996; Pashos 2000). Other confounding factors, such as birth order, parent age, and grandchild age, were reported in the literature to play inconsistent roles (Euler and Michalski 2007; Euler 2011).

Preferential investment hypothesis. Sex-specific reproductive strategies might explain why maternal grandfathers invest more in their grandchildren than paternal grandmothers. Laham (2005) proposed an alternative hypothesis for this biased grandparental investment. In their preferential investment hypothesis, they assume that alternative investment outlets, i.e., alternative investment options in matri- or patrilineal grandchildren, might additionally explain the strong matrilineal caregiving bias. The existence of daughters' children should reinforce the matrilineality and therefore the investment of the maternal grandfather over the paternal grandmother, whereas the missing of daughters' children should reinforce the investment in sons' children and hence the role of the paternal grandmother. Laham et al. (2005) found some empirical support for their hypothesis; other studies did not (Euler 2011). Taken together the empirical evidence supporting the preferential investment hypothesis is rather weak.

Asymmetric genetic relatedness and sex of grandchild. Chastil et al. (2006) pointed out that discriminative grandparental investment might be influenced by asymmetric genetic relatedness between grandchildren and maternal and paternal grandparents. DNA constitutes of chromosomes, which are either autosomes or allosomes (the latter are also known as sex chromosomes). Regarding autosomes, all four grandparent types are equally genetically related to their grandchildren, but this is not the case regarding allosomes. Males are heterozygous regarding the allosomes. Thus, paternal (but not maternal) grandparents are not symmetrically related to granddaughters and grandsons with respect to the sex chromosomes. Following this line of reasoning and assuming that

kin helper alleles are located to a significant extent on the sex chromosomes, paternal grandmothers are more closely related to granddaughters than maternal grandmothers. Further, maternal grandmothers and paternal grandfathers are more closely related to grandsons than are maternal grandfathers. Kirchengast and Putz (2016) found that the contact frequency between granddaughters and maternal grandparents is higher than between grandsons and maternal grandparents. However, the contact frequency between paternal grandparents and grandsons was only slightly (and not significant) higher than between paternal grandparents and granddaughters. Further, Chrastil et al. (2006) could not support the sex-chromosome relatedness hypothesis in two large datasets. Taken together the empirical evidence for this hypothesis is also rather weak.

Sociostructural explanations. Genetic relatedness, the grandmother hypothesis, paternity uncertainty, sex-specific reproductive strategies, preferential investment, and asymmetric genetic relatedness are ultimate, culture-independent explanations for biased grandparental investment. To some degree, the preferential investment hypothesis acknowledges structural features of the family (e.g., family size and number of grandchildren), but it is deeply grounded in kin selection mechanisms. Other, non-biological reasons for biased grandparental explanations are typically ignored in the evolutionary literature. As Coall and Hertwig (2011) point out, such non-biological, sociostructural approaches are not necessarily competing to evolutionary explanations; they simply operate on different levels. Besides the evolutionary analysis of the ultimate causes, which focuses the behavioral outcome of evolutionary mechanisms, behavior can also be explained directly by its proximate causes. Sociologists have identified structural forces (e.g., female participation in the labor force), social institutions (e.g., the taxation of bequest), and cultural values (for example family obligations and roles) as relevant factors in grandparental investment (Coall and Hertwig 2011). Regarding cultural values, for example, cross-cultural research on grandparental investment is noteworthy. Most studies on grandparental investment, as

well as in psychological research as a whole, rely on WEIRD (Western, educated, industrialized, rich, and democratic; Henrich et al. 2010) samples. In these modern urban societies, matrilineal-biased grandparental investment is nearly universal. Traditional rural societies, however, often show high levels of patrilateral grandparental investment. In rural Greece, for example, paternal grandparents, especially paternal grandmothers, provide more caregiving than maternal grandparents. Paternal grandparents were found to be the primary source of caregiving also in Iowa among rural farmers (USA) and in China. These results show the cultural variability of grandparental caregiving (Pashos et al. 2016; Strassmann and Garrard 2011).

Aunt and uncle investment. A possible way to study the proximate mechanisms underlying biased grandparental investment are aunts and uncles. First, individuals are related to the same degree to grandparents and aunts/uncles ($r = 0.25$). Second, there is no difference in kin certainty of an aunt and an uncle; brothers and sisters of the parents have the same certainty of relatedness with their sibling's children. Finally, potential confounds like co-residence are usually ruled out. As the grandparents live together as a couple, the grandfathers' investment in grandchildren might be positively affected by the grandmothers, especially in case of the maternal grandfather who often invests more than the paternal grandmother. These considerations together would predict just a laterality bias of more investment from maternal aunt/uncle compared to paternal aunt/uncle. The research, however, found only partially support for this prediction. Maternal aunts and uncles invest more than paternal aunts and uncles, but aunts also invest more in nieces and nephews than uncles do. Thus, the female role of caregiving neglected by the ultimate approaches described so far seems to be a likely candidate for this pattern of results and perhaps also as explanation for biased grandparental investment.

Family ties as explanations. A proximate explanation for the asymmetric kin investment could also be the stronger family ties of women compared to men, which lead to a matrilineal pattern of close female-female relationships.

The quality of the relationship between the caregiver (grandparent, aunt or uncle) and the parents of the caregiving recipient was also found to have an impact on the caregiving for grandchildren and nieces and nephews itself. Especially a good relationship between the maternal grandmother and the mother was found to have a positive effect on maternal grandmothers' caregiving (Danielsbacka et al. 2015; Matthews and Sprey 1985; Pashos 2000; Pashos and McBurney 2008; Steinbach and Henke 1998). Hence, family relationship networks appear to play a major role in kin caregiving (Cherlin and Furstenberg 1994; Lussier et al. 2002). Moreover, the caregivers' relationships to the parents of the caregiving recipients were found to explain caregiving asymmetries among grandparents and aunts and uncles to a great extent (Monserud 2008; Pashos and McBurney 2008).

From an evolutionary point of view, the stronger female family ties explanation, however, does not argue against an evolutionary explanation. The theory could explain the creation of proximate social pathways through which evolutionarily formed mechanisms of kin investment are passed (Pashos and McBurney 2008). In social sciences research on family relationship networks, the intention for kin caregiving is merely seen as a result of the social framework conditions or the so-called female kinkeeping effect. In evolutionary explanations, however, the motivation for kin investment is seen as a biological mechanism, which interacts with the social environment.

Non-consanguine Grandparental Investment

From an evolutionary perspective, consanguine grandchildren are expected to be favored over non-consanguine, for example, stepchildren. Furthermore, there is no differential genetic interest in step-grandchildren, and consequently the investment in grandchildren should not be asymmetric. Empirically for step-grandparents, the universal asymmetric matrilineal caregiving pattern has not been found. However, step-grandparental caregiving can be substantial and was found to be

differential between the four grandparents. In Western societies, the parents' stepfathers and, in particular, the grandmothers' later husbands (whose marriages took place when the parents were already adults) provided more kin investment than the parents' stepmothers and grandfathers' later wives (Pashos et al. 2016). When the biological grandparents were divorced and not widowed before they remarried with the step-grandparent, this effect was even stronger. The biological grandmothers' later husbands seemed to mirror the discrimination of the biological grandmothers in favor of daughters' children (as maternal grandmothers). The greater step-grandchild caregiving by grandmothers' later husbands might be explained by mating effort which induces them to invest in their new wives and wives' families (Pashos et al. 2016). By contrast, the grandfathers' later wives, aka step-grandmothers, might rather tend to invest their resources in their original, biological families (Dench and Ogg 2002). For biological parents of stepparents (which are also called step-grandparents), no such effects were found.

Conclusion

From an evolutionary view, grandparenthood has developed in our evolutionary past and is a significant kin investment supporting families in rearing children. The grandmother hypothesis assumes that grandparenthood has evolved through post-menopausal women.

Empirical research has shown that grandparental investment is not equal between the four grandparents, but biased. Many studies from modern Western societies, anthropological field studies, as well as historical data found larger investment from grandmothers compared to grandfathers, as well as larger investments from maternal compared to paternal grandparents. Different ultimate explanations refer to this matrilineal kin investment bias (see paternity certainty hypothesis, sex-specific reproductive strategies, preferential investment hypothesis, asymmetric genetic relatedness and sex of grandchild above).

Grandparental investment might be also explained by proximate, non-biological

approaches (see sociostructural explanations, aunt and uncle investment, family ties above). For example, cross-cultural research found no support for the matrilineal bias in grandparental investment in patriarchic organized societies. In such societies, grandfathers invest more in their grandchildren than grandmothers (Pashos et al. 2016).

As all explanations regarding consanguine grandparental investment are based more or less on kin selection mechanisms, other explanations for non-consanguine grandparental investment are required. As predicted, consanguine grandparents usually provide more caregiving than non-consanguine step-grandparents. However, also non-consanguine relatives can be important kin investors, especially step-grandfathers who are married to a biological grandmother. A suitable explanation for kin investment of not genetically related grandparents might be mating effort.

As Coall and Hertwig (2011) point out, evolutionary explanations are not necessarily competing with sociostructural approaches; they simply operate on different levels (ultimate vs. proximate). Thus, the joint acknowledgment of ultimate, as well as proximate explanations for consanguine and non-consanguine grandparental investment, is required to gain better insights in understanding grandparental investment in future research.

Cross-References

- Euler and Weitzel (1996)
- Father's Father Versus Mother's Mother
- Grandparenting
- Increased Grandchild Survival
- Maternal Grandmother Invests Most
- Paternal Grandfather Invests Least

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Grandparental Investment and Genetic Relatedness

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Synonyms

Grandparental involvement; Grandparental solicitude

Definition

Grandparental investment refers to all support that grandparents channel toward their grandchildren. Grandparents can invest in their grandchildren either directly or indirectly via a third party (e.g., via parents). Evolutionary theory claims that the

ultimate reason why grandparental investment exists is because grandparents are genetically related to their grandchildren, and by investing resources in their grandchildren, grandparents can improve their own inclusive fitness. Thus, genetic relatedness is a crucial element behind the evolutionary idea of grandparental investment. Biological grandparents have on average a 25 % chance of having the same genes as their grandchildren.

Introduction

Humans are a cooperative breeding species, meaning that other people besides biological mothers invest large amount of time and resources in children (Hrdy 2009). These allomothers often include the child's father, aunts, uncles, and grandparents. Based on inclusive fitness theory (Hamilton 1964), it is beneficial for these allomothers (e.g., grandparents) to invest in their kin because by doing so they can improve their own inclusive fitness. Due to the assessment of the reproductive value of the receiver, investments are usually predicted to go toward the younger generation. In particular, for post-reproductive grandmothers who cannot have own children anymore, helping their already born offspring in descending line tends to be the most efficient strategy to spreading their genes in future generation. Thus, grandparents should favor and invest in (all else being equal) their children and grandchildren over more distant relatives, older relatives, and non-related friends.

Nonbiological Grandparents

All humans have exactly four biological grandparents either they are alive or not. Due to the increased rates of divorce in parental as well as grandparental generations in Western societies, the proportion of nonbiological grandparents is also increasing. Children can have several types of nonbiological grandparents (Coall et al. 2014; Pashos et al. 2016). For instance, step-grandchildren may appear in the family because

the grandparent himself or herself has divorced and has acquired a new spouse who has grandchildren. The child of a grandparent may also have divorced and remarried with a new spouse who has children, who are thus stepchildren to the grandparent's child (Tanskanen et al. 2014; Westphal et al. 2015). In addition, grandparents or their children may have foster or adopted children. If children are adopted by their parents, they may have up to four living nonbiological grandparents. Obviously, the variety of ways children can have nonbiological grandparents makes the study of nonbiological grandparenthood very complex.

Since to date, there are only few studies concerning the difference between nonbiological and biological grandparental investments. This is the case although several previous studies have shown that in biological relationships parents invest more in their children compared to nonbiological parents (see Anderson 2011 for review). Two previous studies have investigated directly the difference between biological and nonbiological grandparental investments. These both have shown that nonbiological grandparents tend to invest less in grandchildren compared to biological grandparents. Using data from Germany and the USA, Pashos and colleagues (2016) found that step-grandparents invested less and were more distant to grandchildren than biological grandparents. Similarly, Coall and colleagues (2014) showed with data from 11 European countries that biological grandparents more likely looked after their grandchildren in a daily or weekly basis compared to nonbiological grandparents. However, the study by Coall and colleagues (2014) showed that biological grandparents more likely than nonbiological grandparents invest nothing at all in their grandchildren.

All nonbiological (grand)children are not necessarily treated the same way. Due to the variety of ways to one can have nonbiological children and grandchildren, the investment in them might be different. For instance, adopted children may be more desired than stepchildren, because in the case of stepchildren, it is more often a question of mating effort which involves children whereas

adopted children are usually wanted *per se*. Thus the investment made in adopted children may not differ from that made in biological children (Segal et al. 2015). However, in the case of grandparents, the mating effort may increase the investment in step-grandchildren if the remarriage happens in grandparental generation compared to the situation that both grandparents are step-grandparents (i.e., remarriage happens in parental generation) (Pashos et al. 2016).

Usually in situations described above, the non-biological relationship between grandparent and grandchild is well known for everybody involved. There is, however, a possibility that a grandparent may not be genetically related to grandchildren if the father is not the genetic father, through, for instance, infidelity or fertility treatments, and this fact may not be known to the grandparents, parents, and grandchildren involved.

Paternity Uncertainty

In humans, paternity uncertainty may affect the relationship between grandparents and grandchildren (Euler and Weitzel 1996). Because of the paternity uncertainty, human fathers can never be absolutely sure the child is related to them. In contrast, women who give birth to the baby do not meet this problem and can be sure that they really are related to the child. Paternity uncertainty creates an adaptive problem for human males, meaning that it is likely that there are some psychological adaptations regulating the amount of resources males are investing in offspring according to paternity uncertainty. In humans, paternity uncertainty may not influence only potential father's behavior but may also expand to extended kin, namely, grandparents.

In the case of grandparents, paternity uncertainty (also called relationship uncertainty) means that only the maternal grandmothers can be sure that they actually are related to their grandchildren, because they can be certain that both their daughters and their daughter's children are genetically related to them. Maternal grandfathers have one link with paternity uncertainty (via them and their daughters). Also paternal

grandmothers have one kinship link with paternity uncertainty (via their sons and sons' children). Paternal grandfathers are in most uncertain positions, because they may not be related to their sons and their sons may not be related to their children. Thus paternal grandfathers have two links of paternity uncertainty.

Based on paternity uncertainty, grandparents can bias their investment according to relationship certainty. Thus, maternal grandmothers are predicted to invest the most, following maternal grandfathers and paternal grandmothers. Finally, paternal grandfathers are predicted to invest the least. Several studies from contemporary societies investigating several types of grandparental investments (e.g., child care help, financial transfers, and contact frequencies) have shown support for this prediction (see Coall and Hertwig 2010; Euler 2011 for reviews). These results hold even after several potential confounding variables, including geographical distance, grandparental age, and grandchild age, are controlled for.

Sex Chromosome Relatedness

Although biological grandparents share on average 25 % of their genes with grandchildren, this holds only in the case of autosomal relatedness, while the unequal sex chromosome inheritance makes the relation more complicated (Chrastil et al. 2006; Fox et al. 2010; Tanskanen et al. 2011). Girls inherit one X chromosome from their mother and one from father. Their fathers have inherited these sex chromosomes from their own mothers (i.e., the girl's paternal grandmothers), and mothers have inherited them from both own mothers and fathers (these are the girl's maternal grandmother and grandfather). Also boys inherit one sex chromosome from mothers, and it includes genes from both maternal grandmothers and grandfathers. However, boys inherit Y chromosome entirely from their fathers who have inherited it from their fathers (these are the boy's paternal grandfathers). Based on the asymmetrical inheritance of sex chromosomes, paternal grandfathers share more genes with grandsons than granddaughters, and paternal

grandmothers share more genes with granddaughters than grandsons. In addition, paternal grandmothers are more related to granddaughters than maternal grandmothers, while maternal grandmothers are more related to grandsons than paternal grandmothers.

Based on sex chromosome relatedness, it could be expected that grandparents allocate their support according to grandchildren's sex. Previous studies investigating this topic have, however, produced mixed results. Using data from seven traditional populations, Fox and colleagues (2010) found some support the prediction. However, an increasing number of studies using data from contemporary societies have not shown convincing evidence for the sex chromosome relatedness predictions (see Chrastil et al. 2006; Kaptijn et al. 2013; Tanskanen et al. 2011).

Conclusion

Nonbiological grandparenthood is a complex subject to study. Different ways of having nonbiological grandchildren may affect the grandparental investment behavior. Studies comparing the investment of nonbiological and biological grandparents are scarce. Those few studies (Coall et al. 2014; Pashos et al. 2016) that exist implicate that especially intense investments are more often made by biological grandparents than by nonbiological grandparents. As Pashos and colleagues (2016) suggest, in addition to biological relatedness, it is important to separate different types of having nonbiological grandchildren. For some, the investment in grandchildren may be more related to the mating effort than the others which may in some cases generate more investment from nonbiological grandparent than is expected.

The possible effect of the degree of genetic relatedness is related to the grandparental investments through paternity uncertainty and unequal sex chromosome relatedness. One of the most robust result of grandparental studies is that maternal grandmother invests the most following maternal grandfather paternal grandmother and paternal grandfather. This can be explained by

uncertainty in genetic relatedness created by paternity uncertainty. Unequal sex chromosome relatedness would predict different investment according to grandchild sex, but these predictions have not been systemically supported by previous studies.

Although studies have found support for the inclusive fitness theory (Hamilton 1964) showing that greater genetic relatedness is often associated with higher amount of investment among grandparents, there is need for future studies showing in what circumstances socio-ecological factors can override the effect of genetic relatedness. Moreover, in contemporary societies with increased amount of blended families, it is important to compare the possible effect of genetic relatedness to grandparental investment in different family situations more carefully. Finally, longitudinal studies on the topic are needed.

Cross-References

- [Grandmother Hypothesis of Menopause](#)
- [Grandparents and Grandchildren](#)
- [Importance of Grandparental Investment](#)

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Grandparental Involvement

- ▶ [Cross-Cultural Research on Grandparental Investment](#)
- ▶ [Euler and Weitzel \(1996\)](#)
- ▶ [Grandfather Investment Versus Grandmother Investment](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Importance of Grandparental Investment](#)
- ▶ [Predictors of Grandparental Investment](#)

Grandparental Solicitude

- ▶ [Euler and Weitzel \(1996\)](#)
- ▶ [Grandparental Investment](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Importance of Grandparental Investment](#)
- ▶ [Predictors of Grandparental Investment](#)

Grandparenting

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Definition

Grandparenting including serving as alloparents may be beneficial for the development of the grandchildren and may provide role satisfaction, yet the longer duration of caregiving comes at a cost for grandparents.

Synonyms

[Alloparents](#); [Custodial grandparents](#); [Discriminative care](#); [Grandparental investment](#); [Kin selection theory](#); [Parents-as-mediators](#); [Paternity uncertainty](#); [Preferential investment hypothesis](#)

Introduction

Becoming a grandparent can be one of the most jubilating moments in one's life. In many cultures, grandfathers and grandmothers are revered and called “big father/big mother,” “big papa/big mama.” The addition of a new family member completes the basic intergenerational triangle of the family that includes grandparents, parents, and grandchildren (Van Ranst et al. 1995). Grandparents find a grandparenting role to be

generative, meaningful, productive, and full of satisfaction (Thiele and Whelan 2006), while communities and macro culture consider the role of grandparents to be multidimensional, dynamic, protective, and powerful.

Across cultures and centuries, the depth and breadth of grandparenting have been infinite. The role ranges from being an alloparent/care-giver, or a sibling, friend, teacher, therapist, mentor, a reservoir of the cultural traditions, and transmittals of cultural values and spirituality (Stelle et al. 2010). Custodial grandparenthood (aka skipped generation households) and residential grandparenthood are increasing rapidly. Custodial grandparenthood refers to grandparents that are legal guardians and are sole caregivers when biological parents are not present. Residential grandparenthood refers to grandparents who live with their children and grandchildren, are co-caregivers, but are not a legal guardian or sole provider.

Although it is debatable whether the increase in custodial and residential grandparenthood is a recent change, many cultures have always considered the role of grandparents an intrinsic part of the social fabric and natural way to preserve cultural values and heritage. Perhaps that is why, in Tongan communities, grandparents act as a bridge between ancestors and present and future generations and grandparents raise their grandchildren like their own (Ofahengaue Vakalahi et al. 2008). Similarly, in Asian cultures, *filial piety* and *respect for elders* sustain and strengthen the grandparents and grandchildren bond (Yee et al. 2008).

To further corroborate, in the USA alone, 7.3 million grandparents care for their grandchildren who are under the age of 18. Out of 7.3 million, 2.6 million grandparents are responsible for the basic needs of their grandchildren (US Census Bureau 2017). Likewise, in Europe, the grandparent's investment in their grandchildren is so extensive that Albertini (2016, p. 14 & 26) in his report on Survey of Health, Ageing, and Retirement (SHARE) suggested that grandparenting is "the most relevant downward flux of time resources." The amount of time that the respondents devote to this activity... seem to act as

substitutes of a weak public provision of formal childcare."

Notably, a remarkable increase in global life expectancy has added another layer to grandparenting. Globally, life expectancy has doubled since the 1800s. In the USA alone, the average life expectancy has increased from approx. From 60 to 80 years from 1950 to 2014 (Max Roser 2019).

In light of global improvements in life expectancy, the contributions of grandparents to an individual's development are not only protracted but also strengthened. Despite grandparenting being an intrinsic part of culture, in research, in the USA, little attention has been given to grandparents. Therefore, most of the studies included in this review are from European or Asian countries.

The entry will begin with a discussion of theoretical frameworks followed by the impact of grandparents on grandchildren' developmental outcomes, grandparenting role and grandparents, factors moderating grandparenting, and implications for social law and family policy and research and practice.

Theoretical Frameworks and Grandparenting

Allen et al. (2019) suggested the importance of integrating theoretical frameworks while researching grandparents. Applications of the theoretical frameworks describe and clarify the social mandates of role expectations and commitments to support each member of the dyad: in this case grandparent and grandchild. The authors also emphasized that grandparenting is a multidisciplinary area. Therefore holistic approach is necessary to appreciate the depth and breadth of the relationship thoroughly. For instance, grandparents as a social status can be a function of the family, community, and macro culture. How each of these interacts to provide dimensions and refinement to the grandparenting role and relationship needs to be further examined. To theorize, Allen et al. (2019) applied five theoretical frameworks. These theoretical frameworks are:

- (a) **Family Ecological Theory (Bronfenbrenner 1986, as cited in Allen et al. 2019).** The theory takes into account how various systems such as *micro*, *meso*, *exo*, *macro*, and *chrono* interact and strengthen the processes of grandparenting. As stated above, the increasing life expectancy and existing values related to *filial piety* may contribute to grandparents experiencing role enhancements (*chrono*). Conversely, the relationship may remain weak if the parents (*micro*) do not consent or approve of the relationship. Subsequently, the relationship between grandparents and their children along with other factors may dictate the frequency of contact and investment in grandchildren (Uhlenberg and Hammiii 1998).
- (b) **Family Systems Theory (Kerr and Bowen 1988, as cited in Allen et al. 2019).** The micro-level theory explains that families are a system and each member has a responsibility of sustaining the smooth functioning of the system to prevent disequilibrium. A loss or change in the life of one member, for example, the death of parents, reverberates throughout the system, and unless other members, in this case, grandparents, take over the role of custodial parents, the family system will remain in disequilibrium.
- (c) **Life Course Theory (Elder et al. 2003; as cited in Allen et al. 2019).** The life course theory focuses on the concept of linked lives across generations and suggests that changes in one generation will reverberate across generations impacting individual trajectories. To illustrate, *intergenerational solidarity* in many cultures mandates individuals to care and support each other. Thus, grandchildren's feeling of commitment toward their grandparents can be an act of reciprocity to repay for the care and support grandparents provided them in early or later years or could be an observational impact of watching their parents taking care of their parents (Even-Zohar and Sharlin 2009).
- (d) **Social Exchange Theory (as cited in Allen et al. 2019).** The theory takes into

consideration evaluation of interactions between individuals in a dyad. Thus, according to the theory, the members of the dyad in this case grandparents and grandchildren before becoming invested in their relationship carefully consider available resources, its associated costs to them, and how they would be benefitted. Imaginably, many grandparents may continue to be invested in their children as they see role satisfaction as a benefit (Allen and Henderson 2017).

- (e) **Family Stress and Resilience Theory (Hill 1958, as cited in Allen et al. 2019).** The theory, when applied to custodial grandparents or parents of low SES, offers a robust rationale behind the emergence of stress and mental health issues in grandparents as a result of increasing demands. The theory also brings into light the importance of social support in buffering the negative impacts of increasing demands on grandparents.
- (f) **Feminist Theory and Intersectionality (Allen and Henderson 2017).** Although an underutilized framework, Allen et al. (2019) suggested that the feminist theory accounts for grandmothers being more involved in caregiving and emotional labor than grandfathers. It also explains how the intersectionality of race, gender, SES, disabilities, and age may influence grandparenting.

Please note that other theories, such as kin selection theory and paternity uncertainty, are discussed in the section on factors moderating grandparenting.

Grandparents and Grandchild's Developmental Outcomes

It is a common knowledge that differences in extended family relations of an individual contribute to the differences in his/her developmental outcomes because of the alterations in the child-rearing environment. Among extended family members, grandparents contribute significantly to the development of their grandchildren and

remain prominent parental figures into adulthood (Mills et al. 2001). Even when grandchildren do not live with their grandparents, the indirect effects on the grandchild's development are significant. Perhaps that is why De-Guzman et al. (2018, p. 520) consider grandparenting and grandparents' role as a "vibrant influence and a synergistic force of endearing, endowing and enduring."

The direct and indirect effects of grandparenting on the developmental outcomes of an individual have been observed in all domains of development ranging from enhancements in interpersonal relationships to academic performance and physical activities.

In terms of physical and competitive activities, a study of Latino families reported that grandparents might provide direct support by taking grandchildren to sports camps, may advise on the positive impacts of physical activities, or offer tangible rewards to motivate grandchildren to participate in sports (Xie et al. 2017). The engagement in physical and competitive activities may further boost their grandchildren's sense of industry (Silverstein and Marengo 2001).

In the same vein, Møllegaard and Jaeger (2015) found that Danish grandparents' cultural capital (noneconomic resources such as knowledge, skills, and education) had a significant impact on grandchildren's academic performance and educational success. Likewise, Anderson et al. (2018) conducted a systematic review and reported that in 58% ($n = 69$) of the studies, grandparents' SES had a positive and significant effect on the grandchildren's educational outcomes regardless of the parents' SES.

Lastly, many researchers have reported that grandparents transmit positive attitudes and values, which may promote positive social-emotional development (Yusuf 2014). The positive emotional bond between grandparents and grandchildren is associated with improved prosocial behaviors, a stronger sense of self, development of healthy relationships and connections with peers, improved emotional regulation and resilience, and a decrease in aggressive behaviors (Kemp 2005; Sheridan et al. 2011; Hammer 2017; De Guzman et al. 2018).

Grandparenting Role and Grandparents

Overall, grandparents are essential agents of positive individual outcomes among the grandchildren. Having said that, grandchildren also play a crucial role in the development of physical, mental, and social outcomes of grandparents.

Kivnick (1982) proposed to shift the focus of research and emphasized grandparenting as a dyadic relationship rather than an individual experience. He then conducted a factor analysis of five factors related to grandparenting. These five factors were grandparents/grandparenting as (a) centrality to identity and meaning to life, (b) valued elder, (c) immortality through the clan, (d) reinvolvement with personal past, and (e) spoil/indulgence. The author validated the symbolic interaction theory and suggested that grandparenting offers ample opportunities to create meanings and identities for grandparents including enhancements in social status. Grandparenting is associated with positive health outcomes and well-being, closer relationships with grandchildren and children, higher levels of role satisfaction, perceptions of meaningful and productive life, and lower depressive symptoms among grandparents (Hayslip Jr. and Kaminski 2005; Choi and Zhang 2018).

Nevertheless, the grandparenting role comes at a cost and may have physical, psychological, and financial consequences on grandparents. Notably, the negative consequences are amplified among custodial grandparents of children with developmental disorders and mental illnesses in comparison with noncustodial and nonresidential grandparents. Given below are justifications for the unfavorable outcomes.

First, custodial grandparents have to shift their role from being a grandparent to a parent (Newman 2004) at an age and a developmental phase when parenting might not be conducive to their mental and physical health. Second, grandparents have reported to experience role ambiguity, higher levels of stress and anxiety, shame, guilt, conflict, anger, resentment, and financial drain because of adverse behaviors of not only grandchildren but also their children.

Finally, many grandparents after the loss of their children may worry about the well-being and future of their grandchildren (Minkler 2005; Waldrop and Weber 2001; Smith and Palmieri 2007).

Consequently, custodial grandparents may experience a decrease in the quality of social relationships and marital satisfaction (Minkler et al. 1992; Jendrek 1993) which may further result in poor mental and physical health of grandparents (Goodman et al. 2008).

Factors Moderating Grandparenting

Several factors may moderate grandparenting and their investment and involvement with grandchildren. Given below is a review of some of these factors.

Genetic relatedness and paternity uncertainty. Contributions of grandparents were measured in terms of unequal investment in their grandchildren. Although the definition of an investment may vary in research, it is often reported in terms of emotional closeness, degrees of contact, preferential treatment among grandchildren, and allocation of resources/or giving gifts.

At a theoretical level, the issue of unequal investment (aka discriminative care by paternal and maternal grandparents) is explained by paternity uncertainty, kin selection theory, and preferential investment hypothesis. Paternity uncertainty refers to perceptions of genetic relatedness; kin selection theory refers to the regulation of investment in kin, based on genetic relatedness; and the preferential investment hypothesis refers to preferential treatment in case of more certain kin. Studies that provide evidence for the positive associations between genetic relatedness and investment by grandparents are reviewed below.

Even though grandparents and grandchildren share 25% of their genes, maternal grandparents and paternal grandparents may invest differently. According to the paternity uncertainty and preferential investment hypothesis, maternal grandparents, especially the maternal

grandmother, are completely certain of the genetic relatedness. On the contrary, paternal grandparents, especially the paternal grandfather, are completely uncertain of the genetic relatedness.

The theoretical framework was tested and supported by researchers who applied preferential investment hypotheses to grandparenting. DeKay (1995) and Laham et al. (2005) concurred with the idea of unequal investment and discriminative care by paternal and maternal grandparents and suggested that maternal grandmothers invested the most, followed by maternal grandfather and paternal grandmother. The paternal grandfathers invested the least in their grandchildren. Unsurprisingly, maternal grandmothers and their grandchildren experienced a higher degree of emotional closeness and contact (Euler and Weitzel 1996; Bishop et al. 2009).

Furthermore, Tanskanen et al. (2014) added another layer to the issue of genetic relatedness and found that grandparents' involvement is higher for biological grandchildren than compared to step-grandchildren, thus providing another corroboration for the positive associations between genetic relatedness and investment in grandchildren.

Despite support in earlier studies, recently, researchers have criticized the emphasis on genetic relatedness and argued that the issue of discriminative care is complex and an agreement with the preferential investment hypothesis is questionable. Igel and Szydluk (2011) and Coall et al. (2014) suggested the integration of a comprehensive framework that includes sociological, economic, psychological, cultural, and political factors to examine grandparents investment.

Personal and Contextual Factors

In order to examine personal and contextual variables that influence grandparents' involvement in terms of frequency of contact, Uhlenberg and Hammiii (1998) categorized them into three main variables. These variables were a) opportunity variables that include geographical proximity, number of grandchildren sets, grandparents' health, and their employment status; b) gender/

family variables that include being a female, marital status of grandparents, and quality of relationship between parents and grandparents; and finally c) sociodemographic variables that include age, race, and educational status of grandparents.

In terms of opportunity variables, Uhlenberg and Hammiii (1998) reported that geographic proximity was the strongest predictor of frequency of contact, yet relationship with their children can mediate frequency of contact and quality of relationship. Thus, grandparents who live further away cannot be involved in day-to-day routines of their grandchildren consistently. Even when grandparents live closer to their grandchildren, their children and their relationship with them can influence the frequency and intensity of care provided. Thus, parents can act as gatekeepers of grandparents' involvement aka parent-as-mediators.

In terms of gender and family variables, first, the number of grandchildren or more sets of grandchildren may result in splitting time between sets and lower involvement or increased preference for a particular set of grandchildren. Second, unsurprisingly, grandmothers were found to be more actively involved than grandfathers and maternal grandmothers were more engaged in grandparenting than paternal grandmothers. Finally, married grandparents were more involved than widowed, remarried, and divorced. The findings on married and divorced/remarried grandparents may be the consequence of the negative ramifications of divorce on the relationship between parents and their children. Divorced and remarried grandparents either move farther away or get more involved with their new family (Uhlenberg and Hammiii 1998).

In terms of sociodemographic variables, advancing age resulted in lower physical competence to care and thereby resulting in infrequent contact and lower involvement. Interestingly, race and educational status did not significantly impact the frequency of contact (Uhlenberg and Hammiii 1998).

Recent research. Most findings of Uhlenberg and Hammiii (1998) have been replicated with similar findings. Silverstein and Marengo (2001) and King (2003) reported that divorced

grandparents and grandchildren share a weaker bond, are less involved in grandparenting, and contribute less frequently and intensely than married grandparents. The reasons for lower levels of involvement can be many such as grandparents live farther away or they may not have a good relationship with their children who serve as mediators between them and their grandchildren.

However, for custodial grandparents, Sands and Goldberg-Glen (2000) and Choi et al. (2016) contradicted the idea of advancing age and lower involvement. The researchers suggested that the younger (middle-aged), not older, grandparents invest less in their grandchildren. Lower involvement with grandchildren can be because middle-aged grandparents are still employed and therefore may often experience higher stress and anxiety due to competing demands between caregiving and professional commitments. Likewise, the cumulative negative impacts of role conflict, competing demands, and developmental disorders in grandchildren are higher in middle-aged grandparents than older grandparents.

Meanwhile, Mhaka-Mutepfa et al. (2015) suggested that in Zimbabwe, grandparents of higher SES, personal competence in terms of self-esteem and self-efficacy, resilience, and social networks experienced more resilient grandparenting than those who did not have these characteristics. Notably, in this study, advancing age was again associated with decreased caregiving competence and lower involvement.

Conclusions and Implications

Based on the evidence stated above, we can conclude that universally, a significant number of grandparents are involved and invested in grandparenting. Grandparenting provides potential benefits to grandchildren in all domains of their development and buffers the effects of childhood adversity, but the role comes at a cost to grandparents in terms of increased stress, depression, and financial drain. Besides, custodial grandparents may be left to cope with trauma, loss, and legal and medical repercussions of their

dysfunctional children. Interestingly, in the presence of adequate social support, the adverse outcomes may diminish and grandparents may feel more resilient in their role (Mhaka-Mutepefa et al. 2015).

The above findings have important implications for family policy and intervention programs. Similar to any caregivers, grandparents, especially custodial grandparents, require social support to sustain and effectively navigate their role (Kresaka and Gallagher 2014). Parent training programs, case management services, and federal policies and programs such as respite care, financial assistance, SSI, health insurance, and more can benefit grandparents tremendously. Sparng et al. (2015) further argue that custodial grandparents' interventions must integrate a trauma-informed approach to help them cope with grief and loss of their grandchildren, whereas Choi et al. (2016) advocated customized individual interventions to support the dyadic relationship and mitigate the effects of negative outcomes.

Cross-References

- [Cross-Cultural Research on Grandparental Investment](#)

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Grandparents and Grandchildren

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Synonyms

Extended family relations; Intergenerational relations

Definition

Relationships between grandparents and grandchildren are a part of intergenerational family relations. According to sex and lineage, there are four possible types of biological grandparents: maternal grandmother, maternal grandfather, paternal grandmother, and paternal grandfather. Moreover, there are several possible nonbiological grandparent–grandchild dyads that are not the topic of this chapter. Interaction between grandparents and grandchildren is typically not only between those two generations but involves the middle generation that is the parents of (grand)children. Especially when grandchildren are small, the parents may act as gatekeepers between grandparents and grandchildren, and, thus, the quality of parent–grandparent relationship is important for the quality of grandparent–grandchild relationship. In evolutionary literature, the grandparent–grandchild relationship is typically studied from the viewpoint of grandparents' fitness interests, and it often encompasses biased grandparental investments and the child outcomes of grandparental presence and investments.

Introduction

Recent rise in life expectancy have increased shared years of life between grandparents and grandchildren. At the same time, the number of (grand)children has decreased in Western world. This means that the time grandparents spent with each grandchild may increase (Coall and Hertwig 2010). Due to these recent demographic transitions, the relationship between grandparents and grandchildren has nowadays the potential to be more important than ever before.

In evolutionary literature, humans are often defined as a cooperative breeding species (Hrdy 2009; Sear 2015). Cooperative breeding means that human's species-typical child-rearing involves, in addition to the child's biological mother, other caretakers (so-called allomothers) who are needed because of humans' exceptionally long dependent childhood. These allomothers may include, for instance, the child's father, older siblings, aunts, uncles, and grandparents.

Hamilton's (1964) kin selection theory explains why it is beneficial for kin members, such as grandparents, to help their close kin, especially in the descending line. Kin selection theory states that an individual can enhance its inclusive fitness by supporting close relative's reproductive success (indirect fitness), at the expense of its own direct fitness (Hamilton 1964). According to kin selection theory, all else being equal, people should favor and invest more in their close kin than more distant kin or non-related friends. In addition, Trivers' (1972) theory of parental investment, which easily extends to the theory of grandparental investment, accounts all investments (grand)parents make in their offspring. In the case of grandparents, these investments include, for instance, contact frequencies, childcare help, emotional support, and financial assistance (Euler 2011).

In the case of grandparenthood, there are several ways one can have nonbiological grandchildren which makes the study of nonbiological grandparenthood very complex. Moreover, all nonbiological (grand)children are not necessarily treated the same way. Adopted children (and their children) may be more desired than

stepchildren, and thus the investment made in adopted children (and their children) may not differ from the investment made in biological children and their offspring (Segal et al. 2015) although there is evidence that grandparents in general invest more in their biological than non-biological grandchildren (Coall et al. 2014). In this article, the relationship between grandparents and grandchildren is reviewed from the viewpoint of biological grandparenthood.

The relationship between grandparents and grandchildren is almost inevitably influenced by the middle generation (i.e., the parents), at least when the grandchildren are young, because grandparental support may be channeled to the grandchild indirectly via grandparents' own children or their children's spouses instead of a direct support (Euler 2011). Parents can guard access to a grandchild and act as gatekeepers between grandparent and grandchild. This chapter considers different aspects of the relationship between grandparents and grandchildren by concentrating on biased grandparental investment pattern, parents' role as gatekeepers, and grandparents' positive and negative impact on grandchild well-being.

Biased Grandparental Investment Pattern

All grandparents have on average a 25 % chance of having the same genes with their grandchildren, and, thus, according to the kin selection theory, they should invest equal amount in their grandchildren. However, empirically, this is not the case. One of the most robust finding in grandparent studies is that typically maternal grandmother invests the most in grandchildren, following maternal grandfather and paternal grandmother who either invest equally or maternal grandfather invests slightly more, and finally paternal grandfather who invests the least (Coall and Hertwig 2010; Euler 2011). Reason for this biased grandparental investment pattern stems from human's sex-specific reproductive strategies, paternity uncertainty, and a tendency to invest preferentially in more certain kin.

Sex-specific reproductive strategies predict that due to more obligatory maternal than paternal investment, grandparents should allocate their support more probably in their daughter and her children than their son and his children (Euler 2011). Paternity uncertainty in turn assumes differences in the investments according to the certainty of the genetic relatedness. Paternity is more uncertain than maternity, and this creates the pattern where maternal grandmother has no uncertainty that the grandchild is hers, maternal grandfather and paternal grandmother both have one link of uncertainty, and finally paternal grandfather has two uncertain links (Euler 2011).

Paternity uncertainty does not directly explain the commonly found difference between maternal grandfather and paternal grandmother. Maternal grandfathers typically tend to invest more in their grandchildren than paternal grandmothers do, although the genetic certainty is the same. The result is sometimes explained by incidental exposure, meaning that maternal grandfathers' larger amount of investment is due to their spouse, the maternal grandmother, who invests the most (Pollet et al. 2006), but it can also be due to the fact that paternal grandmothers have additional grandchildren via daughter(s) and thus they may prefer to invest in their daughter's (who are more certain kin) than their son's children (Laham et al. 2005). Preferential investment in more certain kin hypothesis has gained support in a large study of European grandparents (Danielsbacka et al. 2011).

Other factors, besides the sex and lineage of a grandparent, are also associated with grandparental investments. These are quality of relationship between grandparent and parent, geographic distance, number of grandchild sets, and marital status of grandparent (Uhlenberg and Hammill 1998). Also grandparent's age and health as well as grandchild's age may matter, because older grandparents who are in poorer health may not be able to have so intense relations with grandchildren as younger and those who are in better health (Danielsbacka and Tanskanen 2012). Also the younger the grandchildren are, the more frequent the contacts with grandparents usually are. In the case of the sex of a grandchild, the

results are mixed. Theoretically, the asymmetric impact of X- and Y-chromosome inheritance could affect the bias in grandparental investment (Euler 2011), because in respect to sex chromosomes the grandchildren are asymmetrically related to their maternal and paternal grandparents. Studies concerning the asymmetric impact of X- and Y-chromosome inheritance have, however, produced mixed results, and no consistent association between grandparental investment and grandchild sex has been found (e.g., Chrastil et al. 2006; Tanskanen et al. 2011).

The above described pattern of biased grandparental investment is remarkably solid in contemporary Western societies even when other potentially confounding factors are controlled for (e.g., Danielsbacka et al. 2011). However, strong patrilocal or patrilineal preference, which was common in previous societies and is in some contemporary societies (e.g., in contemporary China), may override the effects of sex-specific reproductive strategies and paternity uncertainty (Kaptijn et al. 2013; Lahdenperä et al. 2004; Pashos 2000). The reason for this is that in patrilocal societies, the emotional options for attachment to maternal kin do not get an opportunity to develop and at the same time fathers' certainty of their fatherhood is usually enhanced.

Parents as Gatekeepers

If the relationship between grandparents and grandchildren is looked only from grandparents' viewpoint, it is often forgotten that grandparents cannot take for granted that their investment is accepted. Because the relationship and interaction between grandparent and grandchild can be direct or indirect the middle generation (parents) have an important mediating role. The mediating or gatekeeping role of parents is more significant the younger the grandchild is. It is shown in many studies that the quality of the relationship between parental and grandparental generations is associated with the quality of grandparent–grandchild relationship (e.g., Michalski and Shackelford 2005).

In addition, it is often ignored that the relationship between grandparents, parents, and grandchildren includes also in-laws, who are genetically non-related to each other. As an extension to kin selection theory, Hughes (1988) has argued that in-laws, who are usually not closely genetically related, become “inversely” genetically related to each other through common descendants. Thus, in terms of parent–grandparent relationship, the in-law relationship might be more influenced by the advent of a (grand)child than biological parent–grandparent relationship, and the quality of in-law relationship may also be more important for the good grandparent–grandchild relationship than the relationship between grandparent and his or her own child (Danielsbacka et al. 2015).

From evolutionary viewpoint, due to consanguinity, sex-specific reproductive strategies, and paternity uncertainty, the quality of the relationship between eight different parent–grandparent dyads should be expected to be better between genetic kin and among them the best between maternal grandmother and her daughter and worse between in-laws and among them the worst between paternal grandfather and his daughter-in-law, although in empirical studies the worst relationship seems to be between paternal grandmother and her daughter-in-law (Euler et al. 2001). Thus, based on relationship quality between parent and grandparent generations, the gatekeeping role of a daughter-in-law toward paternal grandparents should be the most significant.

The Outcomes of Grandparental Presence and Grandparental Investment

In evolutionary research, it has been a great subject of interest whether grandparents can improve (or could have improved) their inclusive fitness by investing in their children and grandchildren. In studies analyzing the historical and traditional societies, the child outcomes of grandparental presence have been often measured by fertility and child survival. In modern societies, however, grandparents are not anymore needed to keep the

children alive as they were in subsistence societies, and, thus, the outcomes of grandparental investments should be measured with milder indicators of child well-being (Coall and Hertwig 2010).

In high fertility and high child mortality societies, the presence of grandparents has been found to improve grandchild survival (e.g., Sear and Mace 2008), and grandparental presence may have also had influence on parent's age at first birth and the number of children (e.g., Lahdenperä et al. 2004). Also, nowadays grandparents may have an impact on parents' childbearing decisions (e.g., Tanskanen et al. 2014), and they may increase the grandchild well-being measured by, e.g., child development, educational success, and lack of emotional and behavioral problems (e.g., Tanskanen and Danielsbacka 2012). In addition, studies from contemporary societies also implicate that active grandparenting (i.e., caring and spending time with grandchildren) may improve grandparents' own health and well-being as long as caring duties are not overwhelming (Coall and Hertwig 2010).

Grandparental presence is not, however, always beneficial for grandchildren. Local resource competition model takes into account the possible detrimental effect of three-generational household units for the grandchild well-being (Strassmann and Garrard 2011). If local resources are scarce and/or grandparents are very old and in poor health, they may compete with grandchildren over limited resources and parental care and time. Previously, the local resource competition has been studied only in historical and contemporary subsistence societies (e.g., Strassmann 2011). However, resource competition may also explain the results gained in prior studies concerning contemporary societies that have found that child well-being is lower when children are living in three-generational households compared to two-generational families (e.g., Krueger et al. 2015).

Previously found detrimental effects of grandparental presence can also be due to the different fitness interests of different grandparent types which are based on sex-specific reproductive

strategies. For instance, the presence of mothers-in-law has found to have detrimental effects on child survival and well-being in traditional and historical societies (e.g., Leonetti et al. 2007; Volland and Beise 2005).

Conclusion

The relationship between grandparents and grandchildren is a part of an extended family relations which stem from the human's species-typical cooperative breeding system. In evolutionary literature, grandparent–grandchild relationship is often studied as a manifestation of grandparental investment and interest that have focused on its unequal distribution. Sex and lineage are one of the main determinants of grandparental investment, meaning that in contemporary Western societies maternal grandmothers are typically the ones who invest the most in grandchildren, following maternal grandfathers, paternal grandmothers, and finally paternal grandfathers. The pattern tends to remain robust even after several potential confounding variables are controlled for.

The relationship between grandparent and grandchildren is inevitably influenced by the middle generation. That is why the quality of grandparent–grandchild relations are often in some degree contingent upon the quality of parent–grandparent relations. Parents are in important position between the grandparents and grandchildren because they may either act as gatekeepers or enhance the interaction between grandparents and grandchildren. Parent–grandparent couples form eight dyadic relationships, each which quality can be predicted by sex-specific reproductive strategies and paternity uncertainty. In general, in-law relations are predicted to be worse than the relations between genetic kin. In-law relations may also be more easily influenced by the advent of (grand)children.

In evolutionary studies, the positive outcomes of grandparental presence and grandparental investments have been studied far more than possible negative outcomes of them. It has been

found that in previous societies as well as in contemporary traditional societies grandparental presence has associated with grandchild survival and the number of grandchildren born. However, it has also been found out that when there is a lack of resources, grandparents may compete with grandchildren over the local and family resources, and, thus, in some circumstances, the presence of a grandparent may have detrimental effects for child well-being. In addition, due to different fitness interests and reproductive strategies between grandparent types, the presence of mothers-in-law, in particular, may have detrimental effects for grandchild well-being. These potential harmful effects have not been studied in contemporary societies. In modern societies, the positive outcomes of grandparental investment have been confirmed in several studies.

Cross-References

- [Grandmother Hypothesis of Menopause](#)
- [Importance of Grandparental Investment](#)

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Grasslands

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Synonyms

Pasture; Plain; Prairie; Savannah

Definition

A grassy, large open area, often used for grazing, where grasslike vegetation is often the dominant form of plant life.

Introduction

As early hominins developed into eventual *Homo sapiens*, a major step in their change in biological structure and the formation of bipedal locomotion was their change in environment. These early hominins transitioned from living in trees as modern primates do to moving down to savannahs and, as a result, changing their physiological structure through the gradual process of evolution to adapt to hunting and surviving on the African savannah. The savannah, or grasslands, provided a major change from hominins’ previous environment, including climate, elevation, and prey, among various other differences that worked in congruence to illicit change in these hominins – among those changes being bipedal locomotion.

Why Did We Leave the Treetops?

The exact reason as to why we left the treetops is a subject of debate within the evolutionary science community. A common question to evolutionary science is, “Well, if we’re human as a result of evolution, then why are there still monkeys today?” The answer to this question lies within this exact concept – that we left the trees some 5 million years ago to the ground, where we eventually moved out into savannahs. This departure then allowed that group of hominins to evolve differently over the course of millions of years, resulting in the changes that we see in our own bodies today, as compared to the physiological mechanisms still apparent in modern chimps. Some theorize that we didn’t simply go straight from the trees to the savannah – in fact, we may have spent a considerable amount of time living on the grounds of these forests rather than in the trees. This is supported by evidence such as remains of forest animals found nearby early

hominin skeletons – suggestive of hunting these animals on the ground floor of the forest. Modern chimps and gorillas spend a considerable amount of time on the floor; therefore a possible reason for our migration may simply have been our ancestors spending more time on the ground as compared to other apes and, as a result, adapting accordingly. Once enough adaptation was sufficient, our ancestors may then have moved on to other areas that were more suitable for their changes, given their loss of climbing ability and their increased ability to throw and create weapons due to their development of bipedal locomotion (Wheeler 1984).

Climate Change

Others theorize that our moving out into the savannah may have been a result of climate change (Demenocal 2004). Changes in seasonal patterns or climate may have resulted in changes to the forestation of these areas, as well as the kind of vegetation and prey that was available for our ancestors to survive. Certainly a depletion of these resources would have been a logical reason for our ancestors to move out and look for more suitable conditions outside of the forest and into the savannah where the climate change effects would have been less pronounced due to the dearth of trees in the area.

Were We “Pushed Out”?

Another theory is that our relatives such as early chimpanzees simply were more adept at climbing and therefore were in heavy competition for resources and space in the trees (Jacobs 2004). If they became more adept as a result of evolution and began to take all of the resources, it is possible that our early hominins simply migrated further down the trees and began to adapt to a new lifestyle whereby they could hunt for resources by not competing with chimpanzees. Being pushed down to our new environment would have required significant changes in our biological structure, which may have also been a reason for the development of bipedal locomotion.

Conclusion

Early hominins were forced to move into grasslands due to leaving the trees, whereby we developed the ability to walk on two legs in order to accommodate to our new environment and lifestyle. Although the reason why we left the trees is unknown, there are a number of theories that attempt to explain why we felt the need to move out of the trees. Among them are simply spending more time on the ground as many modern chimps and gorillas do, and therefore developing physiologically accordingly, and then moving out into savannahs with more resources. Another could have been climate change, whereby a lack of trees and resources forced us to move lower in elevation and eventually into grasslands to ensure survival. Lastly, it may also have been attributed to a competition in resources with our ancestors and simply pursuing areas where we could lessen competition and still benefit from gaining the resources found at the forest floor. Whatever it may be, it is undeniable that the change from moving out of trees and into flatland savannahs was a major contributing factor to human development through bipedal locomotion.

Cross-References

- [Climate and Habitat Diversity](#)
- [Habitat Change](#)
- [Three Stages of Habitat Selection](#)

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Gratitude, Sympathy, and Empathy

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Synonyms

Einfühlung; Emotional contagion; Empathic concern; Personal distress; Perspective taking

Definition

Gratitude, sympathy, and certain forms of empathy often result in behavior that benefits others at cost to the self. Making sense of these emotional phenomena from an evolutionary perspective is challenging, given they would seem to be non-adaptive for the individual. However, evolutionary processes such as kin selection, reciprocal altruism, and exaptation may give rise to mechanisms for these phenomena when immediate cost to the individual can translate into long-term survival or reproductive benefit. It is essential to clearly identify the nature of the phenomena under examination when evaluating or empirically testing evolutionary explanations for phenomena related to gratitude, sympathy, and, especially, empathy.

Introduction

Gratitude, sympathy, and empathy are challenging phenomena to understand from an evolutionary perspective. Most emotions can be readily conceptualized as evolutionary adaptations that have promoted individual survival and reproductive fitness. However, the terms *gratitude*, *sympathy*, and *empathy* refer to phenomena that may place a burden on the individual in terms of survival or reproductive fitness. Indeed, the phenomena identified by these terms can generate

prosocial behavior that increases the wellbeing of others, often at a cost to the self. Yet, it is possible to understand these phenomena from an evolutionary perspective if one considers how short-term cost to the individual can contribute to the longer-term fitness of individuals or to those genetically similar to them. But before undertaking such an analysis, first one must clearly establish the phenomena to which the terms gratitude, sympathy, and empathy refer.

Gratitude

Gratitude refers to a positive emotion evoked by perception that one has received benefit from the generosity of another (McCullough et al. 2001). The intensity of gratitude is affected by a number of perceptions of the benefactor. People report feeling more gratitude in response to a benefactor who they believe has (a) intentionally sought to benefit them; (b) is more relationally distant; and (c) has provided a benefit that is of high cost or high value. When people experience gratitude in response to a benefactor, research suggests that they are more likely to benefit their benefactor in return. Moreover, research suggests that expressions of gratitude spur benefactors to benefit others in the future (McCullough et al. 2001, 2008).

Sympathy

The term *sympathy* has been used to label two related, but distinct, emotional phenomena. The term was originally used to describe feeling the same emotional or affective experience as another person. However, the term is used by some contemporary social scientists to describe a feeling of concern for another in need. Still other social scientists label this emotional reaction *empathic concern* or *empathy* instead of sympathy (Batson 2011). Indeed, inconsistency in the use of the terms sympathy and empathy to describe related, but distinct, affective phenomena has been a source of much confusion in the literature. Sympathy (empathic concern) is produced by adopting the perspective of another in need. It is more

readily elicited by those who are considered not responsible for their own need, those whose welfare is valued, and those who are perceived as vulnerable or exhibit attributes associated with vulnerability (e.g., childlike characteristics; Batson 2009).

Experimental research suggests that the experience of sympathy (empathic concern) produces altruistic motivation. This mechanism is the focus of the empathy-altruism hypothesis (Batson 2011). Specifically, according to this hypothesis, sympathy produces altruistic motivation to increase the welfare of another as an end itself, rather than motivation to benefit the self. In turn, this motivation can lead to prosocial behavior that is costly to the self. Experimental studies have offered support for this intriguing hypothesis. Yet, these findings have long perplexed those seeking an evolutionary account of human altruism, especially because the vast majority of research consistent with the empathy-altruism hypothesis has involved the effects of sympathy on helping of genetically unrelated strangers (Batson 2011).

Empathy

The term *empathy* was first used by Titchener to describe the process of *emfühlung*, whereby an observer seeks to mentally project the self into the state of another person or object. However, the term empathy is now used to describe at least eight related, but distinct cognitive, affective, and behavioral phenomena. These phenomena include (a) *aesthetic perspective taking* (i.e., *emfühlung*); (b) *imagine-other perspective taking*, whereby one seeks to imagine the mental states of another; (c) *imagine-self-perspective taking*, whereby one seeks to imagine how he or she would think and feel in another's situation; (d) *accuracy in identifying the mental states* of others; (e) *feeling the same emotion or affective experience as another* in response to his or her situation or behavior; (f) *feeling other-oriented concern* (i.e., sympathy, empathic concern) for another in need; (g) *feeling self-oriented distress* in response to another in need; and (h) *adopting the same behavioral postures, expressions, or mannerisms* of another (Batson 2009).

Given the number of phenomena identified by the term empathy, it is unclear whether one can satisfactorily integrate all these concepts or even a subset of these concepts into a single undifferentiated theoretical construct. Also important to note is that it may be inappropriate to consider sympathy as distinct from empathy. Instead, it may be best to consider sympathy as one of many phenomena falling under the umbrella term *empathy*.

Unlike gratitude and sympathy, which appear related to prosocial behavior that benefits others at some cost to the self, a number of phenomena related to empathy are not necessarily prosocial. For example, perspective taking can generate sympathy or other forms of affective empathy that produce prosocial behavior that is costly to the self in some situations (Eisenberg et al. 2010). However, in other situations perspective taking can promote behavior that directly benefits the self, such as ability to more effectively interact with, learn from, and detect deceit in others (Tomasello 1999). In these situations, perspective taking can lead to attainment of positive outcomes or avoidance of negative outcomes that would directly increase one's relative fitness. Certain affective empathy phenomena (besides sympathy) may convey direct self-benefit as well. For example, a tendency to experience emotions similar to those of others in response to witnessing their reactions to situations may promote simulation of mental states that helps guide behavior and understanding of the environment (Decety and Grèzes 2006). Another empathy phenomenon, self-oriented distress caused by witnessing another in need, can lead to costly helping behavior, but this is not the preferred option. Instead, distress tends to evoke an egoistic motive to escape from the need situation (Batson 2011). Thus, it is not clear that all empathy phenomena produce behavior that benefits others at a cost to the self in all situations.

Evolutionary Explanations

Traditionally, evolutionary explanations for prosocial behaviors produced by gratitude and sympathy, and to a lesser extent some empathy

phenomena, involve a consideration of how they are linked to adaptations that promote one's own fitness, or one's inclusive fitness (the fitness of other individuals who share genes similar to the self), despite incurring immediate cost to the self. Evolutionary processes that can speak to the emergence of such adaptations include reciprocal altruism (Trivers 1971), kin selection (Hamilton 1963), and exaptation (Buss et al. 1998).

Gratitude. As noted above, gratitude appears to motivate helping of benefactors directly or to motivate expression of gratitude to benefactors. Gratitude expression then reinforces benefactors to benefit others in the future. Given that this exchange process seems most potent among relationally distant individuals, who are more likely to be nonkin, the emergence of mechanisms that give rise to gratitude and the reinforcement of receiving gratitude expressions suggest adaptations resulting from reciprocal altruism (McCullough et al. 2008). Specifically, gratitude adaptations may have emerged because interactions between individuals who possessed traits for feeling and expressing gratitude and individuals who possessed traits for sensitivity to gratitude expressions produced greater relative reproductive advantage overtime than did interactions between individuals who did not possess such traits.

Sympathy. Upon casual consideration, the psychological mechanism of sympathy (empathic concern) and the altruistic motivation it evokes can be explained by kin selection. That is, those with traits for sympathy were more likely to benefit and promote the fitness of those with similar genes. The tendency for people to experience more sympathy for those in need whose welfare they value seems consistent with this explanation. However, the kin selection explanation cannot account for empirical evidence of sympathy-induced altruism from experimental studies of helping directed toward strangers (Batson 2011). In many of these experiments, there is no anticipation of interaction and no genetic similarity between benefactors and those they benefit.

One possibility is that the capacity for sympathy is an adaptation evolved to promote care of

offspring or young (as a result of kin selection) that can combine with capacities for complex cognitive representation and abstraction that arise from adaptations selected to promote fitness in behavioral domains unrelated to care of offspring. This combination of capacities may permit generalization of sympathy to situationally vulnerable non-offspring (c.f., Batson 2011). Thus, sympathy-induced altruism toward strangers could be a more complex psychological mechanism upon which natural selection did not operate. However, this expansion of parental nurturance to nonkin may well involve the interplay of two mechanisms upon which natural selection did operate for different functional reasons.

Empathy. As discussed previously, the direct benefit to the individual's fitness in cases where the phenomena clearly promote self-benefit (e.g., detection of others' intent to deceive via perspective taking) can readily explain a number of empathy-related phenomena. In cases where empathy phenomena appear to promote benefit of others at cost to the individual, understanding of the phenomena from an evolutionary perspective can be quite challenging. One can seek to identify adaptive functions of such phenomena that may have emerged as a result of either kin selection or reciprocal altruism. Alternatively, some empathy phenomena may be better explained not as adaptations but rather (a) as exaptations, which are earlier adaptations co-opted through the process of natural selection to address a new fitness-promoting function, (b) as spandrels, which are by-products of earlier adaptations co-opted through the process of natural selection to address a new fitness-promoting function, or (c) as by-products of previous adaptations that serve no fitness-promoting function (c.f., Buss et al. 1998).

Conclusion

Gratitude, sympathy, and certain forms of empathy promote behavior that benefits others at cost to the self. Understanding the evolutionary origins of the mechanisms that give rise to these phenomena poses challenges, given that such mechanisms are

not obviously adaptive. However, evolutionary processes such as reciprocal altruism, kin selection, exaptation, and spandrels may account for these mechanisms when immediate cost to the individual can translate into long-term survival or reproductive benefit under certain selection pressures. It is essential to clearly identify the nature of the phenomena under examination when evaluating or empirically testing evolutionary explanations for gratitude, sympathy, and especially the variety of empathy phenomena.

Cross-References

- [Altruism](#)
- [Empathy](#)
- [Imitation and Mimicry](#)
- [Kin Selection](#)
- [Reciprocal Altruism](#)

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Gravidity

- [Implications for Pregnancy](#)

Gravity Hypothesis, The

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Synonyms

[The gravity hypothesis of sexual size dimorphism](#)

Definition

A hypothesis explaining why extreme sexual size dimorphism (SSD), with males being hundreds of times smaller than females, may have evolved (Moya-Laraño et al. 2002). This hypothesis proposes that the race to reach sexually receptive females favors smaller males, particularly in those large species in which females live high up in tall vegetation. The underlying mechanism invokes the Earth's gravitational pull: all else being equal, small males can climb faster than large ones to reach females. Some recent updates and refinements of the hypothesis, including other traveling modes, may actually have stronger explanatory power (Moya-Laraño et al. 2009; Corcobado et al. 2010).

Introduction

In most animal species, males and females differ in many aspects of their morphology, physiology, and behavior, well beyond their fundamental differences in reproductive biology (Fairbairn et al. 2007). Why these differences exist has been a key question biologists try to answer since Darwin (1871). Body size is the most

important characteristic of any individual because body size is intimately related to all other aspects of life, such as physical strength, metabolic rate and thus energy and nutrient requirements, and egg production. Body size is also the trait for which differences between males and females are most common across animal species (Fairbairn et al. 2007). Key questions are: Why do males and females differ in size? Why is there large variation with respect to the degree of these size differences? and When and why are these differences extreme?

Several hypotheses try to explain the evolution of extreme sexual size dimorphism (SSD) in the group of terrestrial animals in which this phenomenon is common, the spiders (Araneae). Indeed, in some spider species, females may be one hundred times heavier than males (Foellmer and Moya-Laraño 2007). The hypotheses put forward so far to explain this phenomenon have been reviewed somewhere else (Foellmer and Moya-Laraño 2007; Moya-Laraño et al. 2013). In brief, the sexual cannibalism hypothesis was initially put forward by Darwin (1871) and states that males evolved much smaller body sizes than females because they would be disregarded by females as potential prey (i.e., too small to be profitable) or because they would be able to enter the female's web without being detected by her in the first place, prior to the onset of copulation. Evidence supporting this hypothesis (e.g., larger males being more likely killed by females) is scant (Foellmer and Fairbairn 2004; Moya-Laraño et al. 2013). On the contrary, recent evidence suggests that extreme SSD (i.e., large female size relative to male size) in spiders evolved first and that sexual cannibalism evolved subsequently in dimorphic species, presumably because females were large enough to catch males without putting themselves at risk (Wilder and Rypstra 2008). In addition, in nonweb building species with moderate SSD females actually prefer to kill smaller, not larger males (Prenter et al. 2006). Another hypothesis, the differential mortality model (DMM), explains the evolution of extreme SSD by selection favoring earlier male maturation at a small size, as large male body size for fighting for access to females is not favored when male mortality is increased relatively to that

of females, due to the fact that males are the sex traveling in search of females. This difference should be therefore more pronounced in species which are sit-and-wait predators compared to actively hunting spiders, as in the latter both sexes move around (Vollrath and Parker 1992). Thus far this hypothesis has only been partially supported and only when real estimates on differences in mobility/mortality between the sexes were used (De Mas et al. 2009). One of the most accepted hypotheses explaining the evolution of SSD in spiders is the fecundity selection hypothesis (FSH) which states that a history of selection favoring fecundity (egg number) has led to the evolution of large body size in females, because in ectothermic animals larger females lay more eggs (Head 1995; Prenter et al. 1999). The evolution of extreme SSD would then be explained by gigantism evolving much faster in females than in males. All of the above hypotheses explain the evolution of SSD by focusing on selection acting on one or another sex. However, none of them can successfully explain the entire range of SSD observed across spiders (Foellmer and Moya-Laraño 2007). For instance, why do some species with very large (giant) females have dwarf males while others have males that are similar in size to females?

The gravity hypothesis (GH – Moya-Laraño et al. 2002) addresses this shortcoming. The GH explains the evolution of extreme SSD as the result of selection acting upon males, favoring those individuals that are more successful at reaching females when these are receptive (sexual selection as a result of scramble competition – Ghiselin 1974). The basic tenet of the GH is that there are marked differences in microhabitat occupancy across different spider taxa, with some spider taxa living on the ground, while others inhabit microhabitat patches on trees, in tall habitats. Therefore, from the point of view of a male that is searching for receptive females, the habitat may show strong verticality; one that needs to be overcome in order for the male to be able to find mates.

A simple biomechanical model (Moya-Laraño et al. 2002) showed that for a male to reach a female that lives in tall vegetation, being smaller is favored, as the speed at which a smaller male

could climb would be higher, thereby facilitating successful encounters with receptive females. Using the comparative method in evolutionary biology, the authors tested two main predictions of the GH: (1) with increasing height of the habitat females live in, SSD increases (i.e., male size relative to female size decreases) and (2) this effect is stronger for larger spider species, as in those the negative effect of gravity should be more pronounced. Both predictions were met by the analysis of Moya-Laraño et al. (2002). However, further research, along with misunderstandings of some of the tenets of the GH, fueled a fruitful controversy in the years following its publication.

More Recent Variations and Improvements of the GH

The Curvilinear GH

Moya-Laraño et al. (2009) published an update of the GH (see also Foellmer and Moya-Laraño 2007). By running spiders on vertical inclines and reanalyzing the data in Moya-Laraño et al. (2002), they showed that (1) there is not a simple negative relationship between climbing and speed, but a curvilinear one with an optimal body size for climbing, and (2) superimposing this relationship on the patterns of SSD across spider species, species in tall habitats showed a clear top threshold on male size which explained a non-linear male (Y) female (X) relationship, which was not predicted (and in fact did not occur) in spiders inhabiting close to the ground. A post hoc model was also built (Moya-Laraño et al. 2009) which explained why we should expect a parabolic climbing speed pattern with body size in spiders. Although this hypothesis further contributed to explain the patterns of extreme SSD across spider species, there was still an unexplained part of the pattern, caused by those gigantic spider taxa that inhabit tall habitats but in which SSD is moderate. The bridging GH solves this puzzle.

The Bridging GH

This hypothesis (Corcobado et al. 2010) considers an additional (and largely neglected) travel mechanism of spider males, moving along a silk thread, or bridging (Moya-Laraño et al. 2007b). During

bridging the spider hangs from a silk thread and releases silk that is carried away by the wind until it finds an anchor point (e.g., a plant) on the opposite end (i.e., in the direction of the wind). Once the silk has been anchored the spider tenses the thread and starts walking upside-down to reach the other end. A biomechanical model (Rodríguez-Gironés et al. 2010) showed how heavier spiders are limited in the use of this mechanism for traveling, especially at longer distances, because the silk released from the minor ampullate silk glands (one of the glands producing silk in spiders) elongates more strongly in the ground direction with a heavier load, ending with the spider on the ground, thus making this dispersal mechanism not efficient. A good solution to travel efficiently using this mechanism is thus also to be small. This hypothesis was tested by inducing spiders to bridge under laminar wind flow (Corcobado et al. 2010). The authors found that (1) both large males and females were less prone to bridge relatively to smaller spiders and (2) the degree of sexual dimorphism in bridging propensity was negatively correlated with the degree of SSD. In a direct test, Morse (2014) found that male size is positively related to bridging speed in the crab spider *Misumena vatia*, as predicted for this species which has small males of a mean size of only 4 mg (well below the bridging threshold of 118 mg predicted by the bridging GH). Females, on the other hand, are up to two orders of magnitude heavier. This hypothesis is the most integrative to date, as it also explains the exceptions; i.e., those spider taxa in which the female is gigantic and inhabits tall places but in which SSD is nonetheless moderate. These correspond to spider groups in which traveling in search for mates is not done by bridging, as for instance the families Ctenidae or Sparassidae.

Findings and Controversy

A complete understanding of the evolutionary processes underlying current trait distributions, such as the different body sizes of males and females, requires investigating the evolutionary history of the traits within a taxon and the factors which currently favor and maintain trait

distributions in populations (Foellmer and Moya-Laraño 2007). Theoretical models, such as the GH and its refinements, make informed predictions for both the evolution and the current maintenance of traits, as these models establish a maximum body size for males. The long-term evolution of characters is best addressed in comparative analyses which are corrected for phylogenetic relationships. To test whether gravitational effects are driving current selection processes in populations, field studies estimating male fitness during mate search as a function of morphology and lab experiments involving locomotion trials are necessary (Foellmer et al. 2011; Moya-Laraño et al. 2013). Importantly, selection processes favoring current body size distributions in males and females do not need to be the same as those that initially led to the evolution of sexual size dimorphism.

All comparative analyses to date find evidence for an important role of gravity in the evolution of SSD, and extreme SSD in particular in spiders, and thus support the GH and its refinements (see above). The predictions of the GH with regards to body sizes favored by selection during mate search and during locomotion trials depend on the male size distribution under investigation, the predominant mode of locomotion (running or bridging), and the habitat context. In many species with extreme SSD, mean male size is well below the threshold for optimal climbing speed predicted by the curvilinear GH (7.6 mm body length or 43 mg body mass) and even the largest males do not reach this threshold (Cheng and Kuntner 2014; Hormiga et al. 2000). For such species, the predicted large male advantage during mate search in the field was found for the orb-web spider *Argiope aurantia* (Foellmer and Fairbairn 2005) and the crab spider *Misumena vatia* (Morse 2014) and in running trials on vertical structures in the laboratory in *Argiope aurantia* (Foellmer et al. 2011). No effect of male body size during mate search was detected in the widow spider *Latrodectus hasselti* (Andrade 2003), the orb weaver *Nephila plumipes* (Kasumovic et al. 2007), and for *Latrodectus hesperus* (Brandt and Andrade 2007), *Argiope keyserlingi*,

and *Nephila plumipes* (Prenter et al. 2010a, b) in laboratory climbing trials. In the orb-web spider *Nephila clavipes*, in which the male body size distribution includes the threshold size of 7.6 mm, the predicted advantage of males of intermediate sizes was found (Vollrath 1980). In the study of climbing speed in the orb weaver *Leucauge venusta*, the body size range was mostly above 43 mg as both males and females were included (Moya-Laraño et al. 2007a). As predicted by the GH, body size was inversely related to climbing speed. In fact, no study has yet yielded results in opposite direction to the predictions of the updated GH, and one non-published study even found evidence for smaller males having better mobility and mating success (Linn 2001). The reason why the predicted relationship between body size and climbing speed was not found for some species is not clear. Apart from gravity effects, morphological aspects such as absolute and relative leg length ought to be important for achievable running speed on structure of any angle of incline (Foellmer et al. 2011). In addition, performance itself is a characteristic based on the metabolic capacity of organisms and can evolve, at least to some extent, independently of body size (Calsbeek and Irschick 2007; Irschick et al. 2008; Lailvaux and Irschick 2007).

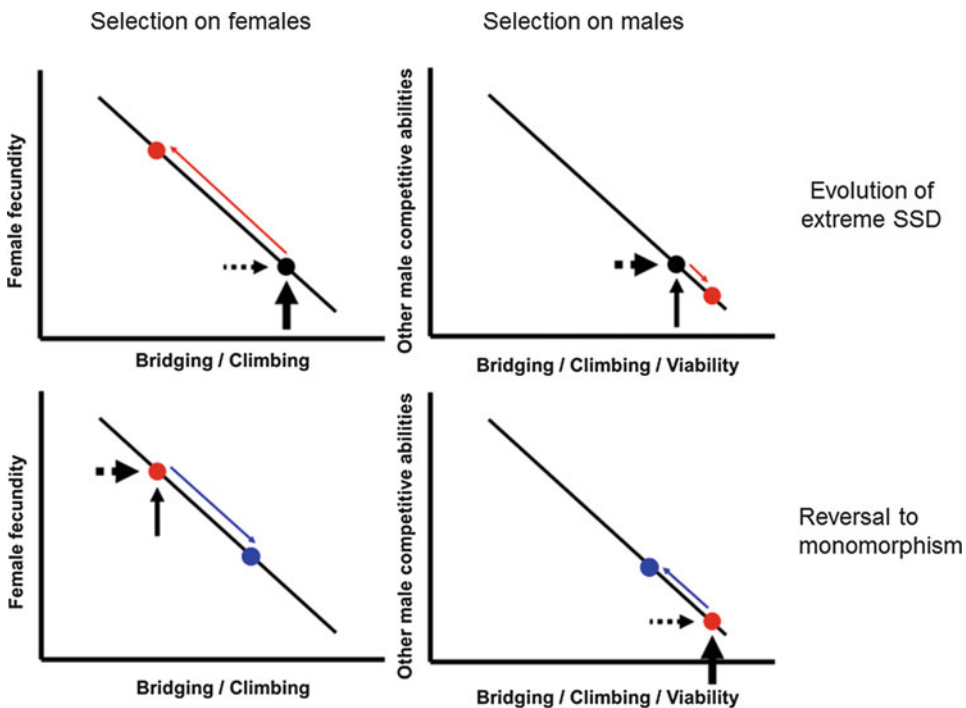
Findings that large male size confers higher mate search success or higher climbing speed was initially interpreted as evidence against the GH (Foellmer and Fairbairn 2005), but the Curvilinear GH has provided an explanation for the pattern (see above). Another implication of these studies is unresolved; however, we still do not have a good understanding about which factors drive the evolution of male body size below the thresholds predicted by the curvilinear GH and bridging GH (Morse 2014). The involved processes may be species specific. What has emerged from the body of literature available to date is that most likely gravitational forces have been the key factor uncoupling the evolution of male and female body sizes, breaking the genetic correlation between the sexes for body size expression (Foellmer and Moya-Laraño 2007; Moya-Laraño

et al. 2009). Below, a general trade-off model is offered that may help explaining these species-specific differences.

A General Trade-Off Model to Explain the Evolution and Maintenance of Extreme SSD

The entire body of hypotheses, models, and empirical evidence on the evolution and maintenance of extreme SSD can be merged into a single graphical model similar to that in Corcobado et al. (2010), as depicted in Fig. 1. Depending on the strength of the selective pressures acting on

each sex, and a size-dependent trade-off involving mobility/viability and other selective pressures, one could explain the evolution of extreme SSD from monomorphism (i.e., males and females of similar size) and even the reversal to monomorphism from clades in which extreme SSD had previously evolved (Hormiga et al. 2000). Assuming that fecundity selection favoring larger females will trade-off with their mobility either during bridging or during climbing, any selective pressure that demands higher female mobility (e.g., high dispersal adult rates) will counter the evolution of female gigantism from fecundity selection or even reverse gigantic females to clades with smaller females. In males, traits



Gravity Hypothesis, The, Fig. 1 A general trade-off model explaining the evolution of extreme SSD in spiders. *Black filled circles* show the original hypothetic ancestral situation in which both males and females were of similar size. *Horizontal dotted arrows* show the strength of selection favoring smaller sizes (*wider arrows* mean stronger selective pressures). *Vertical solid arrows* show the strength of selective pressures favoring larger sizes. Evolution occurs along the trade-off line in the direction

determined by the balance between the two types of selective pressures. If large size from fecundity on females is favored and small size for mobility or viability is favored in males, extreme SSD evolves (*red arrows and circles in top panels*). When mobility on vertical surfaces favors smaller female sizes or large male sizes are favored from other competitive abilities, reversal to monomorphism can evolve (*blue arrows and circles in bottom panels*) (Redrawn from Corcobado et al. (2010))

favoring smaller sizes, such as bridging, climbing, or even viability, when male mortality is much higher than female mortality (the DMM), will trade-off with other male competitive abilities favoring larger sizes (e.g., mobility on flat surfaces, male-male contest competition). When reaching females involves higher male mobility in tridimensional habitats, smaller males will be favored. Strong fecundity selection acting on females and strong selection for mobility on tridimensional habitats on males will lead to the evolution of extreme SSD. However, according to the update of the GH (Corcobado et al. 2010), bridging must be a much more important trait associated with the evolution of small body size than climbing. When these selective pressures on one or both sexes are relaxed, evolution on the opposite direction along the trade-off line occurs, possibly leading to a reversal to monomorphism.

Future Perspectives

Several of the predictions of the extended GH remain to be tested. For instance, a post hoc model for the curvilinear GH (Moya-Laraño et al. 2009) predicts that at smaller sizes the frequency of leg (muscle) striding is constant, at intermediate sizes is inversely proportional to size, and at larger sizes becomes inversely proportional to the square of size, which explains when a negative relationship between climbing and body size arises. Detailed laboratory climbing experiments with high-speed cameras are necessary to test the above predictions. The biomechanical model accompanying the bridging GH (Rodríguez-Gironés et al. 2010) predicts that silk produced in minor ampullate glands in spiders will support much lower weights than those typical of gigantic females and that large spiders will drop to the ground if hanging from such silk. Tests of silk properties released by spider males are needed. Also, evidence that the above silk is economically cheaper than that produced from major ampullate glands (e.g., for capture webs) could be granted. Despite the fact that the “ghost of the evolutionary past” could be at play, further evidence that smaller bridging males have an

advantage finding mates in the field would be appropriate (Linn 2001). Finally, a few of the predictions in the general trade-off model of Fig. 1 could be tested. For instance, documenting the selective pressures in the field (e.g., differential mortality between the sexes – De Mas et al. 2009) in species living in tall habitats versus those living in short habitats could show whether the DMM and the GH interact (e.g., is differential mortality stronger in tall habitats?), possibly leading to the evolution of males even below the size threshold predicted by the updated GH. Or, in species that live in tall habitats and use bridging as a dispersal mechanism, is there a negative relationship between adult female body size and the propensity of females to relocate their webs? In other words, is there evidence of a trade-off between body size and mobility from bridging?

Conclusion

The original gravity hypothesis predicted a negative relationship between climbing ability and body size. However, new data and updates of the hypothesis showed that the relationship between climbing speed and body size was parabolic, with an optimal climbing speed at intermediate sizes. Furthermore, a biomechanical model shows how another mechanism of spider dispersal, bridging, can actually be behind the evolution of extreme SSD, giving rise to the bridging GH. This last hypothesis has a stronger predictive power than all previous hypotheses to explain the observed patterns of SSD across spiders. A size-based trade-off graphical model has been proposed here to explain the evolution and maintenance of extreme SSD, which integrates most of the current mechanisms favoring large or small body sizes in both males and females. Further data are needed to fully understand the GH.

Cross-References

- [Sex Differences](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)
- [Sexual Size Dimorphism](#)

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Great Ape Psychiatry

► Psychiatry of Nonhuman Apes

Great Apes

► Primate Menopause

Greater Polygyny Selects for Greater Risk-Taking

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Synonyms

[Mating market](#)

Definition

When men can have multiple female partners, male mating competition increases, leading to riskier behavioral strategies.

Introduction

Most mammalian species are polygynous, where a male can simultaneously have several female mates (Reichard and Boesch 2003). In polygynous species, male reproductive success is

more highly skewed than female reproductive success, both because of high-status males with multiple mates, and because fewer potential partners are available to lower status males. The greater intensity of intrasexual selection increases male risk-taking in the competition for resources and status.

Sexual Selection and Polygyny

Sexual selection helps explain sex differences in psychology and behavior, including greater male tendencies for risk-taking, competitiveness, and sensitivity to social hierarchy (Cronin 1991). Males compete more intensely for female sexual partners in most animal species because females usually invest more in offspring and are therefore selected to be more discriminating in selecting mates (Bateman 1948). Male mating competition can involve fights with other males for rank or territory; it can also involve competition over traits and displays that females prefer in their mates. Males succeeding in these competitions have more offspring, shaping traits that foster such success, even if those traits also have detrimental consequences (Darwin 1871).

In polygynous species, some males will have many offspring while many others will have none, creating powerful selection pressure for traits that lead to success in mating competition at the expense of longevity (Plavcan 2000). The degree of polygyny is analogous to male reproductive inequality. In highly polygynous species, a few males will have many offspring, whereas many others will have none (Reichard and Boesch 2003). This highly skewed reproductive success creates powerful selection pressure for traits that lead to success in mating competition. Such selection pressure has produced elaborate ornaments (such as the peacock's tail) and armaments (such as a deer's antlers), all with substantial costs. The longevity gap between males and female vertebrates is highest among polygynous species (Clutton-Brock and Isvaran 2007).

Primates vary considerably in the degree of polygyny; humans have a moderate degree of polygyny (Betzig 1986). Still, men's reproductive

success is more variable than women's reproductive success, resulting in male mating competition as a potent force of selection. Polygyny occurs in the vast majority of cultures (84%) documented by anthropologists (Ember et al. 2007). The heightened degree of male mating competition in polygynous cultures leads to higher levels of risk-taking, with resulting detrimental consequences for mortality (Kruger 2010).

Conclusion

Higher degrees of polygyny correspond to an effectively higher (more male biased) sex ratio, increasing the intensity of male mating competition and associated risk-taking.

Cross-References

- [Operational Sex Ratio](#)
- [Polygyny and Male Risk-Taking for Status](#)

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Greater Risk-Taking and Status

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Synonyms

[Status gradient](#)

Definition

The greater the inequality in social status and the greater effect that social status and relative position has on reproductive outcomes, the greater risk-taking will be, especially for men. Greater uncertainty in important aspects of life will also increase risk-taking.

Introduction

Patterns of risk-taking in relation to social status concerns can be understood through the framework of life history theory. Greater risk-taking is associated with greater uncertainty and inequality in reproductive success.

Status Competition and Risk Taking

Life history theory explains variation in behavioral and physiological strategies as partially contingent on conditions in the developmental environment. Individuals developing in relatively uncertain environments will develop riskier behavioral strategies to take advantage of possibly fleeting opportunities (Chisholm 1999). Humans living in chronically risky and uncertain environments are more likely to experience earlier menarche, earlier ages of reproduction, and higher reproductive rates (Chisholm 1999). Community college students who expected shorter life spans and saw the future as less predictable had a higher frequency of risk-taking (Hill et al. 1997).

Neighborhood homicide rates are predicted by neighborhood life expectancy (controlling for the effects of homicide) and neighborhood income inequality (Wilson and Daly 1997). Risky behaviors may have facilitated early reproduction before death occurs, steep discounting of future outcomes is a response to environments where the probability of receiving delayed benefits is uncertain or low, and the expected benefits of safer courses of action are negligible (Wilson and Daly 1997). Urban middle school students who lived in more dangerous neighborhoods were more oriented to present rewards, and time perspectives predicted rates of interpersonal violence and property crimes (Kruger et al. 2008).

When competition for resources and social status is more intense, greater tendencies for risk-taking are evident. The shift in the male allocation of effort from somatic to mating to parenting over the life course helps to explain the pattern of risky behavior underlying the peak in sex differences in mortality from behavioral causes across the life span (Kruger and Nesse 2006). The peak in risky behaviors during young adulthood corresponds with entrance into mating competition (Wilson and Daly 1993).

Men compete for social status and resource control, as these are characteristics valued cross-culturally in intersexual selection (Buss 1989). In ancestral times, men who controlled more resources partnered with younger women, partnered with more women, and produced offspring earlier (Low 1998). Even in relatively egalitarian foraging societies, men with higher status have greater sexual opportunities (Chagnon 1992; Hill and Hurtado 1996).

Over the course of human history, variance in male wealth and power increased through sociopolitical arrangements and intergenerational transfer (Smuts 1995). Where there is greater variation and skew in male social status and resource control, there will be greater competition for positions of power and status. Relative socioeconomic position has a stronger influence on mortality rates for men than for women (Bopp and Minder 2003; Kruger and Nesse 2006). Increased uncertainty in economic opportunities and greater variability in males social status and resource control within

populations are associated with elevated male mortality rates (Kruger and Nesse 2007). The degree of the economic disparity across a population directly predicts the extent of excess male mortality (Kruger 2010).

The degree of male risk-taking is also directly related to male reproductive inequality. The higher the degree of polygyny in a population, where high status men are better able to attract and/or retain multiple female partners, the higher the effective sex ratio will be. For every woman who is polygynously mated, there is one less woman available to other men. Higher degrees of polygyny are associated with greater consequences of male mating competition (Kruger 2010).

Conclusion

Patterns of risk-taking can be understood as an aspect of human life history. Higher levels of risk-taking are evident when important life outcomes are unpredictable and when there is greater inequality in attributes that are historically related to reproductive success.

Cross-References

- [Greater Polygyny Selects for Greater Risk-Taking](#)
- [Polygyny and Male Risk-Taking for Status](#)

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Green Beard Effect, The

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Definition

A concept in social evolution theory where a single gene or a set of multiple tightly linked genes has two phenotypic effects: a trait that allows other individuals to recognize carriers of the gene (such as growing a greenbeard) and

a behavioral trait whereby altruistic acts are directed toward others recognized as carriers.

Introduction

In 1964, William Hamilton published two classic articles on the evolution of social behavior, seeking understanding of the evolution of altruistic traits. The first of these articles (Hamilton 1964a) focuses on mathematical theory. The second paper (Hamilton 1964b) discusses the implications of the theory and gives it further biological context. In a brief section of the second paper, Hamilton also discusses a hypothetical “supergene affecting (a) some perceptible feature of the organism, (b) the perception of that feature, and (c) the social response consequent upon what was perceived.”

Although Hamilton first described the idea, the popular name “greenbeard” comes from Richard Dawkins (1976) who illustrated the idea with an intuitively appealing and visually memorable example where the perceptible feature of the organism is a greenbeard, encoded by a gene such that its carriers not only have greenbeards, but they also tend to be selectively altruistic toward others with a greenbeard. It is not difficult to envision how such a gene can be successful in a population even if the altruistic act is costly, as long as the benefits to the recipient are sufficiently high. Consider a simple and extreme example of a greenbeard gene that causes its carrier to save five other carriers of the same gene from certain death while sacrificing itself: the net effect is of course that a larger number of gene copies remain in the population due to the altruistic act, despite the death of the altruist.

The Green Beard Effect and Kin Selection

Richard Dawkins (1976) used the idea of a greenbeard gene to direct readers into the right mind-set for grasping the empirically more important concept of *kin selection*. Once one realizes that greenbeard genes can become more common in the population by helping identical copies of themselves carried by other greenbeards, it is a

relatively small step to understand that similar logic applies even if it is not guaranteed that the recipient of help carries a copy of the same gene. In kin selection theory, it is more likely (although not certain) that close relatives will carry identical copies of the same gene, when compared to random members of the population. In other words, helping fellow greenbeards and helping close relatives are two different ways a gene can help copies of itself via altruistic behavior. The greenbeard effect is therefore useful as a thought experiment that helps us reason about other evolutionary phenomena.

The greenbeard effect is distinct from *kin recognition*, in which individuals may share a phenotypic marker coded by a marker gene (Gardner and West 2010). In contrast to greenbeard genes, such a kin recognition marker gene need not be directly linked to any behavioral trait. It simply serves as a signal that suggests two carriers may be closely related. And if the carriers are closely related, they are likely genetically similar across all of their genome, not just the marker locus. A greenbeard gene, in contrast, need not indicate similarity elsewhere but at the greenbeard locus and closely linked loci. A greenbeard gene may of course be shared by genealogical relatives, but the greenbeard effect is not reliant on this.

Some authors nevertheless consider the greenbeard effect to be a subset of kin selection. Although the word “kin” suggests interaction with genealogical relatives, the more general theory of kin selection accounts for genetic similarity arising for any reason, including greenbeard effects (Gardner et al. 2011). It is not likely that a full consensus will be found on the precise meaning of the term “kin selection,” but it is useful to be aware of the different uses of the term.

Are Greenbeards Stable?

Intuition might suggest that greenbeard genes are unstable over long evolutionary timescales in two ways, of which only one is correct.

Let us consider first the incorrect idea: Recall that a greenbeard gene does not necessarily indicate similarity elsewhere in the genome but at the greenbeard locus. Given that the gene causes

behavior which is costly to its bearer, it is easy to imagine that there would be selection for a modifier elsewhere in the genome to suppress the greenbeard gene entirely – after all, these genes depend on the survival of the same body, and they pay the cost of altruism, but are not particularly likely to be present as copies in recipients (other greenbeards). But a moment’s thought shows that such a modifier would typically not spread. Imagine a population where everyone is a greenbeard, implying that benefits have outweighed the costs for the greenbeard in the past when it has spread in the population. Now if a mutation elsewhere in the genome suppresses the greenbeard gene, what happens? Carriers of this new mutation will not pay the cost for altruistic behavior. But the flipside is that they will no longer have greenbeards and will no longer benefit from the altruism of other greenbeards. The original greenbeard gene would only have spread if greenbeards were on average fitter than non-greenbeards. The new mutant is for all practical purposes now a non-greenbeard and hence will not be selected for. This is why suppressors of greenbeard genes are typically not positively selected, assuming the greenbeard gene was selected for in the first place (see Ridley and Grafen 1981; Biernaskie et al. 2011).

The more acute problem facing greenbeard genes is that of so-called *falsebeards*. A falsebeard is an individual with a greenbeard, but who does not behave altruistically toward others. Contrary to the modifier gene described above, a gene that suppresses the altruistic behavior but not the beard is at an advantage because its bearer still receives altruism from greenbeards (who cannot distinguish it from other greenbeards) but does not pay the cost of altruistic behavior itself. Falsebeards are an important reason for why greenbeards are expected to be rare in nature and are likely to only be found in situations where the link between beard and behavior is very difficult to break, so that falsebeards are unlikely to arise.

Greenbeards in Reality

So far we have considered greenbeards mostly from a conceptual point of view, and indeed

they were originally conceived as a thought experiment; perhaps unlikely in nature but nevertheless helpful in thinking clearly about reality. Despite their seeming improbability, several examples of greenbeards have by now been discovered (reviewed in Gardner and West 2010; Madgwick et al. 2019). Most of these empirical examples have been found in microorganisms. It has been hypothesized that this is because the potentially simpler link between genotype and phenotype in microorganisms may prevent the evolution of falsebeards (see above), which would require a decoupling of the signal and behavior (Gardner and West 2010). It is likely that in humans and other complex multicellular organisms with complex genotype-phenotype links greenbeards would be highly vulnerable to falsebeards. There is also some disagreement on published empirical examples of greenbeards, and a recent review suggests that they all fall short of fully conclusive evidence for classification as greenbeards (Madgwick et al. 2019).

The prevalence of greenbeards in nature also depends on how strict we are with the definition. For example, Dawkins (1986) used the greenbeard effect to illustrate the evolution of exaggerated sexually selected traits, such as a peacock's tail which would typically be thought of in terms of, e.g., Fisherian runaway selection. Imagine there is some preference for long tails among females. Such a preference implies that a son of a long-tailed father is likely to carry not only genes for a long tail but also genes – inherited from his mother – for a preference for long tails. The latter genes may not be expressed in males but can nevertheless be carried and passed on by males. As a consequence, the long tail of the son acts as a greenbeard-like signal that he is likely to carry genes for long tail preference. The outcome is a system where genes for a signal (long tail) and for fitness-enhancing behavior (choosing to mate with males with long tails) become linked. Genes for choosiness in females are helping copies of themselves by choosing long-tailed males. And if genes for preferring long-tailed males become common in the population, then long-tailed males will be successful and will also become more common in the population.

Another real-world example where the greenbeard effect can clarify our thinking about nature is the evolution and maintenance of sexual reproduction. It is often thought that sex is a costly way to reproduce because a parent passes on only half of its genes to the offspring, giving away 50% of the genetic representation in the offspring to the other parent. If the parent simply cloned itself, it would pass on 100% of its genes. But consider this from the perspective of a hypothetical gene for sexual reproduction. Individuals that do not carry this gene do not reproduce sexually. Hence the act of sexual reproduction is in itself a marker for carrying this gene, analogous to a greenbeard. By mating with another sexually reproducing individual, the parent is helping copies of the gene for sex in the other parent (Lehtonen et al. 2012). Although this suggests that such a cost of “genome dilution” may be illusory, there are many other evolutionary costs to sexual reproduction which is why its prevalence remains one of the big mysteries in evolutionary biology (Lehtonen et al. 2012).

It is reasonable to ask if these two examples are really instances of greenbeards. The answer depends on how far one is willing to extend the definition. But perhaps it does not matter. The original spirit of the greenbeard effect was a thought experiment that helps us reason about nature, and so it does in these questions of sexual selection and sexual reproduction.

Evil Beards

Greenbeards are typically thought of as altruists, but Hamilton (1964b) noted that “if an individual can be attracted towards likes when it has positive effects -benefits- to dispense, it can presumably be attracted the other way, towards unlikes, when it has negative effects to dispense.” If a greenbeard is able to selectively harm those individuals that do *not* carry copies of the greenbeard gene, the outcome is that the non-greenbeard competitor decreases in relative frequency in the population, and conversely the greenbeard gene increases in frequency – again, provided the costs to the evil greenbeard are not too great, and the costs to the individuals being harmed are great enough.

However, the evolutionary dynamics of harming greenbeards are more complicated than those of helping greenbeards, and they tend to be positively selected only once they have reached a high enough frequency in the population (Gardner and West 2010).

Conclusion

The greenbeard effect was originally devised as a thought experiment that clarified reasoning about the evolution of altruistic behavior. It has subsequently become a growing field of study, from a theoretical as well as empirical perspective. The biggest threat to the long-term evolutionary stability of greenbeards is “falsebeards,” in which the signal (greenbeard) is retained, while the altruistic behavior is abolished. For this reason, greenbeards are expected to be found in settings where it is difficult to decouple the greenbeard signal and associated behavior by mutation. Although initially thought to be implausible, examples of greenbeards have been found in nature, particularly in microorganisms.

Cross-References

- [Charles Darwin: Theory of Sexual Selection](#)
- [Fisherian Runaway Selection](#)
- [Genetic Relatedness](#)
- [Kin Selection](#)
- [Puzzle of Altruism, The](#)
- [William Hamilton](#)

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Green Exercise

- [Stress Reduction and Mental Health](#)

Greenbeard Effect

- [Helping and Genetic Relatedness](#)

Grief

- [Nonhuman Reactions to Death](#)

Grooming

- [Cooperation Among Nonchimpanzee, Non-human Primates](#)

Grossed Out

- [Disgust](#)

Group Augmentation

- [Helping and Inclusive Fitness Benefits to Helper](#)

Group Hunting

- [Coalitional Hunting](#)

Group Leaders

- [Coalition Leaders](#)

Group Living

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Synonyms

[Cooperation](#); [Sociality](#)

Definition

Humans are a highly social species, with an evolutionary history of living in cohesive and structured groups. There are many psychological processes specialized for adaptively dealing with intragroup and intergroup phenomena.

Introduction

Animal species vary in the extent to which they are social, and there is broad consensus among researchers that humans are a highly social species. Human sociality is evident throughout the lifespan. Humans are an altricial species, meaning that infants are not capable of sustaining themselves and require a high level of care for a prolonged period. As children grow, acquiring the skills necessary to survive requires a great deal of learning from the older generation and peers. And unlike most mammal species, humans tend to pair bond, meaning that couples form lasting relationships within which reproduction and rearing of children tend to occur. More generally, people of all cultures spend a substantial amount of their waking hours socializing with others, and contemporary psychological evidence indicates that humans have a strong motivation to maintain close relationships with a handful of others (Baumeister and Leary 1995).

Human sociality goes beyond the small circle of immediate family and close friends. Evidence indicates that humans are adapted to living in groups of dozens of individuals (Dunbar 2004). These groups would have presented different kinds of opportunities and threats, as different social interactions are associated with different types and degrees of benefits and costs in terms of survival and reproduction. Accordingly, many aspects of human social cognition are expected to exhibit functional specialization, with distinct psychological mechanisms for optimally managing the diverse kinds of social relationships and interactions (Kurzban and Leary 2001). A crucial part of human social psychology is that, in addition to individual-based thoughts and feelings (e.g., liking one person more than another based on familiarity, attractiveness, reciprocal exchange, etc.), there exist group-based thoughts and feelings (e.g., favoring one person over another, based solely on group membership, separate from individual-based preferences). Group-based psychological processes are likely to have emerged due to the evolutionary benefits of within-group cooperation, benefits which are further bolstered by out-group exploitation, resulting

in the evolution of between-group competition (Kurzban and Leary 2001). Over time, humans best able to cooperate with in-group members and outcompete rival groups would have been most reproductively successful, resulting in a species-wide tendency to be tribal. There is plenty of psychological evidence for humans' propensity to favor in-group members over out-group members (Tajfel 1982).

While *group living* technically encompasses the entirety of human sociality – including pair bonding, parenting, sibling relationships – this chapter focuses on aspects of human psychology associated with “groups” as typically conceptualized in psychology (i.e., collectives of unrelated individuals who cooperate and sometimes engage in competition with other similar collectives). Those other aspects of sociality (e.g., pair bonding, parenting) are covered in other chapters of this volume. For the sake of organization, the remainder of the chapter is divided into two major sections: within-group processes and between-group processes.

Within-Group Processes

To reap the benefits of group living, ancestral human collectives needed to achieve coherence and stability. In this section, various aspects of intragroup processes that were pivotal for successful group living are reviewed. These include (a) being able to navigate social hierarchies, (b) being able to work together cooperatively, and (c) being able to identify nonreciprocators and noncontributors in order to exclude them. As noted above, this section reviews dynamics among individuals in a group that are either distantly related or not related at all.

Navigating Social Hierarchies

For group living to be successful, social order and intragroup structure are essential. In situations where resources (e.g., food and mates) are limited, established social structures minimize the need for confrontation that can arise from competition for these resources. Of course, there is competition for position on the hierarchy, as level of rank in a

social group is directly associated with mate allocation, food allocation, and territory. High-ranking members can be awarded with disproportionately high levels of resources, mates, and territory. In contrast, low-ranking members are likely to get much less resources, mates, and territory. It is therefore a good strategy to attempt to gain the highest possible rank that is available.

There are two techniques that can be deployed to establish social rank. The first one is *social dominance*, the use of force and intimidation in order to induce fear and subordination from those who are ranked lower (e.g., a “bully” who asserts his status through agonistic encounters). The second is *prestige*, the ability to impress others by demonstrating high-level skills and abilities. For example, Mother Theresa was able to establish a high social ranking and was known worldwide, not due to her aggressiveness and dominance, but by her prestige alone.

Social Dominance

Social dominance is a form of establishing social rank that has been observed in many social animal species and particularly in primate species, with dominance being typically achieved with acts of aggression (Trivers 1985). However, humans do not display acts of dominance through physical conflict alone. Social dominance can be achieved by having control over the extent to which others have access to resources, mates, and their own well-being. The threat of losing any of these resources results in lower-ranking individuals being subordinate to higher-ranking individuals who hold this control. Examples of those resources that could be deprived include the loss of resources for their wellbeing, their children, or their livelihoods (Cheng et al. 2010). Despite the negative connotations associated with social dominance, there are also positive aspects. For example, dominance has been associated with high levels of agency and can be indicative of better leaders (Cheng et al. 2013), with trait dominance being a predictor of leadership (Lord et al. 1986).

Prestige

The second form of navigating social hierarchies and gaining social rank is through obtaining

prestige. This involves having a high social standing and commanding a high position in people's minds. Instead of gaining social rank through power and evoking fear, prestige involves being influential. Those who possess prestige tend to be listened to and are able to convey heavily-weighted opinions that are influential rather than being obeyed. Using the example of Mother Theresa, her social standing was based on her influential practices, rather than being able to force her views and opinions on others.

Henrich and Gil-White (2001) provided an evolutionary explanation for why those with prestige hold a high social standing. Human cultural capacity, meaning the capacity for intergenerationally stable social transmission created a new selective environment that favored those who promoted transmission. Social learning through social transmission is adaptive, particularly in group settings, as it saves the learners the cost of individual learning. Once the human cultural capacity was in place, it favored the propensity to identify and copy models who are considered as being better than average. Put more simply, it makes more sense to be able to identify and prefer to learn from those people who demonstrate that they have a high skill level. Copiers (i.e., those that want to learn) therefore evolved to seek out and prefer models who provide this higher level of learning and will, reciprocate by cooperating and offering a range of benefits. This means that those preferred models have a certain level of prestige from the perception that their copiers have of them. Moreover, the level and status of copiers is directly associated with the level of prestige that the model holds. As the level of expertise that a copy model holds is directly related to their own level of prestige and social ranking, this means that there is also an incentive, between models, to outperform each other.

Cooperation

Humans are remarkably adept at working cooperatively and forming social groups. In addition to cooperation among kin, there are other various kinds of cooperation among nonkin including

direct reciprocal altruism, also known as social exchange, and indirect reciprocal altruism, which can be associated with recognition of values and formation of friendships.

Social Exchange

Social exchange, also referred to as reciprocal altruism and dyadic cooperation, is the practice of mutual provision of benefits on the assumption that the receiver will be compliant and reciprocate either immediately or in the future. This practice is observed among humans and only a small number of nonhuman species, such as chimpanzees and baboons. Moreover, the ability to create social exchanges with a variety of different goods and services is an exclusively human trait (Cosmides and Tooby 1992). In situations where social exchange takes place between two individuals who are unfamiliar with each other, the conditions of the exchange are likely to be explicit; in contrast, in situations where individuals know each other, conditions for social exchanges are likely to be implicit and rely upon social norms (Cosmides and Tooby 2005). Furthermore, if social exchange occurs between familiar individuals, reciprocation can be delayed with less urgency for it to be fulfilled. In these social exchanges, the behavior of the receiver is normally factored into deciding whether future exchanges should take place (Cosmides and Tooby 2005).

As social exchange goes beyond associative learning, such as classical and operant conditioning, researchers have proposed that humans have a specialized evolved capacity to engage in social exchange. This suggests that social exchange may be a product of functionally specific cognitive mechanisms, designed to predispose humans to engage in seeking and creating social contracts (Cosmides and Tooby 2005). In order for humans to possess cognitive mechanisms for social exchange, a further ancillary mechanism designed to detect cheaters would be required (see below). Indeed, this view is supported by neurological evidence showing that cheater detection can be selectively impaired and is closely associated with other forms of similar reasoning (Stone et al. 2002).

Friendship

Distinct from social exchange, a direct form of reciprocal altruism, is Tooby and Cosmides's (1996) model of psychological engagement, commonly known as friendship. People possess skills and/or attributes that are valuable to others. During the course of engagement, these individuals create externalities (outward displays) that, as a by-product, can be perceived positively or negatively. As others are likely to seek out those with positive externalities, this can motivate individuals to display positive externalities and minimize negative externalities. For example, it is likely that those who frequently demonstrate good hygiene practices are much more likely to be favored as a potential friend in place of those who demonstrate poor hygiene practices.

This situation is therefore likely to cause adaptations for individuals to seek out those who are sources of these qualities. Thus, a feedback loop is created, whereby *X* seeks out *Y* due to their positive externalities, and *Y* is therefore interested in *X* by virtue of the fact that *X* is interested in *Y*'s welfare (Kurzban and Leary 2001; Tooby and Cosmides 1996).

What differentiates the psychological engagement model from reciprocal altruism is that it does not rely on the direct social contract that one individual will benefit from the other's generosity on the condition that it will be reciprocated in the future. Instead, it is based on the notion that an individual can be valued while pursuing their own goal and at no cost to themselves. The value is therefore not due to exchange of goods but due to individuals valuing each other.

Cooperation and the Supernatural

One of the puzzles of human cooperation is why unrelated individuals would help a stranger who they are likely to never meet again and where reputation effects are absent. Johnson and Krüger (2004) suggested that throughout our history, fear of the supernatural has deterred defectors from avoiding helping others, even if they are strangers, for the common good. This is supported by the fact that supernatural beliefs are universal among human societies and there are associated taboos for not contributing to the common good.

Furthermore, punishment for noncooperation could be the possibility of being deprived of privileges in the afterlife, such as entrance to heaven.

Social Exclusion and Stigmatization

While it is important to work cooperatively as a cohesive group, part of its success will be down to making sure that all members are able to contribute appropriately and that all members do contribute. Even if a group does work cooperatively, there are a number of instances when this can still fail. These reasons include, but are not limited to, those who do not make good social exchange partners or potential friends, those who do not cooperate in the wider context of a group setting, and those who pose a health risk due to being perceived as potentially ill.

Due to the consequences of individuals not contributing or being fit to be part of the group, it is likely that a suite of psychological mechanisms have evolved to promote social exclusion. Kurzban and Leary (2001) proposed that stigmatization originated not from an individual being negatively evaluated for idiosyncratic reasons, but because that individual possesses characteristics or exhibits behaviors that are collectively disagreeable to the group. Kurzban and Leary argued that humans have evolved three specific mechanisms through which social exclusion can occur. The first is dyadic cooperation, a suite of adaptations designed to avoid those who would either make low-value partners, be a greater cost than benefit to the group, or does not possess some or all of the qualities valued to that particular group. The second is the importance of selecting members that meet the standard of the group and exploiting those who do not (this section will only take into account standards for group selection). The third is parasite avoidance, a suite of adaptations that are designed to detect, avoid, and prevent prolonged contact from those that have perceptual cues associated with disease threat.

Dyadic Cooperation

Dyadic cooperation encompasses kin selection, reciprocal altruism, and group-based models. In a hunter-gatherer scenario, a successful hunter may provide their surplus to an unsuccessful

hunter, in order to bridge a shortfall in the supplies that they may have. However, the costs of benefit delivery are only acceptable if the receiver is likely to reciprocate the gesture in the future. This means that in order for this type of cooperation to be successful, cheaters and low-value group members, who are unlikely to be able to reciprocate in the future, must be excluded (Cosmides and Tooby 1992).

In addition to reciprocal altruism, friendship selection also plays a part in the cooperation from those who are considered friends, and the social exclusion of those who are not accepted as friends. Tooby and Cosmides (1996) suggested that humans only have a limited amount of time to form and build friendships. As such, affiliations with some people may mean missed opportunities for forming friendships with others. Particularly for more popular members of a group, this may also lead to the rejection of some due to receiving more offers of friendship than one can have time for.

Restrictions for opportunities with both friendships and social exchange mean that decisions should be made wisely. Kurzban and Leary (2001) suggested that there are three categories that can be used for exclusion from cooperative relationships. The first is unpredictability, relating to whether an individual recognizes that opportunities for social exchange exists. In order to engage in social exchange or to engage in engagement, it has to be possible to coordinate with the other individual and to be able to predict their intentions. Not being able to predict someone's intentions can make these practices very difficult as there is an issue of uncertainty. Unpredictability can occur when they violate social norms. For example, someone who engages in self-destructive behavior (e.g., attempting suicide) could be seen as unpredictable. Indeed, engaging in behavior that deviates from the norm is used to diagnose many mental health issues. Therefore, if an individual is seen as being unpredictable, this presents an element of uncertainty in terms of their future value, and can be a cause for social exclusion.

The second reason for exclusion, both in social exchange and in friendship, if an individual has

poor prospects and offers little capital both in the social and economic sense. Examples include individuals who could be perceived as financially poor, be ill, elderly, or have little social connections. Indeed, there is evidence to show that those who are lacking in social and economic resources are among the most stigmatized (Phelan et al. 1997).

The third is the perception of cheaters, those individuals who take part in a social exchange and do not reciprocate. As discussed, in order for a reciprocal system to be adaptive, it would have had to evolve ancillary mechanisms that are designed to detect cheaters. It is therefore likely that individuals who do cheat will be excluded both from social exchanges and friendships. The term cheating can be applied to those who seek to obtain benefits from goods or services that they need, to satisfy a chemically rewarding substance, or to fulfil a sexual appetite. It is likely that those who are detected as cheaters are actively punished, rather than simply being avoided like those individuals with poor prospects.

Selection for Within-Group Membership

The strength of the group is dependent on the level of cooperation within the group. It is therefore adaptive to ensure that group members are both competent, are able to advance the interests of the group, and willing to sacrifice for the good of the group. Conversely, it is likely that there are psychological mechanisms that have evolved to detect and exclude individuals who do not meet the criteria or standard that the group expects. For example, it is important that all group members both share the benefits of the group in proportion to their social rank and equally share the costs and risks (Kurzban and Leary 2001). It is also important that these individuals conform to social norms and expectations that the group may have. If a group member does not meet these criteria and standards, that member is likely to be removed from the group (Neuberg et al. 2000). Moreover, public displays could be used to shame an individual and ensure that all members of the group are aware of their exclusion, with actions such as locking them in a public stockade.

Parasite Avoidance

As disease has been one of the biggest threats to human survival, it has been proposed that humans, as well as animals, have evolved a behavioral avoidance system (BIS) that is designed to detect and avoid perceptual cues associated with disease threat (e.g., Schaller and Park 2011). As diseases cannot be directly perceived, this system relies upon perceptual cues that are imperfectly correlated with disease threat. Put more simply, not all perceptual cues will mean that a disease threat is present. Due to this imperfect correlation, the BIS is overinclusive, meaning that it is more likely to activate when there is no disease threat present (false positive) rather than the more costly chance of not activating when there is a disease threat present (false negative). Due to the close proximity of groups, it is likely that any disease threat would have disastrous consequences to the community. In ancestral times, many humans lived in small close-knit communities, meaning that any disease could have grave consequences if any of the key members of the group were to become ill. Common effects of disease, such as fatigue and fever, would incapacitate any number of individuals who would then not be able to contribute to the group. The worst case scenario is that one or more individuals die as a result of disease. As such, it is highly likely that those individuals who do appear to suggest disease threat (e.g., visible sores, vomiting, etc.) are likely to be excluded and avoided. Moreover, due to the overinclusive nature of the BIS, it is also likely that those individuals who appear abnormal but carry no disease threat may also be excluded (e.g., obese individuals; Van Leeuwen et al. 2015).

There are functional explanations for why social exclusion and stigmatization of certain individuals has become part of our evolutionary make up. Those individuals who would make low-quality group members and would form poor relationships, either due to cheating, lack of social or economic resources, or due to being perceived as a type of threat, are likely to be excluded. Although these three categories have been presented as being distinct, an individual maybe excluded and stigmatized for being considered

as possessing more than one of these categories (e.g., obese individuals; see Van Leeuwen et al. 2015).

Between-Group Processes

Groups can often achieve more than isolated individuals can. This is true of groups in preindustrial societies (e.g., cooperative hunting, childcare, and farming) and has only become intensified in industrial societies (e.g., modern manufacturing). Clearly, cooperating in-groups often confer many advantages, and this was likely a key driving force underlying the evolution of psychological capacities pertaining to within-group processes discussed above. At the same time, there is evidence that psychological processes underlying groups have also been shaped by a long history of intergroup conflict. There is archaeological and anthropological evidence indicating that intergroup violence has a long evolutionary history within the human lineage (Bowles 2009). Throughout history, as much as 20–30% of men may have died from intergroup violence, and this is also true of contemporary hunter–gatherers (Keeley 1996; Pinker 2011). For these reasons, it has been suggested that humans possess “tribal instincts,” a set of psychological processes specialized for dealing with antagonistic intergroup situations (Van Vugt and Park 2010). These tribal instincts include the propensity to spontaneously divide up the social world in in-groups (us) and out-groups (them), the tendency to favor in-group members over out-group members, and distinctly negative beliefs and attitudes regarding out-group members. Also, these tendencies are flexibly heightened in situations perceived to involve intergroup competition.

Categorization

Humans naturally carve up the social world into various categories, which are partly based on biology but also subject to cultural influences. Some of the fundamental categories that humans routinely perceive and utilize – genders and age categories, for instance – may be due to their adaptive relevance. Quickly categorizing other

individuals in terms of gender and age would allow one to infer important opportunities and threats (e.g., potential mates and potential rivals for mates). Studies have shown that people also tend to categorize others in terms of race (e.g., white vs. black), and this appears to be a manifestation of a deeper psychology of coalitional alliances (Kurzban et al. 2001). A number of studies (with adults and children) have shown that people tend to perceive racial categories as though they are coalitional alliances, but this tendency can be overridden when other, more diagnostic cues to coalitional alliances (e.g., sports team membership, language/accent) are provided (Kinzler et al. 2010; Kurzban et al. 2001). These different types of categories – genders, ages, coalitions – serve different functions and thus deploy different sets of psychological processes. The intergroup processes covered in this section pertain mostly to the psychological processes associated with coalitions. Groups based on coalitional categorizations engage a specific set of psychological responses, particularly in competitive contexts.

Intergroup Psychology

Social psychologists have tended to use the term “group” somewhat loosely, to include common social categories such as genders and ages. However, groups are cohesive collections of individuals capable of cooperating toward common goals, and this definition narrows down the range of actual human groups. And of those, only a subset – those reminiscent of coalitions – activates intergroup psychological processes. So which categories are experienced as coalitional groups? As Kurzban et al. (2001) argued, human tribal psychology should be sensitive to “(i) patterns of coordinated action, cooperation, and competition, and (ii) cues that predict—either purposefully or incidentally—each individual’s political allegiances” (p. 15387). Examples of the former would be sports teams and opposing militaries. As for cues, examples might include religious affiliation and speech patterns (e.g., languages, accents). This may explain the historically ubiquitous antipathy between different ethnic and religious groups. Of course, social categories that do not fulfill the tribal criteria

(e.g., male/female, old/young, lawyer/architect) may give rise to prejudice and discrimination as well, but this is likely to be for reasons qualitatively distinct from tribal conflict.

Upon perception of people as coalitional in-group and out-group members, perceivers experience positive sentiments (e.g., trust) toward in-group members and negative sentiments (e.g., fear) toward out-group members. The specific emotions experienced will depend on the nature of the out-group and the in-group–out-group dynamic in that specific context (e.g., Cottrell and Neuberg 2005). For instance, out-groups do not simply inspire “negative” feelings, but more specific emotional responses such as fear, anger, disgust, and contempt, depending on their perceived status and the kinds of threat they pose (if any). Thus, what social psychologists refer to as “prejudice” may encompass a varied set of emotional responses and motivational tendencies. Out-groups perceived to pose a safety threat may inspire fear and desires for avoidance. Out-groups perceived to pose a health threat may inspire disgust and desires for exclusion (Schaller and Neuberg 2012).

Stereotypes (traits believed to be associated with specific social categories) also provide a window into the underlying psychology, because stereotypes may also motivate adaptive behaviors, with different kinds of stereotypes potentially driving different kinds of behaviors (Schaller et al. 2003). Commonly held stereotypes tend to be either positive or negative, with in-groups typically being ascribed positive stereotypes (e.g., hardworking, trustworthy, intelligent) and out-groups typically being ascribed negative stereotypes (e.g., lazy, devious, superstitious). Among the negative stereotypes, some connote threat (e.g., untrustworthy) whereas others do not (e.g., lazy). In coalitional intergroup contexts, ascribing threat-connoting stereotypes towards out-groups may be functional, as such beliefs can promote potentially life-saving fear and avoidance. Consistent with this expectation, various lines of research have found that out-groups that can be categorized as coalitions (e.g., races, ethnic groups) do often inspire threat-relevant perceptions, including ascriptions of threat-connoting

stereotypes (Schaller and Neuberg 2012; Schaller et al. 2003).

Intergroup Competition and Conflict

One school of thought in psychology holds that in-group favoritism evolved for its own sake, as it confers survival benefits. Humans necessarily rely on intragroup cooperation for survival, individuals must rely on others for information, help, and resources (e.g., Brewer and Caporael 2006). While this perspective likely accounts for a substantial part of in-group favoritism, there is evidence to suggest that it is unlikely to be the entire story. Thus, another school of thought holds that the evolution of intragroup cooperation was further pushed along by intergroup competition and conflict. For instance, people spontaneously perceive intergroup contexts to be more competitive than interpersonal contexts. Also, in-group loyalty increases when intergroup competition is salient (Van Vugt and Park 2010).

Furthermore, the effect of intergroup competition on in-group loyalty may be sex specific. This is because intergroup conflict may have affected the evolved psychologies of men and women differently. Intergroup aggression has historically involved rival coalitions of males fighting over scarce reproductive resources, a tendency that appears to predate *Homo sapiens* (Van Vugt and Park 2010). As a consequence, this aspect of human coalitional psychology may be more pronounced among men, an idea referred to as the *male warrior hypothesis* (Van Vugt et al. 2007). Across many contexts, it has been found that men are more supportive of intergroup conflict. Also, studies have shown that the effect of intergroup competition on increased in-group loyalty is observed only in men (Van Vugt et al. 2007).

Conclusion

Successful group living has required the evolution several psychological mechanisms specialized for navigating both within-group and between-group aspects of social life. Within groups, group members have a set of standards and expectations that current and new group members should observe.

Cooperation is also an essential part of successful group living, being able to take part in social exchanges with a wide variety of goods and services that are either explicitly expressed or implicitly expected. Beyond social exchange is the formation of friendships, which involve being able to recognize and engage in relationships with people who share positive and/or common values. Equally as important as effective cooperation are the ancillary mechanisms designed to detect those who do not benefit the group and subsequently promote social exclusion.

There are also mechanisms specialized for between-group interactions, which have been driven by a long history of intergroup conflict. These mechanisms include those that impel humans to categorize the world between “us” and “them.” This process is functionally flexible, meaning that it becomes particularly salient in contexts involving intergroup competition. Negative stereotyping tends to be associated with outgroups, whereas positive stereotyping tends to be associated with in-group. These trends towards in-group favoritism have been driven by both intragroup cooperation and intergroup competition for limited resources.

The mechanisms and motivations associated with the within-group and between-group aspects of group living are analogous to the rowing boat races, like the annual race between Oxford and Cambridge. On the one hand, each individual wants to compete to the best of their ability in order to be recognized for their individual contribution and receive the subsequent recognition. On the other hand, members of a rowing team have to work together in order to be able to compete against other rowing teams.

With recent changes in technology, such as the creation and expansion of social media, there have been many fundamental changes to the ways in which groups are perceived and how individuals can communicate on a group level. As already discussed, the term “groups” can be used loosely in social psychology, but it becomes a lot clearer when a group is considered as one that is working towards a common goal. When considering groups that are formed and maintained on social media, many of them meet this criteria. For

instance, groups can be created for a number of reasons that include campaigning towards a cause, sharing an interest, or even just arranging a small-scale event. The long-term effects of this substantial shift in these methods of communication remains largely unknown, but it is likely to fuel research in the coming years.

Cross-References

- [Cooperation](#)
- [Dyadic Relationships Versus Group Processes](#)
- [In-Group Versus Out-Group](#)
- [Reciprocal Altruism and Group Living](#)

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Group Mortality During Environmental Stress

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Group Selection

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Definition

The hypothesis in evolutionary biology which holds that natural selection acts at the group level. That is, natural selection favors certain groups over others in a population composed of multiple groups.

Introduction

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

Charles Darwin, *Descent of Man*, 1871 p. 89

Group selection is the hypothesis in evolutionary biology which holds that natural selection acts at the group level. That is, natural selection favors certain groups over others in a population composed of multiple groups. This hypothesis is often contrasted with individual selection, in which natural selection favors traits which confer fitness benefits at the level of the individual organism. Group selection theorists believe that natural selection acts both among groups in a multigroup population and individuals within a group.

The central idea behind group selection is that intergroup competition creates a selection pressure for intragroup cooperation. Under this hypothesis, a population (the set of all individual organisms competing for some common resource pool) may be divided into groups (subsets of the population composed of multiple individuals whose fitness is interdependent and non-zero sum). When such a division occurs, group members have the opportunity to cooperate with one another in order to exploit mutual gains. Groups which achieve high levels of cooperation will outcompete their more selfish counterparts, garnering a larger share of the resource pool and consequently enjoying greater reproductive success.

If the selection pressure induced by intergroup competition is strong enough, group selection may favor not only intragroup cooperation but altruism. Whereas *cooperation* requires only that a behavior be beneficial for the group as a whole, *altruism* imposes the additional requirement that

such behavior be detrimental for the donor. More precisely, “altruism” refers to any trait or behavior which has the effects of (1) lowering the donor’s fitness relative to its group while (2) increasing the average fitness of the donor’s group members relative to outgroup members. In short, within-group and between-group selection are opposing forces, with selection among individuals within a group favoring selfishness and selection among groups within a multigroup population favoring altruism. Notably, altruism in the context of group selection is distinct from other definitions of altruism, such as that employed by inclusive fitness theory, which will be discussed later. Several notable biologists, psychologists, and behavioral economists, including David S. Wilson, Edward O. Wilson (no relation), Martin Nowak, and Jonathan Haidt, have argued that the existence of altruism in humans and other species is best explained by group selection.

Old Group Selection Versus Selfish Gene Theory: A History

Pre-1960s evolutionary biology frequently invoked group selection to explain what was thought to be the abundance of altruism observed in nature. This approach, now called “old group selection,” viewed natural selection as acting both between and within groups and presumed that between-group selection was often the dominant force. Old group selection was advanced by figures like Vero C. Wynne-Edwards and Konrad Lorenz, who regularly conceptualized evolution in terms of group benefit (Wynne-Edwards 1962; Lorenz 1966). Wynne-Edwards, for instance, believed that nature contained numerous “...collective attributes, all possessing the common quality of contributing to the welfare and survival of the group... and when necessary subordinating the interests of the individual” (Wynne-Edwards 1962 p. 653).

For example, biologists noted that animals fighting over mates or territory often engaged in ritualized aggression rather than “total warfare.” Because ritualized aggression was less costly than total warfare, it was thought that such behavior

had evolved through group selection (Lorenz 1966). Similarly, certain species were thought to rear fewer children than they were otherwise capable of. Again, biologists invoked group selection to explain such behavior (Wynne-Edwards 1962). Presumably, groups which exercised reproductive restraint were more likely to sustain their limited pool of resources. Those which failed to exercise such restraint would become overpopulated, and deplete their resources. Group selection was thought to explain other “collective attributes” as well, including territoriality and social orderings.

Old group selectionism was superseded by selfish gene theory from the 1960s through the 1980s due in part to two key theoretical developments – kinship altruism and evolutionary game theory – in conjunction with supporting empirical observation (Williams 1966; Dawkins 1976). According to selfish gene theory, the gene – not the group – is the fundamental unit on which natural selection acts. Although not entailed by selfish gene theory, selfish gene theorists tended view group selection as empirically implausible. While group selection was possible in principle, they argued, in practice within-group selection pressures would dominate between-group selection pressures.

In supplanting old group selectionism as the ascendant paradigm in evolutionary biology, selfish gene theorists were tasked with explaining – or explaining away – numerous ostensible examples of group-beneficial adaptations. Proponents of selfish gene theory noted firstly that much of what was thought to be altruistic behavior was in fact selfish. One notable example is that of the stotting gazelle. A group-selectionist explanation of this behavior might claim that healthy gazelles stot to draw the attention of predators to themselves and away from weaker members of the group. However, stotting could also be explained by selfish gene theory according to the “handicap principle,” in which a stotting gazelle purposefully handicaps itself to signal its fitness and agility both to mates and predators (Zahavi and Zahavi 1999). Other instances of ostensible altruism were explicable as exploitation, a now-famous example being that of enslaved ants (Franks and Scovell 1983). Upon closer

inspection, selfish gene theory argued, there was much less altruism to explain than group selectionists believed.

Moreover, two theoretical developments – kin selection and evolutionary game theory – allowed selfish gene theorists to explain the existence of cooperation and limited forms of altruism as the result of individual selection. Between 1963 and 1964, W. D. Hamilton punished a series of seminal papers expounding the notions of inclusive fitness, kin selection, and kinship altruism (Hamilton 1963, 1964). His central insight was that close relatives are more likely to share a rare allele than two randomly selected members of the population. If such a rare gene were to cause its bearer to exhibit altruism toward a close relative, it would stand a good chance of benefitting a copy of itself housed in that relative. An organism’s genetic success, Hamilton argued, was not merely the number of direct offspring it produced (personal fitness) but the number of direct offspring it produced summed with the number of direct offspring produced by its relatives, discounted by how distantly related they are. This latter measure would become known as *inclusive fitness*. Kinship altruism, Hamilton showed, will be selected for when an organism can decrease its personal fitness to increase its inclusive fitness (Hamilton 1964).

The second theoretical development which shifted evolutionary biology away from old group selection was evolutionary game theory. Under certain conditions, evolutionary game theorists demonstrated, cooperation between two organisms can be mutually fitness-enhancing. For example, it might pay for two organisms to engage in a series of quid pro quo transactions in which one individual cooperates with another under the expectation that cooperation will be reciprocated (Trivers 1971). Such an engagement is known as *direct reciprocity*. More generally, evolutionary game theory provided analyses of how ostensibly altruistic behavior was in fact mutually beneficial cooperation.

In 1973, John Maynard Smith and George R. Price applied a game-theoretical analysis to ritualized aggression, formerly thought to be an example of a group-level adaptation, and

demonstrated how such behavior could be mutually beneficial (Smith and Price 1973). The stage game they employed is called the *hawk-dove game*, in which two organisms or “players” compete for a common resource through one of two strategies: the aggressive strategy (hawk) or the nonaggressive strategy (dove). If both players choose hawk, they will each receive half the value of the resource $V/2$ but, in doing so, incur a cost from fighting $C/2$. When one player chooses hawk and the other chooses dove, the dove retreats leaving the hawk to claim the full value of the resource V . Finally, when two doves encounter one another, they will engage in minimally costly ritualized aggression before splitting the resources evenly for a payoff of $V/2$. The hawk-dove game can be represented in the following symmetric payoff matrix (each cell contains the payoffs for player 1):

		Player 2	
		Hawk	Dove
Player 1	Hawk	$\frac{V-C}{2}$	V
	Dove	0	$\frac{V}{2}$

Note that if the cost C of total warfare (hawk/hawk) is greater than the value of the resource V , the best response to hawk is dove. In a population of hawks, a single dove would enjoy an adaptive advantage. Because payoffs in evolutionary games represent fitness differentials, successive generations would see an increase in the relative frequency of doves and a decrease in the relative frequency of hawks. The composition of the population would converge to the mixed strategy Nash equilibrium, such that the expected payoff from playing hawk was equal to the expected payoff from playing dove. At this equilibrium, dove-dove ritualized aggression would be a common occurrence. The conclusion of this analysis, contra Lorenz 1966, is that ritualized aggression is not altruistic and does not require group selection to explain.

The introduction of dynamic or iterated games into evolutionary game theory demonstrated how repeated interactions create selection pressures for cooperation above what can be explained by static or one-off games (Axelrod 1984; Smith 1982).

A classic example of the potential for cooperation in dynamic games is the iterated prisoner’s dilemma. In the prisoner’s dilemma stage game, players choose one of two plays: cooperate or defect. If both cooperate, they receive a reward valued at R . If one cooperates and the other defects, the cooperator receives the sucker payoff S , while the defector receives temptation payoff T . If both players defect, they each receive punishment P . The values of these payoffs are given by $T > R > P > S$. According to this payoff structure, each player is Tempted to defect and take advantage of a cooperative Sucker, but if both players succumb to this temptation, they will be Punished rather than Rewarded. The cells of the following symmetric payoff matrix represent the payoffs for player 1:

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	R	S
	Defect	T	P

In the static version of the prisoner’s dilemma, the unique Nash equilibrium is mutual defection. However, in dynamic or iterated versions, a new set of equilibrium strategies and payoffs emerge. Many of the subgame perfect Nash equilibria associated with the indefinitely iterated prisoner’s dilemma involve players electing to cooperate with positive probability. For instance, a strategy known as *tit for tat* (TFT) begins by cooperating and thereafter mimics its partner’s last play. Two TFT players will enjoy the reward payoff for the duration of the game. Furthermore, TFT is difficult to exploit, as it immediately punishes defection by defecting itself in the next round. These two characteristics of TFT (its ability to enjoy the benefits of mutual cooperation while remaining largely impervious to exploitation) explain its success in evolutionary simulations (Axelrod 1984). Several cooperative behaviors observed in nature can be modeled according to the iterated prisoner’s dilemma, such as when two individuals take turns grooming one another or sharing food (Dawkins 1976).

To summarize, the key point of departure between selfish gene theory and group

selectionism is that selfish gene theorists view between-group selection as a weak evolutionary force which is dominated by within-group selection, whereas group selectionists believe the opposite. In making their case, selfish gene theorists argue firstly that there is much less altruism to be explained than group selectionists believe and secondly that the few confirmed examples of genuine altruism can be accounted for by inclusive fitness theory and evolutionary game theory. By the 1970s, selfish gene theory had overtaken group selection as the dominant paradigm within evolutionary biology.

New Group Selection and Multilevel Selection Theory

Old group selection was modified and updated by several biologists and evolutionary theorists beginning in the 1970s, the work of whom would eventually culminate in a new group selection theory. While continuous with old group selection, new group selection improved upon its predecessor in at least two key respects. First, new group selection theorists provided mathematical analyses to identify the conditions under which between-group selection will dominate within-group selection. Second, new group selectionists extended the bi-level theory of old group selectionism to multiple levels of a biological hierarchy – a framework known as *multilevel selection* (MLS). Together, these modifications have contributed to group selection’s revival in modern evolutionary biology.

Formalizing Group Selection

To clarify the conditions under which between-group selection dominates within-group selection, new group selectionists divide fitness into “local fitness” and “global fitness” (Sober and Wilson 1998). Local fitness refers to the fitness of an individual relative to its group, while global fitness refers to the fitness of an individual relative to its population. When new group selectionists say that altruism will evolve when the group benefit outweighs the individual cost, they mean that altruism will evolve when the increase in global



fitness, averaged across individual members of the donor's group, is greater than the decrease in local fitness incurred by the donor. According to this framing, altruists simultaneously incur a cost in terms of local fitness while gaining a benefit in terms of global fitness. Consequently, the altruistic trait will decrease in frequency within the group but increase in frequency within the population (Wilson 1975a).

The causal hypothesis identified by group selection – that intergroup competition is a selection pressure for intragroup cooperation – lends itself to various mathematical formalizations. One notable formalization utilizes the Price equation, which models the changing frequency of traits over successive generations, to decompose the effects of between-group selection from those of within-group selection (Price 1970). According to the Price equation, altruism will be favored when there is high intergroup heterogeneity and intragroup homogeneity, that is, when altruists cluster in groups with other altruists. In this way, the altruistic trait will benefit from high levels of mutual cooperation while ensuring the same benefits are not reaped by selfish free riders.

For example, consider a group with n individuals. The rate of altruism within this group is r . Altruists act in such a way that confers a benefit of b to the group (b/n per individual) at a cost of c to themselves. For simplicity, suppose the outgroup population is composed of a large number of selfish individuals with a base rate fitness of x . The fitness of altruists (A) in such a group and the fitness of average group members (avg) are given as:

$$w(A) = x + rb - c$$

$$w(\text{avg}_{\text{group}}) = x + rb - rc$$

There are three important points to note in these equations (Sober and Wilson 1998). First, the fitness of altruists exceeds the population base rate if $rb > c$. When this occurs, the altruistic trait will increase in frequency within the population. Second, the fitness of altruists never exceeds the group average. When $r = 1$, the group is

composed entirely of altruists, in which case the within-group rate of altruism is intergenerationally stable. However, in the more realistic scenario when $r < 1$, the local fitness of altruists will decline. Together, these two points demonstrate the mathematical possibility of altruism evolving due to global fitness enhancements despite being locally costly.

Third, because of local fitness costs, the rate of altruism within this group will erode over successive generations. As the erosion becomes more severe, the group will reach a point where the fitness of altruists no longer exceeds the population base rate ($rb > c$ will no longer hold). Several mechanisms have been proposed to avoid the erosion problem, most notably preferential assortment (Grafen 1984) and group fission (Traulsen and Nowak 2006). In the case of preferential assortment, altruists selectively interact with other altruists and avoid cooperating with selfish individuals. In the case of group fission, groups are assumed to split once they reach a given capacity. After fissioning, the subgroups will compete with one another, allowing the more cooperative subgroup to outcompete the less cooperative subgroup. Fissioning models have been shown to maintain high levels of altruism under certain parameter values, even when intergroup migration is permitted (Traulsen and Nowak 2006).

Multilevel Selection Theory

In addition to mathematically modeling the causal process of group selection, new group selection theorists extended the bi-level theory of old group selectionism (between-group and within-group levels of selection) to multiple levels of a biological hierarchy (Wilson and Sober 1994; Okasha 2006). This extension is known as *multilevel selection* (MLS) *theory*. According to MLS, altruism at lower levels of the biological hierarchy evolves through competition at higher levels. For example, altruism at the genetic level can evolve through competition at the cellular level; altruism at the cellular level can evolve through competition at the individual level; and altruism at the individual level can evolve through competition at the group level. Rather than a rare and

exceptional evolutionary phenomenon, MLS maintains that the causal process underlying group selection is ubiquitous in evolutionary transitions.

A core concept of MLS is that selection can act on both replicators and vehicles. A vehicle, in this context, is an entity created by multiple replicators to enhance their reproductive success. Typically, these vehicles house the replicators which create them, thereby binding their reproductive fates. For instance, cells, multicellular organisms, and groups are all vehicles for genes. The biological hierarchy posited by MLS is composed of a series of nested vehicles, whereby genes are nested in chromosomes, which are nested in cells, and so forth. MLS argues that it is possible to speak about selection operating at every level of this biological hierarchy so long as it is clear that the fitness of these vehicles is determined by their ability to enhance the reproductive success of the replicators which created them (Sober and Wilson 1998).

Selfish gene theorists have argued against MLS, claiming that the application of natural selection at the group level is overreaching (Dawkins 1976). While selfish gene theorists acknowledge that selection can operate on the level of certain vehicles, such as multicellular organisms, they maintain that groups are not the right sort of vehicle on which natural selection can act. Multilevel selection theorists counter that there is no principled reason for the conclusion that selection can act on individual's *qua vehicle* but not group's *qua vehicle* (Sober and Wilson 1998).

Both formalized models of group selection and multilevel selection theory contributed to group selection's revival beginning in the 1970s. Even though these developments put group selection on firmer theoretical ground, new group selectionists still had to contend with the objection that the best explanations for altruistic behavior were kin selection and evolutionary game theory. If the existence of altruism could be explained in terms of individual selection, then invoking higher levels of selection would seem unparsimonious (Smith 1982).

New group selectionists responded by claiming that kin selection and game-theoretical

explanations of altruism were not, alternatives to group selection, but were rather equivalent frameworks describing the same underlying causal process. The concept of equivalence is discussed in the following section.

The Equivalence of Group Selection, Kin Selection, and Evolutionary Game Theory

Kin Selection

Despite the fact that kin selection was originally conceived of as an individual-level explanation for the evolution of altruism (Smith 1964), new group selectionists argue that kin selection is a specific instance of group selection for a group composed of close relatives (Wilson 1975a). According to the Price equation, what matters for the selection of altruism is not relatedness per se but rather a high covariance of altruistic traits within groups (Price 1970). Under this interpretation, kin selection is a type of group selection in which an altruistic trait achieves high intragroup covariance through common ancestry (Wilson 1975a; Grafen 1984). This interpretation of kin selection was subsequently adopted by W. D. Hamilton, who first formalized the conditions under which kinship altruism will evolve (Hamilton 1975).

To see how this works, consider a group composed of n relatives, each of whom is related to one another with an index of relatedness r . Now suppose some of these individuals contain allele A for kinship altruism which causes them to confer some benefit b to the group (per organism benefit b/n) at a cost of c to themselves. If A is rare within the general population, the number of altruistic individuals in the group is $r * n$. The respective payoffs for altruistic individuals and average members of the group are given by:

$$w(A) = x + rb - c$$

$$w(\text{avg}_{\text{group}}) = x + rb - rc$$

where x is the base rate payoff for members of the general population.

Note that these equations are identical to those in Formalizing Group Selection, and describe the same causal process by which altruism will experience positive selection. Namely, kinship altruism will increase within the population when $rb > c$ (Hamilton 1964). Moreover, altruists incur a cost in terms of local fitness, further supporting the contention that kin selection is an instance of group selection.

Evolutionary Game Theory

New group selectionists further contend that certain applications of evolutionary game theory also constitute group selection. Notably, it has been suggested that game-theoretical models of direct reciprocity which utilize iterated prisoner's dilemmas are specific instances of group selection with a group of size 2 (Sober and Wilson 1998). According to new group selection theory, the iterated prisoner's dilemma exemplifies a situation in which direct reciprocity evolves as a consequence of altruists incurring a cost in terms of local fitness while benefitting the group in terms of global fitness.

The intuitive explanation behind direct reciprocity parallels that of group selection. Within a mixed pair, selfish players beat cooperative players, but pairs of cooperative players outcompete pairs of selfish players. Between-pair competition favors altruism over selfishness – a miniature version of group selection.

The mathematical equivalence of new group selection, kin selection, and direct reciprocity has been used to argue that group selection is not an alternative mechanism by which altruism and cooperation evolve. Rather, group selection is a more general description of the causal mechanisms responsible for the evolution of altruism, which unifies kin selection and evolutionary game theory, and extends their logic to explain altruism in groups of varying sizes and degrees of relatedness (Sober and Wilson 1998). While group selection, kin selection, and evolutionary game theory are equivalent in their population dynamic predictions, new group selectionists contend that their theory offers certain conceptual advantages. For instance, group selection provides a useful lens through which to view the evolution of

altruism under complex conditions, such as cultural group selection and selection between multiple locally stable equilibria.

The Imprint of Group Selection on Human Psychology

One of the basic tenets of evolutionary psychology is that social behavior, including human social behavior, has its roots in biology. Therefore, any complete explanation of human social psychology must include the ultimate mechanisms by which sociality evolves (Wilson 1975b; Wilson and Wilson 2007). Kin selection, for instance, largely accounts for the psychology of nepotism, while moral emotions such as a sense of fairness can be explained as a logical consequence of direct reciprocity (Haidt 2012). If group selection played an important role in the evolution of *Homo sapiens*, its influence should be reflected in features of human social behavior. Indeed, a growing body of research from several fields, including psychology, behavioral economics, and anthropology, argues that it is (Fehr and Gächter 2002; Gintis et al. 2003; Haidt 2012; Greene 2014). There are at least two broad categories of evidence for group selection's influence on human psychology: altruistic punishment as an explanation of human ultrasociality and “groupish” psychological tendencies.

Altruistic Punishment as an Explanation of Human Ultrasociality

A unique feature of human behavior is our ability to cooperate in large, unrelated groups, often in one-off interactions where the potential for reputational gains is slight or nonexistent. This is known as *ultrasociality*. Human ultrasociality, it has been suggested, cannot be accounted for by the usual mechanisms postulated to explain cooperation: kin selection, direct reciprocity, indirect reciprocity, and network effects (Fehr and Gächter 2002). One mechanism to enforce ultrasocial levels of cooperation is altruistic punishment, whereby certain individuals pay a price to punish those who violate social or moral norms. If punishment is severe enough, this changes the

incentive structure facing group members, making it beneficial *at the within-group level* to engage in cooperative behaviors which, absent the threat of punishment, would be detrimental at the within-group level. Simply put, altruistic punishment makes otherwise altruistic behaviors selfish (Sober and Wilson 1998). Simultaneously, altruistic punishers experience a depreciation of local fitness, implying that punishing behavior is explicable only in light of group selection (Fehr and Fischbacher 2003).

Altruistic punishment in the context of group selection can be illustrated using a public goods game with punishment (Fehr and Fischbacher 2003). In the standard public goods game, n participants are given an endowment and offered the opportunity to contribute a portion of it to the “public good,” real-world analogues of which include government budgets, public services, the environment, and collective knowledge. The value of the public good is then multiplied by a factor m between 1 and n and distributed evenly among the participants irrespective of their contribution. Because the public goods multiplier falls strictly between 1 and n , contributing to the public good is an example of altruistic behavior, as the returns to contribution are m/n . In the original setup of the public goods game, a contribution of 0 is the dominant strategy, which should be unanimously adopted if all players are performing optimally. This game-theoretical prediction has been borne out in laboratory experiments, which show that participants in a public goods game decrease their level of contribution over successive iterations towards the unique Nash equilibrium (Fehr and Gächter 2002).

Variations of the public goods game which incorporate an element of punishment yield different results both theoretically and behaviorally (Fehr and Gächter 2002). In these variations, players are given the option to pay to punish one another after each round. If every player was reluctant to punish non-contributors, it would be in the interests of a single player to unilaterally deviate by choosing to punish those who failed to contribute to the public good. Severe punishment then acts as an enforcement mechanism. Players can expect to secure a higher payoff by

contributing to the public good and avoiding punishment than by failing to contribute and receiving punishment. In sum, what would have been altruistic behavior in the public goods game *without* punishment is selfish behavior in the public goods game *with* punishment.

Laboratory experiments which test the public goods game with punishment behaviorally find that human participants engage in altruistic punishment even when the element of repeated interactions is absent (Gintis et al. 2003). Because participants are willing to punish in one-off interactions, their behavior cannot be explained as a payoff-maximizing response to the game’s structure. Some behavioral economists suggest that a sense of fairness and inequity aversion are the proximate psychological mechanisms responsible for altruistic punishment (Fehr and Fischbacher 2003). These proximate psychological mechanisms, in turn, are indicative of group selection’s influence in shaping human psychology. While altruistic punishment is detrimental at the within-group level, it is beneficial at the between-group level, as groups with higher degrees of altruistic punishment exhibit greater intragroup cooperation and are therefore more successful in intergroup competition.

Groupish Psychological Tendencies

A number of moral and social psychologists have invoked group selection to explain the “groupish” characteristics of human psychology. In the same way that selfishness is the tendency to exhibit preferential treatment toward oneself over others, groupishness is the tendency to exhibit preferential treatment toward one’s own group over other groups (Haidt 2012). Such preferential treatment extends both to the individual members of one’s group and to the cultural norms of one’s group.

For example, anthropological surveys have identified norms of egalitarianism as a cultural universal (Brown 1991). Egalitarian norms, however, only hold insofar as they benefit the group. In general, equality within the group is considered less important than ensuring the group’s collective welfare (Henrich et al. 2004). Similarly, psychological research reveals that moral norms – particularly those relating to care, fairness, and liberty –

apply more strongly to ingroup members than to outgroup members (Greene 2014). Other types of moral norms – specifically those related to loyalty and respect for authority – arguably evolved to ensure group cohesion. Two prominent moral psychologists, Joshua Greene and Jonathan Haidt, suggest that the main evolutionary function of morality is to bind individuals together into a single group (Greene 2014; Haidt 2012).

Other demonstrations of ingroup bias come from the field of social identity theory (Tajfel et al. 1971). According to this theory, humans tend to identify as members of certain social groups on the basis of shared characteristics. Once these groups are established, individuals display ingroup favoritism (or intergroup discrimination), for instance, allocating larger rewards to ingroup members relative to outgroup members (Tajfel et al. 1971). Ingroup favoritism has been demonstrated experimentally even when groups are randomly assigned on the basis of arbitrary criteria, suggesting that ingroup favoritism can function as a cognitive bias (Tajfel 1970).

In addition to preferences for members of their group, psychological and anthropological research suggests that humans universally prefer over the norms of other groups (Richerson and Boyd 2005). While group selection hypotheses might explain partiality toward the *members* of one's group, it is less obvious why partiality toward the *norms* of one's group would have evolved. To explain this aspect of groupishness, some evolutionary theorists have invoked cultural group selection and gene-culture coevolution (Richerson and Boyd 2005). If group membership is contingent upon adherence to group norms, natural selection will favor individuals who are capable of adhering to the norms of their group. Successful groups, in turn, outcompete less successful groups, which increases the frequency of their norms within the population (cultural group selection). In effect, natural selection favors certain cultural norms via group selection, while cultural selection pressures favor individuals capable of adhering to the norms of their society. Once individuals have acquired the norms of their ingroup, they will tend to prefer them over the norms of the outgroup.

Criticism

Despite its decline in popularity in the late 1960s to early 1970s, group selection has experienced a revival in recent decades and is now one of the more contentious topics in modern evolutionary theory. Of the contemporary criticisms, at least three have emerged as the most common and substantive arguments against group selection. First, the language of new group selection is often seen as terminologically confusing, imbibing standard terminology with nonstandard definitions. Second, some theorists view equivalence as an argument *against* group selection, wondering why one would prefer a group selectionist account over, say, a kin selectionist account if they are ultimately equivalent theories. Finally, critics since John Maynard Smith have argued that new group selection suffers from anisomorphisms with respect to individual or gene selection and therefore should not properly be considered “group selection.”

New group selectionists see themselves as having updated the terminology of old group selection so as to clarify its underlying concepts (Sober and Wilson 1998). Critics, however, argue that new group selectionists are not merely “updating” their lexicon but are rather employing idiosyncratic redefinitions to standard terminology (West et al. 2007). For example, new group selectionists use “individual selection” to refer to selection for traits which enhance the fitness of individuals within their group, whereas “individual selection” traditionally refers to selection for traits which increase personal fitness (as opposed to inclusive fitness). Similarly, “altruism” is standardly used in reference to traits which decrease the personal fitness of their bearer in order to increase the personal fitness of another organism. Hence, kinship *altruism* evolves if individuals can increase their inclusive fitness by paying a price (in terms of personal fitness) to benefit a close relative. New group selectionists, however, call traits “altruistic” when they decrease the fitness of their bearer relative the group. Ultimately, these critics conjecture, much of the debate over group selection is attributable to

terminological confusion for which new group selectionists are at fault (West et al. 2007).

Another common argument against group selection runs as follows: New group selectionists contend that inclusive fitness theory, evolutionary game theory, and group selection are equivalent. Indeed, mathematical formalizations of group selection yield identical population dynamic predictions to those of inclusive fitness theory and evolutionary game theory. However, if these mechanisms are indeed equivalent, then what novel contributions does group selection make to evolutionary theory (West et al. 2007)? According to this line of reasoning, group selection collapses into a redescription of the previously established selection mechanisms. New group selectionists have responded by noting that, while group selection is equivalent to kin selection and evolutionary game theory in certain respects, group selection may offer certain conceptual advantages (Wilson 2015). For instance, group selection provides a useful lens through which to view the evolution of altruism under complex conditions, such as cultural group selection and selection between multiple locally stable equilibria.

Perhaps the deepest conceptual issue surrounding the group selection debate regards the anisomorphism between group selection and other levels of selection, such as selection at genetic or individual level. Specifically, certain critics (most notably John Maynard Smith) have argued that group selection fails to provide a convincing account of how group-level adaptations are inherited (Smith 1987). Whereas, in individual selection, parent organisms spawn characteristically similar offspring organisms, group selection does not involve parent groups spawning characteristically similar offspring groups. While Maynard Smith concedes that intergroup competition may select for intragroup cooperation (and other intragroup traits), he argues that this is insufficient to establish group selection. Because such traits are inherited through individual (rather than group) reproduction, they are best viewed as arising from individual (rather than group) selection (Okasha 2006).

Conclusion

Group selection is the hypothesis that natural selection acts at the group level, favoring certain group-level characteristics over others. According to group selection theorists, natural selection acts both between groups in a multigroup population and between individuals within a group. Within-group and between-group selection are opposing forces, with selection among individuals within a group favoring selfishness and selection among groups within a multigroup population favoring altruism. Old group selectionists believed that selection between groups would typically dominate selection within groups, resulting in adaptations “for the good of the group.” This paradigm was replaced by selfish gene theory in the 1960–1980s due to both theoretical and empirical developments in evolutionary biology. Most notably, kin selection and evolutionary game theory purported to explain how cooperation could arise from individual selection, obviating the explanatory necessity of group selection.

In the 1970s, several evolutionary theorists began revising and updating old group selection in at least two key respects. First, new group selection theorists provided mathematical analyses to identify the conditions under which between-group selection will dominate within-group selection. Second, new group selectionists extended the bi-level theory of old group selectionism to multiple levels of a biological hierarchy, resulting in the framework of multilevel selection (MLS). Although group selection is a causal hypothesis – not a formalism – mathematical analysis helped put group selection on firmer theoretical footing. Moreover, analogizing group selection to other evolutionary transitions using the MLS framework lent credibility to new group selection theory.

One notable result of new group selectionists’ mathematical analyses is that the population dynamic predictions of group selection theory are identical to those of inclusive fitness theory and evolutionary game theory. In this sense, group selection, kin selection, and non-zero sum evolutionary games can be viewed as equivalent mechanisms underlying the evolution of cooperation

and altruism. To the extent that these mechanisms are not equivalent, some evolutionary theorists (e.g., David Sloan Wilson) have argued that group selection offers certain conceptual advantages, such as the ability to understand the evolution of altruism under complex conditions.

A growing body of research from several fields, including psychology, anthropology, and behavioral economics, claims to have found evidence of group selection's imprint on human social behavior. First, several behavioral economists have argued that altruistic punishment, in which the altruistic punisher incurs a personal cost to punish those who violate social or moral norms, is a mechanism for ensuring ultrasociality. Because the administration of punishment is individually costly, group selection may explain why altruistic punishment evolved. Second, social psychology and anthropology have uncovered a number of "groupish" psychological tendencies, in which humans favor the members and norms of their own group over those of other groups. The prevalence and universality of ingroup favoritism is often seen as further evidence for group selection's influence on human psychology.

Group selection theory continues to be the subject of numerous criticisms. Opponents of group selection theory argue that group selectionists utilize idiosyncratic redefinitions of standard terminology and note that the concept of equivalence calls into question the explanatory utility of group selection. Perhaps the deepest conceptual criticism regards the anisomorphism between group selection and individual or gene selection, with detractors arguing that group selection theory fails to provide a convincing account of group heritability. Ultimately, these and other issues surrounding group selection contribute to its status as one of the more controversial topics in modern evolutionary theory.

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Altruistic Punishment Enhances Reputation](#)
- ▶ [Benefit Group Relative to Other Groups](#)

- ▶ [Competition Between Groups](#)
- ▶ [Cooperation](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [George Williams on Group Selection](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [In-Group–Out-Group Bias](#)
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- ▶ [Reciprocal Altruism and Group Living](#)

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Group Size

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Synonyms

Colony size; The size of a group

Definition

The total number of individuals comprising in a social group.

Introduction

Animal groups vary greatly in size. Male wild turkeys form coalitions of two to four members to attract females. Cliff swallows breed in colonies ranging from a few pairs to thousands of individuals. Antarctic krill aggregate in dense swarms, which number up to a trillion individuals and can be visible from space. As these examples illustrate, not only does group size differ between species but it can also highly differ within species

(Krause and Ruxton 2002; Ward and Webster 2016).

What determines group size? How are animal group sizes distributed? Adaptive explanations for social grouping posit that there are a wide variety of fitness costs and benefits associated with group membership and that each individual would prefer the optimal group size, i.e., the size that maximizes his/her own inclusive fitness (Pulliam and Caraco 1984). This entry explores how natural selection will act to shape the optimal group size and why there is such a variation in the distribution of actual group sizes.

Optimal Group Size

Living in a group entails both costs and benefits. Potential benefits of group living include predator avoidance (e.g., group defense, improved vigilance, dilution of predation risk), increased foraging success (e.g., information sharing, group hunting), aerodynamic or hydrodynamic advantages in locomotion, protection from climatic extremes (e.g., huddling for warmth), cooperative territorial defense, and increased probability of winning intergroup competition. Group membership, however, may impose costs such as intragroup competition for resources, increased attack rate on larger groups, disease transmission, brood parasitism, and cuckoldry (Alexander 1974; Krause and Ruxton 2002; Wilson 1975).

Clearly, the costs and benefits of group living will vary systematically with group size. In most cases, as group size increases, the benefits to each group member would increase with diminishing returns (a newly added individual has less impact than the last). By contrast, the costs to each member would increase with increasing returns (a newly added individual has more impact than the last). As groups become very large, the costs of grouping will eventually always exceed the benefits. Under those conditions, the fitness function will reach a maximum at an intermediate group size, i.e., the optimal group size, and decrease thereafter. Natural selection should have favored individuals that form groups of

optimal size (Caraco and Wolf 1975; Pulliam and Caraco 1984; Rodman 1981; Wilson 1975). Note that the fitness function with an intermediate optimal group size may not always hold. In some situations, grouping may be always disadvantageous and individuals will be selected to be solitary.

The optimal group size model rested on several simplistic assumptions; subsequent models relaxing the assumptions were developed, as discussed below:

The Rules of Entry into Groups

The aforementioned model tacitly assumes that existing group members have full control over a newcomer's entry into the group: they would recruit solitary outsiders when the group size is below the optimum, n_I , or prevent solitaries from joining the group when the group size is at the optimum, n_I (Fig. 1). Under this group-controlled entry, the maximal benefit of group living can be attained (Caraco and Wolf 1975; Rodman 1981; Wilson 1975). However, things change when a solitary outsider is assumed to exert full control over her own entry into a group: a series of solitary individuals arrive sequentially and each would freely decide whether to join the group or to remain alone. Under the free entry, solitary outsiders are expected to enter the group as long as the fitness of a group member exceeds that of a solitary outsider. Group size continues to increase up to a certain size, n_O , at which joining the group no longer increases a solitary outsider's fitness (Fig. 1) (Clark and Mangel 1984; Sibly 1983).

Therefore, the group size favored by a group insider, n_I , is less than the group size favored by a solitary outsider, n_O . It means that there is a potential genetic conflict of interest between insiders and outsiders over group size. Within the zone of conflict between n_I and n_O , a solitary outsider "wants" to enter the group, whereas a group insider "wants" the outsider to remain outside (Giraldeau and Caraco 1993; Higashi and Yamamura 1993). It is worth mentioning that models identifying the potential for insider-outsider conflict over group size do not themselves make testable predictions about what group size should be predominantly observed in

nature (Godfray 1999). For such predictions, a different class of models are needed that seek to predict how the potential genetic conflict is resolved at the level of phenotypic interactions between group insiders and a solitary outsider (Cant 2011; Higashi and Yamamura 1993; Port et al. 2011).

Effect of Genetic Relatedness

Initial models of optimal group size were based on regular (direct) fitness, i.e., the number of progeny an individual produces over lifetime. They thus treated group-forming individuals as if they were unrelated. As many instances of animal groups are actually composed of genetic relatives, later models took into account the effect of genetic relatedness on the size of groups (Giraldeau and Caraco 1993; Higashi and Yamamura 1993).

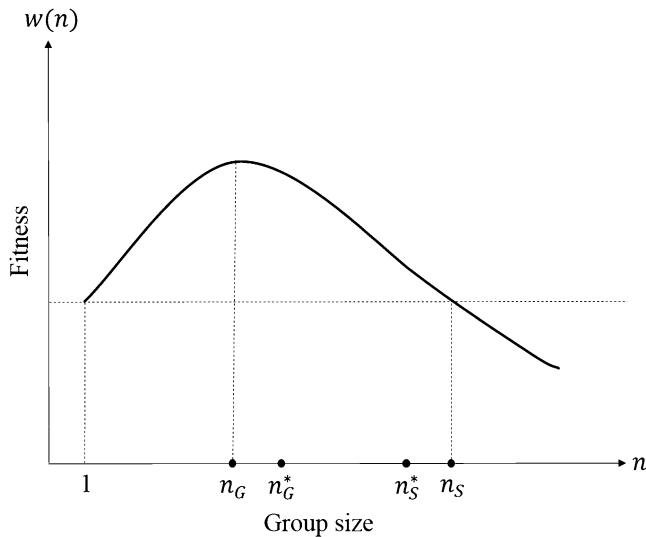
Under the group-controlled entry, an insider living in a kin group of the “optimal” size, n_I , will still tolerate the joining of a related outsider to the group, as long as the indirect benefit to the outsider outweighs the direct cost to the insider herself. That is, the inclusive fitness (IF)-based group size favored by an insider, n_I^* , is equal to

or larger than the regular fitness (RF)-based group size favored by an insider, n_I (Fig. 1). Further, increasing relatedness may ordinarily increase, and will never decrease, the IF-based group size favored by an insider, n_I^* .

Under the free entry, a related outsider may choose not to enter a kin group that has not yet reached the RF-based group size favored by an outsider, n_O , as long as the indirect benefit to the insider outweighs the direct cost to the outsider herself. That is, the IF-based group size favored by an outsider, n_O^* , is equal to or smaller than the RF-based group size favored by an outsider, n_O (Fig. 1). Moreover, increasing relatedness may ordinarily decrease, and will never increase, the IF-based group size favored by an outsider, n_O^* (Giraldeau and Caraco 1993, 2000; Higashi and Yamamura 1993).

Effect of Dominance Hierarchy

In reality, individuals in a group may differ in their competitive abilities. As a consequence, each group member may prefer different group sizes according to their relative ranks in the dominance hierarchy. Reeve and Emlen (2000) applied



Group Size, Fig. 1. The fitness, $w(n)$, of an individual in a group, where n is group size. The optimal group size from the viewpoint of a group insider, n_I , is less than the optimal group size from the viewpoint of a prospect joiner, n_O . Further, the inclusive fitness (IF)-based group size favored

by an insider, n_I^* , is equal to or larger than n_I . The IF-based group size favored by an outsider, n_O^* , is equal to or smaller than n_O .

reproductive skew theory to predict the size of a group in which a single dominant individual and multiple subordinates exist. They assumed that (1) expected group output is an increasing, but decelerating function of group size, (2) the dominant should yield just enough reproduction to each subordinate to induce them to stay in the group rather than to breed solitarily, and (3) the dominant has the ability to eject a subordinate from the group. Their model predicted that increasing relatedness would decrease the “optimal” group size from the viewpoint of the dominant individual. Interestingly, this prediction is in stark contrast with those of the “group-controlled entry” version of the earlier models, which predicted that increasing relatedness would generally increase the “optimal” group size from the viewpoint of group insiders (Giraldeau and Caraco 1993; Higashi and Yamamura 1993). The divergence occurs because, in Reeve and Emlen’s (2000) skew model, the dominant individual is more likely to eject a closely related subordinate from the group. By doing so, the single dominant member will gain greater indirect fitness benefits from the solitary output of the closer relative. In contrast, the earlier models not assuming the dominance hierarchy in social groups find that each and every group insider will gain indirect fitness benefits from the entry of a related outsider (Giraldeau and Caraco 1993; Higashi and Yamamura 1993).

Group Size Distributions Observed in Nature

How do theoretical predictions about the optimal group sizes compare with empirical observations of the actual group sizes? As shown above, theoretical models predict that group size distributions should have a single peak at the optimal group size and a very narrow variation around this maximum (Caraco et al. 1980; Clark and Mangel 1986). However, the variation in the observed group sizes for a number of animal species is usually much wider than predicted by these models. In such species as ungulates, fish, and social spiders, group size distributions are

highly right-skewed and long-tailed: while there are lots of small groups, a few exceptionally large groups do exist that are often several orders of magnitude larger than the modal group size (Avilés and Tufino 1998; Bonabeau and Dagorn 1995; Bonabeau et al. 1999; Gerard et al. 2002; Sumpter 2010). Such long-tailed distributions often follow a power law. For instance, plotting the logarithms of tuna school sizes against the logarithms of their frequencies, Bonabeau and Dagorn (1995) showed that the data in the log-log plot were fitted by a straight line with a slope of -1.5 , meaning that a group size n occurs with a frequency of $n^{-1.5}$.

Long-tailed distributions of group sizes in the wild have sparked the interests of many theoretical physicists. Instead of asking which group size an individual should be selected to prefer so as to maximize his/her inclusive fitness, researchers tried to find the simplest set of rules for the fission and fusion of social groups that can generate long-tailed group size distributions, including power law distributions (Bonabeau and Dagorn 1995; Sumpter 2010). Bonabeau and Dagorn (1995) developed a model of group formation based on an extremely simple assumption: when groups meet they always merge to form a larger group. Their model predicted a power law distribution of group sizes, which appeared somewhat consistent with the empirical data of fish schools. Bonabeau and Dagorn’s (1995) model, however, has been criticized for its biologically unrealistic assumption that the population should keep increasing to infinity with time in order to get a power law in group size distributions (Ma et al. 2011; Sumpter 2010).

Niwa (2003, 2004) proposed another model of animal aggregation and breakup. The model’s assumption about aggregation were identical to Bonabeau and Dagorn’s: when groups meet at any site they always merge. Yet Niwa further assumed that each group may split into two sister groups – the size of which is chosen uniformly at random. Niwa (2003, 2004) showed that, simply by measuring the expected group size experienced by a randomly chosen individual for a particular species, one can predict the whole distribution of group sizes in that species (Ma et al. 2011).

Moreover, the predicted long-tailed distributions of group sizes for six different fish species fitted well with the empirical data.

Note that the mechanistic approach seeking the simple rules of group fission and fusion that agree well with observed group size distributions is distinct from the functional approach seeking the optimal group size resulting from the balance between the costs and benefits of group membership (Sumpter 2010). In other words, although mechanistic models make implicit assumptions about the set of behavioral rules by which individuals join and leave groups, they fail to take into account how such rules could have affected the inclusive fitness of a group member over evolutionary history. Obviously, it would be desirable to investigate models of group fission and fusion in the context of optimizing group size (Krause and Ruxton 2002; Sumpter 2010).

Conclusion

The size of group in which animals live may reflect the optimal balance between the fitness costs and benefits of group living. From the viewpoint of each individual in and out of a group, however, the optimal group size is likely to differ between them according to whether (1) the individual is an existing group member or a prospective joiner, (2) the individual is genetically related to others, and (3) the individual occupies a dominant or subordinate position within the dominance hierarchy in the group. Consequently, there should be a potential genetic conflict of interest between individuals over the size of the group. Future studies should pay more attention to at what group size the conflict will be resolved. Ideally, such a resolution model should generate long-tailed distributions of group sizes, thereby accounting for the observed group-size distributions in the wild.

Cross-References

- [Group Size Optimality and Stability](#)
- [Grouping and Predation](#)

- [Inclusive Fitness](#)
- [Living in Groups](#)
- [Skew Theory](#)

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Group Size Optimality and Stability

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Synonyms

Optimal versus stable group size

Definition

The group size that maximizes the average fitness of group members; the group size which, if prevalent in a resident population, cannot be evolutionarily invaded by any slightly different group size.

Introduction

Adaptive explanations for group living have suggested that individuals choose to live in groups of

optimal size where the inclusive fitness of each group member is maximized (Caraco and Wolf 1975; Pulliam and Caraco 1984; Rodman 1981). Yet Sibly (1983) pointed out that the optimal group size may not be stable; the stable group size to be observed in nature will frequently exceed the optimum. This happens because a solitary outsider will do better by joining a group of optimal size rather than by remaining alone, even though the average fitness of group members is reduced by the addition of a newcomer (Clark and Mangel 1984; Sibly 1983). The size of a group is expected to increase until group insiders do not fare any better than solitary individuals, which seems paradoxical (Giraldeau 1988; Giraldeau and Caraco 2000). This entry examines whether the optimal group size is indeed unstable.

Is the “Optimal Group Size” Unstable?

As stated above, earlier models for the evolution of group formation have viewed that selection would favor individuals residing in groups of optimal size. Let $w(n)$ be the average fitness of group insiders within a group of n individuals. As n grows, the fitness function $w(n)$ is typically assumed to initially increase, to attain a maximum at an intermediate group size n_I , and to decrease afterward. It is further assumed that $w(n)$ drops below $w(1)$ once n goes beyond a certain value n_O (i.e., $w(n) \geq w(1)$ for $n \leq n_O$, while $w(n) < w(1)$ for $n > n_O$). Then n_I is the group size that maximizes $w(n)$ for its members, the “optimal group size” (Caraco and Wolf 1975; Pulliam and Caraco 1984).

Sibly (1983), however, contended that groups of optimal size may rarely be found in nature. The argument was based on his specific assumptions regarding how groups are formed: (1) a series of solitary outsiders arrives at a site singly, (2) each outsider has a choice between living alone and entering a group at no cost, and (3) group insiders leave a group individually. Under these circumstances, solitary outsiders will join a group of size n as long as the resulting fitness they would gain in that group size, $n + 1$, is larger than the fitness of being on their own (i.e.,

$w(n+1) > w(1)$). Note that solitaires will join the group even when their joining decreases the average fitness of group members (i.e., $w(n) > w(n+1)$). Group size continues to grow up to n_O , at which solitary outsiders no longer enter the group (i.e., $w(n+1) < w(1)$ when $n = n_O$) and no group insiders leave the group singly. Then n_O is called the “stable group size.” Accordingly, self-interested animals would cause the stable group size to be larger than the theoretically predicted optimum (Sibly 1983). Thus, a paradox arises where gregarious individuals end up in a group of stable size for which group membership bestows no benefit over living alone.

Stable from Whose Point of View?

In order to investigate whether the “optimal group size” is unstable, one should observe that Sibly’s (1983) model was constructed on his strict assumption that a solitary outsider has complete control over her own entrance into a group. As covered in the chapter entitled ▶ “Group Size” in this volume, different assumptions about who is in control over a newcomer’s entry can make markedly different predictions regarding group size. Under the assumption of free entry, the “optimal group size” n_I maximizing the average fitness of group insiders is certainly neither optimal nor “evolutionarily stable” from the viewpoint of a solitary outsider. As shown above, the optimal and evolutionarily stable group size for an outsider is the “stable group size” n_O . It is worth noting that evolutionary stability can be determined by verifying whether a resident population fixed for a particular strategy is resistant to the invasion of any mutant strategy (Otto and Day 2011).

Consider the opposite assumption that group insiders exert full control over a newcomer’s entry. Under the assumption of group-controlled entry, the “optimal group size” n_I is both the optimal and evolutionarily stable group size from the viewpoint of a group insider. As Sibly (1983) cogently argued, the “optimal group size” n_I for an insider is neither optimal nor evolutionarily stable for a solitary outsider. Hence,

the baffling conclusion of Sibly’s (1983) model largely arouse from semantic confusion over *from whose point of view* the “optimal group size” is evolutionarily stable. The “optimal group size” for a group insider is evolutionarily stable from the viewpoint of an insider; however, it is unstable from the viewpoint of an outsider.

Resolution Models Predict the Observed Group Size

Which group size could we expect to observe in the wild? Given that group insiders and solitary outsiders have different fitness optima concerning group size, so-called “resolution” models are needed that would predict how the evolutionary conflict between insiders and outsiders is likely to be resolved in behavioral terms (see the entry ▶ “Group Size” in this volume). The evolutionarily stable group size predicted by such a resolution model is what we actually should expect to see in natural populations. For instance, Higashi and Yamamura (1993) found that the resolution of the insider-outsider conflict over group size should eventually result in a “compromise groups size” that lies between the group size favored by an insider (the “optimal group size” n_I) and the group size favored by an outsider (the “stable group size” n_O). Seno (2006) constructed a resolution model of group size that takes into account the influences of fusion and fission within and between groups.

Viewed in this light, it can be seen that Sibly’s (1983) model has brought about some unfortunate difficulties in making general predictions about actual group size in nature. Undoubtedly, the free entry assumption will hold in some cases, such as the formation of sea birds’ breeding colonies or the formation of some animal species’ nocturnal roost sites, where existing group members have little chance to prevent a solitary outsider from joining them (Giraldeau and Caraco 2000). It seems reasonable, however, to suppose that in most situations neither insiders nor outsiders would have complete control over an outsider’s entry. Thus, the evolutionarily stable group size found in the wild is highly likely to represent

a compromise between the different fitness optima of insiders and outsiders. The mere fact that the observed group size of a particular animal species turned out to be larger than the theoretically “optimal group size” for an insider (e.g., Caraco and Wolf 1975) in no way demonstrates that the optimal and evolutionarily stable group sizes do not normally exist in natural populations.

Conclusion

Sibly (1983) argued that, since the optimal group size is unstable, the mean group size observed in nature will be generally larger than the optimum. Semantic confusion exists in the literature concerning from whose point of view the “optimal group size” is evolutionarily stable. The “optimal group size” for a group insider is certainly stable from the viewpoint of an insider, whereas it is unstable from the viewpoint of an outsider. It is so-called “resolution” models that do predict the mean group size that should be predominantly found in natural populations.

Cross-References

- [Game Theory](#)
- [Group Size](#)

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Group Social Structure

- [Primate Dominance Hierarchies](#)

Group Socialization Theory

- [Peer Socialization](#)

Grouping and Predation

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Synonyms

[Aggregation](#); [Living in groups](#); [Sociality](#)

Introduction

The formation of groups is one of the most conspicuous and striking behaviors seen in animals. It is observed across a diverse range of living organisms, from colonies of multicell slime molds to human cities that rely on extensive and complex infrastructure. The reasons we may observe a set of individuals in closer proximity to one another than expected from a random distribution are varied. Animals that are usually asocial may

aggregate around a food resource, such as brown bears (*Ursus arctos*) feeding on migrating salmon in rivers, or aggregation may emerge simply from a lack of dispersal, where offspring tend to be found in close proximity to their parents and other relatives. In many other cases, however, aggregations are a result of *social attraction*, where individuals actively seek out the company of others. Once such groups form, they can be very stable, with the group moving as a unit, synchronizing their activity and behavior over space and time. This stability of group membership can then give rise to complex social behaviors such as dominance hierarchies and altruism.

The question of why animals actively form groups is a long standing question in animal behavioral research (e.g., Miller 1922). Competition for resources (e.g., food or breeding sites) often leads to aggression, and close proximity to others can have a significant negative impact on an individual's reproductive success. A number of mechanisms for why group living may be favored in evolutionary terms have been supported with theoretical, experimental, and observational studies: moving through space may be energetically less costly via hydro- and aerodynamic effects, and resources may be more easily found and/or exploited in groups (Ioannou 2017). The most common and widespread explanation for why animals live in groups, however, is because predation risk is reduced in groups (Rieucou et al. 2015).

The Social Response of Prey to Predation Pressure

Evidence that animal groups have evolved to reduce predation risk comes from studies demonstrating that social tendencies are greater with higher levels of predation. This trend exists at the short time scale of individuals detecting and responding to cues indicating higher predation risk. For example, using a carefully manipulated experimental design, Hoare et al. (2004) demonstrated an increased group size in the banded killifish (*Fundulus diaphanous*) when exposed to a nondirectional predator odor cue. An alternative

approach is to compare social behavior between populations found in low versus high predation habitats, where exposure to predation risk varies at a much longer time scale (i.e., generations compared to minutes or hours). Beauchamp (2004) demonstrated that populations of various bird species tended to form smaller flocks on islands compared to mainland populations, where predation risk is reduced in island habitats. Over a small geographical range but across multiple populations, Seghers (1974) similarly showed that populations of the guppy (*Poecilia reticulata*) in the Northern Range Mountains of Trinidad have a reduced shoaling tendency in habitats with fewer and less dangerous predators. Additionally, it was shown that these shoaling tendencies were heritable.

Mechanisms for the Reduction of Predation Risk in Groups

In addition to studies of how social tendencies vary with predation pressure, a number of mechanisms which drive the reduced risk in prey groups have been proposed and are supported from studies of behavioral predator-prey interactions. These mechanisms reduce the overall predation rate by reducing the chance the prey are detected or captured and/or, for each attack, shifting the risk to less aggregated individuals. Disentangling the mechanisms that reduce the risk of predation in groups can be problematic; although through careful experimentation, analysis of data, and knowledge of the biology of predators and prey, each of the mechanisms detailed here is well established in the literature. These antipredation grouping mechanisms are ordered from those requiring simple behaviors in the prey to those that are more advanced.

The Dilution Effect, Attack Abatement, and Detecting Groups of Prey

The simplest mechanism for reducing predation risk in groups is the dilution effect. As group size increases, the probability that any single

individual is selected for attack decreases, so that the per capita risk of predation is $1/n$, where n is the prey group size. Foster and Treherne (1981) were the first to provide strong evidence for this effect, by observing rates of predation on a marine insect, the ocean skater *Halobates robustus*. Due to the biology of the system (the prey cannot detect and respond to imminent attacks from below by the fish predator in the study, *Sardinops sagax*) and a close match between observed and expected risk at different group sizes, Foster and Treherne convincingly showed that the dilution effect could reduce risk in larger groups in a naturally occurring predator-prey system. They also showed that the dilution of risk between group members had a greater effect on risk than a reduced attack success in larger groups, possibly caused by the confusion effect (see below), suggesting that risk dilution is the dominant mechanism explaining group living in this species.

Although intuitive, further work refined the circumstances under which risk would be reduced due to a dilution effect. Turner and Pitcher (1986) argued that in addition to risk being diluted between group members, the number of attacks on groups would need to be less than proportional to the group's size ("attack abatement," also referred to as encounter-dilution). In other words, if a group twice as large is attacked twice as often, the dilution effect would be canceled out. While Foster and Treherne (1981) did show there was no relationship between group size and the rate of attacks per group, there are a number of reasons why larger groups may receive more attacks in other predator-prey systems. Larger groups are more conspicuous simply due to their increased size, although the relationship between group size and conspicuousness tends to be less than directly proportional (Treisman 1975), suggesting that attack rates are still lower in larger groups per individual prey. Recently, Ioannou et al. (2011) argued that rather than considering groups of different sizes, a more ecologically relevant question is how a population of prey should distribute themselves to minimize detection by predators, i.e., whether to form a single, large group, or to distribute themselves in smaller groups or as individuals. Using a combination of an

experiment and a simple model, Ioannou et al. (2011) found that while larger groups are more easily detected, the reduced encounter rate between predator and prey when there are fewer groups is a stronger effect, leading to an overall decline in the rate at which predators are expected to detect prey as group size increases. These studies, however, have used (Ioannou et al. 2011) or assumed (Treisman 1975) simple prey that do not change their behavior in larger groups. There may be greater per capita activity in larger groups, for example, through increased competition for food, and this may make larger groups disproportionately more conspicuous and hence preferentially targeted.

Once detected, there are other ways in which the number of attacks could increase with group size. Predators often attack and consume multiple prey per encounter, for example where predators can ingest numerous prey simultaneously, as with filter feeders (Rode et al. 2013), or when multiple predator individuals are simultaneously attacking a group. When foraging on cryptic prey that do not flee or show other evasive behaviors, predators often conduct "area restricted" searches once a first prey is found (Hill et al. 2003). When aggregated, this increases the foraging success of the predator, and increases risk to prey. In cases where multiple prey are consumed in each encounter, it may be advantageous for prey not to be social, and instead distributed themselves throughout the habitat (Treisman 1975). However, the time taken to handle and process each prey item will place a limit on the rate of consuming prey (Holling 1959), and this is likely to mean that attacking larger groups may provide little benefit for the predator relative to smaller groups if handling time restricts the rate of prey consumption. Thus, there may be a reduced incentive to attack larger groups, especially if other mechanisms, such as the confusion effect and group vigilance (see below), reduce the likelihood an attack is successful.

The Selfish Herd

A mechanism often discussed alongside the dilution effect is Hamilton's selfish herd effect (Hamilton 1971). As with the above mechanisms,

the selfish herd can explain group living simply through the spatial distribution of prey, without the prey needing to move, coordinate, or otherwise communicate with one another. The selfish herd model assumes that predators can appear anywhere in the environment and will attack the nearest prey. Thus, to avoid predation, prey should position themselves to be closer to other prey, selfishly reducing their “domain of danger” (the space closer to that individual than any other), and hence forming densely packed groups. Prey often show a short-term response of reducing interindividual distances upon detecting a predator (Hoare et al. 2004; Viscido and Wethey 2002), although this could be a response which increases the efficacy of confusion and group vigilance effects (see below), rather than solely to reduce domains of danger. Few studies have quantified domains of danger in prey groups and shown them to be directly proportional to the risk of mortality, or to what extent proximity to individual prey in groups affects a predator’s selection of which individual to target relative to other variables.

Confusion Effect

The confusion effect is a popular concept and is rarely omitted from the reasons why animals live in groups. Aggregation of prey results in more prey individuals within the visual field of a predator, which can overwhelm a predator’s cognitive ability to quickly select and successfully attack a target prey when many other possible targets are visible. This can reduce the rate of attacks made, make attacks less successful, and/or shift attacks to targets with fewer prey nearby, such as those on the periphery of the group or those that are separated from the group. The confusion effect can also explain the targeting of phenotypically odd individuals (the “oddity effect”), which stand out more against the background of their similar-looking group mates (Landeau and Terborgh 1986). This oddity effect can help account for assortment of phenotypes in groups, and synchronization of behavior, as behaviorally odd prey can also be preferentially targeted by predators. Evidence that targeting prey in groups is cognitively demanding includes experiments using three-

spined sticklebacks (*Gasterosteus aculeatus*) attacking groups of *Daphnia*, where detection rates of the sticklebacks’ own predator decreased when they were attacking a high, rather than low, density prey group (Milinski 1984).

Current evidence suggests that the high synchronization and coordination seen in some bird flocks and fish schools is not necessary to induce a confusion effect (Ruxton et al. 2007), although studies on a greater range of animals are needed to generalize this conclusion. Neural network models (Tosh and Ruxton 2010) have been used to explain how the confusion effect arises as an information-processing constraint of predators. Only group size and spatial arrangements of prey are used as the visual input into such models, with no interaction between prey or even any prey movement, suggesting that the confusion effect may be widespread in predators of aggregated prey. The effect is unlikely, however, to be important in predators which do not target individuals, such as flamingoes which filter feed (Rode et al. 2013).

Group Defense

Living in groups can allow collective defense of the group to stop predation by predators that may otherwise be too dangerous for a single individual to defend themselves (or their offspring) against alone. A classic example of group defense is the arrangement of adults around young in bison herds, where the wall of horns and muscle creates a formidable defense against attacking wolves. However, most studies of group defense come from birds, particularly from nesting colonies. Rates and effectiveness of mobbing potential predators typically increases with colony size (e.g., Hoogland and Sherman 1976), and experiments using artificial nests show predation is decreased when these are closer to larger, rather than smaller, colonies (Andersson and Wiklund 1978). As well as stopping successful attacks, mobbing can function to signal to a predator that they have been detected, which may deter attacks if the predator relies on surprise to be successful. The close proximity of prey to predators during mobbing also allows prey to learn about the level of threat an individual predator

poses, and can allow less experienced prey to learn about potential threats from more experienced individuals (Graw and Manser 2007).

Group Vigilance (the “Many-Eyes” Effect)

Vigilance for predators and other threats is common in prey animals. When in groups, the “many-eyes” looking out for danger mean that predators are more likely to be detected (Siegfried and Underhill 1975). If this information can transfer between individuals and through the group, it can significantly reduce the rate of successful attacks on groups if appropriate behavior is performed, such as fleeing or signaling to the predator that they have been detected. As well as a mechanism reducing risk in groups, this collective detection is an example of social information use, as it allows individual prey to respond to publically-available information (the response of near neighbors or intentional alarm signals) without all prey having to directly detect the threat (Herbert-Read et al. 2015).

Of the mechanisms that reduce predation risk in groups, group vigilance is the only one that relies on information transfer between individuals. Information transfer may be through intentional, active signals, such as alarm calls, or via unintentional cues such as the fleeing response of near neighbors. Collective detection also applies outside of a predator-prey context; for example, collective detection of food can show a similar pattern (many eyes are more likely to detect a food source, which is information then transferred through the group). Ward et al. (2008, 2012) elegantly showed that the same collective response rule (quorum decision making) could describe the collective detection of either a predator or a food source in a Y maze using three-spined sticklebacks (*G. aculeatus*). There is growing interest in the way that information (regarding possible threats or resources) flows between individuals in groups, and this has been greatly facilitated by recent technological advances where the movement of individuals in groups can be tracked in detail (e.g., Herbert-Read et al. 2015).

Vigilance is also important for studying aggregation in animals because it can indicate the level of risk perceived by individuals. Rates of vigilance typically decrease in larger groups (Roberts 1996), suggesting lower perceived risk, and this lower risk can be via any combination of the anti-predatory grouping mechanisms described above. It will, however, lessen the extent that collective detection improves detection of predators. Competition for food and other resources may also explain why vigilance decreases in larger groups, as individuals need to pay greater attention to finding food when competition is more intense.

Conclusion

Almost all animals face predation at some point in their lives, even if this is just in vulnerable juvenile life stages. Living in groups is a common strategy to mitigate the risk of predation and has evolved independently and repeatedly in numerous taxa. However, there are a number of limitations on our current understanding of grouping and predation. Most studies have considered visual detection only (both of prey by predators and vice versa), and relatively little is known about whether the conspicuousness of larger groups, the confusion effect, and group vigilance alter when other sensory modalities are used. Similarly, little is known about whether environmental variables, such as turbidity in aquatic habitats, have an effect on the mechanisms that make groups safer for prey. A challenging but worthwhile aim for future work would be to bring together the common antipredation grouping mechanisms under a single framework to determine and predict which combination of mechanisms would be favored under different conditions. For example, prey that cannot detect the first attack by a predator are unlikely to benefit from group vigilance, but may benefit from a confusion effect if they are moving before the attack occurs (Foster and Treherne 1981).

There also remains a bias in predator-prey studies, with much greater focus on prey behavior rather than the behavior of predators. As with prey, predators are under evolutionary selection

pressure to forage optimally, although there has been relatively little work studying the foraging behavior of predators searching for (Ioannou et al. 2008), attacking (Cresswell and Quinn 2004), and consuming (Rode et al. 2013) prey that live in groups. In some cases, predators have appeared to have evolved to exploit the grouping and social tendencies of their prey (Rieucau et al. 2015; Rode et al. 2013), even in carnivorous plants (Bauer et al. 2015). The confusion effect and increased conspicuousness of larger groups suggests that predators are under considerable cognitive constraints in predator-prey interactions. The reduced success from the confusion effect should result in a preference for attacking smaller groups (Cresswell and Quinn 2004), but the difficulty in detecting smaller groups constrains the choice of prey available; frequent, but relatively unsuccessful, attacks by predators on larger groups may result in a greater net intake rate compared to maximizing success per attack. Predators may respond to the reduced attack success from confusion and group vigilance effects by spending a greater proportion of their time foraging, so that overall predation rates remain constant. In contrast, they may shift their diet choice to nonsocial prey species that are more profitable once the difficulty in finding and attacking aggregated prey is considered. A full understanding of predator-prey interactions needs a balanced approach where the behavior of predators is also studied, ideally through both theoretical and empirical approaches.

Cross-References

► Predator Swamping

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Groups and Categories

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Synonyms

Social organization; Social categorization; Social identity

Definition

Groups and categories are the elements of social organization in human societies of any size. Whereas the term ‘group’ primarily refers to sets of identifiable individuals, the term ‘category’ primarily refers the mental representation to the building blocks of the social world. Social organization and its mental representation have co-evolved to striking degrees of complexity; yet, simple – even crude – behavioral patterns such as ingroup-favoritism or parochial morality persist.

Humans are social animals, both in their dependency on interaction with individual conspecifics and in their embeddedness in a social structure comprising groups. The nature of these groups varies greatly with ecological, economical, and historical conditions, making it difficult to uncover the essential characteristics of a group-shaped psychology. Studies of the fossil record and surviving hunter-gatherer societies suggest that hominid social life has long been hierarchically organized. Small units, such as temporarily pair-bonded mates and their close kin, are vital for reproduction; bands comprising a few dozen individuals cooperate in hunting, gathering, and shelter-making; communities comprising multiple bands share a language or dialect, and they may intermittently congregate for ritual activities or common defense. This multilevel social organization has evolved during the Pleistocene, and it distinguishes the only surviving human species from the great apes and other social animals (Layton et al. 2012; cf. Darwin 1871).

Evolutionary psychology seeks to understand how and why this prevalent social organization obtained its present form, and inasmuch as the properties of human social organization are functional, what are the adaptive problems they have solved. Moving to the individual human being as the unit of analysis, evolutionary psychology explores elements of cognition, affect, and behavior that can be properly understood only with reference to the evolutionary legacy of past generations.

With regard to the first question, research highlights the co-evolution of neocortical size, mental

capacities, and social organization. Compared with other primates, humans can keep track of a greater number of individual conspecifics, who they are, and, more importantly, how they have acted in the past. Humans can even represent and keep track of those conspecifics who are currently out of sight, often for a long time, and even the deceased. From this knowledge, humans can compute expectations about future behavior and choose between aggression and appeasement, trust and suspicion, pursuit and avoidance. The complexity of these perceptual, memorial, and executive functions is correlated with the size of the neocortex relative to total body size over living species of social animals, and, very probably, over extinct hominid species in evolutionary time (Dunbar 1993). The extraordinary evolution of the human brain is thus intertwined with the complexity of the social organization humans can afford.

A key correlate of advanced psychological functioning is the human capacity to sustain a sophisticated social organization while being able to tolerate very low population density – lower than in any of the great ape species. Bands of hunter-gatherers can roam over large territories, exploiting scarce resources, while occasionally congregating with other bands to affirm shared community identities. Shared language and ritual practice afford community cognition, affect, and behavior. Although some of these shared psychological features reside within the individual and may remain unexpressed (e.g., certain types of affect or elements of the self-concept), many features are expressed in a way that signals shared group identity to others. The evolutionary bedrock of shared identity is genetic relatedness (Dawkins 1976). Social structure is often superimposed on and often correlated with genetic distance, but sometimes it is not. Humans have developed cross-cutting social categories that further complicate social structure. Many hunter-gatherer communities subdivide into clans and totem-defined structures that mimic sympatric bands, by, for instance, imposing taboos on endo- or exogamy, but that are, from the outside observer's perspective, arbitrary (Stanner 1965).

While the hierarchical and multilevel organization of social life is a human universal, its observed forms vary greatly. The flexibility of the social brain and especially the ease with which it creates, changes, and eliminates categories or groupings spawns ever-new structures. The minimum criterion for a social structure to become mentally represented and socially consequential is a signal that communicates inclusion versus exclusion. The totem-based clan is the evolutionary archetype of the influential minimal-group paradigm (MGP) in social psychological research (Tajfel 1970). The MGP mimics social groups or categories that have no basis in genetic relatedness, differential familiarity, or intended future interaction. Research participants are categorized at random, with the only mark of distinction being a quasi-totemic label, such as “The Greens” or “The Blues.” After the typical hour-long experiment, participants are disbanded. In contrast, many arbitrary marks of group belongingness in the wild are irreversible, such as circumcision.

Despite its skeletal and fleeting nature, the MGP produces many of the shifts in cognition, affect, and behavior observed among groups in the field. Most prominent among these phenomena are perceptual contrast and assimilation effects (cognition), ingroup love and positive social identity (affect), and ingroup cooperation versus outgroup competition (behavior). Moving to the second question with the individual as the unit of analysis, we can now consider the three sets of phenomena in turn. Cognitively, the categorization of people into mutually exclusive groups leads to the accentuation of intergroup differences where such differences exist (contrast). If, for example, differences in body height covary with an arbitrary criterion of demarcation, the shorter ones will be collectively viewed as shorter and the taller ones as taller than they would be in the absence of such a criterion. At the same time, individual differences within categories are minimized (assimilation) (Krueger and DiDonato 2008; Tajfel 1969). Affectively, categorization affords identification with those who are like us, even if by label only. In turn, this shared positive affect affords a sense of positive social identity, which extends – usually in mitigated form –

positive self-sentiments to the group (DiDonato et al. 2011) and inversely reflects positive features of the group back to the self (Van Veelen et al. 2016). Behaviorally, categorization affords coordination and cooperation with ingroup members, which, in turn may set the stage for group selection effects over evolutionary time (Wilson 1975).

A minimally sufficient theoretical account to explain the correlated patterns of categorical ingroup perception, ingroup love, and ingroup cooperation (Balliet et al. 2014) assumes that most people possess positive self-images, which they selectively project to ingroups but not to outgroups (Robbins and Krueger 2005). This differential projection results in comparatively positive ingroup perceptions and a comparatively high level of trust in ingroup members (Brewer 2008; Krueger et al. 2012). These models, built on assumptions about learning and inductive reasoning, do not require that people actively compare ingroups and outgroups. Learning about ingroups is sufficient so that competition with and discrimination against out groups can begin as a mere byproduct of parochial learning.

Whereas most social psychological theories assume – and show – that the social or arbitrary introduction of criteria for categorization triggers multifaceted psychological discrimination, some basic distinctions arise from even simpler processes. Human infants are highly sensitive to human and human-like faces. An innate positive response is available, providing a stepping-stone for the building of a mental archive of familiar faces. Infants quickly learn individual identities and thus person-to-person differences. The proximal benefit is that they know from whom to expect love and protection. As a result of this identity learning, infants pick up any variable that is correlated with identity, such as sex and race. Computerized simulations of such learning suggest that it is not necessary to introduce infants to ideas of sex or race; they will induce them from observed patterns of variation (Kramer et al. 2017). The appearance of an individual's face varies somewhat from occasion to occasion, depending on the lighting, the angle of viewing, or the observed person's mood. The learner's challenge is to abstract identity from these

variable observations. However, a person's identity does not cross gender or racial boundaries once it is detected – in most cases. Therefore, sex and race information is implicit in identity information and can be easily extracted. Once the infant (or the algorithm) harvests a categorical distinction from observation, the door is open for accepting other distinctions between social groups and categories, including those provided by social learning.

The title of this essay, “Groups and Categories,” signals the unsettled nature of these concepts in the behavioral sciences. Biologists and social psychologists tend to prefer the concept of group as a general way of referring to any non-random sorting or the lumpiness of social organization. Cognitive scientists, in contrast, tend to prefer the concept of category, as it supports theories of general category learning, which just happen to include social stimuli. On this view, the lumpiness of the mind is prioritized over the lumpiness of the social world. From an evolutionary perspective, the two concepts are too closely intertwined to allow a strictly separable usage. As we have seen, it seems likely that the physical separation into seen and unseen groups coevolved with the ability to represent seen and unseen categories of greater abstraction. At the present time, there is little reason to assume that one concept preceded the other.

Cross-References

- [Competition Between Groups](#)
- [Human Groups](#)
- [In-Group Versus Out-Group](#)

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Group-Serving Biases

- [Self-Enhancement Relative to Others](#)

Growth

- [Cancer](#)
- [Development](#)
- [Social Development in Nonhuman Primates](#)

Gua the chimpanzee

- [Kellogg Chimpanzee Study, The](#)

Guns, Germs, and Steel

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Synonyms

[Civilization division](#); [Development of civilizations](#); [Evolutive competitions of civilizations](#); [History of civilizations](#)

Definition

Comprehensive historical analysis of how environmental pressures shaped the development of the societies, playing a key role in the supremacy of the Eurasian peoples, aided by weapons, germs, and steel.

Introduction

Guns, Germs, and Steel, written by Jared Diamond, was published in 1997. The book attempts to answer Yali's question, a New Guinean who quizzed him about how Europeans had colonized New Guinea within 200 years and why

they developed so much goods, but they had little goods of their own. By historical explanation, the book intends to understand the interactions among disparate people and how it shaped the modern world through the reverberations of conquest, epidemics, and genocide. The history's broadest pattern question is why did human development proceed at such different rates on different continents.

One of its main ideas is that all great civilizations have had some things in common: advanced technology, large populations, and complex government forms. The arguments are developed in four parts that cover historical examples of how the environment can interfere in a civilization formation and interaction, how and why they evolved from hunter-gatherer to food-producer societies, how the food production has fostered a complexification of societies, and finally how these elements made possible the domination of the Eurasian peoples over the others.

Environmental Pressure on Very First Civilizations

The author investigates, in a Darwinian perspective, the influence of environmental pressures on the formation of human societies, from *protohumans* to the last 13,000 years of history. In analyzing the societies' diversity on the Polynesian, Diamond provides clues to understanding the plural formation of the civilizations. The author investigates the main factors that contributed to further technological, economical and social development of some societies, especially the world supremacy of the Eurasian people in terms of wealth and power. The climate and geography conditions of the very first civilizations were very similar. These aspects shaped the way to acquire resources for survival. Understanding the development of technologies is determinant to discern the capacity of some people to dominate others. Even there were people in similar environmental conditions, the rise of practices like food production by agriculture instead of hunt-gather lifestyle allowed the development of societies and their technologies.

Food production spreads at different rates on different continents. Middle East and Chinese peoples were the first farmers; they started to control nature interrupting the environmental cycle to produce wheat and barley and rice, respectively. New Guinea type of food, taro roots, has a difficult process to grow and has some disadvantages: it is necessary to plant taro roots one by one; it can't be stored because it rots quickly and it is low in protein. Besides, the hunt-gather lifestyle wasn't economic and took a lot of effort and poor results. In most places where farming emerged, a relatively large advanced civilization followed.

Another element of the societies' development was the animal domestication. This package was mutual beneficial for humans, animals, and plants. When human started to control their moving, feeding, and breeding, it was possible, without hunting, to have meat supply, milk, muscle power to the plows, and leather. Thus, exceeding food production could feed the animals, which would aid in the production of more food because of their strength and also the ability of their excrement to fertilize the soil. The best animals to domesticate were those plant-eating and sociable mammals, as ox, horses, pigs, sheep, and goats, native from the Middle East. The only domesticated mammal in New Guinea was the pig, which can't produce milk, leather, or muscle force for plows.

Diamond assumes that it is the shape of the continents, their crops, and their animals that allowed some cultures to flourish while others were left behind. Also the type of farming was most important than only farming, because most productive and nutritious crops allowed most productive farmers. The people in New Guinea didn't advance technologically; they spent too much time and energy feeding themselves.

From Germs to Guns and Steel

Therefore, two main arguments for the development of societies are presented: (1) surplus of food production allowed the social division of work and the raising of class specialized in other activities and (2) human contact with animals allowed

interactions with germs, which caused several diseases, an important element to understand colonization processes. The crops, the animals, and the increasing food production started to feed new social groups: the artists, the inventors, and the soldiers. Thus, years of agriculture development allowed to evolve the writing, the new technologies, and a central government and religion. The writing emerged independently at the Fertile Crescent, Central America, and China, where there was plenty of food and cultural interactions. This knowledge facilitated communication, dissemination of information, and other technologies, placing literate civilizations ahead of others. Technology is developed through two processes: creation and diffusion. Creation is more difficult because it involves high cost and requires more time. Diffusion, in turn, primarily requires a contact between peoples for the exchange of knowledge. In addition, technology is an autocatalytic process, that is, the more it develops, the greater its advancement potential. In this way, technological development, as well the political complexification, depends on the contact between independent civilizations and higher food production. Food production is related to technology, as larger population increases the exchange of knowledge and the chances for geniuses.

In turn, germs as well evolved with writing, guns and political organization as a modern agent of conquest. Europeans and Central America Indians had a developed civilization, with central government, writing, and food production; however, genocide was not caused only by guns and steel but predominantly by the diseases brought by European. The dominance of European societies occurred mainly because they had the writing, complex government, technology (as guns and steel), and germs. Diamond's arguments highlight that the differences between the civilizations do not derive from the biological capacities of the peoples who formed them but were primarily determined by the environment. For example, Yali's people did not produce metal or steel tools and did not use writing, and their social structure wasn't complex. Besides, their land, geography, and plant and animal species did not allow a development of a complex society. Similar patterns were found in

other civilizations. They were limited by environment dispositions, such as low diversity of food sources and fragmented or isolated lands, precluding the populational growth and the social development. Furthermore, the low cultural exchange with other people and isolation hindered the high technological development.

Conclusion

The civilization collisions created reverberations that have still not died down after many centuries and that remain continuing in some of the world's most troubled areas today. There are four main types of differences to understand the development of civilizations: first, continental differences in the plant and animal available species; second and third, the rates of diffusion and migration among and between the continent, which allowed the knowledge of new technologies and the political and linguistic progress toward its unification; and fourth, continental differences in total area or population size, because they mean potential inventors, competing societies, and innovation. In short, the book indicates that some environments provide better starting materials and favorable conditions for utilizing inventions than do others. The culture and the individual, although they are important elements in history, are scarcely relevant for the purposes of the book, because it would be difficult to interpret history's broadest pattern in terms of a few individuals. *Guns, Germs, and Steel* is ultimately a comprehensive history analysis. Its subject matter is not just of academic interest but also of overwhelming practical and political importance.

Cross-References

- [Australopithecus garhi](#)
- [Competition Between Groups](#)

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Gut Feelings

► Moral Instincts and Morality

Gut Microbiome

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Synonyms

Gut microbiota

Definition

The human gut microbiome is a community of roughly 40 trillion bacteria, fungi, archaea, and protozoa which reside within the human gastrointestinal tract. Variations in gut microbiome composition have been implicated in a variety of psychological, physiological, and behavioral traits.

Introduction

A variety of environments, including many human organs, contain within them communities of microorganisms, including bacteria, fungi, archaea, protozoa and viruses. This community is collectively referred to as the microbiome or microbiota. Traditionally, the term microbiota was used to refer to the community of organisms, and microbiome to refer to the collective genomes of organisms within those communities. While the term microbiome can still refer to a set of collective genetic material, these two terms are also now used synonymously to refer to the community of organisms within a given environment (Ursell et al. 2012). The human gastrointestinal tract contains roughly 40 trillion microorganisms which collectively form the

gut microbiome (Sender et al. 2016). Of these organisms, bacterial species are the best understood, of which there are approximately 1000 species, belonging to 4 dominant bacterial phyla: *Firmicutes*, *Bacteroidetes*, *Actinobacteria*, and *Proteobacteria* (Guarner and Malagelada 2003).

Human gut microbiomes are established at birth, when an infant is seeded with microbes from the mother's vaginal canal, skin, and feces. Infants born via caesarean section present with different compositions of gut microbes, which resemble microbes found on their mother's skin, compared to those born vaginally whose gut microbiomes more closely resemble the mother's vaginal canal (Dominguez-Bello et al. 2010). These caesarean-associated early gut microbiomes have been implicated in the risk of later diseases such as celiac disease, type 2 diabetes, and asthma (Mueller et al. 2015). The gut microbiome is further colonized during breastfeeding and continues to change throughout development in response to the environment. By 3 years of age, the infant gut microbiome is structurally similar to those found in adults (Palmer et al. 2007).

There is a lot of individual variation in gut microbiome composition, though those differences remain relatively stable over one's lifespan (Costello et al. 2009). However, this stability can be altered by diet, disease, and the use of medications like antibiotics (Becattini et al. 2016; Power et al. 2014; Turnbaugh et al. 2009).

Microbiome diversity is understood using metagenomics, which uses bioinformatic techniques to identify multiple species from environmental samples of large amounts of DNA. In 2012, a reference database for the human gut microbiome was completed, as part of the first phase of the Human Microbiome Project (Human Microbiome Project Consortium 2012).

Symbiosis and Evolution

Gut microbes exist in a symbiotic relationship to their human hosts. Many are thought to be commensal, imparting no direct harm or benefit to their human host. Other relationships are mutualistic. For example, some gut

microorganisms help to metabolize compounds so that human hosts can access otherwise inaccessible nutrients. Others digest carbohydrates, ferment dietary fiber, and synthesize vitamins, fulfilling important digestive roles (Turnbaugh et al. 2007; Liang et al. 2018). Parasitic relationships also exist where microorganisms in the gut harm their human hosts, causing disease and, in extreme cases, death.

Mutualistic relationships suggest a persisting evolutionary history between microbiomes and their hosts, as each relies upon one another for vital functions, and thus are thought to have coevolved. This type of coevolution is sometimes understood as a holobiont – an entity which includes both the host (macroorganism) and its symbiotically related microorganisms (microbiomes). A related concept is the hologenome – which in this case is the complex of genomes of microbiomes and their hosts (Rosenberg 2013).

There is emerging evidence that gut microorganisms can influence human behavior. This has led some researchers to consider whether the evolution of some human behaviors can be explained in light of the benefits to their associated microorganisms (Turnbaugh et al. 2007). For example, Alcock et al. (2014) have theorized that food cravings and eating behaviors with negative human health impacts have originated as a mechanism by which some microbes acquire nutrients and defeat competitor microbes in the gut, in order to maintain their own existence.

Human Physiological and Disease Associations

Differences in the composition of the gut microbiome have been implicated for various human diseases. Microbiomes associated with disease states are termed “dysbiotic” and often display reduced diversity, along with under- and overrepresentations of certain bacterial phyla. Inflammatory bowel disease, which includes Crohn’s disease and ulcerative colitis, has been associated with decreased overall microbial

diversity, as well as compositional differences when compared to healthy individuals. It is thought that these diseases develop from an interaction of gut microbes with the mucosal immune system (Kostic et al. 2014).

Asthma and many allergies are also associated with compositional differences in the gut microbiome. Mechanisms of gut microbiome alteration in these cases may be due to diet or because of lack of early life infections which alter the T-cell response in immune system (the hygiene hypothesis) (Shen and Wong 2016).

The gut microbiome has also been implicated in cancer, with both *Bacteroidetes* and *Clostridium* associated with increased tumor growth rate and fewer tumors observed in germ-free (thus microbiome free) rats and mice. Specific bacteria, such as *Helicobacter pylori* (associated with gastric ulcers), are thought to contribute to cancer with epithelial injury and inflammation. Other kinds of bacteria are thought to prevent tumor formation, such as *Bifidobacteria* and *Lactobacillus* (Schwabe and Jobin 2013).

Individuals with a higher relative abundance of *Firmicutes* rather than *Bacteroidetes* are more likely to be overweight, and humans who have lost weight through dieting reduced their increased abundance of *Firmicutes* (Ley et al. 2006). However, it is not known in this instance whether microbiome composition is a cause of obesity or obesity is a cause of microbiome composition. In order to investigate this further, experimental manipulations in animal models have extensively addressed the obesity question (discussed below).

Human Behavioral Associations

Interestingly, the human gut microbiome has also been implicated in many behaviors and mental capacities. The proposed mechanism of influence is the gut-brain axis, which encompasses a bidirectional pathway between the central nervous system and the digestive system. This axis includes the vagus nerve, hormone secretions, inflammatory molecules, and signalling molecules (Carabotti et al. 2015).

The gut microbiome is thought to influence mood via its effects on serotonin and tryptophan – hormones which regulate stress responses and influence cognition. There is some evidence that people with depression have altered microbial compositions in their gut, though no differences in species richness have been observed (Dash et al. 2015). There is also some evidence that probiotic usage can decrease the likelihood of depressive and anxiety-related symptoms in humans (Foster and Neufeld 2013).

A large number of children with autism also present with gastrointestinal problems, and an increase in the relative abundance of *Clostridium* has been observed in autistic children. However, interventions on the microbiome via diet and probiotic use have so far proved unsuccessful for the treatment of children with autism (Chen et al. 2013).

A major issue with associative studies is identifying the causal structure of each association. Microbiomes may be causing human differences in behavior, psychology, and disease, or it may be that human behaviors and human diseases causally impact upon microbiomes. It is also possible that a third factor is a common cause of both microbiome compositional differences and the trait of interest. For instance, autistic children are often picky eaters, and so differences in diet may account for differences in microbiome composition. Relatedly, obese individuals often have markedly different diets and lifestyles compared to nonobese individuals.

For this reason, researchers have used animal models in an attempt to uncover the causal processes underlying gut microbiome associations. Animal models provide the advantage in that microbiomes may be manipulated and other confounding variables minimized.

Evidence for Behavioral Influences in Animal Models

Animal models, particularly using rodents, have been used to make inferences about the causal role of human gut microbiota. Germ-free (GF) mice are most often used, which have been birthed

surgically and raised in sterile environments, meaning that they have no gut (or other) microbiomes. GF mice are then artificially colonized by the microbiome of interest. Fecal matter (representing the donor gut microbiome) is transplanted surgically into the host GF mouse via gavage in a process termed fecal microbiota transplant (FMT). The fecal transplant is sourced either from another mouse with a particular phenotype of interest (mouse-mouse FMT) or from a stool provided by a human donor with a phenotype of interest (human-mouse FMT). Transfer of phenotype from both donor mice and humans has been demonstrated most compellingly for obesity. Recipient mice which receive FMTs from obese mice, or from obese humans, become obese themselves, suggesting strongly that the gut microbiome is a causal factor in the development of obesity (Turnbaugh et al. 2009).

The success of transfer of phenotype studies for obesity has spurred experimental research investigating other microbiome associated traits in humans – including human psychological attributes. These include developmental disorders, such as autism, and mood disorders like anxiety and depression. To date, there has only been one successful transfer of behavioral phenotype study using human donor FMTs. FMTs from depressed humans into antibiotic-depleted rats induced depression and anxiety-like behavior (Kelly et al. 2016). Mouse-mouse FMTs have also been shown to decrease anxiety-like behaviors (Bercik et al. 2011). Other evidence for the microbiomes influence on behavior comes from indirect interventions on the gut microbiome. Autism-like behaviors were observed in mice which had in utero disruption, altering the microbial composition of their guts (De Theije et al. 2014). Probiotic administration has been shown to decrease anxiety and the severity of stress response in mice, thought to act indirectly via changes in microbiome composition (Sudo et al. 2004; Diaz Heijtz et al. 2011).

One problem with the animal model approach is that complex psychological traits are measured using behavioral proxies in mice and rats. For instance, tests of depression are made using the forced-swim test, where animals are placed into a

water-filled cylinder and their attempts at escape are timed. Individuals who stop swimming or “give up” after a shorter period of time are deemed depressed, compared to those which continue to try and escape for longer. Anxiety tests include recording the amount of time an animal likes to spend in an exposed environment (prominent examples are the light-dark box test and the elevated plus maze). The least amount of time spent in a very light or exposed environment, the more anxious the animal is thought to be. Autistic-like mice are characterized by reduced socialization, increased anxiety, fewer vocalization, and obsessive behaviors like grooming and marble burying. Given these limitations, some (Hooks et al. 2019, Lynch et al. 2019) have questioned some of the scientific conclusions made about microbiome causality, suggesting that claims about the influence of the human gut microbiome on behavior have been overblown or at the least are premature.

Concluding Remarks

The human gut microbiome is the most well-studied and complex microbial community on the human body. Without these microbes, humans would be unable to perform many vital metabolic functions, and so many microbes persist with their human hosts in a mutualistic symbiotic relationship. Differences in the relative abundance of microbes, or microbiome composition, along with increases or decreases in overall diversity, are implicated in a number of health in disease states, such as inflammatory bowel disease, cancer, obesity, allergies, asthma, autism, and mental health. The gut microbiome is thought to influence human behavior via the gut-brain axis, and some human behaviors are hypothesized to be due to the evolutionary interests of gut microbes.

Associative evidence for physiology and behavior are potentially confounded, and so manipulative experiments colonizing germ-free rodents with microbes provide the majority of evidence for microbiome causality. These experiments have successfully demonstrated manipulations on the microbiome resulting in disease states, obesity, anxiety, depression, and

autism-like behaviors. However, critics of these studies point out that murine behavioral analogues are not sufficient to demonstrate the causal role of microbiomes in human health, disease, and behaviors.

Cross-References

- [Anxiety Disorders](#)
- [Autism](#)
- [Depression](#)
- [Obesity](#)
- [Stress Reduction and Mental Health](#)
- [Symbiosis and Mutualism](#)

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Gut Microbiota

► Gut Microbiome

H

Habitat

► [Ecological Niche, The](#)

Habitat Change

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Synonyms

[Migration](#)

Definition

The changing of a habitat for a given species, whether voluntarily or involuntarily.

Introduction

Much of the way we are shaped by evolution is indicative of the kind of environment we had to survive in. Early records show that we, as humans, had to survive at one point in trees as we often see modern primates do. Many primates today are confined to forests, whereby they have developed

mechanisms physiologically to be able to climb high distances, especially given the usage of their opposable thumbs. In addition, the diet that keeps them nourished is very indicative of living in trees, such as having to seek out fruits like bananas that may grow at a higher altitude. Therefore, a major question for someone who does not understand the concept of evolution is how we are living as *Homo sapiens* today despite there still being monkeys in the wild. Many people choose to understand evolution as a “progression toward perfection.” This is a common misconception – evolution is not a progression toward perfection. In fact, the idea of “perfection” is highly debatable – what exactly constitutes a “perfect” organism? Evolution is simply biological and psychological changes in an organism that are best suited and adapted for survival in their respective environment. A classic example is Darwin’s discovery of finches on the Galapagos islands. Their beaks are by no means perfect, but their beaks were also well-suited to be able to eat the kinds of foods that were best suited for that respective bird’s diet. A similar concept is true between chimps and humans – the reason chimps continue to look the way they do is due to the environment that they are in. They are in an environment whereby getting to high elevations is essential to not only find food sources but to also have a better visual scope of the environment around them and avoid predators. Humans, on the other hand, do not have the mobility and grip strength that is evident in primates, as we have a much harder time

climbing than do many modern monkeys. We also stand in an upright posture with our spines straight, and walk with what is called *bipedal locomotion*, or the ability to walk on two legs. Monkeys often depend on their arms as a means of locomotion, as is evident in the way many primates walk, such as gorillas. This difference, however, is by no means a coincidence, nor did we evolve such a difference because of “perfection.” The difference lies within specifically habitat change. Given that we have so much in common genetically with modern primates, there had to have been some kind of change or a point at which a divide was necessary and occurred to have so much genetic similarity but such a monstrous difference in behavior and physicality. The bigger question that evolutionary scientists are still trying to figure out to this day is precisely, “Why and how did this change occur?”

Our Original Habitat

Oddly enough, one of the key components that demonstrates how our early ancestors may have lived in trees is exhibited by our shoulder development. Genetically, we are most similar to chimpanzees and also share their shoulder structure most similarly. Despite us sharing most of our genetic similarity with apes, it seems as though our shoulder development is actually more similar to orangutans than other apes, suggesting that at some point we had a mechanism by which we had to swing between trees in the way orangutans do. Through studying evolution, we must operate under the assumption that no physiological change is the result of a mere coincidence, rather, there must be some adaptive purpose to have developed the kind of structure the organism did. In this case, there must be some reason why we share so much genetic similarity with other apes, but our shoulders specifically seem to model orangutans that swing between trees as compared to heavier apes (Young et al. 2015).

If we did indeed live among the trees, then an obvious question of course would be why we ever had a reason to move out if our bodies were already accommodated to living in those conditions for

survival. The answer is not fully understood, although there are an abundance of theories that attempt to explain why through various means of measurement. As will be discussed in later chapters, there are numerous popular theories such as climate change or simply being pushed out by other animals that could explain why we eventually moved out of the trees after successfully living in them for such a long period of time. (Potts 1998)

The climate theory, in short, essentially states that there are constant fluctuations in our climate that can have profound effects on our environment. The theory also states that the fluctuations in climate are more dramatic than ever, especially with the advancement of the industrial revolution and the ever-increasing population, having a more profound effect on the environment than ever. However, we also see climate change far before human civilization, whether due to catastrophes such as volcanic eruptions, the supposed meteor that wiped out the dinosaurs, or even the last ice age that wiped out vegetation and livestock across many continents. Therefore, it is suggested that perhaps some kind of major catastrophe happened at the time that would result in a change in the local environment. Thus, a lack of vegetation or even deforestation resulting in a lack of trees would have made survival infinitely harder for primates and early hominids, and thus they likely decided to migrate further down to look for resources that would be scarce at higher elevations (Demenocal 2004). This also likely resulted in a *population bottleneck* or an event that significantly decreases the population of a given organism. These changes likely resulted in the vast majority of our species dying from either being unable to survive in the trees due to lack of resources or moving onto the forest floor and being unable to survive due to new predators and an unfamiliar environment (Potts 1996). Those that did survive, however, likely were eventually able to migrate out onto the African grasslands, where they then started experiencing evolutionary change over the course of millions of years to adapt to their new environment.

Another such theory is that we simply got “bullied out” by our ancestors which would

eventually become modern day primates. It is possible that they gained some kind of evolutionary advantage that allowed them to get resources faster than early hominids could, giving them no choice but to move to another location to ensure survival. Again, those that could survive did, but it likely resulted in a massive decrease of the population whereby migrating to a new environment and reproducing with viable mates was the only way that the species could survive. As a result, the species slowly but surely had to make adjustments neurologically and physiologically to accommodate for an environment that they were not evolutionarily suited for, similar to the *evolutionary mismatch* effect. (Foley 1994)

Given that grasslands were often much higher in visibility due to the lack of obstruction from trees and a wider horizon, it became pivotal that our vision and hunting skills change. Hence, we developed bipedal locomotion as a more efficient means of traversing the grasslands and being able to hunt our prey. We adapted from having short bursts of speed and having the strength to be able to climb trees and instead endure long distance running to tire out our prey, as well as our shoulders changing to be able to accommodate for weapon making and throwing. It was precisely this change that paved the way for eventual *Homo sapiens*, given that with the ability to make weapons, we evolved from a creature that was confined to trees and using our body as our means of hunting prey and instead creating objects that we can attack prey with from a distance – maximizing resources and food and minimizing risk. With this cycle came a population resurgence and therefore eventually the entire hominid species moving out into the African savannah.

The African Savannah

The savannah represented a radical departure from the forest that we had previously lived in, and therefore the reason we see ourselves as so different from chimps is because of that divide

that occurred to keep them in trees and us on the grasslands. The chimps had no reason to have to change given that whatever the reason may be (climate change, being pushed out by predators or our ancestors, or another reason we have not been able to deduce), they were able to survive in the trees whereas early hominids could not. While the hominids' new environment requires new means of adaptation to be able to hunt different kind of prey on a different terrain, the primates kept doing what they had been doing all along. This, in essence, is the answer to why we have evolved into *Homo sapiens*, but monkeys still exist – they simply had no reason to change given that they continued to live in the environment that their bodies were always suited to, as they continue to do today. Hominids were forced out, and therefore the evolutionary changes we see in ourselves today that differentiate us from primates are remnants of how we would survive on the savannah (Reed 1997).

Savannahs typically have a wider horizon, and therefore our vision became essential to not only avoid being killed by predators but to more easily seek out prey that represented food and a means to survive as a group. As such, our spines began to straighten out rather than have curvature and we developed *bipedal locomotion*. Not only did this allow us to traverse long distances, but it made a huge difference in terms of our vision and even our communication. Instead of lifting our heads to look at what was in front of us, we now could look at our surroundings with ease and could turn our heads horizontally in a manner that was not possible before. This was no coincidence, of course, as the savannah is often called “flatlands” for their constant altitude and lack of elevation – generally, it was important to be able to have a wide scope of view of the entire landscape and to see as far as the horizon to be able to hunt for prey. Not only did this structural change help our vision, but it also helped us communicate with other hominids. By being able to look directly at their face, face-to-face communication became much easier, by being able to read emotions and eventually develop language and dialects that allowed for

more coordinated execution of group activities. As a result, enhanced communication came which would eventually lead the way to more advanced concepts such as music, stories, and much of the art world we see today in the form of human creativity.

Conclusion

Our habitat change was essential to the way that we have developed physiologically as *Homo sapiens*. We now stand in an upright position because of *bipedal locomotion*, which gave us an enhanced and extended scope of vision, as well as enhanced communication which led to the development of speech and language. Getting out of the trees also allowed for free use of our upper body that was previously essential to be able to walk as well as swing from tree to tree. Our shoulder muscles then evolved to be able to do things such as create weapons and more importantly throw them, maximizing our potential as predators in the environment to hunt prey. The ability to throw objects was essential to survival especially on the African savannah, not only given the newfound predators and the lack of obstruction from trees, but also simply to maximize reward by attacking animals from a distance, but also minimize risk by avoiding getting close to potentially dangerous animals. In short, many people fail to understand the concept of evolution by not comprehending why chimps are still in the wild today, but humans exist alongside them. This difference is explainable by our division from chimps for a number of possible reasons, such as climate change or being pushed out by other predators or ancestors. Ultimately, habitat change was paved the way for us to evolve into the *Homo sapiens* we see ourselves as today, physiologically and with our remarkable ability at communication and cooperation.

Cross-References

- [Bipedal Locomotion](#)
- [Climate and Habitat Diversity](#)

- [Climate Change](#)
- [Climate Fluctuations in the Last 200 Ky](#)
- [Three Stages of Habitat Selection](#)

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Habitat Selection

- [Savanna Hypothesis, The](#)

Habitual Processing

- [Procedural Knowledge](#)

Habituation

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Synonyms

[Familiarization](#); [Nonassociative learning](#)

Definition

Habituation is a process of diminishing responsiveness due to the presentation of a repeated stimulus.

Introduction

Habituation constitutes an essential process of behavioral adaptation, as it assists in filtering out the large amounts of information received from the surrounding environment that are likely irrelevant or less important, thus shifting attention to more important to survival or urgent information. The latter gives an evolutionary advantage as a result.

Theoretical Background

Several influential nonassociative theories have historically been proposed Thompson (2009). These theories constitute the early work of Sokolov (1960) and Wagner's (1979) revision of Konorski's Gnostic Hypothesis, and Groves and Thompson's (1970) dual process theory.

Sokolov (1960) was the first to propose a comprehensive theory of habituation ("*Stimulus-Model Comparator Theory*"). In short, Sokolov's theory stated that when a stimulus appears repetitively, the brain cortex forms a model (or a memory) of the stimulus. Each incoming stimuli were compared to the model and if the incoming stimulus matched the model, responding was inhibited; otherwise, an orienting response was evoked. The exertion of inhibition was thought to yield habituation; thus, habituation was perceived as purely inhibitory. Even though Sokolov's work intrigued a great bulk of follow-up investigations in habituation in the human kind, the theory was not applicable to animals who do not possess a cortex, contrary to the dual process theory.

Another comparator theory constitutes the work of Konorski's on habituation which shared many similarities with Sokolov's theory. Wagner (1979) revisited Konorski's ideas but he concentrated on the roles of short-term memory and

associative mechanisms. A stimulus is carried by afferent/sensory neurons toward a memory system, the Gnostic assembly, and to the arousal system. With repeated stimulation, a gnostic unit is formed, that is a near accurate neuronal model or memory of the stimulus. As this model develops, it increasingly activates an inhibitory system that inhibits the arousal system, consequently causing habituation. Wagner added a process mediator, an associative network where contextual cues have to pass through in order to excite stimulus models in memory and a process of transient memory (short-term memory). In short, what these scientists advocated is that long-term habituation requires the storage of a stimulus in long-term memory and that it is associated with external cues for retrieval from long-term memory.

Finally, the most prominent nonassociative learning theory was proposed by Groves and Thompson (1970). Neurophysiological concepts were combined with concerns of human ethology and evolution to create the *dual process* theory. This theory advocated that repeated stimulation would produce two independent processes that could both be active at the same time; decreased responsiveness (habituation) or increased responsiveness (sensitization). The authors believed that the two processes take place in different parts of the nervous system. Scientists believed that habituation took place in the so-called S-R system (reflex arc) that controls reflexes whereas sensitization occurred in the "state system" which is responsible for the level of readiness to respond. The state system requires arousal to become activated while the S-R system is activated with the presentation of an eliciting stimulus. Further, habituation is thought to be stimulus specific and involves learning, in contrast to sensitization which is not highly specific and does not require learning. However, both are of relative permanence; they are expected to decay at the absence of stimulation. Contrary to Sokolov's model, the *dual process* theory does not propose an inhibitory system.

Nevertheless, all these studies of cellular processes which facilitate learning and memory, which were mostly held in invertebrates, most

certainly add to the understanding of the underlying physiological processes of learning in the majority of living animal organisms, but mechanisms such as habituation and sensitization are far more complex and necessitate further exploration.

The Nature of Habituation

Habituation constitutes an essential process of behavioral adaptation, as it assists in filtering out the large amounts of information received from the surrounding environment that are likely irrelevant or less important, thus shifting attention to more important to survival or urgent information. The latter gives an *evolutionary* advantage as a result. Habituation is the simplest form of non-associative learning and it can be defined as a decline in behavioral responsiveness to the continual presentation of a stimulus. While there is a strong response initially, the strength of the response reduces and eventually disappears with repeated stimulation. The reduction in responsiveness is neither the result of motor (muscle) fatigue nor sensory adaptation; however, it is likely to be disrupted when another strong stimulus appears (dishabituation). Other factors influencing habituation include stimulus repetition, interstimulus interval, and stimulus intensity. These factors are determinant of whether short- or long-term habituation will occur. Short-term habituation is characterized by rapid stimulations with short intervals in between, habituation is observed early; however, it is short-lived as soon as stimulation ceases. On the other hand, long-term habituation is characterized by fewer stimulations over longer periods; habituation is slower but its effects are long-lived as recovery is delayed.

In addition, in earlier writings, habituation was thought to only have short-term effects (Hinde 1970); however, existing literature has demonstrated that its effects can last long. Apart from its simplicity, habituation is thought to be ubiquitous; it is both a highly automated yet learned phenomenon occurring in the central nervous system (CNS) of all animal species, ranging from single-celled protozoans to humans Thompson (2009), with studies demonstrating its occurrence

in plants as well Gagliano, Renton, Depczynski, Mancuso (2014). Thompson and Spencer (1966) presented a list of nine parameters of habituation, shared by all species. A tenth parameter was added to the list of behavioral characteristics of habituation by Rankin et al. (2009) and are all presented as follows:

1. Given that a particular stimulus produces a response, repetitive applications of that stimulus will result in a reduced response (habituation). Most of the times, the decrease is a negative exponential function of the number of stimulus presentations.
2. If the stimulus is withheld, the response tends to recover over time ("spontaneous recovery").
3. After a multiple series of stimulus repetitions and spontaneous recoveries, habituation becomes more rapid ("potentiation of habituation").
4. The more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation.
5. The weaker the stimulus, the more rapid and/or more pronounced is habituation. Stronger stimulation might yield no significant habituation.
6. The effects of habituation training may proceed beyond the zero or asymptotic (minimum level of response) response level.
7. Habituation of response to a stimulus displays stimulus generalization to other stimuli.
8. Presentation of another strong stimulus results in disruption or recovery of the habituated response ("dishabituation").
9. After repeated application of the dishabitatory stimulus, the amount of dishabituation produced habituates ("habituation of dishabituation").
10. Some stimulus repetition protocols may result in properties of the response decrement that last hours, days, or weeks. This persistence of aspects of habituation is termed long-term habituation.

Importantly, the aforementioned characteristics of habituation were observed and collected

through numerous studies on a variety of species; therefore, they do not imply particular theories or inferences. They could be considered, however, as a detailed definition of habituation.

Several scientists who have studied the process of habituation provide valuable information regarding the underlying mechanisms of habituation and associated processes, demonstrating at the same time its complexity Thompson (2009). It has been noted that the occurrence of habituation is determined and/or influenced by variations in interstimulus interval and by the organisms' ability to generalize and discriminate between the presented stimuli. Additionally, spontaneous recovery is another process thought to influence habituation's maintenance. All these concepts are further analyzed in the section ► [“Interstimulus Interval”](#) that follows.

Interstimulus Interval

The concept of interstimulus interval is frequently encountered within processes of nonassociative learning, specifically habituation and sensitization Petrinovich (1984). Interstimulus interval can be defined as the time interval between the end of one stimulus presentation and the onset of another stimulus presentation. Interstimulus interval experiments were extensive under the work of Davis (1970) on habituation of the acoustic-startle response in the rat. Generally, through Davis's series of experimental studies, it was demonstrated that the length of interstimulus interval, as well as variability (regularity), determines habituation in animals. The author compared the responsiveness of two groups of rats to a 50-ms, 120-db tone of 4000 Hz during pretest, training, and posttest periods. During both the pretest and the posttest periods, both groups of subjects received 300 tone exposures at intervals of 2, 4, 8, and 16 s, the intervals being scheduled in an irregular order. During the training period, both groups received 1000 tone exposures; however, the interval between stimuli was 16 s in one group and 2 s in the other group. Among other findings, greater reduction in responsiveness was

observed in the group who received stimulation every 2 s.

In the second experiment, startle responsiveness was lower following training with regular as opposed to variable interstimulus intervals. Simply put when interstimulus interval is longer and constant, habituation is greater. Also Davis (1970) reported a quite an interesting finding; when rats were tested at 1 min or 24 h later with a variety of interstimulus intervals, habituation was greater for the group that was trained on the 16 s interstimulus interval schedule suggesting, thus, that short- and long-term habituation processes may be distinguishable on the basis of the presentation and the intervals between stimuli. Specifically, it was demonstrated that short interstimulus intervals were involved in the progression of short-term habituation, while long interstimulus intervals were involved in the promotion of long-term habituation. Also, apart from the fact that high-frequency stimulation leads to more rapid response decrement, it results in faster spontaneous recovery as well Leaton (1976).

Similarly, Groves and Thompson (1970) noted that increased frequency should lead to increased habituation in the “S-R” pathway, but in the “state” pathway, it would lead to increased sensitization. All the aforementioned experiments considered together are indicative of the importance of interstimulus interval making it obvious that it can have a major effect on learning; it may delay or improve learning. Lastly, the organism's ability to determine the interval and duration of sensory stimulation is central to sensory processing; therefore, impairments in that domain are likely to interfere with the process of learning.

Variations in the time between the presentations of one stimulus to the next have a determinant effect on the forms of nonassociative learning; habituation and sensitization and the occurrence of long- and short-term habituation are dependent upon the length of interstimulus intervals Leaton (1976). Further manipulation of interstimulus intervals will provide valuable information regarding disruptions in learning processes or even suggestions as to how to enhance learning.

Stimulus Generalization and Discrimination

The concepts of stimulus generalization and stimulus discrimination are encountered within the context of associative and nonassociative learning. *Stimulus generalization* refers to a set of stimuli sharing similar properties with the original stimulus that provoked a response. *Stimulus discrimination* is the ability of an organism to respond only to the original stimulus and not to other similar stimuli.

Both concepts are inherent mechanisms in the processes of associative and nonassociative learning, and for both processes to take place, it is essential that a stimulus model should be stored in memory in order for comparisons with new stimuli to take place.

To begin with, generalization occurs when an organism *produces the same response to different stimuli*. Stimuli who exhibit analogous properties to the stimulus that was originally presented and provoked habituation, are more likely to provoke a similar response, that is habituation. There could be variations in terms of the level of pitch, brightness, loudness, and so on; however, if these variations deviate significantly from the properties of the original stimulus, generalization will not occur; hence, it is more likely that habituation will not occur either Teyler, Chiaia, DiScenna, Roemer (1984). Stimulus generalization of habituation can only be determined when a second habituation series is done with the use of a novel stimulus. With a comparison of the rates of habituation between the original and the novel stimulus, the amount of generalization will be demonstrated. More rapid habituation in the second series would be indicative of generalization, whereas similar rates between the two series would be indicative of a lack of generalization Petrinovich and Widaman (1984).

On the other hand, if stimuli are rather dissimilar than similar, the opposite process of stimulus generalization, the so-called *stimulus discrimination*, will be activated. In *stimulus discrimination*, the organism shows the ability to differentiate between similar stimuli and only to respond to a specific stimulus; hence, the

organism responds *differently* to the two stimuli. *Stimulus discrimination* is particularly important in the process of habituation, as it can be used to dismiss sensory adaptation and fatigue as an alternative explanation of the occurrence of habituation. Further, *dishabituation* is indicative of the ability to discriminate, therefore ending habituation Thompson & Spencer (1966). It is important to clarify, however, that dishabituation occurs due to repetitive stimulation of a completely irrelevant stimulus and should not be thought of as the same as stimulus discrimination. Finally, stimulus generalization is useful because it allows for learning to take place quickly in new situations that share similarities with past experiences and promotes the transfer of skills into similar situations thus saving time and effort. Stimulus discrimination offers assistance in a practical level as well.

Stimulus generalization and discrimination are crucial processes in learning and both are of paramount importance to adaptation. Clearly any organism that lacks such abilities would have minimal chances of survival. There are well-known experiments undergone within the concept of conditioning (Pavlov's and Watson's experiments) that illustrate the stimulus generalization and the stimulus discrimination concepts more elaborately.

Spontaneous Recovery

Spontaneous recovery refers to the recovery of a habituated response. When a sequence of stimulus presentations is interrupted, the object at hand will return to its earlier stage, the behavior will recover over time. In a series of experiments undergone by Rankin and Broster (1992) on the nematode *Caenorhabditis elegans*, mechanical stimuli were delivered at four interstimulus intervals (2, 10, 30, and 60 s) in order to investigate the effect of interstimulus intervals in the development and maintenance of habituation. Results indicated that recovery from habituation was dependent on some factors. One of these factors is the length of interstimulus intervals; it was observed that recovery from habituation was faster when short interstimulus intervals were applied rather than longer interstimulus intervals.

That is, long-term habituation prevents recovery. Also, the rate of recovery varied according to which response level each subject exhibited on the habituation curve. The recovery of animals on the lowest response level appeared to be determined by interstimulus interval and not by the further addition of stimuli. Interstimulus interval recovery rates did not differ even though the number of stimuli the worms received was significantly bigger (60 vs. 10) in the second group. In short what was evident is that the frequency of stimulation during habituation training was the one to determine the rate of spontaneous recovery.

Moreover, Rankin et al. (2009) upon revisiting the characteristics of habituation, originally described by Thompson and Spencer (1966), revised a point concerning spontaneous recovery. It is described in the characteristics that when a sequence of stimulus presentations is interrupted, the object at hand will return to its earlier stage, the behavior will recover over time. Rankin et al. (2009) revised this characteristic by adding that sometimes the response recovers completely, but sometimes it recovers only partially depending on the time frame that recovery was examined.

Further, when stimulus presentations and spontaneous recoveries are given repeatedly, the phenomenon of *potentiation of habituation* is observed. Here, the decrement in response that follows spontaneous recovery (i.e., habituation) becomes gradually more rapid with each application of spontaneous recovery. Moreover, the process of spontaneous recovery can be disrupted with the presentation of a new, strong stimulus, i.e., sensitization.

Lastly, it is crucial to note the importance of spontaneous recovery; it is the second way, with stimulus discrimination being the first way, to distinguish sensory adaptation and fatigue from habituation. With regards to learning, this process demonstrates that even though a response might disappear, it does not necessarily mean that it has been withdrawn from memory and that it will never reoccur.

Experiments on the lowest living forms illustrate the phenomenon of spontaneous recovery and those indicate that spontaneous recovery is highly determined by the frequency of stimulus presentation. These experiments

provided a special insight on the underlying processes of habituation.

Conclusion

Habituation is one of the simplest forms of nonassociative learning, it is found in all animal species, and it is a highly complex yet essential process of the evolution of learning. It has been demonstrated that underlying processes as interstimulus interval, stimulus generalization, and discrimination, and spontaneous recovery are interconnected and influence the occurrence and maintenance of habituation.

Cross-References

- ▶ [Aplysia](#)
- ▶ [Associative Learning](#)
- ▶ [Classical Conditioning](#)
- ▶ [Interstimulus Interval](#)
- ▶ [Long-Term Potentiation](#)
- ▶ [Sensitization](#)
- ▶ [Stimulus Generalization and Discrimination](#)

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Half-Siblings in Human Evolutionary History

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Synonyms

One parent's offspring whose other parents are different

Definition

Half-siblings are either sired by the same father (paternal half-siblings) or born by the same mother (maternal half-siblings), but not both.

Introduction

In altricial species, such as primates, maternal half-siblings and full-siblings live usually in the proximity of each other and are raised up by the same mother. In contrast, the relation between paternal half-siblings is much less tight. The outcome of this difference in terms of social interactions, such as cooperation, aggression, and agonistic behavior, has been studied extensively in many mammalian species. Most research studying human behavioral ecology and the role of kin network, however, focused on full-siblings only. The current knowledge about the mating behavior of *Homo sapiens* and extinct *Homo* species suggests that this form of relatedness had always been present during the evolutionary history of the genus. Therefore, studying the interactions between half-siblings is expected to contribute significantly to our understanding of how resources are allocated between, and how support is given to, human individuals with different degrees of genetic relatedness.

Relation of Half-Siblings

Though the degree of genetic relatedness is the same, a distinction has to be made between maternal and paternal half-siblings. The relation of siblings within the two types is qualitatively different: on average, maternal half-siblings exhibit more interactions with each other, compared to paternal half-siblings (e.g., Pollet 2007; Tanskanen and Danielsbacka 2014). The main reason for this is that after a couple splits up, the children usually stay with the mother, so children from a new relationship grow up with the mother's other children. The shared family environment is an influential determinant of the half-siblings' relation (Pollet 2007).

Half-siblings – just as full-siblings – could either compete for resources (social, emotional, material, etc.) or provide resources to each other or both. Both types of relation can be explained within the frameworks of evolutionary theories, such as: (1) kin selection, (2) parent–offspring conflict, and (3) parental investment theory.

Siblings as Rivals

From an evolutionary point of view, the rivalization between siblings can be explained by kin selection (Hamilton 1964) and parent–offspring conflict (Trivers 1974). Trivers assumed that competition among full-siblings is less intense than among half-siblings. The results of empirical research, however, are contradictory (Pollet 2007; Tanskanen and Danielsbacka 2014; Salmon and Hehman 2015; Tanskanen et al. 2016).

In their study, Tanskanen et al. (2016) compared older (62–67 years) and younger (21–50 years) siblings. They proposed that the fact that they lean on the resources of the very same providers puts more strain on the relation of full-siblings. In general, the older generation showed less conflicts. Members of the younger generation had indeed more conflicts with full-siblings than with half-siblings. They also had more conflicts with maternal half-siblings than paternal ones, just like the older generation. However, the older full-siblings in the sample reported an increased likelihood of having conflicts with full-siblings over paternal half-siblings only, but not over maternal ones. The data were also controlled for emotional closeness, contact frequencies, and other demographic and socioeconomic family variables. This suggests that these within-family relations might be more successfully explained within the frames of the parental investment, rather than the inclusive fitness theory.

Siblings as Resources

Studies inspired by the kin selection theory yielded confirmatory data in the case of resource allocation. It was suggested that individuals will invest more in full-siblings than in half-siblings or step siblings (Emlen 1997). This view received support from Jankowiak and Diderich (2000), who found that half-siblings displayed significantly lower solidarity in a polygamous Mormon community in the USA. Solidarity was expressed in monetary gifts, requests to babysit, feelings of closeness, favoritism, and attendance at birthday and wedding celebrations. This happened despite

a strong cultural ideology for equal treatment of half-siblings.

Half-Siblings and Sexual Selection

In *The Mating Mind* Miller (2001) suggested that the mating pattern of the human ancestors in the Pleistocene might be best described as *serial monogamy*. This is similar to what is observed in extant hunter-gatherer communities. Exclusively monogamous pairs are formed for a couple of years and may split up either because of the death of one party or because of deserting. Then, new relations could be formed. On average, 3 months with regular copulations is necessary for conception. Therefore, in a relation which lasted for several years, one baby was likely to be born in every 2–5 years. Just like in most of the recent human societies, the major part of the costs of rearing a child was inflicted on the ancient hominid females. After the couples split up, this was even more the case.

Because of the serial monogamy, it is likely that the mating behavior of hominid females with one or more dependent offspring was combined with their parental behavior. Miller suggested that males hardly had any chance to court childless females. Hence, the main question was not whether a female has any children; her attractiveness and other reproductively important qualities were more of a concern. Sexual competition between females was, therefore, competition between mothers. It was proposed that mothers in the Pleistocene paid attention to how their children judged the prospective sexual partner. So the mothers' choice was influenced by the children's choice. Therefore, the courting of hominid males was directed partly on the offspring of the potential female sexual partner. An inevitable but somewhat surprising consequence of the children's preference was that through influencing their mother's choice, they influenced sexual selection and the genetic constitution of their younger half-siblings.

Conclusion

The kin network might have been much more complex during human evolutionary history than

it is often suggested by the traditional view of families in Western societies. “Patchwork” families of nowadays may stand closer to what was common in the evolutionary past. As the number of such families is increasing, and the relations between full- and half-siblings are getting more complicated, and eventually stressful, the reconsideration of the view of a “normal” human family is warranted both from a scientific and a therapeutic perspective.

Cross-References

- ▶ [Adaptive Problem of Detecting Kinship](#)
- ▶ [Hamilton’s Rule and Genetic Relatedness](#)
- ▶ [Hamilton’s Rule and Kin Investment](#)
- ▶ [Kin Selection Theory](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Parent-Offspring Conflict](#)
- ▶ [Siblings](#)

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Hallucinations

- ▶ [Visual Illusions](#)

Hamilton’s Forces

- ▶ [Selection Pressures as a Function of Age](#)

Hamilton’s Rule

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Synonyms

[Inclusive fitness theory](#); [Kin altruism](#); [Kin selection theory](#)

Definition

According to Hamilton’s rule, the cost of an investment must be less than the benefit weighted by the genetic relatedness of the investor and recipient. Based on the condition “all else being equal,” individuals are predicted to invest more in closely genetically related kin compared to more distantly related kin or non-kin.

Introduction

William D. Hamilton (1964) formulated a rule that defined the conditions under which

altruism can evolve and spread in sexually breeding populations. Altruism refers to a behavior that decreases the fitness of the actor while increasing the fitness of another individual (West et al. 2011).

The Rule

Hamilton argued that in addition to the parent–offspring relation, other relatives who share a common descent carry identical copies of the same alleles (Mock 2011). Therefore, individuals can spread their own genes (inclusive fitness) not only by reproducing themselves (direct fitness) but also by supporting their relatives' reproduction (indirect fitness), even at the expense of their own direct reproductive success. Hamilton's rule, a mathematical formula of the above-described inclusive fitness theory, specifies the conditions under which altruistic behavior spreads in a population. The simplistic version of the rule can be formulated as follows:

$$Br > C$$

In the equation, B refers to the benefits of an investment, and C refers to the costs of the altruistic act. Benefits and costs are measured in terms of the investor's inclusive fitness. The coefficient *r* refers to the genetic relatedness between individuals, indicating the probability that the investor and recipient have an identical allele at a random locus by common descent (Salmon and Shackelford 2011). In theory, the degree of relatedness may vary between 0 and 1. For instance, among humans the degree of relatedness is 1 with monozygotic twins; 0.5 with a biological child and sibling; 0.25 with a half-sibling, grandchild, niece, nephew, aunt, and uncle; 0.125 with a great-grandchild and first cousin; 0.0625 with a first cousin once removed; 0.0313 with a second cousin; etc. The coefficient *r* mediates the benefit–cost ratio, and the greater the *r*, the easier the benefits exceed the costs. Hence, all other things being equal, the level of altruistic acts between individuals should correspond to the degree of their genetic relatedness.

Conclusion

According to Hamilton's rule, for the “altruistic gene” to be selected for and spread in a population, the fitness benefits weighted by the degree of relatedness must exceed the fitness costs of altruistic behavior. By contrast, if the altruistic gene decreases the inclusive fitness of individuals, it will be selected against by natural selection. Hamilton's rule is a simple but elegant equation that defines the circumstances in which altruism can evolve. Hamilton's rule also explains and predicts the variation in the level of altruistic behavior among kin.

Cross-References

- ▶ [C < Rb](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Helping and Genetic Relatedness](#)
- ▶ [Helping and Inclusive Fitness Benefits to Helper](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
- ▶ [Kin Selection](#)

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Hamilton's Rule and Genetic Relatedness

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Synonyms

[Altruism](#); [Comparative phylogenetic analysis](#); [Inclusive fitness](#); [Kin selection](#); [Relatedness](#); [Social evolution](#)

Definition

Hamilton's rule predicts that individuals will be more likely to support closer kin altruistically, and thus more likely to get support from closer kin (Hamilton 1964). This refers to a biological law that defines whether an animal is going to participate in altruistic activity that does not appear to benefit their own well-being. The Hamilton law, named after the evolutionary English biologist W.D. Hamilton, says an animal will only engage in altruistic behavior if the indirect benefits it derives from such behavior are greater than the direct reproductive costs it entails. For example, when an animal shares similar genes with another animal requiring support, it is likely to demonstrate altruism. This has led many biologists to believe that at the gene level altruism could be simply selfish behavior.

Introduction

W.D. Hamilton in 1964 implemented the most famous law in evolutionary biology. He proposed a concept in two back-to-back papers and derived from it a law that we now know as Hamilton's rule. The rule states the selection favors altruistic conduct if the recipient's benefits times the relationship between actor and recipient outweigh the actor's costs. This captured both a qualitative perspective – genes can make people do things that are bad for that particular person, but good for copying the

gene in other people – and an elegant, intuitive, and easy quantification of that phenomenon.

Both the rule of Hamilton and the notion of “inclusive fitness,” which the rule suggests is maximized through evolution, have become standard material for both theoretically and empirically inclined biologists since. As is usual for a pioneering article, indications came that this is a key indication for outsiders as well. The paper contains almost half as many quotes as Darwin's (1859) “On the Origin of Species” and is one of the key ingredients in Richard Dawkins' (1976) “The Selfish Gene” and is one of the books that anybody with a general interest in science wants to read. Hamilton's law is not only a historic development but also the subject of a controversy. Karlin and Matessi (1983) and Matessi and Karlin (1984, 1986) also proposed in the early 1980s that not all evolutionary scenarios lead to a maximization of inclusive fitness, but those papers did not receive sufficient coverage to make it into the collective memory of evolutionary biology.

A renewed criticism of the generality of inclusive fitness has emerged in the last 7 years, the most notable of which was articulated in a paper by Martin Nowak, Corina Tarnita, and E.O. Wilson. Wilson. The latest debate on the generality of inclusive fitness does not yet display any signs of convergence and positions range from “nearly never holds the law of Hamilton” (Nowak et al. 2010) to “Inclusive fitness is as general as the genetic theory of natural selection itself” (Abbot 2009).

Hamilton's Rule

In the mid-1960s British evolutionary biologist William D. Hamilton offered the main insight for understanding the nature of self-sacrificing behavior. He argued that natural selection favors genetic success, not reproductive success per se, and that individuals should carry to future generations copies of their genes. Genes are transferred from direct parentage (rearing offspring and grand offspring) and aiding the reproduction of close relatives (such as nieces and nephews), a phenomenon known as “inclusive fitness” or “kin selection.”

Hamilton developed a theorem, now called Hamilton's law, which defines the conditions under which reproductive altruism develops: $r \times B > C$, where B is the gain (in number of offspring equivalents) gained by the beneficiary of altruism C is the cost (in number of offspring equivalents) sustained by the donor when participating in altruistic behavior and r is the genetic relation of the alt. Relatedness is the likelihood that the potential beneficiary of the altruistic behavior shares a gene in the potential altruist. Altruism can develop in a population if a potential donor of assistance can more than compensate for the loss of C offspring by adding a fraction r of its genes to population B offspring. For example, a female lion with a well-nourished cub gains inclusive fitness by nursing a hungry cub of a full sister because the profit to her sister ($B =$ one offspring who would otherwise die) more than compensates for the loss to herself ($C =$ about one quarter of an offspring), because her own, nonstarving cub's survival probability is only slightly reduced. If the mean genetic association (i.e., " r ") between two sisters is 0.5, so according to Hamilton's law (0.5×1) > 0.25 . Basically, altruism genes spread by encouraging help to replicate themselves.

Based to this view, popularized by the British zoologist Richard Dawkins, from a gene-selection viewpoint, the most acceptable way of understanding natural selection is as expressed in Hamilton's law. Genes that are best able to direct the species that carry them for successful transmission should survive and proliferate over generations. A description of the role of a specific action will also provide how the action encourages the performance of the genes underlying the behavior. Obviously, since an animal's actions almost always encourages genetic success by helping the animal survive and spread its genes, conduct research usually addresses the survival and reproductive value of the behavior.

Hamilton's Rule and Genetic Relatedness

Hamilton showed mathematically that, because other members of a population that share one's genes, a gene may also increase its evolutionary

success by indirectly encouraging the reproduction and survival of other people who also carry that gene. This is alternatively known "kin theory," "kin selection theory," or "inclusive fitness theory." The most obvious group of these individuals is close genetic families, and the application of inclusive fitness theory is often approached more straightforwardly by the narrower kin selection theory where these are concerned.

In addition to reciprocal altruism, Hamilton's theory is considered one of the two main reasons for the evolution of social behaviors in human organisms and a significant contribution to the field of sociobiology, which holds that all behaviors can be determined by genes and can therefore be passed on to future generations and can be selected as the organism evolves.

If there is a "altruism gene" (or gene complex) that affects the behavior of an organism to help and protect the relatives and their offspring, this behavior also tends to increase the proportion of the altruism gene in the population, as the families are inclined to share genes with the altruist because of common descent. In formal terms, if such a complex of genes occurs, Hamilton's rule defines the selective criteria for such a trait to increase the frequency in the population (in terms of cost, gain, and relatedness). Hamilton noted that inclusive fitness theory by itself does not assume that these altruistic behaviors will automatically evolve as an incentive or context for interaction among individuals is a more primary and necessary requirement in order for any social interaction to occur in the first place. "Altruistic or selfish acts are possible only when a suitable social object is available, as Hamilton puts it. In this sense behaviors are conditional from the outset" (Hamilton 1987, 420). In other words, while the inclusive theory of fitness specifies a set of conditions required for the evolution of altruistic traits, it does not prescribe a sufficient condition for their evolution in any species. More primary essential requirements include the presence, as described above, of gene complexes for altruistic traits in gene pool and in particular that, as Hamilton noted, "an acceptable social object is available."

Though presented in seemingly anthropomorphic terms, these concepts refer to all living

organisms and can explain the evolution of innate and acquired behaviors across a wide variety of species like insects, small mammals, or humans.

The ground squirrel from Belding offers an example. The ground squirrel is giving an alarm call warning its local group of a predator's presence. It gives away its own location by emitting the alarm, putting itself in further danger. However, in the process, the squirrel will defend its relatives within the local community (as well as the rest of the group). Consequently, if the effect of the trait influencing the alarm call typically protects the other squirrels in the immediate area, it will result in more copies of the alarm call trait being passed on in the next generation than the squirrel could leave by reproducing itself. In such a scenario, natural selection tends to increase the characteristic that influences giving the alarm call, provided that the gene(s) predisposing to the alarm call are included in a sufficient portion of the shared genes. (Mateo 1996)

Synalpheus regalis, a eusocial shrimp, is also an illustration of an organism whose social traits meet the set of criteria of inclusive fitness. The bigger defenders safeguard the colony's young teenagers from outsiders. The genes will continue to be passed on to succeeding generations, by ensuring the longevity of the young (Duffy et al. 2002).

Inclusive fitness is more universal than strict kin selection, allowing the shared genes to be of the same by descent. Inclusive fitness is not confined to cases affecting kin.

Application of Hamilton's Rule

Hamilton suggested that inclusive fitness provide a basis for the evolution of altruism in the sense of sociobiology. He believed this would lead to natural selection preferring species that are behaving in ways that correlate with optimizing their inclusive fitness. If a gene (or gene complex) that causes altruistic behavior has copies of itself in

others, helping others survive will ensure the genes are passed on.

Gardner et al. (2007) suggest that Hamilton's rule can be applied to multilocus models, but that it should be done at the point of interpreting theory, rather than the starting point of investigation. They propose that one should "use traditional population genetics, game theory, or other methodologies to derive a condition when selection favors the social character of interest and then use the law of Hamilton as an aid to conceptualize this outcome."

This insight has significantly extended population genetics, the genetic theory of natural selection and the Modern Synthesis, because it shows that natural selection of any gene depends on the effects of the gene, or lack of effects, on the direct fitness (number of offspring) of the copy bearers themselves. In terms of fitness, specific individuals are not sealed off from each other and traditional "individual selection" is, in the end, gene selection. All higher rates of organization, such as genomes, multicellular organisms, and populations, emerge from significant evolutionary transformations that are conditional on cooperating genes seeking a correlation of inclusive interest in fitness in bringing them about (Queller 2000).

Hamilton's rule offers a clear but powerful formalization of inclusive fitness theory (Grafen 1982). This states that a gene for any social change shall be selected if the sum of indirect fitness (rb) and direct fitness (c) exceeds zero, where r is the relatedness of the social actor and beneficiary and where c and b are the changes introduced about by social action in the number of offspring of the actor and the receiver, respectively. From the rule of Hamilton follow the well-known conditions for the four possible forms of social action defined by the signs of c and b , which include cooperation or mutual benefit (+, +), altruism (−, +), selfishness (+, −), and spite (−, −) (West et al. 2007). Specifically, in its most celebrated application, Hamilton's rule puts that altruism (net loss of direct fitness) is selected if $rb - c > 0$. Through defining this condition the

inclusive theory of fitness solved the altruism problem (Dawkins 1976).

The theory provides the best present basis for a unified understanding of social evolution because of its foundation in fundamental theory, its incorporation of the four types of social action and its universal taxonomic scope (Lehmann and Keller 2006). For example, it allows for a common understanding of conflicts between family groups and intragenomic conflicts (Haig 1997). This offers an overview of the biological structure itself as applied to the main transitions.

Proof for the inclusive theory of fitness is extensive, diverse, and growing. Nevertheless, there are relatively few clear empirical tests of Hamilton's law in natural populations. Hamilton's law states that any social activity can occur only under certain configurations of r , b , and c values. Factors that produce the required r , b , and c values inside natural populations create the conditions for social evolution. Variation in such values may then trigger social evolution in the sense of making the difference between whether or not social behavior undergoes selection (given the correct genetic variation). For instance, Hamilton's rule shows that positive relationships are a sufficient prerequisite for altruism evolution, and that altruism develops quite easily when b is high and c is low. So the identification of factors affecting the relative values of b and c gives insight into the causes of altruism for a specified relatedness structure (Korb and Heinze 2008).

Significance of Hamilton's Rule

First, Hamilton's rule introduces the gene's eye view of natural selection, noting that the important aspect for a gene to be evolutionarily successful is that it tends to leave more copies of itself to future generations regardless of the fitness effects experienced by individuals. This gives him a theoretical point of entry into the altruism problem and places the research within a systematic, population-genetic context.

Second, Hamilton's rule goes on to point out that, even after decreasing the reproductive fitness of the altruist, a gene encoding altruism may leave more replicas of itself in the future if the recipient also carries replicas of the altruist genes. This pinpoints, qualitatively, the selective benefit of the origins of altruism.

Third, being quantitative and using the vocabulary of "concentration" and "dilution," Hamilton states that it is the "regression" in the recipient of the altruistic genotype that defines how well the recipient transmits the genes of the altruist. He points out that Sewall Wright's correlation coefficient of relationship will well estimate this regression coefficient: that is, one-half for full siblings, one-quarter for half-siblings, and so on, in typical scenarios. This regression method to relatedness tests genetic similarity with respect to the average population, rather than in absolute terms, and it is in this sense that we can only be compared to our siblings by half despite sharing 99% of our genes with chimpanzees.

Fourthly, Hamilton puts together these observations into a single inequality, defining the required and sufficient condition for the gene to be favored by natural selection: $k > 1/r$, where k refers to the recipient's fitness gain ratio and the actor's fitness cost and r refers to the degree of relatedness. This basic finding now forms the cornerstone of social evolution theory and is referred to as "Hamilton's Rule" in its various forms" (Charnov 1977).

Fifth, by putting aside genes and paying attention to individual species, Hamilton derives from the evolutionary process a moral law, noting that "an animal operating on this theory would sacrifice its life if it could save more than two friends, but not less" (p. 355). This reflects a profound shake-up in Darwinian understanding, as it demonstrates that natural selection does not need to lead individuals to act as though they were trying to maximize their personal reproductive success and that, in certain circumstances at least, they will value their kin's lives.

Sixth, Hamilton clarifies that, in addition to nepotistic behavior toward known relatives,

natural selection will favor even indiscriminate altruism, such as birds' alarm cries, because adjacent individuals appear to be genetically related in viscous populations.

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Hamilton's Rule and Kin Investment

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Synonyms

[Altruism](#); [Inclusive fitness theory](#); [Kin selection theory](#)

Definition

Hamilton's rule predicts that, all else being equal, individuals will invest more in their closely related relatives compared to their distantly related relatives.

Introduction

Inclusive fitness theory (Hamilton 1964) argues that individuals can spread their genes in future generations (inclusive fitness) by investing in the reproduction of their relatives (indirect fitness) in addition to reproducing themselves (direct fitness). Hamilton's rule is an equation of the above-described theory and can be described as follows: $Br > C$. In the equation, B stands for benefits and C refers to the costs, which are both measured in terms of reproductive success. The coefficient r represents the genetic relatedness between the investor and the recipient, indicating the probability that these individuals have an identical allele by common descent at a random locus (Salmon and Shackelford 2011). According to Hamilton's rule, the benefits of an

investment, weighted by the degree of relatedness, should exceed its costs. The theory has been investigated especially in nonhuman populations and empirical results have provided extensive support for the validity of Hamilton's rule in many species, such as eusocial insects, birds, primates, and many other mammals (Hepper 2011).

Hamilton's Rule and Human Populations

The benefits and costs of investments are difficult to measure because they are defined in terms of the overall reproductive success of an individual. Therefore, research on humans typically focuses on the genetic relatedness of individuals, which is the more measurable parameter of Hamilton's rule. On average, the degree of relatedness is 0.5 with parents, children and full-siblings, 0.25 with half-siblings, grandparents, grandchildren, nieces, nephews, aunts, and uncles, and finally 0.125 with great-grandparents, great-grandchildren, and first cousins. According to Hamilton's rule, all other things being robust, the investment between individuals should correspond to the degree of genetic relatedness.

The prediction is relatively well supported by ethnographic, experimental and self-report-based studies, which have shown that people typically invest more in their close relatives than their distant ones and, in general, the investments among kin or the willingness to invest reflects the patterns of their genetic relatedness (Burnstein 2005; Madsen et al. 2007). For instance, individuals are more willing to make sacrifices for the benefit of their siblings than their cousins and, respectively, individuals are closer with and provide more support to their full-siblings than their half-siblings (Neyer and Lang 2003; Pollet and Hoben 2011). Moreover, twin studies have shown that genetically identical monozygotic twin-pairs have higher levels of closeness and cooperation than dizygotic twins, whose relatedness is equivalent to full-siblings (Segal et al. 2007).

Conclusion

Hamilton's rule is widely applied in evolutionary studies. Nonetheless, it has also been criticized. The universal applicability of inclusive fitness theory was questioned in a recently published article by Nowak et al. (2010). In the following debate, almost 150 scholars stated that the critics had ignored an extensive amount of empirical studies that has accumulated over several decades and provide strong evidence for Hamilton's rule (Abbot et al. 2011). Overall, Hamilton's rule can provide a prediction and an explanation for kin altruism and it has gained extensive support from empirical studies.

Cross-References

- [Genetic Relatedness Affects Aid to Kin](#)
- [Hamilton's Rule](#)
- [Hamilton's Rule and Genetic Relatedness](#)
- [Helping and Genetic Relatedness](#)
- [Helping and Inclusive Fitness Benefits to Helper](#)
- [Helping More Likely with Close Kin than More Distant Kin](#)

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Hamilton's Rule and Theoretical Implications

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Synonyms

Altruism; Group Selection; Inclusive Fitness;
Kin Selection

Definition

Hamilton's rule is that an altruistic behavior can be selected for in a population under the circumstances that

1. The behavior is heritable (variance explained by genetic difference).
2. The gene underlying it provides a benefit to those who share that gene by common descent that is higher than the cost exerted, multiplied by the coefficient of relatedness.

This is usually simplified to $rB - C > 0$. In this formulation r is the relatedness coefficient between actor and beneficiary of behavior; B is the reproductive benefit provided to the recipient;

and C is the cost to the actor in terms of direct reproduction.

Introduction

The term “paradigm shift” should come with a health warning. Hamilton's rule, formalizing inclusive fitness, is one of those very few developments in science that genuinely deserves the accolade. Inclusive fitness is a central, axiomatic concept in evolutionary biology. Darwin's discoveries, concerning descent with modification from common ancestry directed by natural selection, were the result of years of painstaking observation and the synthesis of vast amounts of empirical data. Hamilton's rule is an extension of Darwin's insight, based on pure deductive reasoning as laid out in (Hamilton 1964) and further developed in papers of equal mathematical sophistication (e.g., Price 1972).

While the complexities of these original papers are rarely directly engaged with, the take-home message seems simple: Namely, that altruistic behavior can be selected for just in case that the benefit bestowed on the recipient (B) multiplied by the coefficient of relatedness between actor and recipient (r) minus the cost to actor (C) is greater than zero.

This is typically expressed as $rB - C < 0$.

Rarely has such a deceptively simple formulation had such profound consequences or provoked such large misconceptions and fights over interpretation. It has been argued that the rule as it stands is too simple to permit simple predictions on the basis of it (Frank 1998). Whether or not this is true, it has been tempting for scholars to rush to predictions based on it, perhaps in a version of physics envy. The upshot of this haste can then be that, following a supposed failure of Hamilton's rule to apply, scholars seek for other explanations for the source of a social behavior. In this vein it is worth emphasizing that there are a large number of things that Hamilton's rule does not imply and does not apply to – much though it may appear to.

Why does all this matter? It is not hyperbole to say that Hamilton's rule explains the otherwise miraculous. Miracles are, strictly speaking, things

that cannot be explained by appeal to natural laws. Darwin's insight explains how the world appears to be designed but without needing a designer. Hamilton's extension of Darwin's insight is no less momentous. It explains how moral behavior – which at its bedrock – requires the capacity to benefit others at a net cost to oneself (in other words, true altruism) can come into the world without a divinity to underwrite it.

Throughout history, humans have typically sought for supernatural explanations for the way that the universe contains both beauty and goodness. As Kant famously put it “Two things awe me most, the *starry sky* above me and the *moral law* within me.” Darwin's discoveries showed us that no designer was needed to create functionality and in the process reminded us that not all functionality was beautiful. Hamilton's rule unites all of nature in terms of how genuine altruism – a crucial social behavior – can exist at all without supernatural interference. In the process he similarly showed us that our intuitions about what is truly good cannot be relied on. Of course, this mathematical extension of evolution by natural selection has far more implications than simply that it is the most general formulation of natural selection yet devised.

Useful Terms

Adaptation: A trait that improves fitness – defined in terms of representation of genes in the next generation. Since Darwin and the modern synthesis, the only non-supernatural force that explains the appearance of design in this fashion is natural selection, although other forces (such as drift) can explain differential representation of genes.

Altruism: A behavior that imposes a cost on the actor and gives a benefit to the recipient. The word is usually applied to behaviors, but any trait could be altruistic – such as a physical trait that acts to benefit others at a cost to the user like a honey-bee's sacrificial sting.

Gene: The basic unit of selection. Whatever has the requisite properties of longevity, fecundity, and fidelity is a gene in the sense needed for evolutionary biology. Since the double-helix

nature of DNA has been uncovered (which has those three required properties), this has become the focus of research. However, interesting complexities such as the various kinds of interactions between genes make judgements that rely on a single “gene for x” potentially misleading. A useful way to think of genes for evolutionary biology purposes is as a catalyst whose catalyzing reactions influence its representation in the next generation (Dawkins 1976; Haig 1997).

Green beards: A putative tightly aligned property linking genes to phenotype that would allow them to recognize one another directly. It is controversial whether any genes do this, but no one claims that they do in the case of humans. However, humans do possess adaptations allowing them to recognize kin at better-than-chance levels.

Group selection: There are a number of meanings for this term, and not all are mutually consistent. The original use of the term, by Wynne-Edwards, to refer to voluntary limitation of fitness-producing behaviors so as to benefit the group has fallen out of favor as being shown to suffer from being fatally vulnerable to selfish invaders. While other uses do persist, there is to date no additional explanatory power that has been shown to be dependent on modeling social behavior in this way, rather than in terms of existing mechanisms such as inclusive fitness and mutualism. Group selection in the way precisely defined by Price (1972) can exist but only in extreme situations that do not pertain to human beings (such as groups budding and reproducing faster than their constituent elements do). That a group persists or expands is not itself an instance of group selection because the group is not, in this case, the unit of selection. Humans have a number of adaptations to groupishness, however, and these are important.

Heritability: The proportion of variance in a trait accounted for by genetic factors. It is important to note that heritability is not a fixed property. For example, as shared environments become more similar, then heritability increases. Heritability is sometimes confused with “genetic determinism” which is a largely meaningless phrase. The development of human heads can be safely said to be encoded in genes. The actual possession

of a head has a heritability of 0, because variance in the number of heads possessed by a specific human (0 or 1) will be entirely explicable in terms of environmental factors.

Inclusive fitness: Individuals can affect the transmission of their genes into the next generation either directly (their own reproduction) or indirectly (that of relatives). Inclusive fitness is an extension of Darwin's principle of evolution by natural selection so as to include social behaviors – indirect as well as direct benefits. It is inclusive fitness that Darwinian individuals can be assumed to maximize – making it the most generally applicable model for explaining adaptation yet formulated. Inclusive fitness can be measured through measuring the effect on offspring in general (direct and indirect) multiplied by the degree of relatedness. As such it is foundational and true by deduction once one accepts that evolution is through differential survival of genes in the gene pool. Attempts to disprove it are thus misguided, unless one first attempts to disprove the concept of fitness or the concept of genes. Hamilton's rule for inclusive fitness is often simplified to $rB - C > 0$, where r is the coefficient of relatedness, B is the benefit in terms of fitness, and C is the cost to the actor.

Kin selection: A term coined by Maynard Smith (1964) to explain the indirect fitness benefits that accrue from aiding kin reproduction and to distinguish this from group selection. In one sense kin selection refers to relatedness due to common descent. However, a broader use of the term refers to the degree of shared genes at particular loci – whether or not these happened to come from shared ancestry. However, given that green-beard effects (where genes can recognize copies of themselves) are likely to be rare, the differences between these uses are unlikely to matter much in humans. Hamilton does not use the term in his writings. Inclusive fitness (unlike kin selection) does not require actual kinship, just genetically non-random altruism (Hamilton 1975). This could occur through situations of comparatively low dispersal, for example.

Mutualism: Behaviors that provide fitness benefits (not necessarily equal) to both actors and

recipients. It is easy to mistake mutualistic behaviors for altruistic ones.

Relatedness: Although this is commonly thought to refer to shared genes, this is a simplification with consequences. A much better definition is to put relatedness in terms of the degree of genetic similarity between individuals related to the average background shared genetic similarity. See Box 1 (taken from West et al. 2011 and used with permission) for a more complete description.

Selfish: Behaviors that benefit the actor but impose a cost on the recipient.

Social behavior: Any behavior that has consequences for other individuals (Hamilton 1964). Mere presence may have consequences but it is not a behavior, per se. There are four types of consequence that can occur: altruistic, mutual, selfish, and spiteful.

Spiteful: Behaviors that impose costs on both recipient and actor. One of the strengths of Hamilton's (1970) formulation of social behaviors is its successful prediction of spiteful behaviors in cases where relatedness coefficients are negative.

Implications of Hamilton's Rule

Good theory both explains and predicts. It explains what we see and frames what kinds of questions we can ask of our observations. And, it makes (one hopes) surprising predictions about things that we might see and the things that, despite persistent search, we don't see. The more surprising the prediction, the more confident we are of the theory if it is confirmed. Darwinian evolution by natural selection explains the appearance of design in the natural world and places constraints on the sorts of traits that can exist by limiting the ways that they can come to exist. For example, Darwin could famously predict the existence of a particular kind of moth and its traits prior to its discovery, based on observations of a deep flower with nectar at its base.

Hamilton's rule makes similar surprising predictions and offers constraints on the sorts of social behaviors that can evolve. Its predictions are somewhat more complex to follow than

natural selection alone, however. The rule also makes predictions, but often not the ones attributed to it.

Inclusive fitness implies that organisms can be assumed to be acting so as to maximize their average lifetime fitness (even if individuals may deviate from this). Hamilton's extension of the Darwinian insight was to realize that this included not just the fitness of the individual themselves but also of their relatives. Social behavior involves more than one entity, of course. For ease let's call them an actor and a recipient. Either one, both, or neither can benefit from the interaction. This gives us four possibilities. If both benefit, this is mutualism. If neither benefits, this is spite. If the actor gains at the expense of the recipient, then they are truly selfish (in the technical sense of the word – they may or may not have selfish motives), whereas if the actor loses out but the recipient benefits, this is altruism (West et al. 2007). Once again, "altruistic" here means what it means in a technical biological sense. For everyday usage behaviors that are mutualisms (like both parents giving loving care to a child) might be felt to be altruistic when they are mutually beneficial. It is important not to be misled (by our natural tendency to be hypervigilant for our fellow humans' potential to be exploiting us) into thinking that these behaviors are somehow not really altruistic.

Questions That Biology Can Answer

Tinbergen (1963) helpfully defined the four types of biological questions that can be asked of a trait.

1. How does the trait contribute to fitness? (Evolutionary question.)
2. How does it function? (Mechanistic question.)
3. How does the trait develop? (Ontogenic question.)
4. How did the trait evolve? (Phylogenetic question.)

There is resemblance to Aristotle's four causes (material, formal, efficient, and final) with some scholars insisting that final causes

(teleology) correspond to the evolutionary explanation of a trait, and, possibly, Darwin himself may have flirted with this idea. However, teleology is end directed and evolutionary fitness is something that can only be seen in retrospect. Other than as a shorthand (i.e., organisms behave as if they are trying to maximize their fitness), the resemblance of evolutionary causation to teleology is misleading. Organisms are driven neither by an inner elan vital nor pulled by an external divine plan.

A useful general distinction following from Tinbergen (1963) is that ultimate answers are given to "why" questions, whereas proximate answers are given to "how" questions. Thus, in answer to a question about how eyes develop, a proximate answer might look at the development of eyes and ask questions such as "do neonates see color?" On the other hand, a question that asked "why do humans discriminate red and green" might make reference to our phylogenetic history and how the ability of our ancestors to discriminate ripe fruits from unripe ones increased their fitness. These would be ultimate questions.

Information and Price's Formulation of Altruism

The general application of game theory to evolutionary problems begins with the work of Smith and Price (1973) which showed how limited conflict between animals could be modeled without assuming some benefit to the species model. These insights depended in turn on Price's (1995 posthumous) formulation of Hamilton's rule. Here he realized that any useful mathematical definition of selection is needed to exclude "psychological factors of preferences and decision making" (p. 389).

This is important for a number of reasons, but one of them is that human beings – hypervigilant as they are to signs of possible fakery and betrayal in acts of apparent altruism – can be led astray by the notion that all altruism is somehow not real – by which they usually mean that the appropriate feelings associated with it may be absent in a

particular case. It may well have made a lot of evolutionary sense for our ancestors to test one another in the group for the presence or absence of particular moral sentiments. Indeed, we likely still do this in the form of gossip and similar behaviors. However, the proximate moral emotions of, for instance, empathy or shame, which mediate social behaviors, are not to be confused with the ultimate causes of how the gene underlying altruistic behaviors might be selected for by evolution.

Price (1995) makes an explicit analogy with how Hartley's (1928) definition of information, which made no reference to meaningfulness, was foundational to Shannon's (1948) insights into information theory. Hartley's (1928) definition of a practical measure of information was in terms of the logarithm of the number of possible symbol sequences. It is a striking fact, not lost on contemporary physicists, that this definition of information:

$$W = K \log m$$

(where W is the speed of transmission of information, K is a constant – to be empirically determined – and m is the range of voltage levels to choose from in the signaling system) Has so much in common with Ludwig Boltzmann's formulation of entropy

$$S = k_B \log W$$

(where S is the entropy of an ideal gas, k_B is Boltzmann's constant – an empirically determined number – and W is the number of microstates in that system).

The fact that energy and information can be put in terms of one another should alert scholars to the fact that the information referred to here does not require psychological meaning. This is important because many might otherwise assume that information requires some sort of irreducible semantic content – e.g., a mind that understands it – and it does not. In the same way, altruism (and aggression for that matter) can be modeled without any necessary ascription of proximate mechanisms by which they are manifested (such as loving feelings).

Genes, Selfish, and Otherwise

Genes can be helpfully thought of as catalysts whose catalyzing reactions affect their own representation in the next generation (Haig 1997). Another way to think of this is that they are as replicators that build vehicles through which they interact with the world, including one another (Dawkins 1999).

Game theory has become central to modeling these complex interactions of vehicles, providing testable and often surprising predictions (Smith and Price 1973). Gene frequency can be held in various kinds of dynamic equilibrium – helpfully referred to as evolutionarily stable strategies (ESS). This is a term borrowed from game theory to describe a set of strategies adopted by actors in a population that is stable. By “stable” it is meant that an invading (and rare) alternative strategy cannot invade and become dominant.

To a first approximation, an individual's gene's success is synonymous with her own. However, this isn't necessarily true when the fitness of relatives who share particular genes by common descent is factored in, and this is when Hamilton's (1964) insight comes into play. At this point a suite of possibilities for modeling and predicting behaviors opens up. Of course, analysis may not stop there. As Haig (1997) has pointed out, the genes may well be in conflict with one another at the level of expression within the individual as well. Indeed the latter provides a powerful test of how powerful the “selfish-gene” model really is (Dawkins 1976). To illustrate this consider the conditions of Angelman and Prader-Willi syndromes – both of which are usually considered as developmental abnormalities.

Unless genes are taken to be “selfish,” i.e., that they seek representation in the next generation even at the (possible) expense of their hosts, then a number of phenomena are inexplicable. A good example would be maternal/paternal drives for gene expression – genomic imprinting. Here, some proximate mechanism (typically methylation) causes some genes to prosper (be expressed) at the expense of others. Some genes know if they are derived from the father or the mother. A classic example would be genes on

chromosome 15 which code for the growth of the hypothalamus (Buiting et al. 1995). The father’s genes would benefit – i.e., maximize their representation – from an offspring which demands a lot from the mother, and the genes from his line try to force expression at the expense of the mother’s genes. At the same time, her gene’s interests (and her own) would be served by hedging her bets and not investing all in one highly demanding offspring.

Normally the conflict of these genes is held in dynamic tension – neither set winning out. However, the evidence that they reached this impasse through conflict lies in the conditions that (rarely) result if one set does happen to win out over the other. If the father’s genes win, then the baby develops Angelman syndrome (and is highly demanding), whereas if the mother’s win, Prader-Willi syndrome (also known as “happy puppet syndrome” for the relative undemandingness of the baby) is the result. If the fight for expression was silenced, then the offspring would be perfectly viable (Moore and Haig 1991). Therefore, the existence of the syndromes (which occur when the mechanisms are not in dynamic equilibrium) constitute evidence for selfish gene theory. They are the classic “signs of a struggle” that detectives see when they enter a crime scene; nothing else explains the syndromes in question. Note that these are not cooperative strategies because the more efficient ones (where both sides drop their weapons) are not evolutionarily stable strategies.

However, these examples are not per se social interactions, and at the level Hamilton’s rule operates, it is social interactions that are the normal focus of attention.

Cooperation and the Major Biological Transitions

It might be thought that evolution by natural selection implies universal conflict. It is true that, without a struggle for resources, there is nothing that counts as outcompeting others. However, the means of achieving this is frequently cooperative in nature. Selfishness of genes does not imply that

they cannot cooperate in many ways to achieve their goals. Cooperation is ubiquitous in nature. One way to see this is in terms of the eight major transitions that have occurred, each increasing the level of complexity and requiring a cooperative mechanism to do so (Smith and Szathmary 1997).

(1) Replicating molecules	=> Populations of joined molecules
(2) Independent replicators	=> Chromosomes
(3) RNA (gene and enzyme)	=> DNA and protein (genetic code)
(4) Prokaryotes	=> Eukaryotes (cells with nucleus and organelles)
(5) Asexual clones	=> Sexual reproduction
(6) Protists	=> Multicellular organisms with organs
(7) Solitary individuals	=> Colonies with sterile castes
(8) Primate societies	=> Human societies with language

Some might argue that cultural evolution also belongs in this line as the next step, but the majority view is that cultural evolution represents a separate process rather than a biological transition per se (West et al. 2011).

Direct and Indirect Fitness

Fisher (1930) made a crucial distinction between direct and indirect fitness. To increase direct fitness is to increase the representation of the actor’s genes in the next generation. It is also possible to have fitness modulated by the behaviors of neighbors. For a variety of obvious reasons, neighbors are more likely to be kin and this is indirect fitness.

Relatedness

Organisms have traits, and those traits can be quantified. The trait (phenotype) can be meaningfully separated into the heritable component and environmental component. Natural selection acts upon genes and changes the average value of the phenotypic quantity of interest in populations (not individuals) as Fisher (1930) showed. This is how

increases in fitness are defined. Furthermore, Fisher (1930) usefully separated such fitness increases into direct and indirect effects – the latter including improving the fitness of kin (see Fig. 1).

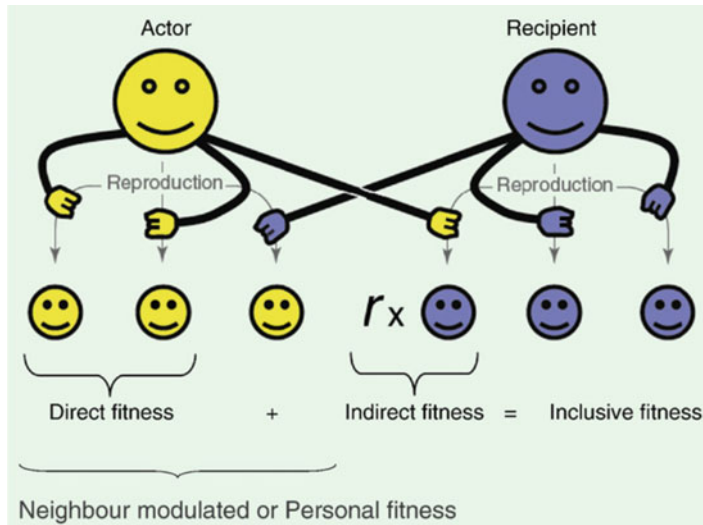
One of Hamilton's key insights was to realize that shared-gene underlying altruism could exist linearly as well as vertically in a population. "There is nothing special about the parent-offspring relationship except its close degree and a certain fundamental asymmetry" (Hamilton 1964, pp. 1–2). In Hamilton (1970) kinship by common descent can be calculated from shared genealogy. Subsequently it was appreciated that the direction of selection for social behaviors could be driven by appropriate statistical associations between individuals (Hamilton 1972; Price 1970).

Hamilton's early work takes an expressly population genetic approach – for example, he showed that the net effect of allele frequency on

related individuals can be expressed in terms of the fitness effects on those partners in relation to their degree of relatedness. This is exactly what $rB - C > 0$ implies. Later work (Queller 1992) showed that this is a special case of a more general model of covariant traits in a socially linked population. This later work fits Hamilton's insights into a quantitative genetics model but should not be seen as superseding these insights – rather as extending them to even further generalizability.

The "r" refers to the probability that a particular allele is shared through common descent. It does not imply anything about the proportion of shared genes in common. Humans share over 99 % of their genes – r measures the greater similarity between relatives above the background similarity between members of the same species.

An example of r: Let us assume the frequency of a particular allele in humans is 0.9. If I have a brother, then he is related to me with a coefficient of relatedness of 0.5. For us as a pair of siblings,



Hamilton's Rule and Theoretical Implications,

Fig. 1 Inclusive fitness is the sum of direct and indirect fitness (Hamilton 1964). Social behaviors affect the reproductive success of self and others. The impact of the actor's behavior (*yellow hands*) on its reproductive success (*yellow offspring*) is the direct fitness effect. The impact of the actor's behavior (*yellow hands*) on the reproductive success of social partners (*blue offspring*), weighted by the relatedness of the actor to the recipient, is the indirect fitness effect. In particular, inclusive fitness does not include all of the reproductive success of relatives (*blue*

offspring), only that which is due to the behavior of the actor (*yellow hands*). Also, inclusive fitness does not include all of the reproductive success of the actor (*yellow offspring*), only that which is due to its own behavior (*yellow hands*; adapted from West et al. 2007). A key feature of inclusive fitness is that, as defined, it describes the components of reproductive success which an actor can influence and therefore which they could be appearing to maximize (Reprinted from West et al. (2011) with permission)

half the time my brother will get the allele in question from the same parental chromosome as I did and half the time from the other parental chromosome. Therefore the probability of him sharing the particular allele with me is $\frac{1+0.9}{2} = 0.95$. This is (intuitively) halfway between the background frequency of the allele and 1. It is possible that using the concept of gene frequency rather than fitness might forestall confusion.

Families and Tribes

For parents to invest in offspring is species typical across taxa, with the types of investment varying according to a host of factors. In humans it might be thought that, as human children are so labor-intensive, investment would be total and preclude other behaviors. However, there is plenty of scope for the interests of parents and offspring to diverge somewhat. Parent-offspring conflict is a theme developed by Trivers (1974). The patterns of investment are predicted to alter in accordance with the possibility of investing in further offspring and viability of the offspring in question among other things.

Altruism toward families, both immediate and extended, requires some mechanisms, and Hamilton proposed that both kin-recognition mechanisms and the natural result of populations with a high viscosity could be the local means by which these occur. The various forms of potential markers of kin recognition are a rich field of enquiry. It could involve such markers as facial features, smell, dialects, skin tone, and proximate markers of tribal allegiance. Viscous populations are those where dispersal is sufficiently low that proximate mechanisms that treat mere proximity as sufficient to cue kinship can be selected for. These will form part of what Dawkins (1999) calls an extended phenotype, and, once again, this is a rich source of potential enquiry.

It is even possible that otherwise hard to explain behaviors such as homosexual preference (as distinct from homosexual behaviors which are far more common across taxa) might be explained in terms of inclusive fitness. If so-called helpers at the nest effects could occur with humans with the

benefits conferred offsetting the costs involved, then this could explain the development and preference of such behaviors. No one has, to date, convincingly shown this to happen without other assumptions being built in to the models.

There is a natural consequence of favoring one's kin and tribe and that is potential disfavoring of those who are not kin or who might be threats to resources. Indeed, this is what we find. Not only is in-group favoritism species typical in humans, but there is also a marked Cinderella effect – with those who are not one's offspring – but are still making demands on one's parental care, being at increased risk of neglect or even violence (Daly and Wilson 1998).

Strong Reciprocity and Economic Games

Humans do not just help one another; they also punish those that do not help. This calls for an explanation because said punishment is costly. Evidence for these moral dispositions – such as pride, envy, spite, shame, helpfulness, and similar – can be found cross-culturally and even sometimes in prelinguistic neonates favoring puppets who display such tendencies. A large literature – too large to fully review here – involving economic games, has developed to demonstrate these tendencies across human populations (see West et al. 2011, for an extended discussion of economic games in this context). This tendency to punish transgressors and free riders in a community is sometimes referred to as “strong reciprocity.”

It is especially important in considering models of such behavior to distinguish proximate mechanisms, such as feelings of moral outrage at transgressors, from ultimate causes for the selection of such mechanisms, i.e., how they might have contributed to fitness (Mayr 1961). Such selection may be in terms of altruism *sensu stricto*, but it is at least as likely to be evidence of a mutualistic system. While it is important that we can model human behavior in laboratory, or quasi-laboratory settings, care must be taken with conclusions that appear to be challenging Hamilton's rule. They are not; any more than the fancifully irreducibly

complex systems beloved of the creationists are a challenge to evolution by natural selection. While there may appear to be an elegant symmetry between maximizing utility functions and maximizing inclusive fitness, it doesn't follow that the world acts this way. Often, Hamilton's rule is not being addressed at all.

One of the consistent findings from experimental psychology is that participants do not see themselves as isolated laboratory creatures but as full human beings who also live outside of laboratories and might meet the recipients of their generosity or cruelty at some point – whatever an experimenter might insist. Thus, the use of so-called one-shot games (especially where it appears that people are more cooperative than expected) must be carefully considered. The experimenter might see them as one shot. It does not follow that this is how the participant sees them. Natural selection works by generating proximate mechanisms that maximize inclusive fitness on average. The fact that such systems can be made to misfire does not invalidate natural selection. No one would argue that the existence of pornography undermines sexual selection, just because humans can be fooled by it into generating nonreproductive behaviors.

As an example, consider the data on ultimatum games. These are where one actor makes an offer and the other participant can choose to accept or reject it. It turns out that a robust finding is that people make larger offers that standard economic theory would predict, and it could be argued that this supports a contention that humans are notably more cooperative than utility-maximizing (taken as a proxy for inclusive fitness maximizing) theory would allow for. However, as West et al. (2011) point out, the data could equally well support a rather more depressing conclusion – namely that humans are notably more antisocial (and know it) than we previously wished. If humans have evolved to recognize that other humans are especially spiteful and vicious, then they might expect low offers to be punished. Thus the surprising behavior would be the rejection of lower offers, and we could (equally) conclude that humans are more punitive than previously thought.

It is possible that scholars have been misled by the word “selfish” in the title of Dawkins (1976) work into mistaking the maximizing of representation of genes (ultimate causation) with selfish motives (proximate motivation). Expecting selfish behavior, scholars perhaps have been pleasantly surprised to find that humans are not, in fact selfish. But selfish gene theory never predicted that they were, and showing that they are not doesn't undermine the model of the selfishness of genes.

Even more common than ultimatum games is the prisoner's dilemma. This is an experimental economic situation involving a payoff matrix that allows researchers to model interactions of cooperation and defection. It is common to find it assumed that the prisoner's dilemma has proved that in one-shot games the strategy of defection (selfishness even to the point of spite) should be maximized but that cooperative tit-for-tat exchanges will thereafter defeat all other strategies in iterated interactions. Frank (1998) provides a sophisticated set of ways to model such interactions in a way that does justice to the complexities – modeling the biology of actual interactions rather than assuming that the world must be fitted, procrustean style, to the most elegant mathematical model. It turns out that neither of these assumptions is correct.

Group Selection and Selection for Groupishness

For a variety of interesting reasons, the term “group selection” has become almost synonymous with culture and morality in some quarters. In part, this confusion is that selfish genes make selfish people (and that therefore some special, extragenetic mechanism is required to make them social), but there is more to the issue than this.

Organisms cooperate, often at a cost to themselves. How, given the famous Darwinian struggle for survival, is this possible? In the 1950s and 1960s, many social behaviors were explained in terms of benefits conferred on individuals (e.g., Tinbergen 1951; Lorenz 1966). Group selection

arguments, sometimes even arguments in terms of the benefit to the species as a whole, were frequently invoked. In Wynne-Edwards (1962) proposed that organisms would voluntarily reduce their own fitness – for example, by limiting their own reproduction – so that the wider group could survive. One can still hear arguments of this kind in general circulation, although more rarely among scholars.

Both logic and empiricism were fatal to these sorts of group selection arguments, however. In terms of logic, it was reasoned that any such adaptations would be ruthlessly outcompeted by intruders that exploited them. Then, when the data were explored, it was found that the sort of self-limiting behaviors predicted could be shown to not occur.

There are other forms of group selection, including ones where the unit of selection is itself the group rather than the gene or includes the gene as well in so-called multi-level selection. All scholars agree that this sort of group selection can occur; indeed the covariance equations of Price (1972) could be expanded on one side of the equation without any limit so as to encompass any unit of selection that is desired. However, such expansion comes at a cost that the effect of selection decreases exponentially with such expansion. What this means in practice is that if groups were to bud and reproduce faster than their elements do, then group selection would overtake individual selection. In the absence of this, the effects of group selection are going to be vanishingly small, and no one has convincingly shown that this could occur with human beings.

Advocates of group selection in relation to humans tend to emphasize helping rather than, for example, genocide. But genocide and other activities like suicidal sacrifice for a military cause would potentially provide some of the strongest evidence for group selection, and in humans it is certainly well attested in our histories. Critics of inclusive fitness models are sometimes explicit that they believe that such selection dooms us to being ultimately selfish (Wilson and Sober 1998). But, “selfish” here is equivocal. Humans are very interested in the motives of one another. For example, we are intensely interested

in whether someone's motives can be trusted. To say that someone is selfish is tantamount to saying that, at crucial moments, they cannot be relied upon. But the selfishness of genes – their blind replication at the expense of others (unless those other genes produce mutual benefit) – must not be confused with selfish motives. Genes have no motives.

What Hamilton's rule explains is not that all so-called altruistic motives are at heart a sham. On the contrary, it explains how genuine empathy, self-sacrifice, and love can exist without supernatural intervention. By analogy, if someone were to see a brain scan of a loved one and noted that their ventral-tegmental area was firing strongly in response to a stimulus of them, would they conclude that “love was not real” because they could see its activity in the brain? They would be foolish if they did – because what they have just seen is actual evidence of just what a real thing love is.

Philosophers have struggled for millennia to try to make sense of our sense of morality. Where could it have come from? Is it god? Is it reason? Is morality somehow part of the fabric of the universe? What Hamilton's rule demonstrates is that some aspects of morality – those that give rise to empathy, for example – are indeed part of the fabric of the universe. This is not the whole of morality, of course. And Hamilton's rule certainly provides no guidance (or possibly only provides bad guidance) on a human's actual conduct. However, it provides a non-supernatural source for our proximate social feelings toward one another.

When something persistently reoccurs in human thought, it's likely not simply a misunderstanding but revealing of underlying cognitive architecture. As Lewis Wolpert famously put it, science is profoundly unnatural. We have only been performing science (rather than mere data collection about local regularities) in recent times. The conclusions of science are typically counter-intuitive and require a record of testing and failures to build up gradually. Scientific conclusions often jar with our sensibilities.

For instance, various forms of Lamarckism (inheritance of acquired characteristics) keep cropping up in each generation perhaps because humans, as obligate investors in their children,

probably cannot quite bring themselves to believe that the minute details of what they do as parents – unless they do some truly ghastly things – are normally swamped by the effects of genes. Similarly, perhaps it is the case that group selection keeps recurring as a plausible source of human moral behavior because it feels intuitively evident that we often suppress our needs for the sake of the group.

Indeed, some prominent scholars have made such introspection a major pillar of their arguments for group selection (Wilson and Sober 1998). But intuition and introspection are very misleading here. Given our species' long-documented capacity to have major sections of cognitive architecture opaque to others, it would be premature indeed to consider introspection as final. As Marvin Minsky memorably put it in an interview with Ken Campbell, "all parts of your mind are treating the other parts like tiny robots and finding ways to trick them." There is absolutely no reason to treat our inner emotions about the "good of the group" as anything more than an effective way to get ourselves to advertise ourselves as selfless members of the said group. Indeed, given that the most effective way to fool others is to sincerely believe it oneself, we have very strong reasons to be deeply suspected of introspections in this particular area most of all.

An important implication raised by Hamilton (1975) is that altruism in semi-isolated groups depends on the migration rates rather than the size of the groups. This is a rather surprising finding, but Hamilton showed that the interrelatedness of the groups will gradually tend toward the level of siblinghood if there is, for example, just one migrant per two generations.

Misconceptions About Inclusive Fitness

As well as stating what Hamilton's rule is, it is important to state what it is not. Misconceptions about inclusive fitness abound, leading to a number of attempts to rectify this in the theoretical literature (Dawkins 1979; Griffin et al. 2002; Park

2007; West et al. 2011). Some of the most common of these (that particularly matter in relation to human beings) are:

1. That cooperation is altruistic. This misconception may partly be due to the fact that humans have such exquisitely sensitive reactions to the potential cheaters and traitors in a group. This likely results in the notion that a suggestion that a behavior is somehow not really altruistic (because the actor also benefited) becomes conflated with the idea that the cooperation is itself not genuine. In fact, many cases that are described in the literature as "altruistic" are in fact mutualistic; both actor and recipient benefit from them. It may be better to call "reciprocal altruism" by other names to emphasize this fact (West et al. 2011). Reciprocity (Trivers 1971) can be direct or indirect (mediated, e.g., through reputation in humans), but it is not altruistic, in the strict sense required by Hamilton's rule, if both parties increase fitness through the behaviors. There are a multitude of mechanisms for enforcing cooperation and these have been found across taxa. The most common is simply punishing transgressors (West et al. 2011). None of these mechanisms require Hamilton's rule or require elaborate new types of explanations to be able to explain their occurrence (although they may well require sophisticated and sensitive modeling, of course).
2. That relatedness is merely about shared genes. This is incorrect. Only genes that influence behavior (through possible altruism) can fall under the kind of selection that Hamilton's rule describes. For instance, two clones who had no altruistic genes would not aid one another simply because they were genetically identical. Nor is altruism somehow proportional to shared genes. Humans and mustard grass share 15 % of their genes but do not show any measurable degree of altruism toward one another. As stated clearly by Krebs (1987), "The reason why relatedness is important. . .the coefficient of relatedness between two individuals is equivalent to the probability that they share the gene for altruism, not because they

share a high proportion of other non-altruistic genes" (p. 93).

One consequence of this is that simplistic models of individuals doling out lumps of altruism in proportion to the degree of relatedness of family members are very unlikely to be empirically verified. Generational asymmetries in investment and reproductive value are likely to be important variables, for instance.

3. That there is something special about siblinghood, cousinhood, or other similar kin relationships. This is also untrue. One of Hamilton's insights was to appreciate that parent-offspring relatedness was only one way in which relatedness might matter. In a diploid species (such as humans), each offspring has a 50 % chance (ignoring complications) of inheriting a specific altruistic gene. So as long as the benefits bestowed on the offspring outweighed the costs incurred in fitness by the parent multiplied by 50 % (the coefficient of relatedness), the gene could be selected for. Indeed, non-kin who happened to share a cooperative gene could act altruistically, in principle. While it is unlikely that this happens in humans, limited dispersal patterns and viscous populations can frequently mean that groups of humans who are apparently not close kin are still highly related to one another.
4. That kin selection is group selection. Selection for groupishness is not the same as group selection. There is no space here to explore all the variety of possible meanings of the term "group selection," but some have been discussed above. It is worth noting that evolutionary biologists in general accept the fact that group adaptations (which is one of the meanings attached to the term) can only occur in very specific circumstances that do not apply to humans such as in communities of clones or in situations with no within-group competition. Many evolutionary biologists would argue that putting things in terms of group selection adds nothing in terms of explanation but carries a potential for confusion (see West et al. 2011 for an extended discussion).
5. That kin selection requires the ability of genes to recognize one another. This putative property is sometimes referred to as a "green-beard" ability (Dawkins 1976). If the gene that underlays an altruistic behavior also pleiotropically produced both visible markers (e.g., the eponymous green beards) and the preference for such markers, then the genes could aid each other more directly. This appears to be very rare in nature. However, kin discrimination can occur through a variety of proximate cues. The most obvious of these is a shared early environment. In birds this would typically be a nest, but there is plenty of evidence (such as the famous Westermarck effect that prevents siblings' sexual interest in one another) of humans' assuming (not necessarily consciously) that those they grew up with are close kin. Other likely sources of interest for humans might include the ability of fathers to discriminate likely offspring, patterns of investment that reflect degrees of paternity uncertainty, and the role of infanticide and natal neglect (see West et al. 2011 supplementary material for an extended discussion of the research in this field).
6. That animals, and humans prior to arithmetical ability, need to be able to consciously calculate relatedness (Sahlins 1976) for Hamilton's rule to apply. No conscious calculations are required here; any more than spiders are required to be able to perform Weyrauch's formula of load bearing to be able to build their webs. Mathematics may be used to model and predict behaviors, but not necessarily the mechanisms by which those behaviors occur.
7. That altruistic behavior is too complex to be captured by a single gene and that therefore there cannot be a "gene for altruism." This is misleading. Fisher (1930) noted that phenotypically neutral genes were likely to be very rare in practice. Behaviors grow out of complex interactions of genes, not one single "gene for X." By way of example, a behavior that involves the feeding of chicks in the nest probably relies on a complex interplay of many genes working through proximate rules such as "feed whatever is in your nest, has a large patch of yellow, and is making a noise." This

rule can be exploited by, e.g., a cuckoo in a reed warbler nest. However, a mutant gene that caused the reed warbler to treat its younger siblings as its offspring (say) would be an altruistic gene in the strict sense; it reduces the older reed warbler's fitness but increases that of its siblings. Such a gene would not create the feeding behavior from nothing; it would build on existing behaviors (Dawkins 1979).

8. That Hamilton's rule predicts specific interactions between individuals. For example, it is not true (despite Haldane's famous quip) that humans regularly give their lives for two brothers or eight cousins. Neither does Hamilton's rule predict that they will (or should). Despite this, it is common to see Hamilton's rule presented in undergraduate textbooks as something that will predict specific altruistic acts (see Park 2007, for extended discussion and examples of this misconception occurring). Hamilton's rule describes the circumstances under which a particular altruistic gene can be selected for, not proximate instances of behavior.

Conclusion

Hamilton's rule (1964) is a foundational, axiomatic extension of Darwin's (1859) insights concerning how species develop through natural selection. Where Darwin (1859) explained the apparent miracle of design without recourse to the supernatural, Hamilton (1964) explained the underlying apparent miracle of morality – i.e., altruism – without recourse to anything other than the components of natural selection. This insight isn't the whole of moral behavior of course. Human morality also requires reason to, for example, extend thought and behavior in logically consistent terms. Hamilton's rule certainly does not itself provide a justification for behaviors. Indeed, inclusive fitness would seem to promote (say) nepotism, and this tendency is not a justification – rather the reverse.

One of the things that humans intent on building a better world would be wise to do is to pay

attention to the grain of human nature rather than be in denial of it. Humans are not slaves to their genes but their genes do keep culture on a leash, to echo E. O. Wilson's memorable phrase. Hamilton's rule delineates one of the most important ways in which this occurs. Does this make human morality some sort of mistake, as some people seem to fear? In short, do the nihilists (as H. P. Lovecraft joked) have a point when they say "The world is indeed comic, but the joke is on mankind." Not in the least. The recognition that our (proximate) moral sensibilities evolved in strict accordance with the known rules of biology means that they are real things.

More than that in principle, this realization gives us ways to identify and perhaps deal with those who do not share those proximate sensibilities. Those who lack empathy, for instance, are in principle just as disabled as those born without eyes. Biology is silent on the rational application of such moral sensibilities as shame, pride, and the desire to protect others, however. The rational application of these sensibilities in individual morality, or in the large-scale coordinations that politics requires, is a very human ability too and relies on our ability and need for reason and consistency. Only a highly simplistic moral philosophy would assume that feelings and sentiments alone were the whole of human ethics.

For biologists (and psychologists who accept that psychology must be at a bare minimum consilient with biology), then Hamilton's rule represents a powerful tool. As with all powerful tools, the potential can go both ways. Although it might seem daunting to face up to the challenges that the mathematical formulations require of us to model human behavior, it is also worth bearing in mind that human minds are a collection of complex kludges that evolved over millions of years in response to many conflicting pressures. The promise of an elegant predictive mathematical tool in the manner of the theoretical physicists is a tempting goal, though probably never attainable. That said, Hamilton's rule probably comes as close to being such a realization of the Ionian enchantment – the unification of all sciences through mathematics – as we are ever likely to get in behavioral science.

Cross-References

- [Hamilton's Rule](#)
- [Kin Recognition and Classification in Humans](#)

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"Hammer" and "Anvil" Stones

- [Stone Hammers](#)

Hand Axe

- [Acheulean](#)
-

Handbook

- [Evolutionary Psychology, The Handbook of](#)
-

Handicap Hypothesis

- [Steve Gangestad](#)
-

Handicap Principle

- [Costly Signaling and Altruism](#)
 - [Costly Signaling Theory](#)
-

Handicap Principle, The

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Synonyms

[Costly Signaling](#); [Honest Signaling](#)

Definition

The Handicap Principle suggests that many aspects of animal morphology, behavior, and communication are best understood as *handicaps*.

A handicap reliably advertises an animal's quality because it signals that the organism is of sufficient quality to tolerate the burden the handicap places on it. Central to this principle is the idea that the costliness of the handicap ensures the reliability of the message being conveyed.

Introduction

Upon spotting African wild dogs (*Lycaon pictus*), Thomson's gazelles (*Gazella thomsoni*) will sometimes start *stotting* – repeatedly leaping up and down using all four legs. Instead of fleeing to safety, these gazelles call attention to themselves, squandering valuable time and energy. Why do they engage in such an ostensibly dangerous behavior, and how could it possibly be favored by natural selection? The answer lies in the handicap principle – one of the oddest and most counterintuitive theories in evolutionary biology.

The Logic of the Handicap Principle

The Handicap Principle suggests that a stotting gazelle is sending a message to its predator - and that this message is effective precisely *because* it is wasteful (Zahavi, 1975; Zahavi & Zahavi, 1997). The gazelle is advertising its physical fitness to persuade the predator to pursue a less physically fit gazelle instead. In essence, the gazelle is saying “look at how physically fit I am – I see you coming, but I’m so confident in my ability to outrun you that I can afford to waste time and energy in this otherwise pointless behavior. You would be better off chasing one of my less physically fit peers instead”. The key idea is that only physically fit gazelles can afford to engage in this wasteful display. Consequently, stotting is a reliable indicator of the gazelle's fitness. It is precisely the costliness of the display that guarantees the veracity of the message, rendering it an “honest signal”. And because the message is reliable, it behooves the predator to attend to the information it is receiving. Indeed, studies confirm that predators prefer to chase gazelles who stot weakly or do not stot at all – and they are more likely to succeed in the hunt when they go after a nonstotting gazelle than when they go after a

gazelle that stots (FitzGibbon and Fanshawe 1988).

The key claim of the handicap principle, then, is this: many features of animals – ranging from bodily markings to behavior and communication – are handicaps. These handicaps exist because they convey honest, reliable information about the animal bearing the handicap. It is the costliness of the trait that ensures the truthfulness of the message conveyed.

The peacock's tail provides a canonical example. It requires physiological resources to build and maintain, attracts the attention of predators, and hinders the peacock's ability to escape. From the point of view of natural selection, it seems costly and wasteful – a metabolically expensive burden that decreases the peacock's chances of escaping predation. So why do peacocks build such extravagant tails?

Many readers will know an initial answer: because peahens find it attractive. But *why* do peahens find such a wasteful burden attractive? The handicap principle's counterintuitive answer is that they like it *precisely because* it is a wasteful burden. Because it is so costly, only males of high quality can *afford* such a burden. As such, the size, color, and patterns on a peacock's plumage serve as reliable indicators of the male's underlying genetic quality. The peacock's tail thus provides reliable information about his physical fitness and genetic quality – key information for a peahen's mating decisions. This captures the central logic of the handicap principle: the costliness of the handicap ensures the honesty of the message.

Before we evaluate the theory on its scientific merits, considering other examples of the handicap principle may help bring the logic of the theory into relief and simultaneously offer a sense of its scope.

The Handicap Principle in Nonhuman Animals

Skylarks escaping from falcons sometimes sing in mid-flight (Cresswell 1994). Because singing requires oxygen and energy, only skylarks in the best physical condition can afford to sing while fleeing – it is a reliable signal to the falcon that this particular skylark is healthy and fit, and that the predator would do better to pursue one of the

skylark's weaker peers. And indeed, studies show that if a skylark sings during escape, the falcon often aborts the chase. But if the skylark does not sing, the falcon continues to pursue it, and often succeeds (Cresswell 1994). The handicap principle thus explains a behavior that would otherwise appear inexplicable.

Siamese fighting fish offer another illustration. When two such fish get into an altercation, they may flare their gill covers, holding them erect. This is a wasteful display – it needlessly surrenders partial use of the gills and thereby impairs respiration. Gill flaring is a signal to one's competitor that one is so formidable that victory is assured despite the handicap of partial respiration. Weaker, less formidable fish cannot afford to do this. Sure enough, when such a fight takes place, the fish that holds its gill covers erect for the longest period of time toward the end of the fight is most likely to be the victor (Simpson 1968).

The Handicap Principle in Humans

The logic of the handicap principle is not limited to any particular species and should theoretically apply with equal force to our own. Are there features of human morphology, psychology, or behavior that are best understood as handicaps?

One candidate is female preference for testosterone-dependent traits in men. Testosterone is a known immunosuppressant (e.g., Folstad and Karter 1992) and is one of the reasons why men are more susceptible than women to a range of diseases (Bouman et al. 2005) and die several years earlier than women, on average (Buss 2015). Like the peacock's tail, high levels of testosterone can be a heavy burden in terms of health and survival. As such, only high-quality males can afford to produce high levels of this immunosuppressant. The handicap principle suggests that one reason why women are attracted to testosterone-dependent features such as a deep voice, strong jawline, and high shoulder-to-hip ratio is that these traits are evidence that the male in question is of sufficient quality to be able to tolerate high levels of a harmful immunosuppressant. Just like the peacock, his ability to afford a heavy handicap is a reliable indicator of his

underlying genetic quality (Hamilton and Zuk 1982; Smith 1985).

Is the Theory Likely to Be Correct?

When Zahavi first proposed the handicap principle (1975), many scientists ridiculed the idea. Ethologist Richard Dawkins evaluated the idea unfavorably in his landmark work *The Selfish Gene*, and evolutionary biologist, geneticist, and game theorist John Maynard Smith published a mathematical model showing that the principle was unworkable (Smith 1976). The handicap principle met with much resistance in the scientific community.

With time, attitudes changed. Ethologist and evolutionary biologist Alan Grafen published a mathematical model demonstrating that, under more realistic assumptions than those of the previous model, the handicap principle could indeed work in natural populations (Grafen 1990). This turning point, in conjunction with the continued flow of empirical evidence emanating from the Zahavi research team, gradually changed the opinions of many scientists. The handicap principle now enjoys both a mathematical proof of concept and a wealth of empirical evidence. Some questions remain about the principle's scope – some thinkers regard it as an extremely wide-ranging theory, while others are more circumspect. But the remaining debates no longer center on the conceptual tenability or mathematical feasibility of the concept, and the theory is now well-regarded among evolutionists. Richard Dawkins went so far as to reverse his initial view, saying this in the 30th anniversary edition of *The Selfish Gene*: “If Grafen is correct – and I think he is – it is a result of considerable importance for the whole study of animal signals. It might even necessitate a radical change in our entire outlook on the evolution of behaviour, a radical change in our view of many of the issues discussed in [The Selfish Gene]” (Dawkins 2006, p. 313)

Evaluating the Theory on Its Scientific Merits

The handicap principle has several scientific strengths. First, the hypotheses that fall under its umbrella are eminently testable. Second, the theory is broad in scope, dealing with topics as diverse as mate selection, predator-prey

interactions, parent-offspring relationships, chemical communication, animal coloration, ritualized fighting, parasite-host coevolution, altruism, humans, social insects, and even social amoebas. Third, the theory unifies diverse, seemingly unrelated phenomena by pointing to a deeper logic that underlies their surface variability. Fourth, the theory is parsimonious, and while the biological processes involved can be complex, the underlying logic of the principle is clear and simple. And fifth, the theory has heuristic and predictive power, suggesting new avenues of exploration and making new predictions. For example, because the principle maintains that there must be a logical, nonarbitrary connection between the nature of a signal and the message it conveys, the theory enables one to deduce from the nature of a signal what message it conveys and vice versa.

Novel Hypotheses

We would like to end by advancing a few novel handicap hypotheses in humans. It has been argued that, since immune function may be inversely related to disgust, people may down-regulate their disgust in front of potential mates in order to convey a robust immune system (e.g., Al-Shawaf et al. 2015). Although it has not been framed as such, this is essentially a handicap hypothesis: individuals' decreased disgust exposes them to heightened risk of pathogens, thereby conveying reliable information about their health and immunity.

Second, we suggest that the pride display, which involves a raised chin, lifted arms, protruding chest, and exposed torso (Tracy and Matsumoto 2008), is also a handicap. The person showing pride in this manner is exposing himself to attack and making himself vulnerable. This cost is tolerable for formidable individuals but constitutes a heavier burden on weaker or less capable individuals. We suggest that pride displays therefore convey reliable information about the quality of the individual engaging in them.

Third, we suggest that the practice of fighting for the right to pay the bill in a restaurant (common in the Mediterranean, for example) is a manifestation of the handicap principle. Despite the surface-level variability between this cultural practice,

potlatch dinners in tribal environments, and conspicuous consumption in urban environments, they are all underlain by the same logic: people are attempting to publicly handicap themselves with a financial burden in order to reliably convey their socioeconomic standing to their peers.

These examples represent only a small subset of the many manifestations of the handicap principle detectable in modern cultures, ranging from golf handicaps through chess handicaps to blindfolded skateboarding. The idea is not that humans have evolved adaptations tailored to modern innovations like golf or skateboarding, of course, but rather that selection favored the evolution of psychological mechanisms designed to flexibly use local cultural cues as handicaps, thereby honestly advertising an individual's ability or quality.

Conclusion

The handicap principle suggests that most animal communication is honest and reliable. This honesty is guaranteed by the cost of the communication – the message is too costly to fake. In other words, the cost is prohibitive for liars but not for those who are telling the truth. For example, the investment required to build the peacock's brilliant plumage is manageable for a male of genuinely high quality, but prohibitively costly for a male lacking the relevant physiological and genetic resources. The costliness of the peacock's tail guarantees the reliability of the information it conveys.

Scientists initially rejected this idea but have generally come to accept it. Though strikingly counterintuitive at first, its underlying logic is sound, and it has the hallmarks of a good scientific theory: testable hypotheses, unifying explanatory ability, parsimony, broad scope, and heuristic and predictive power. It is buttressed by both mathematical and empirical support, and it changes the way we look at much of animal communication.

Cross-References

- [Amotz Zahavi](#)
- [Animal Signaling](#)

- [Communication, Cues, and Signals](#)
- [Costly Signaling](#)
- [Costly Signaling and Altruism](#)
- [Costly Signaling Theory](#)
- [Disgust](#)
- [Fitness Benefits of Costly Signalling](#)
- [Game Theory](#)
- [John Maynard Smith](#)
- [Richard Dawkins on Constraints on Natural Selection](#)
- [Signal Reliability](#)
- [Testosterone](#)

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Handy Man

► [Homo habilis](#)

Harassing

► [Child Abuse and Bullying](#)

Harassment

► [Bullying](#)
 ► [Child Abuse and Bullying](#)

Hard to Fake Signaling

► [Steve Gangestad](#)

Harems

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Synonyms

[One-male group](#); [One-male troop](#); [One-male/multi-female group](#); [One-male-multi/female troop](#); [Single-male group](#); [Single-male troop](#); [Single-male/multi-female group](#)

Definition

- (I) Cohesive social group that is constituted by one or few dominant individuals of one sex (usually males) and, respectively, two or more individuals of the other sex (usually females), and in which dominant individuals actively fight nonmember competitors for all or, at least, the vast majority of the copulations with the group members of the other sex.
- (II) The assembly of individuals of one sex (usually females) that is sexually monopolized by one or few individuals of the other sex (usually males).

Introduction

Polygyny (i.e., the mating combination in which one male is paired to two or more females) is found in different forms, including resource defense polygyny, female defense polygyny, scramble competition, and leks (Emlen and Oring 1977). In these mating systems, high-quality males acquire more than one mate because they are more successful than low-quality males in premating competition. However, this higher success is defined in different ways in each of these polygynous systems. In leks and scramble competition, high-quality males are more successful because they are more effective in finding and/or courting females, but they do not actively restrict the access of other males to females. There are situations, however, in which males do not only compete for finding and courting mates, but also defend females, directly (i.e., female defense polygyny) or indirectly (resource defense polygyny). If a mating system/social group is characterized by a male that prevents other males from accessing his breeding partners, this may be termed a *harem*. However, through the decades, the term *harem* has been applied to a variety of contexts, leading to a gamut of different definitions of the concept. The heterogeneous nature of the concept of *harem* is presented in the following sections.

The Different Applications of the Term *Harem*

In behavioral ecology studies with nonhuman species, the term *harem* is most commonly used to designate social groups and mating systems that comprise just one male and more than one female. Social groups of one male and at least two females are found, for example, in arachnids (Gonyleptidae harvestmen), crustaceans (isopod *Paracerceis sculpta*), insects (stone and tree wetas, and bark beetles), fishes (*Centropyge*, *Serranus*), *Agama* lizards, great reed warbler, pheasants, northern harriers, *Sacropteryx* bats, elephant seals, fur seals, geladas baboons, hamadryas baboons, gorillas, langurs, pronghorn antelopes, red howler monkeys, red deer, and zebras. In some of these organisms, the harems can be part of a larger grouping of individuals, such as baboon troops. However, for each sub-grouping inside the troop, there is a cohesive interaction between a specific male and two or more particular females, which characterizes, under this definition, a *harem* (Lancaster 1975).

In the examples mentioned above, once females are clustered in space and/or time, a set of males in the population can monopolize sexual partners and prevent other males from mating. For example, female pinnipeds (seals) concentrate on beaches during the reproductive season and, once they are clustered in an area during a specific period, high-quality males can monopolize them, becoming harem bulls that fight off other males. Female monopolization may be achieved by defending territories (e.g., fur seals) or by defending the females per se from the attempts of competing males (e.g., elephant seals), allowing the dominant male to enhance his fitness.

By naming as *harems* the groups formed by one male and more than one female, it is assumed that one male and two females form a harem. It is also common to describe *harems* as groups composed of one male and several (or many) females. Yet, some authors define as *harems* even the groups of one male and just one female, given the potential of the male to acquire additional mates during the same breeding season. Further

still, some authors also name as *harems* those groups composed by few males that, together, monopolize a larger number of females. These male coalitions are found, for example, in animals such as the chimpanzees, feral horses, lions, and the cichlid fish *Pelvicachromis pulcher*. This joint effort of males may allow the monopolization of females and the maintenance of a harem when there are too many females and/or the females disperse along extensive areas.

Harems can be classified into two categories. Seasonal harems may occur when females are highly synchronized with respect to their sexual receptivity, and their monopolization remains feasible (e.g., red deer, *Cervus elaphus*). And permanent harems may occur when there is little synchronization in the availability of breeding females, and males are forced to defend their partners constantly (e.g., hamadryas and gelada baboons) (Davies et al. 2012).

Lastly, the term *harem* can also be used to designate: (a) social groups in which females are the polygamist sex that monopolizes sexual partners (i.e., *polyandrous harems*; e.g., phalaropes and jacanas), (b) social groups in which an individual of one sex monopolizes conspecific hermaphrodites (e.g., some serranine fishes) (Leonard and Córdoba-Aguilar 2010), and (c) the set of individuals of the most numerous sex in a given social group (i.e., if a single male defends three females, these females can be named *his harem*).

Harems and Their Evolutionary Implications

When few individuals control access to mates, the intensity of sexual selection upon the controlling sex is large. In pinnipeds, for instance, a large male can control a harem with more than a hundred breeding females. Given that one single male controls all the females at his harem by ferociously displacing challengers, many males will remain unmated. Once few males copulate with several or dozens of females and other males gain few or no mates, there is intense sexual selection (i.e., nonrandom differences in mating success;

Kokko and Jennions 2008), and just a few males achieve high fitness.

The great variance in mating success between males tends to lead to the evolution of costly traits that favor males in male-male competition for the access to females. As discussed by Darwin (1871), this may lead to the development of extravagant secondary sexual traits in the non-limiting sex (males, usually). For instance, there are the great differences in size and aggressiveness between the sexes in pinnipeds and red deer. Red deer also presents great antlers, which are used in fights for access to mates. The development of antlers and the fact that several fights for harem control result in males with permanent wounds, such as broken legs or perforated organs (Davies et al. 2012), show that males can suffer extreme costs in highly polygynous systems.

Under the Shadow of Harem Masters

The great mating success of dominant males that hold harems contrasts with the mean mating success of males that do not possess a harem. Among the latter males, some will engage in alternative strategies to achieve some matings. In the isopod *Paracerceis sculpta*, while large males hold harems, and defend females from the attempts of challengers, small males use their low detectability (derived from their reduced size) to sneakily enter the harem and mate. Additionally, medium-sized males mimic the size and behavior of females, enter harems, and mate without being displaced by dominant males (Shuster and Wade 1991; Shuster and Wade 2003). Sneaking behavior occurs in several *taxa*, such as harvestmen, amphipods, decapods, elephant seals, and ungulates.

The existence of harems promotes conflicts between the sexes. These sexual conflicts of interests emerge because, in harems, some males can prevent others from accessing females, which may preclude females the opportunity to choose the identity and number of sexual partners that could maximize their fitness. Moreover, the sexual conflict may emerge in cases in which the dominant harem male kills unrelated offspring,

as has been recorded for lions. This happens when the male has recently acquired the harem, and he is assured that he is not the father of the young. This behavior guarantees that the male will not care for the young of a competitor and may bring the female to a fertile state sooner. However, from a female perspective, this behavior only represents a reduction in her reproductive success.

Controversies Regarding the Term

Given the constrain imposed by harems upon the maximization of female fitness, and the existence of male alternative strategies, it is not surprising that, despite the vigilance of the dominant harem male, various females do copulate with other males (e.g., blackbirds, seals, Gunninson's prairie dogs, *Hamadryas* baboons, and the cichlid *Pelvicachromis pulcher*). This leads to sperm competition and reduction of the dominant male's fitness. If dominant harem individuals are not able to secure the great majority of copulas, it could be argued that they are not monopolizing, *sensu stricto*, sexual partners.

It also has been pointed out that the term *harem* brings problems derived from an anthropomorphist approach of studying animal behavior. Early naturalists interpreted animal mating systems by relating them to some specific human social organizations, particularly the harems (Rowell 1991). However, despite the several slightly different definitions of *harem* in human contexts, the human harem encompasses important political and economic aspects that match no straight analogy in other animals' harems. In several human societies, the harem represents the political power that derives from the position occupied by a particular man in the social stratification. Moreover, in some ancient human harems, the dominant individual could turn his wives into exclusive sexual partners, once eunuch guards were employed to protect his harem. Thus, the harem owner was assured to father all the children of all the women in his harem. Given these differences between human and nonhuman harems and that anthropomorphism is not an exclusive problem of early naturalist, but also a mistake in which

current scientists may incur while studying non-human animals, it has been proposed the use of substitutes to the term *harem*. One such synonym that has been used is the term *one-male group* (Lancaster 1975).

Conclusion

The use of the term *harem* has a long history, while at the same time not having a consistent definition. Harems are a widespread form of social organization in animal reproductive systems. Among species, harems differ in the structure of group composition and in which sex is in the role of dominant individual. The variation among different species in aspects such as group composition is very likely one of the main causes for the lack of a consistent definition of what a *harem* means. Moreover, as the term was first coined to define a form of human social group, carrying human-specific context, it does not readily apply to the reproductive systems of other animals. Presently, there is little consensus as to the definition of the term *harem* and its applicability to different organisms.

Cross-References

- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Polygamy in Humans](#)

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Harlotry

- [Prostitution](#)
- [Prostitution and Women's Short-Term Mating](#)

Harmed

- [Victims Mostly Men](#)

Harming

- [Reproductive Value and the Evolution of Aggression](#)

Harris' Moral Landscape

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Synonyms

[Ethics](#); [Moral values](#); [Morality](#); [Utilitarianism](#)

Definition

In Sam Harris' (2010) book, *The Moral Landscape*, he argues that human values can be interpreted scientifically through the examination of what contributes to the well-being or suffering of conscious creatures.

Introduction

Neuroscientist and philosopher Sam Harris argues in his book, *The Moral Landscape: How Science Can Determine Human Values* (2010), that a scientific approach to morality will be able to establish objective truths about what is right and wrong in terms of what causes conscious human and nonhuman animals to thrive or suffer. Because conscious beings are governed by the laws of nature and are responsible for conceptions of moral values, he proposes that morality can be construed and developed as a natural science. In Harris' view, applying an empirical approach to morality is reasonable because "human well-being entirely depends on events in the world and on states of the human brain" (2010, p. 2). To make this case, Harris observes that experiences that cause human's varying degrees of happiness or pain tend to be evaluated similarly by people around the world. For example, there is likely to be universal agreement that a life in which one is afforded pleasure, freedom, and the basic needs for survival is preferable to a life in which one experiences fear, hunger, and physical and emotional pain on a regular basis. Thus, Harris surmises that there are objective, identifiable conditions that allow for more or less favorable experiences in life.

Overview of The Moral Landscape

Harris first establishes that verifiable accounts about organisms and their environments constitute scientific facts about natural phenomena (i.e., observable events discoverable by empirical study). By extension, Harris asserts that we have the capacity to use the scientific

method to determine facts, or high probabilities, about what will best serve to minimize the suffering of conscious creatures and maximize their success. These facts, Harris contends, should qualify as moral values, which he operationalizes as: "the set of attitudes, choices, and behaviors that potentially affect our well-being, as well as that of other conscious minds" (2010, p. 12).

Harris prudently clarifies that the science of morality he advances does not prescribe drawing from human nature to identify moral values. Specifically, he does not propose that what is natural is right (i.e., he does not claim that something is good because it is natural or bad because it is unnatural) or that we should model morality on basic human motives (e.g., mate acquisition, parenting, etc.). Harris further denounces religion and faith as determinants of morality, arguing that religious belief is frequently in direct contradiction with reason and is responsible for impediments to social progress and human welfare. Harris additionally rejects the doctrine of *moral relativism* (similar to *cultural relativism*), which contends that moral judgements espoused by groups from different cultures are all equally valid and moral in their specific contexts. Like religion and faith, Harris argues that relativism is an obstacle to the pursuit of determining and implementing universal human values. According to Harris, moral facts about the quality of human life revealed by empirical analysis will transcend culture, just as, he notes, physical and mental health do.

Importantly, Harris' proposed science of morality is not absolute or immutable. Because our understanding of human well-being will improve and evolve, he maintains that we should correspondingly revise our definition of what constitutes a moral value. Additionally, Harris recognizes that there may be various methods of increasing well-being or reducing suffering, but disagreements about the best routes to morality do not imply that we should revert to relativism. Overall, Harris' work aims to stimulate a discussion among scientists to establish a normative science of morality in hopes of promoting universal human values.

Conclusion

Many critics of Harris' *Moral Landscape* take issue with his proposal of applying scientific principles to morality and maintain that science and ethics are separate disciplines that should not intersect (e.g., Blackford 2010; Horgan 2010; Isaacson 2012; Jollimore 2010; Nagel 2010; Pigliucci 2011; Robinson 2010). Some of Harris' critics argue that he assumes that minimizing the suffering of conscious creatures should, in fact, be a moral value because science cannot itself determine what criterion are moral (e.g., Pigliucci 2011). However, Harris preemptively addressed this criticism in the final chapter of his book (2010), recognizing it as the key assumption of his argument. In a later response to his opponents, Harris (2011) pointed out that reason and science itself are necessarily founded upon presuppositions (e.g., respect for evidence, logical cohesion, valuing an understanding of the natural universe). According to Harris, if we aspire to act morally, then it is counterproductive to spend time arguing over these inherent assumptions and debating whether it is theoretically important to ask moral questions. Although scientific inquiry into morality may be a challenging endeavor, it does not follow that there are no answers to these questions. Notably, Harris holds that instead of searching for affirmative answers to what promotes the well-being of conscious beings, we ought to more rigorously pursue answers to the question of what causes them measurable suffering. He also suggests that we have reasonable ideas of what some of these immoral practices may include (e.g., enslavement, genocide, the denial of basic human rights).

Other reviews of *The Moral Landscape* are more positive and have offered constructive recommendations to further Harris' science of morality. In their review, Diller and Nuzzolilli (2012) call upon behavior analysts to support and advance an empirical approach to morality by employing behavior change techniques to encourage prosocial (i.e., moral) behavior. Wall and Shackelford (2011) present a largely favorable review of Harris' argument but observe that, while Harris indeed argues for respecting the

well-being of nonhuman creatures, he provides inadequate attention to issues of animal welfare (e.g., animal testing and the consumption of animals). Although a scientific system of morality is not currently attainable in practice, several academics are supportive of its pursuit (e.g., Diller and Nuzzolilli 2012; Wall and Shackelford 2011), including Richard Dawkins, Lawrence Krauss, and Steven Pinker, whose endorsements are printed on the book's dust jacket (Harris 2010).

Cross-References

- Moral Concerns
- Neuroethics
- Philosophical Foundations for a Modern Morality
- Science and Morality
- Utilitarianism

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Harsh Environments

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Synonyms

Extreme environments; Inhospitable environments; Unpredictable environments

Definition

Harsh environments are external conditions that present a heightened or unusual challenge to the fitness of individual organisms, the stability of populations and longevity of species, or even the robustness of ecological communities.

Introduction

Harsh environments are external conditions that are detrimental to survival for most forms of life. These conditions limit the growth, abundance, or

distribution of organisms and populations in an ecosystem. The challenges posed by such environments are typically conceived of as being abiotic in nature. Although by no means an exhaustive list, severe limitations of essential nutrients or vitamins, resources such as water or energy (in the form of heat or light), space or shelter, and extremes of temperature, pH, salinity, or altitude are all limiting factors that contribute to the harshness of an environment. Humans and many other organisms have nevertheless adapted to survive and even flourish in these conditions.

Disambiguating “Harshness”

An environment may be considered “harsh” for a variety of reasons. It is necessary to distinguish these senses of harshness since each may have substantially different effects on the ecological dynamics of a population or community and the evolutionary dynamics of a species. Two distinct but not necessarily exclusive general criteria for harshness can be captured by using the labels *abnormal* and *unpredictable*.

“Statistical abnormality” can be attributed to environments that exhibit extreme values of limiting abiotic factors that fall well beyond the average as calculated across all known species. This form of trans-specific extremeness is typically correlated with lower species diversity. Take, for instance, exposure to sunlight. One extreme value on the spectrum for this limiting factor is realized in habitats hidden well beneath the surface, such as caves and sewers. As well as being a valued source of energy for many species, light is a requirement for even the most basic forms of sightedness. The evolution, ontogenetic development, and maintenance of a complex adaptation like the eye are costly. In many cases, the fitness enhancement that comes with sightedness is well worth the cost. Even the most basic forms of vision, simple photoreceptors, often enable the organisms that have this capacity for detection to evade predators or snare prey that cast shadows, as well as reliably migrate to areas that receive greater or lesser amounts of sunlight and correlated resources. For species of cave-dwelling fish

(e.g., *Astyanax mexicanus*), however, there has been strong selection for the loss of functional eyes and thus blindness because of negligible light levels in their local environments (Cartwright et al. 2017). This is a harsh environment in the sense that relatively few extant species encounter or could survive in conditions where there are no immediate photosynthetic primary producers and no way for them to see.

It is precisely to statistically unusual environments that organisms commonly known as “extremophiles” have adapted (Archibald 2014). Although these are usually microbial life forms that thrive in geochemical or physical conditions that are typically too extreme for complex multicellular forms of life, examples can be found in all three domains of life (Rothschild and Mancinelli 2001). Perhaps, the best-known extremophiles compose a phylum of small invertebrates known as tardigrades (*Tardigrada*) or “water bears.” Species of this phylum can be found in almost every habitat on Earth. They can withstand temperatures ranging from -200°C to 151°C , a complete lack of water or oxygen, boiling alcohol, the low pressure of a vacuum or six times the highest pressures found in the deepest part of the oceans, and more than one thousand times the lethal dose of X-ray radiation for a human (Bordenstein 2019).

A subtly different sort of abnormally harsh environment is one that is unusual for the members of a species when viewed from an evolutionary perspective. A human example is informative in this context. The preference for and occasional overconsumption of fatty or sugary foods was likely adaptive for our hominid ancestors since opportunities to exploit such energy-dense resources were somewhat rare. Evolutionary precursors who exhibited trait variants for effectively exploiting these resources were on average more likely to survive and reproduce than those of our distant ancestors who exhibited less effective trait variants for doing so. Exploitative (i.e., gluttonous) foraging behavior and an enhanced ability to store energy in fat cells thus increased relative inclusive fitness in this “normal” environment for our ancestors, also known as the environment of evolutionary adaptedness, or the environment to which humans became adapted during the

Pleistocene. But in most modern societies, this behavioral strategy no longer maintains the fitness advantage that it once held.

To understand why this is so, it must be mentioned that many aspects of the metabolic control system are established early in fetal development. Among these are the craving for food, insulin sensitivity, and the number of fat-storing cells. Normal maternal constraints during pregnancy can generate an upper limit on how much nutrition a fetus can sense. These constraints have the effect of directing the fetus to anticipate an environment that is not quite as bountiful as the one its mother experiences. The developing fetus responds by exhibiting increased insulin resistance and allocating more resources to the development of fat cells than necessary. When energy-dense environments are rare, there is no problem with this response; it can be a useful strategy in cycles of feast and famine. However, energy-dense foods have been readily available in most developed countries since the agricultural revolution. Worse yet, many of the modern foods we consume are explicitly engineered to falsely exhibit the common cues for high energy density (e.g., saltiness without corresponding high protein content) and thereby trigger virtually uncontrollable cravings. The fetus is subsequently born into a modern environment teaming with such resources. Blood glucose levels rise when these foods are consumed, which results in heightened insulin levels. Due to increased insulin resistance, however, the process of restoring normal blood glucose levels becomes biased toward storage of fat rather than more immediate usage. The outcome, of course, is a situation in which obesity and metabolic disorder have become global epidemics. There is a severe mismatch between the environment of evolutionary adaptedness and our statistically normal but nevertheless “harsh” obesogenic environment (Gluckman et al. 2005).

The foregoing forms of harshness are due to statistical or evolutionary *abnormality*, which involve uncommon extremes of limiting abiotic factors or significant departure from the conditions historically associated with periods of adaptive evolution, respectively. An altogether different form harshness can come in the form of

environments that are unpredictable. Essential resources fluctuate in most environments. There are, for example, regular and thus highly predictable daily changes (e.g., light hours per day) as well as seasonal climatic variations (e.g., colder Fall/Winter temperatures giving way to a warmer Spring/Summer). The relative stability of fluctuations like these over a *geologic* timescale has granted species time to adapt to such conditions on an *evolutionary* timescale.

Predictable fluctuations in limiting factors are contrasted with what is called “environmental stochasticity” in the relevant scientific literature (Lande et al. 2003). Environmental stochasticity refers to *unpredictable* spatial or temporal fluctuations in environmental conditions. Notice that the inability of an organism to precisely predict a future state of the system is due to extrinsic ecological features. This should not come as a surprise. For, upon close inspection, most (if not all) natural habitats exhibit highly localized and effectively random spatiotemporal fluctuations in available resources. Given that there is insufficient time for finely tuned adaptive evolution, survival in such adverse spatially or temporally “patchy” conditions requires adopting a sub-optimal survival strategy (i.e., allocation of available resources). Since no attainable strategy can reliably make perfect predictions about the future, there will be a continuum of (suboptimal) strategic variation along which some strategies fare better than others.

Unpredictably harsh environments are often the background conditions against which constrained trade-offs in the strategic allocation of resources and the evolution of life history traits are examined (Stearns 1992). This is evinced in the theoretical contrast between the reproductive strategies known as *r* and *K*. For present purposes, it is worth noting that unstable or unpredictably harsh conditions generally lead to strong selection for a high fecundity, low investment strategy (*r*), the idea being that at least a few small and quick-to-mature offspring will survive in the face of high mortality due to environmental instability. Niche construction theory – wherein it is argued that organisms significantly modify their environments and

thereby influence selection pressures on some population of recipient organisms – takes the ability of organisms to manage (minimize) the harshness of the environmental conditions to be fundamental (Laland et al. 2014). And research on cooperation suggests that such behavior facilitates the colonization of harsh environments (Cornwallis et al. 2017), which in turn implicates harsh environments as an explanatory factor in the maintenance of altruistic behavior.

The point to note is that environmental harshness due to unpredictability does not involve uniform distribution of or prolonged exposure to statistically extreme and, thereby, unusual values of a limiting abiotic factor. Quite to the contrary, unpredictable environmental fluctuations can mirror the average (statistically normal) conditions present in *both* the environment of evolutionary adaptedness *and* current environments. This can happen when (i) the resources available to a population are distributed in a spatially non-uniform (i.e., “clumped” or “patchy”) way over a limited area, or (ii) there are irregular temporal fluctuations in the available amount of a resource within a population’s habitat. Some of the spatial parts or temporal stages of a habitat accordingly experience statistically extreme values of limiting resources. However, the quantitative influence that these locally extreme values have in the calculation of average (arithmetic mean) conditions for the habitat as a whole can be offset when there are enough complementary high/low values from other parts or stages of the habitat. The arithmetic mean value for a limiting factor in a habitat can, therefore, remain unchanged even as environmental variance in the availability of limiting resource, not to mention corresponding uncertainty regarding resource allocation, increases. Environmental stochasticity thus makes for a “normal” but nevertheless harsh environment insofar as it induces individuals to adopt allocation strategies that maximize actual fitness (especially the fitness component of survival) at the expense of expected fitness (maximum fecundity). Following Matthewson and Griffiths (2017), it might be prudent to label these unpredictably harsh conditions “inhospitable” rather than “abnormal.”

Conclusion

The Importance of Harsh Environments

The recognition and study of harsh environments is of vast importance to ecological and evolutionary theorizing. Simply identifying the range of values for limiting factors over which species can thrive is hugely informative. In astrobiology, for example, it is typically the capacities of extremophiles in harsh environments that bound the possibility space of our thinking about whether and where life is likely to be found. For a more “down-to-earth” illustration, we can turn to conservation biology. Human-induced climate change is an unprecedented threat to human and nonhuman life. One way to understand and possibly predict ecological and evolutionary dynamics in the age of dramatic climate change is to examine how organisms have already adapted to harsh environments, past (via paleontology) and present.

Cross-References

- [Environment of Evolutionary Adaptedness](#)
- [Environmental Stochasticity](#)
- [Fitness](#)
- [Life History Theory](#)
- [Trade-offs](#)

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Head Injury

- [Specific Brain Damage](#)

Headmen

- [Unokais and the Headmen of the Yanomamö](#)

Health

- [Maternal and Offspring Condition](#)

Health Benefits of Nature

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Synonyms

[Nature effects on well-being](#); [Positive impacts of exposure to nature on human health](#)

Definition

Physical and mental well-being may be fostered by being in nature, viewing natural scenes, and bringing natural elements (e.g., indoor plants and natural light) into built environment.

Introduction

The work of several scholars in the area of human-environment relations confirms the notion that contact with nature may be beneficial for human health and well-being. This idea is very intuitive and is reflected in the fact that most people, regardless of their nationality or culture, prefer natural environments over urban environments (Parsons 1991) and that the majority of places that people consider favorite or restorative are natural places (Kaplan and Kaplan 1989). While the relation between contact with nature and human well-being may seem quite obvious and self-explanatory, there are many nuances to be taken into consideration.

In most studies, the effects of natural environments are compared to the effects of urban environments, which usually pose some specific health hazards for people, including pollution, crowding, sensory overstimulation, noise, etc. Natural environments may be beneficial in comparison just because they lack those exact sources of health risks. On the other hand, adverse effects of being in nature are rarely investigated since contemporary humans rarely face the same challenges that our ancestors had been exposed to during the most of our evolutionary past (e.g., encounters with predators, stress and injury from exposure to adverse environmental conditions, etc.). Thus, the scope of research on health benefits of nature is framed by the needs and lifestyle of contemporary humans, majority of which lives in urban environments with limited access to nature.

The most investigated benefits of contact with nature include enhancing people's ability to cope with stress and illness, fostering recovery from mental fatigue, and mood regulation.

Stress and Recovery

There is ample evidence that exposure to natural environments enhances the ability to cope with and recover from stress and recover from illness and injury.

One of the fundamental studies in this area of research found that patients with a natural view from their hospital room recovered faster, spent less time in hospital, had better evaluation from nurses, required fewer painkillers, and had less postoperative complications after gall bladder surgery compared with those who viewed an urban scene after the same surgery (Ulrich 1984). Subsequent studies explained the mechanism behind these effects: natural settings elicit a response that includes a component of the parasympathetic nervous system associated with the restoration of physical energy (Ulrich et al. 1991a).

Similar effects are found in other potentially stress-eliciting environments and situations. Access to nature in the workplace is related to lower levels of perceived job stress, higher levels of job satisfaction, and fewer reported illnesses and headaches (Kaplan and Kaplan 1989). Prison cell window views of nature are associated with a lower frequency of stress symptoms in inmates, including digestive illnesses and headaches (Moore 1981). Recovery from commuter stress in car drivers was quicker for participants who viewed nature-dominated drives than participants who viewed artifact-dominated drives, and the former also experienced greater immunization to subsequent stress (Parsons et al. 1998).

Attention Restoration

Kaplan and Kaplan described "restorative environments" as those settings that foster recovery from mental fatigue (Kaplan and Kaplan 1989) (Kaplan 1992a, Kaplan 1992b). The main four elements of every restorative environment according to them include fascination (an involuntary form of attention requiring effortless interest), a sense of being away (temporary escape from one's usual setting or situation), extent or scope (a sense of being part of a larger whole), and compatibility with an

individual's inclinations (opportunities provided by the setting and whether they satisfy the individual's purposes). Many natural environments and especially urban parks provide an opportunity for restorative experiences due to their ability to satisfy those four elements.

Even a view of nature may have restorative effects. In a study by Tennessen and Cimprich (1995) students who occupied dormitory rooms with natural views from their windows showed an increased capacity for directed attention when compared to students who occupied rooms with built views (views of buildings), so the authors concluded that views of nature may indeed be related to better attention restoration experiences.

Attention restoration effect of viewing natural scenes has been replicated in numerous studies since then, and some practical implications have been purposed both in prevention of mental health and in therapy of various disorders (e.g., attention deficit disorder).

Mood and Outlook on Life

A review of the literature on the psychological response to nature concluded that nature elicits feelings of pleasure, sustained attention or interest, and relaxed wakefulness and mitigates negative emotions, such as anger and anxiety (Rohde and Kendle 1994). It is noted that, in general, people have a more positive outlook on life and higher life satisfaction when in proximity to nature, particularly in urban areas (Kaplan and Kaplan 1989).

From Research to Practice

Environmental approach may be considered along with other health-promoting interventions in fostering and recovering human health and well-being. This approach as a preventive strategy may include both behavioral interventions, e.g., developing healthier habits (like going to nature frequently, tending a garden, keeping indoor plants and animals as pets), as well as design interventions in built environment (such as adding more greenery and water features into urban environment,

planning buildings with natural light, allowing employees to keep photographs of nature in offices, etc.). Recovery from various illnesses may be fostered through nature-based therapy like wilderness, horticultural, and animal-assisted therapy.

Conclusion

There is empirical evidence that beneficial effects of contact with nature for humans include fostering attention restoration, enhancing ability to cope with stress and illness, and mood regulation. Since various mental disorders are among leading contemporary health challenges, contact with nature may be included as preventative and restorative strategy in the domain of mental health and as an aid to recovery from physical illness.

Cross-References

- ▶ [Cross-Cultural Research on Grandparental Investment](#)
- ▶ [Landscape Preferences](#)
- ▶ [Natural Versus Artificial Environments](#)

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Health Cues

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Synonyms

[Honest signals](#); [Signals](#)

Definition

A phenotypic trait that reflects underlying physiological health.

Introduction

Researchers have advanced a range of hypotheses to explain why individuals perceive some phenotypic traits as attractive. One such hypothesis is that these phenotypic traits act as cues that reveal valid information about the bearer's underlying physiological health. Choosing healthy long-term (or even short-term) mating partners confers obvious fitness benefits. Understanding precisely what aspects of health such traits reflect is not always straightforward. Modern medicine and abundant high calorie food (at least in Western diets) has likely weakened, obscured, or even modified ancestral relationships between health and some phenotypic traits. Further complexities arise from the breadth of states (such as current nutritional state, and disease burden) and traits (MHC heterozygosity and immunocompetence) that contribute to an individual's health.

The Evolution of Cues and Signals of Health

One important consideration is whether the phenotypic trait in question is a cue or a signal of health. Signals are traits that have evolved under selection pressures arising from others' – the receivers' – behavioral responses to the trait in question. Cues, on the other hand, are traits that correlate with physiological health in such a way that observers can extract reliable information, but have not evolved under selection pressure to communicate that information (Scott-Phillips 2008). It is frequently difficult to establish whether a trait is an evolved signal of health or simply a cue that correlates with health. For example, fluctuating facial asymmetry (random deviations from bilateral symmetry) are thought to reflect developmental perturbations, resulting from developmental stressors. Thus, high facial symmetry reflects few developmental perturbations and may reliably indicate a robust immune system or a well-nourished development – two factors that would positively contribute to health. For facial symmetry to be an evolved signal of health, however, the human face would need to be under direct (sexual)

selection pressure, arising from the mate choices of the opposite sex, to resist developmental perturbations and develop symmetrically. While more symmetrical faces are perceived as more attractive, it is not clear whether such preferences have translated into the necessary selection pressures. Because of the difficulties in ascertaining whether any given trait constitutes a signal or a cue, no clear consensus exists about this distinction for nearly any given health-related trait. For simplicity, we will refer below to all potentially health-related traits as cues, but do not mean to imply that such traits are definitely not evolved signals.

Theoretically, a health cue might reflect trait-based health or state-based health. By trait-based health we mean an intrinsic, genetic trait that predisposes an individual (and their offspring) to being healthy, like a robust immune system. By state-based health we refer to an individual's current state along any of a number of dimensions (such as being nutritionally replete or free of parasites) that can potentially vary over time.

Trait-based health cues and state-based health cues are not readily separable, with many traits potentially providing information about both trait and state health. For example, fat deposits on women would tend to be thought of as a state-based health cue, indicating adequate energy reserves. However, the capacity to effectively utilize nutritional resources and convert them to energy reserves likely varies genetically. So fat deposits on women could indicate both a genetic predisposition to efficiently metabolize food as well as providing reliable information about a woman's current energy reserves.

It is generally presumed that reliable phenotypic signs of health ought to increase perceived attractiveness. The circumstances under which human health cues (or signals) evolved, however, differ from those in which theories of trait-attractiveness-health links are typically tested. So while links between purported health cues and perceived attractiveness are readily reported (and we provide examples of many such cues below), links between purported health cues and objectively measured physiological health are less common. Modern medicine may have erased the

correlation between an ancestrally reliable health cue and actual health by buffering more susceptible individuals. For example, an individual with a weaker immune system would, in the absence of population-wide immunization, have endured a development with substantial disease and pathogen stressors, resulting in high levels of fluctuating asymmetry as an adult. In the presence of population wide immunization, however, that same individual may experience no more developmental stress, and subsequently exhibit no more fluctuating asymmetry, than an individual with a more robust immune system. By dramatically reducing variation in both health and health cues, modern medicine may make relationships between the two difficult to observe.

It is also true that conscious ratings of health (which some researchers have used, as discussed below) might not adequately reflect evolved responses to health-relevant cues. It is possible, for example, that a cue increases attractiveness (because it serves – or served – as a cue to health) without necessarily affecting conscious perceptions of health. Conscious ratings of health may more reliably reflect adaptive responses to state-based cues, rather than trait-based cues, since the former are generally the cues that we have the opportunity to consciously learn about as indicators of health. However, just because a physical trait increases conscious ratings of attractiveness, without increasing conscious ratings of health, should not necessarily rule it out as a potential health cue. Health cues could, in theory, affect attractiveness without us being aware that they are cues of health. Conversely, attractiveness will also be influenced by factors other than health, and so conscious ratings of attractiveness are by no means pure reflections of subjective responses to cues of health.

Cues to Health

A number of traits have been proposed as health cues, including facial traits such as symmetry, averageness, sexual dimorphism, adiposity, skin quality, and skin color, and body cues such as waist to hip ratio (WHR), waist to chest ratio

(WCR), body size, and body composition. As discussed above, while there is good evidence that these traits are perceived as healthy and attractive, evidence that they reliably indicate some aspect of physiological health is more mixed. Here, that evidence is reviewed.

Proposed Cues to Trait Health

A number of studies have shown that observers perceive symmetrical faces as more attractive, with authors speculating that low levels of fluctuating asymmetry reflects a strong immune system and ability to resist stressors such as pathogens and lack of nutrition during development (e.g., Rhodes et al. 2001). However, recent studies, including one using a large longitudinal database, have failed to find reliable connections to childhood health measures (Pound et al. 2014) in a modern industrialized society (UK).

Having a face that is close to the population average is also perceived as healthy and attractive, with authors suggesting that averageness indicates a lack of extreme, deleterious alleles, and some evidence suggesting that people with average faces may have been healthier during childhood and adolescence (Rhodes et al. 2001).

Sexual dimorphism – the femininity or masculinity of faces – has been found to have a role in attractiveness perception and is thought to reflect levels of sex hormones during development. The femininity of female faces is thought to be associated with estrogen levels, which are important in female fertility, and female facial femininity is perceived as attractive (Law Smith et al. 2006). Male facial masculinity, though hypothesized to be an honest signal of health, has shown mixed results, with most studies showing that women have a preference for slightly feminized faces, which may reflect more prosocial qualities (DeBruine et al. 2010).

Proposed Cues to State Health

Skin quality, including skin color (Stephen et al. 2011), has been shown to affect the perceived

health and attractiveness of faces, with redder, yellower, and more homogenous skin coloration being perceived as healthier and more attractive. These cues have been associated with aspects of health and fertility, with skin yellowness reflecting levels of carotenoids – antioxidant pigments obtained from fruit and vegetables in the diet, and which may be associated with improved immune and reproductive systems (Stephen et al. 2011, but see Foo et al. 2017).

Cues to body composition have also been found to play a role in the perception of health and attractiveness, with low WHR (thought to reflect estrogen levels) in women and low WCR (reflecting upper body strength) in men suggested as attractive cues to health. More recently, studies have suggested that body size (defined by body mass index, a ratio of weight over height squared) is more important than WHR (Tovée et al. 1999). However, BMI is a flawed measure of body size, since it conflates body fat and muscle. A recent study separated the influence of the fat and muscle components of body size, finding that men are perceived as healthiest and most attractive when their bodies contain healthy levels of fat and muscle, while women's bodies are perceived as healthiest with levels of body fat toward the low end of healthy, and most attractive with levels of body fat below the healthy range (Brierley et al. 2016). This has been interpreted to mean that while health is important in determining what appears healthy and attractive, some other influence, such as Western media or the association between youth (strongly positively correlated with fertility in women) and low body fat, may also be influencing perceptions of attractiveness.

The Relative Importance of Cues to State and Trait Health

Studies examining the relative contributions of these cues to perceptions of attractiveness have shown mixed results, with some finding that state cues (color) are more important than masculinity (Scott et al. 2010), while others suggest that trait cues, such as averageness, symmetry, or sexual dimorphism (Foo et al. 2017), are more important.

There may well be no one correct answer to the question of which cues are more important. With different cues reflecting different aspects of health, condition, and genetic quality, their relative importance should be expected to differ from population to population. As threats to health (including pathogen and parasite prevalence and nutritional stress) vary, so too should the relative importance to perceivers of cues to resistance to those different threats. Indeed, state and trait cues are difficult to fully disentangle because of the importance of trait (e.g., immunocompetence, ability to metabolize energy) to health state and of (current or past) health state to expression of trait health in the face and body.

Conclusion

Several cues have been shown to be robustly associated with healthy and attractive appearance of human faces and bodies. However, whether they can be considered valid cues to health depends on whether they accurately reflect aspects of underlying physiological health. Research into this second question is less abundant and results have often been inconsistent across studies. Modern medicine and dietary habits may make it difficult to observe relationships between health cues and actual health that were historically – and in some environments, perhaps currently – reliable. Research into the underlying (developmental and physiological) processes that give rise to purported health cues may reveal mechanistic links between such cues and actual health-relevant traits. Such findings would provide more robust and definitive evidence of the validity of health cues than has so far been reported.

Cross-References

- [Body Attractiveness](#)
- [Costly Signaling](#)
- [Costly Signaling Theory](#)
- [Facial Attractiveness](#)
- [Pathogen Load and Attractiveness](#)
- [Physical Attractiveness](#)

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Health Education

► Goals

Health Markers

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Synonyms

Indicator traits

Definition

Health markers are phenotypic traits that signal some aspect of mate quality, and these indicators may be used during mate choice. Health markers are generally considered honest, condition-dependent signals.

Introduction

Mate preference and mate choice in humans is notoriously complex. However, humans are the product of their evolutionary history and, in particular, two key processes: natural and sexual selection. To put this in perspective, we only need think back to our recent history over many hundreds of thousands of years. Under natural selection, traits that increased survival will have been favored. For example, individuals with a more robust immune system would likely live longer perhaps because they are more resistant to parasites and pathogens. And likewise, traits that indicate high quality, such as “good genes,” could be favored during mate choice. Under this scenario, sexual selection will favor particular individuals or genes because they will have higher reproductive fitness. The role of phenotypic traits in sexual selection has been the subject of considerable research in animals (reviewed in Andersson 1994) and, more recently, has gained traction in

evolutionary psychology (e.g., Thornhill and Gangestad 1996; Barrett et al. 2002; Rhodes 2006).

Phenotypic Indicators of Health in Animals and Humans

In animals, many species have dramatic sexual dimorphism such that males may have elaborate plumage in birds (like peacocks), bright coloration in lizards, or large antlers in antelope, to name but a few examples (Andersson 1994). These traits are clearly the target of selection, and they can be easily measured although what they may signal to a potential mate is far more difficult to discern. On the one hand, a sexually dimorphic trait may be arbitrary such as in the case of Fisherian runaway selection (Andersson 1994), or alternatively, it may be condition-dependent and signal quality (Hamilton and Zuk 1982). In the case of humans, while females are still the limiting sex (i.e., females are more choosy than males), male traits are perhaps not as obvious as in the animal kingdom. This raises two important questions. First, what male traits are important to females when they choose a mate, and second, what do these traits signal to a potential mate? Likewise, we should also ask what female traits are important to males because while females may be more choosy than males, male choice can play a significant role in fitness.

Physical Traits, Symmetry, and Mate Preference in Humans

Particular physical features are found to be attractive both within and across cultures (Langlois et al. 2000). While humans may use a wide range of traits linked to socioeconomic factors, personality, trustworthiness, etc., the focus here will be on phenotypic traits that signal health or quality. One commonly used measure of quality is fluctuating asymmetry (FA), which is a random deviation from perfect bilateral symmetry. Individuals with higher levels of FA are thought to reflect developmental instability – an inability to deal with environmental stressors during

development (Thornhill and Gangestad 1996). Measures of FA are influenced by exposure to pathogens or environmental contaminants, poor nutrition, parasite load, and numerous other factors (Rhodes 2006). Therefore, individuals with higher symmetry are considered more attractive and in better condition/health. In humans, body and facial symmetry are two sources of information available during mate choice.

Symmetrical human bodies are preferred and are likely condition-dependent because they are less likely to be associated with psychosis, premature birth, and inbreeding (Livshits and Kobylanski 1991). Similarly, among women with relatively large breasts, individuals with lower FA were more fecund (i.e., had more children; Møller et al. 1995). While this result suggests that breasts are sexually selected via male preference for larger breasts, more detailed study is required to determine the nature of breast FA relative to health.

The relationship between attractiveness and facial symmetry in humans has received considerable interest in the last two decades, particularly given the ease with which images can be quantified and manipulated on a computer (Rhodes 2006). Importantly, computer-generated images allow for the control of a wide range of confounding traits such as skin, hair, and eye color. So, do humans find symmetrical faces more attractive? It turns out that it depends on the method used to generate a choice of two computer images in which one of them shows less symmetry. In early studies a mirror image was created of one half of a face that was mirrored across a vertical midline (termed a chimera). This technique was later shown to be unreliable because it resulted in some distortion of features (see Rhodes 2006 for details). A more recent technique is facial blending, which produces a more reliable end-product. The two methods yield different results. Humans find symmetrical faces more attractive when the images are produced using facial blending but not when they are produced as chimera images. But do symmetrical faces signal FA, which theoretically is an important index of mate quality? Or, put differently, does facial symmetry signal health in humans? FA in humans is controversial, and

there are instances where studies have claimed to measure FA, but did not, or did not meet other essential criteria such as demonstrating repeatability. In a recent review, Rhodes (2006) concluded that there is little evidence that facial symmetry signals health, and recent meta-analyses have likewise come to this conclusion with respect to nonhuman animals. There is still work to be done before we can say unequivocally that facial symmetry reflects underlying health, but it is an intriguing hypothesis.

Condition-Dependent Signals and the Role of MHC and “Good Genes” in Mate Preference

Immunocompetence, or the strength of an individual’s immune system, has been touted as a target of selection because having offspring with a robust immune system is likely to raise inclusive fitness. This may be accomplished by selecting a mate with a complementary immune system in order to increase major histocompatibility complex (MHC) diversity (the genes governing immune responses; Winternitz and Abbate 2015). Put another way, humans should prefer MHC-dissimilar or MHC-diverse mates because a polymorphic MHC is a better tool kit with which to deal with rapidly evolving parasites and pathogens. It is of course more complicated than simply selecting a mate with a dissimilar MHC because there might be an optimal MHC diversity or there may be a specific MHC that correlates with “good genes” at that moment in time (reviewed in Winternitz and Abbate 2015). But how would an animal or a human know that a potential mate has an appropriate MHC complement? One possibility is that MHC is linked to a cue that is easily accessible to a receiver. In the case of humans, body odor has been linked to MHC such that favorable MHC genes correlate with more attractive body odor. Visual cues may also play a role. For example, men that were heterozygous in three loci for MHC genes were also rated as having more attractive faces than males that were homozygous at one or more of these loci (Roberts et al. 2005). While MHC condition-dependent mate preference in humans has been

controversial, the variation in results can in part be explained by differences in methods, and the weight of evidence is in favor of MHC preference playing a role in sexual selection (Winternitz and Abbate 2015).

Sexual Dimorphism in Facial Traits, Attractiveness, and Indicators of Health

During and after puberty, sexual dimorphism in facial and body features becomes more pronounced as testosterone levels rise in males and females suppress testosterone through estrogen production. Although testosterone plays a key role in reproduction, it is thought to suppress immune responses and therefore comes at a cost. At the same time, relative testosterone levels can be apparent in facial features. During and after puberty, males with higher levels of testosterone may develop higher cheek bones and more pronounced jaws (Winternitz and Abbate 2015). These traits may honestly signal health because males are able to pay the cost of expressing these traits although testosterone is immunosuppressive. Females are therefore predicted to prefer males with these traits. Indeed, populations or cultures from areas of greater parasite/pathogen prevalence place more weight on attractiveness (Gangestad and Buss 1993). This particular study used 37 different societies from six continents and five islands. Participants were asked to rate attractiveness using 18 traits, and this was assessed in relation to the prevalence of seven key pathogens prevalent in humans. Interestingly, this result held true for both sexes even when a range of confounding variables, such as average annual income, latitude, and geographical region, were controlled for.

Conclusion

While a great deal of research has focused on human evolutionary psychology in the past two decades, the field has a long way to go. In part, this has to do with some of the constraints of working on humans in a modern society with easy access to modern medicine and pharmaceuticals. For

example, taking birth control pills alters hormone profiles and may influence mate preference. Nevertheless, the ease with which we can sequence genomes and manipulate imagery for mate preference trials also means we have better tools with which to answer key questions.

How much evidence is there for condition-dependent, or health, signals in humans? As it turns out, the evidence is scattered and not substantial. First, the jury is out on whether facial symmetry, which is thought to be more attractive, is in fact an indicator of health. However, there is evidence that more attractive individuals have greater heterozygosity, which is linked to immunocompetence. Therefore, if females prefer males with more attractive faces and these males are heterozygous at MHC loci, there could very well be fitness benefits to such traits/health markers. Furthermore, attractiveness is also more important in societies where the risk of pathogen transmission is greater. Again, mate choice in these systems could be relying on health markers. Finally, aspects of body symmetry are linked to traits that influence fitness.

We particularly need more studies on societies far removed from Western influence where resources are more limited and, therefore, where health markers may be particularly informative with respect to fitness.

Cross-References

- [Intersexual Selection](#)
- [Intrasexual selection](#)
- [Natural Selection](#)
- [Sexual Selection](#)

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Definition

The sensory process by which auditory stimuli are perceived as sound waves by the ear(s) and then translated to neural signals and comprehended by the brain.

Introduction

The ability to hear (audition) is an impressive skill that differs greatly among species. For humans, the level of auditory discrimination that has developed over time has evolved not only due to outside influences of everyday noise, but also as a result of hearing's role in humans' complex speech and language production and comprehension. Hearing involves external and internal structures, as well as physiological processes that enable sound processing.

H

Healthy Sexual Development

► Positive Sexual Development

Healthy State

► Good Health and Stable Future

Hearing

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Synonyms

Audition; Auditory perception; Auditory system; Aural perception

The Auditory Process

Essentially, the process of audition is catalyzed by changes in air pressure from the normal surrounding atmospheric level, which are the result of a stimulus such as noise from an object creating patterns of molecule vibrations in the air (Zemlin 1998). This change in air pressure results in sound waves, which project outwardly from the source. The sound waves are perceived first by the larger part of the ear called the pinna (outer ear), during which the sound waves are transmitted through the auditory canal. The sound waves reach the eardrum (tympanic membrane) through the Eustachian tube, which vibrates and passes the waves through the three small bones of the middle ear (malleus, incus, and stapes). The higher order processing of sound occurs in the inner ear, which contains the cochlea and hair cells in the organ of Corti that are responsible for transforming sound waves into neural signals and transmitting the signals into the brain via the auditory nerve. The auditory nerve, in conjunction with other cranial nerves, delivers the neural signals to several areas of the brain. First, the primary auditory cortex within the left posterior superior temporal gyrus receives sound input. Sound input is then passed

through secondary areas of the brain and the frontotemporal lobe, which is important for discriminating sounds as speech and nonspeech.

Hearing and processing speech sounds for humans have resulted in the development of mostly left-lateralized areas known as Broca's and Wernicke's areas, which are connected by a nerve fiber bundle called the arcuate fasciculus. These three entities form an important loop for speech production and comprehension in real-time through near-simultaneous comprehension and production, which is seamless in normally functioning auditory systems.

Evolutionary Anatomy of Hearing Structures

The most apparent observation that can be made about the evolution of the ears and auditory system in reptiles, mammals, and humans, aside from contributing to equilibrium and balance, is that they have developed over time to enable maximum awareness of auditory stimuli in the environment. This plays a role in readiness to respond to potential threats and make other important observations regarding safety, such as detecting the presence of others. In reptiles and earlier mammals, deeper auditory structures were present prior to outer structures developing (Webster and Fay 1992); as such, the pinna (outer ear) developed after the middle and inner ear, with the main purpose of enhancing the capture of sound to be processed by the deeper parts of the ear. In fact, recent research has established that the small bones of the ear in humans and other land mammals originated from gill structures that earlier vertebrates used to breathe under water (Brazeau and Ahlberg 2006).

Similar to other features in the human anatomy, the auditory system contains some vestigial structures that no longer dictate any auditory function. The auricular muscles of the outer ear, which in other mammals enable directional movement of the ears to better position the pinna to capture sound, are unnecessary for human audition due to the ability to manipulate positioning of the skull to further locate sources of sound (Hackley 2015).

Evolutionary Process of Discriminatory Properties

Humans can detect and discriminate between a great number of frequencies due to the highly developed auditory system. Due to the variety of speech sounds produced by humans, the complexity of verbal speech is matched by the development of heightened auditory ability in order to process all possible sounds in the social, as well as general surrounding, environment (Fritzsche et al. 2013). The ability to hear other humans' speech enables social interaction that is predicated on speech; goal-based group interaction, one-to-one conversation, and parent-child dyadic interactions are examples of important social relationships enabled by the auditory system's discriminatory capacity.

Conclusion

The evolution of human audition has not only enabled *Homo sapiens* to survive in response to hearing potential threats, but also enables speech sound discrimination essential to social interaction, which may facilitate group behavior and belongingness. The continuous improvement of technology has enabled in-depth study of the bone structure of the ear in the fossil record. Continued technological advances will likely enable even more discoveries regarding human hearing and its evolution.

Cross-References

- [Communication and Developmental Milestones](#)
- [Development](#)
- [Developmental Milestones](#)
- [Evolution of Hearing and Balance](#)
- [Evolution of the Brain, The](#)
- [Language Acquisition](#)
- [Language Development](#)
- [Physiological Mechanisms](#)
- [Physiological Responses](#)

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Heart Pound

► [Heart Rate](#)

Heart Rate

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Synonyms

[Cardiac Rate](#); [Heart Pound](#); [Heartbeat](#); [Pulsation of the Heart](#); [Pulse rate](#)

Introduction

Love is heartbeat of life – *Lailah Gifty Akita*. The human heart is the symbol of love and emotions since ancient times. When we see our beloved, our heartbeats get faster and stronger in response to chemicals release from the brain (Freud Nour 2017). It is a vital organ which circulates the

blood in our body. It is located in the chest cavity in between our lungs and is the size of human fist. It pumps approximately 5 l of blood every minute. It carries oxygenated blood via arteries to the tissues and deoxygenated blood to the lungs via veins. Heart rate is one of the important vital signs and is measured by no. of contraction of the heart in 1 min and varies according to the physical need of the body (*Heart Matters* 2013). Changes in the heart rate can occur by some activities such as anxiety, depression, anger, physical exercise, drugs, disease or infection, and sleep. **According to American Heart Association**, normal resting adult human heart rate is 80–100 beats per minute (*American Heart Association* 2014). Normal fetal heart rate is 120–160 bpm in the in utero period. It can be measured by sonography from around 6 weeks, and the normal range of FHR varies during gestation (Nijhuis 2003). Electrical activity of the heart can be measured by electrocardiogram (Mason et al. 2007). Tachycardia refers to a fast resting heart rate, usually more than 100 beats per minute and when the heartbeats gets too slow, usually slower than 60 beats per minute, called bradycardia. When the heart rate is not beating in regular pattern, arrhythmia occurs (Jensen et al. 2013). An increased resting heart rate is an independent risk factor for mortality and a marker of poor general fitness and cardiorespiratory fitness (Jensen et al. 2013). It is directly associated with indicators of cardiovascular diseases such as hypertension, hyperlipidemia, etc.

Definitions

Heart Rate

According to NCI Dictionary of cancer terms, the number of times the heart beats within a certain time period usually a minute. It can also be defined as number of contractions of the heart ventricle (ventricles are lower chamber of the heart) per minute.

Contractions: **According to Merriam-Webster (1828)**, the shortening and thickening of a function muscle or muscle fiber.

Ventricle

According to WebMd, ventricles are lower pumping chambers of the heart. Heart has two ventricles – the right and left ventricle.

Is There Any Difference Between Heart Rate and Rhythm?

Heart rate is no. of beats per minute, while heart rhythm is regularity of rate or the pattern in which heart contracts. Normal heart rhythm is also known as sinus rhythm. Abnormal heart rhythm is called as arrhythmia which means heart is beating very fast or too slow or rhythm is irregular (Ine van loo 2019). The symptoms may be feeling of skipped a beat or added a beat or beating too fast or beating too slow. The heart has electrical or cardiac conduction system which is group of specialized cardiac muscle cells where electrical impulse is generated (in the SA node or natural pacemaker of the heart), and it sends signals to the heart muscle causing it to contract and to pump blood to the lungs and to the body. The electrical activity of the heart can be detected by electrocardiogram or ECG (Kléber and Rudy 2004). When there is problem with this system, person may feel arrhythmia. The symptoms may be like palpitation, dizziness, breathlessness, loss of consciousness, lightheadedness, etc.

Source of a Pulse: The Heart

Heart is a muscular pump, and a heartbeat is a contraction of the heart's muscle, forcing blood to move in the body through arteries. An electrical impulse causes the cardiac muscle to contract. An average healthy adult heart rate is 60 to 80 beats per minute. For older adults, normal is considered 60 to 100 beats per minute. Women generally have a higher rate than men (Heart Matters 2013).

The Result of Heartbeat: Pulse

A pulse is the expansion and contraction of an artery caused by the ejection of blood from

the left side of the heart. At certain points it can be easily felt (palpated) such as in the wrist (radial) or in the neck (carotid) of adults and older children. In infants and younger children, it can be palpated in the upper arm (brachial) (WebMd 2013).

So, pulse rate is same as heart rate. It varies from person to person.

Genes Affecting Heart Rate

Heart rates are affected through various physiological mechanisms. The predisposition of heart rates not only is wired by physiology but is deep rooted in the genetics. Studies have suggested a large number of genes associated with inheritable capacities generated by exercise. These genes (CDC141, PAX2, SOX5, and CAV, RNF220 and MCTP2, SCN10A and RGS6) are related to four basic attributes, neuronal development, cardiac development, cardiac rhythm, and neuronal life span (van de Vegte et al. 2019).

Arrhythmia

It is also known as cardiac arrhythmias; dysrhythmias or heart arrhythmias are a group of condition in which heart contracts too fast/too slow or with irregular pattern (Kobayashi 2018). Dysrhythmias are grouped from where they occur – in the upper chambers or receiving chambers of the heart (known as the right and left atrium of the heart), in lower chambers or contracting chambers of the heart (right and left ventricle of the heart), or in both chambers (Antzelevitch and Burashnikov 2011).

Bradycardia/Bradyarrhythmia

When the heart rate goes less than 60 bpm, it is known as bradycardia (Brazier n.d.). It occurs when the electrical signals are not formed into the SA node or are not sent to the lower chambers via proper channels. It can cause feeling of dizziness, weakness, lack of energy, or fainting

spells. The diagnosis can be made by doctors by evaluating the ECG, and the main treatment is implanting the pacemaker which is a device that generates the electrical impulses to regulate the heartbeat (*Heart rhythm society* 2015).

Tachycardia

When the resting heart rate is more than 100 bpm, it is known as tachycardia. Many forms of tachycardia depend upon where the heart rate begins. Series of rapid heartbeats that begin in the ventricles are known as ventricular tachycardia and if these fast heart beats starts above the ventricles, it is known as supraventricular tachycardia (Brazier n.d.).

Supraventricular Arrhythmia

Arrhythmia that starts in the atrium or upper chambers of the heart and heartbeat are above 100 bpm at rest. It is very common and less dangerous than ventricular arrhythmias (Tse 2016).

- **Atrial flutter:** it happens when the atria beat very fast causing the ventricle to contract insufficiently as well.
- **Atrial fibrillation:** it occurs when the atrium of heart contracts in irregular pattern and out of synchrony with lower chambers. It is the main cause of stroke, especially in elderly people.
- **Paroxysmal supraventricular tachycardia (PSVT):** this type of arrhythmia begins and ends suddenly. It can happen during vigorous physical activity, tends to occur in young people, and is usually not dangerous (Kobayashi 2018).
- **Premature/extra beat:** when the atrium contracts too soon, causing the heart to beat out of sequence, it leads to atrial premature contraction.

Ventricular arrhythmia: it starts in the ventricles, and these types of arrhythmia are very

dangerous and usually require emergency medical care (Sloman et al. 1971).

- **Ventricular tachycardia:** This type of arrhythmia is rapid, regular heartbeat usually more than 100 bpm lasting for few seconds or longer, and it prevents the ventricles from fully contracting resulting in less supply of blood (Ma et al. 2009). If immediate proper attention is not given, it may result in more lethal form of arrhythmia (Jordaens 2018).
- **Ventricular fibrillation:** Ventricular fibrillation is an abnormal heart rhythm in which disorganized electrical signals leads to the quivering of the ventricles instead of pumping normally and ventricle fails to pump the oxygenated blood to the brain & body resulting in to the sudden cardiac death or cardiac arrest. It is the most dangerous form of arrhythmia (Tse 2016).

Heart block is a type of arrhythmia in which the heart contracts too slow (bradycardia). Usually the electrical signals start in the SA node of the heart which is located in the right atrium and travels to atrioventricular node (AV node) and from AV node to wirelike structure To Bundle of HIS into the right and left ventricle of the heart, and they reach down to the bundle branches into the muscle wall of ventricles causing ventricles to contract (Kléber and Rudy 2004). If the electrical signals block in any step of this conduction, system leads to heart block (Brazier n.d.).

- **First-degree heart block:** it is the least serious type of heart block and usually does not require medical care. In this type of block, the electrical impulses are slowed as they pass through conduction system, but they all successfully reach to the ventricles causing the ventricles to contract (Levis 2011).
- **Second-degree heart block:** the electrical impulses are delayed further and further with each subsequent beat until a beat fails to reach ventricles entirely causing dropped or skipped beats. The person may feel dizziness, and they need pacemaker (Lim et al. 2018).

- **Third-degree heart block:** Complete heart block occur when electrical signals don't travel between upper and lower chambers of the heart. It is usually treated by implanting a permanent pacemaker (DiFrancesco 1993).

Treatment of Dysrhythmia

There are some tests for arrhythmia such as electrocardiograph (ECG), electrophysiological studies (EPS), Holter monitoring, echocardiogram, etc. that help to diagnose an abnormal rhythm of the heart (Jordaens 2018). Depending on the type of abnormal heart rhythm, the doctor recommends the medications (also called as anti-arrhythmic drugs) (Ganjehei et al. 2011), minor invasive procedures (like catheter ablation in which catheter is inserted into the heart via blood vessels to destroy the tissues in the heart which are allowing electrical signals to cause abnormal heart rhythm), implantable devices (such as pacemaker and implantable cardiac devices), and cardioversion (is a treatment modality in which controlled electrical shocks given to convert abnormal rhythm to normal rhythm) or defibrillation to prevent and or control it (Sloman et al. 1971).

Emotional State of the Mind and Role of Heart

The heart is not a merely organ which pumps the blood to the body, but it also sends the message to our brain about our emotional status. Earlier psychologist believed that emotions are purely a brain-generated mental expressions, but now many studies have found that there is a critical link between the heart, brain, and emotions. Many psychological factors such as grief, depression, anxiety, anger, hostility, loss of loved one/job, etc. contribute to poor heart health and cardiac diseases (Radcliffe Shawn). There is a two-way relationship between depression and heart disease (*National Heart, Lung, and Blood Institute* 2017). It has been linked to low-grade inflammation in blood vessels, which leads to

clogging or hardening of arteries and the rupture of cholesterol-filled plaque and also increases the production of stress hormones which increases the workload of heart by increasing the demand of blood flow. It activates platelets (a type of blood cell), making them more likely to clump and form clots in the bloodstream which finally leads to many cardiac problems like coronary heart diseases and heart attack. Depression also increases the risk of behaviors associated with poor physical health and unhealthy behaviors like smoking, drinking, physical inactivity, inappropriate coping skills to stress which can further lead to hypertension, arrhythmia, and heart failure (Smith n.d.). In the same way, people after cardiac surgery, heart attack or with any cardiac disease may have stress or poor response to stress, social isolation, low mood which are common and temporary for the first few weeks of recovery, but unmanaged stress can further increases the severity of depression and other mental problems (*Cleveland Clinic* n.d.). Everyone feels stress in different ways and reacts to it in a different way. Reducing stress or changing the response to stressing situation and maintaining the healthy lifestyle which includes physical activity, well-balanced healthy diet, and avoiding alcohol and smoking can actually lower the risk of cardiac diseases and better mental health (*American Heart Association* 2014).

Heart Rate and Heart Rate Variability

Heart Rate Variability

Heart rate variability (HR) is the time interval between two consecutive heartbeats. HRV is also known as interbeat intervals, R-R intervals, N-N intervals, etc. It is affected by a no. of factors such as age, pattern of lifestyle, diet, exercise, response to stress, etc. It is one of the indicator of health and disease stats of human body (ChuDuc et al. 2013). The intervals between beats are constant but vary between beats to betas; HRV can be used as a biomarker to indicate the influence of nutrition on mental and physiological health. An increased HRV is related to better general health, while decreased variability leads to a no. of

diseases which include diabetes, cardiovascular diseases, and psychiatric disorder. A study showed that a low HRV contributes to poor prognosis in patients who had survived after heart attack (Malik and Camm 1990). A well-balanced diet which includes Mediterranean diet, omega-3 fatty acids, B vitamins, probiotics, polyphenols, etc. can increase HRV, while high intake of saturated fat, flavored/processed food, alcohol, etc. is found to reduce HRV (Young and Benton 2018).

Evidences show that regular physical exercise has a significant impact on HRV. In healthy as well as patients with cardiac disease, regular aerobic exercise results in improvement of heart rate variability, and HRV can be used as diagnostic marker of overexercise and overtraining (Hottenrott et al. 2006), with increasing age function of heart decreases and leads to more cardiac events and morbidity and mortality related to cardiovascular diseases. Regular physical exercise in older people increases HRV, and a higher HRV is associated with high cardiovascular fitness and psychological health (Routledge et al. 2010).

Heart Rate Variability and Psychiatric Disorders

Cardiovascular diseases (CVDs) and mental illness are the most common cause of morbidity and mortality worldwide. CVDs are group of disorder which affects heart and blood vessels which includes coronary artery disease, chronic heart failure, arrhythmias, hypertension, etc. They account for 50% deaths in developed countries and 25% deaths in developing countries. The prevalence of neuropsychiatric illness and use of psychotropic drugs are equal (Shah et al. 2004). There is a strong relationship between CVDs and psychiatric disorders (Bacon 2019). Evidence suggest that people with mental disorders like schizophrenia, bipolar disorder, post-traumatic stress disorder, and anxiety disorder have an increased risk of developing coronary heart diseases (De Hert et al. 2018). Heart rate variability is changes in time intervals between consecutive heartbeats. Patients with depression without any cardiac diseases have low HRV which further

decreases with severity of depression and use of some antidepressants (Kemp et al. 2010). Depression has also an effect on fetuses of pregnant lady. A study showed that the fetuses of non-depressed women have high HRV as compared to women who had prenatal depression (Figueiredo et al. 2017).

Conclusion

The best and most beautiful things in the world cannot be seen or even touched – They must be felt with the heart – Helen Keller. Human heart is a pumping machine which provides oxygen and nutrients to the body and removes carbon dioxide and other wastes. It is also a seat of human emotions and feelings. Cardiac diseases are the leading cause of death for both men and women worldwide. For a healthy heart, one must have a healthy lifestyle (avoid smoking and heavy drinking, proper sleep, etc.), a well-balanced diet (such as use of healthy fats, whole grain, plenty of fruits and vegetables, plenty of water, etc.), regular exercise, and health checkups. Take care of your heart, and your heart will take care of you.

Cross-References

► [Polyvagal Theory](#)

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Heartbeat

- [Heart Rate](#)

Hedge Sparrow Mating System

- [Study of Dunnock Mating, The](#)

Heidelberg Man

- [Homo heidelbergensis](#)

Height and Dominance

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Synonyms

[Hierarchical position](#); [Length](#); [Size](#)

Definition

The relationship between height and dominance refers to a position in a hierarchy based on body height.

Introduction

In many mammalian species, dominance is positively associated with body size. All else being equal, larger individuals should be more likely to win than smaller individuals in contests. Building on findings from the animal kingdom, evolutionary psychologists have argued for similar associations between body size and dominance in humans. Indeed, it seems that both historically and cross-culturally body size is believed positively associated with dominance. One often noted example is that political leaders in Melanesia and Polynesia are referred to as “big men,” and they are often physically big men (Sahlins 1963). Similarly, today, in Western societies, positive associations between stature and political leadership exist. For example, ratings of American presidents’ leadership abilities positively correlate with their stature. Intuitively, one would therefore speculate that across the globe, dominance positively relates to height. In this encyclopedia entry, one aspect of body size, height, is discussed, and the evidence for a positive association between stature and interpersonal dominance is briefly reviewed.

Height and Dominance

Dominance interactions in humans remain understudied, and evidence for a positive relationship between height and dominance thus remains rather circumstantial. For example, research suggests that taller individuals might have more strength (Vaz et al. 2002), have better fighting ability (von Rueden et al. 2008), and are able to generate a larger force when striking (Carrier 2011) than shorter individuals. Taller individuals are also perceived as more powerful and stronger than shorter individuals (e.g., Huang et al. 2002). The reverse also holds that more powerful individuals are estimated as being taller (e.g., Fessler et al. 2012). Tallness also is found to be positively associated with perceived leadership qualities (Stulp et al. 2013). Taller individuals might have more authority in business settings (Judge and Cable 2004) or sports (Stulp et al. 2012). Finally, only a few studies have studied actual behavior which can be labeled as dominant in naturalistic

settings, such as having “right of way” (Stulp et al. 2015). For example, when faced with a narrow passage, taller individuals are more likely to take precedence than shorter individuals, all else being equal.

Conclusion

In conclusion, various strands of evidence corroborate the claim that tallness is positively associated with dominance. Yet, it is important to bear in mind that height is clearly correlated to a whole suite of other traits, including socioeconomic status, and as such teasing apart the independent effect of size itself for dominance could be difficult (especially given that we cannot experimentally manipulate human height directly). Moreover, it should be noted that any relationships found between height and interpersonal dominance tend to be weak. Perhaps, unsurprisingly muscularity appears to be a better correlate of interpersonal dominance, at least in perception studies (e.g., Sell et al. 2012). Finally, it must be noted that there is actually not that much research on height and dominance and that it is mostly limited to men. Therefore, while Western societies might have fewer dominance interactions due to the state monopoly of violence, height and dominance remain an interesting domain for further investigation, but studying the role of stature in dominant behavior in a naturalistic setting might prove challenging.

Cross-References

- Aggression
- Body Posture
- Costs of Aggression
- Dominance in Humans
- Men in Positions of Power
- Sexual Dimorphism

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Helper at the Nest Among Nonhuman Primates

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Definition

A helper is an individual that contributes to breeding by conspecifics through providing alloparental

care. The helper may be nonreproductive, or its own reproduction may have failed.

Introduction

In the majority of primate species, infant care is provided solely by mothers, although other group members may interact with infants and carry them for short periods. In some pair-living primates, social/genetic fathers may provide paternal care. Particularly in night monkeys and titi monkeys, males are the principal infant carriers, while the contribution by helpers is negligible (Huck and Fernandez-Duque 2012). Regular helping behavior through transport of and food sharing with infants occurs in marmosets and tamarins, of the New World primate family Callitrichidae. Callitrichids (except Goeldi's monkey) are characterized by flexible mating systems, including polyandry (particularly in tamarins), monopolization of reproduction by a single female per group, and twin births (Goldizen 1988). The energetic costs of carrying twins which at birth may correspond to 15–20 % of maternal body mass have been postulated as a driver for the evolution of the helper system in callitrichids (Goldizen 1990).

How Do Helpers Help?

In callitrichids, helpers basically provide two types of infant care: transport and food sharing. Transport is by carrying infants on the back. During the first weeks of life, twins are usually carried together, but when they become heavier are transported separately. Infant carrying ceases after 3–4 months of age; thereafter helpers carry infants only in case of danger (e.g., predatory threats).

Food sharing extends for almost the entire first year of life, although it diminishes in frequency when offspring become older. Shared food mainly includes prey (arthropods, small vertebrates) that infants are not yet capable to capture and fruits that require force for opening the husk. Food sharing may be passive through not resisting “stealing” by infants, but in some callitrichids, food may actively be offered, including the emission of “food calls.”

Is Helping Costly?

As infant body mass is high in callitrichids, it can be reasonably assumed that their transport incurs energetic costs. In fact, captive studies have demonstrated that helpers lose body mass during periods of infant carrying (Sánchez et al. 1999). Changes in activity budgets, particularly the reduction of feeding and foraging, in wild callitrichids suggest similar energetic costs (Huck et al. 2004). It is conceivable that infant carrying might also reduce the speed of escape, thus increasing the risk of predation for helpers.

Why Do Helpers Help?

The costs incurred by helping must be compensated by benefits to maintain this behavior evolutionary stable. By helping with the rearing of younger siblings, helpers may gain inclusive fitness benefits. High levels of intragroup genetic relatedness suggest that such benefits might indeed be realized (Huck et al. 2005). However, intensive helping has also been observed in individuals unrelated to infants, suggesting that other benefits must be realized as well. Such a benefit could be an increased probability of survival by remaining in a group until opportunities for own reproduction emerge; helping could then be a form of “pay to stay.” Inheritance of breeding positions by female helpers suggests that such a benefit can also apply (Goldizen et al. 1996).

Helpers may receive more allogrooming from reproductive females (“pay for help”; Lazaro-Perea et al. 2004) which renders social, psychophysiological, and/or hygienic benefits as an additional possibility. Whether or not helpers can benefit from gaining rearing experience for own later reproduction is contended.

Does Helping Make a Difference?

Several studies, both in captivity and in the wild, have shown a relationship between the number of helpers present in a group and the probability of infant survival (Culot et al. 2011; Rothe et al. 1993). Group productivity can thus be increased by

helping, although the ideal measure for such an effect would be the amount of help received per infant rather than the number of helpers.

Helpers in Other Primates

Primate infants are generally attractive to other group members, including older siblings, but also related and unrelated adults who may handle, play, or carry infants. This is particularly noteworthy in capuchins and squirrel monkeys (Huck and Fernandez-Duque 2012), the closest phylogenetic relatives of the callitrichids. However, the amount of maternal care always exceeds the care provided by others, unlike callitrichids, and so far there is no evidence for an influence of the number of caretakers on infant survival.

A special case is grandmothering: post-reproductive females caring for the offspring of her daughters. Grandmothering has been observed in some nonhuman primate species.

Conclusion

Among nonhuman primates, helpers at the nest in the strict sense are uniquely found among the New World marmoset and tamarin monkeys. Helpers provide transport and food for heavy infants to whom they may or may not be related. Benefits of helping may mainly rest in inclusive fitness gains and increased survival by remaining in a group. Helping may increase the probability of infant survival.

Cross-References

- [Alloparenting](#)
- [Breeding Systems](#)
- [Food Sharing](#)
- [Grandparenting](#)
- [Helping and Genetic Relatedness](#)
- [Helping and Inclusive Fitness Benefits to Helper](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Primate Cooperation](#)

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Helpers at the Nest

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Definition

A breeding system in which offspring from the previous breeding period remain with the parents and play a role in raising young.

Introduction

The term helpers at the nest is typically applied to species in which young animals of both sexes delay dispersal and remain in their home territory through at least one breeding cycle. The proportion of young remaining and the period of time that they spend as helpers are both variable. As the name suggests, the phenomenon has been recorded most often in birds with examples known in over 200 species (mostly monogamous, passerine species). Among mammals, the system is seen in most members of the dog family (Canidae) and many marmosets and tamarins (Callithridae) and sporadically elsewhere, e.g., beavers (*Castor canadensis*). There are a few examples from fish (Hatchwell and Komdeur 2000). The term is sometimes applied to communal breeding systems with delayed dispersal predominantly by one sex. In this context, it has been applied to social insects and to humans.

Main Text

The evolutionary costs and benefits to helping need to be analyzed in terms of inclusive fitness where costs and benefits apply both to the individual involved (direct fitness) but also that individual's effects on the reproductive success of genetic relatives (indirect fitness). Indirect fitness is usually a product of altruistic behavior (usually feeding the offspring of other individuals). Some of the first and most detailed studies of altruism directed at kin (kin selection) come from species with helpers at the nest.

Helpers do all the caring behaviors of their parents notably protection (babysitting and chasing predators), carrying young (especially in marmosets and tamarins), and playing with young. However, the commonest and probably most useful action is providing food (often by regurgitation).

Do helpers help? The majority of studies with good quantification show increased fitness of young when helpers are present. However, help can depend on current resources. In African wild dogs (*Lycaon pictus*), there is an overall positive

correlation between pup survival and number of helpers. However, in a time of food shortage the helpers stole food regurgitated to the pups (Malcolm and Marten 1982). In several species, the parents contribute less in the presence of helpers and may benefit from enhanced survival (Heinsohn 2004).

Under what circumstances does helping behavior evolve? Helping depends on the balance between the direct and indirect components of fitness. However, it seems that in most cases the direct components are more important. Direct fitness depends on the chance of successful emigration versus the benefits of stay in the natal territory. Helping is usually seen in saturated habits where there is very limited opportunity for successful dispersal. The benefits of not dispersing can be enhanced through the opportunities for care for siblings, but animals seldom appear to forgo a chance to disperse and have the opportunity to raise their own offspring.

Conclusion

The retention of offspring into the breeding group is a feature of most forms of cooperative breeding. Helpers at the nest is a term for this philopatry mainly studied in birds. Breeding systems with helpers at the nest have yielded some of the most detailed information on inclusive fitness theory.

Cross-References

- [Alloparenting](#)
- [Alloparenting and Female Same-Sex Behavior](#)
- [Communal Breeding](#)
- [Cooperative Breeding](#)
- [Higher Survival with Older Siblings](#)

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Helping

- [Cooperation Among Fishes](#)
- [Primate Cooperation](#)
- [Prosocial Behavior](#)
- [Reputation and Altruism](#)
- [Selection for Cooperative Relationships](#)

Helping and Genetic Relatedness

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Synonyms

[Altruism](#); [Assessing genetic similarity](#); [Degree of relatedness](#); [Evolution of altruism](#); [Extended phenotypic effect](#); [Familiarity-based kin recognition](#); [Greenbeard effect](#); [Hamilton's rule](#); [Inclusive fitness](#); [Kin altruism](#); [Phenotype matching](#)

Definition

Helping can be defined as a voluntary act which directly or indirectly benefits an individual; the helper may be rewarded or unrewarded or pay a price for helping. In evolutionary psychology, for these forms of prosocial behavior the concept of altruism is used. Altruism differs from helping in that there is no expectation of a return. In other words, altruism is behavior which increases the fitness of the recipient at a cost to the actor (reducing the fitness of the actor), who does not expect to be rewarded (Barcaly 2011). Altruism is

an evolutionary puzzle: a trait that appears to reduce the fitness of the individual who possess it. One would expect that natural selection operates against helping others at a cost to oneself, because such behavior probably reduces the resources the altruistic actor has available for survival or for reproduction. The mechanism by which altruism could have evolved is puzzling.

Introduction

Hamilton was the first to demonstrate that a fitness-reducing trait could spread in populations if it had sufficient *extended phenotypic effects*; in other words if a trait produces beneficial outcomes for other members of the same species, who presumably possess the same trait due to genetic relatedness, it can be adaptive. Thus, Hamilton connected kinship to altruism, suggesting a new perspective on evolutionary success: *inclusive fitness*. The evolutionary success of a gene depends on the number of copies of itself it leaves in the next generation, i.e., the maximum number of viable, direct offspring of the individual possessing the gene. Hamilton argued that, to some extent, other members of the population share identical genes so a gene may also increase the number of its copies by indirect reproduction. More specifically, according to Hamilton our genetic relatives (e.g., not only parents, siblings but aunts, uncles, etc.) have the same version of genes or alleles we have in proportion to the ratio of our common ancestors. The support of the reproduction and survival of individuals who may possess the same genes (traits) as oneself (i.e., family members or genetic relatives) increases one's evolutionary success. Without doubt close relatives or kin have the highest number of identical genes. Inclusive fitness can be defined as the result of the number of offspring produced directly by an individual plus his or her contribution to the reproductive success of genetic relatives (Hamilton 1964). For example, the alarm call of belding ground squirrels can be explained by this model. An individual squirrel gives an alarm call to warn others in the local group of the presence of a predator; this act puts the

alarm-sounding squirrel at a disadvantage because the call signals its location to predators, increasing the likelihood that it will be killed; however, by sounding the alarm the squirrel protects its relatives and others in the local group. Belding's ground squirrels live as groups of close genetic relatives, and in this context sounding the alarm can enhance the reproductive success of kin (who share the trait/gene for giving alarm calls) by protecting them from the predator, thus resulting in more offspring with the alarm-sounding trait in the next generation. Of course, altruistic behaviors are only favored by natural selection if they lead to more copies of the gene (trait) concerned being passed on than would be achieved by direct reproduction (Mateo 1996).

Hamilton's Rule

As well as developing the concept of inclusive fitness Hamilton suggested a formula to define the conditions under which altruism could spread in a population: $C < r \times B$. This inequality is also known as Hamilton's rule. C represents the cost of the altruistic individual, like time, effort, and resources utilized for helping, which limits the survivorship or reproduction of the helper. The recipient's possible benefits derived from the altruistic act are represented with B and r is the *degree of relatedness* between actor (altruist) and recipient (individual in need). As explained above, kin probably share common genes, because they have one or more common ancestors or are ancestors or descendants of each other. Accordingly, the degree of relatedness is an arithmetic formula for the probability of sharing genes with relatives. In effect, Hamilton's rule describes the two major factors defining the evolutionary consequences of *kin altruism*. Accordingly, altruism can be an evolutionarily stable strategy, if (1) the probability that the helper shares genes with the individual in need (r) is significant and (2) if the fitness benefit to the helped kin exceeds the fitness cost to the altruist ($B > C$) (Dawkins 1982).

Kinship is privileged in all cultures, and in certain cases (emergency situations) individuals

will give precedence to even the weakest kinship bond over the most beneficial nonkin relationship. Nevertheless, altruism toward kin and reciprocity with nonkin may have common genetic roots because of their functional correspondence. Individuals have to recognize each other and remember the history of their relationship; consequently, humans have to be able to memorize individuals and discriminate them from others according to certain cues or features. Moreover, they have to remember previous outcomes of the relationship, that is, individuals have to be able to calculate the costs and benefits of that particular relationship. The evaluation of a relationship is affected by the frequency of social exchange with a particular individual. Frequent social exchange may lead to creation of a sense of familiarity, and familiarity implies genetic relatedness because in evolutionary environments close and distant relatives lived near to each other. This means that kin altruism is inherently error prone because of the difficulties of evaluating degree of relatedness as well as judging the costs and benefits of altruism, especially in emergency situations, when decisions have to be made rapidly (Burnstein 2005). This problem raises some important questions: How can we assess the benefits and costs of an altruistic act and how we evaluate degree of relatedness?

Hamilton (1964) also suggested the existence of evolved mechanisms enabling individuals to discriminate kin from nonkin. Subsequent work was dedicated to whether and how animals and humans recognize kin, even collateral kin (e.g., siblings, nieces, nephews, aunts, and uncles). These studies showed that humans are able to recognize kin but the interpretation of evidence is ambiguous, because it depends on how we define kin recognition. The broadest definition of kin recognition describes it as the facility for distinguishing kin from nonkin or recognizing kin. In the case of altruism, it is important to have reliable cues for identifying relatives and avoiding deceivers (think of the birds that care for a cuckoo's chick because they use spatial signals to identify their own offspring, assuming "all chicks in my nest are my own"). Evaluations of genetic relatedness should be based on genetic

similarity or on signals associated with kinship (Penn and Frommen 2010).

Estimating Genetic Similarity

Hamilton (1964) proposed that it was possible to evolve for a gene that is capable of recognizing copies of itself in other individuals and that such a gene would trigger behaviors designed to benefit individuals who shared it. This signaling function is also known as the *green beard effect* (Dawkins 1976). Thus, a greenbeard gene (1) produces a rare phenotypic trait (e.g., a green beard), (2) enables the recognition of that trait/phenotype in others, and (3) promotes altruistic behavior towards individuals carrying that trait. The evolution of such greenbeard genes is highly improbable, and it has in fact been observed in only a few species. This rarity is presumably because such genes are vulnerable to cheating: individuals may fake the phenotype in order to gain benefits without acting altruistically (Penn and Frommen 2010). Several mathematical simulations (e.g., Jansen and van Baalen 2006) have shown that genes enabling altruism must continuously change their phenotypical cues to avoid exploitation by defectors or social parasites. Thus, it is plausible to suggest that this continual alteration may lead to more stable evolutionary dynamics of greenbeard genes.

In addition to theoretical assumptions discussed above there are several studies with humans suggesting a genetic locus for kin recognition cues, namely the major histocompatibility complex (MHC), a group of genes that control immunological self/non-self-recognition and are thought to be associated with kin recognition mechanisms (Brown and Eklund 1994). Body odor is influenced by MHC genes, which differ between families, and may therefore act as a kin recognition label. In a double-blind study women were asked to rate T-shirts worn for a few days by men to indicate how attractive they found the men on the basis of their body odor. Women found men with different MHCs more attractive than men with more MHC similarity but only if they were ovulating. The reverse effect was found in women

taking oral contraceptive, that is, the odor of MHC-similar men was rated more attractive than the odor of MHC-dissimilar males (Wedekind et al. 1995). Apparently, women are able to recognize nonkin men and find them desirable in cases where being genetically nonrelated reduces the chances of inbreeding. The reverse effect suggests that detecting MHC similarities facilitate the formation of cooperative bonds.

These findings suggest that evaluations of genetic relatedness are based, to varying degrees, on judgments of phenotypic similarity which involve comparison of a stimulus (e.g., the phenotype/trait of an individual) and a standard. Kin recognition mechanisms can be distinguished according to the source of the standard: *familiarity* or its ecological correlate, *proximity* requires that individuals memorize traits/phenotypes of kin and compare this memory trace with their perception of another person's trait/phenotype in order to judge relatedness. Another mechanism, *phenotype matching* uses self-referential cues for the comparison between stimulus and standard. The individual develops a "kin template" based on phenotypic cues learned through self-observation or from relatives it was reared with. The phenotypic cues presented by others are compared with this kin template to make kin recognition judgments (Penn and Frommen 2010). Both these mechanisms require similar operations and templates derived from experience with others, self-observations or genetic programming. This means that in certain circumstances it is not possible to distinguish between the effects of greenbeard genes and familiarity or phenotype matching. For example, there is a greater genetic similarity in blood antigens between spouses than between randomly chosen couples, and likewise long-term friends have more similar blood antigens than unacquainted pairs (Holland 2012). However, individuals of similar ethnicity and nationality tend to live near one another, even in modern societies (Glazer 1975), and these cues (i.e., ethnicity and nationality) predict blood group and are associated with proximity, which is a reliable predictor of relationship choices, so spouses and friends could share the same blood type whether or not they are able to detect genetic relatedness.

Familiarity-Dependent Kin Recognition

In species where young individuals stay with parents and other family members during the first period of their life – as humans do – offspring learn kin phenotypes and use the information later on to recognize kin (e.g., Westermarck 1921). The *Westermarck effect* was the demonstration of this kind of discrimination in humans: children who live in close proximity during the first few years of life become negatively imprinted and consequently in adulthood they reject each other as sexual partners.

There is a large body of evidence suggesting that social learning influences human kin recognition, principally in where matching abstract, alterable phenotypes such as personality traits is concerned. Some studies have shown that infants are able to identify kin even after limited experience: they can distinguish the voices of their mother and an unrelated woman a day after birth. Several weeks after birth infants are able to discriminate between their mother and unrelated women on the basis of their faces while mothers can identify their child from a set of photographs five hours after birth (see Bjorklund and Pellegrini 2002 for a review).

Phenotype Matching

The other group of kin recognition mechanisms is based on evaluation of self-resemblance, i.e., individuals compare the cues presented by others with their own cues for a given trait. The most salient social cues for humans are facial characteristics, and it is therefore assumed that facial resemblance plays an importance role in the detection of genetic relatedness.

Studies investigating the effects of facial resemblance use facial morphing techniques, such as merging images of two different faces to give a “compound face” (i.e., a morph) that shares features of both original faces. Facial morphs which are intermediate between the two original faces enable researchers to compare the impact of self-morphs (i.e., composite faces combining the subject’s face and a stranger’s face) and non-self-

morphs (i.e., compound faces combining the facial features of two strangers) on social judgments. A considerable body of experimental evidence confirms that individuals are able to detect self-resemblance in faces and that they treat such faces differently; subjects trust self-morphs more than non-self-morphs, even when the non-self-morph is familiar. Facial morphs of celebrities provide familiarity but no self-resemblance. Subjects favor self-resembling morphs over non-self-resembling faces and even over familiar non-self-morphs (DeBruine 2002). Moreover, Bressan and Zucchi (2009) found that both dizygotic (DZ) and monozygotic (MZ) twins preferred self-morphs over morphs based on the face of their twin.

Assessing Costs and Benefits of Altruism

Several factors were identified to have influence on fitness costs and benefits of helping. For example, helping only occurs, if the actor has available resources or control over required resources or skills. Another significant factor is the value of the recipient, which is defined by several characteristics of the individual (e.g., age, sex, status, etc.). Accordingly, for example, age of the recipient can change the cost-benefit ratio: Older individuals have less capacity and opportunities to use help efficiently and convert to reproductive success than younger individuals. Consequently, evaluating cost and benefits depends on contextual parameters and on the characteristics of the recipient (Kurland and Gaulin 2005).

Field studies have provided some evidence for the existence of kin altruism, showing, for example, that genetic relatedness influences resource distribution: For example, when fishermen divide their catch they give a bigger share to close relatives than to others (see Burnstein 2005 for more examples). Nevertheless, beside field observations, experimental analyses could provide some insight into the proximate mechanisms to evaluate the ability of individuals to benefit the group and their willingness to help/cooperate.

The prisoner’s dilemma (PD) is an experimental game used as a model for cooperative behavior (and other real-life interpersonal situations). In a

basic PD, two interacting individuals (A and B) have to decide whether to cooperate or betray and the amount of money they win will depend on the decisions both parties make. If A and B both betray each other both lose a moderate amount of money; if one of them betrays and the other offers cooperation the betrayer will win a certain amount of money while the cooperator loses more than in the previous scenario (betray-betray); if both opt to cooperate they will both win a modest amount. Most studies use an iterative PD in which the same individuals play each other repeatedly as thus have opportunities to punish the other player for his or her previous decisions. It has been shown that the most effective strategy is “tit-for-tat” (TFT), i.e., making the decision one’s partner made in the previous round. The evidence suggests that in most cases individuals display a systematic bias towards cooperative behavior, which is not compatible with the predictions of a simple model of self-interested action (Nowak and Highfield 2011; Stewart and Plotkin 2012). Hamilton’s inclusive fitness theory predicts that PD pairs should be more trusting and cooperative if they are genetically related. Studies on facial resemblance provide some indirect support for this (e.g., studies of DeBruine 2002): Subjects were more trusting and altruistic towards self-morphs than non-self-morphs. A study by Segal and Hershberger (1999) provided more direct evidence of cooperation between kin. They compared the performance of MZ and DZ twins in PD game and found that MZ pairs exhibited noticeably more cooperation than DZ pairs. In general, familiarity encourages individuals to display trust and altruism in individuals: For example, subjects judgments about whether a person is typically altruistic or not were improved if they had watched a video clip of that person telling the Little Red Riding Hood story, which created familiarity (experiment 1 in Brown et al. 2003).

Other studies have shown that genetic relatedness has a systematic impact on assessments of the costs and benefits of altruism. Generally, higher genetic relatedness is associated with a higher probability of helping, in accordance with Hamilton’s rule: The larger the benefit-to-cost ratio, the more likely altruists will discriminate

and favor close kin (see Burnstein et al. 1994). Moreover, individuals prefer to distribute their help so as to maximize the reproductive return, based on genetic relatedness (i.e., they will choose to help two siblings rather than one but will prefer to help one sibling rather than two cousins etc.). For example, Wang (2002) asked subjects to imagine situations in which their decisions affect a six-member kin group, containing two close relatives of the same sex, two distant relatives of the opposite sex, and two unspecified relatives. Subjects have to choose one of two options: a medical procedure which certainly saves two male or two female kin (either close or distant kin) and a procedure with a 33 % probability to save the whole six-kin group. Additionally, half the subjects were asked to imagine that the group was made up of their own relatives and half that it was made up of another person’s relatives. When subjects were making decisions about their own relatives 40 % of them chose the certain procedure to save close relatives but only 20 % did so to save a pair of distant relatives.

Conclusion

Hamilton’s theory of inclusive fitness offers an explanatory account of the evolutionary stability of the altruism; according to Hamilton’s model altruism occurs when the costs do not exceed the reproductive benefits, which are weighted according to the genetic relatedness of altruist and recipient ($C < r \times B$). Hamilton’s rule is supported by ethnographic and experimental research showing that in line with the predictions of inclusive fitness theory individuals unequivocally favor kin over nonkin and prefer close kin over distant kin. Furthermore, these preferences are stronger in emergency situations, i.e., when (reproductive) cost-benefit ratio is more salient. Under this model, kin altruism depends critically on how accurately individuals are able to estimate genetic relatedness and evaluate the costs and benefits for helping. Despite a large number of studies, the computational mechanisms underlying these processes remain unclear. There is some evidence suggesting that individuals use a

genetically programmed template to recognize familiarity; however, co-rearing or early childhood experiences could also generate an inner representation of a “family schema” via social learning mechanisms. Familiarity-based kin recognition could also occur via phenotype matching, that is, on the basis of assessing resemblance to self. Whatever the cues used for kin recognition, it seems plausible that individuals have some mechanism for taking into account degree of genetic relatedness when evaluating the costs and benefits of altruism. In conclusion, altruism towards kin is based on complex calculations and assessments which are affected by familiarity, situational cues, and the reproductive “value” of the recipient (based on age, health, etc.).

Cross-References

- [Adaptive Problem of Detecting Kinship](#)
- [Cooperation Varies With Genetic Relatedness](#)
- [Genetic Relatedness Affects Aid to Kin](#)
- [Hamilton’s Rule and Genetic Relatedness](#)
- [Hamilton’s Rule and Theoretical Implications](#)
- [Kin Recognition](#)
- [Kin Recognition and Classification in Humans](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)

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Helping and Inclusive Fitness Benefits to Helper

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Synonyms

[Altruism](#); [Evolution of altruism](#); [Delayed reciprocity](#); [Group augmentation](#); [Hamilton's rule](#); [Helping at the nest](#); [Inclusive fitness](#); [Kin altruism](#)

Definition

Inclusive fitness is the sum of direct (personal) fitness and indirect fitness of the organism. Direct fitness is the number of offspring the individual procreates, whereas indirect fitness is defined by the number of offspring begotten by the genetic relatives of the individual. To the extent of the genetic relatedness, descendants of relatives share a proportion of copies of the individual's genes. Thus, helping genetically related individuals, also aids the reproduction of the shared genes, providing additional (indirect) benefits for the altruist (Hamilton 1964).

Introduction

Both direct and indirect fitness benefits could account for the evolution of altruism, and therefore in several cases it is difficult to separate them. Hamilton suggested a formula to define the conditions under which altruism could spread in a population: $C < r \times B$, also known as *Hamilton's rule*. In this inequality C is the fitness cost of the behavior to the altruistic individual, B is the benefit of altruism for the recipient, and r is the *degree of relatedness*. Since kin share one or more ancestors or are ancestors or descendants of each other they are likely to possess some common genes (or traits). The degree of relatedness gives the probability of sharing genes with relatives. In

effect, this formula states that the evolutionary consequences of being altruistic towards kin depends on the probability that the altruistic individual shares genes with the recipient (kin) (r) and the extent to which the benefit to the kin exceeds the cost to the altruist ($B > C$) (Dawkins 1982).

Indirect Benefits for the Helper

Field studies have provided some evidence for the existence of kin altruism, showing, for example, that genetic relatedness influences resource distribution: when fishermen divide their catch they give a bigger share to close relatives than to distant kin or non-relatives (see Burnstein 2005 for more examples).

However, costs and benefits of altruism depend on several situational factors, such as the availability of resources or the actors' ability to control or utilize these resources. Another key factor is the value of help to the recipient, which depends on several characteristics (e.g., age, sex, status, etc.). For example, as a consequence of aging older individuals are less efficient than younger individuals in using resources to reproduce or nurse offspring. Beside situational factors, genetic relatedness has also a systematic impact on assessments of the costs and benefits of altruism. Based on Hamilton's rule, higher genetic relatedness is predicted to be associated with a higher probability of helping. Accordingly, some studies showed that the larger the benefit-to-cost ratio, the more likely altruists will discriminate and favor close kin over distant kin and over nonrelatives. Moreover, individuals prefer to distribute their help so as to maximize the reproductive return based on genetic relatedness (i.e., they will choose to help two siblings rather than one but will prefer to help one sibling rather than two cousins, etc.; see Burnstein 2005).

Direct Benefits for the Helper

There are two different forms of direct fitness benefits for helpers: (1) direct benefit as a by-product or "automatic" consequence of

helping and (2) social benefits (advantages within the group).

By-Product Benefits

Altruistic behavior toward group members can lead to a larger group size, which can be beneficial to all members of the group, because it lowers the mortality within the group. An enlargement of group size can increase the likelihood of survival through enhancing catering or outcompeting other groups by means of mutual helping between group members (Clutton-Brock 2002). For example, there is a good evidence that subordinate individuals help raise unrelated offspring in order to increase group size but at some later point, if these subordinates obtain dominance, they can take account of being supported by those offspring (*delayed reciprocity*). The help in rearing offspring that are not the individual's own is termed as *group augmentation* and has been suggested to be important mechanism in several social species (see Griffin and West 2002).

If group members are related, the by-product benefits of altruism can provide indirect benefits as well, because if the altruist helps a relative or kin they may share the benefits of the altruistic act. A good example for this effect is the “*helping at the nest*”: adolescent (and often sexually mature) offspring remains in the habitat of the family to help the parents raising subsequent offspring, instead of investing of the own reproduction (West et al. 2007). In several societies, mothers expect their juvenile girls to help with rearing their siblings and encourage them to do housework (e.g., Bereczkei and Dunbar 1997). On the one hand, this assistance could increase the reproductive success of the mother and so it provides an indirect benefit for the older sibling. More direct advantages for the helper might are (Dickinson and Hatchwell 2004):

Protection: staying in the parental habitat could be more safe for the young one, who is yet not in his/hers prime.

Skill training: helping at the nest is attached with practices which are requisites of subsequent

reproduction or survivorship (e.g., nursing babies, cooking, etc.).

Social Benefits

For most of the species, individuals show an enhanced survival in a group rather than alone or few in numbers. Therefore, altruism can provide one of the best strategies for avoiding ostracism or being punished to violate norms. Some empirical evidence support this notion, showing that individuals who help or pretend to helping other in the group can successful avoid punishment (see Griffin and West 2002 or West et al. 2007 for examples).

Under certain conditions, for example, to help someone, who is unlikely able to return the favor advertises the helper's generosity, available resources, and other socially desirable traits. Because helping is associated with significant fitness costs, altruism can be considered as an honest signal of several personal qualities. Advertising such qualities enhances the mate value of the individual, which increases the probability of reproduction, and so it may contribute to the fitness of the helper. Therefore, the most common result of altruism within the group is the increase of social status of the helper (Zahavi and Zahavi 1997). Although evidence for this assumption is limited, in some studies, participants preferred individuals, who tended to be altruistic to others in earlier interactions. In some cases, the reputation rises even if the individual only aims to act altruistically (Bereczkei et al. 2007). Furthermore, individuals with an advanced social status appear to be more beneficial partners in social exchange situations. Thus, such individuals are preferred as partners in establishing cooperative alliances.

Conclusion

There is a considerable overlap in the mechanisms of direct and indirect fitness benefits of helping. More specifically, helping can provide a fitness benefit for more than one reason and because the different proximate mechanisms, direct and indirect benefits can play different

roles in the evolution and maintenance of helping behavior. Moreover, kin altruism does not necessarily imply that indirect fitness is the main factor driving altruism, even if it was presumably required for the initial evolution of helping. One of the major tasks of contemporary studies is to estimate the relative impact of direct and indirect fitness benefits on observed forms of helping.

Cross-References

- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Helpers at the Nest](#)
- ▶ [Indirect Benefits of Altruism](#)

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Helping and Reproductive Value of the Recipient

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Synonyms

[Altruism](#); [Indirect benefits of helping](#); [Kin altruism](#); [Reproductive limitations](#); [Reproductive value](#); [Residual reproductive value](#)

Definition

Considerable evidence support the basic assumption of Hamilton's inclusive fitness theory showing that individuals behave altruistically towards kin (see Burnstein 2005. for a review). However, there are several factors, which affect the probability of behaving altruistically toward kin, like reproductive value of the recipient. The "evolutionary logic" behind this bias corresponds with the variability of an individual's potential to reproduce offspring. The *reproductive value* of an individual is determined through its current and future reproduction, i.e., its expected summarized contribution to the next generation of the population. Future reproduction (or *residual reproductive value*) represents the investment of the individual of its own growth and survivorship. It is suggested that higher investment in current reproduction reduces future reproduction, because it expropriates resources from growth and survivorship. However, resources invested in growth will benefit the individual in the future through the increase of number of offspring and reproductive episodes (Fisher 1930).

Introduction

Several disorders affect the reproductive success of the individual through limiting mating frequency or fertility which induce a decrease of

the likelihood of passing on genes. Accordingly, individuals are less likely to act altruistic toward kin with such *reproductive limitations* because the lower probability of passing on the gene responsible for altruism. There is some evidence to support this notion, for example, it was observed that mothers provided less maternal care (e.g., length of breast feeding) to weakly infants (i.e., low birth weight) compared to healthy infants (Berezkei 2001).

However, reproductive limitations differ in their conspicuousness and in the extent to which they affect the reproductive value of the individual. For example, a homosexual young adult male dispose no visible reproductive limitation, although his homosexuality could (but not necessarily do) impede the production of offspring. The aim of this entry is to provide a short review of factors affecting the reproductive value of an individual.

Sex of the Recipient

In several studies, female relatives are favored over male relatives by altruists of both sexes suggesting the significant influence of the sex of the recipient in evaluation of the cost-benefits ratio of an altruistic act (e.g., Burnstein et al. 1994). Although women have limited reproductive capacity, because the internal fertilization, they can be absolutely certain about being genetically related to their child. Contrarily, men always face the (hypothetical) possibility that the child has been fathered by another man. This phenomenon is called *paternal uncertainty*. Accordingly, it is more beneficial to help a female relative compared to a male relative, since the helper can be more certain that the recipient transmits their shared genes.

Age of the Recipient

Aging affects the reproductive success of the individual and accordingly it also influences the extent to which the recipient can utilize the benefits of the help. As a general rule, older individuals are supposed to be less efficient at converting

resources into offspring. In good agreement with this hypothesis, Burnstein et al. (1994) found that the preference of female kin over male kin in helping fades away with the increase of the age of the target person. At the age level close to the onset of menopause, or over this period, the likelihood of reproducing offspring drops significantly, thus it is no more favorable to support female over male kin. Moreover, supporting younger individuals results a more lasting impact, because it exerts its effect over a longer period of the life span. However, very young and very old individuals are more vulnerable to damages of reproductive value, like diseases or neglect, and therefore when benefits of altruism are significant, very old and very young individuals are less likely to receive help. On the other hand, if the age of puberty is close, or already began, the likelihood to receive help increases. Those of intermediate age are the most likely to receive help from relatives, because their contribution to current reproduction is the highest. Therefore, in life or death situations, the probability of kin altruism is curvilinear with the age of the recipient, but in everyday situations (when benefits of altruism are nearly 0) this correspondence reverses and aid flows to the youngest and oldest individuals (Burnstein et al. 1994). Although, helping relatives with limited reproductive value has moderate direct benefits, but it advertise our generosity, which can enhance the likelihood to get help from others (Zahavi and Zahavi 1997).

Status and Resources of the Recipient

In the case of differences in access to resources, helping is less costly for high-status individuals, thus the cost-benefit ratio of altruism is differing according to the resources available for the individual. Therefore, individuals can use their resources to manipulate others, thus wealth can lead to receiving more help but only under certain circumstances: in life or death situations, altruists do not discriminate between close kin according their status or resources, but they do in relation to distant kin. For example, high-status siblings receive help as likely as low-status siblings,

while wealthy cousins get help more often than less wealthy ones (Burnstein et al. 1994).

Physical Status of the Recipient

Numerous physical features can affect reproductive success through influencing attractiveness, for example, male height, which is associated with reproductive success (Nettle 2002). Another visible and significant factor is weight: both men and women prefer mates who are of average weight over thin or obese mates. Weight affects the reproductive functions of both men and women; therefore, it has a significant impact on the reproductive success of men and women. Women, who are excessively thin or overweight bear difficulties with their fertility. Underweight men display a decreased sperm count, whereas overweight is associated with lower levels of testosterone in men (see Fitzgerald and Colarelli 2009). In addition, there are several more, persistent physical health indicators (e.g., deformity or dysmorphism) which also influence kin altruism (see introduction of this section). Altruists evaluate the apparent health status of the recipient, and in life or death situations they tend to favor healthy kin over those poor in health, but in everyday situations this effect is reversed and altruists prefer relatives in poor health over healthy relatives (Burnstein et al. 1994).

Mental Health of the Recipient

More or less apparent reproductive limitations are mental disorders or problems in everyday mental functioning. Psychological problems can impair reproductive success, for example, depression (and many other psychological disorders) is associated with decreased sexual motivation or limited social functioning. These characteristics are less appealing for mates, thus helping kin with mental disorder produces a lower fitness payoff than helping kin who are not mentally ill. Moreover, individuals with mental illness are presumably less altruistic or cooperative, thus helping these people is likely to remain unrequited (see Fitzgerald and Colarelli 2009).

Sexuality and Reproductive Value

If an individual engage in sexual activities without reproductive possibilities, it is a sexual reproductive limitation. For example, as mentioned above, homosexuality (and to a lesser extent, bisexuality) is a behavior which is associated with a decreased probability to reproduce offspring. Sexual orientation is less conspicuous and not necessarily rigorous reproductive limitation since homosexuals are physiologically capable of reproducing (see Fitzgerald and Colarelli 2009).

Conclusion

In accordance with Hamilton's inclusive fitness theory, assessing cost-benefit ratio of helping involves proximate mechanisms to evaluate the reproductive value of the recipient. Recipient's handicap in reproduction can lead to a less advantageous return to fitness of the helper, hence altruists have to be able to take these limitations into account. Accordingly, individuals are less likely to help those, with a limited reproductive potential. However, there are many different forms of reproductive limitations, which may have different impact on reproductive value of the individual. In good agreement with this notion, empirical evidence showed that people are more willing to risk their lives to save a relative with a temporary reproductive limitation than a relative with more persistent limitation (Fitzgerald and Colarelli 2009).

Cross-References

- [Mate Value](#)
- [Reproductive Value](#)

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Helping at the Nest

► [Helping and Inclusive Fitness Benefits to Helper](#)

Helping More Likely with Close Kin than More Distant Kin

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Synonyms

[Altruism](#); [Hamilton's rule](#); [Inclusive fitness theory](#); [Kin selection theory](#)

Definition

Evolutionary theory predicts that when all else is equal, individuals will help their closely related relatives more than their distantly related relatives.

Introduction

Humans are prosocial species and typically provide help to one another. The term help can be defined as active and voluntary acts, including the transfer of any resources (e.g., time, money, material) from one individual to another. In evolutionary studies, contact and emotional closeness are often used as proxies for help because they tend to strongly correlate with several forms of support. According to kin selection theory, with all other things being equal, the likelihood of providing help should correspond to the degree with which individuals are related to each other and individuals are predicted to provide more help to their closely related kin than their distantly related kin (Hamilton 1964).

Empirical Evidence

On average, individuals share 50% of their genes with their parents, children, and full-siblings; 25% with half-siblings, grandparents, grandchildren, nieces, aunts, and uncles; and 12.5% with their great grandparents, great grandchildren, and first cousins. An abundant amount of empirical evidence shows that individuals tend to prefer kin over non-kin and close kin over more distant relatives (Salmon and Shackelford 2011). For instance, individuals provide more help and are more willing to make sacrifices if the beneficiary is a close relative and the readiness to help decreases with the degree of relatedness (Burnstein 2005; Madsen et al. 2007).

The exclusion of all other things besides the degree of relatedness is difficult because all else is never equal in human populations, meaning that several factors can affect the conditions under which helping takes place. However, different variations of sibling and twin relationships provide a research frame where all other things are closer to equal, but the genetic relatedness varies. Although individuals share an average of 50% of their genes with their full-siblings, the relatedness is only 25% between half-siblings. Moreover, dizygotic twins' relatedness is equivalent to full-siblings, but monozygotic twins are genetically identical.

Research on family relationships shows that the sibling ties are stronger between full-siblings than half-siblings and that the degree of relatedness predicts interactions and support between siblings (Pollet and Hoben 2011; Tanskanen and Danielsbacka 2014). A twin study, where different twin-pairs played the prisoners' dilemma game, found that identical twins were noticeably more cooperative with each other than other twin-pairs (Segal and Hershberger 1999). Furthermore, identical twins are also "genetic parents" of their co-twin's children, while dizygotic twins have customary relatedness to their nephews and nieces. A prior study found that monozygotic twin aunts and uncles expressed greater social closeness and gave more gifts to their nieces and nephews than dizygotic twin aunts and uncles (Segal and Marelich 2011).

Conclusion

Prior empirical studies have shown that individuals tend to favor their close kin over more distant kin and that the likelihood of providing help is associated with the relatedness of the individuals. These findings are consistent with the kin selection theory.

Cross-References

- [Genetic Relatedness Affects Aid to Kin](#)
- [Hamilton's Rule and Kin Investment](#)
- [Helping and Genetic Relatedness](#)

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Heraldry

- [Birthrights and Bloodlines](#)

Herding

- [Types of Sexual Coercion](#)

Herding Culture of Violence

- [Culture of Honor and Nepotism](#)

Hereditary Transmission

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Heredity

- [Good Genes](#)
- [History of Inheritance](#)

Heritability

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Synonyms

Genetic inheritance; Inheritance

Definition

Heritability is the statistical metric that estimates the relative influence of genetic variation (measured as genetic variance) on phenotypic variation (phenotypic variance), relative to the influence of environmental differences (environmental variance).

Introduction

Heritability is a statistical parameter that is often used in discussions of genetic causation and the nature versus nurture debate. The heritability of a trait, represented by either H^2 (for broad heritability) or h^2 (for narrow heritability) is between 0 and 1. Traits with a high heritability are generally seen as genetically influenced, and those with a low heritability as environmentally caused (Lynch and Bourrat 2017).

The heritability concept most often invoked in psychological science is broad sense heritability. Broad sense heritability estimates the proportion of phenotypic variance (V_P) that can be accounted for by genetic variance (V_G), relative to the influence of environmental variance (V_E):

$$H^2 = \frac{V_G}{V_P} \quad (1)$$

$$V_P = V_G + V_E \quad (2)$$

Narrow sense heritability (h^2) is an alternative heritability measure which is primarily used in

breeding experiments by quantitative geneticists using animal models. It is concerned only with additive genetic effects (V_A), as these are reliably transmitted between generations. This is opposed to other kinds of genetic effects like dominance and epistasis (V_{D+I}), which encompass gene–gene interactions.

$$h^2 = \frac{V_A}{V_P} \quad (3)$$

$$V_P = V_A + V_{D+I} + V_E \quad (4)$$

Knowledge of h^2 allows one to forecast the adaptive potential of a given trait within a population, using the breeder's equation (Lush 1937). Usually these kinds of estimates are confined to traits in agricultural animals such as body weight, milk yield, life span, fecundity, and litter size (Falconer and McKay 1996).

Human research is less concerned about the adaptive potential of traits, and more interested in the sources of trait variation. Because of this, broad sense heritability is used, as it encompasses the total genetic contribution to the trait of interest. In order to calculate heritability, phenotypic data is collected from individuals who share a common family environment, and are genetically related to varying degrees. As environments are assumed not to vary between individuals in a family environment, the phenotypic similarities observed between parents and their children, or between siblings (especially twins), are assessed in light of their degree of genetic relatedness. See ► “Heritability” and ► “Twin Studies” for details.

Populations and Individuals

Heritability is a population-level parameter, and cannot be used to make causal inferences about individuals. For example, the heritability of height is ≈ 0.8 in most human populations. This means that if you lined up a population in accordance to their height, and wanted to know what accounted for differences in stature – you would find that environmental differences between individuals were largely unrelated to height differences, and

that genetic differences were associated with differences in height.

A heritability of 0.8 does *not* mean that only 80% of people have their height genetically influenced. It also does not mean that a given individual has 80% of their height genetically influenced, such that an individual who is 165 cm tall can attribute 132 cm to their genes.

At an individual level, both genes and environment are causally necessary for the production of phenotypes, and assigning values of relative causal importance to each is incoherent. Keller (2010) illustrates this with an analogy. Imagine two individuals, Billy and Suzy, who want to fill a bucket of water. Suzy holds a hose to the bucket, while Billy turns on the tap. Once the bucket is full, one could ask: “How much of the water is due to Billy’s contributions, and how much to Suzy’s?” The example is meant to illustrate that this question does not make sense, as partitioning causes in this case is not possible. Both the hose-holding and the turning of the tap are required to fill the bucket, and it is not possible to assess “how much” each caused the bucket to fill, relative to the other.

The Utility of Heritability Estimates

In addition to the pure explanatory utility of heritability estimates, broad-sense estimates can be used as a tool to investigate the causes of phenotypic variation in detail. For example, they may be used as justification for the search for genetic markers which are the first step of genetic mapping, and can lead to the isolation of candidate genes via methods such as genome-wide association studies.

Broad heritability estimates can also be used to estimate and predict the phenotypes of families and offspring, including complex diseases and behaviors. This information can be utilized for preventative procedures and genetic counselling strategies, as well as to provide extra intervention and support for those who may be genetically susceptible to undesirable phenotypic variants.

The heritability of a trait has also been invoked to discuss broader philosophical issues such as

free will and moral responsibility. For instance, Kaebnick (2006) raises the question: If no environmental interventions (that have yet been studied) seem able to alter the V_P of a trait, how responsible are individuals possessing a certain variant? Kaebnick believes that heritability analyzes help to inform, or at least introduce, some of these broader philosophical questions and should be considered by ethicists. Others such as Parens et al. (2006) have similarly theorized that knowledge about the heritability of a trait can impact on individual feelings of blame, responsibility, and human identity.

Heritability of Psychological Traits

One of Eric Turkheimer’s (2000) three laws of behavior genetics is that all behavioral traits are heritable. This is also true in the study of personality, which indicates that all personality traits are heritable to some degree (Bratko et al. 2017). Studies of personality using the five-factor model (extraversion, agreeableness, conscientiousness, neuroticism, and openness for experience) have yielded significant heritabilities (Power and Pluess 2015), as well as other models of personality such as Eysenck’s PEN (psychoticism, extraversion, and neuroticism), and Tellegen’s (positive affect, negative affect, and constraint) (Bratko et al. 2017). Overall, personality differences have a heritability estimate around 0.40, meaning that 40% of the variance is due to genetic differences, and 60% due to environmental influences (Bratko et al. 2017).

Intelligence is another trait of interest to psychologists. It was one of the first traits to be analyzed using heritability and is to date the most studied phenotype in behavior genetics. The heritability of intelligence is estimated to be 0.5–0.8 (Plomin and Spinath 2004). However, these estimates have been questioned due to phenomena such as the Flynn effect (Flynn 1984) which documents the rise in IQ test performance over generational time scales. While the IQ scores of a population reliably trend towards a normal distribution, the median raw scores of later generations are higher than those of earlier ones,

resulting in a continual re-adjustment raw scores, averaging a 3 point per decade adjustment (Flynn 1984). Another piece of evidence that indicates a significant environment influence on intelligence is observed IQ gains through adoption into higher socioeconomic (SES) homes, as well as through migration into higher SES countries (Sauce and Matzel 2018).

Mental illnesses and disorders have also gained a lot of attention in heritability studies. For example, schizophrenia has a $H^2 = 0.79$ (Hilker et al. 2018), unipolar depression $H^2 = 0.37$ (Sullivan et al. 2000), bipolar disorder $0.71 \leq H^2 \leq 0.77$ (Edvardsen et al. 2008), and Autism spectrum disorder $0.64 \leq H^2 \leq 0.91$ (Tick et al. 2016). Some of these results have been criticized on the grounds of nonadditive effects biasing heritability estimates. These are discussed below.

Nonadditivity

Standard models of heritability assume additivity of genetic and environmental variance. This means that phenotypic variance can be calculated as the sum of genetic and environmental variances as two independent variables. However, empirical evidence suggests that genes and environments interact nonadditively for generating trait differences. This can happen in two ways. The first is gene-environment interaction (GxE), which occurs when the effects of genotypes are differentially expressed depending upon their environment. Likewise, environmental influences act differentially depending upon the genotype of an individual (Tabery 2014). For example, there is a genetic interaction with cannabis usage for development of schizophreniform psychosis. Individuals with a certain variant of the *COMT* gene are more likely to develop psychosis when exposed to cannabis, compared to those with a different gene variant (Caspi et al. 2005).

If GxE effects are not detected, then the resulting heritability estimate will be incorrect, as it is using an erroneous model of variance contributions. When they are detected, they can

be accounted for by updating the heritability model to include an interaction effect:

$$V_P = V_G + V_E + V_{G \times E} + r_{GE} \quad (5)$$

Even if no GxEs are detected, or if they are detected and adjusted for in a nonadditive model (Eq. 5), they still pose a problem for the extrapolation-worthiness of heritability estimates. GxE occurs when genetic differences make a difference to phenotypes in different ways depending upon the environments experienced by the population under study. This makes it difficult to make general claims about the genetic causation of traits across populations. This problem was first identified by Lewontin (1974), who argued that GxEs are problematic for heritability estimates even in cases where none have been identified. Although genes and environments may behave additively in one population, resulting in a particular H^2 , that does not rule out that there could be interactions in different, unstudied environments in unobserved populations. This problem has led some to reject the utility of heritability estimates all together.

The second form of nonadditivity is gene environment correlation (r_{GE}). This occurs when certain genotypes and certain environments are more likely to be found together, and so at a population level genetic variance and environmental variance become associated. There are three forms of r_{GE} (Plomin et al. 1977). The first is passive r_{GE} , which occurs when parents pass on associated genetic and environmental influences to their children. For instance, children of avid readers might inherit genes which provide good comprehension skills, as well as environments filled with many books. Thus, both genetic and environmental influences on reading ability are correlated within the population. Passive r_{GE} s can be isolated using adoption studies, or by controlling for potential correlated environments in study designs. Active r_{GE} s occur when certain genes predispose an individual to seek out certain developmental environments. In this case, the environmental exposure is an indirect effect of genotype, and so genes and environments are correlated at the population

level. For example, bright children with a genetic advantage for academic study may, thanks in part to their genes, seek out more stimulating environments, further advancing their academic performance. A third form of rGE is reactive cases. These occur when individuals experience certain environments because of the way society reacts to some aspect of a genetically influenced genotype. This is thought to occur in problematic society-based reactions to different racial groups. Individuals possess genes which express themselves in physiological traits such as skin color, and because of these traits, those individuals are subject to harassment, or deprived of environmental resources, compared to counterparts with a different genetic background.

Active and reactive rGEs are difficult to detect in the study of heritability, and there is debate as to whether or not active cases should be included as part of the additive effects of V_G (Lynch 2017). Evidence for active and reactive rGEs comes from the heritability of environmental variables, such as socioeconomic status, television viewing, and quality of social support (Plomin and Bergeman 1991). Rutter, Moffitt and Caspi (2006) and Rutter and Silberg (2002) have proposed that rGE contribute significantly to the heritability of psychiatric disorders. For instance, aggressively prone offspring are likely to promote harsher treatment from others, compounding their development along a psychiatric trajectory. This work has been extended by Jaffee and Price (2007) who have identified particular allelic variations and their associations with environments, such as parental rejection. These associations are then predictive of later psychiatric illness, indicating that genetic variation may account rGE with parental engagement. Meek et al. (2013) have suggested that heritability estimates for autism may also be largely accounted for by active and reactive rGEs. Children who begin as mildly autistic are likely to select environments lacking in social stimuli (active rGE), and others around them can react to them in a way which compounds both their autistic phenotype (reactive rGE) and their subsequent environmental selection (further compounding the active rGE pathway).

Conclusion

Heritability is a statistical parameter that estimates the influence of genetic variation on phenotypic variation, relative to environmental variation. Broad heritability (H^2) is the most widely used statistic in the human sciences, and is used to explain the causes of trait differences at a population level. Many psychiatric disorders, personality differences, human abilities, and behaviors have significant heritabilities. These results can be used to understand the causes of trait differences in a population; however, causal claims about relative influences of genes and the environment cannot be made about individuals using heritability results as heritability is strictly a population-level parameter. The population relativity of H^2 has led to some criticisms of the utility of the estimates. In particular, the existence of gene-environment interactions – both within actual and hypothetical populations – is problematic for extrapolating heritability results. Additionally, gene-environment correlations undermine the additive model used for heritability estimates, and are difficult to study and control for. There is growing evidence that gene-environment correlations account for some of the estimated heritability for psychiatric traits.

Cross-References

- [Genetic Determinism](#)
- [Personality Development](#)
- [Problem of Genetic Inheritance, The](#)
- [Twin Studies](#)

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Heritage

- [Birthrights and Bloodlines](#)
- [History of Inheritance](#)

Hero

- [Rescuing Strangers](#)

Heroic Rescue in Humans

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Synonyms

[Courageous rescue](#); [Dangerous rescue](#); [Daring rescue](#); [Heroism](#); [High-risk rescue](#)

Definition

“Heroic rescue” occurs when an individual places himself/herself at risk to save another person in a life-threatening emergency situation.

Introduction

When defining altruism, social scientists usually focus on the intentions of the altruist, and their research has traditionally attempted to isolate the situational factors that determine when people will behave altruistically. Five decades of research have identified the importance of such factors as empathy, rewards, emotional states, social norms, and the number of bystanders in influencing helping behavior. Social science models of altruism do not address the question of why basic motives such as empathy and various situational factors came to be so important. In fact, even most social psychologists continue to study altruism and other social behaviors with little reference to the origins and ultimate functions of altruism, which have been the primary focus for evolutionary psychologists.

Altruism has always been a thorny issue for evolutionary theorists; the idea that an organism would engage in a behavior that comes at a great personal cost and seems to benefit only other individuals was difficult to explain through the basic principles of natural selection. Over time, however, several theories have been developed that may explain such behavior, with each theoretical perspective offering a more suitable explanation for some types of altruism than for others (McAndrew 2002).

Differentiating Heroic Behavior from Other Forms of Altruism

Heroic behavior is qualitatively different from other types of helping behavior. For example, there are many situations in which individuals help others who are not related to them: they loan money and personal belongings to friends, give rides to strangers who are hitchhiking, and go out

of their way to do favors for acquaintances who ask for help. Such acts, however, should not be described as “heroic,” if only because they do not pose any severe risks to the altruist. On the other hand, individuals may put themselves at great risk to save their children or other relatives during emergencies, or they may engage in long-term costly behavior that benefits family members. However, self-sacrificial acts performed for close kin are usually not described in everyday life as being “heroic” or even as “altruistic.” The word “heroism” is usually reserved for those behaviors in which the altruist puts him or herself at physical risk to rescue unrelated individuals who find themselves in a life-threatening situation.

Heroic Rescuing of Relatives

It was not until the concept of *inclusive fitness* was introduced by Hamilton (1964) that evolutionists had a satisfactory theoretical framework for discussing altruism.

Inclusive fitness is often referred to as *kin selection*, because according to this concept, natural selection favors behaviors that benefit others who share our genes, especially closely related kin. Hence, the mother who sacrifices her life so that her children survive may actually be engaging in a behavior that is genetically very adaptive, as the copies of her genes that reside in her children will in the long run lead to greater genetic fitness than if she alone had survived. Although the parent who rushes into a burning building or dives into an icy river to save one of his or her children is admired and the intense emotions driving such behavior are easily understood, the mantle of “hero” is not usually bestowed upon such individuals. The powerful impulse to rescue close kin from harm can most easily be understood through the lens of inclusive fitness and kin selection. Whether such dramatic helping of kin can properly be described as “heroic” is open to question.

The concept of kin selection is somewhat limited in that it cannot explain the whole range of altruistic behaviors observed in humans and other animals. For example, it cannot account for

altruistic acts aimed at other individuals known not to be genetic kin.

Heroic Rescuing of Friends

Reciprocal altruism (Trivers 1971) is defined as cooperative behavior among unrelated individuals that benefits everyone involved. Individual success at reciprocal altruism depends greatly on the ability to identify and cooperate with others who are good exchange partners and to identify and avoid those who are cheaters. Because humans are a supremely social species, the selection pressures faced by early humans in this regard must have been profound. It would have been evolutionary suicide to consistently behave in a selfless, altruistic manner toward unrelated individuals who took as much as they could get while offering little in return. Consequently, it should not be surprising that research has confirmed that humans are primed to recognize true altruists as well as cheaters and to deal with these individuals appropriately (Brown and Moore 2000; Mealey et al. 1996). Reciprocal altruism probably offers the best explanation for heroic rescuing among friends. Friendships are established after individuals have arrived at a mutually satisfying and reliable pattern of equitable exchange. To put one's self at risk to rescue a friend may in fact be something of an obligation but also something that the helper may expect to be repaid in some manner during a future time of need.

Heroic Rescuing of Strangers

Inclusive fitness convincingly explains sacrifice for family members, and reciprocal altruism allows an understanding of individuals who sacrifice for the benefit of unrelated others with whom they have an ongoing relationship. However, anyone who helps others and expects payback will not be thought of as a hero, and in spectacular life-saving acts of heroism, it is clear that no adequate payback could really be possible anyway. It is in the arena of the rescuing of strangers that the term "heroism" is most aptly applied.

The best explanation for the heroic rescuing of strangers may be found in *Costly Signaling Theory* (CST) (Bliege Bird and Smith 2005; Boone 1998; Grafen 1990; McAndrew 2002; Roberts 1998; Zahavi 1977). CST suggests that conspicuous self-sacrificial heroism may be a way for individuals to advertise desirable personal traits. This might increase the likelihood that they will be chosen as a mate or an ally and it might also position them for access to future status and resources, even from individuals who were not direct beneficiaries of the heroic act. For a costly signal to be effective, it must honestly convey valuable information about the individual sending the signal, and it must be impossible to fake.

Evolutionary psychologists believe that even apparently selfless impulses such as the heroic rescuing of strangers must provide some adaptive advantage for individuals; otherwise, such behaviors would have been strongly selected against. Many studies demonstrate that people who sacrifice for the group by engaging in costly activities do in fact achieve elevated social status, respect, and recognition as a result of their public selflessness (Bereczkei et al. 2010; Hardy and Van Vugt 2006; McAndrew and Perilloux 2012a, b; Nowak and Sigmund 2005; Sylwester and Roberts 2010; Van Vugt and Hardy 2010; Willer 2009). No researchers suggest that heroes consciously sit down and calculate all of the benefits that will come their way if they survive the heroic action. Rather, it is thought that such impulses have been selected for because heroic behavior has provided competitive advantages for men throughout human history.

Sex Differences in Heroic Rescuing

There are certainly many examples of women behaving heroically, but physically risky, self-sacrificial heroism is commonly perceived as a stereotypically male behavior (Griskevicius et al. 2007; Iredale and Van Vugt 2009; Lyons 2005). If self-sacrificial altruistic behavior is in fact a "male thing," it should be most likely to occur when males show off and compete directly with each other for status (and ultimately for

mating opportunities). It has been established that altruistic male behavior is most effective if it takes the form of risky heroism, which displays courage and strength (Farthing 2005; Griskevicius et al. 2007; Kelly and Dunbar 2001; Sylwester and Pawlowoski 2011). Also, males are more likely to display altruism in the presence of an attractive member of the opposite sex; the same does not hold true for females (Farrelly et al. 2007; Iredale et al. 2008). This idea has clearly been around for quite some time, as illustrated by a quote from the Sioux warrior Rain in the Face. In describing the effect that the presence of women in a war party has on the male warriors, he said “when there is a woman in the charge, it causes the warriors to vie with one another in displaying their valor” (Philbrick 2010, p. 179).

The *Challenge Hypothesis* developed by Wingfield et al. (1990) provides a framework for predicting the circumstances under which male “showing off” via conspicuous self-sacrifice will be especially likely. According to this hypothesis, physiological changes such as a rise in testosterone occur in response to threats to a male’s status or the imminent threat of male-male competition, facilitating whatever competitive behaviors are necessary to meet the challenge. Thus, showing off may pay off best for a man when there is another man present that one can look superior to. Consistent with the aforementioned hypotheses, McAndrew and Perilloux (2012a, b) have confirmed that self-sacrificial male behavior is most likely to occur when females *and* another male are present.

War Heroism

War is a male activity. Organized fighting and killing by groups of women against other groups of women has simply not existed at any point in human history, and given the wide range of diversity to be found across human cultures, the consistency with which males are the organizers and perpetrators of group conflict has led many scholars to conclude that the male propensity for group violence is rooted in more than the learning of culturally prescribed gender roles.

Evolutionary psychologists have studied war and conflict with the assumption that a predisposition for warfare has evolved in males because it has historically enhanced their reproductive success. Hence, the origins of warfare and war heroism can ultimately be found in the competition between males for status and access to women.

Sexual competition for mates has always been more intense among males than among females, especially in the polygamous societies that appear to have been typical in the prehistoric human world. The stakes were very high for men in this environment, as the winners of this competition would come away with the greatest number of women (and the most desirable women). The losers ran the risk of genetic annihilation by their failure to successfully win the status and resources necessary to attract mates. Historically, powerful men have always enjoyed greater sexual access to women than men lower in the pecking order, and violence, including war, can often be traced to this grim struggle for status and mates among men.

Violence committed against the right people at the right time has commonly been a ticket to social success for men. For example, among the Yanomamo of South America, men who had killed other men, especially during wars and skirmishes with other villages, acquired significantly more wives than men who had not yet killed anyone (Chagnon 2013). Because having killed someone in war was often good for one’s reputation, many societies developed ceremonies for recognizing such accomplishments. In modern societies, these take the form of prestigious awards such as the Congressional Medal of Honor in the United States, and many countries have national holidays to celebrate the heroism of those who have fought and/or died in wars.

War heroes are held in such high esteem because they seem to act in a noble and virtuous manner, setting aside any thoughts of their own well-being for the good of their group or tribe, but conspicuous war heroism may also be a way for men to enhance their long-term reproductive fitness. Dutch psychologist Mark Van Vugt (2007) has proposed the *Male-Warrior Hypothesis* as a way of explaining why men show stronger group identification and more cooperation with in-group

members than do women during times of threat from outside groups. His theory suggests that men have evolved a predisposition to engage in collective cooperative aggression against out-groups, a tendency that has likely been strongly reinforced through culture traditions and socialization.

A team of European psychologists (Rusch et al. 2015) explored the proposition that war provides an arena for men to compete and impress both their male rivals and females who might be potential mates. In one study, they found that 464 American men who had won the Medal of Honor during World War II eventually had more children than other US service men who had not been so heroically distinguished. This is consistent with the idea that heroism gets rewarded with greater reproductive success. In a second study, 92 women rated the sexual attractiveness of men who had behaved heroically in war as being higher than that of soldiers who had served but not been identified as heroes. Tellingly, women did not show this increased attraction toward men who had behaved heroically in sports or business situations. A third study revealed that behaving heroically in war does not increase the attractiveness of female war heroes to men. In summary, heroism in time of war is sexier than any other kind of heroism, but only for men.

Young men are particularly concerned with status and heroic opportunities for sound evolutionary reasons. In early human societies, competitive success or failure in early adulthood determined a man's standing in a social group for the rest of his life. It wasn't possible to simply hit the "reset" button and join another group, so what happened during the teen years mattered a lot. For this reason, high-risk competition between young males provided an opportunity for "showing off" the abilities needed to acquire resources, exhibit strength, and meet any challenges to one's status. Consequently, heroic or even recklessly daredevil behavior was rewarded with status and respect – assuming, of course, that the young man survived the ordeal. Displaying heroism in time of war was a primary way of accomplishing these goals. Hence, it should not be surprising that historical data confirm that the concentration of young men in a population is one

of the best predictors of when a society is most likely to go to war.

War is costly and risky, and for male psychology to have evolved a predisposition for going to war, several essential conditions must be met. John Tooby and Leda Cosmides (2010) have identified four conditions that would be particularly important. First of all, successful soldiers must have greater sexual access to women than non-combatants. Secondly, coalitions of fighters must believe that they will be victorious. Thirdly, the rewards that each warrior receives must be proportionate to the risks he has taken and the importance of his contributions. In other words, cheaters should never prosper. And finally, men going to war must not know for sure who will live and who will die; there must be a protective "veil of ignorance."

Conclusion

High-risk "rescuing" behavior is most appropriately described as heroic when it involves the rescuing of individuals with whom one shares neither genes nor an ongoing cooperative relationship. There is evidence that an impulse toward physically risky heroic rescuing behavior has been more strongly selected for in males than in females. These impulses serve a noble function when they result in altruistic behavior, but these same competitive status-seeking drives are also a component of war and other aggression actions.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruism Advertises Cooperativeness](#)
- ▶ [Altruism Advertises Generosity](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism and Costs to Altruist](#)
- ▶ [Altruism Norms](#)
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- [Genuine Altruism](#)
- [Hamilton's Rule and Kin Investment](#)
- [Helping and Inclusive Fitness Benefits to Helper](#)
- [Kin Selection](#)
- [Men Riskier, More Aggressive](#)
- [Moral Instincts](#)
- [Nonhuman Reciprocal Altruism](#)
- [Psychology of Reciprocal Altruism](#)
- [War](#)

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Heroism

- [Heroic Rescue in Humans](#)
- [Rescuing Friends and Relatives](#)
- [Rescuing Strangers](#)

Heroism in War and Civil Life

- [High-Cost Altruistic Helping](#)

Heschel’s Gyrus

- [Broca’s and Wernicke’s Areas](#)

Heterosexism

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- [Sexual Prejudice \(Personality Correlates of\)](#)

Heterosexuality

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Heuristic Process

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Heuristics

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Heuristics are strategies that ignore information in order to make faster decisions. Traditional theories of decision-making (including the highly influential “heuristics-and-biases framework”; Tversky and Kahneman 1974) suggest that heuristics are suboptimal shortcuts that lead to systematic errors, trading accuracy for speed. These frameworks imply that heuristics are irrational and that decision-makers would be better off if they could avoid heuristics altogether.

In reality, heuristics are extremely sensible, having proven to be reliable tools for successfully navigating diverse situations of uncertainty (Gigerenzer et al. 1999, 2011; Gigerenzer and Gaissmaier 2011). For example, Ortmann et al. (2008) observed that, on average, stock portfolios created using the *recognition heuristic* (i.e., if one option is recognized and the other is not, choose the recognized option) outperformed unplanned portfolios, the market, managed funds, and stock experts. Heuristics are not only useful but, perhaps more importantly, they are efficient; heuristics are both fast and frugal, limiting the amount of information processed while giving comparable (if not superior) results than their more complex counterparts. Consequently, heuristics make perfect tools for situations of bounded rationality, scenarios where decision-makers have limited capacities and resources. This understanding stands in stark contrast to traditional economic

approaches, which assume decision-makers are able to invest unlimited resources in a given problem, making them untenably costly and thus unrealistic cognitive strategies.

Ecological Rationality

Ecological rationality describes robust fit of cognitive mechanisms that have evolved to solve recurrent problems in regularly encountered environments. Fast and frugal heuristics meet the criteria of ecological rationality because they reflect speed and efficiency of cognitive processing; they also reflect robust sensitivity to the structure of decision-making environments. Simon (1990) elegantly illustrated the concept of ecological rationality with a scissor analogy: Human behavior is shaped by the two interdependent blades of (1) the task environment and (2) the actor's ability to carry out a given strategy. Heuristics are useful because they are typically within the limit of the actor's capabilities, but only in certain task environments. Heuristics are also typically more robust than other decision-making tools. They are not overfitted to a single environment and can therefore be utilized in multiple contexts. Heuristics are also very specific in terms of inputs, making dealing with ambiguous contexts more tenable as they do not require having to search through all the data, just the specific criteria outlined.

Building Blocks of Heuristics

Gigerenzer et al. (1999) proposed three main building blocks of heuristics: (1) search rules, (2) stopping rules, and (3) decision rules. Search rules dictate how decision-makers search possible options. Stopping rules detail the circumstances under which the search will stop. Finally, decision rules outline how the final decision is reached.

For example, when deciding what to eat, people appear to use a *lexicographic heuristic*, tending to consider only their most important criteria (e.g., taste) instead of taking a weighted sum of all the possible criteria (e.g., taste plus

price, texture, nutrition content, convenience, ethical concerns, among others; Scheibehenne et al. 2007). In this instance, the individual dining searches through the criteria (search rule). They then find the most important criteria (stopping rule). Finally, the individual chooses the option that rates highest on that criteria (decision rule). These three simple rules outline a process that is fast, frugal, and efficient.

Examples of Heuristics

Heuristics can be used in a variety of settings, including physical, social, and group situations. For example, baseball players use the *gaze heuristic* to catch a ball flying through the air, maintaining a constant optical angle between themselves and the ball, rather than calculating the ball's trajectory in three-dimensional space (McLeod and Dienes 1996). Certain animals also use the gaze heuristic to catch prey or to pursue mates (Gigerenzer 2007; Shaffer et al. 2004).

Heuristics can also be used in social situations. Axelrod (1981) suggested that individuals often use a heuristic "tit-for-tat" strategy in cooperative situations. In utilizing this strategy, individuals initially choose to cooperate. After that, decision-makers simply replicate their partner's most recent choice: if the other person defects, the decision-maker defects. If their partner cooperates, the decision-maker cooperates. This simple strategy leads to a high chance of avoiding potentially harmful social situations, but is also extremely robust and efficient to apply.

Groups also appear to use heuristics. For example, Gonzales et al. (2017) observed that football teams make in-game decisions consistent with *risk-sensitivity theory*, which hypothesizes that decision-makers simply chose riskier options when less risky options are unable to meet a salient need (reviewed in Mishra 2014). Teams were shown to choose the riskier option of passing more frequently whenever running (the less risky option) was unlikely to attain a salient goal (i.e., getting a first down or winning the game).

Heuristics provide a useful tool for navigating a world full of uncertainty. When used in the

appropriate situation, a heuristic can be a mechanism that allows a decision-maker to make good decisions without allocating excessive resources to solving the problem. Traditional approaches to understanding decision-making ignore necessary constraints of human cognition (i.e., they reflect “unbounded” rationality as opposed to “bounded” rationality). However, an evolutionary account requires that decision-making mechanisms be fast, frugal, and robustly fitted to environments of decision-making, thus highlighting the importance of heuristics in decision-making.

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Hidden Ovulation

► [Concealed Ovulation](#)

Hide and Hurry

► [Sneak Copulation](#)

Hierarchical Climbing

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Synonyms

[Chain of command](#); [Pecking order](#); [Ranking](#)

Definition

The Webster Dictionary defines it as “the classification of a group of people according to ability or to economic, social, or professional standing,” or in simple terms, it can be referred to as “a graded or ranked series.” Hierarchy is a social order in which members of an organization are arranged according to their relative authority. This organization can be a simple unit such as a corporate institute or something as complex as the society. Hierarchical climbing in simple terms can be referred to as the process of moving up the hierarchy, up the ranks to reach a higher level which could be in terms of designation, status, money, or power.

Introduction

When you ask a child what he aspires to be in the future, the most frequent answer by any child would be “I want to be rich and successful.” If

further asked to elaborate, they will choose professions that rely on power, fame, or high-ranking officials. When you ask adults what they aspire to be in the future, replies would range from becoming the head of the department, a professor, and a chief executive officer depending on the job description currently with a bigger pay grade. Hearing these answers, one can wonder that all humans are basically similar and want the same things in life to feel content. Success is seen in the form of high-ranking jobs, money, status, and power. So how does this relate with hierarchy? Darwin proved “survival of the fittest.” The same is applicable now to humans as well. If one wants to survive, what does one have to do? Have a secure source of living, a constant, dependable job – a job which is hopefully high ranking. And here, the concept of hierarchy fits in. Hierarchy is a common property of all organizations as seen in almost all biological as well as man-made establishments (Mengistu et al. 2016). Hierarchical climbing is a concept in institutional dynamics and social network. It provides a framework within which individuals can tap their potential best. This increases their productivity, and they become more central to the society. Institutions can be seen as rules that are forced on individuals, or they can be thought of as a group of people with a common belief system (Brousseau and Raynaud 2011). It relates to our society, our offices, our institutions, and even our very own homes. It is closely associated with the concept of power, social status, and standing. This article covers the concept of hierarchical climbing in detail, the aspects related to evolution, the need, and the significance.

Evolutionary Aspects

Hierarchical climbing is not just a concept in institutional dynamics. It is a basic principle in biology and an important reason how evolution has led to the development of more complex organisms. Hierarchy promotes more stability and tenacity in systems and encourages versatility. Hierarchical evolution in biological systems arises out of natural selection: direct or indirect (Mengistu et al. 2016). Hierarchy and leadership

originally came into being to solve problems of coordination in species living in groups. Among humans, it was adapted according to our needs of solving conflicts and maintaining relations among different groups. The reason behind the emergence of hierarchy in social and corporate systems can be best explained by limited resource at disposal or by local interactions. While competing for the same resources, individuals in well-led groups are found to be more efficient. So cost of connections is a driving factor in man-made networks such as the Internet and other corporate institutions (Mengistu et al. 2016). Initially, institutions are “local and voluntary”; gradually, they evolve into more “generic and mandatory” ones. There are two distinct phases in the development of the institutional system – its environment and arrangement. Institutional environment forms the basis of interactions among the agents of a particular institution, whereas arrangement refers to contractual agreements between them. There are certain rules that are mandatory because either they are state-enforced or they represent the cultural norms of that society. New local rules are made after mutual agreements among agents. Over the course of time, these rules tend to be more widely accepted as a result of which they become nonnegotiable and mandatory. This is how evolution of an institution occurs. The best example of the above phenomenon was seen among the stockbrokers of New York in the 1800s. A small group of dealers started to abide a set of informal yet binding set of rules. This group grew in number slowly which made it all the more attractive. Being a part of this group had its own perks, for example, more partners and trustworthy records. Stockbrokers in other states formed similar systems with comparable benefits in order to compete with them. As individual agents had a plethora of options on their plates, it gave rise to competition and a refinement of the institutional network. This development of a common order in an institution is also beneficial in the sense that it supports division of labor (Brousseau and Raynaud 2011). So why do we need to climb this system, this ranking? What would we achieve? How will this affect our lives? Since we are young, what are we constantly pushed toward? To do well. First, it is the basic

academics, tests, and exams in our classes, then competitions which may be extracurricular, then competitive or entrance exams, then jobs, then perfect partner, and the cycle goes on. Life is nothing short of a competition, and to win this said competition, one has to be successful. One has to be the highest-ranking official or the head. This constant rat race which individuals find themselves in is the driving force behind the need to climb, the need to move forward. As if one is not moving forward, then he is just stuck or moving backward and faces it, and no one wants that. This is just not the inner voice in our heads but what our society makes you feel. Let alone the society, if one is not out there achieving something, this voice can take shape of the people in our lives like parents and significant others. In order to push further, add fuel to the fire, and here comes in the concept of ego. One is made to face this reality and think, even if not needed, that they really are a failure. Is everyone around them and are they stuck in actual route? So a push becomes a shove, and an unnecessary need arises in the mind of the said individual to move forward – to move ahead in the pecking order. Rank up, as this is the only way one could find the lost respect in his family and his own eyes. This is then linked up with what will happen if one ranks up – the perks, the status, and the power. Everyone views their superiors in awe – if only they had the life they had, the car they drove, the house they lived in, the clothes, and jewelry they wear. What would happen if that all could be theirs? How the current scenario would change? In this process, one may even imitate his superiors, to feel at the same place as them, the same mentality, to form a common bond. If one ranks up, the social standing and status would also rank up, improving his presence or influence per say. Here, the concept of status which can be explained as “the extent to which an individual or group is respected or admired by others” could be viewed as the benefit one would achieve as most individuals are driven by power and greed, with using hierarchical climbing as a stepping stone to achieve their goals and agendas. In this process, it works by the concept of positive reinforcement. One could reap an award, and for this to occur, one has to move up in order, which could happen if one

works hard consistently. The same concept can be further applied to power, as with a higher pecking order comes in more responsibility and power. The road to success is simple, the path of climbing up the hierarchy of the said institution. Hierarchical climbing as a concept cannot be limited to the workspaces, offices, and restaurants but also in our households. How does it apply to a household? It may seem farfetched or even comical, but the resemblance is uncanny. Running a perfect household requires planning, division of tasks, and complete execution along with someone to look over the swift functioning. Now if, per say, every individual carrying out individual tasks are at the same rank, it may lead to quarrels and constant friction, with one trying to overpower the others. This would in turn lead to a cascade of fights, eventually breaking down a well-functioning machine. So in order to having a smoothly functioning system, there is a need to delineate duties, assign them, and make sure that they are conducted in a proper manner. For this to happen in a sustainable manner, a rank is needed. There will be helps doing the menial jobs, reporting to the housekeeper who in turn will try to ensure a smooth functioning and in return reporting to a particular member of the family. The drivers and watchmen will report to another member. And these will then report to the matriarch. This micromanaging not only helps in equal division of labor but also helps in having a check on all levels. As work is individualized, there tends to be less of overstepping by peers and fewer doubts and questions. And having a superior to report to, they tend to have a satisfaction that in case anything goes down, an option to fall upon will be present. This helps those on a lower rank to have faith in the system, that someone up there will help them, which further leads to the aspiration of moving forward, moving up the order.

Significance

Societal structure depends on the incentives provided to its members. The more these members strive to climb up the social ladder, the more the hierarchical system is reinforced. It works like a

feed-forward loop. Hierarchical model is a sophisticated model of the society in which every person attempts to strengthen his place in the society by trying to become as central as is possible. The basis of hierarchical climbing is organization. It clearly defines the position and the role a member plays in the institution and lays down the chain of command. It helps avoid any uncertainty in goal setting and the path taken to achieve that goal. The person's importance in the network is defined by his centrality. A disordered system creates chaos and confusion as the members struggle to find out with whom they should connect in order to attain a central position in the society (Bardoscia et al. 2013). In institutions requiring high interdependence such as the army or mountain climbing expeditions, the benefits of hierarchy are more pronounced. Individual incentives for high social status are enough to confer this property to the social network, even in the absence of explicit discrimination of particular groups (e.g., caste system or racial segregation) or preferential biases (e.g., hereditary rules). In addition the hierarchical state is more or less stable with reduced social mobility in the extreme sections of the hierarchy. More structured the hierarchy is, a lesser degree of mobility is seen. It is tempting to relate this to the pervasive empirical observation that more unequal societies tend to have lower intergenerational mobility. Wealth or political power is likely to contribute to reinforcing our results. Also, we show that the social climbing game admits a potential function, thereby allowing us to deploy techniques and concepts of statistical mechanics to understand the behavior of the system. The appearance of a social hierarchy in a system of *a priori* identical individuals is an example of a random breakdown of symmetry, in which the resulting ergodicity loss accounts for a reduced social mobility.

Practical Aspects

Hierarchy might as well be considered as a double-edged sword. It has the ability to bring out the best as well as the worst in an organization. Since social mobility has been found to be limited

at the extremes of social order, it brings about a feeling of psychological insecurity (Bardoscia et al. 2013). Members who are low down in the ladder of social ranking become hesitant of voicing their opinions. Quite often, they are dissuaded from doing so. Sometimes individuals avoid contributing with their opinions so as to avoid challenging the hierarchy. Functional accounts of hierarchy propose that hierarchy increases group coordination, whereas dysfunctional accounts claim that hierarchy impairs performance by preventing low-ranking team members from voicing their perspectives. When strong values of hierarchy are instilled in a group, it leads to a well-planned effort, but it can also stifle the voice of the lower-ranking members of the order in the face of adversity. It has been observed that institutions allowing lower-ranked team members to voice their concerns instilled in them a feeling of confidence. They were also able to identify any errors in their methods and could avoid any adverse repercussions of their decisions (Anicich et al. 2015). The hierarchical state is found to be more or less stable with minimal mobility in the extremes. Social mobility is highest in the middle class. More structured societies tend to exhibit lower social mobility. Social hierarchy stabilizes gradually giving rise to social elites that grow over time with wealth and power acting as strong influences.

Conclusion

Hierarchy is necessary so as to encourage people to tap their unmet potential as it encourages competition. Discrimination and development of power elites is detrimental to the social order as it defers the promotion of individuals higher in the social order according to their capabilities. Inequality is admissible if categorization is on the basis of capabilities rather than a result of discrimination (Bardoscia et al. 2013). All members of a society must have access to similar opportunities for growth and must be treated as equal. All in all, this strategy gives a base for not only our institutions but the society as well. This concept applies even on the grassroots level to the

simplest of organizations, for example, a small café serving coffee to the multinational companies with offices spanning the entire globe. History has been evidence enough that this concept helps in the smooth functioning of most and helps restore faith in it as well. It may not only lead to a formation of comradery with peers or individuals at the same level who experience the same hardships but also help in the formation of a two-way channel between different ranks, with each having a particular role to play, helping in the proper functioning. Although it may have a few disadvantages, these are outweighed by the advantages and the evidences. Further, the correlation with ranking up the scale for the opportunity to grasp a higher social standing and power substantiates the need for the same, establishing the practicality. Finally, it helps instill a belief, a hope for a better future, filled with infinite number of opportunities and doors as one moves up this hypothetical ladder to reach a gateway of endless benefits.

Cross-References

- [Imitation of High-Status Others](#)

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Hierarchical Position

- [Height and Dominance](#)

Hierarchies

- [Baringa's \(1996\) Crayfish](#)
- [Status Hierarchies](#)

Hierarchy

- [Dominance, Testosterone, and Cortisol](#)
- [Reputation as a Context for Men's Aggression Against Men](#)
- [Sex Differences in Pursuit](#)

High Achiever

- [Tall Poppy](#)

High Blood Pressure

- [Hypertension](#)

High SES Against Redistribution

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Synonyms

[High SES low egalitarian instincts](#); [High SES low support for redistribution](#); [Opposition to economic redistribution](#); [Resistance to welfare policies](#)

Definition

Individuals with higher socioeconomic status (SES) tend to be against the distribution of resources, aiming at securing advantages over others.

Introduction

Status emerged as an evolutionary solution consisting of the establishment of simple rules to avoid and resolve conflicts in hierarchical groups. In the environments of forage societies, acquisition and sharing of resources were key issues for the survival of individuals and groups. Thus, the process of cooperation and competition was a determinant of survival. Within social groups, these processes of exchange of resources could generate competition or hostility, culminating in conflicts between group members. To avoid this costly relationship, many species of primates have developed ways to minimize possible social conflict by imposing simple systems to determine access and control over scarce resources, such as the concept of status. In modern societies, individuals with high socioeconomic status (SES) tend to oppose resource redistribution. The explanation for this opposition to economic redistribution derives from adaptive cognitive and motivational mechanisms that were selected in the evolutionary process to solve resource allocation problems (Kurzban and Neuberg 2005; Sidanius and Kurzban 2013; Sznycer et al. 2017).

Redistribution and Status

In modern times, redistribution refers to the change in the distribution of resources in a population resulting from a political process. As in other decision-making processes, support for redistribution occurs through the processing of specialized computational systems of human cognitive architecture. It is necessary to understand the evolutionary origins of the motivational processes that result in opposition or support for redistribution. For example, among primates,

dominant males generally have more control over scarce resources, including partners, increasing the likelihood of reproductive success (e.g., greater chance of survival for offspring, more offspring; Kappeler and van Schaik 2002). The same is true for dominant females, as status positively affects their nutrition, which increases their likelihood of reproductive success. That is, resource management impacts on the survival and reproductive success of individuals, so sharing or distributing is an adaptive problem.

Differences in access, control, and redistribution of resources can motivate conflicts. Status and hierarchy relationships are dynamic, and disadvantaged groups can get organized to force redistribution of resources. In the same way, dominant groups or individuals can come together to secure their position within a social hierarchy. Then, status emerges as a strategy for hierarchical classification within groups, signaling access to social (individual or group) and economic resources. This strategy creates implicit social rules about the distribution of resources, with the function of avoiding or minimizing costs with competition and constant conflicts over scarce resources.

In modern societies, the socioeconomic status (SES) derives from this notion of status. Individuals with higher SES are those with higher levels of wealth, such as privileged access to income, education, and occupation. People with higher SES are less likely to support policies that redistribute wealth and have less favorable feelings toward economic redistribution (Brown-Iannuzzi et al. 2015). Humans balance prosocial motivations with self-promotion to deal with social hierarchy relationships (Petersen et al. 2012; Sznycer et al. 2017). Even in scenarios in which cooperative relationships are necessary for group survival, sharing arises only as a form of maintenance of the type of resource distribution. Cooperation through controlled resource distribution functions as a strategy for self-promotion and building alliances or coalitions (Kurzban and Neuberg 2005). Social badges, such as speech or dress code, are used to assess the extent to which others are expected to cooperate in promoting group interests. These cues act as markers that guide the selection of

alliances or coalitions by creating a behavioral expectation through the share of common social norms. Thus, individuals promote self-interest and, at the same time, reduce the social costs of coercive or dominant strategies through prosocial gestures.

Motivations for Redistribution

Humans have interacted with individuals with varying levels of access to resources or SES throughout evolution, and our motivational systems may have been naturally selected to deal with the challenges and opportunities arising from these social relationships. Therefore, the personal standpoint on the redistribution of income and wealth among human beings permeates often unnoticed aspects. For example, in men, physical strength shapes the support for redistribution (Petersen et al. 2013). Among men with lower SES, physical strength predicts support for redistribution and among men of higher SES, the opposite. This is probably because physical strength is a relevant aspect of the ability to fight. Individuals with higher fighting ability will tend to acquire or defend resources rather than less skillful competitors. As personal strength is irrelevant to compensate for economic policies in modern societies, one can conjecture that decision-making on redistribution is shaped by a psychology designed by evolution for small groups. Among human, relations of cooperation, such as sharing of resources, occur mainly between individuals with some degree of kinship. It commonly occurs as a partner attraction/retention strategy or to form/preserve status (White et al. 2013).

Our ancestors were constantly in social situations where they had to solve problems, among others, related to the distribution of resources. The human mind was designed by evolution to seek clues and to provide emotional responses to evolutionarily recurring challenges and opportunities regarding the social distribution of resources (Sznycer et al. 2017). For example, humans are more motivated to share when they are subject to chance-driven interruptions and less motivated

when they think they are being exploited by low-effort free riders. The motivation to share with nongenetically close individuals has evolved as a defense mechanism against opportunists, low-effort free riders. Petersen et al. (2012) found anger and compassion as the main motivators of these mechanisms. Encountering individuals who accept help without contributing, such as intentional avoidance of a productive effort (i.e., parasitic strategies), triggers anger and decreases support. The subjects' perceptions of the recipient's effort (e.g., search for work) regulate compassion and anger which in turn mediate views about well-being. To corroborate this assertion, a research conducted by Kim and Lee (2018) analyzed data from 28 countries and identified that the perception of inequality of opportunity is a potential moderator of attitudes toward redistribution for people at all SES levels. There is an expectation that opportunities can be equal and thus the acquisition of resources would be based on individual efforts in a fair competition.

In this way, individuals with higher SES can interpret redistribution policies as a way to benefit subjects using parasitic strategies, while lower SES are less prone to this interpretation precisely because they have less access to resources. It is only in a scenario where it is explicit that the conditions of opportunity are unequal that subjects of higher SES could support policies of redistribution.

Still, other factors must be considered. A study conducted by Sznycer et al. (2017) mapped the motivations that shape attitudes toward redistribution. For this, they started from the premise that modern redistribution is perceived as an ancestral scene involving three actors: the other in need, the other in a better situation, and the actor himself. This scene would be the central aspect in the individual understanding of redistribution in modernity. The motivation to accept redistribution would then be shaped by a mixture of humanitarian and resentful motives foreseen by this ancestral game model. The motivations that predicted support for redistribution were compassion, envy, and self-interest. Although justice is central to many of the arguments for redistribution, it has had little or no effect on support for

it. Thus, individuals with higher SES faced with this ancestral scene would be led more by the motivations of envy and self-interest rather than compassion or justice. Another motivational aspect that can help explain why people with higher SES tend to be against redistribution is social dominance. From this perspective, individuals would have evolved to achieve and maintain social dominance over other groups (Sidanius and Kurzban 2013). In order to favor group superiority, it is necessary to accumulate resources and resist redistribution.

Conclusion

In general, individuals with higher SES tend to oppose measures of economic redistribution. This is due to a series of cognitive and motivational mechanisms shaped by evolution to solve problems related to the distribution of resources in forage societies. In modern times, these systems end up reflecting individual attitudes about redistribution (e.g., anger, compassion, self-interest). In addition, status, by creating a stable system to distribute scarce resources without constant conflict, is considered to be adaptive. At the individual level, it guarantees access to resources; and at the group level, while creating inequalities, hierarchy provides stability for cooperative relations without open, constant, and widespread competition among group members. Therefore, individuals in a privileged position tend to wish for the permanence of the distribution of resources and oppose redistribution policies. For, in evolutionary terms, it is advantageous for individuals of higher SES to maintain the social hierarchy, both at the individual and group level.

Cross-References

- Access to Resources
- Cooperation
- In-Group Versus Out-Group
- Redistribution Preferences and Low Socioeconomic Status
- Robert Kurzban on Group Processes

- Status and Dominance Hierarchies
- Status and Redistribution of Resources

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High SES Low Egalitarian Instincts

- High SES Against Redistribution

High SES Low Support for Redistribution

- [High SES Against Redistribution](#)

High Status

- [Popular Children](#)
- [Reputation](#)

High Status Individual

- [Tall Poppy](#)

High-Cost

- [Rescuing Strangers](#)

High-Cost Altruism

- [Rescuing Friends and Relatives](#)

High-Cost Altruistic Helping

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Synonyms

[Heroism in war and civil life](#); [High-cost helping](#);
[High-stakes altruism](#)

Definition

In acts of high-cost altruistic helping, substantial risks to the own well-being or considerable losses of social and/or economic capital are voluntarily incurred in order to benefit others.

Introduction

Thomas H. McCann was one of the first recipients of the Carnegie Medal for civil heroism. On June 29, 1904, McCann jumped from a bridge 25 ft high into Portland Harbor and dragged Alfonso Sekosky, an 8-year-old boy, to safety on a boat, but was too fatigued to get into it himself and was drowned. McCann's case is quite representative: since its inception in 1904, the Carnegie Medal has been awarded to almost 10,000 "individuals in the US and Canada who risked their lives to an extraordinary degree saving or attempting to save the lives of others" (carnegiehero.org, September 2016). About 20% of the recipients of the Carnegie Medal did not survive their attempts to help others (Becker and Eagly 2004).

Why is it that ordinary people like McCann, who was only 32 years old at the time of his death, voluntarily take such tremendous risks to their own well-being in order to help others? Or, asking from the biological perspective, how can such prosocial behavioral inclinations be conserved or even be promoted by evolutionary forces, if they substantially increase the chance that their bearers eliminate themselves from the human lineage?

This entry reviews potential answers to these questions in light of the available empirical evidence. After a brief clarification of terms, the first main section focuses on theories that can explain the preservation and propagation of prosocial behavioral traits that cause high costs to their bearers. The second section discusses the problems that research on high-cost helping faces, before the third and fourth sections review the evidence available from controlled experimental studies and the analysis of documented historical cases of high-stakes prosocial behavior in the domains of civil life and warfare. The concluding

section points out important open questions and suggests directions for future research.

Disambiguations

Dying in the course of his heroic action, Thomas H. McCann paid a high price, his own life, for the protection of a boy who, presumably, was a total stranger to him. But what if he had died rescuing one of his sons instead? Would we think of his action as equally honorable? If we take the eligibility criteria of the Carnegie Medal as a proxy for prevalent societal norms about which kinds of actions are considered heroic, then the answer is “yes”: “Persons not eligible for awards are: [...] members of the immediate family, except in cases of outstanding heroism where the rescuer loses his or her life or is severely injured” (carnegiehero.org). Still, callous Darwinian evolutionary logic states that the price paid by McCann is higher, *ceteris paribus*, than the one a father pays when dying for the life of his offspring. Obviously, thus, the Darwinian costs of high-stakes prosocial behavior can differ. Therefore, before we review potential explanations for how such behaviors might evolve, let us briefly recapitulate the underlying evolutionary calculus.

The currency of natural selection is fitness, which can be approximated as the expected number of copies of a given gene that an individual is able to successfully pass to the next generation. Therefore, when analyzing the prospects of evolutionary success of a certain behavioral trait coded for by one or multiple genes, we need to take into account that trait’s *direct* fitness consequences on its bearer, as well as its *indirect* fitness consequences on individuals bearing the same gene or genes. Furthermore, it is important to note that the fitness balance, F , of a certain trait can only be evaluated after aggregation over the *entire lifetimes* of all individuals affected by the behavior, because both direct and indirect fitness consequences, D and I , respectively, can each have an immediate and a delayed component. For short, let us define the fitness balance of a trait as: $F = D_{\text{now}} + I_{\text{now}} + D_{\text{later}} + I_{\text{later}}$. As we will see, all of these components can play crucial

roles in explanations of the evolution of high-cost prosocial behaviors and altruism, which, in terms of direct and indirect fitness consequences, can now be defined as follows.

According to West et al., four types of behavioral traits need to be carefully distinguished, based on their *direct* fitness consequences (i.e., $D_{\text{now}} + D_{\text{later}}$) for the acting individual: *mutualistic* “+/+” behaviors benefit all affected parties, *spiteful* “-/-” behaviors cause costs for all parties, *selfish* “+/-” behaviors benefit the acting individual at a cost to those affected, and *altruistic* “-/+” behaviors benefit those affected at a cost to the actor (West et al. 2007). While natural selection can potentially favor mutualistic and selfish behaviors straightforwardly, because of their positive effects on direct fitness, spiteful and altruistic behaviors can evolve only if their negative effects on direct fitness are offset by sufficiently high indirect fitness benefits, i.e., if their *inclusive fitness* balance is positive.

One important point to note about this definition of altruism is that not only the immediate direct fitness consequences of a behavior need to represent a cost to the acting individual but that their overall direct fitness effects need to be negative, i.e., $D_{\text{now}} + D_{\text{later}} < 0$. Thus, if the immediate direct costs of behaving to the benefit of others are offset by direct benefits accrued later, such behavior does not fall under the category of altruism *sensu* West et al. but represents mutualistic behavior instead. To avoid terminological confusion, thus, we will refer to any kind of action to the benefit of others as “helping” and only speak of altruism if $D_{\text{now}} + D_{\text{later}} < 0$ actually holds for a specific action.

A second important point to note is that the effective costs of a certain type of prosocial behavior can differ between individuals. Obviously, the risk of drowning while swimming to the rescue of a person in distress is much lower for an experienced and athletic swimmer than for someone who swims only infrequently. That means: for the latter $D_{\text{now}} < 0$ likely holds, while the experienced swimmer is more likely to face a $D_{\text{now}} \approx 0$ type of risk. The classification of an action as “costly,” thus, requires a thorough prior evaluation of the fitness effects an action

potentially has on the respective acting individual. As will be discussed later, this second point mainly is a problem for empirical studies on helping behavior. The theories reviewed in the following section, however, can all explain how helping might evolve also when it is effectively costly, i.e., when $D_{now} < 0$.

Theory: How Can Helping Evolve, Particularly if It Is Extremely Costly?

Numerous theories exist that can explain how behavioral traits causing immediate direct fitness losses to their bearers might eventually be preserved and even favored by natural selection (see, e.g., Kurzban et al. 2015; Nowak 2012, for overviews). Using the terminology just introduced, their common rationale can be summarized as follows. In order for such a trait not to go extinct in the long run, its inclusive fitness balance, F , must be zero or positive. If one or more of the terms of this sum are negative, thus, at least one of the other terms must be positive and large enough to compensate for the negative terms.

All theories on the evolution of costly helping behavior start from the assumption that $D_{now} < 0$. They differ in their assumptions about which other components of the inclusive fitness balance are eventually compensating for these costs (see Table 1). The first set of theories – *costly signaling*, *direct reciprocity*, and *indirect reciprocity* – all identify delayed direct fitness benefits to the helper, D_{later} , as the compensating factor. Costly helping of this kind, thus, does not represent altruism sensu West et al. (2007). Let us briefly review these theories in turn.

Costly signaling. The main idea behind the theory of costly signaling is that individuals differ

in characteristics that determine their attractiveness to others as social and/or sexual partners but that are not directly or reliably observable (Spence 1973; Zahavi 1975). By engaging in costly helping, those individuals who can afford the respective costs, e.g., because they are physically fit or wealthy enough to do so, can reliably signal two characteristics that increase their attractiveness: their physical or economic capabilities and their prosociality. Such unforgeable public displays, in turn, increase the chances for the signalers to benefit from social interaction with choosy high-quality partners later on, by whom they might otherwise have been ignored (for further discussion, see, e.g., Barclay 2011).

Direct and indirect reciprocity. While the recipients of help eventually play no role other than causing a cost to the signaler in costly signaling theory, they are more important for the theories of direct and indirect reciprocity (Nowak and Sigmund 2005; Trivers 1971). Direct reciprocity theory assumes that the initial cost of helping is eventually overcompensated by the returns from a longer-term cooperative partnership between the helper and the recipients of help that results from this initial act of benevolence. Indirect reciprocity theory, on the other hand, assumes that helper and recipient might never meet again. Instead, the cost of helping here is compensated indirectly through help that the helper herself receives from third parties later on who base their decisions to help on reputation. In order to maintain a good reputation, and thus to receive help if needed, one must help others if they are in need. Hence, under regimes of indirect reciprocity, costly helping buys helpers access to a community of cooperative social partners and

High-Cost Altruistic Helping, Table 1 Overview of potential explanations for the evolution of helping behavior classified by their immediate direct, D_{now} ; delayed direct, D_{later} ; immediate indirect, I_{now} ; and delayed indirect, I_{later} , fitness consequences

Theory	D_{now}	D_{later}	I_{now}	I_{later}	F	Costs compensated by
Costly signaling	–	+	0/–	0/+	>0	$D_{later} + I_{later}$
Direct reciprocity	–	+	0	0	>0	D_{later}
Indirect reciprocity	–	+	0	0	>0	D_{later}
Inclusive reciprocity	–	–	0/–	+	>0	I_{later}
Kin selection	–	–	–/0/+	+	>0	$I_{now} + I_{later}$
Mismatch	–	–	–	–	<0	Nothing

eventually makes them better off than living in a community of non-helpers (for further discussion, see, e.g., Roberts 2008).

As we have just seen, the three previous theories assume delayed, but positive, direct benefits to the helper, i.e., $D_{later} > 0$. One might be tempted to interpret this assumption as meaning that these theories only work in case helpers always survive, because otherwise they cannot benefit from these delayed direct fitness benefits. This is not the case, though. All that $D_{later} > 0$ requires is that there is a positive chance of surviving for the helper, because what counts from the evolutionary perspective is not the fate of any single individual, but rather the “average fate” of all bearers of a specific trait over a longer period of time, of course. Still, there are at least two theories that can potentially also explain the evolution of traits that lead to their bearers’ death with certainty, i.e., theories that work even if $D_{later} < 0$.

Inclusive reciprocity. The first of these theories, inclusive reciprocity, is an extension of the theory of indirect reciprocity (Albert and Rusch 2013). Its central idea is that reputation is not necessarily limited to individuals, but can span entire groups or families of individuals. If parental reputations are inherited by the offspring, e.g., altruistic behavioral traits can evolve that cause a parent’s death, if they lead to a sufficiently high increase of the offspring’s reputation, i.e., if they make I_{later} sufficiently large. Note that under inclusive reciprocity, altruistic traits can evolve even if they do not benefit the offspring directly in any way and even if they cause immediate costs to them, because inclusive reciprocity works through delayed indirect benefits.

Kin selection. The other theory that is potentially able to explain the evolution of “lethal helping” is kin selection, i.e., inclusive fitness theory. Just like inclusive reciprocity, kin selection theory assumes that direct fitness costs to the helper are eventually compensated by indirect benefits, i.e., benefits to the helper’s kin. The main difference between the two theories is that inclusive fitness theory assumes that the act of helping itself causes these indirect benefits, while inclusive reciprocity assumes that they are mediated by the reputational gains that the act of helping causes for the

offspring of the helper, i.e., by “family reputation.” Inclusive reciprocity, thus, requires that individuals are able to track reputations and to condition their behavior on them, while inclusive fitness theory is less demanding. Kin selection only requires that altruistic acts have positive indirect effects on helpers’ kin in the long run. Note that this does not even require that individuals are able to discriminate between kin and non-kin. All that is needed is a clustering of kin groups in a given population such that the average expected fitness consequences of helping are higher for relatives of the helper than for non-kin (Kümmerli et al. 2009).

Mismatch. Before we move on to discuss how the explanatory value of the theories just outlined could be tested on the background of the available evidence on acts of high-cost helping behavior, one important possibility must not go unnoticed. As is known, natural selection usually works slowly. Given that, from an evolutionary perspective, the time during which humans lived in small bands of quite closely related mobile hunter-gatherers is “just” over, contemporary high-cost altruistic helping, i.e., helping with $D_{now} + D_{later} < 0$, may have become dysfunctional through the rapid changes in human social organization over the last 15k years. Therefore, while such prosocial behavior may have had significant positive effects on kin in ancestral times, the “mismatch hypothesis” states that these effects are no longer present today and that evolution might simply not have caught up with this fact.

The Intricacies of Studying High-Cost Helping

It is not hard to see that testing the aforementioned theories against each other is not a straightforward task. While the mismatch hypothesis makes for a suitable null hypothesis, and may thus receive some support in case all alternative theories should fail, researchers trying to find supportive evidence for these alternative theories face numerous problems.

One intricacy on the theoretical side is, for example, that many of the suggested explanations for the evolution of high-cost helping are not mutually exclusive. As can be seen from Table 1, evidence of delayed direct benefits, $D_{later} > 0$, for

instance, can yield support for costly signaling as well as for direct and indirect reciprocity. Disentangling further which, if any, of these three theories receives more support if evidence for $D_{later} > 0$ is actually found, thus, requires refined research designs and/or more fine-grained data gathering efforts.

On the empirical side, on the other hand, researchers of high-cost helping behavior face even more taxing challenges. For obvious reasons they cannot put experimental subjects into life-threatening situations or confront them with decision situations involving other types of high personal costs. To work around this problem, at least three approaches to approximating such situations under controlled conditions have been used in the literature. Naturally, they all have their respective up- and downsides.

The first commonly used approach is to focus on the question of how – real or fictitious – persons who engaged in high-cost helping are perceived by third parties. Using this approach, researchers can experimentally manipulate certain characteristics of the helper, the recipients of help, the situational context, etc. The second approach is to ask subjects how they would behave in hypothetical scenarios requiring high-cost helping – the characteristics of which can again be experimentally manipulated, including the priming of subjects with mind-sets of interest, like mating motives or high group coherence. Of course, both these approaches face the common problem that the data they yield stem from self-reports and are not readily generalizable to the real-world analogs of the persons and situations studied in the laboratory. They are, however, able to establish causal relations, which makes them an indispensable tool in the study of high-cost helping.

Apart from using self-reports, researchers have also used economic decision-making experiments to study high-cost helping. In these, subjects are endowed with money and asked to decide if they would like to use their endowment to help one or multiple persons in need. In addition to being able to reveal causal relations as well, the second benefit of studies of this kind is that subjects make decisions that have real monetary consequences for themselves and other persons. Through

increasing the size of the endowment, these studies can then approximate situations of helping at high personal costs. Apart from the practical challenge that such studies can become arbitrarily expensive, they face at least three additional problems. The first is that endowments usually are “windfall” money to the subjects, i.e., free money that they might spend more laxly than money they earned outside the laboratory. The second problem is that the same amount of money may be of quite different value for different subjects. Comparisons of economic decisions between individuals, or even countries and cultures, therefore, should ideally simultaneously control for individual- and group-level differences in wealth and in the endowments’ purchasing power. The third problem, finally, is fittingly captured in the commonplace that “money can’t buy everything,” meaning that even decisions involving very high monetary stakes may psychologically not have the same gravity as fitness relevant decision situations involving immediate threats to one’s survival and/or reproductive prospects.

Complementary to studying high-cost helping experimentally under controlled conditions, a second main branch of the literature has developed that analyzes data on documented historical cases of such behavior (also see Rusch 2016). Just like all other studies that are based on historical data, this branch of the literature faces all the problems caused by the impossibility to control the conditions from which these data originate, of course. These problems include, but are not limited to, sampling bias, undetected confounding factors, data availability, and measurement problems.

Sampling bias, for instance, represents a potential obstacle for researchers who gather case data from sources like the Carnegie Hero Fund. Naturally, those cases of civil heroism available from this source were selected for being publicly honored by the fund’s selection committee. The underlying process of nomination, screening, and eventual selection or rejection by this committee might, of course, be influenced by shifts in societal norms, changes in the composition of the committee, adjustments of the eligibility criteria or new views on how they are to be interpreted, etc.

Apart from potentially biasing selection committees' work, societal norms can also represent confounding factors that may affect research using historical data, of course. The fact, e.g., that – to date – there is only one woman among the roughly 3,500 recipients of the highest US military award, the Medal of Honor, must not be taken to indicate that women are very unlikely to behave bravely in combat. Obviously, instead, women simply did not have the opportunity to display such bravery until the fourth quarter of the twentieth century during which they were gradually admitted to all branches of the US military. Other important potential confounders include contraceptives, which interfere with the study of reproductive success after the 1950s, or socioeconomic status and urbanization which may reduce the exposure of individuals to certain types of life-threatening situations.

In addition to being subject to these aforementioned complications, finally, research on historical cases of high-cost helping virtually always suffers from limited data availability. Trying to track the reproductive success of specific individuals, e.g., is a time-consuming endeavor and usually results in incomplete data. A standard problem in this process is the identification of extramarital offspring, which is usually impossible. Furthermore, the available information on specific individuals, even if accessible, often is limited, thus forcing researchers to either base their analyses on sub-optimal proxy variables or even to leave interesting questions unanswered.

In summary, research on high-cost helping faces both theoretical and, maybe more importantly, numerous practical problems. Still, as the following sections will show, a number of instructive empirical studies on this type of behavior exist. They are listed in Table 2. Although each of these studies faces specific limitations, some of which were just outlined, a number of more general insights already become apparent from the overall picture drawn by the available evidence. Therefore, instead of describing each study individually, the following two sections try to summarize these more general insights.

Evidence from Controlled Experimental Studies on Helping Behavior

The standard paradigm for studying costly helping behavior in economic experiments is the dictator game. In this game, subjects are randomly matched into pairs. One subject is then assigned the role of the dictator and the other the role of the recipient. The dictator receives an endowment from the experimenter and can decide how much of it she would like to share with the recipient. The recipient, on the other hand, does not make any decisions. Experimental designs usually ensure that dictators can make their decision in private and that dictator and recipient do not know each other, cannot communicate, and are very unlikely to meet after the experiment. Generally, thus, the aim of dictator game designs is to make sure that dictators do not have to fear any negative consequences, but also cannot expect any positive ones, irrespective of what they decide. Still, across studies (Engel 2011) and across cultures (Henrich et al. 2001), remarkable proportions of dictators decide to share a part of their endowments with the recipient, 28% on average (Engel 2011). As discussed above, however, these endowments are usually comparably small.

Stakes effects in dictator games. What happens, now, when endowments are increased? Two recent meta-studies tried to tackle this question (Engel 2011; Karagözoğlu and Urhan 2016) and arrived at mixed conclusions. Analyzing data on average giving rates in 158 experimental conditions from studies in which endowment sizes were systematically varied, Engel (2011) finds that increasing endowment size seems to have a small negative effect on dictators' willingness to share. However, for his larger sample of 440 conditions from dictator games for which dollar equivalents could be computed, Engel finds no such effect, with stakes ranging from \$0 to \$130. Karagözoğlu and Urhan (2016) arrive at similarly mixed conclusions. Intriguingly, a recent study on the giving behavior of dollar millionaires, furthermore, found millionaires playing with an endowment of €100 to make the most generous dictator game decisions observed in the literature so far (Smeets et al. 2015).

High-Cost Altruistic Helping, Table 2 Synopsis of the existing literature on high-cost helping

Study	Method	Data source/s	Main findings (paraphrased)
<i>Economic studies on voluntary helping</i>			
Engel (2011)	Meta-study, econ	Dictator game studies	Average share given: $\approx 28\%$ ($N = 616$); Small negative effect of endowment size ($N = 158$)
Smeets et al. (2015)	Exp.	Millionaires playing dictator games	Millionaires are much more generous in the dictator game than other samples
Karagözoğlu and Urhan (2016)	Meta-study, econ	Multiple game types	Negative effects of endowment size in multiple dictator game studies
<i>Controlled laboratory studies on high-cost helping</i>			
Kelly and Dunbar (2001)	Rating exp.	Mixed sample ($N = 120$)	Females prefer risk-prone brave males to risk-averse non-brave males, and men are aware of this preference
Farthing (2005)	Rating exp.	Students, two exp. (N 's = 100/117)	Females and males preferred heroic physical risk takers as mates, preference stronger in females
Griskevicius et al. (2007)	Exp.	Students, four experiments (N 's ≈ 200)	Experimentally induced romantic motives produce strategic and sex-specific displays of helping and consumption
Barclay (2010)	Rating exp.	Students ($N = 175$)	Altruists more desirable for long-term relationships than neutral individuals
Moore et al. (2013)	Rating exp.	Mixed sample ($N = 77$)	Reports of helping behavior increased the attractiveness of both men and women as potential long-term sexual partners
Rusch et al. (2015)	Rating exp.	Students, two experiments (N 's = 92/340)	Females regard men more sexually attractive if they are war heroes; no effect for male participants judging female war heroes
<i>Studies analyzing historical case data on high-cost helping</i>			
Blake (1973)	Hist. data	Medal of Honor ($N = 325$)	Potential biases in selection process of Medal of Honor recipients are discussed
Blake and Butler (1976)	Hist. data	Medal of Honor ($N = 207$)	Two types of distinguished actions are identified: "war winning" and "soldier saving"; the former is most clearly associated with officers and the latter with low-ranking enlisted men
Blake (1978)	Hist. data	Medal of Honor ($N = 207$)	"Altruistic suicide" is found to be higher in more cohesive than in less cohesive groups and more likely among enlisted men than among officers
Riemer (1998)	Hist. data	Medal of Honor ($N = 125$)	Partial replication of Blake (1978)
Rusch (2013)	Hist. data	Medal of Honor ($N = 966$)	Altruistic behavior toward comrades seems to occur more frequently when soldiers are on the defensive
Rusch and Störmer (2015)	Hist. data	Medal of Honor ($N = 988$)	Descriptive information on 988 Medal of Honor recipients of WWI, WWII, Korea, and Vietnam
Rusch et al. (2015)	Hist. data	Medal of Honor ($N = 123$)	Proxies for reproductive success are compared between 449 regular veterans and 123 surviving Medal of Honor recipients of WWII; results suggest that the heroes sired more offspring than the regular veterans
Lay et al. (1974)	Hist. data	Carnegie Medal ($N = 101$)	Men directly intervene in emergencies more often than females; responsive bystanders tend to act alone; rural people are more heroic than urban people
		Toronto Metropol. Police Civilian Citations ($N = 147$)	
Johnson (1996)	Hist. data	Carnegie Medal ($N = 676$)	Detailed analysis of actions of Carnegie Medal recipients focusing on the relationship of rescuers with the recipients of help

(continued)

High-Cost Altruistic Helping, Table 2 (continued)

Study	Method	Data source/s	Main findings (paraphrased)
Becker and Eagly (2004)	Hist. data	Carnegie Medal ($N = 8,706$)	Carnegie medalists are disproportionately men, but other actions yield representations of women that were at least equal to and in most cases higher than those of men
		Righteous Among the Nations ($N = 10,343$)	
		Kidney donors ($N > 60$ k)	
		Peace Corps volunteers ($N = 9,622$)	
		Doctors of the World applicants ($N = 76$)	
Lyons (2005)	Articles	UK Newspapers ($N = 286$)	Males were highly more likely to rescue than females, the typical rescuer was a low status male rescuing another male
Rand and Epstein (2014)	Testimonies	Carnegie Medal ($N = 51$)	Self-reports by Carnegie Medal recipients about their decision to act were judged to be overwhelmingly dominated by intuition
McNamee and Wesolik (2014)	Interviews	Carnegie Medal ($N = 30$)	Carnegie Medal recipients' parents' expectation that they help others was the only parenting factor that differentiated the Carnegie Heroes from a random sample

With respect to high-cost helping, thus, the existing literature on dictator games suggests two things. For one, the readiness to share wind-fall money with others may be relatively insensitive to stake size. From a methodological perspective, this could be regarded as good news, as it yields some support for the assumption that costly helping behavior can be studied in the lab using comparably small stakes without losing too much generalizability. Importantly, however, the range of stakes used in the existing dictator game literature is still limited to three-digit dollar amounts. We currently do not know what happens if stakes are increased beyond this (for further discussion, see Karagözoğlu and Urhan 2016). For the other, as the millionaire study by Smeets et al. (2015) indicates, it is important to keep in mind that the same monetary stakes may be of very different value for different subjects. Revealingly, when asked by Smeets et al. to explain their decisions, many of the millionaires gave answers like “With my money, 100 euro is easy to give” (see the supplements to Smeets et al. 2015).

Rating studies. A somewhat clearer picture emerges with respect to the results of studies that asked participants to rate fictitious persons who engaged in high-cost helping. Focusing

predominantly on high-cost helping as an honest signal of desirable qualities as a mate, the existing studies consistently find positive effects of helping on ratings of attractiveness. In addition, Griskevicius et al. (2007) report that subjects who were experimentally manipulated into a mating mind-set self-reported a higher readiness to engage in certain types of costly helping behavior toward third parties. Thus, convergent evidence exists in the literature that costly helping does increase perceived attractiveness and that it may also be used, intentionally or unintentionally, as a means to display personal qualities on the mating market. The literature is less univocal, however, with respect to the question if using costly helping as an honest signal is a sex-specific phenomenon or not. While Griskevicius et al. (2007) report that their experimental manipulations yield stronger effects in men, many other studies find that both men and women positively react to displays of costly helping by rating helpers as more attractive than both non-helpers and neutral persons with otherwise identical characteristics. Furthermore, the literature also is inconclusive with respect to whether helpers are preferred as long-term or short-term partners or both. Unfortunately, because of the focus of most studies on costly

helping as an honest signal in the context of mating, the literature also does not offer a decisive answer with respect to the question of whether there are additional benefits to costly helping through indirect reciprocity. At least, Kelly and Dunbar (2001) report that helpers are also rated as more preferable social partners, i.e., friends, by women.

In summary, the literature on costly helping as a “courtship display” (Barclay 2010) provides quite consistent evidence that various types of costly helping behavior actually seem to increase perceived mate value. However, the questions of whether this effect is sex-specific and whether costly helping is also an effective signal in other contexts than mating are not answered conclusively by the existing studies.

Evidence from Documented Historical Cases of High-Cost Helping

Given these results from controlled laboratory studies, the logical follow-up question of course becomes, if they can help us understand the occurrence of real-world high-cost helping behavior better. To date, however, only comparably few studies have tried to shed light on this question, each of them focusing on rather distinct aspects of this kind of behavior. Their data, furthermore, mainly stem from two sources only: the Carnegie Hero Fund and the official Medal of Honor citations (also see Rusch 2016).

Civil heroism. Recipients of the Carnegie Medal, “civil heroes” for short, have been analyzed in five studies so far (see Table 2). Their main common observation is that the Carnegie Medal is predominantly awarded to men (roughly 90% of all recipients, see Becker and Eagly 2004). Notably, the only study using an alternative data source, UK newspaper articles on cases of civil heroism (Lyons 2005), confirmed independently that civil heroism is more likely to be displayed by men. Two other observations were also made repeatedly. First, civil heroes likely have an increased probability of belonging to the working classes (Johnson 1996; Lyons 2005). Second, civil heroism seems to occur more often in rural regions as compared to urban ones (Johnson 1996; Lay et al. 1974).

It is tempting to take these three repeatedly made observations as evidence supporting two of the theories outlined above. The overrepresentation of men among civil heroes suggests that this type of high-cost helping might be a sex-specific costly signal. The tendency of civil heroes to have low socioeconomic status and the more frequent occurrence of civil heroism in rural areas might indicate that indirect reciprocity is playing an important role, as anonymity is likely to be lower and a good standing in one’s community likely to be more important in rural areas and in social strata in which mutual favors cannot be substituted through buying the same services.

However, with respect to sex bias, Becker and Eagly (2004) argue that the overrepresentation of men among civil heroes might be due to the physically challenging nature of those specific types of acts of helping conventionally subsumed in the category of “civil heroism.” In fact, Becker and Eagly are able to show that for other types of brave and potentially very costly actions, such as hiding Jews from the Nazis or donating a kidney, among others, no such bias exists – and even that women are overrepresented among some of these other groups of helpers. For the findings on social status and region, on the other hand, Lay et al. (1974) and Johnson (1996) point out that similar caution needs to be applied. It could be that those types of situations allowing for actions of the types most frequently honored as civil heroism are just more likely to occur in rural regions and in contexts that members of the lower social strata are more frequently exposed to.

War heroism. The actions of the recipients of the Medal of Honor, “war heroes” for short, represent the second source of historical case data on high-cost helping behavior frequently used in the literature. Seven studies exist that have studied selected characteristics of these men and the contexts of their heroic actions. However, the only finding that has been repeatedly reported across studies concerns cases of “heroic suicide,” i.e., the deliberate sacrifice of the own life by covering an explosive device in order to save the lives of fellow soldiers in close proximity. Analyzing

partially overlapping data extracted from the official Medal of Honor citations from different wars, Blake (1978), Riemer (1998), and Rusch and Störmer (2015) all report that this kind of high-cost helping behavior is observed more frequently in lower-ranking soldiers and in members of the Marine Corps. Other noteworthy, but singular, findings reported in this literature include that surviving Medal of Honor recipients of WWII seem to have had increased reproductive success compared to other veterans of this war (Rusch et al. 2015) and that acts involving direct help to comrades are more frequently observed during defenses (Rusch 2013).

The finding of increased reproductive success of WWII Medal of Honor recipients apparently yields direct support to the idea that war heroism might be a costly signal favored by sexual selection. However, in addition to pending replication using data from other times, regions, and sources, numerous confounding factors could not be ruled out by Rusch et al. (2015), and their finding therefore needs to be interpreted with due caution. To name just one limitation, they could not rule out, for instance, that the material benefits associated with the Medal of Honor might have allowed its recipients to support a bigger family as compared to regular veterans.

With respect to the observation that enlisted men and members of elite troops seem more ready to “make the ultimate sacrifice,” the same caveat applies as with apparent status and provenance effects in civil heroes. It could simply be that enlisted men and elite troops are more frequently exposed to situations in which such a sacrifice can be made. However, data that allow controlling for this potential confounding factor currently are unavailable and, unfortunately, are likely to remain so as gathering them seems hardly feasible.

Conclusion

This entry has reviewed selected evolutionary theories that can potentially explain how behavioral traits causing their bearers to lend help to others can be sustained and also promoted by

natural selection even when the acts of helping cause high costs for the helpers. Subsequently, the intricacies of testing these theories against the results of laboratory and archival data studies were discussed. Finally, the existing empirical literature on high-cost helping was summarized briefly.

Contrasting the broad spectrum of suggested theories to the sparseness of available empirical work on high-cost helping, it becomes immediately apparent that intensified research is needed. The only theoretical suggestion, for which more than a modicum of empirical support has been found so far, is costly signaling. Costly helping does indeed seem to increase the perceived attractiveness of helpers as mates and may even have resulted in increased reproductive success in some historical cases. This should not be taken to mean, though, that the other theoretical suggestions – direct, indirect, and inclusive reciprocity and kin selection – have received no support so far. They simply have not been tested in the study of high-cost helping, yet.

Given the continuously increasing availability of data sources on historical cases of high-cost helping from online databases and the steadily improving accessibility of biographical information on historical persons, significant progress in this area of research can be expected in the nearer future, though. Particularly, since instructive recent studies have already pioneered ways of accessing and analyzing such sources (Lyons 2005; Rusch et al. 2015).

Apart from the imperative need to replicate earlier findings using alternative data sources and better controls to rule out potentially confounding factors, important research questions to be tackled include the following: To which extent is costly signaling in the form of helping a sex-specific phenomenon? Apart from increased mate value, which direct and indirect benefits, if any, do high-cost helpers regularly obtain, and what are their effects on helpers’ fitness balances? And finally, do the available theoretical suggestions suffice to explain the occurrence of the dark flip side of “lethal helping” in the form of suicide attacks (Atran 2003)?

Cross-References

- Adaptation and Natural Selection
- Adaptations for Reciprocal Altruism
- Altruism
- Altruism Advertises Cooperativeness
- Altruism Advertises Generosity
- Altruism Among Nonkin
- Altruism and Costs to Altruist
- Altruism Defined by Benefits Conferred
- Altruism Displays Cooperative Potential
- Altruism in Kin Selection
- Behavioral Economics
- Benefit Provisioning
- Benefits to Kin
- Competitive Altruism
- Cooperation
- Costly Signaling
- Costly Signaling and Altruism
- Costly Signaling Theory
- Culture of Honor
- Evolution of Cooperation
- Genuine Altruism
- Helping
- Helping and Genetic Relatedness
- Helping and Inclusive Fitness Benefits to Helper
- Helping and Reproductive Value of the Recipient
- Helping More Likely with Close Kin than More Distant Kin
- Kin Selection
- Kin Selection Hypothesis
- Kin Selective Suicide
- Kin Selection
- Maladaptive by-Product Hypothesis
- Mate Preferences
- Mate Value
- Mismatch
- Mismatch Between Evolved Morality and Modern World
- Problem of Altruism
- Prosocial Behavior
- Reputation and Altruism
- Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- Reciprocal Altruism and Cooperation for Mutual Benefit

- Reciprocal Altruism
- Reputation
- Risky Behavior
- Sexual Contact and Sexual Disgust
- Status and Reproductive Success
- Status Competition
- Suicide as Kin-Directed Altruism
- Survival and Death
- Survival and Reproduction
- War

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High-Cost Helping

► High-Cost Altruistic Helping

Higher Status in Group

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Synonyms

[Dominance](#); [Informal leadership](#); [Power](#); [Prestige](#); [Social hierarchy](#); [Social rank](#); [Social status](#); [Sociometric status](#)

Definition

Social status refers to differential degrees of social influence and rank in relation to other group members. This definition is used in the current entry. Note, however, that variations in definition exist across disciplines (and sometimes subfields): in some areas of research, for instance, social status is used to describe freely conferred deference or prestige, in contrast to the use of the term here to refer to more general influence that may or may not be associated with respect or prestige.

Introduction

From the most egalitarian societies to the formal organization of contemporary businesses, human groups are inherently structured by social hierarchy (Eibl-Eibesfeldt 2017; Mazur 1985; Von Rueden 2014). That is, differentiation in social rank – defined as relative position within a social hierarchy based on social influence and agency (Báles et al. 1951; Berger et al. 1980) – is persistently observed within and between groups. The

ubiquity of social hierarchy and rank differentiation likely emerged because hierarchies ease the tensions between competing group members who may have conflicting goals, and thus facilitates effective collective action and reduces the frequency of agonistic conflicts (Anderson and Willer 2014). Such rank differentiation is characterized by two dimensions: power and social status (see Blader and Chen 2014 for a review).

Power generally refers to institutionally legitimized and endorsed influence that is characterized by an individual’s ability to influence others through fear and harnessing control over resources (Keltner et al. 2003). Social status, on the other hand, refers to informal rank and influence that can be achieved by those who lack formal power or institutional roles. Power and social status have distinct antecedents and divergent consequences for both individuals and groups (Hays and Bendersky 2015). The current entry will, however, focus solely on the antecedents and consequences of having higher social status in human groups.

Social status in human groups can either be freely conferred to respected and admired individuals by other group members or coercively imposed on group members by a forceful, aggressive and manipulative individual. These two often distinct forms of social status are underpinned by individual differences in prestige and dominance within a group (Cheng et al. 2010). Moreover, social status (also termed *sociometric status*) is conceptualized differently to *socioeconomic status*, which is characterized by an individual’s occupational status, educational attainment, and income (Adler et al. 1994).

The Antecedents of Higher Social Status

Freely Conferred Status

Freely conferred social status is allocated to individuals by others within their group. Unlike power and coercively imposed status, freely conferred status is highly dependent on the collective perceptions of group members about an

individual's instrumental value in a respected cultural domain (Henrich and Gil-White 2001; Leary et al. 2014). There is often consensus among group members in judgments of an individual's social status (Mast and Hall 2004) and those high in social status are often conferred considerable influence over group decision-making (Cheng et al. 2013). As freely conferred status is granted by others, it is an inherently relational process. More specifically, an individual can only be high in status when those around them exhibit deference, and thus social status is not a characteristic of the individual but the property of a dyad or group (Bunderson et al. 2016; Emerson 1962).

Individuals often confer social status to those who they perceive to have an ability to confer benefits to group members. Those who provide skills (i.e., making effective arrowheads), expertise (i.e., botanical knowledge for medicinal practices), and exhibit traits that signpost physical ability (i.e., physical strength and size) are often granted higher social status in their groups (Anderson and Kilduff 2009a; Von Rueden et al. 2008). These abilities and expertise are often associated with narrower personality traits and individual differences – such as extraversion, conscientiousness, and openness – that may motivate the accrual of such skills. Prestige is also associated with agreeableness and genuine self-esteem, which may also help individuals prosocially monitor and maintain their social standing within groups (Cheng et al. 2010). All of the aforementioned traits and abilities are important for a group's success and survival (Ellis 1994), help to establish hierarchical relationships based on respect and admiration, and comprise a *prestige* profile (Henrich and Gil-White 2001). This prestige profile is associated with social or cultural learning, whereby the traits that signpost prestige highlight an individual's propensity as a teacher (or so-called learning model) to observers (so-called *info-copiers*), who in turn aim to maintain proximity and seek advice from that individual (Henrich and Gil-White 2001). Through this learning process, the individual high in prestige may confer adaptive skill or knowledge to the info-copier – such as how to produce a usable arrowhead – and thus

facilitate that individual's own goal accomplishment (Barkow 1975).

Acquiring social status through prestige is not only reliant on an individual's ability, but also their willingness, to bestow benefits to others. Experimental evidence suggests that those who contribute most generously achieve the highest levels of social status within a group (Barclay 2013; Willer 2009). These acts of generosity and cooperation may effectively broadcast an honest signal of an individual's prestige (see Bliege Bird and Smith 2005). More specifically, by signaling generosity and cooperative intent, high prestige individuals relinquish valued resources – be they informational or material – that will benefit other group members and further signal their quality within their group. In return, the individuals receiving the signal freely confer deference to their high-prestige counterpart and further elevate that individual's social status within the group (Boone 1998; Gintis et al. 2001; Roberts 1998). Indeed, a large and growing body of empirical evidence suggests that the most capable individuals who are willing to provide benefits are allocated the highest social status across many small-scale societies (Sugiyama and Sugiyama 2003; Wiessner 2005), among North American task groups (Cheng et al. 2013; Lukaszewski et al. 2016), and also during development (Hawley 2002; Redhead 2016).

Coercively Imposed Status

In some circumstances, individuals may achieve social status through coercion and cost imposition. Individuals acquire such coercively imposed status through dominance, which is related to an individual's ability and willingness to inflict costs on others (see ► “[Individuals That Impose Costs](#)” by Redhead et al., this volume for a detailed overview). Unlike freely conferred status, coercively imposed status is not the property of the group. More specifically, it is not granted through a process whereby group members collectively agree upon an individual's social value to the group. Rather, individuals defer to their high dominance counterparts in an attempt to lessen the costs that the individual high in dominance may impose on them, even if they may not necessarily

wish to. Thus, such coercively imposed status is underpinned by fear (Cheng et al. 2010, 2013). Without such fear, an individual's coercively imposed status would diminish. In many contexts, there are a several mechanisms characteristic of human groups that lessen the efficacy of dominance, such as the ability of group members to form coalitions (Boehm 2009; see ► [“Individuals That Impose Costs”](#) by Redhead et al., this volume).

Often dominance is related to power. Those who have disproportionate control over a group's resources and are willing employ coercive tactics to attain their egocentric goals are more able to leverage such control and successfully spread fear among proximate others (Mazur 1985; Wrangham 1980). In addition, there is variability in the efficacy of dominance's association with social status (Anderson and Kilduff 2009b). In most social groups, dominance typically has no substantial relationship, or a negative relationship, with prestige (Cheng et al. 2010; Redhead 2016). However, in some contexts, dominance and prestige may be positively related. For example, in groups and cultures whereby an ability to inflict harm is respected (i.e., during development, in delinquent gangs, prison populations), dominance may have a positive association with both prestige and higher social status in groups (Hawley 1999; see ► [“Status Competition and Peer Relationships in Childhood”](#) by Redhead et al., this volume). More broadly, individuals may at times both respect and fear their superiors (Barkow 2014). This relationship has received scarce empirical investigation and provides a fruitful platform for future investigation.

The Consequences of Higher Social Status

There are abounding benefits of having higher status in groups. First, evidence from various societies indicates that those high in both freely conferred and coercively imposed status have greater access to sexual resources (Alden Smith 2004; von Rueden and Jaeggi 2016) and have lower offspring mortality (von Rueden et al. 2010). Those high in

freely conferred status are attractive as long-term sexual partners, while those high in coercively imposed status are more attractive short-term partners (Kruger and Fitzgerald 2011). Complimentary to this, individuals perceived as contributing more to the goals of a group – and thus attaining positions of higher social status – are perceived as more physically attractive by their lower-status counterparts (Kniffin and Wilson 2004), and individuals perceive the leaders of their in-group as more physically attractive in comparison to leaders of an outgroup (Kniffin et al. 2014). Alongside these, high status individuals tend to have higher numbers of allies and cooperative partners (Patton 2005; Von Rueden et al. 2008), and have privileged access to a group's valued or scarce resources (Ellis 1994). It seems that having high social status increases an individual's overall fitness (Wiessner 2005) and may be considered a fundamental human motive (Anderson et al. 2015; Barkow 1989).

Having high social status also has a positive impact on the health and subjective well-being of individuals. Among the Tsimane forager-horticulturalist of Bolivia, individuals higher in status had greater nutritional health (Reyes-Garcia et al. 2008). Across cultures, individuals who feel more respected are higher in life satisfaction and positive affect (Tay and Diener 2011). Evidence also suggests that, during adolescence, individuals low in prestige are more likely to be bullied (Sijtsema et al. 2009) and adolescent girls who are perceived as leaders are also perceived as being happier (Weisfeld et al. 1984). Moreover, individuals high in freely conferred status are less likely to exhibit poor mental (i.e., depression: (Cooper et al. 2010) and physiological health (Ghaed and Gallo 2007) than their lower status counterparts. There are, however, several negative consequences of coercively imposed status (see ► [“Individuals That Impose Costs”](#) by Redhead et al., this volume).

Conclusion

Differentiation in social status seems universal for human groups. Individuals are granted positions

of high social status by members of their groups through prestige, a profile grounded by an individual's ability and willingness to confer benefits to others, and dominance, which is centered on the ability and willingness to inflict harm on others. Overall, there are many benefits related to high social status in groups.

Cross-References

- [Individuals That Impose Costs](#)
- [Status Competition and Peer Relationships in Childhood](#)

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Higher Survival with Older Siblings

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Synonyms

Alloparents; Helpers at the nest

Definition

Examination of cultural provisions of childcare suggests that the presence of female alloparents including maternal relatives, friends, and older siblings result in higher survival rates.

Introduction

In comparison to animals, newly born human babies are entirely dependent on their caregivers and need sensitive care and attention to survive. In most cultures, the necessary care and attention are provided by mothers and perhaps that is why, when a mother dies, the probability of infant surviving becomes slim, unless the caregiver is replaced by another sensitive human being (Brittain 1992). The positive correlation between maternal and infant mortality is quite evident in Scandinavian countries with the lowest maternal and infant mortality rates and African countries with the highest maternal and infant mortality rates (World Bank 2018). Citizens of countries with very high maternal and infant mortality rates face the biggest challenge of first surviving their childhood and becoming reproductively successful adults, and then raising their children to adulthood (Volk and Atkinson 2008).

Since, raising a human infant requires immense levels of sensitivity, investment, and care during the child's early years, in case of the death or disability of the mother, caregiving needs to be delegated to multiple caregivers. Ideally, kin caregivers a.k.a. alloparents are considered to be the best choice. Alloparents refer to individuals other than biological parents who assist in childcare or reciprocate childcare. Although most alloparents are chosen from the kin, but may also extend beyond kin as in case of foster children. The role of alloparents in many cultures is extensive and multifaceted. Hewlett (1991) found that among many foraging societies, for the 20–50% of the time an infant is held, it is by someone other than the mother, and most often a close female relative or trusted babysitter. Among the Efe, allomothers on occasions will nurse another woman's child if the mother is not

available (Hewlett 1989). Sear and Mace (2008) examined 45 studies of kin-child rearing patterns among people living in nonindustrialized groups and found that after mothers, maternal grandmothers have the most significant effect on increased child survival (see entry ► [“Mothers and Maternal Grandmothers and Childhood Survival”](#)).

Hence, in most cultures, especially with high maternal mortality rates, raising a child is not the sole responsibility of the parents, but is often executed by other female kin members such as grandmothers, aunts, and sisters as part of kin keeping. Many researchers have shown that kin keeping or investment by extended family members in raising children can be a function of gender, perceptions of genetic relatedness, and discriminative care (DeKay 1995; Laham et al. 2005). Subsequently, it is no surprise that maternal grandmothers and aunts are most involved in childcare due to higher perceptions of genetic relatedness and lower perceptions of paternity uncertainty (Bishop et al. 2009; Milardo 2009).

This brings us to the first question – in the early childhood years, does the relationship between alloparent and the child improve the child's mortality rates and developmental outcomes? Sear et al. (2002) investigated this question and reported that in the Gambia, maternal death was the most significant predictor of infant mortality rates; however, the rates were significantly lower in the presence of maternal grandmothers or older sisters. As anticipated from gendered norms of caregiving and perceptions of genetic relatedness, presence of paternal grandmothers and grandfathers, maternal grandfathers and older brothers had no significant effect on child mortality at any age. For this entry, we will focus on the impact of alloparenting by older siblings (generally sisters) and its outcomes on the survival of young children.

Alloparenting by Siblings and Cultures

In many cultures, older sisters assist their mothers, in taking care of their younger siblings (Weisner

et al. 1977), thereby curtailing net parenting costs (Sieff 1990). These contributions by older sisters may continue to prove beneficial to her younger siblings even after marriage. For example, in Hungarian rural communities, Romani girls contributed substantially in housework and childcare of younger siblings even after their marriage. As a consequence, there is a marked improvement in the longevity of mothers' reproductive careers and reduction in inter-birth intervals (Bereczkei and Dunbar 2002).

Older daughters, being relatively free of financial and more strenuous household responsibilities, are often seen as "Helpers at the nest" and mother's assistants. The term "helpers at the nest" has been borrowed from the study of birds (Emlen 1984) and was initially applied to the human species by Turke (1988). Turke (1988) found that women with older daughters had a better reproductive outcome than those who had sons, and this positive reproductive outcome was enhanced further in families who had two older daughters. To elaborate, a recent study ($N = 338,504$ for children aged 1–5) by Raj et al. (2019) in India drew analogous conclusions; infants with two older sisters had lowered infant mortality in comparison to those with an older brother.

This effect varies across cultures and may depend on the gender of the older siblings. Some researchers (Das Gupta 1987; Kemkes 2006; Muhuri and Preston 1991) found increased mortality when children have older siblings, especially an older brother. The rationale provided in these studies ranged from biased parenting in patriarchal societies to a lack of available resources. For example, preference for a male child in patriarchal societies may result in neglect of a female infant, or if the older sibling is not much older than the youngest child and competes for the same kinds of care and attention, the positive sibling effect on infant mortality can be negated or even reversed.

Now that we have established that females are generally the caretakers of young children more than twice as often as males (Weisner 1987) and improve the odds of infant survival, the second question is, what do sisters do to improve the survival rates of their younger siblings?

Sibling Caregiving

Sibling relationships are one of the longest-lasting relationships (Bank and Kahn 1982), and older siblings may have direct and indirect effects on their younger siblings. In early childhood, responsive and supportive interactions between siblings can be a source of secure attachment for the younger siblings (Ainsworth 1978). As previously noted, female children begin to contribute toward domestic chores, childcare, and the economic well-being of the family at an early age (Hames and Draper 2004). For example, in Dominica, girls as young as 12 years of age, spend a similar amount of time on domestic activities as adult women (Quinlan et al. 2003). Consequently, the mothers are relieved from the domestic burden and spend more time in taking better care of their infants and toddlers.

These tasks can depend on the priorities of the mothers in these cultures, the age of the children providing help, and the age of the children receiving it. In the Toba of Argentina, older girls' tasks depend on the age of the infant; girls focus on domestic tasks when mothers are nursing, so they do not provide childcare as much as free the mothers to provide milk and nurturance at this crucial time. Within these same homes, older girls assist a great deal more than younger girls and are more likely to care for children, and not perform simple domestic tasks (Bove et al. 2002). Overall, the tasks are scaled according to the development of both the helpers and the helped. Among the Kikuyu of Kenya, 7–12-year-old sisters' primary responsibility is sibling caregiving. While young girls may assist with domestic chores, taking care of their brother or sister is the cultural norm (Leiderman and Leiderman 1974). Similarly, in the USA, African American and Latino families, especially single-parent families, expected siblings to provide future support and began delegating age-appropriate caregiving tasks from a younger age (Jewell and Stein 2002; Fields 2003).

Conclusion

Older children in hunter-gatherer societies have several responsibilities and assist parents with

domestic chores, gathering, and other productive work (Sear and Mace 2008). The assistance provided by female offspring lessens the mother's workload and has beneficial outcomes on the survival of a younger brother or sister. Notably, the beneficial effect of older children is moderated by age and gender of the older brother or sister, birth spacing, need for childcare, availability of resources, and alloparents.

Cross-References

► Mothers and Maternal Grandmothers and Childhood Survival

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High-Level Representation

- [Inceptive and Derived Memory](#)

Highly Structured Society

- [Eusociality](#)

High-Risk Rescue

- [Heroic Rescue in Humans](#)

High-Stakes Altruism

- [High-Cost Altruistic Helping](#)

Hilarious

- [Humor Production](#)

Hilariousness

- [Neurology of Humor](#)

Historical Contingency

- [Spandrels](#)

History of Abuse

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Synonyms

[Battering](#); [Child abuse](#); [Child maltreatment](#); [Cycle of violence](#); [Domestic violence](#); [Intergenerational transmission of violence](#); [Interparental conflict](#); [Intimate partner violence](#)

Definition

One of the most consistent predictors of intimate partner violence (IPV) perpetration in prior research is a history of abuse, particularly within the family of origin. However, not all victims of child maltreatment go on to perpetrate violence within their intimate partnerships. A number of theoretical explanations help distinguish who may be most at risk for perpetuating this “cycle of violence.”

Introduction

Historically, intimate partner violence (IPV) has often been viewed as a primarily male-perpetrated phenomenon. However, research in recent years has demonstrated that women also perpetrate violence against their loved ones. National surveys estimate that more than one in three women and more than one in four men have experienced rape, physical violence, or stalking by an intimate partner in their lifetimes (CDC 2010). In community surveys specifically, where less severe forms of violence, often referred to as “common couple violence,” are studied, it is often found that women perpetrate violence at rates equivalent to or even higher than men (e.g., Kaufman-Parks et al. 2017). In order to reduce IPV perpetration and its associated costs to victims, perpetrators, and society at large (e.g., CDC 2010), it is

imperative to understand the potential factors that increase the risk for such violence.

Prior research has documented a number of negative sequelae of childhood abuse and neglect. One of the most frequently researched consequences has been coined the “cycle of violence” hypothesis, whereby it is presumed that individuals who are abused as children grow up to face an increased likelihood of perpetrating violence toward their loved ones. Supporting this hypothesis, past empirical research has documented associations between harsh physical discipline and physical abuse of children and subsequent IPV perpetration throughout both adolescence and adulthood (e.g., Capaldi et al. 2012). Yet, research has also demonstrated that exposure to violence during childhood does not lead in a deterministic fashion to violent behaviors, including IPV perpetration, in later life (e.g., Smith et al. 2011). Rather, it appears that accounting for potential mediating factors is essential if we are to understand why individuals with a history of child abuse are more likely to engage in IPV (e.g., Capaldi et al. 2012). A number of theoretical explanations lend insight into these potential mediating factors, including individuals’ attitudes and beliefs, the ability to develop and maintain healthy attachments with others, cognitive decision-making processes, personality traits and disorders, genetic or neurophysiological risks, and adoption of specific life history strategies.

Social Learning Mechanisms

Social learning theorists argue that attitudes and behaviors are acquired through processes of observation, learning, and reinforcement with key social agents (Bandura 1977). As part of the natural aging and socializing processes, children observe the behaviors of key figures in their lives and encode their observations. At a later time, they may copy or imitate these observed behaviors, which are then reacted to by others. If others reinforce the newly performed behavior through praise or reward, the child is likely to continue performing the behavior. If reactions by others are negative, continued performance of the behavior

is likely to decline or cease entirely. Accordingly, because the family is one of the first and main socializing agents for most individuals, relationships between parents and between parents and children provide models for how individuals should behave in relationships with others.

In the context of IPV, social learning theorists propose that children exposed to violence in their families of origin learn that hitting is an appropriate response to conflict with others. Upon entering intimate relationships as adolescents and adults, these individuals then often have limited resources for dealing with relationship conflict in constructive ways and resort to violence as a strategy for conflict resolution. They may also develop an expectation for violence in their own relationships or feel that violence is necessary to maintain control and power in their lives (Foshee et al. 1999; Kaufman-Parks et al. 2016). For example, in a community sample of young adult men and women, it was found that harsh physical discipline by parents (i.e., physical abuse) in adolescence increased the risk for IPV perpetration in young adulthood among both men and women. Moreover, while the risk of IPV also increased among all individuals when they experienced verbal conflict with their intimate partners, this was especially the case among individuals who had previously been maltreated (Kaufman-Parks et al. 2016). As concluded by the researchers, such findings demonstrated that individuals exposed to childhood physical abuse may have a lower tolerance for verbal aggression in their romantic relationships and react violently as a result.

Despite the evidence linking child abuse and later IPV perpetration, empirical research also has found that the vast majority of individuals exposed to violence in the family of origin do not report IPV in adulthood (e.g., Smith et al. 2011). Similarly, global endorsements of IPV in the general population are often relatively low (Simon et al. 2001). In other words, most individuals with a history of abuse still do not perceive violence as an acceptable way of dealing with conflict in their adolescent and adult intimate relationships. What accounts for whether abuse leads to the adoption of attitudes accepting of IPV may

thus rest in factors considered in combination with and external to childhood victimization experiences specifically. For example, analyzing the development of attitudes toward IPV, Copp et al. (2016) noted a positive, significant association between neighborhood poverty and attitudes accepting of IPV, even after accounting for exposure to violence in the family of origin via interparental violence and “coercive parenting” (i.e., physical abuse). Thus, IPV perpetration among those with a history of child abuse may be especially likely if they are also placed within a greater structural and cultural context (i.e., the neighborhood) that espouses violence as a normative, or at least justifiable, behavior.

It is also important to note that although most social learning explanations of IPV focus primarily on family of origin experiences, the process of learning continues throughout the life course. In other words, individuals’ attitudes toward and engagement in violence with intimate others may be influenced by those external to the family unit and in contexts beyond the childhood years. For example, prior research has indicated that association with peers who perpetrate violence increases risk for individuals’ own IPV perpetration (Capaldi et al. 2012). Relatedly, individuals who experienced controlling behaviors from partners in earlier intimate relationships are more likely to accept violence as a justified response, under certain circumstances, toward an intimate partner in subsequent relationships (Copp et al. 2016). Thus, IPV perpetration among those with a history of abuse may be especially likely if such individuals are exposed to peers and intimate partners who further reinforce violence as acceptable. Conversely, individuals who, despite a history of abuse, are able to surround themselves with others who reject the acceptability of violence may decrease their chances of later IPV perpetration. As noted by Giordano (2010), children are not only influenced by their environments but, because of human agency, are able to influence their environments. Although children are arguably much more constrained than adults in selecting their immediate environments, they may still have the power to attend more to some family members than others or to select role

models outside the family, who do not model and reinforce violence as justified or socially normative.

Interestingly, however, some prior research has indicated that even after accounting for a history of family violence and a number of additional potential risk factors (i.e., sociodemographic characteristics, IPV experiences in previous relationships, current relationship status and duration), women may be more likely than men to endorse the use of violence under a number of different circumstances (Copp et al. 2016). What accounts for this difference is not entirely clear, but it is possible that the general societal belief that female-perpetrated IPV is less problematic or more acceptable than males may lead women to minimize the harms associated with their violent behavior.

Attachment Theory

Prior research has found that children who are abused are more likely to describe relationships with others as threatening or painful, attribute hostile intentions toward social partners, and are less likely to establish or maintain social interactions overall (e.g., Wolfe et al. 2001). This association between childhood abuse and later relationship perceptions may be best understood through an attachment perspective. Attachment theory (Bowlby 1982) rests on the premise that individuals begin to form early cognitive models of relationships with others based on the interactions they have with their parents and other adult caregivers. These cognitive models often entail such notions of others as being predictable and trustworthy, of the self as being lovable and competent, and of relationships in general as being rewarding and worthwhile.

Building from this foundation and illustrating the relative stability of attachment styles throughout the life course, Bartholomew and Horowitz (1991) developed and tested a four-category model of attachment styles based on adults’ perceptions of self and expectations of intimate others. Three of the attachment styles reflected insecure attachments, and two of the three have

been found especially likely to lead to IPV perpetration (e.g., Dutton et al. 1994; Henderson et al. 2005). The first insecure attachment style linking childhood abuse to later IPV perpetration has been labeled “fearful” (Bartholomew and Horowitz 1991). Individuals with a fearful attachment orientation experience a sense of unworthiness and the expectation that others will be untrustworthy and rejecting. This insecure attachment style results when children place blame on both themselves and others for their caregivers’ physically abusive behaviors. However, despite this negative model of self and others, fearful individuals still desire social contact and intimacy. This seeming contradiction results in a chronic sense of frustration, as fearful individuals become enmeshed in, and simultaneously try to withdraw from, relationships with romantic partners due to continual anxieties over rejection and abandonment (Bartholomew 1990). The second style of attachment linking childhood abuse to IPV perpetration has been labeled “preoccupied” (Bartholomew and Horowitz 1991). Preoccupied individuals experience a sense of unworthiness but a positive evaluation of others. This attachment style results when children place blame solely on themselves for the abuse that they have incurred. Relationships with others are sought in order to increase preoccupied individuals’ sense of self-worth. Yet, entering these relationships with a negative view of self, preoccupied individuals are as equally anxious about potential rejection and abandonment as their fearful counterparts. They are only differentiated from fearful persons in their positive evaluation of others, making preoccupied individuals less likely to withdraw from partners or blame partners for their anxieties.

How insecure attachment styles may lead to IPV perpetration can largely be understood as a consequence of negative emotional states (Dutton et al. 1994; Goldenson et al. 2007). For example, in a study of 120 men referred to treatment for wife assault, Dutton et al. (1994) found that both preoccupied and fearful men scored higher on levels of jealousy, borderline personality organization, anger, and trauma symptomology. More specifically, due to insecurely attached individuals’ hypersensitivity to rejection and

abandonment, fearful and preoccupied individuals are much more likely to experience romantic jealousy in their intimate relationships. Faced with the anticipated or perceived loss of their romantic partners, these individuals then attempt to regain partners’ attention and restore their relationships. However, their ability in doing so is limited as a result of dysfunctional parenting practices rooted in violence, which were unlikely to convey the social skills necessary to handle relationship problems in constructive ways. These limited social skills, combined with the trauma symptoms associated with a history of childhood abuse, then lead to increased anger and the potential for violence as an outlet for such anger. Illustrating that such processes are not confined to male perpetrators, a study of 33 female offenders receiving mandated treatment for IPV perpetration indicated that female offenders reported less attachment security, more trauma-related symptoms, and more personality psychopathology than did a clinical comparison group of women who had not engaged in IPV perpetration (Goldenson et al. 2007).

From an attachment theory perspective, these findings demonstrate that IPV perpetration may be a reaction to romantic partners analogous to the angry behavior of a child who has been separated from their caregiver (Dutton et al. 1994; Henderson et al. 2005). Although the consequences of IPV perpetration for romantic relationship functioning generally are not positive, they do often represent an active attempt on the part of perpetrators to maintain or improve relationships they perceive to be in danger. Thus, for those with a history of childhood abuse, IPV perpetration may be likely if individuals also suffer from attachment insecurities.

Social Psychological Processes and Personality Traits

Complementing both social learning and attachment theories, the social information-processing (SIP) model argues that childhood abuse may lead to IPV perpetration in adulthood through SIP deficiencies. Originally formulated by McFall (1982)

to describe social skills among the general population, Holtzworth-Munroe (1992) applied this model to martially violent men specifically, given many therapy programs' focus on addressing social skills deficits as a strategy to treat domestic violence. In later years, recognizing that many of the pathways leading to IPV perpetration may be similar among men and women, this model was later applied to domestically violent women as well (e.g., Fite et al. 2008).

According to McFall (1982), social skills are acquired and performed in a three-stage process. In the first stage, individuals receive and interpret incoming social stimuli, a process known as "decoding." Once decoded, individuals must choose an appropriate response to the social situation. This requires individuals to think of all the available potential ways in which they can respond, determine the response type that best fits the situation under examination, and select the behavior from their behavioral repertoire that best reflects their desired response. This process is referred to as "decision-making." In the final stage, labeled "enactment," individuals must execute their chosen response and monitor the situation to determine whether their response had the desired impact.

For individuals with a history of abuse, there may be breakdowns in the SIP stages that increase the risk for violence in a number of given social situations. For example, in the first stage, and in line with attachment theories (Bowlby 1982), individuals may misinterpret social situations due to various cognitive deficits, including unrealistic expectations, faulty attributions, and irrational beliefs (Holtzworth-Munroe 1992). For abuse survivors, who are likely to view others as untrustworthy and relationships as unrewarding or threatening (e.g., Wolfe et al. 2001), such cognitions might include being hypervigilant toward hostile social cues, perceiving harm, or ill-intent in situations where none exists. Similarly, and in line with social learning theories (Bandura 1977), individuals with a history of abuse may be unable to produce nonviolent response options in the decision-making stage of the SIP model. They may also perceive violent options as superior in producing the desired situational outcome

(Holtzworth-Munroe 1992). Intuitively, each of these breakdowns would be likely if individuals were exposed to violence and come to see violence as an acceptable, or at least justifiable, behavioral response.

Using data from the longitudinal Child Development Project, Fite et al. (2008) provided empirical support for using SIP models to understand IPV perpetration. Specifically, the researchers analyzed whether SIP models mediated the relationship between witnessing interparental relationship conflict during childhood and children's own romantic relationship conflict in young adulthood. Among children who had witnessed interparental relationship conflict, there were SIP breakdowns in both response generation and response evaluation stages, and these breakdowns partially mediated the intergenerational transmission of relationship conflict. In other words, witnessing interparental conflict during childhood inhibited individuals' abilities to generate constructive, non-conflictual social responses when interacting with romantic partners in young adulthood. They were also less able to effectively evaluate the potential outcome of their chosen (and often conflictual) responses. Importantly, no significant gender differences were found; both young adult men and women were equally affected by interparental conflict and SIP deficits in their own romantic relationships.

In addition to potential cognitive deficits, survivors of childhood abuse may suffer from personality disorders or exemplify certain personality traits that increase their risk for IPV perpetration. In regard to personality disorders, results from a community sample followed for over 20 years demonstrated that suffering from either Cluster A (i.e., paranoid, schizoid, and schizotypal) or Cluster B (i.e., borderline, narcissistic, antisocial, and histrionic) personality disorders mediated the effect of childhood family violence exposure and adult partner violence (Ehrensaft et al. 2006). The researchers concluded that individuals exposed to interparental violence were more likely to suffer from Cluster A personality disorders and that Cluster A disorders were suggestive of pre-existing symptoms of mistrust, suspiciousness, and distortions in cognitions, all of which

increased the risk for IPV perpetration. Similarly, individuals exposed to either interparental violence or childhood sexual abuse showed elevated Cluster B symptoms, which increased the risk of IPV perpetration due to individuals' propensity to engage in aggressive and antisocial acts.

In assessing personality traits, a considerable body of research has documented associations between anger and IPV perpetration. In a meta-analytic review of 33 studies, Norlander and Eckhardt (2005) found that IPV perpetrators, compared to nonviolent men, consistently reported higher levels of anger and hostility, and anger levels also helped to distinguish men in low-moderate and moderate-high IPV relationships. Accordingly, a number of hypotheses have been put forward to understand the connection between anger and IPV, given the recognition that anger does not always lead to aggression. As one example, some scholars have argued that anger may reduce inhibitions against violence, either by aiding in the justification of violence as a viable response option or by disrupting cognitive processes that would defend against a violent response (Norlander and Eckhardt 2005). Each of these propositions, in turn, builds upon social learning and SIP theories, where individuals with a history of abuse already face greater likelihood of accepting violence as justified.

Importantly, while most of the research on anger and IPV to date has focused on male perpetrators, a comparably smaller body of research indicates that female perpetrators may also experience a strong disposition toward angry feelings, often referred to as "trait anger." For example, in a study of 80 women arrested for domestic violence, Shorey et al. (2011) found that both traits anger and impulsivity were significantly associated with women's physical and psychological aggression toward intimate partners and that trait anger mediated the relationship between impulsivity and aggression perpetration. Taken together, these findings indicate that individuals with abuse histories may be more likely to perpetrate IPV in adulthood if they also experience SIP deficiencies, suffer from certain personality disorders, or have higher state-trait anger.

Neurophysiological and Genetic Explanations

To date, sociological and psychological theories have dominated the literature in understanding intergenerational linkages of intimate violence. Yet, in recent years, some scholars have argued that attention be paid to potential neurophysiological and genetic explanations. Such explanations compliment more traditional IPV theories, as it is likely that individuals' physiology interacts with such things as expectations about and attitudes toward violence, emotional regulation, and social skill deficiencies (Margolin et al. 2016). Accordingly, a number of physiological and genetic factors may help to explain why some, but not all, individuals who were abused as children grow up to perpetrate violence against romantic partners.

One potential neurophysiological link between a history of abuse and IPV perpetration is the hypothalamic-pituitary-adrenocortical (HPA) axis (Margolin et al. 2016), which regulates many bodily processes, including reactions to stress, and the regulation of moods and emotions. Exposure to early life stressors, such as childhood abuse, may lead to the dysregulation of the HPA axis. In turn, HPA reactivity, specifically in regard to cortisol activity, has been linked to aggression and hostility in adult intimate relationships. For instance, neuroimaging research conducted by George et al. (2004) demonstrated that abusive men had lower cortisol levels, resulting in hypersensitivity to social stimuli, including certain looks or critical statements from romantic partners.

In addition to the more indirect HPA dysregulation processes which may result from early exposure to violence, brain structure and functioning may be affected by childhood abuse more directly via traumatic brain injury. Severe childhood abuse may result in traumatic brain injury, later increasing the risk for IPV perpetration. Prior research has reported that abusive men have higher rates of head injury, with rates ranging between 40% and 62%, compared to an estimated 6% in the general population (Howard 2012). The orbitofrontal and anterior temporal lobes are the most common sites of brain contusion and

laceration. In turn, the orbitofrontal cortex is the area of the brain that maps rewards and punishments through cortical activity. When damaged, this can lead to deficient social competencies in the arenas of judgment and behavior, the ability to experience certain moods and emotions, and the capacity for realizing others' thoughts and feelings.

Finally, some research has noted that genetic susceptibility may help to differentiate between maltreated children who do and do not go on to become aggressive and violent in adulthood. Deficient monoamine oxidase A (*MAOA*) gene activity, which metabolizes neurotransmitters such as norepinephrine, serotonin, and dopamine, may predispose individuals to respond hyperreactively toward perceived threats in incoming social stimuli. Examining the effects of maltreatment status and *MAOA* activity on antisocial behavior, Caspi et al. (2002) conducted research among a sample of individuals assessed from early childhood (age 3) to young adulthood (age 26). When measured by itself, *MAOA* activity had no significant effect on antisocial behavior. However, among maltreated children, low *MAOA* activity predicted four antisocial behavioral measures: adolescent conduct disorder, adult violent criminal convictions, self-reported disposition toward violence, and informant-reports of antisocial personality disorder symptoms. Taken together, these findings lead to the conclusion that, among individuals with a history of abuse, certain neurophysiological deficiencies and genetic susceptibilities may further increase risk for perpetrating IPV in later life. Importantly, while the vast majority of neurophysiological and genetic research on IPV perpetration to date has been conducted among men, it is not implausible that such findings may also hold true for women.

Evolutionary Perspectives

Integrating social psychological and biological models, contemporary evolutionary scientists have proposed a life history strategy for understanding the connections between a history of childhood abuse and IPV perpetration in

adulthood. Life history theory is based on the premise that all living organisms face trade-offs in dividing their energy and effort between important survival goals, given that resources for survival and reproduction are finite (Kaplan and Gangestad 2005). The trade-offs that organisms, or individuals, make determine what is referred to as their "life history strategy," which exists on a fast to slow continuum. A fast life strategy entails making decisions based often on immediate gratification or short-term gain with little investment in long-term maintenance or growth. Fast life strategies are most often exhibited in environments that are considered dangerous or limited in resources. Because individuals in these environments experience shorter life expectancies, it pays more to invest in short-term gains instead of devoting time and energy into long-term planning and relationships. Sexual promiscuity and aggressive behaviors are commonly cited examples of a fast life strategy (e.g., Brumbach et al. 2009). Conversely, a slow life strategy entails making long-term investments that signify the preservation and progression of both physiological systems and "embodied capital" (e.g., knowledge and skills) (Kaplan and Gangestad 2005). Slow life strategies are commonly adopted in environments that are considered safe, stable, and plentiful in resources. Delaying reproduction until individuals are able to sufficiently provide for their offspring financially and emotionally is one example of a slow life strategy.

Importantly, a great degree of variability exists between individuals' life history strategies; and some scholars have argued that such variation may be accounted for by the family. For example, building on Bowlby's (1982) attachment theory, Belsky et al. (1991) suggested that the family environment is central to the social, emotional, and behavioral development of children. Accordingly, when family functioning is disrupted through environmental uncertainty and its consequent stressors, secure attachments between parents and children become damaged, leading children to adopt internal working models of relationship uncertainty. In turn, internal working models of significant others and the environment overall as uncertain and unpredictable increase the

risk for adoption of a fast life history approach. Analyzing data from the National Longitudinal Study of Adolescent and Adult Health (Add Health), Brumbach et al. (2009) provided empirical support for the importance of family in predicting young adults' life history strategies and a wide variety of life history traits (e.g., mental and physical health, sexual attitudes and behaviors, social deviance). Of most relevance to the study of IPV perpetration, the researchers found that environmental harshness during adolescence via exposure to violence was predictive of adolescent delinquent behavior. Similarly, environmental unpredictability, which measured frequent changes or ongoing inconsistency in individuals' childhood environments (e.g., parents failing to provide for basic needs, being removed by social services), was predictive of delinquency during young adulthood. In turn, adolescent and young adult delinquency was associated with other negative life history traits (e.g., mental and physical health, sexual attitudes and behaviors) indicative of fast life history strategy. Considering that aggression is one potential form of delinquency, individuals who (unconsciously) adopt a fast life history approach as a result of childhood abuse may be more likely to perpetrate IPV in adolescence and young adulthood.

Conclusion

Being a victim of or witness to violence in early life is a significant risk factor for perpetrating violence throughout the life course. Yet, most individuals with a history of abuse still do not become violent toward romantic partners in adulthood. As demonstrated throughout, a full understanding of this variance and the complex processes by which intergenerational violence is transmitted requires a multifaceted theoretical framework. Specifically, those individuals exposed to violence in childhood via child maltreatment or interparental violence may be especially likely to perpetrate IPV in adulthood if they are also placed in multiple contexts that model violence as an appropriate way of dealing with conflict. These contexts may include associations

with deviant peer groups and intimate partners, as well as more structural contexts such as neighborhoods (Capaldi et al. 2012; Copp et al. 2016). Relatedly, when combined with a history of abuse, attachment insecurities (Dutton et al. 1994), cognitive difficulties (Holtzworth-Munroe 1992), personality disorders or certain personality traits (Ehrensaft et al. 2006; Shorey et al. 2011), neurophysiological deficiencies (Margolin et al. 2016), genetic susceptibilities (Caspi et al. 2002), and adoption of a fast life history strategy (Brumbach et al. 2009) may each further increase the risk for violence toward a romantic partner in adulthood.

Cross-References

- ▶ [Attachment Theory](#)
- ▶ [Contexts for Women's Aggression Against Men](#)
- ▶ [Defense Against Attack](#)
- ▶ [Early Attachment Experiences and Romantic Attachment](#)
- ▶ [Familial Violence](#)
- ▶ [Fast Versus Slow Strategies](#)
- ▶ [Female-Perpetrated Violence](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Psychological Mechanisms](#)
- ▶ [Sex Differences in Intimate Partner Violence](#)
- ▶ [Social Learning and Social Cognition](#)

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History of Attachment Theory

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Synonyms

[Bond](#); [Relationship pattern](#)

Definition

The bond between two persons, often between an infant and his/her caregiver.

Ethological Beginnings

Ethologists were the first to notice that all species exhibit particular biologically programmed attachment behaviors. These behaviors ensure that adults will care for their young and increase their chances of survival. Current attachment theory was formed by examining the research conducted by ethologists on animals. For instance, an ethologist, Konrad Lorenz (1935), studied imprinting in ducklings and goslings. Imprinting is a phenomenon in which a duckling or gosling will follow a moving object. Imprinting is believed to be innate and most likely to happen during a sensitive period shortly after birth. Harry Harlow's (1958) extensive research with infant and mother monkeys also paved the way for current attachment theory. Harlow separated infant monkeys from their birth mothers and placed them with surrogate "mothers." Infant monkeys were then raised by either a wire-mesh mother who supplied them with a bottle of milk or a wire mother wrapped in a soft cloth. Harlow found that monkeys spent much more time with the cloth mother, especially when the infant monkeys were scared or when they were encountering new surroundings. Harlow's studies directly tested the hypothesis that young infants form

attachments to their mothers because they are the source of food, rather than affection. In fact, the behavioral viewpoint at the time proposed that mothers should limit their affection toward their children (Watson 1928/1972). Harlow's finding that infant monkeys used the cloth mother as an attachment figure emphasized the importance of contact comfort to the attachment process. In addition, Harlow's work found that infant monkeys would use their cloth mothers as a secure base when exploring new situations.

Bowlby's Attachment Theory

Basing much of his work on imprinting and non-human primate studies, John Bowlby (1958) is credited with introducing the notion of attachment from an ethological perspective to the field of developmental psychology. Bowlby proposed that attachment is a bond between an infant and caregiver which increases the likelihood that an infant will survive. Human infants, in particular, are born depending on their caregivers for survival. Bowlby proposed that attachment evolved to keep the infant safe from predators and exposure to outside elements. To ensure that the infant survives, he/she must exhibit behaviors that will elicit attention from a parent and create a need to keep the infant safe. These attachment behaviors can be as simple as a smile, a coo, or a babble early on. As infants get older, they are more likely to show proximity-seeking behaviors such as crawling, walking, following their caregivers, and using visual social referencing. Developmental psychologists believe that this proximity-seeking behavior is later related to separation and stranger anxiety as infants begin to become more independent of their caregivers. It is also believed that evolution has created a biologically predisposed need for caregivers to want to attend to their young. Adults find that they want to attend to their infants' smiling and babbling and to keep them safe. Lorenz (1943) even discussed how the cuteness of many baby mammals, including humans, draws in adults and elicits caregiving behaviors. Unlike imprinting, Bowlby (1969) believed that human attachment develops

gradually. It is not until approximately 6 to 9 months of age that the infant discriminates and prefers to remain in contact with his/her attachment figure. The final stage of his four-stage theory, goal-corrected partnerships, does not happen until the infant is at least 3 years of age. Attachment does not fully develop until the infant has the communication skills necessary to foster a reciprocal interaction between caregiver and infant in which each understands the other person's emotional responses. Bowlby also proposed that an important cognitive mechanism arises as a result of the infant and parent attachment relationship. He called this mechanism an internal working model, a memory of the attachment bond that creates a cognitive representation of the infant's relationships with others. If the attachment relationship was one in which the parent was consistent and responsive to the child's needs, the infant would have an internal working model that people can be trusted. If instead the parent was inconsistent, insensitive, and unresponsive, the child would have a distrustful internal working model for relationships.

Empirically Measuring Attachment

The notion of attachment is a difficult emotional construct to define. Mary Ainsworth (Ainsworth 1973) is credited with creating an empirical examination to describe the attachment bond between a caregiver and infant/toddler between the ages of 12 and 24 months. Infants and caregivers are observed in a Strange Situation paradigm, especially identifying the attachment behaviors of proximity-seeking and using the caregiver as a secure base (Ainsworth et al. 1978). The Strange Situation paradigm is a series of eight contextual episodes which places the infant and caregiver in various situations, each lasting 3 min. In each situation, the infant interacts with his/her caregiver or a stranger or is left alone in an unfamiliar room. Ainsworth classified an infant/caregiver attachment by closely watching for how the infant uses the caregiver as a source of comfort. Secure infants (sometimes referred to as Type B), when distressed, will turn to their caregivers for support

and comfort. They will exhibit proximity-seeking behaviors either visually or physically and explore the room after checking in with their caregivers. Caregivers will also reciprocally meet the needs of their infants, whether it be for comfort or to foster independence. Connecting this to Bowlby's ideas, it is hypothesized that securely attached infants have developed a trusting internal working model after many months of consistent and sensitive parenting responses. The other three categories of attachments are classified as insecure. Infants with insecure-resistant/anxious-ambivalent (sometimes referred to as Type C) attachments respond to the strange situation by exhibiting anxious, resistant, and contradictory behavior toward their attachment figure. They may, at one point, seek comfort from the parent by clinging but moments later show anger and push the parent away. Infants with insecure-avoidant (sometimes referred to as Type A) attachment show little emotion and distress when separated from their parent and disengage and avoid contact when they return. Empirical research has since discovered an additional attachment style category, the disorganized (sometimes referred to as Type D) attachment (Main and Solomon 1986). Infants who exhibit disorganized attachment behaviors may exhibit anger, calm play, cry hysterically, stare blankly, or sometimes freeze or move slowly. More recent developmental theorists have proposed another classification, reactive attachment disorder, for children who have been significantly maltreated or institutionalized (Zeanah et al. 2004).

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History of Civilizations

► Guns, Germs, and Steel

History of Dominance Theory

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Synonyms

[Dominance hierarchy](#); [Pecking order](#); [Rank order](#); [Social hierarchy](#)

Definition

Dominance theory in ethology is concerned with how dominance hierarchies develop and function within human and animal societies in relation to the operation and maintenance of social status, behavioral strategies for survival and reproduction, and gaining preferential access to resources in competitive social situations.

Introduction

This entry will start with a history of dominance theory in ethology, before documenting the history of the understandings of socially stratified relations as they have been developed in some other subjects such as sociology and philosophy. It will then consider component concepts of Denise Cummins' more recent account of dominance hierarchies in more detail, as it was developed as part of the wider evolutionary psychology paradigm.

In terms of a definition, a dominance hierarchy, otherwise known more colloquially as a pecking order or a rank order, is simply a well-defined set of priorities defining the access of different individuals to desirable resources. High-ranking individuals have priority for access to desirable resources over low-ranked individuals, but specific dominance hierarchies often involve complex sequences of priority for various individuals in relation to different types of resources. Higher-ranking individuals are usually more successful in reproductive terms than lower-ranking individuals but this may not always be the case, as lower-ranking individuals can use non-aggressive and/or deceptive means to achieve their reproductive aims (Turner 1992, p. 148).

Dominance hierarchies are both conceptually and organizationally distinct from bureaucratic or administrative hierarchies, even though they do share some common characteristics with them. Bureaucratic or administrative hierarchies are formally fixed structures of dominance and subordination in which individuals occupy specific roles at specific times, and in which authority is formally stratified and the division of labor clearly defined (Jaques 1991). Dominance hierarchies on the other hand, as will be seen, are more organic and less formal than bureaucratic hierarchies, and they allow for greater fluidity in the specified roles and greater flexibility in the hierarchical relationships.

The idea that human societies are hierarchically stratified is, of course, nothing new, the concept of the class hierarchy being found in the work of various nineteenth-century and twentieth-century social theorists such as Karl Marx and

Max Weber (Barnett 2009, p. 122). However, since the notion of a class hierarchy is potentially distinct from dominance hierarchies and bureaucratic hierarchies, the historical origins of dominance theory in ethology needs to be considered.

Origins of Dominance Theory (Ethology)

The origins of the hypothesis of an evolutionary link between human and animal mental states and behavior is often attributed to Charles Darwin (1874 [1871]), but its historical origins goes back much further than this. John Gregory's *A Comparative View of the State and Faculties of Man with Those of the Animal World* explicitly paralleled the human mind both as a material system of instincts in parallel with the human body, and alongside the instincts of animals (Gregory 1766 [1765], pp. 4–7).

Gregory declared in proto-Darwinian fashion that “one [animal] species often runs into another so imperceptibly, that it is difficult to say where the one begins and the other ends,” and he declared that the mental faculties of different species of animals were all “well adapted to the particular sphere of action which Providence has allotted them” (Ibid., 8). In addition, he believed that the scientific enquiry “into the Instincts that are natural to Mankind” should be conducted alongside the study of “the analogous Instincts of other Animals” (Ibid., 16).

While neither Gregory nor Darwin discussed dominance hierarchies explicitly, Darwin did describe what he called “the law of battle” that operated between male animals, with the victors in these battles being characterized as conquerors (Darwin 1874 [1871], pp. 500–514). In a section of *The Descent of Man*, he explained that:

When many males congregate at the same appointed spot and fight together, as in the case of grouse and various other birds, they are generally attended by the females, which afterwards pair with the victorious combatants. (Darwin 1874 [1871], p. 49)

Although in this passage the concept of dominance was not explicitly outlined, it can be suggested that dominance relations were implied through the idea of the victorious combatants in

fight. However, the idea that “the Battles of certain [Male] Animals for the Possession of their Females” was common in nature goes back to well before Darwin, at least as far as J.J. Rousseau (1761, p. 85).

The concept of a dominance hierarchy in its ethological sense was first explicitly studied in the early 1920s in relation to the behavior of chickens (Schjelderup-Ebbe 1921), which is how the term pecking order (*Hackordnung*) originated. The pecking order of chickens is established most significantly in relation to feeding and mating behavior. As has been explained:

When strange[r] chickens are put together, they will at first fight intensively. Each animal will fight every other animal and victory or loss will determine its future standing. A chicken that has lost a fight will remember the victor and avoid it in the future. The victor usually is the stronger animal, but agility, perseverance, and aggressiveness are also of importance. (Eibl-Eibesfeldt 1975, p. 391)

The term pecking order came into being because chickens fight mainly by pecking at other chickens with their beaks. Once the pecking order is established, fights then only occur occasionally, and most of the time the chicken social structure remains peaceful. The pecking order determines which chickens have priority access to any newly-available resources such as food sources and mates.

However, the notion of a pecking order, if not the term itself, goes back at least as far as the early eighteenth century, where peck sparring between young cockerels, and the resultant “well ordering of the Cocks in these their early heats” of battle, was duly noted (Howlett 1709, p. 42, 48). The pecking instincts of various different birds were discussed in detail at the end of the nineteenth century (Morgan 1896, pp. 36–44), and hierarchies within Eskimo dog sledge teams were noted by anthropologists at around the same time (Boas 1964 [1888], p. 125). Dominance hierarchies among both jackdaws and mice were studied more formally by ethologists in the 1930s (Lorenz 1935; Urich 1938), and the effects of social conditioning on dominance behavior began to be studied in the 1940s (Ginsburgh and Allee 1942).

The link between territorial groupings and dominance hierarchies was considered by various authors as early as the 1920s (Howard 1920; Allee 1926). Some animal dominance hierarchies are confined in their active operation to certain marked geographical areas, the individual control of which has been clearly established through previous ranking contests amongst individuals located in the area under dispute (Blount 1990, pp. 430–431). As has been explained:

Dominance behavior can be conveniently viewed as the analog of territorial behavior in which a group of animals coexist within one territory. The result is that one of them, the equivalent of the territory holder, comes to dominate the others ... The expression of hierarchies may shift with the spatial position of the animals. (Wilson 1971, p. 196)

One of the first more general accounts of rank order in the psychology literature in the 1930s linked together behavior, status, and feelings of social dominance (Maslow 1937).

The connection between rank order, constant mating provocation, and the growth of the neocortex region of the brain began to be investigated in the ethology literature in the 1960s. The need to mediate between sexual and aggressive behaviors was seen as a crucial driver in the growth of Hominid brain size, with dominant animals being characterized as those that could hold their aggressive and sexual instincts in most effective equilibrium (Chance 1967). Also in the 1960s, dominance hierarchies among crickets were studied (Alexander 1961).

However, there is an important difference between the dominance hierarchies of crickets and those of chickens. In the case of chickens, individual hens remember which particular hens they have previously beaten in fights, whereas individual crickets only remember whether they have won or lost across a sequence of fights.

The concept of a dominance hierarchy became very well established across the ethological literature on animal behavior and many studies of specific animal dominance relations were published (see Richards 1974 for a discussion of dominance assessment). The concept of a pecking order eventually migrated to other academic subjects. For example, the literature on the structure

of corporate finance (Frank and Goyal 2003) and the literature on the sequence of biochemical reactions (Buettner 1993, both developed their own versions of a pecking order theory.

The related concepts of the teat order and the leap order were then proposed. The teat order refers to the sequence in which piglets get to suckle their mother's milk (Jeppesen 1982), while the leap order refers to a separate form of physical aggression (leaping) that chickens use in addition to pecking (Rajecki 1991). However in addition to its prevalence in the ethology literature, the idea of dominance structures has also been a key part of the social science tradition for a very long time.

The History of Dominance Theory in Human Societies

When stranger human beings are first put together, they do not usually fight each other in order to determine a future pecking order, like chickens do. However, occasionally a few do exhibit similarly aggressive behavior:

Mentally retarded [sic] boys who stayed together in a fairly large room initially fought for certain territories. When at last everyone had claimed a spot, quarrelling became rare ... Each had his place and knew that there he would be left in peace. (Eibl-Eibesfeldt 1975, p. 505)

Even though such first-contact physical aggression is rare among human beings (Esser 1968), when they are first put together, humans do instinctively evaluate each other in terms of a range of different qualities such as looks/beauty, physical strength, size, exhibited wealth, age, sexual orientation, and so on, in order to determine preliminary evaluations of various qualities such as perceived rank order and potential future relationship function (friend/foe; predator/prey; sexual partner/platonic).

Various types of hierarchy in human societies have, in consequence, been documented for many centuries. For example, the ruling Turkish political hierarchy, composed of the Grand Seigneur, his chief councillor the Great Vizier, then the Lords of Lords and then the provincial Sanzacks, was

documented in the UK in the late seventeenth-century (Shirley 1683, pp. 384–385). This political hierarchy could be conceived of as a dominance hierarchy. The familial dominance hierarchy was one of the first hierarchies to be explicitly identified as such in terms that are very close to the contemporary ethological meaning: Thomas Hobbes described what he called “paternal dominion” in the mid-seventeenth century (Hobbes 1983 [1651], p. 197).

Within the social science tradition in the West, one of the earliest works explicitly on social hierarchy in human societies was John Millar’s *Observations Concerning the Distinction of Ranks in Society* (1771), which argued that over time, social authority tended to become less concentrated and more dispersed across society as a whole. Adam Smith was more pessimistic than Millar, arguing that the idea of submitting to higher ranks was a doctrine of nature that was difficult to over-ride (Smith 1976 [1759], p. 53).

By the early twentieth century, the nature of social authority and bureaucratic hierarchy was being investigated by sociologists such as Max Weber, who distinguished between various different types of authority: rational/legal, traditional, and charismatic authority (Weber 1947 [1922], pp. 300–301). Regarding the functioning of bureaucratic hierarchies, Weber declared that:

The organization of offices follows the principle of hierarchy; that is, each lower office is under the control and supervision of a higher one. Hierarchies differ in respect to whether and in what cases complaints can lead to a ruling from an authority at various points higher in the scale, and as to whether changes are imposed from higher up or the responsibility for such changes is left to the lower office. (Weber 1947 [1922], p. 303)

Weber outlined that different hierarchies could sometimes employ different types of authority in tandem, for example, in the system of hereditary charisma. Occasionally, Weber’s work was drawn upon by those studying animal dominance hierarchies (Chapais 1991, p. 191). In the first half of the twentieth century, the philosopher Bertrand Russell identified power as being the fundamental

concept of social science, but Russell’s work on this topic was not influential within the social sciences (Russell 1938, p. 10).

As has been demonstrated in this section, although various types of social, political, and administrative hierarchies were considered by sociologists such as Millar and Weber and by philosophers such as Russell, the concept of a dominance hierarchy as a type of pecking order generally remained limited to the ethological literature for much of the twentieth century, until it was taken up directly by various evolutionary psychologists such as Denise Cummins at the end of the century.

Cummins on Dominance Hierarchies

A few studies applying the ethological concept of dominance hierarchies to humans had been published prior to Cummins, but, with one notable exception (Omark et al. 1980), these studies were usually isolated examples with very specific foci, for example, school playground hierarchies or hierarchies in psychiatrically hospitalized boys (Esser 1968). Cummins was, therefore, in the mid-1990s the first to attempt a more general application of dominance theory to human societies using evolutionary psychology as the overarching theoretical framework. As she explained about the fundamental impetus to her work on dominance theory:

... a look at human history shows quite unequivocally that humans have the unfortunate tendency to organize themselves into dominance hierarchies at both local and global levels. A monarchy, with its social stratification of power and status, is a dominance hierarchy. Indeed, much of human history is a careful record of intrigues and wars aimed at gaining or limiting domination of territory and resources ... The struggle for survival through competition and cooperation with members of one’s own species is as old as life itself. If the data on social norm and theory of mind reasoning show us anything, it is that the winners are most likely to be those with the capacity to exploit or route the constraints of the dominance hierarchy. (Cummins 1998, pp. 45–46)

As will be seen, by “route the constraints of the dominance hierarchy,” Cummins meant to manipulate it to an individual’s own benefit.

A dominance hierarchy is simply a social hierarchy that is governed by a set of rules that enshrine the various rankings that constitute it, e.g., that if *A* has priority over *B* for resource *x*, and *B* has priority over *C* for resource *x*, then *A* also has priority over *C* for resource *x*. As explained by Cummins:

Social living confers both costs and benefits to individuals . . . In hierarchical social groups, how these costs and benefits cash out depend a good deal on an individual's status. Consider that from a cognitive standpoint, a social hierarchy is, essentially, a set of *social norms*, that is, *rules that constrain the behavior of individuals depending on their rank* (Cummins, 2000). In human societies, these may be implicit or explicitly codified as regulations or laws . . . (Cummins 2005, pp. 681–682; italics in original)

The basic distinction between hierarchical and nonhierarchical societies (e.g., some aboriginal societies) is not that the latter are not constrained by any general social rules, but that in the former, adherence to social rules varies in a well-defined way according to an individual's position within the dominance hierarchy (Cummins 2005, p. 681).

How the set of rules that constitute the dominance hierarchy are established also varies for different animal species. For example, rank in chimpanzee hierarchies is not determined by physical size of the individual animal but instead by the formation and maintenance of alliances that provide support during any ranking contests (Cummins 1998, p. 34). In other animals (e.g., chickens), rank is determined mainly by fighting ability. As Cummins explained, in addition to physical abilities, “dominance hierarchies are supported by a collection of specific *cognitive functions*” such as rule learning, behavior forecasting, and alliance formation (Cummins 2005, p. 680). A central distinction here, therefore, is between physicality-based dominance hierarchies and prestige-based hierarchies, although sometimes a combination of both types is involved.

Regarding the origins of her approach, Cummins has cited work on both reciprocal altruism and the social context effect vis-à-vis reasoning tasks as the initial starting-points of her own work. As she explained, from reading the literature on how reasoning processes actually

functioned, she noted that “virtually all of them made reference to status hierarchies, and . . . social norms . . . It seemed apparent to me that status hierarchies were the crucible with[in] which much social intelligence adaptation evolved” (Private correspondence).

Therefore, Cummins' work can be seen as stemming less from the ethological approach to status hierarchies and more from the cognitive psychology tradition of understanding the influence of content effects on reasoning performance, as human social reasoning evolved in direct response to the need to navigate dominance hierarchies. The only partial precursor in this respect is the work of Michael Chance (1967).

Cummins argued that the higher reasoning capacity of human beings evolved in direct response to the pressure to cooperate and to compete with conspecifics within the set of dominance hierarchies that go to make up human societies (Cummins 1998, p. 30). This means that the main function of higher intelligence in human beings is not primarily to solve abstract or mathematical problems, but to solve problems associated with social behavior and the understanding of group dynamics. Successful functioning within dominance hierarchies requires the application of deontic reasoning, or reasoning about rights and obligations with respect to what individuals are permitted, obligated, and forbidden to do within these dominance hierarchies (Cummins 1996a, b, 1998, p. 39, 1999).

Cummins contrasted this deontic reasoning about social norms with indicative reasoning, or reasoning about what is factually true or false, and suggested that humans are “primed” for, or have evolved psychological mechanisms devoted to, responding to violations of these hierarchical social norms (or to cheating) by means of ongoing deontic calculations. One piece of evidence for the importance of deontic reasoning was that this form of reasoning emerges early in a child's development and operates separately from indicative reasoning, with children as young as three exhibiting behavioral sensitivity to transitive dominance hierarchies (Cummins 1998, p. 42).

Even so, some references to work on the social order of turkeys suggest that ethology was certainly

an influence on Cummins' approach (Cummins 1998, p. 34, 50; Watts and Stokes 1971). Hence, although her work on dominance hierarchies is an important part of the evolutionary psychology paradigm, it also fits to a significant degree within the comparative psychology tradition, which aims to understand the parallels between animal behavior and human societies (Vonk and Shackelford 2012; Romanes 1898 [1878]).

A modern form of the comparative psychology tradition, which Cummins' work can be said to resemble to a degree, is comparative developmental evolutionary psychology, which "integrates frameworks from developmental psychology and evolutionary biology" (Parker 1990, p. 3). It has been suggested that Darwin's approach to studying comparative cognition searched for human-like behaviors in animals (Shettleworth 2012, p. 529, 532); in which case, Cummins' work can be described as searching for animal-like behaviors in human beings. This would characterize it as drawing on the contemporary cognitive ethological tradition, or on the evolutionary comparative cognition framework.

Other Aspects of Dominance Hierarchies

Dominance hierarchies are not static structures but are open to challenge and are subject to ongoing conflicts and change, a fact that was acknowledged early on in the ethology literature (Lorenz 1935). They are dynamic structures in which some individuals challenge others above them in the hierarchy for greater resource-access rights and where established hierarchies can be reversed or overturned, at least for a period of time.

This dynamic property of dominance hierarchies is one important way in which they differ from bureaucratic or administrative hierarchies. It is certainly possible for individuals in bureaucratic hierarchies to be promoted or demoted, and therefore to change position within the hierarchy, but this is a formal process that follows fixed administrative procedures. Changes within dominance hierarchies are less formal and more open-ended, and are also subject to more frequent and ongoing challenges.

In addition, the dominance hierarchies of different species can have different levels of dynamism. In one species, the dominance hierarchy might only rarely be subject to challenge and experience changes only very infrequently, for example, after the death of a dominant individual, whereas in another species the dominance hierarchy might be subject to almost continuous challenge and in consequence experience very frequent changes in position.

Interestingly, dominance hierarchies are not always linear (or transitive) in function. For example, in most circumstances, if *A* has priority over *B* and *B* has priority over *C*, then *A* necessarily has priority over *C*, i.e., a simple linear relationship exists between *A*, *B*, and *C*. However, in other circumstances it is possible for non-linear (or non-transitive) hierarchies to develop. For example, a high-ranking individual *A*, who was dominant over both *B* and *C* because they had been victorious over them in previous fights, might then lose to *D* in a fight, *D* having previously lost to both *B* and *C*, possibly because *A* was temporarily weakened by their last fight. Then *A* would still be dominant over *B* and *C*, but would be below *D* in the hierarchy, even though *D* would still remain below *B* and *C* (Eibl-Eibesfeldt 1975, p. 391). It is likely that such non-linear hierarchies are often transient phenomena.

Sex Differences and Dominance Hierarchies

So far, the discussion about dominance hierarchies has been presented as if all individuals of the same species had the same nature, when in fact this assumption is certainly false. Males and females have, in some respects, very different natures (Davies and Shackelford 2008). One example of this is that *Homo sapiens* women tend to use subtler and more indirect means of conducting intra-sexual competition, in order to denigrate and defeat rivals, whereas men use more direct and physical means of intra-sexual competition. Put differently, women tend to use relational verbal aggression as a means of intra-sexual competition, whereas men tend to use

direct physical aggression (Cummins 2005, p. 691; Mavin 2008).

Other differences relating to sex have also been outlined in the literature. For example:

An important implication of men's stronger tendency to compete over status is that the male status hierarchy is steeper and has a more pinched distribution: that is, we find more men at both the highest and lowest end of the status continuum, while relatively more women lie in the middle of the hierarchy . . . Given their motivation to obtain status, men have been more eager to become leaders than women. (Buunk and Dijkstra 2012, p. 41)

However, just because there have been, historically, more male leaders than female, male leaders are not always superior to female leaders, and there are observable patterns that have been identified in the literature for when male and female leaders are preferred. For example, it has been suggested that female leaders are preferred in order to manage instances of intra-group conflict and competition, whereas male leaders are preferred in order to manage instances of inter-group conflict and competition (Ibid.).

Another aspect of dominance and sex differences is that there are three forms of dominance hierarchy that are found in the animal world: male-male hierarchies, female-female hierarchies, and male-female hierarchies. If male-male hierarchies were the first 'default' dominance hierarchies to be investigated in the 1920s, as was also implied in Darwin's notion of "the law of battle," then female-female dominance hierarchies began to be studied as separate phenomena in more detail in the 1960s (Kawamura 1965).

Male-female dominance hierarchies are heavily affected by the degree of sexual dimorphism present in the particular species in question. In species with no or low sexual dimorphism, male-female hierarchies are either ambiguous or mildly in favor of females. However in species with high sexual dimorphism, male-female dominance hierarchies usually operate strongly in favor of males. Female-female dominance hierarchies are often matrilineal, i.e., rank is transmitted from mothers to daughters, although they are not always so. Male-male dominance hierarchies are

often based on size and fighting ability but other factors such as skill at making cooperative alliances are sometimes also involved (Chapais 1991, pp. 199–200).

Conclusion

Historically speaking, the formal concept of a dominance hierarchy started out in the ethological animal behavior literature (in its "default" male-male form) in the early part of the twentieth century, before it migrated to various other subjects, then broadened out to include female-female dominance hierarchies, and was eventually adopted by evolutionary psychologists such as Denise Cummins at the end of the twentieth century. In this protracted adaptation process, the concept was transformed from its early more narrow "pecking order" meaning, which was initially confined to chickens, to a broader concept that could be applied to both other animal species and to human societies.

However, it is important to distinguish between the concept of a dominance hierarchy meant in its ethological sense, and other types of hierarchies such as class, administrative, or bureaucratic hierarchies. These latter types of hierarchy do share some features in common with dominance hierarchies, for example, that position within them is usually connected with an individual's status, but they also have some features that may differ from them, for example that positional changes are usually accomplished by more formal and/or bureaucratic means.

Although, as has been suggested, the importance of the class hierarchy for a long time involved "the profound influence which it exerts upon the intermarriage of different families," with legal penalties sometimes applying to illicit inter-class marriages (Fisher 1930, p. 210) – similar to how an individual's dominance hierarchy position usually affects their reproductive success – such strict marriage prohibitions are now no longer in place in most of the Western world. This may mean that class hierarchies are now less important

than dominance hierarchies in determining mating success in some instances.

Finally, one potentially interesting further extension of dominance theory might be to widen its scope beyond the intra-species level, as has been discussed in this entry, to the inter-species level, in order to investigate how some species may dominate over other species. As Darwin related, human beings are currently the dominant species in the world (Darwin 1874 [1871], p. 51), but all other species below them are not of equal rank with each other. How the long-term evolution of different species affects various inter-species dominance hierarchies might prove an illuminating topic.

Cross-References

- [Access to Resources](#)
- [Dominance in Humans](#)
- [Primate Dominance Hierarchies](#)
- [Social Dominance and Sexual Access](#)
- [Status and Dominance Hierarchies](#)

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History of Inheritance

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Synonyms

[Hereditary Transmission](#); [Heredity](#); [Heritage](#)

Definition

In living organisms, inheritance is the sum of genetic and epigenetic characteristics transmitted from the previous generation to the offspring.

Introduction

From a historical perspective, inheritance is a multifarious epistemic object. Discussions of biological inheritance have crossed various eras leading to multiple explanations of the processes of hereditary transmission. Scholars have retraced the stages of the scientific debate on inheritance from the early modern theories of generation to modern molecular genetics. When considering the historical evolution of the debates on heredity, there are however shifts in meaning and conceptual transformations that must be tackled. Until the beginning of the twentieth century, the circumstances of conception, pregnancy, and development were not seen as separable from the processes of inheritance. Still in the mid-nineteenth century, the belief that the child was susceptible of acquiring likeness to a particular individual at the moment of conception was widespread among physiologists and physicians (Bowler 1989).

For many years, discussions of biological inheritance were meant to include a range of phenomena, i.e., social learning and cultural transmission, which started to be considered as specific – and often independent – levels of inheritance only between the nineteenth and the

twentieth centuries (Stocking 1968). Over time, theorists of inheritance assumed the existence of various physical substances responsible for the transmission of both body and behavioral characteristics and proposed different mechanisms of transmission. These were often explained through linguistic metaphors taken from diverse historical frameworks that mirrored social practices. For this reason, historians have put effort towards highlighting how the knowledge of inheritance cannot be disembodied from technological practices and cultural contexts (Müller-Wille and Rheinberger 2012). Accordingly, the periodizations of the history on inheritance must take into account not only the turning points in the history of biology but also how the study of heredity has developed in relation to other areas, absorbing elements from medicine, farming, breeding, cybernetics, and computer science.

Inheritance and the Theories of Generation

Terms such as “heredity” and “inheritance” were absent from the medical literature until the mid-nineteenth century. Yet the first methodical investigations of transgenerational biological traits date back to the early modern studies of embryological development, which revived the ancient Greek theories of generation and the atomistic view of reproduction within a context of scientific inquiry based on microscopic observation and empirical investigation.

The works of the French natural philosopher Pierre Louis Moreau de Maupertuis (1698–1759) best exemplify this approach. In *Vénus physique* (1745) and *Système de la nature* (1751), Maupertuis provided a statistical analysis of the inheritance of polydactyly focusing on its modes of emergence and frequency. According to his interpretation of embryogenesis, the fetus formed from the combination of elementary particles from both the female and the male germinal line, finding their way in the embryo through chemical affinities

and forces of attraction. Hereditary aberrations were thus explainable in terms of mechanical failures in the distribution of such particles (Lange and Müller 2017).

The stress on the similarities between parents and offspring, as well as the idea that generation stems from the blending of female and male semen, harked back to the Galenic theory of “double semen” and the atomistic doctrine of “pangenesi” originally supported by Hippocrates and Democritus. According to this hypothesis, each part of the body would produce, through duplication, particles that convey the mold of the somatic structures to the gonads. In this way, the mixing of the two germinal lines was meant to imply the union of the somatic history of the parents.

This model of inheritance was widely diffused among French natural philosophers of the middle eighteenth century. In *Histoire naturelle de l’homme* (1749–1804), Georges-Louis Leclerc de Buffon (1707–1788) used the observational data gathered by the anatomist Louis-Jean Marie Daubenton (1716–1800) and the biologist John Turberville Needham (1713–1781) to maintain the double semen theory and the idea that organic molecules congregate in the genitals preserving the essence of the body part where they had originated.

Historians have often regarded this model of inheritance as the foundation of the modern conception of hereditary processes (Roger 1963). Furthermore, it played a major role in the pre-modern disputes on generation, highlighting the limits of the preformation theories of development, according to which each individual existed preformed either in the maternal ovum (*ovism*) or in the male semen (*animalculism*). The preformation theory could not give account of the manifest similarities between the parents and offspring, as well as of hybridization. Such new evidence came to reinforce the doctrine of *epigenesis* already theorized by Aristotle (384 BC–322 BC), René Descartes (1596–1650), and William Harvey (1578–1657), which has become the standard view of development since the middle eighteenth century (Canguilhem et al. 2003).

Inheritance and Hybridization in Natural History

The growing interest in hereditary processes between the middle XVIII and the XIX centuries can be scrutinized from various perspectives. The study of the patterns and fluctuation of hereditary characters in the cases of hybridization was of primary concern in the Colonial era, since it intertwined with the knowledge of human pathology and anthropology, as well as with breeding and botanic practices. For instance, the conceptual distinction between constant and variable characters was connected with animal crossbreeding and the attempts to acclimatize exotic plants to the temperature of European botanic gardens (Müller-Wille and Rheinberger 2012).

The dichotomy between constant and variable characters also underlay the broader debate on morphological deviance in species description. According to Swedish botanist Carl Linnaeus (1707–1778), hybridization (*mixtura*, *generatio hybrida*, *generatio ambigena*) showed a definite pattern of traits in plants: the medullar substance and reproductive organs were a copy of the maternal line, while the external features resembled the male (Linnaeus 1760). As the director of the *Jardin des plantes* of Paris, Buffon regarded the domestication and acclimatization of plants and animals as one of the primary sources of biological “degeneration” which could lead to the production of new species.

Speculations on hereditary mechanisms became part of medical and veterinary studies of animal crossbreeding. Among the most discussed phenomena of heredity was *telegony*, i.e., the idea that the characteristics of previous mates can influence the hereditary constitution of the female parent. In his communication published in the *Philosophical Transactions of the Royal Society* (1821), George Douglas Earl of Morton (1761–1827) stated he had bred a chestnut mare and a quagga stallion and then observed that the offspring produced by the mare mated to a black Arabian sire was more plainly barred across the legs than even the pure quagga (Burkhardt 1979). Similar accounts appeared among veterinarians

throughout the nineteenth century. James Law (1838–1921), dean of the Edinburgh Veterinary School, maintained that the impregnated ovum impressed the tissue of the placenta with the sire’s characters, which were then transmitted to the subsequent embryos. The geologist Louis Agassiz (1807–1873) acknowledged telegony as a real fact in natural history and stated that the female horses, once they are impregnated, are irreversibly modified in their hereditary constitution (Greene 2009, p. 101).

Inheritance and Evolution

The attention towards hybridization, domestication, and acclimatization had a remarkable role in the shaping of the nineteenth-century evolutionary debate. In France, Jean-Baptiste de Lamarck (1744–1829) proposed a systematic synthesis of the doctrines of Maupertuis and Buffon. In the *Philosophie Zoologique* (1809), Lamarck exposed his doctrine of transformation stating that environmental circumstances could drive organisms’ habits towards new adaptive scopes. By means of nutritional and nervous fluid dynamics, habits modified organic structures as well as the germinal fluids, which, in turn, transmitted the modified pattern of fluid distribution to the offspring. Throughout the nineteenth century, such form of hereditary mechanism, commonly known as the theory of the inheritance of the acquired characters, ended up being regarded as a synonym of Lamarckism (Burkhardt 2013).

Charles R. Darwin (1809–1882) never denied the supplementary contribution of use-inheritance processes in evolution. In *On the Origin of Species* (1859), Darwin traced back inheritable variations to various laws, including the conditions of life and the use-inheritance factor:

Variability is governed by many unknown laws, of which correlated growth is probably the most important. Something, but how much we do not know, may be attributed to the definite action of the conditions of life. Some, perhaps a great, effect may be attributed to the increased use or disuse of parts. The final result is thus rendered infinitely complex. (Darwin 1859, p. 31)

However, Darwin highlighted the nearly indefinite outcomes of the external conditions:

All such changes of structure, whether extremely slight or strongly marked, which appear among many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism, in nearly the same manner as the chill effects different men in an indefinite manner, according to their state of body or constitution, causing coughs or colds, rheumatism, or inflammation of various organs. (ivi, p. 3)

In *The Variation of Animals and Plants Under Domestication* (1868), Darwin exposed his provisional hypothesis of pangenesis to account for the inheritance of acquired characters. According to his interpretation, which was later expanded by William Keith Brooks in *The Law of Heredity* (1883), somatic cells produce minute and discrete particles he called “gemmules” which would be able to circulate throughout the body and finally congregate in the gonads.

However, the dispute on the physical basis of the inheritance of acquired characters took a multifaceted form in the years of the post-Darwinian debate. Among the alternatives to the discrete view of heredity was the so-called dynamic theory originally proposed by the German physiologist Ewald Hering. On the occasion of the 30th anniversary of the Imperial Academy of Natural Sciences of Vienna (1870), Hering stated that the nervous system could convey the nerve vibrations to the whole organism, including the genitals. These could transmit all the qualities of the organisms, including acquired habits and instincts, thus making the individual development a record of memory. In *The Perigenesis of the Plastidule* (1876), Ernst Haeckel (1834–1919) reified Hering’s analogy between heredity and memory postulating the existence of the *plastiduels*, the hypothetical basic units of living matter whose wavelike movements, activated by external stimuli, transferred their acquired memory to the offspring.

The analogy between heredity and memory spread in the Anglo-Saxon-speaking countries especially thanks to the British novelist Samuel Butler, who first translated Hering’s work in the book *Unconscious Memory* (1880). The idea that

both memory and biological inheritance were based on the persistence of vibrations accentuated the role of mental factors in evolution and was often used to counteract the Darwinian view of heredity and evolution (Ceccarelli 2018). The American neo-Lamarckians Alpheus Hyatt (1838–1902) and Edward Drinker Cope (1840–1897) strongly opposed Darwinian pangenesis, as it was quite impossible for them to imagine that the gemmules could find their exact place in the growing embryo. The transmission of “a mode of motion” organized in a central nervous system was considered less inconceivable than any discrete model of inheritance (Cope 1896).

The work of the German cytologist August Weismann (1834–1914) represented a major breakthrough in the debate. Since early 1885, Weismann had maintained that the germplasm was unaffected by the activity of development and isolated from indirect environmental influences. In 1888, he affirmed that somatic modifications do not affect the germ line after he demonstrated that the descendants of mice whose tails had been detached continued to grow tails. This was the start of the so-called neo-Darwinian school, since sexual reproduction (*amphimixis*) became the only source of variability for natural selection to act upon. Even though many naturalists accused Weismann of having mistaken accidental modifications for acquired characters, his conclusions were generally considered the fatal blow to the inheritance of the acquired characters and habits. Furthermore, Weismann’s experimental work questioned the very idea of the interchangeability between biological and social inheritance, which, in turn, favored a first fundamental separation between biological heredity and cultural learning in social sciences (Ceccarelli 2018).

Experimental Biology and the Discontinuous View of Inheritance

Between the nineteenth and the twentieth centuries, the debate on inheritance underwent significant technical and methodological changes. Innovative cytological studies expanded the

knowledge of the cell's architecture. During the 1870s, the Swiss chemist Friedrich Miescher (1844–1895) and the biochemist Albrecht Kossel (1853–1927) identified nucleic acids. In 1882, Walther Flemming (1843–1905) coined the term “mitosis” to describe the longitudinal division of those nuclear corpuscles that, in 1888, the German anatomist Wilhelm Waldeyer-Hartz (1836–1921) first termed “chromosomes” (Wall 2015).

It was the experimental studies on plants' hybridization that provided the ground for the quantitative description of hereditary processes. Gregor Mendel (1822–1884) conducted his well-known crossing experiments with peas (*Pisum sativum*) between 1856 and 1863. His results were published in the paper *Versuche über Pflanzenhybriden* (1866), where he exposed his main generalizations. By analyzing an amount of about 28,000 plants, Mendel observed that the hybrids, instead of presenting a fusion of the parental characters, showed specific morphological patterns. He assumed these characters were linked to distinct hereditary factors which come in pairs, one from each parent. The combination between the variants (*alleles*) of these factors determined the character of the offspring. Organisms with two identical alleles were *homozygous*, while those with different alleles were *heterozygous*. However, the physical appearance of the hybrids showed that some variants prevailed over others. For instance, in heterozygous plants for pea seed color (*yellow/green*), the yellow variant prevailed over the green one. In spite of this, the unexpressed variant remained unaltered and thus transmissible to the offspring. Although the separation and recombination of factors occurred randomly, the expression of the hereditary constitution of the plants revealed proportional relationships that Mendel described in terms of dominant-recessive factors.

The idea that the organisms carried unexpressed hereditary discrete factors, as well as the broader attitude towards a quantitative description of inheritance, determined one of the deepest breaks in nineteenth-century life sciences. It has been suggested that the very dichotomy between “blending” and “non-blending”

inheritance is a product of the post-Mendelian biology (Müller-Wille and Rheinberger 2012). Mendel's work provided an explanation to many mysteries of inheritance (Watson 2003), although his conclusions were scarcely noticed by his contemporaries, at least until 1900.

Even before the rediscovery of Mendel's researches by Hugo de Vries (1848–1935), Carl Correns (1884–1933), and Erich von Tschermak (1871–1962), several scientists had however developed a discontinuous view of inheritance. In *Hereditary Genius* (1869) and *Natural Inheritance* (1889), Darwin's cousin Francis Galton (1822–1911) critically assessed the Darwinian view of inheritable variations. According to his studies on statistical correlation and regression, minimal variations tended to regress to the average value. It followed that the only evolutionary-relevant variations had to be discrete alterations (*sports*) at the germinal level. In *Materials for the Study of Variation* (1894), William Bateson advanced the hypothesis that the discontinuity among species mirrored discrete variations.

In 1902, the American physician Walter Sutton (1877–1916) observed that, in the body cells, chromosomes occurred in pairs, while in germ cells, they appeared in single structure. This architecture well-matched Mendel's description of alleles' behavior. In parallel with the German cytologist Theodor Boveri (1862–1915), Sutton laid the foundation to the chromosome theory of heredity, which turned the Mendelian factors into material and localizable objects. In *The Genotype Conception of Heredity* (1911), W. L. Johannsen coined the term “gene” to designate the Mendelian “unit factors.” He further proposed the well-known dichotomy between “genotype” and “phenotype,” which is widespread in the science of genetics throughout the twentieth century.

The endorsement of Mendelism was however not undisputed. During the 1910s, Thomas Hunt Morgan maintained a skeptical view as to the epistemological significance of Mendelism. Indeed, Morgan initially saw in Mendelism a methodological fallacy common to many nineteenth-century studies of inheritance, i.e., postulating the existence of unverified

processes and physical units. By assuming the existence of factors responsible for hereditary processes, Mendelism was still implying an unknown material basis (Morgan 1909, p. 365). About a year later, Morgan became one of the foremost proponents of Mendelism thanks to his now famous experiments on *Drosophila melanogaster* he had carried out at Columbia University between 1907 and 1910. Not only did the experiments confirm Sutton-Boveri's chromosomal theory, they also showed that the phenotypic expression of certain characters (the white-eye recessive trait in flies) was linked to the chromosomal spot of Mendelian factors and, in particular, to sex.

The study of phenotypes in Mendelian terms did not just involve body characters. As a matter of fact, in the early twentieth century, eugenicists used to trace back individuals' behaviors and personal attitudes to the action of single genes (Watson 2003). As a result of the Mendelian revolution and the Weismannian turn in the 1880s, nineteenth-century environmental determinism often turned into genetic determinism.

The Century of the Gene

In the 1940s, the study of biological inheritance did benefit from the groundbreaking researches on organic molecules. The achievements in X-ray crystallography help scientists determine the molecular structure of organic macromolecules, thus revolutionizing organic chemistry (Mitchinson 2014). Even though the analysis of the conformation, function, and interaction among organic substances was not originally aimed at scrutinizing hereditary phenomena, it laid the foundations for what has been later called the "molecularization" of genetics (Müller-Wille and Rheinberger 2012).

Between 1940 and 1952, scientists identified the deoxyribonucleic acid (DNA) as the material basis of genetic information. In 1944, Oswald Avery (1877–1955), Maclyn McCarty (1911–2005), and Colin MacLeod (1909–1972) of the New York Rockefeller Institute discovered that the DNA could transmute

the characteristics of the cell while studying the *Streptococcus pneumoniae*. In 1952, Alfred Hershey (1908–1997) and Martha Chase (1927–2003) of the Cold Spring Harbor Laboratory confirmed that DNA was the transforming factor as well as the very material basis of heredity. It was only a year later that D. Watson (1928) and F. C. Crick (1916–2004) famously proposed the double-helix model to describe the structure DNA macromolecules.

Watson and Crick showed that each DNA chain was composed of sequences of nucleotides (*adenine*, *cytosine*, *guanine*, and *thymine*) that coded for molecules with specific functions. While molecular biology provided the technologies and operational methods for the understanding of the material basis of heredity, modern communication technologies and cybernetics allowed scientists to shape the informational conception of biological inheritance. As a matter of fact, the nineteenth-century energetic conception of inheritance came to be replaced by expressions such as "biological information," "genetic program," "transcription," and "genetic code" (Fox Keller 1995; Maynard Smith 2000; Müller-Wille and Rheinberger 2012). As early as 1944, Erwin Schrödinger's essay *What is Life?* had introduced the notion of "hereditary code" to designate the information enclosed in the chromosomes. As Watson affirmed (2003), many of the pioneers in the field of molecular biology assumed Schrödinger's idea that the transmission of characters followed definite set of instructions.

Between the 1950s and the 1960s, such instructions had their quintessential reification in the so-called central dogma of molecular biology, the idea that molecular information could only flow from DNA to proteins via messenger RNA (mRNA). The first phase of the process is that of *transcription*, where DNA segments are replicated into mRNA. During the second phase, called *translation*, the copied information is conveyed in the ribosomes and finally translated in proteins.

This one-way conceptualization of biological information did play a major rule in reinforcing the neo-Darwinian view of germ line inheritance, creating "an impression of straight-line progress

in genetics and from Mendel to Weismann to Morgan to [Watson] and Crick's decoding of DNA to the Human Genome project to gene therapy" (Depew 2017, p. 75).

Between the 1960s and the 1970s, the analysis of genetic sequences in relation to the genetic variants involved in hereditary diseases gave rise to the "genomic revolution" (AA.VV. 2006). The use of enzymes and plasmids to modify and manipulate the genetic material in the cells (Morange 1994) made a methodological switch that redefined the institutional, disciplinary, and epistemic status of genetics. In this regard, the milestone was reached in 2001 and 2003 with the Human Genome Project and the determination of euchromatic human genome.

Behind the applicative side of these researches, new theoretically significant evidence was brought to the attention of scientists. The sequencing of the human genome did raise questions about the actual functioning of the genome. Scientists discovered that it required "more than just knowledge of the order of the base pairs" to cure human disease and started to focus their attention to those regions of the genome "devoid of traditional protein-encoding genes" (Chial 2008) that play a major regulative role in gene expression during the individual development.

At the same time, new experimental evidence questioned the "central dogma." As early as 1970, Howard Temin (1934–1994) and David Baltimore discovered a viral polymerase that could transcribe RNA molecules into DNA molecules. The enzyme that appeared to break the central dogma was named "reverse transcriptase." Further anomalies were brought to light in the studies of development and evolution. Between the 1940s and the 1950s, the British embryologist Conrad Hal Waddington (1905–1975) and the Russian zoologist Ivan Schmalhausen (1884–1963) had independently showed that developmental and genetic variations could lead to phenotypic plasticity and genetic canalization. In *Canalization of Development and the Inheritance of Acquired Characters* (1942) and *Genetic Assimilation of an Acquired Character* (1953), Waddington argued that environmentally

induced adaptations could become inherited characters without implying the Lamarckian mechanism of inheritance. Waddington called such process "genetic assimilation" and explained it as the outcome of the plastic abilities grounded in organisms' genetic potentialities. Through the perturbation of development, Waddington argued, the individual ontogeny escapes its standard pathway (*decanalization*) which, in turn, may reveal cryptic genetic variations.

Waddington termed the branch of biology "epigenetics," whose aim was that of studying the causal interactions between genes and their products which bring the phenotype into being (Waddington 1942). However, it took decades for evolutionary biologists and geneticists to fully grasp the operational and theoretical potentialities of Waddington's proposal. For decades, biologists found DNA, the genetic code, transcription, and translation "far more exciting" (Lamb 2009, p. 118).

Inheritance in the Post-Genomic Era

There is enough agreement that contemporary biology has undergone a "holistic turn" by now. Terms such as "post-genomics" and "epigenetics" have come to the fore in the last three decades leading to a systemic view of hereditary processes and organisms' complex development (Müller-Wille and Rheinberger 2012). In post-genomics, phenotypes are no longer considered the mere expression of genetic information but rather as the manifestation of "systems of development," which include factors that have been traditionally considered as environmental (Griffiths and Stotz 2006). The genome is more frequently conceived as a broad and hierarchical regulatory network that interacts with external inputs (Dupré 2012).

Along the lines of Waddington's research agenda, the Evo-Devo studies are now proposing a new synthesis among molecular biology, embryology, genetics, and epigenetic inheritance. Since the early 1990s, the phenomenon of transgenerational epigenetic inheritance has been deeply reconsidered by molecular biologists.

Scientists have surveyed several examples of inheritable gene alteration and deactivation (*silencing*) in response to environmental stimuli, with specific regard to the process of DNA methylation by which the genes' expression is modified. There is increasingly evidence that information is also conveyed through non-DNA portions of chromosomes, self-sustaining metabolic loops, chromatin-marking systems, and small RNA molecules able to suppress gene activity (Jablonka and Lamb 2015).

All this has unsurprisingly stimulated a historical and epistemological reflection, which largely deals with the uses of terms such as “epigenetics,” “epigenesis,” “epigenetic inheritance,” and even “Lamarckism.” To designate nongenetic inheritance, scientists have sometimes used the more general term “epigenetics,” i.e., the study of the processes that underlie developmental plasticity and canalization (Jablonka 2009). Moreover, the very term “epigenetic inheritance” has a double meaning:

Epigenetic inheritance in the narrow sense refers to the cellular epigenetic inheritance [...] in which the unit of transmission is the cell. Epigenetic inheritance in the broad sense includes body-to-body (or soma-to-soma) information transfer between generations of individuals. This can take place through developmental interactions between mother and offspring, through social learning, through symbolic communication, or through the transmission of symbionts and pieces of DNA between individuals. (ivi, p. 151)

In some cases, the narratives of the epigenetic turn have revived the interest in Lamarckism. Since epigenetic inheritance can lead to a form of soft inheritance, scholars have advanced the hypothesis of a revival of Lamarckian issues. This has stimulated further historical discussions of the conceptual parallelism between epigenetic inheritance and the classic notion of inheritance of acquired characteristics (Loison 2018).

Conclusions

The history of biological inheritance has been characterized by various discussions. Concepts from other areas have played an operative role in

the shaping of the various theories of inheritances throughout the centuries. A thorough analysis of the subject easily reveals how discussions of inheritance have long referred to a wide and complex phenomenology (genetic and epigenetic inheritance, cultural transmission, social learning) whose inquiry has undergone further specialization between the nineteenth and the twentieth centuries.

Beyond a seemingly constant alternation between reductionists and holistic stances, recent developments in the field of post-genomics seem to challenge the classic accounts of genetic determinism and hereditarianism, according to which the organisms' phenotypic as well as behavioral characteristics would be reducible to the genotype alone.

Cross-References

- Cultural Inheritance
- Eugenics
- Evolutionary Change
- Genetic Determinism
- Problem of Genetic Inheritance, The

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History of Natural Selection

► Dual Inheritance Theory

History of Sperm Competition in Humans

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Synonyms

[Adaptations to human sperm competition; Human sperm competition tactics](#)

Definition

Many species have faced sperm competition (when sperm from two or more males compete to fertilize an egg in a female’s reproductive tract) in their ancestral past to varying degrees. In the history of human evolution, the common mating system of social monogamy led to decreased levels of sperm competition relative to some other primates; however, it was not completely absent. Evidence of this history of sperm competition is seen in both men and women in terms of their genetic makeup, anatomy, and evolved mating psychology.

Introduction

In humans, there is evidence that they repeatedly faced sperm competition in their ancestral past. That is, women mated with two or more men in a sufficiently brief window of time to allow sperm from more than one man into their reproductive tract that subsequently would compete to fertilize ova (Parker 1970). Because the most common mating system in humans is social monogamy (Brown et al. 2009), sperm competition can have a large impact on men's reproductive success through their regular partner's engagement in extra-pair mating and subsequently producing offspring sired by another male. This scenario leads to men unwittingly investing in genetically unrelated children (Trivers 1972).

This situation does occur in contemporary human societies, with an average rate of 3.1% of children having a different biological father than the one socially regarded as their father (Voracek et al. 2008). However, this rate sharply increases with degree of paternity uncertainty as men who reported having low confidence in paternity of their children experience a nonpaternity rate of 29.8%, while those with high paternity confidence experience only a 1.7% nonpaternity rate (Anderson 2006). Additionally, women report "double mating" or mating with more than one male within a 5-day span at least once in their lifetimes at a rate of 17.5% (Baker and Bellis 1993a). As such, men currently exhibit both physiological and psychological adaptations to sperm competition in order to avoid cuckoldry (and the subsequent reproductive cost of raising unrelated children) and women exhibit adaptations to manipulate the outcome of sperm competition in their favor (Shackelford et al. 2015). These adaptations would not have arisen without the presence of sperm competition in humans' evolutionary past. The following presents evidence of this history of sperm competition in humans.

Evidence in Men

In some primate species, females commonly mate with multiple males (polyandry) and in other

species they mainly mate with one male (monandry; Harcourt et al. 1995). In species practicing polyandry, the risk of sperm competition is greater, and the male genitalia of these species evolved to adapt to this greater risk. Specifically, more sperm is needed to be produced to outcompete that of rivals, and polyandrous species have larger testes capable of producing enough sperm to meet the demands of sperm competition (Harcourt et al. 1981; Short 1979). Relative testis size and the number of sperm per ejaculate correlate positively with the degree of polyandry; for example, monandrous gorillas have relatively small testes, while highly polyandrous chimpanzees have rather large testes in proportion to body size (Harcourt et al. 1995). Humans have testes that are intermediate in size (in proportion to body size) compared to both the gorilla and the chimpanzee, which signals an intermediate level of sperm competition risk in humans (Smith 1984).

Similarly, the length and shape of the human penis has been noted as evidence of a history of sperm competition. The length is longer than that of any other ape (Short 1979) which is argued to give men an advantage in sperm competition. Specifically, the long penis can deposit sperm close to the cervix which gives the sperm an advantage in the race toward the egg as they would have a shorter distance to travel (Baker and Bellis 1995; Smith 1984). In terms of shape, it has been proposed that the coronal ridge of the penis is designed to displace rival semen that was previously deposited in a woman's reproductive tract (Baker and Bellis 1995). Empirical evidence to support this hypothesis was provided by Gallup et al. 2003, who used artificial genitals to conclude that phalluses with a coronal ridge displaced up to 90% of simulated semen while phalluses lacking a coronal ridge only displaced 35.3%. In further detail, this displacement seemed to function by the coronal ridge allowing semen to flow back and collect under it; however, this only was able to occur when at least 75% of the length of the penis was inserted into the simulated vagina (suggesting again that length is important for sperm competition). Finally, the refractory period that men experience after an ejaculation (period in

which an erection cannot be achieved) can also be argued as evidence of the semen displacing ability of the human penis, as it would be reproductively costly for a man to displace his own sperm (Gallup and Burch 2004).

At the genetic level, there also exists evidence of some history of sperm competition in humans. Upon examination of protamine genes (genes involved in the production of functional spermatozoa), they seem to be somewhat similar to those found in polygamous rodents as well as being thought of as comparable to the more polygamous chimpanzee in primate terms (Martin-Coello et al. 2009; Wyckoff et al. 2000). Other research looking at genes that encode seminal fluid proteins suggest a more moderate history of sperm competition. Specifically, in many nonhuman species (including other primates such as the gorilla and chimpanzee), proteins in seminal fluid function to form a “mating plug” within the female reproductive tract as a means of blocking sperm from rival males in subsequent matings (Lievers and Simmons 2014), and the rate of evolution of a certain gene involved in the production of the proteins necessary to form the mating plug is positively correlated with the level of sperm competition within a species (Clark and Swanson 2005). Among primates, the rate of evolution of this gene is only moderate in humans compared to the highly promiscuous chimpanzee (Dorus et al. 2004).

Beyond anatomical evidence, men try to boost their paternity confidence of offspring that may result from sexual relations with a given woman and therefore have evolved preferences for mates that will provide them with the least amount of sperm competition, even in short-term contexts (Shackelford et al. 2004). Consistent with these preferences, men are most likely to report a desire to pursue a short-term relationship with a woman who is neither married nor involved in casual sexual relationships as this situation presents no risk of sperm competition; men were least interested in a short-term relationship with a married woman, as frequent inseminations from a husband present a high sperm competition risk (Shackelford et al. 2004).

Another part of men’s mating psychology related to the threat of sperm competition is the strength of male sexual jealousy. Not only do men attempt to choose mates that pose a low sperm competition risk, once finding a low-risk partner they try to further minimize the opportunities for her to engage in extra-pair copulations with other men, and this is often motivated by jealousy (Shackelford et al. 2015). Men react with stronger jealousy to just imagining their regular partner engaging in sexual intercourse with someone else compared to women (Buss et al. 1992). This jealousy and its use as a mate retention tactic tend to keep men’s regular partners away from potential rivals in order to avoid the consequences that can be attached to that jealousy. In the most extreme of cases, male sexual jealousy can lead to men murdering their partners; this is also the leading motive for men to kill their partners (Buss 2006). Such strong reactions to potential extra-pair copulation are evidence of sperm competition as a recurring theme among humans’ evolutionary past.

Evidence in Women

While men’s adaptations to sperm competition are designed to avoid cuckoldry, women’s adaptations to sperm competition are designed to ensure its outcome serves their best reproductive interests. These adaptations concern both pre-copulatory and postcopulatory female mate choice (Shackelford et al. 2015). In precopulatory mate choice, women have the most reproductive success from forming a long-term relationship with a man who is willing to invest in her and her children to increase the chances of offspring survival (Trivers 1972). However, the type of mate that a woman can secure as a long-term investing mate and the type of mate that can offer the most in terms of good genes that could be passed to her offspring may be different from one another (Gangestad et al. 2015). Specifically, men with traits signaling “good genes” such as muscularity, masculinity (in the body, face and voice), symmetry, and social dominance typically have high testosterone levels and subsequently are

less likely to display a willingness to be faithful and invest in one woman (Pollet et al. 2011). Therefore, it is adaptive for women to strive to obtain both paternal investment and good genes to maximize reproductive success by having a long-term mate and engaging in extra-pair copulations with men of superior genetic quality when conception risk is the highest (Gangestad et al. 2015).

This speculation has been supported by research finding that while women's sexual attraction to their regular partner remains unchanged across the ovulatory cycle, their sexual attraction to and likelihood of sexual fantasizing about men other than their partner is more likely to occur during the fertile window of the ovulatory cycle (Pillsworth and Haselton 2006). This also translates into behavior as women are more likely to engage in extra-pair sex when conception risk is high, especially when their regular partner is not of relatively high genetic value (Garver-Apgar et al. 2006). Not only do women engage in extra-pair mating during high fertility, but they also strategically schedule copulations with their regular partner to manipulate sperm competition outcomes as well. When women have recently engaged in an extra-pair mating, they tend to delay copulation with their regular partner in order to give the rival male an advantage in sperm competition (Gallup et al. 2006).

In postcopulatory mate choice, female orgasm seems to be the driving force in sperm competition outcomes. It has been speculated that the female orgasm is an adaptation for selective sperm retention, as its occurrence causes uterine contractions that facilitate the retention and transfer of a greater number of sperm into the reproductive tract (Baker and Bellis 1993b, 1995). Because women want the best quality genes for their offspring, the finding that women mated to more symmetrical men (a sign of genetic quality) have more copulatory orgasms than women mated to less symmetrical men (Thornhill et al. 1995) might be support for the argument of female orgasm being an adaptation. In addition to the presence of female orgasm during copulation for sperm retention, the timing of such orgasms may be just as (if not more) important for this purpose (Smith 1984). According to research by Baker and Bellis

(1993b), the optimal timing for female coital orgasms for greater sperm retention is between 1 min before and 45 mins after male ejaculation. This was concluded after examining seminal and vaginal fluid that was ejected from the vagina after copulation (known as flowback), and less sperm was ejected when female orgasm occurred during this time frame. Furthermore, for women with extra-pair partners, they report having more of these high-retention orgasms within this time frame with the extra-pair partners compared to their regular partners (Baker and Bellis 1993b). This is also indicative that women may promote sperm competition and bias the outcome in favor of an extra-pair partner that likely is of greater genetic quality.

Related to female orgasm as an adaptation concerning sperm competition outcomes is men's interest in ensuring their partner achieves orgasm. One study found that men who spent more than 50% of time away from their partner since the couple's last copulation reported a greater interest in their partner's copulatory orgasm than men who spent less than 50% of time away from their partner (McKibbin et al. 2010). More specifically, sperm competition risk (as measured by percentage of time spent away from partner) moderated the effect of relationship satisfaction and investment on interest in partner orgasm, such that men who reported a greater sperm competition risk and greater relationship satisfaction and investment were particularly likely to report an interest in and attentiveness to their partner's copulatory orgasm. The association between relationship satisfaction and investment and interest in partner orgasm was not significant for men who reported lesser sperm competition risk, suggesting this interest is motivated by wanting to get an advantage in potential sperm competition.

Conclusion

Humans have faced a significant degree of sperm competition in their evolutionary history. Between the highly promiscuous chimpanzee and the monandrous gorilla, the level of sperm

competition in human mating systems is moderate, but this moderate amount is enough to warrant the development of adaptations in response to sperm competition in both men and women. For men, they have evolved adaptations to both avoid sperm competition and to also have an advantage in winning such competition on the occasions in which it does occur. Their genitalia evolved to generate enough sperm to be competitive in a lottery or scramble scenario and also to displace rival sperm that may already be present in a woman's reproductive tract. Genetic indicators of moderate sperm competition exist in men as well. Psychologically speaking, men have evolved preferences to avoid choosing a long-term mate that would be of high sperm competition risk and, once in an exclusive sexual relationship, men have evolved strong sexual jealousy to deter their partners from engaging in extra-pair copulations.

In women, sperm competition adaptations function to manipulate its outcome in their favor. In terms of reproductive success, it would be optimal for women to have a regular partner from which they can secure paternal investment and also strategically engage in extra-pair copulations during periods of high conception risk to secure genes superior to those that can be obtained from the long-term partner. To aid in utilizing this strategy, women's sexual preferences change throughout the ovulatory cycle such that they are more attracted to men other than their regular partner during times of high fertility. Women also can manipulate the outcome of sperm competition in the incidence of "double mating" by strategically having orgasms during copulation with the partner that is deemed genetically superior to retain more of his sperm. For being a moderate selection pressure on human mating dynamics, sperm competition has had considerable influence on the evolution of human sexuality.

Cross-References

- [Female Orgasm and in-pair Copulation](#)
- [Infidelity Risk](#)

- [Paternity Uncertainty](#)
- [Physiological Evidence for Human Sperm Competition](#)
- [Psychological Evidence for Human Sperm Competition](#)

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Holistic Sexuality Education

► Sex Education in Schools

Hollywood Actors

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Synonyms

Attractive; Celebrities; Muscle; Strength

Definition

Individuals who are perceived as the most attractive individuals in society who work in film and television.

Introduction

Hollywood actors have the ability to transform their stage into another dimension for their

audience. With this ability, many people covet these Hollywood actors and their lifestyle that comes with the territory. However, being a successful Hollywood actor depends largely on the physical attractiveness of their appearance to the population. Each gender of Hollywood actors conforms to the common perception of what makes an individual attractive. By being able to abide by these perceptions of attractiveness, many Hollywood actors manage to find roles that remain within their levels of attractiveness and portray a character that their audience will find appealing. With the pressure of abiding by the common belief that Hollywood actors must remain attractive in order to stay successful, some Hollywood actors can be seen as being more prone to anger. Although Hollywood actors have the stress with remaining physically attractive to their audience to earn more work in their trade, some would argue that the stress is not what makes them more prone to anger. Rather, Hollywood actors, because they are attractive, are more prone to anger because of their appearance not because of their trade.

Attractiveness and Hollywood Actors

The common belief that in order to be a successful actor in Hollywood comes from the perception of attractiveness of the individual. Thus, each gender of Hollywood actors must adhere to the common perception of what makes each gender attractive to others. For example, females are perceived as attractive when they have lower body weight, whereas males are perceived as attractive when they have a higher body weight (McCreary and Sadava 2001). Female Hollywood actors follow the common belief that having a smaller body structure will make them more appealing to their audience. As a result, females are more likely to diet and are more likely to use unsafe weight-loss strategies to remain physically attractive (Connor-Greene 1988). In addition to a lightweight body structure, females are perceived as more attractive when they maintain an element of youth to their physical appearance. Females are considered more attractive, and thus a more successful Hollywood actress, when they reduce the effect of aging in

film roles (Lincoln and Allen 2004). Age changes the facial structure of females that make them dissatisfied with their physical appearance. When females age, their lips, eyes, and cheeks are making structural changes to their facial structure that distance themselves further from cultural beauty standards set by Hollywood (Franzoi and Koehler 1998). So with both youth and a lightweight body structure, these females have a higher perception of attractiveness in Hollywood. As a result, those females who are considered attractive are portrayed more favorably in film and television than characters who are considered unattractive (Smith et al. 1999). Females use both age and body structure to influence their perception of attractiveness, and Hollywood actresses that can abide by the cultural standards of beauty are considered more successful in their trade.

Like females, males also adhere to cultural standards of beauty to obtain success in Hollywood as an actor. Unlike females, males' body structure is to have a higher weight because it perceives the males as having muscle and strength. With having a higher body weight, males can distort the perception of their body to have others perceive them as attractive. For instance, body structure can perceive certain facial characteristics, specifically a prominent jaw line, to associate these facial characteristics with masculinity and strength (Windhager et al. 2011). Males who are considered muscular have more success in Hollywood as an action star and remain within that field of acting for several roles. Males view these Hollywood actors as successful because it remains their ideal body structure that cultural standards have promoted (Leit et al. 2002). In addition, younger men who perceive a larger body with more muscle mass and less body fat is what both males and females would find attractive (Lynch and Zellner 1999). Therefore, similar to females, emphasis on body structure influences the perceptions of what males consider to be attractive.

Attractiveness and Anger

Anger is an emotion that every individual expresses in their lifetime and has been examined to determine who are more likely to be anger-

prone. Hollywood actors and actresses consistently argue that anger is a response to the stress and pressure of their career. However, research shows that the pressure and stress of working in Hollywood may not be the reason why some Hollywood actors are anger-prone. Children who have been reported as some of the most aggressive students toward teachers have also been perceived as being some of the most physically attractive children (Hawley et al. 2007). Thus, the argument that the stressful work environment creates the response of anger does not sufficiently address that more physically attractive individuals tend to have more aggression and anger in their lives. Females' perception of attractiveness is related to their emotion of anger, and males are more prone to anger when they view themselves as physically attractive (Sell et al. 2009). Accordingly, being perceived as more physically attractive makes an individual more prone to anger regardless of their career choice. Therefore, Hollywood actors and actresses, because they are perceived as some of the most physically attractive individuals within the population, will be more prone to anger than others.

Research has shown that individuals who are physically attractive are more prone to anger. In addition, individuals who are considered some of the most successful actors and actresses in Hollywood have been considered some of the most physically attractive individuals. As a result, media consistently reports on incidences of anger, aggression, and violence of Hollywood actors and actresses. In 2014, a Hollywood actress physically fought with her brother-in-law in a hotel elevator. In another incident in 1992, a different successful Hollywood actress was arrested for battery after being involved with an altercation with another female. However, Hollywood actors also have a lower threshold for anger and aggression to handle disputes. Over the years, several Hollywood actors have been involved with physical disputes with paparazzi in the public streets. In one incident in 2013, a successful Hollywood actor was engaged in a shoving match with a member of the paparazzi. Hollywood does have several different pressures placed on actors and actresses, but research helps understand that its more of the

belief that attractive individuals have a lower threshold to anger and aggression in handling disputes.

Conclusion

Hollywood actors and actresses are considered as the most attractive individuals in society. By adhering to the cultural beauty standards, certain individuals are able to obtain a successful career in Hollywood, while others are considered not as successful. Females are perceived as attractive, and therefore more successful, when they maintain a lower body weight and youth. Aging is believed to make Hollywood actresses less employable and less appealing in Hollywood making them less popular in media. However, males are perceived as attractive in Hollywood when they have a higher body weight compared to females because it perceives them as muscular and having strength. While Hollywood actors and actresses are some of the most attractive individuals in the population, individuals who are perceived as more attractive are more prone to anger and aggression. Several incidences that have been seen in the media involving Hollywood actors show how attractiveness leads to a higher likelihood of anger.

Cross-References

- [Attractiveness and Anger-Proneess](#)
- [Sex Differences in Aggression](#)
- [Strength and Anger-Proneess](#)

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Holmes and Sherman (1982) on Ground Squirrels

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Synonyms

[Comparing phenotypes](#); [Phenotype matching](#).

Definition

Phenotype matching refers to the ability to detect genetic relatedness based on phenotypic cues of the self or close kin.

Introduction

In laboratory studies it was found that Belding's ground squirrels (*Spermophilus beldingi*) are able to recognize kin with which they did not share natal burrows. Related female individuals, even if they were unfamiliar to each other, were less agonistic than unrelated individuals. Field studies also showed that littermate full-sisters treat each other differently than maternal half-sisters. This suggests that both rearing environment and relatedness have crucial contribution to nepotistic behavior in ground squirrels. Similar results with other rodent species imply that learning and recognition of cues of probable genetic relatedness, known as phenotype matching, might be a mechanism which influences social interactions.

Mechanisms of Kin Recognition

Hamilton's inclusive fitness theory suggests that it would be advantageous for individuals to show a biased behavior for conspecifics who are genetically more closely related. Preference for kin could help optimize prosocial behavior within the group (nepotism) and mate choice decisions (inbreeding avoidance, optimal outbreeding, see Bateson 1983). However, for nonsedentary species, as dispersal from the native group is common, differentiating between kin and nonkin could be a challenge. At least four possible mechanisms of kin recognition were outlined (Mateo 2003).

First, *spatial cues* (i.e., co-residence) can inform individuals about relatedness.

Second, *early association* is a somewhat better heuristic for the estimation of kinship. For species which disperse after the juvenile period and, therefore, may easily find themselves in the proximity of nonrelated conspecifics, co-residence is an uncertain cue of genetic closeness.

Third, as a theoretical possibility, it has been proposed that *recognition alleles* could serve the recognition of related individuals. This allele should be expressed phenotypically,

recognized by others and it is expected to increase the likelihood of preferential treatment of the individuals with that cue.

Fourth, if there is a correlation between the similarity of phenotypic traits and the amount of shared genes, *phenotype matching* can provide individuals with the necessary information about relatedness. During the juvenile period they can learn either the cues (e.g., odors) of their littermates and other co-residing conspecifics (other-referent phenotype matching), or that of their own (self-referent phenotype matching), and later use these as a recognition template to assess genetic relatedness to unfamiliar individuals.

Ground Squirrels as Model Animals

Holmes and Sherman (1982) used Belding's ground squirrels (*Spermophilus beldingi*) and Arctic ground squirrels (*S. parryi*) as model animals to test whether phenotype matching is used for kin recognition in these species. They cross-fostered preweaned pups in a laboratory environment and tested the behavior of related and familiar individuals and related and unfamiliar individuals in pairs. It turned out that ground squirrels which were reared together treat each other as siblings, that is, they are not more agonistic than sibling pairs. Besides, female siblings reared apart showed less aggressiveness than unrelated female pairs. Field observations of Belding's ground squirrels revealed also females' ability to discriminate between full-sisters and maternal half-sisters, despite they shared the natal burrow with both sibling types. They are more cooperative and less agonistic with full-sisters than with half-sisters – an impressive demonstration of the inclusive fitness theory. Hence, it was suggested, shared environment shape prosocial behavior and so does genetic relatedness.

In subsequent experiments, the role of phenotype matching in kin recognition was studied further. It was shown that females of *S. beldingi* treat paternal half-sisters differently than unrelated females (Holmes 1986a). In this case, as these

siblings were reared apart, familiarity could not contribute to the biased behavior. When female ground squirrels were cross-fostered and reared in a mixed group of related and unrelated littermates, paired arena tests confirmed that both shared natal environment and relatedness affects the frequency of agonistic acts (Holmes 1986b). On the one hand, when females encountered unrelated females, the level of aggression was modest. Note that due to cross-fostering they were mutually the sisters of each other's littermates. This shows that exposure to a certain phenotype in the natal burrow is used later as a template to which other individuals are compared (Holmes 1984). In this case, information about phenotypic cues of nonrelated littermates is used to recognize kin of that littermates (other-referent phenotype matching). On the other hand, unfamiliar sisters are recognized and preferred as well, even in case the pup does not share its natal environment with any relatives, preventing the use of phenotypic cues other than her own (self-referent phenotype matching).

Conclusion

The ability to recognize kin, and to prefer them over conspecifics who are genetically not related, has been observed in many taxa, including insects and mammals. It has been suggested that this bias was selected for during evolution and might be best explained by the theory of inclusive fitness. Several mechanisms have been put forward to account for kin recognition, most notably *phenotype matching*. In their influential paper, Holmes and Sherman (1982) provided evidence that ground squirrel pups (*Spermophilus sp.*) learn phenotypic cues of both their littermates and their own, to which unfamiliar individuals are compared at later encounters. Though theoretically both sexes might use this ability the discriminate between conspecifics with different degrees of relatedness, biased behavior is limited to female–female interactions. This suggests that kin-recognition is used in these rodent species as a means of nepotism, rather than that of optimal mate choice.

Cross-References

- ▶ Adaptive Problem of Detecting Kinship
- ▶ Facial Resemblance and Kinship Detection by Strangers
- ▶ Hamilton's Rule
- ▶ Hamilton's Rule and Genetic Relatedness
- ▶ Hamilton's Rule and Kin Investment
- ▶ Hamilton's Rule and Theoretical Implications
- ▶ Inclusive Fitness
- ▶ Kin Detection by Odor
- ▶ Phenotypic Resemblance and Kinship Detection
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ William Hamilton

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Home Language Acquisition

- ▶ Language Acquisition in the Home

Home Literacy

- ▶ Language Acquisition in the Home

Home Ranges

- ▶ Unknown Territory

Homeostasis

- ▶ Physical Health

Homicide

- ▶ Contexts for Men's Aggression Against Women
- ▶ Employment Status
- ▶ Female Age as a Predictor of Men's Aggression Against Women
- ▶ Humans: Within-Group Conflicts
- ▶ Marital Status
- ▶ Nonhuman Primates: Within-Group Conflicts
- ▶ Reproductive Value and the Evolution of Aggression
- ▶ Risk Variation with Parent Age
- ▶ Sex Differences in Death by Filicide
- ▶ Sex Differences in Death by Homicide
- ▶ Violence from Women's Kin

Homicide Adaptation Theory

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Synonyms

Homicide modules; Killing; Murder

Definition

Evolved psychological mechanisms to facilitate killing other humans.

Introduction

Violence has been a recurrent and persistent occurrence throughout the expanse of human history (Daly and Wilson 1988; Pinker 2011). An evolutionary psychological perspective proposes that violence is inherently and inextricably entrenched in human psychology. Accordingly, this perspective suggests that over deep evolutionary history, humans have evolved adaptations for aggressive behavior as means of solving a variety of adaptive problems (Buss and Shackelford 1997). Thus, the capacity for violence disposed by modern humans may be the result of selection favoring aggressive tendencies. In particular, aggressive behavior may have emerged as a pattern of solutions to the many problems presented by group living.

Buss and Shackelford (1997) proposed seven domains for which aggression may serve effective means: (1) co-opting resources from others, such as fertile land, water access, or tools; (2) defending against an attack from conspecifics, which can result from others employing the previous strategy and poses a serious threat to the survival of the victim; (3) inflicting costs on intrasexual rivals, typically within the context of intrasexual competition for mates; (4) negotiating status and power hierarchies in relevant contexts; (5) deterring rivals from future aggression, which can include creating and maintaining a reputation for aggression; (6) deterring mates from sexual infidelity as a means to ensure paternity or paternal investment; and (7) reducing resources expended on unrelated children by means of infanticide. Two of these domains in particular – inflicting costs on intrasexual rivals and reducing resources expended on unrelated children – often include the killing of another human.

Homicide as an Adaptation

In every culture studied, people have been documented killing other people. Although many species kill members of their own species via competition, the sophistication of human killing is observed in only one other species – chimpanzees (*Pan troglodytes*; e.g., Mitani et al. 2010), the phylogenetically closest living relative to humans. Duntley and Buss (2005, 2011) proposed *homicide adaptation theory* to explain why people kill other people. Homicide adaptation theory states that humans have evolved adaptations to facilitate killing in specific, and evolutionarily-recurrent, contexts for which the benefits of killing outweigh the costs. The majority of killings perpetrated by humans are believed to be the product of evolved psychological mechanisms designed by natural selection to ensure the death of conspecifics.

Homicide has not been perpetrated indiscriminately over human evolutionary history. Rather, killing of conspecifics occurs in highly specific contexts that have posed recurrent adaptive problems over human evolutionary history. Duntley and Buss (2005, 2011) propose specific contexts for which homicide may have been ancestrally advantageous, including: (1) preventing the exploitation of self, kin, mates, or coalitional allies from conspecifics; (2) reputation management to avoid appearing exploitable; (3) protecting resources; (4) eliminating individuals who utilize resources, but who provide no fitness benefits to the aggressor (e.g., step-children); (5) eliminating genetically related individuals who pose a significant fitness cost to the perpetrator; and (6) gaining access to mates. Homicide adaptations could therefore have evolved if, on average, homicide increased the fitness benefits of the perpetrators, relative to the fitness costs.

Homicide adaptation theory does not propose that homicide is the preferred strategy as a solution to any of the above adaptive problems. In most circumstances, the costs of homicide are far too high to make it a viable strategy. Instead, according to homicide adaptation theory, homicidal behavior may have been the best solution for some adaptive problems in some circumstances.

Converging lines of evidence provide support homicide adaptation theory as an explanation for the ubiquity of homicide in human history and cultures (Duntley and Buss 2005, 2011).

Homicide adaptation theory proposes that selection has shaped distinct homicide adaptations for men and women (Duntley and Buss 2005, 2011). More generally, men are significantly more likely to engage in violent and potentially lethal behavior than are women. Pioneering work by Daly and Wilson (1988) demonstrated that the proportion of male-male homicides substantially exceeds the proportion of female-female homicides in every culture studied. National statistics reported by Daly and Wilson (1988) are corroborated by a network of evidence demonstrating physical, psychological, and behavioral adaptations for aggression specifically in men (Goldstein 2001; McDonald et al. 2012; Sell et al. 2012). Male-male homicide is committed for a variety of reasons including the escalation of petty disputes, reputation management, and – most often – because of intrasexual competition (Daly and Wilson 1988).

Spousal homicides are overwhelmingly committed by men and are most often fueled by sexual jealousy, with young, reproductive age women disproportionately represented among the victims (Shackelford et al. 2000). Men may benefit from wife-killing if the wife has committed sexual infidelity which disposes risk of investing resources into genetically unrelated offspring. Men with adulterous wives may also incur substantive reputational costs which may be alleviated by uxoricide.

Men and women are both hypothesized to have evolved adaptations for the killing of infants, though for different reasons (Duntley and Buss 2005, 2011). Because internal fertilization and gestation occur in women, ancestral men could not be certain of the genetic relatedness of their offspring. Men with low paternity confidence are at increased risk for killing their offspring. Men that enter a relationship with women who have offspring from a previous mateship(s) may kill the women's offspring to reduce resource expenditure on genetically unrelated offspring and increase the

likelihood of subsequent breeding – a pattern found in nonhuman species, such as lions (*Panthera leo*; e.g., Packer and Pusey 1983). Women, in contrast are certain of maternity but may kill their offspring they perceive a net cost of continued investment (e.g., severely ill or deformed offspring) or if there are not sufficient resources to adequately care for the offspring (e.g., food scarcity). Infanticide may be considered a particularly powerful force driving its own set of adaptations in males and females (See ► [Infanticide](#), ► [Infanticide in Nonhumans](#), Infanticide as a Selective Force for Group Living, Infanticide Risk).

Other lines of evidence converge to support the key proposition that adaptations for killing conspecifics has evolved (reviewed in Duntley and Buss 2011), such as it being more likely that an individual's killer is someone known to the victim, cross-species documentation of killing conspecifics in similar and predictable contexts to those of humans, evidence on ancient human remains that are consistent with homicide by another human with a weapon, archeological evidence of weapons designed for homicide, extensive cross-cultural evidence of homicide, and consistency of contexts for homicide across diverse cultures. Taken together, existing evidence suggests the longevity of killing conspecifics in human and nonhuman evolutionary history.

Conclusion

Humans have a long evolutionary history of aggression (Pinker 2011). Duntley and Buss's (2011) homicide adaptation theory explains how homicide has evolved. The theory proposes that humans have evolved psychological mechanisms for killing. Homicide may have emerged as an advantageous strategy in specific contexts when the fitness benefits of committing homicide outweighed the fitness costs. These benefits suggest explanations for the cross-cultural and cross-generational ubiquity of homicide in humans.

Cross-References

- ▶ [Child Homicide](#)
- ▶ [Evidence of Intentional Killing](#)
- ▶ [Homicide by Design](#)
- ▶ [Homicide Fantasies and Evolved Homicide Module Theory](#)
- ▶ [Infanticide](#)
- ▶ [Infanticide and Parenting](#)
- ▶ [Infanticide in Nonhumans](#)
- ▶ [Marital Status and Infanticide](#)
- ▶ [Partner Abuse and Homicide](#)
- ▶ [Partner Homicide](#)
- ▶ [Partner Killing](#)
- ▶ [Predictors of Infanticide](#)
- ▶ [Same-Sex Homicide](#)
- ▶ [Sex Differences in Death by Homicide](#)
- ▶ [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)

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Shackelford, T. K., Buss, D. M., & Peters, J. (2000). Wife killing: Risk to women as a function of age. *Violence and Victims*, 15, 273–282.

Homicide and Life History Theory

- ▶ [Sex Differences in Death by Homicide](#)

Homicide by Design

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Synonyms

[Murder by design](#); [Premeditated homicide](#); [Premeditated murder](#); [Proactive homicide](#); [Proactive murder](#)

Definition

Homicide by design is the premeditated killing of another person that is calculated and deliberate.

Introduction

Homicide is regarded by society as one of the most extreme and immoral crimes a person can commit. However, the act has persisted throughout human history and its prevalence is still unmistakably common today. Types of homicide (and human aggression in general) can be understood in two distinct groups: proactive and reactive. Reactive homicide entails an individual committing murder as a direct reaction to someone else's actions (Wrangham 2017). Common occurrences of reactive homicide include self-

defense and “heat of passion” murders. Conversely, proactive homicides lack the same emotion and physiological arousal as reactive murders (Wrangham 2017). They are premeditated, being consciously calculated by the offender against a specific individual or group of victims. This form of murder is also referred to as homicide by design, and its evolutionary advantages date as far back as the very beginnings of human history.

Homicide Adaptation Theory

Historically, homicide by design was an effective and adaptive method of solving evolutionary problems present in hunter-and-gatherer cultures and early human civilizations. The benefits gained from strategically killing others included preventing one’s own death, eliminating rivals, and acquiring valuable resources (Buss and Duntley 2001). In addition, the very limited or complete lack of legal and judicial repercussions in these times resulted in aggressive acts such as homicide enjoying these many evolutionary payoffs while avoiding the negative consequences these crimes face today. This theory was developed by Duntley and Buss (2011), who named it Homicide Adaptation Theory.

Homicide Adaptation Theory explains and predicts many statistics of today’s homicide prevalence, especially in the case of sex differences. For instance, the theory details why homicide rates are much higher in males (87%) and why males are also more likely than females to be the victims of homicide (75%): the early adaptive gains from homicide by design were mostly experienced by males, as they were the ones competing against each other to earn mates and obtain resources (Duntley and Buss 2011). Males who were better at planning their calculated attacks and successfully eliminating rivals would have thrived in this time period. Thus, the adaptive traits linked to homicidal ideation and planning would have survived and been passed on to future generations of males.

Ideation and Design

Even today, homicidal ideation is still a common occurrence in humans. Most people fantasize about killing at some point, even if they have no intentions or desire to follow through with their thoughts. These ideations often include detailed scenarios in which the individual contemplates and calculates the possible methods and consequences of their plan (Buss 2006). When faced today against a rival for adaptive resources such as access to food, mates, or money, the initial thought may be to strategically plan a way to eliminate the competitor entirely. The vast majority of people suppress homicidal thoughts and never commit or attempt murder due to the high risk of costly consequences following these acts. This suggests that homicidal ideations come from leftover psychological pathways from our ancestors which cause people to consider murder as a solution to different adaptive problems (Buss 2006). Despite premeditated murder now having more evolutionary costs than ever before, homicidal ideation in humans has not dissipated accordingly. Rather, the new consequences often force individuals to rethink their homicidal strategy and develop a different plan to solve their evolutionary problems.

Signal Affects

Individuals committing homicide can also benefit from more indirect evolutionary rewards, one of which being signal effects (Dahlén and Söderlund 2012). Somewhat counterintuitively, infamous murderers in recent human history such as Ted Bundy and Charles Manson achieved fame and even admiration from people all across the world. At first thought, it may be hard to understand why these criminals are admired and seen in a positive light despite committing heinous and immoral deeds; however, evolutionary perspectives of psychology explain that the killings can operate as a signal of the individual’s fitness, augmenting others’ perception of that person. The “homicidol effect,” coined by Dahlén and Söderlund (2012), described that individuals aligning themselves

with another individual prone to commit homicidal acts was evolutionarily adaptive and likely developed during ancestral times. By associating with a known and proven killer, the individual decreases the likelihood of becoming the culprit's next homicide victim, thus improving the individual's own fitness and chance of survival.

Conclusion

Despite being one of the most socially and morally impermissible acts a human commit, planned homicide has persisted throughout human history and still remains common today. The adaptive benefits and lack of costs of homicide in hunter gatherer cultures likely played a large part in wiring homicidal ideation into human brains through evolution over many generations. Committing homicide in this time also involved acquiring more indirect adaptive benefits including signal effects. While the costs and risks of homicide are much greater in today's world, ideation carries on, suggesting that the primitive drive to kill may be deeply rooted in our genes.

Cross-References

- [Partner Abuse and Homicide](#)
- [Same-Sex Homicide](#)
- [Sex Differences in Death by Homicide](#)
- [Strategic Aggression](#)

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Homicide Fantasies and Evolved Homicide Module Theory

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Homicide refers to the intentional act of killing another human. Buss and colleagues (Buss and Duntley 2001; Buss 2006; Duntley and Buss 2011) proposed that homicide is an evolutionary adaptation (i.e., *Evolved Homicide Module Theory* or *Homicide Adaptation Theory*). Psychological factors, such as cognitions or behaviors, are adaptive when they function to resolve challenges, leading to increased fitness. In human evolutionary history, there have been specific contexts where killing another human may have solved specific, recurring problems, and such actions had fitness benefits that outweighed the costs (Duntley and Buss 2006, 2008, 2011). Homicide was hypothesized to arise as an adaptation to prevent premature death, remove cost-inflicting rivals, gain resources, abort rival's prenatal offspring, eliminate stepchildren, and reduce future competitors of one's children (Duntley and Buss 2008, 2011).

One approach to studying homicide as an adaptation is through homicide fantasies. Our ability to form cognitions or fantasies about homicide suggests it allows people to explore scenarios in which murder may be a beneficial solution. Because these adaptive problems are complex (e.g., kin retribution), it would be important for mechanisms to weigh all the potential costs and benefits, resulting in either motivation or inhibition of homicidal behavior (Duntley and Buss 2006, 2008; Duntley 2005; Liddle et al. 2012; Shackelford et al. 2000). Since the homicide mechanism is triggered under specific contexts, this type of adaptation is considered facultative

and developmentally flexible. Buss and colleagues collected data on homicide fantasies from a very large sample (approximately 5000) across multiple nations. Generally, they found homicide fantasies to be quite prevalent, where 91% of men and 84% of women have had at least one homicide fantasy. These data also show some support for homicide as a facultative response to specific conditions. For example, Buss and Duntley hypothesized that spousal homicide functions by preventing being labelled a cuckold and reducing a rival's mating opportunities and found that many spousal homicide fantasies involved estrangement or infidelity (Buss 2006). Others studies found patterns of homicide fantasies that match patterns found in actual homicides, such as sex differences (Kenrick and Sheets 1993).

An alternative view is that homicide may function as a by-product of other adaptations (see, e.g., ► [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\] \[Daly & Wilson\] entry](#)). Much more empirical and theoretical work is needed to test whether various types of homicide are adaptive or a by-product of other adaptations. These studies need to demonstrate that homicide has fitness benefits that outweigh the many costs.

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Homicide Modules

- [Homicide Adaptation Theory](#)

Homicide, to Kill

- [Murder](#)

Hominid

- [Largest *Homo* Brain](#)

Hominidae

- [Largest *Homo* Brain](#)

Hominids

- [Why Humans Are Unique](#)

Hominin Evolution

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Synonyms

[Human evolution](#); [Previously hominid evolution](#)

Definition

The evolution of *Homo sapiens*, its ancestors, and closely related species from the last common ancestor with chimpanzees onward (~7 million years ago to present).

Introduction

Early evolutionary biologists answered the question of human origins by searching for the precise location of “man’s place in nature,” in T.H. Huxley’s phrasing, based on comparative anatomy between living species. Research has moved from viewing humanity at the top of the *scala naturae* to seeing it as “just” a big-brained, bipedal primate, and the focus shifted to explaining how we *arrived* at “our” place. The post-nineteenth-century focus has been on understanding the evolutionary circumstances that produced *Homo sapiens*, based on the idea that human-specific traits are the product of the same evolutionary processes that led to all other species. This effort is notably multidisciplinary: human origins fall within the remit of anthropology, biology, genetics, zoology, primatology, geology, and psychology. The (occasionally contentious) synthesis of work within these fields has produced a coherent, albeit pixelated picture, of which this summary is a sketch. It first reviews hominin evolutionary history chronologically and then explores evolutionary patterns, including the evolution of cognition, in more depth.

Hominin Evolutionary History

Hominins in Comparative Perspective

Systematics of the Primates

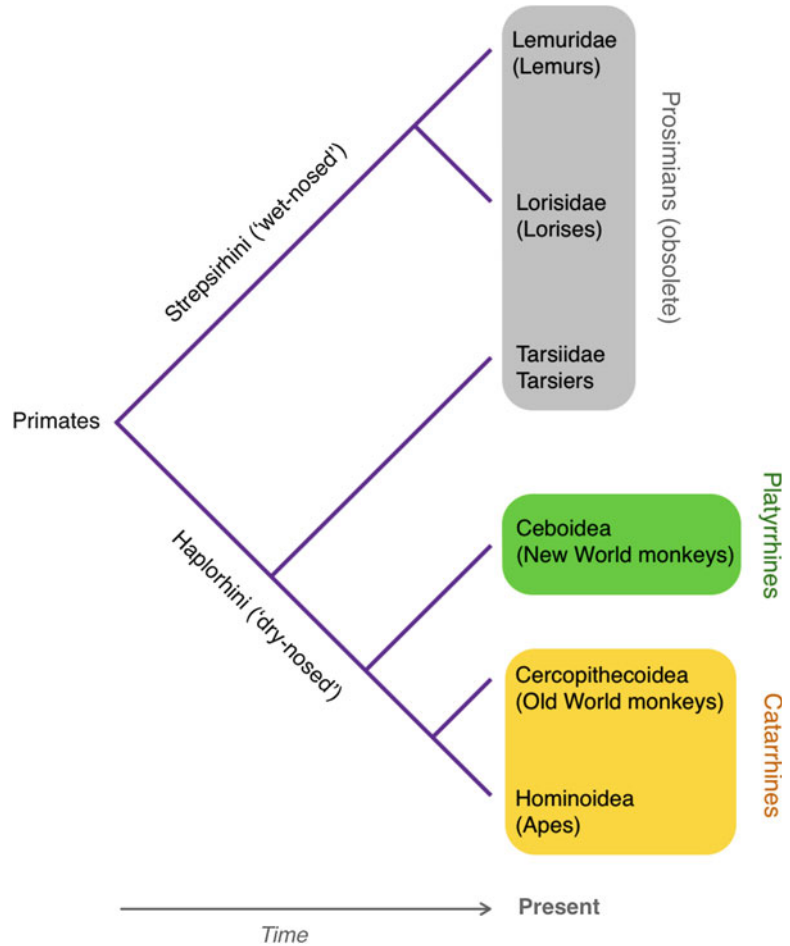
The Order Primates, to which we belong, is characterized by increased body size, dexterous hands, flexible limbs, nails instead of claws, a shortened snout, and associated shift of emphasis from olfactory to visual sensitivity manifested in, for example, stereoscopic vision. Primates are divided into two groups, separated terminologically if rather prosaically by nasal dampness: Strepsirhini (“wet-nosed”) and Haplorhini (“dry-nosed”) (fig. 1). This division

was initially based on purely morphological characteristics and was later refined and confirmed using molecular and genetic data. The Strepsirhini, whose ranks comprise lemurs and lorises, are characterized mostly by nocturnal adaptations (e.g., eyes with reflective layers to improve night vision), heightened olfactory sensitivity, and comparatively small brains. The Haplorhini are split into three major taxa: tarsiers, platyrrhines, and catarrhines. Current genetic phylogenies place tarsiers within the Haplorhini despite their strepsirrhine-like features, but their evolutionary relationship has been debated. The monkey-grade, or simian, primates are again distinguished nasally, but this time by shape: they include platyrrhines (“flat-nosed”) and catarrhines (“down-nosed”). Platyrrhines – of which the only living representatives is the Ceboidea superfamily which includes capuchins, marmosets, and howler monkeys – are restricted to the New World. They are mostly arboreal and are the only group to include monkeys with prehensile tails. Catarrhines, by contrast, are found in Africa and Asia: these are the Old World monkeys (Cercopithecoidea) and apes (Hominoidea). The Old World monkeys are unlike the apes in that they have tails, and include baboons, mandrills, and macaques. The Hominoidea comprises the arboreally specialized lesser apes (gibbons, or Hylobatidae) and great apes (Hominidae). Humans are therefore catarrhines, hominoids, and hominids.

Outline of Primate Evolution

There is an element of arbitrariness inherent in the idea of a “beginning” of the evolution of a lineage: after all, evolution is a continuous process, and consequently there are no real starting points within it. For this reason, the evolutionary events (like the splitting of lineages) requiring chronological estimates are based on *taxonomic* frameworks.

The current chronological outline of primate evolution is based on convergences between anatomical, fossil, and molecular approaches, of which the “molecular clock” gives the most frequently used dates. By assuming a constant rate of mutation during evolution, the molecular clock uses similarities and differences between biomolecules to estimate lineage-split times. The

Hominin Evolution,**Fig. 1** Phylogeny of living primates

divergence between primates and closely related lineages is estimated somewhere between 70 and 80 Ma, in the Cretaceous epoch. The Strepsirhini and Haplorhini diverged from each other around 55–90 Ma, and recent genetic estimates suggest they last shared a common ancestor ~87 Ma, at the very beginning of the primate radiation. Debate continues about the most likely location of their common ancestor – but Asia is a strong contender, because the basal clades of both lineages (the haplorhine tarsiers and strepsirrhine lorises), as well as the closest relatives of primates, Dermoptera and Scandentia, are exclusive to Asia. Fossil evidence of this common ancestor remains elusive. Tarsiers diverged from the rest of the Haplorhini early, around ~81 Ma. Platyrrhines last shared a common ancestor with catarrhines ~43 Ma, but the fossil record is equivocal

about where this last common ancestor lived and the platyrrhine route of dispersal to the Americas is therefore also unclear. Platyrrhines remained entirely arboreal, whereas some catarrhines (including humans) adapted to a terrestrial life. The Catarrhini further subdivided into Cercopithecoidea and Hominoidea ~25 Ma. Within the Hominoidea, the consensus order of divergence is an early Hylobatidae (gibbon) split with the rest of the clade at ~21 Ma, followed by *Pongo* (orangutan) at ~15 Ma and *Gorilla* at 8–9 Ma, and a final split between the *Pan* (chimpanzee and bonobo) and *Homo* lineages between 6 and 7 Ma.

Hominin Relationships to African Apes

Collectively, all modern and extinct great apes, including humans, are currently referred to as

hominids. The African contingent of the family Hominidae (comprising *Homo*, *Pan*, and *Gorilla*) is known as the subfamily Homininae. Within the Homininae there are three tribes: Gorillini, Panini, and Hominini. Humans are therefore most closely related to the two *Pan* species, chimpanzees and bonobos

Previously, “hominid” was also used to refer to the human lineage, including our ancestors and related species, after the split from *Pan*; but nowadays, humans and extinct species more closely related to humans than *Pan* are known as *hominins* (see Fig. 2). In practice, this means that we can start speaking of hominins around 7 million years ago, since molecular dates suggest the Hominini-Panini lineages diverged around this time – although the proposed split times range from 13 to 5 Ma.

Implications for Hominin Origins

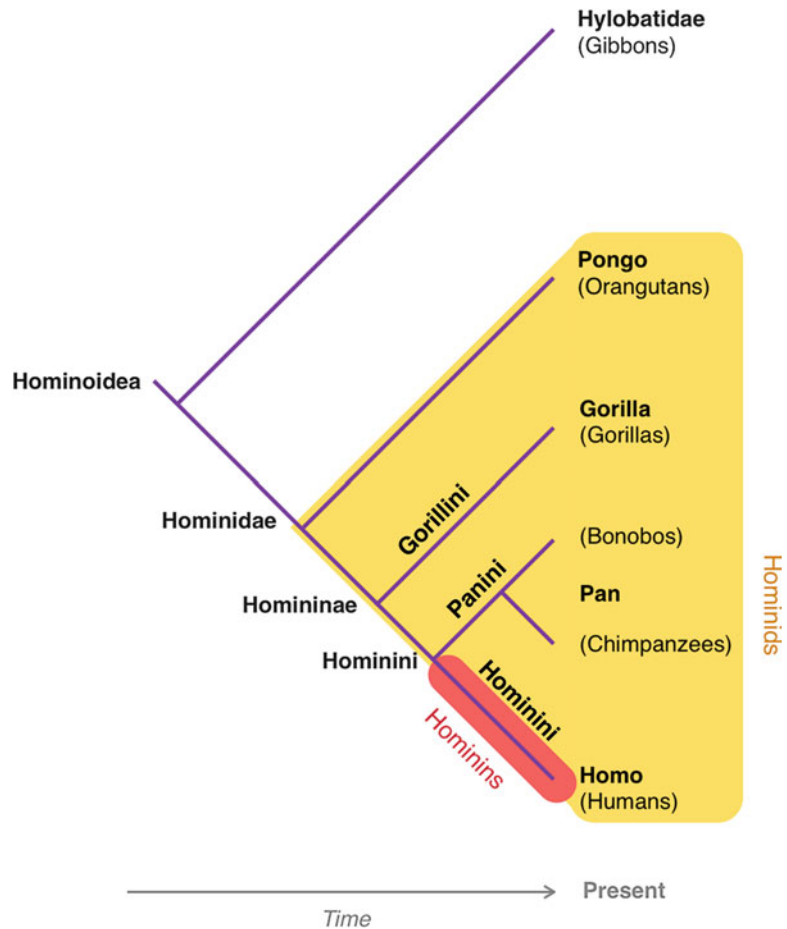
In the context of the range of living species, hominins share the closest evolutionary history with the African apes and in particular with chimpanzees and bonobos. This evolutionary proximity implies that features we have in common with all Hominidae genera are the consequence of shared ancestry. The list of shared features, which were presumably present in our common ancestors, has expanded considerably over recent years and now includes behavioral traits, potentially including a capacity for “cultural,” or socially transmitted, behavior (Whiten 2011).

The features *not* shared with African apes are most probably the product of our lineage’s evolution after it diverged from our modern ape cousins’ lineages – in other words, the features

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Hominin Evolution,

Fig. 2 Hominin relationships to African apes. Within the family Hominidae, the African apes, or Homininae, comprise three tribes: Gorillini, Panini, and Hominini. The term *hominid* is used to refer to all great apes, while *hominin* refers to humans, the direct ancestors of humans, and other closely related species *after* the split from *Pan*



that arose specifically during hominin evolution. In this perspective, it is implicit that some features unique to other ape genera are the consequence of their independent evolution, so apes cannot always be used as direct analogues or homologues for human ancestors. This phylogenetic framework is essential in exploring the origins of hominin characteristics, as it is a precursor to discovering *why* and *when* these “human” features appeared and what *consequences* they had.

Environmental Context for Hominin Evolution

The problems to which hominin adaptations provide solutions derive from the physical environment: the ecological context in which hominins evolved. Hominins diverged from the Panini clade at the end of the Miocene (23–5.3 Ma), around 7 Ma. Important climatic changes coincide with their emergence: long-term decline in temperatures (culminating in Pleistocene Ice Ages) and associated fragmentation of habitats (involving the breaking up of Miocene tropical forests and expansion of grassland, woodland, and bushland, producing mosaic habitats). These more open environments played significant roles in hominin evolution. Furthermore, the increased fragmentation probably promoted speciation through population isolation and also produced dynamically changing selective pressures associated with changing resource type, distribution, and seasonality.

Hominin Origins

The Hominini-Panini split is poorly documented in the fossil record, reflecting an overall paucity of Miocene fossils. Hominin origins consequently remain an elusive paleoanthropological problem. The problem has two key elements: first, the environmental and evolutionary context in which the split and, second, the lineages involved – the last common ancestor (LCA) of humans and chimpanzees, and its daughter species, the earliest member of the hominin clade.

To date, no potential chimpanzee-human LCA is known from the fossil record. This precludes empirical reconstruction of the context in which

the ancestral species split into two independent lineages. Even the geographical context of that group is unclear; although hominins belong to the African ape clade, and this clade might have a prolonged African ancestry, an alternative scenario is a Eurasian ancestor that migrated back into Africa in the Late Miocene. Two potential Eurasian ancestors have been proposed: *Graecopithecus* and *Ouranopithecus* – but there is insufficient fossil material to conclusively resolve the issue.

There are three African Late Miocene contenders for “early hominin” status: *Sahelanthropus tchadensis* (7.43–6.38 Ma), *Orrorin tugenensis* (6.14–5.52 Ma), and *Ardipithecus* (6.7–4.26 Ma). These three genera are classed as potential basal members of the hominin clade due to probable bipedal adaptations and, where sufficient evidence, dental traits shared with later hominins. Found in Chad, *Sahelanthropus* has an anteriorly positioned foramen magnum (the opening at the base of the cranium through which the spinal cord passes) compared to quadrupedal species, indicating that its head was held on an upright body consistent with some level of bipedal locomotion. However, the incomplete nature of the fossil makes reconstruction of the position of its foramen magnum, along with the behavioral inferences based upon it, contentious. By contrast, East African *Orrorin* is only known from fragmentary postcrania. Its femoral morphology suggests it shared distinctive hip biomechanics with the unequivocally bipedal australopithecines (Richmond and Jungers 2008). Finally, *Ardipithecus*, an Ethiopian genus comprising two species (*ramidus* and *kadabba*), shows a mosaic of terrestrial and arboreal features, indicating it was a facultative biped – in other words, that it moved bipedally on the ground, but quadrupedally in trees. Dentally, *Ardipithecus* showed reduced sexual dimorphism of the upper canine: a hallmark of later hominins, contrasting with marked canine sexual dimorphism in chimpanzees.

Opinions are divided about early hominin taxonomy: the fossils may represent three individual genera, may belong to one basal hominin genus, may not belong to the hominin clade at all, or a

combination of these. The real difficulty in assigning Late Miocene apes to a species, genus, or lineage is not just ascertaining the presence or absence of derived traits shared with later hominins, as their evolution may have been paraphyletic. The divergence of later Miocene African hominids may have involved complex speciation with prolonged gene flow among populations and the evolution of extinct lineages with no direct ancestral relationship to later hominids. Further uncertainties about genetic mutation rates and generation times compound these paleontological considerations, because they influence molecular clock split-time calculations. Slow mutation rates produce dates as early as ~13 mya for the Hominini-Panini split, while fast ones estimate it at ~5 mya.

Early Hominin Evolution

Early hominin evolution (~4.2–2 Ma) is usually taken as synonymous with the emergence, diversification, and partial extinction of the australopithecines, defined broadly (see Table 1). This is correct, in a sense, although there is no clear consensus as to which early hominin species should be included formally in *Australopithecus*. The period might have seen the emergence of at least two other genera: *Paranthropus* (sometimes referred to as the “robust” australopithecines) and *Kenyanthropus*. The exact nature and extent of taxonomic diversity is debated; some researchers advocate a minimal level, but most support at least some degree of diversification. The evolutionary history of the early hominins coincides with the early Pliocene and

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Hominin Evolution, Table 1 Early hominins

Species	Age (Ma)	Mean cranial capacity (cm ³)	Mean body mass (kg)
<i>S. tchadensis</i>	7.43-6.38	365	-
<i>O. tugenensis</i>	6.14-5.52		
<i>Ar. kadabba</i>	6.7-5.11	-	-
<i>Ar. ramidus</i>	4.6-4.26	300-350	32
<i>Au. anamensis</i>	4.37-3.82	-	46
<i>Au. afarensis</i>	3.89-2.9	433	39
<i>Au. africanus</i>	4.02-1.9	454	31
<i>Au. sediba</i>	1.98	420	26
<i>Au. garhi</i>	2.5-2.49	450	-
<i>Au. bahrelghazali</i>	3.85-3.31	-	-
<i>P. aethiopicus</i>	2.73-2.23	443	32
<i>P. boisei</i>	2.5-1.15	493	46
<i>P. robustus</i>	2.27-0.87	536	30
<i>K. platyops</i>	3.54-3.35	Within the range of <i>Australopithecus</i> or <i>Paranthropus</i>	-

Source: Boyle and Wood (2017)

“–” indicates absence of fossil data. Shaded species have been proposed as primitive members of the hominin clade, but their exact phylogenetic affinities are uncertain. Age ranges take into account dating error

consequently takes place in the context of increasing habitat fragmentation. In this ecological context, the high degree of species diversity (however it is interpreted taxonomically) during this period is frequently interpreted as an adaptive radiation, although the scale, relative to other primate groups, is relatively small.

As a whole, this diverse group shares bipedal adaptations, reduced canines and canine sexual dimorphism, relatively large postcanine dentition, apelike life histories, body sizes, and cranial capacities. Broadly speaking, the latter three remain relatively constant across early hominin species (see Table 1), while the first two contribute to the fundamental trends underlying australopithecine diversity. These are:

1. Varying levels of terrestriality, with morphological adaptations to ground-dwelling. Mosaics of locomotor features are indicative of a spectrum of bipedal adaptation, with species incorporating arboreal climbing in their locomotor repertoire to greater or lesser degrees. *Au. afarensis*, a well-represented species (with around 300 individuals found so far) that lived from 3.89–2.9 Ma, has clear derived bipedal adaptations, like a humanlike pelvis and non-grasping big toe, but also primitive features indicative of arboreality, like long, curved fingers and a strong shoulders. A set of footprints found in Laetoli, Tanzania, dated to ~3.7 Ma and likely made by *Au. afarensis*, are commonly interpreted as the product of a form of bipedalism not unlike that of modern humans (Raichlen et al. 2010). *Au. africanus* (4.02–1.9 Ma) provides evidence of an increased reliance on arboreality than its older relative, with a grasping big toe and longer arm to leg ratio. *Au. sediba* (1.98 Ma) moved with a distinct combination of arboreal and terrestrial features, again implying a unique form of bipedalism (Zipfel et al. 2011). So, while early hominins were clearly united in their increased reliance on bipedal locomotion compared to their Miocene ancestors, accumulating evidence suggests at considerable diversity the *nature* and *degree* of bipedalism each species exhibited.
2. Specialization of subsistence behavior with a trend toward postcanine megadonty. The general “australopithecine” trend toward postcanine megadonty reflects increasing specialization in subsistence behavior over ~2 million years. From an ecological perspective, this makes sense: as new environments (such as those resulting from decreasing temperatures in the Pliocene) become saturated with opportunistic species, the evolutionary advantage shifts to specialized species who extract energy from specific resources more efficiently (Foley 1987). Subsistence specialization is especially pronounced in *Paranthropus* (later “robust” Australopithecines (*aethiopicus*, *boisei*, and *robustus*), ranging from 2.73 to 0.87 Ma), which share adaptations for chewing extremely hard and brittle foods like nuts and seeds. These adaptations include prominent sagittal crests for the attachment of massive chewing muscles, large and robust cheekbones to accommodate these muscles, and thick dental enamel. Some researchers consider their degree of subsistence specialization sufficiently different to that of the “gracile” Australopithecines to suggest they are a separate genus, *Paranthropus*, in accordance with one definition of a genus as a clade sharing a single adaptive zone (Wood and Collard 1999).

The Origins of *Homo*

The exact ancestry of *Homo* is unclear, but the genus tends to be seen as the evolutionary product of the gracile australopithecines. In general, *Homo* differs from *Australopithecus* in its trend toward ecological generalism, reflected in efficient ranging behavior, encephalization, and behavioral flexibility. The candidates at the center of the debate about the origin of our genus, which first appears at the start of the Pleistocene (2.5–0.01 Ma), are *Homo habilis* (2.6–1.65 Ma) and *Homo rudolfensis* (2.09–1.78 Ma). Their status as members of *Homo* is contentious. The problems with assigning fossils from around 2 Ma to either *Homo* or *Australopithecus* are twofold: first, the process of macroevolution and, second, uncertainty regarding the exact defining characteristics of the *Homo* genus.

In a now familiar tune, exact taxonomic affinities between species around this time are hotly debated. This derives, in part, from the debated definition of “genus” in the context of macroevolution, where the central question is *when* differences between species or groups of species are sufficient to merit their distinction at the generic level and of what *nature* these differences should be. A character-based distinction between *Homo* and *Australopithecus* – where *Homo* is defined on the basis of enlarged absolute brain size ($>600\text{ cm}^3$) and “complex” behavior, including tool use and language – long formed the bedrock of investigation into the origins of *Homo*. This essentially amounts to a “checklist” of features true *Homo* species should exhibit, but its validity has been questioned in recent years.

On the one hand, the apparent simplicity of a trait list for *Homo* membership is deceptive, because inferring the presence or absence of “complex” behavior is difficult. Language leaves no direct trace in the fossil record, and no stone tools have so far been found associated directly with Pliocene hominins. In the context of multiple coexisting hominin species around 2 Ma, this precludes assigning makers to lithic assemblages. The synonymy of technological ability and the *Homo* genus, moreover, is an artifact of the incomplete archaeological record: until 2015 the earliest known stone tool industry was the Oldowan, dated to 2.5 Ma, coincident with the appearance of the first bigger-brained hominin species (*H. habilis*). The beginning of the archaeological record has now been pushed back to 3.3 Ma with the discovery of the Lomekwian industry (Harmand et al. 2015), implying either that *Homo* originated much earlier in hominin evolution or, more parsimoniously, that the evolution of technological behavior preceded the emergence of our genus. Simple stone tool use by chimpanzees and capuchins in order to crack nuts supports the latter.

On the other hand, the usefulness of a trait checklist is undermined because it oversimplifies distinctions between genera by assuming a definable moment in time at which these distinctions appeared. This might not have been the case, and it has recently been suggested that the abrupt

Homo-Australopithecus divide that the checklist approach is based on has been exaggerated and that the emergence of *Homo* from *Australopithecus* is better conceived of as an accumulation of small transitions (Foley 2016).

So, theoretical problems abound. What this means in practice for the putative earliest members of *Homo*, *habilis* and *rudolfensis*, is that they likely represent “intermediate” species between *Australopithecus* and *Homo*, with features linking them to both genera. They have larger absolute brain sizes than Australopithecines and likely made and used stone tools, but the *habilis* hand and foot indicate it might have retained some arboreality in its locomotive repertoire. Both species have been suggested to have similar life histories to Australopithecines and certainly have considerably smaller bodies than later *Homo*. A phylogenetic approach to *Homo* by Wood and Collard (1999), where they define a genus as a “monophylum [common ancestor and all descendants] whose members occupy a single adaptive zone,” suggested *habilis* and *rudolfensis* do not belong in the genus. In summary, the emergence of *Homo* appears to be characterized by greater complexity than previously assumed.

The Evolution of *Homo* in the Pleistocene

After 2 Ma, human evolution is characterized by a general trend toward bigger brains, reduced dentition, increased technological complexity, and the development of a body plan adapted for long-distance ranging (see Table 2 for a list of *Homo* species after 2 Ma). The development of these traits contributed to the first hominin dispersals out of Africa, currently estimated at ~1.8 Ma. Despite these distinct overall patterns, specific evolutionary relationships between hominins in this period are unclear.

While its membership to the *Homo* genus is uncontested (based on its large brain, tool use, and modern body proportions), the precise phylogenetic affinities of *Homo erectus* are not. Its ancestry, descendants, and classification are debated, especially in relation to *Homo ergaster*, which is exclusively found in Africa. Some researchers assign *ergaster* and *erectus* to a single evolving lineage, called *Homo erectus*; others support a

Hominin Evolution, Table 2 The *Homo* genus

Species	Age	Cranial capacity (cm ³)	Encephalisation quotient	Geography
<i>H. habilis</i>	2.6-1.65	611	~3.6	Africa (Kenya, Ethiopia, Tanzania, South Africa, Malawi)
<i>H. rudolfensis</i>	2.09-1.78	793	~3.8	Kenya
<i>H. erectus</i> *	1.85 Ma - 27 kya	981	~3.6	Asia*
<i>H. ergaster</i> *	2.27 Ma - 870 kya	796	~3.3	Africa*
<i>H. heidelbergensis</i>	700 - 100 kya	1158	~5.3	Eurasia*
<i>H. floresiensis</i>	100 - 60 kya	417	2.5 - 4.6	Flores, Indonesia
<i>H. naledi</i>	~0.3	460 - 610	~2.4	South Africa
<i>H. neanderthalensis</i>	197 kya - 39 kya	1420	~5.5	Europe and Western Asia
Denisovans	50 -28 kya	-	-	Siberia
<i>H. sapiens</i>	200 kya - present	1457	~5.8	Archaic forms evolved in Africa, now worldwide

Sources: Age, Cranial capacity, and Geography from Boyle and Wood (2017); Encephalisation quotients from Schulkin (2011)

*indicates this is debated; see text for discussion. Shaded species have been proposed as the earliest members of *Homo*, but their exact phylogenetic affinities are uncertain

variation on this argument, where *ergaster* is the “African variety” of *erectus*. From this perspective, *Homo erectus* sensu lato (s.l.) refers to the lineage as a whole, whereas *Homo erectus* sensu stricto (s.s.) is used to refer to its Asian representatives (Lordkipanidze et al. 2013). Alternatively, *Homo erectus* and *Homo ergaster* can be seen as two distinct species, where *ergaster* is older and African and *H. erectus* younger and Asian (Klein 1999). These contrasting perspectives are based on interpretations of morphological variation between fossil groupings (with the unresolved issue being how much variation can be exhibited within a distinct species unit). An unusually large set of contemporaneous hominins found together in Dmanisi, Georgia, illustrates the complexity. The site was inhabited from 1.8 to 1.7 Ma

(making these the earliest hominin fossils outside Africa), and its inhabitants exhibit wide morphological variation with features linking them to *H. habilis*, *H. ergaster*, and *H. erectus* (s.s.). This mosaic suite of features, combined with the range of variation, it has been suggested, shows a single evolving *Homo* lineage with some geographically stratified variation around 1.8 Ma (Lordkipanidze et al. 2013). However, across the range of possible *Homo* paleodemes of the Lower Pleistocene, it is likely that several lineages existed in relative geographical isolation, some becoming established as stable species – for example, *Homo erectus*.

Regardless of systematics, the *Homo* lineage is characterized as a whole by fully modern (i.e., humanlike) bipedalism reflected in a rounded pelvis, long legs relative to arms, and arched feet, as

well as reduced postcanine dentition and large brains (~900 cm³). They made simple (Mode 1) stone tools and might have used fire.

Whatever their ultimate phylogenetic status, hominins first dispersed out of Africa in the Lower Pleistocene. The earliest evidence possible claim for a dispersal are some disputed stone tools from Pakistan (Dennell et al. 1988), at around 2 Ma; a less contested earliest date outside of Africa are from the hominin remains at Dmanisi (1.8 Ma) and lithic assemblages in Israel (1.9–1.7 Ma). There is considerable uncertainty about the timing, route, and direction of early hominin dispersals, but archaeological evidence implies at least three waves of migrations. The first, around 1.8 Ma, involved the makers of Oldowan core-chopper tools; the second, around 1.4 Ma, makers of Acheulean hand axes; and the third, around 0.8 Ma, is represented by Acheulean assemblages with numerous flake cleavers. It is commonly proposed that these dispersals were facilitated by behavioral flexibility (manifested in greater levels of hunting and cooperation and dependence upon technology) resulting from increased intelligence, as well as changes in body plan reflecting adaptations for long-range walking.

The best-known later descendant of these dispersing hominins is the larger-brained *Homo heidelbergensis* (0.7–0.1 Ma). As a whole, this species was larger than preceding hominins, stockily built, and had thick cranial bones and massive brow ridges. Its brain size was almost as large as that of modern humans at around 1200 cm³, although its encephalization quotient (the allometric relationship between the brain and body size) is smaller. Technologically, it is associated with the Acheulean industry (Mode 2) and is likely to have hunted and potentially cooked its food. Its relationship to later hominins is controversial. *H. heidelbergensis* is known from Africa and Eurasia and is sometimes divided into geographical lineages (*H. heidelbergensis* and *H. rhodesiensis*). Whether they are a single species or two, *H. heidelbergensis* represents the core Middle Pleistocene lineage, widespread across the Old World and ancestral in some way to the later hominin lineages in Africa and Eurasia; namely, modern humans and Neanderthals.

Later *Homo* Diversity

Late Pleistocene species and their evolutionary relationships are relatively well understood, no doubt because they are better well represented in the fossil record, and more significantly because they existed recently enough for ancient DNA to be preserved. There are three lineages of later Pleistocene hominin currently recognized – Neanderthals, Denisovans, and *Homo sapiens*. The first two are Eurasian, the last African, and all evolved in the last ~300 ky or more.

The Neanderthals are the best-known extinct hominin, and past misconceptions unfairly characterized them in Hobbesian terms as “nasty, brutish, and short.” Relatively short they might have been – they were stockily built, with males averaging 166 cm and females 154 cm – but the archaeological record associated with them suggests they were capable of behaviors that are very similar to those of modern humans. Key questions about Neanderthals concern the degree of behavioral complexity they were capable of and the nature of their distinct morphological features. Anatomically, Neanderthals appear particularly well-adapted to cold Pleistocene European climates: their limb proportions appear to conform to Allen’s Rule (cold-adapted species tend to have short limbs), and their shape and relative robusticity conforms to Bergmann’s Rule (bodies tend to be rounder in colder climates). Neanderthal facial features have also been explained with reference to climate: for example, their relatively large sinuses could have been useful for warming inhaled air. However, this explanation has been challenged, and the distinctive Neanderthal morphology might simply be the consequence of genetic drift in an isolated population.

Neanderthals made standardized stone tools, but this is where consensus about their behavioral repertoire ends. Broadly speaking, there are two major positions: one contends they lacked behavioral flexibility, did not have language, did not bury their dead, did not use fire, and scavenged rather than hunted, and the other suggests the opposite. Current evidence best supports a mild version of the latter. Neanderthal genomes contain the human version of the

speech-related FOXP2 gene, and the Kebara Neanderthal hyoid bone shows features consistent with a capacity for speech – although these features do not necessarily imply “modern” language. Archaeological evidence suggests at proficient hunting: the oldest known wooden spears in Europe date to 300 kya, and lithic spear points date as far back as 185 kya. Claims for advanced “cultural” capacities have been based primarily on the French Châtelperronian industry, which included ivory rings, grooved and perforated animal teeth, and other potential ornaments, but this has been contested on the basis of likely stratigraphic mixing (Higham et al. 2010). It appears Neanderthals used bird feathers, perhaps for decorative purposes. Controversial archaeological evidence aside, their large brains and similar encephalization quotient to humans make it unlikely Neanderthals were incapable of at least *some* “advanced” behavior.

The Neanderthals were not the only Eurasian hominin lineage. The “Denisovans” were first introduced to the paleoanthropological lexicon by Reich and colleagues in 2010, following the successful sequencing of ancient mitochondrial and nuclear DNA extracted from a distal manual phalanx found in southern Siberia. Based on the aDNA evidence, which suggested the individual belonged to a sister group of Neanderthals, the group was named Denisovans after the cave in which their remains were found. So far, they are represented by very fragmented and undiagnostic anatomical elements, and so their phenotype is unknown, but they may have been widespread over large parts of East Asia. When both are compared to modern human genomes, the Denisovan has an unexpected excess of divergent regions in comparison with its Neanderthal sister species, leading Prüfer and others (2014) to propose that these regions could have been contributed by an as yet unidentified species. Alternatively, the similarity between Neanderthals and modern humans might be the result of gene flow from AMHs into Neanderthals, and this is a more parsimonious explanation (Posth et al. 2017).

The Evolution of Modern Humans

It is now almost universally accepted that while Neanderthals and Denisovans evolved in Eurasia, *Homo sapiens*’ roots lie in Africa. This is known as the “Out of Africa” model, in which AMHs are a distinct African species that replaced existing Eurasian hominins as it dispersed out of Africa around 50 kya. Earlier models proposed a more widespread evolution of modern human traits, with regional continuity from archaic to modern forms, rather than dispersals and replacement. Genetic studies have formed the basis for the Out of Africa model.

Genetic Evidence

The coalescence date of the modern human and Neanderthal lineages gives a lower bound for our species’ independent genetic history. Prüfer et al. (2014) suggest a date of 553–589 kya based on two Neanderthal genomes. All lines of genetic evidence point toward an African origin of AMHs. The highest level of mitochondrial DNA diversity is found in Africa, which can be explained as a result of African populations having a longer period of time to accumulate genetic diversity compared to the populations of AMHs that colonized the rest of the world *after* their emergence in Africa. Mitochondrial DNA lineages coalesce ~200 kya (implying their LCA lived around this time), in accordance with fossil evidence. The same goes for the Y chromosome, although it coalesces at ~150 kya (Jobling et al. 2014). The relatively low amount of whole-genome genetic variation worldwide compared with, for example, chimpanzees, is suggestive of a relatively small founding population resulting from a genetic bottleneck associated with the AMH migration out of Africa.

Fossil Evidence

The oldest fossils showing significant *Homo sapiens* traits are found in Africa: in Jebel Irhoud, Morocco (300 kya); Omo, Ethiopia (195 kya); Herto, Ethiopia (160 kya); and Laetoli, Tanzania (120 kya). Some of these are clearly AMH, while others show mixed traits, suggesting a complex population history. Modern humans are characterized by a rounded cranium with a vertical

forehead and reduced brow ridges, a small orthognathic face, a chin, and a tall, relatively gracile skeleton. These earliest AMHs are considerably more robust than current forms, and they exhibit a mix of archaic and modern features concurring with an African origin.

Archaeological Evidence

There is a general association between the evolution of modern humans and the Middle Stone Age in Africa, although it is the case that both archaic forms in Africa and Neanderthals used Mode 3 technologies (see section “[Technology](#)”). The African archaeological record is dramatically understudied compared to its European counterpart, but despite this, more derived traits such as blades, use of ochre, and use of aquatic resources first occur between 280 and 120 kya in Africa, compared to around 50 kya in Eurasia.

A historically contentious concept is “behavioral modernity.” On the one hand, some scholars have argued the archaeological record is indicative of a mismatch between anatomical modernity and behavioral modernity. The most extreme variety of this standpoint is a “human revolution” where modern human culture, linguistic ability, and cognition suddenly appear at 50 kya, 150,000 years after the emergence of morphologically modern humans (e.g., Mithen [1998](#)). On the other hand, Mcbrearty and Brooks ([2000](#)) and others suggest there was a slow, sporadic development of modern human cognition in Africa over a period spanning at least 300,000 years; so, behavioral modernity evolved in tandem with its biological correlates (i.e., large brains and the modern human form). Current evidence supports the latter view, with increasing evidence for unambiguously symbolic behavior as early as 100 kya, and modern human cognition generally, as manifested in various technologies and subsistence behaviors, at ~250 kya (for a full discussion (McBrearty and Brooks [2000](#))).

Admixture Between Modern Humans and Archaic Hominins

Interbreeding between Late Pleistocene hominins appears to have been a common occurrence. At current count, there is genetic evidence for three to

five cases between four distinct populations (Prüfer et al. [2014](#)): between modern humans and Neanderthals, modern humans and Denisovans, Neanderthals and Denisovans, and Denisovans and an unknown hominin. The evidence for interbreeding is debated: it has been shown that ancient population substructure generates highly similar genetic patterns to gene flow, and the two scenarios are difficult to differentiate statistically. If assumptions hold, however, and the genetic patterns are the consequence of gene flow, coding sections of introgressed DNA can provide a clue as to the functional consequences of interbreeding. It looks, for example, like Neanderthals and Denisovans contributed immune system genes to modern Eurasian and Oceanian populations, and altitude adaptations in modern Tibetans have been linked to Denisovan-like DNA (Jobling et al. [2014](#)).

The Evolution of Human Diversity

The observed degree of modern human diversity depends on analytical category: on one end of the scale, sociocultural differences between human groups are vast (although all cultures share universal elements), while at the other, we are biologically relatively homogenous – at least compared to other great ape species. These discrepancies reflect differential rates and transmission of change: genetic evolution is transmitted from one generation to the next and is therefore limited by long human lifespans, while cultural change can occur many times within one lifetime and is transmitted both within *and* between generations. What biological variation does exist between human groups tends to be geographically stratified: that is, it is the consequence of populations’ individual genetic histories after dispersals into specific regions (or, in the case of Africa, remaining in a region). Although there is disagreement about exact timings, the history of continents’ colonization is summarized in Table 3. Population-specific traits, whether invisible (molecular) or visible (morphological), tend to be explained first with reference to specific ecological circumstances. Ethnic differences in hemoglobin genes are linked to geographic malaria persistence, and lighter skin has been

Hominin Evolution, Table 3 *Homo sapiens* geographic dispersals. Data from Jobling et al. (2014)

Continent	Date(s) of dispersal(s)
Australia	First colonized ~50 kya
Asia	First colonized 80–120 kya
Europe	At least 3 independent waves of colonization First colonized ~50 kya
Americas	3 (independent) waves Date of first colonization disputed, but probably between 15 and 20 kya

explained as a response to less intense sunshine in northern latitudes. Other processes, such as genetic drift or sexual selection, may have played an equally significant role: blonde hair, for example, confers no direct evolutionary benefit and has instead been shown to be the likely product of sexual selection.

The Out of Africa model of human evolution emphasizes the genetic homogeneity of humans as a species. Biological differences are thus relatively minor and are the product of differential dispersals, local adaptation, and genetic drift under conditions of isolation. Older models that related major racial divisions in the human population have been abandoned.

The Pattern of Hominin Evolution

Hominin evolution is not just a question of phylogenetic and phenotypic change, but is a pattern of adaptive change in response to changing ecological and selective conditions. The fossil record shows a sequence to these adaptive changes.

Bipedalism

Anatomically, obligate bipedalism is one of the most obvious and fundamental differences between our ape relatives and us. The consensus among paleoanthropologists is that bipedalism is a defining feature of the hominin clade and that adaptations for upright locomotion can be used to assign putative hominin fossils from 7 to 5 Ma to the lineage (see section “[Hominin Origins](#)”). Accumulating evidence suggests at multiple

“versions” of bipedalism in the hominin clade (see section “[Early Hominin Evolution](#)”). A key issue in the analysis of locomotor features is interpreting “primitive” arboreal traits shared with Miocene apes: these could be preserved due to functional relevance *or* be inconsequential vestigial remains that were not selected against. In any case, mosaics of locomotor features in early hominins imply bipedalism need not be monophyletic, meaning it could have evolved several times independently within a rapidly diversifying lineage.

The absence of early chimpanzee fossils complicates reconstruction of the precursor to hominin bipedalism. Suggestions for the ancestral condition have included a knuckle-walking ancestor, an orthograde arboreal clamberer, and pronograde clambering similar to orangutans. It is likely the LCA did not brachiate; the Miocene ape *Proconsul*, which likely belongs to the common ancestry of African apes, shows no adaptations to brachiation.

The question of *why* bipedalism evolved remains, and while as many as a dozen explanations have been proposed, they are united in their specific reference to the ecological context within which it did. This context was one of increasing habitat fragmentation. Energetic models suggest bipedalism allows the exploitation of larger areas than the knuckle-walking of modern chimpanzees, with obvious advantages in terms of food acquisition in patchy resource distributions associated with mosaic habitats. Others have suggested a bipedal posture was first habitually adopted in threat displays against predators or as a form of vigilance in increasingly open environments. Thermoregulatory advantages of reducing the surface area exposed to direct sunlight and raising the trunk further from the ground have also been proposed. A further possible advantage of bipedalism was that it freed the hands for carrying, an idea originally proposed by Darwin. These hypotheses are not necessarily mutually exclusive; indeed, it is likely selective pressures associated with changing environments produced multiple challenges (like increased predation, exposure to heat, and more dispersed resources) to which an upright posture provided evolutionary

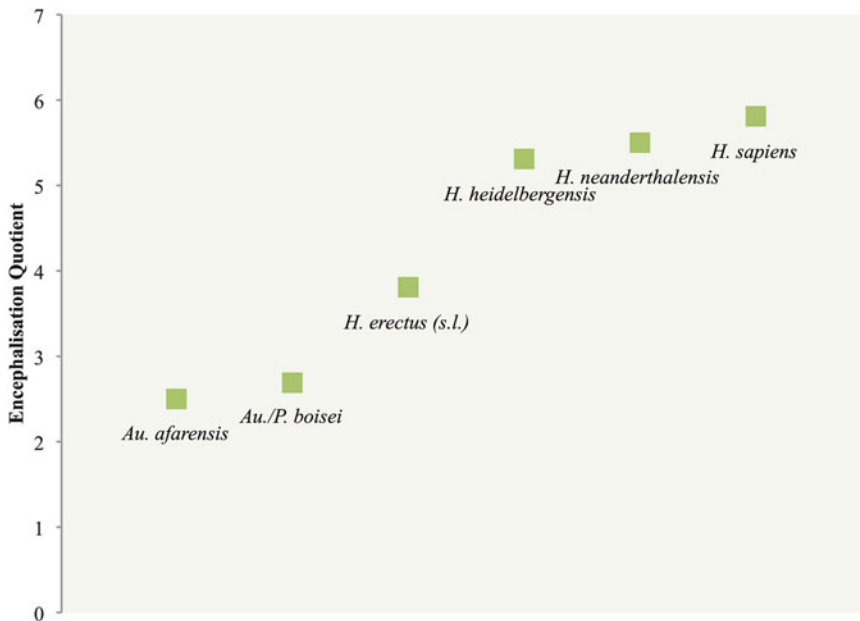
solutions. And while it provided solutions, bipedalism also engendered energetic costs requiring explanation in comprehensive models of its origins.

Encephalization and Life History

If developing bipedalism is the defining feature of the earlier phase of hominin evolution, encephalization is that of the later phase. Encephalization entails brain growth beyond that *expected* for an animal's body size and is measured as a ratio of body size to brain size known as the encephalization quotient (EQ). High values imply greater intelligence as they reflect "more" brain than that required to merely coordinate bodily functions. Australopithecine brains stay relatively stable at chimpanzee-like volumes from ~4 to 2 Ma, contrasting with the increase observed in the *Homo* lineage (see Fig. 3). Even within the comparatively encephalized order Primates, *Homo* is exceptionally large-brained, and various adaptive explanations have been proposed to explain the trend (see section "The Costs of Cognition"). As with the evolution of bipedalism, these causal factors are not mutually exclusive,

and it is likely the ultimate selective pressure arose from their interactive effects.

Regardless of their evolutionary advantages, larger brains entail clear energetic costs (see section "The Costs of Cognition" for a full discussion) for parents and offspring alike. They require a longer period of postpartum growth to reach adult size because the narrow human birth canal, the product of selection for a rounded bipedal pelvis, limits the maximum brain volume attainable in utero. This period of growth creates increased and prolonged energetic demands, met by secondary altriciality – high and prolonged dependence on others, including conspecifics other than parents. The *Homo* "solution" to these demands is a changed life history (the timing of key events in an organism's life cycle). Human life histories differ from those of African apes in two key ways: they include a long period of childhood after weaning, and women live long after reproductive cessation. By contrast, female apes' physiological systems usually fail together with menopause. These life history shifts appear in tandem with encephalizing brains: analyses of dental and femoral development of fossil hominins have indicated that *Australopithecus* is



Hominin Evolution, Fig. 3 Hominin encephalization quotients. Data from Schulkin (2011)

more similar to African apes in its rate of development, whereas the development schedules of *Homo ergaster* and Neanderthals are more similar to that of *sapiens* (Smith 1994).

Technology

A key difference between extant primates and humans is our extreme reliance on technology for survival – while some primates (chimpanzees and capuchins) do use stones to crack nuts, there is no evidence (yet) of nonhumans purposefully manufacturing lithic tools in the wild. Technology is a specific trait within a species’ behavioral repertoire, but it is especially ecologically significant as it provides a foundation for other behavioral traits like hunting.

Lithic technology dominates most of human evolution; other raw materials, like bone, antler, and metals, were first used only relatively recently. Hominins have been making stone tools for at least 3 million years; the earliest simple flaked tools come from Lomekwi in Kenya and are dated to ~3.3 Ma (Harmand et al. 2015). Lithic technology has been classified in several ways reflecting technological, morphological, and stylistic differences, of which the most commonly used are Clarke’s (1968) technological modes. He recognizes five modes (see Table 4) which are very loosely arrangeable as a chronological framework cataloguing increasing complexity

over time, but with a very strong caveat: the modes overlap considerably, with the “simpler” modes occurring continuously after their first appearance, and the introduction of a novel technology often did not result in the complete replacement of older forms. Obviously, in the frequent absence of hominin fossils associated with lithic assemblages, it is challenging to generalize about species-specific technological abilities. Broadly speaking, however, the earliest simple flaked tools (represented by Mode 1) were manufactured by late australopithecines and early members of *Homo*; Mode 2 bifacially flaked hand axes are frequently associated with *Homo ergaster* and *Homo heidelbergensis*; and prepared core technologies (Modes 3 and 4) appear with later forms of *Homo*. Modes 4 and 5 are currently exclusively associated with AMHs. While increasingly complex technological manufacture probably reflects changing cognitive capacities to a great degree, especially in the context of progressively encephalized brains, it should be noted that lithic technology was likely only *one* component of early toolkits and “simple” technology is thus not necessarily synonymous with “simple” cognition. The long stasis of the Asian archaeological record associated with *Homo erectus* (s.l.) has been interpreted this way, for example, but it is highly likely they supplemented their lithic technology with other

Hominin Evolution, Table 4 Hominin Technology. Adapted from Foley (1987)

Technological mode	African classification	European classification	Characteristics	Distribution
1	Early Stone Age	Lower Paleolithic	Simple, direct percussion producing flakes and chopping tools	From late Pliocene; especially in Africa, but occurs continuously
2			Production of large flakes, extensively retouched; hand axes	Early and middle Pleistocene; extensively in Africa, Europe, and parts of Asia
3	Middle Stone Age	Middle Paleolithic	Systematic preparation of cores prior to striking	Early parts of late Pleistocene in Europe and Africa
4		Upper Paleolithic	Reduced striking platforms with blade production	Late Pleistocene onward; in many parts of the world, especially Europe
5	Later Stone Age	Mesolithic	Microlithic flake and blade production with retouch	Global post-Pleistocene distribution, with some late Pleistocene presence

locally available materials – possibly bamboo. *Homo heidelbergensis* definitely made wooden tools, evidenced by eight throwing spears from Germany dated to ~400 kya. Vegetation-based non-lithic technology was thus within the technological repertoire of species before *Homo sapiens*, but that based on materials such as bone and antler tends to be seen as evidence for increased behavioral complexity and intelligence, mainly because they are found only in association with AMHs.

Culture

Technology is one element, among many, of human culture. “Culture” is commonly seen as the sine qua non of our ecological niche as it is essentially a storage and transmission vehicle for human behavior. The comparative study of culture in an evolutionary context is an increasingly important field, one example of which is cultural primatology. Paleoanthropologists and cultural primatologists are concerned with, first, *when* and *why* “culture” evolved and second, its biological consequences.

The time depth of “culture,” as well as its evolutionary causes, is entirely subject to definition. Cultural primatologists operationally conceive of “culture” as a process, rather than a product: i.e., as information or behavior acquired from conspecifics through some form of social learning. This definition dramatically deposes human culture from its long-held pedestal of exclusivity in one sense, because in this conception culture can be attributed to other modern taxa such as killer whales and chimpanzees. Despite cultural behaviors in nonhumans, human culture remains unique in its scale and complexity, often summarized as the capacity for cumulative culture. The empirical question that follows on from this perspective is, “when did *human-specific* (cumulative) culture appear, and under what selective pressures?” Broadly, two models of cultural emergence prevail: one advocating a “revolution”: a relatively late sudden emergence of culture as a complete “package” associated with the development of language and consciousness (e.g., Mithen 1998). The other posits a gradual accretion of elements that comprise modern human culture

(e.g., Mcbrearty and Brooks 2000). The expanding archaeological record, especially as more evidence in Africa is discovered, tends to support an accretionary pattern, with some elements, potentially including symbolism, appearing before the emergence of AMHs, and others, like blade technology, appearing after. That said, it is true that human culture has markedly increased in complexity over the last ~10,000 years, and this probably reflects an important transition in cultural evolution, and equally that culture probably played relatively little role in the Pliocene and earliest Pleistocene phases of hominin evolution. If a tendency toward cumulative culture is a process that occurred in the last half million years or so, it raises the question of the “cultural status” of different hominins. The limited evidence of the archaeological record would certainly point to marked contrasts between modern humans and, for example, Acheulean-bearing *H. heidelbergensis*, but more subtle differences with Neanderthals, who may have shared considerable cultural complexity with AMHs.

The biological consequences of human culture are significant. By any standard, it is unique in the extent to which it has transformed our surroundings and thus our selective environment. This has contrasting evolutionary effects: on the one hand, it *removes* selective pressures (a culturally constructed environment buffers the genome from “natural” pressures, removing the need to genetically adapt to newly colonized habitats). On the other, it *creates* them, as the constructed environment exerts new evolutionary stresses culminating in gene-culture coevolution. The classic example of this process is lactase persistence in populations with pastoralist ancestry, where individuals in pastoralist communities who continued producing lactase would have been at a nutritional advantage.

Adaptive Radiations

The patterns in hominin evolution can be interpreted as seven adaptive radiations (Foley 2003), where an adaptive radiation is defined as (rapid) diversification of a group with common ancestry. These radiations are:

- (I) The African apes and earliest hominins in the later Miocene, the products of which are *Sahelanthropus*, *Orrorin*, and *Ardipithecus*.
- (II) The bipedal apes (early australopithecines), whose diversification mainly occurred within mosaics of locomotive features.
- (III) The megadontic specialists (the *Paranthropus* genus): it is unclear whether this was a monophyletic (single ancestor) group or the outcome of a general trend toward megadonty within the Australopithecines and, as such, whether it is a true radiation.
- (IV) The earliest *Homo*: this is the most problematic of the radiations, because the phylogenetic positions of the species within it are precarious (see section “[Hominin Origins](#)”), and it shows relatively little taxonomic diversity or scale of geographical dispersal.
- (V) Pleistocene *Homo*: specifically, *Homo erectus* (s.l.) and its descendants. Underlying this radiation is a major shift in adaptive complex, reflected in changes in morphology and behavior.
- (VI) Larger-brained *Homo*, in the last 0.5 Ma, with the emergence of the Neanderthals, Denisovans, and AMHs.
- (VII) The radiation of *Homo sapiens*, which mostly involved social rather than morphological diversification.

Hominin Diversity

These patterns are, in practice, more continuous, but emphasize the role of diversification and geographical spread in the process of becoming human, rather than the classic *scala naturae* of early reconstructions. The hominin family tree is now speciose, although this is subject to splitting/lumping controversies, where the underlying problem is one of variation – specifically, how much is acceptable between individuals classed as the same species. A splitting perspective would identify about 28 hominin species, and this does not seem unreasonable in the context of modern-day primate diversity (with approximately 60 genera and 200 species) (Fleagle [1995](#)).

Transitions in Hominin Evolution

An alternative way of making sense of these evolutionary patterns is as a series of transitions (within which adaptive radiations, or other degrees of evolutionary diversification, may have taken place). The question, here, is whether these major changes occur continuously or only during particular periods in prehistory. The distinction between *Homo* and *Australopithecus* is often seen as an important transition, but it is probably more accurate to recognize three major transitions (Foley [2016](#)). They are, in order:

1. Ranging and energetics (~5–4 Ma), with the appearance of habitual bipedalism and changes in ranging behavior as habitats became increasingly fragmented
2. Technology and niche expansion (~3–2 Ma), with the first appearance of lithic technology and animal food processing, as well as features associated with the *Homo* lineage (large brains, reduced dentition, more humanlike body plan)
3. Cognition and cultural processes (~0.5–0 Ma), with the first appearances of “advanced” behavior: depending on definition, this is human seen in humans *or* is common to the Neanderthal and human lineages.

The Evolution of Human Cognition

Evidence for Evolving Cognitive Capacity

Reconstructing the evolution of hominin cognition is fundamentally different to that of other physical features. Thoughts do not fossilize (although their products are occasionally preserved in the archaeological record), but most crucially, the end product – the modern human mind – is more difficult to define than basic anatomy since it is currently not fully understood biochemically nor psychologically. “Cognition” comprises multiple skills and it is possible that these evolved independently, simultaneously, or in a mosaic fashion; but accurate reconstruction of these patterns is difficult. Broader trends in cognitive evolution, however, are clear: as a whole, hominin cognition evolved increasingly

complex functions capable of innovation and abstraction.

This is directly evidenced in increasing brain size, particularly within the *Homo* genus, where both absolute and relative cranial capacities increase exponentially (see Fig. 3). Relative brain size (captured as an allometric relationship between brain and body size in the encephalization quotient [EQ]) is particularly informative about evolving cognition because it suggests “excess” brain presumably used for higher mental processes as opposed to basic functions. Hominin EQs demonstrate a pattern of increasing excess capacity that accelerated during the evolution of *Homo*. This is classically interpreted as evidence of expanding cognitive abilities or intelligence. Beyond broad patterns, elucidating *which* cognitive skills evolved *when* requires finer-grained analysis of where in the brain, specifically, growth occurred. This was long held to be exclusively within the prefrontal cortex, strongly implicating increased social intelligence (Dunbar 1992); but recent reanalyses suggest greater expansion occurred within the cerebellum, implicating fine motor skills (Barton and Venditti 2014).

Evolving cognition is also indirectly captured by its behavioral consequences, which are preserved in the archaeological record. The manufacture of lithic technology is particularly informative because it provides a long and consistent record of change, although other markers of advancing cognition could be used. Two variables – duration of technological tradition and complexity of technology – reflect cognitive states well, but it is important to note that these data are proxies and therefore provide only a scale of the *relative* cognitive abilities of stone tool-producing hominins. Faster turnover of technological traditions and increased complexity within them, manifested in numbers of stone tool “types,” are generally taken as evidence for more advanced cognition; but there are caveats. Stability of tradition is taken as evidence of socially transmitted “culture” in nonhumans, with associated inferences about advanced cognition; and classifying “complexity” within technocomplexes is subjective. In any case, both variables evidence

trends toward advancing cognition over time: technologies change from simple flaked chopping tools to assemblages comprising highly diverse tool types (see section “Technology”), and there is much faster turnover of later technocomplexes, on average, than earlier ones. Within-species change suggests change was not always in the direction of greater complexity, with later Asian *Homo erectus* (s.l.) displaying fewer technological “types” than earlier African forms – although this might reflect the use of alternative local materials like bamboo. The clearest shift toward complexity in both variables occurs with the emergence of *Homo sapiens*, which produced dramatically more variable and rapidly changing technology than all other hominins.

Crucially, when direct and indirect evidence are analyzed together, it becomes clear that markers of cognitive evolution do not change simultaneously. Encephalization is a universal temporal trend in the *Homo* lineage, but this is not directly translated into equal rates of change in technology. This suggests a complex interaction between encephalization, changes in behavior, and evolutionary processes such as speciation. These patterns demonstrate that elements comprising cognition may have evolved independently. The idea of a sudden emergence of “modern” human cognition as a single, unified package comprising culture, language, and consciousness relatively recently is currently not supported by the evidence, and a more cumulative model is more likely.

Social and Ecological Models for the Evolution of Hominin Cognition

What selective pressures and advantages underlay the observed pattern of hominin cognitive evolution? Various ecological and social answers have been proposed. Clutton-Brock and Harvey (1980) examined the relationship between primate brain sizes and relative home ranges, concluding that larger brains are linked to frugivorous diets and larger home ranges. For hominins, whose diets were likely omnivorous and who became increasingly specialized for long-distance ranging in fragmented habitats, this link strongly implies a selective role for sophisticated mental processing

of large amounts of spatial data. In this view, encephalization was thus primarily ecologically functional.

An alternative model is the “social brain hypothesis.” Nicholas Humphrey, Alison Jolly, and Robin Dunbar suggested the problems of living in social environments prompt selection for larger brains. Dunbar (1992) observed a correlation between the relative size of the neocortex and the size of primate social groups. Larger group sizes and associated social complexity thus created selective pressures for bigger, more cognitively advanced brains. This model fits well with the very high levels of social complexity and activity found among humans, with a particularly high degree of social cooperation.

Not all encephalization, however, is found in the neocortex. Recently, Barton and Venditti (2014) demonstrated that the cerebellum, which contains four times more neurons per unit of space than the neocortex, underwent rapid increase during hominin evolution. Consequently, humans have larger cerebella relative to neocortices than other extant primates do. In this “sensory-motor hypothesis,” selection for technical intelligence played a more significant role in cognitive evolution than did social or ecological factors.

These factors, of course, need not be mutually exclusive, and there are clearly interactions between social and ecological factors. Group size, for example, is largely determined by availability and distribution of resources, and equally the size and structure of a group can affect how resources are acquired – for example, hunting among chimpanzees and almost certainly also among hominins.

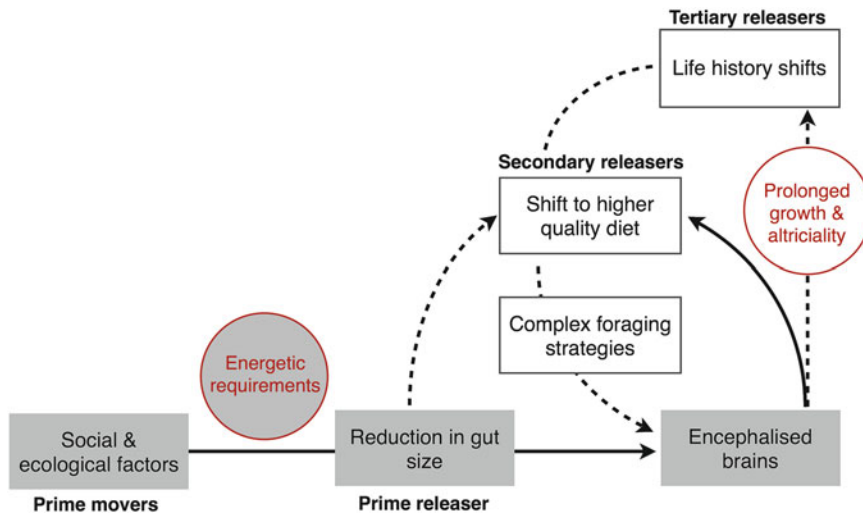
The Costs of Cognition

Acknowledging evolutionary complexity does not necessarily require the sacrifice of analytical power in favor of untestable description. Falk (1995), for example, does this by making the point that evolutionary models must account for both “prime movers” (major selective agents) and “prime releasers” (changes in physiology that relax constraints on traits, thereby permitting their evolution). “Costs,” in the form of evolutionary tradeoffs between traits, are implicit in the

concept of prime releasers. Explaining how these costs were physiologically mitigated answers the question of *how* cognition evolved, while prime movers explain *why*. The direct costs of evolving cognitive capacity are increased energetic demands. Aiello and Wheeler (1995) suggested these metabolic costs were met, at the individual level, by a redirection of energy from the gut to the brain, necessitating a reduction in the size of the gastrointestinal tract. Falk categorizes these physiological changes, which *permitted* selection for larger brains, as “prime releasers” (1995). Since gut size is strongly determined by diet, Aiello and Wheeler proposed that this reduction was only possible in the context of a shift to higher-quality diets achieved through more complex foraging strategies – that is, smaller quantities of highly digestible food. These shifts in diet and behavior, then, acted as secondary releasers permitting evolving cognition, and to a degree, they exemplify an evolutionary feedback loop, because complex foraging strategies themselves necessitate increased intelligence. Encephalizing brains, however, also entail secondary energetic costs met by relatives. Humans have a prolonged postpartum growth period – childhood – necessitated by limitations on maximum brain size attainable in utero due to the narrow human birth canal. In addition, human infants have 9% greater energetic requirements than similarly sized ape infants due to their encephalized brains (Foley et al. 1991). Life history shifts, like the evolution of a long female postmenopausal lifespan, allowed alloparental investment in offspring to account for some of these energetic costs (Hawkes et al. 1998) and thus acted as tertiary releasers (Fig. 4).

The Evolution of Language

The evolution of language is closely related to that of human cognition. Language both *facilitates* cognitive functions (as internal language, or the language of thought) and their *externalization* (speech). Models of language evolution range from an extremely recent, non-Darwinian emergence in *Homo sapiens* alone to extreme time depth with incremental evolution of its component parts throughout hominin evolution. These contrasting paradigms reflect both differences in



Hominin Evolution, Fig. 4 A model for the evolution of cognition. *Shaded shapes* represent “primary” factors in this model of cognitive evolution, while *clear shapes* represent secondary and tertiary factors – factors produced as consequences of “primary” factors. *Unbroken arrows* indicate the direction of this evolutionary cause-and-effect.

Circles indicate evolutionary constraints, or costs, mitigated by so-called “releasers” (Falk 1995). Accounting for evolutionary costs involves energetic redistributions or life history shifts to account for tradeoffs between traits, and this process is indicated by *dashed arrows*

definitions of language and the paucity of direct evidence.

Elucidating the evolution of human internal language falls far out of the traditional reach of paleo-anthropology (although ingenious attempts have been made), but genetic and anatomical proxies for externalized language suggest at least some form of language in pre-*sapiens* hominins. Neanderthals possessed the derived human version of the speech-related FOXP2 gene (Krause et al. 2007), but its exact role has been debated and its genetic presence alone is insufficient evidence for completely humanlike vocal language. The single Neanderthal hyoid bone from Kebara, Israel, was essentially modern, suggesting a capacity for articulated speech. However, the hyoid provides tentative evidence at best: a modern form is not equivalent to a modern position in the vocal tract. Other attempts to reconstruct speech production by extinct hominins, like analyzing endocast shapes to infer relative sizes of Broca’s and Wernicke’s areas and linking the size of the thoracic vertebral canal to voluntary control of breathing required for speech, have provided highly ambiguous or statistically unsupported conclusions. “Modern”

behavior is linked to both speech and internal language. To the extent that human language is interdependent with symbolic thought, we can infer its existence from “symbolic” artifacts of which the first evidence might extend as far back as shell engravings to 430 kya or a more recent package of evidence for symbolism around the last interglacial (130–70 kya), particularly in Africa. Overall, the evidence suggests language is not the prerogative of modern humans alone; linguistic capacity was likely shared with Neanderthals, also implying a form of language in the LCA they shared. This would place some level of language competence to closer to half a million years ago.

Conclusion

“Our” place in nature is specifically characterized by striding bipedalism; slow life history strategies; large brains capable of complex cognition; human-specific culture based on abstract, symbolic, and internalized thought with a metacognition; articulated language; and an extreme reliance on technology. These traits are related and

interdependent, evolving both in a serial sequence and in parallel, depending on the trait. Fossil, archaeological, and genetic data suggest clear patterns, with bipedalism evolving earlier in human evolution as part of a general shift in ranging and energetics, followed by a technology-based niche expansion. The final period of human evolution was marked by the development of advanced cognition and its behavioral corollaries. However, within each of these phases, there would have been associated coevolution of traits; for example, the coevolution of brain size and changes in life history or diet and technology.

One hundred and 50 years of research into human evolution has revealed much about the tempo and mode of human evolution, showing a complex pattern of novel traits and diversification of lineages, set against a dynamic ecological background. Recent research has been increasingly interdisciplinary, and will continue to be so, with evidence coming from both direct studies of the past – the paleosciences – and inferences from contemporary populations at every level, from the genomic to the cultural.

Cross-References

- [Ardipithecus Group](#)
- [Australopithecus africanus](#)
- [Australopithecus garhi](#)
- [Australopithecus Group](#)
- [Brain Evolution Resulting from Cooking](#)
- [Evolution of Intelligence, The](#)
- [Extended Postmenopausal Lifespan](#)
- [Grandmother Hypothesis](#)
- [Homo habilis](#)
- [Homo heidelbergensis](#)
- [Homo neanderthalensis](#)
- [Homo rudolfensis](#)
- [Human Tool Making](#)
- [Linguistic Evolution](#)
- [Modern Theories of Language](#)
- [Orrorin tugenensis](#)
- [Paleoanthropology](#)
- [Paranthropus aethiopicus](#)
- [Paranthropus boisei](#)
- [Why Humans Are Unique](#)

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Homo economicus

► Rational Actors

Homo erectus

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Definition

Homo erectus is a species on the hominin lineage that appears in the fossil records approximately 1.8 million years ago. *Homo erectus* is associated with a significant increase in brain size,

developments in stone tool technology, and dispersal out of Africa.

Introduction

The appearance of *Homo erectus* around 1.8 million years ago marks a significant shift in the hominin lineage (the lineage leading to modern humans after the divergence from the chimpanzee lineage). There is debate among paleoanthropologists as to the unity of *Homo erectus* as a species and some choose to designate early African fossils as a separate species *Homo ergaster*. The discovery of five complete skulls at the site of Dmanisi, Georgia demonstrates remarkable anatomical variability within a *Homo erectus* group from a single time horizon leading some paleoanthropologists to identify a series of distinct species (Lordkipanidze et al. 2013). Setting aside debates about the anatomical variability within *Homo erectus*, the fossils attributed to this taxon possess an increased cranial capacity relative to body size in comparison to all preceding members of the hominin lineage (Elton et al. 2001).

Chronology

The first appearance of *Homo erectus* is dated to approximately 1.8 million years ago at sites in South Africa and East Africa (Antón et al. 2014). By approximately 500,000 years ago, populations of *Homo erectus* are replaced by derived taxa trending towards modern humans in Africa and Neanderthals in Europe, although the chronology for the end of *Homo erectus* in Africa remains poorly defined. Based on dates of fossils from Indonesia, it appears that remnant populations of *Homo erectus* might have persisted in East Asia as recently as 50,000 years ago (Swisher et al. 1996).

Behavioral Innovations

There are several major behavioral innovations associated with *Homo erectus*. The development of shaped tools known as handaxes and cleavers

(also called bifaces or large cutting tools) formed by bifacial flake removals begins at about the time of the first appearance of *Homo erectus*. These tools become increasingly refined over time (Chazan 2015). The initial use of fire is dated to ca. one million years ago based on archaeological evidence from Wonderwerk Cave, South Africa, although based on theoretical arguments there is a possibility that already 1.8 million years ago *Homo erectus* habitually used fire for cooking (Berna et al. 2012; Wrangham 2009). *Homo erectus* is associated with an expansion of the hominin range outside of Africa across Europe and Asia. The earliest site outside of Africa is Dmanisi, Georgia, dated to 1.8 million years ago (Ferring et al. 2011). Oddly, the dispersal of *Homo erectus* is not associated with use of handaxes and cleavers and the stone tools found on early sites outside of Africa are restricted to simple flakes and cores. The dispersal of *Homo erectus* provides evidence of the behavioral flexibility of this species and the ability to adapt to novel ecological contexts. However, there is a consistent tendency for archaeological sites associated with *Homo erectus* to be near sources of fresh water.

On archaeological sites, stone tools are often associated with accumulations of faunal remains including the bones of large animals such as elephants. There continues to be debate over the question of whether *Homo erectus* was a hunter or scavenger, although the current data strongly supports the position that *Homo erectus* was a hunter (Domínguez-Rodrigo 2002). One particularly interesting question is what types of weapons *Homo erectus* would have used for hunting as there is no surviving evidence for the use of spears before 500,000 years ago. There is also considerable debate about the role of social learning in *Homo erectus* with most archaeologists agreeing that the production of refined handaxes was a skill transmitted by some degree of learning (McNabb et al. 2004).

Phylogenetic Position

With *Homo erectus* the hominin radiation that saw the diversification of the hominin lineage into

multiple contemporary genera comes to an end and genus *Homo*, represented by a limited number of species, becomes the only surviving genus in the hominin lineage. In a general sense, *Homo erectus* can be considered ancestral to modern humans, Neanderthals, Denisovans, and *Homo floresiensis*, although there is considerable question over whether modern humans and Neanderthals share a common ancestor derived from *Homo erectus*.

Conclusion

With *Homo erectus*, we see a narrowing of the diversity of the hominin lineage to a single genus, genus *Homo*, and the spread of this genus across much of the globe. Reconstructing the cognitive capacity and social organization of this unique and distinctive human ancestor is a key challenge in the study of human evolution. Based on the archaeological record, it is clear that *Homo erectus* was a species capable of both adaptive flexibility and technological innovation.

Cross-References

- [Hominin Evolution](#)
- [Homo floresiensis](#)
- [Homo habilis](#)
- [Homo heidelbergensis](#)
- [Homo neanderthalensis](#)

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Homo floresiensis

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Synonyms

[Early homo](#); [Human evolution](#)

Definition

Homo floresiensis is a new species of hominin discovered in 2003 during archaeological excavations by an Indonesian-Australian team in Liang Bua cave on the island of Flores, Indonesia. The species is dated to ~90,000 years ago; the presence of an archaic-looking species living at such a recent period is an extraordinary occurrence. This

entry focuses on the discovery, morphology, phylogeny, and controversies surrounding this enigmatic hominin.

Introduction

A series of bones, including a partial skeleton, was discovered in 2003 during an archaeological excavation in Liang Bua cave, on the island of Flores in Indonesia (Brown et al. 2004). The excavation team of Indonesian and Australian researchers was led by the late Professor Mike Morwood and Dr. Tony Djubiantono under the auspices of the Indonesian National Research Centre for Archaeology. The excavation aimed to find insights into the origins of the first Australians but instead the team discovered a number of very different and very small, individuals. The strata in which the remains were found have recently been redated to between 58.3 ± 0.05 and 80.8 ± 0.8 thousand years ago (kya) (Sutikna et al. 2016). This is considerably earlier than the previously reported dates of 13.4–10.2 kya to ~100 kya.

Discovery, Description and Evolutionary Scenarios

The most spectacular find was at a depth of 6 m. It comprised a partial skeleton, labeled LB1, an archaeological reference to the cave in which it was found. These remains include the skull, leg bones, the pelvis, hands, feet, and some other fragments. It was so small that, at first, it was thought that the remains were those of a *Homo erectus* child. But the jaw had a full complement of adult teeth which suggested that, relative to modern humans, this hominin was the equivalent of about a 30-year-old. Although it is not known how death occurred, archaeological evidence shows that the body had not been deliberately buried but, rather, after death, had sunk into mud in a shallow pool of water where it was slowly covered by silt.

There were more than 85 other hominin bones from a number of adult and juvenile individuals

found throughout the 13-m deep excavation. They were all from small individuals. At these levels of the archaeological site there were no bones from individuals with the stature of modern humans.

Brown et al. (2004) compared the Liang Bua remains with those of *Homo erectus*, *Homo ergaster*, *Homo georgicus*, *Homo sapiens*, and *Australopithecus africanus* and found that they showed a mix of archaic and modern characteristics, unlike any other hominin species and was attributed to a new species, *Homo floresiensis*.

The cranium is relatively low with and its widest part at the level of the ears, unlike *Homo sapiens*. Its forehead slopes back from behind a mound of bone that frames the orbits: The jaw lacks a chin (Fig. 1).

Wrists and shoulder joints are quite unlike those of modern humans, and in fact Tocheri et al. (2007) found that the wrists are more like those of African apes and the hands could not open as expansively as ours. As well, Larson et al. (2007) discovered the shoulders face somewhat forward and the arms could not rotate quite as much as ours and, in this, *Homo floresiensis* was more like *Homo ergaster*, which lived 1.5 million years ago in Africa and *H. georgicus*, the 1.8 mya hominins excavated at Dmanisi, Republic of Georgia. Stature is estimated to be just over



Homo floresiensis, Fig. 1 The skull and mandible of Liang Bua 1 (LB1) (Image credit. Debbie Argue)

1 m, and it was a bipedal hominin – it walked upright. Its feet are 70% the length of its shins; in *Homo sapiens* the ratio is 55%. This configuration meant that when walking, these beings had to bend their knees more than modern humans do, just to get ground clearance (Jungers et al. 2009).

It had a small brain in its small skull – 426 cc, similar to the Australopithecines that lived ~4–2 million years ago in Africa. Absolute brain size does not directly measure the cerebral capabilities of an individual; rather, it is the complexity and organization of the brain that is important. Although brains are not usually preserved in ancient fossil remains, sometimes marks on the inside of the skull reveal the presence and form of arteries and of convolutions of the brain. This was the case for LB1. Falk et al. (2005) studied these marks and found that the skull of LB1 had housed a relatively large frontal lobe. In *H. sapiens* this part of the brain is associated with capabilities for planning, for learning from mistakes, and for passing on knowledge from generation to generation. The implication, therefore, is that though *H. floresiensis* was tiny and had a small brain, it probably had some of the same mental abilities as us.

Brown et al. (2004) proposed two possible hypotheses for *H. floresiensis*: (1) that they belong to a new species of small-bodied hominin, *H. floresiensis* that derived from an early lineage of *Homo* and (2) that they represent a new species, *H. floresiensis*, but in this scenario the species derives from an as yet undiscovered early population of immigrant *H. erectus* on Flores that subsequently dwarfed in response to the Island Rule (below). When new skeletal remains comprising a second mandible, a radius, a tibia, and the right humerus and ulna of LB1 were described, however, Morwood et al. (2005) concluded from the new evidence that the ancestors of *H. floresiensis* could **not** be attributed to *H. erectus*. Nevertheless, these two hypotheses continue to be rigorously debated.

Many researchers support the hypothesis that *H. floresiensis* represents a remnant population of a very early member of *Homo*. For example, Falk et al.'s (2005) study of the brain highlighted its archaic characters; Argue et al. (2006) used metric

analyses of hominin crania and showed that *H. floresiensis* sits in with early *Homo* from 1.5 mya in Africa and does not cluster with modern humans; Tocheri et al. (2007) discovered the ape-like characteristics of its wrist bones; Larson et al. (2007) showed that its shoulder bone configuration was last seen on 1.5 mya hominins; Jungers et al. (2009) draw attention to the extraordinary long feet of *H. floresiensis*; and Peter Brown and colleagues undertook a detailed analyses of the two *H. floresiensis* mandibles, in which it is clear that it possesses very archaic characters that do not appear on *H. erectus* (or, indeed, *H. sapiens*). In 2009, Argue and colleagues analyzed and compared the characters of *Homo floresiensis* with those of other *Homo* species – including *H. sapiens* – and some Australopithecines. The analysis showed that *H. floresiensis* probably branched off the human evolutionary tree at a very early stage of the evolution of the genus, *Homo* 1–2 million years after the disappearance of similar hominins from the African continent. They conclude, therefore, *H. floresiensis* is likely to represent a remnant population of a very early hominin on this remote Indonesian island.

The alternative hypothesis is based upon the island rule for insular dwarfing that stipulates that body size of mammals alters when a founder population reaches an island, becomes reproductively separated from its mainland group, and faces an environment different from those of its mainland sister species. For example, a smaller body size would be expected as a response to a limited food supply, a larger size in the absence of predation. In this case, it is assumed that *H. erectus*, known from further west in Indonesia, at Sangiran, arrived on Flores and then, as an evolutionary response to the conditions encountered on Flores, dwarfed. This hypothesis may be tested by analyzing the similarities between the two species. Kaifu et al. (2011) undertook a detailed morphometric and morphological comparison of the LB1 cranium with *H. habilis*, *H. erectus*, and *H. georgicus*. They assessed 67 cranial characters and found that only a few traits support a relationship between *H. floresiensis* and *H. habilis* while 17 characters

supported, or are compatible with, the hypothesis that *H. floresiensis* is an island dwarfed form of *H. erectus* from Java. More recently, Kaifu and colleagues reiterated this hypothesis based upon a comparative study of dentition. There are several other studies in which this hypothesis is supported.

A third hypothesis was proposed almost as soon as the original publication that described the new species came out. Rather than *H. floresiensis* representing an archaic hominin, Henneberg and Thorne (2004) claimed that *H. floresiensis* represents a modern human population with microcephaly. Successive publications have proposed a range of metabolic or genetic disorders in modern humans to explain the morphology of *H. floresiensis*, such as Laron's syndrome, hypothyroid cretinism, and, more recently, Down syndrome. Each of the hypotheses has been fully tested and none has been corroborated. Whether the new dates for *H. floresiensis*, in which an overlap with modern humans on the island is very unlikely, will impact on these hypotheses is too early to say. In any case, the problem with the "pathology" hypotheses is that they do not account for all the facts. Firstly, they are based upon limited aspects of the one skeleton, LB1. But LB1 is not the only individual represented in the Liang Bua cave excavations. The skeletal parts of all other individuals represented are of the same small stature as LB1. Microcephaly and Laron syndrome, and, to a lesser extent, cretinism and even Down Syndrome are rare conditions and one would expect that, even if an archaeological excavation did reveal such a rare skeleton showing evidence of any of these syndromes, most of the skeletal remains would be of a normal, nonpathological population. The *absence* of modern-looking, modern-stature human skeletal material in the deposit is not explained by the proponents of the various pathology-based hypotheses.

Further, the skeletal remains span a long period. The pathology hypotheses fail to explain how a rare condition such as microcephaly or Laron Syndrome could be sustained in *all* known members of a single population for such a long time.

Nor do the pathology hypotheses account for the non-*H. sapiens* mandibular structure, the archaic head shape, archaic facial features, archaic shoulder, and ape-like wrist structure, the relatively short legs in relation to arms, and very long feet on a very short body.

While *H. floresiensis* is known from excavations at only one site, Liang Bua cave, recently a partial mandible and isolated teeth were excavated from Mate Menge in the Soa Basin on Flores. These fossils are dated to ~700,000 years ago – and are therefore more than 600,000 years older than *H. floresiensis*. The new fossils are said to be *H. floresiensis*-like but the researchers await the discovery of more material before they can determine if the remains are indeed *H. floresiensis*.

Conclusion

Homo floresiensis remains a puzzle, and its place on the human evolutionary tree is unresolved. It is not known where these hominins came from; when they first arrived on Flores; or how they got there, given that this island has, it is supposed, never been attached to a mainland. The recent discovery of *H. floresiensis*-like hominins at ~700,000 years ago hints at a long existence of this species and opens up the tantalizing probability that more fossil remains will be discovered on this island.

Cross-References

- [Homo erectus](#)
- [Homo habilis](#)
- [Homo rudolfensis](#)

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Homo habilis

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Synonyms

Handy man

Definition

Most ancient species of *Homo* found in East Africa between 2.3 and 1.6 million years ago.

Introduction

Based on anatomical similarities between the African apes and humans, Charles Darwin and Thomas Henry Huxley forecast that the oldest fossil evidence for human ancestors would be found in Africa (Huxley 1863). In 1924 Raymond Dart recognized a child's skull from South Africa as a potential ancestral human and named it *Australopithecus africanus* ("southern African ape"). Sometimes referred to as "ape-men," these early hominins were found in abundance at a number of sites in South Africa and were assigned to several distinct species.

After Mary Leakey's discovery of a 1.8 million-year-old cranium at Olduvai Gorge in 1959, field research began to focus more extensively on East Africa and the Great Rift Valley. The cranium, Olduvai Hominid 5 (OH 5), popularly known as "Nutcracker Man," due to its massive molars, was ultimately placed in its own species, *Australopithecus boisei*.

Oddly enough by 1959 much more was known about the anatomy, adaptations, and diversity of the genus *Australopithecus* than of the human genus *Homo* (Latin for man) to which modern humans, *Homo sapiens* (sapient, or wise man), belong. Most scholars were searching outside of Africa for the earliest members of the human genus, and many focused on Europe as the finishing school for modern humans.

Discovery and Anatomy

In 1960 the discovery at Olduvai Gorge of OH 7, a partial mandible containing 13 teeth, much smaller than those of *A. boisei*, was thought to represent a very different kind of early human ancestor from OH 5 (Leakey et al. 1964). Further excavation recovered other fossil bones presumably belonging to the same individual as the lower

jaw. These included hand, wrist, and finger bones, left and right parietal bones (sides of the braincase) of the cranium, an upper molar, and a partial foot. The foot, mandible, and cranial bones exhibited carnivore tooth marks perhaps inflicted by a hyena responsible for the death of this individual.

This fragmentary, juvenile skeleton, also dated to 1.8 million years, indicated the presence of a second kind of hominin at Olduvai Gorge. Discovered by the Leakey's eldest son, Jonathan, the find was dubbed "Johnny's Child." In 1964 Louis Leakey, Phillip Tobias, and John Napier published a new species, *Homo habilis*, in the journal *Nature* (Leakey et al. 1964). The species name meaning "handy man" was suggested by Raymond Dart, making reference to Oldowan stone tools found nearby likely made by this early human.

Oldowan tools include scrapers, choppers, spheroids, and proto-hand axes made by simple stone on stone percussion. The raw material, predominately quartz, was obtained from a source area several kilometers away from the lakeside where they were utilized to butcher meat that was scavenged from carnivore kills. The oldest Oldowan tools date back to 2.6 mya (million years ago), but there are no associated hominin remains.

Features such as the reconstructed cranial capacity for *H. habilis* of approximately 674 cc (roughly three cups of coffee) as well as the slender anatomy of the mandible and the narrow, elongated molars all pointed in the direction of *Homo* and not *Australopithecus*. Compared with *A. africanus* from South Africa, the cranial capacity for "Johnny's Child" was some 50% greater justifying its placement in the genus *Homo*.

Controversy and Further Finds

This new species was widely contested by other paleoanthropologists, but further remains of *H. habilis* fossils from Olduvai Gorge added legitimacy to this new taxon as a valid species. These included OH 24, an adult, crushed, female cranium, referred to as "Twiggy," OH 13, a female upper and lower jaw associated with cranial fragments, nicknamed "Cinderella," and OH 16, a

fairly complete male cranium, lacking a face, was dubbed "George." *H. habilis* was an upright walking, early member of our genus, *Homo*, with a cranial capacity greater than *Australopithecus* and with hands capable of stone tool making, bearing jaws and teeth reduced in size and gracility compared to *Australopithecus*. Fossils assigned to this species have been found in Kenya, Ethiopia, and perhaps South Africa, but there is continued debate as to which of these finds are identical to *H. habilis* (Tobias 1991) as defined at Olduvai or constitute or another species of *Homo* (Wood 2014).

While the definition of *H. habilis* rests on cranio-dental features, little was known about the postcranial anatomy (below the neck) until the 1986 discovery by the Institute of Human Origins team from Arizona State University, Tempe, Arizona, of a partial skeleton, OH 62, of this species (Johanson et al. 1987). This specimen eroded from 1.8 million-year-old strata where some 302 fragments were recovered.

Parts of a right arm, humerus (upper arm), two forearm bones, radius and ulna, a fragmentary left femur (thigh bone), and a scrap of right tibia (shin bone) were recovered as well as associated splintered fragments of teeth, small shards of cranium, and fortunately a partial maxilla, the upper jaw. Reconstructed from 32 fragments, the maxilla held the key to the species identification of the skeleton. Not only did the maxilla resemble other *H. habilis* finds at Olduvai Gorge in anatomy and size but it also lacked the megadont teeth so characteristic of *A. boisei*.

The recovery of OH 62 constitutes the first time upper and lower limb bones of *H. habilis* were securely associated. This presumably female individual was relatively elderly as inferred from the heavily worn adult teeth. Estimated to be approximately a meter tall (39 inches), OH 62 is the smallest ancient hominin ever recovered, suggesting that the larger *H. habilis* at Olduvai Gorge such as OH 7 were probably males, indicating a large degree of size difference between males and females, a condition referred to as sexual dimorphism.

Although fragmentary, the humerus and femur afforded estimated lengths used in calculating a

ratio of upper arm and lower thigh bones. In chimpanzees, quadrupeds, the humerus is 100% the length of the femur indicating that fore and hind limbs are used in locomotion. In modern humans, the humerus is only about 70% of the length of the thigh, a biomechanical arrangement reflecting our dependence on bipedal locomotion. Surprisingly in OH 62 the humerus is 95 per cent the length of the femur, similar to the condition seen in *A. afarensis*, the ‘Lucy’ skeleton. The implication is that evolutionary change toward modernity first centered on the cranio-facial region and only later on the postcranial skeleton.

Reconsideration of *Homo habilis*

In 2015 a state-of-the-art computer reconstruction of the original OH 7 mandible and cranium has thrown new light on the anatomical nature of this type specimen for *H. habilis* (Spoor et al. 2015). The mandible was severely distorted as a result of lateral forces during fossilization resulting in a significant distortion of the shape of the dental arcade. After mirror-imaging the undistorted left half of the mandibular dental arcade and correcting for a damaged area along the midline, the correct shape of the dental arcade could be reconstructed. Surprisingly the dental arch was not rounded, as is the case in modern humans, but exhibited relatively long, parallel tooth rows, reminiscent of *Australopithecus*.

A computer visualization of the cranial bones of OH 7 also revealed something surprising in that the cranial capacity for this specimen was significantly underestimated. Previous cranial capacity calculations centered around 674 cubic centimeters, but the new estimates suggested a much higher value around 729–824 cubic centimeters, falling within the range of *Homo erectus*, known from Java and elsewhere.

Conclusion

The mixture of more advanced features like an enlarged brain and more ancient features such as a

long, parallel sided dental arch in OH 7 has significant implications for the placement of *H. habilis* on the human family tree. The more rounded, human-like dental of a 2.3 million-year-old maxilla, upper jaw, from the site of Hadar, Ethiopia, would not have articulated with the reconstructed OH 7 mandible. This suggests that prior to 2.3 mya, the *Homo* lineage had already split into two lineages implying that *H. habilis* from Olduvai Gorge is not necessarily the progenitor to later species of *Homo* as previously proposed.

The recovery of a 2.8 million-year-old partial mandible at Ledi-Geraru, Ethiopia, exhibits a mandibular anatomy and a dentition that places it comfortably within *Homo* (Villmoare et al. 2015). Other anatomical features of the jaw suggest evolutionary affinities with older *Australopithecus afarensis* mandibles. This suggests that Lucy’s species, *A. afarensis*, that disappears around 3 mya, should be considered the ancestor to the *Homo* lineage (Johanson 2017).

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Homo heidelbergensis

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Synonyms

Broken Hill Man; Heidelberg Man; Rhodesian Man

Definition

Archaic *Homo* found in Europe, Africa, and possibly Asia between 70,000–200,000 years ago.

Introduction

In 1907 a heavily built mandible, containing a complete set of teeth, was discovered by workers at a sandpit just outside of Heidelberg, Germany, in a village called Mauer. Initial observations of the jaw suggested similarities with *Homo neanderthalensis*, but the combination of a massive mandible and quite small teeth suggested something different. Paleontologist Otto Schoetensack gave a new species name to the fossil, *Homo heidelbergensis* (Heidelberg Man) (Schoetensack 1908). It has been a challenge to determine a precise geological date for this middle Pleistocene mandible considered to have lived sometime between 475,000 and 700,000 years ago.

Unfortunately, no cranial remains were found at Mauer, but a number of skulls from other sites in Europe, Africa, and, perhaps, China, dating to the same geological epoch as the Mauer mandible, are referred to *H. heidelbergensis*. The best preserved European specimens were found at Petralona, Greece, and Arago, France (Harvati 2007; Rightmire 1998).

Additional Finds

Comparative anatomical study of skulls from Petralona and Arago led to the conclusion that the Mauer mandible would have been a good fit for these skulls, and therefore they should be placed in *Homo heidelbergensis* (Harvati et al. 2010). It has been difficult to geologically date the Petralona skull which was found in 1960 by shepherds in a cave close to Thessalonika, but associated animal bones provide an estimate of 350,000 years. The rugged male skull has a cranial capacity of 1220 cc and a massive supraorbital torus resembling other skulls (see below) that have been assigned to *Homo heidelbergensis*. Analysis of the anatomy of the Petralona specimen confirms a mosaic of primitive (*Homo erectus* like) and Neanderthal anatomy.

In 1971 a 400,000-year-old skull, Arago XXI, was excavated in the eastern Pyrenees in a limestone cave located near Tautavel, France. Initial impressions of the heavily built skull, presumably a male, with strong brow ridges and a low cranial capacity of 1166 cc suggested that it might belong to a primitive species well known in Asia called *Homo erectus*. More comprehensive analysis of Arago reveals many resemblances with the Petralona specimen and is now placed in *Homo heidelbergensis*. This decision is supported by the recovery of mandibles at Arago that resemble the Mauer mandible.

African Finds

In Africa the most complete crania assigned to *H. heidelbergensis* come from Bodo, Ethiopia, and Kabwe, Zambia. The Zambian cranium, found by workers at the Broken Hill Mine in what was then called Rhodesia, is sometimes referred to as Rhodesian Man or the Broken Hill skull (Smith-Woodward 1921). Today it is known as the Kabwe skull. No stone tools were recovered, but associated parts of a pelvis and lower limb provide a glimpse into the postcranial skeleton, suggesting that Kabwe was a very tall and robustly built male.

The Kabwe skull has a cranial capacity of 1325 cc and was incredibly massive, sporting a prominent supraorbital torus at the front of the cranium. The majority of the dentition exhibits very heavy wear, with cavities and root abscesses that must have been painful. An undiagnosed lesion on the left wall of the cranium, above the ear canal, may also indicate disease.

Debate on Naming

Considerable debate has swirled around placement of all these specimens in a single species, *Homo heidelbergensis*, a taxon that was based on a single mandible. However, the European and African crania share many details of morphology and are collectively considered to be the kind of skull that would have had a Mauer-like mandible. Found in 1921 the cranium from Kabwe was given a separate species name, *Homo rhodesiensis*, leading some anthropologists to retain that name for the African material (Stringer 2012).

The Bodo skull was found in 1976 in Middle Awash Valley, Ethiopia (Conroy et al. 1978). Hand axes and cleavers made on lava, of the Acheulean industry, were found nearby, and the associated faunal remains suggested a Middle Pleistocene age. The geological age of the Bodo specimen was confirmed with argon dating to be 600,000 years old.

The powerfully built Bodo skull with a very thick, projecting supraorbital torus possesses the largest face in the human fossil record and a cranial capacity of 1250 cc. Upon close examination, numerous cut marks were found on the cheeks, in the eye orbits, and on the frontal bone, indicating intentional defleshing of this individual (White 1986).

Sima de los Huesos

More than 5000 human fossils were excavated at Sima de los Huesos (“Pit of Bones”) located in the Atapuerca Mountains of northern Spain (Arsuaga et al. 2014). These bones come from the Middle

Pleistocene epoch and have been dated to 400,000 before the present. Initially these fossils were placed in *Homo heidelbergensis*, because of anatomical similarity to other skulls placed in *Homo heidelbergensis*. Some anthropologists also drew attention to many anatomical resemblances of the Sima de los Huesos bones shared with *Homo neanderthalensis*. The amalgam of older *Homo heidelbergensis* anatomy with later, derived Neanderthal features has attracted widespread debate. Perhaps it is useful to view Neanderthals within the accretion model that posits the gradual accumulation of Neanderthal features over time. With the recovery of diagnostic Neanderthal DNA in Sima de los Huesos bones (Matthias et al. 2016), a plausible interpretation is that they represent an early stage in the Neanderthal lineage that led to later “Classic Neanderthals.”

Conclusion

It is now widely agreed that the great number of anatomical similarities shared by all *Homo heidelbergensis* fossils justifies their inclusion in a single species. In Europe, as a result of their isolation due to Pleistocene glaciations, they evolved into Neanderthals. The African fossil record for *Homo heidelbergensis* such as Bodo and Kabwe supports an African origin for modern humans who migrated into Europe and replaced the Neanderthals.

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Homo neanderthalensis

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Synonyms

[Neanderthal man](#)

Definition

Archaic *Homo* found in Eurasia between 400,000 and 40,000 years ago.

Introduction

Although Neanderthal fossils were first recovered in Belgium in 1830 and in Gibraltar in 1848, it

was not until 1856 when skeletal remains found by miners in the Feldhofer Cave in the Neander Valley, Germany, that scientists entertained the idea that the bones might belong to an extinct form of an ancient human (Shreeve 1995). In 1864, the bones were assigned to the species *Homo neanderthalensis* (Neander Valley Man). This was the first recognition of an extinct human relative. At that time, the prevailing view considered Neanderthals as an extinct kind of human that played no role in the ancestry to modern humans. In the 1930s several scholars challenged this interpretation and entertained the view that Neanderthals were progenitors to modern humans. Today Neanderthals are seen as an evolutionary lineage close to modern humans that exchanged some genes with us but died out roughly 40,000 years ago.

Geographical Distribution and Geological Age

Numerous Neanderthal remains have been found from Great Britain to Spain and eastward to the Middle East and Uzbekistan; no Neanderthal fossils have ever been recovered from Africa. Neanderthal DNA can be traced back to roughly 400,000 years ago in fossil bones from the Atapuerca Mountains at Sima de los Huesos in northern Spain, tracing the roots of Neanderthals much deeper in time than anticipated (Meyer et al. 2016). Carbon 14 dating places Neanderthal extinction at approximately 40,000 years before the present, shortly after the migration of modern humans, *Homo sapiens*, into Europe (Wood et al. 2013).

Neanderthals evolved as a single lineage in Eurasia and appear not to have spawned any other descendants. The most ancient Neanderthals exhibited incipient skull anatomy that gradually became more distinctively Neanderthal over time due to natural selection and genetic drift as they continued to be isolated in a glacial Europe. By 50,000 years ago *H. neanderthalensis* evolved its full blown “Classic Neanderthal” morphology both in the craniofacial region and throughout their postcranial skeleton. Examples of the later

Neanderthals include some well-known finds such as those from La Chapelle-aux-Saints in France and Amud in Israel.

Neanderthal Anatomy

Neanderthal faces are characterized by a heavy, double-arched, supraorbital brow behind which are enlarged frontal sinuses. The nasal aperture is broad and large with an expanded nasal cavity bordered by big maxillary sinuses. The middle face juts forward, a feature called midfacial prognathism, and gives the impression that the entire nasal region was pulled forward. The cheek bones, immediately below the orbits, slope backward unlike in modern humans where this region presents a flat face where our prominent cheeks define a right angle below the orbit (Harvati 2015).

The distinctive Neanderthal craniofacial morphology is interpreted largely as a response to the glacial and periglacial environments in Eurasia where they lived. A large nasal opening and nasal cavity functioned to warm and humidify the cold, dry glacial air. The large sinuses functioned much like double pane windows as insulators to keep the brain from becoming chilled.

Neanderthal brain cases were long and low from front to back and sported a substantial “chignon” or projecting bun at the rear of the skull. The average Neanderthal brain measured 1520 cc (cubic centimeters) and ranged in size from 1200 cc to as much as 1700 cc. Modern human brains average around 1400 cc, and the larger Neanderthal average probably reflects the additional endocranial space required to house an increased blood flow to keep the brain warm.

Generally Neanderthal teeth fall in the size range of modern humans, but molars are distinct in having large pulp cavities, a condition known as taurodontism. However, the anterior teeth are large and exhibit heavy wear as if they are used perhaps in some activity like chewing hides. The mandible lacks a chin, and in lateral view a large space (retromolar gap), maybe associated with midfacial prognathism, is evident immediately behind the wisdom tooth (third molar).

Neanderthal bodies are short in stature, stocky, and heavily built with strong, thick-walled bones. Relatively speaking the lower leg and forearm bones are shortened compared to modern humans. The short, stocky bodies, and abbreviated limb segments undoubtedly reflect an adaptation to the cold environment of glacial Europe. Thus with a reduced skin area to body mass ratio their bodies served as heat conservers. In contrast modern human bodies, especially in tropical regions, are tall and slender with long limbs, thus increasing the ratio of skin area to body mass enhancing heat dissipation allowing for cooling of the body.

Neanderthal Behavior

Neanderthals led stressful lives in Arctic-like environments under rugged conditions as is seen in frequent evidence of trauma, perhaps brought about during close encounter hunting episodes employing thrusting spears. Bone fractures occur in both male and female individuals implying that both sexes participated in hunting. Studies of the age of death suggest that Neanderthals did not have long life spans. A number of Neanderthal skeletons show healed fractures, possibly a reflection of some level of compassion and care by other individuals.

Archaeological evidence suggests that Neanderthals did not lead culturally sophisticated lives (Marean 2005). The stone tool technology traditionally associated with Neanderthals, known as the Mousterian, was named after the site of Le Moustier in the Dordogne region of France. The tools of this Middle Paleolithic period consisted of stone flakes that were modified into points, scrapers, and even small hand axes. Employing a knapping technique known as the Levallois, a number of smaller flakes are first removed from a larger stone core. This prepares the core that is then struck with a single percussive blow, fabricating a large disc-like flake. Tools were fashioned exclusively on stone unlike the more recent Upper Paleolithic technology, brought into Europe by *Homo sapiens*, where bone, antler, and ivory served as a source for

making tools and carvings. While there are minor regional differences in the shapes of flake tools throughout the geographic distribution of the Mousterian, the extensive variation in Upper Paleolithic blade technology reflects a significantly more sophisticated cultural diversity associated with *Homo sapiens*.

Faunal remains recovered from excavations of Neanderthal living sites indicate that they were principally carnivorous eating large amounts of meat from a variety of mammals such as the aurochs, horse, deer, and bison, as well as wild boar and ibex. Neanderthals living closer to the Mediterranean Sea included marine mammals and even shellfish in their diet (Stiner 2006). Studies of stable isotopes recovered from Neanderthal skeletons, like nitrogen and carbon, confirm a diet dominated by large, cold adapted herbivores such as woolly rhinos and woolly elephants (Richards and Trinkaus 2009).

The lack of art associated with Neanderthals, with some minor exceptions such as an engraved figure, similar to a hash mark found on the floor of a Gibraltar cave in strata containing characteristic Mousterian artifacts, suggests that Neanderthals were not capable of symbolic thought. Neanderthals must have had some level of communication, but it is unlikely they possessed symbolic language that is one of the defining hallmarks of *Homo sapiens*.

Neanderthals occasionally buried their dead, but their graves show a paucity of ritual grave goods in characteristic of later *Homo sapiens* interments. Discovery of crayons of variously colored ochre and even manganese suggest that Neanderthals may have practiced some degree of self-adornment.

An abundance of eagle, falcon, and vulture wing bones recovered from a number of Neanderthal sites implies that feathers were intentionally collected and worn as ornamentation. Cut marks and polishing on eagle talons recovered from a Neanderthal site in Croatia and Italy imply that these were worn as jewelry (Peresani et al. 2011). Discoveries such as these are beginning to paint a somewhat more “humanlike” view of Neanderthals in contrast to the long-prevailing view that they were dim-witted brutes.

Neanderthal Extinction

Not everyone agrees as to why Neanderthals went extinct 40,000 years ago, but they vanished only a few thousand years after modern humans arrived from Africa. The Upper Paleolithic industry associated and brought in by *Homo sapiens* is significantly more advanced and varied than the Mousterian. In the Upper Paleolithic, sophisticated techniques were employed to make blade tools, tools with long cutting edges like knives. Blade tool technology is a more efficient use of stone than Mousterian flake technology. *Homo sapiens* used spear throwers, also known as atlatls, and perhaps also the bow and arrow, both of which greatly enhanced their hunting prowess compared to Neanderthals that killed by jabbing spears in dangerous close encounter episodes. Neanderthals were unable to compete with these technologically advanced peoples who may even have used dogs during hunting (Shipman 2015). Polychrome paintings on cave walls and exquisitely carved mobiliary art objects further attest to the cognitive superiority of the modern humans over Neanderthals.

Neanderthal and Modern Human Interbreeding

Migrating out of Africa, modern humans may also have brought with them pathogens against which Neanderthals had no immunity. Paleogenetic studies confirm that moderns and Neanderthals interbred, opening up the possibility that tropical infectious diseases could have been a factor in Neanderthal extinction.

It is clear that the Neanderthal lineage went extinct and *Homo sapiens* prevailed, but genetic analysis confirms that our direct ancestors and Neanderthals did interbreed with humans, perhaps during three separate time periods, before their extinction (Green et al. 2010). Both Neanderthal mitochondrial DNA and a complete nuclear genome of Neanderthals have now been sequenced and compared with modern humans. Modern Eurasians have inherited between 1 and 3% from Neanderthals.

In this early stage of paleogenetics, understanding the function of the genes we inherited from Neanderthals is difficult, but it is certain that some of these genes were beneficial and other are deleterious to humans (Gibbons 2016). For example, it appears that some archaic genes actually conferred an increased immune response in modern humans. While other genes may not have been so beneficial and may have contributed to depression, the risk of nicotine addiction, increased risk of blood clots, and even urinary infections.

According to the biological species definition, different, even closely related species should not be capable of interbreeding and exchanging genes. However, in the case of *Homo neanderthalensis* and *Homo sapiens*, these two species were similar enough to have experienced some level of interbreeding. No fossils retaining intermediate hybrid morphology have been recovered. Although a 24,000-year-old subadult skeleton from Lagar Velho, Portugal, was thought to be a Neanderthal-human hybrid, unlikely since Neanderthals had already been extinct for 16,000 years. The Lagar Velho find may be a modern *Homo sapiens*, with cold adapted features in its postcranial skeleton as in Eskimos.

Conclusion

Current thinking views Neanderthals as a separate, successful, and geologically long-lived Eurasian lineage of humans that were morphologically and behaviorally distinct from anatomically and behaviorally modern humans, *Homo sapiens*. And while Neanderthals did interbreed with us and contributed some favorable genes to *Homo sapiens*, as a lineage, they went extinct.

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Homo rudolfensis

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Synonyms

Early Homo; Human Evolution

Definition

Homo rudolfensis is a species of early *Homo* that is known from ~1.8 million years ago in East Africa. Despite more than 40 years of research and analyses, it is still unclear where this hominin sits on the human evolutionary tree.

Introduction

Fossil hominin bones found in Kenya in 1973 remain enigmatic despite 43 years of discussion and analysis. The bones comprise a partial cranium and face and leg bones. The cranium and face have the Kenya National Museum name KNM-ER 1470. Just where they fit on the human evolutionary tree has long occupied researchers, but a resolution has not been forthcoming, and it is unclear as to what other fossils might belong in the same species as KNM-ER 1470.

History of Discovery and Taxonomic Challenges

In 1973 Mr. Bernard Ngeneo discovered a relatively intact cranium in the East Rudolf area of Kenya during fieldwork led by Mr. Richard Leakey. The cranium is known by its museum reference KNM-ER 1470 (Kenya National Museums-East Rudolf). Possibly associated postcranial bones were also found – a right femur (KNM-ER 1472), discovered by Dr. J. Harris; part of a second right femur (KNM-ER 1475; discovered by Mr. Kamoya Kimeu); and skeletal material (KNM-ER 1481; Dr. J. Harris) (Leakey 1973).

The brain case and partial facial skeleton were found in deposits under a volcanic tuff that was at that time dated to 2.6 mya. We now know that the skull is from deposits dated to 1.8 million years ago (Mcdougall et al. 2012) and are thus contemporaneous with cranium KNM-ER 1813 *H. habilis* (East Africa) that was at the time the earliest member of our genus.

At the time of discovery the taxonomic status of the remains was not clear. Not only did KNM-ER 1470 differ from fossil hominins known at the time, it also had an unexpected mix of Australopithecine and *Homo* characters. The size and form of the cranium suggested that it should be included within the genus *Homo*, but the flat fronted, wide palate, and form of the supraorbital region are suggestive of the Australopithecines; and the postcranial (femora – leg bones) cannot be distinguished from *Homo sapiens*. Leakey (1973) therefore attributed the fossils to *Homo* sp. indet (Fig. 1).

Since its discovery, opinions have differed about the species into which this cranium should be placed. In a joint publication Alan Walker and Richard Leakey “agreed to disagree,” Walker preferring to place KNM-ER 1470 in *Australopithecus* and Leakey would place it to *Homo* (Walker and Leakey 1978, p. 54). The challenge facing us is the unexpected mix of characters in the specimen. It has a domed calvarium with steeply sloping sides that have parietal eminences; the frontal (forehead) rises relatively steeply (but not as greatly as modern humans), which are



Homo rudolfensis, Fig. 1 *Homo rudolfensis* cranium KNM-ER 1470 (Image credit: Debbie Argue)

characteristics of *Homo*. But the size and flatness of the face and the shallow, broad, and short palate are reminiscent of *Australopithecus*, although the wide palate in relation to its length differs from the shape of the *Australopithecine* palates (Leakey 1973). Its cranial capacity is 752 cc while *Australopithecines*' cranial volume range from 387 to 560 (Holloway et al. 2004).

Because KNM-ER 1470 existed at the same time and in the same general region as *H. habilis* it became customary to include KNM-ER 1470 in that species, although Groves (1985, p. 264) notes that there was never any attempt to justify this assumption. The differences in the cranial capacities and general morphology of KNM-ER 1470 and crania attributed to *H. habilis*, however, led some researchers to suggest that the fossils might better be assigned to two species, while others attributed these differences to sexual dimorphism within *H. habilis*.

The first to separate the species into two was Groves and Mazak (1975) who attributed a mandible KNM-ER 992, at the time included *H. habilis*, to a new species, *H. ergaster*. Wood (1985) showed that the KNM-ER 1470 parietal bone is within the *H. erectus* range in some aspects but different in others and that the base of KNM-ER 1470 is metrically similar to *H. erectus* (OH 9, KNM-ER 3733 and 3883). He, therefore, asks, in relation to KNM-ER 1470 and *H. habilis* KNM-ER 1813 "Are we dealing with one taxon, or two?" (Wood 1985, p. 211). Using statistical methods applied to expected cranial capacities in a population, he finds that the chance of the two crania being from the one population is <5% and that KNM-ER 1470 and KNM-ER 1813 should not be uncritically regarded as being sampled from the same taxon (Wood 1985). He concludes that even more tantalizing than the differences between KNM-ER 1470 and KNM-ER 1813 is the possibility that not two but three species existed in the East Africa in the Early Pleistocene: *H. habilis*, *H. erectus*, and a taxon that included KNM-ER 1470.

Questioning the coexistence of more than one species of *Homo* in the human evolutionary journey occurred in an intellectual milieu that viewed the evolution of *Homo* as unilineal. That is, until

the question of KNM-ER 1470 was raised it was thought that *H. sapiens* evolved from *H. erectus* that evolved from *H. habilis*. To maintain this paradigm, any variation around any of these species was considered a "grade." In this context, Groves (1989) tested the unilineal concept of human evolution by applying cladistic analysis to the *Australopithecines* and *Homo*. His cladograms consistently returned results in which KNM-ER 1470 was on a separate branch to other species in the analyses, *H. habilis* and *H. erectus*. He attributed KNM-ER 1470 to a new species, *Homo rudolfensis* (Alexeev 1986). This species name is a derivative from Alexeev (1986), who, 3 years earlier, had attributed KNM-ER 1470 to *Pithecanthropus rudolfensis*. Under the rules of taxonomic nomenclature the name first published in accordance with the rules is the correct name for a taxon so, in this case, *rudolfensis*, is retained, but the genus name is amended, and the originator of the name is appended. The unique characters that distinguish *H. rudolfensis* are the flat form of the zygomatic root, lack of internal buttressing of the mandible, and some morphologies of the premolars (Groves 1989: 264).

Those that would retain KNM-ER 1470 in *H. habilis* regard the species as being highly sexually dimorphic, regarding the larger KNM-ER 1470 as a male of the species and the smaller crania as females (such as KNM-ER 1813 that has a cranial capacity of 509 cc; Holloway et al. (2004)). In this case, the species name *H. habilis sensu lato* is used in the literature, and *H. habilis sensu stricto* is applied if the researcher includes only the smaller crania in *H. habilis*.

A further challenge within this somewhat complicated situation is the lack of agreement as to the composition of *H. rudolfensis*. For example, William Kimbel and colleagues include KNM-ER 1470, KNM-ER 1590, KNM-ER 3732 *H. rudolfensis*; David Strait and colleagues' sample comprised 9 fossils; Lee Berger and colleagues included 11 fossils in their compilation of *H. rudolfensis*; David Lordkipanidze and colleagues include KNM-ER 1470, KNM-ER 62000, and OH65 in the species; while other studies limit the species to KNM-ER 1470.

H. rudolfensis, then, is somewhat of an enigma. Where does it fit on the human evolutionary tree? What is it most closely related to? In 2001, Leakey et al. (2001) announced a new hominin genus and species discovered in East Africa, *Kenyanthropus platyops* sp. nov. The species comprises a largely complete cranium KNM-WT 40000 and part of an upper left jaw and face KNM-WT 38350. The former has an estimated age of 3.5 mya; the latter has an estimated age of 3.3 mya. Leakey et al. (2001) draw attention to the similarity of KNM-WT 40000 to KNM-ER 1470, *H. rudolfensis*. Both have a flat face, a vertically oriented cheek region, lack of a supraorbital sulcus, and an anterior origin for the root of the zygomatic arch. The main differences between the KNM-ER 1470 and *K. platyops* cranium KNM-WT 40000 relates to the more primitive nasal characteristics of KNM-WT 40000 and the higher cranial vault (larger braincase) of KNM-ER 1470 (Leakey et al. 2001). Cameron (2003) sees similarities among *Kenyanthropus* and *H. rudolfensis* in the pattern of growth stages in brain morphology and cranial and dental development that differed from *Paranthropus*. He suggested *Kenyanthropus* and *H. rudolfensis* may form a sister group relationship to the exclusion of *Paranthropus*. This led him to propose that *K. platyops* was the ancestor of *H. rudolfensis* and the species should be renamed *Kenyanthropus rudolfensis*. So it seemed that at last that the ancestor of *H. rudolfensis* had been identified, but others have questioned this and a possible phylogenetic relationship between *Kenyanthropus* and *H. rudolfensis* needs further clarification.

Conclusion

Just what *H. rudolfensis* is, where it sits on the human evolutionary tree, and even the tantalizing prospect that its ancestors may have been discovered are unresolved questions despite more than 40 years of comprehensive research. Is there hope for a resolution? Yes, probably. In the last 15 years, a remarkable suite of

discoveries of new hominins has been made, so there is more comparative material with which to compare *H. rudolfensis*, and, judging by the recent increase in the rate of new fossil discoveries, there is every chance that more *H. rudolfensis* fossils will be found that will fill out our understanding of its morphology so that we can better assess its place on the human evolutionary tree.

Cross-References

- [Australopithecus africanus](#)
- [Australopithecus Group](#)
- [Homo erectus](#)
- [Homo floresiensis](#)
- [Homo habilis](#)

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Homogamy/Heterogamy

- [Assortative Mating](#)

Homology of Ear Ossicles to the Reptilian Jaw Bones

- [Reichert-Gaupp Theory](#)

Homonegativity

- [Genetic Hypotheses of Homophobia](#)
- [Sexual Prejudice \(Personality Correlates of\)](#)
- [Social Hypotheses of Homophobia](#)

Homophily

- [Peer Socialization](#)
- [Specific Friendships](#)

Homophobia

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Synonyms

[Heterosexism](#); [Sexual prejudice](#)

Definition

Generally, homophobia refers to prejudice, stereotyping, and/or discrimination based on sexual orientation – particularly directed by heterosexuals

toward lesbian, gay, and bisexual individuals (hereafter referred to as LGB). *Prejudice* refers to the specific emotional reaction to a person because of one's sexual orientation. *Stereotypes* refer to the beliefs about others due to classifying them according to their sexual orientation, and *stereotyping* refers to the process of applying stereotypes of a certain sexual orientation group to an individual member of that group. *Discrimination* refers to differential behavior toward an individual as a function of their sexual orientation.

Introduction

Homophobia is a term often used to describe prejudice and discrimination directed toward non-heterosexual individuals. As the name implies, the concept *homophobia* denotes a fear-based response toward those who are attracted to and/or engage in sexual behavior with members of the same sex. While still used colloquially, researchers more often employ the term *sexual prejudice* to refer more generally to prejudices directed toward members of a particular sexual orientation group, especially toward lesbian, gay, or bisexual individuals (LGB). Researchers only recently considered prejudices against LGB individuals as part of the prejudice and intergroup relations research, which historically focused primarily on interracial and interethnic prejudices. As such, research on sexual prejudice derives from only a few theoretical perspectives (e.g., focusing largely on gender role violations and threats to sexual identity), and just recently have researchers begun applying an evolutionary perspective to understand the range of sexual prejudices. This entry provides a summary of the existing research on sexual prejudice in light of an evolutionary analysis.

Using Evolutionary Psychology to Understand (Sexual) Prejudice

How can evolutionary psychology explain stereotypes about, prejudices toward, and discrimination based on sexual orientation? Human

cognition, emotion, and behavior evolved to effectively manage recurring threats and opportunities to survival and reproduction, including those posed by other people (i.e., affordances). Throughout evolutionary history, humans faced a consistent set of challenges to survival and reproduction, including successfully mating and raising children, avoiding disease and danger, and successfully navigating the social terrain provided by group living (Kenrick et al. 2010). Successful cognitive, emotional, and behavioral responses to these challenges and opportunities increased the likelihood of an individual's survival and reproduction, which, through differential reproduction over time, led to evolved psychological mechanisms for addressing these recurring challenges and opportunities.

Evolutionary approaches to inter- and intra-group relations argue that (1) humans evolved as social, group-living animals, (2) effective group functioning requires psychological processes facilitating group functioning, and (3) evolution shaped mechanisms to manage threats and opportunities of group living (Cottrell and Neuberg 2005). This affordance management perspective contends that inter- and intra-group prejudices stem from perceived threats attributed to outgroups and perceived threats to ingroup functioning (e.g., threats to health, physical safety, sexual autonomy, socialization). Stereotypes, as socially transmitted information about others, convey threat and opportunity-relevant information. Likewise, specific affective emotional responses to perceived stereotypes characterize the prejudices underlying inter- and intra-group dynamics. These perceptions and emotional reactions facilitate specific behaviors designed to respond effectively to the perceived threats and opportunities attributed to specific ingroup and outgroup members, thus characterizing discrimination based on social group identity.

This functionally driven, affordance-based perspective on intergroup dynamics and prejudice allows researchers to predict specific emotional and behavioral tendencies based on the threats associated with stereotypes of different groups. For example, threats to physical and sexual autonomy elicit fear, avoidance, and escape. Threats to

health elicit physical disgust, avoidance of the contaminant, and if contaminated, expulsion of the contaminant via cleansing or aggression. Moral transgressions elicit moral disgust, aggression, and suppression or expulsion of the moral violator. Obstacles to desired outcomes elicit anger and aggression to remove the obstacle. Mating, parenting, and social affiliation opportunities (i.e., positive affordances) elicit positive emotions (e.g., lust, love, compassion) and approach behaviors to facilitate successful mating, parenting, and affiliating. This entry combines the affordance management approach to prejudice with the fundamental motives theory to demonstrate how perceptions of threats to fundamental human motivations elicit affective prejudices and behavioral responses to respond to the perceived threats.

Overview of Stereotypes of, Prejudices Toward, and Discrimination Against LGB

This entry summarizes and interprets the existing sexual prejudice research through the lens of an evolutionary, threat-based framework. Specifically, it examines how the perception of threats to fundamental human motives (e.g., disease threats, parenting and childrearing threats, values threats, status threats, and mating autonomy threats) engage emotional and behavioral reactions to effectively manage these threats.

Disease threats. Relative to a variety of other social groups (e.g., European Americans, African Americans), gay men are perceived as more likely to pose threats to physical health (Cottrell and Neuberg 2005). This perception of threats to health predicts increased disgust and negativity toward gay men (relative to other social groups; Cottrell and Neuberg 2005), and individual differences in general disgust predict greater negative attitudes toward gay men (and lesbians, albeit using a measure confounding attitudes toward gay men with attitudes toward lesbians; Terrizzi et al. 2009). In addition, activating concern for disease increases sexual prejudices and contamination-avoidant behaviors specific to gay men. Specifically, activating disease concern by

exposing people to a disgusting odor (relative to no odor) decreased warmth toward gay men but not lesbians, heterosexuals, or other social groups unassociated with disease (Inbar et al. 2012). Further, imagining an interaction with a gay man (vs. heterosexual man) increased heterosexuals' desire for physical cleansing, measured by greater activation of words associated with physical cleanliness, greater liking of cleansing products, and greater likelihood of selecting a sanitary wipe over a pencil as compensation (de Zavala et al. 2014).

Parenting and childrearing threats. Heterosexuals believe that gay men and lesbians (relative to heterosexuals) are more likely to influence children's gender and sexual orientation development by making them more likely to become non-heterosexual (Filip-Crawford 2015) and therefore decreasing one's inclusive fitness by proxy. Parenting enhances these stereotype-based concerns about children's safety. Comparing parents to nonparents in a random sample of adults, parents reported greater levels of sexual prejudice (using scales measuring a myriad of negative beliefs against "homosexuals"), even after controlling for sex, number of nonheterosexual friends, religiosity, education, and age (Gallup 1995). College students who simply imagined having children reported similar prejudices – heterosexual college students rated their distress to a scenario depicting their (imagined) 8- or 21-year old child spending the night at a friend's house (the friend's parent was gay and either the same or opposite-sex to the child); participants reported the greatest distress to the scenario involving a young child staying with a same-sex gay parent (Gallup 1995).

Experimentally activating parenting concerns increases sexual prejudices. Activating traditional family roles (i.e., viewing a photo of a traditional family vs. a photo of a garden) caused participants to judge a gay father more negatively across a series of traits than a heterosexual father (Vescio and Biernat 2003). Further, activating the importance of family values (i.e., writing about the importance of family/friends vs. the importance of one's sense of humor) increased sexual prejudice toward gay men and lesbians (i.e., a measure assessing a myriad of beliefs about gay men and

lesbians), as mediated by increased endorsement of traditional husband-wife family values (Lehmiller et al. 2010).

These prejudices map onto behaviors designed to keep LGB men and women away from children. Specifically, heterosexuals report increased discomfort with "homosexuals" participating in roles and occupations in which they interact closely with children and could potentially socialize them to be gender or sexual orientation non-normative or have intimate contact with children – roles as teachers, school bus drivers, and doctors (especially pediatricians), but not auto mechanics, bank tellers, airline pilots, construction workers, lawyers, or sales clerks, relative to a control condition with the sexual orientation unspecified (Gallup 1995).

Values threats. Relative to other social groups (e.g., European Americans, welfare recipients, heterosexuals), LGB individuals are often perceived as more likely to hold nontraditional values that potentially undermine and violate traditional values based on parenting, romantic relationships, gender roles, and religion (e.g., Brambilla and Butz 2013; Cottrell and Neuberg 2005; Haddock et al. 1993; Henry and Reyna 2007; Pirlott and Neuberg 2014). For example, homosexual behavior directly defies many explicit religious teachings and values – all three of the Abrahamic religions (which represent a large proportion of the world's religions) explicitly prohibit homosexuality. Perhaps unsurprisingly, a meta-analysis of measures of religiosity and sexual prejudice revealed associations of religiosity and greater levels of sexual prejudice (Whitley 2009). Specifically, more frequent religious attendance, greater levels of religiosity, greater levels of fundamentalism (belief that one set of religious teachings exist which contain absolute truths which must be followed absolutely), greater levels of Christian orthodoxy (agreement with core beliefs of Christianity), and greater intrinsic religiosity (internalizing religious teachings) predicted greater prejudices toward gay men and lesbians (Whitley 2009). Extrinsic religiosity (using religion to achieve nonreligious goals; e.g., socializing) was unrelated to sexual prejudice, and quest religiosity (using religion as a search for

existential meaning) predicated greater tolerance toward gay men and lesbians (Whitley 2009).

Such perceived threats to traditional values predict elevated prejudices toward LGB. Perceived threats to sexual morality predicted elevated negative attitudes toward gay men and lesbians (Crawford et al. 2014). Perceived threats to ingroup values predicted disgust toward gay men (Cottrell and Neuberg 2005). Finally, manipulating normative gender role behavior affects sexual prejudice; for example, heterosexual men reported greater dislike for feminine male targets more than masculine targets (Blashill and Powlishta 2009).

Experimentally activating traditional values and threats to ingroup values elicits prejudices against LGB. For example, priming a general symbolic values threat (reading an editorial commenting on the worsening of values and traditions in participants' home country) suppressed warmth toward gay men relative to nonsymbolic threat (editorial about climate change) and non-threat conditions (Brambilla and Butz 2013). Subliminally activating Christianity (using Christian words relative to neutral words) increased coldness toward gay men relative to heterosexual men (Johnson et al. 2012). As previously mentioned, activating the importance of traditional family values increased sexual prejudice toward gay men and lesbians, driven by elevated endorsement of traditional husband-wife family values (Lehmiller et al. 2010). Finally, both the situational activation of and individual differences in endorsement of traditional family values (as discussed above) predicted harsher evaluation of a gay father relative to a straight father (Vescio and Biernat 2003).

Perceived threats to heterosexual values predict the endorsement of aggression and aggressive behavioral responses against LGB. For example, perceptions that gay men and lesbians violate traditional values related to relationships, sexual morality, religion, and family predicted opposition to same-sex marriage and adoption rights (Henry and Reyna 2007; Reyna et al. 2014). Priming a symbolic values threat suppressed support for gay rights relative to nonsymbolic threat and nonthreat conditions (as previously discussed;

Brambilla and Butz 2013). In addition, a large body of research suggests that aggression against LGB may stem from perceived gender role violations, particularly violations performed by men (e.g., Gordon and Meyer 2007). Finally, research examining reasons why college students verbally or physically aggressed against a gay person identified a religious and moral values threat component – i.e., “because of my religious beliefs” and “because of my moral beliefs” (Franklin 2000).

LGB values are also perceived as “transmittable” – i.e., that pro-gay ideologies are contagious and that interacting with a gay man or lesbian increases a person's support for gay rights (Filip-Crawford 2015). Further, the degree of “contagiousness” of gay behavior and pro-gay ideology also depends upon community structure, as a particular individual's social influence is stronger in more tightly knit social communities. Perceptions of greater community connectedness predicted greater aggressive intentions toward gay men and lesbians (Filip-Crawford 2015). Filip-Crawford (2015) also manipulated social community connectedness by telling college students that the university social scene is either highly or loosely connected and asked students to write about a time consistent with this. Highly connected communities increased highly prejudiced participants' intentions to aggress and increased actual behavioral aggression (noise blasts) against gay men and lesbians relative to weakly connected communities.

Threats to status via stigma by association. Simply interacting with another person potentially causes others to characterize one as similar to their companion, despite salient differences, especially if the target's companion belongs to a stigmatized group. This phenomenon is known as *stigma by association* – the process by which associating with members of a stigmatized group similarly stigmatizes “normal” individuals (Neuberg et al. 1994). Associating with LGB individuals can stigmatize heterosexuals as gay, therefore, affecting their social status and mating potential. For example, highly prejudiced heterosexual men assumed a man (with an unspecified sexual orientation) who voluntarily chose a gay roommate was

as likely to be gay as a man specified as gay and more likely to be gay than a man with a heterosexual roommate (Sigelman et al. 1991).

Why might the labeling of a heterosexual as gay upset heterosexuals? Mislabeling heterosexuals as gay can reduce future mating opportunities if opposite-sex potential mates are no longer interested in mating with the stigmatized individual, and thus can have reproductive costs. In addition to mating costs, stigmatization as nonheterosexual can have the same social ostracism costs as those afforded to LGB individuals. For example, persons interacting with an LGB individual experience similar discrimination as LGB men and women: Heterosexual men display increased negativity toward another man seen interacting with a gay man – they feel less comfortable interacting with the stigmatized man, rate him as less social and civil, and even socially distance themselves from him by rating themselves as less similar – than when he was interacting with a heterosexual man (Neuberg et al. 1994).

Heterosexuals are often aware of the potential stigmatization from interacting with LGB men and women (Buck et al. 2013), and the anticipation of stigma by association threatens from associating with LGB men and women predicts anxiety toward LGB individuals (Buck et al. 2013). This anticipation of stigmatization also predicts both physical and psychological avoidance of same-sex gay/lesbian individuals. For example, stigma by association concerns predicts an increased desire to avoid interacting with a same-sex gay/lesbian person (Plant et al. 2014) or roommate (Buck et al. 2013). Buck et al. (2013) induced threats of stigma by association by randomly assigning heterosexual participants to create an LGB-supportive poster and either sign their name (stigma by association condition) or not (control), which elicited public avoidance of LGB people as assessed by refusal to sign a petition for LGBT rights. Swim et al. (1999) examined women's use of social distancing to avoid stigma by association. Women participated in a panel comprised of two male confederates and one female confederate; the female was either a lesbian or presumably heterosexual. Each panel member publicly reported their preferences to a

series of questions, and whether the participant's response was different from the female confederate indicated public social distancing. Highly prejudiced women's responses more frequently differed from the female confederate posing as lesbian than as heterosexual, suggesting they used social distance to avoid stigma by association.

Threats to mating autonomy. Perceived unwanted sexual interest from certain sexual orientation targets concerns many heterosexual individuals. For example, when asked to imagine a negative interaction with a gay man, the most prevalent scenario generated by heterosexual men involved unwanted sexual interest (42% of scenarios generated; McDonald et al. 2014). Furthermore, a primary concern reflected in heterosexual women's stereotypes about lesbians is that lesbians seduce heterosexual women (Eliason et al. 1992).

Pirlott and Neuberg (2014) measured perceptions of unwanted sexual interest by asking heterosexual college students to rate their own sexual interests toward heterosexual, bisexual, and gay/lesbian male and female targets as well as their perception of each of these groups' general sexual interest in heterosexual people of their same sex. They calculated sexual interest discrepancies by subtracting the perceivers' own sexual interests in the target group from their perceptions of the target groups' sexual interests in heterosexuals of their same sex, for each group. Heterosexual women perceived bisexual men, bisexual women, and lesbians to pose threats of unwanted sexual interest, yet not heterosexual men (mutual sexual interest targets) or gay men and heterosexual women (mutual disinterest targets). Heterosexual men perceived threats of unwanted sexual interest from gay and bisexual men but not from heterosexual men (mutual sexual disinterest targets) or from heterosexual and bisexual women (mutual sexual interest targets) or lesbians (unreciprocated sexual interest targets).

Perceptions of unwanted sexual interest map onto prejudices toward certain sexual orientation targets. Pirlott and Neuberg (2014) found that heterosexual female participants expressed more negativity toward bisexual men, bisexual women,

and lesbians (unwanted sexual interest targets) relative to heterosexuals and gay men (mutual sexual interest/disinterest targets). Heterosexual male participants also expressed more negativity toward gay and bisexual men (unwanted sexual interest targets) relative to heterosexuals, bisexual women, and lesbians (mutual sexual interest/disinterest targets), and perceptions of unwanted sexual interest mediated the relationship between sexual orientation groups and general negativity (Pirlott and Neuberg 2014). Further research demonstrates that heterosexuals avoid same-sex gay/lesbian individuals, particularly in potentially intimate situations. Imagining a same-sex gay/lesbian roommate increased likelihood of private avoidance of that roommate relative to a heterosexual roommate (Plant et al. 2014), which could serve to minimize threats of unwanted mating.

Conclusion

Stereotypes, prejudices, and discrimination against LGB individuals are not *evolved*, *per se*. The human social psychology of cognition, emotion, and behavior, however, evolved in response to recurrent threats to and opportunities for survival and reproduction. Consistent recurrent threats to physical safety, sexual autonomy, health, ingroup functioning and group living, parenting, and mating, for example, exerted significant selection pressures on humans to evolve a threat management system (Schaller and Neuberg 2012) to detect and respond effectively to perceived threats and opportunities in the environment, including those posed by other people.

Accordingly, although the stereotypes, prejudices, and discriminatory behaviors against LGB individuals are not evolved, the perception of and affective and behavioral responses to the threats (and opportunities) attributed to LGB individuals are evolved. As discussed above, heterosexuals believe certain LGB men and women pose threats to health, child socialization, ingroup norms and values, status via stigma by association, and sexual autonomy via unwanted sexual interest. The stereotypes of LGB individuals convey perceived

threat and opportunity affordances, which elicit specific affective and behavioral reactions to functionally respond to these affordances, as predicted by evolutionary theory. Perceived threats to health predict elevated disgust toward gay men and contamination-avoidant and cleansing behavior (Cottrell and Neuberg 2005; de Zavala et al. 2014). Perceived threats to child socialization predict elevated prejudices and sequestering children from LGB individuals (Filip-Crawford 2015; Gallup 1995; Henry and Reyna 2007; Lehmiller et al. 2010; Reyna et al. 2014; Vescio and Biernat 2003). Perceived threats to ingroup norms and values predict increased negative prejudices, disgust, and aggression against LGB individuals, as a way to prevent the social influence and block counter-normative behaviors of LGB individuals (Blashill and Powlisha 2009; Brambilla and Butz 2013; Cottrell and Neuberg 2005; Crawford et al. 2014; Franklin 2000; Filip-Crawford 2015; Gordon and Meyer 2007; Lehmiller et al. 2010; Vescio and Biernat 2003). Perceived threats undermining social status (e.g., appearing gender nonnormative or non-heterosexual) via stigma by association predict anxiety and public avoidance of LGB individuals to minimize potential stigmatization (Buck et al. 2013; Plant et al. 2014; Swim et al. 1999). Perceived threats to sexual autonomy predict elevated negativity and desires to avoid these individuals in potentially intimate situations to minimize the risk of unwanted sexual activity (Pirlott and Neuberg 2014; Plant et al. 2014).

In conclusion, although the research exploring prejudice toward nonheterosexuals (i.e., homophobia or sexual prejudice) is somewhat recent and less extensive than research on race- or ethnicity-based prejudices, this does not undermine the evolutionary underpinnings of the stereotypes, prejudices, and discriminatory behavioral responses toward LGB individuals. Stereotypes relevant to prejudices and discrimination reflect perceived threats to survival and reproduction. These perceived threats engage affective and behavioral responses designed to mitigate these threats. This functional set of cognitive, affective, and behavioral responses arise reliably from evolved mechanisms. Using an evolutionary

approach to examine LGB prejudices and inter- and intra-group dynamics more broadly provides a powerful framework for truly understanding human behavior.

Cross-References

- Genetic Hypotheses of Homophobia
- Homophobic Bullying
- Outcomes of Homophobic Abuse
- Sexual Prejudice (Personality Correlates of)
- Social Hypotheses of Homophobia

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Homophobic Bullying

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Synonyms

Antigay bullying; Homophobic victimization; LGB victimization; Negative school climate

Definition

Experiences of harassment or discrimination on the basis of actual or perceived sexual minority status.

Introduction

Lesbian, gay, and bisexual (LGB) youth show a number of health disparities relative to heterosexual youth, including greater psychological distress, suicidality, sexual risk behaviors, and substance use (Kann et al. 2016; Saewyc 2011). Similar patterns have been identified for transgender youth, although less is known about this population due to the lack of items to identify transgender respondents in population-level surveys (Reisner et al. 2016). A substantial body of research has linked these disparities with experiences of homophobic bullying and victimization (e.g., Collier et al. 2013; Kosciw et al. 2014). Homophobic bullying can take a variety of forms (e.g., verbal harassment, physical assault) and is experienced differentially by subgroups of LGBT youth. School climate also plays an important role in shaping LGBT youths' experiences of homophobic bullying, and supportive resources can promote resilience among LGBT youth.

Prevalence of Homophobic Bullying

Homophobic bullying can take a variety of forms. A nationwide survey of lesbian, gay, bisexual, and transgender (LGBT) students conducted by the Gay, Lesbian, and Straight Education Network (GLSEN) in 2013 examined some of the most common forms, including hearing biased language (e.g., "That's so gay") and anti-LGB remarks (experienced by 71% of LGBT youth in the past year), verbal harassment (e.g., name-calling or verbal threats, experienced by 74% of LGBT youth in the past year), physical harassment (e.g., pushing or shoving, experienced by 36% of LGBT youth in the past year), physical assault (e.g., being punched, kicked, or injured with a weapon, experienced by 17% of LGBT youth in the past year), and cyberbullying (e.g., verbally harassing or anti-LGB text messages or social media posts, experienced by 49% of LGBT youth in the past year). A more recent population-level survey found similar patterns: LGBT youth reported higher prevalence rates of bullying on school property, electronic bullying, feeling

unsafe at school, and a number of other violence indicators relative to heterosexual youth (Kann et al. 2016). Although peers were the most common perpetrators of homophobic bullying, 51% of LGBT youth reported hearing teachers or school staff making homophobic remarks (Kosciw et al. 2014). Encouragingly, the GLSEN survey also found that experiences of homophobic victimization are declining over time as social attitudes about sexual minorities change (Kosciw et al. 2014). This may reflect the links scholars have drawn between homophobic bullying, societal attitudes, and broader relationships to structures of power (Payne and Smith 2013).

Demographic Differences in Homophobic Bullying

Although LGBT youth experience higher levels of homophobic bullying than heterosexual youth, research also documents variation between subgroups of LGBT youth. Youth who are questioning their sexual orientation experienced higher homophobic teasing and peer victimization than LGB or heterosexual youth (Birkett et al. 2009). Bisexual youth and youth who report both male and female sex partners, particularly boys, reported more fighting, skipping school due to feeling unsafe, property theft, or damaged than lesbian, gay, or heterosexual youth (Russell et al. 2014). LGBT youth of color experienced greater victimization than white LGBT youth. Also, middle school students experienced greater victimization than LGBT high school students (Kosciw et al. 2014). Middle school appears to be a period of elevated developmental risk, as LGBT middle school students reported lower access to supportive resources, lower school belongingness, and higher truancy than high school students (Kosciw et al. 2014; Robinson and Espelage 2011). There is also evidence that although more overt forms of homophobic bullying decline across development, more indirect forms persist into adolescence (Russell et al. 2014). Homophobic bullying may also be experienced by children of LGBT parents (Clarke et al. 2004; Kosciw and Diaz 2008), and additional research is needed to understand the experiences of these students.

Students in different educational contexts also reported different prevalence rates of homophobic bullying. LGBT students in public schools reported higher victimization than students in private or religious schools (Kosciw et al. 2014). LGBT students in rural or small town schools reported higher victimization and fewer supportive resources than students in urban schools (Kosciw et al. 2014). Across the United States, LGBT students in the South and Midwest reported higher levels of homophobic victimization than LGBT students in the Northeast and South; LGBT students in the South also reported fewer supportive resources than students in other regions (Kosciw et al. 2014).

In addition to experiences of victimization on the basis of sexual orientation, youth may experience bullying on the basis of actual or perceived gender minority status. Transgender youth experience a range of forms of bullying on the basis of gender expression (Kosciw et al. 2014). Additionally, violation of gender norms may drive many instances of bullying for both sexual and gender minority students (Payne and Smith 2013). Research is needed to better understand the experiences of transgender students and to examine how homophobic bullying and bullying on the basis of gender identity and expression may intersect and overlap.

Impact of Homophobic Bullying

Homophobic bullying has been linked with a number of adverse outcomes for LGBT youth, including psychological well-being, attendance and academic achievement, and educational aspirations and future plans. In terms of psychological well-being, it has been associated with greater depression, traumatic stress, alcohol and substance use, and suicidality as well as lower self-esteem (Collier et al. 2013; Kosciw et al. 2014). In terms of school attendance and academic achievement, LGBT youth who experienced high levels of past-year victimization had lower grade point averages (GPAs) and were three times more likely to miss school in the past month than youth with low levels of past-year victimization (Kosciw et al. 2014). Other research has found that homophobic bullying is associated with higher truancy

and lower school belonging (Collier et al. 2013) and that feeling unsafe in school mediated the relationship between identifying as a sexual minority and experiencing higher truancy and lower grades (Birkett et al. 2014). In terms of educational aspirations and future plans, LGBT youth who experienced high levels of past-year victimization were twice as likely to report not planning to pursue post-secondary education than LGBT youth with lower levels of past-year victimization (Kosciw et al. 2014). As homophobic bullying impacts both short-term (e.g., attendance and achievement) and long-term (e.g., educational aspirations and future plans) academic outcomes, it likely leads to disruptions in LGBT youth's educational trajectories (Collier et al. 2013).

Although it is important to understand how experiences of homophobic bullying lead to negative outcomes for LGBT youth, it is also important to highlight that many LGBT youth demonstrate resilience despite these experiences. In fact, most sexual minority youth thrive and achieve health and well-being similar to heterosexual youth, despite greater experiences of adversity and risk factors (Saewyc 2011). To understand these processes of resilience, research is needed that attends to contextual factors, particularly protective factors. Research on school climate has provided important contributions in this area.

Homophobic Bullying and School Climate

School climate is important to understanding homophobic bullying, as school climate has been found to moderate the relationship between homophobic bullying and negative psychological outcomes (with students in more positive school climates experiencing fewer negative outcomes; Espelage and Swearer 2008; Hatzenbuehler et al. 2014). Similarly, school-based supportive resources are associated with lower victimization and better academic outcomes for LGBT students (Kosciw et al. 2013). Incorporating a focus on school climate is consistent with a social-ecological approach, which underscores the role that risk and protective factors play on multiple levels (e.g., families, schools, communities, societies) in shaping the impact of bullying on LGBT

youth (Hong and Garbarino 2012; Hong and Espelage 2012).

In addition to moderating the impact of homophobic bullying on psychological and academic outcomes, school climate may play an important role in shaping responses to homophobic bullying. Most LGBT students (57%) who experienced harassment or assault in school did not report this experience, primarily because they doubted this would result in effective intervention. This perception appears to be founded, as most LGBT students who did report the experience (61%) said that school staff did nothing in response (Kosciw et al. 2014). More effective school responses to homophobic bullying are an important area of future growth to foster more positive school climates and more positive outcomes for LGBT youth.

Similar to demographic differences in experiences of homophobic bullying, demographic differences in perceptions of school climate have been found. Transgender youth report the most hostile school climates of all sexual and gender minority groups (Kosciw et al. 2014). In terms of sexual orientation, questioning students report a less positive school climate than LGB or heterosexual youth. Both school climate and homophobic teasing moderated the relationship between sexual orientation and depression, substance use, and truancy, with questioning youth who reported more negative school climates or higher levels of homophobic teasing most likely to report negative outcomes (Birkett et al. 2009).

Several kinds of resources that contribute to a more positive school climate for LGBT students have been identified, including anti-bullying policies, gay-straight alliances (GSAs), and other LGBT-related student organizations, inclusive curricula, and supportive school personnel (Hatzenbuehler et al. 2014; Kosciw et al. 2014). The most recent GLSEN School Climate Survey found that LGBT youth have reported an increase in all of these forms of support over time (Kosciw et al. 2014). In terms of anti-bullying policies, most LGBT students (82%) reported their school had an anti-bullying policy; however, only a small minority (10%) reported the presence of a comprehensive policy that included sexual orientation

and gender identity (Kosciw et al. 2014). In terms of GSAs and student organizations, half of LGBT students reported the presence of a GSA or similar organization in their school. Those students who reported the presence of such a student organization reported higher levels of school connectedness and lower levels of homophobic bullying (Kosciw et al. 2014). Other research has found that students in these schools also reported improved mental health and lower harassment (Saewyc 2011). In terms of inclusive curricula, a minority of students reported being taught positive representations of LGBT people or history (19%), and almost as many (15%) reported being taught negative representations (Kosciw et al. 2014). Additionally, curricula that do address LGBT people or issues may do so only in superficial, limited, or problematic ways, such as through onetime events or representations that reinforce pathological representations of LGBT people (Payne and Smith 2013). Finally, in terms of supportive school personnel, almost all LGBT youth (96%) could identify at least one supportive school staff member; however, less than two-thirds (61%) could identify at least six (Kosciw et al. 2014). Supportive school personnel are an especially important resource, as support networks are important buffers of the impact of homophobic bullying on LGBT youth (Espelage and Swearer 2008).

Conclusion

LGBT youth report a range of forms of homophobic bullying, including antigay remarks, verbal and physical harassment, and cyberbullying. Some subgroups are especially at risk for homophobic bullying, including LGBT youth of color, questioning and transgender youth, and middle school students. School climate plays an important moderating role, with students in more positive school climates reporting more positive health outcomes. A number of factors contribute to more positive school climate, including anti-bullying policies, LGBT-related student organizations, inclusive curricula, and supportive school personnel.

Cross-References

- [Bullying](#)
- [Cyberbullying](#)
- [Homophobia](#)
- [Outcomes of Homophobic Abuse](#)
- [Procedures for Dealing with Bullies](#)

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Homophobic Victimization

- [Homophobic Bullying](#)

Homosexual Behavior

- [Homosexual Receptivity](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Same-Sex Sexual Behavior](#)

Homosexual Orientation

- [Lesser-Known Theories of Homosexuality](#)

Homosexual Preference

- [Lesser-Known Theories of Homosexuality](#)

Homosexual Receptivity

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Synonyms

[Homosexual behavior](#); [Intra-sex sexual behavior](#); [Same-sex sexual behavior](#)

Definition

Courtship displays, mounting and/or genital contact, and stimulation between same-sex individuals.

Introduction

Various authors use different definitions of homosexual behavior. The one used is after Sommer and Vasey (2006). Bagemihl (1999) characterizes homosexual behavior in terms of courtship, affection, interactions involving mounting and genital contact, pair bonding, and parenting activities between same-sex individuals. More recently, Poiani (2010) defines homosexual behavior as an interaction that is sexual or of sexual origin and that is performed between two or more individuals of the same sex. He distinguished homosexual behavior from homosexuality, which is a sexual orientation characterized by sexual attraction to individuals of the same sex.

Homosexual Behaviour

Homosexual behavior either in males or females is common and widespread among social

nonhuman species (Bagemihl 1999; Poiani 2010; Sommer and Vasey 2006). It is rarely associated with sexual orientation, however. Domestic sheep *Ovis aries* is so far the only mammalian species where spontaneous sexual orientation of up to 10% of rams to other males has been repeatedly reported (Perkins and Fitzgerald 1992). The proximate causes of same-sex preferences may be induced by specific situations. Steroids and other hormones, genetic and epigenetic mechanisms modified by stress during prenatal or perinatal period have been shown to have potential to induce homosexuality mainly, but not only, in mammalian males (Balthazart 2016). Also, early postnatal social environment such as removal of other sex from the rearing environment that affected sexual orientation in some mammals and birds has been reported (Poiani 2010).

In most of the cases, animal homosexual behavior is not associated with sexual orientation and the animals involved may and do reproduce. There are numerous situations when depriving individuals of members of the opposite sex causes them to engage in sexual interactions with members of the same sex. Though, when the deprivation is ceased, such formerly deprived animals immediately renew regular heterosexual behavior (Bailey and Zuk 2009). Still, most of the cases of homosexual behavior in animals are not primarily associated with clear sexual context. Understanding social relations requires correct interpretation of the significance of such behavior. While male-male mounting is a common behavior, female-female mounting is also widespread. For some farm ungulates, intra-female mounting has been understood to be a normal element of behavior associated with estrous aimed to signal to males the female is ready to mate. However, observations of female-female mounting outside the rut have been frequently reported as well. Female bonobos, *Pan paniscus*, for example, embrace frequently each other ventroventrally and rub their genital swellings against each other (Hohmann and Fruth 2000). Hohmann and Fruth (2000) observed bonobo females and investigated five hypotheses on the function of this behavior. During 5-year-lasting study, they found support for multifunctional origin of the behavior, most of

all to reconciliation and social tension regulation. They concluded that genital contacts may express quality and dynamics of dyadic social relationships among female bonobos. Similar function can also be seen in many other primate species where homosexual behavior also often promotes alliance formation between sexual partners.

Same-sex mounting in socio-sexual context has been classically suggested to signal dominance. It was first suggested for primates, but later also for many other taxa. When reviewing literature, there are a number of papers supporting dominance signaling hypothesis. On the other hand, many other reports are not consistent with the view that actors are dominant and recipients subordinate (short review in Bartoš and Holečková 2006). The dominant individuals mount subordinates, solicit mounting by subordinate conspecifics, or prevent subordinate to mount them. Opposition against being mounted may but need not occur. As a result, there is a wide variation between as well as within species in who is mounting whom and how the mounted individual responds. Thus, who mounts whom may, in fact, reflect decision of the dominant individual involved rather than signaling the dominance per se.

What is misleading with dominance signaling hypothesis is that even when a dominant male mounts subordinate one, male-male mounting can be associated with penile erection, occasionally anal intromission, and ejaculation. In this context, erection has been regarded as indicative of sexual arousal and thus evidence of a sexual motivation underlying same-sex mounting (Bagemihl 1999). Moreover, mounting is apparently testosterone dependent, because bulls mounted others more frequently than steers, male-male mounting of fallow deer bucks was associated with the start of a seasonal increase in testosterone levels following seasonal minima (Bartoš and Holečková 2006), and testosterone treatment of cows increased their mounting behavior (Bouissou 1978). Here it should be emphasized that there is also a lot of obviously nonsexual situations such as serious fighting associated with penile erections (e.g., Bartoš and Holečková 2006). This seeming

contradiction may most likely lie in a mix-up of motivations. For example, androgens, testosterone in particular, in males shape and modify sexual as well as agonistic behavior (Michael and Zumpe 1993). Therefore, it frequently happens that some elements of behavior typical for sexual behavior can occur in agonistic context and vice versa regardless if such a behavior was functional or even dangerous. Moreover, it is also known that disturbance and tension associated with a stressful situation can be linked to mounting. Thus, penile erections, anal intromission, and ejaculation during male-male mounting cannot be taken as real evidence of sexual motivation. Rather, it might be attributed to excitement associated with serious fighting (Bartoš and Holečková 2006).

Conclusion

In conclusion, same-sex orientation in non-human animals is extremely rare. In contrast, same-sex sexual behavior is quite common. It does not seem to have any special, exclusive function. In particular, it cannot be clearly linked to roles of a dominant actor and subordinate recipient. Instead, intra-sex behavior is likely to be a consequence of deprivation from the other sex or a side effect of excitement, not necessarily sexual. Hence, depending on circumstances, various proximate factors and ultimate functions may be involved.

Cross-References

- [Alloparenting and Female Same-Sex Behavior](#)
- [Ancient Homosexuality](#)
- [Female Homosexuality and Bisexuality](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Hormonal Component of Homosexuality](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Non-Western Homosexuality](#)
- [Same-Sex Sexual Behavior](#)

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Homosexuality

- [Sexual Orientation and Human Sexuality](#)

Homosexuality Paradox, The

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Synonyms

[Evolutionary puzzle of homosexuality](#)

Definition

The heritable components of human homosexuality are not immediately explicable according to basic evolutionary principles because they entail reduced average individual reproductive success relative to alternative genotypes.

Introduction

Evolutionary psychology generates research questions by considering the ancestral survival and reproductive challenges faced by humans and human ancestors. At the heart of evolutionary thinking is reproductive success, as every trait informed by genetics must allow for its own replication in the next generation. For example, a genetic mutation that causes early death or sterility will not replicate under normal circumstances and is thus quickly removed from the population. Less extreme cases of limited reproductive success also tend to be outcompeted by prevailing alternatives. If a mutation merely reduces fertility (i.e., lower probability of fertilization at each copulation, all else equal), one may expect it to be outcompeted by alternatives and exit the gene pool after some number of generations. Homosexuality appears to be a trait that, like sterility or reduced fertility, reduces the likelihood of reproduction. One can think of exclusive homosexuality as analogous to sterility and non-exclusive homosexuality as analogous to reduced fertility. This has led researchers to wonder how homosexuality continues to appear at a relatively consistent rate in the human population. Strictly speaking, a paradox is an inconsistent or logically contradictory premise; the maintenance of homosexuality is better described as a puzzle or a mystery, since a solution exists, even if it is not forthcoming. Before looking at how researchers have responded to this puzzle, it is necessary to consider whether it is appropriate to apply evolutionary thinking to homosexuality in the first place.

Williams (1966) encouraged evolutionary thinkers to avoid invoking evolutionary theory whenever simpler mechanisms are sufficient in explaining a phenomenon. If the expression of

homosexuality is not influenced by genetics or other heritable elements, then evolution will not help explain its existence. If the expression of homosexuality is not common or culturally universal, then evolution may be unnecessary to explain its existence. Likewise, if the expression of homosexuality is not an ancestral human condition, evolutionary theory may be unnecessary. Finally, if the expression of homosexuality does not reduce reproductive success relative to alternatives, then it is not fundamentally mysterious according to evolutionary theory. Evidence regarding each of these conditions is discussed ahead.

Does Homosexuality Have Heritable Components?

Heritability estimates (h^2) describe the proportion of phenotypic variance that is attributable to genetic relatedness. These estimates are calculated by looking at the probability of expressing a particular phenotype (in this case, homosexual identification) as a function of genetic relatedness to others who express that phenotype (in this case, homosexual relatives), compared to the probability of expressing the phenotype in the general population. In other words, a trait is heritable to the extent that it is more likely to reoccur within families than between unrelated people. Especially useful for these estimates is data on identical twins who were reared apart and thus did not also share identical developmental environments. Depending on the methods and statistical assumptions used, twin studies provide heritability estimates between roughly $h^2 = 0.3$ and 0.6 for men and $h^2 = 0.2$ and 0.7 for women (e.g., Alanko et al. 2010). These are considered moderate to large estimates for psychological variables; personality variables cluster around $h^2 = 0.5$ and intelligence is between $h^2 = 0.5$ and 0.8 . As long as a trait is heritable, it can be subject to natural selection; thus, it is irrelevant in this context where the genes that contribute to homosexuality are located or what they do. That said, one popular hypothesis for males is that differences in genes on the X chromosome of mother and child cause developmental feminization of male brain

regions involved in sexual behavior (Mustanski et al. 2005). No specific genetic hypotheses are available for females, although prenatal androgen exposure appears to be important.

Is Homosexuality Universal and Frequent?

Rates of homosexual identification vary by region, but anthropological studies in every region of the world find homosexual expression of some description. These expressions can differ wildly. Egalitarian homosexuality is the predominant form in modern Western societies, wherein two adult, gender-typical individuals enter into short- and long-term sexual relationships. However, transgendered forms of homosexuality, wherein homosexuals adopt opposite-sex gender roles and appearance from a young age, have also been well documented in populations like the *fa'afafine* of Samoa, the *hijra* of India, the *kathoey* of Thailand, and the *berdache* of Native America. Some researchers argue that transgendered homosexuality represents the more ancestral form of male homosexual expression, as evidenced by its preponderance in societies with more ancestral cultural practices (VanderLaan et al. 2013). Others argue that the oldest and most widespread form of male homosexual behavior is transgenerational, wherein young men become sexual apprentices to older men until they reach maturity. This form of male homosexual behavior is likely distinct from male homosexuality as a preference for same-aged male partners but has been documented as a common and socially sanctioned practice in cultures ranging from Ancient Greece and Rome; to the Azande and Zulu tribes; to India, Pakistan, and Persia; to Imperial China, Japan, and Korea; to Melanesia, Polynesia, and aboriginal Australia (Greenberg 1988).

Unfortunately, female homosexuality is less well documented by anthropological and historical sources, partly because in many cultures no terminology was developed to define female homosexuality and (relatedly) because female homosexuality has been marginalized by male historical perspectives that disbelieve or discredit female homosexual preferences. Despite these

limitations, female homosexuality is understood to be universal and diverse. Native American women frequently inhabited a similar transgendered homosexual role as homosexual men. For example, the *hwame* of the Mohave possessed unique spiritual faculties, and their marriage to women was viewed as normative (Blackwood 1984). Similar practices are observed in many African societies in Nigeria and Kenya, where women may take on the role of husband and father. Women in Lesotho are known to develop intimate sexual friendships with other women in which they engage in the full range of sexual acts but do not consider their acts sexual because no penis is present. In the West and elsewhere, female homosexuality is expressed in long- and short-term relationships, and females who practice homosexual behaviors range from highly masculine to highly feminine and everything in between.

Like heritability estimates, global rates of homosexuality are imprecise as a result of differences in methods and populations. The best estimates for the number of men who identify as homosexual are between 2 % and 5 %, although somewhere between 5 % and 15 % of men report some attraction or sexual behaviors toward the same sex (e.g., Bagley and Tremblay 1998). Between 1 % and 3 % of women identify as homosexual, although somewhere between 10 % and 15 % report some attraction or sexual behaviors toward the same sex (Mercer et al. 2007). Non-heterosexual women are more likely to report being bisexual or queer, whereas non-heterosexual men are more likely to report being exclusively homosexual. This has led to the suggestion that females experience greater “sexual fluidity” than males (Diamond 2009). Regardless, rates of both male and female homosexuality are greater than would be expected to be the result of random mutation, and the breadth of cultures in which homosexuality is found recommends that it is not the result of particular environments.

Does Homosexuality Reduce Reproductive Success?

Western male homosexual identification is associated with roughly a third the number of

offspring that are had by heterosexual males. Males who identify as homosexual are much more likely than heterosexual males to never have offspring, and when they do, they tend to have fewer across the life span (Schwartz et al. 2010). Data on females suggests that homosexuality is associated with about a 20–30 % chance of at least one offspring, compared to an 80–90 % chance of motherhood in the general population (Morris et al. 2002). However, when thinking about the evolution and maintenance of a trait, one must not confuse current reproductive outcomes with the ancestral reproductive outcomes that prevailed for the vast majority of human existence. Measuring reproductive success in industrial cultures across the last several decades says almost nothing about the ancestral conditions in which the trait was designed by natural selection to replicate itself. For example, modern obese Americans have shorter life spans than the nonobese, but this does not cause scientists studying obesity to rule out adaptive theories for the development of genes that promote slow metabolism and the accumulation of body fat. Rather than recording current reproductive success as a benchmark of adaptiveness, considering how a trait may have been expressed and the outcomes of that expression in ancestral environments can be more illuminating.

One window into ancestral reproductive success is simply to look at patterns of sexual attractions that would have encouraged or discouraged mating in ancestral environments. Male sexual desire is usually considered category specific, strongly favoring either one sex or another (Chivers et al. 2005), such that there is a negative correlation between sexual attraction toward one sex and toward the other sex and men of all orientations with higher sex drives have more sex with a single preferred sex (Lippa 2007). This is not true of females, who show a weak positive correlation between attraction to one sex and the other (Lippa 2007). Looking across women of all orientations, the number of past sexual partners of one sex is positively correlated with the number of past sexual partners of the other sex (in contrast to a negative correlation in men; Kanazawa 2016). This may suggest that women who express same-sex attraction and

engage in more same-sex activities also report greater opposite-sex attraction and engage in more opposite-sex activities, potentially improving reproductive outcomes. However, this description may not apply to exclusively homosexual women, who show reduced attraction to males as a function of their attraction to females (Lippa 2007). In general, homosexual males express sexual attractions and behaviors that can be expected to have reduced reproductive success in ancestral environments, but it is less clear whether ancestral females would have suffered reduced reproductive success as a result of same-sex attractions.

Is Homosexuality an Ancestral Condition?

Comparative research has identified thousands of species that engage in homosexual acts, from house flies, beetles, and dragonflies; to shorebirds, geckos, and sunfish; to dogs, dolphins, and elephants. The particular practices, apparent purposes, frequencies, and phylogenies vary as widely as one could expect for a set of behaviors that span so many taxa. In almost every case, however, individual homosexual acts represent an infrequent, contextual, or strategic deviation from a typically heterosexual repertoire. The few exceptions to this include the domesticated male sheep (rams), of which only about 75 % show interest in mating with females, about 15 % show no mating interest whatsoever, and about 10 % are strictly interested in mounting other males. Among the apes, homosexual contact is frequent, particularly in our closest relatives, the chimpanzee and bonobo. Male-male cohorts dominate chimpanzee social structures and female-female cohorts dominate bonobo social structures; in both species, homosexual contact is used to maintain relationships, facilitate cooperation, and signal social dominance or submission (de Waal 1982). A recent phylogenetic analysis discovered that the frequency of same-sex genital interactions in primates is associated with social complexity and that male and female same-sex genital interactions may evolve independently (Fernandes et al. [in press](#)).

Deciding whether the character of human homosexual expression has changed substantially across the past several thousand years requires some speculation, but that humans have expressed some form of homosexual attraction and behavior since our common ancestor with the extant primates is nearly indisputable. Debate surrounds the translation and interpretation of texts and artworks that appear to describe homosexuality, but the debate centers on the exact nature of those sexual relationships, their exclusivity, and how they were perceived, not whether same-sex relationships occurred. It is an open question, for example, just how exclusively homosexual men and women may have been in ancestral hunter-gatherer societies. Across recorded history there have existed cultural entities that form in celebration of homosexual desire (e.g., the sixteenth century *mignons* of France, the seventeenth century *fanchonos* of Portugal, and the seventeenth through twentieth century *mollies* of England; Fone 2000). The term “homosexual” was coined at the emergence of the first large-scale homosexual cultural movement in the late nineteenth century in protest of German anti-sodomy statutes and has served to unite individuals under a broad conception of sexuality. When thinking about ancestral forms of homosexuality, cultural identities and sexual norms may not be applicable. For example, in ancestral communities on the scale of 20–80 individuals, perhaps no more than a couple of homosexuals of either sex would be present. These men and women would have been disconnected from an understanding of sexual variance and identity. Sexual norms likely included sexual fidelity and consent, but one can only speculate whether concepts of categorical sexual preferences or disgust toward same-sex activity were ancestrally significant.

As described, female sexual fluidity may suggest that the genes associated with homosexuality in females may not have suffered greatly reduced reproductive success in ancestral environments. A promising hypothesis for female homosexuality will be outlined ahead, but the high frequency of apparently exclusive homosexuality among males poses a greater challenge. The following two sections present evidence regarding whether human

male sexual orientations are fundamentally exclusive, i.e., psychological and behavioral data may help illustrate how male sexuality would have been expressed in ancestral environments.

Evidence Against Male Sexual Fluidity

Western men’s reported sexual orientation skews toward exclusivity, producing a bimodal distribution clustering on exclusive heterosexuality and exclusive homosexuality. This distribution is corroborated by implicit, physiological, and neural measures of sexual attraction in men. Self-reported sexual identity tends to match implicit associations of male and female stimuli as sexual targets in the implicit association task, with homosexual men showing rapid associations between sexual categories and male, more than female, stimuli (in contrast to heterosexually identified men; Snowden and Gray 2013). Several studies show that self-reported identity also aligns with penile arousal responses, with homosexual men showing larger responses to male stimuli than female stimuli and bisexual men showing no difference in response to male and female stimuli (Chivers et al. 2005). Regarding neural responses, the broad activity patterns of self-identified homosexuals exposed to male stimuli measured in an fMRI are similar to those of heterosexuals exposed to female stimuli, and differences in activity between preferred and non-preferred stimuli are similar in magnitude for heterosexuals and homosexuals (this study also found no evidence for conscious inhibition). Additionally, a taxometric analysis of sexual orientation in a sample of 14,118 American men demonstrates that homosexuality is a nonarbitrary sexual taxa defined by broad uniformity in sexual behaviors and attractions as well as mental health variables (Norris et al. 2015). Heterosexual and homosexual men report similarly stable sexual attractions across 6- and 10-year periods, whereas homosexual women and bisexual men and women show less stable sexual attractions (Savin-Williams et al. 2012).

Evidence in Support of Male Sexual Fluidity

Individuals of all orientations report overlapping and inconsistent sexual identities, behaviors,

and attractions, with anonymous and non-categorically framed studies showing higher reported identity-inconsistent sexual feelings. Just over half of exclusively heterosexual men and all homosexual men in a college sample reported questioning their sexual identity, indicating experiences ranging from hypothetical thoughts to sexual exploration (Morgan et al. 2010). Several studies have reported that just over half of self-identifying homosexual men report having had heterosexual sex at some time (e.g., 64 %, Whisman 1996). Whisman also found that 45 % of homosexually identified men report having had a romantically meaningful heterosexual relationship. In a longitudinal study of New Zealanders, among men who reported same-sex attraction at age 21, only half reported same-sex attraction at the final assessment at age 26 (Dickson et al. 2003). In a large retrospective study assessing lifetime sexual partners, 90 % of the 5.8 % of men who had at least one same-sex sexual partner since puberty also had at least one opposite-sex sexual partner during that time (Laumann et al. 1994). Although only 0.58 % of sexually active men studied by Laumann et al. reported exclusively homosexual sex since puberty, more than four times that percentage (2.4 %) reported exclusive attraction to the same sex, and 2.0 % reported a homosexual identity. These data suggest that behavioral bisexuality is common among men who identify as homosexual even if such behavior is transient or contextual.

Thus, homosexual and heterosexual identities are, for modern Western men, statistically and personally reliable and honest predictors of sexual attractions and behaviors. Yet the evolutionary and developmental sources of these patterns remain unclear, and when the boundaries of sexual identities are probed, inconsistency and diversity can be found. There is no consensus regarding how to interpret male sexual orientation; some researchers imply that ancestral male sexualities resembled modern categorical identities, and others argue that ancestral male sexuality was likely to be more fluid than modern identities suggest.

Is There an Evolutionary Puzzle?

Homosexuality in humans is heritable (Alanko et al. 2010; Mustanski et al. 2005) and currently responsible for reduced fecundity (Schwartz et al. 2010). In addition, human homosexuality is prevalent (Bagley and Tremblay 1998), and same-sex attractions and behaviors are ancient and likely to be deeply ancestral. These facts constitute an evolutionary puzzle, one that has generated fascinating evolutionary hypotheses and fruitful research avenues.

Proposed Solutions

There are several compelling theories for the maintenance of human homosexuality. Some of these theories describe homosexuality as the result of genetic abnormalities, developmental instability, social irregularity, or a pathogen. These hypotheses are interesting, if speculative, but the purpose of this discussion will be to review testable evolutionary hypotheses for human homosexuality. While male and female homosexuality both appear to have genetic components, the associated genes and etiology of homosexuality are believed to differ between the sexes. In particular, there exist reliable prenatal and childhood predictors of homosexuality in men, for example, greater numbers of older brothers and more female-typical interests are positively associated with homosexual identification (Bogaert 2006). Female homosexuality is more difficult to predict, has greater variability in its expression, and may evolve independently from male homosexuality (Alanko et al. 2010; Fernandes et al. *in press*). Differences of this kind may be attributable to differences in the selection pressures faced by ancestral males and females or differing modern cultural pressures (or both). Consequently, evolutionary theory may be applicable to both male and female homosexuality, but there is little reason to expect identical theoretical considerations. Thus, male and female hypotheses are presented separately. It could be argued that male homosexuality is more difficult to explain in an evolutionary framework. This is not only because females

show higher levels of sexual fluidity but also because male mating strategies benefit more than female sexual strategies from rapid, repeated, and diverse opposite-sex copulations. Thus, homosexual men who would refuse sex with women may be further removed from their maximally successful reproductive strategy than are homosexual women. Perhaps as a consequence, there exist more diverse hypotheses for the evolution of male homosexuality, although this may also be because there are more male researchers investigating these topics.

Male Hypotheses

The sexual antagonism hypothesis proposes that the genes that contribute to homosexuality in men facilitate reproductive success when expressed in women. In this view, the expression of male homosexuality is a costly by-product of selection for reproductive adaptations in women. This hypothesis was inspired by the finding that the female relatives of homosexual men show greater fecundity than the female relatives of heterosexual men, particularly in the maternal line (Iemmola and Camperio-Ciani 2009). Several studies have failed to replicate these findings (e.g., Schwartz et al. 2010), but the hypothesis remains tenable.

The overdominance or heterosis hypothesis describes the possibility that homosexuality is reported by men who carry homozygous recessive alleles that, when expressed in the more common heterozygotic form, confer selective advantages (e.g., such men are more cooperative, more lingual, and less aggressive; Zietsch et al. 2008). Here, androphilic men represent the tail of a distribution experiencing selection for a linked set of traits that produce female-typical behavior. In theory, only a small heterozygote advantage is necessary to produce a stable proportion of homozygotes, leading to the persistent, low rate of exclusive homosexuality. Sexual antagonism and overdominance are often supported via computer modeling techniques that allow researchers to set the parameters on a population and to simulate the gene frequencies that unfold over generations. Critics of these techniques argue that such models demonstrate only that the hypotheses are possible given the tidy parameters included in the

model, parameters which are not always empirically validated.

The genes that contribute to male homosexuality may survive via kin selection by supporting the reproductive success of kin who carry copies of those genes. If, by providing care to close relatives, a man enhances the overall reproductive success of his kin group, he may recoup the cost of his abstinence from reproductive sex. Evidence for elevated investment into kin among male homosexuals has been directly demonstrated on the island of Samoa among the fa'afafine (Vasey and VanderLaan 2010) but is not found in Western cultural environments (Rahman and Hull 2005). VanderLaan and colleagues point to elevated childhood separation anxiety in Western homosexual men as a sign that Western men are concerned for kin but may be culturally constrained from providing care. Kin-investing, transgendered forms of male homosexuality are also more frequent in cultures with more ancestral characteristics (smaller communities, simpler agriculture), which may suggest that ancestral male homosexual expressions were maintained via kin-directed investment in the context of transgendered homosexuality (VanderLaan et al. 2013).

The coalitional mating hypothesis emphasizes the comparative evidence for benefits gained by male chimpanzees from male-male alliances built upon sexual favors. The alliance or affiliation hypothesis thoroughly develops the human anthropological evidence for peripheral males gaining status through their sexual relationships with other men (Muscarella 2007). The homosocial hypothesis describes homosexual behavior as a natural extension of male-male and female-female cooperation serving to reduce violent mating rivalries. Underlying these hypotheses is the suggestion that direct, individual, and ultimately reproductive benefits can be gained via sexual behavior as a form of social influence. In other words, these hypotheses recommend that ancestral homosexual expressions were reproductively beneficial in certain social arrangements. Hypotheses of this kind have remained largely untested but are indirectly supported with reference to comparative and anthropological research. For

example, high-status male chimpanzees have been observed allowing low-status male grooming partners to mate with estrus females (de Waal 1982). Grooming between males frequently results in arousal and penile erection, and subordinate males can placate aggression by handling the genitals of dominant males. Similar patterns are observed among female bonobos. Anthropological research provides examples of lower-status human males gaining resources, status, and reproductive access via sexual relationships with higher-status males (Greenberg 1988). These relationships are typically intergenerational or transgendered in context, elevating younger or more feminine males in the mating market through sexual relationships with higher status men.

Female Hypotheses

Evolutionary theories for female homosexuality take a common form, closely resembling the affiliation hypotheses described for men just above. It is typically argued that female same-sex attractions aided ancestral females in creating and maintaining cooperative partnerships with other females. The function of these partnerships may have varied from interpersonal and sexual defense, to alloparenting and reciprocal child care, to status management and mate retention (Diamond 2009; Kanazawa 2016; Kuhle and Radtke 2013). Diamond points to the independence between arousability, or the capacity to become aroused, and proceptivity, or the motivation to initiate sex, in apes that lack conspicuous estrus (signs of fertility). If arousability is decoupled from proceptivity and continuous throughout the menstrual cycle, there is little evolutionary reason for it to discriminate between sexual stimuli of different sexes, i.e., becoming aroused by female stimuli will usually not inflict opportunity or energetic costs. Diamond argues that female sexual fluidity is thus a consequence of reduced pressure to curtail arousability in homo lineages (although she offers no direct adaptive benefits; Diamond 2009). Kuhle and Radtke (2013) highlight the benefits to child-rearing that can be gained by females who are willing to recruit female sexual partners. Bonobo females

provide the clearest nonhuman example of life-long female-female sexual coalitions, the members of which provide significant care to the unrelated offspring of their partners. Bonobo offspring receive basic care such as food sharing, defense, and transportation. These relationships involve sexual activities including genito-genital rubbing which frequently leads to orgasm. Human offspring are particularly altricial, requiring a lengthy and costly period of development before becoming self-sufficient. Without some form of outside care, researchers have argued that ancestral human mothers would have found it extremely difficult to raise offspring, particularly in cases where the father was not present. In modern hunter-gatherer societies, alloparental care from unrelated females (usually other mothers) is common and is associated with improved offspring survival. Sexual activity and especially orgasm promotes associations between the sexual partner, positive sensations, and social-bonding hormones including oxytocin. It is hypothesized that ancestral females took advantage of this capacity to manufacture social commitment in order to facilitate reciprocated child care. Recently, Kanazawa (2016) underscored the conflict resolution functions of same-sex interactions, proposing that in ancestral polygynous arrangements, females who found reliable ways to diffuse conflict would have been better able to collaborate for their own benefit. In other words, women who lacked a capacity for sexual fluidity may have suffered from an inability to function in recurrent polygynous mating situations. Each of these theoretical perspectives seeks to explain female sexual fluidity without necessarily addressing the appearance of exclusive female homosexuality. Exclusive female homosexuality is uncommon, often transient, and appears to be linked to higher than average prenatal exposure to androgens (Savin-Williams et al. 2012). This leads many researchers to consider it inappropriate or unlikely to fit a directly adaptive theory to the phenomenon. Again, one can only speculate as to the influence that social environments and identities may have upon modern sexual orientations, but such effects may be worth considering.

Conclusion

Human homosexuality has puzzled evolutionary thinkers for decades, its existence challenges basic principles of natural selection, and this problem has inspired creative thinking on the topics of ancestral mating patterns, comparative sexuality, reciprocal and kin altruism, and genetic inheritance. Many advances in our understanding of sexuality and mating in general are owed to the study of homosexuality, and it is a research avenue that continually reveals new questions and invites original answers. The study of homosexuality also has unique implications in the social and political world, as homosexuals around the world suffer immeasurably for harboring desires deemed taboo. One hopes that a growing understanding of homosexuality, particularly its evolutionary and developmental origins, will help to illustrate how deeply ancestral, universal, and ultimately healthy same-sex attractions and behaviors are. Progress on this topic is encouraging and indicates that public perception can be effected by conversations in science and that the public are interested in learning more about human sexual variance.

Cross-References

- [Bonobo Sexuality](#)
- [Evolution of Homosexuality](#)
- [Female Homosexuality and Bisexuality](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [George Williams](#)
- [Heritability](#)
- [Homosexuality](#)
- [Human Sexuality](#)
- [Kin Selection](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Non-Western Homosexuality](#)
- [Sexuality](#)
- [Sexual Orientation and Human Sexuality](#)

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Honest Signaling

- ▶ [Costly Signaling Theory](#)
- ▶ [Signal Reliability](#)
- ▶ [Handicap Principle, The](#)

Honest Signalling

- ▶ [Observations of Sexual Dimorphism](#)
- ▶ [Reliability and Deception in Language](#)

Honest Signals

- ▶ [Health Cues](#)

Honesty

- ▶ [Reliability and Deception in Language](#)

Honor Code

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Synonyms

[Honor concern](#); [Moral values](#); [Social identity](#)

Definition

Honor is defined as a person's worth in his/her own and others' eyes (Rodriguez Mosquera et al. 2010). This set of socially accepted norms further

highlights the significance of a person's reputation and social image (Rodriguez Mosquera et al. 2008).

Social and Cultural Underpinnings of Honor Code

According to Pitt-Rivers (2001), honor, simultaneously, is a person's self-reflection and representation of their moral values in the social setting. Consequently, honor is a cohesive measure for determining social identity, which exists in one's interpersonal relationships established in the society. They further added that honor code applicable in a culture regulates individuals by guiding their moral evaluation and judgment of others, influencing people's actions before society, and measuring of social status (Pitt-Rivers 2003). Blincoe and Harris (2011) suggested that we use other people's perception of our social image to draw our own social image in their eyes. Other people's behavior toward us translating respect or disrespect for us is an important indicator in this regard. Such opinions may be a result of our own behavior, or may be behavior/s exhibited by the members of our closest social groups like our family. Moreover, these perceptions may be based on gender roles prevalent in a culture.

Cultures with highly traditional attitudes toward sex-roles associate gender-specific honor trepidations (Rodriguez Mosquera 2011). Moreover, *family honor* refers to a concept, which requires a person to behave in a certain manner, which defends the honor of the entire family as well as improves the reputation-damaging behavior of other family members. A person's reputation significantly revolves around protecting and respecting their family name (Rodriguez Mosquera et al. 2010). Literature associates different factors like importance of family's reputation, the existence of family secrets, and satisfaction of a family with this aspect of respect (Vangelisti 1994) in addition to their tendency not to report sexual attacks (Lewis 2003).

Integrity, on the other hand, is the status of a particular person given to them because of their

fairness in dealings and honesty. This states the image of a person to the social group as loyal and trustworthy (Rodriguez Mosquera et al. 2010). Whereas a person's reputation being assertive as a male gender role, supporting their family, working hard, having sexual capability, and defending themselves against invectives are the measures of their *masculine honor* (Nisbett and Cohen 1996). Many violent crimes and behaviors have been strongly associated to male honor (Guerra et al. 2013), as well as being directly related to other concepts like fearlessness, superiority, respect, and bravery (Neff 2001). On the contrary, *feminine honor* is deemed as the responsibility of a woman to submit to the gender role ascribed to her by her culture and to uphold the reputation by behaving with chastity and sexual restraint. Because it is considered that a disgraceful behavior can bring shame men's associated and bring down the family name also. For that reason, proper conduct is significant to defend the family's name (Rodriguez Mosquera et al. 2010).

Conclusion

Generally, our behavioral expressions are related to our sense of inclusion in a social group, as well as the status ascribed to us by the group. A person's self-worth and their social image are strongly interconnected in cultures, which adhere to honor codes. Traditional cultures, in particular, strongly emphasize on honor because elements like family values, harmony, and respect are emphasized in such cultures (Markus and Kitayama 2003).

Cross-References

- [Human Enculturation](#)
- [Morality](#)
- [Rite of Passage](#)
- [Spiritualism](#)

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Honor Concern

- [Honor Code](#)

Honor Cultures

- [Culture of Honor and Nepotism](#)

Honor Killing

- [Sex Differences in Death by Homicide](#)
- [Violence from Women’s Kin](#)

Honor-Related Violence

- [Culture of Honor and Retaliation](#)

Hooking Up

- [Friends with Benefits](#)
- [Impersonal Sex](#)

Hookup Culture

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Synonyms

[Casual sex](#)

Definition

A culture that involves and supports hooking up or uncommitted, short-term sexual acts between two people who are not involved in a long-term relationship with each other.

Introduction

One of the most primal human desires is the want to engage in sexual behaviors. Traditionally, the most important goal of sexual intercourse was mating for reproduction and the continuation of genes, which has favored long-term relationships. However, reproduction is not the only goal for people to have sex. There are also other goals like physical gratification and fulfillment of emotional needs (Birnbaum and Gillath 2006). Over the past 60 years, many societies have become more sexually liberated, and the use of birth control (e.g., condoms, oral contraceptives) has increased (Garcia et al. 2012). With these changes, the sexual goals of physical gratification and emotion fulfillment have increased their prominence. Unlike reproductive goals, which tend to favor long-term relationships, these goals may be fulfilled with long-term or short-term relationships. Currently, hookups are one of the most common ways of achieving these goals in short time and have been told to become a culture. A “hookup” occurs when two people who are not involved in a long-term relationship with each other engage in a brief sexual encounter, which may involve kissing, sexual touching above or below the waist, oral sex, or sexual intercourse.

Creation of the Hookup Culture

The roots of the hookup culture go back to the 1920s where societal norms started to change, mobility increased, and medicine and science had advanced developments. For example, with the advent use of cars, people’s mobility increased, which led to a decrease in the time spent with parental supervision, which led young men and women to have more freedom (Stinson 2010). The 1920s was just the beginning of many changes, and the number of women who wanted to follow the role of wife and mother reduced after the advances in the contraceptive technology in 1960 (Heer and Grossbard-Shechtman 1981). Again in the 1960s with the sexual revolution, young adults became more sexually liberated,

making them more open to short-term mating practices (Garcia et al. 2012). This movement toward sexual liberalism continued with the rise of feminism and increased numbers of females in the workforce and university students. Long-term relationships were viewed as potentially interfering with career goals, so young adults started to substitute quick hookups for long-term relationships that usually require longer investments (Heldman and Wade 2010). As a result, the age of first marriage increased, creating time for young adults to be sexually active but not ready to settle down (Garcia et al. 2012).

Although it seems as if culture and sexual lifestyle has changed in the new millennia, data from the Generals Social Survey (GSS) indicates otherwise. Since 1972, the GSS has been conducted by the National Opinion Research Center to assess the experiences, attitudes, and practices of United States residents. GSS data indicate that there is only a modest difference between the waves from 1988 to 1996 and 2004 to 2012 in sexual behavior. Young adult (18–25) respondents from the 2004 to 2012 waves did not report more frequent sex or more sexual partners than young adults in the 1988–1996 waves. However, respondents from the 2004 to 2012 waves were less likely to report sex with a regular partner, and more likely to report sex with a casual dating partner or friend (Monto and Carey 2014). This small change between the two groups suggests an increase in the hookup culture and is consistent with changes in “sexual scripts.” *Sexual script theory* argues that sexual behaviors are initiated with a set of these “scripts” that people use to shape and understand sexual encounters (Simon and Gagnon 1986). Scripts are a representation of the conceptualization of social behavior, and they direct behaviors for what should be done and who should do it in a context. So if people are living in a hookup culture today, it appears to be similar to the culture of the previous generation just with a different name (Monto and Carey 2014).

The origins of these scripts are not defined thoroughly, but evidence indicates that popular media influences the design of these scripts; and media is also an important factor in the growth of this culture (Garcia et al. 2012). As time passes,

people are exposed to more mass media than ever before, and TV programs use sexual images, themes, and references more than in previous generations (Aubrey 2004). In the same vein, a content analysis shows that more than 90% of the songs in Billboard's Top Ten lists include sexual messages in their lyrics (Hobbs and Gallup 2011). A similar trend in the use of sexual themes can also be seen in print media in the depiction of smartphone apps designed for matchmaking. Currently, matchmaking applications are one of the most used mediums for people to meet new potential mates, "Tinder" being the app with the most users. Although studies show that people's motivation to use this application is more for "love" than "casual sex," the application is presented as the "hookup app" (Sevi et al. 2017). This increase in sexual exposure has been argued to be a possible reason for the endorsement and participation in the hookup culture, just as the relation between aggression and media violence (Heldman and Wade 2010).

Conclusion

The emergence of the "hookup culture" can be traced back to the early twentieth century. Throughout the decades, advances in science and technology and changes in societal norms have contributed to shifts in the goals of sexual behavior and the structure of interpersonal relationships. Hookups include a broad range of sexual behavior from kissing to sexual intercourse and may consist of a single encounter or multiple encounters. This culture has started to emerge with sexual liberation and has been going on since. However, it has not had a name. With the help of media and the evolution of sexual scripts, this culture of brief and uncommitted sexual acts has found its name as the "hookup culture."

Cross-References

- Casual Sex
- Sexual and Reproductive Development
- Sexual Behavior

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Hookups

- Casual Sex

Hook-Ups

- Costs of Short-Term Mating for Women

Hopelessness

► [Depression \(Randolph Nesse\)](#)

Horizontal Family Relations

► [Sibships](#)

Hormonal Component of Homosexuality

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Synonyms

[Courtship orientation](#); [Intercourse sexual orientation](#); [Partner preference](#); [Sexual preference](#)

Definition

Sexual orientation is defined as “an enduring pattern of emotional, romantic, and/or sexual attractions to men, women, or both sexes” (APA 2008).

Introduction

Sexual preferences are focused to be expressed during the whole process of courtship and mating. Thus, depending toward which gender those behaviors are aimed to, a person may be defined as heterosexual, homosexual, or bisexual. In this sense, sexual orientation has a motivational (desire) component and also a behavioral component (courtship behavior). In homosexual persons both components (motivational and behavioral) are orientated toward their same sex group. These feelings are expressed during all the life span, while the behavior might be expressed or not. Psychological research (questionnaires, tests)

through many years and in different historical periods has demonstrated that sexual orientation ranges along a continuum, from exclusive attraction to the opposite gender to exclusive attraction to one's own gender (Kinsey et al. 1948; see the Kinsey Scale in this volume), suggesting different motivational and behavioral brain networks for sexual orientation. Only 3–10 % of the population are exclusively attracted to individuals of their own sex, but this minor number cannot be reason for exclusion, discrimination or a phobic social attitude toward them, because there are none objective links nor serious correlation data at all that might proved any relation between homosexual orientation to antisocial or social disruptive behaviors.

Perhaps Sigmund Freud was pointing a second type of mainly late-onset homosexuality in human when he stated parental styles and childhood experiences might have an effect on adult sexual orientation. However, psychoanalysis was not so correct when assured male homosexuality might be due to an authoritarian father and a wrong erotic relation toward the mother (Puts et al. 2006). Other wrong interpretations as sexual orientation like a choice might have been derived from this late-onset explanation: it has been wrongly considered as a bad habit that could be changed, and many people have unfairly suffered for this confusion. Besides psychoanalysis, many other methods have been used in the attempt to bring about changes in sexual orientation: castration, administration of testosterone or estrogens, apomorphine, psychosurgery, electroshock, etc., but none of these interventions have led into a well-documented change in sexual orientation (see Savic et al. 2010). In the 1960s and 1970s, in the context of the behaviorism and its *tabula rasa* concept about unlimited brain plasticity for sexual identity, some clinical practices have had quite devastating effects, such as in the John-Joan-John case (for revision, see Garcia-Falgueras and Swaab 2010).

Genetic information coming from a father (man) (XY) and from a mother (woman) (XX) are inherently part of all of us. However, sexual preferences for having a life partner, for creating a family with another adult in a human being commitment and taking care of an

offspring, are a complex set of feelings that might be defining the whole complexity of sexual orientation as a path for life.

Main Text: Orientation and Organizational Changes

It is important to notice female and male homosexuality are not equivalent nor similar but depend at least partly on different interactions with hormones during fetal development which creates, organizing for later activation, specific brain networks for each gender. It has been proved the production of testosterone and its conversion into dihydrotestosterone between weeks 6 and 12 of pregnancy are essential for the completion of a boy's reproductive system, while in the girl's reproductive system, it might be essential not having such high amounts of plasma androgens during the same period (Garcia-Falgueras and Swaab 2010). In men, testosterone levels and the efficiency of its receptor during the process of their body development in the womb are relevant for sexual orientation and gender identity. In women higher testosterone levels may also have an effect on adult game preferences and spontaneous drawing, for congenital adrenal hyperplasia cases (CAH). On the other hand, homosexual women have been shown to have higher free cortisol stress concentration compared to heterosexual women, while homosexual men have lower overall cortisol concentration compared to heterosexual men (for review, see Garcia-Falgueras and Swaab 2010). Due to these differences in early organizational hormonal effects during embryonic development, adult activation might also be different for homosexual orientated people: for instance, homosexual men are more sensitive (react more intensely) after oxytocin administration when facial stimuli are presented compared to heterosexual men (Thienel et al. 2014).

In the brain *in vivo* studies have proved that the hypothalamus, in homosexual man and woman, has a different activated areas to specific smells related to reproduction than the hypothalamus in heterosexual subjects (Savic et al. 2010). These results have been replicated with other methods

and different subjects: it was found gray and white matter are differently concentrated in certain brain areas for man and woman homosexual and heterosexuals, such as those related to olfaction as the perirhinal cortex. In the resting state, the amygdala is asymmetrically connected in homosexuals (men and women) (Savic et al. 2010; Garcia-Falgueras and Swaab 2010). Left-handed people are slightly more likely to be homosexual than right-handed people (Puts et al. 2006). Such a balance between our inner masculinity and femininity, as well as that equilibrium between symmetry for both sides of the body, seems to be organized early in the womb. For further details, see chapter entitled ► [“Relationship Between Sexuality and Gender”](#) in this volume.

Reviewing current scientific literature on the topic, there are several effects during gestational critical period (i.e., organizational changes because of hormonal modifications in plasma levels or in hormone receptor efficiency) that might cause or have a consequence together with sexual orientation. Their presence in the womb might lead to an organized specific grown-up characteristic. Some examples about the possible effects of changes in hormonal levels during gestation on adult behaviors, phenotypes or morphologies have been proved to occur in (a) female humans with adult polycystic ovaries, (b) specific length of fingers and length proportion between them in adulthood, (c) brain laterality for right or left handed, (d) large percentage of bi-/homosexuality in female offspring during the 1950s because of early exogenous diethylstilbestrol (DES) treatment for pregnant mothers, and (e) large percentage of bi-/homosexuality in females because of specific steroid mutations such as congenital adrenal hyperplasia (CAH), androgen insensitivity syndrome (AIS), etc. (for rev. see Savic et al. 2010; Garcia-Falgueras and Swaab 2010), and hormones that might affect the mother's immune system and having an effect toward her male offspring's sexual orientation, depending on the order of birth for boys and the amount of previous brothers (Puts et al. 2006). Experimental procedures pursuing a causal relationship between these variables are simply not possible to implement because of ethical principles, but correlations do strongly exist.

In some few cases, sexual orientation has been expressed later in life, as it has been described for gender dysphoria patients, in a late onset (Auer et al. 2014). This is happening in some particular cases in humans, for instance, while they are in prison, but there are no good experimental evidences to describe it as an adult change in sexual orientation. Cases in humans about plastic adult learnings have been described but they might be related most likely to another brain region such as the hippocampus, as it has been reported to occur in taxi drivers and musician (Hahn et al. 2016). The existence of a biological substrate of sexual orientation is unquestionable, because human existence is rooted in our biology, but the neural basis of motivational versus behavioral sexual orientation is not completely established yet, for heterosexuality nor homosexuality (Gooren 2011).

In animal kingdom curious cases in beetles have been described. In some species of insects, in which the recognition cues of females and males overlap to a certain degree such as beetles, homosexual behavior is a consequence of an adaptive discrimination strategy with a functional meaning of avoiding the costs of making rejection errors. This studies might be suggesting that sexual orientation in certain species is a result of a balanced calculation between low/high costs of a rejecting female versus low/high costs of an accepting male (Engel et al. 2015). Although currently there are no experimental evidences about this hypothesis in humans.

However, animals and not human beings have another set of determinant variables strongly linked to reproductive goals and defining their intercourse behaviors. Patterns of behavior in vertebrate species, such as those related to territorialism or aggressiveness, vary and change as stages during the reproductive seasons in the life cycle progress while it is activated by specific hormone signals (Wingfield et al. 1997). Concerning to animal research, there are plenty examples of homosexual behavior: in rodents and rams, those behaviors have been related to the hypothalamus neuromorphology, i.e., in rams, ovine sexually dimorphic nucleus, (oSDN) and in rats, medial preoptic nucleus (MPON). Some parallelisms in humans, i.e., suprachiasmatic nucleus (SCN) and

interstitial nucleus of the hypothalamus-3 (IHAN3), were found as well in extension to human homosexual behavior (Swaab and Hofman 1990; Levay 1991; Garcia-Falgueras and Swaab 2010). As far as our knowledge, no histological tissue studies have been done to localize the motivational aspects of sexual orientation. More relevant information is available for the reader in the chapter of this volume entitled ► [“Biology of Human Gender, The”](#).

Many times in history, love potion antidote has been tried to supply for heterosexual love in some cultures. Further details can be read in the chapter of this volume ► [“Mate Retention and Romantic Attachment”](#). Love has been considered as a serious illness. Indeed George Bernard Shaw defined love as one of the “most violent, most insane, most delusive and most transient of passions” (for revision, see Earp et al. 2013). Those data are pointing out that extreme passions, any sort, might be a considerable dangerous factor against life survival and contradictory in evolution terms. Much research suggests that while sexual orientation might be malleable at certain stages of the life span, it is fixed by the time we reach adulthood and is beyond further influence (Savic et al. 2010).

Conclusion

Sexual orientation is defined as “an enduring pattern of emotional, romantic, and/or sexual attractions to men, women, or both sexes.” In this sense, sexual orientation has a motivational (desire) compound and also a behavioral compound (courtship behavior). The production of testosterone and its conversion into dihydrotestosterone between weeks 6 and 12 of pregnancy are essential for the completion of a boy’s reproductive system, while in the girl’s reproductive system, it might be essential not having such high amounts of plasma androgens. Changes in this proportions might caused adult behavioral and motivational modifications. Some cases of late onset for sexual orientation have been described, i.e., prison, although there are no experimental evidences. Specific brain areas in mammals have been found to have a connection with sexual orientation behavior (i.e., ovine oSDN, in rats MPON,

humans SCN, and IHAN3). Those data are pointing out the fact that sexual orientation might be fixed by the time we reach adulthood and is scarcely beyond further influence.

Cross-References

- [Biology of Human Gender, The](#)
- [Mate Retention and Romantic Attachment](#)
- [Relationship Between Sexuality and Gender](#)

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Hormonal Contraception

- [Effect of Birth Control on Women's Preferences](#)

Hormonal Contraceptives

- [Birth Control](#)

Hormonal Cues to Attractiveness

- [Male Perception of Cycle-Related Fluctuations in Women's Attractiveness](#)

Hormone Effects on Human Fetal Development

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Prenatal Programming, Cortisol

The evidence that phenotype is set partially based on prenatal hormonal exposure is overall strong.

Such effects make sense within the evolutionary psychology framework.

Hormone levels that a developing fetus experiences can result in long-lasting phenotypic differences in the individual. Because the maternal blood supply is the route by which a fetus will be exposed, mother's levels – and her experiences – can affect development.

High levels of stress during pregnancy result in higher levels of the hormone cortisol as does exogenous ingestion of certain medicines (e.g., steroids) or certain foods (i.e., licorice). In any case, there is evidence that exposure of the fetus during prenatal development will alter early programming, causing differences in metabolism and other physiological parameters. The effects are long term or permanent. Combined with experimental methods employing animal models (see Weinstock 2008), there is converging evidence implicating a causal pathway for human development. The human placenta features 11 β -hydroxysteroid type 2 (HSD2) that works as a barrier to prevent excess cortisol exposure for a fetus; the enzyme converts the active form into an inactive form when it crosses the placental barrier. Animal research suggests that this enzyme can be more or less active due to starvation, various kinds of inflammation, or general stress, thus altering fetal exposure to glucocorticoids. Broadly, high levels of glucocorticoids in the mother result in lower birth weight and increase in HPA activity and changes in the overall metabolic profile. For example, increased cortisol, higher susceptibility to diabetes, and cardiovascular risk have all been well documented (see Reynolds 2010; Reynolds 2013). The general patterns suggest that *more* cortisol encountered prenatally results in generally *more cortisol* when there is not an acute stressor present and a *blunted increase during times of acute stress* (O'Connor et al. 2013). Also of considerable interest are the effects on the developing brain. McEwen in 1999 demonstrated a definite susceptibility of the developing brain to glucocorticoids. Since that time, several key findings have emerged. Buss et al. (2012) have found evidence for an early window of

sensitivity to cortisol in girls. Specifically, early exposure to high cortisol during gestation was associated with significantly increased size of the amygdala in seven-year-old girls. The amygdala is associated with linking and responding to fear or anxiety-producing external stimuli. Research has documented that levels of cortisol (measured in utero) predict later impairments in measured cognitive development (Bergman et al. 2010).

Evolutionary psychologists generally conceptualize an individual as a combination of genotype framing allowing for a range of final outcomes that are fine-tuned based on expected or encountered environmental circumstances. As a whole, it appears that prenatally experienced increased cortisol leads to alterations of the offspring's HPA, thus causing myriad changes, including low birth weight and altered glucose processing (e.g., later susceptibility to type 2 diabetes) and altered response to experienced stressors throughout life. From an evolutionary psychology perspective, it is interesting to observe that deleterious effects may be most pronounced when a mismatch between utero environment programming and experienced adult environment is likely greatest. For example, low birth weight in tandem with adulthood obesity was a stronger risk factor than either variable alone (Li et al. 2010). This suggests the possibility that the function of prenatal programming may be to somehow prepare for adult environment most likely to be encountered.

Conclusion

Certainly, the environment encountered determines which behaviors and phenotypes are the most adaptive. Hormones may serve as a signal to alter the developing fetus toward a phenotype more adaptive to expected circumstances. Alteration of the physiology and behavior of offspring via the levels of maternal corticoids could be plausible vehicle for such fine-tuning to occur. In any event, evidence that hormonally based prenatal programming alters the phenotypic outcome of the individual, especially glucocorticoids, is strong.

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Hormone-Based Contraception

- [Birth Control](#)

Hormones

- [Music and Hormones](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)

Horrors

- [Fears](#)

Hostile Masculinity

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Definition

A latent personality construct comprised of aggressive, defensive, and narcissistic traits and a tendency to derive sexual gratification from dominating and controlling women. Hostile masculinity predicts sexual and nonsexual violence against women, and it is one of the two proximal trait constellations directly predicting male sexual violence against women in Malamuth et al.'s (1991) Confluence Mediation Model of Sexual Aggression.

Introduction

The Confluence Mediation Model of Sexual Aggression (CMM or Confluence Model) is a multifactorial, evolutionary-based model of sexual violence perpetration first proposed by Malamuth (1986). This groundbreaking model has proven robust in cross-sectional, longitudinal, and laboratory studies, and it has been replicated in a variety of populations, including incarcerated, university, and community samples of men (for a review, see Malamuth and Hald 2016). The central premise of the CMM is that two major constellations, hostile masculinity and sexual promiscuity/impersonal sex, are synergistic (interactive) and predict sexual violence perpetration better than an exclusively additive model of the individual risk factors. In the absence of the sexual promiscuity constellation, hostile masculinity predicts nonsexual violence against women (Malamuth et al. 1991).

Factors Contributing to Hostile Masculinity

Hostile masculinity is conceptualized as an antagonistic, insecure, grandiose personality profile exemplified by manipulative, callous, distrustful, and hostile attitudes against women (e.g., Malamuth and Hald 2016). Although seemingly similar to constructs like hypermasculinity, men with high levels of hostile masculinity direct their aggression toward women specifically, whereas hypermasculine men are less discriminating when selecting their targets of aggression (Malamuth et al. 1996). Childhood maltreatment (e.g., abuse, neglect, domestic violence) appears related to the development of psychopathic/narcissistic traits and hostile masculinity. There are several hypotheses for the development of the malevolent personality styles that lead to hostile masculinity. These involve men modeling the violence against women that they witnessed in childhood, as well as engaging in antisocial activities at an early age (e.g., Malamuth and Hald 2016; Malamuth et al. 1991, 1996). Additionally, neglectful maternal relationships lead to anxious maternal attachments and cognitive distortions, which contribute to the perception that women are unreliable and unworthy of respect (Russell and King 2016). These early life experiences, along with living in subcultures encouraging the expression of stereotypically masculine traits (e.g., dominance, competitiveness) and punishing the expression of stereotypically feminine traits (e.g., kindness, empathy), foster attitudes supporting violence against women and hostile masculinity (e.g., Malamuth and Hald 2016; Malamuth et al. 1991, 1996).

From a statistical perspective, the CMM is a structural equation model, and hostile masculinity is an endogenous latent variable with a direct path to sexual violence perpetration. Hostile masculinity serves as a mediator between broad, general personality types (e.g., psychopathy, narcissism) and sexual aggression. Observed variables loading on hostile masculinity include scales assessing hostility toward women, sexual dominance, and rape myth acceptance.

Exogenous personality predictors of hostile masculinity relate to narcissism, psychopathy, and sadism. Hostile masculinity also mediates the relationship between childhood maltreatment and sexual violence (e.g., Malamuth et al. 1991; Russell and King 2016). In an answer to Malamuth and Hald's (2016) call for research to "elucidate more precisely the mechanisms that link 'higher order' general hostile/antisocial factors...to the 'narrower,' more proximate factors predictive of sexual aggression" (p. 66), Russell and King (2017) found hostile masculinity mediated specific facets of psychopathy and narcissism. These lower order facets included grandiosity, cognitive/perceptual dysregulation, traditional/conventional beliefs, and interpersonal suspiciousness.

Evolutionary Theory and Hostile Masculinity

Comparing and contrasting the evidence for sexual violence being an adaptation or a by-product of an adaptation is beyond the scope of the current entry (for a discussion of this topic, see ► "Aggression for Sexual Access"). However, Malamuth et al. (2005) make a convincing case for sexual arousal to force being a specialized psychological adaptation motivating sexual violence that can be briefly summarized. Malamuth et al.'s (2005) contention is that, in order to be an adaptation, sexual violence must have contributed to some men's fitness increases some of the time, and it had to occur often enough to overcome fitness costs (e.g., injury, death). If that occurred, and assuming all humans evolved with common psychological mechanisms, then a sexual violence mechanism could have evolved. Implicit in these assumptions is that all men have the potential to become sexually violent when individual experiences (e.g., childhood maltreatment, anxious maternal attachment) "activate" the evolved psychological mechanism. The factors loading on hostile masculinity (sexual dominance motives, hostility toward women) seem to be a manifestation of

this evolutionary specialization. Thus, men with sufficient levels of the sexual violence mechanism exhibit a relatively persistent hostile masculinity *trait*, as opposed to transient *states* of hostile masculinity.

There is empirical support for the sexual violence adaptation hypothesis. Beyond the considerable evidence for the CMM and hostile masculinity, laboratory research has demonstrated men can be primed for sexual arousal to force by simulating female rejection of sexual advances. For example, college men who were insulted by a woman became more sexually aroused by non-consensual sex descriptions than consensual sex descriptions (Yates et al. 1984). Baumeister et al.'s (2002) development of a narcissistic reactance theory for rape and coercion also described numerous studies involving narcissistic men becoming sexually violent when rejected by women. Indeed, there seems to be support for an evolutionary adaptation related to sexual arousal to force in the sexual violence literature, although it is premature to discount the possibility of a by-product at this time.

Conclusion

The present summary described factors contributing to hostile masculinity, as well as evolutionary concepts associated with this cluster of personality traits. Hostile masculinity is a latent construct in the Confluence Mediation Model of Sexual Aggression. It directly predicts sexual violence perpetration in men who have co-occurring traits associated with the sexual promiscuity/impersonal sex constellation, and it predicts nonsexual violence against women when sexual promiscuity is absent. Hostile masculinity manifests as hostility toward women and sexual dominance motives, and it mediates the relationship between broad personality traits (e.g., narcissism, psychopathy) and sexual violence perpetration. Hostile masculinity may be the manifestation of sexual arousal to force, a potential evolutionary adaptation for sexual violence, although additional research in this area is required.

Cross-References

- [Aggression for Sexual Access](#)
- [Alcohol and Rape on College Campuses](#)
- [Forced Copulation](#)
- [Rape and Dating](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion and Dating](#)
- [Violence to Control Women's Sexuality](#)

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Hostilities

- [War](#)
-

Hostility

- [Aggression](#)
 - [Meta-analysis of Sex Differences in Aggression](#)
 - [Sex Differences in Aggression](#)
 - [Sex Differences in Anger Proneness](#)
 - [Strategic Aggression](#)
-

Hour Glass

- [Waist-to-Hip Ratio](#)
-

How Evolutionary Psychology Can Still Explain Behavior

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Synonyms

[Applications of evolutionary psychology](#); [Evolutionary psychology's role in behavioral science](#); [Proximate versus ultimate explanations](#)

Definition

The understanding of foundations of psychology in respect to biology and of evolutionary psychology's ability to coalesce various academic domains that advances the modern science of psychology.

Introduction

The battle between *nature* and *nurture* continues to be incessant within the social science communities. Evolutionary psychology, however, is a field that takes initiative to become an exemplar of academic consilience. The inception of psychology and biology itself segregates themselves from the other, which distorts the perspective that behavior can be adaptations like physicality. Humans are organisms that possess brains that abide to the laws of evolutionary biology. Societies similar to modern Western ones exploit the operations of psychology as well as the ancestral conditions in which psychology evolved. When the comparisons between ancient and modern environments are established, evolutionary psychology will become a pertinence to the modern study of mind and behavior.

Psychological Attributes as Biological Adaptations

Like organisms, academic disciplines evolve. Psychology is widely accepted as a descendent of biology; however, parsing one from the other has resulted in academic complications and controversies. Behavior as an adaptation, sometimes called an *instinct*, serves as an intersection of psychology and biology. Behavior of all sorts rests on the foundations of the nervous system or the brain, which has and always will be subject to the principles of biological evolution.

Because the rates of both biological and cultural evolutions are far from identical, adaptations from exponential generations ago endure the journey to the contemporary generations. Like a biological adaptation, a psychological adaptation is a feature that ultimately enhances its genes reproductive fitness as a result of gradual modification generation to generation. Any adaptation or any seemingly designed characteristic is not *always* of service to the organism that possesses it. *Mismatch theory* posits that evolved features that were adaptive in certain environments are maladaptive in others (Buss 2015; Barkow et al. 1995).

Modern society and enduring cultures, intuitively, are distinct from one another; however, many, if not most, of them share similar qualities. Language, religion, sexual preferences, division of labor, and hierarchal structures, for example, are never identical culture to culture but certainly are in respect to their service to those who practice them. As a perspective of psychology, evolutionary psychology unites a variety of academic domains, which poses original questions on behavior. The lens of evolutionary psychology is capable of enlightening the current conundrums traditional psychologists frequently confront. As a truly integrative discipline, evolutionary psychology could contribute to the sciences of most, if not all, of the branches of psychology.

Psychology as a Descendent of Biology

The foundations of psychology lie within the nervous system. The central nervous system of modern humans or *Homo sapiens* is the brain, the hub of cognition and behavior. Like any organ, the brain is a product of gradual modification on the basis of evolution via natural selection. The accumulation of selective forces and environmental pressures that humans encountered throughout their evolutionary history ultimately forged, like any other biological entity, the brain (Palanza and Parmigiani 2016).

Distinction between the mind and body has been under debate since their inception. Science, today, advocates the dualistic view of the mind and body by delegating their studies into two different disciplines: psychology, which imperialized the study of mind and behavior, and biology, which imperialized the study of the body and its operations. This dualistic view yields unexplained discrepancies between neurological psychologists and molecular biologists. While every brain and mind is popularly believed to be different between every individual, merely every bodily aspect is inherited, including neurochemistry (Pervin 2009).

The terms *psychology* and *biology* themselves are a mean to their academic segregation. The underlying causes of mental illnesses and bodily diseases are almost indistinguishable from each other. The notion that psychological and

biological principles are related is frequently condoned from both disciplines, yet one cannot survive without the other. As a descendent of psychology and biology, evolutionary psychology is the first scientific discipline that applies established biological principles to the study of human mind and behavior.

Life history theory predicts the pace of a species' maturation when given its ancestral history and modern environments. Furthermore, life history theory can be used to predict characteristics such as lifespan and degree of social cohesion. Mental traits that foster socialization develop non-randomly from species to species. Even major brain regions like the amygdala, hippocampus, and frontal lobes begin and finish developing during specific times of an organism's lifespan (Figueredo et al. 2006).

Somatic effort, an organism's pursuit for self-growth and maintenance, transforms into *reproductive effort* or the will to obtain the means to procreate. Reproductive effort may then evolve into *mating effort* to select a particular mate from a selection of potential mates, which may transform into *parenting effort*, which is an organism's nature to bear and rear its offspring they can sustain themselves. The relationship from somatic to parenting efforts enables life history theory to predict the number of offspring typically reproduced, sex differences in mating strategies, years of adolescence, risk-taking tendencies, and even social deviance (Figueredo et al. 2006).

Sexual selection theory also has implications on the nature of parenting. Sexual selection is the preference of one sex to choose to mate with members of the opposite sex. Generations of sexual selection result in more unique characteristics that distinguish one sex from the other. Sexual selection influences almost all of the nuances of a species' reproductive nature. Relative to males, females more often invest both more and a variety of efforts to the overall fitness of their young, especially within the mammalian kingdom. Evolutionary psychology endorses the relationship between sexual selection and *parental investment theory* as it provides new insights to explain human parenting and mating behavior (Buss 2015; Geher 2014).

Behavior or acts of expression may be viewed as a physical adaptation enhancer. Scientists within the domain of ethology effortlessly explain animal behavior from an evolutionary standpoint, yet the nature of biology is condoned when examining behavior of *Homo sapiens*. Physical structures that characterize an organism are designed by biological evolution (Cosmides and Tooby 1997; Palanza and Parmigiani 2016); the architecture of the brain changes in order to guide its host to survive without excessive discomfort.

Mental traits, like their physical counterparts, are adaptations. Behavior is a result of *both* genes and environments (Cosmides and Tooby 1997). From an ultimate perspective, the origins of behavior can be traced to the principles of biology. This perspective does not assert that every action or single behavior is of a survival or reproductive service; rather it posits that psychological phenomena are not completely dependent on experience and are partially inherited qualities from previous generations.

Evolutionary Mismatch Theory

Traditional social sciences have an extensive history of putting nurture before nature. This standard social science model (SSSM) originates from the false conception that mind and behavior is a product of only experience, which is also called the *blank slate* (Barkow et al. 1995; Figueredo et al. 2006). Given that numerous regions of the brain are functionally specific (Cosmides and Tooby 1997; Palanza and Parmigiani 2016), an adaptationist approach to psychology may be scientifically advantageous (Buss 2015; Barkow et al. 1995; Geher 2014). The SSSM significantly lacks this perspective, which transcends to a plethora of unasked questions.

It is necessary to reiterate that the rate of cultural evolution is far beyond the rate of biological evolution, for biologically complex organisms. The human brain's evolution predominantly derives from when early humans were hunter-gatherers (Cosmides and Tooby 1997). The persistent problems human ancestors faced – droughts, famine, competitions for resources, predators, and disease, to name a few – serve as ultimate and unique selective pressures.

Individuals with cognitive advantages over the others better adapt to evolutionary pressures over time. The more consistent the evolutionary pressures, the more time the mind has to specialize in each evolutionary hurdle (Buss 2015; Barkow et al. 1995; Geher 2014).

The position that human psychology is chronologically displaced due to the rapid rate of change of culture and society leads evolutionary psychologists to espouse *evolutionary mismatch theory*. A psychological trait is either an adaptation, a by-product of other adaptations, or a random effect (Buss 2015). A central theme of evolutionary mismatch theory is that an adaptation is not always adaptive or maladaptive (Caporael 2001). Evolutionary psychological theories and hypotheses frequently result from this popular theory, many of which assist the field to explain contemporary psychological phenomena.

A lucid example of mismatch is the penchant for sugary and fatty foods. Hunter-gatherers would not be called *hunter-gatherers* if there were a McDonalds or a supermarket in their environments. The conditions hunter-gatherers evolved from had a dearth of food and nutrition. Humans who yearn and seek for fatty foods have advantage over those without it or those with a lesser degree of it. Today in developed nations, fast-food restaurants and supermarkets are ubiquitous, which result in maladaptive responses, such as heart disease, high cholesterol, and obesity (Geher 2014).

Modified pictures and popular movies with slim women and men have significant influence on its audiences. Teenagers and young adults prioritize their physical appearance so high that they become malnourished or spend masses of money for unnecessary surgeries. Both the absence of images of slim women and men throughout *Homo sapiens'* evolutionary history and the social-behavioral phenomenon to imitate individuals with seemingly desirable traits exploit humans' evolutionary mismatch of environments (Ferguson et al. 2011).

Evolutionary mismatch theory may also explain the rise of the epidemic of clinical depression. Evolutionary psychologist, Stephen Ilardi, advocates for a lifestyle similar to those of earlier

humans. Actively participating in social relationships, getting daily exercise with a diet similar to the *Paleolithic diet*, being awake and outside in broad daylight while maintaining a proper sleep schedule, and being mentally engaged to minimize rumination comprise Ilardi's new therapeutic regime. Healthy diets, proper exercise and sleep, exposure to sunlight, and living in the present moment are painstakingly difficult to obtain in modern developed nations. The vast majority of clinically depressed individuals who participated in Ilardi's program reported to have obtained an overwhelming degree of success and recovery without the use of antidepressants (Ilardi 2010).

Although there are cogent instances of evolutionary mismatch when comparing the ancestral environments with those of developed nations, social scientists urge evolutionary psychologists to demonstrate the phenomenon in all nations and cultures. Universal behavior across independent cultures would elucidate evolutionary psychology's role on modern behavior.

Any two cultures are far from identical, but the variations between them are not completely random (Schmitt et al. 2016). Evolutionary psychology with the cultural and multicultural psychology perspectives provides viable predictions within esoteric cultures. Women with a waist-to-hip ratio of .7, for example, is rated as the most attractive by men from both developed nations and indigenous tribes (Singh and Young 1995; Buss 2015; Schmitt et al. 2016), which bolsters the hypothesis of universal behavior as evidence for a biologically evolved psychology.

Evolutionary Psychology and the Subdisciplines of Psychology

Any mental capacity or ability that *survives* and is passed down to the next generation, one way or another, is technically an *evolved* psychology. Evolutionary anthropologists and psychologists claim that human psychology is derived from early humans as hunter-gatherers (Cosmides and Tooby 1997), and despite that it was designed for prehistoric environments, it *survived* or *adapted* to modern environments. More simply, modern psychology is prehistoric psychology "but on steroids" (Pinker 2011).

Stimuli from contemporary cultures and environments act on the same biological frameworks that stimuli from ancient cultures and environments did. The difference between how the mind operated and functioned in hunter-gatherers and how it operates and functions in modern human beings is not due to a biological change; it is due to an environmental and cultural one. Reading, going to school, and living in large cities are examples of evolutionary novelties. Although many novelties engender admirable behaviors, many yield abominable ones.

It is a common misconception to view evolutionary psychology as a justification for malicious or any sort of behavior. Individuals who support this *naturalistic fallacy* fail to recognize that the study of evolutionary psychology can provide powerful insight of how to proactively control unwanted behaviors (Wilson et al. 2003). With the understanding of any complex system, one can do more than just control unwanted behaviors. The philosophy of evolutionary psychology can produce viable predictions of behavior within various branches of psychology. An adaptationist perspective will yield unasked questions that traditional psychologists neglect.

The *modularity hypothesis*, the position that the brain is like a computer with programs that are installed for various functions, is still at the center of debate within cognitive psychology. Evolutionary psychologists espouse the modularity hypothesis in a manner similar to why evolutionary biologists espouse that almost every characteristic of an organism specializes in a particular function (Cosmides and Tooby 1997). Certain cognitive traits and capacities develop at certain rates and are nonrandomly situated in specific locations of the brain (Caporael 2001). Cognitive traits do not arise from oblivion for no reason (Buss 2015; Barkow et al. 1995).

The cornerstone of human culture, language, is a truly universal attribute among *Homo sapiens*. A social species with the ability to express unlimited information can quickly dominate those without same ability. Evolutionary psychologists explain the origins of verbal language as an exaptation or by-product of human social nature and intelligence (Pinker 2010; Caporael 2001) that has

transcended into an adaptation. Traditional cognitive psychology does not refute that language has a biological basis, but it does assert that the capabilities for verbal language are primarily obtained through practice. The controversial *critical period*, the time when humans are most prepared to acquire verbal language skills, suggests that language can only be learned within a human's specific time window. With the fact that language is localized within Broca's area, the region of the brain associated with human speech, evolutionary psychology sits at the forefront of investigating the biological bases of verbal language (Pinker 2010).

Social psychology is a prime disciple of the SSSM. Cultural and social psychologists frequently claim that cultural norms and experience strictly shape human psychology; however, *culture* is not an adequate explanation for behavior. Moreover, explicating behavior via culture may be a redundant and even a stalling explanation (Barkow et al. 1995). Social psychology supports that committing altruistic acts are strictly motivated by intrinsic satisfactions. Ethology and evolutionary psychology, on the other hand, well explain and predict the instances of altruistic behavior.

Kin-selected altruism rests on evolutionary biological principles that can be observed in many nonhuman species. From a gene's perspective, putting oneself in harm's way in situations where the gene can continue to survive via its host's biological relatives sheds light on the unconditional nurture between biologically related organisms (Geher 2014). In low-risk or low-cost situations, humans are more likely to act altruistically toward friends, which can be reciprocated, whereas humans in high-cost situations are more likely to help their kin or family (Stewart-Williams 2007).

Life history theory may ultimately predict the development of the brain maturity and certain mental abilities (Figueredo et al. 2006), which is also subject to the study of developmental psychology. The onset of puberty and the relationship between infant mobility and fear of heights suggest that both bodily and mental changes are not completely random (Swanepoel et al. 2016).

Applying life history theory, a biological evolutionary theory, to developmental psychology may help social scientists learn when and how to intervene various behaviors.

Attachment is fundamental to the development of healthy social relationships. Both traditional and evolutionary developmental psychologists stress the importance of establishing interpersonal relationships on one's well-being and fitness. Renowned scientist, John Bowlby, examined the functions of the development of an unconditional attachment between an infant and caregiver. Bowlby (1982) recognized that many primates and mammals evolved behavioral-motivation systems to have both their physical and emotional needs met by a caregiver (Palanza and Parmigiani 2016). If these needs are met, individuals will develop a healthy and secure attachment style toward others; if not, individuals are likely to develop an insecure attachment style that could lead to severe issues within subsequent social and personal relationships.

Evolutionary psychology can also contribute to the field of personality psychology. Each of the Big Five personality traits (openness, conscientiousness, extraversion, agreeableness, and neuroticism) can be portrayed as a behavioral adaptation. Evolutionary theory hypothesizes that extraversion is rated as more attractive than introversion (Nettle and Clegg 2008). Not only was the hypothesis supported; it was also found that the more extraverted an individual reports to be, the more sexual partners that individual is likely to have (Buss 2015). Beyond personality traits, evolutionary psychology traces self-esteem, subjective well-being, and mental disabilities to their origins and uses. Additionally, the variation of personality characteristics across cultures is not due to chance, but is due to the environmental conditions (Schmitt et al. 2016).

Treating mental disorders like anxiety and depression is incredibly rare in indigenous tribes that are independent from other cultures, whereas developed societies treat mental disorders on a daily basis (Ilardi 2010). Evolutionary psychology poses unprecedented questions that gravitate around a variant of functionalism. Mania and periods of low energy and activity fluctuate with

the four seasons, which is a relationship that cannot be depicted without the evolutionary lens (Geher 2014). Most, if not all, psychiatric disorders are considered to be results of the mismatch between ancestral and modern environments. Clinical depression, among other mental illnesses, is now under immense scrutiny since the evolutionary perspective advanced depression treatments within clinical psychology (Buss 2015; Palanza and Parmigiani 2016; Ilardi 2010).

Conclusion

Psychology is, in a perspective, a branch of biology; however, psychologists and biologists are reluctant to inspect phenomena from the other domains. Established theories of evolutionary biology, such as sexual selection and life history theory, indirectly influence behaviors that take advantage of physical attributes and abilities. While the brain shelters the human soul, it abides by the laws of biological evolution.

Although cultural evolution complicates the means to observe evolved behavioral adaptations, by-products, and random effects, evolutionary mismatch theory disambiguates one from the others. Modern tools and technology facilitate many endeavors, yet their consequences accumulate to a seemingly incessant burden. Human psychology evolved from humans with the predominant occupation of hunting and gathering, yet the once adaptive traits betray our physical and mental health today. Whether or not culture is responsible for one's actions, it is not a cogent explanation of behavior.

Universal behavior across modern and indigenous cultures, like mating preferences and social altruism, is an evident support for psychology possessing a heritage. Despite that evolutionary psychology is mistakenly accused for justifying unwanted behavior, it has made prominent advances in cognitive, social, developmental, personality, and clinical psychology. With the adaptationist frame of mind that can be applied to, perhaps, all psychologies, evolutionary psychology cannot be sufficiently identified as a sub-discipline of psychology. Given that psychology

is a descendent of biology, evolutionary psychology is not an opposition of traditional psychology; it is a missing property of the study of mind and behavior, psychology.

Cross-References

- [Environment of Evolutionary Adaptedness](#)
- [Hunter-Gatherer Societies](#)
- [Mismatch](#)
- [Non-human Primates](#)
- [Selectionist Models: Implications for Behavior](#)

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How the Mind Works

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Synonyms

Pinker evolutionary psychology; Steven Pinker
How the Mind Works

Definition

A 1997 book by Steven Pinker.

Introduction

Steven Pinker's *The Language Instinct: How the Mind Creates Language* (1994) played a vital role in refuting many myths regarding the development of language abilities. Pinker argued against the behaviorist perspective that language acquisition was primarily or entirely the result of operant conditioning process and presented substantial evidence to attest to the fact that, despite its complexity, understanding and using spoken language is a relatively easy accomplishment for most children. Language acquisition is largely dependent on evolved psychological mechanisms, which result in a predictable developmental sequence of language abilities.

In *How the Mind Works* (1997), Pinker extends his work on language from *The Language Instinct* while simultaneously broadening the focus to include myriad other areas of psychology and cognitive science: vision and the senses, emotion and affect, ideology, sexual attraction and love, gender roles and identity, learning, judgment and decision making, social behavior, and much more. Pinker's expansion of his range of topics is necessary to address the goal of *How the Mind Works*: to attempt to explain the many functions of the mind, including those that are poorly understood, in evolutionary terms. Or, as Pinker himself puts near the end of his book, "To get you to step outside your own mind for a moment and see your thoughts and feelings as magnificent contrivances of the natural world rather than as the only way that things could be." (p. 563). The work is largely inspired by and uses the frameworks of cognitive psychology and evolutionary psychology, and Pinker highly utilizes the work of prominent evolutionary psychologists such as John Tooby and Leda Cosmides.

Main Assertions

Pinker's two main assertions in *How the Mind Works* are taken from cognitive and evolutionary psychology. First, Pinker utilizes the information processing metaphor from cognitive psychology/cognitive science, which posits that the human

mind is like a computer, which utilizes sets of algorithms (“modules” or “programs”) to process data and produce behavioral output. Second, Pinker asserts that these mental programs represent evolved psychological mechanisms that were crafted by natural selection to efficiently solve specific adaptive challenges: acquiring language, choosing mates, avoiding danger, etc. Pinker even uses an evolutionary framework to explain negative emotional states such as sadness, which may elicit social support when we need it most, and disgust, which motivates us to avoid contamination by potentially lethal pathogens. Because natural selection results in evolved psychological mechanisms that on average improve the odds of an organism passing on its genes, Pinker’s viewpoint explains why our minds are often predisposed to believe things that are untrue but that enhance our ability to survive and reproduce.

Conclusion

Toward the end of *How the Mind Works*, Pinker poses the question “[I]f the mind is a system of organs designed by natural selection, why should we ever have expected it to comprehend all mysteries, to grasp all truths?” (p. 563). Indeed, a mind that evolved to efficiently navigate the relatively small-scale social dynamics and primitive survival pressures of our early human ancestors should not be expected to easily grasp macroeconomic, geopolitics, or the mysteries of the cosmos.

Cross-References

- [Language Development](#)
- [Pinker’s \(1994\) The Language Instinct](#)
- [Steven Pinker](#)

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Human

- [Largest *Homo* Brain](#)

Human and Nonhuman Behavior

- [Observation of Altruism](#)

Human Artifacts

- [Human Products](#)

Human Behavior

- [Human Nature and Biocultural Evolution](#)

Human Behavioral Ecology

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Synonyms

[Human evolutionary ecology](#); [Human sociobiology](#); [Studies on adaptation of human behavior and behavioral outcomes](#)

Definition

An evolutionary approach to human behavior, and its outcomes, that attempts to understand the adaptation at the phenotypic level in a current ecological and social environment.

Introduction

Human behavioral ecology (HBE) is one of the major approaches in evolutionary behavioral sciences. HBE investigates adaptation of human behavior, and its outcomes, in a current environment in terms of the theory of fitness maximization. HBE covers a variety of research topics (the whole of life history, for example: foraging, livelihood, mating, reproduction, parental care, health, cooperation, and sociality), study subjects (people in traditional small-scale, pre-industrial, historical, and modern developed societies), and methodologies (ethnographic fieldwork, interviews, questionnaires, experiments, statistical analyses of secondary datasets, and mathematical models). This entry briefly explains HBE's trends, recent representative studies, and an integrated theory with closely related other fields, that is, evolutionary psychology (EP) and cultural evolution (CE).

Note that this entry uses different names for each academic discipline (like anthropology, psychology, or demography) just for convenience and never stick to the terms themselves.

Trends

This entry deals with the recent (since the mid-1970s) trends of HBE and does not refer to the whole history, such as Charles Darwin's huge contribution to the evolutionary understanding of human behavior (see Laland and Brown 2011 for detailed history). Around the same time as Edward O. Wilson's *Sociobiology: The new synthesis* in 1975, HBE came to be recognized as a powerful approach to evolutionary behavioral sciences. According to previous reviews (Nettle et al. 2013; Winterhalder and Smith 2000, see also invited commentaries to Nettle et al. (2013) in the same issue), HBE began especially from studies on foraging and production in hunter-gatherer populations and then grew with further investigations on resource distribution and reproduction in traditional small-scale societies (in addition to hunter-gatherers, horticulturalists, and agropastoralists). In these early phases, field anthropologists took leading roles.

Thereafter (since the mid-1990s), the proposition of studies on reproduction and that in industrialized

societies have been increased. In this later phase, researchers in not only anthropology but also other disciplines, such as psychology, demography, public health, and sociology, participate in HBE actively. In the light of evolution, HBE can provide a concise theoretical framework and ultimate explanations. One of the most epochal papers is Kaplan et al. (1995). This study conducted an interview survey at a driver's license center in New Mexico, USA, and collected reproductive and socioeconomic information on three generations (i.e., children, parents, and grandparents). Using this dataset, they analyzed a trade-off between children's quantity and quality, and the relationship between socioeconomic success and reproductive success. In the three-generation analyses, their sample did not maximize fitness (here, the number of grandchildren), while there were trade-offs between parental fertility and offspring socioeconomic status (see also Morita 2018 for a review). As well as Kaplan et al.'s pioneering study, statistical analyses of secondary datasets also contributed to the development of HBE. Rich demographic data of individuals are useful to test evolutionary hypotheses in human populations (e.g., Mattison and Sear 2016; Morita 2018).

Below, two representative studies published very recently are introduced. One is an achievement from a field survey in Africa and the other is a statistical analysis of longitudinal historical data in Europe. These two studies will show recent developments in HBE clearly.

Case Study 1: Children's Time Allocation and Schooling in Tanzania (Hedges et al. 2018)

In modern competitive labor and subsequent mating markets, acquiring high skills, knowledge, and experience during childhood should be critical to win the peer competition in the near future. This situation will favor reproductive strategy in which parents aim to have a small number of high-quality children. The large amount of parental investment in children's education is a principal driver of fertility decline (low birthrates), a paradoxical and puzzling phenomenon for HBE (e.g., Collieran and Snopkowski 2018).

Parental investment has strong effects on reproductive outcomes for both parents and children. However, how such parental attitudes influence children's time allocation and trade-offs between schooling and other activities were rarely investigated quantitatively. Hedges et al. (2018) conducted an interview survey in Tanzania where the socioeconomic modernization and demographic transition to low fertility are undergoing right now. They found that there existed several trade-offs in children's time allocation depending on their sex, age, and residential area (i.e., town or village, a proxy for modernization). For boys living in the village, there was a trade-off between time spent in education and that in farm work. For elder (14–19 years old) girls, especially living in the town, time for education decreased that for chores. They also showed that a robust trade-off appeared between schooling and leisure time. The economic and opportunity cost of education, sexual division of labor, and degree of modernization led to different patterns of trade-offs in time allocation of children in the region. These findings are valuable for deep understanding of reproductive strategies in a novel environment (in other words, socioeconomic contexts) that humans are facing at present.

Case Study 2: Temporal Changes of Grandmotherhood Patterns in Finland (Chapman et al. 2018)

In humans, many individuals other than mothers and fathers, such as grandparents, siblings, other kin, and also nonkin, participate in childcare. This reproductive system is called cooperative breeding (a narrow sense), communal breeding, or alloparenting (broader senses). Through evolutionary processes, the presence of helpers has facilitated human's shorter birth intervals than other great apes. In particular, it has been suggested that grandmothers make an immense contribution to grandchildren's care (but see Sear 2017 for the cross-context variation of kin effects on fertility).

In some (especially Western) countries, abundant parish registers from local churches are available and these resources of pedigree data are quite useful for HBE. Chapman et al. (2018) investigated how grandmotherhood patterns varied across the

demographic transition to low fertility and low child mortality by analyzing longitudinal data in Finland. Their dataset included detailed records of individuals' births, deaths, dispersal, marriages, and reproduction for up to 15 generations. The subjects were 66,160 grandchildren born between 1790 and 1959 and their 7,349 grandmothers. They analyzed changes of the grandmother-grandchild relationship over time and found that both the percentage of grandchildren who had grandmothers (maternal and paternal) at births and their shared time were increased during/after the demographic transition. This study revealed temporal changes of grandmothering for the past about 200 years and also provided further implications to interdisciplinary fields, such as biology (the evolution of family and alloparenting), demography (age structure changes in the population, due to fertility and mortality transitions), public health (post-reproductive longevity of grandmothers and its effects on social care), and sociology (family structure changes associated with modernization).

Integration with Evolutionary Psychology and Cultural Evolution

HBE has close connection with other evolutionary approaches to human behavior, EP, and CE (see Laland and Brown 2011 for details). EP sheds more lights on psychological mechanisms or decision-making algorithms underlying each observed behavior. EP assumes that humans have acquired psychological foundations in ancestral environments (the so-called EEA: environment of evolutionary adaptedness) and a current environment may much differ from the past ones. CE pays primary attention to cultural traits that can be inherited to the next generations independently of biological fitness in a genetic sense.

As well as HBE, EP, and CE seek evolutionary adaptation of human behavior (but not limited to behavior). However, EP and CE attempt to find it in different levels (i.e., not in observed behavior but in psychological mechanisms or nongenetic cultural transmission underlying behavior). Therefore, EP and CE will enable researchers to better understand (seemingly) evolutionarily maladaptive outcomes (e.g., fertility decline, child

abuse, and suicide). Environmental mismatches and maladaptive culture sometimes may result in behaviors that decrease reproductive fitness. Advanced integration of HBE, EP, and CE can enhance more holistic theories in evolutionary behavioral sciences (e.g., Morita 2018).

Conclusion

HBE explores adaptation of human behavior in a current environment. Since the 1970s, HBE has varied its main contents but grown definitely. In addition to “traditional-type” studies on foraging and resource distribution in small-scale societies, a number of “new-type” studies on reproduction in industrialized populations have been performed. Both fieldwork with unique perspectives and statistical analyses of secondary datasets are recent remarkable achievements. HBE contains a variety of research topics, study populations, and methodologies, which promotes further evolutionary understanding of human behavior. By integrating with EP and CE, maladaptive outcomes will also be explained better in future studies.

Cross-References

- [Alloparenting and Grandparenting](#)
- [Cultural Evolution](#)
- [Cultural Transmission](#)
- [Fertility](#)
- [Field of Behavioral Ecology, The](#)
- [Grandmother Hypothesis, The](#)
- [Hunter-Gatherer Societies](#)
- [Life History Strategies](#)
- [Parental Investment Theory](#)
- [Reproductive Strategies](#)
- [Sociobiology Wars, The](#)
- [Towards Methodological Pluralism in Psychological Sciences](#)

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Human Brain Evolution

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Definition

There have been significant changes in brain development, anatomy, and molecular biology over the course of human evolution.

Introduction

Modern humans are characterized by remarkable specializations of cognition, including a language that is rich in syntactic complexity and symbolic meaning, a nuanced understanding of the mental states of others, a strong motivation to share in pursuing joint goals, an ability to manufacture sophisticated tools, and an extraordinary capacity for cultural learning. What are the evolutionary changes in brain structure and molecular biology that underlie these cognitive faculties? A comprehensive understanding of human brain evolution requires data from multiple perspectives, incorporating information from fossils, archaeology, comparative neuroanatomy, and genetics.

Evolution of the brain in the human lineage

Compared to other primates and our earliest hominin ancestors, modern humans have very large brains. Weighing approximately 1,400 g on average, our brains are roughly three times bigger than those of other great apes and also significantly larger than expected for a primate of our body size (Jerison 1973; Martin 1990). Because great apes (chimpanzees, bonobos, gorillas, and orangutans) are the closest living relatives of humans, they provide the most relevant phylogenetic basis for comparison. More broadly, there are several mammalian species, including elephants, dolphins, and whales, that have bigger brains than humans in absolute size. Pilot whale brains have even been shown to contain more neocortical neurons than those of humans (Mortensen et al. 2014). But humans are the most extreme outlier from the typical mammalian brain-body size scaling relationship. Although the average adult human brain is only approximately 2% of body size, it consumes about 20% of the whole body's energy budget (nearly 400 kcal per day) due to the high level of activity of neuronal firing and signal transmission across synaptic connections (Kuzawa et al. 2014).

The hominin fossil record indicates that there has been a general trend over time for steadily increasing cranial capacity, accompanied by reorganization of cerebral morphology (de Sousa and

Cunha 2012; Falk 2012; Holloway 2015). The cranial capacity of hominin ancestors shows very gradual increase in brain size early in the evolution of the lineage, with a period of more accelerated growth within the last two million years since the origin of the genus *Homo* (Du et al. 2018). There are some notable exceptions to this apparent trend, however, such as *Homo naledi*, a southern African hominin which had a small cranial capacity of 460 ml at about 300,000 years ago (Holloway et al. 2018), and *Homo floresiensis* from the island of Flores in Indonesia, which had a cranial capacity of approximately 400 ml at 190,000–50,000 years ago (Falk et al. 2005). Additionally, it is apparent that evolution of endocranial morphology in fossil hominins has not always been tightly synchronized with brain size changes (de Sousa and Cunha 2012; Falk 2012; Holloway 2015). For example, there are differences in endocranial shape between recent modern humans and similarly large-brained close relatives, the Neandertals, and the earliest *Homo sapiens*. The endocranial shape of modern humans is more globular, or rounded, due to bulging of the parietal and lateral cerebellar regions (Bruner et al. 2003; Neubauer et al. 2018).

Several interrelated features of life history biology are associated with the large brains of modern humans, including elevated nutritional and metabolic requirements, slower development, a longer lifespan, and more involvement in raising offspring by fathers and grandparents to assist mothers (Sherwood and Gómez-Robles 2017; Hawkes and Finlay 2018). Also, likely due to obstetrical or energetic constraints on the timing of parturition (Rosenberg 1992; Dunsworth et al. 2012), a larger fraction of brain growth in humans occurs after birth compared to other primates (Halley 2017). This means that significant neurodevelopmental events that lay the groundwork for brain function, such the refinement of synaptic connections and myelination of axons, take place over a prolonged period of time in a rich social and ecological context (Petanjek et al. 2011; Miller et al. 2012; Bianchi et al. 2013). The plastic brains of our helpless human infants incorporate these experience as neuronal circuits are being constructed, paving the way for more elaborate cultural learning (Buřill et al. 2011; Sherwood and Gómez-Robles 2017).

Detailed comparisons of human brain anatomy to that of other primates, particularly chimpanzees, have shown that the association regions of the prefrontal, posterior parietal, precuneus, and temporal cortex involved in higher-order cognitive functions have become especially expanded (Buckner and Krienen 2013; Rilling 2014; Bruner et al. 2017; Mars et al. 2017; Smaers et al. 2017). These cortical regions also mature particularly late in development (Sakai et al. 2011; Fjell et al. 2015). Some have argued that change in the absolute and proportional size of the prefrontal association cortex is tightly correlated with corresponding changes in other brain areas (Barton and Venditti 2013; Gabi et al. 2016), whereas other analyses show that human prefrontal cortex is enlarged beyond what would be predicted from primate brain scaling trends (Smaers et al. 2017).

To some extent, evolutionary changes to human association cortex have involved differential expansion of regions that have clear and well-established homologs in other primates (Donahue et al. 2018). Notably, many regions of the prefrontal cortex, including Broca's language area, have been shown to be homologous among humans, great apes, and various other anthropoid species (Gil-da-Costa et al. 2006; Schenker et al. 2008; Wilson et al. 2015). Furthermore, cerebral hemispheric asymmetry is not entirely unique in human brain evolution, and seems to be an extension of trends that can be observed in other primates, especially great apes (Balzeau et al. 2011; Hopkins et al. 2015). Some other changes in human association cortex, however, appear to comprise proliferation of novel and functionally distinct areas. For example, data suggest that, compared to rhesus macaques, human intraparietal sulcus includes four additional motion-sensitive areas dedicated to processing of three-dimensional form in relation to motion (Orban et al. 2006). As a result, human parietal cortex might include more regions dedicated to processing of shape. Addition of these and other posterior parietal areas likely enhanced processing of visual and somatosensory information involved in manipulative abilities associated with tool production and handling (Stout and Chaminade 2007). More detailed comparative mapping of parietal cortex in great apes, however,

is needed to resolve whether the observed intraparietal sulcus organization in humans is truly unique or shared with our closest primate relatives.

In addition to changes in the size of neuroanatomical structures, it is also apparent that there has been significant rewiring of fiber tract connections in human brain evolution. Several of the long-range pathways that interconnect the association regions of the frontal, parietal, and temporal cortex with each other and to the cerebellum are differentially expanded in human brains compared to other primates (Rilling et al. 2008; Balsters et al. 2010; Hecht et al. 2015). These circuits, which include the arcuate and superior longitudinal fasciculi, are involved in language, tool making, and imitation. Furthermore, reward systems utilizing the neurotransmitter dopamine in the striatum have been reshaped, likely to increase attention to social signals and facilitate vocal learning. Notably, comparative molecular and anatomical examinations of the basal ganglia show human-specific increase in dopaminergic innervation of the medial caudate nucleus (Raghanti et al. 2016; Sousa et al. 2017), a highly interconnected region of the striatum that is involved in language production, among other functions.

The evolutionary changes in the genome underlying distinctive molecular and cellular process of human brain development have also been investigated extensively. These studies have shown how single nucleotide substitutions, gene duplications, and modifications that regulate gene expression have impacted fundamental aspects of human neurobiology. Uniquely human genetic changes increase cell proliferation as the brain is being formed or stimulate neurons to grow more complex dendritic branches with a higher number of synaptic connections (Enard 2011; Florio et al. 2017; Suzuki et al. 2018). One particularly striking case is the gene *SRGAP2*, which has a human-specific duplicate (*SRGAP2C*) that functions to increase the density of synaptic spines on dendrites (Charrier et al. 2012). Relatedly, analyses of RNA transcript level in brain tissues of humans and other species have revealed increased gene expression in the human brain compared to non-human primates, which is not evident in non-brain

tissue, such as the heart and the liver (Enard et al. 2002). These human-specific upregulated genes are enriched for functions including synaptic transmission and energy metabolism (Cáceres et al. 2003; Uddin et al. 2004; Somel et al. 2013; Muntané et al. 2015), supporting the idea that human brain evolution is characterized by molecular modifications to increase levels of neuronal activity (Preuss 2011).

Cross-References

- [Brain At Birth](#)
- [Brain Development](#)
- [Brain Growth in the First Year](#)
- [Environmental Unpredictability and Bet-Hedging](#)
- [Resources for Brain Development](#)

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Human Brain Size Evolution

- [Brain Size Growth in Humans and Nonhuman Primates](#)

Human Computer Interaction

- [Repeated or Iterated Prisoner's Dilemma](#)

Human Constructed Elements

- [Human Products](#)

Human Cooperation

- [Evolution of Human Sociality, The](#)
- [Jonathan Haidt's The Righteous Mind](#)

Human Copulation

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Synonyms

[Copulate](#); [Mate](#); [Sex](#); [Sexual intercourse](#)

Definition

Both copulation and sexual intercourse have been used to refer to penetrative, heterosexual sexual activity, that is: penile-vaginal sex. Here, however, the term “copulation” will refer to both penetrative (i.e., vaginal or anal sex) as well as nonpenetrative (e.g., oral sex) forms of intercourse that occur between same-sex and opposite-sex partners.

Introduction

Defining sex is – perhaps surprisingly – the subject of significant debate and disagreement in lay as well as scientific circles. Several works have investigated the ways in which individuals define “sex” or “having had sex” and have arrived at disparate findings, depending on when these attitudes are assessed (Rosenthal 2013), the age of the respondent (Sanders et al. 2010), and even how the question is asked (Peterson and

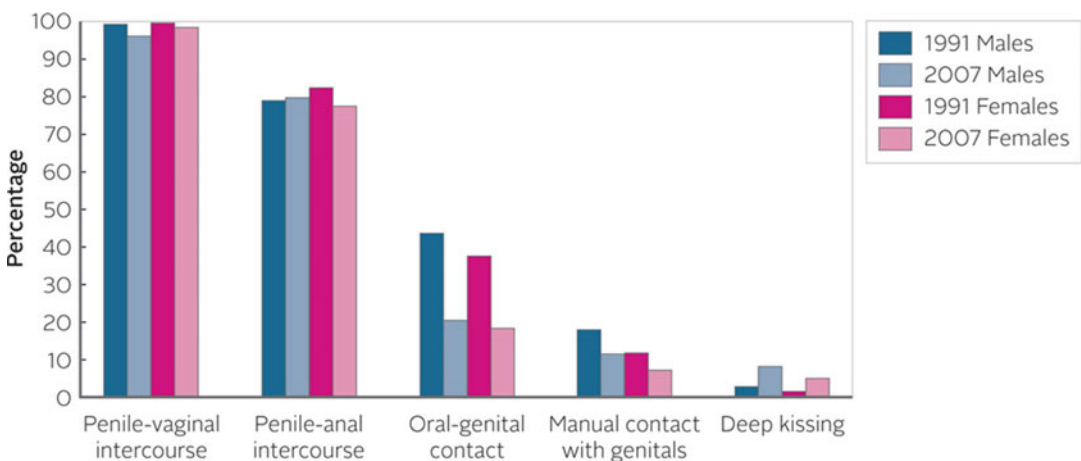
Muehlenhard 2007). This ambiguity is mirrored in the scientific community, where “copulation” and “sex” have been used to refer to exclusively intromission (i.e., penile-vaginal sex) as well as intromission between opposite-sex conspecifics and penetrative sex, oral sex, and manual stimulation of genitals that occurs within both same and opposite-sex pairings (Bailey and Zuk 2009). Herein, human copulation, colloquially referred to as “sex” or “sexual intercourse,” will adopt an inclusive definition, including (1) oral sex, (2) vaginal sex, and (3) anal sex. The various expressions and function(s) of human copulation will be explored through the review of psychological, cross-cultural, and phylogenetic evidence.

Human Copulation

There is considerable debate and disagreement when it comes to answering the following question: What is sex? When discussing human copulation, or “sex,” with a partner, individuals have many different definitions as to the nature of the sexual contact implied. Generally, individuals are most likely to consider penile-vaginal intercourse as “sex,” while considerable disagreement appears with considerations of anal intercourse, oral sex, manual genital contact, and kissing

(Peterson and Muehlenhard 2007; Sanders and Reinisch 1999). The nature of the lay disagreement as to the classification of nonintromission sexual contact as “sex” seems to depend on several factors, including when these attitudes are assessed. As demonstrated in Fig. 1, more recent college student samples are *less likely* to define oral sex and manual genital contact as “sex” compared to college student samples assessed 20 years ago (Rosenthal 2013).

This difference in lay definitions of “sex” is also represented as an age difference, wherein men aged 18–29 are less likely to define oral sex and manual genital contact as “sex,” compared to men over the age of 30 (Sanders et al. 2010). Interestingly, the same cross-sectional study of definitions of “sex” found that all men *but* those in their oldest age group (65+) were significantly more likely to indicate that anal sex was defined as “sex” (Sanders et al. 2010). All of these works have used a similar approach when assessing disagreement as to the definition of “sex,” that is, asking participants if, after engaging in these various behaviors with a partner, they would say that they have “had sex” with that partner. In other words, these studies have all relied upon a methodology wherein they ask participants if various sexual behaviors “count” as sex. However, this methodology involves the implicit assumption that participants have clear (that is, not



Human Copulation, Fig. 1 The percentage of males and females that indicated that they would “say you ‘had sex’ with someone if the most intimate behavior you engaged in

was . . . ?” (Sanders and Reinisch 1999, p. 276; figure from Rosenthal 2013)

contradictory) definitions of what contact constitutes “sex.” Conclusions about how laypersons define “sex” may change if these attitudes are assessed in a manner which allows for the representation of uncertainty.

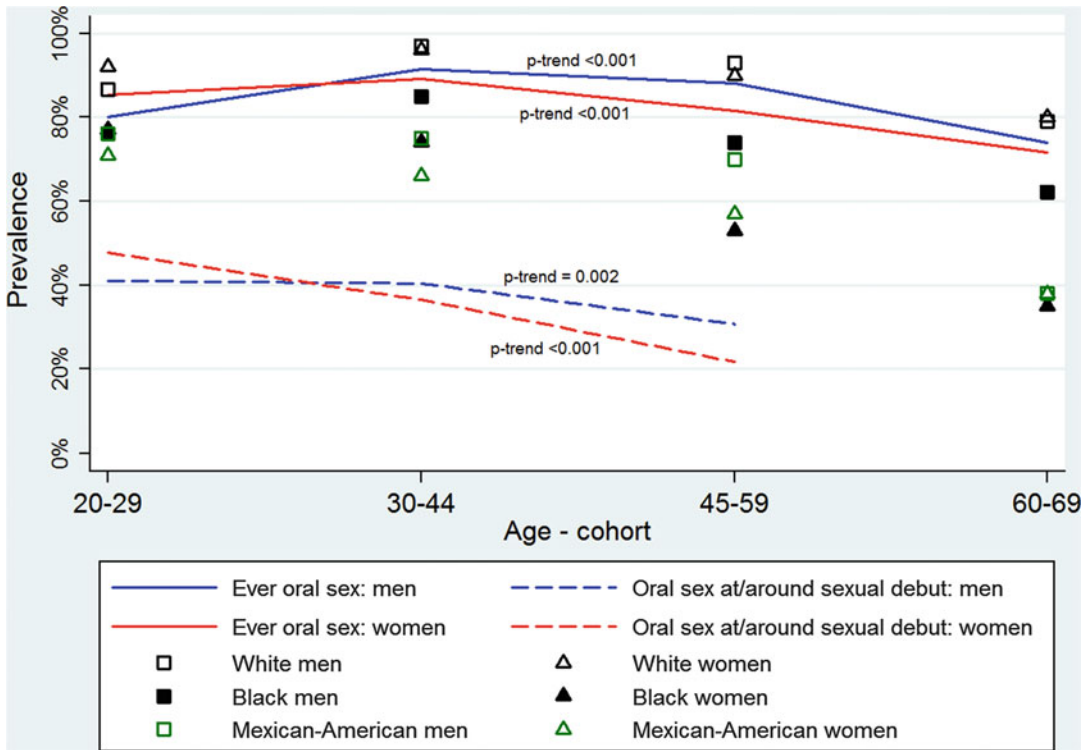
Work does suggest that the way in which participants are asked to define sex can affect the definition of sex that they provide (Peterson and Muehlenhard 2007). Specifically, Peterson and Muehlenhard (2007) asked participants to share experiences which were “almost but not quite. . .” or “just barely qualified. . .” as sex and thereby employed a methodology that allowed for representations of uncertainty or ambiguity in definitions of sex. Activities that “almost but not quite. . .” fit participants’ definitions of sex included brief or partial intromission, genital to genital contact without penetration, oral sex, and manual genital stimulation. Interestingly, these same activities were represented (albeit, to a lesser degree) as behaviors that “just barely. . .” fit participants’ definitions of sex. Participants explained that these nonintromission types of sexual contact “fit” within their definitions of sex because they contained what participants perceived to be other, critical defining features, such as genital contact, orgasm, “an exchange of fluids,” sexual arousal, and/or nudity. Taken together, it seems as though individuals have an overwhelming tendency to define sex/copulation as intromission, while expressing some uncertainty as to whether or not other types of genital contact such as oral sex, anal sex, and manual genital contact fit within this definition – among other factors (such as age, the specific ways in which definitions of sex are elicited from participants, etc.) it seems as though these definitions depend upon the *anticipated consequences* of labeling a specific type of sexual contact as “sex.” Specifically, when the consequences of labeling a specific type of sexual contact as “sex” are negative, individuals’ are more likely to label these experiences as “not quite sex” (Peterson and Muehlenhard 2007). For example, some individuals reported a motivation to define sexual contact with a same-sex partner as “not quite sex” in order to preserve their identity as heterosexual.

Disagreements as to the definition of copulation/sex are also present in the scientific community, where “copulation” and “sex” have been used to refer exclusively to intromission (i.e., penile-vaginal sex) as well as penetrative sex, oral sex, and manual stimulation of genitals that occurs within both same *and* opposite-sex pairings (Bailey and Zuk 2009). Studies of copulation in nonhuman primates often define copulation as sexual contact between opposite-sex conspecifics that *must* include intromission. Alternatively, comparative studies of sexual activity and contact between same-sex pairs have defined a variety of activities between same-sex conspecifics (e.g., oral sex, manual stimulation of genitals) as “copulation” (Bailey and Zuk 2009). The following evolutionary analysis of human copulation will adopt the latter, more inclusive definition, including (1) oral sex, (2) vaginal sex, and (3) anal sex. These various expressions and function(s) of human copulation will be explored through the review of psychological, cross-cultural, and phylogenetic evidence.

Oral Sex

Oral sex can be classified as either the stimulation of the female genitals (*cunnilingus*) or the male genitals (*fellatio*) with the mouth. The incidence of oral sex has been steadily increasing in the United States, and recent estimates indicate that over 80 % of individuals over the age of 20 have engaged in oral sex (85.4 % of men and 83.2 % of women; D’Souza et al. 2014). While oral sex is overall a very common form of copulation, individuals that are most likely to have engaged in oral sex are White men and women, individuals under the age of 60 (see Fig. 2), and individuals that have attended college (Baumeister 2001).

Evolutionary analysis of a given behavior, cognition, or affect typically follows one of the two paths of inquiry: (1) from form to function or (2) from function to form (Buss 1995). The former refers to the process of identifying a particular behavior of interest and searching for the adaptive problem for which that particular behavior may have been preferentially selected and perpetuated; in other words, what is the function of this behavior? The latter refers to the process of identifying a



Human Copulation, Fig. 2 The percentage of individuals (by race, age, and sex) that have engaged in oral sex and have engaged in oral sex proximate to their age at sexual debut (Figure from D’Souza et al. 2014)

particular adaptive problem of interest and searching for the behavior, cognition, or affect that might have solved that adaptive problem in ancestral environments; in other words, what psychological mechanism might have evolved to address this problem? Therefore, an analysis of a given behavior of interest – oral sex – will take the following form; what is the function of oral sex?

Oral sex has long been colloquially understood as a form of sexual contact that often serves as a substitute for other forms of sexual contact during one’s sexual debut (Duberstein Lindberg et al. 2008). As Duberstein Lindberg puts it, “There is a widespread belief that teens engage in nonvaginal forms of sex, especially oral sex, as a way to be sexually active while still claiming that technically, they are virgins” (Wind 2008). Indeed, oral sex is more common among teens than vaginal sex, and teens perceive oral sex to be less likely to precipitate many negative emotional and social outcomes, compared to vaginal

sex (e.g., less likely to get them into trouble, cause them to feel guilty or bad about themselves, less likely to conflict with their ethical, religious, or moral values; Halpern-Felsher et al. 2005). However, recent work suggests that oral sex often closely corresponds with the initiation of other types of sexual contact (including vaginal sex), rather than serving as an alternative for these other types of sexual contact (Duberstein Lindberg et al. 2008). Findings from a national survey indicate that the proportion of teens and young adults that engage in oral sex *before* other forms of sexual contact (26 % of females and 24 % of males) is strikingly similar to the proportions of teens and young adults that engage in oral sex *after* other forms of sexual contact (27 % of females and 24 % of males; Copen et al. 2012). It seems as though oral sex is common in both teens and adults but does not serve the function of initiating sexual activity or delaying other forms of sexual contact.

Comparative analysis of a particular behavior – such as oral sex – is often illuminating when determining the evolutionary function and adaptive importance of that behavior. Phylogenetic evidence, comparing the prevalence and function of a behavior in other species, supports the proliferation of an adapted behavior through generations of selection pressures. Oral sex is quite common in nonhuman animals, appearing in bonobos, stump-tail macaques (Chevalier-Skolnikoff 1974), lemurs, and orangutans. In nonhuman primates the function of oral sex is often affiliative between same-sex conspecifics. For example, observations of oral-genital contact in male stump-tail macaques suggests that such contact is most likely to occur between an adult male and a juvenile that has not yet reached sexual maturity, in the context of other positive, affiliative behaviors (such as grooming, carrying, and other parental care; Chevalier-Skolnikoff 1974). Also, the frequency of same-sex oral-genital contact between primates of disparate age suggests that this contact likely serves an educational function, critical to subadult primates' sexual development (Gray and Garcia 2013). Alternatively, it is possible that oral sex in nonhuman animals is simply reflexive, a response to attractant pheromones secreted near the genitals. In nonhuman animals, there is little consensus as to the function of oral sex, but the behavior may serve the complex function of assisting in the sexual development of subadults or fostering social ties between same-sex conspecifics.

Recent work has illuminated three potential functions of oral sex in humans (Pham and Shakelford 2013) – which, unlike other types of sexual contact (i.e., kissing), is a practice that is quite common cross-culturally – (1) the detection of rivals' semen, (2) the increase of partner's relationship satisfaction (and thereby, fidelity), and (3) the facilitation of sperm retention. The first proposed function of oral sex in humans, the detection of rivals' semen, is detailed in the *infidelity-detection hypothesis* that suggests cunnilingus may allow heterosexual males to test for the presence of rival semen in the vulva and therefore determine (at least in part) the sexual fidelity of their current mate. If cunnilingus serves this

infidelity-detection function, one would expect that these concerns would be particularly great during female peak fertility (when the likelihood of conception is greatest); indeed, nonhuman animals display more frequent oral-genital stimulation during female's peak fertility and humans indicate that the odor of vaginal secretions during peak fertility is more pleasant, compared to secretions during low fertility (Doty et al. 1975). Furthermore, men that are at a greater risk of experiencing sexual infidelity (operationalized as having a partner high in sexual and physical attractiveness) are more interested in performing oral sex and perform oral sex for longer durations than those with lower risks of experiencing sexual infidelity on part of their heterosexual partner (Pham and Shakelford 2013).

The second proposed function of oral sex – that it increases partner's relationship satisfaction – is partially supported throughout literature exploring the relationship between sexual satisfaction and relationship satisfaction. Frequency of oral sex has been repeatedly linked to sexual satisfaction, in same-sex and opposite-sex couples. Oral sex seems particularly important for the sexual satisfaction of individuals in same-sex couples, as lesbians report oral sex as their most-preferred technique for achieving orgasm and oral sex has been found to be the most-frequently engaged in sexual contact for gay men (Ekstrand and Coates 1990). What seems clear from this work is the relationship between oral sex and sexual satisfaction – the relationship that is more contentious in the literature is that between sexual satisfaction and relationship satisfaction.

Evident in the literature are *both* strong correlations between sexual satisfaction and various indicators of relationship satisfaction, such as overall satisfaction with one's marriage, satisfaction with one's dating relationship, and feelings of love and commitment, *as well as* longitudinal works indicating that relationship satisfaction and sexual satisfaction seem to change concurrently (Sprecher 2002). However, these findings are qualified by works which have failed to demonstrate strong evidence that changes in relationship satisfaction can account for or explain changes in sexual satisfaction or that changes in

sexual satisfaction can explain observed changes in relationship satisfaction (Byers 2005). Instead, it seems as though the relationship between sexual satisfaction and relationship satisfaction is mediated by the quality of communication in an intimate relationship (Byers 2005) and the similarity of sexual desire between partners in an intimate relationship (Davies et al. 1999). Overall, it seems as though oral sex can facilitate greater sexual satisfaction in both same-sex and opposite-sex mateships, but evidence providing a direct causal link between sexual satisfaction and relationship satisfaction is lacking.

The third proposed adaptive function of oral sex in humans – the facilitation of sperm retention – has received support in literature exploring the relationship between cunnilingus and the experience of female orgasm. Originally termed the *Upsuck Theory* by Masters and Johnson, recent work indicates that the experience of female orgasm (and the associated release of oxytocin) is associated with uterine contractions that act as a peristaltic pump, promoting the travel of sperm and other fluids in the reproductive tract towards the oviduct (Zervomanolakis et al. 2009). Therefore, if a female experiences orgasm during a heterosexual encounter, the likelihood of conception is promoted as the experience of female orgasm decreases the distance that must be traveled by spermatozoa to reach the ovum. Using both objective and subjective estimates of sperm retention (that is, sperm retained in the reproductive tract following penile-vaginal copulation), Baker and Bellis (1993) find that female orgasms occurring within a specific time window relative to male ejaculation (between 1 min before male ejaculation to 45 min after male ejaculation) increased the amount of sperm retained in the reproductive tract. This sperm retention theory appears to be relevant only to penile-vaginal copulation, rather than the current behavior of interest – oral sex. However, the likelihood of experiencing female orgasm through penile-vaginal copulation alone (that is no clitoral stimulation with the hands or the mouth, etc.) is quite low. Data from a national survey suggests that the likelihood of experiencing female orgasm during penile-vaginal copulation is dramatically

increased (from around 12 % to around 32 %) if oral stimulation of the clitoris (e.g., oral sex) occurs (Richters et al. 2006). Therefore, the likelihood of retaining sperm in the reproductive tract and the travel of spermatozoa and seminal fluid to the oviduct are both facilitated by the female orgasm, which is more likely to occur when the clitoris is stimulated, particularly via cunnilingus.

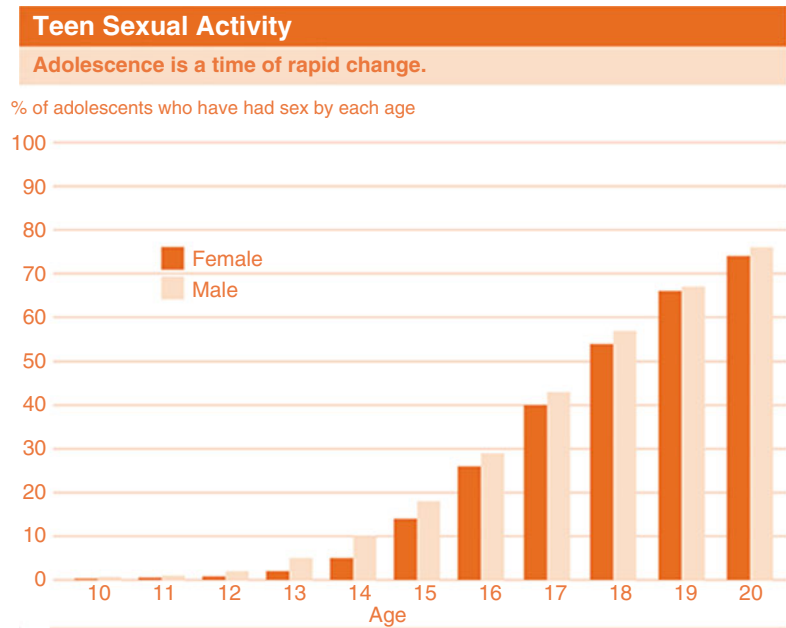
Vaginal Sex

Vaginal sex refers to penetrative copulation, which can be classified as the penetration of the vagina with the penis (penile-vaginal copulation). Contrary to contemporary rhetoric, the age at which heterosexual individuals initiate penile-vaginal copulation has been increasing in recent years; in 1995 around 20 % of young adults reported initiating penile-vaginal copulation before the age of 15, while estimates from 2008 indicate that only 11 % of females and 14 % of males report initiating penile-vaginal copulation before the age of 15 (Finer and Philbin 2013). Recent estimates indicate that the average age of penile-vaginal sexual debut is 17 years of age in the United States, with the likelihood of initiating penile-vaginal copulation dramatically increasing for both males and females after the age of 16 (see Fig. 3). The age of penile-vaginal sexual debut varies dramatically cross-culturally, with 40 % of Brazilian males and over 50 % of Bangladeshi females initiating penile-vaginal copulation before the age of 15 (Wellings et al. 2006). Penile-vaginal copulation is the most *common* form of sexual contact in heterosexual couples (98.5 % of couples surveyed experienced penile-vaginal copulation during a 21-day span; Hurlbert et al. 1993) and is reported to be the most *pleasurable* form of sexual contact in heterosexual males and females.

Vaginal sex can take many forms in primates, including (1) male on top, female supine (*ventro-ventral position*), (2) female on top, male supine (*ventro-ventral position*), (3) rear entry (*dorso-ventral position*), (4) inverted rear entry (*inverted dorso-ventral position*), and (5) side by side (*latero-lateral position*). The ventro-ventral position of vaginal sex, with the male on top, female supine (i.e., “missionary position”) is by

Human Copulation,

Fig. 3 The percentage of individuals (by sex and age) that have engaged in penile-vaginal sex (Figure from “American Teens Sexual and Reproductive Health”, 2014)



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far the most common among humans (Gray and Garcia 2013) and has even been demonstrated to be common across cultures, appearing in the Alorese, Hopi, Marshallese, Tikopia, Balinese, among others (Dixon 2012). While occurring less frequently in other primates, orangutans, bonobos, and gorillas also engage in ventro-ventral vaginal sex, both with the male and with the female on top (Dixon 2012); some researchers hypothesize that this face-to-face copulatory posture evolved as primate intelligence increased, which gave way to variations in copulatory postures (specifically, variations from the dorso-ventral “norm”). Also, this face-to-face copulatory posture facilitates communication between opposite-sex conspecifics during vaginal sex, and such eye contact can be used to assess interest in sexual contact (Dixon 2012); indeed, eye contact has been demonstrated to be used as a method of communicating sexual intent. However, ventro-ventral vaginal sex with the male on top, female on bottom has been associated with low female sexual satisfaction and female difficulty achieving orgasm (Rosenthal 2013), as this position does not afford the female control over the depth, speed, or angle of intromission and often does not stimulate the clitoris. Variations

on the ventro-ventral position that involve manual stimulation of the clitoris *are* associated with a greater likelihood of females achieving orgasm during vaginal sex. It is important to note that it is uncommon for females to achieve orgasm when engaging in penile-vaginal copulation alone, that is, without additional clitoral stimulation orally or manually (“vaginal orgasm”; Gray and Garcia 2013). There is some evidence to suggest that the vaginal orgasm might play a role in mate choice, wherein longer penises are associated with a greater likelihood of achieving female vaginal orgasm and females that report a preference for longer penises are more likely to experience vaginal orgasms (Costa et al. 2012). These differences in orgasm outcomes might create a selection pressure favoring longer penises, particularly for females that experience vaginal orgasm.

Dorso-ventral copulatory positions (i.e., “doggie style”), less common but still preferred among male and female humans, are much more common among nonhuman primates. These positions allow the, typically larger, males to remain standing, while the female crouches on all fours. In primates the dorso-ventral copulatory position is often accompanied by the use of the feet (termed the “leg lock” position) or the hands to restrain the

female, particularly common during long duration vaginal sex (between 15 and 35 min; Dixon 2012). Importantly, the dorso-ventral copulatory position allows the males to retain a grip on tree branches with their prehensile tails and/or their feet. A fascinating variation on the dorso-ventral copulatory position is the inverted dorso-ventral position, wherein both the male and female primate are suspended, upside-down, by a tree branch. This position, common in the slow loris, slender loris, and the aye-aye, is thought to provide protective benefits, allowing the partners to hide during copulation and to quickly drop from their tree limb if disturbed or pursued by a predator (Dixon 2012).

As above, evolutionary analysis of a given behavior, cognition, or affect typically follows one of the two paths of inquiry: (1) from form to function or (2) from function to form (Buss 1995). Again, an analysis of the given behavior of interest – vaginal sex – will take the following form; what is the function of vaginal sex? There are two prevailing explanations as to the function of human vaginal sex, (1) (the somewhat obvious adaptive function) the production of offspring and therefore the proliferation of one's genes in future generations and (2) the increase of partner's relationship satisfaction (and thereby, fidelity). The former function refers to the fact that in the Environment of Evolutionary Adaptedness (EEA) for humans (roughly 10,000 years ago) – a time characterized by significant selection pressures in the environment which provided significant advantages in survival and reproduction for certain members of a species, with specific traits – modern medical technologies which enable individuals to conceive in the absence of penile-vaginal copulation were not available. Therefore, the production of offspring depended entirely upon fertilization as a result of penile-vaginal copulation between opposite-sex conspecifics. The necessity of sexual behavior (such as vaginal sex) for the survival and perpetuation of one's genes has likely produced natural rewards for engaging in such behavior, such as the production and release of neurotransmitters that produce feelings of desire and pleasure (e.g., dopamine and serotonin) in the nucleus accumbens and the

ventral tegmental area in the midbrain. Sexual behaviors are a “natural reinforcer” along with other behaviors that have been historically critical for survival and reproduction, such as eating, drinking, and seeking social connectedness. Activity in specific pathways of the brain (e.g., the nucleus accumbens and the ventral tegmental area) *rewards* individuals for and *motivates* individuals to engage in behaviors – like vaginal sex – which have been critical for the perpetuation of genes into subsequent generations. Put simply, were it not for the existence of vaginal sex and a desire to engage in vaginal sex, the human species would not continue to exist.

The second proposed function of vaginal sex – that it increases partner's relationship satisfaction and fidelity – is partially supported throughout literature exploring the relationship between sexual satisfaction and relationship satisfaction. As mentioned above, the existence of a *direct* causal relationship between sexual satisfaction and relationship satisfaction is somewhat contentious; however, the use of vaginal sex to maintain a long-term bond between mates is supported in both the human and nonhuman animal literature. Among nonmonogamous species of primates, such as lemurs and chimpanzees, almost all of their vaginal sex takes place during periods of female peak fertility, ovulation (Gray and Garcia 2013). Therefore, one might infer that in these nonmonogamous species, vaginal sex serves the primary function of producing offspring and that vaginal sex is motivated by cues indicative of female receptivity. These cues can be detected by scent or sight; male tamarins display increased erections and mounting behaviors when exposed to the scent marks of an ovulating female tamarin and vaginal sex increases in frequency while female bonobos display a swollen perineum, which is indicative of female ovulation. It is important to note that while these cues have evolved to signal times of peak fertility to sexually mature males and therefore motivate vaginal sex behaviors, the accuracy of these cues is a matter of some debate. According to the *graded-signal hypothesis*, in nonmonogamous species that live in multi-male, multi-female groups, signals of ovulation vary in their strength to indicate

variations in the probability of conception (Nunn 1999). For example, sexual swellings would vary in terms of their size with their largest expression indicative of the greatest probability of conception. This type of variable signaling provides benefits to both males and females of nonmonogamous species; it allows the males to preferentially engage in vaginal sex with fertile females, and it provides a sufficiently wide window of *possible* ovulation (i.e., “graded”) to produce paternity uncertainty – if males in these multi-male, multi-female social groups are unsure as to which offspring are their genetic relatives or that of their rivals, they will be less likely to engage in infanticide.

Alternatively, in monogamous species, such as gibbons and siamangs, vaginal sex (while taking place relatively infrequently) does take place during periods of female infertility (e.g., when a female is currently pregnant; Gray and Garcia 2013). There are several physical markers that indicate a species evolved to engage in monogamous mating in the context of long-term pair bonds – such as small testicles (indicative of infrequent sperm competition) and low sexual dimorphism (indicative of *similar parental investment* provided by males and females, and relatively infrequent male physical competition for access to mates). In fact, some scholars argue that monogamy may have evolved, in part, to solve the adaptive problem of producing and caring for offspring that require significant investment; for instance, due to a long juvenile period or ecological constraints that make acquiring enough resources to produce healthy offspring difficult without male–female cooperation.

It is possible that the vaginal sex that takes place during periods of female infertility, observed in gibbons, siamangs, and many monogamous bird species (Eens and Pinxten 1995), may serve a function of increasing relationship satisfaction and protecting against threats to the fidelity of the mateship. For example, female sterlings have been observed courting and initiating copulation with males whom were seeking the attention of other females even after they have laid fertilized eggs (Eens and Pinxten 1995). Humans also engage in several mate retention tactics,

including enhancing one’s appearance to appear more attractive to one’s partner and engaging in more frequent sexual contact, in response to perceived threats to their relationship. Interestingly, both men and women have reported faking orgasm during vaginal sex in order to increase their partner’s satisfaction (Muehlenhard and Shippee 2010) and women are more likely to fake orgasm during vaginal sex when they perceive that their relationship may be at a greater risk for experiencing partner infidelity and defection.

Anal Sex

Anal sex refers to penetrative copulation, which can be classified as the penetration of the anus with the penis (penile-anal copulation). While often colloquially assumed to be prevalent in gay sexual relationships, 20 % of gay men report never experiencing anal sex (Laumann 1994). Furthermore, the incidence of anal sex has been steadily increasing among heterosexual couples in the United States, with estimates (of having “ever” engaged in anal sex with an opposite-sex partner) increasing from around 20 % in 1995 to approximately 36 % in 2013 (Chandra et al. 2013). While anal sex is overall a relatively uncommon form of copulation, individuals that are more likely to engage in anal sex are typically those that report higher levels of education and lesser religiosity (Baumeister 2001). Interestingly, women report anal sex as being their least preferred and the least satisfying type of sexual behavior (Hurlbert et al. 1993). While oral sex is reported as being the most preferred and most frequently engaged-in type of sexual behavior by gay men, anal sex is still a relatively frequent type of sexual contact in male same-sex couples; 75 % of men reported engaging in the “insertive role” while 81 % reported engaging in the “receptive role” (Laumann 1994).

Anal sex in the primate world is rare, and often occurs during isosexual encounters (male-male mounting and intromission; Dixon 2012). The male same-sex mounting and anal sex which take place in nonhuman primates is proposed to serve a developmental function – occurring frequently in juveniles and decreasing in frequency

as the primate reaches sexual maturity – and is proposed to be maintained and motivated by the pleasurable sensation associated with engaging in anal sex from the “insertive role” (Dixon 2012). This type of male same-sex anal intromission has been observed in orangutans, stump-tail macaques (Chevalier-Skolnikoff 1974), and rhesus monkeys, among others. As discussed relevant to oral sex above, same-sex sexual contact via anal sex in nonhuman primates likely serves the adaptive function of facilitating sexual development (Chevalier-Skolnikoff 1974). Interestingly, some documented cases of anal sex between same-sex conspecifics do not seem to be developmental and transitory in nature; in the case of two male rhesus monkeys raised in captivity, the two monkeys were capable of successfully mounting and achieving ejaculation during mating with a female, but demonstrated a preference for social and sexual contact with their male partner when given the option to interact with a female.

Conclusion

In the current discussion of human copulation, it has been demonstrated that the definition of copulation or “sex” is the topic of significant debate and disagreement, both within lay and scientific circles. Overall, one’s individual definition of “sex” or “having had sex” seems to depend on when these attitudes are assessed (Rosenthal 2013), the age of the respondent (Sanders et al. 2010), and how the question is asked (Peterson and Muehlenhard 2007). This ambiguity in the scientific community may be indicative of a transition away from heteronormativity, where “copulation” and “sex” have historically been used to refer exclusively to penile-vaginal sex but are now adopting more inclusive definitions which can capture partnered sexual contact between same-sex conspecifics (Bailey and Zuk 2009).

Taken together, human copulation in the form of oral sex is becoming increasingly common and likely serves the adaptive function of promoting social connectedness (in nonhuman primates) or is simply a reflexive response to appetitive vaginal

secretions. Furthermore, oral sex in humans may serve the adaptive function of allowing for the detection of infidelity, increasing relationship satisfaction, and facilitating sperm retention (Pham and Shakelford 2013). Vaginal sex is the most common and most preferred form of sexual contact between heterosexual couples. While dorso-ventral forms of vaginal sex are most common in the primate world, the appearance of ventro-ventral (face-to-face) vaginal sex in some primates (including humans) may have evolved to facilitate communication or is simply indicative of increasing species intelligence. Vaginal sex likely serves many functions, including the propagation of one’s genes into subsequent generations, increasing relationship satisfaction, and increasing the likelihood of partner fidelity. Anal sex, while relatively uncommon in the primate world, is becoming increasingly common in heterosexual human mateships (Chandra et al. 2013). It likely serves affiliative and relationship maintenance functions in humans, as well as functions relevant to sexual development in nonhuman primates (Chevalier-Skolnikoff 1974). Overall, it is clear that human copulation, in its many forms, serves important functions for developing and maintaining social connections, sexual development, and satisfaction in intimate mateships. Many of these behaviors have been present throughout evolutionary history, as evidenced by the many copulatory behaviors shared with nonhuman primates. Future work will continue to illuminate the nature of the changing social and sexual world and the implications these changes might have given the ways in which evolution has shaped humans into sexual creatures.

Cross-References

- ▶ [Alloparenting and Female Same-Sex Behavior](#)
- ▶ [Casual Sex](#)
- ▶ [Four-Stage Model of the Sexual Response](#)
- ▶ [Long-Term Mating](#)
- ▶ [Masters and Johnson](#)
- ▶ [Oral Sex](#)
- ▶ [Orgasm](#)
- ▶ [Penile-Vaginal Sex](#)

- Same-sex Sexual Behavior
- Sexual Intercourse
- Short-Term Mating

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Human Courting

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Synonyms

Dating; Courting; Courtship; Mateship

Definition

The process of social and cultural processes whereby one attempts to gain another as a mate.

Introduction

Courting as we know it has gone through a drastic change in the last century, with an almost insurmountable level of change in the past decade due

to technology. The word courting itself is old fashioned, bringing images of ice cream socials in the 1950s – now we commonly use words like dating. Once upon a time, and currently in some cultures, a man and a woman did not choose to spend their lives together, their bond was chosen by parents or other authority figures. When mateships are decided upon by outside people, there was/is no courting necessary. In modern times (with some exceptions), this tradition of having a mate chosen by an outside party has gone by the wayside and has been replaced with courtship – a period of time wherein a couple gets to know one another, often wherein one person (usually the male) competes for the attention of the other.

Courting, or dating, comes down to a much more simple concept than it immediately appears – courting and dating is the human equivalent to the procurement of a mate for reproductive purposes. Courtship, or dating, is the modern human equivalent to sexual selection and the displays that certain species engage in when seeking a mate. Much of evolutionary psychology is focused around the attainment of a mate – how it is done for different species, how the attainment of a mate has changed over time, and what sort of variables affect mate attainment.

Parental Investment

Humans are no exception to the rules put forth by Trivers’ (1972) theory of Parental Investment – the sex which possesses a larger minimum investment in offspring is the sex that chooses a mate, while the sex which has a smaller minimum investment in offspring competes for access to mates. In the context of humans, like most species, females hold the larger minimum investment (9 months gestation and labor at the absolute minimum), thus they are the sex that gets to choose mates, while males (whose minimum investment is the ejaculation of sperm) hold the smaller minimum investment is the sex that must compete for access to the females through intrasexual competition. What all of this investment and competition information adds up to is

quite simple: men compete more for access to women, while women are choosy in picking a man to mate with. In dating terms, this simply goes together with the generally accepted gender roles associated with human dating – men pay for meals and compete with access with other males for female attention. A clear and concise way to understand and remember courting practices and their ultimate goals is to realize that, especially in the animal kingdom (particularly with non-human species), courting is merely a series of events that must occur in order for copulation to be allowed, agreed upon, or desired.

Human courting varies dependent on historical context, religion, cultural norms, and family norms. Currently, in a Western context with a secular religious emphasis, males and females seek each other out for dates and exhibit a long courting period before (if) marriage happens. Previously, males and females used courting as a prerequisite of sorts for marriage – courting was used to determine whether a male and female were a good fit for marriage, marriage being the ultimate, paramount goal. Now, it is common for humans to date for the sake of dating, without marriage as an ultimate or proximate goal in mind. It is particularly interesting that, while the goal of dating may have gone from ultimate (marriage is the point) to proximate (dating for the sake of dating), the gender roles devised by biological differences such as minimum parental investment have not changed – even if a man is not courting a woman to test her for marriage material, he is still the one seeking and competing, while she is the one who makes decisions about whether or not she wants to date the male, and what type of relationship she is willing to have with him (short-term – sexual, or long-term – committed).

Sexual Intent

Another important variable when discussing human courting is perceived sexual intent – the “friendzone” is somewhat of a joke on sitcoms like *How I Met Your Mother* and *Raising Hope*, often discussed more seriously in the bowels of

the internet where men who perceive themselves as “nice guys” lament over the “friendzone” and how they are always placed in it despite their best efforts. The “friendzone” is a fictitious place where men go when they befriend a woman and take too long to make their move, thus appearing as nothing more than a friend in the eyes of a female. The friendzone is mentioned as an easy way to understand perceived sexual intent. When males and females begin to court one another, in modern times where women and men are friends (and modern cultures, where women are allowed to be in the presence of a man without a male relative with her for protection), there is not always clear sexual intent. The question “could this individual only want to be my friend, or are they interested in a copulatory relationship with me” is often raised in the minds of individuals beginning a courtship. One can plainly see how a misunderstanding of sexual intent could lead to trouble: from mere discomfort between the two individuals to the possibility of sexual assault or misconduct (see subsection below).

Operational Sex Ratio

There are numerous variables that affect dating behaviors. One such variable that drastically changes behavior in dating is operational sex ratio (OSR). Operational Sex Ratio is the ratio of reproductively viable males to females in a given mating market. It is important to understand the logistics of mating markets in order to better understand mating and dating behaviors. Operational sex ratio generally is divided into three major categories: equitable, wherein there are an even number of reproductively viable males and females in a given market; female disadvantaged/male advantaged, wherein there are proportionally more females than males in the mating market; and female advantaged/male disadvantaged, wherein there are proportionally more males than females in the mating market. It makes sense from a simple supply and demand point of view that operational sex ratio would affect dating habits and behaviors. Males and females have different wants and desires, and it

stands to reason that male wants and desires would be put ahead of female wants and desires in a male advantaged/female disadvantaged ratio, and vice versa. Because of this, we do see behavioral changes in courtship and dating across different OSRs.

Conclusion

Human courting is an incredibly complex process that has evolved with us over hundreds of thousands of years. Many factors can affect the outcome of a relationship between two individuals, especially Paternal Investment and Operational Sex Ratios in their immediate environment. Though humans display indices of Parental Investment our courting behavior can still be incredibly plastic depending on a multitude of variables, including environmental factors.

Cross-References

- [Advertising](#)
- [Aggression for Sexual Access](#)
- [Appearance/Beauty in Girls](#)
- [Benefits of Short-Term Mating](#)
- [Benefits of Commitment and Marriage](#)
- [Body Attractiveness](#)
- [Casual Sex](#)
- [Competition for Resources Desired by Females](#)
- [Conflict of Mating](#)
- [Dating](#)
- [Hookup Culture](#)
- [Intersexual Selection](#)
- [Intrasexual Selection](#)
- [Life History Strategies](#)
- [Mate Choice](#)
- [Mate Poaching](#)
- [Mate Retention](#)
- [Mating Strategies](#)
- [Nuptial Gift](#)
- [Perceiving Sexual Intent](#)
- [Sex Differences](#)

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Human Deception

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Synonyms

[Betrayal](#); [Deceit](#); [Duplicity](#); [Lying](#); [Treachery](#); [Trickery](#)

Definitions

Deception is notoriously difficult to define given that there are so many forms across human and nonhuman animals (Mitchell 1993). Here, we define deception as the intentional or unintentional misrepresentation of information. This misrepresentation can be conscious or unconscious and may serve a multitude of purposes including (but not limited to) survival (e.g., physical defense), resource acquisition (e.g., acquiring food or resources), or increased inclusive fitness (e.g., reproductive advantages).

Introduction

Deception is common in human interactions (Kashy and DePaulo 1996). It can be intentional such as in the case of lying, self-presentation, or withholding important information. Deception may also be unintentional or unconscious, such as in the case of self-deception (e.g., von Hippel and Trivers 2011). Deception may stem from

good intentions or a desire not to harm, or it may come from a place of selfishness or malevolence.

In the animal kingdom, deception is often used for survival. Some researchers have argued that survival of primates is calibrated on deception and that “Machiavellian intelligence” is required for survival (Byrne and Whiten 1989). Despite its benefits, deception also poses risk. To deceive and fail can pose fitness costs in the form of ostracism or death. To deceive and succeed could mean fitness enhancement.

Although a tremendous amount of research and theoretical attention has been paid to the evolution of cooperation and reciprocal altruism in modern society (Trivers 1971), players in a cooperative society may not merely fit a cooperator vs. cheater distinction. Instead, some deceptive individuals may engage in cooperation for long periods of time in order to cultivate trust and the appearance of cooperation. This cultivation of trust, however, may ultimately be in the service of large-scale defection. In this way, individuals in cooperative societies might be better categorized as cooperators and cheaters.

Deception and defection are pervasive in modern society. At the corporate level, financial fraud costs a cooperative society more than 680 billion dollars annually (Wells 2007). However, the costs of defection are not solely financial. Individuals suffer severe psychological consequences as a result of being victims of fraud or financial misbehavior. Such consequences include (but are not limited to) increased anxiety, depression, and even suicide (Titus and Gover 2001).

In humans, examples of deceptive strategies can take either long- or short-term forms. In the short term, individuals may execute strategies which are direct and are designed to reach broad communities, in short intervals of moderate payouts; these individuals are often referred to as con-artists or swindlers. A successful confidence artist or “con-artist” may prey on a wide variety of victims (e.g., elderly women, college students). One example comes from Pratkanis and Shadel (2005, pg. 35) where an individual would call and ask elderly individuals to donate money to a fictitious “Say No to Drugs Program.” He used very broad and flexible persuasion techniques and was

successful in getting a wide variety of individuals to “donate” to his organization. One particularly clever swindle occurred when this con-artist was arrested. Using his phone call from the Federal Marshal’s office (where he was being held), he called one of his previous victims claiming that he was a Federal Marshal and that he could recover all of the victim’s losses for a processing fee of \$20,000 (Pratkanis and Shadel 2005; pg. 42).

In contrast, some individuals execute strategies designed to reach very specific communities for long-term intervals of large payouts. These individuals are often guilty of antitrust or business/trade violations (Benson and Simpson 2009). One successful long-term cheater of this type is Bernie Madoff. Most evidence indicates that Madoff first began his fraudulent trading back in the early 1970s and eventually was responsible for the largest documented Ponzi scheme in history (Arvedlund 2009). Ponzi schemes are difficult to perpetuate because one must have great patience and build a reputation within the financial community over a significant period of time. Even more difficult, one must show initial returns in order to gain more clients to participate in the Ponzi scheme.

Although Madoff’s primary charge was running a Ponzi scheme, he used what is known as “affinity fraud” to perpetuate his fraudulent trades (e.g., Babiak and Hare 2006; Perri and Brody 2011). Affinity fraud occurs when an individual integrates her-/himself into a community for the purposes of eliciting trust and then proceeds to defraud that community. Madoff, however, went far beyond general integration into financial communities, serving on many financial advisory boards and forming long-standing relationships with important people in governmental positions (Collins 2011). Operating for almost 40 years, Madoff was able to defraud investors in excess of 65 billion dollars (Arvedlund 2009).

Although both successful con-artists and white-collar offenders (such as Madoff) have cheated innocent people out of money, they presented themselves differently. A con-artist, on the one hand, can be considered an intentional and direct defector. Con-artists and short-term deceivers use only temporary and superficial

deceptive techniques, techniques of which people are immediately suspicious (Pratkanis and Shadel 2005). On the other hand, Madoff worked himself into the fabric of the financial community through more complex deception, giving every appearance of cooperation and contribution. In essence, he imitated or “mimicked” cooperative behavior in every facet of his public life.

A comparison of human and nonhuman animal deception was proposed by Mitchell (1986, as cited in Mitchell 1996). Mitchell (1993, as cited in Mitchell 1996) argued that researchers could learn a lot about human deception by studying deception within different kingdoms of living creatures. In particular, Mitchell (1996) walks the reader through levels of deception starting with simple camouflage or mimicry all the way up to memory and perspective taking. Indeed, these more sophisticated deceptions generally require more planning and cognitive ability.

Mitchell further (1996) articulates the process of deception insofar as one must convince a target of fictional information without raising issues of suspicion. Suspicion, according to Mitchell, is the enemy of deception. This assertion makes sense, given that the human default in most cases is to believe others (Levine 2014). In fact, Levine argues that deception sometimes requires self-deception on the part of the deceived. This finding of course raises the issue of motivation. Individuals are most vulnerable to lies when they want to believe them in the first place. Take for example, someone who is uneasy about their savings with respect to retirement. This individual meets Madoff and is motivated to believe that the solution to their financial woes may be the impressive payouts that Madoff offers. Rather than raising red flags about unrealistic returns, the individual is motivated to believe that they are simply lucky to have found such a wise financial genius.

Differential Temporal Strategies

Jones (2014) argued that all deception falls on a long- to short-term continuum, and there are four key components that exist for long-term deception: complex deception, slow resource

extraction, community integration, and difficulty in detection. These four components are absent in short-term deceptions. Empirical evidence supports the idea that these four components do indeed intercorrelate (Jones and de Roos *in press*). Below we review further evidence for these claims.

Among predators and prey in the animal kingdom, mimicry is an adaptation utilized to confuse other organisms to an adaptive end (Wickler 1968, as cited in Jones 2014). In fact, many kingdoms, viruses/bacteria, plants, nonhuman animals, and humans (both children and adults), are replete with examples of some form of mimicry (Damian 1964 & Gilpin 1975, as cited in Jones 2014). Mimicry is especially prevalent when deception is adaptive for the organism (Gilpin 1975, as cited in Jones 2014).

Much in the same way that Madoff displayed characteristics of a cooperator, when in fact, he was a cheater, some animals will display characteristics that appear similar to other organisms but are actually quite different. In contrast, con-artists engage in direct parasitic and/or predatory behaviors, behaviors that are analogous to traditional infections (Damian 1964 as cited in Jones 2014) or predators (Gilpin 1975, as cited in Jones 2014).

Strategies of fraud resemble viral and bacterial infections of cooperative hosts, and as such, virulence provides a useful analogy for fraudulent behavior. Virulence refers to the rate of infection of a microorganism. Some infections spread quickly in a broad fashion, while others tailor their infection to a specific host, making the spread of infection slower, but the virus more difficult to detect (Levin and Bull 1994). Virulence, however, comes at a cost: widespread detection and destruction by antigenic entities within the host (Levin and Bull 1994). On one end of the virulence spectrum, certain microorganisms will infect a broad range of hosts. Examples of such microorganisms are *Streptococcus pneumonia* and *Haemophilus influenza*. Such microorganisms are transmitted via droplet infection (e.g., sneezing). The mechanism for infection, among these parasites, is similar in most hosts, and these microorganisms infect similar

locations within the host (e.g., nasopharyngeal passages or respiratory systems).

By contrast, certain forms of meningitis and viral infections, such as the human immunodeficiency virus (HIV), have a different approach to infection. Such infecting agents evolve within the host, in order to mimic naturally occurring cells and entities. HIV, for example, is not easily transmitted (i.e., not through droplet) and will often lie undetected for years within a host, before causing damage. These differential parasitic strategies can be viewed as two separate “defection” strategies utilized by microorganisms in compromising a “cooperative” host (Zimmer 2000). Thus, it appears in the evolutionary arms race between infecting microorganisms and multicellular hosts that many parasitic organisms have utilized mimicry strategies to appear similar to naturally occurring substances within the host’s system (Damian 1964, as cited in Jones 2014).

Mimicry also occurs in the animal kingdom when an animal or species gives the appearance of possessing characteristics of an unrelated animal or species, but actually does not possess these traits (Holling 1965, as cited in Jones 2014). Common examples can be found in organisms such as butterflies, frogs, fish, and lizards. Mimicry, which evolved for the purpose of predator confusion and defense, is often referred to as *Batesian mimicry* (Malcolm 1990, as cited in Jones 2014). Such creatures may display bright coloring or similar markings to creatures that are unpalatable or even poisonous. However, the mimicking organism is either palatable, nontoxic, or both.

Mimicry can work in the other direction as well, in favor of a predator. Some animals appear to be harmless, when in fact they are predatory. This type of mimicry is referred to as *Mertensian mimicry* (Wickler 1968, as cited in Jones 2014). For example, the Venus flytrap, which looks quite harmless to unsuspecting insects, but is carnivorous, will strike when an insect is inside.

Mimicry represents an evolutionary arms race in its own right between organisms utilizing mimicry and organisms attempting to detect mimicry (Caley and Schluter 2003). These selective pressures and arms-race style evolutionary

mechanisms are intensified by the trade-off that exists between costs associated with missing opportunities (e.g., the chance to feed on palatable prey) vs. the costs associated with making mistakes (e.g., dying from biting into poisonous prey). In other words, the cost/benefit to trusting or avoiding mimics is often based on consequences associated with false positives or false negatives. For example, if the consequence of mistaking a palatable fish with an unpalatable fish is merely an unpleasant taste, then there will be mild selective pressure placed on predators to distinguish between the two types of fish. On the other hand, if one of the fish carried lethal poison, selective pressures placed on predators for distinguishing between the two types of fish would be intense (Caley and Schluter 2003). However, as aforementioned, motivation (and therefore, self-deception) may play a role in deception as well. Take, for example, a fish that is starving, he/she may be more likely to fall for the mimicry deception, given that the trade-off of poison vs. starving increases risk-taking behaviors.

When detecting potential mimicry or deception in humans, differential pressures also produce divergent abilities for detection. For example, when consequences are low and familiarity is sparse, humans are not much better than average at detecting deception in other humans (von Hippel and Trivers 2011). In such situations of little consequence or closeness, most individuals lack the motivation and/or ability to detect deception. This lack of motivation is analogous to the lack of selective pressure on predators that face little consequence for mistaking bad-tasting fish with palatable ones. However, when consequences are high (e.g., the individual is high in closeness or the event high in consequence), detection of deception is much improved.

Deception and Evolution

Frequency Dependent Selection

The proportion of cheaters vs. cooperators follows the basic principles of frequency-dependent selection (Pfenning et al. 2001). Frequency

dependence means that too much or too little of a particular trait will create an imbalance. This imbalance is then corrected through selective pressures. Several publications have reviewed the impact of frequency-dependent selective forces on cheater vs. cooperator strategies (Mealey 1995; Wilson et al. 1996). In particular, Mealey (1995) argued that psychopathy was likely to fit in an evolutionary model mixed of cheaters and cooperators (p. 526). Mealey (1995) also noted that other variables (e.g., competitive disadvantage) played a role in determining a player's strategy (in this case, disadvantaged individuals were more likely to cheat).

In the case of mimicry, if there ends up being an exceedingly high level of harmless (Batesian) mimics when compared to harmful (e.g., poisonous) organisms, it becomes too advantageous for predators to take a risk and attack both harmful and harmless organisms, because probability is in favor of non-poison. By contrast, if the balance of mimicry to harmful organisms is such that there is an exceedingly high percentage of harmful (e.g., poisonous) organisms, then selective pressure would favor (a) finding an alternative source of food (i.e., predators would avoid both mimics and harmful prey altogether) and (b) evolving stronger mechanisms for differentiating mimics from non-mimics (Caley and Schluter 2003). In this way, a positive imbalance of cheaters might pave the way for mimics.

Among humans, some who mimic cooperation with selfish intentions may never defect unless they feel it is "necessary". However, until necessity strikes, the most effective cheaters may maintain their cooperative veneer, and thus, a positive reputation. It should be noted that necessity may be perceived differently by different individuals.

Single vs. Dual Selective Pressures on Mimic Cheaters

Frequency dependent selections also are context specific. In areas familiar to a particular type of dangerous predator or unpalatable prey, mimicry is quite effective (Pfenning et al. 2001). In such cases, predators and prey require highly evolved mechanisms to detect differences and mimicry

will often work. In areas unfamiliar to these organisms, mimicry is unnecessary. For example, Pfenning et al. (2001) placed coral snake look-alikes in eastern regions of the United States, as well as regions of Central America. They found that snake predators in the United States would readily attack these coral snake look-alikes because they had no prior exposure to such snakes or to their mimics. By contrast, coral snake look-alikes placed in regions of Central America were left alone.

By analogy, detection of deception in humans may operate in a similar fashion. For example, individuals planning affinity fraud are more likely to go undetected in certain environments once introduced (e.g., religious communities) as compared to other environments (e.g., Wall Street). Communities used to dealing in fast-paced monetary exchanges (e.g., Wall Street) are more likely to be flooded with deceptive attempts. Thus, within these communities, there is likely to be greater selective pressure placed on deceptive individuals to emulate both being a cooperator and simultaneously avoid looking like a cheater. Less pressure may be placed on someone in a community where deception is not expected (e.g., religious community).

Differentiating Human Deception Strategies

Indeed, research and theory in evolutionary models of cooperation have alluded to several permutations of cooperation that might differentially benefit the individual at the (slight) cost to the group. For example, Trivers (1971) noted that appearing to be a good cooperator with mild levels of selfish bias provides long-term benefits of resource allocation without incurring direct cheating costs. However, it should be noted that such strategies require social dominance to execute. When caught taking slightly more than one is supposed to take, it would require either refined social skills, status, or intimidation (Tooby and Cosmides 1990) to avoid having group members act in punitive ways based on unfairness.

Moreover, as Axelrod (1984) points out, strategies are contextually based, and one might cheat when costs are low, others are submissive, detection is unlikely, payoffs are great, or one feels cheated in their own right. As aforementioned, frequency dependence and the presence of others' strategies greatly influence the strategy employed by a given group member (Tooby and Cosmides 1990).

However, there is a second way an individual may engage in deception is through self-deception. For example, von Hippel and Trivers (2011) reviewed a body of evidence suggesting self-deceptive enhancement bestows advantages with respect to interpersonal deception. They argue that through deceiving oneself, detection of deception by others is rendered extraordinarily difficult. The absence of truthful leaks and/or hints of deception stem from the fact that self-deceptive individuals genuinely believe that they are cooperators, they benefit others, and they are not cheating. In sum, mimicry may be split into two forms: mimicry stemming from intentional and planful strategy vs. mimicry stemming from self-deception and exaggerated overconfidence.

Self-deceptive enhancement is a fairly broad strategy that can be beneficial (at least in the short-term). It should be noted, however, that exaggerations come at a cost. At best, these self-deceptive exaggerations represent a "mixed blessing" (Paulhus 1998, as cited in Paulhus et al. 2003), because they wear off over time.

Personality and Deception: The Dark Triad

The dark triad is a term that refers to three commonly studied personality traits in the realm of interpersonal harm (Paulhus and Williams 2002). All three of these traits are linked to deception under different circumstances (Jones and Paulhus 2016). Machiavellianism is associated with strategic and planful deception (Jones and Paulhus 2009). Such individuals are cautious and anticipate future moves from others (Bereczkei et al. 2013). In contrast, psychopathy is purely short term and aggressive in their deception,

wearing a temporary mask of deception (Book et al. 2015). Finally, narcissistic individuals deceive through self-deception (Paulhus et al. 2003). In this way, the dark triad traits cover a wide array of deceptive dispositions.

It should be noted that all deception requires some level of skill. Individuals who are convincing "talkers" often rise in corporate ranks with little substance (Babiak and Hare 2006). Skill is likely to be even more necessary for deceptions that are long term or planned. Turner and Martinez (1977) found that individuals high in Machiavellianism but low in intelligence were the least successful individuals. In contrast, those high in Machiavellianism and high in intelligence were the most successful.

Conclusion

Deceptions can take predatory and defensive forms. Further, deception ranges from simple (e.g., camouflage) to complicated (e.g., planned). In many ways, mimicry can be split into more nuanced categories, which suggests that there may be multiple forms of mimicry operating in humans as well as nonhuman animals. Moreover, there is a wide variety of deceptive tactics. Some are likely to be perpetuated by planful mimic cheaters, such as intentional information omission (DeScioli et al. 2011). By contrast, other tactics are simple and direct lies based on emotional manipulation or fabrication (Patrick and Zempolich 1999). Still others involve overconfidence and entitlement (Campbell et al. 2004). Simply put, understanding human deception is complicated because there are infinite ways to deceive, but few ways (perhaps even, just one) to tell the truth.

Cross-References

- [Female Deception](#)
- [Male Detection of Deception](#)
- [Reliability and Deception in Language](#)
- [Self-deception](#)

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Human Dietary Predispositions

► Food Preferences

Human Diversity

► Cultural Variation

Human Enculturation

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Synonyms

Adaptation; Morality; Social organization; Social values; Socialization; Spiritualism

Definition

The progressive adaptation of human species within organized social norms that are characterized by values and social order.

Introduction

The values that describe human societies managed to create a culture that renders humans as the only species to be separated qualitatively from other animals. It is argued that the tendency of

early humans to be curious in their nature fostered the learning of useful strategies that selectively became genetic capabilities and which rendered the ongoing development of culture as a remarkable achievement. Human species evolved over generations, and communication became more complex. Arbitrary cultural meanings are found to be assigned to animate and inanimate objects in the environment, allowing for a vivid indication that early culture initiations were occurring. As communication is a vital component in the realm of enculturation, language appeared to develop in parallel with human cultural values. Throughout a continuous, systematic progress, there is evidence of memory expansion and brain size increase that facilitated and possibly co-interacted with the development of enculturation and the entry of humans in social norms.

Evolutionary Adaptability

Adaptability is of central importance to the evolutionary process. It is through adaptation that organisms are able to survive in changing environments, become better suited to their existing environment, or expand into new environments. Interpretively, organisms that are more adaptable can be expected to be more successful in evolutionary terms; a major improvement in adaptive ability is a major evolutionary advance. It is important to underline that genetic evolution has developed the superior adaptive mechanisms that have the potential to replace it in humans (Stewart 2001). The adaptive arrangements that operate within organisms during their life were discovered and established by genetic evolution. The first adaptive mechanisms established by genetic evolution searched for better adaptation by trying out changes within the organism using trial and error. As it has been mentioned above, the acquisition of language was a critically important step forward in human ability to construct mental models. Language and associated forms of communication enabled humans to share the knowledge used for building models (Popper 1972). Communication enabled all members of a society to acquire and use the knowledge discovered by any individual.

It also enabled knowledge to be accumulated across generations. The progressive accumulation of knowledge allowed the individual to model greater range of interactions with the environment and to predict the consequences of their actions (Stewart 2001). Consequently, this notion encouraged human species to discover effective ways of achieving adaptive goals and obtaining positive reinforcement from internal reward systems. Nevertheless, human species have a very large evolutionary blind spot. Humans are not motivated to explore an immense variety of adaptive possibilities, regardless of how useful they may be in evolutionary terms. Until this limitation is eliminated, continuous use of genetic engineering, artificial intelligence, and other technological advances will be needed to satisfy past evolutionary needs and conditioning, rather than to achieve future evolutionary success.

Social Values

Societies seek to establish congruence between social values associated with their activities and the norms of acceptable behavior in a larger social system (Weigert 1983). Values foster harmony within a human society and function as the foundation of organizational legitimacy. The absence or violation of cultural common values leads to disparity that can threaten congruence and undermine unity within a society (Cooley 1953).

Emergence of Identity within Culture

In developing their sense of identity, people identify successively with values of influence over their well-being. The primary processes involved in identity development are ones of enculturation of cultural elements (Berry 1980). Enculturation references the agentic individual's process of identification with whatever cultural elements of influential others are accessible to the person (Weinreich 1983). In the main, the young child identifies with mother and father in the first instance but identifying only with limited aspects of them apprehended from the child's perspective. Subsequently, the person as older child, adolescent, and then young adult successively identifies

with members within their direct environment, and beyond with agents of the wider community, and part-identifies with their salient features according to increasing levels of comprehension (Erikson 1950, 1968). As a consequence, over a formative period, the child who becomes the adult migrant will have enculturated major aspects of heritage culture including some elements that are incompatible with others, since cultures are not entirely monolithic (Liebkind 1989). According to ISA, identity is a modification of earlier ones and emphasizes people's construal of their biographical past and their aspirations for the future. For human species, their biographical past scenarios can be located in their heritage locations and cultures, while their future aspirations may entail considerations about their intended modes of engaging with their receiving communities (Weinreich 2003).

Morality

Contrary to the belief that wants morality to encompass a trait unique to humans, it is argued that other animal species may possess moral behaviors including community concern, reciprocity, and empathy. Although it is not supported that a fully developed moral system is present in other animals, it is indicated that human morality is embedded in phylogenetic relationships with ancestral animal species. Evolutionary scientists depict the phenomenon of homology by rendering the presence of shared behaviors as the result of a common ancestor between humans and other animal species. They also support that two distantly related species can share a behavior while they inhabit similar environmental niches as it results from convergence due to shared environmental constraints. Intriguingly, examining behavioral patterns of other species might explain mechanisms of human behavior and depict that a multitude of phenomena concerning morality are the result of continual evolution (Dennett 1995).

Darwinism and Moral Emotions

Charles Darwin proposed that the basis of morality is innate and that humans and animals share an

evolutionary background. He mentions in his book *The Descent of Man and Selection in Relation to Sex* that nonhuman primates possess social instincts, such as parental affection, and they are consequently characterized by a sense of conscience that would be otherwise intellectual power if it was well developed as it is in humans. It is argued that other animals experience some level of sympathy for others in their environment that also includes a strong need for familial interactions (Darwin 1964).

Darwin does not disregard the importance of advanced intellectual ability for meaningful judgment, but he underlines that well-marked social instincts are present in animals indicating moral constraints and conscience in species other than humans (Darwin 1981). He supports that this notion functions as an evidence for evolutionary continuity between humans and other animals as he relied on comparative data regarding facial expressions across human cultures and other species. He addressed the reasons why universal behaviors are expressed in the form that they do (Darwin 1998).

Adam Smith appears to support Darwinian theory. In his book *The Theory of Moral Sentiments* discusses that both positive and negative passions are seen in animals and that they share many traits that are considered human. To support his views, Smith mentions that all animals, including children and dogs, are likely to become angry at inanimate objects that hurt. He highlights that human instincts were in place to promote survival and reproduction. He further believed that instincts were initially experienced as emotion, rather than rational thought, and were often laid outside conscious awareness (Smith 1817). The idea of evolutionary continuity of behavior and the recognition of moral emotions has its roots embedded in the ancient past.

The Empirical and Normative Senses of Morality

Morality from a scientific perspective refers to a set of empirical phenomena, such as the observed capacity of human beings to make normative judgments and the tendency to have certain sentiments including sympathy, guilt, or blame as well

as intuitions about fairness and violence. Scientists speak of the evolution of morality in empirical sense while utilizing tools as comparative genomics and primate studies to analyze the subject of interest. While morality in the normative sense is not an empirical phenomenon to be explained, there are vital points that require attention regarding evolutionary theory and principles (Rosenberg 2006).

The normative sense of morality questions one's evolutionary background for moral guidance; through the normative approach, scientists might attempt to gain insight into the content of morality as claimed by proponents of prescriptive evolutionary ethics. Evolutionary theory can potentially explain metaethics and allow to resolve inquiries about the existence and nature of morality (Biniolo and de Anna 2006). Once topics of interest are selected, scientists begin to consider scientific explanatory projects concerning morality in the empirical sense.

Moral Behaviors in Nonhuman Species

Moral emotions have been identified as the principle mechanisms that uphold the rules of behavior underlying social norms and conventions (Mead 1934). They constitute vital components in interactions as they normalize the behaviors of group members and foster the tendency to be in line with the norms (Haidt 2003). Equity and equality are the two primary elements that synthesize justice. Adam Smith refers to justice as “the main pillar that upholds the whole edifice of human society.” This perspective lies within the rationale that wants animal species to react in the face of unfair treatment. This notion argues that based on instincts of moral behavior, primates tend to respond negatively when others are treated less well, a fact that contributes to the maintenance of harmonious coexistence among group members (Brosnan 2006).

Studies on Moral Behavior in Primates

Naturalistic studies have shown that long-term behavior of the partner is more important than the outcome of the individual. In an experimental cooperation task, subjects were more likely to cooperate if they and their partner evenly shared

the rewards. In one study, monkeys had to work together to pull a heavy tray of food. The foods differed every time, and the monkeys had to decide whether they were willing to work for the food reward they were offered. Pairs in which the partners shared the good food about half of the time were successful in the cooperative task, while pairs in which one partner eliminated the other rarely obtained cooperation. Aside from the fact that non-sharing dominants received higher value rewards than their partners, their success rate was lower; thus, they tended to receive fewer rewards. The subjects seemed to expect that working together on a task leads to equity if reward outcome and dominant partners who failed to do this received a form of punishment (Brosnan et al. 2006). The findings indicate that a critical factor in a cooperative task is the partner's behavior to be equitable, rather than the actual value of reward. In experiments where participants are humans, responses to inequity differ depending on the source (Silk et al. 2005). Humans change their responses if there is a reason for inequity (Tajfel 1981). Individuals offer less, and partners accept inequity more readily if the subject is perceived to have earned the right to it. Interestingly, humans tend to respond more negatively to inequity that is caused by another human directly than to inequity that is the result of chance.

Evolution of Justice

The sense of justice is seen in nonhuman primates as they are likely to respond negatively to earning less preferred rewards than a social partner. In respect to natural selection, researchers argue that it might have been a critical environmental factor that led to selection for the behavior (Darwin 1964). It is important to underline that evolution of shared behaviors does not indicate identical approaches from species as well as it does not eliminate the novelty of behaviors that are unique to specific primates, but not others, due to their complex nature. Nonetheless, inequity can be explained as the byproduct of another behavior that led individuals to selectively focus on

conspecifics, such as social learning, which is present in many species and can be beneficial (Kelly 1955). On the other end of the spectrum, inequity superficially might not be perceived as rewarding from species due to unjust circumstances; however, reacting negatively to unfair treatment can cease harmful interactions with opponents and encourage them to seek out equitable partners (Brosnan 2006). There is also evidence that human and nonhuman species actively take steps toward rectifying inequity when the moral sense of justice is violated, and they receive less than they deserve (Brosnan 2008). In this stage, primates react by punishing others who do not play fairly (Fehr and Gächter 2002). It can be argued that reaction to disadvantageous inequity is more salient as there is immediate benefit to the partner. On the other hand, advantageous inequity leads individuals to abandon their own good and act against their short-term self-interest in order to give up rewards to benefit others. The definition in itself might seemingly appear disastrous for the individual; however, it derives long-term benefits for the community and the conservation of healthy social norms.

Embodiment of the Self in the Community

Rites of Passage

A rite of passage is a ceremony and marks the transition from one phase of life to another. It plays a critical role in the evolution of human civilization as it defines the common values of a society. A rite of passage manages to conserve social order and the sense of community among the members of a group who come together to celebrate an occasion and practice traditions and customs on the foundation of shared social values. Rites of passage are characterized by the ordeals with which a youth is formally invested with adult status in a community. Intriguingly, these rituals and ceremonies allow adults to transition into new life roles along the path of adulthood, all the way into meaningful elderhood. When humans design rite of passage experiences, they work to assure

that initiates come out of the experience with a new and empowering story that helps them take responsibility for the decisions that set the course of their future. Members of a social group initiates create the story of who they are and the kind of life they wish to build based within the exploration of their own personal values. Initiates are encouraged to select the story that connects them to their community. Through this self-exploration, they emerge with a stronger sense of personal responsibility to all aspects of their lives, stretching all the way out to the larger world of which they are a part of (Carrithers et al. 1985). Consequently, both the community and the initiate benefit from a rite of passage. An intentional rite of passage experience provides the space for the community to transmit its core values and ethics and confer the role responsibilities appropriate to the initiate's stage of life, hence insuring cultural continuity and knitting together of the generations.

The Role of Honor Code

A fundamental aspect of culture is its embodiment of the societal processes of substantial groups of people who perceive themselves as belonging to a commonality of values and beliefs, moral imperatives and religious beliefs, dress and behavior, history, and modes of living, whereby one group is culturally distinctive from another (Henry 2008). From evolutionary perspective, honor codes appear to maintain cohesive order within communities. The role of an honor code is to encompass a set of ideals in a society and govern accordingly a group of individuals that abide by moral rules. It is based on what constitutes honorable behavior among group members, and its use depends on the notion that individuals within the group can be trusted to act honorably. In many cultures, an honor code exists parallelly to ethics that require proper compliance according to societal rules, by members who seek to be recognized for their individuality and be inviolably included in community. Punishments upon disregard of the honor code underline that values-driven individuals ought to be more successful within a society.

Development Levels for Compliance and Ethics

From evolutionary perspective, crucial components that characterize honor codes of human societies appear to be diachronic as they influence critically the man of today who seems to adhere to values that had always fostered healthy functions in communities since ancient times. Modern society has adopted these values and incorporated them into organizational honor codes. Foundation-level programs set the basis for establishing a healthy organizational culture and preventing, detecting, and resolving legal and regulatory compliance violations. The behavioral focus is on compliance, and the business focus is on the organization. Transformation-level programs support a shift from a compliance focus to a compliance and ethics focus. The behavioral focus is on compliance and ethics promoted by values-based leadership. The business focus is on the organization and primary stakeholders which might be customers, suppliers, investors, financiers, and communities in operating area. Sustainability-level programs foster aspirational behavior and contribute to the organization's continued success. The behavioral focus for this level is on compliance, ethics and honor, collaboration, and meaning, all promoted by values based on leadership (Keegan 1994). Hence, the business focus is on the organization, primary stakeholders, and secondary stakeholders which might be special interest groups, media, government, competitors, consumer advocates, and global society (Henry 2008).

Spiritual Development

Humans have assembled a remarkable body of knowledge about how they can develop new psychological capacities. Such knowledge is embodied in religious and spiritual systems. Even though systems differ in the expression of their goals, the world's major religious systems advocate the cultivation of the human ability to free oneself from particular emotional responses, desires, and motivations. All systems contain methodologies that

aim to assist the development of such capacity. Religious systems generally promote the emergence of the new self through practices that separate the mind into an observing part and an observed part (Nicol 1980). The observing part is the precursor to the new self. These practices typically operate by turning attention and awareness inward and directing it at mental contents such as sensations, emotions, motivations, mental images, and thoughts as they arise in the mind (Goleman 1988). For instance, many religious systems require adherents to struggle against the dictates of their lower desires and impulses facilitating significantly the process of human enculturation. Doing so renders these mental states objects of attention and begins the separation of the mind into an observing part and an observed part.

The Role of Spiritual Meditation in Enculturation

Intriguingly, the concept of culture is not only characterized by participation of the individual in community but also by the separation from the massive group in an attempt to grow intellectually, enrich their mental capacities, and acquire identity for the inner and outer self. Meditation involves turning attention inward and making thoughts as emotional states objects of attention. Mindfulness practices and self-observation promote the development of the new observing self during ordinary life. These practices focus attention on the physical sensations, emotions, mental images, and thought that arise as the individual goes about daily activities and interactions; these techniques emphasize that self-observation is to be passive and non-judgmental (Nicol 1980). Evolutionary scientists argue that mental capacities of this kind characterize the primitive man and his spiritual practices back in the old antiquity. They have always allowed the individual to accumulate knowledge about the operation of their motivational and emotional system and improve their capacity to manage them. The result is a new emerging self that can remain functionally separate from motivations and emotional impulses and can decide whether or not to be influenced

by them. This separation enables the new self to control the disposition of attention. The individual can direct their attention and energy at activities that serve the aims of the self. As a result, he/she can be motivated and emotionally satisfied in the activities that serve their goals. If an individual decides to pursue evolutionary success as their ultimate objective, they will be able to align their internal reward system with evolutionary goals (Stewart 2001).

Conclusion

Enculturation of elements represented by moral and social values is a process of incorporation of cultural elements to become elemental aspects of one's overall identity. The continuous process of human enculturation is the foundation of the person's identification as well as the coexistence of mixed cultural elements within the person's identity. Ultimately, the goal is the creation of elemental identification that is characterized by common values and is expressed within social boundaries, honor codes, and moral incentives. A better understanding of the evolution of moral behaviors can be achieved through examining outcome behaviors that allow for insight in the past. According to the notion of natural selection, salient behaviors were practiced more than others, rendering certain moral tendencies as vital for survival. Values of justice and equity appear to be among some of the most crucial components to maintain social norms and community order intact in communities of human and nonhuman animals. Undoubtedly, intellectual ability and moral judgment of humans are not comparable with those of other species; nevertheless, the presence of social instincts functions as an evidence of moral conscience in other species. With respect to moral behaviors and emotions, through approaching the precursors, such as the inequity response, scientists may gain a better insight into the outcomes of evolution of moral behavior. Since clear continuity has been determined between the species, it can function as the foundation of future research on evolutionary approaches to human morality.

Cross-References

- [Honor Code](#)
- [Meditation](#)
- [Morality](#)
- [Norms](#)
- [Social Values](#)

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Human Estrus

- [Women's Preferences During Ovulation](#)

Human Evolution

- [Alfred Russel Wallace \(1858\)](#)
- [Evolution of Long-Term Pair-Bonding in Humans](#)
- [Hominin Evolution](#)
- [Homo floresiensis](#)
- [Homo rudolfensis](#)

Human Evolutionary Ecology

► Human Behavioral Ecology

Human Genome Project, The

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Definition

The Human Genome Project was an international research project that mapped and stored all 3.2 billion base pairs in the human genome.

Introduction

The Human Genome Project (HGP), successfully completed in 2003, was an international collaboration that accurately sequenced and mapped the entire euchromatic portion of the human genome. Two separate drafts of the human genome DNA sequences were published in 2001 as a consequence of the race between Celera Genomic's privately funded and the International Human Genome Sequencing Consortium's publicly funded initiatives. Their goals were to sequence all the nucleotides of the human genome, create databases to store this information, and develop tools to analyze this massive amount of information. Completing the project required collaborators from the UK, France, Japan, Italy, Canada, and Germany and costs approximately \$3 billion (International Human Genome Sequencing Consortium 2004).

History and Significance

In 1986, over 30 years after James Watson and Francis Crick first discovered the structure of DNA, Italian Nobel laureate Renato Dulbecco supported the creation of a project aimed at

sequencing the complete genome of an organism. While he was not the first to propose such an undertaking, his commentary in *Science* propelled the concept of a HGP into scientific mainstream. Its independent origins stem from Dulbecco, Robert Sinsheimer of UC Santa Cruz, and the Department of Energy's (DOE) Charles DeLisi (Berg 2006). Though each with his own specific reasons, ranging from understanding cancer to detecting chemically induced mutations, they understood that this colossal feat was needed to completely understand the genetic basis of human illnesses and diseases. The project was officially launched in 1998 by the DOE and the National Institutes of Health.

Before the HGP, stretches of genetic material had only been examined through individual small-scale experiments. DNA is the code that makes thousands of genes that keep a cell living. This code is made of four chemical bases, called nucleotides, ordered along a sugar-phosphate backbone of the DNA double helix. An organism's genome is the entire DNA sequence of one set of chromosomes. Humans have 23 pairs of autosomal chromosomes, which are identical in males and females, and a set of sex chromosomes, which are different between males and females. Each chromosome consists of around 50–300 million nucleotides, but because of DNA's double helix complementarity, the makeup of one strand provides exact information about the other strand. The complete human genome consists of 3.2 billion nucleotides, however knowing just the arrangement of the bases (called a sequence) does not give any information of where the genes are located on the chromosome (called a map), the function of each genes, or what genes correspond to which proteins. The difficulty of the HGP was to both sequence and map every single nucleotide (International Human Genome Sequencing Consortium 2001).

The laboratory techniques in the 1990s were not able to yet read the three billion sequence from end to end. Sequencing at this scale was a laborious process as the HGP Consortium started by using clone-by-clone sequencing to create a crude physical map of the genome before sequencing the DNA. In this method, long strands

of DNA are cut into smaller 150K base pair long pieces and then into a bacterial artificial chromosome (BAC) vector, an artificial chromosome from a bacteria. A BAC is a piece of circular DNA that can reproduce inside a bacterial cell, so each time the bacteria divides, the inserted human DNA is copied. All of this DNA is broken down into small overlapping pieces, sequenced, and then pieced back together using areas of overlap to reform the large original pieces originally inserted into the BAC (International Human Genome Sequencing Consortium 2004). While each piece is from a known region of the chromosome, making clones and creating genome maps is expensive and time-consuming. Furthermore, this type of sequencing cannot be used on centromeres or telomeres, the tightly packed middle and ends of a chromosome, because they contain long repetitive sequences (Venter et al. 2001).

Craig Venture and his company Celera instead pushed forth a method that bypassed the step of using BAC clones entirely. In this method called shotgun sequencing, the whole genome is broken down into small pieces that are easy to sequence. Then, using massive computing power, the pieces are assembled by a computer program that looks for small overlaps between the pieces (Venter et al. 2001). Because this eliminates the physical mapping stages needed for BAC clones, sequencing is faster and less expensive.

The HGP used genetic material from five anonymous donors in order to create the reference map we have today. Scientists collected blood and sperm samples from individuals of European, African, American, and Asian ancestry, so the completed genome was a composite of DNA and not a specific individual's genetic information, called a reference genome. A major finding of the HGP was that all humans contain the same large set of genes and genomic regulatory regions that direct development (International Human Genome Sequencing Consortium 2004). People only deviate in 1 out of 1000 bases, so this reference genome is 99.9% identical across all humans, regardless of race (Venter et al. 2001). While each person's genome does contain individual variations, the conclusion of the project dismissed many genetically based ethnic differences.

Scientists were also surprised to discover that humans only contain 20,000 genes, a number far lower to pre-HGP predictions of 100,000 genes (International Human Genome Sequencing Consortium 2004). As humans are arguably the most complex organisms on earth, researchers assumed that we would contain the largest number of genes. While 20,000 is more than a rodent, it is not much larger than other apes. Even more astonishing was the discovery that genes only make up 1% of the genome. The rest, once considered junk DNA, is vital in regulation when and where genes are turned on and off.

The project had an immense impact on all of science, chiefly because it accelerated the advancement of DNA sequencing technologies. The first genome took around 13 years to complete, but since then scientists have been able to sequence the genomes of other organisms within a year. The price to sequence an entire human genome now only costs around \$1000 which allows for detailed comparisons across thousands of individuals. Moreover, since the completion of the HGP scientists have identified the genetic basis of more diseases, like autoimmune disorders and specific types of blindness. Research studies have also linked over 200 genes to types of cancers – triple the number that was known before the HGP. The completion of the project has heralded in a new age of personalized medicine and revolutionized genomic technology.

Conclusion

The HGP was an international collaborative project that identified and mapped the 3.2 billion base pairs that make up the human genome. Initiated in 1990, the project took 13 years to complete and led to many significant advances in sequencing technology. Using wholegenome random shotgun method and hierarchical shotgun methods, the collaboration built a genetic and physical map of the genome. Most striking, researchers discovered that the genome only contains around 20,000 genes and 99.9% of nucleotides are identical between any two people.

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Human Groups

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Synonyms

[Collectives](#); [Social groups](#)

Definition

Aggregates of individuals united by specific relations or characteristics, which make them distinct from other aggregates.

Introduction

Social life in human societies relies on interactions and cooperation between their members. At the same time, the distribution of these interactions is not equal across the whole population. Instead, social life goes on within collectives, or groups, uniting a number of individuals. Such collectives are distinct from other collectives and exist in many different forms, from small family groups to states and nations. Although it might seem intuitively clear what a “group” is, its scientific description turns out to be very difficult. There are two general approaches to understand the nature of human groups. The first one is based

on researchers’ goals and interests, whereas the second one is based on lay people’s perception of groups.

Social Group as a Researcher’s Construct

The first approach to understand human groups is more analytical and based on researchers’ decisions on what constitutes a group and how can it be identified. Depending on research goals, many alternative criteria for group identification can be proposed. For example, an evolutionary biologist can make this decision on the basis of genetic similarity, an anthropologist can rely on spatial characteristics of residence, a sociologist can group people according to the statistical analysis of survey results, a psychologist may focus on self-identification with a group, a social network analyst will probably look at the density of electronic connections between users. The multitude of the possible criteria underlying group identification and multitude of groups in which humans can be included is a challenge for any science treating groups as separate units of analysis and especially for any science treating them as real entities.

Such difficulties are evident in evolutionary biology and, particularly, in group selection approach because of the necessity to determine to what types of social collectives any group-level evolutionary mechanism should be applied. When evolutionary arguments are applied to human groups, they are typically refer to those ones, which are common in primitive societies and more resembling animal groups. The two most important forms of social organizations in such societies are families and local groups. Whereas the former are directly involved in daily routines, child-rearing, and mutual aid, the latter are based on a more large-scale cooperation necessary for complex tasks, wars, or rituals necessary for maintaining group solidarity (Johnson and Earle 2000).

Such groups are considered by some evolutionary biologists as examples of “adaptive units” which are the object of natural selection as well as individuals (Wilson 2006). According to this multilevel selection approach, group-favoring

behavior should be understood in terms of individual's absolute fitness rather than relative fitness within a group. At the same time, direct application of the kin selection theory to larger ethnicity groups faces difficulties due to enormous complexity of larger groups' social and normative organization (Jones 2018). Within large social groups, psychological processes necessary to cooperate and regulate social relations become extremely important. The multilevel selection theory argues that such psychological processes (e.g., underlying collective decision-making, imitation, or social control) can still be understood as group-level adaptations, because they make possible the existence of specific types of groups (Wilson 2006).

The argument of the multilevel selection theory that groups are adaptive units in the same sense as individuals raises another question: Are they real? Or, to be more exact, Should human groups be treated as entities? This question, albeit in a varying forms, underlies long-lasting discussions in sociology and other social sciences often treating collective forms of social life such as corporations, states, or institutions as social entities within "social reality". However, both in evolutionary and social psychology, such views are seldom. Within these disciplines, psychological processes and behaviors are attributed to individuals even if collective phenomena are under consideration. Any group-level effects are seen as resulting from interaction and communication between individuals. Unlike individuals, groups are unobservable as entities, have no clear boundaries comparable to those of an individual, and cannot perceive, feel, think, or behave in the strict sense, i.e., irrespective of individuals' cognitions and behaviors.

Another difficulty is the great amount of group types in which humans exist. In modern societies, individuals participate in numerous collectives which can be called groups: families, local communities, organizations, nations, ethnic groups, religious groups, political parties, customers, sports fans, etc. Treating each of them as a real entity is theoretically challenging.

To overcome these difficulties, an American psychologist Donald Campbell introduced the

notion of group's *entitativity*, i.e., the degree to which a particular aggregate of persons can be considered as an entity (Campbell 1958). The matter of group's reality thus becomes a matter of degree rather than yes-or-no question. Relying on psychology of visual perception, he proposed a number of principles, or criteria, which could be used to treat human groups as more or less entitative. Those are common fate, similarity, proximity (as condition of face-to-face communication), permeability, and some other. This approach is more realistic and allows thinking about human groups in terms of many specific group characteristic, although it depends a lot on the choice of measurement procedures used to describe a group.

Lay Theory of Social Groups

An alternative approach for understanding the nature of human groups refers to individuals' own perceptions of group and intuitions about what constitutes a group and how it differs from other groups. A number of studies conducted by B. Lickel, D. Hamilton, S. Sherman, and several other psychologists revealed important regularities of people's perception of social groups. They used several methods: explicit rating of 40 different groups according to their characteristics, voluntary sorting of these groups into categories, analysis of identification errors during face recognition (Lickel et al. 2000; Sherman et al. 2002). In the explicit rating task, participants rated each of the 40 groups according to their perceived entitativity and 8 properties: interaction between members, importance of a group for its members, shared goals and outcomes, similarity of group members, permeability, group size, and the duration of its existence. Analysis of participants' choices allowed to identify four different types of groups:

Intimacy groups (family, small group of friends, romantic partners, etc.) are the highest in entitativity and are characterized by high interaction and personal importance for their members, as well as common goals and outcomes.

They are small in size, have low permeability, and relatively long duration. The level of perceived similarity among their members is also the highest among the all group types.

Task groups (e.g., sports team, rock band, coworkers, etc.) are also high in perceived entitativity, small in size, moderate in permeability, have moderately high level of interaction, shared goals and outcomes, personal importance, and members' similarity.

Social categories (e.g., women, Jews, Americans, Blacks) have intermediate perceived entitativity, are very large, and have the longest duration. At the same time, they are low in members' interaction, shared goals or outcomes, as well as personal significance and similarity.

Loose associations (e.g., people at a bus stop or in line at the bank) are the lowest in their entitativity and highest in permeability. Other group's properties for loose associations are low; they exist for a short time, their members have little interactions, are not similar, and don't share goals and outcomes much. Their personal significance for the members is also the lowest among the all group types.

The analysis of the studies' findings led authors to the conclusion that in terms of subjective perception, entitativity is strongly correlated with members' interaction and similarity, shared goals and outcomes, and personal importance. Additional studies showed that when people treat the groups to which they belong, their perceived self-importance and entitativity are also strongly correlated (Lickel et al. 2000). It is also supposed that other contextual and motivational factors, such as intergroup relations or personal goals can influence perceptions of groups. Culture is another important factor, which can determine the subjective perception and meaning of groups. In particular, collectivist societies are supposed to attribute more entitativity and agency to groups than individualist societies (Tsukamoto et al. 2018).

Subjective perceptions of groups and their properties are psychologically meaningful and

related to many aspects of human cognition and behavior. They are used to explain and predict the social world, necessary to choose appropriate strategy. Defining group boundaries and perceiving their entitativity and other attributes is a necessary prerequisite of most effects associated with group membership: social identity, intergroup biases and prejudices, in-group favoritism, intergroup relations, perception and regulation of social relations (e.g., Lickel et al. 2001; Effron and Knowles 2015).

The four types of groups listed above are identified in various studies using different samples and methods. Recent studies show that the differences among these group types appear in childhood, so that 5–6 years old children differentiate between them and ascribe some degree of entitativity to all of them except for loose associations (Plötner et al. 2016). This allows to suppose that the lay theory of groups is a part of those universal psychological processes which, according to the evolutionary approach, underlie human ability to compose groups which can be considered as real social unities (Wilson 2006). Thus the two approaches described above are not necessarily contradicting each other.

Conclusion

Groups are the key element of the social organization of human societies studied by various social disciplines. The main difficulty of studying human groups is their enormous diversity and the fact that individuals belongs to a great amount of them, contextually change their memberships and relations to other groups. For psychological science, identification of group types is crucial as it helps to systematize behavioral and relational patterns of social life. The idea that humans organize their knowledge of groups according to some common principles is crucial for understanding these regularities and bridges the gap between evolutionary notion of groups as adaptive units and psychological reality of actual group perception.

Cross-References

- [Group Size](#)
- [In-Group Versus Out-Group](#)
- [Living in Groups](#)
- [Out-Group Members](#)

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Human Improvement

- [Eugenics](#)

Human Leukocyte Antigen (HLA) System

- [MHC Compatibility](#)

Human Locomotion

- [Humans Crawl: Species Atypical Movement](#)

Human Mate Poaching

- [Costs and Benefits of Mate Poaching](#)

Human Mate Poaching (Schmitt and Buss, 2001)

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Synonyms

[Hunting out of season](#); [Mate stealing](#)

Definition

Strategies, communications, and actions that have the intention of attracting someone who is already in a romantic relationship, with the purpose of

dissolving that relationship and forming a new relationship with that person.

Introduction

A significant portion of human mating research considers male and female intrasexual competition as limited to competing for available mates in a pool, for either short-term or long-term relationships (or both). Much of this is captured well by sexual strategies theory (Buss and Schmitt 1993). However, competition can continue well into established relationships, as Schmitt and Buss (2001) demonstrate and develop in a series of studies on human mate poaching (“behavior intended to attract someone who is already in a romantic relationship,” Schmitt and Buss 2001, p. 894). This topic clearly extends human mating research to include ongoing relationship issues, including relationship maintenance and dissolution, and the fact that aspects of these issues involve others outside the actual relationship. Across most of human evolutionary history, it would have generally been advantageous to secure additional mating experiences via poaching and correspondingly detrimental to have one’s mate poached. Therefore, we can expect that modern humans also, to some degree, utilize mate poaching as a method of securing mates. This behavior, operating at both a conscious and subconscious level, can be directed at either short- or long-term contexts. Whether a brief affair or a more permanent coupling, there is some degree of premeditation involved from the mate poacher because they engage in actions meant to draw their desired partner away from the already-established relationship.

Patterns of Human Mate Poaching

Schmitt and Buss (2001) predicted that patterns would emerge that could be predicted from an evolutionary lens. For example, one method of mate poaching occurs through engaging in extra-marital affairs, which (depending on the study) occurs between 20% and 50% of the time. While

many of these affairs are short term, there is a pattern of poaching for long-term partners as well. Another example is that of serial monogamy, viewed as long-term mate poaching, which is a feature of mating in many cultures. Therefore, an argument that long-term mate poaching might be part of our evolved mating psychology is feasible. These patterns of mate poaching are extensively historically documented and have been found in literature and mythology.

Empirical Evidence for Mate Poaching

Four studies are reported in Schmitt and Buss (2001), supporting and developing the idea of human mate poaching. The first study found that substantial proportions of people had personal experiences related to mate poaching, across both undergraduates and a broader convenience sample of participants. This included experiences attempting to poach a partner from someone else and experiences with someone trying to poach them away from a committed relationship. Of the participants that reported being in a relationship, between 12% and 27% indicated that their current relationship resulted from poaching their partner away from someone else and between 20% and 41% reported that their current relationship was a result of them being poached from a previous relationship. Higher scores on the personality traits of agreeableness and conscientiousness were associated with less likelihood of poaching attempts, whereas higher scores on the traits of extraversion and openness to experiences were associated with being more likely to experience poaching attempts directed toward themselves. Personality features related to accepting poaching attempts included being disagreeable, neurotic, and unconscientious, as well as having low relationship exclusivity scores, a masculine gender orientation, and low emotional investment.

As a preliminary step for Study 2, small groups of some of the prior participants were asked to generate potential short- or long-term costs or benefits of mate poaching, for either men or women, within moderated focus groups. These

were transcribed and summarized into 73 distinct items that were themselves grouped based on conceptual similarity. Study 2 had four hypotheses:

- (a) Men should view the physical beauty of the person they were poaching as a larger benefit than the women in the sample.
- (b) Women should see potential partners with more resource control as a larger benefit than would men.
- (c) Men should perceive short-term poaching opportunities as more beneficial than women because it satisfies evolved desires for sexual access and variety.
- (d) Both men and women should view commitment threats in the long term as costlier than those that threaten short-term fidelity.

Ratings of the 73 mate poaching costs and benefits by undergraduate participants (focusing on variables of temporal context, sex of actor, and sex of rater) supported all four of the above hypotheses.

The structure was similar for Study 3, in that an initial group of participants generated 60 individual behaviors and tactics associated with mate poaching (i.e., male and female attraction methods). Separate undergraduates then rated each of these 60 tactics for effectiveness for either attracting a short-term partner or a long-term partner. The results of these ratings supported five hypotheses for Study 3:

- (a) Enhancing one's own appearance and derogating a rival's physical appearance should be less effective as an attraction technique for men than for women.
- (b) Men should have better success when drawing attention to their resources and their willingness to devote those to a potential partner.
- (c) The suggestion of low-cost sexual access should be more effective for women trying to poach a mate in the short term.
- (d) When attempting to poach a partner, men and women should experience different levels of success when they make that person question their current partner's fidelity.

- (e) There should be an interaction between sex and temporal context (i.e., poaching for a short-term or long-term relationship), such that men attempting to poach for the short term should be rated as most effective when displaying dominance over the rival mate. (This final hypothesis was qualified by the finding that dominance display, although rated as more effective for men in a short-term context, was not rated as the most effective tactic in terms of absolute ratings.)

Study 4 extended the results of Study 3 by changing the relatively vague relationship context of Study 3 (short and long term) to a broader and more specific set of relationship contexts: married, dating, living together, long distance, highly committed, not committed, just beginning, and about to end. The same five hypotheses generated for Study 3 were utilized again and were again supported by the results. Furthermore, the more diverse set of relationship contexts in Study 4 produced several more nuanced findings that go beyond those original hypotheses. For example, women's use of appearance enhancement (as a mate poaching tactic) was judged least effective when targeting married men and most effective for targeting men in noncommittal relationships. Similarly, men's use of resource control demonstrations was judged as less effective when targeting women in a very committed relationship and most effective when targeting someone just beginning their relationship.

Limitations and Impacts

Schmitt and Buss (2001) set out a theoretical and methodological framework for studying a previously unexplored area within human mating, mate poaching. Their empirical results then provided evidence of the validity and value of this topic. As the authors noted, though, some limitations existed with these studies. The Schmitt and Buss (2001) studies are almost entirely based on university undergraduates, and it would be beneficial to employ more diverse samples – particularly utilizing various age categories. Additionally,

these studies evaluated the reported perceived effectiveness of various mate poaching tactics, not the actual or absolute effectiveness of any of these tactics. Finally, it is possible that the artificiality of these study methods (i.e., text descriptions) did not capture the complexity and subtleties of mate poaching in the real world. There likely are nuances in the tactic, timing, and deployment of each of these techniques allowing them to co-occur and depend on the skill or relationship status of the individual enacting them. Addressing each of these limitations required more extensive and difficult research projects, with Schmitt and Buss (2001) serving as a foundational springboard for cross-cultural studies (Schmitt 2004), examinations of tactics poachers use (Schmitt and Shackelford 2003), and in-depth research on specific personality characteristics (for examples, see Jonason et al. 2010 or Kardum et al. 2015).

Since its publication, Schmitt and Buss (2001) have received a strong and consistent level of citation in the research literature and elsewhere. Google Scholar (<https://scholar.google.com/>) counts a total of 442 citations of Schmitt and Buss (2001) between its publication and November 2019. Furthermore, the citation rate for this publication has been increasing over time. During the 2000s, it received 10–20 cites per year, but in the 2010s it has been consistently receiving about 30 cites per year. This is a relatively unusual pattern of citations over time, indicating a seminal paper on a topic that is becoming increasingly relevant.

Conclusion

The broader discussion of human mating strategies in Schmitt and Buss (2001) opened a new vein of research in the area of mating relationships. It was the first article to systematically explore the evolutionary case of mate poaching, including questions about how frequently the tactic is employed, associated individual differences, costs and benefits for both sexes, and the relative success of different strategies. It also

provided valuable contexts for work on rival derogation and self-promotion by pointing toward powerful situations in which those phenomena would be particularly prominent. This laid a foundation for extensive research that followed.

In agreement with broader infidelity studies, mate poaching is a frequent strategy that succeeds in a larger-than-expected number of cases. This strategy is associated with several distinct individual personality characteristics (a finding further supported by Sunderani et al. 2013, in addition to those mentioned previously), and the success of this strategy is likely dependent on both the characteristics of the poacher and the poached (for another example, Parker and Burkley 2009). Similarly, there are unique costs, benefits, and response options for each party involved in a mate poaching scenario, and, given that a large portion of mates in any given mating pool are already partnered, mate poaching inherently creates adaptive problems for the person whose partner is being poached (for further research on costs and benefits, see Davies et al. 2010). Schmitt and Buss anticipated that mate poaching likely coevolved with methods for mate guarding and retention tactics. Since its publication, further findings have broadened our understanding of, among other things, how individuals cope with mate poaching (Ein-Dor et al. 2015) and its coevolution with mate guarding (Buss 2002).

Cross-References

- [Compensatory Mate Retention Tactics](#)
- [Concurrent Mate Retention Tactics](#)
- [Costs and Benefits of Mate Poaching](#)
- [Mate Guarding](#)
- [Mate Poaching](#)
- [Mate Retention](#)
- [Mate Retention Strategies](#)
- [Personality and Mate Poaching](#)
- [Sex Differences in Costs and Benefits of Mate Poaching](#)
- [Use of Mate Retention Strategies](#)

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Human Milk

- [Breast Milk Composition](#)

Human Nature

- [Cross-Cultural Universality](#)
- [Psychic Unity](#)

Human Nature and Biocultural Evolution

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Synonyms

[Evolution of culture](#); [Genes and culture interaction](#); [Human behavior](#)

Definition

Human nature refers to psychological aspects and behavioral traits that are common to most people. Biocultural evolution is the process by which biological and cultural aspects interact to shape human nature throughout human evolutionary history.

Introduction

One of the most intriguing topics of scientific investigation is human nature, why humans behave the way they do, having been the object of study of a wide variety of disciplines, including psychology. Despite the volume of research, human nature has not been completely unveiled. This is partly due to the controversy over the extent to which human behaviors are a product of their environment or of their genetics, resulting in the “nature versus nurture” debate that has been the focus of scientific discussion since classical times (Thorpe 1974). Philosophers such as Locke and Rousseau, for example, adopted the nurture side of this debate, advocating that the newborn child is a *tabula rasa*, a blank slate, and as such, the essential nature of a human being is inscribed as a result of learning and other interactions with the environment during the life course. Conversely, thinkers as Hobbes and Spencer believed that genetic makeup determines to a very large extent essential human nature. Nowadays, this

dichotomy between nature and nurture is largely deemed false with the view that an interaction between the two results in human behavior: that “every bit of the behaviour (...) of every single organism living on the face of the earth results from the interaction of genetic information stored in the developing organism and the properties of its environment” (Richerson and Boyd 2005, p. 9).

There is little doubt that in all mammals, including humans, early behavior in life is a result of the activation of structures that are largely a result of genetic endowment (Plomin et al. 2014). However, human behavior is highly flexible in its expression, and humans appear to have a much greater latitude for learning than other animals as seen in, for example, our many and complex languages. Each person’s behavior is made up of the evolutionary past embodied in the genetic apparatus and of the experiential past incorporated in the various forms of specialized brain mechanisms formed by evolution which include mechanisms dependent on environmental input such as learning and memory. As a consequence, another factor that has also to be considered is *culture*, variation caused by learning from other humans both past and present, facilitating a population’s adjustment to a given environment. Human nature is, therefore, a result of the interaction between genes and culture, known as biocultural evolution (Gintis 2011).

The human organism is an integrated and coordinated system, adapted to its environment, and at the same time, a member of a population with a unique evolutionary history adapting it to the environment it presently occupies. Because the evolution of the psychological mechanism’s underlying culture was so powerful, they resulted in cultural change (Mesoudi et al. 2004). As such, the transformation of sociocultural systems can best be explained via analogy to the synthetic theory of biological evolution, applying concepts as variation, selection, and adaptation. With that in mind, in this chapter, we discuss how the interactions between genetic evolution and cultural evolution, i.e., biocultural evolution, have shaped human nature. Before going further, understanding the concept of culture and how culture has

evolved throughout humans’ evolutionary past is an essential step to a comprehensive understanding of the nature and diversity of human behavioral adaptations.

A multifaceted process like culture is complex to conceptualize using one single definition; however, in this chapter, we will consider culture as a set of information that impacts individuals’ behavior and is acquired from other members of their species through teaching, imitation, and other forms of social transmission (Richerson and Boyd 2005). Culture here is considered as an autonomous inclusive fitness-seeking adaptive system that functions to maximize inclusive fitness under present-day conditions (Tooby and Cosmides 1989). According to Tooby and Cosmides (1992), our evolved information-processing mechanism should be context dependent in a way that different informational inputs should generate different behavioral and representational outputs, usually as an adaptive response to different environmental contexts. As a result, although humans share the same evolved information-processing mechanisms, people living in different areas or experiencing different environments can display different responses that may be adaptive under those different conditions.

Culture affects the success and the survival of individuals and groups; as a result, some cultural variants spread, and others diminish, leading to evolutionary processes that are every bit as real and as important as those that shape genetic variation. These culturally evolved environments can then also affect which genes are favored by natural selection. Over the evolutionary long haul, it has been argued that culture has shaped our innate psychology as much as the other way around (Richerson et al. 2010). According to Ruyle (1973), selective pressures result from the material conditions of life and of the society influencing individual members of a population which then determine both the genetic and cultural heritage of humans. Thus, the genetic characteristics humans share in different degrees with other members of their species along with psychological principles that have evolved genetically constitute the heart of “human nature.” As such, the

most fundamental question of how humans came to be what they are can be answered by considering culture as intimately intertwined with other aspects of human biology.

Genetic evolution created a psychology that allows the cumulative cultural evolution of complex cultural adaptations. One classic example relates to the coevolution of genes related to lactose digestion and the cultural practice of acquiring dairy products from other animals. Although the cultural evolution of animal husbandry practices emerged in at least two geographical locations independently, detailed genetic studies demonstrate that different genes evolved to generate tolerance to lactose in adults in each case (Ingram et al. 2007). It may have been the case that the evolution of dairy farming traditions increased the relative fitness of the gene that allows whole-milk consumption by adults in each environment. As that gene spread, it may have changed the environment, shaping cultural practices, perhaps favoring more milk consumption and as such tolerance to lactose (Richerson and Boyd 2005). This example illustrates how biocultural evolution operates to shape different human traits.

Likewise, biocultural evolution has been believed to have also played an important role in the genetic evolution of human psychology. While natural selection shaped variation, different modalities of transmission biases mold the distribution of cultural variants. To illustrate, we will borrow the example given by Richerson and Boyd (2005) regarding the development of language. It is indisputable that the human vocal tract and auditory system have been modified to enhance our ability to produce and decode spoken language and along with a special-purpose psychological machinery for learning the meaning of the words and grammatical rules. Selection, however, could not have shaped those in an environment without spoken language. The most plausible explanation is that simple culturally transmitted language arose first and then selection favored a special-purpose morphology and psychology for learning, decoding, and producing speech.

To explain how coevolutionary processes occur, Cloak (1975) proposes an ethological

model to understand the interaction between culture and biology: Cloak divided culture in two components that mutually influence each other: (1) *i-culture* that is a set of cultural instructions we carry in our nervous system and (2) *m-culture*, which encompasses the material instructions, including features of human behavior, technology, and social organization. Natural selection would, in turn, operate to shape cultural practices. Those cultural instructions whose behavior (m-culture features) helps to determine its occurrence, replication, or endurance in several places would therefore survive and propagate. Thus, the evolution of both genes and culture is governed by natural selection, which means that different environments will lead to different culture types, just as they can lead to different genotypes (Richerson and Boyd 2005).

Conclusion

Human nature is a controversial concept. Some thinkers have claimed that there is an innate human nature, emphasizing biological aspects governing behavior. Others have defended the idea that humans are unique and able to take decisions that are not governed by their biology and that humans are molded along their lives in interaction with the surrounding environment. There are also those who have advocated that there is no such thing as human nature and that the term should be abolished (Visala and Fuentes 2015). In this chapter, we highlighted that a biocultural view on human nature that resolves the nature versus nurture debate and considers the capacity for the interaction between biological factors and cultures is the key to understand what makes us unique.

In light of these arguments, we can conclude that any attempt to understand how humans came to be what they are that disregards either biological or cultural factors may fall into reductionism. Human beings are too complex to be understood based solely on one or another cause. A more comprehensive approach is one in which the role of both genetic and cultural

factors and their interaction contribute to human evolution resulting in what we can call human nature.

Cross-References

- [Evoked Culture](#)
- [Evolution of Culture](#)

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Human Ornamentation

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Synonyms

[Body Modification](#); [Clothing](#); [Modification](#); [Mods](#); [Ornamentation](#); [Piercings](#); [Tattoos](#)

Definition

The deliberate or purposeful additions to the human body/anatomy, including clothing choice, jewelry, and various forms of body modification.

Introduction

Humans have always showed a propensity toward ornamenting ourselves. From an evolutionary perspective, ornamentation leads to unique gains in the mating market – allowing individuals the ability to bolster their appearance to potential partners by using environmental cues. Ornamentation can exist in a multitude of forms; clothing, jewelry, and even tattooing/piercing the body. Yet, all forms of ornamentation share one very important criterion in common: they are all cultural artifacts. Much of our evolutionary history has deep cultural roots across the world. The mechanisms of evolution shape many of our behavioral tendencies, including our capacity for culture and cultural artifacts (i.e., the way we ornament ourselves).

In the time long before written record, we made relics of elaborate adornments, hinting at an interesting unfolding of development within our uniquely human psyche. Before the Phoenician's paved the way for modern

language, humans were already pro's at creating ways to ornament ourselves; each culture (and various subpopulations within) unique, with types and levels of ornamentation varying in permanence. The headdresses of Native American's, the armor of a samurai, the makeup of a geisha, the stacking neck rings of numerous cultures, and full-body tattoos are just a few examples of the ubiquitous nature of body ornamentation. This human universal – the push to ornament oneself – is rooted in evolutionary theory. In proximate terms, it allows an individual to stand out in a crowd, and, depending on type of ornamentation, signal to a potential mate underlying fitness (in a way, it could be considered an extended phenotype). Nonpermanent forms of ornamentation like clothing have practical proximate outcomes: Ornamenting oneself in decorative clothing that either accentuates form or signals financial status can attract the attention of potential mates in a general sense. More permanent forms of ornamentation, like the neck-rings of the Padaung women, or full body tattoos not only promote uniqueness but also are a form of costly signaling. If an individual is able to successfully “pull off” a more permanent form of body ornamentation without any deleterious side effects, they are essentially self-handicapping (Zahavi and Zahavi 1997). This will be further expanded upon in the body modification section.

The Conscious Ape

At the heart of our complex system of body ornamentation lays a spark of consciousness that glows brighter than any other animals on Earth – including our closest living ancestors, the Chimpanzees. Our higher-order thinking quite obviously stems from their ancient thought processes, yet consciousness is something that had classically been considered uniquely human. Being able to be conscious of *oneself* (i.e., “have an identity”) and further, to understand that ones' own experiences are different from the next person, has allowed humans to excel in ways that no other animal has before us. Yet, it is important to keep in mind that humans did not just wake

up one day suddenly conscious of themselves; Evolutionary theory claims that in order for a structure to evolve, mechanisms will only build upon/shape lasting structures. Nonvocal forms of language within various types of great apes (especially chimpanzees) have been demonstrated many times over the past few decades (which hints at the idea of a common ancestral mechanism that was further shaped and built off of). This connection with symbolism (through language) arguably leads way to the idea of *consciousness* – which was classically thought of as a uniquely human attribute.

In 1977 Gallup Jr. demonstrated the bidirectional properties of consciousness in a sample of chimpanzees. Consciousness can be broken down into two streams: the outward stream (attention directed toward environment/surroundings) and the inward stream (the thought processes within your own mind) – hence, *bidirectional*. As many pet owners can attest, when cats and dogs are presented with their own reflection, they either do not seem to care at all or look into their reflection as if they are seeing another animal for the first time. In chimpanzees, this is not the case. Interestingly, recognizing your own reflection can indicate an evolutionary step in the formation of consciousness. When wildborn preadolescent chimpanzees were given access to mirrors, they were startled at first, but then began using the mirror to groom themselves in areas they could not normally see, or pick food out of their teeth – or even make faces at their reflection. After nearly 2 weeks of mirror exposure, the chimpanzees were anesthetized and a bright red mark was painted on their forehead. They recovered without a mirror in their cage, but once the mirror was re-introduced they immediately noticed and began touching the colored spot on their head, supporting the idea of self-awareness and essentially, a more simplistic form of consciousness in our closest ancestors. Unlike many other species (including many other primates), chimpanzees reacted to their own reflections and supported the idea that they hold part of the evolutionary building blocks that make up our consciousness. Human uniqueness is arguably due to our higher-order forms of consciousness, and through

that form of consciousness, human ornamentation was born. As the most conscious animal on this planet, it should not be surprising that we display some of the most complex forms of ornamentation.

The Building Blocks of Human Ornamentation: Behavioral Modernity

As mentioned earlier, evolutionary theory teaches us that for any structure to evolve or become specialized, it must build off a more basic form. Essentially, the birth of symbolic thought is linked to our drive to ornament ourselves and thus, when we became truly “human” is when we began forming these symbols of our culture. Approximately 200,000 years ago anatomically modern *homo sapiens* were already roaming across much of the old world, yet, signs of modern human behavior did not emerge for another 150,000 years. According to “The Human Revolution” reconstruction of human evolution, anatomically modern *Homo sapiens* experienced an exceptional shift between 40,000 and 50,000 years ago that marked the birth of behavioral modernity (signs of behavioral modernity include planning ahead and effectively using/manipulating resources) (McBrearty and Brooks (2000)). Some opponents of this model claim that modern human behavior was a structure that was slowly built upon, starting around 300,000 years ago and sculpted over hundreds of thousands of years. From this perspective, the transmission of cultural (and not genetic) processes over the course of many years is what eventually led to the culmination of behavioral modernity. Again, we see this strong link between body ornamentation and culture or cultural transmission. Yet, regardless of which model one ultimately sides with, we see a dovetail of modern human behavior and the birth of symbolic thought (along with body ornamentation).

Apart from the general idea of behavioral modernity, *Theory of Mind* is important to consider when attempting to understand human ornamentation from an evolutionary perspective. At a basic level, *Theory of Mind* is the ability to

attribute mental states to not only oneself and others but to recognize that other individuals might not share the same views as you. Similar to the idea of consciousness, being able to effectively rationalize that *I* is separate from *you* can lead to evolutionary advantages that play out in the form of human ornamentation. If an individual is ornamenting themselves in ways that are considered “attractive” culturally and socially, they are taking in cues from their environment, processing them, and providing an output via ornamentation that will potentially increase their reproductive success (due to the ornamentation practices being seen as “attractive”).

Some of the earliest examples of body ornamentation are perforated shell beads found in Africa. These beads date back 150,000 years – after anatomically modern humans, but before the proposed shift to behavioral modernity. This early form of body ornamentation is a testament to the snowball effect of evolution; ornamentation was essentially once shells with holes and today takes a multitude of forms that can affect an individual’s phenotype on numerous levels (i.e., extended phenotype). Remember, a phenotype is typically explained in terms of being the physical expression (or output) of a genetic code. All living things are essentially vehicles for our genes: transporting them throughout the generations via sexual reproduction. Yet, the reach of our genes is not limited to our own bodies; it can actually extend out into the environment itself via behavioral manipulation (Dawkins 1999). Nonhuman examples include beaver dams and birds’ nests; human examples can include everything from clothing and houses to more extreme forms of ornamentation like piercing, tattooing, and scarification.

Group Membership

From an evolutionary perspective, human ornamentation is essentially used to increase the potential for reproductive fitness. One way to enhance reproductive fitness is via group membership. Since we are ultimately self-interested, the formation of groups was necessary in order

to control various levels of coercive power within different populations. Ancestrally, we went from small communities that averaged approximately 150 individuals to living in cities with populations of over a million. As the population began to grow exponentially, ornamentation practices became more ornate and elaborate to meet the demands of large communities.

The Human Canvas and Upping the Ante

The evolutionary forces that nudged us into groups also encouraged the cultural behavioral output of human ornamentation. Though human ornamentation has many outputs, one of the most fascinating is tattooing due to its permanence. *The human canvas* hypothesis is based on the idea that our propensity for symbolic thought and our need to be unique from one another lead to an explosion of creativity that began on the walls of caves but eventually turned to our skin (Carmen et al. 2012). The subject matter and placement of a tattoo can either enhance or impede an individual's likelihood of getting approached by a potential partner.

As populations began rising and healthcare became more advanced, ornamentation practices became more costly to meet this demand. In many cultures across the globe, we see tattooing and piercing in the general population. Because of large modern populations, individuals must *up the ante* in order to stand out to potential mates by means of costly signaling, often doing so via tattooing and piercing (Carmen et al. 2012). The more elaborate or specialized the tattoo or the more unique the piercing, the more costly and potentially attractive.

Of course, ornamentation is not typically permanent. In fact, it can often be used to signify a momentary emotional state or to enhance a specific feature depending on what an individual wishes to highlight, specifically when it comes to cosmetics. The type of ornamentation can vary drastically within and between cultures. Black pigment referred to as *kohl* was used as eyeliner in ancient Egypt and much of the Arab world. In India, Henna (dye) is used to make complex

designs on the skin, outlining the fingers and highlighting certain areas of the wrist, and in Japan, geisha wore rice powder to paint their faces white. Cosmetics were used historically and cross culturally as a way to enhance appearance, ultimately aiding individuals in finding a mate.

Modern Ornamentation

In today's society, cosmetics, clothing, tattooing, piercing, shoes, and hairstyles can all be ways in which individuals ornament themselves. Though some forms of ornamentation are "dishonest" in nature (think waist trainers, magnetized piercings, and spray tans), they are all momentary and can be removed in one way or another.

The plastic surgery industry prides itself on the quality of the (mostly permanent) ornamentation it provides to individuals. If people are unhappy with the way they look, they can change their phenotype if they have the cash to pay for it. A few years ago, there was a case in China where a man sued his wife for essentially having unpleasant looking children. It turns out that she apparently had plastic surgery prior to their marriage that he was unaware of, and their children looked like the mother's genotype, not her current phenotype. Plastic surgery is perhaps the most extreme yet discrete example of body ornamentation. Of course, there are many forms of body modification that are considerably extreme, but individuals that commit to these acts are often fully committed in that everyone knows they are. If plastic surgery is done well, no one will know (that is, unless they reproduce and their offspring look drastically different from them).

Conclusion

Body ornamentation has many faces in many cultures across the world and across time. As complex animals, we have always had a propensity to ornament ourselves in increasingly novel ways. As we grow and learn, it will only be a

matter of time until we find new ways to ornament ourselves, though, ultimately, we will always use an ancient algorithm to push us forward.

Cross-References

- [Advertising](#)
- [Appearance/Beauty in Girls](#)
- [Art](#)
- [Beneficial Side Effects](#)
- [Burials](#)
- [Camouflage](#)
- [Carving](#)
- [Emotions](#)
- [Facial Attractiveness](#)
- [Facial Disfigurement](#)
- [Good Genes](#)
- [Greater Risk-Taking and Status](#)
- [Health Cues](#)
- [Male-Male Competition or Male Provisioning?](#)
- [Manipulation and Dishonest Signals](#)

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Human Play

- [Social Play](#)

Human Precopulatory Sexual Conflict

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Introduction

In sexually reproducing species, some degree of cooperation between the sexes is an inevitable result of the dependence of each sex on the other for reproduction. Some degree of conflict should also be expected, however, because each member of a reproducing pair has conflicting genetic interests. This conflict is termed “sexual conflict” and is responsible for the evolution of an arms race, or antagonistic coevolution (Rowe and Day 2006), between the sexes, whereby the evolution of offensive and defensive adaptations in one sex creates the selection pressure for the evolution of counter-adaptations in the other and so on.

The two major categories of sexual conflict are “intralocus” and “interlocus” sexual conflict (Parker 2006; Rowe and Day 2006). Intralocus sexual conflict describes the contradictory effects of two autosomal alleles at a particular genetic locus within an individual. For example, males are usually physically stronger than females due to the selective effects of male-male competition on size and strength (Frontera et al. 1991). Conflict may therefore occur between a male-linked allele associated with greater physical strength and a female-linked allele associated with lesser physical strength. Interlocus sexual conflict describes conflict between sex-linked genes at different loci, usually manifested as conflict between the reproductive strategies of individual males and females. Both types of sexual conflict can be *precopulatory* (i.e., occurring prior to mating).

Human Paleontology

- [Paleoanthropology](#)

Precopulatory sexual conflict describes the costs that individuals of one sex inflict on individuals of the other sex prior to copulation. This is the period during which males and females are typically evaluating the suitability of their prospective mate(s). Because females invest more physiological and behavioral resources in childcare (Trivers 1972), they evolve strategies aimed at securing more parental investment from males than males are willing to apportion. Males, on the other hand, evolve strategies aimed at avoiding parental investment in favor of pursuing casual sexual encounters with multiple females. Therefore, much of precopulatory sexual conflict consists in the tension between female reluctance and male eagerness to engage in sexual intercourse.

Sexual conflict may create opportunities for sexual cooperation. For example, when male aggression is correlated with genetic worth or ability to secure resources, it may benefit a female to mate with a male exhibiting aggression even if he harms her in the process. The reason for this is that any son sired by such a male will likely inherit his father's traits (Eberhard 2005). If the son's aggression helps him to spread his mother's genes, such a benefit may outweigh a prospective mother's cost of mating with an aggressive male. Even if females are only benefited by male aggression because other females find aggressive males more attractive (a phenomenon referred to as the "sexy son" hypothesis; see Gwinner and Schwabl 2005), a female preference for aggressive males may evolve. According to Eberhard (2005), instances of sexual conflict may provide "the original 'nudges' that set off rounds of traditional Fiesherian runaway female choice" (p. S21). Thus, what may be an instance of sexual conflict may actually be, either in whole or in part, an instance of sexual cooperation. Albeit speculative, the courtship rituals of some species may reflect such conflict-turned-cooperation scenarios, as suggested by the manner in which a female resists a persistent suitor only to accept his advances once he has "proven" himself worthy (see Crean et al.'s 2000, discussion of female mate choice for large males in contexts of premating struggles between male and female seaweed flies). Another possibility is that male aggression is, in fact,

costly to females, but the costs pale in comparison to the costs of resistance, which may involve harm or even death. As such, instances of sexual conflict may contain some degree of compromise and cooperation (Crean et al. 2000; Crean and Gilburn 1998; though see Parker's 2006, discussion of the decreased theoretical and empirical likelihood of sexual "concurrence" in comparison to sexual conflict).

Sexual Conflict Before Puberty

Sexual conflict pervades the entirety of the human lifespan. Even children and juveniles experience its effects. A good example of this is the practice of "*sim-pua*" marriages in Medieval China. *Sim-pua*, or "little daughter in law" practice, involved the adoption of a young, prepubescent girl by the parents of an infant son. The fact that such marriages were often unsuccessful is often presented in evolutionary discussions as an example of the "Westermarck effect" (Wolf 2005), which describes the activation of evolved incest avoidance mechanisms that prevent individuals who grow up in the same household from being sexually attracted to one another. *Sim-pua* marriages are also a good example of sexual conflict between the reproductive interests of male children and female children. Insuring the virginity and betrothal of a prospective daughter-in-law to one's son may have conflicted with the reproductive interests of the daughter-in-law if the son in question was of low genetic worth or if he and his family were less wealthy than they claimed to be.

Similar conflicts may occur in cultures that practice bride pricing and dowries. For example, parents who are vying for the betrothal of their son or daughter to a girl or boy whose parents are asking for a bride price or dowry may exaggerate the actual worth of their son or daughter (who may turn out to be unhealthy, unkind, or lazy) or their resources (e.g., the livestock turn out to be sick, the land turns out to not be arable). In such instances, the reproductive interests of a girl may already be in conflict with the reproductive interests of a boy, even if those interests are represented by parents rather than the boy or girl

in question. In effect, shared genes – and, hence, shared reproductive interests – among family members allow sexual conflicts between individuals to expand into conflicts between families.

An intriguing possibility is that unique imitative and linguistic abilities allowed humans to erect entire cultural systems as extended phenotypic expressions (see Dawkins 1982) of sexual conflict. In aforementioned examples of *sim-pua* marriages, dowries, and bride pricing, cultural traditions and explicit and implicit rules, norms, and principles are passed down alongside biologically older adaptations for sexual conflict. Certain Middle Eastern and African cultures, for example, enforce strict codes regulating interactions between men and women. Usually, the heavier burden is placed on girls and women. A girl who speaks to the wrong boy or a woman who wears something immodest is risking being harmed and even killed by a father, brother, husband, or entire community for having violated a law or tradition. An example of a more harmful cultural manifestation of sexual conflict is female genital mutilation, a cultural practice aimed at limiting a girl's sexuality by associating intercourse with excruciating physical pain. Effectively, such cultural traditions may be examples of society-spanning expressions of male adaptations for sexual conflict. Although a young girl and her parents perceive the alternative as much worse (i.e., prohibition from marriage and possible excommunication), female genital mutilation may nonetheless be situated in a context that favors male reproductive interests such as sexual proprietariness and decreased cuckoldry risk stemming from female pain during intercourse (Wilson and Daly 1998, 1993).

When examining such examples of culture-spanning sexual conflict, it is important to note that male adaptations to sexual conflict might benefit some women (e.g., the male's female kin; Gwinner and Schwabl 2005) just as female adaptations to sexual conflict might benefit some men (e.g., the female's male kin). Thus, it is no surprise that women often enforce restrictions and punishments on girls and other women in cultures advocating female decency (BBC Monitoring 2016), just as it is no surprise that men enforce the

criminalization and punishment of rapists and domestic abusers in cultures that value women's rights. This point also highlights the importance of not thinking of sexual conflict as a dualistic struggle between all men and all women. Humans are genetically heterogeneous creatures who can compete and cooperate with others regardless of their biological sex. As such, sexual conflict and its cultural expressions are simply the manifestations of the reproductive interests of individuals and not some universal patriarchies or matriarchies. From an evolutionary perspective, adaptations to sexual conflict are built by the differential survival and reproduction of individual men and women rather than by all men outcompeting all women or vice versa.

Sexual Conflict After Puberty

Men's sexual eagerness and women's sexual reluctance. The conflict between male eagerness and female reluctance to engage in casual sexual encounters is most clearly on display in a now classic study by Clark and Hatfield (1989). In the study, female college students were randomly approached by a male confederate, and male students were randomly approached by a female confederate who made various sexual propositions, ranging from less explicit (i.e., "Would you go out tonight?") to more explicit (i.e., "Would you go to bed with me?"). (Note that male and female confederate attractiveness was controlled for.) Unsurprisingly, all women refused the more explicit sexual offer, whereas a majority of men accepted it. It is easy to interpret Clark and Hatfield's findings in terms of sexual conflict dynamics. Specifically, by engaging in casual sex with the wrong man, a woman risks getting pregnant and being abandoned by the man – an outcome whose time and energy costs weigh heavily on the woman and her future offspring. A reluctance to engage in casual sex therefore evolved as part of women's arsenal in sexual conflict with men. Men, on the other hand, are reluctant to pass up any sexual opportunity, as doing so might jeopardize their reproductive

interests – which are marked by increasing the quantity, as opposed to the quality, of sexual partners.

Men's eagerness to engage in sexual behavior is often in conflict with female reluctance. According to Haselton and Buss's "error management theory" (Haselton and Buss 2000), men are expected to maximize realized sexual opportunities and minimize missed sexual opportunities. In practice, this leads to men's overperception of women's sexual interest, even if it is nonexistent. Such overperceptions were responsible for an eventual lawsuit on the part of women employed at the Safeway supermarket chain who were told to smile and act friendly toward all customers (Haselton 2003). The problem was that some male customers interpreted the female employees' friendliness in sexual terms, which led to many awkward and a few relatively serious consequences, such as harassment. Along similar lines, Abbey (1982) revealed that male participants are more likely than female participants to report sexual intent in an actress's performance (but see Perilloux and Kurzban 2015, for an alternative interpretation of error management theory).

Women must also contend with error management, but their dilemma concerns maximizing opportunities to find a committed long-term partner and minimizing the possibility of falling for – and possibly getting pregnant by – men who are not interested in commitment or paternal care. In practice, women realize this strategy with an enduring skepticism toward men's professions of love, devotion, and commitment (Haselton and Buss 2000). Men can presumably override this skepticism only if they lavish a sufficient amount of material and emotional investment on women to prove their honorable intentions. Inevitably, however, some men who are truly willing to commit are often passed over by women too skeptical to accept their shows of devotion as being genuine. Thus, women's underperception of men's commitment is often in conflict with men's eagerness to profess commitment (whether actual or false) in order to obtain or maintain sexual access to women.

In the context of romantic relationships, men's sexual eagerness and women's sexual reluctance

manifest itself in sex differences in the preferred timing of sexual intercourse (Buss and Schmitt 1993). In general, a man is ready to have sex a week or so after first meeting a woman. Women, however, only reach the point of sexual readiness about 6 months into the relationship. This difference in the preferred timing of sex probably leads to many instances of precopulatory sexual conflict marked by men's pressuring of women into sexual activity and women's prolonged reluctance to acquiesce. Such divergent sexual strategies also fuel men's increased interest both in pornography and prostitution (Ellis and Symons 1990; Schmitt 2003), both of which may exacerbate existing tensions within a relationship by causing women to question men's level of commitment. On their part, women's increased interest in romance novels and films may create unrealistic expectations for men by causing women to demand greater displays of love and commitment than their partners can provide, which only adds to men's costs of pursuing sexual relationships with women.

Deception in the mating market. Sexual conflict in human mating often centers on men's and women's mate preferences. One such preference is the desire for physically attractive mates (Buss 1989; Jones et al. 2001). Other preferences include a desire for mates who have resources and a desire for mates who are capable of long-term romantic commitment (Buss 1989; Haselton et al. 2005). Evolutionarily, attractiveness is associated with genetic health and fertility (Jones et al. 2001; Pflüger et al. 2012). When judging the physical attractiveness of prospective mates, individuals are specifically attuned to features such as symmetry, averageness, clear skin, voluminous hair, and youthful eyes (Apicella et al. 2007; Fink et al. 2008; Gangestad et al. 1994; Mesko and Bereczkei 2004; Peshek et al. 2011). All of these features can be passed on to offspring and are the most prize-worthy outcomes of short-term mating, reproductively speaking. Having resources may likewise be associated with having good genes, but is also associated with being able to provide for one's offspring. Similarly, being willing to commit to, or form a pair-bond with, a romantic partner signals a prospective partner's

willingness to stick around long enough to invest in any resultant offspring. As such, the ability and willingness to invest resources in one's partner and one's offspring are characteristics that are usually sought for in long-term mates.

Males tend to pursue a short-term mating strategy to a greater extent than females (even though the males of some species, such as human males, do invest in long-term mating and paternal care) (Trivers 1972). This is why men are generally more interested in prospective mates' physical attractiveness than are women (Buss 1989), whether in short-term or long-term relationships. Men's mate preferences focus on women's physical features such as youth, breast size, lumbar curvature, a 0.7 waist-to-hip ratio (i.e., an "hourglass" shape), and facial femininity (Burriss et al. 2011; Buss 1989; Karremans et al. 2010; Lewis et al. 2015; Zelazniewicz and Pawlowski 2011). Whereas women are generally more interested in long-term relationships and value characteristics such as maturity, ambition, industriousness, kindness, and commitment (Buss 1989; Buss and Schmitt 1993; Haselton et al. 2005; Lukaszewski and Roney 2010), they, too, engage in short-term mating and value men's characteristics such as height, masculinity, symmetry, and dominance (Gangestad et al. 2004; Pawlowski and Jasienska 2005; Penton-Voak et al. 2003; Quist et al. 2012). In general, women seek short-term mates either prior to finding committed partners or in order to procure good genes while deceiving existing committed partners (Pillsworth and Haselton 2006). In other words, sometimes a prospective mother's strategy may be to make sure that her offspring thrive in the genetic lottery regardless of who, if anyone, is providing paternal care.

When it comes to sexual conflict, men and women deceive each other about different things. This is suggested by Haselton et al.'s (2005) investigation into which types of deception men and women are differentially upset about. In general, men are more upset about women's false promises of sex (i.e., being "led on"), whereas women are more upset about men's exaggeration of their social status, resources, and willingness to commit. Although both short-term- and long-term-oriented men are upset about being led on,

short-term-oriented men experience greater discomfort over this type of deception, which is likely a reflection of their greater interest in casual sexual opportunities with multiple women. Women's greater distress over men's exaggeration of commitment and – especially for women seeking long-term mates – inflation of status and resources suggests that women are primarily interested in finding long-term mates who are able and willing to provide paternal care. In short, what Haselton et al.'s study suggests is that deception is an integral aspect of human precopulatory sexual conflict and that men and women deceive each other by pretending to cooperate with each other's reproductive strategies.

Intrasexual competition and sexual conflict.

When adaptations to sexual conflict are directed at other individuals whose behavior is likely to augment the reproductive success of an individual's would-be partner, it is helpful to consider this a form of *indirect* sexual conflict (see Thompson and Alvarado 2012, for a similar distinction between direct and indirect sexual coercion and the evolution of different adaptations in relation to each). All of the aforementioned examples constitute direct sexual conflict wherein males and females target their offensive and defensive adaptations at one another. Indirect sexual conflict entails that men and women target their attacks at their reproductive rivals. So, for example, when a male or female derogates or drives off an intended mate's other, otherwise valued, mating prospect, it can be said that the male or female is engaging in indirect sexual conflict. Although successfully driving off a competitor may indicate something about the successor's reproductive value, derogating rivals (which depends on cognitive and verbal abilities possessed by most humans) and seizing an opportunity to sabotage them (which depends highly on chance) are strategies that can be pursued by individuals of high and low reproductive value alike. Individuals of low reproductive value may even depend on these strategies to a greater extent than they do on strategies such as intrasexual physical combat and direct partner seduction – strategies that are more reflective of high reproductive value (see Miner et al. 2009b, for evidence that men of low

mate value may rely on cost-inflicting, as opposed to benefit-provisioning, mate retention tactics).

Direct and indirect sexual conflict are often indistinguishable, as driving away reproductive rivals of high mate value inflicts a direct cost on one's intended future mate. Sometimes, the cost is also felt by the individual engaging in such aggressive tactics, in which case it is a non-adaptive byproduct of sexual conflict or intrasexual competition. For example, the mere act of battling or driving off a reproductive rival may be fatal to a potential mate, as instanced by the occasional killing of a female red-sided garter snake, recently arisen from hibernation, by a pack of male garters that coil up into a swarm of aggressive reptiles wrestling one another in a destructive melee that crushes the fought-over female in its depths (Arnqvist and Rowe 2013, pp. 49–50). The distinction between direct and indirect sexual conflict is valuable, however, because anticipating the two types of conflict allows scientists to formulate testable hypotheses about specific adaptations that may have been differentially selected for either type.

One tactic that humans use to drive away reproductive rivals is competitor derogation (Buss and Dedden 1990). In general, men are more prone to disparaging a male rival's income and willingness to commit, whereas women are more prone to disparaging a female rival's looks and sexual behavior (Buss and Dedden 1990; Fisher 2004; Schmitt and Buss 1996). The reason for this is that women prefer mates who have – or have the potential to acquire – resources and who are willing to enter into a committed relationship, whereas men prefer mates who are attractive and, in the context of a long-term relationship, are sexually faithful (an important factor for men given the evolutionarily recurrent threat of investing in genetically unrelated offspring). By derogating competitors, men and women are essentially engaging in competition with their reproductive rivals by disparaging them to their prospective mates. This competition is not as extreme as a barroom brawl, but it is competition nonetheless, and may engage multiple cognitive adaptations.

On the one hand, if a derogator is correct about her rival's deficiencies (e.g., her rival is not as young as she claims to be), then this may be valuable information for her prospective mate, who may take appropriate steps to avoid mating with her rival. If the derogator is higher in mate value than her rival, then her derogation of her rival's age was an instance of cooperation between her and her prospective mate. On the other hand, if her rival is in fact as young as she claims to be, then the derogator is inflicting a cost on her prospective mate by denying him a reproductively valuable mating opportunity. Such instances of competitor derogation can therefore be considered as specialized weapons employed by men and women in the context of sexual conflict.

Various emotional adaptations are likewise aimed at deterring one's future or current mate from mating with, or investing in, one's reproductive rivals. One such set of adaptations is associated with the experience of romantic jealousy. In general, men are much more likely to experience sexual jealousy, whereas women are much more likely to experience emotional jealousy (Buss et al. 1992). Sexual jealousy is felt as discomfort at the prospect that an intended or current romantic partner has had sex with someone else. Men's greater susceptibility to this form of jealousy arises from their vulnerability to cuckoldry (i.e., an instance of a female having sex with a male who is not her long-term partner). Humans, along with only a few other species, are marked by both maternal and paternal care. In most cultures, paternal care is an essential component of the total care received by a child (though it still does not measure up to the level of care provided by mothers). As a result of the high cost of paternal care, natural selection designed various psychological adaptations to ensure that a man does not waste resources on genetically unrelated children. One such adaptation is sensitivity to any prospect of sexual infidelity, i.e., sexual jealousy. Due to the recurrent evolutionary costs of relationship abandonment and a redirection of resources to other women and their children, however, women are more prone to emotional jealousy, which is felt as discomfort at the prospect that

one's intended or current romantic partner has formed an emotional attachment (i.e., has fallen in love) with a reproductive rival. Both forms of jealousy may inflict costs on current or future romantic partners and can therefore be thought of as evolved, specialized emotions evoked in the context of sexual conflict.

As with many other sexually reproducing species, humans seek to neutralize their reproductive rivals by, among other methods, simply restricting their proximity to an intended mate, a technique known as "mate guarding." This can be done either by fighting off approaching rivals or by monitoring the movements of, or secluding, a prospective or current mate in order to make sure that he or she has no opportunity for a dalliance with a reproductive rival. Because males are typically stronger than females, they are more successful at mate guarding their prospective or current mate with threats and actual uses of force. Humans, for example, exhibit a continuum of mate-guarding behaviors, from benefit-provisioning, whereby individuals bestow gifts, care, and affection on partners in order to keep them happy, to cost-inflicting, whereby individuals inflict verbal and physical abuse on partners to deter them from ending the relationship or to punish them for actual or perceived infidelity (Holden et al. 2014; Miner et al. 2009a, b). Note that, although research on mate guarding mostly examines interactions within existing sexually active relationships (hence the term *mate guarding*), similar tactics can be employed by individuals prior to copulation.

Even though men and women engage in both benefit-provisioning and cost-inflicting mate-guarding behaviors, the costs of violent mate-guarding are mostly felt by women (Whitaker et al. 2007). Notwithstanding that men and women engage in similar levels of domestic violence (and, in some studies, women are actually shown to be the primary culprits; Whitaker et al. 2007), it is women who bear the most serious injuries, including death, as a result of a partner's abuse (Daly and Wilson 1998). This is unsurprising given men's greater physical strength, on average, compared to women's. Of course, some men are more reproductively successful than others,

and so they are expected to exhibit less jealousy and mate-guarding behaviors overall because they have no need of them. In partial support of this, tall men (who are high in mate value) exhibit less jealousy and engage in fewer benefit-provisioning mate-guarding behaviors (e.g., "love and care") than short men (Brewer and Riley 2009). Unlike short men, however, tall men engage in more cost-inflicting behaviors (e.g., monopolization of a partner's time). The authors hypothesize that this is because men of high mate value can more easily get away with guarding mates by engaging in costly mate-guarding behaviors, whereas men of low mate value might risk being abandoned by their partners if they were to engage in such behaviors. Other studies, however, suggest that men of low mate value are *more* likely to engage in cost-inflicting mate-guarding behaviors (such as verbal insults) than men of high mate value (Miner et al. 2009a, b).

Sexual harassment. Due to both methodological and political roadblocks, the evolutionary study of harmful sexual practices such as sexual harassment and sexual coercion continues to garner much controversy and debate. Nevertheless, notwithstanding the gap in our theoretical and empirical understanding of these phenomena, the evolutionary biological framework provides an important starting point for their scientific examination. However flawed the attempts at tracking harmful sexual behaviors through the lens of evolution by natural selection – and, in particular, the framework of sexual conflict – might be, such attempts are necessary if these behaviors are to be understood and remedied. As with any discussion of controversial topics with far-reaching social and political implications, it is important to keep in mind that any attempt at explaining such phenomena from a scientific perspective should not be conflated with an endorsement of them.

The definition of sexual harassment varies across time, region, and even across individuals. Nevertheless, its legal parameters within the United States often confine it to two more-or-less independent categories: (1) *quid pro quo* sexual harassment, which involves pressuring someone into sexual activity with either threats (e.g.,

the loss of employment) or inducements (e.g., job promotion), and (2) the creation of a hostile environment via the persistent expression of unwelcome explicit or implicit sexual content (e.g., sexual jokes, suggestive comments about someone's clothing, etc.). Note that, although these categories are not the final word on what constitutes sexual harassment (as both the legal and lay understanding of sexual harassment continue to change), they are sufficient starting points for a discussion of how sexual conflict can illuminate instances of coercive sexual behavior.

Because men are generally more prone to favor casual sexual encounters and to pursue promiscuous sexual strategies to a greater extent than women, it is predicted that they would be the primary sexual harassment offenders. And, indeed, they are. As cited by Studd and Gattiker (1991), women – especially women who are young and single – are overwhelmingly more likely to report being victimized by workplace sexual harassment than men, and men are almost always the perpetrators. From an evolutionary perspective, be it quid pro quo or hostile environment sexual harassment, the fact that men are the primary culprits suggests that sexual harassment is a manifestation of men's evolved propensity to maximize sexual access to as many women as they can. As such, sexual harassment is an example of sexual conflict because it often exacts costs on its recipients.

In cases of quid pro quo sexual harassment, women who do not acquiesce to sexual advances may risk the loss of resources if their job security or career prospects are threatened. Women who do acquiesce to such advances, however, may risk unwanted pregnancy or the possibility of exposure to sexually and nonsexually transmitted diseases as the costs of maintaining their employment or furthering their career. Similarly, women who encounter a hostile work environment may suffer both financial and psychological costs due to the loss of productivity and emotional security. It is also possible that women may suffer reputational damage if they are perceived to not be “team players” due to their not taking part in crude office banter or sex talk – damage that could threaten both their career and mating prospects.

That sexual harassment may be a manifestation of sexual conflict is evidenced by instances of similar conduct that is less likely to be perceived as harassment when exhibited by attractive or high-status individuals. In examining sexual harassment vignette ratings, for example, LaRocca and Kromrey (1999) found that college students rated sexual advances as being less harassing when coming from attractive opposite-sex individuals (e.g., female students rated attractive male professors as being less harassing than unattractive male professors). Similarly, female flight attendants reported less negative affective responses to verbal and physical sexual harassment exhibited by high-status pilots than by low-status airline workers such as cleaners and ticket agents (Littler-Bishop et al. 1982). These findings indicate that sexualized behaviors are only perceived as harassment when they are suggestive of sexual conflict – i.e., conflict between incompatible mating strategies. When there is no conflict, as when sexual overtures come from opposite-sex individuals who are of a high mate value, recipients are less likely to interpret such overtures as harassment.

Rape and sexual assault. The most extreme forms of sexual conflict are sexual assault and rape. Although women's sexual assault of men does occur, men's greater sex drive and women's decreased physical strength collude to make women's vulnerability to sexual assault and rape by men a more prevalent phenomenon. (Men's sexual assault and rape of other men are not presently discussed.) Furthermore, rape and sexual assault can be studied in the context of precopulatory sexual conflict because forced copulation need not occur for individuals' physiological and psychological adaptations associated with it, and in response to it, to be activated. For example, a man planning on committing a sexual assault in the future may very well be acting out a behavioral pattern that is a product of innumerable generations of sexual conflict between the sexes, even if the man happens to be arrested prior to committing the assault. Similarly, even if she is never attacked herself, a woman who is wary of strange men may be exhibiting a behavior pattern that was selected because it helped ancestral women to

avoid unwanted sexual attacks. Despite the lack of an actual rape, each scenario highlights the possibility that specific precopulatory mechanisms (i.e., the planning of a sexual assault in the former scenario and its avoidance in the latter) selected in ancestral contexts of sexual conflict may be at play.

Whether rape is an adaptation whose selected function is to allow men to maximize their reproductive opportunities is still a topic of contention for both scientific and political reasons. Nevertheless, the prevalence of forced copulations among nonhuman animals attests to its occasional evolutionary advantages (Palmer 1989), which necessitates its inclusion in discussions of human sexual conflict. According to McKibbin et al. (2008), human rapists can be sorted into at least five categories: disadvantaged men (i.e., men who rape because they have no other avenue for consensual reproduction), specialized rapists (i.e., men who exhibit specific physiological and psychological adaptations for rape, such as greater arousal to sexually violent stimuli and discriminatory targeting of rape victims), opportunistic rapists (i.e., men who only exhibit sexually coercive behaviors in contexts where doing so poses fewer punitive risks, as in warfare – see Chang 1997, and Morris 1996), high-mating-effort rapists (i.e., men who are otherwise sexually successful, but who rely on sexual assault to obtain reproductive access to unwilling partners – see Lalumière et al. 1996), and partner rapists (i.e., men who rape their romantic partner when under threat of sperm competition following a partner's actual or perceived infidelity).

If rape and sexual assault were a regular part of life for ancestral women, it is likely that women evolved counter-adaptations aimed at preventing and countering such attacks. Hypothesizing this, McKibbin et al. (2009) developed a “rape avoidance inventory” by extracting four principle components from women's ratings of various rape avoidance behaviors. Each of these components may reflect a suite of specific defensive adaptations, and the components are as follows: “avoid strange men,” which includes behaviors such as avoiding men with a reputation for sexual assault and not letting strange men into one's home;

“avoid appearing sexually receptive,” which includes behaviors such as avoiding wearing revealing clothes or drinking alcohol in unfamiliar places; “avoid being alone,” which includes behaviors such as turning on the television or music when alone and not going out alone; and “awareness of surroundings/defensive preparedness,” which includes behaviors such as looking around before getting out of the car and carrying a defensive weapon.

If the sexually coercive strategies on the part of men and the defensive strategies on the part of women constitute adaptive solutions to recurrent reproductive problems that members of each sex posed to members of the other sex over evolutionary time, then such solutions are examples of adaptations wrought by generations of sexual conflict. These strategies may even exhibit elements that are specifically tuned to the precopulatory period. For example, disadvantaged rapists and high-mating-effort rapists may exhibit adaptations specifically suited to assessing their own mate value and to responding to such an assessment by developing a sexually coercive mating strategy. Similarly, the development of specialized rape adaptations may depend on critical periods during which adolescent boys and young men are drawn toward, and positively rewarded by, violent sexual cues. In response, women may have evolved the ability to pick up on some of the specific cues given off by these men as a subcomponent of an avoidance-of-strange-men adaptation and may consequently avoid being alone or appearing sexually receptive when in the vicinity of these men. Opportunistic rapists may exhibit selective attunement to contexts wherein they could sexually coerce unconsenting women with impunity, and partner rapists may exhibit adaptive psychological and physiological precopulatory adaptations that are sensitive to contexts of partner infidelity and that bring about a more rapid sexual response as a result. In turn, women may discriminate between environments and contexts wherein they would be more or less vulnerable to rape and sexual assault and may modify their behavior accordingly. For example, women's awareness of their surroundings and attendant defensiveness may be activated in contexts wherein the costs of

men's sexual violence are low or when their partners suspect them of infidelity.

Women's antirape adaptations, such as avoiding strange men, avoiding appearing sexually receptive, avoiding being alone, being aware of one's surroundings, and being prepared to defend oneself, all occur prior to the onset of forced copulation. In addition to McKibbin et al.'s (2008) proposed suite of women's antirape defenses, Thornhill and Thornhill (1990) advanced evidence for the adaptive function of psychological pain such as fear and social disturbance following sexual victimization. Specifically, Thornhill and Thornhill report that women of reproductive age (as opposed to prepubescent and postmenopausal women) and married women experienced more psychological pain after being raped than women who were neither of reproductive age nor married. The authors suggest that this is because psychological pain following a reproductively costly event functions to redirect one's efforts toward preventing such events in the future and that the evolutionary costs of rape are greatest for women of reproductive age (who suffer from the circumvention of mate choice) and married women (who may suffer an increased risk of partner abandonment). As such, psychological pain following rape or sexual assault should likewise be counted as an adaptation for precopulatory sexual conflict, being as how it is aimed at preventing future instances of forced copulation.

Conclusion

The previous discussion suggests that much of human mating may be imbued with adaptations and counter-adaptations whose features were shaped by ancestral arms races between men's and women's competing reproductive strategies. Much is still unknown, however, about whether some of the previously mentioned examples – particularly with respect to instances of rape and sexual assault – indicate the presence of specialized adaptations on the part of men and women. It may be that, for example, men's proclivity for sexual violence is not adaptive in itself but is rather a byproduct of a more general male

proclivity for sexual variety. Likewise, women's antirape defenses may not be adaptive in and of themselves but may be extensions of more general defensive behaviors whose function is to ward off both human and nonhuman predators – behaviors that may be shared by both sexes. More research is needed in tracking both the evolutionary history of human sexual conflict and its physiological and psychological manifestations in modern humans.

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Human Products

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Synonyms

[Human artifacts](#); [Human constructed elements](#);
[Man-made items](#)

Definitions

Human products represent goods (articles, items), ideas, methods, information, and services produced by humans.

Introduction

As sources of data, human products can be analyzed from the perspective of several inclusive fitness-related functions (inclusive fitness is referred here as the abilities of an individual to further pass its genes on to the next generations; Hamilton 1964). These functions can be centered on the individual physiological needs in the physical environment (e.g., clothing for the regulation of body temperature, food preparation, access to

water) on intraspecific interactions (couple, family, cultural groups and other types of institutions) or on interspecific interactions (e.g., human-animal interactions). Having in mind these multiple levels of functional analysis of human products as data sources and being aware that these levels are generally overlapping, a synergic frame of analysis of human products as data sources is proposed here in terms of identifying the connections of human products with individual, developmental, and evolutionary human motives. This synergic analytical frame integrates the model of the renovated Pyramid of Human Needs (Kenrick et al. 2010), the niche construction theory (Laland and Brown 2006, with references to the extended phenotype, Dawkins 1982), the idea of evolved aesthetic preferences (Miller 2001; Tooby and Cosmides 1990), and the principles of Positive Design applied to human products (symbolic meaning connected to subjective happiness and quality of life; Cassais et al. 2016).

Human Products as Indicators of a Pyramid of Human Needs

Maslow's Pyramid of independent sets of human needs (Maslow 1943; immediate physiological needs, safety, affection, esteem, and self-actualization) offers generous possibilities of interpretations of several aspects of human developmental and social functioning, including the human motivation to produce items, methods, and information (i.e., human products) corresponding to their needs.

A revised version of Maslow's Pyramid of needs is offered by Kenrick et al. (2010) in the light of theoretical development at the interface of evolutionary biology, psychology, and anthropology. The renovated Pyramid of Needs highlights the connections between fundamental motives and immediate situational threats and opportunities in human existence, hence anchoring the hierarchy of human motives in the field of modern evolutionary theory (Kenrick et al. 2010). The updated Pyramid examines human motives at three levels of analysis: (a) their ultimate evolutionary function; (b) their developmental

sequencing, and (c) their cognitive priority as triggered by proximate inputs.

The most important updated aspect of the Pyramid of Needs is the functional reconsideration of the self-actualization, which is not regarded anymore as a functionally distinct human need. Based on their new interdisciplinary framework of analysis, Kenrick et al. (2010) removed self-actualization from the top of the pyramid and subsumed it within status (esteem) and mating-related motives. In the process of the Pyramid's updating, the authors combined the development level of analysis with the biological framework of *life history theory*, which addresses the trade-offs between the organisms and their environment, in terms of how the time and energy should be allocated in activities and traits that have the potential to maximize their fitness (e.g., Kaplan and Gangestad 2004). Hence, the updated Pyramid includes the following fundamental human motives, starting from the base: (1) Immediate Physiological Needs, (2) Self-Protection, (3) Affiliation, (4) Status/Esteem, (5) Mate Acquisition, (6) Mate Retention, and (7) Parenting. One can notice that the top of the Pyramid contains three reproductive goals, appearing in their developmental order. The authors stress that the later developing goal systems are overlapping, rather than replacing earlier developing systems; once a goal system has developed, its activation can be triggered by salient relevant cues (Kenrick et al. 2010).

The updated version of the Pyramid of Human Needs and the three levels of analysis proposed by Kenrick et al. (2010) provide a frame for the identification of developmental, individual, and evolutionary data provided by human products.

Several human products are parts of tactics of benefit-provisioning behaviors, which "...are *mate retention behaviors that are intended to increase the incentives of staying mated to the current partner and, in turn, deter defection from the relationship. These behaviors can include things such as buying gifts for the partner, altering one's appearance, and different sexual behaviors*" (► [Benefit Provisioning](#)). From an evolutionary perspective, a wedding ring, for example, might indicate a resource display within

the positive inducement tactic, such as the ability of a partner to provide resources to the female and her offspring and/or intentions of emotional investment – love and affection – in the relation. Also, wedding rings may offer indications about another tactic within the benefit provisioning process, which is the possessive ornamentation, meaning that a male might offer a wedding ring (or another symbolic product) to his female partner to convey to same-sex individuals the status of the relationship (Holden et al. 2014). While a wedding ring can generally be associated with relationship status in nearly any type of human cultures, other forms of human products might be either more ambiguous regarding the information they convey or be presented with specific explanations to the persons expressing interest in the history of the product (e.g., the story of a scarf received as a gift from a former romantic partner in a specific moment of life).

If the example of the wedding ring is taken through the multilevel analysis framework provided by the updated Pyramid of Human Needs model (Kenrick et al. 2010), such an item may offer data on two reproductive human motives (mate acquisition and mate retention), but also on the status/esteem motive. Moreover, the acquisition of reproductive-related human products, such as wedding rings, for example, may offer data on the developmental stage of an individual. Hence, a man who purchases a wedding ring is at a sexual maturity stage rather than at an earlier stage of his ontogenetic development. The value of the wedding ring might offer data not only on the status/esteem of the person, but it may also indicate that a person who can afford to offer an expensive ring to a potential partner probably has no difficulties in terms of the fulfillment of the individual needs situated at the base of the Pyramid (i.e., immediate physiological needs: access to food, water, and shelter).

Human Products as Indicators of Niche-Construction Process

The idea of individuals changing the environment according to their contextual, developmental, and

evolutionary needs is a focus of the *niche-construction perspective* (Laland and Brown 2006). The interaction with the environment is considered bidirectional, in that organisms adapt to their environment and they also adapt the environment to their needs. Like other animal species that manufacture nests, holes, webs, burrows, etc., humans can change, adjust, and construct their physical and social environment. Laland and Brown (2006) point out that niche construction implies not only building environmental components, but regulating the environment “*to damp out variability in environmental conditions.*” Hence, human products may convey data on the environmental variability the humans are faced to and the solutions they came up to minimize this variability. The authors argue that niche construction is not an end product of evolution but a continuous cause of evolutionary change (Laland and Brown 2006).

The large variety and intensive dynamic of human products (including digital information) indicates that, compared to other animal species, humans appear to be effective niche constructors that are continuously challenged by the interaction between their cumulative culture and their evolutionary and developmental needs, as well by contextual threats and opportunities (see Laland and Brown 2006). Culture is seen here as “*the ability to acquire and transmit learned knowledge, beliefs and skills and to devise ever more efficient solutions to problems that build on this reservoir of shared knowledge*” (Laland and Brown 2006). While some human products can be interpreted as parts of the extended phenotype of individuals, based on the effects that the candidate genes for that type of product has on the environment (Dawkins 1982), there are theoretical studies (mathematical population genetics) indicating that niche construction does not have to be based on genes in order to impact the evolutionary process (Laland and Brown 2006). Hence, it is believed that human culture and the process of niche construction have become self-reinforcing and that the transgenerational culture changes the environment in a manner that favors more culture in order for the human beings to fulfill their needs.

Many human products (elements of the constructed environment), specifically ones that are related to the human motives situated at the base of the updated Pyramid of Human Needs (Kenrick et al. 2010), appear to be resistant to transgenerational culture, in that their basic characteristics indicate their original utilitarian function and that they are generally shaped to suit the human bodies (e.g., cups, forks, knives, clothing, socks, beds, chairs, doors). Typically, niche construction in humans can have immediate fitness benefits to the constructor or to those who acquire the products (Laland and Brown 2006). However, some human products (e.g., medical products, nuclear power plants) may have critical consequences for the environment, which can be translated into negative effects on human fitness. Hence, the presence of these types of products in a specific environment may offer data on the negative effects the products can bring to human individuals and other living species, but also on their potential as selective pressures.

Some human products can be transformed by the users according to their specific needs or body characteristics, e.g., a wheel chair can be adapted to the human body shape and posture and clothing can be adjusted to the length of the legs. Other products, even though they do not fit the personal preferences of the users in terms of aesthetic appearance and proximate needs, cannot be reshaped/adapted due to their built-in characteristics or because they represent unique art-work pieces.

The diversity of traits within the same utilitarian category of human products (variations in shape, color, size, etc.) has attracted a lot of interest toward the analysis of the *aesthetic qualities* of human products in relation to the evolved aesthetic preferences of humans. Such preferences are thought to be based on the aesthetic experiences of individuals while interacting with their environment (in a direction of favoring the inclusive fitness of individuals) and are supposed to be molded by natural selection through the adaptive advantages conferred by emotional responses during the process of problem solving and decision making in relation to elements of habitat (Orians 2001, in Hogh-Olesen et al. 2009). Besides the habitat selection-based explanation of human aesthetic preferences, Miller (2001) has introduced

an updated idea of the connection between human appreciation of beauty and mate-choice (Darwin 1874), arguing that many design features of art products may function as indicators of “*artist’s virtuosity, creativity, intelligence, conscientiousness and other important heritable mental and physical traits*” (Miller 2001 in Hogh-Olesen et al. 2009). In other words, Miller (2001) suggests that the aesthetic judgment can be part of the mate-choice process and social cognition, in that art-work can be seen as an extended phenotype of the artist (Hogh-Olesen et al. 2009). Also, the large variation within the same category of products allows individual aesthetic preferences to manifest at the level of decisions about purchasing one variation over others.

Many human products are nowadays a result of mass production (e.g., cups, glasses, makeup, clothing products, etc.) and their authors are individually unknown to the persons that are purchasing them. Hence, the decision to purchase a product may offer data on the needs of the user, his/her aesthetic preferences, and on the qualities of the product that match the search image of the user. However, in some cases, such as art exhibitions and fashion shows, the authors of the products reveal themselves to the potential buyers. In these cases, i.e., having some information about the persons behind the products, the users/buyers tend to pay more attention to the association between the psychosocial characteristics of the producers and the products, and the decision to purchase the product may be based on this association. Therefore, the labels of several successful human products (in terms of high demand on the market) may offer data not only on the quality of the product itself but also on the socially and economically perceived image of the producer. A highly expensive and rare brand can offer data on the socioeconomic status of the purchaser, thus functioning as a badge of status for the owner of the product.

Human Products as Indicators of an Evolved Aesthetic Preferences

From the perspective of “narrow” evolutionary psychology (e.g., Tooby and Cosmides 1990),

human aesthetic preference is considered a *single integral capacity* (or a genetically based set of beauty detectors, Kogan 1994), regardless of the mate-choice and/or habitat selection advantages it might have provided to our ancestors. Hence, one can infer that, besides their primary utility, human products may offer data on the personality-based and culturally-shaped aesthetic preferences of their users/owners and that the products a person is acquiring during specific moments of lifetime may be considered as elements of that person's extended phenotype. Besides the data on the aesthetic preferences of the user and on the human motives illustrated by the updated Pyramid of Human Needs (Kenrick et al. 2010), human products may also provide data on the personal significance of a product. The personal significance may or may not be related to the aesthetic preferences of the owner of the product.

Human Products as Indicators of Positive Design

Positive Design is possibility-driven design that enables positive experiences in the direction of improving human well-being (Desmet and Pohlmeier 2013). Several studies on symbolic meaning of human products in relation to Positive Design indicate that people from different cultures tend to attribute symbolic meanings to a large variety of products in association with their need for subjective happiness and personal comfort (e.g., Cassais et al. 2016). Human products with symbolic meaning can provide the users with the following additional functions (besides the primarily utilitarian function), most of them indicating individual context sensitivity (see Cassais et al. 2016): preserve memories, remind of goals of aspirations, and help build and signal identity (e.g., Csikszentmihalyi and Rochberg-Halton 1981). The products that are mostly accessible through specific stages of development (e.g., favorite toys during childhood) can be offered symbolic meaning in associations to those stages. These associations between products and specific stages of development may be recalled later in life.

While the process of decoding the personal symbolic meaning of a human product requires access to data based on self-reports (interview, content analysis of a diary, etc.), some products can offer direct cultural specific information (e.g., flags, badges, etc.). Physical characteristics of human products, such as their solid structure, for example, facilitate their preservation through long periods of time (e.g., cups, printed pictures, miniatures, carpets), which favors the construction of symbolic meaning. The symbolic meaning of a product is constructed by the owner of that specific product (in the direction pointed by the extended phenotype theory), meaning that without the communication of the meaning by the owner, the symbolic meaning may never be revealed to other persons. Some products, such as the personal advertisements, are produced and used for specific periods of time and their content offers clear indications on what individual need from a potential partner.

Personal Advertisements: Sources of Data about Mate-Choice Process

Overall, evolutionary psychologists consider mate-choice a negotiation process between two partners, and the way each sex expresses choosiness in the process of mating may vary across human cultures (e.g., Schmitt 2005; Rusu and Maxim 2009). Compared to other animal species, humans sometimes engage in forms of mate search in which they explicitly state what they have to offer to their potential partners and what they expect from them (e.g., Pawlowski and Dunbar 1999). One of the most common forms in which an explicit communication in this respect occurs is the market of personal advertisements, either online or via newspapers (Pawlowski and Dunbar 2001). A personal advertisement typically consists of a list of self-descriptive attributes (i.e., words describing the traits of the advertiser) and a list of attributes the advertisers seek in a prospective partner (Pawlowski and Dunbar 1999). Studies of the matrimonial market in different cultures indicate that the descriptive attributes contained in the personal advertisements reflect the gender-biased mate-choice strategies as predicted by

Triver's theory of parental investment (Trivers 1972), which states that the relative proportion of investment in rearing the offspring varies across males and females. This asymmetry regarding the parental investment of each sex is supported by the facts that a female needs fewer mating episodes to fertilize the eggs she can produce during the entire life, whereas a male has the potential to fertilize a much higher number of eggs than one female can produce. Trivers (1972) has argued that, because of this difference, the reproductive success of females tends to be limited by their access to resources needed for the nourishment of each of their eggs, while the reproductive success of males tends to be limited by their access to females. Given these conflicts of interests between the two sexes, it is expected that the mate-search strategies differ between males and females accordingly. There are numerous studies showing that women, as opposed to men, express a stronger preference for attributes referring to resources necessary for the survival and success of offspring developing from their fertilized eggs. Previous investigations indicate that some of the resource-related attributes that women generally seek are: financial wealth, social status, desire for children, and desire for commitment (e.g., Bereczkei et al. 1997; Buss and Schmitt 1993). Since all these attributes are age-dependent traits in men (i.e., older men in average have greater access to resources critical to female reproduction; Buss 1989), women usually seek older partners. Like the males of other sexually reproducing species, men commonly select their mating partners on the basis of cues that correlate with female fecundity, such as youthfulness, health, and physical attractiveness (Buss 1989; Pawlowski and Dunbar 1999).

Several investigations of personal advertisement markets indicate that these type of human products reflects the evolutionary principles of the theory of parental investment, i.e., male advertisers are more concerned than females about attributes that refer to their partner's fecundity, while female advertisers tend to focus on their future mates' wealth and commitment (Bereczkei et al. 1997; Pawlowski and Dunbar 1999; Rusu and Bencic 2007).

While personal advertisements indicate the proclivity of human individuals to form couples and reproduce, a specific category of human products (e.g., weapons), besides the utilitarian function of hunting animals for survival (food, clothing), indicates the potential of human beings to harm and kill other individuals with the help of weapons.

Human Products (Weapons) as Indicators of Intraspecific Aggression

Buss and Shackelford (1997) start their paper on the evolutionary perspective of human aggression with a reference on the usage of weapons by our ancestors, as indicated by ancient hominid skeletal remains (Trinkaus and Zimmerman 1982). From an evolutionary psychological perspective of human aggression, weapons, as human products and besides their hunting utility, can functionally fit within all the seven intraspecific adaptive problems proposed by Buss and Shackelford (1997) for which aggression might have evolved as a solution: (1) co-opting the resources of others, (2) defending against attack, (3) inflicting costs on same-sex rivals, (4) negotiating status and power hierarchies, (5) deterring rivals from future aggression, (6) deterring mates from sexual infidelity, and (7) reducing resources expended on genetically unrelated children. Within these aggression-related strategies, the individual decision to use a weapon and the need to purchase such a human product is context-sensitive. Besides the evolutionary psychological explanations listed above (which can be associated with the presence of weapons in human existence), and like other types of human products, weapons may offer data on several other dimensions. These include the degree of mastery a person needs to acquire in order to properly use the product, the aesthetic preference of the user, the possibility to be used by a sole person or if it requires cooperative work, and the degree of innovation of the producer.

Conclusions

Many human products appear to be shaped to suit human bodies and to serve human basic needs (immediate physiological needs), while others seem to be associated with individual, intraspecific, and interspecific needs (with all their proximate, developmental, and adaptive aspects and inferences), such as self-protection, affiliation, status/esteem, mate acquisition, mate retention, and parenting. From the perspective of niche construction theory (see Laland and Brown 2006), human products may offer evolutionary relevant data on the potential of human individuals to control the variability in environmental conditions, in the direction of maintaining specific conditions within tolerable limits for their survival and reproduction, which are the two dimensions defining the evolutionary inclusive fitness. Additionally, the decision to purchase a product may offer data on the needs of the user, his/her aesthetic preferences, and on the qualities of the product that match the search image of the user. A synergic framework for the analysis of human products as sources of data is proposed here, by integrating the model of the renovated Pyramid of Human Needs (Kenrick et al. 2010), the niche construction theory (Laland and Brown 2006, with references to the extended phenotype, Dawkins 1982), the idea of evolved aesthetic preferences (Miller 2001; Tooby and Cosmides 1990; Kogan 1994), and the principles of Positive Design and symbolic meaning (Cassais et al. 2016). Also, the behavioral flexibility and context-sensitivity showed by human individuals (Buss and Shackelford 1997) should be always taken into account in the process of identifying the potential functions and significance of human products.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Benefit Provisioning](#)
- ▶ [Clothing](#)
- ▶ [Engagement Rings](#)
- ▶ [Environmental Unpredictability](#)

- ▶ [Extended Phenotype, The](#)
- ▶ [Financial and Hierarchy Maintenance](#)
- ▶ [Human Tool Making](#)
- ▶ [Nuptial Gift](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Pornography as a Human Product and Source of Data](#)

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Human Reproduction

► Size Dimorphism and Locomotion

Human Self-Domestication

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Definition

A longstanding evolutionary process of human sociosexual selection for reduced reactive aggression, leading to correlated behavioral, physiological, and morphological trait changes consistent with “domestication syndrome” as seen in domesticated animal lineages.

Introduction

Domesticated animals are known to show a range of correlated trait changes in common when compared to their wild ancestors or relatives (Leach 2003; Wilkins et al. 2014; Zeder 2015). These traits have been experimentally demonstrated to emerge in response to sustained breeding selection for less reactive aggression (Trut et al. 2009). Modern humans show similar changes when compared to fossil remains of earlier *Homo sapiens* (Cieri et al. 2014). This evidence, coupled with high levels of cooperation and sociability, has led multiple authors to diagnose a process of “self-domestication” in human evolution (Cieri et al. 2014; Hare 2017; Leach 2003; Thomas and Kirby 2018). Human self-domestication is thought to have substantially enhanced our capacity for amicable social interaction, promoting language acquisition, shared culture, and technological capacity.

Domestication Syndrome

Domesticated lineages are known to show a syndrome of correlated traits in common when compared to their non-domesticated ancestors or relatives (Leach 2003; Wilkins et al. 2014).

These traits typically include behavioral docility (especially dampened reactive aggression); reduced sexual dimorphism; smaller brain sizes; lower skeletal robusticity; smaller teeth; floppy ears; pedomorphic morphology, physiology, and behavior; earlier sexual maturity; nonseasonal estrus; less prognathism; and altered pigmentation (Leach 2003; Trut et al. 2009; Wilkins et al. 2014).

Long-standing experimental breeding of farmed silver foxes has shown these traits will emerge in response to selection for lower aggressive reactivity suggesting the existence of underlying correlatory mechanisms (Trut et al. 2009). Similar behavior-based selection has been shown to have the same effect in other vertebrates, including rats, mink, and chickens. Given most traits of domestication syndrome can be associated, directly or indirectly, with various roles of embryonic neural crest cells, the most widely accepted proximate explanation for this collection of traits is mildly altered function in this cell lineage (Wilkins et al. 2014).

Neural crest cell contributions to the autonomic nervous system, especially the adrenal medulla, and the pituitary suggest an influence on bodily endocrine regulation, which could explain both moderated behavior and shifted developmental processes (Trut et al. 2009; Zeder 2015). As such, major heritable shifts could be accomplished via altered neural crest cell function with only minor genetic mutation. Secondary influence from endocrine change could compound any direct effect of altered neural crest cell behavior on specific tissues, organs, or structures. For example, dampened adrenal reactivity might directly moderate aggressive responses while an extended developmental period could maintain juvenile sociability and cognitive flexibility and both would promote enhanced sociability in adults (Wilkins et al. 2014).

Interestingly, a form of “self-domestication” has been described in wild bonobos (*Pan paniscus*) whose features, in comparison to their near relative, the chimpanzee (*P. troglodytes*), strongly resemble those attributed to domestication syndrome (Hare et al. 2012). In this case, aspects of the bonobo’s socioecology – especially

relatively elevated female social status – are thought to have supported sociosexual selection in favor of less reactively aggressive males.

Human Self-Domestication

Interestingly, multiple authors have suggested that modern humans show signs of domestication syndrome when compared to fossil remains of ancestral *Homo sapiens* (e.g. see: Hare 2017; Leach 2003; Thomas and Kirby 2018; Wrangham 2018). Stated evidence for human domestication includes reduced sexual dimorphism; reduced cranial capacity; smaller tooth sizes; lower skeletal robusticity; reduced craniofacial masculinity and prognathism; and enhanced sociability and social complexity (Cieri et al. 2014; Hare 2017; Leach 2003). Given that selection for lower aggressive reactivity has been experimentally demonstrated to cause domestication syndrome in other vertebrates, similar selection appears likely in human evolutionary history (Cieri et al. 2014; Hare 2017; Wrangham 2018).

Mechanisms explicitly proposed to drive human self-domestication via selection against aggressive reactivity include: (1) social benefits derived from dampened aggressive tendencies which may enhance the fitness of cooperative and sociable group members (Cieri et al. 2014); (2) ostracism or capital punishment of particularly aggressive individuals by cooperative coalitions, which would dampen the fitness of aggressive behavioral traits (Wrangham 2018); and (3) female mating preferences which might select against aggressive males in favor of more sociable individuals with elevated capacity for paternal investment (Cieri et al. 2014; Gleeson and Kushnick 2018). Other modes of selection against reactive aggression, though not previously associated with self-domestication, could include the reproductive benefits of increased alloparenting ability, and selection for enhanced group collaboration during intergroup conflict.

Human self-domestication holds substantial implications for the emergence of human sociability and the study of mechanisms which contributed to it, at individual and collective

levels (Cieri et al. 2014; Hare 2017; Thomas and Kirby 2018). If, as suggested by Cieri et al. (2014), self-domestication has operated by dampening expressions of physiological masculinity, the process would be highly relevant to expanded studies of human social evolution and factors affecting social interaction today. For example, self-domestication research might increase our understanding of sexually differentiated aggression and antisocial behavior witnessed cross-culturally across most human groups.

Conclusion

Domestication syndrome is a heritable physiological condition experimentally demonstrated to emerge in a range of vertebrates under breeding selection for diminished aggressive stress reactivity. Fossilized morphological evidence, along with noted capacities for cooperation and social complexity, points to an evolutionary process of human self-domestication occurring via sociosexual selection for reduced aggression. This phenomenon suggests a cumulative evolutionary influence of past social interaction and implies significant fitness benefits from enhanced social capacity in humans.

Broadly speaking, domestication-related research has a long pedigree of useful contributions to evolutionary knowledge. It has enhanced understanding of relevant selective mechanisms and the underlying physiology of inheritance. An expanding literature on this topic suggests ongoing research into the genetic, physiological, and selective factors associated with vertebrate domestication, and human self-domestication, will continue to provide useful insights for cultural and evolutionary anthropology in future.

Cross-References

► [Silver Fox Domestication Experiment](#)

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Human Sexual Activity

► [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)

Human Sexual Response

► [Four-Stage Model of the Sexual Response](#)

Human Sexuality

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Synonyms

[Primate Sexuality](#)

Definition

Human sexuality is most broadly defined as the totality of experiences, systems, attributes, and behavior that characterize the sexual sensation, reproduction, and intimacy of *Homo sapiens*.

Introduction

Human sexuality, a remarkably broad topic, is the purview of numerous academic fields and is a discipline unto itself. Scientific perspectives of human sexuality encompass, variously, its reproductive, social, cultural, emotional, and biological aspects. Evolutionary psychologists frame these facets by asking the following question: What is the design of the system – that is, what are the evolutionary forces that have likely shaped the constitution of human sexuality?

The present chapter is focused on human sexuality from the perspective of the evolved nature of mating systems. The main advantage of this focus is that it facilitates broad considerations about the evolutionary biology and psychology of human mating. By the same token, a mating systems approach leaves many aspects of human sexuality unaddressed, namely, those that have less clear implications for reproduction. Omission of a topic does not necessarily reflect a lack of relevant evolutionary research; on the contrary,

evolutionary psychologists engage deeply with all matters of human sexuality. For further reading on sexual diversity or nonreproductive sexuality, please see entries in this volume such as ► [“Evolution of Homosexuality,”](#) ► [“Same-Sex Sexual Behavior,”](#) ► [“Human Copulation,”](#) ► [“Sexual Identity,”](#) and ► [“Sexual Pathology.”](#)

Human Sexuality and the Comparative Approach

Many aspects of human sexuality are unique among species, but usually by a matter of degree than of kind. This general observation has two implications. First, by using phylogenetic comparative methods (for instance, comparing features of human mating to those of the other, extant great apes), one can attempt to draw general conclusions about the likely ancestral makeup of human sexuality. Second, a comparative approach can also reveal instances in which human sexuality meets or violates expectations (for instance, showing ways in which human sexual adaptations are compatible or incompatible with a given mating system). More generally, a comparative approach has value for informing an understanding of the forces that have led to the current state of human sexuality. A comparative perspective is emphasized in Tinbergen’s (1963) “four questions” (about mechanism, ontogeny, adaptive value, and phylogeny) for explaining behavior. Therefore, a recurring tool throughout this entry will be comparisons with sexuality studies in nonhumans.

A Note on Hormonal Mechanisms Underlying Human Sexuality

Endocrine systems constitute an important class of proximate biological mechanisms underlying human sexuality. Hormones are chemical “messengers” that allocate limited physiological and psychological resources throughout an organism. As detailed below, hormones provide some of the physiological background for many of the hallmarks of human mating systems, including pair-bonding, parental care, and mutual mate choice. At a theoretical level, hormones – both independently and in concert with one another – are mediators of an organism’s life history reproductive

strategy, linking physiology, and behavior in the partitioning of energy between mating, parenting, and nonreproductive activities (e.g., Del Giudice et al. 2015). For these reasons, hormonal systems are frequently discussed below within the context of human mating adaptations.

Defining Mating Systems

An understanding of mating systems is core to recreating how human sexuality might have evolved. In brief, mating systems dictate who mates with whom, when, and how often. Mating systems emerge from the cost and benefit male and female experience from mate choice and competition for mating opportunities, which in turn select for male and female adaptations. The details of a mating system can thus suggest selection pressures that forged reproductive behavior. But mating systems also *cause* adaptations, as they affect the reproductive strategies and tactics most beneficial to males and females. Conceptually, therefore, mating systems anchor the various facets of human sexuality discussed below (for an extended discussion of these issues, see Gangestad and Grebe 2015).

Traditional Mating Systems

Mating systems give rise to the nature and degree of reproductive skew, namely, the partitioning of reproduction among members of a society. The following categories of vertebrate mating systems are considered “traditional”:

Monogamy: Males and females have exclusive sexual access to one another.

Polygamy: Sexual exclusivity occurs, but is not monogamous. Three subtypes of polygamy can be discriminated: (a) *polygyny*, individual males have exclusive sexual access to two or more females; (b) *polyandry*, individual females have exclusive sexual access to two or more males; and (c) *polygynandry*, two or more males have exclusive sexual access to two or more females and vice versa.

Promiscuity: Males within a group mate with any and potentially multiple females and vice

versa. A subtype of promiscuity is *dispersed promiscuity*, in which largely asocial individuals with overlapping home ranges mate with multiple partners during brief periods of social grouping (typically, a female’s fertile period; see Dixon 2012).

Monogamy and polygamy assume forms of sexual exclusivity, whereas promiscuity does not. Whereas monogamous mating systems generate variation in reproductive success that is nearly equal across the sexes, polygynous mating systems generate greater male than female variation, and polyandrous mating systems generate greater female than male variation.

Mixed Mating Systems

The traditional categories of mating systems do not exhaustively cover all possibilities; instead, many animal populations exhibit mixed mating systems. In one case, different forms of sexual exclusivity may exist simultaneously. For instance, in avian species typically characterized as polygynous (such that some males mate with two females), monogamous mating arrangements can also occur in the same population. In other cases, different forms of exclusivity may exist temporally or spatially within the same population or species. For instance, individuals of some mockingbird species will mate both monogamously and polygamously depending on available opportunities. Indeed, across the vertebrate species examined, humans included, there is more fluidity in mating system structure than has been recognized historically: Human groups, large and small, have created and can create an array of mixed mating systems.

Selection Pressures Influencing Vertebrate Mating Systems

Traditionally, sexual selection theorists had widely assumed that natural selection would most likely give rise to mating systems characterized by some degree of polygyny. The rationale behind this assumption is known as the “Darwin-Bateman effect”: the increase in offspring number

as a function of the number of matings each male procures with different females, without a similar increase occurring as a function of the number of matings each female procures with different males (see Drea 2005; Parker and Birkhead 2013). Ultimately, the differential effect by sex of “multiply mating” was attributed to anisogamy – sexual reproduction involving the union of “expensive” eggs and “cheap sperm” – and to differences by sex in the initial investment in offspring. In placental mammals, internal fertilization and gestation delays the female’s production of new offspring until after birth, fetal or neonatal loss, and/or some period of lactation; males, however, do not experience these same delays. According to this paradigm, whereas males should benefit from seeking multiple mates, females should reap little, if any, benefit from mating multiply. Under many conditions, therefore, selection was expected to favor multiple mating by males, but only rarely by females, thereby driving an increase in polygynous mating systems.

Polygyny can take on different forms depending on male features that foster access to multiple females (e.g., Emlen and Oring 1977). In resource defense polygyny, males control the resources valued by females for fueling offspring production. In male dominance polygyny, which involves leks (small territories where males congregate to display and attract females), males are chosen by females for their ability to compete with other males, but offer no material resources to females to be directed toward investment in offspring.

In this “Darwin-Bateman” view, monogamy typically evolves when males cannot defend the resources that permit them to attract multiple mates. Ecological constraints explain why, for instance, most birds (over 90%) are socially monogamous: Resources are dispersed to a degree that males cannot typically secure enough for more than one female’s offspring (e.g., Emlen and Oring 1977). However, with the development of genetic tools in the late 1980s and early 1990s, researchers began testing some of the assumptions about traditional mating systems, and avian biologists discovered that many pair-bonding birds actually exhibited high rates of extra-pair

paternity – paternity by males other than the social partner. This finding, which has now been extended to primates also previously thought to be monogamous (e.g., in gibbons: Palombit 1994), prompted the recognition of an *extra-pair mating system*. Although most of the sexual activity occurs within structured units (e.g., individual male-individual female units, individual male-multi-female units, and so on), some mating – “extra-pair” mating – occurs outside of these units. In recognition of the social unit in which most mating occurs, systems with pair-bonding and cuckoldry are said to reflect *social monogamy with EPC* (extra-pair copulation). Some systems entail little EPC, whereas others may entail frequent EPC. Thus, social monogamy with EPC lies on a continuum of degree of sexual exclusivity.

The Polyandry “Revolution” Within Behavioral Biology

Over the past three decades, behavioral ecologists have increasingly recognized the benefits of female multiple mating, which includes EPC in addition to polyandrous mating more generally. Parker and Birkhead (2013) refer to the sea change as a “revolution.” By mating multiply, females could gain both direct benefits that increase reproductive success and indirect benefits that increase the genetic fitness of offspring. Direct benefits can include increased rates of fertilization, increased attainment of resources offered by males, and reduction in male aggression toward offspring via “paternity confusion.” Indirect benefits can include attaining a sire whose DNA is compatible with the mother’s (whereby selection occurs “cryptically” post copulation – within the reproductive tract of the female), diversification of offspring via multiple paternity (bet hedging), and, in the context of extra-pair mating, attaining a sire who potentially has greater genetic fitness (“intrinsic good genes”) than does an in-pair male. As a result of these benefits, female multiple mating is not a rare anomaly; it is commonplace (Parker and Birkhead 2013).

Benefits of Female Multiple Mating

The benefits of multiple mating can arise from multiple sources. To take the example of EPC,

whereas many socially monogamous birds engage in extra-pair mating, it remains uncertain if females in particular derive *any* benefits from it. Males are assumed to benefit from multiple mating, in which case female engagement in EPC may simply reflect male assertion. In some instances, the costs of resisting copulation (e.g., physical harm) outweigh its benefits. Accordingly, EPC can commonly arise exclusively due to male sexual interests and female tolerance, under a scenario of “sexual conflict” (Parker and Birkhead 2013).

Nevertheless, in some avian species, females clearly solicit EPC (e.g., Parker and Birkhead 2013). In this case, the benefits that have the greatest empirical support are direct ones (e.g., parental care, food provisioning). The most controversial interpretation concerns “good gene” benefits. Some researchers conclude that support for genetic benefits of EPC is weak (Parker and Birkhead 2013), whereas others argue that inconclusive data do not necessarily counter a “good genes” interpretation (e.g., Eliassen and Kokko 2008). The jury is still out about whether or not avian EPC functions in a female to gain genetic benefits, and this same uncertainty extends to humans, as noted below in the section “[Women’s Mating Adaptations](#).”

New Models of Sexual Selection Pressures on Males

In recent years, theorists have also questioned the traditional perspective on male interests. In the traditional view based on the Darwin-Bateman effect, males should possess promiscuous sexual motivations and, whenever ecological circumstances permit, compete for the resources or social standing that promote multiple mating. Yet, there are good reasons why males might not pursue this strategy. Males can instead benefit from providing care for their existing offspring. When the net benefits from providing care to offspring exceed the net benefits from competing for mates, males should be selected to care. These conditions are most likely to exist when (a) competing for mates is costly (e.g., males risk injury), relative to the costs of providing care, (b) the net benefits to

competing are relatively weak (e.g., a male is not competitive or many males compete), and (c) the benefits to care are relatively great (e.g., males are able to discriminate their own offspring; offspring benefit from complementary care from males and females) (e.g., Kokko and Jennions 2008).

This framework offers a different perspective on why pair-bonding with biparental care is so common in birds. In the traditional view, the focus is on the male’s inability (e.g., due to resource dispersion) to defend resources supportive of multiple mates and their offspring. In the more recent view, the focus is instead on the relatively poor gain from competing and the substantial benefits to male care (see Kokko and Jennions 2008). In avian species especially, one parent may need to forage, while the other defends a nest of offspring that cannot yet fly. Thus, avian research has drawn attention to the importance of male care and its benefits in the evolution of mating systems – a framework that is broadly applicable to other pair-bonding species, including humans.

Hominoid Mating Systems

The Ancestral State

Applying a comparative perspective draws attention to selection pressures that can drive benefits of multiple mating and of male care – what mating systems characterized ancestral human groups that drove male and female mating adaptations? To address this question, one must consider some of the defining features of primates. Notably, within the primate order, females evolved from the “primitive” mammalian condition of strictly circumscribed sexual receptivity (limited to the 2–3-day peri-ovulatory or fertile period) to a more “advanced” state, evidenced by anthropoid primates, of situation-dependent receptivity. Thus, in female anthropoids, sexual behavior is decoupled from fertility, and females can engage in copulation at any stage of their cycle (Dixon 2012). In those primates that show “extended sexuality” (sexual activity outside of fertile phases), the social system can have significant

influence over sexual behavior, despite the type of mating system. Such is likely to have been the case for our closest ancestors. But what mating system did this ancestral species possess?

Chimpanzee and Bonobo Mating Systems

Whatever mating systems evolved in humans, they originated from adaptations associated with the system(s) of the shared common ancestor with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) that existed about 5 million years ago. Chimpanzees and bonobos both live in mixed-sex groups and have promiscuous mating systems, in which females advertise their fertility and show extended sexuality. Females of both species possess hindquarter sexual swellings that serve as “graded signals” of fertility; yet, they are sexually active for a significant portion of their ~30-day cycle, mating with potentially all adult males in the group, typically multiple times. Despite these similarities, these species have highly divergent social organizations that likely impact their sexual strategies. Notably, chimpanzee societies are male dominant and despotic (in which males show female-directed aggression and infanticide), whereas bonobo societies are female dominant, peaceful, and more egalitarian.

In the better-studied chimpanzee, the favored hypothesis for the function of promiscuous mating in females is Hrdy’s (1979): Promiscuous mating confuses paternity. If no male can rule out his own paternity, each is less likely to aggress against the future offspring, thereby reducing the likelihood of infanticide. Nevertheless, there is recent evidence to suggest that the sexual interests of female chimpanzees change across the sexual period. During the non-fertile phase, females are most promiscuous, but during the fertile phase, they tend to prefer particular males (e.g., younger males whose status is rising; Stumpf and Boesch 2005). Perhaps females confuse paternity during non-conceptive portions of their cycle, but when they are fertile, they bias sireship toward males that can offer genetic benefits or certain forms of direct benefits (e.g., physical protection). Indeed, male reproductive success is highly skewed in chimpanzees, with one or two high-quality males

typically siring many more offspring than the majority of other adult males, despite female promiscuity (e.g., Stumpf and Boesch 2005).

In bonobos, female coalitions are considerably more powerful than they are in chimpanzee societies. Female-female sociosexual exchanges regulate female social hierarchies and coalitional activity. It would seem that paternity confusion to protect against the threat of infanticide would be an unlikely explanation for female promiscuity in bonobos; it instead appears to be a mechanism for ensuring social harmony. In no study, however, have researchers yet tested for changes in female bonobo sexual activity or male preferences across the cycle. Despite promiscuity, male reproductive skew is strong, suggesting similar bias in mating with certain males at peak fertility (Gerloff et al. 1999).

Human Versus Pan Mating Systems

As Dixson (2012) notes, humans have diverged considerably from both chimpanzees and bonobos in a variety of respects. In chimpanzees, extreme sexual size dimorphism, rank relations in male androgen concentrations, relative testes size and ejaculate volume, structural features of semenogelin proteins (that coagulate sperm), and length of the female reproductive tract are consistent with the high degree of either male-male competition or sperm competition (multiple males’ sperm residing in the female reproductive tract vying for conception) evident in their social and mating systems, respectively. These features in humans are consistent with lower levels of male-male and sperm competition. Nonetheless, human mating adaptations may possess vestiges of *Pan* mating, as discussed below.

Unique Features of Human Systems

Limits on Reproductive Skew

Hominoids – and humans in particular – have extremely slow life histories, which severely constrains female fertility. Because of the energetic demands of producing highly encephalized infants (and usually only one per pregnancy),

hominoid mothers are heavily invested in their young, assuming costs associated with lengthy gestation and lactation, as well as extended infant and juvenile dependency. Women are especially reproductively inefficient, even “infertile”. Beyond the constraints imposed by the concealed release and short-term survival of generally one egg per fertile period, approximately 50% of human cycles are anovulatory or too short to allow implantation. Women also suffer relatively high rates of conception failure, low embryo viability, miscarriage, premature delivery, and perinatal death (reviewed in Drea 2005).

Coupling women’s extended sexuality with the various physiological constraints on her reproduction, there is enhanced potential in humans for non-fertile mating (Drea 2005; Thornhill and Gangestad 2008). The low probability of conception associated with each copulatory act challenges predictions arising from the Darwin-Bateman paradigm about the almost limitless potential for fatherhood as a function of increasing the number of sexual partners. Brown et al. (2009) examined variance in reproductive success across 18 traditional or preindustrial societies. On average, male variance exceeded female variance (median ratio ≈ 1.70); yet, this ratio varies widely (ranging from <1 to nearly 5).

Mating Arrangements and Sexual Exclusivity

One feature entirely unique to modern humans is the influence of cultural evolution on mating systems. Notably, marriage is a near-universal institution in human societies; despite this ubiquity, marriage does not imply near-universal monogamy (or even serial monogamy) in humans. Ethnographic evidence from the standard cross-cultural sample (SCCS) shows that over 80% of present-day, human societies possess some degree of polygyny. Fewer than 20% are completely monogamous, and 1% are characterized by a nonzero level of polyandry. Agriculture, herding, and other relatively recent means of resource production may alter mating arrangements; Western religious traditions promoting marriage do so as well. Marlowe (2003) examined mating arrangements in the SCCS’s 36 foraging groups and found that about 90% exhibit a

nonzero level of polygyny. Monogamy is, however, still the most typical, socially sanctioned mating arrangement in human societies. In about two-thirds of foraging societies, for instance, the percentage of polygynously married women is 12% or less (Marlowe 2003); in only 13% of these societies does the rate reach 50%.

Nevertheless, marital systems may or may not imply sexual exclusivity. Although most offspring may be produced by in-pair partners, some may be produced through extra-pair matings. Questions of interest, then, are how common is extra-pair sex and how often does it result in extra-pair paternity (EPP). Anderson (2006) reviewed studies estimating nonpaternity, largely in developed countries. Nearly all samples give biased estimates, depending on how they were selected. High paternity confidence samples estimate an EPP rate averaging just 2%. Samples of men who suspicion about their partner’s fidelity estimate it to be, on average, about 30%. Once again, tremendous variation exists, ranging from $<1\%$ in high paternity confidence samples (in Switzerland and Germany) to about 12% (in Monterrey, Mexico). For some other traditional societies, ethnographies report very frequent EPC, but systematic data on EPP rates are scant (Anderson 2006). Within developed countries, extra-pair paternity rates have declined in the past century; the advent of effective birth control may reduce incidence of conceptive EPC, suppressing the EPP rate. In traditional settings, then, EPP rates may have been low on average (5% or less) but variable (in some societies $>10\%$).

As with females of other species, the benefits that give rise to women’s extra-pair mating are debated. Some scholars argue that benefits lie largely (or even exclusively) with male extra-pair partners, while others stress the possibility that women too, in many circumstances, benefit (for a review, see Thornhill and Gangestad 2008).

Offspring Care

Consistent with slow life histories, human offspring are, in many respects, remarkably altricial at birth. Compared to other hominoids, humans are born with extreme motor immaturity and brains that represent a relatively small proportion

of adult size. As in other primates, human mothers harvest the overwhelming majority of calories consumed by offspring during pregnancy and lactation. For periods longer than in any other primate (i.e., including postweaning), however, human infants continue to be dependent on mothers and others for food, protection, and social development. Because of their extended dependency and juvenility, evolutionary theorists argue that early humans developed a system for rearing their young (and, thus, ensuring their own reproductive success) in which mothers, along with various helpers, cooperate in raising infants (Hrdy 2009). These adaptations for care stem from the nature of human mating systems and life history that inform the likely structure of ancestral human sexuality.

Mothers and Allomothers

The maternal bond or mother-infant relationship is one of the strongest across mammalian species. Its development, which begins in pregnancy, is influenced by the hormone oxytocin (OT). Most generally, OT (along with related homologs in nonmammalian taxa) is a smooth muscle contractor that plays a highly conserved role in orgasm and sexual functioning, as well as in parturition and lactation. OT also functions as a neurotransmitter involved in establishing and maintaining maternal behavior (see Gangestad and Grebe 2017). It is thought that OT's role in maternity constitutes the "biological prototype" for its functions in facilitating other kinds of social bonds so critical to human society (see section on "[Pair-Bonding and Oxytocin](#)").

Many have argued that the extended period of infant care is intricately linked to the early termination of fertility in women – that the distinct post-reproductive period (i.e., menopause) that characterizes human females allowed reproductively senescent mothers to better ensure their latest progeny's survival and overall reproductive success, relative to aged mothers who continued to engage in risky pregnancies. This "stopping early" hypothesis has been contrasted with the "grandmother hypothesis" that instead proposes that senior women contribute best to their own inclusive fitness by investing in the reproductive

success of their childbearing daughters. Accordingly, the diets of women of reproductive age and their children are subsidized, not primarily by the women's mates, but through the efforts of maternal kin – most importantly, the mothers' mothers (Hawkes 2003).

Paternal Care

Questions intensely debated within evolutionary anthropology over the past two decades include whether human pair-bonding is central to the mating system and whether males possess adaptations for providing care for offspring. Did ancestral conditions that favored male care, at least contingently, exist recurrently in human groups, leading natural selection to shape male features that promoted care? Although pair-bonding need not imply biparental care, the two are strongly associated in the animal world. Male care potentially comes in many forms: Protection, direct care (e.g., supervision), and provisioning are three prominent categories. In the anthropological literature, two research areas have received significant attention: the role of testosterone (T) in men's parenting effort and the importance of men's hunting in provisioning mates and offspring.

Parenting Effort and Testosterone

Across vertebrate taxa, T is a crucial component of a system that functions to facilitate male mating effort by channeling energetic resources to features particularly useful in male-male competition (e.g., muscles, sensitivity to dominance ranks, and cues of social hierarchy) and, due to necessary trade-offs, away from other targets of allocation (e.g., repair, immune function; see Bribiescas 2001). In species in which males exert parental effort, a modification may have evolved: T may also modulate allocations of effort to mating versus parenting (in shorthand, competing vs. caring). In some species in which males invest in offspring (e.g., marmosets, some birds), male T concentrations drop after the birth/hatching of the mates' offspring (discussed in Bribiescas 2001; also see section on "[Mating \(Versus Parenting\) Effort and Testosterone](#)").

Views About Hunting as “Parental Effort”

In most primate species, individuals of both sexes are largely responsible for their own subsistence after at most a few years after birth. In most human foraging populations, however, the average adult male generates more calories than he consumes, with the surplus being distributed among kin and, in some cases, non-kin group members. The primary activity through which men generate surplus calories in foraging societies is hunting (broadly defined to include any activity, including fishing, aimed at harvesting animal meat). Although women forage and extract roots (and, in a meaningful minority of societies, produce more calories than do men), only rarely do they hunt to a substantial degree. Human foragers appear to be adapted to a diet consisting of high-quality, calorie-rich foods. Whereas chimpanzees obtain about 95% of their calories from collected foods requiring no manual extraction (e.g., fruits, leaves), only about 8% of calories consumed by modern hunter-gatherers are from foods requiring no manual extraction, with a large proportion (30–80%) derived from vertebrate meat. The level of male contribution to the diet varies considerably across foraging societies (~40–90+%). Women reproductively benefit from the male-generated surplus. Women’s offspring production or, specifically, their inter-birth interval – the delay between the birth of one offspring and the same woman’s next offspring – is aided by male contribution to subsistence (Marlowe 2001).

Thus, a traditional anthropological view is that male surplus food production evolved as paternal care. According to this view, the nuclear family is a key economic unit in the evolution of human mating relations. For subsidies generated by male hunting to function as parental effort, nutrients that men generate must flow to their mates (and then to offspring) or directly to offspring. Additionally, if one adopts the perspective of T as a mediator of mating versus parenting effort, this view of hunting as an instantiation of paternal care suggests it should be associated with T decreases. An alternative view of hunting – in that it primarily functions as an activity to gain new mates – is discussed below in the section “[Views About Hunting as “Mating Effort”](#).”

Adaptations for Mating

In general, patterns of human mating and reproduction are consistent with human pair-bonding and biparental investment, albeit with modest levels of polygyny, nonzero rates of EPC, and notable variability. How do these patterns inform male and female adaptations for mating? These features, in some instances, serve as telltale signatures of the mating system that led them to evolve. The subsections below address evolutionary forces and mechanisms that (a) contribute somewhat equally to mating adaptations in both sexes, (b) are most directly relevant to men’s mating adaptations, and (c) are most directly relevant to women’s mating adaptations.

Mutual Mate Choice

In species in which male and female pairs bond, “mutual mate choice” typically evolves. Members of both sexes are advantaged through preference of some mates over others (e.g., Kokko and Jennions 2008). Studies of mate preferences strongly point to mutual mate choice in modern human societies. In many instances, choice for mates that exhibit good parenting qualities should be preferred. In seeking a long-term mate, both men and women, on average, rate “kindness and understanding” as the top preference. Many other mate preferences for personality traits, however, are characterized by large sex differences (see Conroy-Beam et al. 2015).

Specific forms of mate preference offer particularly compelling examples of adaptation for mutual choice. The human leukocyte antigen (HLA) system, for example, which controls the immune response and pathogen resistance, has been correlated with both odor preferences and, to a lesser extent, facial preferences in potential mates (Winternitz et al. 2017). The HLA is a highly variable gene complex encoding the major histocompatibility complex (MHC) proteins in humans. MHC genes code for cell surface markers that function to “declare” that a cell is uninfected (when the MHC molecule presents only self-peptides) or infected (when the MHC molecule binds a non-self-peptide structure that is “visible” to the immune system). All else

being equal, it pays to mate with someone who possesses alleles optimally different from one's own, either to avoid inbreeding or to produce advantaged heterozygotic offspring. MHC appears to be detectable through signatures in scent (or facial attractiveness). In a variety of species, females prefer the scent of males that possess MHC genes different from their own. Studies strongly suggest that humans too are most sexually attracted to scents of others who possess non-shared MHC alleles. Consistent with *mutual* mate choice, preferences typically exist in *both* sexes (reviewed and meta-analyzed in Winternitz et al. 2017). Evidence for mutual mate choice also exists in the domains of voice pitch and facial symmetry, perhaps because these traits too are cues of the bearer's condition (of which MHC complement is only one feature; see Thornhill and Gangestad 2008).

Pair-Bonding and Oxytocin

As discussed above (see section on “[Offspring Care](#)”), OT plays a major role in the formation of social bonds; its role in pair-bonds has become a hot topic within social psychology. Classic comparative studies in voles were the first to implicate OT in sexual pair-bonding, showing that brain neuroanatomy and central nervous activity of the OT system underlie the development of monogamous partner preferences. From this foundation, psychologists have recently begun to examine how OT plays a role in human sexual pair-bonding. Some evidence is consistent with a pro-social role for OT in romantic bonding in both sexes. OT administration leads to more engaged, constructive communication about relationship conflicts and more intense orgasms and greater contentment after intercourse with a pair-bond partner. Success of relationship interventions and overall relationship satisfaction are related to OT concentrations, and both men and women in newly involved couples exhibited high serum concentrations of OT (see Gangestad and Grebe 2017).

In other studies, OT has been linked to distress and attachment anxiety in romantic relationships. These conflicting results reflect a more general uncertainty regarding the overarching function

of OT in social behavior (see Gangestad and Grebe 2017). As one possible resolution, it may be that threats to valuable, vulnerable relationships are key triggers of the OT system. This hormonal increase, in turn, then functions to reorient psychological resources toward these relationships. Preliminary evidence from both men and women in romantic bonds is in line with such an interpretation, further suggesting that the role of OT in pair-bonding is central for both sexes. A focus on relationship vulnerability may also generalize to other social bonds regulated by OT – in particular, the mother-infant relationship (see Gangestad and Grebe 2017).

Men's Mating Adaptations

Mating (Versus Parenting) Effort and Testosterone
Evidence from nonhuman studies are consistent with a T-mediated hormonal system that is sensitive to the relative value of exerting mating versus parental effort. There is increasing evidence to suggest men's T mediates a similar trade-off. Men with higher T concentrations exhibit greater frequency and intensity of male-male competition, dominance behavior, and mate seeking; in contrast, men who are mated or have offspring typically have lower T concentrations than do single, childless men (reviewed in Gray and Campbell 2009). Some evidence indicates that the association depends partly on changes in T concentrations following changes in mating or paternal status. Additionally, among fathers, those with lower concentrations of T and smaller testes show a pattern of brain activation when looking at photos of their own children, indicative of greater paternal involvement.

The effect of mating status on men's T concentrations is moderated by men's interest in pursuing extra-pair relationships with women other than their primary partners. Men who have little interest in or history of extra-pair relationships reveal the typical drop in T concentrations when mated, as compared to their concentrations while single. Men who have interest in extra-pair relationships, by contrast, showed no difference: Their T concentrations were just as high when in relationships as when single (see Gray and Campbell 2009).

Paternity Certainty and Male Care

Because male confidence in paternity is variable, men's parental efforts may be contingent on cues of paternity, such as self-resemblance. In a large Western sample, men assisted offspring they report as likely to be their own genetic offspring more so than those they suspect reflect EPP (Anderson et al. 2007). Behavioral researchers have examined possible psychological underpinnings of discriminative parenting. In one design, a digital photograph is taken of a participant. The participant's own face or, alternatively, that of another participant is digitally combined with the face of a small child to create two composite images of child faces – one “self-resembling” and one not. Participants then choose between the children based on their likelihood of investing in (e.g., spending time with, adopting) each child. Men consistently prefer the self-resembling one, an effect not due to conscious recognition of self-resemblance (reviewed in Thornhill and Gangestad 2008).

Views About Hunting as “Mating Effort”

The theory of male-hunting-as-parental-effort, discussed above, faces a fundamental difficulty: Nuclear families are not, in fact, potent economic units in foraging societies. In the Hadza of Tanzania and the Ache of Paraguay, for instance, hunters have little control over the distribution of the meat they generate. Instead, meat (particularly from large game) is shared widely across community members. A Hadza hunter's own family receives no more meat from his large game kills than what it receives from the same-sized animal a neighbor killed. In one analysis, offspring nutritional status covaried with Hadza women's foraging returns, but not with men's returns. Thus, perhaps men's hunting functions as (i.e., is adapted for) mating effort – effort to compete for access to mates through “showing off” – rather than as parental effort. Men garner prestige through successful hunting exploits, particularly big-game hunting, and this prestige translates into mating opportunities.

Of course, male hunting subsidizes the diets of women and their offspring. But these subsidies, in

the male-hunting-as-mating-effort view, are not generated directly by the women's own mates or by the children's own fathers. Rather, they are generated through the efforts of men in general to gain mates. The surplus calories generated by male hunting that benefit women and offspring are by-products of men's showing off – windfalls they enjoy, not benefits men's efforts were designed to achieve.

A Blended View on Hunting in Relation to Human Sexuality

Historically, men may have benefited from hunting in currencies of enhanced viability of offspring *and* mating opportunities (e.g., Gurven and Hill 2009). Patterns of Hadza foraging rates and activities support this relationship (Marlowe 2003). Overall, married Hadza women produce as many calories as do married Hadza men. Women with young children, however, do not, because their childcare interferes with effective foraging. In such circumstances, their husbands forage more than they do; in couples with an infant less than 1 year of age, men produce almost 70% of the total calories generated within the family unit. Hadza men's work efforts (and prey items targeted) adjust in response to the direct food production of wives and the presence or absence of young children. The view that men's work functions solely as mating effort cannot readily explain this pattern.

Other data also support this blended view. Across societies of the standard cross-cultural sample, pair-bond stability (low divorce rate) associates with children being weaned at older ages. Because lactation interferes with women's ability to collect food, male subsidy purportedly permits women to invest in young offspring through nursing. Additionally, if men contribute to the household's consumables, male total contribution to calorie production should predict greater levels of monogamy across societies. This prediction is supported by the available anthropological evidence (see Marlowe 2003; Thornhill and Gangestad 2008).

Women's Mating Adaptations

The Ovulatory Cycle

Women, like the vast majority of other mammalian females, undergo regular cycles that restrict the window in which successful conception from sexual intercourse is possible. It is thought that these cycles arise, at least in part, because (1) substantial time is required to prepare the uterus for implantation and (2) the production of germ cells and behavioral adaptations essential to ensure conception from sexual intercourse are physiologically exhausting. Periodicities in sexuality are regulated by a concert of hormonal changes, involving luteinizing hormone, follicle-stimulating hormone, estradiol (E_2), and progesterone (P_4). Together, these hormones function to ensure successful conception, gestation, and parturition (reviewed in Dixson 2012). E_2 and P_4 have received substantial attention for their roles in the psychology of women's mating as well (for a review, see Roney 2015).

Mating Effort and Estradiol

In line with other phenotypically integrated hormonal systems, E_2 's psychological effects "go along" with its physiological roles to regulate energy allocation – in this case, toward females' mating effort, perhaps at the expense of other activities, such as feeding (see Roney 2015). Historically, some sexuality researchers have argued that E_2 has little, if any, impact on women's sexual behavior, noting, for instance, that the effect of ovariectomy on women's sexual behavior is less than the effect on comparable sexual behavior in other female primates (Dixson 2012). In the most robustly designed study to date, however, researchers sampled women continuously throughout multiple cycles and found that E_2 does, in fact, predict overall levels of female sexual desire (reviewed in Roney 2015).

Social Bonding and Progesterone

The role of P_4 in human sexual behavior has received relatively less attention. Dixson (2012) reviewed studies involving the administration of

P_4 to female nonhuman primates, in which the general finding was that P_4 diminishes sexual receptivity and proceptivity. Roney (2015) argues that because women's P_4 concentrations associate negatively with subjective sexual desire, P_4 is a "stop signal" for sexual motivation that facilitates a shift toward other activities. An alternative viewpoint is that P_4 modifies the nature of sexual motivation. P_4 is most consistently elevated at two times: during the luteal phase and during pregnancy. During these non-conceptive phases, in which women still initiate and accept sexual advances, P_4 may have been selected because it shifted sexual interests to allow focus on pair-bond relationships, perhaps especially when the male partner's interest in the relationship lags behind that of the woman (Gangestad and Grebe 2017). During pregnancy, women may have particularly benefited from consolidating social support from a pair-bond partner, kin, or trusted friends. Preliminary evidence is consistent with an interpretation of P_4 facilitating bonding in a *targeted* manner, rather than it contributing to generalized affiliative motives (see Gangestad and Grebe 2017).

Cyclic Shifts in Women's Mating Behavior and Preferences

Whereas ovarian hormones may be the proximate biological factors thought to underlie changes in women's sexuality, cycle phase (i.e., fertile vs. non-fertile windows) provides a relevant functional distinction for understanding adaptations in women's sexual behavior. Changes in concentrations of E_2 and P_4 that result from the physiology of the ovarian cycle convey information, via the neuromodulatory effects of these hormones, related to fecundity (i.e., the probability of successful conception and gestation). Presumably, because the costs and benefits of sexual activity differ depending on whether or not conception is possible, women's mating adaptations should shift accordingly. A substantial literature has accumulated addressing if and how women's sexual preferences and behavior shift as a function of where they are in their cycle.

In most vertebrate species, females are only sexually receptive during their fertile reproductive phase. Consistent with early views about the minimal influence of E_2 on women's sexuality, initial accounts on the evolution of human sexuality minimized or entirely discarded the idea of a distinct fertile-phase sexuality in women, proposing that it was lost and replaced by continuous, unchanging sexual receptivity across the ovarian cycle. Decades of empirical research have since shown that while sexual *frequency* may not always vary across the ovulatory cycle, women's sexual *behavior*, *preferences*, and *interests* clearly do change (see Thornhill and Gangestad 2008). In an impressive longitudinal study following over 400 naturally cycling women, Arslan et al. (2017) found that women in the peri-ovulatory period, compared to during non-fertile phases, reported increased extra-pair sexual desire and behavior, in-pair sexual desire, and self-perceived desirability. Additionally, when fertile, women may be more attracted to certain male features, such as masculine bodies and behavioral dominance. And, should the women's primary partners lack those desired features, fertile women (only) report greater attraction to men other than their partners (findings reviewed and meta-analyzed in Gildersleeve et al. 2014). Thus, one possibility is that women's fertile-phase sexuality is attuned to certain male features when fertile – namely, those that represent “good genes” that could be transmitted to offspring (Thornhill and Gangestad 2008). In cases in which primary partners lack these features, women's mating adaptations could facilitate EPCs. Nonetheless, other possibilities cannot be ruled out: First, these preferences may reflect adaptive mate choice without any selection for EPCs per se; second, women may have retained a vestigial form of estrous-related sexual interests that carry little adaptive significance (e.g., Thornhill and Gangestad 2008).

Women also exhibit extended sexuality to an extreme degree: In addition to potential receptivity and proceptivity throughout the cycle, women's frequency of sexual intercourse changes little depending on where they are in their cycle (Thornhill and Gangestad 2008). In chimpanzees, the prevailing explanation of extended sexuality is

that non-conceptive sexual behavior functions to confuse paternity and prevent infanticide by males (see above; Hrdy 1979); however, women's extended sexuality does not function in this way. Rather, emerging evidence suggests that sexual interests during the non-conceptive phase function, at least in part, to elicit investment and benefits from male pair-bond partners (see Gangestad and Grebe 2017). This account perhaps provides another example of an adaptation for pair-bonding in the human lineage.

Conclusion

What can be concluded about the evolved nature of human sexuality, as it has shaped human adaptations for reproduction?

First, humans likely evolved systems in which pair-bonding has been important and in which men often exert considerable effort to invest in offspring (e.g., Dixson 2012; Thornhill and Gangestad 2008). Monogamy or serial monogamy is the most frequent mating arrangement, especially when male contribution to subsistence is great, but most human societies possess some degree of polygyny. Both men and women possess adaptations that serve as telltale signs of selection in favor of pair-bonding and paternal investment, but both also exhibit features that suggest some degree of adaptation for short-term mating bonds. Indeed, although typically occurring at low frequencies, nonzero rates of EPP characterize most human groups. Female benefits to EPC are not fully understood and may or may not include genetic benefits.

Second, despite these general patterns, wide variations across human groups exist in degrees of monogamy, sex differences in reproductive skew, and EPP rates. Some variation derives from flexibility in which group members invest heavily in offspring: Reliance on paternal contributions fosters monogamy and relatively low EPP rates; heavy reliance on maternal kin (arrangements of communal breeding) likely leads to increased EPP rates.

Third, human mating systems possess some similarities to the mating systems of several of

our close ancestors, including chimpanzees and bonobos, but the differences also cannot be denied. Evolutionary biologists have intensely debated the order in which humans proceeded through specific primate-like mating systems, as well as the events and adaptations which eventually spurred a transition to the contemporary systems displayed by humans. There is no clear consensus on this issue, although further research may lead to future insights.

Finally, biological mechanisms (and hormonal systems in particular) are central to the development and expression of human sexuality. Sexual behavior in humans, compared to that of most other primates, appears to be less tightly regulated by hormonal mechanisms. Indeed, human sexuality is characterized by its remarkable flexibility and diversity, much of which cannot be parsimoniously explained by biological forces. Nevertheless, there exists some hormonal influence on women's sexual behavior and preferences, which is modulated by partner characteristics, cultural norms, and environmental circumstances.

Cross-References

- [Bonobo Sexuality](#)
- [Chimpanzee Sexuality](#)
- [Mating Systems](#)
- [Sexual Behavior](#)

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Human Sociobiology

► Human Behavioral Ecology

Human Sperm Competition

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Definition

Human Sperm Competition The competition to fertilize a woman's egg between sperm from two or more different men.

Robin Baker has retired.

Introduction

Sperm competition was first studied in insects (Parker 1970), but was soon suspected to occur in other animals, including humans (Smith 1984). A series of publications (see **Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition**) claimed to have found evidence that confirmed this suspicion. These claims triggered a wave of opposition (see **Opposition to human sperm competition**).

Currently, authors are divided into three main groups. The first (e.g., Baker and Bellis 1995; Gallup et al. 2006) considers that sperm competition occurred sufficiently often in the human past to have been a major selective pressure on sexuality. The second (e.g., Dixson 2009; Larmuseau et al. 2016) proposes that human sperm competition happened rarely and has played either a minor or zero role in human evolution. The third (Marczyk and Shackelford 2010) maintains that the actual frequency does not matter. As long as sperm competition occurs with some predictability and carries large fitness costs, even a relatively low frequency can act as a powerful selective pressure.

For the moment this debate continues unresolved. Alongside this discussion, however, aspects of human behavior, psychology, physiology, and anatomy are being demonstrated that seem to make sense only as adaptations to sperm competition (Shackelford et al. 2016). A brief summary follows, divided into three sections. The first considers when, where, and how sperm might compete, and the next two consider the potential evolutionary impact of such competition on first male and then female sexuality.

Competing Sperm: When, Where, and How

The following descriptions are based on the review and extensive references in Baker and Bellis (1995).

Insemination

A man stores sperm in two long narrow tubes in his lower abdomen. Each tube (vas deferens)

extends from a testis to the single prostate gland. Inside this gland, the two tubes join the urethra (the duct that runs the length of the penis). While in the vas deferens sperm are highly concentrated in just a small amount of fluid from the testis. The maximum number of sperm stored in the two tubes at any one time is ~1000 million with older sperm nearer the penis and younger sperm nearer the testes.

A woman's unstretched vagina is more a slit than a tube. Protruding into the upper vagina is the cervix (the lower part of the uterus). The cervical opening ranges in shape from a circular dimple to a transverse slit. Inside the cervix the walls are lightly adpressed on a column of mucus that moves forever downward in glacier-like fashion eventually to drip into the upper vagina.

When copulation begins, the penis distends the vagina, everywhere touching the internal walls. Just before ejaculation a portion of each of the two "columns" of sperm is shunted from the vas deferens into the urethra. Ejaculation then follows. The upper part of the vagina dilates like a balloon, in effect creating a bowl to receive the semen.

While contractile waves force the sperm from the urethra, secretions from first the prostate then the seminal vesicles add volume. On average, ~300 million sperm in ~3 ml of semen are ejaculated in a series of 3–9 spurts, often with a copulatory thrust between each spurt. The result is an inseminate that for two reasons is neither homogenous nor all in one place. First, the seminal fluids differ chemically between spurts. The first part is dominated by prostate gland secretions and the later parts by fluids from the seminal vesicles. The very last spurt is strongly spermicidal. Secondly, the spurts are inseminated with different force by a penis that may change in length and turgor from first spurt to last. The end product is a "seminal pool" next to the cervical opening, plus semen from later spurts and dribbles lower down the vagina.

Sperm Competition It is not known what happens on the, presumed infrequent, occasions that a woman is inseminated by two males

simultaneously nor how the two ejaculates and contained sperm might interact if she does.

In Vagina

Immediately after, or even during, insemination, the cervix dips into the seminal pool, creating a cervical mucus-semen interface. Virtually simultaneously, most of the ejaculate, excluding the part nearest the cervical opening, coagulates to form a soft, gel-like structure which does not become liquid again for 15–20 minutes. Coagulation retains the seminal pool in position while sperm leave to cross the cervical mucus-semen interface.

After the seminal pool decoagulates, the upper vagina contains a mixture of the now-liquid-again seminal fluid, various female secretions, and stranded sperm. If the cervix dips again into this mixture, such as during female orgasm, more sperm can still escape into the cervix. If not, no more sperm can leave the pool. Eventually, the female ejects the whole mixture from the vagina as the "flowback."

The flowback exits the vagina as a discrete series of 3–7 white globules and measures ~3 ml; in effect the female rids her vaginal tract of virtually all of the seminal fluid plus any sperm still contained. This event occurs between 15 and 120 min after the male ejaculated (0–105 min after the seminal pool decoagulates). If expelled during urination, the flowback is sometimes ejected with surprising force.

All flowbacks contain sperm, on average ~35% of the number inseminated (range: 5% to ~100%).

Sperm Competition Only when a woman mates with a second male before ejecting the flowback from the first male do two ejaculates interact inside a vagina. In the UK, ~1% of women with >500 lifetime copulations claimed at some time to have been inseminated by two different males within <30 min (Baker and Bellis 1995). In the USA, ~8% of college undergraduate women claim to have engaged in group sex (1 woman, 2 or more men) at least once (Gallup et al. 2006). On most such occasions, the second male will remove the first male's ejaculate with his penis (see section on '[Penis shape and copulatory behavior](#)' below) before himself ejaculating. If he does not, however, the two ejaculates interact in the vagina.

There are two phases and elements to this interaction. First, for ~15–20 minutes after the first male ejaculated, his coagulated seminal mass can function as a short-term plug, a physical barrier that keeps sperm from the second ejaculate away from the cervix. Secondly, after decoagulation, the spermicidal back part of the ejaculate from the first male could decrease the motility and survival of sperm in the second male's ejaculate. Counteracting this, however, the prostatic first half of the second male's ejaculate provides some protection to its contained sperm.

In Cervix

Cervical mucus has a complex structure with fibrils arranged to form channels. Sperm migrate through the mucus by way of these channels. There are two channel arrangements within a cervix: vertical, aligned more or less parallel to the cervical walls, and diagonal, running from the lower (vaginal) end of the mucus column to crypts in the cervical wall. Compared with a sperm, which is ~3 μm wide, the vertical channels are spacious (30–35 μm), whereas those through the diagonal mucus are relatively narrow (2–6 μm). Proportions of the two types vary over time with vertical channels dominating during the fertile phase of the menstrual cycle.

The dipping of the cervix into the seminal pool allows sperm to escape from the vagina. The mucus-semen interface consists of a series of finger-like projections of semen extending a short way into the mucus channels. Once across the interface, sperm then swim either through the vertical mucus, perhaps directly to the uterus, or along the diagonal channels into the cervical crypts.

Around 65% of sperm from an inseminate successfully enter the cervical mucus, but the vast majority then go no further. Within minutes of first sperm entry, the female floods the mucus with white blood cells (leucocytes). These attack the invaders, killing and removing them by phagocytosis, targeting healthy sperm just as aggressively as the dead, and dying. At their peak, a few hours after insemination, leucocytes may outnumber sperm by up to 3:1. Within

24 hours of insemination, however, leucocyte numbers have returned to base level.

Only ~1% of sperm (~3 million) from the inseminate successfully evade the leucocytes. Some that do so pass straight through into the uterus, but the vast majority instead find safe haven in one of the 10,000 or so crypts that dot the cervical walls. While in these crypts, safe from phagocytosis, the sperm become immotile until expelled. Expulsion occurs suddenly but is staggered over days with a peak 24 hours after insemination.

Sperm Competition Most (~99%) sperm that enter the cervical mucus never leave alive, reaching neither the uterus nor the crypts. Instead, they are either intercepted by leucocytes or simply lodge in the mucus. Even these sperm, however, can play a part in sperm competition. By blocking channels through the cervical mucus and attracting leucocytes, they can greatly hinder the passage of sperm from any second male that inseminates the female over the next day or so.

Competition can also occur in and around the cervical crypts. As sperm from a second male attempt to enter and settle in these crypts, then later jostle after expulsion, the presence of sperm from a previous male can interfere with both maneuvers.

In Uterus

Except when pregnant, a woman's uterus (womb) is roughly pear sized as well as pear shaped with the walls pressed closely together. Vanguard sperm that swam straight through the vertical channels of the cervical mucus arrive within 5 minutes of insemination. These are then helped to the womb's top, the widest part of the pear. In effect, they surfboard, carried on the crests of muscular ripples passing up the walls. At the top of the womb on each side, where horns would be if the "pear" was a bull's face, is an opening (the uterotubal) leading into a narrow tube, the oviduct. Once through the opening, the sperm swim a short distance along the oviduct until reaching a rest area (the isthmus). Here most cease swimming, settle down, and wait.

The wave of sperm that passes through the uterus just minutes after insemination is neither

the largest nor the last. Numbers in the uterus peak ~24 hours after insemination as further sperm arrive following expulsion from the cervical crypts.

Sperm Competition The uterus seems merely a zone that sperm must traverse to reach the oviduct. As it is possible to arrive in the oviduct too soon as well as too late, sperm from two or more men are not really “racing” during the traverse. Only if early sperm can hinder later sperm in some way (e.g., by blocking the uterotubal junction or occupying better positions in the oviduct), does there seem scope for competition during this leg of the journey.

In Oviduct

Fertilization occurs in the ampulla, the region of the oviduct furthest from the uterus. Beyond the ampulla is an opening into the female’s body cavity near one of the two ovaries. Roughly every 2 months, a particular oviduct receives an egg, which then remains fertile for only ~24 hours.

Only ~25,000 sperm from an inseminate of ~300 million ever pass through an oviduct. At any one time only ~3500 are present and of these only ~300 are in the ampulla. Most often, after several hours residing in the isthmus, sperm set off individually to swim to and through the ampulla then on into the body cavity where they die. However, on those rare occasions that an egg is released by the nearby ovary, a chemical “signal” arrives, and many sperm from the isthmus swim to the ampulla simultaneously. Whether an egg arrives or not, 4–5 days after a single insemination, there are no sperm left in the oviduct.

Sperm Competition A sperm’s timing of arrival at the ampulla may be more important than speed. However, when an “egg-approaching” signal is given, the swim from isthmus to ampulla might become a race.

Fertilization

A single insemination is most likely to lead to fertilization if it occurs 48 hours before ovulation, which is roughly the time taken for the sperm

population to peak in the oviduct. However, not all sperm even in the oviduct are able to fertilize an egg: only 1 in 7 have such ability (compared with an even lower 1 in 300 in the original inseminate). This means that of the ~25,000 sperm that pass through the oviduct, only about ~4000 are capable of fertilization, and of the 300 found at any one time in the ampulla, only ~40.

Sperm Competition It is generally assumed that when sperm from two or more males compete inside a female, the male who has most sperm in the ampulla as the egg arrives has the greatest chance of fertilization. Whether the critical factor is “most sperm” or “most sperm capable of fertilizing an egg” is not yet clear. Much depends on the function, if any, of the 86% (6/7) in the oviduct not capable of fertilization. Two explanations have been offered: (1) that these sperm are faulty, hence irrelevant, and (2) that they hinder, divert, or even kill fertile sperm from rival males.

Selection on Men

Human males, whether paired to women monogynously (1:1, male/female) or polygynously (1:>1, male/female), invest significant time, energy, and “wealth” into raising their partners’ children. Evolutionarily, a male gains most if these children are his own genetic offspring (Trivers 1972). Sperm competition, due to a partner’s infidelity, threatens a male’s reproductive success because it raises the possibility of cuckoldry, leading a male unknowingly to expend resources on raising another man’s child. Selection, therefore, favors a man who either prevents sperm competition or, if he fails, ‘wins’ the competition that ensues.

Pham and Shackelford (2014) contrast the “risk” and “intensity” of sperm competition: risk refers to the likelihood that the male’s sperm will face competition, while intensity refers to the number of males that contribute sperm to that competition. Shackelford (2003) proposes that human males encounter three separate adaptive problems from sperm competition: anticipation, prevention, and correction. The first two are

generated by risk and lead to adaptations that motivate mate choice and guarding. The last is generated by intensity and leads to adaptations such as copulatory behavior, genital morphology, ejaculate qualities, and the number and behavior of sperm. Some behaviors, such as routine sex, are adaptations to all three problems.

Anticipation: Mate Choice

Males who choose more-faithful long-term partners are less likely to encounter sperm competition, and evolution should favor men who can reliably identify such women.

Men show agreement on which women are likely to be unfaithful, their judgment seemingly based on female attractiveness. There is also some evidence that this judgment has foundation. Women with features shown to be attractive to men (e.g., low waist-to-hip ratio, bilateral symmetry, and feminine voices) have been reported to accumulate more sexual partners, including committing more acts of infidelity (Baker 1997; Hughes et al. 2004; Shackelford and Buss 1997; but see Rhodes et al. 2005).

Prevention: Mate Guarding

Once committed to a relationship, a man shows some ability to judge his partner's faithfulness (Andrews et al. 2008), in part by analyzing her behavior (Shackelford and Buss 1997). He can also assess to a degree whether any child she bears is likely to be his genetic offspring (Anderson 2006).

Buss (1988) identified 19 male tactics that reduce sperm competition including surveillance, threatening rival men, and direct guarding (i.e., spending as much time with the partner as possible). Such guarding succeeds: in the UK the more time a man spends with his partner between copulations, the less likely she is to be unfaithful (Baker and Bellis 1995). A man can also recruit other family members to keep surveillance on his partner in his absence (Strassmann et al. 2012).

Some men attempt to enforce fidelity through violence and in places have their actions supported by law. The earliest known example, from 4300 years ago, is found in the Mesopotamian Code of Urukagina (French 2008) which

advocated stoning unfaithful women to death. A number of modern societies still allow a death sentence for females accused of infidelity.

Correction

Despite men's attempts to prevent partner infidelity, they do from time to time fail. Estimates of the proportion of children sired by a man other than their putative father range from ~10% (Baker and Bellis 1995; Anderson 2006) to ~1% (Larmuseau et al. 2016) (see **Opposition to human sperm competition**). Perhaps in consequence, men also show adaptations that seem to increase their chance of "winning" any sperm competition that results.

Routine Sex

Men seem motivated to maintain a population of sperm inside their partners, and the greater the risk of sperm competition, the larger the population maintained (Baker and Bellis 1995). This adaptation *anticipates* partner infidelity, *guards* against another male's sperm having uncontested access to the partner's egg, and provides some chance of *correcting* the female's infidelity by still being the male to fertilize her egg.

The strategy a man is suggested to use (Baker and Bellis 1995) is to maintain reservoirs of sperm in his partner's cervical crypts, thereby ensuring a continuous passage of fresh sperm through her oviducts for up to ~5 days after each insemination. Intercourse at least every 5 days is sufficient, combined with varying the number of sperm inseminated according to time since last copulation.

Over a period of 4 weeks, the total number of sperm inseminated into a partner averages about 3000 million and varies little whether the couple have sex 20, 10, or 5 times in that period (Baker and Bellis 1995). However, if the man spends less time physically "guarding" his partner between copulations and the risk of sperm competition increases, the total number of sperm he inseminates also increases (Baker 1997).

Masturbation

A recent (<72 hours) masturbation reduces the number of sperm inseminated at the next copulation but not the number that enter the cervix

(Baker 1997). Such masturbatory “shedding” may increase inseminate competitiveness by removing older sperm. Thus, at the next copulation, the male inseminates younger sperm which could survive longer inside the female. Potentially, masturbation is an adaptation to sperm competition.

Response to Sight of a Copulating Pair

Males of many species respond to perception of a copulating pair by attempting either to oust and take over from the other male or, failing that, to mate with the female as quickly thereafter as possible (review: Baker and Bellis 1995). To achieve this, perception of a copulating couple needs to generate a rapid arousal for copulation and the sperm competition that inevitably follows. In male humans the appeal of hard-core pornography rests on such a response. Surveys have shown that men prefer images of a woman with multiple men, suggesting sperm competition, compared to those of a man with multiple women (McKibbin et al. 2013).

Urgent and/or Forced “In-Pair” Copulation

Just as with directly observed infidelity, a man who strongly suspects his partner of recent infidelity increases his chances of avoiding being cuckolded by inseminating her himself as soon as he can. This is especially the case if he suspects the infidelity to be very recent (<2 hours). Until the flowback from the previous male is ejected, that male’s sperm can still be entering the cervix (Baker and Bellis 1995).

Men who spend a greater percentage of time absent from a partner report greater sexual interest in that partner, greater distress in response to sexual rejection, and a greater sexual persistence if rejected (Shackelford et al. 2007). This increased drive to inseminate a partner suspected of infidelity can lead to force being used (Wilson and Daly 1992): most forced within-pair copulations follow accusations of female infidelity.

Penis Shape and Copulatory Behavior

Until ejected in the flowback, one male’s semen can hinder any second male’s sperm trying to enter the cervix, but this earlier semen can be removed.

The erect human penis is piston shaped with a smooth terminal protuberance (= coronal glans). This shape, the fit of the penis in the vagina, and the pumping/thrusting action during copulation together mean that as a penis pushes forward then pulls back, semen already present is sucked down the vagina. On the next forward thrust, the glans pushes through this material; then on the next backward pull, the back edge of the glans scrapes the material further down the vagina in a “push-pull-suck-push-pull-scrape” process (Baker and Bellis 1995). This process has been verified by Gallup et al. (2003) using artificial penes, vaginæ, and semen. Gallup et al. also reported that after a perceived female infidelity or period of female absence, males thrust deeper, faster, and more vigorously.

Testes Size

Males of primates with high levels of sperm competition have proportionately larger testes (relative to body size) than males of species with low levels (Harcourt et al. 1995). Larger testes produce more sperm at a faster rate. Evolutionarily, in lineages with greater sperm competition, the organs increase in size until the gain from greater competitive success is opposed by some other factor (e.g., cost of maintaining larger testes, or greater risk of damage). Relative testes size for humans is ~4 times greater than for gorillas (with low sperm competition) but ~5 times smaller than for Chimpanzees (with high). This suggests an evolutionary past for humans with intermediate levels of sperm competition.

Testes size varies greatly within populations. Baker and Bellis (1995) hypothesized that men with larger testes are specialized for sperm competition and men with smaller testes for mate guarding. Between the two extremes, men follow a mixed strategy. In support of this hypothesis, men with larger testes: (1) spend less time with their established partner (Baker and Bellis 1995), (2) show less interest in their partner’s children (Mascaro et al. 2013), (3) copulate and ejaculate more frequently (Baker and Bellis 1995), (4) inseminate more sperm at each copulation (Baker 1997), (5) ejaculate more sperm during masturbation (Baker 1997; Simmons

et al. 2004), and (6) are more likely to become involved in sperm competition (Baker 1997; Baker and Bellis 1995; but see Simmons et al. 2004).

Sperm Morphology

Human ejaculates contain a proportion (up to 40%) of strangely shaped sperm. Head shape, for example, can be small, large, pear shaped, cigar shaped, or simply oddly shaped. Tails vary too: short, bent, coiled, or double. Traditionally, such sperm have been blamed on mistakes during sperm formation (Cohen 1977). However, Baker and Bellis (1988) suggested that they were adaptations to sperm competition, some even present specifically to die, a “kamikaze” role (see: **Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition.**)

Selection on Women

Most discussion surrounding sperm competition focuses on males, but females also gain benefits (Smith 1984). If sperm competitiveness is heritable, females fertilized by the most competitive sperm will gain through the greater reproductive success of their sons. To obtain this advantage, a female needs to promote sperm competition via *double mating* (matings that lead to the presence of sperm from two or more males inside her reproductive tract) at around the time of peak fertility.

Weak Signals of Fertility

To double-mate a female must, at key moments, evade mate guarding by her established partner. Several adaptations have evolved to make such evasion easier (review: Welling and Puts 2015).

Female humans are sexually receptive both throughout the menstrual cycle and during pregnancy. This background receptivity makes it more difficult for male partners to identify the critical days to guard the female intensively. Nevertheless, females do not, and maybe cannot, hide their fertile phase completely.

“Oestrous” is the phase of the female cycle leading up to and just following ovulation. During this phase a suite of attributes appear, all of which

are less pronounced at other times. In humans, not only do females travel further and show more interest in mating with multiple males at this time (Baker and Bellis 1995), but also they advertise their phase of cycle through subtle changes in appearance, behavior, attitude, sound, and smell (review: Welling and Puts 2015).

How effectively men can detect and act upon the oestrous signals given by women is still debated, but clearly they cannot interpret the signs with total certainty (see Welling and Puts 2015). For example, men of the agricultural Dogon tribe of Mali forced their wives to advertise menses by temporarily residing in special “menstrual” huts. When menstruation finishes, the wives are then for a while kept under intense surveillance by their husband’s family network. Consequently, the number of Dogon children fathered by a man other than a woman’s husband was low (Strassmann et al. 2012). However, when a section of the population relaxed its use of the menstrual hut, the frequency of such “extra-pair” paternities increased fivefold, suggesting that direct detection of the fertile phase by males was weak at best.

Timing of Double Mating by Women

Nationwide data for women in the United Kingdom revealed that general female infidelity showed no pattern with respect to the menstrual cycle (Baker and Bellis 1995). However, double matings “unprotected” by contraception were most likely to occur during the fertile phase, suggesting that the women were most likely to promote sperm competition when the probability of conception was highest (see **Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition** for more details).

Cryptic Female Choice

Women use a range of information when choosing long- and short-term partners (Shackelford et al. 2016; Welling and Puts 2015) and make comparisons between the two when promoting competition between their sperm. Females also have a variety of adaptations that allow them to bias the chances of fertilization in favor of a particular male.

Although such “favoritism” is not shown by younger nulliparous women, it is shown by women in the main reproductive phase of their lives (Baker 1997). The latter are less likely to use contraception during sex with a male who is not their established partner. They also, by altering the occurrence and timing of their orgasms, seem to retain more sperm from this other male than from their partner.

For further details of this function of the female orgasm plus opposition to the findings, see **Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition**; for a general review of the female orgasm, see Puts et al. (2012).

Conclusion

Debate continues over whether sperm competition occurred often enough in the past to play a significant part in the shaping of human sexuality. Yet at the same time a body of work is amassing, covering many aspects of human behavior, psychology, physiology, and anatomy, that seems to make sense only in terms of adaptation to sperm competition.

Human sperm have a long and complex journey ahead of them when they are first inseminated into a vagina, and most falter within minutes or hours. An average of ~35% never escape the vagina and <1% ever get further than the neck of the womb (the cervix). Each leg of the journey raises its own unique circumstances and, when sperm from more than one male are present, raises different types of opportunity for those sperm to meet, interact, and compete.

The threat of sperm competition appears to have imposed a range of selective pressures on men. Advantages can be gained from preventing such competition, but when preventive measures fail, the only adaptive avenue is to try to win the sperm competition that then ensues. Sexual psychology, mate choice, mate guarding, masturbation, copulatory behavior, ejaculate size, penis shape, testes size, and sperm morphology have all been argued to have been shaped by sperm competition.

The evolutionary impact of sperm competition is not limited to males. Females would also appear

to gain by promoting such bouts. Various behaviors and attributes may all have evolved to aid such promotion; So, too, may responses such as sperm ejection and orgasm (female) that could influence the outcome of any sperm competition the female generates.

If the opposition to the role of sperm competition is justified, then all of these apparent adaptations will need to be explained in other ways. However, if sperm competition has indeed been the force that many scientists claim, it has been a highly significant factor in the shaping of human sexuality.

Cross-References

- ▶ [Opposition to Human Sperm Competition](#)
- ▶ [Robin Baker and Mark Bellis](#)
- ▶ [Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition](#)

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Human Sperm Competition Tactics

- [History of Sperm Competition in Humans](#)
- [Physiological Evidence for Human Sperm Competition](#)

Human Storytelling

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Synonyms

[Literature](#); [Narrative](#); [Recounting](#); [Story](#); [Storyteller](#)

Definition

The process of sharing stories with other people generally for the purpose of entertainment, education, and promotion of cultural awareness and societal values.

Introduction

“Once upon a time” or the less common variant “once there was not” (Sherman 2008, p. 29) probably initiated everyone’s favorite story as a kid. There are many definitions of the words story, narrative, and storytelling, and at times they are even used interchangeably; nevertheless, a story is defined as the conceptualization of a sequence of events, a narrative is the concrete means of communicating a story to other people, and storytelling is the process by which narratives are composed, where the conceptualization of the story is turned into a material product, i.e., a narrative through an available medium, e.g., language and other nonverbal mediums such as pictures and miming (Sibierska 2017). Even though there are different types of stories, they can all, more or less, be separated into four main genres: true stories, folklore, fiction and literature, and fairy tales (Sherman 2008, p. 19).

A Bird’s-Eye View into Storytelling

Sherman (2008, p. 17–18) reported that the oldest record of written storytelling goes back as far as the second millennium BCE; around 2560 BCE, Egyptian records show that the sons of Pharaoh Khufu (or Cheops) used stories to entertain their father. Additionally, he stated that stories most probably predate their written versions. For instance, during the fifth century BCE, the Greek fabulist Aesop and, during the eighth century BCE, Homer (the famous Greek poet who wrote the epics “Iliad” and “Odyssey”) almost certainly recited their tales long before they had a chance to be written down. According to the author, in the course of the Middle Ages, the names of proficient storytellers started to be

systematically recorded, while throughout the Renaissance era, storytellers begun to attract attention and gain popularity.

Dennehy (1999) indicated that the narration of a story is comprised by five steps that are interdependent to each other’s content:

1. “Establishing the setting” – describes the various details of the situation (e.g., names, time, place, etc.) that foster a sense of connection between the story and the audience and also enables the listeners to mentally visualize the story’s circumstances.
2. “Building the plot” – this step builds up the listeners’ excitement and interest to the unfolding events of the story while taking advantage of their emotions so that audience identifies with the plot.
3. “Resolving the crisis” – the “ah-ha” experience which involves the realization of the story’s main point(s).
4. “Describing the lessons learned” – the story’s messages are made clear ensuring that everyone understands since some listeners may not outright realize the main point conveyed in the story (depending on the audience the key lessons of the story may vary).
5. “Explaining how the characters change” – listeners once again are prompted to identify with the story and reflect on how they can adopt the new values and behaviors portrayed in the key lessons of the story (as cited in Yoder-Wise and Kowalski 2003).

Lipman (1999, p. 17–18) described that the storyteller, the audience, and the story constitute the three corners of the “storytelling triangle” and that these three elements are accompanied by relational forces in-between them. The first relationship is between the storyteller and the audience, the second is found between the storyteller and the story, and the third is the one that the storyteller cannot force control over and can only affect indirectly, which is the relationship between the story and the audience. Subsequently, the goal of the storyteller is to form a positive bond between the story and the audience, a relationship that can only be established indirectly by the storyteller’s skills and abilities to persist, create a novel plot,

prepare, and genuinely care for both the story and the audience.

Role in Evolution

Despite the fact that language is considered the most popular way to tell a story, it is by no means the only modality available, which is evident by nonverbal narratives that are expressed through the use of pictures, facial expressions, body movements, and hand gestures (Sibierska 2017). McBride (2014) proposed that storytelling originated from mimes, long before there was any possibility of telling stories through the use of language, which would use gestures to impart their experience of the hunt. In addition, the author advocated that since stories would bestow more knowledge than juveniles could potentially learn on their own, they would eventually lead to mature and socialized adults that assembled the first forms of human cultures, from there on language evolved as the means to make the use of storytelling easier and more efficient. The storytelling brain separates humans from animals as it allows for meaning to be derived from metaphors and narratives to be interpreted and applied into real-life events (Le Hunte and Golembiewski 2014).

Over time human evolution ensured that it would be no longer necessary to live a situation in order to gain insight into potential threats or opportunities and humans would possess the evolutionary advantage to recognize and compare patterns in different situations or narratives allowing them to experience the perspective of others (Le Hunte and Golembiewski 2014). Storytelling is a skill assumed to be favored by natural selection because (a) children would receive important lessons from stories of experience hunters in a playful manner that would make them more adept as future hunters, (b) individuals talented at storytelling would receive more attention from their species hence gain more status and respect in their society, irrespective of rank, that could even make them more likely to be chosen as a sexual partner, (c) by hearing more stories experience troops learned from their peers about dangers and others' failures or successes which they

could later avoid or repeat without wasting unnecessary lives, and (d) storytelling's ability to pass on knowledge without directing communication through a double interaction, i.e., a primary social/interpersonal interaction between two or more individuals that contains a secondary interaction which is the story (McBride 2014).

Throughout years of evolution, neurological mechanisms in the brain have developed that allow the human species to effectively process and reflect on stories (Le Hunte and Golembiewski 2014). The brain components, found in both brain hemispheres, that assist these neurological mechanisms include the hippocampus where its role in storing and recalling information enables listeners to process the details of the story, within the temporal lobes the amygdala's function in processing emotions grants contextual awareness enabling the listener to identify or separate himself from the story, and lastly the frontal cortex act as an inhibiting agent for these storytelling mechanisms so that individuals can choose the story they want to concentrate and focus on (Le Hunte and Golembiewski 2014).

Why Do We Even Bother?

The storytelling occasion is a two-way street: as for the audience it is an opportunity to play, bond with friends, and share an experience together with a group, but for the effective storyteller, it is a moment of unconditional acceptance by the crowd (Sherman 2008, p. 18). To an even larger extent, when a father tells his son a story, societal values are passed down from one generation to the next, and when other groups of individuals hear those stories, it can help promote intercultural awareness (Sherman 2008, p. 18).

Some of the many benefits for students from the educational properties of hearing stories include but are not limited to learning about different cultural backgrounds, increasing the self-worth of immigrant or minority children who listen to their cultural values, aiding children to hone their listening skills, and improving the use of imagination, and by listening to the experienced storyteller, they are indirectly trained to become better storytellers, writers, and readers

themselves (Sherman 2008, p. 29). This is concurrent with current research findings that illustrate that in children there is a positive relationship between receptive and expressive language abilities along with their storytelling abilities (Holmes et al. 2017).

According to Sherman (2008, p. 18–19), individuals who hear a tale are presented with the opportunity to acquire another perspective to an adversity, gain access to an effective role model that prevailed in a challenging situation, expand their imagination to new heights, and overall develop on a personal level, while stories filled with intense emotional content promote a climate of compassion and caring that cultivates the feeling of togetherness among a group of people. What is more, the author stated that children listeners improve on their vocabulary knowledge, understanding of a narrative's structure, verbal ability to retell the story, and sense of self-worth. However, caution is advised when interpreting meaning from tales as the mind is biased toward detecting positive patterns and inferring meaning in stories where none exists (Gottschall 2012, p. 103–105), for example, “pareidolia” is the psychological phenomenon where the mind associates a familiar pattern to a stimulus even though one does not actually exist (e.g., seeing a face from a stain).

Conclusion

As discussed, human storytelling offers many evolutionary and developmental benefits while simultaneously is a largely entertaining and readily available resource to draw upon. For instance, the “catch-phrase” can often conveniently remind us of a tale and the accompanied moral point so that we can reevaluate our course of action (Sherman 2008, p. 18). Without undermining traditional storytelling, the technological advancements that increase exponentially year after year suggest that storytelling's future lies inside the virtual world and toward the direction of MMORPGs (massively multiplayer online role-playing games) where individuals can immerse their selves in a story shared with millions of other people that come from different ethnic backgrounds (Gottschall 2012, p. 177–200).

Cross-References

- Adaptations
- Early Theories of Language
- Evolution of the Brain, The
- Morality
- Natural Selection
- Social Play
- Social Values

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Human Tool Making

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Synonyms

Flintknapping; Human tool manufacture

Definition

Human manufacture of objects designed to achieve particular results.

Introduction

A tool is an object that can be used to achieve a particular desired result. The use of tools and the tools themselves are referred to as technology. Tools may be relatively simple and unmodified objects, such as rocks or sticks, or may result from modification of raw materials, with chipped stone tools or metal objects as examples. It was long assumed that only humans were able to use tools, but subsequent observations of tool use in a number of species like chimpanzees, monkeys, otters, and several types of birds have changed that perception. Nonetheless, human tool manufacture and use is quite complex and has been an important contributor to human adaptation in a variety of contexts.

Human Tool Making

It is likely that the earliest use of tools by human ancestors incorporated organic materials that are unlikely to be preserved in the archaeological record and that these are similar to tools like sticks, leaves, and other objects used by chimpanzees today. After stone was adopted as a raw material, however, long-term preservation became much more probable. At present, archaeological evidence suggests that humans began manufacturing simple stone tools sometime prior to about 2.5 million years ago. These first tools were made through relatively simple flaking along the edge of a rock to create a crude chopping tool. Such tools are inconsistently manufactured and did not require much skill to make, but research has demonstrated that chimpanzees lack the coordination necessary to produce the flaked edges seen on these tools.

The most basic stone tools fall into a small number of categories: manuport, core, hammerstone, and flakes. Manuports (derived from the

Latin for “carry by hand”) are unmodified stones that have been moved to a particular site by human agency. These stones are typically far removed from their source and could not have been moved to the site without human intervention. A core is a piece of stone that has had flakes removed from it. A hammerstone is used to remove flakes from the core. Flakes are small pieces of stone removed from a core, which can either be simple waste (debitage) or could also be used as tools themselves. The raw materials used to make stone tools were quite variable in the earliest examples, while more recent technological complexes show greater care in choosing higher quality stone that will flake more predictably.

The broad divisions of the Paleolithic (Stone Age) fall into the Early/Lower Paleolithic, Middle Paleolithic, and Late/Upper Paleolithic. The Early Paleolithic includes the Oldowan and Acheulian stone tool complexes. The Oldowan is the earliest stone tool culture and is characterized by simple choppers made from fairly crudely flaked stone cores, while the Acheulian is characterized by large, teardrop shaped bifacial handaxes. Unlike the more irregularly shaped choppers of the Oldowan, the Acheulian is more consistent in design and more skill is required to manufacture them. The Middle Paleolithic, sometimes referred to as the Mousterian, is typified by a variety of smaller tools struck from a prepared core. Typically multiple tools could be removed from a prepared core, greatly improving the efficiency of raw materials. The Late Paleolithic is characterized by stone blades, which require high quality stone and significant skill to produce. Additional tool types, such as points, scrapers, and awls, are present in the Late Paleolithic and incorporate a variety of raw materials besides stone, such as bone and antler.

Conclusion

Technology provided an important set of flexible adaptations to a variety of environments, allowing humans to range across the surface of the Earth. The evolution of tools throughout our history,

continuing through our present day dependence on a variety of gadgets, serves to highlight our reliance on innovation as a strategy for dealing with a number of obstacles in daily life.

Cross-References

- ▶ [Nonhuman Tool Use](#)
- ▶ [Primate Tool Use](#)
- ▶ [Stone Hammers](#)
- ▶ [Stone Hammers](#)
- ▶ [Tool Use](#)

Human Tool Manufacture

- ▶ [Human Tool Making](#)

Human Universals

- ▶ [Cross-Cultural Universality](#)
- ▶ [Cultural Universals](#)
- ▶ [Psychic Unity](#)

Human Visual Neurobiology

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Synonyms

[Vision science](#); [Visual cognition](#); [Visual processing](#)

Definition

Human visual neuroscience is an interdisciplinary field of study which seeks to understand the processing of visual information by the eye and brain in humans and provides a well-studied model of how sensory systems enable organisms to interact with their environments.

Introduction

Objects in the environment reflect light rays onto the retina which are transduced by photoreceptors into electrochemical impulses, and this information is sent to the occipital lobe for initial computation before being sent to higher-order brain regions for more modular processing. Visual neurons detect where objects are located in space by signaling only when an object in the visual field is presented in a specific position, known as its receptive field. As an example, a neuron in the right primary visual cortex may only signal in response to a black vertical bar but will only do so if it is located in a specific position in the visual field. Similar to the somatotopic maps of the somatosensory system or tonotopic maps of the auditory system, the visual neurons contained within the lateral geniculate nucleus of the thalamus and primary visual cortex maintain an organized map that detects spatial location and transduces it into a physiological portrayal of the visual field. These topographic maps in the visual system are known as retinotopic maps. The left-hemisphere of the primary visual cortex contains a complete retinotopic map of the right visual field and the right-hemisphere contains a complete retinotopic map of the left visual field (Gazzaniga et al. 2019). The primary visual cortex, otherwise known as area V1, acts as the first level of cortical visual processing. Neurons in the primary visual cortex are activated in response to specific characteristics of the visual world which include orientation, movement, spatial frequency, retinal disparity, and color.

The Primary Visual Cortex

Definition: The primary visual cortical area, anatomically defined as Brodmann's Area 17 or the

striate cortex, receives the axons of third order afferent visual tract neurons projecting from the lateral geniculate nucleus, which in turn receives afferents from retinal ganglion cells. It is the first cortical location that visual information reaches during vision processing.

Structure: Retino-Geniculo-Cortical Tract

It is no secret that many processes in life can be understood through a careful examination of their structure. If you want to know how a car engine works, one approach would be to begin by examining the underlying parts and how they interact with one another. This approach is based on the idea that function and form influence each other. This notion is thought to hold true of the brain as well. Therefore, to begin to discuss the function of the human visual system, it becomes critical to have a fundamental understanding of the underlying anatomy.

To make better sense of the anatomy, an awareness of the terminology related to the visual system must be appreciated. The retina is the portion of the eyeball which contains cells from the central nervous system. It is found at the back of the eye and receives input from the external world in the form of light. It can be grossly separated into the peripheral retina and the macular retina. The peripheral retina, unsurprisingly, makes up our “peripheral” vision. The macula makes up the center of our visual field. A shallow depression in our macula, termed the fovea, makes up the part of the retina with the highest visual acuity. When we speak of our visual field, we often divide it into quadrants, such that we have an upper outer, upper inner, lower outer, and lower inner quadrant with each eye. Due to the location and structure of the eye, and concave structure of the retina, our retina receives information from the visual field that is upside down and backward of its location in the retina. For example, the inferior temporal portion of our retina receives light input from the upper inner portion of our visual field. Similarly, the superior nasal retina receives input from the lower outer portion of our visual field, and so on.

Visual information begins its neurological journey in the retina. Information in the form of photons interacts with first order neurons called

cones and rods, is then converted to chemical and electrical signals, and is transferred to second order neurons called bipolar cells. The information is then modulated by interneurons (amacrine and horizontal cells) and is passed along to ganglion cells. There are two major types of ganglion cells: alpha (or M cells or magnocellular cells) mainly in the periphery, associated with rods and beta (or P or parvocellular cells) mainly in the fovea, associated with cones. A third type of ganglion cell (melanopsin-containing cells), making up a minority of ganglion cells, plays a role in circadian rhythm with projections to the suprachiasmatic nucleus of the hypothalamus which in turn projects to the pineal gland. The M cells and P cells then project to the lateral geniculate nucleus (LGN), where the cell bodies of third order neurons lie.

The journey of these ganglion cell axons is impressively organized as they maintain retinotopographic organization throughout their course. In addition, optic nerve fibers (containing the axons of the ganglion cells) arising from the nasal portion of the retina cross at the optic chiasm to join the contralateral temporal fibers, thus joining fibers from alike visual fields. These joined fibers are now called the optic tract and are destined for the LGN, superior colliculus, pretectal area, SCN of the hypothalamus, and the reticular formation. The LGN is a region located in the dorsal portion of the thalamus. The LGN is constructed of 6 distinct layers from ventral to dorsal. The first two make up the magnocellular layer which receives input from the M cells and thus mainly information from the periphery of the visual field. Layers 3–6 make up the parvocellular layer and receive input from the P cells, or the fovea of the retina.

In what is referred to as the optic radiation, fibers from the LGN making up the geniculocalcarine tract radiate posterolaterally along the lateral ventricles toward the primary visual cortex, again maintaining retinotopic organization. The visual cortex, located at the most posterior aspect of the cerebrum, is divided by a nearly horizontal fissure called the calcarine fissure, which separates the cortex into a superior and inferior portion. The geniculocalcarine tract contains an

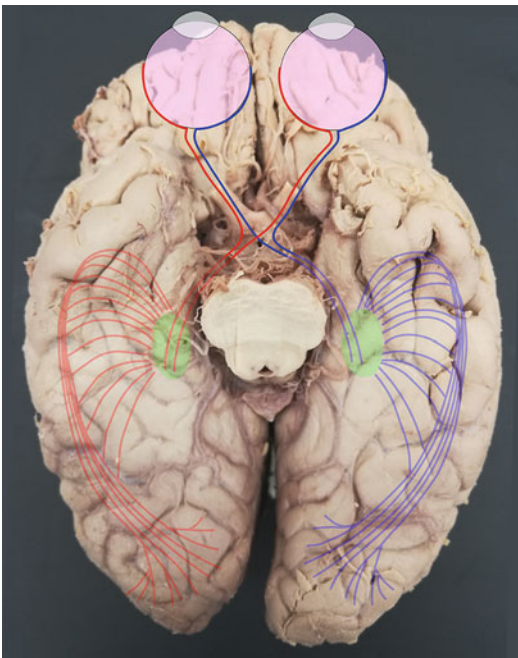
upper division with fibers corresponding to the superior retinal quadrants, lower division (Meyer's loop) with fibers corresponding to inferior retinal quadrants, and an intermediate division with fibers corresponding to the macular retina. The upper division relays information to the superior bank of the calcarine fissure and the lower to the inferior bank of the calcarine fissure. The intermediate division projects to the most posterior aspect of the visual cortex and straddles both inferior and superior portions of the calcarine fissure. Through this convoluted pathway from the eye to the back of the brain, visual information has arrived at the primary visual cortex, also called V1, primary visual cortex, or Brodmann's area 17 (Fig. 1). Straddling the calcarine fissure, V1 is located in the midline of the occipital lobes

on either side of the longitudinal fissure. It is here, at the primary visual cortex, that information from both eyes converges onto a single cell for the first time. From here, visual information is further processed through the visual association cortex, or "extrastriate cortex" (Patestas and Gartner 2016).

Function

Visual Cortical Streams of Processing Two streams are often mentioned throughout the literature: the dorsal stream (a.k.a. the "where" stream or magnocellular pathway) and the ventral stream (a.k.a. the "what" stream or parvocellular pathway). The dorsal stream is thought to process information related to movement and spatial localization, while the ventral stream is thought to be involved in object recognition, color processing, and texture/shape identification. Counter-intuitively, the dorsal stream is roughly associated with the LGN M cells (located in the ventral LGN), whereas the ventral stream is roughly associated with the LGN P cells (located in the dorsal LGN).

From V1, the dorsal stream consists of V2, V3, V5/hMT, and V7a. Thus, information flows from the posterior occipital lobe (V1, V2, V3) to the medial temporal area (V5/hMT) and then dorsally to the posterior parietal cortex (7a) in the dorsal pathway. In the ventral stream, information flows again from the posterior occipital lobe (V1, V2) to the more lateral V4 region and ultimately to the inferior temporal cortex. Specific modalities making up the ventral stream include areas involved in the perception of color (V4/V8) located in the ventral occipitotemporal cortex and areas involved in object recognition such as the lateral occipital complex which is further divided into the lateral occipital and posterior fusiform, and ventral occipitotemporal regions, consisting of the fusiform face area and parahippocampal place area (Grill-Spector and Malach 2004). Additionally, studies conducted regarding object handling suggest that certain dorsal foci appear to be activated by object and shape information (Culham et al. 2003; Goodale et al. 1991). We now know that there is some cross-talk between the two streams. Much of what is understood about the



Human Visual Neurobiology, Fig. 1 An overview of the human retino-geniculo-cortical tract. Visual information is carried in a rostro-caudal direction from the retina to the visual cortex. The optic nerves cross in the optic chiasma and then continue caudally as the optic tracts towards the diencephalon. Fibers from the LGN radiate in a rostro-caudal direction towards the primary visual cortex. The visual cortex, located at the most caudal aspect of the cerebrum, is divided by a nearly horizontal fissure called the calcarine fissure, which separates the cortex into a superior and inferior portion

anatomy of the human visual cortex has been discovered using fMRI techniques in addition to the investigation of the macaque visual cortex. As we will see, the complexity of the extrastriate cortex is bewildering and relatively well studied but not yet fully understood. It is here that we can begin to digest the many elements that make up human vision.

Dorsal Stream Functions The famous experiments conducted by Hubel and Wiesel in a cat model demonstrated that particular receptive fields in the visual cortex were oriented horizontally, vertically, or obliquely and that certain areas demonstrated a preference for movement and even direction of movement as evidenced by strength of their firing response. These experiments paved the way for our current understanding of how orientation and movement are processed.

Before Hubel and Wiesel's experiments came to light, the very important work of Kuffler outlined the receptive fields of retinal ganglion cells. In his work, he demonstrated that ganglion cells responded to circular spots of light or darkness at a specific point on the retina. These are now known as "on-center" and "off-center" ganglion cells, respectively. When an on-center cell is stimulated by light, it increases the rate of action potential firing. In contrast, when an off-center cell is stimulated by light, it decreases the rate of action potential firing. However, if the light stimulus is removed, the off-center cell will subsequently increase its activity. Furthermore, he showed that the circumferential area immediately surrounding the receptive field is antagonistic toward the center receptive field's response when stimulated. For example, if the periphery of an on-center cell is stimulated, it has an antagonistic effect which reduces the firing of the on-center cell. As discussed in the anatomy section, this information is then relayed to and modulated at the LGN and ultimately arrives at the primary visual cortex (Kuffler 1953; Purves et al. 2012).

The incoming visual information is thought to undergo hierarchical processing, such that as information moves further through the dorsal stream, the complexity of a stimulus that a cell

will respond to increases. For example, the stationary "point" stimulus which excites an on-center cell in the retina is a much simpler stimulus than the types we will find higher up in the processing stream. However, the varying types of "simple" stimuli are thought to be combined to build the more complex stimuli which start to resemble reality the further into the extrastriate cortex we get.

Hubel and Wiesel characterized cells in different portions of the dorsal stream (V1, V2, and V3) as simple or complex. The most basic of these cells are located in the primary visual cortex (V1) and are called simple cells. Simple cells were found to be selective to orientation and position. In Hubel's experiments, these cells were found to fire strongest when a linear stimulus (such as a bar or edge of light or dark) was at an optimal orientation and remained quiet when the stimulus was oriented 90° to the preferred orientation. Similarly, strength of response was found to depend on position within the visual field. Complex cells, located in V1 and V2, were also found to be selective to orientation. In addition, motion and direction of the motion were found to be important for response optimization. A stimulus moving across the receptive field of a complex cell with specific orientation and directionality produced a sustained response (Hubel and Wiesel 1959; Purves et al. 2012). In humans, separate studies showed that hMT displays direction-selectivity and may not be confined to simple translational movements (Huk et al. 2001; Tootell et al. 1995; Morrone et al. 2000). Interestingly, studies also demonstrated that tracking of motion seems to increase the response of hMT neurons (Buckley et al. 1998; Culham et al. 1998). Furthermore, evidence suggests that a region lateral and anterior to hMT is involved in the perception of biological motion (Grossman et al. 2000). Clearly, the further into the dorsal stream we get, the more complex the information we are dealing with becomes.

As we can begin to see, the synthesis of more complex aspects of motion appears to arise from the summation of information from earlier visual areas. From a collection of on-center or off-center cells, we can construct edges of a specific

orientation. This orientation excites simple cells in V1. A collection of these simple cells with alike orientation at nearby retinotopographic locations forms a translational plane. A stimulus with appropriate orientation that is moving in an appropriate direction through this translational plane excites a complex cell. This type of hierarchical processing is a theme that is not limited to motion processing but one that is thought to occur throughout the visual cortex. As we will see, a similar story unfolds during object recognition.

Ventral Stream Functions

Spatial Frequency The experiments by Hubel and Wiesel demonstrated that primary visual cortical neurons responded to edges and lines, but later research by De Valois demonstrated that these neurons respond even better to sine-wave gratings. A sine-wave grating appears as blurry long parallel rectangles that alternate in light-dark brightness following a sine-wave function. A sine-wave grating is quantified according to its spatial frequency. For a sine-wave grating, spatial frequency is its alternating change in light-dark brightness expressed as cycles per degree of visual angle. Visual angle is the angle measured where two lines drawn from an object meet at the retinal surface. Primary visual cortical neurons react most strongly when a sine-wave grating with a specific spatial frequency is presented in a certain area of the visual field (Carlson 2014; De Valois et al. 1978).

High and low spatial frequencies supply important information about an image. High spatial frequencies are found in smaller sized objects, the features inside larger objects, and the distinct edges of larger objects. High spatial frequency corresponds to abrupt spatial changes in the image such as edges and gives fine detail and configural information. A picture lacking in high spatial frequency will be perceived as blurry and unfocused. Low spatial frequencies correspond to global information about shape such as general orientation and proportions. A picture lacking in low spatial frequency will only have fine details and not general features. Low spatial frequency has been found to be prioritized in the detection of

faces. For these reasons, low spatial frequencies are more necessary for human vision. Low spatial frequency information is supplied by the evolutionarily more ancient magnocellular pathway, of which axons from the LGN terminate in cortical sublayer 4Ca (Carlson 2014; De Valois and De Valois 1988; Awasthi et al. 2011; Bar 2004).

Color Detection

Retinal ganglion cells that are color selective relay signals to the parvocellular and koniocellular layers of the LGN. From there, axons are sent to neurons inside cytochrome oxidase blobs in the primary visual cortex for color analysis. Wong-Riley found these blobs using a stain for cytochrome oxidase, a mitochondrial enzyme that when found in high amounts signifies a cell with a high metabolic rate. Later experiments showed the existence of a polka-dot distribution consisting of dark columns present in layers 2 and 3 and less intense staining in layers 5 and 6 of the primary visual cortex. On cross-sectioning, these columns appeared oval and about 150×200 micrometers in size and separated by 0.5 mm intervals (Wong-Riley 1979).

Two pathways send color signals to the primary visual cortex from the LGN. The axons of projection neurons in the koniocellular and parvocellular layers of the LGN synapse onto specific sets of neurons in the primary visual cortex. The lower sublayer of 4C, called 4C β receives parvocellular input, whereas the superficial layers 2 and 3 receive koniocellular input in a patchy distribution. Experiments on monkeys demonstrated that lesioning the parvocellular layers causes impairment in visual acuity and color vision, indicating this system is used for detecting object shape, color, and size. The parvocellular pathway sends in signals from red (long-wavelength) and green (medium-wavelength) sensitive cones, and the koniocellular pathway sends in signals from blue (short-wavelength) sensitive cones. It is not fully understood why two separate pathways exist for color detection, although it is believed that the koniocellular pathway is evolutionarily more ancient (Purves 2019; Carlson 2014; Wong-Riley 1979; Horton and Hubel 1980; Humphrey and Hendrickson 1980;

Fitzpatrick et al. 1983; Livingstone and Hubel 1987; Hendry and Yoshioka 1994; Chatterjee and Callaway 2003).

The Function of the Organizational Aspects of the Visual Cortex

Retinal Disparity

Depth is important for determining object shape, surface segmentation, and detecting third dimensional aspects. It is perceived in more than one way and can be detected monocularly using cues such as brightness, perspective, occlusion, size, and movement. However, binocular vision allows for a clearer depth perception utilizing stereopsis. This becomes especially essential for controlling fine movements of the hands and fingers such as playing a violin. The majority of primary visual cortical neurons are binocular, meaning that they fire in response to stimuli arising from either the left or right eye. These cells, and most notably those found in a cortical layer receiving magnocellular pathway input, have firing patterns that play a part in depth perception. These binocular neurons fire most intensely when each retina detects an object in a slightly different part of the retina, meaning that they react to retinal disparity, that is, when an object forms an image on slightly different regions of the retina in each eye. This is how the brain forms stereopsis: the left and right retina detects the scenery in a slightly different perspective, and the retinal disparity points to differences in distance between the person and the object being seen (Carlson 2014; Poggio and Poggio 1984).

Binocular integration in the visual system starts in the primary visual cortex at the point where single neurons receive input from both eyes. The amount of input from both eyes differs among neurons in the primary visual cortex; this property is called ocular dominance. When objects are at different distances from the retinas, these binocular neurons will calculate depth based on retinal disparity. If an object is exactly in the plane of fixation, an image is formed at corresponding retinal positions bilaterally. Any images behind the plane of fixation or in front of the plane of fixation will form an image on the two retinas at slightly different areas. Single neurons in the primary visual cortex are selective for a

tight range of these types of retinal disparities. Neurons selective for objects directly in the plane of fixation are referred to as tuned excitatory and tuned inhibitory cells. Neurons selective for objects behind the plane of fixation are called far cells, and neurons in front of the plane of fixation are called near cells. When the depths of more than one object need to be calculated, the retinas must connect all images to perform a global disparity calculation. When the calculation of depth is known for one part of an image, this data is utilized for other parts of the image where information is missing for calculating depth, in a process called disparity capture. By doing so, the calculation of one region of the image will affect calculations for other parts (Kandel et al. 2013).

Modular Organization of the Primary Visual Cortex

The brain is separated into modules, with populations of neurons per module ranging from one-hundred thousand to several million. Modules are heavily interconnected, sending, and receiving signals from one another while performing complex operations. The primary visual cortex is arranged in a visuotopic order such that the visual field is represented along the cortical surface. Every point in the visual field needs to be detected by columns of neurons with varying functional properties in the cortex. From the cortical surface to the underlying white matter, neurons are grouped together tightly into columns which share comparable functional properties including orientation selectivity, spatial frequency, and ocular dominance. Moving along the cortical surface, the change in visuotopic position of receptive fields is slow, yet the change in columns is extremely fast. Any specific point in the visual field is processed by a single modular unit of cortex that analyzes object orientation, direction, color, and depth. A single module contains every possible column and cell-type needed to analyze a single point in the visual field, and this module is repeated hundreds of times to span the entire visual field.

The primary visual cortex is separated into about 2,500 modules, each with around 150,000 cells, nearly 0.5×0.7 mm in size, and containing all 6 layers of cortex. A single module includes a

single orientation hypercolumn: a full 360-degree cycle of orientation columns; a single pair of left and right eye ocular dominance columns; along with a pair of blobs and corresponding interblob regions. A microelectrode placed straight down into an interblob area of the primary visual cortex will demonstrate that every orientation selective cell will fire in response to edges of the same orientation. Neurons in the blobs detect color and low spatial frequencies, and interblob regions demonstrate detection of movement, orientation, retinal disparity, and spatial frequency; but not to color. Blob neurons signal in response to low spatial frequencies and minor variations in brightness. Within the interblob region, spatial frequency detection increases as a function of distance from the blob center region. The farther away from the blob, the higher the spatial frequencies that these neurons detect.

Each module is divided into two halves, each receiving connection from only one eye through the terminations of LGN axons in the ocular dominance columns of layer 4, which are monocular. Axons from layer 4 neurons in neighboring columns form connections with single neurons in all other layers. Cortical layers located directly above and below the center zone of the ocular dominance columns in layer 4 respond to only one eye, whereas at the vertical zone separating the module, neurons recorded from the surface straight down respond equally well to either eye. In-between these zones, areas tangentially recorded along superficial layers show a continuous and gradual change in ocular dominance: from total domination of one eye to equal input from both eyes. Recordings from the surface straight downward demonstrate that neurons have equivalent ocular dominance, except in layer IV which is entirely monocular.

The cortical arrangement into columns decreases the distance necessary for neurons with comparable properties to signal each other and permits them to share signals from separate pathways that relay data regarding specific characteristics of vision. This allows for more efficient use of brain volume and raises calculation speeds. By grouping cells into columns sharing similar properties, the brain can decrease the

number of cells necessary for calculating different characteristics of an image (Carlson 2014; Purves 2019; Kandel et al. 2013; Livingstone and Hubel 1984; Born and Tootell 1991; Edwards et al. 1995).

Evolution of the Human Visual Brain

Visual ability has played a driving role in primate evolution (Cartmill 2012; Barton 2004). Humans share with closely related primate's visual system specializations in foveal vision, visual acuity, binocularity, and trichromatic color vision that have suggested to be related to brain features. Haplorrhine (but probably not strepsirrhine,) primates possess a retinal fovea which has a higher cortical magnification factor (Ross 2004). Primates' high visual acuity has been related to an increased visual surface area, with more neurons (Srinivasan et al. 2015). Neuron density is 2.5 times higher in primate primary visual cortex than in other cortical regions and in other species (Rockel et al. 1980). About half (52%) of the surface area of the cerebral cortex in macaques is primarily visual in function – although human visual cortex is absolutely larger, the proportion is smaller (27%) due to more multimodal association cortex (Van Essen 2004). Thus, the evolution of vision has an important impact on brain size evolution and is linked to the large brain size of primates (Barton 2004). In primates, visual areas are more numerous; this impacts the network structure of the cerebral cortex, with fewer long-range and cross-sensory connections and more short-range connections between visual areas (Meredith and Lomber 2017; Krubitzer 2009; Kaas 1989). The binocular visual field overlap is enlarged in primates, which have relatively convergent eyes (Heesy 2004).

Macaque monkeys (e.g., *Macaca fascicularis* and *Macaca mulatta*) are typically used as models for human vision in research. However, human and macaques share a most recent common ancestor with humans 25 million years ago and it is important to consider that the visual system of humans could show further specializations (Preuss 2004). Some apparent similarities shared between humans and macaque model species – for example, similarities in the lamination of M and

P cells in the LGN – could potentially be due to convergent evolution (de Sousa et al. 2013). Functional neuroimaging in human and macaques has revealed differences in the organization of higher-order visual areas, compared to more similar early visual areas (Orban et al. 2004).

Yet even subcortical structures and early visual areas show species-specific structural variation among *catarrhines* (humans, apes, and catarrhine monkeys). Compared to monkeys, *hominoids* (humans and great apes) show a reduction in a direct parvocellular-geniculate afferent to primary visual cortex layer 4A; this layer is further derived in humans who show a unique mesh-like organization of presumed magnocellular-related cells (Preuss et al. 1999). More research is needed to link specializations of human visual brain structure to cognitive function. Recent work has suggested ecologically relevant visual processing differences between human and chimpanzees such as in shape from shading (Tomonaga 1998) and the face inversion effect (Kret and Tomonaga 2016).

Humans seem to have among the best visual ability of any animal – tied for highest mammalian visual acuity with chimpanzees – and this relates to our ability to process other complex sensory information as well (Heffner and Heffner 1992). The neural demands of visual processing could have led brain features (de Sousa and Proulx 2014) that even in vision's absence relate to high level cognitive functions such as language (Pascual-Leone and Hamilton 2001).

Conclusion

Human visual neuroscience has revealed much about how the eye and the brain work together to process visual information about the environment. It has, more generally, made important revelations about the relationship of brain structure to function. Research on model organisms has revealed that visual neurons respond to specific features in the environment and work together to map features in the visual field. The visual system is a

well-studied model of how sensory systems enable organisms to interact with their environment. This sensory system is particularly important in humans which show specializations in it.

Cross-References

- [Evolution](#)
- [Neuroscience](#)
- [Primates](#)
- [Retina, The](#)
- [Vision](#)

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Human-Dog Symbiosis

- [Convergent Evolution of Dog and Human Social Cognition](#)

Humans

- [Primate Menopause](#)

Humans as a Social Species

- [Humans as Social Primates](#)

Humans as Social Animals

- [Humans as Social Primates](#)

Humans as Social Primates

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Synonyms

[Humans as a social species](#); [Humans as social animals](#)

Definition

Human beings are typically characterized as social primates, meaning they live in structured social groups, they communicate and interact with each other, and coordinate their activities around their conspecifics – much like other social primates, such as chimpanzees, bonobos, and gorillas.

Introduction

Forming social ties and living in social groups are of the most fundamental behavioral characteristics of human beings. Humans are frequently referred to as *social animals* to reflect this attribute (Aronson 2018). Living in social groups may have increased the chances of survival and reproduction of our prehistoric ancestors, via facilitating protection from the elements of nature and predators, finding resources (e.g., food, shelter, mates), and caring for offspring, and hence may have been selected for throughout our evolutionary history. The fact that our closest primate relatives, the great apes, also display affiliative behaviors (e.g., group living, social grooming, pair bonds), offer evidence for this conjecture. In the following sections, first the main characteristic of being a social species, cooperation, will be discussed, then different social ties human beings form throughout their life span will be elaborated, and

finally the neurobiological processes underlying human sociality will be briefly deliberated.

Cooperation

Living together in coordinated groups is one of the main defining characteristics of being a social animal. It necessitates a well-developed social cognitive skillset to ensure cooperation. Cooperation requires a complex cascade of mental tasks: The individual needs to be able to recognize other people's separate selves, understand their mental states and intentions, monitor their actual behaviors, keep track of past interactions, and detect deceit. Moreover, they need to calculate the costs and potential benefits of engaging in a cooperative act and restraint own behavior should they decide to cooperate. All these require tremendous cognitive capacity, and reaching this capability has been one of the fundamental challenges for human beings in evolving as a social species. Social primates, including human beings, have overcome this challenge by evolving unusually large brains, which is evident in the correlation between the sizes of social groups and the neocortex, also known as *the social brain hypothesis* (Dunbar 1998). Complex cognitive mechanisms that characterize human beings (e.g., culture, language, theory of mind, sense of morality) are argued to have evolved because they enable the social animal to carry out large-scale cooperation in complex social groups (Tomasello 2014).

Although highly adaptive at the group level, via the optimization of resource utilization and environmental risk management, cooperation is very costly for the individual, both due to the cognitive load mentioned above and in terms of tangible resources, so human beings have evolved to cooperate with conspecifics who are reciprocal in cooperation – who are more likely to be as such when they are among one's own group (Happé et al. 2017). As a result, cooperation is more common within social groups as compared to different social groups. Forming affiliative ties with one's group members serves the function of differentiating in-group from the out-group and hence makes the cooperation decisions more

efficient. Such in-group cooperation is largely automatic and guided by neurochemical systems (Crespi 2016), which makes adaptive sense as this reduces the cost of the taxing cooperate/not cooperate decision and hence allows to maintain interactions with several individuals.

Social Ties Throughout the Life Span

Human beings form many different social ties during their life span. Arguably, the most crucial of these ties is formed in early life with caregivers. The human infant is born altricial, meaning they require extensive care for a long period of time to have a chance at survival. Bowlby (1969/1982), in his seminal attachment theory, argued that the early problem of survival for the immature human infant is solved by the *attachment behavioral system*, an evolutionarily adaptive regulatory device which adjusts proximity to supportive others, i.e., *attachment figures*. This system protects the infant from physical and psychological threats and hence ensures the endurance and procreation of the species. The attachment bond formed with caregivers not only protects the infant from threats, but also teaches them how to affiliate with other people in the world and sets the stage for later social ties.

When infants grow into adults, the same attachment system ensures the formation and sustenance of romantic relationships (i.e., pair bonds) (Hazan and Shaver 1987). Human beings are predominantly socially (but not necessarily sexually) monogamous, meaning they live together with one partner and raise their offspring together. Pair bonds not only increase reproductive success by optimizing fertilization and making childrearing more efficient, but they also have major benefits for the partners. Being in a satisfying romantic relationship has been associated with many positive outcomes, such as happiness and subjective well-being (e.g., Easterlin 2003), and health and longevity (e.g., Robles et al. 2014).

In addition to the social ties in these close relationships, people spend the majority of their life socializing with friends, acquaintances, colleagues, and other in-group members virtually in all cultures. Amounting evidence suggests that

forming and maintaining affiliative ties and feeling belongingness are among the most pervasive psychological needs we have (see Baumeister and Leary 1995).

The Neurobiology of Human Sociality

In both humans and other social species (e.g., prairie voles, titi monkeys), the neuroendocrinological systems are hardwired to form and maintain affiliative ties. Several areas of the brain (e.g., the olfactory system, amygdala, lateral septum) and numerous hormones (e.g., oxytocin, vasopressin) have been linked with social behaviors (see Carter and Keverne (2002) for a review). These brain regions and hormones have crucial roles in motivating the organism to engage in social contact, perform sexual behavior, form pair bonds, care for offspring, cooperate, and regulate pain and stress. Endogenous opioids, which are involved in the brain's reward system, have also been identified to be intricately related to affiliation and bonding processes. This link provides a possible explanation as to how social ties have been experienced as rewarding and hence continued to be carried out. The behavioral or neurobiological responses humans and other social animals give in face of the presence or absence of the conspecifics they form ties with (e.g., physical touch, social grooming, separation distress, increased HPA activation) provide further evidence for the role of social ties in the psychophysiological system.

Conclusion

Living in social groups is a defining feature of human beings. Sharing the burden of ensuring protection, finding resources, and raising offsprings has been evolutionarily advantageous for humans, which led to being a social species. Our behavioral and neurobiological systems are hardwired to ensure we form, maintain, and grow our affiliative ties. Being part of social groups is indeed part of who we are: It increases our chances of survival and reproductive fitness, protects us against stress, and even gives meaning to our existence.

Cross-References

- [Cooperation and Social Cognition](#)
- [Evolution of Human Sociality, The](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Group Living](#)
- [Living in Groups](#)
- [Primates](#)
- [Social Development in Nonhuman Primates](#)
- [Tend and Befriend Adaptations](#)

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Humans Crawl: Species Atypical Movement

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Synonyms

Gait; Human locomotion

Definitions

Crawling is a form of species atypical movement for humans.

Introduction

Striding, bipedal walking, and endurance running are the hallmark modes of human locomotion, yet humans locomote in a number of different ways. As young infants we start with a system that is more plastic and flexible than it seems, given the relative uniformity of adult forms of locomotion like human bipedalism. This plasticity is evident in the surprising number of different pathways to upright walking (Largo et al. 1985). In this piece we contrast the divergent pathways that humans and their relatively close neighbor, the chimpanzee, take in the ontogeny of adult forms of movement.

Factors Influencing the Ontogeny of Gait

The ontogeny of animal movement is constrained by factors both within and external to the organisms that both limit certain types of actions and facilitate others. These can be described as organismic constraints which are internal to the animal, environmental constraints that are external to the animal and that are relatively consistent across developmental time periods, and task constraints

that pertain to any specific problem that animal is confronted with at a particular time period (Rosengren et al. 2003). At any one time point, these three different types of constraints interact to produce a particular action pattern or behavior.

A change in one constraint can have cascading influence on the emergence of different action patterns. For example, encouragement by health care professionals to have parents have their infants sleep on their backs to prevent sudden infant death syndrome (SIDS: Skadberg et al. 1998) had the unexpected consequence of delaying the onset of motor milestones such as creeping and crawling, in part because supine sleepers do not gain the same experience using their arm and torso muscles necessary for creeping and crawling as prone sleepers (Davis et al. 1998).

For the developing animal, organismic constraints for movement include the timing and pattern of growth, the organization and maturity of the musculoskeletal system, and the motivation to move from one place to another to gain food or obtain shelter. Environmental constraints include the fact that animals on earth are bound by gravity and the structure and characteristics of the surfaces that one can act on (e.g., a relatively flat horizontal ground or vertically rising trees). Task constraints include whether the animal is interested in seeking food, comfort, or safety. Although traditional models of the development of locomotion emphasized that maturation was the main driving force in the ontogeny of human gait, more current approaches emphasize the importance of the developing infants' active exploration of the interaction of these different types of constraints (Rosengren et al. 2003; Thelen 1995).

Gait Ontogeny in Humans

Human infants enter the world with a relatively immature action system that provides ample opportunity to explore the interaction of constraints and in doing so develop a number of species atypical movement patterns. Over the first year of life they acquire the physical strength and coordination to effectively move through the environment. But the ways individual infants

accomplish the act of locomotion is determined by their motivation, physical layout of their home (e.g., does it contain carpeted surfaces or hard tile floors, flat surfaces or stairs), and the goals of their caregivers in promoting exploration or optimizing safety. For this reason, young infants exhibit a wide range of atypical locomotor behaviors to get from one place to another including rolling, shuffling on their bottom, crawling on stomach, crawling on hands and knees, and crawling on hands and feet, prior to the acquisition of upright walking (Largo et al. 1985). The fact that upright gait is relatively uniform as the species-typical pattern of movement suggests that over the course of evolution the different types of constraints have led to a small number (e.g., walking and running) of highly efficient and effective patterns of movement.

Gait Ontogeny in Chimpanzees

For chimpanzees, infants cling to their mothers' fur for safety, transportation, and feeding. These behaviors lead the infants to develop forelimb-dominated, suspensory grasping abilities. Like humans, infant chimpanzees are more variable in their locomotor modes than juveniles or adults, in part because their size permits it and in part because of differences in parenting styles. As offspring size increases (~ 3 years), mothers carry the offspring less frequently, and they transition to quadrupedal knuckle-walking. This species-typical behavior does not become the dominant mode of locomotion until after 5 years, when the chimpanzees are completely independent of their mothers (Sarringhaus et al. 2014).

Conclusion

This cross-species comparison provides evidence that the same three sets of constraints apply to different species. The transition to species-typical posture and locomotion will depend on organismic-, environmental-, and task-specific constraints. The fact that more limited forms of species-typical gait are found in adults suggests

that these constraints interact over the course of development to select for efficient and effective patterns of movement.

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Humans: Between-Group Conflicts

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Synonyms

Between-group Killing; Feuding; Intergroup Conflict; Intergroup Killing; Warfare; War

Definition

Conflict among human groups or populations, usually of different cultural backgrounds, involves violent interactions. The aggression usually leads to death of part of group members of both sides and to advantages (material or social) to surviving victors.

Introduction

The central aim of evolutionary approaches to the study of intergroup violence is to examine whether between-group violent conflicts and killings are in any way adaptive, and to investigate their evolutionary history. Lethal intergroup conflict among humans during the late Pleistocene and early Holocene is still a controversial subject, with little agreement on its extent (Bowles 2009). It is important to turn to prestate societies, as these are thought to typify the kinds of aggregations that humans belonged to for the great majority of human history. Their study facilitates our understanding of the contexts from which modern behaviors are derived and of those in which human universals had their evolutionary origins. A great deal of interest revolves around illuminating the frequency, intensity, and importance of the types of lethal intergroup killings in small-scale societies such as feuds, raids, massacres, treachery, and warfare. Different hypotheses have been proposed to explain the adaptive value of intergroup conflict, some involving individual-level selection and others group-level selection. Empirical evidences for these hypotheses are reviewed here.

Review

Despite scientific discussions, intergroup killings have been found to occur across a variety of human societies (Guilaine and Zammit 2008). Contrary to the claims of some perspectives, lethal violence between groups did not originate with nation-states. According to archeological data, intergroup killings were already committed by

small-scale societies before the emergence of states. Evidence supporting the occurrence of lethal violence in the past includes Paleolithic, Mesolithic, and Neolithic art in Italy, France, and Spain, as well as osteological evidence, settlement patterns, and weapons retrieved from prehistoric sites across Africa, Eurasia, and North America.

In human subsistence societies, death rates from intergroup aggression are reported to be higher compared to rates of death from intragroup aggression (Heider 1997). The underlying motives for between-group killings in small-scale societies include (Gat 2010): competition for subsistence resources and for mates; contests for prestige and status; retaliation after suffering raids and massacres; elimination of future rivals through pre-emptive attacks; clash of cosmovisions, ideologies, or accusations of supernatural wrongdoing (e.g., witchcraft); and security dilemmas (the actions of one community are misinterpreted as warmongering by another group). Lethal violence in subsistence societies of human hunter-gatherers and farmers occurs in similar average rates (and similar variability in the rates) when compared to those reported for chimpanzee societies. Estimates are considerably high: for instance, in seven subsistence farming societies for which data were compiled, median percentage of deaths accounted for by warfare was 28.5% for men and 6.1% for women (Keeley 1996). These figures are higher than those for hunter-gatherer societies or Western-industrialized societies, especially across recent decades of modern history, although several wars among Western forces in recent decades have resulted in extreme mortality rates that surpass even the upper bounds of war-related mortality estimates for farming societies (e.g., the War of the Triple Alliance between 1864 and 1870). In spite of interpopulational variance in frequency of warfare and mortality rates due to such conflicts, evidence for warfare exists for at least 90–95% of human societies (Keeley 1996), indicating it is a human universal.

A conceptual model for human evolution that has recently gained widespread popularity is the *Ecological Dominance* hypothesis, which claims that modern humans have so mastered the natural environment that the major contemporary sources

of selection are predominantly social. Although this model has much merit, and is related to the “social brain” hypothesis in primatology, it is possible that the case for human autonomy from natural selective pressures has been somewhat overstated. For example, climate change has recently been shown to exert severe selective pressures upon human populations over historical time (Zhang et al. 2007) – e.g., cold historical periods have been associated with elevated rates of intergroup conflict. In such cases, although the more proximal selective pressures behind intergroup conflict and killing might be social (e.g., conflicting views), the more distal selective pressures behind them might be natural (e.g., climate change and reduced resource availability). Game-theoretic models combined with updated information on archeological evidence on causes of death during the late Pleistocene and early Holocene, and with ethnographic and historical reports on hunter-gatherer populations suggest that parochial altruism (i.e., altruism geared toward those of the same group) and intergroup warfare have coevolved during these periods (Bowles 2009). Recent historical analyses in fact support this notion, for instance demonstrating that regions more frequently involved in intergroup warfare throughout Japanese history present higher levels of collectivism (as opposed to individualism or independence; Fernandes et al. 2015). It is important to stress, however, that resource competition is not the only driver of intergroup conflict, and in several human societies studied does not appear to predict warfare.

Comparative studies of hunter-gatherer societies and farmer societies indicate that, although common, material rewards possibly obtained in looting do not appear to be sufficient to explain motivations for individual engagement in group efforts toward warfare (Glowacki and Wrangham 2013). Moreover, capturing individuals who were defeated in battles (thus kept as slaves, for instance) is not a widespread in bands and tribes. On the contrary, when large raids (i.e., massacres) occur, most of the individuals in the attacked group are killed, thus not serving as a direct

socioeconomic boost to victors. Hence, acquiring captives is more of a common practice of chiefdoms or other sociopolitically complex societies. Nevertheless, in those cases where it has been observed, most of the time captives are reproductively active females. Increased status, honor, and prestige appear to be the most common individual benefit for warriors. Increased fertility, be it direct or in the long-term as a result of cumulative combat efforts and recognition, has been observed to be associated with warrior status, such as among the Yanomamo foraging horticulturalists of Venezuela and the Nyangatom nomadic pastoralists of East Africa.

Archeological information permits examining how widespread and prevalent warfare-related deaths were throughout historical periods of human societies. It is worth noting, however, that despite the benefits of relying on the archeological record, its imperfection imposes a limit to the type of inferences that can be drawn. A critical issue stems from the difficulty in distinguishing between violent deaths that resulted from intergroup killings and warfare or from interpersonal attacks within a community. Related to this is the difficulty in ascertaining the number of perpetrators responsible for any given case of violent death. Though these challenges are present, the following sites represent the strongest and most significant examples of likely intergroup warfare in the archeological record (Guilaine and Zammit 2008). The Jebel Sahaba cemetery 117 in Northern Sudan, with an estimated age of 14kya–12kya, offers one of the earliest evidences of seemingly intentional and effective killing between groups, and with a lethality of ~40%. Furthermore, it has been hypothesized that either an increase in population pressure or in ecological distress led to the escalation of competition for resources along the Nile valley, leading to the violence at Jebel Sahaba. Similarly, recent findings from Nataruk, Kenya, provide evidence for intergroup aggression against a band of hunter gatherers in the late Pleistocene–early Holocene (Lahr et al. 2016). However, different for Jebel Sahaba, the remains in Nataruk were not intentionally buried, but rather covered

by the sediment of the lagoon. In Europe many sites exhibit evidence of lethal conflict (Keeley 1996). Furthermore, across archeological sites around the world, the lethality of such encounters has been calculated to be close to that displayed by hunter-gatherers (~23%).

Another line of evidence for the widespread existence of aggressive between-group conflict in human societies comes from cross-cultural and ethnographic analyses. An examination of 11 Amazonian societies found a higher number of deaths as a consequence of between-group conflicts compared to within-group killings (Walker and Bailey 2013). For example, the Ache in Paraguay, as well as the Waorani (precontact) and the Jivaro from Ecuador, experienced considerable levels of lethality (average estimates are 56% for the Waorani, 43% for the Ache, and 42% for the Jivaro). In all 11 societies, males were more likely to be the victims in both between and within-group attacks. Comparatively, only 2% of the aggressors died during the attacks. The intense and escalated competition observed among lowland South American, coupled with (1) comparatively low levels of within-group killing, (2) high genetic differentiation among populations, and (3) small direct individual benefits to warriors, suggest that group selection may be an important force shaping warfare in these societies.

Conclusion

Different lines of study of between-group conflicts emphasize different evolutionary hypotheses for their origin and adaptive value, which involve individual and group selection approaches. However, neither account for the evidence completely, suggesting that complementary explanations employing the integrative multilevel selection theory, rather than relying on one mode of selection, are parsimonious. An adaptationist view of between-group conflict and killing cannot be applied to only a portion of human societies or a portion of human evolutionary history, as comparative ethnographic and archeological data

point to the ubiquity of this phenomenon despite cultural and temporal fluctuations in frequency, specific strategies employed, and death rates.

Cross-References

- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Evidence of Intentional Killing](#)
- [Evolutionary Theory and the Causes of War](#)
- [Evolved Psychology of Warfare](#)
- [Humans: Within-Group Conflicts](#)
- [Nonhuman Primates: Within-Group Conflicts](#)
- [Nonhuman Primates: Between-Group Conflicts](#)

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Humans: Within-Group Conflicts

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Synonyms

Aggression; Homicide; Intragroup conflict;
Intragroup killing, within-group killing; Murder

Definition

Aggressive conflict between individuals within a human group or culture, involving violent interactions, in certain circumstances leading to death of one party and fitness benefits to aggressors.

Introduction

Conflicts of interest and competition are a common feature of social life within groups. Many interindividual altercations lead to escalation of aggression and ultimately to killing. To have an evolutionary understanding of intragroup aggression and killing and assess evidences of adaptive functions, it is important to empirically examine (1) how ubiquitous these phenomena are among human cultures; (2) what social and biological variables explain rates of intragroup aggression and homicide, and if they do so in a predictable way in line with theory; and (3) what consequences these behaviors have.

Review

Registered homicide rates vary greatly among cultures and across time, although they it is a widespread phenomenon in humans (Knauff 1987). While in countries such as Iceland and Japan they are below 0.5 per 100,000 persons per year in recent years, they are more than 100 times more prevalent in the Virgin Islands and Honduras and up to 1000 more prevalent in certain prestate societies. Homicide rates are estimated to have reduced by approximately 20 times in Europe since medieval times (Spierenburg 2008). Some homicides are consequences of individual-level conflicts and altercations and another considerable part are due to gang violence and organized crime. It is important to consider the individual characteristics that may lead to adaptive benefits in lethal aggression, examining the sociodemographics of killing across different sectors of the human population.

Aggression and murder are observed to be a more prevalent behavioral feature of young, unmarried individuals and in those with few resources (such as low socioeconomic status, in modern industrialized societies), especially populations having high levels of inequality, as they have comparatively little to lose by engaging in high-risk behavior such as physical altercations over conflicts of interest (Daly and Wilson 1988). For individuals in such life contexts, expected returns from safe courses of action may be negligible, and relying on delayed benefits may be suboptimal considering socioecological uncertainty; as such, future discounting coupled with aggressive, coercive tactics and elimination of competition may be an adaptive response.

A common reported motive for aggressive and homicidal desires and actions is jealousy and distress over sexual competition (Buss 2000). Even though various behavioral strategies for intrasexual competition exist (involving, e.g., self-promotion, derogation of competitors, mate manipulation, and mate guarding) and various anatomical and physiological features can be argued to be adaptations for intrasexual competition (e.g., penile anatomical characteristics which may facilitate sperm displacement in the female reproductive tract, thus reducing other males'

chances of fertilization), aggressive behavior towards sexual competitors is hypothesized to be an effective strategy for competition. Young men are more likely than individuals in other demographic categories to act on such aggressive desires, suggesting that sexual selection has maximized male competitive prowess during young adulthood. Successfully confronting and attacking other males may not only fend off sexual competition and facilitate mate guarding, but may also permit mate poaching, and increasing status by demonstrating dominance, willingness to take risks, and physical formidability, thus increasing attractiveness.

As such, generally speaking, men are more prone to violence than women. There are various possible nonmutually exclusive explanations for this (Tanha et al. 2010): (1) men are sexually selected to be about one-fifth larger in total body size than women, conferring a greater capacity to deal damage, making violence a more effective means of obtaining goals; (2) men are sexually selected to be anatomically more able to sustain damage in combat (having more muscle and skeletal mass), lowering the costs of violent encounters; and (3) men are sexually selected to possess more cognitive and affective psychological adaptations for violent behavior, making them both more proficient in violent tactics and more predisposed to deploy them.

In a study of six human cultures, 91% of men and 84% of women admitted to having had at least one fantasy of murder (Buss 2000), figures which are more similar than is usually speculated. Although many studies have shown that the frequencies of violent *acts* are also roughly comparable for male aggressing against female intimate partners and female aggressing against male intimate partners, the rates at which these assaults translate into injuries are highly discrepant. This could be because men are more capable of dealing and sustaining damage in physical interpersonal altercations. Thus, such violent interactions more often lead to the death of the female than the male intimate partner. Many special theories have been proposed to explain sex differences in death following intimate partner violence as a result of male sexual jealousy or of other strategic conflicts of interests between the sexes. However, recent

evidence has indicated that the major predictors of between-sex and within-sex interpersonal aggression are virtually identical, rendering these special evolutionary theories somewhat unparsimonious (Figueredo et al. 2018).

It has also been found that in societies where critically important subsistence resources are difficult to defend (such as privately owned livestock) and populations densities are low (which is also typical of herding ecologies), leading to low efficacy of law enforcement (where state authority even exists in principle), a “Culture of Honor” evolves where individuals are selected to take justice into their own hands (Nisbett and Cohen 1996). This system depends upon the maintenance of individual reputations for retributive justice, as this is the only proactive way that vindictive behavior can deter raiding of resources by potential enemies. The maintenance of personal or family “Honor” therefore becomes the psychological mechanism for implementing the implicit threat of violent retribution, by the intentional cultivation of an informal public record for revenge.

The question of how comparable inter-individual aggression and killing are within human populations is also an important one from an evolutionary perspective. Homicide is in no way exclusive to only specific kinds of human cultures or to specific subsistence types (Knauff 1987). Homicide rates in bands and tribal societies exceed those of cities and states. Societies such as the Gebusi in New Guinea, and the Yanomamo in Venezuela, exhibited estimated homicide rates of 683 and 165.9 per 100,000 per year, respectively. These estimates are considerably higher when compared to 2.2 homicides per 100,000 per year in Japan, during 1951–1956 and to 15.1 in the city of Kent, during the thirteenth century. Similarly, societies traditionally considered to exhibit low levels of intragroup conflict such as the !Kung had annual homicide rates of 41.9 between 1920 and 1955. However, it has been contented that these cases may not adequately distinguish between intra- and intergroup killings despite the fact that they have been classified as homicide.

Circumstances and reasons for infanticide are strikingly comparable among human cultures (Daly and Wilson 1988). Although not observed in high rates, filicide is more commonly

committed by parents in life contexts that are not favorable to child rearing and in cases of children illness or deformations, both of which are situations prone to jeopardize parental fitness. Unrelated men most commonly commit infanticide if adulterous conception is suspected. Thus, although extremely distressing, killing of children appears to largely conform to theoretical expectations that would facilitate gene-copying replication, showing signs of adaptation.

The challenges of investigating the archaeological record for evidence of interpersonal violence are greatly reduced compared to those of studying intergroup conflict. Interpersonal violence can be inferred through the evidence of trauma, and injury on skeletal remains such as embedded lithic points, cut marks, and bone fractures (Walker 2001). Additionally, it can be established by a single case exhibiting this evidence. However, a considerable challenge in establishing interpersonal violence is encountered in attempting to correctly distinguish between accidental injury and intentional harm. Another nuance of importance is the recognition that many forms of behavior can be subsumed under the label of interpersonal violence, such as ritualized fighting as a form of conflict resolution, domestic violence, and social execution.

The sizeable quantity and relative completeness of known Neanderthal remains has facilitated analysis into the nature of their numerous injuries. In comparison to a sample of hospital records on fracture injuries, Neanderthals were found to exhibit considerably high incidences of trauma indicative of interindividual aggression (Walker 2001), although part are due to accidents and hunting-related injuries. Similarly, a smaller sample of early human skeletal remains from Africa and the Middle East seems to exhibit a consistent pattern of elevated rates of head trauma and injury (McCall and Shields 2008), like those observed in Neanderthals and modern human assault victims. Further archaeological evidence supports the occurrence of lethal violence during prehistory. For example, in sites such as Grimaldi (27kya-24kya) and San Teodoro (14kya) in Italy, embedded projectiles were found within the remains of juvenile victims.

Finally, ethnographic descriptions have also considered how societies respond after the occurrence of homicide, with responses ranging from indifference to a collective disapproval accompanied by punishment (Boehm 1999). As such, even though it seems that the existence of within-group killing is ubiquitous, societal attitudes toward it may vary somewhat, although they are in no culture positive, as they are in the case of between-group conflicts and warfare. Based on the type of social sanction, killers sometimes prefer to desert the group rather than facing any form of social sanction. Blood money, for example, is the financial restitution to the family of the victim and has been a common practice across prestate societies, such as in Norse cultures during the eighth to tenth centuries. It is worth noting, however, that under some circumstances, societies such as the Hadza, the Alaskan Eskimos, and the Kung resort to executions when other regulatory mechanisms are deemed ineffective. However, due to the risk of retaliation by either kin or allies of the offender, the decision of eliminating the offender is taken collectively, and under some conditions the execution is conducted by the kin of the attacker.

Conclusion

Although cross-cultural variations among modern human societies are observed in terms of homicide rates, sociodemographic predictors and attitudes towards within-group aggression and killing are less variable and more in line with expectations based on evolutionary theory. It is clear that such forms of social interactions are not a product of civilization and are not limited to only a part of human societies, and the evidence strongly supports the notion that within-group killing can be, although it need not always be, an adaptive strategy for competition for reproductive maximization, rather than a dysfunctional or exaggerated outcome of aggression.

Cross-References

- ▶ [Evidence of Intentional Killing](#)
- ▶ [Homicide](#)

- [Humans: Between-Group Conflicts](#)
- [Infanticide and Parenting](#)
- [Intrasexual Rivalry Among Men](#)
- [Nonhuman Primates: Between-Group Conflicts](#)
- [Same-Sex Homicide](#)
- [Sex Differences in Aggression](#)
- [Variability of Aggression](#)

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Humor

- [Components of Humor](#)
- [Daniel Dennett: A Review of His Evolutionary Work](#)
- [Sex Differences in Attractiveness of Humor](#)

Humor and Ostracism

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Synonyms

[Laughter](#); [Rejection](#); [Social exclusion](#)

Definition

Humor refers to “anything that people say or do that others perceive as funny and tends to make them laugh” (Martin and Ford 2018, p. 3).

Ostracism refers to the exclusion or rejection of persons.

Introduction

Most of us have been ostracized, ignored, or rejected at some point and experienced the hurtful consequences of being ostracized. Humor and laughter might have been one way of excluding us. This entry presents a brief definition of ostracism and its consequences, explains how humor and ostracism are related, and summarizes empirical research about the link between humor, laughter, and ostracism. It concludes with suggestions for future research in this area.

The Relation between Humor, Laughter, and Ostracism

When individuals are ostracized, they are ignored, excluded, or rejected (Williams 2007). Humor and laughter can be ways of ostracising individuals and groups. The term ostracism is based on the Greek word *ostraca*. This is a shard of clay that Athenians used to cast their vote on who should be banished from the community for ten years. Ostracism is pervasive – it can be observed in almost all social species, cultures, institutions, age groups,

and groups of different sizes (Williams 2007). In the literature, the terms “ostracism,” “social exclusion,” and “rejection” are not consistently differentiated and often used interchangeably.

In his review of ostracism research, Williams (2007) describes short-term and long-term consequences of ostracism. Even short episodes of ostracism threaten fundamental needs – namely belonging, self-esteem, control, and meaningful existence. Historically at least, ostracized individuals and groups suffered from negative consequences such as restricted access to resources leading to lower chances for survival and reproduction (Alexander 1986).

Two categories of consequences to these threats of fundamental needs can be distinguished (Williams 2007). Ostracized individuals either show more prosocial thoughts and behaviors (presumably to satisfy their relational needs), or more antisocial thoughts and behaviors (presumably to satisfy their efficacy/existence needs of control and recognition). Longer episodes of ostracism deplete coping resources and can lead to helplessness and depression. Thus, for the ostracized individual, ostracism can have very negative consequences. For the ostracizing group, though, ostracism can have positive consequences, because the group can eliminate unsuitable group members and maintain cohesion.

In his groundbreaking work on humor and ostracism, Alexander (1986) puts forth the basic assumption that humor developed as one form of ostracism. Humor “is a broad, multifaceted term that represents anything that people say or do that others perceive as funny and tends to make them laugh” (Martin and Ford 2018, p. 3). Alexander (1986) regards humor as a status-altering activity. This is corroborated by anecdotal evidence about a literal connection between humor and ostracism in some groups (Williams 1997). The Greenland Eskimos, for example, have joke telling contests to resolve conflicts. The person with the most laughs wins, and the one with the least laughs has to go to exile. Alexander (1986) postulates that ostracizing humor singles out a victim, whereas affiliative humor maintains group cohesion. This hypothesis is supported by detailed

analyses of lab group discussions (Robinson and Smith-Lovin 2001). Humorous comments referring to the self or another group member can undermine cohesion in groups; and humorous comments referring to the group as a whole or to outsiders can increase cohesion.

More recent empirical research has examined the link between humor and ostracism. Two experiments illustrate the negative effects of disparagement humor, e.g., sexist humor, for members of the target group (Ford et al. 2019). Disparagement humor occurs when denigration is disguised as harmless amusement or followed by “just a joke.” Individuals who were exposed to humor disparaging their political in-group perceived a social identity threat resulting in feelings of social exclusion (Ford et al. 2019).

Even observing someone else being ridiculed can affect an individual’s behavior. Janes and Olson (2000) labeled this effect “jeer pressure” and examined it in two experiments. Participants saw videotapes with a speaker either ridiculing another person’s physical and behavioral misfortunes, ridiculing his own misfortunes, or using humor without a specific target. Only those participants who saw how another person had been ridiculed were more conforming and more afraid of failing than participants in the other experimental conditions.

Being ostracized can also influence how individuals appreciate humor from others. More specifically, it can lead to ingratiation and finding even unfunny jokes funny (Sacco et al. 2018). In a lab experiment, participants were either ostracized or included in a virtual ball toss game. They then rated the funniness of target persons who were presented with funny or unfunny jokes. Excluded men, as compared to included men, rated female targets as funnier – even when their jokes were unfunny. No such effect was found for excluded women, though. Thus, humor appreciation may help to assure social affiliation after being ostracized.

Besides humor, laughter can also be perceived as a cue for ostracism (Lackner et al. 2018; Papousek et al. 2014). This is especially true for individuals with gelotophobia, which is a fear of getting laughed at. In an experiment, individuals

with and without gelotophobia heard two insulting statements and laughter while solving arithmetic problems. Laughter was presented as ambiguous and in a personally relevant context involving a social interaction. Thus, participants could perceive laughter as a cue of rejection but did not necessarily need to. Results showed that individuals with gelotophobia showed a “freezing-like” physiological response to laughter as indicated by heart rate deceleration. This reaction implies the perception of social rejection. Heart rates slowed down more and for longer in individuals with gelotophobia than without gelotophobia.

A follow-up study with only healthy individuals provided more support for the assumption that laughter as an ambiguous social signal can be interpreted as a signal for social rejection (Lackner et al. 2018). Regardless of whether participants had experienced social rejection or acceptance, all participants showed a “freezing-like” response after hearing laughter as indicated by sustained heart rate deceleration. This response was even prolonged for participants who had been accepted. The result might imply that participants felt being laughed at in an ambiguous social situation.

To summarize, research corroborates an association between humor and ostracism. However, because humor has a multitude of forms, not all humor is necessarily linked to ostracism. Benign forms of humor such as spontaneous conversational humor and unintentional humor (such as physical or linguistic “accidents”) are probably less closely linked with interindividual processes and outcomes.

Conclusion

Ostracism is pervasive and can have negative consequences. Empirical research supports the link between humor and ostracism that was first proposed by Alexander (1986). Disparagement humor can result in feelings of social exclusion (Ford et al. 2019), and observing someone else as the target of humor can result in conforming more strongly (Janes and Olson 2000) – potentially to

avoid social exclusion. Being ostracized leads to changes in humor appreciation, more specifically in finding unfunny jokes funny (Sacco et al. 2018). Finally, even laughter without humor can be perceived as a cue for ostracism (Lackner et al. 2018; Papousek et al. 2014).

Most research to date has focused on the target perspective, on short-term consequences, and has been experimental in nature – enabling researchers to make claims about cause and effect. To examine the complete picture about humor and ostracism, more research is needed on perpetrators of ostracism and the relationship between target and perpetrator, on long-term consequences, and in field studies.

Cross-References

- Bullying
- Components of Humor
- Evolution of Humor, The
- Factors that Influence Bullying
- Humor Production
- Stigmatization and Ostracism

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Humor as a Mental Fitness Indicator

► Humor as a Signal of Sexual Interest

Humor as a Signal of Sexual Interest

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Synonyms

Humor as a mental fitness indicator; Sexual selection and humor

Definition

Humor as sexually selected trait

Introduction

Sense of humor is a sexually attractive trait that is ranked as one of the most desired attributes in a prospective mate. However, men and women are interested in somewhat different qualities of humor when choosing a mate. Women place greater importance on choosing a mate that makes them laugh, while men are more interested in a woman who will laugh at their humor. Sexual selection theory can explain these disparate preferences, and there is abundant evidence to support the view that men and women evolved different psychological adaptations to appreciate and create humor.

Humor as a Sexually Selected Trait

Researchers generally agree that sense of humor is an adaptive trait, though there is no consensus on the nature of the adaptation or the mechanism that explains the evolution of humor (Greengross 2014). One evolutionary explanation that has generated much empirical work is based on sexual selection theory, and the view that humor serves as a mental fitness indicator (Miller 2000). The theory focuses on the asymmetry in reproductive costs for men and women (as with most other mammals), and the fact that women invest more time and energy to care for children. This makes women choosier than men when selecting a mate and drives men to try and advertise mate qualities that would make them more appealing to women. A great sense of humor is hypothesized to serve as such a reliable cue for a high-quality mate, an honest signal of intelligence that underlies genetic quality (low mutation load). This advertisement of high quality humor is similar to the extraverted and colorful peacock's tail, an ornament that functions as a fitness indicator to attract peahens. With humor, choosy women should be attuned to cues of high humor ability in men and be more attracted to men who manifest a great sense of humor, while men should try to allure women with their sense of humor.

Sex Differences in Humor Mate Preferences

Sense of humor is hypothesized to be a product of sexual selection and the differential life-histories of men and women that shaped distinct psychological adaptations. If sexual selection played a role in men's and women's humor mate preferences, we should expect to find sex differences in the way men and women enjoy and use humor. Specifically, women should express more interest in mating with a man who displays a great sense of humor, while men should be more attentive to cues showing that women appreciate their sense of humor, and put less emphasis on women's humor ability. Indeed, several large and cross-cultural studies support the notion that women considered humor to be a more important trait when choosing a mate than men did (e.g., Lippa 2007). Women show a special preference for a man with good humor production ability over a man that appreciated their humor for all relationship types (dating, one-night stand, short- and long-term relationships, and friendship), while men show an overall preference for a woman that would appreciate their humor over a woman that would make them laugh (especially for dating purposes) (Bressler et al. 2006). One study found that the use of humor by an attractive man increased his desirability as a mate for women, for both short- and long-term relationships (Lundy et al. 1998). Other studies that looked at the actual mate choices of men and women uncovered similar trends. When analyzing actual personal dating ads, where people have little incentive to lie about their preferences, researchers found that women desired a humorous partner much more than the opposite (e.g., Wilbur and Campbell 2011).

Sex Differences in Humor Production

Based on sexual selection theory and viewing humor as a fitness indicator, it was hypothesized that women's preference for a humorous mate would foster men to try and make women laugh. It is expected that funny men will be considered desirable as mates, while women's humor ability

should make little difference in how attractive men perceive them. A few lines of research support the view that men and women use and value humor differently. Studies that analyzed natural conversations between men and women in restaurants, shopping malls, sidewalks, and bars found that men were more likely than women to tell jokes and to initiate humor. Men's efforts to make women laugh are quite successful, as evident by the larger amount of laughter displayed by women in response to men, compared to how much men laugh in response to women. Women tend to laugh almost twice as much as men in mixed conversations, and their laughter is mostly in response to men talking (Provine 1993). The larger amount of laughter manifested by women is not just an arbitrary feature, but rather signifies women's sexual interest in men. Men who produce high quality humor are more physically attractive, while women's humor ability makes little difference in how attractive they are to men. In addition, the amount of laughter by women predicts both women's and men's interests in dating each other, while men's laughter does not evoke such interest in dating in either of the sexes (Grammer 1990).

Producing humor does not only make men more attractive to women but can also increase mating success. Individuals with higher humor production ability exhibit greater sexual access to partners of the opposite sex, as measured by actual sexual behaviors. Funny people report earlier age at first intercourse, larger number of sex partners, and having more sex in general, compared to the less funny individuals (Greengross and Miller 2011). These results were true for both men and women; however, the incentives for men to be funny are greater, as women are attracted to funny men but not the opposite. Men therefore are presumed to be more motivated than women to use humor, with the hope of mating with women who find their humor attractive. Further support for the benefits men gain from producing high quality humor comes from a slew of studies showing the men's humor production ability is greater, on average, than those of women, which makes it more likely for men to use humor to attract mates (Greengross and Miller 2011; Mickes et al. 2012).

The allure of having a great sense of humor seems to be true for both short-term and long-term mating. For example, women are more likely to give their phone number to a man, and also find him more attractive, when he is telling jokes to a friend, than to the friend who laughed at the jokes. In addition, spousal humorosity was more important for the marital satisfaction of the wives than the husbands in a cross-cultural study of five countries (Weisfeld et al. 2011).

Conclusion

Both men and women recognize the significance of humor in attracting mates, but they differ in the importance they place on producing and appreciating humor. Women emphasize finding a man who will make them laugh, while men are more interested in a woman that will appreciate their humor and laugh at their jokes. Ample evidence suggests that humor is a sexually dimorphic trait, where women are attracted to men with high humor abilities, while women's sense of humor does little to attract men. Men are more interested in women laughing at their jokes, and women's laughter signals their romantic interest in a man. Men's laughter does not affect how attracted women are to them. A great sense of humor is an attractive trait that translates into mating success, and this is true especially for men, as men are more motivated to create high quality humor and produce better humor than women, on average.

Cross-References

- [Evolution of Humor, The](#)
- [Humor](#)

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Humor Production

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Synonyms

[Comedy](#); [Comical](#); [Funny](#); [Hilarious](#); [Jokes](#); [Silly](#)

Definition

The production of humor leading to laughter and cheerfulness in others.

Introduction

Humor production and appreciation is a human universal and may have evolved as a species typical adaptation in humans (Greengross and Miller 2008). Across the vast majority of cultures, “a good sense of humor” in a partner is listed off among other seemingly more important traits like intelligence and attraction (Bressler et al. 2006). From an evolutionary perspective, we understand that typical attractive features are thought to be indicative of genetic fitness (i.e., lower mutation load) and thus are considered fitness indicators. Taking that idea a step farther, Miller (2001) explains that there are also *mental* fitness indicators – honest signals to genetic fitness via behavioral interactions with the environment: intelligence, creativity (including artistic and musical ability), and humor. In order for an individual to successfully deliver “good” humor, they must possess intelligence and creativity. Essentially effective humor production requires the coordination of a multitude of other (mental) traits that have underlying genetic quality.

Interestingly, though “a good sense of humor” is generally desired, a few research studies found that males were not necessarily attracted to women that were considered “funny.” In actuality, it seems the way in which males and females used the phrase “good sense of humor” differs. While men only emphasize the importance of a partner’s receptivity to humor, women emphasize both humor production and receptivity equally; the difference lies in the attraction to humor production (Bressler et al. 2006). Essentially, from this view, humor production is a mental fitness indicator and humor receptivity/appreciation signals sexual interest.

This interest though seems to be contingent on the way and *type* of humor being produced. Typically, when discussing humor, the first thing that comes to mind are jokes with a distinct set-up and punch lines – yet structured jokes only make up 10%–15% of laughter in typical social contexts

(Greengross and Miller 2008). Surprisingly, most laughter is derived from individuals reacting to spontaneous stimuli within the environment during informal conversations. An ability to react to these situations quickly and respond in a humorous manner hints to the recruitment of a number of processes (like intelligence, creativity, and an assessment of social context) to produce a response quickly. Because of the acuity of these jokes, replication does often not yield the same response due to the change in (social) context.

Humor Styles

From a mating relevant perspective, two specific types of humor forms stand out: self- and other-deprecating humor. Self-deprecating humor takes the form of “making fun of oneself” for perceived deficits in various traits like intelligence or physical attractiveness. Typically this type of humor is found in mating contexts: during courtship or in mated-pairs when a partner is trying to relieve tension after a disagreement (Greengross and Miller 2008). That being said, it can be considered somewhat risky due to the fact that it may actually draw attention to true flaws in an individual. Other-deprecating humor (often referred to as “dissing”) usually arises between potential rivals when the perceived deficits in another individual’s traits (i.e., intelligence, status, attractiveness) are essentially mocked. This form of humor may be taken as more of an insult than a joke, resulting in possible retaliation from the individual being “dissed.” Both forms of humor present potential risks if not delivered properly. The costly signaling theory explains that if an individual can successfully execute a “risky” or potentially costly behavior, they may be considered more attractive. Unsurprisingly, self-deprecating humor is considered more attractive than other-deprecating humor when used by high-status long-term mates.

Conclusion

Humor is an incredibly salient part of our lives: In order to be pulled off correctly, it must be

coordinated by many complex systems, yet it plays an incredibly important role in communicating with potential mates or partners. Our desire for humor (delivered appropriately) speaks to the complexity of our evolutionary mating systems.

Cross-References

- [Components of Humor](#)
- [Evolution of Humor, The](#)
- [Humor](#)
- [Humor and Ostracism](#)
- [Humor as a Signal of Sexual Interest](#)
- [Mating](#)
- [Neurology of Humor](#)
- [Sex Differences in Attractiveness of Humor](#)
- [Social Play](#)
- [Status and Reproductive Success](#)
- [Vocal Competition](#)
- [Why Humans Are Unique](#)
- [Words and Rules](#)

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Hunter

- [Predators](#)

Hunter-Gatherer Lifespan

- [Life Expectancy in Hunter-Gatherers](#)

Hunter-Gatherer Societies

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Synonyms

[Band societies](#); [Foragers](#)

Definition

Hunter-gatherer societies (HGS) are a type of society whose subsistence needs are met by gathering wild plant resources, hunting wild game, and fishing, without reliance on agriculture or domesticated animals except for dogs (Lee and Daly 1999).

Introduction

Throughout the Pleistocene, HGS spread to occupy nearly every habitable corner on the planet and locally adapted to a diverse array of ecosystems. For approximately 95% of the time span during which human evolution occurred, people lived in HGS, that is, from the emergence of *Homo sapiens* until approximately 10,000 years ago (Lee and Daly 1999). Therefore, there is potential to greatly inform our understanding of human evolution by studying the social dynamics and other patterns that characterize modern HGS since their contexts are the

most similar socioecological contexts which exist today to which humans have had the most time to adapt. Given this argument, it should be recognized that extant HGS are not exact models of Pleistocene HGS, but they are the best ethnographic models available and are therefore still useful. This entry will summarize important core aspects of HGS. Attention will be directed toward what could be conceptualized as modal patterns of HGS in the areas of social organization and cooperation (Hill et al. 2009, 2011; Mathew et al. 2013).

Hunter-gatherers live in social groups characterized by fission-fusion dynamics, i.e., people freely travel between subgroups in their daily foraging activities and between other bands seasonally or at much longer timescales (Lee and Daly 1999). Hunter-gatherer bands are therefore comprised of a flexible mix of individuals, with important social bonds among individuals within and between bands. Individuals co-residing in bands are connected by close and distant ties of genetic and affinal kinship, while some individuals in a band are not related at all. For example, among the !Kung and Ache, approximately 25% of individuals within a band are not related in any way (Hill et al. 2011). While, band membership is so flexible that individuals in HGS are likely to encounter many individuals during their lifetime. For the Hadza and Ache, data show that, on average, adults interact with more than 300 other same-sex adults during their lives (Hill et al. 2014).

HGS are broadly egalitarian (Lee and Daly 1999). There are no formally defined positions of social power to which individuals are ascribed by birth or with which they can act unilaterally against the wide interests of their peers (Boehm 1999). Despite this, status dynamics and leadership roles are still relevant but are muted in contrast to more complexly organized societies. Leadership is often context-specific and achieved by those who exhibit qualities that facilitate the coordinate and logistics of achieving group goals, such as knowledge, experience, intelligence, etc. (Glowacki and von Rueden 2015; Hooper et al. 2010). Achieving higher status is associated with higher

measures of biological fitness across small-scale societies independent of subsistence strategy, though the effect size of this association is weaker among humans than in primates generally (von Rueden and Jaeggi 2016). While material wealth stratification is minimal or nonexistent among most HGS, disparities are observed in access to important social relationships, i.e., relational wealth, which have a greater impact on a family's well-being than on material or embodied wealth (Smith et al. 2010). Additionally, relational wealth is moderately heritable across generations, as is the case for Ju/'hoansi *hxaro* partnerships, which importantly assists individuals in surviving particular periods of intensified need and finding marriage partners (Smith et al. 2010).

HGS are also extremely cooperative (Mathew et al. 2013). They universally and intensively share food. Mathew and colleagues summarize that detailed data from three HGS indicates that major pathways of net food transfers occur from husbands to wives, from parents to dependent offspring, and to currently breeding mates from nonreproductive adults (2013). These pathways being the major features of human family organization and reproduction; pair bonded males and females who cooperate in reproduction by dividing specialization in productive strategies by sex; intergenerational resource flows from older to younger; and cooperative relationships among kin and unrelated individuals to reduce daily food variance and provide other forms of childcare (Kaplan et al. 2007). HGS also notably coordinate production activities in varying instances of large-scale collective action, e.g., building game drives, large fish weirs, and coalition formation in warfare (Allen and Jones 2014; Boyd and Silk 2014).

Cross-References

- [Cooperative Foraging](#)
- [Food Sharing](#)
- [Gathering Returns When Nursing Infants](#)

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Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology

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Synonyms

Immediate-return societies; Nomadic foragers; Small-band hunter-gatherers

Definition

Small-band hunter-gatherer societies or nomadic foragers are “immediate-return” societies who lack significant possessions, do not cultivate plants, domesticate animals, or hoard food, in contrast to delayed-return societies who do one or more of these things.

Introduction

Often, people confuse nonmodern types of societies as if they were all the same. The differences among small-band hunter-gatherers, complex hunter-gatherers, tribes, and chiefdoms are quite important. All but the first cultivate plants or domesticate animals, activities that lead to hierarchy and inequality, and typically represent sedentary, patriarchal societies prone to violent management of conflict.

Nomadic foragers are distinctive. Nomadic foraging bands are similar in structure wherever they have been found all over the world (Lee and Daly 2005). They represent the type of society in which humanity spent 99% of its history before agricultural settlement. Nomadic foraging is not merely a subsistence mode but also represents a long-term evolutionary inheritance of social patterns based on equality, cooperation, and partnership. Many groups have persisted to the present day. The collected set of ethnographies from

nomadic foraging societies are relevant to understanding humanity's psychological and social evolutionary legacies (e.g., Kelly 1995; Lee and Daly 2005; Woodburn 1982).

Which Hunter-Gatherers?

Nomadic foraging bands have been ethnographically described for all major world regions. Some bands still exist but they have become increasingly rare in recent centuries and decades due to ecological destruction of their habitats, land grabs, epidemics, and even extermination campaigns. The data from which this discussion is drawn include individual ethnographies (for review see Lee and Daly 2005), studies that systematically sample nomadic forager societies (e.g., Fry 2006; Fry and Söderberg 2013) and comparative forager studies (e.g., Kelly 1995; Woodburn 1982). The focus is on the recurring patterns across foraging societies, from different continents and habitats.

There are several reasons that examining data from mobile groups is useful for social science. First, as noted, most of humanity's evolutionary past was spent in this kind of nomadic foraging society. Thus we can take it as not just an economic subsistence form of life but a stable form of living. Fry (2006) summarized the recurring demographic features reported for dozens of mobile forager societies worldwide. Recurring patterns include small size (25–50 individuals on average) and low population densities, mobility with flexibility and fluctuations in group composition, and interconnections among bands (especially among those that speak the same or similar languages). Territory is loosely defined among groups. Bilateral systems of descent (maternal and paternal) are emphasized.

Second, all over the world nomadic foragers show recurring patterns of behavior and orientations. Nomadic foraging data offers a glimpse into multiple baselines for human societies: (1) they provide humanity's evolved nest to their young; (2) they demonstrate similar cultures and personalities which likely are related to evolved nest provision, including (3) alternative ways of dealing with

conflict; (4) they display a human nature and worldview distinctive from the modern.

The Evolved Nest

Evolutionary systems theory identifies humanity's multiple evolutionary inheritances, which includes genes but also a developmental niche for the young (Oyama 2000). Nomadic foragers provide the evolved niche, which is similar to that of social mammals who emerged over 30 million years ago (Konner 2005). As for all animals, the human nest matches up with the maturational schedule of the young, shaping the wellbeing and nature of offspring through ongoing constructive interactionism. Nomadic foraging data provide a window on the evolved nest and its effects (aka, hunter-gatherer childhood model, Konner 2005). The human nest has been described by anthropologists as a set of recurring patterns among nomadic foragers (Hewlett and Lamb 2005). For young children, the evolved nest includes soothing perinatal experiences (no separation of baby from mother, no painful procedures); responsiveness to infant needs to prevent distress; extensive on-request breastfeeding (2–8 years; 4 years on average); extensive positive (no negative) touch and holding; positive climate and social support for the mother, the child, and the dyad, including multiple responsive familiar caregivers; and self-directed social play. Transdisciplinary studies demonstrate that each of these nest components has measurable neurobiological effects on the child's personality and trajectory for health, wellbeing, and sociality (e.g., Narvaez et al. 2013). A supportive community nest continues past early childhood as can be surmised by the characteristics of flexible communalism described below. In adulthood, nomadic foragers demonstrate similar cultures and personalities which likely are due to similar early life experiences or evolved nest provision.

Culture and Personality

What kind of cultural patterns do the nomadic foraging data show? The data show a human predilection for peaceful living through fostering prosocial behavior, using nonviolent rather than

violent conflict management approaches, including a lack of warfare (Fry 2006). They emphasize cooperation with high egalitarianism, including between genders. Hunting large game is primarily a male activity and gathering primarily a female activity, though these are not exclusive, and each group makes decisions for their realms of activity. There is minimal leadership and no overarching authority within or among groups; in fact they eschew authoritarian leadership. Individuals are highly autonomous while highly communal. Group decision making is by consensus. There is little material property and minimal private ownership of resources. Generosity and reciprocal sharing are expected within and between groups. Band members practice sexual freedom, tend to find spouses in other groups, and can change partners when so desired. Multilocality, rather than patrilocal, is typical among mobile hunter-gatherers (Dyble et al. 2015, p. 798).

What values do they exhibit? Reciprocity of generosity and sharing are expected within and between groups, even those at some distance. No one goes hungry unless all do. The ties of friendship, kinship, marriage, and gift exchange bind individuals and groups together. Landscape resources are shared. This may be especially important because of the fact that groups are ephemeral – membership is always changing in a fission-fusion pattern. In fact, it is speculated that because of evolutionary pressures “co-residence with unrelated individuals set the selection environment for the evolution of hypercooperation and prosociality. . . . This social system may have allowed hunter-gatherers to extend their social networks, buffering environmental risk and promoting levels of information exchange required for cumulative culture” (Dyble et al. 2015, p. 798). Also valued are humility, respectful behavior, and nonaggression (Boehm 1999; Fry 2006; Woodburn 1982). They live leisurely with limited wants and self-restraint. Overall, they display a partnership orientation to social life, characterized by egalitarianism and respect for individual autonomy but also high communalism.

How are these values cultivated and enforced? The evolved nest, described earlier, is the way to establish self-regulation and

sociality. As they grow up, children observe and imitate the typical ways to interact which include self-restraint, patience, and helpfulness. In everyday life, conversation and banter are used to keep people in line. Prosociality is expected but rewarded with reputation. On the other hand, rough humor is used to minimize the ego inflation of a successful hunter or of someone who is demonstrating greed or is less than generous. In extreme cases, group members may expel (thief; regular troublemaker) or even execute (recidivist killers) offenders.

Dealing with Conflict

One of the most common mistaken assumptions about humanity’s past regards aggression. Nomadic forager data shed light on humanity’s predilection for violence. From nomadic forager data, we can surmise that our ancestors tended to avoid lethal aggression, favored nonviolent cooperation and avoidance during conflict, and used social control mechanisms to maintain a peaceful social life (Fry 2006). Nonviolent conflict resolution includes such techniques as avoidance (physical or emotional), toleration, negotiation, and settlement (ibid). The typical response among foragers is to walk away, foment a discussion, or enter into group contests such as song duels or wrestling. Disputes are typically personal (e.g., two jealous men), and sometimes lead to homicide but most often do not.

With the definition of warfare as *lethal aggression between different communities*, war is a highly rare occurrence among foragers according to extensive analysis (Fry and Söderberg 2013). It must be remembered that foragers have few possessions to fight about, egalitarianism is the norm, population density is low, and there are no military leaders. At the same time, reciprocal exchange practices and ties of kinship and friendship are very strong. It is the latter that increase survival challenges.

Human Nature and Worldview

Nomadic foraging data offer a glimpse into human capacities of development and offer a glimpse into the type of worldview that develops in ancestral conditions of living close to the earth

with basic needs met through the evolved nest and ongoing social support.

Nomadic foraging data offer a contrast to the view of human nature as “economic man” – an acquisitive, calculating, and competitive creature always looking for self-advantage. Along with selfish exploitation, economic theory assumes scarcity in the world and that some will be rich and others poor; work and production, at the expense of leisure, are necessary to eat. These features are contrary to nomadic foraging data where generosity is a dominant value, the world is considered to be full of abundance; work and socializing go together; and no one is coerced to do anything in order to share in the group’s food. Following nature’s gift economy of giving and taking, nomadic foragers practice communal sharing, whether of food or possessions.

Conclusion

Nomadic foraging data have often been ignored, minimized, or collapsed into prehistory, perhaps because they challenge received views of human prehistory and human nature. The data challenge views of human nature as selfish, aggressive, and competitive. In contrast to modern views of humanity and its past, nomadic foragers are fiercely egalitarian, even among genders and ages, with high autonomy and communality and an emphasis on generosity. The social patterns shared across mobile societies include reciprocal social networks across vast distances, peaceful exchange, and restraint in conflict resolution.

Nomadic foraging was the form of living for all humanity until recent millennia. As it is the original form of social life, nomadic foraging represents the social and developmental circumstances reflective of humanity’s evolution. Data from societies that live largely like humanity’s 99% allows researchers a glimpse into deep history. Similar features occur among widely disparate mobile foragers around the world, suggesting a stable form of social organization. Comparative studies with moderns, whose characteristics represent civilization’s effects, can be informative

about how much humans are shaped by early experience and by social lifestyles.

Cross-References

- [Hunter-Gatherer Societies](#)
- [Nomological Networks of Evidence](#)

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Hunting Ability

- [Social Status and Economic Resources](#)

Hunting Hypothesis

- ▶ [Male-Provisioning Hypothesis](#)
-

Hunting Out of Season

- ▶ [Human Mate Poaching \(Schmitt and Buss, 2001\)](#)
-

Hunting Strategies

- ▶ [Coalitional Hunting](#)
-

Hyperadrenocorticism

- ▶ [Congenital Adrenal Hyperplasia \(CAH\)](#)
-

Hyperpiesia

- ▶ [Hypertension](#)
-

Hypertension

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Synonyms

[High blood pressure](#); [Hyperpiesia](#)

Definition

A medical condition in which arterial blood pressure remains abnormally elevated, classically >140/90 mmHg.

Introduction

The development of a maladaptive health disorder may seem counterintuitive to the evolution and fitness of a species; however, pathologies such as hypertension are the result of a biological response to inadequate environments that may have been in favor of survival for previous generations.

Blood Pressure

All organ systems within the body receive energy and oxygen via blood transportation; in larger animals and humans, this transportation requires a significant vascular system to deliver these nutrients to the furthest organs and tissues (Weder 2007). The strength of the blood pressing against arterial walls is defined as blood pressure, and this pressure rises and falls with the heart's synchronous pumping as it is forced through the cardiovascular system. Blood pressure is measured at its maximum, during contraction of the heart (systolic), and at its minimum, the resting state between two heartbeats (diastolic), and is presented as a ratio measured in units of millimeters of mercury (mmHg). Normotensive or normal blood pressure is defined as 120/80 mmHg or lower (Hypertension Canada 2015; Whelton et al. 2018). The volume of the blood being pumped through this system affects the blood pressure, with increased volume forcing excess cardiac output. Two salts, sodium and potassium, are required in a balanced state to stimulate the kidneys to remove excess water from the body; when sodium is present in excess, the ability of the kidneys to remove water is inhibited and plasma volume increases, forcing blood pressure to increase, which may develop into the health disorder, hypertension.

Hypertension

Hypertension develops in response to extended periods of stress, whereby the body attempts to adapt through increased energy consumption or, the other way around, stress comes in the form of

excess energy input and the body has an incapacity to utilize the abundant resources. Stress can be defined as anything that poses a threat to the health or survival of an organism, such as bacterial infections, inadequate nutrient intake, injury, or even mental trauma. Many organisms, including humans, are often driven to increase available energy to fuel the metabolic demand of dealing with a stressful event (Pettit and DeBarr 2011; Torres and Nowson 2007). Chronic stress can lead to increased stores of glucose and/or sodium, increasing risk of a number of disorders, including hypertension. The classical diagnosis of hypertension is repeated measures of blood pressure greater than 140/90 mmHg; however, some medical professionals are treating patients with measurements greater than 130/80 mmHg (Daskalopoulou et al. 2018). Short-term high blood pressure can be harmless; however, chronically it has been linked to a cascade of health issues such as cardiovascular diseases, stroke, vision loss, dementia, and metabolic syndrome.

Thrifty Gene and Salt Hypotheses

A promising concept was developed in 1962 by James Neel, named the thrifty gene hypothesis, which predicted diabetes and obesity were diseases that have developed as a survival adaptation, a remnant of the early evolution of the human species. Early humans were faced with famine, immune threats, and disease. The thrifty gene hypothesis argues that for early ancestors who were able to retain the most out of consumed nutrients, a blood pressure sensitivity would increase their chances of survival by maintaining normotension during low-sodium conditions. These ancestors would pass along their genotype to their offspring, propagating a line of humans suited for conservation of nutrients in times of deficit. As noted, sodium consumption plays a significant role in blood pressure regulation, and Gleibermann (1973) proposed a sodium hypothesis that describes a drive by our ancestors who lived in hot, arid climates, to consume salt to replenish loss from sweat. The readily available, abundant, and nutrient-rich foods in industrialized nations render these proposed evolutionary

genotypes maladaptive, rather than efficient, leading to the development of hypertension and other metabolic disorders (Weder 2007).

These theories have been met with criticism over the past few decades, predominantly over genotypes and population studies. Gosling et al. (2015) argues that, during times of nutritional abundance and deficit, these theories do not hold true for Pacific Island populations, noted to be the exemplary model for the thrifty gene hypothesis. A lack of genetic markers linking diseases to metabolic disorders, Gosling continues that the hypothesis has failed to provide sufficient evidence in its current definition. Different conceptions of the thrifty gene hypothesis, however, are presently driving research in the growing field of epigenetics and fetal programming.

Barker Hypothesis

In 1992, Hales and Barker devised the thrifty phenotype or Barker hypothesis which stipulates that stress in the prenatal environment correlates to the expression or inhibition of genes linked the metabolic consumption. This influences the physiology and metabolism of the fetus through permanent changes in transcription factors, a process termed fetal programming. During significant acute or chronic stress, steroidal hormones called glucocorticoids are released into the circulatory system from the mother, in high concentrations, and are able to overcome an enzymatic placental barrier that usually suppresses the passage of hormones to the fetus (Seckl and Holmes 2007). Infection, injury, or lack of adequate nutrition during pregnancy all present either acute or chronic stress states that can lead to increased levels of circulatory hormones during critical and sensitive periods of fetal growth. Glucocorticoids can inactivate or silence genes that are sensitive to metabolism, predisposing offspring to hypertension when faced with nutrient abundance or stress of their own. Research involving both humans, such as Holocaust survivors, and nonhuman animals currently supports this hypothesis providing evidence of links between early-life stress, glucocorticoids, and hypertension (Keinan-Boker et al. 2015; Nguyen et al. 2015).

Conclusion

Adaptation to novel environments promotes the survival of a species; however, total adaption can produce complications when environmental conditions change (Weder 2007). Humans have adapted to environments deficient (or at least lower) in nutritional support and, as such, are now faced with current health challenges linked to abundant resources. The correlation between the availability of nutrients and the presence of early-life stress suggests that the fetus is provided with information about its probable environment; the Barker hypothesis claims maternal nutrition and the presence of hormones adjust the phenotype through silencing or activation of genes to enhance the fetus' ability for survival. If the fetus were born in a nutrient-deficient environment, the sensitivity to dietary sodium and other nutrients would enhance available energy and cardiovascular circulation required to deal with stress; conversely, this phenotype may lead to the development of a number of health disorders, such as hypertension.

Cross-References

► [Increased Cortisol](#)

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Hypoactive Sexual Desire Disorder

► [Desire and Arousal Disorders](#)

Hypodermic Impregnation

► [Traumatic Insemination](#)

Hypodermic Insemination

► [Traumatic Insemination](#)

Hypothalamus

► [Regulation of Body Temperature](#)



I Am Unaware of Any Synonyms for This Place Name

- ▶ [Olduvai Gorge, The](#)

Iberian Peninsula

- ▶ [Western Europe](#)

Ideal Partner Preferences

- ▶ [Men's Mate Preferences](#)

Identification of Animated Actors

- ▶ [Agency-Detection](#)

Identifying Adaptive Functions

- ▶ [Function Versus Capability](#)

Identity

- ▶ [Object Permanence](#)

Identity Formation

- ▶ [Self-Concept](#)

Ill-Matched

- ▶ [Mismatch](#)

Images of Nature

- ▶ [Landscape Preferences](#)

Imagination

- ▶ [Fiction](#)

Imitation

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Synonyms

Copying; Emulation

Definition

Imitation in economics and the social sciences is the process by which individuals adopt the strategies and practices of others. Typically we imagine that it is success that is imitated rather than failure.

Introduction

Imitation plays a key role in the economic study of competition, innovation, and evolution: the imitation of good ideas serves as a crucial way in which those ideas spread throughout a population. A key theme in the literature is that imitation improves economies and tends to foster efficiency. Imitation, however, bootstraps off of innovation: without new ideas to imitate stagnation is likely to result.

Three Types of Imitation

There are three broad strands of literature in economics studying imitation. The first is the role of imitation in competitive economies. The second is the role of imitation in pushing the process of innovation and growth. The third is the role of imitation in determining long-run outcomes in evolutionary economies. In all three cases, imitation serves a positive role in advancing economic progress.

Competition

Competitive equilibrium requires that firms maximize their profits. In a long oral tradition, firms were thought to do so by dynamically imitating the policies of rival firms rather than statically “optimizing.” On the one hand, firms innovate – try new pricing and production policies, combine inputs in new ways and with new production processes. On the other hand, they adopt practices of other firms which seem to be successful.

Some of the earliest work in economics on imitation is the examination of how stochastic imitation combined with a degree of innovation can lead to competitive equilibrium – in effect verifying the earlier oral tradition. The classical paper is that of Winter (1971) who studied a Markov model of evolution in an economy with gross substitutes and shows that indeed convergence to competitive equilibrium is obtained. An element of innovation – the innovating remnant in the title – is needed to make sure that eventually good production plans are discovered. Once discovered they are then spread by imitation leading to competitive equilibrium and an efficient production plan and allocation.

Winter’s paper is very advanced for its time, using as it does a stochastic Markov model similar to those that only became widespread twenty or so years later. It provides a much more compelling account of convergence to competitive equilibrium than the deterministic tatonnement and non-tatonnement models of price adjustment that were widely used at the time.

The early literature on imitation, innovation, and competition is well reviewed in the Nelson and Winter (1977) survey which also reviews some of the empirical literature at that time on the importance of imitation. It covers also their own work simulating the process of innovation and imitation.

Schumpeterian Competition

Schumpeter (1942) focused not on static competitive equilibrium but rather on dynamic competition resulting in the generation of new ideas. In this account, imitation is destructive of the profit of existing ideas: this on the one hand makes it less desirable to generate new ideas as profit will

be lost to imitators, but on the other hand makes it essential in order to gain a short-term monopoly by generating new ideas. In this account, imitation forces firms to run faster to stay ahead.

This idea first appears in the literature on patent races such as Fudenberg et al. (1983). There firms engage in a contest to see who can get the monopoly thereby shutting out the competitors. Such models can lead to “excess” innovation.

This Schumpeterian idea is picked up on and plays a key role in some modern theories of innovation, most notably in Grossman and Helpman (1991) and in Aghion and Howitt (1992). Although different in details, both of these theories focus on imperfect competition and quality ladders. That is production may be carried out with different technologies organized on a ladder with lower cost more productive technologies higher on the ladder. Firms move up the ladder either by innovating and discovering a new step or by imitating another firm higher up on the ladder. In the simplest version, an innovating firm keeps its place on the top of the ladder for some fixed number of periods after which imitators enter the rung and drive profits to zero. On the one hand, the presence of imitators takes some of the profit out of innovating; on the other hand, it provides incentive to innovate as only innovation can provide short-term monopoly profit.

These models with their simple imperfect competition point to intellectual property – patents – as a key incentive to innovate. Boldrin and Levine (2004) observing that empirically patents seem to have little to do with innovation (see Boldrin and Levine 2008 for a review of the evidence) contest this point of view. They observe that the presence of imitators – of copiers even – does not drive profit to zero as a matter of theory. Imitators must pay for a product to imitate and imitation takes time. Moreover, innovators have a number of methods of generating profits such as the complementary sales of expertise and services – the driving force in open source software – with which to profit from their ideas. Hence imperfect competition in general and patents in particular are by no means necessary to generate innovation and growth – it is the movement up the ladder that is key.

This connection between imitation and growth is further reinforced when we recognize that R&D not only is needed in order to innovate but in order to imitate. For example, Griffith et al. (2004) show that R&D is essential in order to imitate existing ideas. This perhaps is not surprising: one who is not actively doing research in an area is unlikely to quickly appreciate the breakthrough of others working in the area. A biochemical formula will mean little to someone who is not a biochemist; we are likely to get better service for our software from the creators than from people who simply copied the code verbatim, and so forth.

This connection is also relevant in the literature on user innovation. Von Hippel (2005), for example, makes the point that it is users of products and imitators who often improve those products. Here imitators also improve upon the original. One of the fascinating things is the “not invented here” syndrome so that producers of products often attribute to themselves improvements that originated either with users or imitators.

Empirically theories of user innovation and competition such as Boldrin and Levine (2002) better match the data than Schumpeterian models. We see this in empirical work of Irwin and Klenow (1994) for example. Their study of memory chips is particularly useful as the quality ladder is clearly defined moving as it does by factors of four. The key fact is that production of a particular quality does not jump up instantaneously but ramps up gradually – long after imitation has taken place – and that a new quality is only introduced when the stock of the old one is fairly large. Each old vintage is phased out gradually as the new one is introduced. The price data shows that the price of each vintage of chip falls roughly exponentially over the product cycle – meaning that the incentive to introduce the next generation chip keeps increasing. Evidence suggests this is the usual pattern in most industries. It makes the point: why introduce a new product if the old one is still doing so well? Rather innovation waits until the market is relatively satiated and there is reason to introduce a new product.

Evolution

In the original work on evolutionary game theory in Kandori et al. (1993) and Young (1993) innovation was central and imitation not present. One conclusion from this literature is that evolution selects not for efficiency but trades off efficiency against a measure of the risk from coordination failure. The subsequent literature shows that when imitation is present along with innovation there is a stronger tendency toward efficiency – reinforcing the conclusions of Winter about competition and Boldrin and Levine about growth.

The contrast between models used by economists to study learning and biologists to study evolution highlights the role of imitation. Traditionally learning models in economics have focused on best response dynamics in which players attempt to do the best they can relative to how other people in the population are playing. This is rather different than biological models of evolution in which the number of offspring a population can produce is greater in a larger population all else equal. However, when imitation is introduced into economic models, dynamics more similar to biological models results.

Consider first how biological models work. Central to biological models of evolution is the replicator dynamic. This asserts that ideas (or organisms) reproduce based not only on how much utility or fitness they provide, but also on their current level of success as measured by their population. In biology, this reflects the fact that a larger population will have more offspring than a smaller population all else equal.

What happens when imitation is introduced into the economic setting of ideas rather than organisms? Schlag (1999) showed how imitation in an economic setting can lead to a dynamic more like the replicator dynamic of biology than the best response dynamic of traditional economic theory. If players they acquire information through imitation then the chances of meeting a player playing a better strategy depend on how many of those other players there are. This means that more popular strategies are more likely to spread all else equal.

One of the peculiar and unattractive features of the replicator dynamic is that it can get stuck – if

everyone is doing the same thing, no matter how stupid, then the system cannot move. If there is only imitation this makes perfectly good sense: if the population is homogeneous there is nobody to imitate. Hence we need some degree of innovation. Imitation alone is never enough – and this is characteristic of all types of economic models.

It is natural to combine the random innovation model of Kandori et al. (1993) and Young (1993) with a model of imitation. This program is carried out in Levine and Pesendorfer (2007) who model a process in which imitation more common than innovation, but in which innovation is present as well. They show in this case that stochastic stability is determined by the outcome of pairwise contests. This favors relatively efficient outcomes – for example, if strategies can identify themselves to each other.

This tendency toward efficiency can be found in other strands of the economics literature. Ellison and Fudenberg (1993, 1995) study how rules of thumb for imitation evolve and find also that there is a tendency towards efficient outcomes.

A particularly clean example of how imitation and evolution lead to efficiency can be found in Ely (2002). Ely studies a model in which there are different locations. Innovation takes place at different locations and imitation has the form of moving to a particular location and adopting the social convention there. Naturally people move to successful locations and unsuccessful – inefficient – locations gradually lose population to the successful – efficient locations. In the long run, the outcome is fully efficient.

Conclusion

Economists have studied a broad range of models where imitation plays a crucial role in spreading ideas. In dynamic theories of competition, imitation plays a key role in establishing competitiveness and efficiency. In the theory of growth and development, imitation may drive down profits from existing ideas, but by doing so creates incentives to create new ideas. In evolutionary game theory, imitation spreads good ideas pushing

toward more efficient outcomes. In all cases, it is the combination of imitation and innovation that results in good economic outcomes.

Cross-References

- ▶ [Evolution and the Theory of Games](#)
- ▶ [Game Theory](#)
- ▶ [Learning Versus Imitation](#)

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Imitation and Mimicry

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Synonyms

[Copying](#); [Echoing](#); [Emulation](#)

Definition

Using someone as a model for one's own actions.

Introduction

Scientific interest in imitation and mimicry in the animal kingdom goes back at least to the times of Darwin. The debate on the cognitive aspects of imitation, however, is more recent. Influenced by serial sensory-motor, stimulus-response models of perception-action coupling, the cognitive mechanisms that make imitation possible were initially framed as the “correspondence problem.” That is, how does retino-centric, visual information about the actions of other people get translated in body-centered information that the imitator uses to copy the observed action? The correspondence problem, and the model of

perception-action coupling that inspires it, obviously assumes no shared representations (or codes) between perceptual inputs and motor outputs. A longtime alternative model to the sensory-motor model of perception-action coupling is the ideomotor model (Hommel et al. 2001). This model assumes at least some level of shared representations between perception and action, thus making the correspondence problem fundamentally irrelevant. The ideomotor model of perception-action coupling, however, is typically framed in terms of intentional actions: whenever I plan to turn on my computer, I can anticipate the sensory consequences of my action plan. While imitation can obviously be intentional (for instance, observational learning is a form of intentional imitation), humans do display very often a type of imitative behavior that is unintentional and pre-reflective, what is typically called “automatic imitation” (Iacoboni 2009).

Top Down and Bottom Up

Observational learning and automatic imitation are perhaps the two imitative behaviors that are situated at the opposite ends of a continuum: the continuum that represents the ever-varying balance between top-down and bottom-up processing of the actions of other people. Observational learning is a top-down intentional imitative behavior that focuses on specific actions and behaviors with very specific goals (how to hit a tennis forehand or how to behave, speak, and even deliberate in specific contexts and situations, for instance). Automatic imitation, in contrast, is clearly a bottom-up process in which the visual input of the actions of others “sweeps us up” so that we cannot help but reproduce that behavior, generally in terms of the postures, facial expressions, and mannerisms of the people we are interacting with. Automatic imitation, however, is not as automatic as its name may suggest. We don’t parrot each other in a zombie-like fashion. Pre-reflective, unintentional imitative behavior is clearly influenced by fairly high-level factors, and in turn, it does influence those factors. For instance, we tend to imitate unintentionally more

people that belong to our social group, compared to out-group members. However, even the influence of social group membership on automatic imitation can be modulated by other contextual factors. Indeed, a competitive situation reduces automatic imitation for in-group members, whereas a cooperative situation increases it for out-group members (Miles et al. 2010). Furthermore, automatic imitation is associated with empathic predisposition. More empathic individuals tend to display more automatic imitation. In experimental settings, being imitated has also been associated with increased liking (Chartrand and Bargh 1999).

Neural Correlates

All these behavioral data suggest that low-level bottom-up processes continuously interact with high-level top-down ones during imitative behavior and that these interactions are modulated by contextual variables and intentional predispositions. Imitation is in itself a complex behavior, and these complex, nuanced contextual modulations make it even more so. What are the neural mechanisms of imitation? Given its complexity, especially in real-world scenarios, for many years, the neuroscience community had largely avoided the study of the neural underpinnings of imitation. A breakthrough discovery in monkey neurophysiology, however, has inspired a recent wave of neuroscience studies on human imitation.

A subset of motor neurons in the monkey brain have surprising visual properties. Even when the monkey does not move at all and is simply watching, these motor neurons fire, as long as the monkey is observing someone else making the same action triggered by the firing of these motor neurons when the monkey moves (or a similar action that achieves the same goal) (Gallese et al. 1996). In other words, the visual properties of these neurons mirror their motor properties, and for this reason, they have been called mirror neurons.

Mirror neurons clearly support more the ideomotor model of perception-action coupling, which assumes shared coding or representations

for perception and action, than the sensory-motor model which assumes independent coding for perception and action. They also seem to have ideal properties to support imitative behavior, especially of the automatic type, since these cells seem to fire in a stimulus-dependent fashion (when the action is seen).

Depth-electrode recordings in both monkeys and humans have provided evidence for mirror cells in a number of neural systems coding for different kinds of actions performed with different body parts (Iacoboni 2011). These findings support the variety of imitative behavior that humans display. However, an outstanding question with regard to the neural underpinning of imitative behavior is also how neural mirroring gets controlled so that the nuanced modulation of imitative behavior due to contextual and dispositional factors can also be accounted for. Early studies pointed to the dorsomedial prefrontal cortex (dmPFC) and the temporoparietal junction (TPJ) as two areas controlling imitation. These areas have been associated with a number of behaviors and cognitive functions, including theorizing about the mental states of other people (theory of mind or ToM). Insofar as imitation control requires a differentiation between the action of the self and the actions of other people and theory of mind requires a differentiation between one's mental state and the mental states of others, the involvement of dmPFC and TPJ in both imitation control and ToM makes sense.

Recent studies have provided more insights on the complex and continuous interplay between bottom-up and top-down neural processes associated with imitative behavior and its control. For instance, a neurophysiological phenomenon analogous to automatic imitation is "motor resonance." When observing someone else making an action, the excitability of our own motor system increases. This increase is "muscle specific," that is, it is restricted to the same muscles used in the action we observe. Motor resonance has been considered for many years a typical automatic, stimulus-dependent process. However, a recent study shows that when planning not to imitate, motor resonance is abolished (Cross and Iacoboni 2014). Note that the plan "not to imitate" is a very

general, high-level plan in this study, because subjects still don't know which action they are supposed not to imitate, which means that fairly high-level intentions ("I am not going to imitate whatever I see") are able to modulate in a top-down fashion a typical bottom-up process like motor resonance.

A brain imaging study on automatic imitation recently attempted a more detailed description of the frontal lobe circuitry for imitation control. Here, dynamic causal modeling (DCM) revealed a circuitry composed of dmPFC and anterior cingulate cortex (ACC) that together trigger top-down inhibitory control – via the anterior insula – of the posterior inferior frontal cortex (pIFC), an area strongly associated with imitation and mirror neurons (Cross et al. 2013). Furthermore, another brain imaging study on controlled imitation, in which subjects were instructed whether to imitate or not, suggested that connectivity changes between brain areas activated by the task was a key regulatory factor for inhibition of imitation (Cross and Iacoboni 2013). Taken together, these findings may explain why the dmPFC is so often implicated in the top-down regulation of imitation. Indeed, dmPFC has a rich connectivity pattern with other neural systems, and this anatomical feature may make it ideally situated for the control of imitative behavior, also in light of the presence of mirror neurons in a number of neural systems. Recent studies using noninvasive neuromodulation have shown that by transiently downregulating dmPFC, it is possible to modulate fairly high-level forms of social conformity (Holbrook et al. 2015), thus suggesting that imitation grounds social conformity processes through bodily synchronization.

Conclusion

The picture that emerges from these recent studies is rich and intricate, yet exciting, due to the fairly rapid progress in knowledge obtained in the last two decades. Progress on our understanding of imitation and mimicry is likely due to the interdisciplinary work of social, cognitive, and neuroscientists.

Cross-References

- [Brain Imaging](#)
- [Cooperation and Social Cognition](#)
- [Empathy](#)
- [Imitation](#)
- [Memes](#)
- [Mirror Neurons](#)
- [Neonatal Imitation](#)

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Imitation of High-Status Others

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Synonyms

[Mimicry, power, and influence](#)

Definition

To follow as a pattern, model, or example (Merriam Webster).

Introduction

“Imitation, is the highest form of flattery.”

What is imitation? Imitation is the innate conative tendency to behave as others behave in the absence of logically sufficient grounds for behaving in that manner, which simply can mean, copying or mimicking the other person. Carried out by animals-primates and humans alike, help one in acting or becoming like the one copied. Often, used by children as a form of mockery, imitation in itself has a complex scientific concept behind it. Mirroring, in its true self, can explain imitation well. The process of copying the person in front of you, consciously or unconsciously, may give us a sense of belonging, a sense of connection. It tries to put both the individuals at the same level.

Neurobiology

Neurobiologically speaking, the theory of mirror neurons comes to play. Describing the process and reason for imitation can easily be explained by this concept. Mirror neurons act when an animal observes an act and then follows it. The basic ideas being visual signals are converted into motor mechanisms. The premotor cortex, the

supplementary motor area, the primary somato-sensory cortex, and the inferior parietal cortex show consistent activity, which favors mirror neurons. These areas are the core areas to be involved in conversion of visual analogues and cognitive processes, thus strengthening this belief (Huber et al. 2007).

Imitation: A Concept

Evolutionary speaking, imitation has been an important skill. It helps in learning of new skills by conversion of visual inputs into fine motor skills. The process, even though be unconscious, can help us learn; thus there is only gain in such situations. Different types and forms of imitation are described-Starting with lower level animals, young ones imitate parents to learn to gather food. They even imitate parents to speak as seen in parrots. Primates, for example, monkeys, can even mimic humans let alone one another, a skill often exploited by circuses. Children grow up learning by, for example, following parents and teachers alike. A baby can be taught new words by making them repeat, establishing that skills needed for daily living as best learnt by copying. People tend to imitate our elders, following rituals and traditions- their seniors in the workplace, and the only conviction needed, that this will make them reach a better place. Also seen by the society as a whole, the youngsters following the latest fashion trends sported by a celebrity, or we as a nation trying to follow the western ways. Baghot stated “society is imitation”, reiterating the belief. Imitation is all around us, be it the aeroplane that flies or the ship that sets sail. Numerous studies have been conducted which establish the importance of imitation, in child-rearing and education. This further justifies the need for good role models as they enhance good behavior. There are three types of mimicry:

1. Automatic imitation which can be defined as a kind of stimulus-response compatibility effect where the action stimulus (either video or image) is paired with a congruent or an incongruent response.

2. Behavioral mimicry which can be defined as the tendency of people to naturally copy others’ movements during social interactions.
3. Facial mimicry which describes the tendency to mimic others’ facial expressions.

The “chameleon effect” can easily explain what happens during a conversation. Given by Chartrand and Bargh 1999, “chameleon effect refers to the tendency to adopt the postures, gestures, and mannerisms of interaction partners.” The best possible explanation is that it is conducted without the idea to copy and not in conscious awareness (Lakin et al. 2003). So, social interactions while linking non-conscious mimicry and rapport building can be enhanced. Studies conducted express the need for further research on how affiliations and non-conscious memory can be linked in greater detail.

Social Status: A Concept

Why is status so important? Or why is it given so much weightage? Why does everyone around us want to be considered as the high and mighty or an influential persona? Us humans constantly find ourselves battling in out among power hungry creatures, so much so that we often find ourselves guilty of the very same charge. If we have a link, a source, and a connection to someone influential or connected, we never refrain to use it. Let alone using, bragging about the same to our friends and families continue for long periods of time. Have you ever wondered, why is it so? Why are we part of this rat race – where in the sole purpose is, who is the most connected, the most influential, and the most powerful. This struggle continues not only for laymen but also those who in fact are the high and mighty themselves. The fundamental remains the same – status. The concept of status can be explained as “the extent to which an individual or group is respected or admired by others.” High status means more admiration in simple terms. If someone presents themselves as having a high status, they feel they would be respected more by the people around them; more people would like to be like them and would in turn copy them.

In turn, this sets of another cycle of imitation, and this may continue up until the very grass root level. Each individual wants to show the world the best version of themselves, the one overshadowing their flaws. What better way than to act like someone else, someone who we admire and consider perfect, is helping them become a better version of themselves in their own eyes. Imitation may or may not raise the respect or admiration in front of others – society per say, but it definitely raises our level in front us; it can help in building a pseudo confidence – that anything is certain now.

“Power is defined as a possibility to influence others.”

In our society, individuals exerting power are perceived to be influential. If they make themselves appear powerful, they become powerful in the eyes of the perceivers, raising their status and standing. Also, making themselves an object of admiration and glorification. Struggle for power and associated high status is not a new idea for us; power play has been evolving through the ages, be it in politics, sports, offices, or even in our relationships. We tend to follow those in power. Feeling powerless automatically makes us feel that we are vulnerable, although it might not be true in reality; our emotions force us to look upon that direction. Concept of high social status and power is also interlinked – a common notion being that high-status individuals are powerful. But this is no sort of guarantee. This favors change in social interactions in two ways. Firstly, one with high-status individuals and secondly, the one with peers but behaving like a high-status individual.

Imitation and High Status: The Connection

The art of copying imitation in its true self can enhance an individual's social standing – reiterates the fact the social status and power play a role which can modify the chances of an individual to imitate. Also, these play a role in cognitive processing and its multiple forms of the perceiver. Studies have been conducted, which had significant results. Studies have drawn various conclusions

when it comes to social gestures and overall body language when dealing with people at the same strata as the individual themselves and those with a higher social status or power entity. Apart from the inherent changes in the overall demeanor of the person, the tendency on what actions and expressions to mimic may even change. High social status and high power definitely have a role to play, and their presence is of much bigger value than perceived directly. Gestures made while interacting and conversing commonly involve shaking hands, nodding, crossing and uncrossing of elbows, waving, even friendly hugs, and kisses. In order to try to come closer to members of the higher social stratas, in a manner to show them we are alike, individuals tend to follow their line of social communication, be it verbal or nonverbal forms of expression. Mostly picking up the motor movements first and then eventually facial expressions, giving them a sense of belonging (Farmer et al. 2016). During the tasks which are based on automatic imitation memory, high and low power-related gestures can cause greater impacts. For example, an individual when approached having clenched fists may open them when faced with a person they admire. This can further even cause changes in facial expressions, denoting a much more dynamic and holistic change in the overall behavior of that said individual. Although, the individual may think of this as the best possible way to approach the social ladder, is it the best possible way? Speaking from an observers' point of view, if two people are standing in front of one another in similar postures, that of a dominating nature, it may appear that they are arguing or even in polite terms disagreeing with one another. The individual mimicking might even make him feel that he is being mocked or made fun of by copying each and every move and rather than building a rapport or acquaintance; it may feel like an attack. What feels like a natural form of interaction if two people conversing maintain a complimentary posture would give an impression of a confrontation, which could finally shorten the already biased conversation or even lead to abandonment of the said individual. Powerful individuals are used to having others bow down and act submissive or in simple terms complimentary to their gestures. Like while shaking hands, we

expect the opposite hand, a complimentary gesture, it feels normal. The imitation behaviour may seem odd or unnatural. Coming to interactions with peers, Lansu et al. 2015 established that among peers, the influential peers tended to be dissuaded in interacting with other popular or influential peers. They further explored nature of self-esteem with the propensity to imitate a powerful peer. Their findings included “Popular young women with low self-esteem were most likely to imitate a popular peer. Unreferred young women with high self-esteem were least likely to imitate a popular peer.” This in turn establishes the same, peer status of influential and powerful alike control our behavior in social interactions. Although this study was conducted in adolescents, results are applicable to older adults as well.

Conclusion

Various studies have been conducted which establish the fact that our conscious and unconscious memory makes us mimic actions and expressions during social interactions. Imitation has been a string suit of the human nature guiding us and making us learn newer skills directly or indirectly. The tendency to mimic those who are at a higher social position than us is tempting and may happen unconsciously. Although, no definitive gain or association has been established between power, status, and imitation, it does seem to have potential advantages. Further, neurobiological aspects need to be explored in greater details to establish causality.

Cross-References

► [Hierarchical Climbing](#)

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Imitation of Sound

► [Bow-Wow](#)

Imitation of Sounds

► [Ding-Dong](#)

Imitative Aggression

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Synonyms

[Aggressive imitation](#); [Imitative assault](#); [Media violence](#)

Definition

The imitation of aggressive behavior, modeled by another individual.

Introduction

Imitative aggression, or the imitation of aggressive behaviors modeled by another, serves an

important developmental process. Specifically, imitative aggression may function to use others as models for appropriate behaviors in specific environments or circumstances. By imitating others' behaviors in similar situations, individuals are able to learn vicariously through the experiences of those they model, decreasing their chances for experiencing negative outcomes and increasing their chances for experiencing positive outcomes in those situations. Thus, individuals who utilize imitative aggression are able to maximize their fitness in situations which they themselves have not yet experienced.

Imitative aggression research dates back to Bandura's seminal works, assessing the effects of modeling aggression directed toward bobo dolls on children's aggressive behaviors. These experiments suggested that demonstrating aggression to children made them more likely to imitate that behavior and increased the aggressiveness with which they played in the subsequent experimental sessions (Bandura 1965; Bandura et al. 1961, 1963a, b). These experiments also contributed to the development of social learning theory, which states that learning occurs through direct experience and observing others' behavior. However, subsequent research has been unable to assess imitative aggression as rigorously as Bandura, due to ethical concerns (Barrett 2007). Instead, recent research generally uses exposure to media violence in place of a more direct and intense experimental manipulation, to assess these relationships.

Bandura's Studies on Imitative Aggression

Bandura and colleagues' first imitative aggression study randomly assigned children to an aggressive, nonaggressive, or control condition. Children in the aggressive and nonaggressive conditions were individually led into a room and provided with art supplies. After the child was settled in, the experimenter led a model into the room as well and had them sit on the opposite side of the room from the child. The model had some tinker toys and a mallet to play with, as well as an

inflated bobo doll. In the nonaggressive condition, the model quietly played with the tinker toys when the experimenter left the room. However, in the aggressive condition, the model acted aggressively toward the bobo doll by sitting on the doll and punching it, striking it in the head with the mallet, and kicking it around the room. Additionally, the model also stated several distinct, verbally aggressive phrases while aggressing against the bobo doll. Control participants, on the other hand, did not have any interaction with the model at all. Then, the child was led into a new experimental room, filled with a variety of aggressive and nonaggressive toys, including a bobo doll and a mallet, and were given 20 min to play freely, while raters observed their play through a one-way mirror and coded it as imitative and aggressive, nonimitative and aggressive, or nonaggressive. Results of the study showed that individuals in the aggressive condition were more likely than either control or nonaggressive participants to verbally and behaviorally imitate the model's actions. On the other hand, subjects in the nonaggressive condition were substantially more likely than subjects in either of the other groups to simply sit quietly, without playing with any of the toys at all. These results were the first to show that the observation of others' behaviors is sufficient to elicit imitative behaviors which an individual almost certainly would not have exhibited otherwise (Bandura et al. 1961).

Subsequent experiments by Bandura replicated his original finding and extended the implications to other similar situations as well. For example, in one experiment, aggressive behavior toward a bobo doll was either demonstrated by a real-life aggressive model, in a paradigm identical to Bandura and colleagues' original study (1961), with a film clip depicting a human model behaving in the same manner as the real-life model, using a cartoon film clip, in which a cartoon character behaves in a similar manner to the model in the above conditions or was not demonstrated at all. When children were allowed to play freely, participants who viewed the non-cartoon film clip displayed the most total and imitative aggression, followed by individuals in the real-

life, cartoon film, and control conditions, respectively (Bandura et al. 1963a). Additionally, in a separate experiment, subjects were shown a film clip in which an aggressive child either gets punished for his aggressive behavior or gets rewarded for his aggressive behavior, and only children who observed the child get rewarded for his actions displayed increased imitative aggression during a subsequent play session; those who saw the child get punished showed similar levels of imitative and total aggression to control participants, who did not view a film clip (Bandura et al. 1963b). Finally, one last experiment showed that the inhibitory effects of viewing an aggressor be punished can be eliminated if the researcher subsequently offers the subject a reward for imitating his behavior. Specifically, Bandura (1965) noted that participants who viewed a model get rewarded for his aggressive behavior showed identical levels of imitative aggression as those who saw no consequences of his aggression, but those who saw him get punished were less likely to imitate his behavior. However, after the children in all conditions were offered rewards for imitating the model's behavior, children who previously saw the model get punished showed identical levels of imitative aggression to those in the other two experimental conditions (Bandura 1965).

Social Learning Theory

When trying to determine possible boundary conditions for imitative aggression, informed by social learning theory, Bandura (1986) concluded that the following four elements must be present in order for imitative aggression to occur: First, the individual must pay attention to whomever is modeling their behavior. Without paying attention, subsequent steps of this process would be impossible, as the subject would have no knowledge of the behaviors they were going to imitate. Next, the individual must retain a memory of the aggressive behavior the model engaged in. In order to ensure that the subject retained a memory of the aggressive actions in his experiments, Bandura et al. (1961, 1963a, b) included both

physically and verbally aggressive behaviors, as it would be virtually impossible for a subject to reproduce both types of behaviors spontaneously. Additionally, the model must be capable of imitating the actions of the model, because if they are unable to properly imitate the model's actions for any reason, they will not be able to aggress in the same way that the model did. Finally, the individual must have the desire to imitate the aggression, and such desire is much more likely to be present if he saw the model rewarded for his aggressive actions than if he seems him punished for the same actions or if the subject is offered a reward for imitating the subjects actions (Bandura 1965, 1986; Bandura et al. 1963b).

Ethical Concerns

Due to ethical concerns, recent research has not used procedures similar to Bandura et al. (1961) when assessing imitative aggression. Specifically, the Belmont Report states that one of the fundamental ethical principles for conducting research using human subjects is beneficence, meaning that one must "do no harm" to human participants (National Commission for the Protection of Human Subjects of Biomedical and Behavioral Research and Ryan 1978). Since experimentally inducing subjects, especially children, to behave in an aggressive manner is considered harmful (Barrett 2007), contemporary research on imitative aggression does not use procedures similar to those used by Bandura (1961). Instead, researchers have used proxies which they may use in place of directly exposing participants to aggressive behavior, with the intention of having them imitate it.

Contemporary Research and Media Violence

The proxy most commonly used by contemporary researchers of imitative aggression is violence encountered by participants willingly, through their consumption of media, including movies, television shows, and video games. While a

limited amount of research has found little to no effect of violent media and real-world aggression (e.g., Decamp and Ferguson 2016), the overwhelming majority of experimental research disputes this and suggests instead that increased exposure to violent media causes increased levels of hostile expectations (Hasan et al. 2013), increased aggressive cognitions and affect (Carnagey and Anderson 2004) short- and long-term increases in aggressive behavior (Huesmann, Moise-Titus, Podolski, & Eron, 2003), and an overall negative impact on the effected population (see Huesmann and Taylor 2006 and Wiedeman et al. 2015 for reviews). Thus, although the study design associated with research assessing aggressive or violent media cannot assess the imitative nature of the increased aggression as stringently as Bandura's studies did, the tenets of social learning theory suggest that much of the increases in aggression caused by exposure to violent media may be due to increases in imitative aggression by those who are exposed to it.

Sex Differences

Since Bandura's initial studies, researchers have also been interested in how imitative aggression may affect male and female participants differently. Early work examining possible sex differences in imitative aggression largely showed that males tended to be more aggressive than females were. However, more recent research has not consistently replicated this finding. Specifically, Bandura's seminal bobo doll studies showed that, in most cases, male participants displayed higher levels of both imitative and nonimitative aggression than females did (Bandura 1965; Bandura et al. 1961, 1963a, b). However, more recent research examining sex differences and the effects of exposure to media violence have been mixed. For instance, a study by Bartholow and Anderson (2002) showed that playing a violent video game caused an increase in aggression relative to a nonviolent game in both sexes but that this effect was larger in male participants than it was in female participants. On the other hand, other studies have found that there are no sex

differences when examining the effect of exposure to violent video games (Hasan et al. 2013) or other violent media (Bushman 1995), on subsequent aggressive behaviors.

Conclusion

Bandura's groundbreaking studies demonstrated that viewing specific, aggressive behaviors causes children to imitate those exact behaviors, especially when they are associated with receiving a reward or even a lack of punishment (Bandura 1965; Bandura et al. 1961, 1963a, b). Although contemporary research does not induce specific aggressive actions for ethical reasons (Barrett 2007), research on the effect of media aggression demonstrates that exposure to violent media causes increases in aggressive cognitions, affect, and behaviors (Carnagey and Anderson 2004; Hasan et al. 2013; Huesmann et al. 2003), which may be due, in part, to increases in imitative aggression. Future research on imitative aggression should more closely examine this relationship, to determine the extent to which the increases in aggression are due to direct imitation, rather than more general increases in aggression. Additionally, research should seek to more definitively determine whether men are more susceptible to the effects of media violence than women are or if this is merely an artifact of cultural influences.

Cross-References

- [Aggressive Fantasies](#)
- [Media Violence](#)
- [Physical Aggression](#)
- [Social Cognition](#)
- [Social Learning Theory](#)

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Imitative Assault

- [Imitative Aggression](#)

Immaturity

- [Duration of Childhood](#)

Immediate or Intermediate Recall of Processed Information

- [Working Memory](#)

Immediate-Return Societies

- [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)

Immigrant Parents

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Synonyms

[Intergenerational language transmission](#)

Definition

Immigrant A person who goes to live permanently in a foreign country.

Bilingualism The practice of speaking or signing in two or more languages, with varying degrees of proficiency. Synonym, multilingualism.

Majority, or Societal Language A language spoken by the majority of the inhabitants of a given region.

Minority, or Heritage Language A language which is not the language of the community, spoken by indigenous peoples or immigrants as part of their cultural heritage, includes the whole

range of mastery, from only a few words and incomplete grammar to full fluency.

Introduction

All humans, except victims of heinous child neglect, grow up speaking the language of their caregivers (Pinker 1994; Rhymer 1993). Indeed, given the right circumstances and enough support for it, people become fluent in two or more languages, such that more than half of the world's population is estimated to be multilingual (Crystal 2004). When children are raised in a language from birth, they become members of their caregivers' language community. Children who master a second language before puberty (Hyltenstam and Abrahamsson 2000; Lenneberg et al. 1967) are most likely to learn it without an accent that would mark them as outsiders and can enjoy membership as "insiders" in a second language community. Beyond the instrumental value of enabling direct communication with a larger number of people and access to more economic and cultural resources, participating in an additional language community gives a powerful sense of belonging and strengthens emotional ties with speakers of that language (Gardner and Lambert 1972).

Patterns of Language Use and Abilities Among Immigrant Children

Immigrant parents migrating together to a country where a different language is spoken generally expect that their children will become bilingual in their language of origin, or "heritage language," and the language of their new host country. The parents might attain some fluency or even deep knowledge of the language of their adopted country, but unlike their children, their speech will likely mark them as foreigners there throughout their lives. Although children may start out slowly, even to the point of having a silent period of several months (Tabors 2008), more typically, they learn a new language to "playground standards" (Basic Interpersonal Communication

Skills) within the first year, sometimes within a few months (Cummins 1979a). Even children as young as 6 years have been observed to take on the role of language broker for their slower-learning parents. It takes the child longer to develop enough proficiency for age-appropriate progress in academic programs in the medium of the new language, acquiring Cummins' "Cognitive Academic Language Proficiency," or CALP, within 3–5 years. Finally, proficiency levels asymptote about 8 years post-immigration (Hakuta and D'Andrea 1992). Most developed countries have school programs to transition immigrant children to the societal language, and children need little encouragement to adopt the language and the popular culture of their new peers.

Less certain is the fate of the language of origin. Immigrant parents are often so focused on their children learning the new language, they take the first language (L1) for granted (Jarmel and Schneider 2009). While learning a second language (L2) does not require the loss of the first, without special attention to the first language in the process of learning the second, a weakening or loss of the language of the homeland is more likely than proficient bilingual abilities (Lambert 1977). Thus, in theory, children of immigrants are in an ideal position to establish robust bilingualism that will allow them to participate as full-fledged members of two language communities. In practice, however, that is not always the case.

Language Assimilation Across Generations

The classic timetable for linguistic assimilation into a new language community spanned three generations (Dorian 1982; Haugen 1972): the immigrants themselves remained stronger, or "dominant," in the old language; their children, the second generation, learned or retained the old language but became native or near-native speakers of the new language; and the grandchildren were dominant, or even monolingual in the new language. However, linguistic assimilation in the USA appears to have been

compressed into two generations (Rumbaut et al. 2006; Veltman 2000), or less (Polinsky and Kagan 2007).

“Generation,” in any event, may be too coarse a term to adequately describe the language outcomes for the many different trajectories of immigrants. Hakuta and D’Andrea (1992), in a study of several hundred Mexican-background teenagers in California, subdivided the generations in order to probe more carefully which children would become robustly bilingual, and who would struggle with one or the other language. In their analysis, three generations became six “depths.” Depth 1 comprised those who immigrated after age 10, (with an average of 3 years in the USA at the time of the study); Depth 2 arrived in the new country between ages 5 and 10; and Depth 3 arrived before age 5. The second generation was split according to whether both parents were born abroad (Depth 4) or only one (Depth 5). Depth 6 comprised the third generation, that is, students with at least one parent and associated grandparents born in the USA.

Proficiency measures showed that children at Depth 3 (from the first generation) and Depth 4 (from the second generation) had the strongest skills in both languages. The English of Depth-2 children showed significant progress over Depth 1, but both groups remained dominant in their L1. At the other end of the spectrum, proficiency levels for Depths 5 and 6 were not significantly different from each other. Both showed weak Spanish scores and strong English scores. Importantly, the high level of skill in **both** languages of Depths 3 and 4 demonstrated that progress in English did not depend on loss of Spanish. Interviews revealed that the choice to speak predominantly in the majority L2 shifted before proficiency did. Parent language preferences shifted later, after Depth 4.

Patterns of Bilingual Language Use in the Home

In contrast to children with two parents who spoke the same heritage language in the home, children with parents who immigrated separately from

different countries, or with only one immigrant parent, have different language resources. A common household arrangement for this group, especially popular in Europe and Canada, is for one parent to speak one language to the child and the other to speak another language – so-called OPOL, “one parent/one language.” One of these languages may be the community language, but often the community language will be a third language. De Houwer (2009) investigated family language practices and bilingual outcomes for 1,450 mostly Dutch/French families in Flanders, and she reanalyzed Yamamoto’s (2002) report of 188 bilingual families in Japan. The analysis took into account whether the family used OPOL or another strategy and whether the mother was the source of the minority language. Like Hakuta, de Houwer found that the crucial element was for both parents to speak in the minority language in the home. Fewer than half of the children with parents who spoke together in the societal language grew up speaking two languages, whereas when the parents spoke together in the nonsocietal language, more than 93% of their children spoke both that language and the societal language.

Conclusion: Language Transmission in Bilingual Communities

According to Haugen (1972) and Fishman (1991, 2001), community bilingualism is transitional. When two languages compete in the same domains, one language will win out. Fishman’s advice to maintain or revive bilingualism is for the weaker language to carve out a location or function – e.g., the home or religious observances – where the minority language is used exclusively and language choice does not need to be constantly renegotiated.

Fishman’s cautions are most commonly understood in the context of indigenous languages at risk for extinction, not with a language that ranks high on the UN Language Vitality Scale like Spanish in Miami-Dade County, Florida (UNESCO 2003). Hispanic immigrants are more numerous than native born, and government,

business, and educational leadership are in the hands of the immigrants who control most of the wealth of the region (US Census 2015). Four-fifths share a global language, with millions of speakers in many localities around the world (Moseley 2010). There should be ample support for the “majority-minority” language to be transmitted to succeeding generations. However, researchers have found in Miami that “Depth 4”/second generation children speak mostly “kitchen Spanish” if they speak Spanish at all, and even fewer are literate in their L2 (DCPS 2015; Hassan 2006; Oller and Eilers 2002).

Why would so few children in the second generation there learn or speak the language of their immigrant parents? Two causal factors stand out. (1) Lack of awareness. With continued immigration fueling the overwhelming presence of Spanish on the street and in media in Miami, there is no sense of threat to the language (Glazer 1966; Eilers et al. 2002). Possibly, parents would be more motivated to take specific steps to transmit the language to their children if, instead of full acceptance, there were harsh suppressions against it, like those for example, imposed unsuccessfully on Catalan in Franco’s Spain. (2) Lack of education in Spanish. In Miami, children of immigrants enter a primarily English-only educational system. In most states, including Florida, there is no law precluding education in two languages, and there is a strong research base to support it (Collier and Thomas 2004; Cummins 1979b; Oller and Eilers 2002), but ironically, it is rarely offered. Only a handful of schools offer a dual-language curriculum (CAL 2004; DCPS 2015).

In a running survey over the course of 10 years, several hundred Hispanic-heritage students in Miami from middle school through university, (Eilers et al. 2006; Pearson and McGee 1993) almost all said they wanted their children to learn Spanish. However, on the very same survey, the students gave evidence against their being able to do so. They reported that they, themselves, spoke to their parents at least half in Spanish when the parents spoke to them in “mostly Spanish,” especially if both their parents were recently arrived in the United States. However, when the students were free to choose their language,

with siblings and friends for example, most reported speaking “mostly English with a few words of Spanish,” a pattern observed within the first generation, within their first months in this country (Pearson and McGee 1993). Unless these students, when they become parents, were to make a more intentional effort than their parents did to maintain their heritage language in the home and advocate for heritage language programs in their schools, they would be unlikely to reverse the natural shift toward the majority language.

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► Bilingualism

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Immoral

► Monoamine Oxidase and Antisocial Behavior

Immune Response to Disgust and Disease Cues

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Synonyms

Disease cues and immune response; Disgust and immunity

Definition

The degree to which the immune system responds to disease cues.

Introduction

Pathogens including viruses, protozoa, bacteria, and parasites, including helminths (worms), ticks, and mites, have been an important selective force for all multicellular organisms. Pathogens and

parasites take energy and resources from their hosts. They use their hosts to reproduce and make copies of themselves siphoning off calories and interfering with physiological processes. There is evidence that some pathogens and parasites alter hosts' behavior and physiology to their own adaptive ends (e.g., some parasites sterilize their hosts). Two systems have evolved to prevent, mitigate, and eliminate infection. The immune system, a set of specialized cells and mechanisms, is mostly engaged when parasites and pathogens have entered the organism. The immune system fights infection by, for example, producing enzymes to destroy the structure of the parasite or creating antibodies that can neutralize pathogens. The other adaptive system, sometimes called behavioral prophylaxis or the behavioral immune system (BIS), is a suite of evolved strategies to minimize the risk or prevent the introduction of pathogens and parasites into the organism. Examples in animals include selectively grazing away from feces or avoiding sick conspecifics. The human BIS is thought to center around the emotion of disgust. Recently, researchers have discovered that the BIS and the immune system are responsive to one another. For example, there is some evidence that immune vulnerability makes people more sensitive to disease cues (Miller) and that disease cues (e.g., seeing a sick looking person) can activate the immune system.

This entry will focus on human literature showing immune response to disgust and disease cues. The functional rationale behind this work is that perceiving disease cues is indicative of likely imminent infection and the most adaptive response is an anticipatory mobilization of the immune system.

Measure of Immune Activation: Cytokines, Antibodies, Proteins, and Body Temperature

Immune response in psychological studies is measured both in blood and in saliva. Blood is often considered a better and more direct method. However, salivary markers are easier to collect. Because the mouth is one of the main entryways

for pathogens, we might expect immune defenses to be mobilized preferentially in the mouth (Stevenson et al. 2011). A few kinds of immune marker are measured in these studies. Cytokines are proteins that act as messengers for the rest of the immune system and can activate other cells (Delves et al. 2011, p. 6). In particular, these kinds of studies are interested in inflammatory cytokines, messengers that recruit cells to sites of infection. However, it's important to remember that cytokines do not have a unitary function and many cytokines have both anti-inflammatory and pro-inflammatory properties. Immunoglobulins are antibody molecules that usually bind to pathogens neutralizing them or tagging them as "foreign" for other cells to clean up (Delves et al. 2011, p. 36). Immunoglobulins have classes based on their variable molecular structure. Most of these studies focus on what are commonly termed "innate immune" markers; these aspects of immunity are the first line of defense against pathogens because they distinguish the body's own cells from foreign and infected cells without previous exposure to the pathogen.

One study (Stevenson et al. 2012) also looked at body temperature. Body temperature may be increased to (1) make the body less hospitable to pathogens that are adapted to live in a certain temperature range and (2) increase metabolism and thus hasten the production of antibodies and other immune components (Kluger et al. 1996).

Thermal and Immune Response to Disease Cues

Five studies have investigated how exposure to disease cues or disgust activates aspects of the immune system. Schaller et al. (2010) conducted the first study, randomly assigning 28 participants (both men and women) to either watch a neutral slideshow and then a gun slideshow (fear condition) or a neutral slideshow and then a disease slideshow (disgust/disease condition). Participants came in on separate days and had blood drawn before and after the neutral slideshow and the experimental slideshow. The blood samples were incubated with a compound that the immune

system perceives as a bacterial infection and then were measured for inflammatory cytokine interleukin-6 (IL-6). Participants in the disease condition showed greater increase in blood IL-6 response (23.6%) than participants in the fear condition (6.6%).

Stevenson et al. (2011) examined salivary immune response to disgust. Stevenson et al. (2011) randomly assigned 92 male participants under 30 years of age to a disgust condition, a negative affect control condition or a neutral control condition. They measured antibody salivary immunoglobulin A (IgA) and inflammatory cytokine TNF-alpha (TNF- α).

They found a decrease in IgA and an increase in TNF- α in the disgust relative to control conditions. Disgust stimulates increased salivation, possibly to protect the tooth enamel from intestinal acids. The authors surmise that this is why there was a decrease in the concentration of IgA.

Stevenson et al. (2012) conducted another study on 74 male participants randomly assigned to look at disgusting food, pleasant food, nonfood-related disgusting images, and a negative affect control. Again they measured IgA and TNF- α , but they also measured core body temperature (BT). IgA showed a different pattern for disgusting food than for nonfood-related disgusting images. The disgusting food condition showed a sharp increase in IgA posttest and a subsequent decrease. The nonfood-related disgust condition showed a decrease in IgA like the previous study. TNF- α increased across both disgust groups (food and nonfood) relative to both control groups (food and negative). This was the first study to demonstrate a significant increase in body temperature from disgust induction; participants in the disgust conditions were 0.3 °C warmer than the participants in the control conditions.

Ersche et al. (2014) looked at salivary immunological reactions in men, 31 cocaine addicts and 30 controls. Like the previous Stevenson et al. study, they compared food and nonfood images in both the disgust and neutral categories.

They measured salivary cytokines IL-6, IL-1beta (IL-1 β), TNF- α , interferon-gamma (IFN- γ), and IL-12, IL-10, and IL-8. All group

comparisons controlled for an inflammatory marker known as C-reactive protein (CRP) which was significantly greater in cocaine addicts. They found IFN- γ , IL-1 β , IL-6, and TNF- α were significantly increased after viewing disgust stimuli in all men.

Stevenson et al. (2015) noted that previous studies haven't found a relationship between self-reported disgust and immune activation. They designed a study that uncoupled disgust and disease stimuli creating three sets of images: (1) disgusting but minimally disease related (e.g., a dead cat), (2) disease related but minimally disgusting (e.g., a woman sneezing), and (3) a negative control. Thirty-nine male participants viewed all sets of images 1 week apart. In this study, none of the conditions caused an increase in salivary TNF- α or IgA. The researchers found that TNF- α increased in the subset of participants with high trait disgust for both the disgust (1) and disease (2) image sets.

Conclusion

The examination of how disease- and disgust-related emotions and cognitions influence immunity is still in early stages; these studies have been conducted on mostly male participants with mostly salivary markers. Thus far it seems that many inflammatory cytokines, some antibodies, and body temperature are influenced by exposure to disgusting and disease-related cues.

Cross-References

- Disease Avoidance Hypothesis
- Disgust
- Immune System Benefits

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Introduction

The immune system is an essential biological system which ensures the survival of the organism by providing protection against offending agents (pathogens – including bacteria, viruses, fungi, parasites, etc.). Intactness of immune system is required for the survival of the individual. Optimal functioning of the immune system is essential for a healthy body. Either a compromised or overactive immune system can be associated with health hazards. A compromised immune system increases the vulnerability to acquire infections, whereas an overactive immune system has damaging effects on body's own tissue (van der Most et al. 2011). Immune system and good health have a bidirectional relationship, one promoting the other (Murray 2013). Many factors related to day-to-day life (e.g., life style, exercise, diet, stress, substance use) influence the immune system (Murray 2013).

Structure and Functioning of the Immune System

The immune system comprises a group of cells and organs distributed in the body which together provide protection against pathogens entering through, or multiplying in, any part of the body (Delves and Roitt 2000; Janeway et al. 2005). It is composed of primary (bone marrow and thymus) and secondary (lymph nodes, spleen, and mucosa-associated lymphoid tissues {MALT}) lymphoid organs. The primary lymphoid organs are responsible principally for the production of immune cells and their education. The developing immune cells undergo a process of positive selection and negative selection in these primary lymphoid organs. In positive selection the cells recognizing their MHC molecules survive. In negative selection lymphocytes that recognize self-antigens are eliminated by inducing apoptosis or anergy (state of unresponsiveness to antigenic stimulus). The secondary lymphoid organs have designated zones for T cells and B cells within them. The naïve T and B lymphocytes get exposed to the

Immune System

► Physical Health

Immune System Benefits

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Synonyms

Defense system

Definition

The benefits an individual receives due to its own immune system.

antigen in these organs, following which they mature and proliferate.

The immune system is divided broadly into innate (natural) and adaptive (acquired) arms (Delves and Roitt 2000). The first line of defense against any microorganism is an intact skin and mucous membranes. *Innate immune system:* This arm of the immune system is not directed against any specific pathogen but instead provides protection against all infection in general. It is present since birth by virtue of an individuals' genetic or constitutional makeup. The components are pre-formed and fully active; thus, they can function immediately upon entry of the microorganisms. The innate immune system includes various cells like – neutrophils, basophils, eosinophils, mast cells, macrophages, and natural killer cells. These cells can kill the pathogen either by phagocytosis and subsequent intracellular killing (neutrophils, macrophages) or by releasing certain chemical mediators (eosinophil, basophil) (Delves and Roitt 2000).

Adaptive immune system: This arm of immune system recognizes and mounts an action against specific components of the pathogen called an antigen. Activation of the acquired immune system requires prior exposure to the offending antigen. It takes several days before becoming fully effective. This arm of the immune system improves with repeated exposure to the antigen by the virtue of its memory component. Adaptive immune system acts by the proliferation of lymphocytes (T and B cells) that possess receptors which can specifically identify and attach with the antigen. Levels of antigen, strength of binding between antigen and its receptor located on the surface of lymphoid cells, as well as period of antigenic exposure determine the immune response (Zinkernagel and Hengartner 2001). Adaptive immune system has two arms, namely, humoral immunity and cellular immunity. B lymphocytes, plasma cells, and antibodies produced by them contribute to humoral immunity. T lymphocytes (classified mainly into helper T cells, cytotoxic T cells, and regulatory T cells) contribute to cell-mediated immunity.

Antigen-presenting cells (APCs) and complement system connect the innate arm with the

adaptive arm of the immune system (Rus et al. 2005; Yatim and Lakkis 2015). Antigen-presenting cells (macrophages and dendritic cells) capture large structures and break them into smaller fragments, mostly peptides. APCs process the antigenic peptides, pack them into major histocompatibility complex (MHC) proteins and present them to T lymphocytes possessing the appropriate T cell receptors. APCs also provide additional costimulatory signals, causing activation of the specific subset of T lymphocytes. This leads to clonal proliferation and differentiation of those T lymphocytes. Subsequently, antigen-specific B lymphocytes become activated (by the APCs and helper T cells) and produce antibodies. There is exponential increase in the number of antigen-specific clones of both T and B lymphocytes in response to any antigen. This is followed by the death of most of these lymphocytes; however, a few of them survive to become the long-lived memory cells. Memory cells ensure rapid and more effective immune response on a subsequent encounter with the same pathogen. Several chemical mediators' including chemokines and adhesion molecules are also involved in signal transfer and appropriate coordinated function of the immune system (Yatim and Lakkis 2015). The complement proteins belong to the innate arm of the immune system. Activation of the complement system can occur via three pathways (classical, alternate, and lectin binding pathways). The classical pathway activation requires antigen-antibody complex formation and thus involves the adaptive immune system. Alternative pathway activation and the lectin pathway are considered as a component of innate immunity because they are activated by various components of the pathogens and do not need antigen-antibody complex formation for activation.

Benefits of Immune System: Evidences

The immune system can be modulated by stress, and it helps in combating stress. The health hazards of stress result from failure of the immune system (activation of the hypothalamo-pituitary-

adrenal axis resulting in hypercortisolemia and increased catecholamines leading to down-regulation of the immune system) (Murray 2013). Life style interventions, stress management, relaxation techniques, and positive mood states are known to boost the immune system and thereby attenuate the stress response (Murray 2013). Optimal functioning of the immune system is responsible for producing a state of subjective well-being. Good sleep is also associated with optimal immune function and vice versa (Murray 2013). Evidence also supports the hypothesis that sex hormones (estrogen, testosterone) have an immunomodulatory effect (Foo et al. 2017). Hence, an optimally functioning immune system is likely to boost sexual function.

The mucosal surfaces of the body (e.g., mucous membranes of the gastrointestinal tract, respiratory tract, urogenital tract) are exposed to varied pathogenic bacteria and antigens daily. Mucosal immunity, which is mainly provided by immunoglobulin A produced locally (secretory IgA) and secreted into mucus, is largely responsible for dealing with these antigens. For example, a variety of foreign antigens enter the gut via food. The local immune system of the gut has evolved sufficiently to balance immune response to ingested pathogens, gut microbiome, and ingested antigens. The gut-associated lymphoid tissue (GALT) is able to detect and subsequently kill pathogens entering the gut. At the same time, it prevents vigorous immune response against food antigens by a phenomenon called oral tolerance. *“Oral tolerance is classically defined as the suppression of immune responses to antigens (Ag) that have been administered previously by the oral route”* (Faria and Weiner 2006). Oral tolerance has therapeutic implications in prevention of autoimmune disorders, hypersensitivity reactions, and other conditions where the immune system is dysregulated (Faria and Weiner 2006; Wawrzyniak et al. 2017). Inability of GALT in balancing these functions adequately may lead to autoimmune disease. Autoimmune diseases (e.g., autoimmune anemias, Graves’ disease, systemic lupus erythematosus, rheumatoid arthritis, scleroderma, multiple sclerosis, etc.) are caused due to self-reacting T cells or autoantibodies.

Inflammatory bowel diseases (IBD), for example, are caused due to an immunological imbalance of the intestinal mucosa. T lymphocytes acting against self-antigens lead to a chronic inflammatory condition in IBD patients (Davies and Abreu 2015). Oral tolerance therapy has been examined as a strategy for preventing and treating these conditions.

Gut microbiome also contributes to the human immune system. The gut microbiome has a symbiotic relationship with the host (human). Gut microbiome produces local immunity (by encountering the pathogens that comes in contact with gastrointestinal tract) as well as helps in development of the brain and regulation of behavior (Heijtz et al. 2011; Round and Mazmanian 2009). Any alterations to the gut microbiome are likely to alter the immune system. Hygiene hypothesis proposed that the increased incidence of atopic diseases including asthma is due to a lower incidence of infection in childhood due to vaccination, increased antibiotic use, and reduced exposure to helminths. Though there is debate surrounding this concept, there is no denying that for a healthy immune system to develop, parasitic helminths and commensal microbial organisms are vital (Bloomfield et al. 2016; Stiemsma et al. 2015). Evidences suggest manipulation of the intestinal microbiome may help to treat and even prevent immune dysregulation in the form of atopic diseases.

Immunodeficiency disease results when the immune system of the body is impaired. Primary immunodeficiency diseases result from inherited defects in any component of the immune system. Secondary immunodeficiency diseases occur as a consequence of immunosuppressive conditions like HIV/AIDS, chemotherapy, autoimmunity, etc. Immunodeficiency conditions (DiGeorge syndrome, Wiskott-Aldrich syndrome, Chediak-Higashi syndrome, etc.) increase the susceptibility of the individual to infections and even certain cancers.

Breast milk contains secretory IgA, and thus, breast-feeding in neonates and infants helps in immune development. The immune system in return protects the infant from infections, allergy, and autoimmune disorders (Jackson and Nazar

2006). Evidence suggests that critically ill patients (following sepsis, postsurgical, and post-trauma patients) receiving immune-enhancing enteral nutrition had lesser infection rate. These patients also spent fewer days in ventilator and had shorter hospital stays (Beale et al. 1999). This indicates that immunomodulation has beneficial effects on general health by facilitating recovery from critical illnesses. The immune system also has an important role in cancer pathogenesis. The pathogenesis of cancer is mediated through disruption of immune regulation, and the immune therapy for cancer treatment restores this breach in the immune system (Andersen 2015). Hence, the immune system has a substantial role in preventing cancer.

The immune system interacts with the neurocircuitry and neurotransmitter system involved in regulation of behavior. The immune system also regulates stress response, neuronal growth, as well as degeneration (Miller et al. 2017). Hence, an optimal functioning of the immune system is highly essential for mental well-being. Recent evidence suggests that aberrations in the immune system (particularly in the cytokine profiles) are associated with development of neurodevelopmental disorders like – autism spectrum disorders (ASDs) (Masi et al. 2017).

An exaggerated response of the immune system during inflammation results in tissue damage. Neuroinflammation results in neurodegeneration, abnormal neurotransmission, and aberrant neuro-conduction. This has been implicated in the development of neuropsychiatric disorders like schizophrenia and mood disorders (Thibaut 2017). Restoring the integrity of immune system may be beneficial in recovering from mental illnesses.

Mind-body therapies (yoga, meditation, tai chi, and qi gong) have immune-boosting effects. These psychological therapeutic techniques produce a relaxation response via reduction of anxiety and stress. Evidence supports the hypothesis that these therapeutic techniques used over 7 to 16 weeks reduce the level of inflammatory markers (c-reactive protein, interleukin –6) and to some extent improves antiviral-related immune response (Morgan et al. 2014).

Conclusion

The immune system plays a pivotal role in protecting the humans from pathogens and harmful agents. An intact and well-functioning immune system is essential for good health and longevity. Across the lifespan of an individual, the efficiency of immune system changes. Similarly, with time, the immune system in the organism evolves to meet the needs of encountering differently evolving pathogens (e.g., mutated microorganisms, new environmental toxins). To receive the continuous benefits from the immune system, appropriate measures (e.g., good diet, better life style measures, appropriate preventive measures) need to be taken so as to maintain the integrity of immune system.

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Immunity

- ▶ Disease Avoidance
- ▶ Pathogen Risk

Immunocompetence

- ▶ Pathogen Disgust and Perceptions of Attractiveness

Immunocompetence Handicap Hypothesis

- ▶ Pathogen Load and Attractiveness

Immunologic Protection

- ▶ Pathogen Protection

Impact of Early Theory on Charles Darwin

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Introduction

Charles Darwin was the one of the greatest minds of the nineteenth century, with remarkable synthetic abilities and powers of observation. However, ideas about evolution had been around for some time. In fact, aspects extend back to the ancient Greeks and Romans. While not every historical development can be incorporated into this essay, taking a historical perspective on the development of evolutionary theory allows one to appreciate more fully the extraordinary clarity and understanding possessed by Darwin.

Pre-Renaissance

Twenty centuries before Darwin, the Greeks were developing an understanding of the origin and development of life. Thales (c. 636–546 BC) presented a mechanistic explanation for the world. He emphasized a physical basis for all things, proposed water as the basic building block of all living and nonliving matter, and was one of the earliest precursors of modern scientific thought. Empedocles (c. 495–435 BC) was responsible for the four classical elements approach to understanding the world – water, air, earth, and fire – but also discussed the evolution and origin of organisms. He believed the parts/organs of organisms formed first and would then come together by chance to form different organisms. Those organisms with good combinations survived; those with bad combinations did not. These mechanistic understandings of how things worked gave way to the Greek Classical Period as illustrated by Aristotle (Bardell 1994; Kirk et al. 1983).

Aristotle (384–322 BC), a student of Plato, was the foremost biologist of his time. His ideas about physiology were so sophisticated that they were not demonstrated to be incorrect until the seventeenth century, while his descriptions of marine species endured until the eighteenth and nineteenth centuries. His notions about embryonic development were elaborated into a theory of epigenesis in which the early stages of a being do not resemble the adult form, radical for the time since it was generally accepted that embryos were scaled-down versions of adults. Aristotle originated the concept of genus and species. Of particular importance for things to come was Aristotle's arrangement of organisms in a static hierarchy according to their complexity. Aristotle discussed the work of Empedocles; Darwin commented upon both Aristotle and Empedocles in the *Origin* (Bardell 1994; Kirk et al. 1983).

Approximately 200 years later, Lucretius (c. 99–55 BC), a Roman philosopher, described the development of the world and all things in it through natural processes, i.e., without any supernatural involvement. While these ideas were not necessarily mainstream, they influenced the approaches of some of the philosophers who

followed. For example, Augustine of Hippo, a fourth-century theologian, argued that the creation story in the Book of Genesis should not be taken literally. Rather, he stated that forms of life had changed slowly over time. Thomas Aquinas (1225–1274) built upon and refined the ideas of both Aristotle and Augustine and “perfected” the Great Chain of Being which went on to influence scientific thinking for centuries to come. However, even Aquinas recognized that nature was a force that worked upon the natural world and its inhabitants – albeit following supernatural guidelines. Darwin's ideas regarding causation can be traced back to Augustine. Darwin also discussed Aquinas' work 600 years later with his colleague Asa Gray (Kirk et al. 1983; Lovejoy 1936; Maurer 2004; Phipps 1983).

Renaissance

The sixteenth and seventeenth centuries saw an explosion in the naming and identification of plants and animals. The greatest classifier of both plants and animals of the period was an Englishman, John Ray (1627–1705), who combined his interests in natural history and theology. Ray made the first distinction between monocotyledonous (having one embryonic leaf in the seed) and dicotyledonous (having two embryonic leaves in the seed) plants. He also identified a group of animals including bats and whales that possessed hair, breathed with lungs, had a heart with two ventricles, and gave birth to live young. These animals would eventually be called mammals, but Ray was the first to identify them as a group based on similar anatomical characteristics. His masterwork, the three-volume *Historia Plantarum* (1686–1704), anticipated the work of future scientists by recognizing the fundamental validity of the species concept and the possibility of variation within breeds, even though he viewed species as unchanging. Ray also made an attempt to synthesize science and religion that had a far-reaching impact. He argued that the order in design of things in nature demonstrated the existence of a benevolent and omnipotent creator, and he suggested most of the familiar examples of

purposive adaptation that some still use today to question the validity of evolution by natural selection. These include the structure of the eye, the hollowness of bones, the stomach of a camel, and the armor of the hedgehog (Eiseley 1958).

Post-Renaissance

Explorations of new and uncharted lands during the Renaissance contributed to a heightened interest in nature among both scientists and philosophers and a decrease in reliance upon the classical writings of antiquity. Georges-Louis LeClerc, Comte de Buffon (1707–1788), a central figure in the intellectual history of eighteenth-century science in Europe and a contemporary of Linnæus, exemplifies this interest in nature. Buffon is best known for his 44-volume work, *Histoire Naturelle* (1749), which dealt with everything then known about natural history. At the time, Buffon was more widely read than Linnæus (Eiseley 1958; Roger and Williams 1997).

Buffon's influence on the development of the theory of evolution is often underestimated. He contributed four major ideas that addressed central themes evolutionists would later address. First, Buffon recognized that there was some type of relationship between apes and humans. This is important because religious opinion at that time denied any relationship and emphasized *man's* domination over the earth. Second, Buffon recognized not only the biological reality of the species concept but also how it is applied in nature. Simply put, he stated that organisms that are not of the same species cannot interbreed. Third, he described the formation of the Earth by existing processes, not by supernatural intervention. Buffon was one of the first to suggest that the world was considerably older than many believed. Finally, Buffon discussed the altriciality (helplessness) of humans as compared to other species, conducted the first longitudinal human growth study, and thought that heat exerted a considerable influence on the growth of the body, thus supporting the importance of the environment in determining bodily changes. Each of these ideas are building blocks upon which others, including

Charles Darwin, stood. Darwin did, in fact, acknowledge Buffon's work in the *Origin* though he did not discuss it in detail (Eiseley 1958; Roger and Williams 1997).

Simultaneously, Swedish botanist Carl von Linnæus (1707–1778) contributed to the development of evolutionary ideas through his interests in classification and ecology. Linnæus' *Systema Naturæ* described all known plants and animals of the time and established the principles of modern taxonomy. Linnæus was more sophisticated than the previous scholars in his use of the terms genus and species, applied to specific levels in his hierarchical classification scheme, as he began with a careful description of species. Then, based upon morphology, he grouped species into genera, genera into orders, orders into classes, etc. *Systema Naturæ* was revised numerous times; the tenth edition (1758) included humans. This was important as, similar to Buffon's discussions of apes and humans, Linnæus explicitly recognized the structural similarities between humans and other animals. Humans were classified under the category Anthropomorpha along with nonhuman primates, bats, and sloths. This classification system has existed, virtually unchanged, for over two and a half centuries. While the Linnæan taxonomy was non-evolutionary, reflecting the static nature of life and unchanging species, it has been key to the development of evolutionary theory as we could not talk about evolution without widely shared and accepted names for genera and species. Darwin incorporated Linnæus' concepts both directly and indirectly via his discussions of nature and, of course, through use of the classifications (Eiseley 1958; Fara 2003).

The French Revolution

Following on the heels of Buffon and Linnæus and exemplifying the French Revolution period, Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1774–1829), was one of the most outspoken intellectuals on the ideas of progress and change. He saw each species as embarked on a journey toward perfection with new species

created at the lower end of the scale by spontaneous generation; thus, there would be no gaps in the ascending progression of forms (Eiseley 1958). He was, in short, an evolutionist.

In *Philosophie Zoologique* (1809), Lamarck argued natural processes could result in radical change in an organism during its lifetime, and organisms could make unlimited progress, not only by adapting to local environmental conditions but also by moving up the evolutionary scale. He suggested that organisms were driven to perfection by an internal force, called vitalism. Somewhat similar to Aquinas' Great Chain of Being, he arranged species in a hierarchical order from one-celled forms all the way to humans; it was a linear and progressive hierarchy of complexity. It was evolutionary as he was addressing the transformation of species. He was the first to recognize the taxonomic importance of a vertebral column and use it as a taxonomic marker for species. He was also the first to use "biology" (*biologie*) to describe the new emerging science (Bowler 1996; Eiseley 1958).

Lamarck is remembered by most people for an idea that he did not originate, the development or atrophy of organs through use or disuse and the transmission of their condition to offspring. In fact, this idea of acquired characteristics was widely held among people at that time. The important point about Lamarck is his emphasis on change. He argued that the discontinuities in the progression of forms were due to local and gradual adaptations by each species to their specific environmental circumstances, achieved through the animals' volition. These ideas are particularly important in the development of evolutionary thought because Lamarck challenged the accepted dogma of the natural world as static (Eiseley 1958). Darwin read Lamarck early in his academic career – while investigating *Flustra* invertebrates and, later, beetles (Desmond and Moore 1991). Near the end of and following the French Revolution period, three distinct local intellectual traditions arose in Europe – French Environmentalism, English Natural Theology, and German *Naturphilosophie*. They, too, played a role in shaping Charles Darwin and modern evolutionary theory.

Environmentalism in France

The importance of the environment in sculpting all life forms had been recognized for roughly 1500 years pre-Renaissance, and the Renaissance conditioned people to expect new animals and plants in each new part of the world explored. Thus, by the 1700s, many viewed the environment as *the* primary factor in shaping all living forms. Environmentalism's influence on understanding the human condition reached an apex with the writings of Jean-Jacques Rousseau (1712–1778) in France. Rousseau developed the idea of the "noble savage," that people who lived away from civilization in simple tribes "with" nature were straightforward, self-sufficient, democratic, and honest. Rousseau built upon the work of Lucretius, speaking of the "noble savage" environment as an ideal against which humanity should continue to measure itself. He recognized that our species had changed physically over time, commented upon the struggle for existence, and discussed the concept of "perfectibility" that had no goal or design. The environmentalist tradition had considerable influence outside of France, and one of its most important supporters was Erasmus Darwin, Charles Darwin's grandfather (Bowler 1996; Eiseley 1958).

Natural Theology in England

Following upon the earlier work of John Ray, William Paley (1743–1805) more fully developed the idea of the perfection of living organisms. Paley's *Natural Theology: or, Evidences of the Existence of the Deity, Collected from the Appearance of Nature* (1802), begins by illustrating the argument from design and the existence of a creator. According to the doctrine of *Natural Theology*, everything in nature reflects the beauty and perfection of the god who designed it. Paley's work contributed to the natural theology position by collecting a large number of examples of the perfection of design. He is best known for his watchmaker analogy. *Natural Theology* was a best seller in its time and was read by Charles Darwin just after completing his

degree at Cambridge. In fact, Paley's works were part of the curriculum at Cambridge, and Darwin remarked upon how much he admired them (Desmond and Moore 1991; Eiseley 1958; Phipps 1983).

Naturphilosophie in Germany

At the same time that *Natural Theology* and *Environmentalism* were becoming popular in England and France, respectively, *Naturphilosophie* was growing in Germany. This approach emphasized observations and comparisons of diverse types of animals and plants with the goal of identifying features shared in common. *Naturphilosophie* saw all life as underpinned by certain basic archetypes (*Bauplans*), which have ever more perfect manifestations as one moves up the Great Chain of Being. Again, there were similarities here with ideas being expressed by Lamarck and previously by Linnæus. One of the co-founders of the *Naturphilosophie* tradition was Johann Wolfgang von Goethe (1749–1832). While Goethe is best known for his literary accomplishments, he was also interested in science and studied, among other things, anatomy. Goethe's observations provided support for ideas about the continuity of anatomical structures across species – as opposed to the uniqueness of humans. He, too, argued that animals are shaped by their environments (Goethe and Naydler 1996; Lovejoy 1936).

Outside of Germany, *Naturphilosophie* had a number of supporters. Among them was Richard Owen (1804–1892), England's most prestigious zoologist and paleontologist. Owen is remembered for a variety of paleontological discoveries; however, it is his careful definition of analogy and homology that is important to the development of evolutionary theory. The terms analogy and homology were widely used at the time, particularly in discussions of comparative anatomy, but they were often used synonymously. Owen clarified the differences based on form and function and believed that evolutionary processes were at work in the formation of species. Owen and Darwin worked together on the specimens Darwin brought back from his time on the *Beagle*

though they eventually parted ways due to Darwin's views on transmutation (Bowler 1996; Eiseley 1958).

The Darwins

The links across the centuries between these various approaches and theorists with Charles Darwin's theory should be apparent. There is almost 2000 years of discussion about the natural processes of organic change upon which Darwin would build. Thus, the stage for the development of Charles Darwin's theory of evolution was set. As can be seen from the preceding paragraphs, Darwin did not originate ideas about evolution, change, or the impact of the environment. Rather, he synthesized them and added much new supporting data. One family member, in particular, played a role in setting the intellectual stage and in laying the groundwork that would make Charles' lifestyle possible. This was Erasmus Darwin.

Erasmus Darwin

Charles Darwin's grandfather, Erasmus Darwin (1731–1802), attended Edinburgh Medical School and went on to become a very successful physician, accumulating the considerable wealth that would provide the financial base allowing Charles Darwin to pursue the life of a scientist/scholar. Erasmus Darwin's most important scientific work, a work that would establish him as the leading medical author of the day, was *Zoonomia: or, the Laws of Organic Life* (1794–1796). It marked the beginning of the Darwin family's interest in evolution. Erasmus was convinced that forms remotely similar to living ones were ancient and were their likely ancestors, based on a comparison of morphologies. He saw nature as dynamic and active; species were not static but ever-changing and developed structures that were most suitable to their environments. He also touched on the problems brought on by overpopulation and competition for resources; affirmed the close relationship between monkeys, apes,

and humans; recognized the importance of sexual reproduction in the evolution of species; and was concerned about male competition. Similar to Lamarck, the processes he described also incorporated the animals' volition. Thus, in *Zoonomia*, Erasmus Darwin laid the groundwork for many of the themes that Charles would go on to explore in-depth in either the *Origin* (1859) or the *Descent* (1871). Although Erasmus died before Charles was born, Charles familiarized himself with his grandfather's work at a young age and read it at least twice more over the course of his lifetime (Bowler 1996; Desmond and Moore 1991; Eiseley 1958; King-Hele 1999; Smith 2010).

Charles Robert Darwin

1809–1827

Charles Darwin (1809–1882; hereafter referred to as “Darwin”) received most of his early schooling from his sister, Caroline, particularly in Biblical studies, until joining his older brother at the Shrewsbury School at age 9. Most of Darwin's early education was unremarkable. He was a lackluster student, at best. However, there were several events throughout his teenage and young adult years that played roles in shaping the naturalist and evolutionist he would become. At age 16, he was sent by his father to Edinburgh to join his brother, Erasmus, who was studying medicine. Although Charles did not ultimately pursue a medical degree as his father desired, he did join a student society for the study of natural history – the Plinian Society – that was known for its radical and heretical ideas and discussions. Doing so introduced him to Robert Grant (1793–1874), a Lamarckian and avowed evolutionist, who mentored Darwin in both naturalist skills and evolutionary thinking. Grant pushed Darwin to read Lamarck while Darwin assisted Grant in investigating the status of marine invertebrates. It was Grant's teachings that shaped Darwin's approach to evolution years later. During his final year at Edinburgh, Darwin took a natural history course taught by Robert Jameson (1774–1854). This course granted Darwin access to the Edinburgh University museum, one of the

largest in Europe, where he spent considerable time learning historical geology. He also learned avian taxidermy there from John James Audubon. Both geology and taxidermy would serve him well on the *Beagle* (Bowler 1996; Desmond and Moore 1991; Eiseley 1958).

1827–1836

Darwin left Edinburgh in April 1827 and, early in 1828, went to Cambridge to study for the clergy, again at his father's insistence. As with the other institutions he attended, Darwin's career at Cambridge was largely unremarkable. However, he became enamored with beetles and developed a reputation for his beetle collection skills among fellow collectors. A significant event in Darwin's intellectual development occurred during his junior year when he got to know and became friends with John Henslow (1796–1861), Professor of Botany. Darwin took Henslow's botany course, and they went on field trips together, becoming close friends. Darwin's interests shifted from beetles to plants, and he wanted to follow in Henslow's footsteps. He also developed strong interests in traveling to distant lands. He was convinced that there were many new beetles, as well as other forms of life, to be discovered (Eiseley 1958). Darwin collected many plant specimens while on the *Beagle* specifically to send back to Henslow (Desmond and Moore 1991).

At the same time, Darwin was invited on a small geological expedition by Adam Sedgwick (1785–1873), a Cambridge geology professor. The expedition with Sedgwick lasted only weeks but served to further Darwin's interests in the wonders of geology. When Darwin returned to Cambridge, he found an invitation to accompany Capt. Robert Fitzroy (1805–1865) on a 2-year survey of coastal South America on the *H.M.S. Beagle*. Darwin went to London to meet with Fitzroy and discovered that the voyage aboard the *H.M.S. Beagle* was scheduled to last 3 years, not the originally proposed 2. In actuality, the journey lasted 4 years and 10 months (from December 1831 to October 1836), and the data, specimens, and observations Darwin collected while on the trip formed the cornerstone of all

his future work (Desmond and Moore 1991; Eiseley 1958; Keynes 2003).

1836–1839

Darwin arrived back at Shrewsbury on October 4, 1836, and set about the huge task of cataloging all the notes and the specimens he had collected during the voyage. He used Cambridge as his initial base of operations and started writing the official version of his diary, *Journal of Researches*, to be published by the British Admiralty. His first presentation in London on the geology of the coast of Chile was warmly received and impressed Charles Lyell (1797–1875), the preeminent geologist of the time. Darwin had read two volumes of Lyell's *Principles of Geology* (1830) while aboard the *Beagle* and later stated it had been a huge influence on him. They became lifelong correspondents. By March 1837, Darwin had moved from Cambridge to London where he continued writing his accounting of the journey and, in doing so, confronted the issue of the changing nature of species. Darwin had concluded that species were not fixed but could form new species gradually over long periods of time. By July 1837, he had begun working on notes about species change which he would call the *Transformation of Species*. These notes are important because they would later serve as proof of Darwin's priority to ideas about species change and evolution in his exchanges with Alfred Russell Wallace (Desmond and Moore 1991; Eiseley 1958).

The period from 1837 to 1839 was among the most productive in Darwin's life as it was then that his ideas regarding natural selection took root in a series of notebooks and manuscripts where he outlined his thinking about science, religion, and evolution. During this period, there were several critical points in his intellectual development. In September 1838, Darwin read Thomas Robert Malthus' (1766–1834) *An Essay on the Principle of Population* (1798) which played a powerful role in shaping Darwin's thinking about competition, population size, and species change. Malthus recognized that human population size

could increase geometrically, while food supplies could only increase in a linear arithmetical fashion, leading to competition, population crashes, and the struggle for existence. While these years were replete with intellectual excitement, Darwin was also keenly aware of the religious, social, and political implications of his ideas (Bowler 1996; Desmond and Moore 1991; Eiseley 1958).

1839–1857

Two and a half years after the return of the *Beagle*, Darwin published his first book. The *Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle* (1839) received generally positive reviews and served notice of the reception his future works would receive. It was also during this period that Darwin read two of Linnaeus' essays regarding the economy of nature. His next book, *Structure and Distribution of Coral Reefs* (1842) was a technical book that Darwin did not expect would have much circulation, and he was correct. By the spring of 1844, Darwin had expanded his notes started in 1837 into a full 189-page essay on evolution. He realized the power of his words and found himself in a quandary about publishing it. After considerable thought, he decided not to publish at that time and moved on to a new project on the geological observations he had conducted while on the *Beagle*. There was a growing interest in ideas about transmutation of species; although not popular in Charles' intellectual circles, evolutionary ideas were in the air (Desmond and Moore 1991).

The year 1851 proved to be an extremely important professional time for Darwin as he met Thomas Henry Huxley (1825–1895). Huxley served as surgeon and naturalist aboard the *H.M.S. Rattlesnake* for 4 years where he also studied marine invertebrates and published a number of influential papers. His association with Darwin was solidified after Huxley reviewed Charles' barnacle books (*Living Cirripedia*, 1851, 1854) and incorporated Darwin's observations into his own natural history articles. The barnacle work provided Darwin with the empirical evidence he felt he needed to convince the critics of

transmutation of species. His evidence for his arguments about the formation of new species was, by then, well-developed. His work on barnacles had convinced him that virtually every anatomical detail varied in some way and that this variation was a natural consequence of reproduction. He used homology among the various barnacles as key to understanding their evolutionary relationships and saw embryology as the key tool for discovering homologies. Here, he was building on Milne-Edwards' (1808–1885) influential work on comparative embryology and classification (Stott 2003).

Darwin next turned his attention to pigeons and chickens, reasoning that what occurred in nature regarding the production of variation also occurred with domestic animals. He became interested in “sports,” forms that differed in some way from the typical forms. He chose pigeons and chickens because of their existing variation, their availability, and abundant available information. It was commonly held among fanciers that each breed was distinct, originating from several wild stocks. Darwin set out to show that all varieties arose from a single common ancestor. Darwin was returning to the contentious themes of his notes and essay from 1837 to 1844, respectively; he was drawn to working on natural selection again. Thus, in the mid- to late 1850s, Darwin was applying his evolutionary ideas to vertebrates. However, he might never have published on these issues if not for the events of 1858 (Desmond and Moore 1991).

1858–1859

It was on June 18, 1858, that Darwin received a manuscript from Alfred Russel Wallace (1823–1913) entitled “On the Tendency of Varieties to Depart Indefinitely from the Original Type” asking Darwin to forward it on to Lyell if Darwin thought it worthy of Lyell’s attention. Wallace and Darwin were both committed to explaining the natural world and had corresponded previously, but it was not until Darwin received a copy of Wallace’s essay that laid out his view of evolution that Darwin recognized Wallace as a true

competitor. Darwin realized that Wallace was advancing a theory of variation and natural selection that was identical to his own. Within a week of receiving the paper, Darwin wrote both Lyell and Joseph Dalton Hooker (1817–1911), a preeminent English botanist, and asked their advice. Both Lyell and Hooker knew of Darwin’s work over the previous two decades, but Darwin knew both would be scrupulously fair in such a serious scientific matter. The question of priority was at stake (Darwin 1958 [1892]).

Lyell and Hooker recommended that Darwin and Wallace present joint papers together – part of Darwin’s 1844 essay and Wallace’s 1858 paper – at a meeting of the Linnæan Society in London. Thus, less than 2 weeks after Darwin’s receipt of Wallace’s paper, the Darwin-Wallace papers were added to the agenda. On July 1, 1858, the Secretary of the Linnæan Society read excerpts from Darwin’s essay, part of Darwin’s 1857 letter to Asa Gray where he repeated the themes of his essay, and Wallace’s paper to the 30 or so assembled members of the Society. Neither Darwin nor Wallace attended, but Lyell and Hooker both spoke, attempting to impress on the audience the importance of both papers. The combined Darwin-Wallace (1858) extract/letter/paper was published by the Linnæan Society on August 20, 1858. Darwin always referred to the work as “our theory.” Wallace, on the other hand, always gave Darwin priority (Desmond and Moore 1991).

Darwin immediately began working on an actual paper based on his essay, promised to Lyell and Hooker, but it quickly expanded into something much larger. He informed Lyell and Hooker that his paper, which was supposed to be ready in October to be published with Wallace’s paper, would have to be published separately, and he was negotiating with the publisher John Murray. By April 1859, *Origin* was at the printers. The corrected proofs were returned to the printer in October, and, on November 2, 1859, Darwin received a specimen copy of *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle*

for *Life*. Over the next 2 weeks, Darwin sent a number of complimentary copies of the book to colleagues in Europe and the United States. To Darwin's surprise, all 1,192 copies (1,250 less the 58 complimentary copies) were sold to retailers on the first day of publication, November 24, 1859. The advertised price was 15 shillings (roughly the equivalent of \$83 today) (Darwin 1958 [1892]).

Darwin continued to be nervous about the reception his work would receive among scientists and, in particular, Charles Lyell who suspended judgment for an additional couple of years. On the other hand, Huxley's reaction was immediately enthusiastic. Once Huxley read the entire work, he recognized its monumental contribution. What impressed Huxley most was the quality of the scientific argument and the amount of biological and geological data that were explained by it. Darwin's ideas were, by far, the most plausible explanations for a variety of puzzling phenomena, and Huxley made it his mission to see that Darwin's ideas were heard. Huxley was acutely aware of Darwin's abhorrence of controversy as well as his own skill and appetite for it, so he immediately became Darwin's self-appointed champion. The publication of *Origin* in 1859 marked the beginning of a discussion about evolution that continues today (Darwin 1958 [1892]).

Conclusion

Over the remainder of his life, Darwin wrote books on the communication of emotion in animals, the role of sexual selection in human evolution, locomotion in plants, fertilization in orchids, variation in domestic animals, and the action of worms. His contributions to natural history and biology are without peer, and today Darwin stands as the greatest scientific thinker of the nineteenth century and one of the most brilliant scientists of all time. The preceding description offers some insight into the historical events that contributed to and influenced his thinking and works.

Cross-References

- [Early Perspectives on Evolutionary Change](#)
- [Erasmus Darwin](#)
- [Nature versus Nurture](#)
- [Optimal Designs](#)
- [Science and Religion Compatibility](#)

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Impairment

► Disabilities

Imperative Knowledge

► Procedural Knowledge

Impersonal Sex

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Synonyms

Casual sex; Hooking up

Definition

Sex that is not based on an emotional context or with a romantic partner.

Introduction

Impersonal sex cannot be oversimplified; instead, for impersonal sex to take place, a number of conditions must be met. Other factors, including the gender and race of the participants play key roles. There are also various reasons why someone may participate in impersonal sex, as well as both benefits and drawbacks of participation.

Impersonal sex, also called “hooking up” in modern culture, is sex that is not based on an emotional context or with a romantic partner. Impersonal sex is sexual intercourse with another person with many purposes including fun, to enhance one’s social status among peers, to assert control over one’s own sexuality, to express one’s sexual freedom, or to have sex without the intention of emotional commitment. These are the

factors used to represent an endorsement of the hookup culture (Aubrey and Smith 2013). In addition to the various reasons that people have impersonal sex, there are also a series of conditions that describe the ideal conditions for impersonal sex among men; women have not been described to the same extent. Weinberg and Williams (1975) describe conditions including having a “safe” setting or location in which the person feels private and does not put them in danger; having good sexual partners and/or good options at a low price (such as dating and hookup-oriented cell phone applications); a situation that promotes an organized reality between both parties in which both parties are on the same page about expectations; limited non-sexual interaction between the two parties outside of the sexual encounter; an ability to mask one’s feelings of rejection and non-harsh solicitation of sex or offers of sex; and a comfortable and relaxing physical setting. There are few studies conducted on the matter of impersonal sex, but they seem to focus on examining age’s role in and risk factors of impersonal sex. For example, some of these risk factors include a range of negative health indicators (Långström and Hanson 2006), with others reporting negative effects of sexual permissiveness on social acceptance (Vrangelova et al. 2014).

Gender appears to be the most common variable researched for its role in impersonal sex. In one study conducted by Monto and Carey (2014), the researchers drew respondents from the General Social Survey (GSS) who were between 18 and 25 years of age and who had attended college for at least 1 year from the year 1988 up to the year 2014 when they conducted their study. They looked at the number of sexual partners each person had since turning 18 and how many sexual partners they had had in the past year, how often they had had sex in the past year, and if the sex they had was with a regular partner, a friend, an acquaintance, a casual date, or hookup, or if the person fit none of those categories. They observed respondents from recent years did not report more sexual partners, more frequent sex, or more partners during the past year than earlier respondents had reported. Thus, these patterns or behaviors have not changed as a function

of time or across generations. However, when they explored gender differences, there were more women reporting sex in those earlier years than there were men. In addition to this difference between earlier and more recent participants, sexually active respondents from recent years were more likely to report sex with a friend and less likely to report sex with a spouse or a partner. This implies many people are leaning toward more casual and noncommittal sex in more recent years, and that men are reporting more sex than in previous years.

Another study conducted by Boot, Peter, and Oosten (2014) examined women’s responses to sexual media and how the personal factor of impersonal sex orientation, along with the situational factor of multitasking, affected their involvement with the media. Impersonal sex orientation refers to someone’s preference for uncommitted sexual relationships, and those who score high on this variable are more focused on appearances and physical satisfaction instead of on emotional closeness with another person. The women were asked to watch a sexual scene, and their involvement was measured by how similar they perceived themselves to be like the woman in the scene, how likeable they found that woman, and how much they wished they could be like her (i.e., wishful identification). Boot and colleagues found women high in impersonal sex orientation had decreased perceived similarity to the woman in the scene and found them less likeable when multitasking. On the contrary, those low in impersonal sex orientation found the woman in the scene more likeable while multitasking. In short, there was a significant interaction between media content and impersonal sex orientation on perceived similarity and wishful identification, as well as a significant interaction between media content, impersonal sex orientation, and multitasking on perceived similarity and likeability. Thus, women’s responses to social media content depend on their impersonal sex identification, *and* multitasking may increase or decrease the influence of sexual content depending on personal characteristics.

Spell (2016) investigated how gender and race impacted one’s participation in hookup culture.

She collected her data from interviews that she conducted herself, along with survey data collected from the Online College Social Life Survey. She argues the importance of both variables in understanding these phenomena. For example, Asian men and nonwhite women face additional barriers to participate in hookup culture compared to other groups, including physical stereotypes and possibly other stereotypes or racism-related concepts. Spell further argues that research must incorporate intersectionality to study hookups. Truly, the relationships between factors such as gender, race, and social class may better describe the nature of and preference for impersonal sex.

Vrangelova and Ong (2014) studied the benefits of casual sex as well the moderation of sociosexuality (described as one's personality orientation toward casual sex) on well-being. They describe the effects of casual sex on well-being as mixed; this is due to the moderating factor of sociosexuality. The positive effects as they described them include satisfaction, confidence, and self-knowledge and are stronger and more common results of casual sex compared to the negative outcomes (e.g., lower self-esteem, coupled with increases in depression, anxiety, and sexually transmitted diseases; Vrangelova 2015). The authors found that those who were sociosexually unrestricted reported higher well-being after casual sex than they reported without sex. On the other hand, those who were sociosexually restricted did not report much of a difference in their well-being before and after sex.

Conclusion

There is still room for additional research on the topic of impersonal sex, though we understand there are many factors that play a role in its frequency and effects. Some of these factors include the setting, one's own reasons for seeking impersonal sex, and the individual and their personal views on impersonal sex. Researchers note various ideal conditions to be met as well as positive and negative outcomes, such as getting praised by one's peers or getting rejected by peers for one's

sexual behavior. Individuals may experience casual sex differently, and its effects may vary in accordance with personal characteristics and preferences. For example, two people could experience the same encounter, but one person could respond positively and be happy with the result, while the other person may have disliked the event to the point of regret or self-loathing. Race and ethnicity, sexual orientation, and well-being appear to be critical factors in these investigations, each requiring additional research as these factors could potentially affect an encounter and its outcome. Overall, the widespread prevalence of impersonal sex necessitates additional research to better understand its impact on individuals and their relationships.

Cross-References

- [Mating Strategies](#)
- [Premarital Sexual Permissiveness](#)
- [Sexual Behavior](#)
- [Sexual Regret](#)
- [Sexual Stigmatization](#)

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Implement

► [Advanced Tools of Neanderthals](#)

Implications for Pregnancy

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Synonyms

[Gestation period](#); [Gravidity](#); [Parity](#)

Definition

A number of adaptations have evolved in women to deal with a tremendous set of physiological and psychological pressures during the 9-month gestational period and labor.

Introduction

Pregnancy lasts approximately 9 months and places many demands on women's bodies. First, growing a fetus is tremendously costly in terms of energy needs, and it also places physical strains on a woman's body. Second, pregnancy greatly

inhibits locomotion and makes women vulnerable to threats. This entry will address (a) the basics of pregnancy, (b) two hypotheses about the length of gestation, and (c) the psychological implications of pregnancy.

The Basics of Pregnancy

Gestation begins after copulation during a woman's fertile window when sperm fertilizes the egg. The zygote (fertilized egg) travels down one of the fallopian tubes as it undergoes rapid cell division before implanting into the uterine wall. For the next 10 weeks, during the first trimester of pregnancy, the embryo and all of the necessary structures for fetal development (placenta and umbilical cord) then develop. After this point, the embryo is typically referred to as a fetus.

Women typically carry only one fetus during a pregnancy, because usually only one egg is released from one of the ovaries during ovulation. However, sometimes women will carry multiples. Twins are most common and can either be dizygotic or monozygotic. Dizygotic (fraternal) twins result from two eggs being released and fertilized during ovulation. Monozygotic (identical) twins result from a single fertilized egg that splits early on in the pregnancy.

Women undergo several physiological changes to accommodate the pregnancy. Endocrinologically, women experience increases in both progesterone and estrogen throughout gestation. Further, women's immune systems become suppressed so that the genetically dissimilar embryo can develop without being rejected by the mother's body (Navarrete et al. 2007). Women typically gain weight during pregnancy as the fetus develops, the uterus enlarges, the placenta becomes filled with amniotic fluid, and the body retains extra fat and water. Although women typically do not start lactating until a couple of days after giving birth, women's breasts develop throughout pregnancy to be able to produce milk, and the areolae typically become larger and darker. Women's blood volume increases by up to 50%, and they experience a number of other cardiovascular and hematological changes.

Consequently, pregnancy brings several challenges. Women need to increase their protein and calorie intake in order to support the development of the fetus as well as all of the other necessary structures (e.g., placenta and other uterine structures, breasts). At the same time, pregnancy makes locomotion difficult, and women become more vulnerable due to the increased necessary effort (or potential inability) to acquire resources and avoid harm. Further, if things do not go well during the pregnancy, women may experience medical problems or can miscarry. Both of these outcomes are very costly.

Not only is the 9 months of gestation physiologically costly to women, but giving birth is also an ordeal. A birth is considered full-term if the gestational age of the fetus is 37–42 weeks. Modern humans and other hominins (extinct human species and all immediate ancestors including members of the genera *Homo*, *Australopithecus*, *Paranthropus*, and *Ardipithecus*) have birth canals that are different from other animals in that they are wider sideways (hip to hip, transversely) than front to back (anteroposteriorly). These physiological constraints mean that babies have to rotate as they are moving down the birth canal; first they face sideways to align their head with the birth canal and then they turn parallel to the mother for the rest of their body to move through the birth canal (Rosenberg and Trevathan 2002). The turning process necessary to align the infant's body properly with the mother's birth canal makes the birthing process more complicated.

Further, childbirth is usually painful and can be dangerous as babies' heads and shoulders are large in proportion to women's rather narrow birth canals. Unlike other primates for whom labor lasts about 2 h, first-time mothers typically are in labor for 9 h (Albers 1999), and about 1% of babies end up having shoulders too large to pass through their mother's birth canal (Rouse et al., 1996). Although this would have been deadly in ancestral times, this problem can be solved with a cesarian section and other modern medicinal interventions. Despite the physiological costs and risks associated with gestation and parturition (labor and birth), selection pressures on women's gestational length must have contributed to the

9-month duration of pregnancy. Several hypotheses exist to explain the length of women's pregnancies and birthing constraints. Two such hypotheses are discussed in detail within this entry: the obstetrical dilemma hypothesis and the energetics of gestation and growth hypothesis.

Hypotheses about Gestation Length

Humans have much larger brains than any other hominin. Consequently, heads of human babies are also large. Although most nonhuman primates are precocial (able to locomote and feed themselves almost immediately after birth) and humans are altricial (unable to locomote and feed themselves immediately after birth), the length of pregnancy is similar (Rosenberg and Trevathan 2002). There are several hypotheses that try to explain the timing of human gestation and birth (parturition). This entry will address the obstetrical dilemma hypothesis, which focuses on bipedalism and the narrowing of the birth canal, and the energetics of gestation and growth hypothesis, which focuses on the metabolic demands placed on the woman by pregnancy.

Obstetrical Dilemma Hypothesis

Human bipedalism and large brains can be seen as conflicting adaptations. Walking on two legs narrowed the pelvis and subsequently women's birth canals. These changes make it harder to give birth to babies with the larger heads necessary to accommodate and foster a large brain. Early hominin skeletons, like those of *Australopithecus afarensis*, show signs of bipedal locomotion. Therefore, at that point human ancestors had already started to undergo skeletal changes that made bipedalism possible, including those to the pelvis. However, the brain size in proportion to the bodies in *Australopithecus afarensis* was still small. It is proposed that later, around the time of *Homo erectus* (when brain size started increasing more rapidly), the birth canal, already narrowed from bipedalism, became a limiting factor to gestation. Like humans, *Homo erectus* infants were likely relatively helpless at birth, as indicated by the fossil record. Thus, the obstetrics dilemma

hypothesis suggests that bipedalism constrains the human gestational period such that the babies are born at this particular (and altricial) point of development because that is the point at which they are still able to pass through the birth canal. The result is an infant born with about 25% brain development of an adult human, almost half of that of nonhuman primates (Trevathan 2011). Two additional physiological adaptations allow for the birth of large-brained babies to bipedal mothers: (a) babies are born with soft cranial bones that continue to develop after parturition, and (b) women have greater hip width compared to men (who can be bipedal without having to give birth).

Energetics of Gestation and Growth Hypothesis

Although human pregnancy is in the same temporal range as that of nonhuman primates, human infants are born at a much earlier developmental stage. They require constant care because they cannot walk, eat, or protect themselves from predators, and they depend fully on their parents for survival. Having this parental role and the associated division of labor adds to both mothers' and fathers' costs associated with reproduction. Is bipedalism the only benefit or constraint associated with pregnancy length? If humans didn't walk upright or have wider pelvises, would they have a pregnancy double in length? To match the gestational development of infant chimpanzees, women would have to sustain an 18–21 month pregnancy (Portmann 1990).

Pregnancy is costly to women's metabolic processes, and greater fetal size would lead to even more energy expenditures. Thus, women may not be able to physically sustain a pregnancy necessary for the fetus to have a more developed brain. The energetics of gestation and growth (EGG) hypothesis argues that labor occurs when women are at the limit of their feasible energetic investment into the pregnancy. Dunsworth et al. (2012) examined infant body and brain size in relation to maternal body size (which is associated with the amount of metabolic resources the mothers have available) and found that brains of human infants relative to their mothers' bodies are larger than brains of infants of nonhuman primates. Thus, although infants are born altricial and with brains

at 25–30% of development, human mothers actually invest more metabolically in gestation than nonhuman primate mothers. Further, by the sixth month of pregnancy, women's basal metabolic rate is double what it was prior to pregnancy. The EGG hypothesis suggests that pregnancy length is directly related to the balance of infant metabolism demands and maternal metabolism capabilities. It would not have been adaptive for women to further invest energy into developing an offspring at a point where their own ability to survive and pursue other important goals would be jeopardized.

Psychological Implications

As discussed in the first part of the entry, pregnancy has immense physical costs. Women's energetic needs are doubled. Further, women become more vulnerable to pathogens because their immune system is suppressed. Especially in the latter parts of pregnancy, it becomes more difficult to move around to gather resources and escape threatening situations. Thus, women in ancestral times would have benefitted from developing different strategies for pursuing their goals when pregnant. This entry will discuss several lines of research in evolutionary psychology that examine these psychological adaptations.

Disease Avoidance

During pregnancy, the mother's immune system is suppressed in order to tolerate the genetically different embryo developing inside of her. The suppression is especially strong during the first trimester of pregnancy. Thus, women (and particularly women in the first trimester) are especially susceptible to pathogen contagion. Moreover, disease is especially pernicious at this stage because it can interrupt fetal development and result in severe issues. Therefore, women who were extra cautious in regard to what and with whom they came into contact would have had healthier offspring and increased fitness compared to women who did not regard their environment with due caution.

People's general psychological mechanism for avoiding disease – the behavioral immune system or behavioral prophylaxis – should therefore be

especially active during this vulnerable time. Indeed, women demonstrate an increase in disgust and aversion to potentially contaminated food in the first trimester of pregnancy over and above any effects of nausea and physical ailments (Fessler et al. 2005). Thus, women are more cautious of what they consume in the early stages of the pregnancy when they are most vulnerable and when it would be most problematic for them to be sick. Additionally, women's disgust reactions to food seem to be specific to foods that are novel and/or more likely to lead to contagion and that are not nutritious dietary staples (Mckerracher et al. 2015).

Further, certain people also pose contagion-related risks. Members of dissimilar groups likely have been routinely exposed to foreign pathogens, and coming into contact with these outgroups may result in contagion. Again, women in the first trimester demonstrate an increased preference toward members of their own groups and weariness of dissimilar individuals (Navarrete et al. 2007). Thus, it seems that women have adapted to be more cautious of pathogens during pregnancy (especially the first trimester).

Motivation to Affiliate

Humans face another set of pressures associated with giving birth that is absent for monkeys and great apes (Rosenberg and Trevathan 2002). For the latter, the infant is born facing the same direction as the mother, who can then easily reach down and assist herself in the process of navigating the infant toward her chest. Human babies are born facing the opposite direction as the mother, who then cannot assist herself as the infant is emerging because that would require bending the infant backward. Coincidentally, women are unlike most mammals in that they do not typically give birth in solitude. It may be that women who were more motivated to affiliate (perhaps because of fear and anxiety) had more successful births (i.e., fewer complications for themselves and the infant) due to the assistance they were able to secure. These pressures may have resulted in an evolved preference for social birth and midwifery.

Consistent with the increased need for assistance during birth and the vulnerability to threats pregnant women face during both gestation and postpartum, research suggests that pregnant women

may engage in nesting behavior as a way to protect themselves from these threats. Specifically, pregnant women prepare their physical and social spaces during pregnancy (Anderson and Rutherford 2013). Like other altricial mammals, human mothers begin preparing their physical space for the infant and do so more during the last trimester of pregnancy. Importantly, women also engage in social nesting behaviors by becoming more socially selective in their affiliation. This behavior serves multiple purposes. First, women are able to build closer networks by reinforcing relationships with their selected friends and family, who can later assist with labor and alloparenting (parenting or caretaking of the infant by anyone other than the parents). Further, by staying away from strangers and novel social environments, women are able to reduce their chances of encountering both physical and contagion threats. These nesting behaviors are not simply due to anxiety, mood, and energy levels (Anderson and Rutherford 2013).

Conclusions

Pregnancy requires a lot from women, and giving birth is further complicated by pelvic changes due to bipedal walking. Pregnant women have greater physiological costs and face heightened threat from disease, other groups, and complications. To mitigate these dangers, pregnant women engage in avoidant behavior of possibly threatening objects and people as well as selective affiliation to strengthen their social support.

Cross-References

- ▶ [Alloparenting and Grandparenting](#)
- ▶ [Conception](#)
- ▶ [Early Stage of Brain Development at Birth](#)
- ▶ [Narrowing Birth Canal](#)
- ▶ [Sexual Reproduction](#)

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Implications of Gossip

► Social Consequences of Initiating Gossip

Implications of Object Permanence

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Definitions of Object Permanence

- (a) Knowledge that an object continues to exist when there is no longer sensory input from the object.

- (b) A sensorimotor organization of schemes, completed by about 18 months of age, that enables the infant's organization of reality into a world of objects, including the infant as one of them. – Piaget.
- (c) Inference, that an infant knows innately or early that objects exist when occluded, based on longer infant looking when an inferred expectation, resting on the assumption of that knowledge, is violated, and on additional assumptions that violation of expectation results in surprise and surprise results in longer looking.

Practical Implications of Object Permanence

Knowing that something exists when not perceived implies that the knowledge exists free of sensory input and suggests it can be used mentally without sensory support. The knowledge has been freed from the limitations and constraints of time, space, and perception. The knower no longer needs perceptual contact with the known for knowledge to exist. Such liberated knowledge underlies mental manipulation of the world, imagination, expectation, memory, and prediction.

Before object permanence, when knowledge depends on, and is essentially equivalent to, perception, disappearance of the object is disappearance of the knowledge. Out of sight is literally out of mind. The difference resembles the difference between following an argument and understanding it. Following requires presentation in some way, such as spoken or written, and depends on engagement with each step of the presentation. Understanding means one can know it without it being presented. It is independent of perceptual processes. Following requires a certain level of comprehension but does not ensure that knowledge endures after presentation ends. Understanding liberates knowledge from perceptual engagement. Object permanence is the analog of understanding with respect to knowledge of the existence of objects and events.

With object permanence, objects can exist in memory, serve prediction, and also

imagination. Object memory, predicting how an object will behave, or imagining what an object might be doing, all require objects that are mentally freed from perception. Object permanence enables mind to transcend the actuality of here and now. The child with object permanence can watch someone drive off in a car but know that the person continues to exist, or watch an airplane fly into a cloud and expect it to emerge. In the predator–prey relation, prey goes behind a tree or a rock but still exists for predator. From prey’s perspective, predator is no longer in sight but is still a problem. Where object permanence is limited, fear maintained by body chemistry can support continued flight even when the out of sight predator may not be mentally represented. Object permanence helps both predator and prey to survive.

Theoretical Implications of Object Permanence

Piaget (1954) introduced object permanence. He discovered that when an object is concealed, 5- and 6-month-old infants seem to no longer be aware that it exists.

In Piaget’s theory, schemes are cognitive structures for assimilating reality and enabling generalization of action to similar situations. Knowledge of the continued existence of objects that are no longer visible results from a progression of schemes, i.e., coordinations and organizations of looking and reaching.

Piaget found that the 9-month-old could remove an occluder to reveal a recently hidden object but still lacked some of the visual-motor coordination that would define complete object permanence. Along the 18-month or so path to completing the sensorimotor stage of development where the child structures the world and itself into a collection of permanent objects, the child succumbs to and then solves a series of puzzles, including the well-known A-not-B problem. If an object is hidden at location A, and then, as the infant watches, is moved to and concealed at location B, when the infant is allowed to reach for the object, reaching occurs

to location A. By 12 months, the infant reaches directly to location B.

By 18 months, the system of coordinations of visual-motor schemes is sufficiently complete for the infant to organize its world into objects that exist independently of action and perception, including the infant itself as one of those objects. As the child constructs reality by comparable coordinations involving space, time, and causality, it is gradually freed to grasp an external world of which it is a part.

From Piaget’s perspective, object permanence implies the completion of the sensorimotor stage of cognitive organization.

Nativist and Other Challenges to Piaget

Might the 5-month-old or younger, in a competence–performance contradiction, know that occluded objects continue to exist but be unable to display that knowledge because it does not yet have the required eye–hand coordination? The child knows but cannot display the knowledge. If so, introduction of a task that does not require removing an occluder might reveal object knowledge at an earlier age than claimed by Piaget.

Bower (1966, 1967) studied this possibility, and Bower et al. (1971) used a visual tracking task in which 20-week-old infants watched an object pass behind an occluding screen and then shifted their gaze to where the object would be expected to appear. If a different object appeared, this disturbed tracking. These findings suggest representation of an occluded object exists earlier than Piaget supposed. But Bower and Patterson (1973) showed that visual tracking movements continued even when the moving object was halted in plain sight, indicating a possible inertial component to tracking rather than occluded object representation.

Baillargeon et al. (1985) habituated 5-month-old infants to rotation of a drawbridge-like screen and then placed a block behind the screen. The infants were shown trials where screen rotation stopped at the point where the block would have kept the screen from further rotating, and trials where the screen seemingly rotated right through the block. In

both trial types, the screen reversed its trajectory revealing the block remaining where it had been placed. Longer looking to the “impossible” event was attributed to surprise resulting from violation of expectation of the block still being there and preventing complete screen rotation. The authors take this to reveal a form of object permanence occurring much earlier than Piaget predicted. Other studies are taken to support this finding (e.g., Baillargeon and Graber 1987).

Spelke and her associates (e.g., Spelke et al. 1992) have argued for innate core knowledge such as movement continuity and object solidity that enable the above apparent object permanence in the very young infant.

Baillargeon frequently invokes high level cognitive processes such as representation, assumption, expectation, surprise, belief, reasoning, inference to explain results in violation of expectation experiments with young infants.

Piagetian theory says that object permanence develops slowly as a result of interaction with the world and the organization and coordination of schemes. The implication of the nativist position with respect to the early occurrence of object permanence is that the Piagetian formulation of the development of object permanence may be wrong and raises doubts about the entire theory.

Challenges to the Nativist Position

The Perceptual Processing Response

Brilliantly challenging the nativist position, Haith (1998) argued that “Since virtually all of the nativist claims for early cognitive processes hinge on how long an infant looks at one display rather than another ... investigators who pursue high-level cognitive constructs must play the default game. That is, one must fend off every possible perceptual interpretation of differences to entertain default cognitive interpretations,” and this will involve many factors that affect looking, including variations in the perceptual dimensions of objects and people, familiarity, novelty, recency, predictability, and the time lapse between stimulus exposures. Haith cites numerous studies that call into question nativist high level cognitive

interpretations (e.g., Bogartz et al. 1997; Cohen, 1995; Cohen et al. 1996).

Bremner et al. (2015) provide another excellent alternative to the nativist position. “Rather than advance object persistence as an innate principle through which events are interpreted, ... persistence is specified by perceptual events such as deletion and accretion, and the developmental question is about infants’ changing ability to perceive object persistence on the basis of these cues.”

Parsimony claims abound. One response from Baillargeon (2000) has been to argue that greater parsimony results from attributing higher level processes to the infant, as opposed to detailed analyses calling for multiple explanations when perceptual processing analyses of the behavior are proposed. One counter to this claim is that it is not parsimonious to attribute higher level processes where lower ones will do.

The Dynamic Systems Approach

Another parsimony counter to the nativist claim is implicit in the Dynamic Systems approach of Schöner and Thelen (2006). They “offer a dynamic field model of infant visual habituation, which simulates the known features of habituation, including familiarity and novelty effects, stimulus intensity effects, and age and individual differences” and “provide simulated visual input of varying strengths, distances, and durations to 2 coupled and interacting fields. The 1st represents the activation that drives ‘looking,’ and the 2nd, the inhibition that leads to ‘looking away,’ or habituation.” By varying the parameters of the field, the authors simulate the time course of habituation trials and show how these dynamics can lead to different depths of habituation, which then determine how the system dishabituates. The authors use the model to simulate a set of influential experiments by Baillargeon (1986, 1987a, b) using the well-known “draw-bridge” paradigm. The dynamic field model provides a coherent explanation without invoking infant object knowledge. “And importantly for the parsimony argument, the authors show that small changes in model parameters can lead to qualitatively different outcomes. Because in typical infant cognition experiments, critical

parameters are unknown, effects attributed to conceptual knowledge may be explained by the dynamics of habituation.” Thus, dynamic systems theory provides a rationale for why multiple explanations are necessary in perceptual processing analyses of the behavior that nativist claim indicate object permanence.

Schöner and Thelen (2006) indicate that all that the Violation of Expectation studies definitely show is that the infants notice a difference between the two events they have been shown. Everything else is an extrapolation from this. Schöner and Thelen argue that there are many reasons why infants might prefer looking at the “impossible” events. For example, in the “drawbridge” study, the “impossible” event involves more movement than the “possible” event. They conclude that Baillargeon has mistakenly assumed that the only difference between her stimuli is that one is “possible” and the other is “impossible.” However, there are actually many differences between the two stimuli, any of which might be the reason why infants look more at one than the other. What Baillargeon and Spelke claim is evidence of innate or early knowledge of the physical world, Schöner and Thelen say is no more than the effect of confounding variables.

Conclusion

The practical implications of object permanence are that knowledge and understanding of a world filled with objects and events require the ability to represent such a world in the absence of sensory input. The theoretical implications of object permanence and its time course concern which of various theoretical approaches to cognitive development hold the most promise for enhancing our understanding of the transformations that take the fetus and build it into the scientist.

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Implicit Memory

- [Different Functions of Memory](#)
- [Multiple Memory Systems](#)

Importance of Grandparental Investment

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Synonyms

Grandparental care; Grandparental involvement; Grandparental solicitude

Definition

Grandparental investment can be defined as all actions that may increase grandchildren's fitness at any opportunity cost to grandparents' own fitness. Grandparental investment includes conscious and unconscious investments grandparents channel toward their grandchildren. Grandparents can invest in their grandchildren either directly or indirectly via a third party (mostly via grandchildren's parents). Grandparental investments include, for instance, contacts with grandchildren, care, financial help, emotional support, and practical help. Evolutionary importance of grandparental investment refers to fitness benefits that grandparents may gain by providing support to their offspring. By investing in their grandchildren, grandparents can increase their own inclusive fitness (i.e., spreading their genes in future generations) by two important ways. First, by investing in their offspring, grandparents can boost parental fertility. Second, grandparental investment may increase grandchild health, well-being, and survival.

Introduction

Because of the demographic changes, grandparents today have a potential to be more important for child well-being than ever before. Increased life expectancy in modern Western countries means that grandparents and grandchildren have more shared years than before. Decreased fertility rates in turn denote that grandparents have fewer grandchildren, and thus they may be able to invest more in any particular grandchild. Regardless of this, grandparental effect in contemporary societies tends to be relatively small.

Grandparental Importance in Past and Present Societies

In premodern and historical populations, grandparental effect is measured by grandparental presence in same household or same village with their offspring rather than grandparental investment per se. In these populations grandparental presence is often found to correlate with both improved parental fertility and grandchild survival. However, all grandparents are not found to have similar effects. Studies have shown that paternal grandparents may improve fertility more than maternal grandparents (Sear and Coall 2011). In contrast, maternal grandmothers tend to increase grandchild survival more than maternal grandfathers or paternal grandparents (Sear and Mace 2008). These results can be explained by different sex-specific reproductive interests between women and men, which can be expanded to maternal and paternal grandparents (Euler 2011). Although, in several studies grandparental presence is found to benefit parents and grandchildren, kin relations include also conflicts. If grandparents push higher fertility and shorter birth intervals in females, this may have detrimental effects for both parents and grandchildren (Mace and Sear 2005). Moreover, in older age grandparents can be net consumers rather than net producers and could compete over local resources with grandchildren. This competition, in turn, may

have detrimental effects for grandchildren (Strassmann 2011).

Grandparental investment can still be associated with parental fertility and grandchild well-being in modern Western societies. In the case of parental fertility, the existing evidence is, however, scarce and mixed. While some have found that grandparental investment is associated with increased fertility (e.g., Tanskanen et al. 2014), some others have not detected such an association (e.g., Aassve et al. 2012). Moreover, the form of grandparental investment is found to influence the results. For instance, a study from the UK found no association between grandparental child care help and parents' childbearing, although emotional closeness between parental and grandparental generations was associated with improved fertility (Waynforth 2011). In contrast, a study from the Netherlands showed that grandparental support with child care was indeed associated with parental childbearing (Kaptijn et al. 2010).

In modern affluent countries, grandparents are not needed to keep their grandchildren alive as much as they were in subsistence societies. However, in present-day societies grandparental investment can still benefit grandchildren by improving grandchild well-being measured by, for instance, early years development, school success, and psychological well-being (Coall and Hertwig 2010). In particular, research has shown that in the cases of parental divorce, severe illness, and other family instabilities, grandparents can provide a buffer against these potentially harmful events (Sear and Coall 2011). As it was in pre-modern and historical populations, also in present-day societies, all grandparents tend to not benefit grandchildren similarly. In contemporary societies maternal grandparents are often found to improve grandchild well-being more than paternal grandparents (Sear and Coall 2011). Although in past populations the importance of grandfathers was small, in modern societies grandfathers may have as beneficial effect on grandchild well-being as grandmothers, at least in some circumstances (Sear and Coall 2011).

Conclusion

Evidence from both past and present societies shows that grandparents often boost parental fertility and child well-being. However, in some circumstances grandparents tend to have no effect at all, or they may have even detrimental effect. Thus, more research is needed to show in what circumstances grandparental investment may increase and in what circumstances decrease parental fertility and child well-being.

Cross-References

- ▶ [Grandmother Hypothesis of Menopause](#)
- ▶ [Grandparents and Grandchildren](#)

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Importance of Maternal Grandmother

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If one asks people which of their four grandparents provided the most care for them when they were a child or to which grandparent they feel closest, the most people will answer the maternal grandmother.

Indeed, many research studies found that the intensity of caregiving by the four grandparents is not the same but regularly different. In most urban societies, grandmothers typically invest more in grandchildren than grandfathers, and maternal grandparents invest typically more than paternal. Thus, grandparental caregiving (i.e., their grandchild care, investment of resources, solicitude, involvement, and contact frequency) follows the asymmetric pattern: maternal grandmother provides on average the most caregiving for grandchildren, followed by the maternal grandfather and the paternal grandmother, and the paternal grandfather provides the least caregiving (Smith 1988; Euler and Weitzel 1996; Salmon 1999; Pashos 2000; Pashos and McBurney 2008; Danielsbacka et al. 2011; Pashos et al. 2016). The same asymmetric pattern exists also for emotional closeness: on average, grandchildren are closest to the maternal grandmother and least close to the paternal grandfather (Russell and Wells 1987; Laham et al. 2005; Pashos and McBurney 2008; Pashos et al. 2016). The asymmetric pattern cannot be explained by the different survival chance or age of the grandparents that follows the same

order (the maternal grandmother is on average the youngest; the paternal grandfather is the oldest), as analyses have shown (Euler and Weitzel 1996; Pashos 2000). Also residential distance, which in general strongly affects the grandparental caregiving, does not explain the caregiving biases. Same is true for other potential confounding factors which are however only inconsistently found, such as birth order, parent age, and grandchild age (for an overview, see Euler 2011).

Grandmother Hypothesis

Also in anthropological studies that deal with the evolution of grandparenthood, the maternal grandmother plays a central role. The classical grandmother hypothesis, also called prudent mother hypothesis, assumes that menopause has evolved in humans to stop the risky female reproduction in older age, in favor of investing in already existing children or grandchildren. According to Kristin Hawkes' newer version of the grandmother hypothesis, grandparenting along with longevity evolved through the grandmothers, who helped their daughters with provisioning the offspring (Hawkes et al. 1998). A number of studies using medical health data (Sear et al. 2000) or historical data (Sorenson Jamison et al. 2002; Beise 2005; Ragsdale 2004) found support for this view. These studies found lower child mortality or a better nutritional status in families where the maternal grandmother was present. In a German study, using historical data from Frisia, the paternal grandmother had even a negative effect on child survival (Volland and Beise 2002). However, other research studies revealed a rather mixed picture. Although most studies showed indeed positive effects for maternal grandmothers regarding child survival, some studies also found positive effects for paternal grandmothers, maternal grandfathers, or other kin, and some studies could not find a particular significance for any grandmothers (Sear and Mace 2008; Strassmann and Garrard 2011). Leonetti et al. (2005), for example, found a positive effect of the maternal grandmother, for maternal health, and child survival among the matrilineal Khasi.

However, among the patrilineal Bengali, they found a positive effect of the paternal grandmother on their daughter-in-law's fertility. From an evolutionary point of view, these mixed results might however very well represent different reproductive strategies. The maternal grandmother is biologically related to both her daughter and her grandchildren and hence also interested in her daughter's health, whereas the mother-in-law's reproductive interest is to invest in further grandchildren, however, not in her genetically unrelated daughters-in-law.

Maternal grandmothers were often found to be related to lower child mortality and this has been usually associated with their grandchild investment. However, cross-culturally they are not always the most important kin investors. In patrilocal societies, for example, maternal grandmothers do not live close to their grandchildren. Furthermore, many grandmothers are already deceased when grandchildren grow up. Some researchers therefore criticized the grandmother hypothesis in general, stating that the role of grandmothers may be overestimated. Their research results showed the importance of males for the provision of food and not the importance of grandmothers (Hill and Hurtado 2009). As an alternative for the grandmother hypothesis, also a patriarch hypothesis was proposed that assumes the evolution of longevity through males and not through females (Marlowe 2000).

Nevertheless, there is a relatively broad scientific consensus that extended kin members such as grandparents can be significant family helpers. Compared to other species, humans have a prolonged childhood, and it requires many resources to raise children to adulthood. Thus, in an ancestral environment, additional family helpers appear to be essential for the mother. Because in mammals most frequently the mother is the only caregiver, these additional offspring-care helpers are often called allomothers in biology, i.e., individuals other than the mother providing childcare. Anthropological research in traditional societies has shown that these caregivers can be typically fathers, older siblings and grandparents, or any other related or unrelated adults (Crittenden and Marlowe 2008; Kramer 2010). Sarah Hrdy

(2005), moreover, argued that humans could be classified as cooperative breeders. In a Pleistocene environment, two parent alone are not sufficient for bringing up offspring. Humans are rather characterized by a network of kinship members providing allomaternal assistance. In her view, help from fathers may be important but unreliable. For Hrdy, female helpers are even more important than male helpers; the most beneficial allomothers are, however, experienced elderly females, especially the maternal grandmothers.

For the consideration of maternal grandmothers as important caregiving helpers, not only nutrition and survival of infants should be taken into account. Also, help with childcare itself (Crittenden and Marlowe 2008) or to take responsibilities for children is already an important offspring investment. On the Trobriand islands, for example, it has been found that it is most often the maternal grandmother or other matrilineal kin (i.e., maternal aunts), who adopt children who became orphans (Schiefenhövel and Grabolle 2005). Also in Western countries, fostering roles were typically most frequently taken on by maternal grandmothers (Perry et al. 2014).

Paternity Certainty Hypothesis Explanation

A mother always knows when a child is hers, a father does not. The average degree of relatedness between a grandparent and a grandchild is $r = 0.25$, or, in other words, 25%. According to the rules of kin selection, under identical framework conditions, all grandparents should thus invest equally in grandchildren. However, due to the male uncertainty of relatedness in the family lineages, the average degree of relatedness to the grandchildren can vary. Therefore, Smith (1988) predicted and found that grandparental investment in grandchildren should be biased: (1) Grandmothers should invest in grandchildren more than grandfathers because of the grandfathers' paternity uncertainty. (2) Grandparents should invest more in daughters' children than in sons' children (i.e., invest more as maternal grandparents than as paternal grandparents)

because of the sons' paternity uncertainty. (3) In combination this means, grandparental investment in grandchildren should follow the order: maternal grandmother (highest investment), maternal grandfather and paternal grandmother (being in the middle), and paternal grandfather (lowest investment, because two times affected by paternity uncertainty).

Russell and Wells (1987) presumed the same differences when they measured in a questionnaire study students' feelings of closeness to parents and grandparents. The authors tried to estimate the level of paternity confidence by equating the measured differences in closeness mathematically with a factor for paternity uncertainty. In so doing, they calculated an average paternity confidence level of $p = 0.874$. In other words, they estimated 12.6% paternity uncertainty. Gaulin et al. (1997) used a similar method and estimated the paternity uncertainty between 9% and 17% for the grandparental caregiving results of Euler and Weitzel (1996). Because, the paternity uncertainty in the Western world was often estimated at that level then, the paternity certainty explanation became quickly popular. Newer studies, however, have estimated the level of actual paternity uncertainty in Western societies much lower, presumably less than 1–3% (Anderson 2006). Moreover, other researchers could not confirm an influence of actual paternity certainty in a society on measured caregiving biases. They therefore interpreted the universal asymmetric caregiving pattern as a reflection of paternity certainty in the environment of evolutionary adaptedness (EEA) rather than by current paternity confidence (McBurney et al. 2002). Reluctance in child caregiving might also be a result of a general tendency of mistrusting men's paternity, which has evolved in order to avoid misinvestment in genetic unrelated individuals. Reluctance in investing in patrilineal descendants might be a result of this general tendency of mistrusting paternity.

Although direct kin recognition mechanisms for detecting kinship such as phenotype matching might exist in humans, from a proximate point of view, the caregiving differences between the grandparents appear to be too great to be only

explained by actual paternity uncertainty. Some authors thus also have expanded the paternity certainty explanation by other explanations such as a sex-specific reproductive strategy which explains an additional bias in favor of daughters' children (Euler and Weitzel 1996; Euler 2011).

Stronger Matrilineal Family Ties as Explanation

In explaining why in particular maternal grandmothers are the most prominent caregivers, however, it is not necessary to assume that differential investment by grandparents is triggered by underlying mechanisms of detecting the certainty of relatedness to a grandchild. The caregiving biases can also be interpreted on a proximate level as a result of stronger matrilineal family ties, which create pathways for discriminative or preferential kin investment (Pashos 2000).

Research results show that women generally have closer ties to their families than men have to theirs (Salmon 1999). Thus, matrilineal family connections are stronger than patrilineal. In particular, the strong relationship between mothers and maternal grandmothers was found to reinforce biased caregiving to a significant degree (Chan and Elder 2000; Pashos 2000). However, also in general, the grandparent-parent and the grandparent-grandchild closeness were found to be interrelated (Michalski and Shackelford 2005). Moreover, the quality of the grandparent-parent relationship can explain the asymmetric grandparental caregiving to a great extent (Monserud 2008; Pashos and McBurney 2008). In addition, the relationship dyad between the daughter-in-law and the mother-in-law is on average the least good of all parent and grandparent relationships (Euler et al. 2009; Lee et al. 2003). This additionally increases the matrilineal bias. If, however, the relationship between the mother and her mother-in-law (i.e., the paternal grandmother) was good, grandchildren were found to have closer feelings to their paternal grandmother (Monserud 2008).

These research results fit very well with the proximate explanation of stronger matrilineal family ties as cause and not as result of

asymmetric caregiving. Because the relationship of a woman to her parents, especially to her mother, is more intimate than to her parents-in-law, and is more close compared to a man's relationship to his parents, a mother brings her children into closer contact with her parents than her husband with his parents. A frequent contact between grandparents and grandchildren enables the development of social closeness which allows or triggers the emergence of emotional closeness and grandparental caregiving through evolutionary mechanisms (Pashos and McBurney 2008). Therefore, caregiving by maternal grandparents, especially by the maternal grandmother, is stronger than that by paternal grandparents.

In the social sciences, similar explanations have been proposed and discussed to explain the asymmetric grandparent-grandchild relationships, however, usually ignoring or rejecting evolutionary influences on human kinship behavior. The parents, in particular the mothers, are seen as mediators or gatekeepers, who can build a bridge or also a barrier between the grandparents and the grandchildren (Chan and Elder 2000). Alternatively, women have been described as kinkeepers, who hold the family networks together. In this view, matrilineally biased intergenerational relationships are seen as a result of the female kin keeping, in which gender is not only relevant for parents but also for grandparents and grandchildren (Dubas 2001; Monserud 2008).

Maternal Grandmother and Divorce

The caregiving by grandparents who live together as a couple, as well as their contact frequency with grandchildren, is higher than by grandparents who are divorced. This effect is in particular true for the grandfathers (Euler and Weitzel 1996; King 2003), whose grandchild caregiving might be positively influenced by the coresident grandmothers (Gaulin et al. 1997). Maternal grandmothers, however, play a special role when it comes to a separation of a grandparent couple. Pashos et al. (2016) found that divorced grandmothers, as maternal grandmothers, did not show a reduction

of kin investment in daughters' children, however, as paternal grandmothers, did invest less in sons' children. This means that the caregiving by divorced grandmothers was even more biased in favor of their daughters' children; in other words, the matrilateral bias was greater. Interestingly, when grandmothers were remarried after divorce, their new husbands mirrored this discriminative matrilateral behavior of the grandmothers pretty strongly (Pashos et al. 2016).

Cultural Variety

The asymmetric grandparental investment pattern is very reliable to measure. It appears to be quite universal in all urban Western societies. However, in rural or more traditional societies also cultural variation in the asymmetric order of grandparental caregiving has been found. In rural mainland Greece, a traditional patrilocal society, paternal grandparents, especially paternal grandmothers, provided more caregiving than maternal grandparents, whereas among urban Greeks, the universal matrilineal caregiving pattern was found (Pashos 2000). Also in the USA, for rural farmers in Iowa, it has been found that grandchildren had more frequent contact with their paternal grandparents and received more help from them as compared to grandchildren from urban Southern California (King et al. 2003). Paternal grandparents who take on the duties of caregiving have also been documented for further countries, for example, rural China (Kaptijn et al. 2013).

Even if one assumes a higher paternity certainty for patrilocal societies where mothers-in-law can exert control over daughters-in-law, the paternity certainty hypothesis can only explain matrilineal biases in kin investment. A patrilinear or patrilinear bias in itself cannot be explained using this theory, because in a society with high paternity certainty, all asymmetric biases should disappear (Pashos 2000). Therefore, additional evolutionary explanations for the investment in sons and grandsons must be proposed, such as the Trivers-Willard hypothesis (Pashos 2000; Pashos and McBurney 2008).

Conclusions

Maternal grandmothers play a prominent role as kin caregivers in urban modern societies. In traditional societies, however, also paternal grandparents can take the place of the maternal grandmother as most important caregivers. Differing cultural rules can superimpose the strong, universal matrilineal family ties. Anthropological studies have shown the need for family helpers in rearing and raising children, what highly likely also led to the evolution of grandparenthood. The mother's mother appears to be especially predestined for this role, because she has not only a reproductive interest in helping her grandchildren but also in helping her daughter to whom she is related, as well.

Cross-References

- [Family](#)
- [Grandmother Hypothesis](#)
- [Grandparental Investment](#)
- [Paternity Certainty](#)

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Imposing Humanlike Characteristics

► Anthropomorphism

Impotence

► Desire and Arousal Disorders

Impoverish

► Redistribution Preferences and Low Socioeconomic Status

Impression Management

► Altruism Displays Cooperative Potential

Imprinted Gene

► Maternal-Fetal Conflict

Imprinting

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Synonyms

Filial imprinting; Imprinting effect; Object imprinting; Stamping in

Definition

The process through which early behavior pattern becomes restricted to a particular type of object as a result of a relatively brief exposure of that object at a particular early life stage.

Introduction

After some animals are born or hatched, they have the instinct to acquire or learn the behavioral characteristics from the object exposed to them. This kind of phenomenon can be easily observed in avian such as domestic chickens and ducklings, and it was described as “imprinting” by Konrad Lorenz in 1935 based on his observations of goslings. The word “imprinting” indicates that the learning process of the characteristics of certain objects in young animals is like an inborn and fixed mechanism. Some advanced behavioral and psychological development, such as social bonding and language skills, are believed to have a close relationship with imprinting process.

Imprinting as an Ethology Topic

The concept of imprinting was developed from the observation with animals. Young birds such as ducklings imprint on the first moving object they observe in life; in most cases the object is the duck’s mother. After imprinting, the baby duck walks just after the imprinting object. This remarkable learning

process was first documented by Douglas Spalding, an English biologist, and the process was described as “stamping in” (Spalding 1873). The similar phenomenon was also described by a German biologist Oskar Heinroth in 1911 (mentioned in Bateson 2000), one of the founders of ethology, who used the German term *Prägung* (means “imprinting”) to describe this phenomenon. However, it was Konrad Lorenz (1935), a student of Heinroth, who made the phenomenon of imprinting well-known through a considerable amount of research work. The most famous experiment was that Lorenz showed his own leg to goslings during a particular period after hatching, and the goslings would follow Lorenz rather than their own mother. Lorenz also found that goslings would imprint on inanimate objects (e.g., a box placed on a running model train) if exposed to it during a particular period. This simple but special act of following was thought to be a determination of social bond between the newborn and their parents (Lorenz 1937).

It was further discovered by Lorenz that the age of the birds influenced imprinting (Lorenz 1937). Imprinting would develop naturally and steadily if the object was shown during the first two days after birth. Otherwise, when the object was shown before or after that period, the phenomenon of imprinting would hardly occur. This indicates imprinting only happens during specific periods of development, and the specific period is called critical period or sensitive period. Learning a particular behavior would be easiest during the corresponding critical period.

The finding of imprinting is regarded as one of the most famous studies of ethology (e.g., Krebs and Sjölander 1992). Unlike behaviorists who estimate the responses of animals to specific stimuli which are usually manipulated in laboratory context, ethologists prefer putting much emphasis on animal’s evolutionary adaptivity. They explore the common behavior patterns under natural conditions among different species and believe that existing animal behavioral patterns are generally resulted from evolution. Imprinting is obviously thought of as an adaptive behavior. The function of imprinting is to enable the young animal to recognize and follow the parent instinctively shortly after birth, which will increase the offspring’s

survival probability greatly. Through imprinting the newborn offspring could recognize its parent for protection from the dangerous situation, such as being hunted by enemies or being isolated by other members of the same species. For the parent, imprinting could help them identify their offspring so they would not waste time and energy caring for those who are not their offspring. Thus, the probability of species' successful genetic transmission could be improved greatly through imprinting.

Furthermore, the imprinting developed at the early age also shows long-lasting influence on the offspring's mating behaviors, which is called sexual imprinting. For instance, male zebra finches preferred to mate with those who looked like the female bird that reared them, rather than the birth parent, in the case when they are born and reared separately by different parents (Immelmann 1972). Though sexual preferences may also be influenced by other predictors throughout later developmental experience, sexual imprinting still has a long-lasting and unavoidable impact on sexual choices across species.

Imprinting and Learning

Some researchers pointed out that imprinting was a special type of learning in nature. In order to emphasize that imprinting is distinct from learning, Lorenz (1970) proposed the process of imprinting with four characteristics: (1) it happened during a restricted time interval which was called sensitive period or critical period; (2) the process of imprinting was irreversible; (3) this type of learning may occur long before it could be behaviorally demonstrated; and (4) it consisted of supra-individual and species-specific characteristics. According to Lorenz the two most important characteristics of imprinting are irreversibility (the property that after imprinted by a specific object, the organism would always prefer the object to other stimuli) and the existence of critical period.

Although the claim by Lorenz of the irreversibility and critical period of imprinting has been refuted with experimental evidence in birds (e.g., Hoffman et al. 1972; Salzen and Meyer 1968), the characteristics of imprinting concluded by Lorenz

still have important significance for differentiating imprinting from other types of learning such as associative learning and perceptual learning.

From the perspective of perceptual learning theory, imprinting is the consequence of being exposed to the particular stimulus at early time. In studies of perceptual learning, animals present behavior pattern similar to imprinting. For example, rats performed better in discrimination tasks if exposed to the similar stimulus from birth (Gibson and Walk 1956), which indicated that similar with imprinting, perceptual learning was also related to the familiarity with objects.

Yet, perceptual learning is more like the formation of internal representation of a specific stimulus, rather than a more complex process in which organisms form a behavioral (van Kampen 1996).

Another stream of research has been focused on the similarities and differences between imprinting and associative learning. Associative learning includes classical conditioning and operant conditioning. Some researchers pointed out that some features of an imprinting stimulus acted as unconditioned stimulus (US), which were motivationally significant, and other neutral features acted as conditioned stimulus (CS). This approach hypothesized that birds got attached to shape and color (CSs) of specific object because they detect the relationship between shape or color information with the movement or sound (USs) of the object (e.g., Hoffman and Ratner 1973).

However, with the emergence of more evidence, the claim that imprinting is similar to associative learning was questioned (Bateson 1966; Bolhuis 1991). For example, even if birds' behavior can be reinforced by presentation of the stimulus on which they are imprinted, evidence also showed that birds, which were not able to imprint, could still learn operant tasks (Bateson and Reese 1969). Besides, both classical conditioning and operant learning refer to the formation of associations between neutral and unconditioned stimulus, which can be demonstrated simultaneously or separately, but imprinting seems more like a process through which an animal can detect an object naturally and form a representation of it, rather than predict a specific event. Thus, imprinting helps the young offspring learn to recognize the

characteristics of the parent, while associative learning helps a subject to predict the environment.

In addition, the mechanism of imprinting differs from that of associative learning. In associative learning, predicting the environment involves detecting the order of separate events. But in imprinting, learning to discriminate one object (or characteristic) from another may be the most important task, and the order in which the features occur is not that important (Bateson 1990). In one of Bateson's studies, birds performed better in discrimination tasks if the two objects were demonstrated 5 min or more separately than those in the control group which had not been exposed to the objects. Interestingly, when the two objects were demonstrated 30 s or less separately, the imprinted birds performed poorer than the control group in discriminating the objects. This result can be explained that if presented separately within a short time, different stimuli can be perceived as the properties of the same event, no matter the order of stimuli. In general, there are some similarities between imprinting and associative learning, yet differences also exist in the functions and the mechanisms of them.

Imprinting and the Development of Attachment

Imprinting also provides an alternative explanation of how the attachment pattern is developed.

Based on the characteristics of imprinting, imprinting might be a way to understand the formation of the deep and long-lasting ties between the young and their caregivers. It was concluded by Lorenz (1935) that imprinting served as a specific way for offspring to learn their species' identity, and it lead offspring to form two behavioral patterns: filial bonding and sexual preferences. Attachment, as a motivational and behavioral system (Bowlby 1982), directs the young child to seek proximity with a familiar caregiver and thus is thought to be highly related to the process of imprinting. For example, both of imprinting and attachment take place on the basis of the relationship between the

offspring and the primary caregiver, and both of them focus on the offspring's early experience. Although Bowlby did not include imprinting theory in attachment theory, he also considered that attachment behavior would be best explained as instinctive. These similarities between imprinting and attachment led much literature (e.g., Reed and Leiderman 1983) to discuss whether the development of attachment is a result of imprinting.

Although observational studies of young children in natural settings provided behavioral evidence that might indicate attachment was similar to imprinting, there remained distinct differences between them. For instance, Bowlby's attachment theory included the idea that attachment involved learning from experience during a limited age period, especially influenced by the early social interaction between infants and the primary caregiver after birth, which is different from imprinting (Bowlby 1982). Another example was when staying within a certain distance of the mother without effort on her part and picking up small objects, young children would bring them to the mother but not to others (Anderson 1972). Such kind of behavior may be evidence of attachment, but it may lack the evidence of the essential sensitive period if explained by imprinting. In addition, by studying behaviors of young children, attachment can be described as a developmental process, related to an infant's entire caregiving history, yet imprinting tends to be a learning process that happens in a comparatively shorter period (Reed and Leiderman 1983).

Conclusion

Overall, the concept of imprinting has been developed from the observations of young animals by ethologists. This phenomenon is regarded as an instinct model of early learning which happens within the critical period and is irreversible. Though similar with perceptual learning and associate learning, they are actually different internal mechanisms. Both of imprinting and attachment behaviors emphasize the young organism's

instinctive behavioral pattern; however, they are distinct with each other in nature.

Cross-References

- [Associative Learning](#)
- [Attachment Theory](#)
- [Classical Conditioning](#)
- [Conditioned Stimulus](#)
- [John Bowlby](#)
- [Operant Conditioning](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)
- [Unconditioned Stimulus](#)

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Imprinting Effect

- [Imprinting](#)

Improprity

- [Sexual Harassment](#)

Improving Competition in Women

- [Enhancing Women's Competitiveness](#)

Impulse-Control Disorders

- [Impulsivity Disorders](#)

Impulsivity Disorders

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Synonyms

[Impulse-control disorders](#)

Definition

Psychiatric diagnoses that include impulsivity or difficulties with behavioral and/or emotional inhibition as a primary symptom.

Introduction

Impulsivity Disorders refer to the numerous psychiatric disorders that involve impulsivity as a primary aspect of the clinical presentation. Impulsivity may present as an inability to inhibit behavior or emotions, a lack of forethought or planning, and a failure to consider the consequences of one's actions. Examples of impulsivity disorders include pyromania, ADHD, and binge-eating disorder.

Impulsivity Disorders

Impulsivity disorders refer to psychiatric disorders with a primary symptom of impulsivity or deficits in behavioral and/or emotional inhibition. Hollander et al. (2008) define impulsivity as “the failure to resist an impulse, drive, or temptation that is potentially harmful to oneself or other” (p. 778). In summarizing the various definitions of impulsivity, Moeller et al. (2001), focused on the lack of thought, planning, attention, or judgement accompanying behavior. Whiteside and Lynam (2001) identified four personality factors related to impulsivity including urgency, lack of premeditation, lack

of perseverance, and sensation seeking supporting the notion that “In addition to its importance in personality, impulsivity also plays a prominent role in the understanding and diagnosis of various forms of psychopathology” (p. 670).

The DSM-5 (2013) includes numerous disorders that involve impulsivity. The disorders outlined in the DSM-5 (2013) section *Disruptive, Impulse-Control, and Conduct Disorders* involve difficulties controlling behaviors and emotions and “are unique in that these problems are manifested in behaviors that violate the rights of others (e.g., aggression, destruction of property) and/or that bring the individual into significant conflict with societal norms or authority figures” (p. 461). Examples of disorders in this section include intermittent explosive disorder, pyromania, and kleptomania. Intermittent explosive disorder involves distinct episodes of impulsive aggressive outbursts that appear out of proportion to the antecedent event or stimulus and remit spontaneously (Saddock and Saddock 2007). The diagnosis of pyromania includes deliberately setting fires on more than one occasion that is not done for monetary gain, to conceal criminal activity, or as a result of hallucinations or delusional beliefs (American Psychiatric Association 2013). Kleptomania is described as an inability to inhibit the impulse to steal objects that the individual does not need (American Psychiatric Association 2013).

Impulsivity also serves as a prominent symptom in the presentation of Attention-Deficit Hyperactivity Disorder (ADHD). Impulsivity in ADHD can occur within the cognitive, behavioral, and emotional domains. Individual's diagnosed with ADHD to experience impulsive errors due to failing to wait for complete instructions, a lack of understanding of what a situation requires, and failing to consider the consequences of actions prior to initiating behavior (Roberts et al. 2014). Trichotillomania, intentional hair pulling that causes visible hair loss, and compulsive skin picking that causes tissue damage have also been cited as impulse-control disorders (Grant 2008). Other conditions that involve impulsivity include

Bulimia and Binge-eating disorder, substance-use disorders, addictions, Borderline Personality Disorder, Bipolar Disorder, and Paraphilias (Hollander et al. 2008).

Conclusion

Impulsivity involves a lack of forethought, judgment, and behavioral and emotional inhibition. Impulsivity is recognized as a prominent feature of various psychiatric conditions including kleptomania, ADHD, substance-use disorders, and addictions.

Cross-References

- [Mental Illness](#)
- [Psychopathology](#)

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In Nonhuman Primates

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Synonyms

[Object permanence in monkeys and apes](#); [Primate object permanence](#)

Definition

Cognitive skills related to the understanding of an unseen object's continued existence in nonhuman primates.

Introduction

Object permanence is the understanding that an object does not cease to exist just because it can no longer be directly perceived. This is a fundamental concept studied in the field of developmental psychology, the subfield of psychology that addresses the development of infants' and children's social and mental capacities. There is not yet scientific consensus on when the understanding of object permanence emerges in human development. Jean Piaget (1952) claimed that children progressively obtain object permanence during the first 2 years of life and that, in its final stages, object permanence extends beyond simply understanding that an unseen object continues to exist to being able to follow the trajectory of an object after its path becomes occluded. Early studies on object permanence were conducted by hiding objects behind screens or in boxes and observing whether infants made a search response and generally supported Piaget's assertion that object permanence is achieved in stages. While some researchers think object permanence is a skill that is gained through innate developmental processes (e.g., Baillargeon 2008), others claim it is a learned skill (e.g., Cohen et al. 2002).

Object Permanence Tasks

Studies examining object permanence in animals have used a combination of visible and invisible tasks. Visible tasks involve moving the search object from to and from hiding locations in the experimenter's open hand or in a transparent "displacer," while invisible tasks involve moving the search object moving to and from hiding locations in an opaque displacer. Both types of tasks may involve either single displacements (i.e., the search object is moved only once and in that hiding location) or double displacements (i.e., the search object is moved first to one hiding location, then from that hiding location to a second hiding location). Single visible displacement tasks provide evidence of whether the subject recognizes that the search object exists even when it is unseen. Double visible displacement tasks provide evidence of whether the subject has the ability to track a visibly moving object. Invisible displacement tasks provide evidence of whether the subject has the ability to track the trajectory of an object once it is out of sight.

Evidence

Tomasello and Call (1997) describe object permanence in nonhuman primates as a type of "physical cognition," which is a term describing the ability to manipulate, categorize, and quantify objects. These complex cognitive skills may be necessary for foraging and extracting food from hidden locations and thereby represent an evolved psychological mechanism (Tomasello and Call 1997). Evidence that object permanence, in particular, is an innate skill is provided by research demonstrating that differences in object permanence between members of the same primate species are small (Call 2000). Object permanence is a cognitive skills shared by a wide variety of primate species. Longitudinal testing of macaque monkeys showed that such skills advance over time providing evidence for an innate mechanism shared between humans and other primates (Hall-Haro et al. 2008). Numerous ape and monkey species have been able to successfully solve

both visible and invisible displacement tasks. However, some highly controlled studies using a series of nine increasingly difficult visible and invisible displacement tasks showed differences between species. Great ape species such as chimpanzees and orangutans have solved all displacements tasks whether visible or invisible and no matter the number of displacements (Barth and Call 2006), while monkey species such as marmosets (Mendes and Huber 2004) and cotton top tamarins (Neiworth et al. 2003) failed invisible displacement tasks.

Conclusion

All primate species have demonstrated some degree of object permanence skills, but those species most closely related to humans demonstrate object permanence abilities that are more comparable to humans.

Cross-References

- ▶ [Cognitive Development](#)
- ▶ [Cognitive Development in Non-human Primates](#)
- ▶ [Implications of Object Permanence](#)
- ▶ [Object Permanence](#)
- ▶ [Theory of Mind](#)

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In Vitro Fertilization

► [Medically Assisted Reproduction](#)

Inaction Regret

► [Sexual Regret](#)

Inbreeding Avoidance

► [Westermarck Effect and Imprinting](#)

Inceptive and Derived Memory

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Synonyms

[Encoded memories](#); [Episodic memory](#); [High-level representation](#); [Memory computation](#); [Trait judgment](#); [Transformed information](#)

Definition

Inceptive memory is a representation of the world stored in the way it was encoded at its inception. Derived memory is a higher level of representation that was derived from inceptive memory stores but was computationally transformed to supply in a form that minimizes the need for further processing by the decision rules that use it.

Introduction

It is useful to distinguish inceptive from derived memories as they serve survival. Inceptive memories are representations of external input stored in the way they were encoded at the time at which they were first experienced. Many episodic memories appear to be inceptive; they often contain perceptual detail, proprioceptive information, emotion qualia, a sense of the self as present in the encoding situation, and the sense that the memory is very similar to the original experience. But not all inceptive memories are episodic. It is logically possible to have an inceptive memory about a specific event involving the self without its being episodic in character. It would not be episodic if it lacked the subjective sense of self in space and time that is diagnostic of episodic memory. A derived memory system together with its inferential machinery prepares answers or preprocesses information into usable and ready forms, to facilitate decisions and judgments of a specific type that would otherwise be detrimental if they had to be computed from raw data on demand.

Human Memory and Computation

The computational operations that generate derived memory are not limited to mere extraction of information from inceptive memory. A derived memory can contain information not present in any of the inceptive memories on which it was based, generated by procedures that made inferences from the inceptive data. A derived memory may, in some cases, be the output of the same

decision process that uses it at a later time. For instance, if one needs to decide at Time 1, on the basis of behavioral episodes, whether Person Y is honest, the conclusion might be stored as a derived memory for use at Time 2. A trait summary is a form of derived memory; a stored episode is an inceptive memory. Because of their advantages, human memory may be full of independent, derived memory stores linked to various inceptive memory stores (Nadel 1994). The linked memory stores of abstracted personality traits and behavioral episodes that exemplify those traits may prove to be a model system that can illustrate properties that are common to many memory stores.

Adaptive Function of Memory and Its Properties

The adaptive function of information storage is intrinsically prospective. It is used to support future decisions and judgments, which cannot be known in advance with certainty. To the extent that the character of subsequent decisions and judgments can be predicted, the memory system can be tailored to flag relevant information and precompute variables that are required to make them – that is, it can develop a derived memory store. This set is indefinitely large and hence precluded by limitations on computational and memory resources. In functional terms, factors that should govern the number and type of derived memory stores include (a) predictability, the existence of factors, either ontogenetic or phylogenetic, that allow the successful anticipation of likely varieties of future judgment or decision types; (b) importance, the value of those judgments or decisions ought to justify the costs; (c) urgency, the requirement that such judgments be made quickly; and (d) economy, the number of judgments or decisions supported by a derived memory store should be proportionately large with respect to its size. The use of trait summaries in making decisions about social interactions meets all four criteria.

Benefits and Disadvantages

Storing semantic summaries has both advantages and drawbacks. Direct retrieval of precomputed

representations (derived memory) economizes on online computation and is fast. But it takes up increasing amounts of memory the larger the set of representations that must be precomputed and on tap and may provide information that is no longer up to date. In contrast, procedures triggered online that take inceptive memories as input economize on derived memory and provide up-to-date information. But they are expensive computationally and increasingly slow, the more computational steps that are involved. An architecture designed functionally would be shaped by these trade-offs, using different mixes of memory versus computation for different types of adaptive problem (Pinker 1997, 1999). Decisions about personality traits provide a case in point.

Trait Summaries

Dynamically, when the data set of relevant events is small, judgments about personality traits appear to be made predominantly based on retrieved behavioral episodes (Klein et al. 1997; Klein and Loftus 1990). As the behavioral evidence grows, judgments are increasingly made by accessing an emerging trait summary and decreasingly by accessing relevant episodes. When the amount of experience is high, the semantic summary is well developed, and trait judgments are made by accessing this knowledge (Klein et al. 1997; Klein and Loftus 1990). This process is faster than retrieving and considering individual instances (Klein et al. 1992), and it bypasses and inhibits this other judgment route. Evidence suggests that semantic trait summaries are constructed on the basis of the same set of behavioral episodes that are input into the episodic store (Sherman 1996), although supplementation from other sources of information has not been ruled out. Neurologically impaired individuals who exhibit an inability to retrieve individual events show no apparent impairment in their ability to make accurate trait judgments (Klein et al. 1999) and even maintain the ability to revise their trait judgments based on new episodes they cannot recall. This suggests retrieval of behavioral episodes for trait

judgments lies outside conscious awareness. It further argues that either updating of semantic information occurs as each episode is experienced or else the procedures involved in updating do not require conscious access to the episodic store (Sherman and Klein 1994).

Stored Episodes

Trait summary is valuable in human evolution and survival as it fosters speedy access to information and avoidance of redundant and costly computation. Nevertheless, a summary lacks information present in the episodes from which it was derived. Retrieving a trait summary may be faster than constructing a judgment online from a database of episodes, but it is necessarily less accurate. Maintaining a database of inceptive, episodic memories solves several problems that a trait summary cannot. New information may cause previous episodes to be reinterpreted, drastically changing one's judgments of a person or a situation. Keeping a database of episodes is helpful even when a drastic reinterpretation of previous events is not called for. Judgments can be revised in light of new information.

Conclusion

Memory allows organisms to adjust their behavior on the basis of information they acquire ontogenetically, through their experiences with the world. This connection between personal experience, memory, and behavior implies a close relationship between learning and memory.

Memory evolved to supply useful, timely information to the organism's decision-making systems. Therefore, decision rules, multiple memory systems, and the search engines that link them should have coevolved to mesh in a coadapted, functionally interlocking way.

Cross-References

- [Episodic Memory](#)
- [Scope Hypothesis, The](#)

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Incest

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Synonyms

[Consanguineous sexual relationship](#)

Definition

It is defined as the sexual activity between individuals who are genetically related.

Introduction

Incest is considered a taboo sexual activity. Incest is derived from Latin word *incestus* which means unchaste. It is defined as “any sexual activity between close blood relatives who are forbidden by law to marry” (Kellogg 2005). The Cambridge English Dictionary also defines incest as “sexual activity involving people who are closely related and not legally allowed to marry” (Dictionary 2017). It is a worldwide neglected social issue both in developed and developing countries. As per a recent data from developing countries like India, nearly three out of ten registered cases of rape are due to incest, and it follows an increasing trend (Verma et al. 2017). Considering its rising trend, importance, and impact on the society, WHO classifies it as a silent health emergency (Organization 2004) and is underreported because of social taboo.

Incest: A Journey Through History

Incest is declared as “prohibited degree” of relationship from Biblical period. There is a bidirectional relationship between incest avoidance behavior and taboo. Incest is discouraged and forbidden; hence, people avoid incest, which may give rise to taboo related to incest. On the other hand, because there is taboo associated with incest, people avoid incest (Wolf 2015). Incest carries many social disadvantages (e.g., breach in social harmony, sexual abuse, role-relational confusion, and cultural violation); hence, taboos are created against incest (Wolf 2015). Freudian belief was centered around spontaneous inclination of human to indulge sexually within the family, though it was strongly criticized by many researchers (Wolf 2015). Incestuous characters also appear in mythology in all ancient cultures worldwide (Oosten 2015; Serrano and Gunzburger 1983). These mythological incestuous relationships are depicted in the context of disastrous outcomes, which might have propagated taboo with incest.

Westermarck's hypothesis contradicted the concept given by Sigmund Freud. Westermarck

postulated that children, who grow together in close association, often develop aversion to sexual contact among themselves as they become adult (Morehead 1999). It maintains the integrity of the family and act as a protective barrier against incestuous sexual contacts among siblings.

Incest: Current Status Across the Globe

Incestuous relationship may be consensual or non-consensual. Non-consensual incestuous relationship amounts to rape. Victims of incest may not pursue legal or retributive actions against the family because of fear, helplessness, negative attitude, and stigma toward him or her (Fontes and Plummer 2010; Yildirim et al. 2014).

Incestuous relationship between parent-children and among siblings is prohibited legally as well as socioculturally, worldwide (Holanda Júnior 2017). In England and other Western countries, it is regarded as a cognizable offense. Both men and women, above the consenting age, are punishable according to law, even if there is consent. In India, however, incest per se is not an offense. Police can take cognizance of such cases only when the offense can be charged under Section 376 (rape), 497 (adultery) Indian Penal Code, or under the provisions of POCSO (Protection of Children from Sexual Offences) Act (Modi 2011). In the current society, some incestuous relationships are socially sanctioned in certain regions, which results in consanguineous marriages. Consanguineous marriages are still prevalent in parts of Africa, Asia, and Middle East. Across the globe, approximately 10% of children are born from parents with consanguineous marriage (Maguire et al. 2018). Consanguineous marriages more commonly happen between cousins (Hamamy 2012). Among other types of incestuous relationships, incest between father-daughter is reported to be most common followed by incest between brother-sister, sister-sister, and mother-son (Sariola and Uutela 1996).

Risk Factors for Incest

There are many risk factors that may encourage incestuous behavior. Early evidence support that

overcrowding at home setting might result in breach in family member's personal privacy, which may increase the risk of incest (Weinberg 1955). Incest aversion refers to negative attitude and feelings of an individual toward an incestuous relationship (Antfolk 2014). It has been believed that incest aversion has an important role in self-regulation and prevention of incest (Antfolk 2014). Incest aversion is stronger among the siblings if they are of opposite gender (brother-sister) than if they are of the same gender (sister-sister or brother-brother) (Holanda Júnior 2017). Similarly females are less incestuous than males due to higher incest aversion (Holanda Júnior 2017).

Incestuous relationships between fathers and daughters may be seen in families where fathers used to have a strong authoritative role and the mother is absent or having significant disability as a result of which daughter is playing the role of mother (Herman 1981).

Impact of Incest

Women who had history of incest are more likely to develop poor self-esteem and often have difficulty in close relationships (Herman 1981). Incestual practice between an adult and their child is usually considered a form of child sexual abuse and may lead to development of sexual dysfunction, depression, anxiety disorder, substance abuse, borderline personality disorder, and post-traumatic stress disorder (PTSD) in later part of life. Incestuous relationship results in inbreeding, which has various health hazards because the expression of otherwise recessive alleles, due to homozygous states, might cause development of complex diseases and reduction in longevity (Rudan et al. 2003). Evidences support increased mortality of children born from consanguineous marriages (Rudan et al. 2003). Consanguineous marriage also increases the risk of recurrent pregnancy loss, stillbirths, early death of child, X-linked disorders, autosomal dominant disorders, mental retardation, as well as limb abnormalities (Shawky et al. 2013). The

children born from incest are often at risk of developing rare recessive disorders like homocystinuria, congenital ichthyosis, deaf-mutism, retinitis pigmentosa, glycogen storage disease, cystic fibrosis, and progressive cerebellar degeneration. They are also at high risk of developing congenital organ malformations (Super 1981).

Incestuous relationship during childhood is often a traumatic experience that adversely affects the mental well-being. The cognitive behavioral and other psychotherapeutic interventions for the victims of incestuous abuse focus on understanding the traumatic stress, psychodynamics, concept of self, as well as the relational aspects with the perpetrator (Courtois 1997).

Conclusion

Due to taboo, incest often goes unnoticed and underreported, even though it is equally traumatizing like any other sexual crime. When it is socially sanctioned and resulting from consanguineous marriage, it is important to look for the health of the progeny born from the incestuous relationship.

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Incest Aversion

► Westermarck Effect

Incest Avoidance

► Kin Recognition

► Westermarck Effect and Imprinting

Incest Avoidance and Dating

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Introduction

Humans, like many other animals, possess information-processing programs that guide mate choice. Inherent in mate choice programs are procedures that weigh the potential benefits versus costs of selecting a particular individual as a sexual partner. The question is, which attributes would have been causally linked to the probability of reproductive success and thus part of the calculation that assesses the costs versus benefits of a given sexual partner? Furthermore, how are different attributes traded off against one another? After all, one rarely encounters a mate that is a “10” in every desirable category. That is, one is unlikely to encounter (never mind attract and retain) a mate that is a 10 in every relevant category. Instead, individuals vary in their value as a sexual partner, and to the extent that certain trade-offs had greater positive feedback with respect to selection, then we should see psychologies sensitive to making such trade-offs.

The field of evolutionary psychology has identified many attributes that contribute to a man's and woman's value as a sexual partner, including attractiveness, intelligence, and resource status (e.g., Buss 1994). There has been less discussion, however, of how these attributes are traded off

against the other factors that might influence mating and dating. One model of mate choice discussed by Lieberman and colleagues (e.g., Tybur et al. 2013; Lieberman and Patrick 2018; Lieberman et al. 2018) suggests there are four major factors that interact to shape perceptions of sexual desirability: (i) the mate value of a potential sexual partner, (ii) one's own mate value, (iii) the perceived availability of mates in the social environment, and (iv) the estimated genetic relatedness between oneself and a potential sexual partner.

In unpacking the factors highlighted by this model, let's first clear up some terminology and distinguish two key terms: *sexual value* and *mate value*. Sexual value is a term for sexual desirability, but it refers specifically to the desirability of another individual as a sexual partner *for oneself*. In this sense, sexual value is a subjective term. Mate value, by contrast, is more objective; it is an abstract assessment that refers to the sexual desirability of another individual *in general*, not for oneself.

Several observations support the notion that sexual value and mate value are related, but distinct, psychological computations. First, individuals from around the globe show surprising consistency in their ratings of physical attractiveness (Symons 1979). Second, people are capable of assessing the mate value of both men and women. Specifically, men and women can rate both men and women in terms of their physical attractiveness, evaluating members of the same and opposite sex on a single scale ranging from extremely attractive to extremely unattractive. But ratings of physical attractiveness do not equal sexual attractiveness to the rater: A man might know his best friend is physically attractive, for instance, yet find the prospect of having sex with him quite disgusting. Third, we can assess the mate value of our genetic relatives (both same and opposite sex), but typically object to sex with our relatives even when assessing their mate value as high. A brother might know his sister is very good looking (and vice versa) but the fact that they have categorized each other as close genetic relatives means that an otherwise attractive

sexual partner is turned into a sexual partner of last resort. Thus, mate value is not sensitive to genetic relatedness, but sexual value is.

In general, then, two factors that get traded off against one another to generate a person's sexual value are mate value and degree of genetic relatedness. Much as mate value is computed based on cues that in ancestral environments correlated with fertility and the ability to rear offspring, genetic relatedness is computed based on cues that correlated with a person being a close genetic relative in ancestral social environments. Extensive research has examined how humans assess relatedness (for review, see Bressan and Kramer 2015). Such research suggests that different cues help to identify different types of close relatives. For instance, men use cues of partner sexual fidelity to identify potential offspring (Daly and Wilson 1988; Apicella and Marlowe 2004; Billingsley et al. 2018), whereas women likely use cues of birth. Children use cues of shared parental investment to identify potential siblings (Lieberman et al. 2007; Lieberman and Billingsley 2016), and likely use information regarding nursing frequency to determine motherhood. It is not yet known how children identify their father, but one hypothesis is that children track which man invests most in them and their mother to discern a likely father from other male relatives and unrelated men in the social environment.

Whatever the cues may be, a model of kin detection in humans posits a specific type of program that computes a *kinship estimate* based on the cues associated with a particular individual. This estimate of genetic relatedness is then one input for the system that calculates a person's sexual value. For instance, a woman who is evaluating a male might find him to have high mate value, that is, he is healthy and is intelligent, he has resources, and appears willing to invest those resources in a mate. If this male is *not* a relative, this positive mate value could lead to a high and positive sexual value. However, if he is a close genetic relative, like a brother, the elevated kinship estimate counteracts the high mate value, promoting incest avoidance by pushing sexual value very low.

How low? Well, this depends on the other two factors mentioned above: the availability of potential mates and one's own mate value. Plus, it depends on one's own gender, specifically, on how the sexual value system was calibrated during development. The availability of potential mates should moderate the estimated sexual value assigned to a given person. For instance, a person of moderate mate value might be assigned a higher sexual value when there are few potential partners available than when the environment is rich with possible sexual partners. Aside from anecdotal evidence of imprisoned heterosexual men who might engage in homosexual activities in the absence of available females, psychological research suggests mate availability is an important factor in our sexual psychology. As an example, Daniel Conroy-Beam et al. (2016) found that for people in a relationship with a partner of relatively lower mate value, the perceived availability of better partners was linked to lower relationship satisfaction. The context of what's available and perceptions of an individual's mate value are somehow interacting to generate sexual motivations and partner preferences.

As Conroy-Beam's study also suggests, one's own mate value also influences assessments of sexual value. Only individuals who perceived themselves to have higher mate value than their partner experienced the reduction in relationship satisfaction. In another study (Morgan and Kinsley 2014), researchers manipulated how men felt about their own mate value and then had them look at both attractive and unattractive faces. They found that all men in the study looked at the attractive faces and did so regardless of whether they were led to believe they were of high or low mate value. But men who were led to believe they were of high mate value looked less at the unattractive faces as compared to the men led to believe they were of low mate value. These results suggest that the mind takes into account one's own condition when making decisions regarding whom to pursue as a sexual partner.

Despite the fact that both men and women likely weigh similar kinds of information when assessing a person's sexual attractiveness, there are good reasons to expect that male and female

brains show different sensitivities to these pieces of information. Take relatedness as an example. Although there are costs of inbreeding that affect both men and women, women are expected to be much more sensitive to these costs because women have a much higher minimum level of investment in a given offspring as compared to men (Trivers 1972). That is, relative to men, women should find a given event of inbreeding more objectionable because women experience larger opportunity costs when it comes to biologically risky sexual encounters. What this means is that the conditions under which a female might consider having sex with a brother need to be far more dire (e.g., on a deserted island with no available mates at all for decades) as compared to the conditions under which a male might consider having sex with a sister (e.g., on a deserted island with no available mates for a month).

In terms of the psychological programming, female minds might be organized to weigh relatedness quite heavily and negatively and not allow for other inputs to change this easily (e.g., number of mates available and one's own mate value). By contrast, in male minds, sexual value might be more labile, and changed more easily given various contexts. Certainly more work is required to determine the veracity of these claims and how the model proposed above fares in comparison to other proposed models of sexual attraction.

What does all of this have to do with dating? By and large, men and women possess sophisticated programming, calibrated and tuned over the course of one's lifetime, to help guide mating decisions. Our evolved systems are well equipped to prevent us from sexually desiring our genetic relatives and those perceived to be of low mate value. However, under novel cultural conditions, our system might not operate in the manner we typically expect. For instance, it is possible that the natural mechanism for detecting kin and thus for avoiding incest, can be disrupted. One example would be siblings raised on the Kibbutz. If most siblings were reared apart in separate children's houses, then siblings would not have categorized one another as kin to the same extent as they would have had they lived under the same roof more regularly. This holds true for siblings

separated at birth. Another modern phenomenon is sperm-banks. As sperm-banks become more widely used, women who have never met might be giving birth to paternal half siblings. Should they meet, no natural aversion will be present that arose due to the operation of a kin detection system. Like two strangers, should they meet, half siblings will be left to evaluate each other based on the desired characteristics in a potential mate. Although the chances of such an encounter in the US are extremely low, in some places it can be a bit higher. For instance, in Iceland, a country with a population of just under 400,000, there is now an app to help people identify potential relatives. Before they date, Icelanders can now find out if they are cousins.

Conclusions

In conclusion, Darwinian insights into mating psychology can help reveal the factors that generate a sense of sexual attraction and the circumstances in which each factor might weigh heavily or not at all.

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Incestuous Behavior

► Adaptive Problem of Detecting Kinship

Incidental Encoding

► Summary Representation

Inclusive Fitness

- Altruism in Kin Selection
- Benefits to Kin
- Cooperation Varies with Genetic Relatedness
- Genetic Relatedness Affects Aid to Kin
- Hamilton's Rule and Genetic Relatedness
- Hamilton's Rule and Theoretical Implications
- Helping and Genetic Relatedness
- Helping and Inclusive Fitness Benefits to Helper

- ▶ [Increased Grandchild Survival](#)
- ▶ [Kinship Psychology Manipulations](#)
- ▶ [Rescuing Friends and Relatives](#)
- ▶ [Triggering Kin Selection](#)

Inclusive Fitness Model of Suicide

- ▶ [Suicide as Kin-Directed Altruism](#)

Inclusive Fitness Theory

- ▶ [Hamilton's Rule](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
- ▶ [Kin Selection](#)
- ▶ [Multilevel Selection Theory](#)

Income

- ▶ [Women's Personal Resources](#)

Income Transfer

- ▶ [Redistribution Preferences and Low Socioeconomic Status](#)

Incongruity

- ▶ [Components of Humor](#)

Increased Cortisol

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Synonyms

[Cortisol reactivity](#); [Cortisol response](#); [Stress reactivity](#); [Stress response](#)

Definition

Cortisol is a major steroid hormone in humans that is secreted by the adrenal cortex during the experience of stress as part of an adaptive coping response. Cortisol has wide-ranging effects, largely functioning to alter an organism's immediate response to the stressor, modulate their response to a subsequent stressor, and aid in their adaptation to a chronic stressor.

Introduction

Cortisol is synthesized and secreted by the adrenal cortex following stress-induced activation of the hypothalamic-pituitary-adrenocortical (HPA) axis – the principal endocrine component of the stress response system. During the experience of stress, HPA axis activation causes a neuroendocrine cascade of events that result in the synthesis and secretion of glucocorticoids (GCs) – primarily cortisol in humans and corticosterone in other species. When environments or situations are judged to be harmful, threatening, or challenging (i.e., they are *stressful*), the central nervous system sends signals to the hypothalamus, which then secretes corticotropin-releasing hormone (CRH) to begin the neurobiological sequence of events that results in increased cortisol levels. CRH

signals the pituitary gland to secrete adrenocorticotrophic hormone (ACTH), which is then taken up by receptors in the adrenal glands – a pair of relatively small endocrine glands laying above the kidneys. In turn, the adrenal cortex, which constitutes the outer covering of the adrenal gland, is stimulated to release cortisol.

As a corticosteroid and glucocorticoid, cortisol has diverse effects on physiological functioning, including: increasing blood pressure; increasing blood sugar levels; suppressing the immune system and reducing inflammation; promoting the breakdown of glycogen, lipids, and proteins; and generally, mobilizing the body's energy resources. Compared to the relatively quick response of the sympathetic division of the autonomic nervous system during the experience of stress, the HPA axis mounts a more delayed, long-term response. However, the HPA system does have rapid effects as well, such as fast negative feedback into the HPA circuit, likely mediated by putative membrane steroid receptors (Nesse et al. 2010). Elevation of cortisol generally starts about 5 min following stressor exposure, with a peak between 10 and 30 min. Some of the effects of cortisol begin after an hour and may be observed for several hours or more. HPA activity is regulated by a hierarchy of feedback loops at different levels in the axis (see Gunnar and Vazquez 2006), and the sensitivity of these feedback loops is a major factor in determining HPA responsivity (Del Giudice et al. 2011).

Cost-Benefit Trade-Offs

As with any trait, the cortisol response is associated with cost-benefit trade-offs. While cortisol plays a role in regulating blood pressure, glucose metabolism, and immune function in order to facilitate acute biological responses to stressors, chronic secretion of glucocorticoids has been associated with various forms of pathology and disease. Chronic secretion of GCs has been linked to depression, insulin resistance and diabetes, hypertension and atherosclerosis, bone loss, and

disorders involving decreased immune function (see McEwen 1998). Chronic GC secretion has also been shown to adversely affect the hippocampus – an area of the brain intimately linked to memory and learning – where decreased dendritic branching, loss of neurons, structural change in synaptic terminal, and neuron regeneration inhibition have been noted (see Sapolsky 1996). Despite the substantial costs that are sometimes linked to chronic GC secretion, natural selection has shaped this stress-responsive trait because the associated benefit to organisms is even more significant.

Functions of the Cortisol Response

Cortisol, and more broadly, glucocorticoids (GCs), modify an organism's response to stress in several notable ways that vary as a function of environmental or situational context. In general, cortisol functions to mobilize available resources and serves as a counterbalance to sympathetic activation during the stress response process. Mobilization of resources may include those that are physiological or psychological in nature (see Sapolsky et al. 2000). Functioning as a counter-regulatory mechanism to help counterbalance the effects of sympathetic activation that can result in wear and tear on the body, cortisol can aid the recovery of the organisms as well (see Boyce and Ellis 2005).

What Does the HPA Axis Respond to?

Cortisol plays a pivotal role as mediator of environment adaptation, but significant physiological costs and side effects associated with elevated cortisol responses contribute to the HPA axis selectively responding to specific types of challenges. The HPA axis generally responds with increased cortisol when people (1) encounter unpredictable and/or uncontrollable challenges that require them to be alert and involve an element of anticipation, and (2) when challenges

involve social-evaluation or relational threat (for review, see Dickerson and Kemeny 2004). The body of literature assessing HPA axis responses to stress overwhelmingly demonstrates that activation of the HPA axis and secretion of cortisol is strongly linked to social feedback. The HPA axis is highly responsive to separation and rejection experiences in family life for infants and children, while a similarly strong response is associated with older children in adults in the context of peer evaluation. Social evaluation was likely important in the context of evolutionary history, as negative evaluation carried with it the potential to incur a loss in social status or result in social ostracism, rejection, and loss of social bonds (Del Giudice et al. 2011).

Sex Differences in HPA Axis and Cortisol Response

Sex differences in biological and behavioral responses to stress likely developed during human evolutionary history. Although the basic architecture of the SRS – including the HPA axis – is the same for both sexes, the types of events or environmental contexts that trigger a response in men and women differ (Del Giudice et al. 2011). Generally, men tend to exhibit greater activation of the HPA axis than women during tasks related to achievement. The heightened response in males may be due to achievement-oriented tasks involving a challenge to status, subsequently enhancing the salience. Compared to males, females tend to demonstrate greater responsivity of the HPA axis in situations where social rejection is involved (Stroud et al. 2002). The enhanced salience of rejection experiences in females relative to males may be explained – in part – by Taylor et al. (2000) tend-and-befriend theory of biobehavioral responses to stress. Following this model of sex differences in behavioral and biological responses to stress, men follow a pattern of responsivity that closely follows the sympathetic fight-or-flight response. However, in females, environmental threats or challenges elicit a “tend-and-befriend” pattern of stress responding. This pattern involves caring for and

protecting offspring as a tending response and also involves affiliation with a group and efforts to seek social support as a befriending response. Given the response preference in females for tending and befriending during times of stress, real or imagined rejection experiences would be expected to be highly salient for females, resulting in enhanced activation of the HPA axis and subsequent cortisol secretion.

Conclusion

Cortisol is a major steroid hormone in humans and end product of HPA system activation during the experience of stress, serving as a critical component of adaptive coping. Cortisol has a diverse range of behavioral and physiologic effects, functioning to alter an organism’s immediate response to a given stressor, modulate their response to a subsequent stressor, and facilitate adaptation to chronic stressors. Like all traits, the stress response associated with HPA system activation and increased cortisol is associated with cost-benefit trade-offs. The HPA axis is particularly responsive to unpredictable and/or uncontrollable challenges and social-evaluative threat. While the basic architecture of the HPA system is the same between sexes, differences in biological and behavioral responses to stress likely arose during human evolutionary history as a consequence of different environmental demands on males and females.

Cross-References

► [Stress](#)

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Definition

The role of cooking in increasing energy uptake from the diet as well as reducing the body's costs of digestion.

Introduction

Cooking food is a unique human activity spanning across all cultures, and humans appear to be evolutionarily adapted to this crucial aspect of their diet (Wrangham and Conklin-Brittain 2003). The value of cooking lies in its ability to widen the range of foods that are safe to eat (whether by making their digestion easier or neutralizing toxic compounds) as well as extract more energy from the foods ingested. Both human and animal studies illustrate that the more cooked food there is in a diet, the greater the net energy gain for the eater (Carmody and Wrangham 2009), and a diet of raw foods is energetically inadequate even when various nonthermal processing methods are employed (Koebnick et al. 1999). The effect of cooking on the energy gain from eating includes several mechanisms: increasing digestibility and thus caloric value of ingested foods, lowering the body's energetic costs of digesting, and mounting an immune defense against food pathogens.

Cooking: Digestion Costs

Eating requires the body to use energy: ingesting and assimilating a meal leads to an increase in the metabolic expenditure – termed diet-induced thermogenesis or DIT – that accounts for about 10% of the total energy budget for those of us on a Western diet (Westerterp 2004). DIT increases with masticatory effort, thus softer foods that require less chewing lead to lower metabolic expenditures. Cooking is expected to lower DIT by reducing the structural integrity of foods (Carmody and Wrangham 2009), though no mammal studies have tested this hypothesis. Only one study with pythons provides direct support, where a cooked meat diet resulted in a 13% decrease of

Increased Energy/Reduced Digestion

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Synonyms

Net energy gain

digestion costs compared to the raw meat version (Boback et al. 2007). Since nonthermal processing methods – such as using tools to pound or grind foods – would also make food less firm (thus facilitating chewing and lowering digestion costs), some suggest that cooking was not a necessary part of ancestral diets as tool use could have increased energetic intake without the need for fire (Cornélio et al. 2016).

Net Energy Gain: Starches

Energy increase from cooked starches is well-known, as heat improves digestibility of such foods in two ways: it causes a collapse of the structures of raw starch granules (termed gelatinization – a process that increases starch degradation in the digestive tract) and it denatures enzyme inhibitors present in the foods leading to better digestion of starches in the human mouth and gut (Svihus et al. 2005).

In order to compare the net energy gain resulting from cooking as opposed to nonthermal processing methods, Carmody et al. (2011) put mice, a model omnivorous mammal, on three versions of a starchy diet – raw, pounded, and cooked sweet potato. A number of studies have already shown that cooking substantially increases digestibility of starchy foods – from 6% to 206% depending on the food item (Carmody and Wrangham 2009). Carmody and colleagues, however, also demonstrate that the effects of cooking specifically exceed the effects of pounding: while mice maintain their weight on the cooked version of the diet, they lose weight on both the raw and pounded versions. In addition, they preferred cooked sweet potatoes the most, after having tasted the raw, pounded, and cooked variations. Since mice were hungry following a fast, the authors suggest that higher preference for the cooked version was partly due to its energetic advantages.

Net Energy Gain: Fats

Cooking also appears to increase caloric gain of dietary lipids: Groopman et al. (2015) show that

for cooked peanuts, lipid digestibility as well as net caloric gain (measured by body mass increases of mice) significantly exceeds that of raw peanuts. In addition, their results indicate that non-thermally processed (blended) peanuts do not lead to increased lipid digestibility or net energy gain. Cooking appears to “predigest” oil bodies (structures where peanuts store their lipids), because heat mimics the disruptive effects of a digestive enzyme peptin on the proteins that protect lipids from digestion.

Net Energy Gain: Meat

The effect of cooking on animal foods has been less clear. On the one hand, some consequences of heat processing should increase meat's energy value, such as heat-induced protein denaturation: as heat unwinds proteins, it increases their susceptibility to protein-digesting enzymes in the small intestine. Other positive effects include compromised structural integrity of cooked meat (heat gelatinizes collagen and makes separation of muscle fibers easier) and deactivation of foodborne microbes (thus, lowering the body's energetic costs of an immune defense). On the other hand, dry heat methods result in caloric loss due to fat dripping, and protein digestibility can be reduced due to the Maillard reaction – chemical reaction during cooking responsible for the appetizing flavors and aromas of cooked foods. These flavors increase meat palatability and attract not only humans but also great apes (e.g., chimpanzees, gorillas) that spontaneously prefer cooked meat samples to raw ones (Wobber et al. 2008). Thus, while the Maillard reaction might decrease protein digestibility in some ways, it may increase the amount of meat eaten due to increased palatability.

Carmody et al. (2011) test cooked and raw meat diets on mice, once again contrasting the effects of cooking with a nonthermal alternative – pounding. Authors predicted weight loss on all three versions – raw, cooked, and pounded – since a 100% meat diet is not expected to be beneficial for an omnivorous species. While mice did lose weight on all three, only cooking (and not pounding) had a positive effect on energy

gain as mice on the cooked version experienced the least body mass loss. Considering that intake on the cooked version was in fact lower than on the pounded diet, the higher energy gain with cooked meat is intriguing. This result can be attributed to decreased effort required for chewing as well as improved digestibility through heat's denaturation of proteins. Denaturation results in unwinding of proteins from their tight structures, making them more susceptible to digestive enzymes in the small intestine. This process increases the proportion of protein digested by the eater in the small intestine, compared to that digested by the gut bacteria in the large intestine – this is important for the animal's net energy gain, because very little energy is returned to the consumer from the microbial fermentation of protein.

Another potentially important mechanism behind the increased energy gain from cooked meat is the decrease in meat pathogens, which lowers the metabolic cost of an immune defense. Such cost can be substantial, as fever alone can increase resting energy expenditure by up to 13% for each degree celsius increase in body temperature.

Carmody and Wrangham (2009) calculate that, without customary cooking, the cost of bacterial infections for a US consumer would be substantial, as one would be expected to fall ill 42 times per year from foodborne bacteria in meat. The annual cost of immune upregulation due to fever would be almost 7 years worth of basal metabolism versus less than 1 day when customary cooking is employed. Thus, incidence of foodborne illness from meat eating is 99.98% lower due to cooking.

The ability of thermal processing to kill pathogens could have played an important role for early hominins, as some scholars propose that scavenging was the main strategy of obtaining meat in our evolutionary past (Smith et al. 2015). Considering that scavenged meat would likely accumulate pathogenic bacteria, it would have been a costly strategy before the adoption of cooking. Smith et al. (2015) examine bacterial loads on meat and bone marrow, demonstrating that open-flame roasting is highly effective at reducing bacteria or entirely eliminating it. Thus, a simple cooking method available to

early humans – roasting over an open flame – would have decreased the risks associated with meat ingestion, facilitating increasing amounts of this high-quality food in the human diet.

Conclusion

Cooking leads to an increased caloric value of foods in several ways: by lowering the body's metabolic cost of digesting through decreased chewing effort; increasing digestibility of foods rich in starches, lipids, and possibly proteins; and reducing the metabolic cost of producing an immune defense against foodborne bacteria. These factors point to cooking as an evolutionarily important behavior, as increases in energy can be expected to have important effects on human evolution (e.g., expansion of the brain due to the rise in the energy value of the diet). This potential significance of cooking in our evolutionary past is challenged by alternative non-thermal processing methods: using tools to pound the foods also reduces their firmness, aiding in digestion. However, work with modern raw foodists, who heavily process their foods without heat, reveals caloric insufficiencies of even such high-quality diets. In addition, animal studies contrasting cooking and nonthermal alternatives show significant net energy increase only with cooking, demonstrating that tool use can not match the effectiveness of heat in increasing energetic intake from eating.

Cross-References

► [Brain Evolution Resulting From Cooking](#)

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Increased Grandchild Survival

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Synonyms

Grandparental investment; Inclusive fitness

Definition

Child survival is one of the most important fitness indicators in evolutionary studies. In our evolutionary past, grandparents may have increased their inclusive fitness by helping to keep their grandchildren alive.

Introduction

Humans have been often defined as a cooperative breeding species, meaning that other people in addition to the biological mother of the child take part in child-rearing (Hrdy 2009). These “allo-parents” are typically closely related to the child and may include the child’s father, older siblings, aunts, uncles, and grandparents. Previous studies indicate that grandparents have often been highly involved in their grandchildren’s lives in both traditional and historical populations and in contemporary societies (Coall and Hertwig 2010). By investing resources in their grandchildren, grandparents can significantly increase a grandchild’s survival (Sear and Coall 2011).

Empirical Evidence

Sear and Mace (2008) reviewed 45 studies that detected associations between kin presence in the same household or village and child survival. In these studies, child survival was indicated among children of different ages, ranging from infants to adolescents. The populations included in the review were mostly natural fertility and natural mortality societies, meaning that modern medical care and welfare services were lacking. These populations included several different types of livelihoods, for instance, historical agricultural societies and hunter-gatherer communities from different countries and continents, providing a comprehensive view of kin effects on child survival.

Based on the review by Sear and Mace (2008), the presence of a maternal grandmother correlated with increased survival rates among grandchildren in 69% of the studies (9/13) and the presence of paternal grandmothers in 53% of the studies (9/17). The effect of grandfathers seems to

be much lower compared to that of grandmothers. The presence of maternal grandfathers was related to increased survival rates among grandchildren in 17% of the cases (2/12) and the presence of paternal grandfathers in 25% of the cases (3/12). Moreover, the presence of paternal grandfathers was related to decreased survival rates in 25% of the cases (3/12).

Even though grandparents (and maternal grandmothers in particular) can often have a positive impact on a grandchild's survival, the effect may vary between ecological and other conditions. Sometimes, grandparental presence can be associated with a decreased survival probability among grandchildren. For instance, a previous study found that the presence of paternal grandmothers was associated with increased mortality rates among grandchildren (Strassman 2011). This could result from resource competition between grandparents and grandchildren, meaning that when the grandparents are old or their health is substantially deteriorated, they may compete with the grandchildren over limited household resources. Even the presence of maternal grandmothers may not always benefit the grandchildren (Sear 2008).

Conclusion

Empirical evidence from traditional and historical populations indicates that grandparental presence in the same household or village has often, but not always, been related to improved grandchild survival rates. These studies have also indicated that the presence of grandmothers tends to benefit the grandchildren more than the presence of grandfathers, with maternal grandmothers often playing the most important role. Therefore, in traditional and historical populations, grandmothers may have increased their own inclusive fitness by helping to keep their grandchildren alive.

Cross-References

- [Importance of Grandparental Investment](#)
- [Mothers and Maternal Grandmothers and Childhood Survival](#)

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Increasing Competitiveness of Women

- [Enhancing Women's Competitiveness](#)

Increasing Longevity

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Synonyms

[Expanding lifespan](#); [Extending the length of life](#); [Rising life expectancy](#)

Definition

Increasing longevity consists in the process by which the individuals' length of life has expanded throughout history.

Introduction

According to Blagosklonny (2010), the progress of civilization has enabled a drastic reduction of

the death rate of young people – who died mainly due to epidemics, famine, and physical violence – and hence the increase of lifespan. A century ago, for example, the odds of reaching the 100-year age group were 100 times lower (Blagosklonny 2010). In this context, currently, studies show that there are several factors that can influence longevity, among them highlighted the issues related to heredity, gender, socioeconomic status, nutrition, social support, medical care, personality, and behavioral characteristics (Robine et al. 1997).

Historical Factors

Kaplan et al. (2000) highlight four characteristics, which distinguish human life histories from other primates and mammals: “a exceptionally long lifespan, an extended period of juvenile dependence, support of reproduction by older post-reproductive individuals, and male support of reproduction through the provisioning of females and their offspring” (p. 156). In addition, *Homo sapiens* has developed, over the humanity’s history, a large brain and, as consequence of its complexity, sophisticated psychological features (Kaplan et al. 2000).

The authors expose peculiarities in the human adaptation, such as the successful existence of humans in virtually all of the world’s major habitats; the capacity of eating a very wide variety of food, both plant and animal; the contributions of individuals of different ages and sex; and the contributions of men and women in the process of producing food (Kaplan et al. 2000). Those characteristics lead to the understanding that human adaptation is broad and flexible (Kaplan et al. 2000).

At the same time, the human species adaptation can be understood as narrow and specialized in the sense that it is based on a complex diet, having the individuals used their great intelligent to extract and hunt those foods. The species’ adaptation is also based in a life history with a long and slow development, having the individuals a great commitment to learning and intelligence (Kaplan et al. 2000).

The authors conclude that the course of human life is based on complex processes and in coevolution of psychology, physiology, and behavior (Kaplan et al. 2000).

Kaplan et al. (2000) suggest that language learning and the mastering of the environment, as major psychological milestones, have a close connection with a lot of factors. Among them, it can be emphasized the timing of brain growth; the growth rates during childhood and adolescence; the developmental changes in survivorship; the adulthood’s behavioral, psychological, and physiological changes; the profiles risk with age; and rates of senescence and aging (Kaplan et al. 2000).

On the other hand, Harari (2015) points out that *Homo sapiens* was an insignificant ape and that he didn’t have relevant changes in his physiology and not even in the size and external shape of his brain. Thereby, the author defines cognitive revolution as the process by which *Homo sapiens*, as a result of the occurrence of discrete changes in the internal structure of his brain, achieve the domination of the other species (Harari 2015). The author also suggest that humans are social animals, defining the ability of cooperating socially as the key for our survival and reproduction (Harari 2015).

Genetic Factors

Research projects related to twins, adoption, and other family studies have been important in understanding the influence of genes on longevity (Christensen and Vaupel 1996). Thereby, an association between certain genetic factors and longevity has already been found (Christensen and Vaupel 1996). As an example, there is the genetic factor apolipoprotein E, which, according to Christensen and Vaupel (1996), is the most potent “longevity gene” that has ever been discovered in humans. However, these authors affirm that recent analyses have shown that the variation of this genetic factor only explains 1% of the variation in lifespan. In this context, in relation to genetic influence more broadly, Iachine et al. (2006) allege that several studies with twins have shown

that genetic aspects cause approximately 20–30% of all variation in lifespan.

Environmental Factors

According to Christensen and Vaupel (1996), the environmental factors are highlighted as determinants of longevity. They affirm that the decrease of the use of cigarettes, changes in the diet, and the practice of physical activities can influence the increasing of life expectancy. In addition, it is emphasized that current studies have found that an excessive consumption of alcohol can increase the risk of mortality (Christensen and Vaupel 1996), which shows another factor involved with longevity. Furthermore, Christensen and Vaupel (1996) consider three other environmental factors that may be influencing mortality and hence longevity. In this sense, these aspects refer to socioeconomic status, education, and occupation.

Resistance to Stress

Minois (2000) defines stress as external and internal events that arise for an individual, to which he must respond adaptively. Thus, it is stated that organisms can present low or high levels of resistance to stress, emphasizing that resistance to certain stress tends to increase resistance to other types of stress (Minois 2000). In this way, according to Minois (2000), if an individual has already been subjugated to a stress, he will be more able to deal with others stresses that appear to him.

In this context, as the contact with stress is related to aging, it is considered that resistance to stress and longevity are closely associated as well (Minois 2000). Therefore, Minois (2000) affirms that a range of studies concluded that high levels of resistance to stress entail high longevity. In addition, it is considered that, as exhibition to stress raises the resistance to other stresses, a moderate exposure to stress can be beneficial for increased longevity (Minois 2000). Thereby, it is proposed that the contact with mild

stresses can have advantageous effects for longevity (Minois 2000).

Positivity

Positive affect, according to Pressman and Cohen (2005), can be defined as sentiments which reflect a level of satisfactory connection with the environment. Feelings like happiness, joy, excitement, enthusiasm, contentment, and pleasurable sentiments in general are directly related with the concept of positive affect (Pressman and Cohen 2005). The suggestion that positive affect can bring improvements to people's health has been made over the years.

In this context, Danner et al. (2001) affirm that literature has indicated increasingly that attitudes and states related to positive and negative emotions are associated with health and longevity. Thereby, the authors associate optimism with longer life, exposing other studies which sustain the idea that an optimistic way of life, which insofar results in the emergence of positive sentiments, may also contribute to the increase of longevity (Danner et al. 2001).

The correlation between happiness and longevity was noticed by Pressman and Cohen (2005) while analyzing studies made in several countries. The authors highlighted the indication that happier people seemed to live longer, while lower levels of happiness, or higher levels of sadness, presented a correlation with an increased risk of mortality (Pressman and Cohen 2005). However, Pressman and Cohen (2005) explained that there is no unequivocal indication that positive effects are beneficial for health, which implies the necessity of more sophisticated studies over those issues.

Religion

George et al. (2000) affirm the existence of plenty of evidence which reveals robust connections between religiousness and health. Analyzing several studies, the authors highlight conclusions that

lead to the understanding that religion is directly related to health mostly in a positive way (George et al. 2000). The influence of religion is associated with the reduction of disease and disability and with the perceptions of health, energy, and vitality (George et al. 2000). In addition, the studies which analyze the relation between religion and mortality indicate that religious people tend to live longer (George et al. 2000). In the same context, according to the authors' analyses, religion seems to imply better recovery from a variety of physical illness, and also it seems to be associated with a greater tolerance of pain and higher quality of life (George et al. 2000).

It is also important to highlight that George et al. (2000) conclude that religion seems to influence positively in the prevention of mental illness such as in the prevention of substance abuse.

On the other hand, the authors admit that there are specific subgroups in the population who were harmed by religious involvement, leading to direct and indirect negative effects for health (George et al. 2000). Although, it is important to emphasize that, according to George et al. (2000), the most recurrent pattern is that religion has no effect or has positive effect on human health.

The reasons why religion positively affect health seem to be related with prohibitions against risky behaviors and with the perspective by which body has both a spiritual and material meaning (George et al. 2000). The fact that religious people believe in a meaningful existence may also have relevant results for mental health (George et al. 2000). The social support among religious people who participate in the same organization seems to be also a determinant for the good effects religion has over health, insofar, in those communities, people tend to protect and support each other (George et al. 2000).

Conclusion

For thousands of years, studies about the duration of life have arrested the interest of people (Christensen and Vaupel 1996). However, knowledge about what factors are involved in determining longevity is still scarce – and the little

that is known has been acquired in the last years (Christensen and Vaupel 1996). In this sense, it is important to emphasize that there is a great amount of aspects in the context of longevity increase still waiting to be investigated.

Cross-References

- [Life Expectancy and Reproduction](#)
- [Life Expectancy In Hunter-Gatherers](#)

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Indicators and Correlates of Status and Dominance

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Synonyms

[Correlates](#); [Dominance](#); [Indicators](#); [Prestige](#);
[Status](#)

Definition

Social status has many definitions; however, it can be considered analogous to “rank” in social

nonhuman animals, whereby the higher in social status a person is, generally the more resources, mating opportunities, and higher fitness benefits they receive. Cues of human status and dominance are discussed below.

Introduction

What does a big bank CEO have in common with a bank teller working at one of its numerous locations? They are both part of the company hierarchy. Their day-to-day experience at work is likely, however, to be very different because they are on opposite ends of the company hierarchy. The CEO has reached the highest possible status, and therefore also holds vast resources, power, and wealth, over and above all others below them in the company. The bank teller, on the other hand, must take orders from all those situated higher in the company’s hierarchy, and can, if there are no safeguards in place, have their salary docked or suspended, be declined a raise, and even be made redundant without much warning.

Status hierarchies are ubiquitous in both non-human and human animal groups where individuals live in relatively close proximity and are in contact often enough for it to be warranted. These hierarchies likely serve a purpose and may be beneficial for individuals within a group to reduce within group conflict. That is, formation of status hierarchies can be beneficial to all individuals in the group as it means that there are less overt and prolonged aggressive interactions between the same individuals. Once a hierarchy is established, most individuals will likely learn their place, although hierarchies can change with members moving up or down the ranks, for example, if an individual dies or is displaced through external factors.

Advantages of High Status

Nonhuman Animals

Being of high social status brings advantages, such as the ability to manipulate resources or even mating opportunities. These benefits have

been well documented in nonhuman animals. For example, studies of red deer have shown that stags of high status displace those of lower rank in order and are able to occupy food areas which have higher nutritional content (Ceacero et al. 2012). Similar results have been observed in a wide range of other animals, such as American bison, crayfish, and willow tits (see Ceacero et al. 2012, for brief review). Thus, being of high status in many animals leads to benefits including the ability to monopolize resources.

Another potential benefit of being high in status is having higher reproductive success or leaving more descendants. While this may in part be linked with the ability to monopolize resources, it is worth discussing as there is a large literature on the subject. In nonhuman primates, for example, the rank a male occupied within the group was positively correlated with reproductive success (Cowlshaw and Dunbar 1991). That is, higher ranked males were more likely to have more mating opportunities and produce more offspring than those which were ranked lower. In a very large study which compiled the research of over 700 published research articles, Ellis (1995) found similar results in a wide range of disparate nonhuman animal groups including rodents, birds, fish, and primates. More recent research has demonstrated many more examples of this link between rank and reproductive success (for example, in Macaques, Schülke et al. 2010). Thus, a major benefit of being a leader in animal societies appears to be higher reproductive success.

Humans

The benefits of high social status or rank are not exclusive to nonhuman animals. High status humans, specifically men, are also likely to increase their reproductive success relative to low status men. Indeed, Hopcroft (2006) presents a comprehensive table of preindustrial cultures in which high status has been positively correlated with higher reproductive success, judged by number of surviving offspring. Other than reproductive success, high status individuals, such as the bank CEO mentioned above, have also been found to have increased economic/resource gains (Cheng et al. 2013). High status individuals gain

not only power but also resources and more mating opportunities, which may then equate to higher reproductive success.

Indicators of Status and Dominance in Nonhuman Animals

Being of high status is important as it can lead individuals to enjoy many of the benefits described above and in nonhuman animals, there is much research linking physical traits with status.

There are many indicators of high and low status in nonhuman animals and these vary based on the species in question. For example, body size and age are indicators of status in some species where larger individuals tend to be the dominant ones (Post 1992). In addition, many animals have secondary sexual characteristics and/or weaponry which can be used as indicators of status or rank, especially in an agonistic setting. Well-known examples include antlers, and caribou and red deer with larger antlers have been shown to be more dominant than those with smaller antlers (Appleby 1982). This research suggests that age, size, and size of ornamentation are all ways in which certain nonhuman animals signal their rank to conspecifics.

Achieving Status in Humans

When looking at humans, in contrast to some of the marked differences between the sexes in some nonhuman animals, it is striking how similar men and women are to each other. That is, one sex does not have prominent weaponry such as antlers or extensively bright coloration which can be used to assert rank/authority. There *are* differences in physical strength, with men generally being stronger (Lassek and Gaulin 2009), and height, with men on average being taller. However, these differences are not as prominent as in many other species, and the examples discussed in the section above. So, how do humans generally reach a position of high status? In many groups, individuals are a part of in everyday life, be it during work, sports teams, or other group-based activities, how do they climb the social ladder?

Recent research suggests that there are two main ways of attaining high status in humans,

dominance and *prestige* (Henrich and Gil-White 2001). Gaining status through dominance usually entails the use of coercion, aggression, or force in order to “make” others follow an individual. Conversely, gaining status through prestige does not require an individual to make others follow them and their orders, but rather intrinsic skills, qualities, and knowledge that they possess motivate others to follow them. The key difference is that while dominant individuals act upon others in order to receive followership, prestigious individuals freely, and somewhat passively, receive followership simply through the characteristics they are perceived to possess.

Examples of the use of two methods of status attainment can be seen in real-world individuals. Billionaire businessman and current US president Donald Trump can be considered a dominant individual. He recently completed building the “Trump International Golf Links” near Aberdeen, Scotland. Even though there was a public attempt to boycott the project, mostly due to the golf course being located on a site of scientific importance, Trump continued with the project. Additionally, Trump continues to fight plans to build a large wind farm close to the golf course claiming that it would spoil players’ views. There is even speculation that Trump has used the law to remove local residents from their homes so that they are not located near his golf course and its adjacent hotels. If these claims are true, then Donald Trump has demonstrated himself to be a forceful, coercive, and dominant individual, achieving his goals despite resistance from others. Even within his presidential campaign/term, Trump has publically berated and been hostile toward candidates, foreign dignitaries, news outlets, people who disagree with him, women, immigrants, and people of different races/ethnicities (see @realDonaldTrump on twitter.com (www.twitter.com) for examples).

In contrast, a real-world example of an individual who might be considered prestigious is the current Dalai Lama. He has championed nonviolence in order to solve conflict, and thus seems unlikely to resort to force in order to get his way. He is also a part of the Elijah Interfaith Institute,

which aspires to open dialogue with many different faiths in order to foster peaceful relations among them with the aim to lead to trust and transparency – in effect the opposite of coerciveness and manipulation. Finally, he has accrued international acclaim and praise, including winning the Nobel peace prize in 1989. It is the Dalai Lama’s many personal characteristics, convictions, and qualities which have led others to hold him very high regard, and he is almost universally acknowledged as an individual who deserves to be listened to and followed.

The stark contrast between Donald Trump and the Dalai Lama is quite evident. While both are high status individuals, holding power and influence over others, the tactics used to achieve this status are very different. While Donald Trump has, in effect, exerted his dominance in order to achieve his goals, regardless of the consequences and who it might affect, the Dalai Lama has earned his status through cooperation, and the many merits and qualities which he shows to those around him.

Recent research has also pointed to social and physical dominance being two different methods of attaining “dominance,” with physical dominance dealing with physical characteristics (such as being able to “win a fistfight”), while social dominance implying more guile (is influential but also tells others what they want; e.g., Puts et al. 2006).

Definitions of Dominance

As the above section implies, there appear to be many ways in which researchers study high status, with some opting to provide definitions while other researchers opt to simply allow participants to use their “gut instinct” to decide what dominance, prestige, power, status, etc., are.

The use or lack of use of a definition can complicate matters, as some researchers divide dominance into physical dominance and social dominance and find differences between the two. For example, studies have found that faces of women which have been manipulated to look more feminine are rated as more

socially dominant, while both women and men's faces manipulated to look more masculine are rated as more physically dominant (Watkins et al. 2012). The definitions used to describe physical and social dominance in these studies were taken from Puts et al. (2006), where participants rated voices for dominance and where physical dominance was described as the ability to win a "fistfight," while social dominance was described as being a respected "leader." This definition of social dominance which also includes words like "influential" was originally used by Mazur et al. (1994) to denote dominance; however, in the context of the dominance and prestige literature mentioned above, where dominant people may not necessarily be respected, this social dominance definition appears to align closer with prestige (Henrich and Gil-White 2001). How exactly social and physical dominance relate to the concepts of prestige and how they relate to, or are potentially subsumed by the concepts of dominance, have yet to be established.

"Status" itself has been used to refer to "an individual [who] is respected, admired, and highly regarded by others" in a recent study (Fragale et al. 2011, pp. 767). This quality was compared with individuals who were powerful, where power described someone who "can control others' outcomes by granting or withholding valued resources" (Fragale et al. 2011, pp. 767). Again the definitions used to describe status and power are similar to those used to describe prestige and dominance, respectively, by Henrich and Gil-White (2001).

It is important to note that the research and studies described below may all have slightly different definitions of dominance and its variants, or prestige, whereby the researchers may either have provided various definitions or allowed participants to use their own internal concepts of human social status to guide their judgments. Moreover, future studies should try to elucidate exactly what individuals are imagining when they are asked about these concepts – for example, what adjectives/characteristics/features would they attribute to a dominant person or a prestigious one?

Overview of Indicators and Correlates to Status in Humans

Many different cues and correlates to social status have been explored in humans within the last 30 years. A few studies pertaining to certain indicators are described below.

Faces

Faces are usually the first thing an individual sees or is drawn to when they enter into an interaction with another person. Faces hold a variety of cues, people use faces to judge people's attractiveness, their trustworthiness, and even their competence (see Todorov et al. 2015 for review), among many other traits.

Dominance has been linked to certain facial characteristics by some researchers, including such as prominent brows, muscular and well-defined jaws, broader faces, and masculinity in men (Mazur et al. 1994). In women, those with more masculine faces are considered as more physically dominant while as those with more feminine faces are considered to be socially dominant (Quist et al. 2011).

Additionally, recent research has shown that facial width-to-height ratio (fWHR) (or the distance between the two zygions with respect to the distance between the lower brow and upper lip) is also related to both self-perceived and other-perceived dominance in men though not to prestige (Mileva et al. 2014). Using self and other report measures, in three studies, the authors found that men with higher fWHR ratios were rated as higher in dominance, and rate themselves as higher in dominance using two different dominance scales. fWHR has also been linked to other behavioral characteristics associated with dominance, such as aggression, where Carré and McCormick (2008) showed, when looking at National Hockey League (NHL) players and varsity hockey players, that those players with higher fWHRs were also more likely to have had longer stints in the penalty box – where players are sent if they have performed an act which is deemed reckless or prohibited in the sport. While some researchers have disagreed that fWHR is linked with aggression, a recent meta-analysis suggests

that the two are positively correlated (Haselhuhn et al. 2015).

Another aspect of dominance which fWHR has been related to is exploitative behavior. Stirrat and Perrett (2010) allowed participants to play a trust game and found that men with higher fWHR were more likely to exploit the trust of those they were playing with than men with lower fWHR. Similarly, Haselhuhn and Wong (2012) found that men with higher fWHR were more deceptive in a negotiation task related to the fictitious purchasing of property, and more willing to cheat in a “dice roll” than men with lower fWHR. As such, at least in men, fWHR appears to be related to dominance characteristics as well as to self- and other-perceived dominance.

The facial features discussed above are static and do not, for the most part, change on a person’s face once they have reached the end of puberty. That is, one cannot easily alter (other than with some types of reconstructive surgery or perhaps through gaining a large amount of weight) one’s facial structure as it delineates the underlying skeletal structure. Facial expressions, on the other hand, are easy to alter and have been shown to interact with dominance attributions. For example, research suggests that men with neutral, angry, and happy expressions are more likely to be perceived as dominant than those expressing fear and sad expressions (Hareli et al. 2009). In women, the pattern is more complex, with some studies suggesting women exhibiting anger expressions are perceived as more dominant (Hareli et al. 2009).

Faces therefore allow individuals to make many attributions about a person, and can also be used to infer their dominance, or perhaps lack of dominance.

Voices

Just as faces are important in signaling dominance during first introductions with a stranger, another important cue individuals can use to gain information about someone’s dominance is that person’s voice. Studies suggest that voices are able to signal dominance, with lower pitched voices being considered as higher in dominance (Puts et al. 2007), especially with respect to physical

dominance versus social dominance. As men tend to have lower pitched voices than women, and men are physically stronger (Lassek and Gaulin 2009), it may not be surprising that dominance is associated with a lower voice pitch. Indeed, masculinized voices (i.e., those with lower fundamental frequencies – equated to pitch) tend to be considered as more attractive by women in general, with the authors suggesting this is due in part to relating to their sexual maturity (Feinberg et al. 2005).

More recent research has again showed that artificially masculinized voices are associated with higher dominance, and are also considered more attractive for short-term relationships rather than long-term relationships by women (Vukovic et al. 2011). This research suggests that voices can be used as valuable cues to someone’s dominance which can in turn impact attractiveness and other judgements.

Height

Another characteristic commonly associated with influential, powerful, and dominant people is height. Indeed, studies asking preschoolers to rate the dominance of men and women of various heights show that height is positively related to other perceptions of dominance (Montepare 1995). That is, tall men and women were considered more dominant than their shorter counterparts.

High dominance would be expected to lead to influence and success, and recent studies have looked at the relationship between height and leadership. In a task where the researchers had participants simply draw a “leader” and a “citizen” using a pen and paper, significantly more participants drew the leaders as taller than the citizens (Murray and Schmitz 2011). In a second study, Murray and Schmitz (2011) also found, through self-report measures, that participants who were taller also thought that they would be more qualified to be candidates for leadership roles than participants who were shorter. In a study examining all previous presidents of the US dating back to 1790, Stulp et al. (2013) showed that presidents were significantly more likely to be taller than other men in their birth

cohort, and that taller presidents were more likely to be reelected, win popular votes, and be considered as better leaders.

Height is therefore an important characteristic, at least for men, in that it can make them appear higher in dominance and consequently higher in leadership characteristics than men who are shorter. In addition, as tall men also rate *themselves* as more dominant and as having greater leadership qualities, this may mean that they are internalizing other's opinions of them and behaving accordingly. Another possibility is that differences in height, perhaps related to differences in circulating testosterone levels, lead to subsequent behavior change (e.g., tall individuals are more likely to exhibit dominant behaviors), which in turn affect other's perceptions. Which and to what degree each of these affects the relationship between dominance and height is not yet known.

Nonverbal Behavior, Personality, and Hormones

Several recent studies have looked at dominance with respect to nonverbal behavior and personality. Cheng et al. (2010) looked at self- and other-rated perceptions of prestige and dominance in a set of undergraduate students as well as male university athletes. They found that high dominance was positively correlated to personality characteristics including extraversion, aggression, and narcissism, and was negatively correlated with agreeableness. In contrast, prestige was positively correlated with extraversion, agreeableness, conscientiousness, self-esteem, and openness, while being negatively correlated with aggression. These results were most evident in the self-ratings of undergraduate students, and provide an interesting insight into the differences between dominance and prestige as separate strategies for gaining high status. Other nonverbal cues related to "aggressive" dominance include a decreased tendency to laugh along with others in a group setting, as well as increased time spent looking around the room as opposed to at others within the group – what the authors consider an attitude of disinterest (Kalma et al. 1993). Additionally, dominant individuals are more likely to have persistent, direct eye gaze, while those who

are lower in dominance are more likely to look away and give only furtive glances at the dominant individual (Mazur et al. 1980).

Color

Bright coloration has been found to be a dominance cue in several animal species including, for example, in face of mandrills (Setchell and Wickings 2006). More recently red has been associated with dominance in humans as well. In a unique study, Hill and Barton (2005) found, when analyzing four different contact sports (i.e., Judo, boxing, etc.) during the 2004 Olympic games, that those contestants who were assigned the color red were more likely to win, and that if there was less ability asymmetry between that individual and their opponent (i.e., where individuals had similar competitive abilities), those wearing red were even more likely to win. Indeed, in a simple study using only shapes of different colors, Little and Hill (2007) found that participants chose red-colored circles or triangles more often than blue when asked which would be more aggressive. Additionally, they found that women were more likely to rate red stimuli as higher in dominance, while men were more likely to rate red stimuli as the "winner" of a contest.

Recent research has shown that men whose pictures have been superimposed onto a red background are more likely to be rated as higher in attractiveness than those posing on blue or achromatic backgrounds, and that this effect is mediated by perceptions of status (Elliot et al. 2010). That is, red is associated with high status, and that leads to higher attractiveness ratings for men on red backgrounds. As such it appears that color can affect attributions of status, dominance, and competitive ability, not only in nonhuman animals but also in humans. Specifically, the color red seems to be linked to dominance, though there may be other colors which have yet to be studied which also appear dominant.

Wealth and Displays of Wealth

Wealth has long been associated with social status and cues to wealth may then be important in

inferring status. Research has focused on the association between wealth and attractiveness. At least in men there are reproductive benefits to being wealthy, with wealthier men having more offspring than less wealthy men both in Western industrialized and more traditional societies (Pérusse 1993). Of course, cues to wealth will be culturally dependent, with specific cues perhaps only being valued in particular cultures. For example, the Mukogodo of Kenya value ownership of livestock but this may not indicate high status to city living New Yorkers, who may look to other cues such as the expense of clothing and items such as watches, jewelry, and cars. Research in Western countries has revealed that manipulations of job titles or clothing linked to wealth is related to attractiveness, at least for men, with professional high-earning jobs making men more attractive to women than lower earning jobs (Townsend and Levy 1990).

Relative Dominance

Research is now emerging on the importance of relative dominance, and while not an indicator of dominance, it is nevertheless worth mentioning. To illustrate, imagine that an individual were approached, somewhat menacingly, by a formidable player in the NFL (or Rugby Union for British readers). In most instances, that individual might respond by being frightened, perhaps for their life, and adopting the decision to run away from the confrontation. However, if that individual is similarly tall, muscular, and menacing, then they might “hold their ground” and opt to continue with the confrontation. This scenario illustrates how important it is to use oneself as a relative marker with which to make comparisons regarding others in terms of dominance.

Recent research in evolutionary psychology has shown that these relativities extend beyond dominance. In one study, women who were not using oral contraceptives and rated themselves as highly physically attractive also preferred men with higher facial masculinity and symmetry, two traits commonly associated with higher genetic quality, than women who thought

themselves less attractive (Little et al. 2001). Thus, relative ratings of attractiveness appear to influence women’s judgments of attractiveness in partners; those who think more highly of themselves, in this case with regard to attractiveness, also believe that they are able to attract and attain a higher quality male, in this case one who is more masculine.

There is relatively little literature regarding relative dominance; however, research by Watkins et al. (2010b) has found that men who rate themselves as high in dominance using a standardized dominance questionnaire are also less likely to attribute dominance to masculinized versions of a face (i.e., they were less sensitive to masculinity when deciding which of two facial images – one manipulated to look low in masculinity and one manipulated to look high in masculinity – was the more masculine one). Taller men have also been shown to be less sensitive to cues of other men’s dominance (Watkins et al. 2010a), and above it was discussed that taller men are also rated by others as higher in dominance. In women, Watkins et al. (2012) showed that those women who rated themselves as higher in dominance and those who were taller tended to be less sensitive to masculinity/femininity manipulations of female faces. These studies suggest that self-perceptions of one’s own dominance can affect attributions of others dominance as well, with those individuals who perceive themselves as being higher in dominance also being less sensitive to cues of dominance from other individuals. Thus, it seems that others’ dominance cues are particularly important to individuals who perceive themselves as being low in dominance, perhaps because they have the most to lose when interacting with a dominant individual (specifically in confrontational scenarios).

These studies indicate that self-perceived and relative dominance are important to address in order to fully explore and understand the nuances of human dominance and dominance perceptions.

Summary

Social status and particularly dominance has been the topic of a great deal of research in the last

30 years. Those who possess high status can earn great rewards (i.e., reproductive success) and as such it is important to know more about the indicators and cues of social status, some of which are briefly touched upon above. However, definitions within the literature differ and it is important to keep this in mind when performing research on social status. In addition, the importance of relative dominance and relative social status is only now becoming elucidated and will no doubt become an important topic of research in the coming years, if for no other reason than to control for individual differences found in research results. In the following sections, some of the above sections and others will be discussed in greater detail.

Cross-References

- [Dominance and Testosterone](#)
- [Dominance Hierarchies](#)
- [Dominance in Humans](#)
- [Effect of Status on Social Reasoning \(Cummins 1998\)](#)
- [Facial Width to Height Ratio and Dominance](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Height and Dominance](#)
- [Nonverbal Indicators of Dominance](#)
- [Serotonin and Dominance](#)
- [Size and Dominance](#)
- [Status and Dominance Hierarchies](#)
- [Vocal Indicators of Dominance](#)

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Indigenous Religion

► Ancestor Worship

Indirect Aggression

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Synonyms

[Relational aggression](#); [Social aggression](#)

Definition

Indirect aggression is a behavior intended to harm others, particularly others' social position and self-esteem, through circuitous means. It is a kind of social manipulation, in which the aggressor manipulates other individuals or the social structure to psychologically harm the victim, without the direct confrontation. The related constructs of social and relational aggression also represent the same phenomena in which social community or peer group serves a mediating role between the aggressor and victim. Indirect aggression is exemplified by behaviors such as gossiping behind back, spreading rumors, social exclusion, slanderous remarks, etc.

Introduction

Undoubtedly, aggressive behavior is problematic and a potential formative factor in adjustment problems for both aggressor and victim. Initial research has quite commonly focused on male-oriented models of physical aggression. However, it is clear that the aggressor may sabotage their peers in more subtle ways without being disclosed as an aggressor. By using indirect aggression, the aggressor usually remains unidentified and is at low risk of retaliation and thus avoids counterattack. Although researchers have started considering less direct forms of aggression in the latter half of the twentieth century, they have taken serious interest in indirect aggression since the last decade of the twentieth

century (e.g., Crick and Grotpeter 1995). The validity and existence of indirect aggression is also supported by factor analytical studies representing two factors of aggression: first, overt, direct, or physical aggression and, second, covert, indirect, or social aggression (e.g., Crick and Grotpeter 1995).

Regarding socio-environmental correlates, the literature indicates that indirect aggression has been linked with harsh discipline and a lack of positive and supportive parenting during early childhood years (e.g., Park et al. 2005). Moreover, the aggressors using indirect means of aggression show certain cognitive biases such as attributing hostile intentions and a lack of empathy (e.g., Crick et al. 2002). Interestingly, these aggressors as opposed to those who use physical aggression often show superior language skills. They are better at predicting other's thoughts and actions as well as at persuading and manipulating others by using their advanced cognitive and language skills (e.g., Bonica et al. 2003).

With regard to consequences, the indirectly offending behaviors may elicit the same intensity of pain, psychological harm, or distress at least in the victim as physical aggression may elicit. Evidence shows that indirect and social aggression leaves a range of potentially negative and long-lasting effects on the victim (e.g., Owens et al. 2000). Specifically, the literature describes that indirect aggression is often associated with psychological problems coming under the rubric of internalizing problems. A meta-analysis report shows that indirect aggression is more strongly associated with internalizing problems, but physical aggression is more strongly associated with externalizing problems. Interestingly, these differential associations do not differ across gender (e.g., Card et al. 2008). However, on the part of the aggressor, the use of relational aggression is generally not associated with social adjustment problems. Maybe because of social manipulation, these children become successful in forming very close but maybe short-lived friendships. Also, though some of their peers may not like them, they often hold some dominant position in the group (Johnson and Foster 2005).

Developmental Perspective of Indirect Aggression

The literature describes the validity and psychological consequences of indirect aggression; however, most of the supporting data comes from cross-sectional research with little research focusing on the developmental associations of indirect aggression with environmental correlates and psychological difficulties. From few available longitudinal studies based on children samples, it has been found that expression of physical aggression reduces, but social aggression increases from early childhood onward (Côté et al. 2006). Also, social aggression increases over time in children who are physically aggressive, whereas, the reverse has not been supported. Accordingly, Bjoerkqvist et al. (1992) have presented a developmental model of aggression in children. The model describes that during early childhood years, children express their aggression primarily through physical means because they have not yet developed other expressive tools such as social, verbal, and cognitive skills. As the children develop verbal and communicative skills, they start using verbal aggression, and at around 4–5 years of age, they start using social aggression. In the subsequent stage, relational aggression becomes the primary technique of aggression because it has less risk of being disclosed and ultimately less risk of retaliation (Bjoerkqvist et al. 1992). Genetic studies also support this developmental model by describing that both forms of aggression have common roots and share the same genetic factors (e.g., Brendgen et al. 2005) but show different developmental trends, which may be due to other related factors of cognitive and language skills.

Gender Differences in Indirect Aggression

A diversity of studies in the psychology of aggression has approached the question of gender differences. Two major gender differences in

aggression have been observed and reported in the literatures: (i) higher levels of physical aggression in boys and (ii) higher levels of relational aggression in girls. With regard to indirect aggression, it has been reported that these aggressive acts are not commonly reported in boys. Other studies have reported that frequent use of indirect aggressive techniques is found in girls (Crick et al. 1997). Contrarily, a few studies report negligible gender differences in relational aggression. Accordingly, a meta-analysis review based on 148 studies have reported that boys are consistently reported to be more physically aggressive than girls, but gender differences with regard to relational aggression are minimal and trivial though somewhat significant. These patterns of relational aggression are similar across different age and ethnic groups (Card et al. 2008).

Therefore, it appears that during childhood, children may use both forms of aggression but when they grow, they are inclined to use indirect and circuitous means of aggression to attack their victims with minimal gender differences somewhat favoring girls.

Conclusion

In short, validity studies have confirmed two forms of aggression, that are, direct and indirect aggression. Regarding correlates, indirect aggression is related to harsh parenting and cognitive biases on one hand but advanced cognitive and verbal skills on the other hand. Also, it is generally unrelated to social adjustment problems but related to psychological problems of depression, anxiety, and other internalizing problems. The developmental perspective explains that during preschool years, children use physical forms of aggression, but as their language and cognitive skills develop, they start using indirect and social aggression. Finally, it has been discussed that gender differences are clear regarding physical aggression being more common in boys but minimal regarding indirect aggression being slightly more frequent in girls.

Cross-References

- ▶ [Aggression](#)
- ▶ [Anne Campbell](#)
- ▶ [Costs of Aggression](#)
- ▶ [Derogation of Attractiveness](#)
- ▶ [Gossip, Rumors, and Social Exclusion](#)
- ▶ [Meta-analysis of Sex Differences in Aggression](#)
- ▶ [Relational Aggression](#)
- ▶ [Sex Differences, Initiating Gossip](#)
- ▶ [Social Aggression](#)
- ▶ [Verbal Derogation Among Women](#)
- ▶ [Women's Use of Direct Versus Disguised Social Aggression](#)

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Indirect Benefits of Altruism

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Synonyms

[Cooperation](#); [Indirect reciprocity](#); [Reputation](#)

Definition

The different benefits gained by altruists that are received from individuals other than the original recipients of the act.

Introduction

Traditionally, two theories have mainly been used to explain how altruistic behaviors between organisms can be adaptive, and these are kin selection theory where individuals aid those with which they share a number of genes (Hamilton 1964) and reciprocal altruism where individuals aid others who can and will return the favor in the future (Trivers 1971). These have been mostly adequate in explaining a vast amount of altruism, particularly in nonhuman animals. However, when it comes to humans, there exist a number of examples of altruistic behaviors that neither genetic relatedness or reciprocity can explain. These include giving to various charities (e.g., overseas causes, animal sanctuaries), donating blood or bone marrow, and risking personal

safety to save others (e.g., rescuing a puppy from a burning building). As such examples are not unusual, this contribution will explore how such altruistic acts can still be adaptive in terms of increased survival and/or reproductive success, by showing how their costs are balanced by other benefits that the altruist receives.

Multi-Level Selection

A previous attempt to explain altruism was that it was somehow beneficial for the group, a theory that was all but abandoned in the latter half of the twentieth century. However, a more recent theory of how altruism could have evolved to indirectly benefit groups has been put forward, named multi-selection (e.g., Wilson and Sober 1994; Wilson 2015). According to multi-level selection, natural selection can act on not only an individual but also on a group level. More specifically, even though altruistic members within a group can be outcompeted by selfish members, if the overall fitness of the group is increased by having altruistic group members, then this will be selected for. This can occur in particular circumstances, and the concept of what constitutes a group can vary between levels of organization.

Indirect Reciprocity

This builds on the original suggestion of Trivers (1971) that reciprocity is the benefit an altruist receives. However, whereas reciprocal altruism concentrates on the recipient of the act returning the favor, indirect reciprocity (Alexander 1987; Nowak and Sigmund 2005) states that another individual or third party will return the act to the altruist. This process can work when altruistic acts are reliably and widely broadcast to others in a group, so is highly possible in a social species such as humans who live in groups. As such, a number of contemporary theories have been put forward that show how indirect reciprocity can work and also what specific benefits it provides to the altruist, which are discussed below.

Image Scoring

Image scoring (Nowak and Sigmund 1998) attempts to explain the mechanism by which indirect reciprocity can evolve. Using a theoretical model, they suggest that every individual in a group has an “image score” that relates to their previous altruistic interactions with other members of a group. This is based on group members interacting repeatedly with different individuals in the group in pairs for one-off interactions (i.e., without interacting with that individual again) where one member of the dyad can choose to help the other individual or not. If they choose to help, they have a score of one added to the image score, but if they choose not to help they have a score of one subtracted from their image score.

Therefore, being altruistic in these interactions can increase an individual’s image score which can be beneficial in future interactions. This is because, according to Nowak and Sigmund, individuals in the new dyads will base decision on whether or not to help their new partner on their own “threshold” for image scores. In other words, each individual will have a personal numerical value of image score that a partner must have or exceed for them to decide to help. Any partner in an interaction who has an image score below this threshold will therefore not be helped. So, as receiving help from others can be beneficial, a higher image score is adaptive as it means an individual is more likely to pass a new partner’s threshold and thus provide help. Therefore, this theoretical model provided by Nowak and Sigmund (1998) can show how indirect reciprocity can evolve in groups such as humans.

Competitive Altruism

Competitive altruism (Roberts 1998) similarly uses a theoretical model of how indirect reciprocity can evolve. He suggests that cooperation among group members is a two-stage process, with an “assessment” stage followed by a “partnered” stage. The partnered stage involves

individuals in a group forming long-lasting partnerships where they engage in repeated cooperative interactions with each other. Therefore, as Roberts (1998) suggests, it is important to ensure that a cooperative partner is gained in this second stage.

Furthermore, Roberts suggests that there is an active choice of partners for this second stage (i.e., individuals are able to choose who they have as their partners). As a result of this, individuals will compete with one another to increase their displays of altruism in the assessment stage so that they are a desirable partner. According to Roberts, this then leads to assortative matching whereby the most cooperative individuals will pair together, followed by the next most cooperative, and so on. If altruism in the assessment stage is an honest signal of altruism, then the most cooperative pairs will benefit the most in the partnered stage through their future interactions.

Although the original theory is based on hypothetical models, additional empirical research has shown that humans do indeed follow the principles of competitive altruism when available. In a study where participants first interacted with one another in a cooperative group game (i.e., an assessment stage), those that had behaved most cooperatively in the game were more desired as partners in a further stage where participants cooperated in pairs, and actually benefited more overall (Sylwester and Roberts 2010).

Altruistic Punishment

The idea of altruistic punishment (Fehr and Gächter 2002) is that individuals within a group will cooperate with other group members, as non-cooperation is punished by other group members. This punishment would be severe to act as a deterrent, but will also be costly to perform (i.e., certain group members will incur the costs of punishing non-cooperators even if they themselves do not benefit). Fehr and Gächter show this empirically in a study using the public goods game, where participants can contribute to a public good so that all group members can benefit. However, as often happens in continuous rounds

of this game, individuals stop contributing to the public fund but still get the benefit from those that do contribute. Fehr and Gächter (2002), however, introduced between rounds the opportunity for group members to punish those that had not contributed and found that this was a deterrent that led to those punished individuals to return to contributing, thus ensuring in future rounds that cooperation to the public fund was maintained.

This was found even though it was costly to punish others (although the cost of punishing was less than the cost of being punished), meaning that punishers were behaving altruistic. So what is the motivation to punish, when it is costly and you do not directly interact again with the individual you punished? Fehr and Gächter state a proximate explanation for this, in that we feel strong negative emotions of anger when exposed to non-cooperation (i.e., cheating). Furthermore, the potential costs of punishing may be quite low if minimal punishment is needed to ensure individuals continue cooperating within a group (i.e., potential non-cooperators are aware of the costs they could incur). Therefore, these findings suggest that potential punishment from others may have been important for indirect reciprocity within a group to be adaptive.

Altruism as a Costly Signal

The reason why altruistic acts can provide indirect benefits to the altruist via an enhanced reputation is due to such acts being costly (Gintis et al. 2001). As a result, these costly acts can signal to others that the actor may be an able coalition partner, potential competitor, or mate. This works on the premise that costly signals of altruism are honest, meaning that they are directly related to the underlying quality of the individual and that they are a handicap (Zahavi 1975). Furthermore, they must also be effectively broadcast to others, beneficial to the receiver and the actor, and a reliable indicator (Eric Alden Smith and Bliege Bird 2000).

An example of how altruism as a costly signal can provide indirect benefits can be seen in the practice of turtle hunting among the Meriam in Australia (Bird et al. 2001). Hunting of turtles is

difficult and risky, so can act as a reliable signal of a hunter's underlying qualities. Therefore when successful, turtle hunters share the catches with all members of their group in large public feasts, instead of keeping it to themselves. This seemingly altruistic act therefore acts as an effective costly signal, as it is a reliable indicator of their ability, a handicap (as the hunter is incurring the cost of giving away their catch), effectively broadcast to other group members and beneficial to the altruist (allows them to display their quality) as well as the receivers (who gain reliable information about the hunter and free turtle meat). As a result, these hunters reap the indirect benefits of increased social recognition and reproductive success (Smith et al. 2003).

Altruism and Mate Choice

Finally, a number of studies have recently explored the possibility that being altruistic provides indirect benefits in mate choice settings. This follows from the view that altruism can be a costly signal, as it can be then used to attract mates by reliably displaying desirable traits to potential mates (as happens with turtle hunters among the Meriam). As a result, it has been shown that individuals will behave altruistically in the presence of potential mates (Bhogal et al. 2016; Farrelly et al. 2007; Iredale et al. 2008; Tognetti et al. 2012, 2016), and also that being altruistic makes individuals more desirable to potential mates (Barclay 2010; Farrelly 2011, 2013, 2016; Moore et al. 2013; Oda et al. 2013; Phillips et al. 2008). Furthermore, there is real world evidence of the indirect benefits in mate choice that being altruistic can bring, as single individuals who are altruistic are more likely to be in a long-term relationship 1 year later than those that are not (Stavrova and Ehlebracht 2015).

Conclusion

As new research into the indirect benefits of altruism built on traditional explanations of how

altruism can be adaptive, we now have a much richer and detailed understanding of all examples of altruistic behaviors and acts that occur in the real world. Although there are different perspectives on how these indirect benefits manifest themselves, what is clear is that the role of enhanced reputation of the altruist is what underlies them. As such, it provides a useful lens through which to view human altruistic acts such as charity, heroism, and generosity amongst others. When understanding that the ultimate explanation for such acts is increased reputation (which in turn can lead to increased survival and/or reproductive success), their origins and motivation become clear. Although this may be a cynical way to view human altruistic acts, it should not ignore the fact that by being "altruistic" is at the heart of our nature as a highly social species.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Cooperation](#)
- ▶ [Costly Signalling](#)
- ▶ [Handicap Principle](#)
- ▶ [Indirect Reciprocity](#)
- ▶ [Mate Choice](#)
- ▶ [Reputation and Altruism](#)

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Indirect Benefits of Helping

- ▶ [Helping and Reproductive Value of the Recipient](#)

Indirect Bullying

- ▶ [Girls Psychological Bullying](#)
- ▶ [Same-Sex School Bullying](#)

Indirect Care

- ▶ [Male-Male Competition or Male Provisioning?](#)

Indirect Reciprocity

- ▶ [Indirect Benefits of Altruism](#)
- ▶ [Strong Reciprocity](#)

Indirect Sexual Coercion

- ▶ [Types of Sexual Coercion](#)

Individual

► [Factors That Influence Bullying](#)

Individual Aspects Related to Criminal Behavior

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Individual Characteristics

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Individual Differences

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Synonyms

[Biosocial](#); [Individual characteristics](#); [Individual traits](#); [Phenotypic variance](#)

Definition

Individual differences refer to the many ways in which people differ in terms of traits or characteristics. In the vernacular of behavioral and molecular genetics, individual differences are known as phenotypic variance.

Introduction

The majority of theoretical and empirical literature in evolutionary psychology tends to focus on the numerous ways in which humans are similar. For example, researchers have illuminated how aspects of the human condition such as sexual

attraction, mating strategies, disgust, fear, and even political strategy transcend cultural boundaries. These widespread similarities are a product of our species' shared evolutionary history and so it is somewhat unsurprising, though certainly fascinating, that members of species share so many similar psychological characteristics. Nonetheless, humans across the globe are certainly not identical; indeed, our species is rich in diversity of behavior and psychology. Phenotypic variance (differences in characteristics or traits) is also not surprising as it is a necessary component of evolutionary change. Thus, in order to understand the etiology or underlying causes of human behavior, researchers must recognize both our evolutionary history and the various ways in which individual differences (i.e., phenotypic variance) can affect behavior and psychology. This entry will provide an overview of some of the ways in which researchers in areas such as behavioral and molecular genetics have demonstrated the underlying causes and influential effects of phenotypic differences.

Behavioral Genetics

Behavioral genetics is a scientific field of study that is primarily concerned with understanding the differential influence of genetic and nongenetic factors on phenotypic difference (i.e., individual differences on any observable or measureable trait). In order to determine the estimated genetic and nongenetic influence on phenotypic variance, behavioral geneticists employ a variety of research designs that incorporate at least two genetically related individuals from a given family unit with known genetic relatedness. People in a family unit vary in terms of genetic relatedness based on the amount of genetic material they share. For example, a parent and their biological offspring share 50% of their genetic material, so too do full siblings and dizygotic (fraternal) twins. Monozygotic (identical) twins, however, share 100% of their genetic material. Using information on the degree of genetic relatedness shared between two people from a family unit (e.g., full siblings, dizygotic twins, monozygotic twins) and

information on a phenotype of interest (e.g., height, IQ, aggression) behavioral genetic methodologies can estimate the influence of genetic and nongenetic factors on variance in a phenotype.

Behavioral geneticists interested in examining the causes of phenotypic variance produce estimates of three latent components that represent the sources of genetic and nongenetic factors on variance in the phenotype of interest. The three latent components are *heritability* (symbolized as h^2), the *shared environment* (symbolized as c^2), and the *nonshared environment* (symbolized as e^2). The heritability component represents the estimated amount of variance in a phenotype that is due to additive genetic variance. The shared environmental component refers to the estimated amount of phenotypic variance that is accounted for by experiences and nongenetic factors which are shared between two genetically related individuals and that serve to make them similar to one another on the phenotype of interest. The final component, the nonshared environment, represents an estimate of the amount of phenotypic variance that is accounted for by experiences or nongenetic factors that are unique to two genetically related individuals and that serve to make them less similar (i.e., different) from one another on the examined phenotype. The nonshared environmental component also captures any random sampling or measurement error associated with a study. In total, these components account for all (i.e., 100%) of the variance in a phenotype within the examined sample (Plomin et al. 2013).

Researchers examining the genetic and nongenetic influence on phenotypic variance have applied behavioral genetic methods to a wide variety of phenotypes. Virtually every phenotype that has been subjected to behavioral genetic analysis appears to be influenced by both genetic and nongenetic factors. Importantly, however, these observations have not been derived from a single type of methodology. Indeed, behavioral geneticists rely in a wide variety of methods such the classical twin design, adoption studies, monozygotic twins reared apart studies, and twin-discordant studies. These methods are outlined in brief below.

Classical Twin Design

Known as the workhorse of behavioral genetic methodologies, the classical twin design takes advantage of a natural experiment of nature: twinning. During a standard conception event, one egg is fertilized by one sperm and a single embryo is produced. During twinning, however, the standard conception event is altered. For example, dizygotic (DZ) twins are the result of two separate eggs that are fertilized by two separate sperm. These embryos are no more similar than full siblings are, but they share the same gestational environment at the same time (i.e., during one pregnancy whereas full siblings are the result of different pregnancies). Monozygotic (MZ) twins, however, result when one fertilized egg separates into two embryos. Thus, MZ twins are genetic copies of one another – which is why MZ twins are always the same sex (whereas DZ twins can either be a same- or different-sex pair). The classical twin study is so popular in behavioral genetic research because comparisons between MZ and DZ twins represent an approximation to a controlled experiment in order to estimate the influence of genetic and nongenetic factors on phenotypic variance. However, the manipulation of the genetic relatedness is not completed by an experimenter but by nature.

The underlying logic of the classical twin study is straightforward. Given that twins within a twin set are born at the same time, reared by the same caregivers (typically), attend the same schools, and share many other experiences they are said to share the same developmental environments. Thus, it is assumed that the developmental environments shared between a pair of MZ twins are just as similar as one shared by a pair of DZ twins. Known as the equal environments assumption (EEA), this concept forms a foundation of the classical twin study. While the EEA has been criticized in the past, the empirical *quantitative* literature indicates that it is generally a sound and fair assumption to make (even when violated the estimates of genetic and nongenetic influences are accurate and largely unbiased; see Barnes et al. 2014 and Wright et al. 2015). Given that an equal environment can only result in twins being more similar, any differences

between the sets of MZ and DZ twins must be due to factors that are not shared between the twin sets. Thus, if MZ twins are more phenotypically similar than DZ twins (on the same phenotype), it can be assumed that the increased concordance among the MZ twins is due to the greater similarity in genetic relatedness relative to the DZ twins (MZ twins share 100% of their DNA while DZ twins share 50%). This is the essence of the logic underlying the classical twin study.

Twin studies employ complex quantitative methodologies to compute estimates of genetic and nongenetic influences on phenotypic variance and have refined their methods over the past 30–40 years. Over that time researchers have illustrated that virtually every observable phenotype is impacted by genetic factors. Indeed a recent meta-analysis of 2748 published twin studies covering over 17,000 traits from over 14 million twin pairs indicated that approximately 49% of the variance in all traits was due to genetic factors (Polderman et al. 2015). What this means for the study of individual differences within an evolutionary framework is that any empirical examination needs to be cognizant of the potential influence of genetic factors on phenotypic variance. Note, however, that the classical twin design indicates that not all phenotypic variance is due to genetic factors; nongenetic or environmental factors also clearly play a role in how people differ on a variety of characteristics. This aspect of behavioral genetic methodologies is often glossed over by its critics. While the classical twin design offers a powerful tool in which to elucidate the genetic and nongenetic factors responsible for phenotypic variance, other methods are uniquely suited for examining the influence of nongenetic/environmental factors. The following three subsections outline such methods.

Adoption Studies

Researchers have long recognized the value of adoption studies in determining the influence of genetic and nongenetic factors on individual differences. The rationale of the adoption study method relies on a comparison method. In order to conduct an adoption study, measurements of the phenotype of interest must be available from

the adoptee (child), the adoptive parent(s), and the biological parent(s). If these measures are all available then the researcher can compare the phenotypic similarity between the adoptee and the adoptive and biological parent(s). If the adoptee is more phenotypically similar to the adoptive parent(s) than the biological parent(s) then the researcher can conclude that nongenetic (environmental) factors have more influence than genetic factors. Conversely, if the adoptee is more phenotypically similar to the biological parent(s) than the adoptive parent(s) then the researcher can conclude that genetic factors are more influential than nongenetic factors. The comparison relies on the assumption that the adoptee is not genetically related to the adoptive parent(s) and does not share any substantial environmental factors with the biological parent(s). Sarnoff Mednick and colleagues' (1984) well-known adoption study on criminal convictions provides an illustration of the adoption-based examination of individual differences. Mednick et al. (1984) observed that those adoptees who had *both* a biological parent and an adoptive parent with a criminal record were most likely to also have a criminal conviction. Additionally, the researchers found that adoptees who had a biological risk of crime (i.e., a biological parent with a criminal record) but not an environmental risk (i.e., an adoptive parent with a criminal record) were much more likely to have a criminal conviction than those adoptees with the opposite situation (i.e., an adoptive parent with a criminal record and no biological parent with a criminal record). Given the findings, Mednick et al. (1984) concluded that criminal behavior is influenced more by genetic than nongenetic factors. Nonetheless, the findings also indicate an environmental effect (recall that those adoptees with both an adoptive and biological parent with a criminal record were at the highest risk of having a criminal conviction). Adoption studies are used for numerous other phenotypes and are especially suited to examine the impact of environmental factors on phenotypic variance. However, given that offspring of biological parents only share 50% of their genetic material, there still is the possibility of some unmeasured genetic factors that could

influence the observed associations. The next two subsections deal directly with this issue.

MZ Twins Reared Apart (MZA)

Much like the typical adoption study, MZA research studies rely on a comparison method between the adoptee, biological, and adoptive parents. Additionally, MZA studies allow for comparison between the two monozygotic twins who were adopted apart. Thus, MZA studies allow for multiple ways in which to assess the influence of genetic and nongenetic factors on phenotypic variance. Although multiple comparisons can be made in MZA research, we will focus on the within-twin pair comparisons.

Researchers such as Nancy Segal (e.g., Segal 2000) have used the MZA method to illustrate the often uncanny similarities between genetically identical people who were raised in different environmental conditions. Working with other researchers at the University of Minnesota, Segal employed data from the Minnesota Study of Identical Twins Reared Apart. Given the rarity of adopted apart MZ twins the pool of respondents available to the researchers was relatively small. Nonetheless, the study obtained exceptionally in-depth information on over 100 pairs of MZ twins who were adopted apart. For virtually every phenotype examined by the researchers it was observed that the MZ twins resembled each other more than they resembled their adoptive parents. Furthermore, in what is truly an incredible finding, the MZA twins were observed to be *as similar* on a variety of phenotypes as MZ twins who were reared together. Thus, the effect of being raised apart for MZA twins was minimal in terms of phenotypic variance. The MZA method is an exceptionally strong method for illustrating the effect of genetic factors on individual differences but it is not the only way in which MZ twins have helped inform behavioral genetic research. Indeed, MZ twins have been vital to illustrating what *nongenetic* factors have an influence on phenotypic outcomes beyond the influence of genetic factors. The next subsection describes the MZ twin discordance method and how it is used to isolate nongenetic (environmental) effects on individual differences.

MZ Twin Discordance Methods

Although behavioral genetic research is often perceived as seeking to only identify genetic influences on phenotypic variance, the methods used in behavioral genetic studies are perfectly suited to assess nongenetic (environmental) influences as well. Indeed, given that virtually all phenotypes are influenced by genetic factors those methods which do not account for the influence of genetics are likely confounded (i.e., they are unable to rule out the possibility that genetic factors are influencing the outcome). Thus, methods which examine the influence of environmental factors that are also genetically sensitive are ideal for isolating nongenetic effects. Perhaps the most powerful method for doing so is the MZ twin discordance method.

Recall that MZ twins share 100% of their DNA. Additionally, by definition MZ twins also share 100% of their shared environment. Thus, the only way in which MZ twins will exhibit phenotypic variance will be due to unique, nongenetic factors. These factors are referred to as nonshared environmental factors. Such influences can be isolated using the MZ twin discordance method. The process is relatively simple: a researcher creates difference scores of a particular phenotypic measure by subtracting one MZ twin's score from their co-twin's score on the same measure. This process is done for all variables of interest. The difference score is a measure of the nonshared environmental component of the variable of interest since it measures the *discordance* within the MZ twin pair. Using quantitative methods, a researcher can then examine the associations between multiple difference scores to assess whether a particular component of the nonshared environment is influential in terms of why MZ twins differ on an outcome measure of interest. Doing so controls for the effects of shared genetic and shared nongenetic factors on the phenotype and isolates a particular environmental effect. Thus, the MZ twin discordance method is a powerful and robust method to identify *environmental* influences on individual differences. To illustrate, Nedelec and colleagues (2016) employed the MZ twin discordance method to examine the effect of a variety of criminologically relevant

environmental variables on long term antisocial behavior and substance use. The researchers observed that most of the associations were not statistically significant (indicating that long term antisocial behavior and substance use are primarily the result of genetic factors, or unobserved nonshared environmental factors). However, they did note that twins who had more exposure to delinquent peers relative to their co-twins engaged in higher rates of antisocial behavior and substance use as adolescents than their co-twins. The effect, however, did not persist into adulthood. Nonetheless, this genetically sensitive method provided strong support for an environmentally based theory of adolescent delinquent behavior. These types of studies once again highlight the need to account for genetic influence when examining individual differences on phenotypes of interest to social scientists, including evolutionary psychologists.

As a further example, life history theory (LH) indicates that organisms take key clues from their environmental conditions to guide the allocation of resources to development, mating strategies, and reproduction. Numerous evolutionary psychologists have applied this established mid-level evolutionary theory to human behaviors. Researchers have illustrated, for example, that environments which are highly unstable tend to engender an earlier timing of puberty, earlier timing of first sexual behaviors, and earlier timing of first pregnancy. However, all of these phenotypic outcomes have been shown to be partially heritable. Thus, the potential for genetic confounding is a valid concern. Incorporating a genetically sensitive design, such as the MZ discordance design, could yield results that are not potentially confounded by unmeasured genetic factors.

While behavioral genetics methods are extremely valuable in illustrating the influence of environmental and genetic factors on phenotypic variance, they do not indicate which particular genes are responsible for the variance. The next section describes processes of examining individual differences which focus on identifying specific genes and/or clusters of genes that can affect phenotypic variance.

Molecular Genetics

The identification of genetic influence on phenotypic variance outlined above results in understanding the overall or additive effect of genetic factors. In order to identify specific aspects of that overall influence, molecular genetic methodologies are employed. In general, molecular genetic research on phenotypic variance is focused on three general methods: candidate gene studies, gene-by-environment interactions, and gene-environment correlations. Each of these methods is briefly described below.

Genome-Wide Association Studies (GWAS)

As noted above, behavioral genetic studies have convincingly illustrated the influence of additive genetic effects on phenotypic variance across almost all aspects of the human condition. However, in order to identify which specific genetic material is affecting the observed variance molecular researchers seek out specific genes using candidate gene methodologies. Thanks to the incredible technical advances in researchers' ability to scan a large sample of genetic material provided by research participants, these studies are able to correlate any observed difference in specific genes with reported or observed differences in phenotypic outcomes. Often referred to as genome-wide scan or GWAS, the method relies on genetic differences at certain places in the human genome. For example, genes can vary in a number of ways but one way that is convenient for research is called a single-nucleotide polymorphism. Briefly, genes are comprised of four different bases or nucleotides (A, C, G, and T) that make up the genetic alphabet. At various segments along strands of DNA, contiguous base pairs work together to code for a particular function. These contiguous base pairs are called genes. Most people's genes are identical across 99% of the genome. The reason for such similarity is because humans are from the same species. The remaining 1%, however, can lead to some drastic differences in personality, behaviors, health outcomes, and a number of other factors. Polymorphic genes – those which have two or more versions in the population – can lead to such

phenotypic variance. One way genetic variance can arise is via single nucleotide polymorphisms (SNPs), which are genes that vary in the population due to one base pair (single nucleotide) differing across individuals. While most SNPs (pronounced “snips”) have little to no effect, some have been identified as affecting a variety of outcomes related to neuronal functioning, personality, and behaviors. Studies which employ GWAS methodologies scan the genomes of participants to identify SNPs and any association with a variety of outcomes. GWAS and similar techniques (e.g., genome-wide complex trait analyses or GCTA) have been applied to outcomes ranging from psychiatric disorders to overall health to impulse control and intelligence (Barnes et al. 2014). One caveat that is often brought to bear in candidate gene studies is that the overall influence of a SNP is often minimal. This is not a surprise given that behavioral and psychological outcomes are so complex. However, individual differences in these outcomes would not occur if not for the genetic variance seen in GWAS analyses (i.e., while the effect is minimal with one SNP, the effect would be null if not for the difference between SNPs; see Dawkins 2006).

Gene by Environment (GxE)

While candidate gene studies provide valuable information regarding the underlying specific genetic material influencing individual differences, it is always key to remember that genes also interact with environmental factors to produce phenotypic variance. Thus, molecular geneticists also examine how specific polymorphisms affect phenotypic outcomes when paired with particular environmental conditions. As with any analysis of interactive effects, GxE research has indicated that certain genetic influences are enhanced or dampened when paired with certain environments (and vice versa). An informative way to conceptualize this dynamic is to think of two circles which represent the risk associated with a particular outcome. One circle represents the genetic risk (e.g., a candidate gene) and the other circle represents an environmental risk (e.g., abusive home environment). While on their own each aspect increases the likelihood of some

outcome, but the risk (or probability) of the outcome is greatest where the two circles overlap (i.e., like a Venn diagram). Perhaps the most well-known example of GxE research that illustrates this point was conducted by Caspi, Moffitt, and colleagues in 2002. The researchers were interested in assessing the independent and interactive effects of the MAOA genotype and an abusive rearing environment on antisocial behaviors. Caspi et al. (2002) observed that the effect of the risk allele for MAOA (a version of the gene that had been independently associated with antisocial outcomes in prior research) had a greater effect on the likelihood of antisocial behavior when those who possessed it were also raised in an abusive family. Importantly, the effect of these two factors on their own was minimal compared to the interactive effect. Other researchers studying a wide variety of phenotypic outcomes have illustrated similar GxE effects.

Gene-Environment Correlation (rGE)

While GxE research can illustrate the manner in which genetic and environmental factors combine to influence phenotypic variance, gene-environment (rGE) research highlights how genetic factors can lead to variance in exposure to different environments (Beaver 2009). In other words, this type of research illustrates that genetic variance can lead to phenotypic differences in individuals but can also affect environmental variance as well. Thus, in rGE research environmental factors are considered the outcomes (in the same manner as phenotypes in behavioral genetic and other molecular genetic research). In order to better understand this counter-intuitive claim, the three varieties of rGEs are discussed below.

Passive rGE

The passive rGE typology illustrates that children receive both genetic and environmental influences from their parents (provided they are raised by their biological parent or parents). As a result of the two influences emanating from the same source (i.e., parents), they are bound to be correlated. Consequently, the environment in which a child is raised is an expression of the genetic propensities that they share with their biological

parents. A common example is the observed association between the number of books in a household and a child's eventual cognitive abilities. Social scientists have long observed such an association and have assumed that if one has more books in their house, one will help increase the cognitive capabilities of one's child. However, given that a child shares 50% of their genetic material with each of their parents, they will also share the propensities towards activities that the parents also enjoy (e.g., reading). Additionally, behavioral genetic research has illustrated that cognitive ability is highly heritable. Thus, the books may not be the sole cause of the observed variance in cognitive ability but rather is a manifestation of genetically influenced propensities (i.e., people who have higher cognitive ability tend to read more and have more books in their home; they also tend to have children who also possess strong cognitive abilities). Consequently, passive rGE research illuminates how a developmental environment can be correlated with, but not necessarily cause, phenotypic variance in children.

Active rGE

Active rGE refers to the nonrandom selection into various environmental conditions and situations (e.g., employment type, hobbies, peer groups) that are driven in part by genetic propensities that are best expressed within the selected environment (Plomin et al. 2013). In other words, people often self-select into environmental conditions that suit their personalities and other genetically influenced propensities (and actively select away from environments that do not suit those propensities). This process is often referred to as *niche-picking* and research has illustrated that it occurs partially due to genetic factors (i.e., the niche to which one selects is associated with a nonzero heritability value). Finally, behavioral and molecular genetic researchers have also shown that as people age and gain increased degrees of independence the active rGEs become much more salient. Thus, while it may at times appear that environmental conditions lead to individual differences it is, according to active rGE research, in fact the opposite: variance in environmental conditions for many individuals is due in part to variance in genetic factors.

Evocative rGE

Psychology has long illustrated that different people elicit or evoke different reactions from others. Variance in factors such as personality, physical attractiveness, and sense of humor (among other traits) across individuals leads to differential social interactions with others. Stated differently, genetic differences generate phenotypic variance which in turn elicits differential reactions from one's environment. As a result, there is a statistical association between an individual's genotype and their environment. Additionally, researchers have shown that this evocative process exhibits a nonzero heritability value. Along with passive and active rGEs, evocative rGEs illustrate the need to recognize the ever-present influence of genetic and nongenetic factors when examining phenotypic variance, including in the context of evolutionary processes.

Conclusion

While evolutionary psychology is often focused on how humans are similar across time and cultures, it is still important to recognize the manifest ways in which individual differences arise and can influence behavior and personality. Indeed, without variance in terms of genetic differences, the processes of natural and sexual selection are unable to function. Thus, as a discipline evolutionary psychology has worked to incorporate a greater increase of the research and methodologies of behavioral and molecular genetics. Scholars such as David Buss (2009) and Penke (2009) have described the various ways in which evolutionary psychology can integrate examinations of individual differences and how such examinations can be employed to test, as well as refine, theories derived from an evolutionary paradigm (e.g., life-history theory, frequency-dependent selection, mutation load, among others). For example, Buss (2009) argues that individual differences in personality should be viewed as strategic differences that individuals can employ when provided with a variety of environmental challenges that are relevant to survival and reproduction. Additionally, both

Buss (2009) and Penke (2009) indicate that the theoretical scaffold of evolutionary psychology can be employed to provide ultimate explanations for the observed individual differences highlighted in the fields of behavioral and molecular genetics. The summary provided in this chapter further illustrated the variety of ways such integration can enhance our understanding of why humans behave and think the way that they do. Additionally, it can help highlight the reasons why people differ in a multitude of ways associated with psychology's primary foci.

Cross-References

- [Adaptation](#)
- [Culture of Honor and Individual Differences](#)
- [Evolutionary Personality Psychology](#)
- [Evolutionary Perspectives on Rape](#)
- [Mate Value](#)
- [Personality and Mate Poaching](#)
- [Sex Differences](#)
- [Sexual Infidelity Versus Emotional Infidelity](#)

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Individual Differences and Homicide

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Individual Variations in Attachment

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Definition

Individual variations in attachment denote interindividual variations in the organization or quality of attachment behavior in relation to the attachment figure, particularly observable when the attachment system is activated following external or internal cues of threat. Individual variations in attachment are typically described using two dimensions (secure/insecure, organized/disorganized) subsuming four distinct categories (secure, insecure-avoidant, insecure-ambivalent/insecure-resistant, and insecure-disorganized/disoriented). Profound difficulties in forming attachments to others (i.e., reactive attachment disorder [RAD]) are typically reserved for children who have not had any consistently available caregiver (e.g., children growing up in some institutions). Variations in attachment quality are

reliably predicted by the caregiver's pattern of responding to the child's signals (e.g., sensitivity), with characteristic forms of caregiving believed to be internalized as the child's internal working models (IWMs, cognitive-affective representations) of self and others, particularly as regards the attachment figure's availability for protection and support (Bowlby 1973).

Introduction

Attachment theory involves postulates about species-normative development as well as development of individual variations. John Bowlby, the founder of attachment theory (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), contested the theories of attachment available at the time (see ► [“Psychodynamic Foundations”](#)). Seeking an alternative explanation, he came to devote a great deal of effort into formulating the core tenets of attachment theory and its normative aspects, drawing from ethology, cybernetics, and cognitive psychology (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). These aspects include his conceptualization of the attachment system as a behavioral control system with a function of maintaining proximity to caregivers, retained through natural selection as it served an adaptive function of increasing chances of survival against predators and other natural dangers (see ► [“Infant Survival”](#)).

Bowlby was also convinced that there are interindividual variations in attachment quality, depending on how available the caregivers have been and how effectively they have responded to the child's signals (i.e., their sensitivity). Bowlby had, for example, found in his own work that lengthy separations caused frustration in children which seemed to follow a sequence of phases in the form of protest, despair, and (if not terminated) detachment (Bowlby 1982; Robertson and Bowlby 1952). Indeed, infants and young children were often showing signs of “insecurity” in relation to the caregiver following long separations, for example, in the form of initial avoidance and unresponsiveness upon reunion with the caregiver. That Bowlby argued for individual

variations in attachment is also clear from his emphasis on the importance of the quality of children's attachment to their caregiver(s) for the development of the self and social development. Bowlby had, for example, found in his own research that delinquent and aggressive children had experienced markedly more frequent early separations from their caregivers than other children (Bowlby 1944).

However, in comparison to Bowlby's careful efforts in precisely delineating the core tenets of the attachment system and the normative aspects of attachment, he did not get around to "systematizing" individual differences in attachment. This was partly due to lack of an empirical method for systematically examining variations in attachment. In his groundbreaking research into attachment, Bowlby therefore focused on the basic need for a continuously available caregiver for the development and maintenance of attachment bonds and the untoward effects of serious separations from or loss of caregivers, which were readily observable during the postwar era. Indeed, in delineating the problems yet to be solved regarding patterns of attachment (e.g., individual variations), Bowlby asked: "...in terms of what dimensions are variations best described. . . what antecedent conditions influence the development of each variety of pattern. . . how is each pattern related to subsequent personality development and health" (Bowlby 1982, 1997, p. 331). Attachment theory therefore owes much to Bowlby's close collaborator Mary Ainsworth and her colleagues and students, most notably Mary Main, for the systematic mapping of individual variations in attachment security and organization. Individual variations in attachment, as initially described by Bowlby and subsequently furthered by the research that followed, are elaborated below.

Bowlby's Notion: Variations in Internal Working Models of Self and Others

As outlined by Bowlby (1982), children come into the world endowed with attachment behaviors and prepared to form attachments, doing so to caregivers who are sufficiently available and

responding to their signals, particularly during stress when the attachment system is activated (see ► ["Offspring-Parent Attachment"](#)). Bowlby and Ainsworth both argued that "strength" of attachment is a misleading term. Children are either attached to their caregivers or not; what varies is the quality or organization (see below) of children's attachments to their caregivers. Rather than systematizing individual differences in attachment, Bowlby focused his theoretical efforts on how variations in attachment-related experiences with caregivers become manifested, eventually leading to observable differences in children's overt attachment behavior.

Drawing from cognitive theory (Craig 1943; Young 1964), Bowlby (1973) argued that individual variations in attachment-related experiences are manifested in cognitive-affective representations of self and others, which he termed internal working models (IWMs, see Bretherton and Munholland 2008). The IWMs are thought to include expectations of others' behaviors in relation to the self and the availability of others (particularly in attachment-related situations), as well as expectations on the self and its effectiveness in affecting the environment (i.e., others, most notably the caregivers). Bowlby argued that IWMs of self and others are complementary as the child gets to know itself as a person through how she/he is responded to by the caregiver (e.g., in line with psychodynamic object relations theories (see ► ["Psychodynamic Foundations"](#)). For example, a child that is responded to sensitively and lovingly by the caregiver is thought to construct both a model of others as loving and available in times of distress and a complementary model of the self as lovable and effective in getting what she/he needs from others.

Drawing from information processing and memory theories, Bowlby also argued that experiences of insensitive caregiving lead to the creation of incoherent (or multiple) IWMs, whereby the later emerging explicit layer of the IWMs differs from the implicit layer (Bowlby 1973). In line with Freud's ideas and those of psychoanalysis, but reformulated in modern information processing and memory function terms, he also argued that experiences of insensitive caregiving

and creation of incoherent IWMs necessitate the use of psychological defenses, such as defensive exclusion, to protect the individual against anxiety and associated dysfunctional behaviors (see ► “Psychodynamic Foundations”).

Importantly, Bowlby stressed that once IWMs are formed, they will come to guide children’s attention, behavior, and displays of emotion in future attachment-related situations with the caregiver (and others), as well as how children perceive various situations. Children who have become attached are therefore, for better and worse, thought to become active cocreators of the experiences they subsequently receive. That is, children will tend to act in ways that confirm their IWMs, which contributes to making them stable and partly resistant to change. Indeed, Bowlby noted that the high synchrony typically observed between attached children and their caregivers should be seen as a result of both the caregiver and the child adapting to one another. Drawing from Piaget (1955), Bowlby also argued that we tend to make small corrections to our models, which also contributes to make them stable since information is assimilated into the current models. However, given sufficiently strong new input, substantial change will occur through accommodation. Thus, the attachment system is seen as an open system, and the quality of attachment is therefore not set in stone (see Hoffman et al. 2006, for an attachment-based intervention).

Systematic Mapping of Individual Differences: Variations in the Organization or Quality of Attachment Behavior

Single Behaviors as an Insufficient Index of Attachment Quality

Bowlby argued that displays of attachment behaviors depend on multiple conditions, and he therefore outlined that observations of the quality of children’s attachment to their caregivers must (as a minimum) include “mother’s whereabouts and movements, presence or absence of other persons, the state of the non-human environment, and the state of the child” (Bowlby 1982, 1997,

p. 335). Accordingly, research has found that no single behavior is enough as an index of attachment quality (Ainsworth et al. 1978; Bowlby 1982). Two explanations for this are that the attachment system is activated by external and internal cues of threat and that it develops into a complex goal-oriented system that can flexibly make use of various behaviors (see “Evolutionary Foundations to the Attachment System and Its Functions”). First, as outlined by Bowlby, children’s “set goal” regarding the degree of proximity they desire to their caregivers varies momentarily depending on both external cues (e.g., strange or familiar environment, presence of strangers or not) and internal cues (e.g., child healthy or sick). Second, due to the complex goal-corrected nature of the attachment system, a child may also use signaling behavior in one situation, such as crying or smiling/vocalizing, and active locomotor behavior such as following the caregiver in another. Children moreover show interindividual differences in their tendencies toward various reactions, partly due to their biological characteristics (e.g., temperament; Vaughn et al. 2008). Using one single behavior to capture such a complex phenomenon as attachment quality, and trying to examine attachment in terms of “strength,” is therefore insufficient, indeed misleading. The insufficiency of any single behavior as an index of the quality of attachment is perhaps best exemplified with displays of aversive signaling behavior (e.g., crying) upon (short) separations from the caregiver, which is often mistakenly taken as an indication that children are securely attached (and conversely, that lack thereof is a sign of insecurity). However, not all secure children cry and protest separations, and some insecure children also display such aversive signaling behavior (e.g., Ainsworth et al. 1978).

Organization of Attachment Behaviors as an Index of Attachment Quality: Children’s Ability to Use the Caregiver as a Secure Base and a Safe Haven

One of the great accomplishments of Ainsworth (Ainsworth et al. 1978) was how she nonetheless

managed to devise a way to systematically examine the quality of children's attachment to their caregivers. She did so by taking into account Bowlby's ideas about the interaction between the attachment system and other behavioral systems, most notably the exploratory system (see ► [“Offspring–Parent Attachment”](#)), and his ideas about the complex goal-corrected functioning of the attachment system.

First, Bowlby argued that the attachment system interacts with an exploratory system and that the two systems are mutually inhibiting. That is, children are seen as having an innate desire to explore the environment (which facilitates learning) so that when there are no cues of threat, and the activation of the attachment system is low, children can explore the environment freely. However, upon signs of danger, the exploratory system becomes inhibited and the attachment system activated, typically making children retreat to their caregiver for protection and comfort. Importantly, Bowlby argued that secure attachment facilitates exploration. Children who feel that their caregiver is available for protection if danger should arise (“felt security”) can devote less energy (or epistemic space) into monitoring their caregivers and potential dangers and instead focus their energy on exploration (see ► [“Effects of Attachment Quality and Organization,”](#) for a discussion of how attachment may affect subsequent development through effects on the exploratory system). An important part in Ainsworth solving the puzzle was therefore that she managed to devise a method for examining the balance that (some) children manage to strike between attachment behaviors and exploratory behaviors.

Second, and referencing Bowlby's postulate that the attachment system becomes goal-corrected and can use various behaviors to reach its set goal, she devised a procedure that captures how children “organize” their behavior in relation to the caregiver, rather than focusing on any single behavior. Variations in attachment are thus not seen in any specific behavior, but in the pattern or “organization” of behavior in relation to the caregiver (Sroufe and Waters 1977; see below for specific “patterns of organization”). Ainsworth described the functions that caregivers need to fill

for children to be securely attached, simultaneously delineating what is meant by a “secure organization of attachment behaviors,” using two related terms. First, the caregiver must be a “secure base” for children, a reference point from which they can explore the environment freely. That is, caregivers must convey to the child that the environment is safe and that the caregiver is monitoring the child's whereabouts should danger arise. Moreover, the caregiver must also function as a “safe haven” to which the child can retreat upon signals of threat, being warm and accepting of the child's bids for proximity, cooperating with the child, and responding sensitively to the child's signals. When caregivers fulfill these functions, their children are seen to display a balanced and flexible (e.g., “secure”) organization of behavior, exploring the environment when there are no signs of danger and retreating to the caregiver for comfort when distressed. Wanting to show his appreciation of Ainsworth's contributions to attachment theory, Bowlby named his final book “a secure base” after her concept (Bowlby 1988).

The Development of the Strange Situation Procedure and Measurement of Children's Organization of Attachment Behavior

Using Bowlby's ethological approach, Ainsworth initially conducted extensive naturalistic observations in Uganda of children and their caregivers during the children's first years of life. She observed that children tended to show three distinct patterns in their organization of attachment behaviors in relation to their caregivers, patterns which tended to be associated with the caregiver's sensitivity in responding to the children's signals.

However, when Ainsworth sought to replicate and expand on her findings in American children, she ran into a notable problem. Whereas her mere presence as a white woman in Uganda (a strange and potentially threatening stimulus) had activated the attachment systems of the Ugandan children, making it possible for her to observe variations in the organization of attachment

behaviors, this was not the case in American children. She therefore came to devise the semi-structured laboratory observation called “the strange situation procedure” (SSP), which is still to date widely used for examining variations in attachment security and organization in infants (aged 12–18 months).

The SSP was specifically designed to enable observation of how children organize their attachment behavior in relation to the caregiver by using well-known triggers of the attachment system such as an unfamiliar environment, the presence of a stranger, and two (short) separations from the caregiver. The child (in the caregiver’s presence) is first given some time to explore the room and its play materials after which stress is gradually induced by a stranger entering the room, the stranger trying to interact with the child, the caregiver shortly leaving the room (leaving the child with the stranger), and (after a short reunion) the caregiver leaving the child alone in the room for a short time (before a second reunion). Importantly, the SSP is meant to be mildly to moderately (not very) stressful. The goal is to create a situation that is just enough stressful to activate the child’s attachment system so that variations in the organization (or lack thereof) of behavior can be observed. Indeed, research has shown that too much stress, such as from letting separations go on too long despite marked distress, may make the behavioral organization of otherwise organized children break down (Granqvist et al. 2016).

The SSP was moreover designed to activate the exploratory system. The physical environment of the SSP is not meant to be threatening. On the contrary, it is designed to be welcoming and interesting and is usually filled with age-appropriate toys to trigger children’s desire to explore. In other words, by triggering both the exploratory system and the attachment system, the SSP enables examination of whether children can use the caregiver as a secure base from which to explore and as a safe haven to return to for comfort when distressed. Importantly, by triggering both systems, children’s ability to strike a flexible balance between the two can be observed.

Ainsworth and her colleagues conducted a groundbreaking study of more than 100 children

and their caregivers, wherein 26 dyads were followed particularly intensively using over 70 h of home observations to examine caregiver sensitivity. When the children were 12 months, they were subsequently seen along with their caregiver in the SSP. Using four different behavioral scales (i.e., proximity-seeking, contact-maintaining, avoidance, and resistance) and focusing on variations in children’s organization of behavior, three distinct patterns emerged. Although behavior throughout the observation was important, behavior in relation to the caregiver in the two reunion episodes was particularly informative. Notably, Ainsworth et al. (1978) found a very strong correlation between the caregiver’s sensitivity in relation to their children’s signals during the first year and the children’s attachment security.

Organized Patterns of Attachment: Secure, Insecure-Avoidant, and Insecure-Resistant/Insecure-Ambivalent Attachment

Secure Attachment

Children classified as secure are characterized by a flexible balance between attachment behavior and exploratory behavior in the SSP. They typically use the caregiver as a secure base during the initial pre-separation episodes, playing elaborately with the toys and sharing their experiences with their caregiver. Secure children vary in their reactions upon the entry of the stranger, but most eventually accept interacting with the stranger. Secure children again show varying reactions during the two separation episodes, with some children displaying aversive signaling behavior (e.g., crying, searching), whereas other children are content exploring (see “[Secure Attachment](#)” for a fuller description).

Secure children who have become distressed by the separation use the caregiver as a safe haven in the reunion episodes. That is, they approach the caregiver and/or signal that they want proximity and comfort (proximity-seeking behavior), and they are effective in maintaining the contact for as long as they need in order for the attachment system to become inactive, for example, clinging

on attempted release (contact-maintaining behavior). Thus, they are eventually soothed and can go back to exploring the play material. Secure children who have not become distressed during separation tend to greet the caregiver happily and to try to involve the caregiver in their play. Importantly, this description of variations in “specific” behaviors shown by secure children underscores the need to examine the organization or patterning of behavior and not focus solely on any individual behavior.

Ainsworth and colleagues found that secure children tend to have caregivers who, during the home observations, were sensitive, perceiving the children’s signals and responding to them timely and appropriately. They both acted as a secure base, supporting children’s exploration, and as a safe haven, effectively comforting the children when distressed. Meta-analytical research has indicated that about two thirds of children tend to be securely attached in normative samples, with lower rates in children from high-risk groups (van IJzendoorn and Sagi 1999). Secure attachment is associated with positive development, such as high social competence and low levels of behavior problems (see ► [“Effects of Attachment Quality and Organization”](#)).

Insecure-Avoidant Attachment

Avoidant children show another distinct pattern in the SSP, which is seen as organized but less optimal than the secure pattern. First, avoidant children’s play often lacks the complexity shown by secure children, being stereotypic and shallow, and they share their experiences with the caregiver less often than secure children do. Thus, avoidant children’s ability to use the caregiver as a secure base seems to be impaired. Avoidant children, who typically do not protest during the separations, are particularly characterized by their behaviors in the reunion episodes, whence they often avert their gaze, turn and move away, or actively ignore the caregiver for an extended time (e.g., avoidant behaviors). Thus, their level of proximity-seeking and contact-maintaining behavior is often conspicuously low, and they do not show the same striking specificity of preference for the caregiver. The avoidant pattern is

often referred to as a “minimizing strategy,” denoting these children’s limited display of attachment behaviors and affect in relation to the caregivers (Cassidy 1994). (See ► [“Organized-Insecure Attachment”](#) for a fuller description.)

Importantly, avoidant attachment cannot be explained by stable dispositions such as temperament (Vaughn et al. 2008). Ainsworth and her colleagues, and the research that subsequently followed (Isabella and Belsky 1991), have shown that avoidant children tend to have caregivers who are less sensitive than caregivers of secure children. Specifically, caregivers of avoidant children have been found to more often “reject” their children’s bids for proximity and comfort (Ainsworth et al. 1978). Meta-analytical research has found that about 15–20% of children in normative samples tend to be avoidant (van IJzendoorn and Sagi 1999). Avoidant attachment is a risk factor for suboptimal development, for example, in the form of behavior problems (see ► [“Effects of Attachment Quality and Organization”](#)).

Insecure-Ambivalent/Insecure-Resistant Attachment

Ambivalent (or resistant) children show another distinct pattern of organization in the SSP. They often have difficulties with exploration, and it is not uncommon for them to show negative affect and distress even before the stranger enters the room, demanding attention by and proximity to the caregiver. They often retreat to the caregiver when the stranger enters and show limited acceptance of interaction with the stranger. Thus, their ability to use the caregiver as a secure base is impaired. (See ► [“Organized-Insecure Attachment”](#) for fuller description.”)

The ambivalent children typically show intense negative affect during the separations and often show moderate to high levels of proximity-seeking and contact-maintaining behaviors in the reunion episodes. Their behavior is, however, particularly characterized by an inability to be soothed by the caregiver’s overtures in the reunions, in combination with angry behaviors such as arching the back when in close contact with the caregiver and/or batting or throwing

away toys (resistant behaviors). Thus, the caregiver is insufficient as a safe haven. Ambivalent/resistant attachment has been described as a “maximizing” strategy, denoting these children’s heightened activation of the attachment system and high frequency of attachment behavior (Cassidy 1994).

Ambivalent/resistant children tend to have inconsistently sensitive caregivers, sometimes responding sensitively and sometimes not (Ainsworth et al. 1978; Cassidy and Berlin 1994). Meta-analytical findings have indicated that about 5–10% of children in normative samples are ambivalently attached (van IJzendoorn and Sagi 1999). As for avoidant children, this pattern is also associated with suboptimal development in the form of behavior problems and lower social competence (see ► “Effects of Attachment Quality and Organization”).

Insecure-Disorganized/Insecure-Disoriented Attachment

A minority of children were found impossible to classify using Ainsworth’s coding scheme to the SSP (Main and Solomon 1990). For example, some children behaved as an avoidant child in one reunion, but as an ambivalent child in the other one, or showed avoidant and ambivalent behaviors simultaneously. Some children also showed inexplicable, bizarre, or fearful behaviors in the presence of the caregiver, such as falling prone on the floor or freezing/stilling or covering the face with the hand or approaching the stranger upon seeing the caregiver in the reunion episodes (see ► “Disorganized Attachment and Reactive Attachment Disorder” for a fuller description).

Mary Main, a student of Ainsworth, discovered that the children showing these behaviors had one thing in common: an inability to maintain an organized strategy of behavior in relation to their caregiver (hence the label “disorganized”). Thus, whereas the avoidant and ambivalent patterns are also insecure, disorganized attachment differs from these patterns in the form of a breakdown in behavioral and attentional strategies (Hesse and Main 2000). Accordingly, disorganized attachment is seen as even less optimal than the organized-insecure patterns.

Mary Main, together with her close collaborator Erik Hesse, has theorized that an important antecedent to disorganized attachment is fear in relation to the caregiver and that disorganized attachment may follow from frightening/frightened behaviors on behalf of the caregiver (Hesse and Main 2000). Upon activation of the attachment system, disorganized children are thought to become stuck in an unsolvable approach/avoidance conflict of being both motivated to approach their caregiver for support and simultaneously being alarmed by the caregiver and motivated to avoid the caregiver. This unsolvable conflict is thought to lead to the breakdown in behavior shown by disorganized children. Importantly, and to avoid common misconceptions, disorganized children are attached to their caregivers. Being attached, and thereby motivated to approach the caregiver upon activation of the attachment system, is a prerequisite for disorganized attachment.

Research has shown that disorganized attachment is common in abused and maltreated children, supporting Main and Hesse’s theoretical proposal of fear as key in disorganization (Cyr et al. 2010). However, research has also shown that 15% of children in normative samples tend to be classified as disorganized (van IJzendoorn and Sagi 1999). Importantly, not all children assigned a disorganized classification have been maltreated, which is another common misconception. For example, research has also shown that unresolved traumatic experiences in the caregivers can lead to momentary frightening/frightened parenting behaviors in the absence of maltreatment, such as becoming dissociative and unable to contact and thus leaving the child psychologically alone, or being momentarily frightened by the child. Such frightening/frightened behaviors have in turn been shown to predict disorganized attachment (Schuengel et al. 1999).

It cannot be stressed enough that one cannot infer a characteristically disorganized attachment system merely from observing disorganized behaviors. Research has, for example, also found that temporary over-stress and neurological vulnerability, such as having early difficulties regulating attention and emotion at birth, are risk factors for disorganized behaviors (Granqvist

et al. 2016; Padron et al. 2014). There is also an association between high levels of ADHD symptoms and disorganized behaviors (Forslund et al. 2016), and pharmacological treatment of ADHD has been found to lead to large reductions in disorganized behaviors (Storebø et al. 2014). Thus, neurological problems may result in children behaving in disorganized ways without these behaviors necessarily being the result of a certain relational history with caregivers.

Disorganized attachment is the category of attachment that shows the strongest association with concurrent and later problems, particularly with externalizing problems such as aggression and symptoms of oppositional defiant disorder (see ► [“Effects of Attachment Quality and Organization”](#)).

Following the addition of the disorganized category, variations in attachment may be conceptualized using two dimensions: secure vs. insecure (avoidant, ambivalent, disorganized) and organized (secure, avoidant, ambivalent) vs. disorganized. Children classified as disorganized are typically given (if possible) a best-fitting secondary classification using Ainsworth’s original coding scheme. That is, if the child had been able to maintain an organized strategy, which one would that have been?

Reactive Attachment Disorder

A (small) minority of children do not show clear signs of attachment behaviors in relation to their caregiver and can therefore not be captured with the main dimensions of attachment quality and organization (Dozier and Rutter 2008). One cluster of children shows a marked unresponsiveness to the caregiver in the SSP, neither initiating interactions with the caregiver nor responding to the caregiver’s bids for interaction and/or bids to comfort the child. Another cluster of children fails to check back with the caregiver in the unfamiliar setting of the SSP and exhibits a lack of age typical social reticence by showing a willingness to go off with and approaching the stranger. These patterns are considered two subtypes of reactive attachment disorder (RAD): an emotionally withdrawn/inhibited type and an indiscriminately social/disinhibited type, respectively (Zeanah

et al. 2011) (see ► [“Disorganized Attachment and Reactive Attachment Disorder”](#) for a fuller description).

RAD is mainly found in children who have experienced severe social deprivation, being rare to nonexistent in low-risk samples but among the most common problem found in children who have experienced institutionalization (Zeanah et al. 2011). RAD is therefore thought to stem from a lack of a consistently available caregiver to direct attachment behaviors toward, with a severe lack of species-typical experience compromising the development of the attachment system. Attachment disorders often remit when caregiving conditions improve, such as following adoption, attesting to the resilience of the attachment system, but attachment disorders can persevere long after adoption, possibly indicating that the attachment system may have a sensitive period for typical development to occur (Dozier and Rutter 2008).

Conclusion

Bowlby argued that children, depending on the caregiver’s sensitivity, develop interindividual variations in attachment quality that are manifested in cognitive-affective representations of self and others. Subsequent research, most notably by Mary Ainsworth and Mary Main, has supported Bowlby’s claims and furthered them by systematizing individual differences in attachment. Specifically, Ainsworth discovered three organized patterns of attachment that vary in quality (e.g., secure, insecure-avoidant, insecure-ambivalent/insecure-resistant) and Main a group of children that fail to maintain an organized strategy, the “disorganized-disoriented” category. A final group of children, who have not had any consistently available caregiver, develop attachment disorders, as captured in reactive attachment disorder.

Cross-References

- [Adult attachment](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)

- Effects of Attachment Quality and Organization
- Evolutionary Foundations of the Attachment System and Its Functions
- Infant Survival
- John Bowlby: Pioneer of Attachment Theory
- Offspring–Parent Attachment
- Organized-Insecure Attachment
- Psychodynamic Foundations

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Individualism Collectivism

► Language and Economic Cooperation

Individuals that Impose Costs

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Synonyms

Aggression; Dominance; Formidability; Power

Definition

In humans, individuals that impose costs are those who signal both an ability and a willingness to inflict harm upon others.

Introduction

Traits that successfully signal an ability and willingness to impose costs comprise a dominance profile. Attaining social rank through dominance is reliant on an individual’s propensity to induce fear of psychological, material, and physical costs that the individual may impose upon their conspecifics (Buss and Duntley 2006; Chance 1967). Dominance has a deep phylogenetic legacy and likely persisted due to the prevalence of intergroup conflict throughout human prehistory that created a selection pressure for both physical and behavioral formidability (Manson and Wrangham 1991; Wrangham and Peterson 1996).

Physical Formidability, Resource Control, and the Ability to Impose Costs

Given the importance of discerning who is most able to inflict harm upon others, it seems that humans have evolved cognitive capacities for extracting formidability-relevant information from morphological, or nonverbal, signals to dominance (Sell et al. 2009). Some of these signals may be the individual’s physical strength and size (Blaker and Van Vugt 2014), which may indicate to others their perceived aggression and ability to succeed in agonistic encounters (Archer 1988; Gallup et al. 2007). Other visual characteristics, such as masculine facial characteristics (i.e., height-to-width ratio, more prominent feature brow), are believed to be signals of an individual’s dominance (Little and Roberts 2012). These facial characteristics, with links to testosterone, signal an individual’s formidability, fighting ability, and propensity for dominance-related behaviors (Carré et al. 2009; Stirrat et al. 2012). Alongside this, auditory cues may signal an individual’s dominance. Deeper vocal acoustics can convey an individual’s threat potential through its stable relationship with physical strength and size and testosterone (both endogenous and exposure during development) (Bruckert et al. 2006; Feinberg et al. 2005). Expressions of vocal pitch are, however, dynamic, and it seems that those high in dominance are disposed to modulate

their pitch to invoke signals of their formidability, while those lower in rank or dominance reactively modulate their pitch to accommodate their high-dominance counterpart (Cheng et al. 2016). While some evidence indicates that these markers do predict an ability to impose costs on others – and have further been observed to predict an individual's social rank (Keating et al. 1981; Klofstad et al. 2012) – recent evidence suggests that these relationships are likely to be small (Haselhuhn et al. 2015).

Individuals high in dominance may maintain power through a monopoly over resources, be they material or sexual (Mazur 1985). Individuals who are physically formidable, and thus have a greater chance of success during agonistic encounters (Archer 1988), are more able to aggressively control group resources and face fewer costs (Hammerstein and Parker 1982; Petersen et al. 2013). The defensibility of these resources has broad implications for the steepness of social hierarchies. When resources are scarce and certain individuals have disproportionate control, competition and rank asymmetries become heightened (Pierce and White 2006). Low-ranking individuals are likely to acquiesce to the wishes of a physically dominant individual through fear of both physical harm and also of the individual withholding valuable resources (Hawley 1999; Mazur 1985).

However, physical formidability alone is a noisy signal and can also signpost an individual's ability to generate benefits for others (Blaker et al. 2013; Lukaszewski et al. 2016), thus also being an attribute associated with prestige. Physical formidability is a form of embodied capital, whereby the narrower traits that comprise formidability (i.e., muscle mass and height) are biologically costly investments that take a great deal of time and energy to develop (Kaplan et al. 2003). The information conveyed by physical formidability is multidimensional as the development of such traits can improve an individual's hunting and foraging ability (Apicella 2014; Gurven et al. 2006; Jones and Marlowe 2002) and aid in community defense (Van Vugt et al. 2008), alongside cueing an ability to inflict harm. The combination of physical formidability and individual

differences in personality, motivations, and emotional profile that signal an individual's willingness to inflict harm upon others (Cheng et al. 2010) delivers a distinct profile that disposes certain individuals to propagate fear among group members.

Dispositional Dominance and the Willingness to Impose Costs

There are stable individual differences in the psychological profiles that make certain individuals disposed to dominance (Henrich 2016). Individuals high in dispositional dominance are high in a combination of narrower personality traits, having high levels of aggression and extraversion, and dominance being marginally associated with neuroticism (Cheng et al. 2010). Moreover, those high in dominance are also narcissistic self-aggrandizers, and dominance has a negative association with genuine self-esteem and agreeableness (Cheng et al. 2010). This profile is linked with hubristic pride, which is marked by arrogance and conceit, and is further associated with poor mental health, lack of conscientiousness, and an inability to forge and maintain stable, positive relationships (Tracy et al. 2009). However, hubristic pride may have evolved to motivate a willingness to impose costs on others. The related subjective and egocentric ideals of grandiosity and superiority may provoke antisocial behaviors that induce fear among conspecifics, which has reproductive and social benefits that balance the negatively associated outcomes (Ashton-James and Tracy 2012). Furthermore, the combination of these stable traits and egocentric status motivations increases an individual's willingness to inflict costs on others to obtain goals (Sijtsema et al. 2009).

There may be gender differences in cost imposition. Evidence suggests that males are more likely to impose direct costs on others through direct aggression (i.e., imposing physical costs on others), while females are more willing to indirectly aggress (i.e., gossip: Card et al. 2008; Griskevicius et al. 2009). For instance, a key tactic in female mate competition involves spreading

information aimed at maligning the reputation of her romantic rivals (Reynolds et al. 2018), whereas males often focus their efforts on inflicting (or threatening to inflict) costs on rivals and mates in addition to provisioning benefits to the latter (Miner et al. 2009).

The Costs and Benefits of Dominance and Cost Imposition

There is a plethora of individual benefits for high-ranking individuals whose positions are derived from signaling an ability and willingness to impose costs on others. In several small-scale societies, males high in dominance have greater reproductive success (von Rueden and Jaeggi 2016) and achieve positions of considerable influence (Konečná and Urlacher 2017). Experimental evidence has also indicated that males perceived high in dominance are more attractive as short-term mates (Kruger and Fitzgerald 2011). Those high in dominance also have a greater likelihood of becoming leaders and to receive deference and achieve positions of high rank in both formal (Magee and Galinsky 2008) and informal hierarchies (Cheng et al. 2013).

While individuals high in dominance may impose costs on their counterparts, evidence also suggests that groups may, on certain occasions, benefit from the dominant inclinations of certain group members. There are fewer individuals vying for influence in dominance hierarchies, which may ease tensions within a group and facilitate effective coordination (Ronay et al. 2012; von Rueden et al. 2014) and punishment of norm violators (O’Gorman et al. 2009). Individuals high in dominance may also provide group benefits during times of intergroup conflict (Wilson et al. 2001). Such individuals may inflict costs on an out-group, increasing the competitiveness and success of an in-group (Halevy et al. 2008). It is important, however, to note that these group benefits are by-products of those high in dominance creating fear to attain their egocentric goals. Recent evidence indicates that dominance-related social rank does not depend on (mis)perceptions of contributions from high-

dominance individuals (Cheng et al. [in prep](#)). Thus, the benefits that may result in rank relations weighted by dominance are a result of the fear of retribution that subordinate individuals harbor.

Constraining Dominance and Cost Imposition

In many human groups, there are several mechanisms that restrict an individual’s ability to impose costs on group members. Humans are unusual in the ease with which they form cooperative groups and coalitions (Gintis et al. 2015). Coalitional groups can attain a multitude of fitness-enhancing outcomes in comparison to individuals acting in isolation (Price et al. 2002). One such outcome is the ability to coordinate action against those who impose costs on others (the so-called *reverse dominance*, Boehm 2009). Many groups exhibit an aversion toward exploitative dominance-related strategies, and groups members are more likely form alliances (Eibl-Eibesfeldt 2017; Gavrilets 2012), spread negative gossip (Feinberg et al. 2014), dislike (Anderson and Willer 2014), or exit the group when there are available options (Price and Van Vugt 2014) to counter the influence of an individual high in dominance.

Conclusion

The ability and willingness to impose costs on others comprises a dominance profile. The diminished potency of physical and overtly violent cost imposition, and the increased reliance on manipulation (Clutton-Brock 2009) and coercion through psychological fear (Henrich and Gil-White 2001), has distorted dominance relationships, constraining the efficacy of dominance to certain contexts. Such contexts when individuals can impose costs are those where no strong norms sanctioning dominance-related strategies have developed (Pandit and van Schaik 2003); when the structural properties of a group make interactions between subordinates incredibly difficult (i.e., transitive or non-cohesive groups: Pellegrini and Long 2003), in formal hierarchies

(Magee and Galinsky 2008); and when groups have norms that may promote dominance (i.e., in delinquent gangs: Henry et al. 2000; Redhead 2016). Nevertheless, group members may coordinate and, in some cases, effectively develop counter dominance strategies to level the influence of dominant individuals (Boehm 2009).

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Individuation

- [Differentiation](#)

Induced Altruism

- [Kinship Psychology Manipulations](#)
- [Manipulative Use of Kin Terminology](#)

Induced Nepotism

- [Manipulative Use of Kin Terminology](#)

Induced Ovulation

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Definition

Induced ovulation is the phenomenon of females of a species having their ovulation be triggered by the act of coitus.

Introduction

Jöchle (1973) challenged the research at the time that argued that “induced” or “provoked” ovulation did not exist in the human species. According to others, the phenomenon was almost considered mythical, existing only in “old wives tales” with no evidence in the medical literature. Jöchle, however, reviewed the existence of coitus-induced ovulation in several species, where it “synchronizes semen disposition, transport, and capacitation, as well as of ovulation” (p. 523).

Jöchle (1973) reported that induced ovulating species were most likely induced by nervous stimulation of the genital tract, which triggered luteinizing hormone release (luteinizing hormone is the hormone responsible for ovum release or ovulation). However, current research in induced/spontaneously ovulating species shows that not only it is the seminal fluid that induces ovulation but also it is a factor that is a potent stimulator of luteinizing hormone (Adams and Ratto 2013). These Ovulation Induction Factors (OIFs, bioactive pro-hormone forms) are absorbed through the female reproductive tissue into the bloodstream. This process has been documented in rats (Aiyer et al. 1974), Bactrian species (Pan et al. 1992; Chen et al. 1985), alpacas (Sumar 1994), koalas (Johnston et al. 2004), Llamas (Bogle et al. 2011; Silva et al. 2011a; Ratto et al. 2006), cows (Tanco et al. 2012), mice (Bogle et al. 2011), and rabbits (Silva et al. 2011b). It is important to note that many induced ovulation species do not show ovulatory signals (Takahashi et al. 2009).

Ovulation Induction Factors in Humans

Jöchle (1973) argued that coitus induced ovulation occurs in humans as well. In the past 40 years, it has become clear that just as in other species, this may be occurring via seminal plasma. Human semen contains ovulatory hormones, immunosuppressants, pregnancy maintaining compounds, and psychoactive compounds (Burch and Gallup 2006). The following ovulatory hormones are present in human semen: estrone (Ney 1986), estradiol (Luboshitzky et al. 2002; Ney 1986), follicle

stimulating hormone (Ney 1986), luteinizing hormone (Ney 1986), and luteinizing hormone releasing hormone (Chan and Tang 1983). Of these, luteinizing hormone releasing hormone is the most appropriate as an ovulation induction factor, acting in physiologically similar ways to the ovulation induction factors in species listed above. However, human males also have five times more luteinizing hormone in their semen than circulating blood levels (Ney 1986). Other ovulation induction factors may not be needed when luteinizing hormone is in such high levels. Induced ovulation in humans could be due to luteinizing hormone, luteinizing hormone releasing hormone, both, or another ovulation induction factor.

Coitus Induced Menstrual Shifts in Humans

Cutler et al. (1979) first investigated this when seven of the eight women studied who experienced extreme cycle lengths also had sporadic sexual behavior. These same authors in 1980 showed that there were no aberrant short menstrual cycles and relatively fewer cycles that lasted over 33 days among the regular sexually active women. Veith et al. (1983) investigated the effect of exposure to males (sexually or sleeping) to ovulation. Around 92% of the women who spent two or more nights with a male ovulated, as compared to only 56% of the women who only spent one night or less with a male. However, no relationship was found between sex and ovulation. It was suggested that it was not the number of sexual encounters but the consistency that had an effect on ovulation. Given that consistent intercourse was key, it would be very difficult to determine induced ovulation with this methodology.

In 1985, Cutler, Preti, Huggins, Erickson, and Garcia found that women who maintained a weekly coital frequency had a zero incidence of short cycles and very long cycles. Women who reported regular weekly sex with men had a greater incidence of fertile menstrual cycles. Finally, in 1991, Burleson, Gregory, and Trevathan studied the effect of heterosexual activity on menstrual cycle variability. Celibate women had more variable cycles than women having

regular, frequent sex, even when gynecological maturity was controlled for. This is similar to the Whitten effect in rodents where females isolated from males display irregular cycles (Nelson 2011). It is important to note that all studies found that sex had to be consistent to have an effect on the menstrual cycle. The data indicate that unprotected sexual activity influences the female menstrual cycle, thereby indicating the role of seminal compounds.

The Selection Pressure for Ovulation Induction Factors

Various hormones that work in concert to trigger ovulation are found in human semen, and several studies have found an effect of unprotected intercourse on the human menstrual cycle. There is mounting evidence that human seminal fluid can trigger ovulation if women are exposed to it at the appropriate time. The next question is why seminal fluid may have evolved to do this. What is the selection pressure that led to the ovulation induction factors in human semen?

The data indicate that human seminal fluid evolved to counteract the ambiguity of concealed ovulation in humans. Sillén-Tullberg and Moller (1993) concluded that in the majority of instances when ovulatory signs have disappeared, it has been in a non-monogamous context and concealed ovulation is more tightly coupled with monogamy than any other mating system. They also concluded that the absence of ovulatory signs could be an important, though not necessary, prerequisite for the evolution of monogamy if concealed ovulation evolved first. Essentially, concealed ovulation could have been a factor pushing humans into a monogamous mating system.

The most cited hypothesis regarding the evolution and adaptivity of concealed ovulation was put forth by Alexander and Noonan (1979) that females concealed ovulation as a strategy to obtain male aid for females and children. This would be a limiting factor on male reproductive success; time spent investing in partners and children would subtract time and effort spent reproducing with other women. If concealed ovulation forced males into monogamy, it created a selection pressure in human males to develop counter strategies, such as semen chemistry. Males who were better able to

“synchronize semen disposition, transport, and capacitation, as well as of ovulation” as Jöchle (1973) stated, would not have to stay at home with one partner to ensure fertilization. Fertilization would become more efficient, allowing men to reduce investment in a given female partner and move on to another. Moreover, this relationship between concealed ovulation and induced ovulation has been seen in other species (Takahashi et al. 2009). Ovulation induction factors in semen actually appear to be a relatively common response to concealed ovulation.

Conclusion

Induced ovulation appears to be a common male response to female concealed ovulation, made possibly through ovulation induction factors in seminal fluid in several species, and may occur in humans through the same mechanism. Further research is needed in the relationship between concealed ovulation and induced ovulation across species, and exactly how and how often induced ovulation occurs in humans.

Cross-References

- [Concealed Ovulation](#)
- [Placental Proteins in Semen](#)
- [Reproductive Timing](#)
- [Semen and Vaginal Chemistry](#)

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Inequity Aversion in Primates

- [Fairness in Primates](#)

Infancy

- [Early Childhood and Adolescence](#)

Infant

- [Age of Child](#)
- [Early Stage of Brain Development at Birth](#)

Infant Abandonment

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Synonyms

[Infant survival](#); [Parental investment](#); [Parenting decisions](#)

Definition

Terminating investment in an offspring by abandoning the offspring.

Introduction

It has been well established that parenting is a complex behavior. Parental investment theory posits that this complexity is partially due to the lack of resources in the environment and the high cost of parental investment (e.g., physical energy during gestation, breastfeeding, and postnatal protection of the offspring; Trivers 1972). These factors may collectively compel parents to (both consciously and unconsciously) make harsh decisions about whether it may be more beneficial to invest in themselves or in their offspring. Evolutionary theory suggests that it may indeed be favorable for parents to, under certain circumstances, terminate investment in a given offspring to either (a) invest more in the other more viable offspring or (b) invest in the parents' own growth and development so that they may have more viable offspring in the future. In any case, parents may be susceptible to reducing investment in their offspring in the context of a less favorable environment. One such case is infant abandonment.

Infant abandonment is the practice of completely terminating parental investment in an offspring with the intent of never again providing care for the offspring (Maestripieri and Carroll 1998). Although it may be considered to be a form of child abuse or neglect, it appears that infant abandonment may be one example of characteristically “maladaptive” parental behavior that may provide adaptive benefits under certain environmental conditions. This is because infant abandonment, unlike other forms of child abuse or neglect, results in immediate termination of parental investment and costs associated with parental care (Maestripieri and Carroll 1998). This suggests that infant abandonment may indeed be a parental, and more specifically maternal, adaptation in an unfavorable environment that limits parental care.

Infant Abandonment as a Maternal Adaptation

Parenting decisions, including decisions to invest in or abandon the infant, are especially pertinent for mothers compared to fathers. This may be due to a number of important evolutionary differences between paternal care and maternal care. First, in accordance with Bateman's principle (1948), the larger gamete size and reduced availability of gametes in females, as compared to males, suggests that the reproductive strategy should differ in women and men. Specifically, because the production of an ovum is more somatically costly, women should pursue a reproductive strategy that emphasizes selectiveness whereas males can afford a relatively less restrictive sexual strategy as sperm is minimally costly and more readily available. Second, partially due to these reasons, females typically have a lower reproductive variance compared to males and therefore should be more selective of their parental investments in especially lower quality offspring compared to males (Dawkins 1976). Third, because mothers give birth to the offspring and are therefore already have invested quite a bit in the offspring compared to males, in conjunction with also being the primary source of nutrition for the offspring (e.g., breastfeeding in mammals; Hrdy 1999), infants across species are almost entirely dependent on their mothers to provide warmth, nurturance, protection, and other resources (Hrdy 1992).

However, as previously discussed, in certain adverse environments, the resource requirements of an offspring may be greater than the resources a mother is able to provide. For example, breastfeeding in some smaller species (e.g., rats) is sometimes metabolically more expensive than pregnancy itself and has the potential to deplete a mother's fat stores and jeopardize her health (Prentice and Prentice 1998). Therefore, a "greedy freeloader" baby who is less viable and in need of more sustenance may put an extra strain on a mother's resources (Hrdy 1999). To illustrate, baboon mothers who carry their unweaned infants are twice as likely to die, and half of the unweaned baboon infants will die, within the first two years

of life due to the energetic and physical costs associated with providing care for an offspring and themselves. As such, both parties are faced with an adaptive challenge (Hrdy 1999). This example demonstrates that it may sometimes be beneficial for a mother to forgo investment in a present offspring for later investment in a more viable offspring when more resources are available. Consequently, rejecting an offspring could mean increased resources for her, a chance at finding better quality mates, and an opportunity to invest more in a future offspring that may be more viable, all of which lead to increased evolutionary fitness for the mother.

Infant Abandonment in Humans

Therefore, cases of infant abandonment (mostly by the mother) are found across species, including humans. Historical records suggest that parents in medieval Europe abandoned their infants with the presumption that the child may be raised by another caregiver who is better able to provide for the child (e.g., the tale of Romulus and Remus being raised by a mother wolf; Hrdy 1992). Indeed, between the antiquity and the renaissance in Europe, it was common for couples without children to care for abandoned infants. Some of the abandoned infants were not claimed by anyone and would subsequently die; however, parents would still choose to abandon them knowing that this was a possible outcome (Hrdy 1999). Cases of infant abandonment still occur today. For example, it is common practice for mothers in economically poor areas of northeast Brazil to abandon their newborns, especially when the infants show cues of low survivability (Scheper-Hughes 1984). A common example of a more socially acceptable form of abandonment that is prevalent in both developed and developing countries is putting a child up for adoption (Hrdy 1992).

Potential Factors Associated with Infant Abandonment

Examining the patterns of infant abandonment across species, including nonhuman and human

animals, provides some insights into some of the important factors associated with such behavior.

Environmental Factors

Environmental factors appear to be a consistent correlate of infant abandonment across species. In nonhuman animals, extreme environmental scarcity/adversity and intra-sexual competition, especially for lower ranking females, are strong predictors, as such contexts will likely result in lower resource availability for both lower-ranking females and their offspring to survive on (Hrdy 1979). Similar environmental factors along with lower levels of social support appear to be important for infant abandonment in humans. For example, among Malaysian mothers, being unemployed, having unemployed partners, and having a rape-related pregnancies were all risk factors for infant abandonment (Suan et al. 2018). Additionally, mothers who were observed to abandon their infants in Kazakhstan had less stable incomes and were single mothers, compared to mothers who did not abandon their infants (Yelissinova et al. 2015). Although extreme environmental adversity alone is shown to sometimes be sufficient for parents to make the decision to abandon the infant, other factors may also play a role.

Child Characteristics

Another important factor associated with infant abandonment is the infant's health. A less healthy child may deplete parents' resources and limit the propagation of parents' genes (Volk and Atkinson 2008). Therefore, parents may be predisposed to prefer and invest more in offspring that exhibit cues of high health (Volk and Quinsey 2002). Indeed, various nonhuman animals are observed to terminate investment in offspring that appear to be weak or low in health (Mappes et al. 1997). Similar findings are also seen in humans' caregiving perceptions as well as their actual behavior and investment decisions toward less healthy, or even less healthy-looking, infants and children (see Franklin and Volk 2018 for a review).

Additionally, the child's age may also influence abandonment decisions. Most infants in the ancestral environment failed to survive through their first year of life (Volk and Atkinson 2008).

This is also the case, albeit to a lesser degree, in modern environments. Newborns are more likely to die due to infections, diseases, and lower quality care compared to older infants (Voora et al. 1982). For these reasons, parents may be inclined towards investing in older infants (Franklin et al. 2018). Moreover, terminating investment in an offspring may be easier if it occurs relatively early, as opposed to later, in the offspring's life. For example, infant abandonment in fish, known as brood desertion, occurs under conditions of food deprivation early in the breeding season when parents have not yet put in much investment in their eggs (Maestripieri and Carroll 1998). Similarly, marsupial mothers are especially prone to abandoning their infant presumably due to their relatively low-investment gestation that favors relatively easy and low-cost abandonment (Wasser and Barash 1983). Even in humans, abandonment is more likely to occur at the newborn stage, as seen in Kazakhstan (Yelissinova et al. 2015) and northeast Brazil (Scheper-Hughes 1984). These findings suggest that parents may be less emotionally attached to younger offspring due to less time spent with the offspring and the costlier investment in newborns due to their lower chance of survival (Bowlby 1980; Franklin et al. 2018).

Parent Characteristics

There are also patterns of some parental characteristics associated with cases of infant abandonment. Studies show that infant abandonment may be more prevalent among younger females across species, including humans (Wasser and Barash 1983). A study that examined the characteristics of infant abandonment among unmarried mothers in Malaysia suggested that being a first-time mother and being a younger mother were important correlates. Similarly, Yelissinova et al. (2015) compared a cohort of 17 mothers who gave up their babies in a maternity hospital in Kazakhstan to a cohort of mothers from the same hospital who did not choose to give up their babies. The results suggested that the women who gave up their babies were more likely to be teenagers. Additionally, Kim (2017) conducted a media report analysis that examined stories of newborn

abandonment in South Korea from 2011 to 2016. The mothers of these infants were usually young women in their 20s. Younger mothers are more likely to abandon their infants compared to older mothers likely because younger mothers have more opportunities to have offspring in the future (Maestripieri and Carroll 1998). Younger mothers may also lack the emotional regulation and resources that older mothers may have and therefore, may have negative attitudes towards parenting, demonstrate less responsiveness towards their infant, and engage verbally with their infant less often (see Belsky 1984 for review).

Additionally, individual differences, such as personality traits, may contribute to harsh parenting decisions including infant abandonment. Studies have found that personality traits, such as lower levels of Honesty-Humility (tendency to exploit others; Lee and Ashton 2004), Emotionality (tendency to feel attached toward kin; Lee and Ashton 2004), and Agreeableness (tendency for willingness to be exploited; Lee and Ashton 2004) on the HEXACO Personality Inventory are associated with negative perceptions and lower hypothetical investment toward infants, especially toward newborns (Franklin and Volk 2018). Moreover, higher levels of Neuroticism (tendency to experience negative emotions, such as anger, anxiety, and worry; Jeronimus et al. 2014) on the Big Five Personality Model is shown to be associated with rejecting behaviors toward children (Kochanska et al. 1997). These traits may have evolved as an adaptation to adverse environmental contexts (Buss and Greiling 1999). With regards to parenting behaviors such as infant abandonment, more specifically certain callous and less prosocial personality traits, such as the ones discussed in this section, may have served an adaptive purpose to help parents make harsh parenting decisions, such as terminating investment in an infant, when necessary.

Finally, mothers' psychological well-being that arises from their developmental histories is also shown to be an important factor associated with the infant abandonment. Mental illnesses, such as anxiety, panic disorders, attachment disorders, and postpartum mood disorders, have been suggested to impair the capacity for parenting and

increase the likelihood of infant abandonment (Megahead and Cesario 2008). These seemingly maladaptive disorders and illnesses may in fact have evolutionary benefits for parents by triggering certain parenting behaviors, when environmental pressures may not support a parents' investment in an offspring. An important example of this is Postpartum Depression (PPD).

Postpartum Depression

PPD is an affective disorder that affects are in seven women after giving birth, that is characterized by a period of emotional disturbance and depression that interferes with the developing bond between mother and child and detracts the pleasure of motherhood from the afflicted woman (APA; Stuart and O'Hara 1995). Symptoms of PPD include tearfulness, dependency, mood lability, feelings of guilt and inadequacy, disturbances in appetite and sleep, excessive worry about the health of the infant, subjective evaluation of themselves as "bad" mothers, and suicidal ideation (Stewart 2005). PPD is strongly associated with the lack of social support, life stress, reduced marital relationship quality, and other stressful life events (Beck 2001; Belsky 1984; O'Hara and Swain 1990).

The gestational and following postpartum periods are a time of rapid hormone fluctuation and cognitive change designed to prepare the mother for her new role as caregiver, regardless of how favorable her current environment may be. Specifically, Hagen (1999) proposes that postpartum affective disorders, such as PPD, may be adaptations that compensate for costs associated with gestation and parenting by informing the mother that she has suffered a social injury, or a "fitness loss." This may motivate her to reduce reproductive costs by reducing parental investment.

Conclusion

Infant abandonment is undoubtedly a heavily stigmatized behavior. However, evolutionary theory provides some insight into why some parents throughout history may feel as though abandoning their infant may be their only option. More specifically, evolutionary theory not only provides an

important framework for understanding the underpinnings for such decisions but also provides insights into the ways in which we can reduce these incidences. While infant abandonment is by no means a desirable decision, even the most developed societies lack adequate resources for supporting parents and reducing such behavior. For example, we know that harsh environments, such as economic hardship, across cultures may be an important and consistent predictor of infant abandonment. Thus, it may be beneficial for parenting interventions to provide support and services for parents such as providing family planning resources, access to abortion, and subsidized family counselling as these parents may be more at-risk for abandoning their infants and making other harsh parenting decisions (Hrды 1999).

Cross-References

- [Infanticide and Parenting](#)
- [Maternal Abandonment and Maternal-Fetal Conflict](#)
- [Postpartum Depression](#)

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Infant Mortality (as Opposed to)

► [Infant Survival](#)

Infant Survival

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Synonyms

[Infant mortality \(as opposed to\)](#)

Definition

Human infants are very vulnerable and dependent on their caregivers for survival into reproductive age. The attachment system, as defined by John Bowlby, is a behavioral control system with a set goal of maintaining proximity to caregivers, which has been retained through evolution as it increased the chances of survival against predators and other natural dangers (i.e., the functional consequence). Bowlby also argued that caregivers have a complementary caregiving system making

them responsive to children's attachment behaviors. Thus, although children (the weaker part) attach to their caregiver(s) (the stronger part), and not the other way around, children's forming of attachment is a collaborative effort. Mary Ainsworth subsequently discovered three organized patterns of attachment (i.e., secure, insecure-avoidant, and insecure-ambivalent/resistant), which have all been argued to be evolutionarily adaptive in that they enable children to adapt to their particular local environments and thereby increase chances of survival.

Introduction

Human children are born very vulnerable and are thus dependent on their caregiver(s) support in order to survive into reproductive age. Indeed, the proportional amount of time that human children are dependent on their caregivers is largely unparalleled in other species. Behavior systems enabling children to take an active part in affecting their caregiver's caregiving behaviors therefore constitute an evolutionary advantage. Universally, human infants are also seen to form strong bonds – attachments – to their caregivers, seeking to maintain proximity to and protesting separations from their caregivers and using them as a reference point, a secure base, from which to explore the environment. John Bowlby, a child psychiatrist and psychoanalyst, sought to understand the nature of children's ties – attachments – to their caregivers; why do children form attachments to their caregivers, and what is the function of attachment? The specific function of attachment according to Bowlby – increasing chances of survival by means of proximity to caregivers – is discussed below.

Infant Survival by Means of Maintaining Proximity to Caregivers

Bowlby could not accept the theories of attachment available at the time, since they deemed attachment secondary to processes such as feeding and/or other motivational processes (i.e.,

drives). Bowlby (1997/1982) deemed these theories unscientific and contrary to evidence and therefore sought an alternative explanation for attachment as a primary motivation in itself (see ► [“Psychodynamic Foundations”](#)). He came to draw from multiple sources, including his own experiences working as a child therapist, clinical research he had done on children with externalizing behavior problems (e.g., Bowlby 1944), scientific collaborations in which he examined effects of early child-caregiver separations (e.g., Robertson and Bowlby 1952), and research and theory from multiple scientific disciplines (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)).

Bowlby became particularly influenced by ethology, cybernetics, and cognitive psychology (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). Bowlby argued, following Darwin (1859) and the theory of natural selection, that humans (like all other animals) should be endowed with behavioral systems that whence evolved have been retained in evolution because they have been associated with adaptive functions in our ancestral species-typical environments. He consequently argued that we must search for an adaptive function of attachment in our environment(s) of evolutionary adaptedness (EEA), which have provided the pertinent selection pressures for an attachment behavioral system to develop. With the words of Bowlby, “Just as Darwin found it impossible to understand the structure of an orchid flower until he knew what insects flourished and visited it. . . , so, it is held, it is impossible to understand man’s instinctive behavior until we know something of the environment in which it evolved” (Bowlby 1997/1982, p. 61). Bowlby argued that ethology was the best present-day application of Darwin’s theories to behavioral systems in animals, drew heavily from ethology, and argued that the human attachment system should have prototypes in other animals. Bowlby also found that imprinting in birds and attachment behavior in other primates bear notable similarities to attachment behaviors in human children, which he argued may stem from convergent selection pressures as other animals have faced the same survival-related threats from

predators (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)).

More specifically, Bowlby argued that the attachment system must have been retained due to it serving the specific function of increasing the chances of survival. Bowlby argued that in humans’ primeval environment and ecological niche, humans were living as nomads in small hunter-gatherer societies, in environments comparable to that of other large ground-living species of higher primates. A key characteristic of our ancestral environments, according to Bowlby, was a risk of falling prey to predators and other natural dangers. Thus, he argued a behavioral system that monitors the whereabouts of and promotes the maintenance of proximity to caregiver (s) should have served an important function that increased the chances of survival. Indeed, Bowlby argued that proximity to caregivers is the predictable outcome of activation of the attachment system, which has served an adaptive function in reducing the risk of falling victim to predators and other natural dangers (i.e., the functional consequence); “Because immature organisms are usually very vulnerable they are commonly endowed with behavioral equipment that produces behaviors specifically likely to minimize risk, e.g. behavior that maintains proximity to a parent” (Bowlby 1997/ 1982, p. 143).

Children are thought to be endowed with attachment behaviors and prepared to form attachments to caregivers who are continuously present and responding to their signals. Attachment behaviors, which are triggered by internal (e.g., sickness, pain) and external (e.g., separations from caregiver, strangers) cues of danger, include all behaviors that children use to maintain and increase proximity to their caregivers, and they are thus defined by their function, with increasing development expanding the repertoire (see ► [“Individual Variations in Attachment”](#)). Attachment behaviors are often grouped into three broad classes of behaviors: aversive signaling behaviors (e.g., crying, screaming), positive signaling behaviors (e.g., smiling, vocalizing), and active behaviors (e.g., following, clinging). Terminating signals, which decreases the activation of the attachment system, includes signals conveying

that there is no more cause of alarm. For young children this typically pertains to close physical proximity to the caregiver whereas older children can often be soothed by other means. Importantly, children's attachment relationships are hierarchical; children (the smaller, weaker part) form attachments to their caregivers (the stronger, wiser part), not the other way around. Bowlby however also argued that caregivers are endowed with a caregiving system that typically makes them biased and responsive toward their children's signals, for example, retrieving children following signs of danger. Children's forming of attachment is therefore a collaborative effort.

Bowlby's close collaborator Mary Ainsworth (Ainsworth et al. 1978) and Mary Main (Main and Solomon 1986) subsequently discovered specific categories of individual variations in attachment security and organization, corresponding to particular patterns of caregiver sensitivity in relation to their children's signals (see ► [“Individual Variations in Attachment”](#)). These categories are (currently) secure attachment (see ► [“Secure Attachment”](#)), insecure-avoidant attachment and insecure-ambivalent/resistant attachment (see ► [“Organized-Insecure Attachment”](#)), and disorganized attachment (see ► [“Disorganized Attachment and Reactive Attachment Disorder”](#)). From a developmental psychology perspective, secure attachment is typically regarded as the optimal way of organizing one's attachment behaviors, with the insecure patterns judged suboptimal due to their links to increased risk for maladaptive development (see ► [“Effects of Attachment Quality and Organization”](#)). All three organized patterns of attachment (i.e., secure, insecure-avoidant, insecure-resistant/ambivalent) have however been discussed in evolutionary terms as adaptive ways of organizing attachment behaviors so as to maintain as much proximity as possible in relation to the caregiver(s) and thereby aiding survival, with no organized pattern of attachment inherently superior to any other one (Main 1981; Simpson and Belsky 2008). Indeed, Bowlby argued that the attachment behavioral system is open to learning so as to function adaptively in children's particular environments. Avoidant attachment (minimizing expressions of

vulnerability in relation to a caregiver that has previously rebuffed the child's bids for proximity) may thus constitute an adaptive way of ensuring some level of proximity to the caregiver without risking further rejection and potential abandonment. Similarly, ambivalent/resistant attachment (showing high levels of negative affect and maximizing attention toward a caregiver that has previously been inconsistently sensitive) may constitute an adaptive strategy for not being overlooked in the presence of danger.

Bowlby was very specific that the set goal of attachment is the maintenance of proximity to caregivers due to caregiver proximity facilitating protection against predators (and other natural dangers). Bowlby discarded a hypothesis that attachment facilitates learning skills necessary for survival from caregivers with the argument that the biological function of a behavioral system cannot be any favorable outcome its performance may have; “Biological function is defined more narrowly: it is that consequence that in course of evolution has led the behavior in question to become incorporated into the biological equipment of a species” (Bowlby 1997/1982, p.224). Hence, he argued that a specific advantage in terms of survival and reproduction must be conferred by the behavior, leading the individuals who display it to achieve higher rates of survival and reproduction (i.e., leaving more progeny). As rhetorically asked by Bowlby (1997/1982): if attachment serves a function of facilitating learning, why does attachment persist into adulthood, when critical learning is complete? (see also ► [“Attachment in Adulthood”](#)).

In support of his argument, Bowlby noted that observations of many species of animals indicate that an isolated animal is more likely to be attacked by predators. Attachment behaviors are moreover elicited particularly easily in animals which “by reason of age, size, or condition, are especially vulnerable to predators, for example the young, pregnant females, the sick” (1997/1982, p.226). Attachment behaviors also tend to always be elicited at high intensity when an animal is alarmed (e.g., in danger). Bowlby also noted that the finding that young offspring attach even to caregivers who are hurtful and

frightening to the offspring is hard to explain by any other theory.

In a possible critique of Bowlby's position, he also argued, however, that variations in the quality of children's attachments to their caregivers are of substantial importance for their personality development. He argued that children construct cognitive-affective internal working models (IWMs) from attachment-related experiences with the caregiver(s) that whence constructed will influence perceptions and expectations of the self and others and thereby how we will behave in relation to others (Bowlby 1997/1982). Although this may be regarded as a secondary side effect of variations in attachment security and organization, not a primary functional consequence in itself, it does raise the possibility that attachment has functions beyond immediate survival against predators, such as learning skills to function adaptively in one's broader social group. Indeed, Main and Hesse (1992) argue that the attachment behavioral system likely serves multiple survival functions, including protection from unfavorable temperature changes and attacks by conspecifics. Relatedly, although Bowlby was right in arguing that attachment is not secondary to feeding, proximity to caregivers also increases chances of getting fed as well as learning what is edible (Harlow and Zimmerman 1959). Current research is also examining the importance of attachment for adult functioning, such as for reproductive strategies, with some findings indicating that attachment security and organization may affect onset of puberty (Simpson and Belsky 2008).

Conclusion

Children's attachments and attachment behaviors are the result of an attachment behavioral control system that continuously monitors the whereabouts of the caregiver(s) and has the maintenance of proximity to caregivers as a set goal. This system, which bears similarities to imprinting in birds and attachment in other primates, has been retained in evolution as it, according to Bowlby, has served a specific function of increasing

survival against predators and other natural dangers. The attachment system is moderately open to learning, and children develop different patterns of attachment in relation to their caregivers depending on the caregiver's pattern of responding to the child's signals, with all organized patterns argued to be evolutionarily adaptive in maintaining proximity to the caregiver in children's specific environments.

Cross-References

- [Attachment in Adulthood](#)
- [Charles Darwin: Theory of Natural Selection](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Infant Abandonment](#)
- [Individual Variations in Attachment](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Organized-Insecure Attachment](#)
- [Psychodynamic Foundations](#)
- [Robert Hinde](#)
- [Secure Attachment](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Infant-Directed Speech (IDS)

- [Motherese](#)

Infanticide

- [Filicide](#)
- [Maternal Abandonment and Maternal-Fetal Conflict](#)
- [Methods of Filicide](#)

Infanticide and Parenting

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Introduction

From humanity's distant past, there has existed a range of archetypal narratives relating to the

murderous actions and intent of parents toward their children, whether they be biological offspring or adopted. The Hebrew God, for example, tested Abraham by ordering him to sacrifice his son Isaac. The Greek myths of Oedipus Rex, Medea, and many fairy tales from a range of different times and places reflect the enduring and cross-cultural expression of this aspect of human behavior over millennia.

Infanticide has often been used as a generic term to refer to this complex phenomenon. However, it has had different meanings depending on time and context. In Biblical times, the term infanticide included any young children murdered by either parent or the State. The modern medicolegal interpretation of the term infanticide is, in contrast, more restrictive.

Although infanticide legislation varies cross-nationally, it only includes certain mothers who kill their young children while considered to have been under the adverse effects of giving birth when they killed. However, for research purposes, the generic term “infanticide” is too broad to reflect the heterogeneous patterns in the way parents have killed their children. An expanded classification taxonomy is thus used to identify specific subtypes of parental child killing as part of this complex phenomenon.

Definitions

The term neonaticide refers specifically to the killing of an infant at birth born within the first 24 h of life (Resnick 1970). The term infanticide is most commonly used to mean the killing of an infant during the first year of life (Friedman et al. 2005). The term filicide is used in relation to the killing of any other child under the age of 18 by either parent (Friedman and Resnick 2007).

Without medicolegal constraints in definition, there has been a proliferation of academic literature in recent decades seeking to understand both epidemiological and typological aspects of parental child killing. Different patterns have been identified depending on the age and gender of the child and the parent, and the nature of the parent-child relationship (whether biological or step-parental).

Furthermore, differences in parental motives, stressors, and rates of mental illness have also been identified.

However, until recently there had been no unifying theoretical framework to assist in this area of academic research. Evolutionary social psychology has begun to provide such a heuristic theoretical framework for a range of social and biological sciences. The application of contemporary evolutionary theory to the broad field of study relating to parental child killing provides unique perspectives into this ancient aspect of human behavior that may assist academics, policy makers, and clinicians alike to further inform their respective disciplines and practice.

Infanticide Law

Infanticide laws exist in approximately two dozen nations. The British Infanticide Act allows for charge akin to manslaughter (rather than murder) for mothers who kill their infant while suffering from a mental disorder. It is based on the 1920s beliefs about delivery and lactation hormonally affecting such women to the extent that “the balance of her mind is disturbed by reason of her not having fully recovered from the effect of giving birth.”

Most international laws have followed the British tradition, significantly decreasing the sentence for women who kill their infant. Nations with infanticide legislation include Australia, Austria, Brazil, Canada, Colombia, Finland, Germany, Greece, Hong Kong, Italy, Japan, Korea, New Zealand, Norway, the Philippines, Sweden, Switzerland, Turkey, and the United Kingdom (Friedman and Resnick 2007). In New Zealand, the penalty is decreased for mothers who kill their child up to age 10 and infanticide can be either a charge or a defense. Despite such variances, international infanticide legislation is invariably limited to mothers and remains legally based on very narrow criteria.

Despite their shaky and often unscientific foundation, these Acts were meant to extend compassion rather than punishment to those struggling mothers – indicating societal acknowledgment of

the point whereby a woman could not be held culpable for killing her children under certain circumstances (Friedman et al. 2012a).

However, many women who successfully utilize the defense of infanticide do not suffer from enduring mental illnesses per se. Somewhat ironically, other mothers who are severely mentally ill and kill older children while psychotic would be unlikely to qualify for the defense in most nations. In medicolegal terms, they would be similarly treated to fathers who were mentally unwell at the time of killing their child.

The state then has not relinquished its influence in determining how society interprets and applies the law in relation to parents who kill their children. Nor has the state completely shed the vestige of its ancient role in sanctioning the termination of unwanted children.

Patterns in Neonaticide (Murder in the First Day of Life)

Dating back to at least ancient Greece, when human infants were deformed or weak, they would be abandoned to die from the elements, if not more actively killed (West et al. 2009). Early philosophers including Plato and Aristotle believed that the Greek custom of killing, or leaving to die, deformed or weak infants preserved the population’s integrity (West et al. 2009). Implicit in this custom was the view that a deformed child was somehow an undesirable burden on either the parent or the society.

However, a child’s anatomical traits need not be the only factor determining a parent’s perception of the “undesirability” of the child. Patterns of neonaticide are distinct in the developed world verses the developing world, for example, suggesting different cultural and social influences (Friedman et al. 2012a).

In Japan, for example, there were two types of neonaticide with different terms to describe them (Sakuta and Saito 1981). Japanese cases of *anomie* are similar to neonaticide in the rest of the developed world. In *mabiki*, translating to “thinning out,” the parent or parents kill the newborn because they lack the financial ability to care for

the baby. Similarly, sex-selective neonaticides occur in some countries where a female infant is seen as a liability.

By definition, neonaticides are committed at birth or within the first day of life and the perpetrator is therefore usually the mother acting alone. The infant's biological father is quite often not a part of the woman's life by the time of delivery or, if he has remained in the relationship, the man often does not know of the woman's pregnancy (Friedman and Resnick 2009). Only very rarely is the father known, present, and assisting with the murder.

Most typically, the mother is a young woman, often in her teens or early 20s, who is afraid of the repercussions of both her pregnancy and the infant's existence. This may be due to external pressures such as religious or cultural taboos, extramarital paternity, or unmarried status. Pregnancies and deliveries are often hidden, and both psychological denial of pregnancy and deliberate concealment of pregnancy are common (Friedman and Resnick 2009).

Denial or concealment of pregnancy usually precedes the neonaticide, and both may interfere with the acknowledgment of pregnancy, without which there may be little or no maternal bonding with the pregnancy and the young baby. In concealment of pregnancy, the woman knows that she is pregnant but hides it from others. In affective denial of pregnancy, women do not acknowledge their pregnancy emotionally but may be cognitively aware. In pervasive denial of pregnancy, the woman is not aware that she is pregnant. She may not experience physical signs or symptoms of pregnancy and does not realize she will give birth (Friedman et al. 2007; Miller 2003).

In psychotic denial, the woman by definition has a psychotic illness (like schizophrenia or bipolar disorder) and may intermittently deny her pregnancy. However, mothers with severe mental illness are uncommon in cases of neonaticide. Nor is neonaticide commonly associated with suicide. In fact, young mothers who kill at birth or in the first day of life are much less likely to have mental illness or to commit suicide compared to older mothers who kill their older children (Friedman et al. 2012b).

Patterns in Infanticide (Murder in the First Year of Life)

Infanticides when taken outside of a medicolegal definition form only a subset of parental child killing. Studies of child murder in the first year of life have found that these parents often have multiple life stressors. Economic stress, unemployment, and young parent perpetrators are commonly occurring factors (Friedman et al. 2005).

Many deaths in this age group occur after a period of sustained and chronic child abuse rather than a single homicidal act. Crying children are sometimes believed to be a final precipitant for the parent (disenfranchised and with poor coping and parenting skills) to inflict lethal violence on the child. These victims may be more likely to have physical anomalies. Mothers who kill infants in this age group have variable rates of depression, substance use disorders, or other psychiatric disorders.

Patterns in Filicide (Murder Up to Age 18)

Maternal Filicides

Mothers who kill their children have typically been victims of violence themselves. They have multiple life stressors and are often socially isolated, poor, and the child's primary caregiver (Friedman et al. 2005). Over one-third of maternal filicides happen either while the mother is pregnant with another child or during the first-year postpartum (Friedman and Resnick 2007). Chronic abuse or neglect, substance abuse, and mental illness are not uncommon among these mothers (Friedman and Resnick 2007).

Among the women who purposefully killed their child and who suffered from mental illness, suicide attempts were not uncommon. Some 16–29% of maternal filicides do end in suicide (Nock and Marzuk 1999).

Mothers who do commit filicide - suicide often kill children who are older; these mothers would be unlikely to have qualified for the age range required for an infanticide defense had they survived. In contrast to fathers, mothers are more

likely to only kill their biological child, and possibly themselves, but not their partner.

Paternal Filicides

Less research exists regarding fathers who kill their children. However, they are more likely to be incarcerated than to be psychiatrically hospitalized after their child's murder. Chronic abuse, mental illness, and revenge were, similar to that for the mothers, common themes (West et al. 2009). Approximately one-fifth of children killed by fathers were infants (West et al. 2009).

Studies have indicated that fathers who kill were often under significant financial stress, relationship stress (including separation or looming divorce), and had limited supports (West et al. 2009). Precipitants to paternal filicide included: domestic disputes, anger and rage, abuse or neglect, punishment for misperceived child behavior, revenge, and mental illness (West et al. 2009).

Fathers who kill their children are more likely to commit suicide after their act than mothers (Nock and Marzuk 1999). Fathers who kill their children are also more likely to kill their partner in the same act. When the father kills the whole family, in an act of familicide, Wilson and colleagues described two categories. Angry men killed because of hostility toward their wife whereas depressed men killed to save their families, having nihilistic beliefs of saving them from a fate worse than death (Wilson et al. 1995).

Filicide by Step-Parents

Step-parents kill step-children at much higher rates than biological parents kill biological children. Step-fathers rather than step-mothers are often thought to be the more common perpetrators. However, this is likely related to the percentage of children who live with step-fathers rather than step-mothers rather than a true base rate. In times past, when there were higher maternity mortality rates, many more step-mothers lived with step-children.

Motives

The motives for child murder by a parent tend to fall into one of five categories, initially described

by Resnick (1969). These motives include: most commonly (1) *fatal maltreatment*; less commonly (2) *partner revenge*; (3) *unwanted child*; (4) *altruistic*; and (5) *acutely psychotic*.

Fatal maltreatment was initially termed “accidental” because the death in these cases is usually not anticipated specifically – but instead is the cumulative effect of chronic abuse or chronic neglect by the parent (Friedman and Resnick 2007).

Partner revenge, also known as spousal revenge or Medea syndrome (after the mythical Medea who killed her children to punish her cheating husband Jason), occurs in the context of a divorce or a breakup when one parent kills the child in order to emotionally wound the other parent. (If only one of the children is killed, it will be the other parent's favorite child.)

In *unwanted child* cases, the murder occurs because the parent, rather than seeing their child as a person, sees the child as a hindrance to their own goals. In neonaticides, the infant is often murdered right at birth because they are *unwanted*. It has been suggested that these cases may sometimes represent a delayed effort by the mother to terminate the pregnancy.

The final two motives – *altruistic* and *acutely psychotic* – are usually associated with parental mental illness. In *altruistic* filicide, the parent holds a belief, cognitive distortion, or frank delusion that the child's death is in that child's best interest. This could include when a child/infant was seriously medically ill and the parent believed it was a mercy-killing similar to euthanasia. Alternately, when the parent was severely depressed and planning suicide, they may not wish to leave their child alone in the world. A parent who was psychotically delusional may also hold a nihilistic delusion that a fate worse than death was awaiting their child. In contrast, in an *acutely psychotic* filicide, when the parent is suffering an episode of acute psychosis or mania and kills their child, there may be no comprehensible motive or explanation.

Evolution and Infanticide

Darwin first published *The Origin of the Species* in 1859 and proposed a theory of evolution of

species by a process of natural selection. Through the accumulation of minor trait mutations over millennia, some individuals will be able to better compete for reproductive resources to favor the genetic proliferation of their own offspring and those traits. The so-called “survival of the fittest” of those interspecies rivals is thus assured.

Although contemporary evolutionary theory has advanced considerably in recent times, the five central tenants of Darwinian theory remain at its core: that there is variation in every population; individuals within the population compete for limited resources; more offspring are produced than can survive; individuals pass genetic traits to their offspring; and those with the most adaptive traits are more likely to survive and reproduce.

Early evolutionary scholars were limited to studying the anatomical and behavioral expressions of these traits without fully understanding how they were transmitted. They did, however, understand that aggression, violence, and lethal violence toward offspring was prevalent in nature and sought to understand how killing one's offspring could be an adaptive strategy for an organism to pass on its genes.

Parental investment theory (Fisher 1930) noted that the 1:1 sex ratio of human offspring was an evolutionarily stable gender ratio, suggesting and hypothesizing that parents should be equally invested in their children. However, Trivers' (1974) theory of a parent-child conflict focused upon the extent of the “investment” of the parental resource as being a function of gender, genetic relatedness, and the degree of benefit to the parent in relation to the child successfully having more offspring.

In the case of social animals who often rely upon one another for survival, Hamilton (1964) proposed an arithmetic algorithm to explain an evolutionary basis to altruistic behavior. Hamilton's Rule, $rB > C$ stated that altruism could arise as an adaptive evolutionary strategy when the genetic relationship of the recipient (r) multiplied by the benefit to the receiver (B) is greater the cost (C) to the beneficent party.

The killing of unrelated infants is particularly common among many animals and would in evolutionary terms, seem to make sense. Indeed,

when males commit infanticide in nature, therefore, they primarily kill infants who are unrelated to them, most likely to secure new potential mating opportunities for their own offspring (Liddle et al. 2012).

For example, in pride of lions, when a new lion comes into power, he kills other males' cubs and thus subsequent new cubs are his biological offspring. In mammals, females are often infertile while lactating such that the death of the infant leads the mother to new fertility and subsequently new genetically related progeny for the father (Liddle et al. 2012).

In humans, fairy tales like Hansel and Gretel, Snow White, and Cinderella have also warned for centuries about the dangers posed to children by evil step-parents. Step-parents do not have a biological vested interest in maintaining the unrelated child's genetic material when compared to the significant investment of time and effort in step-parenting.

When females kill the infants of other females, it may instead be in order to secure additional resources for herself and her own offspring, and has been observed in a range of species from squirrels and birds, to monkeys and chimpanzees (Liddle et al. 2012). However, when females kill their own offspring, this too may confer an adaptive advantage in some circumstances due to the disproportionate investment of reproductive resources for females.

Females have limited numbers of eggs and fewer opportunities to reproduce compared to males and their ability to sire multiple offspring. There are also high physiological risks and other costs to the mother in carrying the pregnancy, giving birth, and feeding the offspring. Not paying this investment can be an advantage to the female when resources are sparse. For example, when a young primate is born in the wrong season or is defective which would require extra parental effort, they may be killed to enable the mother a better chance to raise another healthy offspring to reproductive age (Hrdy 1979).

Advances in understanding the anatomy and neurophysiology of the brain throughout the twentieth century enabled a more sophisticated understanding of these complex behaviors.

Behavioral psychologists, ethologists, sociobiologists, and primatologists have described any number of animal models based largely on the limbic system (and its interactions with the forebrain and hindbrain), to identify and explain evolutionary remnants of complex behavior in our own species, including parental child killing.

Animal studies of the genetic inheritance of certain innate instincts, the capacity for emotional expression, language, and variably complex motivational patterns of behavior have all been presented as analogous to parts of the evolved human behavioral repertoire. However, it has been only recently that these behaviors have been seen as responses to inherited cognitive mechanisms from our distant evolutionary past.

Evolutionary psychology proposes human beings have evolved specific cognitive programs, with neurophysiological substrates, to enable us to process significant species-specific environmental stimuli. Attending to and processing that information in an evolutionarily adaptive and stable way has resulted in predictable behavioral responses in our species. However, the behavioral responses need only to have been adaptive to distal evolutionary selection pressures and not necessarily adaptive in a proximal and contemporaneous social context (Cosmides and Tooby 1987).

Daly and Wilson (1988) then postulated four evolutionary based reasons for parental child killing that resonate with other motivational taxonomies, including: a low quality of child, limited parental resources, paternal uncertainty, and coercion by others.

The fact that homicide is most likely in the first day of life is consistent with this evolutionary view because the child's reproductive value to the parent increases with the child's age, relative to the degree of ongoing parental investment required (Friedman et al. 2012a). The parent is most commonly a single mother of limited means who kills the neonate when the father is not present or does not know about the pregnancy (therefore lacking in any paternal investment).

Scarce financial, emotional, and sociocultural resource availability to care for an unwanted child are similarly consistent (Friedman et al. 2012a).

Examples of coercive motivations vary but it is notable that sex-selective neonaticides in the developing world could be considered as adaptive in response to social coercion (Friedman et al. 2012a).

It is also not surprising then that step-parents (including both step-fathers and step-mothers) kill with different motives than biological parents. Fatal maltreatment of older children is notable for higher rates of step-fathers. This is also reflected in their methods of murder. Biological parents more often kill in rapid ways such as shooting or smothering whereas step-parents more often kill "accidentally" after chronic beating and or maltreatment (Weekes-Shackelford and Shackelford 2004).

Evolutionary psychology is thus helpful in establishing sets of patterns whereby some forms of parental child killing appear "predictable" and may be consistent with ancient cognitive processes that evolved in response to similar proximal selection pressures to those of our distant past. However other subtypes of parental child killings do not so obviously follow evolutionary principles.

Mental Illness and Infanticide

An analysis of parental child killing in humans from an evolutionary psychological lens enables us to conceptualize circumstances under which a parent killing their child may once have been an adaptive reproductive strategy, albeit in a prehistoric setting. Altruistic homicide, however, is something of a misnomer in evolutionary terms since there is no way a deceased child can directly pass on their genetic inheritance to offspring.

A nuanced consideration of this evolutionary conundrum could envisage loving parents making a reality-based assessment about relieving a child of severe pain or suffering. However, this decision would require a parent to be able to make an accurate and informed assessment of the child's suffering. Killing an older child, from a parental perspective, is a less sound evolutionary strategy. The degree of parental investment is significantly higher and, as a child ages so do the parents who

are generally older and with arguably less time to raise another child to adulthood.

It is interesting, then, that research supports increasing rates of mental health problems among parents of either gender in relation to killing older children. It is more probable that many of these parents develop nihilistic cognitive distortions in assessing the perceived circumstances of their child. They may, for example, misinterpret the extent of the environmental stressors or feel guilty as part of a depressive illness. Indeed, the further the circumstances of a filicide move away from an evolutionary informed prediction, the more likely there is to be a more florid failure of reality testing in the parent.

One could consider a hypothetical composite case of a 38-year-old professional woman, married with no other children. She has a university education and is wealthy and has a supportive extended family network and yet is found to have killed her 3-week old son in a bath.

There would be a little apparent adaptive advantage in this scenario although the mother in the vignette is a common presentation to mental health services with the onset of depression in the perinatal period. Clinical understanding indicates both depression and psychosis in the postpartum period can also result in psychotically motivated homicides. Predictably unpredictable, the nature of the delusional motivation of a woman with postpartum psychosis to kill their child may be so bizarre as to defy any rational analysis, let alone an evolutionary one.

Consideration of parental developmental disorders are also important as these too may lead to distortions in cognitive impressions and that may be relevant to child killing. Narcissistic-personality disorder has, for example, been noted as part of the parental psychology in cases of revenge killing. Low intelligence or intellectual disability may also potentially limit the capacity of the parent to consider and accurately evaluate the true extent of support or resource availability.

The suicide of a parent is particularly notable when older or multiple children are killed. Suicide has had a social function in some societies, such as Japan and Samoa, to defer stigma and shame from individual acts that may disgrace the wider family

and thus reduce their combined genetic viability. Some evolutionary theorists would argue this is then an adaptive behavior as way of protecting resources for an extended genetic heritage.

However, psychological autopsies on such parents are rare and are at best retrospective. Committing suicide after killing one or multiple biological children is such a devastating violation of evolutionary prediction, that these perpetrators are likely to have had elevated rates of serious mental illness.

Evolutionary Psychology on the Law, Science, and Medicine

Understanding that humans have evolved to have cognitive mechanisms that process and evaluate relevant environmental information has enriched our understanding of parental child killing. Identifying which individuals facing certain stressors in our contemporary environment that most resemble those of the past is essential in identifying those who are most at risk of killing and of being killed.

For neonaticides, and most filicides, the scarce resources are a common factor strongly implying a need for better social programs and support for parents. Similarly, the evolutionary risk of “poor quality offspring” is noted in physically and psychologically disabled children being at greater risk. More could be specifically put in place for parents of these children and clinicians should be aware of this potential risk.

Education for at-risk age groups could target sexually active teenagers in relation to primary prevention measures for unwanted pregnancies. Relationship awareness and parenting courses could potentially highlight the increased risk of step-parental violence and target more specific therapeutic or social assistance.

A key finding often overlooked in evolutionary theory is when things go awry. Rather than attempting to reconcile errant examples of child-killing with evolutionary theory, accepting the role mental illness can play in distorting prehistoric cognitive mechanisms within a modern setting is also informative. Early screening for

mental illness and substance abuse, and their appropriate treatment is paramount.

More recently, our understanding of the human genome and discoveries in field of molecular genetics have advanced our understanding still further. Informed by evolutionary theory, the field of epigenetics seeks to identify how early environmental conditions may variably affect complex molecular cascades leading to the expression of specific DNA sequences. The biochemical expression of these may predispose an individual to certain complex behaviors under certain conditions.

The implications of such research will continue to further help identify target groups and further interventions in the future. It no doubt also is of interest to clinicians in assisting society in the assessment of those parents charged with killing a child. An understanding of evolutionary principles can thus help a clinician judge what is often a fine line between cognitive reality, cognitive distortion, and delusion.

However, clinicians are only ever able to advise a court in relation to the possible motives whether they be aggravating or mitigating. When revisiting infanticide law at the end of this chapter, it is interesting to note that it mitigates and (at least partially) partially exculpates younger women who behave in way that evolutionary theory would predict, effectively younger mothers who kill their younger children.

Infanticide legislation does not include parents of either gender who actually kill due to mental illness, who tend to rely of defenses of legal insanity. Using evolutionary psychology as an explanatory model, it has been “argued that infanticide legislation is at best unnecessary and at worst misapplied, in that it exculpates criminal intent and fails to serve those for whom an infanticide defense might otherwise have been intended” (Friedman et al. 2012a, p. 585).

Conclusions

Where a society positions itself on this legal continuum is for that society to determine in light of

its own views on childbirth. However, it is certainly notable that most societies have a clear understanding of where a child homicide by a parent is considered a crime or not. Moreover, many societies have laws allowing the state to assist in the termination of an unborn child. The relative availability of legal termination to mothers, young or old, at risk of an unwanted pregnancy varies greatly and is an ethically and emotionally fraught topic.

Nevertheless, the act of parental child killing has been a stable expression of human behavior for millennia and its universality is expressed in a range of cultural archetypes over millennia. Perhaps more surprising however has been the persistence of a social acceptance of the behavior at least to some degree. The fact that at least our partial collective tolerance for infanticide under certain circumstances exists implicates us as holding complicit the same universal cognitive programming of shared evolutionary heritage.

Cross-References

- [Child Abuse](#)
- [Child Homicide](#)
- [Cinderella Effect, The](#)
- [Murder](#)
- [Parental Investment](#)

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Infanticide by Females

- [Infanticide in Nonhumans](#)

Infanticide by Males

- [Infanticide in Nonhumans](#)

Infanticide in Non-human Mammals

- [Infanticide in Nonhumans](#)

Infanticide in Nonhumans

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Synonyms

[Adaptive hypotheses of infanticide](#); [Counter strategies against infanticide](#); [Infanticide by females](#); [Infanticide by males](#); [Infanticide in non-human mammals](#); [Sexual selection hypothesis of infanticide](#)

Definition

A set of aggressive behaviors destined toward the elimination of younglings, usually a dependent infant or hatchling. The attacker often obtains a fitness benefit by targeting the offspring of conspecifics. Due to the costs associated with losing a youngling, parents often employ an array of physiological and behavioral tactics to decrease the risk of infanticide.

Introduction

Although nowadays research on nonhuman infanticide has lost most of its controversial nature,

three decades ago studies on this subject generated heated debate concerning the adaptive function of eliminating infants (Sommer 2000). Due to the costs associated with producing and rearing offspring, killing younglings was interpreted as a pathological behavior with no apparent adaptive benefits. This view considered that selection would favor the inhibition of lethal aggression against conspecifics, which, when observed, was the product of abnormal conditions. Adaptive hypotheses developed during the late 1970s and early 1980s contraposed the notion that infanticide was a pathology (Hrady 1979; Sommer 2000). The following sections provide an overview of these perspectives.

Adaptive Hypotheses on Infanticide

Sarah Hrady (1979) provided a detailed classification of infanticide based on its underlying adaptive function. Therefore, eliminating infants could be due to (1) exploitation, (2) resource competition, and (3) parental manipulation (4) or as an alternative sexual strategy. Infanticide is exploitative if the death of the infant provides a direct benefit to the attacker, such as in instances of cannibalism (Hrady 1979). Exploitative infanticide may also occur as a by-product of agonistic interactions in which an adult may sequester a youngling with the goal of decreasing the risk of experiencing aggression from a third party. However, in the process, the infant may die due to starvation or injury (Hrady 1979). Similarly, curious individuals mishandling the offspring, such as dominant members of the group, could also lead to unintentional infanticide.

Due to the finite nature of resources, some organisms may decrease the costs associated with agonistic interactions by killing vulnerable individuals. Conditions of intense resource competition may positively select for the occurrence of infanticide, with the attacker, and his kin, gaining access to resources and removing future rivals (Hrady 1979). Although aggressors could target both male and female infants, depending on the type of resource contested, the sex of the infant may increase the risk of being the target of

lethal aggression. For example, if females are scarce in the group, males should eliminate male infants, whereas if food is limited, females are predicted to kill female infants (Hrady 1979).

The third type of infanticide, parental manipulation, is observed when the costs of producing and rearing an offspring jeopardize the survival of the parent or its siblings (Hrady 1979). According to Hrady (1979), infanticide as a form of parental manipulation is associated with an array of socio-ecological conditions including resource scarcity, inhabiting high-risk environments, the presence of older siblings, or the inherent fragility of the infant due to morphological or physiological abnormalities. For Hrady (1979), this type of infanticide may also be the outcome of parental neglect. In some avian species, females are known to have more hatchlings than the number for which they are certain that can provide. Brood reduction functions as insurance against complete clutch failure such as during unpredictably dire ecological conditions (e.g., famines, droughts, or high predation risk; Mock and Forbes 1994; Mock 2004). It is not uncommon, however, for all hatchlings in a brood to survive under better environmental settings. The occasional resource scarcity imposes considerable costs on the parents that risk losing all offspring due to energetic and temporal constraints. In response, the adults allocate most of their resources to few younglings, such as first- and secondborn hatchlings, increasing the risk of the rest of the offspring dying due to weather exposure, disease, or starvation. In some species adults do not interfere when younglings attack their siblings (Mock 2004), blurring the line between siblicide and infanticide.

Hrady provided a fourth hypothesized adaptive function for the elimination of younglings. Observations conducted with eutherian mammals indicated that most of the individuals who killed younglings were males, and frequently the animals killed were infants. This pattern was hypothesized to occur due to the fact lactational amenorrhea reduces males' mating opportunities. By eliminating infants, males were able to restart the estrus cycle of females. Moreover, rather than avoiding the infanticidal male, the targeted female often copulated with the aggressor. Therefore, this

view often referred to as the sexual selection hypothesis, considered infanticide as an alternative sexual strategy.

Risk of Infanticide by Males in Nonhuman Mammals

Among the various socioecological factors, life history traits have been found to predict infanticide. The ratio between the lactation and gestation in eutherian mammals influences the presence of postpartum matings. Species with a gestation period longer than lactation will be more likely to exhibit postpartum estrus, facilitating postpartum copulations restricting the evolution of infanticide (van Schaik 2000). Although a longer gestation decreases the likelihood of infanticide, species with large litters may still be at risk of due to the negative association between the number of offspring and future reproduction (van Schaik 2000). Alternatively, species with a shorter gestation period relative to an extended lactation will be less likely to have postpartum estrus and have a higher risk of infanticide. However, clades with a prolonged lactation and short gestation can decrease the likelihood of infanticide if the species breeds seasonally (van Schaik 2000). A cross-species comparison revealed that infanticide by males in nonhuman primates exhibited a high lactation/gestation ratio (van Schaik 2000).

Counterstrategies Against Infanticide by Males in Nonhuman Primates

Since females are expected to invest more heavily in offspring production than males (i.e., parental investment hypothesis; Trivers 1972), according to the sexual selection hypothesis of infanticide, females should develop a series of counter strategies to decrease the risk of having their infants killed by male conspecifics. Females can therefore either confuse the males' paternity certainty or concentrate it on a single male (Palombit 2012). Concerning the former, confusing paternity is achieved through an array of behaviors and physiological changes such as mating with multiple

males, extending the estrous period, copulating before ovulation and after conception, and either concealing ovulation or increasing the advertisement of sexual receptivity (e.g., sexual swellings, vocal displays; Palombit 2012). Instead, physiological and behavioral correlates of paternity concentration include limiting the matings to the male most likely to protect infanticide, advertising sexual receptivity and ovulation to increase the likelihood of mate guarding, and copulating with the potentially infanticidal male (Palombit 2012).

Females could also modify their reproductive schedules to counter the risk of infanticide. For instance, they may block their pregnancy, accelerate the weaning period, synchronize the period of ovulation with that of other females, conceive while pregnant (i.e., superfetation; Palombit 2012), or abandon the infant (Palombit 2012). However, due to the fact physiological strategies are less flexible and plastic than behaviors, it is expected females should also display individual and social defenses against infant killings. Attacking infanticidal males, increasing the level of protectiveness and vigilance, as well as avoiding or distancing from the group, are among some of the individual reactions reported by the literature (Palombit 2012). In addition to responding by themselves, females had been known to employ social strategies such as establishing long-term aggregations, developing coalitions and alliances with other females, preferring small groups (therefore decreasing the risk of male immigration), and rejecting immigrant females to maintain the current group size (Palombit 2012). In addition to developing alliances with other females, mothers with infants can also establish relationships with protecting males (Palombit 1999). However, depending on the socioecology of each species, these associations can range from short-term coalitions to long-term bonds (Palombit 2012). Comparative phylogenetic examinations suggest infanticide and social monogamy coevolved across 230 nonhuman primate species (Opie et al. 2013), a result that not only draws a clear connection between the coevolution of social monogamy and infanticide, but it also calls into question the notion that biparental care preceded pair bonding.

Infanticide by Females

Infanticide by females, though considerably less common than infanticide by males (especially in eutherian mammals), has also been observed. According to Digby (2000), infanticide poses a considerable risk for younglings living in multi-female groups. For the author (2000), additional species-specific risk factors include the presence of altricial offspring, leaving the infant alone or unprotected, the physical proximity of infanticidal females, the presence of alloparental care, and the degree of power variation across individuals in the group. The benefits obtained by female as opposed to male perpetrators of infanticide fit better with the predictions made by the resource competition and the exploitation hypotheses. Parental manipulation is also hypothesized to be associated with infanticide by females, with young and subordinate mothers facing a life history trade-off of investing either in current or in future offspring. In cooperative breeders, killing the infants of subordinate females increases the likelihood of allocating resources and attention to the offspring of dominant individuals. Social systems in which there is active suppression of the reproduction of subordinate females, the costs of female dispersal are higher than remaining in the local group, and the dominant female holds a reproductive monopoly, increases the risk of infanticide by females (Digby 2000). Although sexual selected female infanticide also occurs, in most instances, this behavior is correlated with sexual reversals, wherein males invest more in parental care than females (some females of sexually reversed species also exhibit ornaments and armaments). By eliminating the offspring of other females, the perpetrator can obtain additional resources and care.

Conclusion

Even though initially infanticide in nonhuman species was interpreted as the product of pathological behavior, the current evidence supports an array of adaptive hypotheses wherein eliminating infants decreases resource competition, serves

nutritional purposes, buffers against the aggression of other individuals, and increases the fitness of relatives. Concerning nonhuman primates, the current evidence provides strong support for the sexual selection hypothesis. Some of the risk factors associated with infanticide in non-human primates are 1) a slow life history; 2) a lactation period longer than the gestation period, and 3) living in societies with high male reproductive skew. In response to this persistent threat, females evolved a repertoire of physiological and behavioral tactics, ranging from altering their reproductive schedules to developing coalitions and alliances with other females or resident males. Although, in eutherian mammals, males are often the perpetrators of infanticide, females may also eliminate infants to decrease future competition with other offspring.

Cross-References

- [Cinderella Effect, The](#)
- [Infanticide and Parenting](#)
- [Marital Status and Infanticide](#)

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- [Personality and Mate Poaching](#)
- [Seeking Extra-Pair Partners](#)
- [Sex Differences for Pursuing](#)
- [Sexual Jealousy](#)

Infidelity Risk

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Infection

- [Disease Avoidance Hypothesis](#)
- [Pathogen Risk](#)

Inferior Frontal Gyrus

- [Broca's and Wernicke's Areas](#)

Inferior Longitudinal Folliculus

- [Ventral Stream, The](#)

Inferiority

- [Downfall of “Tall Poppies”](#)

Infidelity

- [Evolutionary Psychology and Intimate Partner Violence](#)

Synonyms

[Adultery](#); [Extradyadic involvement](#); [Extradyadic sex](#); [Extra pair copulation](#); [Unfaithfulness](#)

Definition

The factors that increase the prevalence of infidelity within the context of exclusive relationships.

Introduction

Infidelity may include a broad range of behaviors depending on the perspective of the individual. Different behaviors from flirtatious acts, to emotional involvement, to sexual intercourse may or may not be considered infidelity. Although it may be hard to pinpoint infidelity with absolute precision, its negative consequences are easy to detect. Infidelity is related with negative health outcomes and is the most common reason for marital dissolution around the world. There are different factors that increase the risk of infidelity, and these factors that make people more prone to infidelity can be examined in three levels: personal level, relationship level, and contextual level.

Personal Level

Some individual differences are reported with a higher risk to engage in infidelity. One of the most consistent examples is gender. Although recent studies note that the gap is closing, men are still more likely to engage in infidelity than women (Treas and Giesen 2000). The personality of the individual is another factor. People with higher levels of neuroticism and narcissism are more likely to engage in infidelity (Fincham and May 2017; Whisman et al. 2007). In addition, people with insecure attachment are more likely to search out for alternative mates (DeWall et al. 2011; Russell et al. 2013).

Other than individual differences, the attitudes and experiences of the individual may also play a role in the risk of engaging in infidelity. It has been shown that permissive attitudes toward sexual interests and a general willingness to have casual sex are related to higher levels of infidelity (Treas and Giesen 2000). Moreover, people who have previously engaged in infidelity, who were exposed to parental infidelity, and who had had greater number of sexual partners before marriage are more likely to engage in infidelity (Fincham and May 2017).

Relationship Level

Infidelity can happen in any relationship, and relationship-related factors can play a role in infidelity. Yet, research investigating the risk factors of infidelity focuses primarily on the personal level. Therefore, relatively less is known about how relationship dynamics influence the likelihood of infidelity. Nonetheless, some studies have examined infidelity in the relationship level. Two of the main findings from the level of relationships are that sexual dissatisfaction and decrease in commitment toward the partner predict infidelity (Allen et al. 2005). Moreover, when a partner perceives threats internal to their relationship, such as partner's expression of criticism, they possess less sexual desire for their partner which in turn predicts greater attraction to

alternative mates (Birnbaum et al. 2019). In other words, thinking about moments when they felt intensely disappointed, hurt, or let down by their partner leads the ruminating partner to engage in more approach-related behavior like overt flirtation toward attractive, alternative mates.

Contextual Level

The people in the relationship and the relationship itself impact the risk of infidelity. But contextual factors also have the power to influence an act of infidelity. For example, traveling to another city is one of the contextual factors that increase the risk of infidelity. The number of days spent for work travel away is highly associated with infidelity since there is less risk of getting caught by one's primary romantic partner (Træen and Stigum 1998). Even if a partner is not travelling and staying in your location, you might be in a higher risk for infidelity depending on your location. It is shown that people living in warmer and urban areas are more likely to engage in infidelity. Lastly, people around the individual may also influence the risk in engaging in infidelity. Infidelity is more likely when individuals' peers also engage in infidelity or support their infidelity-related behaviors (Fincham and May 2017).

Conclusion

Personal, relational, and contextual factors discussed in this entry provide several lenses through which to understand the risk factors of infidelity. It should be noted that this entry focused on the factors that are related with higher infidelity risk. Yet, there are also factors that have been identified with lower risk of infidelity, for example, dyads who have similar characteristics (e.g., same religion, education level) and dyads in which both partners are employed are less prone to infidelity (Brooks and Monaco 2013). For more information on prevention of infidelity, see the entry by Sacco and Brown (2018).

Cross-References

- [Frequency of Infidelity](#)
- [Perceptions of Infidelity Cues](#)
- [Prevention of Infidelity](#)

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Infinite Capacity

- [Infinite Storage](#)

Infinite Storage

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Synonyms

[Infinite capacity](#); [Unlimited storage](#)

Definition

Infinite storage refers to the unlimited capacity that is assumed to exist for long-term memory.

Introduction

Long-term memory (LTM) has always been viewed as a rather distinct type of memory compared to short-term memory (STM) or working memory (WM), not only for its long-lasting maintenance of information but also because of its enormous capacity. It was always assumed that storage capacity in LTM is unlimited and thus one can remember an infinite number of things. Difficulties with memory capacity in LTM have usually been attributed to problems in encoding and not so much due to limitations in storage. In this section, the idea of infinite storage of LTM will be briefly discussed, in light of the latest research findings.

Infinite Storage: Is It Really?

One of the seminal papers in the history of memory research was published by George Miller in 1956, who estimated that STM has a limited capacity of seven plus or minus two digits or items, which meant that the range of STM capacity was between five and nine items. More recent studies argue for an even smaller capacity, at least for visual information, of around four items (Brady et al. 2011). Interestingly, the capacity of

STM or WM rather is strongly associated with performance in cognitive tasks and intellectual capacity in both animals and humans, and luckily, it seems to improve with practice (Constantinidis and Klingberg 2016). Despite the possibility of increasing the capacity of WM, it is still greatly limited and in no way its capacity can be compared to that of LTM.

LTM is believed to have infinite capacity for memory storage although nobody has been able to measure it. It is likely that the capacity is very large. Brady et al. (2008) evaluated the capacity of visual LTM and found that even subtle differences in visual stimuli were remembered by the participants who showed good recognition for 2,500 objects. It is logical that larger memory capacity may be more advantageous compared to smaller memory capacity. Perhaps practice in a particular domain may be important (Constantinidis and Klingberg 2016) but genetics probably also plays a significant role (Montag et al. 2014).

Storage of information in LTM can be viewed in terms of concepts or nodes that are interconnected in the brain, as it is proposed by the spreading activation networks, emphasizing the connections established during learning (Collins and Loftus 1975). It turns out that there is tremendous capacity to retain information learned and that is indeed reflected in the brain by increased branching and synapses in the neurons involved, known as the physical traces of memory or engrams (Tonegawa et al. 2015). People who are highly skilled in certain domains seem to have larger brain areas that support those skills, suggesting increased dendritic branching and synapses associated with that knowledge, compared to people that may lack that level of training as documented in musicians, for example (Schneider et al. 2002). So, if memories have a physical trace, can it be that a maximum capacity can be reached, when one may no longer remember more? Can there be such thing as infinite storage if the nature of the stored information is physically coded?

The hippocampus may help to answer the above questions and enhance our understanding

as to what may be happening in other areas of the brain, when it comes to increasing knowledge in a limited space. Recent studies suggest possible mechanisms through which the infinite storage of LTM may be possible. It is well accepted that following learning, the new information is stored for longer-term use through the process of consolidation which renders newly learned material permanent, at least until the next retrieval (Tonegawa et al. 2015).

Most studies have looked at hippocampus-related memories and showed that consolidation initially takes place in the hippocampus and then the information is dispersed to other areas of the neocortex, which were involved during the encoding phase (Davis and Zhong 2017). In addition, a specific pattern of neuronal firing emitted from the hippocampus during slow-wave sleep (SWS) known as sharp-wave ripples (SWR) seem to weaken the synapses between hippocampal neurons which encode old memories but not those which encode newly learned information (Norimoto et al. 2018). Thus, instead of considering LTM as an infinite storage capacity construct, LTM should be instead redefined as a construct involving not only the hippocampus but also numerous areas of the neocortex which themselves become the hosts of memory traces. In addition, the capacity never reaches maximum capacity due to the fact that there are processes in place that actively pursue the elimination of memory traces which are thought to be unnecessary or redundant (Davis and Zhong 2017).

Thus, although the findings regarding the aspects of LTM which have to do with its infinite ability to store information are very exciting, there is still a great deal of work to be done in order to fully understand the nature of this infinite capacity in regards to the different types of memories, different animal species, and the molecular players involved in both enhancing memories and erasing memories. So far, it seems that LTM can maintain this condition of “infinite storage” because it may be very selective. Moreover, given that memories are dispersed throughout different areas of the brain, its capacity can indeed be quite enormous.

Conclusion

It turns out that the idea of infinite storage of LTM is indeed true but not because our brains can expand endlessly. It is because the brain is equipped with mechanisms which allow itself to delete information and create space for new learning. So, in principle, there is no limit in what may be learned and memorized. LTMs which are judged to be important will be saved at the expense of other bits of knowledge that may be lingering without much use and thus will be erased. The infinite storage is made possible, not because of a truly unlimited space but an efficient system which makes the most of a limited space, the hippocampus and the brain as a whole, and an amazing ability to adapt to a changing environment. Decisions on what information is important and thus should be saved and which information is useless and thus should be deleted are made constantly, especially during sleep, throughout life.

Cross-References

- [Encoding and Sleep](#)
- [Episodic Memory](#)
- [Long-Term Memory](#)
- [Multiple Memory Systems](#)
- [Working Memory](#)

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Influence

- [Dominance and Territory](#)
- [Manipulation and Dishonest Signals](#)

Informal Leadership

- [Higher Status in Group](#)

Information About Likely Combat Success

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Synonyms

[Combat](#); [Deception](#); [Overconfidence](#); [Performance enhancement](#); [Sex differences](#); [War](#)

Definition

The same psychological strategies that often lead to unnecessary war may often prevent war as well

when overconfidence and bluffing encourage others to back down rather than fight.

Introduction

If both sides in combat made accurate assessments of their likelihood of success, war should not have to occur at all from a classical economic notion of rationality. If one side believes it is going to lose, it should not fight unless attacked but rather should make accommodations to the dominant side that preserve more life and treasure than would likely be lost in war. However, given the endemic nature of war, such accurate calibration clearly does not take place much of the time. But if that is the case, then the puzzle for evolutionary models is why so many people make so many mistakes so much of the time in making decisions about their likelihood of victory in combat. In other words, as Wrangham (1999) asked, “Is military incompetence adaptive?” This is plausible once observers realize that the same strategies that often lead to unnecessary war may often prevent war; those cases of the dog not barking in the night are not observable and thus hard to measure objectively. But if fitness gains accrue differentially to those who manage to win without fighting by employing these strategies more often than having to fight and losing, it is possible to see how such strategies might be preserved. And indeed some evidence in support of this hypothesis exists.

Standard Explanations from a Rationalist Perspective

There are several standard explanations for war from a rationalist perspective that have been and can be dismissed. And evidence exists for the operation of some adaptive mechanisms that inadvertently lead to systematic and even predictable errors in judgment under some specific environmental and ecological conditions. In addition, since we would expect combat to have been largely differentiated by sex across millennial time, the appearance of these biases should occur more in men than in women, and indeed this appears to be the case, in a process facilitated if not instigated by, specific hormonal pathways.

Several models in political science argue that war can occur within the context of an economically defined notion of rationality. In perhaps the most influential of these arguments, Fearon (1995) argues that state leaders can make rational miscalculations, often due to lack of information. He suggests that this can result from a number of causes including commitment problems; difficulties dividing up seemingly indivisible issues, such as sacred territory; and access to private information, such as when one side has information the other sides does not, such as number or quality of weapons, and the incentive to withhold or misrepresent this information. Other arguments from within a rationalist framework make similar arguments based on the notion that leaders wish to stay in power and often they can facilitate that goal, even at great cost to their population, by initiating war (Bueno De Mesquita et al. 2005). Although these models remain influential in political science and the study of international relations, they can be criticized for numerous failings, not least, the conflation of individual decision making with state level outcomes, as well as their failure to align with empirical demonstrations of individual decision-making strategies and biases.

Potential Sources of Adaptive Military Incompetence

Richard Wrangham’s (1999) framing of the question regarding the value and utility of seeming military incompetence allows for a deeper investigation into the reasons why such behavior might have emerged and persisted. In his original work, he discounted contrary explanations that focused on individual stupidity, psychological maladjustment, or cognitive limitations to explain decisions that result in inaccurate assessments of the likelihood of success in combat. Importantly, he provided a critical distinction between raids, where assessments tend to be accurate, and therefore costs are low, and battles where assessments are often inaccurate, and therefore costs are often high. He proposed two possible explanations for this latter miscalculation: (1) performance enhancement, wherein negative perspectives are suppressed, as, for example, might occur when one side underestimates the

quality of the other sides' warriors and (2) opponent deception through bluffing. Subsequent work by Johnson et al. (2002) provided empirical support for the latter hypothesis using data from the US Historical Evaluation Research Organization.

Opponent deception hypothesis rests on the notion that positive illusions can serve an adaptive function. Opponent deception may be most successful when leaders are able to deceive themselves as well; this kind of self-bluffing proves particularly effective because it reduces the risk of behavioral leakage, whereby observers can see that the leader is faking. Such overconfidence also saves the energy that self-deception might require, thus freeing additional resources for labor recruitment or combat itself. Highly confident leaders may be able to recruit more labor from fence sitters because they convey a feeling of inevitable victory, and everyone likes to be on a winning side where they can derive benefits from the gains of victory. More importantly, opponent deception may scare off the opponent without having to fight at all, or may deter potential aggressors from instigating a fight they fear they may not win.

Thus, opponent deception may prove adaptive in several different ways. Before the emergence of the militarized threshold, victory in combat was secured largely through size and surprise, although some element of superior strategy may have helped as well. But if leaders could increase the size of their following through overconfidence, they would be more likely to prevail in actual combat. In addition, if they could prevent opponents from attacking or get inferior powers to acquiesce without fighting through successful bluffing, then fitness gains would accrue to those who possessed such tendencies, even if some percentage of the time, resulting combat led to many deaths.

The role of overconfidence in triggering war and the consequences of positive illusions in instigating conflict have been explored in depth in Johnson (2009). In their work on the evolution of overconfidence, Johnson and Fowler (2011) present a model showing that overconfidence maximizes individual fitness, thus leading to its prevalence in populations despite the obvious costs. They showed that as long as the benefits of scarce or disputed resources outpaced the cost

of competition, overconfidence would remain a stable strategy. This can happen, for example, because overconfident people may be able to get others to back down without a fight, securing resources without cost. In addition, overconfidence can often encourage followers to join, thereby increasing numbers and making victory more likely. By contrast, they also demonstrated that more economically rational models remained robust under much more limited conditions.

Sex Differences

An additional important consideration has to do with the sex-specific nature of these occurrences. Women would be more likely to place a higher premium on their physical safety because in the environment of evolutionary adaptation, children required more investment from mothers than fathers in order to survive (Campbell 1999). According to Campbell, the evolved mechanism designed to secure the greater safety of women, in part by reducing their own aggressive behavior, involved a lowered threshold for fear in the face of activities that risked physical injury. By contrast, men, particularly low status ones, may have been able to secure greater reproductive access by achieving success in battle, either through obtaining resources such as livestock, bride capture, or simply as a result of higher status.

Work which has examined the characteristics of these sex differences in positive illusions in the context of simulated war games investigated some of the conditions that might prompt or prohibit aggression (Johnson et al. 2006). In these studies, individuals were overconfident in general in their expectations of success, although men vastly more so than women. Interestingly, those who were more overconfident were more likely to attack their opponents, even if they had not been attacked first. Finally, testosterone levels did seem to be predictive of expectations of success, suggesting at least one potential hormonal pathway by which overconfidence and beliefs about success might be endogenously generated. However, these differences only explained the divergences between men and women and not the differences that emerged within each sex, suggesting that hormones

alone do not mediate the entire process, although they may contribute to differences between the sexes. As these authors conclude:

[O]ur key finding is that males were overconfident; and males who *were* more overconfident were *more likely* to launch wars. This remains a concern irrespective of its origin: overconfidence among decision-makers may increase the chance and/or costs of war because it leads to inflated estimates of success – not necessarily of winning outright, but of likely performance, the costs involved, vulnerability to risk, and the ability to control events if things go badly. (2518, italics in original)

In addition, narcissism predicted both overconfidence and unprovoked attacks in males. In this study, one of the interesting findings related to changes in assessments that men and women made after they received feedback about their performance in the wargame. At the outset, everyone was asked how likely they thought it would be that they would win relative to everyone else who played. Men proved vastly more confident in these assessments than women. After they played their game, each person had some direct and immediate feedback about their performance relative to at least one other person: their opponent. When asked after they received this feedback, sex differences in perceived performance also changed differentially. Men who had won their game vastly increased their assessments, whereas men who lost only slightly downgraded their evaluations. By contrast, women who won only slightly increased their perceived rankings, if at all, while women who lost drastically decreased their sense of their overall performance. This matters because past experiences help condition future expectations and behaviors. Men who become more confident after small victories then prove more likely to attack in the future, raising prospects for overall conflict.

Conclusion

Assessments about likelihood of victory are important because most individuals would be loath to launch an attack they believe they will lose, although most would certainly be prepared to defend against an unwanted attack, highlighting the importance of offensive versus defensive contexts in undertaking combat. But the information

that goes into calculating these expectations of victory is not as straightforward as it may seem. Like many other biases in human judgment and decision-making, the biases that lead to overconfidence, particularly in men, may, counterintuitively, be adaptive. Overconfidence can spur the ambivalent to action, bluff and bully the weak or scared into submission, and provide valuable benefits at lower cost on average. Various hormonal and experiential pathways may help precipitate these actions, beliefs, and behaviors. However, these inclinations in information calibration seem to apply more strongly to men than to women, precisely because the damage wrought by physical injury to women exerted higher fitness costs than on men.

Making accurate assessments of the likelihood of success in combat constitutes only one of several factors that may go into decisions about going to war, along with the other variables such as the nature of the risk and threat, the potential benefits to both leaders and followers, and the expected costs. The expectations of success influence most heavily these assessments of relative costs, but from an evolutionary perspective, such costs cannot be determined exclusively according to immediate costs, either financial or physical, but must also be analyzed in terms of the long-term consequences of overconfidence on fitness outcomes.

Cross-References

- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Contexts for Men's Aggression Against Men](#)
- [Male Adaptations That Facilitate Success in War](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Sex Differences in Same-Sex Aggression](#)

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Information Age

- [Loneliness in Modern Life](#)

Information Exchange

- [Communication, Cues, and Signals](#)

Information Processing and the Interdisciplinary Perspective

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Synonyms

[Computation](#); [Computer metaphor](#); [Instructionist](#)

Definitions

Information – A statistical measure of uncertainty involved in the selection of a communicative message in a particular situation (Weaver 1949); a measure of unpredictability of which of a set of possible messages is selected or transmitted by an information source.

Information-Processing – a set of instructionist models of brain and cognitive activities that assume meaningful (communicative) environmental stimuli instruct internal, brain-based, algorithmic programs on how to build or organize an adaptive response to environmental stimuli.

Introduction

Biological and cognitive psychologists rely heavily on the concepts of information, information-processing, and symbolic representations to describe neurocognitive activities; they seldom consider brain activity in other ways (Epstein 2016). Unfortunately, when an idea or paradigm becomes orthodoxy, it stops us from asking questions that could lead to more productive theoretical conceptions of neurocognitive activities (Brette 2019; Epstein 2016). The present entry describes the use of information-processing terminology in Psychology, acknowledging its descriptive utility, but describes problems with regarding information and information-processing as causal explanations of bio-psycho-social events. It also outlines a proposal that brain systems and behavior work by selectionist rather than information-/instruction-based processes (Edelman 1987).

Information Is Distinct from Meaning and Often Reified in Psychology

Psychologists sometimes reify “information” and treat it as a concrete, meaningful mechanistic explanation, anchored in physical (environmental, biological, and biochemical) causality. But, confusing *information* with the *meaning* of individual communicative messages, or with the knowledge contained in messages, is misleading (e.g.,

Weaver 1949). Information, in the Shannon-Weaver sense, is a *statistical description* of uncertainty regarding the “choices,” from a set of possible options, a receiver makes from a meaningful message:

The concept of information developed in this theory at first seems disappointing and bizarre-disappointing because it has nothing to do with meaning, and bizarre because it deals not with a single message but rather with the statistical character of a whole ensemble of messages, bizarre also because in these statistical terms the words information and uncertainty find themselves partners. (Weaver 1949, p. 14)

Because information in the Shannon-Weaver sense is a *statistical-mathematical* description, not a *mechanistic* explanation of events, “information-based models” are only a descriptive step toward models of biological *mechanisms*. Reified “informational” descriptions focus attention on attempts to understand a statistical invention that summarizes and describes, but does not explain, physical mechanisms. Because this sense of information is neither meaning nor a message containing one meaning, reified physical “copies” (e.g., neurally coded symbols/representations computationally manipulated) of environmental information held and processed in the brain mislead biological explanations of neural activities. Similarly, with respect to biology, Wilkins (2009, p. 1) argued:

...“information” is a homonym for a range of distinct notions, and that these notions are either of concrete properties, in which case they are little more than a periphrasis for correlation and causation, or of abstract properties, in which case they are observer-dependent. In short, if information is in the concrete world, it is causality. If it is abstract, it is in the head.

Though Useful, Information-Processing Models Aren’t Necessarily Correct Descriptions

Information theory is often instantiated within an information-processing approach to produce descriptive models of natural phenomena (e.g., human thinking). Tooby and Cosmides (1992) and Pinker (1997; 2009) wedded Evolutionary

Psychology to an information-processing approach that relies on at least three ideas: (1) despite obvious physical (and other) differences, “...brains and computers embody intelligence for some of the same reasons,” (2) our brains are *processors* of symbols that “carry information,” and (3) a set of complicated computer-like programs (complex sets of instructions/algorithms), sculpted by natural selection, produce human thinking and behavior (Pinker 1997).

Information-processing “programs” are sometimes taken literally, not metaphorically. For example, Cosmides (see Monticello and Gillespie 2015) stated:

...behavior is generated by programs in your head, and I don’t mean it metaphorically—devices that are designed by natural selection to process information and guide your behavior. Evolutionary Psychology focuses on that intermediate step of what’s the structure of those programs. And without understanding that, all you can have is sort of fuzzy relationships between insights about selection pressures and behavior as opposed to a real science of the mind.

Following assumptions of information-processing theorists, Tooby and Cosmides (1992) write:

Much of great interest can be learned by investigating the brain in neurobiological terms, but its adaptive dimension will remain invisible unless and until its mechanisms are described in a language that is capable of expressing its informational functions.

By their perspective, studying the physical properties of the brain isn’t likely to help us understand the “...functional structure of the brain” as well as an information-processing-based description can (Tooby and Cosmides 1992, p. 66). In short, although the brain is organized around physically instantiated, algorithmic programs, direct study of brain activities isn’t particularly helpful in developing descriptions of adaptive algorithms.

But, neuroscientists do attempt to study the physical implementation of information-processing concepts like neural-coded representations or memory engrams. If the brain is organized around physical information-processing devices, we should discover how information-processing programs are physically instantiated and how

brains represent “information” (the *meaning* of symbols) at each step of cognition. Some are troubled by the approach. Brette (2019) writes “[the] neural coding metaphor is a way to think about the brain that is disconnected from its causal structure” because brains are dynamically coupled with the environment, neurons are dynamically coupled to one another through timed spikes, and the neural coding idea implies “...that one part of the brain can be understood independently of the way it interacts with the rest of the brain” and the way it interacts with the environment. Furthermore, he argues “...the causal structure of the neural coding metaphor is incongruent with the causal structure of the brain” and “...cannot form a valid basis of a theory of brain function” because “...coding variables are extended measurements of activity linked to the temporality of experiments”, not “...causal variables of the underlying dynamic system.” This suggests that reified information-processing concepts (e.g., neural codes) misdirect proper brain theory: Neural “codes” may not be physically instantiated at all.

Abstract Meaning of Environmental “Information” Is in the Head

Pinker (1997; 2009) defines information as “...a correlation between two things that is produced by a lawful process.” When we consider “information” as a statistical description or a lawful correlation, however, it behooves us to avoid reifying “external” information as independent of a receiver with the mental capacity to generate (perceived) meaning.

In contrast to objective “information,” meaning/knowledge is the *perceived* structure of the surrounds and associated adaptive problems. The existence of meaning/knowledge depends on the biological and experiential nature of the receiver/interpreter. Although information may carry meaning, meaning (1) is independent of the carrier, and (2) cannot be derived from the carrier alone. Hence, meaning/knowledge is a *theoretical* term referring to pre-action use and something an organism makes/creates only

partially from the structured physical information carrier. To achieve meaning, from an information-processing perspective, an organism’s brain machinery must decode novel information in ways that create meaning for adaptive action (Ittleson 2017). Claiming that thoughts are internal representations, Pinker (1997; 2009) argued that talk of homunculi that “read” and “interpret” data structures is common in computer science, but “the homunculus that ‘looks at it’ is not a miniaturized copy of the entire system, requiring its intelligence” and “...each homunculus is required only to react in a few circumscribed ways to some of the symbols” (p. 79), so these “interpreters” are “mechanical” devices that do not require the intelligence of the whole system (p. 79).

Edelman’s Theory of Neuronal Group Selection Rejects Information-Processing

Edelman (1987) rejected information-processing (instructionist) approaches to brain organization/function in favor of a selectionist approach. He argued information-processing approaches, problematically, require precise algorithmic programs and an environment that is organized for objectively “meaningful” categorization, independent of the individual interpreter. In Pinker’s (1997) terms, “A computer is the most legalistic, persnickety, hard-nosed, unforgiving demander of precision and explicitness in the universe.” But, given that environments constantly change in novel and unanticipated ways, precise *pre-prepared rule-bound algorithmic programs* are not equipped to deal with novel or unexpected environmental change:

How and where are “programs” constructed capable of context-dependent pattern recognition in situations never before encountered? Processors of information must have information defined for them *a priori*, just as the Shannon measure of information (see Pierce 1961) must specify *a priori* an agreed-upon code as well as a means of estimating the probability of receiving any given signal under that code. But such information can be defined only *a posteriori* by an organism (i.e., the categories of received signals can be defined only after the signals have been received, either because of

evolutionary selection or as a result of somatic experience). It is this successful adaptive categorization that constitutes biological pattern recognition. In assuming the existence of informational categories in the environment or of computational programs in the brain that can produce a broad range of plastic adaptive behavior, information-processing models are forced to take a position similar to the argument of creation from design, which dominated pre-Darwinian thinking about species (Mayr 1982). Edelman (1987, p. 43)

When we reify information-processing programs, we imagine information and natural processors of it to be anchored in biological reality. Edelman's argument suggests such "programs" are anchored only in researchers' meaning-filled heads.

A strength of a theory of natural selection is that it provides an explanation of the functional adaptedness of organisms to their environmental conditions *without* the need to invoke an intentional "planner" *guiding* the design of organisms, without an entity *teaching organisms through instructions* about how to regulate their features to overcome adaptive problems. Selection, over evolutionary time, proceeds *without the environment "programming" (i.e., transferring instructions ("meaning")* the organism. Thus, we shouldn't expect organisms to possess machinery that deciphers and responds appropriately to informational messages about how to best adapt to novel environmental changes.

Edelman's "Neural Darwinism" permits environmental features (through epigenetic rules, which are useful descriptive inventions) to *select* from evolutionarily prepared "contents" of human (neural) nature during proximate developmental time. This contrasts sharply with an approach claiming the environment *instructs* and/or rearranges neural wiring based on built-in programs and their interpretation of environmental information.

Conclusion

Information and information-processing talk is used by thinkers in various fields attempting to explain the organization of cognition and behavior. Some find this terminology indispensable for

descriptions of neurocognitive mechanisms and for a rigorous Evolutionary Psychology (Tooby and Cosmides 1992; Pinker 1997). But, reifying information creates a dualistic system of explanation. Although useful for describing regularities in how brains respond to stimuli, an information-processing approach is a potentially misleading biological explanation. A search for "information," "programs," "symbolic representations," or "sets of instructions" in the neural tissue might be replaced by a search for physical causation in that tissue (Wilkins 2009). Selection, not instruction by or information transfer from the environment, shapes biological adaptations. Since natural selection rejects an "informed" programmer that builds adaptations over evolutionary time, it's plausible that the brain evolved to operate, in proximate time, by principles analogous to natural selection (Edelman 1987).

Cross-References

► [Selectionist Models: Implications for Behavior](#)

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Information Theory

► Psychological Determinism

Ingredients of Reciprocal Altruism

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Synonyms

Cooperation; Reciprocity

Definition

A mutually beneficial exchange of goods or services.

Introduction

The term “reciprocal altruism” was introduced by Robert Trivers in his seminal 1971 paper to characterize exchanges of goods or services between two or more unrelated members of the same or different species that increase the fitness of each partner to the exchange. Trivers’ (1971) paper had a great deal of impact on the field of evolutionary biology because it offered an explanation for the evolution of altruism that could not be accounted

for by kin selection. However, the term reciprocal altruism is ambiguous. Although the proffering and reciprocation of goods and services by each member of a reciprocal exchange may be considered altruistic because actors suffer costs to bestow benefits on recipients, the ultimate effect of the exchange is biologically selfish when it produces a net gain in fitness for both participants. Adaptations that enable such exchanges have evolved because they have produced return benefits that increase participants’ fitness. Reciprocal altruism may best be viewed as a form of return-benefit mutualism (+/+ vs. −/+).

Reciprocal Altruism in the Animal Kingdom

In his 1971 paper, Trivers cited cleaning symbiosis and warning calls in birds as examples of reciprocal altruism, and suggested that reciprocal altruism was prevalent in the human species. Among the best-documented reports of reciprocal altruism in other species are those of Hart and Hart (1992), who found that impalas engage in alternate grooming, and Wilkinson (1990), who found that vampire bats are more likely to regurgitate blood for nonrelatives who have regurgitated blood for them than they are to help nonrelatives who have not helped them. In addition, primatologists reported observations of chimpanzees engaging in calculated forms of delayed reciprocity. The chimpanzees remembered who helped them, kept track of whether they owed or were owed by other members of their troupes, and repaid them – either in the same currency or in some other currency. For example, de Waal and Luttrell (1988) found that chimpanzees helped members of their groups who had helped them in agonistic exchanges (“one good turn deserves another”) and aggressed against group members who had sided with others against them (“an eye for an eye”). These researchers also found that the probability of chimpanzees sharing food with other members of their groups increased when these members had groomed them earlier in the day. With respect to the human species, Tooby and Devore (1987) included ingredients of reciprocal

altruism among three of the 15 unique hominid characteristics displayed by early humans.

Following the publication of Trivers' 1971 paper, there was a general expectation among biologists that reciprocal altruism would be prevalent in the animal kingdom, but this did not turn out to be the case. Although some biologists reported incidents of reciprocal altruism in non-human species, the prevalence of this form of conduct was lower than expected, and critics questioned whether many of the exchanges of goods and services that researchers classified as reciprocally altruistic met the criteria for reciprocal altruism, suggesting for example that they might be more appropriately classified as byproduct mutualism (Dugatkin 1997; Hammerstein 2003). In his early paper, Trivers (1971) suggested that reciprocal altruism should be prevalent in the human species because early humans satisfied such preconditions for its evolution as "long life span; low dispersal rate; life in small, mutually dependent, stable social groups . . . and a long period of parental care" (p. 45). Such conditions increase the probability that individuals who help others will encounter them in the future and receive goods and services from them in return.

The Structure of Reciprocal Altruism

To engage in reciprocal altruism, two or more members of the same or different species must behave in ways that increase each other's fitness. Participating individuals play two roles: donor and recipient. Individual A donates fitness-increasing goods or services to Individual B at a fitness cost to himself or herself, and Individual B donates fitness-increasing goods or services to Individual A at a fitness cost to himself or herself. Although two or more individuals may donate goods or services to one another simultaneously, most incidents of reciprocal altruism involve a delay: Individual A, in the role of donor, suffers a cost to proffer a benefit to Individual B, in the role of recipient, then Individual B (now the donor) repays Individual A (now the recipient). Although two or more individuals can gain significantly more

fitness-increasing benefits by engaging in reciprocal altruism than they can by failing to reciprocate, there are significant obstacles to the evolution of reciprocal altruism. One pertains to the origin of adaptations mediating the exchanges. How could donors acquire adaptations to make the first costly helping overture, and how could recipients acquire adaptations to suffer the immediate costs of reciprocation? The second obstacle pertains to the temptation to cheat and engage in free-riding. How could individuals acquire adaptations that induce them to resist the temptation to receive without reciprocating or to take more than their share and give less in return?

Ingredients of Reciprocal Altruism

The main ingredients of reciprocal altruism are (a) exchange partners, (b) goods and services, (c) giving and receiving, (d) costs and benefits, (e) gains in trade, (f) strategies, (g) direct and indirect returns, (h) antidotes to cheating, and (i) group contexts.

Exchange Partners

To engage in reciprocal exchanges, individuals must have one or more partners. The range of potential partners may vary across species and within species at different times and in different places. In some contexts, individuals have virtually no choice of partners, whereas in other contexts they have a wide range of choice. Investigators have found that partner choice favors cooperation in such species as yucca moths, fig-wasps, and clearer fish (Dugatkin 1997). Potential partners may vary in their capacity to maximize the benefits of recipients. It is in individuals' interest to select dependable and generous partners who possess resources of value to them and who are most likely to pay them back and to maximize their benefits. The ability to select and reject partners, as well as the value of forming long-term partnerships and friendships with members of one's group,

probably played an important role in the evolution of reciprocal altruism in the human species (Tooby and Cosmides 1996).

Goods and Services

The types of goods and services that are reciprocated in the animal kingdom pertain directly or indirectly to survival and reproductive success. The main goods that are exchanged are the types of food consumed by the species in question – for example, meat, grubs, worms, eggs, ectoparasites, and blood (e.g., in vampire bats). Among the most prevalent services exchanged are protection and defense, coalitional support, mating privileges, and grooming. Individuals may exchange the same or different goods or services. For example, chimpanzees engage in reciprocal grooming and exchange grooming for food and coalitional support (de Waal and Brosnan 2006). The range of goods and services exchanged in the human species is vastly larger than the range in any other species.

Giving and Receiving

Reciprocal altruism consists of giving and receiving, which may vary in terms of the number of exchanges individuals have with one another, the time interval between giving and receiving, and the balance of giving and receiving.

Number of exchanges. Individuals may engage in one-shot exchanges of goods and services or in a large number of successive exchanges. The number of exchanges engaged in by reciprocating partners may have a significant effect on the form of the interaction and the evolution of reciprocal altruism because, as demonstrated in game theory research using the Prisoner's Dilemma, the optimal strategy in one-shot exchanges is to behave selfishly, whereas the optimal strategy in repeated exchanges is to cooperate. The source of this difference lies in the costs experienced by selfish individuals who are treated selfishly or rejected as partners in future exchanges. However, when

individuals anticipate that they will engage in a finite number of exchanges and are able to predict the final exchange, each individual may anticipate that his or her partner will fail to reciprocate in the final exchange and decide not to reciprocate on the second to last exchange, and so on back to the first exchange, precipitating the disintegration of the reciprocal relationship through backward induction.

Timing of giving and receiving. Individuals may exchange goods and services simultaneously or after delays that range from moments to years. For example, primates may groom one another simultaneously or sequentially. Impalas groom one another in short bursts (Hart and Hart 1992). Humans engage in both simultaneous (giving with one hand; taking with the other) and sequential forms of reciprocity. It is unclear whether strict or flexible patterns of alternation affect the evolution of reciprocal altruism in nonhuman animals (Dugatkin 1997).

Balance of giving and receiving. In most types of reciprocally altruistic exchanges givers and receivers reverse roles at some point in time. Individuals may give goods or services worth the same as, more than, or less than they receive. In delayed exchanges, individuals may require repayment of the goods or services they proffer to their partners in a particular exchange before engaging in subsequent exchanges, or they may donate two or more times before receiving anything in return. Game theorists have found that generous forms of reciprocal altruism such as Two Tits for One Tat may pay off better than strict Tit for Tat forms of exchange (Nowak 2006). As pointed out by Tooby and Cosmides (1996), it can be in individuals' adaptive interest to give hundreds of small low-cost favors to a dependable recipient in return for one high-value life-saving favor, and we know that humans may be willing to assist friends and loved ones for many years as long-term investments without receiving anything equivalent in return. Some theorists have posited that cognitive abilities such as long-term memory and the ability to keep records of giving and receiving – abilities prominent in the human species – favor the evolution of reciprocal altruism (Hauser et al. 2009).

Costs and Benefits

The value of the goods and services exchanged in systems of reciprocal altruism are reckoned ultimately in terms of contributions to fitness, which often are difficult to document and quantify. Some researchers have suggested that it is especially difficult to assess reciprocal altruism when the goods and services that are exchanged are dissimilar in nature because it tends to be more difficult to determine the fitness value of different currencies than the fitness value of the same currency (Seyfarth and Cheney 1988). However, it also may be difficult to assess the fitness value of similar goods or services because the value of the same item (e.g., an ounce of meat) may depend on the recipient's state (e.g., of hunger), available alternatives, opportunities for better deals, and so on (de Waal and Brosnan 2006). The same principles pertain to the costs of giving.

Gains in Trade

The primary way in which reciprocal exchanges pay off for two or more individuals is through gains in trade. Consider two individuals who possess more goods than they can consume themselves. One individual might possess a large quantity of meat that will soon rot and the other individual might possess a large quantity of fruit. When these individuals engage in an exchange of resources, each can come out ahead because the benefits to both individuals of receiving the goods they need more outweigh the costs of giving the goods they need less. The same principle may apply when individuals trade sex for food ("prostitution") and when individuals exchange the same resource at different points in time. For example, when two vampire bats trade a surplus of blood that they don't need to survive at one point in time for blood that they desperately need to survive at another point in time, they both gain in trade.

Strategies

Evolutionary theorists have assumed that individuals who engage in reciprocal exchanges of goods

and services adopt behavioral strategies (which need not be conscious), and game theorists have played a variety of strategies off against one another in simulations of natural selection to determine which strategies will evolve under particular conditions. The best-known examples are the original games created by Axelrod and Hamilton (1981) using the Prisoner's Dilemma in which the reciprocally altruistic strategy called Tit for Tat won. Subsequent simulations found that more flexibly cooperative strategies that were equipped to ward off unending iterations of selfish exchanges and restart reciprocally altruistic exchanges – strategies such as Tit for Two Tats, Generous Tit for Tat, Contrite Tit for Tat, Win-stay, Lose switch, and Firm but Fair could defeat strict Tit for Tat strategies and evolve (Nowak 2006). This research demonstrated that in order for reciprocally altruistic strategies to defeat other strategies, they must be conditional, discriminating, and resistant to cheating. Follow-up research found that more than one strategy may evolve and become evolutionarily stable in some populations, that strategies may fluctuate in populations in frequency-dependent ways, that the ability to discriminate between cooperative and uncooperative members of groups and the ability to identify, avoid, and punish cheaters can facilitate the evolution of reciprocally altruistic strategies.

Direct and Indirect Returns To sustain reciprocal altruism, helping another individual must somehow contribute to the helper's fitness. In nonhuman animals, the return benefits are usually proffered by the recipient of the altruistic overtures. The exchanges that occur in food-sharing and grooming constitute examples. This type of reciprocal altruism is referred to as direct or concrete reciprocity. However, in other cases – notably prominent in the human species – the return benefits may stem from other sources, especially third parties from the helper's group. This type of reciprocal altruism has been labeled indirect reciprocity (Alexander 1987). There are at least four forms of indirect reciprocity. In the first form, one individual helps a second individual who helps a third individual who, in turn, helps the first individual in a daisy chain-like sequence. In the

second form, one individual helps another individual who returns the favor, and a third individual initiates a reciprocal exchange with the individual who returned the favor. In the third form, individuals contribute to some central source that redistributes the goods and services, and in the final form, individuals contribute to groups whose existence increases their survival and reproductive success. In systems of indirect reciprocity, what goes around comes around with dividends through third parties.

Indirect reciprocity may enable participants to reap greater gains in fitness than direct reciprocity can, because the former is equipped to produce greater gains in trade than the latter. Alexander (1987) suggested that systems of indirect reciprocity evolved in the human species because early humans living in hunter-gather groups were able to increase their fitness by initiating exchanges with members of their groups whom they observed behaving altruistically and cooperatively and/or with members of their groups with a reputation for being reliable and generous exchange partners. Alexander also suggested that altruistic and cooperative members of groups could benefit genetically from the increased fitness of their collateral relatives that their altruism and cooperation produced, and from the increased success of their groups.

Antidotes to Cheating

The central reason that reciprocal altruism is not more prevalent in the animal kingdom probably stems from the vulnerability of systems of reciprocity to cheating and free-riding. To evolve, adaptations mediating reciprocal altruism must be equipped to withstand the exploitation of those who either take without giving in return – a phenomenon dubbed “gross cheating” by Trivers – or take more than their share and give less – a phenomenon labeled “subtle cheating” (Trivers 1971, p. 46). When individuals are grossly cheated, they suffer the costs of giving without any compensatory benefits. Although individuals who are subtly cheated obtain benefits, they benefit less than their partners. Krebs (2011) has

characterized the susceptibility of systems of reciprocal altruism and other forms of cooperation to cheating and free-riding as a “tragic irony,” because, in favorable conditions, if everyone cooperated, everyone could reap copious gains in trade without suffering the costs of guarding against free-riding and punishing cheaters. In contrast, if everyone behaved selfishly, cheated, and attempted to free-ride, no one would reap the fruits of cooperation.

Adaptations to cheat and adaptations to counteract cheating would be expected to evolve in an arms race manner. In direct forms of reciprocity, individuals can avoid being cheated by exchanging goods or services simultaneously, in effect giving with one hand and taking with the other. In delayed forms of direct reciprocity, individuals can guard against cheating or minimize its negative effects by demanding reciprocation soon after making relatively small donations, by making additional giving contingent on receiving a fair return (such as, for example, in tit for tat type strategies), by threatening or punishing cheaters, and by rejecting cheaters as future partners and ostracizing them from groups.

Systems of indirect reciprocity tend to be more vulnerable to cheating than systems of direct reciprocity are, because it usually is easier to identify those who fail to pay you back than to identify those who fail to pay third parties back, and the biological and genetic benefits of punishing individuals who have cheated others do not tend to be as great as the benefits of punishing individuals who have cheated you.

Inasmuch as punishing cheaters entails a cost, how could it be in the adaptive interest of individuals to punish third parties who have cheated others (a phenomenon that has been labeled “altruistic punishment”)? The main answers to this question offered by evolutionary biologists are (a) punishing third party cheaters may benefit one’s relatives; (b) punishing third party cheaters may help one’s group function more effectively, which in turn may produce collateral benefits for the punishers; (c) some forms of punishment, such as avoiding and shunning those who have cheated others or those who have a reputation for being cheaters, proffer direct benefits to those who

employ them; and (d) individuals may reap indirect benefits by acquiring a reputation as someone who is willing to suffer the costs of punishing third party cheaters (see Alexander 1987). On the other side of the coin, cheaters may suffer losses in fitness (a) through rejection as a partner by third parties who have observed them cheating, (b) through losses in status, (c) through ostracism, and (d) through negative effects on the group that filter back to cheaters and their relatives. In groups practicing indirect reciprocity, we would expect members to be vigilant for cheating and free-riding, to gossip about the social behaviors of others, and to be concerned about their reputations and the reputations of others. Alexander (1987) suggested that the problem of cheating in indirect systems of reciprocity can be solved if members of groups interact with others in a selective manner, favoring cooperators and discriminating against cheaters.

Studies from several areas have supported Alexander's (1987) theory of the evolution of indirect reciprocity. Game theorists such as Nowak and Sigmund (1998) have found that systems of indirect reciprocity can evolve when members of groups tag others with positive or negative images ("image scoring"), depending on whether they are seen to behave altruistically or selfishly toward third parties, and favor those with positive images. Psychologists have found that people's willingness to cooperate increases when they are in public and when they expect cooperation to enhance their reputations (Barclay 2004). Anthropologists have found that members of small societies who contribute more than their share to communal projects, who behave in ways that promote the public good, and who are courageous in battle, are sought out as partners more frequently than their fellows (Hawkes 1983). And economists studying large business firms have found that the social status of employees is positively correlated with their perceived generosity (Flynn 2003).

Although the individuals who participate in systems of indirect reciprocity behave in immediately altruistic ways, the mental mechanisms that induce them to behave in these ways evolved because they increased their long-term fitness,

and this renders the behaviors biologically selfish. Systems of indirect reciprocity evolve because they produce return benefits for those who participate in them. Evolutionary theorists expect people to be tempted to exploit systems of indirect reciprocity and to manipulate others into behaving in ways that increase their fitness. As expressed by Alexander (1987), "the long-term existence of complex patterns of indirect reciprocity may be seen as favoring the evolution of keen abilities, first, to make one's self seem more altruistic than is the case and, second, to influence others to be altruistic in such fashions as to be deleterious to themselves and beneficial to the moralizer, for example to lead others to invest too much, invest wrongly in the moralizer or his relatives and friends, or invest indiscriminately on a larger scale than would otherwise be the case. Thus, individuals are expected to parade the ideas of much altruism and of indiscriminate altruism as beneficial, so as to encourage people in general to engage in increasing amounts of social investment whether or not it is beneficial to their interests. They may be expected to locate and exploit avenues of genetic relatedness leading to nepotistic flows of benefits. They may also be expected to depress the fitness of competitors by identifying them, deceptively or not, as reciprocity cheaters; to internalize rules or evolve the ability to acquire a conscience...and to self-deceive and display false sincerity as defenses against detection of cheating and attributions of deliberateness in cheating" (p. 190).

Group Contexts

Characteristics of groups may constitute significant ingredients in the evolution of reciprocal altruism. Among these characteristics, those that pertain to the probability of reciprocal altruists encountering other cooperators, and those that pertain to the probability of selfish individuals encountering other selfish individuals are probably the most important. Cooperative and selfish individuals may be distributed in different ways within relatively large groups. The higher the probability of an individual who is disposed to

engage in reciprocal altruism encountering another cooperative individual, the greater the payoff for reciprocal altruism will be. In the extreme case, reciprocal altruism could pay off well for all members of groups consisting entirely of reciprocal altruists. When reciprocal altruists are able to identify one another and differentiate themselves from cheaters (in whose interest it will be to mimic them), they may seek one another out, form subgroups, and exclude selfish individuals from their cooperative groups. Assortment of cooperating and cheating individuals favors the evolution of reciprocal altruism (Dugatkin 1997). In large groups, constraints on members' opportunity to "rove" and interact with new partners favors the evolution of reciprocal altruism because it enables reciprocal altruists to discriminate against cheaters and favor cooperators (Dugatkin 1997).

It is generally agreed that small groups favor the evolution of reciprocal altruism. Indeed, theorists such as Boyd and Richerson (1992) have asserted that reciprocal altruism cannot evolve in large groups. However, Trivers (2006) has questioned this conclusion, pointing out that it is based on the assumption that if a selfish (or "defecting") member of a group decides to cooperate, every other member of the group must benefit. Trivers insists that the costs and benefits of most incidents of reciprocal altruism are confined to the individuals involved in the exchange.

The Origin of Adaptations for Reciprocal Altruism

Evolutionary theorists have offered two main explanations for the origin of systems of reciprocal altruism. First, they have suggested that such systems could grow out of reciprocal exchanges supported by kin-selected adaptations (Axelrod and Hamilton 1981). For example, adaptations for blood-regurgitation by vampire bats, which surely originated as a way for mothers to feed their young, may have generalized to collateral kin, then to nonkin. Second, systems of reciprocal altruism could have originated in low-cost

exchanges that increased in value as participating individuals experienced gains in trade and acquired confidence in the relationship (Roberts and Sherratt 1988).

Proximate Mechanisms

Such theorists as Hauser et al. (2009) have attributed the dearth of documented cases of reciprocal altruism among nonhuman animals to the absence in most species of the cognitive abilities necessary to engage in calculated forms of reciprocal altruism – abilities that enable animals to discriminate between reciprocally altruistic and nonaltruistic members of their groups, remember who has helped them and cheated them over relatively long periods of time, quantify costs and benefits, detect inequities, delay gratification, and distinguish between intentional and accidental behavior. However, as pointed out by other theorists, the sophisticated record-keeping abilities that enable animals to engage in calculated forms of reciprocal altruism are not necessary for all forms of reciprocal altruism (de Waal and Brosnan 2006). Many other adaptations, such as those that give rise to such emotional reactions as love, sympathy, gratitude, guilt, forgiveness, vindictiveness, righteous indignation, and the desire to reconcile, could support reciprocally altruistic relations (Trivers 2006).

Conclusion

In 1971, Trivers introduced the concept of reciprocal altruism to explain how mutually beneficial exchanges between nonrelatives could evolve. The main ingredients of reciprocal altruism are (a) exchange partners, (b) goods and services, (c) giving and receiving, (d) costs and benefits, (e) gains in trade, (f) strategies, (g) direct and indirect returns, (h) antidotes to cheating, and (i) group contexts. The central problem that animals seeking to benefit from the gains in trade they can obtain from reciprocal exchanges must solve – and therefore the central obstacle to the evolution of reciprocal altruism – is the temptation

for exchange partners to cheat, either by taking without giving in return, or by taking more than they give in return. Game theorists have identified strategies that are equipped to solve this problem. Adaptations for reciprocal altruism probably evolved from kin-selected adaptations for altruism and as extensions of low-cost exchanges. Although reciprocal altruism is prevalent in the human species, it is relatively rare in the rest of the animal kingdom.

Cross-References

- [Competitive Altruism](#)
- [Cooperative Grooming](#)
- [Food Sharing](#)
- [Iterated Prisoner's Dilemma Model](#)
- [Nonhuman Reciprocal Altruism](#)
- [Psychology of Reciprocal Altruism](#)
- [Reciprocal Altruism](#)
- [Reputation](#)

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In-Group

- [Out-Group Members](#)

Ingroup Favoritism

- [Benefit Group Relative to Other Groups](#)
- [Prejudice](#)

In-Group Morality

► [John Hartung \(1995\) Love Thy Neighbor](#)

In-Group Versus Out-Group

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Synonyms

[Alliances](#); [Coalitions](#); [Tribalism](#); [Tribes](#)

Definition

The evolution of the cognitive architecture humans use to sort themselves into coalitions of us versus them.

Introduction

Considerable attention across the social sciences has been paid to understanding how people categorize individuals into groups and create group identities. Throughout human history, conflict between groups was founded on categorizing relationships into “us” and “them” and social psychologists have long recognized the importance of group membership to human social organization. The “minimal group paradigm,” established as a method for investigating the minimal conditions required for discrimination to occur between groups, has continued to show that even virtually meaningless distinctions between groups, such as shirt color, can trigger a tendency to favor one’s own group over others. It is clear that the ability to readily distinguish between in-groups and out-groups played a key role in our evolutionary history.

Kinship

Understanding the potency of human group identification is often constructed around theories of kin selection – favoring one’s genetic relatives at a cost to one’s own survival and reproduction (Hamilton 1964). If ancestral human groups were composed primarily of closely related individuals, then a shared culture, background, or belief system may have served as a reliable phenotypic marker of genetic relatedness (Swann et al. 2014), and kinship may therefore have played an important role in building the cognitive architecture employed in group identification and formation. Anthropological studies of group fissioning along kin-lines, such as occurred within Yanomamo tribes of the Amazon, confirm this prediction. A cross-cultural study of 32 hunter gatherer groups, however, suggests that kinship may be overstated by evolutionary psychologists and that inclusive fitness (Hamilton 1964) – the ability of an individual organism to transfer genes to the next generation either directly through offspring or indirectly through the offspring of close relatives – cannot explain the composition and cooperation of hunter gatherer social structures. For example, close kin (e.g., siblings, spouses, parents) often make up less than 10% of a residential group and in some groups like the Ache of Paraguay, the mean genetic coefficient of relatedness (r) between adults was estimated to be 0.054 suggesting that kinship may not fully explain group cohesion (Hill et al. 2011).

Kin Psychology

Regardless of the average relatedness of early human groups, many explanations of self-sacrifice for a large group of unrelated individuals are built on kin selection and rely on something called “kin psychology” – forming kinship like bonds with unrelated individuals. These types of explanations tend to focus on cultural adaptations which harness cognitive mechanisms that direct our interactions with genetic relatives. For example, researchers have suggested that applying kinship terminology to a group of close friends

(e.g., a band of brothers) or a nation (e.g., “the motherland”) can trigger emotional responses that are similar to those activated by kin selection. Building on these ideas, Whitehouse (2018) developed the theory of “identity fusion,” arguing that extreme self-sacrifice results when individuals align their own identity with that of the group through bonding over intense shared experiences (e.g., the horrors of war) or from perceptions of shared biology (e.g., recognizing putative kin by looking for individuals with similar traits called “phenotypic matching”). As a result, certain social connections might enable one to view others with such shared experiences or traits as kin. Interestingly, identity fusion is expected to be particularly powerful when combined with a strong outgroup threat. Together, these theoretical arguments and empirical results suggest that extreme self-sacrifice is made possible by exploiting psychological pathways dedicated to kin-biased altruism.

Parochial Altruism

A long history of lethal between-group competition is also likely to have played an important role in generating attitudes towards in-groups and out-groups in humans and Bowles theorized that these biases depend on the frequency of conflict between rival bands in the evolutionary past. The willingness to sacrifice for an in-group, combined with out-group hostility, has been called “parochial altruism” and this phenomenon may help to explain why clear boundaries between human groups are so pervasive. Using simulations, Choi and Bowles (2007) found that groups whose members are hostile towards other groups and are altruistic towards their own groups are more likely to succeed when the frequency of lethal intergroup conflict is high.

Phenotypic Matching and Strategic Coalitions

What cues do humans use to infer shared genes (i.e., phenotypic matching), beliefs, or interests

(i.e., shared experiences) and thereby create boundaries between in and out-groups? There is considerable evidence that when being asked to remember an unknown person, humans are automatically able to remember three “primary” traits – sex, age, and race. Hirschfeld (1998) argued that categorizing individuals by their race is a byproduct of essentialism – the idea that every organism has a set of qualities that forms their identity – and evolved due to our need to reason about natural types, and Gil-White (2001) has suggested that humans process racial and ethnic groups like species. Some ethnographies provide tentative support for this sort of essentialist thinking. For example, the name Yānomamö that a group of horticulturalists living in the Amazon rainforest call themselves is often translated as “human beings” and other enemy tribes or non-Yanomamo groups are not considered to be human. Other researchers see in-group biases as evolving to reap the advantages derived from forming and being a member of a coalition. Here, categorizing people by their race is viewed as byproduct of cognitive structures that evolved to detect coalitional alliances. The likelihood that humans would rarely, if ever, have traveled far enough to have encountered individuals from a population different enough to qualify as a race lends support for this view. Both essentialism based on shared beliefs or ancestry and the ability to form flexible strategic coalitions based on shared interests are likely to play an important role in human group affiliation, however.

Religion

Humans also form coalitions around shared beliefs, and religion has the ability to redraw boundaries between groups and create group identities. Indeed, several studies have suggested that a key function of religion is to bind individuals into groups, and members of religious groups often favor individuals who share their faith. Furthermore, religions frequently have specific rules that promote the defense of their group while simultaneously propagating hatred of out-

groups. In a Jamaican sample, hostility towards out-groups was positively predicted by extrinsic religiosity (i.e., using religion to achieve non-religious goals) but negatively associated with religious devotion (e.g., belief in God) (Lynch et al. 2017).

Political Beliefs

Although religious beliefs, race, sex, ethnicity, and age are some of the most salient cues humans use to categorize other people into groups, other cues may also be relied on as a reflection of an individual's beliefs. For example, in recent years, political views have often been used to assess group membership. In 1960, a poll found that 5% of Republicans and 4% of Democrats would "be unhappy" if their child married someone from the opposing party. In 2010, half of Republicans and a third of Democrats surveyed reported that they would be either "somewhat upset" or "very upset" if this happened. Today, implicit association tests (which measure how quickly people categorize positive and negative words with groups) have shown that people show greater prejudices against political foes than those of different races or religions.

Humor and Laughter

Laughter and sense of humor are also frequently used to categorize individuals into groups. For example, laugh tracks amplify real human-generated laughter only when individuals believe it comes from members of an in-group. This suggests that laughter may function to reinforce within group social bonds. People also report liking others who laugh at their jokes and share their sense of humor, and laughter is more common in the presence of others, especially friends, which suggests that it may be connected to both social bonding and communication. Sharing a sense of humor has also been shown to be extremely important in mate selection and sense of humor may help to assess in-group status or potential mates by determining when others share

our unconscious biases and beliefs (Lynch and Trivers 2012; Lynch 2010).

Conclusion

The formation of boundaries between human groups and groupish behavior can be understood within an evolutionary framework. In general, it is thought that a decreased trust of unknown individuals and groups would have provided fitness advantages to our ancestors and helped to protect them and their offspring from risks posed by other humans. If this interpretation is correct, then we should expect that cognitive structures specifically designed to quickly categorize people into "us" and "them" would have been targeted by natural selection. Although many of the mechanisms remain unclear, such as whether in-group loyalty and outgroup hate are linked, an evolutionary viewpoint provides a functional explanation for why these biases are so fundamental to human behavior.

Cross-References

- ▶ [Alliance Formation Theory](#)
- ▶ [Alliances](#)
- ▶ [Altruism](#)
- ▶ [Cheater Detection Adaptations](#)
- ▶ [Cliques](#)
- ▶ [Coalitional Relationships](#)
- ▶ [Competition Between Groups](#)
- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Cooperative Alliances](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Group Living](#)
- ▶ [Group Size](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Indirect Benefits of Altruism](#)
- ▶ [Indirect Reciprocity](#)
- ▶ [In-Group–Out-Group Bias](#)
- ▶ [Kin Detection by Odor](#)
- ▶ [Kin Recognition and Classification in Humans](#)
- ▶ [Kin Selection](#)
- ▶ [Male Coalitions for Hunting](#)
- ▶ [Male Warrior Hypothesis](#)

- ▶ [Manipulative Use of Kin Terminology](#)
- ▶ [Men but Not Women Will Have Adaptations for War](#)
- ▶ [Moral Tribes](#)
- ▶ [Phenotypic Resemblance and Kinship Detection](#)
- ▶ [Psychic Unity](#)
- ▶ [R = Coefficient of Relatedness](#)
- ▶ [Racism](#)
- ▶ [Religion](#)
- ▶ [Same-Different Categorization](#)
- ▶ [Sex Differences in Attractiveness of Humor](#)
- ▶ [Suicide Terrorism](#)
- ▶ [Tribalism](#)

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In-Group–Out-Group Bias

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Synonyms

[Intergroup bias](#); [Social bias](#)

Definition

A tendency to react differently and asymmetrically toward others, depending on whether they are from the in-group (to which an individual belongs) or from the out-group.

Introduction

Unlike other species, humans live in large and complex social groups, which are based on numerous and diverse social relations, extended cooperation, and cultural norms. To deal with this “ultra-sociality” (Tomasello 2014), humans needed advanced and specialized skills to accurately represent the complex social structure, identify and regulate social relations, predict others’ behaviors, and develop own behavioral strategies. The foundation of such abilities is social categorization, i.e., perception and representation of others in terms of their group membership and common, typical traits. Social categorization helps to reduce the complexity of social environment by applying a limited set of rules to unlimited number of social agents.

The simplest and basic form of social categorization is a binary distinction between a group and category, to which an individual belongs (in-group) and other groups (out-groups). Although there are many types of social groups, identified on the basis of various criteria (kinship, race, ethnicity, age, gender, profession, political attitudes, language, class, etc.), the basic in-group/out-group opposition can be applied in any case. As the evolution of human societies relied

significantly on the combination of intragroup cooperation and intergroup competition, the in-group/out-group categorization became a basis of a wide range of asymmetrical reactions to other people, depending on their identified in- or out-group status.

Types and Effects of Intergroup Bias

In studying asymmetrical reactions to others as a function of their group membership, social psychologists use several terms, often interchangeable: bias, prejudice, stereotype, and discrimination. Among them, the term “bias” is the least univocal. By prejudice, researchers mean specific attitudes toward groups and their members. Typically, in-group members are evaluated more positively and elicit more positive emotions. Stereotypes are specific sets of traits and characteristics associated with particular group. For example, in-group members are often considered as more trustworthy, whereas out-group members can be perceived as more aggressive. Discrimination refers to overt behavior, depended on group membership. People typically make unfair decisions in favor of their in-groups, for example, distribute more resources to them.

As regards the term “bias,” its definition is not so clear. Often researchers use it as a general concept embarrassing various types of group-based asymmetries in cognitive, affective, or behavioral domains. For example, John Dovidio and other authors of *The SAGE Handbook of Prejudice, Stereotyping and Discrimination* define intergroup bias as “the systematic tendency to evaluate one’s own membership group (the ingroup) or its members more favorably than a non-membership group (the outgroup) or its members” (Dovidio et al. 2010, 3) and see it as encompassing prejudices, stereotypes, and discrimination. Although such or similar definitions are widespread, they are problematic in at least two aspects.

First, evaluation is only one type of group-based asymmetrical responses, and there are other processes, which are known to be regulated by the in-group/out-group distinction. For

example, intergroup biases in such basic cognitive processes as attention and memory are well-documented (e.g., Kawakami et al. 2014; Meissner and Brigham 2001). They cannot be described as evaluative biases and are neither prejudices, nor stereotypes, nor discrimination.

Second, it implies that intergroup bias is always a kind of an *advantage* and, moreover, an advantage in favor of the in-group. This is however not necessarily so. For example, a well-documented tendency to pay more attention to in-group members or to remember them better can hardly be called an advantage. Rather, it reflects the difference in the perceived or expected significance of social information. If the evolution of humans was primary directed by the needs for within-group cooperation, greater vigilance to any in-group-related information is explainable. The preference for in-group is also not always the case and can be reversed by other factors, and especially social status, so that a high-status out-group is preferred as compared to the in-group (e.g., Rudman et al. 2002; Newheiser et al. 2014).

For these reasons, it is more accurate to describe intergroup bias as a wide range of asymmetrical reactions to members of various social groups and to in-/out-groups at the most general level. Social categorization, even in its simplest form of in-/out-group distinction, underlies asymmetrical reactions in a wide range of psychological and behavioral processes: perception, memory attention, evaluation, judgments, emotions, decision-making, and approach-avoidance behavior. Intergroup bias was documented in respect to many different types of social groups and categories: racial, ethnic, gender, age, political, religious, etc. The fact that intergroup bias was found even in the so-called “minimal” groups (in-/out-groups defined according to an arbitrary, situational criterion, which exist only during an experiment) confirms that the tendency to respond differently to various groups is deeply rooted in human mind. Studies in cognitive and neuroscience demonstrated that many types of bias are implicit and can be evoked automatically and unintentionally. Further, intergroup bias and preference for own group are common in primates and other animals. Thus, there is strong evidence that the diversity

and strength of intergroup bias effects have evolved to support the specific needs of social life and, particularly, within-group cooperation. At the same time, effects of intergroup bias in specific contexts can vary and depend on many intermediate factors such as personal goals and motivation, familiarity and the history of intergroup contact, time course of social information processing, availability of alternative social information, social norms, etc.

Conclusion

Social categorization is the foundational ability necessary to represent and navigate the social complexity of human societies. Even the simplest and basic social categorization, i.e., in-group–out-group distinction, has a profound impact on human cognition, emotions, attitudes, and behavior. The differentiation between “Us” and “Them” triggers cognitive mechanisms supporting, in a normal situation, preferential processing of in-group-related information and emotional and behavioral predispositions in favor of the in-group. These mechanisms provide the basis for cooperation and affiliative relations, which are crucial for social life and survival of human groups. At the same time, they underlie a wide range of problems in intergroup relations varying from subtle symbolic discrimination to overt and aggressive conflicts.

Cross-References

- Biases
- Benefit Group Relative to Other Groups
- In-Group Versus Out-Group
- Racism and Prejudice
- Social Neuroscience of Self-Categorization

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In-Group–Out-Group Dynamics

- Tribalism

Inheritance

- Birthrights and Bloodlines
- Heritability

Inherited Disease

- Genetic Abnormalities

Inherited Status

- Birthrights and Bloodlines

Inhibited Ejaculation

► [Orgasmic Disorders](#)

Inhibited Sexual Desire

► [Desire and Arousal Disorders](#)

Inhibition

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Synonyms

[Cognitive control](#); [Inhibitory control](#); [Motor control](#); [Response inhibition](#); [Self-control](#)

Definition

The process of suppressing an automatic/prepotent response or mental representation.

Introduction

Inhibition is an executive function that serves to reduce behavioral or cognitive activity, either consciously or unconsciously. Whereas behavioral inhibition refers to the suppression of a prepotent motor response (i.e., any response associated with a history of positive or negative reinforcement), cognitive inhibition refers to the suppression of mental processes. Inhibition may involve the complete cessation of a behavior or mental process, the slowing down of a behavior or mental process, or a decrease in the probability that a behavior or mental process will occur.

Behavioral Inhibition

Behavioral inhibition refers to the process of inhibiting prepotent responses, delaying immediate, ongoing responses, and preventing extraneous information from interfering with response processes (Logan and Cowan 1984). Logan and Cowan (1984) seminal horse race model suggests behavioral inhibition depends on the relative completion times of independent go and stop processes that are initiated by prepotent stimuli and stop signals, respectively. Inhibition occurs when the go process (i.e., prepotent response) is unable to overcome the stop process. Deficits in behavioral inhibition are theorized to be upstream of deficits in other executive functions, such as working memory and self-regulation, which lead to impaired motor control (Barkley 1997).

Behavioral inhibition has been examined using several paradigms in experimental research. The go/no-go (GNG) paradigm (Donders 1969), for example, has been used to examine internalized, automatic responses to stop signals, while the stop signal (SS) paradigm has been used to examine behavioral inhibition within the context of more complex cognitive processes (Verbruggen and Logan 2009). GNG and SS tasks are similar such that they both require individuals to respond to go stimuli that are presented successively across go-response trials and inhibit responses to no-go/stop stimuli (e.g., an auditory tone) that are typically presented during approximately 25–33% of experimental trials (Alderson et al. 2007). However, whereas the GNG paradigm presents intermittent stop trials in context of a simple reaction time go-task, the go-task of the SS paradigm is a choice reaction time task. As such, the GNG task is deemed more suitable for the examination of inhibition processes involved in automatic prepotent responses, while the SS task may be more appropriate for the examination of speed/accuracy trade-offs and attention processes associated with inhibition. Examples of other behavioral inhibition paradigms include antisaccade tasks, delay-of-gratification tasks, flanker tasks, and the Simon task.

Cognitive Inhibition

Cognitive inhibition refers to the process of inhibiting prepotent mental representations associated with an external stimulus or internal thought (Dagenbach and Carr 1994). This process involves blocking and/or removing irrelevant information from working memory or preventing attention from being directed to information that has been previously rejected. Cognitive inhibition includes reducing extraneous information access to attention as a whole, as well as reducing attention to specific psychological pathways (Dagenbach and Carr 1994). For example, when a child ignores what is happening outside their classroom window so that they may instead attend to a teacher's lesson, they are using cognitive inhibitory processes to direct their external focus of attention away from irrelevant external stimuli. Similarly, cognitive inhibition is involved when a child directs their internal focus of attention to class-related information rather than daydreaming (Dempster and Brainerd 1995).

Cognitive inhibition has been examined extensively using the Stroop Color-Word Task. This task involves reading a word and indicating the color in which the text is written while ignoring the content of the text (MacLeod 1991). For example, the correct response to the word *red* presented in green font would be *green*. A prototypical task compares average reaction times obtained from compatible (word meaning and font color are the same) and incompatible (word meaning and font color are different) trials, with slower reaction times during incompatible trials, relative to compatible trials, providing evidence of increased demands on cognitive inhibition. That is, incompatible trials require participants to inhibit the text's meaning that is irrelevant to accurate task completion. A variant of this procedure administers a control condition that presents swatches of color and asks participants to correctly name the color (MacLeod 1991). The task was originally designed to measure interference or reduced performance when conditions contain multiple distracting stimuli but is now used more frequently as a measure of inhibition (Dempster and Brainerd 1995). Additional

common examples of cognitive inhibition paradigms include singleton distractor tasks and directed forgetting tasks.

Inhibition in Psychopathology

Deficits in inhibition have been implicated in the development and maintenance of psychopathology. Deficits of motor control (i.e., behavioral disinhibition), for example, are predominantly associated with disorders related to poor impulse-control and self-regulation, such as attention-deficit/hyperactivity disorder (Alderson et al. 2007; Patros et al. 2016). In contrast, deficits of cognitive control (i.e., cognitive disinhibition) are predominantly associated with disorders related to distorted mental representations of internal and external stimuli, such as anxiety and depression (Clark and Beck 2010).

Conclusion

Collectively, inhibition refers to any mechanism by which an individual intentionally or unintentionally suppresses behavioral or cognitive activity. Inhibition is assessed using cognitive or behavioral tasks that require an individual to withhold, delay, or cease responding while resisting distraction of competing events (i.e., interference control). Deficits in inhibition are highly associated with deficits in other executive functions, such as working memory and self-control, and play a large role in the development of psychopathology among children and adults, including ADHD, mood disorders, anxiety disorders, substance use disorders, and psychotic disorders.

Cross-References

- [Attention](#)
- [Attention and Memory](#)
- [Executive Functioning](#)
- [Impulsivity Disorders](#)
- [Interference](#)

- ▶ [Selective Attention](#)
- ▶ [Working Memory](#)

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Inhibitory Control

- ▶ [Inhibition](#)

Inhospitable Environments

- ▶ [Harsh Environments](#)

Injured Party

- ▶ [Victims Mostly Men](#)
- ▶ [Victims of Violence](#)

Innate

- ▶ [Study of Instinct, The](#)

Innate and Learned Tool Use

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Definition

Innate tool use normally means that it is a highly heritable evolved adaptation, found in at least one age-sex class, or not learned.

Introduction

The concept of innateness is surrounded by controversy. Some claim it is a meaningful notion, while others argue it has no explanatory power. Innateness is commonly pitted against learning, but definitions vary widely. There are at least nine different meanings of innate: “present at birth or particular stage of development; not learned; genetic – highly heritable; adapted during evolution; develops before function is established; shared by all members of species/sex/age group; a functional behavioral system; controlled by a specialized neural module; and developmentally robust – well-canalized” (Bateson and Curley 2013). For the sake of clarity, it is therefore more appropriate to talk about specific meanings than innateness in general.

Tool use in nonhuman animals has often been described as either innate or learned, but a deeper distinction is necessary for meaningful discussion.

Here we discuss the most commonly used meanings of innate tool use, which we compare with the possibility of learning. Following Shumaker et al. (2011), tool use is defined as “the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.”

Is Tool Use Found in at Least One Age-Sex Class?

Tool use is customary when it is present in at least one age-sex class of the species. Although the exact criteria vary, tool use appears to be customary in (some populations of) chimpanzees, orangutans, bearded capuchin monkeys, Burmese long-tailed macaques, California sea otters, bottlenose dolphins, Egyptian vultures, brown-headed nuthatches, New Caledonian crows, Hawaiian crows, woodpecker finches, satin bowerbirds, green-backed herons, and archerfish (Hunt et al. 2013; Meulman et al. 2013; Rutz et al. 2016; Shumaker et al. 2011; Tebbich and Teschke 2013). Customary tool use might be more prevalent in invertebrates, although it is not often investigated as such. For example, hermit crabs use shells for protection, worm lions throw sand to capture prey, digger wasps use object to compact the soil around their burrows, leaf beetle larvae use physical and chemical shields for protection, boxer crabs use anemones to catch food debris, bolas spiders throw sticky bolas to catch prey, and octopuses throw sand over their bodies for camouflage (Shumaker et al. 2011).

However, customary tool use in some vertebrate species is a product of social learning. The frequency of certain tool modes in different populations is often monitored in studies on their cultural transmission. A tool behavior is usually said to be cultural if it is only found in some populations and if this variation cannot be explained by ecological or genetic factors (Meulman et al. 2013).

In contrast, tool use in invertebrates is often widespread within the species or genus, arises from little to no social contact, is highly context specific, involves relatively little working memory, and is only rarely innovated. Such tool use is therefore called stereotypic, which bears many similarities with innateness and instinct because learning plays only a minor role (Hunt et al. 2013). There is notable variation within the aforementioned vertebrates too. Flexible tool use typically develops later in ontogeny, through a more error-prone process, and involves different types of social transmission. Nonetheless, such learning may be supplemented by inherited behavioral predispositions that scaffold tool use, such as object manipulation and exploration (Meulman et al. 2013). Thus, although tool use in many species is found in at least one age-sex class, this does not directly oppose learning.

Is Tool Use Highly Heritable?

Heritability is the proportion of total phenotypic variation that is attributable to genetic variation (Hopkins et al. 2014). Intelligence as measured by IQ is heritable in humans in the sense that it has a strong genetic component, but it is also influenced by environmental factors. Similar results based on a cognitive test battery have been found in chimpanzees. Individual score was stable when tested again 2 years later, and sex and rearing history played only a minor role (Hopkins et al. 2014). Of all 13 tasks the highest heritability score was for tool use, which was passed if the subject could retrieve out-of-reach food with a stick within 2 min. It also had the highest phenotypic variability, so the ability to use tools appears to be strongly influenced not only by genetics but also individual experience. Tool use had the largest variability in studies comparing primate species, which suggests the findings in chimpanzees could be similar for other primates, and that tool use strongly affected primate evolution (Woodley of Menie et al. 2015).

However, this notion of heritability is simplistic because it overlooks the complex interactions between genes and environment. The heritability

ratio is not an absolute quantity but depends on many factors, such as the population, rearing history, and test circumstances. Moreover, heritability does not necessarily oppose learning. For example, walking on two legs is a fundamental property of being human, but it requires extensive learning nonetheless (Bateson and Curley 2013).

Is Tool Use an Evolved Adaptation?

Tool use is likely to be adaptive if it contributes significantly to daily food intake. Woodpecker finches from the Galápagos Islands use sticks and cactus spines to extract invertebrates from tree holes and crevices. The prevalence of this tool use varies strongly between areas and seasons. They rarely use tools in a stable zone with more abundant prey. In the dry zone, they use tools for 12 % of the foraging time during the wet season and nearly 50 % during the dry season. Tool use enables them to obtain prey that otherwise would be inaccessible, and although it takes longer to extract them, they are larger and more energy rich than other prey types. It allows these finches to change their foraging style between habitats and seasons. In contrast, the closely related large tree finch has evolved a powerful beak to extract arthropods. This morphological adaptation limits pecking and probing and is associated with niche specialization, whereas the tool use by woodpecker finches is a temporary solution that allows for more foraging flexibility. It develops through individual learning and does not require social input. Young finches learn to use tools whether they come from the stable or dry zone, which suggests that a genetic predisposition develops into tool use if it is learned during a sensitive ontogenetic phase (Tebich and Teschke 2013).

New Caledonian crows also use tools for extractive foraging on remote islands. Among others, they use sticks to extract fat-rich larvae from wood. Three larvae are sufficient for a crow's daily energy intake, and on average they consume 1.8 larvae per day. Tool use is thus responsible for a substantial proportion of their foraging ecology. However, these larvae are not always available across the crows' distribution, and the ecological significance of their other tool

use remains largely unknown. Similar to woodpecker finches, New Caledonian crows develop tool use in the absence of demonstrators but with individual practice. However, tutored crows handle and insert twigs more often than untutored crows (Rutz and St Clair 2012).

Hawaiian crows, which are only distantly related to New Caledonian crows, were recently discovered to also use sticks to extract food from logs. Although they are extinct in the wild, tool use seems to be part of their natural behavioral repertoire because most captive individuals use tools and juveniles develop this ability without training or social input. Determining the importance of tool use in their foraging ecology can only be done in wild populations, but its species-wide occurrence suggests it is an evolved adaptation (Rutz et al. 2016). Tool use is similarly widespread in some other species, notably invertebrates (Hunt et al. 2013; Shumaker et al. 2011).

Morphological adaptations to tool use can also show its impact on the evolution of a species. Similar to an aye-aye using its elongated digit or a woodpecker its elongated tongue, chimpanzees, woodpecker finches, and New Caledonian crows use sticks to extract wood-living prey. These are different adaptive solutions to the same ecological problem of extractive foraging. Human hands enable dexterous manipulation, and tool use seems to have played a large role in their evolution, although this cannot be directly determined. New Caledonian crows also appear to have several morphological adaptations to or predispositions for tool use. Compared to other crow species, they have a wide binocular overlap, and their beak is relatively strong and straight, which allows them to monitor the working tool tip during probing. This strongly suggests that at least some of these features evolved for improved tool manipulation (Matsui et al. 2016). Hawaiian crows might have independently evolved similar morphological features (Rutz et al. 2016).

Conclusion

The question of whether tool use is innate or learned can only be answered by deconstructing

what is meant by innateness (Bateson and Curley 2013). Many species use tools and most meanings of innateness have never been directly investigated, so a clear answer is impossible at this time. Currently tool use seems to be both innate and learned with varying degrees depending on species, and this answer is unlikely to change when asked as an absolute question. The link between genes and behavior is long, and learning itself has genetic components. Nonetheless, research continues to address some of these issues and has revealed that some species have widespread tool use, have morphological adaptations to tool use, strongly rely on tools for daily energy intake, and partially inherit tool-using skills. Ultimately, the deconstructed meanings of innateness will prove to be useful in understanding tool use in the animal kingdom.

Cross-References

- [Evolution of Tool Use](#)
- [Nonhuman Tool Use](#)
- [Proto-Tool](#)
- [Role of Experience in Tool Use](#)

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Inner Ear

- [Auditory System, The](#)
- [Cochlea](#)

Inner Ear Structure

- [Semicircular Canals](#)

Inner Ear, The

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Synonyms

[Balance system](#); [Cochlea](#); [Vestibular system](#)

Definition

One of the three parts of the ear where the cochlea and the balance system is contained.

Introduction

The inner ear is responsible for the analysis of sound, since it contains the cochlea, the most significant structure of the inner ear responsible for the analysis of sound. The inner part of the ear contains the vestibular system responsible for balance and movement.

The Physiology of the Inner Ear

The physiology of the inner ear is consisted of the cochlea and the balance system (the vestibular system). It is notable that the human cochlea and the cochlea of other mammals were firstly discovered in 1561 (von Bekesy 1948) and resonance, as the foundation of the perception of sounds, was proposed by Duverney in 1683 (Mudry 2000) after observing the phenomenon of the resonance of two strings in tune with each other in the musical instrument Piano during the seventeenth century (von Bekesy 1948). Based on Johnsson and Hawkins (1967), our understanding of the structure of the inner ear is based on the work of many researchers who are associated with specific cochlear cells. Of particular reference were the detailed drawings of Magnus Gustaf Retzius (Jelliffe 1920) of the cytoarchitecture of the human organ of Corti, depicting the membranous labyrinth and its parts, cross sections of the cochlear duct, and surface preparations of the organ of Corti on different developmental stages of humans (Johnsson and Hawkins 1967).

The Cochlea

The cochlea has a shape like a snail and contains fluid compartments in a spiral form. The organ of Corti is contained there, one of the main structures responsible for the analysis of sound waves. There

are more than 15,000 hair cells in each cochlea, and are stimulated by the vibrations of the inner ear fluid – its movement producing electrical signals perceived as hearing from the brain (Balkany and Brown 2017). The cochlea is also responsible for separating the sounds based on frequency (Moller 2013).

The Vestibular System

The vestibular system is comprised of the vestibule, which is the space shared by the cochlea and the semicircular canals. The osseous labyrinth or bony labyrinth is made up by the cochlea, the vestibule, and the semicircular canals. In the osseous labyrinth rests a structure called membranous labyrinth, which can be thought of as a sac filled with fluid. The movement of the fluid in the semicircular canals is pushed on a structure called the cupula, which consists of hair cells that transduce the mechanical movement into electrical signals in the brain (Boulpaep and Boron 2005). Each inner ear has three semicircular canals, a utricle, and a saccule (Balkany and Brown 2017).

Conclusion

The physiology and function of the structures of the inner ear were briefly reviewed. These include the cochlea and the vestibular system.

Cross-References

- [Cochlea](#)
- [Organ of Corti](#)
- [Vestibular System](#)

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Inner-Directed Phase

► Self-Observation

Innovation

► Boredom as an Adaptation

In-Pair Copulation

► Semen from In-Pair Partner

In-Pair Female Attractiveness

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Bodily and Physical Cues

Women's attractiveness indexes health, fecundity and successful mothering potential (the ability to most successfully raise offspring independent of the ability to become pregnant), femininity,

and pathogen resistance (Buss and Schmitt 1993; Cunningham 1986; Cunningham et al. 1990, 1995; Henss 1992, 1995; Kenrick et al. 1994; Singh 1993, 1994, 1995; Singh and Luis 1995; Singh and Young 1995; Symons 1995; Wade 2000, 2003). Thus, men seek female partners based on facial and bodily cues and physical qualities that signal these characteristics. Singh and Luis (1995), Symons (1995), and Singh and Randall (2007) report that the most important and most visible physical cue for judging women's attractiveness is the waist-to-hip ratio (WHR). The WHR is related to crucial endocrine states associated with fecundity and successful mothering, and femininity is inferred from it (Singh 1993, 1994, 1995). Singh (1993, 1995) and Björntorp (1987a, b) report that gynoid fat is distributed on the thighs, legs, buttocks, waist, and hips of women. The lumbar curve is also important. Men execute an adaptation that allows them to tell which women have the optimal level of vertebral wedging that allows for a shift of the center of their mass back over their hips during pregnancy. This shifting of the center of mass allows for less: hip torque, lower back pain, spinal injury, and compromised fitness (Whitcome et al. 2007; White and Punjabi 1990). Thus, Lewis et al. (2015) report that men find women whose lumbar curve is closer to the optimal angle of 45.5° most attractive. Additionally, women's waist size is an indicator of their risk for disease, is used to assess their hormonal status, and is correlated with cardiovascular disorders, diabetes, and gallbladder problems (Björntorp 1993; Singh and Young 1995). Therefore, women who appear to have small hips, small waists, medium to small buttocks, and medium legs (Wiggins et al. 1968) are considered more attractive, healthier, more feminine, most fertile, and better potential mothers (Singh 1993, 1994, 1995; Singh and Young 1995; Symons 1995). Women's breasts and the appearance of their stomachs also play a role in attractiveness, health, and fecundity assessments (Singh 1993, 1994, 1995; Singh and Luis 1995; Singh and Young 1995; Symons 1995). Gynoid fat is distributed on the abdomens of women (Björntorp 1987a, b; Singh 1993, 1994, 1995), and women with large breasts are

considered more attractive, more feminine and healthier, and consequently most desirable for long- and short-term relationships (Singh and Young 1995). Physical fitness is also important. Kenrick and Keefe (1992) and Symons (1979) report that good physical fitness is related to fecundity and may also signal phenotypic quality (Symons 1995). Women's sex drives also play a role. The consequences of sexual activity have a greater impact on women (Bailey et al. 1994). Women must bear the offspring that result from sexual activity and experience the body and life changes that are concomitant with that. Thus, men use women's sex drive as a criterion for long- and short-term mate selection. A higher sex drive is associated with both long- and short-term mating (Buss and Schmitt 1993, p. 213, Table 2) preferences. Vocal pitch also plays a role since vocal pitch indexes developmental stability (Hughes et al. 2002). Collins and Missing (2003) report that men find women with higher pitched voices more attractive, and Hughes et al. (2014) report that men find women with hoarser voices more sexually attractive.

Facial Characteristics

Men also seek female partners whose facial characteristics indicate that they are healthy and fecund and have successful mothering potential. So, women with high cheekbones are considered more attractive, feminine, fertile, and healthier (Cunningham 1986; Cunningham et al. 1995; Symons 1995), because women's cheekbone size indexes pathogen resistance (Folstad and Karter 1992; Iwasa et al. 1991; Zuk 1990). Additionally, women with smaller noses are considered more fertile, more attractive, and more feminine (Cunningham 1986; Cunningham et al. 1995; Enlow 1990; Symons 1995; Wade 2000, 2003). The lips are also important. Lip size is also an estrogen-mediated trait (Johnston and Franklin 1993) and an indicator of femininity and attractiveness (Symons 1995). Thus, men rate women with full lips as more attractive (Baudouin and Tiberghien 2004). In addition, since the eyes get smaller with age (Wade 2000,

2003), eye size becomes a heuristic for youth and fertility. So, women with large round eyes are considered more attractive, fertile, and healthier (Cunningham 1986; Cunningham et al. 1995; Symons 1995). Similarly, since the limbal ring, a dark annulus around the iris, gets thinner/lighter due to health problems and/or aging (Peshek et al. 2011), women with a dark and distinct limbal ring around the eye are rated as more attractive than women whose eyes do not have a limbal ring (Peshek et al. 2011).

Conclusion

Both bodily and facial characteristics are important for men's selection of mates. Also, this is not a random process. Men engage in assortative mating where they select mates whose attractiveness matches their respective mate value (Buss and Schmitt 1993; Vandenberg 1972).

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In-Pair Mate Retention

► Direct Guarding

Inquisitiveness

► Attention and Memory

Insect Intrasexual Competition

► Insect Sperm Competition

Insect Sperm Competition

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Synonyms

[Insect intrasexual competition](#)

Definition

“...competition within the female reproductive tract, between the ejaculates of two or more males for fertilization of female’s eggs” (Parker, 1970).

Introduction

Insects display perhaps some of the most bizarre adaptations to sperm competition in the animal world. Indeed, the first studies of sperm competition, and the consequent definition of the term, were as a result of studies of insects. Geoff Parker’s 1970’s studies of yellow dung flies (*Scathophaga stercoraria*) led him to postulate that:

...copulation with internal fertilization may have arisen by a selective advantage conferred upon males able to eject sperm nearer to the ova than did their fellow males.

Parker was far ahead of the curve. Victorian notions of male and female sexuality had persisted well into the latter half of the twentieth century, and this in turn was reflected in scientific researchers’ understanding of the natural world.

In the *Origin of Species*, Darwin suggested that the cause of differences between male and females in the intensity of selection acting upon them was variation among males in numbers of mates. Yet it was not until 1948 that Angus Bateman was able to experimentally demonstrate in *Drosophila* fruit flies that Darwin was correct (Bateman 1948). However, it was Bateman himself who suggested that when it comes to mating, there is:

...an indiscriminatory eagerness in the males, and a discriminatory passivity in the females.

So, it was considered that whereas males were keen to mate as frequently as possible, and with different females, females themselves preferred quality over quantity.

In the 1980s, following the advent of the molecular age of science, we came to appreciate that females of most species can actually be highly promiscuous, or polyandrous, as a female that remates with different males is termed. For example, DNA fingerprinting in order to ascertain paternity showed that while female birds tend to be socially monogamous, genetically their broods tend to be sired by multiple males. Now, it is known that genetic monogamy is actually extremely rare in the wild. Females of most taxa will mate with multiple males for varied reasons including “trading up” on the quality of the male if their first mate was of poor quality and acquisition of food in species where males provide nuptial gifts (reviewed in Simmons 2001).

Sperm Competition in Insects

Parker (1970) defined sperm competition as:

...competition within the female reproductive tract, between the ejaculates of two or more males for fertilization of female’s eggs.

At its simplest, sperm competition can be viewed as a race or lottery; the faster a male’s sperm travels through the female reproductive tract, or the more sperm he invests in a given ejaculate, the greater the probability that he will “win” fertilization of the female’s eggs.

To date, more is known with regard to sperm competition in the insects than in any other

taxonomic group, due to the ease with which researchers can observe and manipulate them, both in the laboratory and, to an extent, in the wild. There is huge variation in the ways males have evolved to be successful in sperm competition, which is an extremely powerful evolutionary force. Classic early studies showed that in the dark-winged damselfly (*Calopteryx maculata*), the end of the male penis is spoon shaped, allowing the male to scrape any residual sperm from a previous mating from the female reproductive tract, before ejaculating his own. In some butterfly species such as the green-veined white (*Pieris napi*), males transfer a chemical “anti-aphrodisiac” or pheromone to females during mating; this chemical is extremely efficient in deterring subsequent rival males, who will not even attempt to court with the female (Andersson et al. 2000). Finally, male Indian meal moths (*Plodia interpunctella*) are able to determine whether a female has previously mated and adjust accordingly the amount of sperm they ejaculate into the female reproductive tract (reviewed in Wedell et al. 2002). This “strategic sperm allocation” allows males to maximize the chances of their sperm fertilizing the female’s eggs, when sperm competition operates in the manner of a lottery.

Battle of the Sexes

It is not only males that are able to influence the outcome of sperm competition. In 1996 Bill Eberhard published a landmark text, “Female Control: Sexual Selection by Cryptic Female Choice,” which overturned much of sperm competition theory. In it, he suggested that while males were under selection to maximize their success under sperm competition, females were also under to selection to maximize their reproductive success. As noted above, it was well known that females were choosy when deciding to mate with, but Eberhard suggested that they were also choosy after copulation had ended. By manipulating sperm storage and use within her reproductive tract, females could bias paternity toward the sperm of preferred males and thereby influence the outcome of sperm competition.

Concrete experimental evidence that females could bias paternity, thereby exerting what is now called cryptic female choice, was not forthcoming. Indeed, the term cryptic female choice refers to the fact that it occurs within the female reproductive and is therefore difficult – if not impossible – to observe. In 2000 it was showed that in the red flour beetle *Tribolium castaneum*, the intensity of male courtship behavior during mating – in this species the rubbing of the female wing cases with his legs – is directly correlated with male fertilization (Edvardsson and Arnqvist 2000). This was potentially the first experimental study to suggest that females were choosing males on the basis of the intensity of their courtship and biasing utilization of their eggs accordingly.

There are now increasing numbers of studies reporting cryptic female choice in insects. In the cricket *Teleogryllus oceanicus*, females have been shown to assess how closely related a mate is and bias sperm storage toward that of unrelated males (Tune et al. 2013); presumably this is a mechanism of avoiding producing poor quality offspring as a result of inbreeding. In some dragonflies and damselflies, females eject the sperm of non-preferred males prior to oviposition while presumably favoring the utilization of preferred males.

Although covered elsewhere in this volume, it is worth noting here that such interactions between males and females can result in a coevolutionary arms race or “sexual conflict” (Parker 1979). Males of numerous species have evolved tactics which assist them in preventing females remating with other males, or in biasing female utilization of their sperm, to maximize their reproductive success. Conversely, females may wish to remate, if, for example, their first mate is of poor quality, or if they gain food from the male during mating, as noted before. Such conflicting selection pressures can result in coevolutionary cycles whereby males evolve an adaptation to minimize female remating, which results in females evolving a counter-adaption in response to the male adaptation. The classic example is seen in the fruit fly *Drosophila melanogaster*, where males incorporate seminal fluid proteins in their ejaculate which induce female oviposition and reduce

remating, but also decreases female lifespan (c.f. Wigby and Chapman 2004). However, it has been shown that females can evolve a counter-adaptation; when subjected to several generations of increased mating rates and thereby increased levels of sexual conflict, females evolved to reduce the impact of male seminal fluid and their lifespan increased (Wigby and Chapman 2004).

Into the Twenty-First Century

As noted previously, it was the advent of the molecular age and revolutions in technology that allowed researchers to investigate sperm competition in ways that had not previously been possible; indeed, many long-standing paradigms were overturned as a result. As technology has become increasingly cheaper, and increasingly refined, we continue to make breakthroughs in the study of sperm competition in insects. In 2010, for the first time, a team led by Mollie Manier and Scott Pitnick used green- and red-fluorescent proteins to stain sperm in *D. melanogaster* and were thereby able to visualize the movement of competing sperm, *within the female reproductive tract*. The technique led to them discovering that, as explained in the previous section, females were ejecting the sperm non-referred from their reproductive tract after mating.

By essentially artificially inseminating bumblebees (*Bombus terrestris*), Boris Baer and coworkers were able to show that the males produce a mating pug inside the female reproductive tract that physically prevents the female from remating. Additionally, chemical analyses showed that the mating plug contains a fatty acid called linoleic acid, which alters and manipulates the behavior of the queen into not remating. Thus, bumble females are essentially monandrous, mating only once during the course of their lifespan, as they are forced into doing so by the male.

Finally, in 2014, Michal Polak and his group used microscale laser surgery to manipulate the size of a sexually selected ornament of male *Drosophila* flies. These “sex combs” are a microscopic patch of bristles on the front of the forelegs. They found that in addition to being

sexually selected via female preferences, the sex combs also functioned to assist the male in keeping hold of the female during copulation; males who had them removed entirely were unable to copulate.

It is estimated that approximately 10% of species are largely monandrous, with females only mating once during their reproductive lifespan (Taylor et al. 2014). We are still unsure why they are monandrous and therefore not subject to sperm competition, but one thing is clear. In animals that are subject to sperm competition, the little things really matter, and only now do we have the techniques to explore why.

Conclusion

The reproductive lives of insects are remarkable and continue to fascinate the scientists that devote their lives to their study. It has been a long and winding road since Darwin first defined sexual selection in 1869 and Parker first defined sperm competition a century later. Yet we still continue to reveal the marvel that is the inner workings of insect sex, and no doubt, with the arrival of the genomics era and the ever advancing march of technological advancement, there is more to come.

Cross-References

- [Avian Sperm Competition](#)
- [Human Sperm Competition](#)
- [Non-Primate Mammal Sperm Competition](#)
- [Primate Sperm Competition](#)
- [Sperm Competition Theory](#)

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Insight

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Synonyms

[Insightful behavior](#); [Rule extraction](#)

Definition

Insight can be attributed to animals' ability for fast integration of behaviors gained from their past experience and effectively applying this

experience for solving a problem as a meaningful whole, in the context of a situation. W. Thorpe (1963) defined “insightful behavior” as “the sudden production of a new adaptive response not arrived at by trial behavior” and “the solution of a problem by the sudden adaptive reorganization of experience”.

Introduction

Wolfgang Köhler (1924) first revealed experimental evidence of insight in chimpanzees basing on ideas of Gestalt psychology. His experiments showed chimpanzees as using planning and foresight, that is, cognitive reasoning to solve a problem. Köhler devised an arrangement in which all of the elements necessary for the solution of the problem were in full view of the animal. One of the most often referred-to examples of problem solving by insight concerns Sultan, a chimpanzee, whom Köhler regarded as the brightest of a number of apes he worked with. Sultan sat in his cage, in which there was also a short stick. Outside the cage there was a longer stick, which was beyond Sultan's reach, and even further away was a reward of fruit. Sultan first tried to reach the fruit with the smallest of the sticks. Not succeeding, he tried a piece of wire that projected from the netting in his cage, but that, too, was in vain. Then he gazed about him and after a long pause suddenly picked up the short stick once more, came to the bars directly opposite to the long stick, dragged it towards him with the auxiliary, seized it, and went with it to the point opposite the objective which he secured. From the moment that his eyes fell upon the long stick, his procedure formed one consecutive whole.

However, in his late publications, Köhler considered a notion of insight rather fuzzy and was frustrated about not understanding the nature of subject's awareness about relations between things that he called insight. In particular, Köhler distinguished two kinds of mistakes related to the problem solving in chimpanzees, that is, “good mistakes” and “bad mistakes”. If the chimpanzee tried to affix a box to a wall in order to reach a

banana from the top of the wall, it is a “good mistake” that can serve as evidence of the animal’s understanding about dimensions; the chimpanzee is simply unaware of box’s properties. But chimpanzees in Köhler’s experiments also demonstrated a lot of “bad mistakes”. For instance, in one setup, chimpanzees could only get bananas by removing a box. Here was something, Köhler expected, that even his awkward chimpanzees could “do at once.” And yet, to his astonishment, the chimpanzees had difficulties in solving such problems; they often drew into the situation the strangest and most distant tools and adopted the most peculiar methods, rather than removing a simple obstacle which could be displaced with perfect ease. Many years later, Elisabetta Visalberghi (2002), referring to her observations on adult male capuchin pounding an unshelled peanut with a boiled potato, raised a question why capuchins were doing something smart in a silly way, or something silly in a smart way.

Insightful behavior in Human- and Non-Human Animals

The concept of insight introduced by Köhler has been immediately appreciated in human studies. Psychologists identified this phenomenon as “aha!” (“Eureka”!) solutions referring to the well known Archimedes legend. Maier (1931) suggested problems for studying human insight similar to those that were solved by apes, for example, the two-string problem: two strings hanging at two arm-span widths apart need to be tied together, and the items in the room may help. Many human studies are based on human-specific skills such as solutions of Checkerboard problems (Kaplan and Simon 1990) and verbal problems (Jung-Beeman et al. 2004). At the same time, many modern comparative studies of insightful behavior are performed simultaneously on animals and human infants.

In modern cognitive ethology, insight is considered a part of rule extraction, that is, of the learning class which includes casual reasoning

and concept formation. Insightful behavior is based on the animals’ capacities for formation of “what-leads-to what” expectancies which, in turn, are closely connected with their exploratory activity (for details see: Reznikova 2007).

Currently experimental paradigms for studying insight in animals are often based on “folk physics” of animals, that is, their common-sense understanding of how the world works, as well as why it works in the way it does. For example, many experiments testing birds’ abilities to use a physical object to obtain food that is out of reach have involved the string-pulling task known since ancient times. In experiments of Heinrich (1995) with common ravens, it is required that the bird repeats the following sequence several times: reaching down from the perch, grasping the string with the beak, pulling the string up, placing the pulled-up loop of string on the perch, then pressing a foot down on the loop and letting go with the beak, so that the bird can reach down to pull up another loop. Keas (New Zealand parrots) completed the first trial within a few seconds, by showing only goal-directed behavior, thus executing the solution in a manner that could not be improved upon in further trials (Werdenich and Huber 2006). Hooded crows could successfully solve tasks in which the strings did not cross each other but were arranged in such a way that the bait was opposite the end of an “empty” string. They also solved a task in which the bait was attached to each of two strings but one string was broken, preventing it from pulling the bait (Bagotskaya et al. 2012). All these results demonstrate birds of several species as understanding of means–end relationships, i.e., the apprehension of the cause–effect relation between strings, food, and certain body parts.

Another problem also known from ancient times which is involved in insight studies comes from the Aesop’s fable in which a thirsty crow threw stones into a pitcher to raise and drink the otherwise inaccessible water. In the experiment of Bird and Emery (2009), the rooks solved a similar problem: they dropped stones into a tube of water in order to bring a floating worm within reach. Orangutans

(Mendes et al. 2007) and chimpanzees (Hanus et al. 2011) also have insightfully solved an analogous version of the problem. Apes were presented with a tube quarter-filled with water. Floating on the surface of the water was a peanut. To solve the problem, the apes needed to collect water from a drinking container in their mouths and spit it into the tube in order to raise the water level and gain the peanut. After trying to reach the peanut with their fingers or mouths, animals spat water into the tube in order to raise the level and so gain the reward on the first trial. Chimpanzees and orangutans performed better than 4-year-old children and worse than 6- and 8-year-olds in the same experiments.

Conclusion

Insight can be considered a part of the mental process that relates to understanding relationships. In problem solving, the experience need not be directly associated with the problem at hand. Sometimes, when presented with a new problem, an animal will solve the problem on the first attempt using the previous experience in dealing with the component parts of the problem, although they were never met together in just such a way before. There is much work to be done to extend our understanding of whether at least some species can take into account imperceptible physical forces or they are only capable of reasoning about perceptible things. To clear up this problem to a lesser or greater extent, developmental studies are needed that will allow a distinction to be made between inherited and acquired behavior.

Cross-References

- [Evolution of Tool Use](#)
- [Innate and Learned Tool Use](#)
- [Intelligence Testing](#)
- [Nonhuman Tool Use](#)
- [Primate Tool Use](#)
- [Role of Experience in Tool Use](#)
- [Smarties Task, The](#)

- [Technical Intelligence Hypothesis, The](#)
- [Tool Manufacturing](#)
- [Tool Play](#)

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Insightful Behavior

- [Insight](#)

Insist on No More than Equity

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Synonyms

[Distributive justice](#); [Equity](#); [Reciprocity](#)

Definition

“Insist on no more than equity” is one important aspect of reciprocity and a way of solving social dilemmas cooperatively.

Introduction

Equity can be defined as the distribution of resources between people according to their contribution or necessity. Insisting on no more than equity is a characteristic of successful cooperative strategies in social dilemmas, that is, situations in which individuals interests are in conflict and they may be tempted to adopt selfish choices. Axelrod (1984) states that “a strategy based on reciprocity can allow the other player to get the reward for mutual cooperation, which is the same payoff it gets for itself when both strategies are doing their best” (p. 137). In other words, reciprocity means that individuals will receive back from others the equivalent of what they invested, and equity in reciprocity means that everyone in an interaction will eventually get their fair share. Thus, equity seems to be a condition for reciprocity.

Whereas equity means treating others according to their characteristics and actions, equality means treating other in the same way. For instance, someone sharing food equitably will give more food to those who are hungrier or worked harder, while someone sharing food equally will share the same amount to everyone regardless of effort or need. Equity concerns and

reciprocity in humans underlie our sense of fairness and social institutions, most prominently our justice systems. This entry explores how equity and fairness manifest in humans, from an evolutionary perspective.

The Relationship Between Reciprocity and Equity

Evolutionary models of altruism are in essence attempts to explain the occurrence of altruism in what otherwise are considered selfish individuals, from a genetic standpoint. The reason for this is that evolution tends to favor the survival and reproductive success of lower levels of organization. Thus, any strategy that favors the reproduction of genes will tend to spread in a group, even if at the expenses of organisms and groups. This is why group selection is considered rare in nature, because selection at an individual level will tend to be more powerful than at the group level. This reasoning can be applied to the evolution of cooperation from a previous non-cooperative state; if selfish individuals benefit from cooperation, but have less costs or more benefits than cooperators in a group, they will tend to outperform cooperators in the long run (that is, leave more descendants in the next generations).

Axelrod (1984) introduced “insist on no more than equity” as one of the strategies to promote reciprocal cooperation in the long run, based on computer simulations of multiple rounds of an economic game called the prisoner’s dilemma. In these simulations, called computer tournaments, several strategies submitted by game theorists competed in repeated interactions, until one or more of them became victorious. The prisoner’s dilemma is illustrated by the example of two accomplices who have been arrested by the police and are kept in separate rooms. They cannot communicate with each other and have to make one of two decisions: either “cheat” and denounce the other prisoner, thus getting a shorter sentence; or “cooperate” and keep quiet, therefore receiving a longer sentence. However, the length of the sentences are dependent on both prisoners’ decisions, in such way that cheating the partner is

always the best individual choice in the short term. In this scenario, the strategy that was classically victorious in the computer tournaments used a simple heuristic: always cooperate first, repeat the partner previous move in subsequent interactions. Due to its simple reciprocal rule, the strategy was called Tit-For-Tat, and it is an equitable strategy because in the long run partners who adopt this strategy will end up with the same amount of points.

Reciprocity in humans and other species has probably evolved as a social strategy to maintain mutual cooperative relationships (Baumard et al. 2013; Trivers 1971). Reciprocity can be either direct, that is, when an individual is reciprocated by the same individual they have helped before; or indirect, that is, when an individual is helped by someone else than those they have helped before (Alexander 1985). It can also be either immediate or delayed. When immediate, it does not pose much problem for those involved, given that cheating is difficult. Delayed reciprocity, in which an individual receives a return for his helping actions some time in the future, leaves room for exploitation. Humans are among the rare examples of delayed direct reciprocity in the animal kingdom (another famous example are the vampire bats, Carter and Wilkinson 2013; Trivers 1971).

For reciprocal interactions to take place and promote successful cooperation, individuals must be able to judge other actions based on past behavior, contribution to the interaction, and chances of having the helping act reciprocated within their lifetime (Stevens et al. 2005). Or, in absence of these skills, individuals should be able to detect environmental cues such as territoriality or similarity, which make repeated interactions between the same partners possible without sophisticated mechanisms for recognition (Axelrod and Hamilton 1981; Riolo et al. 2001). In addition, social groups must be constituted in ways that allow for non-reciprocators (also called cheaters or free-riders) to be excluded or punished. Obligatory reciprocal interactions, such as collaborative foraging, could have led to the evolution of unique cooperative skills regarding the equitable sharing of resources, and the

subsequent creation of social norms and institutions (Tomasello et al. 2012).

Equity in Human Societies

Morality can be defined as cooperative behavior (Curry 2016). Several authors proposed that the mechanisms of direct and indirect reciprocity underlie human moral systems. If an individual is not helpful with or good towards others, they might lose the others support when they need it. The same logic is applied in interactions with friends and romantic partners (Buss 2000), and it is even more relevant in the context of small-scale societies, which rely on mutual interdependence to survive in harsher environments (Cronk et al. 2019).

The Golden Rule can be summarized by: “do to others as you would have them do to you,” and it appears in different forms across many religions and cultures (Blackburn 2001; Wattles 1996). It is considered, in its purest form, as a call for generosity towards others. However, the Golden Rule as it is practiced within societies takes up meaning more closely associated to the notions of reciprocity and equity. Thus, the Golden Rule is an example of the application of the principle of insisting on no more than equity across societies and an indication of the universality of this trait in humans.

The way societies organize themselves around their moral systems, however, can vary across social and economic conditions. One popular way of measuring reciprocity, equity, and fairness across societies is the use of economic games. Henrich et al. (2005) ran experiments using three of such games (the ultimatum game, the dictator game, and the public goods game) in 15 small-scale societies with varied levels of social and economic conditions. They found significant differences across societies in the amount donated in these games, more specifically with regards to the level of market integration and local importance attributed to cooperation in each society.

Consider, for example, the Aché and the Hadza, both considered small-scale foragers. Both societies are often used as models to test

hypotheses about the mode of living of early humans (Apicella et al. 2012; Marlowe 2005) and are widely viewed as egalitarian societies. However, they differ with regards to their sharing behavior. The Aché spontaneously share more meat with other members of the community, while the Hadza reluctantly share meat with others, and mostly due to social pressure. Thus, when asked to play the ultimatum game (in which a participant receives a certain amount and makes an anonymous offer to another participant, who can then accept it or decline it; if they decline it, both participants get nothing), the Aché had had higher offers (40% or more of the amount) and lower rejection rates than the Hadza, thus showing greater concern with equity in their decisions in the game.

Equity Across Development

There is mounting evidence of universally evolved sense of fairness in humans, even though with differences in developmental trajectories influenced by cultural and demographic factors. In Western countries, earlier evidence from classical psychological studies indicated that children only developed equity concerns by the age of six or seven (Damon 1977). Piaget (1932), based on observations of Swedish children's games, proposed an even later stage: "between 7 and 10 sheer equality in all its brutality still outweighs equity" (p. 216). More recent evidence, however, shows that preschool children are able to take effort and merit into account when distributing resources (Baumard et al. 2012).

However, this apparent contradiction might explained by the developmental trajectory of prosocial behavior, as revealed by a study across several different cultures (House et al. 2013), which shows that young children in these cultures show a similar pattern of behavior around the age of three, which then declines until the age of five or six, and increases again but in diverse ways across different cultures. More importantly, these differences were only found for costly prosocial behavior, which indicates the role of culture in influencing patterns of behavior that are socially

enforced, even when individual interests are in conflict with those of the group.

Western European 3-year-olds are able to judge others' contribution in a joint task and share accordingly, thus taking merit into account (Baumard et al. 2012; Paulus 2015). Moreover, children seem capable of distinguishing between different characteristics while sharing goods. Thus, they take merit, but not gender, when making sharing decisions, thus sharing equally among gender, but not among those who contribute more and less to the activity (Rizzo et al. 2018). Children in the United States increasingly take effort into account, even more than productivity (Noh et al. 2019). Children from more individualist cultures such as the United States, however, may tend to share more with less wealthy individuals, even if they make less effort in a task (Paulus 2015); whereas children from more collectivist societies such as China may tend to focus on the effort and ignore wealth inequality as a factor in their sharing decisions (Chai and He 2017). Thus, though humans show a universal propensity to develop equity concerns and a sense of fairness, both traits may vary across development according to social and cultural factors.

Conclusion

Insisting on no more than equity is a successful strategy in the context of reciprocal cooperation. It is likely that equity concerns in humans have given rise to our sense of fairness and, in interaction with cumulative cultural evolution, led to the evolution of our social institutions (Boyd and Richerson 2009). Equity is a component of fairness, and it protects individuals from exploitative relationships, while also promoting more equitable relationships between those with different amount of resources.

In human societies, these principles are present in many institutions, even if it did not prevent the rise of social inequality. This is probably due to a combination of reciprocal and nepotist systems, in which individuals will seek to profit the maximum for themselves and their families and closest relatives and friends, while also seeking from the

same support when they need. In an individual level, humans and other animals will seek reciprocity from their allies and close kin, but in a group level, social institutions will be often in conflict with individual interests to assure cooperation among its members. A relevant aspect of this is that, once social groups are in competition with each other, those societies who foster more cooperation among its members will tend to out-compete those who do not. In this context, equity tends to be a rule among the members of the same group (Romano et al. 2017) but not necessarily with regards to other individuals.

Cross-References

- [Morality](#)
- [Morality Is Cooperation](#)
- [Prosocial Behavior](#)
- [Reciprocity](#)
- [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)
- [Strategies for Successful Cooperation](#)

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Instil Confidence

- [Projected Confidence](#)

Institutional Anomie Theory

- [Sociocultural Theories of Violence](#)

Instruction

- [Scaffolding in Learning](#)

Instructional Design

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Synonyms

[Organising instruction](#); [Teaching procedures](#)

Definition

How to design instructional procedures.

Introduction

Governing principles of instructional design can be derived from our knowledge of human cognition. In turn, the characteristics of human cognition are intricately bound in the structures and processes of evolutionary psychology. Cognitive load theory (Sweller et al. 2011) uses human cognitive architecture and evolutionary psychology to devise novel instructional procedures. Only some categories of knowledge can provide substantive subject matter for instruction with evolutionary psychology determining which subject matter can be meaningfully taught. Furthermore, the processing characteristics associated with teachable information closely mimic the information processing characteristics of biological evolution allowing us to use the well-known processes that guide biological evolution as a template to assist in understanding aspects of human cognition relevant to instructional design. Categories of knowledge that are relevant to instruction will be discussed first, followed by the cognitive architecture that governs the manner in which instructionally relevant information is processed, and ending with cognitive load theory's use of this base to generate instructional procedures.

Categories of Knowledge

Most knowledge categorization schemes do not have instructional implications. One scheme, introduced by David Geary, is directly relevant to instructional design (Geary 2008; Geary and Berch 2016; Sweller 2016). Geary divided knowledge into biologically (or evolutionary) primary and secondary knowledge. All knowledge can be placed into one or other or a combination of these two categories depending on the evolutionary status of the relevant knowledge.

We have specifically evolved to acquire biologically primary knowledge. Examples are

learning to listen and speak a native language, learning to recognize faces, generalizing learned knowledge, regulating our thought processes, or using general problem-solving strategies. Biologically primary knowledge has several important characteristics. It tends to be acquired relatively easily and automatically without conscious thought. As can be seen from the above examples, it is frequently associated with generic-cognitive skills (Tricot and Sweller 2014) that we have specifically evolved to acquire because of their importance. Biologically primary skills are usually acquired at different evolutionary epochs, and as a consequence, they tend to be unrelated and modular. From an instructional perspective, while they can be improved with practice, they cannot be taught because they are naturally acquired without instruction.

In contrast to biologically primary skills, secondary skills are much more closely related to instructional issues. These are skills that we can acquire but that we have not specifically evolved to acquire. They are important for cultural reasons. Examples come from virtually every topic taught in education and training institutions. Such institutions were devised precisely in order to teach biologically secondary skills that were deemed to be culturally important but which we had not evolved to acquire. While most such skills rely on biologically primary knowledge for their acquisition (Paas and Sweller 2012), the manner in which they are acquired is very different to the acquisition of primary knowledge. Secondary skills can be difficult to acquire despite encapsulating far less information than biologically primary skills. They require conscious, deliberate effort rather than being acquired automatically. Most commonly they are domain-specific rather than generic-cognitive in nature. As an example, while we may have evolved to automatically acquired a general problem-solving strategy to attempt to solve any problem that we encounter, we have not evolved to automatically acquire the means to solve a problem such as $a + b = c$, solve for a . We must deliberately and consciously learn the relevant procedures, and we are assisted in that task by explicit tuition (Kirschner et al. 2006; Sweller et al. 2007).

Instructional design is largely concerned with the best procedures for assisting learners to acquire biologically secondary knowledge. Those procedures depend on aspects of human cognitive architecture associated with the acquisition of secondary knowledge. That architecture allows humans to process information analogously to the manner in which evolution by natural selection processes information.

Human Cognitive Architecture

Five basic principles may be used to describe how the human cognitive system processes biologically secondary information. Those five principles also can be used to indicate how evolution by natural selection processes information. Both human cognition and evolution by natural selection provide examples of analogous, natural information processing systems (Sweller and Sweller 2006).

The Information Store Principle

In order to function in a natural environment, a natural information processing system relies on a very large store of information. In the case of evolution by natural selection, a genome provides that store. Long-term memory has a similar function in human cognition. If anything is learned, if a new skill is acquired, it has been stored in long-term memory. Without such storage, nothing is learned. It follows that the major goal of instruction is to assist learners to store biologically secondary information in long-term memory. Our ability to store information in long-term memory is biologically primary. Cognitive load theory and its instructional prescriptions are based on the assumption that a major purpose of instruction is to store large amounts of information in long-term memory.

The Borrowing and Reorganizing Principle

Given the enormous size of natural information stores, how such information is acquired becomes an immediate question. In the case of evolution by natural selection, the process is well-known. Genomes are borrowed from ancestors during

sexual or asexual reproduction. In the case of sexual reproduction, two immediate ancestors are required allowing the information to be reorganized. In the case of human cognition, the acquisition and storage of large amounts of information in long-term memory also require the information to be borrowed from others before being reorganized. We imitate other people, listen to what they say, and read what they write in order to obtain information to be stored in long-term memory. Information is reorganized during storage when it is combined with previously stored information. Our ability to obtain biologically secondary information from other people is biologically primary. Given the importance of obtaining information from other people, instructional design needs to be organized in a manner that facilitates information transfer. Cognitive load theory was designed for this function.

The Randomness as Genesis Principle

While obtaining complex information from elsewhere using the borrowing and reorganizing principle is efficient, it is not always possible. The information may not be readily available to be borrowed or may not as yet even been assembled in a form that allows borrowing. Information that is borrowed must at some point have been initially assembled or created. The manner in which evolution by natural selection creates novel information is well-specified. Random mutation is the core of the process with all variations between all life forms assumed to be ultimately sourced to mutation. It is a random generation and test process with successful mutations retained for subsequent generations and unsuccessful mutations resulting in fewer or no offspring.

The randomness as genesis principle plays the same role in human cognition as in evolution by natural selection. When required information cannot be obtained from others via the borrowing and reorganizing principle, it may be created during problem-solving. If we do not have access to information because we do not have access to the required people or to their writing or if the required information has never been assembled by anyone else, we can attempt to assemble it ourselves by conducting research. Just as all

novel genetic variations can be sourced to random mutations, all novel ideas ultimately can be sourced to a random generation and test process during problem-solving.

While we sometimes have to engage in problem-solving to obtain information, it is neither an effective nor an efficient mode of learning. Obtaining information from others via the borrowing and reorganizing principle is far more effective and efficient, a factor that needs to be considered when designing instruction.

The Narrow Limits of Change Principle

The randomness as genesis principle has structural implications. The number of possible random combinations of elements increases exponentially with increases in the number of elements that must be processed. Both evolution by natural selection and human cognition have structures and functions designed to limit the number of novel elements of information that can be processed at any given time.

In the case of evolution, the epigenetic system is used to limit the number and the genome location of mutations. For example, if environmental pressures require diversity, the number of mutations can increase by a factor of many thousands. Nevertheless, in general, the number of mutations tends to be limited in order to ensure that the organizational integrity of the genome is not destroyed. As a consequence, the randomness as genesis principle is constrained by the narrow limits of change principle.

Working memory plays a similar role in human cognition as the epigenetic system plays in evolutionary biology. When dealing with novel information, working memory constrains the number of elements of novel information that can be processed and the duration that they can be held. The contents of long-term memory are protected by these limitations.

This principle is central to the instructional design prescriptions of cognitive load theory. When instructing learners, it is important to organize the instruction to minimize the working memory load imposed. Ignoring the working memory limitations of learners invites instructional failure. Cognitive load theory has generated

a large number of cognitive load effects indicating instructional procedures designed to lessen extraneous cognitive load and so facilitate learning which consists of the transfer of information to long-term memory.

The Environmental Organizing and Linking Principle

The narrow limits of change principle apply only to novel, unorganized information from the environment. It does not apply to the organized information stored in the information store. With respect to evolution by natural selection, the epigenetic system permits large amounts of stored, genomic information to be used to govern activity. Based on environmental signals, the epigenetic system can activate some genes and suppress others to determine activity appropriate to that environment. There are no known limits to the amount of stored information that can be used. In that way, a liver cell and a kidney cell with identical DNA have vastly different phenotypes resulting in vastly different structures and functions.

Similarly, the capacity and duration limits of working memory relevant to the narrow limits of change principle disappear when dealing with organized information from long-term memory. Environmental signals are used to activate relevant information stored in long-term memory while ignoring irrelevant information. Relevant information then can be transferred to working memory to govern environmentally appropriate action, with no known limits to the amount of information transferred. It is in this manner, that education transforms us. We can successfully act in a manner that would be impossible without acquired, biologically secondary information.

Conclusions: Cognitive Load Theory and Instructional Design

This cognitive architecture provides a base for the instructional procedures generated by cognitive load theory. The procedures apply to biologically secondary, domain-specific information that we have not specifically evolved to acquire. That information provides the instructional content of

education and training. It needs to be explicitly presented to learners in a manner that reduces working memory load. Once learned, it is stored in long-term memory to be transferred to working memory in order to govern behavior that is appropriate for a given environment.

There are many instructional procedures generated by cognitive load theory (Sweller et al. 2011) with new procedures under constant development (Chen et al. *in press*). Each procedure is designed to facilitate the transfer of information to long-term memory by reducing unnecessary working memory load. All recommended procedures are tested for relative effectiveness using multiple, randomized, controlled trials. The considerable variety of cognitive load effects generated by the theory all have in common the assumptions that the domain-specific, biologically secondary information that forms the subject matter of instruction must be stored in long-term memory for later use and that storage is best effected by explicit presentation of the information in a manner that reduces working memory load during acquisition. These assumptions flow directly from the evolutionary psychology base and consequent cognitive architecture that undergirds the theory.

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Instructionist

- ▶ [Blank Slate, The](#)
- ▶ [Information Processing and the Interdisciplinary Perspective](#)

Instrument

- ▶ [Advanced Tools of Neanderthals](#)

Instrumental Associations

- ▶ [Associative Learning](#)

Instrumental Conditioning

- ▶ [Conditioning and Association](#)
- ▶ [Operant Conditioning](#)

Instrumentation

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Intelligence

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Synonyms

[Cognitive ability](#); [Intellect](#); [Intellectual ability](#); [Learnability](#)

Definition

An influential definition of human intelligence is “a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It is not merely book learning, a narrow academic skill, or test-taking smarts. Rather, it reflects a broader and deeper capability for comprehending our surroundings – ‘catching on,’ ‘making sense’ of things, or ‘figuring out’ what to do” (Gottfredson 1997a, p. 13).

Introduction

One of the striking facts about our universe is that it contains intelligence. Somehow, planet Earth went from a barren, scorching planet into a flowering display of life. Eventually, *Homo sapiens* (“wise man”) was the first species on Earth, and possibly in the universe, that started to talk, generate rich cultures, send conspecifics and electronics to space, and invent abstract algebra and calculus.

Why did intelligence evolve in the first place? This question seems unreasonable at first sight because it is hard to imagine anything more useful than intelligence. Nevertheless, intelligence comes packed with disadvantages. A key hint about the cost of intelligence is the fact that it is relatively rare in nature. In fact, many organisms do just fine without a brain at all. Moreover, intelligence has evolved independently only a few times (convergent evolution) in some mammals, cephalopods (e.g., octopi), and birds (Emery and Clayton 2004). Further, although just 2% of the total body weight of humans, the brain consumes 20% of the calories consumed (Aiello and Wheeler 1995), and Mother Nature does not spend calories unnecessarily. Nevertheless, the brain expanded threefold in just under 2 million years, suggesting that selective pressures forcefully aligned to produce intelligence in the *Homo* line.

This entry will briefly discuss (1) the science and psychometrics of human intelligence, (2) how intelligence works from an information

processing point of view, and finally (3) models and evidence on why human intelligence evolved.

The Psychometrics of Intelligence

Key parts of human intelligence are the abilities to learn, reason, and solve problems (Plomin and von Stumm 2018). These abilities to learn and reason also differ dramatically between people and can be reliably measured with tests such as the Wechsler intelligence scale (Wechsler 2008) and Ravens progressive matrices (Raven and Court 1998). The latter test consists of a series of multiple choice questions based on matrices. The subject is shown a 3×3 matrix containing symbols where the last one is omitted, the subject then chooses a symbol from multiple possible responses based on identification of the underlying rule generating the matrix. In modern measurements of intelligence, a person's intelligence is estimated by taking the subject's raw score on several mental abilities and comparing it to the average performance of a representative group in the subject's age range. This is called *deviation intelligence quotient* (IQ) (Urbina 2011). The normalized IQ distribution has an average of 100 and a standard deviation of 15. Intelligence tests are important clinically, because they are used to diagnose intellectual disability in children and adults (a diagnostic criteria being IQ below 70) and to assess milder cognitive deficits caused by brain injury and neurodegenerative disease.

A classic empirical finding, first made by Spearman (1904), is that test scores on several specific and different intellectual abilities covary and hence form the statistical abstraction called general intelligence (*g*). In other words, people who score well on one particular cognitive ability tend to score well on others. Based on these findings, general intelligence is understood psychometrically as a latent trait, meaning that it is not measured directly, but inferred from several measured cognitive abilities such as verbal and spatial abilities. However, every cognitive domain also has some degree of specificity. For instance, it is possible for an individual to score above average in logical ability but below average in verbal

ability. In fact, a large controversy in the history of intelligence theory and research concerns how to understand both the general and the specific aspect of intelligence. Many theoreticians agree that *g* is important for all mental abilities (Jensen 1998), while others claim that humans have multiple and separate intelligences, such as interpersonal and musical ability (e.g., Gardner 2011). However, the latter theory seems to be a synthesis of general and specific intelligence, as well as noncognitive abilities and personality traits (Visser et al. 2006).

Today intelligence has emerged as a generalist concept that influences many real-life outcomes. Most obviously, it predicts educational attainment (Jensen 1998), but intelligence is also a strong predictor in a wide range of nonacademic areas. In fact, intelligence predicts general health and longevity (Hart et al. 2003), and it is the single best predictor of success in job training and performance, with predictive power increasing with job complexity (Schmidt and Hunter 2004). Overall, intelligence is the best single predictor for both favorable socioeconomic outcomes, such as good education, occupation, and income, and negatively for unfavorable outcomes such as adult poverty, incarceration, and chronic welfare use (Gottfredson 1997b; Gottfredson and Deary 2004).

How Intelligence Works

How can a vast collection of unintelligent neurons produce intelligent behavior? Intelligence cannot, of course, arise out of lumps of brain matter alone. Instead, intelligence is produced by the *computations* going on within the neural tissue. That is, human minds can do intelligent things because nervous systems represent, process, and transform information (Clark 2014). One key property of a computational system is the ability to change its operation based on information (Cosmides and Tooby 2002). Hence, computational processes can be seen as independent of the physical machinery in which it occurs. For example, the plastic cover on a thermostat is not a computational system, but the thermocouple that responds to a particular room temperature and turns on the

switch that activates the heat-generating parts of a furnace is a computational system. Similarly, the visual system in the human brain that detects the presence of a predator and activates muscles that either makes a person run away if the predator has seen it, or freeze if it has not, is a computational system (Cosmides and Tooby 2002).

How does the computing in neural circuitry actually work? One approach in cognitive science, called *connectionism*, uses the insights gained from artificial neural networks to shed light on how intelligence can be produced (Elman et al. 1998). The design of computer-programmed artificial neural nets works by many interconnected nodes that are modified by a learning rule that, over time, strengthen particular connections to produce the desired outcome (Striedter 2005). Hence, in the connectionist perspective, the knowledge base residing within neural structures are composed of sets of simple processors linked by a daunting mass of wiring and connections (Clark 2014).

However, another important approach, called the *physical symbol system*, is that computation works by more abstract symbol manipulation (Newell and Simon 1976). This is akin to how a digital computer works, namely, by manipulating symbols (the famous zeros and ones), while the CPU do operations on them.

Although you can get far with simple connectionist models for modeling intelligent human behavior, it also runs into problems. Generally, they can fail to capture the flexibility and power of everyday reasoning. For example, when representing complex relations between bits of knowledge or generalizing abstract relationships, hence, brain circuitry that produces intelligent behavior might best be construed as a complex combination of both connectionism and symbol manipulation (Marcus 2003).

Modularity

Within classical evolutionary psychology, it is often thought that the mind consists of several special-purpose modules that solve particular problems that were relevant in past evolutionary environments (Barrett and Kurzban 2006). This has been dubbed the *massive modularity*

hypothesis. In this view, the mind contains a vast array of tools that solve particular problems, rather than content-independent, abstract reasoning devices.

There are good reasons to believe that complex brains are modular. For example, within robotics research, installation of special-purpose tricks is often the only effective ways of generating adaptive behavior in real time (Clark 2014). It is likely, therefore, that the mind consists of many specialized subsystems running in parallel, rather than a few general problem solvers.

However, how can the modularity view explain intelligence, that clearly involves usage of content-independent reasoning to solve novel problems? This is in itself a difficult problem because it is hard to conceive how the alternative, namely, content-free and general-purpose minds, could generate intelligence. This would be akin to a smart phone solving complex tasks (reading maps, taking pictures, and so on) without any special-purpose apps installed on it.

A useful distinction is to consider two types of intelligence: (1) dedicated intelligence and (2) improvisational intelligence. Dedicated intelligence is the degree to which a neural program, or module, is able to efficiently solve a particular set of computational problems. Improvisational intelligence, on the other hand, reflects the ability to exploit transient or novel conditions to achieve adaptive outcomes (Cosmides and Tooby 2002).

How is improvisational intelligence achieved? An answer might be that human *g* relates more closely to evolution of *interactions* between evolutionarily recent neural circuitry, rather than the evolution of evermore specialized modules alone (Jung and Haier 2007). Although brain networks are highly modular, there is evidence that individual differences in human general intelligence is not associated with the number or size of modules but in the connectivity between and within modules, particularly in frontal and parietal brain regions (Hilger et al. 2017). Nevertheless, concrete knowledge about how this connectivity produces intelligence might depend more on progress in artificial neural nets and general artificial intelligence than from the direct study of the messy biochemical reality of neuroscience.

The Evolution of Intelligence

Around 2 million years ago, *Homo erectus* (also known as *Homo ergaster*) appeared in Africa. This was the ancestor of ancient *Homo sapiens* and *Homo neanderthalensis* (Klein 2000). The size of the brain of *Homo erectus* was twice as large as any living nonhuman apes and had roughly 75% the brain capacity of modern humans (Gabora and Russon 2011; Ruff et al. 1997). *Homo erectus* has left evidence of human-like characteristics; they made stone axes, engaged in long-distance hunting, and had the ability to adjust lifestyle based on season (Gabora and Russon 2011).

Two major brain expansions occurred during the evolution of the homo line. The first was around 2 million years ago (Klein 2008), and the second one was between 600,000 and 150,000 years ago, marking the appearance of anatomically modern *Homo sapiens* (Gabora and Russon 2011; Ruff et al. 1997).

The fully grown human brain weighs around 1500 g, which is more than three times heavier than for every other living primate (Striedter 2005). Nonetheless, brain weight correlates with the overall size of an organism, so information about brain weight alone is not a useful proxy for the relative intelligence of a species. Therefore, it is more informative to look at ratios between brain and body weight. However, this ratio can be misleading too because smaller animals generally have higher brain to body ratio than larger ones (pocket mice have a higher brain-body ratio than humans do, for instance). Given this nonlinearity, the most useful measure of relative interspecies brain size is the encephalization quotient (EQ). EQ is the ratio between predicted and actual brain mass of a particular species given information from several reference species (Striedter 2005). Examples of EQ scores for various species are the African elephants with an EQ of 1.3, the mouse with 0.5, chimpanzees 2.2–2.5, dolphins 5.3, and humans, with the highest score of all species, 7.4 (Roth and Dicke 2005).

The cradle of humans was in equatorial Africa (Klein 2000), and it was here that humans first

occupied and exploited what has been dubbed the *cognitive niche* (DeVore and Tooby 1987). A niche often refers to what an animal does in its local ecology: It can be said to describe the profession, biologically speaking, of an organism (Odum 1959). Rather than exploiting resources by purely physical and chemical means (e.g., running faster, stronger toxins, and so on), humans are able to extract resources from the environment by using cognitive models of causal relationships in the world. This allows humans to invent tools and weapons, extract poison and drugs from other living organisms, and engage in coordinated action with other people; all embedded in culture (Pinker 2010).

The Cost of Evolving Intelligence

As mentioned in the introduction, evolving large amounts of brain tissue is calorically expensive. Furthermore, greater intelligence requires larger brains and therefore a larger cranium in which to contain it, and giving birth to increasingly big-brained children was risky due to the close correspondence in size between the maternal pelvis and the neonatal cranium (Rosenberg and Trevathan 2002). This evolutionary problem leads to humans being born at an earlier stage in development, giving the brain time to grow postnatally instead. This gives rise, in part, to the particularly long childhoods among humans, years that are spent in apprenticeship within the local culture, using ever-increasing intelligence to acquire skills for survival and social know-how (Bjorklund and Hernandez Blasi 2016; Pinker 2010).

All the extreme traits that are characteristic of humans such as language, sociality, long childhoods, and long investments from fathers and grandparents, and usage of different food sources, have likely all contributed to the development of *Homo* intelligence (Street et al. 2017). Language, for instance, allows for effective communication of know-how, which in turn allows for more sophisticated problem-solving and social cooperation.

However, evolution of the human brain and human cognitive ability was probably not just simply due to cooperative hunting, meat eating, or tool usage because the fossil records show that

these behaviors preceded the main brain expansions in humans (Klein 2000).

Another set of unusual human traits that might have coevolved with increased intelligence are the unusual sexual characteristics of humans. The human species have a reduced sexual dimorphism: Men are still larger than females but less so compared to other apes, suggesting selection for monogamy, biparental care, and general mating cooperation. This might be a crucial step given the extended childhood of humans. Babies require very costly parental investment in order to survive to reproductive age themselves, and human males do provide care and protection toward their offspring to a greater degree than other male apes (Flinn et al. 2005; Gabora and Russon 2011; Pinker 2010).

What selective pressures drove the brain expansions, despite all the costs, within the homo line and in anatomically modern *Homo sapiens*?

Models of the Evolution of Human Intelligence

There are several models on why intelligence evolved in humans. The following section will briefly discuss two important models on how it got started: ecological dominance and the social brain model. Then, lastly, we discuss the possible role for sexual selection in explaining the extraordinary intelligence of humans.

Ecological Dominance

The ecological dominance model on the evolution of human intelligence stresses that the hominin line was able to increasingly master the hostile forces of nature, such as procuring food, keeping warm, survive, and finding mates (e.g., Flinn et al. 2005). Several parts of the human mind are useful for ecological dominance. For example, more than any other animal, humans have “scenario-building” abilities, including foresight, planning, and “autonoetic” functions – the ability to do mental time travel. All of these functions are related to the most recently evolved parts of the brain, namely, the prefrontal cortex.

In fact, humans are the only species that can mold its environment and even entirely remove other aspects of nature, including other species,

from its environment (Alexander 1990), suggesting that intelligence evolved at least partly as a means to overcome classic ecological challenges.

Ecological dominance is likely to be an important factor in the evolution of human intelligence. However, a problem with the model is that it does not explain why humans evolved the *exceptional* cognitive abilities that they have. Many other species hunt, live on savanna habitats, have extended lifetimes, and have generally gone through similar selection pressures in their ecology without ever coming close to evolving the relative brain size and intelligence of *Homo sapiens* (Flinn et al. 2005).

Social Brain

The social brain model postulates that human intelligence evolved due to the social chess humans have played throughout evolution – namely, in dealing with *other* intelligent hominin creatures. After humans dominated and mastered their ecology, these social selective pressures might have been even more consequential. Predicting future moves and countermoves of competitors and cooperators is complex, especially when amplified by deception and shifting coalitions. Climbing social hierarchies is crucial for mating success, a complicated game that strongly rewards intellect (Dunbar 1998; Flinn et al. 2005). Hence, a crucial part of the social brain model is that people who are more sophisticated socially can manipulate other individuals to gain control over resources and other people's behavior. Moreover, humans have also evolved the capacity for prosociality and cooperation. That is, individuals display moral and altruistic sophistication toward both kin and nonkin, making them more attractive as social partners (Nesse 2007).

There is a correlation in group size of a species and brain size (Dunbar 1998). Many highly developed mental abilities in humans are also directly related to social functioning. For example, theory of mind (ToM), the ability to ascribe and understand the intentions and mental states of others, is well developed in humans and have severe negative consequences (autism) when dysfunctioning (Baron-Cohen 1997; Dennett 1989; Nesse 2007).

Sexual Selection: Is Human Intelligence a Fitness Indicator?

In sexual courtship many animals advertise their genetic quality with their bodies and minds (Miller 2000, 2011). The male bowerbird, for example, is famous for its exquisite architectural abilities (Day et al. 2005). Male bowerbirds arrange their bowers out of twigs and ornament them with petals, glossy beetles, and even colorful human-made objects such as pens and dollar bills. Arguably, the male applies its skills as an architect, carpenter, and interior designer sending potential mates a signal saying “I am able to build this particularly complicated bower because my genome contains below-average numbers of mutations and hence my brain was able to develop properly, therefore you should mate with me, because my high-fitness-brain is likely to be passed on to your children.”

Miller (2000, 2011) has argued that human intelligence, too, is a “fitness indicator,” analogous to the bowers of bowerbirds and the tails of peacocks. Like any signal, signalers can deceive their receivers. Therefore, the signal has to be reliable and hard to fake (see Zahavi 1975). Hence, the traits that evolve through sexual selection are typically very different from normal survival adaptations. In particular, sexually selected traits are usually characterized by:

1. Higher phenotypic and genetic variation.
2. Positive correlations with other fitness-relevant aspects of an animal, such as parasite resistance, longevity, and body symmetry.
3. They can evolve quickly due to the runaway interplay between display of the trait and the preference for it (Andersson 1994; Miller 2000; Miller and Penke 2007).

All of these attributes fit human intelligence well (see Prokosch et al. 2005).

Hence, a strength of the sexual selection perspective on intelligence is that it can account for facts about human intelligence not accounted for by other models. For example, that intelligence is highly heritable, meaning that about half of the observed variation in intelligence across people are attributable to genetic differences (Plomin and von Stumm

2018). Another example is that intelligence in men is related to sperm quality (Arden et al. 2009), indicating that intelligence is associated with other conceptually unrelated but fitness-relevant traits. Furthermore, and more straightforwardly, intelligence is sexually attractive and one of the most desired traits for long-term sexual partners for both sexes (Buss 1989; Geher and Miller 2008).

Sexually selected traits in the animal kingdom often portray large sex differences, typically with males competing by showing off conspicuous displays and females choosing the best fit males (although this is sometimes flipped around, depending on which sex invests more in the offspring). Among humans, there are no sex differences in *general* intelligence (Jensen 1998). However, the evolution of fitness indicators does not *require* that one sex displays a sexually selected trait and that the other prefers it. Human mate choices are often best described by *mutual mate choice* (MMC) – both sexes are choosy about their mates, and both men and women select for intelligence (Stewart-Williams and Thomas 2013). However, the average fitness payoff for *showing off* high intelligence might still be higher among human males (Miller 2011). If the latter scenario is the case, it would result in high-intelligence men having more high-quality offspring and low-intelligence men being kept out of the mating game entirely, causing more variance in intelligence and general fitness among men. Indeed, this is the observed pattern among humans: There is greater variance in intelligence among human males (Deary et al. 2003; Stewart-Williams and Thomas 2013), with the consequence that there are slightly more men with extremely low and extremely high intelligence.

The fitness indicator model is a very unlikely explanation for why intelligence started to evolve in several *Homo* species (and in other mammals) in the first place. This is because, in general, traits that evolve into fitness indicators are selected (e.g., by female choice) for their hard-to-fake complexity and hence high mutational target size, but the trait is typically arbitrarily chosen (Keller 2008; Miller 2011). That these evolutionary events arose independently across species is therefore unlikely.

Moreover, some argue that the coevolution between language, sociality, and cognition alone can account for why the human brain expanded so quickly and hence regard sexual selection as explanatory superfluous (Pinker 2010). Future empirical research and analysis of genomic data will help shed light on how important or unnecessary the fitness indicator model is in explaining the evolution of human intelligence.

Conclusion

Intelligence, the ability to learn, reason, and solve problems, can predict many fitness-relevant life outcomes such as educational achievement, income, and health. There is still much to learn about the nuts and bolts of intelligence. However, connectionism and other approaches in cognitive science have shed some light on how neural circuitry can process information.

There are several models on why intelligence evolved in humans. Some highlight the mastery of the hostile forces of nature, such as finding food and keeping warm (ecological dominance), as a tool for social deception, competition, and cooperation (social brain), and that intelligence evolved for the purpose of displaying fitness in mate competition (fitness indicator).

The models on the evolution of intelligence are not always competing perspectives but rather different pieces of the puzzle that belong together (e.g., Flinn et al. 2005). It is nevertheless scientifically useful to differentiate them to derive clear testable predictions, in order to find out where they compete and where they align (Dunbar 1998). For example, one study found that human-sized brain and bodies were predicted by a model where individuals faced selection pressures that was 60% ecological, 30% socially cooperative, and 10% between-group competitive (González-Forero and Gardner 2018) (the fitness indicator model was not included), suggesting that several models are important but to different degrees.

The fitness indicator model can potentially explain why intelligence evolved so quickly and is sexually attractive and highly heritable and why it correlates with other fitness-relevant traits.

However, simpler models are probably better accounts for how the evolution of intelligence in the *Homo* line got started, and it is still debatable if sexual selection is superfluous or essential in explaining the existence of our big and costly brains.

Cross-References

- [Brain Size and Intelligence](#)
- [Evolution of Intelligence, The](#)
- [General Intelligence Factor *G* \(Reader, Hager, and Laland, 2011\)](#)
- [Nonhuman Intelligence](#)
- [Michael A. Woodley of Menie, Yr.](#)

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Intelligence Quotient

► Intelligence Testing

Intelligence Scales

► Intelligence Testing

Intelligence Test

► Intelligence Testing

Intelligence Testing

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Synonyms

Binet-Simon tests; Cognitive capacities; Intelligence quotient; Intelligence scales; Intelligence test; Stanford-Binet intelligence scales; Wechsler adult intelligence scale; Wechsler intelligence scale; Wechsler intelligence scale for children; Wechsler preschool and primary scale of intelligence; Wechsler-Bellevue intelligence scale

Definition

Intelligence testing is a collection of tasks designed to measure cognitive capacities such as abstract reasoning, ability to solve problems, and ability to acquire knowledge, which may be the most important elements. The specific structure of this test depends on the definition of intelligence adopted by each psychometrician. Snyderman and Rothman (1988) reported that psychologists and educational researchers reach a general consensus supporting the validity of IQ testing.

Introduction

The precursor of intelligence tests was Francis Galton, the genius of diverse disciplines such as anthropology, statistics, geography, and psychology. He made the first attempt to establish standardized tests to assess one's intelligence. Galton believes that intelligence is inherited, thus there may exist a correlation between intelligence and some observable physical traits, such as visual acuity, reflexes, muscle grip, and head size. After collecting a large number of data on a variety of physical variables, he failed to demonstrate any such correlation (Carroll 1993).

Although Galton's work is quite illuminating for the intellectual testing boom in the twentieth century, later researchers turned back to the traditional viewpoint that intelligence is correlated with one's behavior and performance instead of physical traits. In 1905, French psychologist Alfred Binet and psychiatrist Theodore Simon developed first formal intelligence tests, the Binet-Simon Tests. The Test consisted of 30 cognitive subtests including measures of language skills, memory, reasoning, digit span, and psychophysical judgments. In the 1908 revision, Binet and Simon added nonverbal tests and applied the year scale, each test was assigned to the age level at which most children performed it successfully. The Binet-Simon scales have served as both a model of form and source of content for later individual intelligence tests (Boake 2002). Internationally, the most widely used intelligence tests are the Stanford-Binet Intelligence Scales and the Wechsler-Bellevue Intelligence Scale. The Stanford-Binet, revised from the original Binet-Simon Scale by psychologist Lewis M. Terman at Stanford University in 1916, extended the age range into adulthood and, most important, adopted intelligence quotient (IQ). The battery of Wechsler Intelligence Scale (1939) contains different versions for different age groups, that is Wechsler Adult Intelligence Scale (WAIS 1955), Wechsler Intelligence Scale for Children (WISC 1949), Wechsler Preschool and Primary Scale of Intelligence (WPPSI 1963) (Wechsler 2008). Wechsler's major contributions were not the

subtests themselves but rather the technical innovations of deviation scores, combining verbal and performance tests into a single scale, and selecting the adult standardization sample by occupation (Boake 2002). For various reasons, mostly the validity of rating person's intelligence and various psychological abilities, these two scales have achieved almost monopoly status in individual intelligence testing. However, these intelligence tests and their underlying definition of intelligence are not the most optimal framework to study intelligence from the perspective of evolutionary psychology. To do so, we focus on the theory of general intelligence and its relationship with evolutionary psychology in the following parts of this article.

Spearman (1904) investigated previous studies referring to various mental tests and argued that many cognitive abilities those were claimed to be unrelated by former researcher because of lacking adequate system of investigation, were actually related. He employed the factor analysis to testify the correspondence between the tests. The correlations between mental abilities are consistently positive, which indicates that there is a general foundation underlying these mental abilities. This common factor, namely, general intelligence or *g* factor, is rooted in many forms of intellectual activity such as in-school Cleverness, out-of-school Common Sense, Sensory Discrimination, and Musical Talent. Besides *g*-loaded components, every specific task contains a specific factor.

When the evolutionary psychology meets *g* factor, it is easy to draw the picture of the information-processing mechanisms. When our ancestors deal with multiple survival problems, such as finding food, shelter, or a mate or detecting danger, it is more economical to assume that we use multiple, overlapping sets of processes for each task, rather than thinking of each of these tasks as being solved by an independent, encapsulated piece of neural machinery, hard-wired for this purpose (Mackintosh 2000). Evolutionary psychologists are also concerned about whether intelligence is adaptive, and if it is, how it evolved, what its biological basis is? And, why

are there such individual differences in human intelligence, especially in IQ tests? The *g* factor theory may be the best framework of intelligence testing to answer these questions. According to Kanazawa (2004), general intelligence originally evolved as a domain-specific adaptation to solve evolutionarily novel problems. Through genetic mutations, our ancestors adapted successfully to solve problems such as mate selection, raising offspring, and navigation, which may be the *g* factor with past adaptive significance.

There has been a historical debate about the biological basis of general intelligence, particularly the relationship between intelligence and brain size. Some researchers reviewed the evidence regarding the relationship between intelligence and craniometrics, like head length, breadth, and weight, and argued that the relationship between brain size and general mental ability is now a well-established and widely-accepted fact (Bouchard 2014; Mackintosh 2000). The correlations between IQ scores and brains size is about 0.30. Besides, a number of studies shows that the *g* factor exists in a wide range of species, including mice, dogs, birds, and primates (Bouchard 2014). Since *g* has been shown to be correlated with brain size, it is natural to wonder the relationship between *g* and the structure and function of brain regions. Many neuroimaging studies have been devoted to studying the neural mechanisms of intelligence. A profound review published by Jung and Haier (2007) summarized the fruitful results and proposed the Parieto-Frontal Integration Theory (P-FIT) of intelligence, which report a striking consensus suggesting that variations in a distributed network predict individual differences found on intelligence and reasoning tasks.

Some critics argue that, Intelligence should not be adaptive because it is an individual variable (Borsboom and Dolan 2006). Adaptation is universal, a constant trait shared by all members of an ethnic group; In contrast, there are significant genetic individual differences in intelligence. Some individuals are more intelligent than others. These critics argue that adaptation and genetic

individual differences are mutually exclusive. These critics clearly have a deep misunderstanding of the nature of adaptation. Evolutionary adaptation can also be a variable of individual differences. In fact, most adaptations show individual differences.

There is another problem for concern. In the construction process of mental tests, the internal consistency procedure demands the selected items should be positively correlated with the total score of all the items in pool of all the tryout group. This process is inevitably affected by the tryout group's genetics and yields a test which is not representative of the item universe, resulting in a genotype-item interaction which have a solid and largely forgotten history of research in testing (Harrington 1997).

Cross-References

- [Brain Size and Intelligence](#)
- [Convergent Evolution of Intelligence](#)
- [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- [Cultural Intelligence Hypothesis, The](#)
- [Evolution of Intelligence, The](#)
- [General Intelligence Factor *G* \(Reader, Hager, and Laland, 2011\)](#)
- [Intelligence](#)
- [Intelligence Versus Natural Selection](#)
- [Nonhuman Intelligence](#)
- [Social Intelligence Hypothesis, The](#)
- [Technical Intelligence Hypothesis, The](#)
- [Theory of Mind and Nonhuman Intelligence](#)
- [Vygotskian Intelligence Hypothesis, the \(Moll Et Al., 2007\)](#)

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Intelligence Versus Natural Selection

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Synonyms

[Behavioral plasticity vs. natural selection](#)

Definitions

Natural selection is the main mechanism that brings populations to new adaptive optima when the environment changes, but intelligence may also contribute by helping individuals devise behavioral solutions to the novel challenges.

Introduction

Environmental conditions where organisms live are changing continuously, often creating mismatches between current phenotypes and those that would be optimal under the new circumstances. These mismatches may be reduced through evolutionary responses, provided that there is enough standing genetic variation for natural selection to act upon. However, animals can reduce adaptive mismatches through yet another mechanism: their “intelligence.” By enhancing plastic behavioral responses, intelligence can place the population close to the new adaptive peak with no need of genetic change. In this sense, intelligence can be seen as an alternative to natural selection. The present chapter describes how intelligence allows dealing with environmental changes, in which scenarios it should be an alternative to natural selection and what are the potential consequences for the evolutionary diversification of animals.

What Is Intelligence?

Intelligence is a slippery concept. From an ecological perspective, however, intelligence can be operationally defined as a domain-general cognitive ability of animals to devise plastic behavioral solutions to novel or unusual ecological problems. This definition thus includes advanced cognitive abilities, like causal reasoning, insight, self-awareness, and theory of mind but also less advanced abilities such as trial-and-error learning, associative learning, and behavioral inhibition. Intelligence should be seen as a complex adaptive system that may vary both qualitatively and quantitatively across individuals, species, and superior clades.

How Behavioral Plasticity Helps Dealing with Environmental Changes?

Like other mechanisms underlying plasticity, the intelligence of animals is thought to be an adaptation to cope with environmental changes

(Allman 2000; Sol et al. 2016). Intelligence can help animals develop new learnt behaviors (i.e., innovations) or modify behaviors already present to solve problems individuals have never or rarely experienced before, including periods of food shortages, irruption of novel predators, or sudden changes in climatic conditions (Sol 2003). Woodpecker finches (*Cactospiza pallida*), for example, build tools that allow them to consume caterpillars from wood crevices. However, this technique only replaces the more usual gleaning technique when seasonal droughts drive insects into crevices. By buffering individuals against environmental changes, intelligence enhances individuals' survival when the environment changes, bringing the population into the realm of attraction of the new adaptive peak (Price et al. 2003). Unlike natural selection, however, the response is rapid and often reversible.

Intelligence as Alternative to Natural Selection

If behavioral responses are enough to move a population close to a new adaptive peak, this should hide genetic variation from natural selection and hence inhibit evolutionary change. This is the so-called Bogert effect. Huey et al. (2003) illustrate it with a hypothetical example of selection on temperature regulation of a lizard distributed along an altitudinal gradient. Being ectotherm, if the lizard uses the environment randomly with respect to factors that influence body temperature, those individuals living at higher altitude will be selected toward progressively lower “optimal” body temperatures, as temperature decreases with altitude. However, if the lizard actively adjusts its behavior to the local thermal conditions, for example, by occupying shaded habitats at low altitude but more open habitats at high altitude, the mean optimal temperature will be similar regardless of altitude.

Despite the widespread influence of the Bogert effect, it is unlikely that behavioral responses completely replace natural selection. Losos et al. (2004), for example, showed that although *Anolis* lizards shift to use safer places when exposed to

predators, this change in behavior does not prevent natural selection to alter their morphology. Even in humans, who are masters in protecting themselves from the external environment by constructing and managing their own niches, natural selection is still acting (Barreiro et al. 2008).

When Intelligence Is More Important than Natural Selection?

Natural selection is ultimately the mechanism that brings the population's genotype to a new adaptive optimum when the environment changes and hence explains how organisms adapt to their environment. However, if intelligence functions to buffer individuals against novel ecological challenges, it may sometimes play a stronger role than selection in helping reduce adaptive mismatches, at least in the short term. This role will depend on both the degree of intelligence of the animal, which determines the extent to which individuals rely on behavior to solve ecological problems and the extent to which the new selective pressures can be dealt with behavioral adjustments. Moreover, it may also depend on the life history of the animal. All highly intelligent animals – like primates, cetacean, ravens and parrots – are long-lived. One reason is that developing a large brain and the behavioral skills needed to survive takes time, and only long-lived animals can afford it. Yet, a long-lived strategy reduces the power of natural selection both because it increases generation time (delaying genetic changes) and decreases population density (reducing standing genetic variation and the probability of new mutations, and increasing stochastic loss of beneficial mutations). In long-lived species, therefore, intelligence should often be more influential than natural selection as a mechanism to reduce adaptive mismatches when the environment changes, at least in the short term.

There are other scenarios where natural selection alone is less likely to bring the population close to a new adaptive peak. High variation in food resources over time and space, for example, makes natural selection to fluctuate in direction,

making adaptive specialization less likely. Under this scenario, intelligence may act as an alternative to natural selection by enhancing the individuals' ability of exploiting a wide array of foods (Ducatez et al. 2014).

Can Plastic Behaviors Promote Evolutionary Diversification?

The existence of the Bogert effect may lead to think that evolution should proceed more slowly in animals with enhanced behavioral plasticity. However, this is not necessarily the case if plastic behavioral shifts expose animals more frequently to new selective pressures. A change in behavior, like learning to exploit a novel resource, is likely to expose individuals to a new set of selection pressures favoring those mutations that improve individual's proficiency. This idea, called "behavioral drive" hypothesis (Wyles et al. 1983), is supported by two lines of evidence. The first is the observation that changes in behavior generally initiate changes in other phenotypic traits. The second is that, according to some studies (e.g., Sol and Price 2008; Wyles et al. 1983), animals with high propensity for behavioral innovation tend to evolve at a faster rate than those with less propensity. Although changes in behavior followed by morphological and physiological adjustments may be a potent force in driving evolution toward novel directions, the existence of the Bogert effect suggests that intermediate level of plasticity should be optimal to produce a peak shift (Price et al. 2003).

Genetic Assimilation

While a new behavior derived from intelligence can influence evolution of other traits by making individuals interact with the environment in novel ways, the behavior itself is learnt and hence cannot be selected. However, the behavior can later become genetically encoded via natural selection through a process called genetic assimilation. This only requires that the likelihood of producing the

behavior depends on a set of heritable traits (like appendages to manipulate objects or cognitive abilities to adopt the appropriate motor actions) and that individuals that are better at using the behavior attain higher fitness. If these conditions are met, natural selection will increase the frequency of individuals possessing the combinations of traits that predispose to perform the behavior. After many generations, individuals will end up looking like if they have an innate ability to do so. Genetic assimilation helps thus understanding how complex behaviors may become genetically encoded.

Conclusion

No organism can totally escape from the influence of natural selection. Yet natural selection is not all-powerful, and some degree of plasticity is always necessary in an ever-changing world. Intelligence functions to buffer individuals against novel ecological challenges, often playing an antagonistic role to selection. However, intelligence and natural selection cannot be simply seen as alternative mechanisms. Under certain conditions, both processes can jointly contribute to facilitate phenotypic change.

Cross-References

- [Cognitive Buffer Hypothesis, The](#)
- [Technical Intelligence Hypothesis, The](#)

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Intention

- [Goal Detection](#)

Intentional Stance

- [Daniel Dennett: A Review of His Evolutionary Work](#)

Interactive Decision-Making

- [Predicting Events and Behavior](#)

Interactive Language Development

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Synonyms

Child-directed speech (CDS); Evolution-based theories; Language stages; Neurological approach; Pragmatics; Social interaction

Introduction

The primary function of language is communication. Speakers and listeners make adjustments in order to accomplish their communication goals. This interaction begins when children are neonates as they smile, coo, and establish eye contact with caregivers (e.g., mothers, fathers, siblings, aunts, grandparents, etc.). Language is dynamic rather a final product. Language is an instrument for social interaction and speaker intents (what the speaker wishes to communicate). Pragmatics is the study of speaker intentions, conveyed messages, and listener interpretations (See discussion on pragmatics).

A brief review of language acquisition and how theoretical perspectives have evolved is presented. The behavioral approach was first presented by Skinner in “Verbal Behavior” (1957). According to Skinner, language learning depends on environmental variables, i.e., imitation, practice, and selective reinforcement of language structures. Language is gradually accumulated. Parents are crucial because they model the appropriate utterances. Parents also shape the child’s utterances until they are grammatically correct. This approach has been criticized because Skinner (according to Chomsky): (1) ignores the content of language learned; (2) children seem to acquire language repertoires far quicker than behavioral learning can account for; (3) children produce novel utterances; and (4) parents rarely correct their children’s productions.

The psycholinguistic/syntactic approach was developed by linguists in the late 50s and early 60s. Influential among this group was Chomsky. According to Chomsky (1965), the human brain contains an internal mental plan to understand and generate sentences. Children are born with an innate linguistic mechanism (i.e., the Language Acquisition Device or LAD). According to Chomsky, the LAD is activated by exposure to linguistic input. The LAD contains a set of rules or general principles for forming sentences, and procedures for discovering how language principles apply to the particular child. Chomsky focused on language being innate with universal features (i.e., a universal grammar) found in all languages; thus, all children were said to possess an internal and innate ability with the brain being pre-wired for language. This approach is criticized because Chomsky treats language as if it occurs independent of thought, cognitive development, and external factors.

Vygotsky, a Russian psychologist, espoused the theory that social development, social interaction, and play are important features of cognitive and language development in children (Vygotsky 1962). Vygotsky viewed social interaction as the prime factor in children’s learning. Wosensdregt and Smith (2017) state that the biological evolution of language is genetically transmitted. However, cultural evolution is transmitted through social learning. And subsequently, it can be said that pragmatics is crucial to social learning, language development, and cognition.

Pragmatics views language within the context of interaction with others. Child–caretaker interactions are seen to be the originating force for language learning. McLean and Snyder-McLean (1999) summarize the pragmatic model in four steps: (a) Language is acquired if and only if the child has a reason to talk. The child has learned (or not learned) that he/she can influence their environment through communication; (b) Language is acquired as a means of acknowledging existing communication functions, i.e., language supplements and replaces existing, less effective communication methods; (c) Language is learned in dynamic social interactions involving the child and an older, more mature language user. This occurs in the child and

other's environment; (d) The child is an active participant in the communicative exchange process and must contribute to it in a manner that allows for the child to benefit from the interaction. Hence, language development is a social, interactive process that also includes cognitive development.

The neurological approach states that all language and cognition is reflected in neurological brain structures. The developing brain in infants and children is about making neuronal connections. Neural cells must connect with other neural cells in the early stages of brain development (a stage labeled as mass migration or neural cell proliferation). Neural cells reach their final destination (i.e., making a connection with other neural cells) with the help of radial glia that spans the entire length of the neural tube. Defects in migration can result in neurological conditions such as epilepsy, mental handicaps, etc. Address selection is where the brain fires the neurons down a pathway, but not selectively, hence all the connections "light-up." The brain strengthens certain connections through repetitive use (i.e., from external stimulation) and eliminates random connections (i.e., pruning). The brain, thus, selects strong, appropriate connections and prunes less efficient and weak connections. This begins and occurs in the womb.

Experience (from external stimulation) drives maturation and development. With experience from the environment, neuronal cells can refine their circuits or connections and influence which connections are stabilized and which connections are lost. Learning is about neuronal connections. The temporal lobe, Wernicke's area, inferior parietal lobe, and the frontal lobe anterior to Broca's area are larger in human beings. Consequently, these areas are important for language and cognition. The temporal lobe is the seat of auditory processing (listening and comprehension). The auditory association area known as Wernicke's area is also important to the use of language.

Evolution-Based Theories

Evolution-based theories state that over time humans have evolved to learn language, not

because we have language acquisition devices (built-in devices), but rather our brains have evolved from previous brain structures. Evolution-based theories stress the relation between how the brain and language have evolved over time in different species, how they develop in children, and how adults perform language functions. In humans, speech and language has developed from brain structures and brain functions based on action recognition and action production (Rizzolatti and Arbib 1998).

In the brain, mirror neurons are activated when an action is performed or when the said action is observed. "These neurons are called mirror neurons because the observed action seems to be "reflected," like in a mirror, in the motor representation for the same action of the observer" (Buccino et al. 2004, p. 371).

The human brain evolved to recognize actions of others as a survival mechanism. Mirror neurons in monkeys (premotor area, anterior to the primary motor area) correspond with actions and observations of the same action the F5 area. Gesture recognition and observations of gestures also appears in humans in the F5 area (which is part of Broca's area (Rizzolatti and Arbib 1998). Buccino et al. (2004) also report that in the F5 area there are mirror neurons associated with the implementation and observation of mouth actions. It is speculated that Broca's area (important for speech production) evolved from F5. Thus, what is seen is that humans evolved actions, observation of those actions, and possibly speech from mirror neurons. The left inferior frontal gyrus (Broca's area), inferior parietal lobe, and posterior middle temporal gyrus involve action recognition, speech, and language functions (Rizzolatti and Arbib 1998). In conclusion, Rizzolatti and Arbib state that language evolved from an initial ability to recognize actions and which later evolved into language.

Stages of Language Development

Language develops along predictable developmental stages. All children experiment with language as active participants. Children learn

linguistic forms that easily fit into their current communication strategies. Children rely on similar sound patterns and environmental contexts to learn linguistic and nonlinguistic forms. Counter to Chomsky, attempts by parents to correct children's syntax is ineffective. And, children vary in the amount of spontaneous imitation that they do. Communicative language milestones are as follows:

1. Birth–1 month – the child uses different cries to express desires/needs or displeasure (i.e., differentiated cries).
2. 2–3 months – the child coos, pleasurable noises; open vowel-like sounds; smiles, squeals; and pitch changes appear.
3. 4–6 months – the child engages in sound play; consonant-like sounds, single syllable-like sounds; and engages in babbling.
4. 6–8 months – the child engages in reduplicated babbling (repeated consonants and vowels, e.g., ba-ba-ba); begins to look at objects that are named; and begins to imitate sounds.
5. 9–10 months – the child uses jargon (sounds like words) and imitates adult speech if the sound is in their repertoire.
6. 11–17 months – the child uses true words (the words are symbolic); gestures; understands “no”; and starts to label familiar objects/people.
7. 18 months – the child uses up to 50 words; combines 2 to 3 words; and understanding progresses rapidly.

Child-Directed Speech (CSD)

Child-directed speech is language directed at younger or less mature language users. It was formerly referred to as “motherese” or language directed by mothers to children. However, it was found that fathers, family members, older siblings, and caregivers also utilized this type of language. CDS typically occurs from 0 to 20 months (Paavola-Ruotsalainen et al. 2018).

Child-directed speech is when the caregiver perceives the child's communication and responds accordingly. During routinized social

activities, the caregiver interprets the child's communication and attributes meaning to the exchange (e.g., “Oh yes, that is a doggie”). This attribution on the caregiver's part is known as perlocutionary effect. The caregiver follows and maintains the child's focus (i.e., joint focus of attention). This joint focus communicates that what the child is communicating is important and reinforces the behavior to be repeated.

CDS consists of simplified syntax, and an exaggerated prosody adapted to the child's levels. Joint attention is shared attention by the child and adult. In addition, “here and now” language aligns with use of familiar words. Child-directed speech is more influential when the child is at the one word stage. Attention following is more important than attention redirections at 18 months of age. CDS also depends on the speaker's own language abilities.

A direct, high interactional style is when the caregiver attempts to control the child's behavior, gives commands, and/or redirects the child's attention. The direct, high interactive style is used extensively in the Anglo-American culture. It is characterized by: (a) Children are seen as equal conversational partners, on the same level as adults; (b) Speech is child directed; and (c) Parents are actively involved in speaking with their children.

An indirect, low interactional style is passive in terms of the caregiver's involvement. Some cultures refer to this style as the “look and listen” approach. It involves watching, understanding, and trying stages. Specifically, the phases or stages include

1. **Watching:** The look and listen phase. The child observes language use and interactions. Receptive processing is involved. Multiple exposure to the utterance and its use is key to learning.
2. **Understanding:** The child tries to process information and make sense of the world and how language is used.
3. **Trying:** This phase is divided into passive trying and active trying:
 - (a) *Passive trying* is mental rehearsal of the utterance and use of language. This is

characterized by mental practice and repetition of practice.

- (b) *Active trying* is when the child attempts the utterance and its use by speaking, i.e., physical practice. The active trying phase is not attempted until near mastery of the utterance is achieved.

Caregivers may employ any of the following strategies:

Context mapping: Using words to describe objects, actions, and events that the child is observing [similar to Brice-Heath's 1982 label quests and event casting].

Bridging: Relating one word used in one context to another new context.

Modeling: Showing use of a particular structure, behavior. Forced imitation is not required. Modeling may be paired with imitation; however, it does not require it.

Prompting: Providing some sort of cue to what she/he is trying to say. This may include saying part of the word, giving the word, or some other sort of clue.

Questioning: Purposely trying to elicit a response through a question.

Recasting: Changing the ungrammaticalness of an utterance while preserving its meaning. This is similar to modeling.

Repairing: Recasting or repeating the utterance in order to seek clarification.

Acknowledging. Any response to show that the listener is following the conversation.

Expansions: Making the utterance more grammatically complete.

Extensions: Adding new information to the utterance. Extensions can be added on to an expansion.

Conclusion

Language development is multifaceted and multiphasic. It appears that language abilities have evolved from earlier brain structures; yet, environmental stimulation plays a key role in furthering brain growth. In sum, language

development is about social interaction and communication.

Cross-References

- [B. F. Skinner and Behaviorism](#)
- [Cognitive Development in Non-human Primates](#)
- [Early Perspectives on Evolutionary Change](#)

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Interbirth Interval

- [Optimal Clutch Size](#)

Interbirth Interval (IBI)

- [Ancestral Birth Spacing](#)

Interbreeding

- [Neanderthals and Humans](#)

Interbrood Conflict

- [Conflict Between Parents and Offspring](#)

Intercourse

- [Sexual Behavior](#)

Intercourse Sexual Orientation

- [Hormonal Component of Homosexuality](#)

Interdependence

- [Morality Is Cooperation](#)

Interdisciplinarity

- [Towards Methodological Pluralism in Psychological Sciences](#)

Interference

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Synonyms

[Inhibition](#); [Interference effect](#)

Definition

Interference refers to the impaired ability to remember an item when it is similar to other items stored in memory.

Introduction

It was John A. Bergstrom who started to study the phenomena associated with interference. But it was the work of G. E. Müller, a German experimental psychologist, that inspired many other psychologists to become interested in interference. In 1894, Müller and Schumann observed that the learning of the second list of items interfered with the memory of the first list (reviewed in Dempster and Brainerd 1995). This observation was extended and studied in greater detail by Müller and Pilzecker in 1900, and the phenomena was called retroactive interference (or retroactive inhibition).

For the next 70 years, psychologists proposed many theories to explain forgetting associated with interference. Researchers describe interference as the competition between items that share a common retrieval cue (Anderson and Neely 1996). A retrieval cue is a clue or prompt that is used to trigger the retrieval of specific memories. Thus, if a retrieval cue connected with more than one item, it might make these items more susceptible to interfering with each other and less likely to be recalled.

The Most Important Phenomena in Classical Interference Research

Retroactive Interference

Retroactive interference (or “retroactive inhibition”) refers to the phenomenon that newer memories would interfere with the retrieval of previously learned memories.

Müller and Pilzecker were the first to study retroactive interference around 1900. In their fundamental experiments, tasks of different characteristics were added into the intervals between original learning and recalling, and it

was found that some interpolated conditions were followed by poorer recall than others. The phenomenon of such new learned materials interfering with the retention of previously learned material was termed by them “Rückwirkende Hemmung”, which should be translated as “retroactive inhibition” (reviewed in Britt 1935). Moreover, several factors have been concluded that can increase the magnitude of retroactive interference, such as the similarity between materials and the unfamiliarity of the previously learned material (Postman and Underwood 1973).

Proactive Interference

Proactive interference (or “proactive inhibition”) refers to the phenomenon that memories learned previously would interfere with the retrieval of newer memories.

The pioneer in the field of proactive intervention is Benton Underwood. In his studies, participants were asked to learn a list of paired words and to recall them after 48 h. After that, a new list was learned on the following day, followed by several additional lists. The learning and recall of each list were completed before a new list was learned. The results showed that the greater the number of previous lists learned, the greater the forgetting of the latest learned list. It was explained that the increasing decrements in recall were caused by the proactive interference from previous lists, and it was further discussed that the Ebbinghaus curve of forgetting was also due to interference from materials learned previously (Underwood 1957).

Researchers conclude that the magnitude of proactive interference depends on the categories of newer and older materials, the depth of original processing (i.e., materials learned more thoroughly may be less susceptible to proactive interference), and the length of the time interval between learning trials (i.e., longer intervals result in less proactive interference).

Of the two typical types of interference, retroactive interference causes more problems during learning and has a stronger impact (Edwards 2010). And retroactive interference is more obvious at short retention intervals, but at long

retention intervals, the influence of the proactive interference will be greater.

Output Interference

Output interference refers to the interference of the act of recall with the retrieval of the learned information. Tulving and Arbuckle (1966) conducted the first systematic study of output interference. Participants were presented with lists of paired associates in which the digits 1–10 were the stimuli and common words were the responses. In the recall tests, participants were asked to recall the words according to the randomly presented stimuli. Results showed that the recall performance declined with the increase in the sequence of stimuli. In subsequent studies, researchers used categories as the cues of recall tasks and asked participants to recall the given words. The results also supported the finding of output interference (e.g., Roediger and Schmidt 1980).

Furthermore, output interference could happen in not only short-term memory but also long-term memory. The recall of organized information from long-term memory has a detrimental effect on subsequent recall. Such kind of output interference effect is dependent on the size of the input categories and the amount of time allowed for recall (Smith 1971).

Based on the findings of output interference, Anderson et al. (1994) found that retrieving a subset of items from a category caused the forgetting of other items from that category. This phenomenon similar to output interference was referred to as retrieval-induced forgetting, which inspired a new wave of research.

Conclusion

Interference is a notion closely related to forgetting, and it is believed that interference is caused by competition among items that have a common retrieval cue. The most important phenomena in classical interference research are retroactive interference, proactive interference, and output interference. Interference effects also exist in other psychological fields, such as cognition and motor skills.

Cross-References

- ▶ [Long-Term Memory](#)
- ▶ [Working Memory](#)

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Interference Effect

- ▶ [Interference](#)

Intergenerational Language Transmission

- ▶ [Immigrant Parents](#)

Intergenerational Relations

- ▶ [Grandparents and Grandchildren](#)

Intergenerational Transmission of Violence

- ▶ [History of Abuse](#)

Intergroup Aggression

- ▶ [Chimpanzee Raiding](#)

Intergroup Bias

- ▶ [In-Group–Out-Group Bias](#)

Intergroup Competition

- ▶ [Coalitional Relationships](#)
- ▶ [Competition Between Groups](#)

Intergroup Conflict

- ▶ [Chimpanzee Raiding](#)
- ▶ [Competition Between Groups](#)
- ▶ [Evolutionary Theory and the Causes of War](#)
- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Nonhuman Primates: Between-Group Conflicts](#)
- ▶ [Out-Group Members](#)
- ▶ [Reputation as a Context for Men's Aggression Against Men](#)
- ▶ [Tribalism](#)
- ▶ [War More Likely with Higher Likelihood of Success](#)

Intergroup Killing

- ▶ [Humans: Between-Group Conflicts](#)

Intergroup Killing, Between-Group Killing

- ▶ [Nonhuman Primates: Between-Group Conflicts](#)

Interindividual Male Gamete Rivalry in Oocyte Fertilization

- ▶ [Non-primate Mammal Sperm Competition](#)

Interlocus Sexual Conflict

- ▶ [Conflict Between the Sexes](#)

Internal

- ▶ [Factors That Influence Bullying](#)

Internal Status Hierarchy

- ▶ [Coalition Leaders](#)

Internal Working Model

- ▶ [Early Attachment Experiences and Romantic Attachment](#)

International Brides

- ▶ [Mail-Order Brides](#)

Internet Brides

- ▶ [Mail-Order Brides](#)

Internet Questionnaire

- ▶ [Online Survey](#)

Internet Survey

- ▶ [Online Survey](#)

Interparental Conflict

- ▶ [History of Abuse](#)

Interpersonal Aggression

- ▶ [Sexual Assault and Intimate Partner Violence](#)

Interpersonal Perception

- ▶ [Dyadic Processes](#)

Interpersonal Rejection

- ▶ [Peer Rejection, Sex Differences in Initiation of](#)

standard deviation. In a one sample t-test, a researcher sample is compared to a claim made of the population mean. In an independent samples t-test, researchers compare two sample groups against each other. Finally, when using a dependent sample t-test, researchers compare the means of various paired scores and then compare those means against a null hypothesis.

Analysis of Variance (ANOVA)

An ANOVA compares two group means against each other. The ANOVA is essentially an extension of an independent samples t-test, just on a grander scale. The two main types of ANOVAs are the one-way ANOVA, which only compares one independent variable against one dependent variable. For example, you could look at running and how it could elevate levels of happiness. In a two-way ANOVA, researchers compare two independent variables against one dependent variable. An example of this would be researchers looking at running AND gender and its effects on elevated levels of happiness.

Conclusion

There are many statistical tests used in psychological research, and this was just a brief overview of the main tests. Researchers use t-tests and ANOVAs primarily when looking for statistically significant evidence when trying to disprove a hypothesis. Attempting to read and decipher the meaning of results in peer-reviewed may cause one to become dismayed; however, interpreting these results and discovering which test was used is rather easy.

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Intersexual Competition

- ▶ [Conflict Between the Sexes](#)
- ▶ [Counteradaptations/Female Counterstrategies](#)
- ▶ [Mating Rivalry](#)
- ▶ [Nonhuman Sexual Conflict](#)

Intersexual Deception

- ▶ [Violation of Short-Term Mating Preferences](#)

Intersexual Negative Inducements

- ▶ [Manipulation](#)

Intersexual Relations

- ▶ [Mating Strategies](#)
- ▶ [Sexual Strategies Theory](#)

Intersexual Selection

- ▶ [Benefits of Short-Term Mating](#)
- ▶ [Bright Male Hypothesis](#)
- ▶ [Desire to Be Included Among Desirable Women](#)
- ▶ [Differential Parental Investment](#)
- ▶ [Production of Eggs and Sperm](#)
- ▶ [Same-Sex School Bullying](#)
- ▶ [Sexual Selection in Evolutionary Psychology](#)

Intersexual Strategic Interference

- ▶ [Violation of Long-Term Mate Preferences](#)

Interstimulus Interval

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Definition

Interstimulus interval can be defined as the time interval between the end of one stimulus presentation and the onset of another stimulus presentation.

Introduction

The concept of interstimulus interval is frequently encountered within processes of non-associative learning, specifically habituation and sensitization Petrinovich (1984).

Experimental Research on Interstimulus Interval

Interstimulus interval experiments were extensive under the work of Davis (1970) on habituation of the acoustic-startle response in the rat. Generally, through Davis's series of experimental studies it was demonstrated that the length of interstimulus interval, as well as variability (regularity), determines habituation in animals. The author compared the responsiveness of two groups of rats to a 50-ms, 120-db tone of 4000 Hz during pretest, training, and posttest periods. During both the pretest and the posttest periods, both groups of subjects received 300 tone exposures at intervals of 2, 4, 8, and 16 s, the intervals being scheduled in an irregular order. During the training period, both groups received 1000 tone exposures; however, the interval between stimuli was 16 s in one group and 2 s in the other group. Among other findings, greater reduction in responsiveness was observed in the group who received stimulation every 2 s.

In the second experiment, startle responsiveness was lower following training with regular as opposed to variable interstimulus intervals. Simply put when interstimulus interval is longer and constant, habituation is greater. Also Davis (1970) reported a quite an interesting finding; when rats were tested at 1 min or 24 h later with a variety of interstimulus intervals, habituation was greater for the group that was trained on the 16 s interstimulus interval schedule suggesting thus that short-term and long-term habituation processes may be distinguishable on the basis of the presentation and the intervals between stimuli. Specifically, it was demonstrated that short interstimulus intervals were involved in the progression of short-term habituation, while long interstimulus intervals were involved in the promotion of long-term habituation. Also, apart from the fact that high frequency stimulation leads to more rapid response decrement, it results in faster spontaneous recovery as well.

Similarly, Groves and Thompson (1970) noted that increased frequency should lead to increased habituation in the "S-R" pathway, but in the "state" pathway it would lead to increased sensitization. All the aforementioned experiments considered together are indicative of the importance of interstimulus interval making it obvious that it can have a major effect on learning; it may delay or improve learning. Lastly, the organism's ability to determine the interval and duration of sensory stimulation is central to sensory processing; therefore impairments in that domain are likely to interfere with the process of learning.

Conclusion

Variations in the time between the presentations of one stimulus to the next have a determinant effect on the forms of non-associative learning; habituation and sensitization and that the occurrence of long-term and short-term habituation are dependent upon the length of interstimulus intervals. Further manipulation of interstimulus intervals will provide valuable information regarding disruptions in learning processes or even suggestions as to how to enhance learning.

Cross-References

- ▶ [Habituation](#)
- ▶ [Non-associative Learning](#)
- ▶ [Sensitization](#)

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Interstitial Cell-Stimulating Hormone

- ▶ [Luteinizing Hormone](#)

Interview

- ▶ [Self-Reports](#)
- ▶ [Surveys and Questionnaires](#)

Intimate Partner Homicide

- ▶ [Partner Homicide](#)
- ▶ [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)](#)

Intimate Partner Sexual Violence

- ▶ [Partner Rape](#)

Intimate Partner Violence

- ▶ [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- ▶ [Contexts for Women's Aggression Against Men](#)
- ▶ [Defense Against Attack](#)
- ▶ [Female Age as a Predictor of Men's Aggression Against Women](#)
- ▶ [History of Abuse](#)
- ▶ [Men's Violence Against Female Partners: The Role of Culture](#)
- ▶ [Partner Abuse and Homicide](#)
- ▶ [Self-Defense and Female-Perpetrated Violence](#)
- ▶ [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)](#)
- ▶ [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)
- ▶ [Violence as Coercive Control](#)
- ▶ [Violence to Control Women's Sexuality](#)

Intimate Partner Violence (IPV)

- ▶ [Men's Suspicions of Partner Infidelity and Women's Defection](#)

Intimate Terrorism

- ▶ [Coercive Control](#)

Intrabrood Conflict

- ▶ [Conflict Between Parents and Offspring](#)

Intragroup Competition

- ▶ [Peer Competition and Cooperation](#)

Intragroup Conflict

- ▶ [Humans: Within-Group Conflicts](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)

Intragroup Cooperation

- ▶ [Peer Competition and Cooperation](#)

Intragroup Killing

- ▶ [Nonhuman Primates: Within-Group Conflicts](#)

Intragroup Killing, Within-Group Killing

- ▶ [Humans: Within-Group Conflicts](#)

Intralocus Sexual Conflict

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Synonyms

[Cross-sex antagonistic pleiotropy](#); [Genetic conflict between the sexes](#); [Sexual antagonism](#); [Sexually antagonistic genetic variation](#); [Sexually antagonistic polymorphism](#)

Definition

The evolutionary genetic conflict describing the causes and consequences of alternative alleles at particular genetic loci being selected oppositely in the two sexes, such that one allele at a given locus

will pose fitness benefits to male individuals but fitness detriments to female individuals, and vice versa for the alternative allele at that locus.

Introduction

Intralocus sexual conflict is the genetic conflict between the sexes (Lande 1980; Bonduriansky and Chenoweth 2009; van Doorn 2009). As opposed to interlocus sexual conflict (IeSC), where the conflicting traits of males and females are underlain by different genes (i.e., loci), intralocus sexual conflict (IaSC) occurs when the same genetic locus or loci control the trait in conflict between males and females (Arnqvist and Rowe 2005).

The term “conflict” refers to the outcome of selection in one sex being detrimental to the survival and/or reproduction (i.e., fitness) of individuals of the other sex. Thus, “conflict” over a particular trait refers to selection on that trait operating in opposing directions in males and females. This is known as sexually antagonistic (SA) selection and is the driver of sexual conflict (be it IaSC or IeSC). SA selection is explained more thoroughly below and in the coming section(s). For now, know that selection is differential fitness among individuals. If a particular version of a given trait benefits the bearers’ fitness, it is said to be under positive selection. Likewise, the particular genetic variant (i.e., allele) of the gene responsible for such a trait is also said to be under positive selection. So when a trait or gene experiences SA selection, it means that the version of the trait or gene that benefits male fitness also detriments female fitness and vice versa for the alternative version of the trait/gene. Thus, IaSC is the conflict that ensues due to SA genetic variation for fitness.

Genetic variation refers to the different versions/alleles of a given gene. So, specifically, IaSC occurs when one allele of a given gene benefits male fitness but detriments female fitness and the other allele of that gene benefits female fitness but detriments male fitness. Hence, “*intralocus*,” i.e. the conflict, is over the

genetic variation *within* a gene. One allele of such a gene experiences positive selection in males but negative selection in females and vice versa for the other allele. The gene is therefore under SA selection. But selection ultimately operates on the traits produced by genes, so if a gene is experiencing SA selection, it must mean that the trait it produces is under SA selection. One version of the trait (owing to one allele) benefits the fitness of male individuals but detracts that of female individuals, and the other version of the trait (owing to the other allele) benefits the fitness of female individuals but detracts that of male individuals. There can be many such genes exhibiting IaSC, but the conflict is over the genetic variation (alleles) within each gene.

So how does this happen? How does a gene that underlies a trait that is expressed by both males and females come to exhibit two alternative alleles, each posing benefits to one sex but detracts to the other? In answering that question, we must first think of the fate of new mutations in a population. If the mutation is 'good' for individuals of both sexes, relative to the original allele, then bearers of that mutation (i.e., that new allele) will survive and/or reproduce more than individuals bearing the original/old allele of that gene. The new mutation/allele will therefore become more frequent each generation, as its successive bearers continue to out-reproduce those lacking the mutation. Over generations, that new allele will eventually become fixed, i.e., everyone in the population will have the new allele and the original allele will die out along with its bearers. Alternatively, if the mutation is 'bad' for individuals of both sexes, relative to the original allele, bearers of that new allele will survive and/or reproduce less than individuals bearing the original allele, and the mutation will quickly be eliminated/lost from the population. It will die out with its bearers. But if a new mutation/allele is good for individuals of one sex and bad for those of the other (relative to the original allele), this places the gene under SA selection. Each allele is selected for via one sex but against in the other. Which allele is ultimately lost and which is fixed depends on the strength of positive and negative

selection acting on the two alleles in each sex. If the strength of positive and negative selection acting on each allele is equal in magnitude (but opposite in sign) in males and females, then both alleles of such a gene will be maintained in the population indefinitely (Kidwell et al. 1977). Even upon deviations from perfect symmetry in the strength of sex-specific selection at SA genes, there are a variety of conditions under which both alleles will still be maintained indefinitely over generations (e.g., Kidwell et al. 1977 and other examples given below). This has important implications for the maintenance of genetic variation for fitness, a concept addressed in more detail below.

So IaSC is an outcome of SA selection *and* a genome that is largely shared across the sexes (Lande 1980; Arnqvist and Rowe 2005; Bonduriansky and Chenoweth 2009; van Doorn 2009). So how likely are these two precursors? How likely is it for the above scenario to happen? With the exception of the sex chromosomes (accounting for a small proportion of genes), the genome is definitely mostly shared by both sexes, so presumably most genes are used by both sexes and are therefore vulnerable to SA mutations (described above). As for whether or not there will be SA selection, as long as there are two sexes that reproduce in fundamentally different ways, individuals will experience sex-specific selection for traits that disregard, and are inevitably bad for, the fitness of individuals of the opposite sex (Kokko and Jennions 2014). So there will be SA selection, at least acting on traits, as long as there are two sexes. And since much of the genome is being used by both sexes, the same genes in males and females encode many of those SA traits. So IaSC would seem unavoidable. Indeed, theoretical models predict the inevitability of IaSC and show its profound influence on the evolutionary trajectory of sexually reproducing populations (Connallon and Clark 2014). Furthermore, since most of a population's genetic variation that is either good or bad for both sexes should be rapidly fixed or lost, respectively (see above), most of the remaining standing genetic variation for fitness should be SA (Connallon and Clark 2012).

An Empirical Example

There are plenty of examples of wild and laboratory populations exhibiting significant levels of SA genetic variance for fitness (e.g., Chippindale et al. 2001; Fedorka and Mousseau 2004; Brommer et al. 2007; Foerster et al. 2007; Berger et al. 2014). However, the best empirical evidence/example for a specific gene experiencing IaSC comes from Barson et al. (2015). Their study of Atlantic salmon revealed a single gene explaining 39% of the observed variation in age at reproductive maturity. This is a very large percentage of the variation to be explained by a single gene for a trait that is likely governed by many genes. There are two versions/alleles of this gene in their study population. Being homozygous (i.e., having two of the same allele, one from each parent) for one of the alleles caused individuals to grow to sexual maturity quickly and consequently have a smaller adult body size – traits that are beneficial to males, but not females (see below). Being homozygous for the other allele caused individuals to grow to sexual maturity more slowly and consequently have a larger adult body size – traits that are beneficial to females, but not males (see below). However, in a heterozygous state, having one copy of each allele, individuals were *not* simply of intermediate growth rates and sizes; instead, one allele exhibited dominance over the other in a sex-specific manner. That is, which allele was dominant over the other in heterozygous individuals depended on the sex of the individual. The male-benefit allele was dominant over the female-benefit allele in males, and the female-benefit allele was dominant over the male-benefit allele in females (Barson et al. 2015).

This is an especially exciting example of IaSC for three reasons. First, it is one of the few, if not the only, definitive empirical examples of a specific gene exhibiting IaSC. As mentioned above, there is plenty of empirical evidence for SA genetic variance natural populations, but identifying specific genes underlying SA genetic variance has been challenging. Second, the traits (largely) controlled by this gene – growth rate and size – exhibit a widespread and well-understood life history trade-off (i.e., grow fast/be small or grow

slow/be big). Thus, it advances our understanding of this classic life history trade-off, and it provides solid empirical evidence for the common assumption that life history traits are vulnerable to IaSC (described below). Lastly, this is the first empirical example of sex-specific dominance partially resolving IaSC, consequently maintaining both of the population's allelic variants of this SA gene. Sex-specific dominance was the first of many conditions predicted to maintain alternative alleles at SA loci when the strength of selection is not perfectly equal between the sexes (Kidwell et al. 1977; Fry 2010). As discussed above, even if the strength of selection is only slightly different between the sexes, the allele that is favored by the sex experiencing stronger selection will become fixed, and the other lost, if it were not for additional mechanisms acting to stabilize the maintenance of both alleles at SA loci. Knowing that such mechanisms can, indeed, help to maintain alternative SA alleles in wild populations provides confidence that IaSC is widespread in nature, posing fundamental consequences to a variety of evolutionary processes.

Consequences and Outcomes of IaSC

The consequences of IaSC for evolutionary outcomes are potentially vast. The prevalence of some of these outcomes (e.g., the near ubiquity of sex chromosomes in sexually reproducing species) supports the notion of IaSC being inevitable. In other cases, the implications of a given outcome (e.g., the potential for extinction) can be so drastic that it deserves further research/understanding regardless of how common it might be. Some of these consequences and outcomes will be covered in more detail in later sections, and some of them are far beyond the scope of this section. Still, in the coming paragraphs, I will try to at least introduce most of these.

The Maintenance of Genetic Variation for Fitness

As hinted at above, SA genetic variation can act to maintain a population's genetic variation for fitness. One of the most long-standing questions in evolutionary biology has been: What maintains genetic variation for fitness? Evolution requires

genetic variation. There must be alternative alleles producing alternative versions of traits in order to provide some variation among individuals upon which selection can act. But even with genetic variation at the start, as selection gradually fixes or eliminates certain alleles, that genetic variation gradually disappears. So how does evolution continue in the face of selection? There are many explanations for what maintains genetic variation for fitness in the face of selection, and one of those explanations is that selection is actually SA. Again, SA selection on a gene can maintain both alternative alleles over generations, and there are many plausible mechanisms that enhance the likelihood of maintaining SA genetic variation (e.g., Kidwell et al. 1977; Fry 2010; Arnqvist et al. 2014). This could effectively maintain a population's genetic variation for fitness depending on what proportion of the population's standing genetic variation for fitness is SA. Remember, since the genetic variation that is either good for both sexes or bad for both sexes should be rapidly fixed or lost, respectively, a population's standing genetic variation for fitness is expected to be disproportionately SA (Connallon and Clark 2012). Thus, IaSC may have a very prevalent role in the maintenance of genetic variation for fitness in wild populations and therefore may help to explain one of evolutionary biology's most long-standing questions.

Sex-Chromosome Evolution

Another major research focus in evolutionary biology is sex-chromosome evolution. SA loci play an important role in the evolution of sex chromosomes (van Doorn and Kirkpatrick 2007; Blaser et al. 2014). Sex chromosomes, among other things, determine the sex of an individual. They do this via the action of sex-determining genes/loci. So there are sex-determining genes that determine the sex of an individual, e.g., one version of the gene *produces* females and the other *produces* males. And there are SA genes, which you are familiar with by now – one version of the gene *benefits* females and the other *benefits* males. There is selection for SA mutations to occur on the same chromosome near sex-

determining genes (Jordan and Charlesworth 2012). This is because if a SA mutation occurs (by chance) near a sex-determining gene, the two versions of those two genes that are on the same chromosome will tend to be inherited together. The value of this for lucky individuals/lineages is that, for example, if a male-determining allele (at a sex-determining gene) is co-inherited with a male-benefit allele (at a SA gene), this will produce males that are particularly good at surviving and/or reproducing as males. Likewise, the same is true for females possessing female-benefit genes. Such individuals/lineages will out-reproduce those with mismatched sex-determining and SA alleles (e.g., males with female-benefit alleles). So there is selection for SA mutations/genes to occur near sex-determining genes due to the benefits posed to individuals of a given sex of being 'good' at being that sex (Jordan and Charlesworth 2012). This in turn generates selection for the homologous pair (i.e., mother/father pair) of chromosomes to stop recombination – to stop exchanging genetic material during meiosis – so that 'good' combinations of sex-determining and SA genes are always co-inherited together (Bull 1983; Rice 1996) or, in other words, so that male-benefit alleles are only passed on to sons and female-benefit alleles are only passed on to daughters. This arrest of recombination causes such 'neo-sex-chromosome' pairs to diverge further and further in genetic sequence and functionality over many generations. For example, the familiar X and Y chromosomes of many species are extremely different in size, gene content, and mutation load. The proximity and chronology of sex-determining and SA mutations, as well as the potential arrest of recombination that follows, influence which chromosomes are coopted for sex determination (i.e., become sex chromosomes), and whether or not they will be kept indefinitely as the sex chromosomes or cyclically abandoned for a new set of neo-sex chromosomes over and over (van Doorn and Kirkpatrick 2007; Blaser et al. 2014). So IaSC plays an important role in sex-chromosome evolution and therefore an important role in the evolution of most eukaryote life.

Sexual Dimorphism

Sexual dimorphism (sex differences beyond reproductive organs) is another large domain of research within evolutionary biology, but also in medicine and conservation, and fields outside the biological sciences (e.g., psychology, sociology, philosophy). In many species, males and females are far more different from each another than are two members of the same sex from different species. IaSC both promotes and constrains sexual dimorphism. The sexes reproduce in fundamentally different ways and therefore accrue and maximize their reproductive fitness in fundamentally different ways (Arnqvist and Rowe 2005). Recall the classic life history trade-off discussed above – grow fast/be small or grow slow/be big. Females tend to take time to incubate offspring and therefore require long, reproductively active lives in order to maximize their reproductive success. They also tend to benefit from being big in cases where larger body size enables greater fecundity (Fairbairn et al. 2007). They tend to achieve long life and large body size by having lower metabolic rates, slower growth rates, and allocating resources toward things like immune system function and somatic tissue maintenance. Alternatively, males tend to maximize their reproductive success by fertilizing as many females as possible. They typically benefit from growing fast in order to reach sexual maturity before their competitors and being fast, strong, and/or aggressive adults so as to win the competition for mates. They tend to achieve this by having higher metabolic rates, faster growth rates, and allocating resources toward reproductive traits, potentially at the expense of being able to invest in their immune system and/or somatic tissues, consequently having shorter life spans (the so-called ‘live-fast/die-young’ life history strategy). Thus, the sexes tend to exhibit different physiologies, metabolic rates, growth rates, body sizes, mating behaviors, patterns of aging, etc. (Arnqvist and Rowe 2005; Fairbairn et al. 2007). These life history traits are commonly underlain by the same genetic bases in males and females since they are some of the most basic features of an organism, but they are also commonly sexually dimorphic (Arnqvist

and Rowe 2005; Fairbairn et al. 2007). So how does this happen?

Using mostly the same genome, males and females of a given species must achieve very different life histories in order to survive and reproduce successfully. They accomplish this in a number of ways (e.g., cellular and hormonal processes during development, epigenetic processes, phenotypic plasticity, etc.), but the most common and most well understood of these ways is via the few small genetic differences between them, the sex chromosomes. As discussed above, the sex chromosomes tend not to recombine and therefore diverge in sequence and functionality over time. Thus, the sex chromosomes can enable sexual dimorphism in two ways. The first is via sexually dimorphic traits being underlain by genes located on the sex chromosomes (i.e., sex-linked genes). For example, in an XY sex-determining system, the product of genes on the Y chromosome will only ever appear in males, and the product of some genes on the X chromosome may require two copies in order to produce enough product (e.g., RNA or protein) to carry out their function, meaning that such a gene will only be effective in XX females. But sex linkage only accounts for a relatively small percentage of the genes in the genome of a given species. The second and more prevalent mechanism via which sex chromosomes enable sexual dimorphism is sex-biased (and sex-specific) gene expression. The sex chromosomes house, among other things, regulatory genes that can turn other genes throughout the genome on or off or up or down; and since they are sex chromosomes, this enables sex-specific gene regulation. This can allow individuals with the ‘wrong’ SA alleles for their sex to survive and reproduce better than they otherwise could have. In this way, sex-specific/biased gene expression can alleviate some of the genetic conflict between the sexes. So, IaSC sets the stage, i.e., generates selection, for the conflict to be resolved so that the sexes can achieve sexual dimorphism and maximize their reproductive fitness, which would essentially allow the sexes to evolve more independently from one another than they could otherwise. Thus, the genetic conflict that constrains sexual dimorphism in the first

place thereby generates selection for other genes to enable sexual dimorphism. One can therefore consider every sexually dimorphic trait of a given species as evidence of a previous IaSC that has been (partially) resolved. But the conflict cannot be completely resolved. New SA mutations can always arise, and many genes are not regulated by genes on the sex chromosomes. So IaSC is expected to still be a severe constraint on achieving sexual dimorphism (Lande 1980), as has been shown in many species, from fruit flies (Griffin et al. 2013) to humans (Stearns et al. 2012), preventing the sexes from achieving their sex-specific fitness optima.

The Tragedy of the Commons

As mentioned, IaSC can cause individuals with the ‘wrong’ alleles for their sex to perform poorly, and this can affect a population’s viability/persistence. Specifically, if females of a population perform poorly then the population may decline in numbers, which can lead to inbreeding depression and extinction (Kokko and Brooks 2003). Females are the limiting factor in population growth rate. This is because, as mentioned above, females take time to incubate offspring, whereas males can fertilize many, many females in a relatively short period of time. Further, females typically receive enough sperm from a single mating to fertilize their entire life’s worth of eggs. Thus, there need only be relatively few fertile males in a population to fertilize all the females, whereas the fewer females there are the fewer offspring a population will produce. When a population’s genetic variation for fitness is largely SA, the ensuing IaSC inevitably causes some males and females to have the ‘wrong’ alleles and to perform poorly (hence “conflict”). When this happens to males, it has very little effect on the population, since relatively few fertile/good males are absolutely needed for a population to persist. Alternatively, when some females do poorly the population as a whole will produce fewer offspring. A population’s offspring production will be proportional to the number and fecundity of its females. If each subsequent generation produces fewer offspring with fewer fecund females, the population could enter into a

downward spiral of declining population size, which can lead to inbreeding depression from breeding among related individuals, and potentially population extinction (Kokko and Brooks 2003). For example, using a wild caught SA population of seed beetles, we have shown that genotypes exhibiting relatively high-male/low-female fitness exhibit relatively low potential to contribute positively to population growth rate (Berger et al. 2016a). This was interpreted as a consequence of both IaSC and IeSC (see second sentence of this article, above). Genotypes with the alleles that are good for males are those with the alleles that are bad for females (i.e., IaSC), and genotypes with high male fitness feature aggressive males that physically harm females upon mating attempts and copulation, lowering female lifetime offspring production (i.e., IeSC; Berger et al. 2016a). In our example IaSC is not acting alone, but it can nevertheless play an integral role in the fate of populations.

Same-Sex Sexual Behavior

Lastly, IaSC provides an explanation for same-sex sexual behavior such as homosexuality in humans. It should first be clear that there are vast mechanistic differences between same-sex sexual behavior in something like an insect (e.g., same-sex mounting, which is observed in many species in nature) and homosexuality in humans, other mammals, birds, or fish, for example. The former can have rather simplistic potential explanations (e.g., strong selection in males to mate frequently and weak selection against brief mistaken encounters), whereas the latter certainly entails far more complexity in terms of the neurological, biochemical, and physiological bases of attraction and conscious behavior. Nevertheless, the SA underpinnings of something like same-sex mounting in an insect and homosexuality in humans have been shown to exhibit strikingly congruent quantitative and population genetic bases (Gavrilets and Rice 2006; Camperio Ciani et al. 2015; Berger et al. 2016b). Camperio Ciani et al. (2015) nicely reviewed the literature on this topic, concluding that, at least for male homosexuality, the predictions from IaSC (modeled by Gavrilets and Rice 2006) fit the available relevant pedigree and

population data well, supporting a SA genetic basis for male homosexuality in humans. I urge readers to refer to Camperio Ciani et al. (2015) for a more thorough and careful handling of this topic. I will only summarize some of their key points here. Two key observations of the data on male homosexuality in contemporary human populations stand out: (1) it persists at low frequency, and (2) pedigree analyses reveal an elevated likelihood of homosexual males in family lineages with particularly high maternal-line female reproductive success. Thus, the genetic factors/alleles involved must be stable at low equilibrium frequencies (i.e. robust to alleles becoming fixed or lost (recall discussions above on the maintenance of SA genetic variation)) and there must be some maternal-line mode of inheritance. A two-locus population genetic model, consisting of one autosomal gene and one gene on the X chromosome, with SA selection, proposed by Gavrilets and Rice (2006), provides the best fit to these two key empirical observations (Camperio Ciani et al. 2015). Thus, one might generate the following mechanistic hypothesis based on IaSC: female-benefit alleles causing females to be particularly attracted to males experience positive selection because this results in females having relatively more offspring, and those same alleles have the same effect (attraction toward males) in their male offspring. However, *female* homosexuality in humans is more difficult to explain – it is less dichotomous than male homosexuality, it is more variable over the course of individuals' lifespans, and it is more vulnerable to environmental/social influence (see Camperio Ciani et al. 2015).

Trans-generational SA epigenetic processes possibly offer an explanation that is even more accurately representative of the observed data and is also capable of accounting for female homosexuality (Rice et al. 2012). Furthermore, this would also explain why identifying a particular gene or genes reliably associated with homosexuality in humans has been so difficult, as epigenetic processes would not be revealed by genetic association studies. By this mechanism, SA epigenetic marks ("epimarks," e.g., methyl tags that bind to DNA and affect gene expression) masculinize or

feminize the genome during development and are typically erased and reapplied upon fertilization according to the sex of the zygote (Rice et al. 2012). Mistakes or epimarks that escape erasure can result in the genome of males/females being feminized/masculinized, respectively (Rice et al. 2012). This explanation does, however, move us away from IaSC per se, as the mechanism is not entirely genetic (so we are no longer talking about "loci" but rather "marks" on loci), but as mentioned, the epimarks in this model *are* necessarily SA (Rice et al. 2012).

IaSC *can*, however, explain male *and* female same-sex sexual behavior in other animals, for example, insects. We have shown, using the same SA population of seed beetle discussed above, that lineages artificially selected over generations for increased male-male mounting behavior exhibited higher female lifetime reproductive success (Berger et al. 2016b). Reciprocally, we also revealed that lineages artificially selected over generations for increased female-female mounting behavior exhibited higher male lifetime reproductive success (Berger et al. 2016b). The evidence implicates IaSC over the genetic components of both male and female same-sex sexual behavior (Berger et al. 2016b).

Conclusion

As the sexes achieve/maximize their reproductive fitness in fundamentally different ways, they benefit from different versions of the genes they share. This is the genetic conflict between the sexes known as IaSC. It is an inevitable outcome of having two sexes share the same genome. This conflict constrains sexual dimorphism, inhibiting males and females from achieving their sex-specific fitness optima, and therefore generates selection for other genetic mechanisms to enable sexual dimorphism. As there are many mechanisms that act to maintain alternative alleles at SA loci over generations, IaSC may play an important role in the maintenance of genetic variation for fitness in natural populations. SA loci also play a central role in sex-chromosome evolution, meaning IaSC has heavily influenced the

evolution of the eukaryotic branch of life on Earth. IaSC has implications that reach far beyond the study of evolution. For example, its implications for population viability and extinction are informative for conservation biology.

Perhaps the broadest appeal of IaSC is its capacity to inform us about the fundamentals of sex differences, which poses insights to fields as diverse as medicine, psychology, sociology, and philosophy. Although IaSC is understood well from a theoretical perspective, we are still building its empirical foundation. Many studies have provided evidence of populations exhibiting sizeable proportions of SA genetic variance for fitness. Recently, the most convincing case of a specific gene exhibiting IaSC was identified by Barson et al. (2015), an empirical finding that was supportive of much of theoretical expectation for IaSC. As the intrigue with this genetic conflict between the sexes continues to grow, more research will continue to uncover more details, eventually revealing just how widespread and influential IaSC has been, is, and will be to biological evolution.

Cross-References

- [Ancient Homosexuality](#)
- [Conflict Between the Sexes](#)
- [Evolutionary Arms Race](#)
- [Fast Versus Slow Strategies](#)
- [Female Homosexuality and Bisexuality](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Sexually Antagonistic Hypothesis](#)
- [Sex Differences in Variance Traits](#)
- [Sexual Orientation and Human Sexuality](#)

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Intralocus Sexual Conflict Across the Genome

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Synonyms

Cross-sex antagonistic pleiotropy; Genetic conflict between the sexes; Sexual antagonism;

Sexually antagonistic genetic variation; Sexually antagonistic polymorphism

Definition

How the loci harboring alleles with opposite fitness effects on the sexes are distributed across the genetic material in a cell: the sex chromosomes, autosomes and organelles such as mitochondria.

Introduction

Female and male reproductive roles are different, and consequently many phenotypic traits are selected in opposite directions in the two sexes, a process called sexually antagonistic (SA) selection. How traits respond to SA selection in each sex is, however, not straightforward. Depending on species, males and females possess a majority or all of the same genes. The shared gene variants (called alleles) cause a strong genetic correlation between the sexes, and the opposing selection pressures therefore lead to a tug-of-war, termed “intralocus sexual conflict,” over optimal expression of phenotypes (Bonduriansky and Chenoweth 2009).

An important consequence of SA selection is that it can maintain genetic variation, and therefore diversity, in a population that could otherwise quickly disappear if alleles were similarly selected in the sexes. Population genetic models have been developed to understand the conditions under which this can happen. A chief outcome of such models is that it matters where in the genome loci harboring SA alleles reside. Regions with asymmetric inheritance between the sexes, such as sex chromosomes and organelle genomes, can accumulate SA alleles more easily than autosomes because they are more often (or exclusively) exposed to selection in one sex than in the other.

Sex Chromosomes or Autosomes: Model Predictions

An influential early work by Rice (1984) concluded that SA alleles are more likely to be

maintained on the X and Z sex chromosomes in male (e.g., in mammals) and female (e.g., in birds) heterogametic systems, respectively. This is the case for recessive alleles beneficial to the heterogametic sex (males with XY, females with ZW) but harmful to the opposite, homogametic sex. Such alleles need to be recessive because in that way their effects are always visible to selection in the benefitting sex, but protected from being selected against in the disfavored sex when paired with a dominant, unharmed allele (which masks the effect of a recessive allele in heterozygotes). On the other hand, dominant alleles that benefit the homogametic sex are also likely to accumulate on the X and Z. While such alleles can readily be selected against in the disfavored sex, what helps with their invasion is that X and Z linked alleles occur more often in the favored sex (2/3 of the time in fact, because the homogametic sex has always two copies) allowing more opportunities for selection to keep the alleles in the population. In line with the Rice model, experimental work using *Drosophila melanogaster* has demonstrated a disproportionate role for the X chromosome harboring SA variation (Gibson et al. 2002). Also recent work on humans finds that most of SA loci associated with sex differences in survival map to the X chromosome (Lucotte et al. 2016).

There are, however, conditions that can make autosomes also attractive to the accumulation of SA loci. Rice (1984) stated that autosomes can maintain SA variation if selection acting on each sex is (nearly) equal in strength. This is an unstable situation and hence happens rarely. However, Fry (2010) expanded the possibilities by concluding that if the dominance effect of alleles is different in each sex – so that the favorable allele will always increase the fitness of the focal sex when paired with a disfavored allele – it will lead to balancing selection maintaining both female- and male-benefit alleles. Such a dominance reversal occurs in an autosomal locus *vestigial-like family member 3* (*VGLL3*) of salmon, resolving sexual conflict over body size at maturation. Alternative alleles for early and late maturation are dominant in males and females, respectively, leading to heterozygotes that are identical in genotypes at this locus but express

different sizes at maturation to achieve optimal fitness in each sex (Barson et al. 2015). Other examples of autosomal SA alleles maintained by balancing selection include *arginine vasopressin receptor 1a* (*Avpr1a*) in bank voles, with roles in reproductive behaviors, and a gene *Cyp6g1* encoding cytochrome P450 in *Drosophila*, which confers resistance to DDT but also increases female fecundity while suppressing male mating success (Mank 2017).

Organelles Are Special

Organelle genomes can accumulate SA variation because they are uniparentally transmitted and therefore respond to selection only through the transmitting sex. For example, in most species only mothers pass on mitochondrial genomes. This allows mutations harmful to males to be maintained, especially when favored but even when they confer no fitness benefit to females (a phenomenon termed the “Mother’s curse”). Work on *D. melanogaster* shows how mitochondrially encoded enzyme cytochrome oxidase II damages sperm development (Patel et al. 2016). Male fertility problems in humans and mice are also often associated with impaired function of mitochondrial genes (Nakada et al. 2006).

The Genomic Legacy of Sexual Conflict

Sexual conflict shapes genomes leaving molecular characteristics that can tell us about both present-day and past antagonistic selection. Intralocus conflict selects for a genetic resolution, leading to sex-specific genetic architecture of traits that allows independent responses to selection in each sex. One way to achieve such a resolution is through evolution of sex differences in gene expression. Sex-biased gene expression (i.e., higher relative expression in one sex) can therefore be indicative of a history of SA selection acting on the transcriptional patterns of such loci. Compatible with the theory, there is excess of sex-biased genes in the sex chromosomes across taxa (Ellegren and Parsch 2007). The conflict

resolution via sex-biased expression may, however, be only partial: evidence from humans and flies shows that genes with moderate levels of sex-bias are still subject to ongoing SA selection (Cheng and Kirkpatrick 2016).

Evolution of homomorphic sex chromosomes (X and W) is also a resolution to the conflict. Sex chromosomes are the product of evolution for recombination suppression between the X and Y (or Z and W), and studies on fish suggest that selection on reduced recombination has occurred to maintain male-benefit alleles on the Y chromosome (Wright et al. 2016). The conflict is resolved because Y-linked genes are simply never present in females. In species where parts of the Y chromosome still recombine with X, the positive feedback-loop between accumulation of SA variation and subsequent selection to expand the area under which recombination with X is suppressed is still ongoing (Mank 2017).

Conclusion

Sexually antagonistic loci can be studied using candidate gene approaches, gene expression analysis, and genome-wide association studies (GWAS). More recently, also population genetic methods have been applied to identify SA loci by testing how allele frequencies change due to sex differences in survival in humans (Cheng and Kirkpatrick 2016; Lucotte et al. 2016). Although these techniques have already provided important examples of SA loci and their genomic locations, many more need to be discovered to answer important open questions including how often the same loci are subject to antagonistic selection across populations and species, and, importantly, which phenotypes do the genes involved encode for. Sexually antagonistic selection truly is common and humans are no exception. With the democratization of the sequencing technologies this important field will continue to shed light into the outstanding question of how sexually antagonistic selection shapes the genomes of humans and other organisms alike.

Cross-References

- [Conflict Between the Sexes](#)
- [Evolutionary Arms Race](#)
- [Intralocus Sexual Conflict](#)
- [Sex Differences in Variance Traits](#)
- [Sexual Dimorphism and Sex-Biased Gene Expression](#)

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Intra-Sex Sexual Behavior

- [Homosexual Receptivity](#)

Intrasexual Aggression

- [Anne Campbell](#)

Intrasexual Competition

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Intra-sexual Competition

- [Status Competition](#)

Intrasexual Competition Between Females

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Intrasexual competition refers to competition between individuals of the same sex for access to mating opportunities (Andersson 1994) and is expressed through both direct aggression (e.g., physical combat) and indirect aggression (e.g., competitor derogation, self-promotion) (Campbell 2004; Vaillancourt 2013). Although direct aggression among women clearly does occur (Stockley and Campbell 2013), intrasexual competition among women more commonly takes the form of indirect aggression (Vaillancourt 2013). These indirect competitive strategies can act to increase a woman's own access to her preferred mate (e.g., through self-promotion) or decrease a rival's access to mating opportunities (e.g., through competitor derogation).

Self-promotion involves attracting attention to and enhancing one's own attractiveness, typically through the use of attractive clothing and makeup (Buss 1988; Grammer et al. 2004; Schmitt and Buss 1996). Self-promotion is an effective tactic for mate attraction due to the importance of physical attractiveness for men's mate preferences (Buss and Barnes 1986). Indeed, women frequently report using these self-promotion tactics to compete with rivals and attract members of the opposite sex (Cashdan 1998; Tooke and Camire 1991; Walters and Crawford 1994). By contrast, competitor derogation involves decreasing the appeal of a rival to members of the opposite sex (Buss and Dedden 1990). Competitor derogation can be achieved

through disparaging a competitor's appearance and through gossip or reputational damage, particularly related to the rival's fidelity or promiscuity (Vaillancourt and Sharma 2011). Additional derogation tactics include excluding a rival from peer groups and derisive actions aimed at lowering a rival's willingness to compete for mates (Campbell 2004). Competitor derogation is an effective tactic, with negative information about conspecifics predicting low attractiveness rankings of those individuals (Rucas et al. 2006). While women use both self-promotion and competitor derogation tactics, some research has suggested that self-promotion is used more often (Fisher et al. 2009).

Given that attractive individuals achieve greater mating success and are more successful at mate-poaching (Sunderani et al. 2013), these individuals pose a greater threat to mating opportunities and mate retention. Unsurprisingly, intrasexually competitive tactics are more often used against these attractive rivals compared to less attractive individuals (Arnocky et al. 2012; Massar et al. 2012; Vaillancourt 2013). For example, women are more likely to discriminate against attractive same-sex candidates in the workplace (Agthe et al. 2011), are less willing to introduce an attractive same-sex individual to their partner (Vaillancourt and Sharma 2011), and are more likely to have negative responses to a "sexy" rival than a conservative rival (Vaillancourt and Sharma 2011).

A growing body of research has suggested that female intrasexual competition is influenced by reproductive status, suggesting that women have a greater desire to outdo attractive rivals to obtain a high-quality mate when conception is possible. In line with this idea, intrasexually competitive behaviors have been shown to increase during adolescence (Archer 2004) and young adulthood (Hess and Hagen 2006; Massar et al. 2012). Conversely, intrasexually competitive behaviors decrease following menopause (Jones et al. 2011; Vukovic et al. 2009). This rise and fall in intrasexually competitive behavior parallels changes in general fertility across the life span (Dunson et al. 2002). In young adult women, intrasexually competitive behaviors have also

been shown to increase during the fertile phase of the menstrual cycle as compared to non-fertile phases (Beall and Tracy 2013; Durante et al. 2008, 2011; Fisher 2004; Haselton et al. 2007; Lucas and Koff 2013; but see Arslan et al. *in press*; Cobey et al. 2013). Research investigating the hormonal correlates of within-woman changes in intrasexual competitive behaviors has shown links to testosterone levels (Hahn et al. 2016; López et al. 2009). Priming intrasexual competitive motivations in women also increases testosterone levels in women (Maner and McNulty 2013; Ritchie and van Anders 2015).

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Intrasexual Homicide

► Same-Sex Homicide

Intrasexual Killing

► Same-Sex Homicide

Intrasexual Male Competition

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Synonyms

[Intrasexual selection](#); [Male-male competition](#)

Definition

Competition between males for access to females or the resources desired by females.

Introduction

Sexual selection leads to the development of traits and behaviors that improve reproductive success. Darwin recognized two types of sexual selection: intersexual and intrasexual selection. Intersexual selection occurs when one sex chooses which members of the opposite sex to mate with, while intrasexual selection occurs when members of the same sex compete for mates (Darwin 1871).

In many species, males compete through intrasexual competition to gain access to females. Critical work in *Drosophila* in the 1940s revealed that the mean number of offspring a male can produce increases with the number of mates he has, while the mean number of offspring a female can produce does not vary greatly and is not limited by access to mates (as long as there is at least one mate) (Bateman 1948). This finding also applies to mammals. For example, male red deer have more reproductive potential and greater reproductive skew than females. Some males will successfully fight for mates and produce ten times more offspring than a female will produce, while many males will sire no offspring at all (Lewin 1982).

This chapter will first provide an overview of the different forms of both direct and indirect male-male competition. It will go on to discuss how male-male competition relates to other forms

of sexual selection, and will conclude with a description of the role that intrasexual male competition has been proposed to play in human mating behavior.

Direct Intrasexual Male Competition

Contest Competition

Since females are usually the choosier sex, males often compete with one another directly for mating access. This competition has led to the evolution of a diverse array of weaponry among animals. For example, many deer and elk species in the family Cervidae have large antlers that can be used in direct competition during the mating season to gain access to females. Further, in many primate species, males have large canines that can be used as lethal weapons in contest competition. Perhaps unsurprisingly, in species where males have weapons, weaponry is often one of the most variable morphological traits within the population (Emlen 2008).

Direct male-male competition does not always have to end in a fight. Sometimes, species with the deadliest weapons have a reduced likelihood of sustaining injuries from contest competitions because weapon size is hypothesized to provide an honest signal of a male's fighting ability (Smith and Price 1973). Before any conflict occurs, a male can gauge the strength of his competitor and decide whether he will be able to successfully compete against him. As a result, some of the most common fights that occur between males are those where male weaponry is equally matched.

Dominance Hierarchies

In populations where individuals spend time together and have repeated interactions with others in their social group, dominance hierarchies may emerge as a product of male-male competition. Among different species, dominance structures can vary based on the strength, stability, and linearity of the dominance hierarchy. Often, males will compete directly with one another to achieve dominance. However, it remains unclear whether variation in strength and fighting ability between males or social constructs such as winner-and-loser

effects more strongly influence how dominance is determined in a social group. While the former hypothesis is well supported in the literature, research on baboons indicates that winner-and-loser effects may also play a role in the construction of dominance hierarchies (Franz et al. 2015).

In species that fight for dominance, high-ranking social status may serve several functions. Dominant males often have priority of access to resources, including females and food, which increases their reproductive success and may improve their health, respectively. Dominance hierarchies also create a social order that prevents individuals from having to constantly fight potentially deadly battles with conspecifics.

Just as weapon size is thought to signal strength in many male mammals, in species where males fight for dominance, dominant males will sometimes display a badge of status. Gelada males compete to be one-male unit (OMU) holders, with each OMU containing multiple females. Males that have an OMU have the reddest chest patches, with patch redness reflecting the number of females in the OMU (Bergman et al. 2009). In male mandrills, red coloration displayed on their face and anogenital region indicates social rank, and more fights occur between males of similar colors than those that show a large difference in red coloration (Setchell and Wickings 2005). Therefore, dominance hierarchies and badges of status provide mechanisms by which males can compete for access to females while limiting the number of potentially deadly contests.

Indirect Intrasexual Male Competition

Sperm Competition and Mate Guarding

Intrasexual male competition can also act indirectly. One common form of indirect intrasexual competition occurs through postcopulatory sperm competition. In species where females mate with several different males, the males' sperm compete to fertilize the female's gametes. In polyandrous and polygynandrous mating systems, males will have larger testes than in monogamous or polygynous mating systems (Harcourt 2005). In primates, the size of the testes is often related to the

mating system of the species: males in polygynous mating systems have smaller testes weights while males in polyandrous and polygynandrous mating systems have larger testes weights. In other taxa, such as insects, males in a polyandrous or polygynandrous mating system may have enlarged accessory glands to produce more seminal fluid (Mikheyev 2004). Finally, in species with a polyandrous or polygynandrous mating system, a male's ejaculate may form a copulatory plug that is made up of a coagulation of seminal fluid and prevents the sperm of other males from reaching the ova (Dixon and Anderson 2002).

In addition to sperm competition, another postcopulatory indirect form of intrasexual male competition is mate guarding. This form of competition is most common in taxa where multiple males mate with one or more females during the mating period or in cases where sperm is a limited resource. After copulation, a male may prevent other males from mating with the female or may prevent a female from seeking out additional mates. Mate guarding can be accomplished by staying close to the female for an extended period, postcopulatory mounting, extending copulation, or coalitionary guarding, depending on the species (Edward et al. 2015). Sometimes, only certain males in the population will guard females. This may be due to the fact that mate guarding is energetically expensive and affects a male's feeding time and energy balance (Girard-Buttoz et al. 2014).

Endurance Rivalry

Males can also compete indirectly prior to copulation. When reproductive skew is low in a polygynandrous group, several males may mate with several females over an extended period and reduce the amount of time they spend on other activities. In these scenarios, the males who spend the longest amount of time actively mating with females are the ones who sire the most offspring. For example, rhesus macaque males experience increases in their fat reserves prior to the mating season but during the mating season, males lose up to 10% of their body weight by focusing on mating and mate guarding rather than activities such as feeding (Bercovitch 1997).

Endurance rivalry is not limited to species with moderate reproductive skew. Elephant seals are one of the most sexually size dimorphic mammals with some males weighing more than three times as much as females. Over the 3-month reproductive season, a few of the largest males fight off smaller males to achieve high rank, defend large groups of females, and sire almost all of the offspring. While males compete directly, they also engage in endurance rivalry since females stay on land for the duration of the mating season while feeding occurs in the water. Reproductive success is greatest for males with the largest fat reserves and can invest in mating and mate guarding rather than feeding (Andersson 1994).

Alternative Reproductive Tactics

In populations where males experience a shallow reproductive skew, selection may favor the development of alternative reproductive tactics. These tactics include any behavior that is distinct from the most commonly used mating strategies and may be maintained by frequency-dependent selection, heterozygote advantage, or condition-dependent selection (Neff and Svensson 2013). For example, males may employ sneaking behaviors, morphologically resemble females, or mate guard their mates. These mating strategies enable males to avoid intrasexual conflict while gaining access to females.

Side-blotched lizards provide a notable example of alternative reproductive tactics. In populations where a majority of males occupy large territories and monopolize females, sneaker males secretively mate with females without having to compete with other males for territory thus increasing their reproductive success compared to males who cannot acquire territory and do not use this tactic (Zamudio and Sinervo 2000). In primate species such as Japanese macaques and Hanuman langurs, where males often live in multi-male multi-female groups, some males may choose to live alone or in all-male groups (Setchell 2008). These males will mate with females opportunistically during the mating season thus avoiding competition with dominant males in the social group.

Intrasexual Male Competition in the Context of Total Sexual Selection

Although intrasexual male competition and female mate choice are often studied in isolation, it is important to acknowledge the role that female choice plays on intrasexual male competition. In populations where mate choice occurs, the preferences of the female should influence the type of competition that occurs between males. If females require a home territory, males should compete for the resources that the female needs, such as land, rather than directly competing for females. In contrast, if a population is structured into one-male, multi-female groups, males should engage in contest competition with other males to gain access to these one-male units.

Intrasexual male competition may also influence mate choice. Some argue that, over time, weapons that were originally used for male-male competition may have become intersexual signals used by females to determine preferred mating partners. Further, in species that exercise female choice, direct intrasexual male competition may provide females with information about the strongest male and influence their mating preferences. This will reinforce selection on traits used in competition (Hunt et al. 2009).

Intrasexual male competition and female mate choice rarely act independently. To better understand the selection pressures on a male sexual trait, it is essential to determine total sexual selection on the trait (Hunt et al. 2009). Total sexual selection encompasses the strength of selection imposed on both sexes by competition and mate choice. When male-male competition and female mate choice interact on the same trait, the effects of these processes can be reinforcing, such that total sexual selection is similar to the strength of each selection pressure independently or opposing, with the resulting total sexual selection differing from either of the selection pressures on its own (Hunt et al. 2009). Intrasexual male competition and female mate choice can also act on different temporal scales. When male-male competition occurs prior to female mate choice, male-male competition will eliminate some of the phenotypes from which females can choose. When

the two processes overlap temporally, both processes select male traits from the same pool of phenotypes and some males may gain access to females by obtaining exclusive mating opportunities while other males gain access to females by displaying attractive traits (Hunt et al. 2009).

Intrasexual Male Competition in Humans

Over our evolutionary history, intrasexual male competition has been an important component of human behavior. One way to evaluate mating and social systems of the past and make assumptions about intrasexual competition is through studies of sexual size dimorphism. Since body size is heritable and helps males win contests, the larger the size dimorphism between male and female primates, the more frequently males compete directly for females (Andersson 1994). Our hominin ancestors, such as *Australopithecus* and early *Homo*, likely displayed a significant sexual size dimorphism. Over the course of hominization, however, this body mass dimorphism was reduced and modern human populations show a modest body mass dimorphism of about 15% (Smith and Jungers 1997). Humans have also lost the canine size dimorphism that is present in many primate taxa. However, since human females store more body fat than males, some have argued that fat-free body mass should be used to measure sexual size dimorphism. Using this method, the ratio of fat-free mass in males compared to females is 1.41, indicative of a significant, moderate size dimorphism (Lassek and Gaulin 2009). Thus, humans experience some degree of body size dimorphism that, while reduced compared to our hominin ancestors, highly suggests that males compete both directly and indirectly for access to females and resources desired by females (Triveres 1972).

Direct Intrasexual Male Competition

One method of intrasexual competition in human males is violence. Beginning early in life, males are more aggressive than females and more frequently engage in rough-and-tumble play (Ellis et al. 2008). Further, males generally have a

higher pain tolerance than females (Ellis et al. 2008). In the tribal Yanomamo society, males engage in contests that involve shouting matches and fights with clubs, axes, machetes, and arrows (Chagnon 1988). In a rural population in Senegal, Sereer wrestling is a traditional fight that occurs regularly in villages and winners often increase their access to mates (Llaurens et al. 2009). According to the Global Study on Homicide, 95% of the perpetrators and 80% of the victims of homicide are male (Caman et al. 2017).

As in primates, human males have also been proposed to compete directly through displays of dominance. Men of high status may procure more opportunities to mate and high status has been shown to be a necessity for women in a mate-screening process (Li et al. 2002). One suggested mechanism by which males display dominance is voice pitch. Studies indicate that when voice pitch is artificially lowered, men perceive these voices as more dominant than higher pitched voices (Puts et al. 2006). Further, men who believe they are dominant to another man will lower their voice pitch when speaking, while men who believe they are less dominant will raise their voice pitch (Puts et al. 2006). Among the Hazda, lower voice pitch has been suggested to increase reproductive success in males but not in females (Apicella et al. 2007). However, the relationship between voice pitch and dominance has recently come into question, with some arguing that it lacks evidence or is simply the product of an innate assumption that larger objects and organisms emit a lower pitch than smaller ones (Feinberg et al. 2019).

In addition to voice pitch, facial characteristics may also serve as a dominance display. Across two distinct cultures, men were considered more aggressive and of higher social status if they had a beard than if they were clean shaven and this sensitivity was stronger in men than in women. This may occur because beards increase the perception of the size of the jaw and length of the face (Dixon and Vasey 2012). Further, computer-manipulated masculinized faces are perceived by men as more dominant than feminized faces and a negative correlation exists between one's self-rated dominance and perceived dominance in masculine faces (Watkins et al. 2010a, b).

Indirect Intrasexual Male Competition

Men have been proposed to utilize two distinct alternative mating tactics: a “quality” strategy or a “quantity” strategy (Hirsch and Paul 1996). The former strategy usually involves long-term relationships, while the latter occurs over a much shorter time frame of a few months to a few hours. Through the “quantity” strategy, men attempt to gain access to a large number of females while minimizing costs and the potential for commitment using tactics that often involve threats and psychological pressure. Using the “quality” strategy, men attempt to ensure high partner commitment, paternity certainty, and female reproductive value using tactics such as resource expenditure and honest advertisement (Buss and Schmitt 1993; Hirsch and Paul 1996).

Men have also been proposed to compete indirectly for access to mates through mate guarding. The Mate Retention Inventory catalogs 19 tactics that males use to guard women such as calling at unexpected times and preventing a woman from going to events without her male partner (Buss 1988). These mate-guarding tactics are more commonly used when the male’s partner is young and attractive and when confronted by males who are more economically successful (Buss 2002). Failure to mate guard can result in reproductive costs such as providing parental investment to another man’s offspring and losing the female to another male.

Similar to many mammalian species, humans also employ sneaky copulation tactics and may engage in sperm competition. In a survey of Australians, 28% of men and 22% of women reported engaging in extrapair copulations (Simmons et al. 2004). The rate of extrapair paternity can vary greatly, ranging from 0.03% to 31.8% in a modest number of studies, with Western populations generally having lower rates than pastoral and tribal populations (Scelza 2011; Simmons et al. 2004). Consistent with the statistics above, male relative testes size is greater than expected for a monogamous species suggesting that sperm competition may occur (Simmons et al. 2004). Men have a higher percentage of motile sperm in their ejaculates when viewing a sexually explicit image depicting two men and one woman

than an image depicting three women, which has been proposed to suggest that evocation of sperm competition alters sperm composition (Kilgallon and Simmons 2005).

Conclusion

Intrasexual male competition occurs when males compete with one another for access to females or resources desired by females. This competition can occur directly, such as through contests, or indirectly through several methods including sperm competition, mate guarding, endurance rivalry, and sneaky copulations. Importantly, intrasexual male competition does not occur in isolation and intersexual competition often operates conjointly with intrasexual competition. Finally, over our evolutionary history, human males have had to compete for access to mates and modern males experience intrasexual competition that occurs both directly and indirectly.

Cross-References

- ▶ [Competition for Resources Desired by Females](#)
- ▶ [Male-Male Competition](#)
- ▶ [Resource Competition](#)
- ▶ [Sexual Selection](#)
- ▶ [Sperm Competition Theory](#)

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Intrasexual Rivalry

- [Derogation of Promiscuity](#)
- [Verbal Derogation](#)

Intrasexual Rivalry Among Men

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Synonyms

[Intrasexual competition](#); [Intrasexual selection](#); [Within-sex competition](#); [Within-sex selection](#)

Definition

Intrasexual rivalry is a driving force behind sexual selection. Men's intrasexual rivalry surrounds competition over reproductive opportunities and resources.

Introduction

Men's reproductive potential is higher yet more variable than that of women, owing to women's substantial (and men's relatively lower) obligatory parental investment. For ancestral men, outcompeting same-sex rivals for access to desirable and varied mating opportunities would have benefited their total reproductive success. Evidence of adaptations for increased intrasexual rivalry among men can be seen in modern human physiology, mating psychology, and related behaviors such as epigamic displays and aggression, which differ between sexes. Mating systems and other contextual factors influence sex differences in competition, such that male rivalry

is stronger in polygynous versus monogamous systems, and when female are abundant rather than scarce.

Male rivalry has been shaped over deep evolutionary time by *sexual selection* – or the variability among same-sex conspecifics in fertilizing the gametes of the opposite sex. Sexual selection is the driving force behind evolution (Darwin 1871) and is the product of two interrelated phenomena: *intersexual selection* and *intrasexual selection*. Intersexual selection refers to the nonrandom choice of mating partners between the sexes. Intrasexual selection refers to the competition between members of one sex for reproductive access to members of the other sex. Same-sex competitors exhibit morphological, psychological, and behavioral traits which directly bear upon their ability to attract mates (intersexual selection) and to defeat rivals in coopting and retaining reproductive access and resources. To the extent that the phenotypic qualities exhibited by individual organisms benefit their success in inter- and intrasexual competition for mates, those organisms will be more likely to produce viable offspring who will themselves be more likely to bear competitively efficacious traits allowing them to, in turn, outcompete intrasexual rivals lacking in those adaptive traits for mating opportunities.

In most species, intersexual selection is driven largely by females, who choose their mates carefully from the male population. Males, on the other hand, more often engage in intrasexual selection, vigorously vying for mating opportunity with selective females. Male intrasexual competition is so ubiquitous that in *The Descent of Man*, Darwin (1871) wrote “it is certain that amongst almost all animals there is a struggle between the males for the possession of the female. This fact is so notorious that it would be superfluous to give instances” (p. 143).

The sex difference in the frequency and ferocity of intrasexual rivalry can be understood in light of disparate obligatory parental investment between the sexes (Trivers 1972). Females produce a limited number of energy-rich eggs and males produce many energetically cheaper sperm (Trivers 1972). Females are limited by the number

of eggs and hence the number of offspring they can produce over their reproductive lives. Because females bear the heavier parental investment, they have the most to lose from making poor mating decisions and are thus selective in their mate choice (Trivers 1972). In contrast, male reproductive potential is limited only by the number of fertilizable females they can access. Yet because, on the whole, the number of offspring sired by males and females in the population is the same, successful males who reproduce with multiple females impose a significant cost upon other males, many of whom will thus be less-successful or will be shut-out from reproducing altogether. Accordingly, males more than females have evolved phenotypes oriented toward competing for mating opportunities.

Intrasexual Rivalry in Humans

Unlike the vast majority of mammalian species, humans tend to pair-bond, as evidenced by social monogamy, serial monogamy, and even pure genetic monogamy that has been observed across diverse cultures. This, coupled with substantial bi-parental care of offspring, has likely tempered sex differences in intrasexual competition. Men are also highly selective in choosing their long-term mates, and thus intrasexual rivalry among women is not uncommon. Intrasexual competition can take on many forms, which can be distinguished in terms of combat (i.e., contest) and noncombat competition. Humans exhibit a diverse menu of intrasexually competitive acts including direct combat (i.e., trying to physically threaten, dominate, injure, or kill a rival), verbal derogation of competitors, social manipulation, as well as many forms of noncombative self-promotion (i.e., trying to enhance the positive qualities of oneself, relative to same-sex others) (Buss and Dedden 1990).

Noncombative Tactics

Many of the noncombative tactics employed by men relate strongly to the mate-preferences of the opposite sex. For example, men more than women believe in the efficacy of, and more frequently utilize, tactics of intrasexual competition involving resource possession and display (e.g., driving

a fancy car, flashing money, buying women expensive goods, bragging about accomplishments), which correspond to women's relatively greater preference for mates who possess resources. Another related strategy that may be used during men's intrasexual competition is *derogation* of other men's financial resources, physical strength, and athleticism. Indeed when newlyweds were asked to self-report their use of derogation tactics as well as those used by their spouses, men more than women reported derogating a rival's strength (Buss and Dedden 1990).

Male Intrasexual Aggression

Men compete more violently than women in the domains of status, resources, and dominance. Wilson and Daly (1985) showed that homicidal conflicts in 1972 Detroit were prodigiously committed by men. These findings mirror those from semi-nomadic hunter-gatherer societies, such as the Yanomamo of Venezuela, where one in four adult males are killed by others individuals within their tribe or in wars with other tribes, with nearly half of all men over the age of 25 having participated in killing someone (Chagnon 1988). Aggression directed toward same-sex rivals may solve a variety of adaptive problems, including the coopting of resources, defense against attack (avoiding loss of status and resources), inflicting costs (on one end making rivals less desirable as mates through reputational damage; on the other end, eliminating them as a potential mate altogether by killing them), negotiating the status hierarchy (such as when Aché males who survive many club fights gain increased status, fear, and admiration), and deterring rivals from future aggression (by having a reputation as a dangerous or violent threat to rivals). The extent that male aggression exists within a culture or subculture hinges upon a variety of factors, such as the likelihood of retaliation and whether the aggression is situated within a "culture of honor," wherein failure to aggress upon being insulted can result in status loss.

At its core, men's intrasexual aggression is driven by efforts to achieve and maintain status, resources, and mating opportunity. To test this hypothesis experimentally, Griskevicius and

colleagues (2009) primed men with status and mating motives by exposing them to short stories. Results showed that status motives increased men's willingness to engage in direct aggression (face-to-face confrontation). Men's aggression was also increased by mating motives within the context of being observed by other men. Male sexual jealousy is also a driving force behind men's intrasexual violence, whereby over 90 % of same-sex killings involving "love triangles" are perpetrated by men and fewer than 10 % by women (Daly and Wilson 1988). Some researchers have observed links between male aggression, victimization, and mating outcomes. Arnocky and Vaillancourt (2012) found in a prospective longitudinal study that male adolescent indirect (but not direct) aggression was associated with being more likely to have a dating partner 1 year later.

Collective Male Aggression

Warfare and intergroup rivalry can also be understood within the context of competition for reproductive success. Greater male, relative to female, participation in organized collective violence is seen at various cultural and subcultural levels, from street-gangs to international warfare. Durham (1976) developed and tested a model showing that the costs of participating in collective aggression can be outweighed by its survival and reproductive benefits when access to scarce and valuable resources is at stake. Accordingly, men may have evolved psychological mechanisms enabling them to form coalitions centering upon perpetrating acts of aggression against outgroups with the goal of acquiring or protecting reproductive resources. For instance, among the Yanomamo, collective groups of men often raid neighboring tribes as acts of revenge, and also to forcibly take food and women (Chagnon 1988), suggesting that men form aggressive coalitions to coopt valuable reproductive resources and opportunities.

Adaptive Physiology for Competition

Men's adaptations for engaging in physical combat are well-exemplified by studies of sexual dimorphism in body size. In most sexually

reproducing species, males are substantially larger than females; sexual dimorphism in body size is owed greatly to intrasexual competition, whereby larger males often achieve greater mating success than smaller rivals (e.g., McElligott et al. 2001). Compared to other Hominids such as orangutans and gorillas, modern Humans exhibit relatively less sexual dimorphism in body size. It is important to note, however, that the relatively less extreme sexual dimorphism in humans (at least, in terms of body size) does not imply that observable physiological sex differences are somehow vestigial in relation to intrasexual competition. Indeed, Archer and Thanzami (2007) found that young Indian men with greater size and strength reported more frequent physical aggression in the previous year. Lassek and Gaulin (2009) examined the relationship between fat-free mass (FFM) and limb muscle volume (LMV) and mating success. Results showed that although FFM and/or LVM are positive predictors of daily energy intake and negative predictors of C-reactive protein and white blood cell count, indicating a tremendous physiological cost to production and maintenance of increased musculature, FFM and LMV were also predictive of men's total and past-year self-reported sex partners as well as age at first intercourse. Men's body size and strength also relates to various characteristic associated with intrasexual rivalry. Fessler et al. (2014) found that men's chest compression strength was inversely related to their perceptions of the size and strength of various rivals (supporter of a rival sports team or as a man armed with a handgun), suggesting that assessment of rival physical threat varies as a function of one's own strength. Male adolescents with more handgrip strength are also more likely to highly estimate their own fighting ability, which in turn predicted actual use of physical aggression (Muñoz-Reye et al. 2012).

Whereas physical size and stature may be implicit in men's ability to fight and to provide protection or resources, other associated morphological traits also relate indirectly to men's intrasexual rivalry as signals of their mate-value and/or formidability. For instance, men with lower

pitch voices are perceived as being more physically dominant and are also rated by others as being larger, more masculine, and older (see Puts et al. 2012 for review). In samples drawn from both the USA and from Hadza foragers, Puts and colleagues (2012) showed that various sexually dimorphic vocal parameters predicted men's body size, strength, testosterone, and/or physical aggressiveness. In North American samples, women have reported lower pitched men's voices as being more attractive, particularly during the fertile phase of the menstrual cycle, men with low-pitched voices report having had more sex partners, and Among Hadza hunter-gatherers, low voice pitch correlates with having more offspring (see Apicella et al. 2007).

For men, components of facial masculinity such as protruding cheekbones, large and well-defined chins, heavy brow bones, and facial hair might also be important correlates of rivalry among men (see Arnocky et al. 2014a for review). Bearded males are rated by women as being more masculine, aggressive, socially mature, and older (Neave and Shields 2008). Research has shown that a marker of facial width-to-height ratio predicted men's reactive aggression as well as aggression (in penalty minutes) among varsity and professional hockey players, and subsequent studies have linked the FWHR to achievement drive, self-reported dominance, and reduced likelihood of death from homicide involving direct physical contact (see Haselhuhn et al. 2015). Mueller and Mazur (1996) showed that cadets' facial dominance predicted subsequent status (in terms of promotions) later in their careers. Little and colleagues (2015) found that observers of facial photos of mixed martial arts fighters were accurate above chance in predicting the winners of fights, and that winners' faces were perceived as being more masculine, as well as stronger, and more aggressive. Women in this study also viewed winner faces as more attractive. Taken together, these findings suggest that men with masculinized somatic, facial, and vocal features may be more dominant, more aggressive, more successful in altercations, and are viewed by women as being more desirable, at least within the context of short-term mating.

Testosterone and Men's Intrasexual Rivalry

The common thread between all of the aforementioned morphological signals is that physical size and strength, deeper vocal pitch, and facial masculinity have all been shown to correlate with testosterone (T) – an androgenic hormone that produces male sex characteristics. T diverts resources away from immune functioning; accordingly, only men of sufficient immunocompetent condition can afford the cost of elevated T. A man's condition could therefore be assessed in his T-linked secondary sexual characteristics. T is important to men's intrasexual rivalry for at least two reasons: First, regarding *intersexual* selection, women should prefer men who exhibit features associated with increased T, given that men who can withstand the immunologic costs associated with developing these characteristics are healthier and thus better able to provide offspring with good genes, resources, and protection. Indeed, some evidence has suggested that males with more masculine bodies in terms of height, strength, and with more masculine voices, and faces are indeed healthier than their less sexually dimorphic conspecifics (see Arnocky et al. 2014a for review). T is also positively linked to sperm concentration and motility (Meeker et al. 2007).

Second, regarding intrasexual selection, T is a driving force behind male dominance and aggressive behavior. Archer (2006), in reviewing evidence pertaining to the challenge hypothesis (i.e., context-dependent increases in testosterone levels linked to aggression) in humans, suggested that T rises among young men who are challenged (e.g., men from "cultures of honor" who are insulted), as well as in men who are in a pre-competitive state (e.g., before a sporting match), and among winners of direct competition (e.g., following a successful competition or sporting match). Conversely, T is often shown to decrease among losers of competition (Archer 2006). Notably, T responses to intrasexual competition have been observed throughout the animal kingdom (Archer 2006), suggesting that context-dependent changes in T may serve important adaptive functions. It has been proposed that the costs associated with maintaining elevated T concentrations (e.g., decreased paternal care, increased risk for

physical injury/death, depressed immune function, increased energetic demands) may have led to a highly flexible endocrine system capable of rapidly modulating T in response to social challenges (Wingfield et al. 2001). Also, it has been speculated that acute changes in T within the context of competitive interactions may ultimately serve to fine-tune ongoing and/or subsequent competitive and aggressive behavior (Archer 2006). Consistent with this functional account of T reactivity, a growing body of evidence indicates that increases in T during competitive interactions positively predict aggressive behavior in healthy young men (see Carré and Olmstead 2015 for review). Recent research that acutely increases T concentrations through pharmacological challenge indicates that T rapidly increases amygdala and hypothalamic reactivity to angry facial expressions (Goetz et al. 2014). Importantly, these brain regions are rich in androgen and estrogen receptors and play a key role in the modulation of aggressive behavior (see Carré and Olmstead 2015). More recent work indicates that a single application of T to young men rapidly increases men's perception of their own facial dominance (Welling et al. 2016). Specifically, T led men to perceive themselves as more physically dominant, which ultimately may in part explain links between T and human aggression. That is, T may enhance men's perceptions of their own formidability, which may increase their willingness to engage in intrasexual competition with other men. Together, this body of literature suggests that high T men may be more competitively successful than low T men in domains of intersexual selection (especially for short-term mateships) and intrasexual rivalry. Men's intrasexually competitive behaviors are driven, at least in part, by real or perceived challenges to their reproductive fitness that are mediated by context-dependent changes in testosterone.

Contextual Influence on Men's Competition

The implementation and efficacy of intrasexually competitive tactics may vary depending on a number of factors including but not limited to (1) the mating system and individual mating goals, (2) the number of mates available locally,

(3) men's relative mate-value, and (4) ovulatory shifts in women's mate preferences.

Men's intrasexual rivalry is characteristically different in terms of tactics employed within short versus long-term mating contexts. For instance, Schmidt and Buss (1996) found that emphasizing their immediately available resources was judged as being most effective for men pursuing short-term relationships, whereas showing resource potential as well as derogating a rival's resource potential and achievements were judged as most effective for men pursuing long-term relationships (Schmidt and Buss 1996). Simpson et al. (1999) told men and women they would be competing with another same-sex individual for a date with an attractive opposite-sex person. While being videotaped, participants stated why the potential date should choose them over the competitor. Results showed that men who reported a more unrestricted sociosexual orientation (indicative of greater short-term mating orientation) were more likely to use direct competition tactics than were more restricted men. Restricted men instead highlighted their positive personal qualities. Men's intrasexual rivalry is also subject to differences in the overarching mating system. Male-male competition is most common in polygynous mating systems, where males are more likely to compete over gaining and maintaining mating access to females (female defense polygyny) or reproductively relevant resources (resource defense polygyny). For instance, in polygynous societies, where some men are able to monopolize significant reproductive opportunities and exclude others, the likelihood of civil war (i.e., male coalitional aggression) increases (Kanzawa 2009).

Another contextual factor influencing men's (and women's) intrasexual rivalry is the ratio of reproductively viable men to women within a given population, otherwise known as the operational sex ratio. Recent experimental evidence has shown that when men and women are primed to perceive that mates are scarce, they report a more intrasexually competitive attitude and express more jealousy and willingness to aggress indirectly against a hypothetical mate-poacher trying to steal their partner, with men also reporting a

modest increase in willingness to aggress physically, relative to those participants primed with mate abundance (Arnocky et al. 2014b). Barber (2009), using murder data from the United Nations and homicides from World Health Organization, showed that killings in both data sets increased alongside a female-biased sex ratio (i.e., a larger proportion of females to males). This finding held independent of statistical control for economic development, income inequality, urbanization, population density, the number of police, and whether the country was a major center of illegal drug trafficking.

Men's relative mate-value and social standing has also been linked to their intrasexually competitive behaviors. Poor and single men are more likely to commit homicide relative to men who are married and well-off (Wilson and Daly 1985). Yet some research has shown that self-perceived mate-value (SPMV) positively predicted young Indian men's use of aggression (Archer and Thanzami 2009); with SPMV previously being linked also to willingness to inflict discomfort upon another person (i.e., using the "hot sauce" paradigm) and trait measures of aggression (see Archer and Thanzami 2009 for review). The apparent disconnect between perceived mate-value and discrepant information about actual mate-value may thus be a particularly potent predictor of aggression. In two studies, Bird et al. (2016) showed that narcissistic (high perceived value) men who received information suggesting they were of low objective mate-value in a mock online dating paradigm engaged in more retaliatory aggression toward a same-sex rival in a point subtraction aggression task relative to men who were not narcissistic and received low mate-value scores or men who received high mate-value scores.

Lastly, the efficacy of men's phenotypic markers of dominance and masculinity as well the efficacy of behavioral aggression in being selected for by females may vary as a function of their fluctuating mate-preferences across the ovulatory cycle. Giebel et al. (2013) exposed women to one of four descriptions of a soldier's experience after returning from war, which included trauma related symptoms with (1) high or (2) low appetitive aggression, or no trauma related

symptoms with (3) high or (4) low appetitive aggression. Participants rated the man on desirability as a short term or long-term sex partner. Results showed that women preferred a soldier high in appetitive aggression as a short-term mate but not as a long-term partner, and this effect was stronger for women in their fertile phase of the menstrual cycle. Similarly, Gangestad et al. (2004) showed that when viewing tapes of men competing for a potential lunch date, women who were in the fertile phase of the menstrual cycle were more likely to rate men who displayed social presence and direct intrasexual competitiveness as more desirable short-term, but not long-term, partners. Taken together, these results suggest that women's preferences for aggressive men are higher during fertile windows, especially within the context of short-term mating.

Conclusion

Adaptations for increased intrasexual rivalry among men have been observed in sexually dimorphic human physiology, mating psychology, and related behaviors. Men's intrasexually competitive tactics range from resource displays, to derogation of rivals, to direct aggression, warfare, and homicide. Male rivalry results from intersexual and intrasexual selection, whereby sex differences in obligatory parental investment, reproductive potential, and variability compel the evolution of male rivalry for valuable reproductive resources and opportunities. Contextual factors, including mating systems and individual mating goals, the number of mates available locally, and men's relative mate-value, as well as ovulatory shifts in women's mate preferences, can influence the content and intensity of men's intrasexual rivalry.

Cross-References

- [Anatomical Adaptations for Fighting](#)
- [Dominance and Testosterone](#)
- [Intrasexual Rivalry Among Women](#)
- [Reproductive Potential](#)
- [Upper Body Strength and Fighting Ability](#)

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Intrasexual Rivalry Among Women

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Synonyms

[Intrasexual competition](#); [Intrasexual selection](#); [Within-sex competition](#); [Within-sex selection](#)

Definition

Intrasexual rivalry is a driving force behind sexual selection. Women's intrasexual rivalry surrounds competition over reproductive opportunities and resources.

Introduction

Humans are among the less than 5 % of mammals that engage in biparental care. Men who invest resources toward mates and offspring are compelled to be more selective in their mate choice. Because men vary widely in their investment and in their overall value as a mate, women can benefit their reproductive fitness by outcompeting intrasexual rivals for the best mates. Yet because women must also remain alive to rear offspring, adaptations for same-sex rivalry are characteristically different in many ways from male competitive adaptations. Women are less likely to rely on violent and physically risky strategies. More surreptitious forms of competition by means of verbal derogation and indirect aggression are considered as evolved mechanisms for defeating same-sex rivals. Competition among women varies depending upon contextual factors such as mating systems and the number of mates available in the environment.

In terrestrial mammals, including humans, sex differences in obligatory parental investment are a strong predictor of sexually dimorphic phenotypes associated with intrasexual rivalry. In the vast majority of species, female parental investment is much greater than that of males, conferring males with increased yet more variable reproductive potential and females with a heightened impetus to be more selective with whom they mate. From this perspective, females benefit primarily from selecting among the most desirable and competitively efficacious males, given that their reproductive output (in terms of number of offspring produced) will remain relatively stable, whereas males who are best adapted to attract or otherwise obtain females and/or to defeat same-sex rivals for mating opportunities or relevant resources will pass on their genes with much

greater frequency than those males who are less-well-suited to these tasks. Over generations, males take on the competitively adaptive heritable characteristics of their ancestors, which can include larger physical stature or weaponry for fighting as well as a more aggressive psychological and behavioral disposition that is beneficial for quelling rival males. From this perspective, it has traditionally been assumed that intrasexual rivalry among females does not exist, or if it does, matters only to an extent that pales in comparison to what is seen among males. However, recent reformulated models of sexual selection have countered this view by considering intrasexual competition as centering upon more than mere access to mating opportunities but rather upon competition over any mating-relevant resources (Rosvall 2011). From this perspective, research has shown that female intrasexual rivalry (1) exists in many diverse species and (2) has evolved to solve a wide variety of mating-relevant adaptive problems, including accessing food, nesting sites, social status, and, in species characterized by biparental care, male investment. Rosvall (2011) noted that although females sometimes compete for number of mates, more often they compete for male provisioning of direct or indirect (i.e., genetic) benefits. Ultimately, intrasexual competition among females for such resources can have a meaningful impact upon reproductive success. In some primates, for instance, high ranking females produce more surviving offspring and daughters that reach sexual maturity earlier, whereas females who fall victim to intrasexual harassment can suffer dire consequences, such as spontaneous abortion of pregnancies in some primates (see Arnocky and Vaillancourt 2014; Rosvall 2011 for review).

Humans offer a unique model for the study of female intrasexual rivalry, given that we are among a minority of less than 5 % of mammalian species in which both sexes invest resources and parental care toward their offspring. Men's provisioning of parental care may offset the costs of monogamy by increasing the survival rate of offspring, and might also provide repeated sexual access to a partner, or deter against a partner's extra-pair copulations (see Arnocky and

Vaillancourt 2014). Because men also invest considerable resources toward partners and offspring, they too are highly discriminating in their long-term mate choice (see Arnocky and Vaillancourt 2014). Moreover, not all men are equally desirable to women as long-term mates (whereby men's ability to provide direct-benefits varies) or short-term mates (whereby men's ability to provide indirect/genetic-benefits varies). Differential mate-value among men equates to there being a limited supply of desirable men, for which women must compete. This competition is characterized by two interrelated phenomena: *intersexual selection*, which refers to the nonrandom choice of mating partners between the sexes (applied to sexual selection among women, this often entails the desire to alter one's physical appearances to appear more desirable to men), and *intrasexual selection*, which refers to the direct rivalry between members of one sex for reproductive resources or access to members of the other sex.

Sex Differences in Physically Violent Competition

Women's direct intrasexual competition is characteristically different from that of men. From a fitness standpoint, women have more to lose, relative to men, from engaging in risky physical altercations characteristic of male intrasexual rivalry. Even though humans are considered a biparental species, women still provide most of the *obligatory* parental care required for offspring survival. Whereas ancestral men's inclusive fitness relied upon obtaining reproductive opportunities, women's relied more on their ability to rear offspring through early life stages (Campbell 2013). A mother's death is considerably more debilitating to a child's survival relative to a father's death (Sear et al. 2000). The costs associated with direct aggression and other risky forms of competition are therefore greater for women than for men, and women's intrasexual competition necessitates greater risk aversion (see Arnocky and Vaillancourt 2014; Campbell 2013 for review).

The greater cost associated with women's use of physically risky competition strategies is well exemplified by studies of sex differences in

human physiology and aggression. First, although humans are much less sexually dimorphic in terms of their physical size (males are approximately 15 % larger than females) relative to some early hominin species, such as *Paranthropus robustus*, and other closely related primates (e.g., Lockwood et al. 2007), it is nevertheless evident that “sexual dimorphism and violent male-male competition are ancient and enduring elements of our human evolutionary history” (Daly and Wilson 1988, p. 143). These elements of our evolutionary past are readily observable in the sex-differentiated aggressive behaviors of contemporary hunter-gatherer and industrialized societies. Cross-culturally, women less often exhibit extreme forms of overt physical aggression, including interpersonal violence, homicide, and warfare, relative to men (e.g., Daly and Wilson 1988). These sex differences are evident from a very early age and may be mediated, in part, by differences in fear responses related to aggression, such that females are more likely to express fear within the context of physical danger. In support of this, a meta-analytic review of sex differences in aggression by Eagly and Steffen (1986) found that sex differences in aggression were larger when women perceived that their aggression would pose a danger to themselves. It is important to note here that women’s lesser involvement in direct physical aggression does not mean that they do not engage in such behaviors or that women’s physical aggression is somehow unrelated to intrasexual rivalry in the same manner as men’s aggression. Burbank (1987) conducted a cross-cultural survey of women’s aggression, which ranged between verbal and physical violence, and noted that such behaviors were (1) common (physical aggression by women was observed in 61 % of the cultures analyzed) and (2) most often directed at other women within the context of competition for mates or reproductively relevant resources (e.g., subsistence products). Reasons underlying young girls’ and adolescents’ reports of physical aggression also include fighting over access to boys as well as reputational defense, status enhancement, and avoidance of victimization (see Campbell 2013). However, in circumstances of girls’ and women’s intrasexual

competition, physical aggression remains a much rarer exception relative to more common tactics of verbal derogation and indirect (social) aggression. Next, I describe women’s use of verbal derogation and indirect aggression situated within the context of competition over reproductively relevant resources such as status and mates, as well as describe why these acts of aggression often focus on physical appearance and sexual reputation, and whether there are tangible mating-relevant outcomes for perpetrators and victims.

Verbal Derogation of Attractiveness, Promiscuity, and Other Components of Mate-Value

Verbal derogation refers to negative statements that are made toward other individuals. Verbal derogation is a tactic used by both men and women in intrasexual rivalry. However, rival derogation often differs between the sexes in terms of content, such that same-sex rivals tend to derogate facets of others that are crucial to mate-value or desirability to the opposite sex. For instance, Buss and Dedden (1990) showed that women, more than men, reported derogating the physical attractiveness of a rival, calling a competitor promiscuous, and suggesting that other women fail to provide reproductive value through intercourse (i.e., calling other women a “tease”). Similarly, Campbell (2013) noted continuity in the epithets which frequently appear in recounts of girls’ fights with other girls, which include verbal barbs such as “slag,” “slut,” “whore (ho),” “tart,” “ugly,” and “fat.” Targeting these aspects of a girl’s or woman’s mate-value directly counters boy’s/men’s preference for mates who best display various physical cues to health and fertility, such as feminine and symmetrical facial features, a low waist-to-hip ratio, clear skin, and lustrous hair (see Arnocky et al. 2014a for review), as well as mates who are sexually accessible (especially in short-term mating where conservative or low sex-drive women may be disfavored), yet who are simultaneously faithful (especially in long-term mating) in order to counter paternity uncertainty (Buss and Schmitt 1993).

Individual differences in the use of such derogation strategies exist, with women who express a

more unrestricted sociosexuality being more likely to disparage other women. For example, Bleske-Rechek and Buss (2006) found that an unrestricted sociosexual strategy among both men and women was associated with more frequent use of dominance displays, derogating a rival's physical appearance and popularity, and attempting to dominate competitors. The sexuality of the *target* might also influence the extent to which women are derogated by other women. Grabe et al. (2012) exposed women to clips of a news anchor who was either more sexualized (wearing a dark jacket and skirt that accented her waist-to-hip ratio, bright red lipstick, and a necklace) or less sexualized (wearing a shapeless dark blue jacket and skirt that deemphasized her waistline and no lip color or jewelry). The researchers found that women who were exposed to a sexualized woman news anchor derogated her appearance efforts ("... her lipstick was too red, it was distracting" or her "outfit was terrible for her body"), her agreeableness ("self-centered"), contentiousness ("she stood awkwardly"), emotional stability ("tense and fidgety"), and intelligence ("stupid" and "dumb") more than women exposed to a less sexualized woman news anchor.

Similarly, Vaillancourt and Sharma (2011) showed that almost all women who were randomly exposed to an attractive female confederate (dressed provocatively) engaged in more derogatory behavior toward her relative to when she was dressed in more conservative clothing. Example statements given by the authors included women implying to another participant that the confederate was dressed as if she wanted to have sex with one of her professors or that her "boobs were about to pop out." One participant was reported to have looked the confederate up and down and to have said "what the fuck is that?" while exhibiting a disgust reaction. Moreover, women were less likely to want to introduce their boyfriends to the confederate, to have their boyfriends to spend time with the confederate, or to become friends with the confederate, when she was provocatively versus conservatively dressed.

Ultimately, verbal derogation can have an important and reproductively relevant influence

upon the target. Fisher and Cox (2009) showed that relative to men's initial attractiveness ratings of women's faces, receiving subsequent negative derogatory statements about those faces from a woman who they viewed as attractive significantly reduced their perceptions of the target woman's attractiveness. Derogatory statements made by attractive women were much more impactful than derogatory statements made by an unattractive woman. However, direct verbal derogation tactics can also be damaging to the perpetrator. Fisher and colleagues (2010) examined men's and women's perceptions of women who were purported to have made a derogatory statement about another woman's appearance, personality, or sexuality. Their results showed that men significantly decreased their evaluations of the derogator's friendliness, kindness, trustworthiness, and overall desirability as a mate, relative to when their photos were presented without having made a derogatory comment. Women also rated derogators more negatively along the same dimensions and also decreased their views of the derogator's fitness as a parent and her physical attractiveness, and in the case of appearance derogations, her promiscuity, relative to when the photos were presented as not having made derogatory comments.

Together, these findings suggest that making direct derogatory comments about intrasexual rivals, such as "She's pretty but... She wears a lot of makeup and wears padded, pushup bras all the time (even to the gym!)..." or "I know her really well. She's a virgin and is holding out until she's married..." (Fisher et al. 2010, p. 269) can have negative effects upon the target but also upon the perpetrator's attractiveness to men and appeal as a same-sex ally. This body of research suggests that while verbal derogation is an effective strategy for disparaging rivals, it is also risky, and thus women may sometimes rely on more surreptitious acts of aggression meant to damage same-sex rivals.

Indirect (Also "Social" and "Relational") Aggression

Beyond the study of direct verbal derogation tactics, researchers have also examined a

related but conceptually distinct phenomenon termed indirect aggression (otherwise termed “social” or “relational” aggression; although see Ingram 2014 for some conceptual differences between constructs). Research has shown that women are much more likely to use indirect aggression relative to physical aggression, which involves purposefully and often covertly manipulating interpersonal relationships through acts of social exclusion, veiled criticism, breaking confidences, gossip, and rumor spreading in order to harm others, which relative to physical violence confers a lower likelihood of retaliation, physical, social, or legal consequence (see Arnocky and Vaillancourt 2014 for review). Studies of sex differences in indirect aggression have shown that women are often equally or more likely than men to use indirect aggressive tactics (see Hess and Hagen 2006). Recent evidence suggests that women, more than men, preferentially remember gossip about a potential rival’s physical attractiveness rather than their wealth (De Backer et al. 2007). Beyond a focus on physical attractiveness, women’s indirect aggression is also intimately tied to sexuality reputation. Leenaars et al. (2008) showed that among older adolescents, recent sexual behavior correlated with increased risk for indirect victimization, suggesting that indirect aggression might also be used to regulate sexuality among the peer group (see Vaillancourt 2013). Indirect aggression seems to be motivated by mating and status goals. Griskevicius and colleagues (2009) primed men and women with status and courtship motives and subsequently assessed willingness to aggress directly and indirectly against a same-sex rival. For women, results showed that both status and courtship motives increased willingness to engage in indirect aggression (e.g., socially excluding a rival). Moreover, when women were primed with competition over scarce resources, they became more willing to aggress directly against a same-sex rival.

The use of indirect aggression is functional as a competitive tactic for at least three interrelated reasons: First, it is damaging to targets and has

been shown to promote depression, lower self-esteem, school drop-out, and even suicide among victims (see Vaillancourt 2013 for review). Second, indirect aggression has been linked to increased status (in terms of popularity and dominance, although not likeability or preference) within the social hierarchy (see Ingram 2014 for review). Third, indirect aggression has been related to mating success and victimization with decreased mating success. For example, in a longitudinal study of adolescents, Arnocky and Vaillancourt (2012) explored whether various types of peer-aggression confer mating benefits to perpetrators. Results showed that peer-rated indirect aggression, but not physical aggression, predicted having a dating partner 1 year later, controlling for age, initial dating status, popularity, and physical attractiveness, whereas being a self-reported target of bullying negatively predicted having a dating partner at 1-year follow-up. Similarly, White et al. (2010) showed that women who reported more indirect aggression toward peers had earlier ages at first sexual intercourse, whereas women who were more victimized in adolescence experienced later ages at first sexual intercourse.

Arnocky et al. (2012) explored how individual differences in self-perceived mate-value (in this case, physical attractiveness compared to same-sex rivals) related to use of indirect aggression in a large sample of heterosexual women who were in dating relationships at the time. Results showed that women who believed they were of lower physical attractiveness relative to other women were more likely to perpetrate indirect aggression against peers. Moreover, women who perceived themselves as being more physically attractive than other women were more likely to also report being indirectly victimized by other women with greater frequency. Similarly, Leenaars et al. (2008) found that among adolescents, attractive females were at greater risk for indirect victimization. This makes sense in light of the fact that physically attractive women report greater success in stealing other women’s romantic partners (Sunderani et al. 2013). Together, these findings suggest that women may

preferentially target attractive women for indirect aggression.

Ovulatory Shifts in Women's Intrasexual Competition

Females' intrasexual rivalry has been shown to intensify in relation to ovulatory shifts. Fisher (2004) examined whether women's evaluation of other women's attractiveness differed during ovulation (i.e., maximum fertility) versus during menstruation (i.e., minimal fertility). Results showed that maximally fertile women rated other women's facial photos as being less attractive compared to menstruating women, ostensibly due to increased intrasexual competitiveness during the time when reproduction is most likely. Intrasexual competition during the follicular phase of the reproductive cycle has been shown to be related to hormonal functioning. Moreover, among normally ovulating women, increased conception risk is associated with women's greater dehumanization of other women (but not of men or of elderly women) and greater intrasexual competitiveness (Piccoli et al. 2013). Cashdan (2003) had female participants complete diary entries detailing competitive interactions and noted whether or not aggressive tactics were implemented. The researcher also obtained measures of total testosterone, free testosterone, androstenedione, estradiol, and cortisol in the follicular phase of the menstrual cycle. Results showed that women high in androstenedione (an androgenic steroid produced by the adrenals) were more likely than other women to express their competitive feelings through verbal aggression, whereas women with low androstenedione and total testosterone were less likely to express their competitive feelings overtly. Some research suggests that use of hormonal contraceptives lowers intrasexual competition among some women. Cobey et al. (2013) found that among pair-bonded (but not single) women, endorsement of a self-report scale for intrasexual competition declined during use of hormonal contraceptives relative to when they were regularly cycling at a fertile and a nonfertile cycle stage, even after controlling for age, relationship length, and satisfaction.

Influence of Mate Scarcity on Women's Intrasexual Rivalry

Because competitor derogation, direct, and indirect aggression all require energies that might otherwise be spent on addressing other adaptive problems and because each of these tactics pose varying levels of risk, women would be expected to generally avoid their indiscriminate use but rather to rely upon environmental cues to their necessity. One such environmental cue which might motivate greater use of competitor derogation and intrasexual aggression is the operational sex ratio – or the ratio of reproductively capable males to females in a given population. When potential mates are scarce relative to intrasexual rivals, women may be compelled to compete more vigorously for rarer mating resources and opportunities. In support of this, Arnocky et al. (2014b) primed participants with perceptions of either mate scarcity or abundance using bogus magazine articles and subsequently had them complete measures of intrasexual competitiveness as well as jealousy, direct, and indirect aggression toward a hypothetical mate-poacher. Results showed that women (and men) were more intrasexually competitive, more jealous, and more willing to use indirect aggression against a same-sex rival after being primed with mate scarcity.

Conclusion

Women can benefit in multiple ways from successful intrasexual competition, including in securing and maintaining mating opportunities and social status (see Arnocky and Vaillancourt 2012), and this is consistent with recent studies of other species highlighting the importance of competition among females to reproductive success (see Rosvall 2011 for review). Given differential challenges faced by women relative to men, such as the need to remain alive in order to rear offspring, women's intrasexual rivalry is characteristically different from that of men. Women are less likely to perpetrate physical violence against other women. Women's intrasexually competitive tactics range from verbal derogation of rivals (often in reference to mate-value characteristics such as

physical attractiveness and sexuality) to indirect aggression involving more discrete social manipulations, gossip, and exclusion. Use of these tactics can be effective in harming rivals and in facilitating mating success but also entail risks such as lower desirability to males or reduced likeability. Accordingly, the use of these tactics is not indiscriminate but rather is more likely under contextual pressures including during phases of the ovulatory cycle in which conception is most likely or when mating opportunities are perceived to be scarce.

Cross-References

- Contexts for Women's Aggression Against Women
- Derogation of Attractiveness Among Women (Intrasexual Rivalry)
- Derogation of Promiscuity Among Women
- Enhancing Women's Competitiveness
- Gossip
- Gossip, Rumors, and Social Exclusion
- Indirect Aggression
- Intrasexual Rivalry Among Men
- Reproductive Potential
- Verbal Derogation Among Women

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Intrasexual Selection

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Synonyms

[Intrasexual competition](#); [Sexual selection](#)

Definition

Intrasexual selection can refer to the act of competing with members of one's own sex (for status, tangible resources, or directly for access to mates) as well as the evolutionary process that shapes the traits employed in this competition.

Introduction

In November of 2016, a striking image began making its way around the internet, two Alaskan bull moose, with their antlers locked, drowned, and frozen together at the presumptive site of their final combat – a stark illustration of the risks that animals will endure, or even pursue, in response to intrasexual selection pressures. Intrasexual selection refers to the within-sex component of the broader process of *sexual selection* (Darwin 1871). Whereas the other half, intersexual selection, is characterized by the choice of mates by the opposite sex, intrasexual selection refers to competition with members of the same sex. Among humans, the particular nature of the competition varies by sex and culture, but same-sex competition is motivated by the more fundamental evolved goal of securing a viable mate or mates.

Competition for Mates, Available and Otherwise

The competition for mates includes those who may already be “spoken for” – thereby often

precipitating the jealousy of the existing partner. And there is a rich literature on the evolutionary psychology of sexual/romantic jealousy. That men are more upset than women about their partners' sexual infidelity (actual, suspected, or merely hypothetical) and women more than men upset by emotional infidelity (i.e., development of romantic attachment to another rather than sexual activity per se) is a remarkably consistent finding across cultures (e.g., Brase et al. 2004; Buss et al. 1999; Fernandez et al. 2006; Whitty and Quigley 2008). This is consistent with the evolutionary perspective of jealousy as an evolved response to the adaptive problems of cuckoldry (exclusively for males) and loss of partner's resource investment (primarily for females), both of which emerge as effects of successful intrasexual competition from one's rivals.

Males and females alike may resort to aggression as a way of warding off or retaliating against their intrasexual rivals, but once again there is a key sex difference; the apparent equivalence is the consequence of too broad a definition for aggression. Male-typical (or "covert") aggression entails physical violence, whereas female-typical ("relational" or "overt") aggression relies upon verbal barbs and inflicting reputational damage on one's rivals, without the use or even the threat of violence (Hyde 1984; Werner and Crick 1999). The novelist Margaret Atwood memorably alludes to the latter in her book *Cat's Eye*: "Little girls are cute and small only to adults. To one another they are not cute. They are life sized (Atwood 1989, p. 124)."

Female-Female Competition

Fisher (2013) elaborates with a catalog of specific behaviors characteristic of this sort of aggression, including "breaking confidences; criticizing others' clothing, appearance, or personality;... excluding from the group; writing nasty notes; and spreading false stories and gossip." Indeed, and presumed to function for effectively tracking and engaging in gossip, women are superior to men in recalling details about same-sex rivals (De Backer et al. 2007). Such aggression, though

of a different species from throwing a punch at a rival's face, nonetheless appears to be employed in service of the same goal – intrasexual competition for desirable mates. Buss and Dedden (1990) studied the nature of insults in the context of intrasexual competition and found that women's derogation of their rivals focused on characteristics shown in previous cross-cultural research (Buss 1989) to be important components of their mate value. In other words, it appears that the function of competitor derogation is not simply to demean or hurt the feelings of one's rival as a benefit in its own right but to reduce her chances of being chosen as a mate – which, it should be noted, would also boost one's own chances of being selected.

There are, however, alternate means of competition. In addition to relational aggression (derogation or manipulation of competitors), competition may also take the form of mate manipulation or of self-promotion. The last of these is, based on self-report at least, the type most frequently employed by women (Fisher and Cox 2010). One likely reason is that men are romantically interested in women who, in addition to possessing high physical attractiveness, are perceived as kind and gentle – an impression difficult to convey while attacking one's rivals. Women exhibit increased interpersonal warmth and (perhaps ironically) decreased dominance at mid-cycle, when they are most intrasexually competitive (Markey and Markey 2011). When women have been shown a series of images of beautiful women, they show an increased desire to enhance their own attractiveness, not only through innocuous means such as cosmetics and clothing choices but also through higher risk strategies such as taking diet pills (Hill and Durante 2011).

Male-Male Competition

Sexual selection is attested to in many animal species, including our own, in the form of sexual dimorphism. Natural selection in the traditional sense of selection for traits contributing to an organism's survival should, with few exceptions

(pelvic bones to accommodate childbirth in females, the sex organs themselves, milk glands in female mammals), result in matching phenotypes across sexes. Absent the effects of sexual selection, dimorphism would not be predicted for such characteristics as height, upper body strength, and craniofacial morphology. To the extent that we observe sex differences in such characteristics, we are witnessing the handiwork of intrasexual and intersexual selection. Human males, irrespective of time spent at the gym, divert valuable resources to the growth and maintenance of powerful muscles in the arms and torso, a product of the selection pressure of intrasexual combat. It may not be possible to quantify the contributions from the selection pressures of hunting, fighting, and sexual signaling with great precision, but we know from cross-species comparisons that the contribution from fighting alone can be sufficient to drive a process of *run-away selection* (Fisher 1915) for extreme sexual dimorphism in size and strength.

The walrus is a good illustration of a key principle here, that the intensity of intrasexual selection is proportionate to the magnitude of the available reward. To take the example of the Pacific walrus, adult males are 45% larger than females, a difference entirely attributable to mating competition (Fay 1982). The losers in these competitions are commonly maimed, occasionally killed in combat (or die from their injuries later in the season), and even the victors acquire such injuries that they can rarely maintain their dominant position for more than a couple of breeding seasons. However, as the females prefer to mate exclusively with the most successful fighter in the population, there is (genetically speaking) no incentive for a male to shirk the fight. That nearly all the males then are likely to lose does not dissuade them from attempting to do otherwise. The male-male competition within our own species is generally tame by comparison, albeit more frequently violent than that observed among women.

Gangestad et al. (2004) recorded videos of men who were told that a woman would be viewing the videos and choosing to go on a date with either him or another (unknown) male participant. Each

of these men was instructed to use the video to explain why the woman should choose him. Those who were more intrasexually competitive in their videos, via both self-promotion and derogation of the unknown rival's presumed inferiority, were rated as more attractive by female participants on high fertility days of their ovulatory cycle than by those on low fertility days, specifically in the context of short-term mating. This combination of cycle effect and context effect is characteristic of females' evaluations of males' signals of high genetic quality (see Gangestad et al. 2005).

Sperm Competition

The preponderance of long-term monogamous pair-bonds and rarity of large harems in humans makes such heightened intrasexual competition less common in our own species. We are notably lacking in tusks, for example. However, several convergent lines of evidence (testicular volume relative to body mass, observed rates of extrapair paternity, preference for "polyandrous" pornography) indicate that sperm competition has been a recurrent feature in the human environment of evolutionary adaptedness (EEA). That is, the female reproductive tract acts as a secondary battlefield for intrasexual competition whenever two or more men have been chosen as mates by the same partner (during the overlapping lifespans of the men's ejaculated sperm).

Other things being equal, producing and ejaculating larger numbers of sperm increase a male animal's chance of reproducing. However, the point at which it becomes more valuable to divert one's limited energy into the production or maintenance of muscle tissue, vital organs, bones, etc., rather than producing still more sperm, varies as a function of the chance of sperm competition. Simply put, those species in which the sperm of two or more males never simultaneously occupied one female's reproductive tract have never faced the adaptive challenge of sperm competition and would therefore show no evidence of having evolved in response to sperm competition. Consequently, one can infer the relative degree of

sperm competition in cross-species comparisons of the testicular mass/total body mass ratio.

Short (1979) performs this comparison for great apes, including *Homo sapiens*. The testis/body ratio for humans is intermediate between those for chimpanzees and gorillas, consistent with the different mating dynamics across the species. Chimpanzees mate promiscuously. Gorilla females mate with a single dominant male, though he may have numerous mates. Human females vary within that range, with individual differences in *sociosexuality* (Gangestad and Simpson 1990) as well as temporary circumstances contributing variation to the choice to remain monogamous or not. The position of human males on the aforementioned spectrum of testicular size indicates that this state (frequent but not exclusive monogamy) prevailed in ancestral human environments as well.

Perhaps the strongest evidence of human sperm competition is genetic evidence of extra-pair paternity. The genetic evidence indicates considerable variability in the frequency of human cuckoldry across cultures. At the lower end, Sasse et al. (1994) discovered an extra-pair paternity rate just shy of 1% in a Swiss sample. A subsequent study, using a Mexican sample, revealed that the ostensible father was in fact a cuckold in 11% of cases (Cerdeña-Flores et al. 1999). In any case, given the typical investment contributed by a father over the child's lifespan, mistaken paternity in even one case out of 1000 would provide strong selection pressure for (a) detection and prevention of partners' sexual infidelity, (b) sperm competition, and (c) detection of extra-pair paternity *ex post facto*.

Further evidence comes from investigation of the effects of pornography. That it is intended to create sexual arousal in the consumer is true more or less by definition. However, not all porn is equally successful in this endeavor. Heterosexual males are sexually aroused by (and subjectively enjoy) pornography, provided that it depicts at least one woman. It may depict more than one woman, and it may depict one or more men, or no men at all, and the men will find it arousing regardless. However, the depiction of a woman having

sex with multiple males is more arousing than the other combinations, as attested to by which pornographic videos are most likely to be purchased, as a function of the images used to advertise them (McKibbin et al. 2013).

An experiment by Kilgallon and Simmons (2005) revealed that men ejaculate sperm of greater motility after viewing videos depicting polyandrous sex (i.e., multiple men copulating with a single woman) compared to videos depicting lesbian sex. This is remarkable enough to bear some repeating. While pornography in general is sexually arousing by design, the experiment reveals that men's evolved adaptations for sexual arousal and sperm competition are precisely calibrated to such a degree as to respond differentially to varying levels of sperm competition cues – and that these have an impact not merely at the level of conscious preferences or subjective judgments of arousal but on the more literal output of the sperm themselves, the body's "decision" of which spermatozoa to force through the urethra and which to retain in the epididymides during a particular ejaculation.

Pornography represents a sort of supernormal stimulus, but the ejaculate data similarly testify (so to speak) to our evolutionary history of sperm competition in more ecologically authentic circumstances as well. Men's ejaculated sperm count when having sex with their regular partner varies in direct proportion to the amount of time they have spent apart since they last had intercourse, even after controlling for the total amount of time elapsed since the previous ejaculation (Baker and Bellis 1995).

A Note on Homicide

The most impactful form that intrasexual competition may take is homicide. There is disagreement within the evolutionary community on the question of whether humans possess an evolved adaptation for homicide (Duntley and Buss 2005) or if it merely arises as a by-product of other adaptations (Daly and Wilson 1988). In either case, the phenomenon of murder and the underlying psychology of homicidal ideation are instructive on the

broader question of intrasexual selection. A majority of both men and women report that they have at least once thought about (literally) murdering someone (Kenrick and Sheets 1993). The most common category of victim in these thoughts is an intrasexual rival, and some data suggest that *a majority of men would commit murder*, if guaranteed they could get away with it, in response to being cuckolded, humiliated, beaten up, or robbed by a rival (Buss and Duntley 1998). In the same study, some of the female participants (but none of the males) endorsed rival's physical attractiveness as a reason to commit homicide.

Conclusion

Reproductive success relative to one's conspecifics is the primary metric by which evolution judges an organism's success. Attractiveness perception, sexual arousal, and other evolved adaptations that are directly involved in mating operate in a context of intrasexual selection. In female-female competition and male-male competition alike, the competitive processes of intrasexual selection afford opportunities to increase the quality and quantity of one's potential mates. Sperm competition carries the intrasexual selection process farther still into mating territory. And ultimately, like the antlers of the two bull moose in their watery grave, it may not be feasible to truly disentangle the selection pressures of intrasexual selection from those of intersexual selection.

Cross-References

- [Evolutionary Arms Race](#)
- [Charles Darwin: Theory of Sexual Selection](#)
- [Intrasexual Male Competition](#)
- [Intrasexual Rivalry Among Men](#)
- [Intrasexual Rivalry Among Women](#)
- [Intersexual Selection](#)
- [Intrasexual Violence and Aggression](#)
- [Male-Male Competition](#)
- [Precopulatory Intrasexual Competition](#)

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Intrasexual Violence Among Women

► Urban Gangs

Intrasexual Violence and Aggression

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Synonyms

Contest competition; Intrasexual selection; Mate competition; Same sex aggression

Definition

Intrasexual violence is the intentional use of physical force to inflict harm on another, and it occurs between members of the same sex, in relation to competition over mates. Intrasexual aggression occurs between members of the same sex during competition for mates and is an intentional act to inflict harm on another. It can encompass direct and indirect acts. Aggression can have violent consequences – but not always – for example, gossip, ostracization, and scarification can intimidate without inflicting bodily harm to another.

Introduction

This entry provides a concise overview of the theory and evidence regarding intrasexual selection as a driving force – shaping patterns of human aggression and violence. It tends not to dwell on human violence and aggression as being purely unique behaviors that have unique underpinnings. Rather, it attempts to discuss an ultimate framework for the evolution of human aggression and

Intra-sexual Signaling

► Steve Gangestad

violence by putting humans into context equal with research on many taxa. While there are always within-taxa specificities, this entry attempts to find generalities. The evolution of sex roles, mating systems, and sex ratios are discussed as they relate to the distribution of human violence and aggression. As a necessity, this entry focuses on male intrasexual violence and aggression, simply because it is more prevalent among males, but does also consider intrasexual aggression and violence in women.

Male Intrasexual Violence and Aggression

Sexual selection is an evolutionary process that favors traits that lead to greater success in securing a mate and therefore greater reproductive success (Andersson 1994). It was Darwin (1871) who first referred to sexual selection whereby members of the same sex compete with each other for mates, as intrasexual selection. In vertebrates, males are typically more aggressive than females. Contest competition, when males of many taxa physically compete with each other for access to mates, has led to the evolution of a plethora of armaments – from pincers to antlers to fangs – that males use in battle with one another (Emlen 2008; Puts 2010). Although there are some exceptions, intrasexually selected armaments are rare in females (Berglund 2013). This evolved weaponry suggests that males are typically engaging in aggression during competition for mates more than females. Additionally, with females providing a greater amount of parental investment, a trade-off between parental investment and competing for mates typically exists. Fish are an exception to this because the trade-off is usually weaker or absent altogether (Jennions and Kokko 2010). Some bird taxa are another exception where the bias towards female parental investment is reduced comparative to mammals and reptiles (Goymann et al. 2015).

In humans, studies and crime statistics consistently show that violence and aggression are more prevalent among men than women. There are two caveats to this point: Adolescent girls use indirect aggression more than adolescent boys do

(discussed in more detail when considering female intrasexual aggression) and women use violence in romantic partnerships as often as men do (Cross and Campbell 2011). Sexual dimorphism in aggression begins in childhood from the age of two years onwards (Campbell 1999) and peaks in young adulthood (Archer 2009). Violent crimes are much higher among men, and male on male violent crime is the most prevalent (Campbell et al. 1998). This has led researchers to the hypothesis that differences in human same-sex violence and aggression are part of a greater evolutionary pattern, which is driven by the different strategies that males and females employ to secure mates (Darwin 1871).

Underpinning this sexual dimorphism in violence are differences in potential reproductive outputs for men and women, conventional views state that men are usually capable of siring many more offspring than are women (Archer 2009). Trivers (1972) reasoned that males compete more for reproductive opportunities because they do not extend as much effort towards parental investment in offspring. Bateman (1948) showed in *Drosophila* that females expend more energy in gamete production, than do males in sperm production (anisogamy). It therefore would make it more beneficial for males to seek out multiple mating opportunities in situations where offspring require little parental investment, or where mothers invest a greater amount of energy into caring for their offspring, whereas when parental care is equal or greater in males the strength of intrasexual aggression in males is reduced. Furthermore, in so-called role reversed taxa, such as the polyandrous black coucals, males brood the eggs and care for the hatchlings, whereas the female birds compete and are the larger, more aggressive sex (Goymann et al. 2015).

Consideration of Sex Role Evolution

Considering sex role evolution is imperative to answering the question of whether intrasexual selection could have shaped human aggression and violence. Especially when we consider that

human males follow the same general pattern of being more aggressive and violent than their female counterparts and are often the sex that uses aggression and violence to compete for mating opportunities (Carter and Kushnick 2018). Kokko and Jennions (2008) argue that explaining sex roles is more nuanced than much of the past conventional literature considers. For example, the notion that males are able to produce more offspring than females violates the “Fisher Condition,” which states that males are inevitably limited by a female’s rate of reproduction. Despite this, in humans men on average still have a greater variance in number of offspring than women do (Cross and Campbell 2011). Secondly, the assumption that females (more than males, due largely to anisogamy) cannot afford to lose their past investments in offspring violates the “Sunk Costs” fallacy (also termed Concorde fallacy), a cognitive bias that describes the tendency to think that previous effort expended in an activity makes further effort in that activity more profitable. This argument also assumes that female’s effort in gamete production is linked to greater amounts of parental care later on.

Due to the work of Kokko and Jennions (2008) and others (for examples see: Goymann et al. 2015; Schacht et al. 2014), models that attempt to explain sex role evolution now take into account not only Operational Sex Ratio (OSR) or the ratio of males to females in a population that are of reproductive age, but also the availability of males and females. This highlights the need to consider Adult Sex Ratios (ASRs) and take into account the effect ASRs have on mate competition; this is discussed further in the next section. Other things to consider in sex role models are whether young born are altricial, i.e., underdeveloped at birth and requiring more care such (e.g., humans) or precocial, i.e., more developed and independent at birth (e.g., giraffes), as this will dictate the amount of parental care required. Additionally, mating system, paternity certainty, the strength of sexual selection, and even possible sexual conflict are all interrelated factors that need to be taken into account when attempting to explain sex role evolution (Kokko and Jennions 2008).

The social role theory proposes an alternative to sexual selection theory in explaining sex roles and their relationship to aggression. According to the revised social role theory, the differences in aggressive behavior exhibited by men and women are due to societal divisions of labor, rather than sexual selection (Eagly and Wood 2011). Although the proponents of the social role theory do allow that the social requirements of the sexes are interacting with ecological and environmental factors, they disagree that sexual selection can explain patterns of human aggression for two main reasons. Firstly, that explaining aggression using intrasexual selection relies mainly on the assumption of humans employing a polygynous mating system. Secondly, that sexual dimorphism is lower in humans comparative to other primates (Archer 2009). While most researchers do not deny that social and cultural norms play a role in explaining human violence and aggression, the evidence shows them unlikely to explain the entire pattern. Putting humans into evolutionary context with other taxa – it would be unparsimonious to assume human exceptionalism (Archer 2009).

Nevertheless, it is valuable to address the criticisms of the intrasexual selection explanation. Firstly, as this section addresses, explaining sex roles in all taxa is a complex interplay of factors, of which mating system is only one. Although serial monogamy is common in humans, evidence still shows that polygynous mating, or extra-marital couplings are commonplace and contribute to men having a larger variance in number of children than women (Cross and Campbell 2011). Secondly, it is accurate to say humans are generally less sexually dimorphic in say body size than our ancestors, although issues with gauging this are discussed in the next section. Nonetheless, it is not entirely accurate to say that humans are less sexually dimorphic compared to all primates, even if one only considers apes. For example, the family *Hylobatidae* (gibbons and siamangs) are monogamous (although sneaky mating does occur) and they are much less sexually dimorphic in both body and canine size than humans are – and are the only nonhuman primate to employ monogamy (Kramer and Russell 2015). The

relationship between mating system and intrasexual selection is discussed in the following section.

Mating System can Predict Strength of Intrasexual Selection

Phylogenetic studies show past ancestral mating system can often predict future mating strategies, and in turn mating system can affect the strength of intrasexual selection. A recent cross-cultural study showed that the intensity of intrasexual aggression is highest in societies that sanction polygyny and where the variance in number of wives is the greatest (Carter and Kushnick 2018). Although many of these societies practice serial monogamy more commonly (one partner at a time, or for a number of years), opportunistic polygynous mating is still occurring frequently, as it does even in societies where polygyny is outlawed (Cross and Campbell 2011; Kramer and Russell 2015). This opportunistic polygyny could be driving the intensity of male intrasexual violence and aggression. Granting modern humans are generally considered less sexually dimorphic in size than both the Australopithecines and early *Homo sapiens* fossils from the mid-Pleistocene (Kramer and Russell 2015).

Debate surrounds this point about variation between modern humans and/or hominid ancestors given sex determination and dimorphism are very difficult to gauge from the small sample sizes of fossils available, especially when these fossils do vary in size and are often fragmentary. It is also problematic to determine correlations between mating behavior and fossil size in extinct species (Plavcan 2012). Nevertheless, body size dimorphism in humans is commonly greater than in other monogamous species of apes (e.g., Gibbons), but smaller than in polygynous species (e.g., Gorillas) suggesting some degree of male antagonistic competition (Kramer and Russell 2015). Males (and females) can also compete for mates in aggressive yet nonviolent ways such as scarification for intimidation, which can act as an armament or an ornament. These nonviolent behaviors are unlikely to reduce the strength of

intrasexual competition but are likely to exhibit different selection pressures upon it (Carter and Kushnick 2018).

The Relationship between Sex Ratios and Violence

As touched on earlier, there is a relationship between sex ratios and violence that is mediated by mating behavior. As violence and aggression are usually more prevalent in men, a long commonly held belief is that an ASR skewed towards men will result in more violence. Additionally, due to females providing a greater parental investment, conventional sexual selection theory assumes this skews the OSR towards males. Schacht et al. (2014, pp. 214) termed this the “more men, more violence expectation.” This notion fits with long held views on sexual selection, such as the influential work of Emlen and Oring (1977) who coined the term OSR as a key measure of the potential intensity of sexual selection. The conventional view has been that male biased sex ratios lead to an increase in male-male competition. This explanation seems intuitive, and mathematically if one considers again that males are usually the victims and perpetrators of violent crime, more men additively equal more violent crime. This was the explanation given for the increasing violent crimes in China and India, due to a preference for sons – both countries had a male biased ASR (Oldenburg 1992; Dreze and Khera 2000; Edlund et al. 2007).

Although these notions appear intuitive, they have been challenged recently. Both mathematical and empirical evidence for such commonly held assumptions are not met (Kokko and Jennions 2008; Schacht et al. 2014; Carter and Kushnick 2018). In their review of data from 15 preindustrial societies, Schacht et al. (2014) demonstrated that there is more male-male competition when sex ratios are female biased. Further evidence for this comes from a recent cross-cultural study that found the strength of intrasexual selection was greater in female skewed sex ratios (Carter and Kushnick 2018). Kokko and Jennions (2008) have demonstrated that, under certain

circumstances, male biased adult sex ratios can lead to a decrease in competition. This is because some males will shy from competition when costs are high or probable benefits low – leading to an ASR that is a poor measure of OSR. That the strength of intrasexual competition among males may be higher when females are in excess does not necessarily negate the hypothesis that this could have shaped human male aggression, but it does illustrate a need for further evaluation of the relationship between human violence and mating.

To consider the relationship between human male violence and mating behavior, several points need to be taken into consideration. Firstly, competition for mates is not always violent; it can be aggressive without resulting in physical violence, such as intimidation tactics (Carter and Kushnick 2018). Male tactics depend on female mate choice, in situations where females prefer males who demonstrate their status, wealth, and resources nonviolently – nonviolent tactics will be the prevailing mode of competition. Crime statistics often do not delineate between intra- and intersexual violence and aggression, making gauging accurate relationships difficult. In a recent review of crime statistics worldwide and their relationship to male-skewed sex ratios, results were mixed and dependent on society, type of violence measured, and rate of violence (Schacht et al. 2014). For example, studies of India and China found positive relationships between male-skewed sex ratios and homicide rates, violent and property crime rates (Oldenburg 1992; Dreze and Khera 2000; Edlund et al. 2007). However, studies considering US cities found negative or mixed relationships between male-biased sex ratios and homicide rates (Messner and Sampson 1991). This is further evidence that there is no simple relationship between sex ratios and violent crime (Schacht et al. 2014).

Intrasexual Violence and Aggression in Women

Women consistently use violence less than men do, with the exception of violence within intimate

partner relationships (Campbell 1999). One possible reason for this disparity in intrasexual violence is that in humans it is the largely the female who expends energy towards enhancing their physical appearance. It is in this way females attract a mate and attempt to out-compete other females (Buss 2003). The trend toward monogamy or at least serial monogamy may have meant that men sought higher quality mates than under a polygynous mating system (Cross and Campbell 2011). Due to an expanding hominin brain, human babies became more altricial than previously seen in our ancestors; this meant human babies required more resources and energy to survive – this preceded the emergence of bi-parental care, monogamy, and co-operative breeding. Put simply, women required help to raise a child and therefore had to attract and compete as men do for mates – something that is quite rare in other species (Buss 2003; Cross and Campbell 2011).

While it is true that men's reproductive output will always be limited by female's reproductive capacity (Fisher's Condition), resulting in a reduction in males potential reproductive capacity – evidence still shows that men, even in modern society, have greater reproductive variance than do women (Kokko and Jennions 2008; Jokela et al. 2010). This discrepancy is largely due to opportunistic polygynous mating in societies where serial monogamy is considered the norm. Many traditional societies today still sanction polygyny, (even if serial monogamy is more common) and the strength of intrasexual violence in men co-varies with the relative presence of polygyny, meaning that intrasexual aggression is higher in societies where polygyny is sanctioned (Carter and Kushnick 2018). It therefore follows that men have a collection of adaptations related to competing for mates, while women tend to have a suite of adaptations to attract a mate and for this reason may compete less violently with one another. Women tend to compete with each other by making further changes or enhancements to physical appearance using: makeup, nail polish, tanning, plastic surgery, bras, corsets, and clothing. Men also enhance their appearance but not at the same rate and prevalence as women do (Puts 2010; Cross and Campbell 2011).

When women do engage in intrasexual aggression, it usually results in less violent consequences than it does in men. For example, gossip and ostracization can stigmatize rivals without escalating to physical violence. These acts do however inflict stress on the rival and act to besmirch the competitor's reputation – usually such gossip takes the form of belittling a competitor's physical appearance or casting doubt on her sexual reputation. Young women are more likely than men to question a rival's loyalty and draw attention to her infidelity (Milhausen and Herold 1999). Such tactics act to cloud paternity certainty and may give women who use them an advantage, especially if they do so while highlighting their own fidelity (Cross and Campbell 2011). These encounters can escalate to physical violence, when a female retaliates due to the besmirching of her sexual reputation. This escalation to violence is most likely to occur when resources are scarce, and women are impoverished (Cross and Campbell 2011).

When women do engage in violent intrasexual confrontation, it is usually less grievous than it is in men. As with males, intrasexual violence among women is most common in adolescence and young adulthood: US official crime statistics report 73% of attacks carried out by adolescent girls were on other girls (Cross and Campbell 2011). In a British study, 7% of women reported being attacked by another female in the preceding 5 years (George 1999). In both the UK and USA, female-female assaults occur most commonly between the ages of 15 to 24 year olds (Cross and Campbell 2011). The reasons for these attacks fall (either directly or indirectly) into these three categories: jealousy, retaliation for slander against sexual reputation, and competition for desirable partners (Ness 2004; Cross and Campbell 2011). Again, skewed sex ratios are implicated to explain rates of violent crimes. In African-American communities where the adult sex ratio is heavily skewed towards females, some argue that this ramps up competition between females for mates and thus results in more assaults among women (Cross and Campbell 2011). As presented in the previous section however, considerable evidence suggests that a female-biased sex ratio may result in

higher male-male competition (Schacht et al. 2014; Carter and Kushnick 2018). Though the two are not mutually exclusive and it could be that in certain societies, female biased sex ratios result in increased intrasexual violence in both sexes, or other ecological conditions are at play.

Other such ecological factors are resource availability, and men's resources seem to predict female intrasexual violence. In poorer communities, fighting for a well-resourced mate may be worth the risk, as the variance in income is much larger than it is in the middle classes. Where the differences in resources are negligible, such as between a Doctor and a Lawyer, the costs of engaging in violence may be greater. Overall, rates of intrasexual violence among women are much lower and less serious than that of men. Weapons are rarely used, and punching and kicking are the main modes of violence (Cross and Campbell 2011).

Conclusions

A re-evaluation of sexual selection theory in recent years has challenged some long-held assumptions, stemming further consideration of a multitude of factors – resulting in models that are more sophisticated (Kokko and Jennions 2008). Intrasexual violence and aggression reflected upon here make up only half of the sexual selection story, as intersexual violence or violence between mates occurs frequently (Cross and Campbell 2011). In addition, other adaptive and ecological problems may be solved by aggression that are still rooted in evolutionary theory but fall outside of sexual selection (Buss 2009). Social and cultural roles should be taken into account, but researchers generally agree – they are unlikely to explain the majority of sex differences in aggression – to assume so is committing human exceptionalism (Archer 2009). Intrasexual violence and aggression in humans, when contextualized with other taxa, can elucidate differences between males and females use of violence and aggression and can go some way to predict the patterning of violence and aggression generally.

Cross-References

- [Intrasexual Competition Between Females](#)
- [Intrasexual Male Competition](#)
- [Parental Investment and Sexual Selection](#)
- [Sex Differences in Aggression](#)
- [Sexual Selection via Direct Male-Male Interactions](#)

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Intraspecific Comparisons

- [Within-Species Comparisons](#)

Intrauterine Insemination

- [Medically Assisted Reproduction](#)

Intromission

- [Penile-Vaginal Sex](#)

Intuitive Morality

- [Evolved Moral Foundations](#)

Invasion

- [War](#)

Investment in More Certain Kin

- [Father's Father Versus Mother's Mother](#)
- [Maternal Grandmother Invests Most](#)
- [Paternal Grandfather Invests Least](#)

Investment Versus Future Payoff

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Synonyms

[Cooperation](#); [Life history](#); [Parental investment](#); [Trade-offs](#)

Definition

Varying levels of investment results in different outcomes.

Introduction

There are a variety of situations in which investment results in a future payoff. This research falls into three areas of research: (1) mating versus parental investment, (2) quality versus quantity of offspring, and (3) cooperation.

Mating Versus Parental Investment

Parental investment is the investment in an offspring by a parent that benefits the offspring and comes at a cost for the parent (Trivers [1972](#), [1974](#)). In humans, females have obligatory gestation and lactation. Therefore, reproductive investment in offspring for females is greater compared to males. Because of this differential investment, females are typically highly selective in choosing mates (Trivers [1972](#)). Males on the other hand are not as selective. Since the females are choosing the mates, males invest in competition tactics that increases their likelihood to be chosen (e.g., mating displays, fighting; Cox and Le Boeuf [1977](#)).

Quality Versus Quantity of Offspring

One cost of parental investment is it decreases the investment in future offspring. Because of this, a trade-off must be made in quality or quantity of offspring (Kaplan [1996](#)). For example, as the number of offspring increases (i.e., higher quantity), the level of investment per offspring decreases (i.e., lower quality). According to life history theory, this tradeoff is influenced by cues of the external environment (Gangestad and Simpson [2000](#)).

For example, a child raised in a harsh environment is receiving cues that in the future access to stable pair-bonds and resources will be limited. Therefore, adopting short-term mating tactics,

reproducing earlier, and increasing the quantity over quality of offspring would be more beneficial. The opposite is true for children raised in an environment in which there was stable biparental care and resources available. It would be more beneficial for this individual to adopt long-term mating tactics, delay reproduction, and increasing the quality over quantity of offspring (Gangestad and Simpson 2000).

Cooperation

Unlike the trade-offs of mating vs. parental investment and quality vs. quantity of offspring, cooperation does not have an immediate payoff. Cooperation, especially altruism, has been a puzzle to many evolutionary psychologists. Cooperation is any behavior that gives benefit to someone other than the cooperator. There are two models that try to explain why, despite its lack of obvious benefit, it exists: kin selection and reciprocity.

Kin Selection. Kin-biased cooperation is one of the original theories that try to explain the paradox of cooperation (Darwin 1859; Hamilton 1964). It is found in a variety of species from primates to insects (Bourke 1997; Silk 2002). Kin selection predicts that individuals should preferentially help relatives over nonrelatives and should help according to the degree of relatedness. In order to preferentially help relatives, individuals must first be able to discriminate between kin and nonkin. Many social animals support this prediction and are able to discriminate between kin and nonkin (Griffin and West 2003). Additionally, there is a stronger discrimination of kin versus nonkin in species in which benefits of helping are greater (Griffin and West 2003). Kin selection is very powerful in cooperative breeding species, but it does not account for all types of cooperative behaviors.

Reciprocity. Although the theory of kin selection is widely accepted, other forms of cooperation such as reciprocity are less so. Reciprocity is the mechanism in which cooperative behaviors are favored by the probability of future beneficial mutual interactions. Reciprocity in a population will stabilize cooperation if the following

conditions are met: (i) the benefits to the recipient outweigh the costs to the donor, (ii) individuals interact repeatedly, and (iii) individuals recognize partners, therefore detecting cheaters. Humans evolved in large groups in which they likely spent their entire lifespan within in one to two primary groups. Therefore, in the environment of evolutionary adaptedness, there was a large probability that individuals would interact repeatedly. Even in modern day environments in which they bring strangers into the lab that will likely never see each other again, individuals still choose to cooperate even though cheating is initially more beneficial (Hamilton and Axelrod 1981). This suggests that humans have an evolved mechanism to favor cooperation.

One of the most successful strategies for reciprocity is Tit-for-Tat (Hamilton and Axelrod 1981). Tit-for-tat the strategy in which players start out cooperating and copies the other players behavior (e.g., if player one cooperates player two cooperates, if player one cheats player two cheats). It should be noted that although reciprocity has been shown in a variety of contexts (e.g., food sharing, grooming, mating opportunities), other alternative models may be at play (e.g., kin selection).

Conclusion

There are a variety of situations in which investment in one aspect results in a future payoff. This research falls into three related areas of research: (1) mating versus parental investment, (2) quality versus quantity of offspring, and (3) cooperation. Cooperation is a puzzle to evolutionary psychologist because it does not have an immediate payoff, yet it occurs in a variety of species. There are two models that try to explain why it exists: kin selection and reciprocity.

Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Kin Selection](#)
- [Life History Theory](#)

- [Mating](#)
- [Parental Investment Theory](#)

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IPD

- [Iterated Prisoner's Dilemma Model](#)

IQ

- [Nonhuman Intelligence](#)

Iron Deficiency

- [Iron-Poor Blood](#)

Iron-Deficiency Anemia

- [Iron-Poor Blood](#)

Iron-Poor Blood

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Synonyms

[Iron deficiency](#); [Iron-deficiency anemia](#)

Definition

When the body contains insufficient levels of iron within the blood.

Introduction

Iron is essential for the maintenance and growth of all microorganisms, including the ones that reside within the human body (Denic and Agarwal 2007). Careful internal monitoring of iron levels has to be maintained as excess iron can damage cells and the body has no method of reducing the iron content of the blood (Steinbicker and Muckenthaler 2013). Though excess iron can damage the host, insufficient levels of iron are just as harmful and can lead to iron-deficiency anemia where red-blood cell levels are reduced.

Inadequate iron levels are the most prevalent micronutrient deficiency globally (Bailey et al. 2015) and is present across all ethnic groups (Denic and Agarwal 2007). Children, pregnant women, and women of childbearing age have an increased susceptibility to inadequate levels of iron, and women are twice as likely to suffer from iron-deficiency anemia than men, primarily the result of iron loss during menstruation (Denic and Agarwal 2007).

The cause of the global deficiency in iron has been argued to stem from the agrarian revolution 10,000 years ago. This is when human culture transferred from hunter-gather based food collection to relying more on agriculture (Denic and Agarwal 2007). This resulted in lower levels of iron being consumed, as the staple diet shifted

from meat (containing iron) to cereals. As a result, the human body, which had evolved based on a predominantly meat-based diet, was deprived of iron when culture advanced.

On an individual level within contemporary society, the cause of iron deficiency and iron-deficiency anemia differs according to country. It can either stem from diets consisting of few foods rich in iron (either resulting from unavailability or restricted diets such as vegetarianism) or through conditions/diseases that cause blood loss (Camaschella 2015).

The effects of iron-deficiency anemia can be difficult to detect and can be mistaken for general poor health. As iron-deficiency anemia impacts the oxygen supply in the blood, the effects are generally felt as a decrease of fitness and strength (Camaschella 2015). There is also evidence that this disruption within the blood supply leads to impairments in cognition, ability to concentrate, and occupational performance (Denic and Agarwal 2007). Though the symptomology of iron-deficiency anemia may be vague, the diseases that are linked with it can be severe and include illnesses involving the kidney, heart failure, intestines, and cancer (Lopez et al. 2016).

Fighting Infection

One controversial debate concerning iron deficiency is the degree to which it protects the host from certain infections (Tansarli et al. 2013). During the aforementioned agrarian revolution, community size and animal domestication increased dramatically, creating an environment which promoted the transmission of pathogens from animals to humans (Denic and Agarwal 2007). As iron is vital to the maintenance of microorganisms (including pathogens), it has been argued that human evolution has failed to adapt to the lessening iron in the human diet because iron deficiency provides an adaptive advantage for protecting the host from certain diseases (Denic and Agarwal 2007).

The evidence for this protective effect is limited due to the amount of empirical investigation within the literature (Tansarli et al. 2013). While

the amount of studies directly investigating the effect may be limited, the evidence that has been conducted appears to support the protective effect (Tansarli et al. 2013). An example of this is a study by Jonker et al. (2012) who analyzed Malawian children living in areas with higher risks of contracting malaria. They found that, after controlling for baseline iron levels, children with iron deficiency were less likely to have malaria after a year.

Another example is Wander et al. (2009), who conducted a study investigating the effect of iron levels on the risk of infection for Kenyan children. The results suggest that the restricted iron available in their diet had a protective effect from contracting infection, provided that the levels of iron had not dropped too far. This is due to evidence that differing severities of iron deficiency can also be detrimental to protecting from infection by comprising the effectiveness of cell-mediated immunity (Wander et al. 2009). This would suggest that the pressure of infectious disease in the immediate environment determines the efficacy of iron deficiency as a protective force (Wander et al. 2009).

Safety of Iron Supplements

When pathogens infiltrate the body, an immunological response reduces the levels of iron in the blood to diminish their growth and spread (Wander et al. 2009). As such there is considerable debate pertaining to the safety of providing iron supplements for individuals residing in areas that confer a higher risk of contracting infectious disease. As removing the iron supply for pathogens is a vital aspect of an immunological response, increasing the amount of iron in the body of the host could risk making the infection worse (Hurrell 2012).

One study especially highlights the dangers of the use of supplements in areas that have a high risk of certain infectious diseases. Sazawal et al. (2006) attempted to study the effects of iron and folic acid supplements on children from Pemba, Zanzibar. The study had to be finished prematurely following safety concerns relating to

increased mortality and hospital admission from the participants.

Conclusion

Poor levels of iron impair the ability of the blood to carry oxygen around the body. This manifests in feelings of fatigue, poor concentration, and generally poor fitness. Despite these effects on the body, humans may not have adapted from the change in diet (resulting from the agrarian revolution) due to an evolutionary advantage provided by poor levels of iron reducing the growth of pathogens that have gained entry to the body.

The evidence for this protective effect from infection requires further evaluation and evidence than is present from the current literature. This is especially the case regarding the safety of iron supplements in areas prevalent in infectious disease where the benefits of having slightly reduced levels of iron may be beneficial.

Cross-References

- [Adaptation](#)
- [Diet](#)
- [Disease Avoidance](#)

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Irrational Fears

- [Phobias](#)

Isolation

- [Loneliness in Modern Life](#)

Is-Ought Problem

- [Naturalistic Fallacy, The](#)

Issues Associated with Not Having Intimate Bonds with One's Relatives

- [Benefits of Profound Kinship Connectedness \(and Problems from a Lack Thereof\) Through an Evolutionary Mismatch Lens](#)

Issues Related to Adolescent Development

► [Adolescent Issues](#)

Item Manipulation

► [Cephalopod Tool Use](#)

Iterated Prisoner's Dilemma Model

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Synonyms

[IPD](#); [PD](#)

Definition

The Prisoner's Dilemma is a non-zero-sum game played by two players in which each player decides between two options – cooperate or defect – with the payoffs dependent on the combination of choices. The best payoff for players occurs when they sucker their partners by defecting while their partners cooperate. The second best payoff occurs when both partners cooperate. The third best payoff occurs when both partners defect. The worst payoff occurs when a player gets suckered. In iterated, or repeated, Prisoner's Dilemmas, two or more players play multiple rounds in succession, and players are able to change their strategies in response to previous moves of their opponents.

Introduction

The Prisoner's Dilemma game was formulated in 1950 by Merrill Flood and Melvin Dresher of the

RAND Corporation and exemplified by Albert Tucker of Princeton University in terms of choices faced by two prisoners. The game acquired its name from a hypothetical dilemma faced by two criminals who are imprisoned and placed in separate rooms. Each is offered a deal: if one confesses (defects on the other prisoner) and the other remains silent (cooperates with the first prisoner), the defecting prisoner goes free and his cooperating partner gets 3 years in jail. If both prisoners remain silent (cooperate), both get 1 year. If both confess (defect), both get 2 years. In a classic article, Robert Trivers proposed that the evolution of reciprocal altruism could be modeled in terms of Prisoner's Dilemma games, asserting that "The relationship between two individuals repeatedly exposed to symmetrical reciprocal situations is exactly analogous to what game theorists call the Prisoner's Dilemma" (Trivers [2002](#), p. 23).

The Prisoner's Dilemma game can be generalized to any situation in which two players simultaneously decide whether to cooperate or to defect. If both players cooperate, they each receive reward R . If both players defect, they each receive punishment P . If one defects and the other cooperates, the player who defected receives the temptation payoff, T , and the player who cooperated receives the sucker's payoff, S . The payoff matrix between Player 1 (bold) and Player 2 (italics) is (Table 1).

In all Prisoner's Dilemmas, $T > R > P > S$. On each move, defectors who exploit cooperators fare better than two cooperators, who fare better than two defectors, who fare better than cooperators exploited by defectors. This creates a dilemma because although mutual cooperation pays off better than mutual defection, the choice to cooperate is irrational from an individual, self-interested perspective, because on each move, defecting reaps greater rewards than cooperating does no matter what move one's partner makes. Players gain more points by defecting than by

Iterated Prisoner's Dilemma Model, Table 1 Payoff matrix for Prisoner's Dilemma games

	<i>Cooperate</i>	<i>Defect</i>
Cooperate	R, R	S, T
Defect	T, S	P, P

cooperating when their partner cooperates ($T > R$) and when their partner defects ($P > S$).

The payoff matrix for Prisoner's Dilemma games distinguishes them from other social games. For example, the payoff matrix for Chicken is $T > R > S > P$ (e.g., players who stay the course (T) win big when the other player (S) chickens out to avoid harm; both players avoid harm when both chicken out (R), but both suffer a great deal of harm when neither chickens out (P)).

Iterated Prisoner's Dilemmas

Prisoner's Dilemmas may involve one exchange or a series of successive exchanges. In iterated Prisoner's Dilemmas, two or more players play multiple rounds in succession. To ensure that mutual cooperation yields a higher payoff than alternating cooperation and defection, the payoff matrix for iterated Prisoner's Dilemmas must also satisfy $2R > T + S$.

In iterated Prisoner's Dilemmas, players are able to change their strategies in response to previous moves of their opponents. Iterated Prisoner's Dilemmas are more challenging than one-shot Prisoner's Dilemmas because although the optimal strategy on each individual round is to defect, it is in players' interest to avoid repeated chains of low payoff P-P mutual defections. The rational choice is to defect on the last turn, because the other player will not have an opportunity to retaliate. However, knowing that it is optimal for their opponent to defect on the last turn, players will realize that the optimal move on the second to last turn is to defect, and so on, which will give rise to low-payoff P-P exchanges. In contrast to one-shot Prisoner's Dilemmas, the rational defection strategy pays off poorly in iterated Prisoner's Dilemmas and is rejected by most human players.

Notable Characteristics of Prisoner's Dilemmas

Prisoner's Dilemmas model problems in which individuals are faced with decisions between

pursuing their selfish interests at the expense of their partners or cooperating with their partners to maximize their combined gains. Prisoner's Dilemmas are challenging because the outcomes for each player depend on the choices made by the other player. In most contexts, the optimal outcome for two or more players considered as a group is to cooperate because a group of two or more cooperating players gains more than (a) groups of two or more selfish players ($R + R > P + P$) and (b) groups containing both selfish and cooperative players ($R + R > T + S$). However, paradoxically, on each move that players make, the optimal strategy is to defect. Individuals may choose to defect as an offensive strategy – to maximize their gains by exploiting their partners – or as a defensive strategy – to minimize their losses by avoiding being suckered. However, if both players choose to defect, both players end up with the second worst outcome – in effect doing one another down.

Prisoner's Dilemmas abound in the real world because people frequently encounter situations in which they are able to advance their interests in selfish ways that, if adopted by others, would produce undesirable results. Some examples are partners deciding whether to do their share of the housework, politicians deciding whether to go negative in campaigns, gas station owners deciding whether to lower their prices, and arms races.

Modeling Social Evolution with Iterated Prisoner's Dilemma Games

Game theorists have used Prisoner's Dilemma games to model the evolution of reciprocal altruism and other forms of cooperation. In a classic study, Axelrod and Hamilton (1981) contacted a number of game theorists and invited them to submit strategies for an iterated round robin Prisoner's Dilemma tournament that modeled the natural selection of social strategies. In Axelrod and Hamilton's tournament, the points won in each game represented offspring inheriting the winning strategy. Each round of the Prisoner's Dilemma game constituted one generation, and the winners (therefore the offspring) populated the next

generation. The strategies (or alleles) in each new generation competed against one another in an iterated manner for 200 generations. The “climate” of the population (the number of replicas of each strategy or allele) changed from generation to generation, because the most successful strategies became increasingly prevalent, and the less successful strategies diminished in number or became extinct. As winning strategies became increasingly prevalent, they interacted with replicas of themselves increasingly frequently. It follows that successful strategies had to fare well against replicas of themselves.

Axelrod and Hamilton's iterated Prisoner's Dilemma games modeled several basic principles of social evolution. Groups of two or more cooperators produced more offspring than groups of two or more defectors, and each member of the group of cooperators produced more offspring than each member of the group of defectors. However, within groups that contained both cooperators and defectors, defectors produced more offspring than cooperators did. Thus, Axelrod and Hamilton's contests captured the tension between between-group selection that favors the evolution of cooperation and within-group selection that favors the evolution of selfishness (Dugatkin and Reeve 1994).

Tit for Tat

Axelrod and Hamilton's initial simulations of the evolution of cooperation using iterated Prisoner's Dilemmas produced two main findings. First, “Always Defect” (the most selfish strategy) constituted an evolutionarily stable strategy – in other words, this strategy could not be defeated by any other strategy. However, even though “All-D” was stable, it paid off poorly, because as this strategy increased in number, it interacted increasingly frequently with replicas of itself, which produced low payoff (P-P) outcomes. Although evolutionarily stable, the “All-D” strategy was not optimal.

Another finding from Axelrod and Hamilton's tournaments ended up garnering a great deal of attention. Axelrod and Hamilton found that a

cooperative strategy called Tit for Tat could prevail over other strategies under certain conditions and indeed won the first tournament they sponsored. Players invoking the Tit for Tat strategy make a cooperative choice on the first move and in subsequent moves, copy their opponent's previous move. If their partners cooperate, they continue to cooperate; if their partners defect, they cut their losses by defecting. Axelrod and Hamilton found that Tit for Tat produced more offspring than “All-D” because it produced as many offspring as “All-D” did subsequent to the first exchange, plus a greater number of offspring in exchanges with other cooperative strategists, without suffering the costs of being repeatedly suckered. “TIT FOR TAT won the tournament, not by beating the other player, but by eliciting behavior from the other player which allowed both to do well. . . . So in a non-zero-sum world you do not have to do better than the other player to do well for yourself” (Axelrod 2006).

There is a great deal of evidence that contemporary humans employ Tit for Tat strategies in their everyday lives, as captured by expressions such as “quid pro quo” and “don't get mad, get even.” On the positive side, individuals are prone to help those who help them and to repay favors. On the negative side, the Tit for Tat strategy can give rise to blood feuds.

The Evolution of Nicer Forms of Cooperation

In a review of research on reciprocal altruism, Trivers (2006) wrote, “TfT and Axelrod and Hamilton (1981) spread like wildfire through the literature, so that soon all reciprocal interactions seemed to be formulated in terms of the PD [Prisoner's Dilemma]” (p. 70). In addition to game theory research employing human participants, investigators found that other species, including viruses and bacteria, engage in iterated Prisoner's Dilemma types of exchanges and employ Tit for Tat strategies to propagate replicas of themselves. However, as pointed out by Trivers (2006), “it soon seemed that theorists and empiricists alike were forgetting that iterated games of PD amount

to a highly artificial model of social interactions; each successive interaction simultaneous, costs and benefits never varying, options limited to only two moves, no errors, no escalated punishment, no population variability within traits, and so on" (p. 70).

In studies that followed Axelrod and Hamilton's simulations, researchers modified the conditions in which Prisoner's Dilemma games were played to reflect more validly the conditions in which strategies evolve in the animal kingdom. "Modifications to the IPD [iterated Prisoner's Dilemma] include variations in population structure, number of players, number of strategies, relatedness of players, stochasticity of strategies, stochasticity of environment, amount of memory, possibility of individual recognition, norms, ostracism, mobility of players, and mistakes by players" (Dugatkin 1997, p. 24). Follow-up studies found that several strategies were able to defeat Tit for Tat in environments that corresponded more closely to actual environments than those modeled in Axelrod and Hamilton's original research (Nowak and Sigmund 1992). One of the most significant findings from these studies was that the kinds of errors and random events that inevitably occur in the process of evolution may exert significant effects on the selection of social strategies. In particular, investigators found that the Tit for Tat strategy was vulnerable to selfish mistakes that launched iterated streams of low-gain defect-defect exchanges. For this and other reasons, most of the strategies that ended up winning modified computer contests were more cooperative or "nicer" than Tit for Tat – strategies that paraded under such banners as "Generous Tit for Tat," "Tit for Two Tats," "Firm but Fair," "Contrite Tit for Tat," and "Pavlov" (win-stay, lose-switch) (Ridley 1996). One of the main principles exposed by this research was that although unconditional cooperation is a losing strategy, several forms of conditional cooperation that enable players to cut their losses against cheaters can evolve in some environments. Other notable findings from studies following Axelrod and Hamilton's research were: (a) more than one strategy may evolve in some populations, and

strategies may fluctuate in the population because they are frequency-dependent, (b) strategies such as Pavlov that "learn" tend to defeat inflexible strategies, and reputation may play a significant role in learning (Ridley 1996), (c) ostracism may favor the evolution of cooperation (Hirshleifer and Rasmussen 1989), and (d) punishing defectors and establishing cooperative norms may facilitate the spread of cooperative strategies (Stephens et al. 1996).

Conclusion

The iterated Prisoner's Dilemma models problems faced by humans and other animals in which behaving selfishly is the rational choice on each individual round or encounter, but cooperating can reap greater benefits in the long run. After pitting different Prisoner's Dilemma strategies against each other in simulations of natural selection, theorists found that a cooperative strategy called Tit for Tat prevailed. Follow-up research that more accurately modeled natural selection found that even "nicer," or more cooperative, strategies than Tit for Tat could defeat Tit for Tat and evolve, primarily because they were equipped to correct never-ending strings of low payoff mutual defections.

Cross-References

- [Competitive Altruism](#)
- [Ingredients of Reciprocal Altruism](#)
- [Nonhuman Reciprocal Altruism](#)
- [Reciprocal Altruism](#)
- [Reputation](#)

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1954; Charnov and Schaffer 1973; Stearns 1976). Both reproductive strategies are observed in the plant and animal kingdoms. Humans (*Homo sapiens*) are an example of iteroparous species – humans are biologically capable of having several offspring during their lives. Iteroparous vertebrates include birds, reptiles, fishes, and mammals (Angelini and Ghiara 1984). Among invertebrates, most Mollusca and insects (e.g., cockroaches and mosquitoes) present an iteroparous reproductive strategy (e.g., Fritz et al. 1982). Most perennial plants reproduce multiple times during their life span, thus are considered iteroparous species (Watkinson and White 1986).

Theoretical Models

The evolution of iteroparity (and semelparity) has been subject of several theoretical models. One set of models attempts to explain the differential evolution of iteroparity by examining the trade-offs between reproductive effort involved in offspring produced and offspring forgone (for a review, see Roff 1993). According to the trade-off models, the reproductive effort of an organism occurs optimally when the benefits of offspring produced outweigh the costs of offspring forgone. That is, the greatest distance states the optimal reproductive strategy for a given species. For species with higher life expectancy (i.e., low forgone offspring rate), the optimal reproductive strategy is to reproduce several times in a lifetime. Trade-off models have found limited supportive evidence from living systems. Moreover, the bet-hedging models investigate whether iteroparity was selected over the evolutionary time because it functions against unpredictable infantile survival rates (see Fox and Rauter 2003). The bet-hedging models have not found empirical support – in living systems, many semelparous species live in habitats with high environmental unpredictability.

The models based on demographic parameters have good support from living systems. Cole (1954) studied demographic explanations for the evolution of iteroparous and semelparous reproductive strategies. Cole's models resulted in an

Iteroparity

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Synonyms

K strategy

Definition

A reproductive strategy characterized by multiple reproductive cycles over the course of a lifetime.

Introduction

The term *iteroparity* refers to a reproductive strategy characterized by multiple reproductive cycles over the course of a lifetime and contrasts with *semelparity* (see ► “*Semelparity*”). The iteroparous and semelparous reproductive strategies received special attention in the study of reproductive strategies of species (e.g., Cole

iteroparous species bearing annual litters of an average of three offspring having the same rate of population growth than a semelparous species that has one litter of four and dies afterward. This suggested that an advantage of just one offspring would select for semelparity. Charnov and Schaffer (1973) then identified that sensible variances in adult and infantile mortality were responsible for costs of a semelparous reproductive strategy that were not accounted by Cole's model. These demographic models have been successful when tested with real-world systems. That is, according to these models, humans are an iteroparous species because the benefits of devoting reproductive efforts to multiple offspring outweigh the risk of infantile mortality.

Conclusion

The iteroparous reproductive strategy played a key role in the evolution of human's reproduction and parenting systems (Jones 2009). Although optimal reproductive strategies may vary between species, theoretical models have shown that iteroparous species have higher life expectancy, making it more optimal for humans to devote reproductive effort to more than one reproductive occurrence in a lifetime.

Cross-References

- [Reproductive Strategies](#)
- [Semelparity](#)

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Jack Kevorkian

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Synonyms

[Assisted suicide](#); [Doctor](#); [Physician](#)

Definition

A physical best known for his work in assisting suicide.

Introduction

Occasionally, history conveniently presents us with an event or a movement personified by a single man or woman. Such an occasion is the melding of Dr. Jack Kevorkian with the physician-assisted suicide (PAS) movement in the 1990s. Pathologist, author, musician, and painter, he is best remembered for having escorted at least 130 patients to their death by assisted suicide and euthanasia.

His Armenian parents had fled persecution in the Turkish Ottoman Empire and immigrated to Pontiac, Michigan, where he was born on May 26, 1928. He attended the University of Michigan

Medical School from where he graduated in 1952. Subsequent to graduation he entertained several radical ideas, including using death row inmates for medical experimentation, and transferring cadaver blood into living recipients, including himself (Nicol and Wylie 2006).

In 1990, he met a 54-year-old Janet Adkins, who became his first assisted suicide. He had cobbled together a homemade device he called a Thanatron (Greek for “death machine”), consisting of a mechanism that initially delivered IV saline, followed by a barbiturate, and finally a lethal dose of potassium chloride. Although initially charged with murder, there were no laws in Michigan that made assisted suicide illegal. The charges were dropped. As his activities increased, the state legislature frantically pieced together a law that made PAS illegal. However, the bill had been so poorly written that Kevorkian was tried four times between 1994 and 1997 and never convicted. But as the legislature had been unsuccessful in convicting him, they were able to deprive him of his medical license, thereby denying him access to controlled substances. From these circumstances, he contrived another mechanism, a Mercitron (mercy machine), that delivered carbon monoxide through a mask that permitted patients to initiate suicide (Jackson 2011).

Throughout his legal escapades, he was inextricably linked to his equally colorful attorney, Geoffrey Fieger. Mr. Fieger had gained such notoriety that he eventually, though unsuccessfully, ran for governor. Dr. Kevorkian continued to

push the limits of the legal system and eventually “fired” Mr. Fieger when he needed him the most, prior to his eventual conviction (Lessenberry 1994).

His last, most controversial patient was Thomas Youk, a 52-year-old with end-stage ALS who had requested his own death with the support of his family. Kevorkian had videotaped himself actively injecting Mr. Youk with a lethal dose of drugs. Through an intermediary, he had the tapes sent to CBS News where they were later aired nationwide on the television show - ‘60 Minutes’. This was not only flaunting the law, it was a departure from PAS to euthanasia, which was construed as second-degree murder by a Michigan jury. By refusing legal counsel and choosing to represent himself, he had lost opportunities to call witnesses and present useful evidence. Judge Jessica Cooper sentenced him to the maximum extent of the law, 10–25 years in prison. He eventually served over 8 years before he was paroled at the age of 79 due to good behavior and failing health (Schneider 2011).

Upon release from prison, Kevorkian was a much sought-after speaker and in 2008 ran for the US Congress, though only received 2.6% of the vote. His story was made into a critically acclaimed HBO movie in 2010, starring Al Pacino in the lead role for which he won an Emmy and a Golden Globe. Dr. Kevorkian died at 83, of natural causes and without artificial or mechanical assistance, on June 3, 2011.

Conclusion

Dr. Kevorkian’s notoriety was vast and varied. Hailed by some as heroic and others as fanatical, he nevertheless brought a meaningful and potent conversation from the dark ages into the twenty-first century.

Cross-References

- [Assisted Suicide](#)
- [Death](#)
- [Suicide](#)

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Jackals

- [Canines](#)

Jamaican Symmetry Project

- [Robert Trivers](#)

Janet Hyde (1984)

- [Janet Hyde \(1986\)](#)

Janet Hyde (1986)

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Synonyms

[Janet Hyde \(2005\)](#); [Janet Hyde \(2014\)](#); [Janet Hyde \(1984\)](#)

Definition

An early meta-analysis showing that gender differences in aggressive behavior are moderate in

size but persistent, yet decreasing in magnitude, over the life span.

Introduction

Are men and boys more aggressive than women and girls? Janet Hyde (1986) conducted the first modern meta-analysis concerning this question. Meta-analysis is a quantitative statistical technique in which a researcher seeks to compute an estimate of an effect size. The effect size that Hyde (1986) sought to quantify was the magnitude of the gender difference in aggression, including physical aggression and verbal aggression. The effect size that Hyde used was Cohen's d , a standardized effect size. A standardized effect size is a ratio of the magnitude of the difference between groups, relative to how much individuals within a group vary from one another. Positive effect size estimates indicate that men and boys have higher levels of aggression than women and girls, and effect sizes of 0.20, 0.50, and 0.80 are considered small, medium, and large differences, respectively (Cohen 1988).

Building on her previous work (Hyde 1984) stemming from Maccoby and Jacklin's (1974) review, Hyde (1986) sought to apply newer meta-analytic techniques to the question. In particular, Hyde was concerned with testing and accounting for *heterogeneity*: the notion that characteristics of studies might be associated with differences in effect size estimates. The characteristics she examined were type of aggression, method of measurement, study design, and age of participants.

Type of Aggression

An important question in the literature historically has been whether there is a gender difference in aggression, depending on the type of aggression investigated (physical vs. verbal). Hyde reported that although the effect size for physical aggression appeared larger ($d = 0.60$, based on 26 studies) than the effect size for verbal aggression ($d = 0.43$, based on 6 studies), this difference

was not statistically significant. Both effect size estimates were positive, indicating that men and boys showed higher levels of both physical and verbal aggression than women and girls.

More recently, researchers have asked whether women and girls show more indirect or relational aggression than men and boys. Indirect aggression differs from direct (verbal and physical) aggression in that when directly aggressing, the perpetrator of aggression directly engages a victim, whereas with indirect aggression, the perpetrator seeks to harm the victim by damaging a victim's reputation. A more recent meta-analysis (Archer 2004) found a small negative effect size such that women and girls were more indirectly aggressive than men and boys, but this newer meta-analysis also replicated Hyde (1986), finding a positive effect size of moderate size for both physical and verbal direct aggression.

Method of Measurement

The method of assessment of aggression varied across studies in Hyde's (1986) meta-analysis. Most studies used direct observation (42 studies), whereas other studies used self-report (14 studies), parent or teacher report (8 studies), projective assessment (1 study), or peer report (4 studies). Hyde (1986) reported significant heterogeneity based on method of assessment, implying that there were differences in the effect sizes observed depending on measurement method. However, the effect size for self-report ($d = 0.40$) was not statistically smaller than the effect size for direct observation ($d = 0.51$).

Study Design

Hyde (1986) contrasted observational and correlational studies with laboratory experiments. In a true experiment, the researcher manipulates and controls an independent variable (in this case, usually a provocation to aggress) and observes its effects on a dependent variable (here, an aggressive behavior or cognition). In observational/correlational studies, a researcher tests for

an association between measured variables – in this case, typically gender and a self-report of unprompted aggressive thoughts or behavior.

In her meta-analysis, Hyde (1986) reported that effect sizes were larger in observational/correlational studies than experimental studies, with effect sizes of $d = 0.56$ (a moderate effect size) in 42 observational/correlational studies versus $d = 0.29$ (a small to moderate effect size) in 27 experimental studies.

Developmental Effects

Hyde (1986) reported that gender differences decreased in magnitude over the course of development. That is, gender differences were larger among preschool-aged children ($d = 0.58$) than they were among college students ($d = 0.27$).

It is noteworthy that in a more recent review of over 350 studies, Archer (2004) reported effect sizes of 0.56 for elementary school-aged children (ages 6–11), compared to 0.29 for emerging adults (aged 22–30 years), and -0.01 for adults over age 31. Importantly, Hyde (1986) explained that methodological factors in different studies (e.g., method of measurement, type of aggression studied) are confounded with age of sample, making firm developmental conclusions difficult.

Conclusion

Janet Hyde's (1986) meta-analysis was a groundbreaking work in early investigations of gender differences in aggression. The paper is important because it was one of the first to use newly developed tests of heterogeneity to determine whether effect size estimates for gender differences varied based on type of aggression, method of measurement, study design, and developmental period. Hyde reported that effect size estimates did vary based on study design and developmental period, but there were no significant differences between physical and verbal aggression, nor between studies assessing aggression using self-report versus direct observation. Overall, estimates were moderate in size

and positive in magnitude, indicating support for the notion that men and boys are generally more aggressive than women and girls.

From a modern vantage point, Hyde (1986) leaves some important questions unanswered. In particular, it fails to correct effect size estimates for publication bias, a well-known cause of overestimation in effect size. Archer (2004) reported some attempts to assess publication bias in this literature, but an update of this meta-analysis with more modern bias correction techniques would be warranted at this point.

Cross-References

- ▶ [Aggression](#)
- ▶ [Aggressive Fantasies](#)
- ▶ [Costs of Aggression](#)
- ▶ [Development of Aggression](#)
- ▶ [Female-Perpetrated Violence](#)
- ▶ [Imitative Aggression](#)
- ▶ [Indirect Aggression](#)
- ▶ [Men Riskier, More Aggressive](#)
- ▶ [Meta-Analysis of Sex Differences in Aggression](#)
- ▶ [Physical Aggression](#)
- ▶ [Relational Aggression](#)
- ▶ [Sex Differences in Aggression](#)

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Janet Hyde (2005)

► [Janet Hyde \(1986\)](#)

Janet Hyde (2014)

► [Janet Hyde \(1986\)](#)

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Synonyms

[Developmental psychology](#); [Evolutionary psychology](#); [Father absence](#); [Life history theory](#)

Definition

Predictions about how cues to accelerated life history will be visible in maturation.

Introduction

Jay Belsky had a breakthrough moment – in his own words “the best idea I would ever have” – early in his career while teaching a graduate seminar. Having been trained in traditional developmental psychological theories (Freudian, attachment theory, and social learning theory) he was familiar with the idea that good developmental trajectories followed naturally from positive parental involvement. Parents who were responsive, financially and emotionally secure, and possessed of an acceptable level of intellectual and social skills would produce children who were similarly capable of love and social interaction in later life. A paper by colleague Pat Draper

(Draper and Harpending 1988) changed all that. Viewed from the perspective of life history theory, human notions of good and bad parenting take a back seat to effectiveness of passing genes on to the next generation – and this is true whether you are a human or a haddock. Viewed through this radical lens, violent and abusive human parents are preparing their offspring for a world where trust and love will not be rewarded. The fact of this being a social and moral evil says nothing about its being a reproductive dead end. This perspective, life history theory, has informed most of Belsky’s subsequent work.

Life History Theory

Life history theory is a set of well-validated interlocking biological predictions about the differential allocation of resources to different fitness-related aspects of an organism’s needs throughout its life. It is well-validated across a huge range of taxa. At the most basic level, organisms can be impelled down slow or fast life history paths. Slow paths are ones that emphasize greater time taken to reach maturity, the low acceptability of risk, and other modifications to take advantage of a predictable and supportive environment. On the other hand, fast life histories are favored in risky, dangerous environments where ultimate fitness is increased by maturing early and favouring reproductive quantity over quality. From a gene’s eye perspective, either set of strategies is as good as the other – both have been favored by selection to maximize fitness (Stearns 1976).

Human Development

Humans are obligate investors, and even minimum parental investment is still considerable. That said, there is plenty of opportunity for parents to cue offspring to a life of likely threats or opportunities. What Belsky realized was that what was traditionally regarded as bad parenting – e.g., unresponsive care-giving, spousal abuse, and frequent conflict was resulting in developmental

trajectories that likely maximized that child's fitness later in life.

This concept is not unknown to popular culture. In the classic country and western song "A Boy Named Sue," the father abandons his son at age three after naming him in a way that will ensure daily conflict. When they meet, later in life, and fight, they are reconciled over the realization that this treatment toughened the son up for the life he was to lead – the song even mentions his speed of maturation. This pattern (minus the sentimental reconciliation) is a distillation of Belsky's key insight as it pertains to what others would regard as developmental insults. Specifically, early maturation should be predictable from what others would regard as bad parenting (Belsky et al. 1991).

The implications of this are profound. The organism can be viewed as a fitness maximizer who can be conceptualized as saying (not consciously) to itself, "given that I am born into an environment that is harsh and unforgiving, in which I can't take my time to choose the best mate, ensure mutual commitment, and invest time and energy in healthy pursuits and a small number of much cared for children; my best reproductive bet is to start reproducing early, be a lot less choosy about with whom I do this, and have as many offspring as possible given that their chances of survival to reproductive maturity are so much less than they could be in this untrustworthy and unpredictable world." The question then is – what sort of early cues might set humans down one path rather than another. Given the need for biparental investment in our ancestral past, Belsky and others (e.g., Belsky et al. 1991) hypothesized that father absence in key developmental periods would predict earlier maturation.

These sorts of predictions have been confirmed strongly in females, but this is only part of the story. The mechanisms are far from perfect, and early calibrations of organisms to their likely environments might go awry. Genes that underlie these mechanisms may thus increase their fitness by hedging their bets somewhat. This results in a set of hypotheses about differential individual susceptibility (Belsky et al. 2007).

The observed effect of this is that some children are likely to appear more resilient to early markers of abuse than others. This is what we do find. Some children are highly reactive – with certain gene markers underlying these individual differences – and these children do both especially poorly in adverse conditions and especially well in supportive ones (Belsky 2012; Belsky and Pluess 2013).

Conclusion

Belsky has summed up these insights in terms of "biological gravity." Engineers cannot ignore the force of gravity when designing a building. Evolution is, similarly, a force that cannot be ignored when considering how biological organisms are designed. And, ultimately – this is cashed out in terms of differential survival of genes. The nature/nurture debate itself needs to grow up.

Cross-References

- [Life History Theory](#)
- [Parental Investment Theory](#)

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Jealousy

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Synonyms

Emotional jealousy; Male sexual jealousy; Platonic jealousy; Sexual jealousy

Definition

Jealousy is a cognitive or emotional response of insecurity or inferiority that occurs when there is a perceived threat to a valued social relationship, resulting in actions that mitigate the threat.

Introduction

Jealousy refers to a cognitive or emotional response of insecurity or inferiority that occurs when there is a perceived threat to a valued social relationship, resulting in actions that mitigate the threat. Different types of jealousy are based on different contexts under which threats to relationships occur, including intimate relationships, siblings, rivals, friends, and peers.

Sexual and Emotional Jealousy

Sexual and emotional jealousy within romantic relationships seems to have evolved in response to conflicting interests between the sexes. Due to concealed ovulation, men faced uncertain paternity and the possible investment in their rival's offspring, known as cuckoldry risk. Since many humans form long-term pair bonds, cuckoldry risk significant loss of time and resources to raising unrelated offspring. Traits that identified and reduced the risk of cuckoldry, such as sexual jealousy, would have been adaptive; thus, sexual jealousy may function by protecting paternity in men (Buss 1992; Trivers 1972; Daly et al. 1982).

Women, on the other hand, have 100% certainty in maternity, so they did not have the same risk of unknowingly investing in genetically unrelated offspring (Buss 1992). However, women risked losing their partner's time, resources, and abandonment to other women (Daly et al. 1982). Because of this risk, women may have evolved to be more susceptible to emotional jealousy (see ► "Emotional Jealousy"). Sexual and emotional jealousy can be understood as an adaptive response to sexual conflict, which is when reproductive interests of the sexes do not align (see ► "Sexual Conflict Theory (Middle-Level Theory in Evolutionary Psychology)").

There is a large body of evidence to support sex differences in these types of jealousy. For example, women are more distressed by scenarios involving emotional infidelity and the possibility of their partner directing affection elsewhere, whereas men are more distressed by scenarios involving sexual infidelity and possible cuckoldry situations (Buss 1989, 1992, 1995; Wiederman and Kendall 1999). These patterns emerged using both self-report and electrodermal measures and confirmed using meta-analyses (Sagarin et al. 2012).

Jealousy may be more pronounced in committed relationships due to the amount of time and resources it takes to form and maintain such a relationship (Harris 2003). There appears to be an increase in the use of mate guarding tactics as relationships increase in duration and seriousness (Buss 1988). Relationship experience impacts jealousy responses among men, where 55% of men with experience in committed sexual relationships, compared to 29% of men with no such experience, reported they would experience greater distress over sexual infidelity (Buss 1992). Among women, the impact of emotional infidelity was not impacted by their history of committed sexual relationships.

Historically, infidelity was often illegal with punishments as severe as death, highlighting the importance that men, who largely or exclusively controlled judicial systems, placed on marital fidelity. Examples of such punishments were found cross-culturally, including European, African, Central American, and Mediterranean cultures (Bullough 1976; Daly et al. 1982).

Jealousy may motivate various actions to secure exclusive access to one's mate, and these actions differ between the sexes. For example, since women's mating strategies involve being more selective based on a potential mate's resources, men who engage in resource display are more likely to retain their mate. Men are also more apt to use violence or threats of violence as a form of coercive control (Wilson et al. 1995). Buss and Shackelford (1997) found that men with younger, more attractive mates were more likely to engage in mate guarding, resource display, and violence in order to retain mates, likely because these women are of higher reproductive value at that age, motivating greater competition for them.

In contrast, women's jealousy may motivate them to enhance their appearance. Appearance enhancement functions by modifying physical attractiveness to appear more youthful, and thus more fertile, to garner stronger interest from a partner (Symons 1979). Similar mating strategies are more pronounced when women have a mate with greater resources. Women in relationships with lower-income men are less likely to engage in vigilance and respond less severely to intrasexual threats (Buss 1988; Buss and Shackelford 1997; Daly et al. 1982). There is some information to suggest women may obtain an equal or greater benefit by choosing a partner whose resources are considerable enough to support multiple mateships (Buss and Shackelford 1997).

Both sexes may engage in behaviors meant specifically to incite jealousy in their partner, known as *jealousy induction*. The most common methods of induction are flirting with members of the opposite sex, making comparisons to past relationships, and infidelity. It is reported, by both men and women, that the goal of such acts is to increase the security of their relationship and retain their chosen mate by increasing their motivation to protect that mate (Mattingly et al. 2012; Wegner et al. 2018).

Jealousy can sometimes lead to positive outcomes, such as signaling partner investment, but there is also a significant risk of negative outcomes, such as abuse, physical violence, and even homicide. It has been found that sexual jealousy is the

leading cause of violence among romantic partners, and sexual jealousy in men is the primary motivation behind physical violence like homicide. Psychological mechanisms associated with emotional and sexual jealousy sometimes malfunction, leading to pathological jealousy (see ► [“Jealousy: Psychiatric Diagnosis”](#)).

Siblings

Jealousy also provided an adaptive function for sibling relationships. Jealousy is triggered when exclusive access to parents is threatened by a new sibling who also wants exclusive access (Buunk and Bringle 1987; Hart 2018). According to Trivers (1974), jealousy between siblings can be attributed to discrepancies over how parent resources are directed. Since parental resources are limited, especially in ancestral environments, conflict arises when there is a change in how those resources are allocated. This conflict is particularly prevalent when a child is first introduced to a new sibling. The firstborn child risks a reduction in access to its mother's breast milk or a premature weaning in order to accommodate the new sibling. Reducing intake by sharing food and nutritional resources would have increased the chance of death, and so protecting exclusive access to those resources would have been adaptive for children and infants (Hart 2016a, b, 2018). Supporting this view, shorter intervals between births increase the likelihood of infant mortality. If a new sibling was born within a time period of 2 years, the risk of death for infants increases by up to 50%. The US Agency for International Development, whose work assists in assessing infant mortality and health, has even suggested parents try to restrict birth intervals to 3 to 5 years and 2 years at minimum (Berg and Brems 1989; Conde-Agudelo et al. 2012; Fotso et al. 2013; Thapa et al. 1988; United States Agency for International Development 2002).

Rivals

Jealousy may occur in other contexts, such as professional, occupational, and social relationships.

According to Buunk et al. (2010), jealousy in professional environments may be a response to intrasexual competition. For example, since women prefer men who have greater resources, status, and physically and socially dominant characteristics, men compete with one another in these domains. Meanwhile, women compete in domains involving physical appearance (Buunk et al. 2010; Campbell 2004). Therefore, high status and physical dominance invoke jealousy between men, whereas traits relating to appearance would invoke jealousy between women.

There are several lines of research to suggest that jealousy occurs between rivals over social communal qualities (i.e., interpersonal skills in groups), because those who are adept at such skills may threaten other people's inclusion in a group or may deny their advancement and promotion within a group. We place importance on our status in occupational settings because inclusion and status in a group have significant benefits. Individuals may seek to protect relationships with supervisors because supervisors make decisions about employee status. Jealousy is invoked when an individual believes a rival has more desirable characteristics or performs in ways that are viewed more favorable by a supervisor.

Jealous reactions in these contexts lead to various actions, including gossip, which is used as a potential source of damage to inclusion, status, or advancement a group, potentially enhancing one's own opportunity for advancement (Buunk et al. 2010; Buunk and Dijkstra 2015; Leary 1990; Zurriaga et al. 2018). Studies also suggest that these phenomena are found cross-culturally. In Dutch, Argentinian, and Kurdish samples, all groups were found to be primarily concerned and jealous toward rival characteristics, with men reporting jealousy toward social power and physical dominance, whereas women reported on feelings of jealousy directed at physical attractiveness (Buunk et al. 2010; Buunk 2015).

Friends and Peers

Being part of a social group increases the likelihood of survival due to the protective, psychological, and

material benefits of group membership. Protecting these relationships from external threats would serve to increase one's fitness; therefore, jealousy can function to protect group relationships, like friendships (Hill 1987; Hill and Davis 2000; Leary 1990). While friendships do not carry the same fitness benefits as do sexual relationships, they may help with solving other adaptive problems, such as acquisition of food, shelter, and introduction to potential mates. Bleske and Buss (2000) found that friendships also provided a psychological outlet, a boost self-esteem or self-worth, and insight into members of the opposite sex.

People also experience jealousy of opposite sex friends because it seems as they are viewed as potential mating partners and sources of sexual contact (Bleske and Buss 2000). Both men and women display regular attraction to opposite sex friends, with men reporting slightly higher levels of attraction than women. Women also showed a greater distinction between sexual relationships and opposite sex friendships. However, these friendships were generally found to be kept separate from one another for both sexes (Kaplan and Keys 1997; Sapadin 1988). Since these friendships sometimes lead to possible mateships, it would make sense that protecting access to these friends would be adaptive; thus jealousy serves the purpose keeping access to potential mates through friends.

Limitations to Jealousy Research

There are several limitations to research on jealousy. For example, a number of studies exploring distress responses in men and women toward emotional and sexual infidelity rely heavily on imagined scenarios, and while some have used physiological measures such as electrodermal activity and heart rate, there still remains a gap in the literature on this subject (Buss 1992, 1995). Furthermore, much of the current body of evolutionary research relies on individuals from samples of undergraduate students who may not have as strong a need for mate retention and guarding compared to older adults in committed relationships (Buss and Shackelford 1997). Despite the

vast amount of effort dedicated to understanding the differences between the two sexes on the activation and function of jealousy and how they react, there is little explanation on jealousy among same-sex samples, variability of jealousy within each sex, and how cultural variation may impact variation in jealousy. For example, in Kurdish samples, there was a surprising lack of difference between men and women on the scenarios and rival qualities that would evoke jealousy and competition (Wiederman and Kendall 1999; Buunk 2015). Furthermore, much of the research relies heavily on self-report measures which introduces response and reporting biases (Buss 1988), focuses on emotional and sexual jealousy, and pays little attention to jealousy between siblings, friends, and co-workers.

Conclusion

There is a fairly large literature supporting jealousy as an adaptation in response to threats to social relationships. More specifically, there is support for jealousy functioning as a mechanism to protect valued, usually sexual, relationships. Theoretical and empirical work have focused on intimate relationships and are mostly based on self-report assessments. Future work in this area would benefit from considering jealousy in other contexts, such as between siblings, friends, and co-workers.

Cross-References

- [Emotional Jealousy](#)
- [Jealousy: Developmental Trajectory](#)
- [Jealousy: Psychiatric Diagnosis](#)
- [Morbid Jealousy](#)
- [Sex Differences in Morbid Jealousy](#)
- [Sexual Jealousy in Long-Term Relationships](#)

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Jealousy and Infidelity

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Synonyms

Emotional jealousy; Emotional unfaithfulness; Extradyadic involvement; Sexual jealousy; Sexual unfaithfulness; Unfaithfulness

Definition

Infidelity is defined as unfaithfulness to a primary partner, which can take the form of a sexual and/or emotional extradyadic involvement with another person. Jealousy is explained as a reaction to threat to the relationship, reaction to loss of a partner, or response to a degradation of relationship’s individual values. This reaction can be triggered by real and/or potential rival.

Introduction

In various studies, infidelity has been related to disintegration of relationships across different cultures and societies. It has also been identified as one of the most common divorce predictors in the world (Hall and Fincham 2006). In general, infidelity tends to evoke strong feelings of jealousy. Evolutionary psychology distinguishes between sexual and emotional jealousy and infidelity. Emotional jealousy focuses on partner’s real or potential emotional involvement with a third person, while sexual jealousy is elicited by partner’s real or potential extra-pair sexual relations.

It has been claimed these two types of jealousy evolved in part due to selective pressures, namely as a response to sex-specific problems linked to reproduction. In humans, although there exists significant paternal care, minimum women's investments into reproduction are considerably higher than men's (pregnancy, childbirth, lactation, childcare, and protection), while male contribution can be minimal, in the form of sexual act. In the case of woman's sexual infidelity, the primary partner risks investing his resources in offspring who may not be genetically related to him, resulting in a loss of his reproductive success. Men thus face the adaptive problem of paternity uncertainty. Nevertheless, recent research shows that greater sexual jealousy in men may be driven by fears of loss of paternity opportunities more than by paternity uncertainty (Edlund et al. 2019). Women, on the other hand, in case of men's emotional infidelity are at risk of loss of time, resources, and partner commitment. Women therefore tend to prefer men with whom they can form an emotional connection and who can provide them with sources that increase the survival chances of their offspring. As a result, jealousy develops as an adaptive mechanism in both men and women who perceive threat to their reproductive success and it motivates behavior aimed at reducing that threat (Buss et al. 1992).

A considerable body of evidence suggests that while the magnitude of sex differences can vary, the existence of sex differences in jealousy is culturally universal (e.g., Harris 2002). In particular, women tend to feel more threatened by partner's emotional involvement, while men tend to respond more to a sexual threat (e.g., Buss et al. 1992; Edlund and Sagarin 2017; Harris 2002; Sagarin et al. 2012). In general, it has been argued that jealousy has three main aims: (1) it warns individuals about threats to a relationship, (2) alerts to possible same-sex competitors, and (3) prevents partner infidelity and relationship abandonment by modification of one's own behavior.

Jealousy

Although there are many different definitions of jealousy in romantic relationships, all agree on

viewing it as a reaction to the relationship being compromised. One of the basic definitions describes jealousy as one of the most common automatic responses to a threat posed by a third party (Buunk 1997; Dijkstra and Buunk 2001). The perception of threat arises from suspicion of actual or potential affection between one's partner and a rival (Dijkstra and Buunk 2001).

My Sex, Partner's Sex, or Rival's Sex: Three Main Explanations of Differences in Sexual/Emotional Jealousy

In studying jealousy from an evolutionary perspective, three main explanations of differences between men and women in their experience of sexual/emotional jealousy have been proposed. The first explanation, mentioned above, suggests that the type of jealousy depends on an individual's biological sex.

A pioneering study in this area was conducted by David Buss and his colleagues (1992). They used a forced-choice design where respondents were supposed to imagine their partner being interested in another person and asked to specify whether they would feel more upset by the idea of their partner falling in love with another person or by partner's sexual involvement with someone else. The results showed that 60% of men would be more upset by sexual infidelity, while only 17% of women chose sexual infidelity as the worse scenario. Regarding emotional infidelity, 83% of women and 40% of men chose it as being the worst case. Numerous other studies produced similar results. The forced choice method leads to relatively clear and easily repeatable results which seem to correspond to sex differences in response to jealousy stimuli (Carpenter 2012).

Some recent studies, on the other hand, work with the assumption that jealousy depends on partner's biological sex (e.g., Harris 2002). Specifically, several studies on homosexual individuals show that homosexual men tend to feel more anxious about the idea of partner's emotional infidelity and homosexual women about the idea of sexual infidelity of their partners. This seems to support the hypothesis that sexual/emotional jealousy depends on the biological sex of one's partner. The authors explain this finding by the fact that even though homosexuality and

homosexual behavior does not lead to direct reproduction of an individual, the mechanism of sexual selection will work in a similar way in homosexual men and women as in heterosexual individuals (Lippa 2007). In this case, the type of sexual/emotional jealousy would depend purely on the partner's biological sex, and sexual orientation should not play any role.

A third possible explanation of differences in experiencing sexual/emotional jealousy suggests that these different types are linked not to partner's biological sex, but rather to the potential rival's biological sex. Sagarin et al. (2012) showed that sex differences are present only in heterosexual individuals when they imagine their partner's infidelity with a person of the opposite sex who is reproductively compatible (similarly Frederick and Fales 2016; Sheets and Wolfe 2001).

Infidelity

There are many different definitions of infidelity, ranging from those limited to defining dichotomous sexual/emotional infidelity to those giving concrete accounts of activities which fall under the term infidelity (Brand et al. 2007). Recent literature often distinguishes between *sexual infidelity*, i.e., extradyadic sexual behavior without emotional involvement, and *emotional infidelity*, which refers to romantic feelings without sexual involvement to a person other than the primary partner. This typology does not exclude the possibility of these infidelities occurring simultaneously. Infidelity thus cannot be defined as a phenomenon or condition that has in all cases certain objectively existing characteristics. It seems therefore that from the perspective of the person who is cheated on, infidelity falls into the category of a subjective experience (Luo et al. 2010).

According to Luo et al. (2010), most studies do not offer a comprehensive definition of extradyadic behavior. The issue of different types of infidelity, i.e., what infidelity is and what it is not, and responses to them is difficult to grasp in quantitative studies, since the typologies presented cannot consider everything a person

could think of as infidelity and cannot take into account all possible reactions to infidelity in real life.

Definitions of infidelity commonly applied in research can be grouped into three broad categories: infidelity as sexual intercourse, infidelity as extradyadic sexual activity, and infidelity as emotional betrayal (Moller and Vossler 2015).

Infidelity as Sexual Intercourse

The definition of infidelity as having sexual intercourse with a person other than the primary partner is commonly used by large studies on the prevalence of infidelity (Whisman et al. 2007). This definition, however, fails to capture the experience of people who are involved in other than traditional exclusive relationships, for instance, open-relationship couples, such as polyamoric relationships, swinging couples, or some homosexual individuals (Moller and Vossler 2015). The definition also seems to assume that sexual intercourse has one generally understood meaning, while research shows that the meaning associated with expressions of sexuality depends on various factors, including context and culture.

Infidelity as Extradyadic Sexual Activity

Contrary to the previous definition, infidelity is understood not only as sexual intercourse with a other person than the partner, but also as other extradyadic activities. In previous studies on extradyadic behavior, all of the following has been classified as infidelity: masturbation in the presence of another person, oral sex, engaging in sex games, kissing, flirting, visiting strip clubs, watching pornography, and sexual fantasy about a person other than the primary partner. Furthermore, internet behavior that can be defined as sexual infidelity includes cybersex, the exchange of one's own sexual photos, online dating, online flirting, and the use of online pornography (Whitty 2003).

Infidelity as Emotional Betrayal

Emotional infidelity has been defined variously, for instance, as falling in love with another person or deep emotional attachment to another person, investment and dedication of love, time, and attention to a person other than primary partner,

or sharing confidential information (Luo et al. 2010).

This overview of the definitions used in various studies highlights the absence of a consistent definition of partner infidelity (Moller and Vossler 2015). Existing inconsistency in research definitions leads to significant differences in reported prevalence of infidelity, with lifetime prevalence ranging between 1.2% and 85.5% (Luo et al. 2010).

Prevalence of Infidelity

In general, it is believed that if an individual is in a long-term relationship, sex and intimate intercourse will be limited solely to the primary partner. Although previous research shows that infidelity is considered immoral, unethical, and unacceptable in the United States (Boekhout et al. 2003), statistics show that 2–4% of the population commit it annually (Treas and Giesen 2000; Whisman et al. 2007). A recent meta-analysis of 50 studies had shown that 34% of men and 24% of women have engaged in extra-marital sexual activities (Tafoya and Spitzberg 2007).

Although one can find cultural differences in the prevalence of infidelity, one type of infidelity is universal, namely *mate poaching*, meaning the effort to attract a person who is already involved in a different short- or long-term relationship (Schmitt 2004). According to Schmitt (2004), 70% of individuals have encountered someone who tried to poach them, while 60% of men and 40% of women admitted to trying to poach someone else's partner. To prevent mate poaching, there evolved an adaptation for *mate guarding*, i.e., the behavioral strategies used to ensure romantic partner's fidelity. Mate-guarding behavior can vary and range from vigilance to violence. Its main trigger seems to be sexual jealousy (Buss et al. 1992).

Correlates of Infidelity and Jealousy

Different and inconsistent results of studies on jealousy and infidelity may be due to various

definitions of romantic jealousy and infidelity and/or by the complexity of individual and relational factors which influence the experience of jealousy and infidelity.

Individual Factors

A large body of evidence associates sex with infidelity, especially in men. Some studies show that men tend to be the ones who commit sexual infidelity in long-term partnerships/marriages, and who also more frequently engage in online infidelity (Luo et al. 2010). Moreover, according to Boekhout et al. (2003), men are better at separating sexuality from love. More recent studies, however, show that differences in the prevalence of reported infidelity between men and women are diminishing (Brand et al. 2007). According to Whisman et al. (2007), men and women under the age of 45 report identical rates of extradyadic behavior but reasons for committing infidelity differ between the sexes. Men are more likely to seek sexual diversity, while women often resort to sexual infidelity as a way of acquiring a new romantic partner. Women who are unhappy in a partnership are more likely to commit infidelity and select partners who appreciate their attractiveness and make them happier (Brand et al. 2007).

Other commonly studied factors that can influence the experience of jealousy and infidelity are personality traits. Research indicates that jealous people show high levels of neuroticism, hostility, and social anxiety, which points to an anxious-ambivalent attachment style that is also associated with higher levels of jealousy (Buunk 1997).

Mate value discrepancy (MVD) is another factor that tends to be associated with forgiveness in romantic relationships. In particular, persons who perceive their partner's *mate value* as higher than their own are more likely to forgive their partner's indiscretions. Furthermore, the higher the value of the partner, the more likely it is that the lower-value partner experiences jealousy (Sidelinger and Booth-Butterfield 2007).

Qualities of the potential rival can influence the experience of romantic jealousy. Persons who perceive someone as a rival try to assess the threat such rival poses to the relationship by comparing rival's qualities to their own, by comparing qualities which are of importance to the romantic

partner, and by assessing how much of a threat the rival poses to the relationship and their self-esteem (Dijkstra and Buunk 2001). According to some studies (e.g., Massar et al. 2009), jealousy in men is caused mainly by rival's characteristics which are related to status. This is explained by the fact that in long-term relationships, women particularly value social status. Men are therefore are jealous of rivals whose socioeconomic status is higher than their own. Moreover, Massar et al. (2009) showed that a higher socioeconomic status is related to height, which is also why men are more prone to being jealous of higher rivals. In women, jealousy is elicited mainly by physically attractive rivals (in terms of body curves and facial features). This is because men tend to be attracted to young and physically attractive women, in other words to qualities that indicate women's fertility. A more attractive rival can therefore pose a more serious threat.

Another important factors related to infidelity are sociodemographic characteristics, such as the place and region of residence. Some studies indicate that persons living in large urban areas are more likely to engage in some form of extradyadic behavior than persons who live in rural areas (Treas and Giesen 2000). Thus, infidelity is also often seasonal: most frequent extradyadic behavior takes place in the summer, mainly because it is a travel-related time of the year. Travel offers opportunities for engaging in extradyadic sex away from one's place of residence, thus reducing the likelihood of being discovered (Adamopoulou 2013). There is no consensus on how religion and beliefs influence the occurrence of extradyadic behavior (Liu 2000; Martins et al. 2014). The relationship between the level of education and tendency to commit extradyadic behavior is also not unclear. Some studies suggest that more educated individuals tend to cheat more (e.g., Treas and Giesen 2000). Other studies, however, do not confirm this correlation (e.g., Martins et al. 2014).

Another important individual factor is sociosexual orientation. Research suggests that although people have generally negative attitudes towards infidelity, many commit it. It also seems that the higher the tolerance of individuals to the notion of infidelity is, the greater the chance to engage in extradyadic behavior in future (Liu

2000). Previous experience with engaging in infidelity has been repeatedly proven to be a significant predictor of extradyadic behavior in future (Adamopoulou 2013). In a study by Rodrigues et al. (2017), individuals who had experience with sexual infidelity had higher sociosexual desire, were less engaged in their primary relationship, and were more tolerant of various forms of infidelity. This study also found a complementary correlation, namely that individuals who had no experience with sexual infidelity were more involved in the relationship and had stricter views on infidelity.

Relationship Factors

Another possible explanation for infidelity is the *investment model* (Rusbult 1983). According to this model, three factors form the key components of romantic relationships: satisfaction in the relationship, investment in the relationship, and alternative options one may have. People who are satisfied in their relationship, had invested in their relationship, and are not aware of better alternatives are more likely to be highly committed to the relationship and therefore less prone to extradyadic behavior (VanderDrift et al. 2012). A correlation between infidelity and relationship quality has been found especially in marriages and partnerships of long duration where partners share households. It has been found that when such relationships become stereotypical and marital/partner benefits (e.g. sexual intercourse) become less frequent (Traent et al., 2007), and/or individuals experience lower relationship satisfaction, respondents list it as one of the main extradyadic motivators (Maddox Shaw, Rhoades, Allen, Stanley & Markman, 2013). In women, both married and cohabiting ones, some studies claim that the longer they are in a relationship, the more likely they are to engage in some form of extradyadic behavior (Træen et al. 2007).

Conclusion

Evolutionary psychology makes a distinction between sexual and emotional jealousy. Numerous studies found that there are differences between men and women with respect to these

two types of jealousy. Explanations of this phenomenon point to different reproduction investment in men and women and threats that arise from this disproportion. In general, men tend to be more distressed by the idea of sexual infidelity, whereas women tend to be more distressed by emotional infidelity. The idea of a strict correlation between one's sex and the type of jealousy has, however, been under some criticism. Varying and inconsistent results and explanations seem to point to numerous problems related to methodology and data analysis. Most quantitative studies which focus on jealousy experience neglect the wider context. For example, they do not take into account the incentives based on which respondents choose to answer. It may not be entirely clear whether they are comparing their priorities within the current relationship, past relationships, or base their responses on a purely hypothetical situation. According to some studies, answers may be influenced by the length of the relationship (e.g., Davis et al. 2018), but other studies do not confirm this result (e.g., Frederick and Fales 2016). Another problematic factor may be the choice of the research method itself. Results may vary depending on whether a quantitative or qualitative method of data collection is used. Carpenter's meta-analysis (2012) of 54 articles about the experience of sexual/emotional jealousy indicates that in general, the results were not fully consistent with the evolutionary explanation. Specifically, Carpenter's analysis had shown that when forced-choice measure was applied, both men and women were more likely to identify emotional infidelity as the worse option. When, however, a continuous scale was used, both sexes reported sexual infidelity as being more upsetting. Nevertheless, a recent review of different methodologies used to study romantic jealousy and other meta-analyses confirmed sex-specific differences in experiencing sexual/emotional jealousy (Edlund and Sagarin 2017).

There are various definitions on romantic jealousy and infidelity, and they lead to different figures on the prevalence of extradyadic behavior. This is exemplified, for instance, by a study of Brand et al. (2007) whose results indicate a similar prevalence of sexual infidelity in both sexes.

Another factor which influences the experience of jealousy and the likelihood of engaging in extradyadic behavior are cultural aspects. According to some studies, jealousy is culturally conditioned and sex differences are based on sex-specific socialization, which affects the perception of various jealous stimuli (Sheets and Wolfe 2001). As described above, motivators of infidelity differ between the sexes, while individual and relational factors are a crucial component of the jealousy experience and of willingness to engage in extradyadic behavior and should be therefore considered in future research.

Cross-References

- ▶ [David Buss](#)
- ▶ [Emotional Jealousy](#)
- ▶ [Female Infidelity](#)
- ▶ [Frequency of Infidelity](#)
- ▶ [Personality and Mate poaching](#)
- ▶ [Sex Differences in Jealousy](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)
- ▶ [Sexual Jealousy](#)

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Jealousy: Developmental Trajectory

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Introduction

Jealousy typically refers to an emotional response that occurs when an interpersonal relationship is impacted by another person (Campos et al. 2010). This experience may be adaptive because it provides an alert of potential threats to an intimate relationship that would impact fitness (Campos et al. 2010). Jealousy can also function by protecting social relationships that enhance fitness at particular points in an individual's life

(Dillon 2013). The recognition of a potential rival triggers both negative affect and overt behaviors, such as imitation of the rival, aggression toward the rival, and attempts to redirect a loved one's attention to oneself (Dillon 2013). The developmental trajectory of jealousy is not well-researched; however, cross-sectional research shows how jealousy is manifested during different periods of development.

Jealousy in Infancy

There is conflicting opinion around the capacity for an infant to experience and express jealousy because scholars disagree on whether infantile emotional experience is limited to basic emotions such as joy, fear, sadness, anger, distaste, surprise, and possibly pride and shame (Campos et al. 2010). It is unclear how much social awareness is required to experience jealousy. Research examining jealousy in the first year of life may oversimplify the construct, and behavioral demonstrations of jealousy are not well differentiated from other possible emotional experiences.

Early in human development, survival depends on parental investment. Infants have a high level of dependency on a caregiver, typically the mother. Parental investment is reduced if there are siblings, thus, Dillon (2013) suggested that infants may exhibit jealous behavior to direct parental care away from their siblings and onto themselves. Jealousy is not limited to mothers attending to siblings but also to mothers attending to other social rivals (Mize and Jones 2012). It is difficult to ascertain whether infants are exhibiting jealousy or if they are expressing some other emotional indicator (Campos et al. 2010). However, studies have identified observable behavior patterns presumed to be the response to feelings of jealousy, due to the context of the behaviors (see Dillon 2013; Hart 2010).

Early research on infant responses to loss of maternal attention has found that infants tend to exhibit approach behaviors and negative affect more so when the loss of attention is to a rival. Mize and Jones (2012) found that infants ages 11–14.5 months old gazed more toward the

mother, stayed closer, and had more physical contact in the presence of a social rival (i.e., life-like doll). The infants also exhibited more anxiety and aggression, as well as negative affect and vocalizations. If negative vocalizations did not regain the attention of the mother, the infants would switch to positive vocalizations. Attempts to regain the attention of the mother in social rival conditions, but not conditions where the loss of maternal attention is to a nonthreatening object, suggests infants attempt to protect maternal attention when they perceive a social threat. This study replicated results from previous studies, suggesting it is a robust effect (Hart and Carrington 2002; Hart et al. 1998).

Infant jealousy may still be adaptive in modern environments. While resources in general are not as scarce as they were in ancestral environments, child mortality rates are still consistently affected by birth spacing and maternal fertility (Hart 2010). Particularly in developing countries, close age spacing of children contributes to early termination of breastfeeding (Hart 2010). Children born within 2 years of a previous birth are twice as likely to die (Hart 2010). Termination of breastfeeding prior to the first year of life also increases the risk of death, compared to those who continue breastfeeding (Hart 2010). Jealous responses in infants appear to have a survival function because it emerges in response to a valid threat of a peer or sibling, not nonthreatening stimuli such as inanimate objects or other adults. Parental investment is still necessary for infant survival, and even in modern times, factors such as breastfeeding can be impacted by sibling competition.

Jealousy in Childhood and Early Adolescence

Similar to infancy, children and adolescents compete with their siblings for parental investment. In ancestral environments, resources were scarce, and so parental investment in one child could have posed a threat to the survival of another (Hart 2010). Thus, if a mother were to pay more attention to one child, it would be adaptive for a sibling

to redirect her attention to oneself. Jealousy would evoke behavioral displays to meet the goal of regaining the attention of the primary caregiver in order to secure the resources needed to promote survival (Hart 2010). In childhood, attaining more resources for oneself by means of competition contributes to survival and eventual reproductive success (Weisfeld and Woodward 2004).

Research on jealousy in early and mid-childhood is also limited. Many studies focus on negative features of the sibling relationship, such as conflict or aggression, which may be the consequence of jealousy, but this distinction is not clear (Volling et al. 2010). Many studies on childhood jealousy are observational, where jealousy is inferred from actions. For example, Volling et al. (2010) examined displays of jealousy in siblings ages 4–6 and in toddlers at age 2 by manipulating how much time parents had with both the toddler and the child, alternating direct interaction and attention to one child for three minutes (involved condition) while the other child was encouraged to go play independently (challenged condition). They found that both the toddler and the child exhibited significantly more negative affect and less positive affect when in the challenged condition in both the sibling-mother and sibling-father trials. Toddlers were found to exhibit two types of behavior, interference and seeking comfort, when in the challenged condition. Older children exhibited these same behaviors and attention seeking. Volling et al. (2010) suggested that attention seeking is more sophisticated at distracting parents than physically pushing oneself between the parent and rival sibling, as a toddler would do. As children get older, jealousy is still a response to a “rival” sibling, but methods of regaining attention to oneself become more refined and effective.

In addition to sibling jealousy, children exhibit jealousy in the context of friendships (see Dillon 2013, for a more exhaustive review). Jealousy is observed when a friend interacts positively with another child, or when there are perceived inequalities within the friendship, leading to behaviors to regain the favor of the friend or ultimately terminate the friendship. Parker et al. (2010) posited that jealousy may arise because the

actions of the friend infer that the person is not socially desirable and is being rejected by the “unfaithful” friend. Sex differences in relationship jealousy have been identified. Girls are more prone to friendship jealousy, presumably because girls tend to have fewer, more intimate friendships, and boys tend to establish a social hierarchy in the context of a larger peer group.

In early to mid-adolescence, sexual competition emerges due to sexual maturity. Individuals with a higher social status have more reproductive success, and so achieving and maintaining this status is important. de Bruyn et al. (2012) found that sexually precocious middle adolescents were more popular, attractive, and aggressive. A threat to an individual’s social status by a rival could evoke jealousy, a possible driving force behind physical aggression among male and relational aggression among female adolescents. By showing off their strength and dominance through behaviors such as bullying, adolescent boys could intimidate their rivals and reduce the rival’s reproductive success. Adolescent females have more of a tendency to lower a rival’s status through use of relational aggression and hurting the reputation of rivals, thus decreasing their reproductive success (de Bruyn et al. 2012). This study does not examine jealousy specifically; however, there is recognition that an individual perceiving a threat from a rival elicits behaviors that decrease the status of a rival, and increase the individual’s reputation and appearance of being reproductively superior.

Jealousy in Late Adolescence and Adulthood

In late adolescence into adulthood, the function of jealousy increasingly changes from protecting parental and peer attention and resources to guarding one’s own reproductive success (Dillon 2013). Research on early to mid-adulthood jealousy has been more prolific. Displays of sexual and emotional jealousy are more pronounced during early to mid-adulthood because of its function of alerting one to the threat of a mating rival. There is competition in both attaining and then

retaining a desired mate, as well as ensuring fidelity. In humans, adulthood typically marks a period of establishing long-term mateships and cooperatively raising offspring. Sexual jealousy in this context exists when there are potential threats to extra-pair mating. Sexual jealousy alerts an individual to the presence of an interloper and triggers the use of tactics to secure or maintain sexual exclusivity with a partner.

An evolutionary framework posits that there are sex differences in jealousy due to different types of infidelity uniquely impacting male and female reproductive fitness (Sagarin et al. 2003). When alerted to the threat of a rival, males are likely to be more jealous of sexual infidelity, due to risks of paternity uncertainty, leading to potential investment of resources into someone else's offspring (i.e., cuckoldry risk). Conversely, females are likely to experience more jealousy around emotional infidelity because emotional investment in a rival female could lead to resources being diverted from her offspring to the offspring of a rival (Sagarin et al. 2003).

Shackelford et al. (2004) proposed that one way to look at the effect of age on jealousy was to determine if sex differences in jealousy from a young sample of young adults are also found in older adult samples. When female partners reach menopause, sexual infidelity no longer poses cuckoldry risk to the male, suggesting there should not be as large of a sex differences in sexual jealousy. For older women with children in adulthood, the effect of emotional infidelity would not be as significant because resources for dependent children are no longer needed. Shackelford confirmed sex differences were still found in the older sample of older adults, but that the magnitude of the difference decreased. Interestingly, older women were less likely to choose a partner's emotional infidelity as more upsetting than sexual infidelity, contrary to younger women.

Jealousy in the context of a romantic relationship can be detrimental because it evokes negative feelings of anger, fear, and sadness. However, it can also be argued that experiencing jealousy can enhance commitment to a relationship, and so inducing jealousy can help to achieve relationship goals (Wade and Weinstein

2011). By fostering doubt regarding one's commitment to their partner, jealousy can be induced to help preserve the existing bond and fend off interlopers.

Jealousy in Late Adulthood

Research on the incidence and function of jealousy in late adulthood is limited, and so firm conclusions cannot be made. Some studies are now examining jealousy in late adulthood in terms of delusional jealousy associated with neuropathological disorders such as dementia (Hashimoto et al. 2015; Cipriani et al. 2012). Future research will need to control for the effects of neurological or mental health deterioration on jealousy.

Conclusion

Across the lifespan, jealousy serves as an important indicator of a threat to significant social relationships, prompting behaviors to divert a valued party's attention from a rival and back to oneself in order to maintain ongoing benefit from the relationship.

At the earliest stage of life, it is difficult if not impossible to determine if infants are experiencing jealousy or even capable of that specific emotion. However, observational research has repeatedly found that infants engage in behaviors to gain the attention of their caregivers when it is diverted to a sibling or another social threat. This suggests that jealousy may exist as one of human's earliest emotions, functioning as the emotional trigger to retain the attention of a caregiver.

As children age and become more independent, they still largely rely on parents to assist with their growth and survival. When parental attention is diverted to a rival sibling, efforts to regain the attention are triggered by feelings of jealousy. In this sense, jealousy functions in quite the same way as in infancy, but an older child's methods to gain and retain the attention of a caregiver become more sophisticated.

In later childhood and early adolescence, the function of jealousy appears to expand from the protection of caregiver attention for survival to also include the promotion of oneself as socially desirable. Jealousy again appears to be the alert of a threatening third party, but the threat is to a significant social relationship that is adding to the social status of the individual. Social desirability becomes more important in adolescence because reproductive success is contingent on social status. It can be argued that jealousy is the emotion that evokes the behaviors that attempt to diminish a rival's social status while strengthening one's own. Sex-specific forms of jealousy start to emerge at this age.

Once long-term relationships are pursued or established, typically in adulthood, jealousy's function is primarily to alert an individual about the threat of an interloper. For a male, the threat of sexual infidelity evokes more jealousy due to cuckoldry risk, whereas for females, jealousy is more prevalent when the threat of emotional infidelity is present. This is likely due to a female's reliance on the male for time and resources to contribute to their offspring, which could be diverted to the rival's offspring if the male was emotionally involved. Maintaining a partner's fidelity is reproductively important for both sexes throughout adulthood.

In later adulthood, a sex difference generally still exists but the magnitude of the difference decreases. Men still find sexual infidelity as more upsetting than emotional infidelity, but one difference is that post-menopausal females experience sexual infidelity as more threatening than emotional infidelity. The higher distress level in older women around sexual infidelity could be in response to the fact that their male partner is still able to reproduce and could do so with a woman with higher mate value. It would be interesting to see if an older woman's degree of jealousy around emotional versus sexual infidelity would differ depending on the perceived mate value and/or fertility of the threatening woman. Sexual infidelity with a younger female could be more threatening than emotional infidelity because pregnancy could lead to relationship defection and investment of resources in the new partner.

If the threat was from an older, postmenopausal woman no longer able to reproduce, perhaps emotional infidelity would still be perceived as more threatening. This could help to clarify if it is the age of the woman that is the source of jealousy or if it is the reproductive viability of the threat. More research on the function of jealousy in late adulthood is needed, controlling for the possible effects of organic brain disorders.

Cross-References

- [Jealousy](#)
- [Sexual Jealousy in Long-Term Relationships](#)

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Jealousy: Psychiatric Diagnosis

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Synonyms

Conjugal paranoia; Delusional disorder - jealous type; Morbid jealousy; Pathological jealousy; Othello syndrome

Introduction

Jealousy refers to an emotional response that emerges when an interpersonal relationship is impacted by another person. Jealousy is functional because it alerts individuals to the presence of a rival and motivates behavioral responses to minimize the impact of a rival on valued interpersonal relationships. For example, people become

jealous in response to partner infidelity, new members of social relationships, and parent-sibling interactions. However, some people experience jealousy in the absence of a threat or rival and maintain such beliefs even in the presence of disconfirming evidence (Cipriani et al. 2012). In these cases, jealousy is no longer functional because it can lead to expending energy and resources fending off a rival that does not exist (Kingham and Gordon 2004). In the context of intimate relationships, when jealousy is not based on a real threat and is persistent despite contrary evidence, it is known as *delusional jealousy* (similar constructs include *pathological jealousy*, *Othello syndrome*, *morbid jealousy*, *conjugal paranoia*) and is applied to sexual jealousy. There are no psychiatric disorders that encompass pathological jealousy between siblings, friends, or other non-intimate social relationships. A person afflicted with delusional jealousy interprets their partner's actions based on how they feel, and irrational thoughts about their assumptions being true initiates even more fear, rage, and insecurity (Seeman 2016). This form of jealousy may be characterized by an individual making unfounded accusations to their partner, demanding reassurances, wanting to know the thoughts of their partner, or spying (Seeman 2016).

Delusional jealousy is characterized by a range of irrational thoughts and extreme behavior in response to the belief that one's partner is being sexually unfaithful (Kingham and Gordon 2004) without reasonable or objective evidence (Easton et al. 2008). These individuals will continue to insist on the occurrence of infidelity, even if evidence to the contrary is presented (Kingham and Gordon 2004).

Delusional Disorder-Jealous Type

Delusional jealousy is not classified as a stand-alone disorder and is often considered a syndrome rather than a diagnosis (Kingham and Gordon 2004). A clinical diagnosis relevant to sexual jealousy is in the Diagnostic and Statistical Manual (DSM-5; American Psychiatric Association 2013) which includes diagnostic criteria for delusional

disorder-jealous type. The current criteria for delusional disorder includes: (1) having one or more delusions over the course of a month or longer; (2) does not meet criteria for schizophrenia; (3) a person is not necessarily severely impaired or oddly behaved; (4) if person also presents mania or depression, their duration must be less than the duration of delusions; (5) symptoms are not due to other physiological issues or use of substances and cannot be better explained by another diagnosis. In addition to the general diagnosis, the DSM-5 (APA 2013) uses specifiers to identify the central theme of the delusions being experienced. These include Erotomantic type, Grandiose type, Jealous type, Persecutory type, and Somatic type, Mixed type, or Unspecified type. Diagnoses also specify if there is bizarre content, and after a year's duration of the disorder, the number of episodes a person has experienced must be identified, in addition to the current state of their episode (acute, in partial remission, or in full remission). While not necessary for diagnosis, there is also a severity specifier to note the frequency of symptoms (APA 2013).

The subtype of delusional disorder, *jealous type* is applied when the central theme of an individual's delusion is that his or her spouse or lover is unfaithful. The belief of infidelity is without due cause, based on incorrect interpretations of small bits of evidence. The delusional individual often confronts the partner and attempts to intervene in the imagined infidelity (APA 2013). A problem with the DSM-5 criteria regarding sexual jealousy pathology is an over-emphasis on delusions, which does not account for other types of sexual jealousy such as Othello syndrome, morbid jealousy, or conjugal paranoia. This lack of differentiation leaves it unclear if these represent different types of sexual jealousy or if they are part of a broader category of jealousy-related disorders (Easton et al. 2008).

Prevalence of Delusional Disorder-Jealous Type

Delusional disorder-jealous type is considered the "purest" diagnosis of delusional jealousy,

because it is not accompanied by additional psychopathology (Kingham and Gordon 2004). The APA (2013) estimates that the lifetime prevalence of delusional disorder is about 0.02%; however, the estimated prevalence of jealous type specifically is not noted.

Easton et al. (2008) studied case histories that included delusional jealousy and alternative titles that are often used to indicate the same disorder (morbid jealousy, pathological jealousy, conjugal paranoia, and Othello syndrome). All 398 case histories reviewed included some form of morbid jealousy, and 283 of these experienced delusions around partner infidelity for over 1 month. This is the first and most relevant DSM diagnostic criterion for delusional disorder-jealous type. Easton et al. (2008) identified the frequencies of the cases that matched each individual DSM-IV-TR diagnostic criteria for delusional disorder-jealous type, and then ultimately the frequency of cases that met all five of the criteria among psychiatric patients with delusional jealousy. Of the 398 case histories, it was determined only 16 (4%) of cases met all five DSM-IV-TR diagnostic criteria and were thus determined to have delusional disorder-jealousy type (Easton et al. 2008).

The Easton et al. (2008) study elucidates an important point, that individuals who experience delusional jealousy can meet some of the criteria of delusional disorder-jealous type but not enough to earn the diagnosis. Also, considering that only 4% of the jealousy-pathology cases reviewed met all criteria for delusional disorder-jealous type, it is possible that the current criteria are not inclusive enough to capture other jealousy pathologies (Easton et al. 2008).

Soyka and Schmidt (2011) analyzed case histories from 2000–2008 at a psychiatric inpatient facility in Germany. Seventy-two of 14,309 case histories were found to have delusional jealousy, with delusional disorders accounting for 11.1% of these cases specifically (Soyka and Schmidt 2011). This study did not separate delusional disorder-jealous type from other typologies, thus the relative frequency cannot be determined. The case histories analyzed in this study all had psychiatric diagnoses, so in the other 88.9% of cases,

delusional jealousy was attributed to another mental disorder (Soyka and Schmidt 2011).

Other DSM-5 Diagnoses

In the DSM-5, there are psychiatric diagnoses that are comorbid with jealousy. Depression can accompany delusions of infidelity that stem from feeling inadequate in the context of a romantic relationship, though it is unclear if the depression leads to the delusions or is a result of them (Kingham and Gordon 2004). In Easton's (2008) sample which had some form of pathological jealousy, 309 of the 398 cases reviewed were determined to have some type of psychological disorder, 40 (12.9%) of which were diagnosed with depression, making it the second most common psychological disorder in which pathological jealousy was present. The case analysis conducted by Soyka and Schmidt (2011) did not examine depression specifically but found that mood disorders (as diagnosed by the ICD-10) accounted for 19.4% of cases identified as having delusional jealousy. To distinguish the cause of delusions in these cases, it is important to review the chronology of the mood disturbance, the delusions, and the severity of mood symptoms (APA 2013). If delusions are only present in a depressive or bipolar disorder during a mood episode, the primary diagnosis would be that particular mood disorder (i.e., "bipolar disorder psychotic features" would be added as a specifier to explain delusional jealousy as being present during an episode; APA 2013).

Soyka and Schmidt (2011) found that the highest prevalence of delusional jealousy occurred in patients diagnosed with a psychotic disorder, and Easton et al. (2008) found that 27 of 309 cases with delusional jealousy also had an official diagnosis of schizophrenia/paranoid schizophrenia. Delusions of infidelity may arise as a component of schizophrenia, in the form of persecutory delusions experienced during psychosis (Kingham and Gordon 2004). However, the bizarre associations that are characteristic of schizophrenia are not necessarily focused on sexual infidelity, and these individuals experience other unrelated symptoms of

psychosis. Individuals with delusional disorder-jealous type do not describe bizarre associations, but coherent descriptions of plausible situations in which their partner is being unfaithful (Kingham and Gordon 2004). The DSM-5 confirms that individuals diagnosed with delusional disorder will not exhibit symptoms characteristic of schizophrenia, such as "prominent auditory or visual hallucinations, disorganized speech, grossly disorganized or catatonic behavior, or negative symptoms" (p. 104).

Organic brain disorders can also lead to delusional jealousy. In fact, delusional jealousy has been found to occur most frequently in patients with neurological disorders (Graff-Radford et al. 2012). At least 30% of cases with a delusion of infidelity can be linked to some form of neurological condition (Cipriani et al. 2012). For example, delusional jealousy is not uncommon in different forms of dementia, such as Alzheimer's disease (Tsai et al. 1997; Cipriani et al. 2012).

In their analysis of clinical and imaging features, Graff-Radford et al. (2012) found that of the 105 patients that met criteria delusional jealousy, 73 met criteria for a neurological disorder. Neurodegenerative disorders accounted for 76.7% of these neurological disorders, most commonly Alzheimer's disease, Lewy body disease, and a behavioral variant of frontotemporal dementia (Graff-Radford et al. 2012). Compared to matched neurodegenerative patients without delusional jealousy, those with it exhibited greater grey matter loss predominantly in the dorsolateral frontal lobes of the brain. Graff-Radford et al.'s (2012) main finding was that delusional jealousy is found in a variety disorders often related to frontal lobe dysfunction and/or damage.

An individual with a neurocognitive disorder may present with the same symptoms identified in delusional disorder-jealous type. As with mood disorders, it is important to review the chronology of the onset or exacerbation of delusional jealousy to see if it parallels the course of the neurological disorder or damage to the brain. If it does, the associated DSM-5 diagnosis would be a neurocognitive disorder, with delusional jealousy as a result of this disorder (APA 2013).

Similarly, an individual with substance or medication induced psychotic disorder could meet the

criteria for delusional disorder. In reviewing the timeline of substance use and onset and remission of the delusions, the substance can be considered or ruled out as the cause (APA 2013). For example, dopaminergic medications used to treat Parkinson's disease have been linked to delusional jealousy (Poletti et al. 2012). Graff-Radford et al. (2012) found that individuals who had Parkinson's disease without dementia exhibited delusional jealousy after an increase in dopamine agonist medication. When the medication was reduced or stopped, the delusions dissipated. They found a similar trend with patients who were treated with stimulant medications, which also affect dopamine (Graff-Radford et al. 2012).

Conclusion

Delusional jealousy is not currently recognized as a stand-alone diagnosis, even in the most recent version of the DSM (APA 2013). While Delusional disorder-jealous type does capture the presentation of delusional jealousy, the exclusion criteria for this specific disorder leave many instances of pathological jealousy unidentified. Perhaps if delusional jealousy were an independent disorder, it could be categorized into typologies by its relation to different disorders (i.e., delusional jealousy, resulting from active mood disorder). This way, if delusional jealousy were a prevalent psychological condition, it could be clinically identified and given more specific attention in the context of treatment. The identification of delusional jealousy could also be the presenting symptom that may lead to the identification of treatable underlying conditions such as disorders of mood, psychosis, and neurology. It also could inform the treatment of such underlying disorders, perhaps alerting providers to find alternatives to medications that are dopaminergic in nature or using an antipsychotic medication to counter its effects.

Cross-References

- Conjugal Paranoia
- Morbid Jealousy

- Othello Syndrome
- Pathological Jealousy

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Jean-Baptiste Chevalier de Lamarck

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Synonyms

Evolution theory; Lamarckism; Philosophie Zoologique; Theory of the descent; Transmutations theory

Definition

The French naturalist Jean-Baptiste Lamarck is one of the most representative figures of modern biology in the nineteenth century. Botanist and zoologist, he was a great systematic taxonomist establishing the current division of the animal kingdom in invertebrates and vertebrates. He also defined the term biology with its modern sense as a set of vital processes. And he was, above all, the first to use the idea of evolution to explain the history of life. His well-known book *Philosophie Zoologique* gathers his way of thinking about evolution. He is, together with Charles Darwin and Gregor Mendel, one of the key elements to understand the formulation and subsequent development of the theory of evolution.

Introduction

Nature is for mankind a collection of surprising beings and occurrences. Discovering which objects comprise it, observing its phenomena, and determining its laws are endless – perhaps interminable – tasks. The desire for knowledge arises in the minds of men trapped by necessity, curiosity, and vanity. Under this scenario, scientists have applied two master formulas to represent it. First is the fixism model, representing a closed, timeless system. A snapshot of beings who eternally are born, grow, reproduce, and die. Then there is the contemporary theory of evolution with its changing and perishable world. The application of one scheme or the other depends on the significance attributed to fossil remains. Leonardo da Vinci and Bernard Palissy, for example, both understood their value as living matter. However, until 1600, there was complicity to consider them as artifacts unconnected to life. Afterwards, naturalists started to abandon speculation by experimentally testing their organic condition. In the following century, another twist on the theme occurred when extinction was accepted as a phenomenon of life. As a result, species known from their remains were recognized to have inhabited Earth in the past. This

theory of lost species divides the natural system into two existential categories: geological time and biological time. The universal and the particular.

The botanist Carl Linnaeus promoted the temporal idea. In *Disquisitio de Sexu Plantarum* (1760), his explanation of organic diversity as a biological process is a pre-evolutionary theory scientific approach. Linnaeus considers hybridization as a phenomenon capable of producing new plants, and, in this way, they diversify over time. Creation is limited to the origin. Nature then acts alone. His hybridization model is a restrictive, regulated application of the fixism theory. God is the creator, but the act has lost its supernatural condition, becoming an actualist, reproductive process.

Around the same time, the celebrated naturalist Count Buffon proposes a more ambitious, complex, and refined version of this fickle nature. According to his *Les Époques de la Nature* (1778), Earth's history consists of seven stages. The first and second stages are abiotic and form the conditions necessary for life, which bursts through during the third stage. The first animals are aquatic. They would also be the first victims, the first species to be lost when the environment changes. The fourth stage is the era of the plants. In the fifth, a green carpet awaits the arrival of the gigantic animals known from their fossilized remains. It is also the time of uncivilized humans. The current continental division occurs during the sixth stage, and, in the last, man takes possession of the Earth. The big question is: How does life emerge from inanimate matter? In the theory of organic molecules – a fantastic hypothesis – organisms are formed through the aggregation of indestructible living particles, formed by the heat that acts on the malleable material. After species become extinct, the molecules are released to organize themselves in different ways into other species. Buffon develops a materialist concept of life but without a biological nexus, far from any notion of common descent. The idea of organizing nature through a philological law appears in other texts of his well-known *Histoire Naturelle*, suggesting its possible interpretation as an evolutionary event. The first step towards

evolution had been taken. It consisted of replacing creation with a self-sufficient world. It was under this context that Lamarck, from 1800, would reveal his transmutationist ideology and propose a different way to think about nature as a demystified entity, reduced to physical processes and composed of species with a common origin. Lamarck changed the analytical scene by converting organic function into the true reference of living beings. The science of biology was born.

The Chevalier de Lamarck

Jean-Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, was born on Saturday, the 1st of August 1744, in Bazentin, a small town in northern France. He was the 11th child of Philippe de Monet, a knight of Saint-Louis and commander of the Château de Dinan. It was noble family with military roots whose prominence had been in slow decline for the last 300 years. Too many brothers and a diminished heritage led Lamarck to a seminary run by Jesuit fathers in the city of Amiens. It was the start of his ecclesiastical career, during which he earned the nickname the *petit abbé*. After his father's death, at the age of 16, Lamarck replaces the *Bible* with the saber. Looking to enlist in the *Beaujolais* regiment, which was waging war on the northern border, he was admitted as a volunteer. In July 1761, he participates in the Battle of Villinghausen, a well-known episode of the Seven Years' War, in which the French troops suffer a bitter defeat. Lamarck, however, is appointed an officer for his heroism, though he would leave the army as abruptly as he joined it. After the war, in 1763, the regiment is stationed in Toulon and then in Monaco, where he suffers a serious injury. He spent over a year convalescing in Paris: a time to read and meditate, to learn botany and meteorology, and to understand that he could progress in life without losing it. He left the army and entered medical school. Hard times. He worked to survive, combining his studies with his job as a banker. But Lamarck was not born to be a doctor. After 4 years, botany replaced medicine. In 1778, he writes *Flore Française*: an effective methodological treatise to recognize the

name of plants using easy dichotomous rules. The work was a success, earning the favor of the powerful Count Buffon who had it printed with the stamp of the royal printing house. Between 1781 and 1782, Lamarck travels throughout the territories of Germany, Austria, Hungary, and Holland, accompanying the count's son as his tutor – a task that earned him an appointment as a royal botanist. Upon his return, he would manage the botanical section of the famous *Encyclopédie Méthodique*. In 1788, thanks to Marquis de Billarderie, manager of the Jardin des Plantes, the King's Garden, he is appointed as curator of the Royal Cabinet's herbariums. He was in charge of fixing and organizing them, which earned him a salary of 1,000 francs. In 1793, he becomes chair of the invertebrate department at the French National Museum of Natural History. No professor wanted the post. His knowledge of “white-blooded” animals, as they were called at the time, was scarce. They were a group forgotten by nearly everyone. Land, aquatic, and underground animals. Walkers, flyers, swimmers, jumpers, and crawlers. Thousands of species: some 135,000 were known at the time compared to the around 10,000 known of the other groups. Lamarck knew how to order the chaos. He separated crustaceans from insects, defined arachnids, distinguished annelids among the worms, differentiated the echinoderms from the polyps, and, fundamentally, had the intelligence, intuition, and success to call them animals without vertebrae. The animal kingdom was divided into two universally accepted groups, vertebrates and invertebrates, as he explains it in his book *Système des Animaux sans vertèbres* (1801). Professor Lamarck remained faithful to the museum until his death on the 18th of December 1829. He even turned down a position as chair of zoology at the Faculty of Sciences. Nearly 30 years in which life and work were intertwined. Three decades also represented by works such as *Hydrogéologie*, *Recherches sur l'organisation des corps vivans*, *Histoire naturelle des animaux sans vertèbres*, *Système analytique des connaissances positives de l'homme*, and, particularly, *Philosophie Zoologique* (Lamarck 1802a, 1820). Lamarck is a man of revolution. He wrote books for a

magnanimous and victorious people. He wants to be useful to his fellow man, to his brothers, and to his peers, as evident in the printed dedication of *Recherches sur les causes des principaux faits physiques*. A committed citizen, he was not in tune with the Napoleonic era. Neither the empire nor the restoration fit him well. Many scientific institutions welcomed him with open arms. He trained, in part, at the Institute of France, the Parisian Philosophical Society, the French Royal Academy of Sciences, the Moscow Society of Naturalists, the Royal Academy of Sciences of Munich, the Berlin Society of Friends of Natural Science, the Strasbourg Society of Agriculture, and the Agricultural Society of Lyon, among others. The twilight of his life was sad and difficult. He fell upon hard times. He buried three wives and several of his eight children. To scrape by, he sold his library, his herbarium, and all of his collections. He died blind and poor. His body was buried in a mass grave in the Parisian cemetery of Montparnasse. Life did not do him justice. History also does not, conceding him a secondary role in the cast of the historical blockbuster entitled *Evolution*. However, it was Lamarck who courageously used the evolutionary idea to explain the history of terrestrial life (Simpson 1953). What were the terms of the proposal?

A New Philosophy on Life

The philosopher Henri Bergson explained his interest in organic evolution at the Huxley Conference of 1911 (Bergson 1919). Briefly, species are generated from other, simpler ones. A hypothesis confirmed by comparative anatomy, embryology, and paleontology since the time of Lamarck and Darwin. In his testimony, we recognize two foundational arguments of the evolutionary theory. First is the general nature of the phenomenon to generate new species by modifying existing ones. It is a descriptive argument, the “what is happening,” from which the different theories develop their own explanations for how and why it happens. Second is the empirical condition of the theory based on data contributed by different disciplines. These two arguments form

the general ideological framework of the theory, as outlined by Lamarck and maintained by successive evolutionary models. In Yves Delage’s view (1895), before Lamarck, it was unthinkable to attribute a natural cause to the origin of species. Or more precisely, the impossible was not to think of life in physical, chemical, or biological terms. It was to close the circle and to explain the genesis of living beings by their genealogy, relating them to each other and to the environment. The impossible was to define a sequence of continuous biological information from the past to the present through reproduction. Lamarck’s wisdom is epistemological: it consists of giving nature a new status, renewing the classical concept of the *scala naturae* or the great chain of beings – a scheme, since Plato and Aristotle, that related organic forms by their morphological proximity to comprise a rectilinear sequence of increasing complexity and perfection up to the human race. Living beings represented a unique, unilateral, one-dimensional, and unidirectional natural group. For Lamarck, nature represents a well-organized group but one not related to the *scala naturae*. In 1800, he publically rejects the concept and abandons the uniformity. He does not interpret it as a regular, linear series but rather a sequence limited to the organizational system of classes and major taxonomic families, a common trunk from which species emerged as lateral branches. It is a new treelike symbolism of the natural order, initially bifurcating into the animal and plant kingdoms that later develop through continuous phyletic series. Nature is composed of living beings grouped into species whose persistence is relative. They are only temporarily invariable. The individual is the essence of the whole, the circumstance that defines and maintains it.

In 1802, during the opening of the zoology course at the natural history museum, Lamarck explained that he had long accepted the principle of species invariability. It was an error that he would not repeat. Reformulating the concept of species was a consequence of observing nature from an evolutionary perspective. Now, a species would be a collection of similar individuals over a long period of time with the exception of small,

accidental differences. Then, after an implausible amount of time for human existence had passed, environmental conditions gradually change, and individuals adjust their topology to accommodate their new needs. They acquire another conformation that is inherited by their descendants. The group now constitutes a different, equally perishable species. A subgroup could also become accidentally separated from the collective and experience different environmental conditions elsewhere. Lamarck hypothesizes that it would develop new habits to survive and thus form another species, thereby incorporating a mode of speciation by geographical isolation into the evolutionary process. A future look to evolutionary biology of the twentieth century. Species, therefore, are not a product of Linnaean time but rather of the environment, and adaptation would be the evolutionary causation – a necessary condition for the survival of individuals. In this context, the phenomenon of extinction is meaningless since there is no existential interruption in individuals, just a continuous adaptive conversion. Indeed, fossils do not identify lost species but rather only show what they were like before the change in form. They are expired pieces of a process of nonselective substitution, because there is not intraspecific neither interspecific competition.

Lamarck, in his outline of his biological theory on the origin and the development of life, emphasizes organic instability as a quality of nature. But if the hypothesis, in general, culminates with the idea of an independent nature that is capable of achieving such achievements on its own, the underlying message is a sea of doubts about the truth of nature as it was then known. The remedy for such ignorance would be an innovative research program. A naturalist would have to be ambitious and not just spend time and effort on describing and classifying. To identify an object is not enough to know it. It is necessary to discover how nature forms and renews its output. The priority would be to analyze the set of relationships that allows a living organism to be expressed as an anatomical-functional model. The idea is to know its organization by studying what phenomena occurred during reproduction and

development and to relate the effects of environmental conditions and lifestyle on the body. This is the biological significance of Lamarck's *Philosophie Zoologique*. A work on the principles of animal life written in order to determine what life is and what conditions are necessary for it to manifest itself. The general conclusion is that, to survive, an individual undergoes adaptive transformations in response to the environment. Adaptation, phyletic continuity, and chronological variation are the foundational pillars of the Lamarckian evolutionary archetype (Galera 2009). The formula has since then travelled through time generating an intense, controversial, and unending debate on the origin and transient nature of species. Because it is one thing to be an evolutionist but another to explain the how and the why of evolution (Simpson 1951). Thus, far from falling into oblivion, Lamarckian thought is today considered an asset of the evolutionary theory because his transformist vision of nature, imbued with knowledge, comprises a bouquet of possibilities not previously considered. It is not so much for his well-known hypothesis on the inheritance of acquired characteristics itself but its understanding that habits can guide future evolution.

In the 50 years that passed from the first appearance of *Philosophie Zoologique* to the first edition of the *Origin of Species*, Lamarck's transmutationist ideology certainly circulated the academic circles. He had supporters and detractors (Galera 2017). Charles Darwin himself acknowledges that he had reached similar conclusions, as he relays in a letter dated 11 January 1844 to the botanist Joseph Hooker. His testimony underlines a consensus with Lamarck to define life as a process of adaptive substitution. The difference essentially lies in the proposed mechanism, in the adaptive model, and in the determination of whether the cause is teleological or random. However, historians often underestimate the figure and the ideology of Lamarck by using a categorical argument: evolution only makes sense in light of Darwinism. Is this true? To address this question, we analyze the role of Lamarckian ideology within the scientific community prior to the publication of the *Origin of Species*.

The Transmutation of Species Doctrine

From 1800 on, Lamarck explains his *theory of the descent*, as it was also known, to his zoology classes. It is immortalized in his book *Philosophie Zoologique* (1809), although it emerged earlier in treatises such as *Système des animaux sans vertèbres* (1801) and *Recherches sur l'organisation des corps vivans* (1802b). The building of his transformist idea of nature continues in *Histoire naturelle des animaux sans vertèbres* (1815–1822). In 1830, *Philosophie Zoologique* is reissued, but it would be another 40 years before a new edition is published in 1873 by Charles Martins, director of the Botanical Garden of Montpellier. By then, Lamarck had already passed away. In Britain, the Lamarck's *Philosophie* was available relatively quickly. In the October 1811 issue, *The Monthly Magazine* communicated to readers the possibility of buying the book. That same year, the literary journal *The Monthly Review* published an extensive review explaining its content – continued in 1813. A brief informative note published in *The New Annual Register*, 1812, recalled the naturalistic interest of the work and the convenience of translating it to English. However, it was not translated until 1914. Previously, the journal *The American Naturalist* in its 1888 issue included the translation to English of the seventh chapter of the first volume. No doubt. The limited editorial projection of the book impaired its dissemination. So, what scientific impact did his theory have?

In 1813, renowned Swiss botanist Augustin Pyrame de Candolle showed his opposition to the theory of the *non-permanence of species* in his book *Théorie élémentaire de la botanique*. His rejection has a taxonomic sense, defending the constancy of species as a basic systematic condition. In his mind, nature is permanently ordered, and only those characteristics that do not change the identity of a group are modifiable. The slow and gradual change of species proposed by the theory of transmutation was an unacceptable idea that violated the general principles, and to attribute the morphology of beings to their habits was an absurd hypothesis. Another case. The year is 1817. For the

German philosopher Friedrich Hegel, as he expresses in *Enzyklopaedie der philosophischen Wissenschaften im Grundrisse*, the unique vision of a changeable nature was but one of those nebulous, sensitive, and ineffable representations that the human intellect should reject. To attribute a material origin to life and to conspire a fickle, inconstant, uncertain, incoherent world was simply an outlandish notion. That same year, in the prologue of the third English edition of Georges Cuvier's *Essay on the Theory of the Earth*, the Scottish geologist Robert Jameson expresses a different view (Cuvier 1817). Jameson identifies two sides: the paleontologist Cuvier leading the anti-transformist camp and Lamarck carrying the evolutionist banner by interpreting nature as an unstable group of living beings subjected to the modifying action of the environment.

The Reverend John Fleming, a famous Scottish botanist, geologist, and zoologist, knew of and rejected the theory of transmutation, as evident in his *The Philosophy of Zoology* (1822). True, the geological strata contain remnants of extinct plants and animals that, to some extent, differ from current species, with those most similar being found in the most recent deposits. This stratigraphic sequence was the relatedness argument used to support the common descent of modern flora and fauna by environmental causes. Fleming arbitrarily rejected the idea. Life simply has limits, and the transmutation of species was one. “It never happened,” he declares, foreshadowing the arduous task proponents of the theory would have to face to prove it. He was right, at least in pointing out the difficulty of the task. He wrote no names, but the Lamarckian connection is discernible in both the modus operandi and the reference to the first volume of *Histoire naturelle des animaux sans vertèbres*. More testimonies. In 1826, the *Edinburgh New Philosophical Journal* published “Observation on the nature and importance of geology” by Professor Robert Edmond Grant, historically known for his professorial relationship with Darwin. The question of the origin of living beings was one of his concerns. His favorite response was the unequivocal theory of “Mr Lamarck.” The organic world originated from simple animals,

such as infusorians, by spontaneous generation. The others gradually had evolved, driven by external circumstances – a hypothesis supported by the *doctrine of petrification*.

In *Éléments de géologie*, published in 1831, the Belgian geologist Jean-Baptiste d’Omalius explains that the most plausible hypothesis to justify the concatenation of species occurred during the world’s geological history, the reproductive substitution of ones for others caused by external circumstances. Even Charles Lyell was surprised to find that his colleague had opted for the Lamarckian system of transmutation. A year later, Lyell made his position clear in the second volume of *Principles of Geology* in which he uses the term *evolution* to refer to the Lamarckian concept of a chronologically modifiable nature that is linked to a space – an ideology that he rejected until the 1860s (Lyell 1830–33). The volume faithfully reflects the contents of *Philosophie Zoologique*. It is, in fact, its first attestation in the English language. In Lyell’s rebuttal, there is a hesitant tone against a hypothesis that had internal logic and consistency and that might not have been wrong. It was Lamarck who revealed the theory of evolution to him in anticipation of Darwin.

In 1833, parish priest William Kirby, a prestigious English entomologist who was considered the founding father of the discipline, published the seventh volume of the *Bridgewater Treatises*, a famous collection on natural theology. It was entitled *On the Power, Wisdom and Goodness of God as Manifested in the Creation of Animals and in Their History, Habits and Instincts*. Kirby had clear ideas. Addressing the theme of God and nature, he would not forget Laplace and Lamarck, two of the most eminent philosophers of the century. A physicist and a zoologist who ignored God by attributing Creation to secondary causes. Lamarck’s great error was his steadfast materialism leading to an irrational, inanimate nature, composed of laws and parts that do not go beyond their sensations. Nature transformed into a *genealogical tree* based on a microscopic organism indifferent to reason. Kirby knows the biological significance of the theory. Heat, electricity, and physical attraction penetrate inorganic matter,

producing excitability and life – cellular tissue. Components that will give rise to primitive beings capable of reproducing by splitting and budding. Then, life made a virtue of necessity. The stimulus to feed formed the mouth; the digestive capacity fostered the stomach and intestines. And so on, moving towards the complexity and diversity of living beings. He believes that nothing new could be added to Lyell’s works to demonstrate the stability of nature. In another volume of the *Bridgewater Treatises* entitled *Geology and mineralogy* (1836), the Reverend William Buckland, renowned geologist and paleontologist, reveals his view of Lamarck as an anti-creationist enemy. He does not hesitate to inform the reader of the ideological danger of a doctrine that excludes the Creator by explaining the origin of species through development and transmutation.

More arguments. The influential British philosopher William Whewell, in the third volume of his *History of the inductive sciences* (1837), explains that the controversy between supporters and opponents of the *doctrine of the transmutation of species* was one of the most outstanding issues of the scientific debate. Geologists and paleontologists had shown that different groups of animals and plants inhabited the Earth successively. It was a scientific fact. The dilemma was to accept the doctrine of transmutation – species of a geological age transforming into other forms due to natural causes – or to acknowledge the miracle of successive creation of species after the extinction of previous ones. The philosopher picked the latter option. Whewell maintained his opinion in the revised edition of 1847. When writing the third volume of *Cours de philosophie positive* (1838), Auguste Comte did not forget the Lamarckian transformist discussion. The theory was a philosophical problem against the method – against the natural method and the immutable hierarchical order. The relationship between the environment and morphological variation were indisputable principles, but, poorly applied, they formed a clever and false hypothesis. A theory far from reality of a nature whose living beings are perpetuated by obeying the law of repeating the characters that identify the group.

In the first volumes of the British periodical *The Oracle of Reason* (1842 and 1843), William Chilton, co-founder and editor, published the article “Theory of regular gradation.” A world without God was possible thanks to Lamarck. And the best way to learn more about his theory was to read *Principles of Geology*. In 1844, *Vestiges of the Natural History of Creation* by Robert Chambers was published. He ignored Lamarck’s name for years, only including a laughable note from the sixth edition (1847) on. Why? In the preface to the tenth edition (1853), Chambers recognizes that he knows the Lamarckian hypothesis, which he considered inappropriate to explain the existence of living species. To understand Chambers’ disregard, it is necessary to read the thorough and extensive review published in 1845 by the *North British Review* on the occasion of the fourth edition of the *Vestiges*. An anonymous columnist raises the injustice of forgetting to include the *system of progressive development* of the skilled and esteemed Professor Lamarck that, conceptually identical to the *Vestiges*, was superior because it establishes intelligible causes to justify the hypothesis of successive changes that transform species.

In the mid-1840s, owing to the French botanist Frédéric Gérard, a follower of Lamarck, the master’s approach took identity as the *théorie de l’évolution des formes organiques* (1845). Gérard used the Lamarckian model to explain Earth’s history. The fossil record indicated what had happened in nature from the origins to the present. The *theory of evolution* was a possible biological law that was simple, direct, and comprehensible. In contrast, the geologists Alonzo Gray and C. B. Adams were not in favor of the widely known theory of transmutation (Gray and Adams 1854). They believed in the miracles. As evident in their book, *Elements of Geology* (1852), they have no doubt about the direct intervention of the Creator. However, it is from a position that does not prevent them from discussing the transformist option, which allows them to recall Lamarck’s theory as an explanation of a correlative natural order from the simple to the complex through the progressive increase of anatomical structures.

Other evidence. At the academic meeting held on the 20th of April 1855 at the Royal Institution, Professor Thomas Huxley took to the floor to discuss some of the zoological arguments on the hypothesis of the progressive development of animal life. He wondered what was the significance of extinct species. The answer was essential. Living beings differed in every era, and the chronological substitution of species was something accepted by all. An undeniable fact. For Huxley, the issue under debate was not what happened but to explain how changes happened. The law regulating the phenomenon remained to be determined. He had to wait 4 years to know that natural selection was the answer. Huxley explains it in his article “The Darwinian Hypothesis” for *The Times* (26 December 1859). In his exposition, the figure of “the famous naturalist” Lamarck appears, one of those privileged rare minds able to reject miracles. Minds willing to refuse the creationist dogma. Lamarck correctly interpreted the process but was wrong to establish evolutionary law as organic modification induced by the environment and inherited by offspring.

The end. In 1859, oblivious to the *Origin*, the French botanist Dominique Alexandre Godron recognized the merit of Lamarck as a leader of the transmutationist movement. In his treatise *De l’espèce et des races*, he advocates that his compatriot deserved to be considered head of the naturalist school, in defense of the theory of the mutability of species through the action of external agents and reproduction. The Swiss naturalist Louis Agassiz, a self-confessed anti-Darwinist, also recalled Lamarck’s role. In his book *An Essay on Classification* (1859), Lamarck, along with his *Philosophie Zoologique*, is emphasized as a defender of species variability. An approach in which the structural complexity of animals is defined by a succession of organizational degrees arranged according to continuous series.

Conclusion

The reputed French biologist Jean Rostand writes in *Esquisse d’une histoire de la biologie* (1945) that *Philosophie Zoologique* was a failure that

soon fell into indifference. Rostand was wrong. It was not so. The Lamarckian hypothesis did not leave his contemporaries indifferent. The theory was known, discussed, and integrated into the naturalist discourse as an alternative to the conservative creationist model. In Great Britain, Lamarck's ideas provoked a major debate. A relevant occurrence as some of the scientists involved – Lyell, Huxley, etc. – were part of the scientific group in which Darwin conceived of natural selection. Huxley's testimony, in particular, presents Lamarck as responsible for the debate on the chronological substitution of species. For its part, *Principles of Geology* was a fundamental element for the dissemination of the Lamarckian ideology, for both its detailed analysis and its widespread circulation. Huxley was right to assert that in England, thanks to Lyell, they did not forget Lamarck. For decades, *Philosophie Zoologique* was the evolutionist reference. Until the publication of the *Origin of Species*, no other treatise existed on the subject. It is the first one. It created the school. It established a new concept of nature by applying another method of investigation. It laid the foundations of the transformist, transmutationist, and evolutionary model – the adjective does not matter. It was, as the Darwinist Ernst Haeckel writes in his *History of Creation*, the first rational exposition on the *genealogical doctrine* that reached the final consequences (Haeckel 1876). And it was by the Chevalier de Lamarck. In short, *Philosophie Zoologique* changed the perspective of nature, leading to the beginning of modern biology. It was not a coincidence. The author explains it in the preamble. His goal was to write a monograph on living bodies entitled *Biology*. In the end, he presented his research on the characters, organization, development, diversity, and abilities of the animal kingdom using the classic format of philosophy. A dull title for a clear, innovative, and revolutionary idea: the origin of living beings through evolution.

Cross-References

► Charles Darwin

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Jerome H. Barkow

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Definition

Jerome (Jerry) Barkow is a biosocial anthropologist whose work has emphasized how our evolved psychology provides the infrastructure of culture and whose work has been a prescient call (Barkow 1973, 1994) for an evolutionary psychological anthropology. His often pioneering work embraces how our pan-primate tendency to form hierarchies helps to generate – and always underlies – human social structures (Barkow 1975a, b, 1980a, 2014b). He co-edited the foundational text and rallying cry for evolutionary psychology, *The Adapted Mind* (Barkow et al. 1992), drawing together his earlier recognition for evolutionary approaches to ground our study of human behavior. Barkow's work runs a broad gamut, including work that was a forerunner in the evolutionary study of gossip (Barkow 1992), happiness (Barkow 1997), and, more recently, the likely psychology of extraterrestrials (Barkow 2000,

2014a, forthcoming). He has also been vocal that explanations at different levels of organization (such as those at the individual versus sociological levels) must always be compatible with one another but can never be in competition (Barkow 1989a, 2006a).

Introduction

Jerry Barkow is an interdisciplinary, biosocial anthropologist who has spent his academic career at Dalhousie University, Canada. He has been a visiting professor at the Institute for Cognition and Culture at Queen's University Belfast (QUB) and, following his retirement and appointment as a Professor Emeritus at Dalhousie, served as an honorary professor at QUB for 7 years.

Private Life

Jerry Barkow was born on January 18, 1944, in Brooklyn, New York, to Philip Barkow and Rebecca Gendler Barkow, the younger of two sons. He spent the first 20 years of his life in Brooklyn and worked selling ice cream, as a photographic technician, a postal worker, and finally a Social Investigator for the New York City Department of Welfare. He has lived most of his adult life in Canada and identifies as Canadian. Jerry was the first in his family to earn a university degree. He is married to Irma Juuti and has one son, Philip, one daughter, Sarah, and two grandchildren.

Academic Education

Jerry received his B.A. from Brooklyn College. While majoring in psychology, a course taken just prior to graduation with the late Gerald Henderson in Culture and Personality led him to seek interdisciplinary graduate training. He was accepted by the University of Chicago's Committee on Human Development, where he worked with psychological anthropologist Robert A. LeVine and ethologically oriented psychologist Daniel

G. Freedman. During his first summer, he was hired by a project on ethnocentrism that LeVine was conducting with then-Northwestern University psychologist Donald Campbell. Campbell gave Jerry a stack of his publications and he read them all carefully and with delight; Campbell's thought has been a lifelong influence on Jerry's own work and prepared him for his introduction to the work of Darwin and to ethology that Freedman provided. LeVine was beginning a project (involving infants) among the Hausa of northern Nigeria, and Jerry went off to Ahmadu Bello University and then to a small town nearby where he built a compound and lived for 15 months conducting his first fieldwork. His thesis topic addressed prestige and relative standing, comparing the ethos of Muslim Hausa and the more rural Maguzawa, a non-Muslim Hausa people. He substantiated his findings using four distinct methods. One of the findings was that the Maguzawa had lower self-esteem than did the Muslim Hausa, reflecting the Maguzawa's lower political power. This lesson that personal self-esteem, membership, group standing, and political power are intricately interlinked and apparently are the human heritage of the general primate tendency to form, maintain, and see the world through hierarchies ("hierarchizing") informed much of Jerry's subsequent evolutionary thinking about the relationship between our evolved psychology and our social structures.

Contributions to Evolutionary Psychology

Fieldwork Contributions

In keeping with his social-cultural anthropological training, Jerry's work has a substantial degree that is field-based. Several of his publications provide empirical data on the relationship between culture and our evolved psychology. For example, Barkow (1982) found that when the age grading social hierarchical system of the Migili (Koro) of Nigeria's Middle Belt collapsed, reciprocal and kin-directed altruism replaced them. An age grading system is a social organization based on a series of ranks, and one is

promoted as one gets older and shows appropriate qualities. For the Migili, the age grade of younger men was responsible for doing most of the heavy labor, including making the hills for the all-important yam crop. This is arduous labor and that age grade performed it for everyone, including women and older people. When the social organization collapsed, individuals were on their own. Data on who made hills for whom and whether or not there was reciprocity combined with coefficients of relatedness showed that the higher the relatedness the less likely that aid would be reciprocated; in contrast, among non-relatives, it was always reciprocated. Thus, a fundamental aspect of evolved psychology, reciprocal and kin-directed altruism, came to the fore when the social structure that had over-ridden it (for this task, at least) ceased to operate.

Working with a medical team in Indonesia, during the late Nineties, Jerry came across an evolutionary paradox (Barkow et al. 2001), which he framed as "why the Bugis know more about cooking than about nutrition." Why, apparently, did Bugis women have a stronger interest in their cooking ability rather than nutritional knowledge? Jerry wondered would not evolutionary theory predict a maternal ability to monitor her offspring's nutritional status and thus strive to provide the healthiest diet possible, given the local environment? As Barkow details, a physician member of the team explained why indigenous knowledge of infant and child nutrition was poor: how would a mother know whether the child's ill health was caused by a parasite, a disease, or diet? Barkow notes that evolution needs something to work with, and in this case there is no way that even the most observant and caring mothers can provide natural selection with genetic variance to select on. Skill in cooking, however, is an important cultural realm of competition, locally, and not just among the women themselves, so we get the historical development of an excellent cuisine (cookies, in particular). Ever the anthropologist, Jerry notes that a lesson for evolutionary psychology is that both evolution and their field have their limits.

Working in the city of Maradi in Niger during the first half of the Seventies, Jerry studied a

small panel of men intensively (Barkow 1975b). A status conflict existed between the ruling, French-speaking bureaucratic elite, and ordinary people. Jerry observed that the response of the latter was to seek to invalidate the prestige claims of the elite by arguing that only Islamic learning and practice merit respect – something the elite did not have, and so many people spent countless hours in religious study; those who had not had sufficient early Islamic education to have this option open to them suffered low self-esteem. Decades later, it is apparent that Jerry may have described one of the processes that has led to the spread of a fervent Islam in the region. The evolved psychological trait of hierarchizing is at the base of a vertically integrated explanation for a major socio-political phenomenon.

Links with Social-Cultural Anthropology

Jerry has repeatedly sought to engage his discipline with evolutionary thinking. At times he has done this with data, at other times by explaining how their view of human behavior is fundamentally flawed (Barkow 1978a, b, 1980b, 1984, 1989a, b, 1994, 2001; Barkow et al. 1978, 2013). “Sometimes the Bus Does Wait” (Barkow 2006b), the amusingly titled introduction to his edited book (Barkow 2006c), *Missing the Revolution: Darwinism for Social Scientists*, is at once a powerful deconstruction of the myths many social scientists hold of evolutionary psychology and a heartfelt plea for them to join the major human science intellectual revolution of our time. The tragedy here is that without evolutionary psychology’s theories of human nature the social sciences are condemned to explaining endlessly recurring fires whose ultimate causes they can never understand, a point made in the title of Jerry’s article (Barkow 2003), “Biology is destiny only if we ignore it.”

An important theme in Jerry’s work is that if cultural features were simply replicated, culture would be nonadaptive because environments change; old practices may no longer work or no longer be sustainable, while new opportunities appear: culture must not only be transmitted but added to and *edited* (Barkow 1975b, 1989a, 2014a; Barkow et al. 2012, 2013). Much of our

evolved psychology, he has long argued, was selected for in order to edit culture. Whom we attend to determines from whom we learn. Status shapes this strongly, biasing us to learn from those high in status as we attend to them (Barkow 1976a, b, 2014; Barkow et al. 2012).

Jerry has also incorporated other concepts into his work that are more commonly found in the animal behavior literature. Jerry has presciently looked at the notion of local adaptation, where the environment of adaptation is the culture (Barkow 1980a). In a quantitative study of conformity to the local ethos and reproductive success among Hausa townsmen (Barkow 1977), he provides evidence for selective pressure from culture in that men who conformed better to the ethos of their community (by not mentioning emotion-laden topics in a standardized setting) had more children than did those who did not conform as well. Population mobility and sociocultural change preclude the process from having any real genetic impact, in this example, but the results are compatible with the possibility that genetic impact from cultural traits may have played a role in our evolutionary history.

Links with Extraterrestrial Intelligences

Jerry is on the Board of Directors of Messaging Extraterrestrial Intelligence International (METI) and has ties to the SETI (Searching for Extraterrestrial Intelligence) Institute as well. In his articles (cited earlier), he reviews the processes believed to have led to our own species’ evolved psychology and then asks what if, on an exoplanet, those processes varied. For example, suppose an ETI (extraterrestrial intelligence) evolved in competition not with bands of conspecifics but with members of other species, would they therefore be selected to be obligate xenophobes? Suppose an ETI species did not have sexes and moved genes laterally but nevertheless evolved a high technology through a history entirely different from our own: what would their psychology be like? Competition is a human universal and is deeply implicated in our science, technology, and art and was likely produced at least in part by sexual selection: would the evolved psychology of a sexless species that could not have been

subject to sexual selection lack competitiveness? These are the fascinating questions Jerry has been asking in his most recent work, perhaps the ultimate exercise for an evolutionarily minded scholar! As we move to being a space-faring species the need for advice from evolutionary psychologists about what we may meet out there will only grow.

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JMS

► [John Maynard Smith](#)

Joanne Raio, Joannis Raii [Lat.]

► [John Ray](#)

John & Leda

► [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

John Bowlby

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Synonyms

[Attachment Theory](#); [Edward John Mostyn Bowlby](#); [Environment of Evolutionary Adaptedness](#); [Maternal Deprivation Hypothesis](#); [Monotropy](#)

Definition

A twentieth-century scientist who integrated principles from ethology, ecology, and evolutionary biology with developmental psychology, Bowlby is most renowned for his scientific contributions of *attachment theory* in humans.

Introduction

John Bowlby’s early interest in child psychiatry and the influences of Sigmund Freud and Konrad Lorenz steered his career to become one of the most influential scientists in biology and psychology. His most famous works, such as *monotropy*, *attachment theory*, and the popular *environment of evolutionary adaptedness* (EEA), are still studied by numerous biological and psychological scholars. Evolutionary psychologists accredit Bowlby for being one of the first scientists to integrate biological and psychological principles in the study of human attachment.

Early Academic Training

Bowlby graduated from the University of Cambridge in 1928 after primarily studying developmental psychology (Rubinstein 2015); nevertheless, the young John Bowlby beheld a passion in working with children and medicine, which precipitated his pursuit to study child psychiatry. After receiving rigorous training as a child psychoanalyst at the British Psychoanalytic Institute, Bowlby began to behold an unorthodox perspective of the development of early human attachment (Bretherton 1992).

Professional Career and Scientific Philosophy

Konrad Lorenz’s research on *imprinting*, the behavior popularly associated with ducklings identifying any apparent caregiver as their parent, made Bowlby revise his conception of the child-parent relationship development (Cicchetti and

Greenberg 1991). Bowlby believed that ethological theories and principles like Lorenz's imprinting theory might apply to his understandings of psychology (Rubinstein 2015). As a psychologist who viewed Freudian psychology as being pertinent to behavioral science (Bretherton 1992), Bowlby encountered difficulty answering questions about the origins of human attachment or the development of children's affectionate relationships with their caregivers.

When Bowlby began considering that innate qualities may have contributed to human attachment, he concluded that the bond between the infant and caregiver is as crucial to the infant's survival as any other helpless and premature offspring (McLeod 2007). Bowlby observed that children's behaviors and habits that reflect their attitudes of intimate relationships were not learned, but he hypothesized that these behavioral qualities are innate to the human species (Bretherton 1992). To better understand what it meant to be *human*, Bowlby went on to become one of the first scientists to apply evolutionary theory to human psychological research (Rubinstein 2015).

Contributions to Evolutionary Psychology

Bowlby understood that unconditional love between the infant and caregiver is necessary for the infant's development until he or she can physically take care of his- or herself (Rubinstein 2015). Infants need relentless attention from others, and it is typically one caregiver that can establish a deep relationship with one infant at a time, which is a concept derived by Bowlby called *monotropy* (McLeod 2007). Contemporary research focusing on this attachment to an infant supports that the infant-caregiver attachment is unique to other familial attachments (Bretherton 1992; McLeod 2007). Monotropy is reported to be so significant to both the infant's personality development and relationship attitudes that failure to establish the bond entails negative consequences for the infant (McLeod 2007).

The maternal deprivation hypothesis conceived by Bowlby predicts that if the infant-

caregiver attachment is not established, deleterious habits and behaviors are likely to develop (Rubinstein 2015). However, the maternal deprivation hypothesis and collaboration with developmental psychologist, Mary Ainsworth, led to Bowlby's most famous contribution to the psychological community, *attachment theory* (McLeod 2007).

Bowlby's and Ainsworth's attachment theory posits that the absence of an infant's attachment to the caregiver ultimately affects the nature of subsequent relationships with others when the infant is mature (Bowlby 1982). Delinquency, reduced cognitive function, increased aggression, heightened risk for depression, and psychopathic traits have been observed in older individuals with little to none attachment to a caregiver during infancy (McLeod 2007). Observations in the pattern of occurrences when the infant smiles or cries while in the presence and absence of the caregiver are used to indicate attachment formation. As the emotional expressions grow with the infant, psychologists scrutinize them in order to learn more about mental disorders and how to treat them (Cicchetti and Greenberg 1991).

The significance of a successful infant-caregiver attachment to human survival led Bowlby to believe that the environmental pressures and problems endured by our ancestors were more extreme than the ones modern humans endure today. Bowlby was the first to coin a term that is ubiquitous to the science and research of evolutionary psychology, *the environment of evolutionary adaptedness* (EEA). Bowlby believed that a species' properties, biological and psychological, originated and evolved during its ancestral history. The EEA is not a single or specific time, place, or environmental condition; it is the broad range of times and environments that the species' properties adapted to (Bowlby 1982).

Evolutionary psychology countlessly derives many of its hypotheses and theories from Bowlby's concept of the EEA. Human psychological adaptations, such as memory, classical conditioning, fear, etc., are designed to solve problems encountered throughout human evolutionary history. On the other hand, modern environments, like Western societies, contain some drastically

different problems and selection pressures on humans. These novel environments and environmental features were not what molded human psychological and biological adaptations. Evolutionary psychologists acknowledge that discerning a species' EEA may help identify and understand the behavioral phenomena observed within that species.

Conclusion

John Bowlby's original interests in developmental psychology and medicine fostered his career interests to apply a different perspective to traditional psychology. As a trained psychoanalyst who was influenced by ethology, Bowlby was pressured to ask questions that concurrent psychologists condoned. Theories he has contributed to, like attachment theory, continue to be viewed as exemplars of the consilience between psychology and biology. Bowlby's position that innate psychological qualities facilitate and nurture human psychological phenomena, like the infant-caregiver attachment, made him one of the first scientists to think like an evolutionary psychologist.

Cross-References

- [Competition for Parental Investment](#)
- [Early Stage of Brain Development at Birth](#)
- [How Evolutionary Psychology Can Still Explain Behavior](#)

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John Bowlby and Attachment Theory

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Synonyms

[Affective bond](#); [Emotional bond](#); [Theory of close relationships](#)

Definition

Edward John Mostyn Bowlby (1907–1990), British child psychiatrist and psychoanalyst, author of the evolutionary theory of attachment.

Introduction

Since its origin attachment theory has become the most important paradigm in contemporary developmental psychology and its author, John Bowlby, is considered to be one of the greatest psychiatrist of the twentieth century and father of contemporary psychotherapy. Attachment theory is one of the most important psychological theories that can be applied to explain personality growth, behavior, and human relationships across the life course. Bowlby's theory of loss, grief, and mourning is acknowledged as one of the major theories of bereavement (Shaver and Fraley 2008).

The Origin of Attachment Theory

Bowlby's theory has its roots in ethological and evolutionary sciences, cybernetics, information processing, control and systems theory,

developmental psychology, object theory, and psychoanalysis (Bowlby 1958; Bretherton 1992). His interest in ethology is particularly noteworthy as it constitutes the basic structure of the theory (Ainsworth 1990) and its main tenet according to which relationship between mother and infant is a result of biologically rooted need for proximity that has its origin in the process of natural selection (Bowlby 1958, 1969/1982). In this way, Bowlby rejected the current psychoanalytic notion that relationship between mother and infant derives from oral gratification (Bretherton 1992) and simply occurs because the pleasure of being fed becomes associated with mother's presence (Cassidy 2008). He was dissatisfied with social learning theory as well, where dependency was seen as based on secondary reinforcement. He also negated precedence of fantasy over real life experiences. All that placed him on the margin of psychoanalytic circles, that he wished to belong to, despite notable differences in thinking. Although Bowlby's ideas were different from psychoanalytical ones, he remained interested in psychoanalysis and merely intended to reformulate clinical thinking with ethological concepts by taking into account the impact of real life experiences on children's psychopathology and by gathering empirical findings to support theory. When it comes to the method of building his theory, Bowlby was closer to Darwin than Freud, as he especially valued "hard data" obtained by observation (van der Horst 2011).

Two papers, *Forty-Four Juvenile Thieves: Their Characters and Home Life* (1944) and *Child Care and the Growth of Love* (Bowlby 1965), are the first publications where Bowlby's major conclusion about what are the conditions of infant's mental health was outlined (Bretherton 1992). He proposed that separation from primary caregiver and maternal deprivation are main factors in explaining children's psychopathology. He wrote, "the infant and young child should experience a warm, intimate, and continuous relationship with his mother (or permanent mother substitute) in which both find satisfaction and enjoyment" (Bowlby 1951, p. 13) in order to grow up mentally healthy and to develop effective personality functioning. Paper from 1951, which

was the WHO report on consequences of maternal deprivation on child development, is marked as the beginning of so-called *ethological era* in Bowlby's scientific development (van der Horst 2011).

According to Bretherton (1992), the following three papers are regarded as the first formal statement of attachment theory: *The Nature of the Child's Tie to His Mother* (1958), *Separation Anxiety* (1959), and *Grief and Mourning in Infancy and Early Childhood* (1960), and never published two papers on defensive processes in mourning (1962).

In 1969, Bowlby started working on the first volume of the attachment trilogy: Attachment and Loss. volume 1. Attachment (1969/1982); volume 2. Separation (1973/1985); volume 3. Loss. Sadness and Depression (1980/1991).

Basic Tenets of Attachment Theory

Attachment can be described from two perspectives: as a behavioral control system with its specific predictable outcome or as an emotional bond, a relationship between two individuals.

From evolutionary perspective, attachment is one of the innate motivational systems that provides survival advantage (Bowlby 1969/1982; Cassidy 2008). It has behavioral, affective, cognitive, and neurophysiological components. The main goal is to obtain and keep the proximity or accessibility to a discriminated primary caregiver, which gives the child protection (survival function) and a feeling of security (psychological function). The biological nature of the system is responsible for instinctual activation of attachment behaviors on the part of the child. These behaviors operate in a goal-corrected manner, which means they are flexibly used according to the needs of the child and current situation (Bowlby 1969/1982). When attachment system is activated – by cues of external danger or any kind of distress – it causes neurophysiological arousal and inhibits working of other behavioral systems (such as exploration). In this state a child seeks proximity and comfort from attachment figure, whose role is to respond to the signs

of distress in an effective manner. Individual differences in organization of the attachment system are shaped by interaction with a specific caregiver (attachment patterns, attachment styles, attachment strategies). Moreover, attachment experiences are represented in internal working model – cognitive–affective representations of *self*, attachment figure, and interaction between them. These structures shape expectations, memory, perception, and behaviors. They are also used to appraise the situation, plan one's own action, and its consequences. They act predominantly in an automatic manner. What plays vital role in organizing memories of attachment experiences is an affect (Pietromonaco and Feldman-Barrett 2000). In addition, affect activates content of working models of attachment.

Attachment described as an affectional bond refers to an intimate emotional bond a weaker and less experienced individual has with another one, regarded as stronger and/or wiser (Bowlby 1969/1982, 1973/1985, 1980/1991, 1988). It is formed first between a child and a care provider, and between adults in later life. According to Ainsworth (1989) it is not a dyadic tie but a characteristic of an individual. Therefore, one can be attached to someone who is not in turn attached to him or her. Attachment bond was described by Bowlby and Ainsworth as a specific type of affectional bond. It is persistent, involves a specific person with whom one has emotionally significant relationship, and desires to maintain proximity and contact with (Cassidy 2008), as it is in the case of any other affectional bond. But additionally, attachment bond serves a specific function: security and comfort are looked for in this relationship. As Bowlby outlined, breaking of this bond (caused, for example, by separation or loss) has profound impact on well-being of an individual, which does not take place to the same extent when other, nonattachment bonds are lost (Bowlby 1969/1982).

Bowlby emphasized the importance of emotions that arise in attachment relationships (Bowlby 1969/1982, 1988) – joy and sense of security when proximity with caregiver is maintained; jealousy, anxiety, and anger when the bond is threatened; and sadness, grief, and depression when the bond is broken. He stated

that these affective responses are a product of evolution. According to Bowlby, positive affects accompanying attachment relationship and negative affects accompanying loss or threat of loss motivate child to maintain this bond. They serve to alert the caregiver to the child's interest in maintaining the relationship (Bowlby 1973).

Attachment theory is described by some researchers as the joint work of John Bowlby and Mary Ainsworth (Bretherton 1992; Cassidy 2008). Ainsworth introduced the notion of individual differences in patterns of attachment, administration of Strange Situation, the concept of the attachment figure as a secure base of exploration, and the concept of maternal sensitivity.

Conclusion

Attachment theory has a lot to offer in the field of infants' mental health. Within the attachment framework, where mental representations of attachment (working models) are considered to give an access to organization of attachment system in adolescence and adulthood, there is also a possibility of studying attachment and its contribution to personality development and psychopathology in adulthood as well. There is growing body of research in the field of intergenerational transmission of attachment and its stability throughout life cycle. It is not surprising then that the attachment theory is used in the prevention and intervention programs for supporting early attachment security, in foster and adoptive care, in child care policies, in psychotherapy – just to enumerate few ways of applying it in practice.

Cross-References

- ▶ [Attachment Theory](#)
- ▶ [Evolutionary Foundations of the Attachment System and Its Functions](#)
- ▶ [History of Attachment Theory](#)
- ▶ [John Bowlby](#)
- ▶ [John Bowlby: Pioneer of Attachment Theory](#)

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who founded attachment theory, drawing on evolutionary theory and ethology, cybernetics, and cognitive theory.

Introduction

John Bowlby, a psychoanalyst and child psychiatrist, sought to reform and modernize psychoanalysis to give it a scientific basis, as he was unsatisfied with parts of its metatheory. Bowlby was particularly concerned with the psychoanalytic explanation of why children develop strong emotional bonds – attachments – to their caregivers, monitoring proximity to the caregiver(s) and showing distress upon separations. Attachment was at the time considered secondary to other processes, such as special forms of psychical energies, which Bowlby argued was unscientific. As outlined below, Bowlby came to draw on ethology, cybernetics, and cognitive psychology and argued that humans and other primates over the course of evolution have developed an attachment behavioral control system with a goal of maintaining proximity to caregivers. This attachment behavioral control system was proposed to have served an evolutionary function of protection from predators and natural dangers, thus increasing survival and reproduction. Bowlby, who himself had experienced an influential separation from a caregiver (i.e., his nanny), also emphasized the importance of actual experiences with caregivers (i.e., quality of caregiving) for children's psychological development and the need for testable psychological theories and empirical methodology using prospective designs.

John Bowlby: Pioneer of Attachment Theory

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Definition

Edward John Mostyn Bowlby (1907–1990): A British child psychiatrist and psychoanalyst

Childhood and Education: Development of an Interest in Close Relationships with Caregivers and Effects of Early Separations

In keeping with the proposals of attachment theory – that early experiences with caregivers affect the development of the person and how we come to view ourselves and others – roots to Bowlby's lifelong interest in the importance of close and

enduring relationships between children and their caregivers may partly stem from his own early experiences. Bowlby was born as the fourth of six children in an upper middle class family in London, his father a doctor and surgeon to the royal family. The family situation was typical for its social class of the time, with nanny's taking care of the household and the children. Bowlby's interactions with his mother were therefore limited and, apart from holidays, typically restricted to her reading aloud to the children during an hour in the afternoon. It is thus not surprisingly that Bowlby formed his first strong emotional bond to one of his nannies, Minnie. However, Minnie left the family when Bowlby was only 4 years old. Bowlby admitted that this was a painful loss to him, and he likened it to losing a mother figure (Van Dijken 1998). During the First World War, when he was 10 years old, Bowlby was sent to boarding school together with his brother so that they would escape the presumed bombings of London. Bowlby however thought this was just an excuse, and that he would have been sent to the boarding school anyway, as this was the traditional first step towards becoming a gentleman (Holmes 1993). Thus, these early experiences may have affected his interest in the potential negative effects of early separations from caregivers and the importance of children's experiences with their caregivers.

After boarding school Bowlby went to the navy cadet school to embark on a career as an officer. However, Bowlby soon got tired of this life, partly as he thought it would not give him opportunities to change the world for the better (Van Dijken 1998). Bowlby then studied medicine at Cambridge University, following in the footsteps of his father. He then came in contact with developmental psychology, gave up medicine, and chose to work as a teacher for a year. This experience, which included 6 months at a school for maladjusted children, came to have a marked influence on him, as he observed that many of the maladjusted and antisocial children he was working with had experienced a difficult childhood, including separations from their caregivers and being cared for by multiple substitute caregivers. Through a colleague Bowlby also got in contact

with psychoanalysis. Indeed, Bowlby regarded this as the most important 6 months of his career, realizing that psychological problems should be understood at a developmental level and being influenced by experiences with caregivers. After his year as a teacher Bowlby studied psychology at Trinity College and worked with maladjusted children before eventually enrolling at University College Hospital in London to qualify in medicine and pursue a career as a child psychiatrist.

Bowlby and Psychoanalysis: A Complicated and Conflicted Relationship

To become a child psychiatrist he also enrolled himself at the institute for psychoanalysis, as psychoanalysis was a good basis for working with children. However, he first had to train in adult psychiatry, which included going through psychoanalysis himself, which he did with a coworker of Melanie Klein (his supervisor), Joan Riviere, as his analyst. Bowlby agreed with Melanie Klein and her colleagues that children's first year are important for their subsequent development but disagreed heavily with the psychoanalytical explanations of the processes responsible for children's development and functioning. When discussing attachment theory in relation to psychoanalysis, Bowlby (1980) referenced Rapaport and Gill (1959), who described the psychoanalytical metatheory in terms of postulates regarding five principles (see ► [“Psychodynamic Foundations”](#)). Bowlby specifically questioned the “dynamic” and “economic” principles of the metatheory, which he termed the “psychical energy model.” According to this model humans are endowed with distinct types of psychical energies that builds up and needs discharge in order for homeostasis and that children's development is affected by the channeling of these energies and infantile fantasies about their caregivers. Bowlby felt that this postulation was unscientific and that it did not sufficiently acknowledge the importance of children's actual experiences with their caregivers. Indeed, according to these theories attachment was secondary to processes such as feeding

and psychical energies. Bowlby thus termed these theories “secondary drive theories.” After being blocked several times Bowlby eventually got accepted into the British Psychoanalytical Association, stubbornly outlining his own ideas in his thesis “The influence of early environment for the development of neurosis and neurotic character” (1940). Interestingly, Bowlby called Klein his anti-thesis and felt that he learned more from the social workers he was working with at a child psychiatrist clinic than he did from his psychiatrist colleagues.

Bowlby was part of a “third-wave” psychoanalytic school, often referred to as the British school of objects relations, and which also included for example Donald Winnicott, Michael Balint, Harry Guntrip, and Ronald Fairbairn. Bowlby was particularly influenced by Donald Winnicott, who shared his view that children come into the world sensitive to social interactions and in need of healthy interactions to develop well. Although the object relation theorists agreed on some things there were also notable differences. A major difference, according to Bowlby, was that the other object relation theories, in comparison to his attachment theory, lacked an alternative to the instincts/drives proposed by Freud. Indeed, Bowlby felt strongly that in order for change to occur there had to be alternatives to Freud’s theory. Of course, the alternative that Bowlby came to suggest was attachment theory. Bowlby was however careful to state that attachment theory is a much more narrow theory than psychoanalysis, pertaining to one behavioral system, and not a theory that could exchange psychoanalysis as a whole.

Given that Bowlby contested some of the core tenets of psychoanalytic theory, that psychoanalysis at the time was rather territorial, and that the scientific methodology Bowlby argued for was largely alien to the psychoanalytical field, it is maybe understandable that Bowlby’s ideas were largely rejected by the psychoanalytic community and that Bowlby was deemed a reductionist that was willing to sacrifice central psychoanalytic concepts for what was observable. Bowlby was vice president in the British Psychoanalytical Association 1956–1961, under Donald Winnicott,

but got increasingly ostracized, and after his position as vice president ended he gradually decreased his involvement and settled for passive membership. Bowlby was saddened, and puzzled, that his work in trying to modernize the psychoanalytic theory was rejected, particularly as he thought that attachment theory was in many ways in accordance with some of Freud’s ideas, although formulated in modern scientific terms. For example, Bowlby agreed with Freud that we have psychological defenses against anxiety, although he formulated the defenses based on information processing and memory in terms of cognitive-affective strategies for dealing with threatening information (i.e., defensive exclusion and shifting of attention).

Attachment theory, together with the empirical research it has generated, has however become an important part of several modern psychoanalytical approaches and is now often seen as an important empirical foundation of psychoanalysis (Fonagy et al. 2008). An important factor in this rapprochement was the advent of the Adult Attachment Interview and other representational and linguistically based methods used for examining attachment in older children, adolescents, and adult (Main et al. 1985), which were developed based on Bowlby’s concept of internal working models of self and others (see ► [“Offspring–Parent Attachment”](#)).

Scientific Work and Collaborations: Scientific Evidence for the Importance of Close Relationships with Caregivers, Negative Effects of Early Separations, and the Development of Attachment

After the Second World War, Bowlby became head of the Tavistock clinic’s child department, where he remained until his retirement in 1972. Tellingly, he immediately renamed the department “the department for children and parents,” to acknowledge a family perspective on children’s psychological problems. In 1944 Bowlby published a collection of clinical case reports, in which he compared the background of 44 children treated for antisocial behaviors with an equal

number of children treated for other behavior problems. Bowlby found that the antisocial children had experienced markedly more losses and separations from their primary caregivers. Negative effects of separations from caregivers were also reported in children who were evacuated from their families in London (i.e., separated) so as not to have to suffer the bombings (Freud and Burlingham 1943). Reinforced by these findings, Bowlby went on to seek more evidence for the untoward effects of separation and the development of attachment.

Bowlby started up various scientific collaborations, most notably with James and Joyce Robertson and Mary Ainsworth. The Robertson couple, inspired by an ethological approach, conducted extensive, videotaped observations of children's reactions prior to, during, and after being separated from their caregivers in the context of hospital or orphanage care. These now classic observations demonstrated with brutal clarity how the children suffered (e.g., Robertson and Bowlby 1952). Bowlby and the Robertson couple attributed the ill effects to the (temporary) loss of the caregiver(s): "from empirical observation we suggested that the young child's hunger for his mother's love and presence is as great as his hunger for food" (Bowlby, p. xiii). The validity of the observations was initially questioned, and the reactions attributed to factors other than the separation from the caregiver(s) per se, such as the strange environment. However, the observations eventually initiated a revolution in child health care in the beginning of the 1950s. In this regard Bowlby was particularly thankful to Winnicott, whose clinical work helped influence policy change.

Mary Ainsworth initially conducted naturalistic observations of children's attachment behaviors in Uganda where she followed a number of children and their parents during the children's first year (Ainsworth 1967). This provided Bowlby with invaluable information about the early development of attachment (see ► ["Offspring-Parent Attachment"](#)) and how individual variations in caregiver behavior are related to systematic variations in children's organization

of attachment (see ► ["Individual Variations in Attachment"](#)). As regards the development of attachment, Ainsworth found that most children seemed to develop an attachment during the second half of the first year, whereby they started to direct their attention and behaviors selectively towards their caregivers and monitor their whereabouts, used the caregivers as a reference point for exploration of their environment (i.e., as a secure base), retreating specifically to the caregivers in times of distress (i.e., as a safe haven), and seeking to remain in proximity with their caregivers and protesting separations from them.

The WHO Report and the Seminar Group: Developing a Theory of Attachment Based on Evolutionary Theory and Ethology, Cybernetics, and Cognitive Psychology

In 1950, Bowlby was asked by the World Health Organization to make a report on the available knowledge concerning factors that may affect children's psychological health, particularly as regards the effects of separations. The report "Maternal Care and Mental health" was published in 1951, and through his work with the report Bowlby learned that other researchers and clinicians shared his ideas about the effects of early separations from caregivers. However, as discussed by Bowlby the WHO report had one major limitation, "whereas it had much to say about the many kinds of ill effects that that evidence shows can be attributed to maternal deprivation. . . it said very little indeed about the processes whereby these ill effects are brought into being. . . how does it come about that one or another of the events included under the general heading of maternal deprivation produces this or that form of psychiatric disturbance" (Bowlby 1980, p. xii)? Bowlby thus started turning his attention more towards understanding the nature of the special relationship – "tie" – between children and their caregivers.

After the WHO report Bowlby received funding that he used to start a seminar group, to

which he invited participants from various academic disciplines including biology, psychiatry, psychology, and social anthropology. If attachment is not a secondary drive but a primary motivation in its own right, what is it then, and how to explain it in scientific terms? The contact with ethology, through the pioneering control system ethologist Robert Hinde, got Bowlby in contact with the ethological work by, for example, Konrad Lorenz (1963) and Niko Tinbergen (1951). Their work included the phenomenon of imprinting seen in some species, such as birds, which shows some similarities with behaviors in mammals (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). Bowlby realized the potential of explaining human children’s propensities for developing strong and enduring bonds to their caregivers using ethological principles. Birds, although able to find food for themselves nonetheless developed bonds to their parents and followed them wherever they went. Thus, the bond must have served some other evolutionary function than feeding.

Bowlby also got in contact with Harlow’s (e.g., 1958) research with infant rhesus monkeys and surrogate mothers, extending the findings on imprinting in a species more closely related to humans. This became particularly important for Bowlby’s subsequent formulation of the attachment system as a primary motivational system (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). Bowlby visited Harlow, and although he explicitly questioned the methods Harlow used in his experiments with rhesus monkeys on ethical grounds, Harlow’s experiments gave Bowlby invaluable information. Indeed, they clearly indicated that the need for a close and enduring relationship with a caregiver – or attachment figure – is a primary motivation (cf. instinct) and not a secondary result of feeding. Bowlby, drawing from Darwin’s evolutionary theory as well as ethological concepts and research, argued that this “instinct” is a behavioral control system that has evolved and been retained because it has served a particular function in our evolutionary history. This function, according to Bowlby, is

protection from natural dangers such as predators, which follows from the predictable outcome of activation of the attachment system, proximity to caregivers. The similarities between humans and many other species regarding attachment bonds could, according to Bowlby, be explained with the notion of convergent evolution, as protection from predators have been common to many species of animals.

Bowlby also drew from cognitive theory and cybernetics in his formulation of the attachment system and its development. Bowlby was for example inspired by Piaget’s (1955) theory about children’s cognitive development, which came to influence Bowlby as regards the importance of cognitive development for the development of attachment during the early years. For example, older children are more able to endure separations due to their more advanced cognitive ability and perspective taking. Young’s (1964) and Craik’s (1943) theories, postulating that animals construct cognitive representations of the world, also influenced Bowlby in his proposal that the child’s experiences with his/hers attachment figures give rise to internal working models (IWMs; see ► [“Offspring–Parent Attachment”](#)) or affective-cognitive representations of self and others. Bowlby used the terms organismic and environmental models for these IWMs, which he argued were complementary. If a child is responded to in such a way that (s)he comes to perceive others as accessible and loving, (s)he will perceive him-/herself as lovable. Thus, when the IWMs are formed they are believed to affect how the child sees him-/herself, and how (s)he behaves in relation to close others, particularly in situations when the attachment system is activated. These models are hence important for predicting future situations with caregivers and important others and for efficient goal-directed behavior whereby the individual organizes his/her behavior based on the IWMs. This also provided Bowlby with an explanation of why children showed individual differences in attachment behavior and why children who had suffered from separations from their caregivers, and/or dysfunctional caregiving (i.e., had become insecurely attached),

many years later could come to show difficulties in developing close relationships, be described as affectionless and cold, or display antisocial behavior problems (see ► [“Individual Variations in Attachment”](#) and ► [“Individual Variations in Attachment”](#)).

Bowlby published the main tenets of attachment theory in three articles, “The nature of a child’s ties to his mother” (1958), “separation anxiety” (1960a), and “Grief and mourning in infancy and early childhood” (1960b). These articles, although initially largely ignored within psychoanalysis, were well received by researchers within developmental psychology, and Bowlby became a member of the medical research council in England. Bowlby thus got more time to think and write and subsequently published his classic book trilogy – attachment and loss – (1969, 1973, 1980), where he outlined the tenets of attachment theory in more detail, expanding on the three articles he had previously published.

Research Immediately Following in the Footsteps of Bowlby: Individual Differences in Attachment

Ainsworth (1967) had noted that the Ugandan children seemed to develop different strategies for maintaining proximity to their caregivers and that this seemed to depend on how the caregivers responded to the children’s signals. Seeking to replicate her Uganda findings in America, Ainsworth later devised a semi-structured laboratory observation, for which she methodologically drew on the ethologically inspired separation and reunion observations that the Robertson couple and Bowlby had used (e.g., Ainsworth et al. 1978). This laboratory observation, which induces slightly increasing levels of stress by means of a strange environment, a stranger, and two short separations from the caregiver, was deemed necessary to be able to observe children’s varying strategies for organizing their attachment behaviors in relation to their caregiver. Indeed, whereas the mere presence of Ainsworth in Uganda, where white women were uncommon,

had triggered the attachment system of Ugandan children, this was not the case in American children. The laboratory observation, which is called the strange situation procedure (SSP), is still today the most widely used method for observing children’s organization of attachment to their caregivers.

Briefly (see ► [“Individual Variations in Attachment”](#) for a thorough discussion), Ainsworth and her colleagues’ research indicated that children whose caregivers noticed the infants signals and responded timely and sensitively (particularly during distress, i.e., when the attachment system was activated) became securely attached to their caregivers, as indicated by a balance between the attachment system and an exploratory system. That is, secure children are able to use the caregiver(s) as a secure base from which to explore the environment when there are no signals of danger and to use their caregivers as a safe haven to return to for comfort and protection when distressed. Ainsworth and colleagues also identified two patterns of insecure attachment, insecure-avoidant and insecure-ambivalent/resistant, who do not show the same ability to use the caregiver as a safe haven and secure base, and which respective organization of behavior in relation to their caregiver could be predicted by specific patterns of caregiver insensitivity. Although Bowlby had argued from the start that the quality of caregiving is crucial to variations in attachment, he lacked an empirical method for examining caregiving in relation to attachment and hence focused on the effects of separation which were readily examined during the aftermath of the Second World War. He was therefore hugely grateful to Ainsworth for her contribution, and to acknowledge her Bowlby named his last book about attachment after one of her concepts, “A secure base” (Bowlby 1988).

Mary Main, a PhD student of Mary Ainsworth, later identified a fourth quality of attachment, disorganized/disoriented attachment, when seeking to understand the inexplicable and contradictory behaviors shown by some children who were therefore unclassifiable using Ainsworth’s established patterns (Main and Solomon 1990;

see ► [“Individual Variations in Attachment”](#) and ► [“Disorganized Attachment and Reactive Attachment Disorder”](#) for a more thorough discussion). These children, she found, had one thing in common: a (momentary) breakdown in the organization of attachment behaviors in relation to the caregiver. As opposed to secure and organized insecure children (i.e., avoidant and ambivalent), these children could not maintain an organized strategy in relation to their caregivers in the strange situation. Main argued that a cause of this breakdown in behavior is that the attachment figure (i.e., source of safety) is simultaneously represented as a cause of alarm. She termed this “fright without solution,” an unsolvable behavioral paradox of simultaneously seeking to approach and avoid or escape the caregiver. Bowlby’s (1980) notion of “segregated systems” provided important guiding principles for Main’s theory of the development of disorganized attachment, which was in turn received favorably by Bowlby (Duschinsky 2015). Main and colleagues argued that disorganized-disoriented attachment is most consistently predicted by frightening/frightened behaviors on behalf of the attachment figure (e.g., Main and Hesse 1990).

Conclusions

Bowlby sought to develop a scientifically based theory for the phenomenon of attachment between children and their caregivers, to reform the parts of the psychoanalytical metatheory that he could not accept. In so doing Bowlby drew on his own work as a child psychiatrist, his scientific collaborations and the information he gathered from the seminar group he started and which included participants from various scientific disciplines, most notably ethology and cognitive psychology. A notable feature of Bowlby’s work was thus an openness to draw on and integrate available knowledge from various scientific disciplines. Bowlby concluded that humans, as some other animals, are endowed with an attachment behavioral control system, which functions to seek and

maintain proximity to (usually) protective caregivers and which thereby increases the chances of survival and reproduction.

Cross-References

- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Individual Variations in Attachment](#)
- [Psychodynamic Foundations](#)
- [Robert Hinde](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)

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John Hartung (1995) Love Thy Neighbor

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Synonyms

In-group morality; Neuroethics; Religion

Definition

People are more likely to harm those perceived to be members of an out-group in a manner in which they would not harm members of one's in-group. When someone in one's in-group transgresses against a social contract, we are more likely to "look the other way" than if it were a member of the out-group performing the same behavior (Jost et al. 2008; Staub 1999; Tajfel 1982).

Introduction

In 1995, John Hartung's article, *Love Thy Neighbor: The Evolution of In-Group Morality*, appeared in *Skeptic* magazine. In it, the SUNY anesthesiologist and anthropologist explains how the Bible is a blueprint for in-group morality, out-group homogeneity, and world domination. The article uses passages from the Old Testament to highlight the interplay between religion, a proximal factor, and ultimate factors described by evolutionary psychology. Specifically, he shows how moral and ethical decrees against murder and theft outlined in the Bible apply to one's in-group but not to an out-group – for the sole purpose of competitive gain. Realistic conflict theory (Campbell 1967; Sherif et al. 1961), a concept heralded by many proponents of the Standard Social Science Model (Cosmides and Tooby 1992), is cast in Hartung's article as an analogue to the distal concepts of kin selection and to the co-opting of resources of one's rivals (Buss 1999). Hartung's article resurfaced in 2006 in Richard

Dawkins' *The God Delusion* and given the current state of polarization in social relations at the time of the drafting of this submission; there is hope that a new dialogue may emerge.

Intergroup Dynamics

From the standpoint of evolutionary psychology, it makes perfect sense to love, be friendly, and to be open with our tribe, family, or race. However, this dynamic is bidirectional. Humans also have a biological preparedness to protect one's in-group from outsiders and be suspicious of those who are "other" or "not like us" (Cikara and Van Bavel 2014; Kappeler and van Schaik 2006). Indeed, we not only have positive feelings about those who are perceived to be "one of us" in terms of norms, customs, and values, but we also have strong *negative* reactions toward those who are deemed to be somehow "other." For example, when African Americans and whites were shown pictures of one another, they both showed elevated levels of activity in the amygdala (the brain region associated with fear and aggression) (Wheeler and Fiske 2005). Perhaps even more chilling, 15–20% of Republicans and Democrats (US citizens) feel as though we would all be better off if large numbers of the opposing political party "just died" (Kalmoe and Mason 2019).

This in-group/out-group effect extends to features significantly less salient than race or political affiliation. Arbitrary and trivial features such as insignias on T-shirts (Cialdini et al. 1976) and art preferences (Tajfel et al. 1971) form what psychologists call minimal groups and known to trigger tribal tendencies and parochial biases. Whether from an evolutionary standpoint or from a social scientific one, preferences for one's group allow for benefits to flow to in-group members and justify hostilities toward out-group members. Interesting, and less discussed in the literature, a strong preference for one's in-group has been shown to be a better predictor for prejudice than overt hatred of an out-group. In other words, disgust for "the other" may not be as powerful of a motive for hostility as is a strong preference for one's in-group (Greenwald and Pettigrew 2014).

The Biology of Morality

In Hartung's article, he cites the work of Nancy Segal (1984) showing that identical twins are more likely to use the word "we," cooperate, and get the job done quicker than fraternal twins. This is hardly surprising given the work of W.D. Hamilton (1964) who showed that acts of altruism will be directed more toward identical twins (the degree of relatedness, or r , being equal to 1) than those who are more distantly related (full siblings, $r = 0.5$; half siblings, $r = 0.25$; first cousins, $r = 0.125$; etc.). According to Hartung, this is the scientific principal which Moses' edict to love thy neighbor as thyself rests upon. For if one was directed to love thy neighbor as thyself, it would be no problem doing only so as long as one's neighbor was construed to be "like us" in a very fundamental way. But if a group or individual was considered "other" or "less than," whether in some real or perceived way, mandates to avoid murdering them could be given a pass. In short, "thou shalt not kill" meant "thou shalt not kill another Jew," and "love thy neighbor" meant "love thy neighbor, as long as that person is also Jewish."

Who Is Thy Neighbor?

According to Hartung's quoting of the Old Testament, one's neighbor isn't merely a person who is being victimized or in need of help as some have interpreted it. In fact, Hartung goes to great length to show that murder in the OT is not only *not* wrong, but it is in certain instances, divinely commanded. When the Lord of the OT commanded Moses to tell others to not kill their countrymen, it should be noted that this was at a time where one's countrymen were essentially people living right next door. What this meant was that one's neighbor was both (a) nearby and, therefore, (b) similar to one's self. Hartung summarizes this succinctly: "...when the Israelites received the love law, they were isolated in a desert. According to the account, they lived in tents clustered by extended families, they had no non-Israelite neighbors, and dissention was rife."

As predicted by literature supporting in-group/out-group theory, the law to not kill one's neighbor was given a pass when the person being killed was no longer construed as a "neighbor."

John Hartung's analysis of the Old Testament has received strong criticism from Jews and Christians not only for his use of evolutionary theory to describe cultural practices, but for his tongue in cheek style in doing so. He quips that "although Moses may not have known about natural selection," it is as if he "had a sense of Hamilton's inclusive fitness." Although Jews are one of the most persecuted groups in modern times, Hartung pulls no punches when he suggests they did not hesitate in committing genocide themselves.

They should be utterly destroyed and should receive no mercy but be exterminated as the LORD commanded Moses. (Joshua 11:20)

Utterly destroy all that they have; do not spare them, but kill both man and woman, infant and suckling. (I Samuel 15:3)

Some may read this in Hartung's paper and jump to the conclusion that he is biased on this topic merely due to his association with Noam Chomsky. However, it should be noted that Napoleon Chagnon, Richard Dawkins, Robert Trivers, and many others were included in the list of people Hartung corresponded with for the drafting of his document (1995).

Religious Justification

"The point, however, is not that such phenomena were unique to the ancient Israelites. Far from it. Indeed, given the ubiquity of in-group/out-group double standards around the globe and throughout history, the propensity for in-group morality appears to be an attribute of human nature" (Hartung 1995). Hartung is correct, but his article only weighs in on the OT. Had he delved into the passages from other sacred works, this author is certain he would have had no difficulty in procuring additional verses to support his thesis. One reason most people do not hear of these verses as often is because they are cherry picked to "play nice" and keep things clean and friendly. Take for example this oft cited verse from the Quran:

...if any one killed a person, it would be as if he killed the whole of mankind; and if any one saved a life, it would be as if he saved the life of the whole of mankind. ... (Surah 5:32)

On the surface, this sounds reasonably in line with a universal code of humanitarian action and has been used to posit that very perspective. But the extension of the altruism, like with decrees in the OT, comes to an abrupt end when one reads the very next verse (not surprisingly, a verse often omitted when the previous one is cited):

The punishment of those who wage war against God and His Apostle, and strive with might and main for mischief through the land is: execution, or crucifixion, or the cutting off of hands and feet from opposite sides, or exile from the land: that is their disgrace in this world, and a heavy punishment is theirs in the Hereafter. (Surah 5:33)

It's difficult to know precisely why Hartung chose one holy book (over others) to exemplify intergroup rivalry, but he is correct in saying that this human propensity is ubiquitous and likely universal.

Realistic Conflict

In virtually every single social species studied, including ants (Shaffer et al. 2016), elephants (Plotnik et al. 2011), and vampire bats (Wilkinson 1984), selfishness is limited in order to increase the reproductive fitness of the group. The spat over group selection has been ongoing and there are few signs of feuds subsiding. In fact, heated debates over this issue have been documented between such learned individuals as E.O. Wilson and Richard Dawkins (Johnston 2014). Despite this disagreement, the evidence is clear: *genes* replicate – groups do not. However, what is also clear is that some groups thrive, while others fall into the evolutionary dustbin. In the *Extended Phenotype* (1982), Dawkins draws this analogy through the literary use of the Necker cube. At one instance, Dawkins shows, it is incontrovertible that genes replicate; however, the story can gestalt into the nearly simultaneous view that successful groups pass their genes on, while unsuccessful groups do not.

This issue is especially poignant when one considers the Israeli and Palestinian conflict. While supporters on either side feel they are unanimous, correct, and infallible, the evidence not only does not support their naive reality, it completely contradicts it. Indeed, this is exactly what the psychologist Lee Ross (2002) found when he studied in-group/out-group dynamics in these populations. He and his colleagues asked Palestinians and Israelis to draft peace proposals that were to be submitted to the “other side.” Predictably, both sides’ proposals favored their own narrative. However, before the research team reintroduced the proposals to their respective populations, they switched the names on the documents. Peace proposals drafted by Israelis that favored Israelis were entitled “Palestinian Proposals” and peace proposals drafted by Palestinians that favored Palestinians were entitled “Israeli Proposals.” Unsurprisingly, and sadly, Israelis and Palestinians rejected their own proposals that would have otherwise favored their group – simply because of the perception that it carried of the “other.”

Conclusion

Humans are by nature social creatures and it is in our nature to compete against environmental conditions as well as with one another. This has helped us not just survive – competition has helped humans achieve greatness. But as Dawkins pointed out in the *Selfish Gene* (1976), selfishness and cooperation could not have evolved independent of one another. These evolved strategies are not mere ideas painted on a blank slate. If humans are to continue to survive into the deep evolutionary future, the main out-group must not be limited to humans, but must include climate change, asteroids, and the incontrovertible finitude of our star. Carl Sagan (1994) said it best:

...every surviving civilization is obliged to become spacefaring – not because of exploratory or romantic zeal, but for the most practical reason imaginable: staying alive.

Cross-References

- [Evolutionary Psychology](#)
- [In-Group Morality](#)

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Synonyms

2D:4D; Digit ratio; Finger length; Prenatal hormones; Symmetry

Definitions

Prenatal effects of sex steroids on fertility, behavior, and health.

Introduction

John Thomas Manning (b. 1942) is best known for his work on digit ratio (or 2D:4D), i.e., the relative length of the index finger (2D) and the ring finger (4D), as a biomarker of prenatal sex steroids. He has pioneered this work by investigating relationships of 2D:4D with various measures of fertility, health, and behavior. Over the past 20 years, Manning has published numerous papers and two books that have stimulated digit ratio research in animals and humans. In addition to his work on 2D:4D, he is an expert on symmetry and has contributed a number of significant studies in humans and animals, especially on symmetry-performance relationships.

Sex and Symmetry

John Manning studied biology at the University of London (BSc) before he moved to the University of Liverpool, where he completed his MSc in Evolutionary Studies and his PhD in Zoology. He devoted a series of early scientific contributions to questions in theoretical biology related to mate selection, sexual reproduction, and the evolution of sex (e.g., Manning 1975, 1982a, b, 1984). Later he developed a strong interest in the biology of symmetry and began to investigate relationships of fluctuating asymmetry (a measure of developmental stability) and directional asymmetry (laterality) in humans and animals. Most notable of this work is the insight that asymmetry of canine size in old world primates is related to sexual dimorphism and male competition (Manning and Chamberlain 1993), and that these asymmetries are sensitive to environmental stress (Manning and Chamberlain 1994). Manning reported that fluctuating asymmetry (FA) in the legs and heads of racehorses correlates negatively with their racing ability, suggesting that FA could predict animal performance (Manning and Ockenden 1994). For humans, he reported a negative correlation of FA with body weight in men and a positive correlation in women (Manning 1995), leading him to speculate that selection pressures operate differently on male and female

size. Manning also showed that temporary, within-individual changes across the ovulatory cycle in asymmetry exist. Women were less asymmetric in mid-cycle, and this information may be used by males to assess female fertility (Manning et al. 1996).

By applying insights on FA-performance relationships in animals to similar tests in humans, Manning and Pickup (1998) demonstrated that symmetry in middle distance runners (800 m and 1500 m) indicated good running ability, i.e., symmetrical athletes had higher rankings for athletic ability. Given his considerable contributions to the study of symmetry in biology, it is not surprising that Robert Trivers teamed up with Manning and colleagues in the Jamaican Symmetry Project (JSP) to investigate long-term effects of FA on development in children (Trivers et al. 1999). The JSP has produced a number of significant findings on FA relationships with physical and behavioral correlates, including recent evidence on knee symmetry in children as a predictor of sprinting performance in adulthood (Trivers et al. 2013).

Digit Ratio (2D:4D)

Finger lengths of left and right hands are typically measured in studies that investigate relationships with a composite measure of FA, and Manning had included this trait in previous studies on relationships with, for example, male ejaculate size and sperm quality (Manning et al. 1998a). Manning and colleagues reported that the ratios of the 2nd and 4th digit length of left and right hands are sexually dimorphic (males < females), and that this dimorphism is likely established in utero under the influence of testosterone and estrogen concentrations (Manning et al. 1998b). This classic study found that in men 2D:4D negatively correlated with testosterone concentration and in women 2D:4D positively correlated with estrogen concentration. In addition, sperm number was negatively related to 2D:4D. Importantly, 2D:4D showed sex differences as early as 2 years and the values of 2D:4D and the sexual dimorphism remained relatively constant across childhood

and through puberty. Subsequent studies showed that the sexual dimorphism in 2D:4D is found across societies (although 2D:4D shows ethnic variation) and correlates with various measures of developmental health, morphology, and performance. To date, digit ratio research includes more than 700 publications stimulated by Manning's suggestion that 2D:4D provides a noninvasive measure of prenatal hormonal action.

In 2005, John Manning contributed to a large-scale web-based survey, commissioned by the British Broadcasting Corporation (BBC), designed to investigate sex differences, which collected data from 255,000 participants. With this large dataset, Manning has continued investigations of 2D:4D relationships across nations by considering national means of 2D:4D. These studies have revealed insights into prenatal hormonal effects on, for example, sexual orientation (Manning et al. 2007), handedness (Manning and Peters 2009), reproductive success (Manning and Fink 2008), gender inequalities (Manning et al. 2014a), personality (Manning and Fink 2011a), nicotine and alcohol consumption (Manning and Fink 2011b), and masculinity/femininity (Manning et al. 2017). In addition to large sample studies, Manning emphasizes that correlations of 2D:4D with testosterone- and estrogen-dependent behavior are particularly evident in studies that consider organizing effects of 2D:4D on activating effects of sex steroids (Manning et al. 2014b).

Conclusion

John Manning has contributed significantly to the study of symmetry in biology. His work on digit ratio as a noninvasive measure of organizing effects on behavior and health has stimulated numerous studies in animals and humans since the late 1990s. He has published two books on this topic (Manning 2002, 2008). The results of his recent research on 2D:4D across nations provide insight into global patterns of prenatal hormonal activity by highlighting communalities and ethnic variation in relationships with sex-dependent behavior and health.

Cross-References

- [Bernhard Fink](#)
- [Biology of Human Gender, The](#)
- [Digit Ratio](#)
- [Fluctuating Asymmetry](#)
- [Hormone Effects on Human Fetal Development](#)
- [Robert Trivers](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)

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Synonyms

JMS

Definition

An evolutionary biologist who pioneered the application of game theory to understand behavioral evolution across many species.

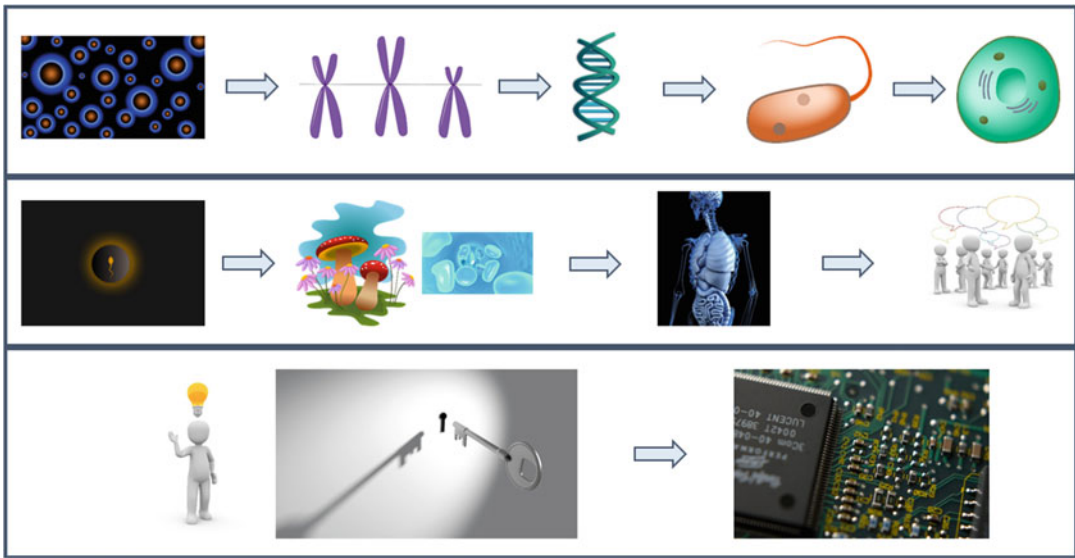
Introduction

John Maynard Smith (1920–2004) was a theoretical and evolutionary biologist, known as one of the pioneers in applying mathematical models to the understanding of behavioral evolution and diversity across many species. He developed a very early interest in natural history as a young boy and was educated at Eton before taking his first degree (Engineering) at Trinity College Cambridge, and then working on military aircraft design during World War II. He subsequently studied zoology at University College London (UCL), where he trained later as a graduate student of JBS Haldane (1892–1964) working on *Drosophila*, although he did not take his PhD as he was offered a faculty position in the same department. He left UCL to become the founding Dean of the School of Biological Sciences at the University of Sussex, retiring in 1985 but still continuing to work and publish until the later years of his life. After his death from mesothelioma, he was survived by his wife Sheila (deceased), two sons and one daughter. He was the recipient of numerous awards and fellowships, including Fellow of the Royal Society, Foreign Associate of the National Academy of Science of the USA, the Darwin, Royal and Copley Medals of the Royal Society, the Crafoord Prize, the Kyoto Prize and (posthumously), the Darwin-Wallace Award. His major books included *The Theory of Evolution* (1958), *The Evolution of Sex* (1978), *Evolution and the Theory of Games* (1982), *The Major Transitions in Evolution* (1995) (with Hungarian biochemist Eörs Szathmáry), and *Animal Signals* (2003) (with David Harper). He was influenced by, among others, the work of Charles Darwin, JBS Haldane, Ronald Fisher, and Helen Spurway. His contemporaries included George Williams, and he had robust debates with many academics including

Richard Lewontin and Steven J Gould. His exchanges and recorded interviews put him across both as an excellent debater and communicator and a kind and caring person. He published extensively (244 papers) in high profile journals including *Nature*, *Proceedings of the Royal Society of London B*, and *Proceedings of the National Academy of Sciences*, primarily with sole-authored work but also with colleagues including Brian Spratt (microbial genetics) and George Price. His work on the evolution of sex and recombination, aging and molecular evolution and population genetics were also very influential (e.g., Maynard Smith and Haigh 1974; see also Charlesworth 2004 and Charlesworth and Harvey 2005 for further discussion and personal accounts).

Major Contributions and Phenomena of Interest

The few talks and interviews of JMS preserved online at the time of writing include his interviews with writer Robert Wright in 2003 and biologist Richard Dawkins (*Web of Stories*, 1997) and his lecture *The Origin of Life* delivered as part of *The Royal Institution Discourse* in 1995. This latter talk outlined some of the key principles and ideas informing his theoretical work including one central reoccurring theme where evolution is conceptualized as the transmission of information through time via genetic and cultural means (Maynard Smith 2000). Indeed, with his colleague Eörs Szathmáry (Maynard Smith and Szathmáry 1995), he analyzed the key transitions in evolutionary history, representing changes in how information is transmitted and stored over time (see also Szathmáry and Maynard Smith 1995. Illustrated in Fig. 1). First, replicating molecules transition into populations of molecules. Next, storage transitions from independent replicators to chromosomes and then to ribonucleic acid (RNA). In a wonderful exposition of these ideas for a general audience, David Deutsch (2011) outlines how we have a catalytic process with RNA – something that promotes change in another entity while it remains unaltered, in this instance depending on the sequence of the constituent



John Maynard Smith, Fig. 1 Illustration of key transitions in evolution. Groups of molecules to chromosomes, RNA, and DNA. The first living organisms to eukaryotes, sexual reproduction, multicellular organisms, eusociality and the emergence of hominins, language, and technology.

The very recent emergence of the industrial revolution and new technologies underpinned by Enlightenment ideas (i.e., the expansion of information and knowledge through culture). (All images used under Creative Commons license (Pixabay))

molecules within RNA. Then, Maynard Smith and Szathmáry suggested that evolution transitions from storing information via RNA to the storage of information via DNA, which may have been due to the selective force of greater chemical stability in the latter versus the former, enabling the storage of larger amounts of information. With this stage we see a shift from prokaryote cells (meaning “before” the “kernel/nut”), related to the first living organisms Archaea and bacteria, to eukaryotes, where cells now have a nucleus enclosed within a membrane. Next, evolution transitions from asexual to sexual reproduction, followed by multicellular organisms with unlimited heredity, leading to animals, plants, and fungi where “like begets like.” These provide the conditions, eventually, for hominin evolution where a key transition in many species including our own was from individual to group living (eusociality) and the final key stage represented the transition to language in humans. With the presence of finite rules of vocabulary to convey a large number of meanings, humans in very recent evolutionary history could develop early technologies and would eventually expand their

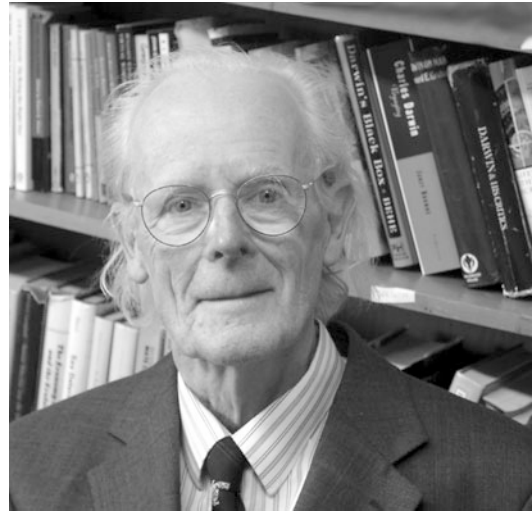
“reach” over the planet via Enlightenment ideas, as technology combined with language enables faster cultural evolution relative to genetic evolution (see also Deutsch 2011 for further discussion). Collectively, their speculations on these issues generated much discussion within behavioral science and science more generally.

Over the latter part of his career, Maynard Smith primarily conducted theoretical work, and used modeling to explain a wide variety of phenomena including avian flight, locomotion, contest competition, female mate choice for good genes, foraging, and the population sex ratio. His debates with contemporaries were important in cementing a theoretical shift from a focus on behavior that could be considered adaptive from the point of view of the species to that which was beneficial, in Darwinian terms, from the point of view of an individual’s reproductive fitness. He illustrated these phenomena and his game theoretic models using empirical work from many different species. For example, he examined badges of status in Harris Sparrows (*Zonotrichia querula*) and Evening Grosbeaks (*Coccothraustes vespertinus*), ownership of territory and contest

competition in Hamadryas Baboons (*Papio hamadryas*), Funnel-web spiders (*Agelenopsis aperta*), Great tits (*Parus major*), and Speckled wood butterflies (*Pararge aegeria*), and the locking of antlers and vocalizations in contests for mates among red deer (*Cervus elaphus*).

Colleagues commented on JMS' exceptionally clear communication of the biology of complex systems and his commitment to public engagement with science, albeit without supervising many graduate students himself (Charlesworth 2004). In one example of his scientific writing (Maynard Smith 1978), he outlined the assumptions involved in optimization in evolution, and offers a fair and engaging response to one critic of these ideas, Richard Lewontin. In his review paper, he notes that there are constraints on what is possible in evolution. If not, to paraphrase, species would be immortal and/or invincible to predators with an unlimited capacity to reproduce (see Maynard Smith 1984). As such, we can use mathematical models from engineering and economics in order to explain biological diversity. For example, we can study the optimization of anatomical structure or skills such as foraging, reflecting a gradual process of change where different species may have evolved different solutions to an identical problem. Here, according to his argument, we can understand the selective forces responsible for the trait and form testable hypotheses based on careful assumptions. He was clear to point out that nature itself does not generate optimal solutions but traits or behaviors can have functional explanations if they are widely observed even when maladaptive – “perfect” adaptation would equate to no further evolution of that trait (Maynard Smith 1984). Models can then be revised in light of the evidence and are of use if they capture some essential feature of a complex system.

Perhaps one of John Maynard Smith's (Figs. 2 and 3) most notable achievements in his academic career was his application of game theory to explain animal behavior, using a framework originally applied to understand political conflict (von Neumann and Morgenstern 1953). Critically, however, his concept of the Evolutionary Stable Strategy solved a problem within population



John Maynard Smith, Fig. 2 Portrait used with permission by Professor Adam Eyre-Walker. (Copyright Sussex University)

genetics, by examining the behavioral strategies that prevail in a population that cannot be invaded by a rare alternative. Here, he noted that as the environment a species finds itself in is not fixed, genetic variation within different local ecologies will be frequency dependent. Put another way, traits and behaviors will vary depending on the behaviors adopted by others in the population, where the fitness of a phenotype will be contingent on the other phenotypes present (see, e.g., Maynard Smith 1982). Perhaps his most well-known model in this area is the Hawk-Dove game (Maynard Smith and Price 1973). He used this model to explain contest competition in different species, including tournaments such as the locking of antlers among red deer and displays without physical contact, where the winner is the most persistent (Maynard Smith 1974). Here, resource holding potential (RHP) and honest signals of RHP play a role in settling disputes among species, such as size and weaponry and asymmetries in other traits irrelevant to fighting outcome such as ownership of territory. The Evolutionary Stable Strategy in his models is the strategy that, if adopted by the population, cannot be invaded by an (alternate) mutant strategy under the conditions of natural selection.

John Maynard Smith,
Fig. 3 Pictured with
 Sewall Wright (1980).
 (Used with permission
 (Professor Brian
 Charlesworth))



One example of the logic from his models concerns contest competition. In simple versions of the Hawk-Dove game (Maynard Smith and Price 1973), it pays to follow a combination of hawkish and dovish strategies in competitive encounters when the costs of competition are greater than the value of the contested resource. By contrast, it pays to be a hawk if the value of the contested resource is greater than the cost of competition (Maynard Smith 1982). This game calculates the evolutionary payoff to pursuing one of two strategies and how, over several generations, hawks or doves may reproduce and proliferate within a population (i.e., the change in fitness due to pursuing a given strategy). For example, when cost is greater than reward, if one hawk or dove invades an entire population of opposites, the hawk proliferates when outnumbered by doves, as hawks can enforce costs with impunity. Doves proliferate when outnumbered by hawks, as they avoid costs to fitness by retreating and leave the hawks to inflict costs on one another (Maynard Smith 1982). Developing these classic ideas, new evidence using biological perspectives is emerging on the potential evolutionary conditions of warfare. In experiments and theoretical models, overconfidence appears to be an

important cause of warfare (Johnson et al. 2006) and this trait develops when the rewards of conflict sufficiently outweigh the corresponding costs (Johnson and Fowler 2011). Work such as this suggests that psychological mechanisms and the genetic basis underpinning different behavioral outcomes can sit within Maynard Smith's framework and motivate further work in the human animal.

Influence on Evolutionary Biology and Behavioral Science

In an interview with Robert Wright in the latter part of his life, Maynard Smith expressed some reservation about the application of evolutionary game theory to some aspects of human evolutionary psychology. Nonetheless, his concepts have influenced human ethologists and psychologists either directly or indirectly and will continue to do so. For example, his ideas are relevant to diverse topics in human behavior including physical formidability, asymmetries in male contest competition and “welfare trade-off ratios” (e.g., Puts 2010; Sell et al. 2009; Watkins 2018; Watkins et al. 2010), Darwinian medicine, human health

and aging, cues to cooperation and deception and their behavioral manifestations, facial expressions, primate vocalizations, and language as signals. A collection of essays in honor of John Maynard Smith (Greenwood et al. 1985) provides a very useful starting point for his contribution to science more generally.

Conclusions

John Maynard Smith stands as one of the primary theoreticians in evolutionary science during the latter half of the twentieth century. His mathematical models and clarity of argument helped shift focus within evolutionary biology from understanding behavior for the “good of the species” to understanding the diversity of life within specific environmental contexts. His work emphasized an understanding of how information is transmitted through evolutionary history, the structure of the population the animal is situated in and how its form and behavior within these environments suggests evidence of behavior that improves inclusive fitness. His work is important to biologist and zoologists, geneticists, and public health researchers, and his ideas are relevant to psychologists interested in human behaviors such as contest competition and mate choice in specific contexts.

Cross-References

- [Darwinian Medicine](#)
- [Game Theory](#)
- [Male-Male Competition](#)
- [Sex Ratio](#)
- [Size and Dominance](#)

Acknowledgments I am grateful to Professor Brian Charlesworth for comments on an earlier version of this manuscript.

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John Ray

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Synonyms

Joanne Raio, Joannis Raii [Lat.]; John Wray

Life

John Ray (1627/8–1705, known as Wray until 1670) was an English clergyman whose work in natural history led to the modern scheme of the classification of species. Born of a blacksmith and his pious wife at Black Notley in Essex, Ray studied at Trinity College, Cambridge, where he subsequently held several teaching and administrative positions. He was ordained in 1660 after flirting with nonconformity, in order to maintain his college connection (Mandelbrote 2005). Ray was a member of the newly formed Royal Society and was subsequently honored by the foundation of the Ray Society in 1844 (Fig. 1).

Ray's contributions to biology and philosophy are manifold, but the most significant ones are his contribution to the design argument for the existence of God in natural theology, and to the definition of the notion of a species, which was the first singularly biological definition.

Much of Ray's natural history work was funded directly by Frances Willughby, son of a wealthy family from Warwickshire. Willughby and Ray collaborated in both zoology and botany, although an agreement was made that Ray should focus on botany and Willughby on zoology (Mickel 1973). After traveling with Willughby, Ray moved to his estate at Middleton. Willughby died in 1672 and left a bequest to Ray that allowed him to continue his researches, as well as publishing Willughby's own research, so long as he tutored Willughby's two sons. Ray married Margaret Oakley, a member of the household, and lived at the estate.



John Ray, Fig. 1 Woodcut frontispiece of John Ray, 1693, from *Synopsis methodica animalium quadrupedum et serpentinum generis*. (Source: Wikimedia Commons, Public Domain)

After Willughby's mother, Lady Cassandra, died in 1675, Frances' widow removed her sons from Ray's care and effectively ejected him and his wife from the household. They moved back to his birth village and he remained there until his death. He had four daughters, who aided his research when they were older.

Natural Theology

Ray's most widely read work was his *The Wisdom of God Manifested in the Works of Creation*, which he published at 64, just 4 years after Newton's *Principia* (Ray 1691; Berry 2011). The book was a revision of sermons and talks

he had given over 20 years earlier while at Cambridge and forms one of the major foundations of the rise of natural theology, in which the existence and nature of God is derived from the “book of Nature” rather than the book of revelation. One of the other major initiators was Robert Boyle, whose essays on reason and religion suggested that the empirical turn in natural history was appropriate for people of faith (Gillespie 1987). Unlike Newton’s later posthumously published writings on scripture, Ray was quite orthodox in this work.

However, Ray had to justify natural history as something that could be adopted faithfully. He asserted that “to contemplate the works of God is part of the business of a Sabbath-day” (Ray 1691, p. 124). Arguably, his success in this respect made natural history popular with the leisure classes, and so added to its growth in popularity over the subsequent decades. This generated a popular and learned tradition of doing theology through natural history in the British tradition.

Ray was convinced that everything had a purpose – if not a human purpose, then a divine one (Berry 2011, 329f). But he did not insist, as his contemporaries (such as Gilbert White) tended to, that all of nature was provided by a beneficent deity for humans:

It is a generally received opinion that all this visible world was created for Man [and] that Man is the end of creation, as if there were no end of any creature but some way or other to be serviceable to Man . . . But though this be vulgarly received, yet wise Men nowadays think otherwise. (Ray 1691, 127f.)

According to Berry, Ray held these “physico-theological” views at the very beginning of his scientific career, in the 1660s. These views led to the rise of natural theology leading directly to William Paley’s *Natural theology* in 1802, which was in turn influential upon Darwin’s early investigations.

Wilkins and Linguistics

Bishop John Wilkins’ *An Essay Towards a Real Character and a Philosophical Language* (1668, 2002) was an ambitious project to classify not

only all organisms but all ideas (and it was the foundation for Phillip Mark Roget’s *Thesaurus*). In reviewing the contributions of Wilkins, Ray, and Linnaeus to the history of systematics, Stearn (1986, pp. 111–113) wrote:

The botanical tables prepared by Ray for Wilkins had to fit the latter’s formal prescribed scheme, i.e. herbaceous plants had to be divided into three groups as nearly equal as possible, these then divided again into nine groups and the species then in pairs. So artificial a classification was inevitably unsatisfactory from a botanical standpoint; indeed, only a botanist with Ray’s detailed knowledge of plants and his obliging nature would have had the ingenuity and kindness to construct one at all.

He contracted Ray to do the species lists, but, as Stearn notes, had a very rigid logical schema into which these tables (indented lists with braces) had to fit. This garnered significant criticism from Robert Morison (1620–1683), Professor of Botany at Oxford, who both attacked the artificiality of Wilkins’ scheme and claimed that Ray had plagiarized his own work (Stevenson 1947, p. 253). Ray was stung by this, being still very junior in botany, and thus began his careful and systematic method of classifying and enumerating species of plants. (Sloan (1972) gives a good account of both the results of Wilkins’ strictures and the reactions of Morison and Rivinus.)

Wilkins’ system was part of what has come to be known as the Universal Language Project (Wilkins 2018, Chap. 4), and Ray and Willughby contributed somewhat, under the influence of Ralph Cudworth and the Cambridge Platonists. Ray published *Collection of English Words Not Generally Used* (1674) and *Trilingual Dictionary, or Nomenclator Classicus* (1675) (Cram 2016). More to the point, Wilkins used the standard Latin terms for inclusive and included groups of things, *genus* and *species* (roughly equivalent to our “set” and “subset”), and thus Ray was forced to refer to living things as species in genera. This was not original to him, as Bauhin had used it much earlier, given that both the terms were “vernacular” in academic Latin, and the Aristotelian logic was common to the educational curriculum of the time, but it led directly to his defining, for the first time, a purely biological notion of species.

Species and Systematics

Ray's greatest claim to fame is his work in botany, and in particular his publication first of a flora of Cambridgeshire, and then of Britain, starting a tradition of florae in botany. Subsequent to these works, he published the *Historia Plantarum* in 1686, with volume 2 in 1688. (The former in 1660, *Catalogus Plantarum circa Cantabrigiam nascentium*, the latter in 1677, *Catalogus Plantarum Angliae* (Lankester 1846, pp. 111–113).) His *Methodus Plantarum Nova* (Ray 2015, second edition 1703) introduced the distinction between monocotyledons and dicotyledons, although he also retained much of the older Aristotelian classification of plants as herbaceous, woody (ligneous), and so on.

In the *Historia Plantarum*, Ray wrote:

In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called “species.” After a long and considerable investigation, no surer criterion for determining species had occurred to me than distinguishing features that perpetuate themselves in propagation from seed. Thus, no matter what variations occur in the individuals or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as to distinguish a species. For these variations do not perpetuate themselves in subsequent seeding. ... But variations that never have as their source seed from one and the same species may finally be regarded as distinct species. Or, if you make a comparison between any two plants, plants which never spring from each other's seed and never, when their seed is sown, are transmuted one into the other, these plants finally are distinct species. For it is just as in animals: a difference in sex is not enough to prove a difference of species, because each sex is derived from the same seed as far as species is concerned and not infrequently from the same parents; no matter how many and how striking may be the accidental differences between them; no other proof that bull and cow, man and woman belong to the same species is required than the fact that both very frequently spring from the same parents or the same mother. Likewise in the case of plants, there is no surer index of identity of species than that of origin from the seed of one and the same plant, whether it is a matter of individuals or species. For animals that differ in species preserve their distinct species permanently; one species never springs from the seed of another nor vice versa. (Ray 1686, Vol. I, 40, Trans. Edmund Silk. Quoted in Beddall 1957, pp. 133–134)

While *species* had been used routinely in natural history to denote kinds of living beings, Ray's is the first definition of the term that applies solely to living things (in contrast to species of minerals, etc.), and his definition relies upon (i) reproduction or generation (propagation through seed) and (ii) similarity of progeny to parents and pace sexual differences. In this respect he formalizes the practice of the past century of botany and zoology, but he also indicates operational tests for specificity and for distinguishing between varieties and species. I have called this traditional sense of living species *the generative notion of species* (Wilkins 2018).

Moreover, he denied that species were mutable, and that they would go extinct, or at least that we could know this (Lankester 1846, pp. 207–214). He rejects the variation in species as evidence of new species, ascribing it to changes in climate, etc., which are “accidental differences.” As to extinction, he asks:

whether . . . any species lost or destroyed? To which I answer, 1. That though it is absolutely and physically possible, yet it is highly improbable, that any species should be lost. 2. Though some species should be destroyed, yet it is impossible morally that any man should be sure thereof.

It is unclear if he thought this because of some adherence to the principle of plenitude – that God would fill the world with all kinds that he could and would not permit them to be lost. In *Wisdom*, he held that no new species would be produced by spontaneous generation, which he rejected, but he also allowed that fossils were remnants of species. His argument depended upon the principle “Nature makes nothing in vain” (*Miscellaneous Discourses*, 1692). Hence no fossil teeth, bones, or leaves would be made unless they were remnants of past organisms. Nevertheless, he still thought they might live in some other part of the world, such as deep oceans. He objected that the loss of species out of the world:

which Philosophers hitherto have been unwilling to admit, [meant] esteeming the destruction of any one Species a dismembering of the Universe, rendering it imperfect: whereas they think the Divine Providence is especially concerned to secure and preserve the Works of Creation. . . . (Ray 1692, p. 119)

Influence

The extent of the influence of the genius of Ray on the science of natural history is far greater than can be estimated by the number or size of the volumes which he wrote, and is to be traced to his habit of acute observation of facts and the logical accuracy with which he arranged them. He made his knowledge of the structure and physiology of plants subservient to a great plan for their arrangement, and this plan, when carefully examined, will be found to contain the fundamental principles of all the more recent scientific systems in natural history, and to have laid the foundation of the views of a natural classification of the vegetable kingdom put forward in later times. (Lankester 1846, pp. viii–ix)

Edwin Lankester's estimation of Ray's importance in 1842 was not retained in the era after Darwin, despite his influence over those who preceded Darwin and Darwin himself. In botany, Ray established some of the basis for Linnaeus' classification of plants and was inclined to use empirical methods first and foremost in describing species. In natural theology, his *Wisdom* set the tone and many of the arguments that resulted in the later examples of that genre. But his greatest contribution remains as critical today as when he first made it: the biological definition of *species*. It is at once a traditional definition, one that later influenced Cuvier and established the fixity of species as a viable and perhaps only orthodox view until the end of the eighteenth century and also one that at its base is still employed by systematists: a species is a lineage of reproductive linkages that tend to produce progeny that closely resemble their parents. This is the prior meaning of "common descent" that Darwin employed later.

Cross-References

► Early Definitions of Species

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John Tooby

► Founders of Evolutionary Psychology

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Definition

An influential British social psychologist and Professor of Psychology at Australian National University in Canberra.

Introduction

John Turner was born in South London to a -working-class family which lived in a small council flat. He was the son of a construction worker and the firstborn of eight children. At the age of 11, he received a scholarship to attend Wilson's School in Camberwell – a boys' grammar school. His working-class accent differentiated him from his more conventional middle-class peers. He received his Bachelor of Arts Honors in Social Psychology at University of Sussex in 1971. Under the tutelage of Henri Tajfel, he received his PhD in Social Psychology from the Bristol University in 1975. He continued at Bristol University as a research associate and lecturer after earning his doctorate. He spent 1 year at the Institute for Advanced Study at Princeton from 1982 to 1983 and then moved to Macquarie University in Sydney. In 1990, Dr. Turner moved to the Australian National University in

Canberra. In 1999, he was awarded the Henri Tajfel Memorial Medal by the European Association of Experimental Social Psychology (Reicher and Haslam 2011; Haslam et al. 2011; Bourhis 2012).

Career and Contributions

While an undergraduate at University of Sussex, Turner worked at a printing factory. During this time, he gained experience as a trade union organizer and started noticing how collective action could nurture a sense of in-group belongingness, group unity, and pride in one's group. At Bristol University, his advisor had noticed that once people created groupings, they tended to emphasize the similarities of themselves within their in-groups and the dissimilarities of themselves from groups of which they do not belong (Tajfel and Turner 1979; Turner 1999). Together, Turner and Tajfel developed *social identity theory*. This theory asserted that people have a strong tendency to categorize themselves into groups in order to gain a greater sense of who they are; consequences for these categorizations play a role in self-esteem for the individual and prejudice and stereotyping for those that belong to other groups.

John Turner is also credited with the formation of *self-categorization theory* – which describes the circumstances in which an individual will recognize groups of people, themselves included, as a group (Haslam 1997). A major principle of the theory is that one should not consider the self as a foundation to cognition but that the self is actually a product of our cognitive system (Turner and Onorato 1998; Turner et al. 1994; Reynolds and Turner 2006). Self-categorization theory has been applied to topics such as social influence, group polarization (Turner et al. 1987), outgroup homogeneity, power (Turner 2005), and leadership (Haslam 2001; Haslam et al. 2011b).

In his book *Rediscovering the Social Group* (1987), he explored the connection between the individuality of the person and the social reality of the group identity. He found that when humans

view others as “us” instead of “them,” people will be motivated to help or work with these other individuals. He described that working together with a shared identity is vital to our future.

Conclusion

Dr. Turner died on July 24, 2011. He was a captivating figure who attracted students to both his research and his causes. His contributions include the development of two key theories regarding individuals acting as group members. He was also quite knowledgeable in politics. He has left a lasting impact on social psychology through not only his research but also through his students. His former pupils have gone on to occupy senior positions around the globe.

Cross-References

- [Peer Socialization](#)
- [Same-Different Categorization](#)
- [Self-Concept](#)
- [Self-Stereotyping](#)
- [Sex Differences in Social Development](#)
- [Social Aggression](#)
- [Social Context](#)
- [Social Development](#)
- [Social Learning](#)
- [Social Roles](#)

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John Watson

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Synonyms

Behaviorism

Definition

Well-known psychologist, founder of Behaviorism.

Introduction

John Broadus Watson (1878–1958), a comparative psychologist, is considered as the person who tried to divert researchers' attention from introspection toward a behavioral understanding of the world, and he was the first who introduced the term "Behaviorism" (Rakos 2013). He was a proponent for the use of scientific approach to examine everyday phenomena (Bakan 1960), a strong supporter of the importance of environmental factors in influencing behavior (Morris and Todd 1999), and an advocate for the use of research findings to reduce or eliminate social problems (Bakan 1960). His hard work, his passion for his beliefs, and the innovations he brought to research stirred up a lot of controversy even long after his death (Horowitz 1992).

His Personal Life

John Broadus Watson, born and raised in the village of Travellers Rest in South Carolina, was the fourth of six children, growing up in a financially underprivileged family. His father, Pickens, was a civil war veteran with a strong preference for alcohol and women. Pickens was close to his son John while he was growing up and he taught him how to master various masculine skills and interests such as handling tools, managing a farm and its equipment, and carpentry, interests he kept throughout his life. His mother, Emma, a devout Baptist who held an active role in the Baptist Church, strongly urged her son to become a minister (Hergenhahn 2000; Moore 2017). Despite her husband's lifestyle that strongly opposed to the Baptist's beliefs, Emma was trying to hold the family together and at the same time to instill to her children her love for the church and her belief in professional advancement through education (Morris and Todd 1999). The family moved to Greenville in 1890 with hopes for greater financial opportunities, but this move brought an extra strain to the marriage and resulted in Pickens leaving the family for good in 1891, when John was 13 years old. Pickens departure was very painful

for John who never forgave his father and resulted in an adolescence of great rebelliousness, where he became disinterested for his studies and engaged in frequent fights with others (Hergenhahn 2000; Morris and Todd 1999).

John managed to graduate from high school even though his academic record was not superior, and he realized that academic education would offer him the means to follow a profession that would provide better living circumstances. At the age of 16, he succeeded in getting accepted at Furman University, a small Baptist college in Greenville (Morris and Todd 1999). At Furman, he studied philosophy and psychology, from where he graduated 5 years later earning a master's degree in 1899. Despite his degree, he was living poor and with few friends and, in addition, at 1900 his mother Emma became ill and died. Wanting to pursue further studies, and with the support of one of his philosophy professors from Furman University, he enrolled at the University of Chicago to study philosophy. He arrived at Chicago with almost no financial resources and he had to work simultaneously different jobs as a waiter and at the psychology laboratories in order to survive (Hergenhahn 2000).

During his graduate studies, Watson pursued a major in experimental psychology supervised by Angel, a first minor in philosophy supervised by Dewey and a second minor in neurology supervised by Donaldson. The intensive studies along with his hard labor work to support himself financially led him to a state of exhaustion which he managed to overcome, and eventually completed his dissertation in 1903 (Moore 2017). In his dissertation, he studied whether myelination in the rat's brain obstructed rat's ability to perform complex behavior, especially maze learning (Moore 2017).

After receiving his Ph.D., Watson accepted a position as an instructor in University of Chicago, where he taught experimental psychology and continued his research with the rats in his laboratory. He met and married Mary Ickes, one of his students, daughter of a prominent Midwestern family. John and Mary had two children together, Mary (born in 1905) and John (born in 1908). The Icke's family never approved of Mary's marriage

to John, whom they thought was a gold-digger (Moore 2017).

In 1907, Watson accepted an offer for the position of full professor at John Hopkins University, one of the most prestigious Universities of America, and soon after he stepped up in the hierarchy, a move that further increased his developing reputation (Moore 2017). The research he was developing at Hopkins on the conditioned reflex process in rats was interrupted in 1917 because he joined the US Army during World War I. In the army, he worked on screening aviators and studying the effects of oxygen deprivation on their skills until 1918 when the war ended and he returned to the academia describing his experience in the military as highly dissatisfactory (Watson 1936, as cited in Moore 2017).

His return from the army and back to Hopkins marked a shift in his research interest. He began studying human development, especially child development from a behavioristic point of view; he studied the conditioned reflex and the conditional emotional reactions of children that led to his famous study on Little Albert (Watson and Rayner 1920, as cited in Moore 2017).

His assistant in this new turn of his research was another student of his, Rosalie Rayner, a lively and beautiful young woman of a wealthy and prominent Baltimore family, with whom John got romantically involved (Hergenhahn 2000). This extramarital affair was the “last straw” of a marriage already shaken by different problems (Moore 2017). Mary and her family – who always disapproved of Watson – got so enraged with his love for another woman while still legally married that used all their social and financial power to pressure the John Hopkins Administration to fire Watson. Hopkins University, in turn started pressuring Watson who, finding no support from any of his former colleagues and friends, resigned from Johns Hopkins in October 1920 (Moore 2017).

Unemployed and with no support, and while his divorce was pending, Watson went to New York and accepted a job in J. Walter Thompson advertising company, thus marking the beginning of a new chapter in Watson’s life and career in business (Moore 2017).

The Ickes family insisted on embarrassing Watson further by initiating formal divorce proceedings and publishing articles about the divorce in newspapers. Watson’s divorce from Mary was finalized on December 24, 1920, and he married Rosalie on December 31 (Moore 2017); he was 42 and she was 21 at the time. Rosalie and John had two sons together, William (born in 1921) and James (born in 1924).

Watson’s success in the world of advertising led him to the position of Vice President of J. Walter Thompson in late 1924, while he continued to give lectures in New York. John and Rosalie continued to study and share their views on childrearing with the public until Rosalie’s death in 1935 of dysentery, at the age of 36. Although devastated from Rosaline’s death, John continued his advertising career by leaving Thompson in 1936 for the position of Vice President at William Esty, another advertising company, until his retirement in 1945. In the early 1950s he moved to a small estate in Connecticut, where he spent his last years devoted to his land, his animals, and drinking excessive amounts of alcohol. He died in 1958 at the age of eighty of cirrhosis, only a year after he was awarded (in 1957) the Gold Medal by APA for his significant contributions to psychology (Hergenhahn 2000; Moore 2017).

The Precursors

A number of different academic, cultural, and personal factors prepared the soil for Watson’s theory and research and led to the need for a more objective psychology: (a) modern philosophy and Rene Descartes’s attempt to bring together the mind and the body; (b) Wundt’s methods of studying in the first psychology laboratory in 1879, and (c) the evolution of biology and neuroscience. At the same time, the changes in American culture toward the increase of technical knowledge, institutional control, and industrial development became the cornerstone into building a nation based on science, technology, and progressivism (Morris and Todd 1999). Watson, although not prepared by his poor rural family to survive in this new way of living, soon realized that in order to survive successfully in a

progressive culture, university education and a profession, and in particular psychology, could generate the means (Buckley 1989 as cited in Morris and Todd 1999).

Before Watson, research in psychology was monopolized by the concept of “consciousness,” that is, the examination of conscious processes and their analysis through language (Malone 2017). Instead, Watson proposed to study psychology in an objective way by concentrating on behavior, thus making it an objective science (Moore 2011; Todd 1994). He claimed that by restricting research on “introspection” and on training people to examine their conscious experience on predetermined subjective labels, we eliminate our field of study only on sane humans who are able to understand and use language, at the same time excluding children and other individuals who lacked the ability to communicate, people with psychopathology, and subhuman animals (Malone 2017).

The Beginnings of His Career: The Birth of Behaviorism

When Watson entered University of Chicago in 1900, he found academia in a process of change (Buckley 1989, as cited in Morris and Todd 1999). He began studying philosophy under Dewey but turned his attention toward Angell’s functional psychology who encouraged him to describe and analyze behavior. This led to a career in comparative psychology, a field of studying the behavior and evolution of different animals, at the laboratory and outside of it as well, and this area became the topic of his research for years. Between 1903, where he received his doctorate, and his 1913 famous Columbia lectures, Watson studied the importance of the sensory system for learning in rats; he conducted field observations on birds’ homing abilities (Tinbergen 1951, as cited in Malone and García-Penagos 2014) and successfully designed equipment to assess the visual capacities of nonhumans, all significant steps for the assessment of nonhuman perception (Boakes 1984).

In Watson’s agenda, the results from the study of comparative psychology could be equally applied to humans, since throughout his life he

strongly believed that the behaviors of humans and animals had no essential differences except from the use of language (Malone and García-Penagos 2014).

During his work as an experimentalist Watson equipped two animal laboratories, designed complicated apparatus, and carried out pioneering experiments on rats, birds, monkeys, and human babies, attacking multiple problems related to neurological developments of different species, instincts and performances, and the early emotional development of the human child (Dewsbury 1994).

Watson’s Career After 1913

By 1913, Watson was professionally established, had a big reputation as a scientist, published more than 65 articles and reviews, and had attained significant professional status (Buckley 1989, as cited in Morris and Todd 1999). He concluded that for psychology to become a science, it had to produce observable results, much like other sciences, at the level of behavior, and it had to become popular (Morris and Todd 1999). His strong beliefs about examining behavior as the only scientific method and his introduction of the term “behaviorism” awarded him the fatherhood of the term, and despite strong arguments against it, he managed to make behaviorism an established entity (Logue 1978; Woodworth 1959).

Watson’s 1913 publication of “Psychology as the Behaviorist Views It” (Watson 1916), taken from a lecture delivered at Columbia University, was later referred to as the “Behaviorist Manifesto” for its innovation and forceful tone that launched the “Behavioral revolution” and signified behaviorism as a separate orientation in psychology (Moore 2017). Even though at the time the impact of that publication was not significant (García-Penagos and Malone 2013), it was later judged as “the single most important publication in the 50 years of the *Psychological Review*” (Langfield 1943). In that publication, Watson presented the three main features of his theory. First, he emphasized the importance of using observational and experimental analyses in order to predict and control behavior, stressing the role of the

environment in human development and criticizing conclusions made about heredity. Thus, he presented psychology as a natural science aiming to predict and control behavior, with an emphasis on environment as a determinant of behavior (Logue 1994; Watson 1913). Furthermore, beyond promoting the concept of learning he argued that scientifically validated behavioral principles could be applied to a variety of social needs and problems, such as education, advertising, psychotherapy, in order to improve society and make life better (Hart and Kritsonis 2006; Salzinger 1994; Samelson 1981). Second, he rejected consciousness, mind, and image as the subject of psychology and took the position that consciousness did not exist as an entity (Morris and Todd 1999; Watson 1913b). Instead, he argued that there is no such a thing as “mind” because it is an abstract concept. There are activities like seeing, hearing, listening, remembering, and imagining, but they do not constitute a “mind” that is separate from the body. Thus, the mind/body distinction is a false one (Malone 2017). His rejection of consciousness and the mind resulted in a confusion as to whether he was a methodological or metaphysical behaviorist or, as Skinner later named it, “radical behaviorist,” a term that “holds that mental terms are fictional products of folk psychology and that the mind/body distinction is a false one” (Malone 2017, p. 4).

Third, he addressed the activities historically associated with consciousness and mind, namely, thinking, feeling, and imagining in a behavioral manner. Thus, he developed the theory that thought processes are motor habits in the larynx, emotions in the glands, and imagery in the movements of the eye (Watson 1913). For him, learning was part of the organism’s interaction with the environment, even though a sometimes private but real environment (Morris and Todd 1999). The 1913 manifesto was the first clear conflict with other approaches and the first to argue for the use of empirically derived principles with the aim to improve society (Rakos 2013).

From Animals to Humans

Until 1916 Watson worked exclusively with animals influenced by the Darwinian thought in the

evolution of the species and believing that human behavior could be explained sufficiently by the examination and explanation of behavior of non-human organisms (Logue 1978; Malone and García-Penagos 2014). In 1917, he switched into postulating that human beings might have unique instincts, different from those of lower organisms, and thus, generalizations from studies on animals to humans was not a safe practice (Logue 1978; Todd 1994).

In his book *Psychology From the Standpoint of a Behaviorist* first published in 1919 (1924, 1929), he asserted the following basic principles. First, he recognized that the human body was a complex organismic system integrated with the behavioral system. Second, although he acknowledged the role of structural change, he clearly postulated that learning was almost exclusively responsible for behavioral development. Third, he insisted on the need for developmental research examining infants, the role of their emotions, and the principles of their learning, by using the experimental method (Horowitz 1992).

Watson identified five categories of objective methods and procedures for psychological research: (a) systematic observation available for analysis through descriptive statistics; (b) conditioned reflex method, as used by Pavlov (1906, as cited in Morris and Todd 1999); (c) verbal reports of implicit and explicit responses and stimuli; (4) standardized testing, and (5), social experimentation (Morris and Todd 1999).

Organization of Behavior

Watson’s organization of behavior included three main categories depending on (A) the origins and loci of behavior (Formal Organization), (B) function (Functional Organizations), and (C) natural-language categories. In “Formal Organization” of behavior, he presented: (1) the distinction between heredity responses (i.e., instinctive, such as reflexes or emotional, such as love, fear, and rage) and habits (i.e., learned responses); (2) whether behavior was explicit (e.g., reading) or implicit (e.g., mental counting); and (3) whether it was manual (e.g., eye-hand coordination), laryngeal (e.g., talking aloud), or

visceral (e.g., emotional reactions) (Morris and Todd 1999).

In *Functional Organization*, although he identified 6 determinants of behavioral regulation, it was the determinants of: (a) recency, the most recent response to stimulus; (b) frequency, the most frequent response to stimulus; and (c) the response most closely connected to the overall situation or context (e.g., responses appropriate for one context but not for another) that he emphasized the most (Morris and Todd 1999).

In his classification of behavior in terms of natural-language categories, he included categories such as emotion; manual, motor, or bodily habits; language; thinking; memory; work; and personality (Morris and Todd 1999).

Reflexes and Habits

While at Chicago University (early 1900s), Watson was studying the sensory modalities that underlay maze learning in rats, as well as the various “instinctive” behaviors of sea birds. Although he got confusing results, the most crucial was that instinctive behavior is not static; it develops through interaction with the environment and takes its different forms according to relevant environmental stimulation (Watson 1914, in Moore 2017). Progressively, Watson was influenced by Pavlov’s ideas on conditioned reflexes and adopted the same views, to the extent that after his election as president of the American Psychological Association in 1914, his presidential address in 1915 was on “The Place of the Conditioned Reflex in Psychology” (Watson 1916, cited in Moore 2017). He postulated that the organism is comprised of a large number of reflexes, or unit acts, that, although they may vary depending on heredity, they “can be shaped” depending on the environment. The organism selects and eliminates the useless movements; thus, with the constant selection of the correct movements, habit formation develops in the service of adjustment. A number of simpler “reflexive” units selected by the environment compose a much larger unit that form a “response.” He believed that the principles of frequency and recency account for simple habit formation (Malone and García-Penagos 2014). Specifically,

he discussed how stimuli that did not instigate a response can do it later indicating his recognition of the complexity of human behavior (García-Penagos and Malone 2013). Progressively, he attributed more importance in the concept of conditioning in his theory. Specifically, he considered conditioning as the mechanism by which words come to be integrated into habit systems, and eventually, he used his same ideas about the conditioned reflex to explain all other habits, which were now defined as “a series of conditioned reflexes.” For him, conditioning could explain how habits are formed, maintained, and rejected (García-Penagos and Malone 2013).

Today this viewpoint is known as *classical S–R behaviorism*. He used the terms *Stimulus* meaning any general environmental situation or internal condition of the organism, and *Response* as anything the organism did (Horowitz 1992). This approach in research represented the first phase of the “behavioral revolution” and was very popular until it was recognized as inadequate and researchers inserted “organismic” variables between stimulus and response as a way to mediate this relation (Moore 2011).

Thus, the principal unit of analysis for all the studies of Watson was the “habit,” defined as “the coordinated and consistent act that develops in a given situation through repetition, rather than some supposed phenomenon from mental life” (Moore 2011, p. 451).

Watson further devoted his professional attention on conditioned reflexes on behaviorism and established it as the main orientation in psychological science at the time upon his return to Hopkins after the end of his military service to World War I (Moore 2017).

The end of the second decade of the twentieth century found Watson in the laboratory turning his attention to human behavior, and particularly to child development. He proposed 3 basic emotional responses for human infants: (a) fear, caused by loss of support or sudden sounds, (b) rage, caused by restricting an infant’s movements, and (c) love, caused by stroking the skin, especially in sensitive erogenous zones. He suggested that through conditioning, the emotional responses produced by different stimuli

expand throughout life and account for the diversity of human development, a position he tried to prove through his famous experiment with Little Albert, his last formal research in academia (Moore 2017).

In 1920, even after the end of his academic career, he continued giving lectures at local universities that resulted in his popular book “Behaviorism” (Watson 1925, cited in Moore 2017) where he incorporates the data from different studies before Little Albert in a book about child rearing (Moore 2017).

On Environmentalism

Watson was identified as a strong environmentalist. Up until 1917, he was holding a middle ground on the power of heredity and environment in development. Progressively, as he came to believe that the differences between species were too large to allow any conclusions from one species to another, he came to adopt the position that eventually environment is responsible for change (Morris and Todd 1999). This shift became prominent in his 1924 book on “*Behaviorism*” where he stated that humans have only a small set of instincts compared to animals, and he narrowed the concept of emotions in only three responses: fear, rage, and love (Rakos 2013). For him, genetics were responsible for the prevalence of instincts in nonhumans and the relative lack of them in humans. Furthermore, although he acknowledged that physical characteristics are inherited, he did not say the same about “mental traits” (Rakos 2013). In one of his most famous and frequently quoted statements, he says:

Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select – doctor, lawyer, artist, merchant, chief and, yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors. I am going beyond my facts and I admit it, but so have the advocates of the contrary and they have been doing it for many thousands of years. (1924/1970, p. 104) (Logue 1978)

In the last three lines, not usually quoted, it shows that what appeared as an extremist environmentalist position was a result of his effort to

counteract the equally extremists hereditarian psychologists of the time who, according to him, had based their views mostly on prejudice rather than scientific analysis (Logue 1978; Todd 1994). Thus, although Watson's position on the heredity versus environment dilemma progressively changed, it was only in 1924 in “Behaviorism,” 4 years after the termination of his academic career, that this division was emphasized.

In conclusion, Watson asserted that the organism's inherited biological structure interacts with the environment to produce behavior. Any change on any of those factors (i.e., biological structure or environment) through learning, injury, etc., changes behavior (Morris and Todd 1999).

Application of the Principles of Behaviorism on Child Rearing

After the end of his academic career from Johns Hopkins, Watson continued only with the studies conducted by his supervisee, Mary Cover Jones (1896–1987) on the elimination of children's fears (Jones 1924a, b, as cited in Morris and Todd 1999), a continuation of his studies on “Conditioned Emotional Reactions” (Watson and Rayner 1920, as cited in Morris and Todd 1999), both studies now considered a landmark in the history of behavior therapy (Krasner 1988).

Watson's interest on children began in 1916 where he studied, along with his wife, their emotional development. Results of his infant studies led to a number of books and publications as well as popular articles in magazines. They concluded that the root of adult psychological problems lies in childhood, and especially in too much pampering. As a result, they suggested treating the child as an adult. Any forms of emotional display (i.e., kissing and hugging) needs to be eliminated in order to reduce conditioned emotional reactions. They further encouraged parents to promote greater self-sufficiency to their children, to be honest and open to them, and to abstain from any form of corporal punishment (Morris and Todd 1999).

Watson and Advertising

At the age of 42, Watson turned his attention to advertising. He used the behavioral approach in

advertising and launched a very successful second career, by using his findings on infants' innate emotional reactions on how to attract the viewer's attention. Furthermore, he used behaviorism principles in personnel selection and management (Malone 2017).

Watson on Psychopathology

Watson approached the concept of psychopathology through his belief about adjustment. He postulated that we go through life adjusting to the different situations by producing a set of reactions organized in a way to help us adjust into new situations. When new circumstances we encounter in life resemble old, familiar ones, the adjustment is easier. The adjustments we learn through life become our personality, and a well-adjusted personality can deal with new situations. Psychopathology develops when new situations are so novel that the person is unable to adjust because it would mean to break up the present habit patterns. This novel situation can cause a trauma, and recovery from trauma, although possible, can be difficult and lengthy since it requires personality restructuring (Malone 2017).

Watson as a Person

John Watson was considered to be a controversial man (Horowitz 1992). He was disciplined, articulate, straightforward, and self-assured; he kept close and long friendships with Titchener and Angell, while also his second marriage was successful (Brewer 1991; Morris and Todd 1999). Furthermore, he was considered attractive, strong, and scientifically accomplished. For others, Watson was arrogant, rigid, and unreflective (Brewer 1991; Horowitz 1992; Morris and Todd 1999).

Memories of his son James present Watson as having a sense of humor, charming, bright, sociable (yet shy), fastidious, and masculine. He was concerned with manly activities, courage and personal capabilities, and manual work. Yet, he was afraid of the dark and of driving (Hergenhahn 2000). He displayed more affection for animals than for people including his children. According to James, the lack of warmth and affection by his father was the reason for the lack of the self-

esteem necessary for a healthy life that led to his brother's suicide. After Rosalie's death in 1936 Watson changed; he was devastated and seemed "confused" and depressed for several years (Malone 2017; Moore 2017).

Conclusion

John Broadus Watson appears to be one of the most controversial researchers in the psychology of twentieth century. He is known as the person who used innovative methods in examining animal behavior and specifically learning. Early on in his career, he challenged the subjects and the methods of studying humans in psychology of the times. He is most known as the person who emphasized the importance of examining behavior and for this reason the term "behaviorism" was attributed to him. Even though his research on humans is limited, his writings are being examined for decades long after his death and have influence in research and practice in psychology.

Cross-References

- [Adjustment](#)
- [Behaviorism](#)

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John Wray

► [John Ray](#)

Joint Activation of Derived and Inceptive Memories

► [Scope Hypothesis, The](#)

Joint Family

► [Extended Kin Role](#)

Joint Intentionality

► [Morality Is Cooperation](#)

Jokes

► [Humor Production](#)

Joking

► [Neurology of Humor](#)

Jonathan Haidt

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Synonyms

[Author](#); [Researcher](#)

Definition

Jonathan Haidt is a psychologist best known for his work on moral psychology.

Introduction

Most of Jonathan Haidt's work has focused on moral psychology. His first major contribution to the field was the Social Intuitionist Model of moral judgment. This model posits that, unlike the assumptions of many previous philosophers and psychologists, moral judgments were not conscious, logical processes, but instead the product of multiple automatic processes (Haidt 2001). Other major contributions include his work on developing a scale of moral disgust and moral elevation. More recently he continued work on his Social Intuitionist Model, expanding it to cover the most important categories of moral intuition. This new model was called the Moral Foundations Theory.

The Social Intuitionist Model

The Social Intuitionist Model proposes four specifics of moral judgements: Moral judgements are primarily intuitive, justified after the fact, created to influence others, and influenced by others. This theory differs from previous theories by positing that humans do not come to moral judgements in a rational way, but that they come to moral decisions based on intuition and then

later find information to justify these judgements. This conclusion was drawn after research on moral dumbfounding demonstrated that humans will frequently come to very strong moral reactions without being able to justify their reasoning. The most common scenario demonstrating this involved siblings that slept together once. No one knows they slept together, no harm comes to anyone, protection is used, and it makes them feel closer. Most people have very strong negative reactions to this scenario, but are unable to rationally justify why other than by appealing to a belief that incest is bad as a rule (Haidt 2012).

Moral Disgust and Elevation

Haidt, along with others, developed a widely used scale of moral disgust. The scale is designed to measure individual differences in disgust sensitivity (Haidt et al. 1997). They argue that disgust evolved to protect the body from pathogens which enter through the mouth and later was expanded through cultural evolution to protect social and moral order. Research into moral disgust led Haidt to examine moral beauty, also termed moral elevation. Moral elevation was illustrated by Algoe and Haidt (2009) who exposed participants to stories about moral beauty that causes common sets of responses such as a desire to be a better person, calmness, and loving feelings. Further research demonstrated that feelings of moral elevation could cause breastfeeding mothers to lactate (Silvers and Haidt 2008), drawing a possible connection between moral elevation and the hormone oxytocin.

Moral Foundations Theory

Moral Foundations Theory was produced as an extension of the Social Intuitionist Model through collaboration with many authors (Graham et al. 2012). This theory states that human morality is derived from five major moral domains, or foundations: care/harm,

fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation. These foundations are the product of specific mental modules evolved to solve recurrent problems for our ancestors. The presence of each of these modules would have functioned to solve common problems for our ancestors, such as caring for children (care/harm) or avoiding pathogens (sanctity/degradation).

Conclusion

Throughout his career, Jonathan Haidt is best known for his development of the Social Intuitionist Model and his work on Moral Foundations Theory. These two models have fundamentally changed how many in social psychology view moral psychology and provide one of the most comprehensive examples of an evolutionarily informed approach to moral domains.

Cross-References

► [Moral Foundations Theory](#)

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Jonathan Haidt's The Righteous Mind

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Synonyms

[Evolution of human sociality](#); [Evolution of morality](#); [Human cooperation](#)

Definition

Jonathan Haidt introduces moral foundations theory in his book and tries to challenge the way we think about the origins of political differences and good and evil.

Introduction

Haidt's *The Righteous Mind* consists of three main chapters. In the first part, he argues that moral judgments are realized through intuitive thinking based on the social intuitionist approach. In the second part, some theoretical approaches based on harm and justice are criticized and it is claimed that morality corresponds to more than harm and justice. In the third part, it is argued that morality is intertwined with (in particular, religious) group behavior and that moral intuitions underlie our group psychology and political differences.

Haidt (2001) endorses the Humeian point of view on morality and criticizes Kohlberg's rationalist moral understanding based on Kant's moral philosophy. According to Kohlberg's rationalist perspective on morality, when we see a moral violation, we decide rationally whether this is morally right or wrong. However, as Haidt demonstrates in his moral dumbfounding studies, when people are exposed to a set of moral scenarios that do not involve harm but include a moral violation, such as incest, they automatically judge that it is morally wrong, but use their rational

processes only to justify the initial moral judgment. For example, Julia and Mark are often used in moral dumbfounding studies:

Julie and Mark are brother and sister. They are traveling together in France on summer vacation from college. One night they are staying alone in a cabin near the beach. They decide that it would be interesting and fun if they tried making love. At the very least, it would be a new experience for each of them. Julie was already taking birth control pills, but Mark uses a condom too, just to be safe. They both enjoy making love, but they decide never to do it again. They keep that night as a special secret, which makes them feel even closer to each other. What do you think about that? Was it ok for them to make love?

When most people read this scenario, they make an automatic (intuitive) response and state that this behavior is morally wrong. However, when asked why, they try to legitimize their judgment in a post-hoc manner. Haidt argues that we are not interested in the truth when making moral judgments like scientists. Rather, we justify our behavior as a lawyer. This approach is called the social intuitionist approach.

In the second part of the book, the moral foundations theory (Haidt 2012) is introduced and it is claimed that morality consists of at least five different dimensions. In Kohlberg's theory, the moral principles that are at the "highest levels" are not to harm and to be fair. Kohlberg's perspective has dominated moral psychology. However, inspired by the anthropological work of Shweder et al. (1997), Haidt (2007) mentions that, apart from these two dimensions, there are at least three other moral dimensions, which he calls loyalty, authority, and sanctity. It is argued that these five dimensions are evolutionary adaptations. While harm and justice constitute the individualizing foundations, loyalty, authority, and sanctity constitute the binding foundations.

In the last chapter, Haidt argues that groups, in general, and religious groups, in particular, come together based on a number of shared moral principles, and crucially, that the differences in moral foundations drive intergroup (i.e., political) disagreement. As morality ties groups together, it also blinds them to the fact that members of other groups can also be good people. Instead,

people view the world from the perspective of their own group.

In general, Haidt's approach suggests that in order to eliminate the conflict between political groups, liberals should appreciate loyalty, authority, and sanctity more than they are generally inclined to. However, an opposing approach (Sauer 2015) argues that since both sides already value individualizing foundations, conservatives should question their emphasis on binding foundations. Although there are a number of empirical studies on what the core moral foundations of humans are (Alper and Yilmaz 2019; Napier and Luguri 2013; Wright and Baril 2011; Yilmaz and Saribay 2017), the current evidence is inconclusive and further empirical studies are needed.

Cross-References

- [Evolution of Cooperation](#)
- [Evolution of Human Sociality](#)
- [Puzzle of Altruism, The](#)
- [Theory of Moral Development](#)

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Joseph Henrich

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Definition

Joseph Henrich is an American evolutionary social scientist whose work is primarily concerned with human psychology, decision-making, and culture. Originally hailing from Philadelphia, Pennsylvania, he obtained bachelor degrees in anthropology and aerospace engineering from the University of Notre Dame, followed by master's and doctorate degrees in anthropology from the University of California in Los Angeles. Throughout his academic career, he has incorporated a diverse range of methodologies into his research, integrating ethnographic tools from anthropology with experimental techniques drawn from psychology and economics (Henrich et al. 2004). Using this multidisciplinary approach, he has spent a substantive amount of time studying indigenous peoples in Amazonia, Chile, and Fiji, as well as individuals living in modern industrialized societies across the globe. Henrich applies principles of evolutionary theory to the study of human culture and has investigated a variety of topics both in the laboratory and in the field, including cultural evolution, human sociality, large-scale cooperation, and the social processes that give rise to complex human institutions.

Introduction

Joseph Henrich argues that culture has driven human evolution to the point of complexity that we see today (Henrich 2016). That is, the reason

why humans have been so successful as a species is because we have the ability to create and acquire culture, which provides us with invaluable information on how to survive in a given environment. In only a few million years, our species has emerged from a lineage of primate ancestors to become one of the most successful species on planet Earth. Particularly, within the last 12,000 years following the end of the last ice age, human societies have expanded from relatively small groups of hunter-gatherers into vast nation states with complex social structures and hierarchies. Although genetic evolution laid the foundation for the cognitive processes necessary for the emergence of culture, our subsequent success as a species, Henrich (2016) argues, has been made possible by culture. Culture may also steer genetic evolution by altering the selective environment faced by genes.

Much of Henrich's work investigates how culture shapes our psychology and the structure of the very societies that we live in. Using evolutionary theory, Henrich explores how people both learn and transmit culture. The application of evolutionary principles to studying culture allows for a theory of *cultural evolution* – a way of understanding the mechanisms that drive human innovation and the cumulative cultural processes that shape human societies. The theory of cultural evolution considers the variation in human psychology across the globe, assessing how different environmental inputs interact with our evolved psychology to produce a diverse range of stable cultural systems comprised of adaptive cultural practices. Using this theoretical framework, Henrich has examined phenomena such as social status and prestige in human societies, and their implications for cultural transmission. He has also explored how small-scale cultural transmission provides the building blocks for large-scale cooperation and the emergence of widespread cultural institutions, such as organized religion and political movements.

Cultural Evolution

Similarly, but not analogously to genetic evolution, culture evolves (Chudek et al. 2015; Henrich

and Boyd 2002; Henrich et al. 2008). Culture, like genes, can meet the three criteria of evolutionary adaptation: (1) information varies, (2) variability is heritable and information is transmissible, and (3) some variants are more likely to survive and propagate than others. However, unlike genes, culture can spread *horizontally* across individuals rather than solely *vertically* (as is the case with parent to offspring genetic inheritance; Chudek et al. 2015; Henrich et al. 2008). Furthermore, according to Henrich and colleagues, cultural transmission differs from genetic transmission in subtle, yet important ways – for example, it neither requires replicators (i.e., as compared to discrete, gene replicators) nor random variation for cumulative, adaptive cultural evolution to occur (Henrich and Boyd 2002; Henrich et al. 2008). That is not to say that natural selection does not play a role in cultural evolution; cultural evolution simply attempts to take into account the interaction of psychological processes and the environment in which cultural systems inhabit. For example, some cultural systems may be more useful in one environment, whereas others more useful in different environments.

Henrich asserts that simply understanding how evolved psychological mechanisms and cognitive structures (due to natural selection) can give rise to culture is insufficient in predicting how cultural representations can spread between individuals, be modified, and diffuse across societies (Henrich et al. 2008). To comprehend the bigger picture of how culture develops and spreads, it is necessary to construct formal cultural evolutionary models. Using the cognitive and evolutionary foundations of human social learning, Henrich has created formal, mathematical models of cultural evolution, and such mathematical models reveal how individual cognitive processes can give rise to complex social phenomena through social interaction between individuals. With simple psychological assumptions and decision rules, such models illustrate how a wide range of phenomena, such as the evolution of economic specialization and the emergence of large-scale cooperation (Henrich and Boyd 2001), technological advancement (Henrich 2004), and the spread of innovations (Henrich 2001), can occur systematically. By consulting these models, Henrich has

also developed theories about the emergence of higher-level social phenomena, such as complex institutions (e.g., governments, organized religion), large-scale social groups (e.g., ethnic groups), and social hierarchies (Atran and Henrich 2010; Chudek et al. 2015; Henrich 2009; Henrich and Boyd 1998; Henrich and Gil-White 2001; Shariff et al. 2011).

The products of cultural evolution profoundly influence human behaviors as well as the ecology of human civilization. Interconnected sets of skills, beliefs, values, and institutions have been assembled by cultural evolutionary forces and are defining characteristics of human societies. Culture affects people's motivations, goals, and reasoning processes by compiling the very belief systems and skills that individuals rely on for survival and group living.

Culture-Gene Coevolution

Joseph Henrich contends that there are elements of human social behavior that cannot be understood without considering the joint interaction between culture and genes. Because humans have relied on cultural learning in order to survive for hundreds of thousands of years, culture may have influenced our species' genetic evolution. The cognitive and behavioral capacities that make human culture possible – complex communication skills, social learning mechanisms, and domain-specific information processing systems – evolved because these capacities allow individuals to readily adapt their behavior to novel and changing environments at rates much faster than genetic evolution (Henrich and Boyd 1998; Henrich and Gil-White 2001). Similarly to genetic evolution, cultural evolution is a cumulative process, where human innovation is transmitted and aggregated by individuals. Because of the transmissibility of culture and its utility in aiding our species' survival, culture has shaped human genetic evolution, including our physiology, anatomy, and psychology (Chudek et al. 2015; Henrich et al. 2008). For example, the structure and function of human teeth, changes in digestive processes, our lack of body hair, and acquisition of manual dexterity cannot be understood without

considering that our genes responded to the cultural transmission of cooking with fire, wearing clothing, and tool use. Similarly, culture has likely shaped human cognition by changing the selective environment faced by genes. This process is referred to as *culture-gene coevolution*.

Cognition and Culture

To understand how culture is made possible, it is necessary to investigate the underlying cognitive processes that facilitate learning, problem-solving, and social intelligence. For cultural learning to occur, humans rely on cognitive processes that organize and interpret information coming in from the social world (Chudek et al. 2015). Henrich has tested hypotheses about how these cognitive processes function, taking into consideration how natural selection has shaped human cognition to allow individuals to acquire new ideas, beliefs, values, and practices from other individuals. In order to accomplish this, he has constructed formal mathematical models of cultural learning and generated predictions on how cultural information is both transmitted and shaped by the human mind. Using a wide range of methodologies and techniques drawn from different fields of study, Henrich has investigated how individuals learn and transmit information from others, both in the laboratory and among traditional societies.

Henrich has identified two key components of human psychology that are crucial for acquiring culture, as well as the ongoing process of cultural evolution. The first involves understanding how cognition directs social learning toward particular individuals, ideas, and beliefs, and how cognition makes sense of the available social information. By applying evolutionary theory to understand the processes underlying social learning, Henrich predicted that individuals should use model-based cues of skill, success, health, prestige, and self-similarity (e.g., sex and ethnicity) to decide with whom to pay particular attention to for cultural learning (Henrich and McElreath 2007; Henrich and Gil-White 2001). Similarly, individuals should rely on copying the behaviors exhibited by others around them in the absence of high-

quality social information from skilled cultural models (Henrich and Boyd 1998). The second component pertains to the ways that cultural learners avoid exploitation during cultural learning: natural selection leads cultural learners to rely on inferentially potent (i.e., costly) displays when acquiring cultural information that can be cheaply transmitted via verbal or other symbolic communication. Costly displays are actions that would likely only be performed by cultural models that actually subscribe to the cultural information that they have expressed verbally (Henrich 2009).

Prestige

Prestige can be seen as an emergent product of psychological adaptations that evolved to assess the quality of information obtained through cultural transmission (Henrich and Gil-White 2001). Not to be confused with dominance (e.g., status maintained through force and threats), prestige is more closely analogous to freely conferred deference on behalf of cultural learners, who perceive a prestigious individual to be a purveyor of high-quality information. Natural selection favored cultural learners who could evaluate and imitate successful cultural models that demonstrate mastery of skills as well as knowledge relevant to survival and reproduction (i.e., high-quality information). Cultural learners evolved the tendency to ingratiate themselves with successful cultural models in order to gain close proximity to, and prolonged interaction with, these models. This adaptive bias granted cultural models deference on behalf of their adherents, and some models accumulated more prestige than others. Cultural learners could identify which cultural models have been bestowed the most deference from others and decide which models to emulate. As a result, this led to a general preference for cultural models who appear to be “popular” relative to others (Henrich and Gil-White 2001).

This type of cultural transmission is adaptive because it saves cultural learners the costs of individual learning, and natural selection favors efficient social learning capacities. Furthermore, natural selection favors behaviors that direct cultural learners toward greater interaction with

successful cultural models, as well as establishing cooperation with them. Cultural learners therefore evolved the capacity to provide benefits to targeted cultural models in order to gain greater access to and cooperation with such models. In a sense, preferred cultural models can be seen as having prestige with respect to their subordinates (cultural learners). The most skilled and knowledgeable cultural models will end up with larger followings of cultural learners – a direct indicator of the quality of information that a cultural model possesses (Henrich and Gil-White 2001). Thus, natural selection favors cultural learners who select their cultural models on the basis of their associated prestige. Because high-quality information (e.g., expertise, skill, wisdom) attracts groups of cultural learners who show deference to prestigious cultural models, models benefit from such deference and are incentivized to compete with one another for greater prestige (Henrich and Gil-White 2001).

Credibility Displays

Natural selection shaped our cognitive processes in regard to cultural learning, such that certain inferentially potent behavioral displays – or *credibility displays* – represent honest cues of belief, commitment, and group involvement (Henrich 2009). Ancestral humans faced the adaptive challenge of verifying culturally transmitted information from other people in order to avoid being exploited or misled. Humans evolved to look for credibility enhancing displays that indicate an individual's degree of commitment to, or belief in, verbally expressed mental representations. Natural selection favored a reliance on credibility displays in determining how much to commit to, engage in, or believe in a particular representation.

Credibility displays are a costly display or behavior that provides other individuals with a reliable measure of a person's beliefs or degree of commitment to a group, an ideology, set of values, or beliefs (Henrich 2009). Credibility displays are actions that must be both consistent with a model's professed beliefs and are also actions that a person would be unlikely to perform if this person were to believe something different from

what they expressed symbolically. As a result, these behaviors are often “costly” with regard to how much time, energy, resources, or risk of bodily harm are involved. In other words, credibility displays are seemingly detrimental to the individual when taking into account the costs of engaging in them. Although such behaviors appear expensive, harmful, or otherwise wasteful, engaging in costly, credibility-enhancing displays confers an overall benefit to participating individuals by signaling to others one's honest commitment to certain beliefs or to a community, thereby reinforcing one's credibility within a group and providing access to the benefits of cooperation and group living.

Credibility displays promote group cohesion between individuals, as performing such behaviors can encourage collective commitment if many individuals partake. Joseph Henrich argues that there is a connection between credibility displays and levels of commitment to group ideologies, religious beliefs, and shared values that promote solidarity and cooperation within groups, such that a greater number of credibility displays indicate greater levels of commitment (Atran and Henrich 2010; Henrich 2009). Participation in such costly displays is associated with prosocial in-group behavior because credibility displays indicate commitment to beliefs that may benefit the group as a whole. Groups that require these displays are favored by cultural evolution because they represent honest signals of beliefs and group commitment, which in turn promote cooperation and success in intergroup competition. *Cultural group selection* then spreads interconnected combinations of beliefs and practices, where stable combinations of beliefs and practices promote a group's success over others (Henrich 2009).

Religion

According to Joseph Henrich, religion is the result of coevolutionary phenomena. That is, religion emerged from the interaction between genetic evolution of certain psychological properties and cultural evolutionary processes that further shaped human behavior and sociality. In other words, religion is comprised of by-products of

psychological adaptations (Atran and Henrich 2010) working in tandem with adaptive cultural learning processes (Henrich 2009; Henrich and Gil-White 2001). Religions often consist of counterintuitive beliefs in supernatural agents (e.g., gods, spirits), costly commitments, and ritual behaviors (Atran and Henrich 2010; Henrich 2009; Shariff et al. 2011), and these features of religious belief systems are deeply rooted in our evolutionary history.

Culture and genes may have interacted to make certain aspects of religion – such as the belief in *moralizing high gods* – more appealing and believable (Atran and Henrich 2010; Shariff et al. 2011). Beliefs in omniscient, policing supernatural agents, or moralizing high gods are theorized to be partly the by-product of psychological processes that once served the purpose of overcoming recurrent evolutionary obstacles but have been repurposed as the selective environment changed. For example, psychological mechanisms devoted to agency detection were selected for their ability to detect environmental threats (e.g., predators, prey, other humans) but later may have become instrumental in the conceptualization of unseen, supernatural agents that exert their influence on the natural world as well as human affairs (Atran and Henrich 2010). The development of large-scale human societies brought about evolutionarily novel challenges to human group living as large, sedentary populations faced difficulties in coordinating group behaviors, monitoring the actions of group members, preventing free riders from exploiting other group members, and maintaining group cohesion. To accommodate these new developments in human civilization, beliefs in moralizing high gods emerged to reinforce the punishment of noncooperation, defection, and free riding within groups (Shariff et al. 2011). Moralizing high gods became prominent in religious belief systems as cultural evolution proliferated combinations of rituals and beliefs that instilled greater degrees of commitment to gods who demand cooperation between group members, punishment for those who do not follow certain behaviors, and who monitor behavior at all times (Henrich 2009). Therefore, the existence of moralizing high gods in many modern religions is the result of long-

term cultural evolutionary processes and competition between emerging human societies.

Religions require credibility displays on behalf of their adherents (Henrich 2009). These costly displays or behaviors provide other individuals with a reliable measure of a person's degree of commitment to a religious ideology, set of values, or belief system. This can take the form of behaviors that are seemingly detrimental to an individual's fitness, such as ritual scarification, celibacy, fasting, self-imposed poverty, sacrifices, and even martyrdom (Henrich 2009). However, costly behaviors are potent displays that transmit beliefs to other participants and observers, and religions with such requirements will tend to survive and grow because such costly acts invigorate others' commitment and represent honest signs of dedication to the group's belief system. Religions that demand credibility displays facilitate the cultural transmission of devotion to deities, moral guidelines, and the group as a whole.

Belief in moralizing high gods, costly rituals, and acts of devotion will be more likely to proliferate when the most prestigious individuals in a group display them (Henrich and Gil-White 2001; Henrich 2009). In learning which behaviors to imitate and what to believe, group members will attend to the behaviors of prestigious individuals in an attempt to replicate cultural knowledge that may benefit the learner, resulting in the transmission of religious beliefs. Further, religions that encourage costly credibility displays (e.g., avoidance of food, sexual abstinence, body modification) among prestigious individuals will spread because these individuals are influential models of such behaviors. *Cultural group selection* will favor religions that demand costly credibility displays and that have prestigious cultural role models who effectively transmit beliefs as well as practices that facilitate in-group cooperation, promote group solidarity, and increase competitiveness against out-groups.

WEIRD Societies

Although the majority of psychology research is conducted in the western world, the psychological and behavioral patterns observed in Western,

Educated, Industrialized, Rich, and Democratic (WEIRD) societies may not be representative cross-culturally (Henrich et al. 2010). Henrich and colleagues have noted that, although most research is conducted on WEIRD populations, there are significant differences in many psychological characteristics between the western world and small-scale societies. For example, the Müller-Lyer illusion trumps westerners, whereas individuals in traditional societies tend to not fall for the illusion. Differences in fairness and cooperation have been documented, such that westerners tend to give more fair offers in game theory paradigms (e.g., dictator and ultimatum game). When comparing industrialized civilizations and small-scale societies, there are notable differences in everything from scores on visual perception tasks, fairness and cooperation in economic decision-making, spatial cognition, and even the perception of color. This has led Henrich to conclude that, for behavioral researchers to make generalizable claims with respect to human psychology, a more concerted effort must be made to collect data from societies around the world (Henrich et al. 2010).

According to Henrich, the same principle applies when attempting to draw conclusions from comparisons between industrialized societies, western societies, and even within American samples (Henrich et al. 2010). As for the differences between western and non-western societies, preference for choice, the motivation to conform, prevalence of analytical versus holistic reasoning, attribution errors, moral reasoning, and self-serving biases contrast with one another significantly. Among westerners, Americans (for whom the majority of psychology research is conducted) and other westerners share notable differences. For instance, Americans are consistently the most individualistic and most patriotic and are among those who work the longest hours and are the most productive. Further, Americans significantly differ from other western societies such that they have the highest divorce rate, highest poverty rate of poverty, highest income inequality, and commit more crimes. Even among American research samples, subjects tend to not be representative of other Americans, usually consisting

of college educated, psychology majors, who tend to be children of highly educated and high socioeconomic status families. These individuals are also often more individualistic, less conformist, and less prejudiced than the general population. In sum, there are considerable differences in psychological characteristics and behaviors between large, industrialized societies, western societies, and even the population of North America, signifying that findings in most studies using WEIRD samples may not be generalizable cross-culturally (Henrich et al. 2010).

Taken together, these findings outlined by Henrich and colleagues suggest that the majority of behavioral science research may be drawing far-reaching conclusions from a rather small, atypical subset of the world's population. Researchers often mistakenly assume that their findings are universal, when in fact their findings may, by and large, only be generalizable to undergraduate research participants found in WEIRD societies. Because of the considerable population variation commonly found in behavioral science research, WEIRD subjects may be an inappropriate population from which to make generalizations due to their unique characteristics. As such, research topics may also be limited by the heavy reliance on WEIRD populations. Henrich contends that understanding human diversity is crucial for not only understanding the breadth and scope of psychological phenomena but also for constructing evolutionary theories of human behavior.

Conclusion

Joseph Henrich has made significant contributions to evolutionary science by applying evolutionary principles to the study of human culture. His work demonstrates not only how our minds shape culture but also how culture shapes our minds. In investigating the ways that humans acquire and transmit culture, he has helped pave the way for an understanding of the psychological underpinnings of culture, as well as the ways that cultural processes lay the foundations for complex sociological phenomena. Such insights shed light

on the interplay between cultural and genetic evolution on the development of human civilizations.

Cross-References

- [Credibility Displays](#)
- [Religion](#)
- [Religious Beliefs](#)

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Joseph Henrich on Religion

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Synonyms

[Author](#); [Religiosity](#); [Religious views](#); [Researchers](#); [Rituals](#); [Spirituality](#)

Definition

An interconnected set of rituals, beliefs, and norms that emerged due to competition among societies and institutions, often consisting of counterintuitive representations of supernatural agents and culturally acquired beliefs, rooted in the commitment-inducing power of devotions and rituals.

Introduction

Religion is a coevolutionary phenomenon. That is, religion arose from the interaction between genetic evolution of psychological characteristics and cultural evolutionary processes. Religion is

comprised of byproducts of psychological adaptations (Atran and Henrich 2010) and is also a product of adaptive cultural learning processes (Henrich and McElreath 2007). Although modern religions are rooted in our evolutionary history, they are not solely the consequence of genetic evolution, but rather the belief systems themselves are the result of dynamic cultural systems working in concert with natural selection. Indeed, religion can be adaptive by imposing beliefs and practices (e.g., dietary rules, hygiene, eating rituals) that can shape human habits in adaptive ways. However, religion itself is not an adaptation per se; it is a converging set of cultural products, rooted in features of our evolved psychology. The converging components of religion consist of counterintuitive beliefs in supernatural agents (i.e., moralizing high gods), commitment (credibility-enhancing displays, costly displays), and ritual (Atran and Henrich 2010; Henrich 2009; Shariff et al. 2011).

Moralizing High Gods

Beliefs in omniscient, policing supernatural agents, or *moralizing high gods* (e.g., god of the Abrahamic religions), are the byproduct of psychological processes that emerged to serve non-religious functions (e.g., agency detection), combined with cultural evolutionary processes that favored cooperation-enhancing beliefs (Atran and Henrich 2010). With the development of large-scale human societies, evolutionarily novel challenges emerged as large, sedentary populations faced difficulties in coordinating group behaviors, monitoring the actions of group members, preventing free riders from exploiting other group members, and maintaining group cohesion. For civilization to accommodate these new developments in group living, it was necessary to invent and enforce beliefs in “moralizing high gods” that punished noncooperation, defectors, and free riders within groups (Shariff et al. 2011). The central features of religions, such as moral guidelines, traditions, and the belief in one particular god or a specific pantheon of gods, have proliferated due to competition between different cultural groups, with the more

successful groups spreading their respective religious beliefs and practices.

The preponderance of moralizing high gods across world religions is the result of long-term cultural evolutionary processes driven by competition among cultural groups. Moralizing high gods became prominent in religious belief systems as cultural evolution favored combinations of rituals and beliefs that instilled greater degrees of commitment to gods who demand within-group cooperation, punishment of those who do not follow certain behaviors, and who have the power to monitor behavior at all times (Henrich 2009). Beliefs in such gods helped expand human cooperation; the fear of moralizing supernatural agents helped overcome the constraints imposed by the growth in the size of human social groups and the subsequent difficulty in coordinating behaviors and maintaining group solidarity. Thus, the emergence of religions with beliefs in moralizing high gods has been a cumulative process built by our evolved psychology and shaped by changes in the size and scale of competing human societies.

Credibility-Enhancing Displays

According to Henrich’s view, religions will culturally evolve to possess beliefs in counterintuitive supernatural agents, such as moralizing high gods, which demand *credibility-enhancing displays* (CREDs; Henrich 2009). CREs are costly displays or behaviors that provide other individuals in a group with a reliable measure of a person’s beliefs or degree of commitment to an ideology, set of values, or beliefs. For example, practicing celibacy, fasting, eschewing material wealth, performing sacrifices, and even martyrdom can act as CREs of deep commitment to a belief system (Henrich 2009). Sacrifices (including self-sacrifice) are potent CREs that transmit beliefs to both participants and observers, and religions with such rituals will tend to survive and grow because these costly acts invigorate commitment to a set of beliefs. Religions that demand CREs allow for the transmission of deep commitments to the supernatural agents and gods that are found in a given belief system and further spread the belief in the agent(s) (Henrich 2009).

Counterintuitive beliefs, such as supernatural agents and moralizing high gods, will be more likely to proliferate when the most prestigious individuals in a group express CREDs (Henrich 2009). In learning how to behave and what to believe, group members will attend to the behaviors of prestigious individuals and the CREDs that they are performing. Cues of prestige influence people to pay attention to specific individuals for learning cultural information, and prestigious individuals performing CREDs convince group members that they are truly committed to their professed beliefs. Religions that encourage CREDs (e.g., avoidance of food, sex, and wealth) among high-status individuals will tend to proliferate because they have made their leaders to be powerful models of such commitment. Therefore, successful cultural practices involving deep commitment to counterintuitive beliefs will tend to involve prestigious individuals performing CREDs. Cultural group selection will favor religions with role models who effectively transmit beliefs and practices that strengthen in-group cooperation, promote group solidarity, and increase competitiveness against out-groups.

Conclusion

Religion is the result of long-term cultural evolutionary forces that helped shape the complex, large-scale institutions that now dominate the modern world. Religion serves to coordinate human affairs in large, genetically unrelated groups by encouraging cooperation between individuals within groups and enforces these belief systems by invoking supernatural agents. Omniscient, moralizing supernatural agents (e.g., high gods) reinforce interconnected series of religious beliefs that were culturally selected based on their ability to facilitate cooperation in larger groups, promote within-group cohesion, and foster competition with other social groups. Religious beliefs are more likely to proliferate when promoted by prestigious individuals, and CREDs function as honest signals of commitment to belief systems while encouraging the transmission of specific religious beliefs.

Cross-References

- [Joseph Henrich](#)
- [Religion](#)
- [Religious Beliefs](#)
- [Scott Atran](#)

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Journalist

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Judgment and Decision-Making

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Evaluations or estimates (*judgments*) inform the intention to pursue a course of action among alternatives (*decision-making*). All of the behavioral

sciences – economics, biology, and psychology – have made judgment and decision-making (JDM) a focus of substantial research. However, JDM has been variously characterized in multiple disciplines and has lacked overarching theoretical integration (Mishra 2014). Evolutionary theory offers such a point of overarching integration. Because all organisms are necessarily products of natural selection, all behavior must be (at least in part) a manifestation of evolutionary pressures (whether positive, negative, or neutral).

In the following, we first summarize theoretical work suggesting that JDM research requires an overarching normative approach (guided by evolutionary theory) and further requires explication of universal currency of decision-making (proxies of biological fitness). Second, we outline that JDM mechanisms must be calibrated around ecological rationality: Decision mechanisms should be fast, frugal, and sensitive to historical and recurrent environmental pressures. Third, we provide examples of how an evolutionary approach can shed light on key topics in the JDM field.

Evolutionary Theory and the Currency of JDM

Normative theories are concerned with quantifying what organisms *ought* to do in a particular situation. In contrast, descriptive theories involve a bottom-up approach based on empirical observations of actual behavior. Descriptive theories are typically constructed from apparent violations of normative theories and are concerned with describing *what* organisms actually do. In evolutionary parlance, normative theories are concerned with functional explanations for behavior, whereas descriptive theories are concerned with proximate explanations for behavior (Scott-Phillips et al. 2011). Both normative and descriptive theories are integral to understanding JDM processes and outcomes given that quantifying both function and mechanism are essential to fully understanding the etiology of any behavior.

The first (and arguably most influential) normative theory of decision-making is *expected*

utility theory (EUT), which was developed in the field of economics (Friedman and Savage 1952). EUT posits that decision-makers seek to maximize *utility*, which is a measure of happiness, gratification, or satisfaction derived from a behavior. Although EUT has been, and continues to be, extremely influential, the currency of utility is vague and has typically been operationalized only at the proximate level (Mishra 2014). In contrast to normative economic theories of decision-making (e.g., optimal foraging theory, risk-sensitivity theory) do not suffer from the problem of vague quantification of a currency of utility. Rather, biological theories explicitly codify that decisions are made around the currency of fitness (Stephens and Krebs 1986).

Humans and nonhuman animals are products of evolution by natural selection and should therefore have cognition shaped by sensitivity to inclusive fitness (that is, the differential reproductive success of self and kin; Hamilton 1964). In humans, however, the pursuit of fitness is not direct; rather, people make decisions based on *proxies of fitness*, which are outcomes that are (or have been) historically statistically associated with reproductive success (Mishra 2014; Mishra et al. 2017). Positive proxies of fitness include access to material resources, mates, status, and positive reputations, among others. JDM should therefore reflect sensitivity to proxies of fitness. Quantification of proxies of fitness as the central currency in decision-making has two key virtues. First, such a currency is not as vague as utility. It can be explicitly quantified, measured, and empirically examined. Second, this currency is derived directly from evolutionary theory, and therefore grounds any understanding of JDM in a broader overarching explanatory framework.

Ecological Rationality and Mechanisms of Decision-Making

Normative approaches to JDM have focused on understanding “rational” or “optimal” decision-making (i.e., seeking to maximize or optimize a particular currency). Key pushback against the

idea of “optimal” decision-making in economics came in the form of the descriptive “heuristics-and-biases” program of research, which quantified the various ways that actual human decision-making countered the predictions of EUT.

Proponents of the heuristics-and-biases program argue that human reasoning is prone to systematic errors (*biases*; Tversky and Kahneman 1974). However, this tradition treats biases as failures of a flawed mind. By contrast, evolutionary theory suggests that while biases may appear to be “irrational” at first glance, they may actually be part of a cognitive system designed to maximize proxies of fitness (reviewed in Haselton et al. 2009). Given the fundamental constraints of cognitive processing – it takes time, energy, and effort to collect information, and almost every real-world decision is made under some constraint of uncertainty or incomplete information – it is necessarily the case that JDM mechanisms must be “bounded.” Most decision-making is characterized by satisficing, which involves seeking outcomes that are “good enough” to meet one’s needs (versus optimal; Simon 1956).

Fast-and-frugal heuristics are simple satisficing cognitive “rules of thumb” that can be simply applied to a wide range of situations. Such heuristics are time, knowledge, and computationally efficient (Gigerenzer and Gaissmaier 2011). However, to be effective, fast-and-frugal heuristics must be well-fitted to the environment of decision-making. In this sense, fast-and-frugal decision-making reflects *ecological rationality*, which describes robust fit between cognitive decision mechanisms calibrated to recurrent structures of regularly encountered environments (Todd and Gigerenzer 2012). The use of heuristics may not always be “rational” in the context of modern environments. However, some heuristics can be considered adaptively rational in that they reflect fit to recurrent past (rather than present) ecologies.

Evolution-minded theorists have posited that human bias occurs for three reasons (see *Bias* entry). First, fast-and-frugal heuristics can be prone to breakdowns in reasoning in systematic ways. Second, humans may have become prone to bias because they developed a preference for errors that impose lower fitness costs. Third,

some instances of bias may be an artifact of environments incompatible with the evolved mind (reviewed in Haselton et al. 2009). Together, this theorizing and research suggests that people make satisficing decisions in accordance with an account of bounded rationality, and that people’s JDM mechanisms reflect ecological and adaptive rationality.

Applying Evolutionary Theory to JDM Problems

An evolutionary perspective suggests that JDM is centered around maximizing proxies of fitness, and JDM mechanisms must reflect bounded and ecological rationality. In the following, we provide examples of how an evolutionary approach can shed light on several commonly studied topics in JDM.

Judgments and cognitive biases. Canonical mainstream understanding of cognitive biases is that they represent systematic errors as a consequence of deviation from “rational” normative judgments. However, many of these supposedly “irrational” biases reflect evolutionary architecture. For example, the *primacy effect* and *recency effect* describe people’s tendency to overweight initial and recent events (respectively) in memory. The *availability heuristic* describes the tendency to overweight salient events in memory. *Attentional bias* describes people’s tendency to differentially attend to recurrent thoughts. The *base rate fallacy* describes people’s tendency to ignore base rates and focus on salient anecdotes.

The list of cognitive biases that have been identified is very large. However, a common thread emerges: most biases involve overweighting salient events in memory, independent of how statistically likely they are. Such biases are obviously ecologically rational: particularly hazardous, dangerous, or important events *should* be overweighted so as to prevent negative fitness outcomes. Ecologically rational judgment mechanisms (especially regarding risk assessment) should overweight salient threats in order to motivate appropriate behavior. In this sense, cognitive biases reflect deep evolutionary logic (an

argument made persuasively elsewhere; e.g., Haselton et al. [in press](#)).

Risk and uncertainty. Risk and uncertainty are inherent properties of essentially every decision. Risk is most widely defined as payoff or outcome variance (reviewed in Mishra [2014](#); Mishra et al. [2017](#)). Uncertainty occurs when decisions involve unknown outcomes (by contrast, risk canonically involves choice only among known outcomes; Volz and Gigerenzer [2012](#)). There are few “real-world” (i.e., nonlaboratory) decisions that do not involve uncertainty. It has thus been argued that uncertainty can be considered a form of immeasurable risk, and that decision mechanisms must be sensitive to (and potentially integrate) risk and uncertainty (Volz and Gigerenzer [2012](#)).

How do people make decisions around risk (and uncertainty?). The recently proposed *relative state model* suggests that there are two pathways to risk-taking: need-based and ability-based (Mishra et al. [2017](#)). Need-based risk-taking is a product of competitive disadvantage, consistent with risk-sensitivity theory (which posits that decision-makers seek risk when unable to meet their needs with low variance options). Those who are competitively disadvantaged (i.e., far from a desired goal) thus upregulate risk-taking. This pathway is inclusive of such widely documented empirical phenomena as the young male syndrome (Wilson and Daly [1985](#)), which describes increased risk propensity among young males who are competitive. By contrast, ability-based risk-taking is a product of an assessment of competitive advantage, where people engage in risk-taking when they possess abilities or traits that increase the expected value of risk-taking and/or have signaling value (e.g., Sell et al. [2009](#)). The relative state model provides an evolutionary account of why both competitively advantaged and disadvantaged individuals engage in (differential) patterns of risk-taking, offering clarification of longstanding arguments about domain-specificity and generality of risk-taking.

Framing and loss aversion. One of the most renowned findings in the JDM literature is that decision-makers are risk-prone when facing losses and risk-averse when facing gains (summarized in highly influential *prospect theory*;

Kahneman and Tversky [1979](#)). Evolutionary theory offers a normative explanation for these findings. Experiencing a loss may bring an organism to the threshold of not being able to reproduce or survive (Hurly [2003](#)). As a consequence, organisms should elevate risk in the face of losses because risk-taking might represent the only way to potentially avoid such dire biological outcomes (consistent with risk-sensitivity theory; McDermott et al. [2008](#)).

Temporal discounting. Human and nonhuman animals engage in temporal discounting: the active preference of smaller, immediate rewards over larger, distal rewards. A large literature suggests that the degree of temporal discounting is dependent on an individual’s perceived time horizon. Those who perceive themselves to have short time horizons (e.g., shorter life expectancy) are substantially more likely to engage in temporal discounting (Daly and Wilson [2005](#)). Such behavior is often interpreted as irrational (why choose outcomes with lower expected values?). However, viewed through an evolutionary lens temporal discounting makes adaptive sense. Individuals who do not anticipate that tomorrow is guaranteed choose options that are available today, especially when making decisions about behaviors related to proxies of fitness (e.g., Krupp [2012](#)).

Perceived time horizons are associated with individual differences in life history orientation, which range from “fast” (comprising a constellation of impulsive, present-oriented behaviors) to “slow” (comprising a constellation of patient, future-oriented behaviors). Substantial research has shown that individuals who exhibit “fast” life histories typically have experienced developmental and/or environmental conditions that cue short time horizons (e.g., high extrinsic mortality, low life expectancy, parental absence, abuse; reviewed in Mishra and Lalumière [2008](#)).

The four broad areas summarized above represent some of the core areas of research and knowledge in JDM. An evolutionary framework offers an integrative, normative understanding of behaviors in all of these areas in that it (a) grounds currencies of decision-making in concrete and quantifiable proxies of fitness, (b) offers an ecologically rational account of decision-making

mechanisms, and (c) has broad explanatory power and scope.

Cross-References

► Predicting Events and Behavior

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Judgment of Cheating

► Perceptions of Infidelity

Judith Jarvis Thomson

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Synonyms

Author; Ethics; Philosopher

Definition

Judith Jarvis Thomson is a researcher and philosopher who works mainly in the fields of moral theory and metaphysics. She is also well known for her role in the development of variations of the *Trolley Problem* and for her controversial 1971 essay *A Defense of Abortion*.

Introduction

Judith Jarvis Thomson was born in New York City on October 4, 1929. She received her B.A. in Philosophy from Barnard College in 1950, another B.A. in Philosophy from Cambridge University in 1952, a M.A. in Philosophy from Cambridge in 1956, and, finally, a Ph.D. in Philosophy from Columbia in 1959 (Gendler 2009; MIT Philosophy Department 2016). She began teaching at Barnard College in 1962 and married British philosopher James Thomson (they later divorced in 1980). Next, Jarvis Thomson spent a year teaching at Boston University before being appointed to the faculty at MIT in 1964 (Gendler 2009). She has held visiting professorships at the University of Pittsburgh (1976), Yale Law School (1982, 1984, 1985), and the University of California at Berkeley Law School (1983). Moreover, she has held academic fellowships from the Fulbright Foundation (1950–1951), the American Association of University Women (1962–1963), the National Endowment for the Humanities (1978–1979, 1986–1987), the Guggenheim Foundation (1986–1987), and the Center for Advanced Study (Oslo, Norway, 1996) (Gendler 2009). She was also elected to the American Academy of Arts and Sciences in 1989 and served as president of the Eastern Division of the American Philosophical Association from 1992 to 1993 (Gendler 2009). Currently, she still works at MIT as a Laurence S. Rockefeller Professor of Philosophy.

Research

In her 1967 essay *The Problem of Abortion and the Doctrine of the Double Effect*, ethics researcher Philippa Foot discussed the moral distinctions between intended and unintended consequences, and between the duty to do no harm versus the duty to help others, using several examples, including the ethical dilemma now known as *the Trolley Problem* (Grimes 2010). The Trolley Problem outlines an ethical dilemma faced by the driver of a runaway trolley that is speeding toward five workers. The driver must decide whether to divert the trolley onto another track where only

one worker is present, thus sacrificing the life of one person to save five other people. After its initial conception by Foot, Jarvis Thomson created two variations of the Trolley Problem; the first is known as the Loop Variant, which requires a bystander to choose whether to throw a switch to divert the trolley (sacrificing one life to save five, similar to the original dilemma) or not to intervene at all. The second variation is known as the Fat Man Variant, which requires a bystander to choose whether or not to throw an obese man onto the tracks to derail the trolley and save five lives (Cathcart 2013). These two problem variations introduce the options of less action (the Loop Variant) or more direct action (the Fat Man Variant), which can influence moral perspectives and perceptions of blame. Collectively, using the Trolley Problem and its variants to study morality has become known as *trolleyology* (Cathcart 2013).

However, Jarvis Thomson is arguably most famous for her controversial 1971 essay *A Defense of Abortion*. In this essay, Jarvis Thomson argues that, even if contending that the fetus has a right to life, the rights of the fetus do not supersede the rights of the pregnant woman's right to bodily autonomy (i.e., to control her own body) and her body's life-support functions (Thomson 1971). In one example, she defends the permissibility of abortion using the following thought experiment:

You wake up in the morning and find yourself back to back in bed with an unconscious violinist. A famous unconscious violinist. He has been found to have a fatal kidney ailment, and the Society of Music Lovers has canvassed all the available medical records and found that you alone have the right blood type to help. They have therefore kidnapped you, and last night the violinist's circulatory system was plugged into yours, so that your kidneys can be used to extract poisons from his blood as well as your own. [If he is unplugged from you now, he will die, but] in nine months he will have recovered from his ailment, and can safely be unplugged from you. (Thomson 1971, p.48–49)

According to Jarvis Thomson, it is permissible to unplug yourself from the violinist even though your actions will cause his death because of limits on one person's right to life. Specifically, one person's right to life does not supplant the rights

another has to their own body. Thus, unplugging the violinist does not violate his right to life, but, rather, deprives him of the use of your body, to which he has no right (Thomson 1971). Jarvis Thomson extends this argument to the aborted fetus; abortion does not violate the fetus' right to life, but, rather, denies the fetus the nonconsensual use of the pregnant woman's body, to which it is not entitled (Thomson 1971). She therefore concludes that induced abortion is morally permissible.

Conclusion

Judith Jarvis Thomson has authored or coauthored several other notable works, including, for example, *Acts and Other Events* (published in 1977); *Rights, Restitution, and Risk* (published in 1986); *The Realm of Rights* (published in 1990); *Moral Relativism and Moral Objectivity* (published in 1996); and *Goodness and Advice* (published in 2001) (see Gendler 2009). Most recently, she published a book entitled *Normativity* in 2008 and published an article on trolleyology in Frances Kamm's *Trolley Problem Mysteries* in 2015 (MIT Philosophy Department 2016). As of the writing of this entry, Judith Jarvis Thomson was working on a new book on moral theory entitled *Ethics* (MIT Philosophy Department 2016).

Cross-References

- Development
- Philippa Foot
- Trolley Problem, The

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Judith Rich Harris

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Introduction

Judith Rich Harris is an American psychologist with a scholarly career that has become quite exceptional after a century of professionalized and compartmentalized science. Although blessed with a well-developed faculty for rigorous analytical thinking, two mishaps conspired to sidetrack her from the beaten academic path. First, she was dismissed from Harvard's PhD psychology program in 1960, because she was considered insufficiently capable of original and independent thinking. Second, she was diagnosed with an auto-immune disease in 1977, which confined her to her home and made a career in science even more implausible. Unable to give up on her love for science, she found a way to feed her interest in psychology as an author of textbooks from 1970s up to 1990s. This enabled her to read widely and to familiarize herself with different psychological paradigms, which proved to be of great importance eventually, when she emerged out of the shadows of textbook-authorship with an article in a peer reviewed psychological journal in 1995, followed by the monograph *The Nurture Assumption: Why Children Turn out the Way they Do* in 1998, and yet another monograph in 2006, *No Two Alike: Human Nature and Human Individuality*. Both books engage in detailed criticisms of developmental psychology, while reaching out to evolutionary psychology and

behavioral genetics to develop alternative accounts for the factors that govern the process of human individuation.

Both books address lay audiences. They do not contain any unexplained jargon, and they excel in the art of persuasion through wit, verbal virtuosity, the staging of scientific *personae* (Wesseling 2004) and clever choices of genre. *The Nurture Assumption* combines the expository mode with autobiography (Harris 1998), which enables the author to establish a rapport with the reader. *No Two Alike* has been composed as a whodunit, with the mystery of human individuation posing as the culprit, the author as a private detective (or “academic investigator” as she calls it), who first has to eliminate five false leads before she can identify the culprit, who turns out to be a threesome. One could therefore fit her under the rubric of science popularization, were it not for the fact that this label evokes unwarranted derogatory connotations. Science popularization is often regarded as derivative, as a continual watering down of science proper as information is passed on from one audience to another, producing ever less of the same. Hence, science popularization can only produce cognitive loss; it can never produce new insights. This view of science popularization is wrong, as sociologists and historians of science have argued at length (Whitley 1985; Hillgartner 1990; Nowotny 1992; Lewenstein 1995; Clark and Illman 2001). The argument is that scientists are communicating their theories to diverse audiences all the time, both inside and outside of the academy, and that every act of communication is a translation that may actually produce new insights. The case of Judith Rich Harris substantiates this perspective on science communication. The ability to put different research fields in dialogue with each other without being subject to the “publish or perish” pressure of professional science may help to move beyond entrenched positions and to explore new explanatory models, as we shall see.

Parental Power: A “Cherished Culture Myth”

Harris’s first book, *The Nurture Assumption*, stages a frontal attack on a sacrosanct tenet of

developmental psychology, while taking the child-rearing advice industry that follows in its wake in her stride. Harris argues that psychological research has focused rather narrowly on the formative influence that parents supposedly exert on their offspring, at the expense of other environmental and genetic factors that may also explain “why children turn out the way they do.” The methodological rigor of psychological research leaves much to be desired, as Harris sees it. The confusion of correlation with causation is rampant, and researchers have only been alert to parent-child effects, while ignoring the possibility of child-parent effects, which would make for different relations between causes and effects. Moreover, control groups are often lacking, which makes a longitudinal project such as Judith Wallerstein’s inquiry into the effects of divorce upon 131 children between ages 3 and 18 virtually useless in Harris’s eyes (Wallerstein and Resnikoff 1997; Wallerstein et al. 2000). More specifically, developmentalists hardly ever control for genetic factors according to Harris, which is a further reason why the bulk of their research cannot reveal how the home environment shapes personality in the longer term with any degree of reliability. To top it all off, Harris emphasizes that learning is highly context-specific. Parents may teach their children all sorts of things inside the home, but this does not necessarily carry across to spheres outside the home, which constrains parental influence considerably. Harris therefore concludes that the impact of parents on their children has been grossly overestimated, while evidence to the contrary has been systematically ignored. After half a century of research in developmental psychology, this idea is still just an assumption or “cherished cultural myth” as she calls it, and the author thinks it is about time that we discard it in favor of other, more viable hypotheses.

Genes and Peers

Harris offers two alternative explanations for why children turn out the way they do, namely, one’s genetic make-up and the shaping influence of peers. True enough, intelligent parents tend to

have intelligent children, but this is not because these parents used flashcards or read books to them at length, but because intelligence is largely hereditary. Furthermore, because of the context-specific nature of learning and because we spend only a limited portion of our lives in a family setting, the interaction with peers is bound to exert a stronger influence on the development of our personalities than relationships with parents. Thus, Harris subscribes to the well-established view that both nature and nurture determine how children turn out, but she redefines “nurture” quite drastically, by privileging peers over parents.

Harris’s exposure of methodological flaws in psychological research does not only deal a sensitive blow to academic developmental psychologists but also to science-based child-rearing experts who administer advice to parents through diverse media. If the nurture assumption cannot stand up to critical scrutiny, then it inevitably follows that the dos and don’ts of the child-rearing advice industry are unfounded as well. Harris does not hesitate to drive the message home. Advice-givers likewise exaggerate the impact of parents on children, making impossibly high demands on parents, which degrades parenthood into an anxious, guilt-ridden affair. This does not mean that Harris claims that parents “do not matter,” as many a newspaper article suggested. Clearly, parents have the power to make their children miserable or happy during the time they are together, but they cannot determine their personalities in the long run. As the reception of her book demonstrates, this two-pronged attack gained a wide hearing. *Newsweek*, *New Republic*, and *Commentary* put Harris’s story on their covers. *The Nurture Assumption* was reviewed in leading American newspapers and weeklies, and was a topic on radio and television talk-shows. The British media likewise lavished attention upon Harris’s book (see <http://judithrichharris.info/tna/index.html> for a complete overview of its reception in the press) and it has been translated into some twelve foreign languages (French, German, Italian, Greek, Danish, Finnish, Hebrew, Spanish, Polish, Japanese, Chinese, and Dutch). Determined to get a firmer grip on the “genes and peers” factors, Harris went on to write another book.

The Mystery of Human Individuality

In *No Two alike*, Harris sets herself the daunting task of solving the riddle of human individuality. How come human beings differ from each other to the extent that “no two are alike,” not even identical or conjoined twins? Comparative research into identical twins (genetic similarity is almost 100%), siblings (genetic similarity is around 50%), and adoptive siblings (genetic similarity is zero) enables researchers in behavioral genetics to distinguish between the contributions of genetic and environmental factors to the shaping of human personality. This has led to the insight that genetic factors account for around 45% of human variation. Parenting, Harris repeats once more, accounts for virtually nothing, nor do other factors of the shared home environment appear to have much impact: identical twins, when reared apart, differ just as much (or just as little) as identical twins reared in the same home. Differences within the home environment such as birth order cannot be credited with causing long-term personality differences either, as Harris argues in a lengthy dialogue with Frank Sulloway’s *Born to Rebel* (1996), since systematic comparisons of first-born with later-born children do not reveal consistent patterns of variation across different contexts. Differences between siblings, then, are to be attributed to the “non-shared environment” as the world outside of the home is called in behavioral genetics, which includes the peers that Harris already touched upon in her previous book. However, this nebulous concept may include basically anything and everything, and cannot have much explanatory power as such. Therefore, Harris has made a concerted effort to specify which aspects of the “non-shared environment” could explain why even Ladan and Laleh Bijani, identical conjoined twins who died during the operation that was to separate them, had developed different personalities, while their genes were well-nigh similar, and the one could not go anywhere without the other.

The Modular Mind

Having drawn upon behavioral genetics to account for around 0.45 of human variation,

Harris resorts to evolutionary psychology for the unexplained other half, proceeding from the premise that human variation serves some purpose, that “evolution provided humans with a certain amount of plasticity in behavior so they can profit from their experiences” (Harris 2006, 115). Learning is another word for profiting from one’s experiences, therefore Harris searches for clues in theories of learning, which are necessarily embedded within theories of the human mind. Since humans have lived in groups since time immemorial, it is theories of social learning we need to look for. How is the human mind equipped to fit us to social life? Harris takes her cue from modular theories of mind as elaborated by Jerry Fodor (1983) and Steven Pinker (1997), who claim that cognition is distributed over various functions, and argues that the brain is not a single organ, but rather a conglomerate of mental modules, each taking care of its own specialized function. In other words, modularity of mind implies that there is a specific division of labor between the different modules constituting the human brain. Harris goes on to argue that three specific mental modules are crucial to social learning, namely, the “relationship system,” the “socialization system,” and the “status system,” which she deduces from the different tasks a human being needs to fulfill to function in human society. The first stores information about significant others and helps to establish and maintain consistency in individual relationships; the second gathers information about how we could conform to a specific group that we want to belong to (this is where the “peers” come in); and the third collects information about where we stand vis-à-vis other members of our group, suggesting how we may stand out from or compete with them. The third system is particularly important with a view to explaining non-genetic human variation, for we develop this mental faculty relatively late in life, perfecting it all throughout adolescence and adulthood, whereas the first two develop in early childhood already. This would tally with Harris’s point that the home environment is not of much consequence to the shaping of human individuality. The status system is the faculty that drives us to distinguish ourselves from others and to find our own

little niche in society, in collaboration with the relationship system and socialization system, fitting us to specific divisions of labor that seem to be characteristic of how groups of human beings get things done.

Harris’s Legacy

What is it that Harris has bequeathed to psychology in her late-life, uncredentialed, unpaid, but widely discussed appearances upon the academic scene? Clearly, Harris has engaged in both demolition and construction work. She has not only invested a lot of energy in exposing unwarranted assumptions, flawed research designs, self-serving bias, and immunity to critique in academic psychological research, but she has also attempted to raise new structures after clearing the ground, namely, group socialization theory in *The Nurture Assumption* and the modularity of mind in general and the status system in particular in *No Two Alike*. It has clearly been Harris’s ambition to change the agenda of psychological research, diverting scientific energies away from assessing parental impact on their children in early childhood, to the ways in which human beings adapt themselves to different social environments beyond the home, by offering a theoretical model that could be tested. If we take this ambition very literally, we have to conclude, 12 years after the publication of her last book, that it has not been realized, in the sense that one is hard put to point to researchers that have put her theory to the test. There may be both social and intellectual reasons for this absence of follow-up in a narrow sense. First, it is a mission impossible for a single individual operating outside of the university to set the agenda for groups with vested interests working within this institution. Institutions outnumber and outlast individuals, in science and elsewhere. Moreover, there are also certain self-defeating elements in her bold speculations themselves. If social learning is highly context-specific as Harris emphasizes all throughout, meaning that there is hardly any transfer of lessons learned from one social domain to another, then it cannot be a shaper of personality, understood as a pattern of

traits that remains stable across different contexts and stages in life. The only consistency we would then be left with would be entirely genetic, for genes are impervious to social contexts. Beyond that, we cannot be anything other than shape-shifters if we follow Harris's theory of social learning to its logical conclusion. We would then not only differ from others, but we would also continually differ from ourselves as we move from one social context (e.g., work) to another (e.g., sports), a notion that is hardly conducive to empirical testing.

Having said as much, this does not mean that Harris's publications have remained without consequence in the academic world, as we may infer from specific signs of scientific acknowledgement that are also indicators of impact. First of all, having your work published in peer reviewed journals is a clear sign of scientific recognition, which she managed several times (Harris 1995, 2000a, b, c). To receive an award for a publication is another sign of acknowledgement, and Harris received the George A. Miller Award for her 1995 article, which is named after – irony of ironies – the very scientist who dismissed Harris from Harvard graduate school in 1960. When an authoritative peer-reviewed journal makes room for an extensive commentary by an established scientist and an equally elaborate reply from the author, one can be sure the academic world takes this author seriously (Vandell 2000; Harris 2000b). A similar argument applies to the fact that a leading developmental psychologist, Eleanor Maccoby, took the trouble of producing a 27-page paper in response to Harris's book (Maccoby 2000). *No Two Alike* has also been reviewed by scientists (cf. Ronald 2008, Kaighobady and Shackelford 2000; Anderson 2007) in addition to a wide spectrum of journalists (see <http://judithrichharris.info/n2a/index.html>). On the whole, these scientific reviews are fairly positive, with Shackelford even recommending that Harris's model of the modular mind is put to the test, a recommendation that has not been followed yet, as stated before. Clearly, then, the scientific community has taken due notice of Harris's work, demonstrating that works in science communication may feed back into the

research process, although it is difficult to establish precisely how it has done so.

Given the widespread public acclaim her two books have met up with, Harris's major impact is probably on the public understanding of psychological science. First, her work infringes upon psychology's "biopower," to use a term from Michel Foucault, who argued that the biomedical sciences do not only produce knowledge but also exert power by imposing standards on individuals that distinguish between "normal" and "abnormal" behavior. Psychology certainly also has such disciplinary power. There is probably no other academic discipline which has managed to disseminate its ideas so widely amongst lay audiences and to embed itself so firmly in a wide array of societal institutions as developmental psychology (Rose 1985, 1992). Most citizens of Western welfare states understand themselves and their relationships in the terms of developmental psychology. It has been taken for granted that parents are all-powerful (and that children's agency counts for nothing) for several decades by now, which has sustained the equally widespread notion that parents stand in constant need of expert advice, coaching, monitoring, and intervention, as Foucault's pupil Jacques Donzelot already argued in the 1970s (Donzelot 1977, 1980). After Harris's widely read books, this assumption can no longer be taken for granted, which is sobering for developmental psychologists and the experts who sell their theories to a wider public, but potentially liberating for parents (and their children).

More specifically, Harris's books are bound to have had an effect on the public understanding of the relative merits of evolutionary psychology, behavioral genetics, and developmental psychology. In the shadow which national socialism cast over the twentieth century, it took a long time before behavioral genetics could cast off its detrimental associations with eugenics and racism, a blight that developmental psychology has always been free from, with its emphasis on the environmental plasticity of the child. Harris has certainly done her share in redressing the balance between these fields of inquiry, thereby paving the way towards dialogue and exchange. If she has

deflated the public image of developmental psychology, she has certainly boosted the reputation of evolutionary psychology and behavioral genetics, through her crystal clear expositions of their founding assumptions and basic methods. Thus, even though Harris may not have had a direct impact on the research agenda of developmental psychology, she may very well have had an indirect impact, making it less acceptable for developmental psychologists to ignore the role of heredity in the shaping of human personality.

Third, on the meta-level of knowledge production, Harris's work demonstrates that casting the occasional glance over the walls of one's own area of expertise is a necessary anti-dote against disciplinary bias and career-motivated overinvestment in theories that are sinking under an increasingly heavy burden of anomalous findings. If we grant that professional experimenting scientists are hard put to develop such a broader perspective, given the labor-intensive nature of scientific experimentation, then we should make a greater effort to acknowledge and cherish the vital role of "independent investigators" such as Judith Harris or Oliver Sacks in the overly compartmentalized landscape of contemporary professional science. They are well positioned to identify blind spots and to open the scientific mind to new theories and hypotheses. Conversely, having all your scientific credentials in place, including an affiliation to a prestigious university institute, is not a watertight guarantee for scientific integrity or validity, as Harris has revealed at length, a lesson never to forget. Outsiders within such as Harris or Sacks help to maintain scientific standards, while their curiosity-driven intellectual work embeds scientific research within broader intellectual and scholarly cultures. Through such embedding, specialized scientific research can be made amenable to societal debate, which is necessary, given science's immense impact on the everyday lives of (late-)modern citizens.

Cross-References

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- [Adaptive Plasticity](#)
- [Adolescent Issues](#)

- [Cognitive Changes in Adolescence](#)
- [Development](#)
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- [Theory of Mind](#)
- [Theory of Mind and Evidence of Brain Modularity](#)

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Just So Stories

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The just-so story was invented by Rudyard Kipling when writing fanciful tales for small children about such things as how the leopard got its spots (Kipling 1902). The term was then appropriated by others to apply to cases in which a critic thought that an explanation was as juvenile and silly as those provided by Kipling. Although use of the just-so story to denigrate someone else's idea preceded Stephen Jay Gould's use of the term (Smith 2016), Gould's repeated application of the just-so story canard (Olsen and Arroyo-Santos 2015) to sociobiological hypotheses and research (e.g., Gould 1978, 1980, 2002) led to the current tight association between Gould's anti-adaptationist views and the just-so story. While it is true that Gould (with Lewontin) did not use the label in their most famous and widely cited article (Gould and Lewontin 1979), they did criticize the adaptationist program in that paper as one that relies “on plausibility alone as a criterion for the acceptance of speculative tales” (p. 581). In other words, adaptationists (i.e., sociobiologists and evolutionary psychologists) are unscientific types whose enthusiasm for plausible selectionist accounts leads them to accept speculations as true even in the absence of evidence in favor of the idea. The hostile meaning of the just-so story as applied to studies by sociobiologists and evolutionary psychologists was clear to all concerned (Alcock 1988; Holcomb 1996; Kurzban 2002).

However, as Brown (1982) pointed out early on, the “just-so story” label really refers to a hypothesis, a possible explanation, which is an initial step in all scientific investigations. The hypothesis is then used as a prediction generator with follow-on tests of a possible explanation involving checks of the predictions taken from that hypothesis (Sesardic 2003). In other words, Gould would have us believe that producing hypotheses based on natural selection theory was a fatuous activity that led nowhere given the

supposed eagerness of adaptationists to accept speculations on the basis of “plausibility alone.” In reality, silly hypotheses are rare and those that are proposed will be quickly rejected when tested. Since no journal accepts untested hypotheses, testable predictions are universally required by adaptationists. Gould’s use of the just-so story was designed not to improve scientific procedure but to block the scientific study of animal behavior, especially human behavior.

Gould’s examples of just-so stories as applied to species other than humans were limited. He apparently felt that the evolution of the giraffe’s long neck was one such “story,” given that high school textbooks all repeated the standard account of evolutionary change driven by natural selection with a longer neck said to be adaptive in the context of feeding competition (Gould 1996). The widely presented idea was that hereditary variation in neck length enabled the variants with longer necks to acquire food that was out of reach of competitor herbivores. According to Gould, little evidence existed in favor of this hypothesis. And yet if we were to predict that currently giraffes would often feed on leaves of trees growing at heights only giraffes could reach, our prediction would be correct inasmuch as giraffes favor taller trees and preferentially feed on plant material growing 2–4 m above the ground where it is out of reach of the next tallest browsers (Cameron and du Toit 2013; Mahenya et al. 2016a, b).

There is an alternative adaptive explanation based on sexual selection in which long necks are favored in males because of their use as weapons in “necking” combat in which two males competing for access to mates swing their heavy heads and necks into one another (Simmons and Scheepers 1996). Gould (1996) appears to like this hypothesis despite the fact that some researchers have noted that some predictions derived from the sexual selectionist hypothesis might be wrong (e.g., Mitchell et al. 2013). Others feel that the evidence supports both hypotheses or that the data do not invalidate either of the two explanations (e.g., Simmons and Altwegg 2010; Danowitz et al. 2015).

The point here is not that Gould was wrong in failing to anticipate work that would be done after his death. It is that Gould’s just-so story criticism,

applied to an easy target, high school biology textbooks, which was designed to ridicule a hypothesis, has not kept others from using the scientific method to explore the possible adaptive value of long necks in giraffes in terms of feeding competition. And the same is true for another of his just-so story victims (Gould 1978) David Barash, author of a short note in the *American Naturalist* based on a very small sample of experimental observations of the mountain bluebird (Barash 1976). This note, which dealt with the possible adaptive responses of male bluebirds to potential cuckoldry, has been cited 55 times as of 2016, an indicator not of the completeness of Barash’s research but rather of the productivity of trying to test the ideas that selectionist thought generated about adaptation in male behavior in paternal birds, which are not predicted to provide parental care to offspring they may not have sired.

Indeed, as DeBruine (2009) notes, the beauty of evolutionary theory is to alert researchers to hypotheses that they would never have considered were it not for the impetus provided by selectionist thinking. DeBruine supplies several examples of novel predictions about human behavior that were derived from evolutionary hypotheses and then tested, such as the context-specific responses to similar faces (a marker for genetic similarity) that are viewed positively in terms of trustworthiness (relatives are generally to be trusted over nonrelatives) and negatively in terms of sexual attractiveness (relatives are generally to be avoided as sexual partners compared to nonrelatives). As DeBruine points out, without the benefit of evolutionary theory, no one would have thought to propose and then test the idea that the perception of apparent genetic similarity would have two different but adaptive effects on human behavior. Likewise, it was the possibility that selection would increase the probability that paternal male birds would try to avoid being cuckolded by their mates that led Barash to his experiments. The selectionist idea that Barash explored has now been examined by hosts of behavioral ecologists who have produced many papers on the subject. The same is true for the analysis of human behavior by evolutionary psychologists.

The rapid development of the field of evolutionary psychology (Durant and Ellis 2003)

speaks to the failure of Gould's efforts. The only persons who continue to follow Gould's lead in vilifying the adaptationist approach to human behavior are philosophers of science like Buller (2005), Fodor (2007), and Kitcher (1985) and non-scientist commentators like Gottlieb (2012) and Slater (2013). Evolutionary psychologists and other adaptationist researchers have rightly come to ignore the just-so story slur that Gould attempted to apply to entire fields of study.

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Justice

- Fairness in Corvids
- Fostering Values of Fairness

Juvenility

- Early Childhood and Adolescence

K

K Strategy

► [Iteroparity](#)

Kellogg Chimpanzee Study, The

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Synonyms

[Gua the Chimpanzee](#), [Kellogg study](#), [Winthrop Kellogg](#)

Definition

A study conducted by Winthrop Kellogg to determine the extent to which a chimpanzee can be taught human behaviors and language skills when raised like a human.

Introduction

Comparative psychologist Winthrop Kellogg (1898–1972) was a strong proponent of conducting research to compare the development of humans and nonhuman primates (Kellogg

1931). In the summer of 1931, Kellogg undertook what was intended to be a 5-year study examining the relative influence of heredity and environment on development. The study was conducted as part of Kellogg's Social Science Research Counsel Fellowship at the Yale Anthropoid Station in Florida. The facility (now the Yerkes National Primate Center at Emory University in Georgia) was opened the year before and quickly became one of the main primate research facilities in the United States in part due to Kellogg's work.

Rationale and Goals

Kellogg was inspired by stories of children reared among wild animals in India and popular fiction such as *The Jungle Book* and *Tarzan of the Apes* as well as by the comparative psychological work of Nadezhda Ladygina-Kohts and was interested in examining the relative role of nature and nurture in creating differences in mental abilities (particularly the capacity for complex language skills) between humans and other animals. However, Kellogg knew that it would be unethical to place a child into the wilderness to be raised among animals for an experiment, and so he decided instead to test his nature vs. nurture question by raising a wild animal, specifically a chimpanzee named Gua, as if she were his own child (Benjamin and Bruce 1982). It was important to Kellogg that Gua was “always treated as a human” (Benjamin and Bruce, p. 467), and accordingly she was reared as a sibling

to Kellogg's son Donald, receiving the same diet, toys, and opportunities for learning.

- [Language Development](#)
- [Pinker's \(1994\) The Language Instinct](#)
- [Steven Pinker and Language Development](#)

Study and Findings

At the start of the study, Donald was 10 months old and Gua was slightly less than 8 months old. The development of both "siblings" was carefully recorded, and Kellogg conducted numerous tests to compare Gua's skills to Donald's (Hearst and Capshaw 1988). Gua was able to acquire a number of behaviors traditionally characterized as uniquely human such as utilizing a spoon to feed herself, and she was noted to outperform her "brother" on some behavioral measures (Kellogg and Kellogg 1933). However, Gua did not make any attempt to communicate using human language, while Donald did imitate many of Gua's ape vocalizations (Shusterman 2010). This difference was enough for Kellogg to conclude that innate differences in the brains and bodies of chimpanzees and humans prevented Gua from fully adopting the behaviors expected from a healthy human child (e.g., use of symbolic language), and the experiment was discontinued in the spring of 1932 after less than 1 year (Kellogg and Kellogg 1933).

Conclusion

While the inability of Gua to learn human language was an important factor in Kellogg's conclusions regarding the limits of environmental influences on behavior, teaching language to Gua was not the primary goal of the experiment. The experiment is thoroughly documented in Kellogg's 1933 book *The Ape and the Child*, which was coauthored by his wife Luella. After the study was concluded, Gua was placed in the Yerkes Regional Primate Research Center where she died of pneumonia in December 1933.

Cross-References

- [Cognitive Development in Non-human Primates](#)
- [Imitation](#)

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Kellogg Study

- [Kellogg Chimpanzee Study, The](#)

Kenyanthropus

- [Australopithecus Group](#)

K-Factor (Figueredo)

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Synonyms

[Arizona Life History Battery \(ALHB\)](#); [K-SF-42](#); [Mini-K](#); [Super-K](#)

Definition

A common factor underlying a cluster of human life history indicators.

Life History Theory

According to life history (LH) theory, individuals allocate resources (such as time or calories) for competing needs. Allocating resources for one need may diminish the resources for the other. This leads to several trade-offs between specific goals. For instance, should an organism invest in current or future reproduction? Should it invest in the quality or quantity of its offspring? Should it exert efforts in mating or parenting? (Del Giudice et al. 2015). The (unconscious) decisions an organism makes regarding these trade-offs comprise LH strategies.

LH strategies tend to generate clusters of traits. These traits include maturation, growth, fertility, parenting, and lifespan. Species differ in their LH strategies. Species that follow *r* (or fast) strategies mature, mate, and reproduce early, producing many offspring (e.g., clams, fish, and frogs). Species that follow *K* (or slow) strategies mature, mate, and reproduce late and produce few offspring (e.g., whales, elephants, and humans).

Individual Variability

Variability in LH strategies exists within species as well. As a group, humans are *K*-strategists since they produce relatively few children and invest substantial resources in each one (as compared with *r*-strategists like fish). However, there is variability among individual human beings regarding the degree to which they exhibit this trait. This variability is a consequence of genetic and environmental conditions.

The traditional approach to measuring both species and individual LH strategy is biodemographic, such as measuring the age of puberty and the number of offspring. Nonetheless, in humans, individual LH strategy can also be measured psychometrically by asking people to disclose their resource allocation preferences. This approach was pioneered by Rushton and continued by Figueredo (see historical review in Figueredo et al. 2013).

Using the psychometric method, Figueredo et al. (2005) collected data from multiple self-

report items related to LH, such as parental and partner attachment, mating effort, and risk-taking. They proposed that there is a common factor – the *K*-factor – that underlies this collection of LH indicators. Using measures of the *K*-factor, people could be divided into high- and low-*K*. High-*K* individuals invest significantly in their family and friends, are long-term planners, and take fewer risks. Low-*K* individuals, on the other hand, invest little in their family and friends, are short-term planners, and take more risks. Figueredo and colleagues showed that the *K*-factor is heritable (Figueredo et al. 2004).

K-Scales

The *K*-factor can be measured using several *K*-scales that have been translated into several languages. The Arizona Life History Battery (ALHB; (Figueredo 2017) comprises 199 items in 7 subscales. Each subscale measures resource allocations of a different domain: (1) insight, planning, and control (e.g., “I try to make sense of the things that have happened to me”); (2) mother/father relationship quality (e.g., “How harsh were they when they punished you?”); (3) family social contact and support (e.g., “During the last twelve months, about how many times have you seen them?”); (4) friends social contact and support (e.g., “During the last twelve months, about how many times have you seen them?”); (5) romantic partner attachment (e.g., “I prefer not to show a partner how I feel deep down”); (6) general altruism (e.g., “I usually vote in local and national elections”); and (7) religiosity (e.g., “I am a very spiritual person”). Most items are rated on a scale of -3 (disagree strongly) to $+3$ (agree strongly). Many of the items were derived from previous scales, whereas others were developed by Figueredo and colleagues. Due to its length, the ALHB is rarely administered.

A more popular *K*-scale is the Mini-*K* (ALHB-SF); this is a short form comprising 20 items (Figueredo et al. 2006). The Mini-*K* is the eighth-AHLB subscale and can be used separately. Its items are not taken from the ALHB; they are generalized statements derived from

the other ALHB items. Each of the seven ALHB subscales is represented by two to three Mini-K items. Sample items are as follows: “I can often tell how things will turn out,” “I avoid taking risks,” and “I have a close and warm relationship with my own children.” The items are rated on a scale of -3 (disagree strongly) to $+3$ (agree strongly). The Mini-K reliability is not high. Both the test-retest reliability and the Cronbach’s alpha are about 0.70 (Olderbak et al. 2014).

Recently, Figueredo et al. (2017) proposed a new short scale – K-SF-42. The new scale incorporates six items from each of the seven ALHB subscales and has better psychometric traits than those of the Mini-K. About half of the items (24) are rated on a scale of -3 (disagree strongly) to $+3$ (agree strongly), for instance, “I am nervous when partners get too close to me.” The other half (18) are rated on a scale of 0 (not at all) to 3 (a lot), for instance, “How much have your friends told you that they liked the way you are?”

The K-factor scales can be placed in a wider context, creating Super-K factors. Super-K factors add general elements to the K-factor. For instance, a Super-K can consist of three components: K-factor, Covitality, and the General Factor of Personality. Covitality includes mental and physical health; the General Factor of Personality is synonymous with the Big-Five personality traits (Olderbak et al. 2014).

Critique

The K-scales have received sharp criticism (Copping et al. 2017; Richardson et al. 2017). The critics claim that the psychometric properties of the K-scales have not been sufficiently studied and, at present, seem inadequate. They question the need to aggregate items from different domains (e.g., parenting, religion, altruism) into one global measure. They also question if the scales measure a single construct and if that construct is correlated with behavioral indicators of LH theory. Last, they claim that some of the subscales (e.g., insight,

planning, and control; mother/father relationship quality) do not measure LH strategy but predictors or mediators of it. They, therefore, consider the K-scales and ones like it as lifestyle – not life history – measures.

Conclusion

The K-Factor is a latent variable underlying a cluster of LH indicators. It aims to measure human individual differences in LH strategy, using a psychometric method. It can be measured using several scales; the Mini-K is the most popular of them. The K-factor and similar psychometric LH scales have been critiqued on psychometric and theoretical grounds.

Cross-References

- ▶ Aurelio José Figueredo
- ▶ Fast Versus Slow Strategies
- ▶ Fundamental Tradeoffs
- ▶ Life History Strategies
- ▶ Life History Theory
- ▶ r/K -selection Strategies
- ▶ Reproductive Strategies
- ▶ Rushton, J. Philippe

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Killer

- [Defending Against Predator](#)
- [Predators](#)

Killer Whale Life History

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Definition

The reproduction, growth, and survival patterns of killer whales (*Orcinus orca*)

Introduction

The killer whale (*Orcinus orca*), or orca, is the largest species in the dolphin family and is commonly recognized as one of the top predators in our oceans. Killer whales are abundant in high latitude coastal waters; however, they reside in all oceans around the world (Forney and Wade 2006). Because of their wide distribution, they are still considered “data deficient” by the International Union for Conservation of Nature and Natural Resources (IUNC; Reeves et al. 2017). Luckily, several populations of killer whales have been studied extensively for several decades to gain important information on their life history.

Killer whales are considered one species, but there has been some debate whether populations should be classified into subspecies, due to differences in diet, genetics, morphological traits, coloration, and movement patterns (Forney and Wade 2006). Groups of killer whales have been distinguished by socially isolated ecotypes, including those in the northeastern Pacific who are categorized as either *resident*, *transient*, and *offshore*. *Resident* killer whales are characterized by maintenance of stable social networks and feed primarily on a variety of fish species, such as salmon. *Transient* killer whales tend to travel greater distances, have less stable networks, and feed on small marine mammals, like seals and porpoises. Less is known about *offshore* killer whales because of their large geographic range and tendency to be further from coastal waters. They feed on fish, including some species of shark (Baird 2000). Much of the information about killer whales has come from long-term studies of *resident* killer whales around Alaska, British Columbia, and Washington state. Along with these well-studied wild populations, individual whales residing in managed care have also helped us gain a better perspective on how killer whales allocate resources for reproduction, growth, and survival patterns (Robeck et al. 2015).

Reproduction

Killer whales tend to live together in social groups that can range from 2 to 20. Each group is defined by one matriline (descent from the female line) with one to three generations. *Resident* killer whales typically stay with their natal group for much of their life, but offspring of *transient* killer whales sometimes separate from their group when they reach maturity (Baird 2000). There is less information about the behavior of *offshore* killer whales who periodically separate and even abandon natal groups (Robeck et al. 2015). Mating occurs between individuals of different pods, which are composed of many matrilineal groups.

Similar to many other mammalian species, killer whales begin reproducing at an older age and produce few offspring. Male killer whales begin to sexually mature starting around 12.4 years old (Matkin et al. 2014). In the wild, the age of first reproduction for females is also around 12 years. Females born in managed care have been known to reach about 7.5 years of age by their first estrus and around 9.8 years by their first conception (Robeck et al. 2015). Killer whales have long reproductive lives; females stop reproducing around 30 to 40 years old. Like all other whale and dolphin species, killer whales give birth to a single calf. Though it is possible for whales and dolphins to give birth to twins, this is very rare. Thus, females may give birth to several offspring throughout their reproductive life span.

The gestation period for killer whales can range from 15 to 18 months (Duffield et al. 1995), which is longer in comparison to many other species of dolphin (typically around 12 months). Having a long gestation period helps balance the cost of producing large offspring, as calves of toothed whales are typically between 40% and 48% of adult female length (Chivers 2018). Gestation requires low energy investment that is compensated by longer calf dependency.

After birth, calves stay close to their mothers for protection, social bonding, nutritional, and locomotor support. For the mothers, lactation may be the most energetically expensive facet of reproduction, as producing milk with high protein and fat content is crucial for the development and growth of their

calf. Weaning is estimated to occur around 1.5 to 2 years when the calf begins to learn foraging techniques from their relatives (Baird 2000). The intervals between calf births range from 2 to 14 years, but the average is typically between 3 and 7 years. It has been noted that these intervals likely increase over time as mothers age (Matkin et al. 2014). Having a lengthy gap between births allows mothers to provide support for successful growth and survival of their offspring.

Growth

On average, the body length during the first year of life for resident killer whales is 2.7 m (Fearnbach et al. 2011). The rate of growth occurs rapidly from birth and throughout weaning and slows until sexual maturity. One sexually dimorphic trait that is apparent in this species is that males tend to reach a larger body size and have longer appendages compared to females. This is because females typically reach their full body length around 14.5 years, whereas males take longer to mature physically and do not reach their full body size until around 18 years (Fearnbach et al. 2011). Also, males have an additional spike in growth around sexual maturity, indicated by an increase in dorsal fin height. The average body length for southern *resident* killer whales in Alaska is 6.5 to 7.2 m for adult males and 5.5 to 6.4 m for adult females, which seems to be consistent with other populations of killer whales around the world (Fearnbach et al. 2011). One factor that may affect growth in killer whales is food availability. For example, one study found that younger adults were 0.3 m shorter than older adults after experiencing nutritional stress due to a decline in salmon stock (Fearnbach et al. 2011). While transfer of energy from mom to calf and food availability may influence growth rate, it also greatly impacts survival.

Survival

Like many mammalian species, killer whales have higher mortality rates for younger and older

individuals (Matkin et al. 2014). The mortality rate for wild killer whales younger than 6 months is estimated to be around 37% to 50%, though this rate slowly declines with age until 12 years for male and 20 years for females (Olesiuk et al. 2005). Calf survival past the age of two in managed care has improved over time and may be greater than some populations in the wild, including southern *resident* killer whales of the northeastern Pacific (Robeck et al. 2015). For individuals residing in managed care, average life expectancy is 41.6 years. Northern residents are similar with an average life expectancy of 42.3 years, while for southern residents, it is 29.0 years (Robeck et al. 2015). The maximum longevity of killer whales is estimated to be around 80 to 90 years of age for females and 50 to 60 years for males.

Females have a prolonged postreproductive life span, like humans, that is an adaptive benefit for aiding the fitness of their kin. For example, older females improve reproductive success and survival of individuals in their matriline by passing on ecological knowledge by leading group movements, particularly when food is scarce (Brent et al. 2015). These matriarchs are likely to be of value in the current environment where killer whales face many anthropogenic threats, including habitat deterioration and reduction in prey abundance due to pollution and overfishing. Boat traffic is also negatively impacting this species along with many other marine mammals through collisions, noise, and presence that disrupts important activities such as foraging, resting, and socializing. Although killer whales have no natural predators, the negative effects of humans have caused several populations to be endangered, threatened, or vulnerable.

Conclusion

Killer whales have a unique social group network based on matrilineal descent. Populations of killer whales differ, leading researchers to categorize them into ecotypes. Though there is still much to learn about killer whales, research on the *resident* ecotype in the northeastern Pacific and individuals

residing in managed care have been essential for gaining knowledge about life history parameters in this species. Killer whales begin reproducing later in life, which requires more involved parental care. However, this high investment strategy involves the risk of some offspring not surviving to reproductive age or reproducing their maximum potential. Killer whales are one of the only species, other than humans, in which females have a lengthy postreproductive period of life. These individuals are valuable for the success of their kin. Further investigation on killer whale reproduction, growth, and survival patterns can help us understand the impact we have on this species, and from this we can educate the public on sustainable practices to help conserve killer whales, as well as many other marine mammals around the world.

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Killing

- [Homicide Adaptation Theory](#)

Kin

- [Adaptive Benefits of Matriliny and “Walking Marriages” in Mosuo Culture](#)
- [Emotional Closeness Predicted by Relatedness](#)
- [Family](#)
- [Kin Elders Encourage Youth to Cooperate](#)
- [Presence of Siblings](#)

Kin Altruism

- [Hamilton’s Rule](#)
- [Helping and Genetic Relatedness](#)
- [Helping and Inclusive Fitness Benefits to Helper](#)
- [Helping and Reproductive Value of the Recipient](#)
- [Monetary](#)

Kin Bias

- [Early Association Cue to Kinship in Primates](#)

Kin Detection

- [Kin Detection by Odor](#)
- [Kin Recognition](#)

Kin Detection by Odor

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Synonyms

[Genetic relatedness](#); [Kin detection](#); [Kin recognition mechanisms](#); [Modified behavior towards conspecifics](#); [Self-referent processing](#)

Definition

Kin detection by odor refers to situations in which an organism recognizes a conspecific using organism specific odor cues. Once recognized, behaviors towards that conspecific may be triggered or inhibited resulting in an increase in overall fitness. For example, humans seem able to identify the odors resulting from differences in the major histocompatibility complex (usually unconsciously), thus avoiding in breeding with close genetic relatives and increasing hybrid vigor because of the increased variability in offspring MHCs.

Introduction

Kin selection, proposed by Hamilton (1964a, b), argues that overall fitness can be increased not only through direct transfer of alleles from parents to children, but also indirectly by aiding the survival and reproduction of relatives (kin) who share copies of the same alleles. Kin selection acts in two main ways: by helping relatives directly and by selectively avoiding mating with conspecifics thus avoiding inbreeding depression with its attendant evolutionary consequences.

Hamilton (1964a) argued that the cost of helping kin must be less than the overall benefit moderated by the coefficient of relatedness. In practice, this means that more altruistic help should be given to close relatives compared to distant relatives, and altruistic behavior should be absent with strangers, and even friends, as they do not share family alleles. But this leads to the question, if you can increase your overall fitness through aiding kin, how do you identify kin to aide?

Both proximate and ultimate aspects of kin recognition have been proposed to be important in kin selection (Reeve 1989). Reeve (1989) proposed a theory of conspecific acceptance thresholds, i.e., the criteria which must be satisfied in order to successfully identify kin. The first criterion was argued by Reeve (1989) to be the perception and identification of “kin” signals; secondly there must be processes which confirm the “other” as kin through matching to a stored template and finally there must be mechanisms which inform an appropriate behavioral response.

Methods of Kin Detection

Over the years several methods have been proposed for the identification of kin in humans. These explanations fall into several main theoretical positions, such as phenotypic matching using visual, acoustic or olfactory cues following imprinting at an early age or familiarity (such as being raised together), or self-reference where an awareness of self allows matching to kin. In humans there is additionally active specification, i.e., when parents directly indicate kin, e.g., *this is your cousin*.

Each method of kin selection has advantages and disadvantages, depending on the physical and social environment of the individual. Using sensory cues, such as self-referenced smell to identify kin, can be considered a reliable mechanism as imprinting and familiarity are open to error via adoption and alloparenting of genetically unrelated individuals. Visual and auditory cues may change over an individual's lifetime, while olfactory profiles in contrast have been found to be more developmentally stable (Curran et al. 2005), i.e., they remain constant over the majority of an individual's lifespan, although

changes occur with aging and ill health. Moreover, olfactory cues have been found to reliably co-vary with genetic relatedness, meaning they are an accurate, long-term cue to identify kin. Importantly individuals do seem to be able to reliably identify their own smell (Olsson et al. 2006), meaning self-referent odor similarity is a possible mechanism for kin selection, which eliminates the need for imprinting or early life experience with kin.

Detection of Kin Using Odor

What then is involved in the detection of kin using odor? This is an important question as our awareness of odor does not always reach the level of conscious awareness, suggesting that our behaviors in relation to odor are likely to be unconsciously mediated. A useful starting point is to identify the areas of the body that are particularly odoriferous.

In humans the axillae seem particularly important for odor generation and therefore kin identification, leading Richard Dawkins to coin “the armpit effect” in Dawkins 1976. The axillae may have gained prominence in odor signaling because of human bipedalism and therefore the relative height proximity of the axillae to the sensory organ of olfaction in others. Both eccrine and apocrine glands are important in odor generation, although the latter are likely more important as they are particularly concentrated in the axillae. A genetic factor influencing individual odor is the highly polygenetic (and therefore polymorphic) major histocompatibility complex (MHC). Each individual possesses a unique set of MHC genes, and these act in combination with the body's other processes (such as sweating) to produce a characteristic odor profile (odor-type) which is singularly their own. Thus, Reeves' first criterion has been met. The second requires the identification of processes that confirm the “other” as kin. Olsson et al. (2006) found that smelling a stranger activated the same parts of the limbic system as fearful stimuli, while the odor of a friend activated areas involved in feelings of familiarity. Thus, we can distinguish friend from foe, but can we distinguish kin?

Emma Marxer-Tobler and Jamie Pineda investigated this by testing whether people could

recognize shared ethnicity using body odor alone. They looked at the ability of participants to use body odor to differentiate between themselves, members of their own ethnic group, and members of a different ethnic group. German, Korean Taiwanese, and Chinese students were asked to wear cotton T-shirts over a period of four consecutive nights without use of de-odorants or other artificial scents (participants were also given information on foods to avoid, such as garlic). They were then asked to rate the familiarity of their own T-shirt and T-shirts from their in-group and out-group ethnicities (participants were naïve as to which were which). A total of 75% of participants rated T-shirts from the same ethnic group as familiar, but could not specifically identify from which condition they came. EEG readings were also taken, and it was found that participants' electrode responses to self-odor were most similar to those for in-group odor (Marxer-Tobler and Pineda 2012). The authors concluded that people can discriminate members of their in-group ethnicity using self-referencing odor and that this can be achieved without conscious awareness.

Several studies have shown that odor identification can be even more specific, for example Weisfeld et al. (2003) found that people can identify genetically related family members by scent alone. Participants could use odor to correctly identify a T-shirt worn by their mother 86% of the time, a stranger 91% of the time, their brother, father or sister 59% of the time, and themselves 50% of the time. Interestingly, errors in identification were symmetric, so that, for example, a sister's odor was confused with the mother's and vice versa, and a stranger's odor was symmetric with a friend or spouse's odor. Odors from kin were rarely confused with those from nonkin. So it seems that we can use odor to identify kin with reasonable accuracy.

Differential Behavior Resulting From Kin Identification Using Odor

The final aspect of Reeve's criteria is whether differential behavior results from kin identification. A great deal of research has looked at

behaviors in a mating context, particularly aspects relating to MHC. Repeated studies have shown that in humans, females are more likely to mate with a male who has a MHC smell profile dissimilar to their own and are sexually repulsed by males with a similar one (Wedekind et al. 1995). Mating with conspecifics is therefore avoided, reducing inbreeding depression and ensuring an enhanced immune responsiveness in any resulting offspring.

There is less evidence as to specific altruistic behaviors resulting from kin identification. Dubas et al. (2009) investigated whether parents could identify their children by smell; 79% of mothers and 67.7% of fathers could do this. But more importantly in terms of behavior, fathers who could identify their children by smell engaged in more positive behaviors with them, such as increased levels of attention and play.

Kin Detection Outside the Laboratory

Research in the laboratory has generally supported olfactory kin selection theory and met Reeves three criteria. However, outside of the laboratory life is not so simple. The majority of people nowadays attempt to over-ride their natural odor through the use of de-odorants and perfumes. But how successful are we at disguising our body odor? Allen et al. (2015) investigated this using a three-fold testing method. Individuals providing odor samples were initially matched on their deodorant brand use. Odors were collected through the use of cotton pads over 24 h in three conditions: (1) no deodorant, (2) their usual deodorant, and (3) an assigned deodorant. Participants in the study were presented with three 500 ml odor samples, two of these were from the same individual, and the third was from a different individual. The participant's task was to identify the odd smell out. The results indicated that the proportion of correct responses was highest for the no fragrance condition, compared to the usual deodorant condition, which was higher than the assigned deodorant condition. The authors concluded that fragrance does not mask information contained in body odor, and moreover that deodorants are chosen (probably unconsciously) to complement an individual's own body odor.

In our ancestral environments, humans probably lived in extended kin groups, meaning that individuals rarely came into contact with completely unrelated others. However, this is not the case in the modern world, so that social behaviors which evolved in the Pleistocene may no longer be adaptive in the twenty-first century. In evolutionary terms, helping nonrelatives is maladaptive, as resources are wasted on nonkin alleles (Hamilton 1964a), and olfactory kin selection evidence supports this idea (Selwyn and Meakings 2015). However, in today's world, we now spend proportionately more time with friends than family, due to increased geographical mobility and the frantic pace of twenty-first century living. Evolutionary mechanisms are often plastic, allowing for appropriate responses to a changing environment. Olsson et al. (2006) found that the odor of a friend could induce feelings of familiarity (and therefore potentially altruistic behaviors), particularly when the friendship had lasted for more than three years.

Conclusion

The term 'olfactory kin selection' is misleading to some extent, as it suggests that the identification of kin is the key biological imperative. The term accords the identification of non kin (via their body odor) to a lower status, when actually this ability is equally important in fitness terms. For example, olfactory cues to kin/non kin have relevance both in avoiding inbreeding depression by selecting a mate that is not closely related, and in bonding and caring for your own offspring rather than offspring which are unrelated. Moreover, despite our modern day obsession with concealing our natural odor through the use of perfumes, we can still detect an individual's body odor over and above externally applied scents (Allen et al., 2015). Furthermore, the warm feelings generated by the body odor of friends, reflects the structure of society as it is today, rather than the close knit kin groups of our evolutionary past. Clearly, there is plasticity in the olfactory kin recognition system, allowing it to respond flexibly to changes in social organization. Perhaps in today's complex

and geographically mobile society, friends (as colloquially suggested), really are the new family (at least in olfactory terms).

Cross-References

- [Kin Recognition](#)
- [Kin Selection](#)

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Kin Detection System

- [Adaptive Problem of Detecting Kinship](#)

Kin Discrimination

► Cooperation Varies with Genetic Relatedness

Kin Elders Encourage Youth to Cooperate

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Synonyms

Family; Kin; Sibling

Definition

Kinship is a “system of social organization based on real or putative family ties,” according to Encyclopædia Britannica.

And when it involves the social fabric which ties families and societies, the sociologists define it as, “Kinship is the most universal and basic of all human relationships and is based on ties of blood, marriage, or adoption” (Crossman 2019, p. 1).

Introduction

Among all social mammals, humans are organized communities of relationships that are focused around everlasting unions between family ties (Koster 2018). When younger siblings co-reside in a family with elder siblings, relationship between them may have significant effect on their growth and developmental, psyche, or behavior (Nitsch et al. 2012). Though social ties through common ancestry are among the oldest forms of sociality where young are nurtured by elder siblings, the psychology of kinship across human societies regularly co-opts sentiments

geared toward genetic relatives and extends them to unrelated strangers also (McNamara and Henrich 2016).

The common phrase, blood is thicker than water, is used to value the importance of family. People, who are related by blood, have stronger cooperation to each other over the people outside their family. Many studies suggest that kin selection with elder and young siblings can have manifold effect on cooperative behaviors in later stage of life, especially in smaller societies (Apicella et al. 2012; Lieberman et al. 2007).

In spite of the evolutionarily ancient roots, facts about the distinctive effects of kin selection on human psychology are mixed. Even, over the time, the phrase also has switched meanings, where it was “the blood of the covenant is thicker than the waters of the womb” (connections made through birth; Jack 2005). This self-contradictory history of the idiom also encases the critical nature of this kinship psychology. As we find that kinship norms establish only one of the several norm systems, we employ to exercise cooperation (Kimbrough and Vostroknutov 2013; Sripada and Stich 2006). And many studies suggest that kin relationship may only manifest a certain amount of human cooperation (Laland et al. 2010; Richerson and Boyd 2006; Richerson et al. 2010). It is also found that in societies with loose kinship, cooperation is promoted through universal moral values; a feeling of guilt; altruistic punishment; and an evident up and down of moralizing religions (Enke 2017).

From our own experience, we find that human being’s tendency toward cooperation may change through the course of stages of life. The present essay addresses effects of kinship interactions on siblings’ cooperativeness.

Context: Kinship and Cooperativeness

During the growing years of life, I have come across many friends and have experienced that the children who have siblings are more considerate and cooperative in nature. I remember that we were a group of elder sisters who would not only take care of our own siblings but also look

after the well-being of our friends and their siblings too. In contrast few of our friends who had no siblings would remain mostly aloof from extending help in time of need. We never even expected cooperation from them.

Antfolk et al. (2014) found that support from parents and similarities in physique and behavior among siblings predict the subjective certainty in relatedness and kin-directed behavior (i.e., cooperative behavior and inbreeding aversion).

Kinship relatedness among siblings is indeed a strong force in cooperation and trust patterns. Kinship mostly the influence of elder sibling on younger promotes social structures and cooperation patterns; similarly psychological, biological, and institutional variables also coevolve through kinship (Enke 2017).

From my own experience, I realized many a times that kinship develops cooperation. During one such experience, Once my elder daughter at the age of 15 accidentally had a dog bite on her nose by a pet dog resulting in profuse bleeding. Incidentally all her friends ran away, but one small unknown child of only 10 years accompanied her to our apartment and stayed with her till he handed over my daughter to me. As I settled with my daughter's condition, I visited the child's home in our premise and understood that he is taken care of by his elder sister along with a keeper, while his mother is at work. The elder sibling relatedness might have induced the cooperative behavior in the child.

Youth mostly cooperate according to their experiences in neighborhood regardless of their previous actions and influence of family values including kinship cooperation (Gutiérrez-Roig et al. 2014).

This is also supported by Greene (2014) who purported that, among youth with tight kinship, societal structure and behaviors evolve through in-group loyalty and cooperation. Kinship promotes cooperativeness even in the absence of parental love and care. Often it is observed that even though a child experiences parental absence due to death or any other reasons, parental love is compensated by the child's other kin to develop the child into a social cooperative being (Winking

et al. 2011). As both of us are working couple and often have work-related trips outside town, we have experienced that our daughters are extremely cooperative to each other and even compensate for our absence from home. They also cooperate with their friends and extend to others in the society as well.

Scientists have found that cooperative breeding from kin has a potentially vital role in the evolution of human prosociality (Hrdy 2009).

It is evidenced that elder siblings can make an advantageous contribution toward younger siblings' social cooperative behavior (Nitsch et al. 2013).

Many observational studies suggest that kin selection helps in increasing cooperation, especially in small-scale societies (Apicella et al. 2012; Lieberman et al. 2007).

Being into the teaching profession for more than 15 years, I have closely observed the students and noted that adjustment, cooperation, and cooperative nature are more among students who have siblings than who are brought up as a single child. This is supported by the work of Henrich (2015) that togetherness and tight kinship systems often contribute to "clannish" social structures and are thereby directly related to the people's cooperativeness toward other members of society.

Context: Kinship, Cooperativeness, and Related Factors

According to cultural anthropologist and social organizations, cooperativeness is largely determined by historical kinship systems (Dousset 2011).

In societies, mankind evolved through kinship system is influenced by culture, different types of rules, and norms that control kin psychology and are used to regulate behavior toward others specifically to all close knit family members. Studies support that cooperativeness among youth is influenced by kinship and aging.

Hulkenberg (2015) in his study shed light on the influence of culture layers of normative kinship build up on the preexisting genetic

relationships to facilitate further more extensive cooperation in the early evolution of increasingly complex social groups.

Despite this relatedness through common genetic ancient roots, humans often co-opt and extend cooperativeness to genetically unrelated others through culturally acquired kinship systems (McNamara and Henrich 2016). They further supported the effect of culture on normative kinship and the preexisting genetic relationships in increasing cooperation during early evolutionary years of complex social groups.

Findings also show the low cooperation found between children with tight kinship and the rest of in-groups but high cooperation by the elderly toward out-groups as they age (Gutiérrez-Roig et al. 2014).

Context: Kinship, Cooperativeness, and Contradiction

Often it is found that kinship norms not only contribute to kin-focused psychological mechanisms more strongly but extend effectiveness to include genetic nonrelatives and sometimes counter activation toward actual genetic relatives even (Henrich 2015). Thus, this set of norms may expand cooperation beyond genes.

Kinship advocates relatedness and coalitions to some extent. In kinship relationship both competition and cooperation are very important issues (Smith 2014).

Not only cooperation mechanisms for youth interactions with genetic relatives matter, human kinship also revolves around extensive cooperation with genetic nonrelatives (Henrich 2015).

Kinship rarely promotes patience in primates and largely fails to protect individuals from hostility. Smith (2014, p. 192) describes that an “individual’s closest friends and follies, many of whom may be kin, are most often an individual’s closest competitors, the siblings within the social groups.”

Although support networks are organized around kinship, covariates that test predictions of kin selection models do not receive strong support, potentially because most kin-directed

altruism occurs within households, not between households (Koster 2018).

Scientists have supported that in societies with tight kinship systems, youth have shown strong in-group favoritism. Youth were found to cooperate less with out-group members in games and even cheated them but have shown highly helping attitude to in-group members (Green 2014).

Contrasts have been drawn where societies with loose ancestral kinship ties have been seen to cooperate effectively and trust broadly (Enke 2017).

Evidence shows that societies with a historically tightly knit kinship structure regulate behavior through communal moral values, revenge taking, emotions of external shame, and notions of purity and disgust (Enke 2018).

Genes from common ancestors are considered the oldest social bonds.

Cooperativeness nature in human beings is influenced by many factors, and from the evidences available, of course kinship mainly, the relation between siblings cannot be attributed as one of the strongest reasons.

Conclusion

The present discussion highlights some aspects of youth cooperativeness and kinship ties especially the influence of elders.

There is a positive relation that exists between kinship tightness and cooperation with in-group members due to underlying trust, however opposite is also found with out group members due to lack of trust (Enke 2017).

It is also evident that the role of genetic kinship among siblings as a fundamental belief principle for constituting cooperative human genre might be less supported in certain cases than previously thought to be (Alvard 2009).

However, several studies purport that kinship norms are one of the many norm systems to facilitate youth cooperation where elders are closely related to young siblings (Kimbrough and Vostroknutov 2013).

In spite of much contradiction, kinship is essentially a helping aspect in bringing up

cooperativeness among human kind. Kinship mostly the sibling relationship boosts cooperation and altruism toward genetic relatives and beyond (Kurzban et al. 2012).

It may be concluded through the writers' own experiences and scientific evidences that kinship encourages cooperative behaviors among youth.

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Kin Interest in Mating Relationships

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Definition

Human mate choice is often strongly influenced by kin, notably parents. This can lead to conflict over mate choice, because these individuals have different evolutionary interests.

Introduction

In many cultures, parents have a strong (if not complete) influence on the mate choice of their offspring. Arranged marriages are a clear example of this. Research across cultures has shown that parents and their offspring do not agree about the importance of various characteristics in a mate. For example, offspring find it more important that their mate is physically attractive, whereas parents care more that they come from a good family background. This conflict over mate choice may be a product of evolution. The evolutionary interests of parents and their offspring overlap, but they do not entirely coincide. Because they are not equally related to their family members, the survival and reproduction of these individuals are not of equal importance to them. This evolutionary conflict can result in a conflict over mate choice in a number of different ways.

The Evolution of Human Mate Choice

The evolution of mate choice is an interesting but complicated topic. Sexual traits evolve in a complex interplay of selection pressures that the sexes impose on each other. The evolution of sexual preferences in the one sex affects the evolution of sexual characteristics in the other and vice versa. This coevolution can lead to intricate

evolutionary dynamics and surprising evolutionary outcomes. There are many famous examples, from the extravagant tail of the male peacock to the huge antlers of the Irish elk, which were so costly to produce that some believe they drove the species to extinction (Moen et al. 1999). Evolutionary biologists have used various methods to model the evolutionary dynamics that result from sexual selection, from evolutionary simulation models to mathematical methods such as population genetics and invasion analysis (reviewed in Kuijper et al. 2012). These models have helped us understand how evolution may have shaped the sexual characteristics that we observe in nature, including exaggerated sexual traits such as the peacock's tail (Fisher 1930; Zahavi 1975; Andersson 1994; Qvarnström et al. 2006). Empirical biologists have gone out to test the predictions of these models, often inspiring a further refinement of models in return. This close interaction between theoretical modeling and empirical research has been essential for advancing our understanding of the highly intricate topic of sexual selection (Andersson and Simmons 2006; Kokko et al. 2006; Kuijper et al. 2012).

In humans, the complex process of sexual selection is further complicated by another important factor: parental influence on mate choice. Parents in many cultures influence the mate choice of their children, both throughout history (Buunk et al. 2008; Apostolou 2012) and across geography (Minturn et al. 1969; Apostolou 2010; Buunk et al. 2010). In some cultures, such as India, China, Japan, and the Middle East, it is common for parents to arrange the marriages of their children, effectively exerting full control over their mate choice (Hatfield and Rapson 2006; Buunk et al. 2010). Also, in almost all present-day hunter-gatherer societies, there is at least some degree of parental influence on mate choice (Apostolou 2007a). Although parental influence on mate choice is less prevalent in most Western cultures, this is a relatively recent development (Apostolou 2012), and some parental influence on mate choice also remains there, especially among immigrant groups (Buunk et al. 2008).

We should expect the impact of parental influence on mate choice to be negligible if parents and their offspring essentially agree on what are the ideal characteristics for a mate. However, this is generally not the case. It has repeatedly been shown that parents and their offspring place emphasis on different qualities when assessing the value of a potential mate for the offspring. Specifically, parents give more importance to characteristics such as family background and social status, whereas offspring place more emphasis on attributes like physical attractiveness and smell (Buunk et al. 2008; Apostolou 2010, 2015; Perriloux et al. 2011). Similar results have been found across various different sample groups, including people from the Netherlands (Buunk et al. 2008; Dubbs and Buunk 2010), Argentina (Buunk and Castro Solano 2010), and Japan (Dubbs et al. 2013).

Why do parents and their offspring disagree on mate choice? This entry will discuss why evolution may have led to the emergence of this conflict. To do this, we will first examine the evolutionary interests of the involved parties and how they differ from each other. Next, we will discuss how these diverging evolutionary interests can result in a conflict over mate choice. Finally, we will briefly go into conflicts over mate choice that individuals may have with family members other than their parents.

Evolutionary Conflict Between Parents and Their Offspring

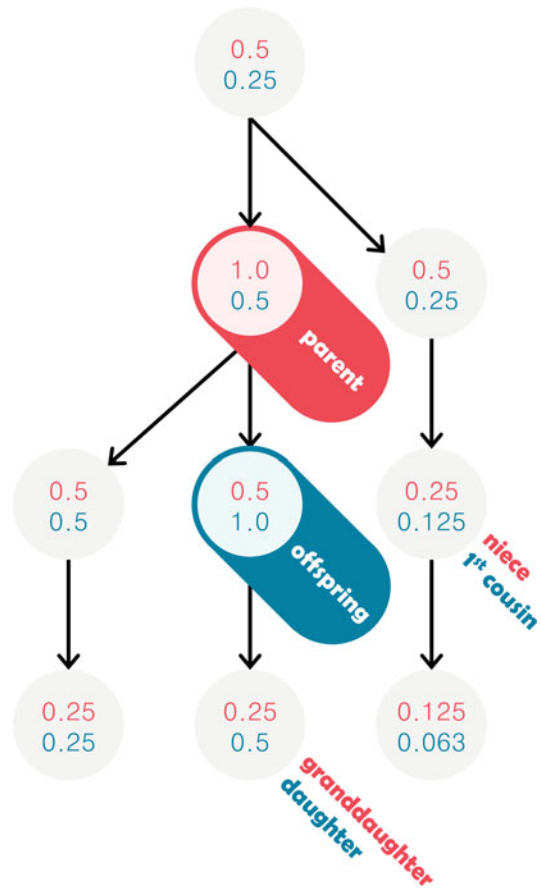
Why would parents and offspring disagree about anything? After all, parents and their offspring share many of the same genes, and both have an evolutionary interest in spreading those genes into future generations. However, even though parents and their offspring have overlapping evolutionary interests, these interests are not completely aligned (Trivers 1974). Parents are equally related to each of their children. This means that their evolutionary interests are served equally regardless of which of their offspring spread their genes. It is in their evolutionary interest that the *total* fitness of all their offspring is as high as possible.

Hence, parents are selected to allocate their parental resources according to that objective. This does not necessarily mean that they should allocate their investment exactly equally among all offspring. Under some circumstances, parents maximize the total fitness of their offspring by preferentially investing in young that are in relatively poor condition, whereas in other circumstances, the reverse is true (Davis et al. 1999; Caro et al. 2016). However, all else being equal, parents have no *a priori* reason to give any of their offspring priority when allocating parental resources. From the point of view of the offspring, matters look quite different. Each offspring has a stronger evolutionary interest in their own reproduction than in the reproduction of their siblings (with whom they do share some of their genes, but not all). Therefore, each offspring prefers a skewed distribution of parental resources, favoring investment into themselves over investment into their siblings.

There are many examples that show the consequences of this evolutionary conflict of interests between parents and their offspring. For instance, in families of Galápagos fur seals and sea lions, older offspring often attack their younger siblings, sometimes leading to the younger sibling's death (Trillmich and Wolf 2008). By doing this, the older sibling secures more parental resources for itself, at the cost of parental investment in its sibling. The mother, however, is often seen protecting the younger offspring from the attacks of the older offspring. This is in line with the theory of evolutionary parent-offspring conflict: the mother should place relatively more value on the survival and the potential future reproduction of the younger sibling than the older sibling does. In this example, evolutionary parent-offspring conflict of interests manifests as an actual conflictual interaction between a mother and her offspring. However, there are plenty of other manifestations of parent-offspring conflict that occur without overt antagonistic interactions, from the exaggerated begging for food of young birds in a nest (Caro et al. 2016) to genomic imprinting, where the expression of genes depends on which parent transmitted them (Kilner and Hinde 2012; Roulin and Dreiss 2012).

Although conflict over the distribution of resources among offspring is one of the best-studied manifestations of an evolutionary conflict between parents and offspring, it is by no means the only matter on which their evolutionary interests diverge. In fact, parents and offspring will in principle disagree about the evolutionary importance of any individuals that they are not equally related to. As a result, there will be some degree of conflict between them about how resources that enhance evolutionary fitness (i.e., survival or reproductive success) should be distributed. To account for the evolutionary importance of relatives, biologists use the concept of *inclusive fitness* (Hamilton 1964). The core idea of inclusive fitness theory is that genes indirectly affect copies of themselves if they cause their bearers to affect the fitness of related individuals (e.g., through the allocation of resources to family members). Hence, the inclusive fitness associated with a trait is not only determined by the effect that it has on the individual that carries it; we also have to add the fitness effects of the trait on other individuals, each multiplied by the *genetic relatedness* (r ; see Fig. 1) of the affected individual to the individual that carries the trait of interest.

As an illustration, consider an individual (“parent” in Fig. 1) that has to decide how to distribute an amount of resources between her granddaughter and her niece (her sister’s daughter). Her coefficient of relatedness to both these individuals is the same ($r = 0.25$; red numbers in Fig. 1), so she will place equal value on the fitness of both these individuals. Hence, she will prefer to distribute her resources such that the summed fitness of both individuals is as high as possible. For her daughter (“offspring” in Fig. 1), the calculation is quite different. From her perspective, the two individuals in question are her own daughter ($r = 0.5$) and her first cousin (the daughter of her aunt; $r = 0.125$). She places a much higher value on the fitness of her daughter than on her cousin’s fitness and does therefore not agree with her mother about how the resources should be divided between them. It is this kind of differential interest in the fitness of family members that lies at the heart of evolutionary conflict between parents and their offspring.



Kin Interest in Mating Relationships, Fig. 1 Family tree depicting a parent-offspring pair and some of their other family members. Numbers in each circle indicate the genetic relatedness (r) of the individual to the parent (top numbers, in red) and to the offspring (bottom numbers, in blue). For illustration purposes (and in line with the example in the main text), the relationship of two family members to the parent and the offspring is explicitly indicated. For example, the circle to the right of the offspring denotes an individual that is a niece/nephew from the point of view from the parent and a first cousin from the point of view of the offspring. All siblings in the diagram are full siblings; half-siblings are not included

To be clear, genetic relatedness is not the only factor that determines how individuals should allocate resources. For example, even though individuals are equally related to their parents, siblings, and offspring ($r = 0.5$ in all cases), they should not be expected to care about the survival and reproduction of those individuals equally. In their resource allocation decisions,

they should also take into account to what extent potential beneficiaries are still expected to contribute genes to future generations (this is expressed by the concept of *reproductive value*; Fisher 1930; Taylor 1990; Taylor and Frank 1996). However, since reproductive value is a property that does not change depending on the point of view of different family members, we should not expect it to affect parent-offspring conflict qualitatively.

Evolutionary Parent-Offspring Conflict over Mate Choice

Based on the previous, we should expect a conflict over mate choice to arise if different potential mates affect the fitness of relatives in different ways. Generally speaking, individuals will be more interested than their parents to attract a mate that confers fitness benefits to themselves or to their offspring. For example, we should expect them to place relatively strong emphasis on traits like parenting ability, which directly increase the fitness of their offspring. Similarly, we should expect individuals to have a stronger preference than their parents for mates that are of high genetic quality; such mates will enhance the fitness of their offspring by conferring genetic benefits (i.e., the offspring will inherit their “good genes”). Parents, in contrast, will place more value on potential mates that confer fitness benefits to other members of the family (the parents themselves and their brothers, sisters, nieces, and nephews; see Fig. 1). For example, we should expect parents to place more importance on whether a son- or daughter-in-law comes from a wealthy or powerful family; an alliance with such a family may benefit extended members through forms of nepotism and reputation. Similarly, parents may be more averse to characteristics that are considered to bring shame on the entire family (e.g., coming from a different religion or ethnic background). We should expect this to be the case if such characteristics reduce the chances of family members to obtain advantageous marriage opportunities or prestigious positions in society, thereby negatively affecting their fitness. Broadly

speaking, these predictions are in agreement with the typical observations about parent-offspring conflict over mate choice in humans, which show that parents care more about traits like family background, whereas offspring care more about traits that might indicate heritable fitness (e.g., Buunk et al. 2008; Apostolou 2010).

It is worth noting that we should not expect conflict between parents and their offspring in all cases where there is a choice between a mate conferring genetic benefits and a mate conferring nongenetic benefits. It has been argued that individuals should be more interested in genetic quality than their parents, because they have a higher genetic relatedness to their offspring ($r = 0.5$) than their parents do to their grandoffspring ($r = 0.25$; e.g., Apostolou 2007b; Buunk et al. 2008). However, as explained above, evolutionary conflict between parents and offspring is about which family members are of more evolutionary importance (and, hence, who should receive fitness benefits) – not about what kind of fitness benefits are to be allocated (genetic vs. nongenetic). When the choice is between a potential mate of good genetic quality and a mate of good parenting ability (i.e., a mate that confers nongenetic benefits to his own offspring only), there is no a priori reason to expect the parents and the offspring to disagree; both potential mates benefit the same individuals. Having said this, in cases where a “good genes” mate is compared to a mate providing benefits to other family members also, we should expect individuals to value genetic quality more than their parents do. This is consistent with empirical observations; parents value traits that might benefit extended family members more than their offspring do (e.g., family background and religious beliefs), but this is not true for traits indicating parental investment (whether a potential mate likes children; Buunk et al. 2008).

Indirect Conflict Over Mate Choice

As discussed above, parent-offspring conflict may arise because mate choice can have direct implications for the fitness of various family members.

Beside this, there are also more indirect ways in which parent-offspring conflict over mate choice can arise. How this may occur is illustrated by an evolutionary simulation model in which females and their parents (either mothers or fathers) both have an equal say in mate choice (Van den Berg et al. 2013). In this model, males vary in their “parenting quality,” a heritable characteristic that determines how much parental investment they provide to their offspring. In addition to parental investment by the males, there is also grandparental investment by the females’ parents. If parents have more than one daughter, they have to distribute their grandparental investment over the children of all their daughters. How they allocate these resources is under the control of a separate heritable locus, which allows for equal allocation (invest equally much in the children of each daughter), compensatory allocation (invest more in the grandchildren that have fathers of low parenting quality), or augmenting allocation (invest more in the grandchildren that have fathers of high parenting quality). The outcome of the model was that parents are selected to use a compensatory resource allocation strategy. In other words, it is in the parents’ best interest to compensate their daughters if they end up with a mate with poor parenting ability. As a consequence, females with a weaker preference for parenting ability in males than their sisters may end up with a relatively poor father as a mate, but do manage to attract an unequal share of resources from their parents. This way, they avoid the costs associated with being choosy, without facing any negative consequences of having a poor father as a mate. This leads to the evolution of ever weaker female preferences for mates with good parenting skills. In turn, this is balanced by a continual strengthening of parental preferences for sons-in-law with good parenting qualities. Hence, the model shows the evolution of disagreement about mate choice that increases in intensity over evolutionary time.

It is worth noting that the results of this model contrast with the general prediction that individuals should place more emphasis on mates that enhance the fitness of their offspring than their parents should. This result emerges because of the specific assumptions that are made in the model

(in this case, that parents are able to compensate daughters for choosing a bad father as a mate). This illustrates the importance of clearly delineating arguments about topics as intricate as the evolution of human mate choice. Constructing a model is valuable in this respect: it requires an explicit consideration of all assumptions, allowing for a precise examination of a line of argumentation. Using verbal reasoning alone, mistakes can easily be made, and implicit assumptions are often overlooked.

The model discussed above shows one way in which the relatively complex dynamics of sexual selection with parental involvement can indirectly result in the evolution of a conflict over mate choice. However, many other ways in which such a conflict can emerge may be conceivable. To discriminate between competing hypotheses, it is important to derive predictions that can be tested empirically. For instance, the model described above predicts a stronger conflict over mate choice between daughters and fathers than between daughters and mothers (Van den Berg et al. 2013). Empirical studies can be designed to test this prediction and can thereby either falsify or provide support for the model.

Interest of Other Kin in Mate Choice

So far, we have only discussed evolutionary conflict over mate choice that individuals may have with their parents. However, although parental interference in mate choice is perhaps the most common and best documented, parents are not the only family members that have an evolutionary stake in mate choice. Siblings, aunts, uncles, cousins, grandparents, and other extended family members also share some (but not all) genes with the individual in question, leaving plenty of scope for evolutionary conflict. However, at first sight, it seems unlikely that individuals will find allies among these other family members in the conflict with their parents. Particularly where the conflict is over fitness benefits for an individual’s own offspring (i.e., choosing a male of good parenting skills or high genetic quality) versus fitness benefits for other family members (i.e., choosing a

male with a good family background), we should expect the other family members to side with the parents, due to their differential relatedness to the parties that stand to benefit. Having said that, these other family members will not fully agree with the parents about the allocation of fitness effects either; they all have their own distinct evolutionary interests.

Conclusion

In this entry, we have seen why evolution may lead to the emergence of a conflict over mate choice between parents and their offspring. Parents and their offspring are not equally related to various family members, causing them to place different value on the survival and reproduction of these individuals. These divergent evolutionary interests can cause a conflict over mate choice, if different potential mates differently affect the fitness of family members. Mates can affect the fitness of family members in various ways, some of which are more direct (e.g., by investing resources in their offspring) and some are more indirect (e.g., by affecting the investment decisions of their parents-in-law). All else being equal, we should expect individuals to place relatively more value on mate characteristics that only improve their own fitness or the fitness of their children, whereas their parents should be expected to care more about traits that (also) benefit other members of the family. However, the complex evolutionary dynamics of parental investment and mate choice can lead to patterns that seem at odds with these predictions at first sight. For instance, in the model discussed above (Van den Berg et al. 2013), it is the parents rather than the offspring who evolve to put more emphasis on parenting qualities in a son-in-law. This example illustrates that it is important to be cautious with verbal argumentation about a topic that is as complex as sexual selection – especially in humans, where parents are also involved.

This entry has focused on examining the evolutionary causes for disagreement between family members over mate choice. However, there are many other important aspects of kin interest in

mating relationships that have not been discussed. For example, we have not considered whether we should expect conflict over mate choice to be different between individuals of different sexes. Sexual selection is rarely a symmetrical affair: in many species, there is more competition of males over females than vice versa, causing the females to be the more choosy sex. In human societies, parents exercise more control over the mating decisions of their female offspring and desire different qualities in a son-in-law than in a daughter-in-law (Apostolou 2010). Another topic we have not considered is how conflict over mate choice may affect the outcome of sexual selection. Parental influence on mate choice constitutes a sexual selection pressure; we should expect it to shape characteristics (since parents especially affect the mate choice of their daughters, we should expect this pressure to be strongest on males). In line with this, we might expect that the degree of kin influence on mate choice (which is culturally variable) affects the evolution of desired characteristics. Modeling approaches can be used to formulate predictions on the outcomes we should expect from the coevolution of mate preferences, parental preferences, and desired characteristics, depending on the degree of kin influence on mating relationships.

Cross-References

- ▶ [Arranged Marriages](#)
- ▶ [Competition for Parental Investment](#)
- ▶ [Conflict Between Parents and Offspring](#)
- ▶ [Female Mate Choice](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Grandparental Investment](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Helping and Inclusive Fitness Benefits to Helper](#)
- ▶ [Helping and Reproductive Value of the Recipient](#)
- ▶ [Human Sexuality](#)
- ▶ [Kin Selection Hypothesis](#)
- ▶ [Mate Choice Effects](#)
- ▶ [Mate Preferences](#)

- Parental Investment
- Parental Investment and Parenting
- Parental Investment and Sexual Selection (Trivers Foundational Theory)
- Parent-Offspring Conflict (Trivers)
- R = Coefficient of Relatedness
- Reproduction
- Sexual Selection in Evolutionary Psychology
- Vigilance Over Kin's Romantic Relationships

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Kin Recognition

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Synonyms

Altruistic behavior; Genetic relatedness; Incest
avoidance; Kin detection

Definition

Kin recognition refers to individuals' ability to distinguish kin from nonkin. Kin recognition helps to avoid harmful consequences of incestuous relationships and is a precondition for nepotistic altruism.

Introduction

There are two major selection pressures for distinguishing relatives from nonrelatives. The first selection pressure is related to inbreeding avoidance. Inbreeding depression – that is, the decreased survival and fertility rates of the offspring of individuals who are genetically related to each other – is well documented among humans and nonhuman species (Charlesworth and Willis 2009). Because inbreeding has extremely harmful consequences in the case of the two most important fitness indicators, survival and fertility, natural selection should have produced strategies for helping individuals to avoid mating with close relatives.

A second evolutionary selection pressure is related to consequences on inclusive fitness (Hamilton 1964). In terms of one's fitness, it is beneficial to help close relatives, even if the costs

are high, because relatedness is also high, whereas helping nonrelatives at high cost is less beneficial in terms of inclusive fitness. By helping genetically related kin, especially when said kin are descendants, it is possible to increase the probability that one's own genes will spread to future generations. An increasing number of empirical studies of humans and nonhuman animals have provided support for this prediction, showing that individuals invest more material and non-material support toward one another according to their degree of relatedness (see Salmon and Shackelford 2011; Tanskanen and Danielsbacka 2019 for reviews).

Direct and Indirect Kin Recognition Cues

To regulate social behavior according to degree of genetic relatedness, individuals need ways to recognize to whom they are related. With the exception of mothers' relatedness to their children, all other kin relationships are more or less uncertain and need to be inferred. Because genes do not directly recognize other genes, individuals have to use cues, which help to determine whether another individual is related to her or him. These kin recognition cues can be either direct or indirect. Direct cues can be either physical or psychological, and they may include, for instance, facial and odor resemblance or personality similarity (Krupp et al. 2011). However, for the most part, humans have to use indirect environmental kin-detection cues, such as residential proximity and familial living arrangements.

Lieberman and colleagues (2007) have argued that the most important indirect kin recognition cues are duration of childhood coresidence and maternal perinatal association (i.e., an individual seeing her or his mother nurse a newborn baby) (Lieberman et al. 2007). Although the childhood coresidence cue would encompass all coresiding relatives, studies have considered kin recognition as it particularly applies to siblings. Several such studies have tested Westermarck's (1921) hypothesis, which states that coresidence during early childhood is the proximate mechanism activating inbreeding aversion among siblings, because

living very close to a person from early childhood provides a valid social cue of actual genetic relatedness. Perhaps the most prominent evidence for the Westermarck hypothesis comes from anthropological investigations that have found that childhood proximity is associated with sexual avoidance among genetically unrelated individuals who been raised in sibling-like conditions (Talmon 1964; Wolf 1995). In addition to inbreeding aversion, childhood proximity tends to be a driver of sibling-directed altruism (Lieberman et al. 2007; Sznycer et al. 2016). Finally, studies have shown support for the argument that maternal perinatal association is an important kin-detection cue among siblings; as a matter of fact, it could be even more important cue than duration of childhood coresidence (Lieberman 2009; Lieberman et al. 2007; Sznycer et al. 2016).

Although sibling recognition has received reasonably good attention among evolutionary scientists, studies detecting how children recognize their parents have been scarce (but see DeBruine 2005; Marcinkowska and Rantala 2012). In particular, there has been lack of studies considering father recognition, although most likely children recognize their fathers as the adult males living with their mothers during childhood (Haig 2011).

Conclusion

This entry has reviewed studies considering how individuals can detect their relatives. To detect kin, individuals can sometime use direct cues, such as facial or odor resemblance. However, most of the time, individuals have to use indirect environmental kin-recognition cues, such as childhood coresidence and maternal perinatal association, which have tended to be correlated with degree of relatedness in the ancestral surroundings (Lieberman et al. 2007). To conclude, empirical investigations have shown that the presence of kin-recognition cues tends to regulate human social behavior in present-day societies.

Cross-References

- ▶ [Adaptive Problem of Detecting Kinship](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Co-residence and Early Maternal Perinatal Association](#)
- ▶ [Early Association Cue to Kinship in Primates](#)
- ▶ [Kin Detection by Odor](#)
- ▶ [Kin Recognition and Classification in Humans](#)
- ▶ [Phenotypic Resemblance and Kinship Detection](#)
- ▶ [Promoting Paternity \(You Look Like Your Father Phenomenon\)](#)

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Kin Recognition and Classification in Humans

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Synonyms

Childhood co-residence duration; Contextual cues; Direct familiarization; Heuristic process; Kin recognition; Kin-directed behavior; Kinship estimator; Kinship index; Maternal perinatal association; Phenotypic cues; Phenotypic matching

Definition

Kin recognition is broadly defined as the ability to identify or distinguish kin from non-kin using genetic similarity or any cues correlated with kinship. However, recognition does not necessarily lead to differential responses toward kin, “just as recognizing a fruit as an orange does not necessarily lead us to eating it” (Barnard 1991). Accordingly, in this chapter, the term *kin discrimination* is used to designate the differential treatment of kin and non-kin, thanks to the ability to distinguish between them. This research shows that the perception of kinship cues may trigger a heuristic process of kin recognition. Here, the

term “heuristic” could be defined as a strategy that ignores part of the information, with the goal of making decisions more quickly, frugally, and/or accurately than more complex methods.

Introduction

Kinship is special. We interact with kin differently than we do with non-kin, behaving more altruistically toward the former and more selfishly toward the latter. And the closer the kin, the bigger the investment. We also avoid sexual relations with close relatives. Because humans have lived among genetic relatives throughout their entire evolutionary history, the study of kinship in human society is a vast interdisciplinary field at the heart of social anthropology and behavioral ecology (but also, to a lesser extent, of sociology, social psychology, and family economy). The family is the primary core of social organization, and, until recently, people were only able to migrate and move to new locations very slowly. It follows that in countless social groups, kinship is inextricable from economic, political, and religious affairs. At the individual level, kinship relations are primarily social relations that influence our pro-social as well as sexual behavior. Thus, we act differently with our relatives than with individuals whom we may or may not know (friends, colleagues, neighbors, etc.).

Why Do We Feel and Behave This Way Toward Related Individuals?

Biologists have observed that kinship is involved in numerous behaviors across thousands of species, be they animal, plant, or bacterial. Kinship does play a crucial role in at least two distinct behaviors: avoiding inbreeding and altruism. Ancestrally (and even today), there was intense selection in humans to avoid mating with close relatives. Genetic endogamy has a tendency to increase the homozygosity of deleterious recessive alleles; inbred descendants are less likely to survive (primarily in utero), and when they do, they show a range of (congenital) physical (e.g., frequent immunosuppression, various

malformations) and psychological afflictions (e.g., lower intelligence levels). Given the enormous costs of consanguinity, behaviors (or motivational processes) that help prevent sexual relations among related individuals can be considered adaptive. The second behavior, altruism, is costly and generally appears ill adapted from an evolutionary point of view. Thus, altruistic acts can evolve if they bring advantages that are greater than their costs. In our human societies, there exist numerous, distinct ways in which this condition can be met, and each of its associated mechanisms is at the foundation of altruistic behavior theory. One of the most relevant mechanisms is kin selection: it postulates that we are more likely to help our close relatives (individuals from the nuclear family) more than distant relations (e.g., cousins) and non-kin, toward whom we act more selfishly. Now, notice that these are two very distinct adaptive problems: avoiding sex with our kin members and helping kin. But one common element of a solution to both is that we need to know who our kin are. Solving both of these distinct evolutionary problems requires some kind of human kin detection system, that is to say a kin recognition mechanism. But recognizing relatives is not an easy task; no method yet exists allowing humans to directly “see” another individual’s DNA and compare it with their own in order to determine their kinship relation.

This chapter argues that to gain general insight into human kinship recognition, it is necessary to take an interest in both the proximate and ultimate aspects of the different components of recognition systems. This research provides a review of the expression component, the sender mechanisms that produce kinship cues, particularly contextual and phenotypic cues, and it will also show how the receiver may interpret these kinship cues. This paper then provides a sketch of the decision-making rules/heuristic process of kin recognition, the mechanisms that enable the receiver to evaluate their likely relatedness to the sender, in order to produce appropriate behavioral outputs. The conclusions of this chapter will be that there is still room for considerable improvement in the human kin detection system.

How Do Individuals Recognize Their Kin?

How do we recognize kin? What are the psychological processes that allow us to overcome the difficulties involved in kin recognition? At first glance, these questions can appear trivial, and their answers are obvious: “We know who our relatives are because we are told [as much], because we give them names, because we have formal marriages, and because we have written records [birth registries, family records, parish records, etc.] and good memories” (Dawkins 1989). In addition, we live by relationship rules that allow us to easily identify new individuals according to different kinship types. By applying these rules, we can deduce that the son of our sister is our nephew, for example. However, verbal communication and kinship terms can also be illusory – without any real information on the links among relatives (in numerous cultures, the same word (e.g., uncle) may designate different levels of kinship or different kinship links) – but undoubtedly contribute to the systems regulating sexual preference and avoidance, along with helping behavior. Kinship terminology presents multiple traits of performative language, since the mere act of calling someone “brother” is a way to act on reality and generate a range of behaviors. Of course, the solutions (verbal communication and relationship rules) to kin recognition problems are relatively recent “contrivances” on humanity’s evolutionary timeline and are due to the evolution of language and symbolic representation ability resulting from structural neocortical development.

If linguistic and cultural information is not enough to provide a stable solution to the kin recognition problem, what then are the relevant cues?

Recognition Cues

Much of the theoretical and experimental biological research suggests that kin recognition mechanisms are also based on specific cues. Given the prevalence of these mechanisms in the plant and animal kingdoms, it is probable that they (or related processes) persist and function in humans, independently of our current additional

cognitive means of kin recognition. A reading of animal literature generally identifies two broad categories of kinship cues (Penn and Frommen 2010): the cues can result from the spatial-temporal context (that is, by contextual or indirect cues) and from phenotypic traits from the sender individual (phenotypic or direct cues).

Contextual Cues

Indirect cues are based on spatial and temporal landmarks; individuals identify as kin all those encountered in a situation or a particular place where any person is likely to be kin (e.g., individuals who are related to their mothers or who live in the same home). In humans, it has been suggested and experimentally shown that the cues reflecting spatial proximity during early childhood can be used as kinship indicators (Lieberman et al. 2007). Two contextual cues are commonly accepted as heuristic cues that signal kinship: maternal perinatal association (MPA) and co-residence duration during childhood.

Maternal perinatal association. One of the peculiarities of the human species is our long period of parental investment; the investment is mainly maternal and is essential for the survival of the child. Maternal investment starts during pregnancy and continues during breastfeeding and weaning, and the child only really becomes independent nearly a decade after birth. The close association between mother and infant (then child) provides reliable support for mutual detection between them and for each to categorize the other as a kin member. Moreover, this support can be used by other people who are present in the family environment to infer kinship. Thus, a child who has the opportunity to both observe the pregnancy of the person he/she identifies as his/her mother and to note the existence of a very close physical relationship between mother and infant can easily rely on the perinatal association cue to infer that the baby is a sibling (or to mentally tag it as such). Thus, Lieberman et al.'s study (2007) suggests that the maternal perinatal association (MPA) is a reliable cue for the recognition of siblings among themselves. The MPA is a relevant cue and a non-costly one from a cognitive point of view. Nonetheless, it is available only for people

already present in the family environment and is specific to older siblings recognizing their younger siblings as such.

Empirical support of the MPA cue comes from surveys with self-reporting responses and from physiological measurements applied to social behavior (e.g., willingness to perform altruistic behavior, real altruistic acts) and/or to the mating context (e.g., attractiveness, moral rejection, and disgust in incest scenarios). Because the MPA cue is absent for later-borns, they must employ an alternative strategy, using one or more other contextual cues to recognize "sibship" with an older brother or sister.

Co-residence duration. As the parental investment period is relatively long, the later-born is mindful that his/her parents care for and allocate their parental investment among one or more older children. Furthermore, as parental investment is costly – and therefore directed as much as possible toward kin members – the later-born may, by observing the children who receive special attention from his/her parents, reliably detect likely siblings. This spatial landmark (individuals who live together and who fully benefit from the investment of their parents) becomes even stronger when it is associated with a temporal landmark. In addition, the longer the investment, the greater the likelihood that the older child (ren) will be kin. The duration of sharing parental care, often formulated as "childhood co-residence duration," is an effective contextual cue to recognizing kinship. Initially enunciated by Westermarck in the late nineteenth century to explain what would come to be known as the Westermarck effect – children raised together during childhood tend to develop sexual aversion behavior toward one another in adulthood – this cue has been intensely studied for the past 15 years, notably with the (i) research of Debra Lieberman (see in particular Lieberman et al. (2003, 2007)) and (ii) fieldwork studies seeking to explain natural observations of inbreeding avoidance behavior in populations under specific cultural conditions.

Several studies have shown that the childhood co-residence cue (its absence vs. presence, along with its duration) is correlated with differential attitudes of participants in terms of altruistic and

sexual behaviors (disgust at the possibility of sex with a family member, choice of sexual partner) (Antfolk et al. 2012a; Lieberman et al. 2007), but also in moral opposition to third-party incest (Antfolk et al. 2012b; Fessler and Navarrete 2004; Lieberman et al. 2003) across multiple cultural groups. And the studies also revealed two more things: First, that prolonged separation between opposite-sex siblings during childhood increases their propensity for incestuous behavior. Second, that co-residence duration predicts altruistic behavior and sexual aversion even when the people involved know their siblings are distant relatives (as with half-siblings) or non-biological kin members (adopted siblings), suggesting that this cue is not affected by such knowledge (Lieberman et al. 2007). This outcome makes sense given the anthropologic observations of sexual aversion behavior in populations where young children (non-kin) grow up together (notably in the observations of kibbutz children).

Although contextual cues – perinatal maternal association and childhood co-residence duration – provide reliable information for the kinship recognition mechanism, they nevertheless have some disadvantages: (i) they are indirect cues, sensitive to the spatial-temporal environment and therefore a source of false-positive recognition errors (Park et al. 2008); and (ii) they only allow sibling members to be categorized as relatives, since the MPA cue only allows elder siblings to recognize their younger siblings, and the childhood co-residence duration cue only allows younger siblings to recognize their older siblings.

The ubiquity of kinship and its importance “are why” natural selection has selected other cues, namely, phenotypic cues, allowing us to recognize kin members in a more direct way.

Phenotypic Cues

Humans are able to use multiple sensory modalities to perceive phenotypic kinship cues in order to discriminate among familiar kin members and to recognize and discriminate among relatives in a group of unknown people. The phenotypic cues (i) must be stable through the generations, which is to say that these are partially inheritable traits but with high variability among family members

and among families themselves; (ii) the cues should be easily detectable from a cognitive point of view, by the receiver; and (iii) the cues may be more or less discreet (namely, the information may be public or private).

The workings of the phenotypic cues are fairly simple: the similarity of phenotypic traits between two people operates as a genetic similarity index. Thus, the greater the similarity of phenotypic traits, the higher the genetic similarity index, and, therefore, the higher the degree of kinship.

Although it is estimated that 40 % of sensory information comes from vision, “public” visual phenotypic cues seem quite rare, except for those shown by the face. Studies on phenotypic similarities have overwhelmingly focused on facial cues. Unlike nonhuman primates, for whom olfaction is a very powerful sensory modality, this system seems less developed in humans. However, given the prevalence, in nonhuman primates, of using olfactory clues in recognizing kinship, a few studies have shown that human body odor also works for kin discrimination. Because kinship cues are relevant when they are hereditary, phonation or acoustic similarities – copiously influenced by the environment – are rarely good candidates.

Acoustic similarity. As acoustic signals are highly dependent on the environment, their use as kinship cues may hypothetically be appropriate in two cases: (i) when the environment is uniform for all individuals (which corresponds to insular populations in a wider sense) or (ii) when the influence of the environment is still relatively weak. Although the study of the first case would require rigorous – but far from insurmountable – methodology, there appears to have been no study conducted from this angle. In the second case, several studies carried out around the perinatal period show that an individual can recognize kin by their vocalizations. Thus, mothers and fathers can reliably recognize the crying of their baby (Gustafsson et al. 2013), the limiting factor being elapsed time together. It has also been shown that fetuses may have increased heart rates when they hear the voice of their mother or father, but seem to prefer the mother’s after birth; again, the difference in exposure time to the

voices appears to be decisive. It is possible – as the first moments of any ordinary phone conversation might suggest – that in adults, the ability to recognize kinship by acoustic cues remains functional, as with other primates.

Olfactory similarity. Like the information carried on our faces, it has been shown that odors provide a variety of information on the transmitter: identity, age, sex, diet, health, but also reproductive status, etc. Furthermore, olfactory cues are excellent candidates for recognizing and finely discriminating among kin because they are known to covary with genetic kinship across a variety of taxa [Body odor is largely influenced by the major histocompatibility complex (MHC). In humans, the proteins coded by MHC genes include human leukocyte antigens (HLA) and other proteins. HLA proteins are exposed on the surface of most cells and play a substantial role in helping the immune system to discriminate between “self” and “nonself.” Greater diversity of the MHC system makes the immune system more heterogeneous and thus more adaptable in response to infection. Further, the heterogeneity of the MHC comes from the heterozygosity in our genes. Thus, two kin members, who by definition have a high proportion of identical alleles, have a highly similar MHC system.]. Thus, it has been shown that infants can discriminate among and recognize the odor of their mothers just a few hours after birth (Porter et al. 1992). Conversely, parents, aunts/uncles, and grandmothers can recognize the odor of their children, nieces/nephews, and grandchildren, respectively, suggesting an olfactory similarity among kin members across different generations and varying degrees of kinship. Siblings can recognize each other (but they do not seem to be able to recognize their half-siblings, just as parents cannot recognize their stepchildren). Studies involving the odor of identical twins even show that parents are able to discriminate between them using only this clue. Concurrently, it is important to emphasize that unknown third parties are also able to correctly match the body odor of a parent (mother and father) and their child, indicating that the detection is based on phenotypic matching. However, unknown third parties are unable to accurately

match the odor of a woman and a man living together. This latter result implies either that olfactory similarities are better reflected through genetic similarities than environmental similarities or that olfactory similarities that are environmental in origin are “masked” by the extent of gender differences. In addition, studies on identical twins where there is a genetic similarity, but also a very high environmental similarity, suggest that odors may also depend on other factors (e.g., epigenetic factors or state of stress).

It is useful to note that the olfactory similarities between two people strongly influence the expression of behavior related to kinship. The more mothers are able to recognize the odor of their infants, the more they exhibit maternal care behavior. In the same way, it has been shown that paternal investment is correlated with the olfactory similarity between fathers and their children (Alvergne et al. 2009). Other correlational studies point in the same direction: fathers feel emotionally closer to and mothers are less punitive toward their children if they recognize their body odor. The odor inhalation of same-sex individuals and those having similar HLA (which thus mimics a state in which two individuals are genetically similar) leads to different behaviors, depending on the receiver sex: it spurs women to social behaviors, particularly those tied to affinity, whereas it causes competitive behavior in men. Similar effects were also observed after the perception by participants of an oxytocin odor. Moreover, many studies have focused on the causal relations between sexual preference and olfactory similarities. For example, mutual olfactory aversion has been observed in father/daughter and brother/sister dyads at the time of menarche. A well-known study (Wedekind et al. 1995) showed that during their ovulation period, women with a natural cycle (i.e., without hormonal contraceptives) prefer the odor of men with a highly dissimilar HLA system, in order to promote HLA system heterozygosity of any offspring [although the study is mainly well known because of its result showing that sexual preferences are reversed for women taking a hormonal contraceptive (thus preferring the odor of men with similar HLA systems)].

Visual similarity. Thanks to the signals they carry, and since they are highly correlated with genotypes, faces are relevant phenotypic cues in recognizing kinship members (Kaminski et al. 2009). However, unlike studies with olfactory and auditory cues, there is little sense showing a face to a person and asking him/her if it belongs to a related or unrelated individual, with rare exceptions.

- (i) One such exception is when the spatial-temporal exposure between kinship members is short. Thus, mothers can recognize their kin among photographs of different 30-h-old infants (Porter et al. 1984). Similarly, unfamiliar and unrelated people are able to correctly match, based on facial cue similarities, a newborn with his/her parents (Kaminski et al. 2010a). Conversely, 4-day-old infants are able to visually recognize their mother, but only in cases when they experience early multisensory exposure to their mother's face and voice; facial exposure is not enough.
- (ii) A second exception is in cases when the main thrust of research is targeted at better understanding the cognitive and neurophysiological processes that are entangled in kin recognition. Thus, faces are often used to test the kin recognition mechanisms and the influence of kinship on our behavior (mating, pro-social, moral appraisal, and decision-making), but instead of directly showing the well-known faces of related members, researchers use composite faces. These composite faces enable them to experimentally modify facial cues in a very subtle manner. By altering individual facial photographs through this morphing technique, it is possible to produce an implicit yet genuine facial resemblance. To create them, the shape of a face (assume it is individual A) is delineated using a large number of facial landmarks (over a hundred). In addition, an average composite face is generated by averaging the shape and color of many same-sex images (usually around 20 faces). Then, about 50 % of the difference in shape between the face of individual A and the same-sex average

composite face is added from the same-sex composite to create a self-resembling same-sex stimuli. This relatively simple technique has been used for 15 years and has progressed along with graphics methods (see DeBruine et al. (2007) for a detailed explanation of the technique); it can be carried out using Psychomorph desktop software or Webmorph apps.

Traditionally, the method is used to test the decision-making of the participant using their own composite face (i.e., the participant and individual A are one and the same); the experimental *self-resemblance* composite face is then considered to be related, with a kinship degree close to 0.5 [*Our own face is related to (i) itself by a kinship degree of 1 and to (ii) a stranger's face by a degree of 0. The morphing of the two faces produces an experimentally altered face that is related to ours by a kinship degree of 0.5 ($r = (1 + 0)/2$)*]. More recently, several studies have dissociated the participant and the face of individual A (individual A is then the twin of the participant, or a sibling or spouse). These facial experiments reveal a modification of our behavior (especially mating and pro-social behaviors) in the presence of a "self-resemblance" composite face, but the change is condition dependent. Consequently, four major conclusions can be reached:

- (i) Be they of the same or opposite sex to the participant, the "self-resemblance" faces bring a greater trust that the composite faces are actually "other morph" and also promote cooperation strategy in economic games (especially in the public good game) (DeBruine 2005; DeBruine et al. 2011; Krupp et al. 2008). These results are consistent with predictions made by kin selection theory.
- (ii) The same-sex composite faces are deemed more attractive in the case of "self-resemblance" face than with the "other-morph" faces. However, in the opposite-sex composite face, no differences have been observed between the attractiveness of the "self-resemblance" face and the "other-

- morph” faces (DeBruine 2004; DeBruine et al. 2011). These results are also consistent with the assumption of an absence of sexual attraction or even of a sexual aversion with kin members of the opposite sex.
- (iii) Our decision-making with the “self-resemblance” composite face can be influenced by several moderators: for female participants, (a) by menstrual cycle, (b) by the emotional ties they have with their parents (primarily their father), and (c) by contextual cues, in particular the sex of their siblings and for male participants, (d) by their stress level.
 - (iv) Following studies that showed that paternal investment was positively related to both facial and odor similarities between fathers and children (e.g., Alvergne et al. 2009), several studies have used composites of an average face that looks like a child’s, in order to explore a possible effect of the sex of participant on decision-making. Results have been mixed; some studies show a detection bias by fathers, others by mothers, and several more found no detection bias.

The Heuristic Process of Kin Recognition

When we encounter a person, perception of contextual cues and/or phenotype cues (e.g., smell, voice, face, or body) induces us to process the information for kin discrimination, and possibly recognition, of the person. Cognitive processing helps to determine a kinship index, which is an estimate or a given probability that the person is kin, or not. To determine the kinship index, it is assumed that the processing is index dependent and operates from one or more implicit mechanisms, called “kinship estimators.” However, the theoretical and experimental research on these kinship estimators is scarce.

Recognition of Individuals from Contextual Cues

Contextual cues only allow siblings to be categorized as relatives. The MPA cue allows younger siblings to be recognized by their elders, while the childhood co-residence duration cue allows older siblings to be recognized by younger ones. Lieberman and coll.’s studies show that there is a

hierarchy in these two cues. Thus, maternal perinatal association overrides co-residence cues, and therefore co-residence duration does not predict aversion or altruism when the MPA cue is present. Rather, the presence of the cue is associated with elevated levels of both types of kin-directed behavior.

Because the MPA is a binary cue (presence or absence), the kinship estimator probably operates with a logical implication rule: “If I observe a strong bond between my mother and a young child (in addition to have seeing the pregnancy of my mother), I will be dealing with this child as a sibling” [Heuristic 1].

The childhood cohabitation cue includes first and foremost a quantitative parameter which reflects cohabitation duration. Studies (primarily those of Lieberman’s team) show that the greater the co-residence duration, the stronger the sexual aversion toward the individual’s elders, and the more significant the pro-social behavior toward them. These results lead to the (implicit) inference that the kinship estimator assigns a kinship index, which increases with the duration of cohabitation. In this case as well, the kinship estimator likely operates with a logical implication rule, such as “If I grew up with a child during x years, then I will treat him/her as kin, but my behavior toward him/her is weighted by the duration (x) of childhood co-residence” [Heuristic 2].

Whichever contextual cue is involved, the kinship estimator applies a simple rule to calculating the kinship index, which in both cases categorizes the person as a sibling or not, although in reality it can be a half-sibling or unrelated child, as in the co-reared peers of kibbutzim or in minor marriages in Taiwan. Such a cognitive mechanism (used to operate Heuristics 1 and 2) can then bring the individual to regulate sexual aversion toward that person and adopt pro-social behavior in competitive situations.

Recognition of Individuals from Phenotypic Cues

When the indices are direct (i.e., phenotypic cues), the appraisal of the kinship index is based on a comparison mechanism or on phenotypic matching. Two cases can result, depending on whether or not the phenotypic cues carried by

the person with whom we interact are familiar to us.

“I have already met this person!” Recognition by direct familiarization is based on learning and memorizing individual characteristics of the people we have already met. Individuals who are regularly present in our environment are categorized as familiar, and we (unconsciously) learn their phenotypic cues, a cognitive process that can then guide our behavior. For this to happen when we encounter someone, we can assume that their phenotypic cues are represented (or coded) as points in an n -dimensional space, wherein each dimension represents some physiognomic aspect (in a larger sense) of the individual’s phenotype, useful for discrimination. Each phenotype (and thus each individual) is represented by a location in space. The distance between two phenotypes represents the perceived similarity of those phenotypes (the smaller the distance, the more similar the phenotypes). Now if we meet the person again, we will compare these phenotypic cues with the known cues stored in our memory. If there is a match among cues, the individual is identified and recognized as a known and familiar person. In this case, the kinship estimator likely operates with a heuristic, such as this one “If I meet a kin member at time t and if I recognize him/her at time $t + 1$, $t + 2$. . . then I will systematically deal with this individual as kin” [Heuristic 3].

Recognition by direct familiarization is thus an individual recognition mechanism and not a mechanism unique to kin recognition (the same heuristic could apply to an enemy or selfish individual). The use of this mechanism for recognizing kin members can be seen as a by-product of a mechanism dedicated to the identification of individuals (thanks to this *bottom-up* type of cognitive processing, we can easily identify one of our former classmates, even decades after our last encounter). However, as the (familiar) environment of a young child is usually composed of kin members (parents, siblings, or in some cases grandparents), the scientific literature often classifies the direct familiarization mechanism as a kin recognition mechanism (e.g., Penn and Frommen 2010). This mechanism is highly context

dependent (mainly on population density, intensity of interactions, etc.) and represents a potential source of kinship recognition errors. Indeed, familiar individuals are not necessarily made up of kin, and unfamiliar individuals may be kin members!

“How do you recognize someone you’ve never seen?” The identification of a previously unknown person and their categorization as a kin member may occur through the use of the phenotypic matching mechanism. Let us then compare the phenotypic cues conveyed by the person to a mental image that we have built from the phenotypic cues of kin members of ours that we have previously met. Let us call this mental image Template K. The latter can be formed from two types of cues: our own phenotypic cues and those that come from our kin members.

- (a) Self-referent phenotype matching (i.e., matched with itself) is a mechanism by which an individual uses his/her own phenotype as a reference to assess relatedness with people he/she has met. The payoff of such a matching mechanism is twofold: (i) it avoids the inherent mistakes of the two other recognition systems (direct familiarization and contextual cues); and (ii) the person does not need to have previously encountered his/her kin members in order to discriminate among, recognize, and categorize all of his/her kin. This person can recognize and categorize as a kin member anyone who has a similar phenotype. However, demonstrating the workings of such a mechanism is both difficult and rare (it has been shown in certain rodents, birds, and fish), because it means that no contact with kin members can have occurred during their lifetime. In humans, it is possible, even probable, that such a mechanism exists (see Krupp et al. 2011). Conversely, visual, olfactory, and acoustic cues are suitable candidates for promoting the use of a phenotypic matching mechanism. Indeed, awareness of visual cues from our own face is quite difficult to achieve (the emergence of mirrors occurred about 8,000 years ago, and the natural reflection of our body/face in water, even when it is

still, is distorted and therefore not really relevant); so it seems unlikely that we use only these cues to build our K template.

- (b) The other-referent phenotype matching is a mechanism by which an individual uses phenotypic cues carried by various kin members (e.g., parents, siblings, grandparents, aunt/uncles) and, plausibly, by his/her own phenotypic cues. As the information revealing age and sex is typically not correlated with kinship cues, one can imagine that Template K neglects the phenotypic differences associated with this information and only keeps the relevant features from a kinship point of view. Furthermore, it is assumed that Template K can either be fixed at some point during childhood, or on the contrary, dynamic and frequently updated during life (Krupp et al. 2011). Just like with the self-referent phenotype matching mechanism, this mechanism is difficult to test experimentally.

Thus, a kin member that one has never met before can be discriminated, recognized, and categorized as such on the basis of phenotypic similarities with their previously constructed Template K (self- and/or other-referent), thanks to a process of generalization [Krupp and Taylor (2013) recently showed that for the phenotypic recognition mechanism to operate, we need additional information on the phenotypic variability of individuals in the population. Thus, this study suggests that a second template corresponding to the average phenotype of the individuals in the population (*Template A*) also be incorporated in the kin recognition mechanism. In this case then, there is twofold phenotypic matching: if the given individual is closer to *Template K* than *Template A*, he/she is thus considered kin, or non-kin in the reverse scenario, and if there is more matching between templates *K* and *A* than with the phenotype of the given individual, he/she is considered *negatively related* (see Krupp et al. (2012) for the heterogeneity of behavior with respect to these three cases: kin, non-kin, and negatively related individuals)]. The kinship estimator allowing kin recognition through phenotypic matching likely operates with two heuristics, such as “If someone

looks like a familiar kin member, I will be dealing with them as a new kin member” [Heuristic 4] and “If there is match between someone’s phenotypic cues and the K Template I built (i.e., the phenotype is a very short distance from Template K in the *n*-dimensional space), I will be dealing with that person as a relative” [Heuristic 5].

Empirical Support of Kin Recognition

As just mentioned, people can recognize kin members from five different heuristics.

Heuristics 1 and 2 apply to contextual cues and help explain our behavior toward siblings (sexual aversion and altruism behaviors). These heuristics have not been tested as such, but are used as explanatory variables (they are essentially the work of Debra Lieberman’s team) to clarify some observed behaviors, or to be used in experimental studies (e.g., surveys or physiological data studies). Although they are used specifically to recognize siblings, they also seem to influence behavior we have toward more distant kin.

Heuristic 3 is activated from phenotypic cues and is frequently highlighted in studies on individual recognition. It is a relatively simple recognition mechanism, but is not exclusive to kinship.

Heuristic 4 is a variant of Heuristic 3. Applied to kinship, it is probably very common in everyday life, but appears more difficult to prove than, and differentiate from, Heuristic 5. The Oates & Wilson study (2002), though it manipulates context cues (family names), seems to confirm the existence of Heuristic 4, showing that we behave differently toward unknown individuals who have the same family name as ours (as opposed to those with another name), behaving more altruistically toward them!

Heuristic 5 was never directly shown in the kinship context, but two lines of research suggest that it does indeed exist:

The first comes from studies involving the “self-resemblance” composite faces. As the composite faces are unknown to us, it is postulated that during interactions with “self-resemblance” faces, we will implicitly treat those faces (through the phenotypic matching mechanism) as those of unknown kin members. The

research (mainly that of Lisa DeBruine's team) has found a fluctuation in our pro-social and sexual behaviors in the presence of the "self-resemblance" composite face versus the "other-morph" composite face, confirming the hypothesis. Some studies also posit that the other-referent phenotype matching mechanism works too. However, a series of recent studies suggests an alternative interpretation of these results, different from the hypothesis above. This interpretation presumes that, in everyday life, we constantly learn the faces of people from our inner circles, be they kin or not (e.g., spouses, friends) – what we categorize as personally familiar faces. When we meet individuals who have an appearance similar to one of the personally familiar faces (like in studies with "self-resemblance" composite faces), the emotional reaction we have when we see them can influence the emotional evaluation of the face we're looking at (the "self-resemblance" composite face), through a simple transfer effect (e.g., Giang et al. 2012; Günaydin et al. 2012; Kraus and Chen 2010). This alternative interpretation of behaviors generated by "self-resemblance" composite faces is interesting and relevant, and further research involving composite face experimentation seems necessary in order to clarify the accuracy of both of these interpretations.

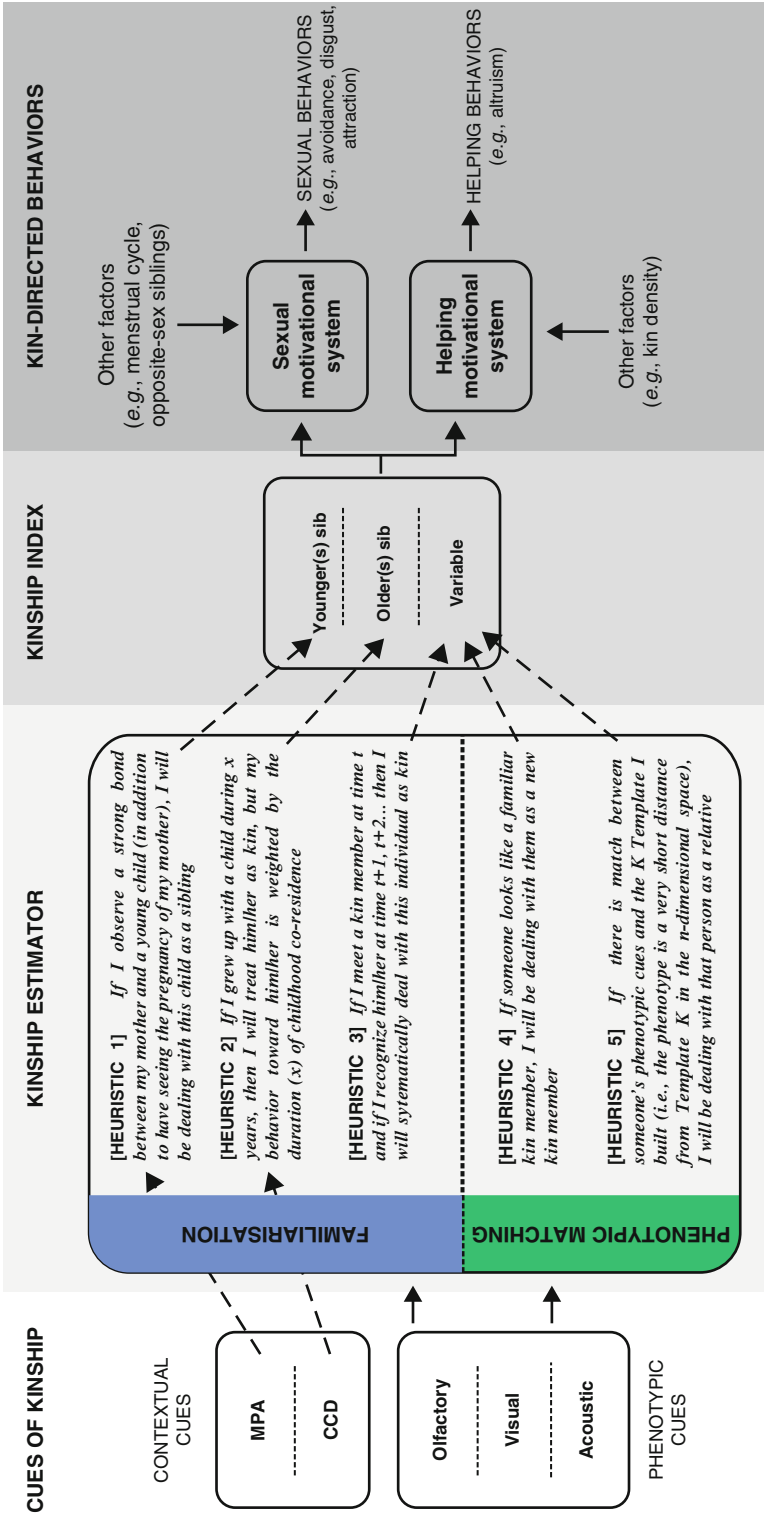
The second line of research comes from approximately 20 studies showing that we are able to, and efficient at, detect kinship among unfamiliar and unrelated individuals, through phenotypic comparison of facial cues. Our ability to recognize kin can be extended to relationships with third parties, i.e., detecting kinship in other individuals. Indeed, because we interact constantly with individuals, be they related to us or not, it is useful (and adaptive) to know who is (biologically) related to whom, in order to best adjust our behavior and ultimately enhance reproductive success (e.g., in non-human primates). Based on this postulate, various studies have highlighted our ability to detect kinship in individuals we do not know, using facial resemblance (e.g., Kaminski et al. 2010a, and one study on odor similarity,

Alvergne et al. 2009). The facial studies suggest that the aptitude is robust and is present early on in life (from the age of five under certain conditions, Kaminski et al. 2012) and that the cognitive process(es) that allow kin detection by comparing faces is not highly specialized by facial category (ethnicity, age, etc.) or kinship degree (Kaminski et al. 2009, 2010b). However, cognitive and social processes associated with this ability have received little attention up until now (see Bressan and Dal Martello 2002).

Human Kin Detection System

The heuristic process of kin recognition may be responsive to specific features in a given situation. One manner in which the situation influences the workings of the kin recognition system is by modulating the nature of the specific psychological outputs that are heightened through perception of a kinship cue. In a potential mating context, the perception of a kinship cue may trigger aversive psychological responses (e.g., disgust and reduced sexual attraction), whereas in other situations, the same kinship cue may initiate responses that should upregulate motivation to provide aid. Currently, the dominant view is that the heuristic process of kin recognition should calculate what researchers call a kinship index (Lieberman et al. 2007), an internal regulatory variable that contributes to the systems regulating sexual preference and avoidance, along with helping behavior (Fig. 1).

Indeed, as kinship cannot be directly observed, this heuristic process of kin recognition must first sort the flow of information (sensory and context dependent), but also select and save only the relevant kinship indices. Based on these cues, the heuristic process of kin recognition will produce an estimate or a given probability (the kinship index) that the other is either kin or non-kin (and if so, of what genetic distance). The thought is that the magnitude of the kinship index should reveal the degree of relatedness of other specific individuals to yourself. For example, if my kinship index for a particular person is high, as when the kinship index reveals that the female child in front of me is my sister, this index should downregulate sexual



heuristic process of kin recognition. Based on these cues, the kinship estimator will trigger one of the five heuristics and then output an estimate or given probability (the kinship index) that the other individual is either kin (and in this case, at what genetic distance) or non-kin. The kinship index will contribute to the systems regulating sexual preference and avoidance, along with helping behavior

Kin Recognition and Classification in Humans, Fig. 1 Proposed model of human kin detection system. In order to recognize individuals as kin or non-kin, people must use cues associated with kinship. These cues can result from the spatial-temporal context (contextual cues), or from phenotypic traits from the sender individual (phenotypic cues). Kinship cues will deliver their outputs to a kinship estimator, or a

attraction by activating disgust at the possibility of sex with a kin member and upregulate motivation to provide aid. The mechanism that calculates kinship indexes was named a kinship estimator (Lieberman et al. 2007). The kinship estimator, or the heuristic process of kin recognition, is likely composed of several subsystems, each dependent on one of the five heuristics of kinship and themselves dependent on the perception of the kinship cues.

Conclusion

The research reviewed in this chapter illustrates how people recognize their kin. In brief, to determine who our kin members are, we can rely on contextual cues, such as maternal perinatal association and childhood cohabitation duration, but also on more direct evidence, conveyed by phenotypes such as body odor or faces. These contextual and phenotypic cues are reliably correlated with the genetic relatedness of kin members in the ancestral environment. The kinship cues feed into a “kinship estimator” that generates a unitary “kinship index” for each individual. This kinship index then contributes, in separate systems, to regulating sexual preference and avoidance, along with social behaviors, as shown in Fig. 1. This chapter argues that the kinship estimator (or the heuristic process of kin recognition) is not a single entity, but rather consists of five distinct heuristics. Thereby, cues to kinship play a crucial role, both direct and indirect, not only in how we choose our mates but also in how egoistic, altruistic, or spiteful we are toward others.

Many questions regarding how humans recognize kin remain unanswered. The questions mainly concern the heuristic process of kin recognition and the two motivational systems that regulate kin-directed behaviors. More research (mainly in psychology) is certainly needed to clarify the nature and boundaries of the heuristic process of kin recognition. For example, to study kin-directed behavior when multiple cues of kinship are simultaneously available, or how Template K is built. Indeed, it is important to know with which people is built the template K (just

me, or my sibling, parents, and myself, or also other people present in my social environment?), (ii) when it is built, and (iii) whether Template K is static or frequently updated and so forth. But it is also necessary to delve into the neural network involved in this process (unfortunately, there are few studies available) in order to yield a complete perspective on the cognitive process. A fuller understanding of the two motivational systems, one causing sexual attraction and the other motivating help toward others, awaits additional research that better incorporates individuals’ internal state’s factors (e.g., menstrual cycle and stress level), social factors (such as emotional ties, number of opposite-sex siblings), and ecological factors (e.g., kin density in the population). Research will help us better understand the functional dissociation between these two motivational systems and how they respond to cues of kinship.

Cross-References

- [Adaptive Problem of Detecting Kinship](#)
- [Co-Residence and Early Maternal Perinatal Association](#)
- [Facial Resemblance and Kinship Detection by Strangers](#)
- [Hamilton’s Rule](#)
- [Heuristics](#)
- [Phenotypic Resemblance and Kinship Detection](#)

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Kin Recognition Mechanisms

► Kin Detection by Odor

Kin Relations

► Children and Sibs Share Same Proportion of Genes

Kin Selection

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Synonyms

Inclusive fitness theory

Inclusive fitness theory and Hamilton's rule are used sometimes as synonyms but are better seen as distinct concepts.

Definition

A foundational component of social evolution theory and a broader view of natural selection where fitness effects on genetic relatives are explicitly accounted for. Kin selection is particularly well known as an explanation for the

evolution of altruism: a trait that is costly to its bearer can spread in a population if it has beneficial effects on relatives, because relatives have a higher than average chance of carrying genes for that trait themselves.

Introduction: History and the Underlying Logic of Kin Selection

“*Nature, red in tooth and claw*” wrote Alfred Lord Tennyson in 1850, in a poem dedicated to his friend who passed away at a young age. This memorable quote later found new meaning as a phrase that evokes the competitive and merciless nature of evolution by natural selection (e.g., Dawkins 1976). Natural selection does indeed seem to be an unfeeling, cruel, and indifferent process, completely detached from any moral connotations. If natural selection is about survival of the fittest, it is difficult to see how more “humane” traits, such as altruistic ones, can arise. Selfishness, where a behavior increases an individual's fitness at the expense of others, is readily explained by natural selection, but altruism is not. Altruism, by definition, increases the fitness of its recipient but decreases the fitness of the donor. Natural selection should decrease the frequency of alleles that are associated with low fitness, so how can an allele that decreases the carrier's fitness increase in frequency or be maintained in the population? Yet altruism and cooperation are commonly encountered in nature, perhaps most strikingly in the sterile workers of eusocial insects who forego reproduction entirely to help their colony.

This problem was already noted by Darwin (1859), and partial explanations were put forward by him as well as two pioneers of the mathematical foundations of evolutionary theory, Fisher (1930) and Haldane (1955). Haldane's brief verbal account came perhaps the closest to William Hamilton's later breakthrough and is quite helpful in understanding the underlying logic of kin selection: “*Let us suppose that you carry a rare gene which affects your behavior so that you jump into a flooded river and save a child, but you have one chance in ten of being drowned, while I do not*

possess the gene, and stand on the bank and watch the child drown. If the child is your own child or your brother or sister, there is an even chance that the child will also have this gene, so five such genes will be saved in children for one lost in an adult. If you save a grandchild or nephew the advantage is only two and a half to one. If you only save a first cousin, the effect is very slight. If you try to save your first cousin once removed the population is more likely to lose this valuable gene than to gain it" (Haldane 1955, p. 44).

Kin selection is a topic with copious amounts of (sometimes complicated) theory backing it up but whose underlying logic is nevertheless simple enough to grasp with minimal mathematics. Haldane's example is a useful starting point here, but as a preliminary step, it may help to review the concept of the *green beard effect* elsewhere in this encyclopedia. Recall that in the green beard effect, a single gene or a set of multiple tightly linked genes has two phenotypic effects: a trait that allows other individuals to recognize carriers of the gene (such as growing a green beard) and a behavioral trait whereby altruistic acts are directed toward others recognized as carriers. An individual with a green beard (hence also with a genetic tendency for altruism) that helps another individual with a green beard is *guaranteed* to aid the propagation of the gene for the altruistic trait, provided that the cost to the donor is lower than the benefit to the recipient. The bearer of the green beard is with certainty a bearer of the gene for altruism because of the tight link between the two. In a green beard scenario analogous to Haldane's example, a green beard gene causes its carrier to save another individual with a green beard from drowning, taking a 10% risk of dying itself while doing so. The net effect is that one copy of the gene will survive with certainty in the individual thus saved and a second copy will survive with probability 0.9 in the altruist. In other words, the expected number of surviving copies in the two individuals is 1.9, while in the absence of the altruistic act, it would be 1 (one would drown with certainty). Hence the altruistic gene can increase in frequency in the population.

Now return to Haldane's scenario where there are no colored beards, and instead an individual carries a rare gene that causes its bearer to help a full sibling: analogous to the green beard scenario, the altruist now saves its sister or brother from drowning, while again accepting a 10% risk of death (we will assume the rescuee is a sibling of similar age so that effects of age can be ignored). The net effect in this case is that the expected number of copies of the gene for sibling altruism after the altruistic act is $1 \times 0.9 + 0.5 \times 1 = 1.4$, while the number of copies that would remain in the absence of altruism would again be 1. As in the green beard case, the altruism gene can spread in the population, although selection for it is not quite as strong. Why does it spread? Being a rare gene as specified by Haldane, the altruist must have received its copy from one of its two parents (the probability of both parents carrying the rare mutation is negligibly low). The altruist's sister would therefore have received a copy of the same mutation from that parent with 50% probability (50% because the probability of one parent carrying two copies of the rare gene is also negligibly low). Therefore, even though the altruist cannot now be *certain* that the recipient of altruism will carry a copy of the gene for altruism, a sibling (or more generally, any close relative) nevertheless has an inflated probability of carrying the same mutation compared to a random member of the population.

This scenario is a simplified one, but it is intended to drive home the central idea that by helping relatives, a carrier of a gene for altruism is likely (but not certain) to help other carriers of the same gene. Because of the uncertainty, the benefit of helping must be discounted by the probability that the recipient does indeed carry the same gene (the factor 0.5 in the calculation above).

William Hamilton and Kin Selection

Although Haldane appears to have touched upon some core ideas behind kin selection and the evolution of altruism, the above verbal explanation still applies only to a very special case, and

much was left unsolved. Haldane and other authors such as Fisher described specific examples, but no one had developed a more general theory that could account for the evolution of altruism. More generally, the time was ripe for a careful reexamination of explanations for the evolution of altruistic traits poorly justified ideas of selection for the “good of the species” or “good of the group” were common in evolutionary biology (later famously critiqued by George Williams in his 1966 book – see also the section “[Kin Selection Versus Group Selection](#)”). The challenge for generalizing the theoretical foundations of altruism was taken up in the early 1960s by a British graduate student, *William Hamilton*. Hamilton took the ideas further than previous authors had and was arguably the first to fully recognize that altruism was indeed a major problem in evolutionary biology that demanded a carefully justified solution. Hamilton made the ideas hinted at by earlier authors more general and mathematically more rigorous and he also showed that under the assumptions of his model, the central results held not only for rare genes as in Haldane’s example but for any gene frequency. This property of frequency independence is important because it implies that the same rules hold from when a rare mutation initially appears in the population, all the way until it has taken over the entire population. It is not obvious that this should be the case, and Hamilton described the result as a “*gift from god*” (Hamilton 2001, p. 543). Hamilton would write multiple papers on the evolution of altruism and social behavior over the next decade (perhaps most easily found in the first two volumes of his collected papers: Hamilton 1996, 2001), with the first of his 1964 papers (Hamilton 1964a) destined to become by far the most widely recognized one, and one of the most widely cited articles in all of evolutionary biology. Hamilton’s work on kin selection was not just an isolated theoretical development; it started an entire field of research, on which many subsequent careers have been built. The following sections review some of the central concepts that Hamilton introduced, while mostly avoiding detailed mathematical treatment.

Kin Selection, Hamilton’s Rule, and Inclusive Fitness

Kin selection, *Hamilton’s rule*, and *inclusive fitness* are three of the most widely known concepts originating from Hamilton’s work, and they are at times used with much overlap in the literature. Here a separation is maintained between these notions, each with its own meaning. Kin selection (a term that first appeared in Maynard Smith (1964) and was later adopted by Hamilton and the scientific community) is the broadest of these concepts, and as will become apparent later in the section on generality, it is in fact broader than its name might suggest because it is not restricted to interactions between genealogical kin. Kin selection can be thought of as an umbrella term that covers the processes, the philosophy, and the methodology originated in Hamilton’s early work (Hamilton 1963, 1964a, b). Hamilton’s rule and inclusive fitness in turn are narrower concepts, and both are ways of encapsulating the central insights of his research.

In mathematical form, “Hamilton’s rule” was first written down in Hamilton’s very first brief article on the topic of social evolution (Hamilton 1963), but the term was apparently coined much later by Eric Charnov (1977). Hamilton (1963) originally described the rule as a “*criterion for positive selection of the causative gene*” for altruistic behavior, and this is how it is still most commonly known. However, in a more general setting, Hamilton’s rule is a criterion for natural selection to favor an increase in *any* character, not just an altruistic one. A common way of writing Hamilton’s rule is

$$-c + bR > 0 \quad (1)$$

where the classic interpretation is that if the costs ($-c$) to the donor of the altruistic act are outweighed by the benefits to the recipient (b) multiplied by the *genetic relatedness* between donor and recipient (R), the altruistic behavior can spread in the population despite decreasing the fitness of the altruist. One of Hamilton’s fundamental insights was the generalized role of relatedness in Eq. (1). Whereas Haldane (1955)

hinted at the importance that close versus more distant relatedness has, Hamilton made the role of relatedness central, mathematical, and general (Hamilton 1963, 1964a). A common misconception is that kin selection requires recognition of kin. This is not the case, and in fact, kin selection requires no cognition at all. All that is required is that interactions are more likely between related individuals, and although this could arise via kin recognition, it can also arise via limited dispersal: if individuals do not move far from their birthplace, they are likely to interact with relatives (e.g., siblings born at the same location), and kin selection can operate in absence of any active recognition.

Ultimately, Hamilton's rule arises from considering the average fitness of all individuals carrying the gene – not just the individual bearing the cost but also those who receive the benefit, and relatedness determines how likely (relative to a random individual) the recipient is to carry a copy of the gene. The three components can take on any sign, and the same criterion is true for traits that are altruistic ($-c < 0$, $b > 0$), spiteful ($-c < 0$, $b < 0$), mutually beneficial ($-c > 0$, $b > 0$), or selfish ($-c > 0$, $b < 0$) (Gardner et al. 2011). But it is the evolution of altruistic behavior where the greatest conceptual breakthrough was focused, expanding our understanding of the evolution of social behavior. In terms of the simple example in the previous section, the cost to the altruist is -0.1 (the risk of dying) while the benefit to the recipient is $+1$ (saved from certain death), and relatedness is 0.5 (full-sib relatedness). Substituting these into Hamilton's rule obtains is $-c + bR = -0.1 + 1 \times 0.5 = 0.4 > 0$, and hence the altruistic behavior is positively selected. Furthermore, because we have $-c = -0.1 < 0$ and $b = 1 > 0$, we can confirm that the act fits the mathematical definition of altruism. We can also confirm Haldane's further analysis for more distant relatives. R equals $1/4$ for a grandchild or nephew, $1/8$ for first cousins, and $1/16$ for a first cousin once removed. Calculating the value of $-c + bR = -0.1 + 1 \times R$ for each of these relatedness values in turn, we notice that Hamilton's rule is fulfilled for grandchildren, nephews, and first cousins, but for first cousins

once removed, we have $-c + bR = -0.1 + 1 \times \frac{1}{16} \approx -0.04$, so that in Haldane's example, it would not be worth saving a first cousin once removed from drowning. Hamilton's rule therefore formalizes Haldane's example in an intuitive way, while allowing the analysis of other, potentially much more complicated scenarios in the same model framework.

Inclusive fitness is a concept closely related to Hamilton's rule and an equally central part of kin selection theory, developed by Hamilton not in the first 1963 paper but in the longer and more widely known article published the following year (Hamilton 1964a). Where Hamilton's rule is a criterion for positive selection on a trait, inclusive fitness is a quantity which, in Hamilton's words "*incorporates the maximizing property of Darwinian fitness*" so that "*species following the model should tend to evolve behavior such that each organism appears to be attempting to maximize its inclusive fitness.*" Hamilton therefore intended inclusive fitness to be a maximand which helps us understand adaptation and the appearance of design in the context of social traits. Whereas Hamilton's arguments in the short 1963 paper are *gene-centric*, inclusive fitness gives selection and adaptation an *individual-centric* objective to seemingly strive towards, and thereby helps us reason about adaptation and evolution of social traits using an analogy where individuals are akin to rational agents pursuing a goal. For example, in the example of saving a sibling from drowning discussed previously, the inclusive fitness of the altruist is

$$1 - c + bR = 1 - 0.1 + 1 \times 0.5 = 1.4 \quad (2)$$

Inclusive fitness takes the actor's perspective and examines the effects that the actor's trait has on individual fitnesses, including the effect on their own fitness ($-c$) and on that of others (b) where the latter is weighted by relatedness between actor and recipient, and these are added to the baseline fitness (here, 1). In Eq. (2), $-c + bR$, which is the same as the left-hand side of Hamilton's rule is the *inclusive fitness effect*, whereas the entire expression $1 - c + bR$ is the inclusive fitness. Hamilton's rule is fulfilled, and

the trait is positively selected when the inclusive fitness effect is positive, while the eventual outcome of selection should lead to maximization of inclusive fitness. However, this maximizing property also makes inclusive fitness more controversial than Hamilton's rule. Not all researchers agree that there is any quantity that is maximized by natural selection even in the absence of social interactions, so it is not surprising that the maximizing property of inclusive fitness is viewed critically by some. The conditions under which individuals can be thought to maximize their inclusive fitness have been the focus of much research (e.g., Lehmann and Rousset 2020), and many agree that despite some limitations, inclusive fitness is a very valuable tool for understanding adaptation and organismal design, particularly when we are interested in the long-term outcome of selection determined by subsequent small changes due to mutations of small effect. Such conditions apply when we examine the origin of adaptation and the appearance of design in nature, typically arisen over a very long time in the past (see also the section on "[Criticism of Kin Selection, and General Versus Streamlined Models](#)").

Inclusive Fitness Versus Neighbor Modulated Fitness

Inclusive fitness may be the most widely recognized conception of fitness in kin selection theory, and the one that best reflects Hamilton's central conceptual breakthrough, but it is not the only one. Neighbor modulated fitness (also known as personal fitness or direct fitness) is a less widely known but nevertheless central concept of fitness in kin selection theory. It is important for multiple reasons. Firstly, the starting point for Hamilton's (1964a, 1970) mathematical analysis of inclusive fitness is in fact neighbor modulated fitness, and it is then shown that inclusive fitness is an equivalent method of analysis (see also, e.g., Birch 2017). Second, modern theoretical approaches (Taylor and Frank 1996; Frank 1998; Gardner et al. 2011) offer powerful methods for analyzing neighbor modulated fitness models – typically more convenient than the equivalent inclusive

fitness analysis (prior to the development of these methods neighbor modulated fitness was considered by many to be the more difficult modelling approach, see, e.g., Maynard Smith (1987)). Because of these developments, many theoretical kin selection analyses now employ a neighbor modulated fitness approach, although the models can typically readily be interpreted from an inclusive fitness perspective. Third, because neighbor modulated fitness is closer to the classical concept of fitness as well as the fitness concept used in other approaches to social evolution besides kin selection (e.g., the multi-level Price equation or contextual analysis), the most straightforward way to study the commonalities and equivalences of alternative approaches is to use a neighbor modulated fitness approach (Lehtonen 2020).

So what is neighbor modulated fitness? How does it differ from inclusive fitness? And how is it linked to inclusive fitness? Technical details are beyond this entry, but intuitive ideas are not. The core idea is that inclusive fitness is an actor-centric concept, while neighbor-modulated fitness is a recipient-centric concept, but in the end both count the same thing. Recall the example of sibling altruism, where one sibling saves another from drowning. To calculate inclusive fitness, fitness effects were assigned to the actors who were causally responsible for them: the altruistic individual was assigned its own fitness ($1 - c$, as altered by the cost of the altruistic action) plus the benefit (b) to the recipients weighted by relatedness between actor and recipient. The point is that the social behavior "*evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors fitness against his own according to the coefficients of relationship appropriate to that situation*" (Hamilton 1964b). This is highly intuitive and allows us to envision the evolution of social behaviors from the perspective of the individual performing them. Inclusive fitness is a quantity that is seemingly under the control of the individual performing the altruistic action.

A neighbor modulated fitness approach would instead focus on each individual in turn, examining their total personal fitness, including all effects

of their own actions *and* the actions of other individuals they might interact with. Consider, for example, the average fitness of a potential rescuee carrying the altruistic gene, swimming with her sibling. Her fitness in the simple model is 1 if she is rescued and 0 if not. What is the probability of rescue if she is swimming with a sibling? It is the probability that the sibling also carries the gene for altruism (which will make the sibling behave altruistically toward the rescuee). And by the same arguments as in the previous section, this probability is 0.5. So the diluting factor of 0.5 appears again despite the causal perspective being essentially reversed compared to inclusive fitness. The fitness of altruists on the other hand, considering a 10% probability of drowning is 0.9. If we assume that a pair of siblings always swims together, with one of them needing rescue, then the average fitness of the altruism allele is $\frac{0.5+0.9}{2} = \frac{1.4}{2}$. The numerator is the same as the result of Eq. (2). But why the division by 2? The reason is that here we are averaging over the fitness of all carriers of the allele, while in Eq. (2), we in effect computed the inclusive fitness of the altruists only. What of the inclusive fitness of the rescuee? Recall that in computing inclusive fitness, fitness effects are assigned to the individual who is causally responsible for them. The survival benefit that rescuees receive is causally attributed to the altruistic actor, not to the rescuee. So because the rescuee would not have survived at all without the altruistic act, her inclusive fitness is in fact 0 – if the benefit was assigned to both the altruist and the recipient of altruism, we would be double-counting that component of fitness. Hence the mean inclusive fitness is $\frac{1.4+0}{2} = \frac{1.4}{2}$, equal to the mean neighbor modulated fitness computed above. And it is the mean fitness of the individuals carrying the allele that matters for evolutionary change. This is closely related to an important observation made by Grafen (1982), who pointed out that there is a simple way to measure kinship effects in a measure of reproductive success: “*simply count the number of the animal’s offspring. Such a measure inevitably predicts the course of evolution for, if animals bearing an allele have more offspring than non-bearers, then the allele will spread. It*

is perhaps not commonly appreciated that this measure also includes kinship effects.” What Grafen is describing here is effectively the connection between neighbor modulated fitness and inclusive fitness. Kin selection, Hamilton’s rule, or the two conceptions of fitness that come with it are no major alterations of natural selection, despite being major alterations of how we can envision and model it. The most successful allele is selected regardless of the presence of kin effects, while the methods of kin selection allow us to reason about the outcome of selection.

Criticism of Kin Selection, and General Versus Streamlined Models

Despite a slow start after Hamilton’s initial papers, kin selection eventually became a major research theme in biology. But at the same time, it has always been the target of criticism, with many articles pointing out scenarios where Hamilton’s rule or inclusive fitness seemingly do not work or where they have significant limitations. An early but still relevant and clear account by Richard Dawkins, partly motivated by such criticisms, addresses many common misunderstandings of kin selection (Dawkins 1979). It is also important to be aware of the structure of contemporary kin selection theory, which has developed in many ways since its inception. Kin selection theory in its modern form can be thought to be composed of a very robust and general, but somewhat abstract theoretical foundation, and a streamlined and powerful set of tools for solving actual biological problems and generating testable theoretical predictions (Gardner et al. 2011). Some critical studies do not take into account these modern developments, and many criticisms are resolved when considered from the perspective of this theory base that combines generality and practicality (Gardner et al. 2011).

The most general forms of kin selection models are based on the Price equation, a fundamental equation in evolutionary theory from which many other central results can be derived (Price 1970). Hamilton was the first to publish a Price equation-based rederivation of his work

(Hamilton 1970), but the most general derivation is attributed to Queller (1992) who derived what is now widely known as the “general” model of kin selection – general in the sense that minimal assumptions are needed in its derivation. The generality of this model arises from the way costs, benefits, and relatedness are defined as linear regression coefficients. The starting point is a multiple regression model of neighbor-modulated fitness (or direct, or personal fitness) with the genotypes of a focal individual and their neighbors (or more generally, those who influence the focal’s fitness) as the independent variables. The partial regression coefficients that arise in this model are analogous to (or generalizations of) the costs and benefits of Hamilton’s rule, and genetic relatedness similarly arises as a regression coefficient. The application of linear regression may sound like the model assumes linearity, but this is not the case. The Price equation shows us that what matters for natural selection – or what natural selection “sees” is the least squares linear regression coefficient, regardless of linearity or lack thereof in the underlying processes. Hence a model of evolutionary change based on linear regression can be exact. Effects of any nonadditivity are subsumed into the regression coefficients, and defined in this way, the model components can accommodate any nonadditivity in fitness effects, or almost any other complexity we can imagine. The fact that genetic relatedness also arises as a regression coefficient which makes no reference to genealogical or pedigree relatedness per se also indicates that what ultimately matters for kin selection is genetic similarity for any reason, not just genealogical relatedness. Genealogical relatedness is however considered to be the most important driver of kin selection, while the green beard effect is responsible for notable exceptions (Gardner et al. 2011). The flipside of the generality of these models is that they are quite abstract, and it has been claimed that such a model cannot make testable predictions (Nowak et al. 2017). The most general models are in a sense “retrospective,” in that they could in principle be applied to any relevant dataset, and model parameters can be calculated from the dataset in hindsight, making the model

true almost by definition. But prediction is not the aim of this type of model, and instead the most general, regression-based formulation forms a robust conceptual and theoretical foundation and provides an organizing framework for social evolution theory, while we typically use less general and more practical methods when solving real biological problems (Queller 1992; Gardner et al. 2011; Birch 2017; Lehtonen 2020).

On the less general but more practical side, a very powerful and popular suite of methods for analyzing kin selection models was developed by Taylor and Frank (Taylor and Frank 1996; Frank 1998). One way to view these models is that they approximate the regression coefficients of general, regression-based models (e.g., Queller 1992) with partial derivatives (Birch and Okasha 2015; Lehtonen 2020), thus making it possible to take advantage of the powerful methods of calculus in kin selection models. In terms of modelling terminology, they are weak selection models where there is very little phenotypic variation in the population at any given time, thus rendering fitness differences between individuals small despite potentially strong and nonlinear relationships between phenotype and fitness. These models provide much flexibility and make it relatively straightforward to model complications such as class-structured populations (Taylor and Frank 1996). Just like the general regression-based models mentioned above, these weak selection models are neighbor-modulated fitness models: the modeler begins with an equation for the personal fitness of a focal individual, from which the costs and benefits of Hamilton’s rule arise as partial derivatives. However, the direct fitness model thus derived can typically be reinterpreted from an inclusive fitness perspective (Taylor and Frank 1996). Where the regression models focus on maximal generality on short-term evolutionary change, the weak selection methodology is best suited for analyzing the outcome of long-term gradual evolution of a character by successive small changes (Eshel et al. 1998). Although the methodology is quite different from Hamilton’s early articles, the underlying thinking and philosophy is well in line with his views: *“Most change comes, I believe, through*

selected alleles that make small modifications to existing structure and behavior. If one could understand just this case in social situations, who cared much what might happen in the rare cases where the gene changes were great and happened not to be disastrous?” (Hamilton 1996, pp. 27–28).

Kin Selection Versus Group Selection

An article on kin selection seems incomplete without some mention of the tension between kin selection and group selection, often seen as competing alternatives in social evolution theory. Central to group selection is the idea that selection favors traits that increase the productivity or persistence of groups, rather than individuals. The debate is an old one, and a culmination of it came in two books in the 1960s. Wynne-Edwards (1962) explicitly explained many seemingly altruistic traits as group adaptations, while Williams (1966) wrote a critique of prevailing views of adaptation and natural selection in general, and group selection in particular, expounding a gene-centered view of evolution (Williams’ book would become a central influence for “The Selfish Gene” alongside kin selection: Dawkins (1976)). Gene-centered thinking was similarly fundamental to Hamilton’s work, explicitly stated in his first, short article on kin selection (Hamilton 1963): “*Despite the principle of ‘survival of the fittest’ the ultimate criterion which determines whether G will spread is not whether the behavior is to the benefit of the behavior but whether it is to the benefit of the gene G .*” Kin selection provides an explicit theory of the evolution of altruistic traits that is not dependent on group selection thinking, and as such was destined to become entangled in the debate surrounding group selection.

For an in-depth account readers are referred to, for example, Okasha (2006). However, three aspects of the debate are worth pointing out: Firstly, one can quite reasonably talk about *selection* at the level of the group when carefully defined, but this does not imply that group *adaptations* can readily evolve (Maynard Smith 1987).

The reason for this is that there is typically pervasive between individual, within-group selection (Maynard Smith 1987), and selection within groups is usually not aligned with selection between groups. Second, inspired by the work of George Price and the famous equation named after him (Price 1970), Hamilton noted early on that group selection (when carefully defined, accounting for selection both between and within groups using a multilevel version of the Price equation) and kin selection are mutually compatible and mathematically equivalent explanations (Hamilton 1975), making it somewhat puzzling that debate between the two has lasted so long. Third, there are in fact several alternative mathematical ways of defining group selection (Okasha 2006), but the three major ones are all mathematically equivalent, and all three can be written using a common mathematical notation which is shared with kin selection, making it relatively simple to transition between kin selection and various forms of group selection models (Lehtonen 2020). Group selection is therefore intimately tied to kin selection and its history and development, but ultimately there is no need to view them as mutually exclusive, competing alternatives.

Conclusion

The evolution of altruism is difficult to explain, because altruistic traits by definition decrease the fitness of the altruist and should hence be removed by natural selection. Yet altruism exists in nature. Partial solutions to this conundrum were proposed, until William Hamilton published a general and mathematical explanation, now known broadly as kin selection. Kin selection explains the existence of altruistic traits but applies equally well to selfish, mutually beneficial, and spiteful traits. Central to the concept is genetic relatedness, which determines the probability that an actor and recipient share genes. Hamilton’s rule is a cost-benefit inequality with benefits weighted by relatedness that tells us when a trait (e.g., altruism) can spread. Inclusive fitness is an actor-centric quantity that is expected to be maximized by selection,

at least under some simplifying assumptions. Neighbor-modulated fitness is a recipient-centric quantity that is equivalent to inclusive fitness; it provides the starting point for Hamilton's (1964a) analysis and is central to modern methods of analyzing social evolution. In its modern form, kin selection is composed of a robust general theoretical framework (regression models) and a set of more practical modelling tools (weak selection models). Kin selection has been the source of considerable debate, and much of this debate has focused on the tension between kin selection and group selection. However, when properly defined, the two are mathematically equivalent.

Cross-References

- ▶ [Alarm Calling and Kinship](#)
- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)
- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Benefits to Kin](#)
- ▶ [Consolidating Familial Power](#)
- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Fisher's Reproductive Value](#)
- ▶ [Genetic Relatedness](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Green Beard Effect, The](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Kinship Psychology Manipulations](#)
- ▶ [Living in Groups](#)
- ▶ [Monetary](#)
- ▶ [Multilevel Selection Theory](#)
- ▶ [Puzzle of Altruism, The](#)
- ▶ [William Hamilton](#)

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Kin Selection Hypothesis

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Synonyms

[Kin selection hypothesis for male androphilia](#);
[Kin selection hypothesis for male homosexuality](#)

Introduction

The following provides an overview of the available literature concerning the evolution of homosexuality via kin selection, which has been reviewed at greater length elsewhere (for review, see VanderLaan et al. 2016, [in press](#); VanderLaan and Vasey 2014; Vasey and VanderLaan 2014). This literature pertains almost entirely to homosexuality in men, especially with regard to empirical studies. As such, this entry focuses on male, not female, homosexuality. In addition, this literature is cross-cultural in scope, and because the term “homosexual” does not always translate to other cultural settings, alternate terminology is frequently employed here. Specifically, rather

than using the term “male homosexuality,” the term “male androphilia” is used instead. *Androphilia* refers to sexual attraction and arousal to adult males; *gynephilia* refers to sexual attraction and arousal to adult females.

Below, the argument that homosexuality is an evolutionary paradox and the logic of the kin selection hypothesis as an explanation of this paradox are summarized. Evidence bearing on this hypothesis is reviewed, including tests of the hypothesis’ basic prediction, evidence of adaptive design, and developmental considerations. A recently proposed model of the evolution of male homosexuality via kin selection is proposed in light of the available evidence. Directions for future research and critiques of the kin selection hypothesis are discussed.

Homosexuality: An Evolutionary Paradox

A number of lines of evidence support the argument that androphilia in males is an evolutionary paradox. First, male androphilia has a familial component and is at least partially influenced by genetic factors. At the same time, androphilic males exhibit significantly lower reproduction rates than gynephilic males. Despite this lowered reproduction, male androphilia appears to be widespread across human populations. Lastly, archeological evidence suggests that sexual behavior between males has existed for millennia. As such, the persistence of genetic factors underlying male androphilia, from one generation to the next over evolutionary time, requires explanation.

The Kin Selection Hypothesis

The kin selection hypothesis has been proposed as one possible explanation for the evolutionary paradox of homosexuality. It suggests that androphilic males offset the cost of not reproducing directly by facilitating the reproduction of kin, who share genes by virtue of descent. In theory, androphilic males could increase their *indirect fitness* (a measure of an individual’s impact on the reproduction of genetic relatives

weighted by the degree of relatedness) via kin-directed altruism, thereby facilitating the maintenance of genetic factors underlying male androphilia in the gene pool.

Empirical Tests of the Hypothesis

The most basic prediction of the kin selection hypothesis is that, compared to others, androphilic males should be more willing to invest resources such as time and money in kin. To date, tests of this basic prediction have produced inconsistent findings across studies. Comparisons of gay and heterosexual men's willingness to allocate time and money toward their kin have repeatedly failed to support this basic prediction in several countries, including the USA, UK, Canada, Japan, Spain, and Italy.

In contrast, this prediction has been well supported in studies focusing on androphilic males in Samoa who are known locally as *fa'afafine*, a "third" gender that is distinct from the categories of "men" and "women." In several independent samples, *fa'afafine* reported greater avuncularity (i.e., uncle-like tendencies or willingness to allocate resources toward nieces and nephews) than Samoan gynephilic men and androphilic women. Given that these Samoan findings contrast sharply with those from tests of the kin selection hypothesis in several other countries, these researchers conducted a series of studies to determine whether some alternate explanation specific to Samoa explained *fa'afafine's* elevated avuncularity. Based on these additional studies, *fa'afafine's* elevated avuncularity – as opposed to the lack thereof among gay men in other cultures – does not appear to be attributable to any of the following:

- Socially desirable responding on the part of *fa'afafine*
- Greater social acceptance of same-sex sexuality in Samoa compared to other cultures
- The fact that *fa'afafine* lack direct parental responsibilities
- The fact that Samoan families typically live in close geographic proximity

The fact that Samoa is a collectivistic society

That *fa'afafine* are simply taking on the childcare role of women as part of their "third"-gender status

That *fa'afafine* have more time to allocate to nieces and nephews because they are not investing in sexual/romantic relationships

That *fa'afafine* or Samoans more generally hold expectations that *fa'afafine* will contribute more than other family members to caring for nieces and nephews

Evidence of Adaptive Design in the Avuncular Cognition of Samoan *fa'afafine*

In addition to examining alternative explanations for the unique Samoan findings, a number of studies have tested more refined predictions derived from the kin selection hypothesis to assess whether the avuncular cognition of *fa'afafine* shows hallmarks of adaptive design (i.e., evidence to suggest that the avuncular cognition of *fa'afafine* has been shaped by kin selection processes). These studies have produced a number of findings consistent with adaptive design.

- First, whereas Samoan men and women decrease their willingness to invest in nieces and nephews when they are in a sexual/romantic relationship, *fa'afafine's* avuncularity remains elevated regardless of their relationship status.
- Second, in light of the issue of paternity certainty, one can always be more confident in their genetic relatedness of sisters' children than brothers' children, and so androphilic males should favor investing in the former to maximize indirect fitness. Compared to Samoan men and women, *fa'afafine* show a bias to invest in their sisters' children, particularly when the consequences of investment are nontrivial (e.g., paying for school or medical expenses).
- Third, because younger children are especially vulnerable to mortality, an efficient means of maximizing indirect fitness would be to bias investment toward younger nieces and nephews. Compared to Samoan men and

women, *fa'afafine* are more likely to show such a bias, and this also translates into behavioral differences in terms of the allocation of monetary resources.

Fourth, as interest in investing in nieces and nephews increases, so too does interest in investing in children more generally, including non-kin children; however, dissociating one's interest toward investing in nieces and nephews vs. non-kin children would allow one to maximize investment in kin. Compared to Samoan men and women, *fa'afafine* show a greater dissociation between these domains. It is noteworthy that Canadian gay men, compared to heterosexual men, also show this greater dissociation, suggesting that the avuncular cognition of androphilic males outside of Samoa might also possess hallmarks of adaptive design due to kin selection despite the lack of support for the basic prediction of elevations in kin-directed altruism.

Development of Elevated Kin-Directed Altruism

Some studies suggest that androphilic males across cultures exhibit a disposition toward elevated kin-directed altruism beginning in childhood. Compared to their gynephilic counterparts, androphilic males in Canada and Samoa reported they experienced higher levels of separation anxiety as children. Separation anxiety is characterized by distress experienced during periods of separation from major attachment figures, who are invariably kin such as parents and siblings. This elevation in separation anxiety might reflect heightened kin attachment among androphilic males, which one would expect from a kin selection perspective given that this heightened attachment might promote kin-directed altruism later in life. Further research has shown that androphilic males' separation anxiety is driven primarily by a concern about the well-being of kin during periods of separation (e.g., worrying kin will be hurt in an accident) as opposed to other circumstances involving separation (e.g., having to go to school). This pattern is also consistent with a kin selection perspective in

that worrying about the well-being of kin would prompt behaviors to secure their well-being and thus the ability of kin to contribute to one's indirect fitness. In terms of other personality correlates, a consistent finding in this developmental literature is that androphilic males also report elevations in female-typical childhood behavior, which is positively associated with their levels of childhood separation anxiety.

The Adaptive Feminine Phenotype Model

The *adaptive feminine phenotype model* attempts to reconcile the mixed cross-cultural and developmental research bearing on the kin selection hypothesis. According to this model, a disposition toward elevated kin-directed altruism on the part of androphilic males is contingent on the concomitant expression of behavioral femininity. If so, this would explain why childhood separation anxiety among androphilic males is associated with childhood female-typical behavior across cultures. Furthermore, it would explain why Samoan *fa'afafine*, who are markedly feminine, show elevated kin-directed altruism throughout life, while gay men, who are more feminine as children but become relatively more masculine in their gender presentation into adulthood, do not.

Some recent findings are consistent with this model. First, among Samoan *fa'afafine*, childhood concern about the well-being of siblings is positively associated with adulthood avuncularity, indicating that the former does prefigure the latter. Second, among Canadian gay men, lifespan expression of kin-directed altruism appears to be linked with lifespan expression of feminine gender expression. Feminine gender expression is not only associated with their childhood separation anxiety but also with their adulthood willingness to invest in nieces and nephews. Moreover, there is a decrease in their disposition toward kin-directed altruism between childhood and adulthood, and this decrease corresponds to a concomitant decrease in their level of feminine gender expression.

The plausibility of this model is further supported by additional lines of research. To begin with, if kin selection produced an androphilic male phenotype that exhibits elevated kin-directed altruism, but only in combination with feminine gender expression, then there should be a close genetic association between these traits. Indeed, research with twins indicates that common genetic variants underpin sexual orientation and gender expression as well as sexual orientation and neuroticism (which is conceptually similar to anxiety).

In addition, if this model is accurate, then androphilic males would have had to be free to exhibit a feminine gender expression in the ancestral environment. Ethnological research indicates that sociocultural factors characteristic of ancestral human societies (e.g., hunting and foraging, relatively small group sizes) are associated with the presence of “third” gender groups similar to the Samoan *fa’afafine*. As such, it appears likely that in an ancestral context, androphilic males exhibited a markedly feminine gender expression as adults. According to the adaptive feminine phenotype model, this feminine gender expression may have then facilitated elevated kin-directed altruism – although the precise mechanisms linking feminine gender expression to elevated kin-directed altruism have yet to be identified.

Limitations

The primary criticism of the kin selection hypothesis concerns its ability to account for the persistence of genetic factors underpinning male androphilia. Some have argued that kin-directed altruism on the part of androphilic males cannot be sufficient to offset the reproductive costs associated with male androphilia. Specifically, because nieces and nephews are only half as related to oneself as direct offspring, kin-directed altruism would have to result in two nieces and nephews for every offspring foregone. The premise that such a degree of kin-directed altruism is possible has been viewed with considerable skepticism, casting doubt on the viability of the kin selection hypothesis.

That said, this critique may be overly simplistic. It is possible that kin selection processes are not sufficient to completely explain the persistence of genetic factors underpinning male androphilia, but they may contribute to their persistence at least in part. In addition, an important consideration is that population growth was only slightly above replacement in the human ancestral environment, wherein the average person produced only two offspring who survived and reproduced in turn. As such, for the kin selection hypothesis to have to be viable ancestrally, androphilic males’ kin-directed altruism would only have had to result in four nieces and/or nephews who survived and reproduced. A bias toward investing in younger nieces and nephews – like that exhibited by Samoan *fa’afafine* – might improve the survival of those kin, thus allowing androphilic males to achieve this mark. Lastly, if the adaptive design features characterizing androphilic male avuncular cognition – such as those described above found among Samoan *fa’afafine* and Canadian gay men – are indeed the product of past selection, then kin selection processes contributed, at least in part, to the persistence of genetic factors underpinning male androphilia *ipso facto*. Thus, additional demonstrations that androphilic males’ avuncular cognition is characterized by hallmarks of adaptive design would further challenge critiques about the viability of the kin selection hypothesis.

A primary limitation of the research literature concerning this hypothesis is the lack of replication studies. Although the basic prediction that androphilic males should be more willing to invest in kin has been investigated quite thoroughly in Samoa, additional tests in other populations where feminine “third” gender males exist would be valuable. Such tests are particularly relevant to evaluating the adaptive feminine phenotype model, which predicts that “third” gender androphilic males in other cultures should also exhibit elevated kin-directed altruism. To date, the kin selection hypothesis for male androphilia has only been tested in one additional population of “third” gender males outside of Samoa: the Urak Lawoi inhabiting Ko Lipe island

in the Andaman Sea off the coast of Thailand. That study found no evidence that feminine, third-gender males (known locally as *na-ning*) exhibited elevated avuncularity compared to gynephilic males from the same culture. Unfortunately, the Urak Lawoi study's value in informing debate over the role of kin selection in the evolution of male androphilia is compromised by the fact that extremely small sample sizes were employed and the statistical analyses employed were characterized by several limitations.

There is also a need to further examine androphilic males in cultures where they identify as gay men to test whether they show the same hallmarks of adaptive design that characterize the avuncular cognition of *fa'afafine*. Even though gay men do not report elevated willingness to invest in kin, they may evince some of the same avuncular cognition design features as *fa'afafine*, which would help clarify the role of kin selection processes in the evolution of male androphilia across populations.

A major gap in the research literature concerns the effects of androphilic males' kin-directed altruism on kin. If androphilic males' kin investments have positive influences on indirect fitness, then one would expect to observe increases in the quantity and/or quality (i.e., physical, psychological well-being) of their kin. To date, no research has provided such an investigation, and such tests are keys to evaluating the kin selection hypothesis.

Another aspect that has yet to be investigated empirically is the relation, if any, between kin selection processes and alternative mechanisms hypothesized to contribute to the evolution of male androphilia. A thorough description of these alternatives is beyond the scope of this piece but suffice it to say that several alternatives have been proposed. If kin selection provides only a partial explanation for the evolutionary persistence of genes underpinning male androphilia, then these alternative mechanisms might interact with kin selection processes to account for the remaining portion. Further advances in theory and research in this area are required to address these possibilities.

Conclusion

The kin selection hypothesis provides one possible explanation for the evolutionary paradox of male androphilia over evolutionary time. This hypothesis argues that androphilic males offset the fitness costs of not reproducing directly by allocating increased altruism toward kin, thereby enhancing kin's reproduction and thus indirect fitness. To date, the majority of evidence in support of this hypothesis has been found among androphilic males who exhibit marked femininity, suggesting that such gender expression might be key for facilitating elevated kin-directed altruism among androphilic males. In addition, several studies have suggested that androphilic males' kin-investment cognition is characterized by adaptive design features that are expected from a kin selection perspective. There is presently a need for further replications of this research and investigations of the impact of androphilic males' kin investment on kin in diverse cultural settings. Such work will help to clarify the role of kin selection in the evolution of male androphilia.

Cross-References

► [Fa'afafine](#)

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Kin Selection Hypothesis for Male Androphilia

► [Kin Selection Hypothesis](#)

Kin Selection Hypothesis for Male Homosexuality

► [Kin Selection Hypothesis](#)

Kin Selection Theory

- [Grandparenting](#)
 - [Hamilton's Rule](#)
 - [Hamilton's Rule and Kin Investment](#)
 - [Helping More Likely with Close Kin than More Distant Kin](#)
-

Kin Selective Suicide

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Synonyms

[Altruistic suicide](#)

Definition

Suicide committed for the benefit of kin.

Introduction

Suicide, the voluntary surrender of life (or more exactly, in evolutionary terms, the surrender of the possibility of reproduction), is the ultimate sacrifice an individual can exercise on behalf of others.

The Christian bible says “No one can have greater love than to lay down his life for his friends” (John 15:13). The pervasive evidence on this extreme kind of sacrifice poses difficulties for superficial interpretations of evolutionary theory, but can be easily accommodated by kin selection and models of local interaction.

Altruistic Suicide: From Puzzle to Redefinition

Durkheim (1897) is probably the first social scientist that dedicated serious effort to defining and understanding altruistic suicide. He starts by documenting that, against common prejudice, suicide was not unknown or uncommon among primitive societies. Rather, egoistic suicide was indeed infrequent, but altruistic suicide was “surely very common among primitive peoples.” He goes on to add that “when a person kills himself, in all these cases, it is not because he assumes the right to do so, but, on the contrary, *because it is his duty*” (Chapter 4, emphasis in the original).

This phenomenon is certainly not restricted to primitive cultures. As Gambetta (2006) shows, from the Second World War Japanese Kamikaze to modern-day Tamil Tigers or Palestinian suicide bombers – as well as present-day conflict in Syria, Afghanistan, Iraq, and Pakistan – altruistic suicide is still a common occurrence. Altruistic suicide occurs in other species, from unicellular organisms (Nedelcu et al. 2011) to genetically unrelated ant co-foundresses (see Pollock et al. 2012 for an empirical example with theoretical explanation). Kin selection predisposes individuals toward altruism, with suicidal parental sacrifice/defense of children being the most relevant case (suicidal altruism is contingent, just as parental sacrifice for young is); but kin selection does not delimit all such extreme suicidal sacrifice. Pollock and Cabrales (2008) provide other models perhaps relevant to, e.g., suicidal altruism in bombing among humans.

Evolutionarily, there is no difference between a suicide and a sterile worker, save that the latter is under indirect reproductive control via helping/

alloparenting; when a suicide also feeds back positively onto others' reproduction, it too is an indirect tool to that end. Adaptive suicide, kin selected or selected by other processes, is not an isolated event; bodily suicide in psychology, however, is generally framed as an isolated event. Thus, adaptive suicide extracts the tragedy from suicide save in a generalized parental care sense.

Altruistic suicide seems superficially incompatible with evolutionary theory. After all, if a genetic trait makes an individual disappear before reproduction, how can it hope to persist in a population? This paradox was already remarked on by Darwin in describing sterile (thus, suicidal) castes in social insects, together with the embryo of an evolutionary explanation. The first mathematically complete evolutionary model arises with the introduction of kin selection. Hamilton (1963, pp. 354–355) summarizes the point simply: “If the gain to a relative of degree r is k -times the loss to the altruist, the criterion for positive selection of the causative gene is:

$$k = \frac{1}{r}$$

Thus, a gene causing altruistic behaviour towards brothers and sisters will be selected only if the behaviour and the circumstances are generally such that the gain is more than twice the loss; for half-brothers it must be more than four times the loss; and so on.” This formulation makes suicidal sacrifice simply a special case of a more general process, although such sacrifice in social insects initially drove the theory (see other encyclopedia entries on ► [Kin Selection](#) herein for references); suicide is simply the greatest personal cost possible for an individual.

But evidence of altruistic suicide even among unrelated individuals (Pollock et al. 2012) calls for further explanation. The best existing theories employ local interaction. The basic idea is straightforward: individuals exist in space and tend to interact with individuals that are close to them. A “suicidal” gene whose acts are beneficial to spatial neighbors will also benefit in general copies of itself (thus, in a loose sense, this kind of suicide can be thought of an extended form of

kin-selected suicide). Clearly, a mutant non-altruist gene introduced within a cluster of suicidal altruists can thrive temporarily, but for the same reasons, it will soon also cluster and act mostly among other non-altruists and can collapse (or not grow) depending on dynamics at the boundary. Spatial models are usually complicated and often require a mixture of analytical and simulation techniques. Examples of such models can be found in Le Galliard et al. (2003) and Pollock et al. (2012).

Some species (e.g., some ants, Hölldobler and Wilson 1990) are able to recognize genetic relatedness almost directly through biochemical cues; humans do not. Sociobiologists saw human kin terminology as a substitute early on (e.g., Chagnon and Irons 1979). This terminology, policed, can force individuals to act on labels rather than more immediate and secure measures of genetic proximity; a biochemical cue cannot be enforced by a third party, but a kin label can. Once social life forces such reification on labels, the original kin-based anchor can be replaced – military loyalty being a prevalent and often extreme case. Once labels become primary, individuals may act on their own, living a group identity with little real referent, an adaptive failure sustained by the usual workings of labeling. Adaptation often endures such recurrent failure. Exactly how far culture can hijack processes originally compatible with genetic trajectories is an outstanding question in gene/culture coevolution (Richerson and Boyd 2008).

Conclusion

Altruistic suicide, either by direct elimination of an individual or by irreversible suppression of its reproductive ability, has been documented for a long time in humans and other organisms. Although apparently paradoxical in evolutionary terms, it can be explained easily if the beneficiaries are direct kin of the suicidal individual, and with some more work even for individuals unrelated in the usual model sense. These latter models may be genetic or a cultural analogue of genetic selection. With the latter, which surely

would include suicidal bombing altruism, one might still expect genetic bounds on realized suicide in terms of sustainable suicide.

Cross-References

- [Altruism](#)
- [Altruism in Kin Selection](#)
- [Altruistic Punishment](#)
- [Hamilton's Rule](#)
- [Kin Selection](#)
- [Kin Selection Hypothesis](#)

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Kin System

- [Ego-Centered Kin Terminology](#)

Kin Term System

- [Ego-Centered Kin Terminology](#)

Kin Terminology

- [Ego-Centered Kin Terminology](#)

Kin Terms

- [Ego-Centered Kin Terminology](#)

Kin Vocabulary

- [Ego-Centered Kin Terminology](#)

Kin-Altruistic Behaviour

- [C < Rb](#)

Kin-Cue Manipulation

- [Kinship Psychology Manipulations](#)

Kinderschema

- [Age of Child](#)

Kin-Directed Behavior

- [Kin Recognition and Classification in Humans](#)

Kindling

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Synonyms

Sensitization

Definition

Upon the cessation of repetitive strong stimulation, the spontaneous elicitation of a response occurs, in the absence of any stimulus. Also as the literal name suggests, a small spark applied to some wood will flare up and eventually grow into a big fire.

Introduction

Kindling became known to the scientific world in the late 1960s through the published work of Goddard (1967) on the neurobiology of learning and later after the application of Goddard's model on the study of epilepsy.

The Kindling Phenomenon Demonstrated Experimentally

Goddard (1967) runs a series of experiments on rats where, in order to investigate their abilities to learn tasks, he administered electrical stimulations in various regions of their brains. With daily repetition of the electrical stimuli, the rats began seizing. That response, however, was astonishing, as the administered stimuli were too low to induce seizures. Even more surprising was the final observation of the rats having unprovoked seizures, that is, seizing without

stimulation. In sensitization, repetitive stimulation produces a full response. A full response can be elicited even with lower stimulus levels than the original stimulus. It appears that a decrease in the threshold of excitability develops leading to the automatic occurrence of the response, without external stimulation. Eventually, with further repetition, the response occurs spontaneously, in the absence of any stimulus demonstrating thus the phenomenon of kindling. The changes caused by kindling seem to be long-term but they are not permanent.

Kindling is universal across species (from frogs to humans) and throughout the brain, and it was the first neuroplasticity phenomenon suggested to give information on memory processes. At a first glance, it may seem awkward to imply that epileptic seizure activity could be interconnected learning; yet, it is plausible that the diverse mechanisms constituting kindling and learning interconnect and share several common mechanisms. In effect, under this conceptualization, both kindling and learning can potentially be considered as phenomena of neuroplasticity. However, when kindling was compared to long-term potentiation as to which neuroplasticity phenomenon was more appropriate for modeling memory processes, long-term potentiation appeared to dominate, mostly because long-term potentiation was observed under normal neural activity contrary to kindling that was observed under seizures.

Further, kindling constitutes the model for the development or recurrence of medical (epilepsy) and psychiatric illnesses such as addictions and mood disorders Post (2007). Goddard's model has been referred to as the "kindling model for epileptogenesis" as it is the most frequently used model for temporal lobe epilepsy with complex partial seizures. It is used by scientists to study the effects of repeated seizures on the brain. What was demonstrated in the experiments with rats, the same applies for humans; a seizure may raise the possibility that more seizures will occur since repeated stimulation "lowers the threshold" and

paves the way for seizures to re-occur (Dennison, Teskey, Cain 1995; Racine 1978). In an attempt to better understand the occurrence of epileptic seizure, many scientists including Racine (1978) have turned their attention to the underlying mechanisms of kindling, in neurotransmitter systems and intracellular mechanisms, as well as genes.

Conclusion

Goddard's experiments suggest that the processes underlying kindling and learning interconnect and possibly have similar underlying mechanisms. Kindling is of particular importance in disorders where recurrence is involved, but its underlying mechanisms are yet to be refined by empirical investigations.

Cross-References

- [Drug Sensitization](#)
- [Non-associative Learning](#)
- [Sensitization](#)

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Kinesics

- [Body Posture](#)

Kinks

- [Paraphilia](#)

Kin-Recognition

- [Westermarck Effect](#)

Kinship

- [Family](#)
- [R = Coefficient of Relatedness](#)

Kinship and Cortisol in Caribbean Village (Flinn et al., 2005)

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Synonyms

[Family Relations](#); [The Stress Response](#)

Definition

A longitudinal study was conducted over 17 years on the island of Dominica that investigated the effects family environment had on a child's stress level. It identified a number of factors such as family composition and instability within the home as key sources of stress to children.

Introduction

Humans have evolved mechanisms that function to increase fitness within their environments. The stress response is one of those mechanisms that

increases the likelihood of surviving a threat in the environment (Flinn et al. 2005). While acute stress is adaptive, chronic stress can negatively affect many aspects of health, and in the modern environment chronic stress can be caused by a variety of sources (Ader et al. 1995; Munck and Guyre 1991). Given how dependent human children are on their caretakers, they may be specifically sensitive to interactions within the family environment (Geary and Flinn 2001), and a stressful family environment may be a salient source of chronic stress to children (Flinn et al. 2005).

The Stress Response

The stress response is activated in response to the perception of a potential threat in the environment allowing the body to adapt to that threat. When triggered, it releases energy and increases both alertness and memory of the threatening event. It also suspends functions that are not immediately necessary to survival such as growth and reproductive and immune function. It does this in order to preserve energy for dealing with the threat or stressor. This response is regulated by two systems. The sympathetic nervous system secretes epinephrine and norepinephrine, and the hypothalamic-pituitary-adrenal axis (HPA-axis) secretes glucocorticoids. Cortisol is the main glucocorticoid in humans and is often released in response to an event that is perceived as unpredictable and requires full attention in order to avoid its potential consequences (Sapolsky et al. 2000).

Essentially, the stress response is a trade-off between long-term and short-term functioning. Processes essential for long-term survival (e.g., the immune system) will be suspended in order to increase the likelihood of short-term survival. This is highly adaptive in response to acute stress, but it can be maladaptive when the stress is chronic. As the stress response suppresses both immune and reproductive functions, chronic stress can result in an increased susceptibility to infectious disease and reproductive issues (Ader et al. 1995; Glaser and Kiecolt-Glaser 2014). Chronic stress has also been linked to damage in

the hippocampus and associated memory dysfunctions. The HPA-axis can be damaged by chronic stress resulting in a stunted cortisol response to stressors which is often called habituation (Glaser and Kiecolt-Glaser 2014). Pre- and perinatal chronic stress has been linked to a malfunctioning HPA-axis in both rats and rhesus macaques (Clarke 1993; Meaney et al. 1991). In humans, individuals who were sexually abused as children have been found to have damage to their HPA-axis. This is thought to be linked to the chronic stress the child experienced as a result of the abuse (Heim et al. 2000). However, it is important to note that there are individual differences in baseline HPA-axis activation and cortisol release. One study found that introverted children had higher levels of cortisol than their extraverted counterparts (Kagan et al. 1988). Regardless, there is sufficient evidence supporting the theory that consistent stressors in one's environment can result in chronic stress and that chronic stress has a negative impact on health.

Stress and the Family

While there are individual differences in response to stressors, there may have been selection pressures to evolve sensitivity to specific situations. Human infants are altricial and, consequently, require a significant amount of parental investment. Their survival, particularly during the early years of their lives, is almost entirely reliant on parental and alloparental support (Flinn et al. 2005). Alloparenting may be particularly important in the absence of maternal or paternal support (Flinn and Leone 2009). Consequently, instability and conflict in the familial environment may be a significant stressor for children.

A longitudinal study was carried out over 17 years in the island of Dominica assessing the relationship between cortisol and family environments (for reviews see Flinn 1999; Flinn and England 1995, 1997, 2003; Flinn and Leone 2009; Flinn et al. 2005). The researchers regularly observed children interacting with each other and their families in order to assess caretaking attention, family environment, daily activities, and

temperament. Researchers also took saliva samples from participants at least twice per day in order to assess baseline cortisol levels and cortisol responses.

One factor that was hypothesized to impact cortisol levels was family composition. Children who lived in a household with a nonrelative such as a step-father had higher cortisol than children who only lived with closely related relatives (e.g., parents, grandparents). Within the same household, children who were genetically related to both parents had lower cortisol than children who were not related to the father (i.e., a step-father). Children who lived in a two-parent household had lower cortisol than children who lived in a single-mother household when there was no kin support (Flinn et al. 2005). Overall, children who lived in a household with two parents, a mother with kin support, or grandparents had lower cortisol than children living in households with a step-father or a single-mother with no kin support. Additionally, children who live in houses with a step-father but who have high alloparental care had lower cortisol than those in the same situation who did not have alloparental care (Flinn and Leone 2009).

Family composition was not the only regulating factor for cortisol. Children who were part of families that were recorded as having more familial stress and conflict had higher cortisol than those who came from less stressful households. Some children from high-stress households who had experienced chronic stress also had a cortisol baseline that was below average during non-stressful times, and they had a stunted cortisol response to nonthreatening stressors such as competitive play. This is most likely due to habituation where chronic stress can damage the HPA-axis and result in a stunted cortisol production and response (Flinn et al. 2005).

There are different stressors in the environment from which the increase in cortisol could be originating from. There is the possibility that in mixed households (i.e., households with a step-parent and a mixture of biological and step-children) there is a risk for there to be higher levels of conflict or for

the children who are genetically related to both parents to receive more investment. In single-parent households, there may be less parental support or more financial issues both of which could lead to uncertainty with respect to basic needs and safety (Flinn et al. 2005). A consistent predictor of cortisol levels was the amount of maternal care. It is possible that even if the single-parent was the mother, there could still be a greater chance of stressors in the environment. This is because the mother may have to spend more time working or even allocate time and resources into finding another mate rather than investing in her children (Flinn and Leone 2009).

Conflict or instability within a family is a negative stressor. However, the stress response does not solely react to negative stressors. It also reacts to nonnegative stressors such as competitive games or situations that elicit positive emotions such as excitement. When comparing participants' cortisol responses to both negative and nonnegative stressors, there are differences in both magnitude and longevity of the cortisol spike. Nonnegative stressors were found to raise cortisol between 10 % and 100 %. However, cortisol levels generally return to their baseline within an hour. Negative stressors were found to raise cortisol 100–2000 %, and, in response, cortisol levels remained elevated for at least 24 h (Flinn and England 2003). The most common source of negative stressors was some form of conflict within the family with 19 % originating from a serious family conflict and 12 % originating from a minor family conflict. Negative interactions at home such as punishment, arguments, or change in family composition (e.g., the addition of a step-parent) consistently resulted in an increase in cortisol levels (Flinn and Leone 2009). Alternatively, positive interaction such as physical touch or encouragement lowered cortisol levels by 10–50 % (Flinn et al. 2005).

When assessing this research, there are a number of considerations such as not all children within the same household responded similarly to stressors. Some showed a spike in cortisol in response to a specific conflict within the home

while their sibling did not. This could be attributed to children's disparity in what they are sensitive to within their environment. When considering the results on family composition, it is important to note that family composition is not consistently predictive of stability within a family. There were single-parent households that were a more stable and unstressful environment than some two-parent households. Therefore, the spike in cortisol is most likely in response to instability rather than the lack of two parents. The presence of both parents or kin support can increase financial, physical, and emotional stability but that does not exclude single-parent households from being stable environments (Flinn et al. 2005).

Conclusion

The presence of chronic environmental stressors can have negative effects on the health and well-being of individuals (Ader et al. 1995; Glaser and Kiecolt-Glaser 2014). Children, in particular, seem to be sensitive to stressors such as conflict or instability within their family environment. The lack of kin support, the presence of a step-parent, or a household with a high amount of conflict can result in children having elevated cortisol or a dysregulated HPA-axis (Flinn and Leone 2009; Flinn et al. 2005). Considering the health repercussions associated with chronic stress, this research suggests the importance of focusing on the home environment when attempting to reduce stress in a child's life.

Cross-References

► [Kinship and Emotional Closeness](#)

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Kinship and Emotional Closeness

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Synonyms

[Alloparents](#); [Extended family](#); [Family](#); [Family of orientation](#)

Definitions

Gharwale, Biradari, Donor families

Introduction

Recent changes in definitions of the family bring forth issues related to defining kinship and concerns over the positive contributions of kinship. Many have alluded that strong kinship is limited to families in developing nations and in light of the lack of societal emphasis on Kin, the topic remains empirically unexamined.

Contributions of Kinship

The family performs crucial functions and satisfies many human needs, such as the provision of economic security, socialization of children, a satisfaction of sexual needs, and love and warmth (Wolf 1966; Choldin 1973). Although other societal institutions can gratify these needs, the family as an institution can execute the above-listed tasks with modest costs and in a more competent manner. Immediate family members and Kin are more competent as they are genuinely concerned and committed, and culturally obligated to carry out these tasks to the best of their ability.

Applications of the concepts of generativity to kinship clarify the rationale behind genuine

concerns, significant investments, and firm commitments of family members towards each other. Since the sense of generativity creates a need to focus on others, as a consequence, it pushes individuals to guide and support future generations. Generative individuals' guide and support future generations by nurturing, teaching, and passing on cultural symbols/traditions (Erkison 1950; Kotre 1984). It is essential to state here, that the process is highly beneficent to both members as acts of generativity are the developmental needs of one member, while the other member is benefited by the support he/she receives.

Correspondingly, Kin are not only "mentors (teach skills, provide guidance), keeper of meaning (preservers of family traditions, family historians), intergenerational buffers (can intercede on behalf of parents, emotion work and resolution of conflict), but also, fellow travelers and companions (help to cope with significant life events, social and emotional support)" (Milardo 2009, pp. 16 & 17).

Besides direct benefits, kin membership provides a sense of identity in the world; for example, the last name may suggest a strong lineage. Daly, Salmon, and Wilson (1997) suggested that belonging to a particular clan is a universally stable attribute. Therefore, for many, the kin membership helps to maintain a sense of higher and more positive reputation in comparison to others, aka, higher social credibility and social capital as members are obligated to share their prosperity (Dasgupta 2005). Nevertheless, how does one achieve social credibility because of the family lineage is a logical question.

Kellerhals, Ferreira, and Perrenoud (2002, p. 215) described the social mechanism of identity transmission among Kin. The researchers suggested that the successful identity transmission process requires three prerequisites. These prerequisites are (a) "normative reference marks such as occupational class, symbols of the family emblem, family name or value code and more, (b) transmission channels such as strict and well-differentiated family codes, intimate exchanges and more and (c) types of cohesion of the actors who personify these reference

marks and who are involved in the transmission channels. These include hierarchy between members (patrimony), family boundaries, and more.” Furthermore, in the process of maintaining membership, kin members develop “social synchronization” (Wolf 1966, p. 9), which is consequential in the development of trust and a sense of cooperation among Kin. Thus, on the one hand, strong lineage and social goodwill offer social credibility, yet on the other hand, it demands harmony and trust among its members.

Despite the significant contributions to human development, research on kinship is underdeveloped and is limited to the caregiving of the elderly (Milardo 2009). Therefore, there is a need to explore beyond caregiving and understand the obligatory and non-obligatory roles of extended family members and their motivations to perform these roles. Hence, the current article reviews the contributions of emotional closeness in strengthening the relationship among Kin.

Emotional Closeness and Kinship

Emotional closeness, although not well- defined in research, consists of a shared sense of security, comfort, trust, and care for another individual (Korchmaros and Kenny 2001; Lee et al. 1990). Kin are defined as individuals related by birth, common ancestry, marriage, or adoption. When applied to kinship, emotional closeness is associated with higher altruistic behavior and assistance (Bell et al. 1995; Clark and Mills 1993), better communication (Roberts and Dunbar 2011), and stronger commitment and investment (Antfolk et al. 2017). All of the above stated variables in relationships can be a lifesaver at the time of crises.

Despite the merits, emotional closeness among Kin can be a function of genetic relatedness, age and stage of development, gender, residential proximity, filial piety and inter-generational solidarity, and more. Given below are some of the factors that moderate or mediate emotional closeness among Kin.

Factors that Impact Emotional Closeness and Kinship

Genetic relatedness. Hamilton (1964) proposed the Kin Selection Theory, which is the foundation of social behaviors and its applications by social psychologists. He proposed that genetic relatedness is the basis of altruistic behaviors towards family members. His theory was later tested and confirmed by several researchers. For example, in a comparative study of full, step and half-siblings; sibling relationships were found to be less intense among step and half-siblings than full-sibling relationships (White and Riedmann 1992). Likewise, Pollet (2007) found that in cases of paternal half-siblings and maternal half-siblings, despite being raised together, half-siblings had a lower degree of an investment than full siblings thus concluding that stronger genetic relatedness is more critical than residential proximity. Recently, Tanskanen and Danielsbacka (2014) applied the Kin Selection Theory to nieces and nephews and found similar findings. The researchers reported that uncles and aunts would meet more frequently with their children of full siblings than half-siblings.

To add to the body of works on genetic relatedness and altruistic behaviors, Daly, Salmon, and Wilson (1997) and Neyer and Lang (2003) suggested the mediating role of emotional closeness between the two variables. Both sets of researchers suggested that although close relationships are based on emotional closeness and connections, but the connections often correlate with genetic relatedness and the concept of near and far relatives. Similarly, Korchmaros and Kenny (2001) tested a model and found that altruistic behaviors facilitate higher perceptions of emotional closeness by mediating the effect of genetic relatedness on altruism. Therefore, we are benevolent to individuals who show connection, cooperation, and solidarity, but most individuals who exhibit these behaviors are also genetically related to us.

Hence, the above researchers provided evidence for the commonly used phrase, “Blood is thicker than water”. However, the extension of the Kin Selection theory does not sufficiently resolve

the question- why, despite the rivalry and competition for the same resources, family members support each other when in conflict with non-family members. Perhaps cultural rules of kin obligations are integral variables.

Life-course development and gender. Especially for females, kinship care begins early in many families with sibling care. In many cultures, especially non-industrialized, girls begin to contribute toward domestic chores, childcare, and the economic well-being of the family at an early age and become mothers helpers/alloparents (Hames and Draper 2004; Quinlan et al. 2003; Bove et al. 2002). Even in industrialized societies, despite the cultural differences; siblings are generally the first friend and mentors who continue to stay part of the social network of their younger siblings for the rest of their life (Cicirelli 1985, 1994).

Once in their young adulthood and adulthood, personal and professional trajectories of an individual offer additional opportunities for building new relationships or renew or renegotiate past relationships. Marriage of self and their siblings extend an individual's kin network resulting in becoming parents, son-in-law, daughter-in-law, aunt/uncle and brother-in-law/sister-in-law (Milardo 2009). The new relational experiences and changing relational landscapes along with age and stability in professional life, may demand a significant investment of effort and time and therefore, commitment. Nevertheless, investment and commitment are not all biological and the strength of investment and commitment are often conflated with the cultural feelings of solidarity & obligations, the similarity of attitudes, perceptions of support, and residential proximity (Milardo). To complicate the matter further, belonging to a female gender can make someone a normed Kin keeper. Perhaps that is why researchers have noted the laterality effect i.e. female Kin such as sisters, maternal grandmothers, and aunts (normed kin keepers) are more invested in raising their siblings, grandchildren, and nieces and nephews (Parent et al. 2013).

During middle adulthood and older years caring for parents and dealing with parents' poor health, disabilities, and death (Lachman 2015) along with professional and nuclear family

commitments become part of life. Furthermore, declining physical and mental health of self or parents may mean additional financial and caregiving pressures (Lai 2012). For example, *filial piety* and *respect for elders* are the underpinnings of grandparents and grandchildren bond in Asian cultures (Yee 2008). Nevertheless, many individuals in their old age are also liable to care for their grandchildren and shift their role from being a grandparent to a parent (Newman 2004). These additional and non-normative responsibilities may decrease the quality of care provider's social relationships and marital satisfaction (Minkler et al. 1992; Jendrek 1993) and result in poor mental and physical health of grandparents (Goodman et al. 2008).

Nationality, cultural and ethnic values. Cultures play a vital role in describing and sanctioning individual expectations, rights, and duties from other family members. In cultures with strong kinship orientation, kin members are considered a form of social insurance at the time of crisis. Nevertheless, this social insurance is built upon, loads of time, energy, and efforts of all kin members with an absolute goal to sustain relationships at all costs. The goal to save the relationship at any cost can be perceived as a burden by individuals from individualistic orientation.

To elaborate, Kim and McKenry (1998) compared the social activities of African Americans, Asian Americans, and Caucasians adults after controlling for their socio-economic background. The researchers found that Asian Americans owing to their collective orientation, were more likely to spend a social evening with their friends and relatives at home and participate in a nationality group event. African Americans were more likely to attend a church-related social event and Caucasians and younger African Americans were more likely to go to a bar or tavern for group recreation.

In terms of reliance for support, African Americans mothers leaned on extended family networks extensively for financial, physical, and emotional support in the absence of the child's father (Sudarkasa 1996). Expectations of support from the father of the child were found to be remarkably low. Perhaps, women hinge more on

the maternal side of the family for support as African American men have a higher rate of unemployment and incarceration (Haxton and Harknett 2009).

Despite the differences in reliance for support, Kin support serves important functions in African American families. Hall (2007) examined the effects of kin and fictive kin support on the development of resilience among African American children of alcoholic parents. Hall reported that children of alcoholic parents in his sample experienced physical, emotional, and financial distress and therefore, the positive support from Kin is a much-needed factor to develop resilience in at-risk families. Since positive support promotes attachment, it detracts children from risky behaviors and enhances their chances to succeed academically and in intimate relationships.

Likewise, Hispanic families have a stronger family orientation than Whites and reported higher intergenerational contact and emotional support (Garcia 1993). However, in contrast to African American families, support is expected from both sets of grandparents (Haxton and Harknett 2009).

Despite the contributions of kinships in families from developing countries and minority groups, many authors alluded to the small role of Kin among families in industrialized nations such as the US (Rodman 1965; Parsons 1943). According to the authors, in the US, the conjugal family is emphasized, and the family-of-orientation of both spouses play an insignificant role in providing economic security and socialization of children. Perhaps that is why, unlike developing nations, they also receive less physical care from their children in old age and rely more on community resources.

European countries. To test the above proposition of weaker kin ties in western nations, Höllinger and Haller (1990) examined the decreasing role of kin ties and the increasing role of non-kin ties among seven European countries. The seven countries were Australia, Austria, Britain, West Germany, Hungary, Italy, and the US. The authors collected data on almost 10,000 individuals and the sample size ranged from 1,000 to 2,800 individuals from each country. The goals

of the study were to compare the frequency of contact between Kin and non-Kin and ascertain the differences in perceived social support.

The authors found that the frequency of contact with Kin was higher among Italian and Hungarian families than American and Australian families. Individuals from Austria, West Germany, and Great Britain were in the middle, with Austrians being closer to the Italian/Hungarian pattern and Brits being closer to the American/Australian pattern. The findings confirmed the effect of the modernization and the diminishing role of kinship in developed countries. It was concluded that Hungary and Italy suggested some evidence of a focus on family and kinship as it had a lower GNP in comparison to other nations in the study.

Nonetheless, in terms of social support, Höllinger and Haller (1990) concluded that close Kin are sought for help in emergencies, even in developed countries. Thus, in the sample from Britain and Germany, even though the spatial distance from parents was more substantial than from Italy and Hungary, the children remained emotionally connected to their family of orientation and would often seek emotional assistance. Finally, Höllinger and Haller (1990) concluded that, except for Italy, the importance of friends in people's social support networks is inversely proportional to the importance of extended kin.

Non-European countries. Among specific Inuit groups, children are expected to carry out kinship obligations from a very young age, and to jump-start the process, adults help them listen to and recite the terms for their kin in infancy and toddlerhood (Douglas 2009).

Harris and Shaw (2009), in their chapter titled - *Kinship obligations of Pakistani immigrants in Great Britain* suggested that kinship relationships in Pakistani immigrant families are complicated, hierarchical, patriarchal, and densely layered with contradictions. Consequently, even though family members may have divergent viewpoints and life goals, they will continue to satisfy the normative expectations and obligations of the kinship from their native culture.

The authors clarified that unlike western cultures, among Pakistani families, the term closed family, i.e., "*gharwale*" includes grandparents,

uncles and aunts and first cousins. The term extended family, i.e., “*Biradari*” includes other individuals who are blood-related, but are not co-residents (p. 129). Despite the larger spatial distance due to immigration, kin members are still obligated to support each other at the time of need.

Evidence of the above necessity to meet kin obligations despite the residential proximity was further presented by Kalra (2008) in case of marriage. Kalra states that Muslims practice clan endogamy and therefore, cross and parallel cousin marriages are normative, permitted, and preferred in Pakistani families as it encourages kin affiliation and bonding. Through marriage and procreation, the kinship is further strengthened as all the “all networks are extremely close-knit and intuned.” However, immigration and exposure to western cultural values pose unique problems. Pakistani immigrants in Great Britain succumb to kin pressure and often marry their children with their nieces and nephews in their native country. Alternatively, they will be considered “anglicized” and socially reprimanded for forgetting their Kin (pp. 35 & 33).

Recent Trends in Kinship Patterns and Care

Wachter (1997) lamented that all kinship ties, especially step ties are getting weaker, leading us to inaccurately assume that kinship ties play a nominal role in an individual’s life. He further cautions that our interpretations of kinship and its contributions cannot be based on current trends as the definition of the family has changed significantly over the years. He further adds that in reality, recent changes in marriage, divorce, remarriage, cohabitation, shared custody and more have contributed to broader kinship and more inclusive families that consist of ex-spouses, step & half-siblings, close friends, neighbors, and even animals. Even today, the sense of security that Kin/family members provide along with positive memories is emphasized in families.

Interestingly, what Wachter stated had been a common practice in other cultures for centuries. For example, among Malays co-residence and sharing food from the same hearth creates kinship ties (Carsten 2004).

Nevertheless, one category that is new and has been created because of medical advancements is donor created families. Cahn (2012) suggested that millions of families have been created from donated sperms and eggs, yet the legal status of these families may not be at par with other families in the light of shared genes, but lack of connections and reliance for support. Although Donor Sibling Registry has created some connections, yet most individuals born out of donated egg or sperm, want to understand and are curious to know more about their biological roots. In the absence of such information, they experience a sense of loss (Turner and Coyle 2000). According to Cahn, who is the parent/family of the donor offspring and the possibility of emotional connections with the donor family can present some unique and complex legal issues.

Social Programs, Family Policies, and Kinship

Kinship care is universal with siblings raising siblings, grandparents raising grandchildren, daughters-in-law/daughters caring for their parents and parents-in-law, and spouses caring for each other in old age or disability. To illustrate further, in the US alone, approximately 2.6 million children lived with a relative who is not a biological parent (Kids Count 2018). The reliance on growing numbers of children and adults on kin members for care brings forth complicated relationship-based care and resilience issues for both care recipients and providers (Connolly et al. 2017).

Most of the time, kinship care is arranged by the child welfare agencies and kin care providers are permitted to make academic, legal, and medical decisions (Rubin et al. 2017) for their adopted children. Many of the relatives who are now legal guardians may have inadequate financial resources and education or training to raise

children or may additionally have mental health issues. To combat the issue, Rubin et al., recommended that the American Academy of Pediatrics and policymakers recognize kinship care and their unique needs in the medical field through training of their medical residents and providing access to community resources. Likewise, Winokur, Holtan, and Batchelder (2018) recommended training, supervision and licensing of kin caregivers to improve permanency and safety of young care recipients.

Bell and Romano (2017) reviewed 54 studies to examine the impact of kinship care on child outcomes in comparison to other placement types (e.g., foster family) in terms of permanence of care and safety. The authors reported that although the positive outcomes diminish over time, most studies suggested that children in kinship care experience a more stable childhood with fewer transitions to receive care from other families and a lower likelihood of adoption in comparison to children in foster family homes.

Future and Limitations of Kinship Research

There had been several limitations and recommendations to improve kinship research. Given below is a very brief account of some recent work.

In terms of theoretical models, Aktipis et al. (2018) criticized traditional models of kinship and recommended the applications of the fitness interdependence model. The model successfully integrates the variations in positive correlations between both kin and non kin and altruistic behavior. The authors suggested that mutual dependence among members gives rise to altruism regardless of genetic relatedness. Similarly, Itao and Kaneko (2020) attempted to understand the emergence of kinship structures (such as generalized exchange and restricted exchange) and the incest taboo through the applications of the degree of cooperation and mating conflict model among indigenous groups. The authors concluded, “incest taboo emerges when the necessity of cooperation, the conflict for mating, and cultural

similarity across generations are sufficiently large.” (pp. 23–83).

In terms of recommendations for future research, Itao and Kaneko (2020) noted that future research must focus on each indigenous group separately. In addition, Furstenberg (2020) recommended that kin relationships and connections can be studied beyond tangible support kin provide to each other, as it is especially relevant in higher income families.

Conclusion

Even though, kinship and emotional closeness remain unexplored in the US, research from other cultures suggests that kinship contributes positively to human development and therefore, there is a need to integrate extended family members in family interventions and social law and policy.

Cross-References

- Aunt Care
- Full Siblings Versus Half Siblings
- Grandparenting
- Kinship is Central to Self-Concept
- Universal Aspects of Kinship

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Kinship Distinctions According to Generation

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Synonyms

Distinction according to genealogical level

Definition

“Kinship distinctions according to generation” refers to linguistic distinctions between kin who are of the same generation and those who are in the generations above or below you. These distinctions exist, to some extent, in all languages. For example, in English, we distinguish three basic generations of kin: ego’s (or the speakers) generation, *brother*, *sister*, and *cousin*; the generation above ego, *mother*, *father*, *aunt*, and *uncle*; and the generation below ego – *son*, *daughter*, *niece*, and *nephew*. To refer to other generations, we can append the prefix “great-” or “grand-” to these basic terms. These generations are often referred to as G^{+1} for the parental generation, G^0 for ego’s generation, and G^{-1} for the generation of

ego's children. This system is extensible, so G^{+2} would refer to ego's grandparental generation.

Introduction

Generational distinctions are found to some extent in all languages and are one of Hérítier's "first fundamental laws of kinship" (Hage 1997). Since kinship systems are largely focused on reproduction and dependency, it is natural to distinguish carers from those who are being cared for (Greenberg et al. 1978). It is also common to make more distinctions in the descending generation, or generation below, than in the ascending generation (the generation above); however this is not the case in English.

Generational distinctions are arbitrary, as people within a society are born and die continuously, and not in distinct sets (Parkin 1997). Equally, men (and to some extent women) can have children over a long time span, meaning kinship ties may often be at odds to what is commonly thought of as generations, people of similar age. For example, if a grandfather has a son after the birth of a grandchild, this child's uncle will be younger than them. Kinship distinctions according to generation, then, could be more accurately described as genealogical distinctions, as they are more directly related to links between relatives than relative ages.

An interesting generational feature, exemplified by the Kariera of North Western Australia, is that of alternating generations (Parkin 1997). This is where kinterms are repeated across generations, often at G^{+2} and G^{-2} . This would mean that the terms used for grandparents are the same as those used for grandchildren. Alternating generations have also been observed between G^{+1} and G^{-1} or between ego's generation and some members of G^{+2} or G^{-2} . Explaining why this feature occurs has long been a puzzle for anthropologists. Possible explanations for why this feature occurs are symmetric prescriptive marriage or a belief in -grandparent-grandchild reincarnation (Hage 1999). However, there is no consensus on the sociological explanation of alternating generations.

There are some special cases where generational distinctions do not occur, and kinterms cover multiple genealogical levels. This is called the *skewing principle* or *generational skewing* (Godelier 2012). An example of this is when people in G^0 are treated as or at least categorized as G^{+1} relatives or higher. This famously occurs in Crow and Omaha systems. These systems are strongly tied to societies that prioritize matrilineal or patrilineal descent patterns (Keesing 1975). Crow societies are associated with matrilineality and use a classificatory term for brother's son, mother's brother's son, and mother's mother's brother's son (Stone 2014). All of these relatives are outside of the matriline and grouped together, using a term that could be broadly interpreted as "son's of men in my matriline." Similarly, within Crow, there will be one term for father's sister, father's sister's daughter, and father's sister's daughter's daughter or "women of father's matriline." Omaha is the patrilineal equivalent of Crow and tends to use a classificatory term for sister's son, father's sister's son, father's father's sister's son, or "son's of women in my patriline." However, there is no consensus on why this principle exists, as it does not appear to solely depend on lineage patterns.

Cross-References

- [Kin Recognition and Classification in Humans](#)
- [Kinship Distinctions According To Sex](#)
- [Manipulative Use of Kin Terminology](#)

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Kinship Distinctions According to Sex

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Synonyms

[Gender distinction](#); [Relative sex distinction](#)

Definition

Most if not all languages make distinction between kin according to gender: for example, in English, mother versus father, brother versus sister, and uncle versus aunt (Greenberg et al. 1978). In each of these cases, the distinction is applied to kin who are otherwise of equal genealogical distance to the speaker (ego). Cousin, in English, is an example of when kin are not distinguished according to gender.

Introduction

Gender is used to distinguish kin in one of three ways: gender of relative name, speaker's gender, or gender of the linking relative (Kroeber 1909). Gender of relative is when the kin term used depends on the gender of the person being referred to; in English, female relatives include *sister*, *mother*, and *aunt*, but not *cousin*, which could refer to a male or female relative. When kin terms depend on the sex of the speaker, the terms used by a man would differ to those of a woman. A special case of this distinction is when kin terms denote that the referent is the same or

different gender to the speaker. This is common in the Pacific; for example, in Tongan, a man would call his elder brother *ta'okete*, and a woman would also use this term for her elder sister. This term could be translated as "sibling of the same gender, who is older than me." The third way gender is used to distinguish kin is through the gender of the linking relative: this is when the term used for a relative that is connected through another relative (e.g., uncle is connected to ego through their mother or father) is determined by the gender of that connecting relative. In English, the term "uncle" makes no distinction between mother's or father's brother, so the parent's gender does not have an influence on kin terms. However, if gender of the linking relative is a constraint on the language, different terms will be used for the mother's brother and father's brother. This distinction is also how cross-cousin terminologies are generated, where parent's siblings of the opposite gender's children are given different terms to parent's siblings of the same gender's children.

Distinctions of gender are overwhelmingly common across languages, so it is of interest when they do not occur. This is the case in Malay, where marking relatives by gender in ego's generation is only reckoned through use of an optional suffix (Banks 1974). However, the core terms, *adek* and *anak*, refer to older or younger siblings regardless of gender.

Discussion

Why gender distinctions occur (or do not occur) is an interesting question and one that is not fully resolved. Possible reasons for distinguishing gender between equally distant relatives could relate to societal gender biases or sexual reproduction, although other explanations are possible (Fox 1967; Keesing 1975). Societal gender biases are when women and men have specific roles or are treated in particular ways within a society, which may be reflected and reinforced through language. An example of this is the comparison of mother and father in English, which have clearly defined parental roles in society (Stone 2014). Other

hypotheses suggest gender-biased inheritance patterns, household roles, or more broadly gender roles may encourage gendered kin terms. Sexual reproduction and gendered kinship terms can relate to one of two possibilities. Firstly, it posits that the biological nature of parenthood leads to gendered distinctions at least within the nuclear family. However, this hypothesis is heavily contested and does not explain many of the cultural differences between men and women (Collier and Yanagisako 1987). Secondly, if a society practices cross-cousin marriage, it makes sense to distinguish those cousins who are marriageable to those who are not. In societies where the language only reckons the gender of the referent relative, then it is necessary to also separate marriage partners for male or female egos. However, within each of the possible explanations for kinship distinction for gender, there are numerous counterexamples. It seems unlikely that a universal explanation for distinguishing kin by gender will ever be established.

Cross-References

- [Manipulative Use of Kin Terminology](#)
- [Kin Recognition and Classification in Humans](#)
- [Kinship Distinctions According To Generation](#)

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Kinship Estimator

- [Kin Recognition and Classification in Humans](#)

Kinship Index

- [Kin Recognition and Classification in Humans](#)

Kinship Is Central to Self-Concept

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Synonyms

[Self-concept and family](#); [Self-concept determined by relatives](#)

Definition

Self-concept refers to an individual's collection of thoughts and beliefs about themselves. It is comprised of multiple mental templates that the individual uses to organize information about the world. These templates include information about the groups one is a member of and central to these are the bonds of kinship.

Introduction

Self-concept describes an individual's collection of thoughts and beliefs about themselves. These self-perceptions involve empirical evaluations, identification with groups and social roles, judgments of personal attributes and abilities, and a concept of the ideal self. Self-concept begins development during infancy and is considerably influenced by an individual's interactions with significant others throughout the lifetime. As such, a person's self-concept continues to develop and change as one ages. This is done through the formation of cognitive structures representing the individual's organization of past experiences. Although often flawed, these *schemas* are mental templates that individuals use to organize and store information about the world (Bartlett 1932). Central to the development of the self-concept are self-schemas, the mental templates that individuals use to process and organize self-relevant information (Markus 1977). These self-schemas not only help individuals to organize past behavior but drive and predict future behavior. For example, the likelihood of a college student consuming alcohol is affected by whether the student's own self-schema incorporates a self-concept in which the students would consider himself a consumer of alcohol (Lee et al. 2018). This suggests that future behavior is less situationally dependent and relies more on that internal template of the self.

Social Identity Theory

As humans are inherently social creatures, we develop self-schemas that reflect both our personal identities and our social identities (Horowitz 2012). Our self-concept is significantly impacted by the groups that we perceive ourselves to be a part of. According to social identity theory, our self-identity is largely defined by membership in various overlapping groups (Tajfel and Turner 1979). These social groups, or social categorizations, help to assist individuals in ordering the social world, providing a sense of self-

identification in social terms and creating boundaries, guidelines, and scripts for functioning in the social world. Thus factors such as one's political or religious affiliation, favorite sports team, or weekly book club influence the way in which one conceptualizes the self. Through these affiliations, persons not only think of themselves as a member of these groups but also think of themselves as the type of person that is consistent with these groups. In other words, individuals integrate their affiliated social groups into their self-schemas.

Kinship

Kinship can be defined as the network of relationships that an individual possesses and regards as close, important, personally influential, supportive, and permanent. Kin are "our people" (Faubion 1996). Anthropologists have formulated various theories of kinship, each theory based upon the purpose of the kin relation. Group viability and reproduction, standards for interactions between groups, and standards for the passing on of wealth have all been suggested as the purpose or role of kin relations. Although each of these theories may have merit, kinship also provides individuals with key social groups (e.g., national heritage, religious faith, or political party identification) around which one may anchor their self-concept. An individual often aligns with a variety of social groups, both biological in origin (e.g., ethnicity) and sociocultural (e.g., footballers). Kinship is unique among social groups in that an individual cannot easily change their affiliation, as one may with sociocultural social groups. Additionally, kinship is the foundation of one's other biological social groups. That is to say, one's biologically based social groups, such as ethnicity, exist as a product of one's kinship.

One long-standing question in evolutionary theory was answered through the development of inclusive fitness theory (Hamilton 1964). Why will humans often assist kin, even at great personal expense? This behavior may be explained by inclusive fitness theory, which suggests that

personal evolutionary success is not determined by the number of personal offspring one has, but by the number of common alleles in the population. Thus, cooperative behavior that may cause one to incur social costs is considered beneficial in that it promotes an investment in the well-being and reproductive success of one's kin. For this to occur, an individual must be able to accurately identify kin. Key indicators of kinship are phenotypic similarity and behavioral similarity. Indeed, we find that humans use facial similarity as a cue to increase prosocial behavior and to decrease sexual attraction, lending empirical support to Hamilton's inclusive fitness theory (DeBruine et al. 2008).

Self-concept is generally a stable characteristic, yet it may fluctuate based on social experiences (DeBettignies and Goldstein 2019). It is for this very reason that kinship is central to the self-concept, as kinship serves as an unfluctuating anchor. Twin and adoption studies demonstrate that genes rather than upbringing cause people to engage in social associations (Rushton 2009). Demonstrating these attributes as fundamental to the self-concept, not only do humans respond favorably to the positive actions of others but also to the phenotypic similarity of others (Parsons et al. 2016). Thus, kinship provides a stable template for the self-concept. Additionally, kinship provides this crucial information at a young age, when individuals are developing their own mental templates of the self. Children use these kinship cues during childhood to not only discern their relationship with others but also develop their own identity (Antfolk et al. 2014). These cues have been found to predict behavior later in life and thoughts about the self. Taken together, this suggests that kinship both prescribes our personal behavior and is central to the development of the self.

Modern Family

Traditionally the family has been regarded as the most basic form of kin. Changes in society over time have led to an increase in households that are not comprised of a traditional nuclear family. This

has challenged the traditional view that kin is defined by shared biogenetic substance (Hayden 1995). Both the traditional Darwinian conceptualization of kinship and cultural conceptualizations of kinship are integrated as the primary support system of individuals. As such, both assist with survival as well as psychological well-being (Shapiro 2014). This expanded notion of kinship develops at an early age. For example, infants are able to grasp social relationships. When observing a common adult comforting multiple babies, infants are able to recognize that there is a common association among babies who were comforted by the same adult, inferring that infants are capable of understanding some level of kinship in others (Spokes and Spelke 2017). This also suggests that when infants are forming their own early self-schemas, they are integrating those around them into those mental templates. Thus, from the moment one is born, one is establishing notions of kinship and using those notions to establish their own identity.

Conclusion

In organizing information about our world, humans develop distinct schemas. Some are about our own unique personality, and others center on our social identity. Kinship is central to both and, as such, central to our own self-concept. Kinship has evolved to provide individuals with unique information about themselves and those that would be beneficial for them to assist. In providing individuals with information about the self, humans are able to develop the self-concept. For it is these very interactions with those that we consider as our kin, biological or chosen, that allow us to see ourselves as both unique and yet simultaneously part of a larger collective.

Cross-References

- [Evolution of Self](#)
- [Self-Concept](#)
- [Universal Aspects of Kinship](#)

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Kinship Psychology Manipulations

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Synonyms

Fictive kinship; Inclusive fitness; Induced altruism; Kin selection; Kin-cue manipulation

Definition

Kinship psychology manipulations in the context of suicide terrorism is a form of deception that effectively tricks individuals into acting altruistically towards non-kin as a result of the activation of kinship cues that over evolutionary history allowed individuals to decipher kin from non-kin.

Introduction

One evolutionary theory of suicide terrorism proposes that terrorist organizations manipulate followers into embarking on suicide missions in part by activating evolved kinship psychology. This theory of suicide terrorism is informed by kin selection (Smith 1964), a form of altruism based on Hamilton's rule ($rb > c$) where r is the degree of genetic relatedness, b is the reproductive benefits to related kin, and c is the cost to the agent (Hamilton 1963). Therefore, an organism should act altruistically if the reproductive benefits to its kin outweigh the costs of the act to the organism, thus increasing the organism's inclusive fitness. Kin selection demonstrates how traits that harm individual organisms can be maintained by natural selection (Liddle et al. 2011). Kinship psychology manipulation is a form of deception that effectively trick individuals into behaving altruistically despite the behavior not serving the reproductive interests of the actor.

Theory and Evidence for Kinship Psychology Manipulations and Suicide Terrorism

Kin recognition is a critical component of kin altruism. An organism must have the ability to calculate the degree of genetic relatedness (r) to a conspecific in order to determine whether to act altruistically; therefore, cues of genetic kinship must have evolved. According to Qirko (2004, 2009), hypothesized cues of genetic kinship among humans include physical proximity during development, shared phenotypic traits, and the use of kinship terminology (Alexander 1990; Fletcher and Michener 1987; Hamilton 1964; Sherman 1985). Applying these concepts to both suicide terrorism and lifetime vows of celibacy, Qirko predicted that institutions that solicit individuals for these practices would tend to (1) seek out recruits who are younger in age; (2) separate recruits from genetic kin; (3) endorse the use of kin referents between members; (4) encourage the use of markers that mimic shared phenotypes (e.g., uniforms or other identifiers); and (5) facilitate close proximity among the in-group members (2004, 2009, 2013). In fact, each of these predictions is supported by empirical data. Terror organization often recruit suicide attackers before they reach their twenties, recruits are separated from their genetic kin and trained in isolation from their natal families and communities, kinship terms are commonly used between members of these groups (Qirko 2004, 2009, 2013). The hypothesis that suicide terrorists are motivated by kinship psychology manipulations is distinct from hypotheses that posit that suicide attack produces tangible benefits to kin such as monetary gain (e.g., Blackwell 2006) (see Suicide as Kin-Directed Altruism).

Conclusion

Kinship psychology manipulations act on evolved mechanisms that over evolutionary time assisted organisms in distinguishing kin from non-kin. Some evolutionary theorists contend that kinship psychology manipulation is the primary vehicle

through which terror organizations convince adherents to forego their own reproduction and self-sacrifice for the benefit of the group. However, as Blackwell (2006) noted, many would-be suicide attackers pledge allegiance to the terrorist institution prior to the use of kinship cue manipulation.

Cross-References

- [Sexual Access Manipulation](#)
- [Suicide as Kin-Directed Altruism](#)
- [Suicide Terrorism](#)

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Kinship Universals

- [Universal Aspects of Kinship](#)

Kissing

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Synonyms

French kissing; Mouth-to-mouth kissing; Romantic kissing

Definition

Research that examines the possible evolutionary function of kissing on the open lips/mouth as a custom during courtship or within a long-term pair bond.

Introduction

Romantic kissing is a custom documented in historical texts (Nyrop 1901), including several types of kiss described in the Kama Sutra of Vatsyayana approximately between the first and sixth century (Burton 1883/2006). Comparative perspectives also reveal analogies between romantic kissing and other coordinated courtship rituals in non-human species. This research, relatively new at the time of writing, examines the extent to which this form of romantic expression has a functional basis, given that it is observed widely across nations, tends to precede other forms of intimacy, and may influence attraction to one's romantic partner. This entry reviews the early accumulation of knowledge in this area and the evolutionary theory that underpins it.

Romantic Kissing: Theory and Data

Romantic kissing, according to the wider anthropological record, is observed in less than 50% of cultures in contrast to nonromantic kissing such as that between parent and offspring and romantic

passion which is regarded as a human universal (see Jankowiak et al. 2015 and other work by this author for discussion). Observational studies suggest that romantic kissing is accompanied by a rightward bias in head orientation (Güntürkün 2003) and, in a study of married couples in Bangladesh, is more likely to be initiated by men than women (Karim et al. 2017). Focusing specifically on mouth-to-mouth kissing (i.e., “French kissing”), Wlodarski and Dunbar (2013a) theorized that romantic kissing may function as (i) a mate assessment tool to assess putative cues to quality via close contact, similar to species that use gustatory and olfactory cues to regulate courtship behavior (Clowney et al. 2015), (ii) to gauge and maintain the quality of a long-term pair-bond, and (iii) to facilitate arousal prior to sexual activity, in light of the sensitivity of the lips and the potential importance of this precopulatory behavior for physical arousal and/or psychological pleasure (see e.g., Basson 2000 for discussion of the female sexual response cycle). None of these hypotheses were intended by the authors to be mutually exclusive to one another.

Using the mate assessment hypothesis as a framework, kissing may incur costs to health (e.g., Posse et al. 2017) which the “behavioral immune system” would be sensitive to (see related entries on ► “Disease Avoidance”). Thus, as a pathogen avoidance mechanism, cues to “quality” in a mate could be valuable to gather during courtship or in short-term relationship contexts more generally. Consistent with this first hypothesis, being perceived as a “good kisser” can enhance desirability as a short-term relationship partner (Wlodarski and Dunbar 2014) and kissing is considered more important, and more likely to influence attraction for women than men (i.e., the “choosier” sex), for choosier individuals of higher “market value” (i.e., attractive individuals) and in contexts where choosing a less healthy mate would be particularly costly (i.e., short-term relationships, Wlodarski and Dunbar 2013a). Of note, although some of these differences are small when examining the accompanying effect sizes, small differences in romantic behaviors and appreciation of intimate acts may still be of theoretical relevance when studying

relationship dynamics, if they have cumulative effects over time on how members of a couple communicate, navigate, respond, and interpret issues related to intimacy within their relationship. For example, even if differences in preference in this area are subtle, it may still translate into one member of the dyad communicating their satisfaction or dissatisfaction first. Secondly, when people are asked about what constitutes a “good kiss,” gustatory and olfactory cues are considered particularly important and women place greater importance on kissing in the very initial stages of a relationship when their progesterone levels are also low, a proxy for conditions related to high fertility (Wlodarski and Dunbar 2013b). Collectively, mate assessment may be an important function of mouth-to-mouth kissing.

Following the pair-bonding hypothesis, kissing would be expected to enhance relationship quality if it is a display of romantic attachment. Consistent with this line of reasoning, frequent kissing and satisfaction with kissing frequency in relationships is correlated with relationship quality, while having a partner who is a good kisser predicts relationship quality at twice the size of the relationship between sexual satisfaction and relationship quality (Wlodarski and Dunbar 2013b). Work to date thus suggests that kissing may be important both as a courtship custom and in maintaining stable long-term pair bonds. While this research does not support the role of kissing in facilitating arousal in specific relationship contexts (e.g., preferred at times preceding sex than at other times, Wlodarski and Dunbar 2013a), further work using more direct measures of arousal (i.e., compared to self-report measures) may shed light on the role of kissing in arousal and generate further discussion within sexology. Indeed, the components of a “good kiss” appear to reflect (i) sensory factors, (ii) technique, and (iii) arousal/contact (Wlodarski and Dunbar 2013b). Thus, kissing may be a fruitful topic for researchers of behavioral synchrony and also for sexual and health scientists, in light of the potential importance of arousal for lowering disgust sensitivity (see

related entries on ► [“Disgust”](#), and ► [“Pathogen Avoidance”](#)). Finally, as proxies for social complexity are thought to predict kissing prevalence in remote societies (Jankowiak et al. 2015) further cross-cultural work can shed light on the factors involved in the development of this romantic behavior in some cultures but not others.

Conclusions

Romantic mouth-to-mouth kissing is not a human universal; however, it is prevalent cross-nationally and is important during courtship and in long-term pair bonds. Further work in this area is of utility for sexual science and empirical work on well-being in romantic relationships, as are comparisons across cultures and species and in research on the developmental basis of intimacy and romantic customs.

Cross-References

- [Disease Avoidance](#)
- [Disease Avoidance Hypothesis](#)
- [Human Courting](#)
- [Long-Term Mating](#)
- [Pair-Bonding](#)
- [Romantic Attachment](#)
- [Sexual Behavior](#)

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Knowledge Enrichment

- [Evolution of Teaching](#)

Kohlberg's Rationalistic Theory

- [Theory of Moral Development](#)
-

K-SF-42

- [K-Factor \(Figueredo\)](#)

L

Laceration

- [Scarification](#)

- [Evolution of Live Birth in Mammals \(140 MYA\)](#)
- [Gathering Returns When Nursing Infants](#)

Lachrymation

- [Crying](#)

Lactose Intolerance

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Lack Clutch Size

- [Optimal Clutch Size](#)

Definition

Lactose intolerance commonly, but not universally, is defined as the inability to digest lactose (found in milk and other dairy products) that often results in symptoms which cause individuals to experience discomfort or pain (Deng et al. [2015](#); Amiri et al. [2015](#); Sahi [1978](#); Misselwitz et al. [2013](#)).

Lack of Respect

- [Derogation of Rivals](#)

Lacrimation

- [Crying](#)

Introduction

Milk and other dairy products are often fed to newborn children during infancy to provide nutrients that assist in growth and development. However, not all humans have the ability to digest milk, specifically a component in milk and dairy products called lactose, without experiencing pain or discomfort. The inability to digest lactose is due to the individual lacking the enzyme lactase that

Lactation

- [Breast Feeding](#)
- [Breast Milk Composition](#)

is found in the intestine that allows lactose to be broken down (Deng et al. 2015; Amiri et al. 2015). Some common symptoms of lactose intolerance are flatus, abdominal pain, bloating, stomach rumbling, diarrhea, nausea, and constipation, among others (Deng et al. 2015; Szilagyi 2015a; Mattar et al. 2012; Misselwitz et al. 2013). Milk provides a variety of nutrients that the lactose-intolerant individual has difficulty consuming. As discussed below, the inability to digest lactose may have been particularly problematic during times of famine and migration through regions in Europe and Africa. Milk and other dairy products were a quick and easy way to gain nutrients; however, for those who could not digest lactose, it meant those individuals were at a nutritional disadvantage (Szilagyi 2015b; Misselwitz et al. 2013). In today's era lactose intolerance is less of a disadvantage or threat to an individual's health because the availability of food and alternative options to milk allow individuals to get the nutrients they require, making the consumption of milk and dairy less important. In addition, the diagnosis and treatment of being lactose intolerant is commonplace and widespread throughout the world, allowing those individuals to understand the issue early on and to more easily manage being lactose intolerant.

Diagnosis

Lactose intolerance is usually diagnosed by one of three ways, the most common is by conducting a hydrogen breath test that measures the amount of hydrogen that is produced in the small intestine from lactose not being digested (Heaney 2013). The second method for testing lactose intolerance is via biopsy of the duodenum of the intestine where the level of lactose can be measured and the rate of lactose digestion can be evaluated to determine if lactose is being broken down (Mattar et al. 2012). The other method to diagnose lactose intolerance is through genetic testing via blood analysis. Each method has drawbacks, and none is considered a gold standard in and

of itself. However, the hydrogen breath test is the most common for its efficiency and easy application (Deng et al. 2015; Amiri et al. 2015; Mattar et al. 2012).

Treatment

Lactose intolerance is usually treated by initially reducing all consumption of dairy/milk products, especially those that contain lactose. This initial reduction of lactose is meant to improve symptoms of the disorder so the individual can begin to feel better (Amiri et al. 2015; Misselwitz et al. 2013). Depending on the individual and the severity of symptoms, dairy and milk products are slowly reintroduced into the individual's diet (Szilagyi 2015a; Amiri et al. 2015). If the individual experiences severe symptoms, non-lactose-based dairy and milk products can be used to help regain calcium in the diet without the risk of symptom flare-up. Complete reduction of dairy- and milk-based foods is not ideal nor is it recommended by clinicians. Rather, lactose intolerance is treated with a careful regime of dairy and milk products that can be easily and safely digested to allow the individual to maintain a healthy diet without having to experience pain or discomfort. In fact, even those with lactose intolerance can safely consume around 12–18 g of dairy/milk containing lactose without experiencing any symptoms (Mattar et al. 2012; Misselwitz et al. 2013; Heaney 2013). However, consumption of more than 18 g of dairy/milk containing lactose within a single sitting can produce painful or uncomfortable symptoms (Mattar et al. 2012).

Biological Details

Lactose is a disaccharide consisting of galactose bound to glucose and is often found within dairy products like milk, cheese, and yogurt (Heaney 2013; Deng et al. 2015; Misselwitz et al. 2013). Within milk is lactase, and it is broken down by lactase, an enzyme, within the small intestine

(Heaney 2013; Deng et al. 2015). However, our production of lactase begins to decline as we age and begin to wean off of feeding in infancy, with production of lactase decreasing to about 10% of its original quantity around 5–10 years of age (Deng et al. 2015; Szilagyi 2015a; Amiri et al. 2015; Sahi 1978; Misselwitz et al. 2013). This reduction in lactase affects roughly two-thirds to three-quarters of the world's adult population (Deng et al. 2015; Amiri et al. 2015). For some individuals the production of lactase reduces to even lower levels, causing an intolerance to any food that has lactose within it (Deng et al. 2015). When lactose is not broken down properly in the bowel, the small intestine begins to break down and ferment the lactose, and the result is the production of gases, primarily hydrogen, carbon dioxide, and methane (Deng et al. 2015; Misselwitz et al. 2013; Heaney 2013). This production of gas can lead to a variety of symptoms including abdominal pain, bloating, stomach rumbling, diarrhea, nausea, constipation, loss of concentration, muscle and joint pain, mouth ulcers, and urinary difficulties (Deng et al. 2015; Szilagyi 2015b; Mattar et al. 2012; Misselwitz et al. 2013; Heaney 2013).

Lactose intolerance and its symptoms are influenced by several variables including the amount of lactose consumed, gut transit time, ingestion with other dietary components, small bowel bacterial growth, and also composition of the enteric microbiome (Deng et al. 2015; Szilagyi 2015a). However, the incidence of lactose intolerance is not equal across races and geographic regions in the world. Next, the history of lactose intolerance and its recent development will be highlighted.

History

Humans have had the ability to consume and digest milk as infants and children throughout history. However, previously in history as we have grown up, our ability to produce lactase to break down the lactose in milk has turned off as

we approached adulthood (Burger et al. 2007). It is speculated around 10,000–100,000 years ago, our ability to digest lactose in adulthood emerged (Szilagyi 2015b; Misselwitz et al. 2013; Burger et al. 2007). A possible reason why lactose digestion emerged around this time is because this is the point in human history when Northern Europeans and some regions of Africa and the Middle East began to use milk to deal with famine (Sahi 1978; Swagerty et al. 2003). Famine occurred due to harsh weather conditions such as long winters in Northern Europe and extreme heats with lack of rainfall in Africa and the Middle East to sustain farming (Szilagyi 2015b; Swagerty et al. 2003). As a result of the inability to farm in these regions, individuals began to start consuming milk to survive. However, many adults still did not have the ability to properly digest lactose and milk, allowing for natural selection to occur. Those individuals who were able to consume milk and survive famine lived, however, those who could not consume milk would have either succumb to famine or likely experienced extreme pain from consuming milk in order to survive (Swagerty et al. 2003; Burger et al. 2007). By Consuming dairy and milk in order to gain the necessary vitamins to survive, our bodies had to adapt and learn to digest lactose (Szilagyi 2015b; Misselwitz et al. 2013). However, not every race and culture underwent this adaptation, and as a result, some populations have a higher incidence of lactose intolerance than others.

American Indians and Asians have the highest rate of lactose intolerance, and up to 80% of Black, Arab, and Latino individuals experience lactose intolerance, whereas the lowest prevalence is detected in northwestern Europeans (Amiri et al. 2015; Deng et al. 2015; Sahi 1978; Misselwitz et al. 2013; Heaney 2013). This difference in racial categorization for those who can and cannot digest lactose provides circumstantial evidence for the proposed geographic and environmental hypothesis for the development of lactose intolerance and digestion (Szilagyi 2015a). Those races and geographic locations within the world that received adequate sunlight, weather

conditions to farm, and received their calcium intake through other food products did not need to consume milk and develop the ability to further digest lactose beyond infancy (Szilagyi 2015a; Misselwitz et al. 2013). As a result of these historical events, it has allowed certain racial groups and geographic regions to be able to digest lactose in milk and force other groups and regions to adapt without the consumption of milk.

Conclusion

Lactose intolerance affects thousands of individuals a year and understanding the mechanism and history of lactose intolerance is integral to understanding how our health and evolution adapts and functions. Our ability to drink milk and consume dairy products is not simple, even though from birth we have evolved to consume breast milk to provide the necessary nutrition to survive as infants. In this chapter, human history, bodily functions and other human attributes have been shown to be more complex than previously thought. It is almost with certainty that seemingly normal activities of the body will reveal different functions and complex histories that question our understanding of what we have developed over millions of years. Lactose intolerance provides us with a small insight into how our body has evolved and why the consumption of milk and dairy is not beneficial to humans as we age because of our adaptation throughout history and should be used as a ideal and straightforward example of how evolutionary adaption for humans can be small but significantly impact how we live.

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Lakatosian Philosophy of Science

► Nomological Networks of Evidence

Lamarckism

► Jean-Baptiste Chevalier de Lamarck

Landscape Aesthetics

- Landscape Preferences
- Savanna Hypothesis, The

Landscape Preferences

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Synonyms

Evolutionary aesthetics; Images of nature; Landscape aesthetics

Definition

The tendency for humans to favor certain landscapes more than others and the theories developed to explain those tendencies.

Introduction

Humans, like all living things, live within an environment. Although that environment contains a wealth of biological and physical elements, ranging from the very small such as radiation and microorganisms to the very large such as geological formations and climate, humans have evolved to perceive only a fraction of these features. Arguably the most highly salient environmental element for humans is other humans, and people spend a disproportionate amount of their time attending to other people. However people also take notice of other things in their surroundings as well. The general term for all these other nonhuman, perceptible things is the *landscape*. People are aware of the physical elements of their landscape such as whether the shape of the land is flat or mountainous, the presence or absence of human-made structures such as buildings, fences, or bridges, and whether or not various forms of water such as rivers, lakes, ponds, or the sea are present. Humans also pay attention to the living elements of landscape, including the presence and density of different types of

vegetation such as trees, grass, or bushes, as well as the presence (or potential presence) and type of domestic or wild animals. Even transitory elements of the landscape are noticed, such as lighting, cloud cover, and weather conditions. At one point in human history, having a keen awareness of all these landscape elements would have been essential since the presence of particular plants or animals, sheltering qualities of a landform and access to potable water would have been fundamental to daily survival. However for the vast majority of humans alive today survival is almost totally a function of human-to-human interactions. As a consequence, most landscape elements, particularly those considered *natural*, are frequently viewed as mere backdrops to life, niceties rather than necessities.

Or so, most people think. In fact, landscapes still represent important dimensions of survival, even if the role they play are more subtle these days. And despite the fact that the presence or absence of particular vegetation or water forms no longer directly impact daily survival, people appear to not just be aware of these various landscape elements, they appear to prefer some more than others. The question is why? It is easy to understand why a person might prefer a particular type of vegetation if their life depended upon being able to travel across or harvest that vegetation for food, but what difference would it make to a person working and living in a city who makes their living as a banker? Even more intriguing is that in general, not only do humans seem to prefer some kinds of landscapes more than others but that these preferences appear to cluster around a relatively few types of landscapes and landscape elements. The most obvious way this convergence in preference is apparent is in the striking similarity in human-made parklands around the globe.

Human Landscape Preferences

One approach to understanding human landscape preference has been through the analysis of historic, worldwide patterns of “pleasure” garden design, i.e., gardens designed for aesthetic rather than utilitarian purposes. The idea being that

when unconstrained by budget or necessity, people would create landscapes that approached some optimal level of preference. One would assume that cultural tastes and traditions would vary considerably, but surprisingly large gardens and estates worldwide reveal some remarkable parallels in the use and organization of certain landscape elements (e.g., Jellicoe and Jellicoe 1975). Particularly in large gardens and estates, where aesthetic preferences could most easily be expressed, park-like settings of short grass and scattered trees have consistently emerged. The English landscape tradition, as typified in the work of “Capability” Brown, is one of the most familiar examples, where random placement of trees gathered in clumps are dispersed throughout an open field. Others have investigated landscapes in Western art (Appleton 1975) and calendars (Dutton 2003) and found a similar preponderance of scenes showing expanses of short grasses punctuated by scattered clumps of trees. In general appearance, all of these created landscapes converge toward a common landscape form, what is biologically called a savanna.

Savannas are ecosystems characterized by the trees sufficiently widely spaced so that the canopy does not close. The open canopy allows sufficient light to reach the ground to support an unbroken herbaceous layer consisting primarily of grasses, grading into either open plain or woodland. Savannas occur worldwide, with the largest occurring in subtropical or tropical regions. Two factors common to all savanna environments are rainfall variations from year to year, and dry season wildfires. Interestingly, recent evidence suggests that many indigenous peoples in both the Americas and Australia artificially created savanna through annual controlled burning (cf., Lentz 2000; Ward 2009).

Research by Falk and Balling (1982, 2010) has specifically shown a strong human preference for savanna-like environments. Additional support for these findings comes from studies that show strong preferences for landscapes containing open meadows surrounded by woods (Zube 1976), and forests are most strongly preferred whether there is little underbrush and an abundance of grass cover (Schroeder 1991).

However it is not just the general gestalt of savannas that appears to be preferred but also the shapes of major elements within them, including and specifically the trees. Orians (1980) demonstrated that horticulturists and landscape designers in Japan have tended to modify the phenotype of native tree-forms toward those found among trees existing in savanna environments. In a crosscultural study of tree preference (Oriens and Heerwagen 1992), subjects from three countries rated as most attractive those trees in which canopies were relatively dense and trunks bifurcate low to the ground. These characteristics of tree-form typify those found in the East African savanna. Sommer and Summit (1995) found consistent findings, with preference for large canopies and small trunks. A later study of tree species preference and context, Summit and Sommer (1999) found that the acacia-type tree-form, typical of the African savanna, was preferred over oak, conifer, palm, and eucalyptus.

In addition to savannah-like elements like short grass and scattered trees, research has consistently identified other specific natural features that increase the attractiveness of landscapes, in particular water elements. Many studies confirm that water is a highly preferred part of any natural scene, and it is not just the amount of water that is significant – clarity and freshness seem at least as important. Mountain lakes and rushing water, especially waterfalls, are extremely well-liked, while swampy areas or water covered with algae bloom receive low rating (Herzog 1985).

Sociocultural Perspectives on Landscape Preference

Like most human preferences, it can be argued that human landscape preferences is best understood as a social and cultural construction (John-Steiner and Mahn 1996); the passing on of aesthetic ideals and social conventions passed on from one generation to the next through human culture. This view of the world, which assumes that all human behaviors are the products of our culture and history, has a long history in the humanities and anthropology but has become

reinvigorated amongst psychologists with the rediscovery of the writings of Vygotsky (cf., John-Steiner and Mahn 1996). And there is certainly evidence to support this view.

According to Nassauer (1995), not only do cultures change the nature of landscapes through various practices such as agriculture or even hunting and gathering, but culture itself is embodied in landscapes. By this she means the humans are inseparably bound to the landscapes they inhabit through their cultures. Hence people from different cultural conventions and customs perceive landscapes in different ways, which directly affects what people notice, find interesting, and prefer about the landscape. People typically assume the prevailing norms of their social/cultural group, believing that a yard, a park, a field, or a forest should look a certain way without questioning the necessity of that appearance (Nassauer 1995). One need go no further for evidence of the cultural influence on landscape preference than the dramatic changes in attitudes toward *nature* and *wilderness* evidenced in modern society over the past 100+ years (e.g., Eisenberg 1998).

At a more fine-grained level, perhaps the most compelling evidence for the role of sociocultural factors in landscape preference is the critical role that familiarity plays. At least amongst adults, living within a landscape appears to result in heightened preference for that landscape (Balling and Falk 1982). For example, in a study of college students, Lyons (1983) found that preferences were highest for the most familiar biome. Subsequent, crosscultural studies reported similar findings, with high correlations between groups in their preference for varied landscapes, with familiarity accounting for much of the variance (Herzog et al. 2000). Herzog and colleagues replicated the earlier study by Kaplan and Herbert, but included a broader sample of settings and examined several subcultural groupings. Familiarity once again emerged as a significant predictor of preference and is consistent with our earlier thesis that preferences can be modified by experience and enculturation. Other seemingly socially and culturally influenced factors beyond familiarity also seem to contribute to preference. For

example, not just familiarity but experience and education (Balling and Falk 1982; Lyons 1983) can play a role in landscape preference. And beyond these findings, no study of people's affinity for different landscapes has ever found complete unanimity of preference. In other words, people do vary in their preferences and those variations almost certainly arise from personal experience as molded by social and cultural forces. However the consistent finding that children across cultures share similar preferences, independent of their cultural background (e.g., Falk and Balling 2010; Newell 1997), suggests that some aspect of landscape is likely innate.

An Evolutionary Psychology Perspective

The perspective that sees landscape preference as a by-product of human evolution has been advocated by a wide range of psychologists. According to this view, human preferences have developed because they have been crucial for human survival as individuals and as a species. These preferences do not appear to be random, in almost all cases these landscape features are exactly the ones which would have offered a good combination of safety and necessary resources to early humans. And particularly related to the seeming preference for savanna-like environments, preferences appear to converge on landscape features that figured prominently in the evolutionary history of human-like organisms in Africa some 1–4 million years ago – favored are places that could support a bipedal African primate's hunting and gathering and basic needs such as evidence of potable water and shelter and refuge from both predators and the elements.

The belief that human biology and behavior were significantly molded by the adaptations of humanity's early ancestors evolved in order to survive in African savanna-like environments were initially supported by a series of major hominid fossil discoveries in southern and eastern Africa during the early part of the twentieth century. The fossil evidence of the associated fauna and flora led anthropologists to the inference that the evolution of modern hominins was guided by

the significant warming events at the end of the Pliocene which resulted in significant changes in available habitats throughout Africa. The increase in aridity was thought to have propelled early hominins away from the comfort of tropical habitats, habitats still occupied by humanities closest primate relatives, into the more hostile habitat of the savanna. This view was challenged at the end of the twentieth century by subsequent research (cf., Foley 1996) which suggested that the landscape of human evolution may not have been exclusively savanna, but rather a mosaic of environments including grasslands, savanna, open and closed forests. However, new research and new analytic tools are once again tilting scientific thinking back toward a savanna hypothesis.

To get a better idea of the environments in which the human lineage evolved, scientists recently analyzed prehistoric soils associated with significant hominid fossil finds for clues about the likely vegetative pattern that existed at the time of fossilization (Cerling et al. 2011). By analyzing the ratio of carbon isotopes remaining in the soil of 1300 soil samples associated with hominin fossils, investigators were able to more reliably extrapolate as to the nature of the ancient vegetation that these ancient hominins once lived in. Researchers found that more than 70 % of the fossil sites were revealed to be savanna-like environments with less than 40 % tree cover. Less than 1 % of the ancient soil tested reflected sites where tree cover exceeded 70 %, which would have made the area a forest. While many scientists think East Africa was forested before 2 million years ago and savannas emerged only afterward, the findings of Cerling et al. (2011) suggest that during the development of bipedalism about 4 million years ago, that is, walking on two legs, savannas were present, even predominant. Thus, savannas appeared to be critical throughout the period of human evolution; seemingly wherever human ancestors were found, there is evidence those ancestors resided in open habitats similar to today's African savannas.

Based on the above evidence, it can be reasonably inferred that semiarid African savanna is likely the ancestral environment in which much of human evolution appears to have taken place.

An important choice for any mobile organism is selecting a good habitat to live in. Thus humans are argued to have a strong modern-day aesthetic preference for landscapes which mirror the attributes of what would be a good late Pliocene/early Pleistocene Afro-Eurasian savanna – a habitat characterized by both open and wooded areas, with trees with broad crowns and branches at a suitable height for climbing and taking foods, a habitat possessing readily accessible potable water and marked by features encouraging exploration such as the beginnings of a game track or a curving riverbed suggesting the possibility of game animals. This idea is not as far-fetched as some might assume. Humans, it seems are far from the only living thing to show distinct preferences for particular landscapes. In fact, species-specific habitat (landscape) preferences are the rule amongst animals of all kinds.

Most biologists would agree that habitat preferences are adaptive, since fitness is likely to be higher in a preferred habitat (Rausher 1984). Natural selection would maintain habitat preferences to the degree that they have a genetic basis, in fact the ability to distinguish and select among habitats is arguably one of the most evolutionary significant traits any organism can possess (Jaenike and Holt 1991; Rausher 1984). A wide variety of investigations have found evidence that vertebrate habitat preferences are at least in part, genetically determined (cf., Falk and Balling 2010). One early study showed that distinct, genetically determined, habitat preferences can exist even within races of a single mammalian species. More recently, research using biochemical markers was able to distinguish between the different alleles for at least one of the genes linked to habitat preference in two closely related species of toads. Previous studies have also identified the genes responsible for habitat preference in several insect species though even in insects there is evidence of learning (Segura et al. 2016). Hence a growing body of data supports the fact that a complex behaviors such as habitat preference can be at least partially genetically determined and that a wide range of organisms, including vertebrates of all kinds, possess these genetic traits.

Landscape Preference Factors

Following on the idea of an innate genetic predisposition toward landscapes, a variety of investigators have developed theoretical frameworks that attempt to dissect landscape preference into predictive variables. Particularly notable amongst these theorists are Jay Appleton (1975), Roger Ulrich (1977; 1983), and Stephen and Rachel Kaplan (1989). Among the earliest models was Appleton's prospect refuge theory. Appleton's initial work was based on an analysis of landscape painting (1975) which he found to consistently include similar landscape elements – depictions of low shrubs and clumps of trees divided by open spaces. He argued that these landscapes offer an attractive combination of *prospect* and *refuge*. Open spaces provide an opportunity for *prospect*, the ability to detect potential hazards – to see, whereas the low shrubs and clumps of trees provide *refuge*, places to hide and escape – to not be seen. Appleton suggested that humans have an affinity for settings that exhibit savanna-like characteristics, but he was careful not to suggest that there exists an optimum landscape preference since the idea of “optimum” implies that human needs are the same at all times. On the contrary, humans have varying requirements at different times, which effect how they interact with their environment. A more specific hypothesis of landscape preference stems from “prospect-refuge theory,” which predicts that within a given landscape preferred locations are found at interfaces between prospect-dominant and refuge-dominant areas. These vantage points combine unimpeded visual prospects with a ready opportunity for concealment and/or withdrawal to a safe refuge. Thus a treeless landscape is less visually attractive than a habitat containing isolated trees that can provide opportunities to hide or escape from potential predators.

Ulrich analyzed informational qualities of various settings and identified five significant variables: *focalcity*, the degree to which a scene contains a focal point or area that attracts the viewer's attention; *ground surface texture*, the perceived homogeneity or heterogeneity of the landscape; *depth*, the ability to see across

distances; *mystery*, the degree to which you can gain more information by proceeding further into the scene; and *complexity*, the degree to which a landscape is perceived to be rich and intricate. Ulrich built on earlier studies of visual preference which focused on complexity as the significant mediator of visual preference. These studies discovered an optimal range of preferred complexity in the visual field. In particular, results showed that visual preference was an inverted U-shaped function of increasing complexity. Stimuli judged to be of intermediate complexity were the most preferred, but for natural landscapes the effect was weak. Although Ulrich and other investigators found support for dimensions beyond complexity influencing landscape preference, Ulrich himself (1977) argued that the most powerful single variable was actually *mystery*. The presence of this factor heightened attractiveness irrespective of the ranges of the legibility variables. This model illuminated the importance of informational determinants but in order to create a more complete model, according to Ulrich the effects of color, water, and other ephemeral landscape elements such as clouds and sunsets should be added.

Like Ulrich, the Kaplans argued that the long-term survival of a highly knowledge dependent organism like hominins would need to depend upon acquiring and processing information about landscapes quickly and efficiently. According to the Kaplans (1989) people and their ancestors should have preferred settings that (1) make the acquisition of landscape information relatively easy and nonthreatening and (2) convey the notion that additional information can be acquired if the setting is explored. Thus, according to the Kaplans, understanding a landscape, which is the comprehension or making sense of the scene, should be predicted on information the needs of what he called *coherence*, landscape scenes where the elements are distinctive and easily identified, and *legibility*, the degree to which different landscape parts fit together, providing a sense of order and assisting in directing attention. While exploration needs should be predicated on a landscape's *complexity*, what a landscape offers in terms of the many different kinds of distinct elements present, and *mystery*, whether or not a new landscape

promises the opportunity for the viewer to go deeper into the landscape. These four dimensions, collectively known as *informational variables*, might refer to what is immediately perceptible, or might refer to what might be perceptible if one moved to another location. Although similar to Ulrich's model, the Kaplans' model has been the most widely used and cited. Considerable evidence over the years has found support for the relationship between each of the Kaplans' four informational variables and landscape preference (see review by Stamps 2004). However a recent meta-analysis of the Kaplan's model by Stamps (2004) failed to conclusively find a consistent relationship between landscape preference and any of the four factors.

Conclusion

Much of the research presented shares an underlying conceptual framework rooted in a Darwinian evolutionary view of landscape preference. Overall, the results reported here suggest there does appear to be strong evidence in support of the basic contention that humans possess some kind of genetically-based, innate landscape preference, particularly for savanna-like settings similar to those in which ancestral African hominins lived and evolved.

However, even if there is an innate basis to landscape preference, whether specific to key features of savanna-like environments like short grass and scattered trees with broad crowns and low branches or generalized as suggested by Appleton's (1975) ideas of prospect and refuge or based on psychological constructs such as Ulrich's (1977) five factors theory or Kaplan and Kaplan's (1989) coherence, legibility, mystery, and complexity theory, it is highly likely that there is more to the story than merely genes. To begin with, recent breakthroughs in genetics and biochemistry suggest that something as behaviorally complex as a visual preference for a landscape must involve multiple genetic loci, suites of epigenetic phenomenon, as well as behavioral and cultural elements (cf., Jablonka and Lamb 2014). Accordingly, the role of psychological factors such as perceived coherence, legibility,

mystery, and complexity as well as cultural sensitivity to the specific affordances of the visual environment are as likely contributors to landscape preference as are genetic loci connected to attraction to water and trees capable of being climbed.

However there is also strong support for the idea that cultural factors as well life experiences also can and do modify landscape preferences. Individual preference generally reflects both macroscale enculturation processes as well as more microscale factors such as social pressure and personal history. Collectively, the research suggests that landscape preference is a complex amalgam of factors, with innate preferences forming a foundation which is then overlain by both socio-cultural and personal experience factors.

In conclusion, the research summarized here provides additional support for the view that human behavior represents an ongoing and inherently complex interaction between human evolutionary history, human social and cultural history, and personal lived experience. Collectively these forces act upon individuals to shape a wide array of both observable and invisible traits and behaviors ranging everywhere from physical features, such as human posture, brain size, and diet, to complex behaviors and preferences, such as aesthetic preference for landscapes. Although human behavior is nearly always individually idiosyncratic and typically culturally diverse, there are times when human evolutionary history significantly restricts the extent of that idiosyncrasy and diversity. Human landscape preference appears to be one of those times.

Cross-References

- [Access to Resources](#)
- [Adaptation and Natural Selection](#)
- [Adaptations: Product of Evolution](#)
- [Australopithecus Group](#)
- [Bipedal Locomotion](#)
- [Cultural Differences](#)
- [Environment of Evolutionary Adaptedness](#)
- [Evolution of Adaptations](#)
- [Grasslands](#)
- [Habitat Change](#)

- *Homo erectus*
- *Homo habilis*
- Imprinting
- Landscape Preferences: Climate and Weather
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- Lev Vygotsky
- Savanna Hypothesis and Landscape Preferences, The
- Savanna Hypothesis, The
- Social Cognition
- Social Learning
- Social Learning and Social Cognition
- Study of Instinct, The
- Unconscious, The

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Landscape Preferences: Climate and Weather

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Introduction

The study of human behavior across diverse environments is certainly not new – this tradition dates back centuries – however, recent research has shed new light on the evolutionary forces that are associated with particular landscape preferences. Collectively, the research summarized here supports the idea that elements of the landscape, including climate and weather, interact with individual psychological processes.

Landscapes, Climate, and Weather

Variation in landscape, climate, and weather all have an impact on the organization of psychological phenomenon. Some cities, towns, and regions may have a geography that is more accommodating for some personalities than for others. Oishi et al. (2015) reported in a multi-study paper that when people wanted to socialize they preferred the ocean over mountains, but overall, mountain-lovers were more introverted than ocean-lovers. The introversion-extroversion disparity was further assessed using photographs of mountains and oceans. Part of the difference can be explained by extroverts' perception that they would have to put forth greater effort to enjoy themselves in the mountains. Extroverts believe that they will have an *easier time* having fun at the ocean.

An analysis of non-students showed that residents of mountain regions in the U.S. were more introverted than those living in flat states. Also, in a clever experimental test, the authors sent participants out to flat open areas or secluded wooded areas. The environment did not cause changes in

personality scores, but introverts were happier in the secluded area than in the flat terrain.

The human tendency to classify individuals as either “ingroup” or “outgroup” can be demonstrated along a continuum. At one end, *individualists* are motivated more by the boundaries between ingroups and outgroups compared to *collectivists* at the other end of the spectrum. The climato-economic theory (Van de Vlier and Yang 2014; Van de Vlier 2011) proposes that collectivism may be an adaptive solution to the existential problem that atmospheric climate can cause human death. They suggest that financial resources enable people to cope with the harsh climate demands of winter and summers. In a study that included measures of ingroup love and outgroup hate across 85 nations, they found that more demanding climates are correlated with stronger collectivism in relatively poor countries but weaker collectivism in relatively rich countries.

These data suggest that economic prosperity influences the impact of atmospheric climate on collectivist culture in that monetary resources enable people to cope with climatic demands of winters and summers. Climate and environmental pressures give rise to solutions that lead to geographical variation in cultural value systems. Collectivism is promoted in countries with demanding climates and economic difficulties. The analysis indicates that the driving force behind the process is ingroup love more so than outgroup hate. The authors argue further that the climato-economic explanation does a better job of accounting for the variance in ingroup-outgroup bias compared to theories of parasitic disease burden.

There is evidence that physical topography also plays a role in building culture and the development of value systems. In frontier regions with formidable terrain levels of individualism are higher than less menacing and more cultivated regions (Conway et al. 2014). Over time, this type of demanding environmental niche likely attracted tenacious individuals with personality traits conducive to surviving in such harsh habitats (i.e., independent and individualistic people).

Other research has concentrated on the effect of ecological stressors (climate stress, pathogen stress, and frontier topography) on vertical and horizontal governmental restriction (Conway et al. 2014). Vertical restriction describes a condition in which select individuals impose asymmetrical laws on others, while horizontal restriction involves laws that restrict most members of a society equally. Across three studies, the authors validated the measurement of restrictions and concluded that ecological stress creates opposing pressures that simultaneously push freedom in two different directions. Ecological stressors tend to inspire more vertically restrictive societies and less horizontally restrictive societies.

Weather and Climate on the African Savanna

There is considerable evidence that humans generally prefer savanna-like landscapes like those found in our ancestral past (Orians 1986). The Environment of Evolutionary Adaptedness (EEA) is the ancestral environment to which a species is adapted, or the set of selection pressures that shaped an adaptation. A central premise of evolutionary science is that forces in our distant past helped make us who we are today. The EEA refers to a group of selection pressures occurring during an adaptation's period of evolution responsible for producing the adaptation (Tooby and Cosmides 1992). A selection pressure can be any factor in a population that impacts reproductive success. Physical, social, and intrapersonal pressures from our ancestral past help to shape our current human design because all animals have heritable variations that are selectively favored or disfavored in accordance with reproductive success (Buss 1995). Each adaptation has its own EEA, or set of adaptive problems, that shaped it over evolutionary time.

According to the savanna hypothesis (Orians 1980, 1986) current habitat biases were shaped by selection pressures in our ancestral past. The theory argues that natural selection favored preferences, motivations and decision rules that attract

us to resource rich environments over resource poor environments. Two perspectives are helpful in addressing evolved responses to landscapes, one spatial and the other temporal. The spatial frame of reference points out three stages of habitat selection: *selection*, *information gathering*, and *exploitation* (Orians and Heerwagen 1992). The temporal dimension concerns short-term and long-term habitat variation in critical survival factors (e.g., weather patterns and seasonal transitions).

The second layer of the savanna hypothesis involves decision making over different time frames (Orians and Heerwagen 1992). Light availability and weather patterns are two time-related factors that impact choices. Long shadows at the end of the day may elicit the desire to set up campsite instead of continuing to move through the environment in darkness. Likewise, daily weather issues can force one to seek shelter quickly. Dark clouds, winds, thunder, and lightning are cues that may initiate the decision-making process.

Along with daily fluctuations, humans are sensitive to environmental changes on a seasonal scale. In general, natural selection favors traits that maximize benefits and minimize costs. People will show preferences for long term signs of robust prosperity because the algorithms that make habitat related decisions were shaped over time in response to specific positive and negative features of the environment. Indicators of harvest, such as fruit, budding flowers, and verdure, are favored over bare trees and impoverished fields.

A number of studies exploring landscape preferences have found support for the savanna hypothesis. For example, participants from Australia, Argentina, and the United States show a preference for savanna-like trees (Orians and Heerwagen 1992). In hospitals, patients who viewed trees outside the window recovered more quickly (Ulrich 1984), and bringing flowers increases optimism and improves the rate of recovery (Watson and Burlingame 1960). When placed in uncertain and stressful situations, individuals who viewed pictures of nature scenery showed less physiological distress (Ulrich 1986).

Research looking at over 900,000 data points found that children who grew up with the lowest levels of green space had up to 55% higher risk of developing a psychiatric disorder (Engemann et al. 2019). Studies in biophilic design demonstrate that people living and working in spaces with vegetation compared to those without vegetation show improved performance on mental tasks, more positive moods, greater ability to refocus attention, stress reduction, and diminished perceptions of pain in health-care settings (Kellert et al. 2008).

Additional support for the savanna hypothesis comes from the body of evidence showing that humans often prefer natural environments over built environments (Kaplan and Kaplan 1982). Using data from 30 studies, Kaplan (1992) summarized the results of participant ratings of photographed scenes of Western Australia, Egypt, Korea, British Columbia, and the United States. Across these varied geographic regions, participants preferred natural environments over built environments. Other data suggest that the addition of trees and vegetation increases positive evaluations of built environments, thus demonstrating the transformative power of foliage (Ulrich 1983).

One of the earliest studies to test the idea that people have a generalized bias toward savanna-like environments hypothesized that “innate predispositions” for the savanna should be more likely to be revealed in children than in adults, given that adults have had greater opportunity to experience non-savanna ecosystems (Balling and Falk 1982). In a study that included six age groups (8, 11, 15, 18, 35, and 70 or over), subjects were asked to rate photos from five natural biomes on scales that measured how much they would like to “live in” and “visit” each one. The researchers found that the youngest group (8-year-old children) preferred the savanna over the other habitats on both scales. The deciduous forest, coniferous forest, and savanna were equally liked among ages 15–70, with ratings for the desert and rainforest coming in lower at all ages. The study also implies that people have an aversion to drought conditions and arid landscapes. Photos depicting greener savanna were rated

higher than similar savanna photos taken during the dry season. Finally, all age groups gave the lowest ratings to the desert environment (Balling and Falk 1982).

Causal Mechanisms

Variation in the distribution of landscape preferences can be explained, in part, by three mechanisms (ecological factors, selective migration, and social influence).

Ecological Factors. Features like the prevalence of disease and urban crowding can affect the psychological processes that give rise to preferences. Regional differences in disease prevalence are correlated with several important cross-cultural differences (Murray and Schaller 2010, 2014). According to this view, ecological variation in the prevalence of infectious diseases gives rise to geographic differences in psychological traits. Thus, pathogens are mechanisms that contribute to regional differences in human behavior. Over evolutionary time, the risk of exposure to parasitic diseases has shaped the way humans interact with the physical and social environments. Murray and Schaller (2014) discuss evidence that disease-causing pathogens contribute to geographic variation in sexual behavior, sociosexual attitudes, value systems, conformity, personality, family relations, ethnocentrism, moral judgments, and political ideology.

Several studies have attempted to rate the prevalence of disease-causing pathogens across countries and regions. Gangestad and Buss (1993) used epidemiological atlases to create a single measure indicating the historical prevalence of pathogens in 29 countries. Employing a similar procedure, Murray and Schaller (2014) calculated an index of the historical prevalence of infectious diseases within 230 geopolitical regions around the world.

Selective Migration. People who choose to migrate to a new region or country are often psychologically different from their counterparts who choose to stay behind. There is mounting evidence that individual personality differences are associated with preferences and decisions

about relocating (Jokela 2009, 2014). For example, high openness and low agreeableness personality scores were associated with between-state and within-state migration in the United States, while high extraversion increased within state migration, but not between states.

Social Influence. People who live in different countries, different regions, or even different neighborhoods often follow different customs and norms which, in turn, influence attitudes and behaviors. In Montana, for example, local norms encourage owning a gun and being emotionally reserved, two factors which appear to be partly responsible for the high suicide rate among Montanans (Rentfrow and Jokela 2016).

Conclusion

Research on landscape preferences has focused on how features of the environment (e.g., climate and weather) contribute to the organization of psychological phenomena and human activity. The savanna hypothesis articulates some of the evolutionary forces that helped to shaped human landscape preferences in ancestral environments. In sum, there is a great deal of variation in landscape preferences and at least three causal mechanisms that help to explain this variation. There is still a great deal to learn about the meaningful outcomes of these preferences in the long run (Bennett et al. 2018).

Cross-References

- [Ancestral Threats Versus Modern Threats](#)
- [Gordon Orians](#)
- [Natural Versus Artificial Environments](#)
- [Savanna Hypothesis and Landscape Preferences, The](#)

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Language

- [Communication and Developmental Milestones](#)
- [Social Learning and Social Cognition](#)

Language Acquisition

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Synonyms

[First language acquisition](#); [Language development](#); [Primary language acquisition](#)

Definition

Process of acquiring the sound system, structures, rules, and symbolic representations of a language and their meanings.

Introduction

How typically developing children universally acquire their primary language(s) with ease before any or without formal schooling is the foundation of research in language acquisition. There have been two general strands of research: nativist and nonnativist. The nativist approach proposes that an innate module gives humans a priori knowledge about the nature of language, specifically syntax, and results in the universal acquisition of language among all typically developing children (Chomsky 1957, 1975). The second strand assumes that there is no innate mechanism specifically dedicated to language, but innate social and cognitive abilities that have evolved for other purposes. There has been no clear winner as research from other disciplines examining infant and child abilities, parent/adult–child interaction, neurobiology have forced researchers to think and rethink, about whether a language faculty dedicated to language evolved, or have general biological structures and cognitive abilities been exapted for languages to be universally acquired.

What Evolved?

Nativism

Chomsky (1957, 1975) perhaps raised *the* question of language acquisition research. How is it that a child is able to correctly generalize from a finite sample of sentences heard from an unfiltered context the rules of a language, and then apply those rules in such a way that they can correctly produce an infinite number of sentences? In other words, how does one account for the *Poverty of Stimulus*, which necessitates that children acquire and know more about language structure than could possibly be gained from the “noisy” ambient language they are exposed to and with little correction? Chomsky proposed that humans have evolved a species-specific innate capacity, a language faculty, encoded in our biology. This faculty is Universal Grammar (UG) and accounts for the uniformly successful acquisition of grammar of typically developing children despite the Poverty of Stimulus. So, knowledge about one’s language(s) will be triggered through exposure to the ambient language and subsequently produced. As the search for universals among the world’s 7000 languages continued, the arguments made in support of a universal grammar became less and less probable, and the technical theories of syntax have had to change over time (Dabrowski 2016; Horgan 2016). Furthermore, while there has been some promising support for a language faculty, researchers have yet to find a plausible genetic or neurobiological substrate (Lenneberg 1967; Lai et al. 2001).

Behaviorism

Prior to nativism, in his book *Verbal Behavior*, Skinner (1957) suggested that we learn language by making and reinforcing associations through the process of conditioning. In this view, language is learned piecemeal using the same innate mechanisms for learning other behaviors and gaining knowledge. New or previously heard instances of language are generalized and inducted into our existing language repertoires. The behaviorist view was considered insufficient as it was believed that young children experience very little

one-on-one language teaching interactions and much learning occurs without direct instruction. It seemed implausible that children had the ability to cut through the “noise” of the ambient language to make associations and generalizations. However, overtime, research in frequency effects and priming suggests that a Skinnerian view of language acquisition may be more reasonable than previously considered.

Frequency Effects

Frequent exposure to language elements strengthens associations. There is a growing body of research demonstrating that infants are highly sensitive to the frequency of events in their experiences, including the features of a language, and can scaffold the understanding, learning, and usage of the elements of a language with minimal instruction (Hasher and Chromiak 1977; Attneave 1953; Shapiro 1969; Underwood 1971). In fact, frequency effects are ubiquitous in first language acquisition (Ambridge et al. 2015). Chang (2006) synthesized studies showing how frequency effects can account for the acquisition of constructions from the natural environment affect and adjust a learner’s usage overtime due to exposure to different linguistic forms and generalize a word’s syntactic roles and associate it to other words in the same category (Boyland 2001; Bybee and Hopper 2001; Hallan 2001). Effects have been found to occur in children as young as 8-months old who can (1) segment words from fluent speech, (2) store and access information about the sound patterns of words that occur frequently in fluent speech, and 3) retain words even when there is no contextual support from the surrounding environment (Juszyk and Hohne 1997). Two-year-old children can learn word meanings across situations and contexts and get better at this skill as they get older (4 years old) (Akhtar 1999). Though not directly addressed, but with frequency, children are able to learn words simply by overhearing (Oshima-Takane 1988; Oshima-Takane et al. 1996; Oshima-Takane 1999; Akhtar et al. 2001; Akhtar 2005; Floor and Akhtar 2006; Skolnick and Fernald 2003). All things being equal, frequency effects in

children have been observed at the word level (nouns, adjectives, verbs, function words) (Ambridge et al. 2015 p. 244), with higher frequency words learned before infrequent words and are associated with better comprehension and lower rates of error (Schwartz and Terrell 1983). Frequency effects have also been suggested for word strings such as routine four word sequences (i.e., a cup of tea, a cup of milk) in child-directed speech (Bannard and Matthews 2008). However, effects at the level of sentence construction are still unclear.

Priming

While frequency effects are related to the facilitative effects of exposure for making associations, priming refers to the facilitative effects of an encounter with a stimulus on subsequent processing of the same or a related stimulus. The effects may be a change in speed, bias, or accuracy of the processing of a stimulus. Each time we attend to a stimulus (i.e., a picture, a face, a word, phrase), a lasting representation is created that aids in later identification of the same or similar stimulus. Priming can occur as quickly as one encounter, has long lasting effects, and has been applied to language acquisition as well. Church and Fisher (1998) compared long-term auditory priming between English-speaking 2- and 3-year-olds and college students and found that all of the age groups performed similarly. Each participant was more likely to identify words that were heard previously regardless of the obvious discrepancies in previous lexical knowledge. Similar studies showed the same priming effects in preschoolers when stimuli were novel non-English words (i.e., yeeg, lell) (Fisher et al. 2001).

Priming may have a central role in the acquisition of syntactic structure as well, though experiments with young children have been limited. Some studies have used the passive form as the target construction as it is rare in children's spontaneous speech (Huttenlocher et al. 2002). One of the earliest studies with 4–5-year-olds (Whitehurst et al. 1974) indicated that children who heard passive constructions were more likely to produce and comprehend the passive form than children who did not. Syntactic priming effects of

transitive and dative constructions have also been observed (Huttenlocher et al. 2004; Shimpi 2007). Non-lexical priming studies are significant because input to young children is often heard without being repeated. Such studies demonstrate, in experimental conditions, that young children are sensitive to and may be conditioned to syntactic form just through *hearing*, and that form may also be reflected in their subsequent speech.

Social Constructivism

While nativism gained momentum, the influence of pragmatic-based philosophers (Wittgenstein 1953; Astin 1960), emphasizing meaning and the role of language acquisition to achieve social ends, did not disappear. The Vygotskian perspective on language as a cultural tool and the fundamental role of social and interpersonal interaction in development advanced among social constructivists (Vygotsky 1978). Among the more notable, Bruner (1957, 1960) rejected the nativist view and proposed that meaningful language acquisition occurs in the context of parent/adult–child interaction with the support of a Language Acquisition Support System (LASS). His research dramatically shifted the field by videotaping the context of naturally occurring language, as opposed to nativists who examined well-formed idealized sentences to uncover the underlying rules, or Universal grammar, that allow children to generate grammatical sentences. Such research indicated that infants are endowed with far more abilities than previously thought that facilitate communicative development (Gopnik 2009). For social constructivists, what is *a priori* are abilities that can be deployed to achieve social ends, including a disposition to attend to and discriminate the sound system, grammatical constraints, facial expressions, and gestures that communicate and intentions. Bruner highlighted the significance of intersubjectivity, or the ability to share and relate experiences with another. In understanding the intentions and meaning of the other, children also learn to appropriately use language (Bruner 1983).

Social constructivists continued to lay the groundwork for research on the capabilities of neonates and prelinguistic infants, which demonstrates that they are born with abilities to interact

and attune to interlocutors. They also continued to promote the study of adult–child dyads and the role of adults or experts in facilitating social interaction, through which valuable cultural knowledge, including language, is learned.

Discriminating Abilities

Infants have been found to make socially related distinctions and preferences. Hours after birth, infants distinguish between rotten and pleasurable odors (Steiner 1979), and 6-day-olds know the smell of their mother's milk (MacFarlane 1975). The capacity to sense touch begins very early in human ontogeny, as early as a preterm in the third month (Barlow and Mollon 1982; Ellis and Ellingson 1972). With regard to the sense of hearing, studies show that 6-month-olds discriminate features of tempo, rhythm, melody, and key in the structures of both song and instrumental sound (Trehub et al. 1993). Human speech is also salient to a neonate among an array of auditory stimuli in its environment (Cairns and Butterfield 1975; Eisenberg 1975). They have been found to be able to discriminate and show a preference between direct and averted gaze, as well as face-like and nonface-like (Maurer and Barrera 1981; Maurer 1985; Farroni 2002, 2004). They differentiate between human and nonhuman sounds (Eisenberg 1975) and between prosodically different languages (Mehler and Christophe 1995). Moreover, infants are able to decompose the stream of speech in their environment when they are as young as 4-days-old (Bijeljac-Babic et al. 1991; Kuhl 2004; Ramus 2002; Saffran 2001; Saffran et al. 1996; Saffran and Thiessen 2003; Vihman 2014). Thus, humans are born with remarkable abilities to sense and make distinctions of their social world, including linguistic input.

Facial Expressions

Newborns seem to also be born with an inventory of distinctive expressions and vocalizations that can be interpreted as communicative and can lead to interpersonal communication. Facial gestalts resembling facial expressions relating to laughter and crying are observed as early as 32.5 weeks in the womb (Reissland et al. 2011). Facial expressions of interest, joy, disgust, surprise, and distress

have also been observed in young infants (Izard 1978). Trevarthen (1979) argued that the posturing of the head during many forms of facial expression seems to be systematically related to particular facial expressions and suggested that all the patterns of body expression are present in infants at birth, and the gesticulations of infants (i.e., hand-waving, index-finger pointing, and fingertip-clasping movements near the face when they are vocalizing) are clearly not imitations of adult partners. Though not linguistic per se, facial expressions can encourage social interaction with interlocutors, creating spaces to be exposed to linguistic input, and to learn to associate expressions with meaning.

Prelinguistic Gestures

Though it is unclear if the phylogentic or ontogenetic origins of language are vocal or gestural (Hirsh-Pasek and Golinkoff 1996; Karmiloff and Karmiloff-Smith 2001; McNeill 2000; Tomasello 2008) research demonstrates a relationship between prelinguistic vocalizations and gestures, and language development. For example, hand banging is a predictor of the onset of canonical babbling (Bates and Dick 2002). Gesture not only provides a way for children to refer to objects (i.e., pointing), but on average, children gesture an object 3 months before they produce the word for that object (Iverson and Goldin-Meadow 2005). Two-word combinations are also preceded by a gesture-plus-word combination (i.e., point at bird while saying nap; point at bird while saying bird). Others have shown that different types of gestures predict different types of word production (Kuvac-Kraljevic et al. 2013). Beat and iconic gestures appear when utterances become longer than two words (Mayberry and Nicoladis 2000). Therefore, some researchers propose that language and gesture are part of a single integrated system (Goldin-Meadow and Wagner Alibali 2013).

Prelinguistic Vocalizations

Babbling was once considered to simply be a reflection of an infant's motor development and sensitivity to and use of the sounds of their native language. Now prelinguistic vocalizations are considered to be a critical part of *social gating*

and may have a significant role in language acquisition (Jusczyk and Hohne 1997; Kuhl 2007; Oller et al. 2010). The consonants used in babbling (CVCV), for example, are good predictors of the consonants used by infants in their first words (Vihman et al. 1985). Babbling is also a predictor of the appearance of pointing and a child's first words (McGillion et al. 2017).

Prelinguistic vocalizations or utterances are also deployed effectively by infants to achieve various communicative ends including requesting and obtaining food and getting the name of objects, to regulate the behavior of others, to maintain contact with others, to express their feelings, and to play with language (Halliday 1975). Infants also modify their vocalizations to be more speech-like or more mature when they receive feedback from their interlocutors (Warlaumont et al. 2014; Albert et al. 2017). In response, mothers prolong the interactions and increase the use of simplified speech, which often contains information about objects in the infant's social context. Mothers also respond more often when infant vocalizations are directed at objects than those that are undirected.

Infant-Directed Speech (IDS)

Infants also have a clear preference for IDS over adult-directed speech (ADS) (Cooper et al. 1997; Cooper and Aslin 1990; Werker and McLeod 1989; Pegg et al. 1992; Soderstrom 2007). Exaggerated, simplified, and adjusted speech directed at infants has long been assumed to facilitate language learning, as it enhances distinctions between the various aspects of their native language (Kemler Nelson et al. 1989). IDS allows infants to easily identify and categorize vowels and consonants (Cristia 2011; McMurray et al. 2013). Infants have been found to remember and learn words better with IDS when compared to ADS (Singh et al. 2009; Ma et al. 2011). IDS exposure is also directly related to vocabulary growth (Weisleder and Fernald 2013).

Though the characteristics or prosodic features may vary from culture to culture, IDS is a species-typical trait (Ferguson 1978; Bryant and Barrett 2007; Falk 2009). Russian, American, Swedish, Mandarin, Hakka, Japanese, Thai, French,

German, Hebrew, Quiche, Lebanese speaking women use IDS with infants (Pye 1986; Fernald et al. 1989; Kuhl et al. 1997; Kitamura et al. 2002; Fernald and Morikawa 1993; Liu et al. 2003; Farran et al. 2017). Men also modify and heighten the pitch of their speech (Broesch and Bryant 2017; Rondal 1980; Fernald et al. 1989; Gergely et al. 2017). Deaf speakers make modifications as well when they sign to infants (Erting et al. 1990; Masataka 1992; Nonaka 2004).

Though IDS may be species-typical, and "may be phylogenetically widespread and evolutionarily ancient" (See Heyes 2016 for discussion, p. 284), it is not a species-specific trait. IDS is also directed toward nonhumans, and the preference for its characteristics is also exhibited among nonhuman animals (Gergely et al. 2017; McConnell 1991). Thus, some have argued that IDS, and other adult and infant abilities that facilitate learning (i.e., gaze, motionese, imitation, etc.) reflects a *natural pedagogy* or predisposition of experts to *ostensibly manifest* their knowledge to novices to ensure the transmission of cultural knowledge, including language (Csibra and Gergely 2006; Csibra and Gergely 2009). This predisposition was selected for in hominid evolution when tool-making practices emerged and confronted a learner with cognitively opaque behaviors to acquire. Heyes (2016), however, argues that such behaviors were adapted not for teaching or learning, but for the promotion of social bonding or to promote attention to other conspecifics. Regardless, both views hold that such aspects of social interaction are not specifically for language acquisition, though research clearly suggests that they can be facilitative in the process.

Contingency

In addition to IDS, caregivers may use gaze, eye contact, eyebrow raising, and pointing as social cues to index relevant information, which infants recognize as signals that the caregiver has communicative intention (Brugger et al. 2007; Csibra 2010). From birth, we are already participating in and anticipating dialogic practices in multiple ways. When adults use both verbal and deictic communicative signals, they assume that they

refer to the same thing. If there is a discrepancy, for example, in a condition when the pointing does not index anything, infants notice and expect that something should be in the direction of the pointed area (Gliga and Csibra 2009). Trevarthen (1979), who observed that infants move their mouth, hands, and eyes in a turn-taking format with an adult, claimed that humans are born with a foundation for interpersonal communication. Bateson (1979) similarly looked at newborns 49–105 days old and also noticed mothers and infants “in a pattern of more or less alternating, non-overlapping vocalization, the mother speaking brief sentences and the infant responding with coos and murmurs, together producing a brief joint performance similar to conversation” (p. 65). Bateson coined this collaboration *protoconversation*. Jaffe et al. (2001) also showed that 4-month-old infants are highly proficient in vocal turn-taking. If interlocutor’s actions are not contingent to an infant’s behavior or vocalization, infants show sensitivity to the lack of contingency with a loss of positive affect and attention (Murray and Trevarthen 1985).

Thus, decades of social constructivists have shown that human beings are born with a remarkable sensitivity to stimuli in the social world, an ability to discriminate and parse the social input, an inherent expectation and use for communicative signals, and an ability to appreciate the communicative significance of social cues, facial expressions, and gestures, crucial to achieving and maintaining social interactions.

Functionalism

From social pragmatists and social constructivists, a functional or usage-based perspective of language acquisition emerged, one that would also suggest that structure is not innate but emerges from interaction and use. For proponents of this view, what evolved, what is universal is not an innate language faculty, but social cognitive skills, again *not* dedicated to or specifically for language. Tomasello (1999, 2003), for example, focused on two cognitive skills. The first skill is the ability to discern the goals and intentions of their interlocutors through joint attention (Tomasello and Farrar 1986). It involves the

ability to share and follow the attention of other persons, and to actively direct the attention of others by pointing, showing, and using non-linguistic gestures. In doing so, children learn the use and intentions of speakers and formulate scripts and routines of how to use linguistic conventions to achieve social ends. For example, pointing produces joint attentional frameworks with interlocutors, in which infants have been observed to use pointing for declarative, imperative, and interrogative motives (Bates 1979; Carpenter et al. 1998; Begus et al. 2014). The second skill, pattern finding, includes the ability to perform statistically based distributional analyses on various kinds of perceptual and behavioral sequences and to form categories of similar objects and events (Tomasello 2003 citing Gomez and Gerken 1999; Marcus et al. 1999; Rakison and Oakes 2003; Saffran et al. 1996). As children try to comprehend and acquire the language in their social environment to achieve their social goals, intention reading allows them to theorize the function and meaning of an utterance, word, or sentence, while pattern finding gives them the ability to isolate and extract parts of the language they hear and allows them to see commonalities in use and function across different utterances. These two universal sociocognitive abilities allow children to construct the grammar, meaning, and function of the language(s) being used around them to achieve social ends, along with other social abilities mentioned earlier.

Socioemotional Approach

For nonnativists, the picture that emerges, thus far, is that human beings have evolved social and cognitive abilities that facilitate attention to social agents, social bonding, and interaction, creating spaces and social contexts in which cultural learning, including language, can occur (i.e., conditioning, frequency effects, priming, pattern-finding, joint attention, etc.). A socioemotional approach proposes a perspective on language acquisition based on evolutionary biology, neurobiology, and complexity theory. Language is viewed as a cultural artifact that emerges as a complex adaptive system (Prigogine and Stengers 1984; Waldrop 1992). The ubiquity of primary

language acquisition is the product of an innate drive to seek out, attune to, and affiliate with conspecifics – an interactional instinct or a social instinct (Lee et al. 2009; Everett 2012; Joaquin and Schumann 2013; Joaquin 2013). This instinct ensures that the language, formed and shaped through interaction, is passed down to succeeding generations. However, the ontogenesis of language behavior (i.e., its acquisition) does not occur without its evolved biology, which support attentional and motivational processes that entrain children on the behavior of conspecifics, or without its evolved cultural practices for socialization (Rogoff 2003, Rogoff et al. Rogoff et al. 2007; Schieffelin 1990).

Evidence for the instinct is found in neonates' and infants' behavior that manifest an underlying motivation to engage in interactional activity. Infants show agency in the initiation of interactional activity. They are not passive participants or recipients of information in interaction. They actively initiate social engagement through the use of inborn abilities (cooing, vocalizations, gestures, smiling, etc.). For example, infants 3–54-hours-old initiate interaction by deploying a previously imitated gesture (Nagy 2006; Nagy and Molnar 2004). Turn-taking interactions are often initiated by infants who also anticipate the end of their interlocutor's turn resulting in high levels of latched turns (Gratier et al. 2015). Infants can also initiate learning. An infant can choose which object they would like information about by pointing. If pointing is followed by information provided by the adult regarding that object, learning is more likely to occur in contrast to objects that the infant did not point or show interest to (Begus et al. 2014). In interaction, infant utterances are longer in duration and have shorter response latencies if the infant initiated the conversation, in comparison to those initiated by the adult (Ko et al. 2015).

Infants also communicate pleasure and distress when desired interaction occurs or fails. This is observed in still-face studies in which a mother is instructed to display an expressionless, "still-face" in front of their child (Tronick et al. 1979; Brazelton and Cramer 1990). For example, when the child sees his mother, he typically "greet" his

mother with a smile. The mother responds with a still-face and he becomes still and then warily looks away. He then looks toward his mother again and finally he withdraws from the interaction. In another study (Murray and Trevarthen 1985), the infant showed signs of distress, such as grimacing, increased handling of clothes, touching the face, sucking the fingers, and frowning within a few seconds of seeing his mother's "still-face." Efforts to communicate or reinstate interaction were also intensified at first, mouthing and tonguing postures were maintained and accompanied by active gesturing. Eventually, the infant withdrew and averted his gaze downward from the mother's face. Thus, infants take into account the visible emotional stances of their interlocutor and use that understanding to deploy their next action.

Moreover, infants demonstrate a bias for interaction with conspecifics. They make a distinction between human and nonhuman acts and they prefer animate entities to inanimate ones. One and two-month-olds respond to physical objects (i.e., a dangling toy) differently than to a person (Trevarthen 1974). Infants look at, listen to, or touch objects. They also seek and interact with physical objects as sources of interest and as potentially graspable, chewable, and kickable, while human beings are perceived as social and are communicated with through expressive movements that are distinct from those with objects. Similarly, other researchers showed that 2-month-olds smile, vocalize, and alternate their gazes with an adult, but if presented with an object that moves and sounds contingently, infants will engage intense arm activity while staring at the object (Legerstee et al. 1987). Neonatal imitation also may be specific to people, such that inanimate objects that attempt to elicit imitative responses from infants fail (Legerstee 1991).

In addition, infants understand the interactional import of communicative and social cues (e.g., gaze, pitch changes) and more generally are attuned to adults' responses and actions (see Lee et al. 2011; Joaquin 2013 for a review).

Collectively, these behaviors are manifestations of an interactional instinct, and are motivated by biological processes. Endogenous

opiates and neuropeptides (e.g., oxytocin, vasopressin, and dopamine) make interaction with caregivers inherently rewarding and serves as a hardwired motivational mechanism (Depue and Morrone-Strupinsky 2005; Thompson et al. 2004; Popik and Van Ree 1992; Blass and Shah 1994). Neuropeptides are also a part of a system that appraises and marks interactions and the contexts in which they occur as pleasurable or not. Thus, as the child grows, the rewarding aspects of the attachment bond become part of the child's memory, which leads to the approach and development of affiliative bonds with caregivers and ensures cultural learning, socialization, and language acquisition through domain general cognitive abilities (Mates and Joaquin 2013). A similar biology guides the behaviors of caregivers, who through IDS, serve to facilitate and increase affiliation and attachment between the infant and caregiver (Storey et al. 2000; Weismann et al. 2012).

Socialization of language use, or pragmatics, may also be subserved, in part by the prefrontal cortex (PFC), known to be associated with monitoring, learning, and memory of the reward value of reinforcers, and the evaluation of punishers (Schumann 1999; Kringelbach 2005a, 2005b). Therefore, as it is involved in the evaluation of reward, it is important for decision-making (Rolls 1998). Its connections to the amygdala and cingulate cortex also involve the PFC in emotional processing, particularly of face and voice expressions (verbal and nonverbal emotional cues) as it receives inputs from the auditory and visual areas (Baird et al. 2006; Hornak et al. 1996; Mah et al. 2004). Furthermore, it is also linked to an ability to infer the likely thoughts or intentions, beliefs, and desires of others (Heatherington et al. 2006; Kelley et al. 2002). As these brain regions subserve such social and cognitive abilities, they have also evolved to subserve language pragmatics, which a child learns as they are enculturated into society. Indeed, there are many anthropological, sociological, and linguistic accounts of how children are socialized to use language. And, indeed, persons with damage to the PFC or frontotemporal dementia, a neurodegenerative disease affecting the PFC, demonstrate social

and pragmatic anomalies (Brickner 1936; Mates et al. 2010; Joaquin 2010a, 2010b).

Conclusion

Language acquisition is the process in which humans acquire and subsequently produce their primary language(s) for social means. It involves acquiring the sound system, structures, rules, and symbolic representations of a language, and then applying, producing, and combining those aspects to suit one's objectives in social contexts. The issue in language acquisition is: What has evolved for children to come to know so much about language if the input they are exposed to is limited, full of imperfections, and is often not accompanied with correction? There are two evolutionary stories. An economical view proposes that human beings have evolved a language-specific faculty in our biology, which accounts for the ubiquity of language acquisition by all typically developing children. However, since its proposal, the language module has not been biologically substantiated and it is still up for debate. What has been substantiated is a vast array of domain general abilities that behaviorist, social constructivist, functionalist, and socioemotional researchers have suggested are significant for cultural learning and language acquisition. Discriminating abilities, prelinguistic behaviors, frequency effects, priming, pattern finding, and joint attention combined with infant-directed speech and socialization practices, and a biologically driven motivation to attune to, affiliate, and bond with conspecifics make language input more accessible than previously thought. Any explanation of language acquisition must also consider these evolved abilities, processes, and biological structures.

Cross-References

- [Language Acquisition in Infants and Toddlers](#)
- [Language Development](#)
- [Learning Versus Imitation](#)
- [Pinker's \(1994\) The Language Instinct](#)

- Socialization Processes
- Spontaneous Language
- Steven Pinker and Language Development

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Language Acquisition Device

► Nativism

Language Acquisition in Infants and Toddlers

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Synonyms

Language development; Learning; Verbal achievement

Definition

How children approach the complex learning of language and speech development.

Introduction

Since birth, it is clear that eye contact is one of the main nonverbal forms of communication for a child and adult, but in these stages, the child begins to acquire the form of language. Language is part of what makes us human since humans are the only mammals to communicate with verbal languages of our own. Language can be best described as a symbolism of thought which allows us to vocalize what we are thinking and feeling. Children all learn at different rates, but much research has shown that the best acquisition comes from gradual interactions between other people and the environment.

Language Acquisition Milestones

Throughout the learning of language, parents/caregivers are their child's best tool for learning, and the way the adult interacts with the child will determine the path of language development they take. From birth to 3 months, the child's main form of communication is crying, whimpering, or screaming. Around 4–6 months of age, infants will have what sounds like their own form of language, such as babbling. Even though we most likely will not understand it, this is a crucial milestone as this is when an infant is learning the rules of language, by moving their lips, teeth, and tongue, they are learning that they can make sounds; it is like a game for them to play. From 7 to 12 months of age, infants make sounds as if they are making sense because they are trying out patterns of sounds in an order similar to mirroring their caregiver which is why reading to children at night is so encouraged. From 13 to 18 months, the infant at this stage will typically be saying one or two words, and what's even more significant is that they will recognize what those words mean (Golinkoff et al. 2015). Around 19 to 24 months, the infant understands much more words than they can speak yet they are learning new words every

single day and start putting short phrases together such as "Carry me." Although some children may take longer to pick up on words, this is simply a guideline for language development.

How Do Infants Learn Language?

Words said by parents/caregivers provide infants with minute artificial languages that embody specific aspects of our natural language arrangement. Once an infant has become accustomed to the sample of this language, a new sample, or a sample from a different language (if bilingual family), is presented to the infant, such as a new word or phrases. Subtle measures of surprise (e.g., the length of time when looking toward the new sounds that were made) are then used to assess whether the infant has learned the new word to be the same or something different. In this strategy, we can ask what the infant learned from the sample language (Christiansen et al. 2016). These repeated patterns are the learning mechanisms underlying the earliest stages of language acquisition for infants.

Language Acquisition and Language Evolution

In 2009, Chater and Christiansen posed an interesting discussion from an evolutionary perspective which highlights on the idea that when it comes to learning language, the child faces a problem of training. For an infant, the objective is to coordinate with others such as the parent or caregiver rather than to model the structure of the natural world. They argue that modeling from the parent is dramatically easier, yet then one is left to question when culture plays a role and how that cultural form arose through processes of cultural revolution. When the child aims to learn an aspect of human culture (rather than an aspect of the natural world), learning language is dramatically simplified – because culture (including language) is the product of past learning from previous generations almost like following in your parents' and grandparents' footsteps since most linguistic researchers will agree that overall language is very stable over the course of the years.

Conclusion

This discussion has aimed to demonstrate that when it comes to language acquisition for infants and toddlers, it is not something that happens without effort nor quickly; it is a gradual progression. Many processes and systems are constantly working together to create a logical pathway for children to learn how to speak that even though we think of it as second nature, it is a complex puzzle which is constantly developing throughout our lives.

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Attention](#)
- ▶ [Language](#)
- ▶ [Speech Volume](#)

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Language Acquisition in the Home

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Synonyms

[Emergent literacy](#); [Family literacy](#); [Home language acquisition](#); [Home literacy](#)

Definition

The process of children acquiring the knowledge and skills of comprehending and using language that takes place in the home context.

Introduction

The past 20 years of language and literacy research has made significant advancement in our understanding of the ways in which children acquire language and literacy skills in the home milieu. Children's early oral and written language knowledge and skills are seen as emergent and continuously developing with increasing importance being attributed to family literacy environments and the role of parental engagement and investment. This entry aims to map out the pathways in which children's language and literacy acquisition is ushered through interaction with various home-based elements.

A Developmental Perspective on Child Language and Literacy Acquisition at Home

The term “emergent literacy” refers to the precursors of formal reading, such as young children's concepts of print, awareness of sound-letter correlation, letter and word recognition, and writing, knowledge of functions of written language. This term, coined by Teale and Sulzby (1986), marked a significant turn of understanding child's language development and education from readiness-based to an experience-oriented perspective. From the early till mid-twentieth century, major work in child development theories and applications in education was dominated by a “maturationalist” perspective, deeming it appropriate for a child to wait until he/she intrinsically progresses to readiness in cognitive and motor skills to begin formal literacy instruction. To distinguish from the “reading readiness” approach, Teale and Sulzby (1986) argued in their foundational work, *Emergent Literacy: Writing and Reading*, that young children's literacy begins

to emerge and develop at very early age, long before what has been conventionally prescribed. More importantly, this perspective of early literacy acquisition recognizes the importance to literacy learning through learners' exposure to and engagement with print and reading and writing practices in real-life settings, especially their home environments.

In the first several years of a child's life, family tends to be a child's primary source of linguistic input. Young learners' exposure to oral and written language in the home context is crucial to their language acquisition in the initial stage. Parents interact orally with their children regularly and systematically throughout their developmental age span. Parents' vocabulary skills have been proven to be a key contributor to the quality of linguistic input that children receive. This holds true not only for monolingual families – Lewis et al.' (2016) study of Spanish-English bilingual children concluded that children's vocabulary skills in English (L2) is especially sensitive to the fluctuations in primary caregivers' language use (although children's early exposure to native language has been proven not detrimental to their second language acquisition). In addition, children's oral exchange with parents also plays a decisive role in cultivating their perception and comprehension of speech, and communicative competence.

The availability of paper-based and digital-mediated print materials is a key constituent of physical literacy environment at home. Children can acquire many things through interacting with books. Once children embark on an exploratory journey into books, they begin to construct fundamental rules of prints. Even young children engaging in pretend reading activities demonstrate their established concepts such as books are for reading, and static pictures are representations of things and events.

It is worth noting that the proliferation of modern technology has dramatically increased young children's access to digital media devices (e.g., iPads) at home in addition to traditional screen activities (e.g., TV, DVD). Although the appropriateness of digital tools in young children's lives has been fervently debated mainly out of concerns

with children's physical and social development in early years, research suggests that children inevitably become socialized into digital practices through their observations of and interaction with adults and peers who use digital tools. Even parents taking precautions to limit best they could their children's access to electronic media view digital tools as a source of positive learning experience for their children (Teichert 2017). Despite the fact that little existing research explored relationship between literacy outcomes and children's engagement in digital-mediated literacy activities, the new interactive model (e.g., long-distance communication, joint participation) and affordance of multiple modes of texts (aural, visual, linguistic, textual, etc.), which are characteristic of digital media, potentially affect young children's literacy development and outcomes.

Factors Affecting Home Language Acquisition Environment and Outcome

A rich body of qualitative studies have corroborated remarkable predictability of family biographical characteristics (e.g., socioeconomic status/SES, ethnicity, gender) and children's early literacy achievement and later academic development. The relationship between SES and monolingual children's vocabulary development has been robustly demonstrated in many studies; ethnicity has also been indicated to play a role in shaping children's initial reading readiness and later growth. Recent attention has been particularly paid to the correlations of SES with bilingual children's language and literacy competence. For example, Buac et al. (2014) reported that SES was among the factors that strongly predicted Spanish-English bilingual children's English vocabulary skills.

The quantitative strand of research complements the descriptive studies that reveal the ways in which different family variables shape qualitatively different language acquisition experiences at home. James Samuel Coleman's (1988) social theory of family capital maintains that the family as a dynamic entity actively transforms various forms of capital from the parent

generation into the educational attainment of their children. In general, Coleman distinguishes three major forms of capital in the family environment: physical or financial capital (material resources measured by family income and wealth), human capital (individual's level of educational attainment embodied in a person's knowledge, skills, and capabilities to act in certain social structures), and social capital (social resources embedded in the network of social relationships both within and between family and community).

Family capitals are indexical of various components of home environment. The affordance of both traditional paper-based and modern digitalized prints is often symbolic of family physical capital; the educational level and (bilingual) literacy proficiency of parents or primary caregivers and the quality and frequency of them involving in joint literacy activities with children are captured by human capitals. Finally, family social capital signifies the importance of extended family ties and community social and linguistic resources as important contributors to children's language and literacy abilities. Home environments, when properly and actively capitalized, can be transferred to young learners' positive oral and written language outcomes. Therefore, family capital theory serves as a useful tool to unpack the assorted elements that reflect the quality of a child's home environment, and how the intricate embroidery of home environment synchronizes children's early language and literacy development with the contemporary social and technological advancement.

Although family capitals reflect the quality of a child's home environment, not all family capitals are equally transferrable to children's literacy outcomes. Rather, it is the way the family utilizes its existing capitals and invests them in children's learning process that acts a central role. In a major study, Li (2007) explored in depth the home environment of four Chinese immigrant families in Canada (two academic families and two entrepreneurial families). She ascribed academic families' success in cultivating children's English learning to parents' ability to make more educated choices (derived from parents' human

capital), including investing their limited financial capital in materials beneficial to children's learning and building social networks in the English-speaking communities (social capital). Parents from the two entrepreneurial families, despite of their better-off financial conditions, were incapable of mobilizing various forms of family capitals to meeting their children's immediate language needs. Thus, the accumulation of family physical/financial capital is not the determinant of the quality of family learning environments; Li concluded parental human capital is central for the families to transfer other forms of family capital into their children's language learning.

The Role of Parental Involvement in Language Acquisition at Home

While literacy is an amalgam of cognitive and linguistic skills, transferable from one context to another, it is also a social practice (Li 2001; Street 1995). This social practice perspective recognizes literacy as culturally situated and socially coconstructed; and it varies from context to context. Thus, everything a child learns about literacy is shaped by their experience about its functions and values demonstrated by the competent members at home.

Early literacy acquisition recognizes social support systems of learning, especially the role of scaffolding, direct instruction, and modeling that parents provide to facilitate children's participating in home-based reading and writing activities. Yet, specific associations exist between different types of home literacy activities and the development of specific emergent literacy skills. Sénéchal and LeFevre (2002) identified both informal and formal literacy experiences that children are exposed to at home. Informal literacy activities (e.g., parent-child shared book-reading) focus on the message contained in the print rather than the print per se.

Parent-child joint book-reading has been extensively researched as a prototype of white, middle-class home literacy practices. Parental scaffolding (e.g., parents expanding on the

meaning of the story, answering children's questions relating to language/story) creates a developmentally sensitive context with potentially rich source of information and opportunities for children to develop language knowledge and skills. Despite of the consented benefit of parent-child shared reading in children's emergent literacy development, storybook exposure has only been found to contribute to oral language skills (i.e., receptive vocabulary, listening comprehension, and phonological awareness). Rather, it is parent involvement in teaching children about reading and writing knowledge that indicates a more positive relationship with the development of written language skills. Formal instruction draws children's attention particularly to the structural features of the prints, reinforcing knowledge regarding the concepts of prints, alphabetical knowledge, word spelling, etc.

The literacy as social practice approach also validates a wide array of ways in which literacy is taught and learned among low SES and language minority families that fall outside the mainstream purview. While parent-child shared book-reading with young children is an iconic literacy practice in mainstream families, it is foreign to many cultures that value oral storytelling and other forms of literacies (Mui and Anderson 2008). Young children from nonmainstream families may develop literacy through engagement in home-based religious practices, structured play, and use of texts with functional purposes (recipes, notes, etc.) (Li 2001). In many of these families, in addition to parents, other members such as siblings may assume parents' role in home literacy activities. In her study with Bangladesh-origin families in London, Gregory (2001) presented the synergistic model among siblings where older children assume the teaching role to present information to the younger children in various ways while likely enhancing and reinforcing their own literacy in the same time. Existing research also identified the bidirectional flow of literacy knowledge where language minority children play the expert role to assist their parents with second language comprehension and use. This sociocultural approach to emergent literacy maintains that children from

nonmainstream homes, despite of their relatively low reading and writing achievement records in schools, are "*learners and do learn* about the ways in which written language functions to the degree to which they experience it" at home (Purcell-gates 1996, p. 427, italics in original text).

Finally, parents' modeling of literacy activities, although without directly engaging children in the use of reading or writing, facilitates children's acquisition of literacy knowledge by demonstrating the use of written language in different domains of family life. Children continuously gain implicit understanding of the social functions of literacy while observing their caregivers reading books and magazines, using dictionaries, jotting down shopping list, composing and sending emails or text messages, watching Youtube videos and playing video games, etc. Putting altogether, literacy as social practice reveals how forms of family capital are mediated into children's literacy development through active engaging and coconstructing written language knowledge with children in real-life settings across culturally and linguistically diverse households.

Conclusion

Language acquisition at home offers a distinctive perspective of children's language development outside formal instructional settings such as classrooms. The emergence of young children's oral and written language knowledge and abilities at home is a sociocultural process closely woven into the tapestry of physical and social home environment. The existing work in language and literacy research and education has jointly painted the mural in myriad ways in which children acquire language(s) across linguistically and culturally diverse home milieus.

Cross-References

- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Development](#)

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Language Acquisition Outside the Home

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Synonyms

[Language development in formal and informal educational contexts](#)

Definition

Processes by which first and/or additional languages are developed through interaction with language users and resources beyond the immediate family.

Introduction

First language acquisition studies typically observe parent-child interactions longitudinally in order to identify patterns of language development. Studies of language acquisition outside the home may focus on the role of formal education or of social interaction with peers either in face-to-face contexts or increasingly in online environments.

Views of Acquisition

In the second half of the last century, the two broad views of language acquisition, whether the acquisition of a first language or that of an additional language, were an innatist perspective, typified by the work of Chomsky (1957) and a socio-constructivist perspective, building on the work of Bruner (1983) and others. While initially presented as competing models, it is possible to consider a measure of compatibility between these two perspectives, since some basic innate cognitive skills are required to explore and develop language while an absence of social interaction inhibits the acquisition of language. However, the uniqueness of these cognitive functions (Chomsky's Language Acquisition Device) to the development of language is now challenged by many researchers.

In the twenty-first century, work on the acquisition of communicative skills and the development of grammar, by researchers such as Tomasello (2003), Ellis (2002), and Goldberg (1995) among many others, has contributed to a view which links language skills closely to social interaction. Larsen-Freeman and Cameron (2008) present general cognitive functions such as establishing joint attention, understanding the communicative intentions of others, forming

categories, detecting patterns, imitating, noticing novelty, and having the social drive to interact with others as key to the development of first or additional language skills.

Current Fields of Research

In the past, the study of language acquisition outside the home has often been limited to the influence of formal and informal learning in schools, whether through interactions with the teacher or from friends in the playground. The performance of young learners has often been a focus of such research since the plasticity of young vocal chords and the absence of an entrenched first language, among other factors, contribute to young migrant learners, for example, quickly outstripping their parents in second language acquisition through such interactions.

Research into language acquisition outside the home in the twenty-first century tends to focus on the affordances of the Internet in the development of social networks which bring language learners into contact with proficient speakers of the target language. Extensive exposure to online video, social networking, interaction in massively multiplayer online role-playing games and even simply music with target language lyrics has been shown to significantly influence the development of second language skills in particular (Sockett, 2014).

The notion of language identity is key to understanding why learners do not simply reproduce their parents' patterns of language use when learning in a new context. Language is essentially a means by which to represent oneself to others. Researchers such as Norton (1997), Rindal (2010), and Cole and Vanderplank (2016) have shown that subconscious imitation of linguistic conventions used by a social group viewed as desirable by the learner leads to measurable differences in language production. Typically learners focused on formal classroom teaching will adopt the accent and grammatical conventions of that context, whereas learners engaged in informal activities and interactions with target language peer groups will similarly reflect the accents and conventions of those groups.

Conclusion

Future research into language acquisition outside the home will necessarily focus on mobile learning phenomena which have continued to develop in the second decade of the twenty-first century. Since the Internet is increasingly accessed via smartphones which themselves use data about the movement and location of the user to provide services, language acquisition research will increasingly need to study learners holistically as they work, play, and seek to construct plural language identities in interaction with complex networks of other language users around them.

Cross-References

- [Bilingualism](#)
- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Acquisition in the Home](#)
- [Language Development](#)
- [Language Instinct, The](#)
- [Steven Pinker and Language Development](#)

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Language and Economic Cooperation

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Synonyms

Cooperation; Cross-cultural psychology; Individualism collectivism; Linguistic relativism; Linguistics; Neo-Whorfianism; Social hierarchies; Whorfianism

Definition

Language and linguistic features have long been speculated to affect various aspects of human behavior. Being intricately linked with cultural systems, linguistic features can encode and make salient specific cultural values, which are then reflected in behavior. Here we talk about two significant linguistic features, pronouns and terms of address, which are hypothesized to have an influence on cooperative behavior. Such effects are said to be mediated by the encoding of social hierarchical structures and contextualization (or decontextualization) of speaker and addressee in speech.

Introduction

The economic literature contains repeated claims that linguistic features such as tense and pronouns influence economic behavior (Weber and Mavisakalyan 2017). This idea comes all the way back from Edward Sapir and Benjamin Lee Whorf who claimed that the particular language one speaks *determines* the way one thinks about reality (Hoijer 1954). Much of

these effects are mediated by cultural constructs which linguistic features symbolize. If economic theory and experimental economics can have a clarifying role with respect to this Whorfian theory (hereafter referred to as the Linguistic Relativity Hypothesis), it is by modeling and probing the plausible mechanisms through which this influence from language and culture is likely to be mediated to behavior.

Language has been implicated as affecting a wide variety of behaviors in humans like patience, future-discounting, and policy support (Chen 2013; Pérez and Tavits 2017); gender roles in household and educational attainment (Davis and Reynolds 2018); hierarchical and social roles (Weber and Mavisakalyan 2017); and individualistic and collectivistic sense of identities (Kashima and Kashima 1998). Linguistic features such as pronominal structures and terms of address also encode information about joint action, coordination, and cooperation. The latter will be the main issue tackled in this entry, following a brief overview of the nature of linguistic relativity and the way it has penetrated thinking about economic behavior.

Linguistic Relativity Hypothesis

The *Linguistic Relativity Hypothesis (LRH)* puts forward a combination of a linguistic and a psychological claim: (a) languages differ in various ways, including structure, syntax, usage (linguistic claim); (b) these differences influence our thinking, behavior, and decision making (psychological claim). In other words, differences in linguistic structures and usage may have a systematic influence on cognition and behavior of their speakers. LRH has been put forward in both general and specific, as well as strong from weak versions (Scholz 2016).

In the general version of LRH, no certain aspect of cognition is pointed out, and it is said that some linguistic features systematically influence certain aspects of thought, whereas in the specific version of LRH, particular linguistic features are said to have an effect on specific cognitive features. In the present discussion, the

specific version of LRH is brought out by pointing out linguistic features that can directly affect cooperative behavior, and an outline of the specific cognitive and cultural features which lead to this. Therefore by validating the specific claims of LRH, the general version automatically gets substantiated. Strong and weak interpretations of the LRH, on the other hand, discuss the *extent* to which language can determine cognition. While the strong version professes that language determines thought and behavior, weak (or moderate) versions propose an influence of language in systematic ways. Here, we deal with the latter by showing various influences of linguistic features via different cultural constructs.

Language, Culture, and Cognition

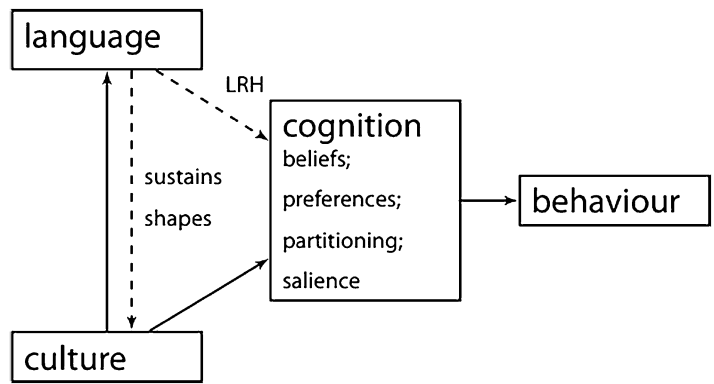
Language represents the symbolic environment of a culture. In a complex web of interactions, language and culture can affect each other in various ways. While language is the major medium through which culture is transmitted, allowing it to be a formative element, it is also a product of various cultural traditions, reflective of cultures and their characteristics (Fig. 1). By being the major mediating element, language can not only shape the content of cultural beliefs, but also lead to preservation, amplification, and diffusion of various attitudes, norms, and values. These, in turn, can have major effects on social behavioral patterns, such as cooperation. For instance, it has been proposed that languages, which grammatically associate the future and

the present, tend to foster more future-oriented behaviors like higher savings, prudent retirement plans, lesser smoking, taking better care of health, etc. (Chen 2013).

Simultaneously, various practices, norms, and structural features of cultures are often reflected in the languages that their people speak. An example is the differences between verbal insults in individualistic and collectivistic cultures. In individualistic cultures, where there is a high focus on the individual and a greater sense of self agency, insults are heavily directed to the individual only. However, in collectivistic cultures, which give high importance to interpersonal relationships, verbal insults are predominantly directed toward one’s significant others along with the individual himself (Semin and Rubini 1990). Therefore, when culture is the issue, language is a major mechanism through which the influence is channeled toward behavior, in turn, bringing us in the presence of a Whorfian hypothesis.

In particular, linguistic features can influence hierarchical structures and interpersonal relations in society. A major cultural dimension that has been linked to language is that of individualism and collectivism. Individualistic cultures are those which have a focus on the individual, characterized by values of high independence of the individual, self-reliance, and a struggle to stand out of the crowd. On the other hand, collectivistic cultures place a larger focus on the social context of the individual by emphasizing interdependent relationships and harmony in the idea of togetherness. Individualism and collectivism

Language and Economic Cooperation, Fig. 1 The web of interactions between language and culture, leading to influences on individual cognition and behavior, in the moderate version of the LRH. (Adapted from Weber and Mavisakalyan 2017)



have been directly linked with cooperative behavior, and distinct patterns of cooperative behavior have been noted in the two different cultural constructs (Wagner 1995; Chen et al. 1998). Moreover, distinct arrangements of interpersonal relationships also have a direct effect on cooperative behavior as was famously shown by a large-scale cross-cultural study by Henrich et al. (2005). Here, we talk about the two specific linguistic features which have been shown to correlate with individualism-collectivism and structures of interpersonal relationships, alongside discussing the implications for cooperation.

Linguistic Features and Cooperation

Terms of Address

A term of address is an expression commonly used to designate the person one is talking to. Languages can widely differ in terms of addresses that they employ and in the ways their speakers are required to use them in conversation. For instance, in Korean, in many contexts, one has to use a term indicating one's "hierarchical" position with respect to the addressee: "eomonim" (mother), "seonsaengnim" (teacher), or "seonbae" (to address a senior). The use of such terms of address, signal deference and make the social distance between interlocutors more salient. This, in turn, leads to a perception of fairness and reciprocity in hierarchies, affecting cooperation (De Cremer and Tyler 2007).

Moreover, the rigidity of such systems can signify the *strength* of the social hierarchies. The use of terms of address in Korean is much more rigid than that in English, leading us to predict that the cultures will reflect a stronger hierarchy, hence have a stronger effect. In English, similar terms exist, but speakers are much less constrained to use them. Inspired by a claim of Kashima and Kashima (1998), it can be hypothesized that the existence of a more hierarchical system of terms of address reflects a higher tolerance to inequality in social roles. Therefore, by affecting interpersonal relationships, these linguistic features can induce various

hierarchical social structures, affect inequality tolerance, and further affect cooperation between people.

Pronouns

Pronouns are primary linguistic features which specify the role of both speaker and addressee, along with placing them in a social context. Kashima and Kashima (1998) have stressed upon the importance of these linguistic features to determine key dimensions of culture, such as individualism versus collectivism and egalitarianism versus hierarchy, in view of economic outcomes. The case of pronoun usage can be further formulated into two further questions: (a) *which* pronoun is to be used; (b) *whether* to use a pronoun or not.

Personal Pronouns

Personal pronouns identify not only the addressee, but also index the speaker in a specific type of social context and relations. In addressing the first question of pronoun usage, both first- and second-person pronouns can have distinct forms in different languages, for instance, those linked with politeness distinctions (Helmbrecht 2005). The existence of these distinct forms affects inequality tolerance and cognitive saliency, which can have implications for cultural norms associated with hierarchy and egalitarianism (Weber and Mavisakalyan 2017). Moreover, by affecting inequality tolerance and cognitive saliency, there are expected effects on cooperative behavior.

There have been seen to be varying degrees of politeness distinctions in second-person pronouns in different languages. While languages like English use only a single term for all (you), others like German and Spanish have two different singular second-person pronouns (e.g., *du*, *Sie*; *tu*, *usted*), whereas Hindi and Bengali have three distinct pronouns (e.g., *Tu*, *tum*, *aap*; *Tui*, *tumi*, *apni*). These are used to designate social distance in interactions. According to Kashima and Kashima (1998), speakers of languages with multiple you's are more conscious of status or social distances than the speakers of other languages, leading to a difference in hierarchies in

interpersonal relations. Such social structuring can be linked to cultural dimensions of individualism-collectivism, conservatism, power distance, etc., reflecting on social behavior.

Some languages also have distinct forms of first-person pronouns, for instance, Japanese. Japanese utilizes multiple forms of “I,” like *watashi*, *boku*, *ore*, depicting the speaker in varying social roles and positions. In such cultural settings, one’s social roles are an important determinant of responsibility in social situations, going back to the idea of collectivism. Conversely, languages with a single first-person pronoun signify the individual as the locus of moral and social responsibility (Kashima and Kashima 1998). This reflects high egalitarianism, making the individual autonomy salient.

Pronoun Drop

Pronominal drop (hereafter referred to as DROP), referring to the second question of pronoun use, is a linguistic phenomenon, in which the pronouns can be omitted in their position of grammatical subject of a sentence, without losing meaning of the utterance. In Spanish one can say, “I am eating” in both the following ways: ‘*Yo estoy comiendo*’ and simply ‘*Estoy comiendo*’. In the second sentence, the pronoun ‘*Yo*’ has been dropped. A DROP language may have the effect of reducing the psychological prominence of the actor (both for the speaker herself and the addressee) and symbolically embed the actor in the context, propagating the collectivist worldview. Contextualization is an important effect of pronoun drop (Weber and Mavisakalyan 2017) that takes place by modulating effects on cognitive saliency and can further affect cooperation (Markus and Kitayama 1991). This can be seen in the examples of South Asian languages, like Hindi, where one can utter the equivalents of both “I ate the cake” and “ate the cake” (without the pronoun).

Conversely, languages necessitating the use of subject pronouns to retain the meaning of the utterance, affords a symbolic prominence of the individual actor in everyday conversation and context, for example, in English. This may

strengthen the psychological effect of affluence, pushing people further in the direction of the individualist worldview. In particular, the mandatory usage (or omission in DROP languages) of the first-person pronoun has been linked to the construction of a social situation, where the speaker is differentiated from the context of speech, which includes the conversation partner. Further, pronoun drop is an emphasizing tool for “autonomy” versus “embeddedness” in cultures, which has important implications for economic, social, and political behaviors (Licht et al. 2007).

The World Atlas of Language Structure Online (WALS Online; Dryer and Haspelmath 2011) identifies many languages that allow dropping of the pronominal subject, most notably in regions of East Asia, Southeast Asia, and South Asia, as well as the Spanish and Portuguese spoken in Latin and Central America, many of which have also been known to have collectivistic cultures.

Further Research for LRH and Cooperation

Any serious discussion on the role of linguistic relativity requires the answering of three questions: (a) Which aspects of language influence which aspects of thought in some systematic way? (b) What form does that influence take? (c) How strong is that influence? A thorough investigation of the first question is the most important step that can lead to answering the following two. Here, we suggest an experimental setup for the particular case of a systematic influence of language on economic cooperation.

A powerful way for validating the LRH for language and economic cooperation is running cooperation experiments on bilingual individuals. By priming bilinguals to one of their spoken languages (with differing linguistic features), the effects of those linguistic features on cooperation can be studied. This methodology was successfully utilized by Pérez and Tavits (2017) to demonstrate the effects of future tense of a language on future time perception and thoughts on

politics. In the case of Estonian – Russian bilinguals (Estonian being a futureless tongue and Russian being a futured tongue), when primed to Estonian, effects of future discounting were observed (hypothesis: a futureless tongue conflates the present and future, making the future seem closer to the present) and on being primed to Russian, the effects of future discounting disappeared (hypothesis: futured tongue use different words for the present and future, making the future seem distinct and distant). Such cases of sampling bilinguals from the same population can be particularly noteworthy, as the influence of language can be directly observed, removing other cultural confounds. Though such experiments have not yet been carried out in the specific realm of cooperative behavior and economic cooperation, given the influence of language on above mentioned social constructs, effects can be expected.

Conclusion

Cross-cultural psychology has been relatively silent about the role of language in culture, but the idea of linguistic relativity is steadily becoming more popular. If language can be regarded as providing symbolic tools with which people construct their symbolic world to render their material environment meaningful, this symbolic tool might have the potential to modify the way in which the material world is understood. Here we discuss such modifying effects of language on social behavior, by implicating various cultural and social constructs. Linguistic features, specifically those that signify hierarchies and contextualize (or decontextualize) interlocutors, can affect economic cooperation in meaningful ways. This can have important implications for areas of psychology and behavioral economics, where task framing can significantly alter behavioral outcomes. It, therefore, becomes important to understand linguistic influences, not only for experimental purposes, but also for a deeper understanding of how the cultural mind works.

Cross-References

- Behavioral Economics
- Cross-Cultural Variation
- Cultural and Moral Relativism
- Field of Linguistics, The

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Language and Handedness

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Synonyms

[Dominant hemisphere](#); [Major hemisphere](#)

Definitions

Hemisphere of the brain considered to play the leading role in hand preference and skill, and in mental processes such as language. The opposite hemisphere is sometimes described as nondominant or minor.

Mirror system: A network in the primate brain that responds to both the production and the perception of voluntary manual actions.

Introduction

Interest in the relation between language and handedness dates from the discovery by Paul Broca in the 19th century that the left hemisphere of the brain was primarily responsible for articulate speech (Broca 1861). Since most people were right-handed, implying left-hemispheric control, the left hemisphere was generally referred to as the dominant or major hemisphere, with the right hemisphere relegated to subordinate status as non-dominant or minor. It was also assumed that dominance was reversed in left-handers, so that speech would be controlled by the right hemisphere. For a time this was known as “Broca’s rule,” but it soon emerged that it did not always hold. As early as

1868, Hughlings Jackson remarked on the case of a natural right-handed man who suffered from expressive aphasia along with left hemiplegia, suggesting that speech was represented in the right hemisphere. Such cases of so-called *crossed aphasia* have since been frequently reported; in their classic monograph, Penfield and Roberts (1959) cited reports of 53 cases of right-handers with aphasia following right-hemispheric lesions, and 63 cases of left-handers, or “predominantly left-handers,” with aphasia following left-hemispheric lesions.

More recently still, it has emerged that the majority of left-handers are actually left-dominant for language. This first became evident from studies of the effects of the sodium amytal test, administered before surgery to determine the hemisphere dominant for language prior to surgery. One large-scale study of 122 left- and mixed-handers showed that 70 % were left-dominant for language, with 15 % showing bilateral representation and only 15 % with right-hemispheric dominant (Milner 1975). Similar figures emerged from studies of the effects of unilateral electroconvulsive therapy. These studies were based on clinical samples, but neuroimaging assessments of cerebral asymmetry for language in nonclinical samples confirm that the incidence of left-hemisphere language dominance is typically in the range 70–80 % (see Badzakova-Trajkov et al. 2010 for evidence and review). This percentage is still lower than that reported in right-handers, which ranges from 95 % to 95 %.

Genetic Models

These findings have been incorporated into models in which handedness is not so much a question of left- versus right-handedness as one of degrees of right-handedness. Left-handers are then considered part of a subgroup lacking a so-called “right-shift” factor, perhaps of genetic origin, where handedness is a matter of chance (Annett 2002). This subgroup, then, is divided between left- and right-handedness, with some displaying ambidexterity rather than consistent

handedness. In genetic versions of this model, homozygotes for absence of a right-shift (or dextral) gene are equally divided between left- and right-handers, homozygotes are all right-handed, while heterozygotes fall in between. Such a model can reasonably account for the relations between handedness and cerebral asymmetry for language, on the assumption that the same gene underlies both. In the case of left-handers, then, it cannot be assumed that cerebral asymmetry is reversed; it is more likely that, relative to right-handers, they show a lower incidence, and perhaps degree, of left-cerebral dominance.

Multiple Genes, Multiple Circuits

Although this approach has proven reasonably successful, there are complications. There has been little success in actually locating the putative right-shift gene, and the evidence now suggests that there are probably several genes underlying handedness, perhaps as many as 40, with each operating to influence the presence or absence of a disposition to right-handedness (McManus et al. 2013). Cerebral dominance itself appears not to be unitary. In one study, indices of cerebral asymmetry were computed across different brain regions in a large sample of individuals in a resting state, and factor analysis of these indices produced four factors, implying four independent lateralized networks, two biased to the left hemisphere and two to the right (Liu et al. 2009). Only one of these was the left-lateralized language network. Using a similar approach, another study of activity in regions of the frontal, temporal, and parietal lobes while participants undertook language tasks and observed manual gestures produced three left-lateralized factors, one representing language and two representing manual gesture (Häberling et al. *in press*). Handedness was only weakly associated with the language network, but was relatively strongly correlated with one (but not the other) gestural network. This network was located in the parietal lobe.

Research is therefore uncovering increasing complexity in the lateralization of networks in

the brain, with different left-lateralized networks for language, manual skill, and handedness itself, and probably different right-lateralized networks for nonverbal components such as face recognition, music perception, and spatiovisual processing. In each case it seems likely that lateralization is a matter of degree rather than a dichotomy, and that there is no systematic reversal. As in the case of handedness, reversal is a matter of chance when a congenital bias is weak or absent.

Evolutionary Aspects

From a more evolutionary perspective, brain development seems to reflect a trade-off between bilateral symmetry and asymmetry. Bilateral symmetry is a natural adaptation in organisms that move, but in which there are no systematic environmental biases from one or other side. So it is that sensory organs and limbs are bilaterally placed, shaping a largely bilateral brain. But with increasing pressure for more complex cognition and increase in brain size, and the demand for multiple specialized circuits, bilateral symmetry would tend to give way to lateralization, with a lessening of duplication and wasted neural space. Lateralized processing is evident in great apes, who show population-level right handedness, albeit at a lower incidence than in humans, and asymmetries in areas homologous to language areas in humans (Hopkins and Nir 2010). In bipedal hominins, these trends increased, with the advent of tool technologies, advanced social cognition, and eventually language. Brain circuits grew more specialized, resulting in what has been termed “hierarchical specialization,” with specialized networks arising from common ancestral ones. New circuits are formed through fissioning of ancestral systems, copying and differential modification of existing circuits, or sometimes through modified circuits fusing to create new functions (Oakley and Rivera 2008). It may well be the case that specialized networks for tool use, gesture, and language fissioned from the “mirror system,” a network in the primate brain dedicated to the production and understanding of intentional

manual acts. Such processes are of course more compatible with evolution through natural selection rather through the creation of new networks, and suggest that language itself evolved from intentional movements of the hands.

Conclusion

The idea that one hemisphere of the brain, usually the left, is dominant for manual action and language no longer holds. Handedness is only weakly correlated with cerebral asymmetry for language, and it is emerging that there are a number of lateralized networks in the human brain, and that handedness is part of a different network from that mediating language. In evolutionary terms, though, networks for language, gesture, and manual operations such as tool use may have emerged from the primate “mirror system,” initially specialized for manual grasping, which became increasingly differentiated and lateralized in the course of hominin evolution.

Cross-References

- [Broca's and Wernicke's Aphasia](#)
- [Gestural Theory](#)
- [Language](#)
- [Mirror Neurons](#)
- [Nonhuman Primates](#)
- [Tool Manufacturing](#)

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Language Deficits

- [Language Dysfunction](#)

Language Development

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Synonyms

[Language learning](#); [Linguistic development](#); [Verbal communication](#)

Definition

Language development is the process by which children come to understand and produce language to communicate with others, and entails the different components of phonology (sounds of a language), semantics (word meanings), grammar (rules on combining words into sentences), and pragmatics (the norms around communication).

Introduction

Language lies at the heart of humanity. The thousands of words and countless nuanced grammatical rules of language enable people to achieve a depth and breadth of social understanding and communication that is uniquely human. Without language, people would be left to rely on imprecise facial expressions and body movements to guess others' intentions, states, and emotions. People would be unable to pass along complex information and fully exploit the expertise of others. Language underpins the transmission of knowledge, traditions, expectations, and values across generations – it is the quintessential cultural tool. Without language, the world would be devoid of poetry, social media, poignant lyrics, folktales, historical documents, novels, and virtually all forms of written artifacts and oral tradition. The past would be lost and the future uninformed.

Developmental scientists have long marveled at children's ability to acquire language. Still, it takes many years for children to achieve the richness, complexity, and fluidity of adult language, and consequently to reap all of the advantages that language has to offer. Nonetheless, the communicative capacities of children fit their precise needs at each point in development. Children's language journey begins at birth (and even prenatally), extends over many years, and is supported by adult caregivers who provide social cues through face, voice, and body that help channel learning. These everyday social interactions are foundational to children's acquisition of the sounds, meanings, and rules of language.

This chapter highlights the functional adaptiveness, developmental changes, and social supports of early communication and language. We begin by illustrating the evolutionary roots to communication in nonhuman animals, followed by discussion of the development of communication in human infants. Next, we describe how caregivers and other adults facilitate infant language learning. Finally, we turn to functions of language in early childhood, with focus on the advanced language skills that undergird social interactions and pave the way for literacy development and school achievement.

Evolutionary Adaptiveness of Communication

Animals of all species communicate. Birds sound a variety of calls that convey meaningful information to their conspecifics (Marler and Slabbekoorn 2004). Bottlenose dolphins whistle to communicate with other dolphins (McBride and Hebb 1948). Whales use vocal calls and songs and nonvocal blows and slaps for reproductive and communicative purposes (Clark 1990). Monkeys howl and squids communicate by regulating the color of their skin (Mäthger and Hanlon 2006). These communications are vital to survival, with different sounds and behaviors conveying specific messages about threats to safety, food sources, and so forth. Over the course of development, the communication of the young grows in specificity and is shaped by adult input.

Specialization

Some species, including primates, birds, and some rodents, produce highly specialized vocalizations that aid survival (Vaughan et al. 2000; Perrins 2009). They produce sounds that are functionally referential, informing others about specific situations (Marler et al. 1992; Macedonia and Evans 1993). For example, songbirds, such as chickadees and thornbills, exhibit a variety of calls to alert conspecifics to potential danger or the availability of food (Perrins 2009). When predators appear, male chickadees shriek in a piercing high pitch and other chickadees freeze in position

until they hear the “all clear” call (Smith 1997). Adult birds alert their nestlings of predators, and the young quickly stop begging and crouch to remain safe (Halupka 1998). When food is present, chickadees chirp loudly, and their conspecifics swoop down to join in the feast. Similarly, prairie dogs produce unique sounds to communicate the size, speed, and color of approaching predators, and their conspecifics respond by diving into their burrows (Slobodchikoff et al. 2009). Bonobos alert others to the quality of food sources by barking loudly when they encounter highly preferred foods, such as bananas and grapes, but merely “peep-yelping” for less tasty foods, such as lettuce or peppers (Clay and Zuberbühler 2009).

Development

Animal young grow over time in their abilities to distinguish among different calls. In the first days following hatching, young black-capped chickadees increasingly respond to specific parental vocalizations by gaping to simulate feeding (Clemmons 1995). Not long after birth, infant vervet monkeys recognize the screams produced by their mothers, but do not yet react selectively to different calls (Cheney and Seyfarth 1980). Over the next several years, they respond accurately to alarm calls, for example by looking up to the sky in response to an “eagle” alarm and down to the ground in response to a “snake” alarm (Seyfarth et al. 1980; Seyfarth and Cheney 1986).

Young animals also produce increasingly complex and referentially accurate vocalizations with age. The vocalizations of young start out relatively imprecise but eventually convey situation-specific information. For example, young vervet monkeys sometimes mistakenly sound “snake” alarm calls to nonthreatening ground animals, or even to long twigs on the ground. With experience, vervet monkeys hone their screeches to dangerous contexts, alerting conspecifics to genuine predators (Seyfarth et al. 1980; Seyfarth and Cheney 1986). Similarly, young infant red-winged blackbirds beg for food by making peeping and chirping sounds – oblivious to their surrounds – which can place them at risk of attack by nearby predators (Redondo and Castro 1992).

Over time, the young learn to confine their begging sounds to times when predators are not around and survival is not at risk.

Social Support

What processes explain developmental changes in animals’ understanding and production of communicative signals? Feedback from and exposure to the vocalizations and behaviors of conspecifics are fundamental to social integration and survival. Notably, adults shape the sounds that young produce through physical proximity and contingent feedback. Chickadee parents respond to nestling begging sounds with alarm calls in attempts to quiet their young and avoid attracting predators (Madden et al. 2005). When vervet monkey mothers are nearby, their young respond with calls that more closely match those of adults than would be seen if mothers were far away (Seyfarth et al. 1980). When vervet monkey infants hear a playback alarm, they are more likely to respond appropriately if they look (versus do not look) to an adult first (Seyfarth and Cheney 1986). Adult monkeys are more responsive to their young’s accurate than inaccurate predator calls (Seyfarth and Cheney 1986).

The refinement of bird songs in the presence of conspecifics further illustrates the power of social feedback. Young male cowbirds sing stereotyped songs earlier and show higher song potency when females stroke their wings or gape in response to their songs (King et al. 2005). Male cowbirds repeat and retain songs that elicit positive feedback from females at three times the rate seen for songs that do not experience this feedback (West et al. 1998). In fact, young male cowbirds often fail to communicate effectively, sing to, and mate with females later in life after being reared in isolation (West et al. 2003).

Communication and Language in Human Infants

The adaptiveness and developmental changes of animal communication likewise characterize that of human infants and children. However, language in humans contains impressively unique

features. People understand and produce an astounding number of words and apply complex grammatical rules to the combination of those words relatively seamlessly. In terms of sheer vocabulary size, native English-speaking 1st graders have an estimated vocabulary size of 10,000 words, which increases to 40,000 by 5th grade (Anglin 1993). Moreover, humans can produce and understand an infinite number of word combinations, including nonsensical, yet otherwise interpretable sentences such as “the purple dog is sitting on the velvet branch.” What is perhaps most notable about the human capacity for language is children’s remarkable facility at learning under natural conditions: Children in all cultures, under strikingly different rearing contexts, become skilled consumers and producers of the language(s) to which they are exposed. How do they accomplish this feat?

Building on a dynamic-systems approach to language, a confluence of interacting factors, internal and external to the child, pave the way for language learning (Smith and Thelen 1993; Smith 2013). From the first days of life, infants are immersed in an abundantly rich multisensory environment that elicits attention and spurs engagement with the world. And, well before infants understand or produce conventional words, they emit sounds, facial expressions, and body movements that are salient to adults who respond with prompt, attuned behaviors. These early social interactions are building blocks to language and critical to survival. In this section, we describe developmental changes in infants’ communicative skills and experiences, and the ways that adults facilitate the language development of infants and toddlers.

Communicating Through Gaze, Gestures, and Emotions

Infants are astute observers of the social world. Prelinguistic infants are highly sensitive to cues in people’s voice, face, and body movements (Bloom 2000; Brooks and Meltzoff 2008; Caza and Knott 2012; Singh et al. 2002), and show impressive gains in their abilities to interpret and respond to these signals over the first 2 years (e.g., Frank et al. 2009; Suanda et al. 2017). Moreover,

well before infants speak, they produce multi-modal signals through gazes, facial expressions, body movements, and manual actions that communicate to the people around them. Over the course of the first year, infants grow in their abilities to follow and pinpoint the target of people’s gaze, respond to gestures like points, and discriminate and understand emotions expressed in people’s faces and bodies.

Following Gaze

Gaze following is central to learning language. Gaze provides information about peoples’ attention and intention – such as when mom looks at an animal in the zoo and exclaims, “Look, a monkey!”, and baby traces her gaze to land on the monkey. Yet, accurate gaze following is not automatic, and it takes several months for infants to identify the target of a person’s interest. Infants begin following gaze to distant targets as early as 6 months (Butterworth and Itakura 2000; Butterworth and Jarrett 1991), and reliably follow gazes that are matched to the looker’s body orientation between 7 and 9 months (Woodward 2003). Later in the first year, around 9–11 months of age, infants shift from simply following an adult’s head orientation to connecting a person’s gaze with the environmental referent (Brooks and Meltzoff 2005). By around 12 months of age, infants follow an adult’s gaze to locations outside their field of view (Moll and Tomasello 2004). During play interactions, infants look at the same objects as their mothers (Deák et al. 2014), and are especially adept at following gazes that are combined with salient cues such as object manipulation or verbalizations (Deák et al. 2017). The importance of gaze following for language development is evidenced by associations between early gaze following and vocabulary size (Brooks and Meltzoff 2005).

Understanding and Producing Gestures

Like gaze, gestures (particularly points) alert people to the referents of talk. Infants at first track a pointing finger by looking at the finger itself, only to later appreciate that a person’s outstretched finger designates an object of interest (Woodward and Guajardo 2002). By about 12 months of age,

infants successfully look where others point (Schaffer 1984; Woodward and Guajardo 2002), and begin pointing themselves to request assistance (protoimperatives) and alert others to interesting things (protodeclaratives) (Bates et al. 1975; Butterworth and Morissette 1996; Cochet and Vauclair 2010). Declarative pointing is thought to reveal an infant's understanding of others as intentional agents (e.g., Liszkowski et al. 2004; Tomasello et al. 2007) and is considered a precursor to language development (e.g., Iverson and Goldin-Meadow 2005; Rowe and Goldin-Meadow 2009; Tomasello et al. 2007). Infants who produced more gestures at 14 months understood more words at 54 months (Rowe and Goldin-Meadow 2009).

Understanding Others' Emotions and Behaviors

Infants' abilities to discriminate among emotions and discern the meaning of emotions are core to social interactions. A smiling face conveys something quite different than does a furrowed brow, and effective communication rests on attuning to the often-subtle emotional cues in a person's face, voice, and body. By 3 months of age, infants can discriminate among mothers' happy, sad, and angry facial expressions (Haviland and Lelwica 1987). At 4 months of age, infants prefer to listen to "infant-directed speech" (i.e., speech characterized by a high pitch and sing-song intonation) rather than adult-directed speech (Fernald 1985), perhaps because positive affect is inherent in most baby talk (Singh et al. 2002). Around the same age, infants look preferentially at their mothers' sad or happy facial expressions that match the tone of mothers' vocal expressions, suggesting they have extracted meaning from the intermodal affective displays (Kahana-Kalman and Walker-Andrews 2001).

Infants' growing emotional understanding allows them to act in line with the valence of social messages. For example, in the famous visual cliff paradigm, 14-month-old infants referenced mothers' facial expressions of fear or happiness when deciding whether or not to cross an ostensibly dangerous cliff (Sorce et al. 1985). The majority of infants crossed when mothers posed happy expressions, whereas no infants

crossed when mothers posed fearful expressions (Sorce et al. 1985). Similarly, 12-month-old infants used maternal vocal and facial cues to determine whether to approach an object for play. Infants responded to their mothers' fearful vocal emotional signals by looking at their mothers longer and showing less proximity to novel toys than infants in a neutral voice condition (Mumme et al. 1996), and displayed avoidance and negative affect after viewing a female stranger's emotional reactions toward novel objects on television (Mumme and Fernald 2003).

Over the second year of life, infants increasingly appreciate that other people can be valuable sources of information, and use social information selectively to resolve ambiguity. For example, 18-month-old infants used verbal, facial, and gestural information provided by their mothers when deciding whether to walk down slopes that were uncertain in their risk, but ignored mothers' messages when slopes were clearly easy and clearly dangerous to descend (Tamis-LeMonda et al. 2008).

The World of Language: Communicating Through Sounds, Words, and Sentences

Infants' growing skills in gaze following, gestural communication, and emotion understanding provide a springboard for learning the sounds (phonemes), word meanings (semantics), grammatical rules (syntax), and social norms (pragmatics) of the language(s) to which children are exposed.

Sounds and Intonation Patterns

Over the first months of life, infants increasingly hone in on the sounds (phonemes) and intonation patterns of their native language(s) (Eimas et al. 1971; Kuhl 1979, 2004; Mehler et al. 1988; Werker and Tees 1984). Babies as young as 2 months of age prefer speech to nonspeech sounds (Vouloumanos and Werker 2004) and respond to the prosody contours of their language (Mehler et al. 1988). Even before they develop grammatical knowledge, English-speaking infants can differentiate the prosody of questions from that of declarative statements (Soderstrom et al. 2011). Infants detect the phonemes of all languages at first, but with time, channel their

attention to the sounds of their native language (Werker and Tees 1984).

Infants also produce a rich variety of sounds to communicate with others (e.g., Oller et al. 2013), progressing through a universal sequence from prelinguistic vocalizations to producing speech over the first 2 years of life (Ferguson et al. 1992). The early cries, grunts, and coos of newborns are salient to parents, who vigilantly respond by feeding, changing, and comforting their infants. Between approximately 5 and 10 months of age, infants' coos develop into strings of consonant-vowel syllables known as canonical babbling, which begin to approximate words. Infants' babbles gradually take on the sounds, rhythm, and intonation patterns of their home language. French adults, who listened to the babbling of a French 8-month-old and an 8-month-old from either an Arabic- or Cantonese-speaking family, were better than chance at identifying which baby was the French one in each pair (de Boysson-Bardies et al. 1984).

Understanding and Producing Words and Sentences

Young infants are able to extract regularities in their environments, which sets the stage for distinguishing familiar phoneme pairings (or "words") from unfamiliar "nonwords" (Saffran et al. 1996). By 4.5 months of age, infants recognize the sound pattern of their own name (Mandel et al. 1995), and by 6 months of age can segment individual words out of speech streams (Bortfeld et al. 2005; Johnson et al. 2014). Infants as young as 6–9 months of age begin connecting words to their referents, often learning the meanings of food words and body parts early on, likely because these words are embedded in repeated everyday activities (Bergelson and Swingley 2012). Around the time that infants produce their first words (~12–14 months of age), they can exploit statistical regularities to map novel words to novel objects in laboratory tasks (Smith and Yu 2008). Over the course of the second year, infants grow in their receptive vocabularies (Hoff 2009) and can follow simple instructions ("Come here!") and understand simple "Wh"-questions ("Where's the rabbit?").

Notably, infants understand many words and phrases several months earlier than they are able to produce them. Infants typically produce their first words around 12–13 months of age (Hoff 2009), with first words typically being the names of objects (Gentner 1982; McDonough et al. 2011). Midway through the 2nd year, infants experience a "vocabulary spurt," producing new words at an impressive rate (Barrett 1985), and soon thereafter combining words into simple sentences (Brown 1973). Advances in grammar and vocabulary enable infants to regulate the actions of their caregivers, for example, through phrases such as "want ball" or "more cookie."

Impressively, infants' first word combinations adhere to the principles of word order seen in their language and can be traced to the months of learning that occurred prior to the first expression of these simple "sentences." To illustrate, well before infants combine words in sentences, they attend to the word order of spoken sentences (Golinkoff et al. 1987; Hirsh-Pasek and Golinkoff 1996): They show comprehension of subject and object questions (e.g., *What hit the keys?* and *What did the book hit?*; Seidl et al. 2003), and process words faster in grammatically correct than incorrect sentence constructions (i.e., looking to the target faster when hearing "Can you see *the* ball?" than hearing "Can you see *and* ball?"; Kedar et al. 2006; see Golinkoff et al. 2013 for a review). Infants can also identify target actions for novel verbs (e.g., "The duck is kradding the bunny") by using their syntactic knowledge (e.g., Naigles 1990), a process referred to as syntactic bootstrapping (Gleitman 1990). As children further develop semantic and grammatical skills, they become increasingly adept at decontextualized speech (talk about the "then and there") and narrative constructions during play and storytelling.

Supportive Role of Caregivers

Children's rapid and impressive gains in language over the first years of life are, at least in part, facilitated by the rich language input and supportive environments provided by caregivers and

other adults. Just as cowbirds' contingent wingstrokes shaped the onset of singing and promoted song potency in the young, human adults support infants through contingent social interactions and by providing concomitant social cues to the referents of their talk. Adults support children's language development by introducing new words, producing exaggerated actions (motionese) and intonation patterns, responding contingently to infant behaviors, and shifting to increasingly complex language as children develop.

Diversity in Language Input

Adults provide infants with a rich and steady stream of interesting words, phrases, and accompanying actions for infants to process. During object play, caregivers describe and label objects that pique infants' interest (Goldstein and Schwade 2010). Mothers' didactic language promotes infants' vocabulary development (Tamis-LeMonda et al. 2012a). Adults repeat words and phrases when speaking to infants, and infants learn to connect sounds to concepts after only a few repetitions, known as "fast-mapping" (Hollich et al. 2000).

Temporal Contingency

Caregivers support infants' understandings of the natural ebb and flow of conversations by tailoring the pace and contours of their speech. Mothers take pauses after speaking to allow time for infants to respond, and they promptly respond to infant gestures, touch, and vocalizations (Jasnow and Feldstein 1986; Hsu and Fogel 2003; Tamis-LeMonda et al. 2013). Infants come to understand the flow of everyday conversations as they learn to take turns conversing with partners (Gratier et al. 2015). Parents' contingent responsiveness fosters early language development (Tamis-LeMonda et al. 2014a, 2006), and relates to infants' own contingent responsiveness to the speech acts and gestures of their mothers (Kuchirko et al. 2017).

Infant-Directed Speech

Parents use a special register of speech characterized by slow pace, short and simple sentences, variable pitch, and high redundancy when talking

with infants (Fernald 1985). Infant-directed speech provides a richly informative context for infants to learn new words (Saint-Georges et al. 2013). The rich prosody cues of infant-directed speech help infants parse units and patterns in speech streams that later become words and grammatical structures (Ma et al. 2011). Infant-directed speech also facilitates infants' long-term memory of words (Singh et al. 2009).

Gestures and "Motionese"

Adults put on a show for infants, sparking infant attention and interest through their enthusiastic and exaggerated manual actions. During object play, mothers direct and redirect infants' attention by pointing, gesturing, and handling objects (Deák 2017). Adults use special infant-directed gestures or "motionese" to communicate with infants (Brand et al. 2002, 2007). Motionese, especially when paired with infant-directed speech, makes adult speech exciting and accessible to the infant, which may explain why infants imitate actions contained in motionese faster than those contained in adult-direct action (Williamson and Brand 2014). Indeed, "acoustic packaging" – the pairing of language input with gestures and other actions – helps infants parse information from speech streams (Hirsh-Pasek and Golinkoff 1996; Wrede et al. 2013) and supports vocabulary learning (Rowe 2000; Rowe et al. 2008).

Increasing Language Demands

Adults are highly sensitive to developmental changes in infant language skill, and tailor their language in line with children's changing skills. Parents use fewer words and less grammatically complex language when infants' language skills are emerging, and increase the amount and diversity of language input as infant language improves (Tamis-LeMonda et al. 2012b). As infants master a growing set of words, parents introduce new words and respond more to children's use of novel words (Masur 1997), and direct an increasing number of questions to their infants (Bornstein et al. 2008). Paralleling infants' transition from using gestures to using words to communicate during the 2nd year of life, mothers decrease their responses to infant gestures and increase

their responses to vocalizations (Tamis-LeMonda et al. 2013).

Language Functions in Early Childhood

Over the course of toddlerhood and early childhood, children show extraordinary gains in articulation, vocabulary, grammar, and narratives. By the time U.S. children reach first grade, they understand between 5,000 and 20,000 words (Moats 2001), can apply grammatical rules to the construction of complex sentences, and engage in elaborate conversations with others (Hoff 2013). At the same time, children venture out of the home into new caregiving and learning contexts that offer unique opportunities to acquire and practice language. Growth in language skills over this period helps children regulate theirs and others' behaviors and emotions, construct elaborate and decontextualized narratives to talk about the past and future, engage in imagination and play, and establish positive relationships with teachers and peers. As such, language provides a vital foundation to cognitive, social-emotional, and literacy developments in early childhood (e.g., Astington and Jenkins 1999; Hoff 2013; Marchman and Fernald 2008; Snow et al. 1998; Tamis-LeMonda et al. 2014b).

Speech to Regulate Behaviors and Emotions

Language supports young children's efforts at self-regulation. Vygotsky (1934/1986) referred to words as symbols or mental tools for manipulating thoughts and behaviors. The development of self-regulation is thus a process in which children internalize caregivers' regulatory speech and strategies (Kopp 1982; Vygotsky 1934/1986). Thus, the richer children's symbolic repertoire (i.e., language skill), the more tools they have at their disposal for regulating their behaviors (Vallotton and Ayoub 2011), as evidenced in associations between language skills and self-regulation in toddlerhood (e.g., Vallotton and Ayoub 2011) and early childhood (e.g., Astington and Jenkins 1999; Cutting and Dunn 1999). Language likewise enables children to verbally communicate their emotions and internal states in

socially appropriate ways (Cole et al. 2010), and to engage in self-managing talk (Eisenberg et al. 2005). Consequently, preschoolers' language skills relate to their ability to cope with frustrating situations (Stansbury and Zimmerman 1999), and conversely, language impairment portends difficulty in emotion regulation (Fujiki et al. 2002).

Decontextualized Speech and Narratives: Time and Space Travel

From infancy through the early childhood years, children's speech shifts from a focus on the highly contextualized "here and now" to the increasingly decontextualized "there and then." By 4 years of age, children are proficient at mentally representing objects, events, and internal states of people and story characters that are not immediately present (see Flavell and Miller 1998, for review). Decontextualized discourse conveys meaning through linguistic devices such as grammar and vocabulary, rather than extralinguistic devices (e.g., gesture), contextual cues (e.g., an object), and shared knowledge (Pellegrini 1985; Scott 1994; Westby 1991). As such, decontextualized discourse is characterized by "literate language features," involving elaborate noun phrases, adverbs, conjunctions, and mental (e.g., think) and linguistic (e.g., say) verbs (Greenhalgh and Strong 2001; Pellegrini 1985), building blocks to literacy development (Curenton and Justice 2004; Pellegrini 1985; Scott 1994; Snow 1991; Westby 1991).

Development in decontextualized language skills enable young children to construct elaborate narratives and revisit the past through reminiscing (discussing shared experiences) or recounting (discussing unshared experiences). However, narrative skills develop over several years, and at first require a lot of scaffolding. At the end of the second year of life, children begin to refer to past events, initially with much prodding and support by adults (Eisenberg 1985; Sachs 1982). At 2 years, children often talk about negative past events, especially injuries (Miller and Sperry 1988), but over the next few years, children tell longer and more sophisticated personal narratives, and increasingly respond to the narratives of their peers (Umiker-Sebeok 1979). The personal narratives of North

American, Caucasian, English-speaking children developed from “Two-Event” narratives at 3½ years, to “Leap-Frog” narratives (i.e., stories that omitted key events) at 4 years, to “End-at-High-Point” narratives (i.e., lacking a resolution) at 5 years, to the final “Classic Narrative” by age 6 years (McCabe and Peterson 1991; McCabe and Rollins 1994; Peterson and McCabe 1983). Children’s advances in narrative skills reverberate across several developmental domains: Reminiscing, for example, solidifies social bonds (Fivush et al. 1996; Nelson 1993; Reese and Brown 2000), and individual differences in narrative skills predict later academic achievement (Feagans and Appelbaum 1986; Feagans and Short 1984; O’Reilly et al. 2004).

Language in Imagination and Pretend Play

Children’s blooming of decontextualized language and the elaboration of narratives allow imagination and pretend play to take off. From the pretend play scenarios of toddlers, to the personification of objects by 3-year olds (such as treating a toy animal as a living, conversational partner), to the creation of imaginary companions, young children enter a fictional world where all things are possible (Singer and Singer 2006). Language is an integral component to the emergence of imagination and pretend play (Andresen 2005; Bruner 1983; Bergen 2002; Singer and Singer 2006). For example, role play – which involves pretending to be the characters of imagined plots – requires decontextualized forms of language to establish the context and generate an altered reality (Andresen 2005). Language helps construct the frame for imaginative role play, as when children establish shared goals through metacommunication (e.g., “Let’s pretend...”; Andresen 2005).

Relationships with Teachers and Peers

The school context allows young children to develop close and meaningful relationships with people outside the family, namely teachers and peers, and language is a primary mechanism for establishing and fostering those relationships (Pence and Justice 2007). It is thus unsurprising that children who exhibit language deficits or

weaknesses in communication sometimes have difficulty developing positive relationships at school (Justice et al. 2008; Rudasill et al. 2006). Children with underdeveloped language skills are more withdrawn, less social, exhibit lower self-esteem, and have more difficulty regulating their emotions than do their peers with strong language skills (Fujiki et al. 1999, 2002; Jerome et al. 2002). These social difficulties could undermine the quality of teacher-child relationships (Howes et al. 2000). Furthermore, children with poor language skills, especially boys, tend to display disruptive behaviors (e.g., Arnold 1997), presumably due to frustration in learning situations (Homrok and Arnold 1995), and disruptive behavior in turn leads to peer rejection (Stowe et al. 2000).

Role of Educators: Language in Educational Settings

Early childhood educators, with whom children spend a significant portion of time during the preschool and early school years, tremendously influence children’s language development. Teachers continually interact with children during circle time, center and playtime, meal and snack times, and book reading (Massey 2004; Pianta and Hamre 2009), thus constituting “the main conversationalists, questioners, listeners, responders, and sustainers of language development and growth in the child-care center or classroom” (Genishi 1988, p. 3).

As might be expected, the quantity and quality of teachers’ language interactions with children powerfully shape children’s skills in language and other domains. Teacher-child interactions that involve cognitively challenging conversations; encourage higher-order thinking skills; and contain a diverse vocabulary relate to children’s cognitive, language, and literacy outcomes (Dickinson and Smith 1994; Mashburn et al. 2008). Cognitive challenging conversations encourage children to provide explanations and personal narratives, analyze experiences, draw inferences, and share opinions and ideas (Smith and Dickinson 1994; Luo and Tamis-LeMonda 2017), and thus support children’s skills decontextualized talk about past and future events (Massey 2004).

Conclusion

Language is uniquely human. Yet, the functions of language and the development of language skills embody the evolutionary adaptiveness of communicative behaviors observed in non-human animals. Throughout evolutionary history, nonhuman animals and humans alike have developed specialized and sophisticated communicative strategies to relay their needs, alert others to danger and resources, and build and maintain relationships – skills that are crucial to survival and social integration. In humans, however, the unrivaled richness and complexity of language make its achievement nothing short of extraordinary. How do the babbling blunders of young infants develop into the decontextualized conversations and imaginative play scripts of young children?

Early on, infants are able to detect statistical regularities and environmental contingencies, requisites for building meaning out of input and resolving referential ambiguity (Tamis-LeMonda and Bornstein 2016). Additionally, infants' interest in and attention to the messages conveyed in others' face, hands, body, and prosody cues in speech are seeds to the understanding and production of conventional words, sentences, and ultimately elaborate stories. But, beyond these child contributions, parents, caregivers, and other adults facilitate language learning at all points in development. Adults not only provide contingent language in response to children's behaviors, but also accommodate young children's needs through infant-directed speech and gestures and by tailoring the complexity of their lexical and grammatical input to children's communicative development. As children become increasingly competent language users, adults "up the ante" by engaging them in interactions that involve and promote higher-order thinking and increasingly sophisticated language functions and forms. In short, animal young and human children develop species-specific communicative skills with the support of adults. As the young mature into competent communicators, they will one day support the development of communication and language in future generations.

Cross-References

- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Acquisition in the Home](#)
- [Linguistic Evolution](#)

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Language Development in Formal and Informal Educational Contexts

► Language Acquisition Outside the Home

Language Disorders

► Language Dysfunction

Language Disturbances

► Language Dysfunction

Language Dysfunction

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Synonyms

Language deficits; Language disorders; Language
disturbances; Language impairments

Definition

Language dysfunction refers to abnormalities in processing of linguistic information.

Introduction

Language is a complex cognitive function that involves multiple levels of linguistic representation, including phonology, morphology, syntax, semantics, and discourse. A huge number of computations are required to sustain and integrate this multilevel information. Language disturbances may arise due to an inability to build or analyze linguistic representations or because of disruption to the computations intrinsic to language function. Since language functioning requires other cognitive domains (e.g., memory, attention, executive function, control processes), language disturbances may appear as a result of dysfunction in these other domains. As an example, sentence comprehension is supported by various memory mechanisms; if the memory demands that are required for assignment of syntactic structure and inference of sentence interpretation based on that structure are not met, there will be

comprehension failure (Caplan and Waters 2015). Given the complexity of language and its interactions with other cognitive domains, it is not surprising that language implicates a wide range of brain areas. Lesions in these brain areas and their anatomical connections lead to language impairments.

Many disciplines study language dysfunction. While neurologists are mainly concerned with associated brain damage, speech pathologists focus on developing speech/language therapies, neuropsychologists investigate residual functional abilities after brain damage, and neurolinguists test hypotheses on patterns of impairment related to specific language components. For a cognitive neuroscientist, the biggest challenge is to find out where exactly in the massive number of computations that enable language function the changes that cause dysfunction occur and how these computational changes map onto brain organization.

Aphasia

Aphasia is an acquired language disorder caused by brain damage. It affects language production and comprehension at the level of single words, sentences, and discourse across different modalities (e.g., spoken language, written language, sign language). Aphasia is present in about 40% of stroke cases, at least in the first few months following the stroke, with the aphasic symptoms persisting in many patients. In addition, aphasia is also common in traumatic brain injury and tumor patients. These conditions do not create ‘neat’ lesions and typically result in complex patterns of language breakdown (Caplan 1995).

Transient language disturbances may appear as a result of epilepsy, migraine headache, drug and alcohol abuse, and sleep deprivation. In contrast, progressive language deterioration is an early symptom of an atypical variant of initially focal fronto-temporal degenerative disease known as primary progressive aphasia. Furthermore, severe language abnormalities characterize later stages of multiple sclerosis, Alzheimer’s disease (AD), Creutzfeldt-Jakob disease, and other progressive

diseases of cortical structures in which many other behavioral and neurologic abnormalities are more salient than language impairments (Benson and Ardila 1996). Language disturbances are common in psychosis, in particular schizophrenia, and in some mood disorders, such as mania.

The extent and type of language disturbances and the brain potential to recover language depend on the lesion type, size, and location. Functionally, the brain can adapt better to slow-growing lesions, such as low-grade glioma, than to sudden lesions such as those caused by stroke (Desmuget et al. 2007). Some evidence suggests that smaller post-stroke lesions are associated with language reorganization in perilesional areas and with better prognosis than larger lesions, which typically involve contralateral homologous areas and have a poor prognosis (Karbe et al. 1998). Other evidence indicates that post-stroke language recovery involves three distinct phases, characterized by a hemispheric shift of function. In the acute phase (~2 days post-stroke), the areas surrounding the lesion show almost no activation; there is also no marked task-related activation in the opposite hemisphere. The beginning of language recovery, which marks the subacute phase (~2 weeks post-stroke), is associated with activation of homologous areas in the right hemisphere. Further recovery of language during the chronic phase (~4–12 months post-stroke) is associated with normalization of activation and a functional shift to the left hemisphere (Saur et al. 2006). Taken together, these findings suggest that a range of brain areas in both cerebral hemispheres contribute to language recovery after stroke, and that a case of chronic aphasia with dominant right hemisphere functionality would be associated with poor recovery. However, the debate regarding whether the right hemisphere supports compensatory, suboptimal, or maladaptive processes in language recovery after stroke has not been settled.

Current models of language dysfunction and the neural basis for language have inherited some basic ideas from nineteenth-century aphasiologists, who established that language is left-lateralized and correlated the site of a lesion with a specific type of language disorder. In the 1860s, Paul Broca recognized that injury in the

inferior frontal gyrus of the left cerebral hemisphere caused a speech deficit, which is known as motor, expressive, or Broca's aphasia. Subsequent developments in aphasiology include Carl Wernicke's finding that damage to the left superior temporal region causes a comprehension deficit, combined with a type of speech production impairment different from the one described by Broca. This type of impairment is known as sensory, receptive, or Wernicke's aphasia (Kljajevic 2014).

Considering that the two types of language disorders – motor and sensory aphasia – followed damage to the left inferior frontal region and left superior temporal region, respectively, Wernicke hypothesized that damage to the arcuate fasciculus, i.e., the white matter tract connecting the two regions, would result in a third type of aphasia, *Leitungsaphasie* or conduction aphasia. Patients with this type of aphasia would have an impaired ability to repeat speech, but spared abilities to produce and comprehend speech. Conduction aphasia was clinically confirmed by Ludwig Lichtheim, who further developed Broca–Wernicke's model and proposed additional aphasic syndromes. The Broca–Wernicke–Lichtheim model was further developed by Jules Dejerine in the late nineteenth century and Norman Geschwind in the mid-twentieth century, who recognized the importance of the left inferior parietal lobe for language. Although the model has been criticized on various grounds, some of its main principles are reflected in current models of functional neuroanatomy of language, such as relative functional specialization of brain areas and the importance of anatomical connectivity for language function (Kljajevic 2014).

There are many classifications of aphasia. Assuming the classical approach, the following seven aphasic syndromes are typically discerned: Broca's aphasia, Wernicke's aphasia, conduction aphasia, transcortical motor aphasia, transcortical sensory aphasia, global aphasia, and anomic aphasia. The aphasic syndromes can be roughly grouped into non-fluent (Broca's, transcortical motor, global) and fluent (Wernicke's, conduction, transcortical sensory, anomic) based on the impression of fluency in aphasic speakers' overt speech production. Spontaneous speech is one of the

features used in the classical approach to assign a person with language disturbances to one of the aphasic syndromes. Other features include auditory comprehension, verbal repetition, and naming abilities, as well as the lesion site.

Broca's aphasia is characterized by non-fluent, effortful, and impoverished speech, with omission of function words and inflection. The type of erroneous speech output in which function words and inflection are omitted is known as agrammatism. Furthermore, speech output in persons with Broca's aphasia is reduced to short phrases, containing two to three words. Due to agrammatism and decreased verbal output, the Broca's aphasic speech pattern is reminiscent of a telegraphic style. Another feature of this type of aphasia is more impaired production of main verbs than nouns, which is in contrast to Wernicke's aphasia, where production of nouns is more impaired than production of verbs. Other features of speech output in Broca's aphasia include impaired melodic line and intonation as well as semantic and phonemic paraphasias (i.e., target words and syllables are substituted with incorrect words and syllables). Speakers with Broca's aphasia also have impaired repetition of words and phrases, their naming abilities are disrupted, and they can have impaired reading and writing. Comprehension of words and phrases is generally preserved, but comprehension of longer and syntactically more complex sentences is impaired. For instance, persons with this type of aphasia comprehend simple active (e.g., 'The boy kissed the girl') or subject relative sentences (e.g., 'The boy who kissed the girl is tall') well, but they find passive (e.g., 'The boy was kissed by the girl') and object relative sentences (e.g., 'The boy who the girl kissed is tall') difficult to comprehend; they also have reading and writing deficits.

Wernicke's aphasia is characterized by fluent but meaningless or 'empty' speech, which may be produced at a normal or rapid rate. The common feature of verbal output in this syndrome is 'press of speech,' which is known as logorrhea. Spontaneous speech of persons with Wernicke's aphasia is characterized by paraphasias, neologisms, and gibberish output termed jargon aphasia. Whereas

Broca's aphasic speakers omit function words and inflection, persons with Wernicke's aphasia select wrong function words and inflection, along with incorrect verb tenses, conditional clauses, and word order. This type of erroneous speech output is known as paragrammatism. Since persons with Wernicke's aphasia are unable to monitor their speech output, they remain unaware of the deficit and thus do not attempt to correct their speech errors. However, their spontaneous speech indicates a relative preservation of syntactic structure. Another key feature of Wernicke's aphasia is severe impairment of auditory comprehension. Verbal repetition, reading, and writing are also deficient, as is naming, and phonemic and semantic prompting does not help.

Conduction aphasia is a fluent syndrome in which there is a marked inability to repeat phrases and sentences, somewhat impaired naming, reading and writing, but relatively spared auditory comprehension and spontaneous speech.

Transcortical motor aphasia is similar to Broca's aphasia. This non-fluent syndrome is characterized by reduced and impoverished speech output, relatively preserved auditory comprehension – except for long and syntactically complex sentences – and impaired naming, reading, and writing. Unlike in Broca's aphasia, repetition of phrases and sentences is relatively preserved in this syndrome.

Transcortical sensory aphasia is similar to Wernicke's aphasia: it is a fluent syndrome with marked auditory comprehension impairment combined with deficits in naming, reading, and writing. However, verbal repetition is preserved in this syndrome.

Global aphasia is a non-fluent syndrome. Of all of the types of aphasia, global aphasia involves the most severe impairments at all levels of language. Speech production is typically reduced to stereotypical and automatic expressions. Auditory comprehension is severely impaired and may be reduced to occasional comprehension of single words. The abilities to repeat words and phrases, name objects, and read and write are absent. The prognosis is generally poor and only some cases evolve to a less severe type of aphasia such as Broca's.

Anomic aphasia is a fluent syndrome characterized by a word-finding difficulty. Auditory comprehension and repetition are typically spared, but mild impairment in reading and writing may be present. Nevertheless, its separate syndrome status has been debated (Benson and Ardila 1996) given that anomia, i.e., difficulty with word retrieval, is a feature that is to some extent present in all types of aphasia.

Crucially, the syndrome approach postulates that each type of aphasia is associated with a lesion in a specific brain area or with a disruption to anatomical connections between the relevant areas. According to this approach (i) Broca's aphasia is associated with damage to Broca's area, i.e., the left inferior frontal region (Brodmann areas 44 and 45); (ii) Wernicke's aphasia follows damage to Wernicke's area, i.e., the left posterior superior temporal region (Brodmann area 22); (iii) conduction aphasia is associated with damage to the left arcuate fasciculus; (iv) transcortical motor aphasia is associated with lesions in the left frontal areas, anterior to Broca's area; (v) transcortical sensory aphasia follows damage to the left parietal-temporal-occipital junction; (vi) global aphasia follows left fronto-temporo-parietal lesions, i.e., the entire perisylvian region; and (vii) anomic aphasia follows damage to the left inferior parietal region.

However, language is much more distributed in the brain than previously thought (Price 2012). It has also become clear that an aphasic syndrome can have different localizations and that different types of aphasia can follow damage to the same brain area. For instance, growing evidence suggests that damage to Broca's area is associated with only transient language disturbances and that Broca's aphasia requires larger lesions, which often involve the underlying white matter (Mohr et al. 1978). In addition, Broca's area itself is functionally not homogeneous, and thus it remains unclear which specific aspect of language this particular region fails to support in Broca's aphasia. Similarly, lesions associated with conduction aphasia rarely affect only the arcuate fasciculus (Damasio and Damasio 1980); damage to this white matter

tract does not necessarily cause conduction aphasia, and this type of aphasia may occur due to damage to other brain areas, sparing this particular white matter tract.

The picture becomes even more complex when deep gray matter structures are considered. As an illustration, lesions in the basal ganglia have been associated with Broca's, Wernicke's, transcortical motor, conduction, global, and anomic aphasia, as well as with no aphasia at all (Nadeau and Crosson 1997). In addition to illustrating a more general difficulty in assigning a certain type of aphasia to a specific lesion site, this finding also suggests that language disturbances of the classic aphasic syndromes may be associated with damage to subcortical structures. Still, subcortical aphasias, such as striato-capsular aphasia, thalamic aphasia, and aphasia associated with white matter disease (e.g., in multiple sclerosis) (Benson and Ardila 1996), appear to be even more difficult to define and categorize.

Apart from poor lesion-function mapping, the syndrome approach to aphasia has been criticized on other grounds: the syndromes are linguistically underspecified (e.g., comprehension is a set of complex processes, not a monolithic task), the same symptoms appear across different syndromes (e.g., anomia, paraphasias), and there is a variation in patterns of aphasic disturbances, both individually and cross-linguistically (Kljajevic and Murasugi 2010). In addition, aphasia evolves. For example, global aphasia evolves to Broca's aphasia, while Broca's, Wernicke's, and conduction aphasias often reduce to anomic aphasia. The instability of aphasic syndromes is probably best illustrated by symptom variation within a single patient, which can occur even within a single testing session, as well as by variation in symptoms in different patients with similar lesions. Regardless, the aphasic syndromes remain useful to clinicians as a quick summary of the most salient, even if not very precisely defined, features of language disturbances in individual cases. However, researchers are developing more sophisticated linguistic descriptions of aphasic language, often using neuroimaging methods to test hypotheses on specific language computations.

Language Disorders Following Right Hemisphere Damage

Most language functions, including the lexicon and grammar, are lateralized to the left hemisphere in more than 95% of right-handed persons and about 70% of left-handed persons. Thus, right-handed persons typically develop aphasia after left-hemisphere lesions. Left-handers often develop aphasia after lesions in the right hemisphere, but a proportion of this population have aphasia after left-hemisphere damage. Patients with atypical lateralization for handedness appear to have less severe aphasia than those with typical handedness.

Early evidence on right hemisphere involvement in language in right-handed persons comes from studies using the intracarotid amobarbital injection technique (or ‘Wada test’), which is a procedure that anaesthetizes and thus temporarily blocks functionality of one hemisphere. These studies showed that the anaesthetized right hemisphere caused additional difficulties in speech production in persons with left hemisphere damage. Additional early evidence on the role of the right hemisphere in language comes from studies with split-brain patients (Gazzaniga et al. 1984). (These are patients who had resection of the corpus callosum, i.e., the white matter tract connecting the left and right cerebral hemisphere, to relieve severe epilepsy not responding to medications.) These studies showed that in some cases the isolated right hemisphere retained a limited capacity for language, such as the ability to comprehend and read words, and to understand simple sentences, but not those that are syntactically complex (e.g., ‘The boy that was kissed by the girl smiled’). Subsequent findings have suggested that only a small portion of split-brain patients retains right hemisphere language.

More recent studies use neuroimaging methods, such as functional magnetic resonance imaging (fMRI) and functional transcranial Doppler sonography, to record brain activation in the cerebral hemispheres and calculate a lateralization index. These methods assess laterality effects based on the extent of activation associated with performance of a task. Functional neuroimaging studies with right-handed aphasic patients who

had a left-hemisphere stroke suggest involvement of the right hemisphere during language recovery. This evidence typically points to rather limited functional support provided by the right hemisphere to ‘core’ language functions (Karbe et al. 1998; Saur et al. 2006) and some researchers associate the right hemisphere involvement in language recovery after left hemisphere stroke with domain-general attentional processes rather than with language per se.

The neurobiological basis of a differential hemispheric role in language is currently not well understood, although some researchers have proposed explanations in terms of neuroanatomical asymmetries between the two hemispheres (e.g., asymmetry in the planum temporale). Current models of language organization in the brain postulate that the right hemisphere supports some language-related functions either in concert with the left hemisphere, as in speech perception, or as the dominant hemisphere for that specific function, i.e., unilaterally, as in communicative and emotional prosody, discourse production and comprehension, and comprehension of distant and secondary semantic relations that are typical for metaphors, idioms, sarcasm, irony, and humor. When the right hemisphere areas supporting these functions are damaged, impairments follow, but they are generally less apparent than those following left hemisphere damage. As a consequence, persons with right hemisphere damage whose language is left lateralized are generally not considered aphasic, even though 50% may have verbal communication difficulties that are socially challenging.

The unique role of the right hemisphere in language remains controversial. For instance, it has been debated whether comprehension of metaphors and other types of figurative language requires support of the right hemisphere. An early behavioral study reported that post-stroke patients with a right hemisphere injury were able to explain metaphoric sentences verbally, but they were correct only half of the time in picture–metaphor matching (Winner and Gardner 1977). An early positron emission tomography (PET) study provided evidence of the role of the right hemisphere in metaphor processing in healthy

adults (Bottini et al. 1994). However, subsequent studies have reported mixed findings, with some indicating that the right hemisphere is involved only in processing less familiar sentential metaphors and others questioning its role in metaphor processing altogether. The discrepancy in findings reported in these studies may be due to the differences in their design, methods, and the populations studied. Regardless, the conflicting evidence illustrates a need for more research on the role of the right hemisphere in language, its contribution to recovery after left hemisphere damage, and its residual abilities after it has been damaged.

Brain Plasticity for Language

Localization of function in the brain is not fixed and the adult human brain retains the potential for changes. This capacity of the brain to reorganize itself structurally and functionally is known as neuroplasticity. Although the concept of neuroplasticity is not new, the potential of the brain to reorganize language function after damage remains relatively unexplored. One general finding is that the extent to which the brain allows functional reorganization after damage depends on the type of lesion: for example, slow-growing lesions, such as low-grade glioma, appear to allow better functional adaption than sudden brain lesions, such as those caused by a stroke (Desmuget et al. 2007).

The most remarkable findings on the potential of the brain to reorganize language function come from studies of low-grade glioma that use intraoperative electrical mapping in awake patients during brain surgery and report patients' performance on language tests at various points in time following tumor resection (e.g., immediately postoperatively, 3–6 months/6–12 months postoperatively). These studies indicate that a language task can be successfully completed even when the brain area that typically supports the task is invaded by tumor or surgically removed. For instance, studies in low-grade glioma patients have shown that removal of the whole left dominant insula (Duffau et al. 2001), Broca's area (Plaza et al. 2009), or Wernicke's area (the posterior two-thirds of the superior temporal gyrus,

middle temporal gyrus, and the supramarginal gyrus) (Sarubbo et al. 2012) did not result in severe language deficits in these respective patients, as would be expected if localization of function in the brain were fixed. To better understand these findings, one must keep in mind that low-grade glioma is a slow-progressing brain tumor with a growth rate of about 5 mm per year (Mandonnet et al. 2003). The relatively slow rate of tumor growth allows a continuous, slow reorganization of functions at risk of impairment. This permits the brain to achieve the level of compensation that appears as (relative) preservation of language function, despite the presence of large tumors in language-related areas and also after their removal.

There are also regional differences in the cortical capacity to reorganize function (Herbet et al. 2016). For instance, the prefrontal cortex, anterior insula, anterior and inferior temporal cortices, and inferior parietal cortex can be compensated for, whereas part of the superior temporal region (including Heschl's gyrus and part of Wernicke's area), the posterior inferior temporal cortex, and the basal ganglia cannot be compensated for. When it comes to white matter, its neuroplastic potential is not as great as the potential of gray matter areas (Herbet et al. 2016). Previous findings in post-stroke aphasia are consistent with this evidence from low-grade glioma, indicating that deep lesions affecting white matter have a worse prognosis than the lesions affecting only cortical gray matter. Finally, while most white matter tracts, including the arcuate fasciculus, cannot be compensated for, portions of some white matter tracts have neuroplastic potential. For instance, the inferior fronto-occipital fasciculus, which is a major ventral white matter tract supporting language, shows a greater plastic potential in its anterior portion than in its mid and posterior portions (Herbet et al. 2016).

On the other hand, developmental data indicate that some language abilities may be compensated for even after damage to the relevant white matter tracts that have a low neuroplastic potential, such as the arcuate fasciculus. For instance, a 15-year old patient who underwent brain surgery for removal of a malignant tumor 10 years earlier

had relatively spared oral language abilities, even with a missing arcuate fasciculus in both hemispheres; however, this patient's reading was completely deficient (Rauschecker et al. 2009). Studies in adults point to a more limited and selective plasticity of the tracts supporting language. A recent study reported that ten patients with low-grade glioma in the left frontal region had normal preoperative language function, but fractional anisotropy values in the left ventral language pathways were increased in these patients compared with healthy control subjects (Zheng et al. 2013). One plausible explanation for the changes in white matter microstructure integrity of the ventral language tracts includes reorganization supporting the patients' normal preoperative language. This interpretation is compatible with the evidence suggesting some degree of regional plasticity of the ventral language tracts (Herbet et al. 2016).

The exciting findings on the brain's potential to reorganize language that come from recent research on low-grade glioma demonstrate what the brain can do, not what it normally does. Nevertheless, these findings are challenging some basic assumptions of the current understanding of language organization in the brain.

Language Deterioration in Dementia

While language disturbances in post-stroke aphasia appear suddenly, language in AD deteriorates slowly and represents a secondary symptom. The main features of cognitive decline in AD, which is one of the most common types of dementia, are impairments in episodic memory, executive functions (reasoning, problem solving, planning), semantic memory, visuospatial skills, attention, and control processes. In addition, language impairments at word-level, such as cued-word generation and confrontation naming, develop relatively early in the disease. At a later stage, word repetition, articulation, and overall production and comprehension become impaired, so that patients in the final stage of the disease experience a profound inability to communicate.

Growing evidence from neurolinguistics suggests that AD patients have a particular difficulty in verb processing (Grossman et al. 2007), which

may be caused not by the semantic content of verbs or limitation of the resources necessary for verb processing, but rather by impaired assignment of thematic roles (Manouilidou et al. 2009). Thematic roles are semantic roles that a verb assigns to a noun to indicate 'who did what to whom' in a sentence. For example, AD patients' comprehension of psychological verbs such as 'fear' or 'frighten' indicates a pattern of spared comprehension of sentences such as 'The boy fears the thunder,' but impaired comprehension of sentences such as 'The thunder frightens the boy.' Findings such as this one escape standard neuropsychological testing of language in AD patients, because it is focused on more general aspects of language.

So far, research on language deterioration in AD has focused on patients who are already at the dementia stage, typically within the range of mild to moderate dementia. However, recently redefined research and diagnostic criteria for AD have promoted a concept of AD as a continuum, including preclinical, prodromal (mild cognitive impairment [MCI]), and dementia stages of AD (Dubois et al. 2010). The new criteria strongly emphasize the role of biomarkers in identifying stages of the disease, such as abnormal levels of cortical amyloid- β and tau-proteins, along with neuroimaging markers of Alzheimer's pathology, such as regional hypometabolism, cortical thinning, gray matter volume reduction, deterioration of white matter microstructure integrity, and changes in networks' connectivity both while performing a cognitive task and while in a resting state. Crucially, specific biomarkers can be mapped to specific stages of the disease.

Neurolinguistic research is lagging behind these important new developments and currently little is known about language deterioration in the initial stages of AD. Evidence so far indicates that MCI patients have deficits in naming and verbal fluency, with some more general speech production and comprehension deficits, as defined in standard neuropsychological test batteries. Moving towards presumably the earliest stage on the AD spectrum – preclinical AD – recent research has suggested that cognitively normal persons harboring Alzheimer's

pathology, such as increased levels of cortical amyloid- β , show considerable changes in network activation related to cue-based word retrieval in comparison with cognitively healthy persons who do not harbor Alzheimer's pathology (Papp et al. 2016). In other words, even though symptoms of language decline are still not manifest at the preclinical stage, the network changes related to the task performance are already present. One methodological problem with current research on language in preclinical AD is related to the type of language tests used. They typically include verbal fluency, naming, etc. from standard neuropsychological batteries, even though such tests are more appropriate for advanced stages of the disease and miss subtle changes. Thus, to advance understanding of language abilities in early AD, research needs to move beyond standard neuropsychological tests and investigate more specific linguistic hypotheses on various aspects of language representations and computations.

Finally, an important topic related to language and AD pertains to the role of bilingualism in cognitive and brain reserves in persons with Alzheimer's pathology. Some evidence indicates that active use of two (or more) languages on a regular basis contributes to cognitive (and brain) reserve and delays the onset of dementia by 4 years (Bialystok et al. 2007). The idea is that regularly switching between two languages strengthens executive control functions, which deteriorate early in AD. A recent study reported that monolingual persons were diagnosed with AD 5 years earlier than those who were bilingual, 6.4 years earlier than those who were trilingual, and 9.5 years earlier than those speaking four or more languages (Freedman et al. 2014). Still, methodologically more desirable longitudinal studies on the topic are scarce and some report lack of evidence for the protective effect of bilingualism on the onset of AD symptoms (Zahodne et al. 2014).

Does Language Decline with Aging in Cognitively Healthy Persons?

Some research on cognitive aging indicates that language declines in cognitively healthy elderly

persons. Examples of language decline include reduced vocabulary, production of sentences with a smaller mean number of clauses per utterance, and difficulties with grammaticality judgments and comprehension of complex syntax. Other evidence supports the view that cognitively healthy elderly persons have largely preserved language abilities, including syntax, but that they appear to experience difficulties with word retrieval. As an example, in tip-of-the-tongue states, the meaning of a word is available but word form remains elusive, so that the person in this state is left with the impression that the word is 'on the tip of the tongue' and yet they cannot retrieve it from the mental lexicon. According to one model, word retrieval difficulties in cognitively normal elderly persons are caused by impaired phonological access. However, there is no persuasive neurobiological argument to postulate this exact type of word retrieval difficulty in cognitively intact elderly persons.

On the other hand, word retrieval deficit is typical in a range of neurological conditions, including MCI and AD dementia. Recent findings indicate that Alzheimer's pathology is far more frequent among cognitively healthy elderly persons than previously recognized (Jack et al. 2014). Besides, until recently it was not possible to study in vivo brain changes associated with Alzheimer's pathology (e.g., increased cortical levels of amyloid- β tau-proteins). Thus, previous research on word retrieval in normal cognitive aging could not differentiate between cognitively normal elderly persons with Alzheimer's pathology and cognitively normal elderly persons without this specific pathology. It is therefore possible that previous findings that suggested impaired phonological access in 'cognitively normal' aging actually pertain to a mix of persons who are healthy and those harboring Alzheimer's pathology, i.e., preclinical AD (Kljajevic 2015). Future studies on language in healthy cognitive aging need to define more precisely the exclusion criteria regarding neuropathology in elderly persons in order to avoid mixing cognitively intact and preclinical AD populations.

Conclusion

Language dysfunction may result from brain injury, as in stroke and trauma, or from a progressive disease, as in brain tumors and neurodegenerative diseases. It appears that the brain can adapt to such changes to some extent, supporting the concept of functional compensation. However, overcoming specific patterns of language disturbances depends on multiple factors and in many cases it may not be possible.

Cross-References

- [Adaptive Plasticity](#)
- [Brain Imaging](#)
- [Broca's and Wernicke's Aphasia](#)
- [Broca's and Wernicke's Areas](#)
- [Brodmann Areas](#)
- [Communication and Social Cognition](#)
- [Field of Linguistics, The](#)
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- [Multiple Memory Systems](#)
- [Schizophrenia](#)
- [Spontaneous Recovery](#)
- [Verb-ing and Noun-ing](#)
- [Working Memory](#)

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Language Evolution

- [Linguistic Evolution](#)
- [Neurobiology of Language](#)

Language Impairments

- [Language Dysfunction](#)

Language Instinct

- [Steven Pinker and Language Development](#)

Language Instinct, The

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Synonyms

[Pinker and Chomsky](#); [Steven Pinker on language](#); [Steven Pinker on universal grammar](#)

Definition

A 1994 book by Steven Pinker.

Introduction

The Language Instinct is a [1994](#) book by Canadian-born cognitive scientist and linguist Steven Pinker (born September 18, 1954). In it, Pinker asserts that the human capacity for language acquisition is innate. In many ways, Pinker agrees with Noam Chomsky's theory of universal grammar, which states that language is hard-wired in the brain; that language skills develop naturally without instruction, rewards, or punishments; and that properties shared by all human languages demonstrate that it is a universal human trait. He does, however, consider himself more credulous than Chomsky regarding the ability of the theory of evolution by natural selection to explain our innate language capacities.

Refuting Misconceptions About Language

Pinker illustrates that children learn a great deal about language without instruction, which he claims is at odds with common conceptions of language learning. In addition, he criticizes common assertions that the typical person has poor grammar and that language is degenerating over time. He also provides evidence against certain

academic linguistic theories such as the Whorfian hypothesis (also known as linguistic relativity), which states that the properties of a specific language affect how its speakers can perceive and talk about the world. He is especially critical of the “strong version” of this hypothesis: that language determines thought. For instance, one could claim, based on the strong version of the Whorfian Hypothesis, that a speaker whose native language has no word for “rebellion” would be unable to express or perhaps even have thoughts of rebellion. Pinker argues in *The Language Instinct* that thought is independent of language and asserts “the more you examine Whorf’s arguments, the less sense they make” (p. 60).

Innateness of Language

Pinker views language as unique to humans and as an ability that allowed our ancestors to adapt to selection pressures whereby hunter-gatherers who could more effectively communicate with each other would have a survival advantage over those who could not. And because language capacity evolved as the result of a domain-specific selection pressure, Pinker asserts that it is a unique mental module rather than a component of a more domain-general skill such as general cognitive ability. Research supports such a view by demonstrating a double dissociation between brain injuries resulting in loss of language abilities and those resulting in loss of general cognitive ability (e.g., Dunn and Kirsner 2003). For example, a condition known as specific language impairment results in impairment of language skills without impairment of cognitive ability (van der Lely 2005), and a condition known as Williams syndrome results in impairment of cognitive abilities but not a direct impairment of language (e.g., Bellugi et al. 1988).

The Universal Sequence

That language is a product of natural selection and an innate part of human nature means that is not the direct product of human culture; it is not a

human invention in the same way as the wheel or the computer. Language is universal across all human cultures, whereas human inventions are not. Pinker asserts that the universal sequence of language acquisition – wherein children first demonstrate language through babbling, then holophrases (single words expressing an entire thought), and other intermediate stages before achieving mature language skills – is apparent even in deaf individuals. He cites research evidence of “manual babbling” (babbling with hand gestures) in deaf infants (e.g., Petitto and Marentette 1991).

Critical Periods

Additionally, Pinker points to so-called critical periods in language development (age ranges during which a child must have a certain experience in order for language skills to develop normally) such as those detailed by Kuhl et al. (2003). Such specialized and rapid learning processes are not explainable by operant conditioning or formal instruction.

Pinker claims that these findings as well as the natural development and acquisition of language skills in the absence of formal instruction are indicative of the innateness of spoken language.

Cross-References

- [How the Mind Works](#)
- [Language Acquisition](#)
- [Steven Pinker and Language Development](#)

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Language Learning

► Language Development

Language Modularity

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Synonyms

Domain specificity; Functional specialization

Definition

The notion that human cognitive architecture includes a module for language, i.e., an innate system of neural tissue that responds only to speech.

Introduction

The concept of a modularized mind, constructed of distinct units devoted to particular psychological functions, can be traced back at least to Gall, the father of the nineteenth-century phrenology. In the twentieth century, a version of modularity (termed “the new organology” by detractors) was advocated by Chomsky, who speculated that some sort of language module would be necessary to support his universal grammar (e.g., Chomsky

1980). Today modularity is most closely identified with Jerry Fodor, whose publication in 1983 of *The Modularity of Mind: An Essay on Faculty Psychology* (Fodor 1983) electrified the still-young field of cognitive psychology. Fodor’s modularity, which depicts modules as hardwired information processing systems, appealed to a generation of psychologists who were intent on peering into the behaviorists’ “black box” of the mind and were hungry for technical language to describe what they had begun to find there. The theory’s impact on the cognitive and language sciences has been broad, deep, and enduring.

Fodor’s Modularity of Mind

The idea of a modular mind emerged from Fodor’s philosophical view of the brain as a computer. Fodor argues that innate cognitive modules, or “input systems,” are necessary to interpret information encountered “at the surfaces (as it were) of the organism” (Fodor 1983, p. 42) such that it is comprehensible by the “central systems” of the brain, where conscious, higher-order cognitive processes occur. Although he sidesteps providing a detailed list of candidate modules, Fodor does grant that there are likely to be modules for at least “the perceptual systems *plus language*” (emphasis original; Fodor 1983, p. 44). He argues that a module for language interpretation is as valuable to humanity as a module for perception of light or odor on the grounds that all of these hypothesized input systems serve the function of generating hypotheses about “the way that the world is” (p. 45) for use by higher-order cognitive systems. Processing the speech of others, Fodor points out, is a generally reliable way of obtaining information about the world – “In the root case, the convention is that we say of *x* that it is *F* only if *x* is *F*” (p. 45) – and thus a module for speech processing is adaptive.

In *Modularity of Mind*, Fodor provides nine criteria that he concludes are useful in identifying a module, two of which have received outsized attention by both supporters and critics of his thesis: *domain specificity* and *informational encapsulation*. Modules are domain specific in

that they respond only to a particular stimulus domain, for example, the purported language module responds to speech, but not to nonspeech auditory stimuli. Modules are informationally encapsulated in that they are autonomous, i.e., they do not interact with central systems or with each other. The primary implication of encapsulation for the language module is that prior knowledge or beliefs – that is, top-down information flow – will not interfere with speech perception. Fodor dismisses evidence of top-down influences on language comprehension, such as the ability to understand acoustically degraded speech, or the phoneme-restoration effect, as post-perceptual (in the case of the former) or as intramodular flow (in the case of the latter).

The modularity thesis has become unfashionable among cognitive psychologists in recent years (“I am well aware of efforts to debunk this view, the arguments raised toward that end, and the disfavor into which a modular view of the mind has fallen,” comments Curtiss (2013, p. 90) in a recent defense of modularity), for a number of reasons. For one, the double dissociations between language skill and general cognitive abilities in lesion patients and individuals with genetic syndromes that are predicted by a language module segregated from other neural tissue have proved elusive (e.g., Stojanovik 2014; although see Barrett and Kurzban 2006, for an account of the unlikelihood of finding perfect dissociations even in a completely modular system). Additionally, advances in neuroimaging in the past 20 years have failed to reveal spatially or connectively “encapsulated” tissue for language or, for that matter, anything else.

Finally, the concept of “computer” has changed considerably since the publication of *Modularity of Mind*. In the past 30 years, connectionist networks that reliably simulate many aspects of cognition by exploiting parallel distributed processing and spreading activation of information have largely eclipsed the serial, symbol-reading devices on which Fodor modeled his view of the mind. If alternative models of the computer had been available in the 1970s and

early 1980s, Fodor could have perhaps conceived of a different architecture of the mind that is nonetheless computational (cf. Katz 2014).

Reconceptualizing Modularity

However, the modularity thesis might remain viable if one is willing to accept a looser definition of a module. The encapsulation requirement now seems fairly untenable, but the same is not necessarily true of the domain-specificity requirement. It is well established that there are certain areas of the brain, and networks of these areas, that are reliably involved in language processing (e.g., Fedorenko 2014). Thus, cognitive psychologists and neuroscientists almost universally allow that there is functional specialization for language. (The terms “domain specific” and “functionally specialized” are used interchangeably here, although others have differentiated them.)

Of those who are willing to declare the language network a module, its provenance is still a matter of serious contention. A spectrum of thinking on the matter stretches from strong nativism on one end to complete emergentism on the other. Nativists such as Curtiss, whose doctoral dissertation examined the famed case of Genie, point to differential activation patterns in response to speech versus other acoustic stimuli in the brains of infants as evidence that neural speech systems are hardwired (Curtiss 2013). Emergentists, meanwhile, are highly dismissive of the notion that a “blueprint” of the mental structures that will develop in an individual is genetically programmed. Karmiloff-Smith (1992) argues that modules are formed wholly through interactions with the environment, and Barrett and Kurzban (2006) provide an evolutionary mechanism for their emergence: natural selection has provided humans with genes that allow the brain to functionally specialize in response to stimuli and environments that have been reliably encountered across human history. It follows that “if the normal environment of development is changed, developmental outcomes might be different” (Barrett and Kurzban 2006, p. 638).

Thus, for the nativist, Genie's brain was denied the linguistic input required at the right moment in development to rouse its innate language module; for the emergentist, because Genie was denied linguistic input at the right moment in development, the gene-by-environment calculus that causes the language module to emerge under normal circumstances was disrupted, and no such module ever formed. Yet another view departs from the nativist-emergentist spectrum altogether, and has languages evolving to fit brains, rather than the other way around (Christiansen and Chater 2008). This view puts any biological adaptation for language as recent, minimal, and falling far short of anything that could be considered a module, even in a relaxed sense of the term.

Conclusion

Despite the increasing skepticism with which the modularity thesis has been viewed in certain academic circles in the past two decades, it is by no means obsolete. It is a touchstone for many evolutionary psychologists, who feel that Fodor was in fact too conservative when he denied modularity to the central systems of the brain. They posit instead that the brain is massively modular, because a large number of functionally specialized cognitive systems should be more flexible in the face of a changing environment than a small number of functionally general systems (e.g., Tooby and Cosmides 1992; Barrett and Kurzban 2006).

When *Modularity of Mind* was first published, one might have assumed that the invention of a noninvasive technology for watching a brain in action would go a long way toward settling the question of the validity of Fodor's theory. Today, nearly 25 years after functional magnetic resonance imaging was first used to watch human brains at work, the debate is far from settled. Modern conceptualizations of modularity are strongly altered from the one Fodor proposed, but the usefulness of the construct for framing central questions in the study of human cognition has ensured its survival to the present day.

Cross-References

- [Evidence of Brain Modularity](#)
- [Linguistic Evolution](#)
- [Nativism](#)
- [Neurobiology of Language](#)
- [Universal Grammar](#)

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Language Origins and Evolution

- [Linguistic Evolution](#)

Language Stages

► [Interactive Language Development](#)

Large-Scale Cooperation

► [Evolution of Human Sociality, The](#)

Largest *Homo* Brain

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Synonyms

[Hominid](#); [Hominidae](#); [Human](#); [Man](#)

Definition

Genus that encompasses modern and extinct human species

Introduction

The brain and cognition have been studied from an evolutionary perspective for many years with size often correlated with aptitude. Still we have seen from animal models that brain size does not always predict ability. For humans, our greatest adaptation has been the development and efficiency of our brains, which many would define as a consequence of their relative size. Therefore to better understand the evolutionary psychology of human development, exploring the largest brain in our genus would be paramount.

Variations of *Homo*

To be classified as a species of the genus *Homo*, the following features – a mean cranial capacity greater than that of members of the genus *Australopithecus*, muscular ridges on the cranium, smaller features such as the mandible and maxillae, and distinct differentiation in bone structures – must be present (Antón and Snodgrass 2012). Within the genus exists the *Homo habilis*, *Homo erectus*, *Homo neanderthalensis*, and *Homo sapiens*. The *Homo habilis* are the most ancient representative of the genus *Homo*. They inhabited parts of the world, roughly two million years ago. *Homo sapiens* are the only surviving species of the genus *Homo*, as well as the only extant human species.

From various gatherings of information known to date, scientists have deemed *Homo sapiens* as the most intelligent species of the genus. Research on intelligence has stated that a relationship exists with anatomical structures, such as brain size and capacity. Neanderthals were known to have larger brains than *Homo sapiens*; however compared to body mass, Neanderthals actually had smaller brains than modern-day *Homo sapiens*.

Consequently, brain sizes, specifically in *Homo sapiens*, were and continue to be researched throughout the years. Several factors have been attributed to increased brain structures. Currently, *Homo sapiens*' brains weigh roughly 1,400 g and are around three times the size of the brains of great apes. It is also larger than presumed for the size of the human body. Fossil evidence of the direct capacity of the cranial size has been linked to the hominin evolution, with increased growth in size over the past two million years. In comparison to the other species, chimpanzees and bonobos have similar brain structures but differ significantly in social skills and behavior (Verendeev and Sherwood 2017).

What Influences Brain Size?

The differences surrounding brain structures and features have led researchers, such as Healy and Rowe (2006), to find that behavioral ecologists

are interested in the ecological factors and life history traits that may be associated with brain size. Through the investigation of these factors, ecologists' research focused on identifying the most important selection pressures. Over the past 10 years, analyses comparing brain size and its evolution have been conducted. Some recent studies have found a relationship between the brain's size and behavioral traits such as migration, deception, and female promiscuity (Healy and Rowe 2006).

In contrast, other studies have explained that there may be a dietary association with the growth in the brain size of mammals. In other times, diet appeared to explain the brain's formation and size in nonhuman primates. Among many other evolutionary researchers, Foley and Lee (1991) have agreed that the variation in the brain structure's size could be attributed to ecological factors, such as life history parameters. A conclusion drawn from the research is that "large brains resulted from various increases in size of parts of the brain, according to their importance" (Mace et al. 1980). Additionally, differences in brain areas could synchronously occur, causing trade-offs between the areas that cannot be measured as whole brain size. Therefore, although brain size was attributed to corresponding ecological factors, it has also been linked to increased function.

From an evolutionary standpoint, these changes in brain size have been linked to many different hypotheses. Among these, the three major theories have focused on the demands of ecology, climate change, and social competition.

Climate change is considered one of the major theories that could explain the increase in brain size, due to the unpredictable changes in the weather. As many ice ages occurred throughout the earth, these unpredictable weather changes accompanied them. As a result, many of our ancestors migrated away from the equator and encountered challenges, such as a depletion of resources. The scarcity of resources led to the development of greater skills used for survival. Among these skills, their ability to find resources and in turn "cleverness" may have resulted in the expansion of their brain capacity. In addition, the climate shifts that caused the migrations to the

north or south of the equator could have further influenced the exposure to the parasites found in the surrounding environments. Because there are fewer parasites found as you migrate further away from the equator, it could be presumed that *Homo sapiens* were not consuming their energy and calories to fight off pathogens, thus allowing for these calories and energy to be used to further influence brain development.

A more commonly known hypothesis is that of social competition for resources which influenced brain size. As aforementioned, the scarcity of resources led to the development of greater skills used for survival due to the competition for resources. As the population grew, the number of individuals contesting for the same resources grew as well. This hypothesis is rooted in the idea that those of higher social status in an environment would have more access to resources, leading to their offspring having higher chances of survival. Those that are not considered as socially adept will eventually die off and consequently influence the group as a whole, by increasing their social "fitness." According to this evolutionary hypothesis, the effects of the social competition could cause the increase in brain size.

In a study conducted in March 2009, 175 skull fossils from humans and other species of the genus *Homo* were studied. Many variables, such as how old the fossils were, the temperature of the environment in which the *Homo* species lived, where they were found, population density, and level of parasites in the environment, were studied (Bailey and Geary 2009). The variables were used in a statistical analysis which concluded that the best predictor of the increase in the *Homo* brain size is population density. This variable further explains the social competition between species since a higher population density would indicate that there is a larger population in an environment. The results of this study also showed that the climate changes contributed to the developments in the *Homo* brain, but were not as significant as the variable of population density. Although the social competition hypothesis seems to be the best explanation for the growth of the *Homo* brain, there is no concrete evidence that certain species,

such as the *Homo erectus*, were in fact in social competition.

Brain Size and Intelligence

The changes in brain size may be linked to differences in the brain development, neuroanatomical reorganization, and modifications at the molecular level (Healy and Rowe 2006). Further studies suggest that the increase in brain size is uniform, as a result of the rate and cessation of symmetrical cell cycles being identical. If differences in cell cycles are among regions of the brain, the result would be a “positive or negative allometric growth” (Roth and Dicke 2005). This kind of growth within the brain has been classified as a source of increase in function; this may be a result of the difference in intelligence levels.

It is probable that the reorganization at certain molecular levels, and not solely the brain size and capacity, produces the distinction in cognition among various species. The increase in human brain size is due mostly to the expansion of the neocortex, specifically heteromodal association regions of the temporal, parietal, and frontal lobes. These evolutionary changes to human association cortex involve the enlargement of structures that “are homologous in other primates and alterations to cortical connectivity” (Verendeev and Sherwood 2017). This rapid growth has been linked to the base of certain genetic mechanisms. As explained by researchers, these mechanisms resulted in a cell division process that has contributed to the expansion of the cranial capacity (Roth and Dicke 2005).

However, some researchers, such as Rogers (2004), do not support that the association between brain and behavior could be explained solely by measuring whole brain size. They believe that the brain must be studied in separate components such as specific brain regions that have changed evolutionarily to allow for advanced functioning. Among these specific regions, the evolution of the cerebral cortex and cerebellum suggests an increase in cognitive and affective functioning among *Homo sapiens*.

As aforementioned, humans are known to be the most intelligent species among animals.

Compared to other mammalian brains, the human brain has been viewed as the most cognitively able, with an overdeveloped cerebral cortex that represents over 80% of the brain mass, with 100 billion neurons (Herculano-Houzel 2009). It is unclear which exact characteristics of the brain determine the difference in intelligence levels among animals. However, studies have found that the following properties – theory of mind, imitation, or a syntactical language – may not be uniquely found in humans, challenging the notion that human beings are the most intelligent species. Other studies have conveyed that controversy has existed among the topic of larger brain capacity associated with greater intelligence due to research that has found that some animals with smaller brain capacities do have higher brain functioning (Herculano-Houzel 2009).

The findings of many research studies have demonstrated that the human brain resulted from the changes in evolution that occurred progressively and explain their advanced cognitive functioning. In contrast to Herculano-Houzel (2009), noting the controversy that exists in explaining intelligence levels in correlation with brain size, Verendeev and Sherwood (2017) discussed the relative size and additional cortical areas that most likely contributed to an advanced neuroanatomical basis for “fine-grained information” and higher levels of processing among *Homo sapiens*. Among these anatomical changes exist the changes evident in microstructure, such as the distribution patterns of neurons and glial cells, which allowed for plasticity and increased learning capacity. These anatomical changes, in combination with cultural and social forces, helped shape human cognition to develop to what it is today (Verendeev and Sherwood 2017).

Although the structure of the human brain continues to be studied and discussed in correspondence to ability and function, other components have been correlated with increased brain size. For example, diet has played a role in increased brain size. A study by Navarette et al. (2011) challenged the “expensive-tissue hypothesis” which claims that the evolutionary changes within the brain are correlated to the evolutionary differences in the digestive tract (Navarette et al. 2011). The hypothesis has been widely supported by

many researchers and scientists but has shown little empirical support. It was found that controlling for fat-free body mass, the brain size is not negatively associated with the mass of the digestive tract or any other organ, refuting the expensive-tissue hypothesis (Navarrete et al. 2011). The notion that early species of the genus *Homo* evolved larger brains due to dietary changes, such as more meat and cooked food, leads to the idea that this allowed for a smaller digestive tract. As a result, the large brains found in *Homo sapiens* have been suggested to act as cognitive buffers against starvation, thus reinforcing the idea that nutrition and diet may have indeed contributed to the evolution of a larger brain capacity.

Conclusion

In conclusion, it is difficult to distinguish the exact properties that contributed to the large brain size of *Homo sapiens*. As mentioned across studies, the combination of neuroanatomical growth, diet, and social function may be attributed to the advanced function of the human mind, such as theory of mind and complex cognitive ability. However, it remains unclear whether an association between the whole brain size or certain brain properties and levels of intelligence directly exists. There is also minimal concrete evidence that supports the evolutionary theories of social competition and climate change to be the ultimate predictors of the increase in brain size. Therefore, additional research on the *Homo* brain and its growth in capacity should be facilitated to further understand the rapid changes which may promote future brain size development.

Cross-References

- [Brain at Birth](#)
- [Brain Development](#)
- [Evolution of Intelligence, The](#)
- [Hominin Evolution](#)
- [Homo habilis](#)
- [Homo neanderthalensis](#)
- [Human Brain Evolution](#)

- [Intelligence](#)
- [Resources for Brain Development](#)
- [Why Humans Are Unique](#)

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Laryngeal Descent

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Synonyms

Descended larynx, Descent of the larynx, Vocal tract reconfiguration

Definition

Laryngeal descent refers to a movement of the larynx away from the oral and nasal cavities in humans or other mammals, either temporarily during vocalization (dynamic descent) or permanently during development (permanent descent).

Introduction

It has been known since the nineteenth century that adult humans are unusual in having a descended larynx. In most mammals, the resting position of the larynx is directly beneath the palate, at the back of the oral cavity, and the epiglottis (a flap of cartilage at the top of the larynx) can be inserted into the nasal passage to form a sealed respiratory passage from the nostrils to the lungs. In humans, in contrast, the larynx descends away from the palate during infancy, and adults can no longer engage the larynx into the nasal passages. This trait was once thought to be unique to humans and to play a central role in our ability to speak, but it is now known that most mammals dynamically lower the larynx during vocalization and in addition that many species have a permanently descended larynx comparable to that in humans. There is thus little indication that a descended larynx plays a crucial role in human speech control or language capabilities.

History

For many years, the descended larynx was believed to be unique to humans, supporting the inference that it was crucially involved in speech production (Lieberman 1968, 1984). Because descent of the larynx in humans also pulls the tongue base, supported by the basihyoid bone, down away from the palate, it leads to a reconfiguration of the vocal tract geometry, with an oral and pharyngeal cavity of roughly equal length and volume. Moving the tongue around within this reconfigured vocal tract allows adult humans to produce extreme vowels that would otherwise not be possible. Particularly when a

descended larynx was thought to be unique, this was thought to be closely associated with the evolution of spoken language.

In 2001, researchers studying deer vocalization discovered that adult males of two European deer species – red deer *Cervus elaphus* and fallow deer *Dama dama* – have permanently descended larynges, with a resting location comparable to adult humans, roughly halfway down the neck (Fitch and Reby 2001). Once alerted to this possibility, researchers have now found comparable permanently descended larynges in many other species, including tigers, lions, jaguars, koalas, and Mongolian gazelles (reviewed in Fitch 2010)

Furthermore, by using x-ray video to observe the vocal tract of living animals while they vocalized, it was found that a *dynamically* descended larynx is observed during at least some types of calls in all mammals yet studied (Fitch 2000), indicating that vocal tract geometry is in fact highly flexible and that any mammal is capable of reconfiguring its vocal tract during vocalization. These new observations clearly indicate that neither a dynamically nor a permanently descended larynx is uniquely human.

Development

Human newborns have a vocal tract configuration like that of most other species, with a high larynx that can be inserted in the nasal cavity but can be retracted during crying. However, starting around the age of 3 months, the larynx begins to retract away from this position, reaching an adult-like geometry by around 6–8 years of age (Lieberman et al. 2001; Sasaki et al. 1977). The mechanical forces that lead to this descent are not known. However, recent data indicate that a similar, though less extreme, extent is seen during chimpanzee development (Nishimura et al. 2006).

It is also well known that a second descent of the human larynx occurs during puberty but only in males (Lieberman et al. 2001). This leads to a sexual dimorphism between adult men and women in vocal tract length, with men having significantly longer vocal tracts, which gives men lower formant frequencies. This vocal tract

elongation is physiologically and acoustically independent of the growth of the larynx itself which, by lengthening the vocal folds, is responsible for men having lower-pitched voices than women. However, both of these changes occur during puberty.

Adaptive Function

When the descended larynx was believed to be unique to humans, only one hypothesis for its adaptive function seemed plausible: the idea that it served to increase the discriminability of speech sounds and thus to improve speech communication (Lieberman 1968, 1984). This led many researchers to assume that the permanent descent of the larynx played a crucial role in the evolution of spoken language. The newer comparative data have called this assumption into question. First, dynamic descent of the larynx allows all mammals to reconfigure their vocal tract by elongating the pharynx, and in some species (such as dogs) this reaches human-like proportions (roughly equal oral and pharyngeal cavities). This suggests that, for any species or at any point in hominin evolution, the vocal tract could be dynamically reconfigured to enlarge the range of producible speech sounds.

The most plausible function of the dynamic descent of the larynx seen in dogs, pigs, monkeys, and other mammals is that it allows vocalizations to be produced through the oral cavity rather than the nasal cavity. Because the nasal cavity, with its conchae and increased surface area, absorbs acoustic energy, orally produced vocalizations will be louder than nasally emitted sounds. Consistent with this, quiet close-contact vocalizations (such as grunts in pigs or whines in dogs) appear to be nasally emitted, and it is only loud vocalizations (pigs' squeals or dogs' barks) that are produced orally with a descended larynx. This hypothesis also explains why human infants lower their larynx during crying.

Regarding permanent descent, those non-human mammals who exhibit a permanent descent of the larynx use it to produce loud

and impressive display vocalizations like roars and do not appear to use it to produce a wide variety of vowel-like sounds (and obviously, deer, lions, and koalas do not speak). Rather, current data supports the idea that laryngeal descent and the concomitant elongation of the vocal tract are an adaptation to make the vocalizer sound larger than it otherwise would. Formants are known to be correlated with body size in many (probably most) mammals, and thus can provide an important cue to body size (Pisanski et al. 2014; Reby et al. 2005). By elongating its vocal tract while vocalizing, an animal can thus match the acoustic properties of a larger animal, exaggerating its own apparent size.

This size exaggeration hypothesis (Fitch and Reby 2001) now has ample support in nonhuman species. But what of humans? The later descent of the human larynx occurs during puberty only in men, and men do not have superior speech abilities to women (if anything the contrary is true). Thus, it is unlikely that this pubertal male descent has to do with improving speech sound discriminability. Rather, it is most likely that this pubertal descent also serves to exaggerate the impression of body size conveyed by male voices.

Conclusion

Although long thought to play an important and unique role in human speech, it is now clear that a descended larynx is phylogenetically widespread among mammals and appears to fulfill multiple adaptive functions. Because most mammals appear to have flexible vocal tracts, a capacity for laryngeal descent is a typical mammalian trait. This means that, were a human brain in control, a monkey or dog's vocal tract would be perfectly capable of producing a wide range of discriminable speech sounds, fully adequate for linguistic communication. Thus, a permanent descent of the larynx was not an important hurdle that human ancestors needed to cross in order for spoken language to be possible. Regarding the permanently descended larynx, the size

exaggeration hypothesis provides the most plausible explanation in those nonhuman mammals that exhibit this trait as well as in adult human males. What remains more difficult to understand is why the larynx descends during infancy, in both males and females. The fact that this occurs in both chimpanzees and humans suggests that this early descent was already present in the common ancestor of humans and chimpanzees and thus that this too serves some nonspeech function, perhaps allowing young animals to produce louder vocalizations.

In conclusion, the widespread idea that the human descended larynx is or was a crucial adaptation for speech is not supported by the comparative data. This also implies that attempts to date the emergence of language by using fossils to determine laryngeal position is misguided. Although a permanently descended larynx probably does allow humans to produce a slightly larger vowel space, with a greater degree of control than would be possible with the dynamic descent seen in dogs or monkeys, the comparative data suggest that this is a matter of degree and not a difference in kind, and in fact may be a by-product of other selective forces (e.g., increasing loudness or size exaggeration by formant lowering).

Cross-References

- [Linguistic Evolution](#)
- [Speech Volume](#)
- [Vocal Attractiveness](#)
- [Vocal Indicators of Dominance](#)
- [Voice Pitch](#)

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Larynx

- [Stereotyped Vocalizations](#)

Lashing

- [Spanking](#)

Last Male Advantage

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Synonyms

[Last male precedence](#)

Definition

The preference for females to be fertilized by the last male they engaged in coitus with. Some species possess first male precedence, the preference for females to be fertilized by the first male they engaged in coitus with.

Introduction

Last male advantage is one example of what some researchers call “sperm precedence,” “sperm predominance,” or “ordinal ejaculation effects.” It is the phenomenon of females being more likely to be fertilized by the last male they engaged in coitus with. While some species possess “first male advantage” or “precedence” (the preference for females to be fertilized by the first male they engaged in coitus with), humans possess a pattern of last male precedence. This is believed to be a result of the semen displacement hypothesis (see ► [“Genital Evolution”](#)).

The semen displacement hypothesis posits that the human penis, with a relatively larger glans and more pronounced coronal ridge than is found in many other primates, may function to displace seminal fluid from other males in the vagina by forcing it back over/under the glans. During intercourse the effect of repeated thrusting would be to draw out and displace foreign semen away from the cervix. As a consequence, if a female copulated with more than one male within a short period of time, this would allow subsequent males to “scoop out” semen deposited by others before ejaculating (Baker and Bellis 1995).

To test this hypothesis, Gallup et al. (2003) used artificial models and measured the magnitude of artificial semen displacement as a function of penile morphology, depth of thrusting, and semen viscosity. The magnitude of displacement was directly proportional to the depth of thrusting and inversely proportional to semen viscosity. The researchers identified the coronal ridge and frenulum as key morphological features in semen displacement. Gallup et al. (2003) also found that males appear to modify the use of their penis in ways that are consistent with the

displacement hypothesis. Sexually active males and females reported deeper and more vigorous thrusting when in-pair sex occurred under conditions related to an increased likelihood of female infidelity.

According to the semen displacement hypothesis, we would expect sperm competition among humans to involve ordinal ejaculation effects. Under conditions in which several males copulate with a female in close temporal proximity to one another, the male who mated with the female last would have an advantage. The last male in the sequence would be in a position to displace the semen left by previous males before inseminating the female with his own semen. This assumes, of course, that other factors such as sperm quality, ejaculate size, penis length, and female control of mating are constant (Baker and Bellis 1995).

Last male advantage is found in several other species, including the honeybee, damselfly, fruit fly, bush cricket, dragonfly, water bug, various beetles, spiders, crabs, finches, butterflies, and other species (see Smith 2012, for a review). In several species, including fruit flies, moths, and damselflies, this effect is clearly due to semen displacement.

This last male advantage would be the major driving factor in the evolution of penile morphology discussed above. This has been well documented in rodent and insect species. Penises in various species have specific features: spines, barbs, spicules, or huge coronal ridges, that function to remove previously deposited sperm or copulatory plugs left by previous males. The type of penile morphology corresponds to the type of copulatory plug the species possesses, with harder spicules or spines for harder copulatory plugs. In the rat, the importance of striated penile muscles has been emphasized (Baker and Bellis 1995).

Conclusion

Many species show a reproductive advantage to being the last male to mate with a female, and the evolution of male genitalia plays a pivotal role in this phenomenon.

Cross-References

- [Genital Evolution](#)
- [Intrasexual Competition](#)

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Last Male Precedence

- [Last Male Advantage](#)

Lateral Geniculate Complex

- [Lateral Geniculate Nucleus](#)

Lateral Geniculate Nucleus

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Definition

The lateral geniculate nucleus (LGN) is a small section of the dorsal thalamus. It relays visual information from the retina to visual cortex.

Synonyms

[Lateral geniculate complex](#)

Introduction

The LGN derives its name from its characteristic curved shape resembling a bent knee (*lat.* “genu” for knee). While the medial geniculate is part of the auditory pathway, the lateral geniculate is concerned with vision. Its primary function is to relay sensory information from the retina to the visual cortex via a large fiber bundle called the optic radiation.

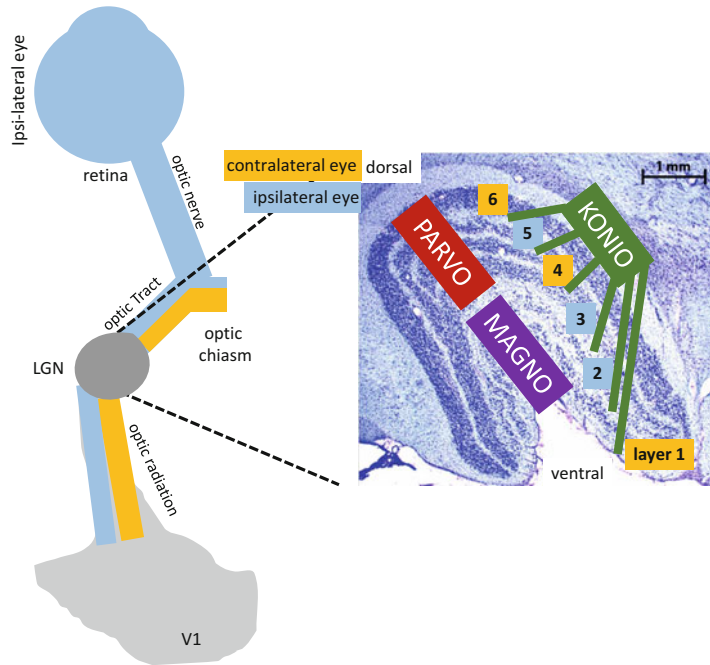
Basic Anatomical Organization

In all mammalian species, the outputs of the two eyes in the form of retinal ganglion cell projections (i.e., the optic nerve) terminate at the LGN of the thalamus (see Jones (2007) for a comprehensive, comparative description of thalamic organization). Both the inputs to and structure of the LGN differ across species. For example, only one third of all retinal output projects to the LGN in rodents, whereas 90% of all retinal output projects to this structure in primates, suggesting a more central role for vision in primates. Across all mammals, LGN neurons primarily project to visual cortex, rendering the LGN a relay between the eye and the cerebral cortex. The LGN is often separated into several layers of similar cell types reflecting ganglion cell-specific input. LGN organization varies across species, with the most prominent lamination present in primates and visually engaged carnivores, such as the cat. The LGN of these species constitutes several cell-rich layers that alternate with comparatively cell-poor interlaminar zones. For example, the LGN of macaque monkeys, arguably the best-studied species with respect to visual function, consists of six distinct cell-rich layers and intralaminar zones, constituting three separate projection systems that each reflects specific aspects of retinal output (Fig. 1). Each LGN layer receives input from one of the two eyes, resulting in a pattern of alternating inputs from each eye across LGN layers, although this patterning is less apparent in some species. In macaques, layers 1, 3, and 6 receive input from the contralateral eye (i.e., the eye that sits on the other side of the skull), and layers 2, 4, and 5 are innervated

Lateral Geniculate Nucleus, Fig. 1

Schematic representation of the retino-geniculate pathway to V1.

Microscopic picture shows LGN's laminar organization



by the ipsilateral eye (i.e., the eye that sits on the same side of the skull). In addition to retinal input, some neurons in the most ventral part of the LGN also receive input from the superficial layers of the superior colliculus, a midbrain structure that also receives direct retinal projections. Although about one third of LGN neurons are local interneurons providing inhibitory input to LGN projection neurons, the main inhibitory input to the LGN is from neurons of the neighboring thalamic reticular nucleus. LGN cell types display different immunoreactive sensitivity, which can be exploited by cell type-specific genetic targeting and immunohistochemical labeling.

Three Parallel Cortical Projection Systems

In primates, the three main LGN projection systems consist of big (magno), small (parvo), and very small and sparse (konio) cell types located in layers 1 and 2 (magno), 3–6 (parvo), and interdigitated layers (konio) (described in detail in Usrey and Alitto (2015)). The magno and konio systems each constitute 10% of primate LGN relay neurons, and parvo neurons constitute 80%. The three

projection systems remain segregated on their path from retina to visual cortex. This is reflected in their distinct retinal inputs consisting of parasol, midget, and small bistratified retinal ganglion cells feeding LGN magno, parvo, and konio neurons, respectively. The segregation into three distinct LGN streams is maintained for the projection to primary visual cortex (V1) but appears to break apart for subsequent cortical processing, where these signals appear more intermixed. The main V1 targets for LGN projections are the granular layers 4A and 4Cb for parvo, 4Ca for magno, and layers 2 and 3 for konio projection neurons, respectively. However, there are also sparser projections to deep cortical layers. A distinct feature of the konio system is that at least part of its ascending projections bypass V1 entirely and project directly to higher cortical areas, mediating residual vision following V1 injury (► “Blindsight”).

Functional Organization

Visual functions of the LGN are described in detail in Hendry and Reid (2000) and Jones (2007). LGN neurons typically receive convergent input from 1–5 retinal ganglion cells, with a

smaller number for the fovea compared to the periphery. Neighboring LGN cells receive inputs from neighboring groups of retinal ganglion cells, resulting in a two-dimensional topography termed “retinotopy.” Electrophysiological measurements of LGN neuron response properties to various types of visual stimuli largely confirm this neuronal convergence. LGN neurons are optimally excited by visual (light) stimulation of a small patch of the retina termed the receptive field. LGN neurons’ responses closely resemble the response properties of retinal ganglion cells in that they either respond to the onset or the offset of light (ON/OFF cells). The strongest LGN responses are evoked if a small bright or dark stimulus is surrounded by the inverse pattern of visual stimulation. The so-called ON cells respond best if the center of their receptive field is stimulated by a patch of light while the surrounding region of visual space resides in the dark. In the same vein, OFF cells respond best if a dark patch is placed into the center of the receptive field while there is light in the surround. Across species, most LGN cells receive inputs from one eye only. However, in rodents some LGN cells are innervated by retinal ganglion cells of both eyes, suggesting that neurons in rodent LGN encode inputs to both eyes. Binocular LGN responses have also been shown for the cat. In this species, the activity of the majority of LGN neurons is different when both eyes are stimulated than when just the eye that provides the main excitatory drive is stimulated. In contrast, most neurons in monkey LGN are sensitive to one eye only, suggesting that activity relating to the two eyes is separated before primary visual cortex. In primates, the most characteristic feature of parvo neurons is their antagonistic response to medium (i.e., green light) versus long (i.e., red light) wavelength stimulation resulting in receptive field color opponency. Parvo neurons often respond tonically and faithfully reflect high spatial frequency content when tested with grating stimuli. The responses of magno neurons have been described as more transient and broadband. They lack spectral sensitivity but exhibit greater sensitivity to low contrast and high temporal frequency stimulation. By comparison, the response properties of konio neurons seem more broadly distributed, with a subset responding preferentially

to the presence of short-wavelength (i.e., blue light) stimuli (Hendry and Reid 2000). This heterogeneity of konio neuron responses may in part reflect their diverse input from several types of retinal ganglion cells as well as the fact that this subgroup of neurons also receives input from the superior colliculus.

Cortical Influences on LGN

About 80% of LGN inputs arise from primary visual cortex (V1) (see Schiller et al. 1990; Sherman and Guillery 2009). This number appears surprising given the close correspondence between LGN activity and retinal stimulation. Closer examination reveals that cortical projections terminate more distally on LGN neurons and may therefore only modulate (i.e., slightly increase or decrease firing rates), rather than drive (i.e., elicit) LGN responses. For example, excitatory input from cortex can shift neuronal responses from tonic to bursting activity. At the origin of this modulatory influence are groups of neurons in layer 6 of V1 that provide stream-specific feedback to the LGN. However, other cortical visual areas also provide sparse feedback to LGN. While there is no direct evidence that cortical feedback is causing cognitive modulation of LGN neuronal activity, modulation of LGN activity has been demonstrated for top-down spatial attention (reviewed in Saalmann and Kastner 2009), possibly resulting in improved efficiency for relaying signals from LGN to cortex.

Cross-References

- [Blindsight](#)
- [Frontal Cortex](#)
- [Retina, The](#)

Conclusion

LGN activity tends to closely reflect its retinal input, more or less faithfully relaying visual information from eye to cortex. It thus remains

somewhat enigmatic why retinal information passes through this nucleus instead of projecting to cortex directly. One feature of the LGN is that the vast majority of its inputs are provided by cortex and other parts of the thalamus and the brain stem. These inputs selectively modulate the two eyes' outputs as they are represented in the three LGN subsystems before they reach cortex. This activity undermines the idea of the LGN as a simple relay between the eye and cortex. Indeed, significant alteration of LGN responses occurs during varying states of sleep and wakefulness, for example, and it is well established that the LGN can act as a state-dependent control that blocks, passes, or amplifies sensory information depending on the wakefulness of the individual. LGN activity has also been shown to modulate with eye movements even in the dark. Moreover, cognitive modulation of LGN activity has been shown to amplify visual signals. The convergence of several retinal ganglion cells onto single LGN neurons as well as the presence of inhibitory neurons within the LGN further suggests additional integration taking place among LGN neurons.

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Law of Effect

- ▶ [Thorndike's Law of Effect](#)

Leadership

- ▶ [Men in Positions of Power](#)
- ▶ [Social Authority](#)

Leadership vs. Followership

- ▶ [Employer Versus Employee](#)

Leading

- ▶ [Non-human Leadership](#)

Learnability

- ▶ [Intelligence](#)

Learned Helplessness from an Evolutionary Mismatch Perspective

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Laughter

- ▶ [Components of Humor](#)
- ▶ [Humor and Ostracism](#)

Synonyms

[Giving up](#); [Learned irrelevance](#); [Passive coping](#);
[Powerlessness](#); [Uncontrollability](#)

Definition

When individuals become passive about a situation that could be detrimental to their well-being following a previous exposure to a similar unavoidable event. Such a sense of helplessness is believed to have been adaptive in many circumstances over the course of evolutionary history but is likely to be regarded as much more problematic in the modern world due to the evolutionarily novel existence of numerous potential avenues of recourse that were conceivably unavailable in general during the prehistoric era.

Introduction

Learned helplessness was originally conceptualized as a phenomenon to describe why canines would appear to be more apathetic about evading noxious circumstances subsequent to previous experiences with comparable conditions that were unavoidable (Overmier and Seligman 1967; Seligman and Maier 1967). The seminal studies on this topic have proffered that canines, which have encountered unavoidable threats (e.g., electric jolts) in a previous experimental phase and were much more likely to defer or to refrain from eluding such stimuli in an ensuing phase (where they were avoidable) as compared to their counterparts that were not exposed to such unavoidable stressors at the outset, were actually demonstrating learned helplessness (Overmier and Seligman 1967; Seligman and Maier 1967). Subsequent to these, such a phenomenon was likewise identified in humans (e.g., Hiroto and Seligman 1975; Thornton and Jacobs 1971), and was consequently modified to account for individual differences in how one would ascribe the source of his/her sense of powerlessness (Abramson et al. 1978).

In addition, Seligman (1974) has also put forth a prominent formulation of depression which was founded on the notion of learned helplessness, while other researchers have similarly utilized such an explanatory framework to describe various other phenomena that ranged from the seemingly puzzling occurrence of certain individuals electing to remain in abusive

relationships (Walker 1977), to apathetic dysfunctional conduct in the workplace (Martinko and Gardner 1982). To these ends, a wealth of empirical research over the last few decades has since largely corroborated the existence of learned helplessness (e.g., Alloy et al. 1984; Cemalcilar et al. 2003), although apathetic responses towards threatening stimuli that have occurred over an extended period of time are now understood to be instinctual and what might instead be acquired through training is the knowledge that some of these stimuli could actually be dealt with effectively (Maier and Seligman 2016). From an evolutionary point of view, such instinctual reactions were likely adaptive at some stage in evolutionary history for them to have been widely present in the modern day.

Adaptive Functions of Helplessness

In this regard, it was contended that passive reactions in certain real-world threatening contexts could actually be beneficial for survival and subsequent reproductive success among a diverse range of living organisms in nature (Eisenstein and Carlson 1997). Indiscriminate efforts to escape a threatening situation when an immobile approach would have been more helpful could potentially make a huge difference in terms of one's survivability (Nesse 1999). Indeed, research work on a variety of animals have typically shown that passive responses in the face of a predator could significantly curtail one's risk of being preyed upon (e.g., Miyatake et al. 2004; Thompson et al. 1981). In addition, such displays of inactivity were also believed to be beneficial in riding out belligerence from more powerful conspecifics across diverse types of animals (e.g., Bilde et al. 2006; Cassill et al. 2008).

More specifically, reacting passively when encountering threats that are unavoidable was likewise conceived to be an adaptive strategy for humans (Peterson et al. 1993). Such passive responses were contended to have been advantageous in minimizing the expenditure of unnecessary physiological resources during attempts to avoid an unavoidable threat, while affording the

individual an opportunity to come through the aversive event by limiting attention to oneself (Peterson et al. 1993). Being inactive when one is being exposed to unavoidable circumstances was also believed to be helpful in promoting remedial and recuperative processes in the body that were initiated by the “ventrolateral” “periaqueductal grey (PAG) region” in the brain (Keay and Bandler 2001, p. 669), activities that could potentially be highly valuable in ensuring one’s eventual survival especially if the individual might likely sustain some forms of injury during the event.

In addition, forgoing any active attempt to evade severe psychological stressors has similarly been argued to be useful in effectively addressing a range of mental health issues (Fogle 1978). Efforts geared towards shunning away from distressing thoughts/emotions were conceived to be ineffective in addressing many different psychological issues including “stuttering, insomnia” and “sexual dysfunction” and could have the paradoxical effect of exacerbating the amount of distress associated with these maladies (Fogle 1978, p. 39). By the same token, desisting from trying to realize an unachievable outcome is an undertaking that has been shown to be linked to a lower degree of stress and a more salubrious level of physical well-being (Wrosch et al. 2007). Feeling helpless and conceding defeat when presented with a situation in which any kind of active involvement would invariably be futile in achieving one’s aims was believed to be instrumental in alleviating the cognitive/emotional discomfort in relation to recurrent unsuccessful attempts (and hence in turn improving one’s physical health) (Wrosch et al. 2007).

Taken together, maintaining/restoring to a healthier level of physical and/or psychological well-being would likely lead to an increase in one’s chances of propagating his/her genes into the future generations and thus it is logical to assume that helplessness must have evolved as an adaptive strategy for humans in certain contexts over the course of prehistory. In spite of this however, it is equally evident that responding passively to a threatening state of affairs could potentially also bring about outcomes in which the severity of resultant adverse effects might

override any functional benefit of inactivity in some other circumstances (such as when certain females opted to stay in a relationship whereby their partners have been repeatedly abusive towards them for instance) (Walker 1977). In this regard, the important question that has to be adequately addressed in order to resolve this dilemma is: why does a supposedly adaptive evolved coping mechanism (e.g., helplessness in the face of a threatening, intractable situation) seem to be so problematic at times? The answer appears to be closely related to the notion of evolutionary mismatch.

Helplessness in an Evolutionary Mismatched Environment

In virtue of evolutionary mismatch, an occurrence in which the rapidity of changes in modern environmental conditions has far exceeded the speed at which certain psychological and/or behavioral characteristics (believed to have been adaptive for much of human evolutionary history) could transform in order to adequately adjust to these recent environmental modifications, adopting a helpless coping style in the face of a threatening situation would likely be perceived as much more counterproductive in the socially advanced and technologically developed present day. Although responding helplessly to threatening stressors (especially if they are unavoidable) could potentially still engender some beneficial physical and psychological effects in an individual in the modern context, such outcomes generally pale in comparison to those that could be derived from more active means of coping because most threatening situations are now no longer generally inescapable but humans would typically still respond to them as if they are truly unavoidable as a result of evolutionary mismatch.

In other words, humans would naturally turn to evolved defensive reactions (e.g., helplessness) when confronted with threatening stressors (e.g., when one is faced with a chronic potentially dangerous situation) in general even when such coping habits might be relatively less useful in the modern world (because it takes time for humans to adapt physically and psychologically

to evolutionarily novel environmental conditions). It was believed that individuals in such predicaments could conceivably only counteract their ingrained helpless responses (e.g., by switching to a more active coping style) if they could obtain the knowledge that some of these adverse circumstances are actually likely to be avoidable at present (Maier and Seligman 2016). The possibility of helplessness being an evolutionarily mismatched coping strategy in the modern context could likely affect humans in a variety of situations.

For instance, although empirical evidence have suggested that active opposition to the perpetrator of ongoing aggression in a romantic relationship could actually bring about additional attacks on the victim in the future (arguably because the perpetrator might perceive the need to intensify the aggressive treatments in a bid to regain dominance) (Goodman et al. 2005), a passive approach is not necessarily the best course of action in the present day. Instead, other active means of coping that are increasingly provided in the modern context such as opting to reside in “a domestic violence shelter” or getting in touch with “a domestic violence victim service program” have been found to be most useful in extricating a sufferer from such a predicament (Goodkind et al. 2004, p. 528). In addition, females, for instance, were also demonstrated to be at a lower risk of being repeatedly victimized by their mistreating partners if they have a self-reliant source of income from work or a personal place of residence (resources that are increasingly attainable for females in modern societies around the world) because these females tended to have a significantly greater amount of flexibility in order to the difficult situation (Goodman et al. 2005). However, because of evolutionary mismatch, victims might generally still attempt to deal with prolonged relationship violence by reacting helplessly, and would likely only turn to more effective evolutionarily novel coping options if they are actively provided with such information and guidance in the current context.

In a similar vein, such a process could analogously be instrumental in informing a better understanding (and in turn potentially more-

effective related interventional strategies) of depression. Widely acknowledged to be one of the most explored utilizations of learned helplessness, depression has been extensively shown to be predicted by passivity when responding to a prolonged overwhelming threat (Peterson et al. 1993; Pryce et al. 2011). While behaving helplessly by forgoing any attempt to actively address an overwhelming threat could actually be evolutionarily useful for one’s continued existence in certain situations (e.g., when evading the threat appears to be an impossible task) (Eisenstein and Carlson 1997), such potentially prehistorically useful, depressive-like symptoms were significantly more likely to presently produce more harm than benefits due to the much greater range of opportunities afforded by the modern world (Trimmer et al. 2015).

For instance, although adopting a passive approach, manifested in the form of depressive symptoms, could be beneficial for recuperative purposes when one has sustained an injury (Keay and Bandler 2001; Kim 2013), such evolved responses (which would have been particularly advantageous in the ancestral context where the availability of other effective forms of therapeutic interventions were conceivably severely limited) are generally substantially inferior to more active coping methods in the medically advanced present environment. Indeed, empirical evidence have suggested that an active approach to remedying an injury via partaking in interventions afforded by modern medicine was linked to significantly enhanced well-being among those afflicted (e.g., Gottlob et al. 1999; Levendoglu et al. 2004). Providing individuals with the knowledge that prolonged suffering following an injury may actually be avoidable (by means of active engagement in the modern-day medical treatments) could therefore likely also be useful in reducing the need for helpless responses (and hence the risk of depressive symptoms) in such a situation. Similar outcomes are also expected in relation to other depression-related events (e.g., marital discord or problems at work) whereby people might be inclined to react helplessly as an evolved coping mechanism. In fact, an evolutionary mismatch perspective

could conceivably also elucidate the evolutionarily novel challenges associated with a diverse range of situations that has been linked to learned helplessness in the modern world.

Conclusion

Reacting helplessly in the face of a prolonged threat could be adaptive in minimizing the extent of harm one might experience in such a situation. Such evolved coping tendencies are believed to have aided humans in their survival over much of prehistory especially when individuals were confronted with circumstances in which active responses might actually result in a greater threat to their well-being. However, given the potentially unprecedented amount of opportunities afforded by the modern environment with regard to dealing effectively with diverse seemingly intractable problems in an active manner (that were generally much more likely to be unavailable in the ancestral context), a passive approach might not be the most useful course of action. The process of evolutionary mismatch could shed some light on why a generally sub-optimal coping strategy (by modern standards) like learned helplessness would nonetheless be adopted in the present day and how such knowledge could inform more effective methods of dealing with prolonged threatening situations.

Cross-References

- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)
- [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)

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Learned Irrelevance

- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)

Learner-Centered Education

- [Child-Centered Learning](#)

Learning

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Synonyms

[Learning disorder](#)

Definition

A developmental disorder that appears during school years, although it may not be recognized until later in life. It impairs one's acquisition of new knowledge even though the individual possesses a normal intelligence quotient (IQ) (American Psychiatric Association 2016).

Introduction

There are 13 categories of learning disabilities (Learning Disabilities Association of America 2017); the diagnostic criteria of which are outlined in the Diagnostic and Statistical Manual of Mental Disorders (DSM-V) under *Learning Disorders*. Learning disabilities affect approximately 5–15% of school children and 4% of adults. Dyslexia is considered the most common learning disability, with approximately 80% of learning disabled individuals bring afflicted with it or a similar reading disability (American Psychiatric Association 2016).

Learning disabled individuals are of normal intelligence range (with an IQ around 100), and the disability cannot be because of insufficient instruction. School environment can impact those with a learning disability, as it is typically where the disability is first noticed. There is, however, special training called *Orton-Gillingham* that educators can receive to help children and adults improve their learning skills. There are also accommodations that school children can receive to help with their studies.

Orton-Gillingham Method

Drs. Samuel Orton and Anna Gillingham, developed Orton-Gillingham for students with dyslexia. Orton-Gillingham combines multi-sensory techniques with the structure of the English language, and it is beneficial not just for dyslexic students, but all students (Institute for Multi-Sensory Education 2016). Although developed in the 1930s, the Orton-Gillingham method is still widely used today.

Orton-Gillingham instructors tailor their curriculum not just to the learning disability, but to the disorders that often accompany disabilities, such as attention deficit hyperactivity disorder (ADHD). According to the Academy of Orton-Gillingham Practitioners and Educators (2012), the instructor engages multisensory teaching to convey curriculum content in an easily digestible format for the student. The multisensory side of this could include the use of chalk, writing with fingers in sandboxes, using smart boards, along with other nontraditional modes of learning. The Orton-Gillingham method also pays attention to the student's emotions, and ensures the student is motivated and self-confident. There are 12 aspects to the Orton-Gillingham approach. Other aspects include diagnostic and prescriptive lessons, direct instruction, systematic phonics, applied linguistics, linguistic competence, a systematic and structured relationship, sequential incremental and cumulative material, continuous feedback and positive reinforcement, as well as cognitive approaches that teach the student why he or she is learning.

Neurological Aspects of Learning Disabilities

While diagnosis cannot be due to a neurological incident, such as a stroke, new evidence shows there is a neurological basis to learning disabilities. Functional Magnetic Resonance Imaging (fMRI) has uncovered differences between the brains of normal range children and the brains of learning-disabled children, specifically the corpus callosum – the bundle of nerves fibers that

connects the two hemispheres of the brain (Semrud-Clikeman 2017). The corpus callosum is moderately linked to reading ability. Specifically, better readers have larger corpus callosums (Fine et al. 2007).

Learning Disabilities in Grade School

There has been much debate on whether students with a learning disability should be included in the regular classroom. While the students with learning disability do not need the special attention that children with other types of disorders require, they do need more specialized instruction than the average student does (Ford 2013). Many positive and negative aspects to having learning disabled children in standard classrooms – known as *inclusive classrooms* – have been discussed (Ford 2013). Inclusive classrooms often occur with one general educator and one special educator, although there are multiple ways that the arrangement can take place. Ford (2013) found that full inclusion in elementary school classrooms possessed moderately positive results; however, inclusive classrooms at the secondary (high school) level were not as positive as their elementary counterparts. The largest weakness in both the academic and vocational classrooms within the secondary level were attributed to the educators lacking knowledge on special education laws, along with ways to support learning disabled students. Ultimately, inclusive classrooms take time to develop, and results for individual students may vary. Direct instruction in an inclusive classroom is difficult to implement, which is why withdrawal may be needed, so it is important that the educator be able to make decisions based on each student's individual needs (Ford 2013).

Learning Disability in College

Students with a learning disability are enrolling in college at the same rate as their peers (67%) but have a lower degree completion rate (41% of students with disability versus 52% of peers) (Showers and Kinsman 2017). Family

background played a significant role in college success for students with a disability but it was mediated by student attributes. Student attributes include, but are not limited to, college preparation, degree expectation, and time of enrollment (i.e., whether or not there was a gap year taken prior to attending college).

Fullarton and Duquette (2016) conducted a case study on four college students with learning disabilities in Ontario, Canada. Although the four patients possessed a range of different learning disabilities, the researchers ultimately found that parental support and university accommodations are essential for the academic success of learning disabled students. One patient, Lauren, stated her gratitude for the support of her parents and the university she attended. It was also found that having accommodations helped her grade point average increase, and thus made her feel less “stupid”. A second patient, Ashley, was permitted to take exams in her school’s resource center, and received individual assistance with reading and math. To prepare for the challenges of college, she attended a 3-week transition program offered by the special services department of her university, and registered to receive needed accommodations. Her accommodations have helped her achieve a satisfactory grade point average. These results illustrate the importance of parental and university support in learning disabled individuals’ academic success at the postsecondary level.

Conclusion

There debate regarding education of learning disabled students continues. While the effectiveness of Orton-Gillingham is generally undisputed, training educators in the method can be costly. With that being said, other methods such as inclusion classrooms are widely debated in their usefulness, as the opinions of educators and peers can have an effect on the services provided to the disabled students. Research has shown that neither educators nor students are able to accurately explain what inclusion is, nor do they seem to be sufficiently knowledgeable on the subject (Ceylan and Aral 2016). Along with this, the conclusion

was made that educators do not prefer children who require more responsibilities in inclusive practice; although educators and peers seem to be more accepting of students with mild disability or impairment. There is still much to learn about learning disabilities, only recently have medical technologies been able to show biological differences between dyslexic children and normally developing children. As this technology improves, so will knowledge on how to properly educate students with learning disabilities.

Cross-References

- Boredom as an Adaptation
- Child-Centered Learning
- Different Functions of Memory
- Disabilities
- Encoding and Sleep
- Language Acquisition in Infants and Toddlers
- Little Albert
- Play and Social Learning
- Role of Experience in Tool Use
- School Environment

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Learning Curve

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Synonyms

Learning graph; Rate of learning

Definition

A graphical representation of the rate of learning (vertical y axis) in relation to number of attempts (trials) at learning (horizontal x axis).

Introduction

A learning curve shows the progression of learning over time in repeated attempts to arrive at the solution of a problem, which may be practical (e.g., open the door of a puzzle box) or mental (e.g., memorize information, find the solution to a mathematical problem, etc.) in nature. Although developed at the end of the nineteenth century, the concept still is used in contemporary research to plot performance progression and skill acquisition over time.

Development of the Concept and First Experiments

In conditioning paradigms, a learning curve is the plot of the frequency of the conditioned response

as a function of the number of reinforcements received (Gallistel et al. 2004). The first recorded use of the concept of a learning curve was by Ebbinghaus (1885), who conducted research requiring participants to memorize a series of nonsense syllables and recorded the success over a number of trials.

Thorndike a few years later introduced his theory of learning, termed as Law of Effect (Thorndike 1898). Using puzzle boxes, he observed an animal's efforts to escape the puzzle box in order to reach food placed outside and recorded how long it took for each successful escape. He plotted the escape times in a graph that he called learning curve. Initially, learning was slow as it took each animal some time to find how to escape the puzzle box but accelerated in successive repetitions of the experiment until the escape time stabilized, resulting in an S-shaped learning curve. The S-shaped (sigmoid) learning curve appears to apply in complex learning; for example, it has recently been documented in foreign language acquisition, in the context of learning foreign words (Murre 2014).

Reflections from Contemporary Uses in Research

Whereas the first uses of the learning curve by Ebbinghaus and Thorndike reported the rate of learning at an individual level, in contemporary research learning curves are reported for groups of individuals. According to Gallistel et al. (2004), there have only been few attempts to specify quantitative properties of the learning curve in individuals, as usually what is presented are group learning curves. However, when the group-average score or performance time is plotted on a learning curve, the information is not representative of individual performance. Using a group-average learning curve confounds important independent parameters of individual learning curves such as onset latency, dynamic interval, and asymptote (Gallistel et al. 2004). Murre (2014) also challenged this practice and argued that taking the average of several learning curves

of individuals may give rise to a power function for a group's performance, even if the individual learning curves are all exponential. He focusing on limited domains of application with more explicit assumptions about the processes involved, as opposed to attempting to generate globally applicable learning functions in order to be able to generate more insightful analyses and more powerful results.

The challenges arising from reporting group learning curves are quite evident if we consider the individual differences approach in psychological research. Plotting average scores can conceal important information; any individual departures from the average are designated as "error" in mathematical models and are discarded. Glautier (2013) reported that from the perspective of an individual differences approach, the error is the data of interest. He proposed a novel associative approach to the analysis of individual learning curves to achieve a more accurate modeling of individual curves, which uses a more detailed representation of the stimuli provided by the learning environment and was able to produce better approximations to individual learning curves compared to other models.

Use of the Term in Colloquial Language: The "Steep Learning Curve"

In colloquial language, a difficult and complex procedure is often described as having a steep learning curve. Whereas in literal terms steepness in climbing a hill equates increasing difficulty, this is not the case in graphs representing learning curves. In fact, quite the opposite applies. A learning curve with a steep start represents rapid progress at the initial stages. Highly complex procedures such as surgical practice are more likely to have more gradual learning curves, with top performance level achieved only after large experience or not at all (Hopper et al. 2007).

Conclusion

The graphical representation of the rate of learning in relation to number of attempts over time is

an illustration of a learning curve. Learning curves can be plotted individually or averaged across a group. Plotting group-average plots can pose a challenge in learning and individual differences research, as important information of interest (i.e., the individual deviation from the average) is concealed. Recent literature has proposed solutions to overcome this challenge.

Cross-References

- [Operant Conditioning](#)
- [Thorndike's Law of Effect](#)

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Learning Disorder

- [Learning](#)

Learning Graph

- [Learning Curve](#)

Learning Process

► [Scaffolding in Learning](#)

Learning Through Associations

► [Associative Learning](#) ► [Classical Conditioning](#)

Learning Versus Imitation

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Synonyms

[Copying](#); [Imitation](#); [Overimitation](#); [Social learning](#); [Trial-and-error learning](#)

Definition

The acquisition of new skills or behaviors through individual effort or by replicating the actions of others.

Introduction

Imagine you have accidentally stumbled across Marty McFly's DeLorean (for the uninitiated, this is in reference to the film *Back to the Future*), and not knowing how to operate it properly, find yourself transported back over a million years to the African savannah. There you encounter a group of *Homo erectus* who are strangely unperturbed by your presence (and, more strangely, unperturbed by the presence of the DeLorean). You eventually notice that most

members of the group are able to manufacture stone hand axes and, being ignorant of how to get the DeLorean to return you to the present, quickly realize that to survive you must learn how to build your own stone tools. The key question is how do you begin doing so? Perhaps you would start by bashing two rocks together. You would quickly discover that approach won't work. What next? Perhaps you would observe someone else making a hand axe and then attempt to copy what they did. But would you copy every step in the observed sequence or would you pick and choose the components that seem to be most relevant? If you are like young children and speculatively like our *Homo erectus* cousins (Shipton and Nielsen 2015), you will precisely and deliberately copy everything you saw being done. Moreover, especially if you are like young children, you are unlikely to engage in much individual learning.

Innovation in Young Children

Building on studies undertaken with nonhuman animals, Beck and colleagues (Beck et al. 2011) investigated human children's emerging tool innovation capacities by presenting them with a narrow vertical tube containing a bucket with a hooped handle. The challenge was to get the bucket out of the tube in order to retrieve a sticker. When given a straight and hooked pipe cleaner, 4-year-olds, but not 3-year-olds, chose the hooked one above chance. Yet when given a straight pipe cleaner, a long piece of string, or some small matchsticks, 3–5-year-olds rarely took the pipe cleaner and bent it into a hook or made any other functional tool. It wasn't until children were 9 or 10 years that high levels of success were achieved. In an analogous study, 4-year-old children needed to pour water into a tube so as to float a toy to the top for it to be retrieved (Nielsen 2013). These children similarly failed to recognize the solution on their own. Testing in remote regions of South Africa suggests this inability to quickly devise solutions to novel problems is not specific to children from Western populations (Nielsen et al. 2014b).

Incongruent with the afore-reported findings, there are multiple reasons why children should engage in individual learning and innovate tools well before their primary school years. From their second year in life, children show an increasing capacity for manipulating and successfully using a variety of tools and for inferring their intended use, design, and means of categorization; and they have an emerging ability for taking what is known and extending it to novel situations, the kind of inductive reasoning necessary for tool innovation. Moreover, from 6 months of age, infants show an ability for acquiring the skills needed to use novel objects by copying others (Barr et al. 1996). It is perhaps in the latter that there lie clues as to the lack of trial-and-error-driven innovation in young children.

Imitation and Overimitation

In a landmark study, Horner and Whiten (2005) had an adult demonstrate to 3- to 4-year-old human children and wild-born chimpanzees how to extract a reward from a novel box. A bolt on the top of the box was first removed, revealing a hole into which a stick tool was repeatedly jabbed. A door located on the front of the box was then opened and the stick was used to extract the reward. Because the box was opaque, the participants could not see how what occurred inside the box was causally related to the outcome. When given their own turn with the box, both chimpanzees and children copied the model's actions, including jabbing the stick tool in the top. However, when the opaque box was substituted for a transparent box (and hence the effect of the internal actions could be identified, making it obvious that when the stick was jabbed into the top hole, it struck a barrier and made no contact with that part of the apparatus from which the reward could be retrieved), the chimpanzees now ignored the jabbing in the top hole and instead copied only the model's insertion of the tool into the front hole. They ignored the initial action which was now visibly, causally irrelevant. In contrast, the children replicated the model's entire sequence of actions, including

the visibly irrelevant insertion of the stick into the top hole.

Now known as overimitation, the tendency of young children to copy others with such high fidelity that they will incorporate visibly, causally irrelevant actions has been replicated in multiple labs and across contrasting cultural groups (Nielsen et al. 2014a; Nielsen and Tomaselli 2010). Though there is currently much research and debate in relation to the specific mechanisms and functions underlying overimitation, there is broad agreement that this phenomenon underpins children's acquisition of object-related skills that is critical in environments that feature many tools and artifacts that lack ready perceptual information about their functional significance and modes of operation. This cognitive opacity makes it challenging for novices to identify which actions or behaviors are appropriate for each artifact and which are not (Gergely and Csibra 2006). Directly and comprehensively copying others thus affords the rapid acquisition of a vast array of essential skills that have been developed and accumulated through multiple past generations.

Conclusion

When we think about the young members of our society learning it might be easy to consider them as blindly copying the acts of those around them, failing yet to have developed the cognitive resources necessary for successful individual learning. While there is an element of accuracy in this, it ignores the overwhelming value accrued to a system that can fast-track skill acquisition while avoiding the potential pitfalls of trial-and-error learning. This is not to say that young children are not capable of invention – the amazing worlds they can invent while engage in pretend play is a testament to their capacity in this regard (Pellegrini and Bjorklund 2004) – but rather highlights the strong evolutionary pressures that have come to bear on our species' peculiar learning proclivities. It is the very same ability that would enable you to make a stone hand axe at a far quicker rate than if you were to focus efforts on developing your own methods. The time saved

could then be spent trying to work out how you can get the DeLorean to take you back to the future.

Cross-References

- [Acheulean](#)
- [Cultural Transmission](#)
- [Evolution of Culture](#)
- [Evolution of Tool Use](#)
- [Homo erectus](#)
- [Human Tool Making](#)
- [Humans as Social Primates](#)
- [Imitation](#)
- [Imitation and Mimicry](#)
- [Play](#)
- [Play and Social Learning](#)
- [Play and Tool Use](#)
- [Social Cognition](#)
- [Social Development in Nonhuman Primates](#)
- [Social Learning](#)
- [Tool Use](#)

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Leda Cosmides

- [Founders of Evolutionary Psychology](#)

Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)

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Synonyms

[Cosmides & Tooby; John & Leda](#)

Definition

Cosmides and Tooby, intellectual kindred spirits, have been leaders in both the theoretical and empirical development of modern evolutionary psychology.

Introduction

They have been leading intellectual influences in the field of evolutionary psychology for over 35 years, but it was possible that John Tooby and Leda Cosmides might have never met.

Yes, they both attended Harvard University, but Tooby's undergraduate degree in psychology (1975) was before Cosmides' graduate work in psychology during the early 1980s. Similarly, Cosmides' undergraduate degree in biology (1979) only briefly intersected with Tooby's work in behavioral biology before he moved on to biological anthropology. But then Irv DeVore got involved.

Meet Cute

Starting in 1971 and running for several decades, Irv DeVore (John Tooby's advisor) held a "Simian Seminar" in the living room of his home. These seminars were incredibly influential due to both the content and the quality of the conversations. It was informal, open to scientists at all levels (and genders), and egalitarian. "At the Simian Seminars, almost no idea or topic was too sensitive, too politically incorrect or too bawdy to be off limits. This openness was made possible by an atmosphere of mutual trust, respect, and affection, which was very deliberately cultivated by the DeVores" (Hrdy 2005, p. 90–91).

John Tooby was already DeVore's graduate student and part of this milieu when Leda Cosmides was invited to attend the Simian Seminars. She was working in both the biology and psychology departments, and the Simian Seminar was one of the few places where these two fields actually integrated well with each other. But the initial experience that Cosmides had at the Simian Seminars was one of intense frustration. She would have questions or comments about the topic being discussed, and she would try to raise her points, but another attendee – John Tooby – would chronically "steal" her thoughts before she had an opportunity to raise them.

This situation eventually led to Leda Cosmides confronting John Tooby about their like minds. Their interchanges of ideas led to collaboration, which also led to marriage. From their first joint publication in 1981 (on intragenomic conflict due to cytoplasmic DNA inheritance), only a handful of publications and presentations by one has not included the other as an author. To this day,

although their graduate students are officially in either the field of psychology or the field of anthropology, most of them consider their advisor to be a single Cosmides/Tooby unit. Together, they have advised over 25 graduate students and postdoctoral researchers.

The Ontogeny of Evolutionary Psychology

Cosmides received her PhD in Psychology in 1985, and Tooby received his PhD in Biological Anthropology in 1989. They then were both postdoctoral scholars at Stanford University with Roger Shepard and Fellows at the Center for Advanced Study in the Behavioral Sciences (1989–1990). Tooby and Cosmides then joined the faculty at the University of California, Santa Barbara, where they continue to run the Center for Evolutionary Psychology. Among the recognitions for their work, Tooby won a Presidential Young Investigator Award from the National Science Foundation (1991), and Cosmides won the American Association for the Advancement of Science Prize for Behavioral Science Research (1988) and the American Psychological Association Distinguished Scientific Award for an Early Career Contribution to Psychology (1993). They have also received an NIH Director's Pioneer Award (2005) and J. S. Guggenheim Fellowships.

Although a number of people were already conducting evolutionary research on human behavior by the 1980s, Leda Cosmides and John Tooby solidified and crystalized this approach by explicitly drawing out the reciprocal relationships between evolutionary biology, cognitive science, human evolution, anthropology, psychology, and neuroscience. According to this *integrated causal* view, researchers can develop meaningful hypotheses about specific functional designs of the human mind by considering the adaptive problems our hunter-gatherer ancestors faced over evolutionary history. In 1992, Cosmides and Tooby along with Jerry Barkow published *The Adapted Mind: Evolutionary psychology and the generation of culture*, an edited volume designed to be a state-of-the-art survey of the new field.

Several seminal chapters were included in *The Adapted Mind*, including those by Donald Symons, David Buss, Bruce Ellis, Margo Wilson and Martin Daly, Steven Pinker and Paul Bloom, Roger Shepard, and Randy Nesse and Alan Lloyd. The opening chapter by Cosmides and Tooby, however (“The Psychological Foundations of Culture”), described this sweeping view of what evolutionary psychology was and how it was done. (More recent treatments can be found in Tooby and Cosmides (2005, 2015).)

The “Psychological Foundations of Culture” chapter runs 118 pages, but a very simplified summary of the key positions includes the following:

- (a) The mind is an information processing system with a multimodular (or massively modular) structure. Specifically, the evolved architecture of the human mind includes a large number of complex, content-dependent computational mechanisms that are specialized for solving adaptive problems. Because good solutions to specific problems are tailored to the structure of those problems, there should be a large number of domain-specific cognitive mechanisms.
- (b) The relevant adaptive problems are defined by, and were shaped by, the ancestral environment of our ancestors, across the Environment of Evolutionary Adaptedness (the statistical composite of environments in which the adaptive problem existed).
- (c) Because sexual reproduction chronically recombines the genetic basis of these complex computational mechanisms in the human mind, these mechanisms must be universal and species-typical in order to be maintained.
- (d) These universal evolved mechanisms generate cross-culturally recurrent concepts and motivations (“they make certain ideas, feelings, and reactions seem reasonable, interesting, and memorable”; Tooby and Cosmides 2005), that is often referred to as “human nature.” Cultural differences arise from the input of “particular ecological, economic, demographic, and intergroup social contexts or environments” (Tooby and Cosmides

1992, p. 24) into these universal evolved mechanisms, yielding different outputs.

The chapter also contrasts these positions with those typical of the “Standard Social Science Model,” or SSSM, and explains why these SSSM positions have major problems. SSSM positions include assumptions of relatively domain-general, content-independent, and equipotential computational mechanisms in the mind, which are not necessarily tied to any evolutionary adaptive problems, and the belief that culture is an irreducible explanation (“*omnis cultura ex cultura*”).

Research Activities, Deep and Wide

Cosmides, Tooby, their graduate students, and other collaborators have published over 150 articles (<http://www.cep.ucsb.edu/publist.htm>) expanding on the theoretical foundations of evolutionary psychology and applying it across a vast range of topics.

Their most well-known application of evolutionary views to a psychological topic is the work (initially from Leda Cosmides’ dissertation; Cosmides 1985, 1989) on human reasoning about social exchanges. Like much of their research, this topic draws on insights not only from cognitive psychology (the nature of human conditional reasoning) but also from evolutionary biology (the significance of cheaters in reciprocal altruism contexts), cultural and biological anthropology (the ubiquity of this phenomena across cultures and times), and economics (the concept of gains-in-trade as a converging line of evidence). Over the years, the evolutionary theory of specialized reasoning mechanisms for social exchange (Cosmides and Tooby 1989, 1992, 2008, 2015) has been bolstered not only by additional reasoning experiments (e.g., Cosmides et al. 2010), but also by supportive findings from neuroscience (Cosmides and Tooby 2000, 2005; Stone et al. 2002), anthropology (Sugiyama et al. 2002), personality (Fiddick et al. 2016), and conceptual priming (Fiddick et al. 2017).

Additionally, research by Cosmides, Tooby, and their collaborators has dealt with a wide

range of topics across most of the major areas of psychology, consistently also drawing upon interdisciplinary insights to guide their development of theories and hypotheses. The topics addressed include: concept formation, social categorization, memory, intergroup relations, emotions, cooperation, aggression, motivations, morality, mate choice, personality, pathology, kinship, hormones, economics, political science and criminal justice, aesthetics, intelligence, and judgments under uncertainty. Throughout all these efforts, a consistent theme has been the conceptual integration of the behavioral sciences. This theme can be traced back to the opening introduction of *The Adapted Mind* (Cosmides et al. 1992), and even to Leda Cosmides' formative years in which her father was "frequently seen pounding the dinner table, insisting that interdisciplinary approaches were the future of science" (Cosmides 1994, p. 269).

Cross-References

- [Adaptationist Program, The](#)
- [Adapted Mind, The](#)
- [Founders of Evolutionary Psychology](#)

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Leech

► [Parasites](#)

Leftist

► [Political Left, The](#)

Left-of-Center

► [Political Left, The](#)

Left-Right Differences

► [Fluctuating Asymmetry](#)

Left-Wing

► [Political Left, The](#)

Lekking

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Synonyms

[Arena display](#)

Definition

Aggregations of males which females visit for the purpose of mating (Höglund and Alatalo [1995](#)).

Introduction

Lekking is a collective behavior: the tendency of males to aggregate during the mating season and perform a communal display at a site restricted in space. This site is called the lek. Males often perform stereotyped displays while attending the lek, and this constitutes the lekking behavior. Females visit these aggregated male displays principally to select and mate with one or several of the males. After, mating females leave the lek and do all the parental care without male assistance. Most lekking species behave in the way just described: males aggregate and display and females select among these males. In a few role-reversed species, females display and males choose. There have been two main reasons to study leks. The first relates to the issue of the evolution of this rare mating system. What factors drive the evolution of lekking behavior? The second has to do with sexual selection. Since no male resources but gametes are transferred during mating: how come females are selective when they chose males on the leks?

Lek Evolution

Lekking is a rare mating system that has evolved independently many times during the evolution of Metazoan animals. It was first described in birds but can be found in many groups of animals including spiders, insects, fish, amphibians, reptiles, and mammals (Höglund and Alatalo [1995](#)). Many hypotheses have been put forward to explain how and why leks evolve. The most influential are (1) the hotspot hypothesis and (2) the hotshot hypothesis. The hotspot model was proposed by Jack Bradbury and coworkers (Bradbury [1981](#)) and revolves around the idea that males aggregate where the likelihood of encountering

females is maximized. Even in a uniform landscape and a hypothetical species without habitat preferences, overlapping female home ranges is enough to generate clustering behavior in males (Bradbury et al. 1989). Under certain assumptions it can be shown that males maximize female encounter rates by aggregating where female home ranges overlap the most.

The hotshot hypothesis is based on the idea that certain males (for some reason) are more attractive to females than others (Beehler and Foster 1988). In such a situation, it may benefit males to abandon solitary display and join an attractive male. If such males are not able to monopolize all females that visit them, it may pay many males to set up display adjacent to a hotshot (Höglund and Robertson 1990). These two main hypotheses for lekking are not mutually exclusive and may work in concert.

Sexual Selection and the Lek Paradox

In almost all species with lekking, it has been shown that females show strong mating preferences in favor of certain males, even if it has been surprisingly hard to pinpoint exactly which phenotypes females prefer (Seather et al. 2005). Perhaps the most common finding is that females select males successful in fighting (e.g., Alatalo et al. 1991). These consistent female mate preferences and exhaustive and costly mate sampling behavior pose an enigma to science. Given that the males do not transfer any material benefits to females, the only conceivable benefits females get from their mate choice are genetic. If so, the persistent selection imposed by females would quickly fix the male genes coding for the phenotypes females prefer, and if there is no variation among males, there is no reason for females to be selective. This is called the “lek paradox” (Borgia 1979). Numerous suggestions have been put forward to solve it including mutation-selection and mutation-drift balance, fluctuating selection in time and space, antagonistic selection between the sexes, antagonistic pleiotropic effects, and balancing selection favoring heterozygote genotypes (Radwan 2008). However, to date, empirical

studies addressing these issues remain scarce (Cornwallis and Uller 2012).

Conclusion

There are two main reasons to study lekking: (1) why do lekking evolve in some species and not in others and (2) why are females selective when the only benefit they get is genetic? These issues have puzzled evolutionary ecologists and geneticists for decades and the debate continues. A general view is that lekking tends to evolve when neither females (the limiting sex) nor resources can be defended. The issue of the lek paradox is related to the larger issue of why there is genetic variation for fitness traits that may be explained by multiple factors including those described above.

Cross-References

- [Leks and Choruses](#)
- [Secondary Sexual Characteristics](#)

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Leks and Choruses

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Synonyms

[Lekking](#); [Male display](#); [Mating aggregation](#)

Definitions

An aggregation of sexually displaying males that females visit solely to appraise male displays and select mates. Females receive no resources from the males they mate with (only genes), and males do not provide parental care to offspring.

Introduction

Derived from the Swedish verb “leka” (“to play”), the word “lek” refers to an aggregation of sexually displaying males visited by receptive females for mate selection. Characterized by the lack of direct benefits obtained by females and the importance of male sexual displays in attaining matings, leks have become the prominent mating system to study sexual selection under natural conditions in the absence of confounding factors. As a result, few mating systems have received as much attention over the past 100 years as leks. Despite this sustained interest, there are still many questions regarding lek breeding that continue to attract researchers, including its relative rarity, the factors that determine male reproductive success and the

maintenance of genetic variation under the influence of strong directional sexual selection.

Defining Leks

Determining what does and does not constitute a lek is sometimes difficult. Classically, leks have been distinguished from other mating systems by the presence of four criteria (Bradbury 1977): (1) male display sites are aggregated within an area that is smaller than the available habitat, (2) male display sites contain no resources required by females, (3) females have the opportunity to select their mates, and (4) males do not contribute to the care of offspring. While these four criteria fit the breeding behavior of many gamebirds (for which lek breeding was originally described) almost perfectly, the discovery of many “lek like” mating systems in species whose breeding behaviors fall on a continuum of one or more of these criteria have resulted in a general relaxation of the definition of lek. For example, the second criterion – male display sites do not contain resources – is muddled on so-called “resource-based leks,” where males situate themselves near resources required by females in order to maximize female encounter rates, but do not control access to those resources. Even the definitive characteristic of a lek – aggregated males – is stretched in some species that display on “exploded leks,” where the distance between males may be so great that the aggregation may not be apparent until evaluated statistically. As such, broader definitions of leks have been proposed, such as Höglund and Alatalo’s (1995) definition that leks are an aggregation of males that females visit primarily for the purpose of fertilization. Generally, a species is considered to be lek breeding if females mate on male arenas and display some level of choice while doing so.

The Evolution of Leks

Five ecological and physiological prerequisites are thought to be required for lekking to evolve (Höglund and Alatalo 1995): (1) resources

required by females are indefensible, (2) male parental care is not required, (3) fertilization is internal, or there is no association between the chosen male and the female's oviposition site, (4) females discriminate between males, and (5) high mobility (i.e., females can accept the costs of searching out male aggregations and males can escape predators while displaying). Beyond this, the factors that lead to the adoption of lek breeding by a population appear to be varied and have received considerable attention from researchers. Why and where males aggregate are interesting questions, as each male faces potentially lower individual reproductive success while also suffering from increased fights by grouping together.

At the basic level, lek-like mating systems should evolve when males in a population cannot defend females nor the resources required by females. Furthermore, leks are likely only economical for males when females possess large home ranges and the density of females is high. In addition to these general characteristics, several hypotheses have been proposed to further explain the factors that lead to the evolution and maintenance of leks within various species (see Höglund and Alatalo 1995). Of these, four hypotheses have received considerable attention: hotshots, female preference, hotspots, and black holes. The hotshot model posits that low-quality males establish territories surrounding high-quality males in an effort to intercept females visiting those males (Beehler and Foster 1988). The female preference model suggests that females prefer to mate with clustered males, as clustering likely reduces the effort required to compare potential mates, and larger clusters may increase average male quality within the cluster (Gibson et al. 1990). The hotspot model proposes that if females possess large home ranges, leks will form in the areas of greatest home range overlap in order for males to maximize their encounter rates with females (Bradbury et al. 1986). Finally, the black hole model has been suggested for some ungulate leks (Stillman and Sutherland 1993). In this model, females in estrus are harassed by males to the point where they are driven out of the male's territory, as male harassment may lead to injury.

Females move through territories apparently at random until they eventually mate. Under these conditions, male clustering allows for higher female retention rates than solitary territories ("thus, like stars in space, females are sucked into black holes"; Höglund and Alatalo 1995, p. 170).

There is some evidence that clustering reduces predation pressure on both males and females, thus providing a selective benefit for leks over solitary displays. However, leks continue to form in captive populations under no predation pressure, and while predators may shape aspects of leks (e.g., male arrival time, lek location, they are unlikely to be the sole explanation for lek evolution.

It should be emphasized that while each of the hypotheses of lek evolution may explain the lekking behavior of some species to some degree (and are not mutually exclusive), no one theory is able to provide a single explanation for lekking; the factors that lead to lek evolution will vary based on ecological and life history characteristics on a species-to-species basis.

Taxonomic Overview

Lek breeding has been described in a wide number of taxa, both in vertebrates and invertebrates, but in a relatively low number of species (for an overview, see Höglund and Alatalo 1995). Lek breeding in invertebrates is almost wholly limited to insects (mainly Diptera), aside from fiddler crabs. Furthermore, many insects that mate in "swarms" (i.e., mass flying aggregations of insects) may reasonably be considered lek breeders despite the absence of male territories, although they are rarely referred to as such in the literature (Höglund and Alatalo 1995).

Among vertebrates, lek breeding is most commonly found in birds with 148 species confirmed to use the mating system (for a review, see Jiguet et al. 2000). In comparison, just over a dozen species of mammals have been confirmed as "true" lek breeders (i.e., meeting the four criteria of lek breeding), although more have been described with "lek like" behavior that resemble

lekking to some degree (for a review, see Toth and Parsons 2013). The mating system has also been described in some reptiles, fish, and a number of amphibians. Like swarming insects, lek breeding in amphibians may be somewhat underreported as herpetologists generally use the term “choruses” rather than “leks” when describing the aggregated male displays used by many frogs and toads.

It is possible that mobility may be a limiting factor for the evolution of leks in many taxa. For example, the relatively high numbers of lek-breeding birds may be a function of the group’s high mobility (however lek breeding may, in turn, be limited by obligate male parental care in the majority of species), and why lek breeding is generally only found in mammals that are capable of travelling large distances, such as ungulates and marine mammals (Toth and Parsons 2013). It is of interest then that only two lek-breeding species of bats have been identified to date, despite the group possessing comparable mobility to birds. However, the apparent rarity of lek breeding in bats is likely due to a general lack of knowledge of bat mating systems as a whole, and it is possible that there may be a higher proportion of lek-breeding bats than birds given that male bats – as a general rule – do not provide parental care. Further research is required.

Leks and Female Choice

Leks provide convenient systems to study sexual selection in a natural context given the apparent absence of confounding factors (i.e., the quality of males as providers and the resources they possess) on female mate choice, and male grouping allows easy assessment and comparison of male traits by females. As a result, a distinctive feature of many leks is a pronounced skew of mating success for males, with few individuals receiving the majority of matings. However, in species where males are arranged within a dominance hierarchy it is unclear if mating skews are a result of female choice or if higher-ranking males are simply able to suppress the mating opportunities of other males to a greater degree. In fact, mating skews generally become less pronounced on larger leks, which may indicate

either an inability for high-ranking males to monopolize matings from subordinates and/or more difficulty for females to assess the differences between all males effectively (Höglund and Alatalo 1995). It is also possible that intrasexual competition between females for access to desirable males may drive some females to mate with lower-quality males on larger leks and further reduce mating skew, although evidence for this is varied between species.

There are some common traits that are correlated with male reproductive success on leks across species. Behavioral traits such as display frequency (i.e., the number of displays over a given time), lek attendance (i.e., the amount of time individuals spent on the lek), and aggression frequency (i.e., the number of fights per unit time) have been found to be positively correlated with mating success, while territorial position (i.e., the distance from the geometric center of the lek) is negatively correlated with mating success across taxa (Höglund and Alatalo 1995; Fiske et al. 1998). The size of male ornaments (e.g., antlers, plumage characteristics, etc.) and male age are both positively associated with mating success (Höglund and Alatalo 1995; Fiske et al. 1998), as is body size in many species. Other predictors of male success include properties of vocal displays, which have been shown to be important in some amphibians, gamebirds, and likely bats, as well as display quality.

The Lek Paradox

Given that females choose males based on their genetic quality and that there is often high agreement among females during mate selection, genetic variation should eventually be exhausted in the population and remove the benefits of female choice. However, persistent female choice continues in lekking populations across generations. This is known as the “lek paradox” and remains one of the most puzzling aspects of lek breeding.

There are several proposed solutions to the lek paradox. Some researchers have suggested “genetic capture” as an explanation (e.g., Rowe and Houle

1996); given that the male traits under female selection are condition dependent and that male condition is in turn encoded by a suite of genes (e.g., those controlling body size, metabolism, etc.), there is likely sufficient genetic variation present in these myriad regions to resist directional female selection. Additionally, mutations and gene flow will also maintain genetic variation and oppose runaway selection by females (Rowe and Houle 1996). Another (not mutually exclusive) hypothesis posits that the effects of predators, parasitic matings, and intrasexual competition can diversify male mating success enough that low-quality males continue to exist in the population, even if there is uniform assessment of male quality by females (e.g., Hamilton et al. 2006). However, empirical tests of such hypotheses are rare and future work is required to determine which explanations represent likely resolutions to the lek paradox.

Conclusions

Leks continue to provide rich systems for the study of male courtship behavior and female selection of good genes in varied taxa. The study of lek breeding will benefit from examining lek breeding in species beyond ungulates and gamebirds, as well as experiments investigating factors that influence lek formation, female choice, and the maintenance of genetic variation in lekking populations.

Cross-References

- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Polygyny](#)

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Length

- [Height and Dominance](#)

Lesbianism

- [Female Homosexuality and Bisexuality](#)

Lesser-Known Theories of Homosexuality

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Synonyms

[Homosexual behavior](#); [Homosexual orientation](#); [Homosexual preference](#); [Same-sex sexuality](#)

Definition

Unfamiliar theories that do not fit the dominant evolutionary theories of homosexuality.

Introduction

There are a number of evolutionary hypotheses about homosexuality that do not fit either of the three main hypotheses discussed elsewhere in this encyclopedia (► [Kin Selection Hypothesis](#); ► [Sexually Antagonistic Hypothesis](#)). Many of these lesser-known hypotheses were initially introduced to explain the occurrence of homosexuality in nonhuman animal species, which may perhaps account for the fact that they tend to be less familiar to evolutionary psychologists. Some of these hypotheses cannot be made to bear on human homosexuality (e.g., *reproductive suppression hypothesis*); others *could* perhaps be made relevant to human homosexuality (e.g., *sperm competition hypothesis*); still others *have* in fact so been applied (e.g., *dominance hierarchy hypothesis*). Finally, there are evolutionary hypotheses that originated in the context of human homosexuality and that do not apply to animal homosexuality (e.g., *kin influence hypothesis*).

Many of the hypotheses discussed below have been the target of criticism from both within and without the evolutionary sciences. First of all, some of them are little more than ► [Just So Stories](#), being notoriously difficult to test, particularly in wild animal species or in human populations. According to Dawkins (1982, p. 37), the *sneaky male hypothesis* is a case in point. Secondly, explaining what some aspect of homosexuality accomplishes is often a far cry from revealing its evolutionary roots: Not all adaptive traits are adaptations. Thirdly, homosexuality can be a complex phenomenon, ranging from a variety of sexual behaviors, such as genital touching, mutual masturbation or copulation, overdesires, and preferences to lifelong orientations. Many of the hypotheses at hand fail to explain what aspects are being targeted – a shortcoming that often leads to confusion and

misunderstanding. Fourthly and finally, evolutionary scientists are often biased toward the “passive” partner in homosexual encounters in animals, while ignoring the “active” partner, i.e., the one who penetrates during a coitus, the one who initiates a series of sexual behaviors, or the one who takes the lead in a courtship session (Fausto-Sterling 2000). A similar critique could be directed against (evolutionary) biological explanations of human homosexuality.

It is important to note that many of these hypotheses are mutually compatible, as they are with nonevolutionary explanations of homosexuality, such as genetic, endocrinological, and even social constructivist explanations (Adriaens and De Block 2006). Like many other organismal traits, mounting and other homosexual behaviors may indeed serve several functions, either simultaneously or successively. The human skin, for example, protects the insides while at the same time regulating body temperature.

There are many ways to classify evolutionary hypotheses about homosexuality. This entry builds on a common tripartition in the evolutionary sciences, identifying and explaining homosexuality as an adaptation, a by-product, or a dysfunction.

Adaptationist Hypotheses

An adaptation is a functional feature of an organism – a feature that evolved through natural selection because it enabled the organism’s ancestors to produce more offspring than rival organisms lacking the same trait. On first thoughts it may seem odd to conceptualize homosexuality as an evolutionary adaptation, given that it is often said to be associated with decreased reproductive success. Now this association may perhaps be true for some aspects of homosexuality, such as homosexual preferences, but it certainly need not be true for other aspects, such as homosexual behaviors and desires. Adaptationist hypotheses about homosexuality can be classified according to whom actually benefits from being involved in a homosexual encounter: the active partner, the passive partner, or both. For each of these options, a number of exemplary hypotheses will be discussed.

In the past half a century, evolutionary scientists have suggested numerous adaptive functions for the active partner's homosexual behaviors and desires. A first hypothesis, the **reproductive suppression hypothesis**, is based on the observation that, in a number of nonhuman animal species, homosexual mounting serves the mounting partner's attempts to reduce the mountee's reproductive success. Mounting may achieve this goal in various ways. In the most straightforward scenario such behavior is part of a harassment strategy aimed at disrupting the mountee's heterosexual reproductive activities. Some evidence shows, for example, that female American bison mount each other to disturb the bull's courtship attempts. In some primate species, such as langur monkeys, estrous females are disproportionately more often mounted by other females (Sommer et al. 2006).

One of the main problems with the **reproductive suppression hypothesis** is that some of its supportive evidence can also be explained by means of other evolutionary hypotheses, such as the **signal mounting hypothesis**. Secondly, it isn't clear why natural selection would favor homosexual mounting as an intrasexual competition tactic if there are obvious and more efficient options available, such as chasing or biting. The latter objection can be met, however, by referring to evidence documenting long-term negative effects (of being mounted) on a mountee's reproductive success. In gray wolves and European rabbits, for example, female-female mounting with pelvic thrusting often causes a kind of pseudopregnancy, i.e., an extension of the mountee's diestrous phase, which suppresses a number of subsequent cycles (Asa and Valdespino 1998). It is doubtful, however, whether the **reproductive suppression hypothesis** would enable one to understand any aspect of human homosexuality (but see MacIntyre and Estep (1993), who argue that homosexual behavior of heterosexuals carrying "a gay gene" could be seen as a reproductive suppression strategy).

A closely related hypothesis, the **dominance hierarchy hypothesis**, fits homosexuality in with findings on dominance behavior in social species. It holds that homosexual contacts are ritualized

behaviors that mirror, establish, or confirm an individual's social position. Penetrating, for example, is an expression of dominance and being penetrated an expression of submission. While this seems to be true for some animal species, such as female stump-tail macaques (Vasey and Sommer 2006), it does not work for others, such as deer, in which dominant individuals are more frequently mounted by lower-ranking rivals than vice versa (Bartoš and Holečková 2006). To complicate matters, it appears that, in some species, high-ranking males take on a dominant position in some homosexual activities and a subordinate position in other such activities. Moreover, the dominance hypothesis only applies to aspects of homosexuality that lend themselves to being an expression of dominance or submission, such as mounting or pelvic thrusting. Such activities, however, are only a limited subset of the total homosexual behavioral repertoire, both in humans and in other animals. What about kissing, masturbation, or courtship behaviors?

In human populations, especially in times past and in non-Western settings, evidence seems to confirm some of the central tenets of the **dominance hierarchy hypothesis**. One of these tenets is that sexual roles are differentiated according to social rank. Historical research reveals indeed that socially asymmetrical relationships between adult and adolescent males always involved a clear-cut sexual division of labor. In classical antiquity, in the Samurai culture in medieval and early modern Japan, in the Islamic world, and in Renaissance Florence, to name just a few, male homosexuality was so common as to be universal. But it was always structured by age, meaning the adult male was expected to consistently fulfill the "active" role in sexual activities. Until well into the twentieth century, a similar sexual tradition could be found among black South African migrant diamond miners. Adult males, some of whom were married back home, took on a so-called boy-wife for both domestic and sexual purposes. Such relationships were governed by a distinct set of rules, including the tenet that "proper wifely behavior did not include ejaculation by the youth, or any kind of sexual reciprocity" (Murray 2000, p. 166).

Contemporary human homosexual relationships, especially in the West, are much more socially egalitarian, so the **dominance hierarchy hypothesis** does not promise well in this context. There is some evidence, however, that homosexual activities in sexually segregated human populations may be reminiscent of dominance behavior. Anecdotal evidence shows, for example, that some male prison inmates in Britain and America, regardless of their sexual orientation before they were incarcerated, are being held as “wife” by their “husband.” A “wife” is expected to fulfill much the same submissive role as the South African boy-wives mentioned earlier, including cooking, washing, and having sex with their “husband.” Some of these men are even forced to take on a female name and identity (Walshe 2012). Criminologists consider prison rape to be an act of violence and power (O'Donnell 2004) – a view that dovetails with the **dominance hierarchy hypothesis**. It is important to note, however, that it is unclear what role the current adaptive value of some aspects of homosexuality has had in driving the evolution of homosexuality as such.

These two adaptationist hypotheses focus exclusively on the adaptive value of the active partner's behavior, which usually consists of penetrating or mounting. Yet sometimes such behavior serves the reproductive success of the *passive* partner, who then acts as (active) instigator in the encounter.

A first hypothesis that fits this description is the **sneaky male hypothesis**. It holds that, in some animal species, some subordinate males mimic salient parts of the female phenotype, in order to appease the dominant male's aggression and to invite mounting or penetrating on his behalf. Thus they, i.e., subordinate males, are able to get full access to the dominant male's territory with all its associated advantages, including protection, food, and access to the latter's females. In bluegill sunfish, for example, males come in three morphological categories – a classification based on two phenotypical characteristics: body size (small, medium, or large) and coloration (light, dark with vertical bars, light with yellow-orange breast) (Roughgarden 2009). Medium males

closely resemble young females, both in size and coloration. During spawning, some large males allow medium males to enter their territory. Both males extensively engage in courtship activities, first with each other and then with a female. As the female releases her eggs, both males fertilize them.

The medium male's reproductive strategy has often been seen as a form of deceit, made possible by the large male's inability to distinguish between females and medium males. Critics have questioned this inability, observing that sunfish have great eyesight. Moreover, even if large males would initially be deceived by the size and coloration of medium males, it is unlikely that the deceit wouldn't come out over the course of their joint activities. According to Roughgarden (2009), both males enjoy a cooperative relationship based on same-sex sexual attraction – a supposition that fits the story of male sunfish homosexuality in with the ► **“Alliance formation theory”** discussed elsewhere in this encyclopedia.

The **sneaky male hypothesis** has also been cited as an explanation for (some kinds of) human homosexuality (Jeffery 2015). Male homosexuals, for example, are often considered “a girl's best friend,” and they are not perceived as sexual competitors by their heterosexual congeners. The main problem with this hypothesis is that it is at least unclear whether, historically, male homosexuals have always had easy access to women, and whether heterosexual men have always been as tolerant to them as they are today, at least in Western countries. Another issue is why being homosexual would be the best way to obtain sneak copulations. If anything, it seems to decrease the possibility of heterosexual intercourse.

The **sperm competition hypothesis** is another adaptationist hypothesis that conceptualizes (male) homosexuality as a trait that benefits the passive partner's reproductive success. In a heterosexual context, sperm competition occurs whenever the sperm cells of two or more males compete to fertilize an ovum, which happens to be the case when a female mates with multiple males over a brief period of time. In some bird species, homosexual behavior has been shown to affect

this competition. Mountees solicit rival males to mount them because allowing themselves to be mounted and penetrated makes the mounters waste their sperm (Birkhead and Møller 1992). In some species mountees proceed by mimicking typically female traits, in which case the *sperm competition hypothesis* can be classified as part of the *sneaky male hypothesis*. Evolutionary psychologists have also invoked sperm competition to explain a number of *human* characteristics, including male homosexuality (Pound et al. 2006). However, the resulting variant of the *sperm competition hypothesis* conceptualizes homosexuality as a by-product, rather than an adaptation, and so it will be discussed in the next section.

Many of the hypotheses, discussed so far, are based on the assumption that homosexuality has adaptive value only for one of the two partners involved. While this may indeed be the case for some instances of homosexuality, many homosexual activities seem to be enjoyed by both partners, and there may be reasons to assume that they do so because these activities are of benefit to both. Regarding the dominance hierarchy hypothesis, for example, Vasey and Sommer (2006, p. 22) note that “mounts by dominant individuals are sometimes associated with affiliative behavior and solicitations by the mountee (...) which, in a heterosexual context, would be taken as a sign that indicates sexual interest.” Given that homosexual encounters are often part of a joint venture, it seems rather naive to consistently distinguish between “active” and “passive” partners. A third and final category of adaptationist hypotheses meets exactly these objections.

A representative example of this third category is the *sexual practice hypothesis*. This hypothesis holds that homosexual behavior among juveniles helps them to practice sexual skills, such as motor and social skills, that may prove helpful in heterosexual contacts throughout adult life. This hypothesis has received support in many mammal species, ranging from rodents over ungulates to dolphins and primates (for an overview, see Poiani 2010). Homosexual play-mounting is an excellent example of the claim that one and the same behavior can fulfill a number of functions, either

simultaneously or successively, in that play-mounting among male juveniles also seems to help in establishing or reinforcing dominance relationships and alliances.

In humans, juvenile sex play, both among siblings and nonsiblings, has been observed to occur in populations as diverse as Trobriand Islanders and North-American undergraduates (quoted in Poiani 2010), even though there seems to be some cross-cultural variation as to its prevalence. Greenwald and Leitenberg (1989) reported that, at least for American boys, homosexual play behavior was more common than heterosexual play behavior. Much like in other animal species, however, juvenile homosexual play does not seem to be a precursor to the development of homosexuality in later life (Poiani 2010). Finkelhor (1980) explains these findings by means of both the *sexual practice hypothesis* and the *dominance hierarchy hypothesis*.

By-Product Hypotheses

Stephen J. Gould and Richard Lewontin (1979) famously argued that many of an organism's features are not adaptations. In their view, some evolutionary theorists tend to underestimate the many constraints imposed on the powers of natural selection, thus limiting the amount of adaptive design in nature. Some adaptations, for example, inevitably come with one or more by-products that are at least initially nonadaptive.

What could it mean to say that some aspects of homosexuality are to be considered as by-products of an evolutionary adaptation? A first hypothesis that fits this description is the *hypersexuality hypothesis*, which holds that some homosexual behaviors (and perhaps some other aspects of homosexuality, such as desires) are by-products of an individual's above-average level of sexual activity and interest (Poiani 2010). Given that hypersexuality is by definition a relative concept, determining whether it is indeed an evolutionary adaptation, as the *hypersexuality hypothesis* assumes, will require a thorough knowledge of breeding patterns and various ecological parameters of the species involved.

In many animal species, hypersexuality is a temporary trait that covaries with the breeding

season(s). During this time, sexual activities are much more abundant than during the nonbreeding season, and they often include homosexual behaviors (Bagemihl 1999). Sometimes these behaviors are facilitated by specific circumstances, such as a species' inability to detect sex differences. Frogs provide a good example. In the breeding season, males will mate with anything that roughly resembles a female, sometimes contenting themselves with females of other species, with males of their own species, or parts of the human observer's body or equipment. Hypersexuality can also lead to homosexuality in the absence of available and suitable partners of the opposite sex. Historically, many instances of animal homosexuality have been explained as the outcome of a Hobson's choice, i.e., a free choice in which only one option is offered. The popularity of this explanation dates back to classical antiquity, where various authors reported instances of homosexual behavior in sex-segregated populations of domesticated and captive animals (Bagemihl 1999).

Hypersexuality can also be considered as a permanent trait, in which case the intensity of an individual's sexual activity and interest is above average on the level of the population *across the individual's mature lifespan*. Levels of sexual activity and interest are known to vary considerably across individuals, particularly in humans. If the **hypersexuality hypothesis** is to account for (some instances of) human homosexuality, then one should expect at least some homosexuals to be hypersexual, which may indeed be the case (Bell and Weinberg 1978). Much like in non-human animal species, the connection between hypersexuality and human homosexuality may be facilitated by certain circumstances, including a biased sex ratio (Poiani 2010).

Another by-product hypothesis about the evolution of homosexuality is the **hypervariability hypothesis**. Hamer and Copeland (1994) have suggested that homosexuality has not been weeded out of the gene pool because it is linked to hypervariable DNA sequences, i.e., sequences in which spontaneous mutations are conspicuously more common than elsewhere in our DNA. There are at least three problems with this hypothesis. First of all, there is little or no research

on the nature of the advantage related to having a flexible genome. For the **hypervariability hypothesis** to be an exemplification of a by-product hypothesis, the trait with which homosexuality is connected needs to be an adaptation. But it remains unclear what the adaptive value of hypervariability would be. Secondly, decades of intensive genetic research have produced very little tangible suggestions as to which DNA regions are involved in the development of homosexuality. Thirdly and most importantly, there is currently no evidence that any of the parts of our DNA that have in the past been associated with homosexuality is in fact a hypervariable DNA sequence.

A third by-product hypothesis about the evolution of homosexuality is a variant of the **sperm competition hypothesis** discussed above. Pound et al. (2006) speculate, for example, that homosexual arousal in men may be caused by (their attentiveness for) cues related to increased sperm competition risk. Pound's earlier evidence (quoted in Pound et al. 2006) indicates that men prefer polyandrous pornography, in which a woman has sex with multiple men at the same time, over harem pornography, in which a man has sex with multiple women at the same time. This preference doesn't seem consistent with the cold reality of paternity uncertainty, unless one invokes a central tenet of the sperm competition hypothesis, i.e., that the presence of rival males stimulates sexual arousal because it increases a given man's number of sperm delivered when copulation ensues, and thus his chances of conception.

Pound's **sperm competition hypothesis** of human male homosexuality leaves many questions unanswered. It is unclear, for example, exactly how homosexuality is to be coordinated with the arousal produced by the presence of rival males. Pound et al. (2006, p. 14) write that the arousal occurs "in response to other men," which obviously differs from saying that it is *oriented towards* them. It seems that their argument is lacking a crucial step, which could consist, for example, in claiming that human male homosexuality is due to a dysfunction in the mechanism regulating sexual arousal in the context of sperm

competition. If that is the case, however, their **sperm competition hypothesis** would be a dysfunction hypothesis, rather than a by-product hypothesis, as the authors themselves would have it. They also mention another hypothesis based on sperm competition (MacIntyre and Estep 1993), which conceptualizes male homosexuality as a (specific kind of) by-product of sperm superiority in heterosexual men carrying gay genes. As such, the sperm competition hypothesis would be a variant of a class of hypotheses discussed elsewhere in this encyclopedia. A general objection to both of these sperm competition hypotheses is that there is considerable debate about the general importance of sperm competition as a selective force in human evolution (Buller 2005).

A fourth and final by-product hypothesis is based on the fraternal birth order (FBO) effect and might therefore be dubbed the **birth order hypothesis**. One of the few reliable epidemiological findings in research on homosexuality, the FBO effect implies a positive correlation between male homosexuality and number of (biological) older brothers. The effect does not hold for the relationship between male homosexuality and number of older *sisters* nor between *female* homosexuality and number of any type of sibling. With further evidence suggesting that the FBO effect is initiated during fetal development, Blanchard and Bogaert (1996) came up with the maternal immune hypothesis to explain the underlying mechanism. Their hypothesis holds that a succession of male fetuses increasingly confronts the mother with specific male antigens, thus triggering an immune response on her part. This response, in its turn, affects the sexual differentiation of her later born son's brain in such a way as to make it more likely for him to develop a homosexual orientation.

Even in a recent review, Bogaert and Skorska (2011) do not examine the question whether the mother's immune response is to be considered as an adaptation. If it is, however, then the FBO effect could be seen as part of an evolutionary hypothesis, explaining male homosexuality in humans as an evolutionary by-product of an adaptation, i.e., a mother's immune reaction during pregnancy. The main problem of the **birth order**

hypothesis concerns exactly this reliance on the maternal immune hypothesis. First of all, even though the latter is certainly testable, it has not, to date, been tested yet. Secondly and more importantly, the maternal immune hypothesis relies on research about structural differences in the brains of heterosexuals and homosexuals, which has aroused fierce criticism in the past quarter century (Stein 1999).

Dysfunction Hypotheses

A third and final category of evolutionary hypotheses considers homosexual behaviors, desires, preferences, and orientations as manifestations of a disruption, rather than a by-product, of some adaptation. Dysfunction hypotheses explain the evolutionary persistence of homosexuality as resulting from the fact that the adaptive mechanisms involved in regulating sexual behaviors and mental states are not always able to perform the function that natural selection designed them to.

Some dysfunction hypotheses are closely related to by-product hypotheses. The **hypersexuality hypothesis**, for example, considers homosexuality to be a by-product of hypersexuality, which in turn is assumed to be an adaptation. In some cases, however, hypersexuality and its connection with homosexuality are the result of a dysfunction. Experimenting with animals shows, for example, that their level of sexual activity and interest can be manipulated by inflicting damage on specific parts of their central nervous system that are assumed to be involved in regulating their sexuality (for an overview, see Poiani 2010, pp. 220–222). Here the **hypersexuality hypothesis** is to be considered as a dysfunction hypothesis.

Apart from lesions, pathogens are also important in understanding why mechanisms dysfunction. Infectious agents, such as bacteria, viruses, and parasitic worms, play at least some part in the etiology of many physical disorders and some mental disorders, such as schizophrenia and tertiary syphilis (Ledgerwood et al. 2003). Some researchers have defended the view that it would at least be worthwhile to consider the hypothesis that homosexuality would also be caused, in part, by some infectious agent (Cochran et al. 2000). This **contagion hypothesis** speculates that infections could cause a dysfunction in any of the

mechanisms involved in the development of brain structures that regulate sexual behavior and desire. To strengthen their case, adherents refer both to the shortcomings of evolutionary hypotheses about homosexuality and to a number of findings that they consider to be supportive, such as low identical twin concordance, geographical variation in incidence, and neurological differences between homosexuals and heterosexuals. One problem with the *contagion hypothesis* is that many of these “findings” are at least controversial (see above). Another problem is that no infectious agent has as yet been identified in the etiology of homosexuality.

A third and final dysfunction hypothesis, the *kin influence hypothesis* (Adriaens et al. 2012), is one of the few lesser-known evolutionary scenarios about homosexuality that do not originate in research on nonhuman animals. Indeed, this hypothesis focuses on an aspect of homosexuality that is generally considered to be rather exceptional in the animal kingdom and is commonly referred to as “modern homosexuality”: long-term, exclusive, and egalitarian homosexual relationships. It is this aspect of homosexuality with which members of WEIRD societies (Henrich et al. 2010) are most familiar. There is considerable debate about the prevalence of such relationships in times past and in contemporary non-Western countries, but there is also a consensus that they have become much more common than ever in the past 150 years (Murray 2000).

The *kin influence hypothesis* relates this rise to the process of economic development and the ensuing disintegration of traditional family ties. Research on small-scale societies reveals that family ties come with a set of norms and beliefs about sexuality and reproduction, which conform to the prediction of Darwinian theory that members of a family-based community will tend to maximize their (inclusive) fitness. Economic development triggers the construction of new sexual norms and beliefs that increasingly diverge from that which is consistent with achieving reproductive success. One such belief is that it is prudent to limit family size – a belief that resulted in a rapid decline in the fertility of most Western populations since 1850. Concomitantly, acceptance of nonreproductive aspects of sexuality has

been on the rise, with ever more people indicating that they believe homosexuality to be justified. According to *the kin influence hypothesis*, these cultural changes have set the scene for a modern kind of homosexuality to begin to flourish. Considered here as a dysfunction hypothesis, it holds that the rise of modern homosexuality is due to a breakdown in the functioning of the mechanisms involved in adopting fitness-maximizing reproductive norms.

Of course, the kin influence hypothesis only accounts for a very specific aspect of homosexuality and that other aspects may rightly be considered as evolutionary adaptations or by-products. Indeed, one of the recurrent erroneous assumptions in evolutionary thinking about homosexuality is that modern homosexuality is somehow representative of all aspects of homosexuality at all times and in all places (Adriaens et al. 2012).

Conclusion

Clearly, there is no lack of hypotheses explaining the evolution of homosexuality, both in humans and in other animals. An optimist would probably consider this abundance as a sign of the imaginative power of evolutionary scientists; a cynic, by contrast, would probably dismiss their scenarios as mere just-so stories. As always, the truth is somewhere in the middle. Some (parts of some) hypotheses have indeed been corroborated or falsified by empirical findings. Moreover, some researchers have indicated that their hypotheses can only account for a specific aspect of homosexuality, or a specific part of the homosexual population, thus leaving the door open for the coexistence of multiple explanations. It is vital, however, that existing hypotheses continue to be tested rigorously against the norms of evolutionary empirical research.

Cross-References

- [Alliance Formation Theory](#)
- [Ancient Homosexuality](#)
- [By-Products of Adaptations](#)

- ▶ Genetic and Prenatal Components of Homosexuality
- ▶ Homosexuality
- ▶ Homosexuality Paradox, The
- ▶ Hormonal Component of Homosexuality
- ▶ Human Sexuality
- ▶ Human Sperm Competition
- ▶ Just So Stories
- ▶ Kin Selection Hypothesis
- ▶ Nonhuman Sexual Conflict
- ▶ Same-Sex Relationships
- ▶ Same-Sex Sexual Behavior
- ▶ Sexually Antagonistic Hypothesis
- ▶ Sexual Orientation
- ▶ Sexual Orientation and Human Sexuality
- ▶ Sexuality

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Lethal Aggression

- Evidence of Intentional Killing

Lethal Conflict

- Evidence of Intentional Killing

Lethal Intrasexual Competition

- Sex Differences in Death by Homicide

Lethal Raiding

- Chimpanzee Raiding

Lethal Violence

- Chimpanzee Raiding

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Definition

Lev Vygotsky is an author and a researcher in the area of general, developmental and educational psychology.

Introduction

Lev Semyonovich Vygotsky (real name – Lev Simkhovich Vygodskiy) was born on November 17 (6), 1896 in Orsha (now the territory of Belarus) to the family of the banker Simkha Leibovich Vygodskiy. Vygotsky spent his childhood and youth in Gomel, where he received comprehensive education, first at home, then at a private Jewish gymnasium. In 1913 Vygotsky started to study law at Moscow University; he also attended classes at the faculty of history and philology of Shanyavsky People's University, where he wrote the *Tragedy of Hamlet* as a graduate thesis. At the time he was involved in literature and theater, about which he would publish more than eighty reviews. During this period he also was in ideological opposition to Marxism and tried to realize himself in essays on Jewish national politics (Zavershneva and Van der Veer 2018).

In the revolutionary years of 1917–1918 he moved from sympathy to Judaism to accepting Marxism, while remaining faithful to the philosophy of Spinoza. Having returned to Gomel in 1917, Vygotsky became one of the central figures of Gomel cultural life and taught the humanities. Vygotsky retained his interest in art until the end of his life and devoted his dissertation *The Psychology of Art* to the problem of the scientific explanation of aesthetic reactions.

In 1923 Vygotsky went to work in the Gomel Teacher Training College, where he conducted his first psychological research. In 1924 at the invitation of Aleksandr Luria he moved to Moscow and later combined scientific and teaching activities in psychological, educational and medical institutions in Moscow, Leningrad and Kharkov. In a short time Vygotsky created a new direction in psychology, which afterwards became known as cultural-historical psychology, and founded a major scientific school (among his associates were Aleksey Leontiev, Aleksandr Luria, Daniil El'konin and others). His work influenced developmental and educational psychology, the psychology of cognitive processes, child psychology, psycholinguistics and neuropsychology. However, the intense activities had a disastrous effect on Vygotsky's health: he suffered from

tuberculosis since 1920 and died on 11 June, 1934 at the age of 37.

Vygotsky's death was followed by a long period of silence connected with an unofficial ban on his publications in the USSR, which ended with the republication of part of his writings in the 1960s and 1980s. The first biographies of the scientist were published in the 1990s (Van der Veer and Valsiner 1991; Vygodskaya and Lifanova 1996) and his ideas acquired new adherents both in Russia and elsewhere (see Cole 1996; Miller 2011; Wertsch 1985; Yasnitsky et al. 2014). Today Vygotsky counts as one of the better-known psychologists of the twentieth century (Haggblom et al. 2002).

Main Ideas and Concepts

At the beginning of his career (1924–1925) Vygotsky toyed with the concepts of reflexology and behaviorism, but the greatest influence on him was exerted by, respectively, the founder of topological psychology Kurt Lewin, the psychologist Jean Piaget, and the Gestalt psychologists Kurt Koffka and Wolfgang Köhler. During the period of “instrumental psychology” (1926–1929), the concepts of sign operation and higher mental functions (HMF) were in the center of his theory (Vygotsky 1997). In the transitional period (1930–1931), and in the period of the psychology of dynamic semantic systems (1932–1934), these notions were supplemented by the concepts of word meaning, sense and semantic field and the study of verbal thinking became the main channel of Vygotsky's thought.

According to Vygotsky, mental processes should be studied in development; for this purpose he elaborated an experimental-genetic method in which mental processes are not simply observed, but also formed. Vygotsky defined his approach as “peak psychology,” focused at studying higher forms of mind, and argued that the mechanisms of human development are not genetically inherited, but introduced by culture and society. Language is the main tool of transforming natural mind into higher mind; it allows

accumulating and transmitting the experience of generations. With the help of speech and verbal thinking the individual gradually becomes an autonomous person capable of free choice.

Sign Operation

In contrast to animal mind, which is based on maturation and adaptation to the environment, human mind is also formed with the help of auxiliary cultural means (speech and writing, the number system, cultural artifacts), which are developed in communication with other people and allow to master human behavior. A system of HMF, developing in the process of anthropogenesis and ontogenesis, arises on the basis of natural functions through their mediation by psychological tools. Thus, voluntary memory in its simplest form is represented by making a knot in a handkerchief, the index gesture is the simplest means for regulating attention, and throwing dice is a prototype of volitional action. Primitive forms of sign operation are based on external material means (a knot, the index finger, a die), however, the mature mind is characterized by the use of internal means of regulation.

The Sociogenetic Law

During ontogenesis the child acquires social forms of behavior and begins to apply them to himself. For example, when he learns to speak, his speech activity is aimed at communicating with other people and is mostly external. Only at a certain stage of development the child uses speech to communicate with himself: first externally, talking aloud, and then internally – as a means of reflection. This process, called interiorisation, is defined as the creation of internal mental structures by “transferring inward” modes of behavior assimilated in the social situation of development.

According to Vygotsky, each HMF passes through three stages:

1. The HMF arises as an interpsychological function, distributed between people and controlled from outside with the help of external means (the adult organizes the activity of the child by pointing to objects, naming them, etc.);

2. The HMF becomes an extrapsychological function: the child controls himself with external means (speaking aloud, counting on his fingers, etc.);
3. Finally, the HMF turns into an intrapsychological function: the external means become internal (inner speech, mental calculations, etc.).

HMF do not work in isolation, they are connected in an integral system. In the process of ontogenesis, the primary, innate connections between functions are destroyed and new, artificial connections are created. They then form a system that can be deliberately changed and in which one function dominates and guides the others. Mature mind is characterized by the presence of flexible and differentiated psychological systems that can be adapted to specific tasks.

The Zone of Proximal Development (ZPD)

The notion of the ZPD appears in lectures read by Vygotsky in the early 1930s, where he argued that teaching should stimulate internal change: it should run ahead of development, rather than follow it. Taking into account the child's actual level of development, the adult must introduce cultural means and teach the child how to use them. This transfer of cultural means takes place in the ZPD, which characterizes the processes that are ripening, but have not yet fully matured. In practical diagnostics, the ZPD is defined as the difference between the level of the child's independent problem solving and his level of problem solving in collaboration with an adult.

Ontogenesis of Verbal Thinking

According to Vygotsky, thinking and speech have different genetic roots, and the relationship between them is variable in phylo-, onto- and functional genesis. In animals, intellect and speech develop independently of each other, but in the process of anthropogenesis these functions merge into the single whole of verbal thinking, which is no longer a natural, but a socio-historical form of behavior.

In the early 1930s Vygotsky proceeded to study word meaning as a unit of verbal

thinking, defining meaning as the internal structure of the sign operation. With the help of the double stimulation technique (in the form of the Vygotsky–Sakharov test, also known as the Kasanin–Hanfmann test), Vygotsky showed how meaning, passing through various stages (syncretic whole, complex, and concept), gradually acquires a stable structure and becomes less dependent on situational factors. The highest form of meaning – the concept – is based on abstraction, free of concrete content, and is not tied to sensory impressions. The concepts acquired by the adult form a network; this internal plane of generalization Vygotsky called the semantic field. It serves as the basis of volitional action and connects cognitive and affective systems.

Egocentric Speech

The term “egocentric speech” for speech addressed to oneself, was proposed by Piaget, whose work served as a starting point for a series of experimental studies by Vygotsky's research group. Contrary to Piaget's assumption that egocentric speech is nothing more than an accompaniment to the child's actions, Vygotsky argued that it has a special function in mental development. In accordance with the sociogenetic law, speech arises as an interpsychological process and then goes through an extra-psychological stage, when the external means (the sounding word) serves to objectify behavior and makes it easier to manage. As the child develops, egocentric speech shifts to the subvocal plane and then, at the intrapsychological stage, becomes inner speech.

Inner Speech and Semantic Dynamics

Thought is not expressed but formed in the word, asserted Vygotsky after the linguist Aleksandr Potebnya. He compared the thought to a hovering cloud, which gushes a shower of words and motivation to the wind that puts the cloud in motion. With the help of this metaphor, Vygotsky presented verbal thinking as a complex dynamic whole, passing through several planes in its development: (1) motivation, (2) thought, (3) inner speech, and (4) vocal speech (Vygotsky 1987). Every single utterance, then, is the result of series of inner processes that defy direct observation.

Using indirect evidence, Vygotsky speculated that inner speech has a number of distinctive features: sense prevails over meaning; it is predicative (the subject is often omitted), abbreviated and idiomatic (intelligible only to the speaker), agglutinated, and detached from vocal speech. In the last years of his life, Vygotsky intended to explore the semantic dynamics of consciousness, but his plans were not realized.

Conclusion

Among the undisputable achievements of Vygotsky's approach are the elaboration of the idea of the sociocultural determination of human development, the experimental-genetic method, the introduction of a number of fundamental categories (HMF, ZPD) and principles (sign mediation, the systemic and semantic structure of consciousness). The practical importance of his approach has been shown in developmental and educational psychology and in the psychology of cognition. In other areas (motivation, emotion, volition, consciousness, and personality) the value of his ideas still needs to be explored. But it seems psychology has not yet exhausted the potential of Vygotsky's cultural-historical approach.

Cross-References

- [Language Development](#)
- [Social Learning](#)
- [Socialization Processes](#)
- [Symbolic Culture](#)

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Level of Grandparental Investment

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Synonyms

[Discriminative grandparental solicitude](#); [Grandparent investment](#); [Paternity uncertainty](#); [Preferential investment in more certain kin](#)

Definition

Any investment by grandparents that increases or contributes to a biological grandchild's survival and/or reproductive fitness at an opportunity cost to the grandparent.

Introduction

Human grandparents often invest heavily in their grandchildren. Enjoying a long post-reproductive period, human grandparents are afforded many

opportunities to direct time and resources to their grandchildren. Grandchildren who receive such an investment are relatively more likely to survive and reach reproductive maturity (Gibson and Mace 2005; Sear and Mace 2008). According to kin selection theory (Hamilton 1964), humans can increase their inclusive fitness *directly* through reproduction or *indirectly* by helping their genetic relatives. Since grandparents share (on average) 25% of their genes with their grandchildren (over and above the large proportion of genes that all individuals share), grandparents can boost their inclusive fitness by investing time, energy, and resources in their biological grandchildren. This investment can take many forms and may change over time. It can range from direct behavioral forms of investment (child care, gift giving, financial support, contact behavior) to the psychological (guidance, advice, settling disputes, sharing of knowledge, showing interest). Whatever form this investment takes, grandparental resources are limited and their allocation should be maximized (Euler and Michalski 2007). Psychological adaptations may have evolved to regulate this investment to maximize fitness benefits.

One of the most consistent findings across the grandparental investment literature is the ordered level of investment of the different grandparents. Maternal grandmothers are often observed to invest the most in their grandchildren and enjoy the closest relationships with their grandchildren. Maternal grandfathers are typically next, followed by paternal grandmothers, and, finally, by paternal grandfathers (Smith 1988; Laham et al. 2005; Euler and Michalski 2007; Coall and Hertwig 2010). This investment differential suggests that grandparental investment is highly discriminative. A number of theories have been proposed to account for this discriminative investment psychology.

Paternal Uncertainty

The role of paternity uncertainty in the psychology of discriminative grandparental investment was first discussed by Dawkins (1976). Because of concealed ovulation, internal fertilization, and

the possibility of female infidelity, human males face a key adaptive problem – they can never be completely certain of their paternity. Thus, human males may unknowingly invest in another male's offspring. In contrast to males, human females are completely certain of their maternity even if they do not know the identity of the father. For human grandparents, this relational uncertainty may be present in two generations of descendants. Because the paternal grandfather cannot be completely certain of his relationship with his son or his son's relationship with his children, he faces two degrees of paternity uncertainty. Consequently, it is predicted that he will calibrate his investment in grandchildren accordingly. The maternal grandmother, on the other hand, is completely certain of her relationship to her daughter and her daughter's relationship with her children. Since the maternal grandmother faces no relational uncertainty, it is predicted that she will invest the most in her grandchildren. The maternal grandfather and paternal grandmother each face one degree of relational uncertainty: consequently, they will invest an intermediate amount in their grandchildren. The selection pressures created by these differing degrees of relational uncertainty are hypothesized to have crafted psychological mechanisms that regulate investment in a discriminant fashion.

Support for the role of paternity uncertainty in the psychology of discriminative investment by grandparents has come from a number of studies using various proxies of investment. The ordered pattern of differential investment has been found in a German sample of adults using retrospective reports of early care (Euler and Weitzel 1996), in a large-scale Dutch study of contact frequencies (Pollet et al. 2006), in the contemporary contact behavior (and closeness ratings) of US college students when all four grandparents are living (Bishop et al. 2009) and in child care in 13 contemporary European countries (Danielsbacka et al. 2011). These studies are notable for the consistency of their findings. An exception to this pattern of investment was reported by Pashos (2000). In this study, adults from both Germany and Greece were asked to retrospectively report on the care each grandparent provided up to the

age of 7. The findings from the urban areas in both Germany and Greece were similar to the above studies; however, for rural Greeks, paternal grandparents were reported as providing more care than maternal grandparents. The author speculated that the close residential proximity with the paternal family may have an increased paternity certainty relative to the urban settings.

Sex-Specific Reproductive Strategies

Studies of grandparent investment often reveal that maternal grandfathers invest more in their grandchildren than paternal grandmothers despite the same presumptive level of relational uncertainty. Euler and Weitzel (1996) suggest that, in addition to paternity uncertainty, grandparent solicitude should also be influenced by the sex of the linking parent. The task of the grandparent is to aid one's child (the parent of the grandchild) in his or her reproductive strategy. Since the maternal strategy differs from the paternal, the behavior of the grandparent is thus conditioned by the reproductive strategy of the linking parent. Maternal grandfathers, supporting the high investment strategy of their daughters, should therefore invest more than paternal grandmothers. In a sample of German adults reporting retrospectively on how much each grandparent had cared for them up to the age of 7, Euler and Weitzel found that paternal grandmothers did provide less care than the maternal grandfathers. In this study, both the sex-specific reproductive strategy and paternity uncertainty were significant determinants of grandparental investment. As they note, this means that the typically solicitous grandmother may become a relatively remote grandmother and the typically remote grandfather may become a relatively caring grandfather – depending on their child's sex. However, the authors acknowledge that partnership (co-residence) may also explain the investment dynamics of couples: for example, maternal grandfathers may invest heavily because they are partnered to high-investing maternal grandmothers.

Preferential Investment in More Certain Kin

In the ordered solicitude relationship discussed thus far, maternal grandfathers are often found to invest more than paternal grandmothers. Since both types share only one uncertainty link, parental uncertainty alone does not predict a differential in investment. Laham et al. (2005) have hypothesized that these two intermediate grandparent types with one uncertain link each will show an investment differential only under certain circumstances. Maternal grandfathers may invest more in their grandchildren relative to paternal grandmothers because *some* paternal grandmothers will have genetically more certain outlets available to them. If cousins are available through the father's sisters, a paternal grandmother will also be a maternal grandmother – she will have investment outlets that are more certain than her investment outlets with her son. Consequently, she may invest in her daughter's children at the expense of her son's children. In contrast, a maternal grandfather will not have a more certain outlet for his investment even if cousins are available through the mother's sister. Thus, relative to paternal grandmothers, maternal grandfathers should invest more heavily in (and be closer to) their grandchildren. The “preferential investment hypothesis” predicts that this investment differential between maternal grandfathers and paternal grandmothers will only emerge when there are cousins through the father's sisters.

The preferential investment hypothesis has received some support. In a sample of Australian psychology students, Laham et al. (2005) had grandchildren retrospectively rate their emotional closeness to each of their biological grandparents (check this). As predicted, maternal grandfathers were rated more highly than paternal grandmothers only when the paternal grandmother had grandchildren via her daughters. Danielsbacka et al. (2011) tested the preferential investment hypothesis in their large multinational study of child care. In this study grandparents self-reported the extent of provision of child care. Controlling for multiple potential confounds, their findings clearly supported the preferential investment hypothesis.

When women do not have more genetically certain investment outlets, the investment differential between paternal grandmothers and maternal grandfathers disappears. However, one test of the preferential investment hypothesis did not find the predicted effect. Bishop et al. (2009) asked college students with four living grandparents to indicate the frequencies of various contact behaviors received from or directed to each grandparent. In contrast to the above findings, grandchildren did not indicate more frequent contact with the maternal grandfather when more certain investment outlets were available to the paternal grandmother.

Reproductive Value

Not all individuals who share the same degree of genetic relatedness are equally valuable as investment outlets. As Hughes (1988) has noted, an individual's *reproductive value* (Fisher 1930) is another factor that may influence how many resources he or she receives. For human females, reproductive value (future reproductive potential) reaches its peak during the early twenties and declines thereafter. If a grandparent has the option of investing in a grandchild who has reached their peak reproductive window or in another grandchild, who is equally related but not yet in this reproductive window, the grandparents should favor the grandchild who has a higher probability of reproducing. Thus, the reproductive value of the grandchild should contribute to the calculus of differential grandparental solicitude. Consistent with this claim, Hughes (1988) has demonstrated that pubertal cohorts (those with the highest reproductive value) have the largest effect on inclusive fitness relative to any other subset of individuals in the population. Direct tests of this hypothesis with grandparents have not been conducted.

Conclusion

The fact that grandparents invest in their grandchildren to further their inclusive fitness and that the discriminative nature of this investment

may be driven by an adaptive calculus designed to solve domain-specific problems does not discount or diminish the important role that grandparents play in the lives of their grandchildren. Many grandparents sacrifice selflessly for their grandchildren and remain devoted even when separated from their grandchildren by great distances. Although the grandparent types often conform to an ordered level of investment in their grandchildren, it is important to remember that this is a differential that often cuts across high overall levels of investment. While many questions remain unanswered, this much is clear: a complete understanding of grandparent psychology cannot be adequately understood without consideration of the adaptive significance of grandparental investment.

Cross-References

- [Hamilton's Rule and Kin Investment](#)
- [Inclusive Fitness](#)
- [Parental Investment](#)
- [Paternity Certainty](#)

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Levels of Explanation

- [Tinbergen’s Four Questions](#)

Lever Box

- [Skinner Box, the](#)

Lexicon

- [Vocabulary](#)

LGB Victimization

- [Homophobic Bullying](#)

LGBTQ+ Identity

- [Sexual Identity](#)

Liberal

- [Political Left, The](#)

Liberty

- [Evolution of Free Will](#)

Life Cycle

- [Stages of Development](#)

Life Expectancy

- [Darwinian Medicine and Survival Problems](#)

Life Expectancy and Reproduction

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Synonyms

[Aging](#); [Breeding](#); [Propagation](#); [Senescence](#)

Definition

Corporeal organisms are vehicles for the prorogation of genetic material, making organismic lifespan an expedient of reproductive output.

Introduction

Humans create machines of metal, plastic, ceramic, and wood that wear with age, eventually degrading and breaking down. It is then natural to think of aging cells, tissues, and organs, as wearing out and winding down as do sprockets, springs, and bearings (Hertler 2014). For all its intuitiveness, the analogy is misleading. Cells need not become exhausted and die. While this is the characteristic of complex, multicellular, sexually reproducing life, it is not invariably characteristic of simple, single-celled, asexually reproducing life (Hertler 2015). This was recognized as early as 1891 by August Weismann, who wrote, “Let us now consider how it happened that the multicellular animals and plants, which arose from unicellular forms of life came to lose this power of living forever” (Smith-Sonneborn 1987). Weismann continued on to qualify his understanding of lifespan as it relates to reproduction:

The immortality of unicellular organisms, and of the germ cells of the multicellular, is not absolute but potential; it is not that they must live forever; they can die – the greater number do in fact die – but a proportion lives on which is of one and the same substance with the others. Does not life, here as elsewhere, depend on metabolism – that is to say, a constant change of material? And what is it, then, which is immortal? Clearly not the substance, but only a definite form of activity. The protoplasm of the unicellular animals is of such chemical and molecular structure that the cycle which constitutes life returns ever to the same point and can always begin anew, so long as the necessary external conditions are forthcoming. This character it is which I have termed immortality. . . . (Weismann quoted by Kirkwood 1987, p. 209)

It required approximately seven decades and four discreet theoretical advances to answer the questions Weismann framed about the complex interplay between *life expectancy* and

reproduction. Together, the *pleiotropic view of senescence*, *The Selfish Gene*, the *disposable soma hypothesis*, and *life history theory* came to explain empirical realities, experimental findings, and biogeographical variation in life expectancy within and between species. In common, these four theories successfully explained lifespan precisely because they studied it in conjunction with reproduction.

The Pleiotropic View of Senescence

Successively, R. A. Fisher (1930), J. B. S. Haldane (1941), P. B. Medawar (1946), and G. C. Williams (1957) progressed toward the first convincing evolutionary explanation of senescence. As described by Hirsh (1987, p. 76), Medawar (1952) provided an analogical experiment for what is a pleiotropic view of senescence. Medawar envisioned 1000 test tubes, 10% of which shattered monthly by random accident and were subsequently replaced. Over time, applying this rule resulted in a population of test tubes that were predictably skewed, with test tubes less than a month old being more common than those a month old, and those a month old being more common than those 2 months old, and so on. It was at this point that Medawar introduced a proxy for senescence by appointing some specific older age at which test tubes would break, not by random accident but by intrinsic shortcoming. The results showed that, if the imposed senescence date was sufficiently late, it would have minimal effect, because, at that point, most of the test tubes would have been already broken through random accident. Lastly, and most importantly, Medawar found that the small cost of test tube senescence for the old could be countered, and even reversed, by a small advantage of test tube replacement for the young (Hirsch 1987). A fundamental transition had been made. Limited life expectancy was perhaps a reproductive strategy that outcompeted its opposite. Dying was not compulsory but competitive. Williams (1957) cited Weismann’s contributions while also critiquing them in his *Pleiotropy, Natural Selection, and the Evolution of Senescence*. With

this culminating publication came a mature theory of senescence that transcended intuitive, but unworkable, views of organisms as machines subject to wearing out and winding down. *Pleiotropy*, specifically, *antagonistic pleiotropy*, is where a gene encodes for a trait that is not decidedly detrimental or beneficial but double-edged. Each instance of antagonistic pleiotropy confers one trait with two repercussions, one that depresses fitness and one that enhances fitness. The fitness enhancing effects do not always exceed and overcome the fitness depressing effects, though by definition, such is the case for those pleiotropic mutations that persist with any frequency within populations. As can be seen, Medawar's test tube experiment was a model of antagonistic pleiotropy because late senescence was overcome by early proliferation.

The Selfish Gene

In theory, an automobile can run in perpetuity; it has no definite expiration date. When the car is new, it requires very little maintenance, generally only oil changes. After about 40,000 or 50,000 miles, slightly more costly service is required, such as new tires and brake pads. Another 30,000 miles more, the car is apt to need rotors, for instance, but by this time, very possibly an essential part has malfunctioned and is in need of replacement or repair. Entering into six-figure mileage will not require a six-figure salary, but it will come with still more costly repairs. Transition to what is unequivocally considered a high-mileage car is the point beyond which major repairs, including transmission rebuilds and engine replacements, become common. When an engine or transmission does fail on a high-mileage car, the driver often chooses to buy another car, and this is often a rational choice because the cost of such repairs will rival, and then exceed, the cost of replacement. Still, it is necessary to recognize that this is a rational turning point in a decision-making process, *not* a necessary decision. One can replace the engine and later, the transmission as well, and go on investing in the high-mileage car with no necessary end point. If the driver is

willing to weld cracks in the chassis, replace steering linkages, bond body damage, and the like, that same first car, becoming like Theseus' ship, can be theoretically driven for the duration. Life is very much like the above-described analogy of *The Selfish Gene* (Dawkins 1976). Adding another blow to the pride of person, in this analogy the organism is the car, and the gene is the driver who jumps from car to car. Dawkins' great insight was to exchange the organism for the gene as the unit of selection. From here, it is not hard to see why bodies are successively replaced. With oxidation, free radicals, and the cellular mutiny that is cancer, organisms in a sense do wear out just like cars, but also like cars, they can be theoretically maintained given sufficient investment. With this in mind, one can see that, with cars, there is some point at which a new car will more cheaply transport the driver; just as with organisms, there is some point at which a new organism will more efficiently propagate the genes. As the driver is economically compelled to trade in his high-mileage vehicle for a new one, the organism is evolutionarily compelled to cease investing in his body and channel efforts toward reproduction and the creation of a new organism. This gene-centric level of selection then clarified the implicit orientation away from the organism and toward the lineage that was contained within the antagonistic pleiotropy view of senescence.

The Disposable Soma

The Disposable Soma, a theory developed by Kirkwood (1977), came to incorporate aspects of August Weismann's work, emphasizing its distinction between the soma and germline, the ideas of Medawar et al. with its distinction between reproductive and post-reproductive life, and Dawkins' reorientation from the organism to the gene as the unit of selection. Like the car in the analogy above, or a disposable piece of cutlery, after the propagating function of the body is finished, so evolution is finished with the body. Consistent with a gene's eye view of selection and the understanding that survival is subordinated to reproduction, the soma is not an end unto itself

but a means to an end. Consistent with antagonistic pleiotropy, energetic saving came from attenuating somatic investment, thus allowing for the bodily deterioration known as aging. Consistent with Weismann and his barrier between soma and germline, the disposable soma hypothesis specified that somatic cells were allowed to senesce, germ cells were not. Sperm cells were constantly cycled, being purged and regenerated. Alternatively, egg cells, though present at birth, were subjected to oocyte atresia, which created an evolutionary process prior to conception, thereby barring mutated eggs from becoming implanted embryos. Yet, the disposable soma hypothesis served more than an integrative function; it pressed the concept of trade-offs to its logical conclusion. Here was the explicit recognition of finite resources being strategically divided between somatic maintenance and reproductive effort. The evolutionary optimum was specified to fall at the convergence of fecundity and somatic maintenance given a particular rate of survivorship.

Life History Theory

As with the antagonistic pleiotropy theory of aging, *life history theory* was developed successively by multiple researchers, with MacArthur and Wilson, Dobzhansky, Pianka, Roff, Charnov, Stearns, Harvey and Clutton-Brock, Rushton, and Figueredo among those making seminal contributions. But unlike antagonistic pleiotropy, or any other theory, life history theory was extraordinarily consilient because it subsumed lifespan and reproduction into a metatheory capable of contextualizing intelligence and personality, attachment and development, and risk-taking and restraint. Even when restricted to the biodemographic variables upon which life history theory was established (Wolf and Figueredo 2011), one can see its range: (1) size at birth; (2) growth pattern; (3) age and size at maturity; (4) number, size, and sex ratio of offspring; (5) age- and size-specific reproductive investments; (6) age- and size-specific mortality schedules; and (7) length of life. While wide ranging, these seven sets of variables can be reduced to

lifespan on one hand, and reproduction on the other, with all else being developmental markers tracking the trade-off between the two. As with the disposable soma hypothesis, life history theory described trade-offs between somatic and reproductive effort, but it did so in a more nuanced manner, which specified the overarching evolutionary development by which one or the other was emphasized. Moreover, within the context of life history theory, the importance of survivorship and mortality became fully apparent. Mortality regime was delineated into extrinsic, threats that could neither be predicted nor controlled, and intrinsic, threats that could be both predicted and controlled. As mortality threats became more extrinsic, life history speed quickened, resulting in the lower somatic effort and higher reproductive effort of a mouse, hare, or shrew, with their short lives and large broods. More than this, life history theory provided a framework by which the interaction between lifespan and reproduction could be more mechanistically understood. High predation, disease, or other hallmarks of extrinsic mortality that could neither be predicted nor controlled resulted in a more disposable soma with short lifespans and rapid aging, but the same evolutionary pressures also necessitated a congruent reproductive strategy replete with many young, produced early, and provided with little or no investment. Where mortality pressures precluded the development of long-lived individuals, it also precluded the development of small broods, enculturation, a long juvenile period, excessive maternal dependency, or large inter-birth intervals.

Experimental and Empirical Validation

These theories of lifespan and reproduction were not separated by a great deal of time, and furthermore developed in parallel, sometimes specifically referencing one another. It is beyond the scope of this entry to trace the precise contributions of each theory, the precedence of ideas, or the nature of their interrelations. Suffice it to say that all four theories, rather than replacing one another, accreted productively, with the end result

being a powerful understanding of lifespan and its relation to reproduction. Jointly, these theories explain a mass of empirically observable facts about the natural world (Wolf and Weissing 2012).

The idea of finite bioenergetic resources being traded off between somatic effort and reproductive effort, so central to the disposable soma and life history theory, is supported by the increased longevity resulting from castration observed in animals and humans (Min et al. 2012). Bioenergetics budgeting is similarly observed in instances of genomic imprinting, wherein resources imparted during gestation are a middle ground between the maternal pull against resource depletion and the paternal push for resource extraction (Burt and Trivers 2006). Though the less than monogamous male maximizes his fitness to the detriment of his mate, the female can only maximize the fitness of her offspring to the detriment of herself (van Noordwijk 2012, p. 322). Still further, Medawar's test tube analogy can be seen conforming to the empirical reality of prostate cancer and breast cancer. Both are deadly cancers of generative organs, both are frequent, and both most commonly afflict the post-reproductive. Like other lethal mutations that persist in the population (Rauser et al. 2009), prostate and breast cancer are often diagnosed in one's 1950s, 1960s, or 1970s after mating, weaning, and rearing. So there then is one of Medawar's conditions met, an attenuated fitness disadvantage. Prostate and breast cancer also meet Medawar's second condition, in that they likely confer a compensatory reproductive advantage. Prostate discharge comprises approximately one-third of ejaculate volume, protecting sperm as they enter the acidic vagina resulting in sperm survival, fidelity of genetic material, and resultant fecundity. What the prostate is to conception, the breast is to completed fertility.

Experimental evidence also supports the validity of characterizing mortality regimes as either intrinsic or extrinsic as a function of predictability and controllability. *Drosophila* experiments conducted by Stearns altered mortality rates, making them more or less extrinsic, which had the effect of decreasing or increasing longevity in

the predicted direction (van Schaik and Isler 2012). Similarly, experimental manipulation of guppies showed that longevity waned and fecundity waxed as a function of augmenting extrinsic mortality (Rauser et al. 2009). Across several treatment conditions manipulating variables such as food availability and temperature, reproductive effort and survival were negatively correlated (Hirshfield 1980). Further still, a population of asymmetrically fissile bacteria exposed to amplified extrinsic mortality were invaded by a highly fecund but rapidly aging morph (Rauser et al. 2009). Lastly, amphibian life histories respond to intensive parasite pressure, a salient form of extrinsic mortality, across markers of life expectancy and reproduction. With high parasite load, the pace of life quickened resulting in amphibians that spent less time growing and living and instead showed more rapid intergenerational turnover (Johnson et al. 2012).

Together, theories of aging also explain variation in life expectancy and reproduction as they are distributed biogeographically. As Gurven notes, low extrinsic mortality, and thus extreme longevity, is found in those desert, polar, or sub-alpine biomes that impose predictably harsh conditions, but which are relatively free of parasitism, predation, and other forms of biotic competition that become extrinsic sources of mortality for so many organisms. Consequently, one can observe long life expectancy and low reproductive effort among Siberian *Actinobacteria*, Antarctic plant species, and many desert succulents. Estuaries, rainforests, and reefs, on the other hand, teem with life. These are generous climatic zones where organisms compete intensively, parasitizing and preying on one another in a manner than can rarely be both predicted and controlled. The evidence for the above-described relationship is reproduced when observing stable micro-niches with low extrinsic mortality, even as they are contained within a larger ecology with high extrinsic mortality. Consequently, one can observe long life expectancy and low reproductive effort among Quahog clams, cave salamanders, and arboreal primates (Hertler 2017).

Beyond explaining variation in life expectancy and reproduction as they occur across species,

these theories also explain variation in life expectancy and reproduction as they occur within species. For example, the four theoretical advances herein described explain mean intrapopulation biogeographical variation in longevity among humans, carefully catalogued by the World Bank (<http://data.worldbank.org/indicator/SP.DYN.LE00.IN>), Central Intelligence Agency (<https://www.cia.gov/library/PUBLICATIONS/the-world-factbook/rankorder/2102rank.html>), and the World Health Organization (http://www.who.int/gho/mortality_burden_disease/life_tables/en/). Looking at the Central Intelligence Agency data set, for instance, shows clear biogeographic trends, with only Afghanistan intruding upon an African monopoly of truncated lifespan. Lifespan among the bottom 36 countries, 35 of which are in Africa, shows mean lifespans of around 55 years. In turn, the top 36 countries reporting mean lifespans of 80 or above contain 5 Asian countries with the remainder being comprised almost exclusively of European countries, their former colonies, or current dependencies. Though the reality of such disparities is irrefutable, explanations are various. War, poverty, disease, and political regime have alternatively been emphasized. The 12-year lifespan discrepancy favoring South Korea over North Korea, and the diminishing gap between what were formerly East and West Germany, validates such situational factors. On the other hand, longevity differentials persist in mixed-raced countries, recapitulating patterns found in the countries of origin, even while attenuating them. Supportive of the theories herein reviewed, these biogeographic patterns in lifespan are paralleled by biogeographic patterns in reproductive effort. According to United Nations data, unintended pregnancies are lowest within Asian and European countries and highest in African countries (Singh et al. 2010). Still further, those of African as opposed to European or Asian ancestry have sex more often before and after marriage. The same racial relationship holds for skeletal muscle, testosterone, combined testes weight, sperm production, secondary sexual characteristics, number of partners, and sexually transmitted diseases (Hertler 2015). Being a mixed-race society containing the extremes of the cross-national

lifespan continuum, the United States provides context. Along with Caucasians having longer lifespans than African Americans, African Americans reach menarche significantly earlier (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4137967/>) and had an earlier mean age of sexual debut (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3064497/>).

Conclusion

Though they have previously been studied in isolation, there now exists an empirically and experimentally supported theoretical framework wedding life expectancy to reproduction. These theories suggest that gene frequency is all that matter. With genes being emphasized above, organisms come to the realization that lifespan is simply an optimized time for genes to reside in a single organism, whereas reproduction signifies the point at which that optimum has been reached. Prior to these theories, it was as if a relay race was being watched, but not for so long that the baton was seen passing from runner to runner. With these theories, one can recognize the relay race for what it is and so focus on the baton rather than the runner.

Cross-References

► [Increasing Longevity](#)

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Life Expectancy in Hunter-Gatherers

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Synonyms

[Hunter-gatherer lifespan](#); [Traditional life-expectancy](#)

Definition

The average period an individual may expect to live among nomadic peoples who rely primarily on hunting, fishing, and harvesting wild foods.

Introduction

Hunter-gatherers do not experience short, nasty, and brutish lives as some earlier scholars have suggested (Vallois 1961). Instead, there appears to be a characteristic life span for *Homo sapiens*, in that on average, human bodies function well for about seven decades. These seven decades start with high infant mortality rates that rapidly decline through childhood, followed by a period in which mortality remains essentially the same to about 40 years. After this period, mortality rates rise steadily until around 70 years of age (Gurven and Kaplan 2007). Of course, mortality rates differ geographically and temporally, especially in the risks of violent deaths and disease. However, these differences are minimal when compared on

a global scale, and the mortality profiles of modern hunter-gatherers living in vastly different environments are remarkably similar.

Specifics of Hunter-Gatherer Lifespan

We know specific details about modern hunter-gatherer lifespan from a few well-studied groups: the !Kung, Aché, Agta, Hadza, and Hiwi (Gurven and Kaplan 2007). Work on these groups show that approximately 60% of hunter-gatherer children live to age 15. Of those who reach 15, around 60–80% of them will live to age 45. If an individual lives to age 45, then on average they will live for approximately two more decades. However, not all modern hunter-gatherer groups show the exact same lifespan profiles. The average life expectancy at birth among these groups varies from 21 to 37 years, and the proportion of individuals living to 45 years old varies between 26% and 43% of the population. These individuals who live to age 45 then have a continued life expectancy between 14 and 26 years.

The generally low life expectancy at birth among modern hunter-gatherers is due to their very high infant mortality rates, which pulls down their average life expectancy significantly. Compared to the United States, infant mortality is over 30 times greater among modern hunter-gatherers, and early child mortality is over 100 times greater (Zopf 1992; Hill et al. 2007). Even late childhood mortality is about 80 times greater among modern hunter-gatherers. Not until the late teens does the relationship start to even out, with over a ten times difference in mortality. This difference then continues to decline until it reaches age 70, where mortality among modern hunter-gatherers is only three times greater than individuals of the same age living in the United States (Gurven and Kaplan 2007).

Does Life Expectancy Among Hunter-Gatherers Represent Humans' Evolved Lifespan?

Given that the average human lifespan estimate was obtained from modern hunter-gatherer

populations, does it represent the evolutionary history of our species, or is it simply the result of modern civilization impacting these groups (Washburn 1981)? Comparative studies predict a human lifespan of 66–78 years from regressions of lifespan on brain and body weight (Hammer and Foley 1996). Converted to average adult lifespan, these results overlap with the observed lifespan from contemporary populations. Similarly, a reestimation of several Paleolithic mortality curves shows a Paleolithic life course pattern similar to those of modern hunter-gatherers (Konigsberg and Herrmann 2006). These types of comparative studies as well as studies on modern hunter-gatherer populations support the conclusion that the evolved average adult lifespan for *Homo sapiens* is around 70 years and thus individuals living long lives in both traditional societies and developed countries is not simply the result of modern medicine and hygiene (Blurton Jones et al. 2002).

There are a number of hypotheses as to why human lifespan is so long and includes a lengthy postreproductive period. Two notable examples are the “embodied capital model” (Kaplan et al. 2000) and the “grandmother hypothesis” (Hawkes et al. 1998). The “embodied capital model” proposes that learning the complexities of hunter-gatherer feeding environments requires a long time to master but provides high benefits later in life, thus favoring an extended life span. The “grandmother hypothesis” suggests that humans live to old age so that women can invest time and resources in their grandchildren.

Conclusion

Excepting outside forces such as violence and disease, hunter-gatherers can live to approximately 70 years of age. With this life expectancy, hunter-gatherers are not dissimilar to individuals living in developed countries. One major area of difference is the high infant mortality rate of hunter-gatherers, which pulls down their life expectancy at birth and influences their overall average lifespan. This pattern of life expectancy among hunter-gatherers is not only a consequence

of the impacts of modern civilization. Rather, humans appear to have an evolved lifespan of approximately seven decades that includes a lengthy postreproductive period.

Cross-References

- ▶ [Extended Postmenopausal Lifespan](#)
- ▶ [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)
- ▶ [Hunter-Gatherer Societies](#)
- ▶ [Life Expectancy and Reproduction](#)

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Life History

- ▶ [Investment Versus Future Payoff](#)
- ▶ [Life History Theory](#)

Life History Model of Psychopathology

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Synonyms

[Etiology of psychopathology](#); [Life history theory](#)

Definition

Life history approaches understand psychopathology as long-term consequences of inevitable trade-offs in investment in reproductive (fast life history strategy) vs somatic (slow life history strategy) effort, interacting with the environment the individual finds themselves in.

Introduction

Psychopathology is characterized by harmful dysfunction, defined by harm to self or others and/or a failure of psychological mechanisms to serve the functions for which they were designed by natural selection. This entry will review evidence that has been collected relating life history strategy (LHS) to various psychopathologies. Early-life experience can lead to adopting a fast LHS, focusing on short-term gains, and consequent risk-taking, or a slow LHS in which resources are accrued and utilized more slowly and carefully. Evidence will be reviewed illustrating the link between these strategies and psychopathology, including a consideration of the

possible underlying mechanisms (hormones, for example), with respect to depression, anxiety, obsessive-compulsive disorders, schizotypal disorders, autism spectrum disorders, eating disorders, gambling, and other risk-taking behavior.

Life History and Psychopathology

Informed by our current understanding of the mechanisms involved in developmental plasticity, along with extensive nonhuman biological research and life history theory (Ellis and Del Giudice 2018; Ellis et al. 2009; Roff 1992; Stearns 1976), theories were developed as a means of explaining between (and later, within) species differences. Life history theory allows for behavioral and physiological adaptation across the life span, suggesting that environmental cues during key phases of development may set individuals on a path to utilize resources in a specific way, particularly with respect to reproductive, familial, economic, and social behaviors/strategies (Ellis and Del Giudice 2018; Ellis et al. 2009; Roff 1992; Stearns 1976). More specifically, life history theory proposes that organisms allocate time and energy differentially as a consequence of a variety of environmental cues and constraints and competing goals (e.g., fitness vs reproduction) (Figueredo et al. 2013; Roff 1992; Stearns 1976). In humans, research utilizing life history theory focuses on the cues and consequences of early life disadvantage in the early environment (Frankenhuis and de Weerth 2013; Nettle et al. 2013). LHT suggests that early-life cues predispose individuals to adopt either a “fast” or “slow” strategy (Del Giudice 2014a; Frankenhuis and de Weerth 2013; Nettle et al. 2013). More specifically, those who experience early-life adversity develop strategies focused on short-term goals and immediate gain (fast). Conversely, those whose early environments were stable, predictable, and abundant in resources adopt strategies, characterized by a more future-oriented, cautious perspective, where the long-term gain is prioritized over short term (slow). For example, with respect to attitudes to food, money, and mating strategies,

individuals at the fast end of the continuum might adopt more risky, opportunistic strategies (e.g., high (vs low) energy food, gambling, unprotected sex), whereas individuals at the “slow” end of the spectrum are more inclined to invest in long-term health and relationship goals (Del Giudice 2014a; Figueredo et al. 2014; Frankenhuis and de Weerth 2013).

The utilization of life history theory as a means of better understanding the nature, development, and outcomes of psychopathologies is a relatively new phenomenon (Del Giudice 2014a). However, an increasing body of literature, both within the evolutionary field and across the discipline, indicates that this perspective may provide a powerful framework informing research and intervention (Del Giudice 2014a; Ellis and Del Giudice 2018). As a framework, life history theory is useful in that it promotes more objective view of psychopathological behaviors (i.e., functional/adaptive vs deficit) (Ellis 2018), which in turn (and in line with traditional clinical approaches) promotes a strength-based approach to symptoms that can improve the efficacy of interventions (Del Giudice 2014a; Ellis 2018). The perspective also accounts for, and strengthens, the case for early intervention. The life history perspective has been useful in highlighting the importance of the function and ontogeny, as well as proximate and ultimate determinants of psychopathology. Psychopathology is characterized as harmful dysfunction, contingent on two conditions, harm to self or others and/or failure of psychological mechanisms to serve the functions for which they were designed by natural selection (Wakefield 1992). The term may refer to the study of, development of, manifestation of, or experience of psychological distress or mental illness.

While psychiatry and psychology frequently focus on descriptive frameworks as a means of diagnosis, the study of development (etiology) of psychopathologies, from genes to environment, is the focus of an increasing amount of research. Life history theory encompasses and promotes a gene/environment model, which encompasses current understanding of developmental plasticity, and incorporates other models (e.g., allostatic load

model, diathesis-stress model). This aligns with the National Institute for Mental Health, where research identifying mechanisms, gene/environment interactions is the focus of the RDoc perspective (Insel et al. 2010).

More specifically, there a great deal of focus on mechanism and ontogeny. The need for an integrative framework can be seen in the controversy around the diagnosis and treatment of mental health disorders (Del Giudice 2014a; Ward and Clack 2019). Current models are based on similarities between symptoms (DSM) and correlations between disorders (e.g., externalizing/internalizing) (Del Giudice 2014a). In this context, life history theory, with its broad, but connected, perspective, also encapsulating function and adaptation, has the potential to promote research and inform interventions. This is particularly the case given the extensive literature linking early-life environmental stress to the development of psychopathologies (Del Giudice 2014b; Pechtel and Pizzagalli 2011).

Life theory research can account for a range of candidate mechanisms in the development of psychopathology across a range of domains. These include developmental plasticity (Ellis and Del Giudice 2014), DNA methylation (Sumner et al. 2018; Vinkers et al. 2015), neuroendocrine system (HPA axis dysregulation, glucocorticoids, etc.), and neural changes, e.g., accelerated/delayed maturation in some areas of the brain (Tyborowska et al. 2018). It is also a useful framework for understanding the link between mechanism and behavioral manifestations (whether that is adaptive or maladaptive). For example, life history theory can explain the link between early environmental stress and delayed or reduced neurodevelopment (e.g., amygdala), leading to antisocial traits and then to psychopathy (Tyborowska et al. 2018). Similarly, life history theory is a useful framework for understanding the link between threat-related stress through telomere length and emotional processing which is linked to depression (Sumner et al. 2018).

The life history approach to psychopathology is well-aligned with the current identified need to reorganize diagnostic criteria along functional lines (Del Giudice 2014a). For example, the

range of symptoms/features of depressive disorders may be better understood in terms of different etiology within life history framework. In other words, for example, there are likely to be differences in symptoms (because of their potentially adaptive functions) between depression as a consequence of adverse life events in adulthood and as a consequence of childhood abuse (Del Giudice 2014a). Similarly, life history theories evolutionary basis provides potential explanations for sex differences in the etiology and presentation of psychopathologies. For example, it is well-established in the literature that the symptoms of depression vary between males and females. Symptoms of depression for males (e.g., aggression) vs females (e.g., self-harm) could be seen in terms of their potential costs – aggression (vs self-harm) may confer benefits or less cost for males (vs females) (Hurst and Kavanagh 2017). Where for females, physical aggression is likely to be costly, and emotional regulation through self-harming behaviors may be more functionally adaptive. Thus life history's functional approach may address limitations of our understanding of internalizing/externalizing disorders (Del Giudice 2014a).

While a number of specific models exist exploring psychopathology in terms of life history (e.g., pace of life, adaptive calibration, psychosocial acceleration), they overlap the sense that they identify the potential for the adaptive value of the psychopathological behaviors (Ellis 2018). This is a main advantage of life history models compared to other models of psychopathology. For example, while all models recognize the role of environmental stress, both historically and currently, life history models explicitly predict that behaviors may be maladaptive or adaptive and that this will depend on context (e.g., time).

Evidence for the utility of the application of life history (evolutionary perspective) in understanding the development of psychopathology can be found in nonhuman biology (Hill et al. 2019), psychiatric and psychological research (Del Giudice 2014a) (see, e.g., (Hurst and Kavanagh 2017; Sumner et al. 2018)), and adaptive (vs maladaptive) value of associated traits, e.g., risk-taking, aggression, early sexuality,

exploitative (fast), risk aversion, agreeableness, inhibition, and delayed sexuality (slow LHS) (Del Giudice 2014a). Psychopathologies implicated include depressive disorders (type dependent: fast/slow) (Del Giudice 2014a), anxiety (fast LHS) (Del Giudice 2014a), obsessive-compulsive disorders (slow LHS) (Del Giudice 2014a), schizotypal disorders (fast LHS) (Del Giudice 2014a), ASDs (slow LHS) (Del Giudice 2014a), and eating disorders (type dependent: dysregulated (fast), reactive (slow LHS)) (Del Giudice 2014a).

The proposed pathways (etiology) to psychopathology according to life history theory (Del Giudice 2014a; Hurst and Kavanagh 2017) include symptoms as strategies/adaptations. For example, psychopathy may be the consequence of traits that enable exploitation, whereas anxiety may be underpinned by adaptive traits evolved to enable survival in fast-changing environments. Another pathway implicates extreme expression/maladaptive levels of useful traits, for example, the pathway from disgust (a useful means of avoiding harmful toxins in the environment) to obsessive-compulsive disorder, the symptoms of which may be seen to be an extreme disgust response. A mismatch between behavior and environment at the individual level may also be utilized as a means of understanding the relationship between, for example, violence in the early environment to hypervigilance and anxiety in the adult environment (fast LHS). Similarly, the life history framework may explain the way life history leads to vulnerabilities. For example, risk-taking (a fast life history strategy) may involve drug use/unprotected sex, which in turn may lead to higher exposure to pathogens/toxins (e.g., infections/cannabis) which in turn increase likelihood of psychopathology (e.g., schizophrenia) (Del Giudice 2014a).

Life history focuses on the allocation of resources towards either reproductive or somatic effort. Increasing energy expenditure in one area necessarily results in a decrease to the other. Thus, an individual must be able to endure physiological and behavioral changes that ideally facilitate successful reproductive strategies. Many of these changes are regulated by the endocrine system, the internal collection of glands that regulate

homeostasis and growth. Responsible for changes in both physiological and behavioral processes through differentiation of hormone secretion, the endocrine system responds to cues in the external environment, by adjusting hormone production, as a means of best equipping the individual to its current environment.

While endocrine function changes throughout the life span, switch points in development have been implicated in the development of specific life history strategies (Del Giudice et al. 2009), where the external environment and the independent state of the organism interact to establish a strategy suited to the current environment. These switch points are established throughout puberty, where onset is arguably at either *adrenarche* (production of androgens by the adrenal glands) or *gonadarche* (production of androgens by the gonads). A key feature of these developmental switch points is the increase of sex-specific androgens, which may be the driving force between the development of specific life history strategies.

Sex-specific androgens are seen as the primary factor in the development of physical traits during puberty. In both human and nonhuman males, both natural variations in testosterone and manipulation of testosterone result in a switch in allocation of somatic effort (Muehlenbein and Bribiescas 2005). Evidence indicates that an increase in testosterone leads to a decrease in select immune functions, which, in terms of life history theory, suggests that increased reproductive effort is coordinated with a decrease in somatic effort.

Bribiescas (2001) theorizes that testosterone plays a role in driving the functional reproductive processes evident in both physiology and behavior. He also theorizes that allocation of skeletal tissue is indicative of a faster life history, the process of which is mediated by testosterone (Bribiescas 2001). This corresponds with evidence suggesting testosterone is associated with competition for mates (Ronay and von Hippel 2010). Further support for this notion can be found in evidence around the immunocompromising effects of testosterone in males, given this effect would be maladaptive for an individual that had more resources to allocate to somatic energy.

While life history emphasizes that reproduction is the ultimate end goal, hormonal output associated with this may have maladaptive effects, leading to the development of psychopathology. High levels of testosterone are associated with aggressive behavior. While aggressive behavior could be advantageous in intrasexual competition for mates, the reduction of such behavior in human societies means violent behavior may be maladaptive. While the association exists between testosterone and aggressive behavior, this may not be due to testosterone itself. Rather males have an increase in testosterone in the presence of competition, which in turn influences aggressive behavior (Archer 2006). This uptake in testosterone has been linked with varying antisocial behaviors (e.g., assaults, use of explicit drugs, etc.) but is likely mediated by individual environment.

While fast life history strategies are typically more likely to include maladaptive behaviors (at least in the long term), slow life history strategies can also lead to psychopathology. While fast maladaptive behaviors are associated with health risks through externalizing behavior (e.g., violence, substance use), internal behavior functioning may be maladaptive as a consequence of lower exposure to circulating testosterone. Low-level testosterone is associated with depressive symptoms. A study by Granger et al. (2003) found that in adolescent males, higher anxiety-depressive symptoms in males were associated with lower levels of testosterone and smaller fluctuations of testosterone levels throughout a day of hormone testing. This highlights the possibility that over-allocation of energy to somatic effort could manifest as overprotection towards survival through anxiety-like symptoms. Despite this link between low levels of testosterone and depressive-like behavior, Del Giudice (2014a) argues that depressive symptoms can be indicative of either fast or slow life history.

The variation in sex-specific hormones and the integration of the endocrine system are illustrations of the usefulness of a life history theory framework in understanding psychopathology. Other hormones (e.g., insulin-like growth factor 1 (IGF-1), cortisol, estrogen, etc.) also interact

with testosterone and have their own life history-related functions, and together their action (and reaction) plays an important proximate role in implementing an individual's life history strategy and so will likely also play a role in the development of psychopathologies. While distinct links between testosterone and male life history have been made, there are very likely to be important links between female hormone functioning and life history, topics for future investigation.

Conclusion

There are ostensibly a number of competing models of the etiology of psychopathology, each of which has some empirical support and each of which shares some features with life history theory, but, as illustrated above, a life history approach has the promise of bringing all such models together. A common, but nonfunctional, approach to psychopathology is the **stress-diathesis model**. The central hypothesis is that stressful environment/life experiences interact with genetic/behavioral/physiological predisposition/vulnerability leading ultimately to psychopathology (Albott et al. 2018; Ellis et al. 2011). There is a vast literature broadly supporting this model, but it necessarily characterizes psychopathology as maladaptive, which, as explained above, may underestimate the complexity of the relationship between early environment and behavioral outcomes. A second, broad approach to psychopathology can be described as **cognitive models**. In such schemes, emotional dysregulation produced by environmental challenges (like stress) results in maladaptive strategies of emotion management in some individuals (like excessive rumination), and that can result in psychopathology (like depression or anxiety) (Dvir et al. 2014; Peters et al. 2018; Sumner et al. 2018). Again, there is ample evidence to support the idea that individual differences in dealing with life's challenges explain some of the variance in psychopathological symptomology, but these models, in isolation, leave unanswered the question of the origin of the individual differences. **Allostatic load** models of psychopathology

propose that increased wear and tear due to the physiological costs of stress lead to a range of health issues including psychopathologies (Ellis and Del Giudice 2018; Del Giudice 2014a; Kotov et al. 2017; Ward and Clack 2019). The fundamental idea of such approaches is that dealing with stressors activates allostatic mechanisms, in order to achieve homeostasis, but that repeated, or excessive, use of these mechanisms “overloads” the system and results in a range of pathologies, some of which manifest psychologically.

One of the main strengths of life history theory, as an approach to psychopathology, is that it brings all of these other approaches together into a unifying, functional framework that provides a deeper understanding of the nature of the psychopathologies and offers the hope of an integrated approach to treatment and (perhaps especially) to prevention.

Cross-References

- Anxiety
- Depression (Paul Gilbert)
- Depression (Randolph Nesse)
- K-Factor (Figueredo)

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Life History Strategies

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Synonyms

Fast and slow strategies; Life history tradeoffs;
R and K strategies

Definition

Life history theory posits organisms face tradeoffs in how they allocate resources to reproduction, parenting, and growth. These patterns of resource allocation can be classified more broadly into life history strategies, which vary on a continuum from fast to slow. These distinctions can be applied to describe within species and between species differences. Slow strategies are marked by increased investment in growth, a delay in reproductive investment, and increased investment in parenting. In contrast, fast strategies are marked by early investment in reproduction at a cost of growth and a reduced investment in parenting in favor of further reproduction.

Introduction

Life History Strategies

Life history theory (LHT) is grounded in a simple premise – resources are limited and thus organisms face tradeoffs in how they “decide” to allocate those resources to growth, health maintenance, and various forms of behavior. These choices involve seeking a benefit on one trait that incurs a cost on another trait. In essence, LHT addresses how an individual’s life-stage, state of health, and local ecology determine that individual’s range of possible allocation strategies, all of which vary in their fitness maximizing potential (Del Giudice et al. 2015). Whereas somatic investment involves growing and maintaining the physical body and mind, reproductive and parental investment involve competition with same-sex individuals, courtship, procreation, the rearing of offspring, and so on. Tradeoffs along these dimensions can further be characterized by another set of key investment conflicts: (1) current versus future reproduction, (2) quantity versus quality of offspring, and (3) mating versus parenting effort. For example, an individual could spend energy on producing a relatively large number of children but limit the amount of parental care devoted to those children, or instead that individual could produce a small number of children and bestow extensive parental care to the growth and development of those children. Importantly, there is no one absolute correct response to these tradeoff conflicts. Whether a given decision is adaptive depends on what the decision maker’s environment affords. Investing in child quality may produce better long-term outcomes for that child, but in a particularly harsh and unforgiving environment, a given child might not survive over the long term. In such conditions, having many children may increase the chances that at least one child survives into adulthood to reproduce himself or herself. Therefore, the particular strategy most functional for an individual depends on the local environment (Del Giudice et al. 2015).

Researchers classify typical response patterns to such tradeoffs as life history strategies, which vary along a continuum from slow to fast.

Between and within species, slower strategies – marked by slower growth and later reproduction – correlate with longer lifespans, later maturation, fewer offspring, lower overall mating effort, and higher parenting effort. In contrast, faster strategies – marked by faster growth and earlier reproduction – correlate with shorter lifespans, early maturation, more offspring, higher mating effort, and lower parenting effort. Researchers have identified a number of correlates of life history strategies within humans, several of which are shown in Table 1. Individual differences in life history strategies have important consequences for our understanding of a variety of human cognitions and behaviors. Below, the origins of life history strategies are explained, and then the effects of slow/fast strategies on a number of important psychological domains are detailed.

Ecological Conditions

Investigations into the particular life history strategies that individuals follow indicate that allocation “decisions” are primarily a function of the

Life History Strategies, Table 1. Correlates of fast and slow life history strategies

Faster strategy		Slower strategy
	Physiology	
Faster	Rating of development	Slower
Earlier	Onset of puberty	Later
Faster	Biological aging	Slower
	Mating	
Earlier	Sexual debut	Later
More	Sexual partners	Less
Casual	Relationships	Pair-bond
	Parenting	
Earlier	Age of reproduction	Later
Higher	Number of offspring	Lower
Lower	Investment in offspring	Higher
	Reward orientation	
Short	Time horizon	Long
High	Impulsivity	Low
Take	Risk for reward	Avoid

Note. Table adapted from Griskevicius et al. (2013)



harshness and stability of the local ecology. Harshness refers to age-specific rates of morbidity-mortality in the environment (Ellis et al. 2009) and may be operationalized by, for example, parenting styles, childhood socioeconomic status (SES), or the extent of childhood illnesses (e.g., Belsky 2012; Simpson et al. 2012; Finch and Crimmins 2004). Unpredictability refers to the degree to which there is stochastic variability in the harshness of an environment across time. If an environment is unpredictable, it may not be optimal from a fitness standpoint to invest energy in long-term outcomes when one is unlikely to survive to benefit from that investment. Following this view, unpredictability has often been operationalized as parental change in residence, job, and cohabitation status (i.e., romantic partners moving in and out; Simpson et al. 2012; Szepeswol et al. 2015).

Whereas individuals who grow up in harsher, more unpredictable environments tend to develop faster strategies, children who grow up in more resource-abundant, supportive, and predictable environments tend to develop slower strategies. Moreover, this effect of the environment on the development of life history strategies appears specific to early childhood environments and experiences (Griskevicius et al. 2011; Belsky 2012; Simpson et al. 2012). For example, Simpson et al. (2012) found that an unpredictable family structure before age 6 influenced adult sexual activity and aggressive behavior more than the family structure after age 6. Additionally, research has identified unsupportive parenting and insecure attachments as mediating factors between environmental harshness/unpredictability and fast strategies in adulthood (e.g., Belsky et al. 2012; Szepeswol et al. 2015; Sung et al. 2016). Children may use cues to harshness and unpredictability in their early environments to forecast the extent and permanence of future resources and receive input from their parents that is either consistent or inconsistent with these cues.

Despite increasing amounts of research on the effects of early-childhood harshness and unpredictability environment on life history strategy development (e.g., Belsky et al. 2012), it is currently unclear under what conditions each factor contributes to specific dimensions of life history strategies. For instance, when harshness and

unpredictability are pitted against each other, harshness seems to be a stronger predictor of menarche (e.g., Sung et al. 2016); however, unpredictability appears to better predict number of sexual partners and criminal behavior (e.g., Szepeswol et al. 2015; Simpson et al. 2012). The differential effects of harshness and unpredictability may indicate that each factor is uniquely associated with specific outcomes.

Individual Differences in Environmental Sensitivity

When environments are highly variable over time or space, natural selection may favor developmental plasticity: biological mechanisms that can respond to cues in an individual's environment in order to "match" that person to the affordances of the environment to better maximize potential fitness. This plasticity can be expressed in at least two ways.

First, plasticity may be important for the initial development of one's life history strategy. Consider the following situations. In a relatively stable environment, or one in which cues to environmental conditions are unreliable and plasticity costly to maintain, selection may favor more fixed genotypes, "specialists" in a given allocation strategy. However, when the environment is variable and cues are both detectable and predictive of relevant social and physical features of the local environment, selection may favor individuals who are more "generalist" in their ability to calibrate their developmental trajectory to fit local conditions (Del Giudice et al. 2011). Given variable environments and the opportunity to change habitats, both specialist and generalist genotypes can exist together in a population. For instance, researchers examining this possibility studied the development of respiratory illnesses in 3–5-year-old children as a function of both their early rearing environments and individual differences in both cardiovascular and immune reactivity. Children with low reactivity – less plastic phenotypes – were no more likely to develop respiratory illnesses in high adversity settings compared to low adversity settings. However, highly reactive children – more plastic phenotypes – had the most

frequent instances of respiratory illness in high adversity settings, but they had the least frequent instances in low adversity settings (Boyce et al. 1995; Del Giudice et al. 2011). Individual differences in sensitivity to the environment can help explain why environmental variables (e.g., family environments, parent–child relationships) often have weak effects on developmental outcomes; effects tend to get stronger when individual differences in stress reactivity are taken into account. For example, Ellis et al. (2011) found that parent–child relationships uniquely predicted earlier puberty for children with heightened SNS/HPA activity, a measure of the stress response system (SRS) (Del Giudice et al. 2011).

Second, plasticity plays an important role in the proximate expression of life history strategies, even in adulthood. Sensitization models of life history suggest that childhood background may have relatively a minor influence on many of the behaviors and decisions adults make in relatively stable and benign environments, but when an environment appears threatening due to some cue, fast and slow patterns of behavior emerge (Griskevicius et al. 2011a, b; 2013). For example, in one set of studies, participants who grew up poor took more risks and discounted the future more than participants who grew up wealthy when presented with a news story about economic recessions, but there were no differences between these participants when the recession cue was absent (Griskevicius et al. 2013). In sum, the work conducted on life history strategies is broad: some studies find that early childhood levels of harshness and unpredictability predict adult outcomes such as risky sexual behavior and delinquency (e.g., Simpson et al. 2012; Belsky et al. 2012), and others demonstrate environmentally contingent responses to threat when cueing current mortality or resource scarcity (e.g., Griskevicius et al. 2011a, 2013).

Influences on Key Life History Domains

Life history strategies have been tied to many outcomes, including outcomes in clearly relevant domains such as physiological development, mating, and parenting. These outcomes also hold

strong implications for psychologically important concepts such as risk-taking, personality, and psychopathology. The following sections explore this research in more detail.

Somatic Development

As mentioned earlier, life history strategies entail trade-offs in investment within somatic, reproductive, and parenting domains. Fast strategists tend to invest less in somatic and parenting goals in favor of reproductive goals. This allocation of bodily resources encourages faster physiological development of sexual characteristics but impairs other forms of bodily growth and maintenance. Kuzawa and Bragg (2012) summarize a variety of studies that find a strong relationship between harsh early environments and impoverished physical characteristics, including (reduced) stature and (accelerated) aging. Such effects may be driven by particular aspects of the environment, including childhood nutrition, environmental stressors (e.g., poverty, authoritative school environments), and infection at childhood.

Much of the research done on aging emphasizes the progression of reproductive stages such as puberty (see Belsky 2012; Del Giudice et al. 2015 for reviews). Consistent with LHT, early childhood psychosocial stress seems to *accelerate* puberty. For instance, girls who were adopted at older ages and who therefore suffered more time in unfavorable orphanage conditions entered puberty more rapidly than earlier-adopted girls (Proos et al. 1991). Factors indexing environmental harshness and unpredictability also predict earlier age of menarche (i.e., first menses). For example, father absence and family conflict are associated with earlier puberty in females (Moffitt et al. 1992; see Belsky 2012 for review on studies on age of menarche). In men, some work has examined peak height velocity, the point at which males reach a maximum rate of growth. Men who were born small and who gained weight rapidly from birth to age 2 (a proxy for environmental unpredictability) experienced peak height velocity earlier (Karaolis-Danckert et al. 2009).

Based on LHT, a person's aging and dying progression should also be determined by how harsh their early environments are. This is because

an individual who is born into a harsh environment and therefore on a fast track may invest less in their personal survival or may just suffer more risk of dying sooner. There is indeed evidence that early life harshness is associated with increased old-age mortality. For instance, Finch and Crimmins (2004) found that in the USA and Sweden, childhood illnesses and nutrition deficits significantly predicted shortened lifespans. In the same vein, in an analysis of hunter-gatherers and forager-horticulturalists, higher infant mortality, infection rates, and violence were tied to a decrease in lifespan (Gurven and Kaplan 2007). Chisholm et al. (2005) went as far as to ask women who grew up in unpredictable environments to estimate their life expectancy; they indeed found that early life unpredictability reduced subjective life expectancy. Together, these findings provide evidence that early harsh and unpredictable environments accelerate maturation in favor of early reproduction, at the cost of more rapid aging and mortality.

Mating

Life history theory predicts that fast strategists should seek to reproduce earlier and at greater rates, implying a greater number of sexual partners and less stable relationships with those partners. Slow strategists, who invest more in embodied capital, should, in contrast, begin sex later in life, have fewer sexual partners, and have more lasting, pair-bonded relationships.

These ideas have been tested in several longitudinal datasets. In an analysis of the National Longitudinal Study of Adolescent Health (Add Health), a nationally representative longitudinal study spanning from seventh grade to young adulthood (ages 18–26), researchers found that environmental unpredictability (i.e., instances of lack of care/needs not being met, being seized by social services) in adolescence was associated with lower sexual restrictedness (e.g., more risky sexual behaviors and less frequent use of contraception; Brumbach et al. 2009). Concordantly, in an analysis of the Minnesota Longitudinal Study of Risk and Adaptation (MLSRA), a longitudinal study tracking approximately 165 individuals and their biological mothers from before birth to

middle adulthood, childhood exposure to harsh (i.e., low childhood SES) and unpredictable environments (e.g., multiple changes in employment, residence, cohabitation) interacted to forecast earlier sexual debut: those exposed to harsh yet *predictable* environments from age 0 to 5 had first sex *later* than average, and those exposed to harsh yet *unpredictable* environments had first sex *earlier* than average (Simpson et al. 2012). High levels of childhood unpredictability at age 0 to 5 (not age 6 to 16) also predicted more sexual partners by age 23. A separate analysis using the same variables measured instead at age 6 to 16 found no such effects.

In a separate study, Belsky et al. (2012) examined data from the NICHD Study of Early Child Care and Youth Development, a study of 1,300 children and their families from infancy to age 15. Here, harshness was operationalized as income-to-needs ratio from ages 0 to 5 (lower scores indicating fewer needs were met). Unpredictability was measured as in Simpson and colleagues' MLSRA project (Simpson et al. 2012). Mirroring Simpson and colleagues' findings, high levels of childhood unpredictability and high levels of harshness (i.e., a low income-to-needs ratio) predicted a larger number of sexual partners. This was serially mediated by maternal depressive symptoms and maternal sensitivity (i.e., responsiveness and care) at childhood. That is, harsh and unpredictable ecologies were associated with greater depressive symptoms; these, in turn, were associated with less sensitivity, and lowered maternal sensitivity led to more sexual partners as the child grew up.

Beyond mating behavior itself, the quality of romantic relationships may be influenced by particular life history strategies. Some work suggests that fast strategists tend to engage in less committed romantic relationships. This could reflect their own insecure attachment orientations which may lead to their having more, and more genetically varied, offspring (e.g., Del Giudice et al. 2015; Barber 1998). For instance, unstable parental relationships in childhood (indexed by larger numbers of stepsiblings) predicted lower college GPA as well as greater frequencies of low-commitment relationships, particularly for daughters (Barber

1998). For the daughters in this study, the effect of unstable parental bonds on lower GPAs was mediated by their orientation towards low-commitment relationships, illustrating the trade-off between investing in somatic capital (operationalized by GPA) vs. investing in current reproduction. In sum, life history strategies affect a range of mating-related outcomes, from specific partner preferences to relationship quality and longevity to sexual behavior.

Parenting

According to LHT, the adaptiveness of parenting investment is dependent on aspects of the local environment. Parenting refers to outcomes related to child rearing, but it also extends to earlier processes such as gamete production and the timing of births. The theory predicts that, relative to slow strategists, fast strategists should devote fewer embodied resources to creation of gametes, have children sooner, and spend less time and effort on rearing behavior. Consistent with this idea, multiple studies have demonstrated the link between indicators of high mortality and age at first birth (e.g., Chisholm et al. 2005). For instance, Nettle et al. (2011) found that experiencing many residential moves during childhood, low investment from parents, and maternal absence each independently reduced age of first birth by half a year. Another set of experimental studies showed that ecological threats to mortality can influence the motivation to reproduce. In these studies, Griskevicius et al. (2011a) primed participants with a mortality cue (reports about violent crime) and then assessed attitudes towards early reproduction. Participants who grew up in resource-scarce environments (i.e., fast strategists) responded to the mortality cue by becoming more open to having children earlier in life. These fast strategists were also more likely to choose starting a family over furthering their own education and careers. The opposite patterns emerged for people who grew up relatively financially well off (i.e., slow strategists).

Less work has been done examining the direct consequences of life history strategies on investment in child rearing (e.g., parenting styles). Overall, LHT predicts that early environmental

harshness and unpredictability should be associated with greater emotional distance and less engaged parenting. However, Parental Investment Theory (PIT; Trivers 1972) suggests sex-differences will exist in parenting outcomes. This latter theory predicts that the sex that incurs higher reproductive costs tends to focus relatively more on their mate's genetic quality and ability to provide consistent resources, elements useful for creating viable offspring. In contrast, the sex that invests less in parenting tends to invest more in mating effort. In humans, women carry most of the burden in caring for children and face higher bodily costs from reproduction (e.g., pregnancy). Thus, PIT predicts men are more likely than women to disengage as parents, thereby increasing their fitness by investing in other domains (e.g., other mating opportunities). In contrast, women may increase their total fertility primarily by having children at a younger age (Belsky 2012).

These hypotheses were tested in another analysis of the MSLRA, featuring 112 individuals (and their low-income mothers) tracked from birth to parenthood (Szepeswol et al. 2015). All individuals completed an interview at age 32 that assessed their general orientation towards parenting. Unpredictability from age 0 to 4 was operationalized by their parents' changes in employment, resident, and cohabitation status during that period. Men (but not women) who experienced early-life unpredictability had a less positive orientation to parenting at age 32 (i.e., lower emotional connectedness and parental involvement, and more hostile parenting). This was serially mediated by maternal supportive presence and insecure attachment, such that unpredictable childhood households had lower maternal supportiveness, leading to the development of insecure attachments, which then was negatively associated with a positive parenting orientation in adulthood and less supportive parenting behavior.

These above predictions and data were corroborated by online survey data from 435 parents, whose early childhood unpredictability was associated with more attachment anxiety and avoidance, which were negatively associated with men's parenting orientations (Szepeswol et al.,

2015). These studies demonstrate that early childhood unpredictability predicts expression of fast strategies through child rearing behavior.

Influences on Other Domains

Risk-Taking

Beyond the three broad domains of investment relevant to LHT (somatic, mating, and parenting domains), life history strategies have important implications for decision-making styles – namely, risk-taking and risk-tolerance. Fast strategies stem from a reaction to ecological cues signaling limited, unstable resources and shorter time horizons. This leads to a preference for immediate benefits and rewards relative to longer-term goals. As fast strategists are looking to jumpstart their reproduction and accumulate a greater number of children, their goal is to amass resources for the present. In contrast, slow strategists exhibit the opposite pattern, with an emphasis on personal survival as well as the survival of a few high-quality children, leading to risk-averse behavior and delay of gratification in favor of future payoffs.

These predicted patterns enjoy support from several studies. A large scale global study found that countries high in ecological harshness (e.g., high infant mortality, high homicide rate, low GDP, lower life expectancy, etc.) are populated by more people with risk-taking personalities who engage in more risk-taking behaviors (Mata et al. 2016). Relatedly, an analysis of the Add Health study mentioned earlier revealed that environmental unpredictability in adolescence (e.g., parents not tending to their children's basic needs and changing living situations) significantly predicted delinquency and impulsivity in young adults (Brumbach et al. 2009). Finally, an analysis of the MLSRA dataset revealed that people who experienced unpredictability (measured by changes in employment status, residence, cohabitation status) between ages 0 and 5 reported more delinquent and aggressive behaviors at age 23, such as lying/cheating, substance use, arguing, and being mean to others (Simpson et al. 2012).

Researchers have also explored risk-taking in experiments highlighting the contingent

expression of life history strategies. Griskevicius and colleagues found that priming people with either mortality or economic instability led people who grew up in poorer environments (i.e., fast strategists) to increase risk-taking in financial decisions marked by probabilistic and temporal differences. For instance, fast strategists preferred to take a chance on a gamble for \$20 rather than receiving a certain \$10, and they preferred smaller immediate rewards over larger later rewards (Griskevicius et al. 2011b, 2013). In contrast, people who grew up in wealthier environments (i.e., slow strategists) took fewer risks and preferred larger rewards later rather than smaller immediate rewards.

Life history strategies also play a role in risk management through bet-hedging. Bet-hedging can enhance long-term reproductive success at the cost of short-term fitness by decreasing variation in outcomes over time (Ellis et al. 2009). From a life history perspective, bet-hedging can help to manage risks in resource/financial decisions: LHT predicts fast strategists will rely more on diversified bet-hedging (i.e., diversifying investments into multiple choice options to reduce the risk of any single choice) and slow strategists will rely more on conservative bet-hedging (i.e., investing more in a smaller number of low-risk options). In related experiments, people who grew up in lower-SES households (i.e., fast strategists) tended to prefer diversification strategies when facing current mortality threat, including preferences for product variety and stock investments (White et al. 2013). In contrast, people who grew up in higher-SES environments and who were primed with mortality threat engaged in more conservative decision-making.

Personality

Variation in life history strategies may correspond with different patterns of stable personality traits. Fast strategies are typically associated with increased impulsivity, aggression, and sensation seeking but decreased sociality (Del Giudice et al. 2015). Borrowing from the Five Factor Model of personality, conscientiousness and agreeableness are often tied to reduced mortality, reduced mating effort, increased parental effort, and increased prosociality/cooperation, all

outcomes associated with slow strategies. Agreeableness, conscientiousness, and emotional stability all load onto the same factor called *alpha* or *stability*, a slow life history trait which negatively predicts impulsivity (DeYoung 2011). In contrast, some aspects of extraversion and openness to experience (e.g., dominance, sensation seeking, imagination) as well as neuroticism can be tied to outcomes associated with fast strategies: increased relationship instability, mortality, sexual partners, and antisocial behaviors (see Del Giudice et al. 2015 for a review).

Other, more pernicious types of personality traits are linked to fast strategies as well. For instance, dark triad traits (narcissism, psychopathy, and Machiavellianism) are associated with impulsivity and pursuit of immediate rewards (e.g., Jonason et al. 2012), characteristics of a fast strategy. Life history strategies themselves have even been construed as highly heritable personality traits (Figueredo et al. 2004). In this framework, the regulatory genes that produce strategic patterns of behavior would likely be conditionally expressed through interaction with environmental inputs, akin to the strategic plasticity discussed in earlier sections.

Psychopathology

Most theoretical work in developmental psychology suggests that negative experiences in early-childhood increase the risk of psychological distress and psychopathology in adolescence and adulthood. Recent evolutionary-developmental theorizing has incorporated LHT in order to, “address the organization of individual differences, the nature of environmental risk, the role of early stress, the nature of gene-environment interactions, and many other critical issues” (Del Giudice and Ellis 2014, p. 3) in our understanding of psychopathology. Del Giudice and Ellis (2014) outline four potential causal pathways from life history strategies to psychopathology. First, life history traits may be diagnosed as undesirable, pathological symptoms. For example, traits associated with psychopathy – low guilt, low empathy, high impulsivity – may increase fitness by increasing the ability to exploit others. Second, typically functional life history traits may express

themselves at maladaptive levels. It is possible that parents who are both high on some trait, but still within an adaptive and socially desirable range, may have a child who expresses the same trait at an extreme, maladaptive level. Third, strategies that are adaptive across individuals may prove maladaptive for a given individual. For example, aggressive behavior yields fitness benefits for males on average (e.g., increased access to mates), even though individual males can suffer devastating costs (e.g., dying in fights). Fourth, life history traits may increase risk for dysfunction. For example, schizotypal personality may increase verbal creativity and interest in short-term mating, thereby increasing fitness; however, when schizotypal personality is coupled with drug use, nutritional deficiencies, and infections, it can increase the risk of schizophrenia, thereby decreasing fitness (Del Giudice and Ellis 2014).

Broadly, factors that determine individual differences in life history strategies are expected to increase risk for some mental disorders and not others. Though psychopathologies associated with faster or slower strategies will overlap to some extent, faster strategies tend to be associated with subclasses of disorders characterized by impulsivity, disinhibition, and bizarre ideation; slower strategies, in contrast, tend to be associated with subclasses of disorders characterized by inhibition, over-control, and cognitive rigidity. For example, both fast and slow strategies are broadly associated with eating disorders and OCD, but faster strategies are associated with bulimia nervosa and OCD featuring autogenous (i.e., unevoked, internal) obsessions, and slower strategies are associated with anorexia nervosa and OCD featuring reactive (i.e., evoked from external stimuli) obsessions (Del Giudice and Ellis 2014). In general, faster life history strategies are associated with externalizing disorders, schizophrenia spectrum disorders, obsessive-compulsive disorder (OCD), bulimia nervosa, and depressive disorders; slower life history strategies are associated with obsessive-compulsive personality disorder (OCPD), OCD, autism spectrum disorders, the perfectionist and over-controlled subtypes of eating disorders, and depressive disorders (Del Giudice and Ellis 2014).

Conclusion

Life history theory is a powerful explanatory tool for organizing patterns of cognition and behavior. The strategies that emerge from differential investment in somatic, reproductive, and parenting outcomes are individually specific and often emerge through interaction between child and adult environmental conditions. Such strategies predict a wide range of outcomes, and many further topics in human psychology await placement within this important theoretical framework.

Cross-References

- [Adaptive Plasticity](#)
- [Bruce J. Ellis](#)
- [Environmental Harshness](#)
- [Environmental Harshness/Mortality](#)
- [Environmental Risk](#)
- [Environmental Unpredictability](#)
- [Environmental Unpredictability and Bet-Hedging](#)
- [Fast Versus Slow Strategies](#)
- [Fundamental Tradeoffs](#)
- [Jay Belsky](#)
- [Life History Model of Psychopathology](#)
- [Life History Theory](#)
- [Quantity Versus Quality of Offspring](#)
- [Reproductive Strategies](#)
- [Reproductive Strategy](#)
- [Risky Behavior](#)
- [Sexual and Reproductive Development](#)

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Life History Theory

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Synonyms

Biological ecology; Life history; Lifespan; Population ecology; Reproductive development

Definition

A theory based on biological evolution that explains variations in organisms' developmental and reproductive strategies in the context of environment pressures and available resources.

Introduction

The core premises of Darwinian evolution are survival and reproduction (Darwin 1859); and biological organisms need energy to achieve these goals. All life requires capturing and allocating energy; however, this energy is limited and comes at a cost – organisms cannot expend unlimited resources, maximizing all life domains simultaneously. Organisms must live within their restricted energy budgets, mandating tradeoffs to

ensure they do not allocate more resources to a particular domain than are available. Selection favors strategies for allocating resources on the basis that they result in the greatest evolutionary fitness for the organism, respective of their environmental constraints. Life history theory explains how organisms allocate energy to survival and reproduction to maximize their fitness; including passing on their genetic material. As a whole, life history theory serves as a framework to organize and understand species differences, sex differences, and individual differences, across a number of domains, including physical growth, sexual maturation, and sexual, social, and parental behaviors.

Human Ecology

Humans are biological organisms and therefore face the same adaptive problems of maximizing fitness through appropriate energy allocation as do all other organisms. It makes sense then, that theories of biological ecology (i.e., life history theory) can be applied to the human species. Approximately two decades ago, evolutionary psychologists started using life history theory to help explain human behavior in the context of reproductive strategies (e.g., MacDonald 1997), early childhood attachment (e.g., Chisholm 1996), and developmental trajectories (e.g., Ellis et al. 1999).

Researchers such as Jay Belsky and Bruce Ellis – who have their own separate entries in this section – have led the way integrating and reforming developmental psychology and development psychopathology with the inclusion of evolutionary psychology and life history theory into developmental models (e.g., Belsky et al. 2012; Ellis et al. 2011). Jay Belsky has been particularly influential in the areas of childhood development, including attachment processes and parent-child relationships (e.g., Belsky 1997; Belsky et al. 1991, 2012; Del Giudice and Belsky 2011). Bruce Ellis's most influential works include investigating the influence of father absence on the timing of pubertal development (e.g., Ellis and Essex 2007; Ellis and

Garber 2000; Ellis et al. 1999). Most contemporary postgraduate developmental psychology and developmental psychopathology books include and/or reference works from these two influential researchers and authors. As such, there are now hundreds of articles and numerous book chapters in the psychological literature using life history theory as a framework to help conceptualize and explain multiple human behaviors as fitness maximizing strategies. The focus of this literature spans from theoretical models of mental health and psychopathology through to explanations about variations in cognitive flexibility (i.e., ease at which we shift tasks).

Life history theory is a middle-level theory that requires the consideration of a number of underlying and associated concepts. These underlying concepts include organisms facing fundamental tradeoffs in the face of energy allocation, the costs and benefits of allocating energy to different domains, how different patterns of energy allocation result in within and across species variations, the influence of environmental factors, varying developmental trajectories, the role of genes (including epigenetics), and the resulting difficulties where there is a mismatch between behaviors and traits selected for an early environment that are no longer adaptive in a current environment.

Fundamental Tradeoffs

Optimal allocation of resources (i.e., energy) toward growth, development, reproduction, and survival varies across an organism's life course. At the most basic level, individuals must make fundamental tradeoffs between reproductive efforts and somatic efforts to enhance their inclusive fitness (Del Giudice et al. 2015). Individuals may prioritize somatic efforts, investing in tasks and traits that affect the age schedule of mortality. Somatic efforts include investing in growth, body maintenance, developmental activity, and survival. Alternatively, individuals may prioritize reproductive efforts over somatic efforts, investing in tasks and traits that affect the age schedule of fertility. These reproductive efforts can be divided into mating effort, parenting effort,

or nepotistic effort (Kaplan and Gangestad 2005); each with its own cost and benefit in terms of maximizing fitness.

The influence of life history traits on an individual's inclusive fitness are expressed through changes in fertility and/or mortality, with strategies that may be targeted at enhancing the longevity or fertility of offspring as well the parents' own fecundity and lifespan. The three main tradeoffs defined within life history theory are the present-future reproduction tradeoff, the quality versus quantity of offspring tradeoff, and the mating effort versus parenting effort tradeoff (Del Giudice et al. 2015). As selected traits contribute to an individual's evolutionary fitness, they involve substantial energy investment, involving both costs and benefits, engendering tradeoffs between different fitness components. That is, most of the selected traits have contrasting effects on fertility and mortality, or contrasting effects on the fitness components of offspring or oneself. For example, at the most basic level, the tradeoff between growth and reproduction means that if an individual is producing offspring, they are reducing their somatic growth and maintenance. On the other hand, allocating energy to somatic growth reduces fertility at younger ages, but subsequently increases fertility in later life; however, at the potential risk of not surviving long enough to reach sexual maturity and reproduce – especially if the organism's current environment has a high mortality risk from predation or lack of resources. If an individual chooses to engage in tasks to increase fecundity, such as increasing mating frequency, they may be simultaneously compromising survival due to a cost to their immune functioning. In the tradeoff between quality versus quantity of offspring, if an individual is allocating energy resources (e.g., time spent nurturing and feeding) to existing offspring, this will increase the quality of offspring, but will reduce an individual's own survival and/or fertility.

Cost-Benefit Analysis

Despite the concept of cost-benefit analysis being largely based in economic literature, this approach has revolutionized evolutionary theory, providing

a systematic way of understanding the effects of selection on inclusive fitness. This cost-benefit analysis and general economic approach to selection greatly expanded the theory of evolution by natural selection (inclusive fitness theory) and shaped evolutionary theory as we know it today. The economic approach resulted in the development of many notable middle-level evolutionary theories, including the theory of parental investment and sexual selection, the theory of parent-offspring conflict, and importantly life history theory (Buss 1995).

An example of the cost-benefit analysis includes the theory of parent-offspring conflict, which explores the disagreement between parent and offspring over the amount of parental investment (Trivers 1974). This theory highlights the cost-benefit analysis demonstrating that both domains (i.e., parental investment and own fertility) cannot be maximized simultaneously – greater energy in one domain results in less energetic resource for the other. Consider a mother feeding her newborn calf; the benefits to the offspring are large, increasing its chance of survival; however, the cost to the mother (measured by the reduction in her ability to produce additional offspring) is relatively small. As the offspring grows and develops, the benefits of being nursed decrease, but the cost to the mother continues to increase. At some point the cost of nursing will outweigh the benefits to the offspring, and if the mother continues to nurse, this will result in substantial costs to the mother's reproductive success. Much like the parent-offspring tradeoff, life history theory is largely concerned with strategic energy allocation, but specifically focuses on the timing of certain life events. Life history theory has increasingly subsumed the cost-benefit analysis into many domains within the theory itself (Kaplan and Gangestad 2005).

Environmental Harshness and Unpredictability

Environmental harshness describes the general physical strain and hardship experienced by an organism. Harsh environmental conditions reflect increased risk of morbidity and mortality, which

can be generated from a number of factors including resource scarcity, extreme climates, intrasexual competition, and threat of predation. Environmental unpredictability describes the variability in the outcomes of adaptive behaviors (Brumbach et al. 2009). That is, when environmental conditions vary in an unpredictable manner, the success of alternate adaptive strategies are arbitrary. Environmental unpredictability is a function of stochastic variation in environmental risk or harshness. As such, environmental harshness can be inconsistent over time and space and is therefore largely unavoidable. This environment unpredictability, especially at an early age, can lead an individual to experience stress reactions than can lead to changes in stress physiology and brain morphology (Ellis et al. 2013), thus ultimately affecting their developmental trajectory. In humans, these physiological changes include earlier pubertal development including the onset of menarche and secondary sex characteristics (i.e., breasts, pubic hair; see Ellis and Essex 2007).

Discounting of Future Returns

Present versus future orientation is a central feature of life history theory. Neither the willingness to delay gratification nor the tendency to discount future rewards in favor of short-term gains is considered inherently better, but the adaptiveness of these behaviors is dependent on the environment. Understanding the future versus present orientation directs attention back to the cost-benefit analysis. For example, in understanding impulsivity and risk-taking behavior in a present-orientated teenager, one must ask how this is benefiting the individual and at what cost. High-risk strategies that may include the expression of aggression, sensation seeking, and impulsivity may produce a number of short-term benefits, such as acquiring multiple sexual partners, acceptance into a certain clique, or early reproduction. However, these benefits are accompanied by long-term losses, such as compromised immune function, loss of job opportunities, or premature morbidity-mortality. In contrast,

future-orientated strategists may tradeoff short-term gains – that is, delaying immediate benefits of employment, marriage, or reproduction by pursuing years of tertiary education – in favor of long-term gains, such as achieving high social and economic status (Ellis et al. 2012). Often long-term planning and a future orientation are considered more socially desirable, whereas short-term planning and a present orientation are considered somewhat undesirable; however, the adaptiveness of these behaviors largely depends on an individual's environment.

Life History Strategies

The costs and benefits of prioritizing one factor over another in each of the fundamental tradeoffs (i.e., present-future reproduction, quality vs. quantity of offspring, mating effort vs. parenting effort) are in part a result of varying environmental pressures and, in turn, produce variation in behaviors in order to secure and allocate resources to the prioritized factor. For example, prioritizing somatic effort over reproductive effort in an unpredictable, harsh environment may result in death before reproduction has been achieved – the opposite of maximizing fitness and not an optimal energy allocation strategy. These differences in resource allocation in reaction to variations in environmental pressures in order to obtain an optimal fitness maximizing strategy are referred to as life history strategies.

Life history strategies can be thought of as functionally complex phenotypes that have resulted from the integration of physiological, morphological, and behavioral traits as an adaptive solution to environmental pressures and fundamental tradeoffs (Del Giudice et al. 2015). Species-level adaptive specializations lead to a number of different life history characteristics that fall along a fast-slow continuum. Furthermore, in response to these ecological variations, most organisms have the ability to slow down or speed up their life history strategy respective of their experienced environmental pressures. That is, life history strategies are not fixed and are subject to developmental adaptive plasticity.

The adaptive plasticity of life history strategies allows developing organisms, human and non-human, to assess their environment through contextual cues and adjust their allocation strategies accordingly (Del Giudice 2014). Adaptive plasticity follows the evolutionary rules of fitness maximizing, enabling organisms to adapt with the intention of increasing inclusive fitness in varying ecological conditions. These varying ecological conditions, which are often referred to within the evolutionary literature, include resource availability, extrinsic morbidity-mortality, and the predictability of environments (Kaplan and Gangestad 2005).

Resource availability within an environment sets the baseline for many developmental activities, including the development of life history strategies. Individuals who experience energetic stress are likely to shift to a slower life history strategy, which results in a more energy-preserving phenotype, characterized by slower growth and development, delayed sexual maturation, and low fecundity. On the other hand, the development of a fast life strategy relies on adequate bioenergetics resources to support rapid growth and development (Del Giudice 2014).

Furthermore, extrinsic morbidity-mortality – the external sources of death and disability – can largely determine an individual's strategy selection. Those who are exposed to higher levels of extrinsic morbidity-mortality, as indicated by environmental cues (e.g., exposure to violence, dangerous ecological conditions), are likely to adopt a faster life history strategy. Faster life history strategies in the context of high extrinsic morbidity-mortality function to reduce the risk of death or disability prior to reproducing by anticipating early maturation and the onset of sexual activity (Del Giudice 2014).

Life history theory and relevant research has shown that organisms are able to electively adjust their life history strategies in response to their environmental context throughout their development. That is, environmental harshness and unpredictability, including varying contextual cues of morbidity and mortality, are important in calibrating the development of life history strategies. For example, individuals who are exposed to environmental cues indicating higher risk of

juvenile mortality, such as increased violence or predation, are likely to select a fast life history strategy. That is, their contextual cues indicate that it would be beneficial to mature rapidly and reproduce in earlier stages of life, reducing the risk of mortality prior to producing offspring (Brumbach et al. 2009). In the case of unpredictable environments, the future is uncertain and therefore resources and energy that are invested in the future will likely be wasted. Rather, the individual should respond to these unpredictable conditions (e.g., erratic residential conditions, fluctuating economic circumstance, and changes in family structure) by selecting a faster life history strategy. Unpredictable environments may infer strategies that maximize reproduction in the face of difficult circumstance, at the risk of reduced life expectancy and decreased social and emotional functioning (Brumbach et al. 2009).

There is substantial empirical evidence exploring the real world application of these processes. For example, studies have demonstrated that greater environmental harshness and early exposure to ecological and social stress have been found to predict early onset of menarche in young girls (Ellis 2004). Furthermore, areas in which residents have a shorter life expectancies and higher risk of mortality (e.g., higher homicide rates) report younger median ages of women giving birth (Wilson and Daly 1997). It could be argued that this tendency to reproduce earlier is not due to a lack of education or family planning, but rather a strategic plan – to reduce the risk of dying prior to producing offspring. Additionally, individuals who are raised in unpredictable environments often have a bias toward strategies that involve producing a large number of offspring – a trait that is indicative of fast life history strategy (Mittal and Griskevicius 2014). By producing a larger number of offspring, there is an increased likelihood that at least some progeny will possess phenotypes that are compatible with the future environment, thus increasing chances of survival. Furthermore, experienced environmental harshness during adolescents, such as exposure to alcohol and substance use, daredevilry, violence, and risky sexual behavior, is predictive of social deviance and sexual promiscuity in adulthood

(Brumbach et al. 2009). Generally, individuals who are exposed to greater levels of environment harshness naturally select a fast life history strategy, allowing them to function logically and suitably, in the context of unsafe and unpredictable environments.

The predictability of an organism's environment may be deemed the most important factor in regulating the development of life history strategies. That is, the unpredictable variation in an organism's extrinsic morbidity-mortality over time and across variable ecological contexts largely impacts an organism's strategy selection. Those who are subject to unpredictable environments may be led to invest in behavioral adaptability and flexibility, enabling them to adapt to ecological variation (Del Giudice 2014). On the timeline of human development, variable and unpredictable contexts tend to infer faster life history strategies, thus imposing similar direction than that of environmental harshness. In contrast, safe and predictable environments are likely to result in the development of a slow life history strategy (Kaplan et al. 2000).

Individuals with faster life history strategies prioritize short-term gains, with little regard for long-term consequences. That is, as faster strategies are an adaptive response to harsh and unpredictable environments with future uncertainty, delayed rewards may never be realized. Conversely, in more stable and predictable environments, future orientation and slower strategies are considered adaptive – as the future is relatively predictable and the risk of mortality is lower, slow strategists are more likely to be long-term planners, who are willing to delay gratification and invest in future outcomes (Mittal and Griskevicius 2014).

Alongside environmental contributions to the development of life history strategies, genetic factors also have a role to play. Life history theory provides a contextualist view of the interaction of genetics and the environment, suggesting that these factors should coexist. Existing literature on human life history traits suggest moderate heritability with epigenetics – the alterations or even the repression of gene expression – playing a pivotal role in the transmission of environmental

effects on life history strategies across multiple generations (see Figueredo et al. 2004).

In short, fast life history strategies develop as a response to environments that are unstable and unpredictable and have greater risks of morbidity-mortality. Individuals with fast life history strategies prioritize reproductive efforts over somatic efforts, and mating efforts over parental investment – producing a large number of offspring rather than investing in the survival of existing offspring. Conversely, slow life history strategies often develop as a response to environments that are stable, predictable, and have fewer risks. These individuals produce fewer offspring, but largely invest in the quality and survival of existing progeny. Neither fast nor slow life strategies are fundamentally better – the benefits of each strategy are contingent on the individual's environment.

Prototypical r-/K-selected species. As a result of varying environmental pressures, some species are classified as r-selected or fast strategists and some as K-selected or slow strategists. So called r-selected species have a shorter lifespan, experience greater risk of mortality, and inhabit areas with varying population size. These offspring often have a small body size, experience rapid growth, and reach early sexual maturation. This shorter lifespan, higher risk of mortality, and tendency to reproduce earlier than most result in optimal discounts to future rewards, in favor of short-term gains. Conversely, K-selected or slow strategy species have a longer lifespan, experience fewer risks of mortality, and inhabit areas that have a constant or equilibrium population size. Offspring from K-selected species often have a larger body size, experience slower growth, and have a later sexual maturation. As a result of the longer lifespan and fewer environmental risks, K-selected species are more likely to be future-orientated, reproducing later in life. Therefore, organisms that are relying on future reproduction need to invest in somatic efforts to maximize their chances of remaining healthy and survival.

There are a number of exemplary species at each end of the fast-slow or r-K continuum. Rabbits are a good example of a typical r-selected animal species. On average they reach sexual

maturity within the first 6–8 months of their life, they have an extremely short gestation period, and they produce a large number of offspring within each litter. These r-selected traits are consistent across a number of small organisms (e.g., mouse, lemur, and frogs) demonstrating relatively short generation times and reaching sexual maturity quickly, as an adaptive response to their high predation rates. On the contrary, typical K-selected species, such as gorillas, elephants, sharks, and humans, have longer gestation times and a larger body size, reproduce later in life, and bear fewer offspring in comparison to faster strategy species (Campbell and Reece 2005). An extreme example of a K-selected species is the Greenland shark, an iconic species of the Arctic Sea, with the longest known lifespan of all vertebrates. Radiocarbon dating of a number of female Greenland sharks revealed that this species has a lifespan of at least 272 years, with the largest shark measured being approximately 392 ± 120 years old. These sharks grow and develop extremely slowly to a total of >500 cm and do not reach sexual maturity until approximately 156 years old (Nielsen et al. 2016).

Life history strategies vary across species, with the distinction between r- and K-selected, as well as within species that results in unique individual differences. Humans are a prime example, in that they differ from other species, but also show large amounts of within-species variation. Typically, compared to other species, humans have distinct life history traits including late onset of reproduction, an extended period of childhood vulnerability, and a longer lifespan. Despite humans being considered typical K-selected species, they also appear to vary along the fast-slow continuum as a response to different environmental contexts. For example, within humans, faster life strategies have been associated with having a more unrestricted socio-sexual orientation and engaging in more interpersonal and intimate partner violence (Figueredo et al. [under review](#)), increases in the ability to cognitively shift between tasks (Mittal et al. 2015), and increases in the tendency to consume more energy than required after a period of fasting (Hill et al. 2016).

Clinical Applications

Psychopathology. As life history strategies are the product of a number of genetic and environmental pressures, as well as constant tradeoffs between somatic and reproductive efforts, they may help to explain the development of so-called psychopathology in humans. That is, variations in life history strategies could be useful in determining individual differences in risk profiles for a range of mental disorders, with a life history theory perspective conceptualizing psychopathology as a reflection of fast and slow life history strategies. The general idea is that the way in which an individual configures their life history strategy may increase their risk of developing a specific disorder or cluster of disorders. For example, Del Giudice and colleagues (Del Giudice 2014; Del Giudice and Ellis 2014) propose four causal pathways for how life history strategies may contribute to the onset of mental illness: (1) adaptive life history traits could be considered as symptoms of psychopathology; (2) life history traits could be expressed at a maladaptive level; (3) certain adaptive strategies may result in individually maladaptive outcomes; and (4) life history traits may increase susceptibility to dysfunction (Del Giudice 2014, p. 269). Although these pathways are considered distinct, they are not exclusive and it is likely that they may co-occur in the etiology of a number of disorders.

A life history approach does not automatically assume that disorders are dysfunctional, but considers alternate explanations, including the possibility that some disorders may reflect adaptive traits and processes that enhance evolutionary fitness. A common example is that of aggression. While aggression is generally considered a socially undesirable behavior, it does provide some fitness benefits such as increased access to resources and mates through dominance over others. Aggression toward outgroup members can also serve to protect and enhance the survival of familial members and offspring. So, although these traits may be considered biologically adaptive, they will often involve substantial cost to an individual in the context of long-term health, wellbeing, and social acceptance in broader

society. Through the lens of life history theory, we may be able to determine the role and function of aggression in people in the context of their personal environmental pressures including their early and current environments. Therefore, a life history approach to psychopathology potentially provides insight into common underlying behaviors, traits, disorder comorbidity, and functional subtypes of specific disorders.

It is largely recognized that fast life history strategies predispose individuals to a number of disorders, whether this is as a result of maladaptive outcomes of life history traits or as an adaptive yet undesirable social behavior (Giosan and Wyka 2009; Hurst and Kavanagh 2016). Fast-spectrum disorders are those that show association with traits such as sensation seeking, risk-taking, disinhibition, and impulsivity, low levels of conscientiousness and agreeableness, and promiscuous sexuality, with early sexual maturation. There is reason to expect that slow strategies may also set the stage for the development of psychopathology with disorders characterized by risk aversion, behavioral inhibition, extremes of conscientiousness and agreeableness, restrained sexuality, and delayed sexual maturation (indicators of a slower life strategy) possibly leading to their own set of difficulties (e.g., obsessive-compulsive disorder, social anxiety disorder).

The classification of mental disorders conceptualized along the fast-slow continuum suggests a number of specific factors that may contribute to the onset of a disorder, irrelevant of their causal pathway, but despite clear associations, these traits may or may not play a causal role in the etiology of specific mental disorders. For example, positive schizotypal traits and autistic-like traits sit at opposite ends of the fast-slow continuum and may be diametrically associated with differences in life history strategies (see Del Giudice et al. 2014). From the life history perspective, schizotypy is considered an adaptive fast spectrum phenotype for its reproductive advantages of high mating efforts and reduced parental investment, whereas autistic-like traits are considered an adaptive slow spectrum phenotype characterized by reduced mating efforts and high parental investment. That is, traits related to

these disorder may be beneficial (greater mating or parental success) or they could be harmful (the expression of the disorder); dependent on genetic quality and the developmental context.

Personality disorders. Individual differences in personality are increasingly thought to serve an adaptive function, but it is less clear whether these same principles apply to extreme variants of personality – personality disorders. If personality were to reflect deleterious variations around a behavioral optimum, it would be expected that individuals with personality disorders would be the most maladapted; however, it is becoming commonly accepted that personality reflects adaptive alternate strategies, and therefore it should be considered that individuals with personality disorders may have the greatest evolutionary advantage (Vall et al. 2016). General criteria for personality disorders are largely focused on self-impairment and limited self-direction, traits that are marked by a present orientation and the opportunistic nature of a fast strategist. Traits such as impulsivity, risk-taking, disinhibition, and presentism are considered indicative of pathological self-impairment as per the personality disorder criteria; however, they could be thought of as behavioral dispositions that allow a person to logically adapt and suitably function in a novel and unpredictable environment. It has been suggested that the general criteria for personality disorders may combine individual differences in life history strategies and pathological dysfunction, reflecting a compilation of the failings of fast strategists (Hertler 2016). Further, despite the harm extreme personality traits may cause in everyday living, some extreme variants are not as disadvantageous to fitness as they may appear to be for social adaptation or wellbeing.

Although the framework is preliminary, the goal of the life history model is to map psychological disorders onto the fast-slow continuum to gain an understanding of how life history traits could be employed as a way to explore the fundamental underpinnings of psychopathology. The life history framework has been applied to a number of disorders, generating some promising results through the replication of the observed structure of psychiatric conditions (Del Giudice

2016). The life history model of psychopathology offers insight into the adaptive function of individual differences in life history traits, but also the differences in risk profiles for a number of psychological conditions. Through the exploration of etiological factors, including genetics and environmental context, the life history model offers an integrative approach to understanding mental illness.

The missing link. Current life history theoretical models of psychopathology (e.g., Del Giudice 2016) provide a solid foundation for conceptualizing mental health problems from an evolutionary perspective and explain the possible development of various disorders; however, the question still remains, why is it that only some individuals develop symptoms of psychopathology and others do not? There are people at each end of, and along, the life history strategy continuum that do not develop mental health problems. What discriminates between those who do and those who do not experience or develop mental health problems? One possible answer might be that of expectations. According to life history theory, organisms react to environmental contexts in preparation to most efficiently allocate energy in a fitness maximizing strategy. That is, there is an expectation that the environment is going to be a certain way and in which the organism has prepared itself *a priori*.

Expectations are about future possible events and are developed from prior experiences and knowledge and encompass both biological and psychological functions. At the basic biological level, examples include our circadian rhythm, with our biological clock expecting sunlight and darkness at certain times of the day. When we travel to the other side of the world, our biological clock's expectations are not met; hence, we experience jet lag until our clock can be recalibrated so that the expectations of the environment and the actual environment match. There is also evidence of this type of circadian expectancy in some plant species. For example, sunflowers have an expectation as to where the sun will rise and set, with the allocation of energy to cell growth unevenly distributed depending on the time of day, so that the sunflower is always facing the sun. That is,

overnight the cells on West side of the stalk on the sunflower grow more than the East side, causing the sunflower to lean toward the East first thing in the morning to catch the morning sun. During the day, the cells on the East side of the stalk of the sunflower grow faster than the West side allowing the plant to follow the sun and make the most of the important ultraviolet light (Atamian et al. 2016). Therefore, there is a biological expectation about the environment, resulting in an allocation of energy that best maximizes fitness.

In the psychological context, our schemas about the environment and relationships are developed at a young age and provide the blueprints for how to navigate our future relationships. If our early relationships are marked by interactions with fast strategists, we will develop schema and expectations about how to best navigate these relationships. Likewise, if we develop in a slower, more stable environment, our schema will likely reflect the best strategies to navigate those relationships with other slow strategists. Therefore differences in interpersonal skills and styles will be in part dependent on context of our early relationships. Indeed, there is evidence to support this notion that fast and slow strategists do indeed see the world differently and have developed different schemas with fast strategists having a more antagonistic social schema (Figueredo et al. [under review](#)) and more likely to engage in intimate partner violence (Barbaro and Shackelford 2016, March 27; Figueredo et al. [under review](#)).

Consider then if a person grew up in and were exposed to a harsh and unpredictable environment; they might reliably develop a fast life strategy. Alongside the prototypical fast life behaviors there would also be the development of cognitions or schema reflective of a harsh unpredictable environment, all of which would be adaptive in that environment. If the person then moved to a stable environment that would be more reflective of a slow strategist context, there would be a mismatch in behaviors and expectations between the fast strategist and the majority slow strategists that constitute the new environment. The fast strategist would bring with them expectations about the environment and interpersonal interactions that were no longer relevant. These might include

behaviors such as impulsivity, or cognitions such as a hostile attribution bias, that in the majority slow strategist environment would be pathologized as they fall out of the norm. Now, imagine this person went to university – a quintessential slow environment – where the environment rewards long-term planning discounting the immediate over the future. The behavioral and cognitive script for the fast strategist is not set up for that environment with greater expectations placed on the individual than are realistic for them to achieve. Failure to adapt and achieve these expectations would lead to confusion and distress.

Consider also the other end of a spectrum where a person grows up in a safe predictable resource-abundant environment. Their behaviors and cognitions would have developed to suit that particular environment. If this person were placed in a situation where their future was no longer predictable, for example, losing paid employment so that their financial future is no longer predictable, or being exposed to uncertainty about an intimate relationship (e.g., perhaps they were attracted to a fast strategist; see Marcinkowska et al. 2016), this would also lead to confusion and distress as their cognitive-emotional blueprint for the future and how to operate in the environment is no longer relevant. There may also be a tendency for slow strategists to set extremely high expectations about themselves and others that may be realistic in one environment given their early experiences; however, completely unrealistic in a different environment. Failure to meet these high expectations can lead to people to experience anxiety, frustration, anger, and low self-worth (symptoms of depression).

While there is no empirical evidence at present to support the notion of rigid expectations leading to psychopathology, there is case study support. The first author is a practicing clinical psychologist who has treated numerous clients who would fall all along the fast-slow continuum and who have all being diagnosed with various “psychopathologies.” Over the years he has observed a tendency for clients to express expectations that do not meet their current environmental context, with these

rigid expectations the apparent underlying cause of their psychological distress, which ultimately manifests itself in various psychological disorders. Conceptualizing mental health problems within a life history framework and removing judgments and assumptions about whether particular behaviors are pathological can help clinicians understand the role and historical function of the behaviors, cognitions, and traits that characterize clients’ presenting problems.

Conclusions

Life history theory provides a robust testable framework that helps researchers to organize their thoughts and their findings in a coherent manner consistent with evolutionary theory. The theory explains across species, within species, group, and individual differences. Application of life history theory to the human experience allows researchers to conceptualize and understand the roles and functions of variations in human behaviors from pubertal timing through to psychopathology. While empirical research investigating the psychological phenomena from a life history perspective is still in its relative infancy in comparison to other theories, what has been done to-date has significantly changed the way people think about human development and gene $\times$ environment interactions. The next step in the process is the application of life history theory to a number of already established subfields in psychology.

Cross-References

- [Bruce J. Ellis](#)
- [Cost-Benefit Analysis](#)
- [Discounting of Future Returns](#)
- [Early Childhood and Adolescence](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
- [Evolutionary Personality Psychology](#)
- [Evolutionary Psychology](#)
- [Fast Versus Slow Strategies](#)
- [Father Absence and Stress Reactivity](#)
- [Fecundity](#)

- Fertility
- Jay Belsky
- Life History Model of Psychopathology
- Mortality
- Prototypical r-/K-Selected (Fast/Slow) Species
- Psychopathology
- Quantity Versus Quality of Offspring
- Sexual Outcomes
- Sibling Studies
- Sociosexual Orientation
- Twin Studies

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Life History Theory and Rape

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Synonyms

Sexual assault; Sexual coercion

Definition

Rape is usually defined as a sexual assault involving some form of oral, anal, or vaginal penetration without the consent of the victim; such penetration may be accomplished either through the use of physical force or threat of bodily harm or when the victim was unable to give consent due to lack of consciousness or intoxication (Koss and Figueredo 2004). The occurrence of a rape may be assessed using self-report questionnaires such as the Sexual Experiences Survey (Koss et al. 1991; Koss and Oros 1982) or the Sexual Acts and Perceptions Inventory (Sisco and Figueredo

2008), typically without explicitly using the word “rape” but instead by providing descriptions of the acts.

Inextricably associated with the formal definition of rape is the question of whether it should be considered to be a “violent” or a “sexual” offense. As with intimate partner violence (IPV), which is highly correlated with marital rape (Figueredo and McCloskey 1993; Figueredo et al. 2001, 2009; Figueredo et al. 2017), feminist theorists consider rape to be a crime of violence against women, whereas evolutionary theorists generally emphasize the sexual dimension of the offense (Figueredo 2001). As most sexual assaults are perpetrated by acquaintances rather than strangers (see Koss et al. 2016), it has even been argued that the difference between rape and IPV is primarily a socially constructed one (Figueredo 2001), perhaps based on the historical definition of “spousal abuse” having required the intimate partners to have been legally married. In rape as in IPV, the sex and the violence cannot be disentwined simply by formulating mutually exclusive definitions. Nevertheless, all reasonable positions considered and in fairness to all parties in this polemic, one might conclude that most sexual assaults are ultimately *motivated* by sex in the perpetrators yet generally *experienced* as violence by the victims (see Thornhill 1996; Thornhill and Palmer 2000).

Introduction

The received view within the standard social science model (SSSM) is primarily derived from the feminist theory of patriarchy (Brownmiller 1975; Figueredo and McCloskey 1993; Figueredo et al. 2001, 2009), which purports to explain both physical and sexual violence toward women as the products of entrenched sociocultural arrangements, such as structural and status inequalities between the sexes disfavoring women that are ultimately founded on the ideology of patriarchy.

The alternative view within evolutionary psychology (EP) is primarily derived from the work of Thornhill and Palmer (2000), who present two alternative evolutionary hypotheses. The first, championed mostly by Thornhill, is that male

sexual coercion of females has possessed adaptive value over evolutionary time and has thus been directly selected for as a behavioral adaptation, analogous to those observed in a variety of other species of insects, birds, and mammals. The second, championed mostly by Palmer, is that male sexual coercion is a by-product of other evolved adaptations, such as greater male size, strength, and aggressiveness as compared with female humans, coupled with elevated male sexual motivation (see Figueredo 1992).

Elaborations of these theories include competitively disadvantaged male (CDM) theory (Figueredo and McCloskey 1993) and the mate deprivation (MD) hypothesis (Lalumière et al. 1996). Both CDM and MD theories predict that perpetrators of sexual coercion will disproportionately be males who are at a strategic disadvantage in the mating competition at obtaining or retaining female partners, as a result of deficiencies in sexually desirable traits such as social status, financial resources, or physical attractiveness. Lalumière et al. (1996) sought to test this hypothesis by demonstrating that sexual offenders were somehow able to obtain comparable numbers of sexual partners to non-offenders, which they were able to document, but failed to provide evidence that these sexual contacts were all consensual; this is an important omission as it has been found that the cognitive distortions prevalent among sexual offenders include heuristics for inferring partner consent that deviate substantially from accepted social norms in contemporary Western cultures (Sisco and Figueredo 2008).

Another important question, even within EP, is whether sexual violence is explained most adequately by theories that are specific to sexual coercion as an evolved adaptation (Thornhill and Palmer 2000) or by theories that are general to social deviance, including other violent but non-sexual offenses (Figueredo et al. 2000a). Recent empirical work has called into question the discriminant validity of the concept of IPV in relation to generalized interpersonal aggression and, thus, by implication, that of sexual coercion (Figueredo et al. 2017); once again, these separate categories might primarily be differing sociohistorical constructions based upon similar or perhaps even

identical phenomena, as seen through various cultural and ideological lenses, as there do not appear to be very defensible demarcations among them that can be derived either from the empirical evidence grounding them or from the nomological network of theoretical constructs surrounding them.

The Role of Life History Theory

Life history (LH) theory is a theoretical framework used in evolutionary biology to describe how and why individuals allocate varying amounts of bioenergetic materials into two competing areas: somatic or reproductive effort (Figueredo and Jacobs 2010). Somatic effort describes the amount of effort an organism invests in its own growth and preservation; the body requires a certain level of caloric energy to complete basic functions like digestion, cell turnover, and homeostatic maintenance (Ellis et al. 2009). Reproductive effort refers to an organism's effort to propagate their genes into the next generation. Under the reproductive effort heading, there are two main goals: mating effort and parental effort (Ellis et al. 2009; Figueredo et al. 2015b). Mating effort consists of investing time and energy into acquiring sexual partners, while parental effort refers to investing energy into the development and survival of an organism's offspring and kin.

LH theory describes how intrinsic and extrinsic threats in the evolutionary and developmental environment update the biology of individuals, selecting for the most advantageous survival strategy. LH theory predicts that when an individual's environment is stable and predictable, one will invest more into somatic effort, rather than reproductive effort. For instance, as the environment is predictable and a future can be reliable upon with a reasonable amount of certainty, an organism can expect time to invest in growing long bones or developing a large brain. Conversely, if the developmental or evolutionary environment was dangerous and unpredictable, with varying degrees of harshness at any given time, an organism would invest more in reproductive effort. When environmental threat levels are high, it is most productive

to develop and reproduce quickly, ensuring their genes will have a chance to be passed on to the next generation.

The latent LH construct consists of a constellation of different manifest indicators. Collectively, these indicators construct an individual's LH strategy along a continuum that ranges from fast to slow (*low to high K*; Figueredo and Jacobs 2010; Ellis et al. 2009). In its original conception, LH theory made predictions about observable, biological outcomes between species such as parental investment, inception of puberty, age of first sexual activity, or age of first birth (MacArthur and Wilson 1967; Pianka 1970). Faster species were predicted to evolve traits that would facilitate reproduction: (1) earlier pubertal timing, (2) more mating partners, (3) earlier first parturition, (4) more offspring, or (5) lower parental investment compared to their slow counterparts. As previously mentioned, slower species were predicted to first invest in their own growth and preservation and then in their offspring; they were predicted to have (1) later first parturition, (2) fewer offspring, (3) high parental investment, and (4) extended lifespan. Humans are slower life history strategists as we have a long juvenile dependency period and life spans that can last up to 100 years (Kaplan et al. 2000). There is visible variation within our species, however, which can be measured in traits such as female initial age of menarche, number of children, or interbirth interval.

In addition to measuring the biological outcomes of humans, LH makes predictions about psychological attitudes (Figueredo et al. 2015a). For example, understanding LH theory can shed light on why some individuals are more inclined to engage in long-term rather than short-term relationships, have few or multiple sexual partners, or maintain negative or positive attitudes toward casual sex (Patch and Figueredo 2017). Faster individuals, due to their more uncertain, unpredictable developmental environment, display a constellation of psychosocial traits selected to increase their proximate (and as such, ultimate) goal of mating effort; they are promiscuous, impulsive, less rule governed, and more likely to engage in risky behavior (Figueredo et al. 2015a;

Olderbak and Figueredo 2010). Additionally, faster LH strategists are more socially deviant (Figueredo and Jacobs 2010). The confluence of an adaptive strategy focused on mating effort and socially deviant behavior might lead to sexually deviant attitudes and behaviors.

Disparate LH strategies have disparate goals related to mating and relationships. Faster LH strategists tend to take an antagonistic social approach toward mating, regardless of the sex of the individual with whom they're interacting. For instance, a faster LH male might display controlling behaviors such as aggressive mate guarding or interpersonal violence more broadly, while fast female LH strategists might engage in competitive, problematic behavioral displays and interfere with a male's other potential mates. These mating differences can be seen cross-culturally (Weiss et al. 2004; Salmon et al. 2009).

Faster LH strategists expend more energy on mating effort and, as such, more energy acquiring mating partners, even those from whom they do not have consent. For faster LH strategists who have disagreeable personalities (Paulhus and Williams 2002), discount the future (Jonason et al. 2016), and are more promiscuous (Patch et al. 2017), rape may be an adaptive tactic. One manifest indicator of LH strategy, early sexual debut, has been shown to predict the level of delinquency later in life in a specific individual and also in their siblings; that is to say, if one sibling has experienced an early age of first sex, early age and level of delinquent behavior can be predicted in not just their own behavior but even that of their siblings (Figueredo et al. 2000). As early sexual debut predisposes adolescents to delinquency, sexual coercion might merely be the interaction between two components of a faster LH strategy: a proclivity for violence and an emphasis on mating effort (Figueredo 1992).

Recently, researchers have been examining a third component of faster LH strategists' personalities that might additionally increase their levels of sexual coercion: dark triad (DT) personalities (psychopathy, narcissism, Machiavellianism; Paulhus and Williams 2002; Jonason et al. 2009; Patch et al. 2017). DT personalities (i.e., callous affect; grandiose, manipulative, and impulsive

nature) have, as of late, been examined through an adaptive lens, particularly because these socially problematical personality traits persist in the population in spite of societal efforts to eradicate them. Among the reasons for the persistence of such traits is the possibility that the latent common factor underlying the three DT personalities is an expression of faster LH referred to as an "exploitative short-term mating style" (Jonason et al. 2009), which is a sexual strategy purportedly based upon the belief by males that they have "divergent interests" from those of females within sexual relationships (Figueredo et al. 2012; Malamuth 1998), generating a greater likelihood of conflict with their partners. Although faster LH does not necessarily imply the possession of DT traits, such an exploitative sexual strategy is more consistent with the uncommitted and promiscuous sexual lifestyle of faster LH individuals. Exploitative sexuality, and especially sexual coercion, would be more clearly inconsistent with slower LH.

For example, faster LH does indeed significantly predict psychopathic personality (Patch and Figueredo 2017). Furthermore, faster LH strategists and psychopathic individuals have similar characteristics and goals, such as a preference for casual sex, higher number of mating partners, and report higher than average levels of relationship conflict and dissolution (Jonason et al. 2009; Olderbak and Figueredo 2010). Both groups' goal is to exploit short-term mating opportunities even if that harms their partners. Both groups, additionally, demonstrate higher than average levels of aggression and criminality (Jonason et al. 2016). As dark triad personalities' common core is a profound lack of empathy, not obtaining consent from a potential mating partner would not constitute a moral dilemma (see also Sisco and Figueredo 2008).

As with the two major EP alternative theories of rape, we may question whether the exploitative sexual strategies represented by DT traits are maintained in the population by selection as a direct consequence of their function in facilitating sexual coercion. Alternatively, it might be the case that the faster LH strategies that might ultimately lead to exploitative sexual strategies, albeit

indirectly, are being maintained in the populations by selection as a consequence of their function in facilitating more generalized antagonistic social schemata and behavioral strategies as psychological adaptations to harsh and unpredictable environments of evolution and development.

Conclusion

We have surveyed the varying definitions of rape in relation to the juxtaposition of its sexual and violent elements. We have then examined the major evolutionary and non-evolutionary theories that have been proposed for the etiology of sexual coercion, including the specific adaptation and by-product hypotheses, following up on some of the novel predictions generated by these two perspectives and evaluating them in light of the empirical evidence. We then considered whether sexually coercive behavior is best explained by domain-specific or domain-general evolutionary theories, calling into question the conventional wisdom that has created arbitrary distinctions between rape, intimate partner violence, and interpersonal aggression in general, whether specifically sexual or not in any given instance.

All of these considerations have been made within the context of life history theory, which provides an overarching framework from which to view sexually coercive behaviors as a subset of sexual behaviors in general, as governed by regulatory mechanisms that control the allocation of bioenergetic and material resources among different components of fitness, including those specifically allocated to mating effort. In so doing, we have considered the specific role of DT personalities as specific manifestations of faster LH strategies that might be evolved and developed with the function of producing exploitative sexual strategies that facilitate the production of sexually coercive cognitions behaviors.

Cross-References

- [Alcohol and Rape on College Campuses](#)
- [Ecological Factors and Rape](#)

- [Evolutionary Perspectives on Rape](#)
- [Intimate Partner Violence](#)
- [Partner Rape](#)
- [Rape](#)
- [Rape and Dating](#)
- [Sex Differences in Intimate Partner Violence](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion and Rape](#)
- [Sexual Coercion and Violence](#)

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Life History Tradeoffs

► Life History Strategies

Life of Charles Darwin

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Synonyms

Biography of Charles Darwin

Definition

The life of Charles Darwin is examined including his education, main writings, and influences.

Introduction

Charles Darwin was an English naturalist who made significant contributions to the fields of geology and biology. His most famous contribution was a theory to explain the mechanism of evolutionary change which he called natural selection. While there were debates during his lifetime about whether or not natural selection is the main mechanism of adaptive change, today his theory is well accepted by mainstream biologists.

Early Years and Education

Charles Robert Darwin was born on 12 February 1809 in Mount House on the outskirts of the English town of Shrewsbury. His parents, physician Robert Darwin and pottery heiress Susannah Wedgwood, were a wealthy property-owning couple who had five other children.

Charles, who was known to his family as “Bobby,” failed to distinguish himself at Shrewsbury School and maintained this trend when, at the age of 16, he went up to Edinburgh University to study medicine. There he proved to be a rather lazy (and queasy) student who spent more time hunting and drinking than studying for his medical degree. Despite this lack of effort, Charles was fortunate in joining a natural history group known as the Plinian Society. There he met and was greatly influenced by physician Robert Grant, who helped to stimulate his interest in marine invertebrates (Desmond and Moore 1991). He also attended a number of talks on natural history where the concept of evolution is known to have been discussed. After 2 years, Charles left Edinburgh and changed direction when he entered Cambridge University to study for the clergy. At this stage in his life, Darwin did not appear to have strong views on religion either

way, but rather found the idea of becoming a country parson an attractive one (Browne 1995). At this time, students studying for a BA degree at Cambridge were allowed a great deal of latitude in which areas they chose to study. Darwin was extremely fortunate in choosing both botany and geology. During the 1820s, Cambridge had two world-renowned naturalists in Professors John Stevens Henslow and Adam Sedgwick, who ran botany and geology classes, respectively. In fact Darwin was fortunate in two respects in taking their classes. First, both of these experts were cutting-edge researchers and captivating teachers, and second, both later played a part in setting up Darwin’s famous voyage on board the *Beagle*. In the case of Sedgwick, a geology trip with Darwin to Mid Wales stimulated the younger man’s enthusiasm and working knowledge of this newly emerging science. This, in turn, stirred his interest in traveling widely in order to examine the rock formations around the world. In the case of Henslow, the link to the *Beagle* was somewhat more direct.

Having graduated in January 1831 (coming a respectable tenth out of a class of 178), Darwin was all set to follow the path of a country parson, when a letter arrived at Mount House which would set him off on a very different path. The letter offered him a position on a 4-year circumnavigation survey voyage of *HMS Beagle*. Interestingly, Henslow had originally been offered the role, but rather than spend this lengthy period away from his family, he suggested Darwin as a young alternative (Workman 2014).

The Voyage of the Beagle

On 27 December 1831, *HMS Beagle* set sail from Plymouth harbor under the captaincy of 26-year-old Robert FitzRoy. FitzRoy was given command of the ship following the suicide of its previous commander Parker King. It’s often reported that Darwin was appointed as ship’s naturalist, but in fact that position was taken by surgeon-naturalist Robert McCormick. Darwin’s appointment at the start of the voyage was as captain’s companion. This rather vague position probably arose as a

consequence of the fact that suicide had become common among commanding officers on such lengthy voyages (Browne 1995). Not only did Darwin have no professional role on board, but the 22-year-old was also expected to pay his way to the tune of more than £1500 (£73,000 in today's money which his father, after some persuasion, agreed to finance).

The young Darwin took some time to find his “sea-legs” and spent much of the early part of the voyage sick in his cabin. As he recovered, he was fortunate that his cabin was also the ship's library containing some 400 books (including a number of up-to-date works on natural history and geology). Of particular importance was a copy of the first volume of Charles Lyell's recently published *Principles of Geology*. Having this groundbreaking work proved to be yet another fortuitous event for Darwin as it introduced him to the concept of *uniformitarianism*. This is the theory that the planet has been, and continues to be, shaped by gradual, but observable, geographical changes. The action of a river running through an area, for example, can lead to the formation of a valley. Moreover, more rapid changes can also occur when, for example, due to an earthquake or the eruption of a volcano, the landscape can alter quite radically. Interestingly, in the third volume of *Principles of Geology*, which Darwin picked up later on in the voyage, Lyell even discusses the gradual birth and extinction of species.

Darwin's Relationship with FitzRoy

During the voyage that was to survey, among others, much of the coast of South America, the Galápagos Islands, Tahiti, Australia, and Mauritius, Darwin's main confidant was, of course, FitzRoy. Their relationship started off very convivially with the two men taking it in turns to read Jane Austin aloud to each other. As the voyage progressed, however, cracks began to appear, and their relationship developed into a love/hate one. Although the two men had great respect for each other, they also engaged intermittently in a number of running debates. While both were from wealthy backgrounds and

both had a prodigious intellect, as the voyage progressed, they fell out on topics such as religion and the slave trade. FitzRoy was a man of religious piety and considered that God had put us on earth to direct those races which he considered inferior to white Europeans. This made the slave trade acceptable to him. Darwin, for his part, perceived continuity between people of different races and saw slavery as an abomination. Despite his unsavory views on race and slavery, or rather because of them, FitzRoy may well have aided Darwin in the formation of his ideas about evolution. When he began to turn his attention to the mutability of species, FitzRoy's counter arguments ensured that Darwin had to be very cautious with how he expressed such radical thoughts on his return home (Workman 2014). This no doubt stood him in good stead when he finally published his theory of evolution some 20 years later (FitzRoy had also read Lyell's book).

The Origin of the Origin of Species

When Darwin made landfall in South America, he determined to spend as much time as possible on land observing the flora and fauna and examining in some detail the geology of the coast. One thing that struck him almost immediately was that fossils of the upper rock layers were more similar to extant species than those of the lower strata. To Darwin, this suggested species had gradually modified over a geological time scale progressively becoming more similar to modern-day ones. Later, when he arrived at the Galápagos Islands on the west side of South America, he began to shift his attention from geology to biology. In fact by the time they reached South America, Darwin had pretty much usurped the McCormick in his role as ship's naturalist (the latter man left the *Beagle* in Rio due to Darwin's developing obsession with geology). On the Galápagos, Darwin made further observations which strengthened his view that species were not immutable. In particular, he noted how the finches and giant tortoises appeared to have specific features which helped them exploit potential food reserves on each island. The shape and size

of the beaks of specific species of finch, for example, allowed them to overcome the challenges of food extraction that each island (and areas within each island) presented. Where seeds required opening, for example, the finches had short robust beaks, whereas when grubs required extraction, then the finches had developed slim probing beaks. In considering the origin of species, these sorts of observation led Darwin to speculate that such species had arisen from a common ancestor and then changed in ways that helped them to exploit food resources (and other aspects of the environment). He did not at this point, however, have the mechanism for such evolutionary change. That was to come much later on.

Back in England

When Darwin arrived home in England (sailing into Falmouth port on 2 October 1836), he brought back with him two major observations. First, organisms change and become progressively more like current living ones as we move up the geological strata, and second, organisms are well designed to deal with the challenges of their local environment. What he needed now was a mechanism or principle to explain these observations. At this stage in his life, he was already gaining a reputation as a geologist. This might sound surprising, given he was away for what became nearly 5 years. In fact he was surprised at how established his reputation had become. There was, however, a logical reason for this rise in standing; every time he put into port, he arranged for letters outlining his thoughts, observations, and samples he had collected to be sent back to Henslow and Sedgwick (Burkhardt and Smith 1986). Such thoughts included an explanation for the formation of marine atolls and the concept of the world being much older than was currently accepted. Note in both of these matters, Darwin was later proved correct. For their part, recognizing the quality of Darwin's field work, Henslow and Sedgwick shared his ideas at prominent meetings and via their published work. Darwin was duly elected a Fellow of the Geographical Society. His reputation as a

biologist was to come later following years of work on barnacle anatomy and later, of course, through his development of the theory of evolution by natural selection (Desmond and Moore 1991).

Marriage to Emma and Family Life

During the late 1830s, Darwin concentrated on two things: first, writing letters, books (including the best-selling *Voyage of the Beagle*), and articles and second, getting married. In both of these endeavors, he demonstrated his usual scientific methodology. His writings, while somewhat long-winded by today's standards, were clear and long-sighted. This was also the case when he decided to begin courtship. The target of his affections was his cousin Emma Wedgwood. It's clear that he had affection for Emma, but prior to determining whether this might be reciprocated, he devised a list of pros and cons with regard to marriage. On the con side, he listed "less money for books," whereas on the pros side, he wrote a "constant companion, (and friend in old age) who will feel interested in one, – the object to be beloved and played with. Better than a dog anyhow." Fortunately for Darwin, he went with the pros side of the equation, and Emma did reciprocate his feelings. The couple were married in a small chapel in Maer on 29 January 1839. Following 3 years living in Upper Gower Street in London, in 1842, the couple bought a country house in Downe in Kent. This large manor house, somewhat confusingly, was known as Down House (note the slightly different spelling), and there, they remained for the rest of Charles' life.

Despite Darwin's apparently utilitarian approach to marriage, it is clear that the couple did love each other and in fact, although his writing style would be considered rather formal by today's standards, he was a man well able to demonstrate affection to his loved ones. Emma, for her part, proved to be a caring and attentive nurse as, following his return, Charles succumbed to regular bouts of ill-health. And despite her strong religious convictions and misgivings

about the concept of evolution, Emma also played a large role in correcting his grammar and spelling. The couple had ten children, seven of which survived childhood. Charles proved to be a caring father, and, in common with Emma, he suffered greatly when three of his children died. He clearly enjoyed the company of children, and when his boys were old enough, he liked nothing better than to play a game of billiards with them of an evening.

Back to Evolution

By the time of his marriage to Emma, Charles had begun to keep notebooks noting down his thoughts on the topic of evolution (although at this time, he largely used the term of “transmutation”). Drawing on his experiences on the *Beagle*, he made a number of false starts, but by the end of 1839, he had managed to put all of the pieces of the puzzle together to complete a picture of how evolution occurred. He called this natural selection. To be clear, Darwin was not the first person to come up with the concept of evolution. The idea of organic evolution had been around since the time of Aristotle. (Interestingly Charles’ grandfather, Erasmus Darwin, had devised his own somewhat fanciful theory of evolution back in 1777 suggesting that efforts animals made during their lives, could alter their characteristics in positive ways and that such improvements are then passed on to their offspring). What the younger Darwin did was to add two elements to the concept of evolution. First, he proposed the mechanism to explain how evolutionary change occurred, and second, he marshaled the evidence to support this theory. The crux of the matter can be seen on page 7 of his first “transmutation” notebook:

According to this view, animals on separate islands ought to become different if kept long enough apart, with slightly different circumstances (Burkhardt and Smith 1986).

According to Darwin, natural selection involves three elements. First, there is heritability, which means that each offspring has similar traits to its parents when compared with other members

of the population. Second, there is variation, that is, members of a population vary in heritable ways. And third, members of a population have differential reproductive success. Hence, due to heritable variability in a population, some individuals have a competitive advantage in relation to survival and reproduction when compared with others in a specific environment. Natural selection later became known as “survival of the fittest,” a term first used by another English evolutionist Herbert Spencer (Browne 1995).

We might ask just how did Darwin derive the concept of natural selection? This was in effect the logical outcome of combining his earlier observations (fossils become more like current living species and organisms are particularly suited to their environment) together with two major works of science. The first of these was Lyell’s *Principles of Geology* and the second was Thomas Malthus’ *An essay on the Principle of Population* (published in 1798). Malthus had argued that, because populations grow faster than food availability, starvation led to the winnowing out of less competitive individuals. Combining this with Lyell’s notion of gradual but constant environmental change, Darwin saw that, as the environment changed, different adaptations were selected by “nature,” hence natural selection.

Friends and Allies

As Darwin’s standing rose, he found he was often visited by eminent naturalists of the day. Many become close friends and supporters. Of particular prominence were three men: the aforementioned Charles Lyell, Joseph Hooker, and Thomas Huxley. It is worth considering each of these briefly as they all proved to be important to him when he launched his radical ideas about evolution onto the world.

Although Charles Lyell had many achievements in the field of geology (for which he was later knighted and then made a baronet), his reputation was secured when he published *Principles of Geology*. By the time Darwin returned to England, Lyell, who was in his 30s, had become professor of geology at King’s College. He

recognized the originality of Darwin's writings, and very rapidly, the two men become close friends. This friendship was to prove beneficial to both men as each drew on the others writings (Darwin would draw on the *Principles of Geology* and Lyell modified later editions of this three-volume work to incorporate Darwin's ideas on evolution). Joseph Hooker was the first person to bring together the fields of botany and geology to create the field of botanical geology. Like Lyell, he was an avid reader of Darwin's work and also become a close friend following an invitation to classify the plants he had gathered in South America. He later went on to become director of the Royal Botanical Gardens in Kew. Despite the close friendship and support of Lyell and Hooker, arguably Darwin's most renowned supporter was Thomas Huxley. As he was only 11 years old when the *Beagle* returned, it was sometime later that he also became a confidant of Darwin. It was during the 1850s that this largely self-taught natural historian took up Darwin's cause and, in particular, defended him when the *Origin of Species* was published. Huxley's strident defense of Darwin would go on to earn him the nickname of "Darwin's bulldog." He later went on to become professor of natural history at the Royal School of Mines in 1854 and was the first person to suggest birds had evolved from dinosaurs.

During the early 1840s, Darwin shared his concept of natural selection with all three of his confidants (and a few others). This included a 35-page essay in 1842 which 2 years later he fleshed out into a more detailed 50,000-word essay (Darwin 1842; 1909). Although all three encouraged him to publish, at this point he held back, probably due to the fact that he was still gaining supportive evidence via his regular correspondence with experts from around the world. During the 1850s, he was working on a mammoth outline of his theory which was planned to be two volumes long. This plan, however, had to be put aside when out of the blue in February 1858, he received a letter outlining the same process in 20 pages. The letter was from another British naturalist, Alfred Russel Wallace, who was conducting field research in the Malay Archipelago. To Darwin's dismay, the letter

outlined the very same theory of evolutionary change that he had spent so many years developing. While Wallace did not have the supporting evidence that Darwin had uncovered, he had also hit on natural selection through deduction.

Publication and Reception of Origin

Darwin was, as can be imagined, greatly disturbed to find another naturalist had stumbled on natural selection, and his initial response was to allow the younger man to publish ahead of him. Fortunately for Darwin, his supporters talked him out of this course of action, and the theory of natural selection was presented to the world when Lyell and Hooker introduced both men's findings at a meeting of the London-based Linnean society on 1 July 1858.

Following this near catastrophic scoop, Darwin quickly got on with editing his Magnum Opus down to a much shorter (but still 540 pages) account of his theory of evolution. Hence the *Origin of Species* was published on 22 November 1859. To give it its full original title *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* is fortunately, by tradition, generally referred to as *Origin*.

Origin become an immediate best seller with the original print run selling out in 1 day and this leading to a series of follow-up print runs. By and large, the scientific community was positive with most prominent figures immediately being converted to what rapidly become known as "Darwinism" (a term coined by Wallace). In providing an explanation for evolution, Darwin also created a grand unifying theory (GUT) for biology. The importance of this development should not be underestimated as even today biology remains the only science to have a generally agreed on GUT (Workman 2014).

Despite this positive reception, Darwin was not without detractors and critics. These came from both the church and the scientific community (and in some cases continue to do so). One high-powered critic from the scientific community was Sir Richard Owen who at the time was a professor

at the Royal College of surgeons. Owen suggested that many young naturalists had been “seduced” by Darwin’s concept of natural selection. Despite being a man of science, it is clear that Owen’s criticism was fueled by his religious belief.

One prominent figure from the church who questioned natural selection was the infamous Bishop Samuel Wilberforce of Oxford. At a notorious meeting of the British Association of Science in the University Museum in Oxford, a discussion of Darwin’s ideas took place in June 1860. Due to ill-health (and possibly due to the fact that Darwin did not enjoy public speaking), he did not attend, and Wilberforce (briefed by Owen) took the opportunity to ridicule the whole concept of evolution. Fortunately for Darwin, this was an occasion when his bulldog Huxley did attend. Wilberforce asked Huxley whether he had descended from an ape on his grandmother’s side or his grandfather’s side? Huxley’s response was to declare that he would rather be the descendent of an ape than a man of learning who ridiculed scientific progress (Huxley 1900).

Life After *Origin*

Although Darwin was a well-known English naturalist and writer prior to the appearance of *Origin*, following its publication, it’s fair to say, he became a world famous figure. One reason for this was that, in addition to its impact on the scientific community, the book made a large impact in the international popular press. As well as a number of positive reviews, there were also some severe criticisms, and on a number of occasions, he was lampooned in popular publications such as the widely read British satirical magazine *Punch* (in which Darwin appeared as a half ape-half human chimera). His lack of appearance to defend himself at prominent public events due to ill-health became a common theme in the Darwin story. It is fair to say that he was a man who disliked, and hence avoided, confrontation. But, as we have seen, he was fortunate in having an illustrious group of acolytes such as Huxley, Hooker, and Lyell (among others). As his reputation grew, however, he became less afraid of

confronting public opinion in his writings. Although he did not write again about evolution for some 12 years after the publication of *Origin*, when he did so it was with two books which did not shy away from issues many of his Victorian audience would find uncomfortable.

Sex and Emotions: Darwin’s Follow-Up Books on Evolution

Despite his growing fame, during the 1860s, Darwin spent most of his time at Down House where he enjoyed a quiet family life (as well as he was able given his intermittent periods of ill-health). During this period of this life, he continued to write about natural history including well-received, but uncontroversial, works on plants and on domesticated animals. In 1871, however, he turned his focus once more to evolution. In his new work *The Descent of Man and Selection in Relation to Sex* published on 24 February 1871, Darwin exhibited a degree of courage in his writing which had arguably been lacking in *Origin*. Whereas in *Origin*, he had devoted a single sentence to human evolution:

Light will be thrown on man and his origin.

In *Descent*, he dispensed with this diffidence, spelling out the fact that we share with the great apes a simian ancestry. In the final chapter, he confidently stated:

We thus learn that man is descended from a hairy quadruped, furnished with a tail and pointed ears, probably arboreal in its habits, and an inhabitant of the Old World.

The *Descent of Man* was a book in two parts. In the first part, Darwin demonstrated how much we have in common with other species, both in terms of physical features and in relation to behavior. This he took as evidence for evolutionary continuity between us and other species. In the second half, he fleshed out an idea he had briefly introduced in *Origin*, that is, of a second evolutionary force which he called sexual selection. Whereas natural selection is based on the ability to survive and reproduce, sexual selection is concerned with impressing and gaining access to

the opposite sex. This means that, rather than the environment, in effect, the opposite sex does the selecting. Sexual selection helped to explain why males of many species, such as peacocks and mandrills, have more gaudy features than females (because it impresses the females). It also explains why males of many species have a lower threshold for aggressive behavior (to compete with other males). Interestingly, this concept of sexual selection has become very important to the development of modern-day Darwinian approaches to behavior (Buss 2019; Workman and Reader 2020).

The *Descent of Man* is not only a confident book; it is also one in which Darwin speculated about the evolution of a number of human features. In particular, he suggested that human language has parallels with bird song and that it evolved, in part, to impress potential mates. Such ideas were prophetic, as today many evolutionists accept both of these arguments (Locke and Bogin 2006; Slater 2011; Zuk and Simmons 2018).

Why, we might ask, had Darwin's writing style become more confident at this point in his life. It is likely that there are two reasons for this. First, as we have seen, when he published *Origin*, he was becoming a well-known geologist and naturalist. By 1871, his reputation had grown to the point where he was almost certainly the most famous scientist on earth. Second, during the 1860s, a number of fossils had been discovered to demonstrate intermediate forms that were predicted by his theory of evolution. In particular, the first bird/reptile intermediate fossil of *Archaeopteryx* had been uncovered just 2 years after the publication of *Origin*.

As with *Origin*, the *Descent of Man* was generally received positively by the scientific fraternity. This was, once again, by no means unanimous. One area of controversy was the idea that females exerted choice in whom they mated with and the idea that this choosiness, in turn, drove some facets of male features (Cronin 1991). This notion remained controversial for almost a century after the publication of the *Descent of Man*, but following recent research, the evidence is currently overwhelmingly in favor of Darwin's view on this (Buss 2019).

In November 1872, Darwin followed up *Descent* with his final book on evolution *The Expression of the Emotions in Man and Animals*. In this new book, he continued his exploration of continuity between ourselves and other species. In this case, he examined similarities in emotional expression between a range of mammalian species and humans. Based on the observations he made on his travels and through his communications with other experts around the world, he also suggested that people from different cultures used the same set of emotional expressions under the same circumstance. For example, when expressing disgust, anger, and fear, people from very different parts of the world make use of the same sets of muscles controlling the eyes, lips, and nose in exactly the same manner. This suggested to Darwin that the expression of our emotional states arose by natural (and sexual) selection for adaptive communicative purposes. Once again, as with the *Descent of Man*, *The Expression of the Emotions* suggested testable hypotheses (do we all use emotional expressions for the same purposes) which were largely ignored for almost a century. And once again, relatively recent research suggests Darwin was largely right here (Ekman 1992).

The Expression of the Emotions received mixed reviews, and sadly, the people for whom it might arguably have had the greatest impact, psychologists, largely ignored it until recent years (Workman 2014).

Darwin's Theory Misused

Although Darwin's greatest impact was on the development of biology from 1859 on, his influence grew (often unintentionally) well beyond this natural science. One area where his concept of natural selection was arguably misapplied was the field that later became known as Social Darwinism (the term was not used at the time). As the American "Barons" of industry became enamored with the concept of survival of the fittest, they began to see Darwinism as a scientific rationale for ruthless competitive business practices. This notion was based in part on the ideas of

American sociologist William Graham Sumner and British evolutionist Herbert Spencer (Caudill 1997; Workman 2015). Both considered that our natural course was to be competitive and that this was our destiny leading ultimately to some races outcompeting others to the benefit of our species. Ironically, Social Darwinism was non-Darwinian as according to his theory of natural selection there is no predetermined evolutionary path for any species, but rather it is simply a description of responses to recurrent environmental pressures. Also Darwin was well aware that natural selection can lead to the emergence of cooperative behavior. Darwin himself was disturbed by such uses of his theory and distanced himself from such misuses. Sadly, the development of Social Darwinism continues to cause some confusion today (Winegard et al. 2014).

Darwin's Latter Years

Following his latter two books on evolution, Darwin continued to write and study aspects of the natural world, including a work on the beneficial action of earthworms on the soil. He spent much of his last decade at home with Emma, but was regularly visited by his associates and famous figures (including George Eliot) who wished to meet the man who had given the world the first working theory of evolution. At the age of 73, following a 3-month decline in health, he succumbed to heart failure and died in Emma's arms on 19 April 1882. Plans were made for a burial in Downe, but following a campaign by his close friends, he was laid to rest a week later close to John Herschel and Isaac Newton in Westminster Abbey.

Conclusion

In the years following Darwin's demise, the concept of natural selection became modified through the integration of the new science of genetics. This led to the development of "neo-Darwinism" which defines natural selection as "differential gene replication." During the last three decades

of the twentieth century and the first two decades of this century, Darwin's ideas have been integrated into a growing number of academic disciplines. These include evolutionary economics, evolutionary anthropology, evolutionary literary studies, evolutionary psychiatry, and evolutionary psychology to name but a few. Of these fields, published output by evolutionary psychologists clearly dwarfs those from other academic disciplines. Given that Darwin wrote a great deal about the relationship between behavior and evolution, it seems likely that he would have approved of this development.

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Life Satisfaction

- [Measuring Well-Being](#)

Lifespan

- [Life History Theory](#)

Lifetime Reproductive Success

- [Reproductive Value and the Evolution of Aggression](#)

Likelihood of Conception

- [Youth and Fertility](#)

Limited Dispersal

- [Viscous Population](#)

Limited Reproductive Fitness

- [Limited Reproductive Potential](#)

Limited Reproductive Potential

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Synonyms

[Direct fitness](#); [Limited reproductive fitness](#); [Restricted reproductive potential](#)

Definition

The limitation of individuals' reproductive potential due to biological and/or environmental conditions that, in case of being optimum (e.g., good immunity against pathogens and/or environment without resources restrictions), the individual would have maximum offspring number.

Introduction

All individuals have distinct capacity of producing gametes and rearing offspring. As well as good nutrition and sex, genetics are biological factors that differentiate individuals' reproductive potential. However, biological elements are not the only ones to influence reproduction. Environmental factors have the same importance (e.g., diseases, resources, mates, competitors).

Sexual Selection

In 1871, Darwin claimed that the existence of some phenotypic characteristics could not be explained by natural selection due to their incapacity to improve individuals' survival. However,

those same characteristics serve to increase individuals' direct fitness as they enable the ability to attract a greater number of sexual partners or sexual partners with a higher mate value. To this, he attributed the name of sexual selection.

While Darwin considered the mating system to guide sexual selection, Bateman (1948) proposed sexual selection to be the factor that modulates mating system.

Bateman's Principle

Based on Darwin's sexual selection theory, Bateman (1948) conducted a study with *Drosophila melanogaster* to verify if there is a sex difference in intensity of mate selection and, in case it is true, a reason why it exists. He concluded that males tend to have an indiscriminate pattern of mating choice whereas females choose males.

Female's fertility is limited by greater investment of the females, relative to males, in gametes production. As males produce much more gametes than females, there is a competition between the sperm to fertilize the eggs (Bateman 1948). Beyond that, mammal females have gestation and breast-feeding as limiting factors of their reproduction. Males, on the other hand, do not have to invest in gestation and offspring nutrition, which allows them to invest more resources and energy in sperm production and mating effort, in order to increase their reproductive success. Therefore, males would have their reproduction limited by access to females (Bateman 1948).

To this idea, Trivers (1972) attributed the name of **parental investment theory**. He proposed that males and females invest differently in reproduction and offspring, which leads them to have differing reproductive success. There is an intrasexual competition between males (which he called the competitive sex) in order to have access to greater numbers of females (considered the limiting reproductive resource) and as women invest more physiologically in the offspring, it restricts the quantity of children they may have.

Strategic Pluralism Theory

Gangestad and Simpson (2000) theorized based on abundant evidence that environment would determine how women would choose their partners, through a trade-off between men's heritable fitness and paternal investment. In environment with high pathogens indexes, for example, women tend to prefer good-looking partners because beauty (e.g., symmetrical body and face) indicates good immunity. If the environment demands biparental care to guarantee children's survival, women tend to prefer men who are willing to invest in the offspring. Men, in turn, adapt their strategy accordingly to the strategy adopted by women and the access to females would be made possible according to quality of males available in the environment.

In this way, it can be noticed that besides the influence that the access to resources exerts on reproductive potential, the social environment also has its influence as the individual's mate value depends on the quality of same sex individuals available in the environment as well.

Limiting Factors of Reproductive Potential

Being too young is a limiting factor for both sexes, men and women, since before puberty they are not able to reproduce. However, younger women, in general, are preferred as mates because of the short period of reproduction when compared to men. While women stop reproducing when they reach menopause, even though there is a decrease of sperm quality (changes in sperm shape and motility), men still are able to reproduce. Thus, age is a factor that limits women's reproduction and decreases men's fitness (Pawlowski 2000).

Because of the effects that age exerts on female reproduction, their mate value decreases with age. Men, on the other hand, have their mate value increased the older they become, since their reproduction is not limited due to age and the probability of having more accumulated resources increases with time (Kenrick and Keefe 1992). Therefore, it can be taken into

account that resources are important limiting factors of human reproductive potential. As women's investment in children is essential for their survival in the first months, it demands a lot of energy from women who need supplies to provide better conditions of offspring development (Trivers 1972).

Hence, a beautiful body is a characteristic that men give high value when looking for a partner (Buss 1989). Low waist-to-hip ratio, for example, is preferred by men for indicating women's fertility and health. Karremans et al. (2010) justified that women's waist-to-hip ratio is associated with the quantity of fat deposited on the waist and on the hip in women's bodies. Fat located in the hip is positively related to the neural development of the embryo, while the type of fat deposited on waist may jeopardize the neural development. Therefore, physical characteristics may be a factor that reduces human reproductive potential.

1. Operational sex ratio may also be a limiting factor, mainly for males. The number of offspring a female has generally does not increase with greater number of mates. However, the statement is true for males. In a male-biased population, it is even easier to notice how the number of females is a limiting factor of males' reproduction, as there are some occasions in which males do not have the opportunity to copulate (Wade and Shuster 2005). Kruger et al. (2010) study corroborated with this idea for humans showing that in men-biased populations, men tend to marry earlier and younger.

Additionally, operational sex ratio is not the only important factor when talking about mating. Even if there is an equal number of mates of both sexes in a monogamous population (which decreases the odds of a man having access to more women), the pairs will be formed by similarity of mate value, and the individuals who have greater mate value, in general, have higher reproductive success for bonding with the best partners available (Buston and Emlen 2003).

Conclusion

There are several factors limiting potential reproduction: resources, operational sex ratio, and genetics are examples of such factors. Throughout the history of evolutionary psychology, authors have given important contributions toward figuring out diverse aspects of human sexual behavior. Together, all of the theories aforementioned are the foundation for understanding human reproductive potential and what may limit it.

Cross-References

- [Hamilton's Rule and Theoretical Implications](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Reproductive Strategies](#)
- [Sexual Strategies Theory](#)

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Lineage

- [Birthrights and Bloodlines](#)

Linear Grammar

- [Protosyntax](#)

Linearity

- [Primate Dominance Hierarchies](#)

Linguistic Development

- [Language Development](#)

Linguistic Evolution

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Synonyms

[Evolution of language](#); [Language evolution](#); [Language origins and evolution](#)

Definition

The multidisciplinary study of linguistic evolution has two overarching goals. The first one is to understand the *origins of language in humans*; in order to do this, anthropologists, archaeologists, geneticists, and linguists examine the biological, cognitive, and technological evolution of our species. Additionally, comparative psychologists and biologists also gain knowledge by identifying similarities and differences between the communicative behavior of humans and other animal species. The second goal of evolutionary linguists is to learn about the *origins of linguistic structure in human languages*. Linguists and psychologists aim at explaining the distribution of linguistic elements and properties as the result of social and cultural evolutionary processes.

Introduction

The term language evolution, or linguistic evolution, is used in two distinct, although related, ways. First, it may refer to the biological evolution of traits that underlie language learning, production, processing, and comprehension in our species. These traits include anatomical features of the language-producing organs and of the nervous system, as well as social and cognitive capacities including advanced imitation learning and cooperation.

Second, linguistic evolution is used to denote the cultural process of language change viewed as a case of Darwinian dynamics or as a complex adaptive system. Linguistic structure adapts to selection pressures originating in modern human cognition and in social factors such as learning and communication processes and population structure.

Language Origin

When Did Language Emerge?

This question “When did language emerge?” has no easy answer. Until recently, language was believed to have emerged with our species,

Homo sapiens, around 100,000 years ago. However, evidence such as the recent sequencing of the Neandertal genome suggests that there are no significant distinctions between the language capacity of that species and modern humans. Therefore, language as we know it may well have been used by the common ancestor of these two species about half a million years ago (Dediu and Levinson 2013).

If the manufacture of complex tools is indicative of the presence of some form of language, the date of language origin may be pushed further back to one million years ago (when Acheulean tools appear in the archeological record) or even to two million years ago (the age of Oldowan tools). Language and toolmaking not only share similar hierarchical, sequential, and combinatorial structure and require similar imitation learning, intention reading, and planned action skills but are also processed by overlapping brain areas (Stout and Chaminade 2012).

Theories of Protolanguage

The structure of early communication systems in the hominin lineage is the subject of extended debate. Questions such as “Did protolanguage have words?” or “Was early language gestural or vocal?” still do not have consensually accepted answers. Describing protolanguage is a difficult enterprise, given the absence of direct evidence. And if we consider language evolution as a gradual cumulative process, protolanguage may never have existed as a single defined stage in the evolution of language (Smith 2006).

Modern languages are mostly compositional (e.g., the meaning of a sentence depends on the meaning of its component words and on the ways in which these are combined) but also some non-compositional, holistic expressions (e.g., “hurray!”, “how do you do?”). Early language could have started off as sets of independent words that were later combined in different ways (Bickerton 1995) or as holistic expressions that were then analyzed or broken down into elements which eventually developed into words as we know them (Wray 2002).

Most of our linguistic behavior occurs in the vocal modality, but vocal control in our closest

ape relatives is poor. Language, therefore, may have begun its existence in the manual, or gestural modality, perhaps as pantomime and pointing, and later switched to the vocal modality (Corballis 2002; Tomasello 2008). Or it may have started off, as the musical protolanguage hypothesis suggests, in the vocal modality, in the form of songs or calls – not unlike the vocalizations of vocal learner species – which were then co-opted for communicative purposes (Fitch 2010). Alternatively, gesture and vocalization may have coexisted in language since its inception. Gesture is well suited to convey meanings iconically – iconic signals resemble their referents. But iconicity has limitations for the communication of abstract concepts. Early iconic gestures may have been accompanied by vocalizations, which gradually became symbolically or arbitrarily associated with aspects of the meaning, until they became the dominant communication medium. This third hypothesis avoids questions about the transition from the gestural to the vocal modality and about the origin of singing or other forms of noncommunicative vocalization, while simultaneously acknowledging that co-speech gesture is an integral component of modern language (McNeill 2012; Arbib 2012).

Biological Language Evolution

The study of the biological evolution of language is informed by evidence from a number of complementary sources. The fossil record of bones and the artifacts left by our ancestors gives us a glimpse of the skeletal structures and the culture present at different stages in our evolution. Comparative studies focus, on one hand, on species closely related to humans, such as chimpanzees and other primates, and, on the other, on more distantly related species including songbirds and marine cetaceans that share a key cognitive capacity with us, namely, vocal learning. The first kind of comparisons allows us to establish which language-related traits were present in our ancestral lines and which have evolved specifically in our lineage, while the second helps us understand which anatomical structures and

cognitive skills underlie the different components of language.

We share with our close primate relatives – and, presumably, also with our most recent common ancestors – well-developed social intelligence and communication skills. Some monkey species have alarm calls to warn the group about specific dangers, and others combine calls flexibly to alter the call meaning (e.g., Zuberbühler 2015). The great apes routinely communicate with each other through gesture and simple vocalizations, and chimpanzees are able to create and use stable signals through ontogenetic ritualization, a social process that gives rise to refined communicative signals, and may happen, for example, when a baby chimpanzee lifts its arms on several occasions in order to climb on its mother; the mother learns to respond to the arm-lifting gesture by picking the baby up before the baby has a chance to climb. Over time, the baby only needs to move its arms up slightly for the mother to respond (Tomasello and Call 1997).

However, monkey alarm calls are mostly innate; nonhuman primate signal combinations are extremely limited; and ritualized signals are confined to the pair who created them and do not spread to the population. Human language, a unique communication system, that is, simultaneously structured, conventional, and socially learned, only exists in the context of the unparalleled scale of human social cognition skills such as imitation and cooperation displayed by humans.

Brain Size

The fossil record attests to a rapid evolution of the brain volume from 400–500 cm³ in the Australopithecines about four to five million years ago to 1500 cc in Neandertals 400,000–30,000 years ago, with a recent volume decrease to the modern human average of about 1200 cc. An increase in brain size, however, provides only indirect evidence of the evolution of language. Changes in brain size and structure may have evolved in response to cognitive demands originating in technological advances or in larger social groups. A cultural novelty, cooking, could have supported these anatomical changes. Cooked food is easier

to digest and provides a much more higher nutrient intake than raw food; the extra resources could then supply the expanding brain (Wrangham 2009).

Speech Production

The speech-producing organs also underwent important changes in hominins, including a reshaping of the oral cavity and the loss of the air sacs present in other great apes, that extended the range of sounds that could be produced. The new elongated pharynx, however, makes us more prone to choking, and this fact has been put forward as evidence for the adaptiveness of phonemic variation – the fitness increase derived from improvements to speech must outweigh the fitness cost of an increased choking risk (Lieberman 2007).

Cooperation

Unlike other apes, humans spontaneously cooperate with and expect cooperation from others from a young age. We are able to direct others' attention toward potential points of common interest, to read others' intentions, and thus to entertain joint goals (Tomasello 2008). We also conform to social norms sometimes against rational judgment (e.g., Asch 1951), and strong conformity allows us to have cohesive societies and also facilitates cooperation. There are close interactions between cooperation, joint intentionality, conformity, and linguistic communication which would boost the fitness of individuals who excel at those traits. Being able to read others' intentions and establish joint attention is important for learning the conventional associations between words and their meanings. Language facilitates cooperation by mediating communication about potential opportunities and risks and by planning and sharing joint goals. And linguistic encoding enables the establishment and enforcing of complex social-cultural norms and traditions.

Imitation Learning

One of the main language-related evolutionary innovations in our lineage is advanced imitation. Humans share a particular aspect of imitation learning called vocal learning with a few other

distantly related species. Vocal learning is the capacity to learn and reproduce the vocalizations of conspecifics and is mediated by an enhanced motor control of the articulators, notably the tongue and of muscles involved in breathing, and by the highly developed capacity for imitation. This high-fidelity transmission mechanism has evolved independently in a heterogeneous group of species that includes some songbirds, cetaceans, elephants, and bats. Some vocal learners produce complex sequences which are made up from smaller elements, or motifs, recombined in different ways, persist for many generations, undergo cultural evolution, and diversify into dialects associated with different populations of the same species (Slater et al. 1984).

In humans, however, imitation is not limited to vocalization. We are, from a young age, avid imitators of all kinds of behaviors, much more so than our closest relatives. While chimpanzees engage in emulation (a form of social learning in which the copier reproduces the goals of an action, but not the precise behavioral sequence to achieve it) and occasionally sometimes in imitation (reproducing both the goal and the behaviors), humans are much more prone to doing imitation and also overimitation (copying actions in a sequence that are irrelevant or unnecessary to achieve the desired goal) (Whiten et al. 2009). The high-fidelity copying enabled by imitation and overimitation is a key causal factor in cumulative cultural evolution. The abovementioned effects of vocal learning on the complexity and diversification of birdsong are but a shadow of the effects of imitation learning on all realms of human culture, including technology, art, and language.

Cultural Language Evolution

The newly evolved social and cognitive traits, notably those that increased the fidelity of social transmission, paved the way for a new evolutionary system, human culture. Traits of cultural traditions such as the length of a spear, the design of a vase, or the set of phonemes in a language can

now persist for many generations and be the subject of evolutionary forces such as mutation and selection.

Language Change as an Evolutionary Process

Historical language change can be construed as the Darwinian evolution of population linguistic traits (Croft 2000; Ritt 2004). These traits include words, phonemes, phonetic variants, morphosyntactic constructions, and prosodic patterns. New variants of the traits arise during the course of language use, when speakers innovate or make mistakes in production or comprehension. Some variants are fitter than others – they are more likely to be adopted or used by speakers and consequently to spread and become the conventions of a language. Cultural language evolution is guided partly by chance factors – in evolutionary terms, by random drift – but also, more interestingly, by selection processes formally equivalent to natural selection, but mediated by cultural instead of biological processes.

Linguistic traits adapt to selective pressures related, among others, to the social prestige of the speakers who use them; to ease of production, processing, or comprehension; or to how well they fit in with the rest of the traits in the language. Some traits – for instance, core vocabulary items – are transmitted with such high fidelity over the generations that they can be traced back thousands of years (Pagel 2009). Most, however, change faster, and as innovations accumulate in separate populations, they give rise to linguistic variants, dialects, and eventually mutually unintelligible languages.

Language also adapts culturally to other aspects of the niche in which it evolves, including the structure of the social group and communicative function. Languages that are spoken in large, open societies tend to be morphologically simpler than those spoken in small, close-knit populations. This may be due to the presence in the open populations of adult learners for whom complex morphology is taxing. In smaller, closed groups, where speakers share more common ground and most learners are children – who are good at learning complex morphology – complexity can accumulate (Lupyan and Dale 2010).

The patterns of variation observed in world languages are, therefore, the result of processes of descent and modification from ancestral languages. From present-day variation, phylogenetic analysis can infer language trees or networks analogous to those used to map biological species. Combined linguistic, geographical, and historical data can not only trace the ancestry of language families but also help establish their geographical and temporal origins (Bouckaert et al. 2012).

Emergent Languages

Occasionally, a new language spontaneously emerges in a newly formed group of speakers who do not share a common language. This is the case of pidgin and creole languages, of sign languages in populations with high prevalence of congenital deafness (Meir et al. 2010), and of sign languages in newly opened schools for the deaf which bring together children who never had full access to language before (Senghas and Coppola 2001). In these groups, an initially ad hoc, variable, and unstructured communication system gradually acquires, usually within a few decades, the properties of modern, full-fledged natural languages, including a phonological system and productive morphology and syntax.

Experimental models of cultural language emergence show that when language transmission is disrupted, linguistic structure becomes simple and compressible; when languages are used communicatively, they develop or maintain distinct words for different meanings. A core property of language, compositionality, whereby a limited number of elements and rules can be productively recombined into countless utterances, emerges as an adaptation to the two simultaneous but conflicting pressures for compressibility and expressivity (Kirby et al. 2015).

These singular cases and models clearly demonstrate that for linguistic structure to emerge, both biologically modern humans and social processes such as communicative use and transmission to new learners are required: a population of members of another species does not spontaneously develop something like a modern human language, nor do humans in the absence of social interaction.

Gene-Culture Coevolution

Genetically transmitted human traits and culturally transmitted linguistic traits coevolve at multiple levels. Early forms of communicative behavior may have introduced selection pressures on humans – if the new behavior improved our ancestors' fitness, for instance, by facilitating cooperation, biological traits that promoted learning, and using the system would be selected for, and spread in the population. This would result in an increase of linguistic skills in the population and in the production of more complex linguistic structures which, in turn, would pose further pressure on biological evolution (Deacon 1997; Dor and Jablonka 2014). Language is an important part of the human cultural niche, and as such it may continue to guide our evolution, as suggested by evidence for rapid recent selection for genes involved in cognitive and linguistic function (e.g., Dediu and Ladd 2007; Ayub et al. 2013).

Conclusion

The evolution of human anatomical and cognitive traits that underlie language probably started early in the *Homo* genus, in close interaction with demographic changes and other cultural developments, such as technology or art. The multiple interactions between cultural and biological traits suggest a coevolutionary history in which humans adapted to language as much as language adapted to humans. The evolution of imitation learning, whether in the vocal or the manual modality, provided a mechanism for social transmission that in turn enabled cultural language evolution: the generation and propagation of linguistic element such as phonemes, morphemes, or morphosyntactic rules and linguistic properties including combinatoriality, compositionality, or arbitrariness in populations of speakers.

In the face of a scarcity of direct evidence, studies of language evolution continue to gather evidence from a diversity of sources, from archaeology to genetics, to decipher the origin and evolution of the unique human skill that is language.

Cross-References

- Adaptation
- Cooperation
- Cultural Evolution
- Cultural Transmission
- Culture
- Emulation
- Imitation
- Language
- Ontogenetic Adaptations
- Overimitation
- Sign Language
- Social Learning
- Toolmaking

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Linguistic Fossils

- [Protosyntax](#)

Linguistic Nativism

- [Pinker's \(1994\) The Language Instinct](#)

Linguistic Relativism

- [Language and Economic Cooperation](#)

Linguistics

- [Language and Economic Cooperation](#)

Literature

- [Human Storytelling](#)

Lithic Technology

- [Evolution of Tool Use](#)

Little Albert

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Synonyms

[Conditioned emotional reactions](#); [Experiment](#); [Learning](#); [Watson](#)

Definition

John Watson's experiment on children's conditioned emotional reactions

Introduction

In 1919, upon Watson's return from the army, he decided to pursue research, along with Rosalie Rayner, on children's emotional response and development based on conditioning processes. The first and only study that Watson and Rayner performed on this topic was the study with Albert B. or, most known, as Little Albert, at the laboratory of a hospital. This experiment became one of the most frequently cited in psychology books and magazines and is described as "one of the classic studies of twentieth-century psychology" (Todd 1994, p. 82).

The Conditions Surrounding the Experiment

Watson's academic career was built on examining animal learning. He was applying Pavlov's principles of classical conditioning, where innate bodily reflexes are conditioned with new stimuli to create new learning by association. Thus, conditioning causes events or stimuli to be associated in time, and learning takes place from the associated (simultaneous) arrangement of stimuli and responses. Watson concluded that the trial ends when the animal chooses the correct response.

The more often a response brings positive results, the higher the probability that it will be repeated by the animal (the law of frequency). Additionally, the animal will tend to repeat the most recent successful response (law of recency) (Hergenhahn 2000).

Upon his return from the army (1918) and before his abandonment of his academic career (1920), he decided to turn his attention to research on humans and especially on how conditioning processes influence human development. While teaching at Johns Hopkins University, he arranged to use a laboratory at Phipps Clinic (Moore 2017). Adjacent to Phipps Clinic was the Harriet Lane Home for Invalid Children, a hospital connected to the Phipps Clinic with a corridor (Watson and Rayner 2000).

Watson's interests centered on emotions; he considered emotions as mere physical responses, and he wanted to prove that emotional responses could be conditioned. For some (Rilling 2000) this was Watson's major contribution to learning theory and an explanation of phobic reactions through behaviorism. He believed that, since birth, infant humans have three unlearned emotional reactions: fear, rage, and love. Fear is evoked by only two stimuli that are unconditioned: a sudden noise and the loss of physical support but those fear-provoking stimuli are learned. Fear in infants can be observed in crying, breathing rapidly, closing their eyes, or jumping suddenly (Watson and Rayner 2000).

The Experiment

It is estimated that in early December 1919, Watson and Rosalie Rayner, his research assistant and later his wife, conducted a series of baseline trials. They chose only one child, Albert B., a healthy, well-developed, stolid, and unemotional child who cried rarely. He was raised almost from birth at the "Harriet Lane Home for Invalid Children" with his mother who was a wet nurse in the home. He had a normal life, and one of the main reasons he was chosen among other infants was that it was believed that the experiment could do relatively little harm to him. Different phases of the experiment were filmed. The experiment was

conducted, with the approval of Albert's mother, in a small, well-lighted dark room, and Albert was placed in a mattress, above a table (Watson and Rayner 2000).

Albert was assessed neurologically at around 9 months, in order to determine whether stimuli other than sharp noises and sudden removal of support can cause fear reactions. Thus, Albert was confronted suddenly with "a white rat, a rabbit, a dog, a monkey, masks with and without hair, cotton wool, etc." (Watson and Rayner 2000, p. 313); he showed no fear, at any time. Independently of the above observations, the experimenters tested whether the child would react to loud sounds by striking with a hammer a suspended steel bar three-fourths of an inch thick and 4 ft long; he reacted with fear and crying. Upon receiving the above results, Watson and Rayner wanted to examine the following: (a) if they could condition fear of an animal under the condition of visual presentation of the animal and simultaneously striking a steel bar, (b) if the conditioned emotional response established can be transferred to other animals or objects, (c) if time has an effect on the conditioned response, and (d) if they can devise methods for the removal of such conditioned emotional responses (Watson and Rayner 2000).

The experimenters had no other interaction with Albert until he became 11 months and 3 days old. He was presented with a white rat, and as he was reaching with his left hand for the rat, the experimenters were striking hard the steel bar behind his head. In the first trial, Albert fell forward and buried his face in the mattress. In the second trial, he jumped violently and began to whimper. A week later, he was exposed to the rat without the sound. Initially he did not reach for it, and when he did start to approach it with his hand, he withdrew it before contact, which indicated that the two joint stimulations of the first week were still effective. Albert had positive reactions to other objects by picking them up. In the next trials of the same day, the rat was presented in association with the sound, and Albert's reaction progressed from sudden bounce to turning away from the rat, then cringing his face and withdrawing his body to the left, and to falling to the right side and beginning to whimper and eventually

violently crying. Watson concluded that the conditioned fear response was completed (Moore 2017; Watson and Rayner 2000).

When Albert was 11 months and 15 days old, they wanted to examine whether the conditioned emotional response can be transferred for another object. Thus, they first presented Albert with different objects, and they noticed that he was comfortably playing with them that indicated that there was no transfer to other objects. When the rat presented alone, the child immediately began to crawl away from it and whimpered. Then, they presented a rabbit, and Albert had the same reactions as with the rat. When a dog was presented, similar reactions were elicited but not from the beginning of the interaction. He had similar reactions to a fur coat, cotton wool, a Santa Claus mask, and Watson's hair but not with other people's hair. Intermediate of the presentations with the aforementioned objects, Albert was presented with blocks, neutral objects that he happily played with throughout the experiment.

A week later, the rat was presented alone to Albert; he was cautious and was following it with his eyes, but he did not cry. As the rod was struck, his reaction was violent initially, but on the next two presentations of the rat alone, his reactions were as strong as before but without crying (i.e., crawling away from it). The experimenters also wanted to present the rabbit and the dog consecutively in connection with the sound of the steel bar and wanted to test whether Albert's reactions were similar in two different contexts, that is, the usual laboratory or a large, well-lighted lecture room. They found that the reactions were similar although less violent in the second room. From this phase of the experiment, they concluded that emotional transfer does take place (Watson and Rayner 2000).

At 1 year and 21 days old, upon Albert's exposure to the phobic objects, the conditioned emotional reactions by transfer persisted, although with less intensity. In the last phase of the test, they observed that when the child was under stress, he would thrust his thumb into his mouth, and he would become impervious to the fear earlier produced by the different stimuli. They suggested that the love stimulation one seeks

under the influence of harmful situations persists throughout life and could be described as a "compensatory" (and possibly conditioned) device, instead of the "expression of an original pleasure-seeking principle" as described by Freud (Watson and Rayner 2000, p. 316) Watson and Rayner did not have the chance to test for the effect of time on the symptoms or whether they could remove them because Albert moved out of the hospital soon after the last trial, but they contended that the symptoms would persist and modify personality throughout life.

Who Was Albert B?

Different researchers tried to discover the true identity of Little Albert. Some researchers (Beck et al. 2009) supported that his real name was Douglas Merritte, son of Arvilla Merritte who was working at the hospital at the time as a wet nurse. Douglas contracted meningitis from his aunt, developed hydrocephalus, and died from it at the age of 6. Fridlund, Beck, Goldie, and Irons (2012, as cited in Digdona et al. 2014) reported findings that Douglas had been neurologically impaired as early as the time the experiment was conducted. The general reactions from the above were that, if this was the case, Watson and Rayner's findings were challenged (Digdona et al. 2014). Other researchers (Digdona et al. 2014) concluded that the child was actually Albert Barger son of a 16-year-old mother by the name of Pearl Barger who was also a wet nurse working at the time at the hospital. One of the points for the defense of this opinion is that Watson typically used real names or initials of the infants he worked with; thus Albert B would be Albert Barger.

Ethical Concerns

Throughout the years, different publications challenged Watson's ethical standards, and some characterize Little Albert as a "victim" (Todd 1994, p. 85). Watson himself reported his hesitation in inflicting fear reactions to a child. His defense in continuing with the experiment was that Albert

was a strong, composed, unemotional child. Additionally, “such attachments would arise anyway as soon as the child left the sheltered environment of the nursery” (Watson and Rayner, 2000 p. 314). At the time, the Little Albert experiment did not raise serious ethical questions, although Watson warned his readers that for the replication of the experiment, considerable training was needed (Todd 1994).

Conclusion

John Watson and Rosalie Rayner planned to examine conditioned emotional responses on children. Specifically, they wanted to test whether they can condition fear reactions of different animals and objects to a 9-month-old healthy infant. The results confirmed most of the hypotheses of the experimenters but stirred up different reactions by researchers and the press for the ethical repercussions of conducting such a study to a child especially without extinguishing the symptoms evoked on the child.

Despite the questionable ethics and its methodological limitations, the Little Albert study (in reprint on Watson & Rayner, 2000) on conditioning became a “landmark” in behavioral psychology and changed the way we examine behavior and the way we practice. Furthermore, the results on fear acquisition and generalization initiated the development of treatments for phobias (Field and Nightingale 2009; Wolpe 1958 as cited in Beck et al. 2009) and other behavioral problems (Masters and Rimm 1987; Rachman 1997 as cited in Beck et al. 2009).

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Littlebrain

- [Cerebellum, The](#)

Living and Dying

- [Survival and Death](#)

Living in Groups

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Synonyms

[Aggression](#); [Benefits](#); [Costs](#); [Cultural transmission](#); [Kin selection](#); [Rank order](#)

Definition

A group can be defined as at least two individuals of the same species staying together for an extended period of time and actively seeking each other out in order to interact.

Introduction

Many animal species, including humans, live in groups of varying size and composition. In order to understand how group living has evolved during evolution, one has to consider which benefits and costs that have led to this. If the costs have been higher than the benefits, it may have led to that a species has developed a more solitary life style. However, living in groups often gives advantages to individuals at different times of their lives, thus pushing animals to choose group living at some stages of their lives. It may also be that the environment and the available resources may differ in different areas leading to that individuals of the same species may choose to live solitary at times and in groups at other times. Humans show all sorts of constellations when it comes to living in large, medium, or small groups, as well as living solitary. Sweden, for example, has one of the highest number of solitary households in the world (<http://sverigesradio.se/sida/artikel.aspx?programid=2054&artikel=5615244>). The reasons can be discussed but having the economic possibilities to live alone can be one of the causes.

What Is a Group?

A group has been defined by Wilson (1975) as “any set of organisms, belonging to the same species that remain together for a period of time interacting with one another to a distinctly greater degree than other conspecifics.” Another definition presented is that “when two or more animals live together they constitute a social unit” (Lee 1994 in Krause and Ruxton 2002). Pitcher et al. (1983 in Krause and Ruxton 2002) assume that the interindividual distance between group members is a function of the trade-off between the costs and the benefits associated with group living, and this has been presented as “the elective group size concept.” This concept requires that animals are close enough from each other for continuous exchange of information, but this distance vary between species (Krause and Ruxton 2002). The animals need to be brought together by

social attraction by actively seeking each other out and not just due to the mere coexistence on the same spot due to access to feed or other resources (Krause and Ruxton 2002). As group behavior show a very large variation across and within species, it may be difficult to find one definition that fits all and Krause and Ruxton (2002) suggests to rather develop operational definitions that fits the study species and the framework of grouping.

It is not really possible to split animals into solitary living and group-living species, as this may differ over time (Krause and Ruxton 2002). Most species will be found together with individuals of the same species at certain times, for example, mother and young, during mating and during other times of their lives. The same species may also have different strategies regarding if it will live in a group or as single due to different circumstances. Singletons or very small groups have often been found when researchers have tried to screen group-living animals for group size. According to Krause and Ruxton (2002), “for many so-called group-living species the group size distribution can have a very wide range and usually will include many singletons.” This may also apply to humans, especially those living in cities, as humans tend to carry out different activities together without knowing each other, for example, training at the gym, watching a movie at the cinema, shopping, etc.

Is There an Optimal Group Size?

Many researchers have tried to find out if there is an optimal group size. However, as individuals in a group tend to have conflicting interests regarding group size, the observed group size is probably a compromise between the various interests (Wittenberger 1981). Wilson (1975) developed a model to predict optimal group size by plotting the separate effects of each selective factor affecting a particular individual's inclusive fitness as a function of group size. However, this method has been criticized by Wittenberger (1981) who means that the model is based on unrealistic assumptions. Another model by Wittenberger (1981) propose

that optimal group size for an average female is reached when the percentage change in mortality rate caused by adding one more individual to the group is equal to the percentage change in reproductive rate. The model predicts that in larger groups, mortality rate may decrease due to increased protection from predators but increase due to higher competition for resources or higher disease prevalence (Wittenberger 1981). Reproductive rate may increase due to offspring being safer in large groups and better fed but decrease due to poorer nutritional condition of females or more malnutrition among offspring (Wittenberger 1981).

Social living in vertebrates is predicted to have evolved in four different ways. The first case predicts that female survival rate increase with increasing group size while the reproductive rate decreases (Wittenberger 1981). An example of this is colonial living rodents who depend on mutual vigilance to detect predators and to dig burrow systems, but competition for food decreases reproductive output. The second case predicts that female survival rate decrease with increasing group size while reproductive rate increases (Wittenberger 1981). Two examples of this are elephants and gorillas where increased group size lead to competition within the group which reduce female survival, but at the same time, social defenses against predators increase offspring survival (Schaller 1963). The third case predicts that female survival rate and reproductive rate both increase initially with increasing group size, but a decline in reproductive rate limit group size (Wittenberger 1981). Examples of this are social ungulates and primates who form groups to get protection from predators, but competition for food limit group size (Geist 1971; Dunbar 1979). The fourth case predicts that female survival rate and reproductive rate both increase initially with increasing group size, but a decline in survival rate limit group size (Wittenberger 1981). An example of this is lions where cooperative hunting increase survival of both adults and offspring in small groups, but as group size increase, female mortality may increase while offspring still survive by suckling other females than their mother (Schaller 1972). Evolution of social living

in humans could have followed the third case as females may have increased their survival rate and reproductive rate by living in groups but access to food may have been a limiting factor.

How Dynamic Is a Group?

It is important to consider that every group of animals can be viewed as a separate population which is characterized by a birth rate, death rate, immigration rate, and emigration rate (Cohen 1969). If it is primarily the birth and death rates that determine group size, it should reach an equilibrium size that reflects the carrying capacity of the home range (Wittenberger 1981). If it is primarily immigration and emigration rates that determine group size, it reflects the adaptive choices and conflicting interests of group members (Wittenberger 1981). In open social groups, individuals can move in and out of the groups, and they do not associate with any particular individuals for longer periods other than their dependent offspring (Wittenberger 1981). In closed groups, individuals stay for longer times in the group.

How close individuals stay relative to other group members mainly depends on food abundance and predator pressure. Competition for food make the animals spread out, whereas predator pressure makes the animals come together. For example Gorillas, Cape buffalos, and Thomson gazelles usually remain in tight social groups when resting or having social interactions, but they spread out into looser groups when foraging (Schaller 1963; Sinclair 1977; Walther 1977). Stable groups may fragment into widely spaced subgroups, as, for example, lionesses that form stable prides that share a group territory, but pride members rarely hunt together as one group (Schaller 1972). Hyenas live on permanent clan territories, but members of each clan hunt alone or in temporary subgroups in the Ngorongoro Crater, whereas they do not defend clan territories or maintain clan integrity on the Serengeti Plains (Kruuk 1972). In hyenas group, size depends on prey size, and the hunting groups is adjusted to the intensity of competition (Kruuk 1972).

In chimpanzees, individuals may join or leave groups frequently with little signs of aggression (Lawaick-Goodall 1968). The social system in chimpanzees can be described as a large group or community comprised of individuals moving among many temporary subgroups (Lawaick-Goodall 1968). Within each group, individuals are familiar with each other and they may share a common home range (Kawanaka and Nishida 1975). Males roam throughout the home range and defend it from males of neighboring groups (Goodall et al. 1979). Females may occupy smaller home ranges and not visit all parts of the unit group range (Wrangham 1979). It may also happen that a female visit neighboring groups or that she moves over to a new group permanently (Nishida 1979). The formation of temporary subgroups in chimpanzees may be caused by the distribution of ripe fruits that they prefer as a food source and if the fruit is clumped or more spread out (Lawick-Goodall 1968). Long-haired spider monkeys that also eat predominantly fruits forage in small subgroups when the fruits are widely dispersed and in larger and relatively stable group sizes when the fruit occur in large localized clumps (Klein and Klein 1975). During other times of the year when the distribution of fruit is more varied, the group size of long-haired spider monkeys are intermediate and has less stable composition (Klein and Klein 1975).

Different Types of Group Living

There are different constellations of group living from pair to anonymous groups. For each group constellation humans may live in them during shorter or longer periods of their lives.

1. Pairs. Male-female, female-female, or male-male. The sexual system is usually monogamous groups for one breeding season or for life. It is often claimed that this is the traditional system that humans live under, but it may not be true for all cultures and places in the world.
2. Maternal groups. Several females of varying age staying together for extended times with

their young up to weaning or when young get into puberty. Often female young continue to stay in the maternal group while the male move away from their mothers group. The sexual system is polygynous groups where the males seek up the females for mating but live solitary or in all male groups for the remaining time.

3. Bachelor groups. Several males living together after having left their mother and the maternal group. This is usually performed by young males, but with increasing age they may become solitary.
4. Mixed gender groups. Both females and males live together in the same group for extended times. The groups may vary in size depending on species and environmental conditions.
5. Anonymous groups. Animals come together at feeding places or to get other resources, but there is no individual recognition or prolonged interaction between the animals. This is typical for schooling of fish or large flocks of birds. However, it also occurs frequently in human society when humans are travelling, shopping, or attending events.

Bases for a Functioning Group and Rank Order

A group is usually an actively formed and maintained unit of animals (Lindberg 2001) or humans. The cohesion of the group needs to be maintained and there are several different mechanisms to do that. Lindberg (2001) mean that “a major feature of the group is that each animal acts (or attempts to act) for its own maximum benefit in its interaction with conspecifics, and this may result in ‘emergent properties’ that affect the group as a whole, such as dominance hierarchies.”

Schjelderup-Ebbe (1935) was the first to study the dominance hierarchy by recording the pecking-order in chickens. Dominance can be explained as “the predictable relationship between a pair of conspecifics, where one animal has learnt to dominate the other (subordinate), which in its turn tends to avoid the confrontation” (Lindberg 2001). The animals need to have

individual recognition for this to work and they learn this relationship for future encounters (Lindberg 2001). When adding up all these dominance relationships in a group, one can talk about a dominance hierarchy, peck-order, or rank order. This dominance hierarchy is unique to each group of animals living together. If one individual disappear from the group due to actively leaving it, being pushed out, or removed from the group, or by death, then the equilibrium is temporarily upset until a new rank order has been set (Keiper and Sambrasus 1986). The rank an animal has in one group may not be the same in another group as dominance ranks are specific to a particular group.

In small groups of animals, the dominance hierarchy may be linear (Craig 1986), which means that the highest ranking animal (A) is dominant over the second highest animal (B), who is dominant over C and so on down to the lowest ranking animal. A dominance hierarchy can also be triangular, where A is dominant over B and C, but C is dominant over A. In a despotic dominance hierarchy, A is dominant over all other individuals, but they do not have clear dominance relationships. A complex dominance hierarchy means that there is not a clear pattern, but rather that each pair of animals within the group has a set dominance relationship. Based on the information of each pair of animals in a group, one can make a dominance index that can show which animals are the dominant, subordinate, and submissive in the group. This has been described in, for example, rats, cows, and other animals kept by humans. There is a lot of research on dominance hierarchies in domesticated animals kept on farms due to the animal welfare problems caused by not considering the problems with mixing animals into different groups of varying sizes. It is also worth mentioning that animals usually try to avoid conflicts with others in the group as this may cause injuries. This can be explained as the “avoidance order,” where subordinate group members avoid provoking those members above them in the rank order (Lindberg 2001). We do not usually talk about humans as having higher or lower dominance rank than other persons in a group, but detailed behavioral observations of a

group of humans would probably be able to identify persons with a higher or lower social rank.

Individual animals within a group may have different tasks depending on their rank. Both the dominant animals and the subordinate animals may be subjected to both advantages and disadvantages from living in a group (see benefits and costs of group living below). In nature, the juveniles usually have a low rank, but as they grow older, they may raise in the dominance hierarchy until they reach a high position. In some species, a top-ranking animal may keep its position just due to its old age, whereas in other species, younger animals may test the top-ranking animal in order to push it down from its position. This is usually happening between males in a group and less often in females.

In order for a group of individuals (animals or humans) to function, they need to be able to communicate. A common definition of communication is “the transfer of information from a signaler to a receiver.” Dawkins and Krebs (1978) argue that communication may be an attempt by the signaler to manipulate the receiver in order to increase its own fitness. This has led to the receiver being selected for its ability to find out which signals are honest and which are not, and thus it has created an arms race between signaler and receiver (Dawkins and Krebs 1978).

The type of communication also differs between species from visual, acoustic, chemical, and tactile to electrical. Humans exchange information also by written and electronic media (telephones, computers, internet, social media, etc.), which makes this dimension even more complicated.

Evolutionary Causes Behind Group Living

Natural selection is usually used to explain the evolution of different behavioral strategies in animals. Krebs and Davis (1993) mean that natural selection can only work on genetic differences, and therefore, the following three criteria must be fulfilled: (1) there must be, or have been in the past, behavioral alternatives in the population;

(2) the differences must be, or have been, heritable; and (3) some behavioral alternatives must confer greater reproductive success than others. When discussing how social living evolved in animals and humans, these criteria therefore need to be considered. Fitness can be explained as the reproductive success of an individual during its lifetime (Dunbar 1982). The more surviving offspring that reach reproductive age, the higher the fitness of the individual. However, as animals share genes with each other, fitness can also be increased by helping relatives to raise offspring. In social living, insects like termites, ants, bees, and some wasps evolution has even gone further so that only one queen in the nest is producing all the eggs and helpers at the nest take care of the eggs and feed the larvae. These insects are called eusocial animals and this is regarded as the highest classification of sociality. In mammals, the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*) are the only eusocial mammals currently known (Jarvis 1981). In the naked mole-rat, one female, the queen, and one to three males reproduce, whereas the others in the colony are workers (Jarvis and Bennett 1993). The other females are sterile, but if the queen dies, another female take over and become reproductive after competition among the females (Jarvis and Bennett 1993).

One can question why animals choose to help each other. However, when an animal is helping its relatives to survive and raise their offspring, an animal increases its probability to get shared copies of its own genes being passed into the future (Mendl and Held 2001). Hamilton's rule (1964) states that "the benefit to the reproduction chances of the helped relative, weighted by the probability that the relative shares the helper's genes, has to outweigh the cost to the helper's own reproductive success incurred through the helping" (in Mendl and Held 2001). Kin selection is when traits are promoted that increases the survival and reproduction of close relatives in addition to those of direct offspring (Maynard Smith 1964). Kin selection may be recorded by using inclusive fitness, which is an individual's own reproducing offspring plus the number of offspring of any

helped relative minus the help received by others to raise offspring (Hamilton 1964). This result in that animals should only help those individuals that it shares some genes with.

However, in some cases, animals also help those that they are not related to, i.e., shares genes with. For example, cooperation to defend resources increases the survival and reproductive chances of all involved. This type of mutual help is called mutualism, and it has been selected for because the fitness of all involved animals increase (Mendl and Held 2001). There are also cases when an individual animal help another animal at a cost to itself, but it does not receive any help in return until sometime in the future, and this is called reciprocal altruism (Trivers 1971). There are risks that helping another individual may never be paid back if animals are not meeting regularly. Therefore, reciprocal altruism has probably evolved when animals live in stable social groups and meet regularly over longer time periods (Mendl and Held 2001). One can summarize this part by proposing that evolution has led animals to cooperate in order to increase fitness, but in order for cooperation to be favored, it has been beneficial for animals to live in more permanent groups.

A review on social evolution in 217 primate species made by Shultz et al. (2011) found that closely related species have tended to organize their societies in the same way. The solitary foraging individual ancestors of primates started staying together as multimale and multifemale aggregations around 52 million years ago, when the ancestors of monkeys and apes split off from the ancestors of lemurs and other prosimian primates. At this time, primates became more diurnal and started to hunt during day time and Shultz et al. (2011) suggest that staying in groups could have decreased the risk of being killed by predators. Today, chimpanzees and baboons live in this type of mixed sex groups. However, gorillas live in harems with one male and multiple females and the New World titi monkeys live in pairs. Living in harems or pairs is a derivative from a second stage of the evolution of sociality in primates occurring 16 million years ago (Shultz et al. 2011).

Humans are suggested to have lived in groups since they occurred as *Homo sapiens* around 200,000 years ago (Roberts 2011). Ancestors to them, *Homo neanderthalensis* (lived 350,000–28,000 years ago), have by archeologists been suggested to have lived in family groups where the males stayed in the family they were born in whereas the females moved to other families when they became adults (Roberts 2011). Human evolution involves the occurrence of at least eight different species during the last two million years, but it is difficult for archeologists to reconstruct how they lived socially. The archeological findings from *Homo sapiens* have shown that as hunters and gatherers they lived in smaller groups that could aggregate to larger groups when there was plenty of food in smaller areas (Roberts 2011). After the last Ice age (11000–4000 years ago depending on place on earth), *Homo sapiens* settled down in more restricted areas and started to grow the land and keep animals. Creating villages with groups of humans living together then became more and more common. Today, millions of people may live in the same city, but then individual recognition is no longer possible.

Benefits and Costs with Group Living

There are many benefits of group living, which may explain why living in groups developed for so many species of animals, including humans. A suggestion of these benefits based on Krause and Ruxton (2002) are:

- Antipredator: many eyes, encounter-dilution, predator confusion, predator swamping, selfish herd effects, defense against parasites, communal defense, predator learning
- Foraging: group hunting, coarse-level local enhancement, public information, information center
- Mate choice
- Keeping warm (heat): reduced heat loss, protection from desiccation
- Reduced cost of transport (movement): in air, on the water, under water

Mendl and Held (2001) suggest that the benefits of group living are:

- Foraging: increased efficiency in detecting, acquiring, and defending food
- Predation: avoiding predation by detection, dilution, and defense
- Thermal regulation in endotherms: especially, small homeotherms can conserve energy by huddling together

Coalition formation in social primates could be another benefit of group living (Dugatkin 1997).

Concerning why early humans started to live in groups, it has been suggested that foraging was one important reason (Roberts 2011). By hunting in groups, they could catch and kill larger prey than one human could manage.

For some species or some individuals of a species, it may be better to live solitary due the costs of group living. A suggestion of these costs based on Krause and Ruxton (2002) are:

- Competition for resource, when more individuals share a finite resource there will be less for each individual.
- Loss of food due to theft by other group members, i.e., kleptoparasitism.
- Aggression between members of the group due to other reasons than foraging.
- Pseudo-interference, i.e., reduced foraging efficiency in individuals that are forced by competition to use poorer feeding sites.
- For sessile foragers, the path that mobile food takes to them can be blocked by the presence of another forager.
- Individuals get in each other's way.
- Prey animals may detect a group of predators more easily and take more effective evasive action.
- Predators may preferentially target larger groups of prey.
- Confusion or interference between fleeing individuals may increase the success rate of predators with increasing prey group size
- Area-restricted search tactics by predators are effective against grouped motionless prey.

- Risk of misdirected parental care when breeding animals are closer to each other.
- Risk of transfer of pathogens when individuals are in closer proximity to each other.

Mendl and Held (2001) consider that some of the following factors may be a disadvantage for group living in animals:

- Resources have to be shared with other group members and defense of resources is negative.
- Groups of animals are more conspicuous both when they are prey animals and predators.
- Increased risk of contact-transmitted parasites.
- Cuckoldry through fertilizations of extra-pair males.

Living in groups may have facilitated the development of more complex social behaviors such as alloparenting, social learning, and helper systems, but we do not know which of these that have been involved in the evolution of group living and which are a consequence of group living (Mendl and Held 2001).

Important Consequences of Group Living for Cultural Development

When animals live in groups, they can learn from each other. This has been called “cultural transmission,” and it can be defined as “the transfer of information from individual to individual through social learning or teaching – both within and between generations of animals (Bonner 1980; Boyd and Richerson 1985). One famous example of cultural transmission is the Japanese macaque monkey “Imo” who learned to wash sweet potatoes to get rid of the sand and where her peers and relatives via social learning also developed the same washing behavior (Kawamura 1959; Kawai 1965). According to (Dugatkin 1997), “Cultural transmission involves a model individual and an observer who learns a specific behavior or response from the model”. If the animal does not learn anything, such as during local enhancement or social

facilitation, it is not cultural transmission. In humans, cultural transmission occurs through social learning and teaching. The main difference between learning by an individual animal or human and cultural transmission is that the latter may be passed on through several generations. This may also be one important reason for why humans evolved and were so successful on our planet (for an overview of human evolution see Roberts 2011).

There are many other areas related to social living in animals and humans that could be discussed, as, for example, social facilitation, synchronization of behavior, learning to interact socially with others, and all aspects of learning in animals that involves transfer of information between group members. Overlapping generations that occur in many animals may also help in the transfer of knowledge from one generation to the next generation. However, the scope of this chapter was to describe different aspects of why animals and humans are living in groups, and I hope the many different aspects of this have been clarified.

Conclusion

Living in groups has evolved through generations because individual animals and humans have benefited from it regarding foraging, reproduction, survival, climatic protection, learning, and for other reasons. In order to manage group life, communication between animals and humans has evolved, and it has been adapted to the species and different circumstances. However, there are also costs of living in groups such as competition for food, reproductive partners and other resources, negative effects of low dominance, increased risk of disease and other risks for the health, and welfare of individual animals and humans. Therefore, animals and humans may choose to leave the group if the cost is higher than the benefits. In human culture, there are so many other aspects of group living which do not occur in wild animals, so one has to be very careful when trying to interpret human behavior in the light of evolution.

Cross-References

► Grouping and Predation

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Local Mate Competition

► Local Sex Ratio

Local Sex Ratio

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Synonyms

Local mate competition

Definition

Ratio of males to females in a local subpopulation, which is not compared to the entire possible population *or* the measurement of females compared to males within a limited sample of a population based on a fixed vicinity relative to the species).

Introduction

Sex ratio is the proportion of males to females in a population. It is often studied on large scales and examined to make inferences concerning an entire population. When examining sex ratio on a localized, specific scale, it is important to recognize the differences between these populations to help indicate what could be causing the variability within different subpopulations of the same species. Genetically speaking, sex ratio should be consistent throughout the entire species and try to achieve a 50/50 balance. But nature is not perfect; external factors from the environment

hinder this balance. Local sex ratio is the measure of those subpopulations of a species, and the “local” is relative to that species and cannot be considered a constant. Fisher’s sex ratio theory explains this in relative cost and gain principles. If there are more females in a population, then it would be in the better interest of the mother to invest more in available males to mate with the abundant females. Similarly, if there are more males in a population, then it would be in the better interest of the mother to invest more in available females to mate with the abundant males. This will eventually lead to a sex ratio of 50:50 in outbreeding populations. However, there are exceptions to this principle. The number of daughters or sons that are born or those that make it to reproduction can be altered in multiple ways. Some, but not many, can control for this through manipulating genetic factors. Species that utilize the method genotypic sex determination (GSD) have sex assignment completely dependent on the genotype – assigned at fertilization (Cook 2002). Environmental sex determination (ESD) is a bit more common but also more easily studied and observed. Species that utilize this method use factors in the immediate environment or the predicted future environment to determine the sex very early in development or decide to foster the well-being of one sex over the other (Kraak and Pen 2002). They will invest in the sex that has a higher propensity to reproduce in the current environment or possibly in the future if predicted conditions are correct. Both methods of sex determination, even genotypic, respond to the proximate vicinity of the individual and the conditions within their niche and usually these mechanisms often coincide. Regardless of how it is achieved, local sex ratio is influenced by some outside factor – be it available mates, temperature, or resource allocation.

Changing Local Sex Ratio by Genotype at Fertilization (GSD)

Different species can determine sex ratio *prior* to birth based on environmental and local factors. These factors may include the number of males or females already present in the population, how

many of those individuals are viable, or resource availability. At fertilization, in most cases, it is the mother that will determine the sex of the offspring, basing her decision on the previously mentioned factors. Various species have been shown to control for sex at conception or during development, primarily insects, such as the common housefly (*Musca domestica*) and the parasitic wasp (*Nasonia vitripennis*).

Controlling of Local Sex Ratio in the Parasitic Wasp *Nasonia vitripennis*

The parasitic wasp (*Nasonia vitripennis*) will alter the sex ratio based on local mating competition. The female wasp will survey the area by detecting chemical signals left by any previous females and will estimate the number of males present in the local region where she will lay eggs – and where her offspring will eventually breed. If the female plans to lay eggs in a host that has been previously parasitized (superparasitized), then she may select to reproduce more males to compete with those males that were previously born. Ultimately, this is to the mother's advantage because if she has more sons that are viable available for hatching females to mate with, there is a better chance that her genes will be replicated (Werren 1980). There are also other factors that could affect the female's bias towards sex. Shuker et al. (2006) found that the emergence time of other broods by other females and the number of other parasitized hosts on the same patch both influenced a female wasp's sex ratio decisions when laying her own brood. These are seen as two other ways that the female is optimizing the chances that her sons will be able to compete with other local mates. The female parasitic wasp is surveying her surroundings and adjusting the sex of the offspring accordingly from the genotypical level, which results in an adjusted local sex ratio for that given population of parasitic wasps.

Changing Local Sex Ratio by Environmental Factors (ESD)

While some species may use the current environment and local population to make assign sex to offspring genetically, others have to leave the

influence towards sex determination to the environment. In these cases, environmental factors, such as latitude, temperature, and air/water composition, will influence the predetermined sex of offspring. Conditions may favor more male development due to signaling that this sex is more viable in these conditions, prompting female offspring to change sex. There are various species, primarily amphibian and reptilian, that practice this type of sex determination.

Influence of Latitude and Water Temperature on the Atlantic Silverside (*Menidia menidia*)

The Atlantic Silverside has a genotype that is acted on by two factors – genetics and environment. The temperature of the water will alter the predetermined sex. This mechanism can be compared between schools found in different latitudes within the same waters to show a difference in sex ratio between cooler and warmer water temperatures compared to those found at a midpoint between the two extremes. Lagomarsino and Conover (1993) examined families within schools of Atlantic Silverside from Nova Scotia and South Carolina to grade how temperature altered sex ratio among these populations. Those in the cooler waters near Nova Scotia saw little influence on sex determination from water temperature, with only 1 of the 23 families examined showing an effect from the cooler temperature. The families in South Carolina (low-latitude population) saw an extremely significant sex determination factor due to water temperature. South Carolina is of a lower latitude which promotes higher water temperatures; all families examined were influenced by these higher water temperatures, which is evident through their sex ratio favoring males and consisting of almost no females. A majority of families in the low-latitude population showed evidence of a shift in sex ratio, suggesting that latitude, and the corresponding water temperatures, causes genetic differences of sex determination. Water temperature plays a major factor due to natural selection – favoring the most “fit” sex to better enhance sexual reproduction. Temperature in the larval developmental stage appears to affect the length of the gestation period – the first born are female, and the second are males. This causes a difference in body size that later on will favor the

female for reproductive success, thus affecting sex ratio (Lagomarsino and Conover 1993).

Temperature-Sensitive Sex Determination in *Emys orbicularis*

The turtle species, *Emys orbicularis*, shows an interesting case of where the sex ratio is affected by the genome as well as directly by the environment. Genes may determine the sex of offspring but that is then limited by influence from the environment through temperature. Entirely phenotypical females will be born when temperatures are above 29.5 °C, whereas entirely phenotypical males will be born when temperatures are below 27.5 °C, regardless of genotypic sex determination. Sex differentiation appears to take place at 28.5 °C, indicating that this intermediate temperature favors the original sex genotype (Zaborski et al. 1988). This is due to the H-Y antigen found in the blood for females being expressed only at certain temperatures regardless of genotypical sex determination (Zaborski et al. 1982).

Changing Local Sex Ratio After Birth and Partial Development

Many species do not have direct influence over the genetic sex determination of their offspring, and therefore, they influence the sex ratio by adjusting care and resources towards the more viable sex. This decision is based on factors within the environment (unpredictability) and resource availability. In an unpredictable environment, one sex may be favored over the other, with the decision of which sex depending on the species. The decision then influences parental investment – resources may be given to one sex over the other due to the environment favoring the vitality of that sex or by practicing brood reduction, focusing on reduction of the less viable sex. In the case for resource allocation, parental investment of resources goes towards one sex over the other, leading the other sex to be negatively influenced.

Brood Reduction and Sex-Biased Provisioning in the Zebra Finch and Crimson Rosella

The crimson rosella (*Platycercus elegans*) will be selective towards the sex that will have the highest

reproductive success in the given, or future predicted, environment. In most cases, this is usually the female chick. Female crimson rosellas usually favor female offspring for the first hatching, causing the sex ratio to be particularly biased towards females. Krebs et al. (2002) found that this is most likely because females can breed within the first year of life and males cannot, making the female chick more immediately successful. Young female crimson rosellas are also a bright green color for their first year of life, making them an easy target for mating. The color may be correlated to reproductive potential; the lighter color being a sign to potential mates that this specific female is young, and therefore may not have hatchlings and most likely has a high reproductive potential. Krebs et al. found that adult males were more likely to breed with subadult females and the opposite, young males with older females, was never the case. An adult female would be biased towards hatching female chicks first to increase her chances of genetic replication through offspring, another cost, and benefit scenario. With all this considered, we can assume the bright green plumage of a young female is acting as a result of sexual selection. It was also hypothesized that male chicks were more common later in the hatching season to eliminate sibling competition between sons (males cannot breed till at least 2 years of age). So, if a male was born early one season and a male was born late in the same season, the younger one would have mate availability disadvantage in the future, and the two sons would ultimately compete for mates. This may also be because males are heavier and mature more quickly, making them costlier than females (Krebs et al. 2002). There are some studies showing that it is possible that available resources greatly affect which sex is provisioned over the other, mainly depending on resources and food supply (i.e., water, seeds availability, seed quality, etc.), especially in zebra finch populations (Burley et al. 1989). The zebra finch (*Taeniopygia guttata*) is a species of bird shown to change the sex ratio through sex-biased laying sequences followed by possible brood reduction. Clotfelter (1996) hypothesized that brood reduction took place through sex-biased provisioning from either parent towards a specific sex, which usually showed

through a father bias for sons. In most cases, this can result in a higher mortality rate of one sex, although in this specific zebra finch population, Clotfelter did not find a bias mortality rate for either sex. The one thing that was noted in this study was that there were more sons born at the beginning of each season, which is suspected to be a retaliation towards inevitable predation – if they have more sons, when a majority die from predators they will still have sons left to reproduce and carry on the family genes. This is most likely a result of the unpredictable environment that these birds tend to inhabit.

Impact on Local Sex Ratio by Experienced Environmental Factors

Humans, similarly to some birds, may select for one sex over the other by using a method of reduction. The Trivers-Willard hypothesis suspects that in times where resources are plenty and the future reproductive stage for offspring looks bright, parents will invest more into their male children. Contrarily, if resources are scarce and future reproductive climate is unpredictable, parents may decide to invest more towards their female children. If resources are available to invest into the child, males are selected for as a “bang for your buck” – males can have more offspring compared to females, which increases the likelihood that the parents’ genes will be replicated. Even with this as a consideration for males, both males and females are limited to the number of offspring they can have in a lifetime, and therefore it is not worth the investment if resources are limited and the environment unpredictable. A study by Davis et al. (2007) showed this phenomenon but only among impoverished Hispanic-Latino populations in a general sample of mothers in Southwestern Arizona. The mothers in this sample were more likely to invest in their daughters when resources were limited, which was indicated by what they regarded as a healthy body size and weight for male compared to female babies. These biases are subconscious and subtle but in some cases may be more severe if negative environmental factors are a heavy influence.

Conclusion

A sex ratio measurement will often times vary among a species based on location but ultimately will work towards achieving an even ratio. While environmental factors may indicate fitness strategies that may increase reproductive success, the genes will always still play a part. In conclusion, every species is attempting different fitness tactics to reach an even ratio of males to females to overall increase the fitness of the entire species – this is just easier said than done, which is why local populations work with what is in the immediate environment.

Cross-References

- [Local Mate Competition](#)
- [Operational Sex Ratio](#)
- [Sex Ratio](#)

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Local Sexual Practice

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Synonyms

[Sexuality in community](#); [Sexuality in neighborhood](#); [Urban sexuality](#)

Definition

Sexuality under norms of a neighborhood or community, including socio-sexuality and adolescent sexual onset.

Local sexual practice, including individual's sexual attitudes and behaviors, could be shaped by many factors, among which local norms and early family environment constitute the two most vital influencing variables.

Norms and Local Sexual Practice

Quite a lot of research indicated Local norms, especially the peer norms, usually exert important

influences on individual's sexual activities. For example, by interviewing with a sample of community young single men, one study (Jacques-Tiura et al. 2015) showed men's sexual violence could be predicted powerfully by the peer group norm that encourage sexual aggression. Another research (Santana et al. 2006) showed adherence to traditional masculine norms would influence men's condom using behaviors.

Actually, the essential role of context on individual's sexual activities has been supported by lots of literature. Based on the multilevel and longitudinal data, research (Browning et al. 2005) showed socioeconomic features of neighborhood context that could exert significant effects on adolescents' sexual activities. Under the context of neighborhoods with low collective efficacy, such as economic disadvantage, residential instability, and racial-ethnic heterogeneity, those who experienced low levels of parental monitoring would show especially high levels of early sexual activities. In addition, a recent research (Kaczkowski et al. 2017) demonstrated that young male who attended to diverse social groups showed a lower level of sexual violence and the effect of social group diversity on men's likelihood to commit sexual violence was partially mediates by male's hostility directed toward women.

The deviant behaviors usually result from the overestimation of the prevalence of these behaviors. One study (Martens et al. 2006) indicated participants tend to overestimate the occurrence of sexual behaviors among their peers. Another research (Kilmartin et al. 2008) also pointed out college males tend to overestimate the level of others' sexism and underestimate their tolerance with sexism. As a result, many social norms-marketing campaigns, which aim at correcting participants' misperceptions by informing them the proper information, have been carried out to reduce individual's deleterious behaviors.

For example, by correcting the cognitive distortions one intervention study (Kilmartin et al. 2008) indicated the level of male's negative attitudes toward female decreased significantly. Another program (Gidycz et al. 2011), which combines social norms and bystander intervention education, found university men in the

intervention program showed a lower level of negative attitudes and behaviors toward sexual aggression compared with those in the control group. Other program (Leone et al. 2017) also supported the important roles of peer norm and bystanders in preventing sexual aggression.

Life History Theory and Individual's Sexual Behavior

According to the Life History theory, in order to pursue the optimal trade-off choices, organisms tend to adopt different life history strategies varying on a slow-fast continuum. People adopting faster strategies would prefer engaging in sexual activities at earlier age, having more sexual partners and building less stable pair bonds (Belsky et al. 1991).

In line with life history theory, one study (Belsky et al. 2012) with large samples demonstrated two dimensions in the environment, harshness and unpredictability, could uniquely predict participants' accelerated life-history strategy, which particularly referred to number of lifetime oral sex and sexual intercourse partners. Based on the longitudinal data, another research (Dishion et al. 2012) also demonstrated that disadvantaged family background at early age predicted powerfully individual's fast strategies, such as early sexual activity, number of partners, unsafe sex, and number of pregnancies or children, through the enhanced role of deviant peer group around them. Other research (Browning et al. 2005) also found parental monitoring would influence girls' timing of first intercourse significantly.

According to paternal invest theory, Draper and Harpending (1982) pointed out the absence of father in early life could exert a vital influence on girl's reproductive strategies. They stated that father-absent females would believe that male parental effort was not essential to reproduction. They would show early expression of sexual interest, engage in sexual activities at earlier age with less discrimination, and also showed poor ability to establish long-term and stable relationship with man. Most importantly, they also stated the timing of pubertal maturation for the father-absent girls would be accelerated.

Conclusion

Local sexual practices can be shaped by local norms and family background at the same time. Individuals usually overestimate the occurrence of deleterious sexual behaviors around them and underestimate the level of their actual sexual activities. By delivering the proper information, the interventions aim at correcting individual's perception and then reducing the level of the deviant behavior. Many intervention programs exhibited ideal effects. In line with life history theory, the existing literatures supported disadvantaged family background at early age could facilitate the selection of fast reproductive strategies, which put the individual at a high level of risk to commit deleterious sexual behaviors. The father-absent girls tend to adopt fast reproductive strategies.

Cross-References

- ▶ [Human Sexuality](#)
- ▶ [Intersexual Selection](#)
- ▶ [Life History Theory](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Robert Trivers](#)
- ▶ [Sexuality](#)
- ▶ [Social Norms](#)

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Localization of Memory Substrates

- [Different Functions of Memory](#)
- [Multiple Memory Systems](#)

Localized Damage

- [Specific Brain Damage](#)

Locomotion

- [Mobility: Crawling and Walking](#)

Logic Game

- [Prisoner’s Dilemma, The](#)

Loneliness in Modern Life

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Synonyms

[Alienation](#); [Digital age](#); [Information age](#); [Isolation](#); [Rejection](#); [Solitude](#)

L

Definition

This chapter delineates loneliness as a universal human condition through the lifespan. This construct is discussed as an individual difference and as a human condition, and explores its evolutionary beginnings. Finally, loneliness is presented as a defining quality of online interactions in the digital age, from chatrooms of the twentieth century to modern-day social networking sites. This chapter concludes with a tentative answer to the decades-old question of whether loneliness is amplified in the digital age.

Introduction

Loneliness may be defined as the distress resulting from a cognitive discrepancy between ideal or desired social relationships and the reality of those relationships. That is, loneliness is experienced when an individual’s connections with friends, family, or romantic partners are less

satisfying than what is desired. The roots of loneliness reach deeply into the very fabric of our society and its constituents – the individuals who conflate isolation and physical removal from others with shame, failure, and rejection. Sadler (1978) wrote that:

we live in a world that is on the move, where people regularly leave loved ones or are left behind. We experience drastic changes that often contribute to the loss of important attachments. We witness regularly the breakup of marriages and families, of communities and neighborhoods, of friendships and working relationships, of organizations and partnerships. (p. 157)

The societal response to these dissolutions forms society’s basic understanding of the phenomenon of loneliness.

Although frequently confounded with isolation or alienation, this phenomenon stems primarily from an individual’s *perception* of his or her integration with a group, rather than the reality. Sadler states that this perception is multifaceted, encompassing the five dimensions outlined in Table 1.

In recent decades, loneliness researchers have continued to operationalize this construct along distinct dimensions that capture its multifaceted nature across social, familial, and romantic domains. Table 2 outlines several commonly used loneliness scales, their distinct dimensions, and example items for each.

Across these widely published and validated scales, it is readily apparent that loneliness is often conceptualized within social psychological literature as an unhappiness with friendships, familial relationships, or romantic relationships;

however, these scales do not tap into the precipitators of – or inclination toward – the experience of this unhappiness. Loneliness may exist as one of two phenomena: (1) a temporary condition brought about by significant life changes (e.g., job loss, relationship conflict) or (2) a more persistent or chronic experience, in which an individual experiences a long-lasting isolation from human contact or socialization. This will explore loneliness as both an acute individual difference and a chronic condition, as an evolved adaption, as unique experiences of loneliness across cultures, and as it exists in a digitally connected world.

Loneliness as an Individual Difference

Because loneliness emerges due to a variety of causes and at different life stages, it is considered a unique individual difference that may appear in many forms across individuals. For example, poor physical or mental health is linked with higher levels of loneliness, whereas individuals of higher socioeconomic status and non-single marital status typically report significantly lower levels of loneliness (Skaff 2008). Furthermore, involvement in organized group activities and higher contact with close relatives are associated with fewer loneliness experiences.

However, many such demographic dimensions may stem from life choices (e.g., physical health, group activity involvement) or life stage (marital status), rather than more stable and unavoidable individual differences. Two such differences on which loneliness might differ are delineated below: gender and age.

Loneliness in Modern Life, Table 1 Sadler’s (1978) five facets of loneliness

Interpersonal	Awareness of separation from individuals
Social	Awareness of being divided in loyalty between competing groups
Cultural	Alienation, anomie
Cosmic	Estrangement from total unity of existence
Psychological	Natural sense of separation stemming from biological individuation

Gender and Loneliness

For decades, a wealth of literature has cited that females from school age to adulthood report higher levels of loneliness than their male counterparts (e.g., Skaff 2008). This is particularly the case when considering females’ higher proclivity toward emotional distress and perceived interpersonal isolation. Whereas females tend to report loneliness as it relates to social domain – friends, acquaintances, and colleagues – males

Loneliness in Modern Life, Table 2 Commonly used loneliness scales

Scale	Number of items	Dimensions	Example items
UCLA loneliness scale	20	Intimate others Social others Affiliative environment (i.e., belonging)	How often do you feel that there is no one you can turn to? How often do you feel that people are around you but not with you? How often do you feel that your relationships with others are not meaningful?
De Jong-Gierveld loneliness scale	28	Deprivation Abandonment Missing companionship Sociability Meaningful relationships	It makes me sad that I lack companionship There is no one who shows a particular interest in me
Social and Emotional Loneliness Scale for Adults (SELSA)	37	Social loneliness Emotional loneliness: Family Emotional loneliness: Romantic	I have friends that I can turn to for information (R) I feel close to my family (R) I have a romantic partner with whom I share my most intimate thoughts and feelings (R)
Differential loneliness scale	60	Romantic-sexual loneliness Friendship loneliness Family loneliness Loneliness in groups	No one in the community where I live cares much about me A lot of my friendships ultimately turn out to be pretty disappointing

(R) denotes a reverse-scored item

show a stronger relationship between loneliness and social experiences with parents and family members. Social network analyses have found that the density (i.e., cohesiveness and interconnectedness) of a social network predicts loneliness only in males, whereas *quality* of dyadic relationships – rather than clusters or groups of individuals – tends to be more important for females.

Age and Loneliness

A wide body of research has found a positive relationship between age and loneliness across the lifespan, with more than a third of older adults in the USA experiencing loneliness. McInnis and White (2001) recorded spoken descriptions of loneliness experiences among widowers living in a senior citizens' apartment complex. The authors clustered over one thousand meaning units into major themes, in which loneliness (1) occurred as a result of the absence of important relationships (i.e., social loneliness described above, or the missing companionship dimension of the de Jong-Gierveld Loneliness Scale)

and (2) accompanied the lost connection with loved ones, both alive and deceased. Old age in particular precipitated a state of anxiety, fear, and sadness stemming from increased dependency on others throughout daily life, which led many individuals to feel as if they were suffering silently, unable to verbalize their loneliness for fear of increasing their burden on others.

But although loneliness is widely perceived as a problem of old age, a growing body of empirical literature suggests that adolescence is the peak age for experiencing loneliness. Adolescent bullying and victimization are widely considered a leading explanation of this trend, and such bullying has been shown to continue to predict loneliness into adulthood (Segrin et al. 2012). Additional factors linking youth and loneliness are depression, low socioeconomic status, proclivity toward aggression, and difficulty with social skills. However, most characteristic of teenage years is the perceived need to conform with peers – a need that is linked with strong experiences of loneliness during this life stage in particular.

Lastly, loneliness can exist as a property of the organization, rather than exclusively of the individual. During the occupational life stage (i.e., post-college and pre-retirement), employees may experience workplace loneliness due to the perceived inadequacy of interpersonal relationships with colleagues and other professionals (Wright 2015). In addition, due to the closely tied nature of most workplaces, loneliness can spread in a contagion effect beginning with a single openly lonely individual. Research has not yet demonstrated a link between loneliness in the workplace and in adolescence or older adulthood.

Loneliness as a Chronic Condition

Loneliness does not exist solely as an acute individual difference but also as a more permanent experience traversing many life stages due to underlying conditions. Loneliness has been associated with mental illness and anxiety (Cacioppo and Patrick 2008) and has been shown to underlie aggression, domestic violence, murder, post-traumatic stress disorder, and suicide. Lonely individuals are more likely to be high in negative affectivity, to act in a socially withdrawn fashion, and to lack trust in the self and others around them. Furthermore, these individuals tend to feel little control over their success or failures and report low satisfaction with personal relationships.

As was stated at the beginning of this , loneliness as a construct is often confounded with the simple state of being isolated or alone; however, when considered as a chronic condition, it is especially necessary to view it as a series of psychological responses to the state of isolation. There is a crucial distinction between the *painful* and the *enriching* dimensions of being alone, depending solely on how the individual chooses to interpret his or her isolation. As such, these chronic precipitators of loneliness should be considered as related phenomena, in which chronic anxiety, depression, negative affectivity, and social withdrawal may be linked with a proclivity toward interpreting isolation in a negative, rather than positive or enriching, fashion.

Antidotes to Loneliness

Not surprisingly, loneliness has become a symbol of depression in global societies – a precursor for agoraphobia (i.e., the extreme fear of public places) or social anxiety. Because it has been linked with mental illnesses and harmful or unhealthy behaviors (e.g., smoking, addiction), loneliness has become synonymous with an aberration or mental disorder – a shortcoming, rather than a human experience. It could be argued that loneliness is – and has always existed as – a universal human condition of varying degrees of severity.

In turn, Mijuskovic argues that loneliness is closely tied with consciousness, in that conscious awareness of the sources and signs of loneliness may help inform individuals of how to avoid isolation and seek social contact. It is through a conscious evaluation of the lonely experience that individuals may partake in any given “antidote” to loneliness, such as seeking a sense of belonging, togetherness, or intimacy with one or more people. This search for belonging is often fostered by empathy as a driving force of connection with other people – that is, sharing lived experiences with family or friends who understand loneliness as a universally shared condition.

The drive to avoid loneliness in search of intimacy and social proximity is possibly the most powerful psychological need of human beings and may have remained so for hundreds of thousands of years.

Loneliness in Evolutionary Beginnings

Loneliness may be considered an individual’s natural response to particular situations across the lifespan, rather than a sign of weakness. Indeed, scholars who support this idea cite a wide array of findings that point toward an innate, biological, and possibly adapted aversion to loneliness and social isolation.

In an illustrative study of the *ball toss paradigm*, Zadro, Williams, Sommer, and colleagues instructed participants to take part in a three-person activity in which they were to toss a ball back and forth with two group members.

Unbeknownst to the participant, his or her fellow group members were confederates instructed to follow a prearranged script, in which after several rounds of ball tosses, the confederates exclude the participant by only tossing the ball between each other. Regardless of self-esteem and personality attributes, the researchers found that participants responded within only a few minutes with negative affect, predominately with anger and sadness. Notably, female participants sought to regain a sense of belonging upon being isolated, demonstrating higher nonverbal engagement with the confederates. Male participants, on the other hand, sought to regain self-esteem by disengaging more quickly and appearing disinterested in the game (Zadro et al. 2004).

The ball toss paradigm has since been replicated in an online environment, in which participants were instructed to toss a ball between two other players, who were believed to be actual participants on other computers but were, in fact, programmed players. fMRI results suggest that even when participants are told that their group members are programmed, responses to social isolation are far from trivial: Researchers found that the emotional region of the brain that is activated in these paradigms (i.e., the dorsal anterior cingulate) is the same region that responds to physical pain (Kawamoto et al. 2012). In other words, the physiological response accompanying the experience of loneliness and isolation mirrors that of actual harm. Further research in this area has illustrated that even innocuous and brief examples of ostracism – and, indeed, even by despised others (with whom the individual logically should *not* desire close contact) – are related to physical pain and psychological distress, possibly because humans have evolved to accurately detect and avoid ostracism.

Further evidence of physiological responses to loneliness are evident in DNA and mortality research. A meta-analysis of findings related to loneliness and mortality found that actual and perceived social isolation are associated with an increased risk for early mortality (Holt-Lunstad et al. 2015), although it remains unclear whether perceived (but not actual) social isolation may be linked with a proclivity toward negative affect,

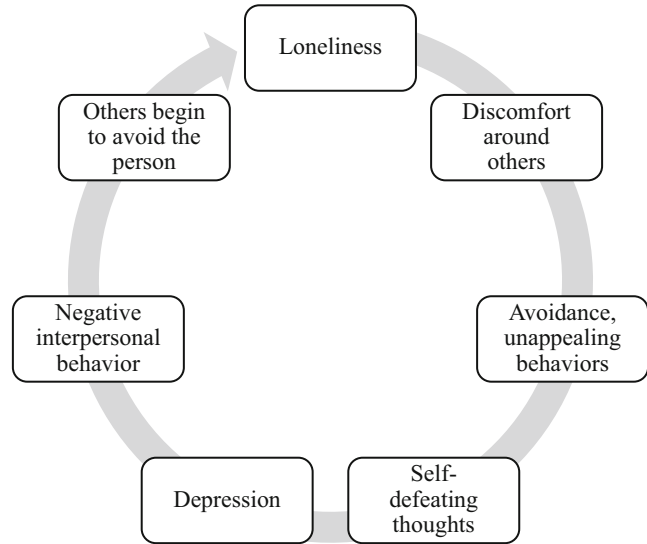
depression, and social anxiety which may, in turn, partially account for this finding. In addition, the mere experience of social isolation has been found to impair DNA transcription in human immune cells, which disrupts thinking, willpower, and perseverance, as well as the ability to read social signals and monitor social skills (Cacioppo and Patrick 2008).

This process, in which social isolation begets loneliness and loneliness inhibits social abilities, is a well-studied finding encapsulated within the self-perpetuating cycle of loneliness and depression (Kenrick et al. 2014), as illustrated in Fig. 1.

This seven-staged cycle shifts from (1) the mere experience of loneliness to (2) a heightened uneasiness around others, particularly those with whom a close relationship has not yet been established (i.e., acquaintances, new partners, coworkers). To circumvent this discomfort, individuals begin to (3) avoid social contacts, and when avoidance is impossible (e.g., in the workplace), unappealing behaviors may surface during interactions – behaviors that, in the modern day, one might refer to as “social awkwardness” stemming from socially evoked anxiety. Among individuals who are aware of this increase in social anxiety, (4) self-defeating thoughts ensue – thoughts that reinforce their fears of loneliness and isolation – which, over time, transform into (5) the experience of depression. Not only does depression predict chronically low mood and (relatedly) low affect, but it also predicts low energy or interest in pursuing sociable activities. It is at this point in the cycle that one witnesses a direct relationship from perceived isolation to active avoidance of social contact, and it is this evasion of contact that predicts (6) negative interpersonal behaviors such as rejection of attempted contact, outward displays of irritation or anxiety, and expressions of guilt, shame, or hopelessness when with others. As a result of these negative interpersonal behaviors, (7) social contacts often begin to avoid the individual, which only furthers (1) the original feeling of loneliness – and thus the cycle continues in a downward spiral.

Returning to the argument posed by Cacioppo and Patrick (2008), however, such a cycle need not be explained exclusively in psychological

Loneliness in Modern Life, Fig. 1 The self-perpetuating cycle of loneliness and depression



terms; in fact, a key argument in the evolutionary realm might suggest that the impairment of DNA transcription occurring in even the earliest stages of this self-perpetuating sequence may jointly contribute to the cycle's later stages.

An Ultrasocial Species

The question that then begs to be asked revolves around the role of loneliness in the human experience. If one were to argue that loneliness is an evolutionarily adaptation, what must follow is a broad understanding of the functions it serves in specific habitats. Cacioppo and colleagues argue for one such example, in which social-environmental factors such as low social support trigger an evolved aversive signal, which draws attention to the varied social risks that loneliness might pose. This signal is particularly important when faced with situations across the lifespan that require social support, such as early and end-of-life dependence on close others. Among mothers, the absence of social support may result in a shortage of child-rearing options or might limit access to food, shelter, and protection from harm during early motherhood. In support of this argument, experimental manipulations of loneliness have yielded an increase not only in depressive symptomatology but also perceptions of unsafety: In times of loneliness, fear and decreased self-esteem jointly predict a heightened caution of

perceived threats in the surrounding environment. Self-esteem in particular is a noteworthy association with loneliness due to its function as a gauge of exclusion and self-confidence, variables that are intricately tied with modern-day conceptualizations of loneliness and isolation.

What follows from this key argument is an *evolutionary model of loneliness* (Cacioppo and Patrick 2008), which argues that when an individual experiences loneliness, a feeling of unsafety should ensue due to an anachronistic survival mechanism that intensifies sensitivity to social hazards. Humans are, in every sense of term, an *ultrasocial species* in the sense that collaboration and cultural identification (e.g., with norms, conventions, institutions) are remarkably strong influences on the ways that humans relate to one another. This ultrasociality is important because for evolutionary ancestors, survival did not necessarily depend on brute strength but rather on the ability to form bonds and collaborations with others; the idea of “strength in numbers” is personified in humankind’s ancestral past. The literal, physical pain associated with loneliness may, therefore, trigger a fear response so disruptive in everyday functioning that it urges the individual to avoid loneliness and seek sociality, no matter the outcome.

A question that might logically follow this insight is why, if ultrasociality was a key ancestral

goal, ostracism existed at all. Many evolutionary theorists have suggested that humans, like social animals including bees, ants, and primates, use ostracism as a tool for social control. Ostracism and social isolation therefore manage deviant or troublesome members of the group by motivating such members to obey norms and contribute to the broader collective. Should these members respond to ostracism with a drive to reaffiliate with the group, the final outcome would be a positive one: Group strength would increase as a product of cohesiveness and the pursuit of a common goal. As such, one component of Cacioppo and colleagues' evolutionary model of loneliness is called the *reaffiliation motive* (RAM), which represents an individual's motivation to reconnect with others – a motivation that is often triggered by perceptions of social isolation.

The Heritability of Loneliness

A second argument for an evolutionary understanding of loneliness revolves around the theorized heritability of loneliness. Researchers have argued that heritability can differ by environment, individual differences such as age or gender, and genetic predisposition to loneliness; furthermore, the expression of genetic factors associated with loneliness may change over the lifespan, potentially accounting for differences observed between children and older adults (Cacioppo and Patrick 2008). Goossens et al. (2015) argue that several genes may account for loneliness, either through immune system functioning or the expression of particular neurotransmitters. Regarding the immune system, past research suggests that the human body functions less efficiently among lonely individuals – an indicator of an impaired or weakened immune system. Furthermore, receptors – chemical substances that are sensitive to a particular neurotransmitter or signaling substance (e.g., dopamine, serotonin) – of *oxytocin* have been linked with prosociality, trust, and social awareness. As such, the oxytocin receptor gene reflects qualities not often seen in lonely individuals as per the evolutionary model of loneliness (i.e., high sociality, trust, social awareness) and therefore stands as a promising genetic marker of the expression of loneliness. Returning to an

earlier mention of social-environmental factors (e.g., low social support) that may trigger feelings of loneliness, it would therefore follow that gene-environment interactions might lead genetically predisposed individuals to feel an increased sense of loneliness when exposed to hostile or isolated situations.

Loneliness and Attachment

Also contributing to the heritability argument of loneliness is the oft-cited link between loneliness and *human attachment styles*, distinct classifications of dynamic long- and short-term interpersonal relationships. These classifications stemmed from a classic study in 1978, when Mary Ainsworth separated infants from their mothers and observed their reactions to the presence of a stranger and, subsequently, to their mother's return. These observations distinguished three clear patterns of response: (1) secure, in which infants respond with minimal distress to a mother's absence and warmth to her return; (2) preoccupied, in which infants remain anxious upon her return, as though wary of future abandonment; and (3) avoidant, in which infants display little emotional response to either stranger or mother.

In the decades since, psychologists have hypothesized that attachment behaviors characterize and define human beings from the cradle to the grave – that is, attachment to primary caregivers might generalize to other prominent relationships formed throughout the lifespan, including adult friendship and romantic love. An attachment relationship is, therefore, an enduring social relationship underscored by expectations of responsiveness and support, which mutually provide confidence to explore and develop independence throughout the lifespan.

To summarize attachment theory, secure, preoccupied, and avoidant attachment styles differ along two key dimensions: anxiety and avoidance. Table 3 illustrates these distinctions, further separating Avoidant attachment by low anxiety (dismissive; the disinterest in social contact) and high anxiety (fearful; the active fear of social contact). Not coincidentally, loneliness has been tied to both anxiety and avoidance, as was

Loneliness in Modern Life, Table 3 Dimensions of human attachment styles

	Low anxiety	High anxiety
Low avoidance	Secure	Preoccupied
High avoidance	Avoidant (dismissive)	Avoidant (fearful)

illustrated in Fig. 1 and which furthermore may stem from gene-environment interactions. It would appear, therefore, that loneliness has roots in childhood and early attachment processes – a theoretical mediation effect in which attachment styles and cognitive mechanisms may partially account for the relationship between loneliness and basic attachment theory.

Supporting a theory of parent-child origins of loneliness, researchers have found that peer attachment strongly mediates the relationship between parental attachment and loneliness (Bogaerts et al. 2006), in which parental attachment – known to influence peer and romantic attachment styles later in life – thereby plays a role in an individual’s experience of loneliness. Although one study found no direct relationship between parent and child loneliness, the researchers did observe a decrease in peer-evaluated cooperation skills among daughters of lonely parents. This decrease, in turn, predicted higher levels of loneliness (Junttila and Vauras 2009). Similarly, Henwood and Solano (1994) found that parents’ loneliness negatively impacts children’s use of relationship-enhancing strategies, such as a willingness to attribute positive factors to a partner’s disposition, and negative factors to the broader situation at hand.

Historically, loneliness has been linked with attachment styles across the lifespan as a function of attachment insecurities (i.e., anxiety and avoidance). High attachment insecurities have been associated with low levels of trust, relationship satisfaction, and closeness – factors also tied with loneliness as per the evolutionary model of loneliness. Laboratory studies of social interactions have found that individuals high in attachment insecurity tend to engage in interactions that are lower in intimacy and warmth (Black and

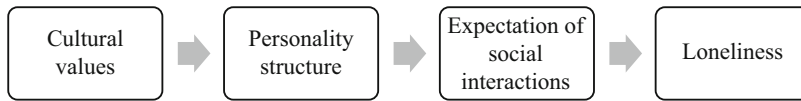
McCartney 1997). As such, it could be stated that the instability of personal relationships among insecurely attached individuals is closely linked with the subjective experience of loneliness. Furthermore, children of parents who socially isolate themselves or are unresponsive to the needs of family members (i.e., symptoms of loneliness) are more likely to develop such attachment insecurities early in life, thereby contributing to a chronic level of vulnerability to loneliness.

Summing across extant literature on the underlying genetics of loneliness, a question that therefore begs to be asked is whether loneliness is actually inherited. Although certain gene expressions may predict a proclivity toward trust and sociability – qualities lacking among chronically lonely individuals – it is clear that environmental characteristics also play a key role in the development of loneliness early in life. Next is presented a body of literature that considers loneliness as a cultural phenomenon, moving from potential gene-environment interactions to a determining factor that is predominately environmental.

Loneliness Across Cultures

A *culture* is defined as an amalgamation of characteristics that not only influence the attitudes, beliefs, and behaviors of a particular social group (e.g., geographic, ethnic, socioeconomic) but that also give unique meaning to various life experiences. Often, cultures are defined through geographic boundaries as a simple function of mobility: Historically, social groups remained relatively isolated from one another with the exception of trade and conflict. In their isolation, these social groups shaped norms, traditions, and values that collectively formed distinct cultures, which set them apart from other groups. Although genetic expression may be highly correlated within any particular group, the cultural environment itself poses many influences on the physical and mental attributes of its members.

Regarding loneliness in particular, Yang and Victor (2011) found that the country in which a person lives shows a greater impact on reported



Loneliness in Modern Life, Fig. 2 Johnson and Mullins' (1987) comparative perspective of loneliness

loneliness than age, which has proven a significant predictor for decades. Whereas Northern European nations (i.e., Scandinavia, Ireland) report the lowest levels of loneliness (i.e., accounting for 6% of individuals), citizens of Russia and Eastern European countries show the highest levels (10–34% across age groups).

One potential explanation for cross-cultural differences in loneliness may stem from a theory posed by Johnson and Mullins (1987), displayed as a process model in Fig. 2. This comparative perspective model outlines a process in which cultural values lend themselves to the development of – and proclivity toward particular – personality structures, which in turn predict expectations of social interactions. The first sentence of this defined loneliness as the distress stemming from a discrepancy or mismatch between an individual's ideal social relationships and the state of his or her actual relationships. Should a person hold high expectations of what constitutes friendship or romantic relationships, and should these expectations not be met (i.e., a deficit in the quality or quantity of a person's desired sociality), loneliness may ensue.

Johnson and Mullins therefore conceptualize a *loneliness threshold* or the minimum level of social contact that an individual requires to *not* feel lonely. The lower the threshold, the higher an individual's proclivity toward loneliness; and should a culture emphasize high expectations of social interactions, members of that culture may be at a heightened risk for experiencing loneliness across the lifespan. Indeed, hypotheses of cultural incongruity support this perspective, in which members of one culture may experience loneliness due to high exposure to a second culture with a different loneliness threshold. More specifically, industrialization itself might explain the curiously high levels of loneliness among elders of recently industrialized cultures. Cultural

ideals of privacy, which have stemmed from Western ideology, may be jarring to members of older and more remote generations. There is, for example, no natural word for “privacy” in Russian: As Eastern European countries have adapted to Western ideals in the past century, increasing levels of loneliness among older generations may be partially explained by this disconnect between old and new.

As such, in the consideration of cross-cultural differences in loneliness, future research should examine the factors that predict social satisfaction as it relates to culturally defined social ideals. Specific to Russia and Eastern Europe, which report the highest levels of loneliness currently on record, researchers cite the dramatic sociopolitical changes that have taken place since the late 1980s as one key cause. For one, younger generations have been encouraged or even forced to emigrate to more prosperous countries, leaving family and friends behind in pursuit of a career. Those who are left behind may consequently report higher levels of loneliness, as has been found among the elderly in China (Yang and Victor 2011). For another, with sociopolitical and economic changes come transformations in the mere definition of social relationships, including expected norms, behaviors, and values. Disconnects with these newly developed social norms may lead to a sense of cultural isolation or ostracism, which may in turn predict loneliness.

Although cross-cultural research on loneliness is sparse beyond Western borders, much research has investigated *hikikomori* in Japan, a phenomenon of extreme social isolation spanning months or even years. Hikikomori, which describes both the social isolate (i.e., as a human) and the social condition of isolation, has been found to stem from dismissive-avoidant attachment styles, oxytocin levels, low social skills, lack of perceived social support, and – in some cases – the

occurrence of a stressful event, lending further credence to the argument for genetic predispositions toward loneliness (Teo et al. 2014). Similar cases of severe self-prescribed isolation have also been documented and researched around the world, including South Korea, France, Oman, Spain, and the USA – countries whose expectations of social relationships may engender distinct loneliness thresholds that have yet to be studied empirically.

Next the impact of a particular form of culture on the expression and experience of loneliness must be considered – namely, *digital culture* or the culture that emerges from the use of information and communication technologies (ICTs).

Loneliness in the Digital Age

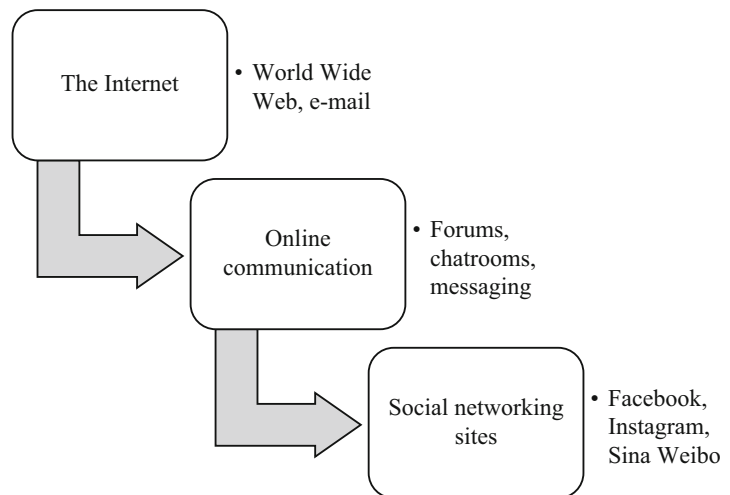
It could be argued that the evolutionary purpose of speech has, throughout history, been the formation and maintenance of social intimacy. The mere act of speech with others allows humans to learn about social contacts and whether they are worthy of trust and collaboration. Social conversation, therefore, has been a cornerstone of community and social organization since the emergence of human life.

However, humans now live at the precipice of a social world that is changing rapidly, and theorists from Sherry Turkle to Clay Shirky now posit that

ICTs are beginning to eclipse human pillars of social intimacy. Such theorists – whether they be cyberpsychologists, cyberneticists, or philosophers – now state that humans are less emotionally fulfilled and more isolated by the same ICTs that have promised for decades to bring them together. (Even so, it deserves noting that Locke predicted the invention of voicemail to be a key culprit in this transition, a prediction that has yet to be realized.) These scholars state that society runs the risk of depersonalization due to an excess of information available at every moment – information that provides human-to-human conversation without necessitating face-to-face contact.

Since the introduction of ICTs into daily life, many have wondered whether the digital age would pose more benefits or detriments to loneliness, social isolation, and mental health – that is, whether online connection would drive down offline connection. This question illustrates the *Internet paradox* (Kraut et al. 1998) or the phenomena by which the Internet is largely used for social interaction but has also been linked with social isolation (i.e., the lack of social interaction), and – among heavy users – depression. In this section, the relationships between loneliness and the Internet, online communication more broadly, and social networking sites (e.g., Facebook; see Fig. 3) are discussed, as well as competing models of Internet use and loneliness.

Loneliness in Modern Life,
Fig. 3 Specification of levels of ICT use



Loneliness and the Internet

As was illustrated in Table 2, the Social and Emotional Loneliness Scale (SELSA) differentiates between social loneliness (i.e., missing companionship) and emotional loneliness (i.e., the inadequacy of familial or romantic relationships). Researchers who have applied the SELSA to Internet users have found that high levels of Internet use are associated with low levels of social loneliness, possibly because such use fulfills these social needs; however, high levels of Internet use are also related to increased emotional loneliness, possibly because those who invest exaggerated amounts of time on online friendships have neither time nor resources to invest in offline relationships.

On the one hand, researchers have found a significant positive correlation between loneliness and Internet use among college students, with males reporting higher Internet use and higher loneliness (Hughes 1999). This relationship is exaggerated among students reporting excessive Internet use, compared with those who exhibit more moderate levels of use. On the other hand, sheer hours of Internet use had no impact on loneliness over time, but rather psychological dependence on the Internet. As such, it is evident that the Internet itself is not harmful, but is rather a tool; heightened compulsions or neediness related to the online world as an escape may be symptoms of related, but separate, conditions (e.g., Internet addiction).

The question that therefore begs to be asked is whether the origin of loneliness – online as opposed to offline – plays a role in Internet use. Odacı and Çelik (2013) found that loneliness while offline does not predict problematic Internet use and, furthermore, this loneliness is not necessarily predictive of social interactions online. In fact, one study found that individuals who score higher on loneliness are more likely to use the Internet for computer-based entertainment and to obtain information about the entertainment world (Whitty and McLaughlin 2007). As such, loneliness while offline might beget – or at least not contest – loneliness online among individuals who use this social tool for predominately informational purposes.

Loneliness and Online Communication

With regard to the Internet as a social tool in particular, a notably smaller body of research has investigated the relationship between computer-mediated communication and loneliness. Although no relationship has been demonstrated between mobile phone use and loneliness among average users, research has pointed to a mediation effect in which loneliness partially accounts for the relationship between social support or social skill deficits and cell phone addiction (Jin and Park 2013). However, Hu (2009) has noted a temporary increase in loneliness after chatting with others online compared with individuals assigned to engage in face-to-face interaction; furthermore, this effect was exaggerated among individuals with high trait loneliness. A second study followed up on these findings by distinguishing between the target of communication as a stranger or known other. In a sample of middle school students, no relationship was observed between online communication and loneliness when communicating with strangers; but contrary to expectations, researchers saw a negative impact on loneliness when chatting with familiar others (e.g., classmates, friends; Li et al. 2013).

This finding may be partially explained by research conducted by Ong et al. (2011), who found that students who spent more time chatting with familiar others online exhibited greater familial loneliness (i.e., as per the SELSA) due to reduced time spent in familial relationships. However, these individuals showed decreased romantic loneliness due to the increased ease of maintaining romantic relationships online, even in the absence of face-to-face contact. Indeed, loneliness may be a byproduct of excessive ICT use because time investment in online relationships comes at the expense of offline relationships.

There are, however, situations in which online communication may pose more benefits than detriments between friends. Internet use may allow anxious children and adolescents to fulfill critical social interaction needs through self-disclosure in an online, physically removed setting that might otherwise feel too threatening in the physical world.

Loneliness and Social Networking Sites

As social networking sites (SNS) such as Instagram and Sina Weibo have reached an alarming percentage of the connected world, research on the effects of SNS use on a plethora of psychological variables has also increased at a rapid pace. Regarding loneliness and self-disclosure in particular, individuals scoring higher in loneliness tend to be more likely to disclose personal and relationship information online, whereas those lower in loneliness tend to disclose personal views (Al-Saggaf and Nielsen 2014). This distinction may be due to a deep-rooted fear of disclosing potentially objectionable opinions and driving away social contact, whereas fact-based information may foster connection without risking objection. Furthermore, lonely individuals on Facebook often engage in positive self-disclosure less but negative self-disclosure more, often in hopes of engendering socially supportive responses from contacts (Jin and Park 2013). Lonely individuals therefore view Facebook as more useful for self-disclosure and social connection than individuals who are not lonely, but their satisfaction while on Facebook is often lower than that of their counterparts – possibly due to a heightened focus on negativity while engaging with friends. Lastly, individuals with access to the Internet but *without* a Facebook account tend to score higher on loneliness; whether this difference is an indication of causal effects or individual differences remains to be investigated.

Although a wealth of research has linked passive Facebook use (i.e., scrolling through news feed) with social comparison and lower self-esteem, much less research has investigated the link between SNS use and the related, but distinct, variable of loneliness. Below, this body of work is separated by the relationship (positive, negative, or neither) demonstrated between SNS use and loneliness.

SNS use increases loneliness. Supporting the argument that SNS use increases loneliness, Schwartz (2011) did indeed observe a positive relationship between loneliness and both Facebook use and Facebook posting behaviors among college students. However, self-esteem

may have confounded this relationship (i.e., due to its historically strong positive relationship with loneliness): Schwartz also found that college students with low self-esteem posted more frequently on Facebook and used Facebook for longer periods of time, while also attributing Facebook more heavily as a key presence in their social lives.

A 2010 survey of more than 1,000 individuals yielded more mixed findings: Although users who engaged in directed interaction with friends (e.g., wall posts, direct messages) reported lower levels of loneliness, those who engaged in passive use without engaging in interaction were more likely to report increased levels of loneliness (Burke et al. 2010). Contrary to expectations, lonely individuals tend to have more Facebook friends than those who are not lonely, possibly as a form of compensation for perceived deficits in offline sociality.

SNS use is not related to loneliness. In a meta-analysis of almost 9,000 individuals across 18 studies, Facebook use did not adequately explain variation observed in loneliness (Song et al. 2014). This null effect is worthy of note due to its lack of bias toward any particular sample characteristic (e.g., college setting, age, ethnic breakdown), researcher bias, or validity of the operationalization of ICT use or loneliness. When averaged together, the *lack* of a signal (in either direction) should be telling.

SNS use decreases loneliness. Lou (2010) found that Facebook intensity may reduce perceived levels of loneliness, regardless of motive for using Facebook (e.g., social, informational); furthermore, both Facebook intensity and motive for use were associated with increased offline friendship.

It is important to note that the research cited above is cross-sectional – that is, causality cannot be inferred based on a positive or negative relationship alone. Whether lonely people are drawn to Facebook or Facebook actively causes loneliness is a distinction that cannot be made through correlational methods alone. However, in 2013, Deters and Mehl experimentally manipulated Facebook use to observe changes in loneliness that could conclusively be attributed to SNS use.

Half of participants were randomly assigned to post more heavily on Facebook than usual, while the other half were given no instructions regarding Facebook use. The researchers found that individuals who posted more frequently exhibited reduced loneliness, partially due to an increase in social connection. This decrease in loneliness remained a robust finding independent of whether individuals had received direct social feedback from friends online.

Competing Models of ICT Use and Loneliness

With the exception of Deters and Mehl (2013), a vast majority of the previously cited research has been unable to tease apart causality due to exclusively correlational methods. Although a few scales have been developed to measure loneliness as it relates to the online world (e.g., the Virtual Environment Loneliness Scale, see Table 4; Usta et al. 2014), most studies have paired responses to inventories such as the UCLA Loneliness Scale with self-report measures of Internet and Facebook use (e.g., *How many hours per week do you use the Internet?*) – a methodology that may yield misleading results due to social desirability biases (e.g., a hesitation to report very high levels of use or loneliness), inaccurate memory for use, or differing definitions of what constitutes Internet or Facebook use (e.g., e-mail, text messaging, Messenger as a distinct entity from Facebook).

Loneliness in Modern Life, Table 4 The virtual environment loneliness scale (translated from the original Turkish)

Dimension	Example items
Virtual socialization (Sanal Sosyalleşme)	I have a lot in common with the people around me when online When online, I feel in harmony with people in my social circles
Virtual sharing (Sanal Paylaşım)	I'm much more comfortable online than in real life I trust my online friends more than my friends in real life
Virtual loneliness (Sanal Yalnızlık)	Nobody knows me very well online I find it difficult to express myself online Compared with the real world, I am often misunderstood online

A second problem with many studies previously reported is an underlying assumption that Internet users are a homogenous group, without taking individual differences into account. Amichai-Hamburger and Schneider (2014), for example, cited personality as a key variable in which SNS use might differ: Mirroring their offline reality, introverts tend to have smaller social networks online compared with extroverts; however, they also take greater care in tending to their online profiles. To their benefit, introverts often find ways to compensate for their social preferences through online communities, including leveraging asynchronous communication to avoid the potentially tiring impact of face-to-face, synchronous contact. Furthermore, social anxiety may act as a confounding variable in the relationship between loneliness and preference for online social interaction; although such a preference may be linked with loneliness, it may also be a function of the social anxiety demonstrated by lonely individuals.

To address these gaps in extant literature, there exist two competing models of Internet use and loneliness that draw this distinction, examining whether lonely people use ICTs differently, or whether ICTs cause loneliness. More specifically, Kraut et al. (1998) argue that Internet use leads to loneliness, whereas Amichai-Hamburger argues that lonely people tend to spend more time online. The latter of the two groups of researchers causally tested both models, in which (A) neuroticism (as one key personality factor) leads to social use of the Internet, which leads to loneliness or (B) neuroticism leads to loneliness, which leads to social use of the Internet. Of the two models, model (B) emerged significant, suggesting more conclusively that lonely people tend to use ICTs more heavily, especially among women.

This study was among the first to challenge the (still predominant to this day) notion that ICT use predicts loneliness in the digital age, regardless of the prevalence of correlational research supporting this claim. These contradictions are succinctly demonstrated in one study by Morahan-Martin and Schumacher (2003), who found that although lonely individuals used the Internet and e-mail with higher frequency, they



were also more likely to use the Internet to secure emotional support; although these individuals were more likely to make friends online and, what's more, to report higher satisfaction with those friends, they were also more likely to use the Internet as a means of modulating negative mood. Finally, and as a result of their motives for Internet use, lonely individuals were more likely to report that their Internet use – although supportive, although friendly, and although satisfying – caused disturbances in their offline functioning, such as interfering with social activities and work.

This compilation of findings summarizes many key points made by decades of research on the issue: Although it does not appear that ICT use causes loneliness, it is difficult to say conclusively that lonely people are more strongly drawn to ICT use. Future research must first take into account the varying effects of individual differences, gene-environment interactions when interacting with the online world, and attachment-related predispositions toward loneliness. Although there are certainly situations in which Internet and SNS use may ameliorate the negative effects of loneliness – for example, fostering social connection even in the absence of face-to-face contact – there are also situations in which ICT use may worsen these effects, as in the case with heavy use and replacement of offline relationships for online interactions.

Conclusion

To conclude, therefore, research suggests that ICTs are nothing more than a tool for communication that is best used in moderation. Although lonely individuals may enhance and expand their social network through online communication, it is also possible that extended time spent on ICTs will limit the ability to enhance existing offline ties. Moving forward, this body of research would benefit from shifting from a predominately cross-sectional methodological base to an experimental or longitudinal focus to better understand the causal effects of loneliness on ICT use and, in some situations, the effects of ICT use on

loneliness. Furthermore, research beyond Western borders is immensely scarce: To be able to make cross-cultural comparisons, researchers must first explore the relationship between ICT use and loneliness in nations or social groups where both variables – whether operational or psychological – may appear and manifest entirely differently. Finally, researchers should consider the use of ICTs to combat experiences of loneliness across age groups and backgrounds; the structured use of social networking sites, online communication venues, and the Internet in general may help ameliorate the negative impacts of loneliness within specific populations that are more vulnerable to depression, anxiety, or ostracism.

This has discussed loneliness in its most basic form as defined by societal aversions to alienation, loneliness as both an individual difference and a chronic condition, and loneliness as an evolved adaption and product of cultural variation. Stemming from this prerequisite discussion, correlational, experimental, and meta-analytic research has been presented that underscores loneliness as it exists in the digital age – an age of sociality and solitude, of connection and isolation. Although it may be a stretch to state conclusively that human-kind now exists “alone together,” it is certainly possible that technology may – in some forms and for some individuals – magnify the experience of social isolation. But it is equally possible that technology can form relationships where there were none that it can foster friendships that would otherwise have been impossible given predispositions toward loneliness, social anxiety, or self-doubt. Wherever technology may drive people apart, it also has the unique power to drive them together; and for those most in need of social connection, it may have a substantial amount to offer.

Cross-References

- ▶ [Adaptations to Avoid Ostracism](#)
- ▶ [Attachment in Adulthood](#)
- ▶ [Bullying](#)
- ▶ [Cross-Cultural Differences](#)
- ▶ [Evolutionary Social Psychology](#)
- ▶ [Friendship and Modern Life](#)

- History of Attachment Theory
- John Bowlby and Attachment Theory
- Peer Rejection

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Longevity

- [Darwinian Medicine and Survival Problems](#)
- [Survival and Death](#)

Long-Term Growth Rate

- [Reproductive Value and the Evolution of Aggression](#)

Long-Term Mating

- [Violation of Long-Term Mate Preferences](#)

Long-Term Mating Strategy

- [Relationship Choices and Sexuality](#)

Long-Term Memory

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Synonyms

[Long-term storage](#); [Long-term store](#)

Definition

Long-term memory is thought to be of unlimited storage capacity and can hold information for a very long time.

Introduction

The ability to learn and remember is essential for survival. Over the course of an organism's life, numerous events take place that have an impact on both the organism, its expectations for the future, and its ability to thrive. Although cases of tremendous ability to remember events have not been associated with great fortune or happiness (Parker et al. 2006), memory is an integral part of our personalities and our life stories. In this section, the nature of long-term memory (LTM) will be discussed in relation to the modal model of memory (Atkinson and Shiffrin 1968). It is now established that LTM is not a unitary structure in which all information is kept, but that it is a very diverse system involving different types of information and various brain areas (Squire 2004). Research has shed light onto the characteristics of the different types of memory as well as the mechanisms involved in the creation and maintenance of LTM.

The Evolution of Long-Term Memory Through Time

Perhaps the most influential model of memory was the modal system of memory proposed by Atkinson and Shiffrin (1968). This model proposed that memory can be broken into different types, based mainly on the duration of the information being held. Thus, three types of memory were proposed: sensory, short-term, and long-term memory (LTM). Sensory memory lasts for only a few seconds and reflects the registering of a stimulus on our sensory organs. That stimulus may be a sound (echoic), an image (visual), or odor (olfactory) but quickly this stimulus decays. Short-term memory (STM) as was initially proposed was the next unit of the modal memory system, where information entering through the senses was maintained for processing for a limited period of time (seconds to minutes) and then would either be stored in LTM or decay. Of particular importance for STM were processes such as rehearsal which would enable the transfer of that information into LTM. Once information is stored in LTM, it will be kept for ever and it will be available for retrieval, if the appropriate cue is used (Shiffrin and Atkinson 1969).

Research has contributed to the emergence of a new way of understanding STM which is rather different from the proposed model (Atkinson and Shiffrin 1968). New evidence gave way to a more complex and more elaborate model of STM, termed working memory (WM), which shifts the emphasis from the maintenance of information for a short period of time to the manipulation of information involving different modalities (Baddeley and Hitch 1974; Baddeley 2000). One may wonder if any changes have occurred and whether our understanding of LTM has progressed in any way that is parallel to the developments made in STM.

It turns out that plenty has changed in our understanding of LTM which seems to be more complex than it was originally believed. It is now established that LTM is not a unitary construct but a rather diverse memory system, involving different types of information supported by multiple brain areas (Squire 2004). The main distinction between

the various types of LTMs is between declarative (or explicit) and nondeclarative (or implicit) type of memories. These two main types can also be distinguished further so that declarative memory can be distinguished into semantic memory, such as memory for a particular topic, i.e., the planets and the galaxy, or episodic memory, such as events associated with a place and time, i.e., attending a concert last year. Non-declarative memory can also be distinguished into different subtypes of memories such as those associated with skills (procedural memory) such as knitting or riding a bicycle, priming (responding faster to previously seen information even if we report not noticing it) or learning that is associated with classical conditioning such as reacting in a fearful way when a bee is approaching, after being stung by one.

Although these types of LTM are all “created” equal at the molecular level (Bailey et al. 1996), they are different in many other ways, as studies have shown in the last 50 years or so. In fact, different types of memories seem to be stored in different parts of the brain so that declarative types of memories are associated with activation in the temporal lobe (hippocampus, subiculum, and entorhinal cortex), whereas nondeclarative memories are associated with activation in areas which were active during learning, such as the basal ganglia (Squire 2004).

The most famous patient in the area of memory or even neuroscience in general is probably Henry Molaison, although he is familiar to all as H.M. (Tonegawa et al. 2015). H.M.’s bilateral temporal lobectomy by the neurosurgeon William Scoville treated his epilepsy but rendered him unable to retain information for more than a few seconds and thus he was unable to form new memories, a phenomenon known as anterograde amnesia. Brenda Milner, the neuropsychologist evaluating H.M. post-surgery, noticed this amazing phenomenon which gave much insight and sparked many research questions as to the role of the hippocampus in learning and memory. The absence of the hippocampus did not affect old (remote) memories and H.M. could recognize people from his past, but amazingly, he could no longer memorize new information and seemed to have lost recent memories. His case was in accordance with other

instances of head injury which have demonstrated that memory loss happens in a distinct fashion, so that more recent memories are more fragile and thus more likely to be lost in an event of injury or disease, compared to older memories, a characteristic known as graded amnesia (Winocur et al. 2013). However, H.M. was capable of learning other tasks such as the procedural task of mirror drawing albeit in the absence of his conscious recollection. Thus, H.M. would practice and improve on this task, but he was unable to recollect having done it before, demonstrating that this motor skill, a procedural type of memory is supported by brain areas other than the hippocampus and so it remained possible even following the bilateral temporal lobectomy (Josselyn et al. 2017; Tonegawa et al. 2015).

This phenomenon of dissociation between old and new memories is rather interesting. How are older memories different from recent memories and why is the hippocampus important? On the one hand, recent memories tend to be richer in terms of episodic information associated with an event. Learning new information is accompanied by details such as perhaps the time of day and the place in which learning took place, but over time, these episodic details tend to fade and what eventually remains in LTM is the main information or the “gist” as it is usually referred to (Feld and Born 2017; Payne et al. 2009).

The main mechanism that differentiates new memories from old is consolidation. Consolidation is the process that takes place in the brain in order to solidify new information and render it stable or capable of withstanding a long period of time without getting lost or erased (McGaugh 2000). Thus, recent memories are more fragile, because they haven’t had the opportunity to become consolidated yet. The process of consolidation was initially proposed by Müller and Pilzecker in 1900 (see review by McGaugh 2000) and it is now known to be consisted of two different types or phases. Synapse consolidation (or fast) and systems consolidation (or slow) (Dudai et al. 2015). Synaptic consolidation takes place at the level of the neuronal synapse and it involves changes in firing of the neurons

involved, such as long-term potentiation (LTP), gene transcription and translation, branching and sprouting within a short period of time following acquisition or learning. Systems consolidation, on the other hand, may take much longer to be completed (days, months, or even years), and it involves reorganization of several cortical areas that participated in the new learning so that these areas can be involved in supporting this learning in the future, thus, LTM (Dudai et al. 2015).

Consolidation mainly takes place during sleep (Pavlidis and Winson 1989; Wilson and McNaughton 1994). More specifically, consolidation of declarative memories seems to benefit from slow wave sleep (SWS) whereas non-declarative memories seem to benefit from rapid eye-movement (REM) sleep (Karni et al. 1994; Gais et al. 2000), although consolidation seems to be occurring also in quiet wakefulness, at least in animals (Diba and Buzsáki 2007).

The area of the brain in which consolidation takes place at least at the beginning or right after acquisition seems to be the hippocampus but this does not mean that the memories are stored in the hippocampus itself. The most accepted hypothesis regarding the locus of memory consolidation is known as the standard model of consolidation which argues that the hippocampus is needed in order for new information or new learning to be established and subsequently its role becomes less important (Frankland and Bontempi 2005). This model is challenged by evidence which argues that perhaps this may not be the way that consolidation works for all memories and that perhaps the hippocampus is also necessary for the subsequent retrieval of episodic memories even if they have been acquired a long time ago, known as the multiple trace consolidation hypothesis (Nadel and Moscovitch 1997).

The idea of a physical trace of memory existed since ancient times, with Plato using the analogy of a wax impression to refer to memory. It wasn’t until the beginning of the twentieth century that the German Zoologist Richard Semon revived this idea of a physical trace of memory and coined the term “engram” to refer to it and he proposed that once this engram is formed, it

remains dormant until it can be awakened by the presentation of information similar to the one which was present when the memory was initially formed (acquisition or encoding) known as “ecphory” or retrieval (Josselyn et al. 2017). But perhaps the person who popularized both the term and the idea of the engram was Carl Lashley (Bruce 2001). Known more for his failed search for the engram, Lashley pursued the engram by lesioning the cortex of animals in order to isolate it and to be able to show that it existed. Partly due to the nature of the tasks that he used and to the crude methodology, he was not able to find evidence for its existence and instead concluded that memories are diffused across the cortex and thus could not be localized.

In fact, with the advent of electrophysiology and the availability of chemical compounds, it was possible to demonstrate that indeed something changes when learning takes place and that there is indeed a physical trace or engram involving the synthesis of new proteins and the anatomical change in the morphology of the neurons involved. Thus, despite the type of memory or brain region involved, there is a uniform way in which learning becomes possible and that is found in the underlying biology (see review Bailey et al. 1996; Nader et al. 2000). Emotional memories are treated differently by our brain as emotion may signify information of great importance for our survival, a possible threat or danger. Thus, a creature able to remember such information well, may be better able to take the necessary measures to keep safe or avoid risk. Emotional memories are better remembered compared to neutral memories and are more resistant to decay due to the role of the amygdala, a structure just anterior to the hippocampus (Squire 2004).

However, the fact that memories are stored for a very long time does not necessarily mean that the memories themselves cannot be lost or that they are kept unchanged for ever, as the process of consolidation may imply. The most widely accepted ideas regarding forgetting seem to merge on the idea of interference, where learning that took place before or after acquisition of the new information interferes with the current

process of learning and memory. This idea has been challenged and rejected based on evidence which instead argues for a type of LTM which is more susceptible to change than previously thought. It is becoming apparent that memories are vulnerable once retrieved and they can be edited and re-edited upon each retrieval, and upon reconsolidation, a different version of the original memory may be stored (Dudai and Eisenberg 2004; Bonin and Koninck 2015). Thus, memories are potentially susceptible to distortion once retrieved (Nader et al. 2000). Research on those types of memories, which are particularly vivid and intense termed “flashbulb” memories, has also shown that there is distortion of memories no matter how intense they are, which can have implications in situations such as eyewitness testimonies, vulnerability towards suggestion, and false memories (see review: Hirst and Phelps 2016).

However, there may be even more active processes that not only hinder memories from remaining pure and intact but may promote the on-purpose removal of memories from the brain. New discoveries in *drosophila* suggest that there may be natural processes which induce active forgetting and that these may be working in order to promote an efficient memory system, which avoids overload and redundancy in the information it stores (Davis and Zhong 2017). These processes are taking place during sleep which seems to be the main platform for the maintenance and update of this complex and multi-process system called LTM memory.

Conclusion

It may well be that research on the acquisition as well as the forgetting aspects of memory will enhance our overall understanding of the nature of LTM as well as the particular phenomena which are closely related to memory. In light of new discoveries regarding the molecular players and the mechanisms involved in memory formation and maintenance, we are beginning to understand this ever-complex construct, which

although we are all familiar with, has remained quite elusive. Thus, although our knowledge regarding LTM has progressed enormously in the last few years, it seems that we are only half way in understanding the complete picture of this construct which is so integral to our daily functioning and survival.

Cross-References

- [Long-Term Potentiation](#)
- [Multiple Memory Systems](#)
- [Working Memory](#)

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Long-Term Partnership

- [Marriage](#)

Long-Term Potentiation

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Definition

Long-term potentiation refers to the persistent increase in synaptic strength following high-frequency stimulation of a chemical synapse.

Introduction

Long-term potentiation of synaptic transmission is a major mechanism for investigating learning and memory in the synaptic level. It is found in several regions of the brain, with the most prominent being the hippocampus thus its obvious involvement in the neural basis of some forms of memory Cooke & Bliss (2006).

Properties of Long-Term Potentiation

High frequency stimulation causes an increase in the efficiency of synaptic transmission, therefore enhancing the efficiency of the signal. For the induction of long-term potentiation, the activation of excitatory receptors is required Cooke & Bliss (2006). Bliss and Collingridge (1993) reported on the properties of long-term potentiation that differentiates it from other forms of synaptic plasticity: *input specificity* (it does not spread to other synapses), *associativity* (when a weak input of a single pathway is insufficient for the induction of long-term potentiation, simultaneous strong stimulation of another pathway can potentiate the weak stimulation), and *cooperativity* (apart from strong stimulation, long-term potentiation can be induced by the cooperation of many yet weaker stimulations). Since long-term potentiation occurs when a neuron shows an increased excitability over time due to a repeated behavior, and the heightened

synaptic transmission leads to the amplification of responses (i.e., pain), its involvement with the process of sensitization is high.

While the long-term potentiation of synapses in localized cell tissues seems to provide an elegant substrate for learning and memory, researchers turn their attention into experiments with the whole living organism (in vivo experiments). Morris et al. (1986) provided for the first time some data from in vivo experiments in which it was indicated that long-term potentiation was essential for the construction of memories. Using rats, Morris and colleagues were able to examine their spatial memory by inserting an *N*-methyl-D-aspartate (NMDA) blocker drug in their hippocampus, a brain structure implicated in learning. NMDA is a glutamate receptor and an ion channel protein within nerve cells, and it is responsible for the control of synaptic plasticity and memory function. Initially rats were trained to swim in a water maze, in order to find the platform hidden beneath (in the center and the sides of the pool) and escape. As soon as the rats were able to locate the platform, they were separated in two groups. One group constituted the control group while rats of the second group received the drug that blocks NMDA. Then both groups of rats were exposed to the water maze spatial memory task with the rats of the control group being successful in locating the platform and escaping the pool. Contrary, the second group of rats exhibited impaired performance, as long-term potentiation could not be induced indicating thus damage in the hippocampus. This series of experiments indicated that long-term potentiation is implicated in learning and memory processes.

Finally, dysfunctions in the process of long-term potentiation are thought to be implicated in mood disorders Post (2007) and neurodegenerative diseases as Parkinson's Cooke & Bliss (2006).

Conclusion

Long-term potentiation is a fundamental process in a cellular level with implications in the process of learning.

Cross-References

- [Non-associative Learning](#)
- [Sensitization](#)

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Long-Term Storage

- [Long-Term Memory](#)

Long-Term Store

- [Long-Term Memory](#)

Loop Variant, The

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Synonyms

[Sidetrack](#); [Single person](#)

Definition

The Loop Variant is a variation of the moral dilemma problem called “the Trolley Problem” where a trolley can be redirected onto a different track with varying consequences and with the known benefit of saving a number of people.

Introduction

The Trolley Problem is a moral dilemma used first by philosophers starting in 1967 and then adopted by psychologists to examine moral thinking in humans (Cathcart 2013). The original problem was made by Philippa Foot in a philosophical paper about abortion. The original problem was simply many variations of a scenario where someone had to make a choice of killing one to save five, one of which was switching a tram to a different track (1967). The Loop variant is generally stated as such:

You are standing near a trolley track, there is a trolley heading down the track toward five workers who are unaware of the trolley and whom will die if nothing is done. There is a lever next to you, pulling the lever will redirect the trolley onto a separate track where one person is standing; redirecting the trolley will cause the one person to die. Do you stop the trolley by redirecting the trolley or let the trolley hit the five workers on the track (Greene 2013)?

The moral dilemma has many variations, including the track reconnecting the original track further from the four or five persons, the separate track having alarms, or the person on the separate track being of different descriptions (e.g., young or old; Bleske-Rechek et al. 2010; Greene 2013).

The Loop Variant

From an evolutionary perspective, the Loop variant is good for analysis of moral and spatial reasoning. For example, participants of the Loop Variant of the Trolley Problem are much more likely to sacrifice the individual when compared

to participants asked the Fat Man variation, which involves physically pushing a fat man onto the tracks (Greene 2013), showing that the difference in action and space has a significant impact on our moral reasoning.

Joshua Greene, April Bleske-Rechek, and Peter Singer are examples of psychologists and philosophers whom have used an evolutionary perspective in their analysis of the dilemma regarding the Fat Man variation. In Joshua Greene's *Moral Tribes* (2013), Greene takes an in-depth evolutionary approach to the Trolley Problem and the problems of many variations, including the Loop Variant. Greene found that only twenty percent of people were willing to push a man onto the tracks to save the five workmen (i.e., the Fat Man variation). However, over eighty percent of people were willing to switch the trolley onto the second track with one person. Pushing the man saves the most lives, but people have a negative emotional reaction to this choice. When instead given the option to switch tracks, this negative emotional response is weakened despite the end result of killing one to save five being the same (Greene 2013). Similarly, Bleske-Rechek et al. (2010) investigated the Trolley Problem using different descriptions of the man on the looped track. They tested this by replacing the man in the Loop Variant with relatives of varying genetic relatedness (0 to .5), people of varying age (2–70), or potential or current mates. They found that younger, more closely related individuals, and those who were current mates or likely to become potential mates, were less likely to be sacrificed for the five (Bleske-Rechek et al. 2010).

Both Greene (2013) and Singer (2005) argue that the reason for the variance in negative emotional reactions when sacrificing the single person is based on innate moral responses or empathy, which is further affected by our spatial reasoning. Pushing the man onto the track is a personally direct action, whereas pulling a lever is an indirect and distant action. This empathy response makes pushing the man difficult, but pulling the lever an easier choice since the five and one share distance, enabling a more objective response.

Conclusion

The Loop variant of the Trolley Problem is used to understand moral thinking in humans. The Loop Variant itself is the general situation where the trolley is redirected and someone is killed at some variable distance instead of having to push or drop a person that is nearby. Similar to variations in the Fat Man variation of the Trolley Problem (e.g., Greene 2013), the emotional response to killing the single individual to save the group of five is stronger when the single individual is younger or more closely related to the participant or is a potential mate (e.g., Bleske-Rechek et al. 2010), suggesting that moral reasoning varies according to context and the traits of the potential victim.

Cross-References

- [Morality](#)
- [Trolley Problem](#)
- [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)
- [Utilitarianism](#)

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Loser Effects

- [Social Dominance Reduces Fighting](#)

Loss of Conceptus

► Abortion

Low Birthweight and Preterm Infants

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Synonyms

Premature infants; Small infants

Definition

Infants who are smaller or have a lower gestational period than is normative.

Introduction

Low birthweight and preterm status of infants is an international source of concern, as is reflected in the priority placed on this issue by UNICEF and the World Health Organization. Although the death rates of such children are much higher in undeveloped countries, they also are a source of concern for many national agencies in the USA (e.g., US Department of Health and Human Services, Centers for Disease Control and Prevention). By their shared definition, infants born before 37 months of gestation or who weigh less than 5.5 lb are at risk for early health problems and a variety of long-term health, behavioral, and learning problems.

Doster et al. (2008) provided specific examples of the long-term outcomes of a large sample ($N = 903,402$) of low birthweight and preterm infants in Norway. They found that surviving children were more likely than other children to manifest cerebral palsy and mental retardation and/or receive public support as a disabled person.

In addition, low birthweight and preterm children create a major economic cost. The Institute of Medicine within the National Academy of Science (as summarized by McCormick, Litt, Smith and Zupancic in the 2011 *Annual Review of Public Health*) reported that the cost of prematurity (which strongly overlaps low birthweight) poses an annual cost (in 2005 dollars) of \$26 billion dollars – which includes costs of medical care, special education, early intervention, maternal health-care costs, and reduced work productivity for those involved.

Interaction Between Mothers and Low Birthweight or Preterm Infants

Preterm infants are exceptionally reactive to the emotions shown by their mothers. For example, they have been observed to demonstrate elevated levels of cortisol (an indicator of stress) when their mothers were depressed. In addition, they show low levels of responsiveness to their mothers' attention bids (Bugental et al. 2008). Thus, children's later development may be influenced by their early exposure to maternal depression. Field (2011) concluded, based on an extensive review of the literature, that children of depressed mothers are more likely to show a difficult temperament and a variety of behavioral, attentional, and emotional problems as well as illness at later ages.

Hagen (1999) argued that mothers who were depressed in our evolutionary past had help readily available from other women present in small groups. A mother who experienced depression, due to her loss of energy and reduced ability to provide care for her child, posed a threat to the larger group in that she is not contributing to their shared welfare. Her state of depression acted as a signal that others needed to provide assistance to her – thus renewing her involvement in community life.

In contemporary times, depressed mothers are more likely to lack access to social support, and thus they and their infants will have more adverse outcomes. This may be one of the advantages when obstetric units in hospitals provide birthing classes to expectant parents – an experience that also provides shared support between participants. As an

example, Feinberg and colleagues (2016) tested the long-term benefits of Family Foundations (a prenatal transition to parenthood program). Indicating a long-term outcome, they found that the program led to a reduced effect of depression and financial stress on infant birthweight, even after controlling for preterm status.

Shared care of infants by females living in small groups has a long history in evolutionary psychology. Hrdy is known for her work on “cooperative breeding” (Carter et al. 2006). According to this model, children were able to survive in the Pleistocene period because other group members (typically female) shared the care of the young (“alloparenting”). This allowed mothers of “costly” children (e.g., small for age or preterm) to continue producing more offspring.

Effects of Remediation

Given the effects of mothers on their premature/low birthweight children, researchers have shown interest in introducing interventions early in life. For example, interventions designed to reduce postpartum, maternal depression can also be expected to produce benefits for preterm children. As an early example, Brooks-Gunn et al. (1993) designed a 3-year intervention for low birthweight, preterm infants. The children in the intervention produced fewer behavior problems than those in the follow-up at age 3. In addition, Collins et al. (1993) not only found that women with high social support showed less postpartum depression, they also found that women with larger social networks had babies with higher birthweight.

Conclusions

Across countries, low birthweight and/or preterm children pose a “cost” to their caregivers (and potentially the community) if they lack an adequate support system. If these events are followed with maternal postpartum depression, infants will react to their mother’s emotional responses with stress. However, across our evolutionary history, mothers have been assisted by other kinfolk. In the present time, support classes are regularly

offered by medical facilities or social services – thus compensating for the absence of relatives who can provide assistance.

Cross-References

- [Maternal Investment](#)
- [Paternal investment](#)

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Low Libido, Female Sexual Arousal Disorder

- [Desire and Arousal Disorders](#)

Low Sexual Desire

- [Desire and Arousal Disorders](#)

Low Social Status

- ▶ [Redistribution Preferences and Low Socioeconomic Status](#)
- ▶ [Rejected Children](#)

Low Weight

- ▶ [Anorexia Nervosa](#)

Lower Classes

- ▶ [Redistribution Preferences and Low Socioeconomic Status](#)

Lowering Partner Standards in a Short-Term Mating Context

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Synonyms

[Casual mating](#); [Mating preferences](#); [Partner characteristics](#); [Uncommitted mating](#)

Definition

Humans are more selective when considering partners for a long-term relationship compared to a short-term one.

Introduction

The characteristics modern men and women desire in a partner differ as a function of mating context. Overall, this pattern reflects a general

“relaxing” of standards in a short-term mating context compared to a long-term one. For example, compared to a long-term partner, both sexes are willing to tolerate a prospective casual mate who is lower in intelligence, kindness, and social status (Kenrick et al. 1993; Li and Kenrick 2006).

However, not all standards are relaxed in the context of casual mating. Desire for physical attractiveness in a potential partner, for instance, appears to be maintained, or even enhanced, in a short-term mating context compared to a long-term one (Kenrick et al. 1993; Li and Kenrick 2006). Understanding why standards are lower in some cases but not others requires both an appreciation of the challenges our ancestors faced when pursuing these two types of mating and how such challenges differed between the sexes.

Mating Strategies

As a species, humans mate within committed pair-bonds and uncommitted casual relationships (Buss and Schmitt 1993). Both types of mating conveyed a reproductive advantage to our ancestors under the right conditions, and each would have presented its own unique set of adaptive problems. As such, we evolved psychological adaptations to help us overcome these problems and draw us, given our circumstances, towards the most reproductively efficient type of mating (Thomas and Stewart-Williams 2018). It is the difference between these two sets of adaptations, or mating strategies, which cause potential long- and short-term partners to be held to different standards.

Global Standards for Long-Term Partners

Humans are a species which engage in mutual mate choice (Stewart-Williams and Thomas 2013). When looking for a long-term partner, both sexes hold high standards across a host of characteristics including physical attractiveness, kindness, and

social status (Kenrick et al. 1993; Li et al. 2002). These modern day preferences exist because human ancestors evolved to be highly selective when pair-bonding to maximize their reproductive success. Ancestral humans who chose long-term mates indiscriminately risked heavily investing in a small number of poor quality offspring, potentially without (or with ineffective) parental support from their partners. Such outcome would have handicapped the reproductive fitness of both sexes. There are, of course, some differences between the sexes in how much they value individual traits within a long-term context. However, it is rare to find traits highly valued by only one sex (Buss 1989; Kenrick et al. 1993).

Men's Standards for Short-Term Partners

Under certain conditions, ancestral humans could have maximized their reproductive fitness by foregoing pair-bonded mating and pursuing casual mating instead. This type of mating presents a unique set of adaptive problems which differ for each sex (Buss and Schmitt 1993). For ancestral men, casual mating offered the prospect of increased offspring quantity, with little to no investment. However, the success of this strategy would have depended on the availability of women willing to be uncommitted sex partners. Men with high standards for short-term partners would have limited this availability, especially given that highly attractive women may have been less likely to benefit from, and therefore pursue, short-term mating (Buss and Shackelford 2008). Thus, men evolved to have substantially relaxed standards for casual sex partners.

These evolved tendencies are visible in the preferences of modern men who, in the context of short-term mating, have lower standards across a broad array of characteristics including intelligence, conscientiousness, dominance, status, sexual history, and kindness (Buss and Schmitt 1993; Kenrick et al. 1993; Li and Kenrick 2006). One noticeable exception to this is the preference for physical attractiveness, which appears to be generally stronger in short-term contexts - likely due

to its association with both fitness and fecundity (Li and Kenrick 2006; Singh and Young 1995). It is worth noting that men are not indiscriminate in their choice of casual partners. This is probably due to the historical risks associated with short-term mating, including harmed reputation, STI contraction, and being manipulated by lower quality women into committed relationships (Greiling and Buss 2000). However, these risks likely constituted a smaller threat to fitness than those faced by women.

Women's Standards for Short-Term Partners

For ancestral women, casual mating could have enhanced fitness in several ways, mostly as the result of access to men of a higher mate value (Greiling and Buss 2000). These men, while reluctant to pair-bond with women of lower mate value, may have been willing to have casual sex with them to potentially increase their fitness with little to no investment. Thus, casual sex would have provided women with a way of securing the genes and resources of these men and may have given them an opportunity to coerce them into a pair-bond. Other benefits of short-term mating, such as manipulating a current partner, or practicing mate acquisition skills, may have been less related to the mate value of a prospective partner. Considering the benefits of short-term mating together, there would have been much less selective pressure on ancestral women to lower their minimum standards for short-term partners. Compared to men, women evolved to maintain higher standards for short-term partners, especially for characteristics that indicate high genetic quality.

Indeed, modern women relax their standards to a much lesser extent than men do. The attributes subject to the largest drop tend to be important for secure pair-bonding, such as family orientation and kindness (Li and Kenrick 2006). The desire for a physically attractive partner, however, tends to be either maintained or increased (Kenrick et al. 1993; Li and Kenrick 2006). Another reason why women evolved to be more discriminate about

short-term partners is that choosing poor quality partners as casual mates has greater fitness consequences for women than men. Obligate levels of parental investment are small among male mammals, who are able to desert a partner after pregnancy. In contrast, immediate desertion is not an option for females who have to carry an infant to term (Stewart-Williams and Thomas 2013). Choosing a poor quality short-term partner would have seen the reproductive resources of ancestral women directed towards poor quality offspring.

Conclusion

In summary, while humans are highly selective about their long-term partners, they appear to have lower standards for casual partners. The intensity of this “mating context effect” differs between the sexes, with men having markedly relaxed standards compared to women. This sex difference likely stems from the different costs and benefits casual mating afforded ancestral humans.

Cross-References

- [Mate Preferences](#)
- [Mating Strategies](#)
- [Men's Mate Preferences](#)
- [Parental Investment Theory](#)
- [Sexual Strategies Theory](#)
- [Strategic Pluralism Theory](#)
- [Women's Mate Preferences](#)
- [Women's Mate Value](#)

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Low-Quality Fathering

- [Children Without Paternal Investment](#)

Low-Status Males

- [Unemployed](#)
- [Young](#)

Loyalty

► Benefits of Commitment and Marriage

Luring Hypothesis

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Synonyms

Female mating strategies; Remating

Definition

A theory that single mothers use their daughters to attract new mates.

Introduction

Most people enter into marriage with the expectation that they've found a life-long mate. However, serial monogamy has been a consistent feature of mating behavior over human history. Today, people regularly find themselves single again well after young adulthood. About half of first marriages end in divorce, and many widowers have years ahead of them following the death of their spouse. Thus, people are frequently in a position to seek out new romantic relationships at later ages after having had children with past partners. Single mothers who have daughters may have a unique advantage when it comes to remating. Specifically, the "luring" hypothesis proposes a strategy in which mothers use pubescent daughters as *lures* to attract new romantic partners (Weekes-Shackelford et al. 2005).

Remating When There Are Existing Children

Between-sex conflict is common (e.g., Buss 1989), and such disagreements can occur over remating when prior offspring are involved. Because women typically get custody of children when a relationship dissolves, women are more likely to seek new mates while encumbered with children from past relationships. In human and nonhuman species alike, one male strategy to deal with a new mate's prior offspring is infanticide. For instance, children are 100 times more likely to be murdered or harmed by stepfathers than they are by their biological fathers (Daly and Wilson 2005). This behavior is advantageous to males, as eliminating previous offspring saves men from having to invest effort into unrelated children. Like males who have strategies to address remating when offspring are involved, females with children may have their own set of opposing adaptations to finding a new partner. Via the tactic of advertising children (specifically daughters), women may successfully attract men, while also countering male tendencies to disregard or dispose of unrelated offspring.

The Single Mother's Advantage

It is well known that men universally place great importance on physical appearance and youth in mates. In fact, men's preference for female attractiveness typically outshines their desire for most other favorable characteristics (Brumbaugh et al. 2014). Consequently, women are aware that men desire physical attractiveness and aim to meet those standards (Buss et al. 2000). Such awareness may have selected for a female psychology that exploits male mating preferences, not only in terms of how a woman behaves and looks (e.g., acting playfully and wearing makeup to appear youthful) but also in terms of how she uses female offspring to her benefit.

Women who are on the mating market and have daughters may find themselves at a unique

advantage over others (e.g., women with sons) in attracting mates. In other words, women who are old enough to have children and have lost some of their own youthful vigor may play into men's desire for physical beauty and youth via their daughters. Women's strategies may also work in concert with the shifting desires of aging men, who increasingly prefer relatively younger females as they get older (Conway et al. 2015). This male preference, paired with female reproductive value being highest immediately before a girl reaches menarche (Sugiyama 2001), may make adolescent daughters especially useful to mothers who are interested in attracting a new partner.

Preliminary Support for the "Luring" Hypothesis

The luring hypothesis is grounded in the idea that men's attraction to youth and beauty provides aging women with a way to secure new mates. Specifically, single women are predicted to benefit from their daughters, because the daughters serve to entice new romantic partners. Thus, mothers with daughters, compared to mothers with sons, should be more successful at acquiring new mates.

Some tentative support for the luring hypothesis exists. Examining the past 8 years of US Census data on living arrangements involving children under 18 years old who do not live with their biological father, 10.14 % of daughters lived with their mother and an unrelated cohabiting male partner, versus 9.89 % of sons who lived with their mother and a cohabiting male. This trend suggests that women may be more successful at obtaining a new mate when they have daughters rather than sons. Although promising, these data provide a broad snapshot. A closer examination of both mothers' and daughters' age could give greater insight into how luring operates. For instance, future work might examine whether luring is more frequent when women are older and nearing the end of their reproductive years, and the specific ages of daughters that make luring more successful.

Future Directions

One question that arises is the exact mechanism behind the luring hypothesis. In other words, is the process driven mainly by men gravitating to women with adolescent daughters or is it driven by women actively flaunting daughters to attract men? Men certainly seek out youthful partners, but there is also evidence of women's potential role in allowing their daughters to be sexual objects for their own new partners. For instance, research finds that mothers are less likely to believe their children's claims of sexual abuse by a stepfather compared to a biological father (Sirles and Franke 1989). Daughters of divorce may further contribute in implicitly helping their mothers lure new partners. For example, compared to girls living with both parents, girls living only with their mothers exhibit an earlier interest in sex (Draper and Harpending 1982). However, teenage girls also appear to display behaviors that may counteract their mother's use of them as lures. For example, compared to boys, girls have more difficulty adjusting to stepfathers (Hetherington et al. 1985). Thus, the role that daughters play in luring a potential male into a single-mother household remains unclear.

Conclusion

In conclusion, the luring hypothesis builds upon prior mate selection theories by postulating that women with daughters have an edge when it comes to remating. Evolutionarily advantageous strategies for obtaining mates are likely unconscious, including women's use of their daughters as lures and men's attraction to those daughters. However, numerous popular examples show that these mating behaviors are indeed in the public conscious. For example, males are portrayed as being sexually involved with their adult girlfriend's teenage daughters in the movies *Fish Tank* and *Mini's First Time*, and women are seen sexualizing their daughters on reality television programs such as *Toddlers and Tiaras* and *You're Grounded Forever*, but *First Let's go*

Shopping. The idea of adult men's attraction to teenage girls and women's use of their own daughters as lures seems unsavory, but the fact that we often see these things play out in pop culture suggests that these behaviors may be surprisingly normative.

Finding a new mate is especially critical for women with children, because it often helps to recover essential resources that were previously provided by one's past partner. However, the mating psychology of parents reentering the dating market has not been well studied. The luring hypothesis illustrates a novel and adaptive approach by which women may succeed in obtaining new partners.

Cross-References

- [Evolutionary Standards of Female Attractiveness](#)
- [Presence of Children](#)
- [Women's Mate Value](#)

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Luteinizing Hormone

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Synonyms

[Interstitial cell-stimulating hormone](#); [Lutrophin](#); [Lutropin](#)

Definition

Luteinizing hormone (LH) is secreted by the anterior pituitary and plays a role in reproductive functions such as ovulation in females and synthesis of androgens in males.

Introduction

The endocrine system plays an imperative role in the management of the human reproductive cycle. LH along with the two other gonadotropin hormones, follicle-stimulating hormone (FSH) and

human chorionic gonadotropin (hCG), are essential for the regulation of sexual and reproductive functioning. LH has an important evolutionary function as it acts on both male and female gonads (testes or ovaries). It plays key roles in biological processes such as sex steroid synthesis (for both sexes) and the critical reproductive mechanism of ovulation in females.

Biochemical Profile of LH

LH along with FSH are both stored in the anterior segment of the pituitary gland – pea-sized endocrine gland sitting at the base of the brain. Their secretion is stimulated by gonadotropin-releasing hormone (GnRH) secreted by the hypothalamus into the pituitary via the hypophyseal portal system (Martini et al. 2012). LH is a member of a heterodimeric glycoprotein family along with thyroid-stimulating hormone (TSH) and the other gonadotropin hormones (Choi and Smitz 2014). Members from this hormone family all share the same 92-amino acid α subunit, yet they each have their own respective hormone-specific β subunit that garners receptor specificity and subsequent functional specificity (Choi and Smitz 2014). In humans, the gene sequence encoding for the LH β subunit is located among a cluster of gene sequences on chromosome 19q13.32. Transcription of the LH β subunit is particularly important as it also happens to be the step in which production rates of LH are modulated (Choi and Smitz 2014). The structure of the highly conserved β subunit amino acid sequence is what provides LH with its essential biochemical behavior and function (Choi and Smitz 2014). Additionally, hCG has a 145 amino acid sequence coded from other genes among the aforementioned gene cluster but in the case of LH, this polypeptide is cleaved, thus shortening it to the complete 121 amino acid polypeptide used to form LH. This cleavage of the polypeptide ultimately results in a shorter circulating half-life for LH compared to hCG. This shorter half-life is key in generating the release of LH in the form of pulses that work in direct accordance with GnRH pulses (Choi and Smitz 2014; Martini et al. 2012). The release of LH in a

pulsatile fashion as opposed to a constant secretion is fundamental since GnRH pulses and corresponding LH pulses vary in frequency (amount released per minute) and amplitude (amount released per pulse), which ultimately drive cellular responses and the regulation of the reproductive cycle at its various stages, especially in females (Martini et al. 2012). LH exerts its action by binding the transmembrane LH/chorionic gonadotropin receptor (LHCGR) that is expressed in thecal cells, luteal cells, and differentiated granulosa cells of the ovaries as well as in interstitial cells of the testes, which is why LH is sometimes referred to as interstitial cell-stimulating hormone among males (Choi and Smitz 2014). This causes a conformational change in the receptor that activates a stimulatory G protein, which in turn activates enzymes such as adenylate cyclase and phospholipase C (Choi and Smitz 2014). Signal transduction pathways such as the phospholipase C/inositol phosphate pathway, the cyclic adenosine monophosphate/protein kinase A pathway, and the extracellular signal-regulated kinase 1/2 pathway result in proliferation and differentiation of the respective LHCGR expressing cells. These cellular developments consequently lead to maturation of the ovarian follicle and residing oocyte throughout the female menstrual cycle (Brown et al. 2010) as well as the regulation of sex steroid production in male testes.

LH Isoforms

Hormones such as LH exist within the human body as a conglomeration of isoforms (i.e., different forms of the same protein) that are created by natural gene sequence variation, metabolism of the hormone, or by posttranslational modification (Choi and Smitz 2014). Posttranslational modification has yielded in the upward range of 30 various LH isoforms and this is achieved mostly by the addition of carbohydrate side chains that are typically sialic and sulfonic acid compounds (Choi and Smitz 2014). These modify the hormones' biopotency (represented indirectly by bioactive-to-immunoreactive LH ratios [B/I]) and serum half-life. Sialylation extends longevity

of the hormone in blood serum while sulfonation shortens it (Choi and Smitz 2014).

Differences and variations between isoforms do exist between the sexes and within the female sexes' own reproductive cycle. During the luteal phase, B/I is low but begins to rise as the follicular phase progresses until it peaks at mid-cycle, which corresponds appropriately with the marked decrease in sulfonation and subsequent high concentration of circulating LH that is associated with ovulatory induction and the LH surge (Choi and Smitz 2014). Men, on the other hand, tend to have greater B/I and LH sialylation than premenopausal women but age progression is yet another factor that influences the LH parameters between the sexes (Choi and Smitz 2014). Women undergo an actual rise in LH B/I after menopause and an increase in LH sialylation and sulfonation, thus they carry a more acidic LH profile (Bergendahl and Veldhuis 2001). Men, on the other hand, actually experience a decrease or unchanged B/I as they age (Bergendahl and Veldhuis 2001). Furthermore, LH variants yielded from genetic sequence variations/mutations also have implications to both male and female reproductive function and success as these variants are frequently associated with fertility problems and dysfunctional LH properties. A common LH variant derived from a mutation in the β subunit gene sequence has been associated with female subfertility and menstrual irregularity (Bergendahl and Veldhuis 2001). In men, this same variant has been associated with the development of generally less favorable traits such as smaller testis, shorter stature, decreased serum insulin-like growth factor binding protein-3, and slowed linear growth rates (Bergendahl and Veldhuis 2001).

Basic Reproductive Function

Evolution hinges upon reproductive fitness – the capacity of an individual to successfully pass on their genes to offspring. LH plays a crucial role in this process by acting as a precursor to important sex hormones involved in this process. The fundamental purposes of LH for the reproductive functions of adult women and men differ with respect to the obvious distinctions between male

and female reproduction. In women, LH works to assist FSH in follicle stimulation and it also has the imperative role of stimulating ovulation and release of the ovum (Martini et al. 2012). This is accomplished by a large LH surge garnered by the positive feedback activity of rising estrogen on the pituitary, which triggers completion of meiosis I in the primary oocyte, rupture of the follicular wall, and subsequent ovulation 9 h proceeding peak LH levels (Martini et al. 2012). In the post-ovulatory phase, LH subsequently forms/maintains the corpus luteum by promoting progesterone secretion (Martini et al. 2012). The corpus luteum is a small yellowish hormone secreting structure that is formed from the remainder of the sac/follicle that once held the developing ovum. It functions in releasing large amounts of progesterone and small amounts of estrogen, which are critical to implantation and preparation for pregnancy (Martini et al. 2012). In men, LH is needed for androgenization during puberty, sexual differentiation, and sexual functioning. Male fertility is closely tied to adequate LH functioning since it is the precursor to testosterone, which in turn is crucial for sperm production, sperm motility, and energy acquisition by the way of augmenting sperm fructolysis and adenylyl cyclase activity (Ramanujam et al. 2000).

Indirect-Reproductive Adaptive Functions

LH appears to serve an important role in fertility-contingent shifts in women's reproductive physiology and psychology across the phases of the menstrual cycle. For instance, women in the peri-ovulatory phase (i.e., around ovulation) of the menstrual cycle when there is a surge in LH, experience changes in body odor (Miller and Maner 2010), adorn more promiscuous clothing (Durante et al. 2008), and are more flirtatious (Cantú et al. 2014). This research tends to be guided by the ovulatory shift hypothesis (Gangestad et al. 2005), from which it is argued that as the likelihood of conception increases toward ovulation pair-bonded women are predicted to be more attracted to men possessing characteristics putatively associated with good

genes (Gildersleeve et al. 2014). This effect is argued to be most pronounced when evaluating a man's desirability as a short-term partner and absent, or heavily attenuated, when assessing his desirability as a long-term mate. This is because women may only obtain genetic benefits from a mate when fertile. For example, men found women's body odors to be more attractive during the periovulatory phase (higher LH) relative to women in a low fertile phase (lower LH) of the menstrual cycle (e.g., luteal phase; Gildersleeve et al. 2012). During the periovulatory phase, relative to the luteal phase, women have also been shown to experience greater interpersonal closeness and satisfaction with their current relationships when pair-bonded to a sexually attractive mate (Larson et al. 2013).

To detect ovulation, researchers use different counting methods to approximate women's menstrual cycle phase position; however, investigators have tended not to verify these estimates using LH test strips to verify whether a surge in LH and ovulation have actually occurred or not (Jones et al. 2019). Recent tests of the ovulatory shifts hypothesis using larger samples, within-subject designs, and LH test strips are casting some doubt on the robustness of earlier evidence. Another challenge with this research is that fertility-contingent shifts in women's mating is influenced by several interrelated complex hormonal mechanisms and not just LH, such as estradiol, progesterone, and oxytocin (Jones et al. 2019).

The impact of LH on men's mating physiology and behavior is also somewhat unclear. Earlier researchers found that increases in men's LH corresponded to viewing sexually explicit material and heightened ratings of sexual arousal (LaFerla et al. 1978). Increases in men's luteinizing hormone-releasing hormone (LHRH) were also found in anticipation of viewing erotic stimuli (Evans and Distiller 1979). It is difficult to gauge the validity of these earlier studies because they are hampered by small sample sizes and low statistical power. In contrast, LHRH agonists (increasing the binding potential of LHRH) have been shown to lower sexual thoughts and behavior among male sexual offenders (Turner and Briken 2018). Elevated LH levels may also be a reliable biomarker of hypogonadism (impaired

sexual function) in older men (see Giannetta et al. 2012). These latter results suggest an inverse relation between heightened LH and decreased sexual arousal and mating effort. It is evident that more work is needed to examine the relations between men's LH levels and their reproductive physiology and psychology, which are complicated by the pulsatile release of this hormone.

Indirect Immune Function

Immune function has been linked to the reproductive hormones of males and females, with LH playing a contributory and noncausal role, as a precursor hormone. Estrogen acts as an immunoenhancing hormone by regulating B cell function, preventing selection of autoreactive B cells, and inducing a Th2 immune response, which includes various Interleukins (IL) that play an important role in immune/B cell function (Taneja 2018). Furthermore, estrogen stimulates T-lymphocyte homing via expression of the CCR5 gene (Taneja 2018). In contrast, testosterone, which is known widely for its immunosuppressive effects in human males and does so by evoking a Th1 immune response, reduces the action of natural killer cells and tumor necrosis factor-alpha (Taneja 2018). Testosterone also enhances the production of the anti-inflammatory IL-10, which inhibits many important immune cells (Taneja 2018). The obvious immunomodulating differences of the reproductive hormones imply an evolutionary link between LH and immune function, due to the principal actions of its downstream hormones.

Areas of Future Inquiry

Scientific evidence of LH's direct immune functions in humans is sparse and limited, but over the past decades animal researchers have suggested potential links between LH as a causal agent of immune function. For example, LH supplementation was found to promote fetal tolerance in abortion-prone female mice (Schumacher et al. 2014). It did so by increasing the number of regulatory T cells, and by reducing the effects of the

tolerogenic dendritic cells – antigen-presenting cells (Schumacher et al. 2014). Lastly, areas of future inquiry may prove beneficial by investigating the direct immunological effects of endogenous LH in humans.

Cross-References

- [Fertility](#)
- [Menstrual Cycle](#)
- [Ovulation](#)
- [Sexual Signaling During Ovulation](#)

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Lutrophin

- [Luteinizing Hormone](#)

Lutropin

- [Luteinizing Hormone](#)

Lying

- [Human Deception](#)

Machiavellian Intelligence

► [Gossip and Grooming Hypothesis](#)

Machiavellian Intelligence Hypothesis

► [Social Intelligence Hypothesis, The](#)

Mail-Order Brides

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Synonyms

[International brides](#); [Internet brides](#); [Picture brides](#)

Definition

Mail-order brides are women who are explicitly seeking marriage and advertise themselves with agencies that publicize their availability.

Introduction

The term “mail-order bride” originated on the American frontier in the nineteenth century. At

that time, the number of men on the frontier far outnumbered the number of available women, and lonely farmers and ranchers would seek wives from “Back East” by placing ads in newspapers and magazines. Interested women would write back and send photographs, and the couple did not usually meet in person until the woman showed up for her wedding.

The Modern Mail-Order Bride Industry

Twenty-first-century mail-order brides advertise themselves through international marriage agencies. These agencies have names such as *AnastasiaDate.com*, *Loveme.com*, *RussianBrides.com*, and *GlobalLadies.com*. What distinguishes mail-order brides from other mate-seeking women is that they are trying to expand their pool of eligible mates across national borders, and they do so in a way that preserves a freedom of choice that would be greatly diminished if they were to employ more traditional matchmakers. Most mail-order brides now come from Southeast Asia (especially Thailand and the Philippines), Latin America (often Colombia and Brazil), and Russia and the Ukraine. The prospective husbands they seek come primarily from the United States or Western Europe, although there is a market for foreign brides in South Korea and Japan as well (Johnson 2007; Ordoñez 1997). As Wilson (1998) has observed, the photographs of these women that are placed on an agency’s

website are in some sense “*passport photos for foreign eyes and a ticket out of Southeast Asia*” (p. 117) or wherever else from which they might hail.

Another factor that may influence a woman to seek a husband as a mail-order bride is family pressure, especially when she has already reached an age by which she is supposed to have been married. Kojima (2001) identified this pressure to escape the social stigma attached to single women in Korea as a primary motive for Korean women’s emigration to Japan in search of a husband.

Recent Research on Mail-Order Bride Mating Strategies

Although the motives of women seeking Western husbands are often driven by economic concerns, this is not always the case (Johnson 2007; Minervini and McAndrew 2006); mail-order brides are drawn from throughout the social spectra of their respective societies. In two studies, Minervini and McAndrew (2006) examined the mate preferences of mail-order brides from Colombia, Russia, and the Philippines. They conducted in-depth interviews with several “brides,” husbands of mail-order brides, and the proprietor of a mail-order bride agency in Colombia. These interviews revealed that a wide range of factors play a role in the mail-order bride mating strategy. When asked why American customers seek Latina women, the proprietor of the match-making service said that American men prefer Latina women as wives because they are believed to take better care of their husbands and are more tender, warm, and dedicated to their home than are American women. The matchmaker also reported that his American customers sought women who were younger than themselves and those who had stereotypically Latin features such as tan skin and long, dark hair. Latina women, he believed, are interested in American men because they are thought to be more faithful, less jealous, and less chauvinistic than Latino men. The interviews captured the irony of situations in which women who were attempting to escape from traditional constraints were being matched with men who were

attempting to find a wife whom they believed would embrace these very constraints.

For example, an American man who married a mail-order bride had this to say about family life:

The husband and wife are equal partners in the family structure, though not the same. Men and women are different in physical and mental abilities. I feel that the wife has her place in the family structure, such as giving more care to children, the house, and things of that nature. The husband should take care of income and things of that nature.

Similarly, another former husband (age 65) of a mail-order bride stated that he felt that American women:

were too interested in what I was worth [economically]. With women’s liberation in the USA, I had them calling me, coming to my house. Before, the man called the woman when he wanted to date her; the woman was not the initiator. Now is so different from what I grew up with, so I thought that the best thing to do was to meet someone that can’t just come to my house.

A woman now living in the United States explained her reasons for becoming a mail-order bride:

I met men in Colombia, I was married, I had my experience. I decided to look for something different, try men from another culture that might be better than ours. American men are more serious; [they] worry and respect their wife.

Thus, the mail-order bride business as it now operates may be in the perverse position of attempting to match independent, nontraditional women with very traditional Western men, a situation which frequently leads to dissatisfaction for both parties.

Minervini and McAndrew (2006) surveyed a group of Colombian women who were attempting to become mail-order brides, and they compared them with a group of Colombian women who were not pursuing a husband in this way. In addition to asking about their preferences for a husband, they also asked them what they thought men were looking for in a wife. The responses of the two groups to open-ended questions about mating were much more similar than different, and the items relevant to what they wanted in a prospective husband were the ones that showed the least

difference. Both groups emphasized the importance of sexual fidelity and commitment as traits to look for in a mate as well as traits to advertise about one's self. These results line up nicely with the responses to a third question in which the women shared what they thought men sought in a wife, as they believed that these were the two most important qualities that men were after. In a second study, Minervini and McAndrew also found a high degree of agreement among mail-order brides from Russia, Colombia, and the Philippines. Across the board, they found a preoccupation with the very same characteristics (e.g., ambition, commitment to a relationship and children, sexual fidelity, a mate that is somewhat older) that have been documented by evolutionary psychologists in a great many studies.

Mail-Order Brides and Domestic Violence

It must also be acknowledged that there is a very dark side to the mail-order bride experience. Women who travel to a far-off country to marry a stranger are putting themselves at great risk, and grim statistics confirm the danger. Many incidents of violence (including murder) against mail-order brides have been well documented, especially in the United States and South Korea (Crandall et al. 2005; Osipovich 2005). It is not unreasonable to assume that awkward or sinister men are overrepresented in the pool of males who choose to pursue mates from so far away, and women should proceed with great caution if they choose to explore mating opportunities in this fashion.

Conclusion

Women willing to become mail-order brides do not appear to have a different agenda than other mate-seeking women; they simply have discovered a novel way to expand their pool of prospective husbands. However, the mail-order bride mating strategy may be putting women at risk for sexual and physical violence, and it may not be the ideal way of connecting with men who value independence in a mate.

Cross-References

- ▶ [Intimate Partner Violence](#)
- ▶ [Marriage](#)
- ▶ [Mate Preferences](#)
- ▶ [Mate Selection Strategy](#)
- ▶ [Mate Value](#)
- ▶ [Mating Systems](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
- ▶ [Opposite-Sex Relationships](#)
- ▶ [Relationship Satisfaction and Commitment](#)
- ▶ [Sexual Assault and Intimate Partner Violence](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Women Marry Up](#)
- ▶ [Women's Long-Term Strategies](#)
- ▶ [Women's Mate Preferences](#)

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Maintaining Rank in Dominance Hierarchy

- ▶ [Salter, Grammer, and Rokowski \(2005\)](#)

Major Depression

- [Depression \(Paul Gilbert\)](#)

Major Depressive Disorder

- [Depression](#)

Major Hemisphere

- [Language and Handedness](#)

Major Histocompatibility Complex (MHC)

- [MHC Compatibility](#)

Makeup

- [Cosmetics](#)

Making Love

- [Sexual Intercourse](#)

Making the Best of a Bad Job

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Synonyms

[Alternative reproductive tactics](#); [Conditional strategies](#); [Mating tactics](#)

Definition

Individuals that are less favored may use alternative reproductive tactics that minimize their disadvantage (Dawkins 1980).

Introduction

The “making the best of a bad job” scenario was derived as a way of explaining how some reproductive tactics are maintained in a population even when those behaviors result in lower fitness compared to dominant/territorial tactics. For example, small individuals may not fair well in direct competitions with dominant males. Rather than competing, small males may find alternative means (i.e., sneak copulations) that downplay their disadvantage to gain some reproductive success. Accordingly, the “best of a bad job” tactic can have lower reproductive fitness than the dominant tactic.

Something Is Better than Nothing

One of the major questions in evolutionary biology is how phenotypic variation is maintained within a population. This is particularly true for discontinuous phenotypes such as alternative mating strategies. When one mating strategy appears more successful than another (i.e., has higher reproductive fitness), why does not selection remove the less successful strategy? One proposed mechanism is that these behavioral differences may not be alternative strategies but one conditional strategy. A conditional strategy involves a “choice/decision” in how to behave dependent upon the relative condition or status of an individual (Dawkins 1980; Maynard-Smith 1982) (see ► [Mating Strategy Equilibria](#)). Individuals of “status A” should perform “tactic X,” and individuals of “status B” should perform “tactic Y” (Dawkins 1980). However, it should be noted that the “choice” in tactic does not have to be conscious. For example, if only large individuals can hold and maintain breeding

territories, small individuals employing a territorial tactic would likely always lose. In this situation, small individuals should use alternative ways of gaining matings that minimize this disadvantage, thus “making the best of a bad job” (Dawkins 1980). It is not expected that these tactics be equally successful, but small males can achieve some reproductive success. In primates it is thought that most alternative reproductive tactics are “best of a bad job” phenotypes. For instance, mandrill (*Mandrillus sphinx*) males of low status may live alone, rather than in groups, and try to increase their reproductive success by visiting multiple groups during the breeding period to obtain opportunistic matings (Wickings et al. 1993). These tactics are not equal in their reproductive success, as alpha males always have higher reproductive success compared to solitary males (Wickings et al. 1993). However, the non-prime male will likely gain higher reproductive success by acting as a solitary transient male than by remaining in a group.

Not “Bad,” Just Efficient

Some alternative tactics are assumed to be “making the best of a bad job” when in fact, this may not be the case. It has often been suggested that “sneaker” tactics, where smaller individuals sneak copulations rather than directly compete with dominant males, are simply trying to minimize their size disadvantage. In both salmon (*Oncorhynchus* spp.) and sunfish (*Lepomis* spp.), the territorial and sneaker tactics often represent distinct life histories. Sneaker males (or jacks in salmon) mature earlier and invest in reproduction, while territorial males delay maturation and invest in growth. Once they reach adulthood, territorial males are much larger than sneakers. Territorial males also fertilize a higher proportion of a brood than sneaker males (Neff 2001; Berejikian et al. 2010). Therefore, at face value it would seem that males using a sneaking tactic are making up for their obvious size disadvantage. However, as juveniles, sneakers in both salmon and bluegill

have faster growth rates than territorial males (Gross 1984; Gross 1991a, b; Neff 2004), and bluegill sneakers have higher survival rates (Neff 2004; Neff and Lister 2007). These are traits more often associated with individuals in good condition rather than poor. That begs the question, are sneaker males really poor-quality males compensating for smaller size? For both salmon and sunfish sneakers, reproductive fitness is related to their frequency within the population (Gross 1984; Gross 1991a, b; Berejikian et al. 2010). When sneaker frequency is high, their reproductive fitness is low, but as they decrease in the population, their reproductive fitness increases (Gross 1991b; Berejikian et al. 2010). This frequency-dependent selection coupled with differences in age to maturity can maintain alternative tactics in an evolutionary stable state, with both tactics having equal lifetime reproductive fitness (Gross 1991b). In addition, some data suggest that bluegill sneakers may even have higher lifetime reproductive fitness than territorial males when differential survival is included (Neff and Lister 2007). Therefore, prior to determining whether a tactic is truly a “best of a bad job,” one must consider a number of additional factors, including frequency-dependent selection, age to maturity, and differential survivorship, before assessing whether the reproductive fitness of one tactic is actually greater than another tactic.

Conclusion

When an alternative reproductive strategy is conditional, low-quality individuals may employ a “best of a bad job” tactic as a way of minimizing their disadvantage. These tactics often have lower reproductive success than dominant tactics, but they do provide some mating opportunities for less favored individuals (Dawkins 1980). While many alternative tactics may appear to have lower reproductive success at first glance, differential survival, maturity rates, and frequency-dependent selection may lead to equal lifetime reproductive fitness.

Cross-References

- [Mating Strategy Equilibria](#)
- [Sneak Copulation as an Alternative Mating Strategy](#)

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Maladaptation

- [Maladaptive By-Product Hypothesis](#)

Maladaptations

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Synonyms

[Adaptation failure](#)

Definition

Failure in the process of adaptation.

Introduction

The Merriam-Webster dictionary defines “maladaptation” as poor or inadequate adaptation (Dictionary 2006). Adaptation is highly essential for the survival of an organism. The process of adaptation makes an organism fit to meet the needs of the environment. The concept of adaptation and maladaptation is applicable to all living organisms. In the ecosystem, degree of adaptation and maladaptation varies across different species of organisms. Adaptation helps in survival and continuation of race, whereas maladaptation may result in extinction. Survival of many organisms depends upon presence or absence of several other organisms. For example, in the ecosystem, certain birds feed on insects. Extinction of birds will result in overgrowth of insects in terms of their number and vice versa. Similarly, in the aquatic ecosystem, fishes feed on algae. Abundance of algae facilitate abundance of the fish population. In this manner, maladaptation of one species may influence the expansion/growth (in terms of abundance) or extinction of other species (Farkas et al. 2015). However, this entry will focus more on the maladaptation processes in human beings and their health significance.

During the life course of human beings, series of physiological transitions (fetal to extrauterine

life, pubertal changes, pregnancy and lactation, menopause) happen. During the physiological transitions, adaptation process plays a role. Failure of adaptation during these phases may result in development of illness. For example, neonatal hypoglycemia may result from maladaptation to the extrauterine environment (Ichord and Bearden 2017). There are various causes of maladaptation. Broadly, certain biological (e.g., genetic), psychological (e.g., personality), and environmental (e.g., sociocultural) factors determine maladaptation. Evidences support that genetic factors – mutation, inbreeding, pleiotropy, etc. – attribute to maladaptation (Crespi 2000).

Types of Maladaptations

Maladaptation may occur in the structural (physical), functional (physiological), as well as behavioral level. Congenital malformations result in structural deformity and may result in maladaptation. For example, cleft lip and cleft palate may cause impairment of speech. Physiological maladaptation results from alteration of the intracellular or extracellular milieu. For example, poisoning alters the cellular physiology (carbon monoxide poisoning results in hypoxia). Similarly, organ failure (e.g., liver, kidney) results in failure in adapting with the physiological demands of the body. Sometimes the structural alteration may result in functional alteration. For example, congenital heart diseases result in alteration in cardiorespiratory physiology. Behavior of an individual facilitates adaptation. Behaviors are often directed to meet the basic needs of life (seeking food, shelter, sex). Maladaptive behavior interrupts the normal integrity of life. For example, addiction as a maladaptive behavior results in impairment of physical and mental health as well as impairs social integrity.

Health Significance of Maladaptation

During the course of meeting the changing needs of environment, at times there may be failure of

adaptation. Maladaptations (failure of adaptations) may result in development of various health hazards (e.g., abnormal neuroplasticity resulting from maladaptation may result in phantom limb pain syndrome, tinnitus) (Nava and Röder 2011). Chronic pain is a form of maladaptation which often results from damage at any part in the course of pain pathway (Hyam and Zrinzo 2018).

Adapting to the changing environment is highly essential for the general well-being. Travellers, travelling long distances in flights across time zones, may develop “jet lag” due to maladaptation, which results from mismatch of the body’s circadian clock with the new time zone (Waterhouse et al. 2007). Mountain sickness (high-altitude sickness) results from acute exposure to high altitude. The individual experiences hypoxia due to reduced oxygen partial pressure at higher altitudes. Pulmonary edema may develop as a consequence (Mohsenin et al. 2017). Certain individuals experience “motion sickness” during travels. This results from maladaptation of the vestibular system and visual inputs with the movement (Golding and Gresty 2015). Individuals, who are not able to adapt with the provocative environmental stimuli (situations), are more likely to experience motion sickness. Successful adaptations diminish the severity of motion sickness.

Maladaptation can occur at the cellular level. Cells of different individuals respond differently to environmental stressors. Even in the same individual, different cells respond differently to a similar kind of environmental stressor. Maladaptation in the cellular responses may occur in bronchial asthma (Agrawal et al. 2009).

Allergy and hypersensitivity reactions often result, when the immune system of the body becomes unable to adapt with a sensitive agent (allergen) and becomes over-reactive to it by releasing various chemical mediators (Tanno et al. 2016).

Metabolic changes in the body can happen as an adaptive response as well as a maladaptive response. Adaptive metabolic changes help in maintaining the integrity, whereas maladaptation

results in disruption of the integrity. Organs in the body are putting continuous efforts to adapt with the environment. Many cardiac diseases (congestive heart failure, cardiomyopathy, hypertension) and metabolic disorders (diabetes mellitus, obesity) result from maladaptive physiological responses (Young et al. 2002). The myocardium has the ability to compensate the environmental stress. Failure of the myocardium to sustain stress leads to decompensation, which is often the resultant of maladaptation process. During this process, excess release of immune mediators (cytokines like tumor necrosis factor, interleukins) occurs, which produces cardiac decompensation (Mann 2003). Similarly, maladaptation plays a role in the pathogenesis of chronic kidney diseases (Ketteler et al. 2013).

Grief is a common phenomenon experienced in life by most of the individuals after losing their close ones. Over a period of time, people able to cope with the loss and recover from the pains of grief. However, it may persist in certain individuals for longer time producing significant distress, which is commonly referred to as pathological grief and is a result of maladaptation (Jacobs 1993). Similarly, anxiety disorders, depression, and stress-related disorders may result from maladaptation. Individual vulnerability plays a pivotal role in development of these disorders. The individuals vulnerable for these disorders often not able to adapt with the environmental needs and hence might be manifesting the disorders (Jacobs 1993). Recent evidences support that exposure to multiple traumatic events result in maladaptation, which might attribute to development of dissociative symptoms (Granieri et al. 2018). Maladaptive personality plays a determining role in development of trauma-related dissociation.

Psychosocial Relevance of Maladaptation

School plays an important role in an individual's life. The environment of school is more structured

than the home environment, and children often face challenges to adapt to the school environment. Adaptation to the school environment is often considered as a key predictive factor of academic excellence (Bravender 2009). Maladaptation to school may result in declined scholastic performance, school refusal, dropout, and truancy (Bravender 2009). Evidence supports the role of maladaptation and adaptation (adjustment) in ego development. Individuals, who successfully adapt, are less likely to experience psychological distress than those who had maladaptations (Noam et al. 1991). Recent evidence revealed that maladaptations in early life (failure of self-regulation in preadolescent period and negative social interactions during adolescence) may lead to development of psychological disturbances in later life (Laceulle et al. 2019).

Evolutionary Significance of Maladaptation

The environment keeps on changing, and the change creates a demand to bring changes in all the living beings within the ecosystem. Every living organism tries to evolve to cope with the changing environment. Those organisms, who effectively cope or adapt with the change by modifying their structure and function, survive harmoniously within the nature, and those who fail to meet the same struggle to survive. Organisms failing to adapt often become extinct.

Evidences suggest that there is continuous change in human brain to meet the changing needs of the environment. During this process there is structural as well as functional changes in the brain, which is commonly referred to as neuroplasticity (Nava and Röder 2011). Natural selection is an important process in evolution. Maladaptation has been linked to natural selection. Maladaptation results from suboptimal designs (programs). George Williams proposed several evolutionary explanations (e.g., mismatch, coevolution, constraints) for the sub-optimal designs that attribute to maladaptation (Nesse 2005).

Conclusion

Maladaptation is an important alert sign. There is a need to identify and understand maladaptation, in order to prevent its occurrence and persistence. Correcting maladaptation, early, may minimize the distress and impairment significantly.

Cross-References

► Adaptation

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Maladaptive

► Antisocial Behavior

Maladaptive By-Product Hypothesis

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Synonyms

Ecological trap; Evolutionary mismatch; Evolutionary trap; Mismatch theory; Maladaptation

Definition

In evolutionary psychology, maladaptive theory holds that some human behaviors are the result of past selective forces that are no longer operative, usually because of changes in the physical and social environment, resulting in behaviors that are no longer beneficial for fitness.

A maladaptation is a feature of an organism that, despite being genetically encoded or influenced, hinders the biological fitness of the individuals that bear it. Rarely is it straightforward to determine that a given trait is unambiguously maladaptive. Indeed, as noted by Crespi (2000), “Conditions for unambiguously identifying maladaptation are considerably more stringent than those for demonstrating adaptation.” Nevertheless, the existence of maladaptive physical and behavioral traits is undeniable and reminds us of the limits of adaptationist explanations for human behaviors.

At its very origin [pardon the pun], modern evolutionary theory has acknowledged the limits of natural selection in explaining every single feature of an organism. Darwin’s insight that, “many structures now have no direct relation to the habits of life” remains a valid, if oft-forgotten qualifier (Darwin 1859). Despite the emergence of the neutral theory of variation (Kimura 1983) and the identification of so-called evolutionary

“spandrels” (Gould and Lewontin 1979), the ghosts of adaptationism persist, particularly in popular science writings, and more specifically in the just-so stories that dominate popular evolutionary psychology. While the tendency to pin every quirk of modern human behavior on adaptation to Pleistocene Africa makes for sciency entertainment, serious theoretical work in evolutionary psychology requires a higher standard.

By definition, a maladaptation reduces reproductive success in some way and therefore calls out for an explanation as to its emergence and/or persistence in a population. This explains both the interest in and controversy of the topic. Perhaps the most frequent explanation for maladaptation is something now called *mismatch* (Gluckman and Hanson 2004). A mismatch trait is one that was adaptive in the ancestral milieu, but is maladaptive in the present, most often due to a change in the environment. A commonly cited human behavioral example is our appetite for sweet foods. For millions of years prior to the dawn of agriculture, human ancestors encountered few foods that were high in mono- and disaccharides, the natural dietary ligands most often responsible for the perception of sweet (Eaton 2006). Those few were mostly fruits, so it is thus inferred that the human sweet tooth was at least partly an adaptation driving us to seek the specific foods that provide an essential nutrient found in many fruits: vitamin C (Breslin 2013). However, beginning with the cultivation and subsequent artificial selection of carbohydrate-rich cereal crops, along with the selection of larger and sweeter fruits, the production of honey, maple syrup, cane sugar, and so on, humans have tremendously increased dietary intake of simple sugars which have been almost completely decoupled from vitamin C (Eaton 2006). Given the mounting evidence that excessive consumption of simple sugars correlates with a variety of poor health outcomes, the human appetite for sugar may fairly be called maladaptive under present conditions (Jew et al. 2009).

Mismatch, an environmental change that has yet to be addressed adaptively by an organism, is but one possible cause of maladaptation. Others include genetic drift, the fixing of a maladaptive

trait by chance; heterozygote advantage, the persistence of a harmful allele, even when a non-harmful alternative exists in the gene pool, due to the advantage that hybrids have over either form of homozygote; genetic linkage, the connectedness of a maladaptive trait with an adaptive one through either pleiotropy or close chromosomal association; and gene flow, the mixture of alleles and traits from two populations that have adapted to different environments. In these cases, with the possible exception of heterozygote advantage, continued selection could presumably correct the maladaptation, though unambiguous examples of this are lacking.

General theories of maladaptation have remained elusive in part because the very concept is strictly context-dependent. This is best illustrated by example. Humans have substantially less hair and substantially more sweat glands than chimpanzees per unit area (Rogers et al. 2004; Zihlman and Cohn 1988). The prevailing view is that both of these traits are adaptations to the much dryer air of the grasslands, compared to that of the rainforest, the habitats of our more proximal and distant ancestors, respectively. Central to this hypothesis is the notion that Pleistocene hominins were persistence hunters, an activity in which the advantage of both hairlessness and copious sweating has been demonstrated (Bramble and Lieberman 2004). However, as archaic humans and other hominins migrated northward, the dearth of body hair represented a distinct *disadvantage* in the colder, wetter climates that greeted them. Hairlessness, then, can convey an advantage or disadvantage based on context. (It is worth noting that adaptationist interpretations of modern hair distribution are not without challenges. See Morris 1994.)

As difficult as it is to apply adaptive and maladaptive interpretations to matters of anatomy and physiology, it is incredibly more so with complex behaviors. The current teleology of a behavior is difficult enough to assess on its own, especially cross-culturally, and the phylogenetic analysis is even more so. Indeed, the substantial behavioral discontinuity between humans and their extant relatives dooms many phylogenetic analyses within human evolutionary psychology. Notwithstanding

that caveat, behavior, particularly reproductive behavior, may be the richest area of maladaptation given how directly sexual selection can act on reproductive success, particularly in highly social animals with marked intrasexual competition, e.g., humans and our close relatives. For example, frequency-dependent sexual selection, the advantage enjoyed by uncommon mating strategies, is inherently fickle. Insofar as they are genetically based, a sexually selected mating strategy can switch from an adaptation to a maladaptation in as little as a single generation (Lande 1980; Pomiankowski 1987).

Suicide as an Adaptive or Maladaptive Behavior

Recently, suicide has come under scrutiny as a possible maladaptive behavior. Tragically, suicide has long been a significant cause of death among humans, especially males. In 2016, 45,000 people died by suicide in the United States, more than double the number of homicides, making this the second leading cause of death of those age 10–34 and fourth most common cause of death among those aged 35–54 (CDC 2017). To call this a conundrum for an adaptationist view of evolutionary psychology would be an understatement, especially given that the peak age of suicide attempts correlates closely with the peak reproductive years in both males and females.

The notion that suicide may provide adaptive benefits in some contexts is controversial but has both theoretical and experimental support (Gyllenberg and Parvinen 2001; McAndrew 2002). In theory, if self-removal from the gene pool results in a net increase in the fitness of close relatives that is greater than the loss of personal fitness, the principle of inclusive fitness holds that suicide could emerge as an adaptive behavior. In this model, kin-selective altruistic suicide could be driven by self-interested genetic elements. In support of this theory, those who survive a suicide attempt very frequently report an overwhelming feeling of being burdensome to their families, which is even more common among those who are beyond prime reproductive

age or who suffer from major chronic illness, a known risk factor for suicide, and are of low reproductive potential more generally (though these are minority of total suicide attempts, successful or not) (Kovacs and Garrison 1985; Juurlink et al. 2004; Gould et al. 2003). Further supporting this notion is the otherwise paradoxical statistic that suicidality shows considerable heritability (Brent and Mann 2005; Voracek and Loibl 2007).

One example of adaptive suicide is found in traditional Inuit culture. During times of severe famine, elderly members of a family have been known to walk as far away from the camp as they can until they collapse from exhaustion or hypothermia where they are left to die (Leighton and Hughes 1955). Because this spares family resources for their children and grandchildren, and because they are beyond reproductive age themselves, the connection to inclusive fitness is direct.

The myriad differences between the modern world and the environment of evolutionary adaptedness could explain suicide as an adaptive-turned-maladaptive behavior. In other words, suicidality may be a mismatch disease due to modern population densities that are orders of magnitude higher than the ones our species experienced for millions of years prior to urbanization. Indeed, a connection between suicide rates and population density has been observed under certain conditions (Galle et al. 1972; Levy and Herzog 1974; Yamasaki et al. 2008). This is not to suggest, however, that suicide is a form of quorum sensing and population control. Indeed, that hypothesis would rest entirely on group selective theory, a shaky foundation.

There is at least one additional adaptationist theory of suicide that warrants mention although full exploration of which is outside of the scope of this entry. The *bargaining hypothesis* holds that suicide attempts are a form of honest costly signaling designed to help an individual in an otherwise untenable situation recalibrate various social relationships and cultural realities (McAndrew 2002; Henrich 2009). This falls under the “cry for help” paradigm of understanding suicidality and is buttressed by the fact that the overwhelming majority

of suicide attempts are both publicly observable and unsuccessful.

Sex differences in suicidality may be relevant to both of these theoretical frameworks because death by suicide is much more common among men, while among women, suicide attempts are more often unsuccessful (Oquendo et al. 2001). It is possible that gender differentially activates the two frameworks of suicide discussed here in ways related to other gender-influenced behaviors such as impulsivity, risk-taking, and sexually selective costly signaling.

Honor Killings as Maladaptive Behavior

While suicide is often considered the most direct affront to one’s personal biological fitness, the murder of one’s children is a close second. Nevertheless, so-called *honor killings* of children by their parents are a noted phenomenon in several different cultures. These murders are wrought upon young women far more often than upon young men and are most often conducted by the father, usually with the assent of the mother, and sometimes with the aid of his brothers and/or sons, the victim’s uncles and brothers. Shockingly, these murders are rarely concealed and may even be conducted in public. Regions in which this enigmatic behavior is observed with some regularity include the Middle East, North Africa, and the Indian subcontinent (Chesler 2010). While its occurrence in Muslim communities, especially those in the West, has attracted the most media attention, honor killings have also been observed in contemporary Hindu and Jewish contexts and the upper classes of Medieval and early modern Europe (Bowman 2007).

Recently, Robert Trivers has invoked kin selection and inclusive fitness theory to attempt to explain the phenomenon of honor killings (Trivers 2018a, b). Importantly, most of the modern cultures in which familial honor killings occur have a high degree of first-cousin marriage. In a society with strong borders and low gene flow, frequent first-cousin marriage markedly raises the degree of genetic relatedness between individuals and their second-degree relatives, e.g., nieces and

nephews. If identical twins show a genetic relatedness (r) of 1, while genealogical nonrelatives show an r of 0, in a society in which first-cousin marriage is rare, siblings have an r of 0.5, as do parents and children, and second-degree relatives have an r of 0.25. However, as rates of first-cousin marriage rise, the r among genealogical relatives increases gradually, can surpass 0.5 within a few generations, and continues rising asymptotically to 1. Within-family genetic diversity thus drops precipitously.

The exception that proves the rule is traditional Hindu culture. Although first-cousin marriage is not common among Hindus, marriage customs have adhered to the caste system since antiquity, which permits only endogamous marriage. This has the same long-term evolutionary genetic effect as frequent first-cousin marriage, raising the genetic relatedness and reducing the genetic diversity within castes.

Under a system of high genetic relatedness, if the murder of an offspring preserves the reproductive potential of the victim's siblings and cousins, it can boost the biological fitness of the murdering father or sibling, despite the total loss of the reproductive potential of the murdered individual. In all of the honor-based cultures listed above, shame carries substantial costs to reproductive potential and passes freely among first- and second-degree relatives, including first cousins. If a young person behaves in a way that brings shame upon her family, and that shame is broadly recognized in the community, the father of the shameful actor may indeed be acting in the interest of his own inclusive fitness when he murders his daughter. While the tight correlation between the two phenomena of honor killings and first-cousin marriage is compelling, a mechanistic explanation has yet to be suggested.

This behavior is very likely maladaptive in industrialized societies. Firstly, the social-reproductive costs of vicarious shame are rapidly attenuating around the world. Secondly, in the West and in developed regions of the East, the modern state imposes criminal penalties for murder with no official amelioration of punishment for honor-motivated killings. (There is some evidence that, the "culture defense" resulted in

lighter sentences for honor killings in the United Kingdom through the 1990s, but this does not appear to the case post-2001 (Gill 2009).) This punishment extends well beyond the adjudication of the murder, as the family of a convicted murderer will experience substantial negative consequences as well, which may very well be reflected in reduced biological fitness, although this has yet to be examined.

Adoption

Parental adoption involves the substantial investment of one's resources into non-kin children at the expense of, or even sometimes *instead of*, one's own genetic progeny. As such, adoption generally confers *negative* biological fitness. While altruistic and group selective theories could be marshaled to attempt to explain adoption (Rushton et al. 1984), such explanations collapse quickly in the light of the increasing frequency of international and/or transracial adoption (Sahlins 1976). From the view of biological fitness, adoption of non-kin children, particularly by apparently fertile individuals, can be seen as a clear, if highly simplified, maladaptive behavior. (Let it be noted that the author of this entry has himself adopted non-kin children and is unconcerned with the apparent maladaptiveness.)

Conclusion

The evolution of maladaptive behaviors, while difficult to demonstrate unequivocally, often highlights just how dynamic the adaptive milieu can be and the imprecision with which selective pressure is applied to behavior. This is tremendously exacerbated in modern humans in whom cultural evolution now dwarfs biological evolution in shaping behavior, a reality made crystal clear by the phenomenon of reproductive choice. In just two generations, technologies for birth control and abortion of unplanned pregnancies have caused the birth rate to plummet in Western cultures as increasing numbers of individuals choose small families or opt-out of reproduction altogether.

Since these behaviors dramatically reduce biological fitness, they are technically maladaptive. This example shows both the fickle nature of selective pressures on reproductive behaviors and the limits of adaptive explanations for human behavior more broadly.

Cross-References

- ▶ [Assisted Suicide](#)
- ▶ [Death by Suicide](#)
- ▶ [Evolutionary Paradox: Adoption](#)
- ▶ [Factors Associated with Suicide](#)
- ▶ [Filicide](#)
- ▶ [Kin Selective Suicide](#)
- ▶ [Mismatch Between Evolved Morality and Modern World](#)
- ▶ [Mismatch](#)
- ▶ [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)
- ▶ [Reproduction, Suicide, Euthanasia](#)
- ▶ [Suicide as Kin-Directed Altruism](#)
- ▶ [Suicide \(Evolutionary Clinical Psychology\)](#)
- ▶ [Suicide Terrorism](#)
- ▶ [Suicide](#)

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Male Adaptations that Facilitate Success in War

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Synonyms

Coalitional psychology; Intergroup conflict; Male warrior hypothesis

Definition

The male warrior hypothesis claims that the sex-specific adaptive pressures exerted by

recurrent lethal intergroup conflicts in our ancestral past favored the evolution of a cognitive machinery enabling men to form and maintain aggressive coalitions with other males to the end of dominating and exploiting out-groups.

Introduction

War is a gruesome phenomenon. Throughout (pre)history, humans engaging in this brutish activity have brought death, suffering, and destruction to an incalculable amount of their conspecifics. And although some scholars' estimates indicate that the relative impact of wars on human survival and living conditions has been on the decline during the last couple of centuries (Pinker 2011), wars still continue to exert their devastating force today.

From an evolutionary perspective, wars pose a nontrivial puzzle. Why is it that humans are obviously ready and willing to put their lives at risk in collective lethal aggression against groups of conspecifics? Why is it that *Homo sapiens* is among the few species that engage in such murderous campaigns? Why is it, finally, that “[w]hile war may be everyone’s business, it has usually been men’s work,” as Keeley (1996, p. 35) trenchantly put it?

In this entry, we review selected previous literature on all three questions. Our focus, however, lies on sex differences in cognitive mechanisms potentially resulting from the differential adaptive challenges posed to the sexes by the frequent recurrence of violent intergroup conflicts throughout humanization. First, we outline theoretical work on the general cost/benefit structure faced by fitness relevant behavioral strategies in war. Second, we discuss how the main components of the resulting models of human belligerent behavior differentiate humans from many other animals. Third, we ask if human prehistory may have actually met the conditions required for war to entail sufficiently intense selection pressures in order to result in adaptive cognitive sex differences. Finally, we review contemporary evidence for the existence of these differences obtained in controlled psychological experiments, field studies, and surveys.

Theoretical Perspectives on Adaptive Problems Posed by Warfare

Modelling approaches to the evolution of human behavioral strategies commonly start from the assumption that most of our species' evolutionarily relevant time on this planet was characterized by living conditions similar to those of contemporary hunter-gatherer bands and wild chimpanzees. For humans, this means living in relatively small, mobile bands consisting of up to a few dozens of individuals, co-residing with primary and more distant kin, spouses' primary kin, other affines, and unrelated others (for recent demographical estimates, see, e.g., Hill et al. 2011). Multiple bands, then, together form clans, tribes, and ethnolinguistic cultures, which are often characterized by frequent exchanges of members between their subgroups. Most recent models of the evolution of bellicose behavior in humans locate violent conflicts at the between-band level (Choi and Bowles 2007; Lehmann and Feldman 2008; for a comprehensive review see Rusch 2014b).

Theorists have identified the main adaptive challenge that individuals living in such groups face when deciding whether or not to engage in intergroup conflicts as the trade-off that must be made between the potential benefits and prospective risks entailed by waging war. While some authors hold that a decision to participate in collective aggression against out-groups represents a genuinely altruistic act (Choi and Bowles 2007), other authors argue that the cost/benefit structure of war often favors the aggressor directly as long as certain conditions are met (Lehmann and Feldman 2008; Rusch 2014b; Tooby and Cosmides 2010). Relevant to this, one of the most important distinctions is the one between coalitionary defensive aggression, which can occur in the forms of preemptive first strikes as well as retaliatory counterstrikes, on the one hand, and unprovoked offensive aggression on the other. While the evolution of defensive aggression is relatively easy to explain because of its self- and kin-protective function, unprovoked offensive aggression poses a more complex problem (Rusch 2014a). Why should an individual be

willing to participate in aggressing against an out-group, if (i) nonparticipation by this combatant would not substantially lower the chances of victory, if (ii) the spoils obtained in case of victory are shared by all members of the victorious group, and if (iii) the risks entailed by participating are high, potentially even as high as losing the own life.

Theorists have identified multiple factors that can provide solutions to this collective action problem (Gavrilets 2015; Rusch 2014b; Tooby and Cosmides 2010). Apart from the commonplace mechanisms – direct and indirect reciprocity as well as peer-punishment – that can of course also promote group-level cooperation in this context, coalitionary offensive aggression likely differs from other collective action problems in a number of crucial respects. For one, in groups as small as the ones our ancestors lived in, nonparticipation by a single individual quite likely had a significant effect on the outcome of an attack (Johnson and MacKay 2015). This makes every single combatant pivotal for the outcome of a threshold collective action problem, a factor which is known to foster cooperative individual decision-making (Barclay and van Vugt 2015). Second, small deviations from the, arguably unrealistic, assumptions that (i) the spoils of war are equally shared and that (ii) all combatants are equal in their contribution capabilities can already substantially alter the incentive structure of coalitionary aggression. This then leads to positive selection for belligerence in the more battle-ready and/or more privileged individuals (Gavrilets 2015; Gavrilets and Fortunato 2014). Third and finally, an interesting structural asymmetry exists between the risks entailed by offensive versus defensive warfare, caused by the greater strategic flexibility that offenders usually have. Normally, attackers can eventually decide if they want to follow through with a strike or not. If, for instance, a lack of numerical superiority or other situational factors discourage an attack, offenders can retreat safely as long as they are not spotted or ambushed by defenders. In addition, the strategic advantage of surprise is usually on the attackers' side. In effect, these structural advantages often minimize the risks faced by offenders.

In summary, various models and simulations suggest that the benefits associated with coalitional offensive aggression can sometimes outweigh the costs. It must be noted, though, that this likely only pertains to single strikes in hunter-gatherer warfare. The long-term outcome of continuous raiding and feuding between such groups can be quite substantial in terms of mortality risks, as we argue later. Assuming that costs are potentially low in the short term, the question is what the potential benefits of hunter-gatherer aggression are. In order for belligerence to be positively selected for in the long run, these must be large enough to offset not only the relatively small risks of single strikes but also the long-term increases in mortality risks, caused by continuous feuding between bands.

A recent model suggests that there are at least two ways through which aggressors can obtain significant direct and indirect fitness benefits through warring. Building on the conventional assumptions about hunter-gatherer population structure, and explicitly focusing on male combatants, Lehmann and Feldman (2008) showed that both (i) direct fitness increases for males obtained through winning additional reproductive access to females of other groups and (ii) the more indirect effect of increased reproduction of in-group females caused by seizing territory or other valuable resources from out-groups can independently suffice for a positive selection of male belligerence and bravery. Unlike other models, furthermore, Lehmann and Feldman explicitly analyze the role of relatedness between combatants. They find that the potentially high costs of warring can be substantially dampened by high within-group relatedness of male warriors. They show that, although an individual combatant may eventually have to pay with his life for victory over out-groups, the inclusive fitness benefits obtained by him through increased reproduction of his lineage can still offset these costs, even in groups of considerable size.

To summarize, various scenarios favoring a positive selection of belligerence and bravery in intergroup conflict exist in the theoretical literature today. They show consistently that warring may have had adaptive benefits, especially in ancestral men. An important question raised by

these theoretical models of human warfare is why only a handful of species show coalitional aggression (Wrangham 1999).

Nonhuman Evidence

One potential reason for the relative sparseness of intraspecific lethal coalitional aggression in other animals lies in the complex social adaptations that are required for warfare. These include sociality, communality, and advanced capabilities for coordinated action. Furthermore, in order for warring to be potentially beneficial in terms of inclusive fitness, the relatedness patterns resulting from a species' way of living must meet certain criteria. As constantly killing close relatives would obviously result in negative selection against this trait, warring can only evolve if its benefits are more likely to be received by close kin while its costs are borne by more distantly or unrelated individuals. Intense lethal intergroup conflicts occur, for example, in some species of colonial eusocial insects. In these, individuals within colonies are genetically very closely related, while relatedness between colonies is much lower. For most vertebrates, however, relatedness patterns are more complex. In group-living mammals, for example, within- and between-group relatedness crucially depends on residence rules, that is, on the question whether groups frequently exchange individuals and if so which individuals.

For understanding the evolutionary roots of human intergroup aggression, and particularly for the question why it is mostly men who engage in this behavior, residence rules are central. A recent meta-study comparing 135 primate species, for example, found that species in which the dominant sex is philopatric, i.e., species in which the physically stronger sex tends to live together with close relatives while members of the physically weaker sex change round between groups, are more successful at defending their territories (Willems et al. 2013; also see Willems and van Schaik 2015). It seems that close family ties are required to foster the cooperation needed to sustain coalitional aggression in animals. Although no commonly accepted theory explaining the

occurrence of lethal animal intergroup conflict exists yet, residence rules of the warring sex show similar patterns in all mammals for which such conflicts have been documented. Among them are hyenas, lions, wolves, and, of course, chimpanzees, and humans (Wrangham 1999).

Chimpanzee “wars,” in particular, are the best studied cases of nonhuman violent intergroup conflicts. Since Jane Goodall made her famous observations in Gombe National Park, documenting the systematic extermination of all out-group males by a coalition of male chimps over a period of 5 years, many careful field studies have been conducted to understand when – and why – male chimpanzees engage in lethal coalitional aggression and how they might benefit from doing so. Michael Wilson and colleagues recently evaluated the available evidence (Wilson et al. 2014). Analyzing 152 killings in 15 communities, they found that (i) males were the most frequent attackers (92%) and victims (73%) in lethal violence in chimpanzees, (ii) a majority of these killings (66%) involved members of different communities, and (iii) attackers used risk-minimizing tactics (median attacker-to-victim ratio 8:1). In addition, Wilson et al. were able to extract two robust predictors of higher levels of intergroup conflict from their data. Violence increased with population density as well as with the number of males living in the respective communities. They conclude that “patterns of lethal aggression in *Pan* [...] are [...] better explained by the adaptive hypothesis that killing is a means to eliminate rivals when the costs of killing are low” (Wilson et al. 2014, p. 416).

Human Evidence

One might be tempted to extrapolate this “chimpanzee model” directly to humans. Like *Pan troglodytes*, humans are a territorial, group-living species. And, like chimpanzees, *Homo sapiens* often lives patrilocally, that is, groups are often formed around “bands of brothers,” whereas females switch groups through exogamous marriage (e.g., 15 of the 32 contemporary hunter-gatherer societies surveyed recently by Kim Hill

et al. 2011, follow this residence rule; matrilocal: 5, ambiguous/unknown – 12).

Support for the notion that residence patterns, and the kinship structures they induce, are key to understanding human warfare comes from early systematic anthropological work. Adams (1983) analyzed evidence from 67 prestate human societies. He found that in nine of these societies, some forms of active female participation in lethal intergroup violence were documented. Strikingly, all of the nine societies followed residence rules that preclude that women may have to fight relatives in enemy groups. Furthermore, Adams found that patrilocally living societies were more likely to exhibit higher levels of intergroup conflict, as compared to societies following other rules for marital residency. More supportive evidence for the relevance of the “chimpanzee model” for understanding human intergroup conflict was recently compiled by Wrangham and Glowacki (2012). Carefully reviewing the available anthropological literature, they identified many additional similarities between chimpanzee and hunter-gatherer warring. Also in humans, victors often seize territory from defeated out-groups, females are frequently abducted in raids, and attackers mostly use risk-minimizing surprise tactics.

Thus, let us assume for a moment that human prestate intergroup violence resembles chimpanzee warring closely enough to follow a similar fitness logic – an assumption which is certainly debatable (see, e.g., Wrangham and Glowacki 2012 for a comprehensive discussion). The remaining question then is if war in ancestral human populations was frequent and intense enough in order to actually create differential selection pressures on human males and females across evolutionary time.

In terms of absolute numbers, the large-scale wars of the twentieth century have certainly been the deadliest campaigns ever carried out. As Pinker has argued, though, their relative impact on human survival may have been comparably small, taking the size of the world population into account (Pinker 2011). Interestingly, Pinker’s calculations are paralleled in the anthropological literature. Where authors have tried to estimate the

mortality rates caused by lethal intergroup conflict in human prestate societies, they have often arrived at similar conclusions. Keeley (1996), for example, in his reconstruction of the prehistory of war, estimates that in some traditional societies, between 8 and 59% of male deaths may have been caused by war, while this figure lies below 1% for the twentieth century Europe and USA. Also, where data is available, Keeley's estimates indicate that men in traditional societies roughly had a 6.5 times higher chance of dying in war than females (Keeley 1996, p. 196). Similar numbers are reported by Walker and Bailey (2013) who recently analyzed ethnographic reports of 1,145 killings in 44 lowland South American societies. They confirm that attackers in individual raids suffered hardly any casualties and that a major reason for raiding was the capture of women (with ca. 0.6 women being displaced per raid). In addition, they found that a total of 1,045 of these events, representing an average of roughly 28% of all deaths, male and female, were caused by war in this sample. Again, though, men had a substantially higher risk of dying in war than women.

Before we move on to review evidence from recent psychological and social science studies supporting the hypothesis that the potentially high mortality rates caused by war under prehistoric living conditions could have resulted in cognitive adaptations for intergroup conflict, one important point needs to be addressed. As, for example, Gat (2015) elaborately discusses, one should not view human prehistory as a history of perpetual extreme intergroup violence. As Fry and Söderberg (2013), among others, point out, many human societies of all times and regions have most likely also been able to sustain long-term peaceful coexistence with neighboring groups (also see Rusch 2014b; Wrangham and Glowacki 2012). When we speak of psychological adaptations for coalitional aggression and intergroup conflict in the following section, thus, these should be understood as domain-specialized, cognitive mechanisms that are being activated only in adaptively relevant contexts and not (so much) as psychological instincts constantly seeking war as the only solution to conflict.

The Male Warrior Hypothesis

Let us assume, for now, though, that warfare and intergroup conflict have been important selective forces for humans, contributing to a relatively unique human coalitional psychology, with some parallels in other species. Then, it is likely that warfare has shaped the coalitional psychologies of men and women differently. This is the basic thrust behind the male warrior hypothesis which claims that specific cognitive machinery has evolved enabling ancestral men to form and maintain aggressive coalitions with other males with the aim of dominating and exploiting members of out-groups (McDonald et al. 2012; van Vugt and Janssen 2007). What cognitive adaptations constitute this specific warrior psychology, what cues activate it, and how do the sexes differ in the activation of these cognitive mechanisms?

We can distinguish between at least four different coalition mechanisms – or psychological systems – that need to be in place to plan, execute, and be victorious in intergroup conflict. First, *coalition detection* mechanisms need to be in place to be vigilant about potentially, hostile coalitions, remember who is in-group and who is out-group, and assess the strength and formidability of these coalitions. Second, an adaptive warrior psychology requires mechanisms to quickly *recruit allies* to form strong and sometimes sizeable coalitions, pick the right members to form a combat force, and form emotional attachments to these coalitional groups quickly. Furthermore, a cognitive adaptation to assume the identity of a male warrior is helpful (cf. the combat identity hypothesis by Tooby and Cosmides 2010) and so is an above-average interest in the aesthetics of warfare. *Coalitional maintenance* adaptations are needed in order to ensure that coalitions remain together and unified, and they include adaptations for reward cooperative members (e.g., war heroes) and punish defectors (deserters and cowards). Finally, *coalition exploitation* systems allow individuals to time a collective aggressive act and reap the benefits of intergroup aggression by converting the spoils of war into reproductive benefits. Cognitive adaptations that enable individuals to make the right trade-offs between the

risks and benefits of coalitional aggression attack and kill members of out-groups only if potential costs are low and potential benefits are high, dominate and exploit members of out-groups, and morally justify these actions are some examples of exploitation mechanisms that together may constitute this warrior psychology.

Such coalitional systems are likely coupled to specific emotions that allow individuals to make adaptive decisions in the domain of intergroup conflict such as feelings of in-group loyalty, out-group hate, anger toward in-group defectors, admiration of war heroes, etc. Furthermore, these mechanisms are activated by adaptively relevant external cues. Seeing a collection of out-group males together, for example, should activate the coalition detection system more so than seeing a group of out-group females and perhaps especially if the men are (i) physically strong, (ii) in possession of weapons, and (iii) in or near in-group territory. Similarly, individual differences in physical formidability, aggression, social class, age, and social networks likely influence how people trade off the risks of engaging in collective violence. Finally, cognitive adaptations for coalitional aggression, although they may partly overlap with interpersonal aggression, are likely to be activated by distinct, domain-specific cues (such as the formidability and power of the leader of a group; Holbrook and Fessler 2013).

This brings us to consider sex differences. Due to differences in parental investment and, as discussed earlier, differences in physical formidability and co-residence patterns, there is an asymmetry in the costs and benefits of engaging in warfare between men and women. This was especially true in ancestral environments where most forms of intergroup conflict involve physical combat. By virtue of a lower paternal investment, coupled with a stronger physique, it may be adaptive for men under certain conditions to be warriors as this can increase their access to reproductively relevant resources (mates, territories). These conditions are specified in Tooby and Cosmides (1988) risk contract theory of warfare that views warfare as a collective action problem in which free-riding dominates unless (i) there are compensating benefits for cooperators,

(ii) defectors are punished, and (iii) there is a veil of ignorance making it impossible to know who will die and who will survive an attack *a priori*.

Coalitional aggression can be directly fitness enhancing for men as one gains access to women (see above). Other benefits of coalitional aggression are indirect fitness enhancers. That is, by killing or injuring the males of rival groups, these out-groups weaken in strength, and their females may eventually migrate to the in-group (analogous to observed behavior in chimpanzees; Wilson and Wrangham 2003).

Research Support for the Male Warrior Hypothesis

The MWH asserts that men will respond more quickly and strongly to cues associated with intergroup conflict and convert coalitional aggression into reproductive opportunities. This hypothesis does not suggest that all men will always prefer war as an option to manage intergroup relations. Whether or not this warrior psychology is activated depends upon cues that are ancestrally linked to be on the winning side in an intergroup conflict. Second, the MWH allows for individual variation between men in their sensitivity to cues associated with warfare. For instance, warrior behavior may be easier activated in men who are physical stronger, have higher degree of dispositional aggression, possess a higher baseline testosterone, and have larger male kin or friendship networks. Nevertheless, we believe that there should be sex differences in the ease with which different coalitional systems that support intergroup aggression and warfare are being activated. The research literature supports this by and large.

Earlier we reviewed the evidence from primatology and anthropology suggesting selection for male warrior traits. Now we turn to the social sciences. There is an abundance of studies in psychology and other fields (political science, sociology, behavioral economics) that show that men have a lower threshold for engaging in coalitional aggression. First, surveys reveal that

men report having more experiences with competitive intergroup interactions (e.g., team sports) than women (Pemberton et al. 1996). In simulated war games between countries, men as the leader of their nation are also more likely than women leaders to make a preemptive strike against another nation (Johnson et al. 2006). Exclusively male groups make more defective choices in prisoner's dilemmas between groups than all-female groups (Wildschut et al. 2003). Finally, in nationwide opinion polls, conducted in various countries, men are always more supportive of military action as a solution to intergroup conflict (van Vugt 2009). This is ironic, of course, considering the fact that men are also the most likely victims of warfare, but it makes sense if we follow the logic of the MWH.

An indirect test of the MWH involves looking at sex differences in preferences for group-based dominance hierarchies, which is the inevitable outcome of warfare. On an individual measure of this preference, called social dominance orientation (SDO), men score systematically higher than women, even in countries where gender roles are relatively egalitarian such as Sweden (Lee et al. 2011). Importantly, scores on SDO are positively associated with a wide variety of social attitudes and ideologies that tend to legitimize intergroup dominance hierarchies, including racism, patriotism, and the explicit endorsement and support for aggressive wars (Sidanius and Pratto 1999). Men, on average, also display more xenophobic and ethnocentric attitudes than women (Sidanius and Ekehammar 1980), and men are more likely to dehumanize out-group members (van Vugt 2009), which may help ease the psychological discomfort associated with killing or injuring men from rival groups.

The way men and women form and maintain their coalitions also differs. In line with the MWH, developmental studies show that boys form larger, more flexible coalitions than girls, which suggests an ability to form flexible war-size parties (Hawley 2014). Men also identify themselves more strongly with large, tribal groups than women. In one study, researchers showed that men had a more collective self-concept, whereas women had an interpersonal self-concept (Gabriel

and Gardner 1999). They asked men and women to complete 20 statements beginning with "I am. . ." They found that men reported a higher proportion of collective self-descriptors (e.g., "I am a member of a fraternity."), whereas women provided a higher proportion of relational descriptions ("I am best friends with Michelle"). In another study (a summary is reported in van Vugt 2009), we asked men and women what their favorite color was and why. More than twice as many men as women mentioned a tribal association with their favorite color (e.g., "I like the color red because it is in our national flag").

Men are also more motivated to defend their in-group and cooperate with fellow in-group members, particularly when there is an intergroup conflict. In a series of laboratory experiments, we found that men contributed more to a public good for their group when their group was in competition with other groups, rather when they were competing individually. This difference was absent for women. Furthermore, men identified more strongly with their group when it was facing intergroup competition, and again this effect was absent for women (van Vugt et al. 2007). Other studies show that men are also more aesthetically attracted to stimuli depicting intergroup conflict, be it war movies or gangster movies, war documentaries, and books depicting intergroup aggression such as biographies of war heroes (Goldstein 2002; van Vugt 2009).

What about the choice for leaders during episodes of intergroup aggression? Both men and women prefer to appoint men as leaders during intergroup conflicts, presumably because they believe that men fit the physical and psychological prototype of a war leader better. In a public goods experiment, participants who thought the study's aim was to compare how teams of different universities were doing were much more likely to appoint men as their team captains than participants who believed that the study's aim was to compare individual team players in terms of their public good contributions – the majority of them chose women as team captains (van Vugt and Spisak 2008). Various studies, using mock presidential election data, revealed that when people are asked to vote for a president when their

country is facing war, a majority of voters prefer a candidate with a masculine-looking face over a candidate with a more feminine-looking face (Little et al. 2007; Spisak et al. 2012).

Finally, consistent with the MWH and in line with sexual selection theory, there are sex differences in the extent to which warfare is driven by sexual motives. That is, for men, warfare may be a platform on which they can show off their physical skills and psychological qualities as valuable coalition partners or sexual mates. Regarding the latter, recent studies found that women were more sexually attracted to men who had shown bravery in warfare than those who had not (Rusch et al. 2015). This effect was both domain and sex specific. Women were more interested in dating a war hero than a hero in a natural disaster. Furthermore, men were not particularly interested in dating female war heroes, showing evidence for a sex-specific war psychology. In addition, an archive study revealed that male war heroes (Medal of Honor recipients of World War II) sired more offspring than ordinary soldiers – suggesting evidence for reproductive benefits associated with war behavior.

Conclusion

Despite the accumulating evidence for the MWH and specific male adaptations for warfare, a number of contentious issues remain. First, are there specific female cognitive adaptations for warfare? We think there are. Ancestral women's reproductive interests were not served by actively joining in physical combat for the reasons we have already outlined. Nevertheless ancestral women could profit from the extra resources that would be gained by warrior males as long as their group emerged victoriously from combat. Thus, under certain conditions such as a food shortage, women could have encouraged their men to go on a raid. Similarly women may encourage male warrior behavior indirectly through selectively preferring male warriors as their mates (Rusch et al. 2015). Nevertheless, on the whole, we hypothesize that women's psychology is probably more geared toward peacekeeping and peace maintenance

between groups as this serves their reproductive interests best. Not surprisingly, both sexes prefer female leaders to keep the peace in intergroup relations (van Vugt and Spisak 2008). This is not to say that women have not evolved specific cognitive adaptations to deal with warfare. First, out-group men pose specific challenges to the reproductive choices of in-group women. Thus, we expect women to have evolved specific mechanisms that are activated in particular after exposure to out-group male warriors. One such adaptation is rape avoidance, and there are findings suggesting that women are particularly fearful of formidable out-group men versus in-group men (McDonald et al. 2012). Second, it would be in a woman's best interest to opportunistically switch sides once a particular coalition of men emerges victorious after battle. Thus we expect women to have evolved a tend-and-befriend strategy (cf. Taylor et al. 2000) toward victorious out-group men to protect themselves and possibly their offspring from danger. This hypothesis remains to be tested in humans.

Third, the MWH does not preclude the possibility of women to play an active role in combat. Although the notorious army of Amazon warriors is likely a myth, women do sometimes join a fight. Female warrior behavior seems to be driven by factors such as the size of the war coalition needed in battle. For instance, Israel is surrounded by a number of countries that are hostile to Israel, and not surprising, it is also the country that has the largest portion of active female soldiers in service (Goldstein 2002). Thus, although women may not be predisposed to be warriors, there may be critical conditions – such as the overwhelming coalition size of the out-group – that override these evolved tendencies. In addition, although offensive coalitional actions such as raids and ambush killings are largely the domain of men, this may be different when a group is defending itself against a hostile out-group.

A final challenge is what specific cues trigger this male warrior psychology and if there are individual differences. Cues of out-group males teaming up together should activate this warrior psychology and probably more so when this male coalition is sizeable in numbers and has a

physically formidable leader. Men should be better at detecting coalitions than women, being able to remember better to which tribal groups a person belongs (Kurzban et al. 2001). Resource scarcities should probably activate male warrior tendencies and so does the presence of young, fertile out-group women. Finally, one's own physique and personality might matter. That is, warrior tendencies are easier to activate in men who are physically formidable, have high base levels of testosterone, and have a fearless personality.

Cross-References

- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Contexts for Men's Aggression Against Men](#)
- [Contexts for Men's Aggression Against Women](#)
- [Defense Against Attack](#)
- [Evolved Psychology of Warfare](#)
- [Humans: Between-Group Conflicts](#)
- [Lethal Violence](#)
- [Male Warrior Hypothesis](#)
- [Men but Not Women Will Have Adaptations for War](#)
- [Rape in Warfare](#)
- [Self-Defense](#)
- [War](#)
- [War More Likely with Higher Likelihood of Success.](#)

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Male Adaptations to Assess Fighting Ability

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Synonyms

Formidability assessment

Definition

Adaptations for assessing fighting ability are perceptual mechanisms designed by natural selection to predict the victor of future bouts of aggression.

Introduction

Nonhuman animals are known to have evolved strategies for the assessment of fighting ability. In short, they “size up” their opponents before and during aggressive contests so as to make more prudent decisions about the fight. Evolutionary psychologists have now gathered evidence that humans also have this competence as a result of several evolved adaptations that extract cues from the body, face, and voice primarily of adult men. This entry reviews the logic of animal assessment and the data showing that humans have evolved adaptations for estimating fighting ability. It also explores some of the new data identifying which cues are used to estimate fighting ability.

The Evolutionary Function of Fighting Ability Assessment

First year psychology students are often told that there are three kinds of neurons: motor neurons to contract muscles and generate behavior, sensory neurons to respond to environmental stimuli, and interneurons to store information and connect the other two. This basic observation reflects a

crucially important point about evolutionary biology: that the function of the nervous system in animals is to make muscle movement (i.e., behavior) contingent on environmental cues. The interneurons, which make up the bulk of the human brain, function to compute and store information that is then used to process sensory data and coordinate muscle movement (along with a contingent of other adaptations, e.g., the endocrine system). Analyzed from the viewpoint of evolutionary biology, the brain is literally a computer that runs behavioral programs that are contingent on calculations made about information coming from perceptual systems.

Perceptual systems, then, will be designed to perceive only a narrow slice of reality, particularly the cues that enabled behavioral systems to be most efficient at overcoming adaptive problems. For an organism of a social species, these adaptive problems would include many aspects of their fellow conspecifics. For example, an individual's access to food, territory, water, mates, and information will often depend on the behavior of others. Therefore, we can expect that natural selection would have designed social species with many perceptual adaptations that function to recognize, categorize, evaluate, and store information about other animals. For example, animals are generally designed to recognize their own species, distinguish their biological kin from non-relatives, evaluate the quality of potential mates, and estimate a conspecific's fighting ability (Alcock 2005; Arnott and Elwood 2009).

Why Do Nonhuman Animals Assess Fighting Ability?

It is difficult to know why animals would assess fighting ability if one does not know why animals fight. Fortunately, evolutionary biologists understand the basics of animal aggression quite well: aggression is a tool designed by natural selection that enables one organism to disrupt the functional integrity of another organism in ways that enable the aggressor to solve an adaptive problem. For example, a lion requires large numbers of calories to survive. The meat of a gazelle contains these calories, but gazelles have evolved to flee from lions. Lions then evolved neck-biting behaviors

that disconnect the gazelle's respiratory and circulatory system which causes loss of function and renders the prey inert so that the lion can consume it.

Excepting predator–prey relationships, conflicts between conspecifics rarely require that one's opponent be killed. Conflicts between individuals of the same species are often over territory, food sources, and mates. Such fights can be “won” if an organism disorders the functional machinery that constitutes the body of the other (i.e., injures them). Thus, aggression is frequently used during these conflicts (Alcock 2005). Typically, the larger more powerful animal will win these conflicts, a pattern found in dozens of species. While physical size and strength contribute to fighting ability, in species where size is less relevant to the likely outcome of a fight, different traits will determine the winner, e.g., weapon size, physical condition, and tactical position (Arnott and Elwood 2009). Assessing these traits is therefore of crucial importance. Any animal that can assess, in advance, whether it is likely to win a conflict can make more prudent decisions about whether to instigate, escalate, or retreat during a fight. Therefore, one would predict that natural selection has designed adaptations that perceive cues of fighting ability in others and in oneself and use those estimates to modulate between different behavioral strategies before, during, and after a conflict.

Evidence shows exactly that (Arnott and Elwood 2009; Huntingford and Turner 1987). Many species estimate fighting ability from perceptual cues (e.g., vocalizations, visual inspections) but also from aggression itself. Given the importance of assessing fighting ability, and the selective damage of an erroneous estimate (i.e., retreating from a fight one could have won and commencing in a fight that one loses), it should not be surprising that natural selection has shaped complex mechanisms for these estimates. For example, domestic hens use a kind of Bayesian reasoning when watching two conspecifics fight, so that when one hen defeats another, the hen watching the fight will credit the victor with greater fighting ability if the opponent they defeated was estimated to be a good fighter (Hogue et al. 1996).

If humans have had a history of aggression, then we should expect nature to have equipped them with adaptations that assess fighting ability as well.

Are Humans Likely to Have Fighting Ability Assessment Mechanisms?

The ancestors of modern humans were highly aggressive (Pinker 2011). In past environments (in which the human mind evolved; see Tooby and Cosmides 1990), being able to accurately estimate the fighting ability of another human would have provided a powerful reproductive advantage. Therefore, one would predict on first principles that humans are designed to accurately assess fighting ability in conspecifics (Sell et al. 2009).

Crucially, human aggression is usually deployed against and by males. In this way, humans conform to a widespread mammalian pattern in which the sex that invests less in offspring competes more aggressively for access to mates and the resources used to keep and acquire them (Daly and Wilson 1983). One result is that the male human morph has been designed for combat at the expense of longevity. For example, compared to women, men have larger bodies, higher basal metabolic rates, larger hearts, better heat dissipation, more hemoglobin, more muscle, less fat, denser bones, and much more upper body strength (see Sell et al. 2012). These differences – and others – demonstrate that men have been engaged in aggressive competition for many generations. Finally, while most aggression is deployed between males, research shows that female mate choice is also influenced by factors related to fighting ability (see Collins 2000; Fink et al. 2007; Hughes et al. 2004). This would contribute to the sex differences in frequency of aggression, but also mean that women would also use mechanisms for assessing male fighting ability. Taken together, this chain of reasoning leads to three predictions: (i) that humans have likely evolved fighting ability assessment mechanisms, (ii) that those mechanisms should be fine-tuned to estimate male fighting ability, and (iii) that both men and women should have these mechanisms.

Adaptations for Assessing Fighting Ability

The primary function of assessing fighting ability is to predict the likely outcomes of fights in a way that minimizes the cost of fighting to the perceiver. Due to the nature of prediction, there is a trade-off between the accuracy and cost of the assessment. For example, one can estimate fighting ability very well by fighting someone to the death, but that comes at a great price. On the other side of the trade-off are perceptual estimates of fighting ability that are energetically cheap and do not risk injury but provide – presumably – less accurate assessments.

Because of their cheap nature, assessments in the animal kingdom frequently start with long-distance perceptual scans for cues that predict fighting ability. It is difficult to gain experimental control over realistic visual images and not possible to ask most animals whether a given opponent looks formidable, but evolutionary biologists have used controlled experiments to test whether animals use visual assessments of fighting ability. Results have shown across a number of animal species that visual assessment provides animals with information about fighting ability (see Arnott and Elwood 2009).

If there exist visual cues of fighting ability in humans, particularly human males, one would expect natural selection to have designed assessment mechanisms for the perception of those cues. Evidence supports this.

Visual Inspection of the Body

Humans have high functioning visual systems, and so it could be predicted that natural selection would tailor this system in particular to respond to any perceptible cues of fighting ability in the bodies of other humans – especially males. Such a prediction would require, however, that there actually be visually accessible cues of fighting ability.

How Could One See Fighting Ability in the Body?

A first principled analysis of human combat suggests that an individual's fighting ability is dependent in large measure on his ability to exert force

against another individual. Humans have no naturally produced poisons, toxins, inks, pincers, horns, or other ostentatious weaponry and fight instead with grips, punches, chokes, bites, and artificially constructed weapons. Such methods rely primarily on upper body strength for the application of force; indeed, no prehistoric weapon has ever been found that relied primarily on lower body strength for the production of force. While core and lower body strength is far from irrelevant, the ability to deliver a strike, choke, or hold will depend heavily on upper body strength. Therefore, one large component of human fighting ability will be upper body strength (see Sell et al. 2009). This analysis is supported by the fact that upper body strength is a highly sexually dimorphic trait in humans, with the more aggressive sex (males) having approximately 75% more of it (Lassek and Gaulin 2009).

Can Humans Visually Assess Fighting Ability?

According to this logic, males with physically stronger upper bodies should be readily perceived as such and be inferred to be better fighters. A team of evolutionary psychologists at UCSB conducted the first test to measure just how accurate assessment of physical strength is from visual inspections of the body (Sell et al. 2009). Sell and colleagues measured the upper body strength of 59 male subjects on four weight-lifting machines and took full body, shirtless, photographs of the subjects standing next to an experimenter (for size comparisons). Raters were then shown the photographs and asked to rate the subjects on how physically strong they appeared. Other raters were asked to rate the photographs on how “tough [he] would be in a physical fight.” Results showed that a static two-dimensional photograph of a man contained enough information that raters could predict about half of the variance in weight-lifting strength. Given that there was undoubtedly error in the lifting strength measure, that the photographs were static, and that the sample was truncated to primarily of young college-aged men, this 50% is certainly an underestimate of how much variance in physical strength can be assessed visually. Importantly, ratings of physical strength were identical to ratings of “toughness”

($r = .96$). This supports the view that upper body strength is a crucial component of fighting ability; in the minds of the raters, they were the same variable.

There is also evidence of specialized design in the assessments that supports the hypothesis that humans possess evolved fighting ability assessment mechanisms. For example, regression analyses showed that ratings of “toughness” and “physical strength” were tracking actual weightlifting strength more so than height or weight. While taller subjects were credited as being tougher (std. Beta = .29), this effect was much smaller than actual strength (std. Beta = .49). Body weight, once its correlations with lifting strength and height were statically controlled, was no longer related to ratings of fighting ability at all (indeed it was negative in some analyses). In other words, raters were not just picking larger males along easily perceptible dimensions (e.g., size, height) but were extracting cues of actual upper body strength, crediting males additionally if they were tall, and penalizing them slightly for being overweight. Additional analyses revealed that subjects were responding to cues of upper body strength over lower body strength. In other words, their ratings were zeroing in on the particular kind of strength that is used in ancestral human aggression.

What Are the Cues of Fighting Ability in the Body that Are Being Estimated?

The question of what actual cues were being perceived has remained largely unanswered. Morphometric measurements of the subjects were taken, and analyses showed that biceps circumference was the single best predictor of lifting strength, but no bodily measurement or combination of measures predicted upper body strength as well as ratings of strength did. It can be concluded, however, that height is being assessed (and taller men are being credited as better fighters), but the ability to accurately assess upper body strength visually is largely independent of height assessments. More research, preferably experimental research, will need to be done to isolate the visual predictors of fighting ability in men.

Is the Visual Assessment of Fighting Ability More Accurate on Male Targets?

Sell et al. (2009) replicated the assessment of upper body strength on a second sample of college students that included both males and females. This necessitated less naturalistic stimuli, e.g., female subjects wore standardized white T-shirts rather than being photographed shirtless, and upper body strength was assessed using proxy measurements validated on the gym sample, specifically, a portable chest compression measure, self-report, and flexed biceps circumference. Unfortunately, the fact that most of female subjects' upper bodies were obscured made it impossible to meaningfully compare the accuracy of assessing upper body strength across the sexes. Raters could still assess female upper body strength from photographs, accounting for approximately 25% of the variance in the composite strength measure. This was less accurate than ratings of male upper body strengths, but little can be made of this difference.

Visual Inspection of the Face

Sell and colleagues (2009) also speculated that humans might assess fighting ability via visual inspection of the face. This was based on three lines of reasoning: (i) there is a precedent in that the human brain is known to possess specialized perceptual mechanisms for processing many kinds of information from the face, (ii) cues of the upper body in ancestral environment may have been obscured by clothing, vegetation, carried objects, tactical cover, and so on, selecting for visual assessment of the face, (iii) decisions that make use of estimates of fighting ability would sometimes need to have been made rapidly, and (iv) the face may contain additional cues of upper body strength not present in the upper body itself (see Sell et al. 2009 for references). Indeed, Fink et al. (2007) had already shown evidence that a man's handgrip strength (a measure of upper body strength) was correlated with ratings (by females) of “dominance,” “masculinity,” and “attractiveness” once one controlled for age and body weight.

How Could One See Fighting Ability in the Face?

There are a number of reasons that the skeletomuscular structure of the face would be relevant to combat. Perhaps of most relevance is that the face is a frequent target of strikes and that strikes to the face can render an individual unconscious. There is paleontological evidence that the structure of the human face (which is markedly different than that of chimpanzees) has been tinkered by natural selection to absorb blunt force trauma more efficiently (Carrier and Morgan 2015). The possibility that differences in human faces track bite strength is also being investigated (Sell et al. 2014). These lines of inquiry suggest that faces are – to some extent – relevant to combat and therefore that different faces could be more or less proficient at aggression. Another possibility is that the face contains cues of fighting ability but that these cues are not themselves causally related to fighting ability. For example, the “masculinity” and “dominance” perceptions of a face often track testosterone levels in the body (Penton-Voak and Chen 2004).

Can Humans Visually Assess Fighting Ability From the Face?

As mentioned above, research demonstrated that handgrip strength in men was tracked by ratings of dominance by female raters (Fink et al. 2007). Sell and colleagues extended this analysis by including both sexes as raters and subjects, using more extensive measures of upper body strength, and including two non-Western cultures: the Tsimane Indians of Bolivia and a group of Andean pastoralists (2009). The correlations between ratings of strength and actual upper body strength are recreated in Table 1.

Results showed that both male and female raters could assess physical strength from a visual inspection of a static two-dimensional photograph

of a man with enough accuracy to predict about a quarter of the variance in upper body strength. Again, given the static nature of the photographs, the imperfect measures of fighting ability, and the limits of the sample, this likely underestimates the accuracy of assessment. Furthermore, accuracy was not diminished at all when assessing males from unfamiliar cultures (which also had no variance in ethnicity). Assessments of strength from female faces were less accurate when rated by either sex and (unlike full body ratings) were not compromised by sex differences in clothing. This suggests that both males and females are all well calibrated for assessing male strength.

Like assessments of the full body, assessments from the face were not overly dependent on estimates of height or weight. Ratings of physical strength from the face also tracked upper body strength over lower body strength; an impressive feat given is that neither the upper nor lower body was visible. This is consistent with two possibilities: either cues in the face that are being assessed are by-products of development or the cues arise because the developmental systems that give rise to upper body strength also coordinate functional components of fighting ability in the face (e.g., blunt force resistance).

One limitation of the Sell et al. studies is that they rely only on upper body strength as a measure of fighting ability. While upper body strength is undoubtedly a large component of fighting ability, there are many additional sources of variance in the ability to fight. Ideally, researchers would use actual fights to measure fighting ability, but this presents a sizeable ethical problem. Fortunately, mixed martial arts (MMA) – in which individuals fight with relatively few restrictions – has become a popular sport with enough data for analysis. Several researchers have looked at mixed martial arts contests and tested the ability

Male Adaptations to Assess Fighting Ability, Table 1 Accuracy of fighting ability assessment from face (From Sell et al. 2009)

	Gym sample (males)	Tsimane males	Andean males	UCSB students (males)	UCSB students (females)
Correlation with upper body strength <i>r</i> (<i>p</i>)	.45 (.0003)	.52 (.0001)	.47 (.01)	.39 (.00001)	.21 (.01)

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of subjects to predict winners based on photographs of the contestants' faces. While these fights are undoubtedly better measures of fighting ability, they unfortunately severely truncate the sample to only the best hand-to-hand fighters in the world and further truncate within samples by weight class.

With those limitations in mind, there have nevertheless been several published studies showing links between features of the face and combat performance in MMA.

Anthony Little and colleagues (2015) produced arguably the most direct test of whether fighting ability can be estimated from the face by showing the faces of MMA fighters to subjects who then attempted to pick the winner of the fight. Results showed that they could do this with better than chance accuracy. These faces were also rated for strength by different subjects, and the results indicated that MMA fighters with stronger-looking faces than their opponents were more likely to win.

One of the first studies to look at MMA fighters was done by Třebický and colleagues (2013) who looked at samples of MMA fighters and correlated their recorded fights against ratings of aggressiveness and fighting ability from photographs of their face. Results were mixed because weight was confounded with ratings of fighting ability (another limitation of MMA studies is that the fighters shed body fat in order to qualify in as low a weight class as possible, leading to an artificially high correlation between body weight and muscle mass). Perceived fighting ability was only predictive of fighting records among heavy-weight fighters who had no weight restrictions.

Another way to mitigate reliance on upper body strength as a measure of fighting ability is to use peer ratings. Doll and colleagues had fraternities give peer ratings of each other's fighting ability. They then had facial photographs taken and rated by strangers on "dominance." Results showed that these dominance ratings tracked peer ratings of fighting ability (Doll et al. 2014). And while dominance and fighting ability are not the same construct, ratings of dominance and ratings of fighting ability are very highly correlated (Toscano et al. 2014).

What Are the Cues of Fighting Ability in the Face?
Compared to research on body assessments, there are many research studies that hint at the cues that indicate fighting ability in the face.

Třebický and colleagues (2013), in their study of MMA fighters, found that aggressive-looking faces had larger chins, more prominent eyebrows, and a larger nose. Zilioli and colleagues (2015) analyzed a sample of several hundred MMA fighters and showed that having a face that was wider but shorter (i.e., facial width-to-height ratio, fWHR) was predictive of having more wins, a greater percentage of wins, and lasting for more matches in the competitive Ultimate Fighters Championship circuit. Artificial faces made to have wider faces were also rated as physically tougher than narrow faces. Toscano et al. (2014) used natural and artificial faces rated on strength and dominance. They found that low brows, large chins, wide noses, and narrow mouths were rated as stronger. Windhager and colleagues (2011) showed that physical strength (i.e., handgrip, shoulder width) was predictive of rounder faces, wider eyebrows, and a more prominent jaw, though the sample size was rather small for such analyses ($n = 26$). Windhager and colleagues also found that perceived dominance was the result of a wide lower face, smaller lips, shorter nose, and smaller eyes.

Research on the design of the anger face illustrated seven features of the face that are used when assessing physical strength. Sell et al. (2014) proposed that the anger face itself is a coordinated modification of cues in the face that indicate fighting ability. They had computer-generated faces rated for physical strength and showed that each of the seven major components of the anger face – independently – increased perceived strength. The features included: a lower browridge, higher cheekbones, wider nose, higher mouth, thinner lips, protruding lips, and larger chin and chin bun. While this demonstrates that these features do influence ratings of fighting ability, they did not demonstrate that these particular features are indeed present in better fighters.

Is the Visual Assessment of Fighting Ability More Accurate on Male Targets?

Sell et al. (2009) found that both males and females were more accurate at estimating male strength from photographs of the face. Most studies of fighting ability assessment, however, do not look at female faces, so this effect should be replicated before strong conclusions are drawn. Female MMA fighters are becoming more common, but so far no researchers have published work on whether female fighters’ records are predictable from facial features.

Cues of Fighting Ability in the Voice

Unlike the structure of the face, which may play some causal role in fighting (be it through biting or blunt force trauma resistance), it is unlikely that the acoustic properties of the human voice played a direct causal role in resisting or inflicting damage on others. Nonetheless, there are several reasons to believe that the voice may contain indicators of fighting ability (see Sell et al. 2010). Firstly, there are numerous animal precedents showing that vocal qualities not only indicate size and fighting ability but that animals evolved to respond to those qualities (see Huntingford and Turner 1987; Sell 2012). Secondly, research demonstrates that women’s mate choices are highly tuned to characteristics of the male voice, which indicates that there are cues of some desirable traits in the voice (Collins 2000; Hughes et al. 2004; Puts 2005). Finally, testosterone modifies the voice of males in ways that generate large sex differences in vocal characteristics (Dabbs and Mallinger 1999). Given that testosterone plausibly affects fighting ability (Bhasin et al. 1996), it is plausible that fighting ability itself can be predicted from cues in the voice.

Can Humans Assess Fighting Ability From the Voice?

There is good evidence that some physical characteristics associated with fighting ability can be assessed from the voice. Acoustic research in perceptual psychology has a long history – over 30 years – of testing subjects’ ability to estimate body size from the voice. The results depend partly on the nature of the voice samples and often have samples too small to detect the typical effect sizes reported elsewhere, but overall the research demonstrates the ability to assess height and weight from the voice (see Sell 2012 for review).

More evolutionary-minded researchers looked at aspects of the phenotype more closely linked to fighting ability rather than just height and weight. For example, Hughes et al. (2004) showed ratings of attractiveness predicted shoulder-to-hip ratio (a measure believed to be predictive of upper body strength).

Sell and colleagues (2010) tested the ability to assess fighting ability more directly by measuring upper body strength and gathering voice samples from four cultures: male and female college students from the USA and Romania, the adult male population of a Tsimane Indian group, and an adult male group of Andean pastoralists. Voice samples were done in the subjects’ normal speaking voice reading or repeating a standardized phrase in their native language. Correlations between measures of upper body strength and ratings of strength are reported in Table 2 and illustrate that males and female can accurately assess upper body strength from the voice.

Again, accuracy was not diminished at all when assessing males from unfamiliar cultures. Assessments of strength from female voices

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Male Adaptations to Assess Fighting Ability, Table 2 Accuracy of fighting ability assessment from the voice (From Sell et al. 2010)

	Males					Females	
	USA-1	Tsimane	Andean	USA-2	Romania	USA-2	Romania
Correlation with upper body strength $r(p)$	.45 (.001)	.35 (.02)	.46 (.04)	.51 (.001)	.48 (.001)	.26 (.07)	.32 (.08)

were generally less accurate when compared to the males of the same culture. As with photos of the face, additional analyses showed that both males and females were well calibrated for assessing male strength and that the assessments were not highly dependent on estimates of height or weight. Furthermore, because photographs of the subjects were available as well, regression analyses were able to be run that demonstrated that assessments from the voice were not redundant with assessments from photographs. In other words, having access to a man's voice as well as visual information about his body enabled a more accurate rating of fighting ability than either did alone.

Other research has failed to find a link between various covariates of fighting ability and ratings of dominance or strength. Doll et al. (2014), for example, found no relationship between dominance ratings of male voices and their acquaintance-rated fighting ability. And numerous studies failed to show that subjects could assess height or weight reliably (see Sell 2012).

Regardless, the weight of the evidence is that various body characteristics associated with fighting ability are linked to different acoustic cues that are produced in the normal speaking voice and spontaneously extracted by the human auditory system (see Sell 2012 for review).

What Are the Cues of Fighting Ability in the Voice? Researchers have suggested numerous acoustic traits that could covary with fighting ability, body size, or the assessments thereof. While some progress has been made, no one has produced an acoustic analysis that can be shown to mimic the ratings of human responses. Regardless, there has been data that demonstrates some recurrent relationships between acoustic variables and various body measurements. The most common are *fundamental frequency* and *formant dispersion*.

F0 – Fundamental frequency. Fundamental frequency is the result of vocal fold vibrations during speech and is not physiologically necessarily related to body size or strength. The vocal folds do, however, respond to testosterone and are highly sexually dimorphic due to a rapid thickening in adult males. The result is that adult men

have much lower F0s (i.e., lower “pitched” voices). F0 clearly distinguishes men from women, and adolescent men from adult men (Hodges-Simeon et al. 2014), but generally does not highly distinguish strong from weak men or large from small men. Nonetheless, experimental manipulation of F0 does show that listeners respond to it and (mis)attribute greater size and strength to men with lower pitched voices. These results were found in Sell et al. (2010) for all tested cultures. F0 did not predict physical strength but did predict ratings of strength (see also Rendall et al. 2007). In her definitive meta-analysis on vocal correlates of body size, Pisanski and colleagues (2014) found that F0 explained less than 2% of the variance in height and weight within adult within-sex samples.

Df – Formant dispersion. Formant dispersion was first proposed by Fitch (1997) who defined it as the averaged difference between adjacent formant frequencies and is – in theory and in practice – linked to the length of the vocal tract and therefore likely covaries with height and perhaps other physical traits. It is an acoustic variable known to predict body size in a number of non-human species (see Pisanski et al. 2014). Sell et al. (2010) found in a single sample of recorded vowel sounds that Df did not predict physical strength and could not account for the accuracy of strength assessment. It did predict height marginally. This is consistent with the larger literature that shows various measures of variance in formant position showing weak negative relationships with height (Pisanski et al. 2014).

Pf – Formant position. Formant position was first introduced by David Puts and colleagues (2011) as a new way of measuring formants which results in a more sexually dimorphic measure similar to formant dispersion (see Puts et al. 2011 for details). Puts and colleagues showed that Pf predicts upper body strength in both a US sample and a sample of Hadza men from Tanzania (correlations were $-.26$ and $-.23$, respectively, though given the smaller sample size, the Hadza correlation was not significant).

While the details of the acoustic variables are still under study, there is good evidence that

speaking voices contain cues of fighting ability and that people extract and use them to estimate it.

Self-Assessment of Formidability

Without an accurate estimate of one's own fighting ability, knowledge of another's would be of little functional use. Thus, it is expected that animals and humans have mechanisms for assessing, tracking, and updating their own fighting ability. Direct evidence comes from experiments such as Richard Alexander's work with fighting crickets (1961). When crickets were allowed to physically dominate "dummy" crickets (i.e., artificial animals created by biologists to resemble crickets), the victors become more likely to challenge live competitors in the future, demonstrating that victory is tracked in the brain of the winning animal as an indicator of the likelihood of future success. Edmonds and Briffa (2016) recently showed that some animals not only track their own fighting ability, but different aspects of their fighting ability. When hermit crabs had the effectiveness of their shell knocking strikes reduced (by buffering their shell), they compensated by switching to an uncompromised and lesser used tactic – rocking their opponent's shell. This switch suggests that the crabs are estimating the effectiveness of at least two kinds of strikes and updating this estimate continuously.

The phenomena of "badges" – in which animals signal their fighting condition via coloring or markings – also demonstrates that animals maintain an internal representation of their own fighting ability (Alcock 2005).

The most direct evidence that humans store representations of their own formidability is data showing very high correlations between objective measurements of physical strength and subjects' own self-assessments (Sell et al. 2009). Similar research shows that individual's self-ratings of fighting ability correspond closely to those of their peers, i.e., men and their peers agree on who are the best fighters (Doll et al. 2014). The mechanisms which humans use to do these computations, and their computational structure, remain to be mapped.

Future Research: Aggression as Assessment

From an evolutionary point of view, perceptual assessment is low cost but low accuracy. There are many factors that determine an individual's fighting ability that will not be vulnerable to a visual or auditory analysis. For example, the following factors are sexually dimorphic and arguably causally related to fighting ability: reaction time, basal metabolic rate, mental rotation and speed of spatial visualization, throwing accuracy, history of combat practice, heat dissipation rates, hemoglobin levels in the blood, heart size, and lung capacity (see Sell et al. 2012). These traits could still be estimated if the developmental programs that gave rise to them were, for example, coordinated by pubertal testosterone levels which left perceptible cues in the voice and face. Regardless, these are imperfect estimates of imperfect indicators.

More accurate estimates of fighting ability can be gained through actual fighting. Evolution has designed mechanisms in many nonhuman animals for engaging in ritualized aggression or "conflicts of assessment" (Huntingford and Turner 1987; Alcock 2005) that function to enable two animals to assess fighting ability during a given conflict. For example, the cichlid fish studied will progress through a series of aggressive stages starting with perceptual assessment (e.g., parallel swimming), to coordinated displays of body size and strength (e.g., "tail-beating" in which the fish take turns shaking their bodies at each other to make waves), and finally actual contact aggression (e.g., mouth-locked wrestling) (Enquist et al. 1990). By following the rules of this "ritual," both animals are able to assess fighting ability through forms of aggression that are less likely to result in injury for both contestants.

Such rituals are found among humans as well (Pinker 2011). A more detailed and thorough treatment of ritualized aggression in humans is needed and will likely be able to explain core concepts in human aggression such as honor, "fair fights," sports, and sportsmanship.

Conclusion

In conclusion, given the long history of human aggression – particularly between males – there is a strong theoretical reason to believe that natural selection would have favored mechanisms for estimating male fighting ability. The computational structures of these mechanisms are now being mapped. Evidence shows that both men and women can estimate aspects of fighting ability from cues in the body, face, and voice. While the exact nature of the cues is still being explored, there is evidence that cues of fighting ability in the face include aspects of the brow, the width-to-height ratio of the face, nose and mouth size, and jaw size. Cues of fighting ability in the voice likely include aspects of formant position that result from the length of the vocal tract and possibly fundamental frequency. Future research will likely show that a great deal of human interpersonal aggression is also designed for assessment.

Cross-References

- Aggression
- Assessment of Fighting Ability
- Combat Sport
- Contexts for Men's Aggression Against Men
- Evolution of Fighting Assessment Abilities
- Facial Width to Height Ratio and Dominance
- Fighting Assessment
- Function of Dominance
- Intrasexual Competition
- Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)
- Male-Male Competition
- Mate Preferences
- Physical Aggression
- Psychological Mechanisms
- Resource Competition
- Self-Assessment of Fighting Ability
- Sex Differences in Ability to Assess Fighting Ability
- Signals of Body Size
- Size and Dominance
- Tactics to Solve Adaptive Problems of Sperm Competition

- Upper Body Strength
- Upper Body Strength and Fighting Ability
- Upper Body Strength From Photo
- Vocal Indicators of Dominance

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Male Aggression

► Perpetrators Mostly men

Male Battles

► Sexual Selection via Direct Male-Male Interactions

Male Bonding

► Male Friendship

Male Coalitional Aggression

► Male Warrior Hypothesis

Male Coalitional Psychology

► Same-Sex Coalitions That Exclude Women

Male Coalitions for Hunting

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Synonyms

Coalitions; Cooperation

Definition

A coalition is a complex social construct that requires a balance between competitive and cooperative behaviors.

Introduction

People coming together to form coalitions, or temporary alliances, for the intent of attaining a shared goal has been observed since the Pleistocene Epoch (Colarelli et al. 2006; Sugiyama et al. 2018). Human ancestral preferences for protein- and fat-rich foods meant that ancestral hunter-gatherer tribes had to form hunting coalitions to capture larger and faster prey, which offered these nourishments, that would have eluded the lone hunter (Boesch 2002). Because coalitional hunting was a highly complex and risky endeavor, the task of hunting fell primarily on males, who possess physical capabilities and psychological adaptations that facilitated the success of a hunt (Bailey et al. 2013), including the physiological build and strength of a male, the tendency to form instrumental relationships, and their propensity toward risk-taking behavior (Apicella et al. 2017; Tanner 1990).

Today, even though hunting coalitions are less common, male coalitions are still evident in

activities involving group-level competition such as warfare and team sports (Apicella et al. 2017; Geary et al. 2003; Lombardo 2012; Van Vugt et al. 2007). Given the extent of the topic, this chapter will limit its review to how ancestral hunting coalitions facilitated the development of certain adaptations that conferred the male certain advantages in cooperative intergroup situations.

Physical Capabilities for Hunting

According to the evolutionary neuroandrogenic theory, during the gestation period of the male fetus, the Y chromosome initiates a series of biochemical actions that lead to significant spikes in testosterone production which results in an androgenized brain (Ellis 2011). Such a development accounted for greater physical size and strength, agility, bone density, and musculature – features that made males better suited for the physical requirements of hunting as compared to females (Geary et al. 2003). Since males with these traits were better able to provide, such indicators of strength also came to be perceived as indicators of a healthy and resourceful mate. Hence, these traits were maintained via sexual selection as they were preferred and sought after by the opposite sex (Apicella 2014; Escasa et al. 2010).

Many of today's sports parallel the skills required in hunting, such as the chasing of the ball in football or the aiming and throwing of a basketball (Lombardo 2012). Even with the surge of female athletes, sport remains primarily dominated by males with male athletes generally outperforming their female counterparts (Lombardo 2012), suggesting the evolved physical skills and qualities that males possess (de Block and Dewitte 2009).

Adaptations for Hunting

Underlying a hunting operation is an intricate system that maximizes cooperation while minimizing intragroup competition, implying that males would have evolved several psychological adaptations that drove these behaviors.

Hunting is a complex skill. The hunter must come to understand the prey being hunted; he must have tactical awareness of other group members, and the understanding of their own role within the group (Boesch 2002). Only then would the group be able to execute complex actions such as fanning out, chasing, distracting, ambushing, surrounding, and capturing (Boesch 2002). In these activities, members would have to cooperate. Doing so would increase the probability of a successful hunt and increase the ability of the coalition to capture a wider variety of prey that differ in size and speed at lower risk of injury and lower cost of energy, as compared to a lone hunter or an uncoordinated group (Bailey et al. 2013). The reduced risk and energy lost per hunter would also mean that hunting could be conducted more frequently to attain larger amounts of food resources to support a larger community (Bailey et al. 2013). The ability to form coalitions for hunting, therefore, carried a significant survival benefit for the group.

Males continue to demonstrate higher tendencies to form large groups that are instrumental in nature and goal oriented (Geary et al. 2003). In organizations today, males continue to show a tendency to form instrumental workplace relationships that revolve around a shared interest or activity, while females were more likely to form workplace relationships that are more communal and support oriented (Morrison 2009). This phenomenon can already be observed in boys as young as 5 years who would form large social groups that display dominance hierarchies and role differentiation, while girls tend to form smaller dyads that focus on intimacy, emotional support, and guidance (Eder and Hallinan 1978). Boys have also been observed to discourage intragroup aggression when faced with intergroup competition, which suggests that when confronted with an external threat to the group, the mechanism for intragroup competition would be suspended in exchange for the formation of a coalition to address the external threat (Colarelli et al. 2006). This could be suggestive of adaptive mechanisms that have evolved to maximize cooperative behavior and minimize competitive behavior in males.

Risk-Taking Propensity

Coalitional hunting, although risky, was a highly rewarding venture (Apicella et al. 2017). Risk-taking behavior in hunts offered opportunities to attain larger payoffs and were selected for, given that it maximizes the potential resources an individual could bring home (Apicella et al. 2008). This innate propensity for risk-taking is evident in activities males partake in today. A study of 1200 children from Colombia and Sweden found that boys as young as 9 years old showed a greater preference for the all-or-nothing coin flip option over the slow incremental option, which demonstrates a greater propensity for risk-taking behavior (Cárdenas et al. 2012). Men were more likely than women to engage in multiple domains of risk-taking behavior such as in between-group competition, in within-group competition, and in the context of reproduction (Wang et al. 2009). Men were also more likely to make risky financial decisions that offer a larger payoff (Apicella et al. 2008). This risk-taking propensity, combined with competitive predispositions, has been cited as one possible reason for why men continue to occupy top positions in the majority of organizations (Croson and Gneezy 2009).

Conclusion

Over the course of human history, males have evolved physical capabilities and adaptations for cooperative and competitive behaviors and the propensity to engage in risk-taking as a consequence of hunting coalitions. Such evolved mechanisms remain in today's world even though the need for hunting has reduced. Taken together, this evolutionary perspective can offer a novel framework for utilizing evolved mechanisms in modified settings to enhance productivity, teamwork, and healthy competition in the modern workplace, while simultaneously identifying and correcting dysfunctional environments (Colarelli et al. 2006; Yue et al. 2019). With the rising influx of women into the workforce, this evolutionary framework may, ultimately, aid organizations in fully utilizing the increasing diversity in the modern world.

Cross-References

- [Coalitional Hunting](#)
- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Male Adaptations that Facilitate Success in War](#)
- [Male Friendship](#)

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Male Counter Strategies to Cyclic Shifts

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Synonyms

[Attractiveness](#); [Concealed ovulation](#); [Fertility](#)

Definition

Women's mating psychology, behavior, and attractiveness shift over their menstrual cycle.

Men may have evolved strategies to mitigate any undesirable effects of these shifts on their own fitness.

Introduction

Human female fertility varies over the menstrual cycle. The likelihood that a single act of intercourse will result in conception is greatest in the days preceding ovulation. At this time, women are more attractive and are more driven to enhance their attractiveness. Androphilic women become more interested in men who are not their primary partner, and their preference for physically and behaviorally feminine men decreases. Because men who are women's primary partners risk desertion or (if their partner engages in short-term sexual relationships with other men) investing in biologically unrelated offspring, they have likely experienced selection pressure to deploy counterstrategies that mitigate the effects of female menstrual cycle shifts. These counterstrategies may include changes to a man's sexual desire, his jealousy and mate-guarding behavior, and his propensity to compete with sexual rivals.

Sexual Interest

Men may respond to female shifts in sexual behavior or appearance by increasing sexual interest in primary partners who are in the fertile cycle phase. Cerda-Molina et al. (2013) collected female underarm and vulvar odor samples while the women were in the periovulatory (fertile) and luteal (non fertile) phases of their cycle. Men sniffed the samples and completed a questionnaire on their interest in sex. Men's sex interest increased after they smelled periovulatory samples but did not change after they smelled luteal samples. Other studies indicate that exposure to the body odor of women in the fertile phase results in men estimating women's sexual arousal as higher and that men are more prone to behaviorally mimic a woman in the fertile phase (Miller and Maner 2011). Increased desire and an overestimation of women's sexual interest may cause

men to more readily and more frequently initiate sex, thereby reducing the primary partner's interest in extrapair copulations, limiting her opportunities for extrapair copulations, or instigating sperm competition with her extrapair sexual partners.

Miller and Maner (2010) hypothesized that men's responses to cues of fertility in non-primary partners should vary depending on whether the man is in a current relationship. They showed that single men are more attracted to fertile than non-fertile women but that partnered men are less attracted to fertile women. Devaluing a fertile non-partner may reduce men's temptation to stray from their primary partner and promote relationship stability.

Jealousy and Mate Retention Behavior

Because men stand to lose more if their female partner copulates with other men during her fertile rather than her non-fertile phase, men may be expected to feel greater sexual jealousy and to behave in ways that minimize the likelihood of a partner straying or being poached when that partner is most fertile. Gangestad et al. (2002) had women rate the extent to which their male primary partner performed each of 41 mate retention behaviors. They found that women reported that their partner performed more of such behaviors when they were fertile, and behaviors were more frequent the nearer women were to ovulation. Proximity to ovulation was related to men's proprietariness and attentiveness, but the strongest relationship was with vigilance (checking up on the partner's location and activities). Less attractive women report that their partner is more jealous and possessive near ovulation, whereas more attractive women report consistently high jealousy and possessiveness throughout the cycle (Haselton and Gangestad 2006). Mate retention behavior also encompasses tactics that are perceived positively, and women whose primary male partner is lower in sexual attractiveness report that their partner more frequently expresses love and commitment during the high rather than the low fertility cycle phase (Pillsworth and Haselton 2006).

The Challenge Hypothesis

The challenge hypothesis posits that men may compete more strongly with male sexual rivals when in the presence of fertile females. Testosterone is implicated in sex drive and competitiveness, and research suggests that salivary testosterone levels increase in men exposed to the body odor of fertile women and decrease after exposure to the body odor of women in the non-fertile phase (Cerdeña-Molina et al. 2013). Similarly, the testosterone levels of men whose primary partners are in the fertile phase of their cycle increase after men view photographs and descriptions of rivals but only if those rivals are competitive and attractive: men whose partners were in the non-fertile phase, or who viewed uncompetitive rivals, did not experience an increase in testosterone (Fales et al. 2014).

Men may have benefited historically by an increased sensitivity to rivals at times when the threat of partner infidelity was greatest. Women are more attracted to men with masculine and dominant traits during the fertile phase of their cycle. Men whose primary partners are in the fertile phase rate male faces as more dominant than men whose partners are in the non-fertile phase but only if those faces appear especially dominant: men do not rate submissive faces differently as a function of their partner's cycle phase (Burriss and Little 2006). This shift in perception may aid men in identifying rivals who present the greatest threat to their relationship.

Conclusion

Women can only accrue the putative genetic benefits of copulating with extrapair men if copulation occurs when fertility is most likely, in the days preceding ovulation. Because women's extrapair sexual behavior is detrimental to the fitness of their male primary partner, it is plausible that men would have evolved counterstrategies to prevent their partner straying or being poached. Research suggests that men are more sexually interested in fertile women, are more apt to be jealous of fertile partners, and respond hormonally and behaviorally toward threatening rivals when

their partner is fertile. If a cost to men of deploying these counterstrategies is the increased likelihood of a partner's desertion, it would be maladaptive to do so uniformly across the partner's cycle.

A limitation of much of the research on this topic is that it relies upon women's reports of men's behavior. It is possible that, just as women's mating psychology shifts over the cycle, so too does their perception of their partner's counterstrategies. Certainly, women resist male mate-guarding more strongly when fertile (Gangestad et al. 2014). Their reports of partner mate retention behavior may, therefore, not be accurate. Also, most research on responses to women's cyclic shifts is laboratory-based and tests unrelated individuals. There is a need for more research on how men respond to cyclic shifts and on how their female partners resist counterstrategies, in real relationships (Haselton and Gildersleeve 2015).

Cross-References

- [Concealed Ovulation](#)
- [Dual-Mating Hypothesis](#)
- [Evolution of Long-Term Pair-Bonding in Humans](#)
- [Menstrual Cycle](#)
- [Ovulation](#)
- [Sexual Signaling During Ovulation](#)
- [Sperm Competition](#)

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Male Defense

► Male Protection

Male Detection of Deception

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Men and women have differing parental investment needs with respect to relationships (Trivers 1972) and place emphasis on different

characteristics when evaluating potential partners. So, not surprisingly, when it comes to mating, both sexes engage in a type of contest, so to speak, where deception occurs on the part of both sexes (Grammer et al. 2000) and both sexes expect the opposite sex to deceive and lie in order to gain a mate (Keenan et al. 1997; Benz et al. 2005). But, both men and women report being upset when they are deceived and lied to (Haselton et al. 2005), and men assume women are being deceiving the majority of the time (Goetz and Causey 2009).

The deception that occurs often centers around characteristics that are preferred by the opposite sex in order to facilitate one's outcome in intersexual competition (Benz et al. 2005; Keenan et al. 1997). The opposite sex's ability to detect deception on the part of a partner would also help them compete intersexually. But, there is an “arms race” between female deceptive skill and male detection of deception skill. Men have evolved abilities that help them detect when women are being deceitful. However, since women's deceptive abilities are also evolving, men are not always successful at detecting deception.

Men place an emphasis on women's attractiveness when they are evaluating partners (Buss 1989, 2006). Not surprisingly, women tend to deceive men by altering their physical attributes, specifically by engaging in self-enhancing behaviors (Tooke and Camire 1991). But, men tend to fail at detecting changes in women's physical appearance, and the research indicates that men's detection of deception tends to be no better than chance (Klaver et al. 2009). A real-life example of a man's failure to detect physical appearance changes on the part of a woman involves the case of a man who sued his wife after discovering her plastic surgery (Li 2013).

One way men could be able to detect physical appearance deception on the part of a woman would be via pheromones. Women are most fertile and most reproductively fit when they are ovulating, and artificial pheromones do not increase attractiveness (Grammer et al. 2005). Thus, even though a woman may alter her appearance to appear more beautiful, a man would still be able to determine if he is being

deceived by focusing on the pheromone profile the woman is emitting.

Another area where women may seek to deceive a man is regarding being sexually unfaithful. Women may engage in this deception because a man's reaction to a female partner's sexual infidelity may involve physical violence against the woman (Daly et al. 1982). If a man fails to detect sexual infidelity on his female partner's part, he runs the risk of being cuckolded into investing in another man's offspring, wasting his resources, and thus reducing his fitness and genetic legacy. Research shows that men are indeed best at detecting sexual infidelity, rather than emotional infidelity on a partner's part (Shackelford and Buss 1997). Men focus on cues such as "increased reference to and time spent with another person"; "passive rejection of partner/inconsiderateness"; "acting guilty and being anxious toward a partner"; "angry, critical, and argumentative toward a partner"; "emotional disengagement from a partner"; reluctance to spend time with a partner"; reluctance to discuss a certain person"; and relationship and dissatisfaction/loss of love for a partner" to detect infidelity on a female partner's part. These points suggest men have developed adaptations to help them detect deception on the part of women.

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Male Display

► Leks and Choruses

Male Dominance

► Origins of Patriarchy

Male Dominance Hierarchies

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Dominance *relationships* refer to asymmetries of control within dyads of individuals. Whether this control is exerted over nutritional resources, space, or sexual partners does not fundamentally matter, as long as framing social interactions in terms of dominance enables the observer to better

predict the outcome of these interactions (Bernstein 1981). For example, the concept of dominance can be invoked when predicting that if A has won over B in the past, then A will also win over B in the future or that if A prevails over B when competing for food, then A will also prevail over B when competing for space or sexual partners.

By contrast, dominance *hierarchies* refer to the transitive manifestation of the aforementioned asymmetries within a social group, such that if one has observed that A dominates B and B dominates C, then one can deduce that A will dominate C. This transitivity criterion plays a key normative role in determining which behavioral metrics are suitable for the assessment of dominance hierarchies. The most famous of these metrics is perhaps the “pecking order” early described in chicken by Schjelderup-Ebbe (1921), where ranks are defined based on priority access to nutritional resources. Yet male dominance hierarchies are now mainly defined on the basis of directional aggression patterns. Although many other transitive metrics can result in stable estimates of hierarchical structures (approach-retreat, facial displays, vocalizations, etc.), aggression is indeed easy to observe and generalizes well across species.

Hierarchical gradients have multiple consequences for the physiology of male individuals which are most often mediated by the influence of steroid hormones and, to a lesser extent, by inflammatory and immune pathways. Individuals of lower ranks have typically higher circulating levels of cortisol, resulting from repeated exposure to social stressors and forewarning fitness-reducing outcomes like hypertension or diabetes (Sapolsky 2004). In some species, these physiological counterparts are so profound that behavioral assays become superfluous to infer dominance. For example, in the African cichlid fish, dominant and subordinate individuals can be readily distinguished on the basis of a specific pigmentation pattern around the eyes (Burmeister et al. 2005). Closer to us, subordinate orangutans retain salient juvenile traits for many years (i.e., lack of cheek flanges, reduced weight, etc.) until the alpha male finally loses dominion

(Pradhan et al. 2012). But it is perhaps in male anole lizards that the most spectacular effects of dominance are observed, as a single social defeat can turn body color from bright green to brown in 1 hour (Greenberg and Crews 1990). Because changes are mostly triggered in subordinate individuals following social defeats and other unfavorable competitive outcomes, some authors have suggested that the term “subordination hierarchy” would better reflect the biological bases of social ranks (Rowell 1974). This shift of perspective is crucial because many of these changes represent more than mere correlates of social rank: instead, they tend to reinforce hierarchical structures themselves by weakening further the competitive abilities of previously defeated individuals – a widespread phenomenon known as the “loser effect” (Rutte et al. 2006).

From an evolutionary viewpoint, the most relevant observation is certainly that subordinate individuals tend to reproduce less efficiently than dominant ones in most taxa, including primates (Ellis and Lee 1995). Although rarely complete, likely exacerbated by captivity and more prevalent in females, this reduction of reproductive success indicates that dominance hierarchies partly mediate the process of natural selection. For example, in chimpanzees, the alpha male routinely sires between one- and two-third of the offsprings (Newton-Fisher et al. 2009). This common observation depends on several causes whose respective contributions vary from one species to another: (i) active guarding of fertile females by dominant males, (ii) delayed acquisition of secondary sexual characteristics in subordinate males due to inhibition of androgen release, and (iii) mating choices of females revealing a preference for dominant males. Complementing prestige- and wealth-dependent mating, this latter effect is significant in humans where it is further gated by women hormonal status (Havlicek et al. 2005; Roney and Simmons 2008). In turn, since dominance hierarchies have exerted a long-lasting pressure in the course of evolution, numerous subordinate traits can be conceived as adaptations selected to minimize the threat to reproductive fitness associated with unfavorable social contexts. In the field of “Darwinian psychiatry”

(Price 1967), the core symptoms of prevalent mental disorders are thus largely envisioned as the downside of mechanisms which used to be adaptive in prehistoric societies before becoming dysfunctional in modern societies. For example, the drive to withdraw which accompanies depression might represent an adaptive response to social defeat, as it can reduce the risk of harm and might even facilitate access to reproductive partners beyond the attentional focus of mate-guarding dominant males.

Finally, it must be emphasized that the manifold consequences of dominance hierarchies depend heavily on the neurocognitive processes which underlie the perception of control over events (Qu et al. 2017). Indeed, it is well known that the lack of control over stressful events dramatically exacerbates their detrimental consequences over physiology and behavior, even when the objective amount of stress is kept equal (Maier and Seligman 2016). Presumably mediated by neuromodulatory systems such as serotonin – which has also been involved in aggression and dominance from lobster to humans (Edwards and Kravitz 1997; Duke et al. 2013) – this overarching impact of control brings us back to the very definition of social dominance. Moreover, because these neuromodulatory systems are highly plastic, because they influence a wide array of brain functions, and because they are ubiquitous in the animal kingdom, they provide a unique window on the interplay of dominance and evolution. Understanding how the evolutionary dynamics has sculpted these systems so as to adapt individuals to the hierarchical social structure surrounding them may eventually help us to understand the origins and the mechanisms underlying the so-called socioeconomic health gradient, which explains why millions of human beings are literally sick of male dominance hierarchies (Adler et al. 1994).

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Male Friendship

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Synonyms

Bromance; Fraternal relationality; Fraternity; Male bonding

Definition

Friendly relationships between related or unrelated males.

The developmental rationale underpinning friendship is well-substantiated in the literature. The process of developing and maintaining friendly bonds with kith is crucial for human children to develop Theory of Mind, interpersonal reasoning, and their faculties for moral judgment. Friendships also serve as a form of social training ground; one in which our earliest instances of developing empathy, forming coalitions, and resolving conflicts begins to take root.

Male-male friendship – what has often colloquially come to be referred to as male bonding or “bromance” (Tiger 2017) – possesses unique dimensions from both an evolutionary and a developmental perspective. From early childhood, male-male friendships are characteristically defined by a greater frequency of rough-and-tumble play, rehearsed belligerence, participation in games governed by systems thinking and strictly codified rules, and the establishment of clearly-defined hierarchies and role positioning. This is in stark opposition to typical female-female friendships during childhood, which tend toward egalitarianism, inclusiveness, and games based more on participation and fair play than rules and rewards (Bjorklund and Pellegrini 2000).

Throughout adolescence and into adulthood, male-male friendship often reflects many of its

early developmental antecedents. Male friendships – consistent with male psychology generally – tend to be more “things-oriented” than “people-oriented”; driven more by mutual interests and activities than by the deeply affectionate personal bonding that is more characteristic of female-female friendships (Robinson et al. 2017). That said, there is a unique affective dimension to male-male friendships that complements the more utilitarian and systemic qualities that are generally more apparent in such friendships. Indeed, one study noted that an overwhelming majority of males preferred to share deeply emotional insights and highly personal matters with their male friends than with their female romantic partners. The authors observed that, for most of the men surveyed in their study, “bromantic relationships were more satisfying in their emotional intimacy, compared to their heterosexual romances” (Benenson et al. 2014).

It seems likely that the capacity for developing and maintaining friendships along same-sex lines generally, and in male-male friendships specifically, had significant adaptive value for the evolution of our species. In ancestral times, males were responsible for the greater preponderance of game hunting; sorties which may have lasted days or weeks depending on the local climate and season, as well as the predatory or grazing patterns of the fauna being pursued (Hildebrandt and McGuire 2002). Such hunting activity would have unquestionably been highly labor-intensive and physically draining, and would also have required significant intra-party co-ordination, division of labor, and collective buy-in as to the relative distribution of the eventual spoils. Time spent away from camp, and thus romantic partners and children, would have likely exacted an additional mental and emotional toll on the participants (Lewis et al. 2011).

Male-male friendship, thus, likely has deep evolutionary roots in humans. The ability to form close bonds with one’s same-sex peers would have allowed males to participate in hunting activity in a harmonious, collectively cohesive manner in spite of the substantial emotional pressure that

accompanied such an emotionally taxing and threat-laden pursuit. It would likely have provided an additional layer of mental reassurance through interpersonal concord, clearly explicated roles and responsibilities, and a unified focus on the particularities of the task at hand. The cognitive and behavioral features of male-male friendship in antiquity likely parallel those found in the “bromantic” relationships of their modern analogues.

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Male Guarding

- [Male Protection](#)

Male Homicide Victims

- [Most Victims Are Men](#)

Male Intrasexual Competition

- [Most Perpetrators Are Men](#)
- [Most Victims Are Men](#)

Male Intra-sexual Competition

- [Male–Male Strategies](#)

Male Intrasexual Homicide

- [Most Perpetrators Are Men](#)
- [Most Victims Are Men](#)

Male Mate Choice

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Synonyms

[Men romantic partner choice](#); [Men sexual partner selection](#)

Definition

Romantic or sexual partner selection by men; characteristics that guide male choice of their romantic or sexual partners.

Introduction

According to the Parental Investment Theory (Trivers 1972), males and females present their mating strategies related to the investment they make in their offspring. In general, females tend to invest more time and energy in their children. Males, on the other hand, do not invest in offspring as much as females do, and the low paternal investment necessity allows them to invest more time and energy in mating effort. For them, engaging more in short-term relationships, with different sexual partners, increases their probability of having a greater reproductive success since they can have more children in a short period of time. Therefore,

men's reproductive success is limited by their access to women, which leads them to compete to have access to females, a limiting resource.

Sexual Strategies Theory

Observing men and women romantic partners preferences, Buss and Schmitt (1993) noticed both sexes focus on different characteristics. Distinct evolutionary pressures have acted on men and women and have led them to valorize different traits in their partners in order to maximize their reproductive success.

Because of women's high physiological investment in children (9 months of gestation, breastfeeding, and the primary care with children), men tend to prioritize physical attractiveness more than women do (Buss 1989).

Physical Attractiveness

As the physiological investment by women is mandatory, men who choose their partners based on characteristics that give them cues about women's good physiology for having children, such as ideal estrogen levels, have increased their reproductive success (Karremans et al. 2010). Karremans et al. (2010) found that women's body in hourglass shape (waist-to-hip ratio of 0.7) is considered more attractive. This proportion of fat distribution is positively associated with the neural development of the embryo, and women who have ideal estrogen levels accumulate more fat in the hip area.

Age

In addition, due to the relation of women's physiology and fertility, another important trait is age (Kenrick and Keefe 1992). Women have a short period during which they can reproduce when comparing to men. Women start being reproductive with menarche, having their reproductive peak around age 24 and stop reproducing at menopause (around 50 years old). With the increase of men's

age, there is a decrease of their fertility because of sperm quality (such as ill-formed sperm) and quantity, but there is no interruption of their reproduction (Pawlowski 2000). Thus, age is a limiting factor of female reproduction and, therefore, important when men are looking for a partner.

Strategy Change

Even though men tend to adopt a short-term relationship, there are some circumstances that might lead them to modify their strategy from short- to long-term. One factor that can influence men's strategy change is the percentage variation of women in a population. A men-biased operational sex ratio forces men to choose a partner and commit to her faster than usual in order to guarantee at least one woman by his side, since some men will not have access to her (Kruger et al. 2010).

Another factor that might influence men's strategy is their perception of social acceptance. Men who perceive themselves as less accepted socially tend to decrease their self-esteem and, consequently, their mate value evaluation (Penke and Denissen 2008). Men with a low self-esteem level, as men in a men-biased population, also tend to commit faster than usual.

Conclusion

In order to maximize their reproductive success, men tend to invest more in short-term relationships, for having the possibility of getting greater access to women. Women invest more physiologically in children when compared to men. This factor leads men to search for characteristics that signal women's capacity to have children. Through physical attractiveness, men assess information about women's youth and fertility, important factors to women's reproductive potential.

Cross-References

- [Female Mate Choice](#)
- [Intersexual Selection](#)

- [Limited Reproductive Potential](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Reproductive Strategies](#)
- [Sexual Strategies Theory](#)

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Male Mating Competition

- [Polygyny and Male Risk-Taking for Status](#)

Male Offenders

- [Perpetrators Mostly men](#)

Male Ornamentation

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Synonyms

[Badges of status](#); [Secondary sexual traits](#)

Definition

Sexual selection has shaped the evolution of extravagant secondary sexual characters in males via female choice (intersexual selection) and male-male competition (intra-sexual selection). Visually conspicuous sexually dimorphic characters can play a purely ornamental role in sociosexual interactions as “badges of status” communicating maturity, social status, dominance, and sexual attractiveness. This entry takes a Darwinian comparative approach spanning monkeys, apes, and man to outline how sexual selection has shaped male ornamentation.

Introduction

Sexual selection theory asserts that female choice, male-male competition, or their combination has shaped the evolution of sexually dimorphic male secondary sexual characters (Darwin 1871). Ornaments embellish and elaborate upon underlying bodily or facial structures and, in some cases, are part of coordinated behavioral displays that serve to attract females (Puts 2010). In other cases, ornaments function as badges of status, enhancing aspects of male sexual maturity, social rank, and dominance during male-male social encounters (Puts 2010). This entry takes a Darwinian comparative approach spanning monkeys, apes, and man to outline how sexual selection has shaped male ornamentation.

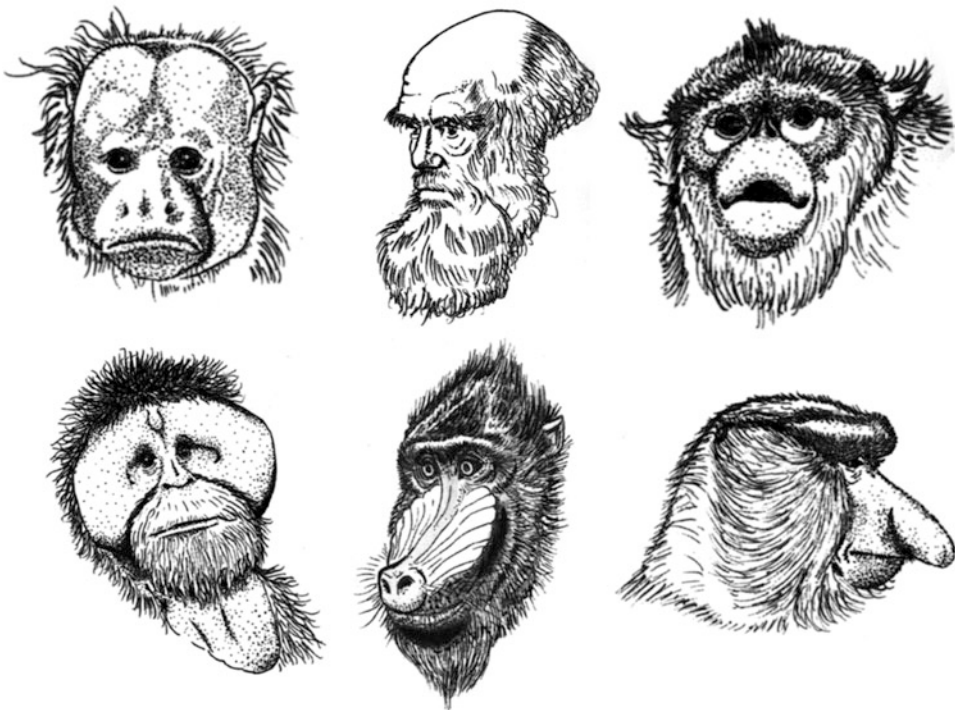
Sexual Dimorphism in Male Ornamentation Among Anthropoid Primates

In *The Descent of Man, and Selection in Relation to Sex*, Darwin noted the pronounced sexual dimorphism in visually conspicuous ornamentation, canine size, and body mass among anthropoid primates and suggested sexual selection had shaped their evolution (Darwin 1871). Particular attention was given to the role of male ornamentation in communicating social rank, status, and dominance that, in turn, may be associated with male attractiveness and reproductive success. Some striking examples of visually conspicuous male ornaments are shown in Fig. 1, which show the red facial coloration of male mandrill (*Mandrillus sphinx*), the white and gray capes of hair in hamadryas baboons (*Papio hamadryas*), the large nose in the male proboscis monkeys (*Nasalis larvatus*), the fleshy cheek flanges in orangutans (*Pongo* spp.), the triangular patches

of red skin on the chest of geladas (*Theropithecus gelada*), and the beardedness in men (*Homo sapiens*; Dixon et al. 2005). The sections that follow discuss the role of mating systems, social group sizes, and social group organizations may have had on shaping ornamentation among male primates.

Sexual Selection, Mating Systems, and Male Badges of Status

The largest sex differences in body mass and canine size occur in primate species with polygynous mating systems, followed by multi-male multi-female mating systems, with monogamous mating systems being the least sexually dimorphic (Dixon et al. 2005). Polygynous systems are characterized by stronger intra-sexual selection for access to females, maintaining harems and protecting females and infants than multi-male multi-female or monogamous mating systems



Male Ornamentation, Fig. 1 Some of the most striking examples of sexually dimorphic ornaments in male anthropoids. The top row shows from left to right the red uakari (*Cacajao calvus*), man (*Homo sapiens*), and golden snub-nosed monkey (*Rhinopithecus roxellana*). Pictures on the

bottom row from left to right show the Bornean orangutan (*Pongo pygmaeus*), mandrill (*Mandrillus sphinx*), and proboscis monkey (*Nasalis larvatus*). (The drawings are used with permission from Alan F. Dixon)

(Dixson et al. 2005). Thus, augmented body size and canine size may play an important role in intra-sexual competition among male nonhuman primates with polygynous mating systems compared to species with other mating systems (Dixson et al. 2005).

Ornamentation in male nonhuman primates may not be biologically homologous to those in men. However, they may play analogous roles as sociosexual signals (Dixson et al. 2005). If these ornaments were sexually selected by female choice, male-male competition, or some combination of the two processes, one would predict that their expression would vary due to the mating system. Quantitative analyses of sexual dimorphism in male primate ornamentation, including all hairy, fleshy, and colorful characters, revealed ornaments were more developed among species with polygynous than monogamous or multi-male/multi-female mating systems (Dixson et al. 2005). Those analyses included men's beardedness, body hair, and patterned baldness. While humans are primarily serially monogamous, in some cultures high status males may be polygynous (Puts 2010). Irrespective of whether men were included in the analyses as monogamous or polygynous, polygynous primates scored highest for ornamentation followed by species with monogamous mating systems, with species with multi-male multi-female mating systems scoring the lowest (Dixson et al. 2005). When men were included as a monogamous species, monogamous primates had higher ornamentation scores than multi-male multi-female species. When men were included as a polygynous species, the differences between monogamous and multi-male multi-female species were no longer significant, and the effects of polygyny on ornamentation was strengthened. Thus, men are similar to species of male nonhuman primates with some degree of polygyny in the mating systems.

Social Group Sizes, Social Organizations, and Male Ornaments

In addition to mating systems, the social environment profoundly affects the strength of mate competition. The complexity of male facial

coloration is positively correlated with social group size in Old World monkeys and apes (*Catarrhini*; Santana et al. 2013). In New World monkeys (*Platyrrhini*), color patterns have evolved to facilitate individual recognition in smaller social groups (Santana et al. 2013). Facial color complexity varies with sympatry among Old and New World primates, so that more gregarious and sympatric species have more complex facial coloration than less gregarious and non-sympatric species (Santana et al. 2013). To further explore how social and ecological factors relate to the expression of ornamentation in male monkeys, apes, and men, Grueter et al. (2015) used a refined classification of primate social organization and social group size as predictors in phylogenetic comparisons of sexual dimorphism in ornaments. Results revealed a positive relationship between ornamental dimorphism and group size, which remained after controlling for other independent variables such as habitat type and fission-fusion dynamics. Ornamental dimorphism also differed according to social organization, being greatest in males from species with multilevel social organizations. Thus, men were similar to species of nonhuman primates with large social groups and multilevel social systems wherein males have well-developed visually conspicuous sexually dimorphic traits. These findings suggest that in complex social systems characterized by larger social groups, individual recognition may be compromised and the need to signal rank, dominance, or attractiveness may be greater.

Sexual Selection and Men's Beardedness as an Ornamental Badge of Status

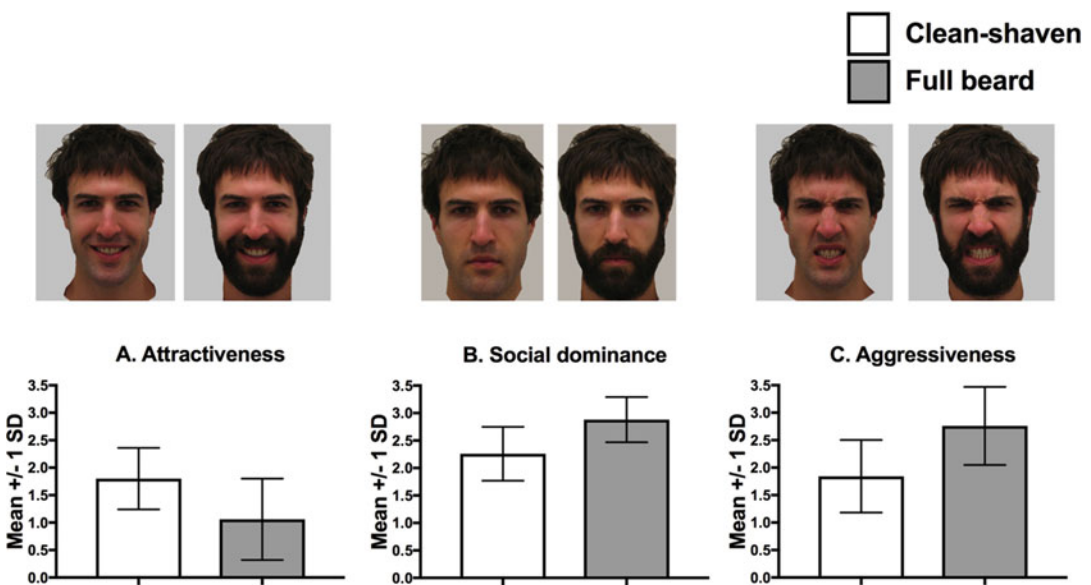
Comparative studies of ornamentation among male anthropoid primates suggest that men's ornamentation reflects sexual selection via male-male competition and female choice (Dixson et al. 2005; Grueter et al. 2015). Beards represent possibly the most strikingly sexually dimorphic ornament between men and women. Sex differences in facial hair emerge during adolescence under the dual actions of testosterone and dihydrotestosterone (DHT), where facial

hair follicles require the conversion of testosterone to DHT via the actions of the enzyme 5 alpha reductase 2 for their activation and growth (Dixon et al. 2016). Dixon and Vasey (2012) showed using images of men with their natural amount of beard growth at 4–8 weeks that bearded faces were judged as more socially dominant and aggressive by men, but less attractive by women, than clean-shaven faces (Fig. 2). This suggests beards play a stronger role in intra-sexual communication between males than enhancing attractiveness to women.

The ease with which men can groom and remove their facial hair suggests that variation in men's beardedness may not communicate underlying genetic quality (Dixon et al. 2016). Indeed, there is little evidence that women's preferences for men's beards are stronger under contexts favoring short-term mating strategies (for review, see Dixon et al. 2018). Instead, cross-cultural research has shown that women's preferences for full beards are stronger in countries with low-average incomes and more male-biased sex ratios and in larger cities where men

tend to be more bearded and life expectancy is higher (Dixon et al. 2017, 2019b). As facial hair communicates aspects of male age, sexual maturity, and social aspects of dominance and status (Dixon and Vasey 2012; Craig et al. 2019), beardedness is preferred under conditions where women may benefit from an intra-sexually competitive partner (Dixon et al. 2017, 2019b). Interestingly, women state stronger preferences for beards when judging male stimuli for long-term relationships and paternal investment where tangible resources that directly benefit the survival of mothers and their children may be acquired (reviewed in Dixon et al. 2019a). Studies comparing ratings of beardedness and clean-shaven male faces suggest that beards enhance perceptions of age, masculinity, dominance and parenting abilities among mothers compared with non-mothers (reviewed in Dixon et al. 2019a). Taken together, men's beards may represent a classic example of a Darwinian ornamental badge of status that enhances men's age, social status, and attractiveness when considering long-term rather than short-term mating contexts.

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Male Ornamentation, Fig. 2 These data show mean ($\pm$ 1 SD) ratings of clean-shaven (Open bars) and full bearded (gray bars) faces made by women and men from New Zealand. A total of 129 women rated stimuli posing smiles for attractiveness (a); a total of 52 men rated faces

posing neutral expressions for social dominance (b); a total of 111 men rated faces posing angry expressions for aggressiveness (c). (This figure is reproduced using data from Dixon and Vasey (2012) and the stimuli are owned by Barnaby Dixon)

Conclusion

Over 150 years ago, Darwin suggested that visually conspicuous sexually dimorphic ornamentation in male primates functions as badges of status during male-male competition that, in turn, influence female mate choice. For many years these hypotheses, particularly as they apply to the evolution of masculine characters in men, remained largely unexplored. A resurgence of interest in how men's ornaments function in sociosexual communication highlights a key role of male-male competition in shaping men's mating success. Future research exploring how the strength of intra-sexual selection on male ornaments relates to men's mating success under variable ecological, social, and economic factors will be valuable.

Cross-References

- [Facial Attractiveness](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Masculinity and Femininity](#)
- [Sexual Selection via Direct Male-Male Interactions](#)

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Male Perception of Cycle-Related Fluctuations in Women's Attractiveness

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Synonyms

[Hormonal cues to attractiveness](#); [Male preferences](#); [Menstrual cycle changes](#)

Definitions

Men tend to perceive female appearance and behavior as slightly more attractive during the follicular phase of their cycle.

Introduction

Women lack the conspicuous morphological and behavioral changes related to their menstrual cycle that are seen during estrus in some old-world monkeys, such as baboons, or in some apes, such as chimpanzees. In these species, changes in morphology and behavior – including genital swelling and active sexual solicitation – tend to peak in the fertile phase of the cycle and elicit elevated interest and sexual activity in their male conspecifics. Although they are not as conspicuous, some cyclic fluctuations in physical appearance and behavior can nonetheless be observed in women.

Cyclic Change in Women's Appearance

Studies of cyclic fluctuations in attractiveness have focused on perception of individual attributes such as faces, body odor, and voice. Several studies have shown that facial images taken during the follicular phase are rated as more attractive when compared to images taken during the luteal phase of the cycle (e.g., Roberts et al. 2004). Attractiveness changes are associated with changes in skin color, skin texture, and facial shape, occurring perhaps due to cyclic fluctuation in fluid retention.

Similarly, axillary and vaginal odor is perceived to be most attractive during the follicular phase, and fluctuations are absent or attenuated in women using hormonal contraception (Kuukasjarvi et al. 2004). Exposure to female body odor collected during the fertile phase may elevate testosterone levels in men, although other studies did not confirm this effect (Roney and Simmons 2012). While the chemical compounds responsible for the aforementioned fluctuations in perception of female body odor are not yet fully characterized, they may include fluctuations in concentrations of short fatty acids.

Vocal attractiveness follows a similar pattern as observed in the perception of faces and body odor. Again, we also know something about the proximate mechanisms involved: the increase in perceived vocal attractiveness is at least partly related to elevated voice pitch during the follicular phase (Fischer et al. 2011).

Cyclic Changes in Behavior

Cyclic fluctuations in attractiveness are not restricted to physical cues; they can also be observed in various behavioral cues. For instance, it has been shown that women at mid-cycle prefer to dress in clothes that reveal more skin and are more likely to wear red and pink colors (Haselton et al. 2007), which are associated with higher attractiveness judgements. Women in the fertile phase also tend to use more cosmetic products. Cyclic fluctuations have also been observed in the perceived sexiness of dance (Fink et al. 2012) and gait, although in the latter case, the reported pattern varies across individual studies – some studies reported a peak during the follicular phase (Fink et al. 2012), while another study found the same peak during the luteal phase.

In contrast to available evidence gathered under controlled conditions, our understanding of how such cyclic effects are perceived in real life is rather limited. So far, only one study aimed to assess whether changes in appearance and/or behavior might have some real-life consequences. In a sample of lap dancers, women earned significantly more in tips during the fertile phase than other parts of the cycle, but again, no similar pattern was found in hormonal contraceptive users (Miller et al. 2007).

Menstrual cycle also appears to affect perceptions of coupled men toward their female partners. Similar to the studies reviewed above, all of which focused on cyclic fluctuations in perceived attractiveness of unfamiliar women, men perceive their partners as more attractive during the fertile window, but such fluctuations are not evident in men whose partners were using hormonal contraceptives. Furthermore, women report their partners as being more possessive and attentive during their fertile phase (Thornhill and Gangestad 2008).

Methodological Considerations

Most studies interpret higher attractiveness judgements in the follicular phase as detection of ovulation. However, this is somewhat misleading as ovulation itself is a relatively short, internal

physiological process which can be detected only by hormonal assays or ultrasonography. Furthermore, many of the published studies did not confirm whether an actual ovulation occurred using luteinizing hormone assays. This is an important issue as a not insignificant proportion of cycles in healthy women appear to be anovulatory – conservative estimates place this between 8 and 12% – although the actual proportion may vary extensively depending, for instance, on women's age, physical activity, and nutritional status. Furthermore, due to significant variation in cycle length and thus also in timing of the fertile window, counting methods only crudely estimate actual fertility. Together with small effect sizes, this might be a reason why cross-sectional studies often fail to find cyclic effects. To avoid these shortcomings, rigorous guidelines on methodology of menstrual cycle-related studies were recently provided and include, for instance, the use of within-subject design and employment of hormonal assays to better estimate the conception probability (Gangestad et al. 2016). Another methodological issue concerns stimulus presentation. Stimuli collected in different phases of the cycle are subsequently presented simultaneously. In principle, this never happens in real life and may thus overestimate actual effect sizes.

Evolutionary Interpretations

In general, effect sizes of the reviewed cyclic effects tend to vary from small to modest, and their evolutionary significance is currently hotly debated. The mainstream view tends to interpret male sensitivity to observable cyclic cues as an adaptation (Thornhill and Gangestad 2008). According to this view, men more sensitive to such cues might increase their chances for conceptive sex and thus increase their fitness. Similarly, coupled men sensitive to cyclic cues in their partners may increase mate guarding to reduce the chances of their partners' infidelity. However, the predictive value of such changes appears to be relatively low. For instance, Fischer et al. (2011) note that the overall variation over the cycle precluded the unequivocal identification of ovulation. Also, there are currently no studies

testing cross-modal integrations of the observed cycle-related effects.

Alternatively, behavioral and perceptual sensitivity to fertile phase cues may be by-products of an adaptation to discriminate ovulatory from anovulatory cycles or indeed as a by-product of more general preferences for women with high potential fertility (i.e., the overall likelihood of being able to conceive) (Havlíček et al. 2015). Male preferences for cues of potential fertility, such as estrogen-related facial cues or low waist-to-hip ratio, have higher effect sizes compared to those for within-cycle changes and are generally considered to be an adaptation. Both within-cycle fluctuations in attractiveness and between-individual differences in attractiveness appear to be based on a shared underlying hormonal mechanism (e.g., levels of estrogen and progesterone). It could therefore be possible that the former arose as an inevitable perceptual by-product (or spandrel) of the latter. This is supported by considerably higher between-individual variation as compared with within-individual cyclic changes. Thus, in future studies, there is a need for more focus on the comparison of cycle-related within-women fluctuations and between-individual differences, in conjunction with measurement of levels of circulating sex hormones.

Conclusions

Changes in menstrual cycle-related attractiveness have been observed in various modalities including facial appearance, body odor, voice, and some behaviors such as gait and appearance enhancements. These fluctuations tend to be absent in women using hormonal contraception, indicating involvement of sex hormones, although exact mechanisms are currently not well understood. Nevertheless, the effect sizes of the cyclic changes are typically small to moderate. Cycle-related changes in attractiveness are often interpreted as men's adaptation to cues of current fertility which may increase probability of conception. Alternatively, perception of cyclic fluctuations in attractiveness may be a by-product of more general preferences for women with high potential fertility, as both within-individual cyclic changes and

interindividual differences are based on a shared underlying hormonal mechanism.

Cross-References

- [Adaptation](#)
- [Attraction During Ovulation](#)
- [Birth Control](#)
- [By-Products of Adaptations](#)
- [Dual-Mating Hypothesis](#)
- [During Ovulation](#)
- [Evolution of Adaptations](#)
- [Facial Attractiveness](#)
- [Fertility](#)
- [Mate Value](#)
- [Men's Mate Preferences](#)
- [Menstrual Cycle](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Sexual Signaling During Ovulation](#)
- [Sexual Strategies Theory](#)
- [Spandrels](#)
- [Women's Preferences During Ovulation](#)

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Male Preferences

- [Male Perception of Cycle-Related Fluctuations in Women's Attractiveness](#)

Male Protection

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Synonyms

[Male defense](#); [Male guarding](#); [Male safety](#)

Definition

The act through which males protect themselves and/or others.

Introduction

Natural selection favors those physical and psychological traits that are beneficial in terms of reproduction and survival (Dobzhansky 1956). Human ancestral times were characterized by prevalent violence, consisting both of within and between group conflict (Duntley and Shackelford 2012; LeBlanc 2003; Puts 2010). As a result, both men's and women's psychology could have been influenced by such violent contexts, leading to preferences for certain physical traits related to protection from partners or allies (men's: Borráz-León et al. 2014; women's: Buss 1994).

Male Protection for Females

On average, women are shorter, smaller in size, less aggressive, and have a weaker body composition compared to men (Daly and Wilson 1988). Evidence from archeological archives suggests that damage of property, homicide, and rape were common practices during human evolutionary history (Keeley 1996; LeBlanc 2003). During this time, conflict was mostly driven by intra-sexual competition between men (Archer and Benson 2008; Little et al. 2013; Puts 2010), hence women's physique could have made them more vulnerable to becoming victims of crime and violence elicited by men (Duntley and Shackelford 2012; Perilloux et al. 2012). The costs associated with men's aggression against women ranged from physical and psychological pain (Thornhill and Palmer 2000) to death (Duntley and Shackelford 2012). In order to minimize or avoid these costs, women are thought to have evolved psychological strategies to protect themselves from potentially being hurt (Duntley and Shackelford 2012).

Women's preferences may have thus shifted toward men with the ability to protect them from violence and therefore decrease victimization risks (Li et al. 2014). Previous studies have suggested that traits that indicate men's protective capabilities, their probability to survive in agonistic encounters, and deter competitors could be their physical formidability, aggressiveness, and

coerciveness (Snyder et al. 2008). Findings on who women prefer as partners have supported this idea. Buss (1994) found that women choosing potential partners had a higher preference for men who could offer protection for themselves and their children. Likewise, Snyder et al. (2011) found that when women felt at higher risk of crime, they preferred partners who looked more formidable and dominant. Taking this idea further, Ryder et al. (2016) found that women's preferences for more formidable and dominant men were exacerbated in crime hotspots and decreased in safespots. Furthermore, women have been found to prefer friends, short-term mates, and extra-pair partners who were described as protective (Bleske-Rechek and Buss 2001; Greiling and Buss 2000). These results suggest that women prefer to be in contact with men (either as partners or friends) who are more capable of protecting them under violent contexts.

Women's higher preferences for more formidable partners are not restricted to bodily features; it extends to facial ones too. For example, men's facial masculinity, which has been directly related to perceptions of dominance (Fink et al. 2007; Little et al. 2013), was preferred by women who were primed with images of male on male conflict (Li et al. 2014). Findings from Li et al. (2014) suggest that when women face danger they prefer partners who would be more able to protect them as well as partners who are more masculine, formidable, and dominant (Windhager et al. 2011).

Men's ability and willingness to protect women can be considered both an asset and a liability. A protective partner would be characterized by being more aggressive, dominant, and physically formidable (Snyder et al. 2011). Although a partner with these traits may seem advantageous in a violent scenario, it could be dangerous as well (Borrás-Guevara et al. 2017a; Li et al. 2014; Snyder et al. 2011). For instance, men's aggressiveness correlated positively with coercion and predicted partner abuse (Lorber and O'Leary 2004). Furthermore, aggression, coerciveness, and getting more involved in fights are more common between stronger than average men (Archer and Thanzami 2009; Sell et al. 2009). While there is a clear association between

men's protective traits and women's risk of being hurt, most research on the influence of violence on women's mate preferences has focused on the benefits women obtain when choosing a protective partner. Only a few studies have done research on the potential costs that women would face as well when preferring such kind of partners (Borras-Guevara et al. 2017a; Li et al. 2014; Snyder et al. 2011). Li et al. (2014) found that when women were primed with images of men punching women, their masculinity preferences dropped. More recently, while studying a Colombian population, Borras-Guevara et al. (2017a) found that women who feared men being dangerous to their children had lower masculinity preferences for male faces.

The findings from Borras-Guevara et al. (2017a, b) and Li et al. (2014) both illustrate the multi-modalism of violence. Indeed, studies on public violence have revealed that this type of violence is mainly driven by intra-sexual competition between men (Wilson and Daly 1985). In domestic violence reports, however, women are commonly the victims and men the perpetrators (Zlotnick et al. 1998; Brewster et al. 2002). Therefore, women's partner preferences should reflect the different roles men and women play during public or domestic violence.

Due to the above, living in a violent environment may not be the only criteria women take into account when choosing a protective partner, they should also take notice of the incidence and severity of different types of violence (Borras-Guevara et al. 2017a, b). That is, choosing a protective partner may be a priority when domestic violence is perceived as infrequent, but public violence is recurrent (Borras-Guevara et al. 2017b). In fact, Colombian women's partner preferences confirm this claim. Women who were asked about their perceptions of domestic and public violence, whose perceptions of within partnership violence were higher, had lower masculinity preferences for male faces (Borras-Guevara et al. 2017b).

The existing research supports the idea that women's mating preferences reflect a need for protection; however, the type of partner they prefer may shift depending on the source of violence. If women face higher public violence,

where conflict is mainly between men, they may be better protected by more aggressive, formidable men. Yet if domestic violence is instead more common than public violence, women may be better off partnering up with someone less likely to be aggressive toward them (i.e., someone less aggressive and formidable).

Male Protection from Males

Men's psychology, like women's, may have been influenced by the high frequency of violence in ancestral environments (Borráz-León et al. 2014; Duntley and Shackelford 2012). In such contexts, men would benefit from recognizing potential allies to approach, from whom they could gain protection from, or potential rivals to avoid (Borráz-León et al. 2014). In support of this idea, Sell et al. (2009) as well as Holzleitner and Perrett (2016) found that men can accurately evaluate other men's fighting abilities by precisely identifying physical cues of strength. An additional explanation, however, is that this ability reflects men's need to protect themselves from potential cuckoldry since during human evolution, male intra-sexual competition for female partners was fierce (Puts 2010).

Previous research has found that men's preferences for other men match that of women (Batres and Perrett 2014; Borras-Guevara et al. 2017a, b; Borráz-León et al. 2014). On the one hand, these findings could support the idea that men's preferences for more formidable males reflect a need to recognize potential rivals, who would be more attractive for potential partners. On the other hand, men's preferences could reflect their ability to identify males that represent a lower/greater threat to them. Following this idea, Borras-Guevara et al. (2017a) reported that Colombian men, who feared about general violence, preferred less masculine male faces, just as women did, suggesting that when facing conflict, men would prefer male allies who represent to them a lower risk of being hurt. How much protection is gained from an ally, however, depends on the physical abilities of both parties involved. That is, a man's own physical strength influences his perceptions of potential

competitors (Fessler et al. 2014). Indeed, Watkins et al. (2010) found that when men considered themselves as less dominant than the average, they were more likely to associate facial masculinity with fighting capacity, compared to men who rated themselves as more dominant.

Men's need for protection, reflected in their preferences for allies, may depend on the source of violence too. Domestic violence is not a matter that only affects women. In fact, in the last 10 years, within-partnership violence against men in the UK has increased by 500%. To date, however, no study has focused on the effects of different types of violence on men's preferences for allies or enemies.

Conclusion

Overall, the existing literature agrees with the notion that women's mating preferences under violent circumstances reflect a need for protection. However, these preferences are contingent on the type of violence women need to protect themselves from. Studies that have taken into account women's fear of public violence, or violence between men, have found that under these conditions women prefer more formidable-aggressive men. When other types of violence were also studied, for example, domestic violence, women preferred less formidable and aggressive partners. In the case of men, it is still not clear if preferences for other males reflect either a desire to gain protection, avoid costs associated with agonistic encounters, or to discern what potential partners want. More studies on both women's and men's preferences for male protection are thus needed to clarify and reach a consensus about their causes.

Cross-References

- [Male Defense](#)
- [Male Guarding](#)
- [Male Safety](#)
- [Male-Male Competition or Male Provisioning?](#)

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Male Provision

► Resources

Male Prudence and Sperm Limits

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Synonyms

[Adjustment of copulatory/ejaculatory investment;](#)
[Strategic ejaculate investment.](#)

Definition

Males do not maximally inseminate females each mating, but rather strategically inseminate sperm according to intrinsic factors such a body condition and extrinsic factors such as sperm competition risk and female quality.

Introduction

The root of the evolutionary differences between the sexes is gametic anisogamy, whereby males produce lots of tiny and relatively cheap gametes, while females produce fewer immotile and relatively more expensive gametes. Despite the relative difference in gametic investment between the sexes, males are clearly not always eager to mate, just as females are not always reluctant to mate to protect their high investment. And even when males do mate, they do not always inseminate females with the largest possible ejaculate or best quality sperm that they can make. Instead, ejaculates are often modified according to intrinsic and extrinsic factors (Wedell et al. 2002).

Ejaculatory and Copulatory Adjustment

Adjustment of copulatory investment in males has been known for decades. The Coolidge effect refers to the observation that a male placed in an arena with multiple females will mate repeatedly with all the females up to the point of apparent sexual exhaustion. However, when a new female is introduced to the group, the male will quickly recover and mate with renewed vigor with the new female (*Rattus rattus*). Males will also adjust their ejaculate investment and inseminate the new female with greater amounts of sperm (*Gallus gallus*). Such strategic investment makes evolutionary sense. Continuing to mate with the same female would likely be wasteful beyond the point at which the female has either acquired enough sperm to fertilize all of her eggs or has been sufficiently stimulated by the male to use his sperm.

Ejaculate Production Is Costly

The physiological cost of ejaculate production, including sperm and seminal fluid production, can be significant. Therefore, sperm prudence is necessary, as males can be limited in the amount and quality of sperm, as well as the amount and quality of seminal fluid they can produce during a reproductive season (Wedell et al. 2002), and males can lose fitness after repeated ejaculation due to sperm depletion. Ejaculatory investment often varies according to the male's body condition. When males are in better condition, they can have larger testes and produce higher-quality sperm than when they are in poor condition.

Extrinsic Factors Affect Ejaculate Investment Across Taxa

Ejaculate investment can be influenced by extrinsic factors affecting male mate choice and sperm competition (Kelly and Jennions 2011). Males will inseminate more sperm when they perceive sperm competition to be high (in the presence of a male that can witness copulations by a pair) than when no other rivals are present.

Males also allocate more or better quality sperm to females that will produce a higher fitness

payoff to the male investment (Kelly and Jennions 2011). Higher-quality females can include those deemed to be more fecund, unmated, more genetically compatible, and more distantly related (Kelly and Jennions 2011).

The combination of the male's own quality and the quality of the females available for mating can also mediate ejaculatory investment: Dominant cocks (*Gallus gallus*) are more prudent in their ejaculatory investment than subordinate males. Dominant males mate more often, and they allocate more sperm to high-quality females, whereas subordinate males have similar ejaculatory investments in the few matings they can achieve.

Ejaculatory Capacity in Humans

Depletion of the extragonadal reserve of sperm in men is rapid, occurring on the second day after an average of 2.4 ejaculations per day, with significant declines in ejaculate volume (47%), sperm concentration (67%), and total sperm (84%) during this period (Freund 1963). During the follow-up period, the numbers of sperm remained well below the original counts before the beginning of the experiment (Freund 1963), suggesting that sperm depletion is a real risk for men after repeated ejaculation and, therefore, that strategic sperm allocation may be evolutionarily favored. Other studies have supported the generality of these findings (reviewed in Shackelford et al. 2005).

Evidence of Ejaculate Adjustment in Humans

In humans, ejaculate adjustment was reported in a study where the authors tested the hypothesis that men may inseminate more sperm to their partners after they had spent time apart, presumably because they could not have mated guarded (Baker and Bellis 1989). Ten couples used a condom to collect ejaculates resulting from intercourse, and their sperm counts were compared to those of ejaculates collected through masturbation. Data from how much time they had spent apart prior to the copulation were collected, and the authors reported that sperm numbers were

significantly correlated with the percent time the couples had spent apart prior to copulation, while no such correlation was found for the masturbation samples (Baker and Bellis 1989). In a follow-up study that added a large survey to investigations of ejaculate number, Baker and Bellis again reported a correlation between sperm numbers and time apart prior to copulation, but their sample sizes continued to be very small (out of 33 recruited pairs, only 15 males produced repeated intra-pair copulation samples, and most did not produce masturbation samples) (Baker and Bellis 1993). They also concluded that men inseminate larger numbers of sperm to larger females (heavier and taller), consistent with the idea that males should adjust their ejaculate when mating with higher-quality females. From the survey data on 3,679 women, they concluded that time apart did in fact reflect the risk of sperm competition, as women who reported having extra-pair sex were more likely to do so when they were apart from their partner.

Although their results are intriguing, Baker and Bellis' studies are correlational in nature, suffer from lack of controls, and small sample sizes (Shackelford et al. 2005; Leivers et al. 2014). Unfortunately, no recent experimental studies with large sample sizes have followed up Baker and Bellis's studies.

The quality and quantity of ejaculates collected from copulatory activities compared to ejaculates collected from masturbation are known to be different (Shackelford et al. 2005). Although this hints at the potential for strategic sperm allocation to take place to avoid wasting too much sperm during masturbation (Shackelford et al. 2005), better/larger ejaculates may be a nonadaptive consequence of higher levels of arousal during copulation when compared to masturbation. Men produce better ejaculate samples through masturbation when allowed to view erotic materials, again perhaps because such materials produce higher arousal levels.

Perceived sperm competition while viewing erotic materials seems to result in ejaculatory adjustment. Men express a preference for erotic materials that depict multiple males engaged in sex with one female than a single male having sex with multiple females as evidenced by sales of

erotic DVDs (McKibbin et al. 2013). This preference seems to be translated into ejaculate quality. When viewing erotic materials, males produced a higher-quality ejaculate when the material included two men and one woman than when it only included three women, presumably because men were viewed as potential competitors (Kilgallon and Simmons 2005). And just as is the case in cocks, ejaculate investment in men can be context dependent, according to the male's own mate value. Men that were rated as having higher mate value invested more in ejaculates only when viewing erotic images of women deemed to be of higher quality (Leivers et al. 2014).

Men have also been found to produce better ejaculates when exposed to novel females during a porn viewing experience (Joseph et al. 2015), just as predicted by the Coolidge effect. Males were exposed to erotic images of the same woman six times, before being exposed to a novel woman. Contrary to expectations, this study failed to find a decrease in the measured ejaculatory parameters between times 1–6 of exposure, perhaps because the men in the study had ample time to recover between exposures (48–72 h), but the introduction of novelty resulted in a significant increase in sperm motility, and ejaculate volume, and a decrease in ejaculation time (Joseph et al. 2015). The extraordinary success and addictive power of easily available porn in the Internet seem to take advantage of men's increased sexual interest in young, diverse, and fertile females. More studies are beginning to delve into the patterns of porn consumption in men and whether these can at least partly be explained by our evolutionary history.

Conclusion

The studies mentioned above provide evidence that ejaculatory adjustment as a response to extrinsic factors appears to be found in men. However, the studies are still relatively few and many are very recent. More experimental evidence testing the general applicability of evolutionary sperm allocation still needs to be gathered. This is

particularly important because ejaculate components such as volume, sperm number, and quality can be highly variable, not only between males depending on their intrinsic factors as mentioned above, but within males (Freund 1963). In his discussion of semen production in men, Freund states that

it is evident that without repeated specimens under controlled conditions, no estimate of the variation among specimens within donors can be made. Without such an estimate of within donor variation, no conclusive test of the significance of the differences among donors, among fertile and infertile groups, or among or among treated and control groups, can be made.

Therefore, experiments with larger sample sizes that control for known factors that cause intrinsic variation of ejaculate quality are badly needed to determine the relative importance of strategic sperm allocation and sperm prudence in men.

Cross-References

- [Adaptations: Product of Evolution](#)
- [Avian Sperm Competition](#)
- [Benefits of Short-Term Mating](#)
- [Competition for Resources Desired by Females](#)
- [Cryptic Female Choice](#)
- [Cues to Infidelity](#)
- [Evolution of Long-Term Pair-Bonding in Humans](#)
- [Female Infidelity](#)
- [Human Sperm Competition](#)
- [Intrasexual Male Competition](#)
- [Mating Strategies](#)
- [Perceptions of Infidelity](#)
- [Polygamy in Humans](#)
- [Primate Sperm Competition](#)
- [Reproduction](#)
- [Reproductive Strategies](#)
- [Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition](#)
- [Semen from In-Pair Partner](#)
- [Sexual Selection in Evolutionary Psychology](#)
- [Sperm Competition Theory](#)
- [Sperm Competition Tactics](#)
- [Women's Mate Value](#)

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Male Qualities and Likelihood of Orgasm

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Synonyms

Attractiveness; Cryptic Female Choice; Facial Attractiveness; Female Copulatory Orgasm; Female Mate Choice; Mate selection; Orgasm; Pair-bonding; The Evolution of Genitalia

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Definition

Male traits and sexual behaviors that predict the likelihood of female orgasm.

Introduction

In contrast to male orgasm, the female orgasm is enormously variable in frequency during penetrative sex. While men almost always ejaculate during penile-vaginal intercourse, women orgasm far less frequently from penetrative sex alone and experience significant variation in orgasm frequency with different partners (Lloyd 2005). While variation in women’s orgasm frequency is poorly understood, evolutionary psychology tends to view variation in behavior as adaptive and responsive to environmental conditions.

Current evolutionary theories regarding the female orgasm can be broadly divided into two positions: those that focus on selection on male sexual function and those that focus on selection on female sexual function. The by-product hypothesis concerns the former and posits that the capacity of women to experience orgasm is a consequence of strong selection pressure on males’ capacity to reach orgasm. This position is based on similarities between male and female orgasm as well as the observation that the male glans penis and female clitoris arise from homologous tissue during development. In contrast, the mate choice hypothesis argues that variation in female orgasm frequency during sexual intercourse is reflective of varying quality of their male partners. Increased orgasm frequency with men possessing desirable traits ought to promote repeated copulations, thus increasing the likelihood of impregnation. This position can be further distinguished by predictions regarding which male traits are likely to influence orgasm frequency.

Mate-Choice Hypotheses of Female Orgasm

Given the high gestational cost of rearing human offspring women should be driven to select mates of high quality. Under the *sire-choice hypothesis*,

quality tends to be defined as the ability to pass favorable genetic traits onto offspring (i.e., heritable traits) that will contribute to offspring fitness. In contrast, the *pair-bonding hypothesis* postulates that male traits that are likely to benefit the woman through increased care and investment in offspring ought to promote orgasm. Traits that have been identified as theoretically important to each theory can be seen in Table 1 below.

Mate-Choice Traits that Predict Orgasm Likelihood

Sire-Choice

The sire-choice hypothesis has been more extensively tested than the pair-bonding hypothesis and some evidence does suggest that women may be more likely to orgasm when their partner possesses traits putatively associated with genetic quality. For instance, several studies have observed that women report higher orgasm frequency with more physically attractive partners (Andersson 1994; Gallup et al. 2014; Grammer et al. 2003; Shackelford et al. 2000). While some of these studies may be subject to bias in the cases that women self-reported their partner’s attractiveness (Gallup et al. 2014; Shackelford et al. 2000), others have obtained independent ratings of male attractiveness, which also corresponded to increased likelihood of orgasm (Puts et al. 2012; Thornhill et al. 1995).

Pair-Bonding

Few studies to date have thoroughly investigated pair-bonding traits in the context of female

Male Qualities and Likelihood of Orgasm, Table 1 Partner traits distinguishing mate-choice hypotheses (For review see Sherlock et al. 2016)

Sire choice	Pair-bonding
Physical attractiveness	Faithfulness
Height	Warmth
Athleticism	Earning potential
Muscularity	Kindness
Voice depth	
Physical fitness	
Humor	
Creativity	
Dominance	
Body odor pleasantness	

M

orgasm frequency. However, Costa and Brody (2007) have observed that greater orgasm frequency is associated with overall relationship quality. Moreover, Gallup et al. (2014) found that women reported greater orgasm frequency during penile-vaginal intercourse when their partner's family had a higher income, suggesting a role for resource provision. It should be noted that neither Thornhill et al. (1995) or Zietsch et al. (2011) replicated the relationship between orgasm frequency and relationship length or commitment, calling into question the validity of the pattern found by Costa and Brody (2007).

Alternative Considerations

While some male traits have been reported to covary with orgasm frequency, this may not represent a causal relationship. Firstly, it is possible that women who orgasm more frequently may be more likely to select particular types of partners than women who orgasm infrequently. For example, women who report a higher orgasm frequency may choose to have sex with more physically attractive men. These men are likely to have more experience in short-term sexual relationships and therefore may be more effective at eliciting orgasm in their partners. Additionally, OkCupid report that of over 42,000 female users, women who reported that exercise is enjoyable also reported reaching orgasm more easily (Rudder 2011). These women, who likely exercise more frequently, may be more attractive themselves and thus more likely to partner with attractive men (Sherlock et al. 2016). Secondly, women vary considerably in their capacity to achieve orgasm, even when masturbating. This variation between women makes it difficult to detect consistent relationships between orgasm frequency and the traits of male sexual partners. However, studying the nature of variation in the same woman's orgasm frequency with different male partners avoids these issues.

Only one study to date has investigated how women's orgasm frequencies have varied with different sexual partners. Sherlock et al. (2016) had single women with more than two male sexual partners report on a range of characteristics of the man with whom orgasm was the easiest and

the man with whom orgasm was the most difficult (or did not occur at all). By comparing high- and low-orgasm men, several traits emerged as important in predicting ease of orgasm. High-orgasm men tended to be higher in humor, attractiveness, creativity, emotional warmth, faithfulness, and body odor pleasantness, consistent with both sire-choice and pair-bonding hypotheses.

Male Sexual Behavior

Importantly, Sherlock et al. (2016) also observed that a number of sexual behaviors differed between high- and low-orgasm males. Specifically, high-orgasm males were more likely to be focused on their partner's pleasure, engage in oral sex, use sex toys, spend more time on foreplay, and stimulate their partner's clitoris during sex. Women were also more likely to communicate their sexual position preferences and stimulate their clitoris when having sex with high-orgasm partners. These results are consistent with two large-surveys of female orgasm during last sexual encounter. Richters et al. (2006) surveyed 19,000 Australians regarding their last sexual encounter and found that the likelihood of a woman orgasm was predicted by the number of sexual practices (i.e., oral sex, digital stimulation, etc.) engaged in prior to intercourse. More recently, Frederick et al. (2017) found that, in a survey of over 50,000 American adults, women who orgasmed more frequently were more likely to receive oral sex, use varied sexual positions, and communicate their sexual desires. Across all three studies, orgasm was more likely to occur with manual stimulation of the clitoris during intercourse (Frederick et al. 2017; Richters et al. 2006; Sherlock et al. 2016). Consequently, any contribution of male traits (e.g., attractiveness) to female orgasm needs to be considered in the context of variation in male sexual behavior. Further complicating these results is the likely association between male traits and sexual behaviors. For example, finding that women orgasm more frequently with men who exhibit higher warmth and empathy could be interpreted as support for the pair-bonding hypothesis: these men may be kinder and more generous spouses/fathers. However, an alternate explanation may be that men

with higher warmth and empathy are more likely to attend to their partner's pleasure during sex.

Conclusion

Despite some consistency in male traits associated with orgasm across several studies, there is reason to be cautious interpreting these results without first accounting for male sexual behavior. The most prominent trait associated with increases in the likelihood of female orgasm is attractiveness (Andersson 1994; Gallup et al. 2014; Grammer et al. 2003; Shackelford et al. 2000; Sherlock et al. 2016), yet the causal pathway between attractiveness and female orgasm could be inverse to the current theorizing. That is, women could come to view their partners as more attractive if they are more frequent benefactors of orgasms. In sum, the most consistent findings regarding males who elicit orgasm more frequently pertain to their sexual behavior rather than their traits. Women are more likely to achieve orgasm with a partner who is attentive, patient, and receptive to instruction.

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Male Reproductive Variance

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Synonyms

Differential male reproductive success

Definition

Within species or breeding population variation in male reproductive success.

Introduction

Within a species, individuals vary in reproductive success. In a sexual reproducing species, where

each individual has one male and one female parent, increased reproductive success for certain individuals of one sex necessitates decreased reproductive success for others of that sex. Put more directly, the more extreme the winners, the more extreme the losers. While the focus of this entry is male reproductive variance, it will by necessity to also discuss female reproductive variance as a contrast, as reproductive variance is a major factor both of and contributing to sex differences, which coevolve with both mating strategies and parental care.

Coevolution with Parental Investment/Care

Across species, males tend to show greater variance in reproductive success than females. This results from females typically having a lower potential reproductive rate relative to males; a fundamental difference is rooted in anisogamy – differential investment in gametes by males versus females, the basis of sexual reproduction. Parental investment is defined as investment in one offspring (or current offspring) to the exclusion of other (particularly future) offspring (Trivers 1972). Because energetic and time investments in particular offspring come at the cost of investing in different behaviors or young, exclusionary efforts toward any particular reproductive event comes at the cost of continued investment in past reproduction, or investment in potential future reproduction.

Even if the only parental investment in a species is initial gamete production, females are obligated to a higher per-offspring investment than males, and this initial difference in investment is thought to be the ultimate basis of the general tendency toward females having higher parental investment than males (Trivers 1972). This difference can be more profound in species such as mammals where females have obligate parental investment far beyond gamete production. Looking at humans as a sample mammal, the maximum recorded number of putative offspring for a man is ~888 (Oberzaucher and Grammer 2014), 12.9 times the maximum of 69 recorded for a woman (in 27 pregnancies, all births were

multiples; Guinness World Records 2016). The fact that females tend to be the “slower” sex – that is, requiring more “time-out” between or resource input into reproductive events – has the consequence of their typically being the limiting sex. Therefore, males, as the usually more reproductively available sex, are faced with a higher likelihood of being excluded from reproduction (as above, because every offspring has one-and-only-one male and female genetic parent), resulting in male variability in reproductive success being typically higher than that in females (known as *Bateman’s principle*; Bateman 1948).

This difference in reproductive success variation *tends* to result in males being relatively more competitive for access to mates (females being a limiting resource for reproduction; Trivers 1972) and females being relatively more choosy about potential mates. It should be noted that this does not exclude the possibility that both sexes are both competitive and choosy – there is no expectation that males mate *indiscriminately* nor that females do not vie for the more valuable (in terms of direct resources or good genes) males. Rather, it means that on average, males will be more engaging in intrasexual competition over mates than females, and females will be more choosy over mates than males.

Coevolution with Mating Systems

Generally speaking, the degree of variation in reproductive success within a sex is closely tied to the species-typical mating system (Davies et al. 2012). For examples, in species where the typical mode is monogamy, both males and females show relatively low reproductive variance, particularly in comparison with systems where females (polyandrous), males (polygynous), or both sexes (promiscuous) have simultaneous multiple mates. However, even in monogamous systems, there is room for variation (e.g., Brown et al. 2009). For example, individuals may differ in their likelihood of ever entering a partnership (e.g., particularly if there is a biased sex ratio), and the number of lifetime partnerships may differ between individuals (and also between the sexes).

Among humans, cultural variation in “exclusive sexual partnerships” or marriage practices is associated with the reproductive variance in the sexes in those cultures. In relatively few cultures, women are exclusively sexual with multiple men (in several of these examples, these men are related to one another), but men “officially” have sexual access only with her. These cultures are often ones where the “cost” of obtaining a wife is high, or there are few available women due to some other cultural or life-history factor (Starkweather and Hames 2012).

More frequently documented are polygynous cultures, where one man monopolizes sexual access to multiple women (this may be associated with strict control of women to prevent her having sex with other men; Chamberlin and Guiora 2014). Such societies often have associated with them reproductive control or expulsion of other men (typically subordinates, sometimes involving castration of non-evicted men; Chamberlin and Guiora 2014). However, not all polygynous cultures have such high male skew, and societies noted as polygynous may express a more mild form of occasional polygyny in the context of overall monogamy or increased re-pairing by men relative to women (e.g., Brown et al. 2009). In fact, many cultures identified as monogamous may be better, from a behavioral ecology perspective, be labelled as mildly polygynous, particularly due to the commonality of serial monogamy.

Complicating matters is the fact that studies frequently show that men *on average* report a higher number of sexual partners than women; while this likely results in part from opposing cultural pressures that drive men to overreport and women to underreport their number of partners, other factors (such as access to sex workers, who are not subsequently surveyed) can help explain this discrepancy. Overall, humans appear to, on average, broadly fit a pattern of moderate polygyny, and male reproductive variance is typically higher than that of females (e.g., Hammer et al. 2008), although as above, this is rather variable, and unlike many animal species, it is difficult to identify a clearly “typical” human mating system, as there is considerable variation of

form even within these broad categories (see discussion in Brown et al. 2009).

Consequences of Variation in Male Reproductive Success

Sexual selection influences the degree of reproductive variance observed within the sexes, and evolution of mating strategies in response to differential reproductive success further propagates sexual selection. The effects of male reproductive variance on mating systems have resulted in myriad complicated expressions of male reproductive behavior, and differential reproductive success among males is often associated with variation (either discrete or continuous) in other aspects of their morphology and reproductive behavior (e.g., Davies et al. 2012). Note that similar variation between sexes within a species (sexual dimorphism), though not invariably the result of sexual selection, can also be rooted in a difference in reproductive success variation between males and females (Davies et al. 2012). For example, if certain traits permit males access to mates through mate preference or through competition, those traits will tend to evolve to become sexually dimorphic (for an extreme example, consider the anglerfish, where females are up to half a million times heavier than males, who become functionally parasitic on the female they adhere to; Pietsch 2005).

The most striking examples of reproductive success coevolving with male reproductive phenotype can be observed in nonhuman animal species where males show profound within-species variation in individual morphology and reproductive behavior. These reproductive phenotypes may represent different life-history pathways (e.g., Ruffs, where alternative types also have a genetic basis; Lank et al. 1995), or different life stages (e.g., orangutans; Knott 2009), with the result males may or may not exhibit multiple reproductive phenotypes in their lifetime. Among fishes, males in species with alternative male tactics may display clearly discrete morphological and behavioral phenotypes, to the extreme that males of the same species may appear to the

naïve observer to be different species (see Taborsky 1994 for an overview of alternative reproductive tactics among fishes). Certain avian species and mammalian species also show similar, though often less profound, discrete variation in male reproductive phenotype (e.g., Leboeuf 1972; Lank et al. 1995; Knott 2009). Typically, alternative phenotypes are associated with different levels of reproductive success, although the strategy with the highest lifetime reproductive success is not necessarily always those large showy dominant males (e.g., Berejikian et al. 2010).

More typically, differences in male reproductive success are correlated with continuous male trait variation of traits involved in mate attraction or intrasexual competition (see overview in Davies et al. 2012). Such traits may be associated with ability to sequester resources (e.g., energetic reserves or mating resources such as territories), attract mates (e.g., by signaling genetic quality, compatibility, or ability to provide direct benefits to offspring), or outcompete other males for mating access (e.g., traits that enhance strength or stealth). Males who possess traits that allow increased control of reproductive resources and potential males have increased individual reproductive success.

From a comparative perspective, the phenotypic variation seen among human males in likely response to reproductive success variation is relatively muted. Data are restricted as there are relatively few studies of human reproduction that directly assess offspring number and outcome; far more frequently examined is mating success or partnership formation. That said, some male traits have been shown to be predictive of reproductive success, both production and survival of offspring, with the caveat that putative offspring are not necessarily fathered by that man, and males may underreport offspring resulting from women they do not have an official partnership with. Relationships are typically in the continuous fashion described above, although it is not always a linear correlation. These traits include voice pitch (Apicella et al. 2007); performance in ritual fights (Llaurens et al. 2009); physical traits such as height (average or moderately tall being most

successful; Nettle 2002; Stulp et al. 2012), weight (Schooling et al. 2011), BMI (Sear 2006), and upper-body strength (Apicella 2014); hunting ability (Kaplan and Hill 1985; Smith 2004); personality (Alvergne et al. 2010); and wealth/higher socioeconomic status (Nettle and Pollet 2008). Also, as males with higher reproductive success are typically judged as more physically attractive (e.g., Jokela 2009), we can expect that some factors correlated with perceived attractiveness should also predict reproductive success. Additional traits that would be expected to correlate with traits above have been shown to be predictive of mating success, and it is therefore reasonable to presume that they are also likely predictive of reproductive success.

Conclusion

Reproductive variance coevolves with parental investment and mating system and influences and is influenced by sexual selection pressures. The initial bias of increased parental investment by females relative to males is related to the typical cross-taxa finding of greater reproductive variance among males than among females. Degree of variation within and between the sexes is tied to mating, and there is a feedback loop between the forces and consequences of sexual selection resulting from male reproductive variation. In nonhuman animals, the consequences of reproductive variance among males can be extreme variation in reproductive phenotype (both morphology and behavior). Similar variation related to reproductive success can be observed in a less elaborate and typically more continuous fashion among human males.

Cross-References

- [Competition](#)
- [Differential Reproductive Success](#)
- [Female Reproductive Variance](#)
- [Mate Choice](#)
- [Sexual Selection](#)

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Male Safety

► Male Protection

Male Sexual Coercion

- [Mate Deprivation Hypothesis](#)
-

Male Sexual Jealousy

- [Jealousy](#)
 - [Self-Defense and Female-Perpetrated Violence](#)
-

Male Sexual Jealousy to Deter Partner Infidelity

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Synonyms

[Cuckoldry](#); [Paternity uncertainty](#)

Definition

The jealousy males feel about female infidelity as an evolutionary reaction to internal female fertilization and paternity uncertainty.

Introduction

When infidelity occurs, males and females experience different biological and social costs. As such, they have developed different reactions toward infidelity. For males, one common reaction is sexual jealousy in order to deter partner infidelity.

The Costs of Infidelity

In species with internal female fertilization, partner infidelity has different costs for males and females. If a male's mate has sexual contact with other

males, the male has a lesser probability of impregnating his mate, and he has greater paternity uncertainty. If the rival male successfully impregnates his mate, the male will have lost the time, energy, nuptial gifts, the female's parental effort, and the opportunity of mating with other females (Buss et al. 1992). Furthermore, in biparental species, where males invest in their offspring after birth, he may unknowingly invest resources in the rival's offspring (Trivers 1972). Because human males invest a great deal in their offspring, evolutionary selection pressures have led to the development of strategies which allow men to exert sexual control over women in order to prevent infidelity (Daly et al. 1982; Nannini and Meyers 2000). Sexual jealousy is one such strategy to prevent cuckoldry.

On the other hand, females do not incur the same costs as males. Regardless of her mate's infidelities, the female is certain of her own maternity. However, infidelities can be costly in other ways for females, as females risk losing the resources, energy, and time of their mates if the male chooses to invest in a rival female. As such, females have been evolutionary driven to be more sensitive to cues of her mate's emotional investment with another female. In this case, emotional infidelity may be more disastrous than sexual infidelity.

Studies of Modern Humans

Studies of undergraduate students have confirmed that males tend to react more strongly – with both jealousy and anger – to sexual, as opposed to emotional, infidelity. Buss et al. (1992) found that 60% of males and only 17% of females reported that sexual infidelity was more distressing than emotional infidelity. The researchers also used physiological measures that recorded sweat activity, pulse rate, and facial activity while subjects imagined various cheating scenarios. Overall, males displayed greater and more consistent physiological signs of jealousy and distress. This research has been replicated in cross-cultural studies as well (Buunk et al. 1996).

Researchers have also studied incidents of intimate partner violence, and they consistently find

that male sexual jealousy is one of the leading motivators for this kind of violence (Daly et al. 1982; Daly and Wilson 1988). Women are most likely to experience battery when her partner either suspects that she is ending the relationship or that she has engaged in sexual infidelity (Daly and Wilson 1988). Both experimental and observational studies therefore show that sexual jealousy is more common among men.

Competing Explanations

Some researchers suggest that the observed differences in male and female jealousy may be due to issues with the validity of measures. This hypothesis, known as the *double-shot hypothesis*, posits that men and women interpret infidelity differently (DeSteno and Salovey 1996). Men are more likely to believe that if a sexual infidelity has occurred, then an emotional infidelity has also occurred. However, in their view, an emotional infidelity can occur without any sexual infidelity. Women are more likely to believe that if an emotional infidelity has occurred, then a sexual infidelity has occurred as well. In their view, a sexual infidelity may occur without an emotional infidelity. Therefore, when asked to pick which scenario is more distressing, each gender will be more likely to choose the scenario in which they think it is likely that both types of infidelity have occurred: men will be more distressed by sexual infidelity, and women will be more distressed by emotional infidelity. In reality, according to this perspective, both men and women are equally distressed by the co-occurrence of both types of infidelity.

Researchers have redesigned studies in order to account for this possible artifactual relationship. When asked to imagine that only one infidelity had occurred, and when asked to imagine that both types of infidelities had occurred, males were more likely to list the sexual infidelities as more distressing, while females were more likely to state that the emotional infidelity was more distressing (Buss et al. 1996). These results show that there are real jealousy differences between males and females.

Other Means of Ensuring Paternity

Jealousy is a tactic meant to prevent infidelity, but in case infidelity occurs, males also have other methods to ensure that they do not invest in another male's gametes (Shackelford and Goetz 2007). Sperm competition strategies may have also developed to decrease the likelihood that another male's sperm will impregnate the female. Differential parental investment, where males invest less in their offspring than females, also decreases the amount of resources that will be allocated to a rival's offspring.

Conclusion

While it is unknown how common cuckoldry was in early human history, one study suggests that between approximately 9% and 13% of modern children have putative fathers who are not actually their genetic fathers (Baker and Bellis 1995). This rate of cuckoldry suggests that there was significant risk of males unknowingly investing in another male's offspring, and this risk may have been sufficient enough that evolutionary selection pressures would develop a mechanism to prevent cuckoldry. Current theories thus suggest that male sexual jealousy developed as a means to deter partner infidelity and the associated paternity uncertainty. This jealousy can range from trivial annoyance to fatal violence.

Cross-References

- ▶ [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- ▶ [Cues to Infidelity](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Jealousy and Infidelity](#)
- ▶ [Male Sexual Jealousy](#)
- ▶ [Paternity Uncertainty](#)
- ▶ [Perceptions of Infidelity](#)
- ▶ [Sex Differences in Jealousy](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)
- ▶ [Sexual Jealousy in Long-Term Relationships](#)
- ▶ [Sperm Competition Tactics](#)

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Male Social Dominance

- [Patriarchy and Feminist Perspectives](#)

Male Status

- [Alpha, Beta, and Gamma Males](#)

Male Strategies

- [Men’s Egoistic Dominant Acts](#)

Male Victims

- [Contexts for Women’s Aggression Against Men](#)

Male Violence

- [Perpetrators Mostly men](#)

Male Warrior Hypothesis

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Synonyms

[Male coalitional aggression](#)

Definition

The male warrior hypothesis is an evolutionary theory that refers to the idea that men’s behaviors and cognitions are more strongly intergroup-oriented than women’s, such that men likely evolved psychological mechanisms that enable the formation of coalitions that are capable of carrying out acts of aggression and violence on members of outgroups as a means to acquire or protect reproductive resources. These mechanisms are purported to have developed as the result of an ancestral history that was largely influenced by frequent and violent intergroup conflict among males, in which success increased their reproductive fitness.

Introduction

Due to reproductive and survival benefits, humans (and other species) tend to come together in groups (Baumeister and Leary 1995). Although

costly, intergroup conflict is, and has been, pervasive among humans (Bowles 2009). When these conflicts involve acts of aggression and violence, research finds that, across time and cultures, men are almost exclusively the perpetrators of such acts (e.g., Goldstein 2003). This greater propensity to engage in intergroup violence and aggression is suggested to have evolved in men due to the resulting benefits to men's reproductive fitness (e.g., Buss 1999; Van Vugt 2009; Van Vugt et al. 2007). Men's reproductive fitness is limited by access to fertile women, whereas women's fitness is limited by physiological, energetic, and resource constraints (e.g., Buss 1999). Thus, men, but not women, can increase their fitness by maintaining exclusive access to large numbers of mates, which can be accomplished through intergroup conflict (e.g., McDonald et al. 2012). That is, groups of successful men in intergroup conflicts may reap the benefits of increased access to mates and gains in prestige. Indeed, research conducted on traditional (i.e., tribal) human societies finds that male warriors have more mates and children and enjoy higher status than other men (Chagnon 1988) and young male street-gang members have been found to have more sexual partners than other young males (Palmer and Tilley 1995). Thus, evolutionary psychologists assert that men may have evolved psychological mechanisms for forming coalitions that are able to plan and execute aggressive attacks on members of other groups and should be more intergroup oriented in general, than women (e.g., McDonald et al. 2012; Van Vugt et al. 2007). This is known as *the male warrior hypothesis* (McDonald et al. 2012; Van Vugt 2009; Van Vugt et al. 2007).

Support for the Male Warrior Hypothesis

The male warrior hypothesis asserts that men are more intergroup oriented than women and have evolved psychological mechanisms that increase the potential for success in intergroup conflicts (e.g., Van Vugt et al. 2007). Evidence for the operation of these mechanisms can be found in research examining the conflict-relevant thoughts, emotions, and behaviors of men in modern

societies (McDonald et al. 2012). Although inclusion of all such research is beyond the limits of this entry, examples of empirical support for some of the major predictions of the male warrior hypothesis, specifically in the areas of intergroup aggression, prejudice, preference for intergroup hierarchies, and ingroup identification and cooperation, are discussed.

The most basic prediction of the male warrior hypothesis is that men should be more likely than women to initiate and engage in aggressive intergroup behavior because success in intergroup conflicts likely increases access to mates and other resources. This prediction has also largely been supported across many studies. As stated previously, in instances of real-world violent intergroup conflicts such as warfare, genocide, and street-gang violence, groups of men are almost exclusively the perpetrators (e.g., Goldstein 2003). And warrior males have also been found to have more mates and children, as well as higher social status (e.g., Chagnon 1988) than other males. Further, on a daily basis, men tend to report a higher frequency of competitive intergroup interactions than women (Pemberton et al. 1996; Van Vugt 2009). These aggressive tendencies have also been found in laboratory manipulations. For example, in one particularly interesting study, pairs of participants played a simulated wargame in which they were asked to imagine that they were the leader of a fictitious country in conflict with another country over newly discovered resources (Johnson et al. 2006). Results revealed that men were significantly more likely than women to attack the other country without provocation and were also more confident that they would win the conflict. Interestingly, even though participants were unaware of the sex of their rival, pairs of male participants yielded the most intense warfare, whereas pairs of female participants yielded the least. In further support for the male warrior hypothesis, men's propensity towards intergroup conflict appears to be specifically tied to mating motives. In a series of studies, Chang et al. (2011) examined whether activating mating motives would increase participants' access to war-related cognition and perception. Men, but not women,

exposed to attractive, opposed to unattractive, opposite-sex photos were more likely to endorse pro-war statements, but not trade-conflict statements. In addition, men who were primed with attractive faces or legs of women, as opposed to unattractive faces of women and national flags, responded significantly faster to war-related words and images, but not farming-related words and images or expressions of general aggression. Taken together, the preponderance of evidence suggests that men are more inclined to engage in aggressive or competitive intergroup behavior than are women, and this tendency appears to be related to mating motives.

The male warrior hypothesis also predicts that men should harbor more derogatory and prejudiced attitudes about outgroup members because this may reduce the psychological discomfort that might result from harming these individuals during violent conflicts (e.g., McDonald et al. 2012). Research has generally supported this contention. Men tend to be more xenophobic and ethnocentric than women (e.g., Ekehammar and Sidanius 1982) and are also more likely to dehumanize outgroup members (i.e., describe them using animal-like words) than are women (e.g., Van Vugt 2009). Further, men are more likely than women to describe outgroup members using danger-related stereotypes when in conditions of ambiguous threat (i.e., when primed with ambient darkness; Schaller et al. 2003). Thus, men do appear to harbor more prejudiced and derogatory attitudes about members of outgroups than women.

Intergroup conflicts inevitably result in intergroup hierarchies because some groups will be more successful than others. As a result, the male warrior hypothesis predicts that men should exhibit a stronger preference for intergroup dominance hierarchies than women (Van Vugt 2009). Consistent with this prediction, in samples taken from a variety of countries and cultures men consistently score higher in social dominance orientation (SDO; i.e., general preference for hierarchical, dominant-subordinate intergroup relations as opposed to more equal intergroup relations; Pratto et al. 1994) than do women (e.g., Lee et al. 2011; Van Vugt 2009). Of particular

importance, higher scores in SDO are associated with a variety of beliefs and attitudes that serve to maintain and justify group-based hierarchies such as political-economic conservatism, meritocracy ideology, nationalism, patriotism, and cultural elitism (e.g., Lee et al. 2011). These results suggest that men do prefer intergroup hierarchies more than women and are perhaps also more likely to harbor beliefs that are involved in maintaining and supporting existing intergroup hierarchies.

Finally, the male warrior hypothesis predicts that men should be more motivated to protect and support the ingroup, especially when threatened by or in competition with another group, because success in intergroup competitions depends, to some extent, on one's ingroup being cohesive, strong, and coordinated (Van Vugt 2009; Van Vugt et al. 2007). In accordance with this prediction, across three studies using a public goods game Van Vugt et al. (2007) found that men increased cooperative donations to their ingroup when in competition with other rival groups, as opposed to a condition in which participants were in competition with other individuals, whereas women's cooperative donations to their group were seemingly unaffected by competition condition. In the same study, men, but not women, also reported stronger identification with the group in an intergroup competition condition than in an interindividual competition condition. Interestingly, men's identification with the group fully mediated the association between their increased cooperative donations and competition condition. Relatedly, research also suggests that men may generally identify more strongly with groups than women. For example, Van Vugt (2009) asked 100 college students to state their favorite color and explain why this particular color was their favorite. Results indicated that 30% of men chose a color because it was associated with an ingroup (e.g., a favorite sports team), whereas no women gave this sort of explanation. Further, Gabriel and Gardner (1999) asked participants to complete the statement "I am..." and found that men were twice as likely as women to make a statement about a group membership (e.g., being a member of a fraternity or being an

American). Taken together, these studies suggest that, when intergroup competition is salient, men are more likely than women to increase cooperation with their group and are also more likely to personally identify with membership groups than women.

Conclusion

The male warrior hypotheses is an evolutionary theory that states men have evolved psychological mechanisms that enable the formation of coalitions that are capable of carrying out acts of aggression and violence on members of outgroups as a means to acquire or protect reproductive resources. The major predictions of the male warrior hypothesis have been largely supported in both examinations of trends in real-world intergroup conflict and laboratory examinations. It is hopeful that future investigations of the predictions of the male warrior hypothesis, and other related theories, will continue to shed light on intergroup behavior and the evolved psychological mechanisms that play a role in such behavior.

Cross-References

- [Aggression for Sexual Access](#)
- [Competition Between Groups](#)
- [Competition for Resources Desired by Females](#)
- [Evolutionary Theory and the Causes of War](#)
- [Humans: Between-Group Conflicts](#)
- [Intrasexual Male Competition](#)
- [In-Group–Out-Group Bias](#)
- [Male Adaptations that Facilitate Success in War](#)
- [Men But Not Women Will Have Adaptations for War](#)
- [Men Riskier, More Aggressive](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Perpetrators Mostly Men](#)
- [Psychological Mechanisms](#)
- [Sex Differences in Aggression](#)
- [Sexual Access as Benefit of Victory in War](#)

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Male Warrior Psychology

- ▶ [Members of Coalition Must Believe They Will Win](#)
- ▶ [Men but Not Women Will Have Adaptations for War](#)

Male Wrongful Discrimination

- ▶ [Second Sexism](#)

Male/Female

- ▶ [Offspring Sex](#)

Male-Male

- ▶ [Cost of Same-Sex Friendships](#)
- ▶ [Same-Sex Friend](#)

Male-Male Competition

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Synonyms

[Intrasexual competition](#); [Intrasexual selection](#)

Definition

Male-Male Competition: Competition between males for access to females.

Introduction

Contest competition in males (male-male competition) is a driving force in sexual selection (Puts 2010). For males, successful competitive displays increase access to valuable resources (e.g., territory, food), mates, and an increase in status. Some mechanisms favor success in male-male competition, such as aggressive behavior and physical characteristics that increase the facilitation of aggressiveness (i.e., size, strength, weaponry). For instance, sea lions establish their dominance through threats and fights, and this has important repercussions to their reproductive success. In a single breeding season, dominant males perform most of the copulations and sire a majority of pups (Daly and Wilson 1983). This intense competition between males was noted in Bateman's classic 1948 study on sex differences in reproductive strategies using *Drosophila*. Because males are dependent on females for their reproductive success, sexual selection, in this case, intrasexual selection, is stronger in males than females. Males can increase their reproductive success by increasing their mating frequency, and to be reproductively successful, they must compete with other males to access those females (Bateman 1948; Darwin 1859).

In human populations, male-male competition reflects similar behaviors observed from non-human species. Competition between males is driven by gaining access to fertile females in an attempt to maximize reproductive success (Daly and Wilson 1983) and in accessing resources and establishing dominance in status hierarchies (Geary 1999), which nonetheless influence reproductive behavior. In preindustrial societies, such as indigenous tribes in South America, conflict is perpetrated by males with motives in gaining status to appeal to prospective female mates as marriage partners. Intergroup conflict between tribes has shown to result in capturing territory,

resources, and women to take as wives which leads to higher reproductive success (Geary 1999). In nomadic pastoralists in East Africa, elders who had a history of engaging in raids throughout their youth had a higher number of wives and children, suggesting that raiding afforded reproductive opportunities (Glowacki and Wrangham 2015). Even in current industrial societies, violent acts are perpetrated by men against other men. Acts of violence are often in response to competing interests, such as access to resources, increases in social status, and in response to sexual jealousy. Since these interests carry fitness consequences, they are valued by men, and competition is stronger for men than they are for women (Daly and Wilson 1988). In violent and homicidal data reviewed by Daly and Wilson (1988), across many societies (e.g., pre-industrial and industrial), homicides are most likely to be committed by men killing other men, with motives ranging from insult to status, domestic issues, sexual jealousy, and attempting to access resources (e.g., robbery) (Daly and Wilson 1988).

Male-Male Competition in Early Development

Evidence for male-male competition is apparent in early development. Compared to girls, infant boys show interest to videos depicting groups, which are an important function for coalitional activities (Benenson et al. 2004). Male physical aggressiveness is apparent at a young age as boys engage in more play fighting and rough and tumble play than females (DiPietro 1981). Male competitive behavior intensifies in adolescence and tends to become more violent compared to childhood. Bullying in males is more likely to include physical aggression, and in adolescence, it is associated with social dominance (Bukowski et al. 2000). Aggressive behaviors in young males are likely to function as a way of establishing social competitive skills, group-level competitive play, and dominance hierarchies (Byrd-Craven and Geary 2013; Geary et al. 2003).

Physical Features in Competition

Compared to women, men are stronger and more physically aggressive. Men have more upper-body mass and musculature compared to women, and the average man is stronger than the majority of women (Puts 2010). Sex differences in physical size suggest an adaptation to male-male competition, and similar conclusions can be made with other animal species that share intense same-sex competition and display notable sex differences in physicality. For instance, fighting ability and behavior associated with male-male competition can be inferred from physical features in males. Studies have shown that features, such as facial masculinity (Perrett et al. 1998) and high facial width to height ratio, can infer aggressiveness and dominance (Carre et al. 2009), which are important attributes in contest competitions. Height has also been shown to be a sexually dimorphic feature shaped by sexual selection. In a study investigating sex differences in height and competitiveness, height was positively associated with intrasexual competitiveness (Polo et al. 2018).

Men are also sensitive to the physical features that are important in contest competitions. For instance, men consider other men with physical characteristics that are considered optimal (e.g., high shoulder to hip ratios) as more attractive and view specific areas of male bodies longer, such as the chest region (Durkee et al. 2018; Pazhoohi et al. 2019). Males who weight lift are sensitive to physical features that are important in contest competitions. For example, males who body build are more likely to use anabolic steroids if they score higher on an intrasexual competitiveness scale and are at the beginning stages of their training (Harris et al. 2017). Much like other species who have sexual ornaments for contest competitions (e.g., elk), males have shown to increase their dominance and aggressiveness by growing out their beards. Even though beards do not increase fighting ability, they signal attributes that are consistent with competitive displays (Dixson and Vasey 2012).

Competition in Sports

Male-male competitive displays are directly observed in sports. Given that males physically compete for access to mates and are more physically aggressive, sports may function as a by-product for those motives as sports can be aggressive and coalitional and serve as an advertisement of mate quality (Deaner et al. 2012). Throughout history, males have been more involved in sports (Guttman 2004), male sports have had more prominence (Roberts et al. 1959), and males have been more interested in viewing sports (Ellis et al. 2008). In three studies examining sports involvement across the United States, males were more likely to play more frequently (study 1), in public (study 2), and be more involved in collegiate intramural sports (study 3) (Deaner et al. 2012).

Hormonal Influences

Hormonal mechanisms play a significant role in male-male competition. In chimpanzees, testosterone levels are higher for males that are high ranking compared to low-ranking males (Muller and Wrangham 2004). In humans, testosterone is related to dominance seeking in males, but not in females (Geary 1999). For instance, in same-sex competitive situations, testosterone levels increase when asked to compete with members of an in-group compared to members of an out-group, suggesting that testosterone influences competitive behavior with known members, as unknown members may pose a greater risk (DeSoto et al. 2009). However, when considering mating opportunities, average levels of testosterone are associated with competing with dominant males if the reward is a high-mate value female (i.e., low waist to hip ratio) (Borraz-Leon et al. 2018). Testosterone has also been implicated in influencing punishing behaviors. When given testosterone compared to a placebo, men were more likely to punish members for an unfair offer in an experimental study, linking its role to aggressive behavior (Dreher et al. 2016). Research has also found that testosterone is linked to adolescent behavior as a function of social context.

Adolescents with nonaggressive conduct disorder are more likely to have higher levels of testosterone if they also have deviant peers. Moreover, in the same study, testosterone in adolescence is also linked to leadership skills, which is an important attribute in dominance but also prosocial behavior (Rowe et al. 2004).

Conclusion

Variation in reproductive success is greater in males than females, and this is apparent in the physical and behavioral differences associated with competition. Evidence from across societies shows that males are physically aggressive early on in development and show interest in behavior associated with coalitional activities (i.e., groups, hierarchies). Male physical characteristics, such as muscularity and strength, reveal the degree of sexual dimorphism that is similar in other species with intense male-male competition. Male-male competition is further underscored by the role of testosterone in aggressiveness, dominance, and mate-seeking, which are similar in closely related species that share similar intrasexual competitiveness.

Cross-References

- [Contest Competition](#)
- [Boys Bully More Than Girls](#)
- [Feelings of Excitement and Brotherhood](#)
- [Intrasexual Male Competition](#)
- [Intrasexual Selection](#)
- [Meta-analysis of Sex Differences in Aggression](#)
- [Sexual Selection](#)
- [Sperm Competition Theory](#)
- [Status and Reproductive Success](#)
- [Status Competition](#)

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Male-Male Competition for Resources

► Competition for Resources Desired by Females

Male-Male Competition or Male Provisioning?

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Synonyms

Cooperative breeding; Indirect care; Intrasexual competition; Paternal investment; Showing-off

Definition

The degree to which a male allocates resources towards competing with male conspecifics or providing indirect care towards mates and/or offspring in order to boost his reproductive fitness.

Introduction

Same-sex competition and intersexual choice are key components of sexual selection. Trivers (1972) proposed that, in sexually reproducing species, intrasexual selection and intersexual choice are related to sex-specific investments (energy, resources, time) in offspring. Sex differences in fitness opportunities and payoffs contribute to sex differences in mating strategies (Geary 2010). In many mammalian species, females are the more ecological sex, meaning their reproductive function is more directly tied to availability of resources like food and safety. Conversely, male reproductive function is more directly tied to reproductive opportunities, contributing to higher rates of physical male-male competition. Females often display more discerning intersexual choice (see: ► “Sexual Reproduction”, ► “Sperm Competition”, ► “Sexual Selection”, ► “Sexual Dimorphism”, and ► “Intersexual Competition” in this volume) than their male conspecifics. Human males are similar to many other mammals in these respects, although humans display more plasticity in their reproductive strategies and more paternal investment than other primates (Gray and Garcia 2013). The highly plastic reproductive strategies employed by human males confound whether men have primarily been shaped by selection to compete with other men or provision their families. Interpretation of contemporary data on male behaviors (such as hunting or breadwinning) that may shape fitness outcomes are fiercely debated (reviewed in Kelly 2013). This entry aims to frame male-male competition and provisioning within life history theory, and highlights the variability with which relevant behaviors can be expressed.

Life History and Socioecology Shape How Men Choose Between Competition and Provisioning

Whether men invest in higher rates of male-male competition or more paternal provisioning depends on intrinsic (e.g., measures of phenotypic quality) and extrinsic (e.g., sex ratio) variables. The expression of a male’s investment in these reproductive behaviors is highly dependent on socioecological context (reviewed in: Gray et al. 2019). A male’s partitioning of time and energy to competing male reproductive behavioral agendas (like mating and parenting effort) can be framed by life history theory. Humans have been characterized as a cooperative breeding species, given the regular involvement of allomothers such as fathers in childrearing. Humans exhibit a unique, derived set of traits including an extended period of dependency (childhood), yet short interbirth intervals (duration between successive births), which lead to “stacking” of dependent offspring (reviewed in: Anderson et al., in prep.; Meehan and Crittenden 2016). When framed in evolutionary and life history theory, each male (unconsciously) decides whether to boost his fitness by investing finite resources (e.g., kilocalories, time) in male-male competition (in order to acquire status, resources, prestige, cooperators, and mates) to ultimately have a greater opportunity to sire a larger quantity of offspring or in provisioning an existing pair bond (reproductive partner) and offspring. Paternal investment may increase offspring survival but likely has a more pronounced fitness effect in contributing to shorter interbirth intervals (Gray and Garcia 2013).

The decision to invest in intrasexual competition or provisioning is, in some ways, a false-dichotomy; an individual can pursue a spectrum of strategies which may not directly reduce to competition for a larger quantity of offspring or provisioning to increase the survival of existing offspring. Some forms of male resource provisioning can both serve as male competitive displays and provisioning. Where forms of male-male competition and provisioning are mutually

incompatible (and thus trade-off with each other), the dichotomy then has merit.

High levels of parental care (such as provisioning) are expected to be favored in socioecologies in which male care helps enhance direct reproductive rates and offspring reproductive potential. If male care has minimal impact on offspring outcomes, there is an increased pressure to mate guard, or if his absence is readily replaced by other allomothers (such as kin, or support from state-level organizations), then men may minimize parental involvement (favoring instead to boost their fertility through male-male competition). The level of provisioning by men is thus influenced by the opportunity costs of foregoing reproductive opportunities with other potential mates, and by the level of support anticipated from the mother as well as extended kin networks (Hrdy 2009).

These factors contribute to the variable and facultative levels of male parental investment observed across contemporary human socioecologies (Gray and Garcia 2013; also reviewed in: Kelly 2013). Furthermore, a male's life history pace (a fast-slow continuum determined by extrinsic risks including pathogen load, lack of caregivers, insecure attachment) may affect how early and how much a male attempts to reproduce, which can further map onto risky attempts at male-male competition in order to secure a mate. In sum, many factors including the evolution of human life history traits, ecology, developmental history, socioecology, and even sex-ratio (see: Geary 2010) may influence whether a male chooses to compete or provision. Proximate mechanisms such as testosterone fluctuations may provide insight into which external stimuli drive a male towards engaging in competition or predisposing him to invest in his mate and children (reviewed in: Gray et al. 2019).

Big Game Hunting: Competition, Showing-Off, and/or Provisioning?

This section describes scholarly ideas on hunting (often attributed as a male activity and a critical

one in the evolution of modern humans), and whether hunting returns can be interpreted as a form of male-male competition, or as a reliable means to provision kin. While men can compete (for reputation, jobs, status, etc.) or provision (financially, vegetable foods, honey, land, social capital) in a variety of venues, big game hunting among foragers remains an area of special attention among many researchers and thus provides a useful focal point for this discussion (Coddington and Kramer 2016). The relationship between big game hunting and reproductive success (RS) has garnered considerable attention among modern small-scale foraging populations. While contemporary (or recently studied within past decades or even centuries) hunter-gatherers are not direct analogues to prehistoric populations, they do provide a window into how men's behavior impacts their reproductive success in natural-fertility settings that more closely resemble those of their hominin ancestors than today's large urban communities.

Among forager societies, male hunting success is consistently tied to higher status, although hunting is not the only way men compete, pursue status, and/or boost their reproductive success (Coddington and Kramer 2016). Theoretically, hunting itself can be viewed as a form of male-male competition in which more successful hunters are viewed as more prestigious within their group. This could allow them to have more access to higher quality mates or simply be more visible within a community. Additionally, big game hunting could be a source of protein and micronutrients which are critical to a group and widely shared due to the large package size that a large kill would create (otherwise most of it could spoil). Men may additionally be sharing preferentially with their household, and while wider sharing would suggest a mix of showing-off (and thus reaping the benefits of "winning" the hunt) and provisioning for the whole group. Hunting itself is a hotly debated topic and may have had many effects related to factors such as increased brain size, tool use, and extended life histories.

So how could hunting lead to an increase in status, and is this a sign of men's work essentially

being expressed as male-male competition? A large literature suggests that there is a link between hunting, men's status, and reproductive success (reviewed in: Copping and Kramer 2016; Kelly 2013), although the exact mechanism for this process is controversial. Men could be signaling their underlying quality as a mate by successfully returning a kill, while also signaling personality features such as generosity by widely sharing game. In this form of male-male competition, group members (and females) would evaluate an individual male based on his success. In fact, it does appear that in many modern small-scale preindustrial foraging populations, individuals can and do recognize who is the "best hunter" (Kelly 2013; Marlowe 2010; Stibbard-Hawkes et al. 2018). Additionally, some evidence suggests that hunting big game is in fact a risky endeavor, with a low success rate, and thus males only hunt (rather than procure easier game or gathered foods) as a costly signal of their mate value (reviewed in: Kelly 2013). In this signaling model, hunting is a more self-serving behavior (relative to if it were strictly a provisioning behavior) and women's work allows the necessary buffer for men to be able to show-off. What exactly is shown-off and how is debated in this model? Stibbard-Hawkes et al. (2018) found that while Hadza hunters are recognized and rated based on hunting ability, it is not necessarily costly to signal through hunting (men feed themselves on the hunt and often bring back alternate foods when faced with failure), and it is unclear if hunting success directly leads to more mating opportunities. That said, it appears the best hunters are often rated as more attractive and often pair with the best foragers (Kelly 2013; Marlowe 2010).

A contrary view to this male-male competitive and status seeking view of hunting is one which supports the positive effects of a provisioning father. Male provisioning, in the form of hunting, can provide critical calories (with a high proportion of fat and proportion) during key moments in reproduction. Females take on a significant caloric cost during pregnancy and lactation while also having noteworthy reductions in their own ability to provision (reviewed in: Meehan and Crittenden 2016). Male provisioning could provide the

necessary buffer during pregnancy and lactation to allow for a reduced risk of infant mortality. Wide sharing (as opposed to sharing within a man's own household) confounds provisioning as a reason for hunting (i.e., men's work), but even if men are sharing for status, it does appear that in many cases the best hunters' families appear to be provisioned more by the group as a whole (Kelly 2013; Marlowe 2010). Pair bonding stability may be an additional benefit of male provision, in addition to increased female fertility (an additional fitness benefit to a provisioning male).

Synthesis and Conclusion

Whether men's work (including the focus here on hunting) is a form of male-male competition or provisioning likely varies along a spectrum, in which men are both simultaneously competing and providing based on a host of factors like those alluded to in preceding sections. Environmental factors such as big game availability, market integration, disease burden, sexual inequality, and cultural norms (along with many others) likely contribute to variation in and changing forager male reproductive strategies. Males both provision and compete, and these behaviors are not necessarily mutually exclusive. It is important to emphasize the remarkable behavioral plasticity found in human males, when compared to other primates and other social mammals. This flexibility may emphasize competition and fast reproduction and indirect care-giving in many socioecologies. But the ability to provision (above as hunting, but also through other means) a slow-growing, costly human child has likely been a critical factor in the evolution of cooperation and modern human life history traits. Men, both competitors and providers, serve as first-line allomothers, even with a vast flexibility in their behavioral motivations.

Cross-References

- [Intersexual Competition](#)
- [Sex Differences](#)

- Sexual Dimorphism
- Sexual Reproduction
- Sexual Selection
- Sperm Competition

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Male–Male Contest

- Male–Male Strategies

Male-Male Cooperation

- Feelings of Excitement and Brotherhood

Male–Male Strategies

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Synonyms

Male intra-sexual competition; Male–male contest

Definition

Direct or indirect competitive interactions over access to females, their gametes or resources to attract females.

Introduction

Male–male competition is, along with female choice, one of two main mechanisms of sexual selection (Darwin 1871; Andersson 1994). However, male–male competition has received much less theoretical and empirical interest than female mate choice, perhaps because it is conceptually more straightforward and easier to comprehend (Parker 2014). Competition among males that increases their fitness (reproductive success) is performed to increase an individual's access to females or their eggs. It is manifested before copulation (precopulatory male–male competition), between copulation and fertilization (postcopulatory male–male competition), or after fertilization. While it has long been believed that male–male competition and female choice are mutually reinforcing, research in recent decades suggests that it is often not the case.

Forms of Male-Male Competition

Traits that undergo sexual selection are sometimes divided between armaments (weapons used in male–male contests and signals of male fighting

ability – status badges) and ornaments (signaling traits used by females in mate choice decisions). However, many sexually selected traits have a dual function and are clearly affected by both forms of sexual selection (Andersson 1994). It appears that many sexually selected traits may have initially undergone selection in the context of male–male contests and then have subsequently been adopted by females as a signal of male quality. This is because male weapons are honest “signals” of male fighting ability since they are routinely put to trial during male contests. Such traits can then be reinforced through female choice, with both intra- and intersexual selection driving the evolution of the trait. The reverse process can also be true. Thus, traits traditionally viewed as ornaments that have been selected through female choice may be used by males in aggressive displays, including such traits as bright coloration and elaborated body appendages (Berglund et al. 1996).

The two mechanisms of sexual selection need not always be mutually reinforcing. Recent research documented that male–male competition and female choice can act in concert, independent of each other or in opposition. A common illustration of concerted evolution is male coloration. For example, red nuptial coloration in the male three-spined stickleback fish (*Gasterosteus aculeatus*) appears to be selected through male–male competition and female choice. Red coloration is a characteristic of dominant individuals that win fights, and females prefer to mate with redder males. Additionally, variation in redness increases under male–male competition and this may facilitate female choice (Candolin 2000). In contrast, conflicting selection pressures are involved in the production of social pheromones by males of the speckled cockroach (*Nauphoeta cinerea*), with differences in male–male competition and female attraction signaling optima. Hence, male cockroaches with a pheromone level that enables them to gain a dominant position are not preferred by females (Moore and Moore 1999).

The form of male–male competition varies widely among taxa and mating system. The most obvious is male–male interference competition. It is manifested as a physical contest (direct fight),

signaling contest (ritualized fight in which an individual matches themselves against an opponent via the expression or display of signal traits), or a combination of both. Most direct fights ensue when a signaling contest does not lead to a clear winner. For example, male African annual fishes (genus *Nothobranchius*) compete for access to females by rapidly approaching an opponent and performing lateral displays that involves spreading the unpaired fins. Males are brightly colored and coloration and body size usually determine the winner of the contest at the signaling stage. Lateral displays expose bright coloration and include tail beating, which directs a stream of water toward the opponent, and mutual threats performed with prominently displayed branchiostegal membranes (Passos et al. 2015). When the difference between males is small and the contest is not resolved with these displays, the contest escalates, with attempts to bite the opponent’s fins and flanks. If the contest is still not resolved, males may lock jaws, sometimes remaining in this position for several minutes (Polačik and Reichard 2009) and with potentially fatal consequences for one of the combatants.

Larger body size or body mass is perhaps the most obvious and probably most common trait that is selected through male–male interference competition. Body size is a good predictor of overall physical strength and performance (McCullough and Simmons 2016). In staged contests, larger males enjoy a substantial advantage, and body size/mass is often the clearest predictor of the outcome of a contest, though it is often correlated with other traits that may contribute to success.

Many direct male–male contests rely on the use of weaponry. Weapons such as horns, antlers, spurs, enlarged jaws and teeth, and other body structures and appendages are used to directly outcompete an opponent. At the same time, weapons often serve as a signal of fighting ability (badge of status) and are used during the signaling stage of a contest. Only when any of the rivals retreats from the signaling contest, a physical interference follows. For example, male red deer fight over possession of females with rivals wrestling with their antlers and attempting to push each

other away. Fights in other species may involve pushing, pulling, or dislodging an opponent. The size of weaponry is often associated with body size and both may be indicators of overall male condition (Andersson 1994). Fighting is costly and potentially lethal, and many contests are resolved at the signaling stage despite males possessing formidable weapons. In the case of red deer, rival males walk in parallel and assess the opponent's antlers and body size. It is only when neither male backs down from a contest that a fight with antlers occurs, potentially with serious injuries.

Other traits selected through male–male competition have a primarily signaling function. While they vary more widely than traits used in direct contests, they supposedly also indicate overall individual performance. Acoustic and visual displays are the best researched signaling traits, though chemical traits appear more common than generally assumed, and other modalities, such as electrical discharges in electric knife fishes (Gymnotiformes), are known to serve for signaling individual characteristics. The function of most signals in the context of male–male competition is intimidation. Hence, many such traits tend to be exaggerated. Yet, for a signal to be evolutionary stable, it must carry honest information about the status of the signaler: his physical strength, body size, condition or prior residence, and ownership of a breeding resource. For example, some aspects of the vocal signals of male red deer (minimum formant frequencies) are constrained by individual anatomical features, directly associated with male body size. Hence, it provides receivers with accurate information by which they can measure a rival's competitive ability (Reby and McComb 2003). Signaling male fighting ability, however, may also include subtler signals. Cuticles of most terrestrial arthropods contain cuticular hydrocarbons, semiochemicals with extensive within-species variation (Ingleby 2015). Cuticular hydrocarbons convey complex information about an individual, including information on male competitive ability. Indeed the composition of these chemical signals can have a profound influence on the outcome of male–male competition (Lane et al. 2016).

The expression of weapons and signal traits may be constrained by direct and indirect costs. First, direct costs arise from increased risk of damage or mortality. In the Asian rhinoceros beetle (*Trypoxylus dichotomus*), the risk of breakage is highest for the longest horns, and overly large horns may, therefore, constrain selection on the continued exaggeration of horn length driven by male–male competition by setting a mechanical limit on maximum horn size (McCullough 2014). Second, exaggerated signals of male–male competition ability may incur a cost of increased predation by reducing escape ability or increasing detectability by predators. In *T. dichotomus*, males with larger horns suffer significantly higher predation rates from avian and mammalian predators (Kojima et al. 2014). Likewise, many conspicuous signals of different modalities carry considerable survival costs by attracting enemies exploiting signal transmission such predators or parasitoids (Zuk and Kolluru 1998). Third, there are indirect costs that include energy depletion (allocation of resources to the trait expression traded off against its use in somatic maintenance, immunocompetence, or sperm production). Fourth, increased expression of factors within particular hormonal pathways that are functionally essential for the expression of the trait or signal can be costly for other phenotypic functions (Blagosklonny 2008). Hence, optimal trait expression to maximize lifetime fitness (reproductive success and survival) is often much lower than the maximum potential expression of the trait.

Lekking males compete for access to females via displays, aggregating in large numbers in specific spots visited by females. Lekking is relatively widespread among insect, fish, and bird species, but also recorded in other taxa such as mammals. Male–male competition on leks is severe, leading to high variance of male mating success. It is generally assumed that reproductive success of males in leks depends on female choice, but competition to obtain a display site on the lek and for the best positions within the lek also contributes to male success (DuVal and Kempenaers 2008). For example, in black grouse (*Lyrurus tetrix*), lekking males fight frequently

and successful males experience high success (Hämäläinen et al. 2012).

Endurance is an important, but often overlooked, aspect of male–male competition and describes the temporal component of male–male competition. To be successful, dominant males must maintain their high rank across a time span of days, weeks, months, or even years. The length of the breeding season varies widely among taxa, environments, and geographic regions. Highly seasonal environments often have a breeding season confined to a relatively short period when most fertilizations occur. In other taxa and less seasonal regions and environments, fertilizations may occur throughout the year. Male–male interference competition is typically highest when female receptivity is temporally clustered within a short period, and the most successful male may secure a large number of fertilizations. However, this scenario is also prone to the evolution of alternative mating behaviors when some males circumvent direct competition with the highest-ranked males and undermine their ability to control access to females. Dominant males typically cannot monopolize all females when they are unable to control their spatial distribution (Reichard et al. 2005).

Harems are examples of mating systems with low temporal clustering of female receptivity combined with an elevated importance of male–male competition for reproductive success. Possession of a harem is physiologically demanding and potentially costly to the territory holder through frequent contests with rival males. Harem holders (and alpha males in social groups with subordinate males) stage many contests from rivals for their position, and there may be substantial turnover of individual males in the possession of the top rank. Defense of harems increases immediate reproductive success (the number of progeny) but has longer-term consequences for survival and may lead to rapid reproductive senescence (Lemaître et al. 2014).

Mate guarding is another mechanism of male–male competition. In some taxa, males restrain female association with other males to ensure paternity of their offspring is not compromised. Males may simply remain in close proximity to a

female and attempt to repel any rivals. Sometimes, mate guarding involves prolonged or repeated mounting of a female, despite no further sperm transfer (Baxter et al. 2015). For example, in the bug *Lygaeus equestris*, pairs can remain in copula for over 15 h and regularly move and feed in this position, with males walking backward or being dragged along. Still, only a period of 1–2 h is needed for successful insemination (Alcock 1994), and the remaining time spent on copulation is probably a form of mate guarding that reduces the likelihood of female remating.

Scramble competition for access to females is a frequent, though relatively rarely examined, form of male–male competition. Successful searches for available females may considerably increase male fitness and imposes selection on superior sensory ability and locomotor organs. Hence, the most mobile males in a population can mate with more females, outcompeting less mobile males. In red-spotted newts (*Notophthalmus viridescens*), tail size is associated with locomotory capacity, and males with the largest tails have the greatest mating success, possibly due to higher ability to capture females (Able 1999). In many arthropods, males have larger eyes, antennae, and other sensory organs than females which have presumably evolved as an adaptation to locate mates, indirectly pointing toward the importance of scramble male–male competition. A temporal component is intrinsically important in scramble competition, and in many anurans (toads and frogs), males intercept females already on their way to a breeding pond and clasp them in amplexus to secure early access to females.

Male–male competition for reproductive success goes beyond direct interference, even at the premating stage. In many mating systems, some males can circumvent direct male–male competition by alternative mating behaviors (AMB). AMB are behavioral adaptations that enable males to compete with their rivals (and sometimes outcompete them) through the use of behavior that is different from the “typical” male–male interference competition. The most common examples are sneak copulations (in internally fertilizing species) or sneak fertilizations (in species with external fertilization). When sneaking, a male deceives

his rival and his access to a female is typically cryptic, at least until copulation/gamete release. Sneak male deception takes the form of camouflage of their external appearance (female-like appearance), hiding in a structured environment, or their combination. For example, in bluegill sunfish (*Lepomis macrochirus*), males may develop either into a territorial male that sexually matures at the age of 7 years and invests in territory defense, nest construction, female courtship, and parental care. Alternatively, males may mature when only 2 years old as a sneaker and compete with parental males (and other sneakers) for fertilization. Young sneaker males “streak” into the nest of a territorial male during female egg laying and may fertilize a subset of eggs before being chased away by the territorial male. Older sneaker males mimic female behavior and coloration and deceive territorial males into identifying them as a second female in the nest (Neff and Gross 2001).

A traditional view of male–male competition considers sneakers to be of low quality, incapable of winning contests and therefore making “the best of a bad job” to gain any reproductive success. However, there is now good evidence from several mating systems to suggest that females sometimes prefer to mate with sneaker males. By preferring sneaker males, females avoid limitation of the expression of their mating preferences by resource monopolization by males winning contests over breeding resources. This leads to an incongruence between male–male competition and female choice where female choice is affecting the final outcome of male–male competition (Reichard et al. 2007). In European bitterling fish (*Rhodeus amarus*), males defend territories with living freshwater mussels into which females deposit their eggs. A limited number of dominant males may control most oviposition sites, forcing females to lay the eggs in their territories, despite a mate choice preference for other males who have not acquired their own territory. Bitterling females sometimes actively engage in a conspicuous behavior that attracts sneaking males and increase the time window for the eggs to be fertilized (Smith and Reichard 2005), modifying the outcome of male–male competition when males are

of unequal competitive ability but when resource defense is crucial for breeding.

Alternative mating behavior may have a genetic basis, depending on the developmental stage or age, or may be entirely flexible and context dependent. In ruff (*Philomachus pugnax*), satellite males tend to steal copulations from dominant males and “faeder” males mimic females. Both alternative male forms differ conspicuously in behavior and coloration from dominant males and the forms are genetically determined. Each alternative male morph possesses a unique, non-recombining chromosomal inversion (Küpper et al. 2016). In many fish (and other) mating systems with breeding resource defense (i.e., nesting sites), males compete with other males by sneaking fertilizations when young and start to compete for breeding resources when they grow older and larger (Wootton and Smith 2015). Yet, in some of these cases, especially in short-living species, differences in body size among males are relatively small, and each male is capable of playing the role of territorial and sneak male, with switches between the tactics within seconds. In the European bitterling, individual males frequently switch between territorial and sneaking behavior, often in a time span of minutes. They attract females to their own breeding territory and, at the same time, attempt to sneak-fertilize the eggs of females laid in the territories of neighboring males (Reichard et al. 2004). In general, the success of alternative mating behavior is dependent on demography (ratio between males and females, population density, male morphs density), environmental conditions (habitat complexity and ability to hide), and the female response to alternative mating behavior (Reichard et al. 2007).

Finally, male–male competition may extend beyond fertilization. In the bluegill sunfish, territorial males care for the offspring for several days. Parental males in this species are often cuckolded by sneakers. However, they have the capacity to assess their paternity level using the visual presence of parasitic sneaker males during spawning and, in addition, using olfactory cues released from the offspring after the eggs hatched. Parental males dynamically adjust their parental care and

cannibalize those clutches for which their paternity share is low (Neff 2003). Another example of male–male competition after fertilization can be found in the three-spined stickleback. Male stickleback signaling effort (red body coloration) actually increases during the post-mating period when males fully engage in parental care and no new partners or fertilizations can be obtained. Parental care is exclusively paternal in this species, and male bright coloration may indicate his ability and motivation to defend the nest and offspring against competing intruders that might steal or cannibalize the nest (Candolin and Tukiainen 2015).

The relative importance of male–male competition for reproductive success arises from variation in resource investment, parental care, fertilization mode, and other parameters. In mating systems with no male contribution to post-fertilization reproductive effort, the largest or strongest males secure access to a large number of females in harems. In contrast, when high parental effort is needed for raising the offspring successfully, stable pairs are formed, and the importance of male–male competition for fertilization is low or restricted to postcopulatory processes. In mating systems with pair bonds, males may compete for the access to females with the highest reproductive value (i.e., fertility), though pairing in such systems is generally relatively unrestricted by mate coercion and dominated by female or mutual mate choice rather than direct male–male competition.

Conclusion

Male–male competition is a powerful mechanism of sexual selection that takes many different forms but is selected to secure access either directly to females (or their gametes) or to breeding resources critical for reproduction. It may be independent of female choice and postcopulatory processes, but often acts either in concert or in opposition to female choice. Interference competition involves direct physical or signaling contests between males, with development of weapons and expression of signals being constrained by direct and indirect costs associated

with their possession. Other forms of male–male competition include scramble competition for access to females, lekking, mate guarding, and alternative mating behaviors (e.g., sneak copulations or mimicking females) that circumvent direct contest with stronger males. Endurance is an important, but frequently neglected, aspect of male–male competition and recognizes that male success integrates over his lifetime. Male–male competition can extend beyond fertilization, and males may adjust the level of their parental care to perceived paternity.

Cross-References

- ▶ [Copulatory Intrasexual Competition](#)
- ▶ [Lekking](#)
- ▶ [Multiple Matings](#)
- ▶ [Precopulatory Intrasexual Competition](#)
- ▶ [Sneak Copulation](#)
- ▶ [Sperm Competition](#)
- ▶ [Vocal Competition](#)

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Maleness

► Masculinity and Femininity

Male-Provisioning Hypothesis

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Synonyms

Food sharing hypothesis; Hunting hypothesis

Definition

The Male Provisioning Hypothesis (MPH) proposes that men have evolved to provision their

mates and children and that this provisioning has resulted in significant changes to the evolution of human biology and life history.

Introduction

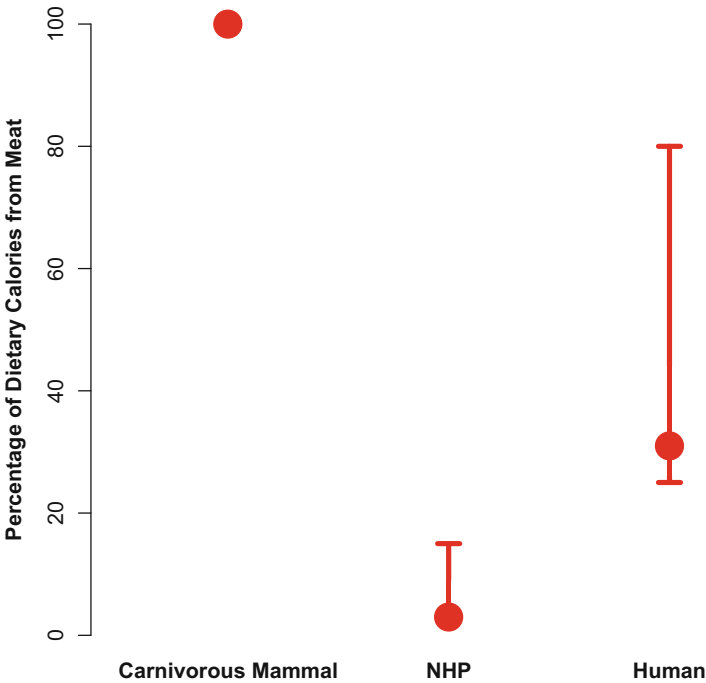
Although the MPH has had many proponents, there have also been many detractors. This article reviews the theoretical underpinnings of the MPH and contrasts the hypothesis with commonly cited alternatives. In reviewing the evidence brought to bear on these alternatives, the article concludes that although male subsistence and provisioning efforts are significantly greater in humans compared to other mammals, the MPH is nonetheless insufficient as a sole explanation for the evolution of humans' extended life histories and attendant adaptations. Rather, men's investments in their children and wider communities are flexibly allocated. Human adaptations are more likely the result of a system of cooperative breeding in which any of a variety of possible caretakers subsidizes a lengthy and expensive period of child-rearing.

Provisioning Does Not Require Hunting and Hunting Does Not Require Provisioning

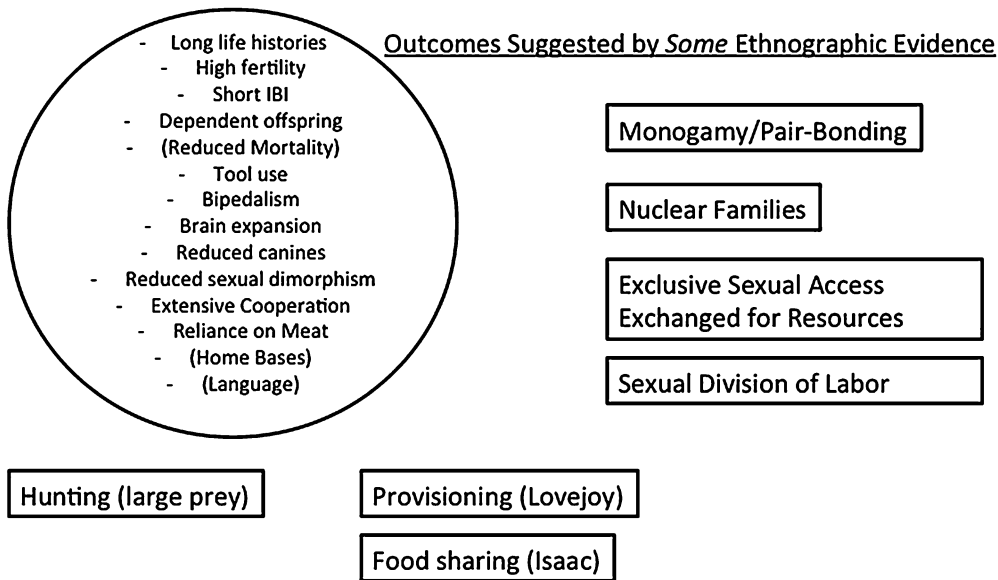
The origins of the MPH reside in part in the observation that the human diet consists of a relatively high proportion of meat (Fig. 1). Indeed, although variable, meat contributes significantly more to the human diet in comparison to the diet of our closest living relatives (Hill 1982). Paleoarchaeological evidence initially suggested that meat consumption became significant concurrently with a number of changes in human life history and biology that are central components of the modern human adaptive complex, including bipedalism, tool use, reduced canine tooth size, decreased sexual dimorphism, extended life histories, higher fertility, lower interbirth intervals, increasingly dependent offspring, and increased cooperation (Isaac 1978; Lovejoy 1981) (Fig. 2).

The MPH links together these features in an evolutionary scenario involving: (1) a sexual division of labor in which men primarily acquired meat and women primarily focused on gathering;

Male-Provisioning Hypothesis,
Fig. 1 Percentage of calories derived from meat among a sample of mammals, nonhuman primates, and human forager groups (Selected data drawn from Hill 1982)



Outcomes Suggested by Paleontological/Archaeological Evidence



Male-Provisioning Hypothesis, Fig. 2 A visual model of the Male Provisioning Hypothesis (MPH). Male provisioning, whether via hunting or food sharing, is thought to be a key driver in the origins and maintenance of the human adaptive suite as depicted by the paleontological and archaeological record, shown in the *circle* on the *left*

(items in parentheses are less commonly emphasized outcomes). Ethnographic evidence that has been used to bolster the case for the MPH is shown on the *right*. As discussed in the text, human families are more variable than viewed in this depiction, undermining some of the key premises of the MPH

M

(2) meat being used by men to provision their mates and biological offspring; (3) a “sex contract” (ibid.) by which women traded fertility for meat; leading to (4) monogamous unions and the establishment of the nuclear family (i.e., a man, his mate, and their dependent offspring) as the elementary human family form. Note that as stated here, the MPH does not require hunting, per se. In fact, in one of the earliest statements of the MPH, Isaac (1978) was careful to distinguish provisioning from hunting, indicating that meat was more likely to have been scavenged than hunted when proto-hominin males began provisioning their mates.

Nevertheless, the MPH has more often been associated with hunting than not (Dart 1953; Gurven and Hill 2009; Gurven and von Rueden 2006; Hill 1982; Kaplan, Hill, Lancaster, and Hurtado 2000; Washburn and Lancaster 1968). Indeed, although the term “male provisioning hypothesis” can be most closely attributed to Owen Lovejoy (1981), the model has its origins

in various versions of the “hunting hypothesis” (HH) dating back at least to Westermarck (Westermarck 1903, cited in Kristen Hawkes 2004) and elaborated most influentially by Sherwood Washburn (Hawkes 2004). Washburn’s (Washburn and Lancaster 1968) original arguments foreshadow modern depictions of the MPH: in his view, hunting evolved alongside bipedalism and tool use, and with bigger brains, which reflected the increased skill associated with hunting as opposed to other forms of foraging. Larger brains would have necessitated the birth of immature offspring to avoid taxing the maternal pelvis. This, in turn, led to increased dependency of offspring on their mother and resulted in the need for male provisioning.

Following evidence that bipedalism, brain expansion, and big-game hunting are separated in the paleoarchaeological record by millions of years (Klein 2009), modern variants of the MPH have shifted emphasis away from the broader linkages envisioned by Washburn and others and

toward its effects on the human life history, *per se*. In the most influential version of this argument, Kaplan and colleagues (Kaplan et al. 2000) have proposed that hunting allows for increased investment into “embodied capital” (i.e., skills, knowledge, health), which is accrued during a lengthy period of juvenile dependency, and pays off when skills-intensive foraging (i.e., hunting) increases the reproductive rate of provisioned females. In this view, male provisioning via hunting is the key to underwriting relatively rapid reproduction among human females, as mothers devote the surplus energy to reproduction and childcare rather than foraging (see also Lovejoy 1981). Females offer fidelity to men in exchange and pair-bonds (Gurven and Hill 2009) and nuclear families result (see also Lancaster and Lancaster 1983, 1987; Lovejoy 1981).

Although the MPH and HH are closely related and share certain features in common, it is important to distinguish between them for at least two reasons. First, male provisioning via hunting presumably requires more skill (if not risk) than scavenging or other forms of provisioning and therefore places a stronger emphasis on men’s increased capabilities as being ultimately responsible for shifts in human life histories. As discussed more fully below, this hypothesis continues to inspire debate over the extent to which hunting functions as a means of provisioning hunters’ families (Gurven and Hill 2009; Wood and Marlowe 2014) or whether it serves more commonly to signal status and high quality to nonkin (Bliege Bird and Bird 2008; Kristen Hawkes et al. 2014). Second, male provisioning, whether or not via hunting, *is* one means by which human allomothers contribute to childrearing. Delineating the factors that predict when and how men invest in children may be more fruitful to our understanding of the origins and maintenance of human life histories than a more narrow focus on hunting, *per se*.

Controversy/Alternative Views

The male provisioning hypothesis has been at the center of one of the most enduring recent debates in evolutionary anthropology. Although this debate

takes different forms, the heart of it concerns (i) the relative contributions to subsistence by males and females and (ii) other possible motivations for male hunting. These two issues have different implications for understanding more generally how men contribute to the evolution of human life history. Undermining the significance of provisioning as a motive for hunting need not imply that men do not or have not in the past chosen to provision their mates. Nor does it need to imply that hunting has lacked an impact on the human life history; even if meat was not used as a form of direct provisioning and was instead widely shared, it would still have been associated with increased energy that could be allocated by women to reproduction instead of foraging (Kaplan et al. 2000; Marlowe 2000). On the other hand, if hunting is not primarily a means of provisioning mates, then pair-bonding and nuclear families do not automatically follow. Moreover, if females are able to supply most of the calories they need in order to subsist, then the degree to which hunting adds to energy reserves is called into question.

Kristen Hawkes (2004) has been perhaps the most vocal critic of the MPH and has provided evidence that supports (i) a stronger role for women in contributing to the diet of hunter-gatherers; and (ii) more self-centered motivations for male hunting than a provisioning model would imply. With respect to (i), evidence suggests that there is more overlap in men’s and women’s subsistence strategies in foraging societies than previously recognized (e.g., Bliege Bird and Bird 2008). This finding is bolstered by cross-cultural evidence of female self-sufficiency in the absence of male support (e.g., Brown 1970; Quinlan and Flinn 2005) and by quantitative evidence of more consistent returns from female rather than male foraging efforts in contemporary hunter-gatherer populations (Bliege Bird and Bird 2008). All of this is not to say that men’s hunting provides negligible dietary input – men contribute as much as 65 % of the calories and 85 % of the protein in forager diets (Cordain et al. 2000; Kaplan et al. 2000) – but it does speak to a more nuanced and flexible system of subsistence than typically advocated by the MPH.

With respect to point (ii), Hawkes and colleagues continue to argue that men’s hunting

targets large game that is both widely shared and unpredictably acquired and therefore that men hunt as a means of “showing off” rather than as a form of provisioning (Hawkes and Bliege Bird 2002; Hawkes 1991; Hawkes et al. 2014). In this view, hunting serves as a costly signal that attracts potential mates and allies to good hunters. Meat is not provisioned, but is instead a publicly shared good. Men benefit reproductively from being good hunters, not by investing directly in their wives and children, but by acquiring more or higher-quality mates and allies. Hungry foragers make for an eager audience and the women who contribute to good hunters’ reproductive success also stand to gain, albeit indirectly (e.g., genetically).

Proponents of the show-off model have furnished a variety of evidence in support of its main predictions, including direct evidence that hunters’ wives and children do not receive more shares of hunted meat than do other foragers and by indirect evidence that pair-bond stability is more sensitive to the intensity of male mating competition than by “father effects” related to provisioning (Blurton Jones et al. 2000). Still, data have also supported increased provisioning during critical periods (e.g., lactation) when women are at reduced capacity to meet their own needs (Marlowe 2003) and contradictory interpretations of hunting data from the same society (Kristen Hawkes et al. 2014; Wood and Marlowe 2014), confound resolution. Solving these empirical conflicts will require more data and clarification of the sources of variability in meat apportionment across hunter-gatherer societies. Regardless, the benefits to females of bonding with males are more than just dietary (Scelza 2013), and human males invest significantly in their offspring in a wide variety of contexts (Gray and Anderson 2010), suggesting that these views are not mutually exclusive.

Determinants of Male Parental Investment

Challenges to the hunting hypothesis and earlier iterations of the MPH are sometimes depicted as a more general challenge to the importance of male provisioning in human family systems, but this

should not be so. Although the degree to which men help is variable across cultures and less consistent than maternal investment, it is nonetheless significant in relation to the majority of nonhuman primates (Hill 1982 and Fig. 1). Several hypotheses explain when and how intensively men invest in their children, and a wide body of empirical literature has tested these hypotheses (see Gray and Anderson 2010 for review). These tests indicate that fathers invest frequently and significantly under a wide variety of circumstances and even in cultures where the significance of their role is downplayed (Mattison et al. 2014). It is also clear that the means of caring for their children extend far beyond provisioning, including both direct and indirect care (Marlowe 2000) and in relation to the support provided by other caretakers (Gurven and Hill 2009; Kokko and Jennions 2008; Marlowe 2003). Critically, however, the support that fathers provide is sensitive to the subsistence base (Hewlett 1988; Mattison et al. 2014), such that it would be unwise to extend the relationship between paternal investment, monogamy, and nuclear families seen in many contemporary Western societies back into a proto-hominin past.

Conclusion

... ‘natural’ parental behavior is often surprisingly flexible, and there are multiple pathways to successful parenting. (Sear 2016, p. 101)

The Male Provisioning Hypothesis in its most virile form has more or less been laid to rest – that is to say, it is no longer generally accepted that men’s hunting alone can explain the adaptive suite that separates humans from nonhuman primates. The current debate centers instead on the relative contributions of fathers, grandmothers, and other kin to the origins and maintenance of our extended life history and relatively rapid reproduction. Whereas it is undeniable that paternal investments in different forms of care (both direct and indirect) underwrite these costs in societies when men benefit reproductively from doing so, it is equally clear that many other care-takers are often as, or more, important (Sear and Mace 2008).

At the same time, the significance of men's hunting in human evolution is not in doubt. It is now "...largely accepted that successful hunters (1) contribute valuable protein and fats to the diet, (2) gain prestige and social status, and (3) tend to have higher reproductive success than poor hunters" (Gurven and von Rueden 2006, p. 81). In light of the available evidence, it seems likely that hunting involves a variety of functions of which provisioning is only one (see Gurven and Hill 2009). This does not diminish the importance of hunted meat as a source of nutrients for hunter-gatherers, but it would seem to weaken the link between hunting, monogamy, and nuclear family formation.

The MPH and the HH, if questionable in their specifics, have nonetheless been useful frameworks to understand how the support of different caretakers might affect the evolution of human life histories. Indeed, the recognition that provisioning and cooperation have played central roles in extending our life history has led to sophisticated applications of the cooperative breeding hypothesis to understand how various care-providers navigate the costs and benefits of providing care under different circumstances (Sear 2016). And unlike the MPH and HH, the cooperative breeding hypothesis implies nothing about universals in the sexual division of labor or the importance of specific caretakers. Rather, it emphasizes our vast flexibility in caring for our unusually dependent offspring.

Cross-References

- Life History Theory
- Mating Strategies
- Mating Systems

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Males and Crime

- [Perpetrators Mostly men](#)

Male-Warrior Hypothesis

- [Same-Sex Coalitions That Exclude Women](#)

Malicious Joy

- [Schadenfreude](#)

Malleability

- [Adaptive Plasticity](#)

Malthus on Population

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Synonyms

An Essay on the Principle of Population;
Exponential growth; Malthusian growth

Definition

An Essay on the Principle of Population by Thomas Robert Malthus (1798) is a book widely viewed as having profound impact on the biological and social sciences by recognizing basic biophysical, demographic, and economic principles that can lead to population growth and possible collapse.

Introduction

Be fruitful and multiply. Fill the earth and govern it. Reign over the fish in the sea, the birds in the sky, and all the animals that scurry along the ground. – Genesis 1:28

The power of population is indefinitely greater than the power in the earth to produce subsistence. – Malthus 1798

An Essay on the Principle of Population by the Reverend, Political Economist, and Demographer, Thomas Robert Malthus (1766–1834), is perhaps the most important document ever published on population, yet its central thesis continues to be highly controversial between natural and social scientists today. First published anonymously during the Enlightenment in 1798, the subsequent five editions bearing Malthus' name (the last in 1826) refined and elaborated on initial arguments, as well as responded to critics with data, case studies, and mathematical and logical proofs. More than 220 years after the first edition, the arguments and counterarguments provoked by *An Essay on Population* (as it became popularly known) are still central to discussions of future human and planetary wellbeing today. In this chapter I (i) introduce the historical context and setting in which Malthus wrote the book, and (ii) provide a brief overview of the *Essay's* general concepts and content, and (iii) conclude with a summary of the enduring legacy of Malthus' *Essay* in modern science and society.

Historical Context

Thomas Robert Malthus was born in 1766 in Surrey outside of London. He studied in Jesus College at Cambridge University where he was later elected Fellow. Malthus was Professor of History and Political Economy for the East India Company College in Hertfordshire. He became ordained by the Church of England in 1788 and was elected Fellow of the Royal Society in 1818. An interdisciplinary scholar, he influenced a vast range of study including theology, biology, demography, public policy, economics, agriculture, labor, commerce, and moral philosophy.

Malthus was educated during the enlightenment when there was much optimism for the recent human progress. During this time, the arrogant view of humans as superior beings on Earth contributed to the growing enlightenment prescriptions for increased fertility, because population increase and economic growth were so intimately coupled. During this time, Adam Smith's *Wealth of Nations* was well received and

paved a path for prosperity through the “invisible hand” of free markets. Malthus was a skeptic of the idea that increasing revenue and wealth would benefit all, citing that a substantial proportion of the population in all societies is in poverty. Malthus' *Essay on Population* was specifically critical of recent utopian views set forth by Marquis (a.k.a. Nicolas) de Condorcet in France and Briton William Godwin's writings on “the perfectibility of society.” The French Revolution, which largely stemmed from the rising disparity between the leisure and working classes, spurred debates among the British aristocratic circles. The inseparable political and religious establishments in Britain were trying to prevent the revolutionary contagion, as they saw it, from spreading across the English Channel.

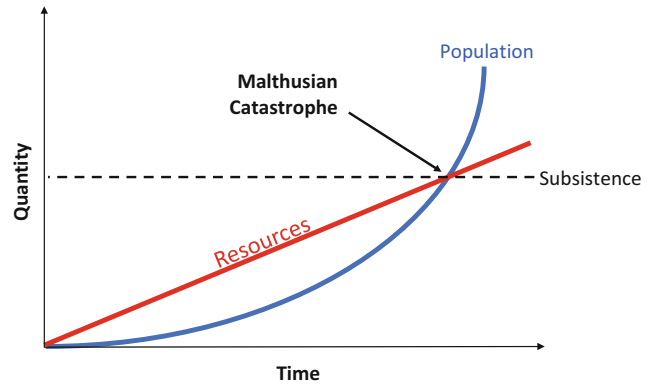
The first edition of Malthus' *Essay* laid out his thoughts and rebuttals to these scholars. It begins with a conversation with “a friend” who turns out to be Malthus' father regarding the speculations on the “future improvement of society” and “perfectibility of man” written by Godwin, Condorcet, Smith, David Hume, and others of the time. Malthus was an empiricist who held that “*acknowledged truth in philosophy is that a just theory will always be confirmed by experiment.*” The second edition provided expanded discussion and data. For example, Malthus cites Benjamin Franklin's observation that the New World colonies of the Americas had a population doubling time of every 25 years (Franklin 1751). In contrast to the Eurocentric focus of much of the discussion on population and society at the time, Malthus' work was global in scope, involving case studies and data from societies spanning the Far East and Pacific Islands as well as the Americas (Bashford and Chaplin 2016).

Malthus' Theory and Implications

Malthus' central thesis addressed the relative rates of food production and population growth, observing that, because human population grew exponentially (geometrically 1, 2, 4, 8, 16, 32, 64, etc.) and food production arithmetically (e.g., linearly 1, 2, 3, 4, 5, 6, 7, etc.), sooner or later

Malthus on Population,

Fig. 1 illustrates Malthus' theory. Over time population growth increases exponentially if unchecked. In contrast, resource production grows linearly. At some future time, growth in population will exceed the supply of resources – known as the “Malthusian Catastrophe” – and the population collapses back to subsistence levels



human population would outstrip resources (Fig. 1). Gains in living standards would be short-lived, and populations would collapse to subsistence levels. This was based on two assumptions that Malthus thought were innate and incontrovertible. First, food is necessary for humans to live. Everyone requires about 2000 calories per day and a healthy balance of fats, proteins, and carbohydrates. Second, the passionate drive between the sexes to procreate and “*be fruitful and multiply*,” will inevitably lead to the birth of more kids and population growth. Malthus predicted that checks on population would come in two forms: *positive checks* that raise the death rate such as widespread “famine, pestilence, and war” and *preventative checks* that lower the birth rate including moral restraints such as birth control, postponing marriage, and celibacy. Infinite growth in population, Malthus proclaimed, is impossible due to finite limits of the Earth.

Malthus' Iron Law of Wages provided one of the earliest economic insights into the biophysical constraints that couple human population to the natural environment. It suggested that growing populations would result in a surplus of laborers, which in turn would drive down wages towards poverty levels. Moreover, increasing population and demand for commodities would drive up the price of provisions, while simultaneously decreasing wages, leading to poverty and misery among the working class. Thus, according to Malthus, in the long-term there will always be poor in all societies. Population growth would exacerbate the problem. Malthus writes that life for the poor would be so miserable “*Even when they have an*

opportunity of saving they seldom exercise it, but all that is beyond their present necessities goes, generally speaking, to the ale-house” (p. 35).

Influence on Biology: First Law of Nature

Malthus had a profound influence on the fundamental demographic models that are still used to study humans and the millions of other plants, animal, and microbe species on the planet today. It was perhaps unforeseen by Malthus that his *Essay* would revolutionize biology. His observation that all living organisms have the capacity to produce more offspring than can survive was a cornerstone in the development of evolutionary biology. All populations that are unchecked, including humans, have the intrinsic capacity to grow exponentially.

The implications of Malthus' theory can be formulated mathematically, where the population growth rate (r) is equal to births (b) minus deaths (d) plus immigration (i) minus emigration (e). So, a

$$\text{Population } (P) \text{ at steady state } = P = 0 = r = b - d + i - e. \quad (1)$$

At the global scale, we can assume net migration of zero and Malthus' theory can be expressed as an exponential function of the form,

$$P(t) = P_0 e^{rt}. \quad (2)$$

where $P_0 = P(0)$ is the initial population size, r = the population growth rate, and t = time. Therefore, all stable populations of all species have an

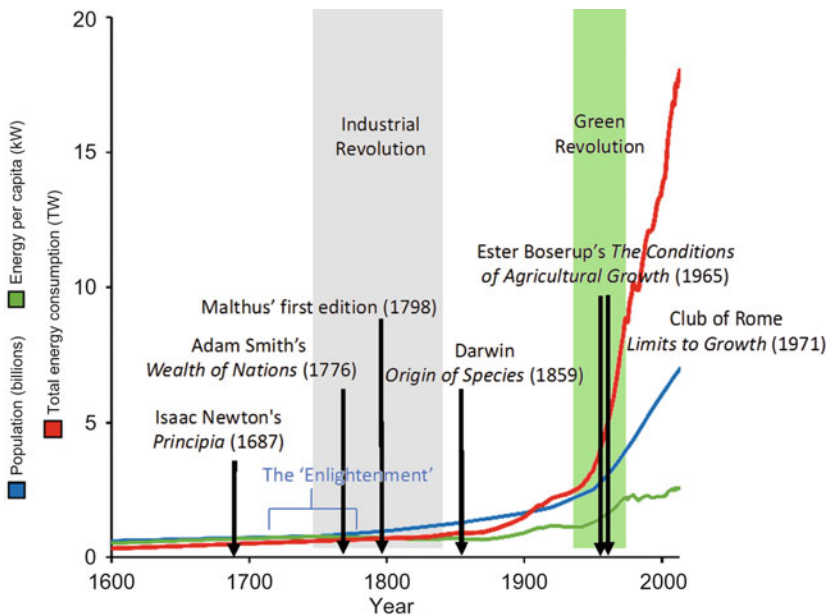
$r = 0$, on average and over the long-term, where births are equal to death rates, and i immigration offsets e emigration. A positive growth rate ($r > 0$) is exponentially. Such species would inevitably fill up the planet, exhaust all resources, and collapse to a steady state population. Conversely, populations with a negative growth rate ($r < 0$) are not sustaining and will inevitably go extinct. Critical for evolutionary theory, is that when populations are in steady state and $r = 0$, most offspring do not survive, selecting for the “fittest” individuals.

Malthus’ law of exponential growth is regarded as the first principle of population dynamics (Turchin 2003). Malthus’ conjecture that all populations have the intrinsic capacity to produce more offspring than can survive, and thus grow populations indefinitely if unchecked, had a profound impact on modern biology as evident by its inclusion in many introductory textbooks spanning the physical, biological, and social sciences today. Despite few scientific laws in biology, and

even fewer in the social sciences, Malthus’ observation on population is even considered a “law of nature” similar to Newton’s laws (Ginzberg 1986) which preceded Malthus in the *Scientific Revolution* (Fig. 2). In fact, Malthus wrote in *An Essay* about the influence of Newton’s *Principia* on his thinking of the fundamental biophysical laws that act on population. In turn, Malthus’ sixth edition published in 1826 had a profound influence on the formulation of evolutionary theory. In Charles Darwin’s *Autobiography* (p. 120) he writes:

I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. (Barlow 1958)

Similarly, Wallace in 1905 in his autobiography *My Life* he wrote:



Malthus on Population, Fig. 2 shows growth in per capita energy consumption, population, and global energy consumption over time reproduced with permission from Schramski et al. (2019). Superimposed are some key publications that influenced or were influenced by Malthus’ *Essay*. The world’s population was about 800 million in 1798 when

Malthus first published the *Essay*. Today there are 7.7 billion people and rising. For much of this time population was growing faster than per capita and total energy consumption. However, around 1960 total energy use began to increase even faster than population. This energy is finite and largely in the form of fossil fuels (about 85%)

Perhaps the most important book I read was Malthus' *Essay on Population*. . . It was the first great work I had yet read treating any of the problems of philosophical biology, and its main principles remained with me as a permanent possession, and twenty years later gave me the long-sought clue to the effective agent in the evolution of organic species. (Wallace 1905: 232)

Equal Fitness Paradigm

In contemporary ecology and evolution, Malthus' first law of nature is a cornerstone of the Equal Fitness Paradigm (EFP; Van Valen 1973; Brown et al. 2018; Burger et al. 2019a). The EFP posits that, over evolutionary time, each parent must exactly be replaced by one offspring, birth rates must equal death rates, and this results in steady-state populations and equal fitness among all species. This is evident by the mere coexistence of the millions of species on Earth. Some fish, plants, and invertebrates produce literally millions of offspring and other species such as birds and mammals, produce very few. Yet, underlying all the enormous diversity of life on Earth are general life history laws: (1) demographic: regardless of the number of offspring produced in a lifetime, on average only two survive to replace the parents (in a sexually reproducing species) resulting in a steady-state equilibrium or non-growing population, and (2) mass-energy balance: each individual exactly replaces themselves in energy and material content, so a mass-energy balance must occur over a generation (Burger et al. 2019a). Thus, despite the enormous variation in biodiversity spanning many orders of magnitude in body size, generation time, and fecundity, all species are equally fit because ultimately each adult is exactly replaced by one surviving offspring that lives to reproduce. The EFP provides a null hypothesis and benchmark to understand the unique circumstances that has allowed the human species to maintain positive population growth. These are just some of the profound insights inspired by Malthus' *Essay*. It still influences modern biology today and can play a pivotal role in extending fundamental evolutionary and demographic theories to understanding the origins of the Anthropocene – the age of global human ecological dominance.

Malthus' Influence on Society

It was evident from the first edition of Malthus' *Essay* that it would have a profound impact on society, influencing the first English census of 1801, and the Poor Law Amendment Act of 1834 which cut subsidies to the poor. Some interpretations of Malthus' work have presumably influenced political ideologies such as genocide and eugenics (Shermer 2016). A number of moral philosophers and historians painted Malthus as being insensitive to slavery, indigenous peoples, and the poor. Yet, in later editions of the *Essay*, Malthus does advocate for educational and economic policy interventions to mitigate the amount of suffering by the poor (Bashford and Chaplin 2016). He further writes about indigenous rights to their native lands, although he was rather vague about how to mitigate imperialism and exploitation of native peoples (Hodgson 2016). Nonetheless, in retrospect Malthus is often considered a forerunner of social Darwinism (e.g., Shermer 2016) because he applied fundamental laws of biology to human populations. However, the naturalistic fallacy instructs that just because things are so, doesn't mean they ought to be.

"Neo-Malthusians" Versus "Cornucopians"

The 1960s witnessed a resurgence of Neo-Malthusian campaigns for Zero Population Growth (ZPG) culminating with the publication of *The Population Bomb* (Ehrlich 1968), written by Paul (and Ann (The editor of *Population Bomb* insisted that Paul Ehrlich be the sole author when Paul and Ann Ehrlich coauthored the book)) Ehrlich, and the *Limits to Growth* (Meadows et al. 1972) report published by the Club of Rome written by a team of scientists lead by Donella and Dennis Meadows at the Massachusetts Institute of Technology. In response, Cornucopians (after the ancient Greek "horn of plenty") have argued against Neo-Malthusians, citing that technological innovations including energy efficiency, health and medical advancements, genetically modified crop breeding, petrochemical fertilizers,

mechanized agriculture, and irrigation have allowed resource supply to outpace growing population demand. Cornucopians extend Adam Smith's "invisible hand" of the free market to believing that supply, demand, and monetary incentives will continue to provide technology that will innovate our way out of environmental problems. This Cornucopian view shared by many neoclassical economists and technologists assumes that growth in the human system (population and economy) can continue indefinitely. In contrast, Jared Diamond's famous book *Collapse* (2005) is critical of Simon and the Cornucopians, stating that their assumptions were not in line with natural limitations.

Perhaps the pinnacle of this discussion culminated with a bet between, Paul Ehrlich (and others), and the American economist and Cornucopian, Julian Simon. Simon argued in the 1970s that we had already accumulated the knowledge required to supply the world's growing population for the next seven billion years (Simon 1981). The business professor Simon challenged the ecologist Ehrlich to choose any raw material and future date and Simon wagered that the real inflation-adjusted prices would decrease because of technology, rising standards of living, and free markets incentives that would drive the prices down (Simon 1980). Ehrlich took the bet arguing that rising demand from population and affluence would result in resource shortages, thus driving up prices. In 1980, in what has become known as the "Simon-Ehrlich wager" Ehrlich chose copper, chromium, nickel, tin, and tungsten with the predicted payoff date a decade later. Ehrlich lost the bet. The prices of all five metals declined during the 1980s. However, the prices of those commodities subsequently increased and other metrics of human well-being (e.g., numbers in poverty, income inequality, and pollution) have gotten worse. So, it is not that straightforward if Ehrlich or Simon was right (Sabin 2013). This debate between Malthusians and Cornucopians continues today (Fig. 3) and has motivated cross-disciplinary research seeking to explain the peculiarity of human population growth. Combining both the Malthusian and Cornucopian perspectives has led to quantitative models that

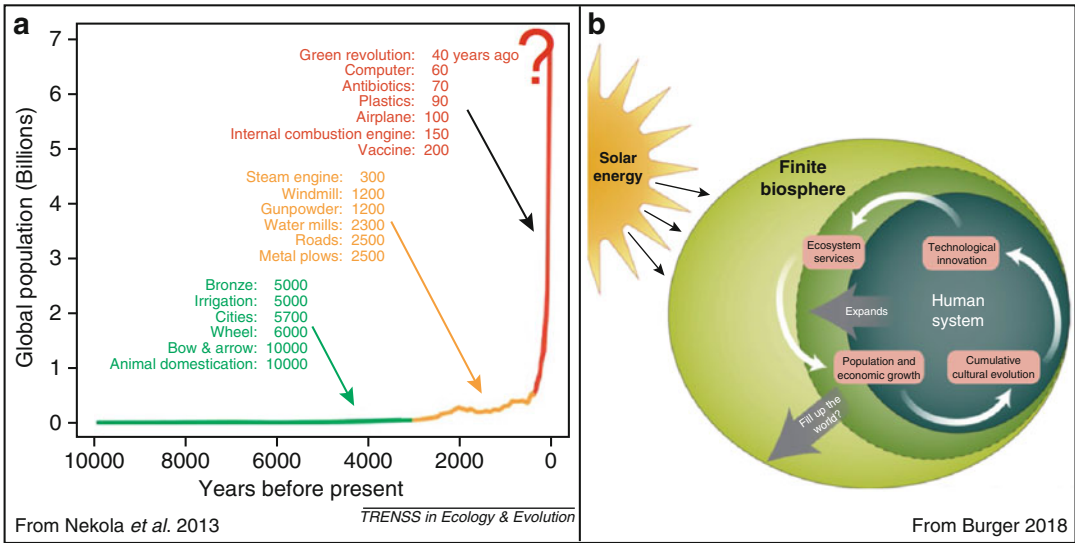


Malthus on Population, Fig. 3 shows climate protestor Brian Maitner holds a sign "MALTHUS WAS RIGHT" featuring Eq. 2 in El Presido Park in Tucson, Arizona, September 20, 2019, demonstrating the legacy of Malthus' seminal *Essay on Population*. Photo credited to Rachel Gallery

incorporate how population growth, interacting with biophysical resource constraints, can lead to biological and/or cultural innovations that allow humans to temporarily circumvent environmental constraints and continue growing (e.g., Boserup 1965; Nekola et al. 2013; Burger et al. 2017; Weinberger et al. 2017; Burger 2018). While these models shed light on how innovations have allowed exponential population growth, indefinite growth in a finite space is impossible and this was central to Malthus' thesis.

Malthus, Darwin, and Boserup

So far, the ascending spiral of positive feedbacks between population growth, innovation, and resource supply has kept pace with growing population and consumption levels (Fig. 4). How have humans been able to continue harnessing



Malthus on Population, Fig. 4 (a) Global human population over the past 10,000 years and some major innovations in human history that have contributed to increasing carrying capacity (Adapted from Nekola et al. 2013). Human population has increased from less than 1 billion before 1800, to ~2 billion in 1927, ~3 billion in 1959, ~6 billion in 1999, ~7 billion in 2011, to the now 7.7 billion on the planet in 2019 and is still increasing. (b) A conceptual model of how growth in the human system (population and economy) is characterized by positive

feedbacks between cumulative cultural evolution, technological innovation, and increased flow of natural and ecosystem services from the environment (adapted from Burger 2018). Cumulative cultural evolution is broadly defined as the accumulated socially learned knowledge and technologies that are tried, tested, recorded, transferred, modified, and recombined over time through social processes like copying, emulating, teaching, and learning. Malthus argued that these exponential processes cannot continue indefinitely on a finite planet

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additional energy sources to temporarily escape checks on populations that seemingly constrain all other species? The Darwinian process of innovation and adaptation has allowed us to continually push environmental limits (Nekola et al. 2013). Thus, Darwinian innovations have allowed birth rates to far exceed death rates resulting in exponential population growth. However, the Malthusian process is that all species have the intrinsic capacity to increase population exponentially until environmental limits are reached. Research at the intersection of evolution and sociology has begun to investigate the role of cultural evolution in accelerating information exchange and innovations leading to continued exponential growth (Fig. 4).

The human ability to innovate and appropriate an ever-increasing resource supply has increased global carrying capacity to current exponential growth rates (Fig. 4). The French and Danish Agricultural Economist Ester Boserup acknowledged

the need to continuously innovate as population growth demands ever increasing resources (1965). As the human population grows, the demand for more resources has led to increased land intensification and higher crop yields culminating in the Green Revolution of the 1950s and 1960s that drastically increased crop yields worldwide. However, the study of complex societies has revealed diminishing marginal returns to growth (Tainter 2011, Strumsky et al. 2010; Diamond 2005) including a global decline of per capita consumption of several important global resources such as oil, phosphate, wood, wild fisheries, agricultural land, and freshwater (Burger et al. 2012). Moreover, the fraction of income spent on food and energy has been increasing since the late 1990s (King 2015). So, the scope for innovation to continue to stave off collapse as we reach planetary limits is an open question (Weinberger et al. 2017; Burger et al. 2017; Burger 2018).

Conclusion

Malthus' *Essay* has had an enduring impact on the natural and social sciences. Its principles continue to influence fundamental models in evolution, ecology, and human demography today. Its central thesis also continues to be a point of contention among Neo-Malthusians and Cornucopians. I end with three concluding points: (i) current population trends, (ii) Malthus' argument for the (im) perfectibility of humans, and (iii) Malthus' solutions and alternatives to the growth paradigm.

Current Population Trajectories

The global population was ~800 million people when Malthus wrote the first edition of *An Essay*. Today there are 7.7 billion people on the planet. There is much optimism that world population will reach a steady state and possibly even begin to shrink by the end of the century due to the demographic transition where the global population growth rate slows as fertility and mortality rates drop as countries urbanize and develop economically (Bricker and Ibbitson 2019; see also Burger 2019). However, per capita resource use and meat consumption (Schramski et al. 2019) increase with shifts in employment from resource-based rural economies to service and technology-based cities (Burger et al. 2019b). Moreover, decreasing fertility rates coincide with increasing per capita energy use across countries and within countries over time (Moses and Brown 2003; DeLong et al. 2010). The increased urbanization that coincides with economic growth, technological innovation, and higher standards of living are fueled largely by nonrenewable fossil fuels. About 85% of the global energy demand is still from fossil fuels despite campaigns and policies to transition to renewables. It is important to note that since 1960 per capita energy use has begun to increase faster than population (Fig. 2), exacerbating climate change. Malthus' *Essay* influenced Jevon's paradox, which states that increasing efficiency has unintended consequences of actually increasing the absolute amount of resource used, accelerating the drawdown of the planet's energy reserves (Jevon 1865).

The (Im)Perfectibility of Humans

Particularly interesting is the timing of Malthus' book in relation to the *industrial revolution* (Fig. 2), when humans began to exploit vast quantities of fossil fuel resources to power mechanized industries including agriculture, manufacturing, and transportation. Malthus' *Essay* does acknowledge technological improvements as a result of human innovations. He merely states the absurdities in thinking that increasing "perfectibility" could happen indefinitely. Malthus pointed out that there are fundamental limits to improvements. For example, he writes that "*One of the most obvious features of improvement is the increase of size. The flower has grown gradually larger by cultivation. If the progress were really unlimited it might be increased ad infinitum, but this is so gross an absurdity that we may be quite sure that among plants as well as among animals there is a limit to improvement, though we do not exactly know where it is.*" (p. 51).

In Malthus' critique of Condorcet's "Perfectibility of mankind" he writes "...*the mortality of man on earth seems to be as completely established, and exactly upon the same grounds, as any one, the most constant, of the laws of nature*" (p. 74). "*I think we may conclude, that we have rather less reason for supposing that the life of man may be indefinitely prolonged, than that trees may be made to grow indefinitely high, or potatoes indefinitely large*" (p. 77). The notion that indefinite growth is impossible on a finite planet has inspired philosophical discussions on alternative pathways for human societies.

Alternatives to the Growth Paradigm

In addition to being critical of the growth paradigm, Malthus' did provide solutions. He proposed that we need to change the "very nature of man?" taking *Preventative* checks to avoid population growth and collapse. To this end, Malthus inspired the pioneering works at the intersection of ecology and economics by Kenneth Boulding, Nicholas Georgescu-Roegen, Herman Daly, Howard T Odum, Vaclav Smil, Charlie Hall, Ken Klitgaard, and others who have advanced transdisciplinary research in the fields of ecological economics and biophysical economics. These

fields set themselves apart from neoclassical economics by placing the human population and economic system as a subsystem embedded within the global biosphere (Fig. 4) instead of being divorced from the natural environment. Malthus doesn't make any specific predictions of the timing of collapse. The central legacy of Malthus' *Essay* is the appreciation that growth cannot occur forever in a finite world. Accordingly, Malthus would argue that the growth paradigm that prevails in neoclassical economics today will ultimately fail. Appreciation of the fundamental biophysical constraints to growth is necessary to develop alternative pathways for sustaining the human enterprise.

Cross-References

- Behavioral Economics
- Cultural Evolution
- John Maynard Smith
- Naturalistic Fallacy, The

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Malthusian Growth

► [Malthus on Population](#)

Mammalian Ear Evolution

► [Evolution of Auditory Perception, The](#)

Mammalian Ear, The

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Synonyms

[Ears of mammals](#)

Definition

The evolution of the mammalian ear and the comparative research with the ears of humans.

Introduction

In order to understand the evolution of the human ear, we must trace its origins and comparison in the mammalian lineage. Therefore, to identify the changes in the hearing capacity of the evolution of humans, a comparison had to be made to the evolution of other mammals (Masterton et al. 1968). It was concluded that high frequency hearing (>32 kHz) is a trait that characterizes mammals. This was due to the short distance of their ears, and the result for the selective pressure to know the accurate source of brief sounds. Sounds with a low frequency (<1 kHz) is a trait that characterizes all mammals, especially humans (Masterton et al. 1968).

The Eutherian Mammalian Ear

Regarding the evolution of the eutherian mammalian ear, Manley (2017) distinguished that during the Paleozoic era (>250 million years ago), the synapsids were no longer under the stem reptiles, forming mammal's ancestors. During the early Mesozoic era, the mammalian ancestors had a short-term middle ear connected to the lower jaw, which was later developed to a more distinct middle ear. The organ of Corti was adopted during this period. The integration of the bone into the

cochlea happened exclusively in therian mammals and took place prior to the cochlear coiling and the split of Eutheria from the Metatheria. The cochlear coil had as a result for the lagenar macula to be eliminated, leading to the evolution of prestins, a motor protein found in abundance in the lateral cell membranes of outer hair cells.

Motor Protein Prestin

This protein lead to a heightened sensitivity in low sound frequencies (see Dallos 2008; Li et al. 2010; Zheng et al. 2000, 2002) and works as a mediator between the somatic electromotility in the outer hair cells of the cochlea. These hair cells are in control for cochlear amplification and the rapid changes of cell length (Franchini and Elgoyhen 2006). They are also responsible for the transduction of mechanical activity into electrochemical activity when the stereocilia structures are bent (Gelfand 2010, p.76).

Additionally, the hair cells compensate for the energy consumed for the course of the traveling wave on the basilar membrane, which has as a result the increased sensitivity of the ear and an increased frequency selectivity at low sound intensities (Moller 2013, p.55).

Moreover, according to Franchini and Elgoyhen (2006), the motor protein has especially evolved in the mammalian species in order to support the adaptation of the cochlea. The researchers concluded that there was evidence for the positive selection of prestin only in the mammalian lineage.

Further evidence supporting the motor protein prestin in the mammalian species was the signatures of positive selection on the $\alpha 10$, but on the $\alpha 9$, nicotinic cholinergic receptor (nAChR) subunits (Franchini and Elgoyhen 2006). The $\alpha 9\alpha 10$ -containing nicotinic cholinergic receptor acts as a mediator to inhibit olivocochlear effects on hair cells on the vertebrate species. According to the researchers, the receptor is significant for physiological processes. Specifically, $\alpha 9$ is essential for the development of efferent synapses in the inner ear, and acts as a distinctive source of extracellular

calcium for Ca^{2+} -activated potassium channels in auditory hair cells (Vazquez 2016).

Comparative Research

Based on comparative methodology, Montealegre-z et al. (2012) discovered that the hearing system of mammals and rainforest katyids are similar. More precisely, the insects showed to possess homologous biophysical mechanisms for auditory processing with the auditory structures of the mammalian species, using the three parts of the ear (outer, middle, and inner) to collect and analyze sound. Further evidence was supported by Hoy (2012) who reported that these stages are likely to have evolved firstly in insects and later in mammals.

Further on the mammalian ear, Radojevic et al. (2015) have found evidence of the Akt isoforms, which have a significant role mainly in evolution of the cochlea. More specifically, the kinase Akt is a key downstream mediator of the phosphoinositide-3-kinase signaling pathway, and it is involved in a variety of cellular processes. Akt contains three isoforms, each encoded by a separate gene. On their study, they have indicated that Akt2 and Akt3, but not Akt1, enhance hair cell resistance to ototoxicity. The researchers have highlighted the significance of these isoforms in normal hearing.

Moreover, Warchol (2011) identified that a regenerative ability of the sensory hair cells was lost during the mammalian evolution. To be more precise, Warchol noted that the regeneration failure in the mammalian ear was the result of a trade-off between phenotypic plasticity of supporting cells and sensitive high frequency hearing.

Conclusion

A brief review of the evolution of the mammalian ear was mentioned, as well as a brief discussion about the motor protein prestin as a contributor to the formation of cochlea in mammals. Comparative research on the mammalian ear with other species was also briefly mentioned.

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Man

- [Largest Homo Brain](#)

Man with Backpack

- [Fat Man, The](#)

Mandeb Strait

- [Bab-El-Mandeb Strait](#)

Manipulation

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Synonyms

[Intersexual negative inducements](#); [Partner exploitation](#)

Definition

Some forms of mate retention involve the use of deception, manipulation, and exploitation of a romantic partner.

Introduction

Some mate retention tactics are used to manipulate a partner. For instance, in the Mate Retention Tactics Scale, the subscale intersexual negative inducements consists of items that measure behaviors used by one partner to get what he or she wants from the other partner and to provoke negative emotions from a partner (Shackelford et al. 2005). For instance, an individual may flirt with someone in front of his or her partner to cause sexual jealousy. Provoking jealousy may be used as a tactic to manipulate a partner into paying more attention to the individual or to discourage a partner from paying attention to someone he or she is interested in romantically.

Mate Retention in Marriage

Research on married couples shows that mate value plays a role in manipulation of a partner. Mate value is higher for younger women because they have more years of fertility remaining before menopause. Additionally, attractiveness in women is related to mate value, partially because it is related to age (and hence fertility) and health. Men who have significantly younger wives use more mate retention tactics, especially the more costly ones, including emotional manipulation, commitment manipulation, intrasexual threats, and violence against rivals. Men married to women that were significantly more attractive than they were used more mate retention tactics – especially the more costly tactics, including emotional manipulation, wife derogation, intrasexual threats, and violence against rivals (Buss and Shackelford 1997). The bottom line here is that when men are paired with wives who have higher mate value, men use mate retention tactics that manipulate their wives into remaining in the relationship and staying faithful. Women with lower mate value than their partner (those who are older and less attractive), actually use fewer mate retention tactics (Buss and Shackelford 1997), indicating that they refrain from manipulation to keep a partner satisfied and interested in the relationship.

Factors Associated with Romantic Partner Manipulation

Not surprisingly, some personality traits are more predictive of manipulative mate retention tactics. Those who score low on agreeableness, conscientiousness, and openness use more intersexual negative inducements as part of their mate retention strategy. In addition, those who are more emotional use more intersexual negative inducements (Holden et al. 2014). In essence, individuals with these personality traits are more manipulative within their romantic relationships.

Men with lower self-esteem also report using more mate retention tactics. Similarly, wives who esteem their partners less report an increased use of costly mate retention tactics by those partners (Holden et al. 2014). Also, men who report

insulting their partners more also report more intersexual negative inducements. Correspondingly, women who report being insulted by their partners more often also report that their partners use more intersexual negative inducements (McKibbin et al. 2007).

Dark Triad and Intersexual Negative Inducements

The Dark Triad is three interrelated personality traits: narcissism (individuals who are excessively interested in themselves), Machiavellianism (individuals who are cold, calculating, and manipulative to get their way), and psychopathy (individuals who lack empathy and behave in an antisocial manner). Taken together, individuals who score high on the Dark Triad personality traits are comfortable manipulating other people, deceiving them, and exploiting others to get their way. Not surprisingly, these same people are more likely to use mate retention tactics that manipulate their partners, including inducing jealousy in their partner and manipulating their partners' emotions (Jonason et al. 2010).

Other researchers have assessed honesty-humility which has been linked with the Dark Triad. Those who score high on measures of the Dark Triad score low on the personality dimension honesty-humility. Research shows that those who are low on honesty-humility have higher levels of mate guarding and use more intersexual negative inducements, including inducing jealousy and being emotionally manipulative; they use more intrasexual negative inducements, including threatening and fighting rivals; and they use more positive inducements (Holden et al. 2014). Although the use of positive inducements as a mate retention tactic seems contrary to the idea that those low in honesty-humility use costly forms of mate retention to manipulate a mate, it is possible that those scoring low on honesty-humility are willing to use a variety of mate retention tactics to keep a partner interested in the relationship, and although they use a lot of the more negative mate retention tactics, they are also willing to manipulate their mate by using positive inducements. Individuals with low levels

of honesty-humility are frequently willing to use any tactic available to manipulate their partner romantic relationships.

Faking Orgasm to Manipulate a Partner

Although there are many reasons for faking an orgasm, including trying to spare a partner's feelings, sometimes women may fake an orgasm to manipulate their partners. This includes faking an orgasm because "I don't want my partner to have sex with another woman" and "I don't want my partner to think that I am having sex with another man" (McCoy et al. 2015, p. 138). Research indicates that faking an orgasm to deceive and manipulate a partner was related to women's self-reported mate retention tactics. Faking an orgasm to manipulate and deceive a partner was most strongly linked with women's self-reported mate guarding, intersexual negative inducements, and intrasexual negative inducements. Faking an orgasm, at least sometimes, is a strategy to manipulate a partner and may be a way to hide an infidelity or otherwise deceive a partner or keep a partner faithful (McCoy et al. 2015).

Intimate Partner Violence as a Costly Mate Retention Tactic

Perhaps the most costly of all of the mate retention tactics, physical violence against one's partner, may sometimes be used to keep a woman from leaving the relationship. Intimate partner violence is hypothesized to be motivated by sexual jealousy, and men who perceive their female partners as more likely to cheat engage in more physically and sexually violent behaviors (Kaighobadi et al. 2009). Kaighobadi et al. (2008) posit that when men suspect or perceive an infidelity, they might begin with less costly retention tactics such as checking up on a partner or keeping her away from other men and then progress to more violent tactics such as pushing or grabbing a partner. Men who are more antisocial, self-centered, and

impulsive are more likely to engage in intimate partner violence. Also, men who are less emotionally stable, agreeable, and conscientious are more likely to engage in intimate partner violence (Kaighobadi et al. 2008). Although it is an extreme behavior, intimate partner violence may have been selected for if it increased a man's paternity certainty. Research indicates that physical violence by men is predicted by proprietary mate retention tactics and that these mate retention tactics are used more when men perceive that their partner is interested in other men. Like men, women who perceive that their partner is interested in another man use more proprietary mate retention tactics, but these mate retention tactics do not predict physical violence in women (Cousins and Gangestad 2007). These studies indicate that intimate partner violence, at least in men, may be a form of coercive control and may enable some individuals to manipulate a partner's behavior.

Conclusion

Within romantic relationships, people may use some forms of mate retention to manipulate a partner. Some personality traits are related to higher levels of manipulation, including people scoring high on the Dark Triad. Additionally, partner manipulation is more likely in married men who have lower mate value, probably as a means to keep a partner faithful and in a relationship. Married women who have low mate value use fewer forms of manipulation, probably because they do not want to risk losing their partners. In its most extreme form, manipulation may take the form of physical violence which may be used to manipulate a partner into remaining faithful.

Cross-References

- [As a Precursor to Partner Violence](#)
- [Coercive Control](#)

- Egg Mimicry
- Prevention of Infidelity
- Problem of Cheating

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Manipulation and Dishonest Signals

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Synonyms

Deception; Influence

Definition

Dishonest signals are displays, calls, or performances that would ordinarily convey certain information about some state of the world, but where the signal being sent does not correspond to the true state. Manipulation is the sending of signals in a way that takes advantage of default receiver responses to such signals, to influence their behavior in ways favorable to the sender. Manipulative signals are often dishonest, and dishonest signals are often manipulative, though this not need be the case. Some theorists have defined signaling in such a way that evolutionarily reinforced signals are essentially manipulative.

Introduction

Signals in the natural world are evolved phenomena, where two actors, the sender and the receiver, use an observable trait or behavior of the sender to direct the behavior of the receiver. The fitness benefits of this relationship for both actors, on average over evolutionary time, help explain why the relevant behaviors evolved. In standard cases, the sender signals conditional on some state of the world which they (alone) have access to, and the receiver responds conditionally to the signal. The conditional strategies of signaling and responding coevolve depending on the fitness

impacts of the receiver's actions (given what the state of the world was), the costs of available signals and responses, and combined effects of the different strategies (Maynard Smith and Harper 2003; Skyrms 2010) (see ► [“Animal Signaling”](#)).

However, evolved response strategies to signals (and other stimuli) are also vulnerable to exploitation via manipulation. If the interests of senders and receivers are not exactly the same, then there will be situations where it is in the interests of the sender to have the receiver behave in a way that is not in the receiver's interests (given the true state of the world). This incentivizes signaling strategies which are dishonest and/or manipulative, and this incentivizes signaling forms and strategies which make dishonest signals more difficult or strategically unwise (see ► [“Costly Signaling”](#)).

Dishonest Signals in Nature

Evolved dishonest signals are well known among insects and other invertebrates, where fitness effects of signaling and manipulation are amenable to study. For example, male fiddler crabs have one large claw used for fighting other males and signaling their capacity to do so (by waving it as a visual signal of relative size and strength). Claws lost in fights can be regrown, but some species cut their losses and prioritize the rapid enlargement of much weaker “dummy” claws, which are ineffective in fighting but can still serve the signaling function dishonestly. Sexual signals such as pheromones are another clear case of manipulable fitness-critical signaling. These signals regulate mating behaviors between partners so that mating occurs when both optimally resourced for the production of viable offspring, with pheromones and other signals triggered by sexual maturity and fertility, and mating behaviors triggered by those signals. One famous manipulator of such systems is the *Ophrys speculum* orchid, which attracts male *Campsocilia ciliata* wasps by producing flowers which mimic the approximate shape of a female wasp and accurately reproduce their pheromones. This is so successful that male wasps preferentially copulate with the flower rather

than with actual females (Ayasse et al. 2003). The payoff for the orchid is pollination, as repeated pseudocopulation carries pollen widely between plants, but the wasp incurs a net fitness cost due to the wasted effort and loss of reproductive opportunity. Developmentally entrenched dishonest signaling between species often involves mimicry, with more common examples being the coloring of some harmless species of arthropods, amphibians, and reptiles to resemble toxic or venomous species, as a deterrent to predators.

Vertebrates, especially those with complex social organization, often exhibit complex, flexible, and voluntary signaling strategies, with a variety of dishonest signals used for conditional advantage against conspecifics. Primate studies show that the use of dishonest signals correlates with cortex size and social complexity (McNally and Jackson 2013). Chimpanzees learn to conceal or suppress signals depending on context, for example, to avoid attention of alpha males, and can be straightforwardly deceptive (De Waal 2007). However, such signaling is often less straightforward and more controversial with respect to measuring fitness impacts and drawing evolutionary conclusions.

This difficulty carries across to the application of signaling theory to communication and deception in humans. Human sociality is mediated by languages and other signals, which in principle can be treated as vast systems of signal and response strategies. However, voluntary human signaling is often based on learned responses rather than developmentally acquired traits; costs and benefits associated with deception or honesty are generally hard to identify with direct fitness payoffs. As with much of ethology, the degree to which animal signaling and manipulation theory is continuous with human social psychology is open to debate.

Contested Definitions

Depending on how signals, dishonesty, and manipulation are defined, dishonest signals and manipulation need not be the same thing. Behavior-altering parasites, for example, clearly manipulate

their hosts without exploiting signal responses. Deceptive manipulation is also possible that exploits environmental responses rather than established signal-response behaviors. For example, the luminescent esca organs of anglerfish are often used to imitate the food sources of prey fish, or otherwise confuse or lure them in for predation. Anglerfish are clearly manipulating their prey via a form of deception, but the responses they take advantage of are not typically responses to *signals* and did not evolve as such, meaning that the traditional “communicative” or co-evolutionary paradigm of signaling does not fit the case well.

In contrast to the more co-evolutionary “information-based” formulation of signaling, some theorists also argue that even honest signals are best seen as cases of manipulation (Dawkins and Krebs 1978; Krebs and Dawkins 1984). Because the fitness benefits of sending a signal are only realized if it influences the behavior of a receiver, it is argued that the primary selected function of signals is to manipulate rather than to communicate or inform. On this way of thinking, all signals are manipulative, but sometimes being manipulated is worthwhile (i.e., when signals are mostly “honest”), and it might sometimes make little difference to the receiver either way. This view therefore retains natural selection as a key component, but only for senders, and its modern proponents argue that it is misleading to link the idea of signaling to the transfer of information/meaning encoded in the signal, or even treat honesty or dishonesty as a primary consideration (Rendall and Owren 2013).

Stability and Dynamics

Regardless of what counts as a signal or as manipulation, the ability of receivers to glean the facts that a sender has access to from their signaling behavior remains evolutionarily significant (sometimes called “mind reading”). Dishonest signals, if treated as veridical, can be directly costly to the receiver. However, in the context of an established, mutually beneficial signaling system, these can also indirectly costly to both senders and receivers more generally due the value of honest, veridical signals being

undermined. This provides incentives for receivers to evolve detection mechanisms and for honest senders to evolve complementary “guarantee” mechanisms.

Among the posited systems of guarantee-detection for mammals (especially humans and closely related primates) are involuntary emotional displays and the ability to rapidly interpret them. Darwin argued that reflexive facial expressions (and other reflexes such as blushing) in humans and other great apes are evolved veridical signals of emotional states (Darwin 1872). Robert Frank goes further, using game theoretic analysis to argue that emotional states themselves evolved as solutions to the threat of dishonest signals. Anger (for example) is seen as an easily identified loss of control which predictably restricts the sender to a dominant course of action, akin to making a show of throwing away the steering wheel of your car in a game of chicken (Frank 1988). Again, the deep human dependence on cultural learning (and potential cross-cultural variation) complicates detailed evolutionary analyses of any particular forms of emotional display or manipulative behavior, though plausible general principles can be posited. In theory, producing and recognizing involuntary, hard-to-fake physiological displays that are directly generated by mental states could be strategically advantageous in competitive social contexts. However, evolving more sophisticated capacities to mimic them would also be advantageous for would-be manipulators, so we should expect to see an evolutionary arms race between intense displays, “acting ability,” and ability to discern genuine anger, fear, and love from manipulative fakery.

The evolutionary dynamics of manipulation therefore follow the general pattern of parasitic relationships. Manipulated receivers often pay a significant fitness cost, so a simple approach to evolutionary theory sees such signals as unstable: the receivers are under evolutionary pressure to alter their strategies to avoid being duped. For example, it might be possible for *Campsoscolia ciliata* wasps to evolve coordination strategies based around alternative pheromone signals that the orchid finds harder to mimic. But this would depend on generation time and other factors in the comparative evolvability of both species. The

persistence of *Ophrys speculum*'s manipulations might therefore be the result of it rapidly adapting to produce any pheromone the wasp uses. Alternatively, there might be an ongoing chemical arms race: with the wasp occasionally switching pheromone signals and the orchid racing to catch up. Another possibility is that the fitness costs to the wasp of being manipulated never rise to the level that a difficult. It is also worth noting that the orchid's breeding strategy makes it an obligate manipulator of the wasp, and therefore it too will suffer if its fitness impact on them is too great. It is therefore possible that the manipulative signaling relationships might be self-regulating, such that selection pressure on receivers stays at levels too low to make adaptive escape worthwhile.

Conclusions

Signaling theory provides a broad framework to approach the evolutionary psychology of communication, deception, and manipulation. Furthermore, evidence from primate studies suggest that deception and the capacity to deceive is linked to need to navigate and exploit social structures and relationships. Deception almost certainly evolved alongside communication, cooperation, and social complexity in our recent evolutionary past, and in principle, it can be understood in simple game theoretic terms that are applicable to evolutionary explanation. In practice though, due to the relative complexity and cultural dependence of humans with respect to their psychology, societies, and signaling systems, the productive application of these principles in psychological research remains a challenge.

Cross-References

► [Evolution of Emotion in Social Context](#)

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Manipulation by Others

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Synonyms

[Deception](#) [kinship](#) [psychology](#) [manipulation](#);
[Sexual access manipulation](#); [Terminal altruism](#)

Definition

Theoretically, manipulation by others into committing acts of suicide terrorism is a form of duplicity in which an individual or group activates evolved mechanisms (i.e., kinship psychology or

mating psychology) that over evolutionary time produced reproductive benefits; however, the benefits in relation to suicide terrorism are not forthcoming and results in maladaptive behavior.

Introduction

Suicide terrorism is an act of outward aggression in which the perpetrating agent willfully sacrifices his or her own life with intent to inflict as much damage as possible on civilian casualties. Suicide terrorism is systematic and often perpetuated by political organizations (e.g., Hamas, Al-Qaeda, Tamil Tigers, among others) that disseminate messages to followers through various media outlets and often train adherents in institutionalized settings apart from their natal residences. Some evolutionary theorists hypothesize that these institutions convince followers to partake in suicide terror missions by manipulating evolved psychological mechanisms i.e., kinship psychology and mating psychology. According to these models, terror organizations use tactics that piggyback on these evolved mechanisms; however, the evolved benefits are not forthcoming as the cues are deceptive. Thus, these hypotheses are distinct from evolutionary models of suicide terrorism, which contend that the act incurs manifest fitness benefits.

Theories and Evidence for Suicide Terrorism as Manipulation by Others

The two most popular evolutionary explanations for suicide terrorism contend that terror organizations recruit suicide attackers by manipulating evolved psychological mechanisms. Informed by kin selection, the first explanation claims that terror institutions effectively deceive would-be suicide attackers by acting on kinship mechanisms, thus facilitating self-sacrifice (Qirko 2004, 2009, 2013). The second explanation argues instead that sexual access manipulations form the basis of the underlying motivation for suicide terrorism (Kanazawa 2007; Thayer and Hudson 2010). Though there is data that backs both hypotheses, each suffers from theoretical and empirical impediments.

Brief overview of kinship psychology manipulation: The hypothesis that terror organization manipulate followers into accomplishing suicide missions by deceptively activating kinship psychology rests on the theory of kin selection (Hamilton 1963; Smith 1964). According to Hamilton's rule (1963) an organism should act altruistically if the reproductive benefits to its kin outweigh the costs of the act to the organism. Mathematically, Hamilton's rule is represented by $rb > c$ where r is the degree of genetic relatedness, b is the reproductive benefits to related kin, and c is the cost to the agent. Kin selection was a groundbreaking evolutionary theory that demonstrated how traits that harm individual organisms could be selected for in a population.

In order for an organism to act altruistically, there must be a means for it to distinguish kin from non-kin, using kin recognition cues to calculate the degree of genetic relatedness (r) between the self and other. Hypothesized cues of genetic kinship among humans include physical proximity during development, shared phenotypic traits, and the use of kinship terminology (Qirko 2004; Alexander 1990; Michener and Fletcher 1987; Hamilton 1964; Sherman 1985). Qirko (2004, 2009, 2013) predicted that institutions that seek out recruits for suicide missions would employ the following tactics: (1) prefer recruits in earlier stages of development; (2) separate recruits from their genetic kin; (3) promote the use of kin referents between group members; (4) encourage the use of markers that mimic shared phenotypes (e.g., uniforms or other identifiers); and (5) facilitate close proximity among the in-group members in the institutional setting. Evidence indicates that, in fact, terror organizations often employ these strategies to foster a sense of kinship among group members.

Brief overview of sexual access manipulation: Alternatively, some theorists have proposed that the promise of access to mates in the afterlife (i.e., 72 virgins) is a central motivator for suicide terrorism (Kanazawa 2007; Thayer and Hudson 2010). The promise of sexual reward, though deceptive, relies on mechanisms for reciprocal altruism wherein one agent assists to increase the fitness of another agent at an initial cost to itself on the assumption that the first agent will be assisted

in kind in the future (Trivers 1971). Kanazawa (2007) claims that the sanctioning of polygyny in Islam creates a reproductive skew, effectively excluding younger males from the mating market. Islamic terror organizations highlight sexual rewards in the afterlife in their discourses, a teaching that is downplayed or contested by other factions of Islam. Furthermore, the acquisition of rewards in the afterlife, including sexual access, is a commonly cited motivator among Palestinian combatants (Hafez 2006).

In a similar vein, the esteem afforded suicide terrorists in death by local communities is an indirect means through which terror networks might access male mating psychology. High social status is correlated with reproductive success in humans and non-human primates (Smith 2004), which is directly linked to risk taking behavior in the realm of intrasexual selection (Daly 2001).

Overall, the empirical evidence to support the sexual access manipulation hypothesis of suicide terrorism is minimal. Sexual access manipulations might factor into cost-benefit calculations; however, this mechanism alone appears insufficient to explain suicide terrorism, especially since many suicide attackers are not low status at least in terms of income and education (Atran 2003; Berrebi 2003). Moreover, as highlighted by Lawson et al. (2008) the rates of polygyny are fairly low in these populations, and the percent of never married males in Islamic populations is about the same as in the West (United Nations. Dept. of Economic and Social Affairs, Population Division 2004).

Conclusion

Terror organizations regularly rely on strategies to solicit followers for suicide attacks that appear to directly act on psychological mechanisms with well-demonstrated evolutionary benefits. These institutions foster a sense of kinship among their members, and they often perpetuate religious teachings that promise sexual rewards in the afterlife for martyrdom.

Cross-References

- [Kinship Psychology Manipulations](#)
- [Sexual Access Manipulation](#)

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Manipulative Use of Kin Terminology

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Synonyms

Fictive kin; Induced altruism; Induced nepotism

Definitions

Humans use language to recognise kin, and this ability can be extended to fictive kin such as close friends and ideological allies. Our closest genetic family ties, denoting one-half degree of genetic relatedness (“sister”, “brother”, “father”, “mother”, “child”), are typically used to signal strong social bonding and manipulate group identity. More distant terminology, denoting one-fourth to one-eighth degree of relatedness such as “cousin”, “aunt” and “grandparent”, appears to be less frequently used. Cross-generational terms denote respect and dominance, while within-generational terms signal solidarity and closeness. The use of fictive linguistic kin terms is a major strategy in the institutional manipulation of individuals.

Introduction

Our first strong attachments are typically formed to parents and siblings. The connotations of these terms have made their metaphorical use common throughout cultures. The aim is to evoke the positive emotions characteristic of close family ties and induce kin-specific behaviour, such as

altruism and loyalty, among individuals who are distantly or not at all related to each other. The manipulative use of kin terminology can concern different social situations, ranging from dyadic bonds to kin lineages, group identity, organisations and mass ideologies.

Language is central for human kin recognition beyond the nuclear family. Linguistic kin recognition can itself be used manipulatively, so that kin membership is expanded or contracted depending on social alliances and individual interest. Such use has been depicted in traditional societies: for instance, an ally can be assigned or deprived of the status of “cousin” (Qirko 2011). In societies where spouses are selected among relatives, individuals may stretch kin assignment in order to allow themselves a greater choice of mates (Chagnon 1988).

Affinal kin, present when kin lineages are joined through marriage, assign each other specific terms, such as “mother/daughter-in-law” (Hughes 1988). This linguistic and emotional capacity to “make kin” through marriage of previously distantly or unrelated individuals appears to be a human universal. If so, it can be assumed to have evolved together with the human cooperative breeding system and language use. In socially complex societies, the ability to “make kin” can further be employed to create kin-like bonds between friends and allies. This allows also for political manipulation, such as referring to neighbouring countries as “brothers”.

It is useful to distinguish between manipulative use of kin terms in dyadic bonds and in large social groups.

Manipulation of Dyadic Bonds

Between two individuals, referring to non-kin as a father, mother, sister, brother or cousin serves to enhance a social relation. The kin metaphor strengthens the mutual relationship as well as signals its significance to others, manipulating social behaviour towards both parties of the dyad. “Like a sister” or “my brother” denotes loyalty, similarity,

trust, and long-term willingness to provide help and support, while “a cousin” – more rarely used in contemporary societies – can denote alliances and cooperation. Cross-generational terms such as “father” or “mother” signify reverence or apprenticeship, and “my daughter”, “son” or “child” a protective and nurturing relationship that may resemble adoption or fostering. (Qirko 2011.)

With the exception of “child”, which can be used for a young lover, the usage of fictive kin terms is usually reserved for non-sexual relations. The grandparental tie is not commonly invoked to describe or manipulate feelings towards non-kin in dyads.

Kin terminology is also employed to signal respect and benevolence. In hierarchical cultures, generic greetings may involve kin terms to denote age and gender hierarchies.

Manipulation of Ideological Communities

Once large and complex social institutions appeared, humans faced the novel problem of enabling co-operation and altruism in groups of several hundred or thousand members and between individuals who may not even have met each other. In this context, kin terminology can enhance group loyalty by tapping into evolved dispositions for kin altruism and fairness (Johnson 1986). People do not actually start believing that they are related to such metaphorical kin. Instead, kin terms are intended to evoke an emotional response that will trigger more altruism and solidarity towards the individual’s own group (Salmon 1998) or more hostility towards the outgroup (Abou-Abdallah et al. 2016). Indeed, as van den Berghe noted (1981, p. 60), large-scale group inequality is “almost invariably bolstered by an ideology that disguises the parasitism of the ruling class as either kin selection or reciprocity”.

Institutions that require costly sacrifice from its members – for instance, putting one’s life at risk or foregoing reproduction – can be expected to encourage close association, similar physical outlooks, and the use of symbolic kin terminology

among its members (Qirko 2013). This is why, for instance, armed groups or ethnic subcultures tend to dress the same way, speak the same way, and refer to each other as “brothers” or “sisters” of the same “family”. Such manipulation can also include measures intended to weaken or destroy bonds to biological family members. For instance, monasteries and the early universities required members to remain unmarried and never have children, and religious sects may encourage members to refrain from contact with their parents and siblings.

Political and religious movements demanding less costly adherence also employ kin metaphors manipulatively. Notions of brotherhood and sisterhood are commonly applied within ideological movements, from the “Freedom, Equality, Brotherhood” slogan of the French revolution to the “Muslim Brotherhood” political movement in the contemporary Arab world. Gods are often provided with paternal or maternal features, as are leaders in authoritarian states. Ideological communities may structurally mimic the nuclear family: the rulers are “parents”, followers are their “children” and “sisters” or “brothers” to each other. The term “spouse” is also metaphorically used within some religious communities, e.g. the “brides of Christ” –perhaps tapping into the psychological similarity of religious and romantic ecstasy (Dunbar 2010).

Monotheistic religions and nationalistic movements have prominently used kin metaphors. It has therefore been suggested that they function as “kinship surrogates” in large populations. These ideologies appear to trigger feelings of belongingness similar to those that would have been induced by kinship in traditional, small-scale societies. However, it may be that the use of kin metaphors on a political level has become less efficient in a multi-racial, multi-national world (MacIntyre 2004), at least among liberal political movements.

Theoretical research on the manipulative use of kin terminology was first developed in the early stages of sociobiology (e.g., van den Berghe 1981). Empirical studies have since been able to demonstrate associations between patriotism and usage of kin metaphors in the United States

(Holper 1996). The effects of kin metaphors on the user have been found to vary with political adherence (Garst and Bodenhausen 1996) and with birth order, so that middle-borns were less likely to be affected than were first and last borns (Salmon 1998). With data from Lebanon and Australia, another study found that metaphors of “brotherhood” boosted the hostility towards out-group members (Abou-Abdallah et al. 2016). However, there is a scarcity of empirical studies concerning the mechanisms and effects of the uses of kin terminology in different societies.

Conclusions

Kin terms can be stretch and assigned as a way of manipulating social relations. In everyday social life, linguistic kin recognition can affect which individuals are treated as if they were genetically related. In complex and hierarchical societies, manipulative and metaphorical use of kin terminology is also common. Institutions and social movements may use kin terminology in order to evoke altruistic behavior and a sense of obligation. Such metaphorical use typically refers to the parent-child bond or to brotherhood and sisterhood. In extreme cases, authoritarian groups manipulatively use kinship terms in combination with a dismissal of biological family ties.

Cross-References

- [Kin Selection](#)
- [Kinship Psychology Manipulations](#)

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Man-Made Items

- [Human Products](#)

Marc Bekoff

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Synonyms

[Animal emotions](#); [Cognitive ethology](#); [Ethologists for the ethical treatment of animals](#)

Definition

Marc Bekoff is an author and researcher in the area of animal behavior, cognition, and behavioral ecology and works extensively for animal conservation.

Introduction

Dr. Bekoff is a Professor Emeritus of Ecology and Evolutionary Biology at the University of Colorado in Boulder, and is a Fellow of the Animal Behavior Society and a past Guggenheim Fellow. Together with Jane Goodall, Dr. Bekoff cofounded Ethologists for the Ethical Treatment of Animals in 2000 and received the Exemplar Award from the Animal Behavior Society for major long-term contributions to the field of animal behavior that same year. He has published numerous books and articles focused on animal emotion, cognition, and welfare, which have been featured in several popular science and news publications, including *48 Hours*, *Time Magazine*, *Life Magazine*, *U.S. News and World Report*, and *The New York Times*. Dr. Bekoff currently writes a science column about animal emotion for *Psychology Today* (Bekoff 2016a).

About the Author

Bekoff is originally from Brooklyn New York, and received his A.B. in Anthropology from Washington University in St. Louis, Missouri. He went on to receive his M.A. in Biology from Hofstra University in Hempstead, New York, and then became a graduate student in Neurobiology and Behavior at Cornell University. He ultimately received his Ph.D. from Washington University in Animal Behavior and has focused his research on behavioral ecology and conservation. He has published extensively on human-animal interactions, emotions, nonhuman morality, and animal protection (Bekoff 2016a, b).

Animal Emotions

Bekoff spent decades studying a diverse group of animals — from coyotes in Wyoming to penguins in Antarctica, viewing their cognitions and behaviors from an ethological perspective (Bekoff 2016a). In his book, *Minding Animals: Awareness, Emotions, and Heart*, Bekoff (2002) offers readers detailed accounts of animal behavior, including grooming and gossip, self-medication, feeding patterns, dreaming, dominance, and mating behavior. Not only does Bekoff provide evidence of advanced cognitions in other animals, such as chimpanzees who medicate themselves with herbal remedies, and elephants who mourn dead group member, but Bekoff also sheds light on many of the more serious issues surrounding these animals. He offers an overview of animal cognition, intelligence, and consciousness, presenting examples of animal passions, and highlighting the presence of deep emotional lives in our animal kin. Bekoff strongly promotes animal protection and well-being in light of understanding animal emotions (Bekoff 2016b). He urges a new paradigm of respect, grace, compassion, and love for all animals.

Following his years of experience studying communication patterns in a wide variety of animals, Bekoff (2007) further advocates the presence of rich emotional lives in all animals in his book, *The Emotional Lives of Animals: A Leading Scientist Explores Animal Joy, Sorrow, and Empathy – and Why They Matter*. Bekoff explains that humans are not exclusive in their emotional experiences of love, empathy, and compassion and that animals of many species feel these same sentiments. This requires humans to think differently about our current domination and abuse of animals, particularly in the field of research. In this book, Bekoff (2007) highlights recent scientific research confirming the existence of emotions in animals, and blends them with related anecdotes of animal grief, joy, embarrassment, anger, and love – emotions that humans have recognized in animals for years. Importantly, Bekoff explores the evolutionary mechanisms supporting these emotions, including underlying brain structures

and cross-species analyses, and advocates the use of noninvasive neurological techniques to reduce negative emotional experience for animals in research. This book exemplifies Bekoff's call for reevaluating how our actions negatively impact the emotional lives of animals, and highlights the importance of ethical and compassionate treatment of animals across scientific domains.

Cognitive Ethology

Cognitive ethology is a branch of ethology concerned with how conscious awareness and purposeful intention influence the behavior of animals (Collins 2012). In this approach, Tinbergen's four questions regarding the evolution, adaptation, causation, and development of behavior (see Ristau and Erlbaum 1991) are applied to investigations of animal cognitive awareness. This combination of cognitive science and ethology promotes the idea that animals should be observed under natural conditions so that researchers can understand the evolutionary explanation, adaptive function, proximate causation, and lifespan development of any species-typical cognition (Ristau and Erlbaum 1991).

Bekoff and Allen (1997) identify three major groups of people with different views on cognitive ethology: (1) *Slayers* deny any possibility of success in cognitive ethology, (2) *Proponents* keep an open mind about animal cognition and the utility of cognitive ethological investigation, and (3) *Skeptics* stand somewhere in between. According to Bekoff (1995) only Proponents converge with animal rights thinking in seeing animal experience as worthy in itself. As a primary example of proponent thinking, E.O. Wilson (1984) coined the term "biophilia" to describe the innate desire shared by living beings to associate and attend to other living organisms. According to Bekoff (1995), researchers can and should investigate the ethology of animal emotions, particularly within their natural habitats.

In this collection of revised essays, titled *Why Dogs Hump and Bees Get Depressed: The Fascinating Science of Animal Intelligence, Emotions,*

Friendship, and Conservation, Bekoff (2013) discusses the expanding field of anthrozoology, or the study of human-animal interactions. A major aim of anthrozoologic research to quantify positive effects of human-animal relationships from either the human or animal perspective (Mills 2010). Bekoff (2013) outlines empirical and anecdotal evidence of emotional cognitions in animals, including empathy, grief, humor, and love. For example, humpback whales protect gray whales from orca attacks, combat dogs suffer from PTSD, and bees display thrill-seeking tendencies. In light of these animal emotions, Bekoff implores others to employ an "ethical compass" when interacting with all species within the animal kingdom.

Furthermore, in *Species of Mind: The Philosophy and Biology of Cognitive Ethology*, authors Marc Bekoff and Colin Allen (1999) make it clear that many animals have rich cognitive lives. They also believe that it is just as important to investigate evolutionary foundations of animals' thoughts and emotions just like comparative studies of physical attributes, such as kidneys, stomachs, and hearts. Although Bekoff advocates the comparative, evolutionary, and ecological aspects of the mental phenomena of animals, this book shows how philosophy and cognitive ethology together can give a more holistic, analytical approach to animal cognition. Philosophy can provide cognitive ethology with an analytical basis for the attribution and assessment of cognition to nonhuman animals, whereas cognitive ethology can help philosophy to explain mentality in naturalistic terms by providing data on the evolution of cognition. This reciprocal relationship between philosophical theories of mind and empirical studies of animal cognition is exemplified by the authors' presentation of case studies, particularly in the areas of antipredator vigilance and social play, where there are many points of contact with philosophical discussions of intentionality and representation. The authors make specific suggestions about how to use philosophical theories of intentionality as starting points for empirical investigation of animal minds. They also discuss cognitive ethology's relevance to questions of ethics, as our beliefs about the mental

lives of animals strongly affect our attitudes toward their moral status.

Conclusion

Marc Bekoff is a central figure in research on animal emotions, cognition, and compassionate conservation. Using his vast experience observing diverse animal species in the natural world, Bekoff promotes the idea that humans are one among many animals and urges his audience to treat all animals with compassion and respect. Because animals feel many of the same emotions as humans (e.g., Bekoff 2002), it is imperative that humans minimize any emotional suffering when interacting with other species. Further research should focus on the evolutionary foundations, adaptive functions, proximate mechanisms, and development of animal cognition, with the hope of understanding the rich emotional lives of animals. With this knowledge, humans have the core responsibility of ensuring both the physical and emotional safety of the animals with whom we share this planet.

Cross-References

► [Moral Instincts and Morality](#)

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Margaret Profet

► [Margie Profet](#)

Margie Profet

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Synonyms

[Margaret Profet](#); [Profet](#)

Definition

Margie Profet contributed evolutionary theories of pathogen and toxin avoidance as they pertained to pregnancy sickness, allergies, and menstruation.

Introduction

This entry focuses on the theoretical contributions made by Margie Profet in the late 1980s and early 1990s. Profet's key contributions included describing the adaptive significance of pregnancy

sickness, menstruation, and allergies. Prior to Profet's work, researchers had not explained these topics through the lens of evolutionary theory; instead, these physiological processes were largely portrayed as biological anomalies or evolutionary by-products. Profet was therefore recognized as a key figure in bridging evolutionary theory with health sciences, but also stirred up controversy among biologists and physicians in the popular media. This entry therefore describes each of the key contributions made by Profet and the social context surrounding her theories.

Background

Margaret "Margie" Profet was born August 7, 1958. She grew up in Manhattan Beach, California, and was the daughter of two engineers (Martin 2012). Margie was a key figure in the development of evolutionary theories of biological processes; however, her educational training did not include formal studies in evolutionary biology. Instead, she received bachelor's degrees in Political Philosophy from Harvard University (1980), and another in Physics from the University of California, Berkeley (1985). She briefly worked as a research associate at UC Berkeley and as a visiting scholar in Astronomy at the University of Washington in Seattle. She began to pursue a PhD in anthropology from Harvard University, but did not finish the degree (Martin 2012). In online interviews conducted with Profet, she is quoted for having a distaste for formal education, and even comparing academia to a jail sentence (McDermott 1994). Thus, instead of completing a PhD, she pursued her research interests independently.

Margie Profet's self-guided academic pursuits led to the development of three formative publications that shaped early understanding of human behavior and health through the lens of evolutionary theory. These novel theories explained the adaptive significance of pregnancy sickness, menstruation, and allergies. She was awarded a MacArthur Foundation Genius Fellowship in 1993 for these theoretical contributions. According to an article published in *Newsweek* (2009), her

award summoned the attention from multiple news reporters who were enthralled by her ideas that altered the way the public viewed women's bodies. Each of her contributions is described below.

Pregnancy Sickness

The first theory developed by Profet proposes that pregnancy sickness evolved as an adaptive strategy to protect women from ingesting teratogenic substances. **Teratogens** are any environmental or chemical agent that can disrupt fetal development. In pregnancy, teratogens can be found in environmental toxins, such as cigarette smoke, or in plant toxins, such as nicotine. Profet's theory was motivated from earlier research by Hook (1978), who proposed that pregnancy sickness evolved during the agricultural revolution because women's avoidances often targeted agriculturally based products, such as beer. Profet disagreed with this hypothesis, suggesting that it failed to account for women's frequent exposure to plant toxins during the Pleistocene Era. According to this model, **plant secondary compounds**, which are produced by plants to deter predators, elicit toxin avoidance mechanisms in humans, with the first line of defense being bitter and pungent tastes. This hypothesis is supported by evidence that pregnancy sickness is experienced primarily during the first trimester of pregnancy, when placentation and embryogenesis occur, making the fetus particularly vulnerable to teratogens. Nausea, vomiting, and aversions to potentially teratogenic substances therefore prevent the ingestion of items that could harm fetal growth and development.

Profet's evolutionary theory of pregnancy sickness was published in *Evolutionary Theory* in 1988, and the book, *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* in 1995. She also published her theory in popular books, entitled *Protecting Your Baby-to-be: Preventing Birth Defects In The First Three Months Of Pregnancy* (Profet 1997b), and *Pregnancy Sickness: Using Your Body's Natural Defenses To Protect Your Baby-to-Be* (Profet 1997a). These books were published as guides for new mothers to better understand the body's evolved defenses during pregnancy. Profet also offered

advice to women regarding the types of food they could safely consume.

News reporters latched onto Profet's pregnancy sickness theory, often bringing attention to her controversial recommendations for pregnant women to avoid plant-based foods. Medical doctors were often cited in these articles, claiming that Profet's theory was unfounded. In a Newsweek article entitled, *Babies, Broccoli, and Birth Defects*, one doctor claimed that the vegetables Profet cautioned against were unlikely to have a harmful level of toxins that would actually cause birth defects (Newsweek Staff 1995). The doctor argued that bitter taste aversions in pregnancy were instead a byproduct of hormonal shifts that occur during pregnancy.

Formal empirical tests of Profet's pregnancy toxin-avoidance hypothesis, however, have generated mixed findings. After her paper was published, Fessler (2002) and Flaxman and Sherman (2000) proposed that women were perhaps more likely to feel averse to meat and dairy products because these items were more likely to harbor pathogens. Flaxman and Sherman (2000) tested their hypothesis with the ethnographic record and found that pregnant women were more likely to avoid meat and dairy products rather than vegetables. More recent investigations of women's pregnancy aversions in non-Western societies have been more varied, with some women reporting aversions to foods with toxins (McKerracher et al. 2016; Placek et al. 2017), staple foods (Young and Pike 2012), and other studies showing that food aversions target animal products (Henrich and Henrich 2010; McKerracher et al. 2016).

Allergies

In 1991, Profet published her second major contribution in the *Quarterly Review of Biology*, arguing that allergies evolved as a last line of defense against toxins, including toxins from ingested foods, injected drugs and venoms, inhaled substances, skin allergens, and helminths. Her motivation for developing this theory originated from former arguments that explained allergies as either an immunological malfunction or as a defense against helminth infections. Profet argued that

these perspectives were inadequate because the symptoms associated with allergic reactions instead show evidence of toxin avoidance. Specifically, mammalian interactions with allergens often result in coughing, vomiting, sneezing, diarrhea, tearing, and scratching. These symptoms may assist the host to rapidly expel the toxins and/or slow the rate of circulation of the toxins. In reference to helminths, Profet suggested that rather than thinking of allergies as responses to helminth infections, that perhaps one should consider the role helminths have in releasing toxins into the bloodstream, which subsequently induce an antibody response via elevated IgE antibodies.

Profet relied on several lines of evidence to support her antitoxin hypothesis of allergies. As an example, the drop in blood pressure during an allergic reaction can reduce the circulation of toxins in the blood stream. Profet also pointed out that allergic reactions become stronger with repeated exposure to toxins. Profet stated that this evidence supports her hypothesis because toxin exposure can have a cumulative effect, whereas the successive contact with a toxin usually implies that it is avoidable, unlike helminths, which are typically unavoidable and can often lead to sudden death (Profet 1991).

The antitoxin hypothesis of allergies also included a discussion of the inverse relationship often found between allergies and cancer (Profet 1991). Profet suggested that although allergies were not specifically designed to fight against cancer, that perhaps they function as anti-cancer agents by expelling mutagenic and carcinogenic toxins.

In contrast to the pregnancy sickness hypothesis, Profet's antitoxin theory of allergies received more positive support, particularly as it applies to cancer. In a review of the literature, researchers Sherman et al. (2008) found support that cancer rates were inversely related to allergies; however, this relationship varied according to the specific type of cancer. The authors concluded that their findings overwhelmingly supported Profet's prophylaxis hypothesis that allergies expel carcinogenic and mutagenic toxins from the body, leading to lower rates of specific cancers. Another study conducted by Cotterchio et al. (2014)

further supported Profet's hypothesis in which hay fever was associated with a significant reduction in pancreatic cancer risk.

Menstruation

Profet's (1993) third major theoretical contribution explained the adaptive significance of female menstruation, which was published in the *Quarterly Review of Biology*. According to popular media, Profet's theory of menstruation came to her during a dream, where she reportedly saw "black triangles embedded in red" and interpreted these symbols as pathogens being washed away by menstrual blood (Martin 2012). Profet relied on evidence from nonhuman mammals to demonstrate that female menstruation was a defense against pathogens transmitted by sperm. The development of this theory was motivated by the fact that no formal theories of menstruation existed. Prior to Profet's theory, much of the research focused on menstruation as a non-functional by-product of reproductive cycling or as a constraint to reproductive effort. Other researchers at the time proposed that menstruation might function to rid the body of dietary phytoestrogens (Garey 1990), or shed fetal cells that might otherwise alter maternal metabolism and behavior if not aborted (Haig 1993). Profet argued that none of these prior hypotheses could account for the ultimate explanation of menstruation in women, or why menstruation evolved in human females during the Pleistocene era. Profet also argued that the prevailing perspectives were limited because menstruation is costly for women in terms of nutritional loss in the form of iron, along with other costs, such as reduced amount of time available for conception to take place.

According to Profet, her theory targeted the key question as to why the body does not simply reabsorb the uterine lining, but instead engages in such an energetically costly act each month of nonpregnant cycling. In her paper, she provides an example from Rhesus Monkeys who absorb a portion of the uterine lining after the menstrual cycle is complete (Profet 1993). Humans, on the other hand, shed the uterine lining. Profet predicted that if menstrual bleeding evolved and

currently functioned as an antipathogenic strategy, that it would be (1) either universal or nearly universal among mammals; (2) if not universal, then menstruation would be less common in species that have a higher probability of pregnancy; (3) the volume of blood expelled during menstruation would be associated with body size of the mammal and mating strategies. In other words, larger bodied animals who engage in promiscuous mating would have heavier menstruation than smaller bodied animals who are monogamous. This rationale was based on the notion that menstruation is energetically costly to maintain; and (4) other forms of uterine bleeding that are not associated with the monthly menstrual cycle would also have an antipathogen effect. Profet relied on evidence from human and nonhuman mammals to support her theory and also discussed other forms of uterine bleeding in relation to infection risk. One study she cited, for instance, indicated that sexual intercourse during the last 2 months of pregnancy resulted in a higher rate of infection, leading to lower reproductive success via premature delivery (Naeye and Ross 1982).

Among Profet's three theories, her predictions for menstruation were perhaps the most debated. After her paper was published, she received mixed reviews. Initial support for her ideas came primarily from evolutionary psychologists who applauded her efforts. Others were more skeptical (Angier 1993). Profet responded to criticisms from reproductive biologists and gynecologists by stating that they had insufficient training in evolutionary theory. Later, Profet's theory of menstruation was further deconstructed by other evolutionary theorists (see Clancy 2009 for a review).

Conclusion

In summary, Margie Profet was among the first to combine evolutionary theory with health sciences. Her primary contributions included three influential theories on the adaptive significance of pregnancy sickness, allergies, and menstruation. Her contributions were significant for her time because few researchers had attempted to understand why these physiological processes evolved.

Soon after the development of these theories, Profet stopped publishing evolutionary theories of human psychophysiology, with possible explanations available on popular media channels (e.g., Martin 2012). Despite the empirical outcomes of her ideas and her own personal trajectory, Margie Profet made a significant impact on evolutionary biology, with contributions that set the stage for further investigations of pathogen and toxin avoidance strategies in humans and nonhuman mammals.

Cross-References

- Allergies
- Food Aversions and Cravings
- Menstrual Cycle

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Margo Wilson

- [Founders of Evolutionary Psychology](#)
- [Martin Daly and Margo Wilson \(Founders of Evolutionary Psychology\)](#)

Maria Montessori

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Definition

Maria Montessori (1870–1952) was an Italian physician and psychiatrist who became the founder of a new “scientific pedagogy” based on careful observation of children and informed by her distinctive approach to evolutionary psychological science.

Introduction

Maria Montessori was born in Chiaravalle, Italy, in 1870. As a child, she insisted – against the wishes of her father – that she be enrolled (as the only girl) in a school for future engineers. By 1890, she was one of first women enrolled in the medical school at the University of Rome. She quickly rose to the forefront of her medical school class and gained the esteem of Guiseppe Sergi, one of the leading psychologists in Italy at the time. Alongside Sante De Sanctis and Giuseppe Montesano, who both went on to play pivotal roles in Italian experimental psychology, Montessori was one of Sergi’s top students. In 1896, she graduated from the University with a thesis in

clinical psychology (supervised by De Sanctis, cf. Foschi 2012). The same year, she served as a representative from Italy to an international women’s conference in Berlin, and she began working in clinical psychology in public hospitals in Rome. By 1900, she was teaching courses in pedagogical anthropology and working in a mental hospital that specialized in the treatment and education of “deficient” children. In this context, she engaged with the writings of Jean Marc Gaspard Itard and Édouard Séguin. She remained involved in public advocacy for women (e.g., at a major women’s conference in London in 1899) and began more actively advocating for children’s education. In 1902, she returned to the University of Rome, now as a student of philosophy, in order – as she put it – to “undertake the study of normal pedagogy and of the principles upon which it is based” (Montessori 1912/1909: 33). At the University, she was exposed to the ideas of Rousseau and Pestalozzi, but also – through professors like Antonio Labriola – to Hegel, Marx, and Nietzsche. Her interest in psychology, combined with an interest amongst Italian students in pragmatism, led her to engage seriously with William James. And she continued her engagement with the evolutionary positivism of Sergi and De Sanctis. By 1906, she was teaching courses in Pedagogical Anthropology at the pedagogical school of the University of Rome.

The pivotal moment in her transition to become a global leader in children’s education came in 1907, when she was invited to run a “Children’s House” that would be part of a progressive new approach to low cost housing in the San Lorenzo district of Rome. She had complete control over this classroom and used it as a laboratory for pedagogical techniques. In this context – described in detail in Montessori 1912/1909 – she developed new teaching methods and materials and formulated the basic principles of her educational philosophy. Her *Metodo della Pedagogia Scientifica applicato all’educazione infantile nelle Case dei Bambini* (1909), translated into English with the regrettable title *The Montessori Method* (1912), made her an instant international sensation. Visitors travelled to Italy to study her educational methods, and she travelled throughout the world (including the World’s Fair

in California in 1915) training teachers in her method and presenting her ideas about children's development and scientifically informed pedagogy. She left her private medical practice, her work at the children's hospital, and her professorial teaching at the University of Rome to spend the rest of her life further developing her pedagogy by applying more theoretical rigor, incorporating further experimental results, and expanding the scope of her education to include all stages of life from infancy through adulthood. She promoted her philosophy through books, lectures, publications and international training courses that would equip others to educate children in accordance with her method.

The core principle of her pedagogy is to "Follow the child," that is, to accord the child complete liberty while providing the resources the child needs to use that liberty well. This liberty is not a reckless license; for Montessori, the indication that a child has an environment conducive to liberty is that a child finds opportunities for sustained attention on self-chosen work. Thus, the educator must provide a carefully prepared environment with sufficient resources for the child to freely choose work that sustains attention and fosters development, and the educator must then allow the child to develop herself. In the context of her observations of children, Montessori noted distinct "sensitive periods" of the development of fine-grained psychological traits and skills. She paid careful attention to the emergence of cognitive and social skills and to the essentially embodied nature of these skills, and she developed activities and material conditions to support progress through sensitive periods. She articulated a unique approach to "character" and to the socialization of human beings from infancy through adulthood. She applied her ideas to understanding human progress in general and even advocated for political change through education.

Montessori's overall philosophy and her approach to developmental psychology are spread throughout her many publications and lectures. The most important sources for specifically understanding Montessori's approach to evolutionary theory are her *Pedagogical Anthropology*

(Montessori 1913/1910), where she directly tackles the evolutionary theories of her contemporaries; her elementary materials (particularly *From Childhood to Adolescence* (Montessori 2007/1948) and *To Educate the Human Potential* (Montessori 1993/1948)), where she describes how the basic nature of the universe should be taught to elementary school children; and occasional essays such as "The Unconscious in History" (Montessori 2012/1948) that directly tackle metaphysical themes. Her approach to experimental psychology comes out best in *Montessori Method* (Montessori 1912/1909), *The Formation of Man* (Montessori 2007/1955), and – specifically in terms of her engagement with Freud – *The Secret of Childhood* (Montessori 1966).

In the rest of this entry, I discuss Montessori's general approach to evolutionary psychology and her account of the proper nature of experimental psychology, and then I briefly touch on how her evolutionary psychology relates to her pedagogy.

Evolution and the Spiritual Embryo

One of Montessori's key theoretical insights was her concept of the "spiritual embryo," the notion that human beings are born in a psychologically embryonic stage. Substantively, this implies that children are forming their basic psychological structures during the first six (especially the first three) years of life. Methodologically, it implies that many of the principles of embryology can be used to understand early childhood development. And systematically, the emphasis on embryology informs Montessori's whole conception of biological systems and even her theory of evolution.

In one of Montessori's earliest publications, she explicitly discusses different theories of evolution, and while she acknowledges "the glorious leadership of Darwin" (Montessori 1913: 5), she describes his theory (alongside those of Lamarck and St. Hilaire) as a "mechanical or materialistic theory of evolution" according to which "the environment is regarded as the chief cause of the evolution of organic forms" (Montessori 1913:

46). In preference to such theories, she endorses “other less familiar theories of evolution” proposed by Carl Naegeli, Gregor Mendel, and especially Hugo deVries (Montessori 1913: 46–51). These theories are informed by close investigation of biological *development*, and they “attribute the variability of species to *internal*, rather than external causes – namely, to a spontaneous activity, implanted in life itself, and analogous to that which is witnessed in the development of an individual organism, from the primitive cell up to the final complete development” (Montessori 1913: 46). Methodologically, the key move here is the suggestion that there is an analogy between the development of individual organisms and evolution of species. Substantively, this leads to a focus on internal drivers of evolutionary development. To some extent, this aspect of Montessori’s position is already implicit in Darwin and has now become standard biological orthodoxy. Natural selection operates only in the context of given variations, so environment can only drive evolution if there is an antecedent cause of sufficient variations of the right kind. Nailing down exactly what causes those variations remains an important problem within contemporary biology, though the discovery of DNA and its operations (and “errors”) has provided a framework for answering that problem. During the early twentieth century, however, Darwin’s unexplained source of variation invited metaphysically loaded accounts of variation, and Montessori offers just such a conception. The universe is teleologically ordered towards the “progress and perfectionment” of living creatures, both as individuals and as species (Montessori 1913: 46–47): “a great universal power . . . is the force of life itself in the process of evolution. It drives every form of life irresistibly towards evolution, and from it come the impulses to action. But evolution does not occur by luck, or by chance, but is governed by fixed laws” (Montessori 1988/1949: 230).

Not only does embryology provide an analogy for understanding macroevolution, both embryology and the evolution based on it provide a basis for understanding *psychological* development. The “spiritual embryo” is “the newborn child [who] has to do a piece of formative

work which corresponds in the psychological sphere to the one just done by the embryo in the physical sphere” (Montessori 1988/1949: 55). Montessori’s emphasis on this “spiritual embryo,” and particularly on the development of children in early infancy, gave her a distinctive perspective on the role of the unconscious in human development. Like Sigmund Freud, Montessori saw the unconscious as an important force in the formation of human personality and even as a driving factor in history (see especially “The Unconscious in History”, Montessori 2012/1948). Unlike Freud, however, Montessori approached the unconscious from the standpoint of a pedagogue constantly engaging with very young children. Rather than “probing the ills of a diseased mind” and making inferences about unconscious influences in a way that is “limited . . . to the study of pathological cases” and “abnormal states,” Montessori develops a method of “observation” of children “from a psychic point of view,” directly grasping unconscious “realities of human life mirrored in the soul of a child” (Montessori 1966: 9, 11). As with Freud, she emphasizes the dangers of various repressions and complexes (e.g., Montessori 1966: 10, 154–176), though for Montessori the most important repressions are not sexual but rather repressions of the child’s desire for freely chosen work. Her conception of the unconscious includes and expands on Freudian accounts of the unconscious and also includes what has recently been called the “adaptive unconscious” (Wilson 2002). She drew from the educationalist Percy Nunn the concepts of “*horme*” and “*Mneme*,” referring to the unconscious correlates of volition and memory (or cognition). *Horme* consists of a “vital force” or “guiding instinct” that “takes the form of a drive towards an ever greater independence,” such that “if we tried to find something resembling this *horme* in conscious life, it might be likened to will-power[, b]ut this would be an extremely poor analogy [because] the idea of will is too restricted, too much a part of a person’s awareness” (Montessori 1988/1949: 76; Montessori 1966: 199–206; cf. Nunn 1920: 23). *Mneme* is that “vital kind of memory, which does not consciously remember, but absorbs images

into the individual's very life" (Montessori 1988/1949: 56–57).

Beyond the general notion that early development is akin to a spiritual embryology, Montessori draws several specific theoretical guideposts for developmental psychology from early embryology and evolutionary theory. One of the most important features of Montessori's pedagogy, one that Rita Kramer credits Montessori as inventing, is the "sensitive period" (what is now typically called a "critical period") in development (Kramer 1976: 373–374; See too Lillard 2005: 122–26). Montessori herself credits this idea to deVries and the embryologist Charles Manning Child (Montessori 1988/1949: 94; Montessori 1993/1948: 76). Her discussion of the latter is particularly illuminating for seeing the connections between embryology, evolution, and developmental psychology. She explains,

It is clear that nature follows a plan, which is the same for atom as for planet. It was in 1924 that the embryologist Child revealed those points of febrile activity called Physiological Gradients, not all starting together, or with the same intensity, but each with its own tempo, pursuing an independent course. To begin with, the unit cells were exactly like all the others, but through their activity they grew to differ and became specialized, for the formation of an organ, and last came the circulatory and nervous systems to link the organ with others, similarly created in independence, but to a different functional end.

These are found to be the basic principles of nature's plan:

1. The freedom and independence of organs in their several developments.
2. Development through specialization of cells.
3. The unification of organs by the circulatory system of the blood.
4. Directive communication established by the nervous system. (Montessori 1993/1948: 76)

Montessori uses these fundamental principles to understand the overall development of natural systems, from atoms and planets through organisms and even "the different centers of civilization [that] have been nursed to strength in isolation [and] then brought into contact" (Montessori 1993/1948: 77). She also uses the specific patterns of embryological development, from sensitive periods to a tendency for fine-grained specialization rather than generic function, as models for

psychological development. Just as we develop different organs for different purposes, and these develop in isolation before being united systematically, so too we develop different psychological structures for different specialized tasks, and these then become integrated into a coherent personality.

In her *Pedagogical Anthropology*, Montessori makes a similar point about the "transformation" that

is not that of a succession of very gradual variations . . . On the contrary, what produces stable characteristics is a *revolution* prepared in a latent state, but unannounced in its final disclosure. A parallel to this is to be found, for example, in the phenomenon of puberty in its relation to the evolution of the individual. (Montessori 1913/1910: 47)

Evolution of biological structures, psychological traits, and even species proceeds through independent cultivation of parts that unite into integrated wholes, and each aspect of this evolution occurs in sudden bursts punctuated by long periods of preparation.

Strikingly, this quotation from the *Pedagogical Anthropology* also reflects a return from embryology and individual psychology back to macroevolution. Montessori brings up deVries's account of sensitive periods and even the comparison to puberty in order to make a broader point about evolutionary processes, that "new species are formed . . . through spontaneous activity" in a way that is "expected" and "not . . . gradual" (Montessori 1913/1910: 47). While the specific example she cites from deVries (the plant "*Enohtera Lamarckiana*") has proven to be problematic, the conception of sensitive periods of development, particularly in the more detailed accounts given by Manning and deVries, suggested to Montessori and deVries something like what has come to be called "punctuated equilibrium" (see Gould 2007); that is, with respect to the evolution of species, "it became possible to envision other possibilities than that of the slow adaptive transformations of the Darwinian hypothesis, which required immense periods of time" (Montessori 1988/1949: 49). For Montessori, the evolution of species, like the development of biological structures in embryos and

psychological structures in human children, involved long periods of latent development and then sudden eruptions as new potentialities become realized.

Evolution, Ecology, and the “Cosmic Plan”

Before turning to her discussion of empirical psychology in particular, two further features of Montessori’s evolutionary theory are important to mention. First, Montessori strongly resisted the individualist versions of Darwinism – popularized most prominently by Herbert Spencer – that insisted on a competitive struggle and the “survival of the fittest.” Instead, under the influence of Louis Bourgeois and other solidarists in France, her approach to evolution emphasized the role of cooperation in evolutionary success (see Frierson 2018). This gave her evolutionary theory a distinctly ecological focus, a point she makes explicit in her *Absorbent Mind*:

Ecology is a study of the different behaviors of animals, and it reveals that they are not here to compete with each other, but to carry out an enormous work serving the harmonious upkeep of the earth . . . Behavior does not merely fulfil the desire to continue to live. It serves a task which evidently remains unknown and unconscious to the being . . . If animals were to become self-conscious, they would be conscious of their habits, of the beauty of the places in which they live, but certainly the corals would never realize or understand that they are the builders of the world, nor would the worms which fertilize the earth consider themselves agriculturists, nor would others consider themselves the purifiers of the environment and so forth. The purpose which places the animals in relation to the earth and its upkeep would never enter their consciousness. Yet life and its relation with the surface of the earth, the purity of the air, the purity of water are dependent upon these tasks. So there is another force which is not the force of the desire for survival, but a force which harmonizes all the tasks. Let us say that each one is important . . . because it carries out tasks which are useful to the whole and the effort of each is to try and reach the place allotted to it and the task which it is to fulfil. (Montessori 1949: 89–90)

As she puts it in her discussion of the elementary science curriculum:

One side of evolution deals with the satisfaction of vital needs, defense, survival of the species, and growth by modifications towards individual and species perfection. Another – and stronger – factor in evolutionary processes is concerned with the cosmic function of each living being, and even of inanimate natural objects, working in collaboration for the fulfillment of the Purpose of Life in the whole . . . The bee who robs the flower of its nectar is aware only of his own need or the hive’s, not that the flower’s need of his visit is as great for its purpose of reproduction, for perpetuating the life of the species. (Montessori 1993/1948: 26–27)

For Montessori, evolution involves not only the survival of the fittest and the development of species but also the increased harmony and mutual benefit of the ecosystems as a whole.

This ecological emphasis shows up throughout Montessori’s evolutionary theory. For example, her approach to adaptation, she explains that “Adaptation to the environment is necessary for all living creatures” (Montessori 2012/1946: 80) but then conceives of that adaptation not in the purely individual terms of the “old idea . . . that we lived in the environment and absorbed as . . . much as possible for ourselves from the environment” but as a process whereby “[e]ach species’ adaptation to the environment shows us what the purpose and useful work of each is, the work which each contributes towards universal harmony” (Montessori 2012/1946: 87–88). Biology cannot be limited to the study of “those things that each species does for the maintenance of its life” but must also include “the important work which is done by each species individually for the harmony of all” (Montessori 2012/1946: 84).

These passages emphasizing the ecological dimension of Montessori’s evolutionary theory already hint at her deeper teleological conception of the “cosmic plan” that all life promotes. In the passage above from the *Absorbent Mind*, not only does she refer to the “force which harmonizes all the tasks,” but the passage goes on:

That is why we said that there was a pre-established plan . . . that . . . puts the animals in relation with the task that they have to accomplish upon the earth. Nor is the [only] purpose of life to perfect oneself, nor only to evolve. The purpose of life is to obey the hidden command which ensures harmony among all and creates an ever better world. We are not created only to enjoy the world, we are created in

order to evolve the cosmos. Today the influence of the existence of a cosmic plan is gradually changing the theory of the linear evolution of past times. (Montessori 1949: 89–90)

In *To Educate the Human Potential*, she explains, “Plant life and animal alike now have to be considered from two points of view, and the more important is that of their function in the cosmic plan” (Montessori 1993/1948: 26). References to this cosmic plan, a teleological ordering of the universe towards increases in harmonious complexity, pervade Montessori’s writings (for discussion, see Frierson 2018).

This teleological, ecological approach to evolutionary theory plays central roles in Montessori’s approaches to both psychology and pedagogy. For one thing, Montessori sees psychology itself – the set of psychological forces at work in human beings – as a stage in the increased complexity of the universe, one that serves to harmonize increasingly complex biological forces into a new – “supranatural” – level of organization (Montessori 2012/1948: 23–24). Moreover, insofar as children’s psychological development is a part of this “cosmic plan,” it too proceeds in accordance with laws of life that have a teleological orientation towards the good of the whole.

There are some immediate implications of her overall conception of evolution for pedagogy, most notably in the series of lessons that make up elementary curricula (particularly the “Great Lessons”). Montessori claims that “When details are presented as being parts of a whole, they become interesting” (Montessori 2007/1948: 20). Thus, her elementary curriculum involves a “study of the whole” (Montessori 1993/1948: 23), a series of stories of the evolution of the universe, life on earth, and the development of human societies. Her conception of the cosmic plan affects the structure of these lessons in the development of life and of human societies. But these direct influences on her lessons are less important than two other crucial implications of her evolutionary theory for pedagogy. First, since children’s development is teleologically driven, the function of education is to provide room for psychological expansion, not to generate or stifle such expansion:

By education must be understood the active help given to the normal expansion of the life of the child. The child is a body which grows, and a soul which develops – these two forms, physiological and psychic, have one eternal font, life itself. We must neither mar nor stifle the mysterious powers which lie within these two forms of growth, but we must await from them the manifestations which we know will succeed one another. (Montessori 1912/1909: 59)

Second, because humans’ cosmic task is an ecological task, and because humans are capable (in ways that other animals are not) of becoming self-consciously aware of that task, one of the central functions of education, particularly for elementary and adolescent children, is to help them orient their immense energies in terms of their place in social and ecological systems of interdependence. Thus, the great lessons that “present . . . the world” (Montessori 1993/1948: 20) also show students how they can contribute to the development of societies and the world; students’ imaginations are fostered through thinking about their place in the great “cosmic plan.”

Scientific Pedagogy

Thus far, I have focused on Montessori’s theory of evolution, but Montessori was an experimental psychologist more than a theoretician of evolution. Her theoretical evolutionary framework supports and is supported by her experimental work; thus, she looks for – and finds – evidence of sensitive periods and the sudden consolidation of organized psychological structures. But her approach to psychology was essentially empirical rather than theoretical. In her *Pedagogical Anthropology*, she strongly endorses her mentor Sergi’s focus on “the human individual taken from actual life, in place of general principles or abstract philosophical ideas” (Montessori 1913: 14), and in her *Montessori Method*, she insists that the basis of a “scientific educational program” must not be mere philosophical conjecture (as in Rousseau) but “the *observation* of free children” (Montessori 1912/1909: 28). Roughly speaking, Montessori endorses Wilhelm Wundt’s “definition” according to which “all methods of

experimental psychology may be reduced to one, namely, carefully recorded observation of the subject” (Montessori 1912/1909: 72–73), but she rejects widespread positivist psychological theories from Fechner and Wundt to her contemporaries, arguing that they are “arbitrary and superficial” (Montessori 1991/1918: 86) and exhibit a tendency in “experimental psychology” to “adopt . . . more or less the standard of laboratories of *physics*” (Montessori 1991/1918: 98).

Montessori’s criticisms of the experimental psychology of her day can be summarized under roughly four basic headings (see Frierson 2015). First, she criticized experimental psychology for being too disengaged and strongly rejected the ideal of merely “objective” and even “blind” inquiry into human mental life:

As long as ‘science’ limited itself to the attaining of further knowledge about children without attempting to rescue them from the many evils which this same science had discovered in the schools . . . , no real claim could be made for any such thing as ‘scientific education.’ (Montessori 1967: 41)

In place of an objectivist model of scientific inquiry, Montessori embraced a broadly Jamesian, pragmatic conception of the search for truth; as she put it, “the *soul of the scientist* is entirely possessed by a passionate interest in what he sees. He who has been ‘trained’ to see, begins to feel interest, and such interest is the motive-power which creates the spirit of the scientist” (Montessori 1991/1918: 102). Second, against approaches to experimental psychology that focus on snapshots of human behavior or childhood development, Montessori argued that one must see the unfolding of the life of the child through extensive observation conducted over long time horizons:

The study of the child cannot be accomplished by an ‘instantaneous’ process; his characteristics can only be illustrated cinematographically . . . [T]he psychologist of today behaves somewhat like the child who catches a butterfly in flight, observes it for a second and then lets it fly away again . . . (Montessori 1991/1918: 86, 99)

[P]sychical researches of a moral order must also, if they are to be of any real value, be based upon prolonged observation . . . [I]t is necessary . . . to observe . . . for a considerable time. (Montessori 1967: 8–9)

Third, Montessori objected to a tendency in experimental psychology to “adopt . . . more or less the standard of laboratories of *physics*” (Montessori 1991/1918: 98), a tendency evident not only in crudely materialist conceptions of mind but also in the sorts of quantitative techniques wrongly – and often absurdly – applied to the investigation of human behavior and mentality. Fourth and finally, Montessori argued that contemporary psychologists studied human beings in a defective and unnatural condition, so that rather than seeing normal human psychology, theories were developed that treated common pathologies of modern life as though they were the normal condition of humanity. She compares the study of children in ordinary schools, where they are “repressed in the spontaneous expression of their personality till they are almost like dead beings” to the attempt to discern the nature of butterflies by their behavior when “mounted by means of pins, their outspread wings motionless” (Montessori 1912/1909: 14). Instead, Montessori insists upon providing a condition within which children can behave in accordance with their natural impulses and latent potentialities. In such contexts, she discovered what came to be called “New Children” (see Radice 1920) and what Montessori herself describes as “normalized” children:

Experience has shown that normalization causes the disappearance of many childish traits, not only those which are considered to be defects but also others which are generally thought to be virtues . . . They also include traits which have been scientifically studied and identified with childhood, such as imitation, curiosity, inconstancy, and wavering attention. The disappearance of these childish characteristics shows that the true nature of a child has hitherto not been understood. (Montessori 1966: 154)

Insofar as psychologists take disinterested snapshots of children (or even adults) in unnatural conditions of development, applying quantitative standards of physics to those snapshots, they will never truly understand human nature and its potentialities.

Montessori’s critiques of experimental psychology paved the way for her own conception of the “teacher-scientist,” who would genuinely love her students (avoiding disinterest), stay with

them for long periods of time over prolonged periods of their development, investigate their development using qualitative measures appropriate to human lives, and work with children in an environment prepared to provide occasions for free activity (rather than inactivity and the repression of their innate tendencies). Mere scientists fail to have the interest and engagement to properly observe children's development, but most teachers are not well trained in scientific praxis. The details of this alternative Montessori vision are laid out in much more detail in Montessori's works (see especially 1912/1909, and see too Frierson 2015), but her basic call is for "a genuine fusion of . . . modern tendencies, in practice and thought; such a fusion as shall bring scientists directly into the important field of the school and at the same time raise teachers from the inferior intellectual level to which they are limited today" (Montessori 1912/1909: 4). Or as she puts it later, "the attitude of the teacher should be at once positive, scientific, and spiritual" (Montessori 1991/1918: 106–107).

Conclusion

Montessori's evolutionary theory was heavily informed by the biological-embryological work of deVries, Naegeli, and Child, the philosophy of William James, Hegel, and Nietzsche, and her own observations of the development of children. The result was an evolutionary theory according to which nature as a whole, individual species, and individual members of species all pursue increased "perfection," understood as an increase in agency and organized complexity. This development happens in a teleologically ordered but discontinuous way, organized around particular sensitive periods within which certain new capacities emerge. Human psychology fits within the broader processes of cosmic evolution as the most recent and most complex source of developmental laws, and it has its own structures of development oriented around "vital impulses" that are actualized during particular sensitive periods in the development of each person. These developments – psychological as

well as evolutionary – are never *merely* for the sake of individual organisms or species, however. As we develop, we do so for the sake of our "cosmic task," to fulfill our role in the unfolding development of the world as a whole. This evolutionary theory was refined in the context of Montessori's careful observation of the development of children, particularly the "spiritual embryos" that during the first 6 years of life are forming their personalities and characters. In turn, her conception of development as motivated by guiding instincts, sensitive periods of development, and an overall tendency towards adaptation that would contribute to a cosmic (ecological) plan fostered Montessori's attention to the innate potentialities of children and the method of freely chosen work as central to proper pedagogy.

Cross-References

► Unconscious, The

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Marital Status

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Synonyms

[Aggression](#); [Competition](#); [Homicide](#); [Young male syndrome](#)

Definition

Males compete for access to female parental investment. Males in long-term relationships have less to gain from that competition, whereas males without ready mating access have much to gain and little to lose. This provides an explanation for why young, unmarried men are the primary perpetrators of violent and deadly aggression.

Introduction

Reproductive fitness is the primary unit of success in the evolutionary game of life. Limited resources and mating opportunities lead to intense competition where the winners successfully pass on their genes to the next generation and the losers face reproductive oblivion. Given the high stakes, it should not be surprising that competition over members of the opposite sex has resulted in violent and deadly encounters. The main participants in these acts of violence tend to be young unmarried men looking to gain respect and resources to improve their reproductive opportunities (Daly and Wilson 1988). This has led to a large disparity between men and women, and also unmarried and married men, in the rates of perpetration of violent crimes. This entry provides an evolutionary explanation for why younger, unmarried men are more violent than married men.

Evolutionary Background

Owing to their reproductive physiology, women invest a significant amount of time and energy to ensure the wellbeing of their offspring from conception to birth, and thereafter (Trivers 1972). In comparison, males' obligatory investment is quite minimal. Given this discrepancy, female parental investment is the resource that limits male fitness and subsequently ignites competition between male rivals. This often takes the form of competition over men's status within a group, their access to resources, and direct mating access. Indeed, men compete for the means to attract mating opportunities and deter rivals (Wilson and Daly 1985). A male's ability to deter rivals may increase his fitness and will ensure that his genes are passed on to the next generation and also lower the fitness of his rivals.

This competition among men is escalated by the fact that many societies are polygamous. According to the ethnographic atlas, out of 849 societies and clusters in Africa, East Eurasia, North America, South America, The Insular Pacific, and the Circum-Mediterranean, 83% practice polygamy (Murdock 1967). This social

structure is a luxury only for men of high social rank. In the demographic survey of the Xavante Indians of Brazil, 40% of married men were polygamous and the rest of the adult men were unmarried. In contrast, no woman of fertile age was without a husband. By age 20, only 1 out of 195 women had not given birth, whereas 6% of men who reached 40 years of age were still childless (Salzano et al. 1967). Muley Ismail, emperor of Morocco, had a harem of 500 concubines. Harems are common in ecologies where it is possible for one or a few men to accumulate vast wealth, and have been documented in Asia, the Middle-East, and sub-Saharan Africa (Betzig 1982). The result of this structure is that only a few men enjoy reproductive success, and the rest face the potential of reproductive oblivion. This incentivizes intense and sometimes deadly competition among men.

Patterns of Violence

Wilson and Daly (1985) reported on a landmark study examining predictors of homicides in Detroit in 1972. The study revealed a pattern of violence supporting the theorizing that most homicides are motivated by competition for status among men.

Wilson and Daly (1985) described two different types of homicide: “crime specific” and “social conflict.” Both terms were coined by Wilt (1974) who examined the 512 closed homicide cases in Detroit in 1972. Crime-specific homicides are cases where homicide was the unintentional result of another crime (e.g., robbery) where the offender did not initially intend on killing the victim. Social conflict homicides are described as heat of the moment actions taken by the offender and not incidental to the omission of another crime. Two-thirds of the 512 closed homicide cases in Detroit were declared social conflict cases (Daly and Wilson 1988).

More than half of the social conflict homicides between nonrelatives were described as “escalated showing off disputes” (e.g., one-upping somebody) and “disputes arising from retaliation for previous verbal or physical abuse” (e.g.,

insulting somebody) (Wilson and Daly 1985). Social conflict homicides are a struggle for status and respect, or in other words, social resources that are valued by men because of their positive fitness consequences. The more respect and social resources you have, the better chance you have at attracting the opposite sex (Wilson and Daly 1985). This makes men more inclined than women to participate in risky competitions to increase status (Weinberg and Ragan 1980). Additionally, participants in these two types of crimes are typically *young* men. In Detroit in 1972, the age group with the most homicide victims was 20–24, while the 25–29 age group had the most homicide offenders (Wilson and Daly 1985).

Men more violent than women. The fact that men are willing to use violence as a means to acquire resources is consistent with evolutionary theorizing. Out of 512 homicide cases in Detroit in 1972, only 90 of them (17.6%) were committed by women (Wilson and Daly 1985). In crime-specific cases, males represent 95% of the 134 perpetrators; in social conflict cases, they represent 75% of 337 offenders (Wilson and Daly 1985). Males were also the perpetrators in 93% of robberies, 94% of burglaries, and 91% of motor vehicle thefts in 1981 (Wilson and Daly 1985). These findings are consistent with the notion that men are more willing to tolerate risk than are women, particularly when resources that could improve one’s reproductive fitness are at stake (Wilson and Daly 1985).

Married versus unmarried men. Across social conflict and crime-specific cases, 73% of offenders and 69% of victims were unmarried compared to 43% of same age men in Detroit (Wilson and Daly 1985). Out of the 134 crime-specific cases, 76% of the men involved were unmarried; out of the 337 social conflict homicides, 58% of the males involved were unmarried (Wilson and Daly 1985). Married men may be less violent than unmarried men for multiple reasons. One reason is that they are typically older. Men are the most violent in young adulthood, a life stage where competition for status, resources, and marriageability is most intense (Daly and Wilson 1988). Married men may also be less violent because they already have mating

access to a reproductive partner, this makes the need to collect resources to attract other mates less urgent. Indeed, married men are more likely to have offspring already, and their energy may therefore be diverted to parenting rather than mating.

In contrast, unmarried men are more likely to be faced with intense competition for a limited number of unpaired females, particularly in polygamous societies. Competition for females will be fiercest at the bottom of the scale where the male on track for total reproductive failure has nothing to lose, and will therefore resort to violent tactics to improve his mating prospects (Daly and Wilson 1988). This may lead unmarried males to commit crimes, such as robbery, to gain the resources necessary to increase status, improve their appeal to females, and deter rivals.

Conclusion

Reproductive success is determined by the ability to gain access to mating opportunities. Given systems of polygamous mating and the ability of some men to monopolize a large share of available females, some men face the prospect of reproductive oblivion. This produces intense competition among men for mating opportunities. The competition for resources and mating opportunities is most fierce among young, unmarried, males. Compared to married men, unmarried men are more violent and have less to lose by resorting to violence as a means to gain resources and status.

Cross-References

- [Contexts for Men's Aggression Against Men](#)
- [Culture of Honor](#)
- [Meta-analysis of Sex Differences in Aggression](#)
- [Most Perpetrators Are Men](#)
- [Physical Aggression](#)
- [Relationship Status](#)
- [Reputation](#)
- [Same-Sex Homicide](#)
- [Sex Differences in Same-Sex Aggression](#)

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Marital Status and Infanticide

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Synonyms

[Child homicide](#); [Filicide](#); [Neonaticide](#)

Definition

This entry concerns the relationship between an individual's marital status (e.g., unmarried, married, widowed) and the intentional killing of infant offspring. While infanticide (the killing of children up to 2 years of age) is sometimes treated separately from neonaticide (the killing of

newborns within the first 24 h of birth), both phenomena are considered.

Introduction

Contemporary evolutionary approaches to infanticide emphasize a life history perspective. Life history theory assumes that individuals will exhibit behaviors that, on average and subject to constraints, maximize their lifetime reproductive success and that of their progeny while minimizing energetic costs (Clutton-Brock 1991; Stearns 1992). Life history theory emphasizes *tradeoffs*; for instance, between quality and quantity of offspring, between current and future reproduction, or between somatic maintenance and reproduction. Parental investment theory is a subset of life history theory that considers how parents optimally allocate resources toward offspring (Trivers 1972). Scholars have applied this lens to human parental investment by examining modulation of investment in relation to socioecological factors and offspring quality (Hrdy 1992; Lawson and Mulder 2016; Minocher and Sommer 2016).

Infanticide, when committed by a parent, constitutes a complete termination of parental investment. A life history approach aims to identify and explain the conditions under which attenuation or termination of parental investment is expected to yield a net fitness benefit to the parent. From this perspective, marital status is expected to influence investment decisions whenever marriage influences the relative costs and benefits of reproduction and investment behavior (for instance, when marriage entails significant material and social support or grants social legitimacy to both parents and children).

Historical Records

Historical accounts suggest that infanticide is recurrent across time and space. They also suggest that consistent demographic similarities exist among individuals who commit infanticide. Resnick's (1970) review of worldwide infanticide records from the seventeenth to twentieth

centuries found that most infanticides were committed by mothers, and that these mothers tended to be young and unmarried. Moreover, he concludes that most were not suffering from mental illness at the time of the infanticides, suggesting that the behavior is not necessarily pathological. Among married women, the most commonly cited motivation for killing newborns was extra-marital paternity, whereas the most common motivation for unmarried women was to avoid the negative social consequences of an illegitimate birth. Resnick also notes that killing of infants rather than neonates tended to be done by older mothers whose motivation was to end some real or perceived suffering (e.g., deformed or sickly infants). This bimodal distribution of behaviors suggests that the relationship between infanticide and marital status is contingent not only upon social legitimacy concerns but also broadly upon factors such as maternal age and infant quality.

In her review of infanticide in Western history, Moseley (1985) similarly concludes that infanticide is generally committed by mothers for "social or economic" reasons (although infanticide threat by fathers was reportedly high during Greco-Roman times, as paternal filicide was legally allowed). Daughters were often perceived as an economic liability among poor feudal farmers. In combination with pervasive androcentric ideology, this led to a disproportionately high rate of female infanticide over the course of Western history. Moseley notes that marital status in the Middle Ages modulated acceptability of infanticidal behaviors: unmarried women were harshly punished for committing infanticide, while married women could kill their infants with "relative impunity." Certain individuals (in this case, married women) were therefore permitted greater control over their reproductive and investment decisions because their offspring were regarded as "legitimate."

Moseley concludes that the decline of infanticide in Europe was linked to both greater financial stability among the poor and an increased availability of breastfeeding alternatives (e.g., animal milk, artificial formula), which reduced the energetic burden of childrearing. Daly and Wilson (1988) credit the historical fall in English

infanticide rates to improvements in social welfare services, access to contraception and legal abortions, and the declining social stigma attached to unmarried mothers.

Contemporary Cross-National Patterns

Drawing statistical inferences from infanticide data is complicated by underreporting, inconsistency in government records (Porter and Gavin 2010), and the relative rarity of the phenomenon. Despite this limitation, records from law enforcement and other government agencies have been used to assess broad patterns of infanticide among industrialized nations during the twentieth and twenty-first centuries. Across nations such as the United States (Overpeck et al. 1998; Oberman 2001), Canada (Daly and Wilson 1988), Italy (Ciani and Fontanesi 2012), Croatia (Marcikić et al. 2006), and Malaysia (Razali et al. 2014), most infanticides are committed by the mother of the infant, many of whom are unmarried or partnerless. In their study of Japanese infanticide, Sakuta and Saito (1981) describe two distinct modes of infanticidal behavior: *anomie*, in which infants are killed by relatively young, unmarried parents (typically mothers), and *mabiki*, in which the parents are married and already have children but cannot afford to raise additional offspring. These patterns parallel the difference that Resnick observed between infanticidal behavior by older, married women and younger, unmarried women in historical cases.

Detailed data regarding infanticide in developing nations are scarce. However, the available evidence suggests that general patterns are similar to those seen in developed nations. In South Africa, young mothers are the most common agents of infanticide, but no information is reported regarding marital status (Abrahams et al. 2016). Interviews with couples in Tamil Nadu, India have revealed that most parents considering infanticide are young (between 20 and 30 years of age), are relatively poor, and already have at least one other child (Giriraj 2004, cited in Tandon and Sharma 2006). This cluster of traits suggests that resource stress exerts notable influence upon parental investment. Though more data are

needed, resource stress may prove powerful enough to drive investment and termination decisions independent of marital status.

It is also worthy to note that cross-national paternal infanticide data displays somewhat different patterns than maternal infanticide data. Paternal killing of neonates (infants aged less than 28 days) is less frequent. Fathers and step-fathers who kill children instead tend to do so when the children are older (West et al. 2009). The demography of infanticidal fathers may, however, parallel that of infanticidal mothers; for instance, in Canada, infanticidal fathers are generally younger (Daly and Wilson 1988).

Patterns in Small-Scale Societies

Small-scale, nonindustrial societies are often objects of scholarly interest because they tend to be *natural fertility* populations, as defined by a lack of access to (or use of) commercial contraceptives. The introduction of commercial contraceptives can significantly alter reproductive behavior. Declining fertility in many industrial nations in recent centuries has been attributed in part to the increased availability of commercial contraceptives, safer abortion procedures, family-planning initiatives, and to changing social norms (Sear et al. 2016). Fertility transitions such as these may shift locally optimal life history and parental investment strategies in ways that are drastic and historically anomalous. Moreover, many contemporary industrialized nations have experienced public health breakthroughs, such as sanitary improvements and development of infectious disease prevention, dramatically reducing infant mortality (Stearns 2016). The potential for both greater reproductive agency and lower infant mortality have serious implications in terms of transforming reproductive behavior and parental investment decisions in human populations. Cross-cultural survey of nonindustrial societies has provided a diverse sample that helps to elucidate the relationship between marital status and infanticide in societies that differ in important ways from industrialized nations.

Daly and Wilson (1984) embraced the cross-cultural approach, surveying ethnographic accounts of infanticide in the Probability Sample Files, a stratified sample of nonindustrial cultures selected from 60 world regions. Of these 60 cultural reports, 39 contained information about infanticide (but note that absence of evidence here is not evidence of absence). Daly and Wilson examined the social context in which infanticide occurred. They found that being an "unwed mother" was a recurrent motivation for committing infanticide. A related motivation, "no male support," was also observed frequently across cultures. In a different cross-cultural study that focused on twin infanticide, mothers were found to be far less likely to kill twins in cultures where they had a high degree of social support (Granzberg 1973).

Culture-specific case studies are also informative. Bugos and McCarthy (1984) describe a similar pattern of infanticide among the Ayoreo of the Gran Chaco region in South America. Some women, due to a lack of guaranteed male support, committed multiple infanticides over the course of their reproductive lives before settling into a stable marriage. Nancy Howell (1979) reported that Dobe !Kung mothers who gave birth before they could safely wean their older children might also opt for infanticide, a possible example of a quantity-quality trade-off. Among the Tarahumara of northwestern Mexico, infanticide may occur when the mother has inadequate male support, when the mother has too many children already, or when the infant is perceived as defective or sickly (Mull and Mull 1987). One of the few detailed, quantitative studies of infanticide in a small-scale society was conducted by Wulf Schiefenhövel among the Eipo, a population of horticulturalists in Highland New Guinea. Schiefenhövel observed an extraordinary rate of infanticide (between 29% and 43%) in a population that he argued was at the limit of its resource base. In interviews with women who committed infanticide, it was determined that extramarital pregnancies, having too many children already, and young maternal age were among the most commonly cited motivations for committing infanticide (Schiefenhövel 1989).

These findings implicate marital status as an important mediator of infanticide, insofar as marital status predicts access to male support, greater material and social resources, and greater social status and acceptance in general. However, there is no single "typical" pattern of infanticide in nonindustrial societies. Investment and termination decisions, as in industrialized nations, are inextricably tied to individualized social and economic concerns and vary based on the support available to mothers.

Conclusion

Cross-cultural and cross-national data are consistent with a life history perspective in which infanticide is most prevalent among (1) young, unmarried mothers who lack sufficient social and material support and (2) among older, married mothers who have insufficient resources to support additional children or who have had extramarital affairs. This relationship between marital status and infanticide is strongly influenced by the levels of social support and material resources available to parents. The comparative evidence is likewise congruent with life history perspectives, which anticipate tradeoffs between current and future offspring and between quantity and quality of offspring. But while infanticidal motivations are similar across time and space, it does not necessarily follow that humans possess adaptations for infanticide per se. As Daly and Wilson emphasized:

The specific act of infanticide may or may not benefit the actor's fitness, whether in an individual case or on average, but the act need not contribute to fitness for a sociobiological analysis to be illuminating. Infanticide can be viewed as one (rare) manifestation of variations in more abstract motivational states such as child-specific parental love and solicitude. Adaptation may then be sought at the level of these more abstract states. (Daly and Wilson 1984)

Patterned relationships between infanticide and marital status can emerge without the need for highly specialized psychological adaptations. A more fruitful approach may be to consider how more generalized parental investment

strategies and life history tradeoffs interact with variable socioecological circumstances and individual differences in reproductive and social status.

Cross-References

- [Infanticide and Parenting](#)
- [Maternal Abandonment and Maternal-Fetal Conflict](#)
- [Methods of Filicide](#)
- [Sex Differences in Death by Filicide](#)

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Mariticide

► Partner Homicide

Marketing Influences

► People's Responses to Personal Ads

Marriage

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Synonyms

[Long-term partnership](#); [Pair bonding](#)

Definition

Marriage is a sociosexual and socially recognized bond of some duration between a man and a woman. This is the traditional definition of marriage, although other sociosexual partnerships may meet the criterion.

Introduction

An evolutionary model of marriage begins with recognition of the centrality of reproduction to the relationship. The economic benefits of marriage, such as economies of scale and specialization of labor, are essentially subordinate to reproduction; raising children is costly in terms of wealth and labor.

Marital behavior that maximizes reproductive success will be favored by natural selection. Marital behavior seems to have evolved in order to keep the parents together and available to raise their common offspring. Infants and children are

highly dependent on their parents and develop better when raised by their biological parents than in most if not all other arrangements. This is true not only of infants but also of children and adolescents and applies to health, psychological functioning, cognitive performance, antisocial behavior, and survival itself (Geary 2005; Cabrera et al. 2000).

The functional hypothesis that marriage evolved mainly in order to promote biparentalism is supported by the fact that pair bonding, the rough animal equivalent, tends to occur in mammals with highly dependent young. In essence, in these species the male tends to remain with his mate rather than pursue other sexual opportunities. However, even in the primates, in which the young are highly dependent on maternal care, pair bonding is the exception rather than the rule. Another factor recognized in the evolution of marriage is the opportunity for effective mate guarding.

Marriage is universal, and almost all adults seek to marry, and most do marry, sometimes more than once. Marriage confers health and emotional benefits on both sexes (Field 2011). People who do not marry tend to fail to attract a partner, such as impoverished men. These facts suggest that adult humans possess what might be called a pair-bonding motive, perhaps best termed amorousness. In a US survey, almost no one not in a romantic relationship renounced seeking such a relationship for any appreciable length of time. Amorousness is distinct from the sex drive, although from puberty on, a sexual component seems invariably to accompany amorous feelings toward the partner. The capacity for amorousness is universal (Jankowiak and Fischer 1992). Even in arranged marriages, amorousness tends to develop afterward, although less often than in self-selected marriages. The evolved basis of amorousness is further supported by the fact that particular brain areas are activated by viewing a photo of the loved one, including the anterior cingulate cortex (Fisher 2006). Brain areas involved in pair bonding tend to have vasopressin or oxytocin receptors; these hormones play a role in pair bonding and parental care in rodents (Bartels and Zeki 2004). Orgasm causes a surge in oxytocin in both sexes that enhances the

bond between them. Relationship satisfaction in women is correlated with oxytocin levels and in men with vasopressin levels (Taylor et al. 2010).

Marriage Rates

The adult sex ratio influences the marriage rate. When men are in short supply, a lower percent of women marry since men can secure sexual opportunities, sometimes with multiple women, without having to marry. When women are scarce, more are able to secure the advantages of marriage for economic security, companionship, and childcare assistance. Under these latter conditions, their marriage rate rises, and the divorce rate falls.

It has been observed that the contemporary African American community suffers from a dearth of marriageable men, with the result that the great majority of children are raised by a single mother, often assisted by her mother. This matriarchal family arrangement is not a carryover from slavery since around World War II when good jobs for black men were abundant, 80 % of adults were married (Harris 1974). Only with the return of white veterans and the subsequent loss of factory jobs for black men did the marriage rate begin its decline. Economic factors more than cultural factors drive marital dynamics.

The marriage rate is low where men have difficulty finding work that allows them to help support a family. A job that allows a man to support only himself generally renders him unmarriageable and raises the likelihood of divorce. The marriage rate in a society tends to be correlated with economic opportunities, particularly for men. Where good jobs for men are scarce, fewer men marry and the age of marriage rises, as men need more time to accumulate sufficient resources and skills to afford marriage. In modern societies with companionate marriage, women's age at marriage tends to track men's, so with the current decline in economic opportunities for young people, men and women are marrying later than in the recent past.

In modern societies with comparatively late marriage, women tend not to be protected against premarital pregnancy by the period of adolescent

subfertility. Hence an adolescent girl can get pregnant and become an unwed young mother, the consequences of which are usually grim for both her and the child. The rate of premarital pregnancy and hence single motherhood is higher in countries such as the USA where confidential, free contraceptive services are not provided in secondary schools.

The marriage rate has been falling in Western societies since the Industrial Revolution. Fewer women are marrying, and more women are divorcing. The main reason seems to be that women's economic opportunities have been rising steadily: salaried jobs are open to them, and they are no longer bound to the family farm (Goode 1993). Many of them can support themselves, and even raise children independently. Cultures in which women and men labor independently tend to have higher divorce rates.

Mate Choice

In most tribal cultures, a man must furnish a bride price or labor in order to procure her from her father. The fact that a man often needs many years in order to acquire the requisite skills or resources helps to explain the fact that husbands tend to be older than their wives across cultures. The age disparity is also explained by the breeding imperative: a woman who is just reaching the onset of fertility is at her maximal reproductive value for a prospective husband. Accordingly, women in tribal societies tend to marry, or be married off, about 2 years after menarche, when the period of adolescent subfertility has just passed. This also ensures that she is unlikely to be pregnant.

The criteria of mate choice show considerable consistency across cultures. Both sexes seek signs of health and genetic quality in a prospective spouse. Physical attractiveness tends to be enhanced not just by signs of health and vigor but also by indications of full reproductive maturation. Masculine men and feminine women tend to be more fertile than less sex-differentiated individuals. Women also seek men who are high in social status, act with self-confidence, exhibit

nonverbal dominance displays, and secure valued resources (reviewed by Weisfeld 1999). Ethologists define dominance as success in fights or in gaining contested resources, and female animals generally seek dominant males. It seems that women also seek a dominant mate.

Spouses tend to be moderately similar genetically. This seems to be achieved by a combination of olfactory and visual cues. The sexes are repelled by olfactory cues that indicate close genetic relatedness (Jacob et al. 2002; Weisfeld et al. 2003). This guards against inbreeding depression effects and enhances the immunocompetence of offspring. Less well known is the phenomenon of sexual imprinting. In many birds and mammals, the offspring imprints on the visual image of the opposite-sex parent and uses this image in seeking a mate at maturity. This mechanism guides the offspring to pursue mates of the right species, gender, and state of maturity. Men and women tend to marry someone who resembles the opposite-sex parent, thus enhancing genetic similarity of spouses. Preference for mates of moderate genetic similarity has been demonstrated in insects, birds, and primates, so it must be generally adaptive. One explanation is that moderate homogamy, or positive assortative mating, preserves combinations of genes that are adaptive in the parents' (and offspring's) environment. Moderate homogamy enhances fertility in humans as well as other species (Rushton 1988).

Another important criterion in mate choice is the apparent commitment of the potential spouse. The resources that a man commands will be of no value to the woman unless they are directed toward her and her children. Likewise, a man may not only squander his resources if his wife is unfaithful; he may wind up aiding a rival. A man may employ a range of tactics to ensure a woman that he is passionately committed to her, including offering gifts, pledging his devotion, and complimenting her extravagantly. A woman may test a man's commitment by deferring sexual involvement, provoking his jealousy, and raising the question of marriage. She can ensure him of her commitment by the unambiguous expedient of having sex with him exclusively. Both sexes may employ various mate guarding tactics to detect cheating by the other, including, nowadays, constant monitoring by cell

phone. The tactics of courtship and marriage may be categorized as self-promotion and disparagement of rivals, evaluation of the potential or actual mate, and retention of the mate.

Marital Satisfaction and Stability

One would expect that these universal criteria of mate choice would, if met, lead to happier and more stable marriages. That is, selection would have favored criteria that led to stable marriages and resulting enhanced fecundity. This seems generally to be the case. Young brides go on to produce more children than older ones. Wealthier men raise more children successfully than do poorer ones. Wealthier men are less likely to divorce and more likely to be polygynous. Couples who are similar tend to stay together.

Analyzing data on scores of cultures, Betzger (1989) identified common reasons cited for a divorce. These included sexual refusal, suspected infertility, husband's cruelty, and wife's infidelity. Other research has pinpointed having a handicapped child, death of a child, sexual dissatisfaction, and rape of the wife. All these factors in divorce make sense in terms of reproductive failure. Furthermore, around the world the more children a couple have, the lower the likelihood of divorce (Goode 1993). Divorce is more likely in marriages without children, and peaks at about 4 years of marriage. The first few years of marriage seem to provide a trial period for deciding to have children or not and for testing fertility with the spouse. After 2 or 3 years of a romantic relationship, the period of intense infatuation has passed, freeing the couple to shift their affection to the newborn. In a sense, the spouses are now kept together by their baby.

Another cross-cultural criterion of mate choice is kindness (Buss 1989). Recent cross-cultural research has shown that lack of kindness is an important factor in marital conflict, along with sexual problems, issues regarding child rearing, disputes about division of labor, and economic difficulties (Dillon et al. 2015). Kindness would seem to be essential for an enduring marital relationship. Similarly, in the same five cultures, it

was found that the spouse making one laugh was correlated with marital satisfaction of both husband and wife, but especially the wife (Weisfeld et al. 2011). Many women seek a mate with a sense of humor, so this criterion seems to be valid in terms of subsequent marital satisfaction. Having a funny husband did not seem to enhance the wife's marital satisfaction because it was a sign of intelligence, however. Mediation analysis revealed that having a funny spouse enhanced the spouse's satisfaction even more by being a sign of kindness, understanding, and dependability.

Developmentally, marital satisfaction tends to decline over time. This does not seem to be related to any adverse emotional effects of having children, at least in collectivist cultures with a thriving extended family (Dillon and Beechler 2010). The probability of divorce declines over time as well. This is one indication that marital satisfaction and marital stability are somewhat independent. This is also the case in cultures that forbid divorce; unhappy couples are forced to remain together.

Sex in Marriage

Sexual satisfaction and sexual frequency are highly correlated with marital satisfaction. In tribal cultures sex is reported to occur nightly except during periods when it is taboo. Sex is usually taboo during menstruation, often taboo during pregnancy, and seldom taboo during lactation. In the absence of contraceptive use, conception typically occurs within 1 year of the onset of coitus. Inter-birth intervals for our species are about 3 years, so women are perennially pregnant or lactating. Breastfeeding typically lasts for about 3 years, with solid food introduced after about 2 years. In simians nursing usually stops when the next pregnancy begins, if it has not already ceased.

Sexual infidelity is associated with low marital and sexual satisfaction, permissive values, low economic status, and opportunities. Men report more infidelity than women, and attractive men with wealth and high testosterone report more infidelity, at least partly because of greater opportunities. In US research, women with low self-

esteem reported more infidelity. In a cross-cultural study, sexual infidelity for both sexes was correlated with low love of the spouse, finding others sexually attractive, and the spouse being unfaithful (Nowak et al. 2014).

Jealousy

Like other valued relationships, pair bonds tend to be defended against interlopers. For example, children tend to show jealousy if their parent favors their sibling (Dillon 2013). Rivalry for parental resources tends to be greater between half-sibling and stepsiblings than full siblings.

Lovers too exhibit sexual and romantic jealousy; mate guarding is typical of pair-bonding species. If in human evolution there had not been at least occasional instances of infidelity, jealousy would not have evolved. Estimates of the frequency of marital infidelity vary but are not insubstantial. Infidelity may raise a husband's reproductive success if he succeeds in fertilizing another woman. Infidelity may benefit a wife if she cuckolds her husband and thus deceives him into caring for a child she has had by a man of greater genetic quality than his or garners resources from her lover. Jealousy in men tends to be evoked by the threat of the wife's sexual infidelity more than by the threat of her desertion; the opposite pattern is more typical of women. Suspected infidelity is the principal cause of homicide around the world.

In a cross-cultural study, both sexes worried about spousal infidelity more if the spouse was attractive (Dillon et al. 2014). Worry was greater when the spouse socialized independently. Individuals who felt possessive about the spouse touched the spouse more. Worry was greater in persons who were themselves unfaithful.

Child Rearing

Since marriage is essentially about reproduction, it seems appropriate to consider child-rearing behavior within marriage. Longitudinal research reveals that when a man marries or becomes a

father, his testosterone level falls, and if he divorces, it rises (Mazur and Michalek 1998). One effect of testosterone is to increase competitive behavior; a married man has less need to compete for mates than before. Similarly, husbands with comparatively low testosterone tend to be more family oriented, whereas those with higher testosterone are more likely to divorce and to earn less money. When a woman becomes pregnant, she and her spouse experience a steady rise in prolactin, one of the several parental hormones (Storey et al. 2000). The higher his prolactin level after the birth, the more nurturant he is, as indicated by emotional responsiveness to a crying baby. Prolactin also suppresses testosterone, resulting in further nurturance.

Pregnant women undergo a rise in at least nine hormones. Several of these, including oxytocin, estrogens, progesterone, and prolactin, enhance maternal bonding and behavior. Prenatal and pubertal hormones contribute to the sex difference in nurturant behavior observed throughout the life span in humans and other primates. Breastfeeding maintains the levels of the lactational hormones prolactin and oxytocin.

Men and women are hormonally disposed to care for their children, but the mechanisms are quite different. Consistent with this, women seem to be closely bound to their infants, whereas men are relatively more attracted to weanlings. When a second child is born, the father is inclined to assume some of the care of the weanling, while the mother attends to the newborn. Some Scandinavian countries provide fathers with their own period of paid paternal care that they can take after the first year or so of parental leave expires. Fathers often take their sons on excursions during this time. Around the world, men specialize in tutoring their sons in subsistence skills, protecting the family, performing tasks with hard and heavy materials, serving as warriors, and providing more resources given that wives devote more time to child rearing and domestic tasks (Mackey 1996). Mothers are the main teachers of girls' subsistence and child-rearing skills.

In every culture, women provide more childcare than men on average. The parents are typically assisted by grandparents, older siblings

especially daughters, other kin, and other women. Some cultures are described not as having the extended family but as having the nuclear family. However, this invariably means that the grandparents do not share the parents' dwelling but do reside nearby in a family compound. Thus the norm for our species is care by the extended family. Bonds of kinship are established and maintained by olfactory cues, kinship terms, social contact, social pressure, and other factors. In addition, adolescents undergo a period of intense tutoring by a same-sex adult. This instruction pertains to social and tribal obligations and often culminates in a puberty rites ceremony. Children also learn from imitating and being instructed by older children in these cultures characterized by little age segregation.

Divorce typically reduces contact time with the father markedly and imposes financial loss due to the need for separate residences and other appurtenances for the ex-spouses. Children of divorce are essentially raised by a single parent in terms of average developmental outcomes. If the mother remarries, the consequences for her children are often no better than if she remains unattached. Stepchildren are at risk for neglect, abuse including sexual abuse, and even homicide and accidental death. In a US study, only about half of stepfathers and one-fourth of stepmothers reported any parental feelings toward their stepchildren (Duberman 1975).

Cultural Factors

What has been presented thus far is an overview of human marriage – the normative pattern for our species. But human behavior is very flexible, and marriage takes somewhat different forms around the world. In most modern societies and in tribal societies where little property is available for bride price, marriages are usually not arranged by parents – although parents seem to exert considerable influence over children's choices. In these cultures a formal marriage ceremony is especially common, perhaps as a way of displaying wealth, discouraging divorce after a public commitment, and arranging economic

alliances with in-laws. Marriage ceremonies occur in the great majority of cultures (Quale 1988). In all cultures the double standard of less acceptance of female promiscuity than male promiscuity is in evidence to some degree. In some cultures sex roles are strictly prescribed, whereas in modern societies these are being mitigated. However, even in modern societies, men gravitate toward jobs involving hard manual labor and women toward service occupations. Cultures vary in the status ascribed to women compared with men. In most cultures, especially bellicose ones, women are expected to defer to men in various ways, and sons are privileged over daughters. Other societies are more egalitarian, and women live much longer than men, unlike “male supremacy” cultures, where the gap is smaller. In most cultures a man must qualify for marriage economically. Among wealthy people in highly stratified societies, a woman’s family may offer her a dowry to enhance her marriage prospects for marrying into another wealthy family. She will also be pressured to remain a virgin until marriage, as a way of raising her mate value and of discouraging her from eloping with a penurious cad. For an analysis of marriage systems, in particular subsistence conditions, see Quale (1988).

One particularly interesting variant is polygyny. This was permitted in the majority of tribal societies, although only a handful of men could afford more than one wife. Highly stratified societies, such as the USA, effectively have serial polygyny when wealthy men divorce and remarry to found another family. Polygyny increases the reproductive fitness of the husband, but at the expense of men left unmarried. Women with co-wives have almost the same fecundity as monogamous wives, and certainly have more children than unmarried women. The availability of the polygyny option seems to benefit women; they may choose to marry a wealthy man who is already married, rather than marrying a destitute man or remaining unmarried.

Polygyny is favored in economically stratified tribal societies. It becomes more common when the sex ratio falls, as after a war: a defeat brings a shortage of able-bodied men; a victory offers women to be captured. Polygyny is also favored

by poor economic opportunities for women, who must marry for a livelihood.

Polygyny has some advantages, cited by its defenders. It raises the marriage rate for women and the percentage of children brought up by their biological parents. Co-wives can cooperate in various ways, such as childcare and conspiring against the husband. Co-wives are often sisters; if so, child survival is higher. A young wife may be favored sexually by the husband, but first wives tend to have more power.

Conclusion

The field of marriage research has been largely atheoretical. Factual data abound, but conceptual integration of these data has been lacking. Many studies deal only with a single society, particularly the USA. Some standard facts are trivial, such as that spouses tend to have lived near each other before marriage and that spouses tend to have similar values. Until fairly recently, most research on marriage surveyed only the wife. None of the commonly used measures of marital satisfaction has been validated by invariance testing for cross-cultural use. Only the Marriage and Relationship Questionnaire (MARQ) developed in England by Russell and Wells (1993) seems to have had scales validated across cultures and genders (Lucas et al. 2008).

The emerging evolutionary approach to the topic of marriage has offered some distinct advantages. The fraught topic of sex differences in married people has been addressed seriously for the first time. Previously, husbands and wives have been treated largely as interchangeable parts. Similarly, much of the social science literature neglects the factor of kinship. Huge effects of stepparenthood have been disclosed by evolutionary scholars. Unfortunately, the US Census Bureau does not inquire about biological parenthood in its surveys of households.

Evolutionary psychologists have been somewhat slow off the mark in studying marriage. In a way, married couples have been victims of the success of the field in studying mate choice. Hundreds of studies have been conducted on mate

choice, many of them on US college students in dating relationships. Conducting research on married adults has been more methodologically challenging. Particularly rare has been ethological research on married couples, along the lines of Weisfeld and Stack (2002), who found that wives gazed longer at the spouse than husbands, whose glances were brief, and wives laughed and smiled more. Also needed is more cross-cultural research, especially on diverse cultures. If, say, a sex difference is found in a variety of cultures, the likelihood of an evolved basis is higher than if it is found only in Western societies. A volume by Weisfeld et al. (*in press*) is intended to address some of these shortcomings.

Another area in need of further work is the emotional basis of various marital behaviors. Mate retention tactics, employed outside and inside marriage, might be analyzed with regard to the emotions involved in execution and the effects on the partner. For example, several emotions seem to be involved in the threat of mate loss; they might be analyzed in detail. The emotion of amorousness is seldom mentioned as being a basic human emotion, yet it seems to qualify as one. Sexual behavior and emotions seem to vary with the likelihood of sperm competition, another topic that has emerged recently.

Also making great contributions to our understanding of marriage is research on the brain and hormones. These findings have the felicitous side effect of helping to dispel the notion, prominent in the social sciences, that social behavior is simply the product of experience and culture. Demonstrating that a particular neural mechanism mediates some marital behavior or capacity is one sort of information confirming the evolved basis of that behavior. Other methods include showing the specific effect of a hormone and establishing that the behavior is universal. Demonstrating that a given behavior has an evolved basis rather than being a product of our domain-general capacities is necessary for delineating human nature. Once a behavior can be shown to have an evolved basis, questions of its function can be addressed.

The great promise of an evolutionary analysis of marriage is that comparative analysis, including analysis of pair bonding in various species, will lead to elucidation of the function of

particular marital behaviors. Function is a unifying concept that can bridge disciplinary boundaries and make common sense of otherwise baffling research findings.

Cross-References

- ▶ [Costs and Benefits of Mate Poaching](#)
- ▶ [Dyadic Relationships Versus Group Processes](#)
- ▶ [Frequency of Infidelity](#)
- ▶ [Human Mate Poaching](#)
- ▶ [Infidelity Risk](#)
- ▶ [Mate Value](#)
- ▶ [Relationship Dissolution](#)
- ▶ [Relationship Satisfaction and Commitment](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Romantic Attachment](#)

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Marriage Transaction

► Nuptial Gift

Martial Arts

► Defending Against Attack

Martin Daly

- [Founders of Evolutionary Psychology](#)
 - [Martin Daly and Margo Wilson \(Founders of Evolutionary Psychology\)](#)
-

Martin Daly and Margo Wilson (Founders of Evolutionary Psychology)

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Synonyms

[Founders of evolutionary psychology](#); [Margo Wilson](#); [Martin Daly](#)

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Definition

Canadian academics whose scholarly contributions and leadership roles in the Human Behavior and Evolution Society and its flagship journal were significant in the emergence of evolutionary psychology.

Introduction

When published in 1859, *On the Origin of Species* received a cool reception in Canada, owing to reservations of the nation's most renowned nineteenth-century scholars, including J. W. Dawson, Principal of McGill College, and D. Wilson, Professor, University College, Toronto (Zeller 1998). The latter, a historian, artist, early archaeologist, and anthropologist coined the term "prehistory" (Trigger 1966). As its first president, he set the University of Toronto on the road to success and international renown. Unlike critiques of Darwin's natural selection theory based wholly on religious grounds, Wilson's complex views included scientific misgivings over the discounting of uniquely human mental qualities in describing the continuity of species (Trigger 1966). It is perhaps somewhat fitting that just over 100 years later, two Canadians, who would be at the forefront of the emerging field of evolutionary psychology, should meet at the University of Toronto, Wilson's greatest legacy. One, coincidentally, would have the same surname. After receiving their Ph.Ds., Drs. Margo Wilson and Martin Daly met at the university in 1974 (Belluz 2009). There they would begin a great academic and personal partnership that would span almost 35 years and help propel and instantiate an evolutionary approach in psychology and behavior not just in Canada but in the USA and abroad.

Margo Wilson: Early Years in Northern Climes

Margo Ings Wilson was born in Winnipeg, Manitoba, on October 1st, 1942 to Edith Helen Ings, a

nurse and daughter of Col. A. Ernest Ings and Clara S. B. Dodge. Before Margo's birth Edith was in England assisting in the war effort. Col. Ings's father had emigrated from Portsmouth, England to Prince Edward Island (P.E.I.) and ran *The Island* newspaper. Clara Dodge's father was a doctor in Halifax, Nova Scotia. Margo's maternal grandfather was originally trained as a barrister, then served in the 104/105th Battalion in WWI, and later held executive positions in a number of PEI utility companies ("Death in Winnipeg" 1944). The Ings family was prosperous and lived in a grand house on the Esplanade in Charlottetown overlooking the water. Margo would not come to know her maternal grandparents, nor their lifestyle, however, as both had died by 1944. By then Edith had returned from the war and was living in Winnipeg with her little daughter and husband, Major Tom Smith.

In 1948, Edith Ings Smith, now widowed, left Winnipeg with 6-year-old Margo and moved to the Gwich'in community of Fort McPherson in the Northwest Territories (Belluz 2009; Krupp and Barclay 2010; Daly 2012; Gaulin and Fessler 2010). Fort McPherson was originally founded in 1840 by the Hudson's Bay Company and called Peel River House. It is located about 65 miles above the Arctic Circle in the Peel River watershed, a place of great natural beauty belonging to indigenous peoples for centuries. As the only medical professional, Edith provided much needed medical care for the local residents, at times even having to do surgery in communication with a doctor from Inuvik via Morse code. Margo went to the little local one-roomed school where she was the only nonindigenous child in attendance. At a young age, Margo began to understand what it was like to be an outsider but, at the same time, showed empathy for those less fortunate. Throughout her life Margo would support and promote "out group" members or those less advantaged (Belluz 2009; Daly 2012). Taken aback by the poverty and inability of the local parents to pay for children's school lunches, to raise money, Margo ran a miniature dogsled to trap muskrats and sell their furs in cooperation with her classmates (Daly 2012; Gaulin and Fessler 2010; Krupp and Barclay 2010).

In 1952, Edith married the Hudson's Bay Company factor, J. E. J. "Jack" Wilson, posted at the fort ("Happenings" 1952), who bought furs from the locals and ran the company store. A kindly, low-key, pipe-smoking man Jack took Margo under his wing, likely offering advice on her fur-trapping enterprise. About a decade earlier, he had provided natural history information about the fur bearing and game species in the Severn area to researchers from the Royal Ontario Museum of Zoology ("Field work" 1940). One wonders if Margo herself had begun studying animal behavior and physiology, while managing her mixed-breed dog team and checking the trap line. In addition, both Edith and Jack were avid readers and possible models for Margo's developing appetite for knowledge and greater understanding. Together, the three Wilsons kept busy, and their minds occupied many dark cold winters and long-lit summers at Fort McPherson.

Margo went to high school in Victoria, B.C., where her mother arranged for her to stay with a family. In 1960, she earned a Queen Elizabeth II Provincial Scholarship and after graduating high school was admitted directly to the University of Alberta in Edmonton. Margo entered the nursing program, but found the restrictions on student nurses, such as having to live in the residence, a 10 p.m. curfew, and prohibitions against male guests and marriage, outdated and intolerable. She dropped out after about 6 months and, according to her, started a bit of a rebellion, as a high proportion of the other women subsequently left and the administration was forced to remove some of the restrictions. Margo switched programs and graduated with a degree in psychology in 1964. She originally intended to become a clinician, but after brief experiences working in an Oregon mental institution, versus an avian embryology lab, she chose a physiological approach (Belluz 2009; Daly 2012). Satisfying both her physiological interests and desire for a milder climate, Margo entered the masters program at the University of California at Davis in 1965 where she worked with Gordon Bermant studying the behavioral endocrinology of chickens and Japanese quail.

After finishing her masters in 1967, Margo won a Commonwealth Scholarship to study at University College, London, England. There she examined the sexual behavior of rhesus monkeys, including the behavioral effects of castration and hormone replacement on males (Michael and Wilson 1974). She and fellow student, Barry Keverne, worked at the Bethlhem Royal Hospital, known as "Bedlam", the oldest mental institution (Belluz 2009). Her supervisor, Richard P. Michael, a psychiatrist, was also an early behavioral endocrinologist. Working doggedly into the night typing her thesis by candlelight, due to power restrictions, Margo completed her Ph.D. in 1972. After earning her degree, Dr. Wilson returned to Canada. She began teaching classes at the University of Toronto as Lecturer (1972–1973) and Visiting Assistant Professor (1973–1975) and cobbled together a research lab without funding. She also sat on a university ethics committee to review proposals for research on nonhuman animals. One day she received an ethics application in person from a recently arrived postdoctoral researcher. His name was Dr. Martin Daly.

Martin Daly: From Toronto to Algeria and Back

James *Martin* Daly was born on November 15, 1944, in Toronto, Ontario. His mother was Ida Simon, the daughter of parents of Ashkenazi Jewish ancestry who immigrated to Canada from Latvia in the early 1900s. Before the first Russian revolution, Martin's maternal grandfather was drafted into the Russian army to tend his unit's horses, but was left behind after being kicked by a horse. Later, in Canada, he worked at a cleaner's pressing pants for a living. Martin's father, James Alexander Daly, was the son of two Irish immigrants. Growing up in Toronto, Martin attended Bennington Heights Elementary School, then York Mills and Don Mills Collegiates. He did especially well in mathematics and won an international mathematics contest award in 1961. After graduating (1962) with an open scholarship, he attended the University of Toronto, obtaining a

B.A. (Honors Psychology) in 1967 and becoming the first in his family to earn a university degree. With his supervisor, Gary Walters, Martin examined the effects of injections of scopolamine on the disruption of memory formation in rats. That same year he married Sandra Fiegehen, whom he had known since high school. They moved to Montreal where she became a teacher, and Martin received an M.A. in psychology at McGill University in 1968 for his thesis on the satiation of hoarding behavior in rats. At McGill, Martin attended a seminar given by Donald Hebb, a highly admired and respected early Canadian psychologist who inspired his students not to just sop up current knowledge but to seek out uncharted academic territories.

Before going to Montreal, Martin had realized that he was far more interested in studying species-specific animal behavior than conducting physiological manipulations. He returned to the University of Toronto for his Ph.D. to work with Jerry A. Hogan, whose ethological perspective he had admired in undergraduate classes (Daly 2015). Hogan transfixed Martin with both his enthusiasm and strong opinions. Martin worked in Hogan's lab, aka the "Chicken House," completing his Ph.D. thesis, *Behavioural development, early experiences, and maternal behaviour in golden hamsters (Mesocricetus auratus)*, in 1971. After studying behavior in the lab, Martin decided to undertake fieldwork to understand how differences in the social behavior of closely related species relate to features of their ecology. He moved to the University of Bristol to work with John H. Crook, the founder of socioecology. Funded by postdoctoral fellowships, Martin undertook research at a French research station in Algeria, where Sandra assisted with the field research on the feeding behavior and socioecology of Saharan gerbils (e.g., Daly and Daly 1973). At the end of the postdoc and looking for a change, Martin and Sandra bought an old Victorian house in Nova Scotia and planned to live off the land. They planted vegetables and bought a goat to make their own yogurt. As the winter approached, however, Martin became intellectually bored, having read all the books in the bookmobile parked nearby. Sandra also had a change

of heart about their lifestyle. Their back-to-the-land experiment and marriage ended.

Martin Daly returned to the University of Toronto in late 1974 where he worked as a volunteer postdoc with his previous supervisor, J. Hogan, and began applying for academic jobs. After first meeting Margo Wilson on campus when submitting an ethics application, they met again in the summer of 1975 at the meeting of the Animal Behavior Society in North Carolina (Belluz 2009; Daly 2012). At that time, the conference was a common meeting ground for those interested in both nonhuman and human behavior. The pair's interests coincided, and according to Martin, at the end of the meeting, "I followed her home back to Toronto, and I wouldn't leave." (Belluz 2009). It was the beginning of a long and productive personal and academic partnership.

Daly and Wilson: A First Book with Longevity

His job search successful, Martin Daly was Lecturer and Assistant Professor in Psychology at the University of California, Riverside from 1975 to 1978. Margo accompanied him and was Visiting Assistant Professor at the University of Southern California (1977) and Visiting Scholar, University of California, Riverside (1977–1978). During their first year, they attended a seminar where participants discussed each chapter of E. O. Wilson's groundbreaking new book *Sociobiology: The New Synthesis* (1975). In the oversized volume, Wilson assembled the foundations of a new discipline encompassing an evolutionary functional analysis of social behavior. Convinced by the approach and wishing to extend its coverage of human behavior, Daly and Wilson decided to write a book to marry proximate and ultimate approaches in the behavioral sciences (Daly and Wilson 1983; Krupp and Barclay 2010). They began working on their first book *Sex, Evolution, and Behavior* (1978), and by 1976, it was largely complete. After Martin attended the conference of the American Anthropological Association in Washington, D.C., they added two final chapters

devoted to human evolution and psychology. The book brought together basic evolutionary concepts and theory, including natural selection, fitness, evolution of sex, sex allocation, parent-offspring conflict, sexual selection, and life history strategies, with numerous applications to the behavior and physiology of both nonhumans and *Homo sapiens*. Filling a new niche in a highly readable way, the volume was immediately taken up by students, academics, and the lay public, with a second edition following in 1983. The clarity and accuracy, with which the chapters covered the theoretical foundations while peppered with real-world examples, resulted in it serving as a textbook for many years, even as recently as a few years ago. Due to the interest and rapid research progress largely inspired by Daly and Wilson's first book and approach, ironically the only chapters that became quickly outdated were the final ones devoted to human evolution and psychology.

In 1978, the pair returned to Canada with Martin taking up the position of Associate Professor of Psychology at McMaster, where he taught some of the earliest classes on sociobiology and human evolution and behavior. Margo became a Research Associate, as antiquated regulations against hiring faculty members' spouses prohibited her from a formal university position for decades (Krupp and Barclay 2010). Every November the couple packed up their station wagon in Hamilton and traveled south. While at Riverside, they had begun conducting field research on the behavior and ecology of Merriam's kangaroo rats at the Boyd Deep Canyon Research Center near Palm Desert, California. Although a research station in the desert sounds completely idyllic, along with their students and postdoc, Daly and Wilson put in long hours tracking kangaroo rats at night. At times, when nighttime temperatures plummeted, they would huddle up under newspapers to keep warm. The fieldwork continued for about three decades and resulted in numerous contributions concerning the ecology and behavior of the nocturnal rodents, including the function of scatter hoarding in reducing major cache loss and modulation of differential predation risk according to

moon phase (e.g., Daly et al. 1992). Each year throughout the 1980s on their way to and from the field station, Randy Thornhill recollects the couple visiting his home in New Mexico, which was also his study site for a project on sexual selection in red junglefowl. True to form, Margo and Martin enjoyed watching and hypothesizing about the junglefowl's behavior. Always up for a good meal, they also joined the Thornhills in feasting on the birds during their many stopovers.

In the late 1970s, during their stay in California or return to Canada, Margo began thinking about undertaking research on *Homo sapiens*. After some time she was struck with the idea that the incidence of human homicide may serve as a porthole through which evolved human passions and biases could be revealed. She readily convinced Martin they should conduct epidemiological analyses of patterns of risk for violence in different kinds of human relationships, such as marital, parent-offspring, and male-male. Thus began a 30-year program of research that would be the focus of much of their later human empirical studies. Soon after, Margo and Martin visited the Detroit police station to discuss researching their homicide records, launching a long-term cooperative enterprise including the police and several other researchers in fields related to jurisprudence and law enforcement (Daly and Wilson 1988; Daly 2016).

Patterns of Homicide and the Birth of a Society

In 1978, Daly and Wilson were invited to an informal conference on human behavior and evolution organized by Richard Alexander and Donald Tinkle at the University of Michigan in Ann Arbor. The meeting also included William Irons, Napoleon Chagnon, and their students from Northwestern University. Over the next 10 years, Wilson, Daly, and their students would regularly drive from McMaster to Ann Arbor for the continuing meetings. Between 1986 and 1995, the *Evolution and Human Behavior Program* was supported by the University of Michigan. In addition to the main organizers, Richard Alexander and Bobbi Low, others affiliated with the program

or attending meetings who would make their own mark on the discipline included David Buss, Barbara Smuts, Laura Betzig, Paul Turke, Monique Borgerhoff-Mulder, Beverly Strassmann, Randolph Nesse, Richard Wrangham, Eugene Burnstein, Elizabeth Hill, Mark Flinn, Warren Holmes, George Williams, William Hamilton, Robert Axelrod, Jack Beckstrom, Mildred Dickemann, John Hartung, and Randy and Nancy Thornhill. Initially the meetings were sufficiently small and informal that a reception was usually held at someone's home, including Richard Alexander's farm.

Cross-border exchanges continued, and in 1984–1985, Wilson and Daly were Visiting Scholars in Biological Anthropology at Harvard University. There they took part in the “Simian Seminars” held by the prominent Harvard primatologist and anthropologist, Irvén DeVore, at his Cambridge home (Hrdy 2005) and attended less formal meetings at North House (Daly and Wilson 1988). During this time Martin and Margo first met Leda Cosmides and John Tooby, who (along with others like Don Symons) would champion a focus on evolved mental mechanisms rather than behavior per se (e.g., Tooby and Cosmides 1989), and David Buss, whose seminal work on human mate selection would establish a new and popular subfield. A special project “Foundations of Evolutionary Psychology” proposed by Buss (Buss 2008) resulted in the four working together in 1989–1990 at the Center for Advanced Study in the Behavioral Sciences at Stanford University where they cemented their mutual and individual approaches. By this time Wilson and Daly had also given numerous presentations to colleagues and students at developing centers of interest in Canada, such as those led by Charles Crawford and Dennis Krebs at Simon Fraser University and Irwin Silverman at York University.

Throughout the 1980s Margo and Martin pursued their epidemiological investigations of human violence. An initial foray with colleague Suzanne Weghorst produced the striking and novel finding that stepchildren were about 100 times more likely to be lethally abused than biological children (Wilson et al. 1980). This they attributed to an evolved bias in parental solicitude

favoring one's own biological children, now widely known as “discriminative parental solicitude” (Daly and Wilson 1980). Predicting that male-male competition over mates would also impact violence, they found that male sexual jealousy and suspicions of infidelity were predominant motives in lethal assaults of wives (Daly et al. 1982). Moreover, they suggested that the heightened levels of violence displayed by young men, or “the young male syndrome,” may reflect sexually selected competitive risk-taking (Wilson and Daly 1985). In 1988, Daly and Wilson published their second book, *Homicide*, a landmark describing many of their previous studies and serving as a model for future research programs. The book began with the theoretical underpinnings of the evolution of motivations toward lethal violence. In subsequent chapters predictions regarding the expected patterns of interpersonal conflict, violence, and homicide were tested citing their earlier findings, other modern samples, and diverse datasets, including those based on hunter-gatherers, indigenous peoples on the Indian subcontinent, a thirteenth-century English sample, and cases of infanticide in the Human Relations and Area files. Interestingly, the book also considered the codevelopment of legal systems constructed to contend with violence. Their investigations had piqued Margo's interest in law, and in 1987, she became the first graduate of the Masters of Studies in Law program at the University of Toronto (Belluz 2009; Daly 2012; Gaulin and Fessler 2010). Although she had not known her maternal grandfather, in later life Margo had come to share his calling, receiving a law degree about 90 years after he was called to the bar.

In 1988, two larger formal conferences, the *Evolution and Human Behavior Conference* and *Evolutionary Psychology and Psychiatry Conference* were held at the University of Michigan. At the latter, Wilson and Daly attended a meeting to discuss future conferences and creation of a formal society. As a result the *Human Behavior and Evolution Society* (HBES) was founded October 29, 1988 with William Hamilton elected first president (Low and Nesse 1989) and the inaugural meeting held at Northwestern University in

1989. A primary instigator, Randy Nesse, remembers that along with others, Martin and Margo were initially skeptical about the success of the new society. However, they quickly became two of its greatest adherents, cheerfully greeting other participants at the meetings each year. Along with Daly and Wilson, several of the early attendees would be recognized as founding members of the society and the new discipline of evolutionary psychology. Thus with the 1980s coming to a close, a new offshoot of E. O. Wilson's *Sociobiology*, focusing more specifically on the functional evolution of human psychological mechanisms and behavior with its own society, had firmly taken root.

Maturation and Internationalization of the New Discipline

During the decades bookending the turn of the millennium, Wilson and Daly played important roles in guiding the further progress and internationalization of evolutionary psychology. Martin Daly was president of the Human Behavior and Evolution Society in 1991–1993 and executive council member from 1989 to 1995. Margo Wilson served as president from 1997 to 1999 and as executive board member from 1992 to 1999. During that time the society's membership and conference attendance rose steeply. In 1996, *Evolution and Human Behavior* (formerly *Ethology and Sociobiology*) became the flagship journal of HBES, and Daly and Wilson became coeditors in chief for the next 10 years. Through their expert stewardship, rigorous standards, and constructive criticism, the journal became a highly cited repository of cutting edge research and theory. For some time it was the primary journal where articles taking a functional approach to human behavior and psychology could be reviewed without fear of disqualification due to antievolutionary biases. Advancement of the journal at this juncture was critical to the expansion and progress of the new discipline.

In concert with the success of the international society came further involvement with researchers in other countries. In 1993, Margo

and Martin spent time with colleagues at Rockefeller Foundation Center in Bellagio, Italy, were Visiting Professors at the University of New Mexico (1996–1997), and fellows at the Wissenschaftskolleg zu Berlin in 2002. In addition to presentations in Canada and the USA, Daly and Wilson gave numerous invited lectures in diverse countries, including Brazil, the Netherlands, Turkey, Japan, Germany, Australia, Sweden, Chile, and the UK. The pair actively promoted international and interdisciplinary research and supported colleagues in other nations, with Margo assisting them in successful grant applications (Daly 2012; Krupp and Barclay 2010). In addition, Martin served terms on the executive committees of the International Society for Behavioural Ecology and Animal Behavior Society, and both sat on editorial boards for other respected journals. With their international reputations firmly established, in 1998, Margo Wilson and Martin Daly were honored in their home country when they were named fellows of the Royal Society of Canada.

With funding from several bodies, including the prestigious Harry Frank Guggenheim Foundation and armed with theoretically derived predictions, Daly and Wilson meticulously raked extant homicide and new datasets, turning up a chain of novel findings. Margo was particularly interested in identifying the determinants of spousal homicide and violence against women and found, for example, that the risk of uxoricide (killing one's wife) was heightened following a separation, and among younger wives and those in common-law relationships (Wilson et al. 1995). She argued that male sexual jealousy and possessiveness or "male sexual proprietariness" was a primary motivation of spousal violence (Wilson and Daly 1996). Building upon their earlier proposition that elevated male aggression is related to risk-taking, Margo reasoned that risk acceptance or future discounting and homicide rates may be heightened when life expectancy is low. Sure enough, a study of Chicago neighborhoods showed local life expectancy was a major predictor of homicide rate and future discounting, as measured by age of first reproduction (Wilson and Daly 1997). Moreover, income inequality was a positive predictor

of homicide rates. A later related experimental study indicated that men shown photographs of attractive women to induce a “present oriented mindset” discounted the future more than those shown less attractive photographs of women (Wilson and Daly 2003). Martin followed up on the findings of increased risk of violence toward stepchildren, dubbed the *Cinderella effect*, finding that women with children from a previous partner were at increased risk of uxoricide (Daly et al. 1997). In 1998, he and Margo published their third book, *The Truth about Cinderella*, a volume in the popular series *Darwinism Today*, covering much of their work on discriminative parental solicitude.

After holding adjunct positions at McMaster University for a decade, Margo Wilson was formally appointed Professor of Psychology in 1998. In their classes and busy research lab at McMaster, Margo and Martin encouraged the academic careers of their students. Genuinely interested in their students’ lives, the pair held get-togethers at their home where tasty dishes always complemented the social menu. Never assuming credit for students’ original work, they published with them as colleagues on diverse topics, such as variability in sociosexuality, birth order and familial sentiment, differential cache pilferage, and evolution of the family. In 2003, Margo was diagnosed with non-Hodgkin’s lymphoma, but nevertheless continued with her active life, teaching, and research. Fulfilling a long-held wish, during the summer of 2008, Martin and Margo took a cruise to the Galapagos Islands, a location fomenting Darwin’s greatest insight (Fig. 1). There they took in the scenery, peered at the peculiar island inhabitants, and added Darwin’s finches to their bird life lists accumulated over many years as avid birdwatchers.

In 2009, Daly and Wilson were honored with a Lifetime Achievement Award by the HBES at the first meeting the couple would miss, due to Margo’s failing health. The society and discipline lost a much-admired pioneer when Margo died in Hamilton on September 24, 2009. In 2010, the first Margo Wilson Award of the HBES, honoring her contributions to the society and discipline, was presented at the annual meeting. Martin retired from McMaster in 2011, but took up a



Martin Daly and Margo Wilson (Founders of Evolutionary Psychology), Fig. 1 Margo Wilson and Martin Daly in the Galapagos Islands, 2008 (Courtesy of M. Daly)

Research Professorship at the University of Missouri the following year, continuing his research alongside his present wife, Gretchen Perry. While in Missouri, he wrote his recent book *Killing the Competition: Economic Inequality and Homicide* (2016). In an engaging, personal style, Martin convincingly lays out the case that economic disparity within populations is not just positively correlated with homicide rates across populations but is causal. His argument builds upon he and Margo’s 1997 findings, as well as those showing reduced homicide rates and income inequity in Canada versus the USA (Daly et al. 2001). Also highly relevant is their finding that the most common form of lethal violence, male-male violence, is the most variable across populations (Daly and Wilson 1988) and perhaps the most amenable to economic intervention. As in *Homicide* (1988), his case is made through the presentation of an array of empirical findings, coupled with established theory and undeniable logic. In the process, Martin dissects and debunks myths including that it is absolute level of resources, not inequity, that drives violence, and that financial policies to reduce inequities inevitably decrease productivity and economic growth.

Conclusion

Together Margo Wilson and Martin Daly introduced a wide audience to evolutionary thinking in

the behavioral sciences through their four books and over 250 theoretical, review, and empirical papers. Their work appears in more than 70 different journals, signaling its broad appeal across disciplines, including criminology, biology, anthropology, law, sociology, and economics. Additionally, they have given at least 200 invited talks or presentations and nurtured the careers of over 20 graduate students and postdocs. Spanning several decades and continents, Martin Daly and Margo Wilson's scientific rigor and zeal galvanized others, helping to carve a clear pathway for the emerging field of evolutionary psychology. Their contributions to the *HBES* and *Evolution and Human Behavior* remain ever inscribed reminders of the extensive and enduring stretch of their influence. Although Darwinism had a slow start in Canada, Daly and Wilson played crucial roles at the frontier of its most modern application to psychology and behavior.

Cross-References

- [Cinderella Effect, The](#)
- [Discriminative Parental Solicitude](#)
- [Homicide](#)
- [Infanticide](#)
- [Male-Male Competition](#)
- [Uxoricide](#)
- [Young Male Syndrome](#)

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Martin Muller

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Definition

Martin Muller, Associate Professor in the Department of Anthropology at University of New Mexico, Co-Director of Kibale Chimpanzee Project and Kibale National Park.

Introduction

Martin Muller is an associate professor and anthropologist at the University of New Mexico. He studies behavioral and reproductive ecology, endocrinology, and evolution in primates including humans. Dr. Muller is the co-director of the Kibale Chimpanzee Project and Kibale National Park. He earned both his Bachelors and Doctorate in Anthropology at the University of Southern California. In recent work, Dr. Muller has co-authored the book *Sexual Coercion in Primates: An Evolutionary Perspective on Male Aggression Against Females* with Dr. Richard Wrangham and has published research on chimpanzees and comparative work on human reproductive behavior.

Kasiisi Project and Kibale Chimpanzee Project

The Kasiisi Project, located in Uganda, was founded in 1997 in order to aid in educating in tangent with the Kibale National Park. The Kasiisi Project serves as a link between locals and the Kibale Chimpanzee Project (Kasiisi Project 2017). The Kibale Chimpanzee Project, founded to study the behavior, ecology, and physiology of wild chimpanzees in 1987 (Kibale Chimpanzee Project 2017), has been dedicated to the survival, welfare, and understanding of chimpanzees (Kibale Chimpanzees 2013). Some recent research by Dr. Muller done with the Kibale Chimpanzee Project involves social customs, reproduction, hormones, and disease in chimpanzees (The Kibale Chimpanzee Project 2017).

Recent Research

Recent comparative work on humans done by Thompson and Muller (2016) has examined human reproductive behavior in comparison to other primates. In this entry, they examine fluctuations of hormones in fertile versus non-fertile periods under such hypotheses as the dual-mating hypothesis. In the discussion, they come to the conclusion that the dual-mating hypothesis is not a suitable explanation for the extended sexuality found in humans when comparing to other primates. They further conclude that additional research is needed on hormone-mediated shifts in female sexual psychology (Thompson and Muller 2016).

In some recent publications of Dr. Muller's work with chimpanzees, he has examined social constructs within chimpanzee groups including grooming behaviors and learning, foraging, and hunting calls. Chimpanzees' have unique grooming styles per group in and out; how these styles developed were unknown. Wrangham et al. found that individuals keep their mother's style and are not influenced by other chimpanzees, impacting community traditions for generations (Wrangham, et al. 2016). Foraging in chimpanzees is primarily done by females; however their

ability to forage is affected by their group, particularly how many males are in the group and if they have children. In a recent article, Thompson et al. determine that having many males in a group has long-term costs associated with reproduction via negative affect on C-peptide levels and foraging capabilities (Thompson et al. 2014). Hunting initiative of chimpanzees has also been examined, finding that groups of male chimpanzees often have constant initiators that spur on the group to hunt, including non-common hunting participants within the group. After the removal or death of the common initiators, fewer hunts are enacted (Gilby et al. 2015).

Conclusion

Dr. Martin Muller studies a variety of subjects in relation to primates. He is the co-director of the Kibale Chimpanzee Project and Kibale National Park. His recent work has compared human reproductive behavior to other primates, and he has examined behaviors in chimpanzees such as grooming behaviors and learning, foraging, hunting calls, and more alongside others in his field.

Cross-References

- [Chimpanzee Raiding](#)
- [Dual-Mating Hypothesis](#)

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Martyrdom

- [Suicide Terrorism](#)

Maryanne Fisher

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M

Synonyms

[Author](#); [Researcher](#); [Teacher](#)

Definition

Maryanne Fisher is a psychologist best known for her work on women's intrasexual competition and applying an evolutionary framework to popular culture.

Introduction

Dr. Maryanne Fisher is a full professor in the Department of Psychology at Saint Mary's University in Halifax, Canada. The majority of her research has focused on women's intrasexual

competition for access to, and retention of, mates. Her first noteworthy contribution to evolutionary psychology was an empirical examination of women's derogation of other women according to ovulatory cycle phase (Fisher 2004). More recently, she has turned her interest towards maternal competition in women. Other significant contributions include examinations of literature and popular culture, including Harlequin romance novels, co-editing *Evolution's Empress: Darwinian Perspectives on the Nature of Women* (2013), and editing *The Oxford Handbook of Women and Competition* (2017).

Women's Intrasexual Competition

In 2004, Fisher published the first empirical study of women's intrasexual competition for mates. She proposed that the decrease in ratings of female facial attractiveness during ovulatory cycle phases marked by high estrogen as compared to low estrogen indicated derogation of potential mating competitors. A similar finding was not obtained for male faces, showing this decrease was potentially related to competition for finding a good mate, rather than simply a decrease in global evaluations of facial attractiveness. She then went on to demonstrate that romantic relationship status, self-monitoring, and sociosexuality did not lead to differences in evaluations of attractiveness, and those who were single and actively seeking a mate did not differ from those single and not seeking a mate (Fisher et al. 2008). These findings highlight that intrasexual competition for mates may not be influenced by romantic relationship status or one's engagement in actively seeking a mate.

She has also examined the strategies that one may use in intrasexual mating competition. Her research shows that there are four primary strategies that people use. Self-promotion is when one attempts to make her/himself seem superior to rivals, such as by dressing nicely or drawing attention to positive personality traits. Competitor derogation instead is when one attempts to devalue a potential rival, relative to oneself, such as by making negative statements about a rival's

sexual history. Self-promotion and competitor derogation had been documented prior to Fisher's research. However, she found the additional strategies of competitor manipulation and mate manipulation. Competitor manipulation is reducing the actual need to compete by manipulating one's rivals, such as telling a rival that a targeted mate has a history of sexual diseases. Mate manipulation is when one attempts to direct the attention of a mate toward oneself and away from a potential rival. She found that self-promotion was the most used strategy, followed by mate manipulation, and that competitor derogation and competitor manipulation were used to the same extent (Fisher and Cox 2010). She has outlined these strategies further in a recent theoretical paper (Fisher 2015) and reviews the area in Fisher (2013).

Until recently, she primarily investigated the ways that young heterosexual women competed for access to, and retention of, mates. However, her focus has shifted from not only examining mating competition but also to study competition between mothers. Women, ultimately, must act in ways to improve their reproductive success, whether it takes the form of mating competition or mother's competing for access to resources that impinge upon their children's health, survival, and their subsequent reproduction. This line of inquiry has, to date, remained primarily theoretical (e.g., Fisher and Moule 2013; Fisher et al. *in press*).

Evolutionary Psychology and Popular Culture

Starting in 2003, Fisher (along with collaborators), began to apply the lens of Darwinian literary criticism towards a variety of media. The premise of this framework is that one may explore media to understand human's evolved motives, cognitions, emotions, and behaviors. In 2012, along with Dr. Catherine Salmon, she co-edited the June 2012 issue of the *Review of General Psychology* on the intersection of popular culture and evolutionary psychology. She has investigated men's and women's mating strategies in Victorian

romance fiction (e.g., Kruger et al. 2003), as well as in contemporary romance novels (Cox and Fisher 2009), television sitcoms (Fisher 2012), graffiti (Fisher and Radtke 2014), and song lyrics (Fisher and Candea 2012). She has also explored the topics of Western paintings, as well as the topics of what women paint specifically, proposing that these topics must at least partly reflect evolved human nature (Fisher and Meredith 2012).

Evolution's Empress and the Oxford Handbook

Fisher co-edited, with Dr. Rosemarie Sokol-Chang and Dr. Justin Garcia, *Evolution's Empress: Darwinian Perspectives on the Nature of Women* in 2013. This volume was inspired by the formation of the Feminist Evolutionary Psychology Society, which showed the need to formally address how women have been active agents during human evolution. The book contains 22 chapters, spanning a range of topics such as health and reproduction, competition and cooperation, parenting, and mating and communication. An offshoot of this book led to working with Sokol-Chang to edit the December 2013 issue of the *Journal of Social, Evolutionary and Cultural Psychology* on the intersection of feminism and evolutionary psychology.

More recently, Fisher has edited *The Oxford Handbook of Women and Competition* (2017). Many but not all of the chapters in this book incorporate an evolutionary perspective. The book contains 39 chapters that range in their focus; topics include social status and aggression, gossip, mating relationships, endocrinology, health and aging, family, physical appearance, virtual considerations, workplace issues, and sport.

Conclusion

Maryanne Fisher is best known for developing the area of women's intrasexual competition for mates and has begun to examine maternal competition in women. Other significant contributions

include examinations of literature and popular culture, co-editing *Evolution's Empress: Darwinian Perspectives on the Nature of Women* (2013), and editing *The Oxford Handbook of Women and Competition* (2017). Collectively, her work has helped to challenge prior assumptions regarding women's passivity in humans' evolutionary history.

Cross-References

- ▶ [Evolution's Empress: Darwinian Perspectives on the Nature of Women](#)
- ▶ [Women and Competition, The Oxford Handbook of](#)

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Masculinity

- ▶ [Biology of Human Gender, The](#)
- ▶ [Culture of Honor](#)
- ▶ [Culture of Honor and Individual Differences](#)

Masculinity and Femininity

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Synonyms

[Femaleness](#); [Gender](#); [Maleness](#)

Definition

Masculinity and femininity refer to an individual's gender in terms of maleness and femaleness, respectively. Gender roles are those socially ascribed normative behaviors with respect to a given gender. Biological sex refers to an individual's reproductive organs as being male or female.

Introduction

Issues surrounding sex and gender roles as they relate to sexuality are among the most divisive across scholarly disciplines. If one adheres strictly to the definitions, sex is biological and defines individuals based on their reproductive anatomy into male and female, while gender refers to one's maleness (masculinity) and femaleness (femininity). Gender roles are those societally constructed normative behaviors ascribed to a given gender that, in turn, are attached to a particular biological sex. For those with backgrounds in social theory, biology may have little to do with how cultural norms color the blank canvas that becomes adult gender identities and roles. An alternative view is that gender bears the stamp of past selective pressures and has been shaped by natural selection. One of the most sexually dimorphic aspects of human behavior and biology concerns reproduction and parental roles. This entry explores the relationships between sexual dimorphisms in morphology and gender-typical parental roles.

Sexual Reproduction and Social Roles in Humans

Parental investment theory proposes that sex differences in reproductive investment should lead to differences in mate preferences (Trivers 1972). Given that females invest more biological resources in offspring than males, they form a scarcer resource, potentially driving male-male competition to attract and retain mates, a paradigm that has become known as the “males compete and females choose” paradigm (MCFC). However, humans have also evolved a cooperative mating system, wherein fathers and alloparents contribute to the survival of children (Sear 2016). Thus, how sexual selection has shaped the evolution of reproductive anatomy, secondary sexual traits, and gender differences in parental roles should be understood as occurring within complex social and mating systems (West-Eberhardt 2014).

Foundational theories in evolutionary psychology suggested that mate preferences were shaped in the early phases of human ancestral evolution to

attend to morphology that provides information relating to biological quality, including fertility, health, and parental skills (Grammer et al. 2003). In a seminal article, Buss (1989) demonstrated across 37 cultures that men stated stronger preferences than women for youth and physical attractiveness in a mate, whereas women stated stronger preferences than men for older partners with greater earning potential. Research among the Hadza hunter-gatherers of Tanzania reported that the most important traits nominated in a spouse were character, foraging ability, and physical attractiveness (Marlowe 2004). The only sex differences in mate preferences were a higher importance placed by men than women on fertility and women's greater emphasis on intelligence than men (Marlowe 2004). These findings provide some support for parental investment theory in shaping the evolution of mate preferences.

It follows logically that if preferences have evolved to attend to characteristics that are associated with health, fecundability and parental qualities then meaningful correlations could exist between sex-typical secondary sexual traits and gender-typical parenting behaviors in women and men. The following sections will discuss the extent to which any such relationship exists and the implications this has for understanding the evolution of mate preferences.

Femininity in Women: Morphology and Maternal Tendencies

Sex-typical or "feminine" traits emerge in women under the actions of estrogens during pubertal development. These include facial traits such as a round overall shape, wide eyes, and full lips and bodily traits such as permanent stores of fat around the hips, buttocks, thighs, and breasts (Grammer et al. 2003).

Given the physiological investments women make in birthing and raising offspring (Jasienska 2009), if sexual selection has shaped men's preferences for femininity as indicators of fecundability and maternal investment, then information about maternal investment capabilities may be reliably conveyed in secondary sexual traits. Facial femininity in women is indeed positively associated with fecundability as measured

in reproductive hormones and women's desire to invest maternally (Law Smith et al. 2012). In contrast, testosterone levels and height were negatively associated with desired number of children and ideal age at first reproduction (reviewed in Law Smith et al. 2012). Higher self-reported maternal tendencies also predict women's motivational responses to infants (Hahn et al. 2015). Men judge more feminine-looking women to be warmer, trustworthy, cooperative, and more sexually attractive than more masculine-looking women (Grammer et al. 2003).

The significant energetic investment in gestation and lactation suggests a healthy distribution of body fat, and fully developed breast morphology might also be associated with maternal tendencies. A low waist-to-hip ratio (WHR), wherein the waist is narrower relative to greater fat reserves in the buttocks and thighs, in concert with a healthy body mass index, is associated with various facets which are reproductive maturity and fecundability in women (Singh and Singh 2011). Thus, the onset of menarche in adolescence and the ability to maintain regular menstrual and ovulatory cycles during adulthood are associated with low WHRs, as is fertility, and healthy offspring birthweight (Singh and Singh 2011).

Fat around the mammary glands provides energy for lactation (Anderson 1983). Although it was once thought that breasts function as storage organs for milk and in rare cases deficiencies in glandular development are associated with reduced success in initiating breastfeeding, the overall size of non-lactating breasts does not indicate actual lactation ability or milk storage capabilities (reviewed in Dixon et al. 2015). Others proposed that permanently enlarged breasts evolved to allow for breastfeeding during bipedal movement and that resting an infant against the breasts is psychologically comforting (reviewed in Dixon et al. 2015). Maternal-infant bonding via breastfeeding is likely an ancient feature of human maternal-infant bonding, and there is some evidence that breastfeeding enhances infant immune response (Duijts et al. 2009) and lowers maternal stress via prolactin and oxytocin release, which may further facilitate maternal-infant bonding (Uauy and de Andraca 1995).

While men's preferences for breast size differ both within and between cultures (reviewed in Dixon et al. 2015), breast size emerges as a strong predictor of female physical attractiveness in multivariate evolutionary studies (Brooks et al. 2015). Likewise, male preferences for specific values of WHR vary cross-culturally (reviewed in Brooks et al. 2015), likely due to greater variation explained by BMI in attractiveness judgments (Swami and Tovée 2005). However, body fat distribution contributes significantly to men's judgments of female physical attractiveness (Brooks et al. 2015). There is also some evidence that men and women judge larger breasts as more sexually mature, as reproductively capable, and as providing greater maternal nurturance (defined as breastfeeding and caring for infants; Dixon et al. 2015). However, empirical data demonstrating that women's body size, shape, or breast morphology are meaningfully associated with self-perceived or actual maternal investment in offspring, infant bonding, or offspring survivability appear to be lacking from the literature. Moreover, how sexual dimorphisms in women's morphology underpin maternal investment in small-scale societies will be critical to ascertain in future research. Thus, although some sex-specific aspects of female body composition are associated with biological aspects of maternal capabilities, for the present, there is a lack of empirical data linking such morphology to behavioral aspects of maternal investment in offspring and offspring fitness.

Masculinity in Men: Morphology and the Masculinity Paradox

Sex-typical male traits develop under the actions of androgens during pubertal development. These include craniofacial masculinity (i.e., enlarged brow ridge, thicker jaw, small eyes, and more robust midface), facial and body hair, vocal pitch, height, and muscularity (Grammer et al. 2003). Boys typically reach sexual maturity later than girls, which suggests that secondary sexual traits manifest when competition to attract viable mates is augmented. According to life history theory, males who attain sexual maturity more rapidly will display earlier development of

masculine secondary sexual characters as they influence mating effort (Muehlenbein and Bribiescas 2005). Earlier recall of pubertal development is associated with greater body size, upper body strength, and aspects of masculine facial shape (Doll et al. 2016), and more dominant-looking teenage boys report greater numbers of sexual partners than their more submissive-looking counterparts (Mazur et al. 1994). In adulthood, men with more masculine faces and deeper voices established higher positions in male dominance-based hierarchies and attained greater mating success (reviewed in Puts 2016).

While masculine secondary sexual traits require androgens for their expression, the allocation of resources toward traits associated with mating effort may come at the expense of some aspects of somatic health (Muehlenbein and Bribiescas 2005) and result in reduced paternal investment (Gettler 2016). Indeed, men with more masculine faces and bodies report engaging in more short-term than long-term relationships, and women accurately judge sexual infidelity from masculinity in static photographic stimuli (reviewed in Dixon et al. 2016). Thus, unlike in women where estrogen-dependent characteristics are to some extent associated with maternal tendencies, in men androgens underpin sexually selected traits that positively predict men's mating success but may be associated with reduced paternal investment.

This suggests there are costs to women in selecting masculine partners. However, preferences for attractive traits have evolved as they confer indirect (i.e., genetic) benefits to offspring or direct benefits such as resources, increased survivability, or enhanced fertility (Kokko et al. 2003). Masculine craniofacial traits are judged as less warm, caring, having less interest in long-term relationships, and providing lower paternal investment (reviewed in Dixon et al. 2016). Thus, reduced phenotypic masculinity may be preferred in a long-term mate, as such men are perceived as more socially amenable, cooperative, and paternally investing as long-term partners (reviewed in Dixon et al. 2016). However, mating strategy theories suggest that the costs associated with selecting masculine

mates are bypassed when women pursue more short-term mating strategies (reviewed in Dixon et al. 2016). Indeed, studies have reported augmented preferences for masculine faces, body shape, vocal pitch, and scents among women when judging short-term than long-term attractiveness (reviewed in Dixon et al. 2016). These preferences may also be greater at the follicular, more fertile, phase of the menstrual cycle when any benefits to offspring fitness gained by selecting a masculine mate are more likely to be realized (Gildersleeve et al. 2014). Although these strategic trade-off models have been popular in the past 15 years of research, a recent large study among identical and nonidentical twins reported that 38 % of the variance in women's facial masculinity preferences was due to genetic variation, while individual differences in sociosexuality, fertility, and pathogen disgust are combined to explain less than 1 % of the variance (Zietsch et al. 2015). These findings call into question the importance of contextual factors in maintaining variation in preferences for masculinity in short-term mates.

Given that androgen-dependent masculine traits are associated with reduced paternal qualities but some aspects of biological quality, facultative trade-offs may underpin the strength of women's masculinity preferences cross-culturally (DeBruine et al. 2010). In a cross-cultural study of women's facial masculinity, preferences were found to be strongest in countries and where national health was lowest (DeBruine et al. 2010). Alternatively, the value of an intra-sexually formidable mate may underpin women's masculinity preferences when resources are scarcer. A reanalysis of the data from DeBruine et al. (2010) reported that national income inequality was a stronger predictor of women's preferences than national health (Brooks et al. 2011). These studies highlight a role of ecological and economic factors in shaping preferences for masculine facial morphology. However, whether variation in preferences reflects any trade-offs in preferences for genetic quality or direct benefits and how either of these forms of sexual selection relate to paternal investment qualities in humans remain to be determined.

It is important to note that aside from the aforementioned cross-cultural analyses (DeBruine et al. 2010; Brooks et al. 2011), the majority of the conclusions in studies of women's preferences for men's facial masculinity are derived from data collected among predominantly WEIRD (Western, Educated, Industrialized, Rich, and Democratic) populations (reviewed in Scott et al. 2014), which represent only a fraction of the current cultural and ecological variation across human societies (Heinrich et al. 2010). Further, they may not reflect the kinds of environments in which preferences are argued to have evolved (Grammer et al. 2003) and instead could represent mate preferences formed within more modern and ecologically novel circumstances. Indeed, a recent cross-cultural study of preferences for sexual dimorphism in facial morphology that included data from several small-scale societies reported preferences for sex-typical facial traits were stronger in cultures with higher human development indexes (Scott et al. 2014). In these settings, people are more regularly exposed to a greater number of anonymous people compared to people living in small-scale societies, which may drive greater sensitivity to small variation in craniofacial masculinity (Scott et al. 2014). Another possibility is that within small-scale subsistence societies where paternal and maternal gender roles are more rigidly defined (Marlowe 2000), asking people to complete mate preference tests that included questions relating to their ecological or social context, such as how much the stimulus or target might invest parentally, may be more effective in exposing any trade-offs in mate preferences. What is clear from these studies is that further comparative cross-cultural analyses among small-scale and multilevel societies would be valuable.

Conclusion

The goal of this article was to highlight that some quite basic questions regarding the relationship between gender roles in parenting qualities and sexual dimorphisms in morphology that have putatively evolved via sexual selection remain

unanswered. A challenge for the next generation of students in evolutionary psychology and human behavioral ecology may be to characterize how variation in culture, ecology, and genetics combine to maintain variation in parental gender roles and mate preferences.

Cross-References

- ▶ [Childcare](#)
- ▶ [Evolutionary Standards of Female Attractiveness](#)
- ▶ [Female Mate Choice](#)
- ▶ [Parental Investment as Mating Effort](#)
- ▶ [Relationship Between Sexuality and Gender](#)

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Masquerade

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Synonyms

Concealing imitation; Procryptic resemblance;
Special resemblance

Definition

When an organism appears to mimic an inanimate object, ostensibly, so that predators or prey misclassify it as unimportant.

Introduction

It is a relatively common strategy among plants and animals to mimic inanimate objects (“models”), such as twigs, leaves, pebbles, and bird droppings (Skelhorn et al. 2010a). Among insects, at least 50 of the 950 species of British

macrolepidoptera resemble inanimate objects. For example, caterpillars of the peppered moth, *Biston betularia*, look like the twigs of birch and willow trees on which they rest; most of the 2500 species of stick and leaf insects (Phasmatoidea), as well as many mantises (Mantodea), also resemble leaves and twigs (Skelhorn et al. 2010b). In terrestrial vertebrates, birds from the genus *Nyctibius*, with bark-colored plumage, are suggested to masquerade as tree stumps by sitting motionless during the day (Caro 2014). Tree-living colubrids, which have long thin bodies, are thought to resemble vines both in appearance and behavior (Caro 2014). In aquatic vertebrates, the nocturnal Amazonian catfish, *Tetranematichthys quadrifilis*, resembles a waterlogged leaf, and the leafy sea dragon, *Phyllopteryx eques*, closely resembles seaweed (Cott 1940). In plants, the variegated leaves of *Silybum marianum* are believed to masquerade as leaves that have been damaged by tunneling insects (Lev-Yadun 2014). Stone mimicry is very common in at least four families of plants, *Mesembryanthemaceae*, *Crassulaceae*, *Euphorbiaceae*, and *Liliaceae*, from arid regions of southern and northeastern Africa and also North America (Lev-Yadun 2014).

This resemblance of inanimate objects has been referred to by a number of terms including “special resemblance,” “procryptic resemblance,” “plant part mimicry,” and “concealing imitation,” but it is now widely known as “masquerade.”

How Does Masquerade Work?

In 2010, Skelhorn et al. showed that domestic chicks that had prior experience of twigs were slower to attack twig resembling caterpillars compared to chicks that had no experience or experience with twigs that no longer resembled the caterpillars because they had been bound in purple cotton twine. This experiment provided the first evidence that experienced birds generalize their learned indifference toward twigs to twig-resembling caterpillars and misclassify caterpillars as twigs. This study also showed that caterpillars benefitted from masquerade even

when they did not match their background, which was the first evidence that masquerade operates in the absence of background matching (crypsis).

Skelhorn et al. (2011) also showed that masquerade is less effective as an antipredatory defense when the density of masqueraders is increased relative to their models. This is because predators are less motivated to search for masquerading caterpillars if their recent experience suggests a high, rather than low, local density of unrewarding twigs and because a greater number of models make it more difficult for predators to detect masquerading prey.

How Does Masquerade Differ from Crypsis and Batesian Mimicry?

Masquerade is distinct from crypsis. Cryptic animals are difficult to detect, whereas masquerading animals are detected but mistaken for inanimate objects (Skelhorn et al. 2010a).

Similar to masquerade, predators mistake palatable Batesian mimics for the defended species (“models”) that they resemble. However, in Batesian mimicry, an increase in the number of mimics causes predators to attack the model more frequently. Therefore, Batesian mimics influence the population and evolutionary dynamics of models, whereas masqueraders do not affect their models in the same way (Skelhorn et al. 2010b).

Masquerade and Behavior

Many species of masqueraders adopt characteristic postures or behaviors that might enhance their resemblance to inanimate objects. When it is windy, several species of stick insects sway from side to side when blown by wind, possibly enhancing their resemblance to the motion of twigs in the breeze (Bian et al. 2016). Twiglike larvae of the early thorn moth (*Selenia dentaria*) settle on branches where twigs are abundant and which they resemble in size.

Nonvisual Masquerade

Theoretically masquerade should also involve nonvisual mechanisms, because most organisms exist in multisensory environments. However, there is not much evidence to support this idea (Ruxton 2009). The fish *Oxymonacanthus longirostris* (Monacanthidae) feeds almost exclusively on corals, associates closely with these corals, and visually resembles a coral branch. The fish is able to chemically resemble its coral habitat by matching the odor profiles, which reduces its detectability to predators, but whether this qualifies as masquerade or crypsis is not yet known (Brooker et al. 2015).

How Did Masquerade Evolve?

Masquerading species may have evolved from cryptic ancestors (Skelhorn et al. 2010a). Animals that developed a minor resemblance to an appropriate model may have been misclassified by predators, leading to reduced attacks. Likewise, predators with a resemblance to models could cause reduced threat perception by prey. Such a resemblance would probably stem from a mutation that may also reduce the animal’s level of crypsis. However, if the benefit of being misidentified was higher than the cost of being detected, selection should favor masquerade. It is likely that the accuracy of the resemblance would then have been gradually improved by selection.

A recent comparative morphological analysis of the wing patterns of *Kallima* butterflies revealed that the leaflike wing patterns in this lineage evolved in a gradual process from ancestors that did not resemble leaves (Suzuki et al. 2014).

Conclusion

Despite a great deal of research attention during the last 6 years, there is still much to learn about masquerade. For example, there are no experimental tests of how masquerade evolves, which

leaves it an open question as to how masquerade evolves. More tests on how behavior or other sensory modalities enhance the resemblance of animals to inanimate objects would be worthwhile. Furthermore, research on the use of masquerade in predators would reveal if prey also misclassify predators as inanimate objects.

Cross-References

- [Camouflage](#)
- [Visual Illusions](#)

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Mass Extinction

- [Population Bottleneck](#)

Master Clock

- [Sleep-Wake Cycles](#)

Masters and Johnson

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Definition

Dr. William Masters and Virginia Johnson were pioneers in the scientific study of sexuality, sexual function, and sexual dysfunction. Beginning their work at Washington University (1957) and continuing their efforts at the Masters and Johnson Institute (1964), they served as one of the first research teams to systematically study the biological substrates of human sexual arousal, orgasm, and intercourse.

Introduction

“Knowledge of history brings order to disorder and imposes meaning on what appears to be chaos, putting the past into perspective to explain the present” – Schultz and Schultz (2015).

An understanding of the current state of any science rests upon the knowledge of, and appreciation for, that scientific field’s history. Specifically, understanding the history of the scientific study of sexuality and sexual behavior provides a context that unites a broad range of disciplines (e.g., evolutionary psychology, social psychology, biological psychology), all of which provide their own unique perspective to the study of

sexuality and sexual behavior. Further, this understanding of history helps to illustrate the complex ways in which scientific findings reflect the time, cultural, social, political, and economic climates during which they were interpreted and disseminated. This entry will explore the significance of the works of Masters and Johnson in constructing the current understanding of sexuality and sexual behavior, as well as the implications of their findings for the study of sex and sexuality through an evolutionary lens. This discussion will begin with (1) the lives of Masters and Johnson and (2) their influential findings, methodologies, and publications.

Masters and Johnson

The history of the study of sexuality and sexual behavior begins as early as 1886, when Richard von Krafft-Ebing published a work detailing sexuality as “the most powerful factor in individual and social existence” (p. 1), entitled *Psychopathia Sexualis*. This text exemplifies the focus of the scientific study of sexuality during the late nineteenth and early twentieth centuries: *sexual pathology* and *the perpetuation of gender stereotypes* prescribing chastity and passivity for women and aggressive, insatiable sexual appetites for men. As von Krafft-Ebing (1886) explains:

Undoubtedly man has a much more intense sexual appetite than woman. As a result of a powerful natural instinct, at a certain age, a man is drawn toward a woman. . . . In accordance with the nature of this powerful impulse, he is aggressive and violent in his wooing. . . . (p. 13)

This reflects the *Zeitgeist* of the time, wherein late-nineteenth-century European attitudes toward sex and sexuality regarded men as individuals driven uncontrollably by sexual impulses, for example, the use of the phrases “white meat” and “dark meat” to refer to poultry being served at meals became increasingly popular, as the use of words like “breast” and “thigh” was impolite as they were considered to ignite men’s sexual passions (Rosenthal 2013). Of women, von Krafft-Ebing (1886) adds:

If she is normally developed mentally, and well bred, her sexual desire is small. If this were not so the whole world would become a brothel and marriage and a family impossible. It is certain that the man that avoids women and the woman that seeks men are abnormal. Woman is wooed for her favor. She remains passive. (p. 13)

Represented herein, Victorian attitudes and expectations of women’s sexuality were extremely repressive. Women were not expected to express (or possess) strong sexual desires, and doing so was often treated as pathological (Degler 1974). Indeed, much of the early scientific study and understanding of sex and sexuality was based on the use of samples of women seeking treatment for some kind of psychological and/or physiological disturbance, dysfunction, or distress. Accordingly, the early study of sexuality emphasized pathology and dysfunction:

Mrs. V. has suffered with a passion for men since her earliest youth. . . . She loved her husband passionately, but even with him she could not keep from demanding coitus of every one with whom she could be alone. . . . (von Krafft-Ebing 1886, p. 55)

Importantly, during the mid-twentieth century, the study of sex and sexuality began to shift away from reliance upon case studies and stereotypes which perpetuated a misunderstanding of men and women’s sexuality. To begin this shift, Alfred Kinsey employed questionnaires and structured interviews to obtain a more representative sampling of human sexual behavior and sexual attitudes, publishing his work in two sequential works, *Sexual Behavior in the Human Male* (1948) and *Sexual Behavior in the Human Female* (1953). In these works, Kinsey contradicted contemporary attitudes by reporting the incidence of same-sex sexual behavior, solitary sexual practices, and sexual intercourse outside of the context of marriage in men and women (Rosenthal 2013). These narratives paved the way for the physiological study of human sexual behavior by Dr. William Masters and Virginia Johnson.

The Lives of Masters and Johnson

William H. Masters earned his medical degree at the University of Rochester in 1943, specializing in obstetrics and gynecology. His career as a sex

and sexuality researcher really began once he accepted a faculty position at the Washington University Medical School in 1947. Masters' research at Washington University began by focusing on a specific population: prostitutes. Masters observed the sexual behavior of prostitutes and conducted interviews with many women involved in sex work; arguably these experiences – quite progressive given they were taking place in the early 1950s – provided unique insights which inspired Masters' later works. For example, historical accounts of these qualitative studies suggest that Masters learned, and was surprised by, the prevalence of faked orgasm in this special population of women (Maier 2009). His structured interviews, which served to debrief sex workers after their sexual experience with a particular client, revealed that his sample believed that faked orgasm was something which often characterized women's partnered sexual experiences, in and out of sex work. Indeed, faked orgasm is prevalent in women's sexual experiences (approximately 50% of sexually active women report having faked orgasm; Muehlenhard and Shippee 2010), and evolutionary scholars propose that faking orgasm may serve the adaptive function of mate retention, particularly when the likelihood of defection or partner infidelity is high. Some attribute Masters' surprise and misunderstanding of women's experiences and perspectives regarding sexual practices with his desire to seek out and hire a female research partner (T. Maier, interview with NPR, October 4, Maier 2013). Given the unrepresentative nature of Masters' early samples, regarding the sexual experiences and attitudes of American women, these findings are largely unpublished and undocumented (Maier 2009).

Virginia Johnson first pursued her education at Drury College as a 16-year-old, but did not complete her post-secondary degree training. She returned to college at the University of Missouri to study music and pursue her ambitions to be a country singer (Fox 2013). After three marriages ended in divorce, Johnson returned to school at Washington University to pursue a degree in sociology (Hayman 2013). It was at Washington University that Masters met Johnson and employed

her as a research assistant and secretary in 1957 (Rogers 2015). Initially assisting with administrative duties, particularly facilitating recruitment of representative samples of men and women for physiological study, eventually Johnson became an equal partner in their research team and cofounded the Reproductive Biology Research Foundation (1964) in St. Louis, Missouri – renamed the Masters and Johnson Institute in 1978 (Fox 2013).

Influential Findings, Methodologies, and Publications

During their collaboration, Masters and Johnson studied the physiological substrates of sexual activity and sexual arousal in individuals aged 18 to 89 (Rosenthal 2013). They employed interview, video recording, electrocardiography, and electroencephalography methodologies to systematically study the physiological activities underlying masturbation and partnered sex with 312 males and 382 females from “the academic community associated with a large university-hospital complex” (Masters and Johnson 1966, p. 11). While this was a more representative sample, compared to early work focusing entirely on male and female prostitutes, Masters and Johnson (1966) do admit that this sample does not represent individuals of lower socioeconomic status. Using these techniques and these community samples, Masters and Johnson were among the first to (a) describe the four stages of the sexual response and (b) the treatment of sexual dysfunction.

The Four Stages of the Sexual Response

Detailed elsewhere in this work (*The Four Stage Model of the Sexual Response*), Masters and Johnson were among the first to detail the physiological stages of the human sexual response (Masters and Johnson 1966). Of note, Albert Moll's work *The Sexual Life of the Child* (1912) and Havelock Ellis' work *Studies in the Psychology of Sex* (1928) both detailed models of the physiology of the human sexual response. What was unique and revolutionary about Masters and Johnson's contribution to the study of sex and sexuality was their use of empirical methods to collect their physiological data (Rosenthal 2013).

Masters and Johnson (1966) described the human sexual response cycle as occurring in four stages, “(1) the excitement phase; (2) the plateau phase; (3) the orgasmic phase; and (4) the resolution phase” (p. 4). During the first phase, they describe a response in the presence of “any source of somatogenic or psychogenic stimulation” (p. 5) wherein physiological arousal begins to build; further, they indicate that a transition to the next phase of the response cycle is characterized by an increase in intensity of physiological arousal (due to continued stimulation). The second phase, the plateau phase, is described via this increased intensity of arousal. Continued “adequate” (p. 6) stimulation during this phase is required for the individual to achieve the third phase, orgasm.

They describe the orgasm as characterized by physiological changes in the penis, prostate, seminal vesicles, clitoris, vagina, and uterus – as well as spasms and muscle contractions observed elsewhere in the male and female body. Interestingly, they have this to say about the difference in the male and female experience of orgasm: “There is great variation in both the intensity and the duration of female orgasmic experience, while the male tends to follow standard patterns of ejaculatory reaction with less individual variation” (p. 6). This is consistent with contemporary evolutionary explanations of the female orgasm; according to the mate-choice hypothesis, the (comparatively complex) female orgasmic experience serves to evaluate the suitability and commitment of a potential long-term mate (Puts et al. 2012). During the final phase of the sexual response cycle, resolution is detailed as an “involuntary period of tension loss” (p. 6) wherein the physiological markers of arousal and orgasm have faded and time (and additional stimulation) is necessary to reinstate excitement and eventually orgasm. Of particular note to contemporary evolutionary psychology, Masters and Johnson (1966) emphasized the role of biological (rather than sociological) forces in shaping sex drives and sexual experiences: “The cycle of the sexual response, with orgasm as the ultimate point in progression, generally is believed to develop from a drive of biological-behavioral origin deeply integrated into the condition of human existence” (p. 127).

The Treatment of Sexual Dysfunction

In 1970, Masters and Johnson published their second influential work (following the publication of *Human Sexual Response* in 1966), entitled *Human Sexual Inadequacy*. This work detailed sexual function and dysfunction in geriatric populations – groundbreaking for the time of its release. Importantly, this work initiated an intellectual movement toward the de-stigmatization of sexual activity in old age – encouraging the maintenance of, and open communication regarding, sexual activity as one ages (Masters and Johnson 1970).

Furthermore, Masters and Johnson’s (1970) work revolutionized the treatment of sexual disturbance and dysfunction. Masters and Johnson admit that their work regarding sexual dysfunction uniquely reflects 5 years of study of the physiological substrates of human sexual behavior and arousal; “. . . categorically the greatest handicap to successful treatment of sexual inadequacy was a lack of reliable physiological information in the area of the human sexual response. It was presumed that definitive laboratory effort would develop material of clinical consequence” (p. 1). Although their work does indeed detail the *physiological* symptoms of vaginismus, dyspareunia, impotence, and premature ejaculation (to name a few) with reference to the physiological substrates in “normal” sexual functioning populations, their explanations for the causes of sexual dysfunction are almost entirely *psychological* (Leiblum 2007).

Prior to the publication of *Human Sexual Inadequacy*, sexual dysfunction was treated with long-term therapy performed on an individual basis. Masters and Johnson (1970) uniquely prescribed short-term (approximately 2 weeks) treatment of sexual dysfunction in joint therapy; “. . . there is no such thing as an uninvolved partner in any marriage in which there is some form of sexual inadequacy” (p. 2). So fervent was their belief in the utility (and necessity) of partnered therapeutic techniques to treat sexual dysfunction, they employed the use of “partner surrogates” for unmarried individuals seeking treatment at their clinic. As Masters and Johnson (1970) explain, “. . . a partner to share the patient’s concerns for

successful treatment, to cooperate in developing physically the suggestions presented during sessions in therapy. . . (is) essential, if effective sexual functioning is to be returned to" (p. 147).

Conclusion

Understanding the history of the scientific study of sexuality and sexual behavior provides a context that unites the many perspectives, and theoretical approaches, to the study of sex. In this entry, the ways in which scientific findings and clinical practice have reflected the Zeitgeist of the time have been detailed – with particular emphasis being given to the work of scholars which paved the way for the first systematic, physiological study of sexual function and dysfunction by Masters and Johnson. Contemporary understandings of the physiology of the human sexual response, the sexual interests and needs of geriatric populations, and the efficacy of fast, coupled therapeutic treatment of sexual dysfunction were made possible by the work of Masters and Johnson. Perhaps most importantly, during a time characterized by stereotype, taboo, and misunderstanding, Masters and Johnson turned a clinical and scientifically rigorous eye to the American bedroom.

Cross-References

- [Female Orgasm and In-Pair Copulation](#)
- [Four-Stage Model of the Sexual Response](#)
- [In-Pair Copulation](#)
- [Long-Term Mating](#)
- [Orgasm](#)
- [Penile-Vaginal Sex](#)
- [Physiological Mechanisms](#)
- [Sexual Intercourse](#)

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Masturbation

- [Sexual Behavior](#)

Mate

- [Human Copulation](#)

Mate Attraction

- [Sexual Behavior](#)

Mate Choice

- ▶ [Bernhard Fink](#)
 - ▶ [Bright Male Hypothesis](#)
 - ▶ [Charles Darwin: Theory of Sexual Selection](#)
 - ▶ [Mate Preferences](#)
 - ▶ [Parental Investment and Sexual Selection](#)
 - ▶ [Physical Attractiveness](#)
 - ▶ [Presence of Children](#)
-

Mate Choice Copying

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Synonyms

[Mate preference copying](#); [Social learning in mate choice](#); [Social learning of mate preferences](#)

Definition

Strictly, mate choice copying occurs when an observer views a target with a mate and the target is more likely to be chosen as a mate by the observer because of the presence of the current mate. More broadly, the phenomenon is related to social learning of mate choice and preferences whereby information about the target's mate, or the absence of a target's mate, affects an observer's preference for and potential choice of the target.

Introduction

It is extremely unlikely that we are born with a template for the ideal mate. Indeed, mate preferences in humans can be learned and change with experience. One source of learning comes from the social domain: observing other people's preferences and partnerships. In recent years, a

number of studies have highlighted social learning effects in women's mate preferences and mate choice.

Why would women be interested in the mate choice of others? There are of course time and energy costs to sampling a range of partners, but there are also major costs to poor mate choice decisions, such as desertion or infidelity. We would then expect individuals to choose their partners carefully using all available information, and information about the choices of other's is presented all around us. In fact, learning from others is common in many domains, and evolutionary selection for social learning mechanisms can occur when there are costs to acquiring accurate behavioral information via individual learning (Richerson and Boyd 2005). Mate preference and choice are therefore a prime domain for social learning as using information about other's choices is a low cost and low risk means to learn who is and who is not likely to be a good partner without the time and effort needed to learn individually by dating and mating with each potential partner. Following or copying other's choices allows an individual to assess potential mates more quickly and efficiently than through individual trial and error as well as avoiding the potential costs associated with poor choices.

Copying

Mate choice copying, whereby individuals are more likely to select mates if that mate has been observed as a mate with a member of the opposite sex, has been observed among females in a wide range of nonhuman animals, including fish and bird species (Galef and Laland 2005). These studies have generally shown that in choice tests where females observe another female (the "model") to be paired with one of two males (the "targets"), female observers are subsequently more likely to prefer the target male they had seen paired over the male they had seen unpaired (Hoglund et al. 1995).

Humans also appear to be very interested in the partnerships of other's. For example, celebrity

gossip magazines and websites often focus on new and failed partnerships. But do women “copy” the partnerships of others like other animals? Inspired by work on nonhuman animals, research suggests that social learning may also influence human mate preferences (for review, see Little et al. 2011) but perhaps in a more sophisticated way than simple copying.

Some studies have manipulated cues to relationship status to examine how this impacts on men’s attractiveness. While some research has shown that the presence of wedding rings on men did not increase women’s preferences for those men, other studies have found that images of men labeled as married were more attractive than those labeled as single (for review, see Little et al. 2011). These results do not suggest a strong pattern of following the choice of other women; however, cues to current marriage in fact may be problematic. For example, while it is predicted that having been chosen as a partner would make a man more attractive, marriage sends a signal that the man may be off the market and unavailable and, at least, that a woman would have to compete with a current wife. Given humans engage in long-term monogamous relationships, being married may indeed indicate a man is attractive to other women, but any increased attraction may be counteracted by the fact that the man is already committed to another woman.

More subtle cues to other women’s preferences show more consistent evidence that women follow the preferences of other women. For example, one study has shown that women appear to follow the preferences expressed by other women for men. Women prefer pictures of men if presented alongside images of other women who look at the target man with positive smiling expressions compared to more negative neutral expressions (Jones et al. 2007). In a more naturalistic study, after observing real interactions on a video recorded during a speed dating event, women were more interested in men they perceived as having a successful date (Place et al. 2010). Women therefore appear to mimic the attitude of other women to particular men.

Bias in Social Learning of Preferences

Another factor in learning from others is that some individuals may be better models than others – women may be more likely to attend to information about partner choice and preferences from particular women. Again, this may be important in explaining why simply being married is not a sufficient cue to be deemed a good likely partner. If a man’s wife was unattractive and disagreeable, perhaps the man himself has negative qualities. In this way we can expect social learning to be biased toward certain models: “model-based biases.”

But which models should women attend to help guide their choices? Models who have greater available choice might make the best models. Attractive women, for example, can select from a variety of men, and so it follows that their choices may be weighted more highly than the choices of less attractive women who may have more limited choice. Indeed, there is evidence to suggest that women attend to the attractiveness of a man’s current purported partner. Sigall and Landy (1973) used real individuals to show that positive characteristics are attributed more frequently to men who are paired with attractive rather than unattractive women. In this way they show that an attractive partner may “radiate beauty.” Such a phenomenon is suggestive of a sophisticated form of mate choice copying, whereby women can use the attractiveness of a partner that a man can acquire in order to judge the man’s own attractiveness. A more recent study using images that were presented with a fictitious partner has shown that both men and women find a face paired with an attractive partner to be more attractive than one paired with an unattractive partner for a long-term but not a short-term relationship (Little et al. 2008). Effects specific to long-term preferences in humans suggest that social information is being used to infer non-physical traits that make a target a good long-term partner, such as resources or intelligence, which may be difficult to determine from physical appearance alone.

Prestige-Biased Learning

Alongside attractiveness, we might also expect popular women to have greater choice, and certainly we see that people look up to prestigious and popular individuals. It has been suggested that prestige evolved from social learning strategies to identify appropriate models from whom to learn and that we preferentially attend to prestigious models. If others consider someone prestigious, then it might be assumed they are useful model for social learning. One study has shown that men are rated as more attractive by women if they are presented with fictitious partners who are believed to be popular in their peer group than if they are believed to be less popular in their peer group (Little et al. 2015).

Effects of Age of Learner

It may be useful to attend to those with the most choice and those who are prestigious, but it is also useful to attend to individuals with the most information. Another model bias has been observed in fish species whereby young guppies are more likely to copy the mate choice of older models than younger models (Dugatkin and Godin 1993). Older guppies are also less likely to be influenced by the choices of younger females (Dugatkin and Godin 1993). In humans, it is likely that as women get older, they have a greater store of knowledge about the quality of potential mates. This greater experience means that older individuals should be less susceptible to social influences, relying more heavily on their own knowledge rather than the choices of younger, less experienced women. This suggests that the balance of social learning is not stable across the lifespan and social learning effects may have their greatest influence when observers are young and relatively inexperienced: women may use social information when uncertain but use individual knowledge when they have relevant experience. In line with these arguments, younger women have been found to be more influenced by the choices of other women than older women in terms of mate preferences (Little et al. 2015).

Conclusion

In conclusion, a number of studies support the idea that women learn about mate preferences and choices from observing the preferences, attitudes, and choices of other women. There appear to be a number of sophisticated biases in humans that move beyond simple mate choice copying, such as preferential attention to the mate choices and preferences of attractive, prestigious, and older models. The social transmission of mate preference highlights the flexibility of women's preferences and the complex mechanisms that determine who we find attractive.

Cross-References

- [Cultural Evolution](#)
- [Cultural Transmission](#)
- [Facial Attractiveness](#)
- [Female Choice](#)
- [Long-Term Mating](#)
- [Social Learning](#)

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Mate Choice Criteria

► Men's Mate Preferences

Mate Choice Effects

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Synonyms

[Partner preference effects](#)

Definition

By suppressing ovulation, hormonal contraceptives alter men's and women's mate choices that depend on women's menstrual cycles.

Introduction

Men's and women's mate choices (i.e., mate preferences) vary according to the normal hormonal fluctuations associated with women's ovulatory cycles. Hormonal contraceptives, however, suppress ovulation by altering these normal hormonal fluctuations and thus affect men's and women's stated mate preferences. This entry will describe the (a) extent to which women's hormonal contraceptive use alters their mate preferences, (b) extent to which women's hormonal contraceptive use alters men's mate preferences, and (c) implications of these mate-preference alterations for men's and women's long-term relationships.

Hormonal Contraceptives Disrupt Women's Mate Preferences

A robust body of research demonstrates that women's mate preferences change across the ovulatory cycle (for a review, see Gildersleeve et al. 2014; for an alternative perspective, see Wood et al. 2014). For example, naturally cycling women demonstrate stronger preferences for cues of male genetic quality (e.g., masculinity, symmetry) near ovulation compared to less-fertile phases of their ovulatory cycles (Meltzer 2016; for a review, see Alvergne and Lummaa 2010; Gildersleeve et al. 2014; Little et al. 2008). Likewise, naturally cycling women display greater sexual attraction and responsiveness to mates whose major histocompatibility complex (MHC) genotype differs from their own MHC genotype near ovulation compared to less fertile phases of their ovulatory cycles (Garver-Apgar et al. 2006). The MHC genotype is a genetic marker of immune functioning, and mating with dissimilar-MHC partners can result in increased variability among and immunocompetence of offspring. Thus, women may reproductively benefit to the extent that they experience increased attraction to such mates at a time when they are most likely to conceive (i.e., ovulation). Moreover, naturally cycling women demonstrate a stronger preference for facial cues of health (e.g., pallor) in potential

mates during the luteal phase of their ovulatory cycles (i.e., when progesterone levels are highest and women's bodies are preparing for pregnancy; Jones et al. 2005). Notably, such facial cues may be indicative of men's immune system strength, and mating with such immunocompetent men would be beneficial for potential offspring.

Researchers have recently demonstrated, however, that women's hormonal contraceptive use can shift these preferences. Indeed, women who use hormonal contraceptives show weaker preferences for facial and vocal masculinity (for a review, see Alvergne and Lummaa 2010) and behavioral masculinity (Meltzer 2016), suggesting that hormonal contraceptives interrupt women's preference for masculine men (but also see Jones et al. 2018). Likewise, women who use hormonal contraceptives demonstrate a stronger preference for MHC-similar mates (Roberts et al. 2008) rather than MHC-dissimilar mates. Given the benefits associated with partner masculinity and MHC dissimilarity, such shifts in women's mate preferences could have negative consequences for offspring fitness. Interestingly, women who use hormonal contraceptives demonstrate a stronger preference for men's facial cues of health than do naturally cycling women – likely because hormonal contraceptives elevate women's progesterone and it is hypothesized that progesterone increases women's attraction to facial cues of health.

Hormonal Contraceptives Disrupt Men's Mate Preferences

Scholars previously posited that because women's ovulation is concealed, men's psychological processes (including their mate preferences) are not affected by women's ovulatory cycle. Recent empirical evidence, however, demonstrates that this may not be the case – there are subtle cues of women's fertility such as appearance, scent, and voice that influence men's mating behaviors, including men's preferences for and perceptions of women. For example, men report greater physical attraction to ovulating women (compared to less fertile women; for a review, see Alvergne and

Lummaa 2010), and they treat such women differently (Miller et al. 2007). Indeed, in a study of exotic dancers, men provided greater monetary tips to dancers near ovulation versus less fertile phases of their menstrual cycle (Miller et al. 2007). Likewise, men rate the scent of ovulating women as more attractive than non-ovulating women (Kuukasjärvi et al. 2004) and exhibit physiological changes such as elevated testosterone following exposure to the scent of ovulating women (Miller and Maner 2009). Additionally, men report an increased preference for women's voices near peak fertility compared to less fertile phases of the ovulatory cycle (for a review, see Alvergne and Lummaa 2010).

Recent research, however, has demonstrated that hormonal contraceptives indirectly alter these preferences. For example, men do not demonstrate an increased attraction to or preference for the mid-cycle scent (Kuukasjärvi et al. 2004) or voice (Alvergne and Lummaa 2010) of women using hormonal contraceptives. Additionally, in that study of exotic dancers, men did not provide greater tips mid-cycle to dancers who were using hormonal contraceptives (Miller et al. 2007). Together, this evidence suggests that women's hormonal contraceptive use influences men's mate preferences by suppressing women's naturally fluctuating hormones and thus the subtle cues of fertility associated with those hormones.

The Implications of Women's Hormonal Contraceptive Use for their Long-Term Relationships

The extant evidence clearly suggests that women's hormonal contraceptive use alters both men's and women's mate preferences and thus may have implications for the mates they choose. If this is indeed true, then women's hormonal contraceptive use could also have lasting implications for long-term relationships. Some empirical evidence is consistent with this notion.

Long-term relationships are long lasting and typically characterized by high levels of commitment. Given women's increased preference for and attraction to men who display cues of genetic

quality (e.g., masculinity, symmetry, MHC dissimilarity; Alvergne and Lummaa 2010; Garver-Apgar et al. 2006; Little et al. 2008), women are most satisfied to the extent that their long-term mates display such cues (e.g., Meltzer 2016). Because these preferences are muted among women who use hormonal contraceptives, however, there may be unintended consequences for women's long-term relationships. Many women begin long-term relationships while using hormonal contraceptives and thus choose their long-term partners while using hormonal contraceptives. But at some point during their relationships, women often discontinue using hormonal contraceptives in order to conceive. Other women, in contrast, choose their long-term partners while not using hormonal contraceptives and at some point during the relationship begin using hormonal contraceptives as they become sexually active. Any changes in preferences for partner genetic fitness associated with such changes in hormonal contraceptive usage may have implications for men's and women's long-term relationships.

Empirical evidence supports this notion. Women who use hormonal contraceptives when they meet their long-term partners and later discontinue those contraceptives report lower sexual satisfaction (Roberts et al. 2014) and relationship satisfaction (Russell et al. 2014) compared to those women who meet their long-term partners while using hormonal contraceptives and continue using those contraceptives (but also see Jern et al. 2018). Interestingly, the association between women's congruency in hormonal contraceptive use and relationship satisfaction depends on their long-term partners' facial attractiveness – women who meet their long-term partners while using hormonal contraceptives and later discontinue those contraceptives report increased relationship satisfaction if their partners have more attractive faces, but they report decreased relationship satisfaction if their partners have less attractive faces (Russell et al. 2014). This finding supports the notion that hormonal contraceptives influence women's long-term relationships because they potentially influence who women select as long-term partners.

Summary

Men's and women's mate preferences fluctuate across women's ovulatory cycles. Specifically, women demonstrate a mid-cycle preference for masculine and symmetrical men, and men demonstrate a preference for and increased attraction to ovulating women compared to less fertile women. Notably, these preference shifts likely have implications for the long-term partners that men and women choose. Hormonal contraceptives, however, suppress ovulation in women and consequently interrupt these effects. Taken together, this growing body of research suggests that hormonal contraceptives interrupt the evolved psychology of attraction, which may have maladaptive implications for offspring fitness and relationships in general.

Cross-References

- [Birth Control](#)
- [Concealed Ovulation](#)
- [Hormone Effects on Human Fetal Development](#)
- [Menstrual Cycle](#)
- [Ovulation Suppression](#)

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Mate Copying

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Synonyms

[Mate quality bias](#); [Mate-choice copying](#)

Definition

Choosing a romantic partner in part or wholly based on information provided via others' preferences and choices rather than relying solely on one's own judgment about the attractiveness and suitability of a potential mate.

Introduction

Choosing a mate is a complex decision for an individual to make: there are myriad personal characteristics that potential mating partners possess which can each affect the chooser's fitness. Some of these characteristics are physical traits which indicate high genetic quality, such as bilateral symmetry and cues to sex hormone levels. Others include a potential mate's likely ability to negotiate their social world to their own benefit and to secure food and other resources. The large number of personal attributes that must be weighed-up in mate choice decisions means that individuals are likely to vary in their skill at choosing the best partner. The best partner in an evolutionary context is defined as the partner who through genetic, parenting, resource and other contributions will maximize the chooser's reproductive success. To make mate-choice decisions even more difficult, some desirable traits are not easy to observe directly: it is difficult to acquire information about personality traits that may contribute to offspring survival and success. For these reasons, evolutionary biologists hypothesized and

Mate Competition

- ▶ [Intrasexual Violence and Aggression](#)
- ▶ [Parental Investment and Sexual Selection](#)

mathematically modeled whether fitness could be maximized by choosing the partner that *other* individuals select as the best partner (mate-choice copying), even if they have made the wrong choice and chose a lower quality partner through copying rather than making an independent assessment. These mathematical simulations suggested that copying others' mate choice decisions can evolve even in cases of mistakenly copying someone who has made a poor choice, because the worst case scenario is that a mate-choice copier will only do as badly as their reproductive competitor (Losey et al. 1986).

Evidence for Mate-Choice Copying

Field research on mate-choice copying began in the 1970s, and by the 1990s evidence had shown that mate-choice copying occurs in a diverse array of birds and fish (reviewed in Witte et al. 2015). Most of this research focused on females copying other females, because in most of the species being studied females were choosier than males about mate quality (Bateman's principle). Early research was typically through field observational studies, but by the 1990s experimental research designs were commonly used to demonstrate mate-choice copying. In fish, experiments could be done by partitioning aquariums using clear plexiglas so that a courting or mating pair could be placed in close proximity while another potential mate was placed in the aquarium in a position that made them appear as the less-preferred male. Partitions would then be removed to assess whether females who were observing the situation were more likely to select the male who appeared to be the preferred partner (Dugatkin 1992). The convention in experimental mate-choice copying studies is to term the individual who is observing and will potentially copy another's choice the "observer" or "focal" female, the individual who is in a position to be copied is the "model," and the opposite sex individual is the "target."

The first published study in humans to directly address mate-choice copying was on what is colloquially called "the wedding ring effect", which is the idea that women prefer men who by wearing

a ring are signaling that they have been chosen for a long-term relationship and are likely to be capable of long-term commitment. The authors failed to find a female preference for men wearing a wedding ring, although this was hypothesized to be because marriage is a legal commitment that is difficult to dissolve (Uller and Johansson 2003). Most researchers studying mate-choice copying in humans have used picture-based preference methods modeled more closely on the experimental study designs being used in non-human research. For example, photos of pairs of models and targets were presented to observers as dating couples. These, and more realistic video-based study designs, demonstrated that humans too appear to mate-choice copy (Waynforth 2007; Jones et al. 2007; Yorzinski and Platt 2010), and that men mate-choice copy (Place et al. 2010), which mirrors recent theory and findings in non-humans: males mate-choice copy when they play a large role in parental care, and hence have more to lose by making a poor mate-choice decision. However, male mate-choice copying may have a lower fitness payoff for copiers if it increases competition for sexual access and sperm competition (Witte et al. 2015). Human mate-choice copying studies have demonstrated that not all individuals are equally prone to copying, for example, women who are younger and those with less sexual experience are more likely to copy (Waynforth 2007; Place et al. 2010; Little et al. 2015), and observers who are more physically attractive than the model and target are less likely to copy (Place et al. 2010; Yorzinski and Platt 2010; Little et al. 2015).

Conclusion

Although to date there is no published meta-analysis, there is growing evidence that humans mate-choice copy, and that it is a variable or facultative behavior depending on a number of factors, such as lack of prior sexual experience. Mate-choice copying research continues to develop into new avenues. One of these is whether individuals exploit mate-choice copying to deceive their competitors by serenading potential

partners who they do not prefer (Witte et al. 2015). Copying others' decisions is by no means limited to mate-choice. One example is following political leaders, where it has been suggested that the personal attributes and experience of a leader are less important in people's decisions about which politician to follow than evidence of others' support and enthusiasm for a leadership candidate: people copy each other's preferences for leaders rather than weighing-up their leadership abilities (Spisak et al. 2011).

Cross-References

- [Conditional Strategies](#)
- [Female Mate Choice](#)
- [Fluctuating Asymmetry](#)
- [Male Mate Choice](#)
- [Pair Bonding](#)
- [Secondary Sexual Characteristics](#)
- [Sex Differences in Same-Sex Aggression](#)

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Mate Deprivation Hypothesis

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Synonyms

[Male sexual coercion](#)

Definition

An evolutionary hypothesis explaining males' sexual coercive behaviors driven by limited access to potential mates.

Evolutionary perspectives provide various explanations for males' sexual coercive behaviors including physical and psychological abuse and physical and psychological aggression. Among them, rape as a specific form of physical aggressive behavior has been evaluated in the context of evolved psychological mechanisms and behavioral strategies to increase reproductive success. Within numerous attempts to explain rape, two different lines of accounts to rape in the evolutionary framework occur. According to one line, rape is an indirect (mal)adaptation or by-product of something else such as promiscuous sex (Symons 1979). Besides, rape is assumed to be a direct adaptation and an evolved mechanism to

maximize reproductive success. Direct adaptation perspective, therefore, implies that rape should be selected in our ancestral past because it results in successful reproduction.

Mate deprivation hypothesis (Thornhill and Thornhill 1983, 1991, 1992) asserts that rape is a specialized conditional mating strategy to maximize reproductive success. Thus, as an evolved mechanism, all males have the potential to use sexually coercive behaviors under certain conditions. Those conditions are defined as limited access to potential partners as a result of environmental and developmental forces such as lack of status, wealth, and/or physical attraction. Therefore, disadvantaged males in the competition to access mates use sexually coercive behaviors to maximize their reproduction success. Research on other animal species displaying sexual coercive behaviors provide indirect support for the hypothesis that rape is an evolutionary adapted behavioral strategy (e.g., Galdikas 2005). Furthermore, Thornhill and Thornhill (1983) reported that arrested rapists are more likely to belong to low socioeconomic status. In another study, it was also found that males from lower socioeconomic status are more likely to rape; besides, those males have higher learning disabilities and psychological disorders (Figueredo et al. 2000). Thornhill and Thornhill (1992) further argue that if rape is an adapted mechanism, then as an implication, sexual coercive behaviors should be arousing. Results of their studies with rape victims and offenders supported this claim (Thornhill and Thornhill 1992). Related to this, it is suggested that sexual coercion and/or female rejection to sexual attempts would not interfere with the sexual desire and performance (Thornhill and Palmer 2000). On the contrary to supporting evidence, some other theorists claim that the hypothesis currently lacks sufficient empirical support. For instance, rape is not a unique behavior for low socio-economic status males; rather rape instances can be found on all segments of status. Likewise, males belonging to low socioeconomic status are more likely to commit lots of different kinds of crimes (e.g., Alexander and Culligan 1979). Besides, mate deprivation hypothesis implies that since rape is

an adaptation to scarcity to reach mates, then males who commit rape should be relatively unsuccessful in their history to reach mates and sexual intercourse. However, it was found that males who commit more sexually coercive behaviors reported higher numbers of sexual intercourse history (Lalumiere et al. 1996). Besides, sexually coercive males in the same study reported more preference for multiple partners and casual sex suggesting that sexual coercion is used as an extreme short-term mating strategy instead of deprived access to mates. Kanin (1985) reported that sexually coercive males are more sexually deprived not because of limited access but because of higher anticipation which results in sexual frustration.

Cross-References

- ▶ [Evolutionary Perspectives on Rape](#)
- ▶ [Hostile Masculinity](#)
- ▶ [Sexual Coercion and Violence](#)
- ▶ [Types of Sexual Coercion](#)

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Mate Desertion

► Partner Desertion

Mate Expulsion

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Marital Satisfaction

Marriage is considered a reproductive union where love is pursued between two individuals. It is seen in every culture around the world (Brown 1991; Buss 1985; Buss and Schmitt 1993; Epstein and Guttman 1984; Shackelford and Buss 1997; Vandenberg 1972). This marital union is a complex state where two individuals tend to share space and begin to have one common life. Also, couples that are satisfied tend to stay together. Shackelford and Buss (1997) report that marital satisfaction is an adaptive function designed to help individuals determine if their relationship is a long-term relationship that should continue. Several factors influence marital satisfaction. From an evolutionary perspective, mate value discrepancies, infidelity, personality attributes, some mate guarding tactics, and abuse affect marital satisfaction (Shackelford and Buss 1997). Also, men's marital satisfaction is influenced by their partner's attractiveness.

Meltzer et al. (2014) report that men with attractive wives have higher marital satisfaction. When couples are dissatisfied, mate expulsion often occurs. For married couples, mate expulsion often takes the form of divorce. Divorce is largely universal, occurring in both industrialized and non-industrialized cultures (Betzig 1989; Marlowe 2010; Anderson et al. 2011). But, mate expulsion can also occur for non-married couples. That mate expulsion takes the form of a breakup since there is no union that has to be legally dissolved.

Frequency of Divorce and Breakups

Mate expulsion in the form of divorce in the USA occurs in 70% of marital relationships (Shackelford 2001). The divorce rate is so high because mate expulsion is adaptive. Mate expulsion allows a couple to end a relationship where the costs exceed the benefits and find a relationship with a different partner that provides more benefits than costs rather than worry about the reputational costs that may be associated with staying in a bad relationship and committing infidelity. This allows individuals to maximize their fitness (Shackelford and Buss 1997). There are sex differences in decisions to divorce also. Since women bear more biological costs in relationships and are choosier with respect to selecting mates (Bailey et al. 1994; Buss 2003), women are more likely to initiate a divorce (Brinig and Allen 2000).

Mate expulsion in non-marital relationships is also very common (Battaglia et al. 1998), and consistent with evolutionary theory, women are more likely to initiate the mate expulsion (DeLecce and Weisfeld 2016).

Infidelity and Mate Expulsion

Jealousy within a couple can be a potent indicator of dissatisfaction with the relationship. Men tend to be jealous and worry about their partners committing sexual infidelity, while women tend to be

jealous and worry about a partner's commission of emotional infidelity (Buss et al. 1992). Not surprisingly, infidelity in married couples is a leading contributor to divorce (Amato and Previti 2003; Scott et al. 2013). This occurs because our evolved sex differences in mating and parental investment are evoked which leads to becoming distraught over different forms of infidelity (Buss et al. 1992; Tagler and Jeffers 2013).

Emotional and Sexual Infidelity

Since women are the choosier sex because they need a higher parental investment from men (Trivers 1972), women tend to seek men who are good financial providers, stable, and emotionally supportive (Buss 1989; Li et al. 2002). So, women are more upset over a partner's commission of emotional infidelity (Wiederman and Kendall 1999) as a male's emotional connection with another woman can lead to a loss of resources and stability from the said male partner (Shackelford et al. 2005).

Since men invest primarily at the genetic level and worry about paternity certainty (Trivers 1972), men are more upset by a partner's commission of sexual infidelity. Female sexual infidelity can lead to a man being cuckolded and the maximization of another man's fitness. A partner's commission of these respective types of infidelity can lead to mate expulsion also.

Forgiveness, or Mate Expulsion

Depending on the type of infidelity committed by a partner, forgiveness or mate expulsion can occur. Since men are more upset by a partner's commission of sexual infidelity, men find it more difficult to forgive their partner if their partner committed sexual infidelity and are more likely to expel their mate for committing sexual infidelity rather than for committing emotional infidelity. Because a partner's commission of emotional infidelity is more upsetting to women, women find it harder to forgive a partner for committing emotional infidelity and are more likely to expel a mate if the mate committed emotional infidelity rather than if the mate committed sexual infidelity (Shackelford et al. 2002).

Access

Emotional and Sexual Access

Emotional access and sexual access each play a role in mate selection. Men seek and desire female partners who are willing to have sex with them (Buss 1989; Buss and Schmitt 1993). Thus, Buckle et al. (1996) and Betzig (1989) report that men place a premium on a woman's capacity to reproduce. Consistent with this, Shackelford and Buss (1997) report that competition among men for sexual access to reproductively valuable women is more intense than competition among women for reproductively valuable men. Therefore, perhaps not surprisingly, Sprecher and Cate (2004) report that men are less satisfied overall when their wives are sexually withholding. Similarly, Buss (1989) reports that men report the greatest anger and upset over women who accepted resources from them but did not provide sexual access in return. Consistent with this, Felmlee et al. (1990) report that sexual intimacy is a positive predictor of relationship steadiness. Further support for the importance of sexual access is the fact that marriages that involve successful reproduction are more likely to continue (Becker et al. 1977; Waite and Lilliard 1991), and some societies allow mate expulsion, that is, divorce, on the basis of a partner's refusal to have sex (Betzig 1989).

Women typically desire a long-term commitment from a male partner, and commitment is a product of emotional involvement (Buss et al. 1992). So, women seek and desire men who are willing to share their feelings/show they care or are committed, i.e., they are emotionally accessible. Since sexual and emotional accessibility are important for men and women, respectively, these factors should play a role in mate expulsion decisions.

Wade and Brown (2012), using scalar measures, found that women were most likely to expel their mates when their partner was emotionally inaccessible 90%, 80%, 70%, and 60% of the time, and men were more likely to expel their mates when their mates were sexually inaccessible 60% of the time. Similarly, Wade and

Mogilski (2013) examined the role of sexual and emotional access in mate expulsion using conjoint analysis and report that men are most likely to expel a mate when there is a low level of sexual access and women are most likely to expel a mate when there is a low level of emotional access; and overall, sexual access is more important for men's mate expulsion decisions than for women's mate expulsion decisions and emotional access is more important for women's mate expulsions decisions than for men's mate expulsion decisions.

Sexual Conflict

Frequency of Sex and Sexual Satisfaction

Sexuality in personal relationships results from an underlying motivation to maximize the transmission of one's genes to succeeding generations (Sprecher and Cate 2004). Thus, Americans consider sex an essential element of relational intimacy that is crucial for ensuring longevity (Michael et al. 1994; Rubin 1990). Thus, sexual intercourse is extremely important. Engaging in sexual intercourse has a significant and positive effect on relationship stability (Simpson 1987). Consequently, as Elliott and Umberson (2008) report, sexual activity in the context of long-term heterosexual relationships may be an important site of relationship vitality and conflict. Sexual frequency is also important. Call et al. (1995) report that a higher frequency of sex is associated with a happier marriage, and happier marriages are less likely to lead to mate expulsion. Furthermore, Sprecher and Cate (2004) report that large discrepancies between the desired and actual frequency of sex are associated with lower relationship satisfaction, and Blumstein and Schwartz (1983) report that this applies to all couples. Similarly, Hunt (1974), Laumann et al. (1994), and Trussell and Westoff (1980) report that couples who have a higher frequency of sex are more sexually satisfied. Thus, sexual satisfaction is also important. Sprecher and Cate (2004) point out that when individuals are satisfied sexually within their relationships, the relationships are more likely to be committed and to continue.

Mate expulsion should be less likely when couples are sexually satisfied, i.e., when there is no sexual conflict.

Most individuals in committed relationships are sexually satisfied. Laumann et al. (1994) report that 88% of married respondents report being extremely physically pleased in their relationships. Similarly, Greeley (1991) reports that one third of respondents report a very great deal of satisfaction from their sexual relationships. Both dating and married couples who are sexually satisfied also report high levels of overall satisfaction with their relationships (Blumstein and Schwartz 1983; Byers et al. 1998; Cupach and Comstock 1990; Davies et al. 1999; Edwards and Booth 1994; Henderson-King and Veroff 1994; Sprecher 2002). Additionally, White and Keith (1990) report that sexual problems or dissatisfaction at one point in marriage are positively associated with the likelihood of divorce later. Similarly, Long et al. (1996) report that sexual conflict is negatively related to sexual and relationship satisfaction. Love, commitment, and the likelihood that a relationship will last are also positively associated with sexual satisfaction (Aron and Henkemeyer 1995; Grote and Frieze 1998; Pinney et al. 1987; Sprecher 2002; Sprecher et al. 1995; Sprecher and Regan 1998; Waite and Joyner 2001; Yela 2000). Not surprisingly, then, changes in sexual satisfaction lead to changes in relationship satisfaction (Sprecher and Cate 2004) which then can lead to mate expulsion.

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Mate Guarding

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Mate Poaching

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Synonyms

[Mate-Stealing; Non-Independent Mate Choice](#)

Definition

Mate poaching is engaging in premeditated behaviors to attract either short-term or long-term mates by luring them away from their already established relationship.

Introduction

Generally, mate poaching refers to behaviors whereby one attempts to romantically attract an individual away from an existing monogamous

relationship. Mate poaching has been defined in two different ways in the literature, with the second definition serving as a clarification of the first definition. Schmitt and Buss (2001) originally defined mate poaching as the process of romantically attracting someone who is already in a relationship. However, Davies et al. (2007) pointed out that Schmitt and Buss' (2001) definition allowed for an overestimation of the frequency of mate poaching, because it did not specify two important criteria that are necessary for mate poaching to have occurred. Davies et al. (2007) stipulated that the relationship must be exclusive such that sex with an individual other than one's partner invalidates the relationship, and poachers must know that the relationship they are poaching from is exclusive. Thus, Davies et al. (2007) revised the definition of mate poaching such that it is said to occur when a person has attracted, or tried to attract, a mate whom they know is already in an existing exclusive relationship, in order to form a new sexual or romantic relationship. Further issues related to definition are discussed by Davies et al. (2019).

It is helpful to distinguish mate poaching from other forms of romantic attraction. Mate poaching is distinct, because it presents costs that are not found during typical, early stages of relationship initiation or romantic attraction. For example, in addition to the potential rejection by the person one approaches, the person's mate may learn of the attempted poaching and seek retaliation. These costs are further discussed in the following sections. Mate poaching also entails a specific set of personality characteristics, which are presented in an upcoming section.

Evolutionary psychology offers a way to make sense of mate poaching. Mate poaching is a form of nonindependent mate choice that is an adaptive solution to the problem of locating a mate of suitable quality from the local pool of those whom are currently available. For men, this problem is thought to have been frequently occurring in ancestral environments where women, in particular, were mated early in life, pregnant much of their lifetime, and/or in situations involving polygyny where a few men dominated local mating contexts. For women, it would have been an adaptive solution to issues around resource

control, such that women could try to invade an existing relationship to secure a mate with ownership of limited resources. Those resources, in turn, may positively have impacted on their ability to successfully bear and raise children, thereby improving their reproductive success and fitness.

Putting all of these ideas together creates an interesting and unique mating-related situation. Mate poachers (i.e., those who poach someone's mate) are theorized to engage in premeditated behaviors to attract either short-term or long-term mates via luring them away from their already established relationship (Moran and Wade 2019; Schmitt and Buss 2001). Mate poaching involves covert behaviors and indirect tactics, unlike other forms of romantic attraction, due to the potential risks involved in luring an already involved mate. Furtive glances, moving into one's social network, and encouraging the target to realize the problems and dissatisfaction with their existing relationship are examples of the sorts of covert behaviors a poacher may perform. The discrete nature of romantic attraction is key, as direct flirting may lead to violence by an existing partner and be seen as in poor taste by the general social community (e.g., Schmitt and ISDP 2004). Of these various strategies of mate poaching, becoming the intended poachee's friend is viewed as a very effective strategy which mitigates risk. However, individuals who use that strategy are perceived by others as less warm, less nurturant, and less friendly than those who merely make the acquaintance of the poachee (Mogilski and Wade 2013).

Occurrence and Prevalence

Estimates regarding the prevalence of mate poaching vary, partly due to whether it is examined with respect to whether one attempts to lure a short- versus long-term mate, or whether it includes any experience versus frequent experience. For example, in a sample of US college students and older adults (average of 41 years), Schmitt and Buss (2001; study 1) report over 70% had experience in attracting an already involved partner, with about equal experience in attracting short- versus long-term mates. Almost 30%

reported frequently trying to attract long-term mates, while 10% frequently attempted to attract short-term mates. Mate poaching specifically, though, was lower, with about 50% having some experience in short- or long-term relationships, with few stating they had frequent attempts. Their sample reported that rate of poaching toward oneself was higher, with an estimated 85% of people reporting someone had attempted to poach them (Schmitt and Buss 2001).

There are some noteworthy sex differences. Schmitt and Buss (2001) found men (60–64%) are more likely to have attempted to poach a short-term mate than women (38–49%, depending on age). As an interesting aside, they reported that mate poaching tactics are perceived to be less effective when one attempts to infiltrate an existing highly committed relationship compared to less committed relationships.

Davies et al. (2007) argued that these frequencies from Schmitt and Buss (2001) may be overestimates due to differences in their definition. They later reported their sampling procedure may also be responsible; using a similar procedure, Davies et al. (2019) found no significant difference in frequencies, as compared Schmitt and Buss (2001).

In addition to the possible causes of variation in prevalence already mentioned, geographic location (as a proxy for culture) is an important consideration. Across a large sample (i.e., 53 nations, almost 17,000 participants), Schmitt and members of the International Sexuality Description Project (2004) found mate poaching was most common in Southern Europe, South America, Western Europe, and Eastern Europe and was relatively infrequent in Africa, South/Southeast Asia, and East Asia. Men were more likely than women to report having made and succumbed to short-term poaching across all regions, but the differences between men and women were often smaller in more gender-egalitarian regions. That is, similar to the rates reported using the US samples, Schmitt et al. (2004) document around 62% of men and 40% of women have attempted to attract someone who was already in a relationship with someone else for a short-term sexual relationship. However,

they argue that cultural differences exist: short-term poaching is less among East Asian men (around 29%), and under 30% for women from Middle East, Africa, South/Southeast Asia, and East Asia. Men seldom engage in long-term mate poaching, with rates higher for women, although there are cultural differences in effects due to sex (i.e., Oceania shows minimal difference whereas Africa shows large differences).

Those who attempt to mate poach tend to be moderately successful at a rate of 65% or higher (Schmitt et al. 2004, Table 4). Women are generally more successful at short-term mate poaching than men (particularly in Western Europe; 90% vs. 84%) but typically not significantly so, with the exception of Africa that shows the reverse trend (65.9% vs. 78.6%). The occurrence and prevalence of poaching for long-term relationships is similar for men and women, with no significant sex differences except for South America where more men report it ever happening (86% vs. 72%), and happening more often. They also found that about 70% of the sample worldwide reported receiving someone's mate-poaching attempt.

Some scholars document minimal sex differences in prevalence rates of mate poaching, which is in contrast to the abovementioned research findings. While the literature on infidelity shows men report higher rates than women, poaching is reported nearly equally by the sexes. However, women, but not men, may show a distinct, increased interest in men who are involved in a relationship. That is, Parker and Burkley (2009) suggest mate copying may be a possible explanation for women's interest in mate poaching. Their experimental evidence shows men are interested in women to the same degree regardless of whether they are single or not, while single women are more interested in pursuing men who are attached than single. By engaging in mate copying, women are ensuring that the mate has been "pre-screened" for quality, resourcefulness, and willingness to commit to a family life, by another woman. This finding does not imply that men are immune from mate copying; Moran and Wade (2019) report that men are more likely to engage in mate copying when a couple is

composed of a man who is more attractive than his partner. This pattern occurs because men view the woman in this couple as possessing very high qualities since she was selected by this highly attractive man. Finding and starting a relationship with a woman with characteristics similar to the woman in this couple would potentially confer benefits to the male copier's future offspring.

Costs Associated with Mate Poaching

Mate poaching is a form of mating competition, and as such, it can lead to various forms of retaliation from the person who loses the mate. There may be immediate repercussions for poaching via violence or other forms of aggression. There may be also a decrease in social standing, given one has breached social norms around exclusivity and relationships (see Sunderani et al. 2013, for discussion).

The poachers who are themselves currently in an existing, exclusive romantic relationship must deceive their partner. They may lie or manipulate their partner, keep themselves out of close proximity to the partner (e.g., "be away for work"), establish their independence (e.g., "I need space"), and perhaps increase their affection and resource allocation toward the current mate in an effort to avoid drawing suspicions of infidelity (Schmitt and Shackelford 2003).

It may also lead to the presence of future infidelity concerns and feeling uncertain about the future of the relationship. There are other costs, too, such as feeling guilty, issues around deception and lying, hiding the relationship, and potential rejection by one's family (Schmitt and Buss 2001). Individuals who then form a relationship with the poacher (or person poached) may experience feelings of jealousy, emotional pain, anxiety, and sadness; they may face serious risks due to these emotions such as intimate partner violence and homicide (see Sunderani et al. 2013, for discussion).

For men, there are also costs related to potentially depleting their resources while engaging in poaching behavior, especially if those resources could be used more productively to gain access to,

and retain mates. Men who lose their partner to a mate poacher face further costs, not only do they experience the loss of a mate (i.e., the poached individual) but also they risk losing any invested resources. Misallocated investments may also stem from the possibility of raising a child who is genetically unrelated, if their partner is poached, becomes pregnant, and then returns to the relationship.

Both sexes face the increased risk of illness; as one accesses new sexual partners, risks of sexually transmitted infections and diseases increase. There is also an increased probability of partner's future infidelity, if they were successfully poached in the past. Women face additional costs of potential unwanted pregnancy, as well as potential feelings of self-degradation, and concerns about future infidelity (Schmitt and Buss 2001).

Reasons to Poach a Mate

The reasons to poach a mate vary. Schmitt and Buss (2001) found several potential reasons, as follows. First, within a long-term context, men may be enticed by a woman's physical attractiveness while women may be enticed by a man with resources. Indeed, highly attractive women are more likely to be the targets of mate-poaching attempts and less likely to remain faithful in a relationship. Women do not show the same benefit of gaining an attractive mate via poaching although men who are targeted by poachers self-report they are physically attractive (Sunderani et al. 2013). Men also report a potential benefit of gaining access to a variety of sexual partners, as well as easy sexual access within short-term mate poaching contexts. Thus, sexual variety, attracting a beautiful partner, and freedom from responsibility for men are considered short-term benefits (Schmitt and Buss 2001).

Men do not consider receiving resources as beneficial as women do, or consider gaining a partner with the ability to accrue resources as beneficial. Interestingly, the benefit of receiving immediate resources was considered strongest in women considering short-term mate poaching, as opposed to long-term mate poaching. Women also

reported the additional reasons of taking revenge on a rival and gaining an already proven mate.

Personality of Mate Poachers and Those Who Are Poached

Schmitt and Buss (2001) examined various personality traits in relation to mate poaching. They found that agreeable and conscientious (i.e., care and think about other's feelings) people are significantly less likely to be poachers regardless of sex. Further, those who self-describe as having erotophilic dispositions more likely to have tried to poach. Individuals who reported success at poaching generally are more sexually attractive and lack sexual exclusivity. Extraverts and those open to experience receive more mate-poaching attempts, as do those who describe themselves as being emotionally investing in a relationship. Disagreeable, unconscientious, and neurotic individuals tended to accept mate poachers' advances, as did those describing themselves as mean, unreliable, adulterous, masculine, and unloving.

A lower level of conscientiousness is associated with increased sexual risk-taking, as well as perceived benefit of such behaviors. The lack of empathy linked to being unconscientious, higher disagreeableness, and disregard for others' well-being may empower individuals to poach a mate when faced with an opportunity and decrease their perception of any associated costs (Mitchell et al. 2019). Indeed, Foster et al. (2014) report that poachers tend to have more uninhibited sexual attitudes and behaviors. Poachers of both sexes self-report a higher number of lifetime sex partners, more lifetime casual sex partners, and more lifetime dating partners (Arnocky et al. 2013).

Sunderani et al. (2013) report that men who poach are better looking, taller, and have higher cortisol levels, which is a hormone that has been linked with impulsivity and extroversion. They also have higher self-esteem, which may lead them to believe they will be more successful at poaching and subsequently more likely to attempt to poach. They have higher criminal tendencies and more of a cold affect (i.e., little concern about others). They suggest that these characteristics

enable the individual to behave without feeling empathy or facing moral objections with respect to poaching. They also surprisingly found that men with lower levels of testosterone were more successful at mate poaching, which requires further study. In contrast, they found for women who poach, the only important factor is that they are attractive.

The dark triad of personality traits (DT) also matters. Kardum et al. (2015) reported that the DT predicts mate poaching experiences better than the Big Five traits, which are openness, conscientiousness, extraversion, agreeableness, and neuroticism. These authors report that the DT trait of psychopathy and the Big Five trait of extraversion are the most consistent predictors of mate poaching experiences. However, there are also noteworthy sex differences. The DT better predicts being the target of a poaching attempt in women and being successfully poached in men. Also, the Big Five traits better predict success at mate poaching for men.

The relationship between personality and mate poaching is small to moderate, according to Kardum et al. (2018). Poaching attempts, poaching success, and being the target of poaching appear to be more strongly related to personality than being successfully poached or being the victim of poaching. They further report that the link between mate poaching and personality are cross-cultural and similar in both short- and long-term relationships.

Targets of Mate Poaching

There are particular qualities of individuals who make them more susceptible targets for being poached. For example, tactics related to mate poaching are perceived to be more effective when the relationship where someone is being poached from is long-distance, not committed, about to end, or that is a dating relationship (Schmitt and Buss 2001). The specific role of the type of relationship within a mate poaching context depends on the tactic. Women are viewed as most effective when they use tactics related to emphasizing their physical appearance, while

men are seen as most effective when they emphasize their resources and generosity. In short-term contexts, women are perceived to be most effective when they advertise, provide, and arrange easy sexual access. Men who manipulated the emotional fidelity of the existing male partner were seen as effective at poaching, while women who manipulated the sexual fidelity of the existing female partner were also seen as effective (Schmitt and Buss 2001).

Individuals who are extraverted and high in openness (sensation seekers), sexy, adulterous, or high in neuroticism are typical targets also. There may be sex differences also. Moran and Wade (2019) report that men are most likely to attempt to poach from a couple where there is a discrepancy in the attractiveness of the members of the couple. Specifically, men are more likely to attempt to poach from a couple where the woman is more attractive than her partner, and men think that a poaching attempt towards this type of couple will be most successful. The duration of the relationship matters also. Moran et al. (2017) and Moran and Wade (2019) report that for short-term mating, men are more willing to poach women who are more attractive than the mates those women are involved with in a relationship.

Disguising Mate Poaching

Since mate poaching can have dire consequences for mate poachers if their behavior is detected, individuals may disguise their poaching attempts. Tooke and Camire (1991) point out that men in particular use a complex repertoire of deceptive tactics to gain access to reproductively viable women. Schmitt and Shackelford (2003) specifically examined tactics within the context of mate poaching, first within the context of how people signal an openness to being poached and then in terms of disguising their poaching.

In the first part, they asked students (11 men and 18 women) to nominate behaviors that they think people perform while already in a relationship to let others know they are open to another relationship. The participants were asked to consider behaviors one might do to advertise an

interest in short- and long-term relationships. Then, they asked students (26 men and 46 women) to rate the effectiveness of the behaviors in signaling interest in a new relationship. They found the most effective tactics for men seeking a short-term relationship were to enhance the potential mate (e.g., boost her ego, compliment her, tell her she deserves someone better), use humor, and be generous (e.g., show they are caring, polite, helps her with work or chores), while for women, it was arranging and providing easy sexual access, and enhancing the potential mate. For men, seeking a long-term relationship effective tactics were the same, while for women, it was to develop emotional closeness (confide in him, try to be a good friend, discuss mutual interests), mention they are looking for a replacement mate, and being generous.

In the second part, they again used an act nomination approach and asked students (20 men, 37 women) to list ways people disguise mate-poaching attempts for short- and long-term relationships. The poachers were stated to currently be in a relationship and who are attempting to disguise their actions in order to maintain that relationship. Then, another group of students (36 men and 44 women) rated the effectiveness of the tactics. The results indicated that the most effective ways to disguise mate-poaching attempts by men are as follows: talk with current partner about their future together as a family, pay closer attention to their current partner, keep constant watch on their current partner to see if they have suspicions, have deep emotional talks with their current partner, spend more quality time with the current partner, pretend one is happy with the current partner, spend less time away from the current partner, tell the current partner he is satisfied with their relationship, and do not discuss the new partner with anyone.

The researchers also examined what the most effective ways for women to disguise their poaching attempts are. Like men, many of these tactics are oriented toward their current romantic partner, such that they are attempting to maintain that relationship. The tactics are: maintain her daily routine to avoid causing suspicion, do not change her physical look, always return home at

same time each day, wear her relationship (e.g., wedding, engagement, promise) ring all the time, do not discuss the new partner with anyone, become more romantic with the current partner, attend fewer parties so as to be seen less, have sex more often with the current partner, rekindle the romance of the current relationship, and do not act like anything is different.

The authors also examined how many of these actions are also effective for men and women to keep their social community from knowing they are engaged in mate poaching (Schmitt and Shackelford 2003). However, while there is overlap in some tactics, there are also tactics that seem specifically oriented toward hiding information about the mate poaching from one's social community. For men, the most effective ways are as follows: do not discuss the new partner with anyone, keep a constant watch on the current partner, think before he speaks in public, have deep emotional talks with the current partner, spends less time away from the current partner, behave affectionately toward the current partner, talk with the current partner about their future together as a family, pretend he is happy with the current partner, and get the current partner pregnant.

A similar list was obtained for women; the most effective ways for women to disguise their poaching attempts are as follows: maintain her daily routine, do not change her physical look, always return home at same time each day, do not act like anything is different, keep her conversation routine and not talk about what is really going on in her life, never tell anyone about her new partner, keep the current partner sexually satisfied, wear her relationship ring all the time, behave affectionately toward the current partner, and rekindle the romance of the current relationship.

Schmitt and Shackelford (2003) concluded that overall, women are most effective at mate poaching when they advertised or provided sexual intimacy and discounted improvements in physical appearance. Women were seen to be most effective at disguising their mate poaching when maintaining daily routines. For men, the most effective tactics are when they advertised their resources and used tactics related to establishing an emotional connection. The best disguise for

men was when they talked to their current partner about their future together as a family.

Some of these findings have been recently replicated. For example, Moran and Wade (2017) performed a two-part study. In study 1, they asked heterosexual men to nominate acts they would use to mate poach someone specifically for a short-term relationship. In study 2, men and women reported which of those acts would be most effective. The most effective acts were spending time together, being attentive, being compassionate, helping her with her problems, and complimenting her. The authors propose these acts, when performed by men, signal altruism and emotional commitment, which women prefer in mates.

Relationships Outcomes

Despite the volume of research on mate poaching, there has been a dearth of investigation into the quality of relationships involving poached individuals. Two studies are worth noting, though, that address this issue.

Foster et al. (2014) examined the relationship quality of 138 heterosexual young adults over a 10-week period. They reported that poached individuals perceive potential relationship alternatives to be higher in quality and have more infidelity in their current relationship than non-poached individuals. Poached individuals are less committed to their current relationship and less satisfied overall, as compared to those who were not poached.

Belu and O'Sullivan (2018) extended this prior work by examining a variety of issues related to relationship quality in 675 heterosexual adults, which included a specifically solicited sample of those with mate poaching experience. They report individuals in romantic relationships formed by poaching rated their relationships as having lower satisfaction, commitment, and trust, higher jealousy, and higher rates of emotional and sexual infidelity compared to those in non-poached relationships (Belu and O'Sullivan 2018; largely replicating Foster et al. 2014). Further, those who were poached compared to those who did the poaching also rated their current relationship as lower in commitment (Belu and O'Sullivan

2018). The link between poaching and relationship quality is influenced by sociosexuality. Poachers tend to have more permissive and less restrictive views of sexual behavior, and require less commitment which is often the cornerstone of exclusive relationships. Thus, is it not surprising that mate poachers have an increased probability of engaging in an infidelity while in a relationship (Belu and O'Sullivan 2019).

Sexual Versus Emotional Mate Poaching

One area for future research may be to further investigate how mate poaching may occur in sexual versus emotional contexts. Research into infidelity has typically examined it in terms of whether the behaviors relate to sexual infidelity or emotional infidelity. Mitchell et al. (2019) extended this work by examining sexual versus emotional mate poaching. They report that mate poachers who engaged in sexual intimacy with their poached partner differed the most from those who did not poach their current partner on several dimensions, including higher antagonism, disinhibition, risk-taking, and lower humility and honesty. They further documented that men who engaged in sexual intimacy with their poached partner reported higher levels of detachment, antagonism, disinhibition, psychopathy, and lower levels of conscientiousness, humility, and honesty. The authors suggest that this combination of traits may allow a mate poacher to maintain a physical relationship with an already partnered individual because it includes a willingness to deceive and manipulate others for personal gain, and the discounting of potential costs.

For comparison, men who engaged in emotional mate poaching still reported high levels of antagonism, disinhibition, and ethical risk-taking, and lower scores for humility and honesty than non-poachers. However, their scores were lower for ethical risk-taking than men who engaged in physical mate poaching. The researchers propose that the differences between the two poaching groups may be due to seeking alternative paths to poaching. That is, men who engage in emotional mate poaching may be attempting to establish a romantic bond with trust rather than sexual

access. Women, for comparison, did not demonstrate as many differences between the two forms of poaching as men, and most of the traits were not exhibited as strongly as men.

Conclusions

In this entry, we briefly reviewed the extensive literature on mate poaching. Our review started with issues surrounding differences in definitions of the behavior, and how it is distinct from other forms of romantic attraction. We then discuss prevalence, showing that there is cross-cultural variation in mate poaching, but also differences according to an individual's sex and according to whether one examines any poaching experiences or frequent experiences. The considerable costs associated with mate poaching were reviewed, followed by a discussion about the potential benefits one may receive. We then shifted our focus to present an overview of some of the findings about personality of those involved in mate poaching relationships, as well as characteristics of targeted individuals. Research on how mate poaching may be disguised was reviewed, along with details about some of the tactics men and women are thought to use. We presented the small body of research on the outcomes of relationships that started with one individual being poached. We then ended our review with an example of an area for future research, which is the examination of mate poaching along sexual versus emotional lines, akin to the large corpus of work on infidelity. Collectively, our review demonstrates the variety of ways mate poaching has been explored using the lens of evolutionary psychology and how the topic has changed in scope over time.

Cross-References

- ▶ [Costs and Benefits of Mate Poaching](#)
- ▶ [Personality and Mate Poaching](#)
- ▶ [Sexual Jealousy](#)
- ▶ [Sneak Copulation](#)
- ▶ [Use of Mate Retention Strategies](#)

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Mate Preference Copying

► Mate Choice Copying

Mate Preferences

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Synonyms

Desires in mating; Mate choice; Mate selection

Definition

Mate preferences are the outputs of psychological mechanisms designed to motivate people to

pursue potential mates who possess particular qualities. Preferred features range widely. They include morphological (e.g., face or body shape), behavioral (e.g., kindness or dominance), or social (e.g., status or connections) attributes. Mate preferences can be species typical, sex differentiated, individually variable within sex, culturally variable, and predictably context dependent.

Introduction

Human mate choice is not random. Given the choice between a kind healthy partner and a disease-afflicted cruel partner, most people would prefer the first over the second. These preferences determine who we are attracted to, who we pine for during absences, and who we write books, plays, songs, poems, and films about. They affect who we select as mates; who we live with, support, and receive support from; and, for some, with whom we raise children. They influence who has experienced mating successes and failures in our evolutionary past, which is key to which qualities increase or decrease in frequency over time. Given this monumental importance, it is appropriate that mate preferences have been one key cornerstone of evolutionary psychological research. This research uses an understanding of what preferences are *for*, that is, their evolved functions, to understand what human preferences are *like*, that is, their content and nature. The study of mate preferences has thus far been extraordinarily successful, generating a large body of knowledge on the content of human desire across cultures and across contexts.

Why Do Mate Preferences Evolve?

Understanding mate preferences first requires an understanding of why they evolve. Humans are a sexually reproducing, social species who bear offspring who are initially helpless and dependent on parental investment for nearly two decades. For our species, a mate is thus a reproduction partner, a potentially valuable cooperation partner, a source of social connections, a parenting

partner, and more. Who an ancestral human selected as a mate would have had direct impacts on that person's health, their resources, their status, the parenting their children received, the traits their children inherited, and, ultimately, through these many routes, their reproductive success. Selection would have strongly favored the evolution of adaptations capable of guiding their holders toward fitness-beneficial partners because individuals with these adaptations would have greatly outcompeted their reproductive rivals.

The challenge for sexually reproducing organisms in mate selection is that they have no way, *a priori*, to determine which mates offer fitness benefits and which mates inflict fitness costs. Potential mates vary on innumerable trait and state dimensions. Some mates are larger than others; some have longer limbs. Some control more resources; others command more status. Some mates are kinder than others; some are more outgoing. Some mates have a larger ratio of dirt on their upper body relative to their lower body. Some have a higher or lower speed of fingernail growth. Only a miniscule subset of the infinitely many dimensions along which potential mates differ would actually be relevant to the net fitness benefits a potential mate offers.

Even if an organism could, against astronomical odds, guess which dimensions of variation should be relevant to its mate selection, it would have no means to know the valence the dimensions should be assigned. Is it better to have a large mate or a small mate? Do older mates offer more fitness benefits than younger mates? Does a healthy mate offer more fitness benefits than a wealthy mate? The answers to these questions will depend on species, sex, mating strategy, and context. A naïve organism could search the environment for its entire lifetime and still never determine the correct valence to assign to even one dimension along which potential mates vary.

So sexually reproducing organisms face a critical adaptive problem in selecting mates who offer them the largest net fitness benefits. Solving this problem appears to be computationally intractable. Each organism has an infinite number of dimensions of variation along which it could evaluate potential mates and an infinite number of

valences it could assign to each dimension. How, then, do organisms ever solve the adaptive problem of selecting fitness-beneficial mates?

One potential solution to the problem of mate choice is mate preferences. Although organisms may never *know* what dimensions of variation it should use to guide its mate selection, random mutations will eventually cause some organisms to have motivational biases in favor of pursuing mates with particular features. Most of these random preferences will motivate organisms to discriminate among potential mates along inconsequential dimensions or with nonfunctional valences. But a very small proportion of these mutations will cause organisms to be motivated to pursue mates who possess fitness-beneficial features or to avoid mates with fitness-harmful features. Those individuals who happen to develop functional mate preferences will be attracted to beneficial mates and, over deep time, will be more likely to select adaptive mates and experience reproductive success. In this way, genes underlying preferences for fitness-beneficial features will tend to reproduce themselves over time, causing sexually reproducing organisms to accumulate mate preferences for fitness-beneficial features.

How Do Mate Preferences Evolve?

The evolution of mate preference adaptations will be favored by selection to the extent that these preferences guide organisms to fitness-beneficial partners. There are at least two routes through which preferences could provide fitness benefits: direct benefits delivered to the mate selector and indirect benefits delivered to the mate selector's kin.

Direct benefits delivered to the mate selector. The most obvious and likely most frequent route to the evolution of mate preferences is through the receipt of direct benefits. Preferences offer direct fitness benefits when they guide organisms to mates who offer fitness benefits directly to the mate selector. A classic example is nuptial gifting in insects. Female katydids prefer to mate with males who offer them

“spermatophores”: packages of food which the females consume during mating. These spermatophores are extremely energetically dense and provide females the energy they need to survive and reproduce. Because these spermatophores meet all of the females' energetic needs, females who are provisioned can focus their time and energy on reproduction rather than foraging. The preference for males who provide spermatophores therefore provides katydid females a direct fitness benefit by allowing them to increase their own rate of reproduction.

Nuptial gifts concern the explicit exchange of benefits between mates; however, direct benefits can also come from less tangible sources. For example, males of many reptile species prefer to mate with larger females (e.g., Shine et al. 2001). These preferences appear to evolve because larger females are generally able to produce more eggs. Males who prefer to mate with larger females consequently receive a direct fitness benefit in that they can produce more offspring with their mates.

What is key about direct fitness benefits is that they increase the reproduction of the mate selector. These fitness benefits can be in the form of mates who offer resources or offspring provisioning that allow the mate selector to direct extra time and energy to reproduction. Benefits can come from access to prime territories or social groups that provide shelter or resources. Or they can come from access to fertile partners with whom the mate selector can produce many offspring. Securing any of these features in a potential mate will allow the holder of a mate preference to produce more offspring and thereby better reproduce the genes underlying their preferences.

Indirect benefits delivered to the mate selector's kin. The benefits of mate preferences need not go directly to the mate selector; fitness benefits can also flow indirectly by benefitting the kin of the mate selector. Selection can, for instance, favor the evolution of preferences for heritable features of potential mates if these preferences lead to offspring who are healthier, more fertile, or more successful in acquiring mates. One commonly hypothesized preference for this class of benefits across species involves the preference for

symmetry (Møller and Pomiankowski 1993). Many species are, by design, bilaterally symmetric: morphological traits on the left half of the body are supposed to be mirror copies of traits on the right half. Although this is the norm at the species level, few if any individuals are ever perfectly symmetrical. Individuals will tend to show random asymmetries throughout their bodies. Among birds, for example, although wings are of equal length on average, most individuals will have one wing that is slightly longer than the other (Møller and Pomiankowski 1993). These asymmetries are typically slight, but can occasionally be large.

Asymmetries are thought to reflect the stability of individuals' development. Because organisms are supposed to be symmetric, asymmetries provide a documentation of developmental "errors": instances where the individual's body failed to organize itself according to design. The developmental errors that cause asymmetries can also cause issues with survivability and health across several species. Further, these errors can result from environmental stresses but can also emerge because of genetic mutations. Symmetry therefore can signal direct benefits, but can also provide indirect benefits: individuals who select symmetric mates are selecting mates with heritable genetic endowments that on average produce healthier, more survivable offspring.

Any feature of a potential mate that provides reproductive benefits to offspring provides, through inclusive fitness, an indirect fitness benefit to the mate selector. This can include heritable features that increase health, fertility, or competitiveness on the mating market; but, particularly in cultural species, indirect benefits can also come from transmissible features such as wealth, status, or knowledge. By selecting mates who can benefit one's offspring, an individual with mate preferences that yield indirect benefits will produce offspring who are more likely to survive and reproduce and thereby reproduce the genes underlying their mate preferences.

Sensory exploitation. Many mate preferences across species appear to be functional, but preferences can also evolve as byproducts of other adaptations. One common evolutionary route to

by-product preferences occurs when perceptual adaptations evolved for other processes are hijacked by potential mates to gain attraction in the mating domain. This process is called "sensory exploitation" and appears to have created mate preferences across several species. Tungara frogs provide the prototypical case of sensory exploitation. Females of this species prefer to mate with males who produce a distinctive chuck sound. However, this preference does not appear to be functional. Rather, female tungara frogs have evolved a species detection system which contains an auditory bias toward sound frequencies produced by tungara frog males but not by males of other frog species. After females evolved this sensory bias, tungara frog males evolved the chuck: a meaningless sound which happens to maximally stimulate females' species detection system (Ryan et al. 1990). Female tungara frogs consequently show a mate preference for chucks that evolved purely as a by-product of a species detection adaptation.

Any perceptual adaptation that can motivate approach or avoidance can in principle be exploited by potential mates to manipulate attraction in the mating domain. The exploitation of existing perceptual adaptations is therefore a potentially common route to the evolution of mate preferences. The result in any case of sensory exploitation is potential for a coevolutionary arms race. Individuals of one sex will evolve adaptations that allow them to better exploit their potential mates; in response, individuals of the opposite sex will evolve sensory defenses to the extent that being exploited is costly. These escalating arms races will craft adaptations that shape how organisms perceive and interact with their worlds as well as shape their mating systems and mating behaviors. Understanding when and how perceptual adaptations are exploited in the mating domain can thus provide researchers insight into the nature of species' perception and mating.

Outstanding theoretical issues in the evolution of preferences. Evolutionary biologists have made considerable progress in developing theory concerning the evolution of mate preferences. But some areas of mate preference theory remain unclear or underdeveloped. One centers on the

distinction between direct benefits to the mate selector and indirect benefits through benefits to kin. These sources of benefits are often considered categorically distinct, but it must be stressed that they can overlap. For instance, a preference for mates willing and able to invest resources in offspring could provide direct benefits to the mate selector by providing supplemental parental investment but also indirect benefits if this provisioning increases offspring reproduction beyond what single parental investment would alone. A preference for good immune functioning could provide indirect benefits by producing healthier offspring but also direct benefits in lowering the risk of being infected by partners. When considering the functions of mate preferences, researchers must take care to consider the many and potentially overlapping functions of preference adaptations.

Indirect benefit hypotheses further focus largely on genetic benefits to direct offspring. But there are many potential ways by which preferences could provide indirect benefits to kin. First, the kin receiving benefits need not be direct offspring. A gene for a mate preference could increase its own reproduction if it were able to provide fitness benefits to siblings or other genetic relatives. A mate whose status or resources are able to spill over and increase the reproduction of siblings can produce fitness benefits by increasing the reproduction of preference genes they probabilistically share with the mate selector. Mate preference researchers must consider the many potential targets of indirect benefits when hypothesizing evolved functions of mate preferences.

What Do We Know About Human Mate Preferences?

Ample theory and evidence documents the ways in which evolution has shaped mate preferences in nonhuman species. Do human mate preferences show the same evolutionary fingerprints? Mate preference research has been a cornerstone of evolutionary psychology since the field's inception (e.g., Buss 1989). This research has discovered an impressive and growing catalog of human preferences evolved to serve a variety of functions.

Direct benefits. Humans across cultures hold mate preferences hypothesized to have offered direct fitness benefits to human ancestors. One well-studied example concerns preferences for resources in potential mates. Human offspring are enormously costly, and they demand relatively large investments of resources to raise successfully. This is particularly true for women, who alone face the substantial energetic, temporal, and opportunity costs of pregnancy and up to several years of lactation. Analogous to female katydids, ancestral women could have partially offset these large reproductive costs by preferentially mating with partners who were willing and able to share resources with them.

Modern women across cultures consequently express a preference for potential mates who control resources that can be invested in them and their families. Buss (1989) surveyed 10,047 men and women across 37 cultures for their mate preferences in an ideal, long-term relationship partner. These cultures varied widely in religion, climate, and economic, political, and marriage systems. Yet despite this incredible diversity, in every culture, women, more than men, expressed a strong preference for potential mates who possess economic resources. This preference is not limited to modern cultures: women among the Hadza hunter-gatherers express a preference for men who are good hunters and therefore good providers of essential resources (Marlowe 2004).

Direct benefit preferences are not limited to women. One critical adaptive problem ancestral men would have faced in the mating domain is identifying mates who are fertile. Men who were able to target their mating effort toward women who were particularly fertile would produce more offspring than men attracted to less fertile women. However, women are fertile during only a relatively narrow period of their lives – after puberty and before menopause. Further, unlike many other mammal species, human ovulation is relatively concealed: whereas chimpanzees develop prominent genital swellings around ovulation, human women show only small changes around the fertile period of the menstrual cycle.

How could ancestral men identify and select fertile partners, since fertility, unlike estrus, is not

directly observable? Men's mate preferences appear to have solved this adaptive problem by drawing men to women who show cues statistically correlated with their fertility. Attributes of physical appearance and behavior provide a wealth of potential cues. One is a woman's body shape and particularly waist-to-hip ratio. Relatively low ratios of waist circumference to hip circumference are associated with young age, non-pregnancy status, fewer diseases, and an easier time getting pregnant. A low WHR is found attractive by men across cultures (Sugiyama 2005). Men's mate preferences also guide them toward mates with beneficial hormone profiles. Higher levels of ovarian hormones, including estradiol, are associated with a higher likelihood of conception (Lipson and Ellison 1996). Facial femininity is strongly correlated with estradiol levels in women; men are also strongly attracted to women who are facially feminine (Smith et al. 2006). This hormone-attractiveness link emerges in facial attraction, but also holds and emerges for body attraction: controlling for BMI, higher levels of estradiol are associated with higher levels of bodily attractiveness (Grillot et al. 2014). Through various probabilistic cues, men's mate preferences are able to guide them to mates who are relatively fertile.

Finally, one particularly important mate preference appears to capture direct benefits related to both resources and fecundity: preferences for the age of potential mates. Age is a key cue to both fecundity – the capacity to produce offspring – and resource acquisition. First, women are not fecund prior to puberty. After puberty, fecundity peaks roughly in the late twenties and early thirties and then gradually declines until menopause. A woman's age is thus a rough cue to her fecundity. Age is also a cue to reproductive value: roughly, the number of future offspring a person can be expected to have. Reproductive value typically peaks in the late teens and early twenties and declines thereafter. By seeking younger partners, ancestral men would have increased their odds of finding fertile reproduction partners. Age is additionally a useful cue to resource-earning potential. In both modern and traditional societies, men accrue more resources when they are older

than when they are younger. By seeking older partners, ancestral women could thus have increased their odds of securing partners with resources available to invest.

People accordingly show strong preferences for the age of their potential mates. Across cultures, men express a desire for younger partners whereas women express a desire for older partners (Buss 1989). This trend has held across decades in India, China, and Brazil (see, e.g., Souza et al. 2016). These preferences manifest not only in what people say but also in what they do: for example, marriage records across cultures show that husbands tend to be older than their wives (Kenrick and Keefe 1992). This difference appears in marriage records extending as far back as the nineteenth century in Swedish records (Low 1991).

Indirect benefits. Providing evidence for preferences evolved through indirect benefits is more difficult than providing evidence for preferences evolved via direct benefits. Nonetheless, humans have some mate preferences that are hypothesized to have evolved because they supplied ancestral humans with indirect fitness benefits. One concerns symmetry: human bodies are bilaterally symmetric by design, but all people show some degree of asymmetry. And just as in other bilaterally symmetric species, humans show a preference for symmetry in potential mates. More symmetric faces are found to be more attractive in both experimentally manipulated and natural faces (e.g., Scheib et al. 1999).

Another prominent preference hypothesized to have evolved via indirect benefits is women's preference for masculinity. Masculine facial, bodily, and behavioral attributes are thought to signal exposure to testosterone. Testosterone plays an important role in energy allocation: testosterone causes bodily systems to shift energy toward the development of muscle and away from maintenance processes such as immune functioning (Simmons and Roney 2009). Therefore, it is thought that only men who have “good genes” – that is, those for robust immune systems – can afford to produce large amounts of testosterone and develop highly masculine features. Consistent with this hypothesis, facial

masculinity and asymmetry are correlated in men, suggesting they tap an underlying dimension of genetic quality (Gangestad and Thornhill 2003). By mating with masculine men, women with a preference for masculinity would bear offspring who inherit their good genes and thereby good immune systems. Evidence for attraction to masculinity is mixed, but women do appear to be more attracted to masculine men in short-term, sexual contexts (e.g., Little et al. 2002).

Despite longstanding research focus on preferences for masculinity, two complications exist for the indirect benefit hypothesis: one methodological and one theoretical. First, evidence is mixed that masculine features reflect circulating testosterone levels as opposed to early life exposure to testosterone (e.g., Whitehouse et al. 2015). If masculine facial features do not reflect circulating testosterone levels, then they do not clearly signal the ability to bear the costs associated with producing large amounts of testosterone. Second, even if masculinity were clearly related to attractiveness and circulating testosterone, these findings would not, on their own, suggest that preferences for masculinity evolved because they provided indirect benefits to human ancestors. An alternative possibility is that preferences for masculinity function to guide humans to healthy partners. These partners would have provided human ancestors direct benefits both in being less infectious and in being more likely to survive to co-parent mutual offspring.

Contextual shifts in preferences. Historically, at least some traits would have offered variable fitness benefits across contexts. Selection should have favored the evolution of mate preference adaptations that are sensitive to these contextual shifts in fitness benefits. Preference mechanisms should take information about the current state of the environment as input and moderate the strength and nature of preferences in response. One context variable studied in the extant literature is pathogen exposure. Pathogens are more prevalent and pose a greater threat under some conditions and in some environments (e.g., warmer climates). Under such contexts, preferences for health in potential mates would have historically provided greater fitness benefits and

so selection would have favored the evolution of preference mechanisms sensitive to pathogen prevalence.

Preferences for physical attractiveness in potential mates appear to be one such context-sensitive preference (Gangestad and Buss 1993). Several studies suggest that physical attractiveness is at least a moderate cue to health (Sugiyama 2005): people who are more physically attractive tend to be healthier across a wide array of indices. Ancestral humans who more heavily prioritized physical attractiveness under conditions of high pathogen threat would therefore have been more likely to select partners who were able to survive disease threats and remain healthy. Additionally, to the extent that immune functioning is heritable, these people would be more likely to produce offspring with strong-enough immune systems to survive in their local, high-pathogen threat environments. Accordingly, modern humans living in ecologies with greater pathogens report stronger preferences for physical attractiveness in potential mates (Gangestad and Buss 1993). Women's preference for masculinity in potential partners specifically varies across cultures related to the health of those cultures: in countries with greater health risks, such as pathogen threat, women express stronger preferences for masculinity in potential mates (DeBruine et al. 2010).

Mate preferences differ across environments, but they also shift within people across contexts. For instance, the traits that are beneficial in a potential mate depend on the mating strategy one is pursuing. For men, a key benefit of short-term, uncommitted mating is access to multiple sexual partners (Buss and Schmitt 1993). This access would be hampered by mate preferences that set high standards for potential mates. Men's mate preferences consequently shift as a function of their mating strategy. When men are pursuing a long-term, high-commitment mating strategy, their preferences set high standards for the intelligence and kindness of their potential mates (Kenrick et al. 1990). When men are pursuing uncommitted, short-term partners, they substantially lower their preferences for kindness and intelligence, which presumably allows them to

mate with a variety of short-term partners. Importantly, men's physical attractiveness preferences remain relatively strong across mating strategies: healthy and fertile partners are always beneficial to men, and so preferences for these traits are relatively insensitive to mating context.

Women's mate preferences also shift across context. One well-studied contextual shift concerns shifts in women's mate preferences as a function of ovulatory status. A growing body of literature suggests that when women are ovulating, they more strongly prefer potential mates who are symmetric, with masculine bodies, and show dominant behavioral displays (Gildersleeve et al. 2014). These preference shifts are generally stronger when women are considering short-term, sexual partners rather than long-term, committed, romantic partners. Because women can only conceive offspring when or just before they are ovulating, these preference shifts have been hypothesized to function in motivating women to conceive offspring with partners who possess "good genes" – including those that allow them to build and maintain symmetric and masculine phenotypes. However, although many of these ovulatory shift effects appear to be empirically robust, the ultimate function of these shifts remains heavily debated. Alternative theoretical accounts include proposals that preference shifts are byproducts of adaptations calibrated to between-women differences in fertility and byproducts of adaptations designed to calibrate preferences to differences in fertility within women between menstrual cycles (see, e.g., Roney 2009).

What Is Not Known About Mate Preferences?

Despite the considerable and growing body of knowledge, many uncertainties remain about the nature of human mate preferences. These questions span the levels of Tinbergen's four questions and include issues of the development, mechanism, and function of human preferences.

Development. Mate preference research has focused largely on the content of adult mate

preferences. Almost no research explores how preferences develop into these mature forms. This developmental question encompasses several sub-questions. For instance, when, developmentally, do mate preferences come online? Because mate preferences presumably function to guide mate selection, one intuitive hypothesis is that mate preferences will not generally emerge until humans begin their mating careers – that is, at puberty. However, some evidence indicates that at least preferences for physical attractiveness appear very early in life (e.g., Langlois et al. 1987). Different preference adaptations may activate and deactivate at different points across the lifespan depending on when they would have been most functional throughout human evolutionary history. The developmental emergence of mate preferences is a very open and important area of inquiry.

A second question concerns the factors that affect the developmental trajectories of mate preferences. For example, mate preferences are known to vary somewhat across cultures (Buss 1989; Gangestad and Buss 1993). These cultural differences could be caused by psychological adaptations that actively calibrate mate preferences to local environments throughout the lifespan. However, an alternative developmental trajectory is that mate preferences are fixed relatively early on in life by environmental cues experienced in infancy or childhood. This relates to a third question: to what extent are mate preference adaptations sensitive to sociocultural cues? That is, do people have adaptations designed to promote learning of mate preferences from their cultures or social groups? Humans are known to engage in some degree of "mate copying": a learning process that appears across species wherein individuals learn to be attracted to potential mates based on the mate choices of others (Waynforth 2007). However, precisely what preference adaptations include these learning features, how long these learned changes last, and just how much learning can adjust the magnitude of mate preferences are still unknown.

Finally, relatively little is known about the developmental course of mate preferences across the lifespan. Many adaptive problems faced in

mate choice would have been age linked throughout human evolution. For example, women's fertility wanes at menopause. After this point, features of potential mates related to heritable benefits, such as the possession of good genes, could no longer provide fitness benefits. Accordingly, women's mating strategies appear to shift around menopause (Easton et al. 2010). These shifts are hypothesized to function in motivating women to take advantage of their fertile years. However, this is just one preference shifting at one point in women's lifespan. Little is known about the extent to which other preferences, such as those for resources, health, or fertility, change across the lifespan.

Mechanism. A central assumption of mate preference research is that mate preferences motivate people to pursue and select mates who fulfill those preferences. But preference researchers do not as yet understand how mate preferences are integrated to make actual mating decisions. Given preferences for mates who are, for example, intelligent, kind, and physically attractive and an array of potential mates who vary randomly on each of these dimensions, how exactly do people determine which mates are worth pursuing and which are worth passing over? How do we weigh a mate who is kind, attractive, and dull against a mate who is beautiful, smart, and rude?

Human mate choice psychology must have some psychological machinery that integrates our many mate preferences into summary decision variables, such as valuable as a mate or not. Several algorithms have been proposed for how this integration is accomplished. These include linear combinations similar to linear regression (Buss and Schmitt 1993), aspiration models involving series of thresholds (Miller and Todd 1998), nonlinear models involving trade-offs between necessities and luxuries (Li et al. 2002), and a Euclidean algorithm that minimizes the distance between desires and potential mates across multiple dimensions (Conroy-Beam and Buss 2016). Understanding the nature of human preference integration will be key to understanding both the content of human mate preferences and the downstream effects of these preferences on mating outcomes.

Function. Finally, mate preference research has been predominantly driven by functional hypotheses that propose mate preferences evolved to solve adaptive problems faced throughout human evolution. However, it is unlikely that all human preferences are the functional outputs of adaptations. At least some preferences are likely to be byproducts of other adaptations. For instance, the most common explanation for why humans prefer symmetry is that symmetry cues health and good genes (Grammer and Thornhill 1994). But it has also been proposed that symmetry preferences can emerge as byproducts of perceptual adaptations designed merely to detect, but not evaluate, mates who happen to be imperfectly bilaterally symmetric (Johnstone 1994). These hypotheses are not mutually exclusive: both functional and by-product preferences for symmetry could act to guide people toward symmetric partners.

Despite an apparent frequency of sensory exploitation in nonhuman animals (e.g., Ryan et al. 1990), sensory exploitation hypotheses for the evolution of mate preferences have not been explicitly explored in human mating. Many preferences whose functions are unclear – for instance, for attributes such as hair color and styling, dressing, dancing abilities, and so on – could exist because they hijack preexisting features of human perception. Exploring these sensory exploitation hypotheses has potential to provide psychologists insight into human perception and human mating.

The number and role of nonfunctional mate preferences remains an open empirical question. Full understanding of the breadth of human mate preferences will require preference researchers to explore by-product hypotheses alongside functional hypotheses as well as conduct empirical tests that compete by-product and functional hypotheses against one another for the ultimate origins of human mate preferences.

Conclusion

Mate preferences have pervasive effects on human life and human evolution. Mating is

central to differential reproduction, the engine of evolution by selection. All living humans are descendants of a long and unbroken chain of ancestors, each of whom successfully mated. Consequently, the study of human preferences has been a large part of evolutionary psychology since the field's inception. This research program begins with an understanding of how preferences evolve, including the receipt of direct and indirect benefits as well as by-product processes such as sensory exploitation. The application of these evolutionary theories has yielded a substantial body of evidence about the content of human preferences. This includes cross-cultural, sex-differentiated preferences for features such as possession of resources, future resource potential, symmetry, masculinity, and many cues to fertility, such as youth, femininity, and low waist-to-hip ratios. Preference research has also uncovered context sensitivity of many preferences, responsive to diverse circumstances such as personal mate value, pathogen prevalence, and mating strategy. Despite this large and growing body of knowledge, many questions remain open about mate preferences for future research. Preference researchers still have little understanding of how mate preferences develop over the lifespan, how multiple preferences are integrated with one another to make decisions about actual mate choice, and how some preferences might have evolved through nonfunctional routes such as sensory exploitation. Mate preference research is a large, successful, and vibrant research area with a long future ahead. The success of preference research contributes understanding of a large and critical domain of human life and underscores the value of applying an evolutionary perspective for understanding human psychology.

Cross-References

- [Benefits of Short-Term Mating](#)
- [Cross-Cultural Expression](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Evolution of Desire, The](#)
- [Fluctuating Asymmetry](#)

- [Intersexual Selection](#)
- [Mate Preferences After Having Children](#)
- [Men's Mate Preferences](#)
- [Older Men](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Sex Differences Versus Gender Symmetry](#)
- [Sexual Selection in Evolutionary Psychology](#)
- [Social Status and Economic Resources](#)
- [Tradeoffs in Mate Selection](#)
- [Violation of Long-Term Mate Preferences](#)
- [Violation of Short-Term Mating Preferences](#)
- [Waist-to-Hip Ratio](#)
- [Women's Mate Preferences](#)

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Mate Preferences After Having Children

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Synonyms

Mate preferences; Parenting effort; Remating; Stepparents

Definition

This section covers the theoretical considerations and existing data relevant to studying mate preferences after having children.

Introduction

Children dominate their parents' time and energy and siphon a significant portion of their accrued resources. Although having children changes people's lives substantially, the extent to which people's mate preferences change after having children is unclear. The current chapter

will address theoretical considerations important to developing hypotheses about mate preferences after having children and will summarize existing relevant data. First, because provisioning and caring for children was a recurrent adaptive problem, human mating psychology may have evolved to calibrate mate preferences to motivate the pursuit of partners who are able and willing to contribute resources and parenting effort and who will not pose a threat to existing children. Any shifts in preferences should be particularly pronounced in females who bear the brunt of obligatory investment costs. However, children also indirectly influence mate preferences because their presence alters parental mate value. Because children have a more detrimental effect on maternal mate value, we should again expect sex-differentiated effects on mate preferences. Finally, it is important to note that extended periods of childlessness in adulthood are a unique feature of modern, WEIRD (Western, Educated, Industrialized, Rich, and Democratic) populations. Observed mate preferences in childless adults may in fact be the product of mechanisms that evolved to guide mate selection of ancestral humans who already had children. Rationale for hypotheses that distinguish pre-children mate preferences from post-children mate preferences must offer evidence that mating mechanisms were shaped in an environment in which this difference was a recurrent selection pressure. Studies must disentangle differences in mate preferences after children from differences caused by potential confounding variables, such as mate value, status, or age.

Women's Preferences after Children

Women's mate preferences are influenced by a variety of contexts, including mate value (Buss and Shackelford 2008), ovulatory phase, and age. Mate preferences research highlights how women's obligate investment in offspring has acted as a recurrent selection pressure, shaping mating mechanisms. However, less research has addressed how sensitive these mating mechanisms are to the presence of current offspring. If

a woman is engaging in a mate search after already having children, she faces not only the adaptive problem of finding a partner who will invest in and help raise future shared offspring but also the adaptive problem of selecting a partner who will contribute towards her current children. This suggests two characteristics that women with children should particularly desire in potential mates: (1) partners who currently have resources to funnel to her and her offspring and (2) partners who are kind and nurturing toward her children and who do not pose a threat to them.

Children impose a particular resource burden on mothers, who are obligated to incur the energetic and resource costs of 9-months of gestation and, ancestrally, years of requisite breastfeeding (Marlowe 2005). As predicted by Parental Investment Theory (Trivers 1972), this difference in obligatory investment has shaped sex differences in human mate preferences. Across dozens of cultures, females place a greater premium on romantic partners' current and future ability to contribute resources than do males (Buss 1989). Existing children are an immediate resource burden. Unmated mothers, or mated mothers looking to mate-switch, should place an even greater importance on a potential mate's *current* ability to provide resources. This may manifest as an increased preference for cues to existing resources or an increased preference for cues to status, status-striving, ambition, and work ethic.

This hypothesis is supported by existing data. In one longitudinal study, the partnering decisions of over 2000 mothers drawn from a sample representative of the United States were assessed 5 years after their child's birth. About half of the mothers no longer with their child's father remained un-partnered. Of those who re-partnered, 60 % did so with a mate of higher economic potential than their child's father, 20 % with a mate of equal economic potential as their child's father, and 20 % with a mate of lesser economic potential than their child's father (Bzostek et al. 2012). This suggests that when women have children they become even more discerning about a mate's ability to contribute resources and may choose to remain unmated if they are unable to find or attract a mate meeting their heightened standards.

Even if a new partner has resources, he may be unwilling to funnel them towards children that are not his. Studies examining step-father monetary investment in children's college education in the United States, step-father monetary and time investment in high school-aged children in South Africa, and step-father time and care investment in children in the Hadza in Tanzania all demonstrate that step-fathers invest less in step-children than genetic children (Anderson 2005; Anderson et al. 1999a, b; Marlowe 1999). Mothers face a daunting task of selecting a mate who can and *will* help provision and care for her existing offspring.

Mothers also face the adaptive problem of selecting a mate that will not pose a threat to, or abuse, her existing children. A mother's new partner gains no direct reproductive benefit from investing in her children and may benefit from encouraging the mother to neglect and inflict costs on her current children to facilitate her investment in him and his children. The presence of a step-parent in the household vastly increases child abuse rates – in one study children living with a step-parent and a genetic parent were 40 times more likely to be abused than children living with both genetic parents (Daly and Wilson 1988). Step-parents are also more likely than genetic parents to kill children, and step-fathers in particular have the greatest tendency to kill step-children (Daly and Wilson 1988, 1994). Mothers would benefit by preferring new mates who display cues to kindness, interest in children, less aggression, and other indicators that they will not pose a threat to children. Women evidence such preferences even prior to motherhood (Buss 1989; Brase 2006). Cobey et al. (2015) found that women's preference for male facial masculinity decreased post-partum compared to their preference during pregnancy. This demonstrates a shift in preferences in mothers toward indicators that a potential mate will not threaten her child's survival. Women without children may be in the position to reap the benefits of mating with more masculine, less pro-social males because of the other benefits they provide. Mothers, on the other hand, may trade-off those benefits to ensure selecting a partner who will not harm her children.

The Effect of Children on Women's Mate Value

Although women would benefit from these shifts in preferences, their mating options and mating decisions will be limited by the effect children have on mate value. In other primate species, males are attracted to parous, older females, possibly because it signals mothering experience which would enhance infant survival or because it signals high genetic quality (Muller et al. 2006). However, humans are unique in that we form long-term pair bonds where males invest heavily in offspring. This has shaped men's preferences for younger women with high reproductive value from which they can maximally benefit. Children may provide a cue to more advanced age and fewer remaining reproductive resources, decreasing women's attractiveness. Although there is evidence that women who do not stay with their child's father are more likely to re-partner with a mate with better economic potential, unmarried mothers tend to mate with less educated men with fewer resources than their childless counterparts (Graefe and Lichter 2007; Lichter and Qian 2008). Men are less likely than women to report being willing to marry someone with a child (Goldscheider and Kaufman 2006). If children reduce a woman's mate value, making it more difficult for her to attract high quality mates, she may be forced to make tradeoffs in her mating decisions. A woman's attractiveness is positively correlated with preferences for a variety of characteristics in a mate, including emotional stability, education, potential income, and physical attractiveness (Buss and Shackelford 2008). Women high in mate value can attract the most sought after mates who embody all of women's preferences. Women with children cannot be highly selective in general but need to be specifically selective to ensure the provisioning and protection of their existing children.

Future studies examining women's mate preferences after having children must account for these competing selection pressures. We may see greater variability in the importance placed on different mate preferences in women with children compared to nulliparous women. Mothers

may place high premiums on characteristics like current resource holdings, willingness to invest in children, and prosociality but be willing to sacrifice other characteristics, like physical attractiveness and dominance, particularly because of their lower mate value. Non-mothers may maintain higher standards across female-typical mate preferences, in hopes of attracting a mate with the best combination of traits.

Men's Mate Preferences after Children

Historical and cross-cultural data shows that men engage in parental care less intensively than women (Geary 2000). As such, we should expect existing children to have less of an effect on men's mate preferences than women's. Any effects may depend largely on the amount of investment a father devotes to his children. Furthermore, children may have the opposite effect on father's mate value than mothers. Observing a father investing in current offspring provides a singular cue to interested females of his parenting abilities, possibly increasing his mate value (Brase 2006). Investigations into how children influence mate preferences need sex-specific rationale that will generate sex-differentiated hypotheses.

Although women bear the greater obligatory investment costs and often invest more in offspring, human males are unique among primates in that they provide high levels of parental care. This care influences their children's survivability and well-being. Having divorced parents predicts higher mortality rates in various countries, including Indonesia, Sweden, Germany, and the United States (Geary 2000). In a study of the Ache in Paraguay, father absence before the child turns 15 is associated with a mortality rate of 45 % compared to a 20 % mortality rate in children with present fathers (Hill and Hurtado 1996). Father's investment also predicts children's ability to compete for social and material resources, educational attainment, and physical well-being (Geary 2000). There is large variability among males in energy devoted to parenting effort – while some display high levels of investment, others invest little in offspring, instead devoting

those resources and energy towards obtaining additional mating opportunities. This is a key variable that should predict whether or not children have an influence on men's mate preferences.

Men who invest highly in offspring, devoting a large amount of their time and resources to their children may experience mate preferences shifts similar to women's, while men who invest less should not display similar preference shifts. Men's closeness to, and investment in, offspring is predicted by both child resemblance to themselves and their self-reported paternity confidence (Anderson 2005; Anderson et al. 1999a, b; Apicella and Marlowe 2004). Paternal investment is also predicted by mating opportunities. Across many species, factors like male phenotype and availability of additional mates predicts parenting effort (Magrath and Komdeur 2003). In humans, a scarcity of females predicts greater paternal investment (Pedersen 1991). Males who can better increase their reproductive success through obtaining additional mating opportunities should trade off parenting effort in favor of mating effort. We should only expect to see differences in mate preferences in fathers if they invest highly in offspring.

Similar to mothers, highly investing fathers should place greater weight on a mate's ability to provide resources and indicators that a mate will not pose a threat to his children. Although men in general place less importance on a mate's current and future ability to obtain and contribute resources, men who invest highly in offspring should be interested in mates who will assist and support their provisioning. They should be less interested in a new mate that will consume their resources at a cost to existing offspring. Step-mothers also pose a risk to step-children, similar to step-fathers. They are more likely to abuse and murder children than biological mothers (Daly and Wilson 1988). Fathers responsible for a significant portion of childcare should prefer new mates who display cues to kindness, interest in their children, and who lack aggression. However, it is unlikely any differences in mate preferences will be as pronounced in fathers as in mothers because even investing fathers generally engage in far less parental care than mothers.

The Effect of Children on Men's Mate Value

As with women, it is important to consider the influence children will have on paternal mate value. Children have a detrimental effect on a mother's mate value. The influence children have on paternal mate value is less straightforward. Although their presence indicates to a woman that some of a man's resources, time, and energy will be devoted to individuals other than herself and her children, his children provide her an opportunity to assess his parenting ability. Having children may even make a man more attractive as a mate because it allows him to demonstrate he is currently a good father and will be a good father to her children, and to any children they have together.

Studies on marriage rates of parents indicate that children have less of a detrimental effect on men's ability to re-partner than women. Divorced and widowed men are more likely to have subsequent intimate relationships and remarry than women (Ahrons 2007; Calasanti and Kiecolt 2007; Lindau et al. 2007). More importantly, when single fathers live with their children, they are far more likely to remarry than single mothers who live with their children (Goldscheider and Sassler 2006). If men's mate value is positively influenced by children, we should expect their mate preferences to adjust accordingly – they may be more selective and interested in higher mate value mates.

Future studies exploring the influence of children on men's mate preferences require assessing paternal investment in existing offspring and determining how children influence men's mate value. Men who engage in low levels of paternal investment should display mate preferences similar to non-fathers. Men engaged in higher levels of paternal investment may demonstrate increased preferences for mates who will help provision and not harm their children, although the magnitude of the differences between non-fathers and fathers should be smaller than differences between non-mothers and mothers. The influence of children on men's mate value remains an important

research question. In addition to providing a cue to parenting abilities, children may influence perceptions of status, resources, and provide a cue to past mating history. Sorting through these possibilities will be necessary to generate predictions about men's mate preferences after children.

WEIRD Populations and Researchers, Children, and Mate Preferences

Comparing mate preferences before and after children requires thinking about the selection pressures that shaped mate preference mechanisms. An extended period of childfree adulthood is a modern phenomenon, particularly for women. Modern birth control and social equality for women have given men and women greater control over reproductive timing and offspring number. A childless 25-year old woman is commonplace in modern, WEIRD (Western, Educated, Industrialized, Rich, Democratic) populations but would have been a rarity through most of human history (Henrich et al. 2010). The design features of mating mechanisms may have been largely shaped in contexts where reproductively viable individuals had children or were already highly invested in the care of siblings and relatives. Researchers must be cautious in distinguishing mate preferences "after" children from "before," which implies a temporal distinction that may be more salient and meaningful to WEIRD researchers than it has been to most humans.

This is especially important to consider with respect to women's mate preferences. Young women high in reproductive value would have been highly sought after as mates, but once mated would have had children quickly. Most of women's mating career would have happened when they were already mothers. Any studies suggesting children alter a woman's mate preferences must parse out the effects of her age, her mate value, and her unmated status on mate preferences, independent from the specific effect the presence of children has. Furthermore, characteristics of the children themselves may be important

considerations. Having particularly unhealthy or burdensome children may negatively influence women's mate value compared to having healthy children, but the presence of healthy children may only negligibly impact her mate value. Children may also actively attempt to manipulate parental mating decisions to benefit their own interests (see Schwarz, this issue ► [“Presence of children”](#)). Any studies of the effect of children on mate preferences may require not just comparing those who have and do not have children but instead require making nuanced predictions about the characteristics of children and how those characteristics affect parents.

Age is another important variable to account for independent of having children. Cross-culturally men prefer younger mates because youth is a cue to reproductive value (Buss 1989). Studies of women in general, and specifically of mothers, have demonstrated that younger women are more likely to remarry after divorce (Bramlett and Mosher 2002; Buckle et al. 1996; Lundberg and Rose 2003). Furthermore, the presence of children provides a cue to age – the older an individual is, the more likely it is that they have children and have more children. Researchers bear the burden of demonstrating that variations in mate preferences are uniquely associated with having children, and not due to age or how having children influences perceptions of age.

Despite these concerns, it is reasonable to think that ancestral humans would have been faced with the adaptive problems of selecting, attracting, and retaining mates at times when they both did and did not have children throughout their life-spans. Even if a man or woman entered a long-term pair-bond when relatively young, their mate could have died, decreased in mate value prompting a mate-switch, or abandoned them. A person's mate value may have increased, or new, better mates appeared, also motivating mate-switching (Buss et al. 2017). It is likely children have acted as a selection pressure in some capacity on mate preferences. However, hypotheses exploring the influence of children on mate preference must consider how the presence of children would have acted as a

selection pressure under circumstances very different from our current environment.

Conclusion

We still know very little about how children alter mate preferences. Mate preferences for resource provisioning ability and for cues that indicate a potential mate is less likely to abuse or threaten current offspring are likely candidates for which we should expect increased preferences in parents, especially mothers. Perhaps even more important will be determining how children influence parental mate value. They likely negatively influence mother's mate value but may have a negligible or positive effect on father's mate value. In this way, children will indirectly influence mate preferences because mate value influences mate preferences. Furthermore, distinguishing mate preferences after children from preferences before may be a WEIRD framing of this area of research interest. Future work in this domain should focus on building rationale that takes into account the environment in which mating mechanisms were shaped. It may be specific characteristics of children, such as their health, that influence mate value, rather than the simple presence or absence of children. In any case, considering how children provide input – either directly or indirectly – to mate preference mechanisms will reveal previously undiscovered nuances to human mate preferences.

Cross-References

► [Presence of Children](#)

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Mate Quality

► Women's Mate Value

Mate Quality Bias

► Mate Copying

Mate Rejection

► Circumventing Mate Choice

Mate Retention

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Definition

Behavioral strategies designed to thwart a romantic partner's infidelity or defection.

Introduction

Humans have regularly and recurrently over evolutionary history formed long-term committed relationships as part of their sexual strategies, consequently facing the adaptive problem of successfully retaining a mate which they have selected and attracted. Thus, successful mate retention is a key human concern, and its importance is amplified to the degree that mate poachers attempt to lure one's mate away, to the degree one is invested in and dependent on the relationship, and to the degree that one's mate is tempted by the prospect of temporary infidelity or total defection.

Retaining a mate requires solving several adaptive problems, including: preventing a partner from leaving, diminishing a partner's interest in other long-term or short-term relationships, and increasing a partner's interest in the current relationship. As a consequence of the number and complexity of mate retention problems that mated individuals have recurrently faced over human evolutionary history, it is reasonable to expect that humans have evolved a large array of adaptations dedicated to mate retention. The behavioral outputs of mate retention adaptations may be broadly referred to as mate retention strategies.

Successful mate retention involves the maintenance of an exclusive romantic relationship over a long period of time. Thus, mate retention strategies include tactics such as continuously providing reproductively relevant resources that fulfill

the mate preferences and desires of a partner. Failure to fulfill these preferences and desires leads to failure to retain that mate (via extra-pair affairs, breakup, divorce, etc.). The hypotheses that humans have evolved adaptations designed to retain their mates, to ward off mate poachers, and to prevent mate defection has received growing support from empirical studies that have outlined some of the "design features" predicted in advance by evolutionary hypotheses about mate retention adaptations.

Performance of mate retention strategies increases to the degree that an individual perceives the problem of partner infidelity. An individual's perception of this problem is influenced by their own information-processing machinery (i.e., stable individual differences) and by informational inputs about their partner (e.g., partner's mate value) and the context (e.g., relationship commitment). These inputs influence perception of a partner's risk of infidelity because this kind of information has helped individuals assess, and therefore mitigate, a partner's infidelity or defection – on average, over evolutionary history. For example, the problem of mate retention is more severe when mated to a partner who has an unrestricted sociosexual orientation – who is more likely to pursue a short-term mating strategy. Another example is that mate retention effort is sensitive to sex-linked components of a partner's mate value such as youth and physical attractiveness (components of female more than male mate value) and ability and willingness to invest resources (components of male more than female mate value). These and other empirical findings support the general hypothesis that humans have evolved adaptations for mate retention that have psychological design features that motivate individuals to increase or decrease effort allocated to mate retention, depending on specific informational inputs outlined below.

Mate Retention Inventory

Buss (1988) developed the Mate Retention Inventory (MRI), a taxonomy of 104 acts clustered

into 19 mate retention “tactics” ranging from subtle to overt (see Table 1). These tactics are organized into five “categories”: (1) Direct Guarding, (2) Intersexual Negative Inducements, (3) Intrasexual Negative Inducements, (4) Positive Inducements, and (5) Public Signals of Possession. One common way to group the five categories into two overarching “domains” is Intersexual Manipulations (those directed at one’s romantic partner; categories 1, 2, and 4) and Intrasexual Manipulations (those directed at same-sex rivals; categories 3 and 5). Another common way to

group the five categories into two overarching domains is Cost-Inflicting behaviors (those reducing the risk of partner infidelity by lowering a partner’s self-esteem, thereby causing that partner to feel unworthy of the current or any other relationship; categories 1, 2, and 3) and Benefit-Provisioning behaviors (those reducing the risk of partner infidelity by increasing a partner’s relationship satisfaction; categories 4 and 5) (Miner et al. 2009). The MRI is a reliable measure overall and has been used to document the prevalence of mate retention behaviors in various samples,

Mate Retention, Table 1 Mate retention (MR) domains, categories, tactics, and sample items

MR domain	MR category	MR tactic	Sample item
Cost-Inflicting	Direct Guarding ^a	Vigilance	<i>Dropped by unexpectedly to see what my partner was doing</i>
		Concealment of Mate	<i>Refused to introduce my partner to my same-sex friends</i>
		Monopolize Mate’s Time	<i>Would not let my partner go out without me</i>
	Intersexual Negative Inducements ^a	Threaten Infidelity (Jealousy Induction)	<i>Flirted with someone in front of my partner</i>
		Punish Mate’s Infidelity threat	<i>Became angry when my partner flirted too much</i>
		Emotional Manipulation	<i>Threatened to harm myself if my partner ever left me</i>
		Commitment Manipulation	<i>Asked my partner to marry me</i>
		Derogation of Competitors	<i>Cut down the appearance of other men/women</i>
	Intrasexual Negative Inducements ^b	Derogation of Mate to Competitors	<i>Told others my partner was “a pain”</i>
		Intrasexual Threats	<i>Confronted someone who had made a pass at my partner</i>
		Violence Against Rivals	<i>Got my friends to beat up someone who was interested in my partner</i>
Benefit-Provisioning	Positive Inducements ^a	Resource Display	<i>Spent a lot of money on my partner</i>
		Sexual Inducements	<i>Gave in to sexual pressure to keep my partner</i>
		Appearance Enhancements	<i>Made sure that I looked nice for my partner</i>
		Love and Care	<i>Told my partner “I love you.”</i>
		Submission and Debasement	<i>Gave in to my partner’s every wish</i>
	Public Signals of Possession ^b	Verbal Possession Signals	<i>Introduced my partner as my spouse or romantic partner</i>
		Physical Possession Signals	<i>Sat next to my partner when others were around</i>
		Possessive Ornamentation	<i>Asked my partner to wear my ring</i>

^aIntersexual Manipulation

^bIntrasexual Manipulation

including undergraduate populations, newlyweds, and longer-married couples. Further, the MRI shows high congruence between self-reports and partner-reports, indicating that partners can reliably describe one another's mate retention behaviors.

Given the importance of assessing mate retention in various contexts, The Mate Retention Inventory-Short Form (MRI-SF; Buss et al. 2008) was developed to provide researchers with a briefer version of the MRI. The MRI-SF is a 38-item instrument that assesses the same 19 mate retention tactics as the MRI, with the same grouping hierarchy of five mate retention categories, and both sets of two overarching domains. The MRI-SF has demonstrated good reliability and validity in various samples.

Mate Retention and Mate Value

Both types of mate retention (Benefit-Provisioning and Cost-Inflicting) behaviors are motivated by sexual jealousy and have likely minimized reproductive losses for ancestral men and women. Because these reproductive losses vary in magnitude across relationships, men and women allocate effort to mate retention based on characteristics of their current relationship, including their own and their partner's "mate value" – a measure of the comparison between a person's characteristics and the characteristics desired by the opposite sex (e.g., a current or potential partner) – and the discrepancy between the two. Men and women may use assessments of mate value to gauge the likelihood, and consequent costs, of a partner's infidelity or outright relationship defection.

Mate value comprises physical traits (e.g., higher shoulder-to-hip ratio and greater height increase men's mate value, lower waist-to-hip ratio increases women's mate value) and social attributes (e.g., social status, generosity, intelligence, resource earning potential) which may signal, for example, genetic quality, fertility, and likelihood of investing in offspring. The mate value of one's partner predicts one's performance of mate retention directed towards that partner.

For example, men allocate more effort to mate retention when the costs of a partner being unfaithful or permanently defecting from the relationship are especially high or when these events are perceived to be particularly likely. Losing a youthful or more attractive partner may be costlier to men than losing an older or less attractive partner because of the difficulty of replacing a more reproductively valuable partner. Additionally, more attractive partners have more opportunities for infidelity, because they are more desired by the opposite sex. For these reasons, men mated to younger, more attractive women allocate greater effort to mate retention than do men mated to older, less attractive women (Buss and Shackelford 1997), and men allocate more effort to mate retention when they perceive that their partner is more likely to be unfaithful (e.g., Buss and Shackelford 1997; Goetz et al. 2005).

Women's mate value predicts men's mate retention behaviors, particularly Benefit-Provisioning behaviors which require known costs from men (e.g., up-front resource and time investments), as opposed to Cost-Inflicting behaviors which have unknown costs for men (e.g., men may or may not be retaliated against). Benefit-Provisioning tactics such as those in the Positive Inducements category are more frequently performed by men mated to women of higher (vs. lower) mate value. Men invest up-front (i.e., provision benefits) only with a woman that they perceive as being of high enough mate value to warrant their time and resources. Men's reports of their partner's mate value also predicts their more frequent performance of Intersexual Negative Inducements (one category of Cost-Inflicting mate retention), which suggests that men may resort to Cost-Inflicting behaviors with a higher mate value partner as part of increased efforts to retain her, if they cannot afford the known costs of Benefit-Provisioning.

One's *own* mate value also predicts one's performance of mate retention. Men of higher mate value are more likely to perform Benefit-Provisioning mate retention, whereas men of lower mate value are more likely to perform Cost-inflicting mate retention (e.g., Miner et al. 2009). Notably, these relationships depend on *who* is assessing men's mate value and mate retention.

The *discrepancy* between one's mate value and their partner's mate value also predicts mate retention behaviors. Although partners in a long-term relationship tend to be of similar mate value, humans detect and magnify differences when that information is important for assessing risks (and has been a reliable cue for that risk in the ancestral past). Mate value discrepancy between members of a couple may indicate important relationship outcomes such as the risk of partner's infidelity and one's ability to secure a better mate. It is especially important to assess these discrepancies, however small, in the context of a long-term relationship because of the large investment in that relationship (and missed opportunities in other relationships). Indeed, mate value discrepancy predicts several relationship processes, including relationship satisfaction, the perceived likelihood of partner defection, and mate retention behaviors (e.g., Conroy-Beam et al. 2016; Sela et al. *in press*).

Mate Retention Across the Ovulatory Cycle

Women can conceive only during the fertile phase of their ovulatory cycle. Thus, historically, women could have obtained genetic benefits through extra-pair sex only near ovulation but paid costs of extra-pair sex throughout the cycle; while men would have paid heavier costs if their partners had extra-pair sex near ovulation. As conflicts of interest between partners change across the woman's ovulatory cycle, so too do specific and predictable forms of behavioral conflict such as the performance of mate retention behaviors. These intersexual conflicts of interest across the ovulatory cycle may have shaped female interest in extra-pair partners and male efforts to track their partner's whereabouts, both increasing near ovulation (vs. the luteal phase). Further, women mated to men of lower (vs. higher) genetic quality might be expected to exhibit these shifts most strongly because these women could only gain genetic benefits from extra-pair sex. In other words, women mated to a partner of higher genetic quality could also gain

genetic benefits from in-pair sex and, thus, may not need to shift strategies across the ovulatory cycle as much as women mated to a partner of lower genetic quality. Finally, men mated to women that are more (vs. less) attractive are at greater risk of their partner's infidelity across her ovulatory cycle and, thus, should not display shifts in mate retention behavior to the same extent as men mated to less attractive women.

Indeed, several studies have documented such shifts in women and their male partners. Women report greater sexual desire for extra-pair partners near ovulation (vs. the luteal phase), but this is not the case for their sexual desire for their *in-pair* partner (e.g., Gangestad et al. 2002). In fact, women report feeling less committed to their in-pair partner and more resistant to his mate retention efforts (Gangestad et al. 2014) during their high (vs. low) fertility phase.

These shifts in women's psychology pose increased infidelity risk to their in-pair partner during the fertile phase and, thus, it is reasonable to expect that their in-pair partner increase mate retention behaviors accordingly, to counteract this threat. Further, men of low (vs. high) genetic quality are at greater risk of their partner's infidelity at peak fertility because their female partner has the most to gain by pursuing this shifting strategy. Indeed, women report that their in-pair partner performs some mate retention behaviors more frequently during the days leading up to ovulation (vs. the luteal phase). Their in-pair partner is reported to be, for example, more proprietary, vigilant, monopolizing of time, jealous and possessive, attentive and loving (but only when he is reported to be less sexually attractive), as women near peak fertility (e.g., Gangestad et al. 2002; Haselton and Gangestad 2006; Gangestad et al. 2014).

Both ovulatory shifts – increased female extra-pair desires and increased male mate retention behaviors – are moderated by men's sexual (but not investment) attractiveness (e.g., Haselton and Gangestad 2006). Increased male mate retention behaviors during their partner's high fertility phase are also moderated by their partner's attractiveness and her increased extra-pair interest. Men mated to a less (vs. more) attractive woman show a greater increase in jealous and possessive mate

retention behaviors near ovulation (even though more attractive women garner higher-frequency mate retention behaviors across the cycle) (Gangestad et al. 2014; Haselton and Gangestad 2006), and women's increased desire for extra-pair partners positively predicts their in-pair partner's increased self-assertiveness and dependence (Gangestad et al. 2014). Finally, women in their fertile (vs. infertile) phase increase their self-assertiveness and resistance-to-mate-guarding behaviors (specifically, those *unobservable* to their in-pair partner, and especially women who report a greater shift toward extra-pair partner desires) (Gangestad et al. 2014).

In sum, a growing body of evidence suggests that men shift their mate retention behaviors as a counter-strategy to their partner's extra-pair desire shifts, according to men's shifts in risk of their partner's infidelity. Countering men's counter-strategy, women increase their resistance to mate retention when they have the most to gain from extra-pair sex.

Mate Retention and Concurrent Sexual Behaviors

Several studies investigating the relationships between the frequency of various mate retention strategies and sexual behaviors suggest that men and women employ various mate retention strategies concurrently with sexual behaviors. Performance of mate retention behaviors is positively associated with frequency of sexual intercourse with one's partner (e.g., Barbaro et al. 2015). Performance frequency of Benefit-Provisioning mate retention, in particular, is positively associated with time, and interest in, performing oral sex on one's partner (Sela et al. 2015a). Men's performance of mate retention behaviors is positively associated with men's use of semen displacement behaviors (e.g., thrusting, longer copulation duration) as an anti-cuckoldry tactic (Goetz et al. 2005). Thus, these sexual behaviors may be part of a broader mate retention strategy.

Pretending orgasm may be another mate retention strategy, used by women, to prevent a partner's infidelity or defection from the relationship.

Men are attentive and interested in their female partner's orgasm, and women most often report pretending orgasm in order to keep a partner interested or excited and to reduce likelihood of a partner's infidelity or relationship defection. Indeed, women who perceive high (vs. low) risk of their partner's infidelity are more likely to pretend orgasm during copulation with him, and women that are more likely to pretend orgasm also report more frequent performance of mate retention across all five categories (e.g., Kaighobadi et al. 2012).

Mate Retention and Individual Differences

Mate retention behaviors require conscious effort, and individuals are likely to differ in their willingness to engage in such behaviors. Individual differences associated with performing, and with being targeted by, mate retention behaviors include personality dimensions, sex, age, parity, sociosexuality, and relationship status.

Personality Dimensions

Neuroticism is a personality dimension that is hypothesized to reflect high sensitivity to social threats, with high scorers displaying greater social vigilance. Those high on Neuroticism are especially sensitive to social threats, including threats to a romantic relationship, which is likely the reason they allocate more efforts toward mate retention. Individuals high (vs. low) on Neuroticism (or Emotionality) perform more frequent Benefit-Provisioning mate retention (Sela et al. 2015b; Holden et al. 2014; cf. McKibbin et al. 2014). They also perform more frequent Cost-Inflicting mate retention (de Miguel and Buss 2011; Sela et al. 2015b).

Agreeableness is a personality dimension associated with cooperativeness rather than aggressiveness (which is the low end of Agreeableness and which is linked to social cost-inflicting tactics). Thus, Agreeableness should motivate less frequent use of negative, Cost-Inflicting mate retention behaviors and more frequent use of positive, Benefit-Provisioning mate retention

behaviors. Indeed, individuals high (vs. low) on Agreeableness perform less frequent Cost-Inflicting mate retention (Sela et al. 2015b; de Miguel and Buss 2011; Holden et al. 2014; McKibbin et al. 2014). This negative relationship also emerges from *women's report* about their *partner's* Agreeableness – and their *own* Agreeableness – and their partner's Cost-Inflicting mate retention (McKibbin et al. 2014). Individuals high (vs. low) on Agreeableness also perform more frequent Benefit-Provisioning mate retention (Pham et al. 2014; McKibbin et al. 2014; cf. women; Sela et al. 2015b). This positive relationship also emerges from *women's report* of their partner's Agreeableness and Benefit-Provisioning mate retention (McKibbin et al. 2014).

Conscientiousness is a personality dimension that reflects a long-term strategy of delayed gratification and tenacity of goal pursuit (vs. a more impulsive strategy that involves low inhibition against seizing immediate adaptive benefits). Individuals higher on conscientiousness are more likely to acquire long-term resources and successfully negotiate hierarchy, both of which are associated with Benefit-Provisioning mate retention behaviors. Individuals high (vs. low) on conscientiousness perform more frequent Benefit-Provisioning mate retention (Sela et al. 2015b; de Miguel and Buss 2011). Individuals high (vs. low) on conscientiousness also perform less frequent Cost-Inflicting mate retention behaviors in the categories of Direct Guarding, Intersexual Negative Inducements (de Miguel and Buss 2011), and Intrasexual Negative Inducements (Holden et al. 2014). Independently of men's conscientiousness, men who report their female partner is high (vs. low) on conscientiousness also perform more frequent Benefit-Provisioning mate retention (McKibbin et al. 2014).

Openness is a personality dimension characterized by novelty- and complexity-seeking and is associated with creativity. Individuals high (vs. low) on openness perform less frequent Cost-Inflicting mate retention behaviors (Holden et al. 2014). According to *women's report*, it is their own high levels of openness that predict their male partner's decreased Cost-Inflicting mate retention behaviors (McKibbin et al. 2014).

Individuals high (vs. low) on openness also perform more frequent Benefit-Provisioning mate retention (Pham et al. 2014; Sela et al. 2015b).

Extraversion (or surgency) is a personality dimension characterized by positive emotions, exploratory and physical activity, and sociability. Extraversion is also linked with aspects of sexuality, such as trying out different sexual positions and acquiring a variety of different sexual partners. Consequently, it is reasonable to expect that those high on extraversion would effectively use Benefit-Provisioning tactics such as Sexual Inducements toward their partner. It also follows that they are likely to be targets of more frequent mate retention *from* their partners, because they may be perceived as having more social opportunities to be unfaithful. Indeed, individuals high (vs. low) on extraversion perform more frequent Benefit-Provisioning mate retention (Pham et al. 2014; de Miguel and Buss 2011) and more frequent Cost-Inflicting mate retention (de Miguel and Buss 2011). Interestingly, women who report that they are high (vs. low) on surgency also report that *their partner* performs more frequent Cost-Inflicting mate retention behaviors (McKibbin et al. 2014).

Honesty-Humility is a dimension of personality that captures the extent to which individuals are concerned with equality, fairness, and honesty in their interpersonal relationships, and the extent to which they are willing to manipulate, deceive, and exploit others; such that those with higher levels are more likely to treat others fairly and to have difficulty lying. These characteristics seem to influence mate retention such that individuals high (vs. low) on Honesty-Humility perform less frequent Cost-Inflicting mate retention behaviors (Holden et al. 2014), many of which involve manipulation of a partner's emotions and commitment (e.g., "Pleaded that I could not live without my partner").

Dark personality traits (e.g., The dark triad: narcissism, psychopathy, and Machiavellianism) have also been linked to mate retention behaviors. Individuals with high levels of the dark triad traits tend to be antagonistic, self-concerned, callous, and manipulative. Not surprisingly, individuals with high levels of the dark triad traits perform

more frequent mate retention overall and especially more frequent aversive mate retention behaviors such as punishing their partners or acting violently toward romantic rivals (Jonason et al. 2010). Those high (vs. low) in dark triad traits have higher rates of their partner defecting, and this relationship is mediated by their increased mate retention behaviors. Each of the three dark triad traits and its association to mate retention documented in Jonason et al. (2010) is reviewed below.

Narcissism is a personality trait characterized by strong self-focus, sense of entitlement, tendency to exploit others, general lack of empathy, extreme confidence in one's abilities, and excessive need for admiration. Individuals high (vs. low) on narcissism perform more frequent mate retention overall and especially more frequent Cost-Inflicting mate retention. They also perform more frequent Benefit-Provisioning mate retention tactics such as resource display, appearance enhancement, emphasize love and caring, and verbal signals of possession. Although, some tactics may not be used as mate retention per-se or exclusively, given narcissists' tendencies to display their resources, enhance their appearance, and attend to alternative romantic partners.

Psychopathy is a personality trait characterized by antisocial behavior, impulsive thrill-seeking, interpersonal manipulation, and cold affect. Individuals high (vs. low) on psychopathy perform more frequent mate retention overall and especially more frequent Cost-Inflicting mate retention tactics such as monopolize mate's time, threaten infidelity, punish mate's threat to infidelity, derogation of competitors, and intrasexual threats. They also perform more Benefit-Provisioning mate retention tactics such as resource display, appearance enhancement, and verbal signals of possession.

Machiavellianism is a personality trait associated with cynicism, distrust, detachment, and willingness to exploit others or use emotional blackmail and little interest in close, intimate relationships. In a long-term romantic relationship context, men and women with high levels of Machiavellianism employ more frequent Cost-

Inflicting mate retention behaviors (e.g., Brewer and Abell 2015), which are centered on reducing self-esteem of, and harming, a partner. Generally, these individuals should be less likely to engage in Benefit-Provisioning mate retention behaviors (which are mostly centered around developing intimacy and commitment), but in one study Machiavellianism was positively associated with Benefit-Provisioning tactics such as submission and debasement, and physical and verbal signals of possession (Jonason et al. 2010).

Pathological personality features other than the dark triad include: negative affect (concerns the tendency to experience an array of negative emotions), antagonism (refers to aggressive tendencies accompanied by assertions of dominance and grandiosity), disinhibition (includes impulsivity and sensation seeking), detachment (characterized by introversion, social isolation, and anhedonia), and psychoticism (involves a disconnection from reality and a tendency toward illogical thought patterns). These pathological personality features are associated with interpersonal difficulties and with increased mate retention – especially the darker, Cost-Inflicting behaviors (Holden et al. 2015). Individuals with high (vs. low) levels of negative affect are likely to be more concerned about their partner's defection or infidelity and as such employ more frequent mate retention behaviors (primarily Cost-Inflicting, but also Benefit-Provisioning; Holden et al. 2015) in an attempt to mitigate these perceived dangers. Individuals with high levels of antagonism tend to be manipulative, cold, and callous towards others which leads them to perform more frequent Cost-Inflicting mate retention behaviors (Holden et al. 2015). Features of disinhibition such as impulsivity are linked to aggression, and individuals high on this trait perform more Cost-Inflicting mate retention behaviors (but this relationship disappears when allowing co-variation with other pathological personality traits; Holden et al. 2015). Individuals high (vs. low) on detachment are likely to be withdrawn from their romantic partner and avoid intimacy and thus be less investing in maintenance of their romantic relationships; indeed, they perform less frequent mate retention behaviors in both

domains (when allowing co-variation with other pathological personality traits; Holden et al. 2015).

Basic and dark personality traits appear to have a profound effect on strategic behaviors within romantic relationships. Personality dimensions actively influence the tactics that individuals use to impact those around them, including keeping a romantic partner from straying.

Sex Differences

Two key sex differences in mate retention usage have been hypothesized: (1) Men more than women should use resource display mate retention and (2) Women more than men should use enhancing physical appearance mate retention. This hypothesis is based on the logic of Trivers' sexual selection theory, and in particular the link between the two component processes of sexual selection – intrasexual competition and intersexual selection. In order to effectively maintain a romantic relationship, the specific mate retention tactics that individuals perform should target the mate preferences of the opposite-sex partner. Because displays of love are highly valued by both sexes in long-term mating, both sexes should use love displays equally as tactics of mate retention. Because women more than men across cultures prefer status and resources when selecting a mate, mate retention behaviors performed by men more than women should include those under the tactic of resource display (e.g., “Spent a lot of money on my partner”; “Bought my partner an expensive gift”). Men, on the other hand, universally place a greater premium than do women on physical appearance when selecting a mate, although this sex difference is more pronounced in short-term mating than long-term mating. Physical attractiveness provides a wealth of information about a woman's age, health, and fertility. Consequently, mate retention behaviors performed by women more than men should include those under the tactic of enhancing physical appearance (e.g., “Dressed nicely to maintain my partner's interest”; “Made sure I look nice for my partner”). These two hypotheses about sex differences in performance frequency of mate retention tactics have been confirmed in American

samples (e.g., Buss 1988), including married couples (e.g., Buss and Shackelford 1997), a Canadian sample (VanderLaan and Vasey 2008), a Croatian sample (Kardum et al. 2006), a Spanish sample (de Miguel and Buss 2011), an Iranian sample (Atari et al. [under review](#)), and others.

Two other robust sex differences in mate retention performance have been documented across samples and cultures. Men more than women perform more frequent submission and debase-ment mate retention behaviors (e.g., “I went along with everything she said”; “I acted against my will to let her have her way”), (e.g., Atari et al. 2017; Buss and Shackelford 1997; de Miguel and Buss 2011; Kardum et al. 2006). The other consistent sex difference is that men more than women perform more frequent intrasexual threats (e.g., “I threatened to hit the guy who was making moves on my partner”), (e.g., Atari et al. 2017; Buss and Shackelford 1997; de Miguel and Buss 2011; Kardum et al. 2006). The greater use of violence and violent threats are consistent with previous research about the vast majority of same-sex violence being perpetrated by men rather than women.

Further support for the idea that individuals employ mate retention behaviors that target their partner's mate preferences has been documented in homosexual individuals (e.g., VanderLaan and Vasey 2008). For example, homosexual women perform more frequent resource display, and less frequent appearance enhancement, than heterosexual women. This suggests that women perform these tactics to target their partner's sex-specific preferences (i.e., female's prioritization of partner-provisioned resources and lesser emphasis on partner's physical appearance). Homosexual men, on the other hand, perform less frequent resource display mate retention than heterosexual men. Thus, it appears that men perform these behaviors to target partner preferences; this tactic used more frequently toward a man's female partner but less frequently toward a man's male partner.

Age, Relationship Length, and Parity

Age and relationship length tend to be positively associated, and both have been documented to

have negative associations with performance of mate retention. Younger individuals, and individuals that have been in their relationship for a shorter period of time, perform more frequent mate retention behaviors than older individuals and those who have been in their relationship for longer (e.g., Buss and Shackelford 1997; de Miguel and Buss 2011). Kaighobadi et al. (2010) documented a decline in frequency of performing mate retention behaviors in the 3-year period immediately following marriage, which could be a function of age, relationship maturation, relationship commitment, or some combination of these. Another important factor that comes along with aging, and relationships of longer duration, is having children.

Parity, however, has been hypothesized to be *positively* associated with mate retention performance frequency. Men and women should be motivated to remain pair-bonded after having children for two ancestrally important reasons: maintaining the distribution of male-provisioned resources to a woman and her offspring and to protect offspring from infanticide. Indeed, Barbaro et al. (2016) documented that both men and women with genetic children with their current partner perform more frequent individual mate retention behaviors and request more frequent coalitional mate retention (see below) behaviors than men and women without genetic children with their current partner. The magnitude of these associations remain, even after controlling for age and relationship length which were positively associated with parity and negatively associated with performance frequency of mate retention in that sample.

Attachment

Another important individual difference relevant to mate retention behaviors is romantic attachment. Romantic attachment functions to maintain pair-bonds and facilitate reproductive strategies. Romantic attachment bonds influence the ways in which individuals respond to relationship threats and are conceptualized as two continuous and independent dimensions of *anxiety* and *avoidance*. Attachment anxiety reflects a hyperactivation of the romantic attachment system and

is characterized by attempts to attain proximity to a romantic partner. Greater attachment anxiety is associated with hypervigilance to cues of abandonment and rejection by a romantic partner and difficulty disengaging from cues to relationship distress. Attachment avoidance, in contrast, reflects a hypoactivation of the romantic attachment system and is characterized by attempts to evade emotional intimacy and physical proximity to a romantic partner. Greater attachment avoidance is associated with independence and self-reliance that facilitate decreased partner dependence and proximity-seeking. More avoidantly attached individuals are more likely to discount cues of relationship threats relative to more anxiously attached individuals.

Romantic attachment dimensions of anxiety and avoidance are associated with distinct behavioral patterns within romantic relationships – particularly jealousy and infidelity – a link that has led to hypotheses concerning unique associations between mate retention domains and romantic attachment dimensions. Indeed, individuals who are more (vs. less) anxiously attached perform more frequent mate retention behaviors, whereas individuals who are more (vs. less) avoidantly attached perform less frequent mate retention behaviors (e.g., Barbaro et al. *under review*). In another sample of nonclinical individuals, those who scored higher (vs. lower) on borderline personality disorder features – strongly associated with attachment bonds characterized by fear of rejection, lack of trust, hypersensitivity to perceptions of, and hypervigilance in acting on cues of potential threats to relationships – also perform more frequent mate retention behaviors (Tragesser and Benfield 2012).

More anxiously (vs. avoidantly) attached individuals also report greater perceived risk of a partner's likelihood of committing infidelity, and this perception mediates the relationship between anxious attachment and performance frequency of Cost-Inflicting mate retention (Barbaro et al. *under review*).

It is suggested that more anxiously attached individuals perform mate retention behaviors more frequently because these individuals are hypervigilant to cues of partner abandonment

and infidelity. In contrast, more avoidantly attached individuals perform less frequent mate retention behaviors, more generally, because these individuals underestimate the extent to which behaviors are indicative of infidelity and are motivated to evade emotional and physical intimacy with a romantic partner.

Relationship Status and Sociosexuality

Theoretically, relationship status, especially the degree of relationship commitment, is expected to influence mate retention efforts such that individuals in more committed, long-term relationships should exert more effort to keep their romantic partner than individuals in less committed, short-term relationships. Indeed, individuals in a more (vs. less) serious, committed romantic relationship perform more frequent mate retention behaviors overall (e.g., Buss 1988). One interesting exception is the Threatening Infidelity mate retention tactic, which is performed more frequently by individuals in a *less* committed relationship (de Miguel and Buss 2011). This finding is consistent with the hypothesis that jealousy induction is a tactic more heavily used by individuals in circumstances in which they are more committed to their relationship than their partner. Individuals more committed than they perceive their partner to be may induce jealousy in an attempt to increase the commitment of their partner.

Another aspect of relationship commitment is perception of a partner's characteristics. One important indicator of a partner's commitment is their standing on sociosexuality, a dimension that reflects a wide range of sexual behaviors and attitudes toward sex, which is defined as the degree to which individuals require emotional closeness and commitment before having sex. Sociosexually restricted individuals prefer commitment and closeness with their romantic partner prior to engaging in sex, while unrestricted individuals tend to engage in sex without commitment or closeness. Accordingly, sociosexually unrestricted (vs. restricted) individuals are more likely to get involved in extra-pair relationships, are more sexually assertive, engage in socially dominant behaviors (e.g., maintaining eye contact and close physical proximity), and are more responsive to situational sexual cues.

A partner that is less (vs. more) sociosexually restricted poses a greater risk of infidelity and should be targeted by more mate retention efforts. Indeed, individuals with a less (vs. more) sociosexually restricted partner perform more frequent mate retention behaviors toward that partner (Kardum et al. 2006). Interestingly, women mated with men who are less sociosexually restricted perform more frequent Intersexual Manipulation mate retention (those behaviors targeted toward their partner), whereas men mated to women who are less sociosexually restricted perform more frequent Intrasexual Manipulation (those behaviors designed to fend off mate poachers) and especially the tactic of violence against rivals (Kardum et al. 2006).

Coalitional Mate Retention

The MRI measures individual's performance of behaviors that aim to thwart a partner's infidelity or defection. However, others may perform behaviors to assist an individual with this goal as well. Coalitional mate retention involves behaviors that one's *allies* perform to reduce the likelihood of one's partner's infidelity or defection. Pham et al. (2015a) developed the coalitional mate retention inventory, which assesses the occurrence frequency of coalitional mate retention behaviors across several tactics.

Coalitional mate retention can overcome some of the costs associated with individual mate retention but may be uniquely costly in other ways. For example, if one performs excessive individual mate retention, one's partner may perceive them as overbearing, excessively jealous, or mistrustful. Coalitional mate retention can overcome these costs by having a friend perform mate retention, and thereby reducing the negative impression on one's partner. Coalitional mate retention can also overcome geographic (e.g., long-distance relationships) and time (e.g., restrictive work schedules) constraints of individual mate retention. Potential costs to coalitional mate retention include same-sex allies poaching a romantic partner, because of their increased interaction, and because requesting help from an ally with mate retention may signal that the relationship is

unstable. Another potential problem is a same-sex ally sabotaging the relationship in order to become romantically involved with the individual that had requested the help.

The quality of the relationship between an individual and their ally is associated with the likelihood of requesting coalitional mate retention (Pham et al. 2015b). Relationship quality of friendships involving women are positively correlated with requests of coalitional mate retention, but relationship quality within male-male friendships is *negatively* correlated with requests of coalitional mate retention. This sex difference suggests that because men, relative to women, inflict heavier retaliatory costs on mate poachers, coalitional mate retention may be less likely to be deployed between male friends in order to avoid risking the loss of an important social resource.

One's standings on several personality dimensions are also correlated with one's requests of coalitional mate retention (Pham et al. *in press*). For example, individuals lower in honesty-humility and higher in extraversion report less frequent requests for coalitional mate retention. Men (but not women) higher in emotionality and lower in openness more frequently request coalitional mate retention, suggesting that coalitional mate retention might be employed more frequently by men who are less willing to communicate with their partner. It appears, more generally, that dishonest individuals are more likely to request coalitional mate retention, suggesting that coalitional mate retention – as compared to individual mate retention – is associated with manipulative and deceitful personality dimensions.

Conclusion

Mate retention strategies are the behavioral tactics that individuals employ to maintain their romantic relationships by reducing the probability of infidelity or defection by their current romantic partner. The majority of research in this area has investigated the mate retention behaviors that individuals perform, as assessed by the MRI and MRI-SF. Recent studies have widened the scope of mate retention strategies to include other sexual behaviors (e.g., oral sex) and behaviors employed by one's allies

(i.e., coalitional mate retention), providing new insights about the complexities and context specificity involved in decisions about how to best keep an exclusive romantic relationship.

Mate retention strategies are outputs of an evolved psychology designed to address one of greatest adaptive challenges humans have recurrently faced in long-term relationships: keeping a desired partner from straying. The hypothesis that humans have evolved adaptations designed to hold on to their mates, ward off mate poachers, and prevent mate defection has received growing support from empirical studies that have outlined some of the design features predicted in advance by evolutionary hypotheses about mate retention adaptations (e.g., sensitivity to partner's risk of infidelity as indicated by their mate value and sociosexuality). Applying an evolutionary framework to the study of mate retention has proven fruitful over the past few decades, and there remain open many profitable avenues of research in this area.

Cross-References

- ▶ [Coalitional Mate Retention](#)
- ▶ [Cost Inflicting](#)
- ▶ [Cues to Infidelity](#)
- ▶ [Evolution of Desire, The](#)
- ▶ [Female Infidelity](#)
- ▶ [Frequency of Infidelity](#)
- ▶ [Infidelity Risk](#)
- ▶ [Jealousy and Infidelity](#)
- ▶ [Male Sexual Jealousy to Deter Partner Infidelity](#)
- ▶ [Mate Retention After Children](#)
- ▶ [Mate Retention and Romantic Attachment](#)
- ▶ [Mate Retention Strategies](#)
- ▶ [Mate Retention Tactic](#)
- ▶ [Mate Value](#)
- ▶ [Men's Suspicions of Partner Infidelity and Women's Defection](#)
- ▶ [Oral Sex](#)
- ▶ [Perceptions of Infidelity Cues](#)
- ▶ [Prevention of Infidelity](#)
- ▶ [Randy Thornhill](#)
- ▶ [Self-Evaluations Track Perceived Mate Value](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)

- Sexual Assault and Intimate Partner Violence
- Sexual Infidelity Versus Emotional Infidelity
- Use of Mate Retention Strategies
- Women's Mate Value

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Mate Retention After Children

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Definition

Mate retention effort after having children that functions to maintain the pair-bond between parents.

Introduction

Several features of normative human life history are unique among the primate order and are particularly unique among our great ape relatives (e.g., chimpanzees, gorillas). For instance, human mothers nurse offspring for a shorter period of time, who have shorter inter-birth intervals, an extended juvenile period, later age at sexual maturity, and longer lifespan relative to

nonhuman primates (Yamagiwa 2015). The most striking human life history traits include the extraordinary length of infant dependency and the formation of long-term pair-bonds.

Pair-bonding in humans evolved as a result of two opposing evolutionary forces: the transition to bipedal locomotion and the evolution of large brains in the genus *Homo*. The evolution of substantially larger brains in *Homo* over the preceding four million years, coupled with the evolution of bipedal locomotion approximately four million years ago, may account for the long duration of infant dependency in humans. Because bipedal locomotion consequently results in a relatively smaller birth canal, a strong selection pressure was imposed on the size of the brain at which human infants could pass safely through the birth canal. Because of these opposing evolutionary forces – smaller birth canal and larger brains – human infants are born at a much earlier stage of brain development than other great apes (Lovejoy 2005). Human infants are, more generally, precocial at birth, but an underdeveloped brain and extreme duration of infant dependency constitute altricial features (Martin 2013). This unique set of traits in human infants may have been a primary selection pressure for pair-bonding in humans (Yamagiwa 2015).

Biparental Care

Humans are among the 3 % of mammals that form long-term pair-bonds, and unique among our great ape relatives. Because of human infants' extreme dependency on caregivers for survival, pair-bonding in humans facilitates biparental care, which increases probability of offspring surviving to reproductive age. Paternal investment is common in humans, although the degree to which fathers invest in their offspring varies cross-culturally (Fernandez-Duque et al. 2009). Variation in paternal investment is associated with the local ecology (e.g., resources, morbidity, and mortality) and the social environment (e.g., availability of mates, availability of alloparents) (Fernandez-Duque et al. 2009; Hewlett 1991; Quinlan 2007).

Biparental investment can reduce the likelihood of child mortality and other negative outcomes for children. In the Tsimane of Bolivia, the death of a father corresponds with higher mortality rates for children (Winking et al. 2011). In the Ache of Paraguay, children whose genetic father lived with them had a mortality rate of 20 %, whereas father absence was associated with a mortality rate of 45 % (Hill and Hurtado 1996). Similarly, in preindustrial countries prior to the twentieth century, father absence was related to increased child mortality (Geary 2000).

Biparental investment and remaining pair-bonded are beneficial to both men and women for offspring survival. A mother's death early in a child's life – especially during the period of time in which a mother is nursing her offspring – has a profound and negative impact on offspring survival (Sear and Mace 2008, for review). And, men with children reliably secure higher fitness pay-offs for allocating greater effort to mate retention and parenting than they do for allocating greater effort to extra-pair mating (Hawkes et al. 1995). But, how exactly does remaining pair-bonded facilitate offspring survival? Two non-mutually exclusive hypotheses concerning the selection pressures that led to biparental investment in humans have emerged in the literature: the *male provisioning hypothesis* and the *male-male competition hypothesis*.

Male Provisioning

The male provisioning hypothesis proposes that men remain pair-bonded to provide their offspring with resources, such as food (Quinlan 2008). Fisher (1987) postulates that the period of time during which a woman nurses her infant may be a “critical period” for paternal investment, in particular. Over humans' evolutionary history – and still today in traditional hunter-gatherer societies – women's foraging returns, on average, account for higher caloric return than do men's hunting returns. Research among the Hadza foragers showed that during the period in which a woman nurses her offspring (about 2–4 years) her foraging returns significantly decreased from average

levels (Marlowe 2003). However, Hadza men with nursing wives compensate for diminished foraging returns by sharing fewer hunting returns with the social group and redirecting these hunting returns to their family.

Men's hunting abilities can also indirectly benefit the nutritional welfare, and therefore survival prospects, of their offspring. In the Hadza of East Africa, for example, a man's own hunting success does not directly impact the nutritional status of his offspring. However, better hunters are, on average, married to better foragers. And, because women's foraging returns account for greater caloric intake than do men's hunting returns, better foraging wives have a direct impact on the nutritional status and, thus, the survival prospects of their children (Hawkes et al. 2001). Therefore, better hunters are able to acquire higher-quality mates – which directly benefits the welfare of their children. These findings demonstrate that both women and men can benefit from pair-bonding and paternal investment (Quinlan and Quinlan 2007, 2008).

Moreover, research further demonstrates how paternal investment, specifically, can indirectly benefit the welfare of offspring. In a cross-cultural ethnographic analysis, paternal investment was positively related to the duration that a woman nurses her infant (Quinlan and Quinlan 2008). Increases in paternal investment may afford women the opportunity to nurse their infants for a longer period of time – which is reliably linked with beneficial developmental outcomes in children.

Male-Male Competition

The male-male competition hypothesis emphasizes a man's role as protector, rather than an investor, of his partner and offspring (Hawkes 2004). Because human infants are extremely dependent on caregivers and require high levels of parental investment for a prolonged period of time, harassment and violence from other adult men, such as infanticide, can impose substantial costs on women and their offspring (Blurton Jones et al. 2000) via abduction, injury, or death.

By remaining pair-bonded following the birth of offspring, a woman depends on the offspring's father to protect her and her offspring from violence and infanticide by other adult men. Married women are at lesser risk of violence from other men (Wilson and Mesnick 1997). Further, a woman with offspring from a previous relationship begins a new relationship with an unrelated male; risk for domestic violence – toward the woman and the offspring – significantly increases (Daly and Wilson 1994). Both men and women can benefit from remaining pair-bonded when they have children because infanticide directly and negatively impacts men's and women's reproductive success.

In nonhuman primates, when a new male usurps a group, he might kill existing offspring to whom he is genetically unrelated. Infanticide brings females into estrus and affords the new male paternity of future offspring (Muller and Wrangham 2009). Infanticide, unfortunately, also occurs in humans. The rate of infanticide in humans is highest when a stepfather – who is not genetically related to a woman's children – is present and when children are younger in age (Daly and Wilson 1994; Weekes-Shackelford and Shackelford 2004). Among the Ache of Paraguay, infanticide is an important cause of child mortality (Hill and Hurtado 1996).

Research has also shown that women prefer dominant men in the context of male-male competition, which is a demonstration of the male's ability to protect her from rival males (Snyder et al. 2008). And, cross-culturally, women prefer high-status men that signal dominance and prestige as long-term partners (Conroy-Beam et al. 2015) – further cues of the man's ability to protect a woman and her offspring from other aggressive men.

Mate Retention Effort

Both the male provisioning hypothesis and the male-male competition hypotheses emphasize how biparental care and pair-bonding can improve the probability of an offspring surviving to reproductive age. Although the specific

selection pressures that facilitated biparental investment in humans are debated, both hypotheses suggest that men and women can both benefit by remaining pair-bonded (at least in the initial years following birth of offspring). Additionally, both hypotheses suggest that men and women are both motivated to remain pair-bonded following birth of offspring and may allocate greater mate retention effort to prevent relationship dissolution.

Mate retention in humans is designed to reduce the risk of a romantic partner committing infidelity and protection against relationship dissolution (Buss 1988). Partner infidelity can inflict costs on men and women and is a leading cause of relationship dissolution. When children are introduced into a relationship, partner infidelity may impose greater costs on men and women than when children are not present. For example, a woman whose partner defects from the relationship is at risk of male violence toward her and her offspring. In ancestral environments and hunter-gatherer societies, a man's defection from the relationship can reduce male-provisioned resources and adversely affect offspring nutrition. A man whose partner defects from the relationship increases the likelihood of offspring mortality, whether by decreasing nutritional welfare of his offspring or by infanticide committed by other men.

Men and women deploy various mate retention strategies concurrently to prevent a romantic partner from defecting from the relationship (Barbaro et al. 2015; Pham et al. 2015). One strategy is *individual mate retention* (Buss 1988). Individual mate retention behaviors are performed alone and function to maintain a romantic relationship. Individual mate retention behaviors can be directed toward one's primary partner or can be directed toward intrasexual rivals. Individual mate retention behaviors can also be positive or socially acceptable behaviors that, more generally, function to reduce the risk of partner infidelity by increasing a partner's relationship satisfaction. But, also, individual mate retention behaviors can be negative and even violent that function to reduce the risk of partner infidelity by lowering a partner's self-esteem, thereby causing that partner to feel unworthy of the current or other

relationship domains (Miner et al. 2009). Another mate retention strategy is *coalitional mate retention* (Pham et al. 2015), whereby an individual requests that a close ally such as a friend performs mate retention behaviors. Coalitional mate retention can reduce the risk of a partner being perceived as “overbearing” or jealous (Pham et al. 2015).

The various normative life history traits that are unique to humans relative to nonhuman primates suggest that mate retention effort may differ for individuals with children as compared to individuals that do not have children. Research conducted by Barbaro and colleagues (2016) recruited over one thousand adult participants that were in a committed, heterosexual relationship from across the United States. In an online survey, participants indicated whether they had at least one genetic child they shared with their current partner and reported the frequency in which they performed various individual mate retention and coalitional mate retention behaviors. The results indicate that men and women with at least one genetic child with their current partner perform more frequent individual mate retention behaviors than men and women who did not have children with their current partner. Additionally, men and women with at least one genetic child with their current partner requested more frequent coalitional mate retention behaviors from both their male friend and female friend than men and women who did not have children with their current partner. That mothers and fathers perform more mate retention than individuals without children points to the importance of both the male provisioning and male-male competition hypotheses in the maintenance of pair-bonds and the ways in which biparental investment facilitates offspring survival in humans.

Conclusion

Pair-bonding in humans originated from the evolution of larger and larger brains in *Homo* and the consequent long duration of infant dependency (Yamagiwa 2015). Pair-bonding in humans facilitates biparental care and promotes offspring

survival. Following the birth of a child, men and women are motivated to remain pair-bonded. The “critical period” in which a woman nurses her offspring may be especially important in regard to biparental investment. Men, in particular, will compensate for reduced foraging returns by their wives during early years. Men also provide protection for their partner and offspring from potentially aggressive men. And, men and women both exert greater mate retention effort to thwart partner infidelity and prevent relationship dissolution when they share children together, relative to men and women in committed relationships with no children. Because of unique life history traits in humans, it is likely that remaining pair-bonded following the birth of offspring increased survival prospects of offspring over deep evolutionary time and, thus, was beneficial to both men’s and women’s ultimate replicative success.

Cross-References

- ▶ [Coalitional Mate Retention](#)
- ▶ [Mate Retention](#)
- ▶ [Parent Influences](#)
- ▶ [Parental Effort Versus Mating Effort](#)
- ▶ [Parental Investment](#)

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Mate Retention and Romantic Attachment

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Synonyms

[Romantic love](#)

Definition

The predictive utility of romantic attachment on performance frequency of mate retention behaviors—behaviors that reduce the likelihood of partner infidelity and/or relationship dissolution.

Introduction

Men and women often form long-term pair-bonds that may span months to years in duration.

Individuals perform mate retention behaviors to reduce the likelihood of a romantic partners infidelity or dissolution of the established relationship (Buss 1988). Performance frequency of mate retention behaviors varies across individuals as a function of dyadic factors and individual differences. Romantic attachment is an individual difference factor that has been documented to predict the frequency with which an individual performs mate retention behaviors (Barbaro et al. 2016; Barbaro et al. *in press*).

Mate Retention and Romantic Attachment

Humans are a socially monogamous species. Men and women typically form multiple, subsequent pair-bonds over the lifespan. Individuals, however, may end a relationship with a partner to pursue a relationship with a new partner, or individuals may surreptitiously pursue extra-pair copulations while concurrently in a relationship with a primary partner (Buss et al. 2017). A romantic partner's infidelity inflicts costs on men and women. A man whose partner commits sexual infidelity is a risk for cuckoldry – the unwitting investment into offspring to whom he is genetically unrelated (Shackelford 2003). A woman whose partner commits infidelity risks losing partner-provisioned resources for her and her offspring (Trivers 1972).

Men and women are motivated to prevent a romantic partner's infidelity or the dissolution of their current romantic relationship. One strategy men and women use toward this end is *individual mate retention*. Individual mate retention refers to behaviors that an individual performs alone that reduce the likelihood of partner infidelity or relationship dissolution (Buss 1988). Mate retention behaviors can be classified into two domains of Benefit-Provisioning and Cost-Inflicting (Miner et al. 2009). Benefit-Provisioning mate retention are behaviors that function to increase the satisfaction of an individual's partner thereby reducing the partner's motivation to commit infidelity or end the relationship. Cost-Inflicting mate retention, in contrast, are comprised of behaviors that

function to decrease the self-esteem of the romantic partner thereby reducing the partner's feelings of being worthy of another romantic partner.

Performance frequencies of mate retention behaviors vary as a function of dyadic-level and individual level behaviors, including relationship duration, age, biological sex, infidelity risk, mate value, and available alternatives, for example. Romantic attachment towards a partner has also been documented to affect performance frequencies of mate retention behaviors. Evolutionary perspectives on romantic attachment (Del Giudice 2009; Hazan and Zeifman 1999) posit that attachment bonds function to maintain pair-bonds between romantic partner by regulating emotional and behavioral responses to perceived relationship threats. Romantic attachment bonds are conceptualized along the two dimensions of attachment *anxiety* and attachment *avoidance* (Fraley et al. 2000). Attachment anxiety reflects hyperactivation of the romantic attachment system such that individuals scoring higher on this dimension report more chronic jealousy, vigilance to cues of abandonment and rejection by their partner, and more intense negative emotional reactions. Attachment avoidance reflects hypoactivation of the romantic attachment system such that individuals scoring higher on this dimension report lesser relationship commitment, a greater need for independence within the relationship, and are more attentive to alternative romantic partners.

Research investigated whether attachment bonds influence perceptions of infidelity-type behaviors (Kruger et al. 2013) by asking participants to rate whether various types of interactions with others (i.e., casual social interactions, close relationship behaviors, and sexual and erotic interactions) were considered infidelity. More anxiously attached individuals rated close relationship behaviors as cueing infidelity, whereas more avoidantly attached individuals discounted the relevance of sexual and erotic interactions with others as cues of infidelity. These results demonstrate that individual's attachment bond toward their romantic partner influences their perception of their partner potential infidelity.

An individual's perception of their partner's likelihood of infidelity is a strong predictor of

the frequency with which an individual performs mate retention behaviors. Because attachment anxiety and attachment avoidance are associated with varying perceptions of partner infidelity (Kruger et al. 2013), Barbaro et al. (2016) hypothesized that attachment anxiety and attachment avoidance may reliably be associated with performance frequencies of mate retention behaviors. The results of a survey studies conducted with men and women residing in the United States (Barbaro et al. 2016) and residing in Iran (Barbaro et al. *in press*) documented that, overall, attachment anxiety is associated with more frequent performance of mate retention behaviors, whereas attachment avoidance is associated with relatively less frequent performance of mate retention behaviors. In a subsequent survey study conducted in the United States (Barbaro et al. *in press*), it was found that an individual's perception of their partner's potential infidelity mediates the association between attachment anxiety and performance frequencies of mate retention behaviors.

Research on the associations between romantic attachment and performance of mate retention behaviors is limited. Empirical findings thus far, however, are consistent with the notion that the association between attachment anxiety and mate retention behaviors is explained, in part, by a hypervigilance to rejection cues and potential infidelity cues by a romantic partner, which may motivate the performance of mate retention behaviors. Attachment avoidance, in contrast, appears to inhibit an individual's perception of their partner's infidelity, possibly due to the hypoactivation of the romantic attachment system. Experimental and dyadic research designs could profitably be pursued to more thoroughly elucidate the associations between romantic attachment and mate retention behaviors.

Conclusion

Individual difference factors influence the frequency with which men women perform mate retention behaviors to reduce the likelihood of their romantic partner committing infidelity or dissolution of the relationship (Buss 1988).

Research investigating the influence of an individual's attachment anxiety and attachment avoidance on performance frequency of mate retention behaviors has revealed that, more generally, attachment anxiety is associated with increased perceptions and a partner's future infidelity and more frequent performance of mate retention behaviors, whereas attachment avoidance is associated with relatively less frequent performance of mate retention behaviors (Barbaro et al. 2016, *in press*).

Cross-References

- Attachment in Adulthood
- Attachment Theory
- Early Attachment Experiences and Romantic Attachment
- Evolutionary Foundations of the Attachment System and its Functions
- Infidelity
- Infidelity Risk
- Mate Retention
- Mate Retention Strategies
- Perceptions of Infidelity
- Sexual Infidelity Versus Emotional Infidelity
- Use of Mate Retention Strategies

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Mate Retention Behavior

- [Female Age as a Predictor of Men's Aggression Against Women](#)

Mate Retention Behaviors

- [Mate Retention Tactic](#)

Mate Retention Strategies

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Synonyms

[Mate guarding](#); [Mate retention](#); [Mating strategy](#)

Definition

The strategies used to ensure the partner's permanence and fidelity in a long-term relationship.

Introduction

Most living beings invest energy, time, and resources in reproductive aspects, especially those related to the selection and retention of partners (Buss 1988; Buss and Shackelford 1997). Partner retention is often not an adaptive problem, since relationships tend to be short in nonhumans in general. Among humans, relationships with the same partner over a long period of time are a central aspect of many individuals' lives (Barbaro et al. 2015). Given the importance of relationships and their implications for survival and well-being, many individuals invest significant time and resources in maintaining these relationships. Some of the strategies used to maintain relationships are to prevent partners from abandoning the relationship or being attracted by rivals.

Men and women present various strategies for retention of their partners. Some associated goals are: to save the energy directed to attracting and conquering a new partner, to ensure parental investment in the offspring, to ensure investment of resources in the partner, and to increase the chances of reproductive success (Gallup Jr and Frederick 2010). In addition, partner retention strategies are associated with various aspects of romantic relationships, such as the frequency of sexual intercourse and violence between partners (Barbaro et al. 2015; Buss 1988).

Composition of Retention Strategies

From an evolutionary perspective, in addition to aspects such as well-being and belonging, long-term relationships are advantageous mainly because: (1) for men, there is a guarantee of transmission of genes with greater control and certainty of paternity; (2) for women, there is

control of the investment and care of the partner towards the offspring (Gallup Jr and Frederick 2010). Thus, both sexes make efforts to retain the partner in long-term relationships. Partner retention happens through various behaviors (or tactics) made with the objective of reducing the probability of the partner engaging in affective or sexual relationships with third parties or leaving the relationship. It involves, for example, attempting to monopolize partner time or slander potential competitors (Buss 1988; Buss and Shackelford 1997).

Buss (1988) proposed the first model to systematize partner retention behaviors in humans. The retention was operationalized through 19 tactics, organized into five strategies and distributed in two domains. Each of the five strategies is composed of some tactics; they are: (1) direct guarding, that is, vigilance, monopolize mate's time, and concealment of mate; (2) intersexual negative inducements, which include threaten infidelity, punishment mate's threat to infidelity, emotional manipulation, commitment manipulation, and derogation of competitors; (3) intra-sexual negative inducements, consisting of derogation of mate to competitors, intrasexual threats, and violence; (4) positive inducements, consisting of submission and debasement, emphasize love and care, resource display, sexual inducements, and enhancing physical appearance; and (5) public signals of possession, which include verbal signals of possession, physical signals of possession, and possessive ornamentation.

The domains organize the strategies into the ones that are costly and the ones that result in benefits (Miner et al. 2009). The strategies of the first domain are those that seek to reduce the risk of partner infidelity by reducing their self-esteem, making them feel sexually or emotionally undesirable, and include the following strategies: direct guarding, intersexual negative inducements, and intrasexual negative inducements. In turn, benefit-provisioning mate retention strategies seek to increase partner satisfaction with the relationship, they are the positive inducements and the public signs of possession (Buss 1988).

Differences Between Sexes in the Use of Retention Strategies

Research has identified gender differences in the use of partner retention tactics (Buss 1988; Buss and Shackelford 1997). For example, men, more than women, tend to resort to exposure of resources, while women, more than men, resort to investments in physical appearance (Atari et al. 2017; Buss and Shackelford 1997; Lopes et al. 2016). These differences corroborate the evolutionary hypotheses that men tend to choose women who appear to have good reproductive capacity prioritizing specific physical aspects related to attractiveness. Women tend to choose partners with characteristics that indicate a greater ability to obtain resources.

Some other differences in the use of strategies include: (a) men with greater partner value use more beneficial strategies and fewer costly strategies compared to men with lower value (Miner et al. 2009); (b) men use more retention strategies with younger or more attractive women (Buss and Shackelford 1997); (c) women married to men with higher incomes use more retention strategies (Buss and Shackelford 1997); and (d) men who suspect partner's infidelity use more retention strategies (Buss and Shackelford 1997). Several factors other than gender differences can help in understanding the differences in the use of retention strategies, individual and contextual factors, such as the reproductive fitness of the individuals, the partner's level of fertility, the operational sex ratio of the environment, the presence of friends within the environment. Thus, research on the topic can help in understanding human romantic relationships and the processes underlying partner selection.

Conclusion

Attracting and securing a partner requires time, energy, and resources. Retention strategies emerge to address threats to the relationship, with the goal of reducing the likelihood of partner abandonment or infidelity. From an evolutionary point of view, retention strategies were selected to

solve these two problems (i.e., infidelity and abandonment) in long-term romantic relationships. They include a wide range of tactics that can be costly or beneficial to the partner. The frequency and intensity of these strategies vary according to gender differences, but also individual and contextual differences. Research on partner retention strategies can provide valuable insights into the workings of romantic relationships.

Cross-References

- [Coalitional Mate Retention](#)
- [Mate Retention](#)
- [Mate Retention Tactic](#)
- [Mate Retention and Romantic Attachment](#)

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Mate Retention Tactic

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Synonyms

[Mate guarding](#); [Mate retention behaviors](#)

Definition

Mate retention tactics represent efforts devoted to retaining a long-term mate, preventing partner's infidelity or defection.

Introduction

Humans usually maintain an intimate sexual bond with the same partner for years or decades. Long-term romantic relationships are one of the most common mating arrangements and a central aspect of many individuals' lives (Barbaro et al. 2015; Buss 2003). Mate retention in this relational arrangement is an evolutionary adaptive problem. People invest energy, time, and resources in reproductive aspects, especially those related to the selection and retention of partners (Buss and Shackelford 1997). Considering this, Buss (1988) proposed a model that systematized human mate retention behaviors, describing 19 tactics. Each of these tactics group together a set of behaviors such as cry in front of a partner to control it (e.g., emotional manipulation) and to gift with jewelry (e.g., possessive ornamentation).

Tactics of Mate Retention

Benefits of mate retention in long-term romantic partnerships include greater chances of survival

for individuals and their offspring, greater certainty of paternity for men, lower risk of loss of partner investment, and greater provision of resources for women (Buss 2003). Tactics are the operationalization of the mate retention behaviors. All of them aim to decrease the likelihood of partner infidelity or the end of the long-term relationship, through, for example, the slander of potential competitors or monopolizing partner time (Buss and Shackelford 1997). Mate retention tactics can be relatively positive, such as praise or bestowing gifts on the partner, or negative, such as the use of threats or punishments.

Buss (1988) proposed the first systematic model of partner retention behaviors in humans. Originally, these behaviors were classified into 19 tactics, organized into 5 strategies, and distributed in 2 domains.

The first of these domains, which refers to intrasexual manipulations and is composed of the tactics directed toward the partner, includes three strategies: (1) direct guarding (vigilance, monopolization of mate's time, and concealment of mate); (2) intersexual negative inducements (jealousy induction, punishment of mate's threat to infidelity, emotional manipulation, commitment manipulation, and derogation of competitors); and (3) positive inducements (resource display, sexual inducements, appearance enhancement, emphasis of love and caring, and submission and debasement). The second domain, which is related to intersexual manipulations and is composed of the tactics directed toward same-sex competitors, includes two strategies: (4) public signals of possession (verbal possession signals, physical possession signals, and possessive ornamentation) and (5) intrasexual negative inducements (derogation of mate to competitors, intrasexual threats, and violence against rivals).

In addition, Miner et al. (2009) suggested organizing the five strategies into two other domains: cost-inflicting mate retention (i.e., direct guarding, intersexual negative inducements, and intrasexual negative inducements), which seeks to reduce the risk of partner infidelity, making him/her feeling less attractive, and benefit-provisioning mate retention (i.e., positive inducements and public signals of possession),

which seeks to reduce the risk of infidelity by increasing relationship satisfaction.

Lopes and Shackelford (2018) found evidence of the relationship between the modes of cost-inflicting mate retention tactics and benefit-provisioning mate retention tactics. Participants formed three mate retention clusters or strategies: (1) disengaged (i.e., rare benefit-provisioning and cost-inflicting), (2) exhaustive (i.e., frequent benefit-provisioning and cost-inflicting), and (3) benevolent (i.e., frequent benefit-provisioning and rare cost-inflicting). Moreover, the results indicated that women, more than men, use a disengaged mate retention mode, and men, more than women, use a benevolent mate retention mode. Individuals who do not have enough resources (e.g., time, money) to use benefit-provisioning behaviors can use more cost-inflicting behaviors to retain their romantic partner; or they may resort to a disengaged strategy (i.e., low use of mate retention tactics).

Sex Differences in Use of Mate Retention Tactics

Mate retention behaviors are sex-differentiated: men and women tend to use different strategies to retain their partners. Such differences corroborate the evolutionary hypotheses. While men prioritize physical aspects related to attractiveness in choosing women who appear to have a good reproductive capacity, women seek to choose partners with characteristics that indicate a greater ability to acquire resources. In general, men use more resource display and protection strategies, and women invest more in appearance enhancement and reproductive value (Atari et al. 2017; Buss 1988; Buss and Shackelford 1997; Lopes et al. 2016). For example, differences in the use of tactics include men report less frequent use of cost-inflicting tactics than do women (Lopes et al. 2016; Miner et al. 2009); women more than men use jealousy induction to retain their partners (Buss 1988; Buss and Shackelford 1997; Lopes et al. 2016); and men who suspect a partner's infidelity perform more retention strategies (Buss and Shackelford 1997).

Different uses of mate retention tactics may be linked with reproductive fitness, fertility, sex ratio, and relationship satisfaction. For instance, benefit-provisioning tactics are positively related to relationship satisfaction, while cost-inflicting tactics are negatively associated (Atari et al. 2017; Lopes and Shackelford 2018). Cost-inflicting tactics are riskier than benefit-provisioning because they increase the chances of relationship defection (Miner et al. 2009) and bring negative consequences for the partner's health (Devries et al. 2013). Research on the use of mate retention tactics can help in understanding human romantic long-term relationships and the processes underlying partner selection. In addition, mate retention tactics knowledge may be useful in contexts such as marital therapy or counseling.

Conclusion

Humans usually engage in long-term monogamous relationships. Mate retention is an evolutionary adaptive problem that requires an investment of time, energy, and resources of individuals. Tactics are groups of behaviors that refer to a retention intent, such as jealousy induction and physical possession signals. The Buss (1988) model cataloged 19 major tactics, which may be cost-inflicting or benefit-provisioning. They are used as a protective strategy against threats to the relationship (e.g., partner defection or infidelity). The engagement in one of these tactics is linked to individual and contextual factors, such as differences between the sexes. Research into mate retention tactics can provide valuable insights about long-term relationships, besides subsidizing practical interventions (e.g., marital therapy).

Cross-References

- ▶ Coalitional Mate Retention
- ▶ Mate Retention
- ▶ Mate Retention and Romantic Attachment
- ▶ Mate Retention Strategies

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Mate Selection

- ▶ Evolution of Desire, The
- ▶ Male Qualities and Likelihood of Orgasm
- ▶ Mate Preferences
- ▶ Mate Value Inflation
- ▶ Presence of Children
- ▶ Selective Attunement to Adaptive Problems
- ▶ Sex Differences Versus Gender Symmetry

- ▶ [Violation of Long-Term Mate Preferences](#)
- ▶ [Violation of Short-Term Mating Preferences](#)

[Mate selection strategy](#); [Reproductive strategy](#); [Sexual conflict](#); [Sexual selection hypothesis](#); [Sexy son hypothesis](#)

Mate Selection Criteria

- ▶ [Men's Mate Preferences](#)

Mate Selection Strategy

- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)

Mate Selection Strategy (Version of Sexy Sons Hypothesis)

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Synonyms

[Evolutionary psychology](#); [Good genes theory](#);
[Good-sperm models](#); [Human sexual activity](#);

Definition

Mate selection has been a topic of great interest and has gained much attention from diverse fields (Zhang et al. 2015, 2016). Mate selection strategies overlap with reproductive strategies that encompass a broad set of behaviors involving the timing of reproduction and the trade-off between quantity and quality of offspring (Buss and Schmitt 1993). Weatherhead and Robertson (1979) proposed the sexy son hypothesis claiming that females are assumed to compensate for the survival of their offspring by increasing the number of descendants produced (Huk and Winkel 2008). The sexy son hypothesis also implies that a potential mate's capability as a parental caregiver are irrelevant to his value as the potential father or the female's descendant.

Introduction

Darwin's theory with regard to the process of sexual selection is the foundation of current theories on the evolution of mating systems. Darwin (1871) thinks that the evolution of characters enhanced its ability to obtain mates. Implicit in this concept is that individuals of each sex differ from one another with respect to characteristics that affect the fitness they will confer on another individual if chosen as a mate. Consequently, the existing selection pressure will promote the evolution of techniques for males to show off their superior characteristics and for females to distinguish the good characteristics from the bad (Weatherhead and Robertson 1979). Trivers, in his review of sexual selection and the role of parental investment, concludes that sexual selection has the same effect only if the investment of each sex in its offspring is approximately equal. Otherwise, sexual selection among each sex will be unbalanced. For example, if females put more effort than males, the competition among males to

increase their frequency of mating will be high. Thus, sexual selection among males will be strong. As Trivers (1972) points out, females initially have a much higher investment in terms of the energy supplied to each ovum relative to the very small amount of energy devoted by the male to each sperm. The difference in the relative contributions of each sex increases due to the limited role played by the male in rearing the young, especially in highly polygynous mating systems. Consequently, in such systems sexual selection will act much more strongly on the male. A poor choice by the female has much greater repercussions on her fitness than a similar poor choice by a male has on his fitness (Orians 1961). Based on this, Weatherhead and Robertson (1979) proposed the sexy son hypothesis, which is one of several possible explanations for the highly diverse and often astonishing ornaments of animals (Mead and Arnold 2004). If females choose physically attractive males, they will tend to get physically attractive sons, and, thus more grandchildren, because other choosy females will prefer their attractive, sexy sons. The theory will work regardless of the physical or behavioral trait a female chooses, if it is heritable (i.e., the trait varies between individuals of the population), because it is possessing the trait that makes males attractive, and not the qualities of the trait. Once a preference becomes established, females choosing males with elaborate secondary sexual traits will produce sons that carry alleles for the trait and daughters that carry alleles for the preference, generating genetic coupling that will drive self-reinforcing coevolution of both trait and preference, due to the mating advantage of males with the trait, creating a runaway selection sexy sons process (Mead and Arnold 2004). Similar models have been proposed for postcopulatory female preferences, such as the time at which females removed the male's sperm ampulla after mating. Sexual selection by direct and/or indirect benefits as well as sexual conflict determines the evolution of animal mating systems (Andersson and Simmons 2006). In its original context, the "narrow-sense sexy son hypothesis" of Weatherhead and Robertson (1979) refers to mating systems with care from both parents. In these

mating systems, females that mate with a polygynous male normally receive less assistance than females that mate with a monogamous male (Ligon 1999), and thus suffer from direct fitness consequences that must be (at least) compensated for by the breeding successes of their sexy sons. On the other hand, a "broad-sense sexy son hypothesis" encompasses both polygyny and promiscuous mating systems, with and without care from both parents. Alatalo (1998) argues that the costs of any additional choice may be so minor that female choice for honestly signaling males, that is, good genes, may evolve even if the indirect benefits on offspring quality are small. A similar argument can be made for the sexy son hypothesis if mates of attractive males do not suffer any direct fitness consequences (Huk and Winkel 2008).

In summary, Weatherhead and Robertson (1979) propose a model of the evolution of polygyny in which female choice of mate is at least partially determined by male "sexiness" characteristics that are advantageous only because they attract females.

Conclusion

The sexy son hypothesis claims that females are assumed to compensate for the survival of their offspring by increasing the number of descendants produced. It provides another insight into investigating human being's mate selection strategy based on the evolutionary psychology.

Cross-References

- [Female Mate Choice](#)
- [Kin Interest in Mating Relationships](#)
- [Male Mate Choice](#)
- [Mate Choice Effects](#)
- [Mate Value](#)
- [Mating Strategies](#)
- [Mating Strategy Equilibria](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Sex Differences in Long-Term Mating Preferences](#)

- Sex Differences in Short-Term Mating Preferences
- Sexual Conflict in Mating Strategies
- Sneak Copulation as an Alternative Mating Strategy
- Sociosexuality and Sexual Conflict in Mating Strategies
- Tradeoffs in Mate Selection

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Mate Stealing

- Human Mate Poaching (Schmitt and Buss, 2001)

Mate Value

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Synonyms

Mate worth; Partner reproductive value; Potential mate or partner fitness value

Definition

The “mate value” of a potential mating partner is the inclusive fitness gain that a focal individual makes from mating or partnering with that individual; also, in humans, it is the value of prospective partners on the “mating market.”

Introduction

Mate value is the total potential fitness value to be gained from a prospective mate or partner. It includes all aspects of fitness, incorporating a mate’s phenotypic condition, genetic quality, and resource holding. These factors must be evaluated as to how they affect the fitness of the chooser; for example, given variation in the chooser’s resource holding or genetic compatibility. It is expected that individuals will be selected to maximize the mate value of their partners, leading to the evolution of the criteria used in mate choice. As it is unlikely that mate value can be directly assessed, it must be inferred from morphological and behavioral traits, which evolve under the selective pressure of the choosers choices. This leads to the evolution of traits that reveal mate value, as well

as to counter-selection for the ability to amplify apparent mate value. In animals, plants, and even unicellular organisms, assessment of mate values involves a variety of sensory abilities that enable discrimination between mates. In “higher” animals, it has also been suggested that the evolutionary assessment-advert feedback was critical to the evolution of cognitive capacities, complex social behaviors, and even human language, rendering mate value a pervasive and important area of investigation.

Here is presented an outline of the component aspects of mate value, how they can vary over time, and how the relative value of each component can depend on specific attributes of potential partner pairs. After this, a wider view is taken, explaining sex differences in mate value, and the role of mate value in social species, human interactions, sexual selection, social evolution, and the evolution of human psychology, cognition, and language.

Aspects of Mate Value and Its Variation

Mate value includes all aspects of fitness that can be imparted, and is thus similar to the broad-sense attractiveness of an individual as a potential mate (Buss and Shackelford 1997; Gangestad and Simpson 2000; Edulund and Sagarin 2014). In humans, mate value is sometimes considered in narrower terms as “the extent to which mating with ... *and retaining* ... a partner would have increased a ... person’s ancestral reproductive success” (Sugiyama 2005). In fact most work on “mate value” conducted in humans has used this narrow sense, while that in animals has used the wider concept of “reproductive value”. Yet the areas are not disparate, and a more serious effort to unify them would be useful.

A list of mate value fitness attributes would include the condition of an individual in relation to its environment (e.g., its fat reserves, disease status), the quality of the individual in terms of its genes (e.g., “good genes,” level of heterozygosity), the quality of the individual’s current resources (e.g., territory size, nest site), and their capacity to hold them over the reproductive period and contribute to the fitness of the chooser (e.g.,

the individual’s resource holding potential, age, capacity to provide parental care) (Gangestad and Simpson 2000). These attributes of mate value are valued by a chooser in as far as they will increase its current or future fitness. Finally, in a human-specific sense, mate value can also incorporate more subtle traits, including the “Big Five” personality traits: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism, as well as complex attributes such as trustworthiness, social status, or aspects of wealth, in relation to the trait-state of the perceiver (Goldberg 1993; Edulund and Sagarin 2014). This list could be extended ad nauseum to cover the particular life history details of a species or the intricacies that surround human social and cultural values. What matters from a biological viewpoint is how the survival and reproductive output of the chooser (and that of their offspring) is improved by the mate choice value they ascribe to potential partners when choosing a mate.

In addition to these traits, which are mate value indicators of signaler quality, it has been widely recognized that attractiveness per se can be a feature of mate value. This came out of one of the first attempts to model the evolution of animal and human aesthetic appreciation, by the statistician and geneticist Ronald Aylmer Fisher in the 1930s (Andersson 1994). Fisher saw that arbitrary sexual preferences could be evolutionarily self-reinforcing, because the trait preferred would be inherited by offspring along with the preference itself, coupling the evolution of ornament size and preference intensity. This force – the so-called self-reinforcing Fisherian runaway – may explain the bewildering diversity of sexual signals used in nature – which are often the only obvious traits that differ between closely related species. What remains unclear is why some mate value traits are stable whereas others turn-over. For example, species of peafowl related to the renowned peacock all have exaggerated tail feathers, but differ in coloration. There are parallels here to the diversity of cultural ornamentation and display found in human populations. It has been suggested, for instance, that courtship traits that have high mate value persist whereas those just serving as attractants are subject to rapid change. This explanation

fits both for changes over evolutionary time in animal species and cultural change in human courtship traits, where it could be the case that being fashionable is the true mate value.

Each of these aspects will be discussed in various contexts below. But it is first important to make the general points that (1) the rating of different parts of an individual's mate value may vary over their lifetime (for example, a female may become more or less fertile with age); (2) that what is, or is not, important in mate value varies among species, mating systems, and across the sexes (for instance, a male may value different attributes of a partner to a female); and (3) the mate value of an individual can be relative to that of the set of competitors or potential partners (a "large" male in one context may be "small" in another; the value of two individuals as partners can depend on their compatibilities).

Mate Value in Mate Choice: Perception and Reflection

A female or male will benefit their inclusive fitness if they mate, or partner, with an individual of the opposite sex with a high mate value: either from direct benefits (for instance, nuptial gifts, or parental input) or indirect benefits to their offspring (such as "good genes," heterozygosity, or "sexy genes") (Andersson 1994; Roberts and Little 2008). Given this, it is in the interest of high-value individuals to signal their quality, for instance through high cost, condition-dependent sexual ornaments, or handicaps (Andersson 1994). This increases the chances that they will be chosen as partners. It allows them to be distinguished from lower value individuals who cannot signal in the same way without incurring punitive costs to their survival chances (Pomiankowski 1988). With handicap signals, individuals signal their quality "honestly" allowing the chooser to discriminate and obtain the highest value mates, albeit within the constraint that errors occur as choosers are always to some degree limited in their abilities to make assessments and to detect cheats (Andersson 1994). A consequence is selection for traits associated with discrimination and

perception, such as visual and auditory senses, or even more complex neurocognitive traits, for instance when "ornament traits" involve aspects of intelligence.

Another consequence of the desirability of high-value mates is selection for self-reflexive perception and discrimination. All individuals "want" to maximize their own fitness and seek to mate, or partner, with high mate value individuals (Andersson 1994). But, the quality of partner an individual can obtain will be relative and dependent on others with whom they have to compete. It is a waste of resources – both in energy and time, and sometimes in risk – to seek partners with unobtainable mate values; for instance, for a low-value male to seek access to a high-value female, if she has the opportunity to be choosy, or vice versa (Andersson 1994). A high-quality individual might therefore "want" to behave differently to one of lower value, becoming choosier, or more promiscuous (dependent on its sex and mating system) (Andersson 1994). Likewise, if compatibility is important, then, in prospecting for potential mates, an individual will "want" to account for aspects of itself (Mays and Hill 2004; Buss et al. 2017). In both cases, the tools used for discrimination and assessment, which are used to make an external choice of partners, may be turned inward and provide a basis, consciously or not, for the assessment of self. While the evolving traits will depend on species, sex, and mate system, the search for high mate value partners will feed back on itself and so play a role in driving the evolution of complex behaviors and cognitive capabilities.

Sex Differences: What Males and Females Want

The two sexes are fundamentally distinct due to differential selection either for numerous, small, motile gametes (sperm) or for few, large, static gametes (eggs) (Beukeboom and Perrin 2014). This gamete dimorphism is absent from unicellular species, but almost universal amongst multicellular forms. It is widely believed that sex differences flow from this number-nutrient distinction, and

lead on to differences in what constitutes mate value in the two sexes (Andersson 1994). A demonstration of this can be found in an iconic experiment carried out by Bateman (1948), on the fruit fly *Drosophila melanogaster*. He allowed males and females to mate multiply and showed males had much higher variance in reproductive success than females. Male reproductive success increases with each mating as this results in more fertilization, whereas female output is limited by the resources available to invest in eggs, rather than the number of times she mates. The implication is that, because male sperm are cheap relative to female eggs, males seek to maximize their mate and offspring numbers, while females choose amongst potential partners in order to maximize the quality of each of their offspring. Although there are notable exceptions – such as sex-role-reversed sea horses (where males carry out the work of parental care) – this number versus quality rule holds out over a wide range of species including insects, fishes, amphibians, reptiles, birds, and mammals (Beukeboom and Perrin 2014).

The translation of this rule into mate value is complex, including many species-specific factors, but is dominated by the mating system of the species in question. For example, in a promiscuous mating system, in which males do not contribute parental care or any resources, a female only gains sperm from a male. Hence, male mate value relates primarily to aspects of a male's genetic quality or attractiveness, as exemplified by the peacock's train or stalk-eyed fly eyestalks, and by material or mental constructions, such as the bower bird's decorated maypole and avenue structures (Andersson 1994) or even human conversational ability (Fitch 2010). In these cases, the male is largely indiscriminate and simply assigns all females a similar mate value (Andersson 1994). In male-dominant systems, typified by the elephant seal or red deer, females largely let male fighting determine which males are potential mating partners, which presumably presorts male genetic quality. Females avoid consorting with subdominant males in order to avoid dangerous conflicts, in order to minimize the costs of mating (Andersson 1994). However, male discrimination has been demonstrated within these systems, as

males can attract or herd several females and cannot necessarily mate with all of them in the same time period. For instance, in stalk-eyed flies, males show a burst of sexual activity at dawn, and evaluate female mate value associated with size and so fecundity, mating first with large females when they have a choice.

Alternatively, the mating system can be more sex-balanced leading to much less difference in male and female reproductive success. In the extreme, there is pair bonding, and both parents contribute equally to parental care. Here, the distinction between male dominance and female choice is far less apparent. Females value males in relation to their condition, and how this predicts parental care (Andersson 1994; Trivers 1972). Males value female condition for the same reasons. Indeed, many examples are known where male and female indulge in mutual mate choice, using ornaments and behavior equally in their courtship displays, as in the albatross (Andersson 1994, Trivers 1972). However, extra-pair copulation can result in greater fertility for males and trade-up genetic quality in females, or other more subtle fitness gains (e.g., outbreeding, avoidance of neighbor aggression), so even within monogamy, subtle differences may persist in male and female mate value.

Sex Differences: What Men and Women Want

Human mating systems are complex and highly variable, but can be characterized, roughly, as serially monogamous, with individuals paired in one or more semiexclusive long-term relationships across a lifetime, with extra-pair copulation more or less present, and phases of polyandry and polygyny common in some cultures (Buss and Schmitt 1993; Gangestad and Simpson 2000). The recent emergence of easier birth control may have permitted greater levels of promiscuity by both sexes (Gangestad and Simpson 2000). Females are often the choosier sex, although males also exert notable choice. Because human mating systems vary across cultures and over time it is difficult to make unifying claims about mate

value and mating system (Gangestad and Simpson 2000). However, there are several reasons to believe that the sort of systems outlined above held true across much of human evolution (Simmons et al. 2004). Human men tend to be larger than human women, that is, humans are sexually dimorphic, which implies sexual selection, with potential roles for female and male choice. Further, men have large testes and produce large ejaculates relative to many primates, indicating that sperm competition was historically common (Simmons et al. 2004). Finally, cross-cultural records and observations show that variants on serial monogamy with extra-pair copulation are, and were, common (Buss and Schmitt 1993; Marlowe 2003), with extreme exceptions, like the “reproductive factories” of the ancient Chinese Imperial Harem or the Ottoman Grand Seraglio intermittently observed (Pinker 2011).

Humans also fit with Bateman’s observations. Men produce large numbers of sperm, and can father 10s, 100s, or even 1000s of children, for example, in the famous cases of Gengis Khan and Ismail ibn Sharif (Zerjal et al. 2003; Oberzaucher and Grammer 2014). In contrast, lifetime reproduction by women is at most in the 10s of children; the current record is held by the Russian Mrs. Feodor Vassilyev, with 69 (Urban 1783). In fact, the averages for total and intersex variation in reproductive output are far lower than these maxima (with means nearer 1–3 children and variance around 1–5 in most modern cultures studied, van Daalen and Caswell 2017, and modest differences between men and women, Brown et al. 2009), but this information can still be informative about mate value.

At a broad stroke then, the traits *expected* to count in women’s assessments of men, when looking for long-term partners, include those associated with a man’s ability to provide parental care, such as his condition, wealth, rank and mental disposition, and with traits associated with his resources, genetic quality, and physical attractiveness (Trivers 1972; Buss and Schmitt 1993). In contrast, attributes counted in women’s assessments of men as short-term or extra-pair partners should relate more directly to a prospective male partner’s genetic quality and attractiveness, or

to additional advantages presented through gifts, wealth, or social connections, with little concern given to direct parental input (Buss and Schmitt 1993; Gangestad and Simpson 2000). Likewise, mate value assessments made by men looking for long-term female partners should relate primarily to traits associated with a woman’s ability to produce and rear healthy children, such as her condition, age, and overall genetic quality (Buss and Schmitt 1993), or related to her attractiveness, though traits such as “curviness,” which may be associated with fecundity. In contrast to assessments made of men by women, however, men’s assessments of women as short-term or extra-pair partners should still be based on estimates of the women’s capacity to produce offspring and provide maternal care (Trivers 1972; Buss and Schmitt 1993). The reason for this sex difference is that additional reproduction is more costly for women. In most cultures, women contribute more to raising children than do men (and must always give birth). If a woman is to have a short-term or extra-pair partner, genes or gifts are required; a man requires only a partner, and can then leave (Andersson 1994; Trivers 1972; Buss and Schmitt 1993; Gangestad and Simpson 2000).

In line with this, recent large-scale cross-cultural studies have found that single women do indeed prefer men exhibiting traits such as wealth, generosity, intellect, dominance, cultivation, sociability, reliability, similarity, kindness, understanding, humorousness, and pleasantness as potential long-term or marriage partners, while single men prefer women who are attractive, creative, and domestic (Schwarz and Hassebrauck 2012). Further, while women will consider long-term male partners 5 years younger to 8 years older, men will consider female partners 10 years younger but only 4.5 years older (Schwarz and Hassebrauck 2012). Finally, women are also less likely to consider an opposite-sex partner for marriage if the individual earns less, is less educated, or is irregularly employed, but are more likely than men to consider a less-attractive opposite-sex partner for marriage (Schwarz and Hassebrauck 2012). However, these observations have only been made in a limited set of cultures and

environments, and may not be as general as is usually assumed.

Additional studies have shown that predicted patterns also follow within relationships. Partnered women are more likely to prefer extra-pair partners with more “masculine” faces, symmetry associated scent, deeper voices, and other behavioral displays associated with intrasexual competitiveness (Gildersleeve et al. 2013), while partnered men focus more on traits like attractiveness and youth, associated with fertility and fecundity (Roberts and Little 2008). An important point though is that in each case, the traits preferred by men and women vary with self-assessment, such as that reflected in self-esteem, self-assessed quality, or complementary mentalities (Roberts and Little 2008; Reeve et al. 2017). A clear demonstration of this relative-to-self mate value is that female mate preferences have been shown to vary with the menstrual cycle. This cycle causes a fluctuation in female mate value, which increases near ovulation, but is very much reduced postmenses. Complementing this, there is temporal variation in female mate preference as a female approaches ovulation, with increased interest in “masculine” traits (Roberts and Little 2008; Gildersleeve et al. 2013). Mate-value feedback plays a role here too, as a female’s awareness of her own reflected mate value – conscious or not – will be crucial to her behavior (Roberts and Little 2008; Reeve et al. 2017). Another example of relative-to-self mate value, for instance, is the finding that women become less choosy after rejection (Reeve et al. 2017), with an accompanying drop in their levels of self-esteem (Schwarz and Hasselbrauck 2012). Likewise, men’s assessment of their own mate value is linked to their partners mate value and influences their self-esteem and retention behaviors (Starratt and Shackelford 2012; Holden et al. 2014). Men with higher self-esteem do more provisioning behaviors, give fewer negative comments and commit less violence, but can be more likely to cheat – as too can women with higher self-esteem and components of mate value (Starratt et al. 2017). All of these behaviors arise though selection for self-perception and the constant assessment of relative mate value. They shape human psychology, playing a crucial role in

influencing the evolution of phenomena such as mate switching and partner fidelity (Buss et al. 2017; Starratt et al. 2017).

In short, as is theoretically expected, women appear to be interested in and to value men in relation to their intelligence, mentality, wealth, and resources, while men value women as mates more in relation to attractiveness, youth, creativity, and domesticity, with variations in the targets and intensity of preference arising in line with partnership status and mate value fluctuations.

Mate Value in Social Evolution

An important class of mate value traits, for animals and humans, are the context-dependent mental traits associated with society and socialization. Forms of society are exhibited by animal classes as diverse as ants, bees and wasps (the eusocial insects; discussed elsewhere in this volume), crows and parrots, dolphins and elephants, monkeys, apes and humans (Whiten and van Schaik 2007). In each case, the social environment influences mate value. A simple near-universal instance, touched upon above, arises from rank or social status. Rank is a social construct, but its consequences are very real. High rank can be inherited by birth, or can emerge from physical strength, or from aspects of intelligence such as the capacity to make alliances or manipulate other members of the social group to obtain “political” power (Chapais 2015). When rank differences are pronounced, they confer advantages to those with higher rank, including but not limited to, better access to resources, reduced stress, reduced effort in food searches, and increased access to sex and reproduction (Rodriguez-Llanes et al. 2009). So rank itself tends to increase an individual’s mate value.

This observation applies to all animals, including humans. In the case of monkeys and apes such as macaques and chimpanzees, rank can be comprised of strength, alliances, and birth, as signified by behavior (Rodriguez-Llanes et al. 2009). In humans, rank is a less concrete trait (Chapais 2015). It comprises traits such as “political” power, wealth, and positional power (e.g., in a work place) (Chapais 2015). All traits associated

with this rank-power will be selected via mate choice, and all traits that assist in obtaining rank-power will also be selected. This is an example of socially context-dependent mate value. Others include the ability to make friends, form alliances, or manipulate individuals/groups (Brent 2015).

Mate Value and Mental Evolution: Cognition, Language and Deception

As can be seen, the need to assess mate value between prospective human mate partners has the potential to enhance discrimination, both through physiological and neurological mechanisms. Moreover, as mate value will be in part determined and assessed in a social context in human societies, it has been suggested that it has contributed to the evolution of mental capacities, including the ability to make accurate self-assessments and to detect inaccurate and deceptive displays of mate value (Shettleworth 2001; Whiten and van Schaik 2007). For instance, as soon as language or proto-language evolves, it is plausible that linguistic ability becomes a mate value focus, similar to how bird and whale song are included in mate value assessments (Fitch 2010). While linguistic ability, like vocabulary, originality, or construct complexity, could be condition-dependent traits used to assess mate value, language could also be used to exaggerate claims about the self, and induce high-value partners to mate (Fitch 2010). The consequence should be selection for better abilities to detect such deception and to direct mate value assessment toward honest expressions of quality, possibly leading to various selective feedback loops leading to better abilities in both language and intelligence (Fitch et al. 2010). In this way, mate value may have played a role on the evolution of human language, cognition, and psychology, but this remains to be fully tested.

Conclusion

Mate value is the total value of a potential mate to the current, future, or inclusive fitness of an individual that is assessing prospective mating

partners. Which traits contribute to mate value will depend on species, mating system, and sex. Further, mate value will vary over an individual's life, and in relation to the current state, situation, or context that an individual is in. Mate value can influence mate choice, social interactions, and behaviors. It must play a crucial role in sexual selection and social evolution. Moreover, selective feed-back between choosers and chosen mean that mate value assessment will have important consequences for the evolution of intelligence, psychology, cognition, and, at last, human language. Looking to the future, it would be useful to more fully integrate across narrow human mate value studies and the wider reproductive value ideas used in animals. This will bring new insight.

Cross-References

- ▶ [Body Attractiveness](#)
- ▶ [Costly Signaling](#)
- ▶ [Cultural Differences in Mate Preferences](#)
- ▶ [Evolution of Intelligence, The](#)
- ▶ [Evolutionary Standards of Female Attractiveness](#)
- ▶ [Facial Attractiveness](#)
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- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
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- ▶ Self-Esteem Tracks Mate Value
- ▶ Self-Evaluations Track Perceived Mate Value
- ▶ Sex Differences in Human Mate Preferences (Buss, 1989)
- ▶ Sexual Selection
- ▶ Sexual Signalling
- ▶ Short-Term Mating
- ▶ Social Dominance and Sexual Access
- ▶ Status and Dominance Hierarchies
- ▶ The Handicap Principle
- ▶ Vocal Attractiveness
- ▶ Women's Mate Value
- ▶ Youth and Fertility

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Mate Value Inflation

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Synonyms

Mate selection; Mate value; Mating strategies; Social media

Definition

Mate value inflation is the process of employing strategies to increase one's value as a potential mate by targeting characteristics preferred by the opposite sex, making oneself more desirable so as to increase the chances of successful mating.

Introduction

Over the course of evolutionary history, characteristics that enhanced survival or held reproductive value were preferred when searching for potential mates (Buss and Schmitt 1993). Possessing these characteristics, therefore, was indicative of one's mate value and allowed one to be successful in the game of sexual selection.

The current chapter reviews the mate preferences of men and women, discusses the strategies men and women engage in to enhance mate value, and highlights some of the consequences that may result from mate value inflation in the context of modern social media.

Evolved Mate Preferences

Men and women evolved to prefer different characteristics in a mate as a result of different adaptive challenges they faced in the ancestral past. Due to women's decline in fertility as a function of age, men tend to look out for traits indicative of high reproductive value and sexual desirability such as physical attractiveness (Buss 1989). In contrast, men offered resources and protection which aided the survival of women and their offspring; hence, women tend to look out for men's social status and industriousness, traits which are ancestrally related to their ability to provide resources and their physical strength (Buss 1989). With these key dimensions being sought after by a big pool of intrasexual competitors, individuals would have to possess a sufficient level of mate value to be selected by members of the opposite sex for mating and reproduction.

Mate Value Inflation Strategies

Mate value is determined by one's possession of the key traits that the opposite sex has evolved to value and prioritize in their mates, and the amount of resources – time, money, and effort – one is willing to expend during the mating process (Fisher et al. 2008). Displaying high mate value facilitates success in the mating game as high mate value attracts potential mates, provides mating opportunities and the option of choosing higher quality mates among a pool of potential mates, and enhances one's position in intrasexual competition (Yong et al. 2016). Thus, with the many benefits high mate value confers, both men and women engage in behaviors that serve to

increase their chances at reproductive success. Strategies that serve to inflate one's mate value are primarily aimed at enhancing the key traits sought after by the opposite sex.

Physical Enhancements

Women, more than men, are likely to enhance their physical appearance (Buss 1988; Buss and Schmitt 1993). They consume diet pills (Hill and Durante 2011), sign up for and attend artificial sun-tanning sessions (Hill and Durante 2011), and undergo cosmetic surgeries (Arnocky and Piché 2014) to enhance their attractiveness despite the negative health repercussions and risks associated with such methods. Women also allocate a larger portion of their financial resources than men to buying appearance-enhancing beauty products (Hayhoe et al. 2000) and continue to do so even when economic times are bad (Hill et al. 2012). In doing so, females portray themselves as more attractive so as to target males' evolutionary preference for physically attractive mates.

Conspicuous Consumption

Owning luxury products also serves to inflate mate value as it signals to potential mates that preferential mate traits are present (Griskevicius et al. 2007). Conspicuous consumption is dominantly used by men to draw attention to their social status and wealth – indicators of resource abundance – which are characteristics that women have evolved to seek (Sundie et al. 2011). Women also seek to own luxury products in efforts of promoting their mate value (Hudders et al. 2014). Women who own luxury products are perceived to be more attractive by other women, and hence are perceived to have higher mate value. This gives women an advantage over their rivals, particularly those who own less luxurious products, in intrasexual competition.

Conspicuous spending on altruistic causes also aids in the enhancement of mate value. In recent times, there has been an increase in spending on products that are perceived to be "green." Because altruistic behaviors that displayed humanistic and moral attitudes suggested better genes and demonstrated ideal mate traits such as good parenting habits (Cela-Conde et al. 2010), spending on such

products are indicative of an individual's willingness to partake in pro-social behaviors over pro-self-behaviors, thus elevating one's mate value. Additionally, individuals are more inclined to make purchases of "green" products only when costs incurred are higher than or equal to their nonenvironmentally friendly counterparts, and when the purchases are done in public (Griskevicius et al. 2010). This display signals that they have enough resources to "give away" without inflicting financial loss (Griskevicius et al. 2010). Thus, conspicuous consumption on both luxury and "green" products is suggestive that an individual possesses ideal mate traits of resource abundance, and arguably, altruism, making displays of such consumptions a fitting way of increasing one's perceived mate value.

Mate Value Inflation Through Social Media

Individuals can also enhance their mate value on social media through technological tools and features offered on these platforms. Less attractive individuals are likely to increase their physical attractiveness with more flattering photos, or older photos in which they look younger, and are also more likely to be deceitful in verbally describing their looks (Toma and Hancock 2010). Additionally, women are more likely than men to have doctored photographs online (Hancock and Toma 2009) and to misrepresent personal characteristics such as their age and weight (Hall et al. 2010). In contrast, men, more than women, strategically misrepresent characteristics such as personal assets, personal interests, and personal attitudes on their online dating profiles (Hall et al. 2010).

With social media, signaling attempts of mate value, where once displayed in natural real-life settings, can now be displayed virtually to a much larger audience than possible during ancestral times. This is especially useful since social media is increasingly being used as a platform for seeking mating opportunities. For example, a study observing conspicuous displays of exercise efforts found that the act of posting workouts

served to inflate one's mate value, tapping on mate preferences for healthy individuals (Vandenbroele et al. 2019). Similarly, signaling efforts in conspicuous spending and consumption, where the outwards display of wealth as an ideal mate trait influences mate value, are more easily displayed through social media.

Consequences of Mate Value Inflation Strategies

Engaging in mate inflation strategies such as those outlined above brings about an array of consequences beyond that of a higher mate value. Mate inflation strategies implicate deception, which is defined as the consequence of an individual's attempt to send signals that specifically appeal to the preferences of the opposite sex (Buss and Schmitt 1993). More often than not, individuals misrepresent their actual mate value in their attempts to inflate their mate value. Women experience higher emotional distress upon being deceived about a mate's resources or social status (Haselton et al. 2005). On the other hand, men – being the sex more invested in short-term mating – experience greater emotional distress than women when sexually deceived, especially when they are misled by a potential partner about their willingness to have sex (Haselton et al. 2005).

Using the tools and nature of social media to inflate mate value also invites several less-than-desirable consequences, especially with social media being a mate-searching platform. Increased access and exposure to potential mates through social media and dating platforms have caused excessive searching due to the massive number of choices available (Yang and Chiou 2010). Excessive searching refers to the search for the best available option among potential mates available online, ultimately resulting in worse mate-choice decision-making (Yang and Chiou 2010). Furthermore, access and exposure to a larger number of attractive individuals reduces males' likelihood to remain committed to existing mates and reduces females' self-perceived desirability (Kenrick et al. 1994). Positive interactions with potential mates on these platforms, such as

receiving likes, swipes, or matches, can lead to an inaccurate sense of self-perceived desirability and increased intentions of infidelity (Alexopoulos et al. 2019).

Conclusion

Humans engage in mate inflation strategies to make oneself more desirable to potential mates and to, ultimately, boost chances of successful mating. These strategies typically revolve around enhancing the key traits sought by the opposite sex – resources and status in men by women and physical attractiveness in women by men. Social media – which increasingly offers mating opportunities – allows quick, low effort displays of conspicuous consumption and enhanced physical appearances, hence adding on to the repertoire of strategies one can engage in to enhance mate value. However, mate value inflation strategies bring about deception attempts, which lead to emotional distress in both men and women. Inflating mate value online also leads to poor decision-making in mate choice and reductions in partner commitment and fidelity.

Cross-References

- Engagement Rings as Modern Commitment Cue
- Evolution of Desire, The
- Female Mate Choice
- Female-Female Strategies
- Male Mate Choice
- Mate Preferences
- Mate Value
- Men's Mate Preferences
- Women's Mate Preferences

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Mate Worth

► Mate Value

Mate-Choice Copying

► Mate Copying

Material Extrinsic Investments

► Resources

Maternal Abandonment and Maternal-Fetal Conflict

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Synonyms

[Infanticide](#); [Neglect](#)

Definition

Withdrawal of maternal caring behaviors after the baby is born; may directly or indirectly lead to infant death.

Introduction

Evolutionary conflict occurs when natural selection acts in opposing directions on different genes involved in an interaction (Burt and Trivers 2008). Conflict can be found at all levels of organization, from conflict between species, to conflict between individuals within a species, to conflict within an individual itself. Most of these forms of conflict revolve around competition for resources and differences in optimal resource allocation among individuals. Between genetic relatives, what is beneficial to one relative may not be beneficial, and may even be detrimental, to another. This situation occurs when there is an unequal probability that genes from one individual will be shared with another. For example, if a mother invests abundant resources in one child, it benefits both that child and, due to shared genes, the mother herself; however it will detract from the mother's ability to invest in other offspring. From the maternal perspective, she shares half her genes with each of her children, so she benefits optimally from maximizing her reproductive output. However, from the perspective of any one child, there is a lower probability that a gene found in that child's genome will be present in other siblings (although there is a 50 % probability that a maternal gene found in one sibling will be found

in the other, the sibs may not be paternally related, thereby reducing their probability of genetic similarity) (Trivers 1974). Therefore there is an unequal benefit for the child relative to the mother when she allocates resources to any one child versus conserving resources for other potential offspring. These situations produce what is known as maternal-offspring conflict.

While the loss of a child will result in a perceived fitness cost for the mother, there are situations in which the long-term fitness benefit will compensate for this initial cost; however this will always come at a cost to the genes present in the child. From mum's perspective, it is better to invest fully in a future reproductive event than to invest in an offspring that is unlikely to succeed. This is most commonly seen in spontaneous abortion, as the earlier the mother stops investing in the child the lower the cost will be to her. However this can be a tricky process, because after implantation the offspring is able to take some control over its own fate (see ► [Spontaneous Abortion and Maternal-Fetal Conflict](#)). After birth the power shifts substantially back into the hands of the mother. Furthermore, in a uterine environment it can be challenging for a mother to accurately assess the quality of her potential offspring, as there are many situations that would be severely detrimental to a child after birth that would not be apparent in utero (e.g., it is difficult to test for blindness in the womb). For these reasons maternal rejection, abandonment, or even infanticide can occur after birth.

Infanticide

In humans, the majority of infant deaths due to injury are caused by homicide. Infant homicide in the first 3 years of life is most commonly committed by an unrelated person, but during the first year of life the mother commits most infant homicides (Overpeck et al. 1998). In fact, it is estimated that over 80 % of all babies killed will die in their first day of life (Bradley 2003), usually at the hands of the mother (Hrdy 2016). There is a ten times greater risk of neonaticide (homicide in the first day of life) than at any other time in life (Herman-Giddens et al. 2003). In one

study of newborn homicide (0–4 days of life; death due to homicide or abandonment) in the USA, mothers were responsible in over 85 % of cases, with the age of the mother ranging from 14 to 35 years, and 35 % of cases occurring in second or subsequent pregnancies (Herman-Giddens et al. 2003). This indicates that, while there are many risk factors of early infanticide, it happens with a broad range of women, often after at least one successful pregnancy has already occurred.

Rates of infanticide increase with economic stress (Hatters Friedman and Resnick 2007), with the USA exhibiting higher rates of filicide (parents killing their own offspring) than any other developed country (Friedman et al. 2005). While older mothers who commit neonaticide are more likely to be psychotic, neonaticide is more often committed by young mothers without many resources or access to help with caregiving (Friedman et al. 2005). In other cooperatively breeding primates like tamarins, mothers are significantly more likely to abandon an infant if she has no help, with most abandonment decisions occurring within the first 72 h after birth (Bardi et al. 2001). This appears to support the evolutionary expectation that a mother is best off cutting her losses as early as possible, especially when she has fewer resources available.

In less extreme circumstances, behaviors that are intended to elicit maternal care in healthy infants, such as crying, are evaluated differently by mothers in response to cues of low health. Some ethnographic reports describe maternal aversion to cries of sickly seeming infants, while cries in fat, healthy looking babies are met with maternal attention (Hrdy 2016). In an experimental paradigm, adults rated faces of babies that had been artificially manipulated to appear skinny (low subcutaneous fat) as less cute and less healthy, and even showed decreased adoption preferences in response to the manipulation (Volk et al. 2005). These results indicate that mothers assess infant health, consciously or subconsciously, and may be weighing the cost of maternal response against the probability of infant survival.

Postpartum Depression

Postpartum depression (PPD) is the onset of clinical depression after delivery of a child. It is quite common, affecting about 15 % of women (Robertson et al. 2004) in cultures all around the world (Tracy 2005). “Baby blues,” a less severe version of PDD which begins within days of delivery, is significantly more common, affecting up to 75 % of mothers (Robertson et al. 2004). Symptoms of PDD can include withdrawal from maternal care behaviors, the most extreme cases of which can result in infanticide (Robertson et al. 2004). Evolutionary psychologists and anthropologists have theorized that PPD evolved as part of the mechanism for allowing mum to decide on the degree of investment to make in a given offspring (Thornhill and Furlow 1998). It may also be used as a signal to increase alloparental support (Tracy 2005); one of the most common risk factors for postpartum depression is perceived lack of support (Tracy 2005), so exhibiting symptoms of PDD may be an adaptive response for soliciting support from family members.

Infant Countermeasures

Although an infant will be genetically related to a future sibling, it is always most related to itself; therefore it is selected to favor its own survival over that of a future potential maternal sibling. It is hypothesized that many traits commonly found in human babies have evolved in order to acquire maternal attention and resources, and reduce the likelihood of being abandoned (Hrdy 2007). These include the extremely high levels of subcutaneous fat that we acquire shortly before birth (Cunnane and Crawford 2003) and a variety of behaviors for eliciting maternal engagement (Hrdy 2007). For example, human babies have much larger sclera (whites of the eyes) than other primate babies. This has been described as an evolved mechanism to elicit maternal care, as it highlights the direction of the infants’ gaze (Hrdy 2007). Not only are features such as round eyes and chubby cheeks perceived as “cuter,” they

have also been shown experimentally to elicit caregiving behaviors relative to photos of infants digitally manipulated to lack these features (Glocker et al. 2009a). These characteristics of infant faces have been shown experimentally to modulate the mesocorticolimbic system, including the nucleus accumbens (reward anticipation), striatum (mutual cooperation and social bonding), and precuneus (attention focusing) (Glocker et al. 2009b).

In addition to these physical features, human infants smile, laugh, and imitate adult facial expressions in ways not observed in other newborn apes (Hrdy 2007). Evidence for the role of genetic conflict here can be found in the literature on Prader-Willi syndrome (PWS) and Angelman syndrome (AS). Individuals with PWS are missing a paternally expressed component of chromosome 15, and are described as weak, quiet, and sleepy (Haig and Wharton 2003). On the other hand, individuals with AS are missing the maternally expressed component of the same chromosome, and these individuals demonstrate increased signals of social engagement, such as frequent smiles, laughter, and sustained eye contact with caregivers, specifically in the presence of other children (Brown and Consedine 2004). This has been interpreted as indicating that, when unopposed, maternal genes benefit from decreased demands on the mother, while paternally inherited genes present in the child (but missing in the mother) elicit behaviors that are likely to attract maternal investment. This supports the notion that many traits found in infants have evolved to evoke increased maternal attention, bonding, and reward circuitry in the maternal brain in order to decrease the chances of maternal rejection.

Conclusion

Since pregnancy is such a costly process for the mother, there is increased pressure on mothers to invest in offspring that have already been born. That being said, there are markers of health and quality that are difficult to assess in utero. For this reason, there is still some degree of maternal-

offspring conflict after birth. While mum might benefit from limiting investment in a low quality offspring, baby would prefer to gain maternal investment even if that comes at a cost of future maternal sibs. This provides evolutionary pressure for adaptations in both mothers and infants to navigate this struggle.

Cross-References

- [Infanticide](#)
- [Maternal-Fetal Conflict](#)
- [Parent-Offspring Conflict](#)
- [Spontaneous Abortion and Maternal-Fetal Conflict](#)

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Maternal Age

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Synonyms

Age of mother at birth of her child

Definition

Age of mother at birth of her child.

Introduction

Timing of parenthood varies strongly within individuals, across societies, and over time. Whether a woman gives birth to a child at ages below 20 or above 40 may have important implications for her well-being, as well as for that of her child. The process of postponement of parenthood has fuelled concerns about the implications of fertility postponement on the health of the children. There may, however, also be important benefits and advantages among those that are born to older parents. This article briefly reviews the characteristics of older mothers and current literature on both the potential positive and negative effects of older-age motherhood.

Characteristics of Older Mothers

A dominant demographic trend in the latter half of the twentieth century that has continued into the early twenty-first century has been fertility postponement and increasing age at first birth. For example, in Germany and the UK, the mean age at first birth exceeded 30 in 2009. In Sweden, the

share of children born to mothers over age 40 rose from 1% in 1975 to 5% in 2015; in the same period, the share of children born to mothers under age 20 declined from 8% to 1% (Human Fertility Database 2017). These processes have been attributed to the contraceptive pill, the expansion of career opportunities for women, and increasing economic uncertainty (Sobotka 2004).

The process of postponement has resulted in changing characteristics of older mothers. Historically, older-age parenthood has been associated with low socioeconomic status and high parity. However, this may have changed. Goisis et al. (2015) analyzed four UK birth cohort studies that covered 1958, 1970, 1992, and 2000–2002 and documented that in the 1958 and 1970 birth cohorts, socioeconomic status based on occupation and education was highest in the households in which the mothers were aged 25–34 years at birth. The pattern however was reversed in the later cohorts, as in the 1992 and 2000–2002 birth cohorts, socioeconomic status was highest in households in which the mothers were aged 35–39 at birth. Similarly, smoking while pregnant was high in all age groups in the early cohorts, but in the later birth cohorts, older mothers had the lowest rates of smoking while pregnant. These findings suggest that the sociodemographic disadvantage that historically was associated with older maternal age has not only disappeared but has turned into a potentially important advantage.

Maternal Age and Child Outcomes

A century ago, Alexander Graham Bell wrote that children born to older mothers have the shortest lifespan (Bell 1918), and a review by Liu and colleagues suggests that “Parental age has been shown to be a major factor, if not the most important factor, in producing variability in offspring”, including health, longevity, and intelligence (Liu et al. 2011). For example, the risk of negative birth and childhood outcomes – e.g., Down syndrome, childhood cancer, and autism – appears to increase with maternal age (Liu et al. 2011).

Moreover, existing literature suggests that being born to an older parent may also have long-term health consequences, and in particular, old-age mortality may be elevated among those that are born to older mothers (Smith et al. 2009).

There may, however, also be important benefits associated with being born to an older mother. Goisis et al. (2017) analyzed three UK data sets, covering the birth cohorts 1958, 1970, and 2000–2002, and found that while child cognitive development was negatively associated with maternal age in the early cohorts, in the 2000–2002 birth cohort, children that were born to mothers aged 35 and above scored higher than those that were born to younger mothers. Barclay and Myrskylä (2016) analyze Swedish data and find that being born to an older mother is associated with higher cognitive ability and higher educational attainment. An analysis of 77 countries across the world using the Demographic and Health Surveys suggests that the positive effect of being born to an older mother may not be limited to the rich world. In particular, in countries in which contemporary development is positive, being born to an older mother may be associated with decreased mortality risk at young ages (Barclay and Myrskylä 2017).

Maternal Age and Parent Well-Being

Parenthood may bring joy but may also come with unexpected stress, responsibilities, and challenges. Research on older mothers suggests that women who postpone childbearing are more “ready” and less stressed by having children (Gregory 2007). Using the World Values Survey data across a large number of countries, Margolis and Myrskylä (2011) document that the association between parenthood and subjective well-being depends on age, being negative at young ages, but reversing to positive at older ages (50+). Another study focusing on Germany and UK found that while having children mostly has only a temporary impact on subjective well-being, among those who experienced their first birth at ages 35 and above, the positive impact of

childbirth on the mother's well-being was long-lasting (Myrskylä and Margolis 2014). This suggests that the age at which individuals have their first children is a strong predictor of how much they are able to enjoy parenthood.

Conclusion

Although most research on advanced maternal age focuses on the risks associated with reproductive aging, recent research suggests that older mothers today differ from those in the past and that there are also benefits to postponing fertility to older ages. Older mothers today observe better health behaviors during pregnancy, are more socioeconomically advantaged, and seem to be happier after childbearing. Furthermore, the children of older parents in high-income countries have better health and educational outcomes.

Cross-References

- [Birth Spacing and Birth Order](#)
- [Family](#)
- [Fertility](#)

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Maternal and Offspring Condition

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Synonyms

[Fitness](#); [Health](#); [Nutritional status](#); [Physical shape](#); [Socioeconomic status](#)

Definition

The Trivers-Willard (TW) hypothesis predicts that parent and offspring condition should effect the ratio of male/female offspring, but the validity and the exact causal mechanisms of this hypothesized relationship are still unclear.

Introduction

According to the Trivers-Willard (TW) hypothesis, offspring sex composition and parental investment postpartum may, under certain conditions, be biased toward either male or female offspring. Maternal and offspring condition play a decisive role in the following three assumptions underlying the TW hypothesis: First, maternal and offspring condition are correlated during the parental investment phase. Second, early offspring condition is correlated with offspring condition later in life. And third, males profit more than females from slight advances in condition in their reproductive success (Trivers and Willard 1973).

The question as to what indicators of maternal and offspring condition specifically are involved in modulating a possible TW effect is closely linked to the question of the specific mechanisms at play in sex ratio variation. Although the authors don't say much about mechanisms, they suggest that in species "in which males determine sex of offspring, female control of the sex ratio must involve differential mortality by sex" either of the sperm or at later stages during the parental investment phase (Trivers and Willard 1973, p. 91). The authors further suggest a few examples of physiological indicators of condition, e.g., health, strength, and body weight, as well as a number of indicators of environmental conditions, e.g., exposure to stressors, litter size, parity, and time of season, that may be relevant with regard to their hypothesis (*ibid.*). Yet, until very recently, little was known about the specifics of how a possible TW mechanism might operate.

The lack of a known mechanism and, in consequence, the lack of a clear specification of the relevant indicators for maternal and offspring condition might have contributed to the as of yet inconclusive state of the TW hypothesis (Cameron 2004; James 2012; Schnettler 2010). In recent years, researchers have tried to systematize findings on the statistical association between some measure of maternal condition and offspring sex ratios. Two meta-analyses, together covering about 400 empirical studies that examine the association between some measure of maternal condition and sex ratios in

various mammalian species, show that support for the TW hypothesis is stronger when maternal condition is measured at around the time of conception as opposed to a later time in the reproductive cycle (gestation, birth) (Cameron 2004; Sheldon and West 2004). This issue of timing has since been taken up by at least two studies examining the TW effect in humans. In one of these studies, based on a general population in Sweden, different timing of resource measurement led to the same conclusion: that there is a null effect with regard to the association between parental condition and sex ratios (Kolk and Schnettler 2016). The other study is based on a US elite sample and finds tentative evidence for a similar timing effect as one of the two meta-analyses elucidated (Schnettler 2013). Yet, in both of these studies, timing of resource measurement is rather coarse due to limited data availability on humans, as compared to the studies on other mammalian species.

The two meta-analyses mentioned above also evidence the breadth of condition measures that have been applied in research on the TW hypothesis so far. In addition to measures listed above, these include, e.g., mother's age, dominance status, food availability, time of insemination, and body weight (Cameron 2004). One of the two studies found that the correlation between maternal condition and sex ratios was stronger in studies that operationalized condition as a behavioral measure rather than a physiological one. Theoretically, the authors made sense of this finding by arguing that behavioral dominance may be a better predictor of future resource access than, e.g., current body weight, but also pointed out that an interaction between physiological and behavioral condition measures may exist that could not be tested in their meta-analysis and possibly complicates an empirical assessment of the TW hypothesis (Sheldon and West 2004).

Both a specification of the timing of maternal condition relative to the specific phase of parental investment and of measures used to proxy maternal condition help to narrow down the set of mechanisms driving a potential TW effect. In recent years, advances have been made in developing explanatory models on the potential

mechanisms responsible for sex ratio variation in response to various environmental influences, going beyond the scope of the TW hypothesis (see, e.g., Schnettler and Klüsener 2014). James (2008) has put forward the hypothesis that hormonal levels of both parents around conception affect sex determination preconception. In his research, he also links various environmental conditions (e.g., external stressors and toxic exposure) to varying hormonal levels, thus at least suggesting to close the theoretical gap between more distant measures of condition and physiological measures of condition directly involved in sex determination. Parental hormones also play a decisive role in a model put forward by Grant and Irwin (2009). Their model is at least in part supported by previous experimental research by the same two authors and suggests more specifically that the level of maternal follicular testosterone prior to conception affects the shape of the outer rim of the ovum and makes it more or less likely to later be fertilized by an X- or Y-chromosome-carrying spermatozoon. In addition to this mechanism around conception, their model further specifies that male fragility during the gestational period is another mechanism that affects sex ratios in a population, the latter being consistent with Trivers' and Willard's suggestion for a mechanism (see above). Taken together, their model allows one to reconcile some previously inconclusive findings on sex ratio variation by allowing that measures of condition may have different effects around conception and at later stages during the gestational period (Grant and Irwin 2009; Schnettler and Klüsener 2014).

Conclusion

In sum, various measures of condition have been employed in previous research on the TW effect, ranging from physiological measures that may be more or less directly involved in sex ratio variation to more distant environmental measures. The challenge in future research will be to elaborate on the causal pathways linking these different types of condition and how they are involved in the

hypothesized mechanisms. For studies examining the TW effect in human societies, where often some measure of socioeconomic status has been employed as a proxy for maternal condition, the challenge will be to examine how socioeconomic status affects physiological measures of condition. The null effect of a TW effect in a modern welfare state like Sweden (Kolk and Schnettler 2016) might well be due to the fact that differences in socioeconomic status are inconsequential with regard to physiological measures of condition, whereas in less developed societies, there might be a stronger connection between measures of condition that are more or less distant from the sex determination process.

Most of the above relates to the physiological part of the TW hypothesis and what maternal conditions might be driving this physiological effect. Much less is known about the behavioral part of the TW hypothesis in humans predicting sex-based favoritism in parental investment. The challenge here is larger, given that the potential causal pathways between indicators of condition and parental investment behavior may be strongly shaped, too, by other cultural and social influences on parental investment (Schnettler 2010). One potential mechanism linking maternal condition and maternal investment behavior that is discussed in the research literature is postpartum depression. The argument here is that postpartum depression can be seen as a withdrawal of maternal investment (Johns and Myers 2016).

Cross-References

- Offspring Sex
- Parental Investment Theory
- Trivers-Willard Hypothesis

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Maternal Behavior

► Maternal Bonding

Maternal Bonding

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Synonyms

Maternal behavior; Maternal love; Maternal motivation; Mother-infant attraction

Definition

The strong attachment of a mother to her infants, resulting in her caring for and protecting them, at least until they reach independence.

Introduction

Parental behavior is any behavior displayed by one member of a species toward an immature conspecific that increases the likelihood that the infant will survive (Numan and Insel 2003). Depending on the species, parental behavior can include maternal, paternal, and alloparental behavior (caretaking behaviors directed toward an infant other than one's own offspring). In mammals, the major infant-caretaking system is a uniparental maternal care system: In 95% of mammalian species, the postpartum mother is the sole caretaker of her offspring (Numan and Young 2016). In a small percentage of mammalian species, paternal and/or alloparental behaviors, in addition to maternal behavior, are essential for infant survival. Alloparental behavior occurs when older siblings, instead of dispersing, remain in the family group and help the mother care for her more recently born offspring (Numan 2015). Alloparental behavior can be divided into allo-maternal and allopaternal behavior, depending on the sex of the alloparent. Hrdy (2009) has hypothesized that allomaternal behavior was essential for infant survival during early human

evolution. The occurrence of paternal and alloparental behavior suggests that when such behavior is essential for infant survival within a social group, natural selection will create alternate mechanisms, which do not require pregnancy and parturition, to enable an individual to form a bond with an infant.

Hormones and Maternal Behavior

In most mammals, the physiological events of pregnancy and parturition influence brain mechanisms to activate maternal motivation (Numan and Insel 2003). This ensures that maternal behavior will be synchronized with the birth of the mother's young at a time when she is physiologically prepared to care for them, since many of these same physiological events also promote lactation. The essential physiological factors that activate the onset of maternal responsiveness at parturition include estradiol (a hormone secreted by the ovaries), prolactin and placental lactogens (hormones secreted by the pituitary gland and placenta, respectively), and the neuropeptide oxytocin, which is produced in the hypothalamus (the paraventricular nucleus) and is released into critical brain regions that regulate maternal motivation. In support of these findings, nulliparous females (females that have never given birth) in most mammalian species avoid and reject infants; they are not maternally motivated. Therefore, dual neural mechanisms regulate maternal behavior in most mammals: an inhibitory neural circuit that depresses maternal responsiveness in nulliparae and an excitatory neural circuit which promotes maternal motivation in the parturient female. The events of pregnancy and parturition have been proposed to depress the inhibitory circuit and activate the excitatory circuit (Numan 2015, 2017).

For many mammalian species, the physiological events that trigger the onset of maternal behavior at parturition are no longer essential for its maintenance during the remainder of the postpartum period (Numan and Young 2016). After a sufficient amount of postpartum maternal experience, it is likely that synapses become strengthened within certain key brain circuits so that maternal behavior can continue without hormonal

and oxytocin stimulation. These neural changes solidify an enduring mother-infant bond.

These results imply that there are neural mechanisms which can regulate mother-infant attraction in the absence of continued hormonal and neuropeptide influences. This fact may be relevant to the evolution of alloparental behavior. For example, a nulliparous allomother is maternally motivated and attracted to young conspecifics, suggesting that the inhibitory circuit is not active and the excitatory circuit is active in the absence of pregnancy and parturition. A good example of allomaternal behavior occurs in nulliparous marmoset monkeys (a New World primate species). These females remain in their family group after they are weaned, and they help their mother care for more recently born infants (Hrdy 2009). Although these allomothers are not lactating, they can help carry the mother's young offspring, and as these younger offspring grow older, the allomother can also provision them with easily digestible food items. The following evolutionary scenario can be proposed: For those species where alloparental behavior is adaptive, being important for infant survival in an extended family group, the mechanisms regulating attraction and bonding to infants may have become relatively emancipated from the need for stimulation by the physiological events of pregnancy and parturition. That is, the neural circuits regulating attraction and bonding to infants may have evolved to allow infant stimuli to gain direct access to these circuits in the absence of pregnancy and parturition, although the release of oxytocin in the brain, in the absence of pregnancy and parturition, may be involved in the initial attraction of an allomother toward infants (Numan and Young 2016). Since alloparents are caring for their younger siblings, kin selection mechanisms may be involved in this evolutionary process.

Since allomothering has been proposed to be important for infant survival during early human evolution (Hrdy 2009), the processes described above may account for the fact that human maternal motivation is relatively emancipated from hormones and that nulliparous women can adopt offspring and show normal maternal behavior. This hypothesis does not rule out the likelihood that an allomother's continued interaction with

young infants improves her allomaternal behavior and further solidifies the bond between the allo-mother and the infant she is caring for (Stolzenberg and Champagne 2016).

The Brain and Mother-Infant Bonding

There are evolutionary conserved core neural circuits that underpin maternal motivation in all mammalian species, including humans (Dulac et al. 2014; Numan 2017; Numan and Insel 2003). A key component of these circuits is the medial preoptic area (MPOA), located in the anterior part of the hypothalamus. Depression of MPOA activity suppresses maternal behavior, and estradiol, prolactin, placental lactogens, and oxytocin act on their receptors in MPOA to stimulate the onset of maternal behavior. Importantly, MPOA inactivation also eliminates allomaternal behavior (Numan and Young 2016). Research has shown that the MPOA interacts with the mesolimbic dopamine (DA) system to regulate a mother's attraction to her offspring (Numan 2015, 2017; Numan and Young 2016). The mesolimbic DA system includes DA neurons in the ventral tegmental area (VTA) of the midbrain that project to the nucleus accumbens-ventral pallidum (NA-VP) circuit in the forebrain. The mesolimbic DA system has been referred to as the brain's reward system and is involved in regulating an organism's attraction to a variety of rewarding stimuli. MPOA activation of the mesolimbic DA system endows infant stimuli with rewarding properties which promotes infant-seeking and infant-caretaking behaviors in the mother. This basic subcortical circuit (MPOA–VTA–NA-VP) is not only involved in mother-infant attraction in animals; fMRI research shows that this system is also active in human mothers that view infant stimuli while they are in an fMRI scanner (Atzil et al. 2017; Numan 2015, 2017). Particular synapses within this circuit probably become strengthened during mother-infant interactions, so that the mother-infant bond becomes solidified, allowing it to endure over long periods of time, even in the absence of continued hormonal stimulation (Numan 2015, 2017; Numan and Young 2016).

Animal studies have focused on subcortical mechanisms in the control of maternal motivation. These studies deal with the behavioral attraction of mothers to their infants, and animal studies cannot deal with maternal feeling states. However, in humans, feelings of love toward one's infant – maternal love – clearly influence maternal behavior. A lack of love for one's infant could lead to neglect and even abuse of the infant. Most fMRI research on feeling states in humans has focused on cortical areas and has correlated activity within the orbitofrontal and insular cortices with a variety of feeling states, including empathy (Numan 2015, 2017). Importantly, neural activity increases in these regions when mothers view infant stimuli and report positive feeling states (Numan 2017). Significantly, the orbitofrontal and insular cortices project to the medial prefrontal cortex, which, in turn, projects to MPOA. This could be a neural route through which maternal love influences maternal behavior in humans (Atzil et al. 2017; Numan 2017).

The Development of Maternal Behavior

Children who have been abused and/or neglected by their parents tend to become abusive or neglectful parents toward their own offspring, and experimental studies on nonhuman mammals, including primates, have confirmed that this relationship is a causal one (Numan 2015, 2017). A variety of mechanisms are involved in how exposure to abuse and/or neglect causes an infant to develop faulty maternal behavior in adulthood, and gene-environment interactions are involved (Numan 2015, 2017). With respect to the core circuits that regulate maternal motivation in animals, it has been shown that the way a mother treats her infants influences the development of the MPOA and its interactions with the mesolimbic DA system (Stolzenberg and Champagne 2016). Therefore, when a young infant is exposed to poor maternal caretaking, the core maternal neural circuits are negatively impacted, and this may be one of many routes that underpin the intergenerational continuity of abnormal maternal behavior. There is also preliminary evidence for humans that poor parenting influences the

development of orbitofrontal/insular cortex projections to the medial prefrontal cortex and MPOA in the affected offspring, which could interfere with the subsequent translation of maternal love into maternal motivation (Strathearn et al. 2009).

Maternal behavior not only influences the development of maternal behavior in her infants but also influences broader aspects of the infant's emotional and social development (Numan 2015). Therefore, an understanding of how faulty maternal behavior affects the development of offspring has wide-ranging significance.

The Neural Systems Underlying Mother-Infant Bonding May Provide a Foundation for Other Strong Social Bonds

Since the maternal care system is a primordial aid-giving system that is present in all mammals, it may have provided the neural foundation for other types of prosocial behaviors that rely on strong social bonds.

Most mammals are non-monogamous, and the female is the sole caregiver to her offspring. However, about 5% of mammals are monogamous. In monogamous species, the mated pair remains together after mating, forming a pair bond, and the male may also engage in paternal behavior. Numan and Young (2016) have compared the neural circuits that regulate the mother-infant bond and the pair bond (the strong attraction of members of the mated pair to one another), and they noted similarities in the underlying neural circuits. Since the strong attraction of a mother to her infants is common in all mammals, whereas monogamy is rare, it was proposed that the neural mechanisms underlying the mother-infant bond may have been modified by natural selection to establish the capacity to develop pair bonds under the particular ecological conditions where monogamous mating strategies are adaptive.

In behavioral studies on nonhuman and human primates, Burkart et al. (2014) have provided further evidence for the proposal being offered here.

They designed a test for unsolicited proactive prosociality which examined whether individuals within their social groups would provide fellow group members with food without obtaining food for themselves and without being solicited to provide such aid. They found that the extent of alloparental behavior within primate groups was an excellent predictor of the distribution of proactive prosociality. Proactive prosociality occurred at high levels in those primate groups that also displayed alloparental behavior but was low or absent in those species without alloparental behavior.

Perhaps alloparental care is linked to the evolution of hyper-cooperation within certain primate groups because, as an initial step, the evolution and development of "trust" in infants toward alloparents were adaptive (Hrdy 2009). But the high level of prosociality in species with alloparents may also be related to the degree to which the maternal care neural system evolved to become a relatively open system, allowing social stimuli from other group members, in addition to those from infants or a mate, to gain access to this caregiving/bonding system in the absence of pregnancy and parturition: The neural basis of alloparental behavior may have served as a preadaptation that allowed for the evolution of strong caregiving bonds between all members within certain social groups.

Conclusion

Understanding the mother-infant bond provides a window into how the most basic social bonding system operates. By understanding its neural mechanisms and how the system can be influenced by physiology, experience, and genetics, we gain an understanding into how abnormal maternal behavior may develop, which in turn influences child development. Such an understanding could give rise to remedial therapies. Finally, understanding the mother-infant bond gives us insight into the mechanisms underlying the formation of other strong social bonds between members of a social group.

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Maternal Caregiving

- [Maternal Investment](#)

Maternal Competency

- [Maternal Sensitivity](#)

Maternal Deprivation Hypothesis

- [John Bowlby](#)

Maternal Grandmother Invests Most

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Synonyms

[Alloparenting](#); [Genetic relatedness](#); [Grandparental investment](#); [Investment in more certain kin](#); [Matrilateral bias](#); [Parental investment](#); [Paternity uncertainty](#); [Pattern of biased grandparental investment](#); [Relationship certainty](#)

Definition

Grandparental investment includes all resources (e.g., time, care, help, money) that grandparents allocate to their offspring. Typically, the maternal grandmother invests more resources in her offspring than other grandparent types (i.e., maternal grandfather, paternal grandmother and paternal grandfather).

Introduction

Robert Trivers' (1972) theory of parental investment applied Hamilton's (1964) general rule to parental behavior. Parental investment theory considers the investments that parents make in their offspring and can easily be extended to

grandparental investment, but to gain the same fitness advantage, grandparents should invest in a larger number of children than the parents do. Humans are cooperative breeding species, meaning that mothers have always needed some alloparents (or allomothers) to help take care of an infant or to help the mother acquire food (Hrdy 2009). These caretakers often include the child's father, older siblings, aunts and uncles, and grandparents, especially the maternal grandmother.

Due to paternity uncertainty and sex-specific reproductive strategies, all grandparents are not in an equal position relative to their grandchildren (Euler and Weitzel 1996). Paternity uncertainty means that women can be sure that the child they gave birth to is biologically related to them, but men can never be 100% certain that the child is actually theirs. The link between parental investment and relationship certainty is evident in many species and males in several species invest in their offspring accordingly as a function of paternity certainty (Platek and Shackelford 2006). Although human males often invest in their offspring, they too have potential uncertainty in their relationship to their children.

In the case of grandparents, no uncertain links of paternity exist between grandchildren and maternal grandmothers. Paternal grandfathers are in the most uncertain position because they have two uncertain links of paternity between them and their grandchildren. Therefore, maternal grandmothers are predicted to invest in their grandchildren the most and paternal grandfathers will invest the least (Euler and Weitzel 1996). In addition, evolutionary researchers have explained women's stronger involvement in kin relations by sex-specific reproductive strategies, which means that due to biological, psychological, and cultural reasons, women tend to invest more in their kin than men (Coall and Hertwig 2010).

Empirical Evidence

One of the most common findings in grandparent studies is that the maternal grandmother usually

invests the most, followed by the maternal grandfather and the paternal grandmother, but the paternal grandfather usually invests the least (see Coall and Hertwig 2010 for review). This is true even in countries where no explicit preference for matrilineal family relations is evident and when many potentially confounding factors such as the age and the health of a grandparent or the geographical distance between a grandparent and a grandchild are controlled for (Danielsbacka et al. 2011). However, cultural traditions and norms can confound the grandparental investment pattern. In patrilocal societies, paternal grandparents are found to invest more in their grandchildren than maternal grandparents (e.g., Kaptijn et al. 2013; Pashos 2000).

A matrilineal bias that is found in many studies may also be enhanced because of the gatekeeping role of parents. Gatekeeping refers to the fact that parents guard access to a grandchild and, subsequently, the quality of the dyadic parent-grandparent relationship becomes important. Studies have shown that the dyadic relationship between mother and daughter is typically closer than other dyadic relationships between parental and grandparental generations, which may further increase the investment made by the maternal grandmother (Danielsbacka et al. 2015).

Conclusion

Alloparenting is an important feature of human species. In historical and traditional populations and in contemporary societies, one of the most important alloparents has been the maternal grandmother. Several studies from contemporary Western societies have shown that maternal grandmothers invest the most in their grandchildren of all grandparent types.

Cross-References

- [Father's Father Versus Mother's Mother](#)
- [Grandparents and Grandchildren](#)
- [Paternal Grandfather Invests Least](#)

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Maternal Investment

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Synonyms

[Maternal caregiving](#); [Maternal support](#)

Definition

Maternal investment involves the provision of resources that provide for the basic needs of offspring.

Introduction

The construct of parental investment was first introduced by Trivers (1972), whose predictions were based on processes that began in our distant evolutionary past. He proposed that mothers served their own reproductive interests best by providing high levels of care to offspring. The proposals made by Trivers were extended by the work of Daly and Wilson (1988), who observed the discriminative levels of care shown to offspring by mothers, whereas males were relatively more concerned with procreating. In both cases, parents were more likely to invest resources in children to whom they were biologically related (Daly and Wilson 1988). However, mothers who gave birth could be certain that the newborn was their own child whereas fathers did not share that same degree of certainty. The resources potentially available to parents in contemporary times include economic resources, social support from others, and time available to spend with offspring.

Researchers focusing on mothers were concerned with the combined effects of maternal resources and the probability that a child would survive. Daly and Wilson (1988) proposed that mothers invest more in low-risk than high-risk children if they have low resources to share across current or future offspring. Low-risk children, in turn, are more likely to reach adulthood and have offspring of their own. In contrast, mothers with high resources can afford to invest in high-risk as well as low-risk children.

Daly and Wilson (1988) observed that children who give cues to some kind of health problem or physical abnormality at birth are more likely than other children to be abandoned at birth. However, of the two conditions, higher levels of rejection occur when the child has a highly visible physical abnormality (Weiss 1994).

Contingent Model of Maternal Investment

There has been emerging evidence that are circumstances in which some mothers invest disproportionately high in high-risk offspring. Bugental and Beaulieu (2003) proposed a contingent model of parental investment in which (1) parents with low resources invest more in low-risk children whereas (2) parents with high resources invest more in high-risk children. In support of the basic nature of this model, Davis and Todd (1999) demonstrated that when food is scarce, the final brood size of birds is optimized if mothers feed the largest chick first, but if food is plentiful, the final brood size is optimized when the mother feeds the smallest chick first. The authors noted the same contingent feeding pattern has been found with actual birds, e.g., pied flycatchers.

Evidence for the proposed contingent model of parental investment comes from many sources. For example, Schepher-Hughes (1985) found that parents in areas characterized by extreme poverty (low resources) were observed to withhold food from sickly children but feed healthy children.

Empirical Test of the Contingent Model of Maternal Investment

In the first test of the contingent model with mothers and children, Beaulieu and Bugental (2008) assessed the resources that depressed mothers versus nondepressed mothers were willing to allocate to a high-risk or a low-risk child. As predicted, depressed mothers (conceptualized as having low attentional resources) invested more in a full-term infant whereas nondepressed mother invested more in a preterm infant.

Bugental et al. (2010) made an experimental test of the contingent model with human mothers. Mothers of preterm versus full-term infant were recruited to participate in a 3-year program. They were randomly assigned to one of three conditions: (1) a condition in which a home visitor provided direct help and guidance to mothers for 1 year, (2) a cognitive reframing condition in which mothers were assisted in solving caregiving

problems on their own for 1 year, and (3) a control condition. Child health was measured when children reached 3 year of age. As predicted, mothers assigned to the cognitive reframing intervention invested more time in the care of at-risk children than low-risk children, which in turn predicted higher levels of health.

The preferential investment in high-risk children among parents with high resources (and reduced investment in low-risk children) optimizes the possibility that both will survive to adulthood. The high-risk children might not survive without additional help; however, the low-risk children are likely to survive with some reduction in parental help. Thus the predicted and observed pattern is consistent with an evolutionary perspective.

Physiological Processes in Maternal Investment

Increasing attention has been given to the role of physiological processes in the early relationship between nonhuman mothers and their offspring. Early awareness of this relationship emerged in the work of Michael Meaney and colleagues. For example, Francis et al. (1999) observed that rat pups who received low licking and grooming at an early age were fearful in novel settings whereas those who received high levels of licking and grooming did not show this response. Associated changes were found in the functioning of the amygdala, a brain that is influenced by stress. In order to remove the effects of shared genetics, rat pups were cross-fostered at birth by an unrelated mother. As a broader conclusion from Meaney's program of research, animal research has demonstrated the clear effects of the postpartum behavior of mothers on brain development, stress reactivity, and capacity for social affiliation.

Research has been conducted on oxytocin for both humans and other species. This hormone plays a role in social bonding at many stages of life but is particularly pronounced in bonding relation between mothers and offspring. The program of research conducted by Feldman and colleagues (e.g., Feldman et al. 2007) has

demonstrated the pronounced effect of oxytocin on maternal behavior and subsequent behavior of the child. For example, higher prenatal levels of the maternal oxytocin present prenatally were found to predict high postnatal maternal bonding behaviors such as gaze, positive affect, unique vocalizations, and affectionate touching.

Conclusions

Variations in maternal investment in their offspring show regularities across measures, cultures, and species. The majority of research has approached this basic process from an evolutionary framework. More recent research often addresses the issue of biochemical mediators. The general conclusion is that maternal responses to the young influence their later behavioral and affective responses – a process (barring pathology) that is typically adaptive.

Cross-References

- [Anne Campbell](#)
- [Biparental Care](#)
- [Birth Order and Parental Investment](#)
- [Maternal and Offspring Condition](#)
- [Paternal Investment](#)
- [Paternal Investment Relative to Maternal Investment](#)
- [Sex Differences in Parenting and Parental Investment](#)

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Maternal Love

- [Maternal Bonding](#)

Maternal Malnourishment

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Introduction

Malnourishment occurs when the body becomes deficient in macronutrients and/or micronutrients. Maternal malnourishment, in particular, appears to be an informative indicator of environmental conditions that has a profound impact on a developing fetus.

Thrifty Genotype

The undernourished fetus of a malnourished mother undergoes metabolic adaptations that

enhance its immediate survival chances (Hales and Barker 2001). Alterations in muscle mass, hepatic structure, and hormone receptor density can all lead to these adaptations becoming permanently fixed and referred to as a “thrifty phenotype.” If the postnatal conditions match the prenatal conditions, these adaptations can be advantageous. However, if there is a mismatch between postnatal conditions and prenatal conditions, such as abundant food sources, the adaptations of the “thrifty phenotype” can be maladaptive.

Parent-Offspring Conflict

Parent-offspring conflict is an idea that was first introduced by Trivers (1974) and can be useful in understanding the alteration of brain growth during fetal development resulting from maternal malnourishment. The idea of parent-offspring conflict is that offspring may be selected to take more from a parent than the parent is selected to give. This period of conflict begins during the prenatal period and lasts throughout childhood and adolescence. During fetal development, this conflict is centered around the transfer of nutrients from the mother to fetus (Haig 1993). Pregnancy is energetically costly, and when food is scarce, a mother will only transfer as much energy to her fetus as she can while maintaining her energy reserves for future reproduction. This occurs even at the risk of a reduction in the likelihood of offspring survival. This phenomenon is apparent when optimal versus actual birth weights are compared. In the majority of human populations studied, the birth weight that is optimal for neonate survival is greater than actual mean birth weights (Frisancho 1993). Early pregnancy, without malnutrition, may also create conflict. For example, teenage mothers are themselves growing, which leads to a competition between them and their fetuses for nutrients (Wu et al. 2004). Thus, in undernourished and in very young mothers, there is an upper limit placed on the amount of energy the fetus can receive from the maternal host, and the rate at which that energy is transferred from the mother to fetus is also influenced by an interaction between maternal and fetal hormones.

Growth Programming

Maternal nutritional intake is not a direct cause of fetal growth rate (Rosso and Salas 1994). Instead, fetal growth rate appears to be determined by the mother’s nutritional state at conception, before the fetus is large enough for its growth to be nutrient-dependent. Indeed, in animal studies, rats which were malnourished before gestation produced offspring with reduced brain volume and DNA content (Harding and Johnston 1995). It is also difficult to increase fetal growth rates once they have been established by the mother’s nutritional state at conception (Rosso and Salas 1994). For example, newborns born to mothers who are malnourished at conception, but have high-energy intakes during pregnancy, will still be underweight. Alternatively, a woman who is in good physical condition who experiences malnutrition during the first half of her pregnancy can still produce normal weight offspring as long as she recovers before the second half of her pregnancy. However, birth weight is more directly nutrient-dependent during the second half of pregnancy, so birth weight will be affected by the mother’s malnutrition during this time.

Maternal Malnutrition and Fetal Brain Development

Nutritional or growth programming of a fetus of an undernourished mother has consequences that extend beyond prenatal life and into adulthood. These consequences include the increased risk of diabetes, hypertension, and other diseases (Lukas and Benjamin 1999). Brain sparing is believed to underlie the phenomenon of growth programming (Barker 1995). Maternal malnutrition leads to the developing fetal organs competing over limited nutrients. In a nutrient-lacking prenatal environment, the size and functioning of most individual organs are sacrificed, but only to the extent to which that sacrifice does not threaten the survival of the organism (Sibly and Calow 1987). Because the brain is an organ that is metabolically expensive and critical to survival, it is a privileged organ that is spared to a great extent (Klingenberg and Nijhout 1998). The heart is also spared to a much

lesser extent. For example, there is a significant size reduction in the liver and thymus of small-for-term infants, while the heart is slightly enlarged and the brain is much larger compared to the rest of its body. Thus, brain growth is maintained through a reduction in visceral mass, and the heart is maintained to supply nutrients to the brain (Lukas and Benjamin 1999).

Conclusion

Maternal nutrition status at conception is a major component of fetal growth trajectories (Rosso and Salas 1994). Therefore, maternal malnourishment at conception often leads to poor fetal growth. Parent-offspring conflict (Trivers 1974) provides a useful framework in which to understand the impact that maternal malnutrition has on the developing fetus. The flow of energy from the undernourished mother to the fetus is limited to ensure the continued reproductive fitness of the mother, sometimes at the expense of the fetus (Sibly and Calow 1987). To increase chances of survival, fetal organs compete for nutrients, resulting in the developing fetal organs being reduced in size and function to better support the developing brain. This adaptation can be advantageous in postnatal life if the child is born into a food-scarce environment (Hales and Barker 2001). However, if the environment is food abundant, the adaptation has the potential of leading to several health problems, making it maladaptive.

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Maternal Motivation

► Maternal Bonding

Maternal Perinatal Association

- Adaptive Problem of Detecting Kinship
- Kin Recognition and Classification in Humans

Maternal Responsiveness

► Maternal Sensitivity

Maternal Role

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Synonyms

Mother-child dyad; Mother's function; Parental investment

Definition

The interactions between the mother-child dyad, what is to be expected from the mother.

Introduction

Maternal care is essential for the survival of human offspring as humans are not able to care for themselves for several years after their birth. Several studies have found that mothers are emotionally closer to their offspring than fathers are and that mothers invest more resources in their offspring than fathers do. Theories in evolutionary psychology posit that this increased care comes from women's natural tendency to nurture and cooperate with others, and this increased investment stems from the fact that women begin biologically investing in their offspring immediately after conception.

Tend and Befriend

In the human ancestral environment, men often hunted for food, while women stayed back and remained with their group to help care for each other and their offspring. This behavior among women helped develop strong emotional connections, reciprocally altruistic behaviors (e.g., food sharing, caring for each other's children, etc.), and cooperative social alliances. This phenomenon has become known as *tend and befriend* – the idea that women respond to stress and obstacles in their environment by tending to oneself and her offspring and befriending others so as to maintain a social network of trusted individuals who can aid in the tending process (Taylor et al. 2000).

Evolution of Maternal Role

The hunter-gather environment was organized in a manner that may have positively selected for cooperative and nurturing behaviors (i.e., tend and befriend) in women. Therefore, it is not

surprising to see that women are usually more nurturing toward their offspring than men. On average, mothers are significantly emotionally closer, and give more care, to their offspring than fathers do (Buss 2000). This is partly explained the mothers' genetic certainty – the idea that because the mother carried and gave birth to the offspring, she is certain that the child is hers (Maestripieri and Mateo 2009).

Women invest significantly more resources in their offspring than men. This is apparent from conception. Once the female's ovum becomes fertilized by the male's sperm, the woman immediately begins investing in the offspring in the form of gestation. The woman must increase her caloric intake – which required more resources – and must care for her body and baby to ensure the health of the unborn offspring. This investment – which takes place before the offspring is born – requires a series of resources, including time (i.e., 40 weeks of gestation), increased food intake, monetary costs of doctor's appointments, and attention to harmful teratogens (things that may harm the offspring in the womb, such as alcohol and caffeine) in one's environment to avoid (Buss 2000). There are also many costs associated with pregnancy – discomfort, severe pain, gestational diabetes and other disorders, death, and many others. Therefore the mother has already invested a vast amount of resources in the offspring before it is ever born. Whereas, theoretically, by this same time, the only investment that the male has to make is the amount of time and energy it took him to help conceive the child. This increased investment also leads to greater maternal care toward the offspring. In short, because they have already invested more, they continue to invest and care more (when compared to fathers). This increased maternal care continues throughout the offspring's development.

Conclusion

Ultimately, the maternal role is usually considered to be a nurturing role. This corroborates the evolutionary psychological evidence which supports

the idea that women may have evolved tendencies to nurture and cooperate with other people. This tendency toward nurturance, coupled with the immense amount of resources that mothers must expend for the sake of their child's survival and development, has produced a strongly nurturing maternal role in humans.

Cross-References

- ▶ [Extended Kin Role](#)
- ▶ [Familial Violence](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Kinship](#)
- ▶ [Paternal Role](#)

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Maternal Sensitivity

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Synonyms

Caregiving sensitivity; Maternal competency; Maternal responsiveness; Parental sensitivity; Sensitive mothering

Definition

A mother's (or any caregiver's) ability to perceive and correctly interpret their infant's signals (e.g., distress, need, social) and then respond to them in a prompt and accurate manner.

Introduction

Maternal sensitivity is one of the key determinants of child outcomes with its vast influence on the way the child learns to perceive and react to the world. Massive empirical work, starting with Ainsworth's seminal Uganda study (1967), has reliably linked maternal sensitivity to infant attachment patterns. Caregiving sensitivity should be considered not only as a trait characteristic of the parent but as a dynamic collection of behaviors that are attuned to the infant's changing needs. These behaviors are orchestrated to react to the needs of the infant in a sensitive and consistent manner while interacting with them. A sensitive caregiver is able to constantly recognize the changes in the infant's physical and psychological needs, attend to these needs in a way that supports the infant's use of the caregiver as a safe haven (i.e., whom the infant can turn to for support and comfort in times of distress) and secure base (i.e., from whom the infant can explore and learn about the world and develop their own personality), and reiterate if the infant is not soothed. What is more, in addition to engaging in prompt and appropriate behavioral responses to infant needs, sensitive caregivers also function as translators between the infant and the environment they cannot yet master on their own. Hence, the quality of sensitive caregiving is directly related to how the child comes to experience the world. In the following sections, first the antecedents and consequences of maternal sensitivity will be discussed, then the measurement techniques that are used for quantifying maternal sensitivity will be explained, and finally the intervention studies aiming enhancing maternal sensitivity will be elaborated.

Antecedents and Consequences

Maternal sensitivity was empirically studied for the first time by Ainsworth et al. (1978) via home observations. Ainsworth and her team then went on to investigate the relationships between maternal sensitivity and infant attachment by the strange situation procedure (SSP), where the infants were observed for their reactions to episodes of separation from and reunion with their mothers in the lab. The researchers assessed a variety of maternal behavior on four rating scales tapping into the sensitivity, acceptance, cooperation, and accessibility of the mother, which were identified to be strongly correlated with the attachment style of the infant as measured in the SSP. Since this pivotal study, numerous empirical studies have consistently reported moderately strong links between caregiving sensitivity and infant attachment security (see de Wolff and van IJzendoorn 1997 for a meta-analysis). Sensitivity, therefore, appears to be a crucial factor in understanding the development of individual differences in the formation of attachment bonds. Caregiving sensitivity has also been identified to be related to a wide array of other crucial developmental outcomes, such as executive functions, behavioral problems, sleep quality, and even body mass index (see Booth et al. 2018 for a review).

It is worth noting that the association between caregiving sensitivity and infant attachment is significantly weaker in studies with low SES or clinical samples (de Wolff and van IJzendoorn 1997), suggesting sensitive caregiving may be superseded by suboptimal child-rearing environments and stressful living conditions. Supporting these conjectures, in their recent review, Booth et al. (2018) show that contextual stress is one of the most important determinants of caregiving sensitivity. Specifically, unfavorable socio-demographic ecology (e.g., low income, low maternal education, young age of parenting, absence of the infant's father), perceived parenting stress, maternal internalizing symptoms (e.g., depressive symptoms), and anxiety have been strongly associated with reduced levels of maternal sensitivity.

Infant characteristics and temperament also play an important role in the degree of caregiving

sensitivity. Sensitive parenting can be harder to achieve with infant negativity, whereas an infant who manifests positivity can be easier to sensitively respond to. Supporting these conjectures, Mills-Koonce et al. (2007) found that the level of caregiving sensitivity decreases for all mothers at high levels of infant negative effect (e.g., prolonged crying, intense protest, venting).

Measurement

Measurement techniques aiming to assess caregiver sensitivity typically derive the sensitivity ratings from direct observations of caregiver-child interactions. These observational tools can be used to assess the quality of sensitive care provided to the child by any caregiver.

The first empirical tool used for these observations was the Ainsworth's Maternal Sensitivity Scale (AMSS) (Ainsworth et al. 1971). The AMSS involves coding several behaviors such as affective expression, appropriateness, and amount of physical contact in a variety of settings (e.g., play, feeding, teaching) on four global scales: *sensitivity* (i.e., the extent to which the mother responds promptly and appropriately to the child's signals), *acceptance* (i.e., how much the mother values the child's will), *cooperation* (i.e., whether the mother's interventions are minimally intrusive), and *accessibility* (i.e., the extent to which the mother is psychologically available as needed). The AMSS can be conducted in the house or laboratory, and it typically takes between 25 min and 2 h to complete.

Another common tool for assessing maternal sensitivity is the Maternal Behavior Q-Sort (MBQS) (Pederson et al. 1990). The MBQS is based on Ainsworth's work, but it concentrates the evaluation of the mother's behavior into 90 items that assess her accessibility, responsiveness, and promptness to the child's needs. Using a card sorting technique, trained raters observe the mother and then classify and rate these 90 behaviors in terms of the frequency she engages in them. The scores are then correlated with expert-based prototypic scores for ideal maternal sensitivity, and the resulting correlation coefficient is used as the global maternal sensitivity score of the mother. The MBQS can be conducted in the house, playground, or laboratory

and is usually filmed. It typically takes between 40 min and 2 h to complete.

Intervention Studies Aiming Enhancing Maternal Sensitivity

As the links between caregiving sensitivity and developmental outcomes have become clearer with amounting empirical studies, intervention efforts in enhancing caregiving sensitivity have increased over the last decades (see Bakermans-Kranenburg et al. 2003; Mountain et al. 2017 for reviews). These early intervention studies typically target caregivers with infants less than 3 years of age and are carried out as home visiting programs where the parents are trained on how to synchronize their behaviors with their infant's needs and develop attachment relationships. These studies have been shown to reduce insensitive parenting and infant attachment insecurity. Not necessarily too lengthy but intensively scheduled interventions with precise behavioral focus are more effective in augmenting sensitivity and attachment security. Intervention programs have also been shown to have long-lasting effects on other crucial child outcomes, such as lessened internalizing and externalizing behaviors, and improved social and linguistic competence.

Conclusion

Maternal sensitivity is one of the central caregiving characteristics that has profound and long-lasting effects on child outcomes; hence, it merits the attention of all scholars interested in child development, parenting, and attachment. It is highly related with the resources a caregiver possesses, and it is a skill that can be enhanced with training. Therefore, efforts toward enriching the parenting environment and educating caregivers are invaluable in improving child development.

Cross-References

- Attachment Theory
- Breast Feeding and Mother-Infant Attachment

- History of Attachment Theory
- Individual Variations in Attachment
- Offspring-Parent Attachment

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Maternal Support

- Maternal Investment

Maternal-Embryo Conflict

► Maternal-Fetal Conflict

Maternal-Fetal Conflict

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Synonyms

Genomic imprinting; Imprinted gene; Maternal-embryo conflict; Matrigene; Parent-offspring conflict; Patrigene

Definition

In humans, genetic conflicts between mothers and embryos may generate phenotypic conflicts, such as gestational diabetes and preeclampsia, which appear to be pathological, but instead arise from differing optima over the preferred level of maternal investment in the offspring.

Introduction

Mothers and their embryos live in intimate though not always harmonious contact during gestation. As Robert Trivers (1974) noted, parents and offspring have shared, but not identical, genetic interests. This asymmetry creates the potential both for conflict and cooperation, and there are circumstances where offspring may be more self-ish than their parent's desire: this is the concept of parent-offspring conflict.

A fundamental conflict arises over how maternal resources are allocated. An increased transfer of maternal resources to the current offspring may impair her ability to invest in other contemporary or future progeny. In humans, the potential for maternal-fetal conflict is heightened by the almost

unparalleled access the embryo enjoys to maternal physiological systems. It is clear that a certain times and places, embryos are able to wrest at least partial control of maternal endocrine systems to the benefit of the embryo and detriment of the mother. The most obvious examples are gestational diabetes and preeclampsia (high blood pressure during gestation) that induce obvious harm for mother. More subtly, embryos may have stolen control of the maintenance of pregnancy from mother via the secretion of counterfeit hormones into the maternal bloodstream. Recent work suggests that there may also be maternal-fetal conflict over thyroid function during pregnancy, and that cognitive disorders such as autism and schizophrenia may arise when genetic accidents favor one side in the tug-of-war between mothers and their embryos.

Some of the most conspicuous maternal-fetal conflicts involve genomic imprinting, where gene expression is conditional on parent-of-origin. These make up a small fraction (~1%) of genes within the human genome but are strongly implicated in a variety of maternal pathologies. Under the kinship theory of genomic imprinting (Haig 1993, 2004), genes of paternal and maternal origin within the embryo are engaged in a tug-of-war over the transfer of resources from mother to embryo, with paternal origin genes favoring greater investment and maternal origin genes resisting. Imprinting involves the silencing of genes depending upon whether they originated from mother or father. As with most parent-offspring conflicts, a pro rata compromise between maternal and paternal interests is the expected result (Haig 1993, 1996, 2004; Mock and Parker 1997), with a rough balance established between the two. But genetic anomalies that generate a maternal or paternal bias in the expression of imprinted genes often reveal the underlying conflict between mothers and their embryos, and in particular between maternal and paternal interests, resulting in conspicuous imprinted gene disorders.

Parent-Offspring Conflict

Parent-offspring conflict theory predicts that parents and offspring will often disagree over the

level of resources an offspring should receive (Trivers 1974). Who wins or loses will rest upon who holds the power in the relationship. If power is shared, the resolution is normally expected to be a pro-rata compromise between the two parties (review in Mock and Parker 1997). In the context of fetal-maternal relations during human pregnancy, it was long assumed that mothers were in complete control. She provided resources to her progeny in a cooperative partnership with her offspring. And even if a fetus desired more than mother was prepared to give, a placental barrier stood between them. How could an offspring act upon its desires? This idyllic view of harmonious relations has been revised in light of both theoretical and empirical work showing that embryos often disagree, sometimes strenuously, with maternal processes. Moreover, they hold the power to enforce their will, sometimes with demonstrable, and occasionally even fatal, consequences for their mother (see “Fatal Conflicts” below). Embryos actively manage the gateway between themselves and their mothers at the placental interface. They are able to ship materials across the placenta into the maternal bloodstream and, in doing so, are sometimes able to “persuade” mothers biochemically to act against maternal interests.

Terminology

A fetus is usually defined as the offspring once all major organ systems are complete, toward the end of the first trimester (8–11 weeks post conception). The embryo is an earlier stage of development that follows the conceptus (the fertilized egg), arising after gastrulation once the tissue layers have differentiated into ectoderm, mesoderm, and endoderm. There are no clear dividing lines among the conceptus, embryo, and fetus because development is a continuum.

The following provides a précis of the key events in early gestation. A more detailed description can be found in Haig (1993). Following fertilization, cell division occurs and at 5–9 days post-conception, a hollow ball of cells, the blastocyst, is formed. It is the blastocyst that implants in the uterine wall, and a process of decidualization

commences around this time. The uterine endometrium thickens, and secretory glands enlarge and become functional; the decidua, so named because this tissue is shed with the placenta at birth, becomes increasingly vascularized being infused with coiled spiral arteries.

The blastocyst contains an inner cell mass that will differentiate into the embryo proper and, an outer cell layer, the trophoblast, that will form the extra-embryonic membranes including the chorion. The trophoblast penetrates the maternal uterine wall, forming chorionic villi that invade the uterine decidua, anchoring the embryo and forming the vascular connections needed for nutrient absorption and gas exchange. The trophoblast eventually breaches the walls of the maternal arteries and veins, and a system of internal cavities forms that fills with maternal blood fed by the spiral arteries. The trophoblast replacement of maternal cells in the spiral arteries reduces mother’s ability to control blood flow through the placenta. In this hemochorial placentation, maternal blood is in direct contact with the embryo’s chorion, giving the embryo direct access to maternal systems. The placenta is a composite of tissue of offspring (trophoblast) and maternal origin (the decidua). Hemochorial placentation is considered the most invasive form of placentation among mammals (Crespi and Semeniuk 2004). A deep trophoblast invasion of maternal tissue increases access of the fetus to maternal resources. Conversely, a shallow placental invasion is associated with subsequent pathophysiology, most notably preeclampsia (Steeger et al. 2010). The placenta is a temporary organ that is key to fetal growth and development. It is built for the exchange of nutrients, gases, hormones, cytokines, immune system components, intact cells, and cellular components and waste products. Importantly, as we shall see below, it is a major endocrine organ affecting both fetal and maternal physiology.

Maternal-embryo or maternal-fetal conflict can occur at every stage of gestation. Here I shall use the term embryo for early gestation and fetus for later gestation, and shall apply the terms maternal-embryo and maternal-fetal conflict interchangeably.

How Embryos Manipulate Mothers

Historically the maternal-fetal interface at the placenta was considered a passive barrier. It is now recognized, however, that there is a considerable transport of materials from fetus to mother and vice versa across this so-called barrier. Fetal cells, cellular debris, hormones, cytokines (proteins involved in cell signaling), microRNA, micro-somes, and exosomes (extracellular vesicles that carry a variety of cargo) all make their way into maternal circulation. In some cases, this may be material that is shed inadvertently into mother's bloodstream, but in other cases, it appears to be anything but accidental. Rather, embryos are attempting to co-opt entirely maternal decisions about provisioning the embryo.

The view of the passive placental "barrier" has been supplanted by the growing recognition that the trophoblast, an extraembryonic tissue of offspring origin, actively regulates the transport of materials across the placenta. Given the more-or-less direct access of the embryo to the maternal bloodstream via its hemochorial placenta, this anatomical arrangement opens the door to fetal manipulations of maternal systems, and the fetus does exactly that using multiple pathways. These include the use of materials shed or secreted into the maternal bloodstream including hormones, cytokines, DNA, RNA, fetal/maternal cells and cell components, and materials packaged inside vesicles.

Hormones and Fetal-Maternal Conflict

Haig (1993, 1996) was the first to suggest that embryos used hormones secreted from the trophoblast to manipulate their mothers during gestation, and introduced the new term "allocrine" to describe a hormone produced by one individual to affect the endocrine system of another. Given that an embryo has the same complement of genes as mother, any time a maternal hormone operates and endocrine system, an embryo can produce the same hormone potentially for its own benefit. Human chorionic gonadotropin appears to be one such example: it appears to have supplanted

maternal luteinizing hormone in corpus luteum "rescue" that is necessary for the maintenance of pregnancy during the first trimester of gestation.

Maternal-Fetal Conflict and Microchimerism

That trafficking of cells occurs between fetus and mother during gestation is now widely recognized. The flow of cells is bi-directional, though more fetal cells are transferred to mother than vice versa (Boddy et al. 2015). Fetal cells remain present in mothers (fetal microchimerism) long after pregnancy, in some cases are found decades later. Some fetal cells yield clear benefits for mother. Fetal stem cells, for example, have been found to aid in wound healing and the repair of cardiac tissue. But fetal cells may also impose costs for mothers, manipulating maternal systems for fetal gain.

Fetal cells are found routinely in the breast, thyroid, and brain, where they could play a role in increasing offspring access to maternal resources – e.g., by shifting the release of hormones toward the offspring optimum (Boddy et al. 2015), but as yet direct evidence is lacking. A maternal immune system response to the presence of fetal cells in the brain has been postulated to contribute to the inflammation linked to postpartum depression, but again direct evidence is lacking.

Maternal cells are also transferred to the fetus via the placenta and during breast-feeding. This maternal microchimerism creates the potential both for cooperation and conflict (Boddy et al. 2015). For example, the transfer of immune system elements to the offspring during breast-feeding is likely beneficial, but the same pathway could be used to manipulate progeny for maternal interests.

Non-coding RNA and Fetal Maternal Conflict

Non-coding RNA (RNA not translated into a protein) plays a key role in gene regulation and

provides another pathway for embryos to manipulate maternal systems. There are a variety of non-coding RNA's with different functions, but much recent work has focused on the role of microRNAs (miRNA) in human pregnancy.

MicroRNA was first discovered in the 1990s, but it was not until the early 2000s that their key role in gene regulation was identified. About 1000 microRNAs are known, and they target the majority of human genes. Individual miRNA can have multiple gene targets. MicroRNA are short (19–24 nucleotides long), single-stranded RNAs that act as negative regulators of gene expression by binding to messenger RNA to prevent protein translation. They can down-regulate a gene by suppressing it directly or suppressing a promoter for a gene. Or they can up-regulate gene expression, a gene by suppressing a repressor for a gene.

Two large imprinted clusters of miRNA genes, on Chromosomes 14 and 19, are directly relevant to maternal-fetal conflict. The Chromosome 19 microRNA cluster (C19MC) is imprinted and expressed from genes of parental origin. The C19MC arose within the primate lineage, and its relatively recent origin suggests that it may have been important in the development of the invasive hemochorial placentation shared among humans and the great apes (Noguer-Dance et al. 2010). The C19MC consists of ~46 tandemly repeated microRNA genes encoding 56 miRNAs. These are expressed primarily in the placenta but are also found in tumors (Noguer-Dance et al. 2010; Flor and Bullerdiek 2012). The C19MC miRNA mediates a variety of biological processes including cellular proliferation and invasion, inflammation and apoptosis, and are important in growth and invasion of the embryonic trophoblast into maternal tissue.

One recently established effect of C19MC miRNA is the upregulation of maternal autophagy. Autophagy is a catabolic cellular pathway that is used to recycle damaged or unneeded cellular components and to clear pathogens. Experimental work has shown that C19MC miRNA increases resistance to viral infection (Bullerdiek and Flor 2012). From the perspective of fetal-maternal conflict, it would appear that embryos,

by secreting miRNA to upregulate the maternal immune system, are promoting their own protection, perhaps against maternal interests. Given that they are of placental origin, it is not surprising that C19MC miRNAs are eliminated from the maternal bloodstream following birth (Donker et al. 2012).

The C14MC is another large gene cluster coding for miRNA located in an imprinted gene domain on Chromosome 14 (Morales-Prieto et al. 2013). The C14MC originated within the mammals well before the origin of the C19MC. C14MC miRNAs are maternally expressed, and some, but not all, are expressed primarily in the placenta. C14MC miRNA plays a variety of roles including neurogenesis and embryo development. Interestingly, the C14MC is the largest cluster of tumor suppressor genes. Conversely, the C19MC miRNAs are associated with tumor development. Given the similarity in molecular pathways shared between tumor development and the invasion of embryonic trophoblast into maternal tissue (Haig 2015), an obvious inference is that C14MC and C19MC miRNAs sit on opposite sides of a fetal-maternal conflict over trophoblast invasion, with greater invasion being favored by paternally inherited genes from the C19MC and restraint favored by maternally expressed genes from the C14MC.

Once produced, placental miRNAs can be packaged in exosomes that are cell-derived vesicles that can be used for the transport of a variety of materials, and exported into the maternal bloodstream.

Maternal-Fetal Conflict and Genomic Imprinting

For most genes in the human genome, the parent of origin has no effect on the action of the gene. But for a small proportion, roughly 1% overall with higher proportions in the placenta and developing brain, it matters a great deal whether the gene originated from mother or father. These are the imprinted genes. Whether the gene is active is conditional upon the parent of origin. A consequence of this genomic imprinting is that

the gene is expressed from only one of the two alleles present, with the other being silenced epigenetically. Genes from mother when found in the embryo are referred to as matrigenes or madumal alleles, and patrigenes or padumal alleles when obtained from father. Under maternal imprinting, the matrigenes are silenced; with paternal imprinting, the patrigenes are silenced. As seen below, imprinted genes are hotbeds of maternal-fetal conflict.

How Are Genes Silenced?

Gene silencing associated with imprinting is achieved via reversible epigenetic mechanisms that include DNA methylation, histone modification, non-coding RNA that regulate gene function, or long-range chromatin interactions (Monk 2015). In many cases, an imprint is established early (during gamete formation) and maintained over the entire lifespan. In other cases, the imprinting pattern is complex, and a specific gene may, for example, be imprinted and expressed from just one allele at certain times and in certain tissues (often the placenta) but be expressed from both alleles elsewhere.

Genomic Imprinting Is Revealed by Genetic or Epigenetic Accidents

In many cases, the evidence of genomic imprinting is concealed by outcome of the tug-of-war between maternally and paternally imprinted genes with the end result being that neither side holds a decisive advantage. The underlying conflict, however, is revealed when a genetic or epigenetic accident tips the balance in one direction. Errors in the establishment of epigenetic marks, or errors in gamete formation, may result in an over or underexpression of alleles of maternal or paternal origin.

Uniparental disomy is one such mechanism. In the absence of imprinted genes, it should not matter if both chromosomes derive from the same parent. But when imprinted genes or gene clusters are present, it matters a great

deal. Uniparental disomy is thought to result from a corrective mechanism to repair trisomies in the earliest stages of gestation. Errors in meiosis sometimes result in extra copies of chromosomes in gametes. Trisomy 21 or Down syndrome is the most common trisomy at birth. In some cases, an initial trisomy is corrected post-zygotically by deletion of one of the supernumerary chromosomes. But in one in three cases (if chromosomes are deleted randomly), this deletion will result in both chromosomes coming from the same parent: a uniparental disomy. If both chromosomes are paternal in origin, this will result in an overexpression of any paternally expressed imprinted genes (patrigenes); and a maternal overexpression if both chromosomes are from mother (matrigenes). Uniparental disomies are often associated with imprinted gene disorders. An overexpression of paternal genes in uniparental disomy of chromosome 15 results in Prader Willi syndrome (Haig 1993). Angelman syndrome is the result if uniparental disomy of chromosome 15 stemming from two maternal chromosomes.

Why Genomic Imprinting?

A variety of hypotheses have been proposed to explain the origin and maintenance of imprinted genes (Holman and Kokko 2014). To date, there is no single hypothesis that provides a comprehensive explanation for the origin and maintenance of genomic imprinting, but the kinship theory (Haig 2004) has garnered the most empirical support and is directly applicable to fetal-maternal conflict.

The kinship theory posits that genomic imprinting arose as a result of competition between the maternal and paternal genomes over the provisioning of the offspring (Haig 1993, 1996, 2004). It builds upon Trivers' (1974) concept of parent-offspring conflict but looks at it from the more focused perspective of genes of maternal and paternal origin in the embryo. In species that are not strictly monogamous, patrigenes and matrigenes will have differing optima for the optimal level of maternal

investment in the offspring. Matrigenes are equally related to all of mother's offspring, present and future. Patrigenes, except in cases of strict life-long monogamy, are not. As a result of this relatedness asymmetry, patrigenes favor a greater investment of maternal resources in the current offspring than matrigenes.

The result is a physiological and developmental tug-of-war between genes of paternal and maternal origin in the embryo, with consequent effects on mother. Patrigenes favor a greater transfer of resources from mother to embryo, resulting in greater fetal growth; maternal genes favoring a more constrained transfer of resources and lower fetal growth. Imprinting is a mechanism to manage the underlying sexual conflict between genes of paternal and maternal origin. Genes that increase the transfer of resources from mother to fetus are maternally imprinted, and expressed from the paternal copy only. Genes that constrain the transfer of resources are paternally imprinted and expressed from the maternal copy only. The canonical example of an imprinted gene is insulin-like growth factor 2.

An Example of Imprinted Genes

Insulin-like growth factor 2 (Igf2) and its receptor (Igf2r) were the first imprinted gene loci to be described in mice. Igf2 acts as an embryonic growth enhancer, allowing nutrients to diffuse across the placenta. It is active (in both mice and humans) from the patrigene. The matrigene, conversely, is silenced by methylation. In mice, the receptor, Igf2r, is also imprinted and is active from the matrigene only. The receptor effectively serves as a growth regulator by capturing and degrading insulin-like growth factor 2. This diametric gene pair accords with the kinship theory where patrigenes favor greater, and matrigenes lesser, investment in the embryo.

The story is slightly more complex in humans as the receptor gene (IGF2R) is not consistently imprinted, being expressed from both alleles in most individuals. In humans, it is a different gene that acts antagonistically toward the paternally expressed IGF2: the H19 gene. H19 is a gene for

a long non-coding RNA that regulates IGF2 in both humans and mice: it is associated with reduced fetal mass and cell proliferation, is imprinted, and is maternally expressed. Similar to the Igf2-Igf2r dyad in mice, the IGF2-H19 dyad in humans is engaged in a physiological tug-of-war, with paternally active genes acting as growth enhancers, maternally active genes acting as growth suppressors.

Maternal-Fetal Conflict over Implantation

An embryo's success in implantation affects profoundly its later access to maternal resources and is where maternal-fetal conflict begins. The process is normally governed by a complex dialog between mother and embryo involves both the immune and endocrine systems results: it is a chemical discussion that sometimes descends into argument. The notion that it is a mutually beneficial dialog and negotiation is almost certainly a too sanguine view of maternal-fetal relations. It is not even clear that implantation requires maternal consent, as illustrated by the ability of the embryo to implant successfully at ectopic sites (Haig 2015). As such, successful implantation can be viewed as sitting somewhere between a maternal-fetal collaboration and a constrained parasitism of mother by embryo.

Preparation for this interaction begins before fertilization takes place, and well before if it is to be maximally successful. A successful pregnancy requires a state of active immune tolerance of foreign paternal antigens of the conceptus. Immunosuppressive regulatory T cells (T_{regs}) are central to this process. Prior exposure to semen and seminal fluid via coitus and/or oral sex plays a key role in inducing maternal immunological protection of the embryo via the production of T_{regs} (Robertson et al. 2009; Robertson and Sharkey 2016). The evidence is manifold and the incidence of preeclampsia (high maternal blood pressure during gestation) serves as a biomarker of an initial conflict between mother and embryo over the depth of implantation, as preeclampsia is associated with a shallow implantation.

Preeclampsia is more common in first pregnancies; it is linked to the period of cohabitation involving unprotected sex between woman and man; the incidence of preeclampsia rises if a woman changes partners; oral sex with the father is protective against preeclampsia but only if there is exposure to seminal fluid. A clear role of the immunological preparation for paternal antigens is revealed with assisted reproduction where donor sperm and/or eggs are used. The background rate of preeclampsia is roughly 1 in 20 to 1 in 12 pregnancies, but this rises to about 1 in 6 if donor sperm are used. That figure soars to 1 in 3 if both donor sperm and egg are used. From these data, it is tempting to suggest that the link between the period of cohabitation involving unprotected sex, and subsequent preeclampsia, is an index of an evolved mechanism whereby mothers can modulate investment in an offspring, investing more if paternal care is likely. Such a suggestion is obviously conjectural.

Maternal-Fetal Conflict over Spontaneous Abortion

Mothers use spontaneous abortion as a mechanism of quality control for the genetic defects that are surprising common in human embryos (Haig 1993; Forbes 2017). Though common at conception, major genetic defects are rare at birth. Depending on maternal age, somewhere between half and 99% of conceptions are spontaneously aborted, and most major chromosomal defects are lost early in gestation, often before a woman is aware that she has been pregnant, if only for a short time.

Haig (1993) suggested that mothers and embryos may disagree over whether pregnancy should continue, with mothers setting a more stringent standard for quality control than embryos, and that a placental hormone, human chorionic gonadotropin (hCG), has played a key role in this maternal-embryo conflict (see Forbes 2017 for a recent review).

During the first trimester of pregnancy, a continued production of the hormone progesterone by the corpus luteum (the structure that forms from

the follicle after release of the ovum) is necessary for pregnancy maintenance. The corpus luteum, in turn, is maintained by a glycoprotein hormone. In many eutherian mammals, that is luteinizing hormone (LH). But in primates, that function has been usurped by chorionic gonadotropins produced in the placenta. In humans, this corpus luteum “rescue” is performed by placentally produced hCG. In the ancestral condition, where maintenance of the corpus luteum was controlled by maternal LH production from the anterior pituitary, mothers could discontinue pregnancy by shutting off LH production, which in turn shuts down progesterone production, resulting in spontaneous abortion.

hCG is a counterfeit hormone produced by embryos to replace maternal control of the corpus luteum. Haig argues that mother and fetus may “disagree” over the whether pregnancy should continue. For example, mothers are predicted to prefer a higher threshold for offspring quality than embryos. Selection would favor embryos to secrete hCG thereby maintaining progesterone production and to escape spontaneous abortion. The initial step appears to have been the placental (embryonic) production of LH when hemochorial placentation first emerged in the anthropoid primates. Hemochorial placentation allows the embryo direct access to the maternal bloodstream and first appears in the tarsiers. Earlier primates had an epitheliochorial placenta. The difference is two additional tissue layers standing between the embryo and the maternal bloodstream, the uterine epithelium, and maternal vascular endothelium. These extra tissue layers stand as a barrier to the free flow of large macromolecules such as LH or hCG into the maternal bloodstream. In short, embryos cannot easily tamper with maternal physiology.

All that changed with the emergence of hemochorial placentation in the tarsiers, monkeys, and apes. Now embryos could use placental LH to wrest control of the corpus luteum away from mother. The expected coevolutional response from mother would be to raise the threshold level of LH needed to maintain the corpus luteum, and thus begins an evolutionary arms race. The next step appears to have been a

duplication of the key LH gene, in particular the gene producing the beta chain of LH that confers functionality in this glycoprotein hormone family. This duplication gave rise to the first chorionic gonadotropin. The expected maternal countermeasure would be to raise the threshold level of hormone production necessary to maintain pregnancy ever further, which in turn favors an increased hormone production by the embryo in an escalating arms race. There is genetic evidence of exactly that. There have been not one but six gene duplications in the primate lineage to create a family of chorionic gonadotropin genes, and in humans the production of hCG is so prodigious during early pregnancy that it spills into the urine where it forms the basis of pregnancy tests (Haig 1993).

hCG and Maternal-Fetal Conflict over Thyroid Function

Human chorionic gonadotropin plays a variety of roles during gestation beyond just corpus luteum rescue. It is often referred to as the hormone of pregnancy and is detectable even before implantation occurs. Measurement of the level of a hyperglycosylated variant on the day of implantation accurately forecasts subsequent spontaneous abortion (review in Forbes 2017). hCG effectively serves as the Swiss army knife of the endocrine system, and it even serves as a bridge between the endocrine and immune systems.

hCG is part of the glycoprotein hormone family that also includes thyroid stimulating hormone (TSH), follicle stimulating hormone, and luteinizing hormone. It cross-reacts with the receptors for these other hormones because of its strong similarity in molecular sequence. It reacts weakly with the TSH receptor, but is produced in such large quantities that it plays a key role in maternal thyroid function during pregnancy. Forbes (2014) suggests this dual control of the maternal thyroid may result from maternal-fetal conflict over the production of thyroid hormone essential for neuro-muscular development of the embryo.

Iodine is a key micronutrient necessary for the production of thyroid hormone, and thyroid

hormone is necessary for brain development (review in Forbes 2017). It is unusual among micronutrients in that there is very little somatic storage. It must continuously be replenished from the maternal diet. Iodine demands rise sharply during gestation, which is especially important in iodine-deficient populations. Most humans over most of human evolutionary history have lived in conditions of iodine deficiency. As recently as 1970, before the advent of universal salt iodization, 2/3 of the world's population lived under conditions of iodine deficiency, and even today, iodine deficiency remains the single greatest source of preventable cognitive impairment.

Although embryos require iodine and thyroid hormone for neurodevelopment, release of their limited supply has heavy long-term costs for mothers, including thyroid disease and later subfertility or infertility. Embryos appear to use hCG production to maintain maternal thyroid hormone production to secure access of maternal iodine. Pregnancy sickness, long associated with hyperthyroidism, may arise as a by-product of maternal-fetal conflict over thyroid function. An extreme form of pregnancy sickness that affects roughly 1% of pregnant women is hyperemesis gravidarum. It is an intractable form of pregnancy sickness that extends well past the first trimester of pregnancy and often requires hospitalization (Verberg et al. 2005). It results in maternal dehydration and malnutrition, and, if untreated, is sometimes fatal.

Though the etiology of pregnancy sickness is still unclear, it has long been linked to hCG production, and its incidence mirrors the production of an inert metabolite of thyroid hormone (Forbes 2014, 2017). Mothers suffering from hypothyroidism, and incapable of producing sufficient levels of thyroid hormone to generate this metabolite, do not exhibit pregnancy sickness.

Beyond its role in corpus luteum rescue and maternal thyroid function, hCG provides a bridge between the immune and endocrine systems. It is key to creating a tolerant micro-environment at the fetal-maternal interface through its effect on attracting immunosuppressive T_{regs} and influencing their function

(Robertson et al. 2009). This is key during the in process of embryo implantation and plays a role in another maternal-fetal conflict over maternal provision of the embryo: preeclampsia.

Maternal-Fetal Conflict and Preeclampsia

Preeclampsia is a hypertensive disorder of pregnancy where maternal blood pressure is dangerously elevated. It affects 5–8% of pregnancies and is a leading cause of both fetal and maternal mortality and morbidity (Steegers et al. 2010). Preeclampsia is associated with a shallow trophoblast invasion of the maternal decidua, resulting in a reduced fetal access to maternal resources. Embryos by increasing maternal blood pressure to increase access to resources. Under Haig's (1993, 1996) kinship hypothesis, preeclampsia can be viewed as a fetal countermeasure to an initial loss in the initial immunological battle over the depth of implantation.

The etiology of preeclampsia is complex and not fully understood. However, a clear role for imprinted genes is emerging. Recent work shows that paternally expressed imprinted genes are upregulated in preeclampsia, and maternally expressed genes are downregulated (Christians et al. 2017); moreover, imprinted genes are more likely to be dysregulated in preeclampsia than randomly selected genes. These data are consistent with the kinship theory of genomic imprinting, where paternally inherited genes favor greater investment in the offspring than maternally inherited genes.

Increasing maternal blood pressure is one fetal tactic employed in maternal-fetal conflict over the transfer of maternal resources from mother to offspring: another diabolical tactic is making mother temporarily diabetic.

Maternal-Fetal Conflict and Gestational Diabetes

Gestational diabetes mellitus, hereafter “gestational diabetes” is a metabolic disease that affects roughly 1 in 7 pregnant women (Buchanan and

Xiang 2005). It is similar to Type 2 diabetes in that it features insulin resistance (the presence of insulin fails to reduce blood glucose following meals) and glucose intolerance (blood glucose levels remain elevated following meals). Gestational diabetes functions as fetal tactic to increase access to maternal resources by increasing fetal access to glucose (Haig 1993, 1996).

The main conflict occurs in the third trimester over the optimal level of blood glucose with embryos favoring a higher threshold level to enhance resource uptake. The pathophysiology of gestational diabetes is largely unknown, but is clearly complex. Placental hormones appear to induce higher maternal blood glucose, but that fetal tactic is opposed by a higher maternal insulin production. That maternal response is in turn countered by further fetal manipulations to induce insulin resistance and increase insulin clearance – e.g., via placental enzymes to degrade insulin; placental insulin receptors to act as an insulin sink (Haig 1993, 1996). Both mothers and fetuses exposed to gestational diabetes are at greater risk for Type 2 diabetes later in life.

As with preeclampsia, there appears to be an immune-system link to gestational diabetes (Shober et al. 2014). Dysfunctional immunosuppressive T_{regs} appear to undermine the normal maternal immune suppression necessary for pregnancy establishment and maintenance in gestational diabetes. Elevated levels of inflammation appear to interfere with insulin signaling, leading to insulin resistance.

Fatal Conflicts

An enigmatic feature of maternal-fetal conflict is that it sometimes results in the death of mother, and consequently her fetus, that obviously is in the interest of neither party. Preeclampsia that serves to increase fetal access to maternal resources by elevating maternal blood pressure and placental perfusion is across the globe, a leading cause of maternal morbidity and mortality (Steegers et al. 2010). Hyperemesis gravidarum, a rare extreme form of pregnancy sickness, may be fatal if untreated (Verberg et al. 2005).

Such lethal outcomes reduce the fitness of both parties and should be selected against. How then could they arise? Why is it unclear but three possibilities that are not mutually exclusive seem likely: (1) rare maternal deaths may be a cost counterbalanced by net benefits that accrue to the embryo; (2) embryos make the best of a bad situation by adopting high-risk high-reward tactics; and (3) the mechanism used by the embryo to manipulate maternal physiology is imperfectly calibrated because the intervention occurs outside the normal negative feedback control circuit.

Haig (1993) suggested that maternal-fetal conflict over hCG production may have driven an escalated evolutionary arms race with alternating bouts of elevated hormone production by the embryo countered by greater maternal resistance to their effects. As Haig notes, arms races usually end when it is too costly for one or both parties to continue. A series of gene duplications have led to human chorionic gonadotropin being produced in staggering quantities in the placenta, with pregnancy sickness a by-product. Most cases of pregnancy sickness subside after the first trimester of pregnancy with little demonstrable long-term cost for either mother or fetus. However, in rare cases of hyperemesis gravidarum, there are marked costs for both mother and embryo, including occasional maternal/fetal death (Verberg et al. 2005).

Here we might use the analogy of a cliff edge. Natural selection will push offspring toward greater selfishness until the costs of such selfishness (maternal morbidity and mortality) exceed the benefits (enhanced growth and survival of the offspring). This leaves both parties near the cliff edge. All biological systems are subject to variation that stems from a variety of sources: developmental, environmental, or genetic. It may simply be the extreme of this natural range of variation that results in a small proportion of maladaptive, fatal outcomes. Both mother and fetus fall from the cliff.

With preeclampsia, it appears that offspring make the best of a bad situation: a shallow implantation in the maternal decidua and limited access to maternal resources. Their solution? A high-risk strategy: elevating maternal blood pressure by biochemical manipulation. Again, it is not in the

interest of the fetus (or mother) to push mother over the edge of the cliff, as they will fall with her. But the fetus may not be able to gauge in real time how close to the edge of the cliff they are. Quite possibly the fetus may lack access or the capacity to monitor mother's current physiological state accurately resulting in missteps that precipitate a fall over the cliff edge.

A further complication is that the fetal intrusion into maternal physiology occurs outside the normal control circuit. For example, maternal thyroid function is normally governed by a negative feedback loop: thyroid stimulating hormone increases thyroid hormone production, that in turn regulates thyroid stimulating hormone secretion. The fetus co-opts maternal thyroid function from the outside, injecting hCG into this maternal thyroid control circuit. As hCG interacts with the TSH receptor, it pushes maternal thyroid hormone production higher, which in turn reduces TSH production. But it has no effect on the production of hCG that is manufactured in the placenta. There is no obvious feedback loop between maternal physiological state and fetal hCG production: that may be by design. Modulating hCG production using maternal cues potentially opens the door to maternal manipulation of fetal production of hCG. Instead, hCG production may be relatively inflexible and not subject to fine-tuning based upon the current maternal physiological state. Again, such a system may be more prone to occasional missteps and maladaptive falls from the cliff.

Maternal-Fetal Conflict and the Social Brain

Though imprinted genes make up roughly 1% of the human genome, they are abundantly expressed during brain development. Recent work suggests that imprinted genes and an underlying maternal-fetal conflict may affect human cognition. The normal tug-of-war between genes of maternal and paternal origin is an integral part of normal cognition, but when the balance is tipped in either direction, cognitive disorders are the result.

Crespi and Badcock (2008) suggest that psychosis and autism represent opposite extremes on a cognitive continuum with normality at the center. Autism is associated with underdeveloped social cognition. Psychosis, conversely, is associated with overdeveloped, dysfunctional social cognition. They further suggest that perturbations from normality are associated with the developmental and metabolic effects of imprinted genes acting in the placenta and brain. Patrigenes contribute to autistic-spectrum disorders whereas matrigenes contribute to psychotic spectrum disorders.

There are multiple risk factors for autism, including environmental, hormonal, and genetic effects, but most cases are of unknown origin. Badcock and Crespi (2006) first suggested that a paternal bias in the expression of imprinted genes was associated with some cases of autism. This led to the complementary suggestion that imprinting in the opposite direction – a maternal bias – would have the opposite effect – e.g., paranoia and related psychotic and mood disorders, and the genesis of the diametric disorders hypothesis.

Diametric Imprinted Gene Disorders

Under the “diametric disorders” hypothesis (Crespi and Badcock 2008), autistic features will be inversely correlated with schizotypal features (schizophrenia, bipolar disorder, and major depression). Prader-Willi syndrome and Angelman syndrome accord with this hypothesis. Prader-Willi and Angelman syndrome are diametric disorders associated with the same imprinted gene cluster on Chromosome 15. Prader-Willi syndrome results from a biased expression of matrigenes; Angelman syndrome from patrigenes.

Prader-Willi syndrome is associated with an elevated incidence of psychosis in adulthood, especially when it is associated with uniparental disomy (review in Crespi and Badcock 2008). Conversely, Angelman syndrome is associated with an elevated incidence of autism and autistic-like syndromes. This pattern accords with the hypothesis of dysregulated imprinted genes, maternally biased with Prader-Willi

syndrome and paternally biased with Angelman Syndrome (Badcock and Crespi 2008).

Crespi and Badcock (2008) suggest that there are two major axes of cognition: the first is determined by the sex of the focal individual. The second is whether there is a paternal or maternal bias in the expression of imprinted genes. They suggest that more common but less severe cognitive disorders occur when the two axes are aligned – i.e., male with paternally biased expression of imprinted genes; female with maternally biased expression of imprinted genes. If the two axes are mismatched, less common but more severe disorders are observed. Autism is less common but tends to be more severe in females; schizophrenia is less common but tends to be more severe among males.

Badcock and Crespi (2008) themselves note that “to propose a single overriding explanation for such a huge range of mental conditions is controversial.” Nevertheless, the explanatory framework that integrates evolutionary biology with psychiatry, psychology, and neuroscience provides new insights and makes testable predictions. Strong tests will require identification of the specific imprinted genes involved and the mechanisms of action. Such work is beginning: Crespi et al. (2018) identified an altered expression of two brain-expressed imprinted genes with paranoid thinking. The traits included imagined and delusional thoughts, actions, and plans, all consistent with a paranoid subtype of schizophrenia. Crespi et al. suggested that small maternal biases in brain-expressed imprinted genes may result in a beneficial increase in theory of mind cognition (i.e., the ability to attribute mental states to oneself and others), but large maternal biases are associated with a pathological, hyper-developed theory of mind, resulting in paranoia.

Maternal Fetal Conflict and Autophagy

The C19MC microRNAs are strong candidates for involvement in maternal-fetal conflict. They are of recent origin in the primate lineage and expressed in the placenta and in tumors. That they are imprinted and paternally expressed

makes them prime suspects as cellular trouble-makers. They are involved in a wide array of processes including trophoblast invasion, immunoregulation (Noguer-Dance et al. 2010; Donker et al. 2012; Morales-Prieto et al. 2013), and experimental work has shown that C19MC miRNAs increase resistance to viral infection (Bullerdiek and Flor 2012).

C19MC miRNAs are also known to upregulate maternal autophagy via miRNA exported into the maternal bloodstream in exosomes (Delorme-Axford et al. 2013). Autophagy (=“self eating”) is a cellular pathway that is used to recycle damaged or unneeded cellular components and to clear bacterial and viral pathogens. It has been described as a double-edged sword, beneficial in some contexts but harmful in others (Shintani and Klionsky 2004). Autophagy allows, for example, the survival of cells in the nutrient poor conditions of a tumor. Given the similarity in molecular mechanisms used by cancer cells and invasive trophoblast (Haig 2015), it is reasonable to suspect that embryos may upregulate autophagy against maternal interests during trophoblast invasion of maternal tissue. Autophagy is also upregulated during periods of nutritional stress, being used as a form of self-cannibalism to redeploy cellular building blocks such as amino and nucleic acids. One might reasonably suspect that embryos upregulate autophagy to gain greater access to nutrients, again against maternal interests. Embryos might also prefer a greater level of autophagy that their mothers as protection against viral or bacterial pathogens; mothers might bear long-term costs associated with autophagy, such as neurodegeneration, or autoimmune dysregulation, not similarly borne by the placenta that is in effect a disposable organ. Although maternal-embryo conflict over autophagy seems plausible, especially given the involvement of imprinted genes, it remains conjectural awaiting further study.

Maternal-Fetal Conflict and Cancer

The similarity between cancer and invasive trophoblast has been known for more than a century

(review in Haig 2015). The challenge in both cases is similar: Mothers and their embryos “disagree” over the optimal access of the embryo to maternal resources, and embryo interests are served by a deeper trophoblast invasion of maternal tissue, and use a variety of biochemical mechanisms to overcome maternal resistance. Invasive cancers face the same physiological challenges and, not surprisingly, use similar biochemical pathways. Many cancers express trophoblast specific genes; hCG, the hormone of pregnancy that also plays a key immunomodulatory role, is considered a cancer biomarker (Haig 2015). And intriguingly, there is a paternal bias in the expression of imprinted genes active in invasive cancers (Summers et al. 2002), as expected under the kinship hypothesis if trophoblastic genes are being retasked in invasive tumors. And as noted above, just as autophagy is upregulated during pregnancy by paternally expressed miRNA of trophoblastic origin, autophagy is upregulated in tumors to facilitate cell survival in nutrient poor conditions.

Conclusion

The view that pregnancy is a harmonious collaboration between mother and fetus has given way to the view that both parties have differing agendas based upon shared but not identical genetic interests as first suggested by Robert Trivers (1974). The discovery of genomic imprinting in the 1990s added a further layer of sexual conflict to potential maternal-fetal conflicts via disagreements between genes of paternal and maternal origin in the embryo, with paternal genes favoring a greater transfer of maternal resources than genes of maternal origin. This conflict perspective (Haig 1993) has helped to explain a variety of otherwise puzzling apparent pathologies of pregnancy, for example, preeclampsia, gestational diabetes, autism, and schizophrenia. The end result of a coevolutionary battle of maternal and paternal interests in the fetus is often expected to be a pro rata compromise with a balanced outcome of the normal result: imprinted genes are one potential outcome. Mothers have been

selected to silence copies of genes that increase the transfer of resources from mother to embryo. Fathers have been selected to silence of copies of genes that decrease that transfer. The underlying conflicts are sometimes revealed, however, and pathologies the outcome, if the balance is disturbed by genetic or epigenetic accidents resulting in a paternal or maternal bias in gene expression.

Cross-References

- Autism
- Embryo
- Fetus Development
- Genomic Imprinting
- Parent-offspring Conflict
- Pregnancy
- Psychosis
- Schizophrenia

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Mating Rivalry

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Synonyms

[Mating competition](#); [Intrasexual competition](#); [Intersexual competition](#)

Definition

Competition among members of the same sex for reproductive partners, opportunities, and resources.

Introduction

Darwin's (1872) theory of natural selection posited that organisms must compete not only for survival but also to reproduce. Through reproduction, organisms then transmit their genetic material to offspring. In sexually reproducing species, organisms must compete with other members of their sex to mate with those of the opposite sex. Humans follow this same pattern. Men compete with other men to mate with women; and women compete with other women to mate with men. Individuals' primary mating rivals are therefore members of their own sex. This competition can take two forms: intrasexual and intersexual. In intrasexual competition, members of the same sex fight against one another directly for mates. In intersexual competition, members of the same sex compete with one another to appeal directly to the preferences of the opposite sex.

Although at the surface, men and women have the same goal – outcompete their same-sex rivals for reproductive opportunities – competition among men and among women relies largely on differing tactics.

Asymmetric Constraints and Benefits

Men and women's mating competition is radically shaped and constrained by the minimum investment they contribute to reproduction. Women, for example, are uniquely responsible for pregnancy, childbirth, and lactation. Therefore, many physiological processes (e.g., umbilical cord development, uterine contractions, milk let down, etc.) must unfold without error for women to reproduce successfully. Because women's bodies are more heavily involved in reproduction than men's, physical injury from violent conflict more strongly jeopardizes women's chances of reproduction. Furthermore, after giving birth, women

are the primary caretakers of dependent children (Hewlett 1992; Hrdy 1999). Women's substantial investment in reproduction (both pre- and postnatally) renders their injury and death costlier for bearing and raising children compared to men's death (Campbell 1999). If a woman were to die from violent conflict, she could no longer care for her dependent children, greatly compromising their chances of surviving. If a man were to die, on the other hand, his female partner could continue caring for the children. Indeed, children are at greater risk of death when their mother dies compared to when their father dies (Hill and Hurtado 1996; Sear et al. 2000). This difference between men and women's investment in reproduction shapes the nature of their mating rivalry. Because the potential risks of physical violence are so substantial for women, women are less likely to use direct physical aggression as a competitive mating tactic than are men (Campbell 1999). Women must find alternate, nonviolent mechanisms of outcompeting their same-sex rivals for the most desirable mates.

Another consequence of men's lower investment in reproduction is that the time it takes a man to reproduce is markedly shorter than the time it takes a woman to reproduce. Men, who are unbridled by pregnancy or lactation, could, in theory, engage in one (or a few) sexual encounter and successfully create a child. At minimum, men must only contribute sperm and the time it takes to copulate, and men are therefore nearly unlimited in the number of offspring they could sire across their reproductive lifespan. Consider one extreme example: genetic analyses reveal that Genghis Khan fathered 0.5% of the entire world's population! From an evolutionary perspective, Genghis Khan won the reproductive jackpot. Although this is an extreme example, it demonstrates that men have a lot to gain from reproductive competition – if they succeed, they can sire many children. Because the potential rewards of reproduction are so substantial for men, taking risks to attract and secure mates is more advantageous for men than women.

Women, on the other hand, are quite limited in the number of children they can produce throughout their reproductive lifespans. Not only is the

timeframe during which women are capable of bearing offspring shorter than men's, women must also endure 9 months of pregnancy for each child (or set of twins, etc.) they produce. Because women are relatively limited in the total number of children they can bear across their lifetimes, women stand less to gain than men from risk-taking or pursuing multiple mates. In theory, women could bear the same number of children with one mate as they could with many mates. Women's mating rivalry therefore is more heavily directed at attracting and securing one (or a few) high-quality mating partner(s) than attracting many mating partners. Men, on the other hand, can produce more children the more women with whom they have sex and therefore stand more to gain from ardently competing for multiple mates.

To successfully attract a mate, men and women must appeal to the preferences of the opposite sex (intersexual competition). To the extent that men and women value different traits in romantic partners, the traits they compete to advertise to potential mates will also differ. The remainder of this entry will outline how mating competition manifests among women and men. Last, it will describe how situational forces (i.e., operational sex ratio) shift the intensity of this competition.

What Are Men Looking for?

Women's ability to bear children across their lifetime is constrained; they are most fecund in their mid-twenties, but their fertility sharply declines thereafter until menopause (Wood 1990). In non-industrial societies, for example, women are, on average, about 35–40 years of age when they give birth to their last child, and the likelihood of having a child past age 46 drops to nearly zero (Hill and Hurtado 1996).

Because women's ability to bear children is so strongly tied to their age, many of the physical traits men find appealing in women are indicative of youth and, consequently, fertility. That is, over the course of human evolution, men who were found sexually attracted to fertile women (and their anatomical features) were more likely to

successfully impregnate those women (because they were fertile) and reproduce. Men who preferred young, fertile women sired more children and transmitted these mate preferences to offspring than did men who were attracted to women who were not fertile. Men who were attracted to prepubescent girls or postmenopausal women would not have successfully reproduced nor passed on their mating preferences to offspring. Over time, then, the human population became filled with men who were sexually attracted to fertile women and the features of women's bodies that indicate fertility.

Men therefore rely heavily on the appearance of women's bodies to ascertain fertility. Although men do not consciously think "she looks fertile" when assessing a woman, men attend to physical appearance when judging a potential mate. Around the world, men more heavily value attractiveness in their long-term mates than do women (Buss 1989). Men's perceptions of female attractiveness are not arbitrary but rather linked to women's underlying health and fertility. Men find bodily cues of women's advancing age, such as gray hair and wrinkles, as sexually unappealing. In sum, because women's bodies are heavily involved in reproduction, men have evolved to be attracted to bodily cues of fertility, and these preferences increase the odds that men will choose mates who are impregnable.

Another consequence of the fact that women are responsible for pregnancy is that women always know they are the biological mothers of the children they birth. That is, women have maternity certainty. Men, on the other hand, never know for certain that the child developing in their female partner's womb is genetically related to them. Men lack paternity certainty, and this uncertainty shapes which traits men find attractive in potential mates. If a man's female partner has likely not had sex with other men, he can be more confident that the child developing in her womb is genetically related to him. Men, therefore, prefer cues of sexual loyalty in their long-term mates. All else equal, men prefer women who are sexually chaste and faithful over women who are sexually promiscuous or unfaithful when selecting which women (and their

children) to invest in. These mating preferences decrease the odds that a man will invest in a child that is genetically unrelated to him, which is called cuckoldry.

Women's Mating Rivalry

Although women are more likely than men to pursue one mate rather than many, the quality of that mate has important consequences for the survival, well-being, and success of women and their children. Throughout history, children have been more likely to die when their mothers were not supported by a male romantic partner (McCalman et al. 2008). Furthermore, when women remain married to their husbands, their children are more likely to later attain social success than if the couple dissolves (Sigle-Rushton et al. 2005).

Polygamy also puts children at risk. In fact, children are more likely to die when their mother shares her husband with another woman compared to when their mother is monogamously married (Omariba and Boyle 2007; Strassmann 1997). When multiple women are polygynously married to one husband, conflict often ensures over access to the husband's material resources and emotional investment (Jankowiak et al. 2005). This conflict may even become violent, harming the fitness of women's children.

If women want to attract a high-quality mate, they must appeal to his mating preferences. Therefore, the domains in which women compete with rivals are shaped by men's mating preferences (i.e., intersexual competition). Because men prefer bodily cues of youth and fertility, women compete with one another to maintain and display physically attractive bodies. To succeed at this competition, women must first size up their competition, assess which are their most threatening rivals, and estimate how they compare relatively. Women consider physically attractive women threatening rivals (Russell et al. 2016). They are most threatened by rivals with feminine faces, large breasts, and a slim waist relative to larger hips (Fink et al. 2014). These physical features indicate youth and fertility and are therefore desired by men (Jasienska et al. 2004). Indeed,

physically attractive women are more successful at securing relationships with wealthy men and luring away rivals' mates, suggesting that women's perceptions of rival threat are accurate (Schmitt 2004; Davies et al. 2010; Sunderani et al. 2013).

To gain a competitive advantage over an attractive rival, women can take one of two approaches: (1) increase their own attractiveness (i.e., intersexual competition) or (2) damage their rival's attractiveness (i.e., intrasexual competition; Campbell 2004).

When women are exposed to an attractive conspecific, they feel less satisfied with their own appearance (Krones et al. 2005). They experience distress when a rival has a relatively more attractive face or body (Buss et al. 2000). This response likely facilitates the first goal: increasing one's own attractiveness. That is, if women feel less satisfied with their appearance, they may be more motivated to augment it. In day-to-day interactions, women report competing to be more physically attractive than their rivals (Cashdan 1998). Women enhance their appearance by applying makeup and donning tight and revealing clothing (Tooke and Camire 1991).

Women also pursue an attractive body shape through diet and exercise to outcompete their mating rivals. In Westernized societies, men prefer slender women, and these women (compared to their heavier counterparts) are more likely to marry men who are taller and wealthier (Fales et al. 2016; Oreffice and Quintana-Domeque 2010). Women report using their bodies and athleticism to compete with other women for male attention (Fisher and Cox 2011). When women are in the presence of attractive rivals who are emphasizing their bodies with revealing clothing, women become less satisfied with their own bodies but particularly if a desirable mate is also present (Ferguson et al. 2011).

Researchers have postulated that mating competition may underlie the more pernicious manifestations of these behaviors (e.g., eating disorders; Abed 1998). Congruent with this contention, women who are prone to eating disorders are not only interpersonally competitive in general but also competitive about mating in particular

than women who are less prone problematic eating (Faer et al. 2005; Schleien and Bardone-Cone 2016). Securing a long-term mate may also ameliorate problematic weight-maintenance behaviors. When women get married, they become more satisfied with their bodies and less motivated to become thin through dieting and purging (Keel et al. 2007; Vogeltanz-Holm et al. 2000). That is, when women have successfully outcompeted their mating rivals in securing a long-term mate, they become less motivated to pursue a thin body, suggesting that some portion of these weight-maintenance behaviors are in pursuit of a mate. However, if women secure a particularly attractive romantic partner and are not attractive themselves, they continue to pursue thinness through dieting (Reynolds and Meltzer 2017). Given that men prefer physically attractive mates, these less attractive women may strive for thinness to preserve the partnership or deter mate poachers.

When exposed to an attractive rival, women not only feel worse about themselves, but they also feel jealousy and anger (Massar and Buunk 2010). These emotions likely facilitate the second mechanism by which women gain a relative advantage: harming rivals' attractiveness. Women are more likely than men to derogate or gossip about their mating competitors' physical appearance (Buss and Dedden 1990; Nevo et al. 1993). Among adolescents, girls critique one another's appearance (Eder and Enke 1991). These comments are effective; men view women as less attractive after they have heard negative comments about their physical appearance (Fisher and Cox 2009). However, attractive women may be especially successful at swaying men's opinions of other women; men were more likely to alter their assessments of a woman if she was derogated by an attractive, compared to less attractive, rival (Fisher and Cox 2009). Given that derogating a woman's appearance can be successful, it is perhaps unsurprising then that women are more likely than men to end a friendship over appearance teasing (Vigil 2007). Women must avoid or socially punish those that might harm men's assessments of their appearance.

Because men could succeed reproductively by pursuing many mating opportunities, men are

relatively open to casual sexual encounters compared to women (Schmitt 2003). Oftentimes, women use casual sex in hopes of securing a long-term committed relationship (Regan and Dreyer 1999). Women must therefore be vigilant toward other women who could lure away romantic partners through sex or by advertising cues of sexual availability. Indeed, women are more likely to have their romantic partners poached by women who are sexually unrestrained than those who are sexually restrained (Schmitt 2004). Women should therefore be sensitive to features that signal sexual openness in their same-sex rivals.

Women are quite hostile toward other women who are sexually promiscuous (Baumeister and Twenge 2002). Women believe that other women judge them more harshly than do men for their sexual behaviors (Milhausen and Herold 1999). Women who embrace their sexuality report that other women often judged, accused, and rejected them (Blumberg 2003). As one woman described, "They see me as sluttie. . . the way they look you up and down. The way they size you up when you walk into a room. The way they watch you when there's a male in the room. And they get upset, or they tend to tense up" (p. 152; Blumberg 2003). Indeed, women are unwilling to befriend sexually promiscuous women (Bleske and Shackelford 2001). Women who are more sexually experienced are more likely to be teased, demeaned, and excluded and have rumors spread about them than their less sexual peers (Gallup et al. 2009). Even indirectly suggesting one's sexual openness is enough to evoke the scorn from other women. In a lab study, when a female confederate dressed provocatively, other women responded with harsh glares, rude comments, and lower willingness to befriend her or introduce her to their boyfriends (Vaillancourt and Sharma 2011).

Although men find women who are sexually open immediately appealing, men are cautious to engage in long-term committed romantic relationships with these women (Oliver and Sedikides 1992). As mentioned, men do not want to mistakenly invest in another man's baby, and so they avoid women who might commit sexual infidelity.

Indeed, men are highly distressed by the thought of their mate's sexual infidelity (Buss et al. 1999). Suspected infidelity is one of the best predictors of divorce and spousal abuse (Betzig 1989; Daly and Wilson 1988).

Because men care about the likelihood their female partner will commit infidelity, questioning a woman's likelihood of staying sexually faithful to a man is an effective way of harming her desirability as a long-term mate (Schmitt and Buss 1996). That is, women can harm their rivals' long-term mating appeal by drawing attention to rivals' sexual openness. One way women accomplish this goal is by transmitting information about their rivals' sexual promiscuity. Compared to men, women are more interested in gossip about their same-sex rivals and more likely to share it with their same-sex friends (McAndrew et al. 2007). Across cultures, women have a higher tendency to gossip than do men (Nevo et al. 1993). Moreover, women are especially interested in information about other women's sexual promiscuity and infidelity, suggesting that this information is valuable in reputational competition (McAndrew and Milenkovic 2002).

One investigation straightforwardly tested the prediction that women would use social information strategically against their same-sex rivals (Reynolds et al. 2017b). Across five studies, women were more likely to transmit reputation-harming information about rivals who were more, compared to less, threatening mating rivals. Women were more likely to disclose that another woman was sexually promiscuous, had a sexually transmitted disease, and cheated on her last romantic partner when the woman was attractive (vs. unattractive), flirtatious with their mates, or dressed provocatively (vs. conservatively). These findings suggest that women compete with one another through strategically influencing social reputations (Hess 2006, 2017).

Although women strategically harm the reputations of women who are threatening mating rivals, women may not necessarily realize consciously what they are doing. Instead, women may simply believe they are concerned about the targets of their gossip. Indeed, women were more likely to disclose that another woman had engaged

in drunken sexual behavior when she was dressed provocatively rather than conservatively, but many of the gossipers phrased their disclosure as concern (e.g., “I am worried about her”; Reynolds et al. 2017a).

Appearing concerned when gossiping may be a competitive mating tactic. Women who believe they are concerned about their gossip targets might phrase their gossip nicely rather than maliciously, which may protect them against the social costs of engaging in overt gossip. For example, people generally dislike gossip, but especially when the gossip is negative, self-interested, or competitively motivated (Beersma and Van Kleef 2012; Turner et al. 2003). Women who found ways to disguise their gossip should have a social advantage over women who gossip in an overtly malicious manner. Indeed, compared to men, women report that their social conversations were less intended to harm their targets and were more strongly motivated by concern (Reynolds et al. 2017a). Furthermore, gossipers are perceived as more likeable, trustworthy, and desirable as romantic partners when they frame their gossip as concern rather than malice (Reynolds et al. 2017a). Therefore, women may believe that they are seeking to help their targets when they gossip, not realizing consciously that they are nonetheless transmitting their target’s social information, and effectively harming their targets’ reputations. Laura Tracy (1991) found support for these misbeliefs when she interviewed women about female-female competition: many women reported that other women were competing with them, but they were not competing themselves.

Men’s Mating Rivalry

Although men do not make similarly large physiological investments toward reproduction as women, men can nonetheless provide in ways that help children’s outcomes. Men’s provision of time and resources enhances the odds their offspring will not only survive but also thrive in society (Geary 2000). Women mated to such men had higher reproductive success than women who mated with men who did not invest in them and

their children. Over time then, the population became filled with women who were attracted to cues of investment and resources in their mates. In order to attract the best mates, men compete with one another to signal these traits to women.

To signal resources to mates, however, men must first acquire them. A substantial component of men’s mating competition involves competing with other men to acquire resources. Men compete against other in-group men for status, which predicts men’s access to the group’s resources. However, across human history, men have also competed *as groups* against other groups of men for access to territories, resources, and mates (Geary 1998). Unlike women’s mating competition, men’s mating competition involves both within-group and between-group components.

Because men competed in groups (e.g., armies), the traits that predict within-group status among men are typically those that aid in between-group competitions. Throughout history, successful male coalitions gained access to the defeated group’s territory, resources, and women. Men who comprised such formidable groups therefore succeeded not only on the battlefield but also reproductively (Carvajal-Carmona et al. 2000). Therefore, the success of the group influenced the reproductive success of the men who comprised it. Men’s intragroup competition therefore rendered their mating competition less zero-sum than women’s.

Likewise, the traits of the men who comprised the group influenced the success of the group. Men who are physically strong, dominant, aggressive, courageous, and loyal to the group increased the odds their groups succeeded in combat. Men have therefore evolved to prefer men who possess these traits as coalition partners and defer to them in exchange for their contribution to the coalition (Henrich and Gil-White 2001; Winegard et al. 2014). Indeed, modern men prefer other men who are dominant, strong, and courageous as partners in competitions. This preference may explain some portion of men’s antigay bias. Indeed, men expect gay men to be lacking in these traditionally masculine traits (e.g., toughness, strength). However, when masculinity and sexual orientation are directly manipulated, men

prefer a partner who is homosexual and masculine over one who is heterosexual and feminine (Winegard et al. 2016). This pattern suggests that men's antigay bias is largely an anti-effeminate bias and likely stemmed from their evolutionary history of coalitionary competition.

To assess the traits of their potential coalition partners, men vet one another using tests of strength, courage, loyalty, and pain tolerance (Sosis and Alcorta 2003). Men who can withstand such challenges are rewarded with respect and deference from other men. This deference creates a hierarchy of dominance, in which the most dominant (and group-benefitting) men are at the top and less dominant men are in subordinate positions. It is within the interests of the subordinate men to defer to the dominant for a few reasons. First, the dominant men are usually more physically formidable and could severely injure or kill their weaker counterparts. Second, dominant men promote the group's success in intertribal warfare. If the group succeeds in these battles, then even the subordinates will benefit from the group's victory, attaining access to the losing group's resources and women. Indeed, genetic analyses reveal that across history, men from successful groups mated with losing groups' women, thereby propagating their genes (Carvajal-Carmona et al. 2000).

This history of warfare and aggression has shaped not only men's psychological but also morphological traits. Compared to women, men are 90% stronger in their upper bodies and 65% in their lower bodies (Lassek and Gaulin 2009). Because of these large differences in musculature, the average man is stronger than 99.9% of women (Lassek and Gaulin 2009). Muscularity enhances perceptions of men's dominance and is sexually attractive to women (Frederick and Haselton 2007). Indeed, muscular men are more likely to be chosen as women's sexual partners than their leaner counterparts (Frederick and Haselton 2007). However, researchers have argued that throughout most of human history, women were not the choosers of their long-term mates. Instead, families arranged advantageous unions (Apostolou 2007), or dominant men used physical force to exclude competitors from their mates (Puts 2010).

Given that muscularity predicts other men's assessments of dominance and deference and women's sexual attraction, men are quite motivated to pursue muscular physiques. When men are unhappy with their bodies, it is usually because they desire to be more muscular (Bergeron and Tylka 2007). Compared to women, men are more compelled to augment their muscularity (Smolak and Murnen 2008), and many men use body building supplements, such as anabolic steroids, to do so (Olivardia et al. 2004).

In modern times, men may use sports to assess and signal one another's strength and athletic prowess. Compared to women, men feel more competitive with their peers over athletic ability (Cashdan 1998) and use physical activity and sports as forms of competition (Apostolou 2015; Kilpatrick et al. 2005). Along with providing a signaling arena for physical prowess, modern-day sports likely appeal to men's interest in coalitional activities. Indeed, men are more likely than women to participate in organized sports but particularly team sports (Deaner et al. 2012).

Men who climb to the top of dominance hierarchies earn status within their groups. This high status grants them priority access to the group's resources and women. Indeed, around the world, women are attracted to men who have high status and access to resources (Buss 1989). Among the Yanomami tribe, for example, men who have killed more enemy males in intergroup conflict have more wives than men who have not contributed as substantially to the group's success (Chagnon 1988).

Another way that men earn status within a group is through hunting. Throughout human history, hunters were primarily men. Men who were successful hunters provided more calorically dense meat for their social groups. These high-contributing men therefore became highly valuable within the social community. Indeed, in foraging societies, men's reputations for hunting ability predict their social standing relative to other men in the group (Kelly 1995; Wiessner 1996). This high social status translates into more mating opportunities. In non-Westernized

societies, for example, men who are better hunters have more sexual partners, marry younger and more fertile women, and ultimately father more children than men who are not as skilled hunters (Blurton Jones et al. 1997; Kaplan and Hill 1985; Smith and Bleige Bird 2000). It is rational for women to be attracted to these highly skilled hunters; although meat is often shared with the group, families of the hunter get a larger share (Wood 2006). Hunting has therefore been a domain of intrasexual competition for men, with the winners attracting more mates and fathering more offspring.

Local Conditions Influence the Intensity of Mating Rivalry

Mating rivalry is not monolithic among the sexes. Instead, the immediate social landscape shapes the degree to which men and women must compete for mates. One factor that dictates the intensity of mating competition is the operational sex ratio – the ratio of fertilizable females to sexually active males within a population at a given time (Emlen and Oring 1977). The sex ratio dictates the number of one's rivals relative to the number of one's potential mates. As the proportion of women relative to men increases, so too does the level of female competition for mates. Conversely, male mating competition increases when there are proportionately more men in the population. When the sex ratio is unfavorable (proportionately more rivals), both sexes increase their intersexual and intrasexual competitiveness.

To increase their intersexual appeal, or to become more desirable to the opposite sex, men and women tend to shift their mating strategies to that of the opposite sex (Moss and Maner 2016). As previously described, on average, women tend to be more selective about their mating partners than men because women incur substantial physiological burdens from reproduction (e.g., pregnancy, lactation). Men, on the other hand, are relatively more open to casual sex because they can substantially increase their reproductive success by impregnating more fertile women.

Although these are the typical strategies of the sexes, these strategies shift to those of the opposite sex when the operational sex ratio is disadvantageous.

When men are more prevalent in the population, men become more willing to invest in romantic partners and less open to casual sex (Moss and Maner 2016). Men's mating strategies therefore more closely match those typical of women. Indeed, historical records indicate that divorce rates are lower and rates of paternal investment increase during times when men are the more prevalent sex (Pedersen 1991; Pollet and Nettle 2008). Furthermore, when men are disfavored, they become more willing to take financial risks to acquire resources (i.e., incur more debt) and are more willing to buy potential mates lavish gifts (Griskevicius et al. 2012). Thus, men must appeal to women's mating preferences (i.e., commitment, resource investment) when they are the prevailing sex. Conversely, when women are more abundant, sex norms become more liberal, divorce rates increase, births out of wedlock increase, paternal investment decreases, and the proportion of single mothers increases (Guttentag and Secord 1983). That is, when women are more prevalent, they can no longer afford to demand high levels of commitment or investment from their male partners and instead pursue a more unrestricted sexual strategy (Moss and Maner 2016).

When the sex ratio is unfavorable, men and women also increase their intrasexual competitiveness (Moss and Maner 2016). That is, they compete or aggress directly against members of their own sex. For men, this increased aggression manifests in the form of increased violence. Indeed, historical analyses indicate that periods when men were more abundant (relative to women) are characterized by more social unrest, violence, and expansionistic military directives (Hudson and Den Boer 2002, 2004). Women, on the other hand, are more likely to turn to mate poaching when they are the more abundant sex. Across the world, women are more likely to lure away other women's mates when there is an overabundance of women (Schmitt 2004).

Conclusion

Although both men and women must compete with their same-sex rivals for desirable mates, this competition manifests quite differently among each sex. Women, who are the physiological vessels of reproduction (i.e., their bodies house and nourish developing offspring), compete to advertise their physical attractiveness (and hence fertility) and sexual fidelity to potential partners. They also derogate these traits in one another. Men, who can provide resources and protection to their female partners and offspring, compete to acquire status (and consequently resources) through hunting and intergroup competitions. Because men often competed in coalitions, which led to increased mating opportunities, their same-sex mating competition may be less zero-sum than women's. Women, on the other hand, were forced to compete among one another for the limited high-status men within their social groups. For men and women alike, the intensity of this mating competition is influenced by immediate social conditions, such as the operational sex ratio.

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Mating Sabotage

- [Circumventing Mate Choice](#)

Mating Selection

- [Good Genes](#)

Mating Sociometer

- [Sociometer Theory](#)

Mating Strategies

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Synonyms

[Intersexual relations](#); [Sexual strategies theory](#); [Strategic pluralism theory](#)

Definition

A set of evolutionary adaptations which evolved to maximize the reproductive success of individuals.

Introduction

A mating strategy can be defined as a set of behavioral and cognitive adaptations which drive reproductive efforts of individuals. The ultimate aim of mating strategies is to maximize reproductive success. These strategies also affect individual investment in mating and parenting (Buss and Schmitt 1993; Gangestad and Simpson 2000). Each consists of specific mating tactics in the form of individual behavior (Gangestad and Simpson 2000). Importantly, mating strategies and tactics are often nonconscious, and their activation strongly depends on specific contexts and circumstances, such as the sex ratio in the mating pool, mate value of individuals concerned, or

cultural norms (Buss and Schmitt 1993). Evolutionary psychologists agree that humans evolved more than one “ideal” mating strategy, which implies that there is no single mating strategy that would be optimal for every individual in any situation. Moreover, human mating strategies are variable and flexible, so that individuals can mix and match them (Buss and Schmitt 2016).

There are two main theories of human mating strategies. The first is *sexual strategies theory* (Buss and Schmitt 1993, 2016). It works mainly with intersexual differences which result from the asymmetry of parental investment. The second is *strategic pluralism theory* (Gangestad and Simpson 2000), which highlights intrasexual variation in mating behavior rooted in individual differences.

Sexual Strategies Theory

According to Trivers’ theory of parental investment and sexual selection (Trivers 1972), men and women face different adaptive problems in mating and parenting, and that leads to different mating strategies and tactics. In mammals generally, investment into reproduction is higher in females than in males: females invest at the very least in pregnancy, childbirth, and lactation, whereas male contribution can be minimal, just the sexual act. This disproportion in reproductive biology led to the development of sex-specific mating strategies. Most generally, we can distinguish between a long-term mating strategy characterized by pair bonding, biparental investment, and relationship commitment and a short-term mating strategy marked by absence of commitment and exclusivity.

As noted above, the sexual strategies theory emphasizes sex differences in mating strategies. Due to high investment in reproduction, women are said to profit more from long-term strategies, which should guarantee resources needed to raise children. Men, on the other hand, are more likely to prefer short-term mating strategy and tactics because a higher number of sexual partners can increase their reproductive success. There is a large body of cross-cultural research which supports these predictions (Buss 1989; Buss and

Schmitt 2016). Furthermore, the sexual strategies theory indicates under what circumstances it is advantageous for both sexes to mix the short- and long-term strategy (Buss and Schmitt 1993, 2016). In fact, short-term strategies can lead to long-term relationships and vice versa (for a review of advantages and disadvantages of short- and long-term mating strategy for each sex, see Buss and Schmitt 2016).

In general, sexual strategies theory posits that both women and men have long- and short-term strategies in their repertoire. This theory has the ambition of using rather straightforward distinctions to produce a complex image of mating. Mating, however, can be influenced by other kinds of factors, such as individual differences, temporal context, or social factors (Buss and Schmitt 2016). By focusing on intersexual differences in mating strategies, sexual strategies theory seems ill-equipped to account for intrasexual variation, which is vast and of undoubted importance.

Strategic Pluralism Theory

The strategic pluralism theory, formulated by Gangestad and Simpson (2000), focuses on differences in mating strategies within each sex rather than between the sexes. It describes how individual characteristics in conjunction with environmental factors can lead to flexibility and pluralism of mating strategies. In general, the strategic pluralism theory views mating strategies through the prism of cost-benefit analysis. It states that individuals adopt a mating strategy based on how “advantageous” it is under given circumstances. Strategic pluralism theory works extensively with *good genes* and *good provider* theories. Depending on circumstances, women make a trade-off between men’s genetic quality and their ability and willingness to support them and their offspring. It is assumed that few individuals meet both of these criteria equally well. Factors which affect the particular form of compromise a woman makes with respect to choosing a partner who has good genes or one who promises to be a good provider fall into three broad categories: first of all, woman’s own characteristics, such as health, age, physical attractiveness, or mate value in the mating market;

second, her access to resources, meaning that women who have sufficient resources either of their own or through their families may be independent of additional resources from a potential partner; and finally, environmental factors in the sense of life in an environment with stable and sufficient resources, presence of various pathogens, and the like. If a woman has sufficient resources and can find a better short-term than long-term partner, it may be more advantageous for her to engage in a short-term relationship, thus “exchanging” man’s parental investment for good genes. If, on the other hand, a woman lives in an environment where biparental care is crucial for children’s survival, it is likely she will favor men with better parental skills. In short, such conditions promote women’s long-term strategy. In human evolutionary history, women have been exposed to a large variety of environments. This led to the development of the range of mating strategies still in use today.

Since women are, generally speaking, more choosy sex, men’s mating strategies are to some extent limited by women’s choices. Short-term strategy may be advantageous for men who display high genetic quality, for instance, by low fluctuating asymmetry, high masculinity, or dominant behavior (Durante et al. 2016; Gangestad and Simpson 2000). In general, men could be expected to pursue a short-term strategy which can increase their reproductive success by mating with more women. This strategy is not, however, universally advantageous. In particular, it does not increase reproductive success of men who do not meet the demands placed on short-term male partners. In fact, according to the strategic pluralism theory, long-term strategy is the most advantageous strategy for most men, although a small proportion of men can achieve higher reproductive success via the short-term strategy.

All in all, both men and women make compromises between mating and parenting and that affects their mating strategies. Both sexes can therefore pursue both types of strategies or mix and match them according to what is beneficial given their circumstances and surrounding conditions (Durante et al. 2016; Gangestad and Simpson 2000). Nevertheless, strategic pluralism theory does not explain how other important

variables, such as self-perceived mate value and sociosexual orientation of attachment style, affect mate choice and how these factors help maintain romantic relationships.

Conclusion

Evolutionary theories on human mating are meaningfully anchored in men’s and women’s different biological roles reproduction. According to Trivers’ theory of asymmetric investment, minimal obligatory investment in reproduction is higher in women than in men (Trivers 1972). Nevertheless, biparental care is the dominant pattern in human societies, and paternal investment of both sexes is relatively high during offspring’s childhood. Both sexes therefore invest in their children and that has a significant impact on their mating strategies and preferences.

Mating strategies are a set of evolutionary adaptations which promote the reproductive success of individuals. In other words, their aim is to maximize the number of children and grandchildren by coupling with the best possible partner. In humans, the range of mating strategies is considerable and varies from exclusively short-term to exclusively long-term strategies. Analogically, people form a wide range of sexual relationships, ranging from commitment-free short-term relationships, such as casual hookups or one-night stands, to committed long-term relationships, such as marriage. Importantly, short-term strategies can lead to long-term relationships and vice versa. Mating strategies include a range of possible tactics which are mostly unconsciously used to attract – and in some cases establish a relationship with – the desired partner. Which strategies are actually employed depend not only on the sex but also on the individual (e.g., his or her age, personality, mate value, sociosexual orientation, life history, and attachment style), on the environment (pathogen prevalence, predictability of resource availability, and ecological stability), and on cultural factors (Marzoli et al. 2018). High levels of variation in mating strategies are therefore found not only between but also within the sexes. Moreover, mating strategies can be influenced by

individuals' families: for instance, a woman who can rely on the support of her family can focus on potential partner's socioeconomic status less than a woman for whom such support is not available. Moreover, not all relationships, and not all sexual activities, lead to reproduction. Romantic relationships can promote the formation of social coalitions (Lancaster 1975); sex can provide safety from physical harm (Hrdy 1981) or be exchanged for food or other items (Hill 1982). Nevertheless, all these factors have the potential to promote reproduction success. All these factors, not only sex, should be therefore considered in further research on human mating strategies.

Cross-References

- David Buss
- Derogation of Attractiveness
- Differential Parental Investment
- Evolution of Desire, The
- Long-Term Mating
- Mate Value Inflation
- Reproductive Strategies
- Self-Stereotyping
- Sexual Strategies Theory
- Sex Differences in Long-Term Mating Preferences
- Sex Differences in Parenting and Parental Investment
- Sex Differences in Short-Term Mating Preferences
- Sexual Conflict and Sex Differences in Parental Investment
- Sexual Strategies Theory
- Short-Term Mating
- Sociosexuality and Sexual Conflict in Mating Strategies
- Steve Gangestad
- Women's Long-Term Strategies

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Mating Strategy

- Mate Retention Strategies
- Parental Investment as Mating Effort

Mating Strategy Equilibria

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Synonyms

Evolutionary stable strategies

Definition

Mating strategy equilibria refers to alternative mating phenotypes being maintained in a population in an evolutionarily stable equilibrium.

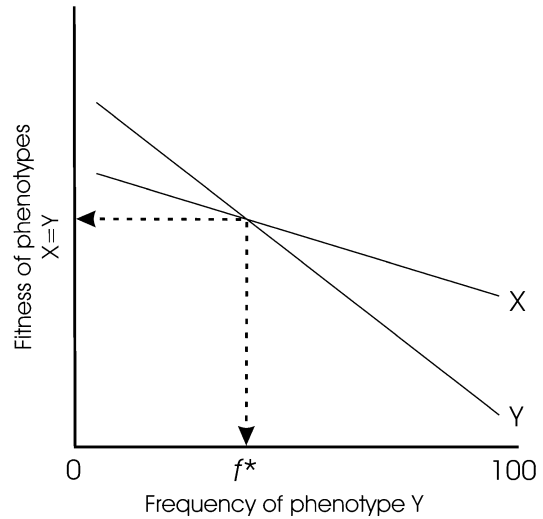
Introduction

In terms of evolutionary game theory, a “strategy” is a genetically determined decision rule that regulates how different behavioral phenotypes (tactics) are manifested (Gross 1996).

Evolutionary strategies are stable; if after reaching a critical proportion within a population, no other alternate strategy can do better (Maynard-Smith 1982). Behavioral strategies can include multiple distinct phenotypes (tactics) that are maintained at an evolutionary stable equilibrium. This is often seen with “alternative mating tactics” in which individuals adopt different behavioral phenotypes to access mates. This section will discuss how alternative mating tactics can evolve and be maintained within populations in a stable equilibrium.

Alternative Strategies

An alternative mating strategy is a decision rule that is governed by inherited genetic polymorphisms leading to distinct behavioral phenotypes. These genetically distinct phenotypes can exist in a population in a stable equilibrium through frequency dependent selection (Maynard-Smith 1982; Gross 1996). Assume a population where the frequency of a strategy X is f , the frequency of a strategy Y is $1-f$, and at least one of these strategies is under negative frequency dependent selection (Fig. 1). The frequency at which the fitness functions of these strategies intersect is the evolutionary stable state frequency (ESS f^*). At this frequency, the average fitness of X and Y are equal, and they are stable within the population (Gross 1996). There are a few examples of alternative mating strategies in natural populations, although they appear rare. In the ruff, *Philomachus pugnax*, alternative mating strategies consist of genetically determined independent (territorial), satellite, and female-mimicking



Mating Strategy Equilibria, Fig. 1 Fitness of strategy X and Y relative to the frequency of Y in the population. The average fitness of X and Y are equal where the fitness functions intersect. The frequency at which the fitness functions cross is the evolutionary stable state frequency (ESS f^*) (Gross 1996)

(faeder) males (Lank et al. 1995). The genetic distinction between these morphs appears to be an inverted region of a chromosome consisting of around 4.5 Mb. Independent males are homozygous for the ancestral state in this region, while satellite and faeder males are heterozygous for the inverted state. Sequences for satellite and faeder males are significantly divergent within an internal region of this inverted section (Lamichhaney et al. 2016). While ruffs are often given as an example of a species with alternative mating strategies due to these genetic polymorphisms, there is still relatively little quantitative data assessing whether the male morphs are under frequency dependent selection or have equal average fitness values. These data will be important to fully establish whether these phenotypes are true alternative mating strategies.

Mixed Strategy

In a mixed strategy, the decision rule is that individuals will adopt tactic X with a probability of p and tactic Y with a probability of $1-p$ (Maynard-Smith 1982). There is no genetic polymorphism

driving these differences, and the likelihood that an individual adopts either tactic is purely probabilistic. As such, there is a stochastic aspect regarding which behavior is adopted. Similar to alternative strategies, mixed strategies can be maintained at a stable equilibrium with equal average fitnesses through frequency dependent selection (Gross 1996). Presently, there is little empirical evidence that mixed strategies actually occur in natural populations. In order for this to happen, it would have to be shown that the tactics have equal average fitness, they are under frequency dependent selection, they are genetically monomorphic, and that the likelihood of adopting one tactic over another is purely probabilistic (Gross 1996).

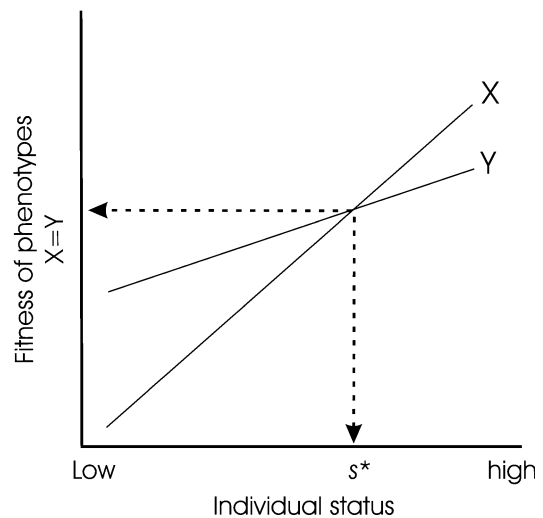
Conditional Strategies

Conditional strategies involve a decision rule where individuals adopt a behavior based upon their condition or status. The behavior adopted should provide the individual the highest fitness given their specific condition. The difference between this and the mixed strategy is that under the mixed strategy scenario, a behavior is assigned randomly with a given probability from a set of possible actions (Maynard-Smith 1982), while for a conditional strategy an action is performed when a specific condition is met (Dawkins 1980). The majority of alternative mating tactics are likely to be conditional strategies. For example, in dimorphic dung beetles, *Onthophagus acuminatus*, males that reach a certain size develop large horns and adopt a fighting tactic to access females, while smaller individuals either developed reduced or no horns and use a sneaker tactic. Both body size and horn length is dependent on larval food intake, and these traits can be experimentally manipulated by altering food quality (Emlen 1994).

Conditional strategies were initially described to be genetically monomorphic (Dawkins 1980) and Gross (1996) proposed that this type of strategy could evolve through “status-dependent selection.” In the status-dependent selection (SDS) model, individuals will vary in their state due to a combination of environmental, genetic, and developmental factors. These factors come

together to influence the “status” of an individual relative to others in the population, which then influences their mating success and fitness. In this case, the average fitnesses of the different tactics do not have to be equal to be at an evolutionary stable equilibrium. Rather, there is an intermediate status, s^* , at which the fitness functions of the two tactics are equal, and this is termed the evolutionary stable strategy switchpoint (ESS s^*) (Fig. 2). Individuals below s^* should adopt tactic Y, while those above s^* should adopt tactic X. The different phenotypes would not have to be maintained by frequency-dependent selection, but shifts in the ESS s^* can alter the frequency of the tactics in the population (Gross 1996; Tomkins and Hazel 2007).

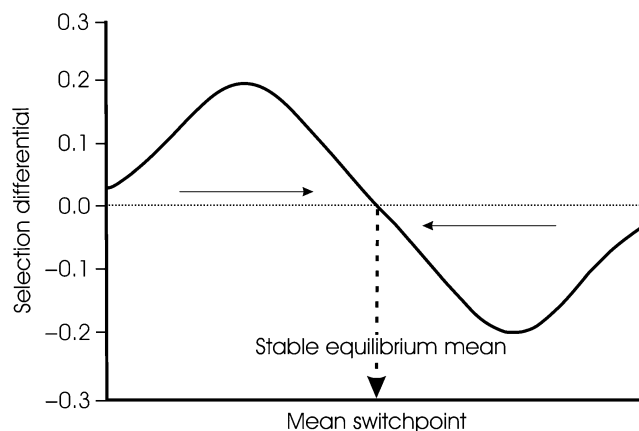
One critique of Gross’s SDS model is that these tactics are described as genetically monomorphic. However, as pointed out by Tomkins and Hazel (2007), this was mainly to distinguish conditional strategies from alternative strategies in game theory models. Without some heritable variation in the switchpoint, evolution cannot act to maintain the switchpoint at an evolutionary stable state. Conditional strategies are



Mating Strategy Equilibria, Fig. 2 The fitness of phenotypes relative to individual status. The fitness of X and Y are equal where the fitness functions intersect. The status at which they intersect is the intermediate status, s^* . Individuals below s^* should adopt tactic Y, while individuals above s^* should adopt tactic X (Gross 1996)

Mating Strategy Equilibria,

Fig. 3 Selection differential relative to the population mean switchpoint. When the selection differential is zero, the mean switchpoint is at a stable equilibrium (Tomkins and Hazel 2007)



more likely regulated by a combination of genetic and environmental (GxE) factors (Hazel et al. 1990; Hazel et al. 2004; Neff and Svensson 2013). Individuals will adopt one tactic or the other depending on whether an environmental regulated cue (such as size) surpasses a threshold value that is individually variable and governed by additive genetic effects. Quantitative genetic models, such as the evolutionary threshold (ET) model (Hazel et al. 1990; Hazel et al. 2004; Tomkins and Hazel 2007), take into account how variation in switchpoint among individuals, the distribution of environmental regulated cues, and the fitness functions for each tactic drive changes in the mean population switchpoint from one generation to the next. Changes in the mean population switchpoint between generations is termed the switchpoint selection differential. In these models, the mean switchpoint is at equilibrium when the selection differential is zero (Fig. 3), and this can occur even when the average fitnesses of the different tactics are not equal (Tomkins and Hazel 2007).

Conclusion

Three strategies have been used to explain how alternative reproductive phenotypes are produced and maintained in an evolutionary stable equilibrium. These include alternative strategies, mixed strategies, and conditional strategies. Both the alternative strategy and mixed strategy models

require that alternative phenotypes be under frequency dependent selection and have equal average fitness values. However, conditional strategies can evolve without frequency dependent selection or equal fitness values among the tactics. While there are some examples of alternative mating strategies, many alternative mating tactics likely fall under conditional strategies.

Cross-References

- [Making the Best of a Bad Job](#)
- [Sneak Copulation as an Alternative Mating Strategy](#)

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Mating Systems

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Synonyms

Effective breeding populations; Polygamy;
Reproductive skew

Definition

The ratio of reproductive variance in men to reproductive variance in women.

Introduction

Most of us take for granted that *Homo sapiens* is monogamous. That hasn't been, is not, and probably never will be the case. Men – like other males – invest little in each of their gametes,

and, like other male mammals, they invest nothing in gestation and lactation. Women invest more. As Charles Darwin, who wrote the book on *Sexual Selection* and attached it to his work on the *Descent of Man*, pointed out: “The female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals, in wandering about in search of the female, in exerting his voice, pouring out odoriferous secretions, &c” (Darwin 1874, p. 224; Trivers 1972).

Over the course of its roughly 200,000-year evolution, *Homo sapiens* has been a polygynous species. Occasionally, a polyandrous (“many men”) woman mates with more than one man – either one after another or at the same time. But more often, a polygynous (“many women”) man mates with more than one woman – either one after another or at the same time. Overall, the reproductive variance of human males has exceeded the reproductive variance of human females: The effective breeding population of women has been greater than the effective breeding population of men.

At the beginning, as at the end, of human time, most people were breeders. Demographic, ethnographic, archaeological, and genetic evidence suggest that in many of the societies of prehistory, reproductive variance for both men and women was low. Among foragers past and present, the most reproductively successful parents probably counted their children in single digits.

But in most of the societies of history, male reproductive variance was high. From the first genetic histories pieced together in the twenty-first century to the first written histories of around 5,000 years ago, the effective breeding population of human males has been extraordinarily small. Heads of the first civilizations were remembered as the fathers of hundreds of children, by thousands, or tens of thousands, or a hundred thousand women. Most lived in enormous palaces or saved places for large numbers of sons in their family tombs. And some left evidence of their reproductive prowess on widespread Y chromosomes.

Low Polygyny

For most of the hunter-gatherer groups for which we have demographic evidence, both ranges and variances in reproductive success tend to hover in, or around, single digits. At the high end, in the forests of Paraguay, Aché men report an average of 6.4 live births, with a variance of 15.05, and at the low end, in the Kalahari, !Kung men report fathering 5.14 children on average, with a variance of just 8.6. Ranges are similarly small. The most reproductively successful foragers we know of were the fathers of from 12 to 16 children. The figures are similar for forager women. At the low end, Aché women report an average of 7.84 live births, with a variance of just 3.57, and at the high end, Hadza women report 4.58 children on average, with a variance of 7.7. Again, all of the ranges are small. The most reproductively successful forager mothers produced 9–12 children. In every one of these forager cultures, the most reproductively successful father had more children than the most reproductively successful mother. And reproductive variances for women were always lower. The highest variance reported for women (7.7 for the Hadza) is lower than the lowest variance reported for men (8.6 for the !Kung). But overall, the sex differences for hunter-gatherers are consistently small (Table 1 and Fig. 1; see Murdock 1984 for ethnographic sources). They might have been larger in the past.

Our best demographic data on living hunter-gatherers were collected in bad habitats. These days, most foragers live on the margins, from the deserts of southern Africa to the Arctic tundra. In the Pleistocene, their environments would have been better. And foragers in better habitats – along coastal strips and inland waterways, where climates are consistent and resources abound year-round – tend to be more sedentary than other foragers. From the Pacific Rim in the Americas to the Pacific Rim in Japan, foragers in consistently rich habitats were more likely to call themselves “big men” and to raise families by more than one woman.

Notes kept by early European explorers corroborate that. When James Cook showed up on the coast of Vancouver in his ship, *Resolution*, in 1778, he was hoping to find a way through to Hudson’s Bay. He found a few Nuu-chah-nulth Indians “hallooming” from their canoes, instead. Most were friendly, if not, as far as the captain was concerned, pretty. As he scribbled in his *Resolution* journal on 26 April, he thought the women were flat faced, crooked legged, and short – “very much so and hardly one, even of the younger sort, had the least pretensions to being called beauties.” Native men thought different. If he’d stuck around, Cook would have found that Nuu-chah-nulth men with high rank liked to collect women like that, especially chiefs. In summer and winter settlements all along the salmon-rich Northwest Coast – from the Tlingit of the Alaska Panhandle to the Haida of the Haida Gwaii, or the Queen Charlotte Islands, off the coast of British Columbia, to the Nuu-chah-nulth of Vancouver, to the Columbia River Chinook – chiefs had sexual access to on the order of ten wives and to dozens of war captives in their cedar-plank houses, and they probably counted their children in double digits (Cook, *Journal*, 4/26/1778).

At the other end of the Americas, half a century later, Charles Darwin sailed into Tierra del Fuego aboard *HMS Beagle* and spent time with the natives. “These were the most abject and miserable creatures I anywhere beheld,” he wrote. He wondered, in his *Beagle* journal, what had made them leave their fine habitats further north and travel down the backbone of the continent, where they lived in wigwams that resembled haycocks – the work of an hour, used for no more than a few days – and slept curled up in the nude on cold ground. They subsisted mostly on shellfish, in groups with no government or chief. But they managed to be polygynous. After a Fuegian woman traded a good supper for scarlet cloth, Darwin wrote: “Her husband, who enjoyed the very universal privilege in this country of possessing two wives, evidently became jealous of all the attention paid to his young wife, and, after a consultation with his naked beauties, was

Mating Systems, Table 1 Means and variances in reproductive success for hunter-gatherers, herder-gardeners, and full-time farmers (After Betzig 2012)

	Male				Female			
	Range	Mean	Var	<i>N</i>	Range	Mean	Var	<i>N</i>
Hunters and gatherers								
!Kung (Botswana)	0–12 ^a	5.14	8.60	32	1–9	4.69	4.87	62
Meriam (Australia)	0–12 ^b	3.63	11.69	19	0–11	2.06	6.43	49
Aché (Paraguay)	0–13 ^c	6.40	15.05	48	0–12	7.84	3.57	25
Aka (CAR)	0–14 ^d	6.34	8.64	29	2–11	6.23	5.20	24
Hadza (Tanzania)	0–16 ^e	4.55	14.31	95	0–12	4.58	7.70	93
Herders and gardeners								
Pimbwe (Tanzania)	0–12 ^f	5.99	9.00	138	0–12	6.14	7.27	154
Tsimane (Bolivia)	0–22 ^g	9.06	19.93	62	0–15	8.91	12.69	112
Xavante (Brazil)	0–23 ^h	3.6	12.1	62	0–8	3.6	3.9	44
Yomut (Iran)	0–30 ⁱ	5.12	8.07	267	0–18	3.87	7.09	216
Yanomamö (Venezuela)	0–43 ^j	5.59	39.64	140	0–14	3.67	8.02	181
Kipsigis (Kenya)	0–80 ^k	12.42	85.58	107	0–12	6.6	5.9	260
Full-time farmers								
Chinese	0–65 D + S ^l							
Egyptians	49+ S ^m							
Aztecs	57 D + 60 S ⁿ							
Indians	101 S ^o							
Mesopotamians	118+ S ^p							
Inca	300–400 D + S ^q							

^aNumber of children born to men ≥ 50 and women ≥ 45 , w/three men w/o “reproductively successful marriages” excluded (Howell 2000)

^bNumber of children born to men and women ≥ 50 . Note that for all adults ≥ 15 , values are for men, $N = 1.74$, $\text{Var} = 5.79$, $N = 114$; for women, $\text{Mean} = 1.56$, $\text{Var} = 4.84$, $N = 163$ (Smith et al. 2003; Smith p.c.)

^cNumber of live births for men and women 50–70 (Hill and Hurtado 1996)

^dNumber of live births for men and women > 41 (Hewlett 1988)

^eNumber of children born to men and women ≥ 18 (Marlowe 2010; cf. Blurton Jones 2016)

^fNumber of children surviving to age 5 for men and women > 45 . Note that sex differences are somewhat higher for number of children born: for men, $\text{Var} = 16.16$, $N = 138$; for women, $\text{Var} = 11.34$, $N = 154$ (Borgerhoff Mulder 2009)

^gNumber of children born to men > 50 and women > 40 (Von Rueden et al. 2011; Gurven p.c.)

^hNumber of surviving offspring for living men and women ≥ 40 , “plus recently deceased individuals for whom information was supplied by a surviving spouse” (Salzano et al. 1967)

ⁱNumber of children born to men and women ≥ 45 (Irons 1979, 2000, p.c.)

^jTotal number of children born to dead men and women in a Shamatari population. Note that for living Shamatari, values are for men, $\text{Mean} = 3.63$, $\text{Var} = 12.40$, $N = 137$; for women, $\text{Mean} = 3.24$, $\text{Var} = 5.19$, $N = 182$ (Chagnon 1974, 1979)

^kNumber of children surviving to age 21 born to men circumcised before 1938 or women by that year. Data were collected in 1983. These figures include all living or dead cohorts from Borgerhoff Mulder 1988, so they differ from values excluding “living Maina” men (Brown et al. 2009). Thanks to Gillian Brown (p.c.) for clarification

^l*Song Shi* in Ebrey 2002

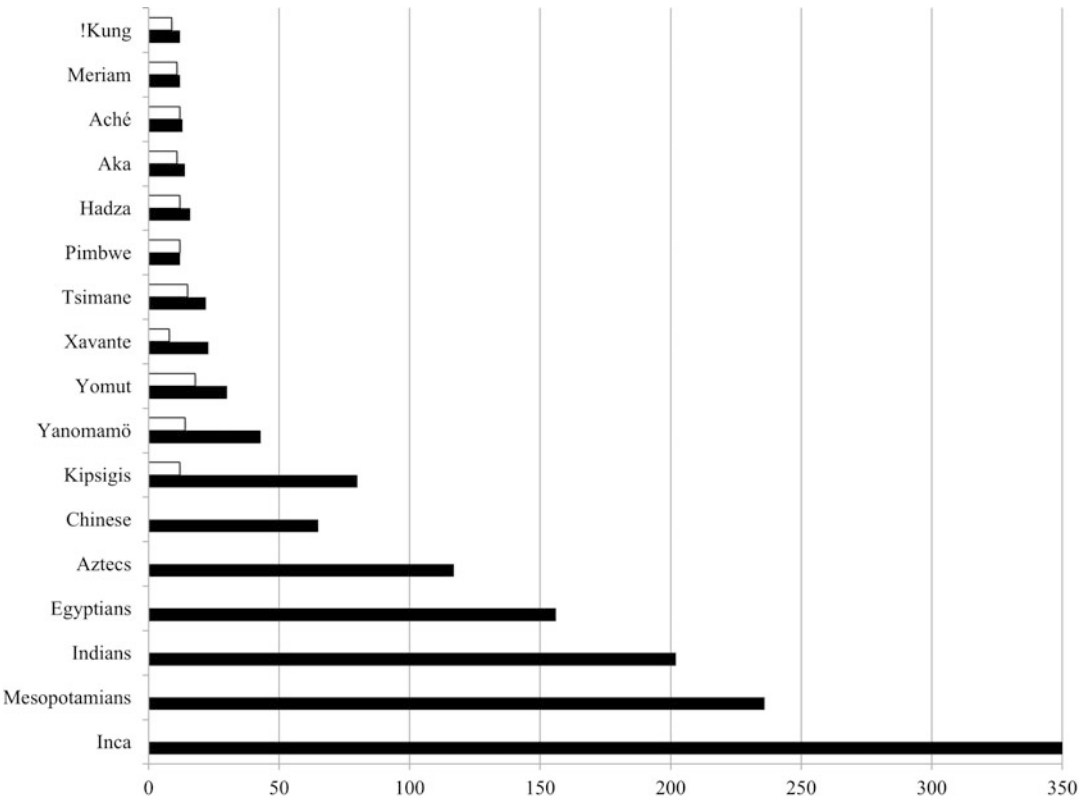
^mDodson and Hilton 2004; Weeks 2006

ⁿAlva Ixtlilxóchitl, *Nezahualcoyotl*, 4.2

^o*Dipavamsa*, 6.22; *Mahavamsa*, 5.18

^pJustin, *Epitome*, 10.1

^qGarcilaso, *Royal Commentaries*, 6.34, 9.36; Betanzos, *Narrative*, 1.23



Mating Systems, Fig. 1 Ranges in reproductive success for men and women in hunter-gatherer (*top*), herder-gardener (*center*), and full-time farmer (*bottom*) populations. *White bars* for women and *black bars* for men (After Betzig 2012)

paddled away by them” (Darwin, *Journal*, 2/25/1833, 3/5/1834).

Archaeologists have uncovered perforated snail shell ornaments and ostrich eggshell beads, ocher and hematite pencils, points and blades, bone tools, and grinding stones from Africa that date to around 100,000 to 200,000 years ago or before. Portable artifacts like those would have been carried in limited amounts, by foragers who lacked significant differences in status, wealth, or reproductive success.

On the other hand, archaeologists have unearthed some evidence of sedentism for almost as long as we’ve been human. From Africa, post-holes for wall supports and deliberately constructed stone hearths from the Middle Stone Age suggest a settled life. And there are burials, with associated grave goods, from around 100,000 years ago in the Levant (Mellars et al. 2007). Sedentary or semisedentary men in

the past, like sedentary or semisedentary men in the present, probably had higher reproductive variance.

Genetic evidence backs that up: Over the long stretch of prehistory, people probably practiced polygyny. Elevated levels of diversity on the human X chromosome, and extremely low diversity on the human Y chromosome, suggest a consistent difference between the sexes in reproductive variance. The effective breeding population of women is likely to have been consistently larger than the effective breeding population of men.

Across contemporary populations including the Khoisan, a group of people in southern Africa that includes the !Kung, genetic estimates of the breeding sex ratio are consistently biased in favor of women. That is, fewer males than females have contributed genes to descendant generations. A larger fraction of the female population has

reproduced; a larger fraction of the male population has not. *H. sapiens* has been polygynous (Hammer et al. 2008; Lippold et al. 2014).

Moderate Polygyny

Both ranges and variances in reproductive success are higher for semisedentary gardeners and herders than for more mobile hunters and gatherers, and they tend to reach double digits for men. Successful, semisedentary fathers in this sample all number their children in double digits, from 12 (Pimbwe) to 22 (Tsimane), to 23 (Xavante), to 30 (Yomut), to 43 (Yanomamö), to 80 (Kipsigis). But ranges and variances for semisedentary women remain in, or around, single digits. The most successful mothers in this sample produced from 8 (Xavante) to 18 (Yomut) daughters and sons. Reproductive variances for herder-gardener men are consistently greater than for herder-gardener women; sometimes, they're more than ten times as high (Table 1 and Fig. 1).

Gardeners put down roots: They are almost always more settled than hunters and gatherers. Some live in the middle of continents, in predictable climates; many inhabit islands or live along coasts. Gardeners in better habitats, like foragers in better habitats, tend to form more permanent groups, and their "headmen" or "chiefs" tend to be more polygynous (see Murdock 1984 for ethnographic sources).

That was often the case on first contact with islanders across the Atlantic and Pacific. After the Genoese sailor, Cristoforo Colombo, made landfall in the Bahamas in October of 1492, he wrote home to Ferdinand and Isabella of Spain: "I assure Your Highnesses that it seems to me that under the sun there can be no better lands." Columbus would make four trips across the Atlantic, with stops in the Bahamas; at Cuba, Jamaica, Hispaniola, and Puerto Rico; in the Lesser Antilles; on the north coast of South America at the mouth of the Orinoco River, and on the Central American coasts of Honduras, Nicaragua, Costa Rica, and Panama. He'd name one island the Fat Virgin, or *Virgin Gorda*, and he'd call an archipelago *Santa*

Ursula y las Once Mil Virgenes, for St Ursula and her 11,000 uncorrupted young women. Wherever he looked there was plenty of water, with cultivated plains where cassava was grown; the men were all handsome and well formed, and there were plenty of fine-figured women. Most men contented themselves with just one of those women, but dozens might belong to a single *caçique*, or chief (Columbus, *Diario*, 11/27/1492).

At the other end of the earth, there was a *tu'i* in Fiji and a *tu'i* in Tonga, an *ali'i* in Samoa, and an *ali'i* in Hawaii, and in the Trobriand Islands off the coast of New Guinea, there were more polygynous chiefs. Centuries after Columbus, and more than a 100 years after the French ship, *Espérance*, first made contact with the indiginies in the late eighteenth century, the Polish anthropologist, Bronislaw Malinowski, stopped by and took notes. From each of their subject villages, a Trobriand chief took a wife, and their families, his in-laws, supplied him with produce. Strong chiefs like Omarakana, who knew Malinowski, married as many as 40 times. "Even now, when his wives number only 16, he has enormous storehouses, and they are full to the roof with yams" (Malinowski 1922, p. 64).

After we left Africa, inequality increased. In eastern Eurasia, in over a thousand Upper Paleolithic archaeological sites, bordered by the Ural Mountains to the east and the Carpathian Mountains to the west, men, women, and children were buried with hoards of Arctic fox bone beads, bracelets, pins, pendants, and Venus figurines. Cave paintings at Maros in Indonesia date from around 40,000 years ago, and there were houses as big as 20 square meters laid out with variable numbers of storage pits and hearths. In western Eurasia, carved Venus statuettes proliferated, and Upper Paleolithic cave and rock shelter art were produced from Altamira to Lascaux and beyond, near the coastal and inland rivers of northern Spain and southern France. Houses varied in size and structure, and graves – in cemeteries that included tens or hundreds of individuals – were richer or poorer. They probably belonged to more or less polygynous fathers.

Greater reproductive variance would have depended, as always, on a rich resource base. Some coastal groups exploited crustaceans or mollusks near oceans and left behind shellfish middens; others settled along inland rivers, where they left fish traps or baskets; some on the plains hunted mammoths, where they left mammoth bone architecture; others harvested and processed mass quantities of wild seeds and left mortars and pestles (Cummings et al. 2014). Many of those artifacts survive from comparatively recent times; other artifacts from the more distant past have inevitably been lost. Wherever edible plants and game animals were abundant, and along fish-rich and shellfish-rich rivers and coasts, societies should have been more sedentary, with more variance in status, wealth, and reproductive success.

Again, the genetic evidence is consistent. Geographically diverse samples of Y-chromosome sequences suggest a couple of reproductive bottlenecks over the course of human evolution. The first, from around 40,000 to 60,000 years ago, coincides with *H. sapiens*' move out of Africa into Eurasia by a small number of colonizers, when the effective breeding population expanded. More females than males contributed to that expansion: The effective breeding population among women was more than twice the effective breeding population among men.

Those differences took off with the Neolithic. A second bottleneck, from around 8,000 to 4,000 years ago, seems to coincide with an increase in sedentism, after *H. sapiens* started to practice agriculture. It overlaps with the origins of civilization. At that point, the effective breeding population among women became as high as 17 times the effective breeding population among men. In short, people became much more polygynous (Karmin et al. 2015).

High Polygyny

After the Neolithic, people settled into full-time farming groups. Many of the first civilizations were formed on areas of circumscribed

agricultural land: They were ecologically constrained. And by as early as 10,000 years ago, the first written accounts were being kept. Emperors consistently fathered children in triple digits, and many of their helpers or workers were facultatively or obligately sterile as a result.

Heads of the first civilizations were consistently reported to have sexual access to hundreds or thousands of women, and in a variety of sources – from Bible chapters to the names of “king’s bodily sons” on Egyptian scarabs, to passages from the Buddhist canon, to Chinese dynastic histories, to narratives by a pair of Inca mestizos, and to a history of Mexico commissioned from an Aztec noble – their children were numbered at over 100. Artaxerxes II (Mesopotamia) was remembered as the father of 118 sons; the names of 60 daughters and 96 sons of Rameses II (Egypt) are known; Ashoka “the Sorrowless” (India), the grandson of the first Hindu emperor, won his throne over the bodies of 100 brothers; the twelfth-century emperor, Huizong (China), was credited with 65 daughters and sons; Nezahualcoyotl, the governor of Texcoco who was a friend of the Mexican (Aztec) emperor Motecuhzoma I, raised 57 daughters and 60 sons, and Pachacuti “the World Seizer” (Inca) was remembered as the father of 300 or 400 children (Table 1 and Fig. 1; for historical references, see Betzig 2012, 2014).

The histories flesh those numbers out. In the Near East, in or around 2271 BC, Sargon the Great put Lugal-Zage-Si, the ruler of Umma, in a dog collar, and patched together an empire. But first, Lugal-Zage-Si overthrew Urukagina, the ruler of Lagash, who wrote: “The houses of the palace harem and the fields of the palace harem, the houses of the palace nursery and the fields of the palace nursery crowded each other side by side.” By the eighteenth century BC, upriver on the Euphrates at Mari, all of 232 women filled the palace of Zim-Rilim – who knew Hammurabi of Babylon. And when by the seventh century, on the Tigris, the Assyrian emperor, Ashurbanipal, left records of Harem Governesses and Weavers in his Nineveh library, he listed 13 governesses, 145 weavers, 52 maids, and 260 miscellaneous

women. The Persians were well known for their harems: Artaxerxes II is supposed to have fathered 115 bastard sons, besides three legitimate ones, and Sisygambis – who was the mother of Darius III and the mother-in-law of Alexander the Great – remembered that 80 of her brothers had been killed in a day. Those estimates fit with the first books put together by Hebrew scribes, who had Solomon collect 1,000 women and his son Rehoboam father 88 children (1 Kings 11:3, 2 Chronicles 11:21).

In Egypt, there were more polygynous men. In the Old Kingdom, when the twenty-sixth-century BC pyramid builder Sneferu went out for a row on his private lake, he took along 20 women with the shapeliest bodies, breasts, and braids, who had not yet given birth, and dressed them in fishnets. In the Middle Kingdom, the twentieth-century BC pharaoh, Amenemhat I, was done after a conspiracy in his harem: “Has discord been fostered within the palace?” And in the New Kingdom, pharaohs collected hundreds of women as tribute (“send very beautiful women, but none with shrill voices”), or as parts of their wives’ dowries (“marvels brought to his majesty”). So the tomb of the thirteenth-century BC pharaoh, Rameses II, held chambers for dozens of sons, and the names of his “king’s sons” and “bodily king’s sons” were written in stone. There were 96 of them, with another 60 or more daughters.

There was more reproductive variance in Asia. Chandragupta Maurya – who might have got a look at Alexander the Great when he was growing up – was the first to bring Indus and Ganges together under one yoke. Tradition had him follow an advisor, Kautilya, who put together an *Arthashastra*, or “Study of Gain.” It asks emperors to build women’s compartments, one within another, blockaded by a defensive wall and moat and circumambulated by three fires. An infirmary was supposed to be stocked with pharmaceuticals and potherbs, for midwives and medics, and nearby, dormitories were supposed to be built for princes and princesses: Bimbisara, who was Chandragupta’s successor, raised 100 sons in those rooms. Hundreds of years later, Vatsayana’s *Kamasutra*, or “Love Threads,”

advised Gupta emperors on how to recruit women. Some were enlisted by village headmen, who won over female villagers by just asking them, and others were conscripted by women already in the harem, who talked up the emperor at festivals in the palace. Compassionate rulers were encouraged to drink milk boiled with the testicles of rams or goats, so they might enjoy many women in a night. And compassionate consorts were persuaded to learn how to sing, dance, draw, sculpt, solve riddles, speak multilingually, practice magic, and make parrots talk, as an emperor may have thousands of other women competing for his attention.

Chinese dynastic histories offer lists of imperial children – 65 are mentioned for the Northern Song emperor, Huizong. But many emperors were supposed to have kept enormous harems and must have fathered more daughters and sons. When the man who unified China in 221 BC, the First August Emperor of Qin, connected his 270 palaces together, he filled them with more than 10,000 beautiful women that he’d taken from the feudal rulers, said China’s first historian, Sima Qian. That number would grow by an order of magnitude. Yangdi, the Sui dynasty emperor who built the Grand Canal and rebuilt the Great Wall, was credited by an official historian with 100,000 women in his secondary palace at Yangzhou, alone. Even before there was a first emperor, records made with the red brush kept track of the health and menstrual cycles of royal women: Court ladies led consorts to the bedchamber on correct calendar days and gave them a silver ring to put on their right hands; they switched the ring to their left hands after congress was accomplished, and consorts who conceived were rewarded with gold rings. And after the Qin brought China together, recorders of imperial intercourse were assigned civil service ranks – 6a under the Tang and 9a under the Song.

As in the Old World, so in the New. In the Valley of Mexico, the fifteenth-century AD *tlatoani*, or “Speaker,” of Texcoco, Nezahualcoyotl – poet, architect, engineer, and friend of the Aztec emperor Motecuhzoma I – had a zoo, gardens, music hall, and ball court in

his palace, where his women, reared in seclusion, raised his 57 daughters and 60 sons. Three generations later, Motecuhzoma II's palaces were indescribably marvelous to Hernán Cortés and the Europeans who came after him. The Spanish were able to get so many Aztecs to help them fight because Motecuhzoma's taxmen had carried off their daughters and wives – said Bernal Díaz del Castillo, who fought with Cortés as a young man. And Motecuhzoma's ancestors had fathered sons on so many women, because it fitted the dignity of a ruler – said Antonio de Mendoza, the Spanish viceroy. Emperors collected raw cotton and textiles, maize, and other staples as tribute, and “provinces that lacked foodstuffs and clothing paid in maidens” – said the Dominican friar, Diego Durán. It got so bad that “since the lords and chiefs stole all the women for themselves, an ordinary Indian could scarcely find a woman when he wished to marry” – said the Franciscan missionary, Toribio de Benavente Motolinía.

In the Andes, it was worse. Inca emperors kept estates all over their empire, and a third part of their revenue was spent on women. “A judge or commissioner named by the Inca was dispatched to each province, and his only responsibility was this matter of collecting girls” – said Bernabé Cobo, the Jesuit historian of New Spain. Houses of virgins were set up all over the empire, and “all of them had many children” – said the conquistador Pedro Cieza de León. Both Garcilaso de la Vega, who was the son of an Inca noble and a Spanish lord, and Juan de Betanzos, who was Spanish but married an Inca noble, suggested some numbers. In the generations before the conquest, the emperor Pachacuti had 300 or 400 children; the emperor Tupac Yupanqui had 300 children; the emperor Qhapaq Yupanki left over 250 sons and daughters, and the emperor Wayna Qhapaq left over 200 *sons*. Guaman Poma de Ayala, a son of Inca nobles, added that access to women was strictly prescribed by law. “Principal persons” got 50, *hunu kurakas* (heads over 10,000 households) got 30, *waranka kurakas* (heads over 1,000) got 15, *pachaka kurakas* (heads over 100) got 8, *chunka kamayuqs*

(heads over 10) got 5, and the “poor Indian” took whatever was left.

Archaeological evidence from the early empires is all over the place. In Mesopotamia, from the third millennium BC, the Great Death Pit in the Royal Cemetery at Ur contained the remains of six male bodyguards carrying knives or axes, with four women harpists, and the ordered rows of 64 women of the court laid out in ceremonial dress – short-sleeved scarlet coats – with carnelian and lapis lazuli on the cuffs, gold and silver necklaces, earrings, headdresses, and dog collars around their necks, and part of the fifth-century BC palace at Persepolis has often been referred to as a harem. In Egypt, the New Kingdom pharaoh, Akhenaten, put up north and south harems in his capital at Amarna, and several letters in his House of Correspondence asked subjects to “send very beautiful women, but none with shrill voices,” 10, 20, or more at a time, and at Thebes, the nineteenth dynasty pharaoh Rameses II's tomb included places for dozens of his 96 sons. In India, the third Mauryan emperor inscribed pillars and rocks all over his empire with reassurances that he would look out for his subjects, “whether I am eating or in the closed female apartments, in the inner chamber, in the royal rancho, on horseback or in pleasure orchards.” And in China, after the third Ming emperor moved the capital from Nanjing to Beijing, he constructed the Forbidden City; it would cover 180 acres and include 980 buildings (apocryphally 999), with nearly 9,000 (apocryphally 9,999) rooms.

So it would go in the New World. Nezahualcoyotl's compound in Texcoco covered over 200 acres and held over 300 rooms, and at the end of the Valley of the Incas, at Machu Picchu, there were over 200 buildings and over 100 burials that included a number of young women.

Genetic evidence is consistent, again. Samples of Y chromosomes from contemporary men suggest an expansion of three East Asian male lineages within the last half a millennium. Those clades show up with high frequency across populations and represent more than 40 % of contemporary Han Chinese. In other words,

roughly 300,000,000 living men are descended from just three ancestor males who lived around 6,000 years ago, in the late Neolithic Age (Yan et al. 2014).

Even more striking evidence suggests a strong genetic legacy of the Mongol emperors who ruled China for roughly a century. A Y-chromosome star cluster has been found in 8 % of all men from the Pacific to the Caspian Sea and in 1/200 of all men worldwide. It has been suggested that the star cluster originated in Mongolia approximately a millennium ago and has been carried on by male-line descendants of the Yuan dynasty ancestor, Genghis Khan (Zerjal et al. 2003).

Conclusion

The first *Homo sapiens* were hunters and gatherers. Some, like most twentieth-century foragers, lived in small groups and moved around a lot. Most of the reproductively successful foragers studied by contemporary demographers number their children in single digits. But many of them live in poor habitats, from the desert to the Arctic. Successful Pleistocene foragers who found and defended rich habitats – where edible plants and game animals were abundant, or along rivers and coasts – might have done better than that. They probably lived in larger societies and were less nomadic. And they were probably more polygynous. Archaeological evidence of sedentism goes back 100,000 years or more in Africa and the Near East, and genetic evidence suggests that, across much of the Pleistocene, the effective breeding population of women was larger than the effective breeding population of men, perhaps by a factor of 2/1.

Gardeners are almost always more sedentary than hunters and gatherers. And many semisedentary men – like the *caçiques* Christopher Columbus found all over the Caribbean, or the *tu'i* and *ali'i* and other Pacific Island chiefs who met James Cook – often have sexual access to a number of wives or slaves. In semisedentary societies studied by contemporary demographers, the most

reproductively successful fathers count their children in double digits. Reproductive variances for herder-gardener men are consistently higher than reproductive variances for herder-gardener women. And again, archaeological and genetic evidence extend those differences back in time. Across Eurasia, Upper Paleolithic shelters varied in size and structure, and burials were richer and poorer: They would have belonged to more or less polygynous fathers. As far back as the African Exodus of around 50,000 years ago, the effective breeding population of women was better than twice the size of the effective breeding population of men. By the late Neolithic, at around 4,000 years ago, after the origin of full-time farming, that ratio was as high as 17/1.

After the origins of civilization, polygyny increased, from the Far West to the Far East. Emperors consistently left children who approached triple digits. In the first written histories, in the book of Kings, Solomon collected a thousand women – 700 *sarah*, or noble women, and another 300 common women, or *piylegesh* – in his bronze and cedar palace, and Rehoboam, his son, became the father of 60 daughters and 28 sons. In histories from later centuries, emperors – from Egypt to India, to China, to the Valley of Mexico, and to Peru – collected hundreds, or thousands, or hundreds of thousands of women and consistently fathered over a hundred children. Many of their palaces still stand, from the ruins at Persepolis to the ruins at Machu Picchu, and in some of their tombs, places were saved for dozens of their sons. Other evidence survives on contemporary Y chromosomes. A star cluster sampled in 16 areas across Asia has been found in 1/200 of all early-twenty-first-century men. It may have originated in Mongolia, in a lineage founded by Genghis Khan.

Genghis' grandson, Kublai Khan – who was a friend to the Venetian traveler Marco Polo, and an inspiration to Coleridge – founded the Yuan dynasty that ruled China from AD 1271. In his *Travels*, Marco Polo remembered that this khan, who was the father of at least 47 sons, kept six women at a time in his bedroom: “And so

throughout the year, there are reliefs of maidens by six and six, changing every 3 days and nights” (Polo, *Travels*, 2.8–9). Half a millennium later, Coleridge ended his opium-inspired poem about the same emperor with these lines: “Weave a circle round him thrice,/And close your eyes with holy dread,/For he on honey-dew hath fed,/And drunk the milk of Paradise.” He was a highly polygynous man.

Cross-References

- [Charles Darwin: Theory of Sexual Selection](#)
- [Differential Reproductive Success](#)
- [Genetic Polygamy](#)
- [Monogamy](#)
- [Polyandry](#)
- [Polygamy](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Polygamy in Humans](#)
- [Polygyny](#)
- [Variance in Female Reproductive Success](#)

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Meaning (Philosophy)

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Synonyms

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Definition

That what our words and sentences refer to, what we intend to convey when we utter sentences, or what we understand when we interpret utterances of others.

Introduction

Among those who think about the nature of meaning in human language are philosophers, linguists, and psychologists, and yet, meaning can still be seen as the most important unsolved problem in these disciplines (Fitch 2010). Numerous different answers to the question “what is meaning?” can be found in the literature, even if we look at philosophical literature alone. This text will give an overview of some of these accounts, starting with an example and some basic intuitions.

When I say “My bicycle is green” I use words to *refer to* an object in the world: my bicycle. But apart from the world, my utterance has something to do with what I think as well. By expressing it, I express a *mental representation* about my bicycle, and whoever hears the sentence will form a mental representation too. Finally, if I would utter the words “Mijn fiets is groen” to a speaker of Dutch, I know that this person will come to understand that my bicycle is green, just because he or she knows what the utterance means: There is an existing *convention* in the language I speak, to connect that meaning

to those words. In what follows I will describe three accounts of meaning in which these basic intuitions are reflected.

Propositional Meaning

Theories of meaning that take reference (and truth) as their central concept are all grounded in the work of Gottlob Frege. Frege (1892) developed his work on natural language against the background of a simple referential theory of meaning. The simplest conceivable theory of meaning in terms of reference defines the meaning of words as the object (or set of objects) they refer to. An example (from Speaks 2016):

1. Obama is the 44th president of the United States.

According to the referential theory of meaning, (1) is true because “Obama” and “the 44th president of the United States” refer to the same person. Similarly, the following sentence is not true, simply because “Trump” and “the 44th president of the United States” do not refer to the same person:

2. Trump is the 44th president of the United States.

A theory of meaning based on reference has the advantage that reference and truth are easy to formalize in a formal or mathematical framework. Reference alone, though, is not enough to form a proper theory of meaning of natural language. One of the problems that have been pointed out has to do with co-reference. Consider the following two examples:

3. John knows that Prince has died.
4. John knows that TAFKAP has died.

During a certain stage in his career, Prince performed under the name TAFKAP, so the names in (3) and (4) refer to the same person. However, John may not be aware of this, meaning that 3 could be true and 4 false, at the same time.

That is something a naive theory of meaning cannot account for.

More advanced theories of meaning (starting in the work of Frege, but for an overview of related approaches, see Speaks 2016) postulate a level in between the word level and the referent level, called *proposition*. Propositions are abstract objects that link words and their referents (and sentences to truth values), and they are often defined in terms of *possible worlds*. In possible world accounts of meaning, the meaning of an expression is not what it refers to in the actual world, but rather a rule that tells you what an expression would refer to *if the world were a certain way*. A simple example: The meaning of a referring expression such as “the tallest man in the world” will not simply be the man that happens to be the tallest, but instead, a recipe or rule for *finding* the tallest man in the world. The advantage of using possible worlds as the middle ground between words and referents is that they work well in formal and mathematical models of language, and a rich tradition of formal theories has been based on this approach. The formal models that are rooted in this approach to meaning are good at capturing the compositional properties of meaning: They show how meanings of individual words plus the way in which they are combined deliver complex, structured meanings. Giving an account of how human minds produce, convey, and process these complex meanings is not the primary goal of propositional accounts of meaning, though. Next, I will discuss an account of meaning that does focus on the mind.

Meaning and Intentions

An account of meaning that focuses more on the language user than on reference can be found in the work of Paul Grice. Grice (1969) defined meaning in terms of *intention*, by the following definition:

a means *p* by uttering *x* if and only if *a* intends in uttering *x* that

1. His audience come to believe *p*
2. His audience recognize this intention, and
3. (1) occurs on the basis of (2)

Thus, according to Grice, meanings of utterances are to be explained in terms of the intentions of their speaker. Moreover, this intention should be recognized by the hearer. As an illustration for this, consider the following example from Grady and Warner (2014):

Imagine you are stopped at night at an intersection, when the driver in an oncoming car flashes her lights. You reason as follows: “Why is she doing that? Oh, she must intend me to believe that my lights are not on. If she has that intention, it must be that my lights are not on. So, they are not.”

Grice’s view ties the meanings of words and sentences closely to the beliefs and mental representations of the language user. Because his work concerns the contexts in which utterances are used, and because of his related work on conversational implicatures, Grice is seen as the founding father of the linguistic subfield of *pragmatics* (see Korta and Perry 2015).

Meaning and Conventions

The two accounts of meaning I have discussed so far focus on very different aspects of language: One emphasizes the aspects of meaning that have to do with truth and reference and are easily formalizable, and the other focuses on language as a social phenomenon. According to David Lewis (1970), these simply represent two different topics, and *only confusion comes of mixing the two* (Lewis 1970, p. 19). Lewis (1975), however, does address these two intuitions simultaneously (but systematically), by starting from distinction between *languages* and *language* and subsequently devising an account of how the two can be connected.

- A. *Languages* can be defined as sets of strings (sentences) and meanings such that to each string a meaning is assigned (Lewis defines meanings in terms of possible worlds).
- B. *Language* is a social phenomenon, a sphere of human action in which speakers produce strings of sounds in order to bring about beliefs or actions in a listener.

Thus, on the one hand, Lewis maintains a very formal definition of meaning that connects sentences to abstract meaning entities, but he recognizes the social aspect of language use at the same time. Looking at linguistic communities in very general terms, Lewis observes that there are regularities between (1) the beliefs held by a speaker and the utterances they produce and (2) the utterances of a speaker and the beliefs or actions they bring about in their listeners. These regularities (or at least some of them), he postulates, are linguistic conventions. Observing that languages are sets of strings and their ascribed meanings (A), and language is a convention-governed social activity (B), Lewis then combines the two views in the following way:

A language *L* is used by a population *P*, if and only if there prevails in *P* a convention of truthfulness and trust in *L*, sustained by an interest in communication.

Truthfulness, in this definition, simply means to say that language users try not to utter sentences that are untrue; trust, on the other hand, represents the intuition that language users assume utterances of others to be true. To apply this to the bicycle example from the introduction, when I say “my bicycle is green,” I believe that my bicycle is green, and I know that this sentence, in English, is generally used to convey exactly that. In other words, I utter this particular sentence because it is true, *and* because I know that other people who hear it, will understand it. See Lewis (1975) for more detail, or Speaks (2016) for an overview of Lewis’s work compared to that of others.

The Evolution of Meaning

Some theorists implicitly conceive of meaning, or of language rules, as a stationary phenomenon, and not necessarily as something that can change over time. When we consider meaning in the context of the emergence and evolution of language, we can no longer hold on to that assumption. In what follows, I will sketch how the

accounts of meaning mentioned above connect to the language evolution debate.

It is not immediately obvious how the formal models that are rooted in truth and reference would fit in an evolutionary picture of meaning. However, they do point us to a property of language that is fundamental and needs to be accounted for in any (evolutionary) theory of language: Human language systems have propositional meaning; our sentences say things about the world that may be true or untrue. Fitch (2010, p. 121) even states that propositional meaning is one of the distinctive design features of language: *a central component of semantics that had to evolve for language in its modern sense to exist.* (pp. 121–122).

Although Paul Grice never discussed the emergence of language systematically, his later work (1975, 1982) discusses the difference between natural and nonnatural meaning. An example of natural meaning would be the usage of “means” in “Those spots mean measles.” This kind of meaning is factive: The spots cannot stop meaning measles. Natural meaning is contrasted with non-natural meaning, such as in “Those three rings on the bell (of the bus) mean that the bus is full.” This kind of meaning is nonfactive: The driver can ring the bell three times while the bus is not full at all. As an example of an in-between case, something that is a case of natural meaning but can grow towards nonnatural meaning, Grice mentions groaning. A groan is a natural sign of pain, when someone groans involuntarily. It is possible, however, to produce a groan voluntarily, to deceive the audience, and the perceiver will then be led to the conclusion that the groaner is in pain, but this happens on the basis of the natural meaning of groaning.

Grice only meant his analysis of groaning as a tentative example, but it brings a characterization of meaning in human behavior closer to the cognitive and communicative observations of animals (see Byrne and Whiten 1989 for a much cited overview of tactical deception in animals). And after all, when the evolution of language is considered, we cannot simply take meaning for granted, and we need well-defined concepts to talk about the transition from nonhuman to human meaning.

David Lewis's work has an explicit connection to evolutionary accounts of language. Lewis (1969) gives an account of how conventions emerge in a community and has laid the basis for mathematical models of the emergence of signaling systems in *evolutionary game theory*.

A key difference between Grice's and Lewis's accounts is that the former focuses mainly on the minds of language users and the latter on the public property of meaning to be grounded in a community. Recent work that discusses the origins of meaning has mainly focused on its cognitive roots (e.g., Jackendoff 2002; Fitch 2010), but accounting for the emergence of meaning in terms of communication and conventions forms an interesting alternative. For instance, Schouwstra (2012, Chap. 3) focuses on two possible sources for the property of *compositionality* in natural language. One postulates that compositionality comes from cognitive biases and was mapped onto language structure in an early stage of language emergence; the other postulates that compositionality is the result of mechanisms of cultural evolution that work on a non-compositional starting point.

Conclusion

Utterances are used to refer to things in the world, to express mental representations (or change those of others), and they rely on conventions that exist in language communities. These intuitions about language can be seen in three main accounts of meaning in philosophy and linguistics. When the evolution of language and meaning are considered, it may not be enough to focus on only one tradition; instead, combining insights from these different emphases is probably necessary to arrive at a complete picture of the emergence of meaning.

Cross-References

- Displaced Reference
- Field of Linguistics, The
- Game Theory
- Linguistic Evolution

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Meaning Making and the Self

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Synonyms

Consciousness; Phenomenological self; Self-agency; Self-concept; Subjectivity

Definition

The construct of self refers to a distinct and coherent mental space of subjectivity that is organized around time, place, and space and which enables humans to reflect on their experiences and maintain a sense of agency, order, and continuity throughout their life.

Introduction

The self is an organic and intrinsically dynamic construct that is constantly evolving and adapting to the complex and dynamic interactions between an individual's internal and external experience (Bonovitz and Harlem 2018). The construct of self refers to the formation of a coherent mental space of subjectivity that is organized around time, place, and space and which enables humans to reflect on their experiences and maintain a sense of agency, order, and continuity throughout their life (Beni 2019). Moreover, this mental space of subjectivity implies a sense of distinctiveness that facilitates the phenomenological differentiation between self and others. Therefore, the self can be functionally conceptualized as the integration of symbolic and sensory-motor representations of internal and external experience into a cohesive sense of a purposive agent. The ability to construct sensory-motor and symbolic representations is intrinsically dynamic and thus constantly evolving organically from birth onward (Labouvie-Vief 2005).

Development of Self and Its Relation to Meaning Making

Humans are born with a biological predisposition for strong affective bonds. The quality of those affective bonds interacts with the infants' genetic endowment and thus influences to a significant extent the developmental trajectory of self (Bonovitz and Harlem 2018). More specifically, the foundational substrate of the self emerges out of the affective sensory-motor contingencies that are constructed during the period of infancy (Riva 2018). The internal and external experiences of

the infant are organized around those affectively charged sensory-motor contingencies, which in turn acquire a structural function and thus shape the sense of one's subjectivity and agency (Beni 2019). That is, in the context of early attachment bonds, infants construct affectively charged sensory-motor schematic representations that are organizing their experiences into pleasurable, unpleasurable, and painful (Labouvie-Vief 2005). These schematic representations enable infants to order their internal experience in terms of phenomenological quality and anticipate similar experiences. In other words, once a schematic representation is constructed, it functions as a lens through which experiences are processed, categorized, and responded to similarly over and over, thus enabling the self to make meaning and adapt to the specifics of its environment. Therefore, regardless of the quality and the degree of complexity of later experiences, the self's sense of agency and subjectivity is significantly shaped by the affectively charged sensorimotor representations that the infant had constructed within the context of early attachment bonds during the early stages of her/his life (Whitebread and Grau 2019).

The Body as a Container of the Self

Moreover, the dynamic interaction between the soma and the external world during the first year of life enables the construction of a psychological space within which somatosensory, affective, emotional, cognitive, and symbolic activity can be held and reflected upon (Feldman 2002). Specifically, during infancy, new-borns have the important task of constructing a mental representation of the skin as a container of their body. The somatosensory experience of their body skin provides them with a psychological frame that enables them to cultivate and gradually solidify a sense of internal and external experience as well as a boundary that distinguishes between the two of them (Riva 2018). Specifically, the body skin provides the foundation for the gradual cultivation of a sense of internal space which is contained within one's body. This is, in turn, cultivates the phenomenological differentiation between the experience of the world, the self, and others (Riva 2018).

Relational Qualities of the Self

Furthermore, neuroscience findings strongly indicate that alignment in attachment bonds constitutes a core quality that provides the underlying substrate for the formation of a functional sense of self (Thompson and Batchelor 2017). Specifically, by becoming attuned to the internal states of the infant's mind, the responsive caregiver provides to the baby a secure, stable, reliable, and predictable environment in which the former feels safe to explore the self while interacting with the world (Fonagy 2002). Moreover, through the experience of emotional attunement and their capacity to use their body, infants become gradually able to identify as well as to set in motion spatiotemporal contingencies (Riva 2018). Through these spatiotemporal contingencies, infants begin to categorize their environment into animate and inanimate objects through the construction of intentional connections with and between perceptual objects. This dynamic process enables infants to develop a sense of a distinctive and unique existence within time, place, and space, which in turn provides the context for the gradual formation and solidification of a sense of self (Scalabrini et al. 2018).

Mentalization, Meaning-Making, and the Self

Mentalization is a functional process that allows people to make use in an integrated manner their perceptual, inferential, and imaginative capacities to reflect on and comprehend the qualitative operations that influence one's and other peoples' idiosyncratic mental functioning (e.g., belief system, incentives, feelings) (Fonagy 2002). Therefore, the capacity for mentalization enables humans to reflect on the phenomenology of the experience of themselves and others and thus fosters to a significant extent the construction of psychological meanings (Luyten et al. 2020).

The responsive caregiver who creates a predictable environment in which the communications and experiences of the infant are empathetically ascribed with needs, intentions, desires, and feelings provide an experience to

the child's self with another who can integrate her/his subjective experience into meaningful narratives (Whitebread and Grau 2019). This dynamic process instills in to the child a sense that her/his intentionality and subjectivity is acknowledged, appreciated, and validated which in turn enables the child to connect to herself as an intentional, real, and integrated agent whose experience is meaningful and can be communicated (Fonagy 2002).

Operational Processes of the Self

In addition, neuropsychological findings indicate that there are qualitatively distinct and dynamically interrelated operational mechanisms of the self that are embedded in underlying activities of brain structures and predispose humans to develop and preserve the qualities of consciousness and subjectivity (Beni 2019). Specifically, neuroscientific research has consistently indicated that the activities of the brain are marked by spatiotemporal contingencies (Scalabrini et al. 2018). This implies that the integration of all stimuli, whether they are sensorimotor, emotional, perceptual, or interpersonal in nature, as well as their primary external properties, must be encoded within the operational context of the brain's internal activity (Thompson and Batchelor 2017). The functional quality of this integration determines to a significant extent how an individual is implicitly and explicitly processing external and internal stimuli, and thus, how she/he subjectively experiences internal and external reality (Scalabrini et al. 2018).

Self-Constitution, Self-Manifestation, and Self-Expansion

Self-constitution reflects the underling foundation of subjectivity and the psychophysiological processes of consciousness (Scalabrini et al. 2018). It involves the construction and meaningful integration of the body schema with a sense of agency and intentionality within time, place, and space. Moreover, it is associated with the construction of a mental representation of the self, which provides

an internal space of subjectivity and enables the differentiation between self and other, phantasy and reality, and thus between the internal and external experience (Scalabrini et al. 2018).

Self-manifestation reflects the operational manifestation of subjectivity and consciousness within time, space, and place in the here and now. It involves the functional mechanisms of perception, motivation, and cognitive-affective mentalization of self and others (Scalabrini et al. 2018). Self-manifestation emerges through the interaction between the processes of assimilation and accommodation (Labouvie-Vief 2005). Specifically, through the dynamic interaction between the processes of accommodation and assimilation, the extent of integration and complexity of the representations of self and others increases gradually (Whitebread and Grau 2019). Moreover, the processes of accommodation and assimilation, in conjunction with the constitutional drive for equilibrium and self-constancy, enable the individual to interact in a meaningful manner with the world and thus adapt to the specifics of it. Specifically, the state of equilibrium in the organism constitutes the driving force for the regulation and integration of ambivalent feelings that stem from conflictual environmental experiences (Labouvie-Vief 2005). The attempt to achieve order, control, and mastery reflects the psychological manifestation of the organismic proclivity to maintain a state of equilibrium as it enables the self to process and make meaning of external stimuli and thus adaptively respond to them (Scalabrini et al. 2018).

The integration of representations of self and others provides a functional framework for the construction of a complex perceptual template, which allows the individual to create subjective meanings about the self, the world, and its people (Labouvie-Vief 2005). Additionally, neuroscientific findings indicate that relational representations are stored in procedural memory (Thompson and Batchelor 2017). The procedural memory refers to a type of implicit and long-term memory system which stores unconscious knowledge regarding procedural ways of relating to other people as well as how to do things (Labouvie-Vief 2005). Furthermore, several research studies have indicated that the unconscious knowledge that is stored

in procedural memory regarding the operational qualities that govern the relationships of the self with others might be dynamically influencing the limbic-frontal circuitry, which is involved in motivation, affects, learning, and memory. This implies that relational representations of self and others might shape to a significant extent the processes of emotion-regulation, which in turn influence the way one's process experiences and responds to intrapsychic and interpersonal stimuli throughout her/his life (Whitebread and Grau 2019).

Self-expansion is associated with the integration of the functional dynamics and the operational properties of the self within an experiential time framework (Scalabrini et al. 2018). Specifically, the autobiographical, relational, semantic-symbolic, and psychological aspects of the self become integrated and then are coordinated within complex mental-conceptual structures (Beni 2019). This process of integration within an experiential time framework brings increasing differentiation between self and others within the time framework of the past, the present, and future experiences of the self. It thus regulates the narrative process of the individual (Scalabrini et al. 2018). Specifically, self-expansion reflects the ability for perceptual processing that integrates the past, the present, and the future and thus the capacity to experience and regulate ambivalent affects through the construction of coherent narratives (Labouvie-Vief 2005).

Conclusion

The self has the capacity for subjectivity, and it integrates implicit, explicit, and intentional states of being. The notion of the self is meaningful only when it is considered within the environment in which the self depends and to which must connect through the construction of psychological, social and cultural meanings (Thompson and Batchelor 2017). One of the core operational functions of experience reflects the process of ascribing meaning upon it. For instance, an experience is idiosyncratically processed by the explicit and implicit operational mechanisms that delineate the construct of the self. This dynamic process

motivates the self to highly idiosyncratic psychological reactions as well as purposive actions. Therefore, meaning-making, physiological and psychological needs, motivational forces, and affective experiences are dynamically interconnected and associated with the construct of self (Thompson and Batchelor 2017).

Cross-References

- Differentiation
- Evolution and Self-awareness
- Evolution of Self
- Personal Memory
- Self-Monitoring
- Self-Observation

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Measure of Relatedness

- R = Coefficient of Relatedness

Measurement: Categorical Versus Continuous

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Definition

Attachment researchers have developed both categorical and continuous measures of attachment, for both theoretical and methodological reasons. More evidence is needed to evaluate whether attachment strategies are fundamentally categorical or continuous in nature.

Introduction

The first assessments of both infant and adult attachment were, without exception, categorical and found to be powerful predictors of behavior. Although there has been some debate as to whether attachment would be best assessed using categorical or continuous measures, as well as the development of continuous measures, the question – is attachment categorical or continuous? – is far from resolved.

Measurement of Attachment

Bowlby's theory of attachment gained considerable momentum when Mary Ainsworth first published, the Strange Situation (SS), an observation method of categorizing infant attachment (Ainsworth et al. 1978). The SS has become the gold standard for measuring infant attachment and the original three categories have endured (secure, anxious/resistant, and avoidant). Over the years,

there have been a few revisions to Ainsworth's original three category model, including the well-accepted addition of a fourth category (i.e., disorganized). Despite some attempts to revise or revisit, infant attachment continues to be viewed as a phenomenon that should be categorized. This insistence on categorization includes methodologies, which could be analyzed using continuous data analytic techniques (e.g., Waters and Dean's Q-sort), but are typically used to categorize infants into secure or insecure categories. There are also several assessments of preschool and school-age attachment which also categorize children into secure or insecure groups. Despite the limitations of categorical measures, from a statistical power perspective, the findings with infant attachment categories are consistent and strong.

Bowlby was quite clear that attachment representations were important "from the cradle to the grave" (Bowlby 1969/1982, p. 208) and in the mid to late 80s researchers began to explore the possibility of reliably measuring adult attachment. Research on adult attachment began with two independent and somewhat different approaches and the two methodologies remain somewhat at odds. First, Main and colleagues developed an interview-based assessment of adults' attachment of their family of origin from a sample of parents of 6-year-old children (Main et al. 1985). The children's attachment had been assessed at 1 year, and the parents' attachment categories were determined by comparing the parents' responses to the interview questions about their own family of origin when their child was 6 years old with their child's attachment category when their child was 1-year-old. Main et al.'s Adult Attachment Interview (AAI) continues to be the primary method of assessing adult attachment in developmental and clinical fields despite the time consuming training and coding of attachment interviews (see Hesse 2016 for a summary). The interview coding protocol which assesses individuals' coherence of their current state of mind with respect to their families of origin (past-focused) results in classification into one of four attachment categories: Autonomous (Secure), Dismissing, Preoccupied, and Unresolved/Disorganized. Over the past three decades, the AAI categories

have proven to be powerful predictors of parenting behavior as well as health and wellness, psychopathology, and romantic relationship outcomes.

Meanwhile, Hazan and Shaver (1987) introduced a simple three-paragraph forced-choice self-report measure of adult attachment using Ainsworth's infant categories as a template and envisaged "how" those infants would behave, in their adult romantic relationships, when they grew up. Hazan and Shaver's three-category measure of current romantic relationships, which differs from the AAI in several ways (i.e., self-report survey, assesses romantic relationships, is present-focused), was met with both enthusiasm and concern by personal relationships researchers. Although no one would question that the measure was ingenious, both in concept as well as in simplicity, researchers expressed immediate concerns with the limitations of this categorical paragraph measure and set out to develop continuous assessments of adult attachment. In fact, most of the debate, concerning whether attachment should be assessed using categorical or continuous measures has been generated from personal relationships researchers.

Over the next decade, several measures of adult attachment were developed but three measures seem to have stood the test of time. First, Bartholomew proposed a four-category model of attachment which highlighted Bowlby's proposition that adult internal working models of attachment developed from a view of the self as worthy of love (or not) and a view that others could be trusted and relied on for help (or not) when distressed, ill, or afraid (See Bartholomew and Horowitz 1991; Griffin and Bartholomew 1994). Bartholomew proposed that these underlying dimensions interacted (self/anxiety and other/avoidance) and resulted in a four-category model – highlighting that this model resulted in two avoidant styles: fearful avoidant (similar to Hazan & Shaver's avoidant category) and dismissing avoidant (similar to Main et al.'s avoidant category). Although Bartholomew's model gained popularity as a measure of both attachment in family of origin and current relationships, the measurement of the model proved

difficult. The time consuming nature of the interview coding proved unwieldy for social and personality researchers who desired large samples to gain sufficient statistical power for their multivariate analyses. Bartholomew also proposed two surveys: the categorical Relationship Questionnaire (RQ) and the continuous Relationship Scales Questionnaire (RSQ). The self-report surveys were more popular than the interviews; however, some researchers questioned the utility of Bartholomew's categorical measure (RQ) despite the strength of the early findings, including stability over time (see Scharfe and Bartholomew 1994). Although the continuous measure proposed by Bartholomew (RSQ) also proved to be moderately to highly stable over time, the scales had lower than desired reliability.

To improve the reliability of self-report attachment measures, Brennan and colleagues developed the Experiences in Close Relationships scale (ECR) using a subset of 323 items which assessed 60 attachment constructs from 14 scales. The resulting factor analysis of the items suggested that there were two orthogonal dimensions: attachment anxiety and attachment avoidance (Brennan et al. 1998). These ECR dimensions were found to have improved reliability compared to the RSQ scales, but the ECR was criticized as an inadequate measure attachment security (see Fraley et al. 2000) and an imprecise assessment of Bartholomew's four-category model (see Mikulincer and Shaver 2007, p. 97). Fraley et al. (2000) reanalyzed the Brennan et al. (1998) data and suggested two revised anxiety and avoidance dimensional scales in the ECR-R but nevertheless concluded that the ECR-R scales were still limited primarily due to the limitations of the existing item pool.

These measures – Bartholomew's RSQ (Griffin and Bartholomew 1994), the ECR (Brennan et al. 1998), and ECR-R (Fraley et al. 2000) – continue to be well used in the literature and each of the three scales have proven to be a powerful predictor of individual differences. Interestingly, researchers are drawn to Bartholomew's four categories and interpret attachment data, regardless of the scale used, using the theory underlying this four-category

model (e.g., neither the ECR nor the ECR-R were developed to assess the four-category model; see Mikulincer and Shaver 2007).

Categorical or Continuous?

Scientists from diverse disciplines have philosophized about and tested the pros and cons of categorical versus continuous measurement. These musings are also part of the fabric of attachment research. Both the SS and the AAI are traditionally categorical approaches, and both categorical methods produce strong results. Social and personality researchers tend to use continuous scales – of the four-category model or the underlying dimensions of attachment anxiety and avoidance – but this choice of continuous measures may be influenced more by their use of multivariate statistical techniques that require continuous variables and/or large samples rather than a philosophical stance on categorical versus continuous measurement. Interestingly, despite the use of these continuous measures and multivariate techniques, many researchers still tend to categorize the data or interpret the data using categorical (e.g., secure individuals) rather than continuous (e.g., security) language.

The problem with categorical thinking – which has been discussed in other fields – also plagues attachment research, and there are many reasons why categorizing attachment may limit researchers' ability to fully understand that importance of attachment representations. First, attachment categories may misclassify some individuals near the boundaries thereby increasing statistical error and reducing the power to detect the effects of particular attachment categories. Somewhat related, it has been suggested that the use of predominant categories may underestimate sex differences in attachment; sex differences are more commonly reported when using continuous measures of attachment. Second, the baseline proportions of attachment categories in clinical and nonclinical groups are different, highlighting that there may be categories that are more or less important depending on the sample or experience of the participants. Likewise, individuals in

clinical samples tend to have lower baseline proportions of secure attachment; however, the degree of security for individuals in clinical samples may be highly associated with coping or success of interventions. Third, categorization assumes that individuals' strategies are "black or white"; however, a more flexible use of different strategies may be more successful. Specifically, Bowlby originally proposed that attachment representations are "survival" strategies, and it may be that the most ideal strategy, in some situations or with some social partners, may include behaviors from two or more attachment representations. Since many infants have one primary caregiver, it may make sense that infants develop one predominant attachment strategy, but adults typically have multiple attachment figures and their internal working models of attachment are correspondingly more sophisticated. Adults may be expected to have developed different attachment representations with their different attachment figures and therefore might not fit nicely into one category. Further work is needed to test when this flexibility is adaptive. Finally, it is important to note that correlational techniques do assume that there is a linear relationship. A more complete exploration of the benefits of categorical versus continuous methods may help to detect nonlinear relationships.

Conclusions

Attachment researchers have developed both categorical and continuous measures of attachment and have only recently begun the dialogue about the pros and cons of categorical versus continuous measurement. In many ways, the choice – categorical or continuous – seems to be one of convenience rather than a decision rooted in theory or empirical evidence. In particular, developmental and clinical researchers, who tend to work with traditionally categorical approaches such as the SS and the AAI, are, of course, satisfied with these categorical methods as they tend to produce strong results. Social and personality researchers who tend to use continuous scales may be influenced more by their use of multivariate statistical techniques that require continuous

variables and/or large samples; however, many of these same researchers interpret the data using categorical (e.g., secure individuals) rather than continuous (e.g., security) language. To fully examine whether attachment is a categorical or continuous variable, researchers need to, in part, provide empirical evidence to support the question (see recent work by Chris Fraley and colleagues). This empirical work could focus on the effects of misclassification, underestimates of differences using categorical measures, importance of sample or experience of the participants, effect of the degree of security (or insecurity), benefit of a flexible use of several attachment strategies, and a more complete examination of linear and nonlinear relationships.

Cross-References

- ▶ [Attachment in Adulthood](#)
- ▶ [Attachment Theory](#)
- ▶ [Individual Variations in Attachment](#)
- ▶ [John Bowlby](#)
- ▶ [Sex Differences in Attachment](#)

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Measuring Well-Being

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Synonyms

Life satisfaction; Satisfaction with life; Welfare; Wellness

Definition

Approaches to the psychometric measurement of human well-being.

Introduction

In psychology, well-being has been defined as “a person’s cognitive and affective evaluations of his or her life” (Diener et al. 2002, p. 63). Within this definition, the cognitive element refers to what an individual thinks about his or her life both as a whole and in domain terms (i.e., in

specific areas of life such as environment, career, relationships), whereas the affective element refers to emotions, moods, and feelings. Similarly, Huppert (2009) considered well-being as the combination of feeling good and functioning effectively. Various instruments have been developed to measure general psychological well-being such as the *Satisfaction With Life Scale* (Diener et al. 1985).

The Measurement of Well-being

Affect is considered positive when the emotions, moods, and feelings experienced are pleasant (e.g., joy, elation, affection) and is deemed negative when the emotions, moods, and feelings experienced are unpleasant (e.g., guilt, anger, shame). A focus on the affective element is known as a hedonic approach to well-being, originating with the Greek philosopher Aristippus, around 400 BC, who believed that the goal of life is to experience maximum pleasure. This view is typically also central to classical utilitarian philosophers in line with the maximization of pleasure (positive affect) and minimization of pain (negative affect). A focus on the functioning element is a *eudaimonic* approach to well-being, originating with Aristotle over a century later. Aristotle considered a purely hedonic happiness to be a vulgar and superficial idea, instead advocating that true happiness is found by leading a virtuous life and realizing potential. These two sides to the phenomenon of well-being are still prominent in the modern debate on defining well-being. In 1948, the World Health Organization (WHO) developed a definition of health as “a state of complete physical, mental, and social well-being – not merely the absence of disease or infirmity.” It has since been argued that this definition was not good enough in line with a eudaimonic approach. In the year 2000, it was put forward that this should include the ability to lead a socially and economically productive life. Indeed, the current WHO definition of mental health includes “a state of well-being in which the individual realizes his or her own abilities,

can cope with the normal stresses of life, can work productively and fruitfully, and is able to make a contribution to his or her community (World Health Organization, 2005).” Furthermore, the practice of considering people who are *Not currently engaged in Education, Employment, or Training* (the acronym NEET is typically applied) as not mentally healthy has become common in many countries such as the United Kingdom and Japan. A NEET individual is someone who is unwilling to work or receive any education or training, and typically lives at home supported by another person or people (often parents). Many of these are physically, mentally, and even socially healthy, but are not productive.

Components of Well-Being

A eudaimonic approach to well-being is central to humanistic psychology, with the key assertion that people have free will and make choices which influence their well-being. In particular, this approach involves the *actualizing tendency*: a fundamental motivation towards self-fulfillment and growth. Underlying this claim is that motives exist to pursue well-being. Indeed, motives can be defined as internal states, triggered by certain needs, which promote thoughts and behavior towards specific goals to rectify such deficiencies (Larsen and Buss 2008). The humanistic psychologist, Abraham Maslow, proposed a hierarchy of five human needs which must be satisfied to achieve well-being: physiological needs, security needs, belongingness needs, esteem needs, and self-actualization needs. The most fundamental and basic four layers of the hierarchy contain what Maslow termed “deficiency needs” which, if not met, will cause an individual to feel anxious and tense and motivated to seek their satisfaction. These needs may be most central to the hedonic element of well-being. The highest level of need, self-actualization, refers to an individual’s desire to realize and achieve their full potential in line with the *eudaimonic* element of well-being. Psychometric measures of Maslow’s hierarchy include the *Need Satisfaction Inventory* (Lester 1990) and the *Need Satisfaction Schedule* (Lollar 1974).

More recently, psychologists have built upon Maslow’s idea from an evolutionary perspective. Kenrick et al. (2010a) argue that Maslow’s hierarchy, although effectively capturing core aspects of human nature and development, is insufficient to capture the specific problems involved in human survival and reproduction. In their paper, the authors first support the notion of a hierarchical model of motivation and then expand the model to place successful reproduction as the primary goal underlying all human motivations. The resultant model incorporates seven levels of needs: parenting/kin care, mate retention, mate acquisition, status/esteem, affiliation, self-protection, and immediate physiological needs.

Kenrick et al. (2010a) base much of their theorization on Life History theory. The premise of Life History theory is that resources (including time and attention, as well as physical resources) are always limited and that development involves trade-offs in when and how to allocate resources (Figueredo et al. 2006). Within a Life History theory framework, behaviors are commonly divided into two broad categories: somatic effort and reproductive effort. Somatic effort is the energy expended to build the body and an adequate resource/skill base for survival (and consequently future reproduction) whereas reproductive effort is directly devoted to replicating the individual’s genes. Put another way, investment in somatic effort promotes the survival and reproductive potential of the organism and is therefore essentially an investment in future reproduction (more or higher quality offspring in the future) rather than current reproduction. Kenrick et al. (2010a) propose that the lower four stages of their hierarchy (status/esteem, affiliation, self-protection, and immediate physiological needs) are highly consistent with somatic effort, whereas the extensions they propose (parenting, mate retention, and mate acquisition) center on incorporating aspects of reproductive effort more firmly into the model. In other works in this area, the motive of *disease avoidance* has been incorporated with less attention given to *physiological necessities* (Kenrick et al. 2010b; Neuberg et al. 2010). Recently, a psychometric

measure of this fundamental motive system from a social standpoint has been developed by Neel et al. (2016).

Conclusion

Within psychology, well-being is measured from various approaches, typically stemming from different theoretical starting points. Broadly speaking, psychological well-being refers to an individual's subjective evaluations of their life, although productivity/functioning is widely advocated as important for true well-being, independent of positive affect and physical health.

General psychological well-being can be measured using short global satisfaction instruments such as the *Satisfaction With Life Scale* (Diener et al. 1985), whereas a breakdown of the components of well-being depends on the theoretical approach, such as a hierarchy/taxonomy of fundamental needs or fundamental motives.

Cross-References

- [Emotions](#)
- [Evolutionary Hierarchy of Needs](#)
- [Fundamental Motives](#)
- [Good Health and Stable Future](#)
- [Harris' Moral Landscape](#)
- [Health Benefits of Nature](#)
- [Life History Theory](#)
- [Physical Health](#)
- [Reciprocal Altruism and Group Living](#)
- [Reproduction](#)
- [Stress](#)
- [Stress Reduction and Mental Health](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Utilitarianism](#)

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Mechanisms

- [Evidence for Modularity](#)

Mechanisms of Altruism

- [Puzzle of Altruism, The](#)

Mechanisms to Detect and Punish Cheaters

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Synonyms

Cheater detection; Defectors/sanctions/violation of social contract

Definition

Cheating violates shared social contracts. Individuals are sensitive to such violations and punish transgressors.

Introduction

Cheating can be broadly defined as any action that violates a social contract (e.g., a shared social norm) and that is intended to obtain personal benefits while inflicting costs on other individuals who have not agreed upon these costs (Cosmides 1989). Cheating occurs in many different contexts – in intimate relationships or in social groups where mutual cooperation increases collective benefits, while cheating benefits only the defector. Consider, for instance, a dyadic interaction in which someone pretends to behave cooperatively, leading another to behave cooperatively as well to maximize collective benefits. In this situation, the first person can exploit the cooperative other by defecting, thus benefiting oneself but inflicting costs on the cooperator. In this regard, incentives are provided for every individual to cheat on the social contract of mutual cooperation, especially when detection rates are low (Trivers 1971).

Detection of Cheaters

Since cheating decreases the relative fitness of cheated-on individuals and social groups as a whole, it is important for them to detect and punish cheaters, particularly in repeated social interactions. Therefore, it is likely that mechanisms to detect cheaters have been selected in human evolution. In order to differentiate between cheating and non-cheating in the first place, individuals must be sensitive to the rules and norms of *social* contracts (Cosmides and Tooby 1992). Individual sensitivity to social contracts can be illustrated clearly with the Wason selection task. In this task, one has to test a social rule, for instance, “If you are drinking alcohol, then you must be over 18.” Four cards are then presented, each with an age on one side and a beverage on the other side, say “16,” “drinking beer,” “25,” and “drinking coke.” The task is to identify the cards that possibly violate the rule. People are typically adept at selecting the correct cards (“16” and “drinking beer”). However, when the same exact task is presented in a less social and more abstract way, for instance, “If a person has a ‘D’ rating, then his documents must be marked code ‘3,’” with cards that read “D,” “F,” “3,” and “7,” then people are typically less adept at selecting the correct cards (“D” and “7”). Hence, individuals have an enhanced sensitivity to violations of social contracts (Cosmides and Tooby 1992).

Cheaters have incentives to mask their cheating, as other individuals are prone to punish and inflict costs on those who violate social contracts. Therefore, people should be sensitive toward the lies of others. Not telling the truth benefits the liar but typically inflicts costs on the interaction partner(s). As such, identifying cheaters in this context, that is, identifying who is telling the truth and who is lying, is important from an evolutionary fitness perspective. However, a recent analysis included several studies and demonstrates an accuracy rate only slightly above chance (54%) when judging whether a statement was true or false (Bond and DePaulo 2006). It is argued that mainly the absence of diagnostic cues and the interpretation of wrong cues (e.g., focusing on nervous facial expressions

instead of logical consistency and plausibility of content) are reasons for poor lie detection accuracy in humans.

Individuals are better in remembering cheaters once they have been identified as such. Although there seems to be no general face recognition advantage of cheaters, it has been shown that people are better at remembering that a face is associated with cheating than that a face is associated with neutral or cooperative behavior (e.g., Buchner et al. 2009). This source memory advantage has been attributed to (1) a greater sensitivity toward negative than positive information and (2) the enhanced memory for information that is emotionally incongruent with the individual's expectation. Accordingly, cheaters are more likely to be remembered if cheating occurs unexpectedly, e.g., if the interaction partner appears at first trustworthy or if the cheater is an in-group (vs. out-group) member (cf. Hechler et al. 2016).

Punishment of Cheaters

In small groups, continuous and repeated interactions between individuals are likely. Therefore, individuals should be prone to punish cheaters once they have been detected to prevent future cheating. Indeed, there is convincing evidence from evolutionary psychology and anthropology, as well as behavioral economics, that cheaters on social contracts are punished (Balliet et al. 2011).

Whether or not a cheater is punished depends on the individuals' sensitivity to cheating on social contracts (Pfafftheicher and Keller 2013). Consider the essential social contract of mutual cooperation in which defectors obtain, on the short term, higher benefits compared to cooperators. In this context, strong reciprocity evolved, describing the tendency to punish cheaters and to reward cooperators (i.e., non-cheaters) at personal cost, leading to the reduction of cheating behavior (Balliet et al. 2011).

Since cheating violates shared social contracts, and while it is important for individuals that these contracts are followed, individuals react with emotion to cheating. The emotion of anger (but not other basic emotions like sadness) is

consistently reported as the emotion that drives punishment of defectors that have cheated on the social contract of mutual cooperation (e.g., Srivastava et al. 2009).

Conclusion

Humans' high levels of cooperation and pro-sociality manifest in a sensitivity to detect cheaters who violate social contracts. When cheaters are detected, individuals are prone to punish the transgressors, even at their own expense. Punishment is important as it reduces the occurrence of cheaters by inflicting costs on them; as such, it is beneficial for social groups to incorporate group members who bear the costs and engage in punishment of cheaters, leading to a selective advantage in the course of evolution (Boyd et al. 2003).

Cross-References

- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Cheater Detection](#)
- ▶ [Cheater Detection Adaptations](#)
- ▶ [Evolution of Punishment](#)
- ▶ [Positive and Negative Reinforcement and Punishment](#)
- ▶ [Prisoner's Dilemma and Cooperation](#)
- ▶ [Prisoner's Dilemma, The](#)
- ▶ [Problem of Cheating](#)
- ▶ [Repeated or Iterated Prisoner's Dilemma](#)

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Mechanisms to Prefer Traits in Coalition Members

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Synonyms

[Coalitional partner choice](#)

Definition

Preferring to form coalitions with individuals who possess certain traits.

Introduction

The conditions under which coalitional aggression is adaptive readily suggest that coalition members ought to prefer certain traits in their coalition partners. Tooby and Cosmides (1988) describe coalitional aggression as a special case of multi-individual cooperation where collective

action entails risk. Tooby and Cosmides (1988) identify two broad adaptive problems that arise due to the intrinsically risky nature of aggressive coalitional acts such as warfare. The first problem is judging the probability of one's coalition attaining success in an aggressive encounter and adjusting one's willingness to participate accordingly. The second problem is judging one's private level of risk relative to the risk faced by other members of one's coalition. When one's own risk exceeds that faced by one's comrades, there is a greater chance that one's costly participation will yield benefits that accrue to one's comrades rather than oneself – that is, unequal risk within a coalition allows some members to parasitically free ride on the efforts of others. To solve these adaptive problems, coalitional actors must possess mechanisms to judge and prefer certain traits in their partners: traits that increase the fighting ability (formidability) of the coalition and traits that are indicative of willingness to participate in aggression despite the risks of doing so, such as courage and bravery.

Judging Coalitional Ability

If coalition partner preferences function adaptively, then those preferences should lead judges to reliably identify individuals who actually perform well in coalitional conflict. Berkun and Meeland (1958) report the results of a study conducted with US infantrymen deployed to Korea in 1953 which suggests that men are able to accurately judge coalition-relevant traits in other men. The combat performance of soldiers was rated by their peers and corroborated by observed combat incidents. These ratings were used to classify soldiers as “fighters” or “non-fighters.” The soldiers were then randomly distributed into new groups made up of people whom they did not know beforehand, which allowed for new impressions to form over the course of living together for 1 week. Although the groups resided behind the frontlines of battle and group members were not informed of each other's combat history, soldiers judged individuals previously classified as nonfighters to be least desirable as comrades in

a combat situation, while fighters judged other fighters to be the most desirable comrades. Thus, soldiers' judgments must have been based on cues that were reliably associated with the targets' previous combat histories.

Coalitional Contribution and Social Status

Winegard et al. (2014) argue that evolved preferences regarding coalition partners manifest in social status systems that allocate prestige to men who contribute to coalitional success. Winegard et al. (2014) point out that in many cultures, men, the primary actors in coalitional conflict, are specifically honored for displays of physical strength and fierceness and shamed for displays of timidity and cowardice. Allocating prestige in this manner not only incentivizes men to cultivate traits that increase coalitional success but also discourages free riding by denying benefits to men who have not or are not likely to contribute to coalitional action.

The connection between a man's social status and his coalitional contributions posited by Winegard et al. (2014) is supported by anthropological evidence. For example, Chagnon (1988) reports that among the Yānomamö, an Amazonian tribe that commonly engages in intergroup raiding, valiant behavior is celebrated, and men who have killed earn the status-elevating title of *unokai*. Additionally, Yānomamö men who frequently avoid participation in raids are shamed for their cowardice (*téhe*). Patton (2000) used informant reports to quantify the social status and capability as a warrior of men from Conambo, another Amazonian site where coalitional violence is common, and found that warrior ability was strongly predictive of social status.

Preferences for Traits in New Coalition Members

While formidability and bravery are important determinants of how much individuals might contribute to their coalitions, whether or not such

contribution will be forthcoming depends on an individual's commitment to the coalitional group. For this reason, loyalty is a valued trait in coalition members. Sosis et al. (2007) argue that cultures in which coalitional conflict is important may test the commitment of male group members by subjecting them to costly rituals, such as scarification, which may involve painful treatment that leaves permanent markings. Using an ethnographic database of 60 societies, Sosis et al. (2007) found that societies that have a high frequency of warfare have costlier male-exclusive rituals. Additionally, societies that engage in external warfare (against other cultural groups) as opposed to internal warfare are more likely to have rituals that leave permanent markings, suggesting that irreversible markers of loyalty may be especially valued when the coalitional context is high stakes and temporally enduring.

The use of costly rituals has also been documented in coalitional subcultures within industrialized nations. Vigil (1996) provides an ethnographic description of gang initiation rituals that are used by Chicano gangs in California "to weed out the weak and uncommitted" (p. 151). The initiation ritual entails a violent encounter with multiple gang members, and initiates who can endure the ritual display both their toughness and their loyalty, traits that are perceived as valuable in the context of fights with rival gangs; those who are unwilling or unable to endure the initiation may be denied gang membership. Testing prospective coalition members by subjecting them to harsh ordeals is even found in the modern US military, as evidenced by the persistence of hazing rituals in the US Naval Academy. Pershing (2006) analyzed interviews with people who attended the US Naval Academy and found that most first year students (derisively referred to as "plebes") were subjected to at least moderate forms of humiliation by upperclassmen (e.g., screaming in their face) and furthermore that a majority of students approve of such moderate hazing. Indeed, a majority of students (midshipmen) agreed with a statement saying first year at the Academy "should be used to identify and eliminate midshipmen who are not committed to the Academy or cannot function effectively under pressure" (p. 481).

What all these examples of initiation rituals make clear is that coalitional entities have a keen interest in screening new members for valued traits and making the social status of coalition members contingent upon the possession of those traits. In many cases, initiation and recruitment procedures appear explicitly designed to give new coalition members a chance to signal their physical strength, their pain tolerance, their psychological fortitude in the face of danger, and their loyalty to the coalition. Insofar as initiation rituals are genuinely difficult and costly, a new member's performance is a credible signal of his ability, and a new member's willingness to endure the trial is a credible signal of his commitment to the group.

Preferences for Masculinity and Risk-Taking

Psychological studies have also tested hypotheses about how coalition-relevant traits impact partner choice among men. Winegard et al. (2016) hypothesized that men prefer to associate with masculine men because judgments of masculinity track underlying traits that are relevant to coalitional functioning, such as strength, dominance, and assertiveness. Winegard et al. (2016) conducted a series of online and laboratory studies showing that male perceivers infer that a man interested in masculine activities (e.g., sports and weight lifting) is more likely to possess aforementioned coalition-enhancing traits and is more likely to perform well as a soldier or an athletic teammate. The conclusion that masculinity is specifically valued as a cue to a man's ability to contribute to a coalition is supported by two other findings. First, while men used masculinity information to guide their choices about whom they would prefer as a basketball teammate, preferences for a masculine teammate in a poetry competition were near chance levels, suggesting that masculinity tracks traits specifically valued in domains where there is potential for aggressive coalitional activity. Second, when the sexual orientation of male targets was varied independently of their masculine interests, participants primarily relied on information about masculinity to judge

whether the target would be an effective soldier or teammate, suggesting that men desire allies who are likely to possess coalition-enhancing traits and not simply men who happen to conform to cultural norms (regarding heterosexuality, in this case). Indeed, compared to straight men with feminine interests, homosexual men with masculine interests were judged to have greater ability as a soldier and were more likely to be chosen as an athletic teammate. Similarly, Winegard et al. (2016) found that participants' expectations about the likelihood of fictional men in vignettes receiving emasculating insults from others were more strongly predicted by whether the fictional men made a sacrifice for their coalition or fled their coalition in fear than by whether the men were heterosexual or homosexual.

Given that coalitional conflict is primarily a male activity, preferences for traditionally masculine traits such as risk-taking should be sex differentiated. Farthing (2005) conducted studies with undergraduate samples to examine sex differences in preferences to associate with risk-taking individuals. Men but not women preferred same-sex individuals who took physical risks (e.g., walking down a dark alley) as friends compared to individuals who avoided physical risks. When evaluating heroic risk-takers who altruistically put themselves in danger (e.g., intervening to stop bullying), both sexes showed a greater preference for heroic friends, but this preference was stronger in men. Taken together, the findings of Winegard et al. (2016) and Farthing (2005) support the conclusion that there is a set of traits (e.g., strength, assertiveness, risk-taking), captured by traditional conceptions of masculinity, that are specifically valued by men when evaluating other men as partners and that these traits derive their value in part from their perceived usefulness in the domain of coalitional conflict.

Conclusion

Analysis of adaptive problems in the coalitional domain, such as increasing coalitional formidability and deterring free riders from obtaining coalitional benefits, sheds light on the evolutionary

origins of preferences to form groups with partners who are strong, courageous, and loyal and to avoid partners who are fearful and uncommitted. Whenever coalitional conflict is relevant, coalitional contribution appears to be culturally valued and frequently becomes directly linked with masculinity. As argued by Winegard et al. (2014), male-specific forms of social status arise not only because of intrasexual competition within groups but also due to the allocation of prestige to men who make coalitional contributions in the context of competition between groups.

Cross-References

- [Male Adaptations that Facilitate Success in War](#)
- [Male Adaptations to Assess Fighting Ability](#)

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Mechanosensor

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Synonyms

[Mechanosensory molecules](#); [Mechano-transduction process](#)

Definition

Molecular structures that trigger biological reactions based on mechanical forces.

Introduction

These molecules are responsible to elicit a procedure known as mechanotransduction. Mechanical forces influence these molecules to trigger biological reactions. Eukaryotic cells contain these mechanosensory structures. There have been attempts to understand the exact functions of these molecules using a number of advanced techniques.

Mechanosensors

These are the molecules or structures that may experience a conformational change and whose interaction with other molecules is affected by mechanical forces. In some cases, the forces applied on molecules are required to trigger biologically significant reactions (Shen et al. 2017).

The mechanosensors in the cell are responsible for the process called mechanotransduction, which refers to the physiological processes through which living cells sense and respond to mechanical stimuli by converting them into electrochemical signals which consequently elicit cellular responses. Mechanosensors are molecular reporters inside the cells that connect external mechanical stimuli at the cell surface to

intracellular signaling events and downstream effectors through mechanosensory proteins (Bavi et al. 2017).

There are three main mechanosensors in eukaryotic cells: (1) those formed by the wrinkling and invagination of the plasma membrane such as caveole, microvilli, and possibly cilia; (2) intra- or extracellular elements such as the actin cytoskeleton, glycocalyx, a cadherin rich cell to cell junction; and (3) mechanosensitive (MS) ion channels, which respond rapidly to mechanical stimuli on a less than millisecond time. A combination of these could also be involved in mechanotransduction (Bavi et al. 2017).

There have been attempts to study the exact role of different mechanosensors in the literature by using magnetic nanoparticles and magnetic fields as well as a combination of other techniques – such as differentiation inducing techniques – in order to understand mechanosensory structures (Shen et al. 2017). Kita et al. (2013) have gone through a thorough description of the birth of a mechanosensor in order to comprehend as much as possible their functional properties.

Evolution Status of the Mechanosensors

Regarding the molecular evolution of mechanosensors, there have been attempts to understand the molecular basis and development of mechanosensation (Fritzsche et al. 2007). Fritzsche et al. suggest evolution of mechanosensors and evolution of auditory organs must be interpreted at the level of the changes in the receptor molecules, which mainly drive sensory evolution. Specifically, they assert that structurally different mechanosensory organs evolved in different phyla, showing a variation of a common theme quantified by a set of transcription factors in their cellular development. Also, a variety of structural designs of ion channels have been identified, which suggest that evolution of mechanosensors has taken place independently many times (Delmas and Coste 2013).

Kung (2005) has created a possible unifying principle for mechanosensation through the use of mechanosensitive ion channels. Specifically, Kung

suggested that these channel proteins sense forces from the lipid bilayer, which are also involved in opening and closing the mechanosensitive channels of animals, plant species, and fungal species.

Conclusion

These molecular structures respond to mechanical forces which consequently trigger a series of biological reactions. They are, also, involved in a process called mechanotransduction

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Mechanosensory Molecules

► [Mechanosensor](#)

Mechanotransduction Process

► [Mechanosensor](#)

Media Violence

► Imitative Aggression

Medical Definitions of Death

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Synonyms

Brain death; Cardiovascular collapse; Coma
dépassé; Deceased; Mortality

Definition

Establishing the point at which a person is considered to be dead.

Introduction

Medical progress has, somewhat paradoxically, evoked more complicated and pressing challenges as more life-sustaining technologies became available. Making determinations about death represents one such medical endeavor. In previous centuries, death was generally accepted as the complete and irreversible cessation of cardiovascular function. Over the past century, advances in the life-sustaining technology have lengthened the interval from an inciting terminal event to the point of complete cardiovascular collapse. Thus, the comparatively simple criteria of the past (e.g., protracted absence of a heart beat) have been rendered unreliable by mechanical and pharmacological support. Thus, updated criteria were required – criteria that remain somewhat controversial at the present. This entry summarizes the

legal definition of death and contrasts the cardiopulmonary criteria utilized in the past with the standardized neurological criteria of today. It concludes by highlighting some controversies surrounding the latter and juxtaposes that medical standard against religious understandings of death that frame this issue.

Main Text: Legal Definition of Death

Along with the proliferation of life-sustaining technologies, there came a need to state specific criteria for death, not only for medical purposes but also as a step in organ donation, as well as in jurisprudence, such as in criminal and civil cases. This led to the Uniform Determination of Death Act (UDDA) of 1981 (President's commission 1981) which asserts that:

An individual who has sustained either (1) irreversible cessation of circulatory and respiratory functions, or (2) irreversible cessation of all functions of the entire brain, including the brain stem is dead. A determination of death must be made in accordance with accepted medical standards.

These standards call for two separate criteria: one assessing cardiopulmonary functions and another assessing brain function. While all states utilize these criteria, some have also amended them to specify who can make such judgments or to further specify particular criteria (e.g., Oregon's version distinguishes "breathing" from "fleeting respiratory efforts or gasps"). Such amendments highlight gaps and areas lacking clarity in the 1981 statute, which often must be elaborated by states or even particular institutions. Still, the UDDA has focused attention on defining death within the cardiopulmonary and neurological paradigms.

Cardiopulmonary Criteria for Death Declaration

No formal, universally followed criteria exist for the determination of death with respect to a cardiopulmonary assessment. In practice, a waiting time

is often followed before patients are pronounced dead, which is the purview of a licensed physician. While the Institute of Medicine recommends a wait time of 5 min (Casell et al. 2000), wait times often vary among institutions. These policies aim to insure that autoresuscitation will not occur. One systematic review reported that autoresuscitation beyond 7 min has never been documented (Hornby et al. 2010). In this interval, patients are permanently dead (i.e., *will not* be resuscitated), but not irreversibly dead (i.e., *cannot* be resuscitated; Bernat et al. 2014). Bernat et al. (2014) also opined that in this context, permanent death is an appropriate surrogate for impending irreversible death. Others have argued that the use of the “permanence standard,” as indicated above, leads to a premature declaration of death (Miller and Truog 2011; Rodriguez-Arias et al. 2011). Such debates are particularly weighty in the context of organ retrieval after death declaration. Organ donation policies must balance the need for optimal organ transplantation with the adequate protection of organ donors in a manner that assures public trust in the integrity of this process.

Brain Death Criteria for Death Declaration

In contrast to the ambiguities that persist with cardiopulmonary death, specific clinical criteria were formulated for the diagnosis of brain death by the American Academy of Neurology (AAN). These criteria, first proposed in 1995, state that brain death consists of coma or unresponsiveness, absence of brain stem reflexes, and apnea (Rosenberg et al. 1995). In addition to a neurological examination, ancillary diagnostic tests such as modified electroencephalography, somatosensory evoked potentials, and brain flow studies may be useful in specific instances. A follow-up study in 2010 reported that no adult had recovered from a diagnosis of brain death rendered in accordance with the 1995 criteria. Still, considerable practice variation in brain death criteria remains evident in leading US hospitals (Wijdicks et al. 2010).

Many argue that the notion of brain death is different in important ways from other biological understandings of death, as brain dead patients are able to perform some degree of integrated functioning such as gestating a fetus, entering and completing puberty, and the maintenance of homeostatic function for some period of time (Youngner and Arnold 2001). Proponents of neurological criteria for death determination have recognized that, “more biophilosophical work remains to be accomplished to solidify the conceptual foundation of brain death to better convince skeptics why they are justified in regarding brain dead patients as dead” (Bernat 2014, p. 7).

As with cardiopulmonary death, this debate is not purely of academic interest because the demand for organs for transplantation far exceeds the supply. Certainly, the number of patients listed on transplant waiting lists has increased steadily. Currently, more than 121,000 people are awaiting transplantation in the United States (Finger 2016). Attempts to increase the donor supply have not met this escalating demand. Significant attention has been devoted to the identification of other sources of organs for transplantation, but the mainstay of organ supply still derives from deceased donors (i.e., cadaveric donation). However, moral and religious objections to organ harvesting prior to cardiovascular death continue to have an impact on organ availability.

Religious Understandings of Death

The introduction of new or unfamiliar diagnostic criteria during the dying process can amplify distress for patients or their families. Different personal and religious beliefs can be more or less compatible with scientific understandings of death. In almost all religions, there are leaders who oppose the concept of brain death, and there are leaders who see the concept of brain death as morally licit (Segal 2014). This was summarized in a 2011 editorial in the British journal, *The Lancet*, in which mainstream

views of the most commonly practiced religions generally accept the concept of brain death, whereas more fundamentalist believers tend to favor the definition in which death is constituted by the irreversible cessation of cardiovascular function (“Religion, Organ Transplantation” 2011).

Given this variety of opinion among religious scholars, lay persons may have a wide variety of beliefs. Thus, it is imperative that clinicians not assume that a patient’s belief aligns perfectly with the stance of their religious doctrine. Rather, clinicians ought to recognize that individuals often generate their own beliefs that may not necessarily align with the mainstream views of their stated religious preference, while at the same time deviating in various ways from medico-scientific criteria elaborated above. Further, it is important to recognize that some religious concepts, such as the departure of the soul from the body at death, will forever remain orthogonal to scientific determination. Regardless of scientific advancement and medical criteria, these patient values must always be considered in end of life care. In such instances, it is prudent to consult with the patient’s family members regarding the patient’s own beliefs and that patient’s view of the value of clerical input. Ultimately, however, in situations of irresolvable value conflicts, providers are typically relinquished of a duty to provide continued futile treatments for patients who meet the scientific criteria for death (particularly the neurological criteria).

Conclusion

Despite the best efforts of medical science, there is still no universal consensus on when death occurs. Religious beliefs vary from the historic definition of brain death as the irreversible cessation of cardiovascular function to those more in line with the American Academy of Neurology’s position statement. In brief, such “brain dead” patients have no evidence of neurological functioning other than the ability to sustain the circulatory system. Therefore, it is important to ascertain the patient’s beliefs through documents such as a

living will or through surrogate decision-making as codified by the governing laws.

Cross-References

- ▶ [Death](#)
- ▶ [Death in Christianity](#)
- ▶ [Death in Islam](#)
- ▶ [Death in the Eastern Religions](#)
- ▶ [Religious Beliefs](#)
- ▶ [Religious Teachings](#)
- ▶ [Reproduction, Suicide, Euthanasia](#)

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Medically Assisted Reproduction

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Synonyms

Artificial insemination; Assisted reproduction; In vitro fertilization; Intrauterine insemination

Definitions

The use of medical technology to conceive.

Introduction

Assisted reproduction is the use of technology to attain pregnancy when traditional methods are unsuccessful. It includes procedures that have entered our vernacular including in vitro fertilization, artificial insemination, and hormonal fertility treatments. Assisted reproduction technology (ART) can help individuals experiencing difficulty conceiving or those who are experiencing infertility succeed in attaining pregnancy. Additionally, assisted reproduction can also help individuals who are hoping to conceive that have communicable viruses, such as HIV and hepatitis A or B, from giving these diseases to their partners.

The first successful use of ART occurred in 1978, when the first baby conceived from in vitro fertilization was born amidst much controversy (Al-Nuaim and Jenkins 2007). Since that time, assisted reproductive technologies have advanced greatly in terms of their ubiquity, safety, and efficacy. The Centers for Disease Control and Prevention (CDC) defines ART as all fertility treatments that handle both eggs and sperm outside of the body. This technology has significant implications for the approximate 80 million people worldwide who are estimated to be infertile, subfertile, or who suffer from viral infections

which could spread to their partner while trying to conceive (Vayena et al. 2002). However, assisted reproductive technology also presents some ethical concerns, as it increases the need for clinical research on preimplantation embryos, can result in multiple pregnancies that may be damaging psychologically and physically to both a mother and her children, and may allow parents to choose the offspring's sex or human leukocyte antigen (HLA) type (i.e., to eliminate immune issues; Pennings and De Wert 2003).

Methods of Treatment

In vitro fertilization (IVF) was the first successful ART used and is still among one of the most popular alternatives to traditional conception. This procedure involves taking both eggs and sperm and incubating them together in a petri dish outside of the body, which results in the formation of an embryo (CDC 2016). Embryos that have been successfully fertilized and are viable are then implanted into a woman's uterus. IVF begins by stimulating a woman's ovaries to produce many mature eggs at once (for an in-depth review of in vitro procedures, see Mahmoud et al. 2013). The first step of this process, known as hyperovulation, begins with pituitary down-regulation, which prevents endogenous hormones from interfering with the timing of ovulating during treatment by preventing the luteinizing hormone (LH) surge that immediately precedes ovulation. Ovarian stimulation treatments are then used to generate many healthy, developing follicles simultaneously. This is typically achieved with injections of gonadotropins extracted either from postmenopausal women's urine or through recombinant DNA technology (Mahmoud et al. 2013). This treatment continues until transvaginal ultrasounds confirm the size and number of the developing follicles are sufficient for extraction.

Once the oocytes are developed enough to be used for IVF, human chorionic gonadotropin (HCG) is injected to mimic the LH surge, which begins the final oocyte maturation process. These mature oocytes are then retrieved from the ovary using a needle attached to the transvaginal probe which aspirates the developed follicles from the

ovary. The oocytes are then incubated with sperm retrieved from the male partner together on special petri plates and monitored for normal development. If normally developing embryos are available after 5–6 days, then up to two (or four, depending on the country) are selected to be transferred back to the woman's uterus to further develop.

There are many other expansive procedures used to combat infertility that are concomitant with IVF that can be used to counter more specific infertility issues. For example, when the source of a couple's infertility is due to abnormal sperm characteristics (male-factor infertility), intracytoplasmic sperm injection (ICSI) in tandem with IVF can help couples conceive over IVF alone (Van Steirteghem et al. 1993). ICSI takes a single spermatozoon and injects it directly into the cytoplasm of an oocyte, which can compensate for structural problems with a man's sperm that may otherwise prevent it from fertilizing an egg (Palermo et al. 1992). If someone is experiencing complete infertility, meaning it is impossible for them to conceive, it is also possible to seek a third party donor to help conceive. In this case, viable sperm may be used from a donor to fertilize the woman's egg, or an oocyte from another woman may be fertilized with the man's sperm via IVF and implanted in the woman. Surrogacy, wherein a woman agrees to carry a pregnancy to term for another couple, is another form of third party ART. This is especially the case when a woman desiring a child cannot safely carry a pregnancy to term, has a congenital defect that has caused the absence of necessary reproductive organs, or does not have fertile eggs (Esfandiari et al. 2003; Goldfarb et al. 2000).

Although IVF is the most effective and most common form of ART (CDC 2016), there are other techniques that are still used, including intrauterine insemination (IUI), gamete intrafallopian transfer (GIFT), and zygote intrafallopian transfer (ZIFT) (Custers et al., 2011). IUI is the injection of prepared sperm into the uterus and is sometimes accompanied by mild or moderate superovulation induction. IUI can be performed during a woman's natural cycle and with fewer possible medical complications than IVF, making

it a safer and cheaper alternative (Goverde et al. 2000). However, whether or not IUI is as effective as IVF is unclear, and in recent years, IVF has provided the highest rate of pregnancy in the United States (Van Voorhis 2006). GIFT and ZIFT are less frequently used methods (about 1% of ART cycles) wherein a laparoscopy is performed and either sperm and an unfertilized eggs or a zygote is transferred to a fallopian tube (Van Voorhis 2006). These procedures have become less common over time because of the risks associated with laparoscopies.

Why Use Medically Assisted Reproductive Technology?

One of the main reasons to use ART is when an individual is experiencing infertility. The CDC (2016) defines infertility as the inability to conceive after 1 year of having unprotected sex, and both men and women can experience infertility. Causes of infertility in women include ovulation disorders, damage to the fallopian tubes, bilateral tubal occlusion (BTO), genital tract disorders, endometriosis, and gonadal dysgenesis (Hull et al. 1985), whereas in men infertility can be caused by seminal defects such as azoospermia (the absence of sperm in semen), oligozoospermia (low sperm number), and asthenozoospermia (poor sperm locomotion; Thonneau et al. 1991). Although both men and women can experience infertility or subfertility, there are fewer treatments that are successful in treating male infertility (Hull et al. 1985; Jungwirth et al. 2012).

As noted above, individuals may also use ART to avoid spreading a disease that could be sexually transmitted to a partner while attempting to conceive. Semen has been shown to carry infection from donor to recipient in the absence of any other sexual contact (Araneta et al. 1995). To prevent the male-to-female spread of a disease in a couple which have different serotypes, some teams have used assisted reproduction technologies such as intrauterine insemination and in vitro fertilization in combination with sperm washing techniques that remove all seminal plasma away from sperm (so that only spermatozoa remain) to help couples successfully conceive and give birth to children without partner contamination (Englert et al. 2004).

A less common and more controversial purpose for using ART is to allow couples to conceive a child of a specific sex to avoid having a child with a deleterious sex-linked disease. For example, consider a woman who is a carrier for a recessive X-linked disorder, such as Duchenne muscular dystrophy (DMD), which causes muscle degeneration and eventually premature death. For a female to express this disorder, she must have two X chromosomes carrying the recessive allele, and for a male to express the disorder, he must have only one X chromosome carrying the recessive allele. The chances that any of her female offspring will inherit the X chromosome carrying the recessive allele are 50%. This means that there is a 50% chance that her female offspring will be carriers of the disease. Her male children, on the other hand, who will receive their Y chromosome from their father and their X chromosome from their mother, have a 50% chance of having DMD. To avoid the chance of having a male child who has DMD, it is possible to selectively fertilize the woman's eggs with sperm carrying an X chromosome to ensure the birth of a daughter. Using flow cytometry, sperm samples can be separated based on mass because sperm carrying an X chromosome are slightly heavier than sperm carrying a Y chromosome (Garner et al. 2013). This enables medical professionals to choose sperm with which to fertilize the mother's eggs to greatly increase the likelihood of her giving birth to a daughter (Karabinus et al. 2014).

Finally, it is also possible to use ARTs in combination with a preimplantation genetic diagnosis (PGD) to select embryos with specific human leukocyte antigen (HLA) makeups for the purpose of conceiving a child who may act as a donor sibling for a child affected by a bone marrow disorder in need of a stem cell transplantation (Verlinsky et al. 2004). This approach can be used to help individuals suffering from a number of diseases which can be treated by a bone marrow transplant in the absence of an existing HLA-matched donor. In these cases, PGD is used to take a single cell from an embryo created via in vitro fertilization and test this cell for the absence of the disease the existing child has and the desired HLA match to the sibling (Rechitsky

et al. 2004). If the embryo has the correct HLA alleles and does not have the gene causing the disorder, it is chosen to be implanted in the uterus and can result in a child who may act as a stem cell donor for their sibling.

Risks Associated with ART

Although ART treatments are becoming much more frequently used for the treatment of infertility, there are some possible risks associated with undergoing IVF and other ART treatments. These include risks to the mother such as ovarian hyperstimulation syndrome (OHSS) and multiple pregnancies and risks to the newborn such as an increased chance of birth defects and increased risk of low birth weight compared to spontaneously conceived infants. OHSS is caused by using gonadotropins and other agents to stimulate ovulation during fertility treatments. It causes the ovaries to increase in size, which causes abdominal pain, and, in more advanced forms, can cause the ovaries to become cystic, negatively impact the cardiovascular and renal system, and impair diaphragm movement and breathing (Delvigne and Rozenberg 2003). Although fatal cases are rare, it is important for physicians to monitor patients undergoing hormonal fertility treatments to manage any symptoms of OHSS. Another risk of ART treatments is that women have an increased chance of a higher-order pregnancy, meaning that they are more likely to deliver multiple babies from the same gestation (twins, triplets, etc.). This is because during most ART treatments, multiple embryos may be transferred back to the woman to increase the chance of a successful pregnancy (ESHRE Capri Workshop Group 2000). A multiple gestation pregnancy increases risk of medical complications for both mother and infants, increases economic costs of pregnancy, and can also have negative social and psychological impacts on the mother and father (Pennings and De Wert 2003). Recent advances in single embryo transfer (SET) IVF have, however, been able to lower the instance of multiple gestations while still providing a comparable pregnancy rate (Forman et al. 2013).

Multiple pregnancies not only have an impact on the mother; they also increase the likelihood

that a child will be born underweight. Interestingly, in a study including 42,463 infants conceived through ART, Schieve et al. (2002) found that twins conceived from ART were no more likely to be underweight than twins from a spontaneous conception. However, they found that singletons born after 37 weeks of gestation had a 2.6 times higher chance of being underweight than the general population, which was not explained by differences between the population of women who conceive spontaneously and those who conceived via ART. The authors cautiously suggest that some aspect of the ART treatment and/or hormonal fertility treatment is associated with birth defects, although more research in this area is required. In addition to increased chance of low birth weight, it also appears that ART treatments increase the risk of a child being born with a birth defect (Hansen et al. 2002, 2005). Davies et al. (2012) found that ART treatments were associated with a significantly increased risk of cardiovascular, musculoskeletal, urogenital, and gastrointestinal defects and cerebral palsy in infants conceived through ART techniques compared to infants which were spontaneously conceived.

Ethical Concerns

As with other topics related to reproduction, ART treatments have historically been surrounded by ethical intrigue and concern. Some of the prominent concerns have to do with the excess embryos created during IVF and the use of preimplantation genetic diagnosis (PGD) to select for desired embryos.

ART treatments are closely associated with research on preimplantation embryos, and embryos that are not used during an IVF cycle or chosen to be used at a later time can be donated for research. The center of this ethical debate is whether or not embryos have the same rights and moral status as children or adults (Pennings and De Wert 2003). From one perspective, embryos are “nonpersons,” and therefore research performed on them should be morally indifferent and depend only on the inclination of the gamete donors (Chervenak and McCullough 1997). On the other hand, some feel that personhood begins

at fertilization and the potentiality of the embryo to develop into a person means that these embryos should be treated with the moral status and respect of a child or an adult (Pennings and De Wert 2003).

Another controversial aspect of ART is the relatively recent ability to genetically screen potential embryos before implantation and select embryos that are most likely to produce healthy pregnancies. One consequence of PGD is that parents are now able to prescreen embryos to avoid the appearance of a sex-linked disorder by selecting the sex of their child. Although PGD is used for medical sex selection and is done with the intent of improving the life of a potential child, it may also be used as a non-medical, social sex selection mechanism (Pennings and De Wert 2003). In countries with more lax regulations or less enforced restrictions on PGD and ART treatments, individuals may take advantage of technology for social sex selection; when there are limitations on the number of children couples are allowed to have and where the birth of one sex is favored over the birth of another, couples may elect to use PDG to select the sex of their child (Whittaker 2011).

Conclusions

Since the first child born through IVF conception in 1978, ART treatments have become more ubiquitous, more socially acceptable, safer, and more efficacious. However, treatments like IVF still face challenges in developed countries like the United States. The financial burden of ART prevents lower-income individuals from accessing treatment, and there is still discrimination against women of older age, poor individuals, lesbians, and single women (Peterson 2005). Additionally, access to ART differs greatly across the globe, and laws regulating the use of ART are inconsistent within and between countries. Although legislation may need to keep pace with innovation, continuing ART advances offer hope to a large portion of the world's population who struggle to conceive.

Cross-References

- [Dysgenic Concerns](#)
- [Fertility](#)
- [Ovulation](#)

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Meditation

- [Stress Reduction and Mental Health](#)

Melancholy

- [Depression \(Randolph Nesse\)](#)

Members of Coalition Must Believe They Will Win

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Synonyms

[Intrasexual competition](#); [Male warrior psychology](#); [Risk contract of war](#)

Definitions

Throughout human history, participating in warfare afforded potential benefits for involved coalitions of males, but also bore a risk of injury or death. Males may have evolved psychological mechanisms that compute the risks associated with intergroup violence, are sensitive to strategic imbalances, and motivate participation when victory seems highly probable. Therefore, coalition members' willingness to participate in warfare rests on whether they believe that they will win.

Introduction

Over the course of human evolutionary history, engaging in warfare with other groups allowed men to expand their territory, acquire new hunting and foraging grounds, and obtain additional mating opportunities (Wrangham 1999; Wrangham and Glowacki 2012). Men could forge coalitions with other male group members to gain access to female members of other groups, by eliminating coalitions of rival males and/or capturing outgroup women. Warfare also presented males with the opportunity to gain additional resources and social status, thereby increasing one's ingroup mating appeal (Buss 1998). Males therefore stood to gain substantive reproductive benefits from strategic participation in intergroup conflict, prompting scholars to propose that men possess an evolved *male warrior psychology* (McDonald et al. 2012; Van Vugt et al. 2007). This male warrior psychology is thought to encourage warfare when it can be carried out with a strategic advantage, because warfare is inherently dangerous for involved individuals.

Strategic Considerations in Warfare

Though there are benefits to be reaped from intergroup conflict, warfare confers an elevated risk of injury or death for participants. Thus, evolution would not have favored individuals, or more specifically, genes, that engaged in frequent, gratuitous violence. However, it is likely that

evolution favored genes that built individuals who engaged in intergroup violence opportunistically, and who can identify as well as take advantage of situations where victory seemed assured (Tooby and Cosmides 1988; Wrangham 1999). Due to the inherent risk of losing one's life (or limbs), natural selection likely favored traits in males that promote warfare when enacted in a way that reduces the risk of injury or death, prompting the evolution of psychological characteristics that encourage participation in warfare when the probability of victory is high. If, for example, a coalition perceives a significant tactical advantage (e.g., opponents outnumbered, unprepared), and the risk of injury or death is perceived to be both small and randomly distributed among participants, then coalition members may be incentivized to engage in warfare (Johnson and MacKay 2015; Tooby and Cosmides 1988; Wrangham 1999). Hence, the male warrior psychology may consist of psychological mechanisms that compute the risks and benefits associated with participation in warfare, and encourage violence when the perceived probability of success is high.

Victory must be Assured

Inferring from modern hunter-gatherers, the dominant style of combat for ancestral humans likely took the form of asymmetric raids in which a male coalition of individuals surround and attack a small subset of rival group members, therefore resulting in a high probability of success in battle (Johnson and MacKay 2015; Wrangham 1999; Wrangham and Glowacki 2012). Modern hunter-gatherers mostly carry out attacks on rival groups when coalitions have a clear strategic advantage, such as possessing superior numbers and the element of surprise (Wrangham and Peterson 1996; Wrangham 1999). This style of combat is structured to reduce potential costs (e.g., casualties), and, as a result, attackers rarely suffer fatalities during such violent encounters (Wrangham and Glowacki 2012). If warfare was not carried out in a strategic manner (e.g., no tactical advantages, equal or lesser fighting strength than opponents) then participants might incur immense fitness

costs (e.g., injury or death). Therefore, to prevent those potential costs, males likely evolved a toolkit of psychological mechanisms that motivate warfare only under certain conditions, particularly when victory is assured. Given this, the willingness of coalition members to engage in warfare is contingent on having significant strategic advantages over ones opponents, and also the perception that such advantages are present.

Thus, certain factors that alter the perceived likelihood of victory may increase the motivation for coalition members to engage in warfare. For example, social inputs (e.g., political ideology) may manipulate male warrior psychological mechanisms to encourage participation in warfare by exaggerating the perceived likelihood of achieving victory. This may be achieved by downplaying the dangerousness, group size, and fighting ability of rival coalitions. Convincing coalition members of their ethnic and cultural superiority, or their prowess as warriors, may facilitate warfare against groups perceived to be weak, inferior, or tactically disadvantaged.

Conclusion

Participation in warfare presented ancestral men with potential benefits, such as additional mating opportunities, but also an increased risk of injury or death. Thus, men have evolved psychological adaptations that promote strategic participation in warfare, and facilitate involvement on behalf of coalition members when the perceived chance of victory is high. This includes psychological mechanisms that are sensitive to information about the group size and formidability of rival coalitions, identifying situations where there is a significant strategic advantage, and motivating participation in warfare when coalitions believe that they will win.

Cross-References

- ▶ [Men but Not Women Will Have Adaptations for War](#)
- ▶ [War More Likely with Higher Likelihood of Success](#)

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Memes

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Synonyms

[Replicating entities of culture](#); [Unit of cultural transmission](#); [Unit of imitation](#)

Definition

Replicating entity able of being transmitted culturally.

Introduction

In 1976, Richard Dawkins published the book *The Selfish Gene*. In its first ten chapters, the author

brings an explanation over evolutionary thoughts, focusing exclusively on genes as units of replication. Only in the last chapter, Dawkins exposes the concept of *memes*, emphasizing its existence as another kind of replicator and showing that genes are not the only components of this class. In this context, exploring the idea of *meme*, the author starts from a notion of culture as a human peculiarity that differs *Homo sapiens* from the others species, passing through the inauguration of the idea of *memes* and then explaining the manner by which *memes* can replicate themselves.

What Is Unusual About Man

According to Dawkins (2006), the human species can be considered unique because of its ability of promoting culture. For him, although cultural transmission is not a characteristic present only in man, it is in this species that cultural evolution proves to be more powerful. Language, fashion, and art are examples of culture in the human species, being transmitted much faster than genetic transmission. Dawkins (2006) argues that cultural transmission, even though it is analogous to genetic transmission, once both can generate a type of evolution, occurs in an accelerated manner.

The New Replicators

Blackmore (2001) predicate that when *memes* arose, everything changed in evolution. In the same way, Dawkins (2006) affirms that, even if the emergence of the new replicator is recent, they are promoting evolutionary changes quite rapidly, surpassing the genes.

A replicator is defined by Dawkins (1976) as an information unit capable of being reproduced with some variations or errors. As discussed earlier in *The Selfish Gene*, Dawkins inaugurates the concept of *memes* as new replicators, disregarding the idea that genes would be the only replicators on the planet. In this sense, *memes* are, at the same time, cultural phenomena and living structures capable of self-replicating, being transmitted from brain to brain (Jarzewicz 2016).

In this way, a *meme* is considered by Dawkins as a unit of cultural transmission (Ambrus 2017). For example, *memes* may refer to melodies, dance steps, and thoughts (Ambrus 2017) or to clothing fashions, customs, and ceremonies (Dawkins 2006).

Discussing over how to distinguish a meme's unit, Dawkins (2006) suggests the existence of large and small units and "units within units." As an example, Dawkins affirms that a tune is one meme, but the whole Beethoven's ninth symphony is also a meme. However, the author implies that a memorable excerpt from the symphony which has become more famous than the rest of the composition deserves to be called a meme.

Survival Value and How Memes Can Replicate

Dawkins (2006) proposes a reflection on why do some ideas have high survival value. The concept of survival value, as the author explains, is related with the stability and the penetrance that some ideas have in the cultural environment. As an example, he brings the ancient and widespread idea of God, replicated over several generations by the spoken and written word, having great music and great art as allies. Dawkins considers that the survival value of the god meme results from its great psychological appeal.

As postulated by Dawkins (2006), *imitation* is the manner by which *memes* can replicate themselves. Therefore, the author explains that, in general, *longevity*, *fecundity*, and *copying-fidelity* are the qualities which define the high survival value of a meme. According to Blackmore (1999), those three words brought by Dawkins mean that, in the process of imitation, the replicator needs to have long-lasting, numerous, and accurate copies. In other words, as suggested by Jarzewicz (2016), while explaining the idea of Dawkins, the three conditions a successful meme must fulfill are lifetime, by which a meme has to survive as long as possible; productivity, by which a meme must be copied as much as possible; and reliability, by which the copies of a meme have to be precise.

Conclusion

In the final considerations of this entry, it is relevant to point out that Dawkins (2006) designates as a remarkable quality of memes their potential of perpetuation in time. The genes' potential, in general, is far more limited than memes' influence over the generations. While the contribution of genes dissolves as each generation passes, when a person contributes to the cultural development with an idea, a music, or a poem, it may live on for countless years. As examples of long-lasting cultural contributions, Dawkins exposes the meme complexes of Socrates, Leonardo Da Vinci, Copernicus, and Marconi.

In addition, considering it as a "serious point," Dawkins (2006) highlights that the evolution of cultural traits may happen with the only purpose of being beneficial to itself. The author's conclusion leads to the perception that, for the analysis of the survival values of memes – like religion, music, and ritual dancing – the conventional biological survival values do not have to be the focus, despite they may also be present. Therefore, Dawkins (2006) understands that memes started to take over automatically in the moment that genes provided brains capable of rapid imitations, with no need of genetic advantages in the process.

Even though the memes replicate themselves in a selfish, compulsive, and potentially harmful way to mankind, Dawkins suggests two unique qualities of man capable of overcome this matter: the capacity for conscious foresight – the ability of imagining the future – and the capacity for genuine altruism. Those particularities, combined, may represent a tool with which humanity can turn against the blind replicators, or as the author states: "We are built as gene machines and cultured as meme machines, but we have the power to turn against our creators" (Dawkins 2006, p. 201).

Cross-References

- [Daniel Dennett: A Review of His Evolutionary Work](#)
- [Richard Dawkins on Constraints on Natural Selection](#)

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Memory

- [Recall of Cheaters](#)

Memory and Survival

- [Evolution of Memory, The](#)

Memory Computation

- [Inceptive and Derived Memory](#)

Memory Enhanced for Cheaters Versus Non-cheaters

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Synonyms

[Cheater memory advantage](#); [Memory for reputations](#); [Reputational memory](#); [Social source memory](#); [Source memory advantage for faces of cheaters](#)

Definition

Enhanced memory for the association between a face and cheating behavior in comparison to the association between a face and trustworthy or neutral behavior.

Introduction

Assumptions about memory are an important component of models of reciprocal cooperation. This can be exemplified using the well-known tit-for-tat strategy, which consists of (a) cooperating on the first move in a prisoner's dilemma game and (b) then mirroring the partner's behavior in the next round of the game. This strategy obviously implies that people are able to remember specific instances of cooperation or defection. All models of direct reciprocity require that the previous history of interactions is remembered to some extent. Increasingly complex strategies make increasing demands on memory. Models of indirect reciprocity often imply that reputational information about third parties is shared and remembered. If assumptions about memory that are implied by a model are unrealistic, the model is likely to be inadequate. Therefore, assumptions about memory for social interactions have to be tested because they have important implications for the evolution and stability of cooperation.

Enhanced Memory for Faces of Cheaters?

A popular assumption in evolutionary psychology is that cheaters should be preferentially remembered (Mealey et al. 1996). This hypothesis can be derived from specific models of human cooperation such as tit for tat. These models imply that cooperation is the norm and cheating is the exception. Good memory for cheaters is essential because individuals with a preference for reciprocal cooperation have to know when to switch to defection. One study (Mealey et al. 1996) has found results that were interpreted as evidence for a recognition advantage for faces of cheaters.

However, this finding could not be replicated in follow-up studies (e.g., Buchner et al. 2009). Instead, face recognition was not affected by whether persons were described as cheaters, trustworthy, or neutral persons. This is neither surprising nor problematic from a functional point of view. Only recognizing a face as familiar does not help to avoid cheaters in social exchange if the cheating context is not remembered as well. Increased familiarity without context or source memory may even lead to enhanced, not decreased, trust. It is therefore theoretically much more important that source memory, but not recognition, was found to be enhanced for faces of cheaters in comparison to those of trustworthy or irrelevant persons (Buchner et al. 2009).

Why Is Source Memory for Cheaters Enhanced?

One way to explain the source memory advantage for faces of cheaters is to assume that people have a specialized module for remembering cheaters. However, given that cheating elicits strong negative emotions, a plausible alternative is that these negative emotions are responsible for the memory advantage. Bell et al. (2014) have observed that people are more likely to remember the immorality of cheating behavior when they have suffered from it than when they have benefitted from it. This may suggest that the source memory advantage is mediated by negative arousal. However, it turned out that another factor is even more important: the degree to which the cheating behavior violates expectations. Cheating is, per definition, a violation of social norms and, therefore, behavior that can be considered unusual and unexpected in most social contexts. This opens the possibility that the source memory advantage for cheating behaviors is, in fact, due to the violation of expectations.

Many results have confirmed that expectancy violations play an important role in explaining the source memory advantage for cheaters. One of the most important findings is that the cheater advantage is restricted to situations in which there is a strong norm for cooperation. For instance, there is a robust source memory advantage for faces of

cheaters when vignettes are used that describe real-world norm violations such as the selling of military weapons to criminals (Buchner et al. 2009). However, the effect disappears when the vignettes describe more common cheating behaviors such as using unlicensed computer programs, which are less negatively evaluated by the majority of the participants (Bell and Buchner 2011). The influence of the relative frequency of cheating and cooperation has been directly examined in social dilemma games. Bell et al. (2010) examined memory for the partners' behaviors in a sequential prisoner's dilemma game. When the majority of the partners in the game were cooperative, participants were more likely to guess that an unknown partner was trustworthy, but memory was better for a partner's cheating than for a partner's cooperation. However, when most of the partners were cheaters, the opposite pattern emerged: participants were more likely to guess that an unknown partner was a cheater, but their memory was better for their partners' cooperation. When the participants encountered an equal proportion of cheating and cooperating partners, they remembered their partners' cheating and cooperation equally well. Similar results have been obtained in a trust game (Barclay 2008). These results suggest that people's memory for cheaters and cooperators is quite flexible. Source memory is not always enhanced for negatively arousing information, but is instead better for information that violates expectations.

These findings are inconsistent with the assumption of a specialized module for remembering cheaters. However, it stands to reason that the flexible and fairly general expectancy-violation mechanism identified by this research is much more compatible with a functional perspective on cognition than a cheater recognition module. First, it is important to realize that people do not have perfect knowledge about social interaction partners because (a) they may not know the person or (b) they may have forgotten the previous interaction because memory is error prone. When uncertain about another person's past behaviors, people may use other information that is available to them to guess the person's character traits, such as the prevalence of cheating or cooperation in the

population (Barclay 2008; Bell et al. 2010) or the person's facial appearance (Bell et al. 2012b), and adjust their own behavior accordingly. Second, a functional perspective suggests that we should not waste our precious memory resources. In a social environment in which the majority of the partners are untrustworthy, it would put a large burden on memory to remember all of them, and it would be more efficient to focus on the few cooperative individuals with whom relationships of trust and cooperation are possible. In an environment in which the majority is cooperative, it makes sense to focus on the few cheaters to avoid trusting them. This ensures that memory resources are not wasted at encoding, and it also ensures that the relevant information can be efficiently retrieved.

The above model is in line with how schema theories account for schema effects on memory in general. For instance, the schema-plus-tag model (Graesser and Nakamura 1982) predicts that the memory trace of an event consists of (a) a pointer to a schema (e.g., about socially appropriate behavior) and (b) tags for bits of information that do not fit into the schema. A tag is only constructed for atypical items such as socially inappropriate or exceptional behaviors. When memory is expressed in terms of memory sensitivity and is, therefore, adjusted for guessing, memory for typical behaviors is often found to be poor because the typical information is produced at test whether it was present at encoding or not. This is exactly the pattern of findings observed in the literature on cheater memory described above. The schema-plus-tag model implies that the memory advantage for the atypical information is based on simple, unelaborated tags. In consequence, atypical information can be robustly encoded even under conditions of depleted cognitive resources (Graesser and Nakamura 1982). In line with this idea, it has been shown that people do not remember the details of the episodes that have led to the classification of a person as a "cheater," but are able to differentiate between contexts that necessitate different types of avoidance reactions, such as immoral and disgusting behaviors (Bell et al. 2012a). Emotional tagging thus integrates the relevant information into a summary judgment that can be quickly

retrieved and may allow for fast decisions in complex and stressful situations.

Of course, the efficiency of this strategy is not restricted to memory for cheaters. Instead, this strategy is generally a simple and frugal way to encode and remember schema-atypical information. Unsurprisingly, it can be shown that the same strategy is used to encode and to retrieve information about other types of items and contexts (Mieth et al. 2016). Thus, a very simple mechanism is able to solve the problem of how to remember efficiently the information that is either (a) consistent with prevailing schematic knowledge and, therefore, expected or (b) inconsistent with prevailing schematic knowledge and, therefore, unexpected. This mechanism presumably provides useful input for a wide range of problems, such as avoiding cheaters in social exchange (Barclay 2008; Bell et al. 2010, 2012b) or avoiding the consumption of spoiled food (Mieth et al. 2016).

Conclusion

Source memory, not old-new recognition, is enhanced for faces of cheaters (Buchner et al. 2009). However, this source memory advantage for cheaters depends on participants' expectations and disappears when people expect to be cheated (Barclay 2008; Bell et al. 2010, 2012b). These findings suggest that it is not the negative arousal associated with cheating but the unexpected nature of the norm violation that is primarily responsible for the memory advantage. From a functional perspective, it generally seems to be a highly efficient and frugal strategy to rely on schematic knowledge to guess information that cannot be remembered and to preferentially attend to information that cannot be inferred from these existing schemas.

Cross-References

- [Ability to Recognize Individuals](#)
- [Adaptations for Reciprocal Altruism](#)
- [Cheater Detection](#)

- ▶ [Cheater Detection Adaptations](#)
- ▶ [Multiple Memory Systems](#)
- ▶ [Recall of Cheaters](#)
- ▶ [Reputation](#)
- ▶ [Reputation and Altruism](#)
- ▶ [Social Reasoning Affected by Rank \(Mealey, Daoood, Krage, 1996\)](#)
- ▶ [Social Reputation](#)

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Memory for Reputations

- ▶ [Memory Enhanced for Cheaters Versus Non-cheaters](#)

Men but Not Women Will Have Adaptations for War

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Synonyms

[Intrasexual competition](#); [Male warrior psychology](#)

Definition

Adaptations that promote warfare are present in men and not women because males stood to gain substantive reproductive benefits from strategic participation in warfare over the course of human evolution. This resulted in the selection of traits that assist the formation of warrior coalitions, galvanize hostility toward outgroup members, and identify of situations where warfare can be carried out strategically.

Introduction

Both past and present, warfare between groups is by and large orchestrated and carried out by men (Goldstein 2001; Wrangham and Peterson 1996). This propensity for men (as opposed to women) to engage in warfare has its roots in the processes of sexual selection.

Sexual Selection

In most species, male reproductive fitness is limited by access to fertile females. Upon reaching

physical maturity, males produce gametes (i.e., sperm) in large quantities for the majority of their adult lives and do not gestate offspring in utero. Males are therefore capable of reproducing throughout much of their lifespan and can sire offspring with multiple females simultaneously. For males, the costs associated with conceiving offspring are relatively low, as it requires only the time, energy, and effort necessary to produce an ejaculate and mate. In contrast, females produce significantly fewer gametes (i.e., ova), are limited in the number of offspring they can conceive at any given time, and incur immense physiological costs carrying and caring for offspring, which in turn mitigates the amount of time and effort that can be devoted to mating (Trivers 1972). This results in a reproductive asymmetry, such that males can potentially produce significantly more offspring than females over the course of their lifespans.

Because males have fewer limits placed on their reproductive capacity, they can continuously seek out mating opportunities. Males may enhance their fitness by monopolizing reproductive access to numerous females. Females, however, do not profit to the same extent from increased access to viable mates given their lower reproductive ceiling. This asymmetry results in notable sex differences in within-sex variability in reproductive success; variance in women's reproductive success is quite low, whereas reproductive success varies considerably for men. For example, some males are hyper-successful (i.e., achieving disproportionately higher number of mating opportunities or access to higher quality mates), while others produce no offspring at all. This disparity in reproductive success outcomes is a consequence of *intrasexual competition* between males.

Intrasexual Competition and the Antecedents of Warlike Behaviors in Men

Intrasexual competition is defined as competition that occurs between members of the same sex for mating opportunities with members of the opposite sex. Intrasexual competition induces

relatively strong selection pressure on traits that assist in competition for mates. These pressures are the precursor to sex differences in size, strength, aggression, and even warlike behaviors observed in males across species, as possessing these traits allows males to optimally engage in intrasexual competition (Geary 2010; Trivers 1972). Intrasexual competition usually entails males competing with one another for access to females, and this pattern rarely occurs in reverse (Trivers 1972). This is in part due to the fact that females stand to gain fewer benefits from participation in intrasexual competition, and also incur greater fitness costs relative to males (Campbell 1999). For most species, and humans in particular, females are essential to offspring survival (Sear and Mace 2008). Thus, for females, engaging in high-risk strategies (e.g., physical aggression) to compete for the “best” mate more acutely impacts their ability to procreate and ensure offspring survival. As a result, females more often engage in indirect intrasexual competition (e.g., gossip) to devalue their same-sex rivals, and therefore optimize their mating opportunities (Campbell 1999). This allows females to engage in intrasexual competition with a significantly reduced risk of injury.

Males, however, must compete rigorously with one another or risk losing mating opportunities. This may take the form of direct competition for mating opportunities (i.e., through displays and/or violence), or indirectly through competition for the acquisition of tangible or nontangible resources, such as dominance and social status within a group. These competitive strategies need not be mutually exclusive, and the latter can readily translate to mating opportunities, because females are more likely and willing to provide mating access to those individuals who display high status within a group (Buss 1998). Therefore, males stand to gain from engaging in high-risk intrasexual competition because it provides men with the potential for greater mating opportunities.

Warfare: A Male Affair

Intrasexual competition among males is not restricted to mating contests within a given

group, but also extends to conflicts with other groups. Engaging in warfare with other groups can similarly increase one's access to direct and indirect reproductive resources. Males may form coalitions with other male group members to obtain mating opportunities with female members of other groups, and eliminate rival males from other groups. Involved individuals may acquire both tangible and intangible reproductive resources, such as direct mating opportunities with outgroup women, as well as greater resource access and social status within one's group, which may increase one's mating appeal. Therefore, males in particular can reap substantive benefits from strategic participation in warfare. Because males stood to gain substantive reproductive benefits from strategic participation in warfare over the course of human evolution, adaptations that promote warfare are present in men but not women.

There are several hypothesized adaptations for warfare that men may possess. For example, men possess a greater proclivity for forming cohesive coalitions of group members (Tooby and Cosmides 1988). Men display greater ingroup favoritism, and are more discriminating and hostile toward outgroup members (Navarrete et al. 2010). Furthermore, men exhibit a greater preference for group-based hierarchies than women, and have a greater desire to establish, maintain and justify dominant–subordinate relationships among social groups (Lee et al. 2011). In addition, men may possess psychological mechanisms that compute the risks and benefits associated with participation in warfare, prompting violence when the probability of victory is high (Tooby and Cosmides 1988). This includes psychological mechanisms that are sensitive to information about the group size and formidability of one's opponents.

Conclusion

Sex differences in minimal parental investment result in reproductive asymmetries between men and women, such that men have a higher reproductive ceiling than women. Because men have a greater reproductive capacity, they can

continuously seek out mating opportunities, leading to intrasexual competition among men for mating opportunities with women. Intrasexual competition induces strong selection pressures on the development of traits such as increased size, strength, and aggression – traits that enable greater success in intrasexual competition. As a result, men evolved the capacity to engage in violent, high-risk intrasexual competition to obtain mating opportunities. Such violence can extend beyond one's social group to other social groups, allowing men to gain access to women in other groups, while increasing their mating appeal within their own group. Thus, men have adaptations for warfare because strategic participation in warfare increased their reproductive fitness over the course of human evolutionary history.

Cross-References

► [Reproductive Benefits Must Outweigh Costs](#)

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Men in Positions of Power

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Synonyms

[Dominance](#); [Leadership](#); [Social authority](#); [Social rank](#); [Social status](#); [Status hierarchy](#)

Definition

An individual or group possesses *power* when holding “asymmetrical control” over valued resources, while an individual or group possesses *status* when having “social prestige” and respect (Fiske et al. 2016, p. 11). Although conceptually distinct, power and status tend to be correlated. In this entry, “male” and “female” indicate biological characteristics and not characteristics of psychological or social identity.

Introduction

Humans are highly social animals. Many scholars argue this characteristic is the result of the advantages in survival and reproduction that humans and other social species gain when individuals band together into groups (e.g., Kenrick et al. 2010). Further, groups with hierarchies tend to gain more evolutionary advantages than egalitarian groups (e.g., van Vugt 2006). In particular, a key feature of social hierarchies is that high-ranking members tend to coordinate their group’s efforts to resolve recurring challenges as well as to

deter and punish members who benefit from the group’s efforts without contributing to them (i.e., free riding). To coordinate a group’s efforts, higher-ranking members usually disproportionately control resources and influence over other members, that is, they hold asymmetrical control over valued resources and others, which is otherwise known as power (Fiske et al. 2016). Consistent with research supporting an evolutionary basis for social hierarchies, evidence is beginning to emerge of an indirect genetic contribution to social hierarchy formation, possibly through expressions of behaviors such as social dominance that are related to support for such social structures (van der Kooij and Sandi 2015).

Male dominance in social organizations has been long recognized. Cross-disciplinary research in diverse fields such as nonhuman animal behavior, anthropology, economics, and psychology documents a direct relationship between biological sex and leadership across time, cultures, and species, suggesting that such dominance may be influenced by evolutionary factors and not only by social construction. With few exceptions (e.g., killer whales, lions, spotted hyenas, bonobos, lemurs, and elephants), male group dominance is nearly universal in primate and mammalian animal groups. Specifically in humans, the relationship is documented going back as far as Egyptian pharaohs; Chinese, Japanese, and Roman emperors; Catholic Popes; and European monarchs (Murray and Murray 2011). The current situation in the political and business domains has not nearly come to parity between the sexes. For example, female leaders represent less than 10% of leaders of UN member states (Geiger and Kent 2017) and of chief executive officers of Fortune 500 corporations (Pew Research Center 2018).

Why Male Dominance?

This question can be evaluated from a demand-supply perspective. That is, there may be a greater demand from followers for male leaders, and/or there may be a greater supply of potential candidates for leadership who are male. In terms of demand, gender stereotyping, role congruity, and

social role theories, all widely supported hypotheses, suggest that consequential leadership traits are primarily associated with males, which makes it more difficult for females to be evaluated positively as leaders (e.g., Eagly et al. 2019). Other research adds that leadership is situational such that male leaders are preferred in some contexts and females in others (van Vugt and Spisak 2008), possibly as a result of evolutionary concerns related to intergroup threat (Murray and Carroll 2019).

In terms of supply, higher-ranking group members gain access to more group resources, have fewer constraints imposed on them, and reproduce more efficiently. While these advantages appeal to both males and females, psychological research suggests that males tend to be more hierarchical socially, as demonstrated by greater social dominance orientation (e.g., Lee et al. 2011), and more motivated than females to lead in hierarchical settings (Fiske and Berdahl 2007). They are also more likely to consider the potential for gaining power in decisions related to leadership and its attainment (Hernandez Bark et al. 2016). Further, widespread gender stereotyping may demotivate females from aspiring to leadership positions as a result of social hurdles faced or self-stereotyping into non-leadership roles. In addition to these psychological factors, evidence suggests that biological factors may also play a role in males disproportionately attaining positions of power. For instance, the hormone testosterone, which males possess at much higher levels than females, has been associated with leadership attainment via dominance, influence-seeking, and risk-taking behaviors (Antonakis 2011).

Does Male Dominance Matter?

There is substantial evidence that the sex of the person in power is consequential to performance and outcomes. For instance, in political governance, female legislators tend to deliver more financial benefits to their constituents and to sponsor more legislation (Anzia and Berry 2011). In the business domain, evidence suggests that increased numbers of female corporate board

members are related to outcomes such as fewer workforce reductions and reduced short-term profits (Matsa and Miller 2013). Further, greater female representation in national legislatures is related to increases in foreign aid to other countries and reallocation of such aid to health- and education-related projects (Hicks et al. 2016). Finally, increased women's representation in leadership positions is associated with future increases in women in leadership positions, presumably related to reduced gender stereotyping (O'Brien and Rickne 2016).

Conclusion

This brief entry has offered a very broad overview of the human preference for organizational hierarchies and the implications related to the attainment and use of power, in particular by males. It suggests there is a long, documented history of "men in positions of power" in social species that can be assessed in terms of the demand for male leaders and the supply of them. It further suggests this may be related to biological *and* social factors. Finally, it shows that it matters which biological sex has power.

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Men Riskier, More Aggressive

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Synonyms

Aggressive behaviors; Risk propensity; Risk-taking

Definition

Evolutionary, psychological, environmental, and genetic processes suggest that men are both riskier (as defined by the willingness to take risks) and more aggressive (as defined by hostile, violent behavior or attitudes directed toward another, as well as the readiness to attack or confront).

Introduction

From an evolutionary perspective, aggression and risk taking are ubiquitous across human societies and are crucial for the evolution of behavior, especially for human males (Bowles 2009). Human nature is in many ways the product of natural selection, and as a result, the traits and behaviors that helped men survive and prosper in hunting-gathering societies still exert powerful influences in the modern world; for the reproductive- and territorial-based motivations that drive men to take stock market risks or fight for the attention of females rest upon the reproductive- and territorial-based motivations to be successful.

Male aggression and risk-taking behaviors have been greatly studied because of their relevance to human behavior, the rationality of thinking, and the relative importance of genetics and environments in determining the expression of such traits among men. Notably, much of this research has documented sex differences in risk taking and aggression (Archer 2004), as well as illustrated a connection between risky and aggressive behaviors throughout evolutionary history – as seen in kinship, securing power, and mating dominance – and the modernized versions of these risky, aggressive behaviors, including financial risks and ethical risks. Overall, these lines of research have led scholars to propose that men are more willing to take risks and act aggressively (Campbell 2006; Bowles 2009). Furthermore, that sex differences are likely a consequence of various evolutionary and social explanations, including male competition over mating opportunities, life-course developmental differences between men and women, and socialized gender roles.

Male Competition over Mating Opportunities

Theories continuously seek to explain why men are riskier and more aggressive than women. Historically, Darwin's theory of sexual selection – a theory of mate choice and competition for mates – provided researchers with a way of understanding these complex sex differences. For Darwin, traits developed for the general purposes of life are due to natural selection, and traits that provide an advantage over a rival in securing a mate are instead subject to sexual selection (Darwin 1871). Therefore, his theory was simple: certain individuals have an advantage over other same sex individuals in respect to reproduction. In this way, male competition is easy to envision: males fight for women, against weaker, less-abled men, using resources associated with their body size; physical conditioning; and weaponry (e.g., horns, guns) to acquire promising mates. The male sex drive is equally as involved in the process of

procuring mates, as well as their song and dance, courting habits, readiness for re-mating, and mate guarding. Biologically, men exhibit higher testosterone levels than women, and higher endogenous testosterone levels in men have been empirically linked to aggressive, dominant, criminal, and violent behavior (McDermott et al. 2007). The male warrior hypothesis, for instance, is another evolutionary theory that refers to the idea that men engage in more aggressive behaviors because of evolved psychological mechanisms that have developed from an ancestral history of violent intergroup conflict among males, in which success increases their reproductive fitness (Daly and Wilson 1988).

Furthermore, among adolescent males, physical aggression is used to achieve social dominance and effectively compete for status, allies, and popularity (Hoff et al. 2009; Pellegrini 2008). As such, males have evolved a range of physical characteristics, biological factors, and psychological mechanisms that they use to improve their chances of gaining access to women and resources, including aggression and risk taking (Buss and Duntley 2006; Geary et al. 2003). Along the same lines, scholars continue to find that male engagement in risky activities, as well as their inclination toward aggression, reflects adaptations to increase ancestral reproductive success. In one study, women were asked to rate the attractiveness of men who were brave (i.e., took risks) or non-brave (i.e., avoided taking risks). In line with evolutionary perspectives, brave males were rated as more attractive long-term mates than non-brave males, suggesting that females prefer males who are heroic and risky (Kelly and Dunbar 2001; Farthing 2005).

Life-Course Developmental Differences Between Men and Women

Sex differences in risk-taking behaviors are even apparent in young children. In one naturalistic observation study, Ginsburg and Miller (1982) observed the behaviors of young children at a

petting zoo, and they found that young boys were significantly more likely to engage in “high-risk” activities, such as riding elephants, feeding animals, and petting the burro, compared to the young girls in the group. Similarly, other studies have shown that young boys, when shown photographs of games that vary from high risk to no risk, generally rate risk potential as lower than young girls do (Hillier and Morrongiello 1998). Additionally, sex differences in the use of direct aggression often appear in the first 2 years of life and persist through childhood and adolescence (Card et al. 2008). Together, these findings indicate that sex differences in risk taking are present early in development, suggesting the existence of a biological sex difference in the predisposition for risk-seeking behavior, with men being more inclined to accept risk than women.

Moreover, sex differences continue to appear throughout the life course. Young males are especially more likely to engage in risky behaviors, such as unsafe sex (DiClemente et al. 1990), substance abuse (Arnett 1992), and reckless driving (Tonkin 1987). This higher propensity for risk-taking behaviors has been referred to as “young male syndrome,” as it so eloquently captures the sex differences present at younger ages that continue to evolve as men develop and mature (Wilson and Daly 1985). Later in adulthood, men take greater financial risks and weigh monetary financial risk attitudes, including the possibility of loss over gain, less heavily than most women (Eckel and Grossman 2002). Men are also more aggressive than women in laboratory settings, as well as in real-life settings, whether measured by self-report (Archer 2004) or by frequencies of arrest for violent crime (Roe et al. 2009). The sex differences in aggression are even consistent across cultures (Archer 2009; Campbell 1999). Scholars have argued that men engage in risky pursuits and aggressive interactions without adequate consideration of the consequences. For example, men are more likely to take part in extreme sports (Murray 2003) and are also more likely to be overrepresented in illegal drug usage (Degenhardt et al. 2008), dangerous driving convictions (Corbett 2007), and deaths from accidents (Pampel 2001). Notably, women

have been documented as less risky, especially when the risks are physical or life-threatening, whereas men are more likely to take risks in everyday situations, such as engaging in conflict and risky sexual activity or even crossing a busy street (Byrnes et al. 1999; Campbell 1999; Poppen 1995). Scholars have further suggested that these sex differences may derive from well-established sex difference in fear of harm or injury (Campbell 2006). In childhood, girls are more fearful than boys (Else-Quest et al. 2006); and among adults, studies have also shown that women experience more intense fear than men (McManis et al. 2001; Brebner 2003).

Socialized Gender Roles

Beyond Darwin’s sexual selection theory, recent hypotheses have surfaced that seek to untangle the evolutionary reasons for sex differences in risk-taking behaviors and aggression. Zuckerman’s (1991) theory of risk as value posits that a consequence of lower levels of arousal and socially instilled beliefs that risk taking is a highly valued masculine trait motivates men to act riskier. Similarly, the masculine psychology perspective adheres to the idea that masculinity has evolved in response to the competitive demands of primitive societies, mainly that competition – in both hunter-gather societies and modern, industrial societies – forces men to engage in risk taking to gain positions of power in nature, at work, and with women (Wilson and Daly 1985).

A more recent line of research posits that differences in risk taking and aggression may be the result of socialization into gender roles that differentially encourage the use of violence among males (Eagly 1997). The observed green light for aggression and risk taking among men is likely due to a societal emphasis on evolution-based, stereotypical dominant and competitive roles understood as “manly.” Therefore, evolved differences between males and females can account for the emergence of the modern division of societal expectations and, consequently, the social roles that have surfaced to account for these differences. Researchers assert that the greater the

degree of gender inequality in a society, the greater sex differences in violence and aggression will be present (Eagly 1997). As long as the “female” gender role promotes communal behavior and the “male” gender role promotes risk-taking and aggressive behaviors, people will continue to expect women and men to possess – and act upon – these characteristics to carry out their sex-typical roles.

Conclusion

Taken together, research indicates that men can be riskier and more aggressive than women in a variety of social and biological domains. These sex differences are present early in development and continue to have a pervasive effect on behavioral patterns in males throughout the life course. More specifically, males are more willing to take risks and behave aggressively, and this propensity for risk and aggression is likely a consequence of various evolutionary and social explanations, including male competition over mating opportunities, life-course developmental differences between men and women, and socialized gender roles.

Cross-References

- [Charles Darwin](#)
- [Charles Darwin: Theory of Sexual Selection](#)
- [Greater Risk-Taking and Status](#)
- [Risky Behavior](#)
- [Sex Differences in Aggression](#)
- [Sexual Conflict Theory](#)

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Men Romantic Partner Choice

► Male Mate Choice

Men Sexual Partner Selection

► Male Mate Choice

Men with Poor Mating Prospects

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Synonyms

[Mating psychology manipulation](#); [Sexual access manipulation](#)

Definition

One model of suicide terrorism proposes that men with poor mating prospects will be more likely to commit suicide attacks as a consequence of either sexual access manipulation or as a means to increase the fitness of genetic kin.

Introduction

Statistics show that the vast majority of suicide terrorists are unmarried, young males. Among Palestinian attackers, the data indicate that 99% are male and 84.2% are unmarried (Atran 2003; Pedahzur et al. 2003), and this sex imbalance is mirrored in other communities with endemic suicide terrorism (Gunaratna 2000). Some evolutionary theorists have latched on to these demographic characteristics, asserting that males with poor mating prospects, as evidenced by their bachelor status, are more likely to commit suicide attacks. (e.g., Kanazawa 2007). While the theoretical argument that those with low reproductive potential would be more likely to self-sacrifice is sound, the evidence that males with poor mating

opportunities are more likely to engage in suicide terrorism is mixed.

Intrasexual Competition

Consistent demographic features of suicide attackers include that they are predominately unmarried males who tend to be in their early twenties (Benmelech et al. 2012). As a consequence, some evolutionary theorists have turned to intrasexual competition to attempt to explain this puzzling act. Kanazawa (2007) argued that polygyny limits younger, low-status Muslim males' access to mates. In conjunction with divine promises of sexual rewards in the afterlife, Kanazawa and later Thayer and Hudson (2010) contended that intrasexual competition and sexual access manipulations are sufficient to explain suicide terrorism from an evolutionary perspective. However, there is no evidence that suicide attackers are less likely to marry than noncombatants nor do they appear to be lower in status (Atran 2003; Berrebi 2003; Krueger and Malečková 2003). Moreover, this hypothesis is theoretically problematic. Lawson et al. (2008) noted that in gerontocratic societies where older males monopolize females, younger males should instead spend their early reproductive years acquiring resources, not engaging in behavior that results in certain death.

Alternative Theories for Demographic Characteristics

Alternative evolutionary explanations for the young age of male suicide attackers, however, exist. First, though polygyny is not likely a direct factor in the social precipitation of suicide terrorism, sexual access manipulation might play a partial role, potentially factoring into cost-benefit analyses (see ► [Sexual Access Manipulation](#)). The belief that 72 virgins await those who sacrifice their lives for religious causes in the afterlife is perpetuated by some Islamic terror organizations, and the hope that one will receive such rewards is cited as a common motivator for

suicide attack (Hafez 2006). Secondly, the veneration of suicide terrorists as martyrs by local communities might act on mating psychology (see ► [Sexual Access Manipulation](#)). Third, the hypothesis that kinship psychology manipulation motivates suicide terrorism entails that suicide terrorists will recruit individuals who are younger in age (Qirko 2004) (see ► [Kinship Psychology Manipulations](#); ► [Young](#)).

Inclusive Fitness

Another possibility is that men with poor mating prospects could improve their fitness by killing themselves and directing resources towards their kin. The inclusive fitness model of suicide proposes that one would enhance his or her inclusive fitness by dying by suicide when he or she has low reproductive potential and is imposing net costs of genetic kin (deCatanzaro 1981, 1984, 1991; de Catanzaro 1995). However, there is no evidence that suicide attackers were a burden on their kin. In fact, many suicide terrorists achieved high educational levels and are employed (Atran 2003; Berrebi 2003; Krueger and Malečková 2003). On the other hand, a preliminary model tested by Blackwell (2006) demonstrated that suicide terrorism can benefit close kin. Using the Palestinian conflict as a test case, Blackwell found that suicide terrorists with middle class backgrounds and large families could benefit their families most through suicide terrorism specifically in light of the resources that could be redirected to male siblings.

Conclusion

Statistics consistently show that suicide attackers are unmarried males in their early reproductive years. Some theorists have argued that these males have poor mating prospects, and hence, will either seek to increase their reproductive success through engaging in violent behavior or alternatively they will attempt to improve their inclusive fitness by redirecting resources to their close genetic kin. More research is necessary to test these various hypotheses.

Cross-References

- [Benefits to Kin](#)
- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Monetary](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide as Kin-Directed Altruism](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Men's Aggression Against Women

- [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)

Men's Egoistic Dominant Acts

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Synonyms

[Male strategies](#); [Social hierarchy](#); [Social status](#)

Definition

Males display a sex-specific pattern of expressions of dominance, which is a universal feature of human psychology.

Introduction

Dominance is the use of aggression, threats, fear, and intimidation to maintain or achieve positions of social influence (Henrich and Gil-White 2001),

and evidence suggests there are important sex differences in the expression of dominance (Buss 1981). Among social animals, dominance is a common mechanism by which multiple individuals produce a linear hierarchy of social rank. When dominance-based strategies are successful, stronger, larger individuals are more likely to attain a disproportionate level of power and influence within the social group (Lukaszewski et al. 2016). Among humans, cultural and ecological context plays an important role in the viability of dominance-based strategies, and among mobile egalitarian foragers, untethered subsistence coupled with an ethos of equality allows the group to effectively resist overly assertive dominant leaders (Boehm 1993). With increased sedentarization and monopolization of resources by kin groups, the importance of dominance in status striving increases (Kaplan et al. 2009). Nonetheless, dominance represents a distinct strategy for gaining social influence across a variety of social and cultural contexts (Chapais 2015; Cheng et al. 2013) and is likely a universal feature of human psychology. Yet sex-specific expressions of dominance reveal the impact of sexual selection on male and female leader-follower psychologies.

The Expression of Dominance Among Men

Among a sample of Western undergraduates, Buss (1981) demonstrated sex differences in dominance behaviors and evaluations of dominant acts. Males showed preference for self-enhancing and egoistic expressions of dominance and rated these behaviors more favorable; similarly, dominant males reported expressing dominance through both communal and egoistic acts, whereas dominant females tended to express dominance exclusively through communal, pro-social behaviors. Both males and females may pursue dominance-based strategies for achieving positions of social influence, yet males are more likely to use dominance to achieve individual goals. For males, expressions of dominance can function to achieve both proximate goals promoting

individual accomplishments, while simultaneously working to achieve ultimate reproductive goals and increased reproductive success.

Dominance and Reproductive Benefits

In addition to the physical underpinnings of social dominance, individuals who achieve and demonstrate competence in a variety of behaviors, including fighting ability, control of fear, the ability to produce coalitions, and the cognitive abilities associated with effective strategizing, are able to more effectively display and express dominance among the group leading to leadership positions and high social status (Chapais 2015). Across a wide variety of cultural contexts, high-status males have increased mating opportunities, have access to higher-quality mates, are more likely to marry polygynously, and ultimately have greater reproductive success (Hill 1984; Neel 1980). The emphasis on status striving and the associated reproductive rewards is a component of human social organization that has remained stable over biological and cultural evolution. In a meta-analysis of 33 nonindustrial societies, von Rueden and Jaeggi (2016) documented a consistent relationship between male social status and reproductive success, independent of domains of status competition and consistent across variation in social stratification. Dominance may be expressed in many forms, including aggressive and nonaggressive mechanisms. For males, dominance is a widespread route to increased social status and ultimately increased reproductive success.

Conclusion

Over the course of human evolution, there have been strong selection pressures shaping and reinforcing status competition among males, building on the primate and mammalian systems of dominance hierarchies (Chapais 2015; Neel 1980; von Rueden and Jaeggi 2016). Males rely on physical markers to signal the propensity and potential for expressions of dominance to

the group but can also use demonstrations of competence in a variety of domains to achieve positions of social influence which may or may not confer authority and coercive power over subordinates (Chapais 2015). At both the proximate and ultimate levels, expressions of dominance among males serve individualistic and egoistic aims, conferring social status and reproductive benefits. From this system, cooperative and pro-social behaviors may emerge as well. Human males have evolved to be status seekers, and the pursuit of dominance-based strategies for achieving positions of social influence remains a universal feature of male psychology employed by at least some males across a wide range of social and cultural settings.

Cross-References

- [Dominant Acts Expressed \(Buss 1981\)](#)
- [Women's Prosocial Dominant Acts](#)

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Men's Mate Preferences

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Synonyms

[Ideal partner preferences](#); [Mate choice criteria](#); [Mate selection criteria](#); [Partner preferences](#)

Definition

The characteristics which men use to evaluate potential relationship partners, especially those in contrast to the characteristics women use to evaluate potential relationship partners. Men place more value on cues of youth and fecundity, whereas women place more value on social status and potential for resource provisioning.

Introduction

Systematic research has documented sex differences in preferences for romantic and marital partners since the early twentieth century. These studies revealed many findings consistent with current theory and research in evolutionary psychology. For example, college-aged women prefer partners older than themselves, whereas college-aged men prefer partners younger than themselves, matching patterns in contemporary census records (Hill 1945). Men and women

showed considerable agreement in preferences for mate attributes, such as agreement on dependable character, emotional stability, and maturity, pleasing disposition, mutual attraction, and good health. However, several sex differences were evident. Women gave more consideration to ambition and industriousness, education and general intelligence, and good financial prospects than men did, whereas men gave more consideration to being a good cook and housekeeper, good looks, and desire for home life and children (Hill 1945). Men in fraternities were more demanding, ascribing more importance to nearly all characteristics than nonaffiliated men. Hill (1945) suggested that fraternity men could insist on higher standards because of their higher social status on campus. Other than this reasonable inference, the researchers made no attempts to explain the patterns of findings. The results were purely descriptive; there were no *a priori* hypotheses reported or tested.

Over the years that followed, the questionnaire from the University of Wisconsin study of campus values in mate selection (Hill 1945) became the foundation for sociologists' studying patterns in marriages and families. Buss (1989) utilized this survey in a study of ideal partner preferences across 37 cultures and framed mate selection in the context of evolutionary selection pressures. The study confirmed theoretical predictions across the human population; although women and men share values and preferences for many characteristics, differences between the sexes are also evident. Women place more value on cues to resource acquisition in potential mates, whereas men place more value on cues to reproductive capacity (Buss 1989). The publication of this study was a defining event in the emerging field of evolutionary psychology, leading to a considerable volume of research on sex differences in mate selection criteria.

Evolutionary Foundations for Sex Differences in Human Mate Preferences

Evolution by sexual selection occurs through two processes, intrasexual competition and intersexual

selection (Darwin 1871). Intrasexual competition consists of contests between members of one sex, where the winner of the contest gains preferential access to members of the opposite sex. The prototypical example of intrasexual competition is buck deer locking horns in combat during the mating season. The winner of the bout gains the territory and access to the females within it; the loser goes home with a broken horn. This process continues year after year, and any heritable variation that promotes success in these contests will spread through the population over many generations (Darwin 1871). Human intrasexual contests may be subtler.

Intersexual selection involves both sexes. If members of one sex have a consensus about the desirable characteristics of the opposite sex, then those individuals with the desired characteristics will have a mating advantage. One example is the size and decorative coloration of feathers seen on many male birds. It is hypothesized that the underlying reason why female birds find a male peacock's tail feathers attractive is their indication of the survival ability of male birds. The feathers would not only be noticeable to females but also to predators and a hindrance in movement, making escape from predators as well as routine tasks more difficult. It would seem easier to survive without this costly display; the females of the species usually possess coloration that blends in well with the features of the habitat. The birds that are able to survive with this handicapping display must also have some characteristics that would be valuable for the female's potential offspring to acquire (Darwin 1871).

Among mammals and most other animals, females are the limiting sex in reproduction because they provide almost all of the physiological resources required for offspring production. The larger investments allocated to offspring result in much lower potential reproductive capacities in females compared to males. Because of these factors, females are more discriminating in mate selection, and males exert comparatively more effort than females in attracting and retaining mates (Trivers 1972). For males in most species, reproduction is limited by access to fertile mates, more so than for their female

conspecifics (Trivers 1972). Thus, cues of fertility and reproductive value will be more prominent in men's mate preferences than in women's mate preferences.

Reproductive value is the expected future contribution to offspring in future generations. Fertility is the likelihood of being able to reproduce at a given time. Although life history patterns will vary somewhat across cultures, women's fertility typically peaks in the early 20s, with a gradual decline until menopause (Bongaarts and Potter 1983). Reproductive value peaks earlier, typically in the mid-teens, and then declines linearly with age. Although cultural norms, reproductive practices, and age-specific mortality will vary across cultures, women's reproductive value and fertility are strongly age-dependent (Williams 1957). Thus, cues of age will be important in men's mate preferences.

Aspects of Men's Mate Preferences

Women and men share preferences for partner characteristics such as kindness, understanding, and intelligence (Buss 1989); however, preferences also show divergence following reproductively relevant currencies. Physical features and behavioral indicators associated with youthfulness are hypothesized to predict women's reproductive capacity and thus men's mate preferences. In addition to studies of attribute ratings, other studies have found that levels of physical attractiveness in photographic stimuli influenced men's evaluations more so than women's evaluations (e.g., Townsend and Levy 1990). These sex differences are evident in preferences for both long-term and short-term partners, although the differences may be smaller in short-term preferences (Li and Kenrick 2006). Several specific aspects are reviewed below.

Facial Features

Cunningham (1986) found that "baby face" features, i.e., large eyes and a small nose, were consistently correlated with attractiveness in women, perceived fertility, and perceptions of few medical

problems. Studies using both actual (Cunningham 1986; Grammer and Thornhill 1994) and computer-manipulated (Perrett et al. 1998) images find that women's faces with more feminine features are perceived as more attractive. The degree of feminine features in women's faces is related to levels of circulating estrogen (Law-Smith et al. 2006), suggesting a connection to health status.

Research has identified other facial attributes that enhance women's attractiveness. Symmetrical faces are more attractive, as they indicate stable morphological development with good nutrition and without significant injuries or contagion from pathogens, as well as a good match between genotype and the developmental environment (Møller 1997). Studies using both unmanipulated images of real faces (Grammer and Thornhill 1994) and sophisticated computer graphic simulations (Rhodes et al. 1998) demonstrate that facial symmetry predicts attractiveness. Individuals with more symmetric faces are perceived to be healthier (Jones et al. 2001). Some studies suggest that these perceptions are accurate, as facial symmetry is inversely related to incidents of respiratory disease (Thornhill and Gangestad 2006) and directly related to features suggesting good physical condition (Little et al. 2008).

Facial averageness, the degree to which one's face resembles most other faces in a population, also predicts facial attractiveness. Average faces may be attractive because they indicate genetic diversity, which confers resistance to pathogens and/or because those with average faces are less likely to be homozygous for deleterious alleles (harmful mutations) than those with less average faces (Mitton and Grant 1984). Facial averageness is in fact predictive of better health status (Rhodes et al. 2001) and genetic diversity in the histocompatibility complex (MHC) genes that code for immune response proteins (Lie et al. 2008). MHC gene heterozygosity in itself is predictive of perceived facial attractiveness (Roberts et al. 2005).

Body Features

Research has demonstrated similar patterns in preferences for women's other bodily features.

For example, breast symmetry is attractive and is positively correlated with fecundity (Little et al. 2011). Skin tone is an honest indicator of youthfulness and fertility (Fink et al. 2001). The number of physical attributes predicting both attractiveness and beneficial attributes will continue to grow with future research.

Waist-to-Hip Ratio

Another salient characteristic in humans is the ratio of the circumference of the waist to the hips. Before puberty, men and women have a similar distribution of fatty tissues, but afterwards women have a smaller waist-to-hip ratio. A smaller waist-to-hip ratio in women is associated with better health status and greater reproductive capacity (Singh 1993). Across decades of cultural and fashion changes in the USA, a small waist set against full hips was a consistent feature of female attractiveness, whereas bust line, overall body weight, and physique varied over the years (Singh 1993). Although the original stimuli were rather crude, male preferences for low waist-to-hip ratios (around 0.7) are replicated with precise digital stimuli disentangling waist-to-hip ratio and body mass covariation (Kościński 2014).

A large pelvis facilitates delivery in childbirth, which is more difficult in humans due to infants' large heads and a pelvis adapted for bipedal locomotion. A narrow waist also signals the absence of pregnancy and therefore current fecundity, one of the few easily perceptible cues of a woman's status (Singh 1993). Women in the optimal 0.7 WHR range have better health status, fewer medical conditions, and lower mortality (Singh and Singh 2011). These women have higher fecundity (Zaadstra et al. 1993) and higher rates of pregnancy (Singh and Singh 2011).

Faithfulness and Paternal Uncertainty

Both women and men are upset by sexual and emotional infidelity in partners; however, sexual infidelity is more upsetting to men than to women because of the threat of diversion of paternal investment to children fathered by other men

(Buss et al. 1992). Men will have mate selection preferences that protect against paternal uncertainty; however, the form of these preferences will vary across history, culture, and population. In natural fertility populations, men may value chaste women as this would provide a cue to paternity confidence both at the current time and in the future (Dickemann 1981). Women's chastity is valued across cultures; however, there is variation in its importance (Buss and Schmitt 1993). Across cultures, men are likely sensitive to women's overt expressions of mating effort. Although men would consider flirtatious women for short-term sexual relationships, they are less likely to desire them as long-term relationship partners (Kruger et al. 2014).

Conclusion

Men's mate preferences include a variety of personality, behavioral, and physiological features all related to the potential to promote men's reproductive success. There will be trade-offs between specific features, and assortative mating will lead to partnering between men and women of similar value in the mating market. Women's intrasexual competition will emphasize features attractive to men in efforts to attract and retain mates.

Cross-References

- [Men's Short-Term Mating Behaviors](#)
- [Women's Mate Preferences](#)

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Men's Mating Psychology

► Psychological Evidence for Human Sperm Competition

Men's Short-Term Mating

► Men's Short-Term Mating Behaviors

Men's Short-Term Mating Behaviors

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Synonyms

[Men's mate preferences](#); [Men's short-term mating](#)

Definition

Mating strategies often differ between men and women, as well as between short-term and long-term contexts. Men seeking short-term mating opportunities are expected to employ strategies that will minimize investment in potential partners and offspring while maximizing opportunities for casual sex.

Introduction

Men and women differ in their minimum investments to their offspring, with women typically investing much more in their children than men. As a result, men and women tend to differ in the genetic benefits they stand to gain from a short-term mating strategy – one in which a person pursues short-term mating opportunities, usually with little investment in their partner. Over a 9-month period, a woman could only give birth to a single child, whereas a man could potentially sire numerous children over the same length of time. Therefore, the potential genetic benefit of a short-term mating strategy is much greater for men than for women. Men and women in all

cultures do tend to gravitate toward monogamy, with both men and women often adopting a mixture of short-term and long-term mating strategies that vary depending on environmental contexts. Nevertheless, data from men and women across many cultures suggests that men may be more likely to pursue a short-term strategy than women.

Strategies

Sexual strategies theory (SST; Buss and Schmitt 2017) asserts that because men and women faced different challenges to reproductive success, they evolved different strategies to overcome these challenges. Men, for example, likely faced the challenge of acquiring multiple, willing sexual partners whereas women faced the challenge of securing investments from their intimate partners. There are also individual differences in mating psychologies within sexes, characterized by Buss and Schmitt (1993) as either short-term or long-term. Short-term relationships often involve sex without considerable investment, such as one-night stands, or friends with benefits. Long-term relationships generally involve prolonged commitment to the same individual, like in marriage. Men and women typically employ a combination of short-term and long-term strategies, and these strategies differ between men and women.

Adaptive Problems Faced by Men Pursuing Short-Term Strategies

Partner Number

Men pursuing short-term mates face a different set of obstacles than those pursuing long-term mates. In general, men who maximized their number of sexual partners would have been more reproductively successful than men who had relatively few sexual partners. In response to these selection pressures, men have developed several adaptive psychologies. Specifically, men typically desire a large number of sexual partners, relax their standards for short-term (compared to long-term) partners, and prefer to

have sex quicker, rather than wait to have sex after first meeting someone (Schmitt et al. 2001).

Minimizing Risk and Investment

Identifying Sexually Accessible Women

When attempting to mate with many different partners, men face the problem of identifying which women are sexually accessible. Men seeking short-term mates would be unlikely to pursue relationships with women who appear sexually reserved or seem unlikely to consent to sex without considerable investment. Although men seeking a long-term partner may find promiscuity undesirable, promiscuity is a good cue to men seeking a short-term partner that they will not have to invest heavily to gain sexual access. Men who could maintain sexual relationships while preventing investments in their partners from escalating were likely able to pursue more short-term relationships (Buss 1994). Men may even pursue short-term relationships with women interested in long-term mating by exaggerating or lying about their willingness to commit for extended periods of time (Tooke and Camire 1991; Jonason & Buss 2012). Where women's preference for sexual permissiveness remains constant regardless of mating context, men considering a short-term mate report a greater preference for sexual permissiveness than do men considering a long-term mate (Oliver and Sedikides 1992).

Identifying Fertile Women

Men seeking a short-term partner face the problem of identifying fertile women. Men seeking long-term partners also face the problem of identifying fertile partners but are predicted to be more concerned with cues to future fertility (maximizing potential future children of the length of the relationship), whereas men seeking short-term partners would likely be more attuned to cues of current fertility. As youth is a reliable predictor of future fertility, men would predictably be more interested in young women when pursuing a long-term strategy. But because age cannot be directly observed, men seeking fertile mates would likely attend to cues that reliably covary with age, such as attraction. Unsurprisingly,

Buss and Schmitt (1993) found that men seeking short-term mates placed more emphasis on attractiveness than did men seeking long-term mates.

Behaviors

Infidelity

Behavioral evidence from large samples of men in various cultures indicates that they pursue short-term strategies more often than women. Both men and women sometimes pursue a mixed strategy, in which they maintain commitment to a long-term partner while seeking mating opportunities with one or more short-term partners. Although both men and women in monogamous relationships sometimes seek extrapair partners, they differ markedly in the type and frequency of extrapair copulations they pursue. A series of surveys from 1991 to 2010 revealed that among American participants who had ever been married, 20–25% of men had cheated on their spouse, compared to 10–15% of women (Carr 2010). Although women could certainly benefit from pursuing extrapair copulations, they historically risked violence and sexual assault at the hands of their monogamous partners if they were suspected of infidelity. Men also face risks to infidelity, such as violence from male relatives and partners of the women they copulated with, and retaliatory infidelity from their own spouses. Nevertheless, men seem to be more interested in extrapair copulations than do women.

Hook-Ups

Men seem to be more interested in casual, one-time sex partners than women. Hook-ups and friends with benefits situations are typically those in which the relationship is sexual, but there are no explicit promises of continued commitment. Men, more than women, report sexual fantasies involving multiple, anonymous women, and men are more likely than women to report having at least one friend with benefits (Garcia and Reiber 2008). Women, on the other hand, report more depression and regret following one-night stands and when asked what they want out of hook-ups, women more often respond with hopes that the hook-up will lead to a long-term

romantic relationship (where men often hope that they get to have more hook-ups). Women do, of course engage in short-term mating, but the motivations for doing so appear to be different from those of men.

Prostitution

The exchange of goods or currency for sex occurs in most known cultures and is frequently referred to as “the world’s oldest profession.” Most solicitors of prostitution are male, and a large proportion of men have solicited prostitution – 69%, according to Kinsey et al. (1948, 1953). The widespread prevalence of male solicitation of prostitution is yet more behavioral evidence for the male preference for short-term mating opportunities.

Sociosexual Orientation Inventory: Behaviors

The sociosexual orientation inventory (SOI; Simpson and Gangestad 1991) and its revised version (SOI-R; Penke & Asendorpf 2008) were developed to measure willingness and desire to engage in multiple, uncommitted sexual relations, as well as frequency of past sexual behaviors. Simpson and Gangestad observed that reports of sociosexual attitudes were generally correlated with reports of sociosexual behaviors. Specifically, individuals who expressed unrestricted attitudes about casual sex were more likely to have engaged in sex with more than one person during the same period of time and reported having sex earlier in their relationships. Conversely, those who expressed more restricted attitudes on the SOI were less willing to engage in sex without commitment and investment from the other partner. Importantly, Simpson and Gangestad (1991) provided evidence that more casual attitudes towards sex, and greater desire for multiple casual, sexual experiences correlated with a greater frequency of past sexual encounters.

Contextual Influence on Mating Strategies

Perceived Effectiveness of Short-Term Strategies

When men do seek short-term partners, they typically emphasize traits that they believe are

desirable to women seeking a short-term relationship (Schmitt and Buss 1996). Schmitt and Buss (1996) observed that both men and women predicted that men displaying cues indicating current ability to share resources and cues indicating dominance would be more successful in pursuing short-term relationships. Indeed, men, more so than women, have been observed to deceive potential partners in order to gain sexual access, exaggerating their future willingness to commit to relationships, inflating their status and earning potential, and acting more agreeable and dominant than they really are (Tooke and Camire 1991). The willingness of men to lie about these cues is unsurprising, given that women tend to prefer cues to high status, high earning potential, willingness to commit, and agreeableness (Buss 1989; Buss et al. 2001; Shackelford et al. 2005) tested.

Father Absence

Pursual of a short-term mating strategy appears to be correlated with father absence in both men and women. Mayan and Ache men without fathers were less willing to invest in a long-term romantic relationship compared to those with fathers (Wanforth et al. 1998). Further, men raised without fathers appear to experience puberty earlier and are more likely to pursue a short-term mating strategy (Ellis et al. 1999; Surbey 1998). It is unclear to what extent genetic heritability plays a role in fatherless men’s unwillingness to pursue a long-term strategy, and the societal impact of growing up without a father should also be considered as a potential explanation.

Life Stage

Men and women also seem to change their sexual strategies across their life spans. Short-term strategies are more common among adolescents and decrease with age. Frayser (1985) explained that adolescents engage in short-term mating as a way of assessing their own mate value and exploring their preferences. It may also be the case that adolescents possess attributes such as attractiveness that make them more successful in short-term contexts, thus making them more likely to pursue short-term mates.

Mate Value

Unsurprisingly, there does appear to be a correlation between self-perceived desirability and number of sexual partners for men. According to Clark (2006), men who perceived themselves as more sexually desirable also reported having more sexual partners. But self-perception of mate value is not the only predictor of more sexual partners; men with desirable short-term attributes such as masculine bodies and faces, and access to status and resources tend to have more sexual partners (Kanazawa 2003; Perusse 1993; Rhodes et al. 2005). These data suggest that men may generally be more likely to pursue a short-term strategy when they perceive a greater likelihood of short-term mating success.

Sex Ratio

The amount of sexually available partners has been observed to influence the adoption of different mating strategies. Specifically, in contexts with a majority of women, men are more likely to pursue short-term mating opportunities. Inversely, when there are more men than women, individuals are more likely to pursue long-term mates, and even to have fewer divorces (Pedersen 1991).

Conclusion

Although men and women generally express preferences for long-term partners and value partners who indicate good parenting skills, men's mating behaviors diverge from women's in several notable respects. Notably, men express greater desire for multiple sexual partners and are more likely to act on this desire by having extramarital affairs and other types of short-term mating arrangements.

Cross-References

- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Sex Differences in Long-Term Mating Preferences](#)
- [Short-Term Mating](#)

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Men's Suspicions of Partner Infidelity and Women's Defection

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Synonyms

Cuckoldry; Forced In-pair Copulation (FIPC); Intimate Partner Violence (IPV); Paternity Uncertainty

Definition

The tendency for men to use intimate partner violence (IPV), forced in-pair copulation (FIPC), and in some extreme instances, homicide as a means of reducing the threat of cuckoldry and relationship defection.

Introduction

More than ten million Americans, both male and female, are victims of intimate partner violence (IPV) each year (Black et al. 2011). Yet women are disproportionately more likely to be victims, with 82% of IPV victims in the United States being women (Truman and Morgan 2014) and are disproportionately more likely to be physically abused by men, with 99% of female IPV incidents being perpetrated by men (Catalano et al. 2009). Although rates of IPV are quite high, being a perpetrator of IPV comes with many potential consequences. Men who physically abuse their partners may lose their partner if she defects from the relationship; lose access to their children; have to serve time in jail; have to pay large legal fees; experience reputational damage from friends or family; and lose out on employment opportunities. Despite these negative, proximal consequences, an evolutionary perspective suggests that physical and sexual abuse may solve adaptive problems recurrently faced by males throughout our species' evolutionary history. Indeed, the two most common reasons men report for having been physically abusive towards their partner is their suspicion of an infidelity and/or the perception that their partner is attempting to defect from the relationship (Wilson and Daly 1996). The purpose of this entry is to explain why men may have evolved adaptations that favor intimate partner violence in the contexts of infidelity and relationship defection, despite the costs associated with IPV.

Evolutionary Foundation

Parental Investment Theory

Parental Investment Theory (PIT) was proposed by Trivers (1972) as an explanation for humans' sexual behavior, including sexual selection and mate preferences. According to PIT, the sex that invests more in its offspring will be more discriminating when it comes to selecting a mate, whereas the sex that invests less in its offspring will be less

discriminating in selecting a mate. In most species, females invest the most in offspring. Women's greater investment in their offspring begins with their gametes; in comparison to men, who produce millions of sperm daily, women produce a fixed number of large (relative to sperm), energetically costly, non-replenishable eggs in their lifetime. Women's larger investment continues with internal fertilization and gestation, which requires a minimum 9-month investment of time and energy, in comparison to just a single ejaculation for the man. Ancestrally, women also engaged in a long period of breast-feeding, and took on a larger role in parental care than men. Because of their greater investment, women are a valuable reproductive resource. In order for a man to pass on his genes, his offspring must survive into adulthood and have offspring of their own to continue passing their father's genes on to future generations. This requires offspring be protected, nurtured, fed, and taught essential survival skills, the majority of which are typically done by the mother.

Because of this immense investment required from the mother, evolution favored women who were selective in choosing high-quality mates, as selecting the wrong mate could lead to decreased reproductive success and fewer of their offspring surviving to reproductive age. Given that women are more selective, they may consider or resort to cuckoldry if their mate is of low mate value. Cuckoldry occurs when a man invests parental efforts and/or resources in offspring that are not genetically his. Cuckoldry may serve as a dual-mating strategy in which a woman remains with a long-term mate who provides resources but simultaneously pursues short-term mating opportunities with high genetic quality partners. Such a strategy is particularly likely to be enacted when the long-term partner is of low mate value. Indeed, research indicates that women who rate their partners as being low on sexual attractiveness report a greater desire for extra-pair mates when ovulating (Pillsworth and Haselton 2006).

Women's mating preferences also shift during ovulation, with women preferring men with symmetrical features, facial masculinity, body masculinity, and vocal masculinity at peak fertility

(Gildersleeve et al. 2014), all of which are indicators of genetic quality. Given that women are most likely to conceive during ovulation, copulating with a short-term partner, especially one of high genetic quality, would allow a woman to secure better genes to pass on to her offspring. By simultaneously remaining with her long-term partner, she would also still be receiving resources from him, provided that he was not aware of the infidelity. The woman would continue to receive resources from her long-term partner through the pregnancy and rearing of the offspring, as the woman would have cuckolded her long-term partner into raising the offspring of another man.

Cuckoldry and Paternity Uncertainty

Although parental investment theory observes that women typically invest more in their offspring than men, men's investment is not negligible, and men who invest in their offspring have a lot to lose in the event that their partner cuckolds them. Men's risk of being cuckolded is heightened by concealed ovulation. In comparison to female chimpanzees, whose genitals swell bright red when their eggs are released (estrus) and thus signal to the male chimpanzees that the females are able to conceive, women give no visible indication that they are ovulating. Most sexual activity for chimpanzees takes place during this phase of genital swelling, whereas humans copulate throughout the menstrual cycle. Given that male chimpanzees are visibly aware of when females are ovulating, a male could mate guard a female as soon as she entered estrus, thus ensuring that he is the only male she mates with during ovulation. This allows the male to be fairly certain of his paternity (Buss 2015, p. 148). Among humans, although women give off subtle cues that they are ovulating, men cannot be certain of when ovulation occurs. As a result, men are not able to mate guard to the same extent that male chimpanzees are, given that it would need to occur for the entire length of the menstrual cycle in the absence of any cues to ovulation. This is not feasible since men have other adaptive problems to solve, such as how to acquire resources. Concealed ovulation coupled with men's inability to mate guard without interruption gives women the opportunity to

furtively mate with other men, thus cuckolding her current mate by tricking him into raising the offspring of another man.

Men who are cuckolded face significant reproductive costs, including: investing wasted time and resources into offspring that are not his; wasting time and effort in selecting, courting, and maintaining the relationship with his mate; losing opportunities for short-term and long-term mating with other women; directing his parenting efforts into a rival's offspring, especially if more effort is directed to his rival's offspring than his own offspring; and acquiring reputational damage (Buss and Duntley [under review](#)). The latter may especially detrimental, as reputational damage may prevent him from raising his status and finding future mates, as well as possibly decreasing his mate value as both men and women may assume that he's unable to prevent mate encroachment or physically protect women. Because the costs of cuckoldry are so significant, men may have evolved psychological adaptations to aid them in identifying and responding to an actual or perceived act of cuckoldry.

Partner Infidelity

Violence

Sexual jealousy has been identified as the leading cause of IPV (Buss and Duntley [2011](#)). Men, in comparison to women, exhibit more sexual jealousy, as a woman becoming sexually involved with another man could signal to her current partner an impending affair, and thus the possibility of cuckoldry (Kaighobadi and Shackelford [2008](#)). From an evolutionary perspective, sexual jealousy is hypothesized to function as a mate retention tactic that solves the adaptive problem of cuckoldry (Daly et al. [1982](#)). By experiencing sexual jealousy, men are able to pick up on circumstances that may make them susceptible to an impending cuckoldry, such as when their partner is flirting with another male. By picking up on such cues, men can use mate retention tactics to prevent their partner from copulating with another man, thus preventing themselves from being cuckolded.

Sexual jealousy can manifest as a variety of behaviors, ranging from seemingly harmless mate retention tactics, such as buying flowers for a mate or sitting next to her when another male is present, to more severe tactics such as IPV and partner rape (Buss [1988](#)). Mate retention behaviors are hypothesized to be performed hierarchically, with less severe or less costly mate retention behaviors being performed first, followed by more severe or more costly behaviors (Kaighobadi et al. [2008](#)). In the event that a woman has been copulating with another man, her partner may be motivated to use physical violence as means of protecting himself from being cuckolded by preventing any further extra-pair copulations. This is especially true if the man initially used nonviolent mate retention tactics, such as verbal threats, to deter the extra-pair copulation, but such tactics were unsuccessful.

According to Wilson and Daly ([1996](#)), men use violence against women as a risky strategy for deterring their partner from an infidelity. When used strategically, violence can increase the credibility of threats. If a man discovers that his partner is copulating with another man, he may initially threaten his partner with violence. However, if the man does not follow through with his threats, they become ineffective at deterring his partner from future extra-pair copulations. In this situation, acting on his threats by inflicting violence on his partner would increase the credibility of any future threats, as this would indicate that he intends to follow through on them. By increasing the credibility of his threats with an act of violence, the man would be able to use threats without having to resort to violence in the future.

Evidence that violence may serve the function of preventing cuckoldry comes from contexts that imply a woman has been involved with another man. One of these contexts is when she is or is expected to be pregnant by another man. Although the hypothesized function of violence as a response to an infidelity is to deter the infidelity and thus eliminate the threat of cuckoldry, the hypothesized function of violence as a response to a pregnancy is to terminate the pregnancy (Buss and Duntley [2011](#)). Although the function of violence differs, infidelity and

pregnancy with another man's offspring represent two very similar adaptive problems, as one signals the possibility of cuckoldry and the other signals that cuckoldry has already occurred. Empirical evidence supports this; Taillieu and Brownridge (2010) found that women who were abused while pregnant were more likely to be pregnant with another man's offspring.

Women's risk of being a victim of IPV is also heightened by the presence of stepchildren in the home (Goetz et al. 2008), as the presence of children fathered by another male implies that her current partner is investing resources in another man's offspring. Interestingly though, a woman's actual interest in another man is not the strongest predictor of IPV – but rather a woman's *perceived* interest in another man (Cousins and Gangestad 2007). If a man perceives that his partner is interested in other men, regardless of whether she actually is, she is more likely to be physically abused. Furthermore, men who make accusations of partner infidelity are more likely to use violence (Kaighobadi and Shackelford 2009). By engaging in violent behavior when accusing their partner of an infidelity, regardless of whether their partner is truly interested in another man, men are using sexual jealousy as a strategy to detect the possibility of cuckoldry. Men then respond to the threat of cuckoldry with violence, which functions to deter their partner from actually cuckolding them.

While an initial act of violence may decrease the likelihood of having to use violence as a mate retention strategy in the future, some men may be especially likely to express sexual jealousy through violence. For instance, men who lack resources may be more likely to use violence to deter an infidelity than men with greater resource access (Wilson and Daly 1993). These men may have to resort to other, more extreme methods of deterrence, whereas high-status men can use their resources as a positive incentive to keep their partner in the relationship. This is not to say that high-status men are not susceptible to cuckoldry, as women may still seek other mates if their partner is high in status but low in genetic quality, just that high-status men may be able to use their resources to manipulate their partner into staying in the relationship. Indeed, research shows that

men with lower mate value have been found to be more likely to engage in spousal violence as a means of hindering an infidelity (Buss and Duntley 2011; Wilson and Daly 1993). Furthermore, in a study examining risks for female homicide in abusive relationships, male unemployment, which would indicate a lack of resources, was revealed as the only demographic risk factor that significantly predicted female homicide risk (Campbell et al. 2003). By failing to provide his partner with necessary resources, a man may thus be inadvertently increasing his chances of being cuckolded by causing his partner to seek out resources from another mate. Without resources, there is little incentive for her to stay in the relationship, and so violence may be the only way to protect himself from a potential cuckoldry and to maintain secure reproductive access to his partner.

Partner Rape

Partner rape, also referred to as forced in-pair copulation (FIPC) may function as another, more extreme anti-cuckoldry tactic. Several studies offer support for this theory of FIPC. Finkelhor and Yllo (1987) found that partner rape was more likely to occur after accusations of female infidelity. Camilleri and Quinsey (2009) reported that convicted partner rapists, in comparison to men convicted for nonsexual partner violence such as physical assault, experienced more situations in which they were susceptible to cuckoldry prior to the crime. Finally, Shields and Hanneke (1983) observed that 47% of married women who reported engaging in an extra-pair copulation were raped and beaten by their husbands.

If an actual or perceived infidelity has occurred, FIPC could be used by the woman's partner as way of ensuring his paternity through sperm competition. Sperm competition occurs when the sperm of two or more males are present in the female's reproductive tract at the same time and compete to fertilize her egg. Evidence for sperm competition comes from changes in men's sexual behavior that occur when there are suspicions of female infidelity. For instance, men's sperm count increases when another man's sperm may be present in his partner's reproductive

tract (Baker and Bellis 1995), thus increasing his probability of securing paternity over his partner's egg. Men's sperm count also increases in proportion to how long they have been apart from their wife: the more time the couple spends apart, the more sperm the man produces (Baker and Bellis 1995), as time spent apart could provide his wife with an opportunity to copulate with another man. In addition to their sperm count increasing with the duration of separation, men's reported sexual interest in their partner increases relative to the amount of time the couple has spent apart (Shackelford et al. 2007). An increase in sexual interest would make it more likely that the couple would copulate upon reuniting, which would subsequently increase the man's chance of fertilizing an egg should another man's sperm also be present in his partner's reproductive tract. It is thus the couple's time spent apart, rather than the time since the couple's last copulation, that is predictive of sperm competition, as the unaccounted time presents a risk for cuckoldry.

FIPC may also be triggered by cues from women. For instance, Thornhill and Thornhill (1992) suggest that women who purposefully resist or avoid copulating with their partner may be doing so because of a recent infidelity. This may be especially true if their partner is low in mate value, and they are employing a dual-mating strategy in which they attempt to secure better genes for their offspring from another man who is high in mate value whilst still remaining with their current partner to continue benefiting from his resources. In order to ensure that her offspring receives the genes of her short-term mate, she would need to avoid copulating with her partner until her short-term mate's sperm fertilized her ovum, as sperm competition would jeopardize her chance of securing better genes. In this situation, the woman's resistance to copulate would signal to her partner that he may be at risk of being cuckolded, and FIPC would function to decrease this risk. Finkehlor and Yllo's (1987) finding that most instances of FIPC occur during or after defection from the relationship lends support to his hypothesis, as men are likely hyperaware of female infidelity during separation as this gives women the opportunity to seek out other mates

Defection from the Relationship

Violence

In a similar manner to a partner's infidelity, a woman defecting from the relationship can also be costly for the man (Buss and Duntley [under review](#)). Defection from a relationship represents a direct loss of reproductive access to his mate. Whereas a man may continue to have reproductive access to an unfaithful mate, any reproductive access to that mate is eliminated once the relationship has been terminated. Furthermore, ending the relationship also means that his partner is now sexually available to other men, including any potential rivals the man may have. A man's reputation could also be damaged if knowledge of the relationship ending becomes public. This could hinder future reproductive opportunities with other mates, as public knowledge of the defection may lead to a decrease in mate value. This would be especially true if the woman defected from the relationship because her partner failed to provide her with necessary resources. If other women became aware of this, this could jeopardize any future reproductive opportunities for the man, as his failure to provide his former partner with resources would signal that he is an inadequate mate.

Because of the reproductive and reputational harm, violence may be used as a strategy to prevent women from ending the relationship (Kaighobadi et al. 2009). Indeed, women who leave their husbands are often pursued, threatened, and assaulted (Wilson and Daly 1996). Men may be especially likely to resort to violence if they expect that their partner is ending the relationship for another mate. Barbaro and Shackelford (2016) found that men who were physically violent towards their partner secured more in-pair copulations per week in the previous month compared to men who weren't physically violent towards their partner. In addition, average monthly rates of violence towards female partners were positively associated with in-pair copulation frequency. By engaging in IPV and subsequently securing more in-pair copulations, the man may be using violence to both deter his partner from engaging in any extra-pair copulations and to keep

his partner in the relationship with him should their increased in-pair copulations result in fertilization. If the woman is pregnant, she may be less likely to seek out other mates as having a reliable source of resources during the pregnancy would be necessary, and it would be unlikely that another man would provide her with those resources if they were aware that she was already pregnant. However, if his partner was already thought to be copulating with another man prior to defecting from the relationship, securing more in-pair copulations through violence would serve as a mate retention tactic by deterring his partner from continuing the extra-pair copulations, as well as a sperm competition tactic by ensuring that his sperm outcompetes the other man's sperm.

Homicide

Using violence as a mate retention tactic is certainly destructive; however, mate retention takes its most extreme and lethal form through another tactic: homicide. Although rare, men may kill their partner to prevent her from defecting from the relationship, and research on homicidal relationships supports the rare instances when homicide is used as a gruesome mate retention tactic. For instance, in an in-depth interview with 30 women who had survived an attempted partner homicide, Nicolaidis et al. (2003) found that 32 women reported that their partner attempted to kill them when they threatened to terminate the relationship. Another study found that women who were separated from a male partner that they had previously lived with were at a heightened risk of being killed, as were women who had ever attempted to leave the home or had asked their partner to leave the home (Campbell et al. 2003). Furthermore, the risk of being a victim of female homicide increased ninefold if their partner was highly controlling and physically abusive *and* if the couple separated after living together. While not true for all men, it seems that a partner's departure triggers a homicidal thought response in men, as husbands who murder their wives justify the murder as a reaction to their wife leaving the relationship (Wilson and Daly 1996). In addition, studies of homicidal fantasies reveal that men often consider killing women who have rejected

them, although they do not act on such thoughts (Buss and Duntley [under review](#)).

While killing a partner may seem counterintuitive and maladaptive, as this would eliminate all reproductive access to that woman, Buss and Duntley ([under review](#)) propose that partner homicide as a response to the woman defecting from the relationship may solve two adaptive problems. First, killing the wife inflicts reproductive costs on rivals. By killing a wife who has terminated the relationship, the rival is denied all reproductive access to her. In addition, if the wife is carrying the rival's offspring at the time of the defection, killing her would also abort the rival's offspring. The second adaptive problem that is solved is preventing reputational damage that may result from the defection becoming publicly known. Although killing a mate may result in reputational damage in and of itself, killing a mate that has defected signals that the man is not someone to be messed with and may deter future mates from defecting the relationship by showing them that defection comes with grave costs. Buss and Duntley predict that the higher the mate value of the wife who ended the relationship, the greater the consequences of killing the wife for the rival as this would prevent the rival from gaining the reproductive benefits, such as good genes, from this woman. Research supports this prediction: young women (e.g., women higher in mate value) are more likely to end unsatisfactory relationships, gain the attention of sexual rivals, and form new relationships than older women (Wilson and Daly 1993). Young wives are also more likely to be killed by their husbands, with wives in their teenage years being at the greatest risk and postmenopausal wives, who can thus no longer conceive and therefore no longer pose a reproductive risk to their husbands, being at the lowest risk (Daly and Wilson 1988).

Conclusion

From an evolutionary perspective, sexual jealousy functions to solve the adaptive problem of cuckoldry. Because men who are cuckolded would be unwittingly investing their resources in another

man's offspring, overtime evolution favored men who were able to detect and prevent cuckoldry from occurring. Violence triggered by sexual jealousy serves to prevent cuckoldry in high-risk situations that indicate that the man's partner could have been involved with another man, most notably during an infidelity and relationship defection. Although IPV may be used to deter the man's partner from having an affair (Wilson and Daly 1996), men may resort to other methods, such as partner rape or homicide, if an affair has already occurred or his partner has defected from the relationship, especially if she is defecting for another mate.

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Men's Violence Against Female Partners: The Role of Culture

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Synonyms

Domestic violence; Intimate partner violence; Relationship violence

Definition

Men's violence against female partners is defined as behavior that causes physical, sexual, or

psychological harm, including acts of physical aggression, sexual coercion, psychological abuse, and controlling behaviors. It has high prevalence rates worldwide, with about 30% of women aged 15 years and over likely to experience violence by an intimate partner in their lifetime. At the same time, rates vary substantially in relation to cultural variables, such as gender inequality, collectivism, societal approval of intimate partner violence, and honor concerns.

Introduction

Men's intimate partner violence (IPV) against women has high prevalence rates worldwide, with about 30% of women aged 15 years and over likely to experience IPV in their lifetime. At the same time, rates vary substantially between cultures. This article reviews current research findings on cross-cultural differences in the prevalence of men's IPV against women and discusses them in relation to culture-level variables, such as gender inequality, collectivism, societal approval of IPV, and honor concerns. These cultural context variables shape the attitudes and norms of individuals about gender relations and IPV. Further research has demonstrated interactive effects between culture-level and individual-level variables in predicting IPV. Challenges for cross-cultural research on IPV in the age of migration and the outline of a gender-inclusive approach to the study of IPV are discussed in the final section.

Men's Violence Against Intimate Partners: The Role of Culture

Across the world, women are at risk of experiencing aggression and violence by men with whom they are in an intimate relationship. IPV is defined as “behaviour by an intimate partner that causes physical, sexual or psychological harm, including acts of physical aggression, sexual coercion, psychological abuse and controlling behaviours” (World Health Organization 2013, p. vii). Although this definition is neutral with regard to

the gender of the victim and the perpetrator, the most common form is men's IPV against a female partner. The main method for studying the prevalence and impact of IPV is through women's self-reports of victimization in large-scale surveys, if possible drawn as a representative sample from the general population.

A comprehensive review of the prevalence rates of intimate partner violence in 81 countries revealed that globally in 2010, 30% of women from the age of 15 had experienced at least one incident of physical and/or sexual violence victimization by an intimate partner in their lifetime (Devries et al. 2013). Despite overwhelming evidence of the negative consequences for women's physical and psychological health and well-being (Coker et al. 2011; Martin et al. 2011), IPV is not uniformly condemned and penalized across the world. A study by the United Nations (UN) revealed that in 2011 no more than 125 out of 193 member countries of the UN outlawed domestic violence (Turquet et al. 2011). This figure means that in more than a third of the member states, women have no legal protection against IPV, and men do not have to fear criminal prosecution when acting violently against their female partner. In the next section, we will present data on the extent to which prevalence rates of IPV against women differ between countries and regions, followed by a review of the evidence on culture-level, societal factors linked to these differences.

Variations in the Prevalence of Men's IPV Between Countries

The most recent comprehensive review of the global prevalence of IPV was presented by Devries et al. (2013). They collected evidence from 151 original population-based studies from 81 countries to assess the lifetime prevalence rate of women's experience of physical and sexual victimization by an intimate partner from the age of 15 years onward. Only women who had ever been in a relationship were included in the calculations. In addition to establishing an overall prevalence rate of 30%, the review yielded specific

information about rates in different regions of the world, as shown in Fig. 1.

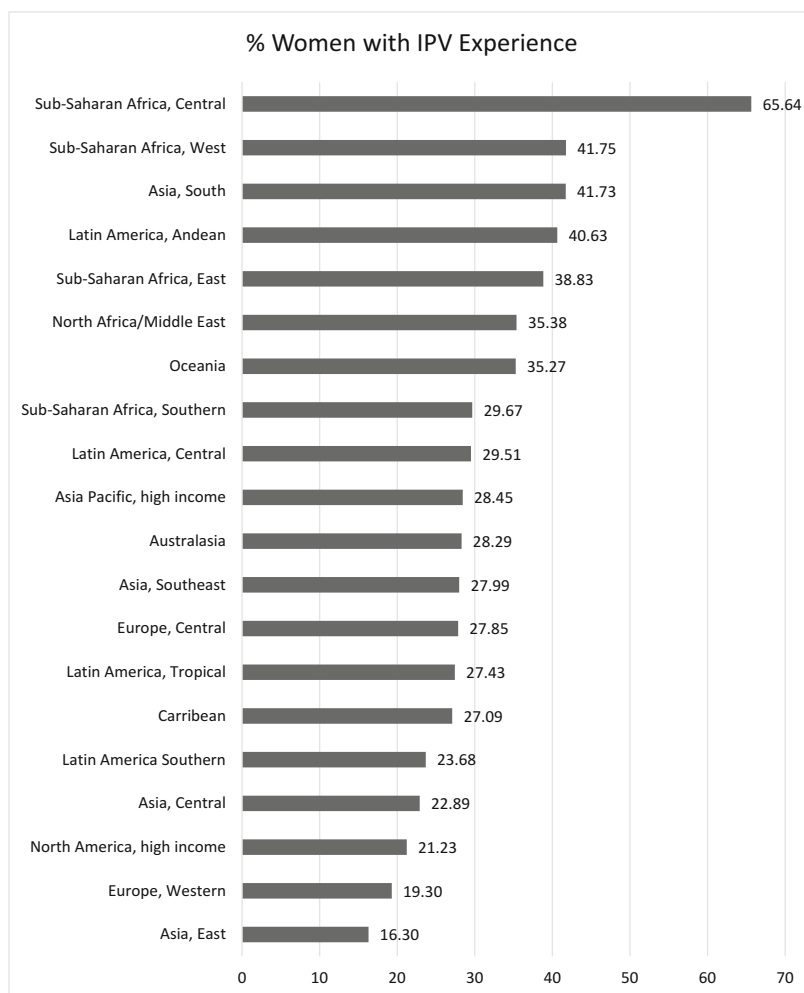
The review shows that prevalence rates of IPV victimization differ markedly between regions, with a difference of almost 40% between the lowest and the highest rates. It needs to be borne in mind that these figures are based on a large number of studies employing different definitions, designs, and methods, so part of the variability is likely to be due to methodological differences (see Krahé et al. 2005). Nevertheless, the figures clearly highlight the need to understand why women are at higher risk of experiencing IPV in some parts of the world than in others so that appropriate measure can be taken.

Looking at homicide as the most extreme form of IPV, a review of the evidence from 66 studies examined the proportion of killings committed by an intimate partner relative to the total number of killings (Stöckl et al. 2013). The results showed that almost 40% of all female homicide victims were killed by an intimate partner, whereas only 6% of killings of men were committed by an intimate partner. The proportion of intimate partner killings in the total number of homicides varied considerably between countries, ranging from about 15% to 60%.

Studies collecting primary data in several countries based on the same methodology also demonstrate substantial differences. A study with nearly 16,000 university students from 21 countries, who completed the Revised Conflict Tactics Scales (CTS2) as a measure of IPV, found rates of experiencing at least one act of physical assault by a dating partner in the last 12 months to range between 12% and 40%. The rates of sexual violence victimization ranged between 9% and 42% (Chan et al. 2008). A comparative study in 9 European countries with about 3,500 university students completing the same survey instrument in each country also revealed substantial differences in the prevalence of sexual violence victimization of female students by a male partner, with rates ranging between 11% and 33% (Krahé et al. 2015). In combination, empirical evidence clearly points to the role of cultural factors in the search for explanations of differences in the level of IPV.

Men's Violence Against Female Partners: The Role of Culture,

Fig. 1 Lifetime percentage of IPV victimization in ever-partnered women aged 15 or over in 20 regions comprising 81 countries (based on Devries et al. 2013)



The Role of Culture in Explaining Men's Violence Against Intimate Partners

Explanations of men's violent behavior against an intimate partner address the macro level of the culture in which they live, the micro level of dyadic interaction patterns between the partners, and the individual level of the aggressor. Although they can be distinguished for analytical purposes, these levels are closely interconnected because cultural norms and conditions also shape interactions within the couple relationship and the attitudes and behavior of individual perpetrators.

Culture-level theories consider causes of IPV that lie in the social structure and value systems of a culture, whereby culture can be a nation or a

particular social group defined by regional traditions, religious beliefs, or other aspects. A critical social-structural variable relevant to IPV is the extent to which a culture is characterized by a *patriarchal power hierarchy* that assigns men a superior status over women (Bartholomew et al. 2015). This power imbalance to the disadvantage of women is seen to permeate not only a wide range of public domains but also the private domain of intimate relationships. The shared view that men are entitled to wield power over women implies that men have the right to expect their female partners to fulfil their demands and expectations and to penalize them if they fail or refuse to do so. The unwillingness to acknowledge marital rape as a criminal offense, which is

still common in many parts of the world, also reflects the understanding that men acquire possession of women with marriage. Several indicators have been developed at a global scale to characterize cultures (mostly defined by national boundaries) in terms of gender equality or inequality. Examples are the Gender Inequality Index (GII) by the United Nations Development Programme, <http://hdr.undp.org/en/content/gender-inequality-index-gii>; the Social Institutions and Gender Index (SIGI) by the OECD, <https://www.genderindex.org/>; or the Gender Equality Index of the European Institute for Gender Equality (EIGE), <http://eige.europa.eu/gender-equality-index/about>.). These indices include access of women to higher education and health, representation of women in senior political positions or leading managerial positions, or entitlement to inheritance and other resources.

To provide empirical support for this line of explanation, studies have related country-level indicators of gender (in)equality to differences in IPV between countries, predicting a negative correlation between gender equality and IPV rates. Based on data from 44 countries representing almost 500,000 women, a significant association was found between women's physical or sexual IPV victimization in the past 12 months and the extent to which women's equal access to land, property, and other productive resources was restricted by law and practice compared to men (Heise and Kotsadam 2015). Moreover, these authors found a significant positive association between the collective acceptance of norms justifying wife beating and norms of male authority and rate of men's IPV across the included countries. These findings suggest that reducing the gender inequality in access to financial resources might be a successful way of strengthening women's independence from men, thereby decreasing their risk of IPV. Microfinance programs that give small-scale loans to women have been introduced in this vein, but systematic research on their effectiveness in reducing IPV has so far been limited and inconclusive (O'Malley and Burke 2017).

Research comparing victimization rates of women against those of men across cultures

further supports the role of gender inequality as a facilitating factor for men's IPV. A study including victimization rates in 16 countries showed that the less power women had in the respective country, the higher women's victimization rates were compared to those of men (Archer 2006).

The same analysis also revealed that women's IPV victimization rates went up compared to men's the more countries were at the collectivism end of Hofstede's (1980) dimension of individualism-collectivism. This dimension describes the extent to which a culture values community goals and ties higher than individual characteristics and autonomy. Because differentiations into ingroup and outgroup members are more relevant in collectivist cultures, it could be argued that intimate partners brought into a man's family are seen as outgroup members who are supposed to follow the family rules. The finding that the gap between rates of female relative to male victimization widens the more a country scores toward the collectivist end of the continuum is consistent with this line of reasoning (Archer 2006).

A further culture-level variable shown to relate to men's IPV perpetration is the emphasis on male honor and the rights granted to men for ensuring their female partners obey the rules of the honor code. This line of research originated in the United States and links higher rates of violence, especially IPV, to cultural differences between the northern states of the United States on the one side and the southern states as well as Latin America on the other. Specifically, the strong emphasis on honor in the southern states and Latin American led Vandello and Cohen (2003, 2008) to identify a "southern culture of honor" in which honor is a salient theme for organizing manhood and gender relations. Honor is defined by status and reputation and – when threatened – may legitimately be restored and defended through the use of violence. In honor cultures, men's standing is critically defined by their toughness, ability to protect their family and possession, and their partners' adherence to accepted standards of female decency. If men see their partner as violating the honor code, violence is legitimate and even imperative in an honor culture to preserve the integrity

of the men and their family. In several studies, individuals from honor cultures were found to be more accepting of men's IPV than those from non-honor cultures, indicating that cultural constructions of manhood and female decency may create a social climate that legitimizes IPV.

Gender inequality and constructions of manhood at the cultural level are the socially shared background that shapes the attitudes of individuals in the course of socialization. Attitudes about gender and violence, in turn, provide a basis for violent behavior toward an intimate partner. An analysis of 52 studies assessing individual attitudes relevant to IPV found that hostile sexism (negative attitudes about women; Glick and Fiske 1996) and the endorsement of traditional gender roles by both men and women were higher in countries with lower gender equality at the macro level. The same was true for men's approval of slapping a partner, whereas women's approval of slapping a partner was unrelated to IPV rates (Archer 2006). Using data from a nationally representative survey in 41 countries in Eastern Europe, Africa, Asia, Central and South America, and the Caribbean, Hayes and Boyd (2017) found that the higher the country-level justification of IPV, the more likely individual participants were to find physical violence justified in different scenarios.

These individual differences in attitudes, shaped by cultural context, play a significant role in understanding individual differences in the propensity to engage in IPV. In the multilevel analysis by Heise and Kotsadam (2015), higher individual endorsement of the belief that men's authority over women is legitimate was found to be related to an increased odds of experiencing IPV over and above the collective acceptance of this belief at the country level. Furthermore, the multilevel approach enabled the authors to show that individual-level variables had a differential impact on IPV risk depending on country-level variables: In countries with a high acceptance of IPV and men's authority over women, spending between 8 and 11 years in education showed a significant negative correlation with IPV, suggesting that education may reduce the risk of IPV. In countries low in acceptance of these

gender inequality norms, the association was nonsignificant.

Adopting a similar approach, a meta-analysis by Mallory et al. (2016) examined the impact of risk markers of IPV at the individual level on the probability of women's IPV victimization in three groups of countries: the United States, as a country ranking high on the individualism dimension as determined by Hofstede et al. (2010), individualist countries other than the United States, and collectivist countries. Of the 11 risk markers considered in their analysis, only 4 differed between the 3 groups of countries: Witnessing parental violence and experiencing emotional abuse in a relationship were more closely linked to IPV victimization in collectivist countries. Younger age and lower marital satisfaction were more closely linked to IPV victimization in the United States than in the other two groups. These findings show that culture and individual characteristics interact in predicting IPV.

Challenges to the Link Between Culture and IPV in the Age of Migration

The research reviewed in this article has provided ample evidence that men's violence against intimate partners, while being a worldwide problem, shows considerable variation between countries and cultural groups. The evidence discussed in this article has illustrated how differences in the way gender relations are organized at the macro level of cultures, such as gender equality, collectivist values, and concerns about honor, relate to differences in the scale of IPV and also shape the attitudes and behavior of individual perpetrators.

In a time that sees migration on a large scale, the evidence of close connections between cultural factors and individual attitudes and behavior relevant to IPV raises a pressing question for research and social politics alike: What happens when individuals socialized in a cultural context with a higher tolerance of gender inequality and IPV move to less tolerant cultures with more egalitarian value systems? How do societies cope with a clash of incompatible constructions of gender relations, including men's dominance

over women, and approval of IPV, and how do individuals moving into a new culture position themselves to the different social norms they encounter? What happens to power relations within couples if women adopt the egalitarian views and opportunities afforded to them in their host society, challenging their partners' traditional conceptualization of manhood?

Evidence suggest that the renegotiation and reevaluation of attitudes and behaviors related to gender roles and IPV that is required by couples in these circumstances may precipitate violent responses as a way of asserting masculinity (White and Satyen 2015). These challenges add to the other stressors involved in the acculturation process that may, in themselves, lower the threshold for IPV. Future studies of IPV among refugees and immigrants therefore need to examine reactions to the clash of norms and attitudes between the culture of origin and the host culture and their role in understanding IPV.

Outlook: A Gender-Inclusive Approach to the Study of IPV in its Cultural Context

In line with the focus of this contribution on contexts for men's aggression against women, only research considering men as perpetrators and women as victims of IPV was discussed. However, it is important to note that women also engage in IPV against male partners, as shown by a substantial body of research (Archer 2018; Swan et al. 2018), even though it has been suggested that women more often engage in reactive forms of self-defense than in proactive forms of coercive control. This research has been conducted almost exclusively in Western countries, leaving the role of cultural variables largely unaddressed. First evidence of the cross-gender impact of power equality comes from a study with university students from 20 countries and showed that male victimization rates were higher the higher social status of women was in the respective country (Hines 2007). However, a different pattern emerged in later studies including nine European countries, which found that male victimization rates were

lower the higher the gender equality in the domain of political participation (Krahé et al. 2015). Finally, it is increasingly recognized that IPV is also a problem in same-sex relationships, with some studies suggesting higher prevalence rates and a more negative impact than for heterosexual relationships (Messinger 2011; Gehring and Vaske 2017). Again, the vast majority of studies addressing the risk of IPV in sexual minorities comes from North America and Western Europe, and the fact that same-sex relationships are still prohibited in many parts of the world raises problems regarding the cross-cultural analysis of IPV in same-sex relationships.

In combination, these developments highlight the need to broaden the scope of our conceptualization of IPV, moving beyond a purely behavioral analysis of IPV to consider its underlying motivation and function, and to develop more comprehensive theoretical explanations that can accommodate both male and female IPV in heterosexual and same-sex relationships. Such explanations are vital to design effective forms of prevention and intervention to reduce IPV and the associated serious physical and mental health consequences in all victims regardless of gender and sexual orientation.

Cross-References

- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Men
- ▶ Men's Suspicions of Partner Infidelity and Women's Defection
- ▶ Sex Differences in Intimate Partner Violence
- ▶ Unique Patterns in the United States
- ▶ Violence to Control Women's Sexuality

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Menarche

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Synonyms

First “period”; First menstruation; Onset of menstruation

Definition

The initial onset of menstruation for a woman, usually occurring during early adolescence.

Introduction

Menarche, or the first menstruation, is a concrete developmental milestone that occurs suddenly and often unexpectedly. It is considered the culmination of pubertal events for young girls, though other gradual sex differentiation continues to occur throughout adolescence. Menarche represents a physiological transition since it establishes girls' reproductive capacity, yet it is also imbued with sociocultural significance and personal meaning. The timing of menarche is influenced by several genetic, biological, and

environmental factors, and much research has shown that both timing and preparation have an effect on girls' attitudes toward menarche.

Onset, Trends, and Timing of Menarche

Menarche is often the last and is considered the most climatic pubertal event for girls, occurring roughly 2 years after the beginning of other pubertal changes. Currently, in the United States, the average age of menarche is approximately 12.5 years, with a range of 10–14 years considered to be a “normal” age at which to reach menarche. Several studies have indicated that African American girls reach menarche up to 8 months earlier than White and Mexican American girls (Chumlea et al. 2003), while other studies have revealed that Latina girls reach menarche earlier than both White and African American girls (Obeidallah et al. 2000). However, most ethnic differences disappear when low SES, conceptualized as an environmental stressor leading to early puberty, is controlled for.

These average ages represent a significant decline over the past several centuries, where the age of menarche fell from 17 years in the mid-1800s to 13 years in the 1950s. Since the 1950s, the average age has continued to decline, but at a much slower, steadier rate, and with a greater increase in ethnic disparities noted above. It is posited that the drastic changes observed over the past century and a half are likely due to improvements in nutrition, sanitation, and treatment of infectious disease (Posner 2006). The slighter changes since the 1950s are thought to be due to continued changes in diet, leading to increased obesity, and earlier exposure to stressful environmental circumstances (Kaplowitz et al. 2001).

The exact triggering mechanism for menarche is unknown; however, the production and secretion of gonadotropin-releasing hormone (GnRH) by the hypothalamus is essential for the initiation of puberty more broadly. There are three widely accepted categories of influence on individual

differences in timing of menarche that interact in a complicated fashion: (1) heredity and genetics, (2) biological factors, and (3) environmental factors.

Heredity

Researchers have historically observed hereditary influence on menarcheal age through assessing correlations between mother and daughter age at menarche. Indeed, such studies have revealed small to moderate positive correlations, though critics have argued that shared environmental influences could account for the observance of such relationships (Graber et al. 1995). Studies seeking to identify particular genes influencing menarcheal age have not yielded conclusive results, indicating that specific genetic contributions remain unknown. However, twin studies also reveal a higher correlation for menarcheal age among monozygotic twins than dizygotic twins (Mendle et al. 2006), and thus, it is still widely accepted that genetics and heredity do account for at least *some* of the variability in menarcheal age (Karapanou and Papadimitriou 2010).

Biological Factors

There are two primary theories relating the triggering of menarche to physical growth. The skeletal growth hypothesis suggests that a girl must reach a particular level of musculoskeletal development in order to reproduce. Specifically, her pelvis must be large enough to bear children. Support for this theory arises from data indicating that most girls who have reached menarche have also achieved a pelvic diameter of at least 26.2 cm (Ellison 1982). The accumulated body fat hypothesis suggests that girls must reach a critical BMI and maintain a certain level of body fat in order to begin and continue menstruation as well as ovulation. It was originally developed by Frisch (1983), who proposed that girls must be capable of sustaining their own health prior to attempting to bear children. This hypothesis suggests that the link between body fat and the initiation of menarche is the hormone leptin. Leptin is largely produced by brown adipose (fat) tissue, and it acts as a signal telling the

hypothalamus to begin secreting GnRH once this critical level of body fat has been accumulated (Allison and Hyde 2013). Support for this theory arises from several indicators, including higher leptin levels in children with higher BMIs, delayed menarche in competitive athletes, and the cessation of menstruation in competitive athletes and anorectics who have a low BMI (Graber et al. 1995).

Environmental Factors

While it has long been accepted that genetic and biological factors affect menarcheal timing, other researchers have proposed more inclusive models taking into consideration the interaction of environmental influences and biology. Perhaps the most popularized and controversial model investigates the role of father absence (sometimes conceptualized as family disruption) on early puberty. Father, but not mother, absence has been consistently associated with earlier menarche; however, the exact mechanisms and reasons for this association have been contested (Moffitt et al. 1992). It is posited by sociobiological theories that father absence triggers early puberty in girls as an adaptive response to a stressful environment, where girls mature earlier in preparation for earlier reproduction in order to ensure the continuation of their gene pool (Belsky et al. 1991; Posner 2006). Paternal investment theory further suggests that girls encode information from their early environments into mechanisms that will influence their later sexual development. Girls growing up in a father-absent home recognize that paternal investment is not necessary for reproduction, and they are hypothesized to mature more quickly, begin sexual activity earlier, and orient to more disruptive child-rearing environments, i.e., unstable relationships with male partners. Some have argued that environmental confounds such as weight, nutrition, and stressful life situations or events have not been controlled for in investigations into the role of father absence in early menarche (Posner 2006). Indeed, a strong relationship between low SES, often conflated with father absence, and early puberty is continuously reaffirmed (e.g., Allison and Hyde 2013). Thus, it is difficult to determine whether it is

father absence per se or a stressful rearing environment more broadly that is leading to early menarche.

Psychosocial and Physiological Effects of Menarche

While other pubertal changes such as breast and pubic hair growth occur gradually and continuously throughout pre- and early-adolescence, menarche is unique in that it occurs suddenly and often unexpectedly. Indeed, many girls report feeling shocked, surprised, or confused at menarche, and this reaction can be magnified in particular among girls who are considered to be early maturers. The literature defines early maturers according to two different metrics: objective and subjective timing. Furthermore, there is not exact agreement as to what constitutes objective early menarche, though most define it as occurring before the age of 11 (Nnoaham et al. 2012). Subjective timing refers to the perception of being “on time” with one’s peers and is perhaps more important when considering the psychological ramifications of early menarche and puberty more broadly (Stubbs 2008).

Early objective timing has implications for a girl’s level of preparedness for menarche, both in terms of knowledge and developmental stage. It has been repeatedly reported in the literature that more preparation for and knowledge of menarche is associated with fewer negative attitudes and less overall worry about menstruation (Cooper and Koch 2007; Stubbs 2008). If girls reach menarche objectively early, then they are at risk for not having adequate preparation or knowledge, missing the education occurring in schools, from family members such as mothers or older sisters, and from peers. Furthermore, it has also been hypothesized that early menarche can lead to a gap between physical maturity and the accompanying psychosocial maturity necessary for facing the challenges and stress brought on by these developments. Peers and adults alike may attribute greater psychosocial maturity and responsibility to physically mature girls, suggesting that they meet new norms and expectations for their

behavior before they are emotionally or cognitively ready (Mendle et al. 2006).

Indeed, there has been a great deal of research suggesting that early maturers are at increased risk for developing a negative body image, disordered eating, and depression (Stice et al. 2001). Explanations for these associations are complex and vary by study, but most ascribe meaning to the changes in social context that accompany menstruation. Girls experiencing early menarche also experience outwardly visible changes to their bodies such as breast development, growth of the musculoskeletal system, and increases in adipose tissue. Experiencing these changes prior to one’s peers can be isolating and alienating and can increase negative social pressure. Early maturing girls often seek out peers who appear outwardly similar to them but are much older in chronological age (Natsuaki et al. 2011), putting them at risk for engaging in behaviors they are not psychologically prepared for from a developmental perspective. It has also been theorized that early increases in fat tissue can make it difficult for girls to fit western cultural standards and ideals for feminine appearance, creating a risk for negative body image early in life. Heightened negative body image is then thought to contribute to eating disordered behavior as girls try to minimize their dissatisfaction with their bodies through engaging in weight-controlling behaviors such as dieting and purging (Stice et al. 2001).

Attitudes Toward Menarche

In general, researchers have observed girls’ attitudes toward and women’s recollections of menarche to be largely negative across socio-cultural contexts. Many girls report feeling shame, embarrassment, confusion, and fear upon seeing menstrual blood for the first time (Lee 2008; Stubbs 2008). Recent studies have revealed that girls in the USA may be meeting menarche with more ambivalence than previously observed, in part as a result of the emergence of more girls and women who are challenging predominantly negative social scripts about menstruation and the body (Lee 2008).

Investigations into how social context and identities might affect attitudes toward menarche have revealed interesting and at times mixed results. While most studies report more negative reactions among black and working-class participants (Cooper and Koch 2007), Martin (1987) observed that her sample of black, working-class participants reported experiencing menarche simply as a life change to be dealt with in private rather than a hygienic crisis. Investigations into Mexican women's recollections of menarche indicate that many reacted with more ambivalence and confusion, though some older generations who knew of menarche prior to its onset recalled positive emotions (Marvan et al. 2006). Fahs (2011) has observed that lesbian and bisexual women recount more positive experiences and the provision of support around menstruation, potentially leading to the transmission of more positive emotions and attitudes among these communities of women.

Conclusion

Menarche is an important event from a biological and social perspective as it prepares a girl's body for reproduction and carries sociocultural meaning. A complex interaction of genetic, biological, and environmental factors contributes to menarcheal age, and a girl's age at menarche can have significant developmental implications, particularly if it occurs early. Societal attitudes toward menarche remain largely negative, though girls have begun to report reacting to it with more ambivalence. Further investigating factors that can trigger early menarche and lead to the maintenance of negative attitudes toward it is imperative as we seek to aid adolescents in their transition to adulthood.

Cross-References

- [Developmental Milestones](#)
- [Puberty in Girls](#)
- [Sexual and Reproductive Development](#)

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Mendel's Experiments

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Synonyms

Mendel's laws; Mendelian inheritance; Plant hybridization

Definition

It is well known that Charles Darwin published his theory of evolution in his 1859 book *On the Origin of Species by Means of Natural Selection*. One of the fundamental problems with Darwinism was the absence of an explanatory mechanism of inheritance that could account for morphological change. In 1868, Darwin would explain the mechanism in his book *The Variation of Plants and Animals under Domestication*. He called it theory of pangenesis. Around the same time, the monk Gregor Mendel

was working on a similar line of research. He was studying the inheritance of characters by experimenting on pea hybrids. Mendel, who published his results in 1866, asserted that resolving the inheritance problem was fundamental to understand the evolutionary history of organic forms. Mendel's research revolutionized the concept of inheritance, but it was disregarded by his contemporaries. However, by 1900, the laws of Mendelian inheritance would be rediscovered, leading to the birth of the field of genetics. How did he do it?

Introduction

In 1843, Johann Mendel (Gregor would become his monastic name) joined, as a novice, the Augustinian Abbey of Saint Thomas, which is in the present-day city of Brno in the Czech Republic. He was 21 years old. Young and without resources, he became a friar to continue his education. First things first, he had to be ordained as a priest, then he could follow the Augustinian motto: through knowledge to wisdom. At the University of Vienna, he studied physics, chemistry, mathematics, zoology, and botany. He had good teachers, such as the experimental physicist Christian Doppler, the mathematician Andreas Ettinghausen, the chemist Josef Redtenbacher, and in particular, the brilliant botanist Franz Unger. The last was an expert in plant physiology and a proponent of the cell theory. Gregor did not forget his teachings on plant fertilization. In short, in Vienna, he learned how to use experimental and quantitative methods in biology.

In 1853, Mendel returns to the monastery. Encouraged by the abbot Franz Cyrill Napp, he devotes himself to horticulture. After 3 years, Brother Gregor begins experimenting with peas. In the spring, he prepares the ground to pick the harvest in summer. During flowering, he manipulates the pistil, depositing previously selected pollen. He studied floral arrangement, plant size, and color and shape of pods and seeds. He examined in total around 30,000 samples. On the afternoon of February 8, 1865, Mendel presents the results of his research at the Brno Natural History Society. By March 8, he would complete his task. He

spoke of the uniformity of the first hybrid generation, the segregation of characters in the second generation, and the independent transmission of characters. The lectures were dry. The audience did not understand Mendel's principles. It was on a rare theme with a mathematical format that obscured the presentation. The work was published in the Society's journal in 1866. Two years later, he was elevated to abbot. He dedicated himself to the governing of the monastery, and as a result, his scientific activity declined. However, he continued to experiment until the 1870s, particularly on plants of the genus *Hieracium* (common name hawkweed). The abbot died suddenly on Three Kings' Day (January 6) in 1884 as he was busily attending to his religious work.

On Tuesday, May 8, 1900, the renowned English biologist William Bateson heads to the Liverpool Royal Horticultural Society to give a lecture on the problems of inheritance in horticulture. He travels by train. During the journey, he reads Mendel's article. By the time that he arrives at Liverpool Street station, his concept of inheritance has changed. Bateson understood the positive significance that Mendel's theory had on his model of discontinuous evolution. He accepted it immediately by disseminating and duplicating the approach (1900, 1902, 1909). Within a few years, a new knowledge, which Bateson called genetics, was formed. Mendel would be its patriarch (Bowler 1989; Henig 2000).

The Experiments

The pea, *Pisum sativum*, was a common species studied by well-known horticulturists such as Thomas Knight, John Goss, Alexander Seton, and Carl Gärtner. It was an ideal plant due to its simple cultivation, the presence of constant and recognizable characters, and the existence of a particular floral arrangement that inhibited pollen contamination. Mendel's selection was not novel. Neither were his observations. The dominance, morphological constancy, and segregation of characters were previously known phenomena. Mendel's originality laid in his differing

interpretation of the observations, which were underlined by his statistical analysis of phenotype and the subsequent conceptual development of genotype.

In 1856, Mendel began his experiments on pea hybrids. The objective is to study how different morphological traits are inherited. He obtained 34 varieties, which he experimented on for over 2 years to determine typological constancy. He selected 22 conserved and invariants lines, and differentiated seven pairs of opposing characters: (1) the round or wrinkled shape of the seeds; (2) the yellow or green color of the seeds; (3) the grey or white color of the seed coat; (4) the smooth or ridged shape of the mature pods; (5) the green or yellow color of the immature pods; (6) the axial or terminal arrangement of the flowers (on the stem or at the end); and (7) the height of the plant (tall or short). He established seven groups of experiments corresponding to each morphological pair. By means of artificial fertilization, he performed reciprocal crosses. That is, in successive fertilizations, he alternated each plant as the egg or the pollen donor. In the first hybrid generation (F1), the individuals are morphologically constant, expressing only one of the characters (the dominant one). The other one (recessive) remains latent. For example, the round seed shape is dominant over the wrinkled one. The phenomenon occurs regardless of whether the dominant trait belongs to the pollen or to the egg donor plant. Moreover, Mendel did not observe intermediate forms. Crossing F1 individuals resulted in the second generation (F2), which showed a dominant to recessive phenotypic ratio of 3:1. Subsequent crosses of F2 individuals determined the actual proportions corresponding to the Mendelian expression $A:2A:a$, that is, a pure dominant individual (homozygous) to two dominant hybrids (heterozygous) to a pure recessive individual (homozygous). The second part of the experiment consisted of crossing plants that carried different traits for the various characters. The results coincided as proven by the independent segregation of the characters. Mendel repeated the study with other plant species to verify the universal value of the laws observed

in *Pisum*. In particular, he used plants of the genus *Phaseolus*: the beans. The hybrids of *Ph. vulgaris* and *Ph. nanus* fully reflected the expected results. However, with *Ph. multiflorus*, the color of the flowers and seeds of the F1 generation were different: they did not show dominance and were distinct from the parental traits. Mendel presumed that tonality in *Ph. multiflorus* was due to the combination of uniformly expressed autonomous colors. In the hybrid, each color was freely combining to modify the coloration. He solved the dilemma by assuming that the anomaly reflected a pea-like combinatorial dominance/recessiveness by interpreting each color as an independent trait.

After publishing the results, Mendel continued his experimental work by collaborating with Carl Nägeli, a prestigious Swiss botanist and a professor at the University of Munich. The professor rejected the validity of Mendel's theory of inheritance but agreed to send him *Hieracium* plants and seeds for experimentation. In the 1869 proceedings of the Brno Natural History Society, Mendel presented his first findings. Mendel had failed. The hybrids did not replicate the hereditary process of the peas. Why? Nowadays, we know the reason: the plant usually reproduces asexually (apomixis). The seed, therefore, has an exclusive maternal origin. As a result, the offspring replicate the mother plant. *Hieracium* is an impossible example to study the dominance and segregation of characters. Nägeli had been working with *Hieracium* for a long time and knew the experimental difficulties of the plant. Was he intentionally seeking to impede Mendel? Suspicion is admissible.

For one reason or another, Mendelian experiments provoked controversy. However, the case of Ronald Fisher is exceptional. In 1936, the English geneticist published an article in the journal *Annals of Science* entitled *Has Mendel's work been rediscovered?* Fisher had thoroughly analyzed Mendel's experimental structure and found that the observed ratios were higher than expected according to sampling theory. Based on this fact, Fisher argued that much of the experimental decisions taken by Mendel were intelligible only if the theory had been formulated a priori. That is,

Mendel's intention would have been to demonstrate experimentally the validity of a theory that was elaborated in the abstract. Did the monk arrange the experiments to prove it? During the first decades of the twentieth century, biologists such as Carl Correns, Erich Tschermak, William Bateson, and Robert Lock repeated the experiments (Johannsen 1926). To a greater or lesser extent, the results all corroborated Mendel's data – Tschermak even obtained more precise percentages. Do these results invalidate Fisher's criticism? Absolutely not. They say nothing about Mendel's intention, just that his experimental method was correct. As the American geneticist Alfred Sturtevant argued, we can attribute the stochastic event to different fortuitous but not completely satisfactory facts (1965). There is only one irrefutable answer: *Mendel was right*. He made a big step in the right direction.

Biological Mechanism

With the inheritance problem solved, the next task was to explain the biological mechanism underlying it. Mendel interpreted it as a simple division process typical of cells in the ovary and pollen. Traits for each character would be determined by individual factors located in the gametes. These factors come together during fertilization, giving the embryo several of the traits of each character whose morphological expression follows the principle of dominance and recessiveness. Gametogenesis, or the formation of gametes, was a crucial process that again separated the factors that united during fertilization. In this simple way, all of the individual morphological potential is again available to the next generation. Implicitly, from these ideas developed the modern concepts of gene, allele, phenotype, and genotype, all of which are, necessarily, rooted in cell theory. Gametes would be the cells characterized by their particular hereditary function, defining two clearly differentiated cell lines: germline and somatic (Galera 2000).

Under the Mendelian approach, hybrids represent reproductive variability. Logically, they are

the cause of speciation. How does this happen? Mendel supported his hypothesis based on the experiments on hybrid stability developed mainly by Carl Gortner, who worked on plants of the genera *Aquilegia*, *Lavatera*, *Geum*, *Dianthus*, and *Oenothera*. Speciation occurs when the hybrid form becomes stable by invariably transmitting its typology to all offspring. A new species then appears. What is the biological meaning? Mendel imagines that stabilized hybrids are formed by the fusion of complementary gametes whose union is permanent. In other words, fertilization brings together the parental traits into a new factor that has its own morphological value that is inseparable during gametogenesis. Individuals, then, only produce gametes of the new hybrid type. If the gametes are not complementary, the hybrid has a transient value, and the parental traits will segregate normally and reappear in subsequent generations (Galera 2000).

Conclusion

Mendel solved the problem of inheritance in the context of the Darwinian theory of evolution. He did so by applying new ideas to known facts and using the experimental and quantitative method. The results are known as Mendel's laws, which form the basis of modern genetics. The evolutionary meaning of these laws is clear: cross fertilization and hybridization manifest an unequivocal tendency to preserve parental types. It is, therefore, an inadequate mechanism to govern the evolution of species under the terms proposed by Darwin. According to Mendelian ideology, chance is responsible for combining parental characters and fixing them in hybrids as pure species, and speciation is a discontinuous biological phenomenon resulting from reproduction. Mendel's laws represent an alternative evolutionary standard, directly linked to the neo-Darwinism of August Weismann and included by Hugo de Vries in his theory of mutation. Certainly, William Bateson had gave reasons to think that evolutionism would have had a different history if Charles

Darwin had been familiar with Mendel's work (1909). It could be that Bateson was wrong, since probably Darwin knew the monk's research (Vorzimmer 1968).

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Mendel's Laws

► Mendel's Experiments

Mendelian Inheritance

► Mendel's Experiments

Menopause

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Synonyms

Climacterium; End of Reproductive Ability; Post-reproductive Life Span

Definition

The biological definition of menopause refers to the irreversible loss of the physiological capacity to produce offspring due to intrinsic biological factors. The term menopause is colloquially used as synonym for the post-reproductive life span in females of all species and covers the life period between the end of reproductive ability and the end of life.

Introduction

Menopause is quite the opposite of menarche. In its broadest sense it refers to the time period when female's ability to reproduce (to bear a child) stops permanently and females no longer have menstrual periods and can no longer become pregnant. The ability to bear children gradually declines throughout a female's reproductive life. This process is essentially caused by a decreased estrogen production of the ovaries. Even though the transition to menopause shows accessory symptoms like hot flashes, mood changes, or an increase in heart diseases, it is a physiological and natural change that concerns all females across all species. When the post-reproductive life span of human females is compared to most other species something different and unique is revealed; women exhibit a very long post-reproductive life span whereas most animals reproduce almost until they die. Even if the proximal causes of menopause are well understood the evolutionary

(ultimate) causes remain still unclear and lead scientists to investigate finding possible answers to the question; why do women go through menopause at an age long before other body functions senesce? To date, some possible explanations to the evolution of menopause exist from which I summarized the most common in the following entry.

The Evolution of Menopause in Human Females

Evolutionary theories predict that selection should operate against living beyond the age of reproduction. Therefore, the observable decline in women's reproductive ability long before end of life seems puzzling. The reproductive ability (reproductive life span) of human females ends long before other body functions senesce (including for example cardiac function, breathing capacity, renal plasma flow, and vital capacity) and that makes – with just a few exceptions – human beings unique. The reproductive ability of women starts with the menarche, about the age of 15 years, and ends with the menopause, between the ages of 40 and 60 years (see Morabia and Constanza 1998; Gordon and Laufer 2005). Menarche and menopause are therefore the two major occurrences in women's reproductive life span due to the fact that they mark the beginning and the end of a woman's reproductive life span. The 10–15 years before menopause are characterized by declining fertility. Consequently, a human female's reproductive life span is compressed into only approximately 20 years of a longer (unfertile) biological life span whereas most other placental mammals (exempt from some primates) retain their fertility almost to the end of their life span (Pavelka and Fedigan 1991; Caro et al. 1995). Thus, compared to other species, human females experience a dramatic loss in ovarian function and subsequent menopause around the age of 50 years and they additionally spend a significant longer time of their life in an infertile state. The proximate cause of this loss of fertility is the cessation of ovulation attended by hormonal

changes in the neuroendocrine system and the advanced depletion of ovarian follicles (follicular depletion) with increasing age.

In most species such a prolonged post-reproductive life span is not observable and females die soon after the last reproductive event, which also demonstrates that a prolonged post-reproductive life span is normally rare. In general, the post-reproductive life period lasts only about 10% of the total life span (i.e., Jones 1975). In addition to some species like elephants, tortoises, and whales, females also experience menopause between the ages of 30 and 40 years, but after menopause their life span is with nearly 14 years, substantially shorter than the remaining time of humans (i.e., Marsh and Kasuya 1984). As a function of general senescence, a decline in age-specific fertility in later life is although common throughout all species, but a significantly prolonged post-reproductive life span as it is the case in human females seems unique. Therefore, menopause is a synonym for a prolonged post-reproductive life span that comprises the period of life between the end of fertility and the end of life (for a review see Levitis and Bingaman Lackey 2011). But why does human female fertility end up by menopause at an age long before general senescence makes gestations biologically impossible?

If menopause can be evolutionary explained in terms of an adaptation, it is necessary that any possible fitness advantages that come along with a shortened reproductive life span outperform any possible disadvantages. Evolutionary psychologists propose that menopause like other observable complex designed characteristics of individuals is, based on the Darwinian logic, the result of natural selection and can be considered as an adaptation. Darwin suggested that individuals should end up with physical and behavioral characteristics that allow them to perform well in the struggle of life in terms of competing with their rivals, finding food, avoiding predators, and, of course, finding a mate. Evolution therefore should have favored ancestors displaying these characteristics that ensure survival and reproduction and in return not allow extravagances or waste. An

essential test for the assumption that menopause is an adaptation shaped throughout evolution could be that it makes quantitative sense and results indeed in increased fitness (higher reproductive success).

It is also important to note that relative to the expected life span a shorter reproductive life span is only characteristic and observable for women, whereas male fertility remains high until the late fifties or early sixties (El-Faedy and Bean 1987; Hill and Hurtado 1991; Irons 1979). Men's reproductive ability additionally does not show a significant decrease up to other body functions also begin to senesce (i.e., Goldman and Montgomery 1989), and the estimated risk of reproductive cessation due to biological causes are also very different between women and men. In contrast to women, men's infertility (impotence) rises very gradually after the age of 50 years, whereas women's infertility rises very sharply between the ages of 40 and 50 years (i.e., Wood 1994).

Physiology of Menopause

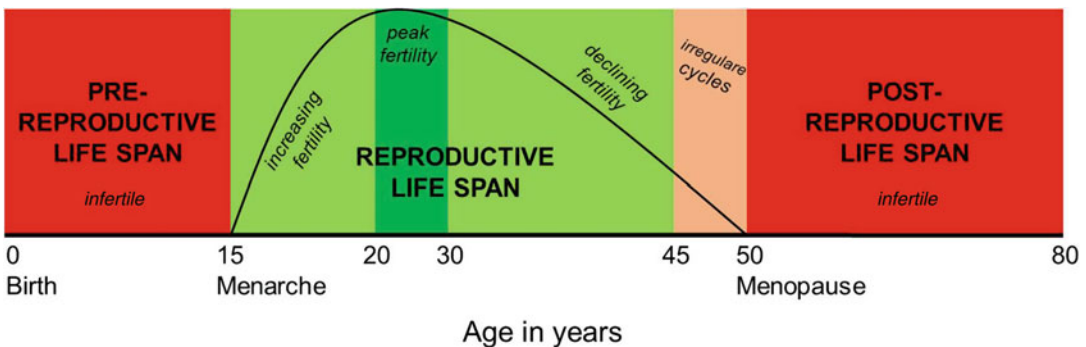
Physiologically, menopause is also known as the climacteric and defined as the permanent absence of menses due to the ever-decreasing number of viable oocytes that are obligatory to maintain the hormonal cycle of normal female reproduction (Leidy 1994; Utian 2004). Human females produce their whole oocytes (approximately seven millions) they will have throughout life span already during the fifth month of gestation. A phenomenon that is only observable in female birds and female mammals. At birth the number of oocytes (follicles) is reduced to two million and declines furthermore to only 400,000 of the originally produced oocytes until the age of puberty. Approximately 1,000 oocytes remain at the onset of menopause (i.e., Faddy and Gosden 1996). This reduction of oocytes is caused by a programmed process of cell death induced by hormone withdrawal and is known as atresia (i.e., Gosden and Spears 1997). In the western world menopause typically occurs around the average age of 50 years and is medically defined as the absence of any vaginal bleeding for at least 12 consecutive months caused by the decrease in

hormone production by the ovaries. The transition from the reproductive life span to the post-reproductive life span is a natural change and not (usually) a disease or disorder induced by the natural depletion of the limited amount of oocytes (ovarian reserve), and associated with the natural occurring aging process (Fig. 1).

The process of ovarian aging (reproductive aging) is dominated by a gradual decrease in quantity and quality of the oocytes within the ovarian cortex and involves endocrine changes. Natural fertility gradually decreases from the mean age of 30 years onward because of the ongoing reduction of follicle numbers caused by ovulation and atresia. The first subtle clinical signs of the advancement of reproductive aging are the onset of cycle irregularities as insufficient availability of follicles leads to prolonged or shortened intervals of menstrual cycles and missed periods. The onset of this menopausal transition period (the period encompassing several years before the final menstrual cycle) occurs on average at the age of 46 years, with a range of 34–54 years. The main causes of the irregular cycles, and therefore the ongoing loss of reproductive ability, are an increase of the two circulating hormones: follicle-stimulating hormone (FSH) and luteinizing hormone (LH), due to the reduction of estrogen producing oocytes and follicles that are normally responding to these hormones. Menstrual cycles persistently become more and more irregular, varying in length from cycle to cycle and complete cycles were skipped.

Periods of amenorrhea (absence of menstrual cycles) of 60 or more days occur. Ultimately, the final cessation of menses (last menstrual cycle followed by 12 consecutive month of amenorrhea (onset of menopause) occurs at an average age of 51 years with a range of variation between age of 40 and 60 years. Even though a small number of follicles remain and estrogen continues to be produced (after menopause) in other tissues, like ovaries and fat tissues, this substantial smaller amount is not sufficient enough to maintain a women's reproductive ability.

Factors possibly affecting the age variations of onset of menopause are until now poorly understood. However, it has been suggested that environmental factors as well as lifestyle factors such as the use of oral contraceptives, parity, and smoking are possibly related to the age of onset. Tobacco smoking for example has been identified to advance the onset of menopause by about 2 years. Additionally, there is little information on possible genetic influences on the timing of menopause as positive correlations between age of mothers and daughters and also between sisters have been found (Murabito et al. 2005). To get further knowledge on the factors that affect the age of onset of menopause is also important from a medical point of view, as it has been found that early menopause is associated with a higher risk of cardiovascular diseases, osteoporosis, and ovarian cancer, and later menopause is attended by a higher probability to come down with endometrial and breast cancer.



Menopause, Fig. 1 Schematic representation of a female reproductive life span

Possible Explanations Why Menopause Has Evolved

Regardless of the precise mechanism, evolutionary theory generally predicts that there should be no selection for living beyond reproductive capacity (Williams 1957; Hamilton 1966). The fact that human females show a prolonged post-reproductive lifespan indicates an evolutionary dilemma and makes possible explanations of menopause somewhat confusing. If natural selection favors those individuals who leave the highest number of viable offspring, for what reason selection has not simply favored ancestors with higher numbers of initial oocytes or those with a slower rate of oocyte degradation or some other mechanism that would prolong reproductive ability instead of prolong reproductive inability? To date, many possible approaches exist about how and why menopause (prolonged post-reproductive life span) has evolved and the evidences are mixed. The two most common proposed hypotheses for the origin of menopause are (i) a change in investment in grandchildren rather than in further own children and (ii) a physiological trade-off between early fecundity and increased longevity. In the following sections you can find a summary of these two theoretical approaches, which perhaps can explain the origin of a prolonged post-reproductive life span in human females, termed menopause.

The Grandmother Hypothesis

The grandmother hypothesis is currently one of the most popular explanations for the evolution of menopause, which suggests menopause as an adaptation and refers to the increased inclusive fitness theory (Williams 1957; Hamilton 1966). It is known that being fertile until the end of life would not be beneficial because maternal risks increase with age. On the other hand, it is unknown whether a woman can gain their fitness (reproductive success) by extending their post-reproductive life span (Williams 1957). Thus, the grandmother hypothesis predicts that post-reproductive life span evolved because females can gain greater fitness by increasing the reproductive success of their own offspring (assisting their children to reproduce successfully) than by

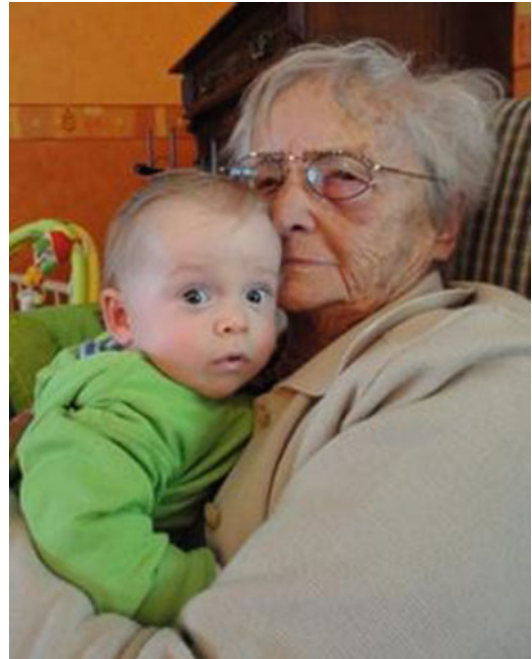
continuing to reproduce themselves (Hawkes et al. 1998; Hawkes 2004). From then on, the benefit comes from increasing the reproductive success of their adult children and the survival of their grandchildren. In the animal kingdom this kind of support of post-reproductive “grandmothers” is mostly uncommon. Previous research on humans provides evidence that post-reproductive mothers can benefit from the reproductive output of their own offspring even though it has not been possible yet to test, whether prolonged post-reproductive longevity indeed can be associated with a higher number of grandchildren, because data covering the complete reproductive histories of several generations are related to the longevity of humans, are difficult to collect, and thus scarce. Most support for the grandmother hypothesis is based on empirical, multigenerational data sets (historical church registers) where all births, marriages, and deaths of each parish have been listed. Parishioners lived in historical rural communities during the eighteenth and nineteenth centuries (e.g., Lahdenperä et al. 2004) or in hunter-gatherer societies (e.g., Sear et al. 2000), where grandparents are known to be a significant part of the family by living in the same household, and together with at least one of their children plus grandchildren. These data sets show that grandparents assist their children by transferring knowledge, by giving a hand in their domestic tasks, and by supporting in child care, which all increase the nutrition and survival of the grandchildren. All are tasks that are known to positively affect the hypothesized offspring’s reproductive success.

Lahdenperä et al. (2004) investigated the fitness benefit effect of a post-reproductive life span by recording the survival and lifetime reproductive details of women (e.g., the number of marriages, number of children and grandchildren, age at first birth, inter-birth intervals, and the age of death). They additionally used this information and tested possible effects of the presence or absence of a post-reproductive mother (grandmother) on the reproductive success of all her children (survival probability of grandchildren), which was embodied by the number of grandchildren reaching minimum the age of 15 years. The results show that the length

of a women's post-reproductive life span as well as the presence of a grandmother have a significant positive effect on the number of grandchildren. Both, sons and daughters, raised more children to adulthood (age of 15 years) when a grandmother was present compared to those families, where a grandmother was absent or died earlier. The presence of a grandmother seems to affect the survival of her grandchildren positively and thus a prolonged post-reproductive life span enhances a women's reproductive success (direct and indirect fitness). Further support is derived from studies that focused on family structures of some traditional societies like the Hadza (ethnic group in Tanzania), the !Kung (ethnic groups in Namibia, Botswana, and Angola), and the Ifaluk (Polynesian ethnic group). In these traditional societies, daughters of post-reproductive women (grandmothers), who provide material goods and other services like helping in child care, raise healthier children compared to those women without such assistance (e.g., Hawkes et al. 1989). The period of time grandmothers can spend helping additionally increases significantly with the age beyond menopause, and grandchildren of older grandmothers show a higher weight and a better health status compared to those with younger (or absent) grandmothers. These findings support the theory that grandmothers contribute to their own (inclusive) fitness by assisting their daughters and sons in raising their own children successfully (Fig. 2).

The By-Product Hypothesis: A Physiological Trade-Off Between Early Fecundity and Longevity

As mentioned before, to understand the evolutionary origin and significance of human menopause has engaged anthropologists and evolutionary biologists for decades. From a Darwinian perspective, natural selection would favor females who become infertile many years before death if offspring requires exceptional duration and intensity of parental care, as is the case with humans. Thus, menopause is an adaptive consequence of natural selection and a solution to the trade-off between investigating in additional offspring or in already existing offspring and their children (grandmother hypothesis). But the grandmother hypothesis seems to be inconsistent with some aspects of



Menopause, Fig. 2 Grandmother providing assistance

the theory about the evolution of aging which leads researchers to the assumption that menopause is rather an artifact of a relatively recent increase in human life span.

This, nonadaptive (nonfunctional) approach for the origin of menopause based on the assumption that menopause has never been directly selected and is not a direct consequence of biological selection for reproductive cessations (e.g., Gosden and Faddy 1998). A better development of health care systems, for example, as well as environmental protection of the contemporary world, improved nutrition, and hygiene, permits women to live beyond the supply of primary oocytes, and thus experience menopause. Adaptations that reduce extrinsic mortality can be generally associated with increased longevity. This idea is supported to some extent by archaeological data on estimated age distributions of skeletal remains and from studies showing that mean life expectancy at birth was close to 40 years in pre-industrial and hunter-gatherer societies. In this context, menopause is seen as a consequence of the increasing life span of humans caused by the industrialization. Thus, as a consequence of the

modernization and the medical progress, menopause seems to be a purely human phenomenon because they are able to live longer after the life period of reproductive ability. But why have these better conditions not affected the reproductive functions (reproductive senescence) in a similar way? According to the life-history theory, increased longevity should come at the cost of reduced fertility. In this view, menopause may represent a trade-off between reproduction later in life, when fertility is naturally lower and birth defects are higher, in favor of some other characteristic that enhances survival and reproduction at an earlier age (e.g., Weiss 1981). Consequently, menopause is considered as a product of antagonistic pleiotropy, favoring early fertility at the cost of late fertility. The antagonistic pleiotropy hypothesis was primarily proposed as an evolutionary explanation for senescence in general. Antagonistic pleiotropy is the phenomenon where one gene controls for more than one phenotypic characteristic in an organism where at least one of these characteristics is beneficial to the organism's fitness and one is detrimental to the organism's fitness. It has been suggested that a gene caused both, increased reproduction in early life and aging in later life, than senescence would be adaptive in evolution.

The Mother Hypothesis

The fact that human females show a gradual decrease in survival and fecundity rates with advancing age (senescence) leads to the assumption that there is probably a close relationship between reproductive fitness and rates of aging and diseases associated with aging. In this context, Williams (1957) developed a further adaptive theory, the "mother hypothesis," to explain the origin of menopause. He proposed that when offspring fitness depends on maternal care and when the risk of maternal and offspring mortality increases with age, then it is more advantageous to stop reproduction to maximize the investment in already born offspring than to continue reproduction with a higher risk of death. The mother hypothesis is supported by the extreme child dependency on adult care of human infants and

the increasing risk of maternal mortality with increasing age. Compared to offspring's of chimpanzees or gorillas, the human infant is proportionally to the mother's weight (on a relative scale) comparatively enormous, which raises in humans the risk of death during childbirth (maternal mortality). Relatively, compared to other species human infants are moreover unusually early born (premature with respect to completion of brain growth and development) and remain highly dependent for extended periods. Infant mortality is high and the onset of puberty occurs late in life. Additionally, child bearing is dangerous and parental care is exhausting and longsome and infant's survival is unlikely if their mother died during childbirth or soon after. This is supported by studies that showed that maternal care significantly influences the change of child survival. The death of a mother, not only soon after birth but also during late childhood and also to prior child's, compromises her child's survival. It is additionally well known that the risk of maternal mortality increases rapidly after the age of 35 years, regardless whether access to modern medicine is available or not. It is also highly supported that the likelihood and frequency of chromosomal abnormalities in new-born children also increase with increasing maternal age.

Regarding the mother hypothesis, menopause occurs because reproductive cessation allows mothers to increase their fitness by investigating on the one hand in survival of immature children and on the other hand in the fertility of their mature children. Thus, older mothers might profit more (genetically) from investing resources in their already existing children than in giving birth to new ones, because with increasing age the risk of stillbirth, birth defects, and the mothers own death during childbirth rise and because of the fact that children need their mothers love and care to survive. Maternal care is therefore a major determinant of offspring survival. So it is more advantageous for a woman to stop reproduction early in life span. In summary, her already living children have a lower risk of dying during their childhood and as a consequence they have a better chance of reaching childbearing age.

Whether a product of natural selection or a side effect, it seems obvious that menopause is strongly linked to aging, which is usually defined as the progressive loss of body function attended by decreasing fertility and increasing natural mortality with advancing age due to complex cellular and molecular changes. There is a general agreement that the evolution of aging is linked to the fact that under natural conditions the organisms' risk to die induced by extrinsic hazards (such as infection, predation, starvation, or cold) increase with increasing age. Furthermore, these extrinsic hazards mainly affect younger individuals and consequently, as a result, most individuals simply do not live long enough to grow old. But reproductive aging in human females takes place long before other body functions senesce which presents an evolutionary dilemma. In order to understand the selective importance of reproductive aging and thus menopause, it is necessary to review some basic facts about the biological system and mechanisms that regulate normal reproductive cycles in adult females. Senescence is described as a decrease in survival and fecundity rates with advancing age. It has been predicted that senescence evolved as a side effect of life-history optimization and longevity has been traded for early high fecundity (Williams 1957). Hence, senescence is supposed to be caused by pleiotropic effects of genes that enhance reproduction at younger ages but suppress also survival later in life.

Menopause is a secondary consequence of the female mammalian reproductive system, which has a physiological limit of about 50 years. From that point on, the egg supply is limited and healthy eggs cannot be maintained with increasing age. The depletion of follicular reserve and the subsequent loss of fertility provide one explanation for how menopause occurs. Female mammals acquire 100% of their primordial follicles prenatal, around the time of birth. Most of this – approximately one million – primary oocytes degenerate before onset of reproductive ability (age of menarche, onset of puberty), so that in case of human females only about 400 primary oocytes are available for reproduction. During the reproductive life span

(adolescence and adulthood) the remaining primary oocytes complete their maturation and are released in series during menstrual cycles. As a result, the female ovarian follicular reserve declines during aging. However, during the reproductive life span the majority of follicles are lost in atretic processes than through to monthly ovulation. At about the age of 50 years, all of the oocytes are depleted and a female that lives according to this age of depletion experiences menopause.

In contrast to what is proposed in the mentioned grandmother or mother hypotheses, menopause is not, itself, adaptive but rather it is the final outcome of a decades-long progress of follicular depletion, which is in turn essential for the maintenance of regular ovarian cycles at younger reproductive ages. Therefore, since follicular depletion in human females causes both, high fecundity in early life (regular menstrual cycles) and loss of fecundity later in life (menopause), it can be selected if the early benefits outweigh the late costs. It is also possible that the physiological mechanisms of the follicular-depletion system and not menopause by itself have influenced the evolution of a prolonged post-reproductive life span in human females. Considering human's evolutionary history, it is also possible that our ancestors rarely survived beyond the age around 50 years, and selection simply produced as many oocytes as would be required, which in turn supports the artifact theory.

The Absent Father Hypothesis

All the previous mentioned hypotheses to explain menopause mainly focused on fitness costs and benefits of women (one-sex models), but it is also thinkable that processes where males are involved and influence menopause (two-sex models). The absent father hypothesis in contrast propose that reduced paternal investment combined with increasing maternal age could be an additional incentive for the evolution of menopause (Kuhle 2007) and represents not an alternative approach to the grandmother or mother hypothesis but is rather an extension of these approaches. The model includes the cross-cultural male mate

preference for female physical characteristics that signal youth and fertility, which is proposed to have evolved because men's reproductive success depends on their ability to gain sexual access to reproductively valuable women. Thus, men show the preference to mate with women displaying those characteristics that can be associated with reproductive ability like youth. Younger women have a higher reproductive value (number of children a woman of a given age can have in the future) compared to older women as younger women have more follicles available for fertilization, have higher fertility, and have lower risks of chromosomal abnormalities. Scientists propose that the evolved male preference for female youth could have prompted our ancestral men to pursue younger women either in place of or in addition to their mates until their mates achieved the age of infertility, to increase their own reproductive success. The evidence for this assumption is that older men prefer women that are increasingly younger than them supports this assumption. Additionally, men wishing to set themselves apart from their middle-aged mates by mating with younger women in addition to or in place of them would probably have reallocated their resources and protection to the younger women which leads to the consequence that the middle-aged women suffered a reduction of paternal investment. There is also evidence that supports the assumption that fathers, who leave their family, spend less parental investment than those who stay in the family. Without the prolonged investment of the fathers, similar to maternal investment, the risk of infant mortality is comparable higher before they reach the reproductive age. Paternal investment seems also to be essential for offspring's survival and because of this a reduction in paternal investment (absent of father) in combination with an increasing maternal age may provide further fitness benefits for the evolution of menopause. Menopause evolved due to the fact that the female abilities to reproduce are terminated and increased women's ability to care for extant offspring's by decreasing the likelihood of having to care for newborns and infants who may not survive until age of reproduction due to decreasing investment of both parents.

Conclusion

In very general terms, according to evolutionary theory, the goal of any organism is to pass on its genes and therefore, the phenomenon of human female's menopause confuses evolutionary theorists and is a highly controversial topic which is still active in research. Menopause refers to the relatively abrupt cessation of the female reproductive ability with about 50 years, when the impact of senescence on most other body functions is still small. Such a decline in age-specific fertility as a function of overall senescence is not uncommon among other species, but in contrast to most other species, human females are unique in experiencing a total cessation of reproductive capacity long before the end of their life. Reproductive aging is based on age-related changes in ovarian function and reduced oocyte quality which lead to menstrual cycle irregularities and changes in monthly fecundity and end ultimately in the total loss of reproductive ability. Whereas neuroendocrine changes that go along with follicular depletion seem to be the proximate causes of menopause; the ultimate causes are still unclear and possible explanations are mixed. To understand and explain the origin and significance of human female menopause has challenged not only evolutionary biologists and anthropologists but also medical scientists for quite a long time. They all investigate possible answers to the questions of why the reproductive ability of human females ends long before other body functions senesce and they thus experience menopause. Trying to find an answer to this question reveals that there are several causes possible and that apparently none of the possible causes can explain the origin of menopause by its own.

The summarized main hypotheses to the origin of menopause are that a prolonged post-reproductive life span could provide grandmothers as well as mothers the possibility to enhance their inclusive fitness by assisting their own children to reproduce successfully instead of raise further own children, or that early infertility could protect mothers from rising risks of age-specific maternal mortality and thereby protect also their highly dependent younger children from death in case the

mother dies. I guess that all theories reviewed here are to some degree possible and played a role in the evolution of menopause. Due to the fact that there is some evidence for each theory and also against, it may be possible that more than one of these models could account for the evolution of menopause. Thus, menopause is probably the result of a dynamic interaction of all the advantages and disadvantages that arise within these theories and that led to a prolonged post-reproductive life span which makes in this manner human females unique.

Cross-References

- [Adaptation](#)
- [Aging](#)
- [Fecundity](#)
- [Life History Theory](#)
- [Menstrual Cycle](#)
- [Natural Selection](#)
- [Sexually Antagonistic Hypothesis](#)

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Menopause Affords Grandparental Investment

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Synonyms

Menopause as a Kin Selection Adaptation
Sessation of Ovulation for Offspring Investment

Definition

It has been proposed (Austad 1994) that menopause is an adaptation that allows older females to provide enhanced care to their kin group. This is one interpretation of the grandmother hypothesis.

Introduction

The grandmother hypothesis proposes that the function of postmenopausal (i.e., post-reproductive) life in females is to provide enhanced care to kin. One interpretation of this hypothesis is that menopause represents an adaptation to make reproduction impossible. Specifically, menopause evolved as an adaptation to reduce the risk of late-life pregnancy in women who have (i) accumulated more germ-line mutations, (ii) become less likely to survive childbirth or produce a live child, and (iii) carry genes that could better benefit from investing in large numbers of kin rather than producing offspring. In this

account, the cessation of ovulation occurs in mid-life to facilitate a new familial role as a grandparent. It may seem counterintuitive for an adaptation to cause infertility, but if a grandmother or aunt can provide enough investment into their developing kin, they can substantially increase the likelihood that those kin survive and reproduce themselves. The theory of kin selection outlines how one can benefit their own genetic replication by improving the odds that their close kin survive and reproduce, because close kin will tend to also carry that same genetic information. A set of genes that promote grandmothering investment will proliferate more effectively if it can identify and support kin members who are more likely to carry those genes.

Evidence

This interpretation of the grandmother hypothesis makes several testable predictions. First, it must be possible to offset the cost of infertility by promoting the survival and reproductive success of kin. Studies of this topic have given mixed results. There is limited evidence that kin investment improves outcomes for children in industrialized societies (Coall and Hertwig 2010; Hawkes 2004) and stronger evidence that child life-expectancy in non-industrialized societies is improved by the presence of a maternal grandmother (Strassmann and Garrard 2011). However, when modeled mathematically, kin assistance provided by older females does not produce positive selection on genes for postmenopausal longevity (Kachel and Jean-Jacques Hublin 2010). In other words, grandmothers do provide measurable improvements to kin survival, but it is not clear whether this is enough to offset the costs of menopause.

Second, if menopause is an adaptation, one would expect to find evidence of special design or clues that the process of menopause is a controlled feature of female physiology rather than a consequence of physiological necessity. Oocytes are immature egg cells (ova) that are maintained in follicle tissue across the life-span. Human females are born with about one million oocytes, but these cells rapidly degrade such that 400,000 remain at

puberty and none remain around age 50 (a total of about 400 are released through ovulation in a lifetime). Oocyte depletion is regarded as a biological constraint on the female reproductive life-span. The process of menopause includes changes in hormone concentrations, psychological processes, and physiological maintenance but does not show the relaxed oocyte maintenance that would be expected if menopause itself were an adaptation.

Third, if menopause is an adaptation, one would not expect to observe the same process in nonhumans as they approach death. This is less an unsupported prediction than a logical challenge to the adaptation interpretation of menopause. Chimpanzees and gorillas observed in captivity show preliminary signs of menopause, and especially long lived chimps appear to show full ovulatory cessation at roughly the same age as female humans (40–50 years; Thompson et al. 2007). Menopause appears to be a conserved primate feature; humans are unique only in continuing to live after menopause has occurred.

Conclusion

The idea that menopause, or the cessation of ovulation, is an adaptation for providing better care to kin has fallen out of favor among most evolutionary theorists. There exists an alternative rationale for the grandmother hypothesis whereby human females have experienced selection for longevity rather than for the cessation of ovulation. Longevity could be selected on the basis that it promotes grandparental investment, and the fact that females will live longer than their oocytes is a by-product of selection for longevity. This rationale is described in extended postmenopausal life-span.

Cross-References

- [Adaptation](#)
- [Alloparenting](#)
- [Extended Postmenopausal Lifespan](#)
- [Grandmother Hypothesis](#)
- [Kin Selection](#)
- [Menopause](#)
- [Senescence](#)

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Menopause as a Kin Selection Adaptation Sessation of Ovulation for Offspring Investment

- [Menopause Affords Grandparental Investment](#)

Menstrual Cycle

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Synonyms

[Ovulatory cycle](#)

Definition

In women, the cycle of regular natural change within the reproductive system that includes ovulation and menstruation and makes pregnancy possible.

Introduction

From puberty to menopause, women who are not pregnant experience a menstrual cycle – a regular set of fluctuations in their reproductive hormones. This entry will focus on several key aspects of the menstrual cycle: (a) a description of the normal menstrual cycle, (b) potential disruptions (e.g., pregnancy, birth control, and amenorrhea) of the normal menstrual cycle, and (c) numerous psychological and behavioral changes associated with the menstrual cycle.

Description of the Normal Menstrual Cycle

A normal menstrual cycle lasts approximately 28 days on average, although some research shows that a normal cycle can range from 24 to 35 days (Stern and McClintock 1998). The menstrual cycle consists of three phases: follicular, ovulatory, and luteal. The menstrual cycle begins with the onset of menstruation, the shedding of the uterine lining from the previous menstrual cycle (which occurs during the follicular phase of the current cycle). During the follicular phase, the follicle-stimulating hormone (FSH) facilitates the maturation of a dominant follicle (sometimes two) that is capable of releasing an egg during ovulation. Estrogen rises, preparing the cervix and uterus for fertilization. At the end of the follicular phase, estrogen peaks and is then followed by a surge of the luteinizing hormone (LH).

The ovulatory phase is the fertile phase of a woman's menstrual cycle. Ovulation occurs approximately 30 h after a detectible LH surge (Bullivant et al. 2004). During this phase, a mature egg is released from an ovary and travels down one of the fallopian tubes where it may be fertilized by a sperm. If the egg is not fertilized, it disintegrates in the fallopian tube. If the egg is fertilized, it begins to develop as it moves down the fallopian tube to implant in the endometrium, or the wall of the uterus. Women are able to conceive on the day of ovulation and up to 5 days prior (Wilcox et al. 1995). In research, the term ovulation (or ovulatory phase) often refers

not only to the day the egg is released but to the whole fertile window (and follicular phase refers to all days of that cycle before the fertile window).

After ovulation, the body begins preparing for possible pregnancy. The luteal phase, which lasts approximately 14 days (Baird et al. 1995), is associated with the creation of the corpus luteum (a temporary structure on the ovary that forms from the dominant follicle after it has released the egg) that begins to release progesterone and, to a lesser extent, estrogen (Gilbert 2000). If the egg is not fertilized in the ovulatory phase, progesterone levels continue to rise until the corpus luteum cannot maintain itself, at which point progesterone plummets and a new menstrual cycle begins with the onset of menstruation (Gilbert 2000). If the egg is fertilized in the ovulatory phase, the embryo produces a hormone (human chorionic gonadotropin, hCG) that aids in maintaining the corpus luteum for approximately 10 weeks until the placenta takes over progesterone production (Yoshimi et al. 1969).

To summarize, the follicular phase occurs at the onset of menstruation and is characterized by a rise of estrogen as the woman's body prepares for possible egg fertilization. The ovulatory phase is the fertile phase of women's menstrual cycle and is conceptualized as the 5 days leading up to and the day of ovulation. The luteal phase is characterized by a substantial rise in progesterone and a smaller rise in estrogen as women's bodies prepare for possible pregnancy. If no pregnancy is detected, the menstrual cycle starts over.

Estimating the Phases

The menstrual cycle phases can be determined in three ways (reviewed in Gangestad et al. 2016). One method involves counting forward from the onset of menstruation. The only information needed for this method is the previous menstruation start date. In this method, the follicular phase includes the first 8 days of the menstrual cycle, the ovulatory phase includes days 9–14, and the luteal phase includes day 15 until the onset of the next menstruation. The forward-counting method is the least accurate but most easily conducted method of determining menstrual cycle phase.

A second method of assessing menstrual cycle phase involves counting backward from the onset of the next estimated menstruation. Two pieces of information are needed for this method – the previous menstruation start date and the average menstrual cycle length (which is used to determine the estimated start date of the next menstruation). In this method, the luteal phase includes the 14 days preceding estimated menstruation, the ovulatory phase includes the 5 days before the luteal phase (i.e., days 15 through 20 when reverse counting), and the follicular phase includes the days between the previous onset of menstruation and the ovulatory phase. The backward-counting method is considered more accurate than the forward-counting method for determining the ovulatory phase because women's luteal-phase length varies considerably less than their follicular-phase length (Baird et al. 1995). This method, however, requires following up with women to confirm the accuracy of their next estimated menstruation, which may complicate the research methodology and may result in fewer qualified research participants due to attrition (a lack of responses to the follow-up from the women who had participated).

The third and most accurate method of assessing menstrual cycle phase involves first estimating women's ovulatory phase (using either the forward- or backward-counting method) and then confirming the LH surge using a urine-detection test. In this method, women typically use an over-the-counter LH test every morning, starting on the tenth morning of their menstrual cycle. Because ovulation occurs 30 h after the detectable LH surge (Bullivant et al. 2004) and the fertile window is comprised of the day of ovulation and up to 5 days prior (Baird et al. 1995), researchers can accurately estimate the fertile window after confirming an LH surge. The days of that menstrual cycle prior to the estimated fertile window are considered the follicular phase, and the days of that menstrual cycle following the estimated fertile window are considered the luteal phase. Further, between-subjects designs require exceptionally large samples in order to detect effects; utilizing a within-subjects methodology is encouraged (Gangestad et al. 2016). Additionally, it is

recommended to recruit a sample with the knowledge that approximately half of participants will not have a detectable LH surge.

Disruptions of Regularity

Although a normal menstrual cycle occurs every 24–35 days, various factors can interrupt or change these normal hormonal fluctuations. Prior research has suggested at least three factors that suppress ovulation: (a) pregnancy and the postpartum period, (b) hormonal contraceptives, and (c) amenorrhea.

Pregnancy and the Postpartum Period

As previously described, if an egg is fertilized and an embryo successfully implants in the uterus, that embryo produces hCG to help maintain the corpus luteum and prevents menstruation from occurring. Throughout pregnancy, progesterone levels rise – produced first by the corpus luteum for 10 weeks and then by the placenta (Yoshimi et al. 1969). This increase in progesterone suppresses the menstrual cycle for the (typical) 40 weeks of gestation. The postpartum period follows childbirth and lasts an additional 6 weeks during which hormones begin returning to prepregnancy levels.

The return of hormones to prepregnancy levels, however, may be interrupted by lactation and consequent breastfeeding for several months (Kippley and Kippley 1972). Indeed, prolactin surges following infant suckling and the disruption of LH production associated with breastfeeding prevent ovulation from occurring. Once suckling declines and the infant is weaned, however, the preovulatory LH surge reoccurs. Notably, the amount of time that women take to return to normal hormonal fluctuations after lactation can vary.

Hormonal Contraceptives

Modern women often use hormonal contraception as a method of birth control to avoid conception during sexual activity. Hormonal contraceptives affect the endocrine system and disrupt the normal menstrual cycle. For example, progestogen-only hormonal contraceptives disrupt ovulation

through a negative-feedback process that disrupts FSH and LH. Likewise, combined hormonal contraceptives that include both progestogen and estrogen more effectively disrupt ovulation through the negative feedback from both hormones. Because ovulation is disrupted, women using hormonal contraceptives do not experience the psychological changes (reviewed in the next section) associated with the menstrual cycle even though they may still experience menstruation (facilitated by a drop in progesterone if women using oral contraceptives take placebo pills). For example, after starting to take hormonal contraceptives, women demonstrated lowered preferences for masculine features when compared to their own preferences when they were normally cycling (Little et al. 2013). Furthermore, some research suggests that there are long-term psychological effects of the disruption of the menstrual cycle for some individuals (see Russell et al. 2014). More details about hormonal contraceptives and their effects can be found in some of the cross-referenced encyclopedia references.

Amenorrhea

Some external circumstances may cause amenorrhea, or the cessation of a menstrual cycle in women of reproductive age that is not due to menopause. One common cause of amenorrhea is low body weight and can be achieved both through dieting and exercising. Thus, intense exercise and weight loss have the potential to disrupt the normal menstrual cycle. A second common cause of amenorrhea is stress. These disruptions in the normal hormone fluctuations within the menstrual cycle would also disrupt the psychological and behavioral shifts associated with those fluctuations.

Psychological Fluctuations Associated with the Menstrual Cycle

The hormone fluctuations associated with the menstrual cycle affect women's behavior and sometimes the behavior of men toward them (Makhanova and Miller 2013). For instance,

women may be especially motivated by mating during the ovulatory phase (when they are most fertile) but motivated by affiliation and self-protection during the luteal phase (when their bodies are preparing for possible pregnancy). In the next two sections, research on both of these motivations is reviewed.

Motivations Associated with the Ovulatory Phase

From an evolutionary standpoint, ancestral women who engaged in more sexual activity during their fertile window would have had greater reproductive success than women who failed to take advantage of the narrow opportunity for conception. Thus, as a result of these evolutionary pressures, it may have been adaptive for women to shift their behavior and cognition toward a mating focus during the ovulatory phase. Indeed, women experience increased sexual desire (Bullivant et al. 2004) and a shift in mating strategies (for a review, see Gildersleeve et al. 2014) a few days prior to and during ovulation. For instance, near peak ovulation, women are more likely to approach desirable partners and distance themselves from undesirable partners (for a review, see Haselton and Gildersleeve 2016). Further, consistent with the notion that such behaviors are perceived as highly attractive, women are more likely to wear more revealing clothing and red/pink colors (Beall and Tracy 2013; Haselton et al. 2007; Prokop and Hromada 2013). Thus, research supports the hypothesis that the ovulatory phase of the menstrual cycle results in behavioral and cognitive changes associated with mating motivation.

Moreover, a growing literature suggests cues of ovulation affect men's physiology, cognitions, and behaviors (for a review, see Makhanova and Miller 2013). For example, men perceive women's scents to be more attractive during the ovulatory phase compared to a non-ovulatory phase (Miller and Maner 2011). Further, men perceive women's dancing as more attractive during ovulation than during a non-fertile phase (Fink et al. 2012). Indeed, one study found that exotic dancers received more tips when they were ovulating than when they were not (Miller

et al. 2007) suggesting that men's behavior may also be affected by cues to ovulation.

Motivations Associated with the Luteal Phase

As women's bodies prepare for possible pregnancy (notably, whether or not the egg is actually fertilized), women may also undergo psychological preparations for dealing with the pressures from pregnancy. Specifically, pregnancy is associated with several threats. Pregnancy greatly limits women's abilities to locomote, acquire resources, and expend energy to pursue their goals. Thus, women may benefit from allies and social support at a time when these threats are more probable and extra costly (Taylor et al. 2000). Accordingly, the luteal phase of the menstrual cycle may be associated with psychological changes associated with an increased motivation to affiliate and protect oneself.

Indeed, women seem to be especially attuned to their social environment during the luteal phase of their cycle. Although women demonstrate greater levels of affiliation during the luteal phase (Schultheiss et al. 2003), women likely benefit from being selective in their affiliations because of the increased threats during pregnancy. Consistent with this notion, women attend more to social stimuli during the luteal phase of the menstrual cycle compared to the follicular phase of the menstrual cycle (Maner and Miller 2014). This increased social monitoring may aid women in achieving both affiliative and self-protective goals. Research has found support for the hypothesis that luteal phase affects social perception. When judging emotions of disgust and fear on others' faces, women judged these emotions to be more intense when they were in the luteal phase compared to the follicular phase (Conway et al. 2007). Furthermore, women seem to be extra sensitive to and overperceive these emotions during the luteal phase (Derntl et al. 2008; Guapo et al. 2009). That is, women may be more attentive to potential threats in their social environment during the luteal phase. Furthermore, an fMRI study found an interaction between cycle phase and neural stress reactivity; specifically women in the mid-luteal phase were more attuned to social stress and experienced greater hippocampal

activation compared to early-follicular women (Chung et al. 2016). Thus, a growing body of literature supports the hypothesis that menstrual cycle phase influences women's affiliation and self-protection motivation. Women tend to pay more attention to social cues and social threat in the luteal phase, when their bodies undergo physiological processes to prepare for a potential pregnancy (a status when women would become extra vulnerable to threats).

Conclusion

Women of reproductive age experience regular fluctuations in their reproductive hormones. The cycle lasts approximately 28 days on average and is comprised of three phases: the follicular phase, the ovulatory phase, and the luteal phase. The follicular phase prepares the ovaries and uterus for ovulation (and includes menstruation). The ovulatory phase is when women are fertile and able to conceive. The luteal phase prepares the uterus for pregnancy. In addition to these physiological changes, research has demonstrated that the normal menstrual cycle is also related to psychological preparations associated with the evolutionary pressures related to the cycle phases. During their ovulatory phases, women report greater mating motivations that correspond with their increased conception probability. During their luteal phases, women report greater affiliation and threat-avoidance motivations that correspond with the increased physical limitations associated with pregnancy and subsequent need for both vigilance to the social environment and allies.

Some scholars have argued that behavioral shifts associated with women's menstrual cycles are illogical because such behaviors should be conscious decisions that are immune to fickle manipulations. Drawing from an evolutionary standpoint, however, it is illogical not to take into account conception risk and pregnancy when examining human psychology because those states have profound implications for women's reproductive fitness and abilities to survive and to achieve other goals.

Cross-References

- [Anorexia Nervosa](#)
- [Birth Control](#)
- [Concealed Ovulation](#)
- [Concealed Ovulation and Pregnancy](#)
- [Conception](#)
- [Harsh Environments](#)
- [Hormone Effects on Human Fetal Development](#)
- [Mate Choice Effects](#)
- [Ovulation](#)
- [Ovulation Suppression](#)
- [Sexual Reproduction](#)
- [Women's Preferences During Ovulation](#)

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Menstrual Cycle Changes

- ▶ [Male Perception of Cycle-Related Fluctuations in Women's Attractiveness](#)

Menstrual Cycle Phase

- ▶ [Problems of Assessing Fertility](#)

Menstruation

- ▶ [Cycle Variation](#)
- ▶ [Ovulatory Hormones](#)
- ▶ [Ovulatory Shifts in Psychology](#)

Mental Grammar

- ▶ [Universal Grammar](#)

Mental Illness

- ▶ [Personality Disorders](#)

Mental Imaging

- ▶ [Sexual Fantasy](#)

Mental Lexicon

- ▶ [Vocabulary](#)

Mental Map

- ▶ [Spatial Mapping](#)

Mental Modularity

- ▶ [Modularity of Mind](#)

M

Mental Processes

- ▶ [Social Cognition and Communication in Chimpanzees and Bonobos](#)

Mental State Attribution

- ▶ [Theory of Mind and Nonhuman Intelligence](#)

Mentalizing

- ▶ [False Beliefs](#)
- ▶ [Theory of Mind](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)

Mental-State Attribution

► Theory of Mind

Messaging

► Communication, Cues, and Signals

Meta-analysis of Sex Differences in Aggression

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Synonyms

Competition; Female-female competition; Hostility; Indirect aggression; Intrasexual competition; Male-male competition; Physical aggression; Verbal aggression

Definition

Aggression is a response by an individual that delivers something aversive to a target. It can be expressed directly, in the form of physical and verbal aggression, or it can be expressed indirectly, in the form of social isolation and ostracism, known as relational aggression.

Introduction

Among humans, physically aggressive behavior in childhood peaks between 2 and 4 years of age and declines steadily in both sexes until adolescence (see below) (Archer 2009). Despite this decline, sex differences persist throughout childhood and into adulthood. There are a fraction of

individuals who maintain the high level of physical aggression seen early in development, and the majority of them are male. Similarly, there are a small fraction of individuals who demonstrate unusually low levels of physical aggression early in development and throughout childhood, and nearly all of those individuals are female. While verbal and relational aggression are more equally distributed between males and females, relational aggression is more common in girls and women, and they are more sensitive to it.

Cross-culturally and to varying extent, men are more likely to use physical aggression than women (Archer 2009). However, where the rate of criminal violence is high, the female rate is also high. The peak of violent behavior in both sexes corresponds to the attainment of sexual maturity, with the female peak occurring earlier than the male peak. In industrialized societies, aggressive behavior is associated with poverty, poor education performance, and dysfunctional parenting for both sexes, which suggests a common underlying mechanism responsive to the same ecological and life history variables. Many have asserted that this may be due to inadequate opportunities to compete for socially valuable resources in other ways, as physical aggression is often redirected in more affluent contexts toward organized coalitions with socially sanctioned aggression (i.e., organized sports) or other forms of competition.

Parental Investment Theory

Parental investment theory provides a useful framework in which to understand sex differences in aggressive behavior. Parents invest resources toward their offspring at the expense of future offspring (Trivers 1972). In most species, investment in gestation and postpartum care creates differences in the potential rate of reproduction and results in the higher investing sex being the limiting resource for the lower investing sex. For most mammals, females are the higher investing sex, and the result in the costs of physical aggression on reproductive fitness is higher (Sear and Mace 2008). In most mammals, the extent of male investment is copulation, with no or little

offspring care or provisioning. This polygynous strategy fuels intrasexual competition for access to mates and the resources they need to successfully raise offspring, and this competition is often physical. Although this strategy can be costly (i.e., potential for death), the benefits of this approach (gene representation in future generations) appear to outweigh the potential costs for males. In many contexts, physical aggression results in control of resources and status, increasing potential for reproductive success.

Physical Aggression

Practice with physical aggression occurs during development, as is the case with many other species. For humans, rough-and-tumble play provides the preparation needed to develop social-competitive skills, at least for most of human history. Though rough-and-tumble play is not exclusive to boys, it occurs with much higher frequency and much more vigor than with girls. This sex difference is robust, as it has been found across all modern and traditional societies in which it has been studied and first emerges around 3 years of age (Eibl-Eibesfeldt 1989; Maccoby 1998). It is consistent with practices for establishing within group dominance relationships as well as coordinating attacks for coalitional maneuvers. The extent and form of rough-and-tumble play can vary across traditional and modern contexts and is dependent on the relative frequency of physical aggression among adults in the culture, including intergroup conflict (Charlesworth and Dzur 1987; Whiting and Edwards 1988). The sex difference in rough-and-tumble play peaks between ages 8 and 10, and as boys move toward adolescence, it often intensifies to outright physical aggression. Importantly, the establishment of a dominance hierarchy is often associated with reductions in aggressive behaviors in boys (Pelligrini and Bartini 2001).

Later in development, physical aggression is predicted by access to resources (including mates), status, and the potential for aggression to result in gains in both. The magnitude in the sex

difference, favoring males, for physical aggression increases as males move through adolescence and into early adulthood. Whether using self-reports, observation, or homicide records, there are significant and substantial sex differences in physical aggression, even in industrial societies, where there are constraints on men's ability to utilize physical aggression (Archer 2009). If one primary function of physical aggression is to gain access to mates and associated resources, then it would be expected to be most intense during years in which reproductive competition is highest. Historical and cross-cultural crime records show that men's involvement in crimes involving physical aggression and in male-on-male homicides is highest between ages 18 and 30 (Daly and Wilson 1990, 2001). Self-reported physical aggression is also highest during this developmental period (Archer 2004).

Relational Aggression

Alternatively, in both traditional and industrial societies, girls and women pursue a less physically risky strategy of competing for resources: subtly organizing their social world in ways that benefit them and their children. Behavior related to this strategy is referred to as relational aggression and involves the use of gossip, rumors, and lies to socially isolate and disrupt the social and sexual reputation of potential competitors (Grotper and Crick 1996). This can be effective in that disruption in the social support systems of women can negatively influence their health and that of their children (Taylor et al. 2000). While both sexes engage in relational aggression, just as in physical aggression, it is the female strategy of choice. There is evidence that women are more sensitive to relational aggression and react more strongly to these social tactics (Benenson et al. 2013). Relational aggression begins as early as preschool age but typically peaks in adolescence, when intrasexual competition is often highest.

Females are tasked with gestation, lactation, and, often, significant postpartum care until offspring reach maturity. Therefore, a mother must provide adequate nutrition and protection from

ecological dangers during the time her offspring are dependent. Females often do not compete for resources physically, as do males. One possible reason for this is that the potential cost of physical aggression is death (Cross and Campbell 2011). Because her offspring's survival is most heavily dependent on the continuation of the mother's investment, the potential cost of physical aggression is often too high a price to pay. This is not to say that women are not competitive and aggressive with one another. This competition is, on average, more indirect than with boys and men, and the focus differs. Unlike many other mammals, paternal investment is common in humans, though the extent is variable across contexts. Paternal investment is linked to the offspring survival rate and social status and is thus a valuable reproductive resource for women (Geary 2010). Further, women would be expected to compete over paternal investment, particularly given that paternal investment is more variable and context dependent than maternal investment (Geary 2010). This creates circumstances in which women must compete for quality paternal investment, while at the same time reducing risks to herself and her dependent children.

The preference for less-risky aggression tactics has also been observed in nonhuman females. This includes behaviors such as establishing dominance hierarchies, territorial aggression (i.e., defending a home range), and coordinated aggression and constraining the reproduction of others (Stockley and Bro-Jørgensen 2011). Chimpanzees have been shown to use a number of these tactics including aggression toward new residents and interfering with their competitors' mating, female-led infanticide, and dominance hierarchies, typically organized around access to food resources (Pusey and Schroepfer-Walker 2013). Female dominance hierarchies have also been observed in other mammals such as vervet monkeys, chacma baboons, bison cows, reindeer, and house mice (Stockley and Bro-Jørgensen 2011).

Emotion

Emotion is a potential psychological mediator of sex differences in aggressive behavior (Cross and

Campbell 2011). The meaning of emotions depends on the outcomes they have been associated with over the course of evolutionary time. The emotions of fear and anger inform approach-avoidance distinctions in behavior that underlie aggression. Anger is positively related to approach motivation and negatively related to avoidance motivation. It increases sympathetic nervous system activity in preparation for exertion and combat. However, there is no evidence for sex differences in the experience of anger.

Unlike anger, fear is negatively associated with approach motivation. The fear system activates responses that maximize survival (i.e., avoidance motivation) in response to perceived danger. There are also marked sex differences in the experience of fear. The hypothalamic-pituitary-adrenal (HPA) axis response to stress is inhibited by androgens and enhanced by estrogens. Further, gonadal hormones lead to the fear system developing differently in males compared to females. Behaviorally, girls begin expressing fear earlier than boys and are more likely to develop on a high fearfulness trajectory. In adulthood, women experience fear more frequently and intensely than men. This lower threshold for experiencing fear leads women to appraise the same objective situation as more dangerous than men do. This evaluation difference explains significant variation in sex differences in aggression (Campbell 2006).

Partner Aggression

Partner aggression is a domain in which aggression occurs at apparent sex-equal rates, though women are more likely to be seriously injured or killed as a consequence of partner aggression than men are (Daly and Wilson 1988; Archer 2000). This suggests that male aggression (typically higher than that of females) is being constrained and female aggression (typically lower than that of males) is being disinhibited (Cross and Campbell 2011). Culture has been suggested as a potential explanation for this phenomenon. For example, in cultures where women are more socially and legally equal to men, women also engage in more partner-directed aggression.

These cultures also typically have strict sanctions against domestic violence, and men are taught from boyhood that it is inappropriate to behave aggressively toward women. However, it is important to note that even in cultures where women are less legally and socially equal to their male counterparts, rates of partner violence committed by women are not trivial (Archer 2006).

Role of Hormones

Oxytocin, a nonapeptide hormone and neuromodulator, has also been suggested to potentially play a role in the sex differences observed in partner aggression. There is evidence that oxytocin is involved in a wide range of cooperative and reproductively relevant behaviors (Pederson 2004; Campbell 2010). Further, oxytocin receptors are upregulated by estrogen, possibly making it a particularly important player in female behavior (Lim and Young 2006). Therefore, women in romantic relationships are producing oxytocin consistently in response to reproductive cues. Oxytocin is associated with a reduction in amygdala activity in response to fear-provoking stimuli and reduces connectivity between the amygdala and regions of the brain associated with sympathetic nervous system responses to threat, thereby reducing the experience of fear. Therefore, oxytocin may be one mechanism by which women are overall less physically aggressive, but similarly physically aggressive within their romantic relationships (Campbell 2010).

In addition to cultural explanations and the possible mediating role of oxytocin, there are sex differences in the motivation for aggressive behavior which may provide some explanation for the sex-equal rates of aggression within romantic relationships. Males and females use aggression for mate guarding. Males use mate guarding as a technique to maximize paternity certainty, while females utilize mate guarding to maximize male investment. In addition to mate guarding, females are also more likely to use aggression toward their partner due to displaced anger (i.e., people aggressing to a target other than the one that provoked them; Archer 2004).

Conclusion

Sex differences in parental investment and associated social selection pressures have resulted in differences, on average, between the sexes in aggressive tactics, particularly those related to intrasexual competition. There are established differences in the extent to which girls and boys self-initiate and thus practice and refine and behavioral competencies that facilitate these forms of competition in adulthood. Cultural demands then direct these sex differences in divergent or convergent directions, depending on the level and nature of competition and access to resources in the current context.

Cross-References

- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Contexts for Women's Aggression Against Men](#)
- ▶ [Contexts for Women's Aggression Against Women](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Same-Sex School Bullying](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)

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Metabolic Changes

- [Cell Death as an Adaptation Against Cancer](#)

Metabolism

- [Energy Consumption](#)

Metacognition

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Synonyms

[Confidence judgments](#); [Metamemory](#);
[Uncertainty monitoring](#)

Definition

Metacognition is the awareness and understanding of one's own thought processes. It involves monitoring processes that ascertain current states of knowledge and control processes that seek information when needed and generate confidence measures.

Introduction

Metacognition refers to the observation that one can be cognizant of one's own cognition and may therefore be in a position to regulate it. Theoretically, metacognition includes two key aspects: (1) The executive monitoring of cognitive states which is an endogenous process that is sensitive to the state of uncertainty in a given judgment or decision context and (2) The information provided by the metacognitive monitoring can alter or control other cognitive processes to

affect decision-making. Metacognition has been extensively studied in humans and is an important concept that captures some of the essence of what it means to be a “conscious agent.”

Comparative research in metacognition illuminates the shared cognitive capabilities of human and nonhuman animals that might be accessible to a metacognitive system while also better defining the uniqueness of human metacognitive capacities. Human metacognitive research often involves verbal reports about one’s own knowledge. However, nonhuman animal (“animal” hereafter) metacognition has been investigated extensively using experimental tasks that infer metacognition by assessing how animals behave when faced with stimuli and choices that might evoke varying degrees of confidence or uncertainty (Smith 2009). Animal metacognitive research could provide evidence of rudimentary forms of self-awareness, or theory of mind, in other species that do not have the benefit of language to mediate its expression. This research area also potentially outlines the earliest emergence of self-reflective minds in animals, including those hominid species that led to modern *Homo sapiens*. As such, this research area provides key insights into the evolutionary foundations of humans’ advanced forms of metacognitive control and monitoring. The procedures that assess metacognition in animals also could be adapted for testing metacognition in preverbal or nonverbal humans or even in young children who lack some of the key aspects of mind that older humans have.

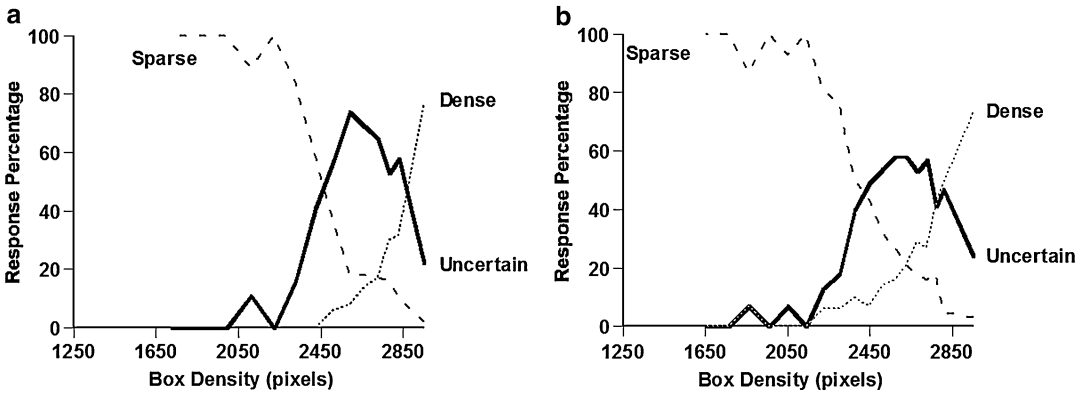
Approaches to Demonstrating Animal Metacognition

Positive Evidence

A diverse range of experimental procedures have been used to assess metacognition in a variety of species. Smith et al. (1995) trained humans and a dolphin (*Tursiops truncatus*) to discriminate between a high pitch tone (2100 Hz) and lower pitch tones (varying between 1200 and 2099 Hz). Along with making a “High” or “Low”

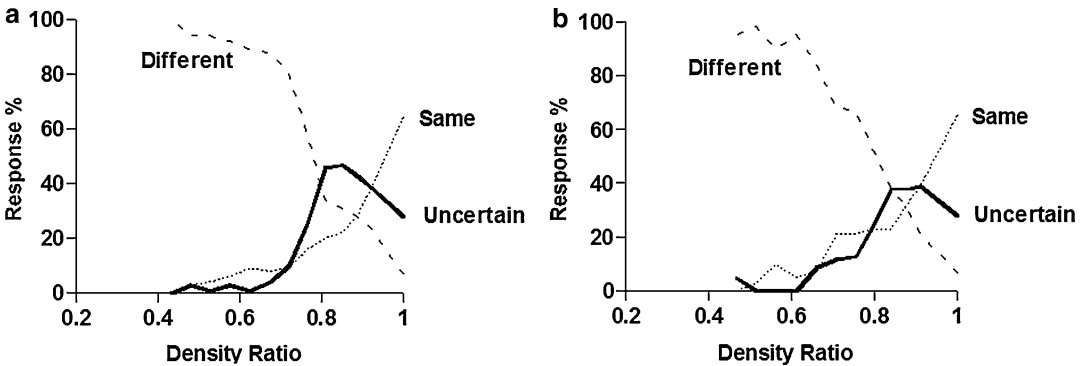
discrimination response, the dolphin could emit an “Uncertain” response to decline the trial and proceed to a trial ending with a guaranteed reward. The dolphin’s Low or High responses were accurate for perceptually easy trials, and his accuracy was lowest at the perceptual threshold (about 2080 Hz) for distinguishing between a 2100 Hz tone and lower pitch tones. Choice of the uncertainty response and hesitation in responding both peaked near the point that High or Low responses were equiprobable. These data provided some of the earliest experimental evidence that animals may experience uncertainty akin to humans, and this methodological approach became one of the dominant approaches in comparative cognition. Smith et al. (1997) arranged a similar perceptual discrimination task separately for humans and macaques (*Macaca mulatta*) using a computer test system. Subjects had to judge whether a stimulus sample contained either a dense (2950 pixels) or sparse (450–2949 pixels) matrix of randomly placed pixels or they could make an Uncertain response and decline the trial and proceed to a guaranteed win trial. Humans and monkeys generated very similar results where the point of equiprobable judgment was approximately at 2700 pixels and the use of the Uncertain response peaked near that location along the perceptual gradient (Fig. 1). The humans self-reported that they felt unsure how to classify the pixelated stimulus when they utilized the Uncertain response, demonstrating that this task generated a conscious self-report of uncertainty that is common in human metacognition studies.

Shields et al. (1997) followed with an experiment where macaques and humans made same/different judgments between two-pixel density samples. This task was more complex because it required a relativity judgment between two samples rather than an assessment of one sample. Humans and macaques performed similarly on the task and efficiently used the uncertainty response to escape difficult trials (Fig. 2). Subsequent approaches demonstrated that macaques also adaptively and appropriately used this uncertain response when they received only deferred feedback for their responses (Smith et al. 2006)



Metacognition, Fig. 1 (a) Performance by a monkey in a sparse-dense discrimination. The horizontal axis indicates the density of the trial. The dense response was correct for 2,950-pixel trials – these trials are represented by the rightmost data point for each curve. All trials with fewer pixels deserved the sparse response. The *solid line* represents the percentage of trials receiving the uncertainty response at each trial level. The percentages of trials ending with the sparse response (*dashed line*) or dense response (*dotted line*) are also shown. (b) The performance of

humans in the sparse-dense discrimination depicted in the same way. To equate discrimination performance across subjects, the data were normalized to place each subject's discrimination crossover at a pixel density of about 2,700 (Data are redrawn from "The Comparative Psychology of Uncertainty Monitoring and Metacognition," by J. D. Smith, W. E. Shields, and D. A. Washburn, *Behavioral and Brain Sciences*, 26, p. 322. Copyright 2003 by the Cambridge University Press. Reprinted with permission.)



Metacognition, Fig. 2 (a) Performance by two monkeys in a same-different task. The horizontal axis gives the ratio between the densities of the comparison box and the standard box for trials of different disparities. The same response was correct for trials at a proportional box disparity of 1.0. These trials are represented by the rightmost data points. All other trials deserved the different response. The *solid line* represents the percentage of trials receiving the

uncertainty response at each density ratio. The percentages of trials ending with the different response (*dashed line*) or same response (*dotted line*) are also shown. (b) Performance by six humans in the same-different task depicted in the same way (From Shields et al. (1997). Copyright 1997 by the American Psychological Association. Reprinted with permission.)

and when monkeys had to work on a concurrent task while also making these discriminations (Smith et al. 2013).

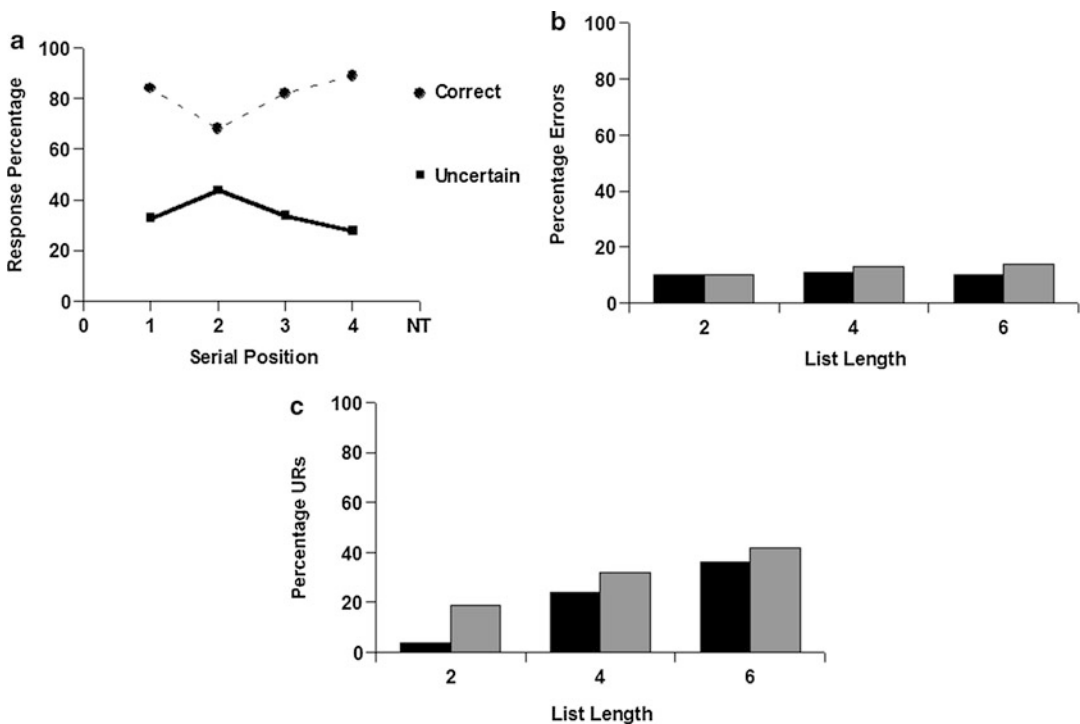
Metacognition also has been investigated using metamemory paradigms where the ability or inability to remember a stimulus is monitored instead of the inability to detect perceptual

features of stimuli. Hampton (2001) conducted an experiment where macaques worked on a delayed matching-to-sample (DMTS) task where the Uncertain response would allow the monkey to "settle" for a less preferred reward than it could otherwise receive for making a correct matching response (but, also allow the monkey to avoid a

costly timeout for an incorrect response). As the delay interval increased in length, the monkeys were more likely to use the Uncertain option. In probe trials, where no sample stimulus was presented (i.e., there was nothing to remember), the monkeys continued to use the Uncertain option appropriately. In a related approach, Smith et al. (1998) designed a serial position meta-memory task where trials presented a list of pictures (ranging from 2 to 6) followed by the presentation of a sample picture. If the macaques correctly remembered that the sample picture was in the preceding list or correctly remembered that it was not, then they would earn a reward. Alternatively, monkeys could escape the test trial with an Uncertainty response. The longer the list length the more likely the monkeys were to escape it (Fig. 3). Also, if the serial location of the list

picture was difficult to remember (e.g., the second item in the list that does not benefit from primacy or recency effects), there was a lower probability of correctly remembering it and a corresponding higher probability of escaping from those trials. Overall, monkeys have demonstrated an ability to avoid taking memory tests on trials where they seem to have forgotten the correct response, and this further supports the generality of this animal metacognition paradigm's claims that uncertainty monitoring is responsible for the use of the escape response.

Uncertainty responding as a means to seek information has been investigated in more naturalistic environments (ostensibly, uncertainty monitoring did not evolve as a means to solve computerized laboratory tasks). Call and Carpenter (2001) presented orangutans (*Pongo pygmaeus*)



Metacognition, Fig. 3 Performance by a macaque in a metamemory task. (a) The serial position (1–4) of the probe picture in the list of pictures is also given along the X-axis for probes. NT denotes probe pictures that were not there in the memory list of pictures. The percentage of total trials that received the uncertainty response is shown (solid line). The percentage correct (of trials on which the memory test was accepted) is also shown (dashed line).

(b) Percentage error rates by two macaques (black and gray bars) when the difficulty of the memory test was increased by increasing the length of the memory list from 2 to 4 to 6 pictures. (c) Percentage uncertainty responses (URs) by the two macaques when the difficulty of the memory test was increased in the same way (From Smith et al. 1998. Copyright 1998 by the American Psychological Association. Reprinted with permission.)

and chimpanzees (*Pan troglodytes*) with a task where a food reward was hidden in one container within an array. If these apes witnessed the baiting of the cups (i.e., they knew where it was hidden), they would immediately point to the baited location without investigating that location first, but if they did not see where the food was located they would visually inspect the container to seek information they needed to make a correct pointing response. Hampton et al. (2004) reported similar findings with rhesus monkeys. Suda-King (2008) presented orangutans with a task that also involved choosing among cups where only one was baited with food. In this case, the orangs could not inspect the cups. Rather, they had the option also to choose a cup which always held a smaller reward rather than risk choosing an empty location and receiving nothing. Suda-King reported that when the location of the larger reward amount was known (i.e., the orangutans saw the baiting), they chose those locations, but when they could not know, they were more likely to accept the small-reward option. Beran et al. (2013) expanded upon the premise of this task using chimpanzees. The apes were tasked with correctly reporting to a naïve researcher what food item they had seen inside of a box. They reported symbolically using a lexigram keyboard where specific objects were represented by various key symbols. In the “known” condition the food was shown to the apes prior being hidden in another location, and in the “unknown” condition the box’s contents were not shown but the apes could travel to inspect the box’s contents. The apes were more likely to travel to inspect the box when the contents were not previously shown, but they were more likely to name the item without inspecting the box when the item already was known.

Confidence judgments also can be assessed by allowing the subject to “bet” on whether its response to given trial is likely to end in reward. Middlebrooks and Sommer (2011) had macaques work on a signal detection task where a sample stimulus appeared in one of four corners on a screen and then after 16.7, 33.3, 50, or 66.7 ms (randomized by trial) all four corners presented identical stimuli. The monkey had to respond to the corner where the first sample appeared.

Following a response, a two-option choice was presented where selecting one option expressed confidence in the prior signal detection response, while the other option expressed uncertainty. Reward amount was calibrated based upon whether the monkey was correct/incorrect and whether the monkey made a high confidence or low confidence bet. A high confidence-correct outcome resulted in five drops of juice, while a high confidence-incorrect outcome resulted in a 10 s timeout. A low confidence-correct outcome resulted in three drops of juice, while a low confidence-incorrect outcome resulted in two drops of juice. Response accuracy increased as the sample-choice delay was increased, and the monkeys’ ratings of confidence in their response increased concomitantly. Thus, the monkeys’ betting behavior tracked their accuracy.

Ambiguous Evidence

In addition to humans, dolphins, and macaques, research has been conducted with pigeons, rats, bantams, and capuchin monkeys (*Cebus apella*) to assess potential metacognitive capacities. Many of these approaches have produced more ambiguous results with regard to whether these species show metacognitive control and monitoring. Inman and Shettleworth (1999) exposed pigeons to a delayed matching-to-sample task where the Uncertain option resulted in a relatively small reward, whereas correct matching responses led to large reward and incorrect responses led to punishment. Even though their matching accuracy decreased with longer delays, the pigeons failed to use the Uncertain response. In a second experiment where pigeons were allowed to reject a difficult trial (similar to Hampton 2001), they again failed to utilize that response. Teller (1989) and Kuroda et al. (2014) demonstrated that pigeons would use an Uncertain response in a DMTS task, but they could not conclusively demonstrate that external stimulus cues (i.e., the delay intervals) were not controlling the use of the Uncertain option. Thus, to date, there is no conclusive evidence that pigeons demonstrate uncertainty monitoring, although there are some suggestive lines of evidence (e.g., Castro and Wasserman 2013).

Rats were trained to classify the duration of auditory streams as being either short or long. For those durations closest to the divide between a true “long” duration and a true “short” duration, the rats were most likely to decline completing the trial (Foote and Crystal 2007). In a second experiment, rats again classified these sound durations, but they were given trials in which they were forced to make a classification (i.e., they could not escape), or forced to replay the sound (i.e., they had to decline making the primary responses), or they were allowed to choose between taking the test or replaying the sound. Here, the evidence for a metacognitive pattern of responding was mixed. Rats did show the accuracy difference that would be predicted by a metacognition account for forced-repeat and choice-repeat trials. However, the other features that would be expected if metacognitive monitoring was occurring were not readily evident.

Ambiguous outcomes from metacognition tests also can occur for primate species. Beran et al. (2009) designed a sparse-dense discrimination task for capuchin monkeys with an Uncertain response option used to decline a difficult trial (as in Smith et al. 1997). Beran et al. also included a control condition where instead of an Uncertain option there was a “Middle” option that was designated as correct for those samples that had intermediate pixel densities between the sparse and dense regions. Although the monkeys were easily able to use the Middle response, only one of the six monkeys used the Uncertainty response – and even then the one successful monkey might have confused the Uncertainty response as a Middle response. Basile et al. (2009) replicated with capuchins Call and Carpenter’s (2001) procedure where food was visibly baited or concealed and searching for the food would demonstrate uncertainty monitoring. Most monkeys did not search for the unknown food items, and when the search effort costs were increased none of the monkeys searched for food. Paukner et al. (2006) also arranged a food search task where capuchin monkeys had to search tubes for baited food. Though some monkeys did search the tubes, they also demonstrated search behavior under conditions where the tubes were transparent or when the

tubes were bent and their inspection would not reveal any useful information. Thus, the appearance of information-seeking behavior in that study was likely due to other reasons (e.g., manipulation of an enrichment apparatus).

To summarize, there is evidence that dolphins, macaques, orangutans, and chimpanzees will demonstrate metacognitive awareness of the likelihood that they know the correct response (uncertainty monitoring), and they utilize that awareness to adapt behavior to improve performance through behaviors such as information-seeking responses (cognitive control). Although pigeons and rats have yet to reliably demonstrate that capacity in a diverse range of tasks and capuchin monkeys appear to demonstrate a metacognitive ability only if the procedure is calibrated to discourage their propensity play the odds, future research efforts may expand the phylogenetic map of metacognitive capacities. The next section discusses the plausible processes and mechanisms that may govern animals’ performances in these tasks.

Controversies About Animal Metacognition

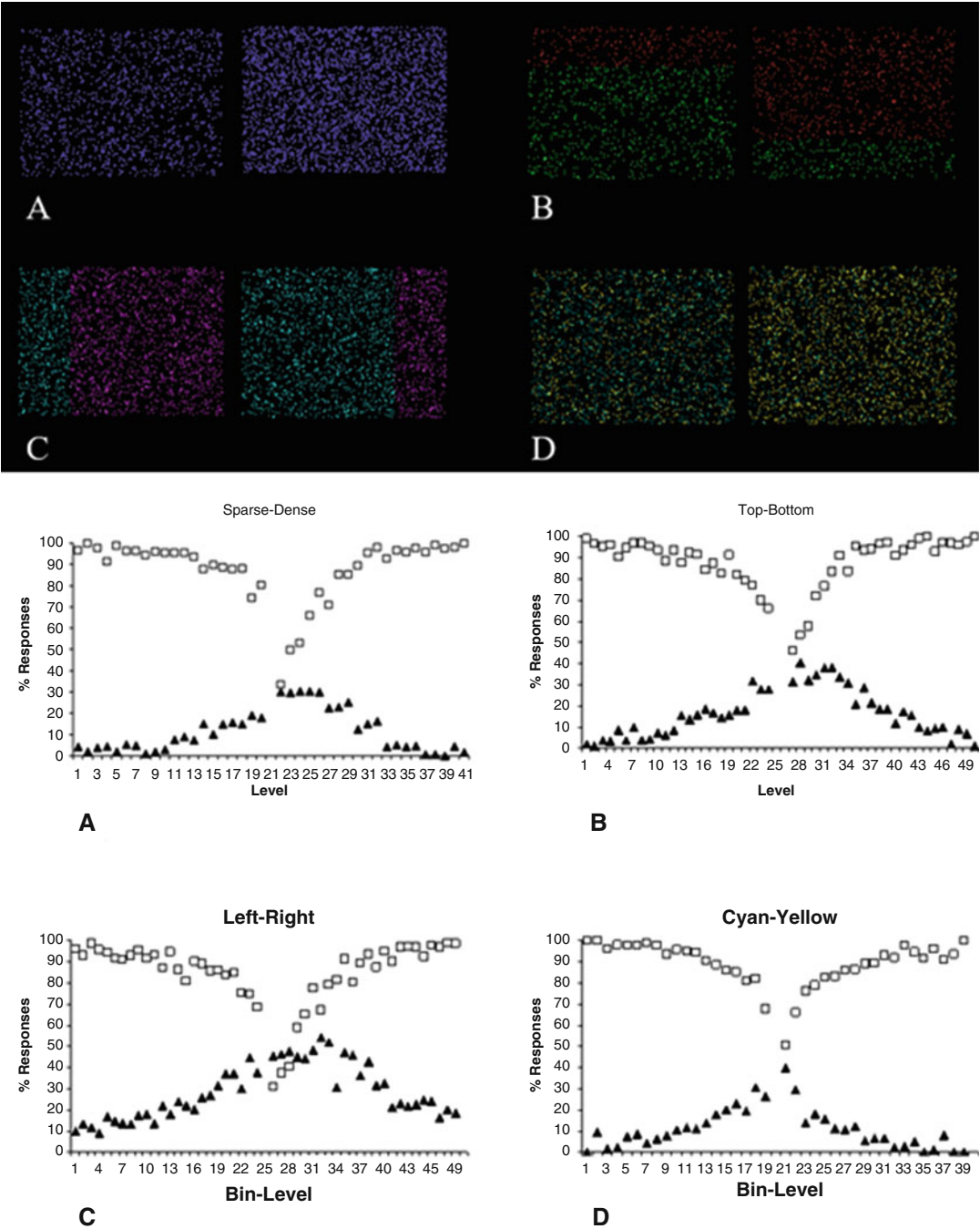
The results outlined above suggest an enticing possibility that the expression of animals’ uncertainty monitoring stems from a similar psychological state shared with humans – thus, animals may also have similar conscious metacognitive experiences. However, such an attribution could be a dangerous overgeneralization that imposes an anthropocentric view on animal psychology. The principal alternative explanation to a metacognitive system is associative conditioning processes that rely on reinforcement, punishment, and stimulus control (e.g., Jozefowicz et al. 2009; Le Pelley 2012). Before a theory of the evolutionary emergence of a metacognitive system that has culminated in adult human capabilities can be advanced there are a variety of associative hypotheses that have needed to be addressed (e.g., Crystal 2014; Kornell 2014).

First, the expression of the uncertainty monitoring could be due to external environmental

stimuli that cue the subject to make an uncertainty response. For instance, macaques may have selected the uncertainty option in a difficult perceptual discrimination trial because in the absence of a clearly correct response the monkeys discriminated their latency to make a response. While Smith et al. (1995) noted that this was a possibility, there is evidence against this explanation given by Shields et al. (1997). Shields and colleagues did not observe a correlation between response latency and the utilization of the Uncertainty option. Alternatively, it is possible that some procedural cue (e.g., the sample stimuli that are often predictive of a timeout in a discrimination task or the delay interval in a DMTS task) occasioned the beneficial use of the Uncertainty option. Indeed, there is evidence that this can be the case. Teller (1989) evaluated metamemory in pigeons and observed that Uncertain responses were used at long delay intervals in the DMTS procedure. The Uncertain response appeared to be due to the pigeons learning the associative contingency of long intervals and Uncertain responses rather than some endogenous expression of uncertainty monitoring. However, this is not always the case. The Hampton (2001) metamemory task occasionally produced a discrimination trial without a sample stimulus where the delay interval was very short, and the monkeys still used the Uncertainty response. Washburn et al. (2010) had macaques work on a DMTS task with brief delay intervals where the monkeys could frequently successfully match. On some trials, the experimenters introduced transcranial magnetic stimulation (TMS) during the delay interval to disrupt discrimination performance by blocking memory for the stimulus. The TMS disrupted discrimination accuracy and increased the likelihood that the monkeys would use the Uncertain response. Thus, despite the procedural aspects being held constant, artificial methods (such as TMS) to disrupt discrimination performance still resulted in the utilization of the Uncertainty response. Smith et al. (2010) exposed macaques to a discrimination task that simultaneously varied the cue difficulty and the type of discrimination being asked when pixels were presented on a screen (sparse or dense samples, cyan or yellow

samples, top or bottom color contrast divider, and left or right color contrast divider; Fig. 4, top panel). The monkeys generalized the use of the Uncertainty response for difficult trials across all tasks, despite there being no single cue that signaled that an Uncertainty response would be efficient (Fig. 4, bottom panel). Perhaps most convincingly, Kornell et al. (2007) arranged a variety of discrimination tasks where correct responses resulted in +3 tokens, incorrect responses resulted in -3 tokens, and the Uncertain response resulted in +1 token. Once 12 tokens were earned then the monkeys would earn a pellet. Monkeys worked on a circle size discrimination task when the metacognitive contingencies were being initially trained. Subsequently, the monkeys worked on a serial recall task with the metacognitive contingencies included but not explicitly trained for this task. The use of the metacognitive response spontaneously transferred from the perceptual task to the serial recall task without training. This demonstrated that the training of the use of the Uncertainty response was not isolated to the specific task that it was originally trained under but rather generalized across procedures. This generalization goes against strict associative accounts for the use of the Uncertainty response, since the response still occurred under different experimental conditions and with very different external cues correlated with a potential difficult trial. Also, the generalization of the Uncertainty response from use in a perceptual task to use in a metamemory task suggests that metacognition and metamemory processes are tied to a similar underlying process.

Second, it is possible that the expression of uncertainty monitoring (rejecting a difficult trial, information seeking, or confidence judgments) is artificially reinforced behavior that does not reflect (or is otherwise influenced by) a metacognitive mechanism. This confound to hypotheses that suggest uncertainty monitoring is due to a conscious process of knowing can be difficult to address. Any conscious metacognitive process would likely develop because it aids in the organisms' adaptiveness to the environment and as such should aid in the attainment of rewards and the avoidance of aversive outcomes. Such a



Metacognition, Fig. 4 Monkeys' performance in four psychophysical tasks. The *top* part of the figure shows the four types of discrimination, and the *bottom* graphs correspond to performance on each of those tasks. In the graphs, the horizontal axis indicates the trial level. The percentage of trials receiving the uncertainty response at each level is

shown (*filled triangles*) along with the percentage of correct responses made when animals completed trials with a primary discrimination response (*open squares*) (From Smith et al. (2010). Copyright 2010 by Springer. Reprinted with permission.)

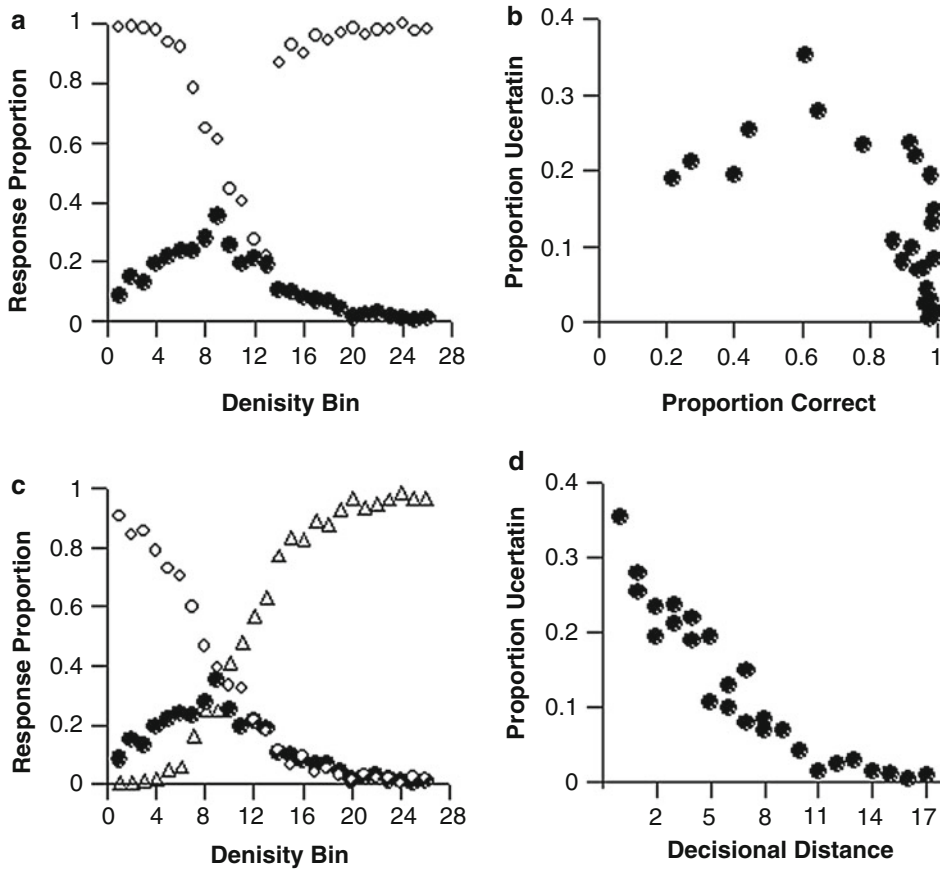
mechanism would be distinct from reinforcement processes, but by using behavioral measures it would be difficult to distinguish between the two. Regardless, there is some evidence to suggest that uncertainty monitoring is not simply a product of reinforcement applied to the uncertainty response. Reinforced behavior does not occur in a vacuum; the behavior must either occur in a discriminated context where the behavior has traditionally resulted in reinforcement or (prior to stimulus control) it should occur indiscriminately across contexts. As discussed above, the expression of uncertainty monitoring occurs under conditions where the probability of making a correct response is low and is not related to any measurable external sources of stimulus control. If the uncertainty response was directly reinforced, then there is no clear reason to predict that it would occur in the absence of external stimulus cues while also reliably occurring under conditions where an incorrect response is likely. Though some procedures have arranged an incentive for using the Uncertainty responses (relatively smaller food reward, Hampton 2001; progression to an easier trial, Smith et al. 1997), the efficient use of the Uncertainty response occurs under conditions where there are no programmed rewards for using it other than to avoid the present trial (e.g., Beran et al. 2006).

In order to even further dissociate the reinforcement from the use of the uncertainty response Smith et al. (2006) prepared a sparse-density pixel discrimination task that deferred the consequences of the responses until the end of a 4-trial block. No response on a single trial resulted in feedback, and at the end of the block the sum of pellet rewards for correct responses and timeouts for incorrect responses were delivered, not in the order of trial presentation, but with all rewards first and then all timeouts. In this way, the monkeys could not directly track each response to its immediate outcome. The use of the Uncertain response option made no contribution to the post-block feedback and effectively rendered the associated trial inconsequential. The question was whether in the absence of this direct feedback the monkeys would continue to use the Uncertain response when facing a

difficult trial. One monkey did, and furthermore the use of the Uncertainty response was well predicted by the subjectively experienced difficulty of trial stimuli rather than the objectively defined difficulty (Fig. 5). In other words, uncertain responses often were made to objectively easy trials and incorrect responses (with few uncertainty responses) were common to objectively difficult trials, because the monkeys were tricked into thinking that truly easy trials were the harder ones they faced. These data support the claim that uncertainty monitoring operates from a process that detects difficult discriminations rather than a process that requires tight feedback (reinforcement or punishment) applied to an Uncertainty response.

Third, the Uncertainty response to escape a trial might be an avoidance response emitted when the sample has been historically correlated with a timeout punishment. Thus, the sample on a difficult trial would not affect any uncertainty monitoring but would be “bad news” because punishment follows it, and therefore the Uncertainty response would remove this bad news sample. Though reasonable, this explanation would not easily account for the expression of uncertainty monitoring using other procedures such as confidence movements corresponding with a correct response or differential cashing out responses to the same stimuli as a function of how many tokens were at risk (e.g., Zakrzewski et al. 2014). This explanation also does not account for some procedures using the Uncertainty response to escape a trial. Shields et al. (1997), for example, did not present difficult trials with a singular sample but rather the relative discriminability between two samples varied the difficulty without allowing any one stimulus feature to be correlated with a timeout. In the absence of a singular stimulus feature correlated with a timeout, it is difficult to isolate what external stimulus cue the monkeys would be avoiding.

Taken together, the weight of the evidence suggests that uncertainty responses are not easily explained by evoking a variety of conditioning processes. However, evidence against particular conceptualizations of an associative explanation does not endorse alternative cognitive



Metacognition, Fig. 5 (a) The performance of a rhesus monkey in the sparse-dense discrimination from the deferred feedback task. The horizontal axis indicates the density bin of the box. The sparse and dense responses, respectively, were correct for boxes at density bins 1–13 and 14–26. The *open circles* show the proportion of trials attempted that were answered correctly. The *dark circles* show the proportion of trials receiving the uncertainty response at each density bin. (b) The monkey's performance in the same task, but now showing his proportion of trials declined in each density bin plotted against his

proportion of trials answered correctly. (c) The monkey's performance is shown in the same task, but now showing separately his use of the sparse and dense responses (*open circles* and *open triangles*). (d) The monkey's performance in the same task, but now showing his proportion of trials declined in each density bin plotted against the decisional distance of the bin from his decisional breakpoint (bin 9 = 0; bins 8 and 10 = 1; bins 7 and 11 = 2, etc.) (From Smith et al. 2006. Copyright 2006 by the American Psychological Association. Reprinted with permission.)

explanations by default. Strong evidence that uncertainty monitoring is a product of a meta-cognitive system comes from Smith et al. (2013). They assessed whether uncertainty monitoring requires cognitive resources to efficiently reject difficult trials. They arranged a DMTS task and then embedded a sparse-dense discrimination trial within the delay interval of the DMTS task. The sparse-dense task either had an uncertainty option associated with it or a

Middle option that replaced the Uncertainty option. They found that the use of the Uncertain option was greatly underutilized, while the use of the Middle option was unaffected. This dissociation of Middle versus Uncertain responding in the context of the concurrent DMTS task is explained by claiming that uncertainty monitoring requires additional cognitive resources to function efficiently, while the reinforcement-maintained Middle response did not. Such results suggest that

Middle and Uncertain response are fundamentally different processes and that uncertainty monitoring is more cognitively taxing.

Another strong and compelling set of results comes from Basile et al. (2015) who evaluated seven hypotheses about alternate accounts to a metacognitive interpretation of rhesus macaque performances during a series of computerized tasks. In these tests, monkeys chose either to take memory tests immediately or to see the answer again before proceeding to the test, a response that could be made when monkeys were aware of weak or nonexistent memory sufficient for taking the test. Basile et al. examined alternate explanations grounded in behavioral cue association, rote response learning, expectancy violation, response competition, generalized search strategy, or postural mediation. None of these accounts could explain the monkeys' pattern of taking tests where they chose to see the answer when memory was poor, either from natural variation or experimental manipulation, and chose to take the test when memory was strong. In addition, there was limited evidence that monkeys also may have monitored the fluency of their memory access, providing an overall pattern in that study that suggested that rhesus monkeys use their memory strength as a discriminative cue for information seeking (also see Templer and Hampton 2012).

Conclusion

Although focused criticisms have been offered in this area of research, often with the consequence of sharpening the quality of the debate and the quality of the methodologies that have been developed, a consensus seems to be emerging that some species may monitor states of knowing and perceiving and may control information use and acquisition to serve adaptive decision-making. The precise mechanics underlying this cognitive process, however, still remain undefined, and there are plenty of future experiments still needed to discover the nature of metacognitive system(s) across species and how metacognitive processes may interact with other systems. Those efforts

will have implications for evolutionary psychological science but also for developmental science and cognitive science more broadly. It is also important to note that the presence of metacognitive processes in nonhuman species does not necessarily mean the presence of human-like conscious experiences of those metacognitive processes. Metacognition is not a "switch" in minds, that is either on or off, and when in on mode equivalent in all instances and across all individuals. Metacognition is a regulatory suite of control and monitoring processes, each of which is subject to competition for attention, resource-dependent in terms of how efficiently such control and monitoring processes can occur, and prone to the influences of other mechanisms, both cognitive and associative. That a monkey, a chimpanzee, or a rat can show analogous control and monitoring capacities to those shown by adult humans does not require the assumption of homologous phenomenology across those species. Nonhuman animal metacognition research may illustrate only the glimmerings of human-like conscious states of knowing and not knowing in other animals, but even such glimmerings highlight from where our own fully conscious metacognitive states may have begun. Such insights can provide valuable information to evolutionary psychological science.

Cross-References

- [Cognitive Development](#)
- [Cognitive Science](#)
- [Executive Functioning](#)
- [Evolution of Self](#)
- [Self-Monitoring](#)
- [Theory of Mind](#)

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Metaethical Relativism

- [Cultural and Moral Relativism](#)
- [Misinterpreted as Cultural Relativism](#)

Metaethics

- [Philosophical Foundations for a Modern Morality](#)
- [Relevance of Evolved Interests to Modern Morality](#)

Metamemory

- [Metacognition](#)

Metaphor

- [Ritual and Speech Coevolution](#)

Metaphor and Analogy

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Synonyms

[Blending](#); [Conceptual integration](#); [Conceptual mapping](#); [Convolution](#); [Metonymy](#); [Parable](#); [Simile](#)

Definition

Conceptual understanding that results from mapping, projection, compression, and elaboration of elements from different ideas, different mental spaces, and different concepts.

Introduction

The mental operation of connecting or combining different concepts has been researched under many names over the last 3,000 years. The rhetorical tradition (Aristotle 1995) uses the terms “metaphor,” “metonymy,” “analogy,” “parable,” and “simile” (μεταφορά, μετωνυμία, ἀναλογία, παραβολή, παρομοίωση). Modern cognitive science has contributed the terms “convolution” (Thagard and Stewart 2011), “blending,” and “integration.”

The system of mental principles that guides and governs these operations is complex. Research on the subject stretches back to at least Aristotle, who wrote that “to do metaphor well is to see (*consider*) likenesses” (*Poetics*, XXII, 17; Aristotle 1995). When Aristotle defines metaphor as the transfer of a noun from one thing to another, he means transfer motivated by conceptual relations – either of category (genus to species, species to genus, species to species) or of analogy. Conceptual connection drives linguistic figuration: “To scatter seed is to sow, but there is no word for the action of the sun in scattering its fire. Yet this has to the sunshine the same relation as sowing has to the seed, and so you have the phrase ‘sowing the god-created fire’” (*Poetics* XXI, 14; Aristotle 1995).

The last century has witnessed constant and energetic investigation of the principles of the mental operations of concept combination, with emphasis on human distinctiveness. C.S. Lewis wrote in 1936 that understanding one story figurally in terms of another story belongs not principally to expression and not exclusively to literature, but rather, *to mind in general*, as a basic cognitive instrument (Lewis 1936, p. 44). By “mind,” he meant, of course, the cognitively modern human mind. The history of these traditions of

research is reviewed in (Cacciari et al. 1998; Turner 2005). Fauconnier and Turner (2002) present a review of the current state of research into such principles.

Evolutionary Psychology

Abilities for mental combination of concepts present an open scientific problem for evolutionary psychology. Remarkably, this combination typically involves concepts that would be maladaptive for a mind ever to *confuse* or to misconstrue as *identical*. For example, one of the most fruitful such patterns of combination for human beings consists in understanding another organism as having a full mind, by taking what we can know of that other organism (its appearance and perceptible behavior) and blending it with things we can know of only ourselves: when we move that way, it is because of pain; when we look in that direction, it is because something has caught our attention; and so on. By such complex combination and adjustment, we can have a very full concept of another person. Other species have some of this ability, and research into concepts other species can achieve of other minds has increasingly discovered subtlety (Call and Tomasello 2008).

Still, by all accounts, human beings are in various ways incomparably beyond other species, including chimpanzees and domestic dogs, in these abilities. Human beings do not confuse themselves with another person; they are not deluded; they do not make the mistake of thinking that these two quite different things are identical. But they can combine the concept of themselves with the concept of another person not only to create a concept of a full mind for another person but also to imagine alternative versions of themselves, and even to blend their current self with memories of their previous selves to create the amazing concept of a personal identity, a character that persists over decades. Without confusion, human beings routinely combine concepts that should not be confused.

How could these abilities have evolved? Deacon, in a range of publications (e.g., Deacon 2010), has proposed a process of human self-

domestication, resulting in a relaxation of selection pressure that made it possible for such abilities to arise and be unmasked. Fauconnier and Turner (2002) and Turner (2014) have provided reviews of some possible evolutionary explanations – all highly speculative – of these abilities. They have proposed that capacities for connecting and combining concepts have been evolving for a long time and that human beings show only a relatively slight increase in this ability but that a slight change in causes can make a dramatic difference in effects: cognitively, modern human beings are able to perform the most advanced form of concept connection and combination, and this ability is indispensable for a great range of downstream cognition and behavior – language, art, music, mathematical insight, scientific discovery, religion and ritual, fashion, advanced social cognition, advanced tool conception, and so on.

The known archeological record makes it clear that cognitively modern human beings have had these abilities for at least roughly 50,000 years; claims for earlier capacity would require more evidence, although these claims are not uncommon. For example, archeological discoveries dating from 175,000 years ago in the Bruniquel Cave in southwest France led to speculation that their purpose was symbolic ritual behavior among Neanderthals. But other interpretations view them as used for routine purposes. Absent a time machine or a radically altered archeological record, it is unclear how such questions could be definitively resolved on archeological evidence.

Conclusion

To the author's knowledge, there is no genetic research dedicated directly to explaining the evolution of these cognitively modern mental operations, although there are hints in population genetics work on genetic variation and language about increasing capacity. There is also the hope of discovering something about the evolution of these cognitively modern mental operations by looking for neural substrates, as reviewed in Turner (2014). But these mental operations of

concept connection and combination are higher order, depending upon the activity of many other operations at the same time; they seem to operate over all conceptual domains and, constantly, in the backstage of cognition. Accordingly, it is difficult to see how current brain imaging techniques could provide research instruments for pursuing the evolutionary question. But they are of very recent invention and continue to be improved every decade. As always, we await the improvement of archeological, genetic, and neuroscientific techniques for the study of the cognitively modern human mind, including its ability to connect and combine concepts.

Cross-References

- [Cognitive Changes in Adolescence](#)
- [Cognitive Science](#)
- [Fiction](#)
- [Field of Linguistics, The](#)

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Metaphysical Freedom

- [Free Will \(Philosophy\)](#)

Meta-tool

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Definition

A tool used simultaneously with a second tool to increase the efficiency or effectiveness of the second tool, where the first tool (the metatool) acts directly on the second, without being used in the manufacture of the second tool. (Shumaker et al. 2011)

Introduction

A chimpanzee searches the tropical forest of Bossou, Guinea, for suitable stones. She has collected oil-palm nuts, which can only be opened with tools. Having localized a large tree root, she places a nut on it and strikes it with a stone held in her hand. This is called *pound* or *hammer* tool use, which amplifies the force exerted on the nut through the use of a stone tool. However, her nut-cracking attempt fails because the wood is too soft. She therefore looks for a heavy, flat rock, which she puts on the ground to serve as an anvil. In contrast to the root, this is a tool because she directly manipulates it prior to use and is responsible for its effective orientation. Together, the hammer and anvil form a *tool composite*, defined as two tools used simultaneously to achieve a single outcome. Unfortunately, she fails again because the anvil stone is unstable. She therefore places a smaller stone underneath it, like a wedge, resulting in a stable, horizontal surface suitable for nut cracking (see Fig. 1). This is a subcategory of tool composites called *meta-tool* use; the small stone does not produce but increases the effectiveness of the anvil and both are used simultaneously (Shumaker et al. 2011).



Meta-tool, Fig. 1 Meta-tools in the form of anvil wedging by Bossou chimpanzees. Shown on the *left* is the hammer stone and on the *right* the anvil supported by two wedges. Reprinted from Journal of Human Evolution, Vol. 55, Carvalho et al., Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking, 148–163, Copyright (2008), with permission from Elsevier. <http://www.sciencedirect.com/science/journal/00472484>

How Widespread Is Meta-tool Use?

The term meta-tool use was first coined by Matsuzawa (1991), involving an old chimpanzee female who was provisioned with nuts and stones at an experimental site. He defined it as using a tool for another tool, but this is very broad and would include other tool combinations, such as using a tool to acquire another tool (sequential tool use) or using a tool to modify another tool (secondary tool use). Shumaker et al.'s (2011) definition considers meta-tool use as distinct from other categories involving multiple tools.

With this more restrictive definition, only a few species have been observed to use meta-tools. It has been mostly documented in chimpanzees. *Anvil propping* (the example from the introduction) has since the initial report also been observed in other age-sex classes of the same population (Carvalho et al. 2008; Hayashi 2015; Matsuzawa et al. 2011; Whiten et al. 1999). In one case, two stone wedges were found underneath an anvil stone (Carvalho et al. 2008; see Fig. 1). It is estimated that anvil propping occurs once every 100 visits to the experimental Bossou site and remains stable over different study periods but is more frequent in uneven terrain (Biro et al. 2010).

Chimpanzees and orangutans have been observed to use leaf sponges or paper to absorb liquids, which they then retrieve with a stick (Shumaker et al. 2011; Whiten et al. 1999). This is meta-tool use because although the liquids could be reached with a stick alone, the leaf sponge or paper greatly increases its effectiveness. Capuchin monkeys sometimes use hammers and chisels. Chisels could be used to break through or remove lids and covers, and the stone hammers allow the capuchins to exert more force. Similar meta-tool use involving a hammer and chisel was observed in a home-reared chimpanzee and a zoo-housed orangutan (Shumaker et al. 2011).

The occurrence of meta-tool use is limited outside of the primate order. Hermit crabs occupy empty shells of sea snails for protection. These shells are tools that the crab can make more effective by applying anemones to them for additional protection. In one experiment, this meta-tool use stopped all attacks by octopuses after initial attempts, whereas all hermit crabs inhabiting shells without anemones were eventually consumed (Ross 1971). Satin bowerbirds attract females by decorating bowers, which they construct for this purpose. Some males paint their bowers with charcoal by using a bark wad as a brush. This brush can be considered a meta-tool if it makes applying paint easier or faster (Shumaker et al. 2011).

Anvil Propping

No systematic studies on the cognition underlying meta-tool use have been done, but its complexity is inferred from the number of actions or movable objects involved, the long development to reach proficiency, and the selectivity of tool types. Matsuzawa (1996) mapped the complexity of chimpanzee tool use by developing a hierarchical tree structure as a kind of action grammar. The level is determined by the number of simultaneous relationships between objects used. For example, picking up a nut is level 0 because the object does not relate to other objects. Using a hammer to smash a nut on an anvil is level 2: the nut rests on the anvil (one relationship) and is smashed by the hammer (one relationship). Meta-tool use is level 3 because it introduces another relationship—

that between the anvil and the wedge. Some researchers believe that anvil propping by chimpanzees is the most complex form of tool use exhibited by wild nonhuman animals (Hayashi 2015; Matsuzawa 1996) and that causal understanding is involved if wedge stones are intentionally used to level anvils (Matsuzawa et al. 2011).

Nut cracking is a skill that takes many years to fully develop. Chimpanzee juveniles in Bossou first succeed between 3.5 and 7 years old and reach proficiency between 8 and 14 years. There appears to be a sensitive ontogenetic phase in which nut cracking must be learned, or else it does not develop at all (Matsuzawa et al. 2011). Adults exhibit selectivity in what tools to use; hammers are typically lighter and smaller than the anvils. This is a sign of their behavioral flexibility that relies on their cognitive abilities (Carvalho et al. 2008). They adjust the height to which the hammer is lifted and the force with which to strike, depending on the nut type, hammer weight, and anvil surface. If their tool use is ineffective, they reposition their tools or switch to others (Matsuzawa et al. 2011).

A 2-year-old infant kept in captivity succeeded at such a young age because it had more experience manipulating objects and watching adults crack nuts (Hayashi 2015). Social learning appears to be an important factor in learning this behavior. Some populations do not crack nuts despite sufficient ecological circumstances, which supports the argument that it is a culturally transmitted behavior (Whiten et al. 1999). The type of nut to crack seems also to be socially learned. When unfamiliar nuts were introduced into the Bossou community, they were mostly ignored even by expert nutcrackers, but one female immediately cracked them. It is likely she migrated at an early age from a neighboring community where these kinds of nuts are commonly cracked. After prolonged exposure to these unfamiliar nuts, more individuals attempted to crack them, and the behavior slowly spread through the community while exploratory behaviors decreased. All juveniles attempted to crack artificial wooden balls that resembled unknown nuts, which suggests that novel nut types may initially

be discovered to be exploitable food sources through the general manipulative and explorative tendencies of juveniles (Matsuzawa 2001; Matsuzawa et al. 2011).

The development of anvil propping has not been studied in detail due to its infrequent occurrence. The youngest age at which a wild chimpanzee has been observed to use such meta-tools is 6.5 years. Children of the Bossou village first succeeded at a similar age (Matsuzawa 2001; Matsuzawa et al. 2011). It is likely that the use of anvil propping in chimpanzees is learned through similar processes as hammer-anvil use. Using these tools is necessary for nut cracking, but meta-tool use is only rarely beneficial. If an anvil is too unstable or slanted, it can be exchanged for another, rotated, flipped over, or moved to another location with a more suitable substrate. Wedging a stone under the anvil may be a final recourse, one that is infrequently used because it requires an additional object and an unusual action (Matsuzawa et al. 2011). One line of evidence for this explanation is that chimpanzees transport anvils and hammers more frequently than wedges (Carvalho et al. 2008). It should also be noted that finding meta-tools does not necessarily point to purposive behavior. In some cases chimpanzees rotated an anvil to find a stable position and accidentally flipped it on top of another stone (Hayashi 2015).

Conclusion

Meta-tools are rarely used by nonhuman animals. One reason for this may be that they are often unnecessary. Simpler solutions are then preferred that do not involve complex relationships and additional objects. However, only little research has been done on meta-tool use, and much of it is confused with other categories that also involve multiple tools due to unclear definitions. Further investigations should establish which other species use meta-tools – in conditions that are ecologically relevant or experimentally induced – and may unravel its cognitive requirements when other solutions are unavailable.

Cross-References

- [Evolution of Tool Use](#)
- [Nonhuman Tool Use](#)
- [Sequential Tool Use](#)
- [Tool Manufacturing](#)

References

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Method of Successive Approximations

- [Shaping](#)

Methodological and Phenomenological Narrowness

- [Towards Methodological Pluralism in Psychological Sciences](#)

Methodological Pluralism

- [Towards Methodological Pluralism in Psychological Sciences](#)

Methodological Relativism

- [Misinterpreted as Cultural Relativism](#)

Methods and Enduring Impact of Behaviorism

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Synonyms

[Applied behavior analysis](#); [Experimental analysis of behavior](#); [Single-subject experimental design](#)

Definition

Behavior analysts rely on single-subject experimental designs in which variables that control behavior are directly manipulated and their effects are directly observed. Because of the high degree of experimental control and powerful intervention effects, behavior analysts prefer visual analysis of data over statistical analysis.

Introduction

The methodology used in behavior analysis is a defining feature of this field. Fundamentally, behavior analysts use experimental methodologies in which direct control over independent variables can be exerted. Behavior analysts manipulate these variables to measure their direct impact on behavior (cf. Sidman 1960). Rate of responding is commonly used by behavior analysts, but other dimensions of behavior are also measured. For example, latency to respond, or percent correct, or the number of intervals in which a response occurs could all be used, depending on the target behavior under consideration (Cooper et al. 2007). The application of these research methods has produced a behavioral technology (i.e., a set of procedures that can reliably be used across settings, individuals, and target behaviors) that has been used to solve behavioral problems in humans and nonhuman animals.

Methodology

The science of behavior analysis focuses on observable behavior and does not appeal to theories that describe the events at another level of discourse (e.g., physiology, mental events; cf. Skinner 1950). This emphasis on behavior itself is at odds with what Tooby and Cosmides (1989) saw as the more important goal of “the investigation and characterization of the innate psychological mechanisms that generate and regulate behavior” (p. 32).

Rather than relying on between-groups experimental designs with large numbers of subjects and statistical inference, behavior analysts prefer single-subject (or within-subjects) designs with experimental control over statistical control. That is, manipulation of controlling variables yields functional relations between their selected independent variables and behavior (their dependent variable). Behavior analysts generally reject statistical analyses (cf. Perone 1999; Sidman 1960) and instead use visual analysis of data. Visual analysis involves systematically examining graphic displays of data to identify how behavior has changed and the extent to which the independent variable or environmental manipulation is responsible for that change (Cooper et al. 2007). To effectively use visual analysis, behavior analysts must select and manipulate variables that directly impact the behavior under study.

Instead of comparing between groups, behavior analysts usually take repeated measures, relying on the individual subject to serve as his or her own control. This tactic reduces the amount of variability that is necessary to control or explain, allowing for powerful demonstration of experimental effects (cf. Sidman 1960). The establishment of a baseline is the first step in a single-subject experimental design.

The baseline is a pre-intervention measure of the behavior of interest. Generally, the baseline phase lasts until behavior stabilizes or reaches a steady state (i.e., there is limited variability in the data, and there is no increasing or decreasing trend). Because behavior analysts attribute behavior change to environmental events, it is assumed that the steady behavioral state would continue until an environmental change occurs; given a consistent environment, behavior should continue, unchanged. This assumption of steady-state methodology allows for the meaningful comparison of subsequent intervention phases with the established baseline. Of course, there may be circumstances that prohibit achieving stability; for example, if the target behavior is too dangerous to continue, as with self-injury, an intervention may be applied before stability is achieved.

Most single-subject experimental designs involve the administration of an intervention following the baseline. For example, if the target behavior is occurring less often than is desired, a reinforcement technique could be employed to strengthen the response. Behavior is then measured for some period of time, usually until stability is regained. A return to baseline conditions (i.e., the withdrawal of the reinforcement) can allow for the assessment of the durability of the behavior change. This baseline-intervention-baseline pattern comprises the simplest single-subject design, the reversal design.

More complex variations of the reversal design can also be employed, depending on the research question. If a phenomenon's generality is of interest, a multiple-baseline design could be used, in which more than one baseline is sequentially established across individuals, participants, or behaviors. By applying the intervention in a staggered fashion (i.e., extending some of the baselines while measuring change in the targeted behavior, individual, or setting), it is possible to demonstrate the generality of an intervention's effectiveness. Maintaining baseline conditions for the other settings (or individuals or behaviors) allows for the demonstration of causality—that is, behavior should only change when the intervention is introduced and not before.

Not all procedures involve a stable baseline before changing environmental events. A multielement (or alternating-treatment) design involves rapid transitions between experimental conditions. Multielement designs are frequently employed when applied behavior analysts conduct a *functional analysis*, a technique which allows the behavior analyst to identify the reinforcers that maintain a particular response. Depending on the function of the behavior (i.e., the relevant reinforcer), an appropriate intervention can be selected to decrease the occurrence of the target response (cf. Iwata and Dozier 2008). Common reinforcers include attention, escape from a situation, access to goods or edibles, or sensory stimulation (Cooper et al. 2007). These consequences may derive their reinforcing efficacy because of the evolutionary history of the organism under study.

If the goal of the intervention is to gradually change (i.e., increase or decrease) behavior to reach a goal, a changing-criterion design could be employed. In this type of design, the experimenter sets a goal level of responding. For example, a teacher may say that a student should answer ten questions correctly on a ten-item quiz. As this goal might be beyond the current performance of the student, a lower goal (e.g., six correct answers) could be set initially. Meeting that goal would result in the delivery of a reinforcer. After a few sessions of successfully meeting the initial goal, the goal can be gradually increased (e.g., seven correct responses) for another block of sessions. Beginning with a goal that is attainable for the learner and gradually increasing the requirement make it more likely that they will successfully achieve the desired performance.

Despite the strengths of single-subject methodologies for identifying variables that directly influence behavior for a particular organism, there are some potential limitations to these designs. Not every relevant variable can be manipulated, due to practical or ethical constraints; this limitation requires that some questions be answered using correlational or between-groups experimental designs. Additionally, the generality of interventions might be limited, since only a few organisms are used in this type of research. However, replication or the use of a multiple-baseline design could help to ameliorate this concern. The influence of any intervention would need to be evaluated on the target individual before knowing that it is effective. This functional, individualized approach to scientific inquiry and intervention epitomizes the behavior-analytic approach. Whereas this approach is well suited for behavior-analytic questions of environment-behavior interactions, it may be less appropriate to answer the questions of “the discovery and characterization of psychological mechanisms as adaptations” (Tooby and Cosmides 1989, p. 32), since behavior analysts would refer more to proximate, immediate environmental events as causal explanations instead of psychological mechanisms. However, the search

for individual-level explanations for group-level processes (Tooby and Cosmides 1989, p. 45) might benefit from the use of single-subject experimental designs.

Impact

Despite the advent of cognitive psychology and the continued reliance on statistical analysis by mainstream psychology, the discipline of behavior analysis continues to be vibrant. Since 1957, the *Journal of the Experimental Analysis of Behavior* has published basic behavior-analytic research. The *Journal of Applied Behavior Analysis* began its publication in 1968; this field uses the techniques of behavior analysis to solve socially significant problems (cf. Baer et al. 1987).

Although applied behavior analysis is known predominately as a technique for providing treatment to individuals with developmental disabilities, there are a host of other applications that have made remarkable contributions to improve life for people across the developmental spectrum. Using the techniques of behavior analysis, researchers and practitioners have reduced self-injurious behavior (cf. Iwata and Dozier 2008), detected landmines and tuberculosis (Poling et al. 2011), reduced drug abuse (Alessi and Petry 2013), and promoted environmental sustainability (Lehman and Geller 2004).

Conclusion

The principles and methodologies pioneered by B. F. Skinner and his fellow behavior analysts have led to the ability to predict and influence behavior of human and nonhuman animals. Wherever there are behaving organisms, their behavior can be understood, and the principles of behavior analysis can be applied to help them live more effectively.

Cross-References

- [B. F. Skinner and Behaviorism](#)
- [Conditioning and Association](#)

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Methods of Filicide

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Synonyms

[Child homicide](#); [Childhood fatalities](#); [Family violence](#); [Infanticide](#); [Neonaticide](#)

Definition

The murder of a child by a parent or stepparent.

Introduction

It would seem as though filicide is a flagship example for a behavior does not seem to fulfill an ultimate goal of evolution: the passing of one's genes onto the next generation. This section seeks to answer the *who* and *with what* questions, rather than the *why* question of filicide. The method in which a parent – or stepparent – uses to murder their child has discrete features and is a source of information into the relationship this person has with the child.

Methods of Filicide

A distinction lies between how different individuals commit filicide: whether or not that child shares genetic material with that individual. In a pivotal article, Daly and Wilson (1994) found stepfathers were more likely to commit filicide by beating and bludgeoning than genetic fathers, who were more likely to use faster methods of killing by shooting or strangulation.

Furthering this line of work, Weekes-Shackelford and Shackelford (2004) analyzed homicide reports for instances of filicide, the perpetrator, and the method of killing in the United States between 1976 and 1994. Children under the age of five were eight times more likely to be killed by a stepfather than by a genetic father and three times more likely to be killed by a stepmother than a genetic mother. For the method of killing, beating by a stepparent comprised 93 % of filicides compared to 67.6 % by genetic parents. For suffocation-drowning-strangling, 5 % of filicides by stepparents utilized this method and 18 % of filicides by genetic parents. For shooting, 1 % of filicides by stepparents utilized this method and 5.8 % of filicides by genetic parents. Stepparents are more likely to choose a method of filicide that is aggressive, violent, painful, and prolonged. Genetic parents are more likely to choose a method that is quick and relatively painless.

Age of the victim can be a factor. Lewis et al. (1998) discovered older children were

significantly more likely to be killed with weapons (e.g., knife, gun) than younger children. Moreover, psychotic women were more likely to utilize weapons to kill their children than non-psychotic women. Young children (less than 10 years of age) tend to be bludgeoned to death, smothered, drowned, or strangled – potentially due to the relative ease to execute these acts on their smaller bodies, negating the need for a lethal weapon. It was only when the woman was psychotic (suffering from hallucinations and/or paranoid delusions) that she would use a lethal weapon on her very young child.

The duration of the act is also a factor when the perpetrator chooses a method. Debowska et al. (2015) conducted a review of filicide in the United Kingdom. Their results supported the notion that genetic parents utilized methods that hastened death, such as carbon monoxide poisoning, strangulation, or drowning while stepparents used methods that prolonged the event, such as battery. In Taiwan, an uptick in mothers burning charcoal to produce lethal levels of carbon monoxide as a means to achieve maternal filicide-suicide was discovered. The inhalation of the gas results in what is colloquially known as a “painless death,” thereby becoming a popular method of filicide in the country (Yasumi and Kageyama 2009). Indeed, Bourget and Gagne' (2002) discovered maternal filicides in Quebec between 1991 and 1998 were most commonly committed by carbon monoxide poisoning, firearm, strangulation, or drowning. The majority of these mothers suffered from major depressive disorder.

The mere presence of an unrelated adult can significantly increase a child's odds of being murdered. Schnitzer and Ewigman (2005) discovered children less than 5 years old living in households with unrelated adults were almost 50 times as likely to die of inflicted injury than children residing with both biological parents in Missouri between 1992 and 1999. The majority of these deaths were caused by shaking or striking that resulted in head, thoracic, abdominal, or multiple traumas – followed by suffocation, firearm, poison, or burns. In 2007, a Canadian study revealed filicide by a stepparent was common and the method of killing involved

protracted abuse and neglect prior to death by beating (Harris et al. 2007).

Another method of filicide is the phenomenon of *unintentional fatality* – death as a result of an event that is an accident. Examples of events precluding childhood death include road accidents, falls, suffocation, burns, drowning, or poisoning. Vigilance against threats of these kinds towards children would be evolutionarily advantageous and ever present in parents hoping to secure the safety and well-being of their genetic off-spring. Tooley et al. (2006) found in Australia, the risk of death due to unintentional injury was between 2 and 15 times greater for stepchildren than for children in complete biological families. Drowning increased this effect of endangerment dramatically. Furthermore, fatalities of children who lived with zero biological relatives were present in every fatality category (violence-related fatalities, drowning, and all unintentional fatalities).

Conclusion

While the motive may vary, it seems as though sharing genetic material with the victim influences the method of killing – even in death the profound impact of the relationship is maintained. The genetic parents act quickly and choose a method that is perceived to be painless. Stepparents, lacking in genetic kinship, utilize methods that are protracted and painful. Devastatingly, children living with unrelated adults are put at an increased risk of suffering fatal harm. While intentional harm from a gun or a fist is an obvious method of filicide, patterns in unintentional fatality from accidents pose a striking resemblance to intentional methods of filicide.

Cross-References

- Cinderella Effect, The
- Child Homicide
- Filicide
- Grandparental Investment and Genetic Relatedness

- Infanticide and Parenting
- Infanticide in Nonhumans
- Kin Selection
- Stepparents

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Metonymy

- Metaphor and Analogy

Mezzosoprano

- Music and Hormones

MHC Compatibility

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Synonyms

Human leukocyte antigen (HLA) system; Major
histocompatibility complex (MHC)

Definition

The *Major Histocompatibility Complex* (MHC) refers to a large, highly dense genomic region found in most vertebrates which encodes proteins that display both self- and non-self antigens to white blood cells called T cells that can eliminate pathogens or malfunctioning cells. In humans, the MHC is also called the Human Leukocyte Antigen (HLA) system. MHC Compatibility refers to the role of the MHC in mate selection.

Introduction

Since the debut of major histocompatibility complex- (MHC) dependent mate preferences in mice in 1976 (Yamazaki et al.), a number of studies have been conducted to determine the role of MHC across species, identify mechanisms of MHC identification, and distinguish among hypotheses about the adaptive significance of having this ability. Three main hypotheses have been suggested (discussed in Penn and Potts 1999): first, that dissortative mating on MHC genotypes produces MHC-heterozygous offspring, which enhances immunocompetence (i.e., heterozygote

advantage hypothesis); second, that a preference to mate with MHC-dissimilar individuals enables the host to be a “moving target” in a coevolutionary arms race with parasites (i.e., frequency-dependent selection hypothesis, or Red Queen hypothesis); and finally, as a mechanism to avoid inbreeding and to identify kin.

Innate and Adaptive Immune System Responses

There are several lines of defense in the immune system; for example, physical barriers such as the skin obstruct the entry of bacteria and viruses from entering the body (Janeway et al. 2001). Once a pathogen has passed this initial barrier, the innate immune system responds immediately (although non-specifically to the particular pathogen). The third layer of defense, the adaptive immune system, is activated if a pathogen survives the innate immune response. This adaptive system has the unique property of antigen recognition and memory, such that the response is improved after the initial introduction of the pathogen. As a result, the adaptive immune system is able to respond more quickly and with a specified target if the pathogen is encountered again.

Both the innate and adaptive immune responses require the ability to distinguish between self- and non-self molecules (Janeway et al. 2001). *Non-self molecules* refer to peptide fragments of invading organisms, such as bacteria, viruses, or pollen. *Self-molecules* refer to peptide fragments originating from a protein created by the organism. Antigens (short for antibody generators) are molecules that bind to immune receptors, eliciting an immune response in the case of non-self molecules. MHC genes play an integral role in self- and non-self distinction. This large, highly dense genomic region is found in most vertebrates; its role in the immune system cannot be understated. The MHC encodes proteins that display both self- and non-self antigens to white blood cells called T cells that can eliminate pathogens or malfunctioning cells. T cells

recognize non-self antigens only after they have been presented by an MHC molecule.

In humans, the MHC goes by a different name: the human leukocyte antigen (HLA) system (MHC and HLA will be used interchangeably throughout this chapter when referring to human research). Most research on human MHC-dependent behaviors assay class I and/or class II molecules. Class I molecules include HLA-A, -B, and -C; these are found on all nucleated cells in the human body and present endogenous peptides (e.g., viral proteins) from inside the cell to cytotoxic T cells. Class II molecules, which include HLA-DR, -DP, and -DQ, present exogenous (e.g., fragments of bacteria or viruses) antigens outside of the cell post-phagocytosis to helper T cells that then activate a B cell immune response (Janeway et al. 2001).

Evolutionary Origins of the MHC

Beck and Trowsdale (2000) review evidence that indicates an origin of the locus predating the adaptive immune system. In fact, several MHC genes occur in the same order on the chromosomes of invertebrates such as *Drosophila melanogaster* and *Caenorhabditis elegans*. The class III region of the MHC appears to be the oldest, based on the conservation of a class III gene in yeasts. Both class I and class II regions seem to have evolved by multiple duplications. For example, HLA-DP and HLA-C show evidence of recent duplications from shared ancestral sequences.

MHC-Dependent Mating

Yamazaki et al. (1976) was among the first to identify MHC-dependent mate preferences. This study was conducted using genetically identical mice except in the MHC region and showed that the mice preferred MHC-dissimilar conspecifics as mates. The preference for dissimilarity was subsequently shown in several other species, such as salmon, sticklebacks, and humans (reviewed in Potts 2002).

Several studies were reviewed in Penn and Potts (1999; see also Havlicek and Roberts 2009) that seemed to provide general support for MHC-dependent mate preferences. Egid and

Brown (1989) showed that female mice preferred MHC-dissimilar mates when they were in estrus, providing support for an adaptive function of this ability. Mating with dissimilar individuals results in offspring heterozygosity, which may provide a selective advantage. For example, when MHC heterozygote mice were infected with HIV, they progressed more slowly to AIDS than homozygotes (Carrington et al. 1999). Similarly, the proportion of MHC heterozygote progeny increased when an epidemic struck a mice colony (Wedekind et al. 1996). A separate study showed that when mice were administered a viral vaccine, virus escape mutants emerged more easily in MHC homozygous mice than in heterozygous mice (Weidt et al. 1995).

At least in mice, MHC-based mate preference may develop postnatally (the case may be different in humans as will be discussed later). Yamazaki et al. (1988) showed that it is mediated by olfactory experience; moreover, mice tended to avoid maternally derived matching MHC haplotypes. Providing further evidence for postnatal imprinting, cross-fostered mice preferred mates dissimilar from the foster family even if it meant mating with more MHC-similar conspecifics (Beauchamp et al. 1988). Interestingly, MHC odor identity may be encoded spatially (Schaefer et al. 2002). This study showed that mice are able to distinguish one another based on a suite of alleles. In addition to identifying individual body scents based on genetic differences in all class I genes, mice can also identify individuals based on a single class I gene alone. Moreover, neural activation patterns in the main olfactory bulb are different and unique for odors from genetically different mice.

An important limitation of the aforementioned studies using mice models is that mice are not tested in their natural environment (Petrinovich 1979), which discounts the role of systemic processes and limits the generalizability of the findings. An elegant solution to this problem comes from research on three-spined sticklebacks (Eizaguirre et al. 2009). This study measured the reproductive success of sticklebacks that were placed in seminatural enclosures located in their natural breeding areas. As a result, these fish were

continuously exposed to parasites that lived in their natural ecology but were isolated from the risk of predators. Eizaguirre et al. (2009) genotyped nearly 4000 eggs using nine microsatellites to determine parenthood and to infer female mate choice. The results of this study showed that females tended to prefer males with an intermediate MHC diversity (i.e., not too similar, but not too dissimilar either). Moreover, in support of a preference for “good genes,” females also tended to prefer males with an MHC haplotype that resulted in stronger immunity against a common parasite. As a result, these males enjoyed more reproductive success than males without this haplotype. This finding seems to indicate that the female mate choice “favored locally adapted genes against the most prevalent pathogens” (p. 3317).

Human Evidence

Several studies have examined the role of the MHC in mating using the so-called T-shirt paradigm because human chemosensory communication is thought to occur via the apocrine glands in the skin, which do not significantly develop in adults until puberty. Apocrine glands are associated with hairs and are concentrated in the axillary organ, or armpits, but are also found around the navel, chest, breasts, areola, and genitals. Mechanisms for MHC identification and discrimination by the main olfactory system (Pause et al. 1996; Schaefer et al. 2001) may lie in its genetic influence of microbial flora (Singh et al. 1990) and concentrations of volatile acids (Singer et al. 1997). Axillary sweat has more volatile organic compounds than saliva or urine (Penn et al. 2007) and thus may be an important medium for MHC information transmission in humans. Importantly, Penn et al. (2007) found “odor fingerprints,” such that humans can distinguish the scent of different individuals. However, in monozygotic twins (but not dizygotic twins), odors are perceived as coming from the same individual (Roberts et al. 2005).

Wedekind et al. (1995) were among the first researchers to study human MHC-dependent body odor preferences, showing that naturally cycling females rated MHC dissimilar odors as more pleasant than MHC similar odors. The

women also indicated that MHC dissimilar odors reminded them of a current or past mate. In a follow-up study, the same authors examined whether MHC-dependent mate preferences aim for a specific MHC haplotype or just general dissimilarity from one’s own MHC haplotype (Wedekind and Furi 1997). Using the same design as the 1995 study, participants who were typed at three HLA loci were asked to rate previously worn t-shirts (the wearers of which were also typed for the same three HLA loci) on pleasantness and intensity, guess the gender of the t-shirt wearer, and to write memories for associations to relatives or mates. While the raters were unable to correctly guess the gender of all of the t-shirt wearers (although females tended to be better at guessing), memory associations for past or current mates were associated with fewer shared MHC alleles. In both the 1995 and 1997 studies, naturally cycling women preferred MHC-dissimilar odors as expected. Interestingly, however, women using contraceptives tended to prefer MHC-similar odors. The authors interpreted the latter finding as a reflection of how hormonal contraceptives work: by simulating pregnancy. Thus, women whose bodies “think” they are pregnant tend to prefer similar odors because they indicate kinship. Who better to associate with than kin if a woman is pregnant?

The role of oral contraceptives in MHC preference was explored more fully in a longitudinal study where women were tested before and after initiating birth control use (Roberts et al. 2008). Using a within subjects design, these authors assessed female odor preferences using t-shirts twice over a 3-month period. For the first assessment period, which occurred between days 10 and 14 of the ovulatory cycle (corresponding to the days of highest fertility and ovulation), all of the women were naturally cycling (i.e., not using hormonal contraceptives). The second assessment period occurred approximately 3 months later during the same window; however, about half of the women initiated the use of hormonal contraceptives in the interim while half remained naturally cycling. During each assessment, the women were presented with three MHC similar and three MHC dissimilar male odors and were asked to rate

them on pleasantness, intensity, and desirability (as a long-term partner), and to write any odor associations with current or past partners or with relatives.

While the results failed to show a significant effect of MHC dissimilarity in either session one or session two, nor did they show an effect of male heterozygosity on any of the three characteristics measured, there was an interesting effect with regard to the initiation of birth control use. The data showed a decreasing preference for dissimilarity across the two sessions for the pill-using group. In other words, after taking birth control, women tended to prefer MHC dissimilar mates *less*, thus showing a direct effect of contraceptives on MHC preference.

There is reason for concern for this shift in preference. For example, there is evidence for spontaneous abortion of MHC-similar pregnancies (Ober 1992), which indicates a mechanism of postcopulatory mate choice. On the other hand, Hedrick (1992) showed that MHC homozygous abortions did not occur at higher than chance rates and concluded that the deficiency of homozygotes in the study sample provides evidence for dissimilar mate selection. Mating with MHC-similar individuals may also result in longer interbirth intervals (Roberts et al. 2008), and homozygosity may be undesirable because it handicaps the organism's ability to thwart pathogens (Carrington et al. 1999; Weidt et al. 1995).

While MHC homozygosity may be undesirable for the aforementioned reasons, too much heterozygosity may be undesirable as well (Eizaguirre et al. 2009; Penn et al. 2007; Roberts 2009). An associated cost of having too diverse of an MHC may lead to the preference for an intermediate preference found in several studies (Eizaguirre et al. 2009; see also Roberts 2009 for a review). In addition to being costly, MHC dissimilarity may be in competition with other desirable traits, such as good genes.

Jacob et al. (2002) conducted a study to determine whether HLA discrimination is based on exposure to family members during development or on inherited HLA alleles. As previously noted, studies in mice have shown a role for postnatal imprinting (Beauchamp et al. 1988; Yamazaki

et al. 1988), but this possibility had not yet been examined in humans. The results of Jacobs et al. showed that odor preference was related to HLA similarity, such that women tended to prefer odors of individuals who had more allele matches with themselves. These preferred HLA similar odors were also *not* rated as more familiar, as has been shown in previous studies (e.g., Wedekind and Furi 1997). The most interesting finding, however, was that the preference was based on the HLA alleles that a woman inherited from her father, but not her mother. In addition, there was a positive correlation between the number of matches to paternally inherited alleles and the rating of the odor. Furthermore, alleles that were not inherited did not influence odor preference even though the women were exposed to them during development.

The findings from Jacob et al. (2002) are complemented by a naturalistic study that measured HLA similarity in a sample of married Hutterites (Ober et al. 1997). They found that fewer married couples matched on HLA haplotypes than would be expected by chance. In those couples that did have matching HLA haplotypes, the haplotype was significantly more likely to be inherited from the father. When maternally inherited alleles were involved, however, HLA dissimilar mate preferences were found. Potts (2002) suggested that paternity uncertainty may underlie the mediation of paternal inheritance in odor preference and that imprinting on paternally inherited MHC would serve as a robust source of paternal information.

Conclusion

Numerous studies have examined the role of the MHC/HLA in human mating preferences with conflicting results. Of the 21 studies reviewed by Havlicek and Roberts (2009), five investigations of body odor preferences reported significant disassortative (i.e., preference for MHC dissimilar to oneself) effects, one intermediate dissimilarity effect, and three nonsignificant tests. Of the tests of MHC influence on mate facial preferences, three showed preferences for heterozygosity, one

for assortative mating, and four were nonsignificant. Among investigations of the role of MHC in marital choices, two reported disassortative pair-bonds, one assortative pair-bonds, and seven were nonsignificant. Thus, while extant inquiries provide some support for MHC-based mate preferences, further research is necessary to elucidate the conditions under which they produce a measurable effect on mating behavior and offspring survival.

Cross-References

- [Kin Selection](#)
- [Mate Choice Effects](#)
- [Ovulatory Shifts in Psychology](#)
- [Paternity Uncertainty](#)
- [Pathogen Resistance](#)
- [Sexual Selection](#)

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Michael A. Woodley of Menie, Yr.

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Professional Life

Michael Anthony Woodley of Menie, Yr. (Younger), is a self-described sociobiologist with interests in traditional and molecular behavioral genetics, community and theoretical evolutionary ecology, evolutionary cliodynamics, and psychometric theories of human intelligence and life history (LH) strategies.

Woodley of Menie is a Lifetime Fellow at the Center Leo Apostel for Interdisciplinary Studies, Vrije Universiteit Brussel, Brussels, Belgium.

His most notable contributions have been: (1) Cognitive Differentiation-Integration Effort Theory, which concerns the systematic attenuation of the correlations among the different components of human intelligence by slower LH speeds; (2) the Co-Occurrence Model of Secular Trends in Human Intelligence, which resolves *Cattell's paradox*, or the apparent incongruity

between the observations of persistent selection against intelligence (which is highly heritable) and rising IQ test performance over time (i.e., the Flynn effect); and (3) the Social Epistasis Amplification Model, which posits that (i) deleterious mutations have been accumulating in certain populations due to the relaxation of purifying selection over recent historical time, and (ii) some of these mutations are “spiteful,” meaning that they have the potential to reduce the fitness of organisms that do not carry them via inter-organismal gene-gene transactions, i.e., social epistasis, and thereby undermine the group-level fitness of entire populations. Since its introduction in the early 2010s, the Co-Occurrence Model in particular has inspired an increasing amount of empirical research and generated some vigorous controversy (see Sarraf 2017).

The sections below discuss a few details of Woodley of Menie's background, his history of education, and his most notable contributions to science.

Background

Michael Anthony Woodley of Menie, Yr., was born in Guildford, United Kingdom, on 16 May 1984. His father, also named Michael Woodley of Menie, is the (28th) Feudal Baron of Menie (Dewar 2001, p. 1530), and his mother is named Caroline, née Cuthbertson. His younger brother is named Anthony, an independent filmmaker, and his younger sister is named Perdita, now surnamed McShan, an Events Organizer. His father's family has its roots in the Scottish landed gentry, and he is related to the twentieth-century Scottish Industrialist William Ritchie, who co-founded the engineering firm Grant, Ritchie & Co. He is also related, through his mother, to Lauren Cuthbertson, a Principal Artist of the Royal Ballet, and to Professor Keith Cuthbertson, a Professor of Finance and Macroeconomics at the Cass Business School, City, University of London.

Woodley of Menie spent most of his childhood in a country house named The Ford, in Northern Surrey, England, which was once owned by

Steven Coleridge, the author of a book about the residence entitled *Digressions*. While living there, Woodley of Menie attended the General Gordon Memorial School, a military school founded by Queen Victoria, and graduated in 2002. Afterwards, he began his undergraduate work at Columbia University, New York, majoring in ecology, evolution, and environmental biology and completing his BS in 2007. He was then accepted into the plant sciences program at the School of Biological Sciences, Royal Holloway, University of London, which conferred his PhD in 2011. He was a 2015 Recipient of an Association for Psychological Science *Rising Star* designation for producing the best-supported model of the Flynn Effect (as evidenced by Pietschnig and Voracek 2015) based on LH theory. Most recently, he was identified as one of the top six most frequent contributors to the journal *Intelligence* (the leading journal of intelligence research; Pesta 2018) and was appointed to the editorial board of that journal in 2018.

Major Contributions

Cognitive Differentiation-Integration Effort Theory

In 2011, Woodley of Menie published a notable meta-analysis of all the data then available on the relation between the general factor of intelligence (g) and the general factor of LH strategy (K), finding no significant or substantial relation whatsoever. This meta-analysis was occasioned by and contradicted the prior predictions of human LH theorists, such as J Philippe Rushton, who argued that g and K should be positively associated at the individual-differences level – meaning that higher levels of g should go with *slower* LH speeds (i.e., higher levels of K). This prediction was reasonable given that slower LH speeds positively correlate with brain size across many nonhuman animal species (see, e.g., Rushton 2004). Nevertheless, nearly every psychometric laboratory in the world that has investigated the relationship between g and K has failed to find any substantial association between these variables at the individual-differences level in humans, consistent

with Woodley of Menie's meta-analytic finding. The Ethology and Evolutionary Psychology (*EEP*) Laboratory at the University of Arizona conducted most of this research and could find no appreciable correlation between g and K over the better part of a decade (the “naughties”). *EEP*'s meta-analysis of this research yielded a negligible, but positive and statistically significant, correlation between g and K ($\rho = 0.06$, $p < 0.05$). What Woodley of Menie did next was something that is widely recommended, although seldom practiced, within empirical science: he made a risky prediction regarding the true nature of the relationship between g and K (Woodley 2011). This prediction was called the Cognitive Differentiation-Integration Effort (*CD-IE*) hypothesis. This hypothesis proposed that higher levels of K may not greatly influence absolute levels of g , but instead attenuate the *strength* of the positive manifold of correlations among the indicators that constitute the common factor of g . To test this theory, he contacted the *EEP* laboratory that had accumulated the preponderance of the aforementioned disconfirmatory data, and shortly thereafter published four successful empirical tests that demonstrated and replicated the *CD-IE* effect (Woodley et al. 2013a). Later that year, the same team (Figueredo et al. 2013) extended this theory to apply to the strength of the positive manifold of correlations among the indicators of K , showing that higher values of K tend to decrease the loadings of that common factor among its own constituent indicators (LH traits); Spearman's Law of Diminishing Returns (*SLODR*) identifies an analogous phenomenon in the case of g . This theoretical generalization was named the *Strategic* Differentiation-Integration Effort (*SD-IE*) hypothesis, in contrast to the previously proposed *Cognitive* one. The hypothesis was immediately supported by the converging evidence of multiple successful replications, which was reported in a publication that also cross-validated *SD-IE* in several demographically heterogeneous samples (Figueredo et al. 2013).

Several years afterwards, an expanded version of the same team of *EEP* researchers cross-validated both the *CD-IE* and *SD-IE* effects cross-culturally in cross-sectional data at the

level of synchronic subnational- and national-level politics (e.g., Figueredo et al. 2016).

All of these differentiation-integration theories hold that the differentiation of these common psychometric factors constitutes an adaptive niche-splitting response to inter-individual competitive pressure, as in the *Coral Reef Model* of the evolution of individual differences in personality (Figueredo et al. 2005); further, they hold that the integration among these factors' indicators represents an adaptive response to the presence of environmental instability and unpredictability, favoring obligate generalism.

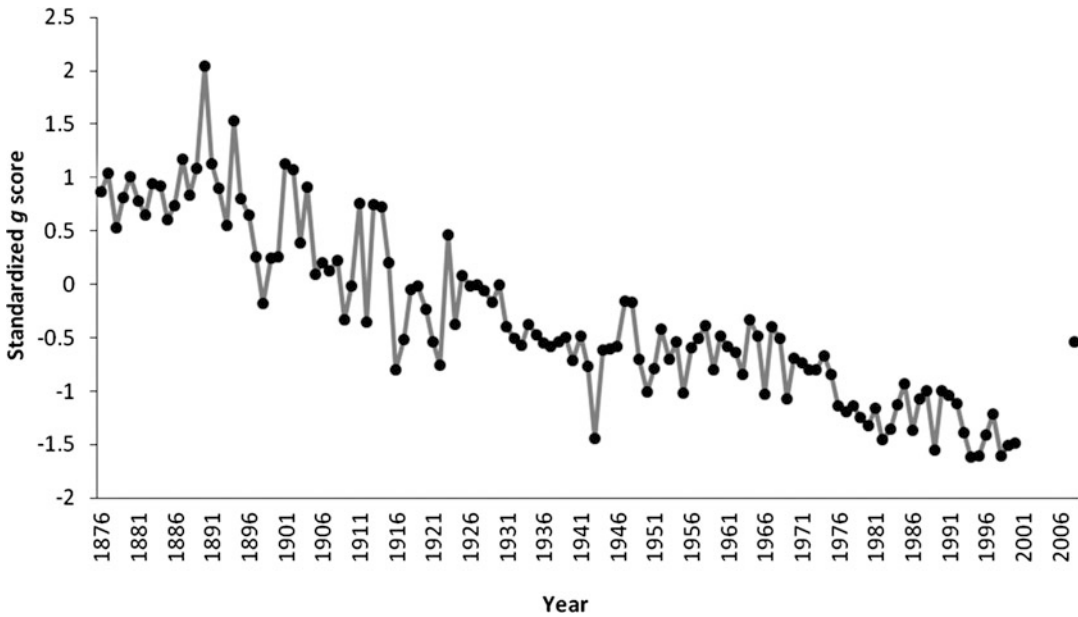
The Co-Occurrence Model of Secular Trends in Human Intelligence: General Intelligence Decline

Woodley of Menie is best known for his work on declining g in Western populations, as distinguished from secular increases in other dimensions of human intelligence (the Flynn effect); these two trends are the *explananda* of the *co-occurrence model* (see the immediately following section on “[Partitioning IQ Change](#)”). He and his colleagues have argued that the primary cause of this decline is the tendency of individuals with higher levels of g to have fewer children than their lower- g counterparts. Woodley of Menie et al. (2017a) argued that industrialization and climatic warming imposed this regime of “dysgenic” fertility (or selection) favoring lower population levels of both g and group-selected altruism in the West, in that these phenomena reduced environmental harshness; both theoretical considerations and empirical evidence support the idea that g advantages the fitness of groups and individuals in harsh environments but lowers their fitness in more benign environments, where selection pressures are reversed. This evolutionary explanation of falling population-level g is called the theory of dysgenic selection.

Woodley et al. (2013b) first documented strong evidence of declining g through examination of an apparent secular slowing of simple visual reaction times, which are moderately negatively correlated with g (faster reaction times go with higher g ; $r = -0.3$ to -0.4), in five Western populations over a span of 120 years (1884–2004).

Evidence of slowing simple reaction times prompted Woodley of Menie and his collaborators, and also prompted some separate research teams, to search for other trends indicative of longitudinal changes in population levels of g . In total, temporal trends in six individual-level indicators of g were discovered from 2013–2016, all of which suggest g -decline. Specifically, measures of working memory, color acuity, spatial-rotation ability, developmental stability, vocabulary usage, and, as already mentioned, simple (visual and auditory) reaction times have all trended in ways that evince temporal decreases in g (see Sarraf 2017 for a review). Notably, apparent declines in working memory, which Woodley of Menie and Fernandes first noted in 2015, have been corroborated through a large- N meta-analysis (139,677 participants) of performance on two working memory tests across 43 years (Wongupparaj et al. 2017). Additionally, per capita rates of genius-level intellects and major innovations, two *group-level* indicators of population g , fell over the course of roughly 150 years in the West, from the mid-nineteenth to early twenty-first centuries (Woodley 2012b; Woodley of Menie et al. 2017c).

These trends that evidence falling g have been termed *Woodley effects* after Woodley of Menie by Charles Murray (Sarraf 2017). Using data sourced from Britannic (mostly Anglo-American) populations, Woodley of Menie et al. (2017a) demonstrated that a representative sample of known Woodley effects load onto a chronometric latent factor, which evidently tracks population-level g over time. This factor in turn loads onto another chronometric latent factor, called the “Co-Occurrence Nexus,” and tracks temporal changes in selection for g , congruent with the theory of dysgenic selection (Woodley of Menie et al. 2017a; see also Woodley and Figueredo 2013). Consistent with these results, Woodley of Menie et al. (2018b) found that the decline in this chronometric g factor is significantly associated with reductions in the frequencies of genetic variants related to g (Kong et al. 2017 offered the strongest evidence to date that such gene frequencies are in decline, and that this decline is due to dysgenic selection).



Michael A. Woodley of Menie, Yr., Fig. 1 Decline in chronometric g factor (the Woodley effect) from 1876 to 2008 in Britannic populations

Figure 1 shows the decrease in the chronometric g factor in Britannic populations (data sourced from Woodley of Menie et al. 2017a). Woodley of Menie et al. (2017a) estimated that this decline in g probably constitutes a loss of 1.21 points per decade in Britannic groups (p. 91), which is severe.

The Co-Occurrence Model of Secular Trends in Human Intelligence: Partitioning IQ Change

Combining the insights produced by the differentiation-integration models for both g and K with those provided by the co-occurrence model of intelligence decline, Woodley of Menie (Woodley, 2012a, b) set about accounting for the Flynn effect in terms of which IQ components might be increasing and which others decreasing. His finer-grained analyses suggested that the observed decreases in g were occurring concomitantly with secular *increases* in s , the IQ components associated with more specialized mental abilities rather than general intelligence. The aggregate rise in total IQ scores observed was thus the product of the increases in s masking the concurrent decreases in g when researchers

do not adequately partition these variance components. For example, this phenomenon is illustrated by the opposing secular trends in *backwards* digit span (a measure of working memory, an ability that exhibits high affinity for g) and *forwards* digit span (a measure of short-term memory, an ability that exhibits high affinity for s), which further evidence the validity of the co-occurrence model (Wongupparaj et al. 2017; Woodley of Menie and Fernandes 2015).

This line of investigation led to the publication of two monographs testing the co-occurrence model and framing it within the evolutionary-biological theory of multilevel selection (MLS). The first of these two monographs (Woodley and Figueredo 2013) examines the historical variability in heritable general intelligence over the period spanning most of the nineteenth and twentieth centuries, such as by tracking the effects of population aggregates of both g and s upon the rates of *eminence* (that is, measures of the prevalence of genius-level intellects) and socially significant *macro-innovations* within the aggregate Britannic population. The main conclusion of the structural equation model comparison performed was that

only *g*, and not *s*, had statistically significant effects upon *eminence* and *macro-innovations*. The second of the recent monographs (Woodley of Menie et al. 2017a) presented a more detailed biohistory of the modern era from the seventeenth century to the present time. This second monograph explicitly tested the theory of *MLS* proposed in the first as a hypothesized set of opposing causal influences upon the balance of *g* and *s* within the aggregate Britannic population. Historical trends indicated that higher intensities of group-level selection (as measured by a theoretically specified set of convergent indicators of between-groups competition) select for higher aggregate levels of *g*, and that higher intensities of individual-level selection (as measured mostly by historical periods of low climatic harshness and instability) promote higher aggregate levels of *s*. Together, these two monographs offer compelling evidence in favor of the co-occurrence model and the hypothesized evolutionary dynamics presumably underlying a wide array of observed phenomena.

The Social Epistasis Amplification Model

The social epistasis amplification model (SEAM) is based on two ideas. The first is that deleterious mutations accumulate in industrializing and industrialized populations, because the high standards of living that industrialization enables reduce the fitness costs of harboring such mutations (relative to their fitness costs under pre-industrial existential conditions). The second is that inter-organismal cross-genomic transactions may occur among the members of populations of some social species – a phenomenon called social epistasis – such that the genotype of one organism can influence the relationship between *another* organism's genotype and phenotype (for example, by epigenetically modifying patterns of gene expression). Given these premises, and assuming that social epistasis occurs in humans, the SEAM posits that the effects of deleterious mutations in carrier humans can be externalized onto non-carriers via social epistasis, and thus that the fitness costs of these mutations can be amplified. In this model, mutations with deleterious effects on both carriers and non-carriers have been termed

“spiteful mutations” (Woodley of Menie et al. 2017c); the SEAM further asserts that the accumulation of spiteful mutations in populations that have industrialized (or are industrializing) has led to an amplification of fitness costs over time. The potential existence of such intensifying fitness costs suggests the possibility that the socially selected extended phenotypes of entire industrialized/industrializing human populations and (consequently) their group-level fitness have been degraded. Indeed, the SEAM was originally developed partly as an explanation of the sharp decline in the fertility rates (a group-level fitness measure) of Western populations over multiple recent decades (Woodley of Menie et al. 2017c).

One of the more provocative hypotheses derived from the SEAM is that socially radical or antiestablishmentarian beliefs, ideologies, and behavioral patterns may at least in part be consequences of the action of deleterious mutations in psychological development that are disruptive of evolved social adaptations; furthermore, it has been argued that these beliefs, ideologies, and behavioral patterns may have proliferated quickly by way of social epistasis, with the effect of lowering the aggregate and relative fitness of groups (Sarraf and Woodley of Menie 2017; Woodley of Menie et al. 2017c). Support for this hypothesis comes from the fact that certain anti-establishmentarian beliefs and ideologies are negatively correlated with fitness both within and across populations (Woodley of Menie et al. 2017c). There is also more direct evidence of a positive association between irreligiosity (an anti-establishmentarian behavioral disposition) and burdens of deleterious mutations. The strongest evidence for this association to date comes from a sequential canonical cascade analysis of the US population, which found that relaxed opportunity for selection positively predicts a factor hypothesized to track mutation load (comprised of converging measures of developmental instability), which in turn positively predicts a “social epistasis” factor (comprised of converging measures of maladaptive social behavior, including irreligiosity operationalized as church absenteeism). This social epistasis factor finally negatively predicts a group-level fitness factor, meaning that

higher social epistasis goes with lower group-level fitness, as the SEAM predicts (Sarraf et al. 2019).

Despite these promising results, the SEAM as applied to humans still lacks fully satisfactory empirical support. Highly compelling evidence for the model has been found in experimental work on laboratory mice, however. Most saliently, Kalbassi et al. (2017) discovered that mice without the gene *Nlgn3* cause mice housed with them that have *Nlgn3* to adopt autistic-like behaviors (deletion of *Nlgn3* is associated with autistic-like behaviors in mice). Sarraf and Woodley of Menie (2017) contended that these findings potentially indicate that social epistasis occurs between mice with and without deletion of *Nlgn3* allowing for the phenocopying of these autistic-like traits therefore, they argued that Kalbassi et al.'s (2017) results may be best explained through the SEAM. Subsequently, Woodley of Menie and Sarraf began working with the team behind the Kalbassi et al. paper. Their first collaborative effort sought to uncover the mechanism(s) by which the apparent *Nlgn3*-deletion-based social epistasis occurs. An experiment investigating this matter determined that mice without *Nlgn3* excrete a urinary pheromone called Darcin, exposure to which “deleteriously modif[ies] the social behavior” of mice with *Nlgn3* (Bachmann et al. 2018).

Controversies

Controversies have attended some of Woodley of Menie's work. Three of these in particular are of note: (1) a number of academics critiqued his and certain colleagues' research on slowing simple reaction times as indicators of declining *g*; (2) a prominent endocrinologist argued that his dysgenic theory of falling *g* is problematic and that an alternative theory invoking neurotoxic pollution to explain this decline is more scientifically sound; and (3) a variety of media outlets condemned the London Conference on Intelligence, for which Woodley of Menie served as secretary in 4 of the 6 years it has been held, for what they claimed were moral and scientific reasons.

Reaction Times

The reaction times controversy began with Woodley et al.'s (2013b) previously discussed meta-analytic finding of slowing simple visual reaction times from 1884 to 2004 in five Western populations. That meta-analysis received one of the largest numbers of critical commentaries ever directed at a single publication in the journal *Intelligence*. In total, five replies were written by six academics: James Flynn, Ted Nettelbeck, Irwin Silverman, Yulia Dodonova and Yury Dodonov, and Scott Parker. David Woods led one other critique that appeared in a different journal, *Frontiers in Human Neuroscience*. (See Sarraf 2017, for a more involved treatment of these papers.)

The criticisms offered in these papers are too numerous to be detailed in full here, but perhaps the most significant alleged problem raised, and the one mentioned the most frequently, was that methods for gathering reaction times data have varied substantially across samples. This potential problem introduced the possibility that apparent declines in simple reaction speed were not substantive, but rather merely artifacts of methods variance. Nevertheless, Woodley of Menie and colleagues replied that profound slowing of simple reaction times still emerged from relevant data even after applying generous adjustments for methods variance (Woodley et al. 2014b; Woodley of Menie et al. 2015a, b). More importantly, studies of modern cohorts using invariant methods to measure simple auditory (Madison et al. 2016) and visual (Woodley et al. 2014a) reaction times also found significant temporal slowing. These results, which have so far received no academic challenges, leave little doubt that the simple reaction times of at least some Western populations have slowed considerably over time.

Neurotoxic Pollution Versus Dysgenic Selection

As already indicated, Woodley of Menie has perhaps done more than any other scientist to revive the theory of dysgenic selection. But competing theories have been forwarded to explain the apparent long-term diminishment of human cognitive ability. One example comes from Demeneix's (2017) book, *Toxic Cocktail*, which

maintains that increasing human exposure to endocrine-disrupting neurotoxic pollution explains at least some significant portion of the apparent decline in intelligence (it is not clear whether Demeneix believes that this decline applies only to *g*). While recognizing that neurotoxic and dysgenic theories need not be mutually exclusive, Demeneix has been clearly skeptical about the latter. Referring specifically to the study of Woodley et al. (2013b), Demeneix (2017) asserts that their dysgenic theory exhibits objectionable “biological determinism and genetic determinism” (p. 87). Further, she argues that their work fails to take seriously the possibility that neurotoxic effects have some role in evident diminutions of intelligence. Demeneix’s (2017) criticisms are purely qualitative, however, making their commensurability with the prior quantitative findings unclear.

In light of these criticisms, and of the lack of adequate assessments of neurotoxic theories of *g* decline, Woodley of Menie et al. (2018b) developed a statistical model to test the dysgenic selection and neurotoxic pollution theories. This model involved the use of composite measures of changes in population-level gene frequencies related to *g* and neurotoxic pollution over time and indicated which of these measures better accounted for trends in a third temporal composite measure, of population-level *g*, statistically controlled for the effect of time. Decreasing *g*-related gene frequencies significantly predicted declines in *g*, whereas trends in neurotoxic pollution were not significantly related to these declines, providing strong evidence in favor of the dysgenic theory and against the neurotoxic pollution theory (Woodley of Menie et al. 2018b).

The London Conference on Intelligence

The London Conference on Intelligence (LCI) is an academic meeting, attended by invitation, devoted to discussion of psychometrics and differential psychology. It has been held for six consecutive years (2014–2019); Woodley of Menie served as secretary for the conference for the first four meetings.

On the 10th of January 2018, an article appeared in *London Student*, a student newspaper of

University College London (where LCI was held from 2015–2017), alleging that LCI had the purpose of promoting racist and eugenicist ideas. Similar claims were published in a variety of other media outlets (see Woodley of Menie et al. 2018a, for discussion of a number of these pieces). The general theme of these articles is that the scientific work presented at LCI was not only morally abhorrent but also represented discredited “pseudoscience.”

In order to refute these claims, Woodley of Menie and a number of colleagues (2018a), all of whom had attended LCI, published a piece in the journal *Intelligence*. This article provides evidence that, contrary to media allegations, the research associated with LCI was mainstream in form and content among experts on intelligence research and had been conducted by persons of diverse national backgrounds. Further to this point, it demonstrates, via scientometric analysis that papers presented at LCI were associated with mainstream scientific publications about as strongly as was research typically presented at biomedical science conferences. Finally, the article offered an analysis of temporal trends in word usage, which provides evidence that past efforts (stemming mostly from the political left) to stop research on “distasteful” psychological issues (for example, group differences in intelligence) have had a chilling effect on such research, despite its manifest scientific credibility. Woodley of Menie and colleagues termed this social psychological phenomenon the *Gould effect*, after the Marxist evolutionary biologist Stephen J Gould. The basic thrust of Woodley of Menie and colleagues’ (2018a) response to media critics was that the work featured at LCI had not been outside of the relevant mainstream of science; instead, it was the critics of LCI who had approached scientific matters in a decidedly politicized and unscientific way.

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Michael Tomasello

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Synonyms

Anthropologist; Comparative psychologist;
Developmental psychologist

Definition

Michael Tomasello has pioneered theoretical and empirical work on the evolution of uniquely human cognition and behavior.

Introduction

Michael Tomasello has developed novel methodological and theoretical tools within the field of evolutionary psychology and, using these, has contributed significantly to the collective effort to understand what it means to be human. A thorough understanding of any object of study requires points of comparison. Nonhuman great apes (henceforth apes) serve as particularly salient subjects for comparative research due to their close phylogenetic tie to our species. Features held in common may be argued to have been present in our last common ancestor (LCA), while differences suggest derived traits in a particular lineage. Tomasello has innovatively implemented controlled comparative experiments

using both apes – chimpanzees in particular – and human children as subjects. In doing so, and by keeping the experimental design as similar as possible across species, Tomasello has been able to illuminate aspects of ape and human psychology in the realms of both physical and social cognition, allowing for the piecing together of the evolutionary trajectory of these traits. In addition, Tomasello has studied children of different ages to further reveal ontogenetic patterns in the development of these cognitive abilities. While it is relatively straightforward to point to contrasts at the species level such as language, institutions, and religious beliefs, it is more challenging to capture the subtle differences in psychology on an individual level which in turn account for the more surface-level species differences. Tomasello's controlled experimental methodology allows researchers to focus on even these more fine differences. The resulting body of work has provided robust support for Tomasello's theory of shared intentionality which posits that apes operate from an individual, or "I," perspective, while humans possess a suite of socio-cognitive skills that allow them to put their heads together in acts of shared intentionality resting on a "we" perspective. It is this ability which allows humans to create the shared realities that give life its distinct character.

This chapter will first provide an overview of the methodological approach pioneered by Michael Tomasello – the comparative approach – through discussion of a representative study. The chapter will then continue in a second section to explore the conceptual foundation of Tomasello's shared intentionality theory and the socio-ecological circumstances that likely played a role in its evolutionary emergence. A third section will offer a concrete example of how shared intentionality transformed ancestral cognitive and social skills used in communication into their uniquely human form.

The Comparative Approach

One overarching question is whether human cognition is more complex than ape cognition across

the board or whether it is characterized by a more targeted species-unique factor. The cultural intelligence hypothesis, propagated by Tomasello and colleagues in a series of influential books and papers, proposes that humans possess a set of species-specific socio-cognitive skills that allow them to participate and exchange information in cultural groups (Tomasello 1999a, b; Tomasello et al. 1993). As the key to isolating differences between apes and children is conducting systematic comparative studies, Michael Tomasello, Esther Herrmann, and colleagues designed a controlled experiment that tested the hypothesis that humans have evolved specialized social cognition skills (Herrmann et al. 2007). In this landmark study, they administered the same comprehensive battery of cognitive tests to 105 young human children, 106 chimpanzees, and 32 orangutans. The three species were exposed to 16 nonverbal problem-solving tasks aimed at measuring skills and motivation related to physical and social cognition. Tasks measuring species' grasp of the physical world measured subjects' understanding of such concepts as space, quantity, tools, and causality. Tasks measuring cognitive abilities in the social world focused on subjects' tendency to imitate others' solutions to problems, subjects' ability to communicate nonverbally, and subjects' understanding of another individual's intentions. If it were simply general intelligence that differentiates human cognition from ape cognition, then one would expect human children to outcompete their primate relatives on tasks relating to physical cognition and on tasks relating to social cognition. If, on the other hand, the cultural intelligence hypothesis holds true and human cognition is marked by unique socio-cognitive abilities, then human children in this study should only differ from the other two primate species on tests relating to social intelligence. Results of this extensive test battery support the cultural intelligence hypothesis and show that the cognitive skills of human children are very similar to those of their primate relatives in the domain of physical cognition, but differ when it comes to navigating the social world. As the cultural intelligence hypothesis argues, young children seem to possess a unique adaptation for social cognition, allowing

them to interact with, learn from, and communicate with others in ways that other great apes do not. These early developing social skills allow human children to engage in the human cultural world which includes learning from others through language, instruction, and other educational tools.

This large-scale test battery not only provides evidence of uniquely human forms of cognition but also testifies to the power of systematic comparisons between human children and great apes in answering questions about species-specific cognitive adaptations.

Shared Intentionality Theory

The test battery's confirmation that humans possess species-unique cognitive abilities in the social realm provides a firm foundation for Tomasello's shared intentionality theory. Tomasello's theory not only recognizes that apes operate from an individual perspective, while humans regularly engage a collective perspective but also asks: How did humans evolve these novel forms of social cognition and become the "ultra cooperative" species that we are today? Which set of species-specific adaptive pressures likely facilitated the emergence of human social skills? One of the most significant achievements of shared intentionality theory is its effort to build a comprehensive understanding of the evolutionary development of human socio-cognitive skills from our divergence from the last common ancestor of apes and humans all the way to our current elaborate forms of social life, including conventionalized forms of interaction (Tomasello 2014). Shared intentionality theory argues that human socio-cognitive evolution over the last 6 million years took place in two key steps (Tomasello et al. 2012). Each of these evolutionary steps involves a new form of social engagement. The first step describes the transition from the individual intentionality of our primate ancestors to the joint intentionality of early humans which arose in the context of small-scale collaborative foraging. The second step focuses on the extension of joint intentionality to collective

intentionality spurred by large-scale forms of collaborative activity, brought about by growing populations and increasing levels of intergroup competition. Shared intentionality theory provides an account of the evolution and ontogeny of the human ability to form a shared agent – a “we” with others – comprising shared goals and intentions, as well as shared attention and knowledge. Shared intentionality theory also provides an account of the socio-ecological challenges that led humans to first collaborate dyadically in acts of joint intentionality and, later, as a group with individuals sharing cultural ties in acts of collective intentionality.

The central adaptive driving force of the first step in this transition was ecological change resulting in increased resource competition between terrestrial primate species and an incentive for early *Homo* to exploit a new niche. After an intermediary stage of scavenging of large carcasses, as suggested by paleoanthropological evidence, this new niche consisted of collaborative hunting of large game. Whereas earlier humans had, like modern-day chimpanzees, likely procured the majority of their food solitarily, members of the species *Homo heidelbergensis* were increasingly forced to depend on one another in their daily foraging: they became obligate collaborative foragers (Tomasello 2014, 2016; Tomasello et al. 2012). This new form of interdependence created two especially pressing challenges. The first challenge consisted of novel pressures of social selection, including partner choice and partner recruitment. Once early humans were dependent on their collaborative partners and choosing the wrong partner meant less food, individuals had to evolve novel ways of reliably interacting with competent and trustworthy partners, i.e., they had to engage in partner choice. Partner choice stabilizes cooperation by allowing cooperators to selectively interact with other cooperators and to exclude cheaters, free riders, and bullies. However, selecting those individuals with stable behavioral dispositions who are both trustworthy and competent in collaborative interactions is not quite enough. Additionally, individuals have to make sure that they are also picked as partners, i.e., they have to engage in

partner recruitment. The prevalence of picky partners in combination with dependence on those partners meant that early humans inhabited a social ecology in which they had to worry about evaluation by others and so they started to manage the impressions they made. Early humans thus had to socially regulate their behaviors in ways other great apes do not so as to align their actions with the expectations of their collaborative partners (Engelmann et al. 2012). Partner recruitment stabilizes cooperation by providing agents with extra motivation to act cooperatively as they must ensure they are chosen for the next collaborative hunt.

The second way in which interdependence in food acquisition created novel selection pressures was the necessity of developing the skills and motivations required for successful joint collaboration and a shift in the conceptualization of dyadic collaboration (Tomasello et al. 2005). Joint agency takes place when two individuals collaborate and relate to one another dyadically and second personally in face-to-face interactions. Joint collaborative activity consists of four elements: joint goals, joint attention, individual roles, and individual perspectives (Tomasello 2014). The emergent dual-level structure of joint collaborative activity is thus characterized by simultaneous jointness (on the levels of goal and attention) and individuality (on the levels of roles and perspectives). Agents form a joint goal, that is, the joint intention to capture the prey together (anchored in common ground). To achieve this goal, individuals assume different but complementary roles, adjusting their respective sub-plans so as to most effectively pursue their joint goal. Individuals engaged in a joint collaborative activity naturally attend together to incidents and objects that are relevant to their joint goals. Joint attention creates common conceptual ground and shared realities with their collaborative partners. In much the same way as joint goals and individual roles are characterized by connection and individuality, joint attention is complemented by the agents' individual perspectives. Indeed, the notion of perspective only gains relevance in the context of an object of joint attention on which two individuals have different perspectives.

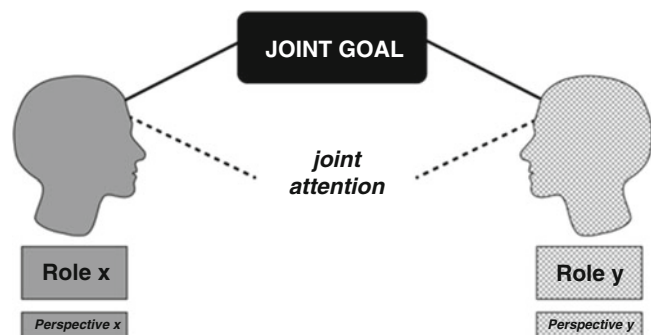
The evolutionary beginning of human uniqueness may well rest in the cognitive representation consisting of a dual-level structure of jointness and individuality, as depicted in Fig. 1. The cognitive, social, and motivational consequences of this dyadic evolutionary revolution can hardly be overstated. Some of its effects on human behavior and cognition will be reviewed in section “A Case Study.”

This dyadic, second-personal, and face-to-face form of collaborative activity was perfectly adaptive as long as humans lived in small groups with an easily manageable number of potential partners and rarely encountered other groups. According to shared intentionality theory, this system was destabilized by two demographic factors (Tomasello 2016). The first was increased competition, direct or indirect, with other groups of early humans which forced dyadic cooperation to be scaled up to collaborative activities by the whole group. If groups failed to turn their dyadic undertakings into full-blown collaborative activities on the level of the whole group, they were bound to be outcompeted by more tightly knit social groups. The second factor destabilizing humans’ early forms of joint collaborative activity was increasing population size. As groups became larger and larger, they tended to split into smaller groupings, with a number of different groups together forming a single culture. As a result, individuals did not face a manageable pool of familiar cooperation partners (as in step 1), but were increasingly forced to collaborate with relative strangers who they had to reliably recognize as members of their group. This challenge was solved by developing various markers of group

identity, allowing agents to collaborate selectively with those individuals that possessed the same skills and values as themselves and therefore likely made for trustworthy and competent collaborative partners.

The second step in shared intentionality theory, from joint to collective intentionality, is hypothesized to have occurred some 150,000 years ago, with the emergence of *Homo sapiens sapiens* (Tomasello 2014, 2016). The interdependence of You and I as part of the same collaborative dyad in the context of obligate collaborative foraging grew into interdependence at the level of the cultural group as a whole. This new form of reliance again created novel adaptive challenges relating to social selection and the ways in which collaborative activities were conceptualized. Most importantly, individuals now not only engaged with one another dyadically but started to view group life itself as one big collaborative activity. They evolved a novel psychological attitude of group-mindedness, consisting not only of skills and motivations for joint intentionality with other individuals, but for collective intentionality with their whole group. Social selection in such large groups required new forces to counter the powerful temptations to free ride under these novel conditions. The basic problem was twofold: in large-scale cooperative activities, each individual was needed less for collaboration to be successful (in comparison to the dyadic situation of step 1) and reputational information was less easy to come by – cheaters and free riders could more easily submerge into anonymity. One solution to this problem was the development of social norms – mutual expectations in common ground –

Michael Tomasello,
Fig. 1 The dual-level
structure of joint
collaborative activity



that specify how individuals are to behave in situations that typically involve non-converging interests. In essence, social norms are conventionalizations of the specific and locally restricted acts of partner choice and judgment of step 1. While failing to act cooperatively at step 1 invited reproach and punishment from my collaborative partner only, free-riding behavior in step 2 is met with protest by my entire group. Due to the generality of social norms, victims can (more or less) easily recruit assistance against cheaters and punishment is in effect not only carried out by the individual but by the whole group. Cheaters not only fail to live up to specific commitments shared by a collaborating dyad but to standards that are endorsed and enforced by the entire group.

Thus, whereas humans' collaborative activities in step 1 were marked by skills and motivations for joint intentionality, human social interaction from about 150,000 years on was characterized by collective intentionality. As suggested in the discussion of social selection in step 2, collective intentionality enabled humans to create various types of conventional practices that were firmly anchored in the cultural common ground of the group. Conventional cultural practices encompass behaviors, standards, and values that all members of our "we" engage in, follow, and endorse and that we expect everyone who wants to be a member of our "we" to engage in, follow, and endorse. Whereas the second-personal common ground of step 1 was created by, and therefore dependent on, the things experienced together during joint collaborative activity, the cultural common ground of step 2 consists of things each member of a group is expected to know – even if the related experiences were not shared or experienced together.

Collective intentionality thus shows the same dual-level structure of jointness and individuality as joint collaboration. The main difference is that the jointness has been scaled up to a kind of objectivity: our shared reality is not only shared between You and I but is shared among the entire cultural group, creating a kind of collective perspective involving various ways of doing things the "right" or "wrong" way and normative judgments of what one "should" or "shouldn't" do.

A Case Study

While so far this review of shared intentionality theory has mostly highlighted the theoretical and conceptual aspects of the theory, the third and last part will briefly discuss one concrete example of shared intentionality theory, focusing on the transition from ape communication to forms of communication unique to humans. Tomasello (2008) argues that the starting point for uniquely human forms of communication is not the relatively hard-wired forms of vocal communication in great apes, but instead their flexible and intentional forms of gestural communication. The flexible nature of chimpanzees' gestures can be clearly seen in their intention movements and attention getters (Tomasello and Call 1997; Tomasello et al. 1997). Chimpanzees ritualize certain intention movements from their social interactions with others and then use these gestures to flexibly and intentionally manipulate conspecifics, for example, when young chimpanzees raise their arm to a peer and then begin play hitting as invitation to play. Chimpanzees also use a number of attention getters in order to manipulate and direct the attention of others. For example, they regularly stomp or slap the ground in order to get others to look at them. The flexibility of their gestural repertoire is clearly evident in the special gestures used when interacting with their human caregivers, such as ritualized reaching and pointing gestures. However, while the range and flexibility of great ape gestural communication is impressive, it is limited in one important regard. When apes communicate with one another or with humans, the underlying motive is always directive and geared toward self-serving ends: getting food from a human caregiver, getting others to look at them, or getting a peer to start playing (Tomasello 2008).

In step 1 of shared intentionality theory, in order to effectively coordinate joint collaborative activities, early humans required a new form of communication. Tomasello (2008) refers to this new type of communication as cooperative communication. Interdependent activities, such as obligate collaborative foraging, invite cooperative communication. If we are hunting together, it is in my interest to inform you helpfully of things that

are relevant to your role. If your spear broke, I will point out an appropriate stick that could serve as a replacement. The first and most basic forms of cooperative communication consisted of the natural gestures of pointing and pantomime long before humans developed conventional languages.

This seemingly small step, from understanding others' gestures only in directive terms to understanding them cooperatively, allowed early humans to make novel inferences in communicative interactions. Consider the following experiment: when a human experimenter hides food in one of two buckets and then points to the location of the food, apes do not reliably use this gesture to locate the reward; they pick the correct bucket only at chance levels (Tomasello 2006). To be sure, apes follow the human gesture and look at the correct bucket, but then they do not make the inference that the gesture was offered with cooperative or helpful intent. Importantly, the problem is not that apes cannot make inferences from human behavior. When apes are exposed to the same setup only within a competitive context, i.e., facing a human experimenter who competes with them for food and who extends his arm toward one of the two buckets, they know right away that this must be the correct bucket (Hare and Tomasello 2004). Apes thus reliably make competitive, but not cooperative, inferences in the context of communication. In stark contrast, when prelinguistic infants as young as 12 months – who may be considered representative of the early humans of step 1 of shared intentionality theory – are exposed to the very same experimental situation (an experimenter pointing to one of two buckets), they readily make the necessary inference and consistently pick the bucket containing the food (Behne et al. 2005).

The evolutionary proposal is thus that early humans evolved a new type of communication – cooperative communication based on prosocial motives – which first emerged in the form of pointing gestures in the context of joint collaborative activities. This not only had significant repercussions for early humans' understanding of cooperative communicative acts, but also for their own transmission of helpful information. When apes work together in experimental studies,

there is a manifest absence of any kind of intentional communication (Hirata and Fuwa 2007; Melis et al. 2009; Povinelli and O'Neill 2000). This is presumably due to the fact that ape communication is directive in nature and not geared toward cooperatively informing collaborators of things helpful to them. Prelinguistic infants again provide a clear contrast. In the context of joint collaborative activities, infants 14–18 months of age use the pointing gesture to coordinate actions with a human experimenter (Warneken et al. 2006, 2007). Even outside of such collaborative pursuits, when infants as young as 12 months observe an adult looking for an object, they spontaneously point for the adult with the simple and pure motive of providing helpful information as to the object's location (Liszkowski et al. 2006, 2008).

The communication of early humans began to veer from intentional ape communication. In a sense, however, the strength of early humans' flexible gestural communication – successful coordination of complementary roles in joint collaborative activities – was at the same time its greatest weakness. Since these early forms of communication were so heavily contingent upon the common ground established within a joint activity, they were almost totally useless when this scaffold was removed and individuals interacted with others who did not share their common ground, or when they faced completely novel situations, or when they could not engage in dyadic, face-to-face forms of communication. To successfully communicate in these situations, early humans had to conventionalize gestures and vocalizations, making the transition from joint intentionality to collective intentionality. While the communication of early humans was locally, situationally, and temporally restricted, the advent of collective linguistic conventions enabled a much more decontextualized and flexible form of communication involving not just collaborative partners but anyone from the same cultural group. While communication between early humans was based on the personal common ground they created with one another as they engaged in collaborative activities, modern humans could communicate even with individuals

they had never met before and with whom they lacked personal common ground, thanks to cultural common ground. In Clark's analysis (1996), cultural common ground refers to pieces of knowledge that all members of a group share and that they know qua membership in the group – even if that knowledge was not gained through direct experience together. Two- and three-year-old children already understand cultural common ground and use it in order to make relevant communicative inferences (Liebal et al. 2013). When children at this age meet an unknown in-group adult and they look together at two objects, a Santa Claus toy and a newly created toy, and the adult asks, “Who is that?”, children unfailingly name the newly created toy, showing a belief that everyone from their culture knows who Santa Claus is and, therefore, would not need to ask. The transformation from communication based on personal common ground in the context of joint intentional activities to communication based on cultural common ground in the context of collective intentional activities thus allowed modern humans to coordinate their actions with all members of their group, independent of whether they had interacted together before or not (for various other consequences of the change from joint to collective intentionality for the communicative abilities of modern humans, see Tomasello 2008).

Although this is only a very brief and incomplete overview of the origins of human communication (for the full version, see Tomasello 2008), it demonstrates the power of shared intentionality theory in explaining how uniquely human forms of communication likely evolved gradually and naturally from the communicative abilities used by the last common ancestor of humans and nonhuman apes.

Conclusion

Based on an extensive body of empirical studies comparing human children and great apes, Michael Tomasello's shared intentionality theory

offers an in-depth and complete psychological analysis of the evolution of uniquely human cognition and behavior. Shared intentionality theory traces the socio-ecological pressures that contributed to the human evolutionary trajectory characterized by novel dyadic and second-personal forms of social engagement based on joint intentionality and, later, by group-based and conventionalized forms of cultural interaction based on collective intentionality.

Cross-References

- [Comparative Evidence](#)
- [Cooperation](#)
- [Cooperation Among Nonchimpanzee, Non-human Primates](#)

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Michelle Scalise Sugiyama

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Definition

Michelle Scalise Sugiyama is a leading evolutionary psychologist/anthropologist who has conducted research on the evolutionary function(s) of art, play, narrative, and story-telling, mainly with respects to human prehistory but also to some degree in contemporary societies. Much of her work investigates the evolutionary origins of various aesthetic, narrative and symbolic human behaviors – i.e., the natural and sexual selection pressures that led to their emergence – the role that these various artistic behaviors played in ancestral human societies, and the cognitive design features of the mind that have made them biologically possible. She has sometimes worked in collaboration with Laurence Scalise Sugiyama, and she is based in the Department of Anthropology at the University of Oregon, USA.

The entry will be divided into two main sections. The first section will simply summarize the most salient content of Sugiyama's work as it has been presented across a range of different publications, and the second section will briefly attempt to develop and extend a particular aspect of it.

Narrative

Sugiyama has conducted innovative work on the evolutionary origins and function of narrative storytelling. In this regard, she has explained that:

The antiquity of narrative is significant. It means that storytelling is a sufficiently ancient phenomenon to have evolved through the process of natural selection and that storytelling might serve an adaptive function – that is, it might have evolved in response to a problem that recurrently impinged upon human survival or reproduction throughout recent (i.e., Upper Pleistocene) human evolution. (Sugiyama 2005, 177)

According to Sugiyama, in order to construct an evolutionary aesthetics of stories, what is needed is to “reverse engineer” the urge to make and participate in such narratives. What survival advantages did narrative stories confer on their creators and on audience participants in the evolutionary past? In this regard, she has explained:

We know that storytelling is verbal and interactive: it involves an exchange between storyteller and audience. We also know that almost without exception, characters are representations of the human psyche; furthermore, characters give us special access to the human psyche that is not available to us in the real world. Finally, we know that conflict is an expression of human problems and plans for solving them, and that setting represents the specific conditions under which those plans are executed, thwarted, accomplished, or undone. The function of narrative, then, would appear to be the representation of the problems humans encounter in their lives and the constraints individuals struggle against in their efforts to solve them. (Sugiyama 2005, 186)

The fitness benefits of modeling human behavior are, according to Sugiyama, as preparation for various important survival-related tasks, such as finding food, building shelters, maintaining group cohesiveness, and so on. In addition, the ability to accurately predict the motives and behaviors of other individuals is enhanced by means of exposure to a wide range of narrative stories, and thus narrative assists individuals in expanding their knowledge of human nature (Sugiyama 1996).

Predators

In the Pleistocene era, violent threats to human life came from two main sources: attacks by animal predators (e.g., lions, tigers, bears) or by other human competitors (either in-group or out-group). Consequently, predator avoidance was a key skill that was required for survival (Barnett 2018). Sugiyama’s work promotes the idea that one important method for passing on useful information about predator attacks was through narrative storytelling.

For example, the oral retelling of “campfire” tales of predator attacks or deadly human conflicts was one effective means by which knowledge of

previous incidents could be transmitted from individual to individual and also across the generations (Sugiyama 2006, 328–329). Early forms of visual art such as cave paintings and ivory, bone and stone carvings may have served a similar function (Sugiyama 2001, 321). Related story narratives such as forager oral traditions contained information about hunting, gathering, and their associated localized dangers (Sugiyama 2010, 485).

However, the folklore and folktales of various cultures were not always presented literally or entirely naturalistically. As Sugiyama has outlined:

Folklore may also convey information metaphorically. For example, a Mataco tale about the bat-spirit informs the audience that the creature only goes out at night and that people “must be very careful not to sleep in the open; otherwise the bat will cut their heads off”. This story appears to be a reference to the menace of vampire bats . . . they are indeed known to prey on humans who sleep in the open: the bite itself is not lethal, but the infection that may spring from it can be. (Sugiyama 2006, 330)

In some areas of the world, bites from vampire bats are more prevalent than venomous snake bites (Ibid., 322). Consequently, there is a direct correspondence between the dangerous animals found in local literatures and those found in local environments (Ibid., 328). Moreover, the symbolic presentation of animal dangers with added supernatural overtones was one effective method of ensuring that such dangers were taken very seriously and received the full attention of the target audience. Often the supernatural enhancements related only to a few additional features of the creatures being portrayed, thus enabling their natural equivalents to be easily recognized (Sugiyama and Sugiyama 2011).

Supernatural creatures such as malevolent spirits, animal-human combines, cannibalistic ogres and giants, are a common feature in the folklore of foraging cultures across the planet. Sugiyama has argued that all these imaginary monsters serve the function of frightening children in order to keep them under control and away from environmental dangers, such as becoming detached from the group and finding themselves under predator attack (Sugiyama and Sugiyama 2011). For example, *Little Red Riding Hood* is a well-known example of a wolf-centered fairytale

set in a wooded location that is likely to contain dangerous wild animals (Sugiyama 2005, 186).

Cultural Variation

One of Sugiyama's most significant contributions to understanding literary universals and context-sensitivity is her work on cultural variation and its relation to universal human nature. She has explained in relation to cultural variation that:

The principle of context-sensitivity is an important stepping stone on the path to understanding cross-cultural differences in literary interpretation ... because all habitats present the same basic set of obstacles to survival and reproduction, we would expect any given literary setting to represent one or more adaptive problems ("the human condition"). However, because literary settings are representations of human habitats, and human habitats vary, we would expect local solutions to adaptive problems to vary in literature as they do in real life. On this view, then, we would expect literary art to express both human universals (e.g., adaptive problems, cognitive adaptations) and cultural variation (e.g., local solutions to adaptive problems). (Sugiyama 2010, 485)

The specific example being considered here is how the Tiv people of West Africa interpreted Shakespeare's *Hamlet*. Sugiyama showed effectively how the Tiv response to *Hamlet* resonated with very much the same universal issues that resonated with Western audiences: kinship, fratricide, revenge, justice, and madness. The small number of interpretive differences that were exhibited when comparing the Tiv and Western interpretations of *Hamlet* were explained by differences in local Tiv customs and economy compared to those of the West, not by wider differences in evolved cognitive architecture or any major distinctions of human nature (Ibid., 489).

Extension

This section will take the argument one stage further than Sugiyama by suggesting that narrative-linked cognitive architecture is, in some ways at least, *genre*-specific or *genre*-sensitive, by which is meant, focused on

assisting in solving very specific evolutionary problems, and "playing" with the particular emotions that have been evolved in association with them. Some scholars have previously considered the concept of *genre* in relation to evolutionary psychology, suggesting that there are three basic *genres*: comedy, tragedy, and satire, each of which links with a specific set of evolved emotions (Carroll 2007, 640; Carroll et al. 2010, 216).

The horror *genre* has not previously been considered in these terms, but it will be suggested here that the emotions that horror narratives are tuned to activate – fear and terror – make this *genre* conceptually prior to all other *genres* such as romance, comedy, or science fiction (Barnett 2010) and thus, it should be understood as "the primal *genre*."

Fear has recently been identified by neuroscientists as one of the four core premammalian emotional systems, and it has been hypothesized that a specific mental module or dedicated neural network has evolved to deal with associated predator avoidance issues (Carroll et al. 2010, 212). The term "the primal *genre*" is therefore appropriate because the adaptive functions of the emotions associated with the horror *genre* – fear/ensuring the survival of an individual under threat – are logically prior to all other functions of the living organism (finding a mate, successful reproduction and so on). Therefore, horror narratives have an enduring popularity in the contemporary world because their evolutionary equivalents rehearsed scenarios of extreme threat and danger that were much more prevalent amongst our evolutionary ancestors than they are today.

Moreover, the emotions of fear and terror should not be understood as corresponding with the themes of the tragedy *genre*, as some have suggested (Carroll 2007, 641), but instead they should be seen as a part of a separate *genre* which is conventionally called horror but could, more literally, be labeled as the predator-prey interaction *genre*, or a *genre* which documents the traumatic association of two separate species or two groups within a species, one of which preys on the other with deadly intent as a result of asymmetric power relations (Volterra 1931, 414).

Conclusion

In her extensive range of work, Sugiyama has pioneered the evolutionary investigation and understanding of the function of narrative storytelling by attempting to “reverse engineer” the need for such stories, especially in relation to an understanding of the function of predator/monster narratives. This entry has attempted briefly to extend Sugiyama’s analysis of the function of narrative by suggesting that the evolved cognitive architecture associated with storytelling is genre-specific and linked to particular systems of emotion, and identifying horror/terror as “the primal genre.”

Sugiyama has also demonstrated how cultural variation in the interpretation of narratives is compatible with the evolutionary psychologist’s conception of a universal human nature. Overall, Sugiyama’s work can be characterized as a valuable, empirically rich, and highly original addition to the body of work that attempts to further develop the Darwinian approach to art and literature (Carroll 2007).

Cross-References

- [Art](#)
- [Fiction](#)
- [Music](#)
- [Play](#)

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Microbial Defense

- [Pathogen Protection](#)

Microbial Resistance

- [Pathogen Resistance](#)

Mid-Cycle

- [Concealed Ovulation and Pregnancy](#)
- [Ovulation](#)
- [Women’s Preferences During Ovulation](#)

Middle Ear

- [Auditory System, The](#)
- [Middle Ear, The](#)

Middle Ear First and Second Pharyngeal Arches

- [Reichert-Gaupp Theory](#)

Middle Ear, The

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Synonyms

[Middle ear](#)

Definition

The part of the ear between the eardrum and the oval window which contains the three bones (malleus, incus, stapes), the tympanic muscles (Stapedius and tensor tympani), the oval window, the round window, and the Eustachian tube.

Introduction

The middle ear has three bones that make the ossicular chain, namely, the malleus (hammer), incus (anvil), and the stapes (stirrup). These are responsible for the sound to reach the tympanic membrane. The oval window, along with the round window, work with an opposite way to each other in order to influence the perilymph of the cochlea to move in response to sound. The two tympanic muscles, Stapedius and Tensor Tympani help to protect the inner structures of the ear from

damage of high intensity and frequency sounds. Further, the round and oval window work together to transmit sound to the structures of the inner ear. The Eustachian tube is to allow mucous to flow out of the middle ear and the air (oxygen) to move into and out of it. It is also used to balance the pressure levels inside the middle ear. Furthermore, the evolutionary patterns of middle ear's ossicles are briefly discussed.

Brief Anatomy of the Middle Ear

The middle ear is a part of the ear which is filled with air and where the structures of the tympanic membrane are located. Specifically, it is comprised of the ossicles – bones of hearing – called the hammer, anvil, and stirrup, or otherwise called the malleus, incus, and stapes, respectively (Hoy 2012). The aforementioned ossicles make the ossicular chain, which are responsible of the sound energy to travel to the tympanic membrane and, ultimately, to the structures of the inner ear (Seikel et al. 2010).

Stapedius and Tensor Tympani

There are, also, two tympanic muscles connected to the ossicles called the Stapedius and the Tensor Tympani. (Seikel et al. 2010). These muscles contract when exposed to high-intensity sounds, and together they compose the middle-ear reflex arc involving the spiral ganglion neurons, the auditory nerve, cochlear nucleus, the superior olive, the facial nerve nucleus, and the facial nerve (Margolis 1993, as cited in Puria and Steele 2008).

The reflex arc can reduce sound transmission through the middle ear at higher intensity (Puria and Steele 2008). As a result, when these muscles contract, they reduce the signal strength of reaching the cochlea, thus protecting the ear from being harmed from high-intensity sounds (Seikel et al. 2010). There are also two more functions attributed to the middle-ear muscle reflex. High-intensity sounds with low frequency tend to mask mid- and high-frequency sounds because of the upward excitation patterns on the

basilar membrane. Therefore, one role of the middle ear muscles is to reduce the level of the low frequency sounds so they do not mask the higher frequency sounds on the basilar membrane (Puria and Steele 2008). The other role of the middle ear reflex is to reduce the hearing of self-generated sounds such as sound made by speech, yawning, sneezing, and chewing (Puria and Steele 2008).

The Stapedius originates from the posterior wall of the middle ear space of the temporal bone. Its function is to rotate the footplate of the stapes posteriorly, thus thickening the ossicular chain. The Tensor Tympani is originated from the cartilaginous portion of the Eustachian tube and the greater wing of the sphenoid. Its function is to pull the malleus anteromedially and reduce the movement of the Tympanic Membrane by placing indirect tension on it (Seikel et al. 2010).

After this process, the eardrum and the three middle ear bones amplify sound waves 26 times before it is sent to the inner ear for further processing (Balkany and Brown 2017).

The Oval and Round Windows

The oval window is a membrane that is located between the cochlea and the inner ear; the sound travels through the three middle ear bones through the oval window. The pressure of the traveling wave on the oval window is amplified 20 times more than on the eardrum due to the difference in the relative surface of the eardrum and the smaller surface of the oval window. The round window vibrates in the opposite direction to the sound vibrations that move in the cochlea through the oval window, therefore, affecting the perilymph of the cochlea (Ruberg 2018). Specifically, the ossicular chain applies sound to the oval window that leads to the cochlea. The round window, located in close proximity to the oval window, moves in reciprocal fashion, expands outwards responding to an inward movement of the stapes footplate, and expands in the opposite direction when the stapes moves away from the oval window (Hawkins 2017).

The Eustachian Tube

An additional part of the middle ear is the Eustachian Tube, which forms the space filled with air between the throat and the nose (Balkany and Brown 2017).

The Eustachian tube is a link between the middle ear and the nasopharynx. The facial nerve (cranial nerve VII) also passes through the middle ear (Munir and Clarke 2013). The function of the Eustachian tube is to allow mucous to flow out of the middle ear and the air (oxygen) to move into and out of it. It is used as an equalizer to balance the pressure levels inside the middle ear – such as in the cases where the atmospheric pressure is altered, i.e., scuba diving and airplane travel (Balkany and Brown 2017).

Evolutionary Status of the Middle Ear

Based on comparative morphology, Reichert's (1837) hypothesis regarding the middle ear in mammals states that two of the mammalian ossicles, the malleus and incus, were derived from cartilages comparable to the lower and upper jaw elements in other amniotes, namely, the articular and quadrate. Additionally, Reichert (1837) suggested that the stapes is comparable to the columella auris in nonmammalians as a component similar to the hyomandibular.

Further evidence from fossil records in South Africa and Russia support the primary jaw joint origin of the mammalian middle ear components. Specifically, these fossils are synsids, a class of animals consisted of the pelycosaurs and therapsids, from which mammals emerged. Also, the mammalian tympanic membrane is assumed to consist of a small dorsal part which is homologous to the reptilian tympanic membrane called parts flaccida, and a large ventral portion homologous to a novel mammalian middle ear feature, the pars tensa (Takechi and Shigeru 2010).

Manley (2010) has reached to a conclusion stating that the tympanic middle ears were developed independently and that the mammalian middle ear is not a better developed single-ossicle

middle ear. Rather, its origin is unique. Manley further elaborated on the fact that evolution in similar groups takes place independently and in parallel most of the time, and the results developed from the same structures could be similar. Also, there is the possibility of a random and opportunistic evolution and that the evolutionary developments of both middle and inner ear were crucial for the development of hearing in very high frequencies. Together with the development of the tympanic middle ear in therian mammals, the brain became larger in size and a secondary palate was developed, having as a result the ancestral pressure-gradient middle ear to be replaced by a pressure system (see Manley 2010, for a review).

Additionally, Maier and Ruf (2016) have explored the question of how the structures of the mammalian middle ear that were developed at the angle of the lower jaw were later relocated to the basicranium (see Maier and Ruf 2016, for a historical review).

Manley (2010) made an interesting comment regarding evolution of the middle ear. He specifically states that

evolution is never goal-oriented. Instead, we must view the evolution of high-frequency hearing in mammals as the fortuitous result of totally unrelated changes in head structures that both led to a new type of middle ear that enabled better transmission of higher frequencies and to pressure-detection middle ears that made the acquisition of high-frequency hearing very advantageous.

Manley (2010) further noted that the process of selection is naturally occurring but the variations are determined genetically between individuals.

Conclusion

The middle ear consists of the three ossicles, namely, the malleus, incus, and the stapes. The tympanic muscles – stapedius and tensor tympani – have as their main function to dampen sound in order to protect the inner structures of the ear. The oval and the round window work to transmit the sound to the cochlea, and the Eustachian tube is to allow mucous to flow out of the middle ear and the air (oxygen) to move into

and out of it. It is used as an equalizer to balance the pressure levels inside the middle ear.

The evolutionary aspects of the middle were also discussed with emphasis to the groundbreaking work done by Reichert (1837). Manley (2010) has provided much insight into the evolution of the middle ear.

Cross-References

► [Stone Hammers](#)

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Migration

- ▶ [Habitat Change](#)

Milieu

- ▶ [Environmental Influences](#)

Mimesis

- ▶ [Ritual and Speech Coevolution](#)

Mimicry

- ▶ [Neonatal Imitation](#)

Mimicry, Power, and Influence

- ▶ [Imitation of High-Status Others](#)

Mind Modules

- ▶ [Modularity of Mind](#)

Mind Perception

- ▶ [Agency-Detection](#)

Mind Reading

- ▶ [Theory of Mind](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)

Mindblindness

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Definition

The inability to interpret behavior in terms of goals, beliefs, desires, and other mental states. It is proposed that, to varying degrees, people with autism suffer from mindblindness.

Introduction

“Mindblindness” is both a concept and the short title of Simon Baron-Cohen’s influential 1995 book *Mindblindness: An Essay on Autism and Theory of Mind*. The term “mindblindness” is meant to be an analogy to “colorblindness,” but whereas colorblindness is a deficit in visual processing, mindblindness is proposed to be a deficit in social processing. The concept of mindblindness attempts to take the disabilities central to autism and frame them in terms of a modular, cognitive, and developmental explanation rather than one that is rooted solely in learning or other environmental influences. Mindblindness, therefore, conceptualizes a person with such deficits not as a person who lacks knowledge, experience, or intelligence, but who lacks the necessary equipment to appreciate what it is like to see the world through the explanatory lens of mental states.

Main Text

The term “mindblindness” did not originate with Baron Cohen’s 1995 publication and was in use at least as early as Gopnik’s 1993 unpublished essay “Mindblindness.” While much of the work in understanding mindblindness focuses on people with autism, there is some controversy surrounding the degree to which the cognitive model associated with mindblindness is a sufficient

explanation for autism spectrum disorders. However, instead of being a strictly clinically focused work, the goal of understanding mindblindness is also to achieve greater insight into how a neurotypical person's brain is organized. The utility of the concept is that it allows us to identify and tease out the functional scope of a very important cognitive module, or related set of modules.

Evolutionary Forces and the Adaptive Problem

In his book, Baron-Cohen begins with the insight from Nicholas Humphrey (1983) that humans must have evolved a truly impressive ability to interpret other people's behavior in terms of mental states. The payoff for this ability was not just mere understanding, however. Once the behavior of another organism is fit into the language of beliefs, goals, desires, and personal knowledge, it becomes possible to gain predictive power over what that organism is likely to do next. As this ability began to emerge over evolutionary time, it became ever more important to be good at it in order to compete in the relatively new game of "social chess," an analogy from Humphrey that Baron-Cohen uses extensively. Baron-Cohen quotes from Humphrey (p. 20):

Thus social primates are required by the very nature of the system they create and maintain to be calculating beings; they must be able to calculate the consequences of their own behavior, to calculate the likely behavior of others, to calculate the balance of advantage and loss—and all this in a context where the evidence on which their calculations are based is ephemeral, ambiguous, and likely to change, not least as a consequence of their own actions.

Therefore, the abilities associated with mindreading (which are absent in mindblindness) are conceptualized in explicitly evolutionary terms as an adaptation designed to solve the adaptive problem of predicting the behavior of highly social peers.

The Intentional Stance

Baron-Cohen borrows from the work of Daniel Dennett (1978) who described several "stances"

that one can take in describing an object. There is the "Physical Stance" (in which one describes the parts of an object just how they are and also the cause-and-effect relationships between them), the "Design Stance" (in which one describes an object in terms of a function that it can fulfill), and the "Intentional Stance" (in which an object is described in terms of what it thinks, intends, and wants). While all three stances (or perhaps more, if they were to be discovered and described) *could* be applied to animate objects like people, only the Intentional Stance is efficient and useful enough to help someone navigate an environment filled with people and animals. That is to say, that if one were to try to describe why a person picked up a box of cookies at a supermarket, looked at the side of the box, and then replaced them with a frown, it is theoretically possible to do so by describing the firing of every neuron and the contraction of every muscle involved in the episode. However, even our best neuroscientists cannot provide such detail under the best of circumstances. Similarly, one *could* describe the *functions* of muscles and nerves, and the function of a brain area designed to create behavior that maximizes caloric intake while another brain system represents longer-term health goals and thus may inhibit the appetite system, but such explanations are lengthy and require a good deal of formal education while still being speculative (at least for particular cases). On the other hand, the natural and useful way to explain the behavior would be to say that the person thought the cookies looked tasty and was hungry for them, but then decided to check to see how many calories they had. Since the person wanted to lose weight, they decided to put the cookies back. This quick and efficient interpretation of the behavior puts us in the extraordinary position of identifying the key factors that went into the behavior so that in the future, if those key factors are again present, we can anticipate what the person is likely to do. We can then adjust our behavior accordingly, now that we know how the person is likely to react to the offer of, say, an unhealthy plate of bacon-cheese fries.

The lack of the ability to take the Intentional Stance, then, would rob an individual of an extremely useful tool in social functioning,

including much that makes the pragmatics of language possible. Baron-Cohen proposes in the book that the lack of the ability to “paint” mental states onto observations is central to the diagnosis of autism. He then uses some examples to illustrate what it must be like to be surrounded by behavior that is inexplicable. To quote Allison Gopnik (1993):

This is what it’s like to sit around the dinner table...around me bags of skin are draped over chairs, and stuffed into pieces of cloth, they shift and protrude in unexpected ways. ...Two dark spots near the top of them swivel restlessly back and forth. A hole beneath the spots fills with food and from it comes a stream of noises. Imagine that the noisy skin-bags suddenly moved toward you, and their noises grew loud, and you had no idea why, no way of explaining them or predicting what they would do next.

This vivid example is an extreme version of what it may be like for a person who can only use the physical or functional stances to be surrounded by things that seem to call out for explanation and prediction, and may be something of an approximation of the anxiety which could come with more severe forms of autism.

Conclusion

Mindblindness is a term that describes the lack of ability to interpret and predict behavior in terms of mental states like wanting, knowing, planning, feeling, and thinking. Individuals with mindblindness are forced to try to understand people and animals in purely physical or functional terms, without the ability to reference the inner lives of others. Some proponents of mindblindness make the claim that it is a parsimonious explanation for the range of deficits typically found in autism.

Cross-References

- ▶ [Autism](#)
- ▶ [Daniel Dennett on Free Will](#)
- ▶ [Theory of Mind](#)
- ▶ [Theory of Mind and Evidence of Brain Modularity](#)

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Mindfulness

- ▶ [Attention](#)
- ▶ [Self-Observation](#)
- ▶ [Stress Reduction and Mental Health](#)

Mindreading

- ▶ [False Beliefs](#)
- ▶ [Theory of Mind and Nonhuman Intelligence](#)

Mini-K

- ▶ [K-Factor \(Figueredo\)](#)

Minimal Obligatory Parental Investment

- ▶ [Bateman’s Principle: Sex Differences in Reproductive Success Variance](#)

Mirages

- ▶ [Visual Illusions](#)

Mirror Mechanism

► [Mirror Neurons](#)

Mirror Neuron System

► [Mirror Neurons](#)

Mirror Neurons

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Synonyms

[Mirroring](#); [Mirror mechanism](#); [Mirror neuron system](#); [Mirror system Neural mirroring](#)

Definition

Mirror neurons are a type of cell in the nervous system that fires during the production of a goal-directed action or expression and during the observation of that same action or expression.

Introduction

Mirror neurons (MN) are a type of neuron, located throughout the nervous system, which discharges both when producing a goal-directed action – such as reaching for an object – and when observing someone else performing that same action. Since the observer's neurons fire as if they are the ones acting, they simulate internally without physically producing the action. Thus, MN provide a link, or a “mirror” between others' actions and our own actions, enabling individuals to experience others'

actions firsthand, as if they were the ones carrying them out. This unique property is how mirror neurons acquired their name.

Main Text

It has been just over 20 years since MN were originally discovered, completely transforming our understanding of the neural underpinnings of social behavior. Indeed, our conceptualization of the motor system has dramatically changed with the realization that the motor system is involved not only in the production of movements but also in the processing of sensory information aimed at supporting the capacity to interpret others' behavior. The team led by Giacomo Rizzolatti discovered MN in the ventral premotor cortex (area F5) in macaque monkeys through extracellular single-cell recordings (di Pellegrino et al. 1992; Gallese et al. 1996), and subsequently these neurons have been recorded in the posterior parietal cortex, an area that is anatomically connected with area F5 (Fogassi et al. 2005).

Since the initial discovery of MN, researchers have made great strides in understanding their properties. Here, some key discoveries are highlighted; however, this is not an exhaustive list. Recent reviews summarize these and other findings in more detail (e.g., a recent edited book on MN: Ferrari and Rizzolatti 2015).

Basic Properties and Related Functions

One of the most intriguing properties of MNs is that their activity appears to be related to the *goal* of the observed or executed actions, rather than simply the body movements. That is, MN are not activated when observing biological movements that mimic a motor act but that are devoid of a goal. MN's activity in monkeys is evident not only for hand actions but also for goal-directed mouth actions (Ferrari et al. 2003). Further, some MNs are sensitive beyond the visual modality, responsive to other modalities, including sound. For example, some MN discharge when hearing actions (audio-visual MNs), such as the sound of

tearing or crumpling a piece of paper (Kohler et al. 2002). Other studies found that these neurons can be activated also when actions are performed with a tool (pliers) that require different movement kinematics and patterns of muscle activity from the natural action performed with the hand (Rochat et al. 2010). The findings clearly support the view that these neurons are capable to code the goal of an action.

MN are hypothesized to have multiple primary functions, including imitation and action understanding (for a review, see Rizzolatti et al. 2014). Imitation refers to the ability to match a modeled action. In order for an individual to match another individual's action, there must be a link between the visual and motor modalities. That is, an individual must be able to see another individual's behavior and match it with motor output. This can be particularly difficult to do if you cannot see yourself perform the action, for instance, if trying to match a facial expression without having a mirror nearby. This is known as the correspondence problem: how does the imitator know what pattern of motor activation matches the model's action? While observing an actor perform an action, the observer's motor representations of that action activates, thereby enabling a first-person experience of the other person's action. Thus, the motor knowledge of the observer is exploited in order to access to the meaning of the observed action. A meta-analysis in humans, involving 11 studies and 361 patients, revealed that lesions within the mirror network are linked to poor action perception and deficits in action understanding (Urgesi et al. 2014). Furthermore, this activated motor representation can be exploited to reproduce the observed action. Brain imaging studies in humans have demonstrated that during the observation and reproduction of simple movements, or also novel patterns of behavior, parietal and premotor cortical regions, corresponding to the human MN system (see below), are recruited.

Existence in Humans

While single-unit recordings have been used to study MN in nonhuman primates, as reviewed

here, this method is not as feasible in humans, unless under specific clinical conditions, given its intrusiveness. One study with electrodes implanted in different brain areas of epileptic patients confirmed the presence of neurons with mirror properties in different brain areas, including the supplementary mesial cortex and the parahippocampal gyrus (e.g., Mukamel et al. 2010). This study, however, did not explore the presence of MN in the homologue monkey areas. The vast majority of MN studies in humans, however, have utilized less-obtrusive neuroimaging techniques – which are indirect measures of MN activity – including functional magnetic resonance imaging (fMRI), positron emission tomography (PET), magnetoencephalography (MEG), as well as neurophysiological approaches, including transcranial magnetic stimulation (TMS) and electroencephalogram (EEG) (for a review, see Oosterhof et al. 2013). These indirect measurement approaches offer convergent evidence of an MN system in humans, namely, the ventral premotor cortex, inferior parietal lobe, and part of the inferior frontal gyrus (e.g., Molenberghs et al. 2012).

Extended Mirror Neuron Network

MN functions are also revealed by the fact that MN exist widely across the monkey brain. In addition to area F5, MN have also been discovered in other cortical areas anatomically connected with F5 and with which they form a functional circuit. These areas include the parietal cortex and the primary motor cortex (M1). Within the parietal cortex, there are MN in both the posterior parietal cortex (area PFG; Gallese et al. 2002) and within the intraparietal sulcus (area AIP; Pani et al. 2014). Other neurons with mirror-like properties have also been described in the monkey supplementary cortex, the dorsal premotor cortex, and in the secondary somatosensory cortex. All these cortical areas have anatomical connections with the parietal and premotor cortices. These new findings support the view of the existence of functional action-observation network with individual nodes decoding different aspects of observed actions, known as the Extended Mirror Neuron Network (Bonini

2016). Studies in humans and in the monkey also suggest that, beyond the decoding of actions, such as grasping and biting, the extended mirror neuron network is involved in the processing of emotional facial expressions. In fact, overlapping brain activity during the observation and execution of emotional facial gestures has been recorded in the anterior insula, a region implicated in integrating autonomic, visceral responses (e.g., Caruana et al. 2011), and also the anterior cingulate cortex.

Development Across the Lifespan

There is also a lively debate surrounding whether MN gain their properties through experience or the extent to which they are genetically hardwired or present already at birth. Like most systems, “nature,” genetics, and “nurture,” everything else besides genetics, including the prenatal and postnatal environments, may contribute to the development of MN and may even work together in interaction through epigenetic processes (Ferrari et al. 2013). Next is a review of evidence that MN are functional from birth and are further tuned through experiences.

There is behavioral evidence that MN are functional from birth, which comes from the discovery of a phenomenon known as neonatal imitation (review Simpson et al. 2014). Neonatal imitation is a precocious capacity to match observed actions, including facial expressions, in the 4 weeks following birth. In other words, if you stick out your tongue at a newborn, the infant is likely to tongue protrude back at you. Neonatal imitation was first reported in humans nearly four decades ago (Meltzoff and Moore 1977) and has since been extensively replicated in humans as well as in chimpanzees and macaque monkeys (for a review, see Simpson et al. 2014). Critically, infants only a few minutes old are able to match facial expressions the first time they see them, suggesting an experience-independent sensorimotor matching ability that is functional from birth. One proposal is that a mirroring system could underlie this early capacity, enabling newborns to solve the correspondence problem (since they cannot see their own faces).

Consistent with this view, neurophysiological evidence also suggests that MN are functional from birth. EEG is a particularly useful noninvasive tool for measuring MN activity for which infants are relatively tolerant and has revealed a functioning MN system is present from birth in monkeys (e.g., Ferrari et al. 2012). Specifically, these studies report that newborn monkeys, while both observing and imitating facial gestures, exhibit similar cortical changes. Termed the “mu rhythm,” cortical activity desynchronizes, or is suppressed, both while observing and producing actions, found in infant and adult human and nonhuman primates.

Role of Experience

Of course, just because MN are present from birth does not imply that they are insensitive to experience. Indeed, EEG studies suggest a functional mirroring system is modulated by infants' early experiences, with macaque infants who have more enriched early social experiences exhibiting stronger MN activation to social gestures, compared to infants with less enriched social experiences (Vanderwert et al. 2015). Further, in the first year of life, infants dramatically improve in their ability to control their own actions and in their ability to understand other goal-directed actions. Developments in infant's action control are intricately linked to developments in their action understanding. MN activation during action observation also depend on whether individuals have a specific action in their motor vocabulary (i.e., whether the observer can produce that specific action). For example, an infant who only knows how to crawl, but not yet walk, will show MN activity while observing a crawling more so than while observing a walking action, whereas an older child, who can walk, will activate MN when observing a walker (van Elk et al. 2008). These results are consistent with findings in adults who vary in their expertise. For example, when dancers observed their own dance style versus another style (in which they were not expert), they exhibited greater brain activity in MN regions, suggesting motor expertise influenced action observation (Calvo-Merino et al. 2005). Similar

findings have been reported for a wide variety of other actions for which you can gain expertise, including musical observation/production (e.g., Vogt et al. 2007).

Evolutionary History

It is relatively uncontroversial that mirror mechanisms are phylogenetically ancient and have a broad evolutionary basis (Bonini and Ferrari 2011). It has been proposed that the different categories of MNs (hand and mouth MNs) might have different evolutionary origins even though, at the cortical level, their functional properties overlap (Casile et al. 2011).

One possibility is that MN began by acting as a monitoring system to track one's own behavior, then evolved as an extended recognition system to enable matching one's behavior with others', and finally evolved to be used in speech perception and production (Bonini and Ferrari 2011). That is, the function of MN may have changed over the course of their evolutionary history, building from more low-level into more complex functions. According to this view, over the course of evolution, the MN system was refined, shaped by each species' unique socio-ecology. MN are found in humans, Old World monkeys (macaque), New World monkeys (marmoset), and songbirds (Prather and Mooney 2015). Both primate and bird MN systems share the fact that they rely on the motor and visceromotor repertoire of the individual (Bonini and Ferrari 2011). Given these similarities, it is suspected that MN are not an evolutionarily recent phenomenon in humans, although MN systems may have been further refined in the human species.

Other Capacities that Involve Mirror Neurons

While the basic roles of MN in imitation and action understanding are relatively uncontroversial, there exist a number of open questions concerning the diverse areas in which MN may

play an important role. Here, a couple of additional areas are reviewed: language and empathy.

While humans communicate mostly by speech, hand gestures are often present as well. In fact, it is widely hypothesized that gestures evolutionarily preceded speech, and the discovery of MN offers support for this view, directly linking two individuals, sending and receiving messages from both hands and mouths (Rizzolatti and Craighero 2007). Imitation is a key factor in learning language; thus in the same way that MN facilitate imitation, they may aid in the acquisition of language. There are several investigations showing that the mirror system is implicated in language processing. For example, Broca's area – a region involved in speech production and considered part of the MN system – is activated by producing or listening to phonemes (i.e., units of sound that distinguish one word from another; e.g., /c/ sound in "cat" vs. /b/ sound in "bat") (Fadiga et al. 2002). Some even speculate that mirror mechanisms are the groundwork from which language evolved, through a first stage in which actions, gestures, and pantomime were involved for social communication (Arbib 2005).

In addition to MN involvement in "cold" action understanding (non-emotional actions, such as grasping an object), MN are also involved in "hot" actions, involving emotions (Rizzolatti and Craighero 2005). The mirror mechanism involved in this case is not confined to parietal and motor regions, but it recruits other brain regions, such as the anterior insula and the anterior cingulate cortex (Wicker et al. 2003). This capacity to share emotions is considered as an important building block for empathy, defined as the ability to share emotions or sensations. While empathy involves a wide array of emotional systems, recent evidence suggests that MN are a critical part of this system. While it is possible to recognize emotions without mirroring or empathy, such as through a more "cold" or cognitive process, more commonly we do so using MN to automatically and effortlessly mirror other people's emotions (Rizzolatti and Craighero 2005). The same principle can be applied to other sensations like pain. Studies have shown that overlapping areas of the brain are activated upon both seeing a loved

one in pain and experiencing pain themselves (Singer 2006). These mirror mechanisms are used to understand how the pain of others feels in order to empathize.

Neurorehabilitation

There are a number of potential clinical applications that may involve MN, particularly those involving motor dysfunction. For example, during a stroke, blood flow to an area of the brain is disrupted and causes damage, often resulting in the loss of voluntary movement. Given that MN are activated both during action production and observation, stroke rehabilitation treatments have focused on action observation, motor imagery, and imitation as part of physical therapy to regain function during stroke recovery (Garrison et al. 2010). MN research has also inspired treatments for autism spectrum disorder (ASD), a neurodevelopmental disorder characterized by motor deficits, language impairment, and social impairment. Although there is much to learn about the role of MN in ASD, there are early promising interventions for children with ASD, which have focused on imitation (for a review, see Iacoboni and Mazziotta 2007).

Conclusion

In summary, it is important to keep in mind that MN systems work in collaboration with other important brain and bodily systems to carry out many of their primary and secondary functions. Neuroscientists recognize that MN are not the *whole story* for explaining the mechanisms that underlie any given behavior or ability. In addition, while there is now a more nuanced and refined understanding of MN since their discovery, just over 20 years ago, there is still much to learn about them. However, despite these limitations, the importance of MN cannot be ignored, as they are widespread throughout the nervous systems of humans, nonhuman primates, and likely many other species, functional early in development, and involved in a variety of foundational capacities.

Cross-References

- ▶ Development
- ▶ Empathy
- ▶ Imitation
- ▶ Infancy
- ▶ Neuroimaging
- ▶ Neuroscience
- ▶ Primate

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Mirror Self-Recognition

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Synonyms

Self-awareness

Definition

An understanding that one's own reflection in a mirror is an image of oneself, as opposed to

believing that one is looking at another individual. This understanding is evidenced by the use of the mirror to touch and/or investigate normally unseen parts of one's body.

Introduction

Do animals recognize themselves? This question prompted the first studies on mirror self-recognition in nonhuman animals, and subsequent research in this area has generated strong debate about the evolutionary emergence of self-aware aspects of human consciousness. Gallup's (1970) results set the foundation for the comparative study of mirror self-recognition with methods that have since become the standard test of visual self-awareness in animals. Gallup (1970) gave four chimpanzees (*Pan troglodytes*) and six macaque monkeys (four *Macaca arctoides* and two *M. mulatta*) 10 and 14 days, respectively, of exposure to a large mirror placed outside of their cages. All three species initially reacted with social responses (e.g., vocalizations and threat behaviors) directed toward their reflections, as if they were seeing an unfamiliar individual. However, within several days of this mirror exposure, the chimpanzees eventually stopped displaying social behaviors and increasingly used the mirror to inspect normally unseen parts of their body, such as picking food from the inside of their mouth and inspecting their anogenital region (Fig. 1). Macaques, on the other hand, did not show a decrease in social behaviors nor any spontaneous self-directed behaviors. Following this period, the mirror was removed and the animals were anesthetized so a nonirritant, odorless mark could unknowingly be placed on one of their eyebrow ridges and the opposing ear, locations that could only be seen using the mirror. Then, the animals were observed for any mark-directed behaviors – first in the mirror's absence and then its presence. In the absence of the mirror, only one mark-directed touch was observed in total across all of the species. However, with the aid of their mirror image, the chimpanzees frequently directed touches to the marks on their faces, occasionally even inspecting the fingers afterwards that they had used to touch the marks, further

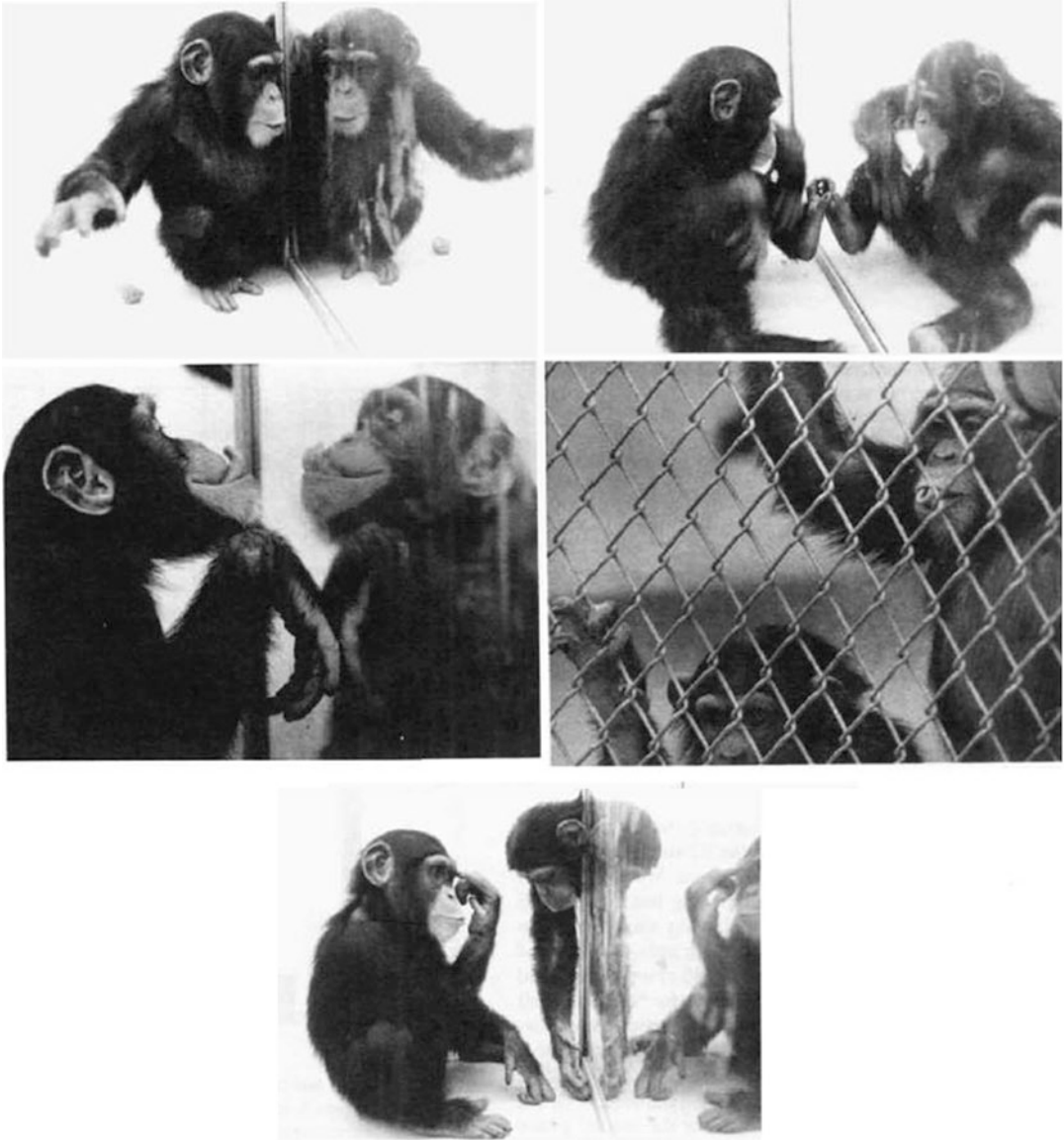
suggesting that they understood the mirror image was an image of themselves. The macaques, however, never made mark-directed responses, suggesting that they may not possess the self-recognition abilities of humans and chimpanzees – a capacity that Gallup (1970) proposed may be limited to humans and the great apes.

Mirror self-recognition thus came to be seen as a behavioral window into self-awareness and the mind. Gallup (1982) defined self-awareness as the ability to become the object of your own attention. Recognizing one's self in a mirror serves as evidence of this "sense of self" (Gallup 1982). Therefore, sessions of mirror image exposure and the mark test provided an objective, nonverbal assessment of mirror self-recognition that could be applied across species, allowing for direct comparisons and study of the ontogeny, phylogenetic organization, and mechanisms of self-awareness. Tests of mirror self-recognition also have been influential for the field of developmental psychology. For example, using similar methods (a mark test and behavioral observations of mirror responses), Amsterdam (1972) documented that mirror self-recognition emerges in human children around two years of age.

Spontaneous mirror-guided self-exploration of body parts that can only be seen with a mirror and the extinction of social responses (as if seeing an unfamiliar conspecific) directed toward the mirror image during mirror exposures, along with mark-directed responses during a subsequent mark test to objectively verify self-recognition, are considered the two criteria necessary to identify an individual's capacity for mirror self-recognition (Anderson 1994; Gallup 1994). Mark tests should be conducted with marks that are unknown and unseen by avoiding any olfactory or tactile cues and by being placed on a part of the body not visible without the use of a mirror (for additional methodological considerations, see Gallup 1994).

Tests of Mirror Self-Recognition with Apes

Given Gallup's (1970) original findings and the strong hypothesis that only humans and great apes have the ability to be self-recognizing, other



Mirror Self-Recognition, Fig. 1 Examples of contingent body (*top*) and facial (*middle*) movements and self-exploratory behavior (*bottom*). From “Self-recognition in chimpanzees (*Pan troglodytes*): Distribution, ontogeny, and patterns of emergence,” by D. J. Povinelli,

A. B. Rulf, K. R. Landau, and D. T. Bierschwale, *Journal of Comparative Psychology*, 107, p. 351. Copyright 1993 by the American Psychological Association (Reprinted with permission)

nonhuman primates soon were tested for mirror self-recognition. Self-recognition in chimpanzees and orangutans (*Pongo pygmaeus*) has been repeatedly demonstrated (e.g., Povinelli et al. 1993; Suarez and Gallup 1981). Spontaneous mirror-guided self-exploration also has been reported in bonobos (*Pan paniscus*; e.g.,

Westergaard and Hyatt 1994), suggesting a capacity for self-recognition in this species as well, although no formal mark tests have been conducted. Research in gorillas (*Gorilla gorilla gorilla*) is less clear regarding their mirror self-recognition ability. Some studies reported no evidence of self-recognition (e.g., Suarez and Gallup

1981) even after close to 400 h of mirror exposure was provided (Ledbetter and Basen 1982). However, instances have been reported of gorillas that passed versions of the mark test, but did not show any mirror-guided self-exploration (e.g., Shumaker and Swartz 2002).

Tests of Mirror Self-Recognition with Other Primates

Prosimians, Old and New World monkeys, and gibbons do not show compelling signs of mirror self-recognition during standard mirror exposure sessions and mark tests (e.g., Inoue-Nakamura 1997; although see Ujhelyi et al. 2000, for an alternative view concerning gibbons). Instead, they seem only able to make social or exploratory responses to their mirror images (see Anderson 1994, for further discussion, and Inoue-Nakamura 1997, for a summary of species tested for mirror self-recognition). This marked difference in responding across primate species supports Gallup's (1970, 1982) assertion that there may be a fundamental qualitative difference in cognition between the self-recognizing primates (humans and the great apes) and all other primates (prosimians, monkeys, and gibbons). However, this hypothesis of an evolutionary gap in primate cognition has been challenged and has inspired numerous efforts to find self-recognition in both primate and non-primate animal species.

Various procedural modifications have emerged in the comparative study of mirror self-recognition to facilitate better evidence of this capacity in species outside of humans and the great apes. One area of focus addresses potential issues of motivation and mark saliency during mark tests. The concern is that mark tests showing a lack of mirror self-recognition in some species may actually be false negatives due to the marks used not being salient (on a perceptual level) and/or motivating enough for the individuals tested. In response to this criticism, Hauser et al. (1995) used a modified mark test with cotton-top tamarins (*Saguinus oedipus*) in which the white tufts of hair on the tamarins' heads were dyed a different color. They reported that while all

of the tamarins that were tested failed a traditional mark test, five of six monkeys touched their dyed hair while looking in the mirror. Hauser et al. (1995) proposed that these self-directed mirror behaviors, while low in frequency compared to humans and the great apes, argue against the hypothesis of phylogenetic discontinuity in self-recognition ability. It should be noted, however, that a replication of this study by Hauser et al. (2001) failed to find the same results, and other studies using food substances as marks in order to increase motivation in several gibbon species (e.g., Suddendorf and Collier-Baker 2009) and marmoset monkeys (*Callithrix jacchus*; Heschl and Burkart 2006) did not find evidence of mirror self-recognition. In addition, Gallup et al. (1980) introduced the use of a directly visible mark (e.g., to the stomach or wrist) during the standard mark test as a control condition to confirm that subjects had at least a general interest in the marks used. This approach rules saliency out as a potential reason for negative results and has been used since by others (e.g., Suarez and Gallup 1981; Suddendorf and Collier-Baker 2009).

Gaze aversion also has been considered a potential reason for the lack of mirror self-recognition in monkeys. Anderson and Roeder (1989) first addressed this concern by presenting capuchin monkeys (*Cebus apella*) with angled mirrors. Similarly, Macellini et al. (2010) presented two pig-tailed macaques (*Macaca nemestrina*) with a modified mark test in which they were prevented from seeing their faces and could only see a mark on their chests using a mirror. However, no self-directed or mark-directed responses were found in either of these monkey species. Attempts to facilitate mirror self-recognition by providing mirror exposure starting early in life and/or for prolonged periods of time (e.g., Anderson 1983; Gallup et al. 1980), physical access to manipulate the mirror (e.g., Anderson and Roeder 1989), and mirror exposure sessions in pairs or groups to utilize monkeys' proficient ability to recognize one another (e.g., Anderson and Roeder 1989; Gallup et al. 1980) all failed to produce evidence of self-recognition in primates outside of humans and the great apes.

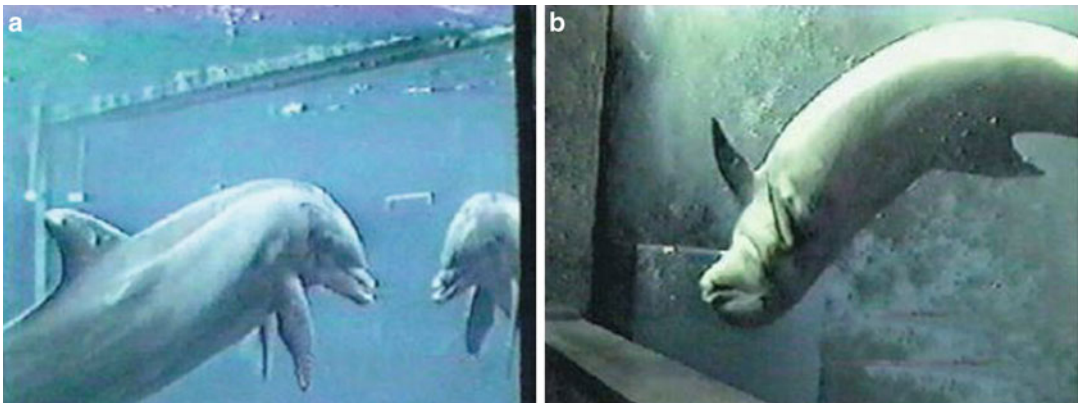
Even with explicit training to touch directly visible marks in their environment and on their body (Roma et al. 2007) and to use mirrors to retrieve otherwise unseen food (e.g., Heschl and Burkart 2006; Macellini et al. 2010) in an effort to aid animals' learning of mirror contingency, monkeys still failed a mirror-mark test. Thus, the evidence at this time suggests that prosimians, monkeys, and gibbons typically do not show a capability for mirror self-recognition.

Tests of Mirror Self-Recognition with Non-primate Species

Various non-primate animals also have been studied with self-recognition tests. Two bottlenose dolphins (*Tursiops truncatus*; Reiss and Marino 2001; Fig. 2), one of three Asian elephants (*Elephas maximus*; Plotnik et al. 2006), and two of five European magpies (*Pica pica*; Prior et al. 2008) were reported as recognizing their mirror image as themselves. However, it should be noted that Plotnik et al. (2006) did not require the elephants to be in front of the mirror during mark-directed touches and no mark-directed touches were observed for any of the elephants

in a retest by the researchers two months later. Four killer whales (*Orcinus orca*) also were presented with mirrors and three of the four were given a mark test (Delfour and Marten 2001). The whales demonstrated contingency testing behaviors only in the presence of the mirror (e.g., repetitive head movements and opening of the mouth). In addition, during the only analyzed mark test, a female whale was observed rubbing her mark off against a tank wall away from the mirror and then returning to the mirror afterward. This behavior occurred three times in succession, suggesting possible anticipation by the whale that her mirror image would be different after rubbing the mark off (although no details were given about the whale's behavior during the sham-mark sessions).

In a replication of Prior et al.'s (2008) study with magpies, the same mark test was given to nine jackdaws (*Corvus monedula*; Soler et al. 2014), another corvid species. However, they did not pass the mark test. Two pigeons trained to use a mirror to respond to an illuminated light behind them and to demonstrate self-directed behavior by pecking a directly visible mark on their bodies were then given the mark test and were reported to pass. This suggested "spontaneous integration" of the two behaviors to



Mirror Self-Recognition, Fig. 2 (a) Mark-directed behavior by a dolphin to a real mirror immediately after release from being marked. The faint white line on the wall indicates the location of the mirror. (b) The dolphin at Wall 1, exhibiting late sham-directed behavior: a continuous and repetitive sequence of 12 dorsal-to-lateral-ventral flips exposing the location of the sham-marked area of his body, the underside and tip of the right pectoral fin, to the

reflective surface. This unusual behavioral sequence continued for 32 s (Image is from "Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence," by D. Reiss and L. Marino, Proceedings of the National Academy of Sciences, 98, p. 5941. Copyright 2001 by the National Academy of Sciences. Reprinted with permission)

demonstrate mirror self-recognition (Uchino and Watanabe 2014). However, self-recognition as a result of explicit training of criterion behavior may be fundamentally different from the spontaneous mirror-guided behaviors seen in great apes (Gallup 1982).

Theoretical Interpretation and Debates About Mirror Self-Recognition

Some theorists do not regard mirror self-recognition as evidence of self-awareness, and a stimulating debate exists around this question. On one side of this debate is the original view of mirror self-recognition as evidence of self-awareness, introspection, and theory of mind (Gallup 1982). However, Heyes (1994) argued that great apes' mirror responses only required the use of visual sensory feedback to guide their behavior and were not different from their ability to successfully navigate their physical environment without running into objects. Similarly, Mitchell (1993) proposed two theories of mirror self-recognition that do not require a self-concept. Instead of recognition of one's own image, Mitchell (1993) suggested that mark-directed responses may only be relying on a combination of kinesthetic-visual matching and an understanding of object and mirror properties. Both Heyes (1994) and Mitchell (1993) also suggested that mark-directed touches may be the result of social responding and imitation.

Conclusion

Despite these differences in opinion about the psychological mechanisms at work, Gallup's (1970) mirror image exposure and mark test procedures have been used for the past 45 years to study mirror self-recognition comparatively. These tests provide a means to better understand the evolution of cognition through testable theories, and mirror self-recognition remains influential to comparative and evolutionary psychology. Although the exact neuropsychological mechanisms of self-recognition have yet to be identified,

there is growing interest in establishing the neural bases for mirror self-recognition (see van Velu and Chance 2014), an approach that likely will add a new chapter to this debate about what it means to recognize oneself in a mirror and how this capacity reflects the nature of nonhuman animal minds.

Cross-References

- ▶ [Does the Chimpanzee Have Theory of Mind?](#)
- ▶ [Evolution and Self-Awareness](#)
- ▶ [Theory of Mind](#)
- ▶ [Theory of Mind and Nonhuman Intelligence](#)

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Mirror System

► Mirror Neurons

Mirroring

► Mirror Neurons

Mirth

► Components of Humor

Misanthropic

► Monoamine Oxidase and Antisocial Behavior

Miscarriage

► Spontaneous Abortion and Maternal-Fetal Conflict

Mise-en-scène

► [Environmental Influences](#)

Misery

► [Depression \(Randolph Nesse\)](#)

Misinterpreted as Cultural Relativism

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Synonyms

[Descriptive relativism](#); [Metaethical relativism](#);
[Methodological relativism](#)

Definition

The concept that cultural norms and values derive their meaning within a specific social context such that each culture must be analyzed on its own terms.

Introduction

Cultural relativism at its simplest is this: *Judgments are based on experience, and experience is interpreted by each individual in terms of his [or her] own enculturation* (Brown 2008, p. 364). As a simple statement, this seems uncontroversial. However, further examination reveals that it has been misinterpreted in ways that are consequential for anthropological theory and practice as well as for more general philosophical positions.

The term cultural relativism may be parsed with several related but very different meanings.

All of them are rooted in reference to the behavior of people individually or collectively in cultures, subcultures, or even smaller social groups within cultures or subcultures. There are empirical and semantic issues even in this preliminary matter of properly referring to people as part of such entities, but we shall ignore those and take it for granted that one may define “a culture” satisfactorily enough to engage further issues about the relativism of cultures.

Historical Context of Cultural Relativism

The concept of cultural relativism cannot meaningfully be separated from the modern concept of culture, which emerged along with the practice of anthropology in the nineteenth century. Culture came to be understood as everything people know, believe, or habitually do and make as a result of their being part of a group. Proposed as a corrective to theories of geographic determinism and theological explanations for differences among societies, this conception of culture countered Victorian ideas about social evolution, progress, and the nature of non-Western people which were ethnocentric, racist, and supportive of European empirical expansion.

In the early twentieth century, anthropologist Franz Boas proposed the notion of *cultural relativism* in the context of several developments: the anthropological articulation and embrace of the concept of culture, the growing body of work of early ethnographers, reaction against the prevailing theories of cultural evolution, the expansion of Western imperial powers, the growing recognition of the power of enculturation, and the recognition of ethnocentrism as a likely cultural universal. It was articulated more fully by his students, most succinctly by Melville Herskovits. Two kinds of cultural relativism are relevant to evidence gathering about behaviors or interpretation of behaviors within suitably defined cultures. These are *descriptive* or *methodological* cultural relativism (Brown 2008; Womack 1995) and *metaethical* cultural relativism (Gowans 2015).

Descriptive Cultural Relativism

Both ethnographers in the field and anthropology professors in their classrooms typically espouse a

descriptive or methodological cultural relativism that follows directly from Herskovits' original formulation: because people think and act on concepts rooted in their enculturation, if ethnographers want to understand the people, they must at least temporarily suspend judgments based on their own cultures' premises.

Descriptive cultural relativism arises from cross-cultural comparison. The classic philosophical example is Herodotus' descriptions of the Greeks' and the Callatians' mutual horror at how they treated their dead: the Greeks burned corpses and the Callatians ate them (Westacott 2016). The behaviors are distinct descriptively and even logically incompatible given that *if* one of these is *somehow* judged to be wrong, then the other may be a member of a set containing at least one behavior judged right. Of course the Greeks and the Callatians judged their own behaviors to be right, and thus strictly contradictory to the other by their own assessments. However, (classically bivalent) logic recognizes that it is possible that, given some objective criterion of what is *right* in these circumstances, *both* the Greeks and the Callatians may be wrong. This logical observation then gives rise to a view about cultures which can be *described* as divergent with respect to some common human condition (here death) but also *may* be mutually inconsistent with some objective standard of being morally correct.

Metaethical Cultural Relativism

If one assumes that either the Greeks or Callatians are right, the other is wrong. That would produce the claim that there is moral contradiction. As allowed above, even if there is some intercultural objective standard of right *that is in fact lacking in all* observed cultural behaviors and beliefs with respect to some common phenomenon, then *all* those behaviors could thus be properly judged wrong. Some investigators, probably motivated by the logical possibility that since many such descriptively divergent behaviors (observed to be different with regard to the traits, behaviors, or beliefs under consideration) may all be wrong with respect to some supposed objective moral standard, made the further argumentative move to conclude that *no such intercultural objective*

standard exists. This is *metaethical cultural relativism*. By this view, no culture may be judged as right or wrong with respect to any behavior as compared with other cultures, even though each culture judges itself in these ways. This eliminates the very possibility of the *moral* contradiction of descriptively divergent behaviors among cultures.

However, no set of such descriptively distinct and culturally relative behaviors – even an open-ended set – can *itself* entail that there is no such objective standard. *There is no valid reasoning – even an inductive basis – to infer from iterated citations of a lack of agreement of descriptive behaviors cross-culturally that there is no objective intercultural standard for all such behaviors* (Gowans 2015; Rachels 1999). The usual way to express this criticism is that one may not infer values from facts (or vice versa) or even, as here, conclusions *about* values from facts (Hume 1983).

No avenue of human reasoning based on descriptive cultural relativism leads inevitably to metaethical cultural relativism. Metaethical cultural relativism may be true, but *no amount of ethnographic data itself demands that it be true*. Any supposition of metaethical cultural relativism, then, creates difficulties for social scientists and for policy makers.

Misinterpretations

Let us look at a number of ways in which a simple idea (one's judgments are based on one's enculturation) has been misinterpreted as or conflated with other ideas which obscure the primary value of cultural relativism to social scientists. First, while culture is a dominant concept in anthropology, cultural *relativism* is not cultural *determinism* and does not rule out other influences on human society and psychology (Spiro 1986). Cultural relativism does not logically entail normative relativism, which claims that there are no universally or absolutely binding moral principles, nor epistemological relativism, which claims that all ways of knowing are equally true. Herskovits, for example, was emphatic that anthropology can be scientific as well as hermeneutic and urged anthropologists to seek universals through empirical research (Spiro 1986, p. 264). Anthropological definitions of culture invariably include some

notion of culture as shared by a group (however large or small). *Cultural* relativism, therefore, does not entail or require *individual* moral relativism, and indeed every group recognizes and negatively sanctions deviant behavior by its members.

Particularly important in the context of a globalized political economy is that cultural relativism does not entail tolerance. The commonly accepted idea that it does was prompted by the debate surrounding the Universal Declaration of Human Rights in the 1940s. The conflation of relativism and tolerance was readily accepted and persists today, especially among anthropologists in the United States. The central insight of cultural relativism is enculturation, not tolerance. Although anthropologists and sociologists practice a suspension of judgment while conducting fieldwork, the attempt at objectivity is a requirement of the scientific method, not of relativism. Nor does cultural relativism require a kind of cultural romanticism, “a naïve glorification of all that is non-western” (Womack 1995, p. 51). There is no necessary connection between cultural relativism and a conclusion that all cultures are equally “good” or that no criticism of varying cultural practices is ever warranted (Edgerton 1992).

Because cultural relativism does not rule out the possibility of absolute moral standards (which could exist in the universe independent of any culture) or of universal moral standards (shared by virtually all human cultures and which could change over time), it does not rule out the possibility that a set of universally accepted human rights can be discovered. The misconception that relativism is opposed to universalism has sometimes made anthropologists ambivalent participants in the support of universal human rights agendas, not least because individual rights, individual autonomy, and democratic practices are so highly valued in Western society. These values could be discovered to have a universal basis, but so far, this has not been demonstrated. Further, cultural relativism does not require that ethnocentric demands, made by one society or group upon another, always be disallowed (Renteln 1988, p. 64). This point becomes more relevant as globalization of the political economy proceeds apace.

Current Social Science Research Strategies

Let us now consider briefly a number of “hot” research topics that engage social scientists, political activists, and philosophers: clitoral excision, honor killing, veiling and seclusion of women, circumcision of infant boys in Western medical practice and in traditional Jewish practice, arranged marriages, rape as a weapon of war, enlisting child soldiers, exploitation of sex workers, gun control, abortion rights, etc. These pose serious challenges to cultural relativism which, although logically flawed and empirically unsupported in its common, metaethical form, continues to be a position held by many and vilified by many more. Understanding such cultural practices is the goal of anthropological research.

For anthropologists, the basic assumption of cultural relativity continues to hold: ethnographers strive to suspend judgment until a belief or practice can be understood within its total context because they generally accept that enculturation powerfully influences ideas and behavior (the ethnographer’s own and those of the observed people). Ethnographers also strive toward objectivity in data collection and analysis to the extent that they wish their work to be considered scientific. Anthropologists in the field today recognize explicitly the collaborative nature of ethnographic research, i.e., the ethnographer doesn’t directly “collect data” but works with informants who share their knowledge. They acknowledge the power differential that may exist between ethnographer and the observed groups, including efforts to minimize the difference by consulting the group about publishing sensitive material, avoiding politicized use of cultural knowledge by states and other outside groups, and enlisting group members in development projects and movements for social change. Although anthropologists originally studied people in non-Western, often colonized, societies, contemporary anthropologists also study up the power gradient, including literate groups who speak the native language of the ethnographer and powerful groups in the anthropologists’ own culture (e.g., organ transplant surgeons, corporate leaders, nuclear scientists).

Conclusion

Although misinterpreted and misused in various ways for nearly as long as the concept has existed, cultural relativism remains an important corrective to imperialistic and chauvinistic ideologies and a necessary insight for conducting ethnographic research. The unencumbered proposition that judgments are based on experience and experience is interpreted by each individual in terms of his own enculturation directs us toward important areas of basic research. We need to better understand, among other things, the power of enculturation, how people acquire the values of their group(s), the nature of interaction, the ubiquity of ethnocentrism, the porous boundaries of social groups, and the effect of power differentials among groups within societies. The empirical search for universal human values, if discovered, would provide a basis for global assertion of a non-Western ethnocentric set of human rights.

Cross-References

- [Cross-Cultural Differences](#)
- [Cross-Cultural Similarities](#)
- [Cultural and Moral Relativism](#)
- [Franz Boas](#)
- [Modern Moral Relativism](#)

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Mismatch

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Synonyms

[Discrepancy](#); [Ill-matched](#)

Definition

The result of the rate of the development of technology and civilization occurring faster than natural selection and evolution can occur.

Introduction

Evolutionary mismatch is a phenomenon by which the rate at which our technology has advanced, especially postindustrial revolution, has effects on our bodies and psychology that were not anticipated and cannot be adapted due to the slow rate at which evolution occurs. Ancestrally, our minds and bodies are still designed to

essentially be hunter-gatherers, with the evolution of bipedal locomotion, our diets, and our intelligence that allow us the use of tools to hunt and use in order to increase the chances of survival. Thus, although it has been a considerable amount of time since our ancestors were forging the African savannah, enough time has not yet passed for our bodies to fully change and adapt in response to the recent advances in technology. Due to the industrial revolution in the late eighteenth and early nineteenth centuries, we have had an exponential rate of growth with our development in technology (Ashton 1997). While the industrial revolution spawned things such as factories and machine usage, it also drastically changed everyone's daily life, generally promoting a cleaner, higher quality living due to the commodities available, plus the surplus of new jobs that came as a result. Since then, we've seen development of technologies that were only figments of people's imaginations – things such as having the Internet, smartphones, self-driving cars, airplanes, and so forth. Mismatch represents the idea that our bodies were simply not created for this kind of lifestyle that happened fairly recently, and therefore we are “mismatched” with our physiological, ancestral minds and our modern, technologically advanced environment (Raichlen and Alexander 2014).

Evolutionary Mismatch: Diet

Evolutionary mismatch occurs in a variety of ways and can yield both positive and negative results, although the lion share of consequences tends to be negative. One of the biggest ways that we see mismatch today is in our diets. Our bodies were designed for high levels of physical activity, being able to run long distances and endure heavy cardioactivity. We also developed the tendency to lean toward sugars, salts, and fats because of their evolutionary advantage. When vegetation and livestock was short in periods such as winters or heavy climate fluctuations, sugars, salts, and fats were essential to survival given their ability to be stored in the body. When long periods of famine would occur, those who had indulged in sugars, salts, and fats when these were available had a

higher likelihood of surviving because of their fat storage and were able to live off of that rather than searching for more food. As a result, these foods were also a rarity and, when found, were extremely valuable. Individuals who had a preference to consume higher amounts of sugars, salts, and fats outlived those who did not stock on such foods.

Nowadays, we live in a civilization where everything can be purchased through an exchange of currency. Our bodies evolutionarily did not anticipate the ability to have a currency within a civilization and therefore be able to pay for anything that we may need. Thus, eating is no longer an arduous task of having to go out, hunt prey, skin and cook it oneself, and consume it – rather, we simply go to the local grocery store, buy some meat, and cook it. This completely eliminates the element of the massive amount of physical energy that was expended to simply get a meal. As a result, we see things such as obesity and heart disease as a result of lack of physical activity. Our ancestors were never required to set aside time to exercise given that physical activity was necessary and automatically came included in the hunter-gatherer lifestyle if one was to survive. Given that now we have commodities such as online retailers that can even deliver things to our doorsteps, the amount of physical activity we do in a day is incomparable to what an early hominid would have had to endure. We generally set aside time to engage in exercise, and when we do, we experience benefits such as drastically lowered risk of cancers, heart disease, obesity, and even psychological benefits such as elevated mood and lowered risk for depression. When this need is not met, we fall victim to many diseases and psychological detriments, which is a classic example of mismatch given that our bodies were meant to endure heavy physical activity every day – something that is simply not necessary with the resources we have available to us today (Frassetto et al. 2001).

With regard to sugar, salt, and fat, we now have the ability to simply pick up any foods we wish at the supermarket. Many of these foods are taken advantage of by their respective companies by using *supernormal stimuli* to appeal to

consumers. Thus, high levels of salt, sugar, and fats are often added to products to appear tastier and therefore keep the consumer coming back for more. This is another example of evolutionary mismatch – given that those foods were extremely rare in ancestral times, we developed an affinity for those tastes because, evolutionarily, our bodies were steering us in the direction of getting tastes and foods suitable for survival. Now that these foods are so often readily and easily available, it is extremely easy to overindulge in them, resulting in many of the health problems that we face today. Our ancestors never had to worry about things like diabetes and heart failure because it was simply impossible for them to encounter such a surplus of sugars, salts, and fats such that it would ever be a concern (Gluckman and Hanson 2004). In addition, by simply trying to get a meal, they engaged in rigorous physical activity on a daily basis which also eliminated much of the risk of health- and diet-related diseases. Given the society we live in, we must be attentive to what we eat, such as our sodium levels, cholesterol, intake of vitamins and minerals, and calorie count to avoid facing these detriments. Having to do so is an example of evolutionary mismatch given that our physiological bodies are still adapted to a lifestyle meant for survival on the African savannah, rather than living in major cities with supermarkets, delivery systems, and transportation.

Evolutionary Mismatch: Social Groups

Another common example of mismatch in humans has to do with the social circles we have today versus the one's in which our ancestors evolved. Prior to the advent of agriculture, our ancestors never stayed put for long. Instead, they lived in small nomadic groups, and because groups of thousands would be impossible to manage and coordinate, early hominin societies consisted of approximately 150 individuals (known as *Dunbar's number*). Additionally, a lot of these clans included many families, to the point that a single individual was probably related to a good portion of the group and the whole group

helped in rearing the children (a term known as *alloparenting* described in another section). After agriculture, however, our clans rapidly evolved into more complex societies, eventually leading to the cities we have today. Within a day alone, we may encounter hundreds, if not thousands, of individuals, and the vast majority of them are bound to be strangers. This may lead to higher levels of stress and feelings of loneliness because we are not meant to be so far away from kin.

If our minds evolved around small groups, then what can we possibly do to solve the mismatch between our EEA and our current metropolises? Wilson's (2011) *Neighborhood Project* seeks to answer part of this question by applying an evolutionary perspective on urban planning. Wilson gathered data on students in Binghamton, NY, and examined the nature of neighborhoods that corresponded to students who were doing well academically and socially and how these differed from the neighborhoods of students who were having problems academically and socially.

Beyond the effects of socioeconomic status, evidence suggested that students who lived in neighborhoods with higher levels of social connectedness and social capital performed better in school and scored higher on indices of natural altruistic tendencies. This was true even for children who came from poor areas of the city. Having signs of social connectedness such as decorations during holidays (Christmas lights in December or Easter eggs for April) or interactions among neighbors seemed to make quite the difference in children's development, both academically and socially.

Evolutionary Mismatch: Education

Gray (2011) applied the idea of mismatch to child development across the school-aged years to assess how modern educational systems compare to systems used in prewesternized societies. In current hunter-gatherer societies, education takes a drastically different form because there are not any lines drawn between work, play, and education. The way through which children learn about

the world and how the group works is by merely being part of the group and playing with all the other children. Furthermore, most of the education that children receive does not come from an adult, but from other children, often those who are slightly older. That most seminomadic societies studied had mixed-age environments suggests our ancestors evolved in similar ways and that our minds are not designed to sit in classrooms of same-age children for long periods of time. Gray's findings also suggest that play is essential for child development and learning.

It is not hard to see the disparity between education in ancestral environments and education in much of the westernized world. Children are asked to remain seated and quietly pay attention to an older, adult figure for hours at a time, with very short breaks between classes that are not enough play for their young ancestral minds. Children who cannot follow these rules or who are jittery in class are typically seen as either problematic or perhaps diagnosed with disorders such as attention deficit disorder (ADD) or attention deficit hyperactivity disorder (ADHD). While there certainly is more to these disorders than just mismatch, it is worth considering that a great part of hyperactivity in children is due to the way we evolved to simultaneously play, work, and learn.

Conclusion

For most of our evolutionary history, we lived in small groups composed greatly of blood relatives. It is under this environment of evolutionary adaptedness that our minds acquired the psychological mechanisms we have today. We are the product of thousands of generations of natural selection, yet because evolution is a slow process, the best these selection processes can do is equip us with the same mechanisms our ancestors had in the probabilistic-based "guess" that the environment will remain more or less the same (Geher 2013). Although this usually works out fine, sometimes contexts change over a short period of time, and that has certainly been the case with our environment.

This mismatch between our EEA and modern life can help explain several of today's problems, such as increased obesity and type II diabetes, particularly among developed countries that can more easily and cheaply produce processed foods and exploit our preferences for sugars and fats. It can also shed light on how current systems of education and urban planning are failing by constantly moving further away from models found in seminomadic societies. Although going back to our hunter-gatherer ways is probably not the solution (especially with today's massive population), we can certainly apply evolutionary theory into trying to overcome any mismatch. By knowing how our minds evolved, we can better understand where mismatches lie, and we can even design methods to overcome it by building our communities to resemble those we had during our EEA.

Cross-References

- [Environment of Evolutionary Adaptedness](#)
- [Evolutionary Mismatch](#)
- [Mismatch Between Evolved Morality And Modern World](#)

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Mismatch Between Evolved Morality and Modern World

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Synonyms

[Adaptive lag](#); [Evolutionary mismatch](#); [Mismatch theory](#)

Definition

Evolutionary mismatch occurs when a trait that evolved in one environment decreases fitness or well-being in a later and different environment.

Introduction

This entry describes evolutionary mismatch hypotheses in general form, provides illustration by way of a pair of nonmoral examples, then formulates the *moral mismatch* hypothesis. It then provides an example of a specific moral mismatch hypothesis focused on the tendency to objectify morality, describing the past benefits of this tendency as well as its current costs and suggesting those costs are due to significant differences between modern and ancestral social environments. The overall aim is only secondarily to defend this particular moral mismatch hypothesis; primarily, it is to identify the conceptual, methodological, and evidential issues that arise when formulating and supporting moral mismatch hypotheses.

Evolutionary Mismatch

An evolutionary mismatch is “a situation whereby an organism that evolved in one environment develops a phenotype that is harmful to its fitness or wellbeing in another environment” (Lloyd et al. 2011). Schematically and more generally, evolutionary mismatch involves the following four

elements: a trait (call this T), at least two environments – the past (E1) and the current (E2) one – and some form of cost (C) of T in E2.

A classic case of evolutionary mismatch is the peppered moth (*Biston betularia*). In preindustrial England, a light-colored morph of this moth predominated. As the industrial revolution proceeded, and as pollution darkened the formerly pale bark of the common trees, a dark-colored morph came to predominate.

To put this case into the framework laid out above, T was color, specifically the light coloration, E1 was the preindustrialization forests while E2 was pollution-darkened forests, and C was a fitness cost: T was selectively disadvantageous in E2, as light-colored moths were conspicuous against dark backgrounds and so faced increased predation risk. (For more detail on this case, see Cook 2003; Grant 1999; Kettlewell 1973.)

A case of mismatch involving humans is, plausibly, our “sweet tooth” (Symons 1992). Humans typically prefer sweet foods to bitter ones; this is T. In ancestral environments (E1) where meeting nutritional needs was challenging and efficient energy capture was crucial, the adaptive benefit of T is clear, since sweeter foods are typically more energy dense (e.g., ripe versus unripe fruit). In many contemporary human nutritional environments (E2), however, energy sources are overabundant and T can prompt overconsumption, leading to health costs.

This second example shows that C can be stated not in terms of fitness (although there may well be fitness costs to T in E2) but rather in terms of welfare or well-being. Obesity and health problems can run counter to the interests of the individual, but not *necessarily* reduce fitness. This example also shows why mismatch hypotheses can matter: understanding the causes of a problem is an important step toward developing a solution, and insofar as a mismatch hypothesis contributes to that understanding, it is significant.

With the framework and examples in place, it should be clear that there is no one thing – the mismatch hypothesis – but rather more and less demanding versions of a mismatch claim, depending on how the placeholders in the hypothesis are filled in. A more demanding version

would be that an adaptation that was adaptive in some past environment is now maladaptive. This version restricts the trait to adaptations and the costs to fitness costs. A less demanding version may be that a previously adaptive trait (whether or not it was an adaptation) is now maladaptive. A less demanding version still would be that some previously beneficial trait (whether the benefits were to fitness or not) is now costly (whether the costs are to fitness or not). Clearly, different evidential standards must be met to satisfy differently posed – more or less demanding – versions of the mismatch hypothesis, and clarifying this at the outset of a discussion is useful in avoiding later confusion.

It is now clear how to develop a moral mismatch hypothesis. Doing so requires specifying a trait *T*, describing relevantly different environments *E*₁ and *E*₂, and identifying the costs *C* of *T* in *E*₂. While this is simple enough as a schema, filling in details swiftly becomes complex.

Specifying *T*

Take the trait first. What is *T* in a *moral* mismatch hypothesis? Defining “morality” is far from straightforward (Gert 2012). Evolutionary explanations of morality target phenomena as diverse as systems of norms (Boyd and Richerson 2005; Richerson and Henrich 2012), moral emotions (Prinz 2007; Frank 1988) and the faculty of moral judgment itself (Joyce 2006; Hauser 2006). There are hard conceptual and empirical questions here, about the nature of morality and about which human features are the proper targets for evolutionary explanations of morality. For current purposes, it is possible to remain neutral on what is necessary and sufficient for something – a belief, judgment, utterance, system of rules, etc. – to count as moral, and on what evolutionary explanations of morality should aim to explain. Focus can be placed instead on features of actual moral thought and talk, and consider their evolutionary explanation and current effects.

An important distinction to make at the outset is between the *content* and the *form* of our moral judgments. Selective forces may well have influenced *what* we think is morally right and wrong, good and bad, favoring judgments that

promote survival and reproduction and shaping the content of human morality to the point that “our moral judgments are thoroughly saturated with evolutionary influence” (Street 2006, 114). A distinct claim is that evolution has affected *how* we think about moral matters, in particular, whether we see morality as objective. Perhaps we have been selected to see morality as objective because “human beings function better if they are deceived by their genes into thinking there is a disinterested objective morality binding upon them” (Ruse and Wilson 1986, 179).

There may well be scope to develop a moral mismatch hypothesis with reference to the content of our moral beliefs. Here, a moral mismatch hypothesis focused on the form of moral judgments will be outlined. In particular, this section will develop the idea that our commitment to moral objectivity is a case of moral mismatch. As befits the aim of this section, the primary concern is to highlight the conceptual, methodological, and evidential issues that arise in presenting moral mismatch hypotheses.

In the moral mismatch hypothesis considered here, *T* is the tendency to objectify morality. A natural question to ask immediately is: do we really have that tendency? There is a growing body of work investigating the metaethical views of ordinary folk and the ways in which those views manifest in behavior: the so-called psychology of metaethics (Goodwin and Darley 2008, 2010, 2012). This literature has been especially concerned with whether the folk are objectivists about morality, and if so how that particular metaethical stance matters. Landmark studies in this field were conducted by psychologists Goodwin and Darley.

Goodwin and Darley start with a definition of “moral objectivism” (following Sayre-McCord 1986): objectivism about morality is the view that “moral claim[s] can be true without reference to the subjective states of the individual making the judgement[s], and without reference to the conventions of any group of people who are making the moral judgement[s]” (2010, 163). The test for objectivism – about moral or any other sorts of claims – worked like this: subjects were given various statements and asked (i) to rate their

level of *agreement*, then (ii) if they thought there was a *correct* answer about whether that statement was true or false, and (iii) whether, if someone *disagreed* about the truth of that statement, then either that person or the subject *must* be wrong. Answering “yes” to (ii) but “no” to (iii) makes sense only if one supposes that the truth of the relevant statement is *not* objective in the above-defined sense. If one thinks that the truth of the relevant statement *is* objective, then one should answer “yes” to both questions. Saying “yes” to (i) and (ii) for any particular statement was therefore taken to mean one was an objectivist about that statement.

Goodwin and Darley found that, for the moral claims, the majority of subjects were objectivists (see their 2008 for details), but that there was variation both across individuals in whether they considered moral statements to be objective, and across moral statements in how likely they were to be considered objective. That is, some *subjects* more so than others treated moral statements as objective, and some moral *statements* more so than others were taken to be objective. Congruent findings about moral objectivity have been reported by other researchers (Wright et al. 2013, 2014; Sarkissian et al. 2011). In sum, empirical investigations paint a complex picture, on which ordinary moral agents are significantly but not universally or uniformly objectivist about morality.

The nuance here helps illustrate how filling in the specifics of a moral mismatch hypothesis swiftly becomes complex. Even defining the trait is far from straightforward. Mismatch hypotheses should be open and sensitive to messy empirical detail. In the case of objectivism about morality, it would be too strong to say the trait is universal and perhaps still too strong to say it is even species-typical. More cautiously, the claim could be that a tendency to objectify morality is a feature of some moral agents’ cognitive profile. What proportion of agents is a further question, but not one it is necessary to settle here. This highlights another important lesson from this case. Consider again the “sweet tooth” example: not everyone *has* a sweet tooth, but formulating a mismatch hypothesis about that trait is not for that reason

impossible. So, insisting that the supposedly mismatched trait be universal is too strong a requirement to impose on a mismatch hypothesis.

Another important lesson from this example is that projecting current traits backward in time is not always straightforward. In the peppered moth example, establishing the presence of the mismatched trait in the ancestral population was simple, since it was a case of observable microevolution over short timescales. When the ancestral population in question is further removed in time, though, establishing the presence of the supposedly mismatched trait is harder. It is far from impossible, of course. Consider again the “sweet tooth” example. Part of the case that this is an adaptation come from comparative evidence: other primates too prefer ripe (i.e., sweeter) to unripe fruit. That the trait is shared across nearby branches of our evolutionary tree helps support (though of course does not establish) the claim that the trait was present in the ancestral populations of interest.

Turning to the moral mismatch hypothesis, the question would be: why think the moral trait under consideration was possessed by our ancestors in the past environments of interest? This question is particularly challenging because the kinds of evidence described above are not available. The timescale obviously means simple observation cannot reveal our distant ancestors’ moral behaviors, beliefs, emotions, or systems of rules. Nor is comparative evidence available. (However permissive one might wish to be in deeming other, nonhuman animals moral, it is implausible in the extreme to think *either* that chimpanzees, for instance, are not only moral beings but also have views about metaethics, specifically objectivist ones, *or*, that even if they did, we could ever be in a position to know.) Establishing the presence of the mismatched trait in ancestral populations is a problem that may not have an easy solution. Here, the goal is simply to highlight the challenge. Any fully developed moral mismatch hypothesis – whatever the particular T is supposed to be – would need to properly address it, which may represent a significant evidential burden.

Specifying C

For a given T, a moral mismatch hypothesis needs detail regarding C, the costs of T in E2. Continuing with the case of moral objectivism, the question would be: what costs does objectivist moralizing impose? Here, as elsewhere, the specific example is intended to illustrate general issues for moral mismatch hypotheses.

Goodwin and Darley's findings suggest that ordinary people's metaethical views, in particular moral objectivism, influence attitudes and behavior, and do so in a way that bears on the case for moral mismatch. Objectivism influences how "open" or "closed" subjects are when confronted with moral disagreement. "Openness" and "closedness" are measured by how comfortable a person is being near others with different moral views, what kind of personality judgments a person makes about others who hold different moral views, and by how strongly a person resists changing their moral views in the face of disagreeing others. Goodwin and Darley found that those who treated a moral issue as objective gave more "closed" responses to disagreement on that issue: they showed more discomfort with proximity to disagreeing others, were more likely to say that a disagreeing other was "not a moral person," and were less likely to admit the possibility of giving up their own belief.

Similar results have been reported by other researchers (Wright et al. 2014) who found that being a moral objectivist predicted greater intolerance across a range of measures, including not only comfort with proximity but also willingness to help and cooperate with people who held conflicting moral views.

So, C in the moral mismatch hypothesis considered here can be stated in terms of the problems moral objectivists face when confronted with moral diversity. In such situations, possessing T seemingly makes one more prone to conflict and less able to negotiate resolutions to conflict when it does occur. Notice this is a quite loose statement of C. The currency is not specified. It is certainly not biological fitness, but rather, something more like a prudential cost, to be understood in terms of agents' prudential interests. And, little

has been said about the mechanisms by which the costs of T are imposed. Is it via brute physical fighting, or social strife, or both, or something else entirely?

Here the concern is not primarily to elaborate on the specific example of a moral mismatch hypothesis, but rather to highlight general issues for any hypothesis of this sort, and here is a significant one: stating C clearly, with reference to both the currency and the mechanisms of the cost.

Still with regards to costs, it is worth considering which individuals are the bearers of a mismatched trait's costs. A natural idea here is that the individual who bears the mismatched trait bears the costs, and in many cases, such as the peppered moth and sweet tooth examples used earlier, this is so. But, for a start, the bearers of mismatched traits need not be the only individuals negatively impacted by those traits. For moral mismatch hypotheses that focus on the content of moral beliefs, the costs of mismatch plausibly also fall on individuals other than the trait-bearers. When racism motivates violence, or limited altruism fails to motivate charity, those affected by discrimination and altruism failure suffer. Indeed, it may be that bearers of the supposedly mismatched traits themselves do not suffer at all; for them, there is no cost to T. While this is all quite speculative, a real lesson remains: mismatch hypotheses must be careful in accounting for costs, not only in terms of the currency paid, but also of who pays.

Returning to the specific example, one might wonder whether the costs of objectifying morality are balanced by any benefits of doing so. This usefully raises several questions for mismatch hypotheses of any sort. One is simply whether T in E2 imposes a cost. Another is whether T in E2 confers any benefits. Yet another is whether T is costly on balance, that is, whether it generates a net cost even when any counterbalancing benefits are considered. As emphasized throughout this section, there is no single way to run a mismatch hypothesis. A mismatch hypothesis could claim only that T in E2 imposes a new cost that it did not impose in E1 (remaining silent on whether

the trait in E2 in on-balance costly), or, it could make the stronger claim that T in E2 is on-balance costly. The important thing is to be clear about which claim is being made.

Specifying E1 and E2

It is not enough for a mismatch hypothesis to show that some trait is costly. That is consistent with the trait always having been costly. If that were so, the notion of *mismatch* would be doing no work. A mismatch hypothesis must show that T is costly *because* of some environmental shift. That is, mismatch hypotheses must specify E1 and E2, and, crucially, identify a difference between E1 and E2 that explains why T in E2 is costly. That last point is important, since it highlights the fact that mismatch hypotheses need not give exhaustive specifications of the two environments, but rather enough relevant detail to draw the significant contrast between them.

For the moral mismatch hypothesis being developed here, the C of T in E2 is being prone to conflict when confronted by moral diversity. In arguing that this is a case of evolutionary mismatch, the key idea is that human social life has undergone a radical and evolutionarily fairly recent shift.

From approximately 75,000 years ago until approximately 10,000 years ago, our Pleistocene ancestors were cooperative hunter-foragers living in small, mobile, multifamily groups of 20 to 30 individuals. Call this our ancestral environment, E1. It was characterized by relatively small-scale, homogenous, and independent social worlds.

In the social circumstances that prevailed in E1, a tendency to objectify moral demands may well have been beneficial. Experimental work in moral psychology (Young and Durwin 2013) suggests that being an objectivist about morality boosts motivation to behave as one believes morality demands. In small-scale ancestral social worlds, this extra motivation could plausibly have provided fitness benefit by encouraging intragroup cooperation. Such benefits may have accrued to individual group members – via increased generation of cooperative benefits and decreased risk of harms associated with selfishness and defection – as well as to the group itself, insofar as intragroup cooperativeness is an

important determinant of success in episodes of intergroup cultural selection (see Boyd and Richerson 2005).

Approximately 10,000 years ago, during the Holocene revolution, human social life underwent a dramatic change. The advent of agriculture saw a great increase in group size as well as social complexity. (Groups also became more sedentary, though that is less relevant here. For more on the Holocene transition, see Sterelny 2014a, b.) Contemporary human social worlds are very large, complex, and interconnected. So, the key change when it comes to filling in the moral mismatch hypothesis being developed here is this: whereas ancestral social worlds were relatively small-scale, homogenous, and independent, modern social worlds – E2 – are relatively much larger, more heterogeneous, and interdependent.

While a tendency to objectify morality may well have been adaptive in small-scale, relatively homogeneous and independent ancestral social worlds, it now operates in a much different social context. As a consequence of the change from E1 to E2, modern humans are currently confronted far more often with diversity along many dimensions, importantly including moral diversity, due to both within-group heterogeneity and intergroup interaction.

Recall the findings of Goodwin and Darley and Cole-Wright et al. concerning the influence of objectivism on attitudes toward moral disagreement. Objectivist moralizing may well be harmful under current social circumstances, insofar as it makes agents faced with moral diversity more prone to conflict while simultaneously less able to negotiate and resolve it. If something along these lines is true, the specific moral mismatch hypothesis outlined here would gain some support.

Of course, a great deal more would need to be done to establish that particular version of the moral mismatch hypothesis, but the point of the exercise here is to identify general issues. One such concerns the kinds of environmental change that can generate mismatch. One possibility is that conditions that once obtained no longer obtain, resulting in T in E2 being costly. That was what happened in the peppered moth case: the trees' bark was no longer predominantly white, so, white coloration was no longer adaptive but

instead became maladaptive. Another possibility is that the past conditions persist but new conditions arise that render a previously (and still partially) beneficial trait on-balance costly. This may well be what is going on in the “sweet tooth” case. A taste for sweetness is not entirely unreliable as a guide to getting sufficient energy and nutrition, even though it is now confounded by the ready availability of modern foods. In the case of moral mismatch sketched here, the environmental change is probably more of the former sort than the latter, but the same need not be true of all moral mismatch hypotheses. The important thing is to recognize scope for variation in how mismatch hypotheses are constructed.

Conclusion

Evolutionary mismatch hypotheses can be stated schematically in terms of a trait T, an earlier (E1) and a later (E2) environment, and some cost C of T in E2. A moral mismatch hypothesis can be stated by appropriately filling in these placeholders. There is no single moral mismatch hypothesis, though, since there are multiple ways of filling in T, C, E1, and E2. Depending on how a specific moral mismatch hypothesis is formulated, different conceptual, methodological, and evidential challenges will arise, some of which this entry has identified.

Cross-References

- [Evolution of Morality](#)
- [Morality](#)

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Mismatch Theory

- ▶ [Maladaptive By-Product Hypothesis](#)
 - ▶ [Mismatch Between Evolved Morality and Modern World](#)
-

Missing Heritability

- ▶ [Problem of Genetic Inheritance, The](#)
-

Misuse/Misapplication of Psychological Mechanisms

- ▶ [Exploitation of Psychological Mechanisms](#)
-

Mitochondrial DNA

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Synonyms

[Endosymbiosis](#); [mDNA](#); [mtDNA](#)

Definition

Mitochondrial DNA is a small circular double-stranded DNA molecule found within mitochondria. Unlike the nuclear genome, it is only inherited from an organism's mother.

Introduction

Mitochondria, covert rulers of the world, are the tiny energy factories of the cell. These membrane bound organelles create energy by using oxygen to burn the food we eat in a process known as

cellular respiration. Floating freely, they exist in hundreds to thousands in the cytoplasm of cells and look much like other rod-shaped bacteria. In fact, over a billion years ago, their prokaryotic ancestors slipped inside other cells and developed a beneficial relationship with their hosts that ultimately facilitated the rise of all eukaryotes, which include protists, fungi, plants, and animals. Only their small circular DNA hints at mitochondria's former independence as free-living bacteria.

Function and Inheritance

Single-celled organisms ruled the Earth for billions of years. Then, around 2 billion years after the first microbe, life got more complicated when cells started dividing up their labor. Some tissues became in charge of digestion while others for motility, storage, and degradation. Cells organized themselves into structures able to communicate and share resources. However, this new complexity demanded a much higher energetic cost. Scientists believe that a large cell swallowed the bacterium ancestor of modern mitochondria, who was then spared from degradation (John and Whately 1975). In exchange for a home, mitochondria produce energy through a chain of chemical reactions that pass an electron down a membrane – giving it the nickname “powerhouse of the cell” (Philip Siekevitz coined this term in his 1957 article “Powerhouse of the Cell.” In recent years, the phrase is usually mocked as an example of useless information taught in schools. In April 2013, a Tumblr user posted several impractical things learned in school, including “mitochondria is the powerhouse of the cell.” In the following 2 years, the post was reblogged and commented on over a million times.) The number of mitochondria in a cell is dependent on what task it needs to accomplish (Robin and Wong 1988). For example, heart cells are powered by thousands of mitochondria while skin cells have almost none. On average, each cell contains around 400, totaling 10 million billion in the human body.

Over millions of years, mitochondrial DNA (mtDNA) has shrunk. Since being engulfed by

our common single-celled ancestor, mtDNA has lost most of its genetic material to the nucleus. In humans mtDNA contains only 37 genes in comparison to the nucleus's 20,000 (Andrews et al. 1999). Most cellular functions are carried out by the host cell, so there is no need for mitochondria to keep redundant DNA. Like bacteria, mitochondria reproduce by exactly replicating their double-stranded DNA and dividing into two. This happens independent of whether their host cells divide because the organelles have their own propagation mechanism, a kind of confined priesthood (Clayton 1982). As each cell contains at least hundreds of mitochondria and each individual mitochondrion has five to ten copies of its DNA, cell division is immensely energy-intensive. MtDNA lost all of its non-vital genes in order to be efficiently replicated and only spans around 17,000 base pairs in vertebrates (Martin and Herrmann 1998). That makes up only .0005% of our entire genome. Unlike our superfluous genome full of transposable elements and repetitive elements, mtDNA genes are compact. (Only 2% of the genome codes for proteins. The rest of it is considered "junk DNA," a term coined by Susumu Ohno in 1972. Whether or not it serves a real purpose is debated among geneticists but may provide new signals for regulation or novel gene functions.) There are no introns, noncoding DNA within a gene, and little noncoding material between genes – a gene immediately starts where another one ends.

Of the genes that remain in human mtDNA, 13 code for proteins involved in cellular respiration and the rest for molecules that transport and assemble amino acids into proteins. All of their functions are closely tied to the control over cellular respiration (Chomyn et al. 1985). The speed of these metabolic reactions is sensitive to the changing energy needs of the cell it resides in, and this can shift rapidly depending on the situation. Mitochondria need to work much faster when we are running a marathon than when we are sitting on the couch watching a movie. (A jog around the neighborhood requires aerobic respiration – oxygen is used by mitochondria to break down glucose to generate ATP or cellular energy. Your breathing rate increases during exercise in

order to adjust for the higher oxygen demands needed by your muscles. Experiments by Gary Dudley in 1982 showed that high-intensity running boosts mitochondrial production.) These changing demands require mitochondria to respond individually to the cell's needs. The mtDNA retains its few genes because they are vital in maintaining a level of on-site control: the chemical reactions needed for energy production are tightly controlled at the level of each mitochondrion. The cell would not be able to respond rapidly or efficiently if mitochondria were controlled by genes nestled far away in the nucleus.

Vertebrates inherit their mitochondria only from their mothers, because the few mitochondria attached to sperm are actively destroyed at fertilization (Sutovsky et al. 1999). The egg contains around 100,000 mitochondria in stark contrast with the wiggling sperm who only has a few arranged around the head to fuel its journey to the uterus. When sperm penetrate the egg, any mitochondria that slip inside are rapidly cut apart by the CPS-6 protein, which first digests the organelle's internal membrane and then the mtDNA (Zhou et al. 2006). This means that the origin of all mtDNA in every cell in your body comes from the few in your mother's egg at fertilization.

Like the Y chromosome, mtDNA has no opportunity for recombination as it is passed down almost unchanged from mothers to their children, both females and males (Giles et al. 1980). Autosomal chromosomes, which contain the majority of your genetic information, go through a complex shuffle every generation, but mtDNA has a straightforward pedigree. Over time, mutations arise in mtDNA which allows it to act as a record of human descent. If a woman acquires a random mutation in her mtDNA, she will pass it to all her children, and her daughters will also pass it onto their children. Therefore, when we find evidence of identical mutations in mtDNA, it indicates that the families who contain them share a common lineage.

MtDNA mutation rates seem to be relatively constant, so scientists can assume that the more mutations there are between two individuals, the longer they have been separated. Specific areas of

the mtDNA evolve at a rate of up to ten times than nuclear genes (Brown et al. 1979), which can be used to study differences at the population level. In 1987, geneticists examined the mtDNA of modern humans living around the world and concluded that they had a common descent in Africa around 200,000 years ago (Cann et al. 1987). But that was not even the most spectacular discovery; their analysis indicates that all people living today can trace their mtDNA back to a single woman – dubbed Mitochondrial Eve. This was not the first human woman but instead the most recent common mitochondrial ancestor; all of the other women roaming the Earth at the same time as her left no heirs living today.

A long time ago in a galaxy far, far away, director George Lucas told us the story of Jedi Knights filled with intelligent microscopic life forms called midichlorians that resided symbiotically in all living cells (In the *Phantom Menace*, Qui-Gon discovers that Jedi Anakin Skywalker has the highest known count of midichlorians. This incredibly high count, and therefore connection with the Force, is the reason why he was the only human who could pod race despite more there being more experienced pilots). In large amounts, they allow for a connection with the omnipresent energy field called the Force. Their similarities to mitochondria in both name and function are indisputable. Like midichlorians, mitochondria are intracellular symbionts related to ancient bacteria with their own separate DNA. This genetic material is also why Princess Leia's son is a Jedi: mitochondria is inherited from your mom.

Conclusion

The mitochondria found in every eukaryotic cell was once an independent bacteria. Over a billion years ago, they crawled inside other cells to form the symbiotic relationship that is found in almost every plant and animal cell. They are membrane-bound organelles that create most of our cells's store of energy and still retain their own genetic information. In comparison to the nucleus's 20,000 genes, mitochondrial DNA contains just 37 genes—the majority of which are involved in

oxidative phosphorylation. Mitochondria, and all of its genetic material, is maternally inherited and passed on to offspring in the cytoplasm of an egg cell.

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Mixed Languages

► Pidgins and Creoles

Moaning

- [Crying](#)

Mobbing

- [Child Abuse and Bullying](#)
- [Predator Confusion Hypothesis](#)

Mobbing Calling

- [Alarm Calling](#)

Mobility: Crawling and Walking

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Synonyms

[Locomotion](#); [Motor development](#)

Definition

Posture – prone or upright – is the position of the torso required to keep balance while stationary (e.g., sitting) and while moving (e.g., crawling and walking). Crawling is locomoting in a prone posture by moving all four limbs, sometimes with belly on the floor for added support. Walking is locomoting forward bipedally without external supports.

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Introduction

One of the crowning achievements in infancy is acquiring the ability to locomote. The study of crawling and walking has a long history (Preyer 1905; Trettien 1900). In more than a century of work, researchers have focused on defining crawling and walking age norms and painstakingly described developmental changes in coordination, movement patterns, and muscle activations (Adolph and Robinson 2013). Much of this work has been conducted in Western populations, overlooking culture and context and assuming universals. Cultural beliefs, practices, and expectations manifest in childrearing practices – how to hold, dress, sleep, toilet, etc. The variability in childrearing – or differences in infants’ experiences – offers different opportunities for posture, balance, and locomotion, which in turn explain variation in motor skills. Moreover, variability in motor skills extends beyond infancy. Examples of this variability and effects of everyday experiences are evidenced in cross-cultural comparisons. The aim of this entry is to show how cultural research illustrates the formative role of experience in motor development and challenges our assumptions that differences in childrearing have no effects on crawling and walking (Adolph et al. 2010; Karasik et al. 2010).

Historical Considerations

In the early 1900s, development was seen as a function of neurological maturation and physical growth. Arnold Gesell (1928) and the early pioneers of motor development led the charge in documenting the developmental progression of postural and locomotor skills based on behavior of infants from a homogeneous sample (infants from middle-class families of Northern European descent living in New Haven, CT), presumably to reduce much of the already existing variability in motor skills. Gesell was first to recognize the enormous variability: In hundreds of pages, miles of film, and dozens of photographs, he meticulously described stages of prone progression and upright locomotion for each month of life

of these children (Gesell and Ames 1940). In this enormous endeavor, Gesell acknowledged the historical and cultural shifts that could underlie variability in motor skills (Gesell and Ilg 1943) but focused on establishing commonalities in infants' skills, assigning ages at onset, and revealing skill order. Gesell's detailed records were condensed to "milestone" charts – a limited list of skills that Gesell considered essential (e.g., hand and knee crawling over other forms of prone progression), ordered by age. Variations of motor milestone charts are still prominently displayed in pediatric offices, featured in developmental textbooks, and are foundational to widely used scales of infant and child development – e.g., Brazelton, Bayley, Peabody – all normed against Western European standards. The World Health Organization took it a step further by publishing standards – requirements for the sequence and timing of infant postural and locomotor milestones – that all infants should meet (Martorell et al. 2006).

Despite their use in clinical diagnostics, norms and standards oversimplify the development of skills like crawling and walking by placing the emphasis on *when* skills should emerge rather than *how*. Ultimately, age is only mildly related to crawling and walking, and importantly it does not determine onset. Instead, infants' experiences created by childrearing practices are a better indicator of what skills develop and how.

Shared Childrearing, Different Practices, and Constraints on Motor Skills

How are babies put to sleep? Where are infants situated when awake? What are parents' choices for diapering and toileting? Universally, caregivers deal with these matters, but how they do so can vary widely by culture and context. Western parents have nearly infinite options on how to manage daily childcare routines, with abundant, commercially available baby gear offering potential solutions. Spacious cribs, thin disposable diapers, baby walkers, and playpens are only a few frequently used childrearing tools readily available to Western parents— and all inadvertently

place a premium on self-generated movement. It is surprising that there are little empirical data describing the frequency and the extent of use of these practices within Western cultures and around the world. Possibly, the paucity of data is because researchers have taken childrearing practices for granted, presuming that variability in these practices present more of a nuisance rather than signifying important differences in infants' experiences.

Handling and Containing Infants

Ask any American parent how to hold a newborn, and they will answer – you must support the baby's head. Western parents deeply believe that babies are to be handled with extreme care, gently cradled in arms with the head always supported against gravity. Specific recommendations published by experts across Europe emphasize safest positions for infants, when to use water for grooming, and whether to rub the skin during bath (Blume-Peytavi et al. 2009). In other parts of the world, caregivers use more vigorous approaches to handling. Intense massage, daily exercise, and close body contact are common childrearing practices documented across Africa in communities such as Kipsigis and !Kung San (Konner 1976), the Gusii (LeVine and LeVine 1966), the Bambara (Bril and Sabatier 1986; Rabain-Jamin and Wornham 1993), Cameroonian Nso (Carra et al. 2014; Keller et al. 2002), and in the West Indies (Hopkins and Westra 1988). Especially during bathing routines, caregivers thoroughly and intensely give infants a rubdown, kneading the head and body, rotating the joints, and pumping the legs and arms. They toss infants into the air, suspend them by the neck or from the ankles, and grasp them by each limb, (Fig. 1a) thus allowing infants to practice supporting their heads against gravity (Hopkins and Westra 1988; Rabain-Jamin and Wornham 1993; Super 1976). Caregivers in these cultural communities believe that the physiological flexion – the tight muscles and joints – infants are born with will not dissipate unless babies are stretched and massaged (Rabain-Jamin and Wornham 1993). The release of



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Mobility: Crawling and Walking, Fig. 1 Culturally specific practices in infancy and adulthood. (a) Suspension by neck, ankles, or limb. (b) Moving the arms and legs to train crawling and walking. (c) Restriction in slings,

“gahvora” cradles, or baby walkers. (d) Locomotion in “lotus” shoes for bound feet, high heels, or “huarache” sandals

physiological flexion may increase the range of motion, thereby providing more opportunities for spontaneous movement.

The vigorous handling may look intense, but only to the Western eye. Caregivers who engage

in these handling routines do so because it is integral to childrearing; it is what caregivers think they should be doing as part of normal everyday interactions to ensure healthy development (Carra et al. 2013; Heidi Keller 2003). In

addition, mothers from West Africa noted that the handling and body stimulation allows for positive social interactions. While infants jump in mothers' laps, babies see mothers smiling and laughing in response (Carra et al. 2014; Super 1976). The reciprocal exchange sets a foundation for turn-taking during these "protoconversations."

Ideas about the importance of childrearing practices are so fervent that even if caregivers emigrate, they often continue their traditional practices rather than relinquish them to adopt those of the host culture. For instance, West African immigrant mothers living in Italy and France and Jamaican immigrant mothers living in Britain maintained frequent body stimulation and exercise routines (Carra et al. 2013; Hopkins and Westra 1990; Rabain-Jamin and Wornham 1993).

Childrearing practices are not without consequence. Infants who were regularly massaged and exercised (Fig. 1b) shortly after birth began walking at earlier ages than infants who did not experience daily massage and exercise (Hopkins and Westra 1990; Rabain-Jamin and Wornham 1993). Experimental data confirm the effects of childrearing. How parents hold their young infants was found to be related to infants' level of postural control in sitting and standing (Duncan et al. 2018). A few minutes of postural training at 2 months of age accelerated postural, manual, and locomotor skills at 12 months (Lobo and Galloway 2012). A few minutes of daily crawling exercises accelerated the development of crawling in 7-month-olds (Lagerspetz et al. 1971). A few minutes of daily stepping exercises in 2-month-olds increased stepping movements 2 months later (Zelazo et al. 1993) and accelerated walk onset age by the end of the first year (Zelazo et al. 1972).

When not tossed, suspended, or exercised, caregivers situate infants in places that keep them safe and occupied or tote them along as they do their own work (Fig. 1c, left and middle panels). African infants in Mali, Kenya, and the Ivory Coast, Papua New Guinea, the Ache infants of Eastern Paraguay, the Zinacanteco of Maya, and Tajik infants in Central Asia spend time confined to slings and sacks tied to caregivers' bodies or gahvora cradles (Bril and Sabatier 1986;

Karasik, Ossmy, Tamis-LeMonda, & Adolph 2018; Kaplan and Dove 1987; LeVine and LeVine 1966; Solomons and Solomons 1975; Tracer 2009). Zinacanteco infants of a Mayan community in Mexico are carried on their mother's back in a "rebozo" shawl that is wrapped around the infant and knotted over the mothers' chest. When mothers are unavailable, older siblings take over carrying but rarely playing with infants. During the first year, infants are not held upright to look around; their face in the rebozo is often covered. Family members avoid talking with or engaging infants in face-to-face interaction and rarely put them on the floor to explore or move on their own (Brazelton et al. 1969). Tajik infants in gahvora cradles are also covered, but caregivers respond contingently to babies' whimpers and cries. During their first year of life, Ache infants spend the majority of their day carried by caregivers and rarely set down on the ground or left alone (Hill and Hurtado 1996).

Caregivers actively discourage exploration to guard children against environmental hazards. To restrict exploration away from caregivers, mothers tie children with a vine around the ankle so that they don't wander into the fire. When camp is moved, infants are carried in a sling with their heads resting on mothers' chest. At 18 months, infants are taught to ride on top of their mother's carrying basket, holding on to her, and ducking branches and vines in the path. As a result, the Ache lag months behind American children; walk onset age is around 2 years of age in Ache infants as compared to 12 months in American infants (Kaplan and Dove 1987). But later in childhood, the Ache children are encouraged to move and explore. At about 5 years of age, children are required to walk 3–5 km over difficult Paraguayan forest terrain when camp is moved; boys are taught to build and use bow and arrow; and girls weave and carry "burden baskets" of personal belongings and food when camps move (Hill and Hurtado 1996).

Caregivers in the USA also reduce opportunities for locomotor exploration by putting infants in playpens and highchairs and installing safety gates that restrict access to stairs. Infants with limited access to stairs learned to go up and

down stairs at older ages as compared to infants with stairs in their home (Berger et al. 2007). Caregivers use mechanical baby walkers in which infants are propped up sitting with their feet dangling (Fig. 1c, right panel). The walkers typically have trays with attached toys for manipulation and play, but these fixtures limit infants' view of the ground and feet, preventing them from visually guiding their movements. Although their feet may reach the floor, infants do not maintain posture and balance on their own as they passively glide across the surface. Infants who used baby walkers crawled and walked later than those who never did or who used baby walkers that did not obstruct infants' view (Siegel and Burton 1999).

Sleeping and Swaddling

Placement and positioning during sleep impose different constraints on movement, and both practices have undergone historical and cultural shifts. Until the early 1990s, caregivers placed infants to sleep in a prone position to prevent aspiration of regurgitated milk. In 1992, the American Academy of Pediatrics instituted the "Back to Sleep" movement, which urged caregivers to put infants to sleep on their backs because researchers found a positive association between the prone sleep position and Sudden Infant Death Syndrome (SIDS). This shift to back-sleeping resulted in a decrease in SIDS ("Changing Concepts of Sudden," 2000). However, the change in infants' sleep position came at a cost: back-sleeping is related to an increase in brachycephaly (flattened back of skull), plagiocephaly (flattened side of head) (Argenta et al. 1996; Chizawsky and Scott-Findley 2005; Holt 1960; Turk et al. 1996), and torticollis (weakened neck muscles on one side of the head) (Boere-Boonekamp and van der Linden-Kuiper 2001). Exclusive back-sleeping position was related to delays in prone skills. Infants who are put to sleep on their backs displayed delays in rolling, tripod sitting, creeping, crawling, pulling to stand, and playing with hands at midline relative to prone sleepers (Davis et al. 1998; Jantz et al. 1997; Vaivre-Douret et al. 2005). It is possible that receiving fewer opportunities to practice

pushing themselves up and developing strength needed to move on all fours delayed infants' prone skills.

Swaddling – which often accompanies back-sleeping – is a well-known form of restriction, characterized by cloth used to wrap infants' body and limbs. Ancient Greeks swaddled infants because they believed it facilitated proper postural development (Lipton et al. 1965). In the traditional Navajo and Mohave cultures, swaddling involves using a cradleboard. Infants are swaddled and bound against the solid surface of the board with their limbs straightened and held in place with straps made of cloth, willow bark, or twine (Chisholm 1978). The cradleboard can be hung by hooks or carried in caregivers' arms or on their backs to keep infants close as caregivers work (Chisholm 1978; Dennis 1941). Recently, swaddling became popular in the USA and Europe likely because research suggested that swaddling reduces excessive crying (Giacoman 1971; Lipton et al. 1965) and improves quality of sleep (van Sleuwen et al. 2007). Although swaddling involves the deliberate restriction of limb and body movement, researchers have found no consistent evidence that swaddling delays motor development (Chisholm 1978; Manaseki-Holland et al. 2010). It is possible that caregivers may reduce how much they swaddle at various points in development or modify the practice, thereby reducing the potential effects of movement restriction (Manaseki-Holland et al. 2010).

Toileting and Dress

Methods of toileting and dress affect infants' spontaneous movements. Caregivers begin to toilet train at widely disparate ages across the world – as early as 4 months among the Digo of East Africa (deVries and deVries 1977) to as late as 2.5 years of age among modern middle-class families in the USA (Brazelton 1962). Before children can fend for themselves, caregivers invent toileting solutions that align with the geographic, economic, and cultural context in which they raise their children. In Tajikistan and other

parts of Central Asia, caregivers toilet using an external catheter that drains waste from infants bound in a gahvora cradle (Karasik et al. 2018). In rural China, caregivers placed infants on their backs for most of the day, buried up to their armpits in a bag of fine sand (Xie and Young 1999). The gahvora cradle and sandbagging are effective methods for keeping infants clean and dry in areas where water and other resources are limited. But, the restrictive bindings and heavy sand prevented infants from moving; infants showed delays in gross motor skills relative to WHO standards (Martorell et al. 2006; Mei 1994). In other parts of China, caregivers dress newborns in split crotch pants and learn to “read” infants’ signals (Dombroski 2018). Similarly, Vietnamese parents potty-train their babies using a whistle. When the baby fusses or gives a sign that they need to go, parents hold them over the toilet and whistle. Caregivers are able to toilet train their babies by 9 months of age, more than a year before Western parents initiate training (Horn 2006). By 12 months, infants could communicate their need to go and by 18 months could go independently without needing to ask (Duong 2013).

Western diapering methods seem less extreme. Until the 1960s, cloth diapers were almost universal in use; by 1971, thin disposable diapers had become the primary means of toileting (Krafchik 2016). However, both types of diapers affect infant movement. While wearing old-fashioned cloth diapers or modern disposable diapers, infants showed less mature walking patterns and displayed more missteps and falls compared to when they walked naked (Cole et al. 2012). Possibly, the diaper pushes infants’ legs apart, making movements more awkward and balance more precarious. Going naked, infants’ gait was advanced by months as compared to when they walked in diapers. Like diapers, layers of clothing can impede infants’ crawling and walking. Infants in Japan, the USA, and Israel show delays in crawling if they are dressed in restrictive heavy clothing (Atun-Einy et al. 2013; Benson 1993; Hayashi 1992). At the turn of the twentieth century, 40% of infants skipped crawling altogether, possibly because the long gowns that were

popular at the time prevented locomotion on hands and knees (Trettien 1900).

Expectations and Activities Shape Ways of Moving

Similar to assumptions made about triviality of childrearing in infancy and extent of variability in infants’ experiences, researchers have assumed the narrow range of motor outcomes beyond infancy. We assume that the epitome of mature locomotion is walking, as exemplified by college-aged participants. But undergraduates that often contribute to psychological research are not representative of the proficiency of adult locomotion. Expectations and culture-specific activities affect typical locomotion for adults and define what is socially accepted and functional in their community.

Expectations

Crawling, a transient behavior displayed in infancy prior to walking, has been documented as a primary mode of locomotion in a few exceptional adults (Humphrey et al. 2008; Tan 2006; Turkmen et al. 2006). Researchers discovered a family living in remote villages of Turkey where the adults crawled on hands and feet instead of walking bipedally. One of the reasons for their stunted development is that children’s parents did not encourage them to walk. Other siblings crawled, thus providing the expected social model of typical locomotion (Adolph et al. 2010).

Expectations about body dimensions, posture, and quality of movement in adults are important factors for social desirability and status in the community. The practice of foot-binding for women prevailed in China for hundreds of years (Ebrey 1999; Kenny and Nichols 2017; Ko 2005). Chinese women bound their daughter’s feet when girls were between the ages of 4 and 6, while bones in the foot are fairly supple, but beyond the developmental time frame when children acquire mature walking gait (Adolph and

Robinson 2013). The ideal female foot (Fig. 1d, left panel) was only 3–4 inches in length (Fang and Yu 1960; Reznikov et al. 2017). The size of the feet created a wavering posture resembling a “lotus flower in a breeze,” which signified women’s tenderness and submissiveness. And the tight binding forced women to take small steps, which was thought to strengthen their vaginal muscles, enhancing their value in marriage (Ping 2000). Moreover, foot-binding limited women’s mobility and productivity and was therefore reserved for wealthy families who did not rely on the labor of their wives and daughters. Women in poor families were still required to do work such as spinning, weaving, tending crops, and food preparation that required skill and strength of hands, not feet. To achieve the ideal foot took years: Mothers submerged daughters’ feet in hot water, scrubbed off dead skin, and wrapped cotton bandages soaked in hot water around the foot folding the four toes under the ball of the foot, leaving the big toe out. Girls were then forced to walk on their folded feet, weakening and breaking the bones, allowing their feet to be tied more tightly (Ko 2005). The practice in China was outlawed in 1912 but continued until 1949 in rural areas (Kenny and Nichols 2017).

High heels (Fig. 1d, middle panel), designed to lengthen and enhance the shape of the legs, also have effects on movement by transferring the center of gravity upward, thereby transforming posture and balance and reducing stability. Wearing high heels also is a century-old tradition associated with upper-class women and men (Vartanian 2011; Wiedemeijer and Otten 2018). High heel use begins in young adulthood and requires extensive practice. Wearers must learn to adjust their posture and modify walking gait to avoid appearing hunched over and stomping ape-like. When walking in high heels, walkers changed the placement of the foot, adjusting their posture at the shoulders and neck, slowed down their speed, and took shorter steps than when walking barefoot (Chien et al. 2013). With experience, high heel wearers learn to adopt a walking strategy to maintain efficient control and minimize trips and falls (Chien et al. 2014).

Daily Activities

People’s daily tasks shape locomotor skills. In Nepal and Africa where transportation is lacking, children and adults routinely carry extraordinary loads up to 70% of their body weight for great distances (Heglund et al. 1995). They carry loads supported on their heads rather than in arms over rough terrain and without compromising efficiency or mechanical energy (Bastien et al. 2016). Walking with head-supported loads begin in childhood to accomplish daily activities and to train for work as porters. Over years of practice, walkers with head-supported loads learn to change the biomechanics of their normal gait patterns to conserve energy, making their walking gait more efficient than adult walkers without such experience (Heglund et al. 1995).

The Tarahumara of the Copper Canyons in Northern Mexico are another prime example of how culturally specific tasks push locomotor abilities beyond what we typically think is the limit. The Tarahumara are known for their extraordinary ability to run long distances, up to 250 miles, without running shoes, either barefoot or in thin, rubber, makeshift sandals called huarache (Fig. 1d, right panel) held on with leather laces (McDougall 2009). Their extraordinary running abilities are not limited to only a select few elites; the entire tribe runs: men, women, and children of different ages, sizes, and body types. And the Tarahumara can run for days. Why do they do it? They run to complete daily tasks, such as delivering mail or persistence hunting for food. They run for comradeship, to maintain interpersonal connections among the tribe. And they run for amusement, competing in races of up to 300 miles. How do they do it? The Tarahumara have inhabited the secluded mountainous region of the Copper Canyons for nearly 500 years (McDougall 2009). Over years of running starting in early childhood, the Tarahumara have adapted their bodies and running ability to the physical constraints of their rugged environment. The trick to their long distance running ability without incurring injury turns out to be barefoot running. When researchers tested participants in the lab running in sneakers and while barefoot, they found that

impact during heel strike was minimized when running barefoot rather than when running in sneakers (Thompson et al. 2015). McDougall's bestselling 2009 book revolutionized the running shoe industry. The minimalist, "barefoot" running movement inspired the creation of new, funny-looking five-finger shoes to mimic the effects of barefoot running (Davis 2014). It is still unclear whether running barefoot or in the minimalist running shoes really does reduce injury (Perkins et al. 2014). But the message seems to be for adults and for walking infants alike: it's best to go naked or barefoot.

Conclusions

What we know about motor development depends on whom we study, what we ask, and where we collect the data. Current cross-cultural work on motor development is narrow in scope. Much of the world is unrepresented. The World Health Organization (2006) that published standards of gross motor skills all infants should meet only included infants from six countries, ignoring many regions of the world (e.g., Central America, Australia, Central Asia). Thus, with respect to daily childrearing tasks, we know little about what caregivers do, when they do it, and how much.

Experience affects every aspect of motor development, and childrearing practices – the most mundane everyday routines – shape infants' experiences. Cross-cultural research helps us realize the extent of the variability in everyday experiences. However, the literature is limited because everyday experience is typically overlooked or poorly documented, studies are concentrated within infancy, and the focus is predominantly on age comparisons. Particularly, the field of cross-cultural motor development is dominated by comparisons with Western practices and age norms established on Western populations, as if Western childrearing practices and developmental outcomes are the barometer for what is universal or at least what is optimal.

Typically, the extent of the variability of experiences or its effects on motor development are not well understood. If experience is considered, it's

treated as a dichotomy – infants are exercised or not, carried or not, diapered or not – because comparisons are made with Western practices where the practice exists or is absent. At best, mothers are asked to self-report whether they engage in an activity: never, sometimes, or often (e.g., Hopkins and Westra 1990). This type of quantification of childrearing assumes that practices either promote or inhibit particular behaviors. But childrearing practices are on a continuum. Take the case of sling carrying, for instance. On the one hand, the practice is restrictive because infants' opportunity to roam and explore their environment is removed. But, to some extent some aspects of posture and balance are actually facilitated: to hang on, infants must be able to adjust their balance and posture to keep upright with mothers' adjustment in posture as she bends and moves (reviewed in Bril 2018). Some researchers have emphasized the effects of carrying in a sling (Goldberg 1972), finding a positive correlation between sling carrying and advanced motor behavior at 6 months but not at 12 months. This finding suggests that there is not a direct relation between postural stimulation during carrying and motor performance; the same experience has a positive effect at 6 months but a negative at 12 months, possibly for different reasons. It is important to examine cultural practices thoroughly, across cultures and age, before concluding that a childrearing practice affects motor outcomes.

The limited work on effects of experience that has been done is concentrated in infancy. But changes in motor skills occur throughout the life span and are specific to a culture. Crawling or walking, teetering on bound feet or in high heels, and running barefoot or in toe pocket shoes are only a few examples of culturally specific expectations and activities that shape movement in adults, well beyond the anticipated endpoint of motor development.

The prevailing focus on age comparisons ignores other outcome measures that can expand our knowledge about motor development (Adolph et al. 2010). In addition to onset ages, experience can alter the rate of developmental change, so we can know how quickly skills

change over time and when asymptote is reached. The very form of movements and which skills are acquired in the first place can also be shaped by experience.

Cross-cultural comparisons serve as a natural experiment about experiences that fit within specific cultural contexts and can lead to the same or different motor outcomes (e.g., Adolph 2018; Bornstein 1995). Thus, cross-cultural research provides an incredible opportunity to understand plasticity, resilience, and effects of experience.

Cross-References

- [Development](#)
- [Developmental Milestones](#)

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Modal Action Patterns

► Fixed Action Patterns

Model Comparison

► Phylogenetic Analysis Within Comparative Psychology

Modeling

► Scaffolding in Learning

Modeling Language Transmission

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Definition

Languages adapt as they are transmitted from one generation to the next. Modeling language

transmission in computer simulations and laboratory experiments shows how this process gives rise to the structure found in language.

Introduction

Language is a defining characteristic of our species, so understanding its evolutionary origins is central to understanding human evolution. In their seminal paper, Pinker and Bloom (1990) argued that the evolution of language is best understood as the result of conventional Darwinian processes, just like other complex biological traits. However, languages themselves also adapt and evolve over repeated episodes of learning and use, providing two evolutionary mechanisms that shape language: the biological evolution of the human capacity for language *and* the cultural evolution of language itself. This entry outlines the consequences of cultural evolution for language and gives examples of how modeling language transmission can shed light on how language evolved.

Cultural Evolution and Language

Like many other human behaviors, language is socially learned and culturally transmitted: Humans learn the language of their speech community by observing the linguistic behaviors of other members of that community. More specifically, languages are transmitted via *iterated learning*: A language is learned by observing the linguistic behavior of another individual who learned their language in the same way. That humans are able to learn language presumably reflects some cognitive capacity or combination of capacities that is unique to humans (Hauser et al. 2002). However, repeated episodes of learning and use also allow for the cultural evolution of languages: Linguistic variants that are difficult to learn, impose substantial processing burdens, or do not meet the communicative needs of language users will tend to be replaced by those that are more learnable, easier to process, or more

functional (Christiansen and Chater 2008). This is because the mistakes that language users make during learning, and the modifications they make while communicating, tend to be in favor of more learnable, more functional forms; poorly adapted variants will be replaced by superior ones. Cultural evolution thus gives rise to languages that are well adapted to being transmitted from one generation to the next.

Mathematical, computational, and experimental techniques developed over the past two decades have made it possible to systematically investigate how cultural processes shape language (see Kirby et al. 2014 for a review). This line of research has demonstrated that some of the fundamental properties of language can be explained as products of cultural evolution, thus highlighting the importance of understanding the role of culture in explaining language design and reframing the debate on the biological evolution of the language faculty (Thompson et al. 2016). This entry reviews some of this work here, focusing on experimental models of the emergence of compositional and categorical structure in language.

Cultural Transmission Gives Rise to Compositionality

Language is compositional: The meaning of a complex utterance is a function of the meaning of its parts and the order in which those parts are combined. By combining a set of linguistic units in a particular order (e.g., *the dog bit the man*), a language user is able to form a complex meaning that is systematically related to an utterance that uses a different set of words (e.g., *the cat bit the man*) or that places the words in a different order (e.g., *the man bit the dog*). This compositional structure is central to the expressive power of language; with knowledge of the linguistic units and rules of combination, language users are able to produce and understand any complex utterance—even those that have never been encountered before.

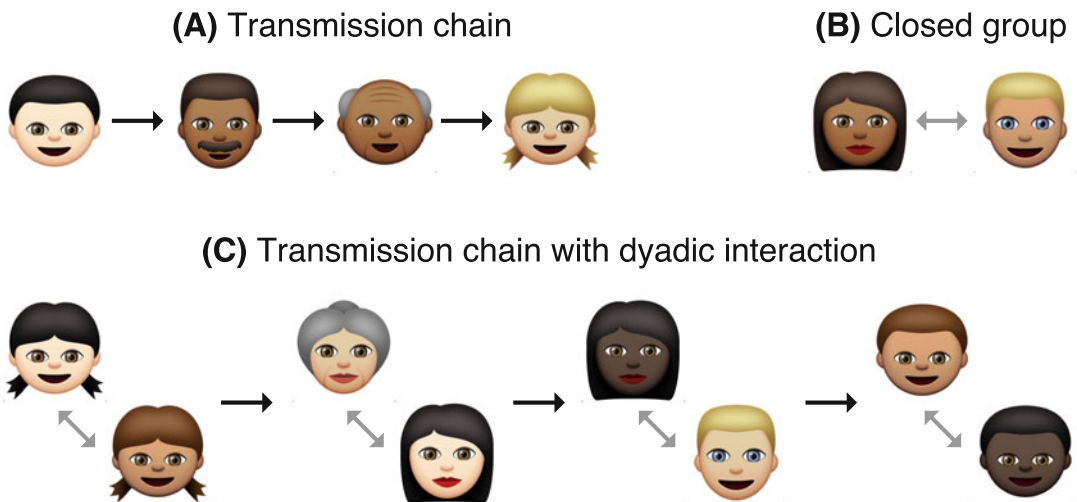
In the first work of its kind, Kirby et al. (2008) ran an experiment showing that the property of

compositionality can emerge as a result of language transmission, replicating the results of earlier computer models (e.g., Kirby 2002). Participants had to learn an “alien” language which consisted of words for colored moving shapes. After a training phase in which participants observed the objects together with their labels, participants were prompted to recall the labels for those objects. The responses of a given participant were then taught to a new participant, whose responses were in turn taught to another new participant, thus modeling what happens when languages are transmitted between individuals (Fig. 1a). Each transmission chain was initialized with an unstructured, non-compositional language in which every object was associated with a randomly generated label. After around ten generations of the iterated learning process, linguistic systems emerged that exhibited compositional structure. An example of this result is shown in Fig. 2a. The initial input language taught to the first participant in a chain contains no system-wide structure, but by the ninth generation, the language had evolved a compositional system in which the first syllable encodes color, the second syllable encodes shape, and the final syllable encodes movement.

Compositionality Depends on Transmission and Communication

Languages are not merely transmitted from person to person via learning and recall; they are used for communication, and the communicative use of language provides the input to language learning. This means that language is shaped by two pressures. On the one hand, a language needs to be expressive—it should allow its users to convey important distinctions when communicating. On the other hand, it also needs to be learnable. These pressures for expressivity and learnability are not necessarily aligned: Languages that convey many distinctions are likely to be harder to learn than languages that encode few distinctions. Indeed, the easiest language to learn would be one in which every concept was conveyed by a single, maximally ambiguous utterance, but such a language would be inexpressive. Kirby et al. (2008), described above, used an artificial proxy for expressivity: If a participant provided the same label for two objects, only one of those labels was passed on to the next learner, thus concealing evidence that languages could be inexpressive. In another experiment in the same paper, Kirby et al. (2008) found that removing this artificial

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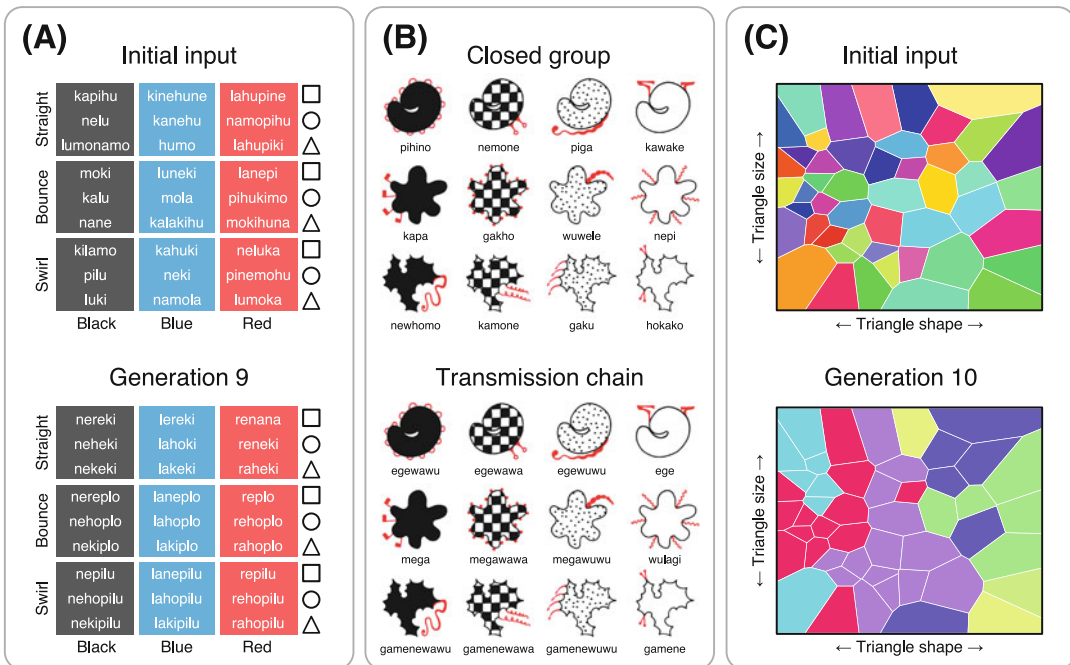
Modeling Language Transmission, Fig. 1 Three models of cultural transmission. (a) shows a simple transmission chain in which a language is passed from one individual to another. (b) shows a pair of language users

who interact back and forth using a language. (c) shows a transmission chain with dyadic interaction at each generation

pressure for expressive languages produced a radically different outcome: Rather than becoming compositional, the languages are rapidly simplified, losing words and distinctions at every episode of transmission.

In a follow-up series of computer models and experiments, Kirby et al. (2015) explored the trade-off between these competing pressures, modeling the expressivity pressure in a more naturalistic way by having participants use the language they had learned in a communication game. In one condition, two speakers had to communicate back and forth about a small set of objects (Fig. 1b). After interacting for some time, the pair of language users developed a system in which each object was described by a unique, idiosyncratic word—communicatively functional but lacking compositional structure (as shown in Fig. 2b). This condition was referred to as a *closed*

group, since unlike Kirby et al. (2008) no new, naïve participants were introduced. In comparison, in the *transmission chain* condition, two participants had to communicate about the same objects, but the language was then passed on from one pair of participants to another: The language produced during communication by one pair became the input to learning for the next pair (Fig. 1c). This combination of cultural transmission to naïve learners (imposing a pressure for learnability) plus communication (favoring expressivity) led to languages with compositional structure (as shown in Fig. 2b). Communication alone, or learning alone, is not sufficient to drive the evolution of compositional structure; instead, compositionality is language’s solution to pressures requiring it to be as simple and as learnable as possible without sacrificing expressive power.



Modeling Language Transmission, Fig. 2 Results from three iterated learning experiments. (a) shows results from experiment 2 from Kirby et al. (2008). The initial input language lacks systematic structure, but after nine generations of cultural transmission, the language evolves a compositional system. (b) shows results from Kirby et al. (2015). Under the closed-group method, a holistic

language emerges; under the chain method, a compositional language emerges. (c) shows results from Carr et al. (2016). The initial input language contains no categories (each color is a different word), but after ten generations of cultural transmission, the continuous meaning space is carved up into semantic categories

Cultural Transmission Gives Rise to Semantic Categories

As described above, languages combine linguistic units, such as words, according to a compositional system. These units pick out *categories* rather than individual items or actions. For example, in English, the space of possible drinking vessels is carved up by a small number of words (e.g., *bottle*, *cup*, *flask*, *glass*, and *mug*). This categorical structure allows language users to refer to an infinite range of possible meanings using a manageable, finite number of labeled categories; this, in combination with compositional structure, is fundamental to the communicative power of human languages.

Carr et al. (2016) show how this categorical structure develops through iterated learning. Previous experiments (including Kirby et al. 2008, 2015) had participants learn and communicate about meanings drawn from a small, finite set. Carr et al. (2016) instead introduced a continuous and open-ended meaning space. Participants had to learn words for, and subsequently label, triangles that were randomly generated by selecting three vertices on a plane, such that there were effectively infinitely many objects participants could be faced with. In addition, participants were always tested on their ability to label entirely novel triangles, none of which they had seen during training. After ten generations of iterated learning using the transmission chain paradigm (Fig. 1a), category systems emerged in which this continuous space of possible triangles was carved up into around four or five categories that related primarily to their shape and size (as shown in Fig. 2c). When this experiment was adapted to include a communication game at each generation (Fig. 1c), as in Kirby et al. (2015), this combination of pressures for expressivity and learnability resulted in emergent languages that exhibited both categorical and compositional structure, thus demonstrating that both semantic categories and compositional structure can arise simultaneously out of cultural evolutionary processes.

Conclusion

Humans are the only known species with a communication system as complex as language, which must reflect unique features of our biological endowment (and thus our unique evolutionary history). Biology can provide an explanation for the basic building blocks required for language, such as the capacity for vocal learning found in other animals or the capacity and motivation to reason about the mental states and communicative intentions of others (Fitch 2010). Nevertheless, it is clear that cultural processes play a potentially important role in explaining the structure of human language. These processes can be studied in the lab, and a growing number of experiments that model what happens to languages when they are transmitted across generations have shown that at least some of the universal properties of language can be explained as a product of cultural evolution. This suggests that biological evolution should be seen as providing the basis on which cultural evolution can operate, with the detailed structural properties of language being a product of cultural evolution. Modeling language transmission therefore has an important role to play in helping us understand how language evolved.

Cross-References

- [Communication and Social Cognition](#)
- [Darwin on the Origin of Language](#)
- [Evolution of Culture](#)
- [Language](#)
- [Language Acquisition](#)
- [Language Development](#)
- [Language Instinct, The](#)
- [Language Modularity](#)
- [Learning](#)
- [Laryngeal Descent](#)
- [Linguistic Evolution](#)
- [Meaning \(Philosophy\)](#)
- [Mother Tongue Hypothesis](#)
- [Musical Protolanguage](#)
- [Pinker's \(1994\) the Language Instinct](#)
- [Social Learning and Social Cognition](#)

- [Symbolic Culture](#)
- [Vocal Communication](#)
- [Universal Grammar](#)

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Modern Human Origins

- [Symbolic Culture](#)

Modern Moral Relativism

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Synonyms

[Moral constructivism](#); [Moral conventionalism](#); [Moral subjectivism](#)

Definition

According to the main version of moral relativism, there are no objective moral facts or properties, and instead moral facts and properties depend for their existence on certain attitudes held by individuals or groups forming moral judgments.

Introduction

This entry first provides some background about how to define moral relativism. It then reviews two different strands of the contemporary discussion of moral relativism. The first concerns the question of whether most people endorse, either implicitly or explicitly, some form of moral relativism. The second concerns the question of whether moral relativism is actually true. Here the focus will be on the influential work of Shaun Nichols, who has proposed an account of the psychology of moral judgments which he takes to provide support for moral relativism. Some problems will briefly be raised with Nichols's main argument (The material which follows is reprinted with permission from Miller 2011).

Defining Moral Relativism

Following the custom in the philosophical literature, it is common to distinguish between three

different versions of moral relativism, each of which will only be given a rough characterization here (for more detailed characterizations, see Wong 1991; Gowans 2008; Miller 2002). The first is:

Descriptive moral relativism: Some human beings have fundamentally different moral standards and values.

This is intended to be an anthropological claim about the existence and extent of the diversity of opinions about central moral issues and can be formulated in stronger and weaker varieties. Just about everyone agrees that at least a weak version of this view is correct and the debate has to do with the extent of these differences.

The second version of moral relativism can be stated as follows:

Normative moral relativism: When the moral differences of individuals or groups cannot be rationally resolved, they should not judge the moral behavior of each other nor act toward each other in such a way as to attempt to bring one side into conformity with the standards of the other.

This view is making a moral claim that people should, in effect, exhibit some degree of tolerance in such cases. And stronger and weaker varieties are on offer here as well.

Finally there is the version of moral relativism which is typically of interest to philosophers and will be the focus in what follows (for further elaboration, see Prinz 2007, Chap. 5, and Gowans 2008):

Metaethical moral relativism: There are no objective moral facts or properties, and instead moral facts and properties depend for their existence on certain attitudes held by individuals or groups forming moral judgments.

Talk of “objectivity” is notoriously hard to make precise in metaethics, but the most common approach is to formulate the notion in terms of the existence and nature of moral facts being mind independent in such a way

that they do not vary with changes in attitudes toward them (for a detailed characterization of objectivity, see Miller 2007, 2009). Someone who thought that moral facts are objective in this way would hold that, for instance, slavery is wrong regardless of whether people thought it was acceptable or not.

The “attitudes” clause gets spelled out differently by different moral relativists. These attitudes could include, for instance, people’s beliefs, emotions, values, reflective desires, or so on. A simple example of a relativist view would be one according to which something is a moral fact for a person if and only if that person believes it to be a moral fact. Hence on this view, slavery is not wrong *simpliciter* – it is wrong for Jones but right for Smith because Jones believes it is wrong while Smith believes it is right.

In what follows, discussion of “moral relativism” will refer to this metaethical version. And the focus will be on two main topics:

- (i) The psychology of folk moral judgments and whether such judgments show signs of an implicit or explicit commitment to moral relativism.
- (ii) A recent account of the psychology of moral judgments by Shaun Nichols and whether it provides support for moral relativism.

Psychological Studies of Folk Moral Judgments

Leaving aside the question of the plausibility of moral relativism for a moment, to the extent that there is one commonsense or folk view about the objectivity of morality, what might it be? Philosophers have been tempted to weigh in on this question for a number of years. For instance, Michael Smith writes that:

we seem to think moral questions have correct answers; that the correct answers are made correct by objective moral facts; that moral facts are wholly determined by circumstances; and that, by engaging in moral conversation and argument, we can discover what these objective moral facts determined by the circumstances are. (1994, p. 6)

Similarly, Russ Shafer-Landau writes that “the semantic norms that constrain truth in ethics do not (even implicitly) relativize such truth to the attitudes of the speaker or the mores of her community. We judge our moral views to be true, *simpliciter*” (2003, p. 31, emphasis his. See also Mackie 1977; Brink 1989, and Darwall 1998).

At the same time, philosophy professors are usually all too familiar with the extent to which many of their undergraduates seem to reject objective approaches to morality in favor of some kind of relativistic view (Stich and Weinberg 2001). So in order to better determine what the common-sense outlook really is, it would be nice to have some careful psychological experiments. Unfortunately, very little has been done in this area so far, although the future looks promising. Here three areas of existing research are briefly summarized.

First, quite a bit of attention has been paid to whether young children are (implicit) moral objectivists. The main approach to assessing this at the present time is to measure whether children distinguish violations of moral norms from violations of merely conventional norms on a number of different dimensions. And the results thus far have been robust. For instance, children overwhelmingly treat moral norms as more serious than conventional norms, as generalizable to other countries, as independent of an authority figure such as a teacher, and as supported with different justifications from conventional norms such as welfare considerations (for reviews see Smetana 1993 and Tisak 1995).

Shaun Nichols (2004a) accepts this work on childhood attitudes toward morality, and in a series of experiments, he examined both whether such default objectivism is still present in undergraduates and, if not, whether relativistic attitudes among students serve to undermine certain other important features of moral judgments. In his first experiment, he surveyed students about four scenarios involving conflicting opinions, two of which were a moral scenario and a flat earth scenario. For each scenario, participants were asked whether they thought one of the sides in the dispute was right and the other wrong or whether there is no fact of the matter in this case.

Six of the 46 participants gave a nonobjectivist response in the flat earth case, while of the remaining 40 subjects, 17 out of 40 gave a non-objectivist response in the moral case (10). These results suggest that by the time they reach college, a significant number of students are such that their default objectivism is defeasible, while at the same time their attitude toward morality does not depend upon a full-blown relativist view about all of reality. Similar results showed up in the remaining four studies reported by Nichols (2004a).

The second part of Nichols’ project was to examine whether those undergraduates making seemingly relativistic claims about moral disputes are still committed to other core elements of moral judgments and in particular whether they continue to distinguish between violations of moral and conventional norms. In the remaining four experiments, Nichols repeatedly found that other core features of moral judgments do still remain. In particular, nonobjectivists drew the distinction between moral versus conventional norms on the dimensions of seriousness, permissibility, justification, and dependence on authority. For instance, here is the set of questions designed to measure each of these dimensions for one of Nichols’ moral scenarios (15):

1. Was it OK for Frank to hit Ben?
2. On a scale of one to ten (with ten the highest), how bad was it for Frank to hit Ben?
3. Why was it bad for Frank to hit Ben?
4. Now what if the teacher had said before the lesson, before Frank hit Ben, that “At this school, anybody can hit someone if they want to.” Would it [be] OK for Frank to hit Ben if the teacher says he can?

Nichols’ conclusion is that, apart from their stance toward whether there is a fact of the matter in the moral cases he devised, “there is little to distinguish objectivists from nonobjectivists in any of these experiments” (23).

The most sophisticated published study of folk metaethical attitudes to date is Goodwin and Darley (2008). In their first experiment, 50 undergraduates at Princeton University participated in a

two-part study. First the experimenters had participants rate their level of agreement or disagreement with 26 statements (on a scale from 1 to 6), as well as how they would answer the following with respect to each statement (1343–4):

How would you regard the previous statement?
Circle the number.

1. True statement
2. False statement
3. An opinion or attitude

The statements were chosen so that they fell into four main categories: ethical, conventional, aesthetic/taste, and scientific.

Next, while the participant was performing an unrelated task, the experimenter chose five statements (two ethical statements and one statement from each of the other three categories) about which the participant had indicated either relatively strong agreement or disagreement. The participant was then instructed as to how to proceed next, the key part being that “None of the statements have produced 100 % agreement or disagreement. In what follows, you will be asked to indicate how you interpret disagreement with your own attitudes” (1344). For each of the five statements, the participant had to select one of the following (1344):

1. The other person is surely mistaken.
2. It is possible that neither you nor the other person is mistaken.
3. It could be that you are mistaken and the other person is correct.
4. Other.

At the end of this questionnaire, participants were asked two more questions which focused on the justification or grounds they had for their moral beliefs.

The results from Goodwin and Darley’s first experiment were striking. While subjects generally agreed to statements about the badness of robbing a bank, the goodness of anonymous donations, and to a lesser extent the permissibility of assisted death and stem cell research, their

willingness to assign truth to those statements varied dramatically: 61 %, 36 %, 8 %, and 2 %, respectively (1346). This led Goodwin and Darley to conclude that “meta-ethical judgments about the truth of ethical claims appear to be highly sensitive to the content of the claims in question, and not merely to whether the claims are generally agreeable” (1346). In addition, using the differences between the kinds of statements, Goodwin and Darley found that scientific statements were treated more objectively than moral statements, which in turn were treated as more objective than conventional statements, followed last by statements of beauty and taste (1348).

Furthermore, the two-part nature of the study allowed the experimenters to construct three categories for the beliefs in question (1345):

Fully objective: Participant regards the belief as true (or false) and regards someone who disagrees with that belief as surely mistaken.

Intermediately objective: Either (i) the participant regards the belief as true (or false) and thinks there is no need for either party to be mistaken or (ii) the participant regards the belief as an opinion and regards someone who disagrees with that belief as surely mistaken.

Least objective: Participant regards the belief as an opinion and thinks there is no need for either party to be mistaken.

For the ethical statements, 50 out of 100 responses were fully objective, 28 out of 100 were intermediately objective, and only 11 were least objective (the remaining 11 were not categorized because the participants chose “Other”) (1348). Finally, Goodwin and Darley examined the responses given to a list of four potential grounds for subjects to check as the justification for their moral beliefs. The more grounds subjects had, the more likely they were to treat moral claims objectively. And three of the four grounds ended up being predictors of moral objectivist attitudes (1349–1350).

In their second experiment, Goodwin and Darley substituted the responses of true, false, or an opinion with the question, “According to you, can there be a correct answer as to whether this

statement is true?" (1351). The results showed a similar pattern as in the first experiment, although in this case moral statements were treated just as objectively as scientific ones, and 70 % of the responses were fully objective (1352–1353).

Finally, in their third experiment, Goodwin and Darley used three short moral scenarios and otherwise employed a similar methodology to the previous experiment. However, this time at the end of the session participants had to rate the extent to which each of the four proffered justifications supported their moral belief, as well as the degree of their belief in the existence of a supreme being and their general political attitudes (1356). They found that grounding moral beliefs in a divine being predicted greater moral objectivism, and more so than political attitudes or merely having religious beliefs by themselves without them playing a role in justifying morality (1357).

Taken together, all of the studies mentioned in this section barely scratch the surface of the empirical work that is needed in this area. There need to be studies which use different adult subjects besides undergraduates and which take place outside of the USA. There need to be studies which are more sensitive to the range of metaethical options available in the literature, such as response-dependent views, expressivist views, error-theoretic views, and so forth. There need to be studies which are more careful in their accounts of what makes a moral statement, belief, position "objective," and so forth. So it is only with great hesitancy that some initial conclusions can be drawn:

- (i) Young children seem to be implicit objectivists about moral claims, and so objectivism is the default position for human beings initially.
- (ii) Our default objectivism is defeasible – many human beings exhibit a nonobjectivist attitude toward at least certain moral claims by the time they reach college.
- (iii) People tend to be neither completely objectivist nor completely nonobjectivist in their thinking; rather the degree to which they are objectivists varies in part as a function of the content of the moral statement in question.

- (iv) Those who offer some grounds for their particular moral beliefs are predicted to be more objectivist in their thinking than those who do not, especially if they ground morality in a divine being.

Clearly much further work is needed in this area.

Nichols on Moral Psychology and Moral Relativism

A separate focus of research in recent years has concerned whether metaethical moral relativism is plausible, regardless of whether people in fact accept it or not. In his 2004 book *Sentimental Rules*, Shaun Nichols has offered an influential argument that the best account of moral judgments points in the direction of moral relativism. He is not out to provide a conceptual account of moral judgments, but rather an empirically informed account of what people are doing when they make what he calls "core moral judgments." Such judgments are concerned with the moral permissibility of actions and in particular whether such actions have violated harm-based norms. Judging the wrongness of an action of hitting an innocent person purely for amusement would be a paradigm example of such a core moral judgment (2004b, p. 5).

There are two central components to Nichols' account of core moral judgments (in what follows "core" will be dropped for the sake of simplicity). The first is a person's normative theory, which is his or her body of information about what actions are wrong. And the second is an affective mechanism that is responsive to harms, where these are understood mainly as pain and suffering. The first component is used to explain why some events can be distressful and involve pain and suffering but are not considered wrong, such as natural disasters and accidents (15). The need for a second component is motivated by Nichols in various ways using cases involving psychopaths, autistic children, and disgust. For instance, psychopaths often understand both harm and conventional norms but have neither backed by an affective system, whereas normal subjects have an affective

system linked to their harm norms. Together, then, for Nichols, these two components of a normative theory and affective system give us an account of actual moral judgments as involving “sentimental rules” or “rules prohibiting actions that are independently likely to elicit strong negative effect. The set of rules or normative theory prohibits actions of a certain type, and actions of that type generate strong affective response” (18).

Nichols is clear that he takes this account to provide evidential support for a relativist position. Indeed, the conclusion of his central argument is that “[n]o action is wrong simpliciter. At best, an action is only wrong relative to a population – the population of individuals that share a certain emotional repertoire” (185). Here is the argument itself (185, emphasis his):

1. Rational creatures who lack certain emotions would not make the moral judgments that we do.
2. There is no principled basis for maintaining that these certain emotions (on which our moral judgments depend) are the *right* emotions. That is, there is no externally privileged basis for maintaining that all rational creatures *should* have the emotions.
3. [Therefore, morality is not objective.]

The opponent here is the philosopher who claims that the moral status of an action is determined “as it is in itself” and so holds that moral judgments are true in a nonrelativistic manner (184). Nichols takes his argument to show that the “common-sense commitment to objectivity is unwarranted. Given the emotional basis of moral judgment, we are not justified in our belief that morality is objective” (185).

Nichols’ main support for the first premise is that “Martians who lacked analogues of human sentiment and affection would not make the moral judgments that we do” (185). Indeed, the Martians might be aware of all the same relevant facts, but judge that torturing puppies is not morally wrong (185). Given the sentimental rules account, affect systems play a crucial role in shaping both the initial moral judgments that people make and the ones that as a culture people preserve over time.

Without those affect systems, the resulting judgments would look very different.

The second premise is really the core of Nichols’ argument. Nichols explains it more fully as follows: “there is no principled basis for maintaining that all rational creatures should have emotional responses like reactive distress and concern. There is no independent reason to think that this emotional repertoire is the right one to have” (187). Instead the burden of proof is supposed to be on the objectivist to “show that all rational creatures *should* have such emotional responses. . . . The difficulty is that it is not at all clear how to argue for such a claim” (188, emphasis his). Note, then, that Nichols does not seem to provide any actual support for premise (2), other than just taking it to be the default position and putting the burden of proof on the objectivist to justify certain emotions over others.

At this point, an objectivist about moral facts could raise at least two concerns about premise (2) and more generally about Nichols’ argument. The first is that premise (2) seems to preach to the choir. A philosopher who is already committed to some version of moral objectivism presumably has good (albeit perhaps mistaken) reasons for countenancing the existence of objective moral facts, including facts concerning the appropriateness of forming certain emotional responses rather than others. So Nichols has offered nothing by way of an argument for why the *objectivist* should accept this premise and rather just seems to be asserting that it is true.

The second concern is that it is not clear more generally why a principled basis for justifying certain emotions over others cannot be found using the agent’s own normative theory. Recall that on the sentimental rules account, the capacity for core moral judgments is constituted by an agent’s normative theory and affective system. And presumably people’s normative theories could provide them with a wealth of important reasons for why, say, emotions sensitive to distress in others are worth having whereas emotions promoting distress in other are not. One such reason, for instance, could be that relieving distress in others is important (for various reasons of its own), and beings with an emotional sensitivity

to distress in others are more reliable at detecting that distress and so are better equipped to try and relieve it. And Nichols would not be entitled to respond at this point by claiming that such reasons provided by people's normative theories are themselves arbitrary and have "no principled basis," since that would assume there are no objective reasons to begin with and so beg the very question at issue against the moral objectivist.

Nichols might reply that the above response underestimates the impact that affective systems have on normative theories. That is, he might hold that affective systems strongly influence the contents of the normative theories people hold in the first place, especially at the cultural level where they significantly impact what moral claims survive over time. Indeed, Nichols devotes an entire chapter of his book to a cultural evolutionary account of harm norms where affective systems play a central role (Nichols 2004b, Chap. 7).

Here the objectivist might make use of one of two strategies to respond. One might be to argue that the best explanation for cultural changes in harm norms over time, and by implication the best explanation for the harm norms the majority of people have today as part of their normative theories, does not involve appealing primarily to their affective systems, but rather to human beings having made progress in getting closer to the objective truth about morality. To his credit, Nichols anticipates this response and argues against it at length (159–164). At this point, the reader should judge who gets the better of that exchange.

The other strategy worth briefly mentioning is to concede that human affective systems have played a significant role in shaping their normative theories, but to note that they are only one of several factors which causally *influence* those theories, rather than being the only factor which causally *determines* them. For Nichols has not offered arguments which come anywhere close to showing that the content of people's normative theories is determined *solely* by their affective systems. Furthermore, the distinction between causal and justificatory influence is worth taking seriously, since the affective system only contributes the former in shaping an agent's normative theory, while other forces might provide both

kinds of influence. For instance, through a process of practical reasoning, an agent might come to a new moral conclusion about, for instance, the need to send money to Africa or the inconsistency between her moral views on two issues. Such processes are familiar and yet often contribute increased justificatory status to their conclusions. Or as another example, the influencing factor could be the social transmission of accumulated wisdom about moral topics through forms of testimony such as parental upbringing and education, some of which corresponds to the objective moral facts. And indeed there might be cases of such social transmission leading to a change in normative theory even in the face of resistance from the individual's affect system. To use one of Nichols' own examples, "[k]nowing that inoculations are for the best does not eliminate the discomfort one feels witnessing a child get inoculated" (155, see also Vranas 2006, 789).

Conclusion

Stepping back, the upshot of this discussion of Nichols' argument is that the sentimental rules account of people's capacity for core moral judgments might not lead to the direction of moral relativism after all, and indeed seems to be compatible in a number of respects with an objectivist metaphysic about moral facts and properties. Thus, Nichols might not be offering a clear path from moral psychology to moral relativism after all.

Cross-References

- [Cultural and Moral Relativism](#)
- [Evolved Moral Foundations](#)
- [Philosophical Foundations for a Modern Morality](#)

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Modern Technology (E.G., IVF)

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Definition

In Vitro Fertilization (IVF) together with Intra Cytoplasmic Sperm Injection (ICSI) are the two major technologies applied in modern Assisted Reproduction Technology (ART).

Introduction

In 1978, the world's first “test-tube baby” was born in England (Steptoe and Edwards 1978). Her name was Louise Brown, and she was the first human born after fertilization of an oocyte by a sperm in a laboratory instead of inside the female body. Such in vitro fertilization (IVF) was at first developed primarily for treating infertility in female patients with obliterated fallopian tubes or other pathologies. Following this initial breakthrough, IVF was accompanied by other technological advances that together constitute modern assisted reproductive technologies (ART). One of these technologies is intra cytoplasmic sperm injection (ICSI). ICSI is primarily used in couples where infertility arises due to a low sperm cell count in the ejaculate. The ICSI operator holds the oocyte in a micropipette and injects it with one of the few sperm cells present under the microscope, thereby fertilizing the oocyte (Palermo et al. 1992). Some of the other technologies constituting modern assisted reproduction are the use of donor oocytes and donor sperm; the cryopreservation of sperm, oocyte, and embryos; the surgical extraction of sperm from the testicle or epididymis, in addition to uterus transplantation and the comprehensive genetic testing; and morphological screening of cells and tissues in both donors and recipients (Niederberger et al. 2018). By putting these technologies to work, assisted reproduction technology has become a common part of most modern health care systems. In several countries ART now accounts for 4–5% of babies born annually (European IVF Monitoring Consortium 2017). In 2017, it was estimated that more than six million children had been born worldwide after ART thus far.

Assisted Reproductive Technologies in Infertile Patients

Assisted reproduction's main use to date has been the treatment of infertile heterosexual couples. The diagnosis of infertility in these couples is based on WHO criteria, which states that infertility is “a disease of the reproductive system defined by the failure to achieve a clinical pregnancy after

12 months or more of regular unprotected sexual intercourse” (Zegers-Hochschild et al. 2017). Treating such couples with IVF has several possible evolutionary effects as selection pressures differ between natural and assisted reproduction (Hanevik et al. 2016). These differences in selection pressures occur at different stages in the reproductive process.

The oocyte: In natural reproduction, the ovaries in general release one oocyte each menstrual cycle. Before ovulation, this oocyte has been through a long phase of growth and development (Hsueh et al. 2015) where at least the final phases of maturation are under tight control by female reproductive hormones. In IVF, this final phase of maturation is manipulated by pharmacological means so that the number of oocytes that are available for ovulation in the ovary is higher, typically around ten. Instead of being released into the female abdomen, the mature oocytes are collected by ultrasound guided aspiration and delivered to the IVF laboratory for fertilization. This means that many of the oocytes that become fertilized in IVF would not have been so in natural reproduction. The selection pressure for timing of oocyte maturation to the naturally occurring variations in female reproductive hormones is thus less in assisted reproduction.

The sperm: After being ejaculated into the vagina in natural reproduction, the sperm has to swim through the cervix of the uterus, pass the uterine cavity and then find its way into one of the two fallopian tubes containing an oocyte that is available for fertilization. Large interspecies variation in sperm morphology is one indication that navigating the internal female genital organs, finding, and finally fertilizing an oocyte is a process with a wide scope for the effect of selection pressures. In IVF, the selection pressures are different in that the ejaculated sperm goes through one or more steps of rinsing and preparation before the sperm is either released in close proximity to the oocyte (IVF) or injected into it (ICSI). Compared to the natural situation, there is very little propulsion and navigation involved for the sperm, and in ICSI the mechanism for fertilization is also very different. Hence, the selection pressures that influence which sperm will have its

DNA represented in the next generation are systematically changed in assisted reproduction.

The embryo: The fertilized oocyte develops into an embryo that in natural reproduction travels down the fallopian tube and implants in the uterine cavity about 7 days after fertilization (Franasiak et al. 2016). In the IVF laboratory, the embryo develops in an incubator under controlled temperatures and gas concentrations, submerged in a commercially available embryo cultivation media. From the ten collected oocytes, typically one embryo will be transferred to the uterus after 1–5 days of cultivation in the lab, and surplus normally developed embryos will be cryopreserved for transfer in a later cycle. The decisions concerning which embryo to transfer and cryopreserve are taken by embryologist, who typically use criteria such as pace of development, embryo morphology and certain developmental landmarks to aid their decisions. The selection pressures for complying with algorithmically determined developmental milestones are not present in the natural situation. Compared to the natural situation, the embryo in assisted reproduction is also exposed to more mechanical stress, strong light, and exogenous chemicals, altering selection pressures.

The couple: Although controversial, a complete analysis of differences in selection pressures between natural and assisted reproduction must include a mention of the barriers that exist for couples to enter an IVF program in the first place. At least in some countries the law prevents people with serious psychiatric illness for instance to undergo assisted reproduction. Also IVF is an expensive treatment, so in many countries infertile couples with low income do not have equal chance of becoming pregnant as those infertile couples who can afford IVF. This is a systematic difference compared to the natural situation, where the chance of pregnancy does not depend on your psychiatric history or your income.

Assisted Reproduction in Fertile Patients

The use of assisted reproductive technologies is ever more common also in patients who are not

infertile by the WHO definition. This includes same sex couples, some cases of oocyte cryopreservation (so-called social freezing), and some cases of preimplantation genetic testing. Assisted reproduction in lesbian couples includes the use of donor sperm either for intrauterine insemination or for conventional IVF. Social freezing occurs when a female wishes to cryopreserve her oocytes at a young age, say when she finishes university, so that she can build a career and find a suitable husband without having to worry as much about her declining fertility if this takes longer than she expects. Assisted reproduction is also very much a part of preimplantation genetic testing, where a couple who either have or carry certain heritable diseases can make sure the “sick” gene for this disease is not transferred to their offspring. In most such cases IVF is preformed, and the resulting embryos are genetically tested to make sure only embryos without the “sick” gene in question are transferred to the uterus. These, and other, applications of assisted reproduction technologies in fertile patients may also have evolutionary implications. The case of genetically testing the embryo for instance is, in principle, applying a very specific selection pressure. However, as the evolutionary implications will vary widely depending on the specifics of the technique, analyzing their systematic difference to natural reproduction is unfruitful.

Cross-References

- Embryo
- Genetic Conflict

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Modern Theories of Language

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Synonyms

Embodied language processing; Emergentist approaches to language; Sociocultural theories of language; Usage-based linguistics

Definition

Modern theories of language represent efforts to account for the evolution, acquisition, and processing of language within an integrated framework. Such efforts acknowledge the relationship of language to sensorimotor experience, social interaction, and general cognitive constraints on information processing.

Introduction

The study of language is a diverse field that engages the applied interests of educators and speech pathologists as well as the academic interests of researchers working in wide range of disciplines including linguistics, speech and hearing sciences, psychology, biology, computer science, philosophy, sociology, and anthropology. Scholars in these different disciplines invariably conceptualize language in different ways, viewing it, e.g., as a biological attribute, a cultural trait, a set of communication skills, or a normative system of signs. This entry reviews modern theories of language that adopt the view of human language as a complex form of human behavior.

The review is organized in accordance with three perspectives considered to be complementary, as opposed to mutually exclusive: an evolutionary perspective that focuses on the origins of what are seemingly unique features of human languages; a developmental perspective that highlights the social-interactive contexts in which children acquire language as well as relationships between perception, cognition, and action in development; and a cognitive perspective that examines the processing mechanisms that determine how language use unfolds in real time.

Theories of Language Evolution and Change

Human languages seem to display many discontinuities when contrasted with the communication systems of other species. These include duality of patterning, symbolic signs, vast vocabularies, syntactic rules, and propositional structure, all of which allow for unlimited productivity in the creation of communicative signals whose meaning transcends the here and now. Modern theories of language evolution attempt to understand precursors to these discontinuous traits and what scenarios may have given rise to their emergence.

The study of the evolution of language presents extraordinary methodological challenges. The comparative method involves the study of homologous traits to uncover potential common

ancestry as well as the study of analogous traits that have emerged across different lineages to understand common selection pressures. This method has revealed strikingly few parallels between the vocal communicative repertoires of humans and their nearest relatives, the great apes, although there may be greater similarities in non-verbal forms of communication such as gesture. At the same time, the comparative method has revealed some striking similarities between humans and songbirds with respect to the imitative behaviors of juveniles and the role of social feedback in shaping immature vocalizations.

The comparative method is fraught with difficulties when trying to establish which exact traits constitute analogues or homologues in species that do not possess the faculty of language. Paleo-anthropological methods are of limited use since the fossil record does not contain clear traces of anatomical prerequisites (i.e., vocal tract structure) or of neural adaptations associated with language. Similarly, archeological methods rely on inferences about the link between the notoriously incomplete record of artifacts and the cognitive abilities involved in their production and use. Finally, the recent applications of molecular biology that try to trace the emergence of language depend on the growing, but currently still limited knowledge about the genetic underpinnings of this unique human ability. Thus, in the absence of “hard” evidence, the extant theories of language evolution and change apply conjecture or reverse engineering, or use computational modeling and experimental studies of specific selection pressures that operate during biological evolution and cultural transmission to provide proof of concept for basic principles that may underlie the emergence of language.

Evolutionary theories of language often differ with respect to what is regarded as the phenomenon to be explained. Drawing on de Saussure’s distinction between language as a system of signs (“*langue*”) and language as the product of the application of knowledge about this system (“*langage*” or “*parole*”), linguistic theory has upheld the conceptual distinction between competence and performance. The concept of language performance describes the behaviors

associated with language use such as the comprehension, production, and learning of linguistic signals. These behaviors and their anatomical, neural, and cognitive underpinnings, including domain-general cognitive mechanisms such as sensorimotor processing, working memory, planning, cognitive control, conceptual representations, and intentionality, have recently been termed the “Faculty of Language in the Broad Sense” (Hauser et al. 2002), and are the subject of study of the discipline of psycholinguistics with its vast arsenal of experimental and neurophysiological paradigms.

Theories of the evolution of the underpinnings of human language have been concerned with abilities like control over vocalization and gesture, vocal and gestural learning (including imitation), sharing of conceptual representations, and intention reading, which is required for the recognition of conspecifics’ behaviors as communicative signals. While there is debate as to whether language is homologous with animal vocal signaling systems like bird song or whether precursors of language may have initially arisen in the gestural modality, there is consensus that many of these abilities constitute adaptations to a variety of selection pressures that may not be related to language, but were likely to be related to social organization, mate choice, and tool use, and are the product of a gradual and continuous process of evolution by natural selection.

In contrast, language competence has been viewed as a cognitive capacity encompassing knowledge of a finite set of rules that can be used to generate an infinite number of utterances. It is this set of rules – called a Generative Grammar – which is seen as being at the heart of the human faculty for language. According to the theory of Universal Grammar, for a child to acquire the Generative Grammar of a specific language they must have innate knowledge of universal constraints that limit the types of structures that occur in human languages. Studying the psychological reality of Universal Grammar (i.e., the innate substrate for acquiring a Generative Grammar) is complicated by the fact that formal descriptions of what constitutes knowledge of grammar have changed since the 1960s: The

Standard Theory encompassed the notions of a deep structure describing the underlying logical relationships between the parts of a sentence, and a surface structure describing the specific manifestations of how those parts are assembled based on a set of transformation rules, the specification of which underwent major revisions in subsequent editions of the theory throughout the 1970s. In the 1980s, the Principles-and-Parameters Framework (aka Government and Binding Theory) viewed Universal Grammar as an innate set of principles comprising phrase-structure rules that specify hierarchical relationships (Government) and relationships of coreference (Binding) between words, and a set of parameters, i.e., values that define variability in language-specific manifestations of these principles, the specific values of which are set upon receiving input during the process of acquisition. Finally, in the 1990s, the Minimalist Program narrowed the human faculty for language down to a basic combinatorial operation, Merge, which hierarchically combines pairs of elements, consisting of a head and its complement, into a superordinate unit that inherits the properties of the head (e.g., in the phrase *big dog*, the adjective *big* serves as the dependent of *dog*, and thus modifies its meaning). Crucially, the product of Merge can subsequently combine with another element (either as dependent or head) to create a new unit (e.g., *the big dog*), thereby implementing the fundamental property of recursion considered at the core of the human “Faculty for Language in the Narrow Sense” (Hauser et al. 2002). As theories of the evolution of language predate the proposal of the concept of the “Faculty for Language in the Narrow Sense” this entry retains the term “Universal Grammar” when talking about the evolution of language competence.

Language as Product of Biological Adaptation

Theories that explain the evolution of Universal Grammar in analogy with the evolution of biological traits can be distinguished with respect to whether evolution is assumed to have taken place continuously or in discontinuous jumps. Adaptationist theories propose that Universal Grammar evolved gradually following principles

of Darwinian selection because it confers reproductive benefits by supporting language acquisition. In analogy to the evolution of the visual system, the central argument is that of complexity of design: In order for a cognitive entity as complex as Universal Grammar to evolve it must have been fine-tuned to fit its purpose through a lengthy process of continuous adaptation. As a result, humans are equipped with a set of innate, *a priori* constraints that enable them to solve the logical problem of language acquisition by allowing children to derive correct structural generalizations from limited input. Nonadaptationist theories argue that Universal Grammar has emerged fairly recently (~90–50 K ago) as the result of a chance mutation. This view draws on two lines of evidence: (a) archeological evidence for a dramatic rise in technological advancement attributable to artifacts that can be dated from 50 K years onward, and (b) evidence for a mutation in the *FOXP2* gene that occurred within the last 100 K years. However, given the exceedingly small likelihood of a complex set of constraints such as Universal Grammar arising through a chance mutation, proponents of the nonadaptationist view have suggested that the mutation affected only a minimal, core element of grammar – recursion (Hauser et al. 2002). Whether the ability to apply Merge recursively provides a sufficient advantage for the language-learning child to derive generalizations about grammatical structure continues to be debated, with some theorists providing evidence that Merge itself could be learned from the input, rather than existing as innate knowledge (Ninio 2014).

Language as Product of Cultural Transmission

Critics of the idea that Universal Grammar is a biological adaptation argue that this view is fraught with a number of fallacies: Given human dispersion and linguistic variability, it is unclear how an arbitrary set of universal rules could have evolved as an adaptation to different specific linguistic environments. Secondly, it is unclear why only innate representations of highly abstract grammatical properties should have evolved, rather than predispositions to learn other specific aspects of an ambient language such as its sound

structure or vocabulary. Finally, it is unlikely that modifications in the genotype could have caught up with the rapidly “moving target” of language which is liable to change over the course of even just a few generations.

Instead, recent theorizing about language evolution views language as a cultural trait that has evolved through cultural transmission via social interaction. Thus, it is not the human brain that has adapted to language but languages have adapted to be learnable and usable by humans (Christiansen and Chater 2016). Language is seen as a product of cumulative cultural, rather than biological, evolution, shaped by requirements to be transmissible across generations and expressive in communication. As a result, language is suited to the capacities of the human perceptual-motor system; the architecture of the cognitive mechanisms that underlie learning, memory, and information processing; the nature of mental representations and thought; and the pragmatic constraints that govern human communication.

Evidence for this view comes from agent-based computational simulations and laboratory experiments that manipulate various aspects of cultural transmission of language-like systems to determine how linguistic structure emerges at various levels. These lines of research suggest that combinatorial structure emerges in response to the need to transmit signals through noisy channels while compositional structure, *i.e.*, the consistent linking of form-based features to dimensions of meaning, emerges from the combined pressure of transmitting signals through limited capacity memory systems coupled with the need for users to be communicatively efficient.

Coevolution of Genes and Language

Gene-culture coevolution theories explore the feedback between genetic and cultural inheritance mechanisms. These theories draw on ideas from domains in which the interplay between genetic and cultural evolution in certain populations had been demonstrated, such as evolution of lactose tolerance as an adaptation to cattle farming, or of light pigmentation as an adaptation to colder climates. The central idea is that culture creates new

environments, which then exert specific selection pressures by influencing mechanisms that enable learning of ambient cultural traits. This view reconciles the traditional juxtaposition of innateness and learning. With respect to language, it implies that although the genotype determines the available learning mechanisms, their selection is governed by the structure of language that arises from the interaction of many individuals over time. This selection, in turn, leads to a weakening of the role of innate biases that shape leaning (Kirby et al. 2007). Indeed, recent modeling work has demonstrated that strong universality in behavior can emerge from weak biases through the process of cultural transmission. Thus, although the process of cultural evolution causes languages to adapt to the human cognitive system, the resultant structural properties of language select for cognitive abilities that are ever better suited to learning and processing of language. Following similar principles, the human larynx and the associated neural and cognitive control of sound vocal abilities may also have evolved in response to the pressure to produce more distinct sounds and words (Lieberman 2012). However, gene-culture coevolution theories that postulate genetic adaptations to language at the level of individual populations need to reconcile this view with the current lack of evidence for individual predispositions for acquiring specific languages, as would be evident if children adopted into different cultural and ethnic backgrounds exhibited specific difficulties in acquiring features of the languages of their adopted families.

How Is Language Learned?

Acknowledging the shift away from the nativist stance that regards language acquisition as a maturational process built on an innate blueprint for a formal generative grammar, modern theories of language development view first and second language learning as a process of skill acquisition (Christiansen and Chater 2016; Ninio 2006), wherein learners develop fluency in processing language in real time, i.e. converting input

consisting of sequences of sounds (or signs) into mental representations of speakers' communicative intentions and generating sequences of sounds or signs to express their own communicative intentions. Under this view, the fundamental context for language acquisition involves joint activities where speakers and listeners share common ground and can make reasonable inferences about their partner's communicative goals (Clark 1996; Tomasello 1999). The relationship between language learning and the social environment is reciprocal: the developing ability to use language facilitates social interaction, and social interaction constrains and guides the process of language learning.

Social Shaping

In the context of social interaction, language learning involves sustained engagement with parents, siblings, and other caregivers. Many theories include social learning as an integral component of language acquisition and consider how feedback from caregivers supports its development. From early infancy, caregivers and infants coordinate the timing of their communicative bids when engaged in face-to-face (dyadic) social interaction, using eye gaze as well as vocalization to modulate the amount and intensity of social stimulation. Such coordination of communicative effort fosters the development of a sense of connection between caregiver and infant while building a mutual awareness of doing something together. Recent experimental work demonstrates how contingent social feedback serves to promote more advanced speech-like vocalizations (i.e., canonical babbling) in prelinguistic infants (Goldstein et al. 2003). In this and similar studies, caregivers were prompted via an earpiece to affirm their infant's communicative attempts by smiling, touching them, or imitating their vocalizations, with half of the infants receiving contingent feedback (i.e., the prompts were timed to immediately follow the infant's vocalizations), while the other half received noncontingent feedback (i.e., the prompts were yoked to the timing of the vocalizations of a different infant from a previously recorded session). Across studies, the provision of contingent feedback was found to

increase both the quantity and quality of infant vocalizations, such that infants who received prompt, contingent feedback made a greater number of communicative attempts to engage their caregivers and produced more mature, canonical forms of babbling relative to the yoked controls. Similarly, in longitudinal designs, individual differences in maternal responsiveness to their infant's communicative bids have been shown to predict the timing of subsequent language milestones, including the emergence of first words, 50 words in expressive language, combinatorial speech, and talk about past events (Tamis-LeMonda et al. 2001), with maternal repetition or imitation of the child's speech proving to be the most impactful form of feedback for later developmental milestones.

Embodied Cognition as Expressed in Gesture and Speech

For infants, one of the major challenges involved in learning a language is to discern the referents of the words heard in the ambient language – a process referred to as word-to-world mapping. Caregivers play an important role in facilitating this process by talking about what the infant already has in mind; for instance, by naming objects that the infant is pointing at or holding. Most early verbs and other relational terms like *up* or *off* are acquired in contexts where the infant is involved in purposeful activity, which allow, for example, the infant to map a word such as *up* onto their efforts to be picked up. Modern theories of language have come to recognize that the semantic representations associated with linguistic forms are multimodal in nature and reflect the sensorimotor experiences of learners. Multimodal representations are one feature of embodied cognition wherein conceptual processing involves simulation or mental reenactment of previously experienced situations (Barsalou 2009). In children, as well as adults, accessing verb meanings is associated with neural activity in motor areas (frontal cortex), which varies as a function of the type of verb, e.g., “hand” verbs such as *clap* or *throw* vs. “leg” verbs such as *run* or *chase*, with self-generated action seeming to play a key role in the development of these neural signatures of

sensorimotor activity during verb acquisition (James and Swain 2011).

Notably, infants are learning the meanings of words at the same time as they are acquiring a wide range of communicative gestures, many of which may be viewed as forms of simulated action, as when the child puts their hands over their heads as a request to be picked up (Tomasello 1999). Young children's gestures seem to convey their thoughts when they are at the cusp of acquiring a new skill (Goldin-Meadow 2009). These gestures provide crucial information to caregivers about what their infant has in mind (i.e., what are the infant's communicative intentions), which facilitates caregivers' provision of relevant input to aid word-to-world mapping. Infants often acquire corresponding gestures prior to learning verbs like *wave*, *sleep*, or *drink*, with the word subsequently mapped onto the gesture as a component of its meaning. Gestures also seem to play a key role in young children's acquisition of combinatorial speech, as infants first combine single words with familiar gestures (e.g., pointing at a cookie while saying *more*) prior to combining two words into a single utterance (e.g., saying *more cookie*). Deictic gestures (e.g., pointing at something), in particular, may be important for the child's acquisition of a general combinatorial operation like Merge, by serving as variable expressions (i.e., with meanings corresponding to pronouns like *it* or *that*) that change in meaning depending on the context of use. Thus, learning to point as a form of request at a multitude of objects (e.g., cookies, milk, out-of-reach toys) paves the way for the child to acquire corresponding phrases such as “get it” which exemplify the situational meanings and flexible utility of linguistic expressions.

Bootstrapping in Complex Dynamical Systems

In order to process incoming information language learners need to rapidly incorporate this information into existing representations. A number of theories provide accounts for how representations of the hierarchical structure of language can be built up incrementally from the input. The evidence suggests that from the

very first moments of contact with language in utero, infants become attuned to the statistical regularities associated with the duration of vowels and consonants and the resulting rhythm of the language (Mehler et al. 1988). During infancy, sensitivity to prosodic characteristics, i.e. intonational and rhythmical patterns, provides a rich source of information that facilitates discovery of the underlying grammatical structure of a language because prosodic and syntactic structures tend to be aligned to a considerable degree (Morgan and Demuth 1996). The process of discovering the sound patterns and structures of the ambient language is aided by the fact that child-directed speech often exaggerates phonetic and prosodic characteristics in ways that support the discriminability of phonemes (i.e., meaning-bearing speech sounds) and discovery of higher order units, such as words, recurrent morphemes, and phrasal constituents. Thus, the rich input supports online bootstrapping of linguistic structure at multiple levels. More generally, the notion of bootstrapping implies that as children acquire aspects of language, such as the meanings of concrete nouns that can be learned ostensively through a process of word-to-world mapping (e.g., pointing at an object to elicit its name), they can make use of familiar forms (i.e., what they have already learned) to aid them in learning unfamiliar and more abstract words and structures (Gleitman et al. 2005).

The notion of bootstrapping and learning as being supported by affordances of the environment extends beyond language input: Language development is grounded in the infant's sensorimotor experience, which undergoes abrupt transitions as infants develop motor skills over the first year of life. Recent work has explored how the transition from crawling to walking provides infants with new ways of sharing their interest in objects with others, which in turn may alter the communicative dynamics of caregiver-child interaction. In a study focusing on 13-month-olds, where half of the infants were already walking and half were still crawling (Karasik et al. 2011), walkers more often carried objects to their mothers, shared their interest in objects from a distance, and communicated their interest in

sharing an object while in motion. The observed differences in how walkers and crawlers shared objects with others had unexpected consequences for communicative development by influencing how the mothers perceived their infants' communicative intentions. Mothers responded differentially to the moving bids (favored by the walkers) in comparison to the stationary bids (favored by the crawlers) by producing more advanced action directives, such as "open it," when the child offered or showed them the object while in transit. These findings suggest that developmental changes in one domain (i.e., motor development) can yield cascading effects on development in a seemingly unrelated domain (i.e., language development) by altering parent-child conversational patterns, which, in turn, enriches the input to the language-learning child.

Usage-Based Learning

In the face of decay, incoming linguistic information needs to be processed rapidly by the learner. As a result, learning is based on local contingencies processed in small chunks rather than on surveying and generalizing over large corpora of previously encountered input. This assumption is built into a number of theoretical frameworks that focus on the dynamics of language usage, chunk and pattern extraction, categorization and generalization, and change over time; these include connectionist, emergentist, and usage-based approaches to language and development. According to these approaches, infants and toddlers learn language in a piecemeal fashion, starting out by acquiring words and phrasal patterns that are relevant to their daily routines, such as mealtime or book reading, using mutually understood activities and predictable communicative formats to make sense of the accompanying language. Through a process of cross-situational statistical learning, young children hone in on the meanings of words and at the same time become sensitive to the unique ways that individual words co-occur with other words, including their frequency of occurrence in different syntactic and situational contexts. Acquisition of item-specific co-occurrence statistics supports priming, wherein the processing of linguistic structure

becomes more fluent and efficient as a function of item and pattern familiarity. Storage of pre-compiled units or chunks of language incurs further benefits by allowing the child to make incremental predictions about what comes next when processing language in real time. By emphasizing statistical learning of distributional information, which includes monitoring how often different lexical items appear in different grammatical constructions, these approaches provide dynamic accounts of how children go from being fairly conservative learners to making the sorts of constrained generalizations that allow sophisticated language users to achieve the unlimited expressive potential of human language.

How Is Language Used?

Language is transient. Humans are able to comprehend language at a rate of about 20 phonemes per second despite the fact that the ability to differentiate nonlinguistic sounds is limited to about 1.5 per second. This implies that current input is rapidly overwritten by new input, urging immediate processing – a phenomenon referred to as the *Now-or-Never bottleneck* (Christiansen and Chater 2016). Similarly, the planning of action sequences, such as those required for speech production, is temporally constrained as planning of long sequences far in advance is hampered by interference and forgetting. These constraints are reflected in a number of basic features of processing systems, which are discussed below. These basic features of the architecture of the language processing system – viewed as consisting of a series of subprocesses that operate in a cascaded manner utilizing different types of information in an interactive manner in order to interpret and even predict upcoming input – are thought to govern both language comprehension and language production, although controversy persists about the extent to which the two systems share parts of their architecture and underlying neural substrate (Pickering and Garrod 2013). Crucially, the principles that underlie language processing and communicative interaction may be shared with processing architectures in a

number of other domains such as visual perception, action planning, or social cognition, rather than being unique to language.

Levels of Processing

Theories of language processing postulate components or stages that deal with different types of information in the signal, such as phonological, prosodic, lexical, morphological, syntactic, semantic, and pragmatic information. Early theories were heavily influenced by the idea of modularity of processing of different types of information (Fodor 1983). As a consequence, language processing was assumed to handle different types of information in several stages assembled in a strictly sequential and independent way, such that information processed at later stages could not influence processing at earlier stages. For example, the process of utterance or sentence comprehension was conceived of as parsing the input to uncover the underlying syntactic structure, formalized as a phrase-structure grammar. Parsing was viewed as incorporating the input into a syntactic tree in incremental fashion following a set of heuristics that minimized memory load by limiting the number of higher-order syntactic units that could be assembled at any given point in time. Semantic processing was postulated to be subsequent to the identification of syntactic structure, and semantic information could not be admitted for resolving processing uncertainties at earlier stages. The idea that processing proceeds from lower to higher levels in strictly sequential fashion was also echoed in early theories of language production where information was propagated sequentially in the reverse direction.

Incremental Cascaded Processing

More recent theories acknowledge that the rapidly fading signal necessitates efficient conversion of sensorimotor input into higher-level representations. This constraint is reflected in the feature of incremental processing, whereby small chunks of input cycle through the various processing stages so that earlier chunks are already integrated with higher-level information while lower-level information is still being processed to create later chunks. For example, studies of speech

shadowing have shown that speakers routinely correct errors in the speech stream, which suggests that spoken word recognition proceeds extremely rapidly based on partial input allowing higher-level lexical information to be used to assemble articulatory commands while lower-level phonological information is still being processed. For larger segments of input, like utterances and sentences, the idea of incremental processing was first introduced by the two-stage sausage machine model (Frazier and Fodor 1978), which proposed that incoming words first get chunked into syntactic phrases, which are then incrementally incorporated into a syntactic representation. Modern theories assume a massively cascaded architecture according to which the processor chunks the incoming input and immediately passes the information on to higher levels of information processing while at the same time continuing to process lower-level information in the subsequent input (Christiansen and Chater 2016).

An incremental cascaded architecture has also been proposed in speech production theories, which show – based on empirical findings from picture-word interference tasks – that higher-level structure, e.g. the semantic and syntactic structure of an utterance, is constructed incrementally and on the fly. Recent evidence from syntactic priming suggests that speech planning involves a syntactic planning phase that is independent from semantic content and phonological form and liable to reusing the structure of recently encountered input (e.g. Pickering and Branigan 1998). The idea of purely syntactic representations derives from earlier theories of speech production, which postulated separate syntactic representations of words called *lemmas* (in contrast to *lexemes* carrying phonological information). In the production of continuous speech, syntactic planning spans somewhat longer time windows than planning at lower levels, e.g. planning of prosodic structure, which, in turn, is planned further ahead than syllabic and phonological structure, attesting to the cascaded nature of the process. Controversy exists with respect to the size of the preplanned components, and the extent to which preparation of multiple components involves parallel processing.

Interactive Processing

In comprehension, incremental chunk-by-chunk processing runs into problems when correct interpretation of current input depends on information that only becomes available in the yet-to-be-processed input. At the level of identifying individual words, ambiguities can arise from distortions in the acoustic signal (i.e., noisy input), from a lack of one-to-one correspondence between the signal and the intended word form (i.e., polysemy and homonymy), or from competition from phonologically related words with similar onsets (i.e., words in a cohort such as *carbon*, *carton*, *carpenter*, etc.). Often, such uncertainties in spoken word recognition cannot be alleviated through bottom-up processing, thus requiring the listener to make inferences about the intended word based on probabilistic contextual cues. Empirical evidence shows that the lexical status of the ambiguous word as well as the coarticulatory properties of the surrounding sounds can affect the sensitivity of early sensory processing of speech sounds, suggesting that the processing system is interactive. In many instances of noisy input, interactive processing includes the use of crossmodal sensory integration (e.g., lip reading) to facilitate rapid restoration of missing/distorted phonemes (Massaro 1987). Moreover, higher-level information can influence processing retrospectively; for example, accessing lexical knowledge about a given word can influence interpretation of ambiguous phonological information that was encountered within that word, for example, a sound with a voice onset time between /d/ and /t/ is perceived as /t/ at the end of /pi/ because /pit/ is a word but /pid/ is not. Such effects have successfully been implemented in connectionist word recognition models such as TRACE (McClelland and Elman 1986).

Ambiguities can also arise in sentence processing. For example, in so-called garden-path sentences, such as *The horse raced past the barn fell* or *Put the frog on the napkin in the box*, listeners may be led down the garden path to form an incorrect interpretation of the sentence. This occurs when information early in the sentence, e.g., the past participle *raced*, is misunderstood, e.g., taken to be the main verb in the

sentence as opposed to a modifier of *horse* (part of a reduced relative clause). Early sequential theories postulated that the processing system commits itself deterministically to just one interpretation using a set of processing heuristics. According to these theories, listeners will subsequently revise their interpretations of sentences only if incompatible information is encountered, with reanalysis manifesting itself in processing cost measurable by error rates, reaction times or electrophysiological markers indicating processing of unexpected information. Crucially, the process of reanalysis is thought to be triggered by various types of information that are independent of syntactic structure, such as semantics, discourse structure, pragmatic inference, and/or real-world knowledge. Reanalysis may not be fully available to young children who show minimal evidence of revising incorrect interpretations of temporarily ambiguous sentences, like the examples given above (Trueswell et al. 1999).

In contrast, interactive constraint-satisfaction theories (MacDonald et al. 1994) permit the processing system to maintain several alternative interpretations of a sentence in parallel, with viable interpretations continuously constrained by multiple information sources (see list above for sources of information guiding the process of reanalysis), thereby limiting the need for second-pass revisions under most circumstances. Thus, a phrase such as *The witness interrogated...* is much less likely to be interpreted as a noun + main verb than the similarly structured phrase *The horse raced...* because a variety of factors, including frequency of use, encourage the listener to interpret the noun phrase *The witness* to be the object of the verb *interrogated*. Such probabilistic information may be obtained through statistical learning of co-occurrence patterns in the input (see subsection above on Usage-Based Learning), although other information may reside in the context of the specific communicative episode. There remains controversy with respect to the amount of information that can be retained in a memory buffer before an ambiguity must be resolved and the types of information that can be considered at various processing stages. It has been suggested that listeners often do not consult all available

sources of information in processing a sentence, but rather engage in satisficing to generate “good-enough” representations that minimize effort and processing cost (Ferreira et al. 2002).

Top-Down Processing

As indicated, higher-level information can be used to resolve uncertainty at lower levels of processing either by aiding in the selection of the correct interpretation among the various alternatives activated by bottom-up processing, or by selectively preactivating just one compatible interpretation at the exclusion of others, even though such top-down processing could lead to misinterpretation of upcoming input. Controversy has arisen about whether context-based facilitation of bottom-up processing reflects top-down processing, or whether it just arises from priming, i.e. from the spreading of lingering, yet rapidly decaying, activation of already-processed input at lower levels of representation. This controversy is of greater relevance in sentence processing than in word processing, where top-down processing has been demonstrated by predictive eye movements in the visual-world paradigm, for example, when participants perform eye movements toward objects predicted by the previous context (Altmann and Kamide 1999). In contrast, in studies of sentence processing there is less agreement on whether high-level information can influence bottom-up processing of lower-level information directly, or whether it merely aids in selection of different alternatives constructed by lower-level processing. One reason for the difference between word and sentence processing lies in the length of the time windows necessary for processing relevant information. Whereas top-down influences on word recognition occur within a relatively short time window (not overly taxing on memory and processing resources), top-down influences on sentence processing require a much longer time window for morphological, syntactic, and semantic processing. However, recent neurophysiological evidence supports the idea of top-down effects in sentence processing: differences in low-frequency oscillatory neural activity indicate reciprocal entrainment of cortical networks associated with lower and higher-level information

processing prior to point at which disambiguating input is encountered (Lewis and Bastiaansen 2015).

Predictive Processing

By definition, introducing top-down influences into a cascaded processing system makes processing predictive. Prediction safeguards the system against loss of information in the input due to noise in the transmission channel and in neural processing. The exact nature of how prediction operates is currently the subject of considerable debate. In its minimal sense, prediction implies that contextual effects from other types of information can influence the state of the processing system before further bottom-up processing has taken place. Theories differ with respect to whether prediction operates in a deterministic or probabilistic manner. As described above, early theories were deterministic in that they proposed top-down processing to favor one possible interpretation, typically the strongest contender of all possible interpretations, which was either the simplest in terms of memory load or the most frequent. In cases of mismatch between the predicted and incoming input (as in the case of garden-path sentences), the processing system had to reanalyze the input to identify the alternative with the greatest plausibility. Recent evidence, however, favors graded prediction effects, which are determined by the surprisal of a given continuation, i.e. by the amount of new information that would potentially be gained by processing this particular alternative: the higher the surprisal, the higher the processing cost. Thus, recent theories propose that several alternatives, each weighted by a certain strength of belief, can predictively be computed and remain active in the processing system until a resolution has been achieved. The process of resolution is proposed to follow an “ideal” or “rational observer” model, which engages in incremental belief updating using Bayesian inference to change an existing prior distribution of probabilities for the various interpretation alternatives to a new posterior probability distribution, which, in turn, becomes the prior distribution for the next processing cycle. Modern theories are trying to illuminate how people trade off the benefits and costs associated with

predictive preactivation in different domains of language processing.

Communicative Interaction

Traditional theories of language processing were developed to account for empirical findings of laboratory studies involving single speakers or listeners subjected to sophisticated manipulations of language input in the absence of a conversational partner. Recent theorizing has increasingly shifted the focus toward understanding how humans use language to engage cooperatively with others (Clark 1996) and how the production and comprehension systems of interlocutors interact when taking turns in conversation (Pickering and Garrod 2013). Modern theories of referential communication attempt to apply principles of interactive processing and Bayesian prediction to explore how speaker intent can be encoded and recovered efficiently in the face of pragmatic constraints on the amount of information conveyed in speech (Frank and Goodman 2012). Processing principles derived from comprehension and production research can also be applied to model the communicative interaction itself by demonstrating how mechanisms like priming, inference, and monitoring of output lead to interactive alignment of linguistic signals at various levels of information processing, with the ultimate goal of achieving an alignment between interlocutors’ internal representations. Here, controversies persist around the question of “audience design” – under what conditions humans engage in strategic and volitional attempts to align the form of their output and adjust its informativeness in relation to the expectations, needs, and assumed mental models of different conversational partners. Furthermore, the question as to how language is embedded in, and governed by, communicative behavior in general has led to proposals about the evolutionary primacy of turn-taking behavior and its ontological independence from language (Levinson 2016).

Conclusion

Modern theories of language try to understand how language use arises from domain-general,

embodied learning and processing mechanisms operating in service of communication that takes place in richly structured social environments. Research has begun to move away from the study of language as the behavior of individuals to consider how it arises as a cooperative enterprise within social groups ranging in size from dyads to global communities. Contemporary theories of language are informed by powerful mathematical and computational models, big-data approaches to the analysis of natural language corpora, neurophysiological methods, and traditional laboratory experiments, designed to illuminate social as well as cognitive mechanisms underpinning language learning and processing. These complementary methodologies have the potential to offer new insights for understanding language as an emergent property of the biological substrate of individuals engaged in complex, hierarchical social interactions.

Cross-References

- [Communication and Developmental Milestones](#)
- [Early Theories of Language](#)
- [Language](#)
- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Development](#)
- [Language Instinct, The](#)
- [Linguistic Evolution](#)
- [Modeling Language Transmission](#)
- [Motherese](#)
- [Nativism](#)
- [Noam Chomsky and Linguistics](#)
- [Phonemes and Symbols](#)
- [Physiology of Language](#)
- [Pinker's \(1994\) The Language Instinct](#)
- [Steven Pinker and Language Development](#)
- [Words and Rules](#)

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Modern-Day European Union

- [Western Europe](#)

Modification

- [Human Ornamentation](#)

Modified Behavior Towards Conspecifics

- [Kin Detection by Odor](#)

Mods

- [Body Modification](#)
- [Human Ornamentation](#)

Modularity of Mind

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Synonyms

[Cognitive modularity](#); [Domain specificity](#); [Mental modularity](#); [Mind modules](#)

Definition

A cognitive system is composed of neural structures and mental processes that to some appreciable extent are distinct, localized with neural architecture, and domain specific. More simply, modularity of mind means functionally specialized mental systems.

M

Introduction

The functional architecture of the mind can be traced back in history into two competing views: (i) the **horizontal view** refers to mental processes as interactions between mental faculties which are not domain specific such as perception, memory, judgment, etc., and (ii) the **vertical view** explains that mental faculties are domain specific, computationally independent, genetically programmed, and linked with localized neural structures. The latter view dates back to the nineteenth century presented by F.J. Gall, who contends that specific mental faculties are linked with specific brain areas.

Afterwards, in the later nineteenth century, the term *modularity* has entered in the *Dictionary*

of *Cognitive Sciences* following the book *The Modularity of Mind* (Fodor 1983). Since then, Fodor has been known to be the major proponent of cognitive modularity. However, Fodor's approach to modularity of mind is a modest approach explaining that mind's input systems are modular while central cognitive systems are not modular. Since Fodor's work, conceptual landscape of modularity has improved radically. Later on, skeptics of Fodor have adopted a less rigorous but a massive approach to modularity by arguing that the mental architecture is more pervasively modular. Recently, the concept of modularity has been extended in related disciplines including epistemology, language, philosophy of science, and ethics.

Fodor's Modularity of Mind

Fodor's approach to modularity of mind is somewhat a modest approach, but the criteria of modularity are very stringent. Jerry Fodor draws his idea of modularity of mind from Chomsky's idea of language acquisition device as well as from other works on linguistics and optical illusions. His approach offers two components: the first component offers that mind's input systems mainly involving language and memory are modular. The second component, however, negates modularity in central cognitive systems involving belief fixation and practical reasoning.

In Fodor's (1983) view, input systems are mind's computational systems through which the world is presented to mind by processing of sensory transducers. A sensory transducer presents the sensory information to the mind into a computationally usable form where input processing draws hypotheses about the object to pass it on to central systems for further processing and in turn for the formation of behavior. Fodor asserts that modularity of input processes means that these input systems have a group of psychologically interesting properties to be recognized as modules, which are listed as nine features of modularity in his classic book (Fodor 1983). He asserts that any system to be recognized as modular must fulfill these features, but not all at

the same time, to some interesting extent. These features in original order are:

- (i) Domain specificity: modules are specialized which function in response to certain kinds of inputs.
- (ii) Mandatory operation.
- (iii) Limited central accessibility.
- (iv) Fast processing speed.
- (v) Informational encapsulation.
- (vi) Shallow outputs: generating a very simple output.
- (vii) Obligatory firing: mandatory processing.
- (viii) Characteristic ontogeny.
- (ix) Fixed neural architecture.

Among all these nine features, "information encapsulation" is the most fundamental of modularity to Fodor as well as to Pylyshyn (1999), who argues that information encapsulation among nine features stands out as being the actual characteristic of a module. To Pylyshyn, encapsulation makes a module encapsulated from both cognitive influence and from cognitive access. One best example of this is the Müller-Lyer illusion which is not even influenced/corrected by the conscious awareness of the illusion.

Although Fodor claimed for lower cognitive systems to be modular, he argued that higher-level central cognitive systems are not modular. As the central cognitive processes are involved in practical reasoning through non-demonstrative inferences, which cannot be understood in an informationally encapsulated system, central processes cannot be modular. He further argues that central cognitive processes are meant for belief fixation which is isotropic. As isotropic processes cannot be informationally encapsulated while modular systems are encapsulated, hence, belief fixation and central systems cannot be modular.

Critically, and even in Fodor's view, the non-modular characteristic of central systems is a serious threat to existence of cognitive science. He supports his pessimistic view of non-modular central system in two ways: First, global and isotropic systems do not seem to relate to specific neural structures, thereby making them a dubious

subject of neurocognitive science; second, global systems are resilient to computational processes, further making them a hopeless subject for psychological study.

Criticisms/Challenges: Skepticism to Fodor's Proposal of Modularity of Mind

Skeptics of modular input systems have challenged information encapsulation and cognitive impenetrability of linguistic and perceptual processes (e.g., Marslen-Wilson and Tyler 1987; McCauley and Henrich 2006). Among them, Prinz (2006) has widely challenged the modularity and encapsulation of perceptual systems by presenting a dual argument: First, likely cross-modal effects in speech perception argue against encapsulation, the best example of which is McGurk effect (McGurk and Macdonald 1976). Second, top-down effects on linguistics and perception processes also argue against encapsulation and cognitive impenetrability. Top-down effects are evident in scientific studies of phoneme restoration effects where subjects fill in the missing phoneme in spoken language. Furthermore, cognitive psychologists contend that lower-level cognitive processes are continuous with higher-level cognitive processes pointing them to be inferential and informationally penetrable.

Massive Modularity

Competing viewpoints on modularity of mind have come from evolutionary psychology whose proponents adopt a less stringent definition of modularity but at the same time claim that mind is more extensively modular from peripheral lower cognitive processes to higher cognitive processes. This view proposes that modules are mental processing units which have evolved over time as a consequence of evolutionary selection. Their proponents suggest that mind is comprised of genetically determined domain-specific computational modules, which are planned to solve particular evolutionary problems, with specific

neural circuits solving specific adaptive problems (Cosmides and Tooby 1994).

Contemporary theorists including Sperber (2002) and Carruthers (2006) assert that the mental architecture is modular from lower cognitive functions to higher cognitive functions including decision-making, reasoning, problem-solving, planning, etc. The theory is sometimes known as massive modularity. Notably, post-Fodorians adopt a less rigorous operative definition of modularity. To Carruthers (2006), "module" means isolated function-specific processing systems, which are domain specific and associated with specific neural architecture, and is likely to have inaccessible inner operations. He excluded many of Fodor's proposed modular features from the operative notion of modularity including encapsulation, shallow output, fast processing speed, transducer computation, and innateness. Importantly, proponents of massive modularity were mainly concerned with modularity of central cognitive systems while being least concerned with modularity at lower-level input systems. Originally spoken and promoted by proponents of evolutionary psychology (Sperber 2002; Cosmides and Tooby 1994; Barrett 2005), the massive modularity view has attained its most comprehensive defense at the hands of Carruthers (2006).

Conclusions

In the late nineteenth century, the term *modularity* has entered in the *Dictionary of Cognitive Sciences* following Fodor's book *The Modularity of Mind* (1983). Since then, Fodor has been known to be the major proponent of cognitive modularity. Fodor's approach to modularity of mind is a modest approach explaining that mind's input systems are modular while central cognitive systems are not modular. However, he adopts a very rigorous definition of modularity with nine rigorous features. Later on evolutionary psychologists and proponents of massive modularity theory adopt a less stringent criteria of modularity while arguing that mind is modular through and through from lower-level input systems up to higher cognitive processes. They propose that mind is comprised of functionally

specialized modules which are domain specific, genetically determined, and associated with specific neural structures and which are designed to solve specific evolutionary and adaptation problems.

Cross-References

- [Cognitive Science](#)
- [How the Mind Works](#)
- [Theory of Mind and Evidence of Brain Modularity](#)

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Molecular Clock

- [Sleep-Wake Cycles](#)

Mollusk

- [Aplysia](#)

Momnesia

- [Mother's Brain Size Decrease During Pregnancy](#)

Monetary

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Synonyms

[Kin altruism](#); [Kin selection](#); [Reciprocal altruism](#)

Definition

Suicide terrorism as directed kin altruism might entail monetary benefits to the kin of the attacker.

Introduction

One tactic used by terror organizations to recruit combatants is to offer monetary compensation to the family members following the completion of a successful attack. Reciprocal altruism and kin selection might factor into decision-making concerning whether one should undertake a suicide mission.

Theoretical Overview: Monetary Benefits to Kin

From an evolutionary perspective, providing monetary compensation to the family members

of suicide attackers might play a role in the cost-benefit analysis of suicide terrorism since genetic kin would ostensibly receive benefits that could enhance their fitness. According to Human Rights Watch (2002), Hamas paid the families of suicide attackers between \$10,000 and \$25,000, and as cited in Bloom (2004) also provided services such as medical care (Blackwell 2006). This represents a form of reciprocal altruism (Trivers 1971) in regards to the exchange between the attacker and the terror organization as well as a form of kin altruism (Hamilton 1963). While there is some evidence that benefits to kin could outweigh the costs of a suicide attack (Blackwell 2006), the evidence is limited that monetary compensation sufficiently outweighs for the total reproductive failure that typically accompanies suicide terrorism.

Problematically, suicide terrorists and their families are often not impoverished. Rather, they tend to be better off financially on average than the general populations from which they come (Krueger and Malečková 2003). Nevertheless, suicide terrorism corresponds to rises in national poverty levels, and suicide attackers tend to come from poorer regions (Pedahzur et al. 2003). In sum, suicide terrorists come from political regions that are relatively impoverished, but the combatants themselves and their families tend to be wealthier than their neighbors.

A preliminary model tested by Blackwell (2006) demonstrated that suicide terrorism can benefit, specifically, close siblings. Using the Palestinian conflict, Blackwell found that suicide terrorists with middle class backgrounds and large families with many male siblings in particular could benefit their families most.

Conclusion

Thus far, the models demonstrating that the potential benefits of suicide attack to kin outweigh the costs to the attacker are preliminary and might not take all of the critical variables into account. Nevertheless, this is fertile ground for future research.

Cross-References

- [Benefits to Kin](#)
- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Monetary Artifacts

- [Cultural Cortical Recycling Hypothesis Applied to Money](#)

Monkeys

- [Primate Menopause](#)

Monoamine Oxidase and Antisocial Behavior

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Synonyms

Asocial; Criminal; Delinquent; Deviant; Immoral; Misanthropic

Definition

Monoamine oxidase is an enzyme that initiates the oxidation of monoamines, which includes neurotransmitters.

Antisocial behavior refers to behaviors or actions that are conflict with societal norms and standards such as conduct.

Introduction

Evolutionary psychology helps to describe how a human may develop biological advantages to antisocial behavior in some circumstances. In a society that values altruism and working together, antisocial traits such as robbery and sexual coercion can prosper in a small minority of people as an alternative means of survival to altruism. Natural selection does not necessarily prioritize overall wellbeing as much as it does general survival fitness. Antisocial behavior (like much of psychopathology) has genetic roots (Del Giudice and Ellis 2016). For antisocial behavior the driving force behind procreation and passing genetic information down to offspring is to dominate other people in an aggressive manner by inciting violence and breaking established rules (stealing of resources), giving them an edge over their more docile and cooperative competition (Woo and

Keatinge 2016). Buss (2009) suggests that evolution in the field of psychology is how people acclimate to their environment, survive, and develop children of their own to pass on their genes to their children.

Environment, Evolution, and Antisocial Behavior

People who exhibit antisocial behavior tend to be charming and have the ability to swindle required resources – like food and money – from other people who earned it by growing crops or trading goods. Deceit is their primary survival skill (Woo and Keatinge 2016). Buss states that particularly in the field of clinical psychology, people may not biologically advance properly causing a disturbance in their overall development – this may allow for maladaptive development strategies to flourish – like antisocial behavior. In the environment, extreme poverty may perpetuate the development of antisocial traits, where many individuals may view conning other people as a way to thrive. A hallmark of antisocial behavior is inconsideration of the rights of other people. People with antisocial behavior may thrive in their development by mating with each other, allowing them to flourish in small enclaves. When the couple has children, they may neglect and abuse their children, perpetuating the cycle of antisocial behavior (Saddock et al. 2015). Eventually, their high-octane lifestyle may come to a halt when they age and vitality begins to diminish (Woo and Keatinge 2016). If one is successful in reproduction they will successfully pass on their genetic information to their offspring – like their monoamine oxidase levels.

What are MAOs?

Monoamine oxidase (MAO) are enzymes that destroy additional neurotransmitters produced in the human body (Carlson and Birkett 2017). MAO-A genes impact three different neurotransmitters: dopamine, norepinephrine, and serotonin

(Godar et al. 2016). Initially, psychiatrists prescribed MAO's to treat major depressive disorder. This would help to improve the moods of patients (Breedlove and Watson 2013). It can also be used to treat social anxiety disorder, while MAO-B can alternatively be used to treat Parkinson's disorder. MAO inhibitors can be rather effective in treating patients; often patients report feeling very well after taking them. However, they are not used as frequently because they can be toxic if taken with foods that have high levels of tyramine, such as cheese (Lovatt 2011). MAO-B impacts mostly dopamine and can also have anticholinergic effects, blocking acetylcholine flow (Carlson and Birkett 2017).

Monoamine oxidase A (MAO-A) is a gene located in the X chromosome, given that MAO-A has a clear genetic link between its level of activation (particularly in males) and violent behavior. Males who participated in a study by Galina and colleagues (2016) had lower rates of MAO-A levels, which is linked to impulsive behavior which may make them more likely to commit violent crimes. Although different strains of MAO's exist to preserve antisocial behavior, for example, MAO-A appears to be the most commonly researched when it comes to antisocial behavior. Lower levels of MAO-A have been found in those who involve themselves in antisocial behavior. Males may be trying to compensate for their low levels of MAO-A by engaging in risky behavior that is highly rewarding, such as unprotected sex, violence, and substance use (Galán et al. 2017).

Given its location in the X chromosome, it is most prevalent to males. In biology, dichotomous "sex" is determined by the X chromosome in males and females. Males have an X and a Y chromosome, while females have two X chromosomes. The two X chromosomes often cancel genetic defects making maladaptive genes more prominent in males. The second X chromosome in females negates most genetic deformities (Xu et al. 2017). Sjöberg found that in prison populations a transcription of the 3-repeat (short) allele means a decreased MAO-A rate and as a result a potentially increased serotonin in the synapse, which may increase the chance that one

may develop aggression in antisocial behavior (Sjöberg et al. 2008).

Environmental Interactions of MAOs and ASPD Development in Males

Low activating MAO-A genes may be partially responsible for weakened verbal functioning in those with ASPD. This could help explain the higher rates of ASPD in males (Jackson and Beaver 2015). In a high-stress environment, low levels of serotonin may influence one's impulse behavior, making them more likely to act without thinking (Sadeh et al. 2013), requiring more frequent behavioral rewards to keep satisfy the individual. Those with decreased levels of MAO-A increase the chance one may be more impulsive than those with augmented levels of MAO-A (Sadeh et al. 2013). Supporting evidence by Checknita et al. (2015) found that those with ASPD and those who have low levels of MAO had higher levels of serotonin. Those with ASPD likely have parents or other initial relatives with the diagnosis, indicating a biological link (American Psychiatric Association 2013). A variety of studies examining the relationship of MAO and antisocial behavior looked at how abuse impacted MAO and antisocial behavior.

Galán et al. (2017) investigated MAO-A and antisocial behavior in a longitudinal study. They found that males who suffered extensive abuse and had lower MAO-A activation were more likely to be involved in criminal behavior such as a history of violent arrests. The same results were not found among males with high activation of MAO-A. Maltreatment as a child also increased the risk of antisocial behavior; however, mistreatment would have to occur before the age of 12 to increase ASPD risk (Haberstick et al. 2014). MAO levels in children are unlikely to be a solid predictor for antisocial behavior. Children with low MAO levels did not exhibit antisocial behavior more than individuals with increased MAO levels.

Derringer et al. (2010) suggests that conduct disorder and antisocial behavior are more extreme in those with lower MAO-A level activation. MAO-A levels alone are not strong enough to predict antisocial behavior among young males.

Males with lower MAO levels had higher rates of violent outbursts than those with high MAO levels. High MAO levels do not increase the chance that one will develop ASPD (Haberstick et al. 2014). Sjöberg et al. (2008) suggest that MAO-A genotype may interact with testosterone in predicting antisocial spectrum behavior. Researchers did not find a direct association between the lower activity variant and aggressive behavior (Sjöberg et al. 2008). In a study conducted on male inmates, researchers found a correlation between levels of MAO-A and violence. Those with an extremely low functioning of MAO-A gene had a higher level of violent outbursts (Tiihonen et al. 2015). Parental neglect damages the amygdala, making emotional processing more difficult and further developing the chances that one may develop ASPD. The amygdala aids in emotional processing. A difficulty or absence of emotional processing is a chief symptom of ASPD (Byrd and Manuck 2014).

Adolescents and Children

Adolescents with ASPD and low MAO-A levels appear to be relatively extraverted, according to one study that used the Minnesota Multiphasic Personality Inventory who wanted to see if MAO-A potentially influenced personality development (Xu et al. 2017). Jackson and Beaver (2015) examined whether nutrition would activate MAO-A genes, impacting antisocial traits. Diet did not explicitly influence MAO-A activation in participants; however, adolescents who had an active MAO-A gene and consumed more fast-food than vegetables showed more antisocial traits during adulthood. Correlational studies have found that diets missing certain nutritional elements such as vitamin C and calcium may cause children to insufficiently develop verbal skills at the same rate as those who were given a proper diet, influencing the development of antisocial traits (Jackson and Beaver 2015). Testosterone levels in children may be a much better predictor of aggressiveness. In a positive environment, low MAO levels may be protective of future development (Nilsson et al. 2018).

Brain Scans in Males

An MRI study was conducted on a group of males with antisocial personality disorder (ASPD). Researchers looked at MAO-A activation in control participants and those diagnosed ASPD. Participants with decreased MAO-A activity were more likely to have an ASPD diagnosis and had lower levels of right basolateral nucleus functioning than healthy participants (Kolla et al. 2017; Kolla and Houle 2019). The prefrontal cortex impacts control and allows humans to solve puzzles. A brain scan was conducted on ASPD patients and non-ASPD patients and found that dorsal lateral prefrontal cortex activity was weakened among those with ASPD. When compared to non-ASPD males who were not incarcerated, incarcerated males with a low functioning MAO-A gene had lower orbital frontal cortexes and ventral striatum functioning. It is possible that because of the lower functioning orbital frontal cortex and ventral stratum, individuals with ASPD were more impulsive and aggressive (Kolla et al. 2017). Kolla et al. (2015) found that impulsiveness may be impacted by a mutation of the eighth axon of the MAO-A gene. Those with the mutation were more likely to be aggressive and impulsive, important traits understanding ASPD. The same results could not be replicated when conducted on incarcerated populations with ASPD (Kolla et al. 2015).

Animal Studies

Antisocial behavior can also be present in some primates. In a meta-analysis conducted by Nilsson and colleagues (2018), they tested MAO-A levels in rhesus monkeys and found that some of the more aggressive monkeys also had lower MAO-A levels. In mice, researchers were able to induce Brunner syndrome by lowering levels of MAO-A in them. Like in humans, this would cause the mice to become riddled with an excessive amount of anger. Brunner syndrome is a genetic defect found in males that have extremely low levels of MAO-A (Godar et al. 2016).

Female Relationship of MAO's and Antisocial

Data involving MAO's and antisocial behavior is not as clear for females as it is for males. MAO levels may not be an excellent predictor of ASPD for females; however, high MAO levels may make one of more emotionally reactive which could eventually positively impact the development of ASPD. For females, lower income helps to predict ASPD development and even some other personality disorders like borderline personality disorder (Byrd et al. 2019). Similar results were echoed by McGrath and colleagues (2012) when it came to cases of abuse for men or women. Abused women with high functioning MAO-A genes were much greater predictors of antisocial behavior than their levels of MAO-A functioning. Mothers with high MAO-A genes may be less sensitive to stress (Kolla et al. 2014).

Fergusson and colleagues conducted a meta-analysis that looked at a twin study and the impact of one's upbringing and their biological history had on their psychopathology. Researchers found that one's personal biology and their non-shared upbringing were both of great significance in the development of ASPD. A shared environment had limited influence on the development of ASPD. Genetic influence related to serotonergic and dopaminergic development have been especially important to researchers in understanding ASPD, particularly involving MAO-A activity. It also has been found to impact the development of other disorders (Fergusson et al. 2011).

Conclusion

In an environment with abuse, neglect, and violence, the evolutionary advantages of ASPD may be much greater than that of altruism. Children who grow up in a home surrounded by violence may be more likely to survive by embracing violence than by being passive towards violence. Unfortunately, as the child grows older, ASPD becomes a maladaptive technique of functioning outside of a criminal enterprise (Del Giudice and Ellis 2016). For these reasons, it may be expected

that MAO-A levels that impact antisocial behavior may be managed by the environment.

Cross-References

- [Antisocial](#)
- [Antisocial Personality Disorder](#)
- [Criminal Behavior](#)
- [Serotonin and Dominance](#)

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Monogamy

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Synonyms

Exclusive pair mating; Pair bonding

Definition

A mating system in which a single male and female form a pair-bond to produce offspring together for a significant period of time (at least one breeding season).

General Considerations

The term “monogamy” has been used to describe a variety of mating systems (Reichard 2003), but typically refers to specific affiliation with one mate, biparental care, and extra-pair aggression (territoriality and mate-guarding). Monogamy is rare in insects, fish, amphibians, and reptiles, but most avian species form monogamous pair-bonds. It is important to distinguish social monogamy, involving social affiliation in the context of pair-bonding, from genetic monogamy, with parentage confined to the socially bonded pair (Reichard 2003). Genetic monogamy is rare compared even to social monogamy (Reichard 2003). The advent of accurate genetic testing methods revealed that many species assumed to be genetically monogamous due to close pair-bonding, were not genetically monogamous (e.g., Quinn et al. 1987).

Traditional explanations for the evolution of monogamy have focused on the importance of biparental care to the growth and survival of offspring (Lack 1968, Wittenberger and Tilson 1980). Logically, if the benefit of biparental care to offspring is high enough (relative to uniparental care) to exceed the reproductive output expected by either sex by desertion, then neither sex should desert.

Later hypotheses focused on a variety of other factors. For example, in their classic paper on mating systems, Emlen and Oring (1977) argued that environmental constraints might limit the ability of one sex (particularly males) to monopolize multiple mates. They focused on the spatial and temporal distribution of females. For example, if females are highly dispersed, then males may be unable to monopolize more than a single female due to constraints on the size of territory that can be defended. Komers and Brotherton (1997) developed a related hypothesis: that when females are solitary and defend a small home range, males may choose to defend only a single female as a risk reduction strategy. Some large scale comparative analyses have lent support to this hypothesis as a general explanation for mammalian monogamy (Lukas and Clutton-Brock 2013).

Another influential hypothesis is that the benefits of protection from infanticide to both females and males may have favored the evolution of monogamy (Van Schaik and Dunbar 1990). This hypothesis has also received some support from comparative analyses, although this remains controversial.

Davies (1989) argued convincingly for the key role of female-female aggression (in addition to male-male aggression) in the context of sexual conflict over parental investment as a key factor affecting the evolution of monogamy. Gowaty (1996) also focused on sexual conflict, highlighting constraints on females as a key factor influencing monogamy. In her “constrained female hypothesis,” which focused on sexual conflict, she argued that all females would benefit from mating with males of the highest genetic quality (and by cuckolding their mates in most cases), but that males of low genetic quality attempt to constrain females from extra-pair matings through helpful coercion (e.g., provisioning), aggressive coercion (e.g., mate guarding), and “resource brokering” (e.g., control of access to critical resources). More recently, there has been increased attention to the potential role of sexual conflict in driving monogamy in a variety of systems.

This is not a comprehensive list of the hypotheses proposed to explain the evolution of monogamy, and as Reichard (2003) argued, it is likely that there have been multiple distinct evolutionary pathways to monogamy in different lineages.

Genetic, Hormonal, and Neural Mechanisms

Prairie voles have been a model mammalian system for the study of monogamy. This species is adapted to life in the harsh environments of the grasslands of the central United States. Early studies on this species revealed male and female pairs sharing nests and having overlapping home ranges (reviewed in Ophir et al. 2012). A key component of monogamy is the phenomenon of pair-bonding, in which a long-lasting preferential

association is developed between two partners, typically involving selective contact, social affiliation, mate-guarding, and copulation. In the lab, prairie voles develop strong pair-bonds with intensive biparental care and partner preferences, consistent with monogamous pair-bonding (reviewed in Ophir et al. 2012).

A series of studies have begun to reveal the hormonal, neural, and genetic mechanisms underlying monogamy in this species. Vasopressin and the vasopressin receptor locus appear to play crucial roles in regulating male pair-bonding, contribution to parental care, and monogamy (Young and Wang 2004). For example, some paternal care behaviors are associated with variation in a microsatellite region upstream of the vasopressin receptor gene, with long alleles showing increased expression. Manipulation of the expression of the vasopressin receptor in the brain of male voles (and mice) increased partner preference for partners in pair-bonds (reviewed in Young and Wang 2004).

In females, oxytocin plays an important role in female pair-bonding and monogamy. The monogamous prairie vole (and pine voles) show higher densities of the vasopressin receptor (in males) and the oxytocin receptor (especially in females) in specific brain regions, compared to promiscuous species like the montane vole (Young and Wang 2004). Recent research has demonstrated that the concentration of oxytocin receptors in specific regions of the brain is associated with monogamous behavior (Ophir et al. 2012). Research suggests that a “pair-bonding neural circuit” may coordinate the effects of vasopressin and oxytocin via a dopaminergic-mediated reward system associated with the mesolimbic network (Young and Wang 2004).

Okhovat et al. (2015) investigated the genetic, hormonal, and neural correlates of variation in degree of monogamy in the field. They found that variation in extra-pair mating was associated with lower levels of vasopressin receptor expression in regions of the brain associated with spatial cognition and memory (e.g., the retrosplenial cortex). Genetic analysis of the receptor genes revealed variation associated with enhancer regions likely to influence levels of gene

expression, suggesting that unfaithful males have poor spatial memory and may consequently range more widely. This trait appears to have both costs and benefits, as males with the “wandering” variant are more likely to engage in extra-pair copulations, yet are in turn more likely to be cuckolded. Molecular evolutionary analyses provide evidence for the footprint of balancing selection at the vasopressin receptor locus variants, which is consistent with the possibility of a tradeoff in which fitness varies with the environment. Okhovat et al. (2015) suggest that lower receptor expression may be favored when densities are high, allowing males to take advantage of readily available opportunities for extra-pair copulations. In contrast, low densities may favor a more monogamous strategy of stable pair-bonding and mate guarding.

The neural circuits and hormonal mechanisms that influence pair-bonding and monogamy in prairie voles may be similar to mechanisms affecting affiliation and love in human mating systems (Ophir et al. 2012). For example, oxytocin has been demonstrated to affect levels of trust in human interactions (Zak et al. 2005), as well as other important components of social cohesion.

Ecological Factors Driving the Evolution of Monogamy

While it has been difficult to identify the ecological factors associated with the evolution of monogamy, progress has been made on this issue in some taxonomic groups. For example, research on a species of South American poison frog has revealed that a specific ecological factor is likely to have driven the evolution of both biparental care and monogamy.

In the South American poison frogs *Ranitomeya imitator* and *R. vanzolinii*, clutches are placed in arboreal oviposition sites (Brown et al. 2010). Males attend clutches and carry tadpoles singly, placing them in small phytotelmata (leaf axil pools). During development, tadpoles are fed with trophic (unfertilized) eggs, and males lead females to each phytotelmata while calling and physically courting them. Genetic

analyses on *R. imitator* revealed the first example of genetic monogamy in an amphibian (Brown et al. 2010; Tumulty et al. 2014). Observations revealed that *R. imitator* uses much smaller pools than a closely related species with male-only parental care with a promiscuous mating system (*R. variabilis*). Translocation and removal experiments in the field demonstrated that both the female and the male make crucial contributions to tadpole growth and survival in *R. imitator* (Brown et al. 2010; Tumulty et al. 2014), revealing the key interaction between pool size and the importance of biparental care.

A complementary comparative analysis across all frogs provided further evidence for the effect of pool size in driving increased levels of parental care in anurans, and for a strong association between the evolution of egg-feeding and biparental care in small pools (Brown et al. 2010). This result is consistent with the argument that the change to using small phytotelmata for breeding drove the evolution of biparental care and monogamy in *R. imitator* (Brown et al., 2010). The increased biparental investment required to raise tadpoles in small nutrient-deficient pools apparently makes mate desertion an unprofitable strategy for *R. imitator* (Tumulty et al. 2014).

Comparative Analyses in Vertebrates

The factors driving the evolution of monogamy in other taxa continue to be the subject of considerable debate. The value of biparental care to offspring has repeatedly been proposed as a key factor favoring monogamy in birds (e.g., Lack 1968), although this is not universally accepted. There is comparative evidence for an association between enhanced levels of parental care and paternity certainty in birds, although cause and effect is not clear. In fish, there are a variety of hypotheses concerning the evolution of monogamy (reviewed in Whiteman and Cote 2004), but no general agreement that any one explanation is valid for all (or most) taxa. In an analysis of 2545 mammalian taxa, Lukas and Clutton-Brock (2013) found that monogamy evolved from solitary female ancestry in which females occurred at

low density and had non-overlapping home ranges. Under these circumstances, males may achieve higher reproductive success by guarding a single female, rather than attempting to patrol the ranges of several females (Emlen and Oring 1977; Komers and Brotherton 1997; Brotherton and Komers 2003).

Monogamy tends to be rare in mammalian species, but is more common in primates than in other mammalian clades. Comparative analysis supports the hypothesis that the risk of infanticide was a key factor driving the evolution of monogamy across primates (Opie et al. 2013), although this conclusion has been disputed. In a comparative analysis across 230 species of primates using a Bayesian likelihood framework, Opie et al. (2013) found significant associations between social monogamy and female ranging pattern, male infanticide and male parental care. However, only male infanticide typically precedes the evolution of social monogamy. Opie et al. (2013) propose that infanticide may have been a key factor leading to pair-bonding early in the human lineage, followed by increased paternal care.

Pair-Bonding and Monogamy in Humans

The evolution of monogamy in human societies is a contentious topic, partly because of uncertainty regarding the reconstruction of ancestral behaviors from paleontological and comparative data, and partly because biologists and anthropologists do not always use the same definition when using the term monogamy. Ethnographic, historical, archaeological, and paleontological data indicate that human mating systems have been highly variable over the course of human history, although monogamy does appear to have been an unusually common social arrangement during much of human history. Phylogenetic reconstructions of pair-bonding and marriage practices across human hunter-gatherer societies suggest that monogamous pairings are an ancient practice (Walker et al. 2011), as do some paleontological reconstructions of ancestral traits. While it is likely that some level of polygamy characterized ancient humans (as it does traditional cultures and

some modern societies), ancestral state reconstruction and other evidence supports the argument that the mating system was characterized by monogamy and low reproductive skew (Walker et al. 2011). Also, arranged marriages in the context of exchange between kin groups (Chapais 2013) are probably an ancient (ancestral) practice in the humans. However, this system of reciprocal exchange (managed by relatives) is unlikely to have evolved until after biparental care and long-term investment in offspring became established.

Any attempt to explain human monogamy must address a large number of unique peculiarities that characterize this lineage. These include: long juvenile period, concealed ovulation, menopause, extensive paternal care, language use and advanced intelligence, coordinated intergroup aggression, among many other traits (Alexander and Noonan 1979).

Richard D. Alexander, in a series of seminal papers, developed a detailed argument concerning the role of monogamous pair-bonding in the evolution of the human social systems, relating monogamy to many of the traits that uniquely characterize the human lineage (e.g., Alexander and Tinkle 1968, Alexander 1979, Alexander and Noonan 1979). Alexander argued that the human lineage was unique in the degree to which members engaged in within-group cooperation to facilitate effective between group competition (Alexander and Tinkle 1968, Alexander and Noonan 1979). This kind of competition is characteristic of chimpanzees as well as human hunter gatherers but is more complex, hierarchical, and extreme in the human lineage.

Alexander argued that females were able to develop and maintain consort relationships with individual males within multimale/multifemale groups, in part through the evolution of concealed ovulation (requiring long-term association and repeated copulation on the part of the male to ensure paternity). These consort relationships benefitted the participating males through paternity assurance and by providing the opportunity for providing effective investment in the male's own offspring. They argued that this would provide benefits to the female in the form of

investment by the associated male, including (possibly) protection from aggression or infanticide by other males. Strassmann (1981) argued cogently that this hypothesis was likely to apply specifically to low status males, as high status males would have much higher incentive to engage in a polygynous mating strategy at the expense of investment in any single female or her offspring. A key issue in explaining the evolution of monogamous pair-bonds is why males would invest in protecting a single female and caring for her offspring as opposed to investing in acquiring further matings (Gavrilets 2012), an issue that Strassmann (1981) addressed directly.

The obvious problem with this hypothesis is that dominant males should break up these exclusive associations between females and subordinate males and mate with the females themselves to enhance their own reproductive success. However, following Alexander and Tinkle (1968), Alexander and Noonan (1979) argued that as intergroup competition increased in importance among rival groups in the human lineage, this enhanced the value of subordinate males to dominants with groups, imposing constraints on the optimal levels of despotism and reproductive skew that could be imposed by dominant males at the expense of subordinates. Alexander (1979) coined the term "Socially Imposed Monogamy" (SIM) to describe this trend. This type of monogamy stood in contrast to what Alexander (1979) referred to as "ecologically imposed monogamy," in which environmental conditions are so harsh that males are unable to co-exist with more than a single female and her offspring in a single territory.

I note here that the idea that pair-bonding may frequently have developed in the context of protection of offspring from infanticide (as supported by comparative analyses across primates: Opie et al. 2013) is not inconsistent with the hypothesis developed by Alexander and Noonan (1979) and Strassmann (1981) for early humans. Certainly, females in multifemale/multimale groups would benefit from protection from dominants who might kill their offspring if there was a significant probability they were sired by another male, and subordinate males might benefit from protecting

the offspring of a female that they were able to mate with. Dominant males might be reluctant to force the issue if subordinates were valuable in intergroup aggression, as posited by Alexander and Noonan (1979).

Using a game theoretic model, Gavrilets (2012) argued that previous hypotheses focused on communal care, mate guarding, and mate provisioning did not have viable mechanisms promoting the evolution of pair-bonding, but that a model incorporating male heterogeneity, assortative mating, and female choice for subordinate paternal males did. This model bears striking resemblance to the hypothesis developed by Strassmann (1981) but does not explain why pair-bonding is tolerated by dominants. Gavrilets (2012) posits that the combination of provisioning as a profitable strategy for subordinate males, and male preference for such provisioning, is sufficient to drive the evolution of pair-bonding. Yet dominant males in primate societies are quite capable of (and intent on) breaking up consortships and claiming paternity for themselves. In this context, Alexander's (1979) hypothesis provides a key missing element: the effect of intergroup competition as a potent incentive to dominants to concede reproduction to subordinates.

Recently, Chapais (2013) developed a comprehensive theory of the sequential evolution of human societies with a focus on monogamy and kinship alliances within and among groups, using a phylogenetic approach and logical arguments concerning likely trajectories based on evolutionary ecological considerations. Alexander (1979) proposed that the ancestral mating system of the common ancestor of humans and chimpanzees was probably multimale/multifemale groups, as found in chimpanzees. Chapais (2013) was skeptical of this idea, arguing instead for multimale polygynous units on the basis of parsimony in comparison with other primate social systems. However, this argument ignores the possibility of a gradual transition from multimale/multifemale promiscuity through the gradual concession of reproductive access to subordinates in the context of increasing intergroup competition.

With specific reference to the transition to monogamy in early human groups, Chapais (2013) proposed four possible explanations (starting from an ancestral state involving groups of multiple one male/multifemale units). Two hypotheses (increasing costs of paternal care and increasing difficulty of herding more than a single female) apply specifically to groups comprised of one male/multifemale units. The other two do not assume this structure. One idea is that dominants face a trade-off when suppressing or displacing subordinates, because subordinates are of high value to dominants for their support in the context of intergroup competition. This is precisely the hypothesis developed by Alexander (discussed above).

The adoption of increasingly sophisticated weaponry may have had a leveling effect on within-group relationships, making it more difficult for dominants to suppress or displace subordinates (Bingham 1999). There is a variety of evidence supporting the leveling effects of (offensive) weaponry (reviewed in Summers 2005). However, this effect is likely to have followed rather than preceded the rise of intergroup competition, which was probably the key selection pressure favoring the development of sophisticated weaponry in the first place (Alexander 1979).

Chapais (2013) argued that once the transition to monogamy was complete, it set the stage for increasing cooperation between mating pairs. One important factor in this context may have been economic collaboration in the context of food acquisition, preparation, and consumption. Wrangham (2010) proposed that cooking rendered food a highly valuable resource, which could have favored the evolution of pair-bonding itself, as females might have required male protection to guard them against other males, in exchange for food. Chapais (2013) argued that monogamy probably predated the invention of cooking but was likely to have been a major force favoring economic cooperation between mated pairs. Chapais (2013) also argued that increasing costs of parental care may have favored increasing male contributions to biparental care. He did not specify the reasons for these increasing

costs, but this possibility fits in very well with Alexander's argument that the balancing act between intergroup competition and within-group cooperation would strongly favor increased intelligence and increasing parental investment in producing high-quality offspring (Alexander 1979, 1989). Chapais (2013) goes on to argue that the establishment of monogamy would have dramatically enhanced cooperation between multifamily groups, due to the development of patrilineal kinship ties through the exchange of females between groups in the context of male philopatry. This is likely to have had a major effect on human social evolution.

Whatever level of monogamy obtained in early humans, the advent of agriculture led to major changes, with many large, hierarchical societies characterized by extreme despotism and polygyny (Betzig 1986). This rise corresponded closely with a sedentary lifestyle, ecological constraints in the form of dependence on (limited) fertile soils, opportunities for accumulation and preservation of wealth, and cross-generational inheritance of resources that characterized the transition to agriculture. However, over the course of more recent human history levels of reproductive despotism began to decline, to the point that the majority of people currently live in societies that consider monogamous relationships to be the norm. Alexander (1979) argued that increasing levels of intergroup competition eventually overcame the factors favoring despotism unleashed by the advent of agriculture and forced despotic (and highly polygynous) rulers to concede more reproduction to subordinates in society, in order to obtain the allegiance of those subordinates in competition against other groups. He argued that intergroup competition increased in intensity in step with the rise of organized nation-states. Betzig (1986) argued instead that the increasing value of specialized skills and labor driven by the rise of industrialization made the value of skilled workers to rulers high enough that they were willing to reduce reproductive monopolization in order to retain such workers in the workforce. Both Alexander (1979) and Betzig (1986) emphasize "concessions" on the part of rulers as a key factor in the rise of monogamy, although they do

not rule out collective action on the part of subordinates.

MacDonald (1995), in a careful historical analysis of the rise of monogamy in Western Europe, agrees that the two factors emphasized by Alexander (1979) and Betzig (1986) were likely important, but argues that their explanations are incomplete and that at least three other factors played major roles. First, he argues that males of low or middle status may have acted collectively to effectively impose social monogamy (as a rule designed as an opportunity-leveling mechanism across males). Second, in some societies women may have been able to exert sufficient political power to push the society toward rules requiring social monogamy (note that polygyny often imposes a high cost on females). Finally, the Christian Church, as a hierarchical nexus of political power that was often in competition for power and resources with the traditional political elites (i.e., traditional royalty), frequently had reason and opportunity to impose rules that restricted the royal power and dominance, in some cases by restricting polygyny and hence the size of royal families. MacDonald (1995) provides an in-depth defense of the importance of these three factors, using a careful analysis of the historical record. He concludes that, while each of the five factors affecting the rise of monogamy is logical from an evolutionary perspective, their interaction is complex and historically contingent, making it difficult to predict exactly which societies would develop monogamy.

An additional factor potentially favoring monogamy is lineage competition. The importance of cross-generational inheritance of wealth on the ability to successfully establish and maintain a family increased with the advent of increasing societal size and complexity (reaching extremes following the demographic transition), and long-term lineage persistence came to depend on high investment in the joint offspring of monogamous pairs, potentially providing a further impetus toward monogamy (reviewed in Low 2000).

A variety of other theories for the evolution of monogamy have been discussed in the recent literature, although none have gained widespread

acceptance. For example, Bauch and McElreath (2016) developed a model of the interaction between sexually transmitted disease and socially imposed monogamy in the context of group size. The evolution of monogamy in humans has been and remains a contentious issue, and vigorous debate about the topic is likely to continue in the scientific (and popular) literature for the foreseeable future.

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Monotropy

► [John Bowlby](#)

Mood

► [Physical Health](#)

Moral

► [Function of Morality \(Haidt\)](#)

Moral Behavior

► [Morality](#)

Moral Codes

► [Social Values](#)

Moral Concerns

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Synonyms

[Bioethics](#); [Eugenics](#)

Definition

Moral concerns describe bioethical issues that have been raised concerning the application of human

biotechnologies, such as abortion, in vitro fertilization, embryo selection, preimplantation genetic diagnosis, and germ line gene therapy, that collectively enhance reproductive choice.

Introduction

The *reproductive choice revolution* has emerged as a voluntary, market-based phenomenon. It presents different moral issues to those associated with the “first-wave” eugenics movement initiated by the Victorian-era polymath Sir Francis Galton. Moral concerns are changing as biotechnology, especially in vitro fertilization (IVF) with preimplantation screening, reduces reliance on abortion as a method of curbing genetic disease, this historically having been an obstacle to Christian approval. Christian opposition to abortion was also an important source of criticism leveled against certain proponents of first-wave eugenics, such as Margaret Sanger. Presently, the Catholic Church continues to condemn the discarding of single-cell embryos as sinful, based on the premise that the right to life begins with the setting of the genotype at conception.

One set of moral concerns raised in response to new *reproductive technologies* (which include IVF and preimplantation genetic screening, among others) involves the existing and rapidly growing market demand for techniques that maximize informed reproductive choice. Other concerns are prospective – the risks posed to children and society by the premature and uneven uptake of reproductive technology. Both sets of issues raise questions, which for many contemporary bioethicists are made sensitive by the historical experience of certain countries that adopted legislation congruent with the first-wave eugenics movement, such as sterilization laws – the issue therefore being: Can government involvement in human reproductive affairs ever be justified?

Review

The Reproductive Technology Market

As early as the 1980s, evidence that consumer demand was driving reproductive technological

innovation was reported by historian Daniel Kevles (1995/1985). The trend had been evident in the genetic counseling movement, in which hospitals offered voluntary advice to parents desiring children. The practice remains widespread, perhaps motivated by the same “eugenic impulse” that influenced the development of medical genetics (Comfort 2012). This motivation is to be expected if evolved strategies for passing on “good genes” are part of humans’ evolved psychology. By the end of the century, the IVF market was booming: a multibillion dollar worldwide industry that offers clients add-ons that are, in the parlance of Galton, “negative eugenics” (i.e., which curb the proliferation of undesirable traits) in the form of preimplantation screening of embryos as a means of avoiding genetic disease. The demand for “positive eugenics” (i.e., which promotes the proliferation of desirable physical or psychological traits) is likely to follow on from the already established negative eugenics, barring multilateral agreements that prevent “procreative tourism” aimed at circumventing restrictive laws (Monni et al. 2006).

Premature and Uneven Uptake of Reproductive Technology

As the sciences of genetics and biosocial sociology are still developing, there is a risk of making maladaptive choices based on bad science. This risk is downplayed by some bioethicists, such as Ingmar Persson and Julian Savulescu (2014) and George Church (2014), who support parents’ right to determine their children’s genome using the full repertoire of reproductive technologies, including the emerging capacity to edit the genome. This view has been criticized based partly on the danger of technological immaturity.

One risky application is recommended by Savulescu and Peter Singer, who propose using gene editing to eliminate ethnocentrism. They envisage producing individuals who do not favor their own children or ethnic groups. Arguably, such an outcome would dissolve the family as a locus of strong interpersonal bonds and prove maladaptive by reducing motivation to invest in genetically similar individuals, whether kin or co-ethnics.

The risk of premature uptake is increased by uncertainty about what is meant by “desirable.” It

is clear from the writings of first-wave eugenicists that “desirable” was synonymous with social good, the aim being to promote civilization-enhancing traits, such as communal orientation and altruism. Modern conceptions of “desirability” may revolve around self-interest to a greater degree. It has been argued that modern populations are relatively more individually selected than historical ones (which tended toward group selection; Woodley of Menie et al. 2017). In as much as the regime of individual-level selection that started in the Late Modern Era has led to *dysgenic consequences* (such as declining general intelligence; Woodley of Menie et al. 2017), conscious control of genetics could facilitate maladaptive outcomes, especially if the sorts of traits deemed “desirable” under the present selection regime enhance individual-level competitiveness in a non-pro-social fashion, such as via the inadvertent promotion of psychopathic traits, a concern first raised by Cattell (1987). Indeed, potentially consistent with this concern are the findings of Latham and von Stumm (2017), who, in a survey of 142 mothers found that they considered extraversion (whose facets include sensation-seeking and dominance) to be more desirable than the potentially more group selected personality dimension of conscientiousness (whose facets include dutifulness and self-discipline) and intelligence in their offspring.

Good science can also engender moral concerns. The uneven uptake of reproductive technological services, including those proven safe for individuals, could reflect and exacerbate existing inequalities. A gynecologist providing preimplantation screening with IVF has noted that the wealthy can find ways to access reproductive technology, but the poor must rely on abortions (Monni et al. 2006). Noah Harari (2015) argues that wealthy individuals will get a head start in using reproductive technologies and other enhancements, giving their children genetic as well as financial advantages. Other early beneficiaries will include slow life history strategists, if their ‘genetic quality’ impulse includes treating preimplantation screening as a form of parental investment. Uneven uptake could lead to structural biological inequalities (de facto castes) between the offspring of those who can afford

access to such technologies and those who cannot. Assortative mating alone can potentially produce dramatic divergence in average IQ (Harpending and Cochran 2015). Harari envisages these castes as a step toward speciation. Even without such fundamental change, castes would risk fracturing democratic communities by impeding social mobility (reviewed in Salter 2015a).

Can Government Involvement in ‘Eugenics’ Be Justified?

First-wave eugenics failed ethically in the eyes of our contemporary, relatively more individually selected population, when it involved curtailment of civil liberties, most notoriously through involuntary sterilization. In that light, socialized eugenics is a known moral risk. Yet government regulation of the eugenics market seems necessary to discourage dangerous choices and to universalize benefits, especially when considered in terms of the regime of individual-level selection that predominates in the contemporary West. Regulation is a relatively passive stance compared to the active government promotion of eugenics responsible for transgressing individual-level liberties in the past. It has been argued that the emerging reproductive technology market that characterizes the modern “second-wave eugenics” may be safest when active citizens are regulated by relatively passive governments (see Salter 2015b).

The scope for ethical government initiative in driving reproductive choice may be small. Government-directed reproductive outcomes may be most acceptable as a secondary effect of policies incidental to this objective or when the latter are sufficient to justify the policy.

Conclusion

The imposition of reproductive choices typical in first-wave eugenics has been replaced by a rapidly growing consumer-led market. The new reproductive technologies, most notably IVF with pre-implantation genetic screening, have shifted moral concerns from civil rights to issues of equality of market access and the potential dangers, to individuals and society, of premature and

uneven uptake. It appears likely for ethical reasons that governments will regulate the reproductive choice market, however their role is likely to be less direct than in the past.

Cross-References

- [Eugenics](#)
- [Moral Instincts](#)

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Moral Constructivism

- ▶ [Modern Moral Relativism](#)

Moral Conventionalism

- ▶ [Modern Moral Relativism](#)

Moral Development

- ▶ [Theory of Moral Development](#)

Moral Dispositions

- ▶ [Moral Instincts](#)

Moral Domains

- ▶ [Evolved Moral Foundations](#)

Moral Emotions

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Synonyms

[Other-focused emotions](#); [Pro-social emotions](#)

Definition

“Moral” emotions are those thought to relate to the capacity for human morality. Examples of

such emotion types include disgust, shame, pride, anger, guilt, compassion, and gratitude.

Introduction

Emotion can be defined with reference to its input conditions, its characteristic output, and the internal mechanisms that mediate input and output. It is generally accepted that at least some emotion kinds are adaptive products of evolution. An appraisal that the environment affords an opportunity or threat is the input condition for such emotion kinds, and the output is some behavior that (if successful) constitutes an adaptive response to the situation. The internal mechanism prompting the adaptive action is a coordinated set of changes in appraisal, expression (facial, vocal), action tendencies (fleeing, threat displays), feeling, and physiological arousal that together explain how the adaptive response takes place and the characteristic internal sensations associated with the emotion.

Moral emotions are those emotion types linked with our capacity for moral thinking or moral action. They are thought to either (i) enable a capacity for moral action or (ii) contribute to the project of grounding or justifying moral norms (i.e., normative statements that define moral obligations). Section “[Grounding Moral Norms](#)” discusses the relationship between moral emotions and the project of grounding moral norms. Section “[Evolved Emotions](#)” introduces the idea that (at least some emotion types) evolved for their adaptive significance. Section “[Moral Emotion Types](#)” discusses some putative moral emotion types that have been studied in recent years.

Grounding Moral Norms

Finding some sort of nonarbitrary ground for moral norms is the traditional “holy grail” of moral philosophy. Virtue ethics, divine command theory, rationalism, and sentimentalism are four broad traditions of thought that engage in this project. Divine command theory takes moral

norms to be grounded by a heteronomous force, namely, the Christian conception of God. Virtue ethics, a tradition initiated by Aristotle in the *Nicomachean Ethics*, grounds the virtuous (good) action of a thing in its ability to perform its “natural” or “proper” function (in the human case, this capacity is the exercise of rationality; see Korsgaard 2008). The rationalist tradition, exemplified by Kant’s *Groundwork for the Metaphysics of Morals* (1785/2003), sees moral norms grounded in autonomous reason – individuals rationally reflecting on the norms appropriate to the situation at hand.

None of the accounts just described support the idea that emotion can, on its own, ground moral norms. It is within sentimental moral theories, however, that emotions perhaps play the most central role in a more modest project, namely, explaining our *capacity* for moral behavior. Sentimentalism is perhaps best understood in contrast with rationalism. Rationalism claims that it is our capacity to reason, not our capacity to feel (i.e., to experience emotion), that undergirds the human capacity for moral behavior. The rationalist approach has a long and venerable philosophical heritage. Plato’s *Timaeus* (360 BCE) presents a myth in which gods invent human heads whose distinctive faculty is reason. Recognizing the heads requires bodies – full of unbridled desires and passions – to help them move through the world. The struggle to live a moral human life is expressed as the struggle of the head to control the body through the sublimation of the body’s passions toward virtuous ends.

In the seventeenth and eighteenth centuries, the sentimentalists Hobbes and Hume instrumentalized practical reason. Hume, for instance, demoted reason, describing it as a “slave of the passions” that can “never pretend to any other office than to serve and obey them” (Hume 1738, p. 462). Hume’s point was that the passions determined which ends were desirable, while reason acted as a conscientious servant, formulating plans to deliver those ends. Moral knowledge was attained by an “immediate feeling and finer internal sense,” rather than a “chain of argument and induction” (Hume 1777, p. 2). For the

sentimentalists, reason alone can enable the inference that a particular action will lead to an avoidable loss of human life, but it cannot tell us whether this loss ought to be avoided.

The focus of Hume (and Hobbes before him) was on casting emotion as (i) a causal antecedent to moral judgment and (ii) a sufficient ground for the legitimacy of moral claims. But this is not to say that sentimentalism offers succor to the moral realist who wants to ground morality in facts extraneous to our nature as embodied beings. We now set aside this latter project and return to the more modest project of explaining our capacity for moral behavior and decision-making and how we foster conditions conducive to its exercise.

Since the Enlightenment, rationalism has exerted an influential hold within moral philosophy. The rationalist tradition takes cool-headed reason to represent the ideal conditions for moral decision-making. Kant (1785) is the canonical representative of this view and has exerted a tremendous impact on modern moral and political philosophers (e.g., Rawls 1971), many of whom have attempted to follow Kant by providing a foundation for ethics derived from the meaning of rationality itself. However, rationalism has also dominated much of twentieth-century psychology. Kohlberg’s work was a sustained attack on “irrational emotive theories” (1971, p. 188), and his cognitive-developmental theory was an important part of the cognitive revolution. More recently, neo-sentimentalists have claimed that moral judgments are produced by automatic intuitive or emotional processes. Cushman et al. (2010) describe two related ideas associated with neo-sentimentalism in contemporary literature on moral psychology. The first “claims that moral judgment takes the form of intuition, accomplished by rapid, automatic and unconscious psychological processes,” while the second “claims that moral judgment is driven primarily by affective responses” (p. 47). Empirical evidence cited in favor of the first claim focuses on demonstrations of people’s inability to articulate a rational basis for many of their most strongly held moral beliefs. Evidence favoring the second challenge draws on neuroscientific data relating to localized brain regions (Ciaramelli et al. 2007) but also

includes behavioral studies of moral judgment that invoke affective manipulations.

Two influential neo-sentimentalist proposals have come from Damasio (2006) and Haidt (2001) in recent years. Both figures emphasize the importance of emotional and/or intuitive processes in moral decision-making. In particular, both claim that moral judgments are produced by automatic intuitive or emotional processes. They also claim that, when we think we are deliberating about the rightness of a given moral principle, we are not so much reasoning from first principles as we are engaging in post hoc rationalization. That is, we are simply reasoning in whatever way will support the emotionally driven judgment we have already pledged allegiance to. Haidt's social intuitionist model aims to explain how this post hoc rationalization occurs. Haidt claims that "moral dumbfounding" occurs when a judgment, solution, or other conclusion appears suddenly and effortlessly in consciousness, without any awareness by the person of the mental processes that led to the outcome.

Proponents of neo-sentimentalism need not be read as claiming that emotional and/or intuitive processes actually ground or justify specific moral claims. Rather they can be seen as showing that the capacity to feel certain emotions (i.e., moral emotions) is tied up with our *capacity* to formulate moral norms (see Kitcher 1994 for discussion). Despite its popularity, neo-sentimentalism has met with skepticism, for instance, by champions of "universal moral grammar" (Hauser 2007). Hauser and others have claimed that moral judgment requires computations performed over representations of agents, intentions, and causal relationships in order to output judgments of right and wrong. Information processing of this sort must precede an emotional response, so the argument goes, and thus it must be that moral judgment leads to emotion, not the other way around. One promising way to make progress in this debate about the role emotions play in our capacity to be moral is to explain the adaptive function of particular emotion types in relation as facilitating conformity to moral norms. The remainder of the article focuses on this project. First, we motivate the claim that emotions evolved.

Evolved Emotions

Evolutionary approaches to emotion describe them in terms of the function they currently perform or performed in our ancestral past. The claim that at least some human emotions evolved and are shared with lower mammalian species is now uncontroversial and began with Darwin's *Expression of the Emotions in Man and Animals* (1872). Darwin himself defined emotions as subjective feelings. Following Herbert Spencer, Darwin distinguished emotions as feelings caused by external states, in contrast to feelings caused by bodily states, such as hunger and pain. Later evolutionary theorists have preferred behavioral and physiological definitions of emotion, and so consequently Darwin's theory of emotional expression has been seen as a theory of the emotions themselves. The central principle Darwin proposed to explain the evolution of expression was the "principle of serviceable associated habits." Darwin believed that instinctive behaviors derive from habits. The consistent acquisition of the same habit for many generations causes it to become hereditary, or instinctive, as a result of the inheritance of acquired characteristics.

The founders of ethology saw themselves as the direct heirs of Darwin's work on mental evolution (Lorenz 1965). They retained Darwin's principles but reinterpreted them to fit the theory of evolution as it emerged in the 1930s in the "modern synthesis" of Darwinism and Mendelian genetics. The principle of serviceable associated habits was transformed into the ethological concepts of "ritualization" and "derived activity" (Tinbergen 1952). Derived activities are behaviors that originally evolved for one purpose but were later selected for another purpose. Ritualized behaviors are derived activities that originally evolved to fulfill some practical function but were later selected to function as signals. For example, grimacing in anger may have originally evolved to enable our ancestors to prepare to attack an opponent using their sharp canine teeth. We have evolved such that we no longer have fang-like canines, and yet we still grimace in anger. The derived activities account sees grimacing serving a derivative, signalling

function of indicating that one is angry and that the possibility of attack is imminent. Grimacing was originally selected to enable direct attack, and through this association came to serve a secondary function of signalling to conspecifics the possibility of attack. The concept of ritualization allowed ethology to reconstruct Darwin's principle of serviceable associated habits while avoiding his commitment to the inheritance of acquired characteristics. Darwin's descriptions of the psychological rewards that led to the reinforcement of emotional behaviors are equally plausible as descriptions of the original selective advantage of those behaviors.

Darwin's detailed accounts of human facial expressions were confirmed and extended during the 1960s and early 1970s, and many of his suggested homologies between human and primate facial expressions were confirmed. It became generally accepted that some emotional expressions, the so-called basic emotions, are found in all cultures and have an evolutionary history at least as long as the history of the human species (Ekman 1973). The basic emotions are usually referred to as fear, anger, disgust, contempt, joy, sadness, and surprise, although in normal usage each of these words has a much wider meaning. Each basic emotion corresponds to an "affect program" stored somewhere in the brain. When activated, this program coordinates a complex of actions that include facial expression, autonomic nervous system changes, expressive vocal changes, and muscular-skeletal responses such as flinching or orienting. The concept of an affect program inherits many of the features of the ethological concept of a "fixed action pattern." Both concepts suggest that certain apparently complex behaviors are, in reality, atomic units of behavior that unfold in the same stereotyped sequence whenever they are triggered. The affect programs are controlled by an "automatic appraisal mechanism." This is a specialized neural system that applies its own distinctive rules for stimulus evaluation to a limited set of data derived from the earliest stages of the processing of perceptual information. Considered together, the appraisal mechanisms and affect programs form a cognitive "module" in the sense favored

by more recent evolutionary psychologists (Barkow et al. 1992).

Evolutionary accounts of basic emotions have inspired work on whether "nonbasic" emotions (such as gratitude) may have also evolved (► [Emotion](#)). This work is discussed in the section below with a focus on emotion types for which an adaptive function related to conformity with moral norms is available.

Moral Emotion Types

Considering the unique adaptive functions of different moral emotion types is the basis of a more complex account of how the "suite" of moral emotions has, as a whole, evolved to support the capacity for moral behavior. Below, we consider a number of putative moral emotion types (disgust, shame, pride, indignation, guilt, compassion, and gratitude). We focus on adaptationist hypotheses that relate to obeying rules or socially sanctioned behaviors, or acting so as to benefit others.

Disgust. Kelly's (2011) influential synthesis of work on disgust suggests that the emotion combines a taste-aversion mechanism with a mechanism for avoiding infection and parasitism. Kelly argues that disgust is uniquely human. It is an example of the co-option and developmental entanglement that occurs as an evolving lineage confronts new adaptive challenges and must solve them by modifying existing features. Both elements of the disgust response have homologues or analogs in other species. It is their entanglement that creates a uniquely human emotion. On this account, moral disgust represents a further piece of evolutionary tinkering in which the emotion of disgust was co-opted to help enforce conformity with in-group norms. More recent work accords with this view, with moral disgust described as disgust that evolved to "respond to sociomoral elicitors [...] such as immoral acts" (Russell and Giner-Sorolla 2013, p. 330).

Pride and shame. Although competing explanations of the evolution of pride and shame are extant in the literature, a consensus is emerging. Behaviors homologous to those we associate with pride and shame are components of displays

employed by nonhuman primates (and other mammals) during the negotiation or affirmation of relative rank. We can label the emotions that underlie such displays as “protopride” and “protoshame.” In a competitive environment, the expression of protoshame signals the actor’s acceptance of a subordinate position in a hierarchy. It functions to deflect aggression from the dominant party. The expression of protopride, in contrast, signals the actor’s dominance. Importantly, protopride is a pleasant feeling, while protoshame is unpleasant. Fessler (1999) argues that protopride and protoshame were selected for in primates because they promoted dominance-seeking behaviors, which increased the chances of reproductive success. These emotions are the phylogenetic ancestors of pride and shame in human beings (Fessler 1999, 2004).

However, Clark (2012) has argued that humans retain the ability to experience protopride and protoshame alongside their more sophisticated descendants, pride and shame. Pride and shame are more cognitively complex than protopride and protoshame. They require that the organism has “theory of mind” – the capacity to attribute mental states to other individuals. They also serve a different adaptive function in the relatively cooperative, nonhostile environments human beings inhabit. In such contexts, pride and shame are experienced in response to the actual or imagined assessment of an actor’s behavior by an audience. If the assessment inspires the contempt or pity of the audience, the actor feels shame. If the assessment inspires the envy or admiration of the audience, the actor feels pride. In the cooperative context, then, pride and shame encourage the actor to seek the admiration and envy of others, which in turn encourages them to act in ways that support the well-being of the group (Fessler 1999). In this way, these emotions inspire adherence to socially sanctioned norm-governed behavior.

Anger. Philosophers sometimes draw a distinction between simple or “basic” anger and more cognitively complex varieties such as resentment or moral indignation. Say that a simple form of anger arises in response to feeling a sharp jolt in the back from an unknown cause while

standing in line at the supermarket. The reflex-like expression of basic anger, consistent with a basic appraisal (however implicit) of goal obstruction, is one we likely share with nonhuman species (Ekman 1973). In contrast, resentment or moral indignation is generally understood as accompanied by a more complex appraisal, namely, the judgment another party or parties are worthy of blame (Wallace 2008). In the supermarket example, resentment might only arise upon turning around and seeing that the cause of the jolt in the back was a person indelicately attempting to queue-jump. This case requires making an appraisal that has a more specific content, namely, that the goal obstruction arousing the initial anger has been caused by a third party and that it was wrong of that party to cause it.

An appraisal of this sort is consistent with Rozin et al.’s (1999) association of anger with violations of the standard of autonomy, which refers to concerns about fairness, reciprocity, and the prevention of harm. Anger elicited in this way could have served three distinct adaptive functions. The first is encouraging behavior that is reciprocal and fair (and therefore likely to lead to the survival of the population at large). The second is motivating an aggressive response to hostility, which would have increased the likelihood of the emoter’s survival. The third is that an angry expression would serve as an important social signal of imminent threat, encouraging the opponent to flee the situation.

Guilt. The case of guilt provides a useful example of the role evolutionary game-theoretic scenarios play in establishing adaptationist hypotheses for emotions and thereby connecting them to the moral domain. Modeling such scenarios is especially useful when considering the role of moral emotions in promoting the survival of the group at the cost of the individual. Unlike the case of anger, guilt-prone individuals act so as to benefit the group at a cost to themselves. That is to say that they behave altruistically, even in cases when they do not expect to be caught. Those who feel guilty after a transgression accept punishment readily and even punish themselves. For this reason, one might think that guilt evolved for its benefits to groups, rather than individuals.

Recent evolutionary game-theoretic modeling (Rosenstock and O'Connor 2018) shows that when actors play an iterated prisoner's dilemma and sometimes err, guilt can evolve to facilitate forgiveness and social reparation. Guilt functions in this setting by either ensuring the trustworthiness of apology or by leading apologizers to pay a cost. This model adds to previous literature on the evolution of apology by showing how both emotion reading and costly apology can interact to stabilize guilt, thereby describing the environmental conditions that would allow guilt to evolve.

Compassion and gratitude. Accounts of the evolution of compassion and gratitude build on the literature on biological altruism. In evolutionary biology, altruism refers to an action that benefits another at a cost to the actor (such as sharing food). The evolution of altruism is explained either by "kin selection" (► [Kin Selection](#)) or "group selection" (► [Group Selection](#)). Kin selection proposes that an altruistic gene will be favored by natural selection when it motivates action that confers a fitness advantage to a recipient of the same kin (Hamilton 1964). Group selection proposes an alternative mechanism by which altruism spreads as a trait in a population: altruistic actions (like helping conspecifics on a hunting trip) increase the fitness of the group even though it decreases fitness for individuals. Groups with larger numbers of altruists will be more likely to survive than those with lower numbers, and so altruism will spread as a trait through the mechanism of group selection.

The relation between altruistic behavior and pro-social emotions is a matter of some contest. However, one influential argument by Trivers (1971) claims that compassion (used synonymously with "sympathy") evolved within a complex system of other emotional states (including gratitude, guilt, liking, and anger) to enable nonkin to initiate, maintain, and regulate reciprocal, altruistic relationships (see also Nesse 1990). Within this system of emotions, compassion emerged as a state that motivates altruism in mutually beneficial relationships and contexts. It is an emotional reaction that involves feelings of concern and sorrow for the other party, based on an apprehension of that party's emotional state.

Gratitude is relatively understudied compared with other moral emotions. Like compassion, gratitude motivates altruistic behavior but stems from the appraisal that one has just received help or aid from another, which creates a motivational state to either "return the favor" (call this "direct reciprocity") or "pay it forward" (by helping someone else, also known as "upstream reciprocity"). Experiments show that gratitude in humans fosters pro-social behavior. In particular, the recipient of a favor is more likely to engage in acts of both direct and indirect reciprocity. Recent modeling scenarios by Nowak and Roch (2007) suggest both that "spontaneous" cooperators are outcompeted by gratitude-related upstream cooperators (i.e., that gratitude is a better motivator of cooperation) and, moreover, that upstream reciprocity greatly enhances the level of altruism in a population.

Conclusion

The surge of literature on the moral emotions over the past 30 years (e.g., Haidt 2003) represents a shift away from the (normative) question of what grounds or justifies moral norms and toward the (descriptive) question of what capacity or capacities in human beings enable moral behavior. While these two projects should be undertaken in tandem, the focus on the latter question holds the promise of explaining much of moral behavior by recourse to "instinct-like" emotional capacities that evolved to encourage norm conformity, especially in relation to norms often described using moral language.

While the hypothesis that basic emotions are adaptations is well-established, the hypothesis that "moral" emotions evolved for their role in enforcing norm conformity is more contested. This is so for multiple reasons. One is that the latter hypothesis requires mapping readily observable behaviors (such as cooperating by sharing food) to normative moral concepts (e.g., fairness, generosity, etc.). Another is that establishing that certain emotion-inspired behaviors increase fitness at the level of kin or group selection (e.g., in the case of compassion and gratitude) requires

game-theoretic modeling of change in frequencies of a trait (e.g., cooperation) in a population over time. Finally, establishing how a “suite” of moral emotions may have evolved over phylogenetic time as part of a multilevel selection strategy would require modeling scenarios of multiple behavioral traits that act as proxies for the suite of emotion types under investigation. The next step would require moral psychologists and moral theorists to determine how much of moral behavior can be explained by exclusive appeal to the behavioral traits under consideration. This is an ambitious and valuable task in and of itself but one quite distinct from the project of justifying or grounding moral norms.

Cross-References

- ▶ [Altruism](#)
- ▶ [Emotion](#)
- ▶ [Evolution of Morality](#)
- ▶ [Evolutionary Game Theory](#)
- ▶ [Group Selection](#)
- ▶ [Kin Selection](#)

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Moral Foundation

- [Sacredness/Purity/Disgust](#)

Moral Foundations

- [Function of Morality \(Haidt\)](#)

Moral Foundations Theory

- [Evolved Moral Foundations](#)

Moral Instincts

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Synonyms

[Moral dispositions](#); [Moral senses](#); [Moral sentiments](#)

Definition

Inborn tendencies to act morally and to experience a sense of morality.

Introduction

Over the years, the concept of instinct has drifted in and out of favor in the natural and social sciences and has been defined in many different ways. Here, instincts are defined as natural inborn tendencies inherited by all members of a species to feel, think, and act in particular ways in response to particular internal and external triggers. Evolutionary theorists such as Pinker (2008) have invoked the concept of moral instincts. Moral instincts can be defined in two qualitatively different, but related, ways – (a) as instincts that induce individuals to *behave* in ways that people consider moral and to refrain from behaving in ways that people consider immoral and (b) as instincts that induce individuals to *categorize* certain phenomena as moral and immoral and to make moral judgments. People experience the second kind of moral instinct as positive and negative feelings, intuitions, and ideas that engender a sense of approval and disapproval about certain forms of conduct, desires, motives, character traits, and people. Darwin (1874) referred to them as the moral senses. The challenges faced by evolutionary theorists are to identify the mental mechanisms that dispose individuals to behave in moral ways and to make moral judgments and to explain how these mechanisms evolved. These challenges entail explaining why people feel that they and others ought and ought not to behave in certain ways; why people view certain phenomena as right or wrong, good or bad, fair or unfair, and virtuous or vicious; and why people pass judgment on themselves and others for behaving in ways that uphold or violate moral standards.

Culturally Universal Moral Norms

Anthropologists and other social scientists have concluded that although people from different

cultures may develop different, culturally relative, moral norms, people from all known cultures view particular types of behavior as right and their opposites as wrong. For example, Boehm (2012) found that members of all the hunter-gatherer groups he surveyed considered generosity, group harmony, and cooperation good and excessive selfishness, bullying, murder, lying, cheating, stealing, incest, and adultery bad. In addition to these forms of conduct, other investigators have adduced evidence that people from all cultures view deference to legitimate authority and purity as moral, and their opposites as immoral. In summary, all cultures possess moral norms upholding (a) altruism, (b) support for one's group, (c) fairness, (d) respect for legitimate authority, and (e) purity.

Culturally Relative Moral Norms

Although people from all cultures consider these five forms of conduct moral, cultures differ in the salience of moral norms upholding these forms of conduct, the relative value they attach to each of them, and the particular kinds of social behavior that instantiate them. As Pinker (2008) has pointed out, Western cultures tend to consider moral norms opposing harming others and upholding care and justice as regnant; Japanese cultures tend to elevate norms pertaining to group solidarity; and Hindu and Orthodox Jewish cultures tend to place a high value on purity (e.g., as reflected in dietary restrictions) and authority (e.g., not insulting Mohammad). Other investigators have found that different groups within Western cultures also tend to place different values on different types of moral behavior. For example, liberals tend to value altruism and fairness more than conservatives do, whereas conservatives tend to value group loyalty, authority, and purity equally highly.

Different cultures and subcultures also may classify particular behaviors in different categories, producing cultural and individual differences in the instantiation of moral norms. For example, people may have different conceptions of what it means to help and to harm others and what it

means to treat others justly and unjustly; and they may harbor different ideas about what makes these forms of conduct right and wrong. Investigators have documented notable differences among cultures with respect to moral norms pertaining to sexual conduct, marital unions, preservation of life, and dietary restrictions. In addition, the threshold for the activation of moral instincts tends to be lower for in-group members than for out-group members (Greene 2013), and cultures may differ in the extent to which moral instincts are activated by nonhuman animals.

Theorists such as Haidt (2001) and Pinker (2008) have accounted for the evolution of culturally universal and culturally specific moral norms by suggesting that all people inherit mental mechanisms that endow them with a set of universal, species-specific moral intuitions, just as people from all cultures inherit mechanisms that endow them with the capacity to produce and to understand language. However, in the same way that people from different cultures acquire different languages, people from different cultures instantiate universal moral norms in different ways.

Origins of Instincts to Behave in Moral Ways

Evolutionary theory generates the expectation that instincts to behave morally originated either because they gave early humans an adaptive advantage or as by-products of other adaptations. Evolutionary theorists such as Alexander (1987), Krebs (2011), and Richerson and Boyd (2005) have suggested that the overriding adaptive function of moral instincts is to motivate members of groups to advance their interests in cooperative ways. Moral instincts induce members of groups to resist the temptation to advance their short-term personal interests in ways that diminish the long-term biological and genetic benefits they can reap from upholding the cooperative social orders of their groups. Cooperation can pay off by enabling members of groups to maximize the acquisition of resources, to engage in superior forms of defense,

and to outcompete selfish groups. “Inasmuch as every member benefits from a unified, cooperative group, one expects them to care about the society they live in, and to make an effort to improve and strengthen it similar to the way the spider repairs her web, and the beaver maintains the integrity of his dam. Each and every individual has a stake in the quality of the social environment on which its survival depends” (Flack and de Waal 2000, p. 14). However, in spite of the potential adaptive benefits of cooperation, there is a significant obstacle to the evolution of cooperative dispositions, namely, the conflicts of interest that inevitably occur within cooperative groups.

As expressed by the evolutionary biologist, Alexander (1987), “agreement seems to be universal...that moral (and ethical) questions and problems arise because of conflicts of interest; I have never found an author who disagrees. If there were not conflicts of interest among people and societies it is difficult to see how concepts of right and wrong, ethics and morality, and selfishness and altruism could ever have arisen” (p. 3). Conflicts of interest give rise to moral dilemmas that, if not resolved in cooperative ways, can diminish the reproductive success of all members of a group.

The anthropologist Boehm (2000) has argued that the central adaptive problems that moral instincts evolved to solve stemmed from “competitive dispositions to dominance” and the social conflicts they produced (p. 97). “Morality is the human invention that addresses such problems, and it is based very heavily upon ancestral dispositions. These were the raw materials, out of which moral communities were forged” (p. 97). According to Boehm, “morality is based heavily on social pressure, punishment, and other kinds of direct social manipulation” (p. 82), and the most significant sources of morality are instincts that induce individuals to obey the social norms of their groups and resist the temptation to dominate others. When members of groups succumb to the temptation to resolve conflicts of interest in selfish ways, it disrupts the cooperative order of the group and prevents everyone, including the cheaters, from reaping the benefits of cooperative exchanges.

Origins of Instincts to Behave in Altruistic and Group-Upholding Ways

It is much easier for evolutionary theorists to explain how dispositions to induce others to behave altruistically could have evolved than to explain how individuals acquired instincts to behave altruistically themselves. How could altruistic instincts have been selected if they decreased altruists’ chances of surviving and reproducing? This problem plagued Darwin (1874), who considered evidence of altruism potentially fatal to his theory. Modern evolutionary theorists have offered three main answers to this question: that altruism can evolve through kin selection, group selection, and sexual selection.

Kin Selection

Although Darwin (1874) focused most extensively on the possibility that altruistic instincts could evolve through group selection (see below), he briefly entertained the idea that even if altruistic members of groups were less likely to survive and to reproduce than selfish members of their groups were, their “tribe would still include their blood-relations” who could pass their altruistic traits on to future generations. Darwin did not fully appreciate the significance of this insight because he did not understand that blood relatives may share genes that code for altruism.

Armed with knowledge that genes are the primary unit of inheritance, Hamilton (1964) recognized that individuals can propagate their genes in two ways: (a) directly, by behaving in ways that increase their reproductive success, and (b) indirectly, by behaving in ways that increase the reproductive success of kin who possess replicas of their genes. This insight enabled Hamilton to predict that mental mechanisms that induce individuals to behave altruistically could evolve when the genetic costs to them (C) were less than the genetic benefits to recipients (B), multiplied by their degree of relatedness (r) – conditions captured in what came to be called Hamilton’s rule: $C < Br$ (also formulated as $Br > C$). The forms of altruism evoked by kin-selected mental mechanisms are most clearly exemplified by the sacrifices parents make for their offspring

($r = 0.5$), but they also extend to other blood relatives, such as brothers and sisters ($r = 0.5$), nephews, and nieces ($r = 0.25$).

Hamilton's rule implies that, all else equal, individuals will favor themselves ($r = 1$) and their relatives such as sons, daughters, and siblings who are most likely to share the genes that code for altruism; it does not imply that individuals will allocate their altruism to others in proportion to their degree of relatedness. Hamilton's rule implies that individuals will be most strongly disposed to help their relatives when the costs of helping them are low and the benefits the helpers receive are high and that helpers will be more prone to make sacrifices for relatives who possess high reproductive potential than for those who possess low reproductive potential. Researchers have amassed a great deal of evidence that humans and other animals behave in accordance with Hamilton's rule.

Triggering Kin-Selected Altruistic Instincts

In order for animals to propagate replicas of their genes in accordance with Hamilton's rule, they must be able to distinguish kin from non-kin and estimate the degree of to which they are related to them. Animals are not able to perceive their degree of relatedness to others directly, so they must derive inferences about genetic relatedness from kinship cues such as how similar others are to them (e.g., in appearance and odor), how familiar they are, and how close to them they reside (proximity). Because non-related members of groups may possess such cues, animals may end up helping those who look and act like their kin, thus contributing little or nothing to the propagation of their genes. Altruistic instincts probably originated as maternal (and in some species paternal) instincts, then were generalized in species such as our own to siblings, more distant relatives, and members of in-groups who looked and acted like kin.

Mental Mechanisms and Emotions Supporting Kin-Selected Altruistic Instincts

Triggers that induce humans and other animals to behave altruistically activate mediating mental mechanisms that affect their emotional and

cognitive states. Although the mental mechanisms that induce animals to help their kin (and those who resemble their kin) are designed in different ways in different species, research suggests that there are significant commonalities across mammals in the ways in which they operate. For example, these mental mechanisms appear to be regulated by hormones such as oxytocin, vasopressin, prolactin, and endogenous opioids, and they appear to generate psychological experiences of attachment, commitment, and love (Brown and Brown 2006).

Sympathy and Empathy

Because kinship equates to genetic similarity, it is not surprising from the perspective of evolutionary theory that people tend to identify with their relatives, to empathize with them, and to sympathize with them when they are in distress. de Waal (2008) has reviewed research demonstrating that empathy is evoked by kinship cues such as "similarity, familiarity, social closeness, and positive experience with the other" and that human "subjects empathize with a confederate's pleasure or distress if they perceive the relationship as cooperative" (p. 16). de Waal cites research showing that "seeing the pain of a cooperative confederate activates pain-related brain areas, but seeing the pain of an unfair confederate activates reward-related areas, at least in men." de Waal concludes that "the empathy mechanism is biased the way evolutionary theory would predict. Empathy is (a) activated in relation to those with whom one has a close or positive relationship, and (b) suppressed, or even turned into Schadenfreude, in relation to strangers and defectors."

de Waal summarizes his account of the evolution of empathy as follows:

Empathy covers all the ways in which one individual's emotional state affects another's, with simple mechanisms at its core and more complex mechanisms and perspective-taking abilities at its outer layers. Because of the layered nature of the capacities involved, we speak of the Russian doll model, in which higher cognitive levels of empathy build upon a firm, hard-wired basis. ... The claim is not that [this basis] by itself explains [all forms of empathy], but that it underpins ... cognitively more advanced forms ..., and serves to motivate behavioral outcomes. (p. 11)

According to Moll et al. (2008), “preliminary functional imaging results in normal subjects point to the involvement of the anterior PFC [pre-frontal cortex], the dorsolateral PFC, the OFC [orbitofrontal cortices], the anterior insula, and the anterior temporal cortex” (pp. 15–16) in the production of feelings of sympathy, pity, and compassion.

Group Selection

Contemplating the problem that altruism presented for his theory, Darwin (1874) considered the possibility that altruistic instincts that reduced the fitness of individuals could evolve if they increased the fitness of other altruistic members of their groups. If altruistic groups outcompeted selfish groups, then altruism could evolve through group selection – a process that selects traits that benefit groups even though they may be costly to individual members of the groups. However, Darwin immediately saw a problem with this idea, namely, that even if altruistic groups outcompeted selfish groups, the selfish members of altruistic groups would fare better than their altruistic cohorts, eventually driving them and their altruistic traits into extinction.

Although most contemporary evolutionary theorists are wary of the idea that altruism could have evolved through group selection, they acknowledge that it is possible under ideal conditions, which, according to some theorists were met during the evolution of the human species. In a prominent defense of group selection, Sober and Wilson (1998) identified five conditions under which altruism could evolve in a population even though it decreased within altruistic groups: (a) there are many groups in the population, (b) the groups contain different proportions of altruistic and selfish individuals, (c) the groups containing high proportions of altruists are more fit than selfish groups are, (d) altruistic and selfish groups compete against one another and form new groups, and (e) the fitness benefits to altruistic groups are greater than the fitness benefits to selfish individuals within the groups. Sober and Wilson suggested that when humans evolved, altruistic groups outcompeted more selfish groups, grew in size, and reconstituted themselves

before within-group selection for selfishness transformed the groups. In recent years, several eminent evolutionary biologists have endorsed the idea that altruism can evolve through group selection.

Many studies have found that people are willing to sacrifice their own interests to promote the collective interests of their groups. Perhaps the most striking examples stem from the behavior of soldiers during battle. As pointed out by Brown and Brown (2006), the US Army Field Manual contains the following passage, “while patriotism and sense of purpose will get American soldiers to the battlefield, the soldiers’ own accounts (and many systematic studies) testify that what keep them there amid the fear of death and mutilation is, above all, their loyalty to their fellow soldiers” (p. 38).

A group of evolutionary theorists has suggested that instincts to uphold large culturally defined groups evolved later than, and through a different form of group selection from instincts to help friends, relatives, and members of smaller in-groups. For example, Richerson and Boyd (2005) suggested that “tribal instincts” evolved relatively recently in the human species through cultural group selection. According to Richerson and Boyd (2005), tribal instincts “are laid on top of more ancient social instincts rooted in kin selection and reciprocal altruism” (p. 191), which causes humans to be “simultaneously committed to tribes, family, and self, even though our simultaneous and conflicting commitments very often cause us...great anguish” (p. 191). Richerson and Boyd view tribal instincts as analogous to Chomskyan linguists’ “principles and parameters . . . of language. . . . The innate principles furnish people with basic predispositions, emotional capacities, and social skills that are implemented in practice through highly variable cultural institutions, the parameters” (p. 191).

The sometimes acrimonious exchanges between evolutionary theorists who have argued for and against group selection are fueled by the different perspectives from which they view evolution. Several biologists have demonstrated that although models of group selection and models of kin selection are formulated in different ways,

they are mathematically equivalent. The essence of both models lies in the idea that genes that dispose a unit of selection to behave altruistically – whether this unit be individuals, families, or groups – can evolve when the altruistic behaviors have the ultimate effect of increasing the frequency of altruistic genes in the population.

Triggering Group-Selected Altruistic Instincts

The basic triggers for group-upholding altruistic instincts are cues to shared group membership. Although it might seem that humans would be evolved to identify with groups that are defined in terms of features such as race and physical appearance, and to sustain such group identifications throughout their lives, social psychologists have found that humans tend to be more flexible. For example, studies have found that individuals who are assigned to groups on an arbitrary basis such as whether they had blue eyes or brown eyes or whether they preferred one form of abstract art or another quickly identify with such groups and favor them when they distribute resources.

Mental Mechanisms and Emotions Supporting Group-Upholding Altruistic Instincts

According to Richerson and Boyd (2001), “we are adapted to living in tribes, and the social institutions of tribes elicit strong – sometimes fanatical – commitment” (p. 215). Social psychologists have attributed the feelings of solidarity that emerge in groups to people’s tendency to identify with in-groups and incorporate “social identities” into their self-concepts.

Sexual Selection

The third way in which altruistic instincts (and other moral instincts) can evolve is through sexual selection. Darwin opened the door to understanding the sexual selection of altruism by recognizing that adaptations that affect reproduction contribute as much – indeed in sexually reproducing species, often more – to the evolution of traits than adaptations that affect survival and that one of the ways in which individuals can increase their reproductive success is by sacrificing their interests for the sake of others. Altruistic traits that are a burden to survival can evolve through sexual

selection when they help individuals increase their reproductive success by attracting mates.

It is in the genetic interest of members of sexually reproducing species to select mates who (a) possess “good genes” that they can pass on to their offspring and (b) are disposed to help them and their offspring. One of the ways in which animals advertise that they possess good genes is by demonstrating that they are able to survive even though they possess a biologically altruistic “handicap” that induces them to make sacrifices for the sake of others. Altruistic behaviors constitute costly signals that advertise that the individuals who possess them are fit enough to survive in spite of them. Although studies on mate choice in humans have featured sex differences in the qualities that appeal to potential mates, members of both sexes rank altruistic qualities at or near the top of their lists.

Triggering Sexually Selected Altruistic Instincts

The primary triggers for sexually selected altruistic instincts are cues that signal the availability of attractive mates with high reproductive potential. Although we might expect the individuals doing the choosing to favor potential mates who signal that they are willing and able to help them and their offspring, individuals also may select mates who display a willingness to help a wider range of recipients, because such behaviors may signal that potential mates possess good genes and high social potential.

Mental Mechanisms and Emotions Supporting Sexually Selected Altruistic Instincts

It seems plausible that sexual selection played some role in the design of mental mechanisms that induce humans to experience feelings of romantic love. According to Fessler and Haley (2003), “a number of investigators...have suggested that some emotions can be understood as mechanisms designed to commit people to behavior that yields long-term payoffs, thus overcoming the temptation for short-term defection. Romantic love, a universal human emotion that underpins pair bonding...appears to be such a mechanism” (p. 10). When individuals are in love, they are motivated to impress their lovers,

to assist them, and to bring them gifts. Neuroscientists have found that feelings of love are correlated with the activation of the ventral tegmental and caudate nuclei of the brain (areas associated with experiences of pleasure), the production of neurochemicals such as dopamine, and the inhibition of neurochemicals such as serotonin.

An Integrative Account of the Evolution of Emotional Sources of Altruism

Brown and Brown (2006) have advanced an account of the evolution of altruism called selective investment theory that integrates other theoretical approaches. The central principle of selective investment theory is that individuals are instinctually disposed to help those with whom they share fitness interdependence. Brown and Brown (2006) review a large number of studies that support their claim that mental mechanisms have evolved in many species that induce them to form emotionally based social bonds with mates, offspring, friends, members of in-groups, and other individuals or groups on whom their fitness is dependent and that these bonds dispose them to treat these recipients altruistically. Selective investment theory postulates that the key to understanding the evolution of altruism lies less in determining whether altruists and recipients share genes or whether they pay one another back than in determining “the direction and magnitude of the correlation between the reproductive success of potential altruists and their recipients” (p. 9).

Origins of Instincts to Respect Authority

In addition to believing that it is right to behave altruistically and to uphold their groups, people from all cultures believe that it is right to respect legitimate authority and to obey rules that uphold the social orders of their groups. Instincts to respect authority probably originated in social species as elaborations of deferential instincts that upheld dominance hierarchies. Deferential instincts induce members of groups to avoid punishment from those who are more powerful than

they are and to accept subordinate positions until they are able to garner enough power to assume more dominant positions in their groups.

In addition to preserving subordinate group members' safety and physical well-being, deferential instincts induce subordinate members to uphold social orders that ultimately contribute to their fitness: “Low-ranking individuals are not simply dominated or exploited; they typically benefit from protection, advice, leadership, and intervention in disputes” (Haslam 1997, p. 300). Dominance hierarchies structure social orders in ways that benefit all members of groups, even if the benefits are distributed unevenly. Well-organized, cohesive groups tend to fare better than poorly organized groups in conflicts with other groups.

According to Haslam (1997), “there appear to be clear continuities between humans and non-human primates regarding the realization and representation of dominance” (p. 304) and, by implication, the realization and representation of instincts to respect authority. Deferential instincts evolved in humans in essentially the same ways in which they evolved in other primates, even though humans define dominance and authority in significantly more complex ways than other primates do and belong to a larger number of groups that are organized in a greater variety of ways. Primitive brain structures similar to those possessed by other primates dispose humans to behave in primitively deferential ways in conditions in which these forms of conduct increased the fitness of early humans. However, in contrast to other primates, humans also possess more sophisticated brain structures that endow them with the capacity to engage in complex forms of abstract and reflective thought and to communicate through symbolic language. The primitive and later-evolved brain structures communicate with each other, which affects the ways in which humans defer to and respect authority.

Triggering Deferential Instincts

Like other animals, humans who are faced with conflicts of interest evaluate the power and status of their opponents and select their strategies accordingly, respecting the authority of those

who have the power to defeat them and those they admire and dominating those who are weaker and of lower status than they are. However, humans are exposed to many more types of authority than other primates are. Although deferential instincts may be triggered by anyone identified as an authority, and even by the rules and norms of groups, humans tend to be more discriminating than other primates in deciding which authorities to obey.

Mental Mechanisms and Emotions Supporting Deferential Instincts

Evidence suggests that instincts to obey authority may be mediated by two types of qualitatively distinct emotions – (a) fear and insecurity and (b) admiration and awe. Fear is evoked by threatening stimuli such as powerful adversaries, whereas feelings of admiration and awe are evoked by accomplished people of high status. Fear is mediated by the autonomic nervous system and primitive brain mechanisms, such as the amygdale, interacting with interpretive mechanisms in the prefrontal cortex. According to Moll et al. (2008), “the neuroanatomy of awe is still obscure” (p. 16). Fear disposes individuals to respect authority in order to avoid punishment, whereas awe and admiration dispose people to make sacrifices for those they “worship” and to curry their favor. Different mixtures of fear and awe may engender different kinds of moral instincts. A spate of research has found that hormones such as androgen and serotonin play an important role in the activation of deferential instincts (Cummins 2005).

Origins of Instincts to Behave Fairly

Social animals induce members of their groups to treat them in fitness-increasing ways by rewarding those who benefit them (and/or their relatives) and punishing those who harm them. Animals that behave in these ways often are motivated to “get even,” which entails behaving fairly. With respect to primates, de Waal and Brosnan (2006) have suggested that “the squaring of accounts in the negative domain. . .may represent a precursor to

human justice, since justice can be viewed as a transformation of the urge for revenge, euphemized as retribution, in order to control and regulate behavior” (p. 88). In the positive domain, “the memory of a received service, such as grooming, induces a positive attitude toward the same individual, a psychological mechanism described as “gratitude” by Trivers” (p. 93).

Game theory research on the evolution of social strategies has demonstrated that individuals who invoke unfair strategies against one another in social exchanges tend to fare more poorly than individuals who invoke fairer strategies. Investigators have found that, in appropriate conditions, fair strategies such as tit for tat and firm but fair outcompete selfish strategies such as All-D [always defect] and therefore evolve. Fair strategies tend to pay off better than unfair strategies because it is in the adaptive interest of members of groups to ensure that cheaters do not prosper. Group members may reinforce fairness by getting even, rewarding those who behave fairly and punishing those who behave unfairly, selecting fair individuals as exchange partners and rejecting or ostracizing unfair individuals, and enhancing the reputation and social status of fair partners and turning others against unfair partners.

Triggering Instincts to Behave Fairly

Evolutionary theorists expect instincts to behave fairly to be triggered in contexts in which behaving fairly paid off better biologically than behaving unfairly did in the environments in which the animals in question evolved, such as contexts that involve repeated social exchanges between members of cooperative groups. These instincts are expected to be sensitive to cues that signal positive and negative consequences of behaving fairly, such as the probability that one will encounter an exchange partner in the future, exchange partners’ willingness and ability to reward fair behaviors and punish unfair behaviors, and the presence of an audience. Individuals are expected to be more strongly disposed to treat members of their in-groups fairly than they are to treat strangers, partners in one-shot exchanges, and members of out-groups fairly. In contrast to deferential instincts, which tend to be activated in relations

between dominant and subordinate members of groups, and in contrast to altruistic instincts, which tend to be activated in relations among friends, relatives, and loved ones, instincts to behave fairly tend to be activated in economic exchanges among equals. Evolutionary psychologists have pointed out that friends and loved ones rarely engage in tit-for-tat-like forms of reciprocity and that they normally are willing to support one another over long periods of time without any expectation of immediate returns. Indeed, people often feel offended when their friends adopt an “exchange orientation” and offer to pay them back.

Mental Mechanisms and Emotions Supporting Instincts to Behave Fairly

Some evolutionary psychologists have asserted that calculating the value of the goods and services that exchange partners give and receive, comparing them, and evaluating them in terms of an appropriate standard of fairness require sophisticated mental abilities that only humans may possess. However, other evolutionary theorists have disagreed, arguing that a sense of fairness may be mediated by less sophisticated mental abilities. In support of the latter position, Brosnan and de Waal (2003) found that capuchin monkeys that were offered a relatively undesirable reward for performing a task (a cucumber) after observing other monkeys receiving a more highly valued reward (a grape) got angry, refused to accept the less desirable reward, and even threw it away. The observers’ anger was intensified when the other monkeys did not have to work for the reward. Brosnan and de Waal (2003) concluded that “capuchin monkeys thus seem to measure reward in relative terms, comparing their own rewards with those available and their own efforts with those of others” (p. 48).

A suite of emotions has evolved to support instincts to behave fairly and through such behaviors to uphold the cooperative orders of groups (Fessler and Haley 2003; Trivers 2006). One set of emotions, which includes feelings of gratitude and a sense of indebtedness and guilt, motivates individuals to even the score by paying their debts and righting the wrongs they have perpetrated. Another set of emotions, which includes anger

and righteous indignation, motivates individuals to induce others to behave fairly. Forgiveness motivates individuals to renew damaged social exchanges. Researchers have begun to identify triggers for these emotions, to map the design of the mental mechanisms that support them, and to identify the areas in the brain that induce them.

Gratitude

In a review of the research on gratitude, McCullough et al. (2008) suggested that gratitude evolved “to stimulate not only direct reciprocal altruism, but also “upstream reciprocity:” passing benefits on to third parties instead of returning benefits to one’s benefactors” (p. 283). According to Moll et al. (2008), people feel gratitude when they experience positive outcomes that they attribute to the agency of a person who intended to improve their well-being. Gratitude engenders attachment to benefactors and the motivation to pay them back. “Activated brain regions include the ventral striatum, the OFC, and the anterior cingulate cortex” (p. 16). McCullough et al. (2008) have found that feelings of gratitude are affected by the value of benefits, the costs of giving, the perceived intentions of the benefactor, and the extent to which the beneficial behaviors are viewed as voluntary, expected, and normative. In contrast to feelings of indebtedness, which people experience as a negative state that motivates them to redress perceived inequities, people experience gratitude as a positive state that motivates them not only to help those who benefited them but also to help third parties.

Guilt

Members of cooperative groups inevitably make mistakes and treat others unfairly. Feelings of guilt evolved to motivate people to uphold the social norms of their groups and avoid punishment from others by making amends, righting the wrongs they perpetrated, repairing damaged social relations, and getting mutually beneficial cooperative relations back on track. Social psychologists have found that people feel guilty when they feel responsible for causing those to whom they feel attached to experience bad outcomes, especially when their behaviors violate moral norms. Theorists disagree about the emotional

origins of guilt. Some assert that it is rooted in fear, whereas others assert it is rooted in sadness. According to Moll et al. (2008), “recent neuroimaging data showed the involvement of the anterior PFC, the anterior temporal cortex, the insula, the anterior cingulate cortex, and the STS [superior temporal sulcus] regions in guilt experience” (p. 13).

Indignation and Vindictiveness

Being treated unfairly and observing others being treated unfairly may trigger feelings of indignation and vindictiveness, which may motivate individuals to right the wrong by punishing those who have behaved in unfair ways. Inasmuch as getting even entails righting a wrong, it entails behaving fairly. In addition, the anticipation of punishment for behaving unfairly motivates individuals to treat others fairly. According to Moll et al. (2008), people feel indignant when they observe others intentionally violating norms: “Indignation relies on . . . engagement of aggressiveness, following an observation of . . . bad outcomes to the self or a third party. . . and “evokes activation of the OFC. . . the anterior PFC, anterior insula, and anterior cingulate cortex” (p. 15).

Research has revealed that feelings of vindictiveness and associated motives to take revenge stem from different mental mechanisms from those that produce feelings of moral indignation (McCullough 2008). Areas of the brain such as the left prefrontal cortex and caudate nucleus that are associated with the pursuit of rewards light up when people feel vengeful, but areas of the brain such as the nucleus accumbens that are associated with feelings of satisfaction light up when people take revenge or learn that those who have treated them unfairly have been punished. According to McCullough (2008), “revenge pays neurochemical dividends. . . Natural selection’s logic here seems pretty easy to comprehend: by paying us back with pleasure, our brains ensure that we’ll go to the trouble of seeking the social advantages that come from returning harm for harm.”

Forgiveness

Although members of all human groups right wrongs and get even by punishing those who treat them and other members of their groups

unfairly, this strategy runs the danger of disrupting mutually beneficial cooperative relations and inviting reciprocally punitive tit-for-tat types of reactions that lead to fitness-reducing blood feuds. To counteract this danger, dispositions have evolved that dispose members of groups to repair damaged social relations by forgiving those who have trespassed against them. Strictly speaking, forgiveness does not support the disposition to treat others fairly unless it is invoked to even the score with those who have forgiven one in the past; however, forgiveness supports fair systems of cooperative exchange by helping to get them back on track after they have been derailed.

McCullough (2008) has reviewed research demonstrating that forgiveness constitutes a culturally universal social instinct that mediates reconciliation in humans, chimpanzees, and other primates. According to McCullough (2008), forgiveness is activated when individuals (a) feel close to and empathize with those who have wronged them, (b) are motivated to guard against the loss of beneficial relationships, (c) are confident that the wrongdoers will not harm them again, and (d) believe that forgiving the wrongdoers will increase their security. When making decisions about whether or not to forgive those who have trespassed against them, people attempt to determine whether the wrongdoers intended to harm them, could have avoided harming them, feel regretful about the harm they perpetrated, and are likely to repeat the offense. Being wronged activates stress hormones such as cortisol that generate unpleasant feelings of anger and anxiety that victims can relieve by forgiving those who wronged them or seeking revenge against them. The neurochemistry of forgiveness involves mechanisms that reduce the stress engendered by ongoing social conflicts.

Origins of Instincts to Uphold Purity

It is in the adaptive interest of group members to ensure that their environments, including other members of their groups, do not contaminate them and cause them to get sick. Rozin et al. (2000) have found that stimuli associated with the risk of harm due to germs, such as bodily

fluids, dead animals, garbage, and rancid smells, evoke feelings of disgust and that this emotion tends to activate negative moral instincts in humans. Rozin et al. (2000) have pointed out that sexual acts involve the exchange of bodily fluids and that sexual prohibitions such as those associated with menstruation, anal sex, and bestiality are often based on ideas of pollution and feelings of disgust. According to Moll et al. (2008), “the neural representations of disgust ... include the anterior insula, the anterior cingulate and temporal cortices, the basal ganglia, the amygdala, and the OFC” (p. 15).

Rozin et al. (2000) have suggested that in humans, moral disgust is an “embodiment” of nonmoral disgust that originated in digestive repulsion. As with other forms of disgust, the adaptive function of moral disgust is to motivate people to avoid potentially noxious stimuli, whether physical or social in nature. It is in the adaptive interest of members of groups to steer clear of those who emit signs of impurity and by implication to behave in pure ways themselves. “Cleanliness is next to godliness.” Rozin et al. (2000) also have suggested that instinctive reactions to physical impurity and purity may be generalized by humans into ideas about spiritual impurity and purity. People tend to view acts that corrupt people as immoral and pureness of spirit as moral. In support of these ideas, research has revealed that disgusting events that have little to do with morality can intensify moral instincts. For example, investigators have found that the harshness of people’s moral judgments is intensified when they are in a filthy, messy room.

Imperfections in the Design of Psychological Mechanisms and the Role of Manipulation in the Activation and Evolution of Moral Instincts

The mental mechanisms that give rise to and regulate moral instincts are not perfect, and imperfections in their design may induce individuals to behave in ways that render their conduct more or less moral than the adaptive forms of conduct that

mediated the evolution of the mechanisms. For example, instincts to avoid contamination may induce individuals to purify themselves in religious rituals and to uphold food prohibitions that foster or diminish their fitness. Instincts to defer to authority may induce people to follow the orders of cult leaders, abide by the dictates of gods, and obey arbitrary rules. Instincts to help kin may be triggered by individuals who look and act like kin, which may contribute little or nothing to the propagation of their genes.

Members of most social species engage in strategic forms of interaction in which they attempt to manipulate one another into behaving in ways that increase their fitness by preying on imperfections in the mental mechanisms that regulate their moral instincts. Like cuckoo birds that trick neighboring birds into suffering the costs of sitting on their eggs, humans attempt to manipulate others into behaving morally by acting like they are their kin, by misrepresenting their value as mates, by acting more dominant and pure than they really are, by exaggerating the value of the assistance they have proffered to them, by persuading others that altruism pays off, and so on. However, because it is in the biological interest of recipients of these overtures to detect and counteract such manipulations, countervailing mechanisms have evolved. In effect, manipulative mental mechanisms have selected increasingly effective countervailing mechanisms, which have selected increasingly effective manipulative mechanisms, and so on in an arm race manner that has caused members of many social species to develop highly sophisticated social strategies. Mutual manipulation probably played a key role in the evolution of the human brain as well as the evolution of moral judgments, moral beliefs, and moral norms (Krebs 2011).

Summing up, people from all cultures are naturally inclined to behave in altruistic, group-upholding, deferential, fair, and pure ways, and people from all cultures consider these forms of conduct right and their opposites wrong. Instincts to behave in ways that uphold universal moral norms are triggered by particular stimuli and are mediated by mental mechanisms that produce emotional experiences such as love, sympathy,

gratitude, and indignation. Although such emotions have been called “moral emotions” because they give rise to forms of conduct that people consider moral, they may be evoked by nonmoral triggers and fail to be accompanied by attributions of right and wrong. For example, people may sympathize with a friend who has been diagnosed with cancer or killed by lightning without feeling that anyone has committed a moral transgression, and people may feel gratitude when they experience a stroke of good luck without feeling that they deserve the positive outcome.

Explaining how humans acquired instincts to behave in ways that they consider moral does not equate to explaining how humans acquired the mental mechanisms that induce them to feel or to sense that these forms of conduct are moral. To fully account for the evolution of moral instincts, evolutionary theorists have attempted to explain how the mental mechanisms that give rise to a sense of morality, or more exactly, to the moral senses, evolved (Krebs 2011).

Origins of a Sense of Morality

All normal human beings possess a sense of morality that induces them to think and feel that certain phenomena are right and wrong, good and bad, and virtuous and vicious. All people make prescriptive and prohibitive moral judgments about how they and others ought and ought not to behave; and all people pass judgment on the moral and immoral behaviors of others. Research has indicated that children distinguish between rules that uphold moral orders and other kinds of rules very early in their lives and that they believe it is significantly more important to uphold the former than to uphold the latter. As expressed by Cummins (2005), “children are significantly better at detecting violations of rules in the social domain, such as those dealing with permissions, prohibitions, promises, obligations, and warnings, than they are at detecting violations of rules in other domains” (p. 698). Children distinguish between moral rules and rules that uphold social conventions by the time they are 3 years old. “When asked to test compliance with social

rules, 3-year-olds have been found to spontaneously seek out potential rule violations just as adults do. . . ., readily distinguish rule-violating behavior from compliant behavior. . . The average 3-year-old appears to have as firm a grasp on the implications of socially prescriptive rules as the average adult” (Cummins 2005, p. 689).

Emotional and Rational Aspects of a Sense of Morality

There is a long-standing debate among scholars about the extent to which people derive moral judgments from emotional and rational mental processes (Denton and Krebs 2016). In one camp, philosophers such as Kant and cognitive-developmental psychologists such as Lawrence Kohlberg have argued that all moral judgments stem from reason and that judgments that stem from emotional sources do not qualify as moral. In the other camp, philosophers such as Hume and social psychologists such as Haidt (2001) have asserted that reason is the “slave of the passions” and that moral judgments are primarily manifestations of emotional states.

Some theorists have attempted to resolve this dispute by demonstrating that two sets of mental mechanisms have evolved in humans – one that induces them to make moral judgments in emotional ways and the other that induces them to make moral judgments in more rational ways. According to Haidt (2001), “The affective system has primacy in every sense: It came first in phylogeny, it emerges first in ontogeny, it is triggered more quickly in real-time judgments, and it is more powerful and irrevocable when the two systems yield conflicting judgments” (p. 819).

In one line of research that has supported dual-process models of moral judgment, neuroscientists have used techniques such as fMRI to assess brain activity as participants make decisions about hypothetical moral problems such as those that are contained in trolley dilemmas. For example, Greene and his colleagues (see Greene 2013) asked participants to make moral judgments about two versions of a dilemma that involved a trolley heading down a track containing five people whom it is destined to kill. In the first version, called the “switch” dilemma, participants are

asked to decide whether they should pull a switch that would cause the trolley to be redirected onto a different track containing only one person. In the second version, called the “footbridge” dilemma, participants are asked to decide whether to push a large man off a footbridge onto the track to stop the trolley. Consistent with the findings of other investigators, Greene and his colleagues found that most participants said that it would be right to pull the switch but wrong to push the large man onto the tracks. In support of the idea that different mental mechanisms mediated this difference in moral judgment, Greene and his colleagues observed an increase in activity in regions of the brain mediating rational moral judgments when participants responded to the “switch” dilemma and an increase in activity in regions of the brain mediating emotional judgments when participants responded to the “footbridge” dilemma. Greene (2013) argued that in contrast to the position advanced by philosophers such as Kant, these findings indicated that emotional reactions induce people to make categorical, deontological moral judgments (e.g., it is never right to violate people’s right to life) and rational reactions induce people to make utilitarian judgments (e.g., it is right to sacrifice the life of one person to save five). However, some philosophers have disagreed with this conclusion.

In another line of research supporting dual-process models of moral judgment, investigators have examined the effects of damage to areas of the brain that mediate emotional reactions to moral issues. In a classic set of studies, the neuroscientist Damasio (1994) found that although patients with damage to the ventromedial area of the prefrontal cortex – an area that mediates emotional processes – made normal kinds of moral judgments to hypothetical moral dilemmas, they behaved in highly immoral ways in their everyday lives. Damasio (1994) concluded that the deficiencies in real-life moral judgment displayed by these patients stem from problems with the activation of moral emotions. People with injuries to their ventromedial prefrontal cortex are able to understand the difference between right and wrong in principle, but they do not *feel* the difference, because they do not experience moral instincts that give

rise to emotions such as shame, guilt, gratitude, and moral outrage in the same way that normal people do.

Denton and Krebs (2016) advanced an “evolutionary-developmental” explanation for the findings from research supporting dual-process models of moral judgment, suggesting that early-evolved brain mechanisms that humans share with other primates give rise to moral emotions; later-evolved brain mechanisms give rise to sophisticated forms of moral reasoning; and the latter increase in power in humans as they develop throughout their life span. According to Denton, “The basic moral emotions produced by primitive brain structures work quite well in enabling social species such as chimpanzees that live in relatively small groups and form relatively simple societies to coordinate their efforts in mutually beneficial ways . . . [and] they also work reasonably well for modern humans in social contexts that are similar to those experienced by chimpanzees and early humans, such as those that include family, friends, and small in-groups. However, because humans are the only species that evolved neocortices capable of performing sophisticated forms of moral reasoning we can safely infer that, early humans experienced adaptive social problems different from those experienced by other species. The high correlation between brain size and group size in social animals . . . suggests that adaptive problems related to complex systems of cooperation and social relations among members of large groups may have played an important role in the evolution of the neocortex.”

The Moral Senses

Although all aspects of a sense of morality induce people to think and feel that certain phenomena are right and wrong, different aspects induce people to experience different kinds of moral sentiments and to make different kinds of moral judgments. Some moral sentiments pertain to one’s self and one’s behavior (e.g., guilt), whereas other moral sentiments pertain to other people and their behavior (e.g., righteous indignation). Some moral sentiments are imbued with positive thoughts and feelings (e.g., moral approbation), whereas others are imbued with negative thoughts

and feelings (e.g., moral disapprobation). Some moral sentiments are activated by thoughts and feelings about how people should and should not behave in the future (e.g., a sense of moral obligation), whereas other moral sentiments are activated by events that already have occurred (e.g., moral outrage). Moll et al. (2008) have suggested that “moral emotions might prove to be a key venue for understanding how phylogenetically old neural systems, such as the limbic system, were integrated with brain regions more recently shaped by evolution, such as the anterior PFC [prefrontal cortex], to produce moral judgment, moral reasoning, and behavior” (p. 17).

Origins of the Moral Senses

Although the basic adaptive function of all moral instincts is to induce individuals to uphold moral norms that support the social orders of their groups, different moral sentiments accomplish this in different ways. The function of some moral sentiments is to induce others to behave in moral ways (e.g., sentiments that induce individuals to approve of group-upholding, cooperative, and altruistic behaviors, to feel vengeful when members of their groups exploit them, and to experience feelings of righteous indignation when they observe third parties behaving unfairly). The function of other moral sentiments is to dispose the individuals who experience them to behave in moral ways (e.g., sentiments that engender feelings of moral obligation, sentiments that induce people to resist temptation, and sentiments that evoke feelings of guilt).

Origins of Moral Sentiments About Others

Moral sentiments triggered by the behavior of others probably originated in positive and negative emotional reactions to social behaviors that had good and bad effects on recipients' fitness and the fitness of their relatives, friends, and members of their in-groups. It is safe to assume that early humans liked being treated in kind, loyal, respectful, fair, and uncontaminated ways by others because these forms of conduct helped them survive, reproduce, and propagate their genes. On the

other hand, early humans surely disliked being treated in cruel, disloyal, disrespectful, unfair, and unclean ways, just as modern humans do. It also is safe to assume that positive reactions to being treated in fitness-increasing ways and observing one's relatives and friends being treated in these ways evoked a primitive evaluative sense that these forms of conduct were right and that the people who emitted them were good, whereas negative reactions to being treated in fitness-decreasing ways and observing one's friends and relatives being treated in these ways would have engendered the sense that these behaviors were wrong and that those responsible for perpetrating them were bad.

Origins of Sense of Moral Obligation

Darwin (1874) believed that the essence of morality lies in a sense of duty and that this sense is engendered by the activation of social instincts: “The imperious word ought seems merely to imply the consciousness of the existence of a rule of conduct, however it may have originated” (p. 112). In contrast to nonmoral feelings of duty, feelings of moral obligation pertain to shared standards of conduct that are prescribed by moral norms, supported by sanctions, and affect the welfare of members of one's group.

Origins of Conscience and a Sense of Guilt

Whereas a sense of moral obligation involves forward-looking motives to behave in moral ways, a guilty conscience involves backward-looking reactions to misdeeds that people have committed. When people's consciences bother them, they pass judgment on themselves. (Anticipatory feeling of guilt also may be evoked when people entertain the idea of committing immoral deeds.)

Darwin (1874) advanced an account of the evolution of conscience in which he suggested that satisfying a pressing but transient antisocial need that leaves a more enduring prosocial need unsatisfied induces people to feel that they made the wrong choice. Supporting such feelings, Darwin suggested that “man would be influenced in the highest degree by the wishes, approbation, and blame of his fellow-men,” and the “deep regard”

people feel for the “good opinion” of their fellows would cause them to regret their misdeeds and feel guilty about them (p. 106).

Findings from research on the development of conscience in children are consistent with expectations derived from a Darwinian framework. For example, in a review of the literature, Thompson et al. (2006) concluded that “one of the strong motivators for morally compliant behavior is the salient emotion that arises from cooperative and uncooperative conduct” (p. 277). “Conscience development has its origins in infancy, where the sanctions (and rewards) of adults in response to the child’s actions have emotional and behavioral consequences. . . experiences of approval and disapproval are important” (pp. 269–270). “Young children are motivated to cooperate with the expectations of parents to enjoy the positive affectionate relationship that they enjoy. Viewed in this light, the parent-child relationship in early childhood can be conceived of as the young child’s introduction into a relational system of reciprocity that supports moral conduct by sensitizing the child to the mutual obligations of close relationships” (p. 282). Moll et al. (2008) have found that guilt stems from “the blending of elementary subjective emotional experiences, which are ubiquitous in mammals, with emotional and cognitive mechanisms that are typically human” (p. 4).

Origins of a Sense of Justice

Trivers (1985) has asserted that “a sense of fairness has evolved in the human species as the standard against which to measure the behavior of other people, so as to guard against cheating in reciprocal relationships” (p. 388), and “such cheating is expected to generate strong emotional reactions, because unfair arrangements, repeated often, may exact a very strong cost in inclusive fitness” (Trivers 2006, p. 77). Evolutionary theory has no difficulty explaining why members of groups would feel that it is right for others to treat them fairly and wrong for others to treat them unfairly, but it is more challenging to explain how the sense that it is right for them to treat others fairly evolved. As expressed by Trivers (2006), “an attachment to fairness or justice is self-interested and we repeatedly see in life. . . that

victims of injustice feel the pain more strongly than do disinterested bystanders and far more than do the perpetrators” (p. 77).

Psychologists have amassed a great deal of evidence in support of self-serving biases in people’s sense of justice. For example, studies have found that people hold themselves to lower standards of fairness than they apply to others, underestimate how much they owe others and overestimate how much others owe them, overvalue the costs of giving to others and undervalue the benefits of receiving, and react less strongly to treating others unfairly than to being treated unfairly by others. Such biases notwithstanding, evolutionary theorists also expect constraints on self-serving biases in people’s sense of justice to evolve for much the same reasons that evolutionary game theorists expect unconditional selfishness to be a nonoptimal strategy in repeated interactions among members of groups. Indeed, some evolutionary psychologists have found that people’s sense of justice may, under some conditions, be biased in favor of others. For example, researchers have found that people may feel worse when they fail to repay their friends than they do when their friends fail to repay them.

The precursors to a sense of justice in other primates observed by investigators such as de Waal appear to be limited to positive and negative reactions to being treated fairly and unfairly by other members of their groups, and humans also display such reactions. However, in addition, humans may react strongly to the ways in which third parties are treated – a phenomenon that has been labeled “strong reciprocity.” As expressed by Wilson (1993), “our sense of justice. . . involves a desire to punish wrongdoers, even when we are not the victims, and that sense is a ‘spontaneous’ and ‘natural’ sentiment” (p. 40).

Conclusion

Although it may seem on the surface that evidence of moral instincts that induce humans and other animals to behave altruistically, to uphold their groups, to respect authority, to behave fairly, and to purify themselves is inconsistent with

evolutionary theory, on close examination it becomes clear that it is not. Instincts to behave in moral ways and instincts to make moral judgments have evolved because they help social animals survive, reproduce, and propagate their genes. Moral instincts induce social animals to sacrifice their short-term interests in order to achieve the long-term biological benefits they can obtain by upholding their groups and supporting those on whom their fitness is dependent. Moral instincts enable members of groups to reap the benefits of sociality and cooperation and to foster their fitness by resolving their conflicts of interest in mutually beneficial ways.

Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Group Selection](#)
- [Kin Selection](#)
- [Moral Emotions](#)
- [Moral Foundations](#)
- [Sexual Selection](#)

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Moral Instincts and Morality

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Synonyms

Gut feelings; Moral intuitionist theory; Moral intuitions

Definition

Moral instincts, or otherwise social intuitions, are unconscious abilities that differentiate between right and wrong actions.

Introduction

Since the advent of psychology, Bargh (1989) stated that people access substantial types of knowledge without phenomenological cognizance. According to Reber (1993), awareness and phenomenological cognizance are comparatively new concepts in comparison to other functions of the brain considered to be unconscious. Lately, some scientific disciplines such as evolutionary psychology and cognitive sciences proposed intuitionist approaches to human functioning (Klein 2003).

Long ago, gut feelings were considered unreasonable. Now, however, things have changed significantly, and often reasoning is considered needless (Cummins 2003). Certain theories, like

the moral intuitionist theories, emphasize people's sudden instinct reactions that they exhibit toward others. As per this view, the intuitive moral judgments are vital part of human moral behavior. These theories further vie that moral intuitive responses result from a person's inherent computational elements obtained from the evolutionary history of the human species and are shaped by the way people were raised in their culture.

Haidt (2001) proposed the “social intuitionist model” of moral functioning. The model suggests that social instincts are a fundamental and quick response that emerges to differentiate between rightness and wrongness without any cognizant of their source. Therefore, moral instincts may or may not be followed by rationale. The “social intuitionist model” was initiated from the data of specific set of scenarios that were designed to provoke repulsive behavior (Haidt et al. 1993). For instance, one scenario details consensual sexual intercourse between adult siblings who, although they both seek pleasure from their experience, decided that they will not do it again. Another scenario describes eating the family dog after it got hit by a car. A third scenario describes a man who bought chicken from the supermarket and cooked and ate it after masturbating on it. After participants were presented with these provoking, repulsive scenarios, they were asked whether the actions in the scenarios were right or wrong and indicated why. Participants were able to decide rightness or wrongness immediately. In contrast, after confronted with an opposite opinion claiming that although the scenarios seem disgusting, no harm could result from people's actions, the participants were unable to give a reason for their judgment. Haidt's “social intuitionist model” had been influential to other approaches followed afterward to support or reject the importance of instincts in moral judgments (Gigerenzer 2008).

Conclusion

Moral instincts are considered important in the study of morality in several aspects. Firstly,

people can differentiate between rightness and wrongness without any cognizant of their source and therefore can shape some moral judgments. Second, moral instincts revolve around the concept of unconscious inherent processes that are necessary for human functioning, and thus these processes lead to moral actions.

Cross-References

► [Morality](#)

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Moral Intuitionist Theory

► [Moral Instincts and Morality](#)

Moral Intuitions

► [Moral Instincts and Morality](#)

Moral Language Regulation

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Synonyms

[Altruism](#); [Evolution of morality](#); [Rule of law](#)

Definition

Recursive language evolved as a precursor to human value systems.

Introduction

In *The Descent of Man*, Charles Darwin identified a moral sense as the cornerstone of what it is to be human. He suggested that, to a social species, the evolution of an ethical brain was essential. This is because no interdependent tribe could succeed if immoral acts, like murder, were to become commonplace. Although the author goes on to claim differences in morality between humans and other animals are a matter of degrees, crucially he suggests only the former can regret actions. Moreover, only they can categorize them in terms of rightness or wrongness. Methods of policing have been observed in other species such as chimpanzees. Yet it seems only humans are able to construct formal moral frameworks, like legal systems, to regulate aspects of life that are not directly linked to reproductive fitness (e.g., obscenity, blasphemy, and copyright legislation). This exception to the general rule within nature suggests that moral systems are a recent adaptation.

Another trait considered distinctly human is the capacity for language. Other animals harbor elaborate communication systems enabling them to alert peers to environmental features, and in some instances, there is even evidence of them attaching distinct sounds to particular targets. For example, vervet monkeys have been found to

produce acoustically different alarm calls in the presence of different predators (Seafarh et al. 1980). Yet human language is thought to be remarkable because of its flexibility, i.e., the ability to combine symbols into understandable structures (Hauser et al. 2002). Humans appear to have been uniquely endowed with the recursive computational mechanisms required to create infinite combinations from a finite set of elements. It is this combinatorial property that has led to the emergence of these two capacities to be considered in parallel.

A Link Between Language and Morality

In addition to the recursive properties of language allowing humans to generate speech creatively, Poulshock (2006) reasons that they let humans moralize creatively. In as much as speakers can use terms to name an unlimited amount of concepts, the author argues they can also discuss them or catalogue them in terms of being positive or negative. People can moralize about cultural etiquette, or important contemporary concerns (e.g., current affairs or the use/abuse of modern technology), along with relatively inconsequential topics (e.g., if a comedian has gone too far). They can also moralize about events that are temporally displaced (e.g., dwelling on past events or considering future ones) or the consequences of things we may never do (e.g., “if I were to do X then Y will be the result”). What’s more, the author points out that speakers can use language to meta-moralize about the nature of morality itself and whether or not it is actually moral to moralize.

Even if nonspeaking animals were to have the cognitive apparatus required for constant reflection, Poulshock argues it is unlikely they would be able to share or enforce morality. For instance, he asks, how would a clan with limited linguistic resources share nuanced ethical judgments beyond approach and avoidance behavior (e.g., violence is acceptable when used for self-defense)? In the absence of language, or paralinguistic features, the author claims it would not be possible to share these values or communicate an

intricate social etiquette for others to abide by. Instead, the direct transference of beliefs and values is most easily achieved through oral or written means. Principles can then be supported by consensually agreed ethical frameworks which are shared within a given population.

Thus Poulshock hypothesizes the uniquely human property of language paved the way for the equally unique property of morality to be shared culturally or intergenerationally. Furthermore, he writes, a recursive communication system that is open to temporally and spatially displaced events can enforce moral behavior with linguistically encoded promises, threats, rewards, or punishments. The result is a socially constructed code which is capable of informing conduct, as well as providing individuals a criterion to evaluate others. On a microlevel, the ease of transmission means communities can establish their own unique information-sharing networks. Members can then be selectively raised or socialized to a specific moral tradition. The author cites the example of religious organizations promoting moral precepts through the use of language. For instance, the Deuteronomic tradition teaches followers to memorize commandments, verbally impart them to others, proselytize with nonbelievers, and record their values in the form of memes (e.g., paintings or signs). Accordingly, our language instinct has historically been treated as critical to the internalization and spread of a moral code.

Ergo Poulshock claims the evolution of language has allowed for members of a community to widen their influence to guide or manipulate the behavior of peers. Linguistically enabled morality lets individuals or groups benefit from cohesion and cooperation through cost-efficient means. It also eases the rapid communal good or bad marking of members, depending on their compliance. The second reason prompts another possible factor in the relationship between language and morality: formal or informal legal structures.

Knight (2008) studies this proposition in detail, theorizing language and the rule of law developed in tandem. Each is thought to stem from adaptations designed to enforce cooperation between strangers. So instead of viewing morality as a

product of language, he contends the two capacities are synonymous in evolutionary history. To illustrate this notion, he juxtaposes the lack of shared morality in primate societies, where conflict is physically resolved, with the self-governing egalitarianism of hunter-gatherer ones. The difference, he suggests, is that the latter are not bound to the same laws of signal operation that are limited to acts of the body. Instead, the advent of language has enabled them to signal in the abstract. This means that humans can utilize institutional beliefs (i.e., protocols) so that important behaviors such as sexual activity and competition can be regulated without conflict. To paraphrase Goodall (1982), this difference may be why human societies exhibit law with order, whereas chimp societies are run by order without law. The role of language in determining these conventions empowers human societies to transcend primate politics, where the key arbiter is dominance.

Boyd and Richardson (2009) also support the coevolution of language and moral structures. They argue that humanity's linguistically determined ability to set social norms is what led to cultural evolution, resulting in the beginning of distinct populations. Within each given group, the extent that conventional behaviors are adopted is influenced by the three Rs, i.e., the impact on reputation, the likelihood of reciprocation, and the possibility of retribution, if they go ignored. In a civilization comprised of small clans, the authors deduce that group-level cooperation would predict the attainment and survival of different communities. They argue that within social systems, where morality is reinforced by punishment or reward, reproductive success is determined by the extent an individual fits in with their community. Accordingly, mating competition would favor those with phenotypes supporting pro-social vs anti-social behavior. Zlatev (2014) adds that an adaptation allowing individuals to be continuously tracked is core to this paradigm. Hence a communication system based upon displacement is highly advantageous for enabling others to compare opinions on fellow group members. Reputations can be systematically enhanced or reduced based upon the extent

to which they deviate from ideals. He concludes that this led to the evolution of traits promoting pro-social behavior, like shame. This hypothesis is akin to Dunbar's (2004) gossip model, which claims one functional role of language is being able to identify individuals who reap benefits from a society they do not contribute to. In his framework, the benefits of being able to identify and share information about "free riders" are twofold. Firstly, speakers may be able to protect other group members from exploitation. Secondly, the spread of such a trait could deter those that wish to exploit them.

As well as the contrivance and enforcement of morals, Poulshock (2006) asserts another adaptive role for language is offering people a means to assess their behavior from its impact on others. Moreover, it lets group members make others privy to their own mental states. This bi-directional mind reading grants greater insight of moral relations than any closed communication system ever could. Similarly, Zlatev (2014) asserts that language and morality both emerged in tandem with capacities to share affective, perceptual, or reflective experiences, including joint attention and empathy. In addition, when met with convoluted circumstances, which can be expected in even the smallest communities, Poulshock (2006) argues oral and written exchanges support discussion and reconciliation. This is particularly common when an understanding of tensions requires third-level intentionality, i.e., knowing someone else who knows someone else who knows something (Dunbar 2004). Language can also be useful in instances where a trusted mediator can communicate an apology or peace offering on another's behalf: another scenario a closed system could not assist.

Moral Development

One way of testing a functional link between language and morality is to study the ontogeny of each trait. If a utility of language is the circulation of communal values, then both ought to emerge and develop simultaneously. However, research into this potential relationship is

constrained by the need for subjects to possess the language skills necessary to describe their moral considerations. Consequently, young children are generally not suitable for testing. This means the modest literature has tended towards theoretical discussions.

Poulshock (2006) suggests parallels in acquisition are commonsense, since an appreciation of complex issues requires the vocabulary to comprehend and discuss them. He cites examples of stumped language and moral development in neglected children, implying a critical period for both that may be owed to crossover modules. Further indirect evidence of a functional link is shown by linguistic analysis from Snow (1990), who analyzed transcripts of 51 h of caregiver and child interactions. At two and a half, she found children spent the most time talking about bad behavior, whereas at three and a half, it was more good behavior. Finally, at four and a half, she noticed they became focused on “should” or “should not” discussions. Based on this, Snow describes the ontogeny of moral sense as following a negotiation of the meaning of words and acts, predicting a correlation between linguistic and moral sophistication. Likewise, Hanfling (2003) advocates a connection, asserting that as children are introduced to concepts (e.g., bullying), they are also taught about their community’s judgments of them (i.e., it is wrong).

Combined, these studies present a consistent picture of language providing a means for parents or guardian to introduce and contextualize specific actions. Children’s moral maturation is then, by necessity, led by language. Its recursive and displaced properties are therefore critical to reinforcing schemas in instances when a behavior does not proceed the lesson. This does not necessarily suggest infants do not possess an innate sense of wrongness. Though it does suggest that the way concepts are first introduced to them goes some way toward determining how they are later regarded.

Conclusion

Humans are not only special in their capacity for language but also in their ability to design,

internalize, and enforce communal values. The key suggestion from the work cited above is that societies based on the collective codification of morality can only be achieved with a flexible means of expression. Unlike their closest evolutionary cousins, people can reason and reconcile with each other in the abstract and establish institutions plus communal values. In particular, the recursive aspect of language and the option to converse over events and people displaced in time and space are thought to play essential parts in regulating morality. A related avenue not touched here is the assumption that, in addition to facilitating moral codes, language facilitates immorality by making deception easier with the option to lie. Although as Poulshock (2006) deliberates, this does not contradict its role in enabling, extending, and maintaining morality.

Cross-References

- [Evolution of Morality](#)
- [Function of Morality \(Haidt\)](#)
- [Morality](#)

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Moral Philosophy

- ▶ [Psychology](#)
- ▶ [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)

Moral Realism

- ▶ [Objectivity](#)

Moral Reasoning

- ▶ [Would You Kill the Fat Man?](#)

Moral Relationships

- ▶ [Social Relations Theory \(Fiske\)](#)

Moral Senses

- ▶ [Moral Instincts](#)

Moral Sentiments

- ▶ [Moral Instincts](#)

Moral Subjectivism

- ▶ [Modern Moral Relativism](#)

Moral Tribes

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Synonyms

[Altruism](#); [Cooperation](#); [Tribalism](#)

Definition

Moral tribes refers to a specifically value-based dimension of tribalism, which is a set of behaviors and cognitive mechanisms that lead individuals to favor themselves and the groups to which they identify. Groups that identify with a set of interests and values distinct from another set of interests and values constitute differing moral tribes.

Introduction

Evolution by Darwinian natural selection appears to be an extremely selfish process by which individuals compete against other individuals in a contest for survival and reproduction. However, Hamilton (1964) showed, and Dawkins (1976) articulated, that “selfish genes” can lead to altruistic and cooperative behaviors at the level of individuals, especially if those individuals are kin and therefore share genes with each other. When individuals are not kin, it can still ultimately favor the helper to aid strangers if it is done under the assumption that the stranger will repay the favor, or reciprocate (Trivers 1971).

Cooperating in groups was likely favored by evolution for a variety of reasons including having greater access to resources, as well as protection from and ability to fight against threats (Greene 2013; Tooby and Cosmides 2010). From an evolutionary point of view, kin selection paired with processes related to and as a result of reciprocal altruism explains a large amount of ingroup activity, including social exchange, helping behavior,

and parental care. These features of human social life likely form a large part of the human moral architecture (Curry 2016). The notion that ingroup activity forms a large part of human life is also supported by the fact that humans evolved in small-scale conditions in which they interacted with a relatively small number of individuals many of whom were kin and close acquaintances (Dunbar 1992).

While reciprocal altruism is one biological mechanism that explains altruism and cooperative behaviors with people besides our kin, ingroup favoritism and cooperation between kin often limits the scope of altruism and cooperation. Greene (2013) argues that while morality evolved for cooperation, it primarily favors cooperation *within* groups and not necessarily between groups. In other words, people's morality is geared towards favoring themselves first along with loved ones and personal acquaintances. However, it becomes a stretch to expand that sphere of morality to strangers. Greene (2013) views this conundrum of human social life as analogous to the Tragedy of the Commons, where the pursuit of individual self-interest leads to a result that is collectively worse off for everyone involved. He refers to this dilemma as the Tragedy of Commonsense Morality.

The tendency for people to favor the groups to which they belong and act with antipathy and hostility towards the groups to which they do not belong is part of a larger psychological phenomenon than morality known as tribalism (Clark et al. 2019). Tribal phenomena include a number of cognitive and behavioral manifestations of ingroup–outgroup dynamics, which can be seen at every level of human social life.

Some of the tribal behaviors and cognitions people exhibit include ingroup favoritism (Balliet et al. 2014; Clark et al. 2019), discrimination and hostility towards outgroups (Balliet et al. 2014; Tajfel and Turner 1979), biased moral reasoning (Ditto et al. 2009; Clark et al. 2019), evaluating identical information more favorably when it supports one's political beliefs (Ditto et al. 2018), avoiding and being more critical of information that goes against one's beliefs (Kahan et al. 2017), ideologically motivated reasoning (Kahan 2013), and political polarization (Stroud 2010).

The Origins of Human Morality

Morality may be a feature that is unique to humans. Indeed, morality is fundamental to human life. Evidence shows that infants are capable of distinguishing good and bad behaviors within the first year of life. Six- and ten-month-old babies not only recognize helpful and hurtful actions in an experimental environment, but also have preferences for a helpful over a hurtful agent (Hamlin et al. 2007). By the second year of life, babies begin to develop the capacity to distinguish fairness (Sloane et al. 2012), prosocial sharing (Brownell et al. 2013), and empathy (Gubler and Bischof 1991).

Sharing behavior in primates exhibits rules and regularities similar to the moral concern in human behavior, to preserve a hierarchy, protect resources, and prevent cheating (Flack and De Waal 2000). After a fight occurs between two chimpanzees, they will sometimes show what looks like forgiveness and reconciliation, for example, “kissing” to reconcile and embracing for consolation (Greene 2013). However, significant differences in moral-like behavior in chimpanzees, such as the absence of anything like a moral conscience that involves internalizing group norms, and the absence of remorse for violent behavior, have prompted Boehm (2017) to make the analogy of chimpanzees to human psychopaths.

Coalitional Psychology

Similar patterns of human and chimpanzee intergroup conflict have led many researchers to study evolutionary parallels between these two species (Wrangham and Glowacki 2012). Intraspecific violence in chimpanzees and humans is often coalitional, where members of the species band together and express intergroup hostility (Wrangham and Glowacki 2012). The capacity to coalesce into coalitions is a necessary condition for intergroup conflict and warlike behavior (Tooby and Cosmides 2010).

Coalitional ties can result in negative judgments towards outsiders, such as representing healthy outgroup members as being infectious

(Petersen 2017). Affiliation helps to explain why people of different group-orientations are differently affected by the same information. For example, differences in moral values between political affiliations affect how disturbed one is to moral violations like kicking a dog, burning a country's flag, and slapping one's father (Graham et al. 2009).

The fact that individuals have a need to belong to a group (Baumeister and Leary 1995) and affiliations are often tied to location (Balish et al. 2013) provides a plausible path for moral tribes to be constituted in sports. Team sports may provide individuals a representation of an adapted form of conflict (Sell et al. 2017). Teams seem to have a form of morality that is enhanced by different regional divides (Balish et al. 2013). The zero-sum nature of sports (i.e., winners imply losers) gives individuals the thrills of winning, but also the pains associated with defeat. Stressful matches being played have been shown to negatively affect one's health, increasing risk of strokes and cardiovascular problems (Wilbert-Lampen et al. 2008). The fact that people are physiologically connected to the outcomes of their team shows how salient an identification with a sports team can be for an individual.

Moral and Political Tribes

Curry (2016) posited a multifaceted nature of morality that corresponds to its many-solutions based nature. These multiple parts of morality evolved as game-theoretic solutions to distinct evolutionary problems of cooperation. The central problems of cooperation outlined by Curry (2016) are as follows: (1) the allocation of resources to kin; (2) coordination to mutual advantage; (3) exchange; and (4) conflict resolution. Curry et al. (2018) describe how humans have culturally and biologically evolved solutions to these moral problems.

For example, the problem of allocating resources to kin is largely solved by kin selection, which explains many instances of altruism and favoring behavior for kin (Hamilton 1964). The problem of coordinating to mutual advantage occurs in a variety of contexts that involve two

or more agents with insufficient knowledge coordinating their behaviors for mutual benefit. Solutions include a host of behaviors that involve signaling, public communicative calls, focal points, among other such behaviors (Curry et al. 2018). In support of his morality-as-cooperation theory, Curry et al. (2018) found that among 60 societies seven cooperative behaviors that encompassed the cooperative domains of the theory were found to be uniformly positive.

Additionally, when it comes to politics, evidence indicates that conservatives and liberals emphasize different moral values, which constitute separate moral tribes (Graham et al. 2009). For example, liberals tend to emphasize harm and fairness concerns more than conservatives (Graham et al. 2009). Harm concerns include actions that make use of violent force against others which results in pain and suffering, while fairness concerns include actions that result in the unequal allocation and access to resources for individuals falls (Haidt and Graham 2007). On the other hand, morality concerns for conservatives are more equally distributed across the five foundations. Concern for the groups to which one belongs, tradition and authority, sacred values, and purity are more salient values for conservatives compared to liberals (Graham et al. 2009).

In addition to fundamental differences in moral values, evidence indicates that conservatives and liberals are equally politically biased and thus susceptible to ideologically skewed beliefs and tribalistic tendencies (Ditto et al. 2018). Together the findings on moral differences and political biases between liberals and conservatives help to explain why they are so often at cross-purposes; they are often not even speaking the same language (Haidt and Graham 2007).

Conclusion

For many decades, research from a variety of disciplines has converged on the finding that humans often engage in ingroup favoritism and express outgroup hostility, which constitutes the essence of tribalism. When this tribal tendency becomes moral, as it often does in intergroup conflict, politics, and when faced with cooperative problems,

people are more likely to be tribal and the tribal behaviors are more likely to be severe. This is because problems that are moral are ones that humans value deeply and strongly identify with and thus are willing to sacrifice for. The last few decades have presented new and unprecedented challenges for the expression of our evolved tribal tendencies with the rise of the internet and social media. Only with a better understanding of our nature, can we better know how to meet these new challenges and successfully solve them.

Cross-References

- [Cooperation](#)
- [Moral Foundations Theory](#)
- [Morality](#)
- [Tribalism](#)

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Moral Values

- [Harris' Moral Landscape](#)
- [Honor Code](#)

Moralistic Aggression

- [Robert Trivers](#)

Moralistic Punishment

- [Altruistic Punishment](#)
- [Altruistic Punishment and Strong Reciprocity](#)

Morality

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Synonyms

[Evolution](#); [Evolutionary psychology](#); [Moral behavior](#); [Natural selection](#)

Definition

Human morality constitutes the by-product of evolution as it emerges from a continuum of shared behavioral characteristics between human and nonhuman species. Natural selection has rendered moral behavior to seemingly constitute a highly developed trait expressed by human primates.

Introduction

Contrary to the belief that wants morality to encompass a trait unique to humans, it is argued that other animal species may possess moral behaviors including community concern, reciprocity, and empathy. Although it is not supported that a fully developed moral system is present in other animals, it is indicated that human morality is embedded in phylogenetic relationships with ancestral animal species. Evolutionary scientists depict the phenomenon of homology by rendering the presence of shared behaviors as the result of a common ancestor between humans and other animal species. They also support that two distantly related species can share a behavior while they inhabit similar environmental niches as it results from convergence due to shared environmental constraints. Intriguingly, through examining behavioral patterns of other species might explain mechanisms of human behavior and depict that a multitude of phenomena concerning morality are the result of continual evolution.

The Empirical and Normative Senses of Morality

Morality from a scientific perspective refers to a set of empirical phenomena, such as the observed capacity of human beings to make normative judgments and the tendency to have certain sentiments including sympathy, guilt, or blame as well as intuitions about fairness and violence. Scientists speak of the Evolution of Morality in empirical sense while utilizing tools as comparative genomics and primate studies to analyze the

subject of interest. While morality in the normative sense is not an empirical phenomenon to be explained, there are vital points that require attention regarding evolutionary theory and principles (Rosenberg 2006).

The Normative Sense of Morality questions one's evolutionary background for moral guidance; through the normative approach, scientists might attempt to gain insight into the content of morality as claimed by proponents of prescriptive evolutionary ethics. Evolutionary theory can potentially explain metaethics and allow to resolve inquiries about the existence and nature of morality (Boniolo and de Anna 2006). Once topics of interest are selected, scientists begin to consider scientific explanatory projects concerning morality in the empirical sense.

Moral Behaviors in Nonhuman Species

Moral emotions have been identified as the principle mechanisms that uphold the rules of behavior underlying social norms and conventions. They constitute vital components in interactions as they normalize the behaviors of group members and foster the tendency to be in line with the norms (Haidt 2003). Equity and equality are the two primary elements that synthesize justice. Adam Smith refers to justice as "the main pillar that upholds the whole edifice of human society." This perspective lies within the rationale that wants animal species to react in the face of unfair treatment (Tinklepaugh 1928). This notion argues that based on instincts of moral behavior, primates tend to respond negatively when others are treated less well (Fletcher 2008), fact that contributes to the maintenance of harmonious coexistence among group members (Brosnan 2006).

Evolution of Justice

The sense of justice is seen in nonhuman primates as they are likely to respond negatively to earning less preferred rewards than a social partner (Frank 1988). In respect to natural selection, researchers argue that it might have been a critical environmental factor that led to selection for the behavior

(Darwin 1964). It is important to underline that evolution of shared behaviors does not indicate identical approaches from species as well as it does not eliminate the novelty of behaviors that are unique to specific primates, but not others, due to their complex nature (Flack 2000). Nonetheless, inequity can be explained as the by-product of another behavior that led individuals to selectively focus on conspecifics, such as social learning, which is present in many species and can be beneficial (Tangney et al., 2007). On the other end of the spectrum, inequity superficially might not be perceived as rewarding from species due to unjust circumstances; however, reacting negatively to unfair treatment can cease harmful interactions with opponents and encourage them to seek out equitable partners (Brosnan 2006). There is also evidence that human and nonhuman species actively take steps toward rectifying inequity when the moral sense of justice is violated and they receive less than they deserve (Brosnan, 2008). In this stage, primates react by punishing others who do not play fairly (Fehr and Gächter 2002). It can be argued that reaction to disadvantageous inequity is more salient as there is immediate benefit to the partner. On the other hand, advantageous inequity leads individuals to abandon their own good and act against their short-term self-interest in order to give up rewards to benefit others. The definition in itself might seemingly appear disastrous for the individual; however, it derives long-term benefits for the community and the conservation of healthy social norms.

Studies on Moral Behavior in Primates

Naturalistic studies have shown that long-term behavior of the partner is more important than the outcome of the individual. In an experimental cooperation task, subjects were more likely to cooperate if they and their partner evenly shared the rewards. In one study, monkeys had to work together to pull a heavy tray of food. The foods differed every time, and the monkeys had to decide whether they were willing to work for the food reward they were offered. Pairs in which the partners shared the good food about half of the

time were successful in the cooperative task, while pairs in which one partner eliminated the other rarely obtained cooperation (Burnham and Kurzban, 2005). Aside from the fact that non-sharing dominants received higher value rewards than their partners, their success rate was lower; thus, they tended to receive fewer rewards. The subjects seemed to expect that working together on a task leads to equity if reward outcome and dominant partners who failed to do this received a form of punishment (Brosnan et al. 2006). The findings indicate that a critical factor in a cooperative task is the partner's behavior to be equitable, rather than the actual value of reward. In experiments where participants are humans (Boesch 2007), responses to inequity differ depending on the source (Silk et al. 2005). Humans change their responses if there is a reason for inequity (Hagan and Hammerstein, 2006). Individuals offer less, and partners accept inequity more readily if the subject is perceived to have earned the right to it. Interestingly, humans tend to respond more negatively to inequity that is caused by another human directly than to inequity that is the result of chance.

Darwinism and Moral Emotions

Charles Darwin proposed that the basis of morality is innate and that humans and animals share an evolutionary background. He mentions in his book *The Descent of Man and Selection in Relation to Sex* that nonhuman primates possess social instincts, such as parental affection, and they are consequently characterized by a sense of conscience that would be otherwise intellectual power if it was well developed as it is in humans. It is argued that other animals experience some level of sympathy for others in their environment that also includes a strong need for familial interactions (Darwin 1964).

Darwin does not disregard the importance of advanced intellectual ability for meaningful judgment, but he underlines that well-marked social instincts are present in animals indicating moral constraints and conscience in species other than humans (Darwin, 1981). He supports that this

notion functions as an evidence for evolutionary continuity between humans and other animals as he relied on comparative data regarding facial expressions across human cultures and other species. He addressed the reasons why universal behaviors are expressed in the form that they do (Darwin 1998).

Adam Smith and Morality

Smith appears to support Darwinian theory. In his book *The Theory of Moral Sentiments* discusses that both positive and negative passions are seen in animals and that they share many traits that are considered human. To support his views, Smith mentions that all animals, including children and dogs, are likely to become angry at inanimate objects that hurt. He highlights that human instincts were in place to promote survival and reproduction. He further believed that instincts were initially experienced as emotion, rather than rational thought, and were often lied outside conscious awareness (Smith 1817). The idea of evolutionary continuity of behavior and the recognition of moral emotions has its roots embedded in the ancient past (Ekman, 1998).

M

Conclusion

A better understanding of the evolution of moral behaviors can be achieved through examining outcome behaviors that allow for insight in the past. According to the notion of natural selection, salient behaviors were practiced more than others, rendering certain moral tendencies as vital for survival. Values of justice and equity appear to be among some of the most crucial components to maintain social norms and order intact in communities of human and nonhuman animals. Undoubtedly, intellectual ability and moral judgment of humans are not comparable with those of other species; nevertheless, the presence of social instincts functions as an evidence of moral conscience in other species. With respect to moral behaviors and emotions, through approaching the precursors, such as the inequity response, scientists may gain a better insight into the outcomes

of evolution of moral behavior. Since clear continuity has been determined between the species, it can function as the foundation of future research on evolutionary approaches to human morality.

Cross-References

- [Charitable Giving \(Peter Singer\)](#)
- [Evolutionary Biology and Feminism](#)
- [Evolution of Free Will](#)
- [Harris' Moral Landscape](#)
- [Human Enculturation](#)
- [Moral Instincts](#)
- [Moral Instincts and Morality](#)
- [Philosophical Foundations for a Modern Morality](#)
- [Psychology](#)
- [Science and Morality](#)
- [Wild Justice](#)
- [Would You Kill the Fat Man?](#)

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Morality Is Cooperation

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Synonyms

[Interdependence](#); [Joint intentionality](#); [Mutualism](#)

Definition

Morality evolved as a mechanism to enhance cooperative behaviors and discourage cheating.

Introduction

Modern humans live in highly collaborative social groups. Although it has been theorized that human sociality only begins to develop as infants internalize symbols of the cultural world around them (Vygotsky 1978), recent research instead suggests that sociality may begin to form before infants are even able to take part in this cultural environment. Research by Michael Tomasello and Amrisha Vaish (2013) has shown that very young infants can already perform cognitive functions that other apes cannot, including cooperative communication. That infants who have yet to embrace any culture or language have performed with higher levels of cognition than adult apes supports theories that human sociality is not embedded entirely in the cultural world, but instead has its roots in the unique human evolutionary history. Additionally, as humans evolved into the ultra-cooperative beings seen today, the competition to be chosen as a partner may have contributed to an environment that became inundated by moral rules and expectations. Ultimately, there is much evidence to suggest that morality exists in humans as a mechanism to heighten cooperative actions and control cheating within groups.

The Interdependence Hypothesis

It is likely that there was a period of progression between the relatively low levels of cooperation of our distant evolutionary ancestors to the high levels that exist in today's human societies. Tomasello et al. (2012) present a theory to describe how humans came to be highly moral and cooperative individuals. They hypothesize that during human evolutionary history, humans began collaborating with others in order to survive and reproduce. Once individuals became interdependent, they also became altruistic, as their success was now contingent upon the success of their partner. This is called the *Interdependence Hypothesis*, and it involves two crucial steps. In the first step, there was a change in the ecology that required humans to search for their food collaboratively. This forced individuals to (a) make the decision to forage together even

when it meant giving up the smaller food they already had, (b) solve the problem of dividing the food after the collaboration was over, and (c) control any potential cheating from individuals wanting the food without participating in the search. Individuals had to communicate their goals during their mutualistic collaboration, which enabled them to create new, joint goals. The joint intentionality present between collaborators forced each member to have an interest in the welfare and success of their partner, as their partner's success was now directly linked to their own. Tomasello and Vaish (2013) further argue that it was this interdependence that originally encouraged helping behaviors. Moreover, the competitive partner choice market would have stimulated cooperation and discouraged cheating, as reputation was undoubtedly an important aspect for being chosen as a partner.

The second step of the Interdependence Hypothesis occurred once group populations grew even larger and they began to compete with other groups (Tomasello et al. 2012). These pressures presented new problems for humans that required a much more dynamic social climate. The increasing group size led to difficulties learning about an individual's reputation, which then led to a decrease in many people's motivation to cooperate. This degradation of cooperation encouraged new group-wide goals and social norms to once again boost collaboration, which in turn created highly enforced mutual expectations for behavior that remained consistent throughout a group. Everyone within the group now had their own role and again depended on other members for their survival.

Morality Improves Cooperation

According to Tomasello and Vaish (2013), children will become moral beings once they can effectively collaborate with other individuals and fully join in the social norms and practices of their culture. Not only do individuals follow the norms of their culture; they also enforce them on others – and themselves – if rules happen to be broken. This leads to a collective morality within the group that individuals will work in accordance

with. In order for a behavior to be considered moral, it requires an individual to either suppress their own well-being for the sake of someone else's or adopt another person's self-interest for their own as well.

According to Baumard et al. (2013), morality is an outcome of the cooperative actions within groups and exists to fairly allocate the benefits of cooperation. They propose a two-step hypothesis to suggest how it has evolved. In step one of the evolution of morality, partner choice would always favor those who were fair cooperators during collaborative activities, even if their motivation for cooperating was selfish. Second, competition among the ultra-cooperative individuals to be chosen as a partner created a further requirement: an individual motivation for fairness. This social selection for fairness contributed to the expectation of highly moral human behavior seen today. They suggest moral behavior exists to benefit one's reputation as a good cooperator, as this can only be done by an individual with a genuine moral sense. The researchers argue morality was adaptive when competition for cooperative partners was extreme, and the most effective way to be chosen was to be fair and equitable with the profits of cooperation.

Conclusion

The studies discussed here have suggested that morality evolved alongside cooperation to encourage cooperators and discourage cheaters. Many other researchers have also suggested the root of morality lies in the evolution of cooperation, with, for example, Joshua Greene (2015) arguing that the function of morality is to support cooperation. Similarly, Tage Shakti Rai and Alan Page Fiske (2011) describe morality by its ability to create and maintain long-term cooperative relationships. Frans de Waal (2006) has emphasized that just because natural selection is a ruthless progression through time does not mean it cannot also proliferate pleasant behaviors like fairness, cooperation, and morality. Natural selection

simply supports organisms that successfully reproduce and ignores the mechanisms that make them successful. Additionally, although the process of natural selection did not classify what our particular morals and norms would be, it did set the groundwork for human kindness and allowed morality to flourish.

Cross-References

- [Cooperation](#)
- [Evolution of Cooperation](#)
- [Evolution of Morality](#)
- [Michael Tomasello](#)
- [Reputation](#)

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Morality of Creating New Life

- [Responsibility for Child Suffering](#)

Moralizing Gods and the Rise of Civilization

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Synonyms

Religion and development of civilization

Definition

Gods and their moralizing values, especially the powers regarding punishment, are related with how civilizations rose and developed into large societies.

The emergence of human civilization is related to the power of large-scale cooperation. Although cooperative behavior is seen in most mammals, large-scale cooperation extends beyond genetically related relatives. This type of cooperation, sometimes called ultrasociality, can be seen even in anonymous and one-time interactions but, without the reputational concern of any kind of large-scale cooperation, cannot be explained by standard evolutionary mechanisms. One of the hypotheses to solve this problem is the supernatural punishment hypothesis (Johnson and Krüger 2004). According to this hypothesis, the human surveillance mechanism does not observe and monitor every situation. However, the possibility of punishment by a supernatural agent eliminates the limitations of punishment for a person who violates moral rules. In other words, the mechanism of fear of supernatural punishment as an evolutionarily stable strategy explains why religions, and especially of religions with a moralizing high gods, spread (Johnson 2016). It is therefore thought that religious belief and

especially the belief in fear of supernatural punishment is an evolutionary adaptation to eliminate the problem of cooperation between large groups (Johnson and Krüger 2004; Johnson 2016). In this perspective, the existence of punishment by an omniscient and omnipotent supernatural agent eliminates the possibility of being not able to observe a moral violator among the communities of human beings with certainty in punishing a person who will make a moral violation. It is thought that the emergence of the idea of supernatural punishment is what underlies the ultrasociality commonly seen in human societies (Purzycki et al. 2016; see also Norenzayan 2013).

In other words, it is thought that there is a relationship between the emergence of moralizing religions and cooperation. For example, the emergence of big moral religions is believed to force people to move together around the temple and thus lead to the agricultural revolution (Norenzayan 2013). The fact that the temples in Göbekli Tepe are dated to a time before the agricultural revolution supports this view (Schmidt 2000).

In addition, different findings using different methods seem to support the supernatural punishment hypothesis. For example, people who believe that God has a punitive character do less cheating behavior on a subsequent task, while participants who believe in God's forgiving aspects show significantly more cheating behavior in the task (Shariff and Norenzayan 2011). In a cross-cultural analysis of national crime rates, Shariff and Rhemtulla (2012) found that there is a negative correlation between the degree of believing in hell and the national crime rates, but there is a positive correlation with the degree of belief in heaven. In a study of 186 different cultures, Johnson (2009) found a positive relationship between the belief in a punitive god and cooperation. Moreover, in a study conducted in eight different cultures, it was observed that a factor that increased the level of helping toward distant coreligionists is the belief that God has a punitive character (Purzycki et al. 2016). Yilmaz and Bahçekapili (2016) also experimentally

showed that activating the punitive aspects of religion caused a significant increase in prosocial intentions. More interestingly, in a way similar to the punitive effect of religion, activating the punitive aspects of secular institutions has similarly led to an increase in prosocial intentions in the same study. This shows that, in addition to religious authorities, punitive secular authorities have similar power in cooperation in contemporary civilization. Likewise, in the study of Shariff and Norenzayan (2007), activating religious or secular institutions had a very similar effect on prosocial behavior.

As a result, these findings support the argument that societies that believe in punitive and omnipotent supernatural powers are more cooperative, and less selfish, which in turn expand and create our large-scale civilization (see Norenzayan 2013).

Cross-References

- [Altruistic Punishment and Strong Reciprocity](#)
- [Evolution of Morality](#)
- [Religious Beliefs](#)

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Morals

- [Evolution of Morality](#)

Morbid Jealousy

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Synonyms

[Pathological jealousy](#)

Definition

It is an intense form of jealousy, mostly involving the intimate interpersonal relationship, and it produces significant distress and impairment.

Introduction

Jealousy is a complex human emotion. The Cambridge dictionary defines “jealousy” as “a feeling of unhappiness and anger because someone has something or someone that you want” (Dictionary 2015). Jealousy is often described as a negative emotional state. Jealousy as an emotion has a close link with anger and sadness

(unhappiness). Jealousy often results in unhappiness or anger. Jealous feelings are often discussed in the context of ownership (power, possession), performance, sexual activity, and love (Bhugra 1993; Zandbergen and Brown 2015). Jealousy is also strongly linked to the emotion “love.” Love gets colored with jealousy, when it demands the “exclusive, unconditional, continued and total possession of the romantic partner” (Maggini et al. 2006).

In the history of literature, the word “jealousy” was frequently used and denoted to a negative feeling state. Interestingly, it had caught the attention of poets and artists to be depicted in popular literary creations (Shepherd 1961). In literature, the words “jealousy” and “envy” are interchangeably used. A finer difference exists between these two words. Envy refers to the feeling that an individual experiences when the individual wants something that he/she does not possess. Jealousy refers to the feeling state that an individual experiences in response to a threat of impending loss of something that the individual possesses (Bhugra 1993).

Sometimes, jealous feelings become very intense, which lead to significant interpersonal impairment and produces clinically obvious distress. It is often referred as “pathological jealousy,” “delusional jealousy,” “erotic jealousy,” or “morbid jealousy” (Miller et al. 2010). Morbid jealousy is often discussed in the context of spousal relationship. Morbid jealousy often results in irrational thoughts and behavior, which are extreme and unacceptable (Kingham and Gordon 2004). It is important to differentiate the feeling of jealousy experienced by normal people from the individuals who experience morbid jealousy. People often experience jealousy after a firm or robust evidence of unfaithfulness, and often they have the readiness to accept alternative thoughts; however, those with morbid jealousy often harbor their belief without robust evidence and offer strong resistance to accept alternative possibilities (Kingham and Gordon 2004). Certain predisposing factors have been identified for morbid jealousy in spousal relationships, which are attractiveness of the partner, partner working at a distant place from

home, and partner having interaction with opposite gender (Singh et al. 2017). Morbid jealousy is broadly classified into two subtypes (Mullen et al. 1990):

1. *Symptomatic jealousy*: Here, jealousy evolves in the background of a psychiatric disorder. As the underlying psychiatric disorder progresses, jealousy evolves concurrently. For example, delusion of infidelity in paranoid schizophrenia or persistent delusional disorder.
2. *Reactive jealousy*: Here, jealousy develops as a reaction to underlying mental state (low self-esteem), psychosocial circumstances (e.g., relational difficulties with partner), or mental illness (e.g., depression). Reactive jealousy is considered as an independent psychopathology, different from the comorbid psychiatric illness or condition that provoked its development.

The Othello Syndrome

The Othello syndrome refers to “delusional jealousy” (Leong et al. 1994). Patients with Othello syndrome often display outbursts of anger and hostility. Their anger may result in verbal threats and physical fights to homicidal behavior in extreme conditions (Leong et al. 1994). Othello syndrome has been reported in the context of schizophrenia and related psychotic disorders, organic mental disorders, personality disorder, substance use disorder, and even some neurotic conditions (Alarcon 1980). The prevalence is almost equal in both genders, but higher prevalence is reported among old people (Seeman 2016).

The etiopathogenesis of Othello syndrome can be linked to certain biological (e.g., neurological conditions like dementia, organic brain syndrome, drug induced), psychological (e.g., paranoid personality, borderline personality, low self-esteem), as well as social (e.g., excessive dependency on the partner, rejection, or altercation with the partner) factors (Seeman 2016).

The core symptom of Othello syndrome is “delusion of jealousy” or “delusion of infidelity”

(Alarcon 1980; Cipriani et al. 2012). When it is developing in the context of dementia, cognitive deficits, hallucinations, and other delusions may accompany (Cipriani et al. 2012). Violent behavior in dementia can be secondary to the delusion of jealousy. Similarly, patients with Parkinson's disease on antiparkinsonian treatment may report about symptoms of Othello syndrome (frequently paranoid and sexual delusions), which often improves with reduction of dopamine agonist agents (Kataoka and Sugie 2018). In the background of obsessive-compulsive disorder, pathological jealousy related to the fidelity of spouse or partner has an obsessional quality (recurrent, repetitive, intrusive, unpleasurable, and irrational). In the context of schizophrenia and related psychotic disorders, morbid jealousy-related spousal relationship is often firmly held and cannot be convinced by contrary evidences. It is often accompanied with keeping a close watch on the partner and partners belongings (Singh et al. 2017).

As the patient may pose threat to self, partner as well as to the rival during the course of the disorder, there is a urgent need of treatment for prevention of untoward consequences (Seeman 2016). Treatment for Othello syndrome can be done pharmacologically (by using antipsychotic medications) or through psychological interventions (e.g., cognitive therapy, couple therapy) (Seeman 2016).

Morbid Jealousy and Alcoholism

Morbid jealousy is often discussed in the context of alcoholism. The prevalence of morbid jealousy among individuals with alcohol use disorder is found to be as common as 34% (Michael et al. 1995). Morbid jealousy in alcoholics can be reported during the state of intoxication, or it can be seen as a comorbid delusion (Michael et al. 1995). Morbid jealousy related to sexual relationships and intimacy is more commonly seen in individuals with severe form of alcohol use disorder (Shrestha et al. 1985). Violence particularly involving the domestic setting and spouse is commonly associated with alcoholism. Morbid

jealousy involving the sexual relationship can be one of the major contributors to alcohol-related violence (Coid 1982).

Morbid Jealousy: Social and Evolutionary Significances

Jealousy has many evolutionary advantages. In the process evolution, there occurs competition in the environment. Those who are able to compete better survive, and those who fail to compete become extinct. Jealousy is one of the determinants of competition. Jealousy related to achievement, possession, power, and procreation (love and sex) acts as a triggering factor for competition. Jealousy as a "mate-guarding" phenomenon is also seen in other primates. Jealousy is capable of producing social pain in a partner, when the other partner is found to be engaged with a new partner or stranger as evident from the study on monkeys (Maninger et al. 2017).

As per the Darwinian hypothesis, jealousy has fitness advantages for both man and woman from evolutionary point of view. Jealousy may be a determining factor for mating (Harris 2004). Jealousy carries different evolutionary significance for males and females. Jealousy in males is mostly related to the risk of sexual contact of their partner with other males (rivals), which reduces their paternity probability, whereas in females, jealousy is not due to reduced maternity probability as females retain their maternity probability, irrespective of their partner contact. The jealousy in females is due to the risk/fear of digression of their committed sexual partner to other female partners for sexual contact (Buss et al. 1992).

Jealousy in sexual relationships may be advantageous as it facilitates the propagation of own genes (Singh et al. 2017). Jealousy may also stabilize the romantic relationship; however morbid jealousy destabilizes the romantic relationship (Sun et al. 2016).

Morbid jealousy may have evolutionary significance. It has been seen that greater percentage of males with morbid jealousy often doubt the sexual fidelity of their partner, whereas greater

percentage of females with morbid jealousy doubt about the emotional fidelity of their partner (Easton et al. 2007). Males and females with morbid jealousy are often preoccupied with the status and attractiveness of their rivals, respectively (Easton et al. 2007).

Evidence supports that morbid jealousy or pathological jealousy falls in the same spectrum of pathological love; however, there are subtle differences in their love style and attachment style. Avoidant attachment is characteristic feature of morbid jealousy, whereas secure attachment is characteristic of pathological love (Stravogiannis et al. 2018).

When compared with healthy individuals, individuals with morbid jealousy are often high in impulsivity, trait anxiety, novelty seeking, and harm avoidance. They have low cooperativeness and self-directedness and poor social adjustment (Costa et al. 2015).

Morbid Jealousy: Neurobiological Implications

Morbid jealousy is seen commonly in the context of organic mental disorders. Evidence suggests that in approximately 30% cases, a neurobiological attribute can be traced for the Othello syndrome (Cipriani et al. 2012). Frontal lobe dysfunction is possibly implicated for morbid jealousy. Dopamine excess has been implicated in the development of morbid jealousy of Othello syndrome. Patients with Parkinson's disease with Othello syndrome reported reduction to resolution of their delusions of jealousy after decreasing the dose of dopaminergic agonists (Kataoka and Sugie 2018). Evidence supports that morbid jealousy (delusion of jealousy) develops after cerebrovascular accidents (stroke), head injury, and brain tumors (meningioma) (Kuruppuarachchi and Seneviratne 2011). Neuroimaging studies found that when people are exposed to scenarios of romantic jealousy, there occurs activation of the basal ganglia. Similarly, the intensity of morbid jealousy related to romantic relationship is correlated with the activation of ventromedial prefrontal

cortex (VMPFC) (Sun et al. 2016). Studies among monkeys revealed that feeling of jealousy produces alteration of glucose metabolism in specific brain areas. During jealous state, there occurred increased uptake of fluorodeoxyglucose (FDG) in the left anterior and posterior cingulate cortex, whereas FDG uptake is lowered in the right medial amygdala (Maninger et al. 2017).

Conclusion

Jealousy is an essential emotion and does have a role in the survival of an individual as well as a race. Morbid jealousy should be always differentiated from non-pathological jealousy. Morbid jealousy can be a core feature of various psychiatric disorders and is treatable. One needs to be familiar with the antecedents and consequences of morbid jealousy for its holistic management.

Cross-References

- Delusional Jealousy
- Envy
- Jealousy: Psychiatric Diagnosis
- Othello Syndrome

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Morning Sickness

► Pregnancy Sickness

Mortality

- Death
- Medical Definitions of Death
- Survival and Death

Mortality Rates

- Calculating Starvation Risk

Mortality Risk

- Extrinsic Mortality

Most Perpetrators Are Men

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Synonyms

Male intrasexual competition; Male intrasexual homicide

Definition

Homicides that occur are overwhelmingly committed by males.

Introduction

Across cultures, homicides are overwhelmingly perpetrated by males. The UN Office on Drugs and Crime (2013) reports that 80–97% of homicide perpetrators are men. Men kill other unrelated men in cases of conflict over social status, face, pride, and reputation, as well as conflict over material resources. Men also often kill women as the result of sexual jealousy. It is very rare for women to kill other individuals. This, however, does not mean that women's level of competition with other individuals is trivial, rather women often use indirect tactics of competition, such as verbal assault or manipulation of other individuals.

Men as the Perpetrators of Homicide

From an evolutionary perspective, men are more likely to be the perpetrators of homicide because there are greater incentives for them to do so. Men's reproductive success is limited by their ability to gain access to mating opportunities. As a result, sexual selection theory predicts that, to avoid the possibility of reproductive oblivion, men must compete with other men for access to women (Trivers 1972). Competition over direct

access to women, as well as competition over resources that will indirectly increase men's mating prospects, may turn fatal.

The homicide rate for male perpetrators increases sharply during the late-teens, peaks during the early 20s, and then rapidly decreases afterwards. A similar peak is present for women, but the magnitude is much lower than that of men. Moreover, across life span, the homicide rate for men exceeds that for women (Daly and Wilson 1988). The evolutionary explanation for this age-homicide curve is that this peak age of homicide corresponds with the life-stage where mating goals loom large, and therefore, competitiveness and the reputation for a readiness to fight is most crucial. Men of this age-category are much more willing to engage in a variety of risky behaviors, such as dangerous driving, sports participation, and excessive drinking, than men in other age-categories. This willingness to accept a high degree of risk likely contributes to the tendency for conflicts between men to escalate quickly to violence and, sometimes, homicide.

Independent of the age effect, male homicide perpetrators tend to be unemployed, poor, and of low education as compared to the general population (Daly and Wilson 1988; Hiraiwa-Hasegawa 2004). These individuals are likely to have difficulty attracting mates using other means and may therefore resort to physical violence to deter competitors. Along similar lines, having a family appears to have an inhibitory effect on men's violence (Daly and Wilson 1988). Although this effect has not yet been demonstrated clearly, it is consistent with the evolutionary perspective – that men who have access to mating opportunities already have less incentive to engage in risky, violent behavior in order to gain additional opportunities.

When men kill women, the most frequent motive is sexual jealousy. Men facing a situation in which their romantic partner leaves them, even when there is no new partner to compete with, may result in a violent, and even deadly, response. Sexual jealousy like this is thought to be an adaptive psychological mechanism for mate-guarding and paternity assurance (Daly et al. 1982). Women usually do not kill their male partners in the same situation, because female-female competition for acquiring mates is weaker among

females than among males, and the costs of violence are greater in females than in males.

Women are generally unlikely to be the perpetrators of homicide, given their large investment in offspring. Indeed, women are essential to the survival of their offspring (Sear and Mace 2008). Thus, engaging in high-risk violent competition poses a serious threat to their reproductive success. Consequently, women adopt more subtle, indirect tactics such as gossip and social exclusion, thereby attacking the competitors without the danger of physical violence.

Conclusion

Across cultures, most perpetrators of homicide are men. Evolutionary psychology can explain this phenomenon from the theory of sexual selection. Men's reproductive success is limited by their ability to gain access to mating opportunities. As a result, men must compete with other men for access to women. Competition over direct access to women, as well as competition over resources that will indirectly increase men's mating prospects, may turn fatal. Men also more likely to kill women for the purpose of mate-guarding than women in the same situation. Women are unlikely to be the perpetrators of homicide, given their large investment in offspring. This does not mean that women do not compete each other, but women adopt more subtle, indirect tactics, thereby attacking the competitors without the danger of physical violence. The homicide rate for male perpetrators increases sharply during the late-teens, peaks during the early 20s, and then rapidly decreases afterwards. This is also explained by the sexual selection theory: that this peak age of homicide corresponds with the life-stage where mating goals loom large, and therefore, competitiveness and the reputation for a readiness to fight is most crucial.

Cross-References

- [Contexts for Men's Aggression Against Men](#)
- [Contexts for Women's Aggression Against Women](#)

- [Meta-analysis of Sex Differences in Aggression](#)
- [Sex Differences in Same-Sex Aggression](#)

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Most Victims Are Men

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Synonyms

[Male homicide victims](#); [Male intrasexual competition](#); [Male intrasexual homicide](#)

Definitions

Homicide that occur overwhelmingly victimize men.

Introduction

Across cultures, when homicides are committed, they overwhelmingly victimize men. The UN Office on Drugs and Crime (2013) reports that

95% of homicide victims are men. Indeed, most homicides are both perpetrated by, and targeted at, men.

Men as the Victims of Homicide

Statics in modern, developed countries show that the homicide victims, as well as the perpetrators, are predominantly men. For instance, the US Department of Justice (2010) announces that murder victims in the United States in 2010 consists of 10,058 men, 2918 women, and 20 cases where the sex was unknown: almost 78% are men. The Office for National Statistics in the United Kingdom (2015) reveals that, in 2015, the homicide victim rate for men was 11.7 per million whereas it was 6.4 per million among women. The same pattern can be found in the WHO's mortality statistics (2016), showing a rate of male deaths by assault that exceeds those of females for nearly all countries reported. The US data is broken down by each age category and demonstrate that across all age categories, with the exception of infant under 1 year of age, males are more likely than females to be the victim of homicide.

An evolutionary explanation of this pattern of findings is linked to the tendency for males to be the primary perpetrator of homicides. Men are more likely to be the perpetrators of homicide because there are greater incentives for them to do so. Men's reproductive success is limited by their ability to gain access to mating opportunities. As a result, to avoid the possibility of reproductive oblivion, men must compete with other men for access to women (Trivers 1972). Competition over direct access to women, as well as competition over resources that will indirectly increase men's mating prospects, can turn fatal. This violence is directed against men, not women, because other men are the obstacle to men's attempts to gain mating opportunities. The violence is not typically directed against women, as they are the desired resource to whom men are competing.

On the other hand, men's attempts to prevent their mating partners from leaving the relationship, or suspected infidelity, may turn deadly. However, this type of homicide is relatively rare

in comparison to the proportions of homicides that are male on male.

Conclusion

Across cultures, when homicides are committed, they overwhelmingly victimize men. Statistics in modern, developed countries clearly demonstrate this pattern; the proportion of men in all the homicide victims usually amounts to more than two thirds. This pattern is linked to the tendency for males to be the primary perpetrator of homicides. Men's reproductive success is limited by their ability to gain access to mating opportunities. Competition over direct access to women, as well as competition over resources that will indirectly increase men's mating prospects, can turn fatal.

Cross-References

- Contexts for Men's Aggression Against Men
- Contexts for Men's Aggression Against Women
- Contexts for Women's Aggression Against Women
- Meta-Analysis of Sex Differences in Aggression
- Sex Differences in Same-Sex Aggression
- Violence to Control Women's Sexuality

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Mother Hypothesis

- Grandmother Hypothesis, The

Mother Tongue Hypothesis

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Synonyms

Proto-language; Proto-Sapiens; Proto-World

Definition

Either a person's native language or a hypothesis about the original human language.

Introduction

The phrase “mother tongue” is often used to indicate someone's native language, as in “what is your mother tongue?” But in linguistics and anthropology “mother tongue” is a hypothesis about the origins of human language. In this context “mother tongue” refers either to the original or first human language or to the most recent common ancestor of all extant or currently existing human languages.

Monogenesis of Language

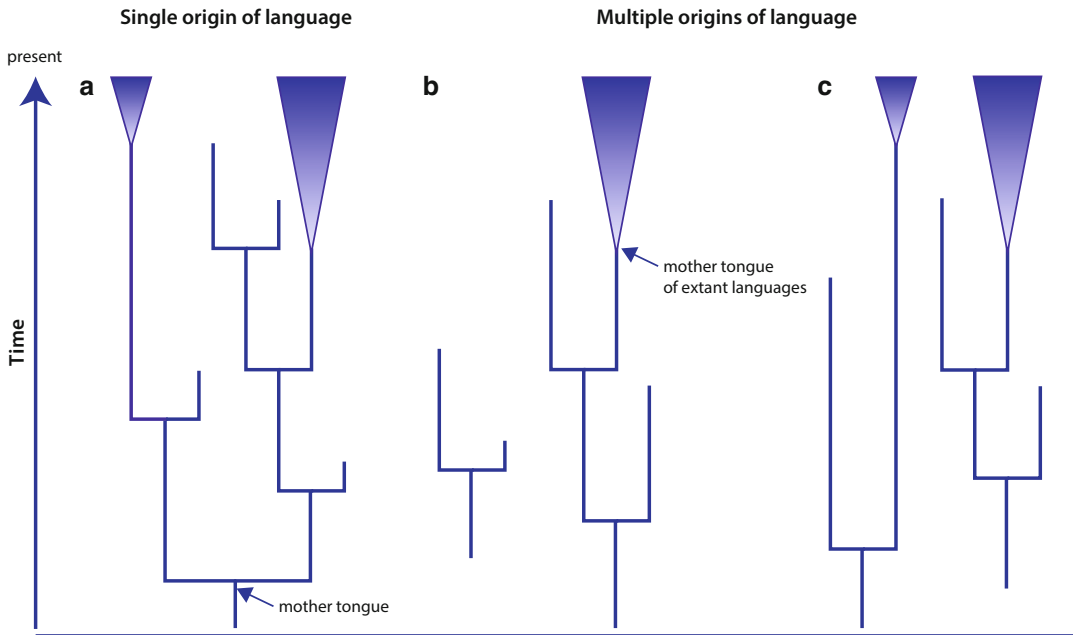
Many scenarios for the origin of human language are possible (Fig. 1). Here “origin of language” can be understood to mean not just people starting to talk, but to the origins of the apparatus – the cognitive, neurological, and anatomical specializations – that make language possible and the genetic architecture that gives rise to them. Some theoreticians believe that this language faculty arose as a specific adaptation for language (Pinker and Jackendoff 2005), while others argue that it evolved for more general cognitive reasons and was only later co-opted specifically for language (Hauser et al. 2002; Christiansen and Chater 2008).

Figure 1a depicts a scenario known as “monogenesis” in which the capacity for language evolved only once, and all modern languages descend from a single original or protolanguage (e.g., Bickerton 1990). Spoken language itself might descend from earlier “gestural” forms of communication (Corballis 2003). Early on in the evolution of spoken language, many private “protolanguages” might have existed within family units (Fitch 2004), but the evolutionary advantages of language meant that it eventually became a public and shared “technology.”

In contrast to monogenesis, there might have been more than one origin of the capacity for language (Fig. 1b, c), and these separate capacities need not have evolved at the same time. In the case of more than one origin, all modern languages might descend from one of these founding events (Fig. 1b) or from more than one (Fig. 1c). Even if the modern languages descend from a single origin, they might trace their ancestry to a more recent common ancestor (Fig. 1b).

Proponents of “polygenesis” believe that the capacity for language arose early in the evolution of our species but that languages only emerged later and independently in various groups around the world (Coupé and Hombert 2005). “Polygenesis” should not be confused with the scenarios expressed in Fig. 1b and c which show separate origins of the capacity for language. Instead, here there is a single origin of the capacity for language, but specific social, environmental, or demographic factors are thought to have encouraged the formation and use of language and at different times in different places. This view of polygenesis has much in common with the argument that the language capacity emerged out of more general-purpose cognitive mechanisms.

Is it reasonable to think there was a single origin of the capacity for language (Fig. 1a)? All human groups that exist today have language, and they share a key gene known as *FOXP2* (Enard et al. 2002). This gene is thought to be involved in language and speech production and influences the fine motor control of facial muscles that are required for the production of speech (Enard et al. 2002). Genetic studies further show that all



Mother Tongue Hypothesis, Fig. 1 The diagrams show two scenarios for the origin and evolution of human languages. Panel (a) A single origin of language occurred in the remote past and all human languages throughout our species' 160,000–200,000 year history descended from that original or founding “mother tongue.” Branches that end in the present represent extant or currently existing human languages. Blue triangles represent collections of languages with a common ancestor. Branches that end

before the present represent extinct languages (such as Latin). Panel (b) The human language capacity arose more than once in separate populations, and not necessarily at the same time, but today all human languages trace their ancestry to just one of these origins. Panel (c) More than one origin of language and currently extant human languages trace their ancestry to these different origins. Other scenarios are possible

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human groups have shared ancestry (e.g., Rosenberg et al. 2002).

In addition, all human languages rely on combining sounds to make words; many of those sounds are common across languages; different languages seem to structure the world semantically in similar ways (Youn et al. 2016); all human languages recognize the past, present, and future; and all human languages structure words into sentences with subjects (S), verbs (V), and objects (O) as in “I (S) kicked (V) the ball (O)” (Greenberg 1963). Finally, all humans are capable of learning and speaking each other's languages.

The similarities among languages and our apparently shared genetic influences on language in the form of *FOXP2* are consistent with the capacity for language having evolved just once, or if this capacity evolved more than once, all

modern languages trace their ancestry back to just one of these events. Genetic evidence points to all modern humans descending from a common ancestor that existed between 125,000–150,000 years ago (Poznick et al. 2013), suggesting that the capacity for language is at least that old.

On the other hand, our species is probably older than this common ancestor (analogous to the scenario for the mother tongue depicted in the right side of Fig. 1b), with fossil evidence suggesting modern humans evolved 160,000–200,000 years ago (Fleagle et al. 2008). Language transmits information using symbols, so it is reasonable to expect that any species that possessed language would show evidence of symbolic behavior. The appearance of symbolic behavior in the form of the use of red ochre pigments (Henshilwood et al. 2002; Henshilwood and Dubreuil 2009) might, then,

indicate that the capacity for language was present by 160,000–200,000 years ago.

Is Language Older than Our Species?

Could language be even older than our species? Might, for example, our genetic cousins the Neanderthals (*Homo sapiens neanderthalensis*) have had language? No one can know because this species went extinct by around 30,000–40,000 years ago. But if Neanderthals could speak, then the capacity for language might already have been present at the time of our common ancestor with them, now thought to be 550,000–765,000 years ago (Prüfer et al. 2014; Meyer et al. 2016).

The *FOXP2* gene in humans and Neanderthals is identical in its coding regions while differing at two key positions from the chimpanzee version of this same gene (Krause et al. 2007). The identity between humans and Neanderthals might suggest Neanderthals could speak. On the other hand, *FOXP2* is not “the language gene” as many genes will be involved in building a capacity for language, and very recent genetic evidence shows that the human and Neanderthal versions of *FOXP2* are expressed or used differently in our two brains (Maricic et al. 2013).

There is also scant evidence that Neanderthals had art or other symbolic behavior (Klein 1999); suggestions that they might have buried their dead or put flowers in the graves divide opinion and do not alone constitute evidence for symbolic thinking anyway. By comparison to Neanderthals, *Homo sapiens* who lived in Western Europe at the same time as Neanderthals had abundant and sophisticated art, they made musical instruments and had a far wider variety of tools and weapons.

We cannot be sure that Neanderthals lacked language, but it would be curious for a species that did have language to show so little evidence of putting it to use. By comparison, modern humans’ cultural and symbolic variety and the evidence of innovation and cooperation are just what we expect of a species that possessed a powerful medium for transmitting information.

A More Recent Origin of Language

Some authors suggest that the human language capacity might have arisen a mere 40,000–50,000 years ago in the modern human populations which had occupied Western Europe by that time (e.g., Klein 1999). The archeological record shows that this was a time of a great flowering of art, symbolism, and technology. Klein (1999) suggests this outpouring of culture indicates that an important genetic development occurred which gave rise to the cognitive abilities that language requires.

The suggestion of a late genetic change making language possible confronts several difficulties. One is that at least some modern human groups had probably left Africa by 120,000 years ago, making it all the way to modern-day China (Wu et al. 2015). Migrating this far would have required adapting to new environments, climates, and sources of food while outcompeting the species already there. Our ability to do this by 120,000 years ago may attest to an already fully developed system of transmitting culturally acquired knowledge, and the most likely medium of this transmission would have been language (Pagel and Mace 2004; Pagel 2012).

The suggestion of a recent emergence of language also struggles to explain the presence of similarly structured languages in human groups all over the world. Thus, for example, the San Bushmen of Southern Africa have the same linguistic capabilities as any other modern human group, but their lineage might have separated from most of the rest of humanity perhaps 100,000 years ago (Knight et al. 2003). For the language faculty to have evolved just 50,000 years ago would require that, somehow, the early Europeans of that time made their way back to Africa, and perhaps interbred with other groups, thereby giving them the capacity for language. There is no genetic or archeological evidence in support of this scenario.

A variant of Klein’s (1999) suggestion avoids the difficulties of proposing a late genetic change, by adopting the perspective of those who support polygenesis, as described above (e.g., Coupé and Hombert 2005). But even polygenesis runs into

difficulties when trying to explain humans' early symbolic behaviors (Henshilwood et al. 2002; Henshilwood and Dubreuil 2009) and apparent technological abilities. These capabilities, expressed early in our history as a species, evidently allowed us to transmit information culturally and adapt to new environments well enough to have occupied East Asia by 120,000 years ago (Wu et al. 2015).

What Was the Mother Tongue Like?

Writing is only around 5000 years old so archeology, beyond identifying symbolic behaviors, is not of much use in identifying traces of a mother tongue or suggesting what it might have been like.

Linguists, on the other hand, can look for words that are shared among enough human languages to suggest that they may be echoes of a shared mother tongue. Statistical investigations of the rate over long periods of time at which words get replaced by new unrelated words lend credibility to this pursuit (Pagel et al. 2007). In particular, some numeral words and pronouns (I, you, who, two, three, five) and the “wh” words or *who*, *what*, *where*, *why*, and *when* tend to evolve slowly enough that it might be possible to trace their ancestry back 10,000 years or more (Pagel et al. 2007).

Evidence that words can retain traces of their ancestry even beyond 10,000 years comes from studies of shared words among language families of Eurasia (Pagel et al. 2013) that probably shared a common ancestor around 15,000 years (Pagel et al. 2013). Two languages that have been evolving separately since a common ancestor 15,000 years before represent about 30,000 years of linguistic evolution over which some traces of similarity in a small number of words have been found (Pagel et al. 2013). Among these words are thou (you), I, we, who, and what.

Still, even 30,000 years of independent evolution doesn't take us back to a common ancestor that might have existed 100,000–200,000 years ago. Historical linguists adopting an approach called mass comparison attempt to identify shared combinations of sounds in widely geographically

separated languages, in hopes that these sounds might be echoes from this more distant past. The work is contentious and controversial among linguists (e.g., Campbell and Poser 2008) but one of its chief exponents, Merritt Ruhlen, working with another linguist, John Bengtson, has proposed 27 “global etymologies” (Bengtson and Ruhlen 1994).

The list of global etymologies includes words for *who*, *what*, *two*, *water*, and *finger* or *one*. For instance, Ruhlen points out that the sounds *tok*, *tik*, *dik*, or *tak* surface repeatedly in the world's languages as a word for the number one or toe or a digit. Other global etymologies include “?ak'wa” (water), “pal” for “two,” “half” for “portion,” “mi (n)” for “what,” and “ku(n)” for “who.” Might these be relics of a mother tongue? Intriguingly, Ruhlen's proposed global etymologies tend to be words that are frequently used in everyday speech, and it is these that tend to change the slowest (Pagel et al. 2007).

Conclusions

Genetics, the shared structure and the universal learnability of human languages, make it reasonable to believe that extant humans have a common language capacity that evolved just once and probably early in our history, perhaps 160,000–200,000 years ago. But the rate at which words evolve means that traces of our common language or “mother tongue” have proven difficult to find. Further clues for evidence linking the world's languages may yet come from studying vocabulary, but other sources such as patterns of tones and styles of prefixes and suffixes (Diamond 2011; Vajda 2010; Hruschka et al. 2015) may also prove useful.

Cross-References

- [Communication and Developmental Milestones](#)
- [Darwin on the Origin of Language](#)
- [Early Theories of Language](#)
- [Human Storytelling](#)

- Language Acquisition
- Language Acquisition in Infants and Toddlers
- Language and Handedness
- Language Development
- Language Dysfunction
- Language Modularity
- Linguistic Evolution
- Metaphor and Analogy
- Modeling Language Transmission
- Modern Theories of Language
- Moral Language Regulation
- Müller's Language Hypotheses
- Neurobiology of Language
- Noam Chomsky and Linguistics
- Pinker's (1994) The Language Instinct
- Universal Grammar
- Verbing and Nouning
- Vocabulary
- Words and Rules

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Mother's Brain Size Decrease During Pregnancy

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Synonyms

Baby brain; Momnesia; Pregnancy brain

Definition

During pregnancy, mothers' brains gradually decrease in size until parturition.

Introduction

During pregnancy, a mother's body goes through numerous physiological changes in order to become adequately prepared with the tasks of motherhood. One change that is not readily apparent to the mother or others is the shrinking of the overall volume of her brain. It has been found in both rats and humans that the size of a mother's brain decreases gradually throughout the gestation period, beginning at implantation of the fertilized egg (Chan et al. 2015; Oatridge et al. 2002). The amount of size decrease can vary between individuals, ranging from a 2% to 7% size decrease (Oatridge et al. 2002). Women with preeclampsia, a hypertension disorder acquired during pregnancy, can experience an even greater decrease in brain size (Oatridge et al. 2002). Although the total size of the brain decreases, there are actually increases in the size of the ventricles and the pituitary gland (Oatridge et al. 2002; Gonzalez et al. 1988). After parturition, the brain gradually returns to its pre-pregnancy size, taking up to 6 months (Brizendine 2006; Oatridge et al. 2002).

Causes of Size Decrease

While there is no consensus about the cause of brain shrinkage during pregnancy, there are a number of possibilities. Holdcroft et al. (2005) note that changes in brain size during pregnancy seem to be related to a change in cell metabolism. Six weeks after delivery, while the brain is returning to its original size, there is a significant increase in intracellular pH. While it is interesting to note that this change is only evident after the pregnancy has terminated, it may be a small part of the mechanism that causes the size change. In research with rats, Chan et al. (2015) postulated that a decrease in taurine leads to the change. Taurine helps prevent cell shrinkage in the brain, and its levels diminish during pregnancy.

Effects of Size Decrease

While the effects of a mother dealing with a shrinking brain are not life-threatening or large

enough to have significant effects on daily life, there are some reported changes that come with brain size fluctuations. When returning to its original size during the postpartum period, there is evidence showing that there are changes in the neuronal connections of certain areas of the brain (Chan et al. 2015; Kim et al. 2010). In rats, there is a reported increase in hippocampal bilateral connectivity during pregnancy (Chan et al. 2015). In humans, there is evidence of gray matter increase in certain areas of the prefrontal cortex, gyrus, parietal lobe, insula, and thalamus (Kim et al. 2010).

There are conflicting results in studies investigating changes in the cognitive abilities of pregnant women. Some find no diminished abilities, while others have found significant impairments in memory (Crawley et al. 2003; Buckwalter et al. 1999). Interestingly, in a study by Crawley et al. (2003), there were no significant differences in the abilities of verbal memory, focused attention, or divided attention between pregnant and non-pregnant women; however, pregnant women rated themselves as less skilled in those areas during their third trimester. This general view of cognitive impairment held by pregnant women is apparent in common media as well; the reported pregnancy-induced dimness is colloquially referred to as “baby brain” or “momnesia” (Knapton 2014).

Evolutionary Implications

Researchers have speculated about the possible evolutionary significance of a shrinking brain during pregnancy. According to the results of the study by Kim et al. (2010), the shrinking and then subsequent regrowing could help facilitate the refocus of neuronal circuitry in areas of the brain that facilitate motherhood and motherly behaviors. Because of metabolic changes, expectant mothers may limit their physical activity keeping them close to home and safe from predators and other dangers.

Conclusion

During pregnancy, there is a significant decrease in the size of the mother's brain up until parturition, after which the decrease is reversed (Oatridge et al. 2002). The effects of this phenomenon are not dramatic, but they are noticed by pregnant mothers (Crawley et al. 2003). While there is some intriguing evidence regarding causes and evolutionary implications of the size decrease, further studies are needed to help provide a more detailed understanding of how and why this aspect of pregnancy occurs.

Cross-References

► [Pregnancy](#)

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Mother's Function

► Maternal Role

Mother-Child dyad

► Maternal Role

Motherese

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Synonyms

Baby talk (BT); Infant-directed speech (IDS)

Definition

Motherese refers to the ways humans (typically mothers or caregivers) alter their speech when addressing young infants or children compared to speech addressed to another adult.

Introduction

“Motherese,” also commonly referred to as infant-directed speech (IDS) or baby talk (BT), refers to the ways in which adults alter various aspects of their speech when addressing children and infants. This can be done in a variety of ways such as using simplified speech, repeating words, shortening sentences, as well as altering the acoustic properties of speech such as using higher pitch, increased pitch range, more pitch variability, and slowing down their speech rate.

The ways in which an individual changes their speech style depends on many factors, including the age and sex of the child as well as the culture they are living in and the relationship to the child (Cooper and Aslin 1994). IDS can be measured using structured or natural observations between an adult and a child (typically a caregiver and their infant) and comparing the speech to that between the adult and another adult in the same setting. Comparisons are then made between the speech samples to determine whether and how the adults modify their speech in the presence of the child. Furthermore, studies have shown that infants as young as 7 weeks prefer infant-directed speech to adult-directed speech.

There is evidence to suggest that this behavior is common across human societies and highly recognizable (Broesch and Bryant 2015; Bryant et al. 2012; Bryant and Barrett 2007; Fernald 1992), although there has been debate about the extent to which some societies address young children and alter their speech style. Research shows that vocal changes happen similarly across industrialized populations (Fernald 1992) as well as in small-scale, traditional societies (Broesch and Bryant 2015).

Several possible functions of IDS have been proposed. For example, IDS might aid in language learning specifically or learning in general (Thiessen et al. 2005; Csibra and Gergely 2009). There is evidence that IDS contains acoustic features that help children learn vowel categories of their language (Kuhl et al. 1997). IDS also likely helps communicate emotional information,

including effectively grabbing and maintaining the attention of infant listeners. In general, IDS also can facilitate an affective relationship between the adult and the child (Fernald 1989; Trainor et al. 2000). Infants demonstrate a preference for IDS over adult-directed speech (ADS) even when the IDS is in a language that is unfamiliar to the infant (Werker and McLeod 1989) suggesting that it is an excellent source of information for infants in early stages of perceptual and conceptual development.

Conclusion

Adults modify various aspects of their speech including acoustic properties, and speech style, often simplifying the nature of their speech and drawing attention to particular aspects of the language or the interactive context. There is evidence indicating that humans across the globe produce motherese. Infants also prefer IDS over ADS and learn more easily from it. It is thought that this behavior facilitates an affective relationship between a caregiver and his/her infant as well as enhances or enables the learning process.

Cross-References

- [Language Acquisition in Infants and Toddlers](#)
- [Modern Theories of Language](#)

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Mother-Fetus Conflict

- [Conflict Between Parents and Offspring](#)

Mother-Infant Attraction

- [Maternal Bonding](#)

Mother-Infant Co-sleeping

- [Co-sleeping](#)

Mother-Infant Proximity

- [Co-sleeping](#)

Mothers and Maternal Grandmothers and Childhood Survival

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Synonyms

Allomothering; Alloparenting

Definition

After mothers, maternal grandmothers have the largest effect on child survival.

Introduction

Arguably the greatest threat to reproduction faced by humans is infant and child mortality. Once an individual reaches adulthood, mortality rates are relatively low, with average lifespan ranging between 68 and 78 years among hunter-gatherers (Gurven and Kaplan 2007). Adults are also likely to find a mate, with virtually 100% of female and at least 90% of male hunter-gatherers doing so (see Volk and Atkinson (2008) for a brief review). The largest fitness challenges humans face, therefore, are first surviving their childhood and becoming reproductively successful adults and then themselves raising children to adulthood. Prior to modern history, infant mortality rates ranged from 25% to 40% and child mortality rates from 36% to 50%. These rates are very similar to modern hunter-gatherer groups (23% and 46%, respectively) (Volk and Atkinson 2008). Indeed, Hrdy (2009) notes that in many hunter-gatherer groups, a woman might give birth multiple times and never raise a child to adulthood.

Given the helplessness of infants, it is not surprising (though only recently acknowledged by scholars) that human mothers require the help

of others in raising offspring. Human mothers are remarkable in their propensity to allow others to interact with infants, even immediately after birth. This is not the case with other great apes, who will not allow any adult contact with infants until 3–6 months following birth (Hrdy 2009). Hewlett (1991) found that among many foraging societies, for the 20–50% of the time an infant is held, it is held by someone other than the mother, usually a close female relative or trusted caretaker.

There are conflicting thoughts on the importance of paternal investment, but collectively, they show that in contrast to mothers, fathers have less impact on child survival (Sear and Mace 2008). However, Gray and Anderson (2015) reviewed the influence fathers have on their children and concluded that paternal investment is typically resource-based (e.g., financial) and may impact on children's survival, health, socio-emotional outcomes, social competence, and educational attainment. Thus, while paternal investment does not seem to affect child mortality rates, Sear and Mace (2008) reported in roughly one-third of the studies where they examined paternal death that father's absence increases the likelihood of child death, but only for a limited time following the father's death.

The question of who keeps children alive then becomes a vital question, and Sear and Mace (2008) after examining 45 studies of kin-child-rearing patterns among people living in nonindustrialized groups, found that after mothers, maternal grandmothers have the largest effect on child survival. Hawkes et al. (1997) found that among Hadza hunter-gatherers, seasonal fluctuations in foraging returns among women predicted variations in child weight for non-nursing mothers. For nursing mothers, the foraging returns of the maternal grandmothers had a positive effect on the child's weight gain. Researchers in the USA have found that among kin, the majority of caretakers are single, African-American grandmothers (Cuddeback 2004), while in the UK, it is married white grandmothers (Aldgate and McIntosh 2006; Farmer and Moyers 2008; Hunt 2003).

Following mothers and maternal grandmothers, it is females in the group who invest

the most in childcare. Barry and Paxson (1971), using a controlled sample of 186 societies, found that after mothers, the principle companions and caretakers of children were adult female relatives, then female children, and then other females. Crittenden and Marlowe (2008) documented that among the Hadza, while female kin are most likely to engage in allomothering behavior such as holding an infant, female nonkin also assist more than males. In their review, Weisner et al. (1977) repeatedly stated that when care is needed, it is a woman more than a man, even if she is more distantly related, who is preferred. Likewise, as mentioned, in foraging societies, when a woman's gathering production decreases after the birth of a new child, the slack is most often picked up by female relatives and then friends (Hill and Hurtado 1996).

Female assistance in childcare and food provisioning begins at a young age. Older children in Bwa Mawego in Dominica take on adult domestic tasks, and in some households, girls around 12 years of age spend as much time in domestic activities as adult women (Quinlan et al. 2003). This activity does not only include childcare and overall relieves mothers' domestic burden which allows them to spend more time caring for their children. Similarly, among the Abuluyia females were the caretaker of small children more than twice as often as males (Weisner 1987). The same trend exists among the Kikuyu of Kenya (Leiderman and Leiderman 1974); Kikuyu child caretakers are usually 7–12 years of age, female, and may be siblings, cousins, or neighbors. They may care for the child for more than half the day, and while they may accompany the mother on various tasks, their primary responsibility is to take care of the child. This care occurs even if the mother is still nursing; the caretakers will take the child to the mother when it is hungry.

Based on the existing evidence from these societies, it seems probable that among humans, there has been selection for food sharing, work sharing, and by extension cooperation, particularly among mothers and grandmothers of young children (Hawkes et al. 1997), and other female group members (Kelly 1995). For

example, Silk et al. (2009) found females who formed strong bonds with their mothers and adult daughters experienced the highest rates of offspring survival (Sokol-Chang et al. 2017).

Conclusion

Overwhelmingly, childcare is prioritized and performed by women, even during childhood and until they are grandmothers. Due to this preference and the prioritization of the care of the child, women are much more reliant on other women, particularly female relatives like grandmothers. This reliance on a cooperative system has a crucial purpose: the care of one's offspring so as to safeguard their investment and, hence, the continuation of their genetic line. This is not only an important relationship but a labor-intensive one as well. When examined in its entirety, cooperation among women has been a vital factor in the survival of the species.

Cross-References

- ▶ [Alloparenting and Grandparenting](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Cooperation](#)
- ▶ [Grandparental Investment](#)

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Motion Parallax

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Definition

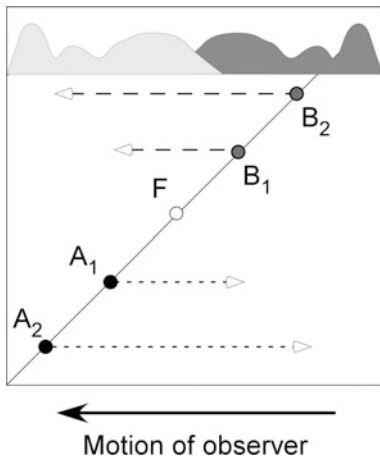
Motion parallax is a monocular depth cue produced by a difference in apparent direction and speed of displacement of the objects located at different distances from an observer, as that observer moves through the environment.

Introduction

Unlike binocular disparity, motion parallax is a monocular depth cue that does not require integrating information from two retinas. However, it is conceptually similar to binocular disparity in that the visual system must still detect the differences between two retinal images obtained successively rather than simultaneously (Rogers and Graham 1982). Motion parallax requires side-to-side (or translational) movement of the body or the head of an observer as depth information cannot be obtained from rotational movement alone. It has comparable precision to binocular disparity (Rogers and Graham 1982), and its use for depth perception is well documented for both humans and nonhuman animals.

Use of Motion Parallax for Depth Perception in Humans and Nonhuman Animals

As an observer moves through the environment, he or she will typically focus on some point in that environment (Fig. 1); in vertebrates, vestibuloocular reflex will trigger eye movements ensuring that the object will remain fixated on the fovea during movement. As a result, the features of the environment will form a bidirectional optic flow: The objects behind the fixation point will be



Motion Parallax, Fig. 1 Pattern of retinal motion created by the translational movement of observer to the left and fixation at the intermediate distance (F). The points located farther than fixation point (B_1 and B_2) will move in the same direction as the observer, whereas the points located nearer than fixation point (A_1 and A_2) will move in the opposite direction. Moreover, the speed with which each point moves across the retina will be proportionate to that point's depth from fixation; for example, the points A_2 and B_2 will be perceived as moving faster than the points A_1 and B_1

viewed as moving in the same direction as the observer, and the objects in front of the fixation point will be viewed as moving in the opposite direction. The speed of the perceived movement will be proportional to the distance from fixation point affording the relative ordering of the objects in depth. Sensitivity to motion parallax is already present in infants as young as 6 months (Condry and Yonas 2013).

Behavioral demonstrations of motion parallax have been carried out in several vertebrate species (barn owl, van der Willigen et al. 2002; gerbils, Ellard et al. 1984; Goodale et al. 1990; rat, Legg and Lambert 1990; rhesus monkeys, Cao and Schiller 2002). In addition, many birds (e.g., pigeons, chickens, gulls, and many shorebirds) also exhibit repetitive backward and forward head movements during walking as well as during landing ("head bobbing") that are thought to provide depth information via motion parallax. Supporting this hypothesis, Xiao and Frost (2013) have recently described neurons sensitive to motion parallax in pretectum of pigeons.

Similarly to vertebrates, many insects show behaviors that appear to produce motion parallax and result in better depth perception. For example, locusts and mantids periodically move their head sidewise prior to striking at a target; if the target is moved in the same direction as the head, then they tend to overestimate the distance to it suggesting that these movements are used as a source of motion parallax information (Kral 2003). Relatedly, bees and wasps circle around objects of interest, presumably using motion parallax to access their three-dimensional structure (Werner et al. 2016). Finally, fruit flies appear to use motion parallax generated by walking toward different objects to judge the distance to them (Collett 2002).

Conclusion

Depth information provided by motion parallax cues is as powerful and precise as that derived from binocular disparity (Rogers and Graham 1982). Unlike binocular disparity, motion parallax does not require binocular integration of information from overlapping visual fields and is therefore likely to be used by the animals with laterally located eyes, even when their visual fields have some degree of binocular overlap (Kral 2003).

Cross-References

- Binocular Disparity
- Depth Perception

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Motivates Punishment

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Synonyms

Functional benefits of punishment; Reasons to punish wrongdoers

Definition

Elicitors of the desire to punish a wrongdoer.

Introduction

People are motivated to punish cheaters, but substantial disagreement exists among philosophers and social scientists regarding why. Evolutionary psychologists have been drawn to human punishment because sometimes it appears to be *altruistic punishment*, costly but non-beneficial to the punisher, making it an anomaly for evolutionary, functional explanations – that is, explanations of how the fitness consequences of a psychological phenomenon enable and shape its adaptive evolution. Functional explanations provide answers to the question of why humans punish – that is, they articulate aspects of human experience that make people want to punish wrongdoers. Evolutionary psychologists have proposed two main classes of functional explanations for human punishment. *Adaptationist* explanations assume that selection is driven exclusively by the punisher's *inclusive fitness* – the fitness effects of punishment on the punisher and the punisher's relatives (Hamilton 1964). By contrast, *multilevel selection* (or group selection) explanations assert that important selection occurs both on the punisher's inclusive fitness (individual level) and at the level of groups by enabling groups to compete against one another based on their complement of punishers. Adaptationists deny the importance of group-level selection, arguing it is too weak to influence the evolution of adaptations. A brief overview of the evolutionary psychology of human punishment provides substantial insight into what motivates humans to punish.

Adaptationist Approaches

Evolutionary theorists frequently used group-level or species-level explanations for biological adaptations until George Williams (1966) showed how individual-level selection could explain adaptive designs better than the prevailing group-level or species-level explanations (i.e., “good for the group” or “good for the species” explanations). Williams persuasively argued that group-level selection is weak compared to individual-level selection, so individual-level

selection should drive the evolution of biological adaptations. Williams not only undermined the credibility of group-level explanations, he also placed a foundational emphasis on the importance of articulating design features of adaptations. This emphasis developed into the form of evolutionary psychology known as *adaptationism*, an approach to evolutionary psychology that relies exclusively on individual-level selection in an empirical search for theoretically derived, a priori characterized design features of adaptations that comprise human psychology. Adaptationism has produced many complementary explanations and predictions regarding what factors motivate people to punish wrongdoers.

Seeking Better Treatment

According to *social exchange theory*, people use punishment as “a bargaining strategy” to enhance subsequent outcomes from their reciprocal interactions with specific individuals with whom they have potentially long-standing relationships (Krasnow et al. 2012, p. 3). That is, punishment modulates later behaviors of relationship partners to provide increased, direct benefits to the punisher. From this perspective, people forage for social exchange partners, using reputation information about how potential partners treat others as a cue to how they might themselves be treated, but preferring to use information about actual treatment by the person toward themselves if available. People invest in relationships hoping for long-term payouts. Such investment includes punishing defection when detected and directing punishment only toward those with whom a long-standing relationship can be expected so that punishment costs can be recaptured through subsequent benefits from that person. This perspective makes the surprising prediction that people will prefer to interact with cheaters more after they have punished compared to before they are punished. This is because punishment is theorized as an attempt to negotiate for better treatment. If however the actor perceives that prior losses are unlikely to be recouped by better outcomes later, the theory predicts the actor will abandon the relationship rather than paying costs to punish. By this approach, people are more likely to punish

someone who defects against them but is expected to continue as a long-term relationship partner but unlikely to punish someone who wrongs another person (a third party) or whose relationship the person is abandoning.

Social Relationships

Lieberman and Linke (2007) argued that an actor’s punitive motivation should be moderated by the degree to which an actor’s biological fitness is tied to others. For example, *inclusive fitness theory* shows how an actor’s fitness is tied to genetic relatives (Hamilton 1964). A brother’s children increase inclusive fitness and more so per child as compared to a cousin’s children. This is because we share more genes with a sibling than a cousin. Inclusive fitness is important for punitive motivation both because punishing a relative reduces one’s own fitness and because one’s fitness is reduced more when the victim is a relative compared to a nonrelative. Lieberman and Linke (2007) also argued that social exchange happens more with members of coalitions and in-groups and less with out-group members, so people should be more concerned with the welfare of coalition and in-group members. In summary, punitive motivation is moderated by the degree of genetic and social interdependence of the punisher with both the perpetrator and the victim: punitive motivation is stronger when victims are more interdependent and when perpetrators are less interdependent.

Reputation

One context in which apparently anomalous altruistic punishment occurs is when people pay costs to punish unknown third parties with whom the punisher expects no future interactions through which costs paid to punish the wrongdoer could be recouped. Kurzban et al. (2007) identified a means by which other sources of benefits and cost avoidance could be reaped by punishers of third parties even in such circumstances. They argue that punishment is costly due to dangers such as retaliation, making punishment itself a *costly* and therefore an *honest signal* – reliable source of information for observers that the punisher is willing and able to punish transgressions.

By punishing wrongdoers a punisher can develop a reputation as being someone who would be costly to mistreat. Kurzban et al. (2007) proposed that reputation benefits of punishment resulted in evolutionary selection for punishment-related adaptation. In particular, they predicted and found that punitive motivation is greater in the presence of an audience.

Offsetting Fitness Differentials

The exceptional cooperativeness observed in human groups is a theoretical problem because human groups produce benefits for members, but members who do not contribute to group efforts while still taking benefits – free riders – would have greater fitness outcomes than those who do contribute. Price, Cosmides, and Tooby (2002) argued that compared to contributors, free riders enjoy a *fitness differential* over contributors. The fitness differential is equal to (a) the costs paid by contributors, added to the (b) benefits free riders take greater than those received by contributors. This fitness advantage must be eliminated for adaptations enabling collective actions to evolve. Price et al. (2002) argued that *punitive sentiment* is an adaptation that evolved to offset these fitness differentials in the context of collective actions. Punitive sentiment is activated by free riders, detected as those “who (1) benefit from a collective action, (2) could have contributed . . . without incurring a cost disproportionately greater than their share of the expected benefit, and (3) did not expend adequate effort towards the collective action” (p. 206). Punitive sentiment’s output is “desire that the target of the sentiment is harmed [and perhaps] that (1) the target be aware of being harmed, (2) the target know why, and (3) others be aware of the reason for punishment” (p. 206). Indeed, participant punitive motivations tracked these and not other variables in response to free riders failing to contribute to a group-defense collective action (Price et al. 2002).

Recruiting Labor

Another perspective that argues punishment is motivated by free riding was provided by Krasnow, Delton, Cosmides, and Tooby (2015). They proposed that punishment can be considered

a labor recruitment method: it can transform would-be free riders into contributors. Krasnow et al. (2015) demonstrated how this could work using individual-level selection in agent-based modeling by enhancing the biological plausibility of model features, such as allowing agents to punish only some defections to avoid excessive costs of overpunishing as occurs when all punisher agents punish every defection, by allowing free riders to become cooperators rather than merely endure fitness reduction while continuing to free ride and by allowing agents to interact with members of other groups to enhance the strength of natural selection. Finally, agents remembered who punished them in the past and selectively cooperated when in the presence of prior punishers.

Multilevel Selection Approaches

As mentioned above, in the 1960s, George Williams largely undermined the scientific legitimacy of group selection theory. Over the last few decades, however, evolutionary scholars have reconsidered the issue. Sober and Wilson (1998) convincingly demonstrated how, mathematically, natural selection could in fact happen at multiple levels, including the group level, within a narrow set of circumstances. They further argued that human morality, including punishment, might be comprised of adaptations formed in part by group-level selection.

The problem for explaining group-level selection of human punishment is articulating how selection could favor individuals who pay costs to punish wrongdoers when the punisher himself or herself would not receive extra benefits as a result of the punishment compared to group members who did not punish. The group-level selection solution, in brief, is that (a) groups with more norm-compliance-enforcing punishers are more cohesive and functional than groups with fewer punishers and so (b) groups with more punishers outcompete and displace groups with fewer punishers, resulting in (c) a relative increase in the number of groups with more punishers, and therefore (d) punishers increase in number overall

despite a reduction in the number of punishers within groups (because within groups such punishers are at a disadvantage relative to non-punishers). That is, punishers proliferate because punisher-rich groups become more common and spread faster than punisher-deficient groups, despite punishers become less common than non-punishers within groups.

Punishing Norm Violators

One prominent multilevel selection theory of human cooperation and punishment is *cultural group selection* (Richerson et al. 2016). According to cultural group selection theory, group-level selection is enabled by diverse, culturally inherited social norms and institutions that produce substantial between-group differences, which in turn impact competition among groups. The phenotypic differences across groups can have strong impacts when groups compete with one another, enabling genetic selection on even small amounts of genetic differences between groups, a form of gene-culture coevolution. Punishment plays multiple important roles in this theory. Punishment of deviant behaviors increases phenotypic homogeneity within groups by enhancing conformity to group-specific norms, which also increases phenotypic heterogeneity between groups. Punishment, sometimes as prescribed by cultural justice institutions such as religion, also enhances within-group cooperation and helps solve public goods dilemmas. Finally, within groups punishment decreases fitness for genes related to antisocial behavior and increases fitness for genes related to prosocial orientation, another case of gene-culture coevolution. Core claims of cultural group selection theory were supported by a study looking at anonymous costly punishment and cooperation across 15 diverse societies. It found that people tended to punish unfair offers in all societies, but critically cooperation was higher in societies whose members punished more (Henrich, et al. 2006).

Conclusion

Evolutionary psychologists have developed many explanations regarding why humans are

motivated to punish wrongdoers based on functional considerations of punishment. Explanations relying on individual-level selection focus exclusively on effects of punishment on the punisher's inclusive fitness. From this perspective, people are motivated to punish others in order to (a) negotiate for better treatment; (b) protect the fitness interests of themselves, their relatives, and their in-group members; (c) develop a reputation that deters defection; (d) offset fitness differentials that free riders reap over contributors in collective action; and (e) recruit labor in collective actions. These explanations are complementary – all could be true – as could the more controversial group-selection explanations, which argue that people are motivated to punish norm violators to enhance their group's ability to compete with other groups.

Cross-References

- ▶ [Ability and Willingness of Victim to Retaliate](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment Enhances Reputation](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Benefit Group Relative to Other Groups](#)
- ▶ [Coalitional Relationships](#)
- ▶ [Competition Between Groups](#)
- ▶ [Costs of Punishing](#)
- ▶ [Cross-Cultural Punishment](#)
- ▶ [Cultural Evolution](#)
- ▶ [Evolution of Culture](#)
- ▶ [Evolution of Punishment](#)
- ▶ [George C. Williams](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Mechanisms to Detect and Punish Cheaters](#)
- ▶ [Norms](#)
- ▶ [Punitive Sentiment](#)

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Motivational States Promoting Survival and Reproduction

- [Relevance of Evolved Interests to Modern Morality](#)

Motor Aphasia

- [Broca's and Wernicke's Aphasia](#)

Motor Control

- [Inhibition](#)

Motor Development

- [Mobility: Crawling and Walking](#)

Mouth-to-Mouth Kissing

- [Kissing](#)

Movement

- [Selectionist Models: Implications for Behavior](#)

mtDNA

- [Mitochondrial DNA](#)

Müller's Language Hypotheses

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M

Synonyms

[Origin of language](#); [Theories of language evolution](#)

Definition

Early speculative hypotheses concerning the origin of spoken language proposed by Friederich Max Müller.

Introduction

Müller was a German philologist who proposed some early theoretical formulations concerning the origins of language. After the publication of the *On the Origin of Species* (Darwin 1859), Müller was fascinated of the idea of human evolution. The tradition of giving disparage names

to the theories regarding how language evolved commenced by him and this was an important factor in his campaign against Darwin's evolutionary theory. Müller (1877) established associations between Darwin's evolution on humans and many other ideas about development, and he concluded that languages are subjected to historical radical change. However, he later realized that he underestimated Darwin's arguments and his suggestions concerning the history of human evolution. In 1864, Müller presented his *Lectures on the Science of Language*. In this period of time, he started to reevaluate Darwin's theory. In his book *The Descent of Man*, Darwin had a section about language, in which he proposed his own theories about the evolution of language. Müller had different ideas about how language emerged, and therefore, he talked in public about "Mr. Darwin's Philosophy of Language" in 1873 (Knoll 1986).

In these talks, Müller suggested that the language faculties of humans are distinguished from other creations; therefore, it was impossible that the human development evolved from a lower form without language acquisition. His point of view was supported by his opinion that the linguistic roots are considered the original building blocks of language. In his *Lectures on the Science of Language*, he proposes that Indo-European verbal communication had developed from hundreds of verbal "cells." Müller hypothesized these linguistic roots as fundamental of the theory of mind. He assumed that they establish the principles for the Kantian intellectual classifications used by the mind to establish cognizance out of raw sense of perception. This capacity of the individual's mental structure separated man from animals since it formed the basis of man's exclusive capacity to form a concept and think rationally. Without these capacities, neither language nor thought was possible. Müller concluded that because animals do not have this intellectual structure, their evolution into humans was impossible (Müller 1877). In 1861, Max Müller published a list of theoretical concepts concerning the origins of language. He later abandoned most of his theories which include the bow-wow

theory, the pooh-pooh theory, the ding-dong theory, the yo-he-yo theory, and the ta-ta theory.

Bow-wow Theory

The overall idea of the bow-wow theory is that the beginning of language can be linked to the era when the progenitors begun to mimic the sounds in their natural environment, a process called "onomatopoeia." The natural world was of paramount importance in the origination of language since the sounds of animals played a significant role in the invention of the vocabulary used in verbal communication. On the one hand, Thorndike (1943) was doubtful about the credibility of this theory as the beginning of language. On the other hand, recent studies support that being able to mimic sounds in the natural environment was of paramount importance in the evolution of language (Malle 2002).

A major drawback of this theory is the fact that people use different words to describe the sounds of animals according to their country and more specifically due to their language. For instance, the sound of a pig can be translated differently across the countries. In English a pig makes the sound "oink-oink"; in Russian it makes the sound "hyru-hyru," while in Chinese it makes the sound "oh-ee-oh-ee." Therefore, the sound and pronunciation of the words are not similar among the different languages. Another challenge is that there are few onomatopoeic words in the languages worldwide. In case the theory was credible, then it should have plenty of words out from the basic rule of onomatopoeia. The hypothesis that language is determined by how a person interprets a sound was rejected, since there are many languages and nobody can suggest that human vocabulary arose from these sounds (Thorndike 1943).

Ding-Dong Theory

The idea behind the ding-dong theory is sound symbolism which is a non-arbitrary connection

between phonetic features of linguistic items and their meanings. Max Müller proposed the ding-dong theory by stating that meaning comes from sounds. According to this hypothesis, the origin of language emerged evolutionary with the names our ancestors gave to objects, activities, and natural occurrences after an identifiable sound associated with it in real life (Mandavilli 2016). An important characteristic of this notion is the fact that words having high front vowels were used to name small or jagged objects in comparison to words having round vowel which were used to name large or round-shaped objects. It is suggested that people used sound symbolism to give meaning to words through onomatopoeia, which is the formation of a word by the imitation of a sound made by or associated with its referent in real space and time. “Boom,” for example, was the word given for explosion (Mitchell et al. 2013).

A major drawback of this theory is that onomatopoeic words are not the same in every country because the sound and pronunciation of the words are not similar among the different languages. People in different nations used their onomatopoeic words which are formed in regard to how they interpret different sounds. These words are a very limited part of their vocabulary since many ideas such as love, hate, harmony, and the sea do not make any noise. Thus, the relationship between meaning and sound is not established by any convincing evidence. For this reason, this theory was later abandoned by Max Müller (1877).

Pooh-Pooh Theory

The early speculative language theory of pooh-pooh refers to the notion that language emerged from unintentional vocal responses to agony, fright, astonishment, enthusiasm, satisfaction, or other emotions (Barber 1965). Although animals produce sounds as well, language is unique only to humans. “Ouch!,” “Aaah!,” and ‘Wow!’ are some examples of the unintentional vocal responses emerged from this hypothesis. This

theory can be found in the literature as “the expressive theory,” “the interjectionist theory,” or “the expressions of emotions theory” (Barber 1965). Max Müller supported the pooh-pooh theory for a while, but later he abandoned it (Müller 1877).

The notion of the pooh-pooh theory that language has many emotional exclamations has been widely criticized by many reviewers. It has been argued that the explanations provided by this theory constitute a very limited part of the vocabulary of different languages. Further, the various languages worldwide have different interjections. For instance, in English pain is “ouch” while in Greek it is “aou.” Therefore, it is indicated that sounds could have been different if their origin was from interjections. To conclude, although early human beings could use words based on interjections, these may have been ultimately overruled by more sophisticated and abstract terms (Mandavilli 2016). Finally, it is important to emphasize that although animals react to the sudden feelings they experience using sounds, they didn’t develop language as human beings did.

Ta-Ta Theory

According to Richard Paget, who was specialized in speech science and the origin of speech, the ta-ta hypothesis supported that speech and the development of sound were produced to endorse the hand and body movements of the individual. So as to better demonstrate the meaning behind the gestures, these sounds developed different words or combinations of sounds unavoidably leading to speech patterns (Paget 1930). For instance, when a person would say ta-ta, he was basically saying good-bye with his tongue. At some point, this theory was even supported by Charles Darwin (Mandavilli 2016). In the literature, there are several theories such as the oral gesture theory and the chew-chew theory that support the idea that the origin of language begun from early human gestures made from their mouth. It is of paramount importance,

though, to understand that it is not feasible to explain the origin of some words using the ta-ta theory.

A major drawback of this early theory on the origins of language is the fact that in order for people to be able to communicate between them, they must see each other in person. Also, there must be daylight, or firelight, and with nothing blocking one's view. In the case of hand gestures, it is important that hands are free from doing something else (Meir et al. 2010). Last but not least, in order for this hypothesis to be the origination of communication, it required a number of gestures be in place already for humans to imitate with their mouth gestures, but it didn't explain how these gestures arose in the first place.

Yo-He-Yo Theory

Verbal communication commenced as growls, moans, and rhythmic chants which occur from the overwrought efforts of ancient menfolk to move a boulder or heave a rock, as it is suggested by the yo-he-yo theory (Mandavilli 2016). Every time these people were working hard to move something heavy, they produced a sound which slowly developed into words such as "heave" and "lift." Therefore, if they didn't want to memorize their favorite growl-sound and use it over and over again, this sound would seem to be random. However, these growls would not be accounted as words in a lingual meaning since they would seem unlikely to fall into consonant-vowel patterns (Rice 1976). The yo-he-yo theory does, however, have a benefit since it is responsible for the inducement, the cause, and the aim of the language. It describes language as emerging from a need to communicate and for making the engagement among men possible in organized activity, rather than seeing language resulting from a cave dweller imitating an animal's howl to assist him while he was away for his dinner (Barber 1965). The yo-he-yo theory can be found in the literature as "Yo-heave-ho theory" and "Social interaction source," all of them proposed that the origin of speech begun as growls and moans (Mandavilli 2016).

Notwithstanding the above, evolution plays an important role since it claims that human society developed gradually because men began thinking of new things to do and began doing them collectively. What makes this theory interesting, however, is the query of what motivates the speechless cavemen move a boulder in the first place since language emerged from the growls and moans of their teamwork. Unfortunately, the origin of grammatical structure is not explained or how a social system got started void of language (Rice 1976).

Conclusion

It is a matter of fact that language is a human trait. All efforts to explain how language emerged have failed because of the absence of knowledge concerning the origin of any language. An important factor for the inability to acknowledge the origin of language is because none of the animals possesses any transitional form of communication. As a consequence, Muller could not differentiate between humans' linguistic faculties and the growls or sounds of animals. Also, the cultural roots of various hand gestures did not suggest verbal communication. Last but not least, most of his theories did not explain the origination of different ideas or things that do not produce any sound, and this resulted to a limited vocabulary of the languages. As a result, there could not be an explanation of the origin of names of such concepts, if his theories were chosen as the origin of language.

Cross-References

- [Darwin on the Origin of Language](#)
- [Early Theories of Language](#)

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Muller's Theories on Language Evolution

► Early Theories of Language

Müllerian Association

► Müllerian Mimicry

Müllerian Mimicry

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Synonyms

Arithmetic mimicry; Müllerian association; Mutualistic mimicry

Definitions

When two or more harmful or unpalatable animals develop similar appearances as a shared protective device.

Introduction

Many prey possess chemical compounds or other noxious substances that they advertise to potential predators via conspicuous warning signals (Sherratt 2008). Mimicry describes the resemblance of one animal (a mimic) to chemically defended species (the model), such that a third animal (usually a predator) is deceived by the similarity. Mimicry is conventionally divided into two separate categories depending on the phenotype of the mimic: Müllerian and Batesian mimicry.

In Batesian mimicry, named for its discoverer, Henry Walter Bates (1862), an undefended harmless species evolves a warning signal (e.g., visual, auditory, or even behavior) that imitates a harmful model species. Batesian mimics gain protection against predators due to their being perceived as harmful. In contrast, Müllerian mimicry describes the phenomenon where two or more defended species, that may or may not be closely related and share one or more predators, mimic each other's warning signals. It is named after the German naturalist Fritz Müller who first proposed the concept in 1878.

A History of the Idea

In his travels in the Amazon, Henry Walter Bates (1862) observed that as well as palatable species evolving to resemble defended species, there were cases where a number of defended species evolved to resemble one another. He proposed that this was due to species sharing similar environmental conditions. However, Fritz Müller suggested an alternative reason. In one of the first clear mathematical treatments of natural selection, Müller hypothesized that to learn to avoid prey with a particular visual signal, predators must kill a fixed (i.e., density-independent) number of that prey. If true, resemblance between a number of prey species would result in a divided cost of educating the predator species. Consequently, an increase in the number of visually similar co-mimics spreads out the costs of predator education between the co-mimics, and Müllerian mimics enjoy strength in numbers: the relative risk of predation on each individual species is reduced. Hence, two defended species that have separate signals pay a higher mortality cost during predator learning than two species that, through mimicry, resemble each other. Although this idea initially met with opposition from Müller's contemporaries (see Ruxton et al. 2004), the benefits of shared resemblance of unpalatable species are now commonly accepted.

Müllerian mimicry has been explored comparatively, theoretically, and empirically (Sherratt 2008). Selection for color pattern similarity among mimetic butterflies in the wild is strong, and research in controlled laboratory settings has uncovered the selective pressures leading to signal similarity.

Examples of Müllerian Mimicry

Müllerian mimicry is common in nature, with perhaps the most obvious example being the black and yellow striping of bees and wasps (hymenopterans). Müllerian mimicry has also been documented in frogs, larval and adult lepidoptera, snakes, coleoptera, fish, and birds (Sherratt 2008). The most celebrated example of

Müllerian mimicry is observed in the heliconid butterflies of South America, which involves a large collection of similar-looking species – a “mimicry ring.”

There is a long and distinguished history of research on mimicry in heliconids. The Heliconiinae is comprised of 46 described species that all contain cyanogenic glycosides and have conspicuous brightly colored wing patterns – aposematism. Mimicry in *Heliconius* often involves convergence between species within the same genus, and frequently between pairs of species. For example, *Heliconius cydno* generally mimics *H. sara*/*H. sapho*, while *H. melpomene* always mimics *H. erato*. These latter two species are distributed throughout South and Central America, and mimic one another wherever they co-occur.

The Evolution of Müllerian Mimicry

There have been two schools of thought on how mimicry evolves. One proposes that shared resemblance evolves through gradual change, the other suggests that mimicry evolves by large mutational leaps toward similarity, followed by gradual evolutionary fine-tuning of the mimic's appearance toward the model. The second proposal, called “the two-step hypothesis,” is supported by recent comparative genomics research showing that large-effect chromosomal inversions give rise to different morphs, but that the evolution of accurate mimicry likely requires a more gradual accumulation of multiple genetic changes (Nadeau et al. 2016). The two-step hypothesis relies on the assumption that predators generalize their avoidance between models and mimics with a level of shared resemblance (Leimar et al. 2012).

Müller's Idea About Predators Attacking a Fixed Number of Prey During Learning

One of the specific assumptions of Müller's theory is that predators must attack and consume a fixed number of each distinct defended species

before learning to reject them. To date this hypothesis has only been tested in laboratory experiments with captive predators. There has been no support for the “fixed n” idea. In fact, several experiments have reported increases in the numbers of unpalatable prey attacked as the abundance of that prey type increases (Sherratt 2008). This is perhaps unsurprising, because animal cognition is rarely expected to be as simple as learning by a fixed amount of experience. An outstanding question of fundamental importance is how predator learning proceeds in a wild setting – how often does a predator meet a model or a mimic in a season, or during its lifetime, and does it ever learn to completely avoid aposematic prey? Questions like these are challenging to address, but could reveal more of the underlying dynamics of mimicry.

Evidence That There Is Selection for Signal Similarity

Several field studies have found evidence for the benefit of sharing a common warning signal (reviewed by Sherratt 2008). In mark-recapture experiments on *Heliconius* butterflies, wild avian predators select against rare and unfamiliar warning signals, and locally common signals have better survival. For example, Mallet and Barton (1989) transferred *H. erato* across the hybrid zone and monitored the survival of the transferred individuals compared to control species which were marked and released. The authors found that more of the rare artificial migrants were attacked and less recaptured than controls. Selection for color pattern similarity among mimetic butterflies in the wild was strong.

However, evidence that predators select for increasing signal similarity is less clear when research is conducted in the laboratory. By observing the foraging behavior of wild-caught captive great tits (*Parus major*) on artificially defended prey, many researchers have found that co-mimics with visually dissimilar appearance can still benefit from strength in numbers, with predators generalizing their avoidance to dissimilar signals (discussed in Rowland et al. 2010). However, mimicry *can* provide substantial

protection during predator learning in the lab, and in the manner proposed originally by Müller, especially if prey are visually distinct and not easily generalized (Rowland et al. 2010), of if the system is more similar to the real world. In a study by Ihalainen et al. (2012), great tits foraged in simple or complex prey communities. Ihalainen et al. found that predator learning was slower and more costly to nonmimetic prey in visually complex prey environments. Therefore, mimicry would be beneficial in complex prey communities, because of the costs of predator education, just as Müller predicted. Interestingly, many studies have found evidence that pattern similarity might also benefit prey in the later stages of the learning process (note that Müller’s ideas are about naïve predators). These findings in conjunction with the field experiments discussed previously suggest that once birds are familiar with a particular warning color or pattern, experienced predators can also select for pattern convergence (Rowland et al. 2010).

Species Differences in Defensive Chemical Concentrations, and Its Consequences for the Evolution of Müllerian Mimicry

Several authors have proposed the existence of a “mimicry spectrum,” of which Batesian and Müllerian mimicry could be thought of as the extremes. This spectrum comes from the continuous range of chemical defense levels of mimics, and the role of predator psychology in selecting for signal similarity (Sherratt 2008). It is well documented that different predators vary in their ability to overcome the chemical defenses of aposematic prey, and it has been suggested by some authors that this can produce a hybrid between Batesian mimicry and Müllerian mimicry. In cases where predators profit from attacking prey with lower levels of chemical defense, model species may not benefit from coexistence with a visually indistinguishable but less-defended mimic, and lose protection when the mimic form is abundant. Therefore, mimicry between two species can be parasitic and Batesian-like (or quasi-

Batesian) and not necessarily mutualistic and Müllerian. Quasi-Batesian mimics could face much stronger selection for signal accuracy than might Müllerian co-mimics (Sherratt 2008).

Müllerian Mimicry and Speciation

Differences in color patterns between co-mimics can lead to reproductive isolation via pre- and post-zygotic mechanisms. This is because recombinant wing patterns are usually nonmimetic and are selected against by predators – a form of hybrid incompatibility. Furthermore, model species are also less attracted, or not attracted at all, to hybrids as potential mates – a form of post-zygotic isolation. Furthermore, *Heliconius* species' mate preference for similar wing patterns is also genetically linked to the genes that underlie the wing color that distinguishes them from other species. This reinforces post-zygotic isolation.

The Molecules Behind Mimicry

Research on heliconius butterflies has unraveled the genomic bases of how mimicry evolves and varies. Advances in sequencing technology and comparative genomics, coupled with recombination mapping have enabled scientists to accurately pinpoint candidate genomic regions responsible for mimicry.

The major loci involved in wing pattern development are collectively referred to as the “wing patterning toolkit” (reviewed in Kronforst and Papa 2015), and comprise: *optix* – a transcription factor that places red patches onto the wings, as well as the black regions on the central part of the wing; *WntA* which is associated with melanization of the fore and hind wing; *poik* – a cell-cycle regulator that is involved in patterning of the central areas of wings, and a gene, *cortex*, that probably regulates pigmentation patterning (Nadeau et al. 2016).

Conclusion

The study of mimicry has been a test bed for the theory of natural selection. Since Müller's

hypothesis, the molecules responsible for mimetic resemblance have been uncovered. We now also have evidence that mimicry evolution is driven by predation pressure: species exposed to the same predators benefit from sharing warning signals. However, there is still a need to investigate how avoidance learning and predators' response to mimetic symbols occurs in the wild. This is an important question because if predators learn to avoid unpalatable prey differently in simple and complex communities in the lab, then how does learning proceed in natural conditions where we don't know how often they meet aposematic prey, if they meet them sequentially or simultaneously, and if they ever fully learn about aposematic prey. There is still much to discover.

Cross-References

- ▶ Aposematism
- ▶ Butterfly Mimicry
- ▶ Communication, Cues, and Signals
- ▶ Frequency-Dependent Selection

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Multi-cultural

► Cross-Cultural Variation

Multiculturalism

► Cross-Cultural Similarities

Multilevel Selection Theory

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Synonyms

Group selection; Inclusive fitness theory; Individual selection; Kin selection

Definition

Theoretical framework that presumes that selection can occur at an array of organizational levels from the gene upwards.

Multilevel Selection Theory

Multilevel Selection (MLS) Theory is the synthesis of individual selection as popularized by researchers including Williams (1966) and group

selection as championed by researchers including DS Wilson (1975). More precisely, MLS theory offers a pluralist and flexible analytical framework that recognizes that selection occurs at different levels of organization as a function of context. As Wilson and Sober (1994) illustrated, when there is both phenotypic uniformity and shared fate at a given level of organization, then selection can be expected to occur. Consequently, if there is no phenotypic uniformity or shared fate among individuals in a given set of individuals, then one would expect selection to occur at the level of individuals. On the contrary, if individuals in a given set do share a common fate with one another and demonstrate phenotypic uniformity, then one would expect selection to occur at the level of sets wherein sets are being selected across evolutionary time relative to other sets in a given population of sets.

In the case of humans, there is obviously not genetic uniformity within any groups (outside of twin-pairs); however, there can certainly exist phenotypic uniformity as well as shared fate within groups since cultural transmission is dynamic and not isomorphic with underlying genetic variation (Wilson and Kniffin 1999). Indeed, Wilson and Sober (1994) review the fact that it is undisputed that genes function as “replicators” as a fundamental level of evolutionary accounting; however, conditions can and do emerge whereby units of organization above genes and above individuals can emerge and function as “vehicles” on which selective retention can occur. For example, Kniffin and Wilson (2010) review three case studies where group-level incentive structures within a population allocated rewards so that individuals would benefit if they served group-level interests.

Among non-human species, there exist numerous laboratory demonstrations whereby selection at group or community levels has been cultivated – often for beneficial outcomes. For example, Swenson et al. (2000) successfully selected for soil ecosystems that more effectively degraded an environmental toxin. More recently, with the benefit of genetic sequencing technology, researchers have demonstrated that selection at the level of soil microbiomes can be effected in ways that yield valuable traits in economically important plants

(Garcia and Kao-Kniffin 2018; Panke-Buisse et al. 2015). Criticisms (e.g., Williams 1966) of group- or multilevel selection have traditionally acknowledged that it can be artificially effected but have been skeptical that it occurs in nature except for species where there is uniquely high genetic relatedness among individuals within groups (i.e., social insects [Seeley 2009]). Reviews of naturalistic evidence from species such as African buffalo indicate, though, that such dynamics are visible in naturalistic conditions (Prins 1996; Wilson 1997).

MLS theory has been the subject of contentious debate at various points over the past five decades partly because it has been central to debates on the evolution of altruism and selfishness where a variety of additional theories (e.g., kin selection and inclusive fitness theories) have been presented as competing frameworks. Consistent with the intention of MLS theory to be integrative and holistic of more specific theories, Wilson and Wilson (2007: 345) summarize the MLS perspective with the pithy set of statements that “Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary.” In other words, selection occurs at the level of individuals when individuals are selfish while selection occurs at the level of groups when individuals are altruistic within their own groups. Debate continues on these perspectives; however, there has, at least, been important refinements over the past five decades in how such positions are argued whereby (1) MLS theory offers an integrative framework that is inclusive of both individual- and group-level selection and (2) relatively new genetic sequencing technologies are increasingly facilitating a better understanding of the mechanisms through which selection at multiple levels (from the gene “upwards”) can be examined.

Cross-References

- [E. O. Wilson](#)
- [Examples of Group Selection](#)
- [Group Selection](#)
- [Kin Selection Hypothesis](#)
- [Problems with Group Selection](#)
- [Selfish Gene, The](#)

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Multilingualism

- [Bilingualism](#)
- [Critical Period of Acquisition](#)

Multiple Mating

- [Polygamy \(Behavioral Ecology\)](#)

Multiple Matings

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Synonyms

Extra-pair copulations (EPCs); Promiscuity

Definition

Copulate with more than one sexual partner.

Introduction

Empirical studies and theoretical models have used the number of sexual partners (i.e., the level of *multiple mating*) as a proxy for lifetime reproductive success (RS) or fitness. This is not surprising considering the close connection between mating and reproduction. In the case of males, the relationship between these variables is considered positive, whereas for females an intermediate optimum is predicted (Fig. 1a). However, when males invest heavily in each mate an intermediate optimum is also expected (Fig. 1b). On the other hand, it is recognized that sperm competition, postcopulatory cryptic choice, and postcopulatory sexual conflict could strongly modify the relationship between reproductive success and number of mates (Shackelford and Hansen 2015). These processes could partially explain why in different human societies the high proportions of cuckolded males, resulting from female multiple mating, are not reflected in high rates of extra-pair paternity (Larmuseau et al. 2016) (Fig. 1).

The relevance of the number of sexual partners for evolutionary interpretations is also evident in

definitions of animal mating systems, which include the number of mates as an essential component. Mating systems are usually considered species-specific, although alternative strategies are included in recent discussions. Mating system definitions have been extremely helpful for organizing interspecific variation in, and identifying selective pressures acting on, reproductive behavior. Nevertheless, even when alternative strategies have been identified, each strategy encompasses individual variation in the number of mates due to strategic decisions, constraints, and chance. Hence, the study of individual variation in number of mates could provide interesting perspectives on the proximate causes and selective pressures acting on individual decisions, especially in species with a long reproductive lifetime, such as humans.

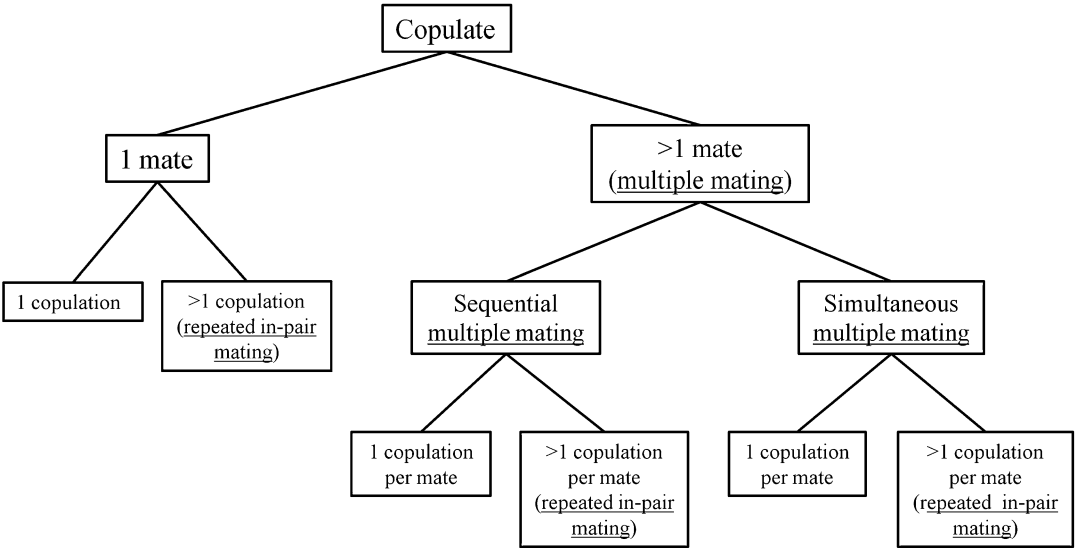
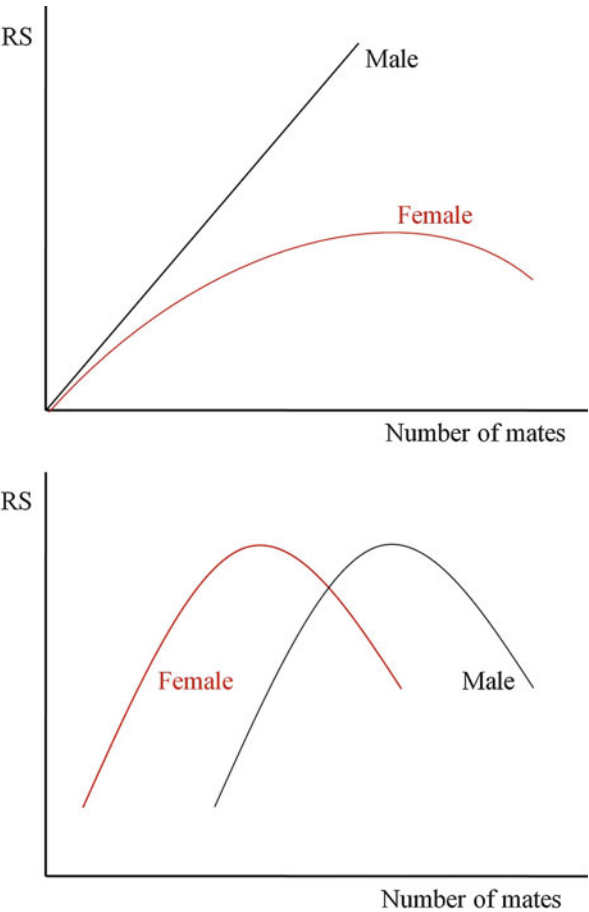
Identifying the Alternatives

When an individual reaches reproductive age she/he will face a number of lifetime options regarding the number of reproductive partners. In Fig. 2 these options are illustrated. An individual could decide or be able to copulate with just one mate or with multiple mates (the alternative of remaining virgin for life is also a possibility). The route taken could depend, for example, on the sex appeal of the individual or the amount of resources she/he controls. For example, an unattractive male or a male without resources could be constrained to mate with only one female, probably of low quality, or try an alternative strategy such as become a rapist. In addition, if he is able to get one female, he could just mate once (this would be the case if he is a rapist or if he is involved in a short-term interaction with the female) or establish a long-term relation in which he performs multiple *in-pair copulations* with the female (which could reduce, for example, the negative effects of female extra-pair copulations [EPCs] or increase the strength of the pair bond) (Fig. 2).

In contrast, if the individual is able, and decides, to copulate with multiple mates, she/he could opt for a series of short-term relationships in which she/he mates once with each partner

Multiple Matings,

Fig. 1 Relationship between individual reproductive success (RS) and lifetime number of sexual partners (number of mates). (a) Male RS is limited by number of mates, while female RS has an intermediate optimum determined by the costs and benefits of multiple mating. (b) Both male and female RS have an intermediate optimum determined by the sex-specific costs and benefits of multiple mating (in the example, the female optimum is smaller than that of males)



Multiple Matings, Fig. 2 Diagram showing the alternatives open to an individual female or male regarding lifetime number of sexual partners (number of mates)

(sequential multiple mating) or she/he could perform repeated in-pair copulations with each of a number of mates; a mixture of these alternatives is also possible, as when a female exhibits simultaneous multiple mating by establishing a long-term relationship with a male and, at the same time, having EPCs with other males (this could benefit the female if she improves the quality of her offspring by mating with a high-quality “lover” who fertilizes her eggs, while being supported by a male that provides better parental care than the attractive male).

Analyzing individual mating frequencies improves the ability to identify ecological and phenotypic constraints on multiple mating and thus to understand the selective pressures and adaptive traits affecting variation in the number of mates and of copulations. For example, several studies have focused either on multiple mating or in repeated in-pair copulations, but trade-offs between these variables (due, for example, to constraints in time or ejaculate production) have been rarely considered, as well as the influence of factors such as health or age on these trade-offs. However, as shown in the following sections, most evolutionary perspectives on human mating frequencies have used the traditional mating systems approach.

Multiple Mating in Humans: Patterns

Although most contemporary human societies practice socially imposed monogamy, this system often enables simultaneous multiple mating. An example of simultaneous multiple mating is EPCs in which sexual couples involved in long-term romantic relationships simultaneously seek EPCs with additional partners. EPCs are very common in humans, appearing approximately in 84 % of societies (Simmons et al. 2004; Anderson 2006). Nevertheless, its frequency and intensity of occurrence is highly variable. For instance, in the “Tsimane,” a forager–horticulturists society living in the lowland rainforests in the Beni region of Bolivia, 31 % of married males reported EPCs during the first 5 years of marriage (Scelza 2013). Similar rates were reported by the Himba

society wives, a seminomadic pastoral population living in the northwest corner of Namibia (Scelza 2013). Female EPCs are also common in several societies from Northwestern Europe and North America, with approximately 20 % of women reporting cases of sexual infidelities, slightly lower than those reported by men (Simmons et al. 2004). Nevertheless, in the “iKung,” a hunter-gatherer society from the Kalahari Desert of Namibia (Anderson 2006), EPC rates of 2–5 % have been reported, whereas in Hong Kong EPC rates of 8 % in men and 1 % in women have been reported (Anderson 2006).

Multiple Mating in Humans: Selective Pressures and Adaptations

The close relationship between mating and reproductive success, as well as the convergence and divergence of male and female reproductive interests, frequently will result in intense selection on male and female traits related to mating frequency and, thus, in adaptations to achieve optimal mating rates (Fig. 1). The RS of men is constrained by the number of fertile women they can mate with, but other factors, such as high paternity uncertainty, also could favor multiple mating in males as a way of increasing the probability of fathering at least some children. On the other hand, selection also can favor male traits that reduce multiple mating in females, such as sexual jealousy, mate guarding, and frequent in-pair copulation (Shackelford et al. 2006).

In the case of women, multiple mating could be selected to obtain genetic benefits for their offspring (Scelza 2013). For instance, female EPCs may allow producing offspring with higher heterozygosity, thus increasing their probability of survival, or offspring whose fathers are of better genetic quality. Moreover, female multiple mating could result in material benefits. For example, a woman could receive resources from each of their sexual partners, she could decrease the time to establish a new marriage when the previous relationship dissolves through death or divorce, or she can reduce infanticide risk (Scelza 2013). However, adaptive EPCs by women select for male

adaptations against female EPCs, such as different forms of punishment, including reductions in paternal investment or even homicide.

An intriguing aspect of human sociosexual behavior is why socially imposed monogamy is exhibited by most contemporary societies, instead of another mating system, such as polygamy, which could allow males and females to gain some of the potential benefits previously mentioned. In fact, most current societies have norms that sanction multiple mating (i.e., EPC), even though such sanctions also affect those who impose the norms (Hauert et al. 2007); for instance, most contemporary societies who practice socially imposed monogamy have a patriarchal origin and punish men (although usually not as hard as women) that incur in EPCs (Hauert et al. 2007). However, besides reducing cuckolding risks, other selective pressures could favor the development of norms against multiple mating. Human pathogens are a fascinating possibility. Exposure to sexually transmitted bacterial infections (STIs), such as syphilis, gonorrhea, or Chlamydia, may impose an enormous selective cost (Bauch and McElreath 2016), particularly in populations living in conditions similar to those experienced by humans during most of their evolutionary time, such as limited access to health services and contraceptive methods (Apari et al. 2014). In these populations multiple mating increases morbidity of STIs and thus the costs for individuals and their offspring, such as high rates of infertility and of mortality (Apari et al. 2014). In addition, there is evidence that seminal fluid proteins have a negative effect on the immune status of females, probably resulting from changes in the expression of immune genes in the cells of the female cervix following reception of a male ejaculate (Sharkey et al. 2012). Furthermore, persistent postmating immune changes produced by multiple mating can result in environments favorable for the invasion of other sexually transmitted pathogens, such as herpes simplex, human papilloma, and hepatitis B or C viruses (STVs; Sharkey et al. 2012). It is interesting to note that the negative effect of seminal proteins on female immune status could be increased not only via multiple mating but also as a result of repeated in-pair

mating, leading to the hypothesis that those seminal proteins evolved as a sexually antagonistic adaptation against female cuckoldry. Thus, norms against multiple mating could be favored not only as adaptations for increasing paternity certainty but also as mechanisms for decreasing the risk of STIs and STVs contagion (Bauch and McElreath 2016).

Conclusion

Multiple mating is observed in most human populations, although at different frequencies, and it seems likely that it has been present during most of the history of the species as attested by the psychological, physiological, and cultural adaptations observed in men and women. Sexual differences in benefits and costs derived from multiple mating indicate that sexual conflict over multiple mating is common. Although sexual selection probably had a strong effect in the evolution of multiple mating in humans, other selective pressures, such as those derived from diseases directly or indirectly related to sexual promiscuity, need to be carefully studied for a full understanding of the causes and consequences of multiple mating.

Cross-References

- [Aggression](#)
- [Copulation](#)
- [Human Copulation](#)
- [Infidelity](#)
- [In-Pair Copulation](#)
- [Marriage](#)
- [Mate Retention](#)
- [Mating Strategies](#)
- [Mating Systems](#)
- [Sexual Behavior](#)
- [Sexual Conflict](#)
- [Sexual Conflict Theory](#)
- [Sexual Reproduction](#)
- [Sperm Competition Theory](#)

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Multiple Memory Systems

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Synonyms

Declarative memory; Episodic memory; Implicit memory; Localization of memory substrates

Definition

“Multiple Memory Systems” is a theory that is based on scientific and evolutionary evidence, which lead us to conceptualize memory, not as unitary system, but multiple systems that work independently, in synchrony, and/or in competition with each other.

Introduction

There are several memory systems, which have been identified (Poldrack and Packard 2003). Depending on the memory function(s) that are needed for the organism to encode, learn, maintain, or recall information, these systems are thought to be able to work independently, in unison/cooperation, or even compete with each other (Sherry and Schacter 1987).

They work independently when, for example, you are driving with memorized directions, given to you for a place in the city, while at the same time you are not forgetting the specific time that you have to attend an important meeting and you are concurrently contemplating the details of your presentation at the meeting.

The cooperation of memory systems is apparent, for example, when positive emotional memories come to you when you walk into a bookstore and the smell of pencils and school supplies hit your nose, and remember suddenly small details from your school years start coming back to you.

Their competition is evident in our everyday life as well. For example, a memory system responsible for encoding factual information could be “interrupted” by a competing memory system responsible for emotional information. For example, the memorized information for a neuro-anatomy test that you are taking in class right now is not very clear in your mind during the test, as you suddenly remember last day’s upsetting phone call from a friend.

We theorized that our memory and its systems have been evolving along with their associated structures in our brain. Our memory systems, which are defined as “...an interaction among acquisition, retention, and retrieval mechanisms

that is characterized by certain rules of operation...” (Sherry and Schacter 1987) are therefore evolved traits that are in place for improving our survival chances and reproductive success as a species. There are a few different approaches in categorizing and defining memory systems, but these approaches are not in contrast with each other, but coexist and represent different types of scientific approaches. Therefore, the neuroscientific approach will naturally approach the matter from a structural neuroanatomical worldview, while the evolutionary perspective will capitalize on the changes observed through the evolution of our species.

Neuroscientific and Cognitive Approach

Murray et al. (2017) postulated that neuroscience and its subspecialties, such as neuropsychology, neuroimaging (e.g., functional Magnetic Resonance Imaging-fMRI, spectroscopy, Computerized Axial Tomography-CAT, just to name a couple well-known neuroimaging methods), neurodevelopment, pushed towards learning massive information about our brains following centuries of knowing minimal information about our brain and its function. This vast amount of knowledge generated more research and thoughts about our memory and its functioning, and therefore, we started developing evidence supported hypotheses and theories about our brain’s memory systems.

In addition, the associations between brain damage in certain locations and the followed behavioral disorders (as in the case of H.M., the famous patient with global amnesia) allowed making inferences about memory dysfunctions and brain areas associated with certain memory systems. The first and second world wars (followed by numerous other regional wars) produced a large number of brain damaged individuals, who needed to be cognitively assessed and, in more recent years, scanned for deciphering the presence and extent of brain damage. These individuals, via their acquired brain injuries, taught us a lot about memory, brain areas that control memories, and in return directed us to theories about memory systems. After all, memory is one of the

first cognitive functions, which are affected by brain injuries (Rabinowitz and Levin 2014).

In neuroscience, it is widely accepted that the following memory systems exist (Murray et al. 2017):

1. A memory system that involves our personal learned experiences and habitual information is associated with our basal ganglia. For example, our memories about the name of a location that means a lot to us or a movie that we really liked.
2. Our explicit memories are mostly connected with functioning in medial structures of our temporal lobes (medial structures). For example, factual information about statistical formulas that you learned for a test.
3. Emotional information and emotional memories are mostly correlated with our amygdala. For example, negative emotions that are brought up after visiting a hospital that reminds you of health issues that you had in the past.
4. Memories about movement and motor processes are connected with the function of our cerebellums.
5. The priming of behavior is connected with our sensory cortices.

A cognitive science and cognitive psychology take on the memory systems follows a similar world view with the neuroscientific approach with mostly semantic differences between the two. Here three memory systems are recognized. Each memory system receives sensory and emotional information and in return, each memory system produces its output. Here are three memory systems:

1. The Procedural Memory System, which is highly associated with the cerebellum and caudate nucleus, processes action-related memories and memories related to motor processes, such as cycling (Hsiao and Chai 2003).
2. The Declarative/Explicit Memory System is mainly associated with the hippocampus and is responsible of mindful encoding of information and memories of facts and events. Our semantic (e.g., news pieces) and episodic

memories (private living experiences) are processed here.

3. Amygdala is associated with our Emotional Memory System, and therefore it is related to our emotional memories.

Evolutionary Science Approach

According to evolutionary cognitive scientists (Murray et al. 2017), there are seven memory systems that were developed through human evolution. These are:

1. Our Reinforcement Memory System, which describes memories that are made stronger or weaker via reinforcement schedules. For example, memories that are strengthened because they are associated with rewards (e.g., remembering your partner's birthday strengthens your relationship).
2. Our Navigation Memory, which we developed in order to store locations and directions to help us find our way in our environment. For example, remembering how to get around and short cuts in a large Business Building.
3. Our Biased Competition Memory, which compares new information we come across to older stored information in order to identify the need for new learning or expanding on older learned information. For example, in a child, learning that a dog is not a larger cat may create a new memory category for dogs.
4. Our Manual-Foraging Memory, which developed after we started walking on two legs and our arms and hands became free for action and collaborate better with our vision on visual-spatial integration tasks. This is the memory that allowed us to learn how to farm, hunt, and work manually in an environment that requires visual motor integration.
5. Our Feature Memory, which stores newly learned information according to its individual features, such as color, size, weight, surface. For example, learning that bears with black and white large spots are pandas.
6. Our Goal Memory, that helps us use stored and new information with our goal-directed

behavior. For example, recalling what history taught us may lead to better politics, in order to avoid wars.

7. Our Social Subjective Memory that encodes information about how we view our selves and how we view others in order to maximize our self-awareness and social behavior. For example, our stored self-image and awareness of our social self is compared with other more social individuals, who seem better than us, and this leads us to improve our social behavior.

Conclusion

There are multiple memory systems and in theory, at least, organize our memories according to their nature, type, and brain location(s) that they are stored or processed. Our Memory systems could work in full cooperation with each other, individually, or compete with each other in our everyday lives. All memory systems exist in order to help us survive and succeed as human species. In order to fully comprehend and keep learning about our memory systems and their evolution and value, we need to work in a multidisciplinary environment that combines knowledge from numerous sciences such as (just to name a few) cognitive psychology, neuroscience, neuropsychology, evolutionary science, and neuroanatomy.

Different approaches in defining and identifying memory systems are not in competition with each other but coexist and are completing each other. For example, a neuroscientific approach to memory systems would certainly focus on brain loci, while an evolutionary approach to memory systems would concentrate on how our memory systems changed through our evolution to better serve our survival and reproduction needs.

Cross-References

- [Evolution of Memory, The](#)
- [Different Functions of Memory](#)
- [Inceptive and Derived Memory](#)
- [Personal Memory](#)

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Murder

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Synonyms

[Homicide, to kill](#)

Definition

Taking the life of another living being unlawfully.

Introduction

The act of murder has existed as long as humanity itself has existed. It is very unlikely, if not impossible, that murder will cease to be an issue during the course of humanity's future.

An Evolutionary Overview of Murder

Murder, or the act of killing another, has been around since the beginning of time and most likely well before recorded history. The act of killing another human carries the greatest cost to

the victim. After all, the recently deceased is no longer able to provide for themselves or their surviving families. From an evolutionary standpoint, this would be the greatest cost to one's fitness; premature death without reproduction is a significant issue. It is important to note, however, that humans are not the only beings that commit murder. The act of murder has been observed within chimpanzees and other primates as well. Researchers Watts and Mitani found that "Observations support the arguments that infanticide has been an important selective force in chimpanzee social evolution and that females with dependent infants can be at great risk near range boundaries, but why male chimpanzees kill infants is still uncertain" (Watts and Mitani 2000).

Historically, there has always been some form of punishment for the act of killing. Some of the earliest recorded history showed records of punishment, including the famous Hammurabi's Code, which was recorded to approximately 1754 BCE. Hammurabi's Code covers one law pertaining to murder which states, "If the wife of one man on account of another man has their mates (her husband and the other man's wife) murdered, both of them shall be impaled (Claire n.d.)." This example demonstrates that ancient civilizations had laws in place to discourage and punish people from committing murder. In ancestral times, it is quite possible that the act of murder carried consequences as well. Ancestral groups are anticipated to have travelled within groups of approximately 150; therefore consequences to murder would have been severe. For example, the murderer could potentially face ostracization from the group and could have disastrous results for the survival of the murderer.

In modern society, there is no country where murder can legally take place. For example, the very definition of murder is the *unlawful* killing of another. The term "lawful murder" can be considered an oxymoron; the very meaning contradicts itself. Further, all modern judicial systems consider crimes that involve murder to be very serious, and these crimes often carry serious punishments. When it comes to murders within the family unit, studies conducted within the realm of evolutionary psychology seem to help offer an explanation. A study conducted by

Daly and Wilson reported that “Most ‘family’ homicides are spousal homicides, fueled by male sexual proprietariness. In the case of parent-offspring conflict, an evolutionary model predicts variations in the risk of violence as a function of the ages, sexes, and other characteristics of protagonists, and these predictions are upheld in tests with data on infanticides, parricides, and filicides” (Daly and Wilson 1988). This study helps shed light into some potentially relevant motives regarding murder in ancestral times.

Conclusion

In conclusion, the act of murder is as timeless as life itself. Humans are not the only species that is known to commit murder, as intentional killings have been documented within certain ape populations. Further research into the motivations of murder will hopefully shed additional light into this topic.

Cross-References

- [Evidence of Intentional Killing](#)
- [Homicide Adaptation Theory](#)
- [Humans: Within-Group Conflicts](#)
- [Nonhuman Primates: Within-Group Conflicts](#)
- [Victims of Violence](#)

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Murder by Design

- [Homicide by Design](#)

Muscle

- [Hollywood Actors](#)

Muscle Conduction Velocity

- [Cortical Neurons and Conducting Velocity](#)

Music

- [Music and Hormones](#)

Music and Hormones

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Synonyms

Ancient music; Art; Artistic expression; Contralto; Dopamine; Early castration; Emotions; Estradiol; Hormones; Mezzosoprano; Music; Nitric Oxide; Octave; Oxytocine; Prepuberal gonadectomy; Soprano; Tenor; Testosterone

Definition

Music is an art form and cultural activity whose language is organized in time with logic and sensitivity the sounds and silences. Originally, the word derives from Greek *mousiké [technē]* that means the “technique of Muses.” It combines harmony, melody, rhythm, pitch, meter, timbre, etc. to create psychoanomic states with hormones, steroids, and other metabolic endogen compounds contributing to those effects.

Introduction

Musical stimuli in humans have been proved to be related with emotional areas of the brain such as insula, cingulate cortex, hypothalamus, hippocampus, amygdala, and prefrontal cortex (Boso et al. 2006). Probably nobody would disagree in the asseveration music has an effect over our moods, reducing stress, increasing well-being, improving social boundaries, and even over our motivation. When people needs to have energy to work, to drive, to train, to have fun, etc. music is a recurrent and common resource for natural energizing. Music has an effect on our metabolism and bodies which might guide toward those desirable mental states; in a human study, it was found an increase in saliva of 26 healthy young men, for their secretions of oxytocin release (positive social ties hormone) and a decrease for their cortisol release (stress, anxiety, and depression hormone) after exposure to music (Further details in chapter ► [“Anxiety”](#) and ► [“Depression”](#) of this encyclopedia.). Moreover, those cortisol levels positively correlated with the arousal level after listening several piano music pieces composed by Chopin (Ooishi et al. 2017). Nitric oxide (NO), endorphins, endocannabinoids, and dopamine have been suggested to play a role being released to the bloodstream with the musical experience (Boso et al. 2006).

Music also informs about our personal stories or cultural backgrounds, since we use to like what we have most listened, whether chosen or not. Or because inside a certain cultural or historical context, a virtuous musicians pursuits to do better than the most of the other people inside a group (Sloboda 1994). For instance, the question *“What kind of music do you like?”* is a very typical question to know someone better, at the beginning of any friendship, next to the question *“Do you come here very often?”* Not only a bidirectional connection to our mood or mental states but also what sort of music we rather, might be giving also information about ourselves, which in turn, enlightens about our personalities, specific personal characteristics, or cognitive styles (Greenberg et al. 2015). Two different forms of well-defined personalities were given

depending on our most pronounced musical preferences: type E (low rhythm, melodic songs, soft arousal) and type S (animated, intense, tension, or thrilling music). For this well-documented classification, they used NEO-PI-R tests results beside the participants physiological reactions to their preferential variety of musical stimuli (Greenberg et al. 2015).

Wherever they come from, most songs and music in general are written in a mathematical language, following cycles, loops, logic sequences (waves, mirror, dialogues) using several parameters well understood by anyone, rhythm, tonalities, accelerations, intensities, etc. The nature of learning to play music will depend on practicing, specifically how much and what is done during that practicing (Sloboda 1994), because playing music combines motor skills besides a high cognitive learning. And it magically happens, that even the simplest tune with the simplest notes in some order sequence might have a sense and good meaning for all of us in many different cultures, languages, latitudes (i.e., Fur Frère Jacques) (Sloboda 1994). Music gives comfort to our brains. However, beyond a doubt understanding music is not a matter of perceiving single stimuli into patters and relating those patterns one another, as Gestalt Psychologist has proved. The same musical stimuli may have many different meanings (Furtger detausk Meyer 1994) (Further details, see chapter ► [“Evolutionary Musicology”](#) in this encyclopedia.).

Although, on the other hand, there are some sort of music with dark legends or “diabolic attributes” associated. These types of music have been affiliated with delinquent manners, such as violence or aggressive actions, drugs abuse, or promiscuous sex. A recent study proved listening to this type of music might have an effect on risk-taking likelihood behavior, although those risks did not happen in areas of health or safety (Enström and Schmaltz 2017). It has been proved that heavy metal might cause different autonomic responses because it’s loud and intensity heavy change heart rhythm rate, respiration rate, and finger temperature in a group of young women (Cheng and Tsai 2016). The soft and most relaxing musical passages induced stronger parasympathetic activity compared with the loud

passages (Cheng and Tsai 2016). Specially for the high intensity or loudness, dancing heavy metal moving head with long hair might cause injuries to the neck or vertebrates. It has been calculated the injury is depending on the constant gravity, the acceleration of movement, and the velocity of the head movements relative to T1 vertebra and the center of balance of the head (Patton and McIntosh 2008). Heavy metal songs have an average tempo of 146 beats per minute and that tempo in head banging of a range of motion of the head over than 45 might predict to cause at least headaches and dizziness (Patton and McIntosh 2008). One clinical teenager case of vertebral artery aneurism after head banging by heavy metal young drummer was described (Egnor et al. 1991).

But not only heavy metal has been considered as diabolic, also pagan music such as folkloric songs or music full of intensity and energy, such as Rock and Roll or Jazz had negative moral values at some point or historical moment. In a study performed over professional women musicians (pianists), it was defined the positive concepts for music in terms of morality and logic are represented by regularity and prediction in musical structures, without much dissonances, roughness, and the narrower pitch range, while the opposite is true for the negativity for music (Mesz et al. 2015).

Castrati: male sopranos in opera

The ancient concept of castrato was given by Jacques Rousseau in 1778, as “*a musician (singer) who, in infancy, has been deprived of his genital organs in order to preserve his high voice*” (Sundberg et al. 2007). Castrati singers were able to produce a distinctive resonance as well as the high pitch, which cannot be matched even by great non mutilated male singers of today (King et al. 2001). They used to be taller than their noncastrated fellows because of the growth plates did not close and growth hormone continued its release. Their facial features used to be feminine (King et al. 2001), consequently they were playing and singing both roles male and female in opera for more than 200 years (1600–1850) (Melicow 1983; Zegers 2009), having their own

specific compositions such as George Frederic Handel did (1685–1759) with opera *Rinaldo* fitting their particular voice range. Castrati had developed the chest of a man, but their vocal cords were like those of a woman having their voices an incredible power, resonance, and control of breathing (Melicow 1983). The ranges of their voices were sometimes of four octaves, and they were carefully educated in vocal art and music (Sundberg et al. 2007). Sometimes they presented obesity, gynecomastia, and steatopygia, but they preserved their heterosexual desires, despite of their sterility (Melicow 1983). The voice of the last castrato, Alessandro Moreschi, can be listened nowadays to gramophone recordings from the beginning of past century. Each castrati voice had their particular color and characteristics; however, they all used to be described as sweet, soft, and ingratiating, or hard, brilliant, and penetrating (Sundberg et al. 2007).

In a study performed over Farinelli's skeleton (Andria, 1705 – Bologna, 1782), who was an Italian singer castrato very famous, it was observed his bones had interesting characteristics probably related to the effects of castration before puberty. Farinelli's real name was Carlo Maria Michelangelo Nicola Broschi. Farinelli presented long limb-bones, periphyseal lines and osteoporosis, bone mineral density, together with skull frontal bone affected by severe hyperostosis frontalis interna (HFI) (Belcastro et al. 2011). It is known the production of interleukin-6 (IL-6) by osteoblast is inhibited by estrogen and androgen, being the bone loss increased by ten times after menopause in woman or following castration in men mainly because of overproduction of IL-6 (Zanatta et al. 2016). Actually, Farinelli's HFI was classified as the most severe grade (type D), because the bone thickness ranges was from 9 mm at the sagittal sulcus to 21 mm at the maximally thickened area. Farinelli was a very good companion for the Spanish King Philip V who suffered for melancholia. He used to listen to Farinelli and his voice helped the King to improve his mood (Melicow 1983).

In general population, a study on 1532 autopsies during 4 years searching for HFI found 13 cases with this disease, 12 women and 1 man

(an incidence of 0.8%). It is characterized by thickening of the frontal skull bone associated with roughness of the endocranial surface in a graduation from type A (less severe) to type D (more severe) (Devriendt et al. 2005). Some behavioral disorders and hormonal diseases have been described with this pathology such as virilism, hirsutism, fatigue, somnolence, obesity, irritability, aggressive behavior, vertigo, polydipsia, polyuria, loss of sense of smell, Pick's disease, Alzheimer disease, cerebral atherosclerosis, dementia praecox, etc. (Devriendt et al. 2005). Many of them are related with the hypothalamus and its homeostatic metabolisms.

The preauricular sulcus was found to be different in castrati too. Farinelli had an absence of preauricular sulcus in his left hip bone, in the male common value range for this parameter (Belcastro et al. 2011). In nonmutilated people, 500 *ossa coxae* were analyzed and it was found a sex difference in this bone morphology, being in males more likely to display a short and narrow sulcus in bone, while in female, probably because of their different pelvic shapes and bells, their sulcus shape was wider and longer (Karsten 2018). Only 10.04% of females analyzed had nonpreauricular sulcus or very narrow.

Farinelli's voice could span over three octaves and his thoracic development allowed him to hold a note without interruptions for breathing during a whole minute. Unfortunately, for his honor and memory, his bones were not well preserved since they were located at the feet of his great-niece grave (Belcastro et al. 2011). He was described as having an inclination to melancholy that got worse with advancing age, perhaps because of T deficiency, having his androgen receptors functional. Perhaps some metabolic loop could have been modified and having some other indirect effect over corticosterone because of a different metabolic instructions for homeostasis balance. On the other hand, castrati were relieved from some testosterone effects over the metabolism, besides the lowering of voice, such as alopecia, thickening of the dermis, development of acne, and formation of male pelvis (Zegers 2009).

Another castrato singer gonadecomized before 12 years old was Gaspare Pacchierotti

(1740–1821) and his skeleton was also studied. He was posterior to Farinelli and also presented in his skeleton some androgen deprivation effects. The posture for singing requires an elongated neck compared with the shoulders, to allow air and sounds passing, specially for acute sounds such as erosion of cervical vertebrae. In Pacchierotti skeleton was found an insertion of respiratory muscles and muscles of the arms, and osteoporosis (Zanatta et al. 2016). The cause of his death was dropsy, being related the liquid metabolism with vasopressin and other hormones in the body, including testosterone. His teeth were white and a dental health preserved. However, an advanced dental erosion, probably due to bruxism, was described that might have happened because of a persistent distress (Zanatta et al. 2016) or for the physical pain caused by muscular atrophies.

As mentioned previously referring to heavy metal, bodily musical performances might induce injuries to the body. Musical ecstasy itself might drive into impossible body postures for long time without perceiving pain, perhaps because of endorphins or other hormones released. Body movements of wrist, torso, and head made by musicians while playing use to be related to specific structural musical features (Sloboda 1994).

Another well-known castrato singer was Domenico Caffarelli (1710–1783). He was a rival of Farinelli but with an unpleasant personality; he refused to sing for Royalty and he returned gifts from Royalty (Melicow 1983). Caffarelli's real name was Gaetano Majorano, but he adopted his artistic name the same of his "benefactor" who castrated him (Melicow 1983). For the surgical intervention of gonadectomy, narcotics such as opium were sometimes used for neutered kids, and the majority of victims died as result (Zegers 2009). A heavy psychological tax after this irrevocable intervention should still be considered for fully understanding of the betrayal happened to them who did not chose to lose their chances for procreation (Zegers 2009). However, a psychological defense mechanism to deal with this injustice might be the arrogance that is a common characteristic for some castrati singers; they used to believe their voices were more than divine, beyond god design. For instance, the castrati Giovanni Battista

Velluti (1781–1861) once quoted “*My throat is worth as much as a queen!*” (Melicow 1983).

However, on the other hand, testosterone might also have an effect over voice on adult singers. A case of a 22 years old man singer with hypogonadism (only one testicle and hidied in the inguinal canal) who was treated with adult exogenous testosterone was described. While hormonal treatment was supplied, his voice control for singing was elusive, a decreased pitch and an alteration of quality for his voice control happened. After hormonal treatment was over, his final voice range changed to a different level from a tenor to a baritone (King et al. 2001).

Many studies have been done trying to understand how these steroids might affect art, quality of sounds, or even long lasting of singer expectancies. A correlational analysis were done just comparing ages of deacease for singers of both genders. They compared mean ages of death for singer women and man in a particular population studied (from years 1900 to 1995, 292 female singers and 505 male singers) and they concluded that androgens might have a protective effect in woman lives (Nieschlag 2003).

Hormones in Musicians

A different gender expression of roles has been described for professional musicians with musical talents; male musicians show a higher rate of female-typical gender role behavior while the opposite (male-typical gender role behavior) is true for female musicians, compared to nonmusicians people (Hassler 1991). As a hypothesis to this fact is an excess of testosterone levels during development embrionary organizational period inside the womb, from weeks 20 of gestation on, has been discussed. Also a different brain hemispheres balance might happened for this particular early hormonal change which leads to a different distribution of tasks among brain hemispheres (Hassler 1991). Men, but not women musicians, have been described more often to be non-right-handed than their fellows nonmusicians (Hassler 1991).

Measuring the digit ratio and musical aptitude some interesting results were found, suggesting

the testosterone levels are related to musical talent but only in female groups (Borniger et al. 2013). Spearman correlation coefficient was found in between those with greater musical ability and their lower digit ratio, supposedly related to higher prenatal androgen exposure. Their musical talented and professionalism in music were measured with the test Advanced Measures of Music Audition (AMMA). A lack of differences in AMMA total raw scores in relation to testosterone was found, but testosterone exposure might facilitate the acquisition of musical aptitude, in terms of competitive skills for music inside a such as an orchestra (Borniger et al. 2013) (Further details, see chapther ► “[Resource Competition](#)” and ► [Status Competition](#) in this encyclopedia). Concerning to this difference in testosterone levels, some autoimmune disorders, related to the immune system and the complex interaction of testosterone with other hormones and neurotransmitters, have been described more often in musicians than in nonmusicians (Hassler 1991).

It has been proved that in humans and rodents, steroid hormones confer some sort of neuronal plasticity but also they have effects over the immune system or mood states. Several empirical evidences would make plausible to assert that music confers neuronal plasticity by affecting steroid hormones and alleviating or relieving stress (Fukui and Toyoshima 2014). Moderately higher levels of testosterone in women (positive correlation) and lower levels of testosterone in men (negative correlation) compared to their basal nonmusicians groups was found, indicating an effect of T in better talents for music. Moreover, a tendency but not significant to a positive relationship between a polymorphism (repeat length) in the androgen receptor (AR) and T levels was described (Fukui and Toyoshima 2014).

Studies with Rodents

A study on rats proved that exposing animals to music during 21 consecutive days significantly enhanced neurotrophins brain-derived neurotropic factor (BDNF) and reducing nerve growth factor (NGF) in rats hypothalamus (Angelucci et al.

2007). Music presented were recordings with no voice added, such as a compilation of New Age songs (Enya).

In a different study, classical music (Mozart) was exposed to Wistar rats and after that, they found changes in dopamine levels (DA), prolactin (PRL), and corticosterone happened in different brain areas (striatal nucleus-SN, prefrontal cortex-PFC, and mesencephalon-MS) (Tasset et al. 2012). Haloperidol is known to block dopamine receptors in the adenohypophysis, having an effect over the PRL releasing inhibiting its secretion. Music exposure was able to prevent the drop in DA prompted by haloperidol administration, specifically marked at the PFC and MS, having a lesser effect over the SN (Tasset et al. 2012).

Conclusion

Music is an ephemeral creation of art that exists in all the cultures in the world. They do happen in our brain while playing and just some time after played, producing emotions and metabolism reactions (For further details see chapter ► “Emotions” of this encyclopedia). Hormones have very relevant aspects for music production such as voice qualities and range of singers. Past century, castrati were prepuberal gonadectomized and their entire metabolism suffered from activational and organizational changes for a forced to a rebalanced not programmed. Even the skeleton, bones, and skulls might have morphological differences after early castration. On the other hand, testosterone has also an effect over good musicians and excellent musical performances. Another molecules related to emotions are involved in musical art, such as NO, endorphins, endocannabinoids, and dopamine; they are released to our bloodstream while listening music as the artistic creation which remains in memory.

Cross-References

- Anxiety
- Depression (Paul Gilbert)
- Emotions
- Evolutionary Musicology

- Resource Competition
- Status Competition

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Music as Auditory Cheesecake

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Synonyms

Music as by-product; Non-adaptationist view of music

Definition

As per Pinker's hypothesis, music is not evolutionary adaptive, but rather is a by-product of other evolutionarily evolved traits, and one that

serves no biological function. Pinker suggests that music is an “auditory cheesecake.” Cheesecake fulfills our evolved desire for fat and sugar, but the desire for cheesecake did not evolve and is merely a by-product, pleasurable but biologically useless. Similarly, Pinker regards music as a highly pleasurable by-product of the evolution of other mental faculties, primarily language.

Introduction

In *How the Mind Works* (Pinker, 1997), Steven Pinker offers an account of how the major faculties of mind were designed by natural selection. However, not all mental faculties have evolved through natural selection. Music, for Pinker, represents a clear example of a nonadaptive “pure pleasure technology, a cocktail of recreational drugs that we ingest through the ear to stimulate a mass of pleasure circuits at once” (p. 528), an auditory cheesecake. Although it may contribute to the well-being of the individual, music is biologically useless: “It shows no signs of design for attaining a goal such as long life, grandchildren, or accurate perception and prediction of the world. Compared with language, vision, social reasoning, and physical know-how, music could vanish from our species and the rest of our lifestyle would be virtually unchanged” (p. 528).

Instead of being an adaptation that was the direct target of natural selection, Pinker sees music as capitalizing on preexisting adaptive mental faculties: (1) language, in particular prosody, which involves the analysis of intonation contours, metrical structure, and hierarchical grouping of phrases; (2) auditory scene analysis, which draws on attention to harmonic relations for the process of segregating components from different sources and integrating components originating from the same source; (3) emotional calls that use acoustic signals associated with specific emotions and thus serve a communicative function; (4) habitat selection which involves attention to evocative environmental sounds; (5) motor control, involved in the rhythmic movement to music. All of these are fitness enhancing and are rewarded by a sensation of pleasure emitted by the pleasure centers of the brain. Music, as a pleasure

technology, pushes all the right buttons, without enhancing fitness itself.

The Pleasure of Music

Before turning to the issue of the biological function of music and its evolutionary roots, it is important not to overlook the emphasis, embedded in Pinker's cheesecake hypothesis, on music's unique ability to evoke pleasure. Whether or not the pleasure derived from music is an upshot of music's ability to stimulate the mental faculties suggested by Pinker as providing the mental machinery for music, research provided support for the notion that music is experienced as a highly potent emotion-evoking pleasure-inducing stimulus. Furthermore, the rewarding effect of music appears to be mediated by the same reward brain circuits as the effect of biologically relevant rewarding stimuli; for example, research has implicated the mesolimbic dopaminergic reward system as involved in musical pleasure (see Chanda and Levitin 2013).

Music: Adaptation or Cultural Creation?

Pinker's position lies at one extreme of the debate regarding music's adaptive function. For Pinker, music is not an adaptation, produced through the process of natural selection for its current function, but rather a spandrel, a by-product of other adaptive mental functions. But moreover, even music's current use is biologically functionless (as suggested by the cheesecake analogy). A less extreme position is Patel's theory that sees music as a human invention, albeit a biologically powerful one (Patel 2010). Like Pinker, Patel argues that music is rooted in non-musical functions, and thus a parsimonious explanation would not assume it has been shaped by natural selection. However, Patel sees music as a "transformative technology of the mind" in the sense that musical engagement and training can have beneficial enduring effects on other brain functions, such as language, attention, and executive function, thereby transforming the biological functions

underlying it. These effects span individual time-scales, as music needs to be learned anew by each generation and does not involve any further modification of the human brain specifically for musicality.

At the other extreme of the debate lie positions that deem music, or musicality, an adaptation. Two kinds of arguments have been advanced in support of music being an adaptation. The first kind of arguments concerns its adaptive function; we will review these arguments in the next section. The second kind focuses on characteristics of music that make it a likely candidate for an evolutionary explanation. For example, music needs to have been around long enough to be shaped by natural selection. Although it is not known at what point in history music came into existence, archeological evidence points to the existence of flutes approximately 40,000 years ago (Conard et al. 2009), suggesting an even older musical tradition. Music is universal and observed across cultures. Furthermore, music needs to be innately constrained to be the target of natural selection. Evidence suggests that at least some aspects of music are indeed innately constrained; for example, even young infants show sensitivity to musical structure, such as melodic pitch contours (see McDermott and Hauser 2005 for a review). However, it is not clear whether music satisfies the criterion of domain-specificity. As suggested by Pinker, sensitivity to pitch can result from adaptations for language and auditory scene analysis (see McDermott and Hauser 2005). The lack of domain-specificity suggests that music may be an exaptation (Gould 1991), not produced by natural selection for its current function but rather coopting traits evolved for other functions. Unlike Pinker's cheesecake idea, the idea of music as an exaptation leaves open the possibility that it does serve a biological function, albeit a novel one that did not result through natural selection.

The Adaptive Value of Music

Different theories have suggested several ways in which music can be fitness-enhancing. One

possibility, suggested already by Darwin in *The Descent of Man*, is that music evolved through sexual selection and functions to attract sexual mates. Music, and the dance that accompanies it, has features that may act as indicators of fitness, coordination, strength, and health (Miller 2000). On the other hand, in contrast to other species in which song is performed by males, mainly during mating season, music is performed by both males and females in a wide range of contexts. Currently, empirical evidence for the function of music in sexual selection is lacking.

Another possibility is that the function of music lies in its role in childcare. Cross-culturally, caregivers use lullabies and play songs to soothe infants and regulate their arousal; such expressive vocal communication also strengthens mother–infant affiliative bonding. Thus, songs and rhythmic vocalizations may have adaptive value for the infant. Infant Directed Speech (“motherese”), with its exaggerated intonation contours and stress patterns, may fill a similar function (Trehub, 2003).

Another potential function of music is in increasing group cohesion. Dunbar (2004) proposed that music functioned as vocal grooming, replacing physical grooming when group size increased too much to allow for physical grooming. According to Dunbar, vocal grooming mimics the endorphin-releasing effects of social grooming, thereby creating feelings of warmth and trust that contribute to social bonding. Music may also promote rhythmic synchronization and coordination at the group level, thereby contributing to group identity and cooperation (Brown 2000).

Conclusion

The idea of music as an auditory cheesecake was suggested by Pinker as a counterexample to his adaptationist account of the major faculties of mind. Pinker suggests that features we see as beneficial or adaptive, in the colloquial sense of the word of contributing to better adjustment, may not be adaptive in the biological sense, and were not the target of natural selection. Music is a

by-product of the evolution of other mental functions, pleasure-inducing, but nonetheless biologically functionless.

Although Pinker’s point regarding the pleasure-inducing effects of music is uncontested, his view regarding the evolutionary roots of music and its function has been disputed by theories that suggested various potential adaptive functions of music. In effect, Pinker’s controversial suggestion has sparked a renewed interest in the evolution of music. However, much of the debate remains speculative and is in need of clear empirically testable hypotheses and empirical evidence.

Cross-References

- [Adaptation](#)
- [Evolutionary By-Products](#)
- [Evolutionary Musicology](#)
- [Music](#)
- [Steven Pinker](#)

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Music as By-Product

► Music as Auditory Cheesecake

Music Evolution

► Evolutionary Musicology

Musical Protolanguage

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Synonyms

Evolutionary precursor to language and music;
Prosodic protolanguage

Definition

Musical protolanguage refers to a hypothetical intermediary stage in the evolution of language, intervening between a non-linguistic stage and the possession of true language. Musical protolanguage at that stage consisted of non-referential song and served as the common ancestor of both language and music.

Introduction

Theories of language evolution often invoke a hypothetical protolanguage stage, a stage that

serves as a precursor and as a scaffold for the evolution of modern language. The idea of such an intervening stage, and the notion that this protolanguage was akin to song and is the common ancestor of both music and language, can be traced back to Darwin. In *The Descent of Man and Selection in Relation to Sex* (Darwin, 1875), Darwin considers the evolution of language and claims that “[. . .] primeval man, or rather some early progenitor of man, probably first used his voice in producing true musical cadences, that is in singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes,—would have expressed various emotions, such as love, jealousy, triumph,—and would have served as a challenge to rivals” (p. 87). Drawing on an analogy to birdsong, which like language needs to be learned and is practiced by the young members of the species, Darwin argues that human vocal imitation was driven by sexual selection. He then traces the emergence of meaningful words to the vocal imitation of natural sounds, other animal vocalizations, or man’s own instinctive vocalizations: “It is, therefore, probable that the imitation of musical cries by articulate sounds may have given rise to words expressive of various complex emotions” (ibid.).

Fitch (2010), in a modern framing of Darwin’s theory, says “prosodic protolanguage was a system with phonological generativity, using a small set of elements to build hierarchical structures. These structures were vocally generated, voluntarily controlled, and learned, sharing core aspects of speech and song” (p. 476). Fitch argues that the musical protolanguage model can explain the design features shared by language and music, such as the use of a vocal/auditory channel, discreteness, productivity, and cultural transmission (for a complete list, see Fitch 2010, p. 469). He further argues that comparative data documenting the evolution of vocal learning in several non-bird species, as well as neuroscientific data showing an overlap in the mechanisms underlying the processing of music and language, provide support for Darwin’s musical protolanguage hypothesis. For example, people with congenital amusia, who are impaired in their ability to process music, also

exhibit reduced ability to process emotional speech prosody, suggesting a common acoustic code (Thompson et al. 2012). It should be noted though that overlap in processing mechanisms, while consistent with Darwin's hypothesis, can be explained by seeing music as dependent on processes that evolved for language or vice versa, and does not necessarily imply a common evolutionary ancestor.

In Fitch's terms, musical protolanguage can be described as bare phonology, that is a system with generative phonology such that units can be hierarchically combined but devoid of semantics, with some elements of syntax (units that can be combined and hierarchically arranged in phrases). The main problem for the musical protolanguage model is explaining how such "bare phonology" evolved into a meaningful system that combines phonology and semantics.

Modern Versions of the Musical Protolanguage Hypothesis

The idea of a musical protolanguage, a common precursor of language and music, has been revived by modern scholars. Brown's (2000) *musilanguage* model provides one such example. Brown traces the emergence of musilanguage to primate emotive referential vocalizations – emotive calls elicited in response to a specific class of objects, for example, the alarm calls of vervet monkeys. According to Brown (2000), in the first protolanguage stage, musilanguage involved discrete-level pitches and the use of pitch for conveying semantic meaning, similar to the way lexical tones can differentiate meanings in tonal languages. The second stage involved combinatorial formation of phrases and expressive phrasing. However, the idea of discrete-level pitches, found in music but not in speech, was later (Brown 2017) replaced with the idea of an imprecise relative pitch system (high vs. low). Another way tones can potentially convey meaning is by capitalizing on cross-modal mappings between pitch and non-auditory properties such as size, brightness, and position (Brown 2017). Indeed, research has shown that such cross-modal mappings underlie some sound symbolic words and can also be

exploited for conveying meaning through prosody (see Perniss et al. 2010).

Another model is Mithen's *Hmmmm* model (Mithen, 2005), termed so because it sees protolanguage as **h**olistic, **m**anipulative (used for manipulation of emotion and behavior rather than for reference), **m**ulti-modal (using movement, such as gesture and dance, as well as sound), **m**usical, and **m**imetic. Unlike the musilanguage in Brown's model that consists of discrete-level tones, in Mithen's *Hmmmm* model, utterances are holistic, rather than combined out of elements that can be recombined. The evolution of modern language then involved the segmentation of *Hmmmm*.

Non-music Models of Protolanguage

Other theories accepted the idea of a protolanguage stage but rejected the notion that this protolanguage was musical in nature (for an extensive review of protolanguage models, see Fitch 2010). One such model is Bickerton's (1990) lexical protolanguage model, according to which protolanguage is a propositionally meaningful system, consisting of a lexicon of meaningful words, but no syntax. Bickerton sees language as primarily representational, rather than communicative. He thus rejects the continuity between language and animal communication systems, focusing instead on the conceptual system as the precursor underlying protolanguage.

Another model is the gestural protolanguage model (see Arbib 2005; Corballis 2002). Although speech can iconically represent meaning through speech sounds or prosody (Perniss et al. 2010), gesture allows far more possibilities for iconicity. Gestural protolanguage is propositionally meaningful, thereby avoiding the difficulty that musical protolanguage faces in explaining the emergence of semantics. The modern discovery of the mirror neuron system suggests a mechanism that enables parity in gesture understanding, which may serve as a precursor to the complex imitation observed in humans and to protolanguage (Arbib 2005). The problem facing gestural theories is explaining the transition from gesture and the manual modality to speech.

Conclusion

The idea of a musical protolanguage, that is a common precursor to both music and language, was originally suggested by Darwin in *The descent of men* and has since been revived and reformulated by contemporary theorists. Although all models share this idea of a common ancestor, the presumed characteristics of the musical protolanguage differ between theories (e.g., synthetic vs. holistic). New evidence for shared brain mechanisms underlying music and language has been interpreted as supporting theories that posit a common evolutionary origin and led to renewed interest in Darwin's musical protolanguage model. The transition from musical protolanguage to meaningful speech remains a challenge for the musical protolanguage hypothesis.

Cross-References

- [Darwin on the Origin of Language](#)
- [Evolutionary Musicology](#)
- [Gestural Theory](#)
- [Music](#)
- [Music as Auditory Cheesecake](#)

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Mutation

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Synonyms

[Genetic alterations](#)

Definition

Mutation is defined as a permanent change occurring in the DNA, i.e., nucleotide sequence of a gene or chromosome.

Introduction

Gene is the functional unit of DNA. The characteristic of an individual is determined by its genetic pool. The genes are transferred to the organism from the parental genetic pool through complex process of reproduction. Mutation is a process of alteration of nucleotide sequence within a gene. Altered gene sequence in DNA ultimately leads to alteration in all copies of proteins encoded by that DNA. The alterations in proteins can lead to change in development and functioning of an organism (Lodish et al. 2000).

The genetic configurations keep on changing due to mutational process (Moorjani et al. 2016). The gene-environmental interaction is involved to

a larger extent in this complex process. By this evolutionary process, the organism attempts to meet the needs for survival, i.e., mutation keeps an organism evolving. However, mutation also attributes to the extinction of species.

Mutation rate is defined as “the probability that a change in genetic information is passed to the next generation” (Sanjuán and Domingo-Calap 2016). The rate of mutation reflects the rate of evolution (Peck and Lauring 2018). The rate (speed) at which the mutation occurs represents the speed at which genetic diversity occurs in a given population. In humans, the most frequently mutated genes are those genes that are associated with various cancers (oncogenes) (Gorlov et al. 2018). Mutability of a gene (i.e., ability of the gene to mutate) depends on several characteristics of the gene. The genes that have higher level of expression, slowly replicating in nature and higher chromatin accessibility, are more associated with somatic mutations (Gorlov et al. 2018; Park et al. 2012). Information is carried by the genes. Genes determine the characteristics inherited from the parents. Germline mutation arrests the passage of information or transmits erroneous information (characteristics) to the next generation (Sally 2016).

Types of Mutation and Their Health Implications

Mutation of various types has been implicated in different health conditions. Mutation that involves germ cells (sperm, ovum) is known as germline mutation. Mutations involving non-germline cells are known as somatic mutations (Loewe 2008). Germline mutations are transmitted to progeny and lead to inherited disorders. Somatic mutations, on the other hand, are not transmitted to the progeny. Somatic mutations are mostly manifested as cancers (Kumar et al. 2017). Mutations in specific genes produce alteration in myeloproliferation in an unregulated manner resulting in hematological malignancies (Ortmann et al. 2015). Genetic mutation too attributes to the development of prion diseases like Creutzfeldt-Jakob disease (Gao et al. 2019).

Alleles are different forms of a gene (e.g., normal and mutant). In diploid organisms, genes occur in pairs. If mutant phenotype appears only when both alleles are mutated (i.e., individual is homozygous for the mutant allele), it is termed as recessive mutation. If mutant phenotype can appear even with one mutated allele (i.e., individual is heterozygous for the mutant allele), it is termed as dominant mutation (Lodish et al. 2000). Recessive mutations mostly lead to a loss of function, whereas dominant mutations lead to gain of function. Genetic disorders thus can be dominant and recessive depending on their pattern of inheritance. Autosomal disorders (due to mutation in autosomes) can be dominant (e.g., Huntington's disease, Marfan syndrome, type 1 neurofibromatosis) and recessive (e.g., sickle cell anemia, thalassemia, cystic fibrosis, phenylketonuria, glycogen storage diseases). X-linked disorders account for almost all sex-linked disorders (mutations occurring in X and Y chromosomes) and are mostly recessive (e.g., hemophilia, Duchenne muscular dystrophy).

Alteration in a single base pair is called a point mutation (Lodish et al. 2000; Loewe 2008). Such mutations lead to either the production of a different protein (missense mutation) or the premature termination of a protein (nonsense mutation). Sickle cell anemia is autosomal recessive disorder due to missense point mutation that causes GUG codon (coding for valine) to replace normal GAG codon (coding for glutamic acid). Alteration in β chain of hemoglobin (Hb) caused due to this mutation causes decrease in oxygen-carrying capacity of Hb and sickling. Nonsense mutations lead to degradation of RNA. Frameshift mutation is a type of mutation that occurs when there is insertion or deletion of one or two base pairs, leading to altered reading frame of the DNA strand. Trinucleotide repeat sequences in an unregulated fashion occur due to certain dynamic mutation processes (Pearson et al. 2005). Fragile X syndrome characterized by mental retardation is an example of trinucleotide repeat where there are tandem repeats of CGG codon in *FMR1* gene. Mutations that result in expanded repeat sequences of trinucleotides result in development of several neurological as well as neuropsychiatric disorders (Pearson et al. 2005).

Mutation in Nonhumans

The process of mutation occurs in all living organisms. Mutation in microorganisms results in their evolution (Peck and Lauring 2018). Mutations can be spontaneous or can be induced by mutagens like UV radiations and alkylating agents (Watford and Warrington 2019). Mutation can alter the pathogenic characteristics of a microbe (Hershberg 2015; Sanjuán and Domingo-Calap 2016). Mutation may accentuate or attenuate the virulence of pathogenic microorganisms. Oral polio (Sabin) vaccine, for example, is produced by attenuating polio virus. These vaccine strains of poliovirus were developed by serial culture in monkey kidney cells. Mutation and selection produced this strain of poliovirus which retains its immunogenicity but has lost its pathogenicity (Fleischmann 1996). Different microorganisms have different rates of mutation. The rate of mutation in RNA viruses is higher than that of DNA viruses. Human immunodeficiency virus (HIV), for example, is a highly mutable virus. Sequential isolates of HIV from the same person can show antigenic variation. Similarly, faster mutation is reported among viruses with single-stranded nucleic acid than viruses with double-stranded nucleic acid (Sanjuán and Domingo-Calap 2016). Viruses with segmented nucleic acid (e.g., influenza virus) also show higher rate of mutation than those with unsegmented nucleic acid. Mutations in HIV lead to development of drug resistance. Drug resistance in bacteria like *Mycobacterium tuberculosis* and *Helicobacter pylori* is mainly due to mutations. Mutation attributes to the continued evolution of acquired resistance genes too, like TEM family of beta-lactamases which are generally transmitted from one bacterium to another by horizontal gene transfer methods (e.g., conjugation) (Woodford and Ellington 2007).

Mutations: From the Perspective of Evolution

In the process of evolution, mutation is always a possibility as well as probability, as gene-environmental interaction is happening continuously in an intricate manner. The genetic

variations seen among organisms during the developmental process are the result of mutation (Lynch et al. 2016). However, the probability of mutations varies according to their nature. Some forms of mutations are more likely to happen, whereas certain others are rare to happen (García and Traulsen 2012). Epigenetic mutations that result from gene-environmental interactions have beneficial effects. They help the organism in adapting with the changing environment. Successful adaptation is highly essential for survival. However, certain epigenetic mutations slow the adaptation process and may stand as a hindrance too (Kronholm and Collins 2016). In the process of evolution, nature selects organisms that are adaptable and fit by shaping their phenotype. The role of mutations in this process of natural selection is still debatable (Svensson and Berger 2019; Uller et al. 2018).

Mutation rate is important from the evolutionary point of view. Mutation rates vary among different species of organisms as well as with same species of organisms. It has been seen that the mutation rates humans have are lower than gorillas and chimpanzee. Similarly, among human race, mutation rate is found to be higher within certain DNA regions of Europeans than Africans and East Asians, as found in some research (Harris and Pritchard 2017).

Mutated genes code for specific proteins that subserve a particular function. The proteins coded by the mutated genes ensemble various permutations and combinations to a final configuration, which is unpredictable. So, as per the existing knowledge, prediction of evolution remains uncertain (Sailer and Harms 2017).

Conclusion

The phenotypic variations among living organisms trace back to mutation. Many illnesses and their risk factors can be understood through the knowledge of mutation. Extensive research for in-depth understanding about mutation and its aftereffects may enable us in understanding the evolutionary process and even may guide us in predicting evolution.

Cross-References

► Genetic Predispositions

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Mutation Accumulation Theory

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Definition

Mutation accumulation theory describes two interconnected bodies of theory: (i) *Germ-line mutation accumulation theory* attempts to understand both the consequences of and the processes by which a population's *load* or *burden* of

spontaneously occurring germ-line mutations increases in the absence of purifying selection, which results from the fitness diminishing effects of these mutations, and (ii) *Somatic mutation accumulation theory* encompasses the related phenomenon of cell lineages within multicellular organisms accumulating mutations as a result of failures of DNA repair in the course of mitotic cell division. These phenomena have important implications for understanding the origin of variance and covariance among fitness salient traits and the maintenance of population viability in the case of germ-line mutation accumulation and senescence and oncogenesis (the mechanisms by which cancer-causing neoplasms form) in the case of somatic mutation accumulation.

Introduction

This entry will start by introducing relevant background concepts, such as the nature of purifying selection, the relationship between fitness, pleiotropy and trait variance, and the sources and rates of new germ-line and somatic mutations. As the target audience for this entry is evolutionary psychologists, whose principal organismal focus is *Homo sapiens*, the entry will then summarize the human mutation load paradox, its resolution, and potential manifestations of ongoing mutation accumulation in human populations. Experimental evidence of the fitness reducing consequences of accumulating germ-line mutations in relation to work on nonhuman eukaryotic taxa will also be discussed. Finally, the possibility that there exists a group-selection level manifestation of purifying selection will be considered.

Review

Purifying Selection

Purifying selection describes the processes by which mutations are eliminated from a population as a consequence of their deleterious effects on fitness. This can occur via *natural selection* under conditions where the carriers of deleterious mutations exhibit suboptimal levels of traits critical for survival, such as in the case of defenses against

predation and disease, or where mutations that interfere with critical biochemical processes lead to prereproductive organismal death at some point in the lifecycle or sterility. A parallel process of *somatic selection* operates at the cellular level, whereby newly acquired deleterious mutations trigger immunological policing responses, such as *apoptosis* or preprogrammed cell-death, which eliminate cells that are at risk of undergoing neoplastic transformations.

Among sexually reproducing organisms such as humans, deleterious germ-line mutations can influence fitness outcomes in ways related to their pleiotropic effects on traits, meaning that they can influence the development of multiple traits simultaneously. This has led to the prediction that there exists a latent *fitness factor* among traits believed to signal the sensitivity of development to perturbation stemming from the presence of deleterious mutations (Penke et al. 2007). Thus, in sexually reproducing taxa, there should exist genetic correlations among seemingly quite distinct traits, encompassing aspects of physical condition, behavior, health, and reproductive viability, high-levels of which are *unconditionally favored* by *sexual selection* across different environments (Penke et al. 2007).

Under conditions where purifying selection occurs in proportion to the fitness costs of spontaneously occurring germ-line mutations, individual differences in and genetic correlations among fitness salient traits will be maintained within a population, as spontaneously arising deleterious mutations conferring few fitness disadvantages to their carriers (by virtue of recessiveness) can persist for many generations, with the addition of each new mutation cumulatively reducing the fitness of the lineage relative to others that are burdened with fewer such mutations. This mechanism by which variance is maintained with respect to fitness salient traits in a population is known as *mutation-selection balance* (Fisher 1930).

Sources and Rates of De Novo Mutations in Humans

Germ-Line Mutations

Paternal age is a major source of common germ-line de novo base substitution mutations (i.e.,

point mutations involving the substitution of single nucleotides) in humans and other eukaryotic taxa also. These new mutations arise via mitosis in germ-line precursor cells (spermatocytes) as a consequence of age-related declines in the efficiency of DNA repair mechanisms and are transmitted via meiotic cell division to the haploid genomes of spermatozoa (Kong et al. 2012). The generational base substitution rate varies widely between mammalian species. In humans, each year of paternal age adds approximately two of these mutations to the genomes of offspring, with fathers aged 35 transmitting around 70 base substitution mutations to their offspring. Mice (which have considerably shorter generation lengths) transmit about half as many mutations per offspring. The chimpanzee generational transmission rate is about equal to the human rate (Lynch 2016). It is important to note that these rates are based on the assumption of linear increases in the numbers of de novo mutations transmitted to offspring. In practice, DNA repair mechanisms undergo accelerated deterioration as a function of advancing paternal age, leading to an accelerating rate of increase in the numbers of de novo mutations (Kong et al. 2012). Maternal age is furthermore a source of additional de novo point mutations, but to a lesser degree than paternal age (the rate is around 0.5 de novo mutations per haploid genome per year of maternal age; Wong et al. 2016).

While paternal age is the principal source of common and mildly deleterious base substitution mutations in human germ cells, other less common classes of germ-line mutation also occur spontaneously, such as insertion-deletion events (i.e., where a single nucleotide is either added or removed), which occur at around 8 % of the base substitution mutation rate. Even less common mutations involving the addition or removal of large numbers of nucleotides such as copy number variation and chromosomal abnormalities also occur spontaneously. It has been estimated that once all sources of spontaneous germ-line mutations are accounted for, the numbers of such mutations transmitted to offspring may be as high as 100 per generation (Lynch 2016).

Human studies examining the influence of paternal age as a strong proxy for the numbers

of spontaneous germ-line mutations on offspring characteristics not only yield information about which trait variances may be maintained by mutation-selection balance but also yield evidence for the existence of the fitness factor, with paternal age effects having been found on diverse traits, such as the risk of offspring acquiring neurodevelopmental disorders such as autism and schizophrenia (Kong et al. 2012) and attention deficit/hyperactivity disorder (D'Onofrio et al. 2014), diminished physical attractiveness (Huber and Fieder 2014), and reproductive failure (i.e., childlessness) (Fieder and Huber 2015).

Finally, a critical factor that moderates a population's load of mutations is endogamy. More inbred (endogamous) populations being more homozygous for mutant alleles.

Somatic Mutations

Among somatic cell-lines, the rates of de novo mutation are much higher than the rate found in germ cells. Each mitotic event is associated with a de novo base substitution mutation rate that is on average 50 times that found in germ cells, with brain cells experiencing the lowest rate (eight times the germ-line rate) and skin cells experiencing the highest rate (112 times the germ-line rate) (Lynch 2016). Somatic mutation accumulation is a major cause of neoplastic transformation in defective cells that fail to be eliminated via somatic selection and may furthermore be a major source of contingency in terms of the underlying risks associated with developing certain neoplasms (Lynch 2016). Somatic mutations are also fundamental to *mutation accumulation theories of aging* (i.e., Medawar 1952), which treat the accumulation of mutations as a major source of the general and progressive cellular dysfunction characteristic of *senescence*.

Critically, somatic mutation accumulation is the principal mechanism through which selection occurs on mutation rate itself, as within an organism, both somatic and germ-line cells share common DNA repair systems, hence differential rates of somatic mutation can serve as a phenotypic target for selection on germ-line mutation rates (Lynch 2016).

The Mutation Load Paradox and Estimates of Human Fitness Loss Due to Germ-Line Mutation Accumulation

The Mutation Load Paradox

Although the human spontaneous germ-line mutation rate is relatively high when compared with that of other species, it is not especially high when considered in the context of human genome and population size and generation length (Lynch 2016). Despite this, it has been estimated that the human germ-line mutation rate, specifically under the assumption that approximately two out of the 100 or so de novo mutations will be harmful, would necessitate the reproductive failure of around 88 % of all humans born. In other words human populations should have undergone *mutational meltdown* whereby the fitness loss causes populations to shrink, increasing the rate at which these new mutations drift to fixation, leading to population collapse. In order to offset this each female should produce in excess of 16 offspring simply to maintain population viability. A *mutation load paradox* arises when this prediction is contrasted with the observation that reproductive failure and excess on this scale is not observed in human (specifically industrialized) populations (Kondrashov and Crow 1993).

One solution to the mutation load paradox is that relative fitness differentials between individuals of different genetic loads might constitute a source of cryptic or soft purifying selection in human populations, operating via factors such as sexual selection, and that large reproductive failure rates and excesses only emerge when mutation load-free genomes are used as the baseline for fitness comparisons against those with relatively high load (Lesecque et al. 2012).

Another interpretation of the paradox concerns the observation that high reproductive failure rates, especially among males, coupled with reproductive excess among females, were in fact a feature of historical, preindustrial populations. For example, among European populations in the year 1600 AD the average individual had around a 25–40 % chance of dying in infancy, a 50 % chance of dying during childhood (Volk and

Atkinson 2008), and only around a 40 % chance of fully participating in reproduction (Rühli and Henneberg 2013). The average family size was close to five in 1600s England (Arkell & Whiteman, 1998) – given the high rates of pre-term, infant, and child mortality, the *numbers ever conceived* would likely have been considerably higher. These historical Western infant and child mortality statistics are similar to those observed in contemporary hunter-gatherer populations (Volk and Atkinson 2008). Furthermore, the historical pattern of reproductive failure does not appear to have been random with respect to indicators of social and economic success, with far higher rates of reproductive failure being found among those with low relative to high social status, indicating that survivorship and reproductive success in this historical context might have been strongly coupled with elevated levels of certain competitiveness and fitness enhancing physical and psychological traits (Clark 2007).

It has been suggested therefore that historically observed levels of infant and child mortality, coupled with low reproductive participation and large compensatory reproduction among females, might account for a substantial portion of the variance in the estimates of both reproductive failure rates and magnitude of reproductive excess required by theory to purify de novo germ-line mutations in human populations (Woodley of Menie 2015). The paradox is therefore *only* apparent when the reproductive patterns of modern industrialized populations are considered, where perinatal mortality is extremely low (~0.5%; Woods 2008), infant and child mortalities are extremely low (~1 %; Volk and Atkinson 2008) and where the opportunity for full reproductive participation is extremely high (90 %; Rühli and Henneberg 2013).

The Consequences of Relaxed Purifying Selection in Industrialized Populations

The modern situation results from the extraordinary degree to which industrialized populations in particular have been shielded from potential sources of purifying selection stemming from reproductive impediments (such as stillbirth and infertility), disease, climate, famine, and violence.

Furthermore, conscious control over reproduction, facilitated by the wide-scale utilization of contraception, appears to have attenuated the correlation between potential indicators of low underlying genetic load, such as physical attractiveness and fecundity in some modern populations (Pflüger et al. 2012). Similarly, while paternal age predicts the risk of childlessness in contemporary samples of the US population, it does not appear to predict fecundity among the fraction of the offspring that go on to reproduce – a situation different from that of historical North American populations in which inverse associations between paternal age and offspring fitness have been observed (Fieder and Huber 2015). Lynch (2016) also notes the potential for cosmetic interventions to mask the effects of mutations on condition in modern populations. Findings such as these have been interpreted as indicating a potentially attenuated role for relative fitness differentials among individuals of differing genetic loads as a source of soft purifying selection in industrialized populations (Lynch, 2016; Woodley of Menie and Fernandes 2016).

These factors have therefore permitted population growth in industrialized nations to occur largely in the absence of major sources of purifying selection, which has facilitated an increase in the generational burden of germ-line mutations. Such mutations may have had significant fitness costs in the face of historical ecological stresses but no longer incur those same costs under modern milder conditions and are thus free to accumulate, perhaps exerting more subtle and direct effects on reproductive fitness. Consistent with this, Lynch (2016) has estimated that under the assumption of strongly relaxed purifying selection, it would be reasonable to expect fitness losses of approximately 1 % per generation among the populations of industrialized countries. Lynch also suggests that this generational fitness loss may even underestimate the true impact of mutation accumulation on fitness salient traits in these populations, as it does not take into account potential interactions between germ-line and somatic mutation rates, stemming from the damaging impact of the former on genes responsible for regulating the latter. Deregulation of the rate at

which somatic mutations accumulate might therefore lead to behavioral deterioration in human populations at a rate greater than the predicted loss in reproductive fitness, owing to the large genomic target size of the brain – with as many as 84 % of all genes in the human genome being involved in some aspect of brain development and maintenance (Hawrylycz et al. 2012).

This should not be taken to imply that there is absolutely no purifying selection operating on modern industrialized populations. Rarer forms of spontaneous mutation involving copy number variation or chromosomal abnormalities or relatively more common mutations interacting via *synergistic epistasis* (Crow 1997) can potentially cause significant functional and reproductive impairment, especially when such mutations lead to loss of viability early in development (such as in the case of spontaneous abortion, which terminates around 10 % of all pregnancies in the West). It is important to note also that some tiny subset of these mutations may even be beneficial for the fitness of certain individuals under certain conditions. Thus, purifying selection continues to operate, even under modern conditions, albeit likely on a much narrower range of the mutational spectrum than was the case historically.

Experimental Evidence for the Effects of Germ-Line Mutation Accumulation on the Fitness of Nonhuman Eukaryotes

There exists an extensive literature on the results of germ-line mutation accumulation experiments conducted on a variety of eukaryotic taxa with short generation spans, which has been taken as support for the approximately 1 % loss in fitness per generation estimate in humans (Lynch 2016). These experiments typically involve the maintenance of a line of descent in which, via experimental intervention, random individuals are selected for mating, thus eliminating the opportunity for purifying selection to operate on these populations via the effects of sexual selection. The impact of accumulated germ-line mutations on fitness is quantified via the measurement of offspring yields, viability (i.e., the proportion surviving to adulthood), and also via direct measurement of levels of fitness salient traits.

Insects

Much of the eukaryotic germ-line mutation accumulation research has focused on insects, with a number of studies having examined *Drosophila melanogaster* (the fruit fly) in particular. The earliest research into mutation accumulation involved fruit flies and found fitness losses (measured in terms of egg-to-adult viability) amounting to 1–2 % per generation in the case of populations that were heterogeneous for a specific chromosome that had been experimentally sheltered (via transmission through the male line) from the effects of purifying selection. Homozygosity for the target chromosome was associated with a larger fitness loss per generation (5–10 %) (Mukai 1964). Subsequent studies involving fruit flies replicated the finding of fitness loss via germ-line mutation accumulation; however, these studies also typically found smaller fitness losses and smaller rates of mutation accumulation than that observed by Mukai (e.g., Fernandez and López-Fanjul 1997). Importantly, it has also been found that in fruit flies the degree to which these mutations impact fitness is sensitive to ecological context, with substantially greater fitness losses occurring under conditions of competition relative to conditions where competition was relaxed (2 % per generation vs. 0.2 %) (Shabalina et al. 1997). This is precisely analogous to the situation as it pertains to the populations of industrialized countries, where aspects of behavior and physiology which have a potentially high sensitivity to spontaneously occurring deleterious mutations may have been far more critical for survival and reproduction historically under conditions of ecological stress than in relatively much more mild contemporary environments.

Indications of reproductive fitness loss have been observed in other insect species bred under mutation accumulation conditions such as in the case of houseflies (Bryant and Reed 1999) and flour beetles, which have been found to exhibit diminished starvation resistance relative to controls (Lomnicki and Jasiński 2000).

Yeasts

Mutation accumulation experiments involving yeasts (a unicellular eukaryote) have also yielded indications of declining fitness (when offspring

growth rates are compared with those of the parental generation), but with considerable line-to-line variability, indicating that some small minority of beneficial mutations may actually raise fitness when allowed to accumulate (Dickinson 2008).

Nematodes

Mutation accumulation experiments involving the roundworm *Caenorhabditis elegans*, which exhibits a lower spontaneous mutation rate than *D. melanogaster* (Lynch et al. 2008), find no indications of declining fitness when viability is used as an indicator (Keightley and Caballero 1997); however, behavioral deterioration in terms of diminished levels of behavioral traits believed to be highly fitness salient, such as those relating to chemosensing and locomotion, has been noted (Ajie et al. 2005).

Mammals

Recent research involving *mutator* strain mice (i.e., mice that are specifically bred for very high rates of germ-line mutation) have found evidence of rapid declines in reproductive fitness when bred under mutation accumulation conditions, relative to *wild-type* mice bred under the same conditions (Uchimura et al. 2015).

Potential Historical Micro-Evolutionary Manifestations of Germ-Line Mutation Accumulation in Humans

It is not possible to run mutation accumulation experiments on humans; however, historically, the nineteenth and twentieth centuries saw the biggest changes in evolutionarily significant aspects of the reproductive ecology of Western populations, such as dramatically falling infant and child mortality rates and rising opportunity for reproductive participation (Rühli and Henneberg 2013; Volk and Atkinson 2008), coupled with the wide-scale utilization of contraception. On this basis, it has been suggested that very recent microevolutionary indications of the effects of germ-line mutation accumulation on fitness salient traits might already be present in secular trend data on population levels of various physiological and psychological indicators of developmental stability (Rühli and Henneberg 2013; Woodley of Menie and Fernandes 2016).

Consistent with this expectation, secular trends towards reduced cranio-facial symmetry have been noted among both male and female European Americans, starting in the early nineteenth century. These have been interpreted as stemming in part from a microevolutionary trend towards declining developmental stability due to germ-line mutation accumulation in this population. Declining developmental stability has also been proposed as an explanation for parallel secular trends in the incidence of neurodevelopmental disorders, such as autism and ADHD, and also for historical increases in the incidence of sinistrality or left-handedness among Western populations (Woodley of Menie and Fernandes 2016).

Also consistent with a potential microevolutionary trend towards reduced developmental stability, Rühli and Henneberg (2013) presented several examples of *medical abnormalities* that have increased in frequency among the populations of industrialized countries over the twentieth century. These include a doubling in the prevalence of anomalous arteries, such as the median artery of the forearm and a decrease in the incidence frequency of individuals possessing the thyroidea ima branch of the aortic arch to zero. The opening of the sacral canal (spina bifida occulta) has also increased in prevalence among those born in the second-half of the twentieth century. Tarsal coalitions are also more prevalent in modern populations, as are skeletal pathologies, such as ossification of the posterior longitudinal ligament and of the spine and diffuse idiopathic hyperostosis.

A recent estimate of the impact of germ-line mutation accumulation on general intelligence (*g*) has been made based on the secular trend towards declining levels of cranio-facial symmetry – measures of *fluctuating asymmetry* and cognitive ability being mildly inversely correlated. The commensurate decline in *g* was estimated to be -0.16 IQ points per decade, with mutation accumulation possibly accounting for around 30 % of this loss or -0.05 points per decade. A small impact of mutation accumulation on *g* is consistent with the observation that *g* likely exhibits a narrow-band sensitivity to the mutational

spectrum and appears to be well canalized against genetic and environmental perturbation in development (Woodley of Menie and Fernandes 2016).

In considering possible historical microevolutionary trends such as these, Lynch (2016) urges caution, arguing that in order to adequately determine the contribution stemming from mutation accumulation, they need to be evaluated utilizing measurement models that can compellingly differentiate between genetic and environmental causes.

Conclusion

Research into mutation accumulation has generated a respectable body of theoretical and empirical work examining the phenomenon from multiple aspects. While germ-line mutation accumulation theory as it pertains to humans remains somewhat controversial, recent (as of this writing) synthetic summaries of this work (Lynch 2016) indicate that the accumulation of both germ-line and somatic mutations is nonetheless likely capable of producing relatively rapid declines in fitness (on the order of 1 % per generation) with noticeable effects arising over relatively short spans of time (i.e., a century). Critical theoretical factors that have not previously been considered in discussions of this phenomenon, such as the potential role of germ-line mutations that deregulate and enhance the rate at which somatic mutations occur and their potential role in behavioral deterioration, could form the basis for fruitful future research involving nonhuman eukaryotes, where behavior is rarely considered to be a key component of fitness (i.e., Ajie et al. 2005). The collection of systematic and detailed data on secular trends in behavioral and physiological variables, especially as these pertain to clinically significant measures, coupled with the use of measurement models that can tease apart causation should allow for fitness deterioration via mutation accumulation to be tracked.

Another potentially critical factor concerns the possibility that mutations with small, deleterious effects on behavior at the individual level can have disruptive effects on the *extended phenotype*

of social ecology in ways that feedback on and amplify the fitness costs to populations. For example, among prosocial species, mutations that lead to reduced sensitivity to social cues or degrade social learning ability could all have widespread effects on fitness, even among conspecifics who do not carry these mutations, but who are nonetheless dependent upon the maintenance of certain social ecological optima for their fitness (Woodley of Menie et al. 2017).

The idea that there may be a *group-selection* analogue of purifying selection may account for Calhoun's (1973) observation of the *behavioral sink* phenomenon in his *mouse utopia* experiments. Calhoun observed that when allowed unlimited resources and space, mouse populations inevitably reach a growth plateau, followed by a decline in fertility, terminating in colony collapse. The decline phase is characterized by the appearance of individual mice exhibiting apparently bizarre behaviors, such as obsessive grooming, a tendency towards either extreme solitariness or crowding, disinterest in communal reproductive activities, and asexuality.

Mice engage in a variety of reciprocal social interactions; they also practice communal nesting and nursing and territory marking behavior. The presence of an elaborated social ecology might be translating the deleterious effects of any mutations on behavior into much larger-scale fitness losses at the colony level in the case of Calhoun's experiments (Woodley of Menie et al. 2017). This mechanism may also account for why the mouse utopia populations did not simply stabilize around some equilibrium number of individuals but instead proceeded to collapse. Accumulating behavior-altering mutations may have been feeding back on the social ecology of the colony, dragging down the fitness of the colony and ensuring eventual collapse. This process of group-level purifying selection strongly resonates with Calhoun's (1973) own description of the terminal phase of mouse utopia:

Autistic-like creatures, capable only of the most simple behaviors compatible with physiological survival, emerge out of this process. Their spirit has died ("the first death"). They are no longer capable of executing the more complex behaviors compatible with species survival. The species in such settings dies. (p.86)

Social ecological systems might actually be quite fragile, containing "tipping points" which trigger group-level purifying selection and collapse once a certain critical load of behavior-altering mutations is present in the population. This is different from the classical mutational meltdown scenario, as it does not necessitate an initially small population in which deleterious mutations are drifting to fixation. Large and potentially genetically viable populations can in this scenario collapse simply via the deleterious pleiotropic effects of relatively small numbers of behavior modifying mutations on fragile features of social ecology. Within the context of human populations, this might help to explain the rapid transition into subreplacement fertility in many developed countries characteristic of the demographic transition. Total fertility rates in the United States, for example, fell from 3.7 in the period 1955–1959 to around 1.8 in the period 1975–1979 (Wattenberg, 1985) – a decline in organismal fitness of 51 % in just two decades – far in excess of what would be predicted on the basis of germ-line mutation accumulation under conditions of relaxed purifying selection alone. These fitness losses are furthermore biggest among those with potentially the lowest mutation loads, i.e. those with high social status. The idea that these rapid declines in fitness may stem even in some small part from the individually subtle behavior-altering effects of accumulated mutations on the generation of a natality-inhibiting cultural feedback loop is indeed a sobering thought, presenting yet another twist on the mutation load paradox, as here is a pathway through which mutations might yet be significantly impacting fitness, albeit indirectly. This possibility serves to amplify Lynch's clarion call that human mutation accumulation is a potentially major existential risk, deserving of our attention (Woodley of Menie et al. 2017).

Cross-References

- [Dysgenic Concerns](#)
- [Fertility](#)
- [Individual Differences](#)
- [Mate Value](#)

- [Mutation](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Reproduction](#)
- [Reproductive Value](#)

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Mutual Grooming

- ▶ [Cooperative Grooming](#)

Mutual Parental Investment

- ▶ [Biparental Care](#)

Mutualism

- ▶ [Cooperation Among Fishes](#)
- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Morality Is Cooperation](#)
- ▶ [Primate Cooperation](#)

Mutualistic Mimicry

- ▶ [Müllerian Mimicry](#)

Myth

- ▶ [Fiction](#)

Names and Titles

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Synonyms

[Designation](#)

Definition

A title is a prefix or suffix added to someone's name in certain contexts.

As discussed elsewhere in this work (Peedicayil 2018), cultural inheritance involves the storage and transmission of information by communication, imitation, teaching, and learning. In this context, there is evidence that complex social behaviors like human altruism and mate choice (Rushton et al. 1986), social attitudes (Martin et al. 1986), personality (Eaves et al. 1999), and the human sex ratio (Lipatov et al. 2008) are culturally transmitted. The cultural transmission of such behaviors, for obvious reasons, will occur effectively only in an animal species that is social, i.e., where the members live in groups and interact freely with one another. Human beings are the best example of that type of animal species and the groups they live in are termed societies (Wilson 2000). Indeed, the famous Greek philosopher Aristotle

had stated “Man is by nature a social animal” (Aristotle 2015). All of man's unique social behavior is pivoted around the use of language (Wilson 2000).

Concerning names and titles, they are products of the highly advanced level of development of cultural inheritance found in humans when compared to other animal species. A title is a prefix or suffix added to someone's name in certain contexts (Wikipedia 2018). It can signify either veneration, an official position, or a professional or academic qualification. Titles include the following types: legislative and executive, aristocratic, titles used by knights, dames, baronets and baronetesses, judicial, historical, religious, academic, and military. Some titles are hereditary. Names and titles vary between different regions of the world and between peoples speaking different languages (Wikipedia 2018).

Cross-References

► [Cultural Inheritance](#)

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Narcissism

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Synonyms

Egocentrism; Grandiose self-esteem; Narcissistic Personality Disorder (NPD); Self-aggrandizement; Vanity

Definition

Narcissism is an epiphenomenon, arising due to various combinations and constellations of underlying traits and motivations. Although the underlying motivations and their behavioral outcomes are heterogeneous, the common core of narcissism is typified by a tendency for these individuals to be entitled, arrogant, self-centered, and vain, using their considerable social potency and tendency towards exploitative behavior to leverage themselves into positions of authority or social prominence (Holtzman and Donnellan 2015).

Introduction

Narcissism has existed in both the psychiatric and early psychological literature since the early 1900s, but this construct has only been under earnest empirical investigation since the latter half of the twentieth century (Raskin and Terry 1988). Only a minority (perhaps 1%) of the population surpasses the clinical threshold for a diagnosis of Narcissistic Personality Disorder (NPD). However, narcissistic personality traits are normally distributed within the population, meaning that there are far more individuals with narcissistic tendencies than there are people with pathological levels (Skodol et al. 2014). For that reason, it is often preferable to focus on narcissistic traits and employ the term “narcissist” to mean someone who scores highly on these traits instead of denoting someone who has received a clinical diagnosis.

Narcissistic traits are rarely associated with the internalizing symptoms of psychopathology (e.g., distress, anxiety, depression) (Miller and Campbell 2012). As such, some researchers have proposed that narcissism should only be considered pathological when it is comorbid with other personality disorders (reviewed by Skodol et al. 2014). In addition, narcissistic traits facilitate a social strategy that allows individuals to garner status, resources, and mating opportunities with desirable partners (Holtzman and Donnellan 2015). Thus, narcissistic traits expressed in appropriate circumstances may provide a selective advantage. Only considering the negative outcomes associated with narcissism under a pathological framework impoverishes our understanding of the construct. Greater insights are gained by considering the proximate and ultimate causes of narcissism, as well as its potential adaptive functions. In other words, a thorough understanding of whether or not narcissism is adaptive is only possible after considering: (1) the behavioral, personality, and interpersonal features associated with narcissistic traits; (2) the etiology of narcissistic traits among individuals, and whether they represent normal development or development gone awry; (3) the fitness benefits (or costs) of narcissistic traits to individual carriers; and (4) the roots

of narcissistic traits in the human lineage, and how they have been maintained across time.

The Narcissist in Context

Narcissism is not a unitary phenomenon. Modern researchers in the field differentiate between several prominent facets of narcissism – grandiose-exhibitionism, authoritative-leadership, and exploitative-entitlement – with the latter two slightly more common in men than in women (Grijalva et al. 2015). Grandiose-exhibitionism is associated with an overly ambitious and inflated sense of self, as well as a tendency to be gregarious and extraverted. Authoritative-leadership is characterized by a strong desire for leadership or authority in a group and the self-assured belief that one's leadership ability outstrips that of rivals. Exploitative-entitlement is marked by a pervasive belief that one deserves high social status and attention and a willingness to use manipulative tactics to get it. Generally, authoritative-leadership and grandiose-exhibitionism are seen as relatively more prosocial and less problematic (for the individual and the group) than exploitative-entitlement (Grijalva et al. 2015; Skodol et al. 2014).

Researchers have noted that individuals who score high on narcissism primarily employ two tactics to gain social status. One tactic is to use charm and assertive social styles to strive for admiration. The second tactic is to raise one's own social standing by bringing others' down (i.e., rivalry), by engaging in hostile and antagonistic social competition, derogating others, or devaluing their accomplishments (Back et al. 2013). The first of these tactics is most strongly associated with *grandiose* narcissism, which encapsulates the grandiose, leadership, and arrogant aspects of narcissism. The second tactic (rivalry) is more closely aligned with *vulnerable* narcissism – typified by emotional sensitivity, pervasive fears of rejection or abandonment, and exploitative tendencies (see Back et al. 2013; Foster et al. 2016; Grijalva et al. 2015). While there are several (nonmutually exclusive) ways to “be” a narcissist, they all share in common a self-centered entitlement,

social competitiveness, and striving for social validation.

Unsurprisingly, narcissistic traits tend to be positively correlated with self-esteem and extraversion and negatively correlated with agreeableness and conscientiousness (Holtzman and Donnellan 2015). Individuals high in narcissistic traits also report that they have an easier time starting new relationships, often perceive a greater availability of viable alternatives to current relationships, and report more lifetime sexual partners along with more favorable attitudes towards casual sex (i.e., higher *sociosexuality*) (Holtzman and Donnellan 2015). These associations are sensible given that converging lines of evidence indicate that narcissists are perceived as more attractive by others (Dufner et al. 2013). These ratings are likely a result of social charm and a focus on appearance enhancement, rather than narcissists being objectively more good-looking (Holtzman and Donnellan 2015). Despite these arguably positive outcomes, narcissistic traits such as exploitative-entitlement (Foster et al. 2016) and rivalry (Back et al. 2013) tend to be associated with poor social outcomes (social isolation, rejection, turbulent relationships, etc.). The confidence and charm of narcissists often facilitates social interaction, drawing people in to their constantly shifting social circles in the short term, whereas their tendency towards un-empathetic and aggressive social competition, along with their persistent ego-centrism, tends to push people away in the long term (Back et al. 2013).

A Selfish Mind: How Does Narcissism Develop?

Narcissism has been shown to be substantially heritable, with as much as 59% of trait variance being due to underlying genetic variation, and the rest resulting from the impact of environmental factors unique to the individual (Vernon et al. 2008). Such a pattern is indicative of an inherited propensity towards narcissism that then interacts with the experiences of the individual, crystalizing ultimate levels of the trait. Specifically, an early desire for social validation and prominence,

coupled with charming and extraverted social strategies, likely kick-starts a spiral wherein narcissists learn to regulate their behavior in ways that maximize the amount of positive social feedback they can garner, with desired outcomes only making these behavioral tendencies more likely in the future (Holtzman and Strube 2010). As noted above, the social strategy of narcissists tends to be relatively short term, and the substantial impact of genes on the development and expression of narcissistic traits calls into question how natural selection has tolerated such a selfish and (at times) exploitative strategy to exist in humans, a decidedly social species.

Selfish by Design? Natural Selection and Narcissistic Traits

Extremely high levels of narcissistic traits are often associated with significant social impairment, heightened alcohol abuse, aggression, and antisocial behavior (Miller and Campbell 2012). Furthermore, certain narcissistic traits (e.g., exploitative-entitlement, antagonistic rivalry) are related to psychopathic and Machiavellian tendencies, whereas the more prosocial facets of narcissism such as authoritative-leadership are associated with high self-esteem and more healthy interpersonal qualities (Foster et al. 2016). While it is tempting to see the socially corrosive nature of some narcissistic traits as an obvious disadvantage or indicator of pathology, such a value judgment should not cloud our evaluations of whether or not these traits (and their associated social strategies) are an advantage *to their carriers*. Indeed, the boldness of narcissists allows them to use their self-assured charm to gain the higher social standing they think they deserve. The enticement of enhanced social standing serves to ensure that narcissists both seek, and often obtain, social status, which in turn allows them to garner resources. In addition to striving for social dominance, narcissists tend to have a less restricted sociosexuality, which facilitates a short-term mating strategy in both men and women. For men, such a strategy usually entails maximizing the number of female sexual partners and hence

their reproductive output. For women, this likely means placing greater importance on the genetic quality (i.e., symmetry, health, masculinity) of her partner than on the partner's commitment to a long-term relationship. The combination of heightened status and a propensity to engage in short-term mating serves to explain both the proximate advantage to carriers and the ultimate origins of narcissistic traits in the human lineage.

Elevated status is a means of controlling resources (both social and physical), which confers a survival advantage. A short-term mating strategy serves to make a high number or greater quality of offspring more likely, with high status facilitating even more opportunity to engage in short-term mating. This dual selective pressure (first detailed by Holtzman and Donnellan 2015) helps to explain why natural selection would favor narcissistic traits and would allow them to persist across generations despite their potential social cost.

Adaptation or Disorder: Is Narcissism an Advantage?

The clinical psychology literature is replete with examples of the social malfunctioning of narcissistic individuals (see Skodol et al. 2014). Despite the potential pitfalls of narcissistic traits at extremely high levels (Back et al. 2013; Foster et al. 2016), new data are challenging old assumptions regarding the *benefits* of narcissistic traits at low to moderate levels (Foster et al. 2016; Holtzman and Donnellan 2015). The substantial heritability of narcissistic traits, and the way they facilitate not only heightened acquisition of status and resources, but also the securing of short-term mates, leaves open the possibility that narcissistic personalities can be thought of as a suite of (largely) adaptive traits, whose benefits tend to outweigh their costs. The psychopathology typically associated with narcissistic personality disorder (NPD) only exists in a small percentage of the population, and even these maladaptations may be better explained by comorbid personality disorders or other psychopathologies (see Skodol et al. 2014). In sum, narcissistic traits can be thought of as an adaptive cognitive and behavioral

style giving carriers not only the entitlement to take what they want (resources, status, desirable mates), but also the social tools to obtain them.

Conclusion

Narcissistic traits are associated with a grandiose sense of self, entitlement, and the use of bold and exploitative social strategies to gain social attention and prominence. While at extreme levels (i.e., NPD) narcissistic traits can be construed as maladaptive, the demonstrable social benefits associated with low to moderate levels of narcissism reveal the possibility of adaptive design via natural selection. Future research should test hypotheses associated with the positive benefits of narcissism, such as status attainment, favorable mating opportunities, and most importantly measurable reproductive output. Such considerations must be balanced against the potential social costs of narcissistic traits – dissolution of social relationships, social isolation, and antagonistic or hostile interpersonal styles. Only rigorous hypothesis testing will inform our understanding of narcissism as an adaptation, a disorder, or both, and reveal whether narcissists see success or failure when they peer into the (gene)pool.

Cross-References

- [Self-esteem](#)
- [Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?](#)
- [Sociosexuality](#)

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Narcissistic Personality Disorder (NPD)

- [Narcissism](#)

Narrative

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Synonyms

[Fiction; Storytelling](#)

Definition

Representational format used to organize, store, and retrieve episodic information.

Introduction

Narrative is a representational format used to organize, store, and retrieve episodic information. As such, it is distinct from associated phenomena such as storytelling and fiction. Narrative includes any representation of a series of interrelated events, such as episodic memories, dreams, fantasies, plans, gossip and, of course, stories. The function of narrative can be inferred from its structural components, upon which there is widespread cross-disciplinary consensus: Cognitive psychologists and literary scholars alike agree that narrative requires a protagonist, setting, causally and temporally linked actions and events, and conflict and resolution. Collectively, these components illuminate the type of information that narrative organizes and stores.

Narrative Structure and Function

Arguably, the most essential component of narrative is causally and temporally linked actions and events (Scalise Sugiyama 2005). In a narrative, something happens: An event occurs or an action is performed that precipitates a subsequent series of events. Events are changes in the state of affairs (Rumelhart 1975) and can be external (e.g., changes in the physical environment) or internal (e.g., changes in mental state; Mandler and Johnson 1977). Actions are events caused by sentient beings (e.g., a boy throwing a ball at a window, causing it to shatter), as opposed to those caused by physical forces (e.g., an earthquake shaking a window, causing it to shatter). Because actions are behavior, and behavior is caused by mental states, narratives that involve sentient beings typically feature internal as well as external events.

Significantly, virtually all narratives involve sentient beings, or characters (Scalise Sugiyama 2005). Characters, in turn, are agents – entities

capable of having goals and capable of acting on those goals. Thus, narrative represents goal-directed action: events that agents cause to happen and agents' reactions to things that happen. Although dreams and memories may appear to lack this focus on agency, the individual experiencing the dream or memory is always an implied agent, because dreams are actual or imaginary events experienced or observed by ego, and memories are recollections of actual events experienced or observed by ego. Overwhelmingly, the agents that populate narrative tend to be human. Although animal characters are common in myth, folklore, and cartoons, they are almost always anthropomorphized: They may retain or be constrained by some of their nonhuman attributes, but they are endowed with a human psyche and human traits (e.g., bipedal locomotion, opposable thumbs, speech) that enable them to manipulate and interact with the environment in a decidedly human manner. Bugs Bunny is a case in point: Although he retains his classification as “prey animal,” he reasons, talks, walks, and manipulates objects as humans do. In myth, characters often take the form of inanimate entities and phenomena – e.g., celestial bodies, weather, topographical features – but like animal characters, they exhibit human intentionality and behavior. In sum, narrative exhibits a pronounced bias toward human-centered action. Even Kafka's “Metamorphosis,” in which Gregor Samsa has lost most of his human attributes, is about a human being with a cockroach body, not a cockroach with a human mind.

Because happenings play out in a physical universe, another key component of narrative structure is setting or the set of environmental conditions under which actions and events transpire (Scalise Sugiyama 2005). These conditions include topography and climate, physical laws and natural phenomena, and objects and their locations relative to one another. Because the human physical environment typically includes people, setting also has a social dimension, which includes such human-generated phenomena as laws, ideology, religious beliefs, norms, and manners. As in real life, the physical and

social conditions that obtain in a given narrative world constrain the kinds of events and actions that can occur.

The last critical component of narrative is conflict and resolution, which arise from obstacles to goal-directed action (Scalise Sugiyama 2005). An obstacle is a problem that must be solved in order for a goal to be achieved. For example, Cinderella is initially prevented from attending the ball by her lack of proper attire and transportation. In order to attain her goal, she must solve these problems. Resolution represents the outcome of conflict: It tells us whether or not the solution deployed by the protagonist solved the problem and whether or not the protagonist attained his/her goal.

In short, narrative is organized around the actions taken by a focal agent in pursuit of a specific goal, problems encountered in the pursuit of that goal (including the opposing goals of other agents), and solutions deployed to solve those problems. Experimental evidence supports the claim that narrative is organized around goals, complications, solutions, and outcomes. Studies have found poor recall for passages containing actions without complications or complications without resolution (Mandler and Johnson 1977). For example, Owens et al. (1979) found that knowledge of a character's motives improves recall of story actions and events. These findings suggest that events and actions are input into and retrieved from memory according to the goals they advance or impede.

When the components of narrative are combined, we end up with a representation of human goal-directed behavior and the set of conditions (including constraints and obstacles) under which it unfolds (Scalise Sugiyama 2005). The basic structure of narrative, then, is SETTING + AGENT + GOAL + ACTION + OBSTACLE + SOLUTION + OUTCOME. Humans appear to make sense of narrative by ascertaining the goals of the characters and using them as a schema for interpreting and organizing the characters' actions and feelings. This strategy mirrors the structure of the agency system, which uses intentional schemas (inference systems activated under specific conditions) to interpret and predict the

behavior of agents in terms of goals (Csibra et al. 2003). By the end of the first year of life, infants evince use of an intentional schema comprising three representational elements: the agent's action, the goal state implied by the action, and the constraints of reality on possible actions (Csibra et al. 2003, p. 128). Experiments show that infants are also capable of discerning contingent action or the modification of behavior in response to events or the actions of others. For example, infants look longer when an animated box continues to use a detour after an obstacle has been removed from its path (Csibra 2008). This suggests that infants expect agents to adjust their behavior in response to a change in conditions relevant to the goal-state (in this case, removal of the obstacle).

The representational elements of the agency system map neatly onto the components of narrative structure: "agent's action" maps onto AGENT and ACTION, "goal state implied by the action" maps onto GOAL, "the constraints of reality on possible actions" maps onto OBSTACLE and SETTING, and SOLUTION maps onto contingency. Narrative structure thus appears to emerge from cognitive mechanisms dedicated to tracking the goal-directed actions of agents in the world. Specifically, narrative appears to be a representational format that guides input and organization of knowledge about problems encountered – or that might be encountered – as agents pursue their respective goals. The AGENT component specifies the person or type of person (e.g., male/female, child/adult, married/single) who encountered the problem in question, the GOAL component specifies the objective and motive of the agent, and the ACTION component specifies the measures taken by the agent to achieve this objective. The SETTING component stores information about features of the local environment relevant to the agents' goals and is closely related to the remaining components: OBSTACLE specifies the nature of the environmental constraint(s) that impeded attainment of the agent's goal, SOLUTION specifies local strategies for surmounting the obstacle, and OUTCOME stores information about the effectiveness of solutions. In short, narrative structure "mimics the format in which experienced events

are mentally represented and stored in memory” (Tooby and Cosmides 2001, p. 24). Indeed, the agency system and narrative structure may effectively be the same thing: Each is dedicated to representing contingent relationships between sets of goal-directed actions. What we experience as “narrative” may simply be outputs of the agency system that rise to the level of consciousness.

Narrative, Storytelling, and Fiction as Discrete Phenomena

As a format for organizing and storing episodic information, narrative is distinct from associated phenomena such as storytelling and fiction. The ability to represent goal-directed action is not unique to humans: We may assume that all animals capable of agency are equipped with agency-detection systems (Barrett 2005). However, one thing that distinguishes humans from other animals in this regard is the ability to access other people’s narrative representations. Once language evolved, humans were able to share the narratives in their heads with conspecifics, and storytelling was born (Scalise Sugiyama 2005, 2011). This is a key point: Storytelling is interactive, narrative is not. Although all stories are built on a narrative framework, not all narrative is storytelling: Many memories, dreams, and fantasies never leave the confines of the mind. Thus, in contrast to narrative, storytelling is a behavior, a by-product of adaptations for (among other things) agency-detection, communication, cooperation, and theory of mind.

The fact that storytelling is a human universal (Scalise Sugiyama 2005) begs the question: What is gained by engaging in this activity? The answer lies in the function of episodic memory, the human memory system dedicated to storing personal experience. This system is hypothesized to provide the raw material for generating plans. As Schank explains, “Figuring out how to behave in a new situation is most certainly helped by being reminded of an old situation that is like the new situation. The old situation then becomes a guide to follow or even a guide to what not to do” (1990, p. 24). It has long been noted that experience is

retrieved from memory as stories (Schank 1990). Moreover, the structural parallels between memories and plans are striking. Both consist of agents, setting, and actions: A memory is a series of causally and temporally related actions that occurred in the past, and a plan is a series of causally and temporally related actions that can be taken to bring about a desired goal-state in the future. The content of plans is thus believed to derive in large part from our memories of past events: To make a plan, the mind consults past experience, gathers details relevant to the target goal, and assembles them into a series of actions tailored to attaining that goal (Schacter et al. 2007). This hypothesis is supported by neuroimaging data showing that the same brain regions are activated by the tasks of remembering the past and imagining the future, and by clinical research showing that memory impairment compromises patients’ ability to imagine future scenarios (Schacter et al. 2007). It follows that, if plans are built out of personal experience, then the greater and more varied one’s experience, the greater the variety of plans one can generate (Scalise Sugiyama 2011). The benefit of storytelling, then, is that it enables individuals to expand their episodic memory by acquiring experience vicariously: When we engage in story worlds, we observe the experiences of other agents and, in so doing, make them our own (Scalise Sugiyama 2011). As virtual experience, storytelling may also increase the audience’s sample size of actions and consequences, which may provide emotional and frequency inputs useful for the calibration of relevant decision-making mechanisms (Tooby and Cosmides 2001; Bechara and Damasio 2005).

Because storytelling involves information donation, it can be characterized as a form of cooperation. The benefit of storytelling for the audience is straightforward: Like all forms of teaching, it greatly reduces the costs of knowledge acquisition. Learning through direct experience is expensive: An individual must spend considerable time and energy seeking out experiences that will provide the needed information, and further time and energy on the experience itself. Moreover, trial-and-error learning can be

dangerous: She who learns from others that moose are dangerous during the rut has a better chance of surviving than she who learns this from personal experience. Social learning is also more predictable: An individual who relies on trial-and-error learning might not encounter the requisite learning experience by the time it is needed or when free from a more urgent task. Thus, like other forms of social learning, storytelling reduces risk and frees up time and energy that can then be invested in other important activities. It also exponentially increases the amount of knowledge that can be acquired in a lifetime: Through storytelling, humans can tap the knowledge of all the individuals in their social network, as well as past generations. Finally, by preventing knowledge from being lost when a person dies, the transmission of stories across generations enables human societies to accumulate and maintain large stores of information (Scalise Sugiyama 2011).

The benefits that accrue to the storyteller can be understood in terms of kin selection and social exchange. Telling stories to close kin may increase their chances of surviving and/or reproducing, thereby helping copies of the storyteller's own genes. Sharing stories with nonkin may motivate reciprocal behavior toward the storyteller, in the form of information or other valuable resources (Cosmides and Tooby 2005). Storytelling can also be characterized as a form of manipulation – specifically, as the strategic deployment of episodic representations to influence the beliefs and behavior of others (Scalise Sugiyama 1996). One drawback of being a highly social species is the ample opportunity group living provides for individual interests to come into conflict. Thus, there are times when a person can benefit from persuading others to modify their goals and behavior in ways that serve his/her interests. Stories are a highly effective means of disseminating information strategically, because both the timing and the content of the story can be tailored to the task at hand (Scalise Sugiyama 1996). For example, storytelling can be used to reinforce social norms by illustrating the rewards of compliance and the costs of deviance. The trickster genre is a case in point: Across forager societies, these stories are used to model antisocial

behavior and the negative consequences of engaging in it. With its implicit message that what befalls the trickster will befall other rule-breakers, this tactic provides a nonconfrontational means of chastising and threatening transgressors (Scalise Sugiyama 2011). Stories can also be used in conjunction with precautions, as seen in the use of monster stories by foragers to compel obedience from children (Scalise Sugiyama 2011). Informants report that they use these stories to discourage children from wandering off, crying at night, and depleting food stores. The monsters in these stories specifically target refractory children, and their predations are described in gruesome detail, which may serve to intensify the attentional salience and emotional valence of the precaution.

On this view, gossip is a subset of storytelling. As a means of exchanging social information and managing reputation (Dunbar 1996), gossip involves both cooperation and manipulation. And, like memories and plans, gossip consists largely of representations of goal-directed action – in this case, who did (or said) what to whom and to what effect. What distinguishes gossip from other types of storytelling is its focus on local social information: Gossip involves the exchange of narratives that reference agents, happenings, and entities in the participants' local environment. These representations are used strategically to provide alliance partners with beneficial information and to shape the beliefs and behavior of the gossip's social network in ways that serve his/her interests (Dunbar 1996; Scalise Sugiyama 1996).

Because narrative representations can be non-veridical, the terms *narrative* and *story* are often used interchangeably with *fiction*. This has led to confusing claims that literature is an adaptation. The term *fiction* refers to nonveridical representations intended to be understood as such and thus includes painting, sculpture, pantomime, and fantasies (Tooby and Cosmides 2001). Clearly, then, not all instances of fiction are instances of narrative or storytelling. Nor are all stories fictions. Fiction is a by-product of our evolved capacity to reason counterfactually – to think about things that aren't present, haven't happened, or don't exist. Counterfactual reasoning, in turn, is the bedrock of improvisational intelligence (the ability to invent

solutions to problems), which was critical to our species' colonization of the foraging niche (Tooby and DeVore 1987; Cosmides and Tooby 2000). As with other key human traits (e.g., bipedal locomotion, language), the importance of this faculty is indicated by its ontogenetic precociousness: The ability to understand pretense emerges by 15 months, and the ability to participate in pretend scenarios emerges between 18–24 months (Onishi et al. 2007). The agency-detection system begins developing even earlier, possibly by the sixth month of life (Csibra 2008).

Conclusion

Narrative, fiction, and storytelling are manifestations of the highly developed ability in humans to acquire, generate, exchange, and apply information (Tooby and DeVore 1987). The foraging niche is characterized by the use of complex techniques to extract nutrient-dense resources (Kaplan et al. 2007). Use of these techniques is supported by a wide range of knowledge and skill sets, which are impossible to acquire through trial-and-error learning alone (Boyd et al. 2011). Thus, occupation of the foraging niche is highly dependent on information exchange. Narrative is a format for representing actual episodic information that, in conjunction with the capacity for counterfactual reasoning, enables humans to generate hypothetical (i.e., fictional) episodic information. Combined, these two faculties enable the representation of possible chains of goal-directed actions. Like emergency drills, fictional narratives are simulations that enable humans to rehearse possible problems and test possible solutions. Language enables humans to exchange veridical and nonveridical narrative representations – to “recreate situations for others and to convey to them what has been found to be of interest and of value” (Bieseles 1993, p. 42) – exponentially increasing the ability to manage risk. Like slings, nets, and baskets, the generation and exchange of stories has “made possible the ‘carrying’ and thus the sharing of adaptively significant information” (Bieseles 1993, pp. 42–43), which in turn has greatly facilitated occupation of the knowledge-intensive human ecological niche.

Cross-References

- [Cultural Transmission](#)
- [Episodic Memory](#)
- [Gossip](#)
- [Human Storytelling](#)
- [Pretense](#)
- [Social Learning](#)

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theory, traveling efficiency hypothesis, postural feeding hypothesis, etc.), it remains that sometime in the evolutionary past (4–7 million years ago), the pressures of the environment affected locomotion to the extent that ancestral hominids began to travel on 2 ft. The shift from quadrupedalism to bipedalism may have been beneficial for a number of reasons, but it was also associated with skeletal changes that became problematic for women's reproduction. For instance, the hips developed larger joints, face changed laterally, and the diameter of the birth canal changed due to the shift in weight-bearing and balance. Further, although men's hips became narrower for optimal bipedalism, women's hip width remained constrained by both the need for a large enough birth canal for successful parturition (birth) and by sexual selection that may favor larger gluteus muscles. The remainder of this entry will focus on (a) the conflicting adaptations between bipedalism and large brains and (b) the mechanics of human parturition through the birth canal.

Narrowing Birth Canal

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Synonyms

[Obstetrical dilemma](#)

Definition

As a result of the evolution of bipedal locomotion, women's birth canals narrowed, making parturition more complicated.

Introduction

Although there are several theories of how bipedalism evolved in humans (e.g., savannah-based

Implications of Bipedalism

Human bipedalism and large brains can be viewed as conflicting adaptations. Indeed, humans have much larger brains than any other hominin, and consequently, heads of human babies are also large. Perhaps due to this increased demand for prenatal brain development, human babies are born altricial (unable to move around or feed independently) and not precocial (able to move around and feed independently) like most nonhuman primates. The obstetrical dilemma hypothesis tries to explain the timing of pregnancy and labor by focusing on bipedalism and the narrowing of the birth canal (Weinger et al. 2008). During the shift to bipedalism (visible in *Australopithecus afarensis*), the pelvis and subsequently women's birth canals narrowed. However, the brain size in proportion to the bodies in *Australopithecus afarensis* was still small. Thus, it is likely that the birth canal only became a limiting factor to gestation later, around the time of *Homo erectus* when brain size started increasing more rapidly. The fossil record indicates that like humans, *Homo erectus* infants were likely

relatively altricial. Thus, the obstetrical dilemma hypothesis suggests that bipedalism constrained the human gestational period such that the babies have the most brain development possible but when they are still able to pass through the birth canal.

Implications of the Birth Canal

Because of the narrower birth canal and the morphological changes in pelvic structure associated with bipedalism, the mechanics of parturition in humans are somewhat peculiar in comparison to that of other species. Unlike most nonhuman animals, modern humans (like all immediate ancestors including members of the genera *Homo*, *Australopithecus*, *Paranthropus* and *Ardipithecus*) have birth canals that are wider sideways (hip-to-hip, transversely) than front to back (anteroposteriorly), and the inlet and outlet of women's birth canals are perpendicular. Furthermore, babies' heads and shoulders are wider in opposite directions as well. To the extent that babies first face in one direction to align their head with the birth canal and then turn in other directions for the rest of their bodies to pass, the physiological constraints mean that babies have to rotate as they are moving down the birth canal (Rosenberg and Trevathan 2002). The baby is normally born facing the opposite direction of the mother, unlike monkeys where the baby is facing the same direction as the mother. These pressures may have influenced the more social nature of human labor and delivery.

Conclusion

Bipedal locomotion evolved in response to pressures from the environment that likely were related to Resources and speed. However, for women, the change in skeletal morphology associated with upright walking facilitated a narrowing of the birth canal. This narrowing is thought to be related to the timing of parturition and the physiological and social aspects of human birth.

Cross-References

- ▶ [Bipedal Locomotion](#)
- ▶ [Early Stage of Brain Development at Birth](#)
- ▶ [Implications for Pregnancy](#)

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Natal Philopatry

- ▶ [Viscous Population](#)

Natalism

- ▶ [Debating Procreation \(With David Benatar\)](#)
- ▶ [Permissibility of Reproduction](#)

Nativism

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Synonyms

[Language acquisition device](#); [Universal grammar](#)

Definition

Language is an innate faculty which humans are biologically prepared to develop in contrast to other species.

Introduction

Naturalistic accounts of language acquisition, such as Chomsky's linguistic nativism, claim that our capacity for producing and understanding verbal correspondence is coded into our brains from birth. On its conception, in his 1959 review of Skinner's *Verbal Learning*, this type of explanation stood in contrast to the dominant empiricist views emphasizing learning and conditioning. Previously, researchers had explained linguistic development as a product of external variables, equating it to the vocalizations of other animals. A knowledge of grammar was then believed to be derived from domain general learning mechanisms, with individuals' capacities for language originating from the conditions of their physical environment. The nativist perspective challenged a prevailing focus on simplistic causal explanations for linguistic development. Instead it addressed the complex organs that allow for language to be produced and comprehended. Accordingly, though the specifics of a language were learned, the human capacity for it was thought to be the product of at least one species specific, genetically endowed, unit. That suggestion marked a paradigm shift in how linguists regarded the internal processes that determine language production and comprehension, and is sometimes credited with spurring the cognitive revolution.

Key Concepts

The nativist hypothesis reasons that language faculties emerge as organically as an ability to walk, with children's brains calibrated to extract content from limited samples of communication. Dedicated linguistic modules are therefore considered a fundamental part of the human genome. Thus rather than thinking of infants as blank slates, nativists characterize them as information processors in possession of an internal knowledge of syntax i.e., the principles and processes which govern form. Ergo people's capacity for organizing language is treated largely independent of that which they encounter in their surrounding worlds.

Chomsky (1980) notes that often a child's knowledge of grammar greatly exceeds the inputs and reinforcement they are given. Moreover, their daily use of language will often comprise novel strings of words that have not been previously spoken by or to them. They will also achieve their creative expertise despite rarely encountering negative evidence i.e., information regarding which strings of utterances are not grammatical. These occurrences make it infeasible that their language capacity is learned through habituation. Instead, despite the relative poverty of their stimulus, their brains must have an inherent means to generatively order its limited vocabulary into, or respond to, a seemingly infinite variety of combinations. Hence they can identify Chomsky's creation "colorless green ideas sleep furiously" as grammatically plausible despite it being semantically meaningless and the odds of them hearing it prior being improbable.

Chomsky (1980) labelled the chief tool, to this acquisition process, universal grammar. This term refers to a set of instinctive language-general principles of categories, mechanisms, and constraints including the ability to distinguish nouns from verbs, or function words from lexical words. One principle is syntax being dependent on structure rather than sequence. In English, a question form of the statement "Dean Robertson will cross the road" sees the third word shifted to before the first and second, to become "will Dean Robertson cross the road?" However, the same technique applied to "the slow chicken will cross the road" results in the ungrammatical form "chicken the slow will cross the road?" Inconsistencies such as this necessitate that speakers have a knowledge of structural components, rather than relying on linearity for clarity. In these examples, "Dean Robertson" and "the slow chicken" are both noun phrases, despite their variable forms. Whereas "will" is future-interrogative and so needs to be moved to the beginning in order to form a question.

Also included in universal grammar are parameters, referring to language-specific variations. For example, English is head-initial, with a noun of verb preceding compliments in the same phrase, while Japanese is head-final. It is these

specifications that allow speakers to create syntactically correct sentences that elucidate the relationships between subjects. The continuity assumption (Pinker 1994) suggests these innate parameters are reliable throughout people's lives meaning, once developed, young children's syntactic competence matches that of adults. The amount and scope of principles and parameters are still subject to rigorous debate, with researchers estimating there being anything from tens to hundreds.

Chomsky draws a parallel between thought and language, conceptualizing the latter to be a means of externalizing the former. In doing so he reverses the Aristotelian view of speech as sound with meaning, by labelling it meaning with sound. Yet he stops short of analyzing its adaptive origins in terms of the specific demands it had to meet. Other researchers have attempted to tackle this issue, so as to align knowledge of why humans have language with how it works. Notably, Dunbar (1993) explored its origins as a means to allow for vocal grooming, or gossip, by permitting simultaneous interactions between multiple members of a social group. Pinker (1994) agrees with language being an instinct akin to spiders weaving webs or beavers constructing dams. Though he suggests its purpose was to meet the reliance on knowledge that would have been crucial to the continued survival of hunter-gatherer societies. What both of these theories have in common is they support the nativist model in suggesting that language acquisition is not a byproduct of general learning tools.

This is not to suggest language acquisition is inevitable under nativist accounts. Rather, it has been claimed that children require access to samples of a naturally occurring inputs to initially stimulate the process. Lenneberg (1967) speculated a salient role of biological age, anticipating a critical period for language acquisition between 18 months and early puberty most people. Similar phenomena have been seen in cross-species, with researchers determining the effects that the timing of relevant environmental inputs can have on how attuned an organism's capacities are to the environment it has been exposed to e.g., imprinting in young animals. As per Chomsky's nativism, this

theory suggests language occurs through maturation instead of feedback. Lenneberg argued that this constraint is owed to a decrease in neural plasticity following hemispheric lateralization, where evidence for lateralization in language is robust.

Outside such a timetable, a child will be neither able to learn, nor meaningfully produce, language regardless of the inputs that follow. But provided this threshold is reached then they ought to learn it without a need for formal tuition. While the critical period has since been revised to a sensitive one, following some exceptional data, there appears to be a consensus that age is a key issue in learning a first language.

Evidence for Linguistic Nativism

The best evidence of linguistic nativism is in the seemingly streamlined process by which language, including sign, is acquired. From any other species, the most intelligent member would be unable to achieve that which we expect from any normally developing one of our own. Whether they are raised in a small mountain village, or a vast metropolis, children encounter equivalent milestones in the same order, despite often considerable variance among their inputs where Brown (1973). Their use will also be creative and not necessarily tied to a context, like the communication systems of other animals empiricists had thought analogous. It would be difficult to explain this humanity-wide mutual incidence, and the resultant grammatical consensuses, through nonbiological models. A uniform schedule, regardless of the quality of exposure, therefore hints at an innate underlying cause. Furthermore, to test the poverty of the stimulus argument Marcus (1993) explored the feedback that young speakers receive. In outlining the inadequate responses, that corrected meaning over grammar, he suggested internal factors and an innate knowledge must be crucial to constraining their generalizations e.g., past tense errors like "maked" or "goed."

A biological premise for language is further supported by consistent patterns of specific

linguistic faculties being deleteriously impacted, following damage to particular neurological regions, despite other cognitive capacities remaining intact (Hickok and Poeppel 2007). Modern imaging techniques, along with neuropsychological data, have revealed a network of regions specialized to comprehending language or articulation. Popular examples include the frontotemporal region, being localized to enunciation, the posterior temporal area being linked to understanding and the bridging tract to repetition. Combined these deficits reinforce language as a natural phenomenon, by highlighting a network of neurological substrates selectively dedicated to its function in the absence of obvious associations with other abilities.

Tragic childhood neglect stories suggest that the roles of these regions are subject to a sensitive period (discussed in Pinker 1994). Famously, Genie was rescued from prolonged isolation at age 13. While she regained some of her language capacities, including basic syntax and an ever-growing vocabulary, she was unable to apply or follow complex grammatical features. This deficit continued despite her being subject to a stimulus-rich environment which actively encouraged her to learn: something that would have nurtured her abilities according to empiricist accounts. In contrast, Isabelle was saved aged six and a half and was soon able to learn language and to use it as meaningfully as her peers. There are ambiguities surrounding the specific role of trauma, or the condition of each subject prior to their mistreatment. Even so, the stark difference in recovery between these examples advocates the existence of a time restricted window important for normal development.

A more routine illustration of the same phenomenon can be found in adults acquiring a second language, with some data showing a linear relationship between age of learning and subsequent struggles (Patkowski 1980). This line of research is considerably less conclusive than the case studies, with many notable instances of learners beginning in adulthood and still achieving fluency. Nevertheless, it is generally acknowledged that some aspects, such as picking up the native accent, are limited to children being raised

with a second language and not adults gaining one. For that reason it may be the neuromuscular components, such as phonology and pronunciation, which are subject to a sensitive period versus the contents of speech per se (Singleton 1995). However, comparisons with the unguided character of first language acquisition are potentially limited since adults learning a second language will typically do so intentionally.

Conclusion

Chomsky's seminal 1950s critique of empiricism provided a new layer of analysis for thinking about language, arguing that previous means had proven inadequate. Here, he extended a topic most frequently thought of through the lens of observable patterns and conditioning into an area ripe for interdisciplinary research. In particular, he called for a computational approach to linguistics that emphasized the species-exclusive nature of its bestowal. Universal grammar is a concrete theory that can be used to explain recurrent findings in the linguistics literature, including standardized procurement and selective dysfunction following lesions. That a young boy will learn to talk, in a way that his puppy never will, ties the aptitude to our unique biology. But prior to Chomsky, there was minimal consideration of its relative contribution or the mechanisms that may underlie it. Nativism changed this by adding modularity to the lexicon with which language, along with how other cognitive functions, was thought about. The details of this model, along with its evolutionary source and the comparative role of culture, are still hotly contested today. Nonetheless, the framework provides a means to better understand how humans are able to generate speech so effortlessly, be it for the most urgent or trivial matters.

Cross-References

- [Language Acquisition](#)
- [Noam Chomsky](#)
- [Study of Instinct, The](#)

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Nativist Approach

- [Steven Pinker and Language Development](#)

Natural Parenting

- [Co-sleeping](#)

Natural Selection

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Definition

Differences in the propagation of genes in a population as a result of survival and reproduction of organisms carrying those genes.

Introduction

Charles Darwin described natural selection in private essays in 1842 and especially 1844 (Darwin 1909; Glik and Kohn 1996, pp. 90–96). He then drafted a large manuscript on natural selection, which he left unfinished. It was subsequently overlooked until recently (Darwin 1975). Eventually in 1858, the Linnean Society published a version of his 1844 essay in conjunction with a communication from Alfred Russell Wallace. Wallace presented some related ideas, but not natural selection as we now understand it (Bulmer 2005). Soon afterward there appeared *On the Origin of Species / By Means of Natural Selection, / or the / Preservation of Favoured Races in the Struggle for Life* (Darwin 1859), which developed the concept in detail.

Introducing natural selection on the first few pages, Darwin emphasized the importance of variation among individuals, in particular hereditary variation, and a “struggle for existence,” in other words, competition, because “many more individuals of each species are born than can possibly survive”. He thus reasoned, “It follows that any being, if it vary however slightly in any manner profitable to itself ... will have a better chance of surviving and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.” He also recognized that natural selection is a means of the “coadaptation of organic beings to each other and to the physical conditions of life” (Darwin 1859, pp. 4–5).

Inherited differences in reproduction, as well as survival, can also lead to natural selection. Darwin emphasized this possibility when he proposed that differences in attracting mates or competing for them could lead to the special case of sexual selection. Attraction of mates proved to be especially controversial for Darwin’s successors. It implied the evolution of behavior, not just morphology. The idea that natural selection might produce preferences for mates, particularly by females, was inconceivable to most scientists in the late nineteenth century.

Darwin’s original theory thus included all of the essential elements of our current understanding of natural selection (see, for instance,

Maynard Smith 1998). Natural selection is a mechanism of evolutionary adaptation that results from a combination of heritable variation among individuals and differences in their survival or reproduction correlated with this variation. Natural selection does not require individuals to change, but it does require new variants to arise occasionally through reproduction. Natural selection requires more than individual differences in survival and reproduction. It also requires heritable variation in these differences. Darwin's presentation of natural selection included these elements but left many uncertainties, largely because the sciences of genetics and ecology had yet to come.

Basic Issues

When Darwin proposed natural selection, no one understood the mechanisms of heredity. Darwin himself conducted extensive experimental investigations of heredity and selection in domestic pigeons, but he was disturbed by his results. Offspring of differing parents often either combined the parental features or had intermediate features. Inheritance in this way, by blending of parental traits, could not produce adaptation by natural selection. Populations would instead converge on an overall average and then no longer change. Nevertheless it was apparent that pigeons did sometimes inherit parental features without complete blending. Within 50 years, examples of particulate inheritance and its infrequent mutations had been thoroughly verified. The inchoate field of genetics had provided Darwin's theory with the requisite mechanisms for heredity and variation, in the form of genes, each with variants (alleles).

Furthermore, it became clear that all steps in the process of natural selection – differences in survival and reproduction, heritabilities, and rates of mutation – were measurable and thus open to mathematical analysis. Within the first decades of the twentieth century, the mathematical theory of evolution by natural selection had established its basic principles. Evolution, that is, a change in the frequencies of alleles in a population of organisms, depends quantitatively on a balance

between selection, mutation, and migration between populations, as well as the inherent randomness in each of these three processes. Selection is included in equations for changes in allele frequencies by adding a coefficient to adjust the relative survival or reproduction of each allele. Random changes in allele frequencies become more pronounced in smaller populations. Within small populations, rare alleles are more likely to be lost, and one allele is likely to become “fixed” (universal), so random genetic variation among individuals is reduced. On the other hand, random genetic variation among small populations is enhanced.

Concurrently with the theoretical advances, experimental studies in laboratories and quantitative studies of populations in natural conditions confirmed all of these processes (Dobzhansky 1937). It was found that individuals in a population often differ in survival or reproductive success, these differences are often heritable, and genetic variation depends on the sizes of populations. Hoekstra et al. (2001) and Kingsolver et al. (2001) provide reviews of the prevalence of selection in natural populations.

The theoretical study of natural selection and evolution has in recent decades developed great sophistication in exploring the manifold complexities of population size and structure, mating systems, social interactions, migration, and isolation. Empirical studies continue to document the relevant processes. These studies, especially in natural conditions, face challenges in verifying small effects of selection and complex contingencies, in conjunction with randomness in finite populations. These effects are just the sort that theoretical investigations tend to explore.

Despite these theoretical and empirical advances, natural selection still has its perplexities and confusions. Natural selection, those who study it agree, results from the correlated consequences of individual variation, heredity, reproduction, survival, and competition and produces adapted change in the composition of a population. In various contexts, these components have raised many contentious issues. Is natural selection the result or the cause of adaptations? What kinds of variation and heredity are affected by natural selection? How do survival and

reproduction interact? What about cooperation as well as competition? Even more important, is natural selection fundamentally misleading? On the one hand, is it so simple that it reduces to a tautology and explains nothing? On the other hand, is there enough complexity to explain the emergence of cooperation, culture, language? Is it even specifically a biological process?

First, a clear definition is needed. Natural selection, along with mutation, migration, and drift (randomness), produces evolution. Evolution is a change in the genetic structure of a population of organisms. In the simplest case, it is a change in the frequencies of alleles in the population. Natural selection then occurs when individuals differ in their survival or reproduction in ways associated with differences in their alleles. It is important to point out that natural selection does not result merely from differences in survival or reproduction of individuals. It also requires heritability of those differences. Natural selection is thus a change in the frequencies of alleles in a population as a result of differences in the survival and reproduction of individuals that carry those alleles. It is a matter of arithmetic: in any population, genetic variants spread when they leave more copies in successive generations.

Such a definition resolves one basic issue above. Natural selection is not tautological. It is not survival of those that survive. It both results from adaptation (of individuals) and produces adaptation (of populations). The general principle is indeed simple and self-evident. If individuals with particular features survive and reproduce better than others (call these individuals adapted) and if reproduction preserves features of the original, with occasional variation, then a population will accumulate adapted individuals. This concatenation of simple arithmetical steps is unarguable.

Heritable Differences

The mechanisms of heredity and variation have become progressively clearer and their complexities better understood. Within 50 years after the *Origin of Species*, the particulate inheritance of discrete features of plants and animals had

become the subject of rapidly expanding research. Fifty years later, a century after the *Origin*, the molecular structure of a gene had been discovered. Now, some 60 years later, many complexities of molecular genetics have been investigated, although challenges remain.

The basis for heredity is an organism's genome, strands of DNA of enormous length duplicated in each of its cells. Segments of this DNA encode the amino acid sequences for several tens of thousands of different proteins, which compose much of each cell's structure and regulate its vital functions. Other segments encode a large variety of RNA molecules, which themselves (without translation into proteins) provide a diverse array of regulatory actions. An organism's DNA also includes parasitic components, which hitchhike on the mechanisms for duplication or which subvert the mechanisms for translation for its own purposes. All of these direct and indirect effects of DNA provide mechanisms for heredity and opportunities for variation.

The genome, we now know, is not the only way that parents can transmit their features to their progeny (Jablonka and Lamb 2014; Robert 2009). The cytoplasmic contents of ova (and sperm, in special cases) are transferred to zygotes and influence their development. The DNA in mitochondria is the primary example of maternal cytoplasmic inheritance, but other components of the cytoplasm can also influence development.

Bonding of methyl groups to nucleotide bases in a segment of DNA can decrease its rate of translation to proteins. This inactivation of DNA by methylation is catalyzed by enzymes encoded by DNA elsewhere in the genome. In some cases, methylation is also promoted by environmental conditions, such as temperature or stress. Furthermore, patterns of methylation are sometimes passed to progeny with the parents' DNA. Plants and animals differ in which nucleotide base is methylated (cysteine in animals, adenosine in plants) and also in the rates of transfer to progeny (greater in plants, which lack the isolated lines of germ cells in animals). Gradual loss of methylation in successive generations eventually attenuates its effects. Nevertheless, rates of methylation and rates of reversion vary markedly in different

regions of DNA (Van der Graaf et al. 2015). Yet whether or not patterns of methylation persist across many generations, natural selection can enhance or diminish their influence on the activity of DNA, just as it can adjust other molecular mechanisms that regulate expression of DNA. Methylation, often called “epigenesis,” meaning “beyond genetics,” expands the possibilities for natural selection. With its susceptibility to environmental influences and its progressive loss, it provides a mechanism for heredity more flexible and less stable than other ways to regulate DNA.

Still less stable influences on development, but nevertheless hereditary, can result from direct responses to an environmental feature sustained across generations. Learned habits and customs are examples that can propagate in families and populations of interacting individuals. The seasonal territorial boundaries defended by many songbirds, as well as features of their songs, provide examples of learned information transferred across generations in organisms other than humans.

Consider even a suggestion by Lamarck that persistent abrasion of parts of the body could result in inheritance of calloused skin. This “inheritance” would occur in human populations, for instance, if children tended to follow parents’ predominant activities, such as using hands for heavy work or bare feet for walking.

Direct environmental influences have often not been accepted as natural selection. Yet the capability for developing callouses, for instance, is likely to require a predisposition to respond to abrasion by thickening of the epidermis, and such a predisposition might depend on particular structural or regulatory proteins (or methylation of particular segments of DNA, or both), all of which would require particular variants of DNA. In other words, development of callouses would depend on a particular interaction of genes and environment. In this case, for a particular genetic structure of the organism, development of callouses would be especially sensitive to environmental conditions.

Other environmental influences on development, including learning, also require physiological mechanisms and predispositions to respond to

features of the environment and thus are also subject to adaptation by natural selection.

The result can take different forms. Development might vary continuously with some environmental feature. Alternatively, developmental switches might produce several alternatives in response to particular environmental features. In other cases, development might be especially sensitive to an individual’s genome, rather than to its environment. An example is human growth to a particular height, in a population of well-nourished individuals. In such cases, genetic influences are more or less “canalized” within a range of frequently encountered environments. Across the entire spectrum from predominant influences of the environment to predominant influences of the genome, the development of an organism is always an interaction of its particular genome and its particular environment.

The influences on an individual’s development span a spectrum of stability from genome to environment. DNA, one of the most stable organic molecules known, retains some of its structure even in the remnants of organisms that died tens of thousands of years ago. In contrast, the most variable features of the environment, for example the weather, can hardly be predicted from day to day. The development of an individual depends on responses to this entire spectrum of influences. At one end is an archival plan, at the other an immediate context.

No successful construction can rely on one of these alone, neither plan nor context. Context alone has too many possibilities; a plan has too few. Trying to build without a plan is just as likely to fail as insistence on following a plan. Successful construction, as much as successful development, results from adaptations at various levels of stability and flexibility. A “tried and true” plan is important. So is attention to immediate context. Success requires stability across generations as well as flexibility in momentary responses.

Development of an organism, its construction, is thus a plan instantiated in a particular context. All contextual influences during the lifetime of an organism, whether temperature, nutritional, or sensory, are mediated by proteins encoded by the genome. An individual’s response to any stimulus

depends on its current state as much as it does on the impinging stimulus. An individual's behavior, for instance, is at any instant an interaction between its present state and the incident stimulation. This interaction of current state and immediate environment continues through the successive, incremental stages of development, throughout an organism's life.

Each individual's survival and reproduction thus result from an interaction of its current state and its current environment. This process occurring in all individuals of a population produces natural selection. So the progressive interaction of genes and environment during an individual's development is embedded in a longer interaction of genes and environment in the evolution of a population of individuals. The pattern of an organism's development is embedded in the pattern of a population's evolution. Natural selection, an interaction between genomes and environment directing the evolution of a population, results from interactions of genome and environment directing the development of each organism.

As a result of such pervasive interaction, we can draw four general conclusions about structure and context: (1) nothing is *determined* by structure, (2) nothing is *determined* by context, (3) everything is *influenced* by structure, and (4) everything is *influenced* by context. In these four conclusions, the general terms, *structure* and *context*, summarize a variety of more specific alternatives: *plan* and *reality*, *physiological state* and *sensation*, *genotype* and *environment*. Each pair of alternatives, substituted for *structure* and *context* in the four statements, produces equally general conclusions.

Variation in Heritable Features

Natural selection, as just described, might produce stability or flexibility in development, to any degree between extremes of "canalization" and "plasticity." In any particular case, the result depends on the nature of both genetic variation and environmental variation.

Genetic variation in a population is produced by mutations in the genome, by genetic drift

(random variation in reproduction or survival), and by migration to and from other populations. R. A. Fisher (1930) first emphasized the importance of variation in his "Fundamental Theorem of Natural Selection," which states that evolution is proportional to genetic variation, for any strength of natural selection. G. R. Price generalized this equation, by partitioning the change in genotypes in a subsequent generation into the covariance between genes and environment. Price's equation makes it clear that this principle can apply to any change, including learning as well as evolution (Okasha 2008; Grafen 2015; Queller 2017). Variation is fundamental to natural selection just as it is to learning.

One consequence is that natural selection must depend on mutation rate. This rate determines the rate of increase in genetic variation in a population; the rate of decrease in genetic variation, in contrast, depends on random loss (genetic drift) and thus on the size of a population. Migration affects genetic variation also, but the principles are similar. Mutation rates, by their effects on natural selection, influence the rate at which a population adapts to environmental change.

The mutation rate at any locus in the genome depends on the regulation of duplication and repair of DNA by proteins encoded elsewhere in the genome. If so, mutation rates might evolve to adjust the stability of DNA at particular locations in the genome. Natural selection might adjust these rates to the rates at which relevant environmental features change. It is known that segments of DNA (and thus the corresponding proteins) differ in their mutation rates. Not well understood, however, is whether or not mutation rates themselves evolve to adjust the rate of evolution by natural selection at different places in the genome.

Environmental variation comes in a spectrum of periodicities, with durations from seconds to many centuries. The stability or plasticity of development or evolution depends on how natural selection responds to different degrees of environmental periodicity. Environmental variation with periods much shorter than an individual's life is best accommodated by direct influences of the environment on an individual's development. Environmental variation over periods of one or a

few generations is often better accommodated by a few alternative sub-plans for development. Variation over intervals of many generations is handled most efficiently by revisions of the basic plan. For biological organisms, these three alternatives correspond respectively to learning, developmental switches (Pfennig 1990), and genomic encoding. These three alternatives are of course points in a continuous spectrum from flexibility to stability. Each of these developmental alternatives results from an interaction of environment and genome, with progressively decreasing reliance on environmental flexibility and increasing reliance on genomic stability.

Nevertheless, the entire spectrum of developmental alternatives rests ultimately on the genome, the most stable form of inheritance. The genomes of organisms must encode the capabilities and predispositions for genetic or environmental stability, for developmental switches, for temporary methylation, or for flexible learning – for development in response to long-term, medium-term, or short-term variations in the environment. The development of individuals thus cannot be separated from the evolution of populations. Natural selection occurs at all periodicities of environmental variation.

Cooperation and Competition

The evolution of cooperation has created another challenge for natural selection. Darwin's initial summary of natural selection emphasized a "struggle for existence," inspired by Malthus' observation that reproduction can outrun resources for survival. This "struggle" implies competition. Ecologists now recognize two forms of competition, aggressive and exploitative. In the first case, direct interaction between two individuals results in greater access to a limiting resource for one of them. In the second, one individual acquires proportionately more of a resource as a result of its greater efficiency at locating or harvesting it, without any direct interaction with other individuals. Both forms of competition can result in the "struggle" Darwin imagined as the basis for natural selection. In his discussion of

honeybees, Darwin acknowledged the challenge that such competition presents for the evolution of cooperation.

Simplistic explanations for the evolution of cooperation prevailed for more than a century after *The Origin of Species*. During the middle decades of the twentieth century, for instance, it was widely assumed that cooperation would prevail in a population whenever cooperating individuals gained an advantage over non-cooperators. Furthermore, it was assumed that competition between groups of cooperators and groups of non-cooperators would lead to the evolution of cooperation.

A path-breaking book, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, challenged these assumptions in their naive forms (Williams 1966, also Dawkins 1976). Cooperation might provide advantages to individuals and thus favor the spread of alleles associated with helping, but it is also necessary to consider possibilities for the spread of alleles associated with *exploitation* of cooperators. Such "cheaters" would have the benefit of accepting help from cooperators without the cost of reciprocating. Cooperators then face the prospect of becoming "suckers," by providing benefits to others that do not return them. Simple math shows that alleles associated with cheating spread at the expense of those associated with helping, even to elimination of the last helper alleles from a population. Group selection, the selection of cooperative groups in competition with non-cooperators, thus appeared in a new perspective. Cooperation had to spread *within* groups before it could spread by competition *between* groups.

Even if cooperation occurred mainly in small and relatively stable groups of individuals, so that some groups might by chance lack individuals with alleles for cheating and cooperators could prosper, these groups would remain vulnerable to any new alleles associated with cheating, which would then spread by natural selection to exclude cooperation.

Nevertheless, persistent cooperation has been documented for many kinds of organisms (Koenig and Dickinson 2016). It is clear, though, that special conditions apply. First, cooperation must

spread within groups before it can spread by selection among groups. Second, reciprocity is a key to cooperation: costly helping must have compensating benefits in return. Third, alleles associated with cooperation can propagate within families as a result of kin selection, a special case of natural selection.

The evolution of cooperation under these constraints requires alleles associated with a behavioral tactic more complex than a simple heritable tendency to help. Perhaps the simplest effective tactic is to try helping occasionally but to continue only if reciprocation ensues (“win stay, lose shift” or WLS). For instance, sedentary individuals, restricted to interacting repeatedly with a few neighbors, can evolve neighborhoods of cooperation, provided neighbors have alleles predisposing them to initial cooperation rather than cheating. More effective is a capability for identifying and tracking individual partners (Wiley 2012, 2015). Alleles associated with tit for tat (WLS directed at recognizable partners) then permit a cooperative resolution of the prisoner’s dilemma. With further behavioral elaboration, individuals might have capabilities for tracking multiple partners. Then alleles associated with such tracking (combined with those for predictable reputations of helping others) can make diffuse reciprocity advantageous (Nowak 2006; Nowak and Highfield 2011).

A different sort of advantage accrues to helping when it is directed toward genealogical relatives. In kin selection, an allele associated with helping kin can spread provided the cost to the helping individual is less than the benefit to its relative, devalued by the probability that the relative carries a copy of the same allele (in excess of the probability in the population at random). The mathematical condition is $C < rB$, where r is the coefficient of genealogical relatedness (the relevant probability when an allele for helping is rare). Individuals do not have to recognize kin directly; they can reliably interact with kin simply as a result of, for instance, birth in the same nest.

Investigation of a wide variety of animals and human societies shows that helping is frequently directed to close kin. Nevertheless, clear exceptions occur. Furthermore, it is rare that the

quantitative condition, $C < rB$, is met. The latter difficulty can be overcome by a combination of some reciprocity in addition to close kinship. Kinship and reciprocity should complement each other in the evolution of cooperation by natural selection.

A further complexity can favor the evolution of cooperation within groups: policing. If cooperators join forces to punish or exclude cheaters, the extra cost imposed on cheating can make it less competitive in relation to cooperation. In this case, the cost to cooperators of policing must not reduce the benefits of cooperation too much. Also, avoiding the costs of policing (while yet enjoying its diffuse benefits) becomes a second-order form of cheating. Finally, if policing results in the expulsion of cheaters from a group, so cheaters face the possibility of receiving no benefit whatsoever from membership in the group, then selection might favor a form of stealth-cheating by sophistication in evading detection. Alternatively, super-cheating might consist of complete disruption of a group in the expectation that strictly individual competition might provide greater advantages for a cheater than expulsion from a cooperative group.

This spectrum of possibilities for the evolution of cooperation by natural selection involves increasing behavioral complexity. Some of the options thus might apply only to humans. For instance, although cooperative interactions with kin are widespread among nonhuman animals, only a few nonhuman primates have enough complexity of individual recognition to support the formation of reputations (Wiley 2012). Evidence for policing by animals, even primates, is also sparse (Flack et al. 2005; Beisner and McCowan 2013). On the other hand, neither theory nor field work has yet plumbed the complexities of helping and cheating, either animal or human.

Constraints on Natural Selection

In the early years of population genetics, a controversy arose between two of the pioneers in this field. Fisher’s Fundamental Theorem suggested that natural selection would move populations in

a particular environment toward ever greater adaptation provided a source of genetic variation, such as mutation, persisted. Sewall Wright argued, on the other hand, that natural selection usually moved populations toward a local optimum in an adaptive landscape with multiple optima. An adaptive landscape, as Wright imagined it, is a multidimensional map of the adaptation of organisms as a function of possible genotypes, in other words, of all possible combinations of alleles at every genetic locus (Wright 1932, 1986). An adaptive landscape in this sense applies to a particular environment. Only if each allele evolved independently would natural selection lead to a unique, maximally adapted genotype for this environment, as Fisher indicated.

Interactions among alleles, as Wright argued, make multiple local optima for genotypes nearly inevitable. Constraints on interactions of alleles at the same locus or at different ones would produce adaptive peaks in any environment. Optima in such an adaptive landscape result from trade-offs in the interactions of alleles at the same or different loci, in one or multiple individuals. Such interactions are frequent in genomes and populations. Any one protein often affects more than one cellular function or trait (pleiotropy), and any one trait or function is often influenced by more than one protein (epistasis). A change in one trait might benefit survival or reproduction only if a concurrent change occurs in another trait. Furthermore, social interactions can involve traits with advantages for one individual but disadvantages for another, or traits with advantages only when present in both individuals concurrently.

Alleles associated with such traits often do not spread in a population when rare. For instance, during sexual selection, alleles associated with a female preference for a male trait do not spread unless their frequency in the population exceeds a threshold (or their genetic correlation with alleles for the male trait exceeds a threshold) (Lande 1981; Kirkpatrick 1982; Andersson 1994). In general, alleles associated with producing a signal cannot spread when alleles for responding to the signal are too infrequent, even if a response would benefit a signaler. Vice versa, alleles for responding cannot spread when alleles for

signaling are rare, even if a response to a signal would benefit the receiver. Only in a population with enough of both sorts of alleles can they both spread (Wiley 2015).

The situation is even more constrained when rare traits have costs for individuals. For instance, when a preference takes time or a signal entails exposure to predators, these individuals are often subject to increased mortality when their counterparts are not quickly located. The associated alleles are lost from the population by natural selection even more rapidly than by random genetic drift alone. Furthermore, alleles for mate preferences interact in counter-intuitive ways with those for ecological differences (Servedio and Kopp 2012; Servedio and Bürger 2014).

Interactions between heritable variants, whether pleiotropic or epistatic, place constraints on evolution by natural selection. Thresholds and isolated adapted optima result. Only genetic drift or extraordinary mutations can move populations past hurdles or valleys where genotypes are associated with disadvantageous traits of organisms (phenotypes). Because alleles cannot persist unless organisms associated with them survive and reproduce disproportionately, thresholds and isolated optima are not easily surpassed. When multiple traits or genes are required for an overall advantage in survival and reproduction, the probability of overcoming disadvantages decreases.

In some cases, it is possible to circumvent hurdles by coopting unrelated traits or functions (Wiley 2017). In the course of natural selection, fins can become repurposed as legs and wings, just as ocelli can become photographic eyes, comfort movements can become signals, and perhaps habituation can become associative learning. Without cooptation of simpler traits to produce more complex ones, natural selection can overcome thresholds and isolated optima only by waiting for fortuitous mutations, either simultaneous combinations or discontinuous effects, occurrences sometimes called “hopeful monsters.” Perhaps, in the long run, such events can occur. If so, evolution would inevitably lead to maximal adaptation of organisms, as Fisher indicated, despite the thresholds and local optima created by interacting alleles in the short run.

Nevertheless, these interactions prolong, even when they do not prevent, evolution toward global optima by natural selection.

Empirical studies of natural selection have so far infrequently reported pleiotropy and epistasis of alleles under selection (Kingsolver and Diamond 2011). Perhaps these interactions in fact seldom constrain natural selection. On the other hand, the constraints might make selection more difficult to study, so that reports have focused on selection with little constraint. It is also possible that selection itself, over sufficient time, tends to reduce these constraints. For instance, duplication of a gene occurs frequently in the course of evolution, often followed by differentiation of the functions of the “daughters.” Duplication and subsequent differentiation would reduce the constraints of pleiotropy on further progress of natural selection. The mechanism of duplication is itself regulated by other proteins and thus subject to evolution by natural selection.

Interactions between alleles at the same or different locations in DNA or between different consequences of the same allele, and the corresponding interactions between traits of organisms, all produce constraints on the progress of evolution by natural selection. As the complexity of organisms increases, it seems possible that these constraints become ever more complex and thus the constraints on evolution by natural selection ever more obstructive. Natural selection itself might produce still more complex genomes to reduce these constraints somewhat.

Evolutionary Computation

Biological evolution is not the only framework for discussing natural selection. Nothing precludes a generalization of its principles far beyond biological evolution. Optimizing structure by means of heritable variation and selection applies equally to evolution, epigenetics, and learning. In recent decades, it has also been applied to computation and molecular synthesis.

Evolutionary computing provides a way to optimize an algorithm (analogous to optimizing

genetic structure) by systematically modifying its components (mutation) and then selecting those versions of components that optimize the output (organism or phenotype) for particular purposes (environments). The process is usually incremental and progressive like natural selection in biological evolution: mutation and selection occur repeatedly until a local optimum is reached.

An example is the use of neural networks to discriminate sets of inputs. In this case, a series of similar inputs is presented to a network of interacting nodes, each of which can promote or inhibit activity in other nodes and all of which combine to provide a response to each input. Randomly adjusting the interactions of nodes at each generation and then selecting those variants that improve discrimination between different sets of inputs eventually yields the best performance possible. In a similar way, pharmacologists search for optimal molecular structures by progressively altering the components of complex molecules (for instance, the sequences of amino acids in synthesized proteins) in order to maximize medical benefits and to minimize undesirable side-effects.

Evolutionary computing or adaptive synthesis occurs in a multidimensional adaptive landscape just as biological evolution does. The adaptive landscape is the performance of an algorithm or synthetic molecule as a function of the hyperspace of possible structures (nodes and parameters or types and positions of chemical functional groups). Any solution encounters two widely discussed problems: too much precision to capture an entire adaptive peak; and too little accuracy to capture a global peak. In evolutionary computing, the first problem is called “overfitting” (Domingos 2012; Srivastava et al. 2014); it applies to algorithms that perform well on initial data but poorly on similar, but previously unseen, data. Such an algorithm has evolved to a local peak but too narrowly. In other words, an algorithm with overfitting has learned some of the noise (non-generalizable features) in the initial data as well as some of the signal (generalizable features). It has learned too much.

Ways to reduce overfitting include early stopping (as soon as errors on previously unseen data increase too steeply) and limitations on structural and parametric complexity (by reducing the number of nodes and interactions and their weights). Constraining weights of parameters often reduces overfitting by reducing the unpredictability of responses to similar but previously unseen data. All of these procedures rely on testing algorithms with unseen data. In terms of an adaptive landscape, they require testing performance on nearby parts of the landscape.

The second problem of evolutionary computing also has its analogue in biological evolution. Natural selection moves structures toward adaptation to a local optimum in the adaptive landscape and thus can miss a global optimum. Any algorithm, just as any population of organisms, evolves adaptation only to those inputs, variable or not, that it encounters. The only way to be sure of finding a global optimum is to test performance throughout the multidimensional adaptive landscape of possible structures. To assure finding this maximum, in the most general case, would require understanding the complete multidimensional structure and connections of the entire universe, down to the last quark. No advance in evolutionary computing, even as quantum computers increase the speed and breadth of learning or adapting, can guarantee discovery of a global maximum (Niu et al. 2019).

These problems in evolutionary computing have parallels in biological evolution. The generality and specialization of algorithms, we noted, can be probed by varying the environment. For natural populations, such probing of adaptations occurs when an environment varies in time. To acknowledge this variation, it has been suggested that a better metaphor is evolution in an “adaptive seascape.” Adaptations of organisms are thus like well-fitted algorithms, both of which perform well over a local optimum with a spectrum of periodicities in input. Yet they do not necessarily perform well in similar environments not previously experienced. Organisms, including human engineers, instead settle for adaptation to a (not too) local optimum.

Humans making decisions with the assistance of evolutionary computing have learned to extend the principles of natural selection. Making decisions based on trial and error, whether by brains alone or by brains assisted by machines, results in optimal responses to each of numerous inputs. It is the basic process of human behavior. Indeed all animals, not just humans, learn to match responses to inputs. Decisions occur whenever an organism discriminates between alternative inputs when choosing what to eat or where to go or whom to associate with or to imitate. They do so because decisions in response to unpredictable inputs allow greater specificity in adaptations. An organism’s capabilities and predispositions are specified by a stable plan, the organism’s genome. Such a plan, as discussed above, is the basis for all forms of learning and culture. This plan then develops in conjunction with its immediate context, the organism’s environment. Evolutionary computing is thus itself a result of evolution by natural selection.

Conclusion

Every organism develops from a particular plan in a particular environment. It persists as long as repair of its molecular components can counteract degradation – as long as its immediate structure can harvest exogenous energy to counteract entropy. Each organism, each instantiation of its plan, eventually decays. Yet, provided an organism transmits its original plan to nascent progeny, a similar organism in a similar environment can develop anew. Provided organisms transmit their plans to progeny with some appropriate level of variability, natural selection can yield a lineage of organisms that persists indefinitely in an environment of complex changes. Organisms with adaptations for learning can improve their survival in environments with short-term variation. These adaptations can extend even to learning the principles of natural selection. In the end, entropy, the ultimate noise in decisions, prevents learning with infallible foresight – and prevents immortality.

In a population of comparable entities, natural selection is no more than the spread of heritable

variants that replicate at a higher rate than others. Natural selection is arithmetic applied to differences. The principles are the same in all cases. The mechanisms of heredity vary across a spectrum of stability, from the relative inflexibility of the genome to the increasing flexibility of developmental switches, epigenesis, and learning, even to quantum computing. Each mechanism is optimized for a pertinent environment by selection itself. Natural selection is potentially constrained by interactions within and between the entities in a population. It leads to greater complexity whenever it can produce more precise and accurate adaptations. The scope of evolution by natural selection thus includes the evolution of culture, cognition, and language. It thus leads to brains so large that they strain the limits of skeletal adaptations. The scope enlarges still further to include even those decisions assisted by machines.

Finally, consider several misconceptions about natural selection. Each misconstrues issues addressed above. All contradict evidence or logic.

The first misconception claims that culture is distinct from biology and thus not subject to natural selection. On the contrary, environment and genome interact in the development of all organisms, including humans. All features of an organism, including their predispositions and capabilities for learning, are influenced by their genetic structure, just as all features of an organism are also influenced by their environmental context.

Another misconception is that natural selection cannot accommodate Lamarckian evolution, in other words inheritance of environmental influences on individuals. We now know that such environmental influences can affect progeny, but natural selection produces and regulates the necessary mechanisms for these influences.

A third misconception is that natural selection, inasmuch as it is a selection, implies the existence of a selecting agent. Darwin was aware of this difficulty with the term “selection.” Clearly rejecting any such agent, he nevertheless felt there was no succinct alternative for the term. Despite any limitations of language, there is no agent of selection.

Finally, it is sometimes claimed that selected individuals are morally superior. On the contrary, natural selection results from the arithmetic of survival and reproduction of genetic variants in limited populations. It has no more moral implications than any other example of arithmetic. Morality (ethics) instead applies to human attitudes toward the various consequences of natural selection. Because such behavioral dispositions are influenced by genes and by context, they are themselves influenced by natural selection.

Natural selection is not the child of morality; instead, morality is the child of natural selection. And not only morality but also philosophy. In the end, natural selection produces not only a philosophy of biology, but also a biology of philosophy.

Cross-References

- ▶ [Alfred Russel Wallace \(1858\)](#)
- ▶ [Darwin on Speciation](#)
- ▶ [Dual Inheritance Theory](#)
- ▶ [Evolution of Adaptations](#)
- ▶ [Evolution of Communication](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolution of Free Will](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Genetic Predispositions](#)
- ▶ [Genetic Relatedness](#)
- ▶ [Group Selection](#)
- ▶ [History of Natural Selection](#)
- ▶ [Kin Selection](#)
- ▶ [Morality](#)
- ▶ [Sexual Selection](#)

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Natural Versus Artificial Environments

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Introduction

Artificial environments first emerged from natural environments approximately 10,000 years ago with the advent of agriculture. Modern artificial environments differ in critical ways from the natural environments of our ancestral past, but psychological mechanisms shaped in our evolutionary past still help us navigate the social and physical complexities of the world today.

Natural Environments

For the first five million years of hominid history, our ancestors lived in small, nomadic bands of hunter-gatherers. On average, group size was likely maintained around 100–250 individuals. Based on correlations between primate brain size and social networks, Dunbar (1992) proposed that humans can comfortably maintain relationships with approximately 150 people. Because neocortex size effectively limits group size, many of our social adaptations are in tune with small cohesive groups with this capacity (Dunbar 1993).

The environment of evolutionary adaptedness (EEA) is the ancestral environment to which a species is adapted or the set of selection pressures that shaped an adaptation. A central premise of evolutionary science is that forces in our distant past helped make us who we are today. The EEA refers to a group of selection pressures occurring during an adaptation's period of evolution responsible for producing the adaptation (Tooby and Cosmides 1992). A selection pressure can be any factor in a population that impacts reproductive success. Physical, social, and intrapersonal pressures from our ancestral past help to shape our current human design because all animals have

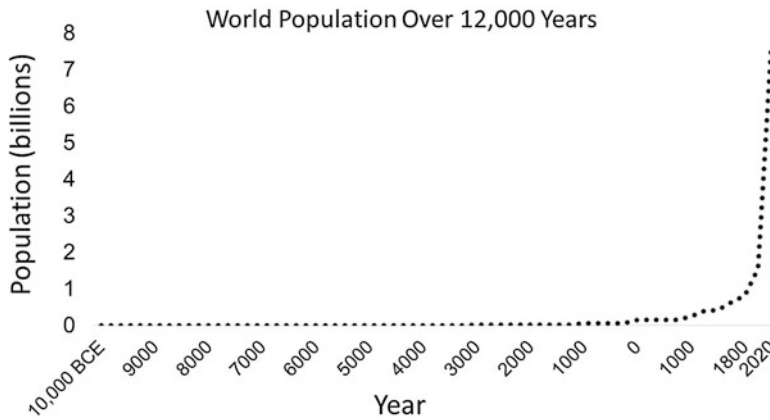
heritable variations that are selectively favored or disfavored in accordance with reproductive success (Buss 1995). Each adaptation has its own EEA, or set of adaptive problems, that shaped it over evolutionary time.

The EEA does not exist as a single geographical location during a discrete period during human evolution. Rather it is a set of selection pressures that formed a given adaptation. For example, ancestral humans faced the adaptive problem of securing and digesting food to maximize energy. Taste buds were shaped in response to this adaptive problem. Our ancestors who showed a preference for salt, fat, and sugar were selectively favored over those individuals who did not have similar preferences. The acquisition of salt, fat, and sugar would have been challenging for our ancestors given the absence of agriculture and the inability to mass produce high concentrations of those items. The probability of survival and reproduction for individuals who showed a preference for those foods would have been greater than for those who did not. Our taste preferences were shaped in response to the problems posed by this environment.

Artificial Environments

Artificial environments first emerged from natural environments approximately 10,000 years ago with the advent of agriculture. The ability for human groups to maintain food and other resources in one geographic area for long periods of time ultimately gave rise to the first small communities, cities, and civilizations. The list of innovations that are present in the modern world but never existed in the EEA includes agriculture, electricity, refrigeration, large-scale weapons, medicines, mass communication, effective contraceptive devices, and virtually unlimited access to all types of proteins and carbohydrates.

The current population of the planet is considerably larger than at any other time in human history. Figure 1 provides some perspective on this time frame by graphically displaying the relevant recent explosion in world population. Our mental machinery, including emotions, decision-



Natural Versus Artificial Environments, Fig. 1 Graph of the global population from 10,000 BCE to 2020 CE, adapted from the US Census Bureau data. The graph shows very rapid growth since the eighteenth century. In the span of 40 years, from 1959 to 1999, the world population

doubled from 3 billion to 6 billion. According to US Census Bureau projections, the world total will reach 9 billion by 2042. (Source: U.S. Census Bureau, International Database, August 2016 Update)

making algorithms, and mate preferences, evolved under conditions that existed more than 10,000 years ago. Since the mid-1800s, the global population has increased tremendously – the blink of an eye on an evolutionary scale. These numbers dramatically illustrate just one of many features of our currently environment that is radically different from previous generations going back to the beginning of human history. Between 1959 and 2042, the world population will grow from 3 billion to an estimated 9 billion (US Census Bureau 2017). In contrast, the prior five million years of human history saw almost no significant population increases during any comparable span of time.

Interactions Between Natural and Artificial Environments

For many residents of urban areas around the world, cities represent the promise of a rewarding due to economic growth, developments in mass transit, and technological innovation. As a by-product of this progress, however, densely populated metropolitan landscapes pose unique psychological challenges not found in other environments. We are navigating our current social and physical world with psychological mechanisms designed to solve problems associated

with survival and reproduction in an ancestral environment much different than the one we live in now.

Websites and applications that enable users to create and share content (i.e., social media) illustrate quite nicely one of the greatest differences between natural and artificial environments. For the past five million years, humans faced problems posed by the social environment (e.g., decoding emotional expressions, communicating internal mental states to others, and detecting cheaters in social interactions, etc.). In response, natural selection shaped a psychological repertoire that includes mechanisms for solving face-to-face social problems. However, human communication has changed rapidly in short amount of time. We now use digital screens more than ever and, as a result, those finely tuned psychological adaptations are being used in a very different way, if they are being used at all.

Humans are particularly good at adapting to diverse surroundings. Harnessing solar power, working in high-rise offices, and navigating via global positioning systems are relatively new experiences that have been widely embraced. While artificial environments offer numerous benefits to health, longevity, and overall well-being, they can also result in unhealthy outcomes. A substantial body of interdisciplinary literature

has accumulated in recent years. Researchers in environmental science, urban planning, architecture, and landscape design have investigated the therapeutic effects of nature on children, adult stress levels in urban spaces, human performance in artificial settings, and criminality (Bennett et al. 2018).

There is now considerable evidence for the positive impact of plants, trees, and other sorts of greenery on physical and mental health. Modern technology, structural designs, and construction materials allows us to comfortably inhabit climates that would have required intense effort just a few generations ago. Still, we carry with us the psychological preferences shaped by generations of ancestors living in a much different world and often customize our environments to resemble that ancient habitat. Most of us prefer physical spaces that offer views of green vistas over windowless basements. Looking at trees might even have a tangible health benefit: Patients who viewed trees outside the window recovered more quickly from hospital stays (Ulrich 1984). Flowers also appear to have a positive impact on hospital patients. Bringing flowers increases optimism and improves the rate of recovery (Watson and Burlingame 1960).

Humans consistently prefer natural environments over built environments (Kaplan and Kaplan 1982). Using data from 30 studies, Kaplan (1992) summarized the results of participant ratings of photographed scenes of Western Australia, Egypt, Korea, British Columbia, and the United States. Across these varied geographic regions, participants preferred natural environments over built environments. Additional data suggest that the presence of trees and vegetation increases positive evaluations of built environments, thus demonstrating the transformative power of foliage (Ulrich 1983).

Other research has focused on the relationship between stress and uncultivated outdoor settings. When placed in uncertain and stressful situations, individuals who viewed pictures of nature scenery showed less physiological distress (Ulrich 1986). Contact with vegetation need not be active, such as gardening, to provide health benefits. Passively viewing vegetation through a window can produce desirable effects as well. Studies in biophilic

design demonstrate that people living and working in spaces with vegetation compared to those without vegetation show improved performance on mental tasks, more positive moods, greater ability to refocus attention, stress reduction, and diminished perceptions of pain in health-care settings (Kellert et al. 2008). Research looking at over 900,000 data points found that children who grew up with the lowest levels of green space had up to 55% higher risk of developing a psychiatric disorder (Engemann et al. 2019). The authors conclude that one long-term approach to improving mental health is to integrate natural environments into urban design.

Conclusion

Agriculture and modern city environments were nonexistent for 99% of human history, emerging only in the past 10,000 years. The modern industrialized world of today differs in many important ways from the natural environments of our ancestral past. This mismatch serves as a useful starting point for understanding the function and design of current psychological mechanisms. Because adaptations evolved over many generations, they are said to be “in tune” with reliable features of the natural environment. Still, we use those psychological mechanisms to navigate the social and physical complexities of the world today.

Cross-References

- ▶ [Ancestral Threats Versus Modern Threats](#)
- ▶ [Gordon Orians](#)
- ▶ [Landscape Preferences: Climate and Weather](#)
- ▶ [Savanna Hypothesis and Landscape Preferences, The](#)

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Naturalism

- [Naturalistic Fallacy, The](#)
- [Philosophical Foundations for a Modern Morality](#)

Naturalistic Fallacy, The

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Synonyms

[Appeal to nature fallacy](#); [Argument from nature](#); [Is-ought problem](#); [Naturalism](#)

Definition

The *naturalistic fallacy*, as it is colloquially used, refers to the logical fallacy made when one derives moral prescriptions from naturally occurring phenomena or factual statements about the world.

Introduction

Moore (1903) coined the term the *naturalistic fallacy* to refer to instances in which one conflates morality with any other construct (e.g., pleasure, fulfillment, social good, God's will). Moore argued that, for instance, while morality and pleasure may both be used to describe a particular act, it does not follow that morality and pleasure are equivalent constructs. The modern usage of the *naturalistic fallacy*, however, most often refers to David Hume's is/ought fallacy, wherein Hume (1739) argues that statements regarding how things ought to be (i.e., moral statements) cannot exclusively be derived from how things are (i.e., factual statements). In other words, moral prescriptions cannot be derived solely from factual statements about the world.

Moral Prescriptions from Evolutionary Principles to Morality

An example of the *naturalistic fallacy* might include statements asserting the morality or utility

of Darwinian natural selection due to its existence in the natural world. Such erroneous reasoning led philosopher Herbert Spencer (1897) to advance a science-based morality in which he proposed that human welfare would be maximized by allowing the weak and poor to essentially die out while the “fittest” thrived in society (but see Wilson et al. 2003). Spencer’s (1897) philosophy was also based in a critical misunderstanding of natural selection, whereby he mistakenly assumed that evolution necessarily leads to human progress or advancement.

The *naturalistic fallacy* is commonly used to describe criticisms of evolutionary psychology that rest upon the notion that factual descriptions of naturally occurring behaviors are equivalent to moral prescriptions or justifications. For instance, critics accused Thornhill and Palmer (2000) of legitimizing rape as a moral behavior and blaming victims for its occurrence by studying rape as a naturally occurring phenomenon (e.g., Kimmel 2003; Rosser 2003; Shields and Steinke 2003). These allegations were made in error; it is not logically valid to claim that descriptions of rape as a natural behavior (i.e., occurring in nature) are equivalent to descriptions of rape as a moral behavior, and Thornhill and Palmer (2000) did not imply as much. Other critics, such as certain feminists, commit the *naturalistic fallacy* by wholly misperceiving the evolutionary investigation of human behavior as “a guide to moral behavior and policy agendas” (Nelkin 2000, p. 20), intended to legitimize and promote the subjugation of women (e.g., Kay 1990; Tang-Martinez 1997).

Conclusion

While the term “naturalistic fallacy” is frequently used in this way within the field of evolutionary psychology (i.e., conflating “is” with “ought”), Wilson et al. (2003) charge evolutionary theorists with misusing the term. Specifically, they assert that evolutionary psychologists inappropriately characterize the above criticisms of their field as

examples of the *naturalistic fallacy*. For example, Wilson et al. (2003) contend that Spencer (1897) was, in fact, not exclusively deriving “ought” from “is,” in line with Hume’s (1739) definition of the *naturalistic fallacy*. Rather, they argue that Spencer (1897) did not invoke “naturalness” in his argument’s factual premise to derive his ethical conclusion; instead, Spencer (1897) defended social practices that favored the strong and the wealthy because he believed that over time, they would produce a better society. Furthermore, Wilson et al. (2003) argue that evolutionary psychologists frequently fail to consider the full moral implications of their findings by neglecting to classify moral behaviors as products of natural selection. However, critics of evolutionary psychology who claim the field seeks to uphold social norms such as sex/gender-based inequality nevertheless misinterpret the intentions of researchers who utilize an evolutionary framework to study human psychology and behavior (i.e., who acknowledge that negative behaviors evolved in response to selection pressures and investigate the underlying causes of such evolved behaviors, but do not necessarily condone their use). Moreover, advances are being made in developing the evolutionary psychology of morality, which investigates the moral behaviors of human beings (see Shackelford and Hansen 2016).

Cross-References

- [Moral Concerns](#)
- [Naturalism](#)

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Naturally Selected Seasonings

- [Darwinian Gastronomy](#)

Nature

- [Emotional Disposition](#)

Nature Effects on Well-Being

- [Health Benefits of Nature](#)

Nature Versus Nurture

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Synonyms

[Behavioral genetics](#); [Biology versus environment](#); [Maturation versus enculturation](#)

Definition

Nature versus nurture is the debate regarding the influence of genetics/biology and environment on human development and behavioral characteristics.

Introduction

Are humans inherently good or bad and intelligent or unintelligent? Are humans born with certain traits, characteristics, and knowledge, or are these developed through experiences? These questions are at the center of the *nature* versus *nurture* debate, stemming back as far as 400 B.C.-E. *Nature* versus *nurture* is the dispute regarding the contributions of biological and environmental factors on human development. *Nature* encompasses genetic, biological, and hereditary factors that are innately present in humans, whereas *nurture* refers to those external, environmental factors that influence human development after conception, including childhood experiences and social relationships. Francis Galton, who coined the phrase *nature* versus *nurture* in 1874, said “Nature is all that a man brings with himself into the world; nurture is every influence from without that affects him after birth” (Galton 1874). Proponents of *nature’s* influence on human

development argue that individual differences are caused by genetic makeup and biology. On the other hand, supporters of *nurture's* influence contend that individual differences are the product of humans' experiences with the physical and social worlds.

Nature

Nature is considered to be humans' "pre-wiring" – the genetics and biology that are present from inception. The idea of nature being entirely responsible for human development and diversity was present as far back as 400 B.C.E. with philosophers such as Plato and Descartes, who proposed the idea that specific traits and characteristics of humans are innate and appear regardless of environmental influences. This idea laid the foundations for *Nativism*, which contends that humans' behaviors and characteristics are the product of genetics and heredity. Nativism segued into other intellectuals postulating on the influential role of inheritance and genes on development (Gordon and Slater 1998).

The struggle to understand heredity and how certain characteristics are shared between parents and offspring led many to speculate on the influence of genetics and evolution on human development. Francis Galton, who introduced the term *nature* versus *nurture*, proposed the idea that intelligence was almost entirely the result of inheritance, and argued that only intelligent people should be encouraged to reproduce, establishing the concept of *eugenics*, or the idea of controlling human reproduction with the intention of producing a "superior" race with desirable characteristics and traits. In 1866, Gregor Mendel published the *Theory of Heredity* and demonstrated how parents pass down traits to their offspring, providing strong support for the idea that much of human characteristics are the result of genetics (Lock and Palsson 2016).

In modern times, nature's influence on human development is still widely accepted and researched. Infants are believed to possess *core knowledge*, or knowledge about phenomena in the

world, such as objects, faces, and numbers, that is present from birth and could not be attributable to life experiences (Spelke 1998). In a study conducted by Pun et al. (2016), the researchers examined infants' perceptions of social dominance by presenting them with scenarios of members of different sized groups attempting to pass one another. In the study, infants looked longer at scenarios when a member of a numerically smaller group had the "right-of-way" over a member of a numerically larger group, indicating this event was unexpected for the infant. The results of this study demonstrated that infants possess elementary knowledge of social dominance by expecting that a member of a numerically larger group will have the "right-of-way" when in contact with a member of a numerically smaller group. Studies such as this provide support for the notion that humans are born with innate knowledge, likely resulting from evolution because of the importance of such knowledge for survival (Pun et al. 2016).

Nurture

Nurture refers to environmental influences on human behavior and development – it is the factors that are "external" to humans and occur after conception. Whereas the *nature* side of the debate was largely developed on the foundations of *nativism*, the *nurture* side was heavily influenced by *empiricism*. Empiricism asserts that learning and experiences are responsible for human behavior and characteristics (Gordon and Slater 1998). Several theories of human development and behavior have their roots in empiricism, such as John Locke's concept of *tabula rasa*. According to Locke, all human minds begin as a "blank slate," and that we learn and develop through our experiences and interactions with the environment. *Tabula rasa* maintains that there is no innate knowledge or characteristics humans are born with, but rather these are gained through life experiences.

Jean-Baptiste Lamarck's groundbreaking research on evolution provided support for the contention that the environment is a powerful

force in determining human characteristics. He proposed the notion that the environment can induce small changes in organisms, which are then inherited by subsequent generations and incorporated into their genetic makeup – this idea led to the *Theory of Inheritance of Acquired Characteristics*, first presented in 1801. Lamarck's theory demonstrated that the environment can have powerful implications for human development and biology (Lock and Palsson 2016).

In more recent times, a study of Romanian orphans has exhibited the undeniable influence of environment on human development and cognition. Researchers Sheridan et al. (2012) compared the brain structure and function of children in Romania who either had never been institutionalized in an orphanage, were once been institutionalized but had been placed in foster care, or were still currently institutionalized. The researchers found that children who had been institutionalized, regardless of whether they were eventually placed in foster care, showed significantly less gray matter in their brains than those who had never been institutionalized. Children who once had been institutionalized but now lived in foster care showed no significant differences in their cortical white matter compared to the children who were never institutionalized, but children who were institutionalized and did not move into foster care showed significantly less cortical white matter, demonstrating that being placed in foster care can improve white matter volume within the brain. This study provides conclusive evidence for the argument that environment plays a significant role in development, as being institutionalized as a child has been shown to have detrimental consequences for neural development (Sheridan et al. 2012).

Conclusion: Nature and Nurture

While genetics and heredity have been found to have a strong influence on the environment humans exist within, individuals' life experiences also determine how genes are expressed. Behavior and development seem to result from an

interaction of environmental and biological processes, and both are responsible for diversity among humans. Many phenomena can be explained in terms of both nature and nurture. Take the example of violence: while many scientists speculate that violence is a learned behavior that is observed from the environment and reproduced, it is equally possible that violence resulted from its evolutionary advantage for survival. Given that there is empirical evidence pointing to the influence of both nature and nurture on human development and characteristics, it is not a question of nature *or* nurture, but rather nature *and* nurture.

Cross-References

- Charles Darwin
- Charles Darwin: Theory of Natural Selection
- Darwin's Education
- History of Inheritance
- Jean-Baptiste Chevalier De Lamarck
- John Bowlby and Attachment Theory
- Offspring Diversity Hypothesis
- Social Learning and Social Cognition

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Nausea

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Synonyms

Biliousness; Feeling Sick; Queasiness

Definition

An uncomfortable sensation of an imminent need to vomit, usually perceived to originate from the stomach and occurring in waves.

Introduction

The term nausea stems from the Greek word “naus” (ship) and was originally used in reference to seasickness (Andrews and Sanger 2014). There are, however, a great variety of external and internal stimuli that can provoke nausea in addition to motion sickness. These range from alternate physiological sources, such as food poisoning or pregnancy, to psychological sources, such as anxiety. In terms of diagnosing the presence of nausea, there is a difficulty due to the lack of known biomarkers (biological indicators) of its presence. As a result, nausea can be challenging to detect without self-reports from the patient (Andrews and Sanger 2014).

Nausea is closely associated with emesis (vomiting) as it is often elicited beforehand. Some research suggests these two sensations utilize the same neural pathways and, as such, form a continuum whereby a nausea-evoking stimulus, when present to a larger degree, will trigger an emetic response (Andrews and Sanger 2014). However, this continuum model is contested, as it fails to account for scenarios whereby vomiting occurs in lieu of nausea, as seen in accounts of astronauts vomiting in space (Stern et al. 2011).

Effects on the Body

There are several alternate effects on the body that occur in combination with nausea. These include a rapid heart rate (tachycardia), sweating, blood vessel tightening (vasoconstriction), and yawning (Andrews and Sanger 2014). Additionally, stomach function has been demonstrated to decline while nauseated, which prevents or slows the toxic food from leaving the stomach to be absorbed into the body (Stern et al. 2011).

Toxin Ingestion

The primary adaptive function of nausea is considered to be the protection of the body from ingested pathogens and toxins, facilitating both immediate and future avoidance of the contaminated stimuli (Stern et al. 2011). Upon consumption of a pathogenic or toxic source, nausea serves as a warning signal to prevent any further ingestion. Concurrently, the progression of the digestive system is slowed to reduce the amount of the toxin that allowed to be absorbed by the body.

The function of nausea, however, extends beyond facilitating the immediate avoidance of the toxic stimuli by also promoting future aversion of the contaminated food, a process called taste aversion learning (Garcia et al. 1955). This form of classical conditioning forms a long-lasting association between the ingested food and the following nausea or further illness (Bayley et al. 2002). From an evolutionary stance, this adaptation facilitates survival through the promotion of future aversion to toxic substances which may otherwise be ingested recurrently.

The evidence for taste aversion learning primarily stems from animal research on rodents, most famously the experiments on rats by John Garcia. Rats are often used in research concerning nausea due to their lack of emetic reflex (they cannot vomit). As such, it is inferred that they rely on taste aversion to avoid consuming lethal doses of toxic food. Garcia et al. (1955) demonstrated the potency of taste aversion learning in a study into the effect of aversion resulting from gamma radiation. Rats typically prefer a solution

of water and saccharin, an artificial sweetener, over plain water; however, after the rats were conditioned to associate the solution with gamma radiation, the rats became aversive to the solution, preferring the plain water.

This taste aversion is specific to food consumption, as demonstrated by Garcia's later experiment with Koelling (1966). In this study, rats were given a water source which emitted an audio-visual stimulus (light and a clicking sound) as the rats consumed the water. When the rats were subject to an electric shock while drinking, the aversive reaction was directed towards the audio-visual stimulus – the rats associated the light and the clicking sound, not the water, with the shock. When the negative stimulus was replaced with an x-ray or a toxin, which elicit nausea in humans, the reaction of the rats was directed towards the water and not the audio-visual stimulus. This suggests that nausea as an adaptive function has evolved to reinforce the avoidance of ingested stimuli and, when there are multiple potential causes for the nausea, to direct the aversion to the ingested stimuli. This is further evidenced by nausea resulting from chemotherapy treatments for cancer patients. While the patients know that the nausea and vomiting are a consequence of the treatment they are receiving, they can still grow averse to the food they consume, associating it with the nausea (Garcia and Koelling 1966).

Pregnancy

A further adaptive function of nausea, interlinked with the ingestion of toxins, is “morning sickness” during pregnancy. This refers to the nausea and vomiting experienced by roughly 66 % of pregnant women that is most prevalent between the 8th and 12th week of pregnancy (Sherman and Flaxman 2002). Though not technically occurring more frequently in the mornings, this elicitation of nausea has the evolutionary function of protecting the mother and fetus from ingested toxins and pathogens. As aforementioned, nausea here also serves to prevent the ingestion of further amounts of consumed toxins and pathogens as well as to avoid the substance that hosted them

in the future. This can be seen in the cravings and commonly avoided foods during pregnancy. This idea has been encapsulated by the maternal and embryo protection hypothesis (Hook 1976; Profet 1992), which suggests that the primary toxins that are avoided during pregnancy are teratogens (chemicals that lead to birth defects) and abortifacients (chemicals leading to abortion of the fetus). Recent research has supported this assertion of aversion, specifically for pregnant women, towards strong-tasting vegetables and caffeinated drinks which host the chemicals. Flaxman and Sherman (2000), however, suggest that aversion to these chemicals were less common than aversions to meats, fish, poultry, and eggs. They go on to suggest that, from an evolutionary standpoint, this could be an adaptive response to the parasites and pathogens these foods can often contain. This would be especially critical for our evolutionary ancestors who were unable to preserve food for extended periods of time or, more recently, that heavily salted their meat which would also be dangerous for the fetus if consumed by the mother.

Motion Sickness

Motion sickness, at first glance, provides a challenge from an evolutionary perspective as there appears to be little adaptive value in nausea and vomiting as a result of motion. Additionally, it can occur in the absence of recently ingested food which would suggest that the immediate expulsion of toxins may not be the sole cause of nausea and that its etiology may be more complex. Treisman (1977), however, suggested that motion sickness is the result of inconsistencies in the spatial representation of at least one of three inputs: visual, vestibular (representation of the position of the head, primarily from the inner ear), and proprioceptive (position of the body, input received from the main body and limbs). Treisman argued that one or more of these inputs being discrepant is a signal of an ingested neurotoxin and, as such, nausea is triggered even in the absence of recently ingested food as a warning signal that a previously ingested food may be

altering the sensory inputs of the body. This theory has received little empirical support however, and the usefulness of regurgitating the remaining stomach contents after the toxins have already been absorbed would not rid the system of the toxins.

Conclusion

Nausea is an evolutionary adaption which has evolved to protect the individual from ingested toxins and pathogens. The immediate function of nausea is the prevention of consumption of further amounts of the toxic substance and to slow the digestive function of the stomach in order to limit the amount of toxins that are absorbed by the body. Furthermore, it serves to create an aversion to the substance containing the pathogen or toxin via taste aversive learning.

Cross-References

- [Adaptation](#)
- [Disease Avoidance](#)
- [Morning Sickness](#)

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Nausea and Vomiting in Pregnancy

- [Pregnancy Sickness](#)

Navigating Social Relationships

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Error management theory (EMT) is a middle-level evolutionary psychological theory that helps explain whether people are more prone to making Type I errors (i.e., believe X when X is not true) or Type II errors (i.e., believe in Not X when X is true). Generally, the theory suggests that people may have evolved cognitive biases to make one type of error if it conferred reproductive benefits, or if it minimized costs of making the other type of error. For example, people are more prone to mistaking a stick for a snake instead of mistaking a snake for a stick because

there are harmful consequences for making the latter error (such as getting bitten by the snake and dying; Johnson et al. 2013). Though early applications of Error Management Theory were applied to explaining men's sexual over-perception bias and women's relationship commitment skepticism bias (Haselton and Buss 2000), this theoretical model is being applied to other domains, including navigating social relationships.

EMT has been applied to two areas social relationships that EMT. First is the *social exchange heuristic*, which refers to a cognitive bias towards cooperation (Yamagishi et al. 2007). Yamagishi et al. (2007) related the social exchange heuristic to concepts from EMT: a Type I Error is when a person thinks there will be a consequence but there is not (i.e., person cooperates when they could have defected without consequence), whereas a Type II Error is when a person thinks there will be no consequence but there is (i.e., person defects, but they were detected and incurred a punishment). EMT may help explain why people are more likely to cooperate in one-shot prisoner's dilemma game, because it may be more costly to defect and experience punishment/sanctions than making an error to cooperate when there would have been no consequence to defecting. This does not mean people will always choose to cooperate – social conditions that change the costs and/or benefits of cooperating or defecting may moderate such an effect. For example, if someone knows they are being watched, they are more likely to cooperate with others because there are more benefits for acting cooperatively and more consequences for not cooperating.

Error management has also been applied to explaining the *negativity bias* (Haselton and Galperin 2011), which is a tendency to believe that others are inherently bad if they committed bad behaviors. Attributions about negative traits after seeing someone act negatively can be wrong in one of two ways: Type I Error is incorrectly judging a person as inherently bad (i.e., believe actions were due to the person) when they are not, whereas a Type II Error is incorrectly judging a person as not inherently bad (actions were due to

the situation) when they are. The suggestion is that making a Type I Error in this case would not be as costly as making a Type II error, because avoiding someone who may not be harmful is not as bad as interacting with someone who is harmful, and so we may have evolved a tendency towards a negativity bias. The negativity bias is well supported in the empirical literature, though direct tests of its function as explained by error management theory are still needed.

Cross-References

- Error Management Theory
- False Negatives
- False Positives

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Navigational Strategies

- Sex Differences in Navigation
- Unknown Territory

Neanderthal Man

- *Homo neanderthalensis*

Neanderthals and Humans

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Synonyms

[Archaic adaptive introgression](#); [Interbreeding](#)

Definition

Homo neanderthalensis interbred with modern humans 50,000 years ago. Approximately 2.5% of the DNA of many individuals living today came from Neanderthals.

Introduction

The only members of the *Homo* genus roaming the world today are humans, but 100,000 years ago *Homo sapiens* and *Homo neanderthalensis* were entwined in an interspecies love affair. Based on the perception of what Neanderthals supposedly looked like, with sloping foreheads, squashed noses, and a nasal voice, it is hard to believe modern humans ever found them alluring. But recent genetic evidence indicates that the two species did indeed fall in love and have fertile offspring. After a 4-year effort led by Svante Paabo and numerous research groups around the world, scientists published the complete Neanderthal genome in 2014 (Prüfer et al. 2014). Researchers compared it with contemporary human DNA and found that on average 2.5% of *H. sapiens* DNA is of Neanderthal origin. Because we all do not share the same genes, 20% of the Neanderthal genome can be found distributed in humans around the world today (Green et al. 2008). *H. neanderthalensis*, a population of humans who once ruled over Europe and Asia, went extinct around 40,000 years ago – but not before a little promiscuity that left foreign DNA in most of us years later.

Interactions with Modern Humans

Our *Homo sapiens* ancestors were never alone on the Earth. While we have been the singular species of the *Homo* genus for the past 10,000 years, the first humans evolved in East Africa approximately 2.5 million years ago. They were descendants of an earlier hominid called *Australopithecus*, who walked upright but had small brains (Their brains were not much larger than apes, usually 500 cc or less. In comparison, *Homo* brains are generally larger than 600 cc and modern humans average at 1350 cc.). Researchers have discovered as many as 27 unique human species, though paleoanthropologists still argue as to where to draw the line of speciation (Darwin was not the first but maybe the most well-known scientist who grappled with the definition of a species. He said, “I look at the term ‘species’ as one arbitrarily given, for the sake of convenience...” Years later Ernst Mayr introduced the biological species concept – species are groups of individuals that are reproductively compatible. However, this definition fails with all asexual organisms or populations that are only geographically isolated. While slightly embarrassing that scientists cannot agree on this basic concept, there are at least 20 valid published definitions and the debate does not appear to be slowing down. In light of current genetic data, some geneticists classify Neanderthals as a subspecies of humans). Some bands of these individuals left their homelands to travel north and settle in Northern Africa, Europe, and Asia. As different adaptations are needed to survive the cold forests in Siberia or hot temperatures of the Sahara Desert, human populations evolved and diversified. *H. neanderthalensis* lived and evolved in Europe for about 250,000 years before early *H. sapiens* moved into their lands (Higham et al. 2014). Our ancestors proliferated in their new environment, and the saga of the Neanderthals ended 10,000 years later when the species disappeared.

For decades, two competing theories were employed to explain the evolution of contemporary humans. One theory proposes that modern humans evolved in unison all over the world.

When *H. sapiens* moved into new lands, they bred with the early humans in Eurasia, and humanity evolved through recurrent gene flow (Wolpoff et al. 2000). In the alternative version, *H. sapiens* emigrated out of Africa and replaced all other hominins they encountered (Stringer 2003). In this tale of incompatibility and competition, *H. sapiens* had little sexual interest in other humans and wiped out all populations they encountered. The theory gained support in the 1980s after genetic studies revealed a recent origin of contemporary humans in Africa around 200,000 years ago (Allan Wilson, a geneticist at UC Berkeley, and his team used mitochondrial DNA to estimate how long human populations have been diverging from each other. All of the unique mitochondrial genomes today descended from a woman who lived in Africa around 200K years ago. Likening her to the first women from The Book of Genesis, scientists named her “mitochondrial Eve.”). Current information on the Neanderthal components in our genome suggests a third theory should be added to the mix: *H. sapiens* moved out of Africa around 100,000 years ago, and a few instances of interbreeding altered their genome. Though the receding chin and stocky frame of a Neanderthal may not be attractive to humans today, maybe being an individual adorned in feathers, with skin thicker than a rhino’s, was just the prettiest thing our ancestors had even seen.

DNA not only contains the blueprint for life but also a glimpse into the past. Frequently, certain populations of individuals around the globe will accumulate mutations in their genome. Most of these are neutral and cause no harm but can be used as markers for scientists to determine where and when a person’s ancestors came from. Based on the mutation rate in humans, interbreeding events took place around 50,000–60,000 years ago (Kuhlwilm et al. 2016). Whether these acts of copulation were clandestine meetings or commonplace is still a mystery, enough hybrid children were born within *H. sapiens* populations to allow Neanderthal alleles into the human gene pool. *H. sapiens* still living in Africa avoided meeting *H. neanderthalensis* and are the only individuals today without any foreign DNA in

their genomes. Contemporary East Asians inherited around 1.4% and Europeans about 1.2% of their genome from our hominin relatives. This Neanderthal DNA is clustered in our genome; some parts are bare, while other sections contain as much as 60% foreign genetic material (Vernot and Akey 2014). Like interbreeding that takes place in other vertebrates and plants, this hybridization happened in a patchy fashion. Advantageous *H. neanderthalensis* genes, like ones tied to the immune system, hair, and resilience for cold weather, survived through time and fixed themselves in our genome. Little Orphan Annie might have been singing a different tune if she knew that the freckles sprinkled on her nose are due to interbreeding – almost 70% of Europeans carry the Neanderthal version of a gene called BNC2 which influences skin pigmentation (Sankararaman et al. 2014). Fair skin and freckles helped *H. sapiens* efficiently synthesize vitamin D from low sunlight in northern latitudes.

Some Neanderthal-derived genes may have helped us in our evolutionary journey, but the vast majority were duds. When Paabo and his team were analyzing the *H. sapiens* genome for Neanderthal DNA, they found significantly less of it in functional versus nonfunctional parts of our genome (Prüfer et al. 2014). Only 1% of our DNA codes for proteins, and the majority of Neanderthal DNA is found in the spaces between our genes, where it has no biological effect. In the estimated 2,000 generations since modern humans and Neanderthals mated, natural selection has been hard at work, removing any of their deleterious alleles from our genome. The variants that escaped this purging also may not always have been a disadvantage. For example, Neanderthal DNA is linked with a blood clot disorder caused by the over-activation of the SLEP genes. In prehistoric times, wounds that closed quickly might have been advantageous when running away from a saber-toothed tiger but now can lead to strokes and heart attacks (Simonti et al. 2016).

Our current understanding of our distant relatives is that they were a sophisticated species who had large brains, used tools, and buried their dead. Scientists do not have a definitive reason for the

Neanderthals's extinction but do know that their entire population was struggling 40,000 years ago (Galván et al. 2014). Archaeological sites indicate that they lived in small bands and rarely interacted with people outside these troops. As men and women continued to mate with their relatives, deleterious genetic mutations remained in their gene pool, and the Neanderthals were reduced to low numbers. Traditional theories speculate that their small population was not able to compete with *H. sapiens* for resources, either through direct warfare or falling prey to evolutionary pressures from the changing climate. Whatever the reason, in the war between the two of human evolution, Neanderthals were cast as the losers, but not before their love affairs left their faint mark on our genome.

Conclusion

Homo neanderthalensis, called Neanderthals, walked the Earth around 200,000 to 30,000 years ago. They closely resembled *Homo sapiens*, though with a prominent brow, larger brain, and stockier build. Like other members from the *Homo* genus, they originated in Africa and migrated to Eurasia. Some scientists estimate that, at their peak, their population was as large as 70,000 individuals. In 2017, researchers found that modern human groups who originated outside of Africa contain around 2.5% Neanderthal DNA. This lends credence to the theory that humans and Neanderthals interbred and produced offspring. While the Neanderthals lived for several hundred thousand years, they died out about 30,000 years ago, from either warfare with modern humans, disease, or absorption into the larger human population.

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Necrotic Cell Death

- Early Stage of Brain Development at Birth

Need-Based Support

- Specific Friendships

Negative Affect

- ▶ [Changes in Self-Esteem Motivate Behavioral Changes](#)

Negative Effects of Gossip

- ▶ [Social Consequences of Initiating Gossip](#)

Negative Frequency-Dependent Selection

- ▶ [Frequency-Dependent Selection](#)

Negative Postcoital Emotions

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Negative Punishment

- ▶ [Operant Conditioning](#)

Negative Reciprocity

- ▶ [Punitive Sentiment](#)

Negative Reinforcement

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Negativity Engagement Bias

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Neonatal Imitation

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Synonyms

Behavioral matching; Copying; Mimicry; New-born imitation; Selective imitation

Definition

The tendency for newborn infants to reproduce, imitate, or copy behaviors as they are modeled to them by an adult.

Introduction

Whether or not newborns have an ability to imitate has been the focus of considerable research effort over the past four decades. It has been considered a unique feature of the human mind and proposed to be the basis of later social-cognitive abilities (Lepage and Théoret 2007; Meltzoff and Williamson 2010; Trevarthen and Aitken 2001). There has, however, been mixed empirical evidence for its existence, placing neonatal imitation at the center of great debate with varied mechanisms and functions being proposed in an effort to explain the inconsistent findings. The most recent and comprehensive research on the topic suggests that there is no longer compelling evidence for neonatal imitation (Oostenbroek et al. 2016).

History of Neonatal Imitation Research

For the majority of the twentieth century, imitation was considered to develop between 8 and

12 months of age (Lewis 1936; Piaget 1945) and was viewed as evidence for the emergence of symbolic reasoning. Challenging this view, Meltzoff and Moore (1977) provided the first experimental documentation that newborn infants are capable of imitating both facial and manual gestures. Their study presented four gestures (tongue protrusion, mouth opening, lip protrusion, and sequential finger movement) to 18 newborn infants. Infants' responses were compared across targets (e.g., infant tongue protrusions when the adult models mouth opening), and it was found that neonates produced significantly more behaviors matching the target gesture when viewing that gesture, than when viewing nontarget gestures. Meltzoff and Moore interpreted this pattern of selective behavioral matching as evidence for neonatal imitation.

Replications and Subsequent Theories

Multiple studies have subsequently attempted to replicate and extend on Meltzoff and Moore's findings and have produced both positive (e.g., Field et al. 1982, 1983; Meltzoff and Moore 1989, 1992; Reissland 1988; Vinter 1986) and negative (e.g., Hayes and Watson 1981; Koepke et al. 1983; McKenzie and Over 1983; Oostenbroek et al. 2016) results. These inconsistent findings have led to a diverse array of proposed mechanisms for the phenomenon. A rich interpretation of these data (as favored by Meltzoff and Moore 1977) suggests that the matching behaviors seen in newborn infants indicate imitation in the truest sense. Alternatively, lean accounts instead propose that these behaviors are simply explained as either generalized arousal (Jones 1996) or the result of primitive reflexes (Anisfeld 1991).

Mechanisms of Imitation

Of the variety of theories detailing the mechanisms of neonatal imitation, five may be considered prominent.

Active Intermodal Mapping

Meltzoff and Moore (1994) describe the active intermodal mapping (AIM) hypothesis as a matching-to-target process that serves as a scaffold for understanding the intentional actions of others (Meltzoff and Moore 1992). Meltzoff and Moore refined the AIM hypothesis over several decades (Meltzoff and Moore 1983, 1989; Meltzoff 1985, 1990) and concluded that imitation is:

- (a) *Flexible*, displaying both variety and novelty
- (b) *Self-correcting*, with subsequent attempts improving in accuracy
- (c) *Specific* to the details of the modeled movements such as the duration and direction of the gesture
- (d) *Temporally flexible*, can be executed by memory after a delay and in the absence of any stimulus

Innate Releasing Mechanism

The innate releasing mechanism (IRM) theory posits that viewing certain stimulus configurations (e.g., an adult's protruding tongue) releases a pre-organized pattern of behavior resulting in the infant producing a behavioral match (e.g., protruding their own tongue). The IRM theory argues that matching behaviors seen in the newborn period are not "imitation" but rather an involuntary, reflexive triggering of a specific motor response that is released upon seeing a modeled gesture (Anisfeld 1991, 1996).

Arousal

The arousal hypothesis states that neonates are visually aroused and interested by the human face and find oral gestures particularly stimulating. Within this perspective infants explore a moving, or arousing, stimulus via increasing their own oral behavior. According to Jones (1996, 2006a), adult mouth and tongue movements are particularly interesting to newborn infants, and any match between the two behaviors is simply coincidental. The arousal hypothesis views other explanations of imitation as simply

misinterpreting infants' coincidental matching behaviors as evidence for true imitation.

Mirror Neuron System

Mirror neurons are activated both when an individual performs an action and when they see another executing the same action. These neurons were first discovered in the premotor cortex of macaque monkeys, and in recent years researchers have claimed evidence of neonatal imitation in macaques (Ferrari et al. 2006; Paukner et al. 2014; Rizzolatti et al. 1996). While these complementary strands of research are interesting, it is notable that monkeys are notoriously poor at imitating (Visalberghi and Fragaszy 2002). Moreover, while there is unequivocal evidence for mirror neurons in monkeys, there is very limited evidence for their existence in humans, let alone their attributed functions in human behavior. Thus as appealing as a proposal linking neonatal imitation and mirror neurons may be, the value accrued to it is unclear.

Associative Sequence Learning

The associative sequence learning (ASL) model suggests that the underlying capacity for imitation is not a specific or innate mechanism (as described by the above theories) but instead part of a general process of associative learning. It is common for parents to enthusiastically engage in imitative interactions, and parents regularly react with effusive positivity when their infant's behavior matches their own (Ray and Heyes 2011). However, according to the ASL model, although reward is not necessary to create sensory and motor associations, it dramatically enhances the rate of learning.

Functions of Imitation

Research has until recently been unable to provide satisfactory answers to whether imitation exists during the newborn period, and as a result there has been little empirical study on the functional relevance of newborn imitation. However,

some theories have been offered which view imitation as:

Communication

Meltzoff and Moore (e.g., 1994) argue that infants' imitation of others helps to establish rapport and identification of familiar people. They see imitation as a primitive means of establishing interpersonal communicative exchange via mutuality and reciprocity of matching the other's gestures.

Bonding

Bjorklund (1987) proposed that neonatal imitation is an adaptive mechanism that evolved to encourage social interaction between a neonate and an adult until the infant can intentionally influence social interactions. Proponents of this theory argue that early imitation elicits and maintains adult-infant social interactions, promoting caregiver attachment to the newborn.

Breastfeeding

Given that oral gestures are more likely to be imitated by newborn infants than any other gesture (Anisfeld 1996; Heimann et al. 1989), it has been suggested that the imitation of oral gestures may play a role in facilitating breastfeeding (Jacobson 1979). There are no published studies empirically evaluating this theory.

No Distinct Function

Finally, some researchers remain agnostic as to what function neonatal imitation might serve. Jones (2006a, b) has suggested that infants produce oral behaviors to explore their immediate environment. However, Jones highlights that this function may be a purely incidental to infants' production of gestures that happen to match an adult's behavior.

Is the Evidence for Neonatal Imitation Compelling?

In the last four decades, more than 80 published experiments have attempted to replicate Meltzoff and Moore's (1977) findings using the cross-

target procedure. Many have failed to find evidence of neonatal imitation (e.g., Anisfeld et al. 1979; Koepke et al. 1983; McKenzie and Over 1983). These inconsistent results and an inability to isolate the precise nature of imitation have led to many differing perspectives regarding its underlying mechanism and function. However, due to the inherent difficulties of infancy research and the relatively small sample sizes, it has been impossible to judge with certainty whether the positive or the negative results are reliable.

The largest longitudinal imitation study to date tested 106 infants at four different time points, 1, 3, 6, and 9 weeks of age, and found no evidence of selective imitation across the four time points (Oostenbroek et al. 2016). Infant responses to adults' modeling of facial gestures, hand movements, and vocalizations were recorded. Infants were just as likely to produce a nonmatching gesture when watching the adult model, as they were to produce a matching one. Regarding tongue protrusion, Oostenbroek et al. (2016) replicated previous studies in finding that approximately 50% of their sample produced tongue protrusions in response to the tongue protrusion model, but they found no sign of consistency across the infants' responses (i.e., infants who "imitated" tongue protrusion at 1-week-old did not consistently do the same at 3, 6, or 9 weeks of age). They argued that their results refute the view that imitation is an inborn ability and instead favor the traditional view that imitation is a skill acquired over the first several months of life.

Conclusion

After 40 years of debate, the best empirical evidence to date suggests that humans' imitative capacity is not inborn. Rather than casting imitation as an innate feature of the human mind, developmental scientists should now reconsider its origins and developmental trajectory and reassess theories regarding its functional significance in early infancy. This also motivates exploration of novel hypotheses about the functions of newborn oral behaviors (e.g., Keven and Akins 2016).

Cross-References

- Cultural Transmission
- Learning Versus Imitation
- Play and Social Learning
- Social Development in Nonhuman Primates

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Neonate

- [Early Stage of Brain Development at Birth](#)

Neonaticide

- [Filicide](#)
- [Marital Status and Infanticide](#)
- [Methods of Filicide](#)
- [Predictors of Infanticide](#)

Neophilia (Antonym)

- [Neophobia](#)

Neophobia

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Synonyms

[Cainophobia](#); [Neophilia \(antonym\)](#)

Definition

A fear of the unfamiliar. Food neophobia refers to the tendency to avoid eating unfamiliar foods.

Introduction

Food neophobia – a fear of eating unfamiliar foods – differs from picky eating or simply being a little fussy. Although there is evidence that these characteristics are correlated (Pelchat and Pliner 1986), neophobia serves as an evolutionary survival mechanism. Some mushrooms, for example, contain harmful toxins, so we are rightly cautious when we come across one in the wild. This initial neophobia could protect us from digesting a possibly lethal substance. In our current, food-saturated, and highly processed eating environment, it is perhaps difficult to imagine these sorts of life-or-death decisions having a great impact on us. However, they would have been very real problems for our ancestors. Through natural selection, then, these problems shaped the behavioral and cognitive mechanisms that underlie our eating behavior today. In the following discussion, to outline the evolutionary significance of neophobia, it will be considered in the context of (1) the Omnivore’s Dilemma,

(2) neophobic behaviors in infancy, and (3) the possible mediating role of disgust.

The Omnivore's Dilemma

The Omnivore's Dilemma (Pollan 2006) or Omnivore's Paradox, as it was initially described (Rozin 1976), refers to the conflict we omnivores face when deciding what to eat. On the one hand, we are *neophilic*, and crave variety, right down to our underlying metabolic processes. As Pollan describes, human metabolism requires Vitamin B12, sourced only from consuming animals, and Vitamin C, which we can only derive from plants. On the other hand, we are *neophobic*, instinctively worried about the unknown, and for good reason. Plants have evolved mechanisms to ward off predators, including producing harmful poisons and toxins. The evolved survival mechanism of neophobia is shared with rats too. In a now seminal paper, Paul Rozin (1976) demonstrated that when faced with a novel food item, rats sampled only a small amount, as a means of testing the dietary consequences of consuming it. In contrast, for specialized eaters such as koalas, no cognitive effort is required to assess the potential danger of a would-be consumed food item. They are hard-wired to treat eucalyptus leaves as food and anything else as nonfood. More complex processing is required in the digestive systems of these more specialized eaters, to derive the nutrients they need from their food source. There are evidently various solutions to the problem of food selection, which have evolved over evolutionary time. For omnivores, more complex cognitive processing (including neophobic reactions) allows us to navigate our food environment, while for more specialized eaters, the guts do the work.

Some of the cognitive processing that occurs to aid us in food selection is relatively low level. However, beyond early processing biases against bitter foods, or initial neophobia, for example, more complex processes have evolved. Notably, enhanced memory capacity, the ability to communicate and share information, and, more broadly, culture have all had an impact on the Omnivore's

Dilemma. As Pollan (2006) suggested, for non-specialist eaters with few constraints on food selection, "if nature won't draw a line around human appetite, culture must step in" (p. 298). Cuisine is one example of a cultural phenomenon that has altered our ability to overcome the Omnivore's Dilemma. This is the set of rules by which a culture prepares and eats food, including what is and is not safe to eat and what flavors and cooking practices are used to prepare food. In a sense, they are an "accumulated wisdom" about how to eat (Pollan 2006). Spices, for example, are used in many cultures to encourage familiarity with otherwise novel foods, working to reduce neophobia. The use of familiar flavors is also noted as important for reducing neophobic behaviors in children (Wardle and Cooke 2008). Thus low-level biases against bitter tastes, which can signal toxicity, work in concert with higher-level mechanisms including the ability to memorize and communicate what is safe, to help overcome the Omnivore's Dilemma, and ultimately to help us decide what to eat.

Infants and Neophobia

Neophobia works in conjunction with highly specified learning mechanisms to help infants navigate their food environment (Birch 1999). As Birch describes, one study from her research group found that neophobic reactions in two year olds do not go away through the repeated opportunity to smell or look at novel food; infants must be given the opportunity to taste the foods directly. This suggests that increased familiarity, which is well documented to enhance preferences in various domains (known as the "mere exposure effect"; Zajonc 1968), is not enough to reduce neophobia. What is important, however, is the ability to learn about the adaptive consequences of eating a novel food. There is some evidence that children prefer to eat food items separately rather than mixed together (Cashdan 1998), which is consistent with the idea that infants are "reviewing" the dietary consequences of novel foods. As described by Birch, this evidence is

consistent with the sorts of processes that are found in rats, who use learned safety as a mechanism in their food selection (e.g., Rozin 1976).

The ability to learn from others is also crucial in deciding what is safe to eat, and there is evidence that social facilitation reduces neophobia in infants. Again, the presence of food alone is not enough to encourage infants to eat, but watching an adult eat something increases the likelihood that an infant will do so also. Interestingly, there may be specificity in this social facilitation, and recent evidence demonstrated that infants learned the edibility of plants, but not artifacts, when watching these objects being placed into an adult's mouth (Wertz and Wynn 2014).

The timeline of neophobia in infants demonstrates a curvilinear relationship with age (Birch 1999). It is minimal in infancy; for example, infants who are just beginning to eat solid food need only a single positive experience with a novel food, to enhance their preference for it, and other similar foods (Birch et al. 1998). Parents also rate infants between 1 and 2 years as most receptive to new foods (Cashdan 1998). This is probably adaptive, as infants who are not yet able to forage for themselves should be fairly open to available food sources provided by their parent, to ensure nourishment. For children between 2 and 3 years, and to a lesser extent 3–4 years, parents report that children are less receptive to new foods (Cashdan 1998). Neophobia then generally decreases with age, as children and adults experience cuisine and learn the rules associated with eating, which can serve to reduce neophobia (as discussed previously).

Neophobia and Disgust

The emotion of disgust has likely evolved to help us to avoid harmful pathogens and parasites. It is possible, then, that disgust plays a role in neophobia, and this has been suggested by various authors in the field. Recent work by Al-Shawaf and colleagues has demonstrated a direct link between trait-level disgust and trait-level food neophobia (Al-Shawaf et al. 2015). Notably, those who were more neophobic had greater sexual- and

pathogen-disgust sensitivity. These researchers also found that males who exhibited higher preferences for short-term mating reported lower food neophobia (more openness to trying new foods). The authors proposed a preliminary hypothesis regarding these findings, suggesting that neophilia could be a form of mating display for short-term mating scenarios. They argue that if (1) a willingness to consume potentially pathogenic and harmful food is a sign of immunocompetence and (2) at least one factor that is considered in female mating decisions is immune health of the male (good genes) – especially in short-term mating contexts – then (3) neophilia (and a lack of disgust around new food) would serve as a mating display, an honest signal of good quality genes. This hypothesis is preliminary, and as the researchers note, more work is required. However, it certainly provides an interesting outlook on neophobic behaviors and evolutionary pressures that may underlie them.

Conclusion

The Omnivore's Dilemma sheds light on neophobia, and neophilia, and a number of other sensory and cognitive tools we have evolved to help solve the problem of eating. For infants, there is good evidence of specified mechanisms present from a young age, which enable them to navigate their food environment. This includes learning mechanisms that enable behavioral flexibility, including the ability to fully overcome their initial neophobia. It is likely that neophobia is related to the emotion of disgust, and preliminary evidence suggests a further relationship with mating strategy. Further research will continue to enhance our understanding of this fascinating phenomenon, and like with many other “quirks” of human behavior, evolutionary reasoning may prove to be an essential basis for this.

Cross-References

- [Disgust](#)
- [Disease Avoidance](#)
- [Sex-Differences in Disease Avoidance](#)

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Neoplasm

► Cancer

Neo-Whorfianism

► Language and Economic Cooperation

Nepotism

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Definition

Nepotism is the favoring of kin over nonkin in resource allocation, nurturing, or attention.

Introduction

At first sight, nepotism is quite obviously a product of evolutionary processes, by virtue of being an extension of genetic self-interest. As Forbes (2005, p. 83) puts it, paraphrasing Richard Dawkins: “Children are the vehicles that carry a parent’s genetic immortality.” The evolutionary origins of the word are visible in its ontogeny, a linguistic route from the mid-seventeenth century: *nipote* “nephew.” The Popes bestowed privileges on their “nephews” who in reality were more often than not their illegitimate sons. This perfectly illustrates the contemporary meaning in social life: patronage in public life on the basis of family relatedness. Some definitions include the favoring of friends, which shall be treated as a special case later in this entry.

Issues and Dilemmas

Yet there are potential conflicts of interest in nepotism, the primary one being the question of why should one bother being nepotistic when you can be purely selfish which is less uncertain in its benefits and less diluted by the genetic interests of other contributors to your progeny’s inheritance. The answer, of course, is that the nepotistic bias is essential for genes to persist – self-interest in one’s own fitness does not ensure the perpetuation of inheritance (Dawkins 1976). This is captured by the evolutionary concept of *reproductive fitness*, which W. D Hamilton demonstrated was embodied *kin selection*, the means by which we do this in infra-species interaction (Hamilton 1964). He extended the insight with the idea of *inclusive fitness* with which it is sometimes erroneously used synonymously. The nuanced difference between them is that kin selection denotes how your genetic interests are advanced by favoring your kin, while inclusive fitness spreads the web of interests more broadly over distant kin.

On the former topic, Hamilton predicted the degree to which we will favor kin by Hamilton’s Rule, $br - c > 0$ – where b is the beneficial on the fitness of the recipient of any social act, c is the cost to the benefactor, and r is the coefficient of

the genetic relatedness of two parties. This codifies an earlier mathematical formulation by Haldane and Fisher, which J.B.S. Haldane humorously captured by replying to the question, would you give your life to save a drowning brother, by saying he would save two brothers or eight cousins: the genetic break-even exchange.

In human tribal communities, scholars have documented numerous socially evolved adaptive norms and practice strategies that are sustained by the weak genetic ties that embrace the whole clan, by linking the strong ties prevailing among the tribe's constituent immediate kinship groups (Cronk and Gerkey 2007; Low 2007). These weak ties are reproduced by the near-universal norm of female-exogamy – young women marry out of their immediate kinship group into other clans, while young men remain importing daughters from other kinship groups. Thus, such generous practices toward nonkin as food-sharing and alloparenting (caring for others' offspring) are commonplace strategies that raise the fitness of the entire tribe (Hrdy 2009). This is reinforced by the human inability to detect relatedness instinctively and unerringly, unlike some other social species such as rodents that can do so by smell. Uncertainty about paternity is further reinforced by (a) the moderately polygynous instincts of our species and (b) the absence of manifest signaling of female estrus (Strassmann 1981). Male parental investment is especially necessary for neonatal survival during the early years of human life, hence uncertainty about paternity serves the group interest by supporting generous habits of social care in inclusive communities where individuals are at mainly related to each other only distantly (Buss 1996).

Hamilton's notable revision of evolutionary theory lies in framing inclusive fitness as the idea that one's genetic self-interest can be advanced without being a reproductive agent oneself. At a stroke this explains many puzzling phenomena, such as alloparenting, infanticide (selective investment in the most viable relatives), cannibalism (raising fitness), and homosexuality (able to foster fitness of kin by nonreproductive means). These phenomena are visible throughout the natural world; most extremely manifest in

what are called insect superorganisms. Among termites and wasp colonies, the queen fertilizing her own eggs to determine their sex results in very high degrees of genetic interrelatedness, such that nonreproducing members of the colony have the nepotistic incentive to engage in various self-sacrificial contributions to support the reproductive fitness of the superorganism, that is, the colony (Gillooly et al. 2010).

Nepotism in Human Society

Inclusive fitness strategies vary across societies. The phenomena discussed earlier – infanticide, adoption, homosexuality – have variously been discouraged or encouraged by cultural rules and norms (Faulkner and Schaller 2007). A multilevel selection view – sometimes crudely referred to as group selection – explains that such norms coevolve with changing material conditions and interests – what we may call the landscape of local ecology (Henrich 2004). This can be multilayered nested strata of a society, so that one can talk of a family, an organization, a social class, or ethnic community, to a nation state, as each having established ways or regulating their interactions to maximize collective fitness benefits. Within these, as the writer has argued elsewhere, much collaborative behavior with unrelated strangers operates on an “as if” principle (Nicholson 2000). We relate to strangers differentially and treat many of them with more trust than is rational. We treat strangers “as if” they were kin from our primal expectation that there is a correlation between relatedness, liking, familiarity, and similarity. This is an adaptive heuristic for the tribe in loosely related kinship groups where we have a common fate regardless of our degree of relatedness to individual members but leaves us vulnerable to being unpredictably cheated in the amorphous, transient, and uncertain networks of modern society.

However, we are highly interested in relatedness and act on the basis of our assumptions and knowledge of kinship. This shows that nepotism is moderated by cognition and judgment (Neyer and Lang 2003). To this we can add the

phenomenon, also present throughout many other species of birds and social animals, of favoritism. Parents especially enter into a calculus that leads them to favor the progeny whose fitness can be raised to the highest levels. Human mothers have been observed subconsciously give more nurturance to the most robust of preterm twins. There is also a substantial literature on how the risks of violent abuse by parents are many thousands of times raised when the victims are step-children (Daly and Wilson 1985).

Nepotism is fuel within the engine of families as political institutions (Bellow 2003), where there are continual contests of interests, shared and divided, including the incipient conflicts between parents and offspring and between siblings (Trivers 1974). Nowhere is this more visible than in the world of family business, where the politics of relatedness, favor, and divided interests continually threaten the stability of the governance of the business (Collin and Ahlberg 2012). Families regularly destroy businesses and vice versa. Yet, paradoxically, family firms frequently outperform their nonfamily counterparts, usually by virtue of their unique cultural strengths. Love is the emotional accompaniment of nepotism, and it hold families together and enables them to achieve superior forms of cooperation, innovation, flexibility, and problem-solving (Dyer 2006). To this extent, family firms could be said to succeed because they capitalize on their status as evolutionary primal forms of working and living together (Nicholson 2015).

Conclusion

Nepotism clearly plays a central role in adaptive evolution. In contemporary discourse about human societies, it is widely seen as pernicious by those who seek a rational rather than an emotional order to govern the ties of association and decision-making, yet we know (a) that the separation of reason and feeling is delusional ideal in human affairs and (b) that bonds of affinity and affection are the glue that hold families, communities, and societies together. If we recognize, absent of moralizing overtones, that nepotistic

impulses are an integral aspect of our common humanity, then it is possible and necessary to create the rational frameworks that ensure they do not corrupt those decisions in our societies that it is believed should be made by other criteria.

Cross-References

- [Adaptation](#)
- [Adaptive Problem of Detecting Kinship](#)
- [Alarm Callers Are Females with Greatest Genetic Representation](#)
- [Alloparenting](#)
- [Altruism in Kin Selection](#)
- [Consolidating Familial Power](#)
- [Cooperation Among Nonchimpanzee, Nonhuman Primates](#)
- [Genetic Relatedness Affects Aid to Kin](#)
- [Family](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Hamilton's Rule](#)
- [Kin Selection](#)
- [Parental Investment](#)
- [Primate Dominance Hierarchies](#)
- [Universal Aspects of Kinship](#)
- [William Hamilton](#)

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Nerve Conduction Velocity

- [Cortical Neurons and Conducting Velocity](#)

Nervousness

- [Anxiety](#)

Nest Abandonment

- [Egg Rejection](#)

Nest Defense

- [Offspring Defense](#)

Net Energy Gain

- [Increased Energy/Reduced Digestion](#)

Neural Development

- [Brain Development](#)
- [Resources for Brain Development](#)

Neural Mirroring

- [Mirror Neurons](#)

Neural Recognition Systems

- [Cultural Cortical Recycling Hypothesis Applied to Money](#)

Neural Structure

- [Olfactory Bulb, The](#)

Neurobiologist

- [Peggy Mason](#)

Neurobiology of Language

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Synonyms

[Biolinguistics](#); [Biology of language](#); [Language Evolution](#); [Neurolinguistics](#); [Neuroscience of language](#)

Definition

Research on language as a biological and neurological object

Introduction

The research area *neurobiology of language* aims to understand the genetic and neurological capacity that enables modern humans to acquire and use language. This language-related neurobiological capacity includes internalized syntactic, phonological, morphological, and semantic structures. Linguistic structures, which are externalized due to linguistic-cultural changes, are therefore not considered. Other relevant approaches comprise relevant genetic foundations, the examination of neural regions and circuits, and comparative studies mainly conducted with songbirds, cetaceans, and nonhuman primates. It is however controversially discussed *what* language is and *how* it might have emerged in the lineage of hominids.

Models and Paradigms

Charles Darwin's (1809–1882) work on natural selection and the evolution of organism represent the foundation for understanding cognitive capacities such as language in an evolutionary context. Already, in his remarkable volume *Descent of Man and Selection in Relation to Sex* Darwin

(1871) explicitly states that the human language system is an “instinctive tendency to acquire an art.” He regards language as a property of the human brain and considers birdsongs as a nearest analogy to the human language. He believes moreover that our ancestors may have used a musical protolanguage to express courtship and basic emotions. Darwin's view on evolution and language was way ahead of his time. He was however also attacked by linguists such as Müller (1866) stating that “language is the Rubicon, which divides man from beast, and no animal will ever cross it . . .” In the same year, the Linguistic Society of Paris even banned any debates on the evolution of modern humans. In the nineteenth century, Paul Broca (1824–1880) and Carl Wernicke (1848–1905) pioneered the field “neuropsychology of language” by discovering and modeling different types of aphasic disorders. Historical studies on language and related disorders were mainly concerned about describing and modeling these clinical disorders in relation to cortical lesions. Biological aspects of language such as the origin or evolution of the language capacity were mostly not considered.

In modern times, Eric Lenneberg (1921–1975) took up the questions about the human-specific biological capacity of language. Lenneberg (1967) argues that language is a species-specific trait, learning of this trait is not possible, and language is not an artifact of culture. He is particularly known for the hypothesis of a critical period for language acquisition. In this vein, Chomsky (1965) introduced in context of a nativist theory of language the concept of the *language acquisition device* and of the *universal grammar*, an innate human capacity to acquire language. He argues that toddlers acquire language reflex-like typically without explicit instructions, and despite of poverty of input and lack of negative evidence.

Today, most researchers agree that the human language is an innate capacity. It is controversially discussed however whether this language capacity evolved (e.g., Pinker and Bloom 1990) or is the result of a sudden mutation (e.g., Berwick and Chomsky 2016). This dispute mirrors to some extent the historical debate between Darwin and the scientific community, which defends a

saltationist view. Noam Chomsky argues that the human language faculty emerged by means of a sudden mutation in the last 50–100 ky. In contrast, others argue that language is the result of a gradual evolutionary process, which took place since the hominid lineage split from genus *Pan* 4–6 mya. Some argue that our closest biological ancestors employed a protolanguage (Bickerton 1981) and that already our sister species Neanderthals or Denisovans used language much like modern humans do (Dediu and Levinson 2013; Hillert 2015). Fossil findings but also limited genetic data provide indirect evidence about the evolutionary stages of language and the human mind. Since empirical data are mostly incomplete or missing, the debate is at present open and undecided.

More recent approaches try to understand the human language capacity in context of other cognitive capacities of the human mind. Numerous studies report comparable computations between the linguistic and other cognitive domains such as music or vision (e.g., Fadiga et al. 2009). The open question is thus whether the acquisition of language relies on a biological capacity, which is specific to language or to the human mind in general. A lion's share of attention received an article by Hauser et al. (2002), who consider the “narrow language faculty” as unique to modern humans, in particular with respect to its property of linguistic recursion. Originally evolved as an all-purpose computation, it refers to a computation, which calls itself such as it is the case when one sentence is embedded in another sentence. In contrast, the “broad language faculty” would share its properties with nonhuman animals. More recently, the operation (binary) Merge, which takes two syntactic objects A and B and forms a new object and which has also the property of recursion, is considered as the fundamental characteristic of language. The linguistic recursion hypothesis, which is part of the Chomsky's minimalist program, has been criticized for various reasons: nonhuman animals are able to discriminate recursive strings, phonological (non-syntactic) recursive structures can be found, some languages do not show evidence of recursive structures, and Merge and recursion can

be also found in nonlinguistic domains such as music (e.g., Corballis 2011).

Other approaches might also provide some clues how the human language capacity might have evolved. For different reasons, particular populations do not use a full grammar but seem to rely on a conceptual strategy to express their thoughts (Jackendoff 2002). Pidgin languages, for example, lack subclauses, grammatical words, and inflections. When a Pidgin language develops to a Creole language in the next generations, it becomes grammatically fully fledged (Bickerton 1981). Another well-known case is the “Idioma de Señas de Nicaragua.” Without the help of teacher or other types of instructions, deaf children developed their own sign language. First, they started to use pidgin-like home signs. Later, younger children modified this pidgin-like signs used by older children and added grammatical features much like when a Creole language emerges. Another example refers to agrammatism in Broca's aphasic patients, who suffer from lesions in Broca's area (pars operculus and pars triangularis) and surrounding areas in the left inferior frontal gyrus (IFG). These patients rely in production and comprehension on a basic subject-verb-object (SVO) strategy, avoid non-canonical sentence structures (e.g., *wh*-questions or sentences with relative clauses) and tend to drop grammatical words and inflections. It is an open question whether these and similar examples mirror an innate and hard-wired language capacity of our biological ancestors.

Our understanding of the neurobiology of language depends thus on the definition of language. The minimalistic program tries to specify the core property of language, that is, the ability to generate hierarchical internalized structures. It is claimed that this property is unique to humans and thus language would not have evolved but emerged when *H. sapiens* dispersed out of Africa about 75,000 ya. Others emphasize that the human language system is the product of a gradual evolution of different cognitive components and consider brain growth in the hominid lineage as an indicator of reorganization and new behavior. The gradual approach usually favors the assumption that the human language capacity

had a precursor in our biological ancestors. Since evidence about the possible evolution of the human language capacity is incomplete or missing, an inductive or empirical approach has at present its limitations.

Molecular Genetics

From a molecular viewpoint, the birth of a new life is a biochemical package, which includes information about development, regulation, and maintenance of cellular structures, which ultimately also determines the neural circuits scaffolding language processing. Our closest living relatives, the chimpanzees, share 96 % and Neanderthals 99.7 % base pairs with our DNA sequence. We might thus assume that Neanderthals' (or Denisovans') biological capacities for cognition were similar as compared to anatomical modern humans. Indirect evidence such as perforated and pigmented shells supports this hypothesis but any evidence about linguistic behavior is missing. DNA analysis shows that Neanderthals and *H. sapiens* diverged from the common ancestor *H. heidelbergensis* or *H. erectus* between 350–400 kya. Our estimates about the age of the language capacity is simply based on the fact about (a) the age of the Omo remains – the first discovered fossils of anatomical modern humans – and about (b) the time period between 50–100 kya when modern humans dispersed out of Africa.

No genetic data can be at present linked to the language capacity. Evidence has been found, however, that the forkhead box protein P2 (*FOXP2*) is expressed in different cortical areas including the basal ganglia and the IFG. Mutations of *FOXP2* in humans cause severe speech disorders and have been associated with verbal dyspraxia (e.g., Fisher et al. 1998). Members of the KE family suffer for three generations from a rare speech disorder while language comprehension seems to be preserved. Genetic analysis reveals that the found mutation was the result of an arginine-to-histidine substitution at position 553. R553H is part of the *FOXP2* transcription factor, represents a loss-of function mutation, and

is conserved in the KE family. Magnetic resonance imaging (MRI) shows that members of the KE family have a bilateral volume reduction of 25 % in the caudate nucleus and basal ganglia. These subcortical structures closely correlate with motor functions. Again, a reduction of gray matter was found in Broca's area, which might be related to the impaired cortico-basal ganglia circuits regulating control of articulation.

The human version of this gene differs from chimpanzees in two amino acid coding positions, which encode protein sequences. In this respect, modern humans and Neanderthals do not differ. We do not know however whether the speech-related mutations took place on these two protein coding regions. The noncoding regions of *FOXP2* seem to be different between Neanderthals and humans. Since the protein differences are minimal between humans and chimpanzees, the efforts focus on finding regulatory changes along with nonprotein coding differences. So far, it appears to be science fiction to establish a link between these findings and linguistic computations (or human cognition in general).

Numerous genes seemed to have contributed to the expansion of the neocortex in the hominid lineage. *SRGAP2* is of particular interest as the occurrence of particular hominids does not only correlate with copies of *SRGAP2*, which trigger brain growth and probably cortical reorganization, but also with the appearance of different artifacts (cf. Hillert 2014, 2015). Again, no conclusions can be drawn regarding the genetic foundation of language. A different approach to determine the role of genetics in brain development is to compare the cortical structures of monozygotic and dizygotic twin pairs. In one study an increasing similarity of brain structures has been found in subjects with an increasing genetic affinity (Thompson et al. 2001). The genetic factors showed a significant impact on Broca's and Wernicke's area as well as on frontal regions. Future studies may thus provide specific information about language-related genetic factors. They trigger the formation of particular neural structures, which in turn support particular linguistic structures such as the computation of inflectional morphology.

The brain of modern humans is highly efficient in terms of acquiring and computing language. Natural selection seems to have preserved the adaptive phenotype language and the brain has the plasticity to keep track of fast-changing linguistic information. It might have been a continuous evolving process, including genetic adaptation and the Baldwin effect, which led hard-wired linguistic computations.

Linguistic Microcircuits

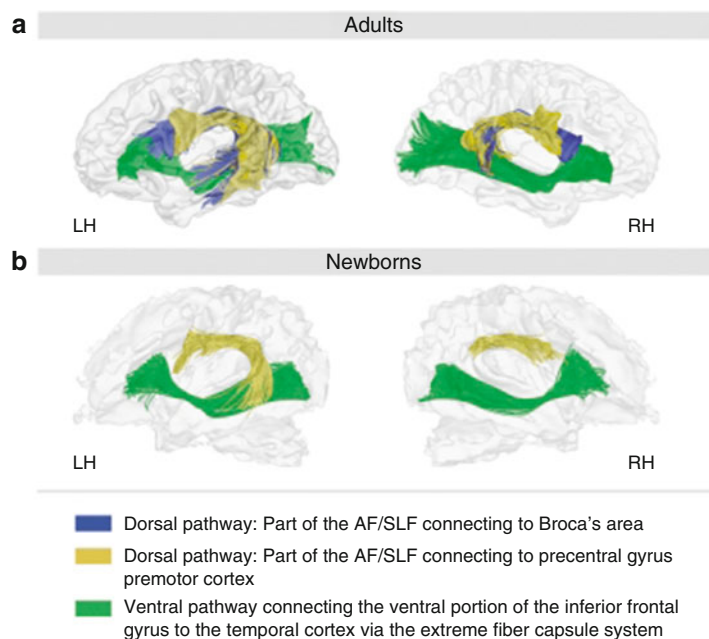
An epigenetic model of language acquisition assumes that genetic expressions of neural growth interact with organism-specific experiences. In the case of humans, it has been argued that neural growth in the perinatal period involves the transition from gene expression to an *experience-expectant* phase, in which ubiquitous stimuli common to all members are required to modify the neural circuits. Neurons, which are in excess, are pruned and dendritic attrition shapes neural circuits. These circuits are thought to be relatively permanent, but can be used for subsequent neural sculpturing. Parameters are set for this critical or sensitive period phenomena. In contrast, during

the *experience-dependent* phase idiosyncratic information, which is unique to the individual, are stored. Thereby, active formation of new synaptic connections in response to the input will be stored. Both mechanisms apparently work against each other: stable and optimized neural circuits are the result of neural pruning and at the same time new neural circuits can be developed to assimilate new information. The formation of particular neural circuits for internalization of linguistic information such as phonology and syntax seems to follow a hardwired program, while other circuits are shaped by neural plasticity to cope for example with new lexical semantic information. For instance, the acquisition of canonical SVO (subject-verb-object) sentence structures can be directly mapped onto our sensory-motor experience. These structures might be acquired by experience-expectant processes, while more complex sentence structures may primarily involve experience-dependent processes. It remains to be seen whether this difference can be verified by the formation of different fiber track systems in young children.

Figure 1 compares language-relevant fiber streams in newborns and adults. The data are based on MR diffusion tensor imaging (DTI).

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Fig. 1 Fiber tracking in newborns (*above*) and adults (*below*) by using MR-DTI (Adapted and modified, Perani et al. 2011; © Proceedings National Academy of Sciences)



Newborns and adults have one dorsal and one ventral stream in common.

The ventral stream (green) connects the temporal lobe (TL) with the inferior frontal gyrus (IFG) via the extreme capsule (EC) and the dorsal stream (yellow) connects the TL with the pre-motor cortex via the arcuate fasciculus (AF) and the superior longitudinal fasciculus (SLF). In addition, children develop a second dorsal stream (purple: as shown for adults). This stream connects the TL with the IFG (including Broca's area) via the AF and the SLF.

At present, the core language model of an adult consists of a dual-stream system: The dorsal route maps auditory input to motor speech representations and the ventral route maps the auditory input to semantic representations. It has been suggested to divide the dorsal stream into an additional temporo-parietal-frontal segment. The anterior and posterior language areas are connected by means of a dorsal stream with the direct AF stream and the indirect MLF and SLF streams and by a multimodal ventral stream. Resting state functional connectivity (RSFC) in humans and autoradiographic data in monkeys suggest the following language-relevant circuits (see Fig. 2):

SLF connects the anterior supramarginal gyrus (aSMG; homolog in monkeys is PF, part of inferior parietal area) with the premotor Brodmann area (BA) 6, the posterior SMG (pSMG; homolog

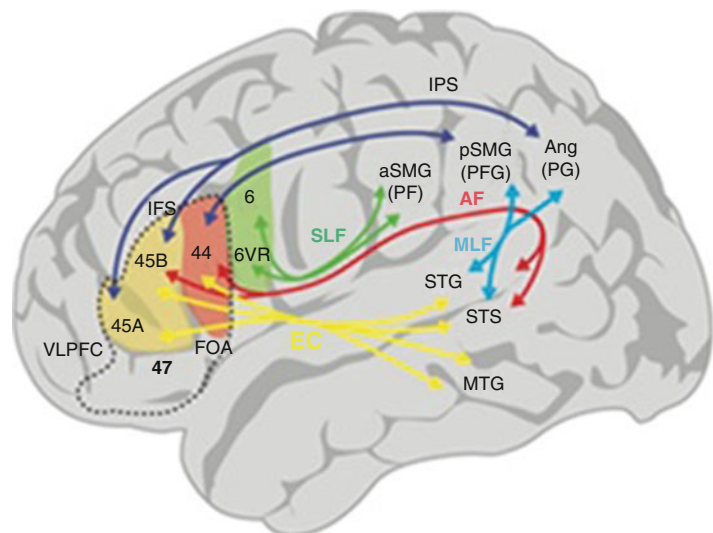
is PFG, part of inferior parietal area) with BA 44 and the angular gyrus (Ang; homolog is PG, middle parietal area) with BA 45B and 45A; AF connects the superior temporal sulcus (STS) and the superior temporal gyrus STG with BA 44 and 45B; the middle longitudinal fasciculus (MLF) connects STS and STG with the pSMG and Ang; the ventral stream connects anterior parts of the STG, STS and MTG with Broca's area (BAs 44 & 45).

In particular, the dorsal stream seems to have undergone significant changes in the human evolution. They assume thus that the development of this auditory-vocal circuit was a key event for enabling modern language. Along with the acquisition of voluntary control over the larynx and the supralaryngeal tract by means of a direct projection to the brainstem, vocal motor neurons and the phonological loop with rehearsal operations may have emerged. Again, phonological computations may have contributed to the development of more complex syntax.

Functional MRI and diffusion tensor imaging (DTI) studies show that BA 44 is connected via the dorsal stream to STG/STS (Wernicke's area). Again, it has been assumed that the frontal operculum (BA 45 & 47) is connected to STG via a portion of the EC fiber system and the uncinate fasciculus of the ventral stream. Again, BA 6, which is part of the premotor cortex and

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Fig. 2 Fiber connections of language circuits based on RSFC in humans and autoradiographic data in monkeys (abbrev. see text; adapted and modified; © García et al. 2014; based on Kelly et al. 2010 © Federation of European Neuroscience Societies and Blackwell Publishing Ltd)

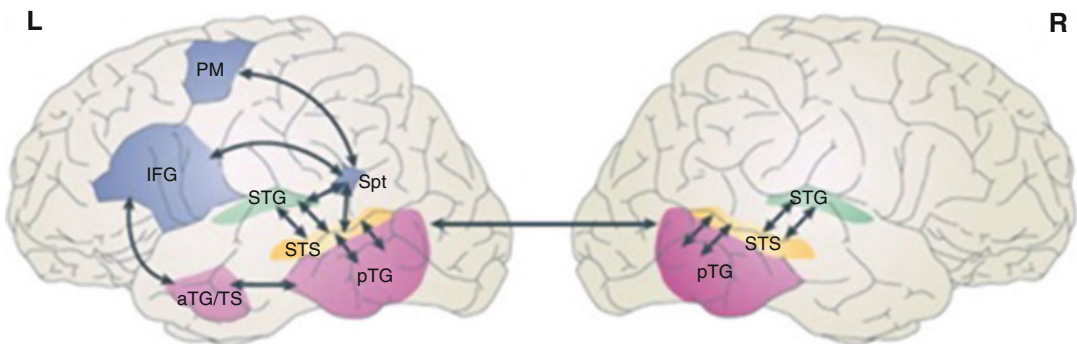


adjacent to BA 44, is mainly involved in orofacial muscular control and seems to be stronger connected to inferior part of the parietal lobe. In contrast, BA 44 connects to the posterior part of the parietal lobe. Similar, RSFC analysis indicates greater BA 45 connectivity to the Ang and to the superior and middle temporal gyrus (STG and MTG) relative to BA 44. This connectivity difference has also cytoarchitectonic reasons. Layer IV sends efferent fibers to the thalamus and has a reciprocal excitatory and inhibitory connection to the thalamus and adjacent areas. BA 45 is granular as it has a well-developed layer IV. BA 44 can be considered as dysgranular as layer IV is only rudimentary developed. BA 6 is agranular, that is, it is lacking layer IV of the cortical structure.

BA 44 seems to be critical for generating rapidly (100–200 ms) hierarchical syntactic structures as verified by early left anterior negativity found in event-related potential (ERP) studies. In contrast, BA 45 and 47 seems to be more involved in generating local phrase structures (Friederici 2009). Similar, it has been proposed that basic syntax (ventral stream) involves phrase structures, lexical retrieval and interpretation and extended syntax (dorsal stream) hierarchical, composed phrase structures, abstract rules and displacements (movements). Analogously basic (ventral) and extended (dorsal) computations were assumed with respect to the morphological and phonological level: Basic morphology requires the generation of whole words such as irregular, derived, or

high-frequent regular forms and extended morphology involves compositional structures as in the case of multimorphemic or regular forms. Again, basic phonology would consist of selecting discrete elements and retrieval of fixed lexical forms and extended phonology involves the composition of complex syllables and higher prosodic structures (Lely and Pinker 2014). Extended computations across all three linguistic levels would be scaffold by the AF, which connects the left IFG with the superior posterior temporal lobe regions. It is assumed that this dorsal route evolved more recently in the human lineage. Also, it has been argued that the extent to which fiber pathways are engaged depends on cognitive demand rather than on the type of linguistic information to be processed.

In addition, right-hemisphere functions such as prosody, intonation, and accentuation contribute as well to language processing in typical right-handers. Accordingly, it has been assumed that a right ventral stream integrates information over longer timescales while shorter timescales seem to be bilaterally represented (see Hickok and Poeppel 2007). Accordingly, the authors assume that during word recognition the left-sided sampling rate ranges between 25 and 50 Hz and the right-sided rate between 4 and 8 Hz. This model is based on the finding that rapid spectral changes such as formant transitions occur in a time window of 20–40 ms, while syllabic and prosodic structures are processed in the range 100–200 ms (Fig. 3).



Neurobiology of Language, Fig. 3 Dual stream model of speech processing (*p* posterior, *a* anterior, *d* dorsal, *mp* mid-post, *ITS* inferior temporal sulcus, *PM* premotor

cortex, *Spt* Sylvian parietal-temporal; other abbreviations used in text; adapted and modified, Hickok and Poeppel 2007; © Nature Publishing Group)

The finding that only severe speech perception disorders can be found if the patient suffers from bilateral (but not unilateral) lesions supports the idea of a bilateral ventral stream for speech. As already pointed out, the dorsal stream involves the posterior planum temporale, the premotor cortex as well as the IFG. The PT, which is typically larger in the left hemisphere as compared to Broca's area, is located posterior to the auditory cortex (Heschl's gyrus). It is the core of Wernicke's area as part of the STG and the parietal lobe. The PT is apparently involved in early auditory processing, in absolute pitch recognition (as found in music), but also in the analyses of many different types of sounds. Phonological information is mainly computed in the STS, whereas the interface of phonological-conceptual information is mainly recruited in the MTG and STG. Again, the anterior temporal lobe area computes semantic-syntactic information, which is basic according to the models mentioned above. The dorsal stream is responsible for auditory-motor integration. In addition to motor areas, STS and the Sylvian parietal-temporal region are involved in sensory-motor integration. Although top-down processing is not crucial for speech perception per se, it can facilitate speech recognition. The model discusses forward predictions: In the case of the ventral stream they are mediated by priming and context, and in the case of the dorsal stream by motor functions.

It is an extremely challenging research task to relate neuroanatomical structures to particular language functions. Future progress will strongly depend on the development of new techniques to examine noninvasively development and function of our cortical structure that enables us to acquire and generate sentences in a reflex-like manner. It is moreover extremely important to develop also appropriate theoretical frameworks to model and predict hardwired and internalized linguistic computations. Another important approach to be mentioned here in this brief review involves comparative studies.

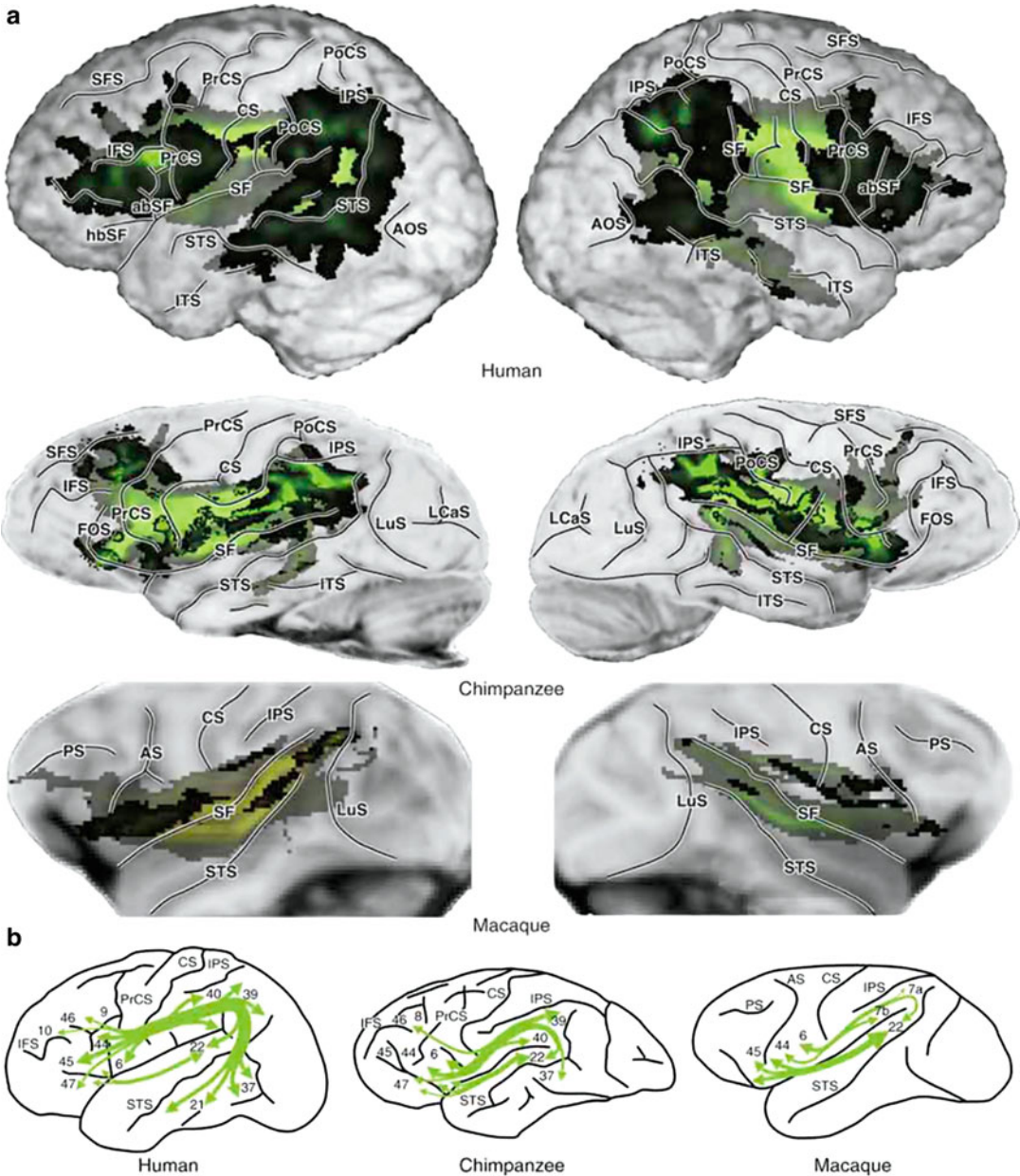
Comparative Models

The study of cortical systems along with cognitive-behavioral patterns in nonhumans can

be relevant for understanding the human language system. This approach can provide valuable analogies how neurobiological circuits evolve and enable cognitive computations. Comparative studies focus in particular on our closest living relatives (great apes and monkeys) or on non-human vocal learners (e.g., songbirds and cetaceans).

The leftward asymmetry of Broca's area, in particular of BA 44, is not human-specific as this asymmetry can be also found in genus *Pan* (chimpanzees and bonobos) and gorillas. BA 44 seems to serve the coordination of gestures and vocalizations in great apes. It is possible that BA 45 expanded on the basis of BA 44 and increased cortical folding in the left IFG. The homolog of Wernicke's area is the left PT in genus *Pan*, which is much like in humans larger in the left hemisphere. Wernicke's area has been considered as an older cortical structure than Broca's area. The temporal-parietal region (Tpt) can be also found in some prosimians (e.g., lemurs and lorises). Macaque monkeys control their facial musculature by means of BA 44 and process meaningful vocalizations in the left hemisphere. The left superior temporal gyrus (STG) and the left inferior parietal lobe are homologs of Wernicke's area.

Based on findings with nonhuman primates, four different segments of the AF-SLF stream have been proposed: three SLF streams and the AF (Petrides and Pandya 2009). The SLF III stream has been in particular considered as a possible language stream as it connects the inferior parietal lobe with the homologs of BAs 44 and 45 (Broca's area). Several studies indicate however that in macaque monkeys the area Tpt (homolog to Wernicke's area) projects to the dorsal and lateral premotor area rather than to the language homologs 9/46d, 6d, and 8Ad. Again, significant differences of the neural pathways between humans, chimpanzees, and macaque monkeys revealed a comparative DTI study (see Fig. 4). In humans, the AF strongly connects in the left hemisphere the frontal lobe with the medial temporal gyrus (MTG) and the inferior temporal gyrus (ITG), including Wernicke's area. This region corresponds in macaque to the



Neurobiology of Language, Fig. 4 Schematic average tractographic results found for macaque monkeys, chimpanzees, and modern humans, (*IFS* inferior frontal sulcus, *IPS* intraparietal sulcus, *PrCS* precentral sulcus, *CS* central sulcus, *STS* superior temporal sulcus, *PS* principal sulcus,

AS arcuate sulcus (BAs in *red/orange*: Broca's area BAs 44 and 45 with extension BA 47; BAs in *blue/turquoise*: Wernicke's area BAs 22 and 40 with extension BA 37; adapted and modified, Rilling et al. 2008; © Nature Publishing Group)

extrastriate visual cortex, adjacent to the primary visual regions. The MTG and ITG enlarged disproportionately in the hominid lineage following the split from genus *Pan*. The pathways in

chimpanzees are slightly more developed as compared to those in macaque and may reflect some prior conditions that enable connections between meanings and motor sequences. However, it is

apparent that along with the increase of the human brain size the white-matter volume increased in frontal and temporal areas, in particular the dorsal stream.

Moreover, a unique set of neurons have been first discovered in macaque monkeys (Rizzolatti et al. 1996). They recorded single visuomotor neurons in the premotor cortex (area F5) of the macaque. The homolog of monkey's area F5 is ventral BA 6, which extends to BA 44 and the inferior parietal area in humans. These premotor neurons fired when the macaque performed an action (e.g., reaching for food). Some of the neurons fired as well as when the macaque observed a similar action by another monkey or by a human (e.g., picking up food). These neurons are called mirror neurons as they do only discharge when an action is performed or observed but not when an object is presented without an action. One-third of the F5 mirror neurons are classified as strictly congruent, that is, they discharge when observing and performing an action (motor encoding). Two-third of the F5 mirror neurons are defined as broadly congruent as they discharge when observing an action without motor encoding. When a macaque, moreover, hears the sound of an action typically associated with an object audiovisual mirror neurons fire in F5, but for most neurons the discharge is smaller for sound per se than for sound and vision. Also, F5 seems not to be exclusively related to manual tasks. For instance, in rhesus monkeys the cortical larynx representations overlap with F5 and BAs 12 & 45 are involved in vocalization. In sum, these single-cell recordings in primates revealed that some properties of mirror neurons are located in the premotor and parietal cortex.

More recently, the role of mirror neurons in the evolution of language has been more broadly discussed as action mirror neurons might have contributed to the evolution of spoken language (Arbib 2011). Accordingly, he divides between seven different evolutionary stages depending on each other. In particular, the evolution of complex vocalization does not need to depend strictly on gesture. It is also possible that the vocalization system coevolved with the gestural system. There is no specific reason to assume that

structures developed by the gestural system have been step-by-step transferred to the vocal system. Most of the communication in monkeys and apes is vocal (besides body language), and it is possible that auditory mirror neurons play a role in vocal imitation. Similar to a motor model for speech, vocal mirror neurons simulate the auditory input and can be therefore used to compare auditory input with own articulation. The basic vocal mirror neuron system may have become more complex by an increase of voluntary control of the vocalization mechanism. This has been probably accomplished by an increase of the auditory working memory in the prefrontal areas.

Research on the evolution of cortical circuits of vocal learning has been also performed with respect to speech and language in humans (Petkov and Jarvis 2012). The auditory pathway of vocal learners such as songbirds and humans was inherited from amniotes, which evolved during the Carboniferous period ca. 320 mya from amphibian reptiliomorphs and include today all reptiles, birds, and mammals. Vocal learning is a process that refers to the ability to acquire vocalization by imitation rather than by "instinct." Thus, a species can modify their vocalization patterns as a result of experience. It is apparent that vocal learning depends on auditory learning but auditory learning does not depend on vocal learning. Dogs, for example, can recognize spoken words but cannot vocalize them. Again, vocal learners must be able to use auditory percepts to correct their vocalization. The mammalian as well as the avian group have members, which can be considered as vocal nonlearners. More recent studies provide evidence that chimpanzees and other primates are also vocal learners but significantly less as for example songbirds. Thus, the capacity of vocal learning did not evolve from a common ancestor of both groups. Most interesting, the acquisition of human speech and of vocalization in songbirds appears to be comparable as both have sensitive periods before adulthood to acquire and maintain phonological or vocal sequences. Humans are highly prolific vocalizers by acquiring virtually infinite new phonological sequences during their complete life span. These sequences typically correspond to particular

meanings. In contrast, vocal learning in birds such as male zebra finch is hardly possible after puberty. Their songs have an emotionally rewarding experience such as mating or defending a territory.

In humans, vocal learning relies on pathway within the forebrain (prosencephalon). It consists of thalamic structures and the cerebrum (telencephalon), which includes the cerebral cortex and the basal ganglia. In contrast to vocal nonlearning birds, complex vocal learning birds such as songbird, hummingbirds, and parrots have particular forebrain neuron clusters (nuclei).

It is said that primates have an innate, involuntary vocalization system, which consists of connections from the amygdala, the orbitofrontal cortex (OFC), and the anterior cingulate cortex (ACC) to the periaqueductal grey (PAG) in the midbrain. Again, PAG neurons synapse to neurons of the reticular formation (RF); in turn, they synapse to the α -motoneurons in the nucleus ambiguus (Amb), which control the muscles of the larynx for vocal production. In nonhuman primates, BA 6 (area 6vr) projects in addition to the RF and from there to the Amb. Area 6vr and the ACC are also connected with the primary motor cortex, amygdala, and thalamic structures (not shown).

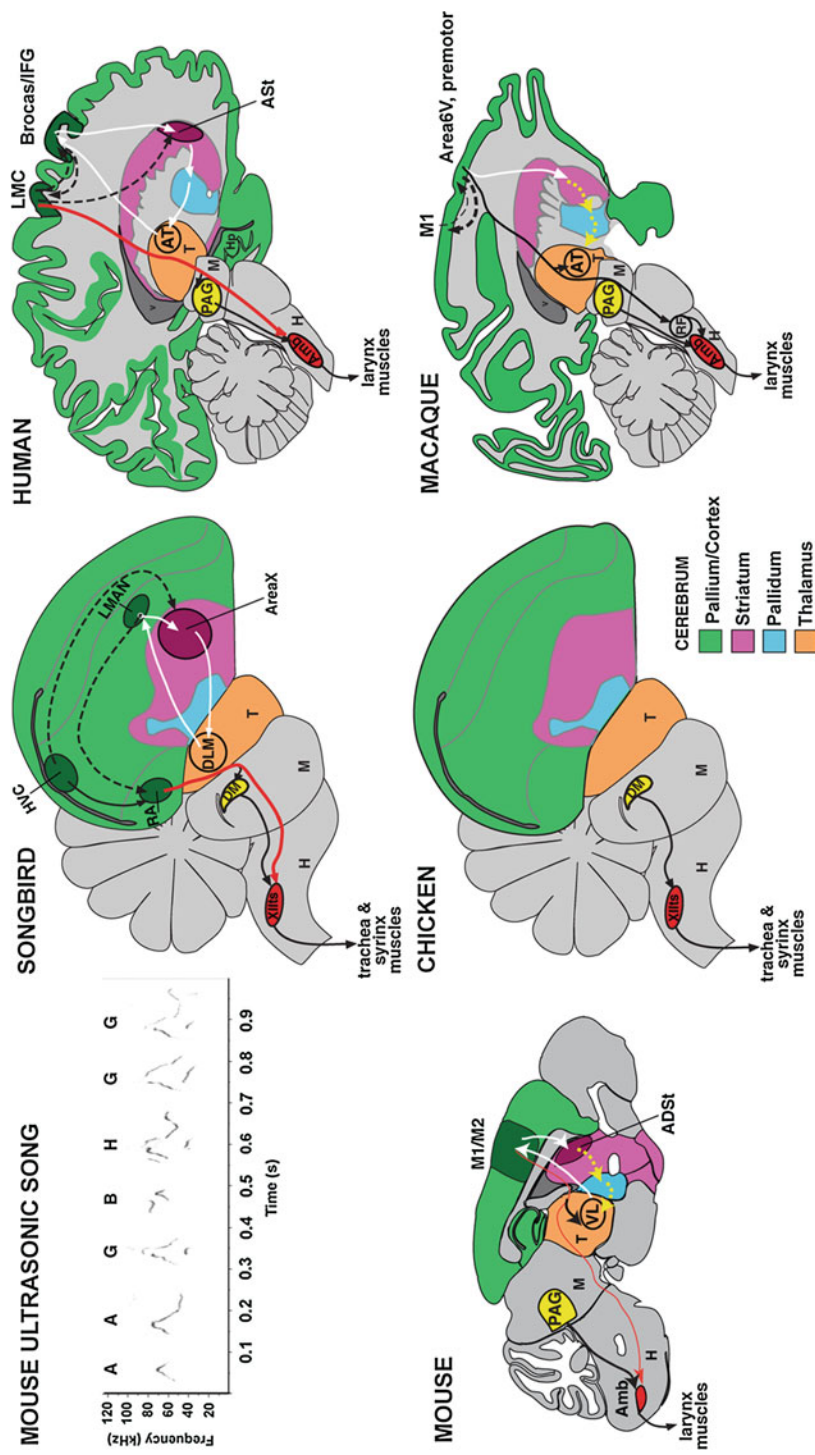
Humans rely more on the learned vocal pathway during speech. The learned vocal pathway projects from the face area of the primary motor cortex in BA 4 (laryngeal motor cortex, LMC) to the Amb (Fig. 5: red arrow) and a cortico-striatal-thalamic loop for learning vocalizations (white arrows). This matches in songbirds the direct forebrain projection to vocal motor neurons in the brainstem, that is, from robust nucleus of the arcopallium (RA) to the twelfth nerve nucleus (XIIIts). It has been stated that there is no direct cortico-bulbar projection in vocal nonlearners such as chickens and monkeys. In the case of a lesion in the LMC, learned vocalization is impaired in humans. Thus, it has been assumed that the humans' ability of speech and spoken language is related to the formation of a direct pathway from the LMC to the Amb. In general, studies with nonhuman primates were not able to report evidence for a direct pathway between

analogous areas of the LMC (e.g., 6vr) and Amb. A recent study with lab mice, however, might have revealed a region, which seems to be homologous: it is active during vocalization and makes a direct but sparse projection to the Amb (Arriaga et al. 2012). Connections between the anterior forebrain and the posterior vocal motor circuits are marked in Fig. 5 with dashed lines. Similar to humans, in mice two pathways converge on Amb, one from PAG and one from the primary motor cortex (M1).

According to new evidence that the vocalization system seems to be more flexible in modulating or mimicking sound patterns in species, which were assumed to be nonvocal learners such as mice and monkeys, a continuum hypothesis of vocal learning has been proposed. In general, auditory processing can be easier modeled in non-human animals compared to learned vocal communication. However, not all patterns of human speech can be modeled in animals and not all vocalization patterns in animals can be modeled in humans. Since a certain group of songbirds and humans are excellent vocal learners, the question arise to what extent human sentences and bird songs can be compared at the syntactic level.

First, human language consists of a lexicon and syntactic rules. This lexical-syntactic system externally interfaces phonological and phonetic information in perception and production and internally it interfaces semantics including concepts, intentions, and emotions. Typically, bird-songs do not express abstract meanings, if at all some intentional or emotive states such as the attempt to attract mates or to defend territories. Thus, we may say that birds (or typically animals in general) use pragmatic meanings rather than semantic meanings. Again, birds make use of a phonetic syntax rather than of phonological syntax as the term phonology refers to the mental representation of an abstract sound system to convey meanings. In contrast to birdsongs and to animal communication systems in general, human language uses discrete semantic units and morphosyntactic rules to combine and create open-ended variations of new meanings.

Birdsongs use variations at the phonetic level but obviously not at the semantic level. For



Neurobiology of Language, Fig. 5 Schematic illustration of the vocal subsystems in (a) humans, (b) macaques, (c) mice, (d) songbirds, and (e) chickens: *ADSt* anterior dorsal striatum, *Amb* nucleus ambiguus, *Area 6/V* ventral part of Area 6 premotor cortex, *Area X* a song nucleus of the striatum, *ASst* anterior striatum, *AT* anterior thalamus, *DLM* dorsolateral nucleus of the mesencephalon, *DM* dorsal medial nucleus of the midbrain, *H* hindbrain, *HVC* hippocampus, *LMAN* lateral magnocellular nucleus of the anterior nidopallium, *LMC* (*BA 4*) laryngeal motor cortex, *M* midbrain, *M1* primary motor cortex, *M2* secondary motor cortex, *nXIIIs* 12th tracheosyringeal motor neurons, *PAG* periaqueductal grey, *RA* robust nucleus of the arcopallium, *RF* reticular formation, *T* thalamus, *VL* ventral lateral nucleus of the thalamus (Adapted and modified, © Arriaga et al. 2012; see Petkov and Jarvis 2012)

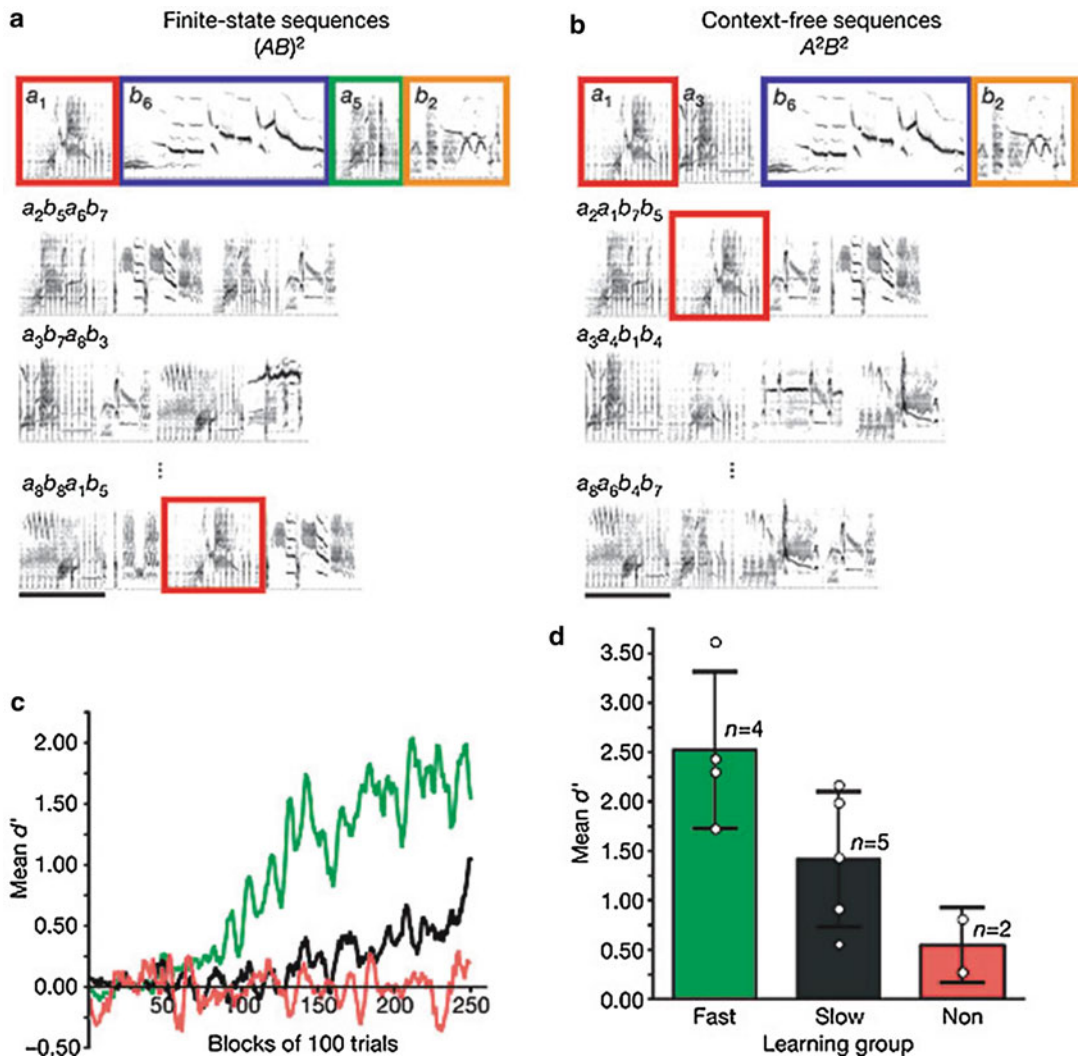
instance, a nightingale can rearrange clusters that generate hundreds of different songs. They may be used for identifying individual birds and express the level of sexual arousal. Canaries use sexy syllables to increase mate attractions, but this does not change the meaning of the song and indicates only the motivation level. Again, humans are able to synchronize the speech-meaning dimension with physical movements (dancing and acting) and/or complex music patterns (beat and harmonics) for a high-coordinated meaningful and/or pleasurable performance. Since a behavioral comparison is not possible at the semantic level, to what extent is the song-syntax of songbirds comparable with the human sentence-syntax?

Human language consists of nonlinear relationships between words. For instance, in the sentence *The guitarist, who plays Bossa Nova, went on stage*, the noun phrase (NP) *the guitarist* has to be linked to the verb phrase (VP) *went on stage* to understand the sentence meaning, that is, it is the guitarist, who went on stage. These kinds of nonlinear links are called nonadjacent dependencies, which are inherently part of the hierarchically organized structure of syntax in human languages. Moreover, nonadjacent dependencies are systematically ordered and require simultaneous processing of different structures to link these codependencies. Our nonadjacent dependency example above involves a nested center-embedded dependency, which are generally called as being recursive. The dependencies are embedded within one another as in the structure $a^1a^2a^3b^3b^2b^1 \dots a^{n-1}b^{n-1}$, whereas a^{n-1} is the unit to be linked to b^{n-1} . In contrast to this context-free grammar version, a finite-state form has the structure $a^1b^1a^2b^2a^3b^3 \dots (ab)^{n-1}$, in which iterations are appended to the end of a pair (Berwick et al. 2011).

In examining acoustic pattern recognition in European starlings evaluated the syntactic recursion hypothesis that the capacity of self-embedding is unique to the human language faculty (see Fig. 6). They conclude that the use of syntactic recursion is not unique to humans as their trained starlings have shown the ability to recognize these recursive patterns.

Berwick and colleagues (2011) emphasize however that the patterns tested do not match those sentence structures used by humans. While European starlings seemed to be able to recognize nesting after training, which needs to be differentiated from natural settings, they did not provide evidence of the bird's ability to recognize dependencies of the kind that pairs specific a 's with specific b 's. The starlings tested above recognized an equal number of a 's and b 's in terms of rattle and warble sound classes (rattle3warble3 patterns), but it has not been examined whether these rattle-warble patterns were properly paired off. Thus, at this point there is lack of evidence that songbirds or any other nonhuman species are able to use a strict context-free grammar. Birdsongs seem not to be able to generate hierarchical structures, which is one basic principle of human syntax.

For example, acoustic features of rattle or warble are not used to classify the rattle-warble sequence as a new unit, which in turn could be then used in more complex structures. Some songbirds however such as Bengalese finches seem to be able to perceive 3–4 notes as a single unit. In one study, the method of the classical psycholinguistic click experiment was applied, in which human subjects were presented with a click in the middle of a phrase (e.g., *ate the apple*). The participants tend to report that the click occurred at the beginning or end of the phrase. In using this click protocol, the authors reported that the Bengalese finches responded in a similar fashion: They perceived the click at the c or e of a cde unit. The Bengalese finches do not only perceive such units but can also produce them. Thus, it appears that they are able to combine notes into units much like humans use words to combine them to noun or verb phrases and to use these units somewhere else. However, in contrast to human syntax, Bengalese finches seem to lack the ability of dependent nesting to manipulate these combined notes. In this vein, it has been demonstrated that cotton-top tamarins (*Saguinus oedipus*) are able to parse synthetic stimuli sequences generated by finite-state grammars, but not those generated by a phrase structure that implies a simple recursively hierarchical structure. It is characteristic for human syntax that not



Neurobiology of Language, Fig. 6 Conditioned European starlings' sonograms of (a) rattle-warble iterations and (b) rattle-warble nesting (Adapted and modified, Gentner et al. 2006 © Nature Publishing Group)

a specific order of individual words is acquired but the specific order of word classes, also called phrase structures. Each single word can be inserted into a syntactic structure that provides a placeholder for this particular word class.

Also, new words can be created or different noncompositional strategies can be used to express figurative meanings. In the case of idioms, for instance, a sequence of different word classes can be treated as a unit that the syntactic structure does not map onto the compositional semantic structure. To understand the meaning of *It rains*

cats and dogs, the phrase needs to be processed as a single unit, as a string of words, and excludes combinatory computations between the individual words. Such kind of linguistic parsing flexibility to express nuances of different meanings seems to be unique to humans.

Conclusion

In context of this brief overview of the field *neurobiology of language*, we were constrained to

focus on the mainstream issues currently discussed. Thus, many important aspects and contributions to the field could not be considered here. In principle, all scientific approaches may provide useful insights about the fundamentals of mind and language. In this vein, humanities, social sciences, and life sciences seem to come closer in the attempt to map linguistic models to neurobiological capacities (and vice versa). It is obvious that this research agenda requires further specializations to accommodate cross-fertilization between established scientific programs. Here, not only the development and use of new technologies are of great significance but also theorizing is most important in terms of methodology and predictions. Advancing the research at both ends is essential for improving our understanding of language as a biological system.

Cross-References

- Auditory Neurobiology
- Broca's and Wernicke's Aphasia
- Charles Darwin
- Darwin on the Origin of Language
- Evolutionary Cognitive Psychology
- Evolutionary Psychology, The Handbook of
- Language Instinct, The
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Neurodiversity

► Psychopathology Versus Adaptation

Neuroethics

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Synonyms

Bioethics; Ethics

Definition

Neuroethics is a relatively new field that covers topics concerning the social, legal, and ethical implications of neuroscience and addresses aspects of neuroscientific research.

Introduction

The field of neuroethics has been addressing issues of neuroscientific research for many years. In the past, many controversial topics have been researched; for example, in the early 1940s, pre-frontal lobotomies were used to treat mental disorders. This procedure involved severing the frontal lobe from the rest of the brain in an attempt to ease symptoms, such as suicidal ideation, obsessions, and delusions. Experimentation during the 1930s and 1940s led to the infamous Nuremberg trials where criminals from the Nazi regime were punished for their crimes against humanity. Among other atrocities, their crimes included neurosurgical procedures such as lobotomies, experimentation on human participants without their consent, and other inhumane experiments. Following this, many boards were formed over the next 30 years, including the International Brain Research Organization and the Society for Neuroscience. These organizations review how research is conducted and how neuroscience is taught to students.

The ethical implications of neuroscience, such as the privacy of a participant's brain scan, can ripple through other aspects of neuroethics, such as its social and legal aspects. If, for example, a participant's information was to be identified, due to the small sample size of neuroscientific studies, the social ramifications could include future discrimination if said participant had a deviance from neurotypical brain scans. Although this could be a very small difference in the brain, the general public may believe it to have a larger impact. Indeed, many people deem information and studies concerning the brain to be more accurate and important (Farah 2005). This misunderstanding could also influence the legal side of neuroethics. For

example, brain scans could be given as evidence in a court system that does not fully understand how to interpret these data. This could lead to swaying a jury, wrongful convictions, and weakening the system that is currently in place, depending on how much the general public values neural data. The three main sections of neuroethics (ethical, social, and legal) are crucial in maintaining a safe practice of research that not only protects the participants but also the researchers that embark on attempting to understand and further science.

Ethical Implications of Neuroscientific Research

If we were to use modern ethic boards and regulations, previous work deemed well-intentioned by the researchers themselves and, commonly, others would fall short of the ethical standards we hold today (Illes and Bird 2006). Neuroethical researchers have attempted to identify the major ethical dilemmas that past and current researchers face. Privacy is a major concern among researchers in this field. A participant's privacy encompasses all information collected from them, including brain images, test scores, and unique identifiers. These data, particularly their unique and limited brain scans, may be more identifying than data collected for other psychological or biological purposes (Illes and Racine 2005).

Another argument under the privacy umbrella is whether to allow researchers to gather information about intimate details of a person's life. Many people speculate that as technology advances, data may be able to estimate what people are thinking (Illes and Racine 2005). The main concern is that these thoughts will not be private and can then be shared among researchers (Illes and Bird 2006). Commonly, the thought of someone being able to read another person's mind is intrusive and scary, so exploration of this topic would be no different. Similarly, understanding what and why people think the way they do is a very appealing strategy for marketing research. The

term "neuromarketing" describes companies using neurological methods to understand how participants react to their marketing materials. The information that is gathered from studies that either appeal to or are conducted by these companies is at risk for being more popularized and, therefore, more susceptible to identification (Farah 2005).

Social Implication of Neuroscientific Research

Neuroscientific research can be arduous to understand even for trained researchers. The general public is poised at a disadvantage because they are not educated in how to properly read and interpret this difficult information; for example, many individuals have heard of magnetic resonance imaging (MRI), but cannot describe how it works, what it measures, or interpret the information that it provides. Advanced technology is commonly used in neuroscientific research, which can enhance the amount of confusion for a layperson trying to understand the data. Neuroethics aims to focus on the social implications that this type of research can have, especially when misunderstood.

Because confusion can stem from limited scientific training or expertise, dissemination is one of the main concerns facing neuroethical researchers. If the average person does not understand a study's findings, but deems them more definite and accurate (Farah 2005), the misunderstanding could be dangerous. Similarly, studies that include brain images have been rated higher in their scientific reasoning as opposed to studies shown with bar graphs, a topographical map of the brain, or no image (McCabe and Castel 2008). Neuroscientific research garners a considerable amount of media attention, and when not properly disseminated can enhance the likelihood of a misunderstanding. This can lead to neuro-determinism, as individuals manifest this belief in neurological data being concrete and accurate. An individual that falls into this category would put more trust into neurological data. This can become increasingly problematic if this level of trust influences the individual to develop

prejudices. For example, if a brain scan was identified, a potential employer may not hire an applicant if they perceive any so-called anomalies on the scan. Even if they were benign in nature, a layperson may not understand that these anomalies would have no effect on behavior, yet their prejudices could lead them to treat the individual differently.

Similarly, the field of neuromarketing grows as an increasing number of companies believe it to be the future of business (Ariely and Berns 2010). This new area will potentially allow marketers to understand a consumer's desire more fully than when they are asked how they feel about a product. Although this domain is still open-ended and largely uncharted, the standards concerning research and ethical codes that these companies uphold are vastly different from a typical experimental setting (Murphy et al. 2008). Even though government, academic, and some commercial settings are required to obtain informed consent and protect the participants' privacy, these requirements are missing when the participant is tapped for a neuromarketing study. The research that is conducted in more privatized and commercialized settings are not required to follow the same guidelines, which can influence the ethical integrity of the research itself.

Legal Implications of Neuroscientific Research

Similar to the social effects of neuroscientific research, data that are difficult to interpret can affect the legal system. New studies have proposed using neuroimaging as a way to detect lying, by viewing specific areas of the brain, including the anterior prefrontal cortices, the parahippocampal gyrus, the right precuneus, and the left cerebellum (Ganis et al. 2003). One study reported a 90% success rate at differentiating deceptions during a test for participants that were asked to lie about an object they were asked to take (Kozel et al. 2005). Although the deceptions in this test were very straightforward, many researchers have called into question the extent that this would be a successful measure for more "real-world" data (Illes

and Bird 2006). Similarly, "brain fingerprinting" uses event-related potentials that are measured with electroencephalographical methods. These tests have been used to identify "guilty knowledge." For example, a participant may be shown information that would only be relevant for an extremist group that they potentially belong to; if this participant displayed an increased amount of activity at the sight of this information, it would be considered guilty knowledge, due to them understanding the significance of the stimulus (Farah 2005). This test has been thought of as a way to determine whether perpetrators have more information on the associated stimulus than they want to disclose, such as would be the case with terrorists and criminals. Although these data can be portrayed as alluring, many neuroethical researchers are concerned with this being heralded as the new polygraph test, which has been shown to be widely inaccurate, especially when participants are privy to counteractions such as biting their tongue or counting backward from a specific number to calm themselves (Honts and Kircher 1994). Because these new measures hold the power to become the new polygraph, it is important to ensure that the public understands the data that are the basis for using any kind of lie detecting test. Similar to the social aspects of dissemination being so important, it is crucial that the legal system recognizes the details of these tests. For instance, if neuroimaging is used, the studies that have been previously conducted have not supported "real-life" deceptions, so this particular test would be of no use in a legal case.

Neuroscientific research also has the ability to undermine the idea of free will by suggesting that humans are nothing more than the product of their anatomical makeup. Although most research would not suggest such a strong declaration, many people may mistakenly advocate that criminals have no choice in their actions due to how their brains send signals to commit an action (Farah 2005). Similar to a reflex, the brain may react a certain way that opens the discussion for whether the human mind can control how they respond to a situation before the physical brain makes them do something else. This could lead to more lenient penalties for criminals, especially those in situations that warrant a reflex or instinct, such as

accidentally wounding a police officer when they felt threatened.

Conclusion

Neuroethics encompasses the ethical, social, and legal aspects of neuroscientific research. Each of these aspects has concerns about how research may affect the public. As discussed, the ethical implications of this type of research are primarily related to privacy. Participants are entitled to assurance that the information they willingly give will remain confidential. Because studies in this field have such small sample sizes, it is more likely that information could be identifying. Similarly, the social aspects of neuroethics are primarily concerned with dissemination and understanding of research findings. If the general public struggles to understand a study, but is able to identify one or more of the participants, this could lead to discrimination, privacy violation, and an overall misunderstanding. The way that research is distributed to the public is crucial to how people may view it; people may view neuroscientific research as more important, but may not be as enticed by other fields of study. Because of this, the legal system can also be affected. Recent work has shown successful deception detection; however, researchers have not investigated complex forms of deception. The general public may also take findings at face value, especially when shown reports of 90% accuracy. Without proper dissemination and explanation, this could become a new form of lie detection that is not as accurate as people believe it to be, similar to the polygraph. The ethical, social, and legal aspects of neuroethics each hold numerous concerns that should be addressed when researchers consider conducting and publishing their work.

Cross-References

- [Ethical Issues](#)
- [Evolution of the Brain, The](#)
- [John Hartung \(1995\) Love Thy Neighbor](#)
- [Neuroimaging](#)

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Neurogenesis

- [Brain Development](#)
- [Resources for Brain Development](#)
- [Use It or Lose It](#)

Neuroimaging

- [Brain Imaging](#)

Neurolinguistics

- [Neurobiology of Language](#)

Neurological Approach

► [Interactive Language Development](#)

Neurology of Humor

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Synonyms

[Comicality](#); [Funniness](#); [Hilariousness](#); [Joking](#)

Definition

Humor is anything that is perceived as funny and makes people laugh.

Introduction

Humor is a heterogeneous concept. There is currently no consensus on how to best define humor, but according to one prominent cognitive account it is a complex experience, which involves detection and resolution of incongruity, followed by the feeling of amusement and laughter. It also refers to creating and expressing something funny. Abnormal humor is characteristic of certain neurological conditions, where specific humor-related deficits depend on the type of condition. The deficits may range from a partial or total inability to comprehend or appreciate humor, to those related to humor production, as reflected in a compulsive need to make disinhibited, often inappropriate jokes. Furthermore, some neurological conditions are characterized by pathological laughter, i.e., inappropriate and uncontrollable laughing, which may or may not be associated with the feeling of mirth.

Defining Humor

Humor is a universal human experience. Even though we can easily recognize humor when we experience it, there is no consensus on how to best define it. This broad term refers to the experiences of perceiving and appreciating something as funny as well as creating and expressing something funny. The complex nature of humor is reflected in the fact that it involves multiple processes, with some types of humor (e.g., comics, strips, cartoons, semantic jokes, etc.) requiring high-order cognition, such as theory of mind (Vrticka et al. [2013a](#)). Also known as mindreading, theory of mind is the ability to understand and predict mental states (e.g., beliefs, desires, intentions, emotions, etc.), one's own as well as those of others (Apperly [2011](#)). Theories of humor processing differentiate between humor detection, i.e., "getting the joke" and humor appreciation, i.e., "enjoying the joke." The former is a cognitive component of humor processing, which is associated with attempts to reconcile disparities between the punch line and the expectations based in the storyline. The latter is an affective component of humor processing, which is associated with the emotional responses caused by the experience (Manfredi et al. [2014](#)). The positive emotional response to humor is referred to as mirth, exhilaration, and amusement, which are used interchangeably in the humor literature. Thus, humor requires comprehension processes (the cognitive component); once detected, it is typically associated with amusement or the feeling of mirth (the emotional component) as well as with laughter (the motor component). Darwin captured the link between humor and laughter in the "tickling of the mind" analogy: "The imagination is sometimes said to be tickled by a ludicrous idea; and this so-called tickling of the mind is curiously analogous with that of the body" (Darwin [1872](#), p. 201).

Experiencing something as funny has evolutionary significance. While other hominids have experiences that correspond to our laughing and smiling, which occur in surprising but nonthreatening situations (e.g., during rough-and-tumble play, when tickled especially under the armpits)

(Darwin 1872), the ability to detect and enjoy humor as “mental play with words and objects” that requires resolving some kind of incongruity is unique to humans (Vrticka et al. 2013a). Detecting and resolving incongruities in humorous events is part of the cognitive component in the tripartite model of humor processing.

Several influential theories have been put forth to explain the ubiquitous role of humor in society. For instance, the superiority theory of humor postulates that humor serves to express negative feelings in a positive way, which allows for the maintenance of social order and reinforces social bonding (Wilkins and Eisenbraun 2009). On this view, aggression – or, as Plato suggested, some kind of malice toward those who are the object of the joke – is a key component of humor. Another theory proposes that humor and laughter serve as a mechanism for tension relief. Yet another account, for instance Miller’s evolutionary theory of humor, is linked to sexual selection theory and proposes that the role of humor in society is to help selection of a potential partner.

In addition to these functional theories, there are cognitive theories of humor. One such theory is the incongruity detection and resolution theory (Suls 1972). It postulates that humor arises due to detection of an incongruity, which is introduced by the simultaneous presence of incompatible elements, involving some unanticipated violation of expectations or social norms. Once the incongruity is detected, it has to be resolved by recognizing the logical mechanism on which the joke is based (e.g., ambiguity, exaggeration). The incongruity resolution allows for a reinterpretation of the information and it is typically associated with the feeling of mirth and laughter. Recent modifications of the two-stage model developed in the 1970s emphasize the emotional response following the incongruity resolution, i.e., the affective component as part of a separate stage in humor processing – the elaboration stage, following the detection and resolution of incongruity (Chang et al. 2018). This view is compatible with the findings indicating that humor and laughter can be differentially disturbed in neuropsychiatric diseases (Granadillo and Mendez 2016).

Abnormal Humor Processing

Disturbances in detecting and appreciating something as funny have been observed in a wide range of neurological and psychiatric disorders. Since humor implies certain cognitive complexity, it requires cognitive skills that are deficient in some disorders. For instance, patients with post-stroke aphasia who have a deficit in language may not be able to understand or produce verbal humor. Another type of a higher cognitive function whose deficiency may preclude humor comprehension is theory of mind, which allows us to understand other people’s minds. Since this ability is impaired in autism and schizophrenia, processing the type of humor that requires theory of mind is poor in patients with these conditions, although other types of humor may be unaffected (e.g., visual puns). For instance, reduced activation in the prefrontal cortex related to the processing of theory of mind-related humor was found in high-risk relatives of individuals with schizophrenia, and reduced ability to comprehend verbal humor together with increased response times and hypoactivation in frontotemporal and limbic cortices was found in chronic schizophrenia compared to healthy controls (Adamzyk et al. 2017). In addition, deficits in humor processing in autism may be related to these individuals’ generally poor processing of social information or poor integration of cognitive and affective information (Vrticka et al. 2013a).

Social cognition and humor processing are also affected in the diseases on the frontotemporal lobar degeneration (FTLD) spectrum, such as semantic dementia and behavioral variant of frontotemporal dementia (bvFTD). Patients suffering from these diseases show impaired accuracy in humor detection as well as proclivity for compulsive punning. While patients with bvFTD show for example preference for simple humor, patients with semantic dementia show a more general impairment of humor processing, i.e., humorlessness (Clark et al. 2015). Similarly, patients with Parkinson’s disease show a blunted response to humor, which is consistent with their overall blunted emotional responses caused by the progressive loss of dopamine-producing

neurons (Mensen et al. 2014). It has been noted that standard neuropsychological instruments are not sensitive enough to capture the alterations in humor processing associated with early stages of neurodegeneration, even though such changes may be an important early feature of the incipient disease (Clark et al. 2015).

Pathological Humor

Apart from deficits in humor perception, there are deficits related to humor production. One striking condition is pathological humor, also known as Witzelsucht (German *Witz* “joke” and *Sucht* “addiction”), which consists in disinhibited, excessive, often inappropriate joking (Granadillo and Mendez 2016). The compulsive need for joking is combined with decreased appreciation of complex, unfamiliar, or humor generated by others, except for simple humor. Witzelsucht is found in patients with brain tumors, bvFTD, strokes, infections and other lesions involving the frontal lobe, in particular the right orbitofrontal region, as well as in developmental and genetic disorders (Angelman syndrome or the “happy puppet” syndrome, Dawn’s syndrome, Williams syndrome, autism) (Granadillo and Mendez 2016; Clark et al. 2015; Rodden 2018). Currently there are no effective pharmacological or other treatments for pathological humor, although the treatment of disinhibition in psychiatric and neurological disorders or low-dose atypical antipsychotics may apply (Granadillo and Mendez 2016).

Witzelsucht, as a compulsive need to make jokes, differs from pathological laughter.

Personality and Sex/Gender Differences in Humor Processing

Humor appreciation appears to be affected by personality traits (e.g., extroversion is associated with enhanced humor processing), which is evident even during development. For instance, emotionality, shyness, and sociability moderate

humor appreciation in typically developing children who are between 6 and 13 years of age (Vrticka et al. 2013b).

In addition to the effect of individual differences in personality on humor processing, some evidence suggests that there exist sex differences in humor processing, with females showing stronger emotional reactions than males, regardless of age (Vrticka et al. 2013b). Females recruit more mental resources than males during the integration of cognitive and affective components in humor processing, and males rely more on automated processes when transiting from the incongruity detection to the emotional response (Chang et al. 2018). Furthermore, it has been observed that women prefer nonsensical and absurd humor, while men prefer humor with sexual and aggressive content. However, when humor was studied in psychological traits of gender identity such as feminine, masculine, androgynous, or undifferentiated instead of biologically defined sex classes (females vs. males), it was found that only feminine females preferred absurd humor to sexual humor, whereas masculine and androgynous females preferred sexual humor (Brodzinsky et al. 1981).

Since personality and sex/gender differences in humor processing may have implications for programs employing beneficial effects of humor in therapy, it is important to extend research on humor processing in neuropsychiatric disorders by considering how it is modulated by these factors.

The Neural Basis of Humor

Given the complexity of humor, it is not surprising that many brain areas support its processing. Attempts to determine which areas are involved in the distinct stages of humor processing suggest that incongruity detection is supported by the right middle temporal and middle frontal gyri, incongruity resolution by the left superior frontal gyrus and left inferior parietal lobe, while the elaboration stage engages the left ventromedial prefrontal cortex, the bilateral parahippocampal gyri and amygdalae (Chan et al. 2012; Campbell et al.

2015). Other evidence indicates the critical role of the left temporoparietal junction in humor detection and incongruity resolution (Slaby et al. 2015) or more generally the involvement of the “language areas”, i.e., the left inferior frontal gyrus, portions of the inferior temporal gyrus and middle temporal gyri in the cognitive aspects of verbal humor processing, and the role of the reward processing system in the affective aspect (Shibata et al. 2014). The integration of cognitive and affective components in humor processing is supported by a network of brain areas including the right middle temporal gyrus, left inferior parietal lobe and left inferior frontal gyrus, and the mesolimbic reward network (Granadillo and Mendez 2016), while the association between facial movements in laughter and the feeling of mirth during humor processing is supported by medial temporal structures (Yamamoto et al. 2015).

Damage to the right frontal lobe leads to deficits in humor processing, affecting the ability to appreciate complex humor (e.g., verbal semantic jokes) and humor generated by others, but sparing simple humor (e.g., violation of plausibility, puns, slapstick, physical humor) and self-generated humor. Deriving from the interpretations of theory of mind, this dissociation has been interpreted as “a dissociation between self vs. other referential network for humor” (Granadillo and Mendez 2016, p. 166).

The literature on the neural basis of humor processing contains some disparate findings, which may be related to methodological issues. Traditionally, lesion studies have been the standard method for establishing which brain areas are necessary for humor processing. Since relatively recently, findings on the neural basis of humor mostly come from functional neuroimaging, sometimes from transcranial magnetic stimulation studies, and to a much smaller extent from the studies using direct electrical cortical stimulation, an invasive technique which is considered the gold standard for brain-function mapping in neurosurgery. To illustrate the point, studying the neural bases of humor using neuroimaging methods such as functional Magnetic Resonance

Imaging (fMRI) is methodologically challenging, because the standard requirement that the person must not move during scanning holds despite the fact that humor is supposed to induce laughter, which would introduce additional movement artifacts in data. On the other hand, suppressing laughter may introduce other confounds and it affects brain activation patterns, even though it does not affect participants’ judgments on funniness (Korb et al. 2012). Furthermore, fMRI studies typically involve small study groups, which may preclude finding true effects and lead to false positives, which in turn leads to the problem of poor reproducibility of neuroimaging findings.

Real-Time Dynamics of Humor Processing

Consistent with the three-stage model of humor processing, event-related potential (ERP) evidence on the temporal dynamics of the contributing processes suggests that in the initial stage, i.e., during the incongruity detection, there is an enhanced negativity component at around 400 ms for funny stimuli compared to unfunny and unrelated stimuli, presumably reflecting surprise or attempts to semantically integrate the incoming information. A sustained positive component at around 500 ms has been discerned at multiple areas as an index of the incongruity resolution stage, and a late positive potential appearing after 700 ms over a range of areas (the ventromedial prefrontal cortex, bilateral amygdalae, and bilateral parahippocampal gyri) has been associated with the affective response to humorous materials (Chang et al. 2018).

Laughter

Laughter is a primal sign of social interaction, which is present in non-human primates, regardless of the presence of chuckling/laughing noise or facial movements like those occurring during human laughing (Darwin 1872). For instance, the nineteenth-century French neurologist G.B.

Duchenne observed that a pleasant surprise, such as getting delicacy during meal times, elicited in a monkey an expression in which the corners of the mouth were slightly rising, indicating satisfaction (Darwin 1872). The term Duchenne smile refers to a type of smiling that is presumably associated with spontaneously occurring enjoyment, i.e., it is a genuine smile/laughter. Unlike voluntary, fake, or deceitful smiling, involuntary smiles of enjoyment are recognizable by the contraction of the zygomatic and orbicularis oculi muscles so that the corners of the person's mouth are raising and the sides of the eyes remind of crow feet (Ekman et al. 1990). This type of smiling is elicited by "proto-humor," including rough-and-tumble play, tickling, physical mishaps, and pleasant surprise, as well as by incongruity-based conceptual humor (Vrticka et al. 2013a).

Different types of laughter are characterized by different vocal signals as well as by different cerebral activation patterns (Kreifelts et al. 2014). Laughter typically indicates safety and play behavior (e.g., tickling laughter), or cooperation, bonding, and affection. A recent study that investigated processing of slapstick (i.e., a type of physical comedy that involves misfortunate situations, like falling down) in cognitively healthy adults found that the feeling of amusement and laughter were generated only when the victim of a misfortunate situation showed bewilderment or disoriented expression, but not if the victim's facial expression showed pain or anger (Manfredi et al. 2014). Furthermore, laughter may convey social status and affect perception of social status in naïve observers. For instance, dominant, disinhibited laughter conveys a higher social status, whereas submissive, inhibited laughter conveys a lower social status; deviations from this norm, as in overt display of high status by a low-status individual, are often punished in society (Oveis et al. 2016).

Laughter is not always related to positive emotions (e.g., taunting laughter with a negative valence). It may communicate negative emotions, such as contempt and strikingly enhance emotions in negative social interactions (e.g., bullying, exclusion). For instance, the presence of a laughing

crowd considerably affects perception of verbal insults, leading to stronger and longer emotional processing (Otten et al. 2017).

In social anxiety, which is one of the most prevalent psychiatric conditions, fears related to humiliation, criticism, and rejection are exaggerated, and so is the fear of being the target of laughter. In a type of social phobia known as gelotophobia the fear of being the target of laughter is pathological (Chan 2016). While gelotophobic individuals fear aggressive humor, katagelastic individuals, in contrast, enjoy such humor, showing high levels of hostility in general and enjoying laughing at others. Not surprisingly, gelotophobic individuals, like patients with major depressive disorder and autism, have a deficit in the reward system. A recent fMRI study reported that relative to non-gelotophobic individuals, gelotophobic individuals showed less activation in the ventral mesocorticolimbic system in response to hostile and non-hostile jokes, suggesting a deficit in the reward system, and more activation in the dorsal corticostriatal system (the dorsolateral prefrontal cortex and dorsal striatum) in response to hostile jokes, which may suggest more voluntary cognitive control of emotions (Chan 2016). Other findings indicate that the left dorsolateral prefrontal cortex is the critical link between social anxiety and the negative attention bias, and that the impact of social anxiety on laughter perception is mediated by the left dorsolateral and dorsomedial prefrontal cortex (Kreifelts et al. 2014).

Sometimes lesions due to strokes, tumors, vascular malformations, or parasitic diseases result in a partial or total paresis of facial muscles, which in turn may affect the patient's ability to smile. Depending on the location of lesion, a weakening or paralysis may affect either one side or both sides of the face. Some patients with lesions in the amygdala and hippocampus experience emotional facial paralysis or contralesional mimetic palsy, a condition in which unilateral lower facial motor weakness occurs only during spontaneous smiling (and weeping), but not during voluntary smiling, which may indicate that these brain

structures link laughter and the feeling of mirth (Yamao et al. 2015).

Pathological Laughing

Disturbances involving involuntary smiling and laughing are present in a range of neurological and psychiatric conditions. Pathological laughter refers to excessive and meaningless laughing, occurring without an external/internal humor-related trigger or due to trivial or minimal stimuli, which may or may not be associated with positive feelings such as joy (Granadillo and Mendez 2016; Rodden 2018). In fact, episodes of uncontrollable laughing may occur even when the laughter is in conflict with the patient's actual mood and emotional state (Chatta et al. 2015). Furthermore, while normal laughter is at least to some extent controllable, i.e., it can be squelched even without affecting the subjective experience of funniness (Korb et al. 2012), this is not the case with pathological laughter, which is characteristically uncontrollable. For this reason, pathological laughter is sometimes classified as an involuntary emotional expression disorder, together with pathological crying and emotional lability, or as a disorder of laughing and crying, or more traditionally as pseudobulbar affect or emotional incontinence (Lauterbach et al. 2013). Pseudobulbar affect is common in neurodegenerative diseases (Lauterbach et al. 2013), including the advanced stages of Parkinson's disease where inappropriate crying occurs more often than acute mirthful or non-mirthful laughter (Chatta et al. 2015). Pathological laughter is also characteristic for post-stroke patients (Morland et al. 2015).

The most common form of pathological laughter is gelastic (Greek *gelos* "laughter") epilepsy, i.e., epileptic seizures in which laughter is a prominent symptom. The laughter during seizures often appears as unnatural and it is not necessarily associated with the feeling of mirth (Granadillo and Mendez 2016). Pathological laughter of non-epileptic nature (*fou rire* or "crazy laughter") was first described by Féré in 1903 as a prodromal sign of an impending stroke (Morland et al. 2015). It

is often related to a stroke in vertebrobasilar territory, with the most severe symptoms appearing in patients with bilateral pontine lesions. Inappropriate uncontrollable laughter may appear as the first symptom of cerebral ischemia affecting the ventral pons, left internal capsule-thalamus, left basal ganglia, or left parahippocampal gyrus. Pathological laughter is found in other conditions, such as frontal glioblastoma, primary progressive aphasia, cerebellitis, obsessive-compulsive disorder among others; it may be substance-induced and it occurs after brain trauma as well. Uncontrollable laughter is treated psychopharmacologically, with or without cognitive therapy (Morland et al. 2015).

Not only that some neurological conditions involve uncontrollable laughter, but sometimes normal laughter can trigger certain abnormal states, such as seizures, cardiac disturbances, syncope, i.e., brief periods of unconsciousness (Rodden 2018), and in particular cataplexy, i.e., a transient loss of muscle tone triggered by strong positive emotions with no change to conscious awareness (Meletti et al. 2015). The mechanism by which laughter induces cataplexy is currently not well understood. Although moments of muscle weakness due to laughter may occur even in healthy individuals, laughter-induced cataplexy is a striking and peculiar symptom, which has been associated with narcolepsy type 1 (Meletti et al. 2015). Laughter- or emotion-induced cataplexy appears to involve the amygdala, the anterior insular cortex, and the nucleus accumbens, i.e., a network of brain areas that supports reward and emotion processing.

Therapeutic Benefits of Humor and Laughter

Since humor processing engages the mesolimbic reward system, the question whether humor and laughter may have beneficial effects on therapy has merit. A positive effect of humor on resilience and coping, and its health-boosting effect have long been recognized (Wilkins and Eisenbraun 2009). Some evidence indicates that laughter has preventive and therapeutic values regardless of whether it is genuine and associated with the feeling of mirth, or voluntarily induced as in

laughter yoga. Evidence supporting the notion that humor and laughter may benefit therapy, presumably by decreasing stress hormones such as cortisol and epinephrine and enhancing activity of the mesolimbic dopaminergic reward system, comes from studies in a range of medical fields. However, the mechanism underlying this beneficial effect remains unclear. Thus, the effects of humor and laughter on mental and physical health and well-being require further studying.

Conclusion

Humor is a complex experience, involving detection and resolution of incongruity that is typically associated with laughter and the feeling of mirth. Different neurological conditions are associated with different humor-related abnormalities, ranging from the ability to comprehend only simple or self-generated humor to impairments affecting specific types of humor (verbal, theory of mind-related) to inability to appreciate any kind of humor. In terms of humor production, a striking condition is pathological humor, i.e., a compulsive need to make jokes. A related set of deficits pertains to pathological laughter, i.e., excessive and meaningless laughing that is found in a range of neurological and psychiatric disorders.

Cross-References

- [Autism](#)
- [fMRI](#)
- [Gender](#)
- [Language Dysfunction](#)
- [Personality Traits](#)
- [Schizophrenia](#)
- [Sex Differences](#)
- [Theory of Mind](#)

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Neuron Proliferation in Humans

► Neurons in the Cerebral Cortex

Neurons

► Early Stage of Brain Development at Birth

Neurons in the Cerebral Cortex

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Synonyms

[Encephalization](#); [Evolution of the human brain](#); [Evolutionary cognitive psychology](#); [Neuron proliferation in humans](#)

Definition

The outermost layer of the brain, the *cerebral cortex*, consists of billions of brain cells or *neurons* that compose perplexing neuronal networks that are associated with humans' higher-order cognitive functioning.

Introduction

Ever since the appearance of mammals around two hundred million years ago, the cerebral cortex has gained an insurmountable reputation as the most significant brain region (Robert 2002). The *cerebral cortex*, or the outer layer of neural tissue of the brain, has grown for as long as natural selection favored its expansion. The cerebral cortex plays a leading role in many higher-order cognitive processes such as memory, attention, thought, language, perception, awareness, and consciousness, which are all hypothesized to have been evolutionarily advantageous among humans.

The Mammalian Brain

Mammals are generally born with the most amounts of brain cells or *neurons* their brain will ever have. As the brain matures, connections are made between neurons and form compact and

complex neuronal networks. In an attempt to save space, the brain folds in on itself to better shelter its expanding neuronal networks, which distinguishes the mammalian brain from others (Hofman 2014; Robert 2002). Among current living species, mammals possess the largest brain-to-body size ratio. The physical sensations mammals can experience by visual, auditory, olfactory, and physical stimuli are a result of the brain's general sensory system that is distributed throughout the cerebral cortex (Robert 2002; Rowe et al. 2011). Among the mammals, primates have the most amounts of neurons in their brain's cerebral cortex (Herculano-Houzel 2009).

Evolution of the Cerebral Cortex

Discovering new means to obtain food and to adapt to ever-changing environments may have been the catalyst of the evolution of the cerebral cortex (Hofman 2014). Eating cooked food is an exclusive feature of modern humans or *Homo sapiens*. Evolutionary anthropologists and psychologists, today, are beginning to accept that superfluous nutrition and sanitation from cooked food paved way the primate brain to become the most advanced nervous system (Carmody and Wrangham 2009).

The homo sapien brain contains about eighty-six billion neurons; sixteen of which are housed in its cerebral cortex (Herculano-Houzel 2009), which makes the homo sapien cerebral cortex larger of any other great ape (Dyer 2016). Although larger size of the brain and cerebral cortex are associated with higher intelligence, size is no longer considered a proxy for number of neurons (Herculano-Houzel 2009). Fossils from the Neandertals, an ancestral relative of *Homo sapiens*, had an even larger brain size than modern humans' (Harari 2015). The complexity of the established neuronal networks within the cerebral cortex, however, is believed to be related to *Homo sapiens*' intellectual gifts (Herculano-Houzel 2009; Hofman 2014).

The cerebral cortex can be divided into four regions called *lobes*. The frontal lobe (1) specializes in higher-order cognitive processes like

abstract thinking and reasoning, problem solving, language, and even the experience of several affective states. The parietal lobe (2) houses neuronal networks for movement and orientation, as well as the recognition and perception of external subjects. The occipital lobe (3) primarily specializes in visual processing, whereas the temporal lobe (4) specializes in the processes of recognition and perception of auditory stimuli, memory, and speech with an emphasis on auditory processing (Kinser 2000).

Psychological Adaptations of the Cerebral Cortex

An increased cerebral cortex expedited the emergence of novel behaviors. While the environmental pressures on *Homo sapiens* diversified, the cerebral cortex evolved to become the most versatile biological system within the species. The creation of tools and weapons, the discovery and manipulation of fire, the ability to discern edible from inedible food, the knowledge of which types of plants would remedy an ailment, and other survival skills are all products of cerebral cortex activity (Hofman 2014). The ability to speak a language further intensified humans' social nature (Harari 2015; Robert 2002), which then contributed to the upbringing of emotional and social intelligences (Hofman 2014).

Humans' capability to learn from experiences, like other organisms', is subject to the laws of biological evolution. Modern behavioral phenomena, such as government, school, marriage, social prejudice, and war, are being linked to the nature of human psychology. Evolutionary psychology seeks to enlighten the behavioral science community about the traces of neurological evolution within universal behavior. Evolutionary psychologists acknowledge that not every observed behavioral pattern today originated as a particular function. The intrinsic pleasure while listening to music, for example, is unlikely to have been an evolved adaptation to a particular problem. Romantic love may be constituted by multiple and independent psychological mechanisms, but by-products and random effects are still subject to

both biological and psychological evolution (Fisher et al. 2006).

Conclusion

The mammalian brain has been in position to surpass any nervous system for millennia. Its talent to fold to conserve space for its neuronal networks deems itself as the most elusive organ to understand. Even while the brain drains a significant portion of the body's energy, early humans' discovery of fire and cooked food provided a plethora of its nutrition. The homo sapien brain may not be the largest hominid brain ever recorded, but its countless neuronal connections, particularly within the cerebral cortex, spoil the species with higher intelligence and the ability to experience affect. Precise environmental pressures that precipitated neuronal proliferation remain uncertain, but novel environmental conditions, such as society and culture, pose as new selection pressures that will continue to drive the evolution of the cerebral cortex and the evolution of human psychology.

Cross-References

- [Costs and Benefits of a Large Brain](#)
- [Energy Consumption](#)

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Neurophysiology

- [Cognitive Science](#)

Neuropsychology

- [Cognitive Science](#)

Neuroradiology

- [Brain Imaging](#)

Neuroscience

- [Cognitive Science](#)

Neuroscience of Language

- [Neurobiology of Language](#)

Neuroticism

- [Five-Factor Model](#)

Newborn Behavior

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Synonyms

Primary circular reactions, Sensorimotor stage

Definition

During the first year of life, children engage into exploratory behaviors in order to become familiar to and learn about the surrounding world.

Introduction

During their first year of life, children engage mainly, in what Jean Piaget called sensorimotor play or practice play (Piaget 1962). This consists mainly of already experienced, sensory and motor activities, which are repeated for the absolute pleasure of doing so (Hughes 2010) and thus considered as “playful” behavior. Piaget (1962) suggested that this form of play is integral for the child’s intellectual development and that the young child moves through a number of different substages of sensorimotor progression. In this section, we will explain the different stages of cognitive development as well as how the newborn child moves through the period of sensorimotor play to acquire the skills and abilities to think on their own.

Stages of Cognitive Development

Piaget suggested that people progress through four cognitive developmental stages: the *sensorimotor* stage, the *preoperational* stage, the *concrete operational* stage, and the *formal operational* stage. In each stage, children demonstrate new abilities, which allow them to

experience and understand the world in qualitatively different ways than they had before (Siegler et al. 2011).

1. In the sensorimotor stage – from birth to 2 years of age – infants experience basic sensory and motor abilities through which adult intelligence develops. Through these abilities young children explore the world and gain information about the objects and people in it (Siegler et al. 2011). In this stage, young children live mainly in the here and now while their intelligence levels are based on their immediate actions and perceptions (Siegler et al. 2011).
2. In the preoperational stage – from 2 to 7 years of age – preschoolers can remember their experiences for longer periods of time and develop more sophisticated ideas as they can now represent their experiences in language and mental imagery (Siegler et al. 2011). Yet, according to Piaget, they still lack the ability to form *mental operations*, that is, forms of reasoning as part of an organized system of mental activities. For example, during the preoperational stage, a young child would be unable to form the idea that pouring a liquid from one glass into a different shaped glass does not change the amount of liquid (Siegler et al. 2011).
3. In the concrete operational stage – from 7 to 12 years of age – children can reason logically about concrete objects and events (Siegler et al. 2011). For example, they can now understand that the amount of liquid is unchanged when it is poured from one glass to a differently shaped one. Yet, they still cannot think in abstract terms, neither to test out their beliefs through scientific experiments.
4. In the last stage of cognitive development, known as the formal operational stage – age 12 and beyond – children can think sophisticatedly about abstract ideas as well as hypothetical scenarios (Siegler et al. 2011). They can also test out their beliefs and gain appropriate conclusions by forming scientific experiments.

With this overview of Piaget’s cognitive development theory, we can examine in greater extent the

changes that occur during the sensorimotor period. Specifically, we consider how newborn children behave during this stage in terms of sensorimotor play and exploration.

Sensorimotor Play

Sensorimotor play is acquired gradually during the first 18 months of life before the newborn child moves to symbolic or make-believe play (Hughes 2010). In fact, Piaget gave a detailed description of the process by which children develop their own capacity for thinking by carefully observing how his own children were behaving (Smith et al. 2015). Based on these observations, he divided the sensorimotor play period into three behaviors, which he called circular reactions (Hughes 2010).

Primary Circular Reactions

This is the earliest form of sensorimotor play – the *primary circular reaction*. During this period, which begins from birth and usually lasts up to 4 months of age, an infant accidentally discovers a pleasing sensory or motor reflex activity that is related to its own body (Hughes 2010). The infant experiences enjoyment and thus repeats the activity (Hughes 2010). Piaget used the term “circular” to emphasize the way that children repeat newly reflex experiences, notably the ones that are pleasing such as scratching or grasping (Smith et al. 2015). The term “primary” relates to basic behaviors that the child learns to exhibit, from the reflexes of the initial period (Smith et al. 2015). Based on his own 8-week-old son’s behavior, Piaget illustrated the concept of primary circular reaction by explaining: “Laurent scratches and tries to grasp, let’s go, scratches and grasps again, etc. . . . At first, this can only be observed during feeding. Laurent gently scratches his mother bare shoulder. [The next day] . . . Laurent scratches the sheet which is folded over the blankets, then grasps and hold it for a moment, then lets it go, scratches it again, and recommences without interruption” (Piaget 1963, p. 191).

In behaving as he did, Laurent’s actions could be perceived, as play with objects rather than play

centered on his own body (Hughes 2010). Yet, according to Piaget this is not the case as he explains that the play is the physical action such as the grasping or scratching (Hughes 2010). According to this idea, an infant is interested in the action itself, rather than being interested in the object they are performing the action on (Hughes 2010). For example, the same action is performed on any object that happens to be around the infant. In this matter, we can appreciate that children, even early on in their life, can manipulate objects once they are given to them. Indeed, such reflex behaviors are purposeless and lack intellectual awareness – two essential elements that characterize object play (Hughes 2010).

Secondary Circular Reactions

From the age of 4 until the age of 10 months, children move to the next stage of circular reactions that is distinctly different (Piaget 1962). They are now interested on objects and the consequences of their actions, instead of being focused on their own body and repeating actions based on early reflexes (Smith et al. 2015). They engage in what Piaget called *secondary circular reactions*, the intentional alteration in their surroundings by making interesting things happen such as moving a hanging object by hitting it (Smith et al. 2015). Particularly, secondary circular reactions refer to the young infant’s enthusiasm to repeat newly initiated actions, aiming to influence their surrounding environment.

To illustrate the difference between primary and secondary circular reactions, Piaget described the behavior of his daughter Jacqueline, at 5 months of age. He describes: “Jacqueline looks at a doll attached to a string, which is stretched from the hood to the handle of the cradle. The doll is at approximately the same level as the child’s feet. Jacqueline moves her feet and finally strikes the doll, whose movement she immediately notices. . . The activity of the feet grows increasingly regular whereas Jacqueline’s eyes are fixed on the doll. Moreover, when I remove the doll Jacqueline occupies herself quite differently; when I replace it, after a moment, she immediately starts to move her leg again” (Piaget 1936/1952, p. 182). Thus, we can see that Jacqueline’s interest

has moved from her own body toward her surrounding environment and the consequences of her actions. In behaving as she did, the young girl seemed to have detected a relation between her movement and the doll's, and was involved in secondary circular reaction.

During secondary circular reaction substage, as children continue to grow, they also start to combine different behavioral schemas; what Piaget called *coordination of secondary circular reactions* (Smith et al. 2015). In the following example, we can see how Jacqueline combined different schemas such as “sucking” or “grasping” an object in a series of coordinated actions when a new toy is introduced to her at 8 months of age: “Jacqueline grasps an unfamiliar cigarette case which I present to her. At first, she examines it very attentively, turns it over, then holds it in both hands while making the sound ‘apff’ (a kind of hiss which she usually makes in the presence of people). After that she rubs it against the wicker of her cradle then draws herself up while looking at it, then swings it above her and finally puts into her mouth” (Piaget 1936/1952, p. 284). Jacqueline's behavior illustrates how children begin to combine several schemas to achieve goals or get through new situations.

Tertiary Circular Reactions

While the newborn child between 8 and 12 months of age would engage in a repetition of their actions in order to enjoy an interesting outcome, the young 1-year-old progresses to the next level. Although children would still repeat the previous stage, they are not repeating it precisely but instead, they try to vary the activity, a new behavior known as a *tertiary circular reaction* (Hughes 2010). Children's behaviors are now more flexible and this could lead to new results (Smith et al. 2015). By repeating actions in alternative ways young children are, essentially, applying already established schema to new situations and needs (Smith et al. 2015).

Consider the example of Piaget's daughter Jacqueline – now 13-month-old – in her bath: “Jacqueline engages in many experiments with celluloid toys floating on the water... Not only does she drop her toys from a height to see the

water splash or displace them with her hand in order to make them swim, but, she pushes them halfway down in order to see them rise to the surface. Between the ages of a year and a year and a half, she amuses herself by filling her sponge with water and pressing it against her chest, by running water from the faucet... along her arm, etc.” (Piaget 1936, p. 273). The playful element in this form of circular reaction is evident, as the child seems to enjoy their time with novel objects as well as actively trying to create new interesting experiences.

As the young child progresses through the previous stages of sensorimotor play, they learn to act directly on their surrounding environment via their sensory and motor schemas. According to Piaget, the sensorimotor play period ends when children finally achieve what we call *internal representation* (Smith et al. 2015). Internal representation refers to the child's ability to act indirectly on the world because they have now a mental representation of the world, and this ability is not acquired until the newborn child reaches the age of 18–24 months (Smith et al. 2015). This means that, children are able to manipulate their mental representation of the world such as being able to think and plan.

Conclusion

According to the Piagetian theory of cognitive development, infants progress through four developmental stages where they gradually acquire the skills necessary to experience and understand the world around them. As Piaget further suggested, young children develop their own capacity for thinking through the period of sensorimotor play. During this period, the young child progresses from very simple and basic reflex actions at birth to more complex behaviors at the end of each stage. At first, infants' motor or sensory activities are related to their own bodies with concrete goals being the ultimate outcome, such as shaking a rattle and listening to the sound it makes. Later, infants' activities are mainly focused on the surrounding world with more abstract goals such as differing the heights from which objects are dropped and watching what happens as well as

how the different effects vary. Young children also acquire the ability to form mental representations such as remembering another person's behavior and imitating it the day after it occurred. It is only toward the end of the period that children develop this ability to mentally represent the world as well as to manipulate their thoughts and construct their own knowledge in response to their experiences.

Cross-References

- [Object Play](#)
- [Play and Tool Use](#)
- [Sensorimotor Play](#)
- [Social Play](#)

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Newborn Imitation

- [Neonatal Imitation](#)

Niceness

- [Benefit to Another at Cost to Self](#)

Nisbett-Reaves Hypothesis

- [Culture of Honor and Nepotism](#)

Nitric Oxide

- [Music and Hormones](#)

No Strings Attached Sex

- [Casual Sex](#)

No Two Alike

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Synonyms

[Book](#); [Nonfiction](#)

Definition

A book, written by Judith Rich Harris, which focuses on the theories and research that explain the individual differences in personality.

Introduction

No Two Alike: Human Nature and Human Individuality is a book written by independent psychological scientist Judith Rich Harris and was published by W. W. Norton in 2006. The book – written in the theme of a detective story – investigates the potential causes of individual differences in personality as though they are suspects in a crime. Throughout this investigation, Harris cites research in many areas of psychology and biology – including traditional developmental psychology, twin studies, animal research, and behavioral genetics, among others. Harris' investigation eventually leads her to present her own theory regarding the causes of individual differences in personality.

About the Book

No Two Alike begins by addressing many of the traditional and popular theories regarding why individuals differences in personality exist. These five theories – considered “red herrings” as they mislead researchers away from the true causes of individual differences – include the environment, heritability, gene-environment interactions, indirect genetic effects (also known as gene-environment correlations), and birth order. Although Harris does not fully discount these potential causes of individual differences, she cites important findings made in the areas of behavioral genetics and social psychology as evidence that these cannot fully account for all of the causes of individual differences across humans.

After eliminating those “red herrings,” Harris posits her own theoretical model that explains how and why individual differences in personality exist. This model contains three evolved psychological systems – each of which is distinct from the other. The first system – referred to as the *relationship system* – accounts for short-term behavioral differences based on interactions with the people in one’s environment. The relationship system allows individuals to store information regarding the people around them (e.g., who is kind, who is aggressive, who is trustworthy, etc.) allowing each individual to know how to act and respond when in the presence of each specific individual. This relationship system allows for variance in behavior but only accounts for short-term changes in behavior – as these behaviors only change when in the presence of different people.

The second system – known as the *socialization system* – is a product of socialization from many sources – parents, peers, etc. This system allows for individuals to develop an understanding of the social norms and accepted behaviors in their environments. This system – which supports Harris’ hypothesis from her previous book, *The Nurture Assumption* – illustrates how parents are not the only source of socialization for their children. Although children are socialized by their parents, they are also socialized by their peers – and peers continue to have a greater effect than

parents’ as the children grow up. These various sources of socialization lead to differences in social behaviors based on what is deemed appropriate within each group. For example, an adolescent knows that s/he may engage in certain behaviors – such as swearing – in the presence of his/her friends, but that adolescent also knows that s/he should not – and therefore usually does not – swear when in the presence of his/her parents.

The third and final system – the *status system* – encourages competition with one’s peers. This system accounts for behavioral differences between individuals and their peers by examining peers as rivals for status and/or resources. The status system then collects knowledge of oneself and interacts with the socialization system to help elevate one’s social status over his/her peers. Harris argues that this system not only accounts for individual differences in long-term personality development, but it also accounts for individual personality differences between identical twins (i.e., identical twins may act differently from each other because they are engaging in different behaviors to achieve higher status than the other).

Conclusion

No Two Alike has been met with positive reviews by journalists and evolutionary psychologists (Kaighobadi and Shackelford 2008; Saletan 2006). It was written in a compelling detective-style format that is often viewed as fun and attention-grabbing. In this book, Harris provides evidence for rejecting some of the more traditional and popular theories regarding the causes of individual differences while also providing a new theory – rooted in evolutionary psychology – that adequately explains individual differences in personality.

Cross-References

- [Judith Rich Harris](#)
- [Nurture Assumption, The](#)
- [Peer Feedback and Norms](#)

- [Peer Relationships in Childhood](#)
- [Personality Development](#)
- [Status Competition and Peer Relationships in Childhood](#)

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Noam Chomsky

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Introduction

Professor Noam Chomsky, born December 7, 1928, as Avram Noam Chomsky to middle-class Jewish working parents in East Oak Lane, Philadelphia, is an American linguist, cognitive scientist, logician, philosopher, and political activist. Often referred to as “the father of modern Linguistics,” “the world’s most important intellectual,” etc., Chomsky has made pioneering contributions to multiple fields, including Linguistics (a field he is primarily credited with founding in its modern form), Logic, Abstract Algebra, Artificial Intelligence and Machine Learning, Formal Languages, Cognitive Science, Cognitive Psychology, Philosophies of Mind and Language, and Anarchist and Syndicalist political theories, and is considered to be one of the pillars of Analytic Philosophy, particularly in the Rationalist tradition. Ranked as “among the eight most cited scholars, ever,” Chomsky is currently Professor Emeritus of Linguistics at the Massachusetts Institute of Technology, where he has held

office for over half a century, and Laureate Professor of Linguistics at The University of Arizona.

Early Life

Avram Noam Chomsky was born on December 7, 1928, in the East Oak Lane neighborhood of Philadelphia, Pennsylvania (Lyons 1978). His father was William “Zev” Chomsky, an Ashkenazi Jew originally from Ukraine who had fled to the United States in 1913. Having studied at Johns Hopkins University, William went on to become school principal of the Congregation Mikveh Israel religious school and in 1924 was appointed to the faculty at Gratz College in Philadelphia. Chomsky’s mother was the Belarusian-born Elsie Simonofsky (1904–1972), a teacher and activist whom William had met while working at Mikveh Israel (Lyons 1978).

Chomsky’s primary education was at Oak Lane Country Day School, an independent Deweyite institution that focused on allowing its pupils to pursue their own interests in a non-competitive atmosphere. It was here, at the age of 10, that he wrote his first article, on the spread of fascism, following the fall of Barcelona to Francisco Franco’s fascist army in the Spanish Civil War. At the age of 12, Chomsky moved on to secondary education at Central High School, where he joined various clubs and societies and excelled academically but was troubled by the hierarchical and regimented method of teaching used there. During the same time period, Chomsky attended the Hebrew High School at Gratz College. From the age of 12 or 13, he identified more fully with anarchist politics (Lyons 1978).

Education

In 1945, Chomsky, aged 16, embarked on a general program of study at the University of Pennsylvania, where he explored philosophy, logic, and languages and developed a primary interest in learning Arabic. Living at home, he funded his undergraduate degree by teaching Hebrew. However, he was frustrated with his experiences at the university and considered dropping out and

moving to a kibbutz in Mandatory Palestine. His intellectual curiosity was reawakened through conversations with the Russian-born linguist Zellig Harris, whom he first met in a political circle in 1947. Harris introduced Chomsky to the field of theoretical linguistics and convinced him to major in the subject. Chomsky's B.A. honors thesis was titled "Morphophonemics of Modern Hebrew" and involved his applying Harris's methods to the language (Boeckx and Piattelli-Palmarini 2005). Chomsky revised this thesis for his M.A., which he received at Penn in 1951; it would subsequently be published as a book (Boeckx and Grohmann 2013; Boeckx and Piattelli-Palmarini 2005). He also developed his interest in philosophy while at university, in particular under the tutelage of his teacher Nelson Goodman. From 1951 to 1955, Chomsky was named to the Society of Fellows at Harvard University, where he undertook research on what would become his doctoral dissertation (Barsky 1998; Lyons 1978; Otero 1994).

Basic Ideas I. Science

Plato's Problem

In Linguistics Chomsky holds a position akin to that of Isaac Newton in Physics during and after enlightenment (Dawkins 2015). Evolutionary Psychologist Steven Pinker remarked, "Whether or not Chomsky provided all the right answers, Linguistics and Cognitive Science will always be dominated by the questions Noam Chomsky has asked." In stark contrast to the behaviorist zeitgeist fashionable in the 1940s and early 1950s, Chomsky brought about a Kuhnian paradigm shift in the study of the human mind, which he claimed is the cradle of language, by directly linking it to mainstream biology and arguing that the adult mind with all its knowledge systems is a biological organ, much like the human digestive system (Chomsky 1959a). Indeed, years after Chomsky kickstarted what came to be known as the *cognitive revolution*, immunologist Niels Jerne compared the human digestive system to Chomsky's theory of Grammar ("Niels K. Jerne – Nobel Lecture," n.d.).

Perhaps the best introduction to Chomsky's thoughts and works in Linguistics is manifest in the introductory lines of *Syntactic Structures*:

Syntactical investigation of a given language has as its goal the construction of a device for producing the sentences of the language under investigation.... The ultimate outcome of [such] investigations should be a theory of linguistic structures in which the descriptive devices utilized in particular grammars are presented and studied abstractly.... One function of this theory is to provide a general method for selecting a grammar for each language, given a corpus of this language. (Chomsky 1957/2002)

For Chomsky one of the fundamental issues in rationalist epistemology concerns the problem of "creativity" (Aarsleff 1970; Bever 2009; Chomsky 2009). Namely, how is it that human beings whose contact with nature is so brief and transient come nonetheless to learn so much of it? Applying this general observation to linguistic phenomena, Chomsky asks how is it possible for a child to instinctively create new utterances to which it has never been exposed specifically, based only on exposure to a fraction of the possible sentences of a language. Indeed, Chomsky points out that the total number of possible sentences in a language is *infinite* and that this infinity (discrete infinity: infinite number of sentences, with discrete whole numbers of words in them, but never fractions of words) itself is made possible by the fact that users can create completely novel utterances at any given instance (Chomsky 2007). Thus, Chomsky observes, the child placed in its natural environment is exposed to a limited amount of experience, and yet what the child comes to possess in the form of knowledge from this limited environment far exceeds its experiences. This gap between what the child is given, and what it comes to possess, and the problems concerning how the child is able to bridge this gap, Chomsky terms *Plato's Problem*, after the classical philosopher who first observed this tendency of the Sapiens' minds (Chomsky 1959b).

This program contrasts, and falsifies, Skinnerian Behaviorism (Chomsky 1959a) which held that language is a result of associations between words. Because users can create completely novel

associations between words in the form of new sentences, such a theory is automatically rendered untenable. While Chomsky's devastating criticism of Skinner's *Verbal Behavior* (Chomsky 1959a, 1967) is often taken to be the most important cause behind the decline of radical behaviorism, the idea that prior constraints on learning space and hypotheses impose severe limits on what can be inductively learned has since spread beyond psychological nativism as evidenced in Wolpert's *No Free Lunch* (Wolpert and Macready 1997).

Principles and Parameters

Chomsky's proposed methodology to scientifically approach Plato's problem was first proposed in *Aspects of the Theory of Syntax* (Chomsky 1965), also known as *standard theory*, and later revised as the *standard extended theory* which was developed and revised throughout the 1970s during the early years of generative grammar. Within this framework it is hypothesized that the child is genetically endowed with an innate hypotheses space, a format for possible grammars of natural language, and the child in the process of growth and development constructs a number of possibilities to externalize. The selection of the ultimate externalized grammar is hypothesized to be the one that selects the least number of rules, that is, one that manifests a minimal implementation of the system to achieve discrete infinity.

However, since this approach proved too cumbersome, Chomsky and colleagues soon proposed a newer alternative in the form of the *principles and parameters approach* (PnP) (Chomsky 1993, 1995). First introduced by Chomsky in *Lectures on Government and Binding, or The Pisa Lectures* (Chomsky 1981/1993), and later elaborated further in *Knowledge of Language* (Chomsky 1986), PnP hypothesizes that the architecture of language is constructed through *Principles*, invariant and constant across languages, and *Parameters*, also universal but adjustable in individual languages, thereby yielding linguistic diversity. One set of principles, for example, restricts the possible distribution of pronominals, reflexives, and anaphors

in sentences of the world's languages to specific predetermined hierarchical spots in phrasal structures and is referred to as *the binding principles*. All languages adhere to binding principles, either explicitly or vacuously. Parameters on the other hand, such as the PRO-drop parameter, are hypothesized to have individual preferences for how they are implemented in individual languages. For instance, Japanese is a PRO-drop language in which certain categories of pronouns are overtly omitted because they are inferable otherwise from the structure. Other languages may choose to not drop the PRO. While parameters themselves are posited to be innate, that is the total number of possible parameters are finite and limited to an universal set, not all languages must instantiate all parameters, unlike principles.

Minimalist Program and the Biolinguistic Link

The system of grammars described above is often referred to as *transformational* and *generative*, or *transformational-generative* (Chomsky 1959b, 2002), because in this framework, grammar is composed of a system of *representations* in the mind, manipulated computationally by innately specified *syntactic rules*, thus deriving structures from elementary primitives (generative) and then modifying existing structures to derive newer ones (transformation). The system can thus be conceptualized in a twofold fashion with regard to how it makes possible and then implements languages in human brains. Traditionally, theories of grammar are *computational-representational* (C-R) (Embick and Poeppel 2015; Poeppel et al. 2012) theories which assume that the human mind is genetically endowed with a set of innate concepts and symbols (representations) which are used as constituents by algebraic computational rules to create bigger and more complex structures. Thus, the meaning (or semantic content) of a structures is derived not *just* from the combined semantic contents of its constituents but also from (a) how the constituents are combined in a given structure to make larger constituent structures and (b) how constituents and (c) constituent structures

in the larger structure relate and refer to each other. For instance, in the sentence

[[John told Mary]_i][that [Bill loves her_i]]

[John, Bill, Mary, love, her, that] form a set of constituents, while [John told Mary] and [Bill loves her] form larger constituent structures capable of being complete utterances on their own but indeed are combined within a larger structure to derive our example sentence. The meaning of this final superstructure, while dependent on the meanings of the constituents, is also contingent on how individual constituents, for instance, “Mary” and “her” relate to each other. Since “Mary” and “her” carry the same index “i,” we know that the “her” that “Bill” loves is in fact “Mary.” Chomsky’s main hypothesis is that such constituent structures, the indices (such as “i”), and the rules that compute and implement them are part of the innate mechanisms of our brains. Thus, “Mary,” the intended listener of our example utterance, can listen to “John” produce the same and, in spite of the fact that linear acoustic speech signals contain neither brackets nor indices, can mentally recompute the intended structure, and therefore the intended meaning, reflexively and without ever being explicitly aware of the fact that she is doing so (Chomsky 1959b, 2007; Hauser et al. 2002; Hauser and Spelke 2004).

In the 1990s, Chomsky’s research focused on what he called the “minimalist program” (Chomsky 1995), which attempted to demonstrate that the brain’s language faculties are the minimum faculties that could be expected, given certain external conditions that are imposed on us independently. In other words, Chomsky began to place less emphasis on something such as a universal grammar embedded in the human brain and more emphasis on a large number of plastic cerebral circuits. And along with this plasticity would come an infinite number of concepts. The brain would then proceed to associate sounds and concepts, and the rules of grammar that we observe would in fact be only the consequences, or side effects, of the way that language works. Analogously, we can, for example, use rules to describe the way a muscle operates, but these rules

do nothing but explain what happens in the muscle; they do not explain the mechanisms that the brain uses to generate these rules.

The specifics of the biolinguistic program (Bever 2003, 2009; Boeckx and Grohmann 2013; Boeckx and Piattelli-Palmarini 2005; Chomsky 2005b, 2007; Medeiros et al. 2016) concern approaching every aspect of language – sound, meaning, and structure – as functions of an organ of the mind. While Chomsky emphasizes that language itself is a function of the biological organ known as *the faculty of language*, a module of the human cognitive system devoted to language specifically, the precise nature and architecture of this module remains a hotly debated avenue of research. Chomsky himself has continuously revised his position on this issue, with the latest version of his theory making a distinction between *the faculty of language-Narrow* (FLN: the core architectural component of the faculty not attested anywhere else in the living world) and *the faculty of language-Broad* (FLB: the aspects of the faculty portions of which may be present in other animals) (Hauser et al. 2002, 2014; Hauser and Spelke 2004). In these versions of his work, along with his colleagues like Mark Hauser, Tecumseh Fitch, and Massimo Piattelli-Palmarini et al. (Berent 2016; Boeckx and Piattelli-Palmarini 2005; Medeiros et al. 2016; Piattelli-Palmarini 2013), Chomsky has claimed that the core component of FLN specific just to humans is a single operation called *MERGE*, which merely takes two constituents and creates an unordered set by merging them together. It is claimed that *MERGE* meets computational minimality requirements by creating simple unordered sets instead of ordered ones.

MERGE $x, y \rightarrow [x, y] (= [y, x])$

The details of how a formal operation like *MERGE* is to be implemented on a biological substrate, how such hierarchical structures get linearized, and what kind of neural structures and operations are involved in doing so constitute the core of biolinguistic research carried out interdisciplinarily by psychologists, linguists, neurobiologists, and evolutionary biologists.

Politics and Activism

Robert Barsky's biography, called *Noam Chomsky: A Life of Dissent* (Barsky 1998), and published by MIT Press in 1997, contains a useful discussion of his early years and the development of his politics. Today, Chomsky is distinguished for his innovative work in the field of linguistics, but his wider public renown is due to his authoritative voice as a critic of US foreign and domestic policy (Antony and Hornstein 2003; Otero 1994).

Turning to sociopolitical issues, we mainly observe Chomsky working on ideas of free development, not unlike those underpinning his approach to language as some have claimed. Chomsky's main idea is that humans do not need much in the way of external control in order to form wholesome and productive social relationships. He has routinely advocated for a society moving toward voluntary organizations and eliminating as much as possible the structures of hierarchy and domination (Herman and Chomsky 2002; Lyons 1978). Chomsky views rigid hierarchical control by structures of authority as antithetical to the nature of human development and argues that such outside interference has a stifling effect on intellectual development and social life in general. While Chomsky maintains that social institutions are a necessity, he rigidly opposes the hierarchical organization of such structure and the privatization of means of production that leads to concentration of wealth. Chomsky argues that concentration of wealth leads to concentration of power (Chomsky 2014).

Chomsky's critique of the state is mainly directed toward his own (Chomsky 2003b). He turns his analytical anger on Washington's cruel maltreatment of third world people, its ruthless foreign policies and disregard for international law, its abuse of US citizens and residents, and its violations of democracy and Constitutional Law (Chomsky 1999; Herman and Chomsky 2002). He argues that this pattern of behavior became dominant after World War II left the US state in a position of unchallengeable power. It was US aggression against Vietnam that has usually been identified, including by Chomsky himself (Chomsky 2003a, 2005a), as the dominating factor that lead Chomsky to become a critic of US foreign policy. His essays

on the war are collected in *American Power and the New Mandarins* (Chomsky 2003a) and in *At War With Asia* (Chomsky 2005a); these books remain relevant today. Chinese readers may have a particular interest in what he has written about the Vietnam War since the US invasion was justified in the USA and around the world by the need to contain China.

Chomsky's logic is to apply universal principles when judging the behavior of government. In particular, Chomsky argues that unlike relativist norms often employed by politicians, an unjust course of action is wrong irrespective of who it benefits. That is, "if its wrong when they do it, then its wrong when we do it." In *Hegemony or Survival: America's Quest for Global Dominance* (p. 4) he writes, "Those who are seriously interested in understanding the world will adopt the same standards whether they are evaluating their own political and intellectual elites or those of official enemies. ... Truth [is] veiled by intentional ignorance that makes a crucial contribution to ongoing crimes" (Chomsky 2004). He regards the quest for truth and the struggle against official evasion and mendacity as the "responsibility of intellectuals" (Chomsky 1967).

Cross-References

► [Pinker's \(1994\) The Language Instinct](#)

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Noam Chomsky and Linguistics

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Synonyms

[Chomsky and language evolution](#)

Definition

The impact of Noam Chomsky on the field of linguistics, particularly the evolution of language.

Introduction

Noam Chomsky (born December 7, 1928) is one of the most influential contemporary thinkers. His huge impact surpasses linguistics to include

psychology, philosophy, or computer science, among other fields. The advent of Chomsky's generative grammar in the second half of the twentieth century challenged the traditional view that considered language to be a purely cultural trait deriving from our great intelligence and unlimited learning capacities, by claiming that language is an innate trait, part of the human biological endowment.

It would be hard to provide an overall presentation of Chomsky's linguistic work, for it has been crucial in many topics: nativism, language and mind, universal grammar, the poverty of the stimulus, language acquisition, language structure, etc. All of these topics have been widely discussed and are well known. Therefore, this piece will discuss a perhaps lesser-known topic, Chomsky's views on language evolution, characterizing the evolutionary processes by which language could have come into being. This is especially relevant, for some scholars (Dennett 1995) have suggested that according to Chomsky language could not have evolved.

The structure of the piece is as follows: first, Chomsky's conception of language is summarized; then, his main ideas about language phylogeny are brought to the fore. Finally, some criticisms are raised to his approach, although without the abandonment of the core theoretical premises Chomsky adhered to.

Chomsky's View on Language

In the 1960s, Chomsky challenged the traditional conception of language by claiming that this trait is biologically rooted (i.e., an innate trait), thus belonging to the human biological endowment. Accordingly, the biolinguistic approach (Jenkins 2000) analyzes language from a biological perspective, by assuming that its study should be conceived of as a branch of human biology (Chomsky 1980). The innate principles (taken to be genetically seated) responsible for language acquisition make up the universal grammar. Language grows in the mind; given a minimum of experience, those principles are triggered, thus making it possible to attain the steady state of

linguistic knowledge that characterizes native speakers. When language development comes to an end, the individual possesses a mental grammar, or I(nternal)-language, by which infinite sentences can be generated/interpreted.

One point is in order: the notion of language is ambiguous, for it covers many different aspects (historical, social, cultural, etc.), but the biolinguistic approach is not concerned with aspects like those. To avoid terminological problems, the notion of faculty of language (henceforth, FL) will be used instead to refer to language as a biological capacity. Its architecture will be briefly presented, for it is such an architecture that is to be explained in evolutionary terms.

From the view of the Minimalist Program (the current Chomskyan model; Chomsky 1995), FL (syntax) is a natural computation system that resides in the mind/brain of all human beings (pathologies aside). In that definition, two notions are to be highlighted: *computational* means that FL is a system of information-processing based on the capacity for manipulating mental elements and performing computations on them, while *natural* means that FL is an innate mental organ restricted to our species (at least, currently).

From the point of view of the mental architecture, FL is a bridge faculty connecting the articulatory-perceptual system (henceforth, A-P), in charge of our visual, oral, gestural, and auditory activities, and the conceptual-intentional system (C-I), responsible for the production of intentional thoughts and attitudes about the world. Both capacities, though, are independent: on the one hand, not every thought needs to be externalized; on the other, sounds can be produced without associated meaning. FL provides the channel by which representations of A-P and C-I systems (sounds/gestures and meanings) become accessible to each other. FL takes elements from the lexicon and "generates an infinite array of hierarchically structured expressions" (Chomsky 2010, p. 45). This capacity is enabled by recursion, which permits to embed constituents within constituents of the same type. FL connects to the A-P and C-I systems through two interfaces: an external sensorimotor interface with the A-P system, in charge of the production and perception of the

expressions generated by FL, and an internal conceptual-intentional interface with the C-I system, which links the mental expressions with their semantic and pragmatic interpretation, concepts, reasoning, etc. Accordingly, any expression generated by FL receives an interpretation at both interfaces.

The next section approaches how the architecture of FL could have come into being evolutionarily.

Chomsky and Language Evolution: A Conceptual Guide

This section will provide the key points of Chomsky's thought on language evolution. For the sake of clarity, the section is organized into questions and answers.

Did Language Evolve from Animal Communication?

Because human and nonhuman animals communicate with conspecifics, many proposals take animal communication and language to be evolutionarily related through a gradual process of descent with modification. However, Chomsky has persistently contended that language could not evolve from animal communication.

The extensive study of animal communication systems has revealed highly complex communicative behaviors that make use of truly referential signals, like those of bees. In addition, animals like birds, whales, bats, etc., possess combinatorial systems that somehow resemble that of language, for they are arranged according to several levels of structure (Berwick et al. 2011).

Despite the great complexity of animal communication, its properties are very different from those of language (Longa 2012). For instance:

1. Animal communication is restricted to the expression of biological needs (food, danger, mating), whereas language makes it possible to communicate any event.
2. Animal signals are restricted to "the here and now" (Hauser et al. 2002, p. 1576), while language may refer to past or future events.

3. Animal signals trigger a unique response: when a monkey hears an alarm call of a conspecific, the only possible response is to escape. This points to a rigid functional association between the signal and the danger the signal refers to. That association does not apply for language: language does not evoke reactions, but properties (Bickerton 1990).
4. Animal communication depends on sensory perception (i.e., experience), but language makes it possible to refer to everything, even in the absence of prior experience. Therefore, language is a powerful representational system, according to which any concept/event (even an unreal one) may be represented and expressed. This means that language constructs our reality but constructs unreality as well. For this reason, it has a key role in human creativity.
5. Animals do have sophisticated concepts, but most of them cannot be expressed to conspecifics: a barrier exists between cognition and communication. That barrier is absent in humans: everything we can represent can be communicated to others.
6. While animal concepts keep a referential relationship with objects/events in the world, human concepts and words lack the relation to mind-independent entities that defines animal signals (Berwick and Chomsky 2016, p. 84). An apparently simple concept like *book*, which seems to point to a real referent, may nevertheless apply to many situations that reside in the mind, not in the environment: a book that has never existed, etc.
7. Although some animal systems have a combinatorial nature that may somehow resemble that of language, those systems lack semantics (see Berwick et al. 2011, p. 118).

Because animal systems "are radically different from human language in structure and function" (Berwick and Chomsky 2016, p. 63), language seems to be biologically isolated. Accordingly, Chomsky (1968) contended that language is a biological emergence, which can hardly be explained through a process of Darwinian descent with modification from animal

communication. A question becomes very relevant: Is language an overall emergence? Not really, according to more recent stages of Chomsky's thought.

Is Language a Unique Trait or Is It Based on Mechanisms Shared with Other Species?

Hauser et al. (2002) propose a divide between faculty of language in the broad sense (FLB) and in the narrow sense (FLN) as a useful methodological tool for guiding research on language evolution. According to these scholars, language is not a monolithic trait, but something like a mosaic, composed of many different components that are evolutionarily superimposed. The divide makes it possible to analyze the evolutionary history of each component, aiming at determining which components are shared with other species and which ones are not. The features that can be thought of as being inherited unchanged from a common ancestor, or subjected to minor modifications, are said to be part of FLB, while the qualitatively new components are said to be part of FLN. Therefore, FLB gathers all the capacities necessary for language that are neither specific to language nor to humans, whereas FLN covers those capacities which are unique to language and to humans.

From the comparative evidence, Hauser et al. (2002) suggest that main mechanisms of the A-P and C-I modules have clear homologues in animals, those mechanisms long predating the emergence of language. The opposite applies for the computational system: this is the only evolutionary novelty and the only component of FLN. A second contention of Hauser et al. (2002) is about the specific contents of FLN: its only component is recursion, i.e., the procedure the computational system makes use of, with its open-ended generativity based on the structural embedding of hierarchically organized phrases. The search for a syntax-like system in animals, whether wild or trained, has been fruitless. Apes appear to be able to acquire symbolic systems, at least under experimental conditions, although no primate has ever been able to acquire a full-fledged language or even rudimentary versions thereof involving combinatorial syntax. This

suggests that FLN is unique to the human species (Hauser et al. 2002, p. 157).

What Has Evolved, Then?

Because FLN lacks any kind of homologues, the computational system had to emerge in the course of human evolution. It is necessary to shed light on what the computational system consists of, given that its very nature will determine the range of hypotheses about its evolution.

From the view of the Minimalist Program, the computational system is mainly reduced to a single operation, named Merge, which applies recursively, giving rise to hierarchical structures through the merging of two syntactic objects (lexical items, affixes, or groups of lexical items) into a new object. One of the two elements becomes the head of the resulting structure. For example, a sentence like *John will read the book* derives from these successive applications of Merge (specific details omitted):

Merge 1: {the, book}

Merge 2: {read, {the book}}

Merge 3: {will, {read the book}}

Merge 4: {John, {will read the book}}

The conclusion can be reached that FL is very simple: it basically derives from a single operation, the conditions of which are simple as well (Longa et al. 2011, p. 599):

1. Binary branching: Merge combines two elements instead of three, four, etc. This greatly reduces the computational complexity.
2. Asymmetric labeling: the outcomes of Merge become identified with one of the two merged elements, not with both of them or with a different one; the projection of a noun produces a nominal phrase, etc. This means that asymmetric labeling presupposes headedness (endocentricity).
3. Structural preservation: each successive application of Merge preserves the structure obtained so far. This condition is computationally efficient: it leaves the two syntactic objects unaltered.

4. Unboundedness: Merge operates in an unlimited way (limitations are due to short-term memory, attention, etc.).

Merge, at the heart of FL, is according to Chomsky the only specifically linguistic and specifically human component of language emerged in evolution. Combined with the prior infrastructure (FLB) and with the appearance of the lexicon (a deep mystery for Berwick and Chomsky 2016), Merge led to language emergence. This is the main contention of Hauser et al. (2002): a specific novelty linked to pre-existing components. The proposal fits in well with evolutionary dynamics (see Chomsky 2010; Berwick and Chomsky 2016): evolution is something like a tinkerer that operates by adding slight modifications on previous systems: “Evolution does not produce novelties from scratch. It works on what already exists” (Jacob 1977, p. 1164).

How Did FL Emerge?

Merge is taken to be the evolutionary key of language (Berwick and Chomsky 2011, 2016; Chomsky 2007, 2010). What evolutionary event gave rise to it? Chomsky’s answer is that Merge first arose in the domain of thought, and was subsequently exapted for language (Chomsky 2010; Berwick and Chomsky 2016), this view implying an evolutionary asymmetry (see below).

More specifically, Chomsky suggests that Merge could have arisen through some slight rewiring of the brain produced by a genetic event, “presumably a small mutation” (Chomsky 2007, p. 14). The mutation could have taken place in an individual pertaining to some anatomically modern human small breeding group from East Africa, from which we are all descendents, this claim deriving from the essential uniformity of FL in the species. However, it should be emphasized that Merge arose in the domain of thought and consequently gave rise to an inner language. Merge led to a substantial modification of the simple system of thought existing so far, based on elementary schemata, and allowed to generate an infinite array of internal expressions made up from (already available) lexical items. The individual who experienced that mutation was

endowed with many advantages, like “capacities for complex thought, planning, interpretation, and so on” (Chomsky 2010, p. 59). Then, the mutation could be transmitted to the offspring also as an internal capacity, in such a way that it began to proliferate among the group.

When that internal capacity spread over the population, “there would be an advantage to externalization” (Chomsky 2010, p. 59). Perhaps through a mutation, such an internal capacity was linked as a secondary process to the A-P system in charge of externalization, intact for hundreds of thousands of years. When the complex language of thought became externalized, FL emerged in its current sense.

To summarize, three stages were involved: (1) a simple system of thought; (2) at a given point, the appearance of Merge produced a linguistically structured system of thought; (3) that system of thought became externalized, giving rise to FL, the specifically linguistic and specifically human component of language. The slight rewiring of the brain triggered by the mutation had nevertheless great effects (FL) because the vast majority of ingredients for language were already in existence.

When Did Language Emerge?

The appearance of FL happened after the speciation event that produced our species, FL consequently being an evolutionary result linked to anatomically modern humans. Its emergence may be dated within a narrow evolutionary window, a timespan between 200,000 and 60,000 years ago (Berwick and Chomsky 2016, p. 110), before the great exodus from Africa. More specifically, it could have taken place more than 80,000 years ago, if the wide symbolic record found in sites like Blombos Cave (South Africa) is considered (Berwick and Chomsky 2016, p. 87). The reason for such a dating is not unknown to paleo-anthropologists (for a review, see Balari et al. 2013): many of them consider that modern behavior arose in that period, including many instances of symbolism (several forms of art, ornaments, engravings, burials with offerings, music), technology unknown to date, etc. Those proxies reveal an unprecedented cognitive flexibility and a

powerful creativity, both factors being very unlikely in the absence of language, which makes it possible to build any kind of mental models (Dennett 1996). Therefore, the emergence of FL is for Chomsky the obvious candidate for those behavioral changes to be explained. The aforementioned proxies would be a visible effect of the externalization of thought, thus indicating the full emergence of language. To summarize, the evidence suggests that (1) FL is a recent evolutionary outcome and (2) it arose in the African Middle Stone Age about 100,000–80,000 years ago.

Why Does Language Imply an Evolutionary Asymmetry?

An evolutionary asymmetry exists between the two interfaces of FL (Berwick and Chomsky 2016, p. 71; Chomsky 2010, p. 55). If we keep in mind that the previous stage to FL was an internal language of thought, the said asymmetry implies that the interface of FL with the C-I system is primary, while the interface with the A-P system (related to externalization) is secondary (although by no means crucial for language to exist). In fact, FL exhibits an optimal relation with the C-I system, for language is just externalized thought (Longa et al. 2011). From this view, there is only one internal language in the species, in charge of generating the expressions of the language of thought.

However, externalization does not hold the same relationship with FL; it is far from optimal, as evidenced by the fact that it causes humans to express common internal thoughts very differently, according to the very disparate mechanisms (case, aspect, agreement, etc.) language makes use of. This secondary process reveals the evolutionary asymmetry, as reinforced by the fact that language is even modality-independent (oral or gestural).

This leads to the question of why there are so many languages if there is just a common internal language of thought. The said asymmetry provides a reasonable answer: the great variation shown by languages is linked to externalization and suggests that this phenomenon is not to do with the biological evolution of language but with

historical and cultural processes (historical change; Chomsky 2010, p. 61), which are very variable and produce heterogeneous results. Therefore, while the computational system is essentially uniform across the species, the morphological and phonological processes that convert hierarchical internal syntactic objects into linearly ordered objects accessible to the A-P system are very different from each other; interlinguistic variation derives from the very disparate solutions to how internal syntactic representations surface in the form of sentences. Thus, language diversity does not lie in the computational system, but in how those internal syntactic objects generated by the computational system become linearized. This is the very task morphology and phonology are concerned with: to map hierarchical internal syntactic objects into linearly ordered strings.

What Is the Role of Natural Selection?

Chomsky has always been reluctant to consider language to have evolved through natural selection, by claiming that “there is no substance to this assertion” (Chomsky 1968, p. 85). This claim should be well understood, because Chomsky does not deny such a mechanism. He acknowledges that “Language must surely confer enormous selectional advantage” (Chomsky 1980, p. 239). However, one thing is to argue that a trait has an adaptive value and a quite different thing is to assume that it is the adaptive value that has driven the evolution of the trait. Actually, Chomsky distinguishes two roles of natural selection: (1) as a creative process which according to Neo-Darwinism is the only mechanism responsible for complex design and (2) as a process which just sifts the results generated by other means. Chomsky rejects the former sense and accepts the latter one. From this view, natural selection would be a “coarse filter that rejects the utter failures” (Goodwin 1994, p. 157). This amounts to saying that “natural selection works on already developed outcomes (so it can not have caused those outcomes)” (Gottlieb 1997, p. 17). Accordingly, evolutionary novelties, like Merge (slight, although endowed with far-reaching consequences) arise abruptly, although they will need

to be sifted by the process of natural selection (see Berwick and Chomsky 2016, ch. 1). To summarize, FLN is not the product of prolonged and gradual evolutionary development driven by natural selection. In addition, that possibility does not fit in well with the brief interval of time within which language evolution appears to have occurred.

Was Communication the Selective Pressure That Guided Language Evolution?

The aforementioned evolutionary asymmetry illustrates a core idea of Chomskyan thought that strongly departs from an adaptive view of language. Adaptationism considers that the traits evolved through natural selection adapt organisms to their environments, thus solving specific needs. Therefore, for adaptationism it is crucial to suggest a selective pressure that guides the evolution of the trait and provides practical, adaptive advantages. As regards language, approaches which aim to explain language origins as an adaptation underline its communicative advantages (Pinker and Bloom 1990), assuming that a selective pressure towards more efficient communication was the driving force that guided language evolution.

Chomsky rejects that view: language did not emerge linked to communicative needs, for communication was a secondary process, derived from externalization. In fact, the idea that the main function of language is communication cannot be sustained, because language, as humans experience it, serves multiple purposes: to communicate thoughts, to be sure; but also to assert the mere presence of an interlocutor, to lie, joke, express beauty, to talk to oneself, to describe instances of nondenumerable expressions in mathematics, and surely many other purposes that any reader can fathom. Any of those is a “function of language,” though none of them seems more natural than the others. Accordingly, “The functions of language are various” (Chomsky 1980, p. 230). Had a function of language to be emphasized, it would be its use for internal thought, because the appearance of Merge gave rise to language as an internal tool, something like a cognitive glue that binds together other

cognitive systems (Berwick and Chomsky 2016, p. 111). Therefore, any approach mainly based on communication is “seriously misguided” (Chomsky 2010, p. 61): if communication is taken to be the driving force in language evolution, then an animal communication-like system would suffice.

Some Criticisms

To summarize in a few paragraphs the main criticisms of the Chomskyan treatment of language evolution (and language) would be impossible, for many approaches strongly disagree with such a treatment (for a wide picture of current approaches on language evolution, see Tallerman and Gibson 2012). For that reason, this section will briefly raise several criticisms that, nevertheless, share the computational approach on language Chomsky adheres to.

According to this scholar, FL is a uniquely human capacity that consists of a specifically linguistic computational system, uniquely involved in language. Therefore, the notion of Merge is taken to be part of the universal grammar (Chomsky 2007, p. 7), the genetic equipment for language. However, doubts can be raised about the alleged specificity of FL: Balari and Lorenzo (2013) contend that the biological machinery of language is neither specifically human nor specifically linguistic. Language emergence would be just one of the far-reaching consequences of a slight modification operated on an ancestral architecture shared with many other vertebrates. According to Balari and Lorenzo (2013), the computational system (named the central computational system) is an unspecific device, used not only by language but also by many other motor or cognitive tasks humans are engaged in (see also Longa 2013). These scholars also claim that the computational system language makes use of is not specifically human; actually, many vertebrates share it, the difference being the amount of computational memory associated with such a system (no memory, a basic memory, or a sophisticated one) that produces several types of computational regimes. The more memory the system has at its

disposal, the more computational power it is endowed with. Linguistic computations are context-sensitive, and accordingly they require powerful memory resources.

This view of the computational system makes sense from a neuroanatomical and evolutionary perspective. Currently, it is clear that the neuronal substrate of the computational system relies on the coordinated activity of both cortical and subcortical brain areas. The unspecific view finds support in the basal ganglia grammar model (Lieberman 2006, p. 207 and ss.). This model characterizes a system composed of circuits that participate, among other tasks, in the motor programming of speech, sentence comprehension, or walking and is comprised of two components: an iterative sequencing device (cognitive/motor pattern generator) located in subcortical areas (basal ganglia) and a working memory component located in cortical areas. It is not difficult to link both components to the computational approach: the differences between the several computational types do not reside in the computational system itself, but in the amount of memory the system is endowed with. Therefore, a common computational system has been combined with a greater or lesser working memory space in different species, depending on the development of the cortex.

For the computational system to be operative, it needs to be connected to some external modules supplying their input and capable of receiving their output. The same unspecific computational system may be thus connected to different modules in different species. This means that the connection of FL with the A-P and C-I systems in humans may be a contingent, i.e., accidental fact.

Therefore, there would be two axes of variation, one of them corresponding to the working memory space the computational system has access to and the other axis corresponding to the number/kind of external modules the system interfaces with.

To summarize, according to this approach, the notion of FLN is not a useful one, for the computational system is neither specifically human nor specifically linguistic, although language can still be considered a species-specific innate trait, this specificity resulting from how its several

components are integrated. FL has not developed a specific machinery but uses a system shared with many other animals. A slight change involving an increase in working memory produced a dramatic qualitative change in humans, by which the access to a computational power unknown to date in other species was reached.

Another problematic idea of the Chomskyan approach is the genocentric stance it adheres to. Since its inception, this approach has assumed the need for the universal grammar or linguistic genotype, the genetic principles that make language acquisition possible. The same geneticism is also assumed for phylogeny, for Chomsky contends that Merge, the key of language, arose through a genetic mutation, and thus became part of the universal grammar (see Berwick and Chomsky 2016).

That gene-centered approach suggests that the genes do contain linguistic information, but this is untenable from a view informed by developmental biology. The notion of a linguistic genotype amounts to saying that the elements contained in it, like Merge, would be directly represented in the genes, in such a way that “there are elements of the genome that stand in a one-to-one relationship with elements of behavior” (Johnston 1987, p. 160). This is untenable, for “Genes store information coding for the amino acid sequences of proteins; that is all” (Bateson 2001, p. 157).

The Chomskyan view conflates the terms *innate* and *genetic* (as Neo-Darwinian biology does), assuming that an innate feature must be a genetic one. However, this conflation is ill-founded, for “being genetic is not necessary nor sufficient for being innate” (Wimsatt 1999, p. 160). Linguistic principles can be innate even though they cannot be seated in the genome, as shown by Longa and Lorenzo (2012).

Chomsky does not offer an overall picture of language evolution but solely of the evolution of Merge. We should be reminded that according to minimalism, the architecture of language consists of FL and two adjacent systems, A-P and C-I (and their interfaces with FL). Therefore, for language evolution to be accounted for, it would be necessary to explain how the internal syntactic objects became linked with the interfaces with A-P and

C-I (Berwick and Chomsky 2016, p. 66). Unfortunately, such a task is not really developed: Chomsky leaves aside the C-I system and its interface with the computational system. As regards A-P system, he assumes that it preexisted long before language, and after the appearance of Merge, internal thought became externalized through its secondary link with A-P. However, no proposals are offered at all about how such a link could happen, with the exception of the rather vague suggestion that a mutation could link the internal thought to the preexisting A-P system. Therefore, the only aspect Chomsky deals with is actually the evolution of Merge, leaving aside how this operation became integrated with the preexisting systems.

As regards the neurobiological foundations of language, works like Berwick et al. (2013) or Berwick and Chomsky (2016) clearly show that the only brain components taken into consideration when accounting for language and language evolution are cortical areas and circuits, like Broca and Wernicke's areas and several cortical (dorsal and ventral) pathways involved in language. Undoubtedly, the importance of cortical areas and circuits cannot be denied, but Chomsky completely ignores subcortical areas and the circuits between subcortical and cortical areas. In fact, the emphasis on cortical areas has recently been criticized by Tremblay and Dick (2016), who assert that the classical Broca-Wernicke model "is based on an outdated brain anatomy" (Tremblay and Dick 2016, p. 66), for it just leaves aside subcortical areas and connections that are crucial for language.

Conclusion

Chomsky has argued that language is part of the human biological endowment. If so, it had to evolve biologically. This entry has summarized the main points of the Chomskyan approach on language phylogeny. Although this scholar has further developed his approach since the advent of the Minimalist Program, his core ideas have remained unchanged since the 1960s: (1) language could not have evolved from animal

communication, (2) language is not an adaptation for communication, (3) FL evolved suddenly, not gradually, which means that (4) FL did not evolve by natural selection, which is a mere filter, rather than the factor responsible for complex design.

Cross-References

- [Broca's and Wernicke's Areas](#)
- [Field of Linguistics, The](#)
- [Linguistic Evolution](#)
- [Modern Theories of Language](#)
- [Nativism](#)
- [Natural Selection](#)
- [Neurobiology of Language](#)
- [Universal Grammar](#)

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Nomadic Foragers

► [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)

Nomological Networks of Evidence

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Synonyms

[Lakatosian philosophy of science](#)

Definition

Schematic overviews of empirical evidence from a wide variety of sources and disciplines in order to evaluate the validity of hypothesized evolutionary psychological adaptations

Introduction

Although evolutionary psychology has been a fruitful and progressive research paradigm (e.g., Cosmides and Tooby [2013](#)), many scientists remain skeptical about the value of an evolutionary approach to unravel the origins of the human mind. For example, in the domain of language

evolution, Hauser and colleagues (2014) have argued that there is still a lack of empirical evidence in favor of the hypothesis that language is an adaptation. They argue that there is no fossil evidence related to language evolution in our ancestors, that the communicative skills of non-human animals are uninformative because these skills do not resemble human language, that our understanding of the genetics of language is poor, and that models of language evolution are based on unfounded assumptions. They conclude that this lack of relevant data and models makes it impossible – now and in the future – to unravel the origin of language.

Although these criticisms are valuable and welcome, they do not result in progressive science. Contrarily, they may prevent researchers from pursuing a research program on the origins of language (or other human cognitive traits, to which these criticisms equally apply), leaving many important research questions open. The question is how scientists build an evolutionary research program that is fruitful and progressive, but in addition takes these criticisms into account. Schmitt and Pilcher (2004) have proposed that evolutionary psychologists need to build a nomological network of evidence around their hypothesized adaptations in order to create a progressive research program.

Nomological Networks of Evidence

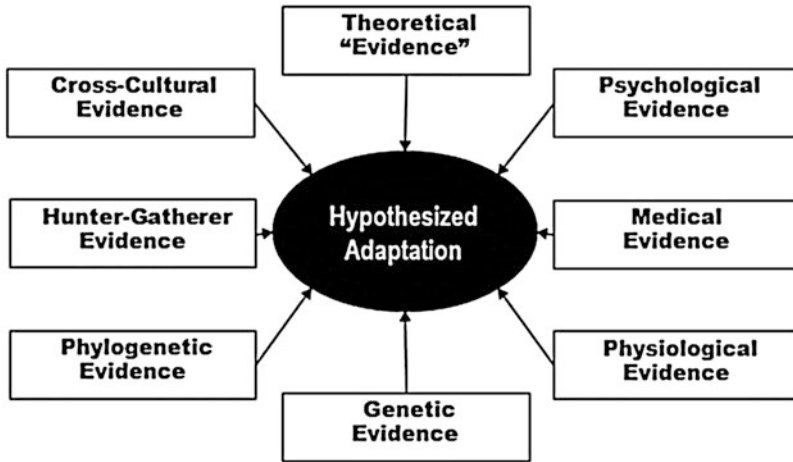
Ketelaar and Ellis (2000) argued that science most often does not follow the path as proposed by the famous philosopher of science Popper, i.e., the path of trying to falsify a hypothesis. In most cases, scientists proceed in a Lakatosian way: they assume that a particular theory is right (the “hard core”) and try to establish evidence in favor of this theory by confirming derived hypotheses (the “protective belt”). Only when the protective belt falls short will scientists abandon or change the hard core.

For example, the theory that language is an adaptation, evolved by natural selection, is the hard core for scientists working on language evolution. They derive hypotheses from this theory

and test those empirically, and, up until today, the results of these empirical studies are consistent with the hard core. There is no reason to abandon this hard core, because there is enough evidence in favor of it, despite the lack of some particular pieces of evidence as pointed out by Hauser and colleagues (2014).

The following question is how we decide whether there is enough evidence in favor of our hard core or not. Schmitt and Pilcher (2004) have proposed that evolutionary psychologists need to develop a nomological network of evidence around their hypothesized adaptation. A schematic example of such a network is presented in Fig. 1.

The oval in the middle of the network represents the hypothesized adaptation, for example, language. The eight boxes represent the protective belt around the hypothesized adaptation. First of all, it is important to start with a well-developed theory why language is assumed to be an adaptation. For example, Williams’ (1966) criteria for identifying an adaptation might be helpful here. Other possibilities are theories about specific selection pressures, cost-benefit analyses, game theoretical simulations, and computer modelling. Second, we may gather psychological evidence in favor of our theory, for example, by performing behavioral tests and surveys or by designing experiments to test for developmental or cognitive specificity. Third, we may gather medical evidence, for example, by collecting the results of fertility and fecundity studies or studies on physical and mental health, including psychiatric disorders. Fourth, we may gather physiological evidence, for example, by doing research on the association between brain and behavior or neurotransmitters and hormones. Fifth, we may gather genetic evidence, for example, by doing twin studies or genotype-phenotype mapping. Sixth, we may gather phylogenetic evidence, for example, by conducting animal studies, comparative research, or paleontological studies. Seventh, we may gather hunter-gatherer evidence, by using studies from cultural anthropology, ethnographic studies, and human behavioral ecology. Eighth, we may gather cross-cultural evidence, for example, by performing research on human universals and ecology-dependent variability.



Nomological Networks of Evidence, Fig. 1 Example of a nomological network of evidence (Adapted from Schmitt and Pilcher (2004) and Ploeger and van der Hoort (2015))

Following Schmitt and Pilcher (2004), nomological networks of evidence may vary along two dimensions: evidentiary breadth and evidentiary depth. In a nomological network such as the one presented in Fig. 1, the breadth may vary from one (only evidence from a single discipline) to eight (evidence from all eight different disciplines). Having filled in only one box of evidence would be considered a minimal level of evidentiary breadth, two or three boxes a moderate level, four or five boxes an extensive level, and six or more boxes an exemplary level of evidentiary breadth.

The evidentiary depth of evidence includes the total number of supportive research findings, but most of all the quality of the studies. So empirical studies with, for example, multiple modes of measurement, a control group and a minimal sampling bias count up more on the dimension of evidentiary depth than, for example, a single self-report survey with only western university students.

Examples of Adaptations for Which a Nomological Network of Evidence Has Been Build

According to Schmitt and Pilcher (2004), the following hypothesized adaptations have reached the level of at least moderate evidentiary breadth and depth:

- *Pregnancy sickness* (both exemplary breadth and depth)
- *Incest avoidance* (exemplary breadth and extensive depth)
- *Men's short-term desire for sexual variety* (extensive breadth and moderate depth)
- *Easily learned fear of snakes* (both moderate breadth and depth)

Schmitt (2014) added to this list:

- *Women's short-term desire for men with "good genes"* (both extensive breadth and depth)
- *Men's long-term desire for women that show fertility related cues, such as youth and physical attractiveness* (both extensive breadth and depth)
- *Women's long-term desire for men that show the ability and willingness to invest in herself and her offspring* (both extensive breadth and depth)

Honing and Ploeger (2012) added to this list:

- *Musicality* (both extensive breadth and depth)

Ploeger and van der Hoort (2015) added to this list:

- *Face recognition* (both extensive breadth and depth)

Conclusion

To conclude, building a nomological network of evidence around a hypothesized adaptation is a fruitful and progressive way to show the existence of a psychological adaptation. Instead of focusing on data that are not available (e.g., Hauser et al. 2014), this approach promotes an optimistic view on the broad range of possibilities to collect empirical evidence, and it motivates researchers to look beyond their traditional ways to gather data and to start interdisciplinary and cross-cultural collaborations.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Controversies](#)
- [Falsifiability](#)

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Non-adaptationist View of Music

- [Music as Auditory Cheesecake](#)

Nonadaptive Hypotheses

- [Spandrels](#)

Non-aptation

- [By-Products of Adaptations](#)
- [Evolutionary By-Products](#)

Nonassociative Learning

- [Habituation](#)

Non-associative Learning

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Synonyms

[Non-declarative learning](#); [Procedural learning](#)

Definition

Non-associative learning is the simplest yet fundamental form of learning that does not require

stimuli association or pairing. This means that animal species alter their response upon exposure to a single event or stimulus. Behavioral responses become attenuated or augmented after repeated or prolonged stimulation. Habituation and sensitization constitute the two major forms of non-associative learning and are opposite to each other in terms of the elicited responses upon continual presentation of the stimulus. In contrary, associative learning involves the presence of paired stimuli in order for change to occur. Naturally, it is suggested that non-associative learning likely came first in the hierarchy of evolutionary history, and then associative learning followed (Pereira and van der Kooy 2013).

Introduction

The mechanisms underlying non-associative learning have received great attention from the earliest of times and continue to puzzle researchers up to this day. There is a growing body of literature exploring these processes and how they influence human behavior and learning, yet there is a vast bulk of delineations to be made. Nevertheless, the current state of literature provided fundamental information that can be further utilized by future investigations. Theoretical frameworks can be applied in context of any field seeking for explanations of human complexity and pathology development.

Theoretical Background

Several influential non-associative theories have historically been proposed (Thompson 2009). These theories constitute the early work of Sokolov (1960) and Wagner's (1979) revision of Konorski's Gnostic Hypothesis and Grove's and Thompson (dual-process theory; 1970).

Sokolov (1960) was the first to propose a comprehensive theory of habituation (*Stimulus-Model Comparator Theory*). In short, Sokolov's theory stated that when a stimulus appears repetitively, the brain cortex forms a model (or a memory) of the stimulus. Each incoming stimuli was

compared to the model, and if the incoming stimulus matched the model, responding was inhibited otherwise an orienting response was evoked. The exertion of inhibition was thought to yield habituation; thus habituation was perceived as purely inhibitory. Even though Sokolov's work intrigued a great bulk of follow-up investigations in habituation in the humankind, the theory was not applicable to animals who do not possess a cortex, contrary to the dual-process theory.

Another comparator theory constitutes the work of Konorski on habituation which shared many similarities with Sokolov's theory. Wagner (1979) revisited Konorski's ideas, but he concentrated on the roles of short-term memory and associative mechanisms. A stimulus is carried by afferent/sensory neurons toward a memory system, the Gnostic assembly, and to the arousal system. With repeated stimulation, a gnostic unit is formed, which is a near-accurate neuronal model or memory of the stimulus. As this model develops, it increasingly activates an inhibitory system that inhibits the arousal system, consequently causing habituation. Wagner added a process mediator, an associative network where contextual cues have to pass through in order to excite stimulus models in memory and a process of transient memory (short-term memory). In short, what these scientists advocated is that long-term habituation requires the storage of a stimulus in long-term memory and that it is associated with external cues for retrieval from long-term memory.

Finally, the most prominent non-associative learning theory was composed by Grove and Thompson (1970). Neurophysiological concepts were combined with concerns of human ethology and evolution to create the *dual-process* theory. This theory advocated that repeated stimulation would produce two independent processes that could both be active at the same time: decreased responsiveness (habituation) or increased responsiveness (sensitization). The authors believed that the two processes take place in different parts of the nervous system. Scientists believed that habituation took place in the so-called S-R system (reflex arc) that controls reflexes, whereas sensitization occurred in the "state system" which is

responsible for the level of readiness to respond. The state system requires arousal to become activated, while the S-R system is activated with the presentation of an eliciting stimulus. Further, habituation is thought to be stimulus-specific and involves learning, in contrast to sensitization which is not highly specific and does not require learning. However both are of relative permanence; they are expected to decay at the absence of stimulation. Contrary to Sokolov's model, the *dual-process* theory does not propose an inhibitory system.

Nevertheless, all these studies of cellular processes which facilitate learning and memory, which were mostly held in invertebrates, most certainly add to the understanding of the underlying physiological processes of learning in the majority of living animal organisms, but mechanisms such as habituation and sensitization are far more complex and necessitate further exploration.

Habituation

Habituation constitutes an essential process of behavioral adaptation, as it assists in filtering out the large amounts of information received from the surrounding environment that are likely irrelevant or less important, thus shifting attention to more important to survival or urgent information. The latter gives an evolutionary advantage as a result. Habituation can be defined as a decline in behavioral responsiveness to the continual presentation of a stimulus. While there is a strong response initially, the strength of the response reduces and eventually disappears with repeated stimulation. The reduction in responsiveness is neither the result of motor (muscle) fatigue nor sensory adaptation; however it is likely to be disrupted when another strong stimulus appears (dishabituation). Other factors influencing habituation include stimulus repetition, interstimulus interval, and stimulus intensity. These factors are determinant of whether short-term or long-term habituation will occur. Short-term habituation is characterized by rapid stimulations with short intervals in between; habituation is observed early; however it is short-lived as soon as stimulation ceases. On the other hand, long-term habituation is characterized by fewer stimulations over

longer periods; habituation is slower but its effects are long-lived as recovery is delayed.

In addition, in earlier writings habituation was thought to only have short-term effects (Hinde 1970); however existing literature has demonstrated that its effects can last long. Apart from its simplicity, habituation is thought to be ubiquitous; it is both a highly automated yet learned phenomenon occurring in the central nervous system (CNS) of all animal species, ranging from single-celled protozoans to humans (Thompson 2009), with studies demonstrating its occurrence in plants as well (Gagliano et al. (2014).

Thompson and Spencer (1966) presented a list of nine parameters of habituation, shared by all species. A tenth parameter was added to the list of behavioral characteristics of habituation by Rankin and colleagues (2009) and is presented as follows:

1. Given that a particular stimulus produces a response, repetitive applications of that stimulus will result in a reduced response (habituation). Most of the times, the decrease is a negative exponential function of the number of stimulus presentations.
2. If the stimulus is withheld, the response tends to recover over time ("spontaneous recovery").
3. After a multiple series of stimulus repetitions and spontaneous recoveries, habituation becomes more rapid ("potentiation of habituation").
4. The more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation.
5. The weaker the stimulus, the more rapid and/or more pronounced is habituation. Stronger stimulation might yield no significant habituation.
6. The effects of habituation training may proceed beyond the zero or asymptotic (minimum level of response) response level.
7. Habituation of response to a stimulus displays stimulus generalization to other stimuli.
8. Presentation of another strong stimulus results in disruption or recovery of the habituated response ("dishabituation").

9. After repeated application of the dishabituation stimulus, the amount of dishabituation produced habituates ("habituation of dishabituation").
10. Some stimulus repetition protocols may result in properties of the response decrement that last hours, days, or weeks. This persistence of aspects of habituation is termed long-term habituation.

Importantly the aforementioned characteristics of habituation were observed and collected through numerous studies on a variety of species; therefore they do not imply particular theories or inferences. They could be considered however as a detailed definition of habituation.

Several scientists who have studied the process of habituation provide valuable information regarding the underlying mechanisms of habituation and associated processes, demonstrating at the same time its complexity (Thompson 2009). It has been noted that the occurrence of habituation is determined and/or influenced by variations in interstimulus interval and by the organisms' ability to generalize and discriminate between the presented stimuli. Additionally, spontaneous recovery is another process thought to influence habituation's maintenance. All these concepts are further analyzed in the sections that follow.

Interstimulus Interval

The concept of interstimulus interval is frequently encountered within processes of non-associative learning, specifically habituation and sensitization (Petrinovich 1984).

Interstimulus interval can be defined as the time interval between the end of one stimulus presentation and the onset of another stimulus presentation. Interstimulus interval experiments were extensive under the work of Davis (1970) on habituation of the acoustic startle response in the rat. Generally, through Davis's series of experimental studies, it was demonstrated that the length of interstimulus interval, as well as variability (regularity), determines habituation in animals. The author compared the responsiveness of two groups of rats to a 50-msec, 120-db tone of 4000 Hz during pretest, training, and posttest

periods. During both the pretest and the posttest periods, both groups of subjects received 300 tone exposures at intervals of 2, 4, 8, and 16 s, the intervals being scheduled in an irregular order. During the training period, both groups received 1000 tone exposures; however the interval between stimuli was 16 s in one group and 2 s in the other group. Among other findings, greater reduction in responsiveness was observed in the group who received stimulation every 2 s.

In the second experiment, startle responsiveness was lower following training with regular as opposed to variable interstimulus intervals. Simply put when interstimulus interval is longer and constant, habituation is greater. Also (Davis 1970) reported quite an interesting finding; when rats were tested at 1 min or 24 h later with a variety of interstimulus intervals, habituation was greater for the group that was trained on the 16-s interstimulus interval schedule suggesting thus that short-term and long-term habituation processes may be distinguishable on the basis of the presentation and the intervals between stimuli. Specifically, it was demonstrated that short interstimulus intervals were involved in the progression of short-term habituation, while long interstimulus intervals were involved in the promotion of long-term habituation. Also, apart from the fact that high-frequency stimulation leads to more rapid response decrement, it results in faster spontaneous recovery as well Leaton (1976).

Similarly, Groves and Thompson (1970) noted that increased frequency should lead to increased habituation in the "S-R" pathway, but in the "state" pathway, it would lead to increased sensitization. All the aforementioned experiments considered together are indicative of the importance of interstimulus interval making it obvious that it can have a major effect on learning; it may delay or improve learning. Lastly, the organism's ability to determine the interval and duration of sensory stimulation is central to sensory processing; therefore impairments in that domain are likely to interfere with the process of learning.

Variations in the time between the presentations of one stimulus to the next have a determinant effect on the forms of non-associative learning; habituation and sensitization and the

occurrence of long-term and short-term habituation are dependent upon the length of interstimulus intervals (Leaton 1976). Further manipulation of interstimulus intervals will provide valuable information regarding disruptions in learning processes or even suggestions as to how to enhance learning.

Stimulus Generalization and Discrimination

Similarly, the concepts of stimulus generalization and stimulus discrimination are encountered within the context of associative and non-associative learning.

Stimulus generalization refers to a set of stimuli sharing similar properties with the original stimulus that provoked a response. *Stimulus discrimination* is the ability of an organism to respond only to the original stimulus and not to other similar stimuli. Both concepts are inherent mechanisms in the processes of associative and non-associative learning, and for both processes to take place, it is essential that a stimulus model should be stored in memory in order for comparisons with new stimuli to take place.

To begin with, generalization occurs when an organism produces the same response to different stimuli. Stimuli who exhibit analogous properties to the original are more likely to provoke a response: habituation. There could be variations in terms of the level of pitch, brightness, loudness, and so on; however if these variations deviate significantly from the properties of the original stimulus, generalization will not occur; hence it is more likely that habituation will not occur either (Teyler et al. 1984). Stimulus generalization of habituation can only be determined when a second habituation series is done with the use of a novel stimulus. With a comparison of the rates of habituation between the original and the novel stimulus, the amount of generalization will be demonstrated. More rapid habituation in the second series would be indicative of generalization, whereas similar rates between the two series would be indicative of a lack of generalization (Petrinovich and Widaman 1984).

On the other hand, if stimuli are rather dissimilar than similar, the opposite process of stimulus generalization, the so-called stimulus

discrimination will be activated. In *stimulus discrimination* the organism shows the ability to differentiate between similar stimuli and only to respond to a specific stimulus; hence the organism responds differently to the two stimuli. *Stimulus discrimination* is particularly important in the process of habituation, as it can be used to dismiss sensory adaptation and fatigue as an alternative explanation of the occurrence of habituation. Further, *dishabituation* is indicative of the ability to discriminate, therefore ending habituation (Thompson and Spencer 1966). It is important to clarify however that dishabituation occurs due to repetitive stimulation of a completely irrelevant stimulus and should not be thought of as the same as stimulus discrimination.

Finally, stimulus generalization is useful because it allows for learning to take place quickly in new situations that share similarities with past experiences and promotes the transfer of skills into similar situations thus saving time and effort. Stimulus discrimination offers assistance in a practical level as well.

Stimulus generalization and discrimination are crucial processes in learning, and both are of paramount importance to adaptation. Clearly any organism that lacks such abilities would have minimal chances of survival. There are well-known experiments undergone within the concept of conditioning (Pavlov's and Watson's experiments) that illustrate the stimulus generalization and the stimulus discrimination concepts more elaborately.

Spontaneous Recovery

Spontaneous recovery refers to the recovery of a habituated response. When a sequence of stimulus presentations is interrupted, the object at hand will return to its earlier stage and the behavior will recover over time. In a series of experiments undergone by Rankin and Broster (1992) on the nematode *Caenorhabditis elegans*, mechanical stimuli were delivered at four interstimulus intervals (2, 10, 30, and 60 s) in order to investigate the effect of interstimulus intervals in the development and maintenance of habituation. Results indicated that recovery from habituation was dependent on some factors. One of these factors

is the length of interstimulus intervals; it was observed that recovery from habituation was faster when short interstimulus intervals were applied rather than longer interstimulus intervals. That is, long-term habituation prevents recovery. Also, the rate of recovery varied according to which response level each subject exhibited on the habituation curve. The recovery of animals on the lowest response level appeared to be determined by interstimulus interval and not by the further addition of stimuli. Interstimulus interval recovery rates did not differ even though the number of stimuli the worms received was significantly bigger (60 Vs 10) in the second group. In short what was evident is that the frequency of stimulation during habituation training was the one to determine the rate of spontaneous recovery.

Moreover, Rankin and colleagues (2009), upon revisiting the characteristics of habituation originally described by Thompson and Spencer (1966), revised a point concerning spontaneous recovery. It is described in the characteristics that when a sequence of stimulus presentations is interrupted, the object at hand will return to its earlier stage and the behavior will recover over time. Rankin and colleagues (2009) revised this characteristic by adding that sometimes the response recovers completely, but sometimes it recovers only partially depending on the time frame that recovery was examined.

Further, when stimulus presentations and spontaneous recoveries are given repeatedly, the phenomenon of *potentiation of habituation* is observed. Here, the decrement in response that follows spontaneous recovery (i.e., habituation) becomes gradually more rapid with each application of spontaneous recovery. Moreover, the process of spontaneous recovery can be disrupted with the presentation of a new, strong stimulus (sensitization).

Lastly, it is crucial to note the importance of spontaneous recovery; it is the second way, with stimulus discrimination being the first way, to distinguish sensory adaptation and fatigue from habituation. With regard to learning, this process demonstrates that even though a response might disappear, it does not necessarily mean that it has

been withdrawn from memory and that it will never reoccur.

Experiments on the lowest living forms illustrate the phenomenon of spontaneous recovery, and those indicate that spontaneous recovery is highly determined by the frequency of stimulus presentation. These experiments provided a special insight on the underlying processes of habituation.

Having analyzed the underlying processes of habituation (interstimulus interval, stimulus generalization and discrimination, and spontaneous recovery), it has been demonstrated that they are interconnected and influence the occurrence and maintenance of habituation. Habituation is one of the simplest forms of non-associative learning; it is found in all animal species, and it is a highly complex yet essential process of the evolution of learning. On the section that follows, the opposite process of habituation, called sensitization, will be explored along with its underlying processes and types.

Sensitization

Sensitization is a non-associative learning process that leads to increased responsiveness to a stimulus and is considered complementary to habituation. The increase in responsiveness or behavior is due to the exposure of a strong, most commonly noxious stimulus that is causing pain. It is therefore logical to infer that sensitization's adaptive value is high, as it protects an organism from predators and other potential dangers (Eisenstein et al. 2001). During sensitization an organism will only respond to high- or strong-intensity stimulus rather to low-intensity stimulus as it happens in the case of habituation. This constitutes a fundamental difference between the two processes, but it is not limited to that; sensitization can occur without necessarily having continual stimulation (a single, strong stimulus can sensitize the organism). Further, sensitization has a limited time course and relatively short-term effects; however that depends on the intensity of the stimulus (Eisenstein et al. 2001).

Petrinovich (1984), based on the "dual-process" theory, outlines eight basic assumptions in relation to sensitization and are listed as follows:

1. Sensitization occurs in the “state” system and not in the “S-R” system.
2. During habituation training, sensitization appears initially but then deteriorates.
3. The amount and duration of sensitization are directly related to stimulus intensity. At high intensities, sensitization is directly related to stimulus intensity and frequency. However, at low intensities there may be little or no sensitization.
4. Sensitization decays spontaneously as soon as the sensitizing stimulus has stopped.
5. Repeated presentations of a sensitization stimulus result in gradual reduction of sensitization.
6. Response sensitization displays generalization.
7. Dishabituation is considered as an instance of sensitization.
8. Temporal conditioning of sensitization may occur.

Sensitization has not received as much attention as habituation did; however especially enlightening was the study of the neural basis of sensitization, in laboratory settings, with the mollusk *Aplysia* and the work of Kandel, as well as with the work of others on *kindling* and *long-term potentiation*.

Long-Term Potentiation

Sensitization and long-term potentiation are similar processes but differ in their site of application. Sensitization occurs in specific pathways (state), while long-term potentiation occurs in synapses. However, the process of sensitization involves the mechanism of long-term potentiation.

Long-term potentiation of synaptic transmission is a major mechanism for investigating learning and memory in the synaptic level. Long-term potentiation is found in several regions of the brain, with the most prominent being the hippocampus thus its obvious involvement in the neural basis of some forms of memory (Cooke and Bliss 2006). It is a form of synaptic plasticity and is defined as a persistent increase in synaptic strength following high-frequency stimulation of a chemical synapse. High-frequency stimulation causes an increase in the efficiency of synaptic

transmission, therefore enhancing the efficiency of the signal. For the induction of long-term potentiation, the activation of excitatory receptors is required (Cooke and Bliss 2006). Bliss and Collingridge (1993) reported on the properties of long-term potentiation that differentiates it from other forms of synaptic plasticity: *input specificity* (it does not spread to other synapses), *associativity* (when a weak input of a single pathway is insufficient for the induction of long-term potentiation, simultaneous strong stimulation of another pathway can potentiate the weak stimulation), and *cooperativity* (apart from strong stimulation, long-term potentiation can be induced by the cooperation of many yet weaker stimulations). Since long-term potentiation occurs when a neuron shows an increased excitability over time due to a repeated behavior, and the heightened synaptic transmission leads to the amplification of responses (i.e., pain), its involvement with the process of sensitization is high.

While the long-term potentiation of synapses in localized cell tissues seems to provide an elegant substrate for learning and memory, researchers turn their attention into experiments with the whole living organism (in vivo experiments). Morris et al. (1986) provided for the first time some data from in vivo experiments in which it was indicated that long-term potentiation was essential for the construction of memories. Using rats, Morris and colleagues were able to examine their spatial memory by inserting an N-methyl-D-aspartate (NMDA) blocker drug in their hippocampus, a brain structure implicated in learning. NMDA is a glutamate receptor and an ion channel protein within nerve cells, and it is responsible for the control of synaptic plasticity and memory function. Initially rats were trained to swim in a water maze, in order to find the platform hidden beneath (in the center and the sides of the pool) and escape. As soon as the rats were able to locate the platform, they were separated in two groups. One group constituted the control group, while rats of the second group received the drug that blocks NMDA. Then both groups of rats were exposed to the water maze spatial memory task with the rats of the control group being successful in locating the platform and escaping the pool.

Contrary, the second group of rats exhibited impaired performance, as long-term potentiation could not be induced indicating thus damage in the hippocampus. This series of experiments indicated that long-term potentiation is implicated in learning and memory processes.

Finally, dysfunctions in the process of long-term potentiation are thought to be implicated in mood disorders (Post 2007) and neurodegenerative diseases as Parkinson's (Cooke and Bliss 2006). Long-term potentiation is a fundamental process in a cellular level with implications in the process of learning.

Kindling

Both sensitization and kindling are forms of learning occurring in some parts of the nervous system, and the common characteristic they exhibit is the increase in responsiveness. Kindling can be thought of as a specific type of sensitization.

Kindling became known to the scientific world in the late 1960s through the published work of Goddard (1967) on the neurobiology of learning and later after the application of Goddard's model on the study of epilepsy. Goddard (1967) ran a series of experiments on rats where, in order to investigate their abilities to learn tasks, he administered electrical stimulations in various regions of their brains. With daily repetition of the electrical stimuli, the rats began seizing. That response, however, was astonishing, as the administered stimuli were too low to induce seizures. Even more surprising was the final observation of the rats having unprovoked seizures, that is, seizing without stimulation. In sensitization repetitive stimulation produces a full response. A full response can be elicited even with lower stimulus levels than the original stimulus. It appears that a decrease in the threshold of excitability develops leading to the automatic occurrence of the response, without external stimulation. Eventually, with further repetition, the response occurs spontaneously, in the absence of any stimulus, demonstrating thus the phenomenon of kindling. The changes caused by kindling seem to be long-term, but they are not permanent.

Kindling is universal across species (from frogs to humans) and throughout the brain, and it

was the first neuroplasticity phenomenon suggested to give information on memory processes. At a first glance, it may seem awkward to imply that epileptic seizure activity could be interconnected learning; yet, it is plausible that the diverse mechanisms constituting kindling and learning interconnect and share several common mechanisms. In effect, under this conceptualization, both kindling and learning can potentially be considered as phenomena of neuroplasticity. However when kindling was compared to long-term potentiation as to which neuroplasticity phenomenon was more appropriate for modelling memory processes, long-term potentiation appeared to dominate, mostly because long-term potentiation was observed under normal neural activity contrary to kindling that was observed under seizures.

Further, kindling constitutes the model for the development or recurrence of medical (epilepsy) and psychiatric illnesses such as addictions and mood disorders (Post 2007). Goddard's model has been referred to as the "kindling model for epileptogenesis" as it is the most frequently used model for temporal lobe epilepsy with complex partial seizures. It is used by scientists to study the effects of repeated seizures on the brain. What was demonstrated in the experiments with rats, the same applies for humans; a seizure may raise the possibility that more seizures will occur since repeated stimulation "lowers the threshold" and paves the way for seizures to reoccur (Dennison et al. 1995; Racine 1978). In an attempt to better understand the occurrence of epileptic seizures, many scientists including Racine (1978) have turned their attention to the underlying mechanisms of kindling, in neurotransmitter systems and intracellular mechanisms, as well as genes.

Goddard's experiments suggest that the processes underlying kindling and learning interconnect and possibly have similar underlying mechanisms. Kindling is of particular importance in disorders where recurrence is involved: in addictions (relapse) and mood disorders (recurrent episodes), but its underlying mechanisms are yet to be refined by empirical investigations.

Drug Sensitization

Drug sensitization is a process frequently encountered in the literature of the field of addictions and pharmacology, and it is an essential process toward the understanding of drug action and use.

Drug sensitization is a type of sensitization, and it refers to an increase in drug effect upon continual exposure to a drug in the organism, which was previously exposed to the drug. With repeated drug administration, gradual and incremental neuroadaptations are produced, that make animals hypersensitive to the specific drugs. Even though users or abusers will be keeping the same dosage levels, drug effects will be greater and greater; therefore they would become intoxicated even in small doses. Using repeatedly a drug but with some pauses in between causes greater sensitization compared to taking a single dosage or even taking repetitively the drug. Moreover, sensitization is promoted if periods of use are alternated with periods of abstinence. When a person who is sensitized let's say to cocaine and abstains from use for some time, he/she is at risk of fatal overdosing at reuse (Steketee and Kalivas 2011; Robinson and Berridge 2008). Known addictive substances, where sensitization has been observed in, are cocaine, amphetamines, morphine, nicotine, and even alcohol; importantly not all drugs are subject to sensitization, mostly stimulants. In addition, the selected route of drug administration as sensitization is influenced by the speed or the time it takes for a drug to reach the brain. Sensitization in the case of drugs is long lasting with its effects on behavior and cognition lasting for years even with abstinence; however factors such as the time lapse between dosages, the choice of drug, the age and sex of the user, and genetics influence the strength of sensitization. Due to these factors, vulnerability to sensitization differs between individuals (Steketee and Kalivas 2011). That provides an insight into the long-asked question of why some users become addicts while others do not get addicted.

The sensitization of behavior and other psychological or psychomotor functions implies neural sensitization. Drugs seem to alter or reorganize neural systems and neurotransmitters, and even though causal relationships are yet to be

established, neuroadaptations seem permanent. The permanency of changes in neurotransmitter circuits have crucial implications on the matter of cravings and relapse. Of special importance is the sensitization of the mesolimbic pathway of the mesotelencephalic dopamine system. Since dopamine is responsible for the motivation to go after pleasure and happiness and fulfill our “wants,” drugs come to jeopardize this process by making dopamine hyper-reactive, consequently increasing the prominence of drug cues, hence the intense cravings (Robinson and Berridge 2008). In the matter of cravings and relapse, kindling is thought to be implicated. The aforementioned comprise the “incentive sensitization” theory of addiction developed by Berridge and Robinson (1998) and is noteworthy of further reading.

Drug sensitization is a complex process influencing drug users in a cellular level and in consequence in a behavioral level.

Having analyzed some types of sensitization and the underlying mechanisms, it has become evident that sensitization is of significant value as it has helped organisms to adapt in potentially dangerous situations and evolve. While sensitization's underlying mechanisms are still under investigation, research thus far has been able to provide data for the better understanding of learning phenomena and the appearance and treatment of pathologies. A significant contribution to the study of sensitization constitutes the work of Kandel with the mollusk *Aplysia*, described in detail in the sections that follow.

Eric Kandel

Eric Kandel is a well-known neuroscientist for his research on memory and learning for which he shared the Nobel Prize in Physiology or Medicine in 2000. His breakthrough came through his pioneering work with *Aplysia*, which provided a wealth of information regarding non-associative learning and its forms.

Kandel was born in Vienna on 7 November, 1929. His mother, named Charlotte Zimels, was born in 1897 in Kolomea, which was at that time part of the Austro-Hungarian Empire. Kolomea is now a part of Ukraine and has been renamed Kolomyia. She came from a well-educated

Jewish middle-class family. His father, Hermann Kandel, was born in 1898 in Olesko, a small town then part of the Austro-Hungarian Empire, now part of Ukraine, and was brought up in a poor family. At the beginning of World War I, his parents moved to Vienna, Austria, where they met and married in 1923. By the time they had their first child, Lewis, his father, was the owner of a toy store. Eric Kandel was born 5 years later. They lived in a middle-class neighborhood, in a small apartment, and as both of his parents were occupied with the toy business, a housekeeper was looking after the children. Approximately when Eric Kandel was 10 years of age, he moved to Brooklyn, in the United States, with his family. His parents had to work hard to bring it along, and adjusting was difficult. However Kandel speaks highly of his parents for their determination and hard work to raise him and his brother; they were not only successful in their jobs but managed to support both of their children on their chosen paths.

After their relocation, Kandel had already involved in an elementary school, of which he graduated in 1944. After he graduated from the Yeshivah of Flatbush Elementary School, he went to Erasmus Hall High School, a local public high school in Brooklyn. By then, Kandel was already fluent in several languages, including Hebrew and Greek, and was involved in several activities including, among others, soccer, music, and writing. He then applied to Harvard College and managed to be admitted and earn a scholarship as well. He majored in European history and literature. After some interactions he had with some psychoanalysts, he became more interested in understanding the human mind, and that was determinant in furthering his studies by becoming a medical doctor. During his studies he became increasingly interested in the biological basis of the mind. By 1956, he graduated from the New York University School of Medicine. He then joined a research team in Harry Grundfest's laboratory at Columbia University where they were dealing with research on a cellular basis. Grundfest was then a pioneer on the use of oscilloscope to measure action potential conduction velocity on the axons of neurons. After the

intracellular recordings of electrical activity of the cerebral cortex of vertebrates done with Grundfest's team, Kandel's interest was directed to the study of the electrophysiology of neurons of invertebrates, influenced by the work of Kuffler. The shift occurred from Kandel's belief that the mechanisms of memory storage were possibly well-preserved in phylogeny and that the cellular analysis of learning in low-level animals would reveal universal mechanisms that were also found in more complex organisms. His belief was validated shortly after The Official Website of the Nobel Prize (2018).

Around 1957, when Kandel joined the Laboratory of Neurophysiology at the US National Institutes of Health, he focused on the study of the hippocampus. William Beecher Scoville and Brenda Milner were working at that time on the hippocampus and noticed that after hippocampus excision, a patient no longer had the ability to form new memories. Kandel was greatly intrigued yet puzzled by the findings of these researchers and begun examining the electrophysiology of hippocampal pyramidal neurons. At that time he was working with Alden Spencer, another great neuroscientist who was also interested in the biology of learning and memory. They managed to provide electrophysiological evidence for the formation of action potential in the dendrites of hippocampal neurons, not only in the axons as it was previously suggested. These dendritic action potentials were the trigger for firing at the axon hillock. They also recorded spontaneous pacemaker-like activity in these neurons; they noticed that firing took the form of bursts of spikes. Lastly their research outcomes indicated the presence of strong recurrent inhibitory processes in the hippocampus resulting in prolonged inhibition. Kandel began to realize that memory storage must rely on modifications in the synaptic connections between neurons and that the complexity of the connections found in the hippocampus made it an inappropriate system for the study of synapses. That's when he selected the simplest animal model for his study, *Aplysia* (sea slug). He conducted electrophysiological analyses of the synaptic changes involved in learning and

memory storage and provided breakthrough information that seemed to correspond to the simplest forms of learning (habituation, sensitization). It is noteworthy to mention that during the years 1963–1965, Kandel begun his academic career as an instructor in the Department of Psychiatry. In 1965, he accepted the position of Associate Professor at New York University, and it was during that time period that he started working with *Aplysia*. By 1974 he became a Professor, in the department of Physiology and Psychiatry, in Columbia University and later the Director of the Center for Neurobiology and Behavior. Around 1984 he became a Senior Investigator at Howard Hughes Medical Institute at Columbia University (The Official Website of the Nobel Prize 2018).

On a personal level, Kandel has already met and married (1956) the French, Denise Bystryin. They had two children, Paul and Minouche, and are currently proud parents and grandparents as well, as all family members have thrived. His wife is a professor in the Department of Psychiatry and in the School of Public Health at Columbia University and has worked extensively on the field of addictions and drug abuse in adolescents. For nearly 40 years, they have been living in the Bronx, and together they enjoy a variety of hobbies and interests: visual arts, classical music, and opera, and they passionately collect art and antiques (The Official Website of the Nobel Prize 2018).

Kandel's experimental research work has been extensive and greatly influential for the scientific world. He counts numerous publications that have not only been enlightening but also determinant for the course of future research. For his excellence and achievements, he has received more than 20 awards among them the Lester N. Hofheimer Prize for Research of the American Psychiatric Association (1977), the American Association of Medical Colleges Award for Distinguished Research in the Biomedical Sciences (1985), the Gairdner International Award of Canada for Outstanding Achievement in Medical Science (1987), the Harvey Prize in Israel (1993), the Wolf Prize in Biology and Medicine (1999), and the Nobel Prize in Physiology or Medicine

(2000) which he shared with two other colleagues. He has also received honorary degrees from nine universities, three of which are European (The Official Website of the Nobel Prize 2018). His awards indicate worldwide recognition of his work.

Eric Kandel's life story and academic path, apart from being motivational, have left the academic society with solid grounds to work on and has provided breakthrough information adding up to the understanding of how the human mind works. His work focused on the physiological basis of learning under which he explored short- and long-term memory, neural circuits, and synaptic processes through experiments with *Aplysia*.

Aplysia

Aplysia became known to the scientific world through the pioneer work of Kandel which provided a wealth of information regarding non-associative learning and its forms (habituation and sensitization).

Aplysia is a species of sea snail, commonly referred to as sea hares because of their posterior tentacles that protrude like ears do in hares. Among low-level organisms, *Aplysia* has become a fitting model for studies of how neurons and neural circuits regulate behaviors. What attracts scientists into studying them is their simplicity and the huge size of their neurons, which are easy to manipulate and work with. Also, *Aplysia* exhibits abilities on learning establishing thus its appropriateness for applying cell biological approaches to the investigation of learning and memory mechanisms (Moroz 2011).

Of particular interest to Kandel and colleagues was the gill and siphon withdrawal defensive reflex of *Aplysia*. *Aplysia* has a mantle cavity on its dorsal surface that protects the gill. The gill lies beneath the mantle shelf, which terminates at the back of the cavity in a fleshy, funnel-shaped spout, the siphon, which contracts to eject water from the gill. A two-component reflex is triggered when stimulation is applied to the siphon (mantle shelf) causing both the siphon and the gill to be retracted, protecting the organism from potential threat. These two components consist of two involuntary reflexes, the so-called siphon

withdrawal reflex (SWR) and the gill withdrawal reflex (GWR). The gill and siphon withdrawal reflex (GSWR) is mediated by distinct neuronal pathways, enabling scientists to record activities on the synaptic and neuronal level and to directly link synaptic plasticity to behavioral plasticity. The neural circuits of these reflexes are comprised of monosynaptic connections from sensory neurons to motor neurons, as well as polysynaptic connections containing excitatory and inhibitory interneurons. Kandel's and associates' work on this invertebrate animal regarding the cellular mechanisms underlying habituation and sensitization observed that while light siphon stimulation would naturally cause retraction, repetitive siphon stimulation produced short-term habituation lasting for a few hours. On the other hand, long-term habituation was demonstrated by repeating multiple training sessions across several days. A single habituation training session consisting of regular trials separated with a time interval of 30 s produced typical reductions in response of the siphon withdrawal reflex. The replication of these training sessions once per day for 4 days produced a progressive buildup of habituation within each session. Habituation preservation was tested the next day and weeks 1 and 3 after training, and when compared to group, the experimental group exhibited greater habituation. The gill withdrawal component of the reflex was also tested for long-term habituation with the same procedures showing that siphon training produces long-term habituation in both components of the reflex (Castellucci et al. 1970). Furthermore, in another series of experiments, noxious shocks at the rear produced an increase in the siphon withdrawal reflex and in the gill withdrawal reflex. A single shock increased the reflex for 15 min to an hour. After repeated shocks sensitization seemed to last up to several weeks. Four brief noxious electrical shocks were applied daily for 4 consecutive days. Sensitization retaining was measured again at day 1 and weeks 1 and 3. Also greater sensitization was observed with the addition of more shocks and by spacing the training sessions (two daily shocks within 10 days) (Pinsker et al. 1973).

Generally it was indicated that short-term and long-term habituation results from homosynaptic depression of excitatory neurotransmission, while heterosynaptic facilitation of the sensorimotor connection caused sensitization. Habituation was not brought up by changes in the activity of sensory or motor neurons. Specifically sensory neurons release less neurotransmitter because of changes in calcium channels regulating neurotransmitter release, leading to the functional inactivation of the synapse in the long term. Nevertheless habituation still occurs after direct electrical stimulation of the motor nerve, avoiding that way the sensory receptors. This is essential as it reveals that the reduction in response is not due to sensory adaptation. Furthermore, motor fatigue is also eliminated by showing that direct stimulation of the motor neurons can still provoke a normal reaction after habituation has occurred. Carew (1984) provides for more detailed description of the work with *Aplysia*.

Conclusion

Research on non-associative learning and its forms indicates that it precedes associative learning in the evolutionary sequence. Associative forms of learning arise from the neural mechanisms used in non-associative learning, making non-associative learning an inevitable component of associative learning.

Habituation and sensitization with their neural substrates are complex forms of plasticity which have been implied as a causal or maintaining mechanism in a wide range of pathologies. Understanding their impact on behavior necessitates constant consideration and evaluation of multiple output measures through the application of the different theories of non-associative learning. Even though mechanisms were studied in the simplest type of existence, they were proven to be remarkably rich and complex. In depth investigations of these processes provide new understandings for the better management and possible prevention of pathologies through the development of effective therapeutic interventions, both pharmacological and psychological.

Cross-References

- [Aplysia](#)
- [Associative Learning](#)
- [Classical Conditioning](#)
- [Eric Kandel](#)
- [Habituation](#)
- [Operant Conditioning](#)
- [Sensitization](#)

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Non-biological Parents

- [Stepparents](#)

Nonconforming Sexuality

- [Paraphilia](#)

Noncooperation

- [Prisoner's Dilemma Outcomes](#)

Noncooperative

- [Defection](#)

Non-declarative Learning

- [Non-associative Learning](#)

Nonexploitative Partners

- [Specific Friendships](#)

Nonfiction

- [No Two Alike](#)

Non-fiction

- [Nurture Assumption, The](#)

Non-fluent Aphasia

- [Broca's and Wernicke's Aphasia](#)

Nonhuman Intelligence

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Synonyms

[Animal intelligence](#); [Cognitive complexity](#); [Intellectual capacity](#); [Intellectual functioning](#); [IQ](#)

Definition

Intelligence in animals can be defined in terms of problem-solving ability, both acquisition to solve problems and the ability to generalize what is learned to novel situations. Intelligence may also be measured in terms of behavioral flexibility, which is comprised of inhibition and innovation components and which concerns adaptability to new and changing environments.

Introduction

Two main categories of inquiry derive from the central topic of nonhuman intelligence. The first category entails questions regarding species differences. Are some species of animals considered more intelligent than others? If so, which species are considered most intelligent? These questions should lead one to ponder whether it is fair to compare different species on the same tasks. The second category entails individual differences. Do individuals within a species vary in their intelligence, and how can these abilities be assessed? It is unknown to what extent nonhumans show the same variability in intelligence that humans do. Variability within a species likely depends upon the environment that it inhabits (Sol 2009). One might not expect intellectual functioning to vary within members of short-lived species whose environments are relatively constant and whose behavior is largely innate or canalized. On the other hand, one would expect variability in intellectual functioning in species that live in constantly changing environments, who face foraging challenges (Byrne 1997), and who live in complex social groups (Jolly 1966; Humphrey 1976). Humans of course live in arguably the most complex social groups and have been the most inventive in terms of extracting sustenance from the environment. They exhibit significant variability in intelligence, ranging from intellectually challenged to extremely gifted. But before delving into possible answers to these broad questions with nonhumans, it is important to define intelligence with regard to nonhumans and to consider how it might be assessed.

Intelligence is difficult to define, even in humans. Most popular tests of the nebulous construct, such as the Stanford-Binet (Roid 2003) and Wechsler Intelligence Scales (Groth-Marnat et al. 2000), focus on assessing processing speed, working memory, analogical reasoning, verbal reasoning, quantitative skills, and other basic reasoning abilities. These tests are based on the notion of a general factor, “*g*” that is innate, stable, and reflects an individual’s capacity to acquire and to apply knowledge (Spearman

1961). Spearman’s view also revolved around the notion that, whereas there may be different types of intelligence, they are all correlated. Other more liberal views of intelligence have been proposed such as Sternberg’s triarchic theory of intelligence that focuses on practical, creative, and analytic components that comprise what he described as “successful intelligence” (Sternberg 2012). In this view, success of the individual in real-world situations, including interpersonal and intrapersonal knowledge, are weighed just as heavily as the kinds of abstract abilities represented in most standard intelligence tests. Gardner’s theory of multiple intelligences (Gardner 2011) stressed the independence of multiple intelligence components even more heavily; this theory encompasses the view that intelligence is not a unitary construct but instead could be measured as multiple traits or abilities, such as body kinesthetic sense, musical ability, and so on, that are not necessarily correlated. That is, a person could be exceptionally skilled as a musician but not have superior verbal or quantitative reasoning skills and vice versa.

Gardner’s conception of intelligence highlights the potential for confusion between particular skills and general abilities. Should a talented musician or artist be considered intelligent in the same manner that a chemical engineer, mathematician, or neurosurgeon would be considered to be intelligent? Should distinctions be made between different types of skills with some qualifying as “intelligence” and others being considered more akin to “talents”? Both intelligence and talent seem to rely on heredity to a large extent, although talent is more likely to be honed by experience and specific training, and is always highly specified compared to the notion of *g*. Studies of the activation of brain areas during different types of tasks seem to support the notion of separate intelligences to some degree as they show that different areas are activated during different tasks (Hampshire et al. 2012). These recent studies emphasize the fact that the study of human intelligence is really still in its infancy despite being the target of much controversy and interest for many decades.

Researchers have not made explicit attempts to apply the same definitions to the question of animal intelligence, and, given that the topic is controversial in humans, it is clear that determining the intelligence of nonhuman organisms is not a straightforward task. However, there may be stronger agreement with a definition of intelligence that focuses on a general capacity to acquire and apply knowledge among researchers studying cognition in nonhumans. For example, working memory is commonly viewed as an essential component of animal intelligence (Carruthers 2014). Other recent approaches have focused on behavioral flexibility, which is defined as an animal's ability to generate novel behaviors to solve problems and includes components such as inhibition along with innovation (Lefebvre et al. 2013). Whereas innovation represents the likelihood of attempting multiple novel solutions to solve problems, inhibition reflects the ability to withhold responses that may have been beneficial in the past but that no longer prove useful. Individuals may vary in the extent to which they show innovation and inhibition with each component predicting success on different aspects of problem-solving. Behavioral flexibility can be exhibited in traditional tasks, such as reversal of learning set (Roberts 1996), which requires an animal to reverse an earlier learned discrimination, learning the new task more quickly than the original task. Reversal learning, thus, clearly depends upon inhibition to a great degree.

Generalization of knowledge or concepts to novel contexts and stimuli is also a hallmark of intelligence. However, given the recent findings from neuroscience suggesting that different brain regions underlie different tasks designed to assess intelligence in humans (Hampshire et al. 2012), it seems plausible that different types of intelligence may have arisen in response to different environmental inputs for species that face unique adaptive problems. That is, the types of adaptive problems faced by, for example, insects, cetaceans, corvids, primates, and carnivores are likely to be quite distinct, leading to separate sets of adaptive skills and abilities. This fact may call into question the notion of one generalized intelligence factor that could be assessed across taxa.

What Makes An Animal Intelligent?

Along with the challenge of defining what is meant by intelligence in general, research into animal intelligence is plagued by a humancentric bias, whereby researchers often conduct “holy grail” type searches for the presence of abilities in animals that have been deemed potentially unique to humans (Vonk and Povinelli 2006). That is, humans have placed themselves atop an imaginary pedestal based on their capacity for language, tool use, imitation, culture, and theory of mind, thus setting the stage for researchers to commit careers to finding evidence for similar capacities in various other species, sometimes with little regard for whether it makes evolutionary sense for the particular species studied to exhibit the behavior in question. It is tacitly assumed that such evidence would allow for a pronouncement of “intelligence” in the species shown to exhibit it. This kind of anthropocentric focus detracts from a more ethological focus on the ability of each species to adapt to its own unique environment. Do factors that define human intelligence necessarily make sense when defining what makes an animal intelligent? For example, would an animal that spent its day calculating abstract mathematical theorems be more intelligent than the bird that was able to build a sturdy nest out of sight of predators and find food for its hungry nestlings? So, intelligence can be defined as a pattern of behavior that serves the individual in enhancing its reproductive fitness and survival or it can be defined as a suite of cognitive capacities that allow it to perform feats considered to be complex, sophisticated, and generally human-like. Different definitions may be applied within the two broad categories of inquiry identified earlier. That is, researchers may focus on the former when examining individual differences but focus on the latter when performing comparisons between species.

The study of animal intelligence has its origins in Darwin's early fascination with the continuity of the mind across species (Darwin 1898)—a topic that was fervently explored by his successor, Romanes (1882). To what some would argue to be the detriment of unbiased study, the

Aristotelian *scala naturae* or Great Chain of Being was at least partly responsible for the widespread idea of the hierarchy of intelligence, with humans poised atop the scale and species more closely related to humans conceived of as superior in cognitive function to those more distantly removed. Later theorists emphasized the fact that evolution should more accurately be represented as a branching bush than a ladder, with concepts such as parallelism and convergent evolution emphasizing the importance of both similarities and differences in cognitive function in animals both distantly and closely related (Novick et al. 2011). That is, distantly related species may evolve similar solutions to similar or different adaptive problems faced in their evolutionary history. Common selective pressures, such as adapting to live in large social groups (Jolly 1966; Humphrey 1976), may lead to the evolution of traits such as theory of mind and analogical reasoning in animals as diverse as corvids, cetaceans, canines, and primates.

In more recent years, researchers from various fields, such as biology, anthropology, ethology, and psychology, have all been intrigued by the question of nonhuman intelligence and have studied it from vastly distinct theoretical perspectives. Researchers studying animals in the field (e.g., Anthropologists, Primatologists, Ethologists, Biologists, Behavioral Ecologists) have tended to focus on questions of how animals adapt to and solve ecological problems, whereas those studying animals in captivity (e.g., psychologists, biologists, zoologists) have focused on questions of generalized versus compartmentalized learning.

Assessments in Nonhumans

Questions of adaptation concern the way in which an animal's sensory and motor capacities, along with cognitive capacities such as attention, memory, and decision-making, contribute to the organism's everyday functioning. That is, a more successful or skilled individual is better able to find food, mates, maintain and defend a territory, and raise young to reproductive age compared to a

less skilled individual. Organisms will vary in the extent to which particular skills are necessary based on the particular set of environmental and social pressures that they face in their natural environment. For example, birds that nest in colonies must develop the ability to recognize individuals, including their young, whereas birds that are solitary may not need to learn to discriminate their parents from other birds and their young from other nestlings. Birds that cache or store their food over harsh winter months might be expected to exhibit superior spatial memory skills relative to noncaching bird species that live in climates where their preferred food is abundant year-round (Shettleworth 1998). Still, within these species, individuals might vary regarding the extent to which they excel at even species-typical behaviors, although it is likely that the skills most pertinent for survival are hard-wired and instinctive and would not reflect a great deal of flexibility. Thus, flexibility in behavior and the capacity to adapt to novel or changing environments seem a good candidate for something akin to intelligence in nonhumans.

However, most scientists would be unlikely to consider insects more intelligent than mammals that live in more restricted environments (e.g., polar bears, lemurs) despite the fact that insects have likely adapted to the largest number of environments in the largest quantities. There is conjecture that insects will be left to roam the earth long after humans have been wiped off the planet. If the ability of an organism to transform the environment to suit its own needs was considered the ultimate form of adaptation, then surely humans would rise to the top of the list. However, this definition might appear anthropocentric as it targets a specifically human cognitive adaptation. Whereas many species of insect exist in a multitude of habitats, only humans have proven capable of building temperature and climate controlled structures or traveling through air, ground, sea, and outer space. Furthermore, scientists might consider the Giant Panda (*Ailuropoda melanoleuca*) not to be "intelligent" given that it has not adapted well to varied environments and is restricted to an extremely limited diet. Given their dependence on a diet of bamboo, large territories,

and a very limited reproductive window, pandas are critically endangered. It is often suggested that their appeal to humans and human concerted efforts to conserve this species is the only reason that they are not currently extinct. But cognitive tests conducted with pandas have shown cognitive skills, such as memory, categorization, and problem-solving (Perdue et al. 2009). Thus, the two different approaches to measuring intelligence are likely to lead to different conclusions regarding species differences and perhaps individual differences as well.

Psychologists and anthropologists tend to focus on questions of what it is that makes human cognition unique, which may lead to biases in the way intelligence is defined. These scientists typically define intelligence as a general capacity for acquiring information and generalizing learned rules and associations to novel events or experiences. This capacity allows an animal to behave appropriately in the absence of specific learning or associations to each independent event or stimulus. Thus transfer tests, which test the generalization of a learned rule to novel stimuli that share some feature with trained stimuli, have become the acid test of intelligent behavior for comparative psychologists. Transfer based on perceptual features is considered less cognitively sophisticated than transfer based on function or conceptual category or rule. The inference of underlying causal mechanisms that would allow the generalization of a rule or outcome is considered one of the hallmarks of intelligent behavior in humans, and researchers have sought to demonstrate this capacity in many other species with mixed interpretations of the results (Vonk and Povinelli 2006).

The application of these types of tests often necessitate that animals in the laboratory are presented with objects that are foreign to them, thus eliminating the role of associative learning and tightly canalized responding, in order to test their inferences about the function or purpose of the object. Removing the organism from contexts for which responses might be instinctive or canalized allows it to demonstrate insight and inferential reasoning. Researchers can thus disentangle

intelligent behavior from hard-wired and automatic responding (Vonk and Povinelli 2010). Although a behavior can lead to success in natural environments, it may not be considered intelligent by traditional definitions if the animal need not engage in any conscious processing or decision-making to achieve the result. For example, many reflexes are highly adaptive, such as blinking when a foreign object approaches an organism's eye, but the blink reflex is not traditionally concerned intelligent because it occurs without any conscious effort or reflection and is generally present from birth.

Furthermore, similar responses can often occur in different organisms through quite distinct underlying processes. Humans, for example, might comfort an individual who is crying because they understand and empathize with emotions of sadness, which are expressed in a crying counterpart. A feline companion might similarly appear to comfort a crying human by climbing into his/her lap and licking his/her face. But these behaviors might result from the cat's desire for the salt in human tears or recognition of cues that the human is amenable to petting it. Tests of cognitive processes in nonhumans are challenged by the difficulty in unearthing the underlying process for behaviors that, on the surface, seem to align with behaviors that arise from complex cognitive processes in humans – the only species whose underlying thought process is easily accessible to researchers (Vonk and Povinelli 2006). Recognition of such challenges has been identified as “failure of arguments by analogy.” One simply cannot conclude that apparently similar behaviors arise from the same underlying cognitive mechanisms.

Because of the importance of underlying processes or mechanisms that support behavior, psychologists have also examined the process of learning. Animals are assessed for their capacity to learn through the use of learning sets and reversal learning. These tests determine whether organisms apply rules or strategies for learning that transcend the particular stimuli they have learned to associate or discriminate. For example, with categorization tasks, researchers aim to

demonstrate that an animal can extract the features of particular stimuli and form an overarching representation of the category to which they belong. They may use two-alternative forced-choice tests in which animals are reinforced for responding to items from one category and not reinforced for responding to stimuli from another category (Hollaway 1969). In addition to learning which category of items is deemed “correct” and will be rewarded when responded to, the animals might also learn the general task, that is, to extract a correct category or set of features that will result in reward and that will define all pairs of stimuli presented within the task. If researchers reverse the reward associations, the animals should learn more quickly to select the previously unrewarded stimuli in comparison to how long it took them to acquire the initial discrimination, thus demonstrating reversal learning, which reflects the application of a general rule for how to solve such tasks.

Researchers also commonly make use of matching-to-sample (MTS) tests where animals are presented with a sample stimulus and required to select the stimulus from among a set of at least two comparison stimuli that best matches the sample (Harlow 1943). Stimuli can be matched based on perceptual features, such as shape or color, or can be matched on more abstract constructs, such as sameness or differences between sets of exemplars (Bovet and Vauclair 2001; Vonk 2003). Sameness and difference can also be defined in terms of identity or similar features but also in terms of same or different relations, which can be social (Bovet and Washburn 2003) or functional in nature (Bovet and Vauclair 2001) as well. The greater the distance from reliance on perceptual features to the inference of underlying unobservable traits, the more abstract the rule, and, the more abstract the rule, the more intelligent the process is deemed to be (Vonk and Povinelli 2006).

In considering whether a species exhibits intelligent behavior or thinking, it is necessary to find only one member of the species that exhibits such a behavior, thus making it possible to test for capacities with small sample sizes in lab settings.

However, then researchers must confront the risk that animals raised or housed in captivity may not be good representatives of their species, and null results cannot be taken to implicate the failure of a species to have a particular capacity (Vonk and Povinelli 2011). Laboratory studies can, on the other hand, be better candidates for exploring individual differences as individuals can easily be tracked and tested in multiple tasks. Surprisingly, few researchers have attempted to track individual differences in cognitive capacities in members of the same species to identify the possibility of a generalized intelligence factor, such as *g*. Vonk and Povinelli (2011) examined the findings from decades of research with a small group of chimpanzees to determine whether acquisition, transfer, retention, and overall performance were correlated across tasks in different domains (tasks that tapped into social versus physical reasoning processes) and found some evidence for individual differences as well as consistency within individuals across measures. Herrmann and colleagues conducted a large scale study of over 100 chimpanzees and over 100 human children and found evidence for a shared general intelligence that reflected physical reasoning, but a uniquely human social intelligence factor (Herrmann et al. 2010). Currently, evidence for general intelligence factors in other species is lacking. Although progress is underway, it is hampered by the difficulties in obtaining large samples of members of the same species and the time investment required to perform dozens of tests. Furthermore, the issue of comparability of tasks across species that have evolved distinct perceptual and morphological features poses a particular problem for interpreting species differences and for being certain that researchers have tapped into the appropriate tests for assessing individual differences within a species. For example, it would not be appropriate to test species like moles (family *Talpidae*) in a visual discrimination paradigm given their poor eyesight and then conclude that a failure to learn the discrimination reflected poor conceptual ability or that there was no variability in conceptual ability within the species. Imagine if humans were assessed for

intelligence based on their ability to echolocate or to navigate using geomagnetic cues.

Brain size has often been implicated as a measure of intelligence in animals, either with or without accounting for body size. MacLean and colleagues (2014) conducted a large scale project to investigate self-control in representatives of 35 different species. They discovered a relationship between absolute brain volume and task performance. Controlling for body mass resulted in a weaker relationship between brain volume and task performance. These investigators also found that, within primates at least, dietary breadth rather than social group size was a stronger predictor of performance. Recently, researchers have examined problem-solving in a large number of carnivores and indicated a similar relationship between brain size and problem-solving success (Benson-Amram et al. 2016), this time when controlling for overall body mass. However, similar to the MacLean et al. (2014) study, there was little evidence for the importance of social group size or complexity. In future, it will be important to investigate the role of dietary factors in predicting success of carnivores in solving foraging related extraction problems and to present animals with more than a single task to assess ability (Vonk 2016). Sol and colleagues (Sol et al. 2005) have examined the role of brain size in a more naturalistic assessment of intelligence. They found that larger-brained birds adapted more successfully to novel environments compared to smaller brained birds after examining a database of over 600 introduction events. These authors were also able to show that the enhanced success of larger-brained birds could be attributed to increased innovation, which as indicated earlier is one component of behavioral flexibility.

Factors Contributing to the Evolution of Intelligence

The research summarized above highlights the factors that researchers have attended to when determining which species might be considered most intelligent. Two main hypotheses have been

advanced, the social intelligence hypothesis (Jolly 1966; Humphreys 1976) and the technical intelligence hypothesis (Byrne 1997). As labeled, the social intelligence hypothesis focuses on the size and complexity of social groups in predicting cognitive ability, with larger, more complex groups predicting more advanced cognition. The technical intelligence hypothesis instead focuses on challenges faced in foraging, such as the need to find and remember the location of patchily distributed and sporadic food sources and the ability to extract food from defenses. Researchers have sometimes postulated that social complexity might predict skills in specific social domains, whereas foraging challenges may predict physical problem-solving skills, although researchers have also made the case that each factor might promote domain general intelligence. More recently Sol (2009) has revisited the cognitive buffer hypothesis, which encapsulates the notion of environmental variability in general in predicting larger brains, which, in turn, appears related to some aspects of intelligence, as described above. The theory proposes that larger brains result in an increased capacity for gathering, storing, and synthesizing information, related to the idea of domain general intelligence, and that this increased capacity may lead to a broader range of new or modified behaviors, which increase the probability of survival in complex and constantly changing environments.

Convergent Evolution

More recent approaches have steered researchers away from the rigid assumptions of the past, which clung to the notion that animals advanced in cognitive complexity along a continuum leading to humans atop the imagined evolutionary ladder. Animals were assumed to exhibit greater cognitive complexity and thus intelligence, with shorter phylogenetic distance from humans. However, researchers have unearthed great behavioral diversity and cognitive complexity in animals ranging from honeybees to corvids and cetaceans. Indeed corvids and canines have surpassed great apes in some kinds of cognitive tasks, supporting the point

that it is important to focus on tasks for which animals might be expected to face adaptive problems in their evolutionary history. Given the increased breadth in species of study within comparative psychology in the last decade, researchers more readily embrace the notion of convergent evolution – animals that are distant relatives and who have adapted to quite discrepant ecological niches might still evolve comparable cognitive abilities to solve problems within their own niche.

Conclusion

In the end, it appears necessary to consider how well animals have adapted to solve the particular kinds of adaptive problems that they will face, with a particular emphasis on flexibility to change, which will increase the odds of both individual and species survival, when determining which species and which individuals are most intelligent. As Vonk and Povinelli (2010) noted, a starting point is to observe an animal's natural behaviors in the wild, but the laboratory may be more carefully controlled to rigorously test hypotheses about how and why specific behaviors may have evolved and how they might be altered under specific conditions. Researchers can then distinguish between behaviors that are plastic and those that are rigid and canalized. Flexible and malleable behaviors will allow an individual to adjust and adapt to an ever-changing, unpredictable environment, which is argued here to be the true mark of intelligence (Sol 2009). By combining field and laboratory approaches knowledge of what animals actually do in their natural environments can be used to further probe what they are ultimately capable of learning when taken out of those comfort zones.

Cross-References

- [Concept Formation](#)
- [Learning](#)
- [Nonhuman Primates](#)
- [Same-Different Categorization](#)

- [Theory of Mind](#)
- [Unobservability Hypothesis, The \(Vonk and Povinelli, 2006\)](#)

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Non-human Leadership

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Synonyms

[Collective action](#); [Flocking](#); [Leading](#); [Swarming](#)

Definitions

Leadership occurs when an individual or subset of individuals within a social group or aggregation has a disproportional influence on the behavioral outcomes of conspecific members within the group regardless of how this effect is achieved.

Introduction

Leadership is ubiquitous within animal societies, occurring when one individual or subset of individuals, the leader(s), exert(s) a disproportional influence on the behaviors of others (followers; Smith et al. 2016). Leaders emerge in non-human groups or aggregations of animals regardless of the how this influence is achieved (Smith et al. 2016). Within non-human animals, most research has focused on collective movements during groups travel (e.g., Reynolds 1987; Boinski and Garber 2000). More recently, the concept of leadership has been extended to also explain collection action within the domains of foraging, conflict resolution and between-group conflicts (Smith et al. 2016). Here, I synthesize what is known about leadership in non-human societies by providing a brief overview of seminal work within domain of group travel and recent developments in this domain of leadership, discussing the ways that leadership permeates into other domains within non-human animals, and then comparing these patterns of leadership in non-human societies to those in human societies.

Collective Movements During Group Travel

Collective movement occurs when two or more individuals maintain spatial proximity while travelling together to a new location (Petit and Bon 2010). Pioneering studies on collective behavior set out to understand the basic rules explaining coordinated, large-scale patterns of movements by aggregations comprised of hundreds of insects, fishes, starlings or hooved migratory animals traveling together in a seemingly coordinated manner. Whereas it was once hypothesized that such aggregations might rely upon a centralized authority, seminal work by Reynolds (1987) proposed an alternative model suggesting that instead complex patterns of swarming, shoaling (schooling), flocking and herding behaviors may be explained by patterns of localized leadership and followership. This parsimonious mathematical model relies upon the following simple rules by which individuals adjust their movements based on information gathered from their local neighbors' movements and positions. For example, flocks of birds coordinate collective movements by following three simple rules: velocity matching, flock centering and collision avoidance. Flocking therefore emerges when an individual bird (follower): (i) matches the speed of nearby flockmates (localized leaders), (ii) maintains close spatial proximity to nearby flockmates, and (iii) avoids colliding into nearby flockmates. These powerful insights have prompted a large body of research confirming these patterns and this model is the most-widely accepted view of how leaders emerge in these contexts. For example, desert locust nymphs (*Schistocerca gregaria*) also rapidly transition from disordered movements to form large swarms comprised of coordinated movement patterns during marching behavior (Buhl et al. 2006).

Extensive studies documenting how and why non-human vertebrates travel in groups suggests that socially-complex mammals also follow simple rules (Boinski and Garber 2000). That is, as in other gregarious animals, social carnivores, birds, and primates living in closed social groups

also seem to adhere to simple rules to navigate group travel from one location to another; these group-living animals often accrue individual fitness benefits, such as reduced predation risk, group acquisition of shared resources and group defense against neighboring social groups from following leaders (Boinski and Garber 2000).

Group travel that requires all group-mates to choose between collectively moving to a new location and remaining together in their current location represents a 'consensus decision' (Conradt and Roper 2005). Because travel decisions often have fitness consequences for all participants, leaders may emerge to resolve consensus decisions that impose conflicts of interest (consensus costs) requiring all members to settle on a single direction, timing or destination of group travel (Conradt and Roper 2005). For groups in which only a few individuals have pertinent information, such as about the location of a food source or a migratory route, patterns of leadership often emerge even in the absence of signaling by leaders, without any active coercion on the part of the leader, and even when followers lack information about which individuals possess information (Couzin et al. 2005; Smith et al. 2015). Importantly, Couzin et al. (2005) showed that only a small proportion of the informed individuals (leaders) are required to lead during collective movement.

Although pioneering models of leadership based on short-term studies in non-human mammalian societies indicated that one or few dominant individuals may consistently occupy leadership roles, more recent work drawing from long-term studies based on recognizable individuals suggests that leadership roles tend to be flexible and shared within groups (Smith et al. 2015). Specifically, Smith et al. (2015) joined others in showing that attribute-based leadership is the most common pattern among mammals, with an individual's motivational state, sex, relative social status and age class at the time of group travel profoundly shaping his/her leadership (or followership) during the group travel (Smith et al. 2015).

Collective Acquisition and Distribution of Food

Although most research to date focuses on leadership during collection movements, leaders also emerge within the acquisition and distribution of foraging (Smith et al. 2016). Most notably, leaders emerge in gregarious species, such as in the social carnivores (carnivorans) when individuals cooperate to acquire energy-rich food items that they would be unable to capture or locate on their own. For example, female elders within groups of African lions, Verreaux's safakas (*Protopithecus verreauxi*), killer whales (*Orcinus orca*) and spotted hyenas all typically enlist more followers than do young, naïve individuals in collective foraging presumably because they possess the greatest local knowledge (reviewed by Smith et al. 2015). Orcas are noteworthy because post-reproductive (menopausal) female resident killer whales lead collective foraging efforts in search of salmon, particularly when food is in low abundance and to promote the survival of their sons who lack local ecological knowledge (Brent et al. 2015). Following the acquisition of food, leadership roles vary widely across taxa. For example, even within carnivorans, lionesses equally distribute food within their egalitarian societies whereas high-ranking adult females control priority of access to food resources within their female-dominated societies (see: Smith et al. 2016). Nonetheless, as in the context of collective movements, leadership also appears to be attribute-based. That is, to the extent to which it has been investigated, those individuals with local knowledge tend to emerge as leaders within the foraging domain.

Leadership During Within and Between-Group Conflicts

Lastly, as in human societies, non-human leaders often emerge to settle or win conflicts within or between groups (de Waal 1990). Because conflict is potentially costly to individuals, natural selection favors mechanisms, such as the emergence of leaders, that mediate conflict resolution within

groups (de Waal 1990). Moreover, because the outcomes of between-group competition often have large fitness consequences for members of a social groups, such as determining the size of a territory containing key resources, natural selection often favors those individuals who join forces during between-group conflicts. Both during conflict resolution within groups and during warfare associated with between-group conflicts, leadership roles in mammalian societies are much more concentrated (less shared) and leaders exert more power than in contexts when conspecifics are simply traveling from one area to another or engaged in collective foraging (Smith et al. 2016). Future studies are needed to elucidate whether this pattern extends to other taxa beyond mammals.

Within these conflict domains, leadership roles also tend to be occupied consistently by one or a few dominant individuals who exert the most power within their societies. For example, among non-human primates, high-ranking apes and monkeys most often take the lead in resolving within-group conflicts through reconciliation; dominants often lead in consoling their former opponents after fights (De Waal 1990). Within spotted hyenas (*Crocuta crocuta*), high-ranking adult females also emerge as leaders, tending to emerge most often at front lines of between-group conflicts and to intervene most often during within-group conflicts (Smith et al. 2016).

Conclusions

Overall, despite the enormous range of taxa across the animal kingdom for which individuals emerge as leaders, common rules appear to explain patterns of leadership within and across leadership domains. Together, studies of collective movements indicate that attribute-based leadership is often shared within groups or aggregations and that patterns on non-human leadership is best explained by simple rules requiring localized decision-making and only a few informed leaders. Thus, despite the enormous disparities in the scales over which animals collectively move and the vast differences in presumed cognitive

abilities across taxa, similar rules appear to explain collective movement decisions, suggesting that general principles may underlie leadership during collective movements.

Although most research to date has focused on leadership during collective movements, leaders emerge across multiple domains within loose aggregations of animals and close social groups ranging from insect swarms to pods of killer whales. Leaders disproportionally influence the collective behaviors of others, determining the direction of travel, foraging decisions and the outcomes of conflicts within and between groups. Synthesis of current data suggests that leadership roles are particularly flexible during group movements, as dictated by current state variables such as age and reproductive status, but that leadership roles are least shared and leaders wield the most power in contexts involving resource acquisition. Indeed, preliminary data suggest that this is also the case for small-scale societies of humans as well (Smith et al. 2016). Moving forward, workers should draw upon the comparative framework of Smith et al. (2016) to evaluate the generalizability of these patterns of human and non-human leadership across the domains of group movement, food acquisition, within-group conflict mediation and between-group interactions. Within an evolutionary framework, workers studying leadership more broadly will gain new insights about the importance and universal principles of leadership that together give rise to collective behaviors in gregarious species of animals, including ourselves.

Cross-References

- ▶ [Coalition Leaders](#)
- ▶ [Coalitional Hunting](#)
- ▶ [Coalitional Relationships](#)
- ▶ [Cooperation](#)
- ▶ [Cooperation Among Fishes](#)
- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Cooperation in Social Carnivores](#)
- ▶ [Cooperation in Social Insects](#)

- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Cooperative Foraging](#)
- ▶ [Cooperative Hunting](#)
- ▶ [Division of Labor](#)
- ▶ [Dominance Hierarchy](#)
- ▶ [Evolution of Human Sociality, The](#)
- ▶ [Non-human Primates](#)
- ▶ [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)

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Nonhuman Primate Tool Use

- ▶ [Primate Tool Use](#)

Nonhuman Primates

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Synonyms

[Comparative developmental psychology](#)

Definition

Study of the physical, cognitive, and behavioral development of nonhuman primates, particularly in reference to human cognition and development. Emphasis is placed on understanding similarities and differences between all primate species to better understand the evolutionary origins of these species and their abilities.

Introduction

The study of nonhuman primates (NHP) can include a wide variety of species that vary greatly in their similarity to human development and psychology. Primates include (in order of ascending genetic relation to humans): New World Monkeys, such as capuchin and howler monkeys, Old World Monkeys, such as macaques and baboons, and the Great Apes (GA), orangutans, gorillas, bonobos, chimpanzees, and humans. This entry will focus on Great Apes as they are genetically closest to humans and used most frequently for understanding the evolutionary origins of human physical and psychological development. Nonhuman Great Apes share many physical and psychological traits with humans and human development but also display substantial differences from human abilities. One might be inclined to assume that in the cases of differences with humans, the other Great Apes are deficient in ability. However, in many cases, specific abilities of nonhuman Great Apes exceed human capabilities, suggesting some interesting

differences in selection pressures. The study of nonhuman primates is a critical piece of the puzzle in understanding evolution as a process in general, primate cognition and behavior, and human psychology and development.

Physical and Brain Development

GA prenatal timing is remarkably similar to humans. For example, the prenatal gestation period for humans is 266 days on average, with chimpanzee (~235 days), gorilla (~250 days), and orangutan (~260 days) (Martin 1981). However, once born, the timing and stages of physical development differ greatly. Chimpanzees move through three distinct developmental life stages, infancy, juvenile, and adulthood. The end of infancy is marked by the cessation of breastfeeding, around 4–5 years, and the end of juvenility is marked by sexual maturity, around the age of 12. Humans, however, have five distinct developmental life stages, Infancy, Childhood, Juvenile, Adolescence, and Adulthood. Human infancy, like that of chimpanzees, is marked by the cessation of breastfeeding. Childhood is a human specific life stage marked by a period where solid foods are eaten but self-sufficiency and survival are impossible. Juvenility in humans is the period between the emergence of adult teeth and the onset of puberty. Adolescence is the period between the onset of puberty and the achievement of consistent reproduction, occurring around the age of 15–16 years and marks the beginning of biological adulthood.

Most noteworthy about comparisons of human physical development with NHPs is the addition of Childhood and Adolescence as life stages and delaying the onset consistent reproductive viability. Given that the process of natural selection ultimately depends upon an individual reproducing, it seems odd that natural selection would favor delaying the ability to create offspring until such a comparably old age. A number of factors likely led to this evolutionary change in human development: humans have large heads relative to body size thus requiring developmentally premature birth when compared to other species, the social complexity

of human life requires time for learning, observation, and cognitive development, and allowing humans time to flexibly incorporate environmental cues into their life-history strategies (Bjorklund and Ellis 2014).

Humans and NHPs have very similar brains; specifically, they have a much larger prefrontal cortex than other animals, the area of the brain responsible for complex cognitions such as critical thinking, cognitive flexibility, and decision-making. Humans have, on average, the largest brains relative to body size among the GAs. However, many believe that increases in white matter connectivity (neural connection within the prefrontal cortex and those emanating to other brain areas) are chiefly responsible for the advanced cognitive feats performed by GAs and even more so the complex abilities that often set humans apart from other GAs (Smaers 2013).

Memory

Human memory is conceptualized as a flexible system with numerous interacting components that serve multiple purposes. Long-term memory (LTM) is the storage and retrieval system that allows for remembering information over the course of hours to years; this is typically what is meant when the term “memory” is used in everyday life. Short-term memory (STM) helps remember information in short time frames on the order of seconds or minutes. Finally, working memory (WM) is the system that keeps information activated in the thoughtful and aware mind in order to perform actions with that information; when you are currently “thinking about something” that information is said to be active in working memory. Decades of research have found these systems to be interactive while also cognitively and neurologically separate. Information that humans can remember can further be divided by its qualities or content. Episodic memories are those that retain a personal quality from a specific time and place (e.g., I remember my grandmother making me homemade donuts on my 9th birthday), whereas semantic memories are simply information (e.g., Alexander the Great was Macedonian).

There is no doubt that NHPs, especially GAs, possess all of these systems and use them in very similar ways to humans. GAs remember family members and social others, the locations of food sources, and how to engage in complex tasks such as tool use. In fact, there is evidence that chimpanzee WM has a greater capacity than human WM. However, debate exists about whether any GA memories can be said to be episodic and include a “personal” component rather than simply an informational component (Sellers and Schwartz 2013). Many have come to call their memories “episodic-like” highlighting the fact that these memories share some characteristics with human episodic memories, but it is experimentally difficult to confirm their exact episodic nature given the limits of communication between humans and GAs.

Developmentally, it is very likely that GA memory over the lifespan follows a very similar course to humans. Memories in infancy are probably not episodic nor semantic in nature, they are purely sensory. However, there is evidence that human children as young as 2 months display memories with some episodic qualities, such as context-dependency (Rovee-Collier and Dufault 1991). With age, LTM, STM, and WM all begin to function in rudimentary ways, with capacity and accuracy increasing with age. Human memories are undoubtedly episodic by the age of 1, as they can generalize knowledge learned in one setting to another (Learmonth et al. 2004). However, little definitive information is known about the exact nature of NHP memory development in early life. It is very difficult to study young primates for a number of reasons, and much must be inferred from day-to-day behavior, leaving many questions unanswered.

Language and Communication

All NHPs engage in communication, both verbal and nonverbal, with social others. Obviously, humans have a natural mastery of complex, representational language that far surpasses the capacity of all other NHPs. However, NHPs can engage in quite sophisticated and varied

communication, as evidenced by chimpanzees' use of different vocal calls to signal different types of danger (e.g., a certain call is used to alert for danger on the ground while a different call alerts for danger in the air or trees).

The most famous developmental-comparative case of language between humans and nonhuman GAs is the case of Kanzi, a bonobo raised in captivity from birth. Kanzi, currently 35 years of age and living at the Ape Cognition and Conservation Initiative in Des Moines, Iowa, exhibits the most sophisticated language abilities of any known NHP. He is able to communicate using lexograms, complex and abstract symbols that stand for physical items and actions. GAs cannot make human vocalizations due to differences in their vocal tracts. One likely reason for his superior abilities is his early exposure to language; his adoptive mother, Matata, was being trained to learn lexograms when Kanzi was young. This early exposure seems to have provided Kanzi with a developmental advantage in language abilities. This can be viewed as analogous to Noam Chomsky's idea for an early critical period in humans when language is most efficiently learned. There is some debate within the scientific community about whether Kanzi's abilities can rightly be called representational language, but even if they fall short of this high bar, his abilities are no doubt impressive and important to our understanding of the evolution of language.

Social Cognition

Social cognition is a broad construct encompassing the cognitions and behaviors used to interact with or think about others and situations involving them. The cognitive ability most closely associated with social cognition is Theory of Mind (ToM). ToM is the ability to think about the contents of another person's mind (e.g., I know that Johnny knows the answer to the trivia question). This ability is important for predicting the behavior of others based on their held beliefs and personal desires so that an individual can formulate appropriate responses and behaviors in reference to this other person. For

example, if I am eating dessert with Erica and I know that she loves ice cream I can give her the ice cream while I eat the brownie. However, I can also purposefully give her the brownie to be mean if I know that she thinks badly of me and has been gossiping behind my back. These decisions rest upon ToM.

Human children typically achieve explicit ToM around the age of 4, with sophistication and proper use increasing with age. There is some debate that perhaps these cognitions occur earlier; however, there is no debate that by 4 years of age children are complex social thinkers who can make appropriate assumptions about the minds of others. Children use this ability to imitate each other and adults in order to learn complex tasks, skills, and appropriate social behavior. They form complex friendships, social groups, and social hierarchies at a young age. Young GAs also engage in observation and imitation of adults, particularly tool use (i.e., fishing for termites or cracking nuts with stones). They also form social groups, understand the adult social hierarchy, and behave differently towards relatives and nonrelatives. These behaviors suggest that young GAs may have social cognitive abilities comparable to those of young human children.

Adult GAs certainly possess complex social cognitions: they can enlist humans to help them in cooperative tasks, can make assumptions about the desires of a human and assist in completing a task the human cannot do alone, and appear to understand that eyes are a source of another individual's ability to gather information (Tomasello and Call 2010). However, aided by language and communication abilities, human adults achieve much more sophisticated social cognitions and collaborations than GAs.

Conclusion

NHPs and humans share many abilities and characteristics that evidence their common evolutionary history and genetic similarities. However, differences abound in both the developmental course of these abilities and in their final adult complexities. However, humans faced

evolutionary pressures that increased the length of childhood and supported an intricately connected frontal cortex, leading to complex, self-referent memory, representational language, and incredibly sophisticated social cognitions.

Cross-References

- [Brain Size Growth in Humans and Nonhuman Primates](#)
- [Convergent Evolution of Hyena and Primate Social Systems](#)
- [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- [Cooperation Among Nonchimpanzee, Non-human Primates](#)

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Non-human Primates

- [Feelings of Excitement and Brotherhood](#)

Nonhuman Primates: Between-Group Conflicts

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Synonyms

[Intergroup conflict](#); [Intergroup killing](#), [between-group killing](#); [Warfare](#), [War](#), [Feuding](#), [Primate aggression](#)

Definition

Aggressive interactions between two or multiple conspecifics from different social groups in primate species usually lead to the death of at least one of the contenders and to fitness advantages to victors.

Introduction

Observations of between-group aggression and killing exist for a wide range of primate and non-primate mammals. Such phenomena occur in different forms, such as coalitional efforts, or independent and individual attacks (i.e., dyadic aggression), and targets may be individuals of any age. This entry will review the current literature on lethal intergroup aggression in nonhuman primates, describing evidences of adaptive value for aggressive interactions and especially killing between groups, in contrast to hypotheses that rely on the concepts of environmental mismatch, trait neutrality, or maladaptation to explain such phenomena. Even though this review will cover reports of lethal aggression between groups which overall also support adaptive hypotheses in

multiple species, special attention will be given to chimpanzees, considering the more intense research effort for this clade and an abundance of aggression descriptions, which permit detailed analyses of evolutionary predictions.

Review

Early theories considered intergroup killings to be exclusive of human societies living in complex political systems such as nation-states. However, observations with chimpanzees (*Pan troglodytes*) during the 1970s at Gombe, Tanzania (Wilson 2013), indicated that lethal attacks across communities were not uncommon. It is now estimated that intergroup killings in chimpanzees exhibit rates that are comparable to those in small-scale human societies, and higher than in modern, industrialized societies (Wrangham et al. 2006). The implications of these reports for understanding the origins of violence and warfare in human societies were met with both skepticism and opposition. According to some researchers, intergroup killings should not be considered a natural trait of the species, but rather a pathological social behavior associated with human interference factors such as ecological disturbance, the size of the protected area, and food provisioning in field sites. Such view is now currently known as the *human impact hypothesis* (HIH; Wilson et al. 2014). Another concern is that human “warfare” is a term sometimes arbitrarily reserved for violent conflicts killing at least 1,000 individuals, and chimpanzee conflicts have never been observed to achieve that dimension.

Alternatively, although the *adaptive strategies hypothesis* (ASH) acknowledged that human activities could not adequately explain the occurrence of lethal encounters, factors such as the number of males in a community and population density were seen as better predictors than human disruption. It is important to note that the HIH does not lead to the prediction that consistent differences would exist in between-group warfare based on the location of the communities (e.g., East–West), the age and sex of attackers and victims, or any variation across species (e.g., bonobos–chimpanzees),

beyond the direct effects of human impact. The ASH, on the other hand, leads to the prediction that natural tendencies for aggressive interactions are exhibited in different levels in different populations, sexes, and life history stages in consistent ways. Fifty years of observations, with 152 cases of intergroup killings reported for chimpanzees and bonobos across East and West Africa, suggest that a model presenting predictors associated with HIH was around seven times weaker compared to models accounting for the number of males and population density, both of which are predictors that are part of ASH (Wrangham et al. 2006; Wilson et al. 2014). From these studies, it is possible to conclude that these intergroup killings (1) exhibit design features that indicate a non-random distribution for characteristics of aggressors and victims, (2) occur in a predictable and organized fashion, (3) are enacted by individuals in sociodemographic categories which are most prepared for, and which would mostly benefit from, intense competition, as is detailed below. Importantly, victims are mostly unrelated to the attackers, in line with expectations from the Inclusive Fitness theory; and the victims and the attackers are mostly males, in line with sexual selection hypotheses.

The inherent costs associated with lethally attacking another individual pose the problem of how this behavior is maintained across chimpanzee communities. According to the imbalance of power hypothesis, intergroup killings would be expected under conditions favoring a maximum cost for the victim and a minimum risk for the attackers. As a supporting example, in the Taï Forest, Côte d’Ivoire, small parties of 1–3 males tend to avoid any direct engagement with adversaries, medium parties containing 4–6 males investigate more actively the territory, and larger parties with 7–9 males pursue physical contact with victims (Boesch 2003). Across chimpanzee communities, intergroup attackers and killers outnumber the targets by a range of 3–9 aggressors per target.

Playback experiments have also demonstrated that chimpanzees in the company of larger parties tend to approach speakers playing the vocalizations of rival males (Wilson 2013). The strategic nature of this behavior has also been demonstrated

based on differences between patrolling (collective travel to the fringes of the territory) and other activities (foraging). Raiding parties spend less time feeding during patrols and more time traveling. Moreover, at the time of the incursion, invaders combine long travel sprints with short rests, periods where they are attentive to cues from members of the rival community. Such organized behaviors further suggest that attacks are not spurious phenomena but rather part of the behavioral repertoire of the species.

Some of the hypothesized functions of intergroup attacks include acquisition of females, territorial expansion, and defense of resources. Supporting this, for example, female chimpanzees in the Taï forest sometime copulate with the attackers within the fringes or their territory (Boesch 2003) or permanently disperse into the group of the attackers (Wilson 2013). Lethal intergroup aggression presents additional fitness benefits to the invaders. Females from invading groups exhibit heavier body mass and shorter interbirth intervals, demonstrating that raiding males improve the reproductive conditions of females and consequently their own, not only by defending the territory but by expanding it (Williams et al. 2004).

Furthermore, intergroup killings in chimpanzee present a median of 271 per 100,000 individuals per year, a rate within the range estimated for human intergroup conflict in small-scale societies (foragers: 164 per 100,000 per year; horticulturalists and pastoralists: 595 per 100,000 per year; Wrangham et al. 2006). Thus, by systematically eliminating lone individuals, attackers are able to reduce the size of rival groups, making them more vulnerable to future attacks. The disappearance of communities such as Kahama (Gombe) or the K-group (Mahale) demonstrates the cumulative effect of such raids (Wilson 2013).

As in other forms of cooperation, the risk of free-riding is a potential destabilizer for collective, organized lethal aggression. Hence, by refusing to participate in any raid, freeloading males may obtain fitness benefits though the group without incurring significant costs. However, analyses with males at Kibale detected a positive relationship between the likelihood of participation,

mating success and the relationship closeness between participants, as measured by the time spent grooming (Watts and Mitani 2001), suggesting that compensating individual fitness benefits exist for those who engage in these intergroup aggressive efforts.

Territorial species living in societies displaying fission-fusion dynamics are more prone to intergroup lethal aggression (Aureli et al. 2006). However, the degree of cohesion and dispersion should not be solely considered as a risk factor. Due to a lower intensity of within-group competition and a higher risk of predation, groups living in the Taï forest have been found to be more cohesive with respect to Eastern communities. This socioecological context provides a protective factor for potential victims. Thus, by decreasing the distance between individuals, lone targets are able to be rescued by other members of the group that may be close to the attack site.

Primates living in fission-fusion societies, such as spider monkeys (*Ateles geoffroyi*; Aureli et al. 2006), have also been observed to form small parties of 3–4 males and invade the territory of competing groups. Moreover, intruders encountering rivals (range 1–3 victims) have been reported to chase the victims. However, there are no reports of intergroup killings as with chimpanzees. Importantly, other primate species exhibit both coalitional and dyadic lethal aggression against individuals from other groups. Red colobus monkeys (*Procolobus badius*) and diana monkeys (*Cercopithecus diana*; Watts et al. 2006) for example, can form small coalitions and kill rivals.

Recently in the Mawas Reserve, Indonesia, a coalitional attack by a male and a female orangutan led to the death of another female, despite the interventions of another male during the attack (Marzec et al. 2016). Only rare evidence of coalitional killings has been described in mountain gorillas (*Gorilla beringei*). In Karisoke, Rwanda, roving males sometimes clash with resident males, and even though the vast majority of these interactions are nonfatal, rare killings have been described (Rosenbaum et al. 2016). In the case of white-handed gibbons (*Hylobates lar*; Palombit 1993), an invading

individual was seen to be lethally wounded by another male. These observations, however, do not approach the mortality rates observed in between-group conflicts in chimpanzees, suggesting that characteristics particular to the socioecology of this species have selected for stronger intergroup competition.

Coalitional lethal aggression against vulnerable lone individuals has also been described in nonprimate species (Watts and Mitani 2001; Watts et al. 2006), including grey wolves (*Canis lupus*), African lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and spotted hyenas (*Crocuta crocuta*). In some species such as grey wolves, the mortality rate due to intergroup conflict may reach considerable proportions, demonstrating significant parallelisms with lethal interactions present in nonhuman primates.

Conclusion

Intergroup lethal conflict can be classified as either coalitional or dyadic aggression. Chimpanzee data clearly demonstrate that intergroup killings are not an outcome of human disruption, but rather an emergent phenomenon based on socioecological features including population density, and the number of males per community, with adaptive consequences. Similarly, intercommunity killings display consistent sociodemographic patterns in that males are more likely to be both aggressors and victims, Eastern communities have higher intergroup lethality rates than Western populations, and chimpanzees have higher intergroup lethality rates than bonobos. Patterns of patrolling and lethal attacks have also been found to be strategic, suggesting adaptation. Raiding individuals spend less time foraging and more time travelling into the territory of rival communities. Similarly, lethal attacks occur based on an attackers/victims ratio. Invaders obtain fitness benefits, including attracting new females, inducing shorter interbirth intervals, and acquiring resources.

Several other anthropoid primate species have also been observed to engage in intergroup lethal aggression, however the mortality rate due to conflict is considerably lower than that of

chimpanzees. Still, these occurrences as well as observations in various carnivorous species disconfirm previous hypotheses considering intergroup lethal aggression to be either adaptively neutral or maladaptive, or a contemporary phenomenon exclusive of complex human societies.

Cross-References

- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Evidence of Intentional Killing](#)
- [Evolved Psychology of Warfare](#)
- [Humans: Between-Group Conflicts](#)
- [Humans: Within-Group Conflicts](#)
- [Nonhuman Primates: Within-Group Conflicts](#)

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atmosphere (Schmidt-Nielsen 1972). However, this is not the case for all walking animals. For instance, spiders lack the muscular structure to extend their legs so they fiddle with their blood pressure to do so, and worms burrow through the dirt using bodily chemicals and muscle contractions (Schmidt-Nielsen 1972). This entry will summarize some of the more common forms of locomotion and specific movements of nonhuman species.

Nonhuman Primates: Species Typical Movement

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Synonyms

Brachiation; Flying; Running; Swimming; Walking

Definition

Unique ways in which different animals engage in locomotion.

Introduction

From swimming to flying, there are a plethora of different movements that are specific to certain animal types and their environments. Animals have specifically developed bodies that allow them to navigate their natural environment. For example, fish have slim bodies that allow them to cut through the density of water, with a natural buoyancy to keep them from sinking to the bottom (Schmidt-Nielsen 1972). Birds are slender with the need to carry their weight against a low-density atmosphere. Walking animals thrive in environments that contain a high-density platform upon which to walk through a low-density

Brachiation

Brachiation is the specific movement or extending and swinging of the upper limbs as a means of moving one's body (Turnquist et al. 1999). This movement is apparent in both human and non-human primates. We see this movement when we watch children on the (aptly named) monkey bars on playgrounds (Turnquist et al. 1999). This swinging motion from bar to bar – in which a child holds one bar and swings his/her weight to a second bar on which to grab – is brachiation. Although humans can engage in brachiation, it is not an efficient form of movement for them. Brachiation is usually exhibited as a form of regular movement by smaller nonhuman primates, such as monkeys and lemurs (Turnquist et al. 1999).

Grip

The hands of primates are used for many things like scratching, pulling/pushing, grasping/gripping, feeding, and grooming (Pouydebat et al. 2011). In both human and nonhuman primates, there are two broad classifications of grip – power grip and precision grip. Power grip refers to instances in which an animal grasps an object between its thumb and palm, so that the object is firmly secured in the palm of the hand (Pouydebat et al. 2011). An example of this would be the way a human grasps a bottle or a baseball. In non-human primates, power grips are what aid the animal in brachiation as it is how the animal can exert enough force to hold on to branches while moving (Pouydebat et al. 2011).

Precision grip refers to when animals use the tips of their finger(s) and thumb to hold an object (Pouydebat et al. 2011). When engaging in precision grip, the object being held does not get placed firmly against the palm. Precision grip is often utilized to hold small individual objects, such as a single berry or grape. Precision group is usually used to hold objects that are so small and lightweight that the added force of holding it against the palm is not necessary (Pouydebat et al. 2011).

Walking and Running

Every legged animal possesses a similar mechanism involved in locomotion. This mechanism, known as leg stiffness, is the measurement of peak ground force to peak leg compression in a stride (Shen and Seipel 2015). SLIP or *spring-loaded inverted pendulum* is the model of locomotion that looks at leg stiffness as a mechanism, which illustrates the similarities between different types of locomotion like hopping and walking (Shen and Seipel 2015). The SLIP model postulates that most legged animals have a spring system of locomotion which allows an animal's individual leg movements to propel it forward. Imagine an animal in stationary standing position. As the animal begins to lift its leg to take a step, the SLIP model is utilized to measure the arch of the leg and the pressures surrounding it all the way until the animal is standing again or taking another step. This arching movement is said to look on paper like a pogo stick springing forward (Shen and Seipel 2015). At each step there are different pressures between the leg, the bend of the knee, and the ground (Shen and Seipel 2015).

Swimming

Fish are special creatures as their movement through a dense medium forces them to be streamlined in shape (Schmidt-Nielsen 1972). This streamlining refers to the elongated shape that deflects the atmosphere smoothly around the fish. This allows the fish to move the water around its body as smoothly as possible, decreasing the caloric expenditure of swimming by moving parts of

their body in a manner that utilizes drag to create propulsion (Schmidt-Nielsen 1972). The two main types of propulsion – anguilliform propulsion and carangiform propulsion – are utilized by different aquatic species. For instance, eels engage in anguilliform propulsion, which is a form of propulsion in which the animal uses its entire body to move forward (Schmidt-Nielsen 1972). Species that use carangiform propulsion, such as sharks and salmon, use the movement of their tail fin to generate propulsion (Schmidt-Nielsen 1972).

Conclusion

Locomotion takes many different forms, each of which is specific to certain animals and the atmosphere of their natural environment. This entry focused on multiple different mediums of motion – swimming, walking, grip, and brachiation – to illustrate how species adaptation to an environment can dictate the type of movement in which that species engages. For instance, animals adapted for land living – such as primates – do not swim as efficiently as animals like fish that have adapted for water living. The evolution of environment-specific locomotion has allowed every species to better navigate and survive in their natural environment by allowing them to search for food, evade predators, and seek shelter from other environmental hazards. However, every type of locomotion utilizes a complex process of muscular movement and metabolic activity and therefore should continue to be researched.

Cross-References

- [Humans Crawl: Species Atypical Movement](#)
- [Kellogg Chimpanzee Study, The](#)
- [Mobility: Crawling and Walking](#)

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Nonhuman Primates: Within-Group Conflicts

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Synonyms

Intragroup Conflict; Intragroup Killing; Within-group Killing; Homicide; Murder; Aggression; Primate Aggression

Definition

Aggressive conflict between individuals within a group or community in nonhuman primate species, involving violent interactions, in certain circumstances leading to death of one party and fitness advantages to aggressors.

Introduction

Intragroup killings are a common phenomenon in primate species. Whereas attacks among adults have been thought to be selected due to the benefits collected by the assailants such as eliminating rivals, gaining access to material and social resources, and ascending in rank, the evolution of infanticide has mainly been attributed to males restarting the ovarian cycle of lactating

females and copulating with them. Furthermore, other adaptive hypotheses interpret infanticide as means of acquiring and retaining mates, eliminating competitors, removing the genetic presence of rivals, and rising in the social hierarchy. Some of the risk factors associated with male infanticide across primate species include a slow life history, the absence of alloparents, the type of social structure, and the prevalence of male take-overs. This review will cover the empirical evidence supporting the adaptive nature of different forms of intragroup killings in primate species.

Review

Similarly to descriptions of conspecific killings due to intergroup attacks, intragroup killings across primate societies have been hypothesized to be associated with various fitness benefits. Primatology researchers have tested them with multiple species, especially in anthropoid primates. For example, in spider monkeys (*Ateles geoffroyi ornatus* and *A. g. yucatanensis*), intragroup killings have been attributed to a male-biased sex ratio producing an increase in male competition (Valero et al. 2006). In capuchin monkeys (*Cebus capuchinus*), rivalry for occupying high ranks (or rank reversals) in hierarchy, as well as attempted expulsions from the community, are considered to better explain violent deaths. Despite the fact that muriquis (*Brachyteles arachnoides*) display low levels of within-group competition, the killing of an old male demonstrates that even tolerant species may resort to violent behavior to eliminate conspecifics due to conflict escalation (Talebi et al. 2009).

However, originally, intracommunal killings were thought to be the product of captivity (e.g., Arnhem Zoo, the Netherlands; reviewed in Watts 2004), with victims unable to flee the scene. This perspective was challenged when cases contrary to this hypothesis were described in wild chimpanzee (*Pan troglodytes*) communities in Uganda and Tanzania (Ngogo, Sonso, Mitumba, and the M-group; Fawcett and Muhumuza 2000). Similarly to the cases of intergroup killings, these attacks were considered by some to be maladaptive. However, rank upheavals, unequal sex ratios, and the elimination of

mating competitors appear to be some of the adaptive problems underlying this behavior.

Within-group victims of attacks usually occupy a low rank in the hierarchy (Watts 2004). The imbalance of power hypothesis, describing a decrease in the risk for the aggressors due to the collective nature of the attack, has also been considered a factor affecting the likelihood of within-group killings. Thus, by targeting a defenseless individual, coalitions of males reduce any risk to themselves, obtain benefits such as protecting their ranks in the hierarchy, and increase their mating opportunities.

Whereas adults and adolescent males had a higher mortality rate due to intercommunal aggression compared to juveniles and infants in chimpanzees, these were more frequently the victims of intracommunal aggression. The primatological literature supports this pattern, with most hypotheses and studies examining the occurrence of infant killings within groups, rather than adult deaths. As such, much of the research examining the adaptive functions of intragroup killing focuses on infanticide, as reviewed below.

Infanticide has been observed in at least 51 primate species. However, despite its ubiquity, infant killings do not occur at random. Targeted younglings are fully unrelated or genetically distant to the attacker, and the identity of the attackers is biased to one of the sexes. Thus, whereas in rodents most of the perpetrators are females, in primates, unrelated males have been found to be mostly responsible. Among some of the functions of male infanticide, observations in patas monkeys (*Erythrocebus patas*) and gray langurs (*Semnopithecus entellus*) suggest that by targeting the offspring of rivals, males eliminate future competitors and remove the genetic presence of the rivals in the group. In other species such as purple-faced langurs (*Trachypithecus vetulus*), infanticide increased the opportunities of gaining access to limited resources. Meanwhile, in chimpanzees (*Pan troglodytes*) and mantled howler monkeys (*Alouatta palliata*), infanticidal males decreased the coalitional power of competitors. Observations in gray langurs also found a relationship between infanticide and rank acquisition.

Other hypotheses have also considered the use of infanticide as a strategy for mate acquisition and mate retention. Thus, by killing the offspring of a female, males demonstrate a lack of protective abilities that competitors can offer. Similarly, according to the sexual selection hypothesis, infanticide is promoted as a consequence of females entering into an anestrus phase shortly after birth, a phenomenon known as lactational amenorrhea (van Schaik and Janson 2000). Hence, by spending more time unreceptive, females restrict the mating opportunities of males, who proceed to eliminate infants as a tactic for returning females to sexual availability. Perpetrators not only have a higher likelihood of copulating with targeted females, but also conceive their offspring. Thus, overall, infant killing in primates appears to be a consequence of both intersexual conflict and intrasexual competition, and appears to serve various adaptive functions.

Social structure and social dynamics also affect the probability of infant killings in predictable ways which suggest evolutionary design. For example, primate species living in one-male units are considered to be especially at risk of occurrences of infanticide compared to other species. Males from such units sire most of the offspring in the group. Therefore, when a dispersing male migrates and takes over, most of the young will be related to the former male. Infanticide allows the new male to obtain a reproductive monopoly and is commonly observed. Infanticide also occurs in primate species living in multimale groups (e.g., chacma baboons, *Papio ursinus*; and olive baboons, *P. anubis*). In contrast to one-male unit species, the average tenure of males living in multimale groups is brief. Thus, due to the risk of being deposed before siring any offspring, males may kill the infants of other males, which has the potential to increase their reproductive output (Beehner et al. 2005).

Paternity uncertainty is expected to be a protective factor against infanticide, as killing an infant when it is possibly one's progeny could have intense fitness costs. An interesting and complex phenomenon is observed with respect to this in primates: Females from species that carry and take care of their offspring on their own are more likely to have their offspring killed compared to

species that rely on the assistance of allocarers (i.e., individuals who engage in communal caring; van Schaik and Kappeler 1997). By having the support of kin or other helpers (e.g., males in marmosets and tamarins), communal females have a shorter interbirth interval, and even display sexual receptivity and proceptivity during pregnancy and shortly after birth. Even though males that copulated during nonconceptive periods do not sire more offspring compared to those that mate during ovulation, the confusion of paternity forces males to inhibit infanticidal tendencies to avoid killing their own offspring. The evolutionary context for females taking care of their young by themselves is considerably different. Due to the high physiological demands of investing in multiple infants at the same time, females limit the opportunities of conception by being unreceptive and in anestrus during periods of gestation and lactation and by increasing the temporal gap between births. However, at the same time, these modifications restrict the mating access of males, promoting the adaptiveness of infant killings by them. Higher infanticide rates are in fact observed in these cases.

An important realization is that evidences for an arms race between the sexes in terms of behavioral strategies to implement against infanticide would suggest that there are in fact evolutionary forces leading to adaptations involving infanticide. In fact, due to the high costs of infanticide, evidence suggests that females have evolved multiple counterstrategies to decrease the risks of losing younglings to attacking males. Depending on the social structure of each species, females can either concentrate or confuse male paternity. Thus, offspring of females who cohabitate or consort with a single male (e.g., OMUs species), receive the protection of the male, due to the copulation exclusivity increasing paternity certainty. Alternatively, paternity confusion occurs in societies with multiple males. In these conditions, concentrating paternity in a single male may not be sufficient to dissuade other males from attacking. Since takeovers in multimale groups are considerably common in multimale species, by copulating with numerous mates, females obscure the paternity of males, forcing attackers to refrain from killing the infant due to the risk of

eliminating their own young. Furthermore, females can advertise their receptivity to males through visual and vocal displays, or through sexual swellings peaking at times of ovulation. Other strategies employed by females to reduce the likelihood of infanticide by males include establishing friendship with a protector; dispersing with a deposed male; forming a coalition with other females or with kin; maternal vigilance and aggression; accelerating the weaning period; abandoning the infant, fetus reabsorption, or induced abortion.

Conclusion

Intragroup killings are observed across nonhuman species. Most of the victims are infants, whereas attackers are frequently adult males. Adaptive benefits obtained by infanticidal males appear to include returning noncycling females to estrus, eliminating future contenders and removing their genetic presence, decreasing the levels of current competition, and gaining access to resources. Support for these hypotheses has been found in various lines of research in different species, with research effort focusing especially in anthropoids. Attacks among adults have also been observed. However, differently from infanticide, victims and attackers in lethal conflicts among adults are mostly males. Gaining access to mates, eliminating rivals, and ascending in the hierarchy are some of the benefits obtained by successful attackers.

Cross-References

- [Contexts for Men's Aggression Against Men](#)
- [Evidence of Intentional Killing](#)
- [Homicide](#)
- [Humans: Between-Group Conflicts](#)
- [Humans: Within-Group Conflicts](#)
- [Infanticide and Parenting](#)
- [Intrasexual Rivalry Among Men](#)
- [Most Victims Are Men](#)
- [Nonhuman Primates: Between-Group Conflicts](#)
- [Same-Sex Homicide](#)
- [Sex Differences in Aggression](#)

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Nonhuman Reactions to Death

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Synonyms

Grief; Ritual; Thanatology

Definition

Death – The action or fact of dying or being killed; the point at which the processes that maintain an

organism alive no longer function. Dead – Deprived of life; opposed to alive and living; reduced to that state of a being in which the organs of motion and life have irrevocably ceased to perform their functions.

Introduction

Awareness of mortality is a human universal, evidenced by the pervasiveness of mortuary behavior and funerary rituals across human cultures, dating to Neanderthals over 40 ka. Humans exhibit diverse cultural variation in mortuary practices, in which treatment of dead bodies ranges from their consumption to the placement of them as far above or below ground as possible (Andrews et al. 2006). Moreover, compassionate behavior toward dying individuals is often regarded as a uniquely human trait, though recent reports of reactions to death and dying in nonhuman animals highlight the value of adopting a comparative evolutionary approach toward these behaviors. Here the diversity of nonhuman animal responses to death is reviewed and explanations for why animals differ so widely in their behavior toward dead conspecifics suggested.

Diversity of Responses to Death

Behavioral Adjustment to a Risk Exposure

If animal responses to carcasses are adaptive, individuals would be expected to view the bodies of dead conspecifics as disease-carrying agents and avoid or isolate them accordingly. Ants and aphids do exactly this, carrying carcasses to refuse piles, while honey bees remove dead brood members from their hives. Rats bury decomposing den mates. Nonetheless, there is information to be gleaned from dead or dying conspecifics, especially in assessing potential risk in an area. In some birds, seeing a dead conspecific induces alarm calling and subsequent risk-reducing behavior (Swift and Marzluff 2015), while in many aquatic organisms (Phylum Protista, Rotifera, Mollusca, Arthropoda, and Chordata), chemical cues perceived from injured, dead, or

digested conspecifics results in complete aversion to the local area.

Intense Interest in Conspecific Carcasses

Alternatively, some animals show intense interest in conspecific carcasses. In perhaps the best known example, African elephants spend unusually long periods at the sites where former herd members' bodies lie decomposing or even where only bones remain. They may also exhibit intense agitation and investigation (Merte et al. 2008). Less known, although behaviorally similar, American bison chase wolves away, before sniffing and nuzzling a calf's rotting body from their herd (King 2013). A similar reaction was reported by Strauss and Muller (2012) in wild giraffes, where following the death of a calf, giraffe mothers, and other herd members exhibited prolonged interest, including extensive vigilance, nuzzling, sniffing, and inspection of the carcass over several days. Intense interest in conspecific carcasses was also observed for a variety of cetaceans (i.e., rough-toothed dolphins, bottle nosed dolphins, Orca). The described behaviors include staying beside injured, dying, or net-trapped conspecifics and supporting sick or dead animals (infant as well as adult) at the surface (Ritter 2007).

Infant Corpse Carrying

Evolutionary biology predicts the extensive interest mothers' exhibit in dead offspring. Mammals that experience long gestation and development will benefit with the successful survival (and subsequent reproduction) of their offspring, thus premature abandonment of a suffering, but viable offspring carries high fitness costs. Examples of responses to dead infants date from almost a half-century ago and seem concentrated in the Order Primates. In numerous species, mothers and other group members carry dead infants from a few days up to several months after their death. Recently, Li et al. (2012) described three cases of mother responses toward dead infants in Yunnan snub-nosed monkeys. They showed that the age at which the infant died influenced the mother's behavior, whereby, for example, there was no carrying of stillborns versus extensive

carrying of dead infants who had survived to at least 1 month. Given that nonhuman primate females are hormonally predisposed to mothering in the last weeks of pregnancy, it is likely that hormones associated with parturition and lactation combined with the formation of a strong mother-infant attachment offer the strongest explanation for these behaviors. Between adults, the pre-dead relationship between the dead and the survivor seems to play an important role. Individuals that are more closely affiliated with the dead exhibit stronger reactions, either immediately or through longer-term behavioral changes. Given the importance of relationships to social animals, from alliance formation in dominance takeovers to cooperative foraging strategies, the loss of an ally can generate tremendous survival cost.

Sexual Arousal and Aggressive Interactions

If removing or isolating a carcass from one's home base makes adaptive sense by reducing potential exposure to disease, spending significant time investigating dead bodies seems maladaptive. However, sociosexual interactions with carcasses appear in several species (Piel and Stewart 2016). In marine mammals, Dudzinski and colleagues (2003) reported six to eight male dolphins spending almost three hours with a female carcass, focusing almost all their attention on its genital area, and simultaneously mate guarding the carcass while aroused. Similarly, mallards were observed to display homosexual and necrophilic behavior toward dead conspecifics, and in one anecdotal observation, a male squirrel was seen to approach and lay down in a copulatory posture next to a dead female. Stewart et al. (2012) detailed the responses of 16 (different) chimpanzees to the recently dead body of an adult female community member in Tanzania. Responses ranged from curious observation and passive investigation (e.g., smelling and grooming) to the shaking, dragging, and frustrated beating of the body. Similar responses were described in a nearby community, where adult male chimpanzees use the bodies of dead members in charging displays. Combined, these behaviors reveal a suite of responses, but they share individuals having

increased arousal levels, and possible confusion at the lack of response and overall state of the dead individual.

Human-Like Grieving in Captive Animals

One of the human universals in responses to death includes people grieving the loss of group members. This is a response to the permanent absence of the individual (e.g., death) versus the examples above, which describe responses to a dead body. Grief can be defined as changes in the survivor's patterns of social behavior, eating, sleeping, and/or of expression of affect (King 2013). While it is both difficult to define and rare to observe, there are documented cases of humanlike "grieving" among nonhuman animals. In captive pottos (*Perodicticus potto*), two individuals who survived a dead cage mate reduced their food intake after the death (and removal) of the conspecific. Captivity, however, allows surviving individuals to adjust their behavior at no cost to their survival. In the wild, natural selection may work against the visible expression of grief, since changes to routine and behavior may make an individual more vulnerable to predation or other lethal aggression from group members.

In perhaps the best description of a sequence of behaviors that approached human grieving, Anderson et al. (2011) reported on the death of an adult chimpanzee at Blair Drummond Safari Park, Scotland. Unique to this report were the detailed video records made before, during, and after the death. The authors described behaviors analogous to those that humans exhibit: chimpanzees appeared to care for the individual before death, to test for signs of life at the point of death, and to show signs of frustration after death, as well as subsequently to avoid the place where the death occurred (after the body was removed). The contrast in behavior pre-, during, and post-death seen in Anderson et al.'s study encouraged the authors to draw conclusions about the possible mental and emotional state of the surviving chimpanzees, specifically whether empathy and self-awareness – traits shared by humans and chimpanzees – allow us also to share with them an awareness of mortality.

What hampers our attempt to understand a nonhuman concept of death is similar to challenges facing any study of nonhuman cognition: How to know what others, unlike ourselves, know? Despite similar neuroanatomy, for example, humans and other primates exhibit vastly different capacities. Thus, it is both anthropocentric and biologically unfounded to expect nonhumans to express rituals as humans do, to communicate and express emotion as humans do. Thus, what can be expected? Besides against that of humans, against what baseline can others' responses to dead group members be compared? Until objective criteria are provided, analysis is limited by a species-specific lens, preventing much beyond a speculative interpretation of responses to death in heterospecifics.

Conclusion

The question of which species conceptualize death and how that is reified has implications for the evolution of human cognition and ritual. Fear of death has been argued to be a human universal. Full self-awareness and a theory of mind were likely propagated by positive natural selection and in some way must have benefitted ancestral hominins, opening the path for a distinction of "death" from "the dead." Others have argued to the contrary that these same traits may actually be evolutionarily detrimental to an individual or species. They would be a dead-end evolutionary barrier and would inhibit positively selected behaviors with large payoffs, like risk. Accordingly, a hominoid conception of death might have been blocked at some point during Great Ape evolution, helping to explain how animals can engage in fatal intergroup encounters, for example. Why then do some animals act as if they understand death? Elephants and other large herbivores investigate the bones of dead conspecifics; primate mothers carry dead infants for weeks or months; and, at least in captivity, animal responses to the dead resemble human grief with remarkable similarity.

If corpse removal from a fixed home base by colony-dwelling insects can be explained as an innate, evolutionary behavior, intense interest in

conspecific bodies may invoke more complex behaviors not as well known to scientists. Behavior associated with extensive vigilance, or high sexual or aggressive arousal, is presumably exhibited in an effort to gather more information about the unusual unresponsiveness of a carcass and demand more complex cognition, although not necessarily a conception of death. Elephant, giraffe, dolphin, and primates share large complex brains and fluid, complex social organizations that are cognitively demanding. It could be that the same faculties demanded to be a member of these groups are similarly useful in creating an awareness of one's position in the group and, in turn, the loss of others.

It is impossible to determine whether any of the animals described above have evolved or, more interestingly, developed an awareness or concept of death; only with concrete attempts to define expectations, look for patterns across anecdotes, and, eventually, test hypotheses can this topic be approached as a scientific question, grappling with the age-old question of human uniqueness.

Cross-References

- [Body Disposal](#)
- [Death](#)

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Nonhuman Reciprocal Altruism

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Synonyms

[Direct reciprocity](#); [Reciprocity](#)

Definition

An evolutionarily stable strategy of enforcing cooperation by conditionally helping based on past experience of the recipient's help.

Introduction

How does the ruthlessly competitive process of natural selection lead to unselfish traits, such as a

tendency to help others? Many birds and mammals give alarm calls that help others escape predators, rather than simply and selfishly running away to get farther from the predator than other group members. Primates spend time and energy grooming the fur of others in their group. Vampire bats regurgitate a portion of their food to feed hungry groupmates, even nonrelatives, which failed to feed. If these costly investments in helping others could have been spent furthering one's own reproductive success, then why would natural selection reward these behaviors? The puzzle is that cooperative individuals pay a cost to increase the reproductive success of others, while more selfish individuals are not paying those same costs. All else being equal, selfishness should outbreed cooperation.

Evolutionary explanations of cooperation solve this puzzle. For example, natural selection rewards altruism when it is targeted to close kin. This is because close kin are more likely to carry the same genes underlying the altruistic trait, so genes linked to altruistic traits favor replication of those same genes in other individuals, a process called kin selection.

Robert Trivers (1971) proposed "reciprocal altruism" as an explanation for apparent altruism between nonkin. Reciprocal altruism theory views acts of helping as cooperative investments that yield a reciprocal cooperative return, and it makes the prediction that individuals will preferentially help those individuals who are likely to later help them, even if those individuals are unrelated. Many evolutionary biologists prefer the term "reciprocity" because "reciprocal altruism" is not truly "altruistic." In the standard terminology of evolutionary biology, altruism is helping behavior that decreases the actor's lifetime reproductive success. Reciprocity, by contrast, provides a long-term mutual benefit to both actor and receiver.

What is Reciprocity?

Here's how reciprocity works: Individual A makes a cooperative investment in individual B, such as social grooming, food

sharing, or risking one's safety to help an individual in need. This investment increases the probability that individual B will later make a reciprocal investment in A. The term "investment" implies that it is in some way contingent on the returns. So if A stops helping B, then B will eventually stop helping A, and vice versa. This contingency prevents free-riding, or cheating, because B cannot continually receive help from A without reciprocating. Reciprocity requires repeated interactions and contingent helping based on past experience (Axelrod and Hamilton 1981).

Some authors contrast "direct reciprocity" where A helps B because B helps A with "indirect reciprocity" where A helps B because B helps C. In this case, A evaluates B as a potential cooperator, and B helps C to build a reputation as a good cooperator. There is also the concept of "generalized reciprocity" where A helps B because A was helped by any other individual. The tendency of humans to both cooperate and punish noncooperators, even in one-shot economic games without repeated interactions, has been called "strong reciprocity," but this behavior is most likely a by-product of natural selection shaping human decision-making in such a way that humans treat most or all social interactions as if they might be repeated (Delton et al. 2011).

What is the Evidence for Nonhuman Reciprocity?

There are many natural examples of organisms in nature making cooperative investments that are contingent on the cooperative returns. Unless otherwise noted, the older examples below are taken from a review by Carter (2014) and the references cited therein, while more recent studies (post-2013) are cited here. In the cleaner-client fish mutualism, small cleaners eat dead skin off larger "client" fish, which benefits both parties. But the cleaners can also "cheat" by eating mucus or live tissue, which benefits the cleaner but hurts the client. Both cleaners and clients enforce cooperation through reward and punishment (direct reciprocity) and through image scoring (indirect reciprocity). Clients abandon or chase cleaners

that cheat, and they avoid cleaners that they observe cheating with other clients. Cleaners behave more cooperatively when they are punished and when they are observed by other clients. Cleaners also enforce good behavior in other cleaners; they will punish cheating cleaners that might otherwise drive good clients away, an example of third-party punishment.

Even brainless organisms can perform a simple version of reciprocity. Plants contingently trade resources with symbiotic partners such as fungi and bacteria. By diverting resources to different structures, plants can selectively eliminate symbionts that do not provide good returns. For example, plants provide mycorrhizal fungi with carbon in exchange for phosphorus. Both parties reward high returns and punish low returns, by delivering more or less of the resource to match the amount of the return.

Some authors consider individual recognition and memory to be a prerequisite for reciprocity, in addition to contingency and repeated interactions. In one set of experiments, rats were trained to pull a lever to deliver food to conspecifics, and the experimenters then showed that the rats were more likely to deliver food to partners that previously delivered food to them. Anonymous help increased pulling by 20 %, which shows “generalized reciprocity,” and help from the same partner increased it an additional 51 %, which shows “direct reciprocity” based on recognition and memory of specific individual’s past behavior.

In nature, contingency in helping is most detectable in scenarios where animals cannot choose their partners. One example involves songbirds on neighboring territories. As male songbirds on neighboring territories become familiar with each other, they tend to reduce aggression towards one another as compared to strangers, which is called “the Dear Enemy effect.” By experimentally simulating territorial intrusions by neighboring males, experimenters found that male song sparrows increase their aggression to previously intruding neighbors but not to those that did not. Either reducing or escalating aggression is based on what the neighboring rival did previously.

Reciprocity might also occur between songbird parents raising offspring together. Great Tit parents were found to feed nestlings in a balanced alternating pattern unexplainable by foraging or begging times. Each parent increased feeding rates after their partners contributed but reduced their feeding rate by about 25 % until their partner contributed (Johnstone et al. 2014). These two examples from songbirds, rival males and allied parents, show that reciprocity results from the mix of cooperation and conflict that occurs in all social interactions that evolve via natural selection.

Some of the best experimental evidence of reciprocity comes from mobbing behavior of birds. Experimenters used fake owls to induce cooperative mobbing in 44 triads of pied flycatcher mated pairs, with each triad consisting of three equidistant nestboxes. One pair (the victims) was exposed to a fake owl near their nestbox to induce mobbing, another pair (the defectors) was prevented from mobbing, and the third pair (the helpers) was left untreated. Therefore, the “helpers” always helped the “victims” with mobbing, but the “defectors” never did. Later, when the authors simultaneously presented the previous “helpers” and “defectors” with owls, the previous “victims” helped the previous helpers in 30 of 32 trials. In a follow-up experiment, when the previous “defectors” were presented with an owl, the “helpers” (but typically not the “victims”) joined the “defectors” in mobbing, as expected if only the “victims” experienced a defection. Later experiments further ruled out the possibility that reciprocal mobbing at nestboxes was purely a by-product benefit of selfish behavior. Astonishingly, the degree of reciprocity was also sensitive to whether the failure of partners to mob was caused by their complete absence. When experimenters used playbacks of recordings to make pairs seem present but unwilling to join, the rate of defection increased dramatically.

Much like mobbing birds, pairs of fish will also sometimes cooperatively approach and inspect predators, such as larger predatory fish. They appear to do this to assess the situation while maintaining the safety of a companion. One hypothesis is that the fish enforce partner cooperation by approaching closer only if their partner

swims beside them. This hypothesis is supported by several experimental results. There are differences in predator inspection behavior of fish from populations with either high or low predation. Predator approach behavior is riskier for single fish and leading fish. Predator inspection involves partner recognition, it is contingent on a partner's past and present predator inspection behavior, and it is more likely to occur with partners that have a history of social interaction.

As in several of the examples above, reciprocity often involves clear turn-taking. Other examples include two hermaphroditic fish that take turns trading egg or sperm and when migrating birds take turns flying in the more costly lead position of a flight formation (Voelkl et al. 2015). But strict turn-taking is not a prerequisite for cooperation, and it does not occur in many long-term reciprocal relationships that may involve the exchange of different kinds of help. For example, primates create and maintain enduring social bonds that involve multiple forms of cooperative investments. Chimpanzees of both sexes appear to exchange several different commodities, including grooming, sex, support, and food, resulting in balanced relationships over extended periods. Similar to humans, nonhuman primates cooperate in a more strictly contingent manner with partners that are actually *less* bonded. Most experimental evidence for strict short-term contingency therefore comes from more simple systems such as those with rats, plants, and fish described, because it is difficult to alter a complex friendship-like social bond in a short window of time.

Many cooperative social bonds form between relatives, which can make reciprocity difficult to distinguish from nepotism. Moreover, reciprocity and nepotism can occur simultaneously because reciprocity can enforce cooperation between relatives. The best evidence for this comes from vampire bats (see ► [“Blood Sharing by Vampire Bats,”](#) this volume).

Many authors view reciprocity as a controversial explanation for cooperation, but this debate is mostly or entirely semantic: it revolves around different definitions of reciprocity that are narrow versus broad or functional versus mechanistic. For

instance, some authors use “reciprocity” for a calculated investment where individuals suppress selfishness to intentionally and strategically help another with the expected outcome of receiving a given amount in return, which requires the ability to plan ahead, value future over present outcomes, and maybe even count. This very narrowly defined kind of reciprocity is the basis for human trade, but it all but excludes its importance in anything but humans. It also departs from the original broader definition, proposed by Trivers (1971) and Axelrod and Hamilton (1981).

One criticism of reciprocity theory is that it historically focused on dyads in isolation and thus ignored the vast importance of partner switching and choice. Why reward and punish a single partner, when one can simply switch to a different partner? Biological market theory (Noë and Hammerstein 1994) addresses this gap by starting with the assumption that cooperative investments lead to cooperative returns and then producing testable predictions for how market effects, such as the supply and demand of available partners, will influence both partner choice and partner control (reward and punishment). When one partner holds more bargaining power, trade can be asymmetric. For example, when experimenters created a situation when only one low-ranking monkey could open a food box, she subsequently received far more grooming. But when a second monkey was given this food-provisioning power, the grooming she received went up, while the grooming the first provider received decreased. The monkeys make cooperative investments based not only on past returns but also the relative value of alternative investments.

Conclusion

Reciprocity is a controversial but important explanation for cooperation.

Cross-References

- [Altruism Among Nonkin](#)
- [Blood Sharing by Vampire Bats](#)

- [Ingredients of Reciprocal Altruism](#)
- [Iterated Prisoner's Dilemma Model](#)
- [Kin Selection](#)

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Nonhuman Sexual Conflict

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Synonyms

[Intersexual competition](#); [Opposing reproductive goals](#); [Postcopulatory conflict](#); [Precopulatory conflict](#)

Definition

Nonhuman sexual conflict refers to any type of conflict that arises between members of the animal kingdom as the result of male and female reproductive interests being at odds with one another.

Introduction

In much of the animal kingdom, mating is not a cooperative process. Instead, it is marked by conflict and arms races between males and females to achieve their opposing reproductive goals (Parker 1979). Such conflict can be manifested in many forms, but they fall into two broad categories: precopulatory conflict and postcopulatory conflict (Parker 2006). The following sections provide brief overviews of the most commonly studied forms of conflict in nonhuman species under these two categories.

Precopulatory Conflict

In general, precopulatory conflict is centered around identification of potential mates before any DNA has been exchanged (Parker 2006). Typically, such conflict arises from discrepancies in mate value between partners. For the majority of species, there are differences in choosiness between males and females when selecting an appropriate mate. This is mainly due to the fact that eggs tend to be larger, more complex gametes than sperm which makes them more energetically costly to produce (Bateman 1948). Additionally, females of most (but not all) species have a larger minimal parental investment in offspring in forms that include gestation, lactation, and incubation (Trivers 1972). Under such circumstances, females typically have lower reproductive potential than males because they are restrained by a limited number of eggs and heavy parental investment. Therefore, they tend to be choosier when seeking a mate as a poor mate choice can be more likely to lead to reproductive failure relative to males (Parker 1979). Males, on the

other hand, benefit the most from a reproductive strategy that involves indiscriminate mate choice in an attempt to produce as many offspring as possible (Trivers 1972).

This asymmetry in choosiness between the sexes has been observed in a variety of species. In some deer species, for example, a routine mating practice is lekking, which refers to males displaying themselves in groups to females and then the females inspecting them and choosing the male of best quality as a mate (Massei and Bowyer 1999). Does prefer bucks with the largest antlers, as this trait is not only indicative of success in aggressive encounters with other males, but it also is an indicator of good genes. Specifically, a study on white-tailed deer found that bucks with the biggest antlers also had better immune function and greater resistance to parasites (Ditchkoff et al. 2001). Choosing bucks with this characteristic will lead to those better genes being passed on to the female's offspring.

Another consequence of greater female choosiness is greater variance in reproductive success between the sexes (Bateman 1948). Because females only choose the highest quality males as mates, there should be at least some males that are not deemed high enough in quality as mates and therefore do not reproduce at all. Hence, males tend to have greater variance in reproductive success than females. However, one reaction to both the higher male propensity to fail to find a mate and the high degree of selectivity in females for males is to engage in sexual coercion. Although this is a known reason for sexual coercion, it is also practiced by reproductively successful males in an attempt to further increase their reproductive success. Such a strategy is favorable to male reproductive interests at the expense of the female's ability to choose the best quality mate (Clutton-Brock and Parker 1995).

This form of sexual conflict is common in nonhuman species, and it is studied more heavily in some than others. For example, in many species of waterfowl, such as ducks, males engage in forced copulations with females that are typically already mated to a regular partner (McKinney and Evarts 1998). Additionally, many of the males engaging in sexual coercion have a regular partner

as well. Male ducks tend to force copulation upon females that are not currently accompanied by their regular male partner, as male partners tend to be able to successfully defend against intruding males. However, in cases where a female is left alone and is forced into copulation by a strange male, if her regular partner arrives during the act of sexual coercion, he will fight off the intruder but will also force his mate to copulate with him immediately after to increase paternity certainty (McKinney and Evarts 1998).

Sexual coercion among ducks has been such a common part of the species' ancestral history that female genitalia has evolved to decrease the chances of successful forced copulation and therefore give the female an advantage in sexual conflict. According to Brennan et al. (2009), the duck penis has a corkscrew shape that spirals in a counterclockwise direction, while the female oviduct spirals in a clockwise direction. This morphology makes it difficult for males to penetrate the oviduct and therefore achieve fertilization during forced copulation.

Precopulatory conflict can also occur among hermaphroditic species. In this case, conflict is usually focused on which member of the mating pair will take on the male and female role in terms of parental investment. Usually, both members prefer the male role as this allows for the highest reproductive potential along with the lowest amount of parental investment (Michiels 1998). Therefore, hermaphroditic species have developed antagonistic ways to approach copulation to compete for the opportunity of paternity. In one such species, flatworms, a mating pair will struggle with one another in an attempt to be the first to inseminate via a stabbing motion with its penis. The individual who stabs first tends to father more offspring in more individuals, therefore increasing reproductive success over other individuals that are not as successful in the stabbing battles (Michiels and Newman 1998).

Postcopulatory Conflict

In cases where females may not be able to choose their reproductive partners as a consequence of

forceful insemination, there are still ways in which they can prevail in sexual conflict. The activities leading up to and including intercourse are only part of the story, as arms races between males and females are just as prevalent after the completion of copulation. Sexual conflict at this point in time usually revolves around which male will achieve paternity.

Sperm competition refers to a situation in which sperm from at least two different males are present in a female's reproductive tract simultaneously and thus compete with one another for the opportunity to fertilize ova. Sperm competition could arise as a consequence of sexual coercion such as in the case of ducks as described earlier. However, in many nonhuman species, females actively promote sperm competition by mating with multiple males during a brief period (such as a mating season) (Parker 1970). It has been suggested that such a strategy still allows for female choice, in that only the most adept sperm (and presumably that also translates to the male with the best genes) are successful in such competition.

For instance, chimpanzees engage in promiscuous mating such that most members of a community mate with multiple members of the opposite sex. Under these circumstances, there is a high risk of sperm competition (Harcourt et al. 1981, 1995). Even though, in terms of precopulatory sexual conflict, the most socially dominant ranking males secure the highest degree of sexual access to females, their rates of paternity do not match their copulation frequency. The males with the highest rates of paternity are those that are somewhat younger than the most dominant males, and this is likely due to the superior quality of sperm from younger males (Wroblewski et al. 2009). Sperm production is vulnerable to senescence, and in older primate males declines in semen volume, count, motility, and morphology are commonly found (Kidd et al. 2001). Therefore, it is likely that female chimpanzees are optimizing their chances of reproductive success in sexual conflict in precopulatory contexts by allowing copulations with high-ranking males and in postcopulatory contexts by allowing copulations

with younger males. Use of both strategies allows ultimately for the best genes to be passed to the next generation.

Not only does the quality of sperm itself help with the outcome of sperm competition, but also penile ornaments play a role. In many species, especially various insects, the penis has spines or some other form of weaponry that actually cause physical damage to the female during copulation. This has developed to discourage the female from seeking additional males and thus produces an advantage in intersexual conflict (Eberhard 1985). In addition to spermatozoa, other chemical components in seminal fluids contribute to sexual conflict. Specifically, substances in seminal fluids have been known to decrease the female's desire to mate with another male and/or mimic her own body's hormones to trigger oviposition as has been observed in grasshoppers, katydids, and fruit flies (Eberhard and Cordero 1995).

Even after accounting for sperm competition, there are still ways to manipulate the outcome of sexual conflict. Female animals sometimes induce abortions in the event that the expected offspring would have poor survival prospects. Mice are known to selectively abort their pregnancies (known as the Bruce effect) when their mate is replaced by a novel male, as unfamiliar males typically commit infanticide when exposed to unrelated offspring (Gangrade and Dominic 1984). Such a strategy saves the female from wasted effort in offspring that are unlikely to survive and prepares them for estrus so they can bear the offspring of the new male. The Bruce effect has even been observed from exposure to just the scent of urine from an unfamiliar male (Gangrade and Dominic 1984). Alternatively, some species use infanticide as a method of inducing estrus rather than spontaneous abortion. For example, when a new male lion takes over a harem of lionesses, he systematically kills all the lion cubs in the harem so as not to invest in unrelated offspring; this also induces estrus in the female lions so that the new male can increase his own reproductive success despite the females' wasted parental effort (Pusey and Packer 1994).

Conclusion

This was just a brief summary of the types of sexual conflict that occur in nonhuman species, and some form of sexual conflict has been observed in virtually all species that have been studied. This type of conflict exists at the precopulatory level in the form of mate value discrepancy or sexual coercion, or at the postcopulatory level in the form of cryptic female choice and sperm competition. For both males and females, they have evolved adaptations to skew the outcome of this conflict in their favor at the expense of their partner. In many nonhuman species, the individuals with the most reproductive success are the ones that are best able to manipulate their partner.

Cross-References

- [Evolution of Genitalia, The](#)
- [Gamete Size](#)
- [Infanticide in Nonhumans](#)
- [Sexual Coercion and Violence](#)

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Nonhuman Tool Use

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Synonyms

Instrumentation; Tool behavior; Use of implements; Use of instruments

Definition

The external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool. (Shumaker et al. 2011, p. 5)

Introduction

Nonhuman tool use has long been a source of much fascination. Claims of human uniqueness have often revolved around the ability to use and manufacture tools. When Jane Goodall discovered the extent of tool use by wild chimpanzees in the 1960s, Louis Leakey commented that “now we must redefine tool, redefine man, or accept chimpanzees as humans” (Goodall 1998, p. 2184). After countless observations of animals using and manufacturing tools, it is now evident that “man the tool-maker” (Oakley 1956) is an erroneous definition of our own species.

Tool use in primates has been known for a long time. Wild chimpanzees and capuchin monkeys were observed by explorers in the sixteenth and seventeenth century to throw stones at intruders and use stones as hammers to crack hard nuts. Alfred Russell Wallace, who independently of Darwin formulated evolution through natural selection, described how three wild orangutans dropped branches toward him as he tried to shoot them (Shumaker et al. 2011). It was often

assumed that tool-use behavior was learned from humans. The variety of tool use in captive chimpanzees had been described before Goodall – notably Köhler’s (1927) experiments on Tenerife between 1913 and 1920 – but her discovery of habitual tool use in wild populations showed this behavior to be independent of human influence (Shumaker et al. 2011).

“Necessity is the mother of invention” is the moral of Aesop’s fable on the crow and the pitcher. It involves a thirsty crow trying to drink from a pitcher, but the water level is too low. He collects stones and drops them into the pitcher until the water reaches the top. Recent research has shown this to be more than a fairytale. Some crow species and their relatives – forming the corvid family including ravens, crows, magpies, and jays – have successfully dropped stones into a water-filled tube to obtain floating food (see Fig. 1). Similarly, some apes spit water into a tube containing a peanut to bring it within reach (Jelbert et al. 2015).

In his final book, Charles Darwin studied the intelligence of earthworms. He noticed how they often used leaves to plug the entrance to their burrows. Such behavior is today defined as tool use. Darwin formulated several functions of this behavior, such as predator protection, insulation, or keeping the burrow free from dirt and water.



Nonhuman Tool Use, Fig. 1 A New Caledonian crow drops stones into a water-filled tube, rather than a sand-filled tube, to obtain a floating reward. Reproduced from Jelbert, S. A., Taylor, A. H., & Gray, R. D. (2015). Investigating animal cognition with the Aesop's Fable paradigm: current understanding and future directions. *Communicative & Integrative Biology*, 8, e1035846. doi: 10.1080/19420889.2015.1035846. <http://www.tandfonline.com/doi/abs/10.1080/19420889.2015.1035846> CC BY-NC 3.0: <https://creativecommons.org/licenses/by-nc/3.0>

The earthworms handled leaves optimally by taking their differing shapes into account, and they incorporated objects never encountered before, such as pieces of paper or leaves of foreign plants (Crist 2002). Such discoveries have been important in lifting animal tool use to scientific level, wherein the study of animals ranging from earthworms to chimpanzees has become acceptable in wild and captive conditions, with questions on the types, function, ecology, evolution, and cognition of tool use.

Modes and Functions of Tool Use

Following Leakey's prediction, tools have been frequently redefined. Most contemporary definitions do not focus on human uniqueness or cognitive requirements and are instead descriptive in terms of actions and objects used. Critically, the user exerts some control over the tool through direct physical manipulation. If all types of interaction with external objects for various purposes are considered tool use, then it would become overly broad, including behaviors such as climbing a tree. After decades of discussion, the definition of Shumaker and colleagues (2011) in their book *Animal Tool Behavior* appears to have the fewest problems and is therefore used here.

They describe 22 modes of tool use, which are operationally descriptive as motor actions and are independent of possible functions. They nonetheless emphasize that tool use, unlike object manipulation and object play, requires purposive behavior. Purposiveness is reflected in the definition of tool use as "to alter more efficiently the form, position, or condition of another object, another organism, or the user itself" (Shumaker et al. 2011). Consequently, an ape passively dislodging branches while fleeing through the canopy does not constitute tool use, but one aiming and dropping branches to discourage gun-wielding naturalists is. That exemplifies the tool-use mode *drop*.

All modes can be assigned one or several of seven functions. For instance, an ape might drop a branch to (1) amplify mechanical force, which can cause more damage to the intruder; (2) extend its

reach, which enables it to inflict damage to the intruder without having to come closer; and (3) create or augment signal value of social display, which could be the case when it intends to intimidate rather than harm the intruder. This example illustrates that although all tool use is purposive, the exact function does not necessarily follow from the assignment to a certain mode. All tool-use modes and functions described by Shumaker and colleagues (2011) are presented in Table 1.

The list of tool-use modes and functions is not exhaustive. Shumaker and colleagues formulated these categories after they catalogued animal tool behavior. Additional observations may thus not fit into these categories. For example, New Caledonian crows are habitual tool users in several modes, and novel findings not only show their tool use to belong to more modes than initially described, but also that novel modes may have to be formulated. They have been observed to insert tools into objects to transport them, with one bird having trouble handling the large target object, which became transportable after inserting a stick into it (Jacobs et al. 2016). Novel modes can also be found in species never having been observed to use tools. Greater vasa parrots held dates and pebbles in their beak and used their tongue to grind them against seashells, which serve as important calcium sources. This appears to be the first report of this kind of tool use in animals (Lambert et al. 2015).

In contrast, Bentley-Condit and Smith (2010) classify tool use based on biological function. Their ten categories are food preparation, food extraction, food transportation, food capture, physical maintenance, mate attraction, nest construction, predator defense, agonism, and other. However, assigning a behavior to one of these categories is often problematic. For example, distinguishing defense and agonism can be difficult, and both categories are excessively broad. When reformulated into the modes from Table 1, defense and agonism can take forms such as drop, throw, slap, club, jab, stab, block, affix, apply, and drape. Furthermore, highly similar behaviors are not forced into different categories because they serve different functions. Bentley-Condit and

Nonhuman Tool Use, Table 1 Tool-use modes and functions described by Shumaker et al. (2011, p. 13–14). The precise definitions are excluded because the labels are sufficiently descriptive for present purposes

Mode	Function
Drop	Create or augment signal value of social display; amplify mechanical force; extend user's reach
Throw	Create or augment signal value of social display; amplify mechanical force; extend user's reach
Drag, roll, kick, slap, push over	Create or augment signal value of social display; amplify mechanical force
Brandish, wave, shake	Create or augment signal value of social display; camouflage; bodily comfort
Bait, entice	Extend user's reach; create or augment signal value of social display
Club, beat	Amplify mechanical force
Pound, hammer	Amplify mechanical force
Pry, apply leverage	Amplify mechanical force
Dig	Amplify mechanical force
Jab, stab, penetrate	Amplify mechanical force; extend user's reach
Reach	Extend user's reach
Insert and probe	Extend user's reach
Scratch, rub	Amplify mechanical force, bodily comfort
Cut	Amplify mechanical force
Block	Amplify mechanical force; extend user's reach
Prop and climb, balance and climb, bridge, reposition	Extend user's reach by expanding accessible three-dimensional space, bodily comfort
Hang	Extend user's reach by expanding accessible three-dimensional space
Contain	Effective control of fluids and small solid objects
Absorb	Effective control of fluids, bodily comfort
Wipe	Effective control of fluids and small solid objects, bodily comfort
Affix, apply, drape	Create or augment signal value of social display, camouflage, bodily comfort
Symbolize	Abstract or represent reality

Smith (2010) consider using a stick to obtain out-of-reach food as food capture, but would classify the exact same behavior as other tool use if the target were a nonfood object. We favor the approach of Shumaker and colleagues because its modes are descriptive with each having multiple possible functions that are independent of the tool actions themselves.

Ecology

Why do animals use tools in the first place? It was long believed that captive animals use tools because they have plenty of time to play with objects or because they copied humans. Some researchers have argued that tool use marks a qualitative difference between animals and

humans, in that we strongly depend on tools for our survival, whereas it is trivial for other animals. However, some species habitually use tools in the wild, which constitutes a significant aspect of their foraging ecology (Shumaker et al. 2011). Tool use takes time and effort, requires dexterity, involves learning, and exposes animals to predators. The habitual tool use of some species suggests that there must be benefits that outweigh these costs.

There are four non-mutually exclusive hypotheses about variation in tool-use frequency and diversity between natural populations (Fox et al. 1999; Rutz and St Clair 2012; Sanz and Morgan 2013). The *necessity hypothesis* follows the proverb that necessity is the mother of invention in suggesting that tool use is an emerging strategy to deal with resource scarcity. For instance, woodpecker finches use sticks and

cactus spines to extract embedded arthropods on the Galápagos Islands. They spend more time and obtain more prey using tools in arid areas compared to wet areas, which have a higher availability of other food sources and therefore also a higher population density. Although tool use is more time consuming than other foraging techniques, it is more profitable during the dry season in the arid zone because larger and more energy-rich prey can be captured (Tebich and Teschke 2013).

The second hypothesis is the *opportunity hypothesis*, which states that increased encounters with target items and tool materials lead to more frequent tool use. For example, orangutans appear to use tools more frequently with increased presence of social insects. Although orangutans are mostly arboreal and frugivorous, insectivory is more common in one Sumatran population because social insects cannot build nests on the swampy forest floor and instead inhabit tree holes. This exposes orangutans to a food source they would not otherwise often encounter, which consequently requires them to use extractive foraging tools, in modes such as penetrating, reaching, inserting, and probing. Without this foraging opportunity, tool use in orangutans in this area would be less frequent or diverse (Fox et al. 1999).

The third hypothesis is the *relative profitability hypothesis*, which proposes that tool use arises when it is energetically more profitable than alternative foraging techniques. Tool use plays an important role in the feeding ecology of New Caledonian crows which, like the woodpecker finches, inhabit islands without woodpeckers or similar competitors. They use three distinct tool types made from plant material. Non-hooked stick tools are made from sticks, grass, and leaf petioles and are often used to extract wood-boring beetle larvae from their tree burrows. Crows use such tools to poke larvae until they bite it, after which it can carefully be withdrawn. Hooked stick tools can be used to extract other kinds of prey and are unique in the animal kingdom. Pandanus tools are made from screw pine (*Pandanus*) leaves, which have barbed edges

that are employed during foraging. Although little is known about tool use by wild New Caledonian crows, it has been shown that these wood-boring larvae comprise a substantial intake of lipids and protein, which indicates the significance of using tools as these larvae would be unavailable otherwise. Other factors that may have enabled the development of habitual tool use are reduced risk of predation, absence of other extractive foragers, and seasonal prey scarcity. New Caledonian crows appear to have evolved several morphological adaptations to tool use, such as a relatively straight beak and a large binocular overlap, which shows its evolutionary significance (Rutz and St Clair 2012).

The final hypothesis is the *limited invention hypothesis*, which suggests that the invention of novel tool use is relatively rare, and its spread and maintenance depend on social learning from conspecifics. This hypothesis is an important explanation of tool use in chimpanzees, which are the most frequent and diverse (20 out of 22 modes) tool users among nonhuman animals in the wild (Shumaker et al. 2011). Nonetheless, there is an enormous variation in the tool repertoire of different populations, which are therefore often considered as different cultural variants. The use of termite-fishing tools by one chimpanzee population in the Republic of Congo is unrelated to temperature, rainfall, fruiting or flowering tree occurrence, or abundance of leaves. Other tool use types have ecological correlates: using tools to extract ants is more frequent with increasing rainfall, and tool use for gathering honey is higher in months with more flowering trees. The chimpanzees consumed more leaves during periods of fruit scarcity, but they did not increase their tool use – a finding that goes against the necessity hypothesis. For the most part, their tool use was not strongly predicted by opportunity either, due to it being mostly independent from ecological factors. The relative seasonal profitability of different foraging techniques may partially explain these results. Party size was relatively small during tool use bouts, and social tolerance may also have enabled less-skilled individuals to learn about the location of tool-use sites, the tools

required, and the techniques involved. Through social learning and conformity, tool-use innovations can spread throughout the population (Sanz and Morgan 2013).

Evolution

Tool use is clearly beneficial for some species, although it can vary strongly between populations and tool-use modes. However, for many species, tool use has only been described in a single subject or mode, in captivity only, or with little to none energetic or nutritional significance. Here follows a brief description of the taxonomic variety of animal tool use, based on Shumaker et al.'s (2011) catalog, which is the most extensive to date. Novel tool-using species and modes are frequently described, so this overview is by no means exhaustive, but aims to illustrate the diversity of tool modes and their occurrence in perhaps unexpected species.

Several invertebrate species use tools, as already described by Darwin in the case of earthworms. Ant-lion larvae dig pitfalls in the sand and wait at the bottom for prey to fall in. If prey attempts to escape, the larva throws sand toward it to bring it into reach. Some digger wasps create subterranean burrows in which they deposit eggs and prey for their larvae to feed on. They seal and conceal the burrow by holding an object in their mandible and then pound the entrance and the surrounding area. Several ant genera construct and repair their nests by moving around larvae that secrete sticky silk that cements parts of the nest together. Sea urchins have been observed to cover themselves with objects for camouflage, which reduces the chances of predation. Boxer crabs attach stinging anemones to their claws, which aids in defense, food capture, and self-maintenance. Nest-casting spiders hold a part of their web between their legs and throw it toward passing prey to capture it. Carrier shells are sea snails that fittingly to their name attach empty shells to their own, which may aid in protection and camouflage. Veined octopuses sometimes carry coconut halves that they use as a shelter when threatened.

Tool use in fish, amphibians, and non-avian reptiles is uncommon. The best-known case of tool use in fish is the archer fish, which shoots water jets at prey above water. They can shoot up to 3 m far, and experienced fish have a near-perfect accuracy at a distance of 1 m. When presented with food in a small pipe, stingrays remove it by using water as a tool by creating currents with their fins or by blowing water through the pipe. Horned frogs throw mud onto their backs with their feet to camouflage themselves. Recently, American alligators and mugger crocodiles were seen to place twigs on their snouts during the nesting season of local birds, which are greatly attracted to nest material during this seasonal shortage. The sticks function as bait that attracts these birds, which can then be caught by the waiting crocodilians (Dinets et al. 2015).

Reports of tool use in birds are more numerous. Egyptian vultures often drop and throw stones on ostrich eggs to crack them. They've also been observed to use stones to kill lizards. Like the crocodilians described above, many birds bait prey with enticing objects. For example, burrowing owls place dung near their burrows to attract dung beetles. Brown-headed nuthatches customarily hold bark scales in their beak to pry away tree bark and expose invertebrates. A Steller's jay and an American crow have once been seen to use a stick as a weapon to jab at each other. Many parrot species use a variety of objects to scratch themselves. A rook plugged water drains in its aviary to create a drinking and bathing pool during hot days. An American crow repositioned a perch to reach an inaccessible location. A gila woodpecker dipped bark into honey for absorption and then transported it to his fledglings. Hawaiian crows are extinct in the wild, but nearly all captive subjects use stick tools for extractive foraging (Rutz et al. 2016). Male satin bowerbirds build and paint bowers to attract females. They hold bark pieces in their beak and dip them into the "paint" (e.g., charcoal, grass, mud, fruit pulp), which they then apply to their bowers. The most widespread tool-use type in birds is anting, which involves applying certain invertebrates, plants, or objects to their plumage.

Many of these tools have acidic compounds that may aid feather maintenance or kill ectoparasites.

Non-primate mammals also use tools in various ways. Beavers managed to overflow their enclosure by blocking pipes with sticks, leaves, and mud. Wood mice place conspicuous objects throughout their home range that might function as orientation points. Polar bears sometimes carry or roll large objects that they throw at prey during hunting. Sea otters place stones on their abdomens and pound hard-shelled prey against them. Some use an additional stone as a hammer. They may also apply kelp to their bodies to increase their buoyancy. Captive giant pandas were seen to clean their undersides by rubbing them with soil held in their front paws. North American badgers capture ground squirrels by blocking the burrow entrances with soil and vegetation. Elephants use tools in various ways. They sometimes destroy electric fences by dropping logs or rocks on them. Throwing, kicking, or rolling objects at intruders and competitors is a common behavior. They often use tools for self-maintenance, such as using leafy branches as fly swatters or sticks to scratch their bodies in places their trunks can't reach. They have been known for a long time to place vegetation and soil over dead elephants and humans. Some bottlenose dolphins carry sponges on their rostra for protection while digging into the ocean floor searching for prey. Several whale species use bubbles to trap fish, but the exact mechanism is unclear.

Tool use in primates is the most studied and perhaps also the most intuitive due to its similarities to human tool use. Only a few cases of tool use in prosimians are known, the most typical being the application of urine or other scents to their bodies. Many New World monkeys drop or throw objects at competitors and intruders. Capuchin monkeys are the most renowned tool users of this group. They habitually pound stones against nuts, dig up roots with stones, use probing sticks in extractive foraging, and apply odorous objects to their fur. Two have even been observed to bait ducks with bread and then kill them. Throwing and dropping objects is also common in Old World monkeys. Some macaque populations frequently use stones to hammer on

hard mollusks or floss their teeth with hair. Many monkeys learn to use reaching tools in captivity. Most ape species use tools extensively in the wild and in captivity. Like in other primates, agonistic dropping and throwing is common. Only a few additional anecdotes of tool use in gibbons are described. The list of tool use modes in great apes is very extensive, but a general pattern is that chimpanzees and orangutans are more habitual and diverse (nearly all modes) tool users than gorillas and bonobos.

The archeological record reveals how tools have affected the evolution of the hominin lineage, with the oldest found tools dating back 3.3 million years. Considering the advanced spatial reasoning and dexterity required to manufacture and use these stone tools, they had likely been around for longer. It is therefore possible that the last common ancestor of hominins and chimpanzees used such tools. Primate archeology aims to uncover the origins and context of tool use through time. Chimpanzees and capuchin monkeys are particularly valuable species because they use stone hammer tools, which are preserved better than organic tools. Assemblages of stone tools used by chimpanzees date back at least 4,300 years, which corresponds with more than 200 generations (Haslam et al. 2009). Similar assemblages have been found in Brazil, where bearded capuchins have been using stone tools for at least 600 years, corresponding to approximately 100 generations (Haslam et al. 2016). The continued use of such tool sites highlights the importance of tool use for these two nonhuman primate species, with similar finding expected for others – possibly even non-primates. Because stone tool use is rare and capuchins are only distantly related to humans, it seems to have evolved independently in these lineages.

In contrast to longstanding opinions of only species closely related to humans using tools, Shumaker et al. (2011) did not find clear ecological or phylogenetic predictors. Hunt and colleagues (2013) recognize two types of tool users. Tool use in invertebrates and fish is mostly innate, stereotyped, asocial, ubiquitous within species, conserved throughout their phylogeny, and highly context-dependent (invariable inflexible). Tool

use in mammals and birds is, in contrast, less stereotyped, more flexible, innovative, requires higher cognitive abilities, relies more on learning (both individual and social), has distinct developmental phases, shows fewer phylogenetic patterns, and has a higher proportion of tool-using species. The only exception is anting in birds and agonistic throwing in primates because they are more widespread and stereotypical. Hunt and colleagues suggest that the rarity of animal tool use originates in a lack of suitable preexisting behaviors. Stereotypical tool use arises from certain object-related mechanical actions, an appropriate ecological context, and phenotypic change. For example, ant-lion larvae dig pits in the sand with stereotyped head movements. Directing this movement toward insects constitutes tool use because the sand serves as a throwing tool with the function of displacing prey. This change in context became adaptive and could be maintained and spread in a species by specifically directing this behavior toward certain stimuli leading to increased prey capture.

Hunt and colleagues (2013) also describe three constraints on flexible tool use: learning that an object can be used to solve an otherwise difficult problem, working memory capacity for dealing with increased sequential and relational complexity, and manipulation abilities necessary for executing the behavior. In a similar vein, Sanz and Morgan (2013, p. 12) claim that ecological opportunity is not sufficient to support widespread tool use and that “emergence of a particular tool behavior may require a certain threshold of abundance: (i) to provide repeated exposure to the target resource, (ii) to make the foraging for this food resource energetically profitable, (iii) to allow the tool user to gain sufficient experience with the tool using task, and/or (iv) to provide exposure to socially transmitted information.”

Cognition

Tool use has long been considered a hallmark of intelligence. For example, Thorpe (1963) asserted that as long as trial-and-error learning can be excluded, tool use is insightful because it shows

an understanding of spatial and mechanical relations. The discovery of novel or sophisticated tool use often receives wide attention, partially because customary tool use is rare in the animal kingdom but plays a prominent role in our everyday life and throughout our evolution (Call 2013). Indeed, media reports frequently show up along the lines of “since tool use is intelligent, and X species uses tools, then X species is intelligent,” or “since chimpanzees use a (specified) type of tool, and X species uses the same type of tool, then X species is as intelligent as chimpanzees” (Shumaker et al. 2011, p. 212).

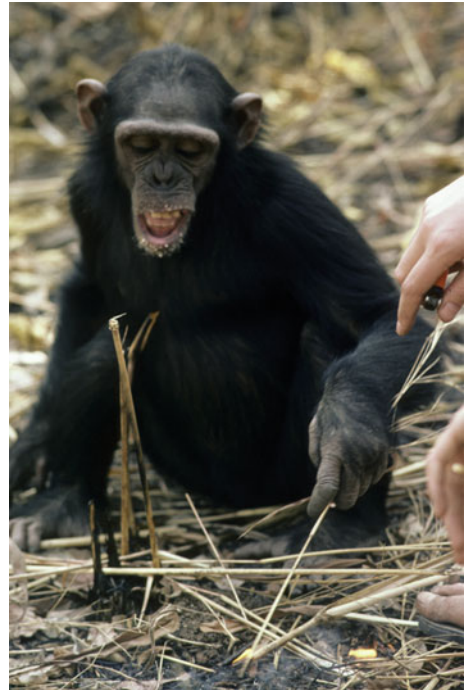
As already mentioned in the previous section, tool use takes many different forms in various species and does not necessarily require complex cognitive abilities. Köhler (1927), who pioneered tool-use tests in chimpanzees, cautioned that stereotyped terms like tool use are clichés that obscure the true details of animal behavior. Tool use is often described as more complex than simple object manipulation because it involves a tertiary relation between own body, goal object, and tool, but this by itself does not mean it is inherently more cognitively demanding than other behaviors (Birch 1945; Hunt et al. 2013).

One of the most intuitively appealing instances of tool use is using a stick to acquire an out-of-reach food piece (Thorpe 1963). This sort of tool use fits most definitions because the tool acts as a functional extension of the body (Seed and Byrne 2010). Many species use tools to extend their reach. Using sticks to reach for food that would otherwise be unobtainable has been reported in yellow-crowned parakeets, Goffin cockatoos, keas, New Caledonian crows, Hawaiian crows, African elephants, spectacled bears, and a host of monkeys, gibbons, and all great apes (Laumer et al. 2016; Rutz et al. 2016; Shumaker et al. 2011; Tebbich and Teschke 2013). Not surprisingly, the frequency and underlying cognition of use of reaching tools varies strongly, which has been an experimental paradigm for a long time. For example, chimpanzees are known to ignore a stick if the food is within reach, choose a stick that is sufficiently long, ignore irrelevant perceptual aspects of the stick (such as color and texture), focus on establishing contact between stick and food, and

flexibly substitute the food for any other goal item (Povinelli and Penn 2011).

Even in species that habitually use tools, experience can play a pivotal role in the development of fully functional tool behavior. Birch (1945) tested six young chimpanzees on a reaching problem. Four of them failed to use a rake to pull in out-of-reach food in the course of 30 min. They kept trying to reach the food with their arms and frequently moved the tool aside as if it was in the way. One chimpanzee accidentally brushed against the tool, after which the food moved closer. He then pulled the tool until the food was within reach. The other successful subject, who often played with twigs and branches, immediately pulled the tool and quickly obtained the food. All chimpanzees were then exposed to sticks (nonfunctional rakes), which they often played with and manipulated, even in the form of poking other chimpanzees and the experimenter. After 3 days, they were tested on the same problem. All six chimpanzees used the tool to rake in the food in 20 s or less. They were also able to use a regular straight stick to retrieve the food, although with more difficulty. When confronted with food in a pipe, three chimpanzees successfully inserted a stick to push it out. This shows their flexible behavior, because although the same objects functioned as a tool (the stick), the required action was the opposite of how they retrieved the food in previous trials. Such reorganization of experience into functional relations is commonly viewed to be at the center of insight, which goes beyond trial-and-error learning (Emery 2013; Köhler 1927; Thorpe 1963).

The goal object does not have to be out of reach for tool use to be advantageous. A tool is a useful way to explore an object if physical contact is best avoided. Chimpanzees (Povinelli et al. 2010) and New Caledonian crows (Taylor et al. 2012) use tools to explore aversive stimuli such as rubber snakes, or to retrieve food that is within reach when positioned next to such stimuli. At least primates, and possibly many other species, include tools into their body schema after sufficient experience, meaning they represent tools as extension of their own limbs. Despite this representation, they use tools in manners they would



Nonhuman Tool Use, Fig. 2 A rehabilitant chimpanzee pokes a small fire with a piece of straw. This exemplifies that using tools in potentially dangerous situations can be advantageous. Reprinted from *Current Biology*, 20, Seed, A. M., & Byrne, R. W., Animal tool-use, R1032-R1039, Copyright (2010), with permission from Elsevier. <http://www.sciencedirect.com/science/journal/09609822>

not use their arms, which has also been an important aspect in human evolution (Povinelli et al. 2010). Using tools to explore fire is one example (see Fig. 2).

Tufted capuchin monkeys are habitual tool users and, like chimpanzees, are able to push a tool into the end of a tube so the contained food falls out on the other side. A popular variation of these tests is the trap tube, which is a transparent horizontal tube with a trap on the bottom that would capture the food if it were moved there. Success thus depends on avoiding this trap and moving the food out on the other side of the tube. It relies on understanding the relationship between the agent, food, tool, and trap, which adds another dimension (the trap) to other kinds of reach tool use. Most capuchins and chimpanzees failed this task, and the successful ones seemed to learn to simply avoid the trap. This

strategy remained present when the tube was inverted so that the trap was nonfunctional because it was at the top of the tube. Many researchers therefore concluded that capuchins and chimpanzees lack the kind of causal understanding that is often assumed to underlie their tool use (Seed et al. 2011).

However, it subsequently became clear that such results do not unequivocally point to that conclusion. Apes performed better when given a thinner tool that allowed them to pull instead of push, when only one tool was present, when the tool was not pre-inserted, and when they could use their fingers instead of tools. Adult humans also continued to avoid the trap in the inverted trap-tube, showing it to be a poor control test. Solving this test is not limited to primates. Rooks, a non-tool using corvid species tested with pre-inserted sticks, and a woodpecker finch also passed. It is possible that the successful subjects relied on arbitrary cues because it took them tens of trials to reach criterion, which allows for plenty of trial-and-error experience (Seed et al. 2011). A reduction in number of trials to reach criterion is not indicative of qualitatively different cognitive abilities (Povinelli and Penn 2011). Another trap was introduced in various configurations, such that the food was between both traps and sometimes had to be pushed into a trap for it to be retrievable. Three New Caledonian crows and a rook passed this test, as did a chimpanzee on the non-tool version, which suggests they were using relevant causal properties rather than arbitrary cues to reach a solution (Seed et al. 2011). Only 3 out of 14 woodpecker finches solved the initial task with two traps, but none performed above chance on the transfer task (Tebich and Teschke 2013).

Seed and colleagues (2011) classify knowledge about object properties into three kinds. Perceptual knowledge is limited to object properties that are immediately available to the senses. Solving the trap tube has to be learned based on perceivable properties that have no causal connection to the task itself, and transfer to novel tests is only possible if some learned cues remain present. Structural knowledge involves encoding functional properties such as continuity and solidity.

It allows for transferring between configurations of the trap tube because the causally relevant principles remain, and a change in perceptual features does not matter. Subjects that passed the trap tube with two traps and its transfers have such structural knowledge. Symbolic knowledge is based on seemingly arbitrary cues having meaning that cannot be reduced to perceptual or structural knowledge. An opaque trap tube where the position of the trap can be inferred from a painted line is an example, which appears to be absent in animals, and starts developing in children at 6 years or older.

In contrast to Birch's (1945) chimpanzees that could use a tool to push out food after having used a tool to pull food from a tube, others fail to do this in the trap tube test. One possible explanation is that the number of elements and their relational complexity simply becomes too high when the trap is introduced (Povinelli and Penn 2011). Goffin cockatoos, which are not known to use tools in the wild, were trained on using two tools, each only functional for one type of apparatus. When given the choice between a functional tool and a non-preferred food, they chose the tool, with which they could retrieve a preferred food item from the apparatus. They instead took the non-preferred food if the tool was of the wrong type for the presented apparatus, such that it could not be used to retrieve the preferred food from within. However, when presented with both tools and both apparatuses, with a different food type in each, they failed to choose the tool that would be functional on the apparatus that contained the preferred food. This suggests that the cockatoos failed to simultaneously consider six dimensions, possibly leading to a relational complexity too great for their attention and/or working memory (Laumer et al. 2016).

One method for quantifying tool-use complexity is categorizing its relational and spatial aspects. Frigaszy and Cummins-Sebree (2005) identify five such properties: (1) number of spatial relations between external elements (e.g., raking in food involves only one relation, that between stick and food); (2) positioning of objects in relation to body and environment, with body-centered actions being more direct (e.g., placing a cup on a

saucer is relatively indirect and difficult compared to just picking it up); (3) precision required for action, with more precise actions being more complex (e.g., hitting a log with a mallet is easier than hitting a nail with a hammer); (4) temporal nature of control, with static actions not requiring any action to maintain a produced relation, and dynamic relations requiring continuous action and monitoring (e.g., a tool can no longer be manipulated once thrown, but raking in food is a dynamic action); and (5) temporal order of production, with concurrent relations requiring more divided attention, coordination, and working memory than sequential relations (e.g., hammering while holding the nail against the substrate is typically more difficult than first securing the nail into the substrate and then hammering it). Systematically varying experimental settings can uncover the properties that influence performance on a given tool task.

Like the cockatoos, chimpanzees and orangutans consider several dimensions of tool-use tasks and take a functional tool over food if it can be used to obtain better quality food (Osvath and Osvath 2008). They even do so with foresight and in the absence of a visible reward, which was often regarded as a uniquely human trait (Oakley 1956; Seed and Byrne 2010). In contrast to these apes, Goffin cockatoos are not known to be habitual and proficient tool users in the wild. Cockatoos may have sufficient general cognitive capacities to succeed on such tool-using tasks. Specifically, they have high behavioral flexibility, inhibitory control, and sensorimotor skills (Laumer et al. 2016).

There are numerous additional examples of non-tool using species performing at similar levels as tool specialists. For example, after their surprising performance on the double trap tube, rooks were tested on a series of tool-use tests. Following training to drop a stone down a tube to collapse a platform containing food, they chose stones according to the size of the tube, used sticks for dropping when they were heavy and for pushing when they were light and long, and even used and manufactured hook tools to retrieve a bucket with food. These results largely mirror those of their tool-using cousins, New Caledonian crows

(Emery 2013). This behavior follows the definition of insight because it is “spontaneous (i.e., not the result of explicit training or trial and error), novel (i.e., not performed before), functional (i.e., solve the problem and be goal-directed), and built from previous, untrained, similar behavior (i.e., not produced from copying earlier learned responses, but adapting previous behavior into new actions)” (Emery 2013, p. 80). However, what insight is – if it indeed reflects a true cognitive mechanism – and what qualifies as sufficient evidence remains a hotly debated topic (Call 2013; Hunt et al. 2013; Jelbert et al. 2015; Seed and Byrne 2010).

In some cases, tool-using species do not even outperform their non-tool-using relatives on tasks that do not require tools. For instance, woodpecker finches did not outperform small tree finches, a closely related species that does not use tools, on two tests of physical cognition and one of reversal learning, although they did perform better on a novel operant task. Woodpecker finches still develop tool use without observing others do so, although it appears there is a sensitive ontogenetic phase during which they have to learn how to use tools or they never will. These results suggest that tool use in woodpecker finches arises from genetic predispositions, trial-and-error learning, and stimulus generalization, which overall do not result in specialized cognitive abilities because their close relatives perform at similar levels. One possibility is that their last common ancestor already had these cognitive abilities and that tool use in woodpecker finches is an adaptation to their ecological circumstances, similar to the foraging specializations of other Darwin’s finches (Tebbich and Teschke 2013).

Emery (2013) describes three lines of evidence that tool use is not necessarily associated with enhanced cognitive abilities. First, tool specialists may not perform well on tool-related physical cognition tasks. Woodpecker finches are an example of this. Second, tool specialists may perform better when a task does not involve tool use, as is the case for chimpanzees using their fingers rather than a tool to solve the trap-tube test. Third, species that do not use tools in the wild may have similar cognitive capacities as their tool-using

relatives, even when the test itself involves tool use. This can clearly be seen in rooks and Goffin cockatoos.

So how plausible is Aesop's fable of the thirsty crow? This question is difficult to answer because we don't know the context and previous experience of the crow – or even what species it was. Nonetheless, recent studies provide ample speculations. For instance, a pet blue jay regularly dropped items into its water bowl if the level was too low for drinking (Shumaker et al. 2011). The first formal experiment was on rooks, but their success might come from generalization because they already had previous experience dropping stones into a tube to collapse a platform. Unexperienced New Caledonian crows did not spontaneously drop stones into a water-filled tube containing a floating food item. All other experiments therefore started with training subjects on the collapsible platform apparatus. Both species stopped dropping stones once the reward was within reach, showing goal-directedness. This was also evident in Eurasian jays, another corvid species, which preferentially dropped stones into baited rather than non-baited tubes (Jelbert et al. 2015).

Overall, most of these corvid subjects preferentially selected large over small stones; sinking over floating objects; solid over hollow objects (which displace less water); water-filled over empty, sand- or sawdust-filled tubes; and narrow over wide tubes when the stone supply was limited. They generally failed when the functional cues were arbitrary or counterintuitive, such as dropping a stone in one tube to raise the level in another. This stark contrast suggests that corvids rely on functional cues, even when noncausal cues give similar visual feedback. Nonetheless, immediate feedback likely enabled subjects to learn quickly, because the proportion of correct initial choices was not above chance. They also seemed to prefer solid objects, even when solidity did not matter as in the platform-collapsing apparatus. Five-year-old children perform at similar levels. In conclusion, stone-dropping behavior in this paradigm is largely explained by object bias, visual feedback, and rapid learning based on causal cues (Jelbert et al. 2015). Aesop's fabled

crow might thus have been less insightful than described.

Conclusion

Tool use is no longer a defining characteristic of humans. It is increasingly often discovered to take novel forms and functions in a wide range of species. There are of course differences between humans and nonhuman animals in how they use and represent tools, but these differences are not as pronounced as regarded some decades ago. Animals only rarely use tools to make tools, seldom cooperate in using or making tools, and power their tools only with gravity and their own metabolic energy (Shumaker et al. 2011). The proposed differences mostly lie in humans having more developed representational abilities, executive functioning, sensorimotor abilities, dexterous manipulation, and collaborative culture (Call 2013; Frigaszy and Cummins-Sebree 2005; Hunt et al. 2013; Povinelli and Penn 2011; Seed and Byrne 2010). Nonetheless, both difference and similarities between species are informative, without the need to redefine tools and mankind or accept other species as humans. If we truly want to understand tool use, we need to clearly define and describe it and look at the ecology, evolution, and cognition of a wide variety of species.

Cross-References

- [Advanced Tool Use](#)
- [Bird Tool Use](#)
- [Cephalopod Tool Use](#)
- [Confounding Use of Tools on Physical Tasks](#)
- [Evolution of Tool Use](#)
- [Fish, Amphibian, and Reptile Tool Use](#)
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- ▶ Sequential Tool Use
- ▶ Social Tool
- ▶ Stick Tools for Foraging
- ▶ Technical Intelligence Hypothesis, The
- ▶ Tool Manufacturing
- ▶ Tool Play
- ▶ What Makes a Tool

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Noniconic Form-Meaning Mapping

- [Arbitrary](#)

Non-independent Mate Choice

- [Mate Poaching](#)

Non-parental Child Care

- [Child Care](#)

Nonparental Childcare

- [Day Care](#)

Non-paternity

- [Seeking Extra-Pair Partners](#)

Non-penetrating Injury

- [Specific Brain Damage](#)

Non-primate Mammal Sperm Competition

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Synonyms

[Interindividual male gamete rivalry in oocyte fertilization](#); [Post-copulation strategies in oocyte fertilization](#)

Definition

Post-copulatory scenario in which the sperm of males of polygamous species competes within the female genital tract to fertilize the oocyte.

Introduction

In many non-primate mammalian species, females may mate with more than one male. According to the sperm competition theory, the reproductive success of the males of such species depends on both the magnitude of inter-male

rivalry and covert sperm competition. When the ejaculates of two or more males must compete to fertilize a set of ova, the quality of the sperm they carry becomes of great importance. The transfer of large numbers of spermatozoa in competitive situations is an effective strategy; males that transfer more sperm per ejaculate, or who copulate more often, are more likely to sire offspring. Usually, males of polygamous species have large testes and produce ejaculates with many sperm cells. Sperm competition also acts as a selective force driving evolutionary change in sperm morphology and function. The degree of sperm pleiomorphy shown by a species varies according to the degree of sperm competition its behavior entails.

Sperm Competition in Polyandrous Species

The sperm of some individuals appears to enjoy advantages over that of their rivals. This is particularly important in polygamous species that practice polyandry, including rodents and many ruminants. Females can benefit from polyandry since males successful in both pre-copulatory (e.g., intra-sexual fighting) and post-copulatory (sperm competition) sexual selection are more likely to sire high-quality offspring.

In many species in which female preference is important in mate selection, males with large and conspicuous sexual selection traits are commonly favored; indeed, male ornaments, to which female attention is paid, play a significant role as part of pre-copulatory strategies. In polygynous species, mate selection focuses mainly on the role played by weaponized male secondary sexual characteristics. Antlers and horns are employed in the pre-coital strategies of several ruminant species, the males using them to establish their dominance. A relationship between horn development and seasonal changes in breeding activity is clearly evident, with wild ruminants attaining maximum horn development just before the onset of the breeding season. However, this weaponry also appears to be a sensitive indicator of genetic stress and a means of providing signals of male vigor to

females. The role of symmetry, a characteristic of genetic vigor, in the attraction of females is well established in many species. Thus, dominant males with larger and more symmetrical horns are likely to be selected for reproduction via their improved access to receptive females, but also via the latter's preference for them.

In some species in which females mate with more than one male, the *sperm competition theory* indicates that male reproductive success depends upon the magnitude of inter-male rivalry and covert sperm competition (Preston et al. 2003). Reproductive success is thus a function of both pre- and post-copulatory strategies. Certainly, larger weaponry is often associated with better sperm quality in polygynous ruminants. Horn and antler size in wild ruminants such as ibexes and red deer is associated with testis size and sperm velocity, and in ibexes, males with the largest and best-developed ornamentation produce semen with a larger proportion of motile spermatozoa and a smaller number of sperms showing primary morphological abnormalities (Santiago-Moreno et al. 2009). This provides some evidence to support the phenotype-linked fertility insurance hypothesis. It may even be that wild bovid and cervid females use horn/antler quality as an index of male genetic and sperm quality. However, when the ejaculates of two or more males compete to fertilize a set of ova, the quality of the sperm they carry becomes of great importance. The transfer of large numbers of sperm is guaranteed by ejaculates with high sperm concentrations, and males of polygamous species usually have large testes and produce ejaculates with high sperm concentrations (e.g., the testis size/body size ratio is higher in promiscuous dogs [*Canis lupus familiaris*] than in monogamous wolves [*Canis lupus*] [Asa et al. 2016]). Successful competition between rivals at the site of fertilization then depends on the number of spermatozoa that enter the oviductal isthmus (sperm reservoir), the proportion of spermatozoa that undergo capacitation and the proportion that respond to ovum-associated signals.

In mammals, sperm length has been positively correlated with maximum sperm velocity.

Although larger sperm heads might be thought a handicap to rapid swimming, several reports show that sperm with longer heads may swim faster (Gomendio and Roldan 1991; Malo et al. 2005). In scenarios of sperm competition, this may afford them a competitive advantage, as may the ability of sperm to maintain high concentrations of intracellular ATP (Tourmente et al. 2015). Indeed, differences in the intensity of sperm competition appear to influence the sperm morphometric variables of wild polygamous ruminant species. For example, in mouflon (*Ovis musimon*), a species with intense polyandry, rams produce sperm with larger heads (and in greater numbers) than other Mediterranean mountain ungulates such as the ibex (*Capra pyrenaica*), aoudad (*Ammotragus lervia*), or chamois (*Rupicapra pyrenaica*). Chamois sperm, which has the smallest head dimensions and is produced in more modest concentrations, may indicate the species to be less polyandrous (Pradice et al. 2016).

Sperm competition also acts as a selective force driving evolutionary change in sperm morphology. The degree of sperm pleiomorphy shown by a species varies according to the degree of sperm competition its behavior entails. Although this is more evident in birds, monogamous mammals (e.g., species of Felidae except for the lion) usually have a higher rate of sperm morphological abnormalities than do very polygamous species, such as many ruminant species.

Sperm variables in polygynous ruminant species in which polyandry plays an important role are related to horn/antler characteristics, revealing a likely strong genetic influence. The social environment may, however, also affect these variables. The social status of an animal varies over its lifetime, even though it might possess high-quality weaponry. The social environment affects physiological variables, such as plasma testosterone and cortisol concentrations, that in turn influence spermatogenesis and sperm maturation and subsequently sperm quality. An impact on seminal plasma composition, e.g., on the seminal fluid proteome composition, might also be expected. Indeed, in some rodents the plasticity of different ejaculate components may be strongly influenced by social environment (Ramm et al. 2015).

Conclusion

Reproductive success in polyandrous species is a function of both pre- and post-copulatory strategies. With respect to the latter, sperm competition plays an important role and is dependent on sperm concentration, sperm velocity variables, and the proportion of sperm produced with morphological abnormalities.

Cross-References

- [Competitive Mating](#)
- [Multiple Matings](#)
- [Polyandry](#)
- [Reproductive Strategies](#)
- [Sperm Competition Theory](#)

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Nonsenescent-Related Mortality

► [Extrinsic Mortality](#)

Nonsexual Social Selection

► [Specific Friendships](#)

Non-transient Ontogenetic Adaptations

► [Deferred Adaptations](#)

Nonverbal

► [Communication and Social Cognition](#)

Nonverbal Communication

► [Vocal Communication](#)

Nonverbal Indicators of Dominance

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Synonyms

[Fighting ability](#); [Formidability](#)

Definition

Dominance in large part is having power or influence over others. An important part of negotiating access to resources, be it food or mates, throughout the animal kingdom and ancestral humans is/has been achieved through physical force, particularly between males. For example, men who repeatedly win fights and contests against other men (intrasexual selection) are often revered in society, and their status within the group is elevated (Hill and Hurtado 1996). This functions as a deterrent to potential competitors from challenge and is known as *physical dominance*, which will be the focus of this section.

Introduction

The ability to make accurate assessments of physical dominance in species with aggressive social interactions is of particular importance as it can ultimately fall within the realm of natural selection. People who have the potential to inflict serious or even fatal physical harm is a strong selective force and it makes sense that our perceptual system has evolved cognitive mechanisms in which to make dominance judgments based off a number of cues.

This section will focus on male cues of dominance as males have productively limited access to mates and have engaged in intra-sexual

conflict, be it one-on-one, or in a coalitional sense (e.g. war) (Keeley, 1996).

Static Cues

It is well known that humans have highly specialized neurological structures to quickly extract information from faces as these hold the key to many social interactions such as the identification of emotions, sex, age, and attractiveness. Aggressive confrontations are often acutely time sensitive and given our affinity with faces, it makes them an ideal structure in which to assess dominance.

Intrasexual selection is thought to have been a strong selective pressure on men's bone structure resulting in thicker skulls, pronounced brow ridges, and more robust mandibles in order to provide better protection from damage (see Puts 2010 for a review). The expression of men's facial structure is thought to be at least in part determined by prenatal testosterone exposure in utero with higher exposure leading to more exaggerated expression of such traits. At puberty these structures are activated by the surge of circulating testosterone thus contributing to sex differences in appearance. Prenatal testosterone exposure also leads to many other organizational effects on men such as increased physical strength and cardiovascular fitness – all of which can be attributed to the ability to fight.

Research has found that exaggerated masculinized features lead to higher ratings of dominance by both men and women (e.g., Neave et al. 2003) and that people are generally accurate when judging strength and formidability (fighting ability) from men's faces (Sell et al. 2009). Furthermore, men with masculinized facial structure typically have higher circulating testosterone (Penton-Voak and Chen 2004; Roney et al. 2006) which is attributed to more dominant behavior (Mazur and Booth 1998).

A rapidly growing area of research has begun to document how the ratio between the width and height of a face (fWHR – bizygomatic width divided by upper facial height to be precise) is correlated with many dominance traits,

particularly aggression. If a man has a high fWHR (they have a wider face), then this seems to be associated with more aggressive reactions to a perceived slight by others, greater sporting penalties resulting from aggressive fouls, as well as socially aggressive behavior such as being self-interested and performing more violations of trust in economic games (Haselhuhn et al. 2015). Furthermore, men with higher fWHR's have also been found to have more circulating testosterone (Lefevre et al. 2013) which might be a mediating factor in explaining these behaviors. Interestingly, these associations appear to be exclusive to men and no relationships are found between fWHR and dominance-related traits in women. Taken together this suggests fWHR is a cue to dominance in men.

Aside from facial structure, another source of dominance information is a man's facial hair. Facial hair does not hold any clear survival value, it is not usually present in women or children, and its expression is dependent on testosterone (Saxton et al. 2015). From an intersexual point of view, facial hair growth does not relate clearly and consistently to ratings of attractiveness. However, dominance ratings show a positive linear pattern with facial hair prevalence indicating that beard growth might have primarily evolved via intrasexual means.

Perceptions of dominance are subject to individual differences, particularly in relation to the observer's own dominance status. Studies have shown that a man's self-rated dominance affects his ratings of faces manipulated for dominance. Shorter men are more sensitive to cues of dominance and rate men's faces as more dominant than taller men do (Watkins et al. 2010, 2013). This has been explained in terms of allowing less dominant men to avoid conflicts that might be costly. However, this moderation effect does not hold true for all studies and there is some debate as to whether these effects are in fact robust (Lefevre and Lewis 2014).

Another indicator of someone's physical dominance status is of course their size and build. Men have around 75 % greater upper body muscle mass than women and are typically taller and heavier with broader shoulders (see Sell

et al. 2012). These traits are easily observable and are perhaps one of the most direct ways in which to assess physical dominance. The reason men have greater upper body muscle mass than women is that this is the primary mechanism for inflicting damage, be it grappling, choking, or punching. As expected, when observers are shown static photographs of men's torsos they are able to quite accurately gauge that man's upper body strength however, this relationship does not hold true for his lower body strength suggesting our perceptions are engineered for detection of fighting strength (Sell et al. 2009).

Dynamic Cues

There are numerous occasions where the static features on which we rely on to make dominance judgments might be concealed, for example, when it is dark, the person is wearing clothing or they are at a distance. As these factors are common in everyday life and the costs of misjudging someone's fighting ability may be grave, we might predict that humans have also developed ways in which to assess dominance using other mediums.

The ability to perceive motion is an ancient information channel and was likely developed before our eyes had sufficient resolution to interpret static detail. Motion is detected and processed very quickly and likely evolved as a result of natural selection in order to detect predators. Several strands of evidence support the hypothesis that movement provides reliable information about an organism's physical condition as unlike many static constructs, movement is very difficult to fake or conceal. In the animal kingdom, for example, it is used to size up competitors before serious intra-sexual conflicts (for example, deer and some species of fish, see Sell et al. 2012 for a review).

The ability to record human movement with sufficient control (for example, removing structural confounds like facial attractiveness and body size) was developed in the 1970s by Swedish psychologist Gunnar Johansson and are known in the literature as point-light displays (PLDs). PLDs are comprised of an array of dots that

typically represent the major joints and structures of the body and when viewed as a static frame, people have trouble interpreting what they are or represent. However, when they start moving a vivid representation of a person's motion.

By observing only very brief presentations of PLDs depicting walking (as it is a motion we see every day), observers are able to resolve the sex of the walker with accuracy (typically in the region of 70 %). A typical male walk involves greater lateral shoulder sway and very little hip movement, whereas the opposite is true of a typical female walk (Troje 2003).

Raters give equivalent answers irrespective of whether they are asked if a PLD is of a female walker or a feminine walk. In contrast, when asked whether a walk is masculine versus whether it is a male walk, a disconnect occurs and observers will report a walker to be male much earlier in the continuum (between neutral and extreme male walk) than to assign the walk as "masculine." This is thought to be attributed "precarious manhood," a term that suggests simply being a man is quite a different concept to being a *real man* (i.e., being masculine) (Kozlowski et al. 2016).

The composition of PLDs means that facing direction is absent as there are no depth cues. When observers are asked the sex and facing direction of a sex neutral, or male walk, they will typically default to reporting that walker as walking toward them. In contrast, obvious female walkers are more likely to be perceived as walking away from the judge. Furthermore, sex neutral walkers are typically judged as being male. This is thought to be a perceptual failsafe as misjudging a male for a female and/or their facing direction may be risky. Men seem to be particularly sensitive to this effect and report extreme male walks to always be walking toward them. This again fits with a threat detection hypothesis as these cues are more relevant to them and may inform them of potential conflict (Schouten et al. 2011).

All of these factors indicate that observers have quite specific perceptions of dominance based solely on walking gait, and we have evolved cognitive mechanisms that help us size up how

dominant a man is, and have built in failsafe's to avoid misperception of facing direction. However, research to date is lacking in evidence that informs us how accurate people's perceptions are, that is, do dominance ratings track the actual dominance status of the walker?

A separate body of research has documented how body postures and gestures lead to perceptions of power and dominance (and even lead to greater feelings of power in the poser) although these judgments have primarily been attributed to more social dominance and leadership rather physical dominance. For example, when observing political candidates, key movement parameters that lead to increased perceptions of (social) dominance are more expansive body postures and gestures as well as greater movement frequency (Koppensteiner et al. 2016). While these ratings are judged in more of a social dominance context, these perceptions are likely to be rooted in the detection of physical dominance. The size of a person is a major factor in how dominant they are perceived to be, and larger men are generally more dangerous than smaller men so making yourself look larger using expansive gestures and posturing is likely to lead to increased dominance ratings.

Conclusion

Intrasexual competition has likely been a very salient selective force in humans, particularly for men. This led to the development of increased aggression, greater upper body muscle mass in order to deal damage, and to stronger, thicker bones to help limit damage incurred in fights. The risk of misjudging a potential rival can lead to serious injury or even death, and research indicates we can call upon a wealth of cues in order to make our assessments from static cues in the face and body as well as more dynamic cues in motion we see every day such as walking gait.

Taken together, the evidence detailed above indicates our perceptual system has evolved cognitive mechanisms in order to assess the dominance status of another person and keep us out of danger from potential threats.

Cross-References

- [Dominance and Testosterone](#)
- [Dominance and Threat or Use of Force](#)
- [Dominance in Humans](#)
- [Facial Width to Height Ratio and Dominance](#)
- [Serotonin and Dominance](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Size and Dominance](#)
- [Social Dominance Reduces Fighting](#)
- [Vocal Indicators of Dominance](#)

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Nonviolent Coercive Control

► Coercive Control

Non-Western Homosexuality

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Synonyms

Sexual expression; Sexual orientation

Definition

Same-sex attraction outside of Western Europe and societies principally characterized by its colonial legacies (e.g., North America).

Introduction

Sexual orientation and homosexuality have been most prominently discussed in Western political and cultural spheres since the late nineteenth century. General understanding of same-sex attraction is thus limited by an absence of perspectives from societies with other cultural traditions and origins. For example, Western scholars and laypeople commonly describe same-sex attraction and sexual behavior using terms like “homosexual,” “gay,” “lesbian,” and “bisexual,” these labels and concepts may not even exist among people living in the cultures to which they are applied (e.g., Nanda 2014). This entry reviews how same-sex attraction might manifest in cultures not informed by Western cultural, social, and linguistic traditions.

The Multitude of Same-Sex Attractions

Western conceptions of sexual orientation typically employ certain linguistic and culturally

normative mental structures to generate representations of same-sex attraction and sexual behavior. Rarely do people in Western societies consider other expressions of same-sex attraction that may be more prevalent in other cultures (see below and Bailey et al. 2016 for examples). The term “same-sex attraction” is therefore a preferred means of describing same-sex relationships because it successfully summarizes the phenomenon of interest while subsuming various manifestations of its expression.

Indeed, although “gay men” and “lesbian women” may not necessarily exist in non-Western cultures *per se* (Blitzer 2011), expressions of same-sex attraction may exist worldwide. Scholars examining the prevalence of same-sex attraction have estimated that approximately 1.5–5 % of the contemporary world’s population is attracted to other members of the same sex (Smith et al. 2003; VanderLaan et al. 2013; Whitam and Marthy 1986). Given a large enough population, then, individuals oriented toward same-sex attraction should emerge though they may express this differently from one culture to another.

For example, *hijras* in South Asian cultures (Nanda 1998), *berdaches* in Native American cultures (Callender et al. 1983), and *fa’afafine* in Samoa (Vasey and VanderLaan 2014) all express nontraditional sexual identities that may or may not include same-sex sexual behaviors. Yet each case represents a relatively different expression of same-sex attraction and gender identity. Whereas *hijras* and *berdaches* occupy largely spiritual and religious roles that symbolize unification of male and female (exemplified in part through crossdressing), *fa’afafine* men are typically raised and socialized in feminine roles due to their more feminine childhood mannerisms and thus evidence greater pragmatism (Bartlett and Vasey 2006).

These differing expressions highlight two interesting phenomena. First, same-sex expressions in non-Western cultures often rely on “switching” between masculine and feminine roles such that the individual almost transitions in gender (e.g., *hijras*; see Tskhay and Rule 2015). Second, non-Western same-sex expressions

largely stem from iterations on defined gender roles. For example, *fa’afafine* tend to be feminine men who have sexual relations with masculine men; it is rather unlikely that two *fa’afafine* would have sexual relations with each other (Bailey et al. 2016). Therefore, even when same-sex attraction is commonly acted upon, its expression still resembles the heterosexual sexual behavior typical between men and women (Tskhay and Rule 2015).

Conclusion

In sum, same-sex attraction appears to be a relatively universal phenomenon, though its expression may vary greatly from culture to culture. Its varieties of expression are clearly shaped by cultural norms, religious traditions, and practices. However, in most cultures, same-sex attraction still follows structures inspired by more demographically common gender roles, such as heterosexual attraction and behavior.

Cross-References

- Culture
- Homosexuality
- Sexual Orientation

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Normal Sexual Development

► Positive Sexual Development

Normative Ethics

► Relevance of Evolved Interests to Modern Morality

Normative Relativism

► Cultural and Moral Relativism

Norms

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Synonyms

Behavior patterns; Common knowledge; Public behaviors; Rule; Social norm; Standard

Definition

Norms are expectations stating that something should or must be the case or socially shared definitions of the way people do behave or should behave. From a sociological perspective, social norms are informal understandings that govern the behavior of members of a society.

Norms have obtained a great deal of attention in the social sciences, such as anthropology, economics, political science, sociology, and psychology. This article will introduce this item from the perspective of evolutionary psychology. Two main topics will be touched in this review: the emergence of evolutionary social norms and the social norms-marketing campaign resulting from the connection between social norms and behaviors.

The Emergence of Evolutionary Social Norms

Being different from the institutional norms, which are formed and enforced by certain individuals (usually the leader of group) or institutions, and voluntary norms, which emerge by the voluntary agreement among group members, the evolutionary norms and the measures for their fulfillment are not explicitly stated (Karl-Dieter 1982). The emergence of evolutionary norms has

been described by several models, among which the emergence of cooperative and altruistic behaviors have been discussed and explored extensively.

The Kin Selection Model

Developed from a biological approach, the Kin selection model indicated that the degree of genetic relationship played an important role in predicting the selection of altruistic behaviors. According to the genetic relationships of the organisms involved, the altruistic behaviors could be explained in terms of natural selection: the organism would provide help to their relatively close kin in order to ensure the successful delivery of their genes. The kin-selection model predicted that altruistic behaviors depended much on the degree of kinship between giver and receiver.

One study (Rachlin and Jones 2008) indicated individuals would give significantly more money for the benefits of their relatives than for the benefits of nonrelatives at almost every social distance. These results were in line with kin-selection theory and supported the important role of genetic relationship in individual's altruistic behaviors.

However, the kin-selection model cannot explain why individuals show cooperative behaviors toward strangers in some cases. It is obvious that strangers could not be helpful for the organism's reproductive success. Another model of "reciprocal altruism" (Trivers 1971) was proposed to explain this phenomenon.

The "Reciprocal Altruism" Model

According to models of "reciprocal altruism" (Trivers 1971), the chance of evolving for the altruistic behaviors was little in random pairings. However, the evolving chance would increase in a social framework because individuals could benefit from building reputations of being altruistic to

other, which would be beneficial to those who perform altruistic behaviors in the long run. Consequently, the altruistic behaviors would also be favored by natural selection in such cases. In the models, Trivers (1971) discussed three instances of altruistic behaviors – behavior involved in cleaning symbioses, warning cries in birds, and human reciprocal altruism – and further explained their evolutionary mechanisms. As for the human reciprocal altruism, Trivers suggested that "friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, and some forms of dishonesty and hypocrisy" could be explained as important adaptations to regulate the altruistic system. Each individual human was seen as possessing altruistic and cheating tendencies at the same time, the expression of which was "sensitive to developmental variables that are selected to set the tendencies as a balance appropriate to the local and ecological environment." According to Trivers, by properly identifying the other agents in a social framework reputation could influence behaviors of the agent: people who show altruistic behaviors would be treated altruistically and people with a reputation of being indifferent would be treated indifferently. Trivers' opinions have been supported empirically by research (Griskevicius et al. 2010).

Simulating the Emergence of Evolutionary Social Norms with Play Games

Based on the Nash equilibrium, quite a few play games were developed to explore the emergence of social norms, especially the cooperative and altruistic behaviors.

By simulating the norms game and the meta-norms game, Axelrod (1986) explored the dynamical processes of the social norms formation. Based on the simulation of norm games, he further proposed the mechanisms that served to support the partially established norms such as meta-norms, dominance, internalization, deterrence,

social proof, membership, law, and reputation. Among the eight mechanisms, Axelrod suggested that reputation and dominance could serve in the origin and content of norms. Axelrod stated "Dominance can work because if only a few very powerful actors want to promote a certain pattern of behavior, their punishment alone can often be sufficient to establish it, even if the others are not vengeful against defections." Actually this conclusion can be confirmed that many norms complied with by people in daily life served the powerful. In line with Trivers' model (Trivers 1971), Axelrod (1986) also believed reputation was an important mechanism of social norms emergence, especially the cooperative or altruistic behaviors.

With the Trust Game, which is role-contingent and like one-sided Prisoner's dilemma, Bicchieri et al. (2004) simulated the emergence of trust and reciprocation. Their study showed as a result of the repeating interaction of several different strategies, which were conditional ones, the norms of trust/reciprocation could come into being and became the dominant observed behavior. This research enriches Trivers' model by describing the emergence of trust/reciprocation based on several, but not single, behavioral strategies.

Skyrms (1996) and Alexander (2007) explored the norms emergence from the cognitive and structured interactions approaches. With a variety of play games, such as the Prisoner's Dilemma, the Stag Hunt, Divide the Dollar, and the Ultimatum Game, they described how the moral norms came into being under different game situations. Both of them emphasized the simpler mechanisms or leaning rules, such as "imitate the best" or best response, in the different norm-formation games. They pointed out agents would rely on their learning rules to select the appropriate strategy. Being different with the model of Bicchieri and his colleagues, who emphasized the several strategies, Skyrms and Alexander believed norms were developed on the basis of single strategy. It is noticeable that both of them emphasized the role of structured interaction in the norms formation and they made some refinement on this structural approach by

differentiating two different kinds of networks: interaction network and update network.

The Spread of Social Norms

How do the social norms spread and change in real life? A vast literature support that social norms are communicated through social interaction. For example, face to face communication constitutes an important approach for the formation and spread of norms (Chwe 2001). Being consistent with Sherif's group norm theory, which states that social norms of prejudice "are the products of contact with members of a group; they are standardized and become common property within a group," one study (Monteith et al. 1996) indicated that participants' prejudiced opinions concerning gay men and blacks decreased significantly under the activation of non-prejudiced opinions made by a confederate.

In addition, Paluck (2009) emphasized that individuals could shape and were shaped as well by their immediate social surroundings, "alone, people become aware of ideas...in groups they [become] aware of other people's awareness [and]... their endorsement creates another vector of social influence." His study (Paluck 2009) suggested the group listening to an emotionally engaging radio drama could result in the change and spread of social norms due to its socially interactive nature. Paluck believed the heated discussion during and after the radio drama listening "creates another vector of social influence" on listeners and "contributed further to socially shared cognition, which is the basis for a social norm."

The Influence of Social Norms on Individual's Social Behaviors

A variety of research supported the influence of individual's normative beliefs on their social behaviors, or in other words, social norms spurred individual's conforming behaviors.

For example, a cross-cultural study (Zou et al. 2009) proved social norms, or the perceived

cultural consensus, could powerfully predict individual's social judgement. A current research (McGuire et al. 2017) explored the influences of group norms on the behavior of resource allocation among children with an age from 8 to 16 years. The result indicated that participants showed the most ingroup-biased resource allocation under the condition of both the ingroup and outgroup peer norms being competitive. In addition, with years when allocating intergroup resources individuals could consider both ingroup and outgroup norms simultaneously. However, only older children changed their reasoning to justify their allocation according to group norms.

In addition according to the information, delivering social norms can be classified to different types, such as descriptive norms, injunctive norms, and situational norms. Different social norms could make particular effects on the individual's social behaviors.

By informing individuals of what behavior is appropriate or adaptive in certain situation, descriptive norms, which refer to how most people behave in a specific situation (Cialdini et al. 1991), could guide individual's private and public behaviors as well. With two experiments study, Goldstein et al. (2008) indicated descriptive norms could effectively motivate participants to engage in the activities of environmental conservation. Especially when people were confronted with threat or danger, they would be motivated significantly to go along with the social environment (Griskevicius et al. 2006).

In addition to the descriptive norms, the focus theory (Cialdini et al. 1991) proposed another type of social information called injunctive norms, which refer to the individual's perceived degree of social approval /disapproval for certain behavior. According to focus theory, the two types of norms are highly relevant to different fundamental human goals. The information provided by descriptive norm is highly relevant to the intrapersonal goal of behaving accurately or choosing correctly. However, the injunctive norm is especially relevant to the interpersonal goal of establishing and maintaining good social relationship by winning the social approval. The main hypotheses above of focus theory have been

supported by the empirical evidence (Jacobson et al. 2011).

Another type of social norms is the situation norms, which refer to "knowledge or mental representations of appropriate behavior that guide behavior in a certain situation or environment" (Aarts and Dijksterhuis 2003). With three experiments, the study (Aarts and Dijksterhuis 2003) suggested that not all situational norms were able to guide individual's social behavior directly. Only those well-established situational norms, which can be regarded as associations between specific situations and normative behavior in memory, could effectively play the role of activating the normal behaviors under certain situations.

Finally, the emotion also plays a role in the connection between social norms and individual's compliant behaviors.

One study (Colombo 2014) explored the role of emotion in motivating social norm compliance. Contrary with resentment hypothesis (Sugden 1998) and hedonistic hypothesis (Fehr and Camerer 2007), Colombo believed that caring, but not resentment and pleasure, might be the source of feeling emotions and the ultimate motive of norm compliance. On the other way, social norms can also make an effect on people's feeling, such as regret. Based on the classic action-effect, which described the phenomenon that individuals regretted actions resulting in negative outcomes more than they did inactions bringing about the same negative outcomes (Kahneman and Tversky 1982), a recent research (Feldman and Albarracín 2017) supported that "negative outcomes resulting from action are regretted more than when resulting from inaction." With four experiments, their study indicated when social norms were for inaction the action-effect was much stronger and the action-effect would be weakened and even reversed in case of the social norms were for action.

The Social-Norm Marketing Campaign

A large number of programs, which were called social-norms marketing campaign, have been carried out based on the two consistent conclusions:

most people tend to overestimate the prevalence of many destructive behaviors, and individuals usually use their perceived norms as a standard to guide their own behaviors. By delivering the normative information that the occurrence of deleterious behaviors is less than most people think, this campaign aims at correcting people's misperceptions and reducing the occurrence of undesirable conducts, such as excessive drinking, drug abusing, disordered eating, and littering and waste of resources.

Based on social norms-based social marketing campaign, most interventions decreased the level of alcohol consumption (Neighbors et al. 2004) and gambling addiction (Neighbors et al. 2015) on campus successfully. However some research (Granfield 2005) failed to confirm the effectiveness of this approach.

One study (Schultz et al. 2007) provided a potential explanation for the mixed results of the intervention programs. Their research (Schultz et al. 2007) demonstrated delivering high-energy-consuming households with descriptive normative information about the average level of home energy usage in the neighborhood significantly decreased energy consumption. On the contrary, the same information resulted in an improvement of energy consumption for low-energy-consuming households. However, when combining the descriptive normative information with an injunctive message of approval, the low-energy-consumption family would decrease their consumption at the desirable low rate, rather than increasing significantly toward the mean.

Conclusion

The emergence of evolutionary social norms has been explained and explored extensively. In addition to the models of "kin selection" and "reciprocal altruism," other models were developed by simulating the forming process with different play games. Social norms can be spread by face to face communicating and social media as well. A vast amount of literature supported that social norms could spur individual's complying behaviors. By correcting individual's misperception of social norms, quite a lot interventions called social

norms-marketing campaign have been carried out to reduce individual's deviant behaviors although the specific mechanisms still await for further exploration.

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Cooperation](#)
- ▶ [Cooperation in Social Insects](#)
- ▶ [Dominance Hierarchies](#)
- ▶ [Game Theory](#)
- ▶ [Kin Selection](#)
- ▶ [Kinship](#)
- ▶ [Nonhuman Reciprocal Altruism](#)
- ▶ [Prisoner's Dilemma](#)
- ▶ [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Reputation](#)
- ▶ [Robert Trivers](#)

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Norms and Social Contract

- [State-Sanctioned Punishment as Deterrent to Violence](#)

Novel Male Effect

- [Father-Absence and Stepfather Presence](#)

Number Sense

- [Quantity Estimation](#)

Numerical Cognition

- [Space, Time, and Number](#)

Nuptial Gift

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Synonyms

[Bride price](#); [Courtship gift](#); [Dowry](#); [Marriage transaction](#)

Definition

Biologically speaking, nuptial gifts are contributions – other than genetic materials – provided by a donor to a recipient during courtship. These materials are often designed to improve the fitness of the recipient, but can also be of little value or even no value (Lewis et al. 2014). In modern human mating, nuptial gifts exist most notably in the form of engagement and wedding rings.

Introduction

Several species of insects, birds, and mammals are known to give or exchange a diverse range of gifts during courtship or copulation including, but not limited to: nongametic organic materials, food items, and apparently worthless tokens (LeBas and Hockham 2005). In human mating, nuptial giving has existed for most of recorded history (Cronk and Dunham 2007). Modern human courtship often involves men offering prenuptial and nuptial gifts which are of high cost to provide, but of little or no tangible benefit to the female recipients (Sozou and Seymour 2005). Engagement rings and wedding bands are often given as examples of such nuptial gifts.

Brief History

In some cultures, traditions of bride price or bride service, which is a payment by the groom or his family for the bride, are still practiced (Anderson 2007). Also common in some cultures is the dowry, which is a payment of property, gifts, or monetary wealth transferred from the bride's family to the groom and his family. Over time, cultural practices can slowly shift between bride price and dowries, depending on the culture and the location (Anderson 2007). The specific practice of giving wedding rings dates back to early recorded history and engagement rings have been given since the Middle Ages, but only in the twentieth century have these practices become commonplace (Cronk and Dunham 2007).

Evolutionary Development and Benefits

In many taxa, nuptial gifts are known to improve several aspects of female fitness (Brockmann et al. 2012). In some specific species, however, males can replace a gift of value, such as food, with a worthless gift and females will still accept it and mate for a certain period of time (LeBas and Hockham 2005). In humans, this is arguably mirrored by the historical shift from bride prices – which transferred tangible property or money to the bride's family – to engagement rings and wedding bands, which are of relatively little inherent value to her or her family.

The above parallel with worthless gifts is not to say that engagement rings and wedding rings do not serve a purpose. Engagement and wedding rings can be used as bonding devices between partners (Cronk and Dunham 2007), and it is generally known that engagement rings are a sign of increased relationship commitment. Research has linked the quality of nuptial gifts with the overall value of the mates involved (Cronk and Dunham 2007). The amount spent on engagement rings reflects certain aspects of both male and female mate quality. Specifically, males with higher incomes spend more on engagement rings, which can indicate more resource control (Cronk and Dunham 2007). Younger women, who tend to have higher mating and fertility potential, and women with higher incomes are also given more expensive engagement rings (Cronk and Dunham 2007). These patterns indicate that investment in a nuptial gift can be a reflection of perceived male and female mate value. The connection between ring value and mate value can give women valuable information about male levels of commitment to a relationship and the extent to which he may or may not invest in her and her potential offspring (Cronk and Dunham 2007; Sozou and Seymour 2005).

Conclusion

In most taxa, nuptial gifts evolved to improve aspects of female fitness and increase the male's chances of mating, but the history of human nuptial gifts is more complicated. Varying by region,

human marriage traditions have slowly shifted from wealth transactions such as bride price and dowry, which provide tangible benefits to at least one party, to the giving of engagement and wedding rings. Wealthier males, unsurprisingly, tend to spend more money on nuptial gifts, and wealthier females with higher mating potential tend to receive more expensive gifts. Both of these patterns are consistent with the idea that the price of nuptial gifts reflects perceived mate value. Even though engagement rings and wedding bands have almost no practical utility, these gifts may provide women with clues as to a potential partner's commitment to their relationship and her potential offspring.

Cross-References

- [Human Courting](#)
- [Mate Value](#)
- [Sexual Selection in Evolutionary Psychology](#)

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Nursing

- [Breast Feeding](#)
- [Gathering Returns When Nursing Infants](#)

Nursing Advantages

- [Breastfeeding Benefits](#)

Nursing Duration in Human Evolution

- [Duration of Breast Feeding in Ancestral Environments](#)

Nursing in Modern Environments

- [Breastfeeding in Modern Environments](#)

Nurture Assumption, The

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N

Synonyms

[Book; Non-fiction](#)

Definition

A book, written by Judith Rich Harris, which explores the effects of genetic influences and peer relations on personality development.

Introduction

The Nurture Assumption: Why Children Turn Out The Way They Do is a book written by psychologist and independent scientist Judith Rich Harris and was originally published by The Free Press in 1998. The book provides a well-supported

argument for Harris' theory that genes and peers influence the development of one's personality far more strongly than the way one was parented. It has been critically acclaimed by several psychologists – including Robert Sapolsky, Steven Pinker, Malcolm Gladwell, and several others – stating that Harris' provided strong scientific evidence for a profound conclusion. However, the book has also been met with negative reviews by some psychologists who argue that Harris did not include important data that contradicts the conclusion in her book (Begley 1998; Kagan 1998). A second edition of the book was published in 2009 with an extra foreword by Dr. Harris addressing the misunderstandings that many critics of the book had made (Harris 2009).

About the Book

The term *Nurture* within the title refers to the latter half of the classical “nature versus nurture” debate in psychology. In *The Nurture Assumption*, Harris addresses this debate – which asks whether personality and behavior are products of our genes (i.e., nature) or our environment (i.e., nurture) – by examining the scientific research in many areas of psychology, including developmental, clinical, social, and evolutionary psychology. Harris' examination reveals two key points: genes strongly influence personality, and although environment (i.e., nurture) also influences personality and behavior, this influence stems mostly from peers. Parents do not have a strong influence on their children's personality development.

Harris takes time to explain the dangers of inferring causation from correlation, and goes on to explain that most child psychology stems from correlational designs as opposed to experimental designs, which makes it difficult to know what is causing a child's personality and behavioral development. She goes on to cite many twin studies that illustrate the influence that genes have on personality. Genes account for approximately half of one's personality and IQ. For example, identical twins raised together in the same home are no more alike than identical twins raised apart – indicating that genes account for most of the similarities between

these personalities, and home environment plays a very small role in personality development.

The book also contains many examples of how a child's peer group influences one's personality development. This is due to many factors, including the fact that people tend to be drawn to similar others – which cause children to be more drawn to peers than parents (as parents and children are rather unlike in many ways – height, social status, intelligence, etc.). For example, as children grow up, they continue to spend more time with their peers and less time with their parents. In addition, children of immigrant parents will learn the language of their social environment and speak with the accent of their peers as opposed to the accent of their parents. Also, peer rejection in childhood has been associated with maladjustment and poorer adult life status.

The Nurture Assumption also addresses other social psychological theories regarding potential influences of personality, including birth order, social comparison, and group socialization theory. Harris notes skepticism of birth order effects – the theory that one's chronological order of birth in relation to one's siblings (i.e., first-born, second-born, third-born, etc.) influences one's behavioral development. However, Harris cites several findings regarding how comparing oneself to peers, as well as one's role within his/her peer group, influences the development of personality and behavior.

Critics' Responses to the Book

Although *The Nurture Assumption* was lauded by many psychologists, it was also met with controversy. Many psychologists have criticized Harris for taking an extreme position on the nature-nurture topic with very limited data (Begley 1998), while other critics have argued that Harris overlooked some scientific findings that refute the theory that parents have very little influence over their children's personality development (Begley 1998; Kagan 1998). Some psychologists – such as Dr. Frank Farley of Temple University – have expressed concern over the idea that, after reading *The Nurture Assumption*, some parents may decide to neglect and mistreat their children

because they do not think it will have any effect on their children (Begley 1998).

Harris has addressed these criticisms in a foreword she wrote for the second edition of *The Nurture Assumption* (2009). She explained that there may have been some miscommunication between the message the book conveyed and the message that some readers received. This may have been due to having the scientific research cited in endnotes – making it less likely that readers would fully investigate the research she cited – or due to confusion regarding terms such as “peer group.” In regards to the concern over whether some parents may neglect or mistreat their children after reading her book, Harris points out that parents love their children not because they are required to. Most parents love their children because they want to; not because loving their children is the only way for the child to grow up to be a decent human being. “A good relationship is one in which each party cares about the other and derives happiness from making the other happy” (Harris 2006).

Conclusion

The key point of *The Nurture Assumption* focuses on the fact that, although children learn from their parents, they seem to learn more from their peers. As children continue to grow, they learn more from their peers and less from their parents, causing their personality development to be influenced more by their peers (and their genes) than their parents. The purpose of Harris’ book was to help decrease the anxiety that parents have when they fear they are harming the development of their children by not being perfect parents. Because children are influenced significantly more by their genes and their peers, Harris explains that her intent with *The Nurture Assumption* was to “make child-rearing a little easier, a little less stressful for parents. Alas, it has not happened, as far as I can tell.” (Harris 2009, p. xxii).

Cross-References

- ▶ Judith Rich Harris
- ▶ No Two Alike
- ▶ Peer Feedback and Norms
- ▶ Peer Relationships in Childhood
- ▶ Personality Development
- ▶ Status Competition and Peer Relationships in Childhood

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Nutrition

- ▶ Obesity

Nutritional Independence

- ▶ Weaning and Maternal-Fetal Conflict

Nutritional Status

- ▶ Maternal and Offspring Condition

Obesity

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Synonyms

Adiposity; Body mass index; Diet; Nutrition; Overweight

Definition

Clinicians define the state of being overweight or obese by body mass index (BMI), which is calculated by body mass in kilograms divided by the square of the person's height in meters. BMI from 18.5 to 25 is considered within a healthy range, or less likely to be associated with increased risk from certain weight-related diseases (González-Muniesa et al. 2017). The categories of underweight (BMI <18.5), overweight (BMI 25–30) to obese (BMI >30) are associated with increased risks of certain diseases, costs to reproductive performance, and life expectancy (GBD 2015 Obesity Collaborators et al. 2017; Global BMI Mortality Collaboration et al. 2016; Hammiche et al. 2012; van der Steeg et al. 2008; Zain and Norman 2008).

Introduction

Conservative estimates suggest that over one billion people worldwide are either overweight or obese (Wang and Speakman 2016). Obesity levels have more than doubled since the 1980s, with the estimate of overweight and obese adults climbing to ~38% of the global population (NCD-RisC 2016; Ng et al. 2014). Obesity is responsible for approximately three to four million deaths per year worldwide, predisposing suffers to a plethora of related diseases such as type 2 diabetes, cardiovascular diseases, metabolic syndrome, chronic inflammatory diseases, and 13 types of cancer (Buescher et al. 2013; González-Muniesa et al. 2017; Ng et al. 2014; Pearson-Stuttard et al. 2018; Whiteman et al. 2015; Wilson et al. 2018). Despite the costly implementation of public health policies, obesity levels continue to rise around the globe due to the complicated epidemiology and etiology of obesity (González-Muniesa et al. 2017). This entry concisely considers some of the possible evolutionary reasons why obesity has arisen, beginning with the evolution of our diet. Next, it will cover the evidence for the longstanding thrifty genotype hypothesis as a possible origin of obesity, and finally, consideration will be given to the role protein targets may play in the rise of obesity in humans.

The Evolution of Our Diet

The diet of an individual consists of many nutrients that are required in various proportions relative to other nutrients. These nutrients interact with each other and with the individual's life stage, genome, microbiota and condition. It is generally true that a single nutrient needs to be consumed at balance, and that over- or under-consumption is harmful to an individual's health (Raubenheimer et al. 2005). Therefore, in order to maximize fitness, an individual must balance ingestion and absorption of nutrients in appropriate proportions. Precisely which foods an organism ingests to achieve this balance is determined by how each nutrient affects appetite and satiety – which is specific to the evolutionary history of each organism (Simpson et al. 2004). The three major energy-contributing nutrients in any diet are carbohydrate, fat, and protein, also termed macronutrients. These macronutrients can explain a great deal of the physiological and behavioral variation between organisms and thus play an important role in determining evolutionary fitness (Raubenheimer and Simpson 2016).

Over the past ~40,000 years since the Paleolithic period, human diet has changed drastically, this change in diet has accelerated even further over the past ~50 years. Fossil studies of past humans show us they were limited for energy because sources of simple fats, starches, and sugars were much less abundant than they are today (Eaton et al. 1996), whereas complex sources of carbohydrate such as roots or tubers and sources of protein from fish or lean game meat were the main staples of a hunter-gatherer diet. Hunter-gatherer populations today, such as the Hadza, have very low levels of obesity (<5%) and rarely experience metabolic or cardiovascular diseases (Pontzer et al. 2018). Importantly, the Hadza people spend a lot longer engaging in physical activity than most of their Western counterparts, accumulating over 120 min each day (Pontzer et al. 2018). When many societies transitioned from a hunter-gather to agricultural lifestyle, diets increased in carbohydrate – mainly starchy grains. Although the shift to agriculture

occurred at differing times across societies, evidence from multiple regions indicate this rise in starch coincided with a reduction in protein. The agricultural revolution also produced an increased disease burden, due to closer living quarters, and increased the risks of famine due to reliance on crops (Prentice 2005; Wells 2012). Due to the availability of mass refining and improved transport of sugar and grains, the carbohydrate content in human diet increased further during the industrial revolution, although still at this time, obesity prevalence was low and considered a luxury of the wealthy (Simpson and Raubenheimer 2012).

In approximately the last 50 years, the macronutrient composition of our diet has changed even more, with most in developed nations having access to an abundance of food. We now have access to an unprecedented amount of simple sugars and fats, and highly processed foods are cheap and plentiful. In tandem with this nutritional shift, we are required to expend much less energy on subsistence activities than did our forebears (Simpson and Raubenheimer 2012). Despite this change in lifestyle, our physiology remains very similar to that of our ancestors. This led many researchers to hypothesize about evolutionary discordance, which suggests significant departures from our ancestral diet but not our ancestral physiology, have greatly contributed to noncommunicable diseases such as obesity (Konner and Eaton 2010). However, research investigating the interaction between our culture, genes, and environment (termed gene-culture coevolution) has shown recent positive selection for mutations such as lactose tolerance, that has arisen in societies that moved toward dairy farming for subsistence ~5000–10,000 years ago (Swallow 2003; Tishkoff et al. 2007). Moreover, the genes that confer some resistance to diabetes may well be under positive selection (Helgason et al. 2007) indicating that an adaptive lag between our genes and diet is not present for all nutritional changes in recent evolutionary history. Such evidence from gene-culture co-evolution studies may lend credence to another possible explanation for obesity: the thrifty gene hypothesis, because

these selection signatures are what one would expect to find under this hypothesis, and this is considered in the next section.

Thrifty Genes?

The thrifty gene hypothesis postulates that obesity may be the result of positive selection for genes that promote fat storage – these so-called thrifty genes may have come under selection during times of food scarcity in our evolutionary history (Gibson 2007; Wang and Speakman 2016). Now that most people in developed, and even many developing nations, have access to an abundance of food – these once thrifty genes – may now be maladaptive and thus lead to obesity. There are several reasons why this hypothesis is alluring to researchers. First, there is variation in obesity and related disease susceptibility in humans, and these traits are both genetically correlated and heritable (Gibson 2007). Second, when we look into our own evolutionary past, we can see shifts in diet, beginning with an energy limited environment changing to an energy abundant one (Simpson and Raubenheimer 2012). Third, when we put humans in context with other extant primates, we see many have an annual body mass cycle where they consume in caloric excess when fruit is abundant and experience the lean season when fruit is more scarce (Irwin et al. 2015). In fact, this type of endogenous cycle where animals eat to a positive energy balance in preparation for energy scarcity is found in other taxa such as barnacle geese, ground squirrels, alpine marmots, bears, and hairy-nosed wombats (Atkinson et al. 1996; Finlayson et al. 2010; John 2005; Körtner and Heldmaier 1995; Portugal et al. 2007). It may appear plausible then that humans are perhaps accumulating weight for a winter that will never come.

However, studies that have investigated positive selection in alleles that may confer a fitness advantage to efficient fat storage have failed to demonstrate any selection signature that would be congruent with the thrifty genotype hypothesis (Ayub et al. 2014; Wang and Speakman

2016). Additionally, there are several other limitations to this hypothesis; they all relate to famine as a selective pressure. It seems that while Paleolithic people were in an energy scarce environment (comparative to now), famines were more likely during the agricultural and industrial revolutions. To confer a great enough selective pressure, famines would likely need to be quite frequent and quite devastating – the mortality rate from the famine would need to be high enough to exert sufficient selective pressure (Gibson 2007; Speakman 2006). There is much debate in the literature about the frequency and severity of famines throughout the past ~50,000 years; some researchers define famines occurring as frequently as every decade, others as only once every century, all with differing mortality rates. This makes determining whether famine is a sufficiently strong and regular selective pressure difficult (Prentice 2005; Speakman 2006). It is also more likely during these times of scarcity that people died from infectious diseases, rather than starvation itself, although interestingly a BMI >30 is associated with an increased chance of survival from some infections such as community-acquired bacterial pneumonia (Corrales-Medina et al. 2011). It is possible therefore that the value of the thrifty gene confers different advantages to those previously investigated, although a BMI >30 is also associated with an increased risk of mortality from other acute infections (Dhurandhar et al. 2015). Nevertheless, little direct evidence exists for the thrifty genotype hypothesis.

Are We Eating to a Protein Target?

Rather than thrifty genotypes, perhaps the more recent changes in our diet have led to obesity, because many organisms, including humans, are eating to specific nutrient targets (Raubenheimer and Simpson 2016). Organisms possess nutrient-specific appetites that maintain homeostasis and alter the consumption of different nutrients (Corrales-Carvajal et al. 2016). If the correct proportion of nutrients required for maintaining

health is not available however, organisms attempt to remedy this by ingesting a range of foods with differing but complementary nutrients (Raubenheimer and Simpson 1997; Waldbauer and Friedman 1991).

Much data across taxa, (including primates, flies, and murids) indicates that protein is the primary determinant of appetite and satiety (Felton et al. 2009; Gosby et al. 2011, 2014; Lee et al. 2008; Simpson et al. 2004; Solon-Biet et al. 2014; Sørensen et al. 2008). Therefore, generally food is ingested in a manner that ensures protein consumption is within a strict range of values, but a wider range of carbohydrate and lipid intake can be tolerated. This may be because protein overconsumption can carry physiological and metabolic costs associated with excretion, whereas underconsumption leads to a decrease or cessation in reproductive output (Piper et al. 2005; Solon-Biet et al. 2015). If excess carbohydrate or fat is consumed however, energy stored as body fat can serve as an important buffer against seasonal variations in energy supply (Prentice 2005; Walker et al. 2017).

Because protein consumption is so closely linked to satiety, it has the capacity to shape feeding behavior, and can be exploited to facilitate the loss of body fat by curtailing appetite through consumption of high protein diets. By contrast, consuming low protein foods to meet a protein intake target can result in overconsumption of sugar and fat, which in the long term can lead to obesity (Gosby et al. 2014; Raubenheimer et al. 2005). Together, this has led to the hypothesis that the current obesity epidemic is fuelled (at least in part) by the unprecedented abundance of low protein, energy dense foods that are highly palatable, yet have little satiety value (Martínez Steele et al. 2018; Raubenheimer et al. 2005).

Direct evidence suggesting that humans are eating to reach a protein target comes from an experiment where participants volunteered to stay in a chalet in the Swiss Alps. They stayed in the chalet for 6 days in total, during the first 2 days they were free to select their own food for each meal from a buffet, which varied in macronutrient proportions. The experimenters were

interested only in protein consumption relative to fat plus carbohydrate consumption. For the next 2 days, participants were split into groups, one group received higher protein food (but lower fat and carbohydrate) than they had self-selected in days 1 and 2, and the other group lower protein (but higher in fat and carbohydrate), food than they had self-selected in days 1 and 2. The high and low protein food was designed to seem identical to the participants. For the final 2 days of the experiment, all participants ate as they chose – the same as on days 1 and 2 of the experiment. The results showed that participants ate to a protein target at the expense of carbohydrate and fat, thus, those put on a higher protein diet (than they self-selected in days 1 and 2) on days 3 and 4 underconsumed carbohydrate and fat, whereas the group on the lower protein overconsumed carbohydrate and fat in an attempt to consume more protein. The researchers concluded that when humans are forced to make choices about food, protein intake is prioritized over carbohydrate and fat (Simpson et al. 2003). This is consistent with many other species studied, including other primates, murids, fruit flies and Mormon crickets, suggesting that leveraging protein intake over carbohydrate and fat is evolutionarily conserved (Gosby et al. 2014; Simpson et al. 2003; Simpson and Raubenheimer 2012).

Conclusion

The origins and increased prevalence of obesity are multifaceted, and evolutionary explanations are paramount to understanding the obesity epidemic. The rapid change in our diet in recent years, as well as a shift to a more sedentary lifestyle, interacts with our nutritional balancing act to attempt to eat optimal quantities of protein, which perhaps leads to overconsumption of carbohydrate and fats. Although an overabundance of highly processed sugar and fat dense foods undoubtedly plays a role, the rise in the prevalence of obesity is unlikely to be caused by positive selection for a thriftier genotype.

Cross-References

- [Body Fat Percent and Distribution](#)
- [Body Reserves and Food Storage](#)
- [Diet](#)
- [Food Preferences](#)

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Object Choice Task

- [Understanding Human Points](#)

Object Imprinting

- [Imprinting](#)

Object Manipulation

- [Bird Tool Use](#)

Object Perception

- [Face and Object Recognition](#)

Object Permanence

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Synonyms

[Continuity](#); [Identity](#); [Persistence](#); [Recognition](#); [Selfhood](#); [Time](#)

Definition

The apparent maintenance of object identity over time, especially during periods of non-observation.

Introduction

Typically-developing human beings and at least some other animals tend to regard the objects around them, including other organisms, landscape features, and artifacts, as maintaining their identities – remaining the “same thing” – over time whether they are observed continuously or not. Objects are, in other words, regarded as “permanent” or “persistent” by default. Both experimental and theoretical practice in psychology largely adopt the “naïve realist” assumption that objects having the properties they are typically perceived to have are ontologically real, i.e., they in fact exist in an observation-independent way and in fact maintain their identities over time. Given this assumption, object permanence is the recognition or understanding of the continuous, identity-preserving existence of objects (see Hoffman et al. (2015) for a critique of naïve realism). As object permanence must in any case be inferred from sensory input and memory, the ontological question of whether objects are in fact permanent can be set aside, in practice, in favor of the more properly psychological questions of how object permanence is inferred, how the ability to infer object permanence develops, and how and why an ability to infer object permanence evolved within animal lineages exhibiting complex cognition. It bears emphasis that “inferences” of object permanence are typically, but not always (e.g., Eichenbaum et al. 2007), automatic: subjects typically “perceive sameness” instead of having to consciously infer it.

Short- Versus Long-Term Object Permanence

The conditions under which human infants, children, and adults infer object permanence during

short (seconds) visual displays have been intensively studied, primarily using visual occluded-motion paradigms (reviewed by Flombaum et al. 2008; Fields 2011). Infants infer trajectory continuity and hence object permanence for a specific range of trajectory shapes and occlusion times beginning at about 3 months old; by 2 years old, infants employ essentially the same trajectory-shape and occlusion-time criteria used by adults. Smooth trajectories and relatively short occlusion times robustly indicate object sameness and hence object permanence; apparent “absorption” of an object by an occluder followed by “emission” of a visually indistinguishable object from the occluder after a long delay or from a position unreachable by a smooth trajectory suggests non-sameness and hence a violation of object permanence. Trajectory-based object permanence is impervious to a wide range of feature changes, e.g., of size, shape, or color of the moving object, in both infants and adults.

While philosophical conundrums such as the “Ship of Theseus” have been discussed since the pre-Socratic period, the inference of object permanence over longer periods – tens of seconds to decades – of non-observation has received relatively little direct experimental investigation. On the shorter end of this temporal range (tens of seconds to minutes), numerous studies have demonstrated that infants are surprised, as adults are, by object permanence violations as early as 2.5 months old (reviewed by Baillargeon 2008). For example, surprise is elicited when an object is placed behind an opaque screen, which after a short delay is lifted to reveal that the object is no longer there. As the period of non-observation increases, however, experimental manipulations become progressively more difficult, and studies tend to be framed in terms of “object recognition” instead of “object permanence.” Object recognition in the sense used here requires object permanence; i.e., it requires an inference of continuing object identity. If for any reason object permanence cannot be inferred, the perceived object is “seen” not as the same thing observed before but rather as novel. Such failures of recognition occur, for example, in severe anterograde amnesia, e.g., Korsakoff syndrome (reviewed by Fama et al.

2012), demonstrating that short-term object permanence may be preserved but long-term object permanence lost. The relative contributions of semantic memory, episodic memory, and causal reasoning to object recognition following moderate to long periods of non-observation (hours to decades) remain to be determined and may vary widely with object type and context (reviewed by Eichenbaum et al. 2007; Scholl 2007; Fields 2012).

Insight into the difficulty of characterizing object permanence inferences across longer gaps in observation comes from fundamental computer science. Recognizing complex objects requires mereological (part-whole) reasoning. In most situations, mereological relations cannot be defined precisely; they are only “rough” or heuristic (Dütsch and Gediga 2000). At low levels of granularity, “parts” become generic and indiscernible, rendering highly similar assemblages effectively indiscernible. At higher levels of granularity, parts may change their properties over time and hence require part-level judgments of “sameness.” In this setting, additional information, e.g., causal or historical information, must be added to track individual object identity. Such information is strictly unavailable during periods of non-observation, so object identity becomes both hypothetical and dependent on the choice of heuristics, e.g., the choice of features or causal constraints to regard as “essential” for maintaining object identity.

The tools and techniques of developmental robotics (reviewed by Baldassarre and Mirolli 2013; Cangelosi and Schlesinger 2015) provide new empirical approaches to object permanence. These range from replicating classic experimental paradigms such as occluded motion using fully specified visual-processing and inference architectures to investigations of self-motivated environmental exploration, multiple object tracking, sensory-motor coordination, and language learning. Such studies make explicit not only the memory resources and inferences needed to establish object permanence but also the role of assumed or inferred object permanence as an enabler of complex cognition and behavior.

Is Object Permanence Innate?

The essential role of object permanence in human cognition has long led to it being considered innate (Baillargeon 2008). In functional terms, object permanence being innate means that the human neurocognitive system already has the organization needed to express behavioral responses indicating an inference of object permanence at or soon after birth. Recently developed protocols for functional imaging of neonates, including preterm neonates, allow the functional connectivity of the long-range networks implementing inferences of visual object permanence (e.g., the visuo-motor, categorization, and salience networks) to be tracked in parallel with emerging infant abilities (e.g., Ball et al. 2014; Gao et al. 2015).

While systematic pathological disruption of object permanence in infants has not been demonstrated, considerable evidence indicates that the perceptual processing pathways that implement object permanence are affected in autism spectrum disorders (reviewed by Gomot and Wicker 2012; Fields and Glazebrook 2017). Hundreds of genes, many of them known to act prenatally to influence neural growth and connectivity, have been associated with autism (reviewed by Geschwind and Flint 2015); these potentially provide a molecular avenue for investigating the emergence of object permanence both developmentally and evolutionarily.

A Special Case: The Self

A particular instance of object permanence is crucial for development of a coherent psychology: the experienced self and its associated body. The experienced self is fixed as a reference point for other objects and object-directed actions early in infancy and may be innate (reviewed by Rochat 2012). How the experienced self is to be defined conceptually, how it is implemented, and how it is updated to track physical and psychological changes remain significant open questions (e.g., Metzinger 2011; Klein 2014). Evidence that the default-mode network, which is implicated in

representation of the self (reviewed by Buckner et al. 2008), is already largely functional in early infancy (Gao et al. 2015) may shed light on the development and assignment of permanence to the experienced self.

Object Permanence and Time

The idea that an object can change its state cannot be formulated without an assumption of object permanence. Conversely, the idea of object permanence cannot be formulated without a sense of time and hence at least one object – a clock – that changes state. An internal not necessarily conscious sense of duration sufficient at least to distinguish “now” from “then” is, therefore, required for object permanence. The human implementation of such an internal “clock” is beginning to be mapped out (reviewed by Merchant et al. 2013; Mathews and Meck 2014); however, a mechanistic connection between time perception and object permanence has yet to be made.

Phylogenetic Distribution and Evolutionary History

Food caching, wayfinding, tool construction and use, long-term pair bonding, and negotiated social relations all require recognizing an object or a location as “the same” after a period of non-perception and hence suggest object permanence. Comparative studies of object permanence have, accordingly, focused on birds (many species, reviewed by Güntürkün and Bugnyar 2016), social carnivores (primarily domestic dogs, reviewed by Zentall and Pattison 2016), cetaceans (primarily dolphins, e.g., Johnson et al. 2015), and great apes (all species, e.g., Karg et al. 2014). The experimental tasks employed typically replicate in a species-appropriate way those used with human infants or children. While both experimental designs (e.g., Jaakkola 2014) and inferences from small sample sizes (e.g., Thornton and Lukas 2012) in this literature have been criticized, there is broad consensus that animals exhibiting complex cognition rely on object permanence.

The deep divergence between birds and mammals (approx. 300 million years; Güntürkün and Bugnyar 2016) indicates either a deep evolutionary origin of object permanence or significant convergent evolution. The question of whether object recognition and wayfinding abilities in rodents, reptiles, or even social insects can be regarded as evolutionary precursors or rudimentary forms of object permanence therefore bears consideration. Conclusive demonstration of a lack of object permanence, e.g., conclusive demonstration of a systematic inability to recognize “the same individual” after some period of non-observation, in a mammalian system would also be valuable in clarifying the evolutionary history of this capability.

Object Permanence and the Social Brain

The Social Brain hypothesis is a pillar of human evolutionary psychology (reviewed by Dunbar and Shultz 2007; Adolphs 2009). The complex social relations envisioned as the primary drivers of human cognitive, emotional, and behavioral evolution within the Social Brain framework inevitably involve abilities to reliably identify particular individual humans over long periods of time and hence moderate to long periods of non-observation. Such abilities require an inference of continuing existence with individual identity maintenance; hence they require object permanence.

Evolutionary Developmental Perspective

Object permanence allows infants and children to exchange fitness-enhancing attachment signals with their mothers, other family members, and nonfamily caregivers. It can, therefore, be regarded as an ontogenetic adaptation (Bjorklund and Pellegrini 2002). It continues, however, to enable qualitatively new capabilities across the lifespan, e.g., the ability to regard abstracta such as religions or social organizations as maintaining their identities over time. As the

selective pressures acting on these later-developing abilities may be different from those acting during infancy or childhood, the robust childhood expansion of object permanence capabilities away from family members to “objects” in general may be regarded as a deferred adaptation.

From a mechanistic perspective, the relevant questions are how the mechanisms enabling object permanence in infancy develop pre- and perinatally, how they later expand as the infant and then the child interacts with her environment, and how this extended developmental system evolved within the animal and particularly primate lineage. The direct mechanistic coupling of evolution and development characteristic of “evo-devo” biology (reviewed by Müller 2007; Carroll 2008) has yet to be achieved within psychology. The centrality of object permanence to complex cognition, together with its broad phylogenetic distribution, suggests that it is an ideal test case for such an endeavor. A deep understanding of how the pre- and postnatal developmental mechanisms that support object permanence have evolved in both avian and mammalian lineages may provide new insights into the generation of novel cognitive and emotional variants and the selective pressures that act on them over evolutionary time scales.

Conclusion

With every new demonstration of quantum superposition or entanglement at macroscopic scales (e.g., Wiseman 2015), the likelihood that observation-independent, time-persistent objects can even be defined at the level of fundamental physics decreases. If the objects of human perception cannot be defined within physics, an understanding of what they are and what it means for them to maintain their individual identities over time must be developed within psychology. Hoffman et al. (2015) have suggested that “objects” are in fact bundles of organism-specific fitness consequences. If this is the case, object permanence is the inference that fitness consequences that are correlated at one time will remain correlated at subsequent times. Sophisticated

neurocognitive mechanisms are required to make such inferences. Developmental robotics, functional neuroimaging of infants, and evolutionary developmental psychology provide new conceptual and empirical tools that can be combined with the traditional methods of experimental psychology to identify these mechanisms and to characterize their development and evolution.

Cross-References

- [Attention and Memory](#)
- [Autism](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Face and Object Recognition](#)
- [Human Visual Neurobiology](#)
- [Kin Recognition](#)
- [Ontogenetic Adaptations](#)

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Definition

Object play involves playful activities with toys or other objects, instead of social or interactive play with peers.

Introduction

Play is certainly an important component in the course of children's development; in fact, it takes up an appreciable portion of their time budgets, considering that all children engage into play activities throughout their childhood. Many definitions have been put forward in an attempt to define what play is and of the different types of play available in the literature. Some have had more examination than others. For example, there is a great amount of literature on children's pretend play, while research on rough-and-tumble play is lacking (Smith et al. 2015). In this entry, we will consider the evolutionary biological perspective on play development, we will address what playful behavior entails, and finally, we will focus on object play and tool use during the periods of infancy and childhood.

Object Permanence in Monkeys and Apes

► In Nonhuman Primates

Object Play

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Synonyms

Construction play; Exploratory play; Playful behavior; Tool play

An Evolutionary Perspective

According to evolutionary biology, the desire to play in specific ways and at specific points in life is shared among a variety of mammals (LaFreniere 2011). Evolutionary biologists have long been intrigued to the origins and functions of play due to its complexity as a phenomenon in young mammals (LaFreniere 2011), not only to observe but also to define it (Pellegrini and Smith 1998). In the evolutionary biology dictionary, the term “functions” with regard to play refers to when a behavior has typically added to the survival or reproductive success of an individual (genes) over many succeeding generations (Pellegrini and Smith 1998b). Functions can also be defined in the context of beneficial outcomes during the life cycle of the individual player (Pellegrini and Smith 1998b).

Evolutionary biologists interested mainly in the study of animal behavior (hereafter ethologists) generally consider play as having been acquired by our species through the process of natural selection, in order to provide deferred benefits to the individual (LaFreniere 2011). In other words, through play a child develops and practices skills crucial to survival and reproduction in adulthood (Smith 2009). Yet, play may also produce immediate benefits to the young individual, and modern ethologists acknowledge that natural selection acts throughout life cycle, a view now called *life history theory* (LaFreniere 2011).

Life history theory is a worldwide accepted analytical framework, used mainly in biology and evolutionary psychology since the 1970s (LaFreniere 2011). It considers an organism as an ever-changing life cycle – not as a static adult – suggesting that certain species-typical characteristics evolve to favor somatic and reproductive efforts throughout life span (LaFreniere 2011). Accordingly, Bogin (1999) postulated that because of a finite amount of time, energy, and resources available, individuals must make choices regarding their behavioral priorities and allocation of resources with respect to developmental periods and life goals suitable to those periods. For example, despite its clear costs, during the early juvenile period, play is prioritized in all social primates, while social play takes up most of the time not spent eating and sleeping (LaFreniere 2011). This fact is considered to be crucial as the main basis for concluding an adaptive function of play, because natural selection favors only behaviors whose benefits clearly outweigh the associated costs (LaFreniere 2011). Play can be costly in terms of time and energy devoted to it as it diminishes the time, effort, and energy spent on other activities.

Despite such costs, there is a natural tendency of young mammals to engage in play as long as and as often as ecological constraints and opportunities afford (LaFreniere 2011); it is in fact indispensable to the development and good functioning of a healthy adult.

Characteristics of Playful Behavior

Although many researchers have attempted to define what we call “playful behavior,” this is not an easy task. Animal ethologist Robert Fagen (1974) proposed two approaches, which can be used to define play: the functional approach and the structural approach. The functional approach suggests that play does not have a clear external goal or an obvious end in itself neither clear immediate benefits to the individual (Smith et al. 2015). In fact, a “functional” way of perceiving play is suggested – play is performed rather for its own sake and for enjoyment instead of for any other external purpose (Smith et al. 2015). Therefore, if an external goal exists such as a need to seek comfort or attention, then the behavior cannot be considered as play (Smith et al. 2015). However, it is important to highlight that, although playful behaviors do not generate any clear immediate benefits for the youth, many theorists do believe that children indeed benefited from playing; there is an ongoing controversy as to what the benefits of play exactly are (Smith et al. 2015).

The structural approach is primarily concerned with behaviors present only during play or the way these behaviors are organized during playful activities (Smith et al. 2015). These behaviors are usually called “play signals” and could, for example, take the form of laughter or the “open-mouth play face” which both signal play (Smith et al. 2015). However, it is arguable that not all play is characterized by play signals. In fact, the structural approach goes a step further and suggests that for behaviors to be considered as playful, they need to be “repeated,” “fragmented,” “exaggerated,” or “reordered” (Smith et al. 2015). Thus, if a child is just running up a slope may not be playing, but if he or she runs up and slides down the slope several times which indicates repetition, runs just halfway up which shows fragmentation, takes unusually large or small steps or jumps which suggests exaggeration, or crawls up and then runs down which indicates reordering, then we could possibly agree that this behavior is playful (Smith et al. 2015).

The two approaches, although logically different, could be considered to be theoretically in parallel and complementary to each other; after all, the child running up and down the slope has no clear, immediate goal except from enjoyment (Smith et al. 2015).

Finally, another approach suggests that play or playful behavior can be identified through a number of different criteria but always in conjunction with the two previous approaches (Smith et al. 2015). No criterion is adequate enough to define playful behavior, but the more criteria are present, the higher the agreement will be on that a behavior is play (Smith et al. 2015). Based on this premise, Krasnor and Pepler (1980) proposed a model, which suggests that playful behaviors are characterized by a form of “flexibility,” “positive affect,” “nonliterality,” and “intrinsic motivation.” Flexibility refers to the form and content of play where objects are being put in different combinations and roles are being performed in new ways – these are the structural characteristics of play (Smith and Pellegrini 2013). Positive affect refers to visible signs of enjoyment such as when children smile and laugh during their time while playing (Smith and Pellegrini 2013). Nonliterality deals with elements of “pretend” during play (Krasnor and Pepler 1980) such as acting out hypothetical scenarios. Lastly, intrinsic motivation refers to the fact that such behaviors are conducted for their own sake with participants being mostly interested with the behaviors themselves (i.e., “means”) rather than the action (i.e., “ends”) of the behavior (the process is more important than any goal) (Pellegrini et al. 2007).

The play criterion approach does not aim to produce an unequivocal definition of playful behavior. It does, however, identify a continuum of play, that is, from nonplayful to playful behavior, as well as how different theorists agree on what to call playful behavior (Smith et al. 2015). As it has been discussed so far, the main “play” criteria for young children are flexibility, enjoyment, pretense, and no specific goal while doing so.

Play and Exploration

The play criteria, as discussed above, distinguish “play” from “exploration.” Play and exploration were often classified together in earlier writings perhaps because both of them were not goal-directed neither guided through reinforcement (Smith et al. 2015). Yet, it is also true that for young infants, during the sensorimotor stage of their development (see ► [Sensorimotor Play](#)), the difference between exploration and play is harder to make, as, for very young children, all objects are unusual (Smith et al. 2015). Once children enter their preschool years, however, the difference is easier to make (Smith et al. 2015). This was illustrated by an experiment conducted by Corinne Hutt (1966) by creating a unique toy – specifically a box where children could sit on, with a lever that could make the sound of a buzzer. Young children around the age of 3–5 years were rather thoughtful when the novel toy was introduced to them by touching it, by feeling it, and by trying out the lever – they were in fact trying to figure out what the novel object could do or in other words “exploring.” Soon after, this changed as the child would regularly relax and sit on the object performing frequently with the lever – perceived as more playful behavior. Based on these observations, Hutt proposed that children typically continue from thorough exploration of different objects to more playful activities.

In addition, exploration in relation to play is characterized by fast heart rate, reduced distractibility, and flat affect (Pellegrini 2016). On the other hand, when playful behavior occurs, there is low heart rate, children are more relaxed, high level of distractibility, and positive affect (Hutt 1966). Exploration was identified as relatively thoughtful and paying attention to details, typically asking, “what does this object do?” – while play was characterized by a variety of behaviors typically asking, “what can I do with this object?” as well as being relaxed while using the object.

Further, exploration usually predates different forms of object use and play in human animals (Belsky and Most 1981). Influential work from

Belsky and Most (1981) showed that toy exploration was the main activity of children aged 7.5–10.5 months, with no signs of playful behavior, while from around 9 to 10.5 months of age, they identified objects as they manipulated them. At 12 months, object play became into view, along with exploration and naming of objects. Indeed, all types of play follow exploration – animal behaviorists suggest that children’s play does not only involve objects but rather ranges also along social and locomotor dimensions (Burghardt 2005). The latter two are being more closely interrelated; for example, play-fighting or rough-and-tumble play has both social and physical dimensions (Pellegrini and Smith 1998a). Most child developmental research, however, has mainly focused on object play dimensions (Smith et al. 2015).

Play with Objects

Jean Piaget’s (1952) theory of cognitive development suggests that young children’s perception and understanding of the surrounding world depend on their motor development – a fundamental skill necessary for the young child to associate visual, tactile, and motor representations of objects. Specifically, the infant has to understand that objects exist even when they cannot be seen, touched, heard, or sensed in any other way – what we call “object permanence” – and this understanding comes through touching and handling objects in different ways (Siegler et al. 2017). Piaget gave a comprehensive description of the varied ways in which children make use of and manipulate objects, including play (Smith et al. 2015). Although initially this is best expressed as exploratory, as the child progresses through the sensorimotor stage, which usually lasts from birth until 2 years of age, exploratory behaviors are repeated and thus perhaps enjoyed – two criteria for playful behavior to be present (Smith et al. 2015). These behaviors become also more flexible, such as that some of them would easily be characterized as playful (Smith et al. 2015). Piaget

suggested that this behavior could also be called “practice play,” in terms of manipulating and bumping objects together and laughing (Smith et al. 2015).

As Piaget’s theory suggests, young children during their first 2 years of life are primarily focused on the activities of their own body (Siegler et al. 2017). Once their attention shifts from basic body reflexes to the events of the surrounding world, the stage is set for the appearance of object play (Hughes 2010). Except from the infant’s interest in the world around them, however, there is another requirement for object play to occur; the motor skills are needed to allow the infant to grasp and handle play objects (Hughes 2010). As mentioned above, Piaget suggested that during the first 2 years of life, children develop their motor skills, and this is when children start engaging into play with objects.

Object play refers to playful behavior involving the use of different objects such as building blocks, jigsaw puzzles, cars, dolls, etc. (Smith and Pellegrini 2013). For instance, when babies engage in play with objects, they usually mouth objects and then they drop them down, while toddlers manipulate the objects such as assembling blocks, or sometimes they pretend play such as feeding a doll (Smith and Pellegrini 2013). In fact, when children are pretending using objects, at first, they imitate someone else’s use of those objects (Pellegrini 2016). Over time, young individuals learn how to use other more abstract objects to portray other objects (Pellegrini 2016). Accordingly, object play is also evident when children use objects in varied ways (Pellegrini and Hou 2011) such as using a pencil to represent a hammer. Play with objects gives the opportunity to children to create new combinations of actions as well as to advance their problem-solving skills (Smith and Pellegrini 2013). Indeed, of all the possible uses of objects, play with objects is most highly akin to creativity (Pellegrini and Hou 2011).

In modern societies, object play typically involves toys which are made to favor children’s

play by being created based on mass media prototypes (Smith 2009). There is a huge production not only of simple toys and objects such as building blocks, jigsaw puzzles, cars, dolls, and toy animals but also of toys used for pretending and fantasy activities, such as farm sets, castles, trains, action figures, and action objects based on either older but ongoing or current TV series or films such as Star Wars (Smith 2009).

As mentioned earlier, before babies, toddlers, and children engage in object play, they must explore the object first (Hutt 1966). In this initial exploration, young individuals extract characteristics of and uses for novel objects, and individuals then use this information as a basis for play bouts (Pellegrini et al. 2007). To illustrate, imagine a child entering the nursery school for the first time, being introduced to a completely new setting (Pellegrini et al. 2007). The child will allow substantial amount of time during the very first few weeks of their experience, to explore the physical and social environment of the nursery school – being a passive onlooker (Pellegrini and Goldsmith 2003). Exploration is used not only to become familiar with a new setting, but it is also needed to identify any potentially dangerous aspects of an environment and discover how to stay away from them (Spinka et al. 2001). Once a child determines that the novel environment is safe, then play can occur (Pellegrini and Goldsmith 2003).

In addition, establishing an accurate time frame for object play during childhood is challenging, considering that object play is usually conflated with other forms of object use (Pellegrini 2016). In a study by Belsky and Most (1981) where object play was clearly differentiated from other forms of object use, they concluded that it begins around 1 year. Further studies concluded that by 3–5 years of age in American and UK preschool settings, object play increases and then declines (McGrew 1972; Pellegrini and Gustafson 2005; Pellegrini and Hou 2011).

Object play becomes increasingly social as the child grows (Rubin et al. 1983). To illustrate, they concluded that less than 2% of preschool and kindergarten children's play is solitary, while 12% and 28% of preschoolers and

kindergarteners, respectively, is social (Rubin et al. 1983). Therefore, not only does object play expand throughout childhood, but it also becomes progressively social. Finally, it should be noted that any benefits of object play should be compared against those of instruction, keeping in mind different external influences such as the age of the child, the type of task, and whether learning is for particular skills or a more general developmental acquirement (Smith and Pellegrini 2013).

Gender Differences in Object Play

Evidence about gender differences in object play as well as in the overall frequency of object play between young boys and girls during the sensorimotor period is lacking (Belsky and Most 1981). However, studies have suggested that the nature and choice of toys do vary, especially after the sensorimotor stage. For instance, Smith and Daglish (1977) found that at 1 and 2 years of age, boys engage more into active play and forbidden play such as playing with wall sockets, pulling curtains, or climbing on furniture and used more transportation toys. Girls, on the other hand, engaged more into play with dolls and soft toys. These kinds of conclusions are also illustrated in other studies with children aged 2, 3, or 4 years, both at home settings and in nursery classes; boys tend to prefer activities such as throwing or kicking balls along with transportation toys, while girls tend to prefer dolls and dressing up (Smith 2009).

Tool Use

According to Bruner (1972), the design features that object play entails make it an appropriate and suitable way of developing tool-using skills. Object play, although highly enjoyable in itself and intrinsically motivated, offers repetition in the practice of a range of relevant skills (Smith 2009).

When considering the early development of tool use in infancy and childhood, the extent to

which young children can indeed explore different objects' functions should be kept in mind (Deák 2014). Ideally, a common definition of "tool use" suggests that individuals make use of objects not attached to the environment or being part of individuals' bodies, in the service of a goal, for example, getting food (Shumaker et al. 2011). To illustrate, using a fingernail to twist a screw would not be considered as an example of tool use but using a screwdriver would (Pellegrini 2016). Tool use is an activity that encourages children's learning on how to use tools according to cultural conventions, such as using a fork (Pellegrini 2016). As mentioned above, using tools appears relatively early in human ontogeny, with an increasing progression in terms of skills from infancy to childhood (Cutting et al. 2011).

Object functions depend on the physical layout and properties of objects such as their material, part configuration, and markings (Deák 2014). These object properties are related to tool use, and this is explained through the concept of *affordances* as suggested by Gibson (1982). An affordance is the extent to which an organism can interact with an object based on the object's properties (Gibson 1982). For example, to humans a cup affords containment of liquids or solids smaller than the mouth of the cup such as flour as well as tracing circles on paper (Deák 2014). Here, it is important to mention that affordances are inherent to the object-organism interaction rather than to the object alone, as they are characterized by a distinct organism's potential for interacting with those properties (Deák 2014). Individual humans can achieve different affordances from the same object too of course such as a skilled player can exploit more affordances on a guitar when compared to an inexperienced person. This concept is relevant when we examine the early development of tool use, because in reality most objects or tools are designed to afford actions of adults and not of infants and young children (Deák 2014). As a result, infants must learn how to use tools and objects in a world with a setup engineered for adults (Deák 2014).

Unfortunately, infants and young children are not frequently or sometimes not at all allowed to

explore object affordances or in other words to explore what they can do with a particular object. This is not only because of young children's physical limitations but also by the limited accessibility to these objects as adults usually design children's environments in such a way that they prohibit children's access (Deák 2014).

However, as infants grow and develop so do their sensory and motor abilities, and these are the necessary skills needed for the development of tool use. Infants aged 6–12 months old readily manipulate novel objects in order to explore their functions and properties – squeezing soft objects or banging hard objects (Bourgeois et al. 2005). As explained above, it is through exploration that children become familiar with novel objects, and once they do so, they enjoy their interaction with them. Exploration is a progressive, embodied, multimodal process that progressively allows children to adapt their reaching and refine their abilities to specific and similar novel objects, in other words, to detect new affordances (Deák 2014). Refinement can be gradual in the sense that younger infants learn how to use a type of tool, for example, a spoon, after a substantial amount of time of experience. Consequently, it has been suggested that tool-using skill depends on infants' and young children's experiences with objects (Deák 2014). The reason why tool use learning is protracted is partly because young children need time also to consolidate their newly acquired sensory and motor skills.

Further, as Tomasello (1999) suggested, tool use is supported by social interaction, with adults having an important role in children's tool use learning. Specifically, infants and young children shift their attention to objects as a consequence of interaction or observation of adults using objects and tools (Deák 2014). For instance, when adults hold objects, children in turn become interested in those objects and reach out for them, to examine and learn about them (Tomasello 1999). Thus, it is suggested that social learning and sensorimotor development are combined in an attempt to favor tool use learning in infants and young children.

In summary, as the young child moves from infancy to childhood, their tool use skills

depended on active, sensorimotor development. Through the acquisition of their sensory and motor abilities, infants and young children are able to explore novel objects and gradually learn how to use them in different ways, just like adults.

Conclusion

This chapter has presented a short introduction about the evolutionary biological basis of “play development” as studied among a variety of mammals. As it has been suggested, it is through play that children develop and practice skills crucial to survival and reproduction in adulthood. While play can be costly in terms of time and energy devoted to it as it diminishes the time, effort and energy spent on other activities, there is a natural tendency of young mammals to prioritize and engage in play activities during the early-juvenile period. Importantly, play allows the young individual, after they have determined that a novel environment is safe, to generate play behaviors and explore different object functions they can afford performing in terms of their age and current skills. Overall, research suggests that play is indispensable to the development and good functioning of a healthy adult while it is through the acquisition of their sensory and motor abilities that young children can develop their tool-use skills and learn how to use novel objects in different ways.

Cross-References

- ▶ [Newborn Behavior](#)
- ▶ [Play and Tool Use](#)
- ▶ [Social Play](#)

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Objectivism

► Objectivity

Objectivity

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Synonyms

Absolutism; Moral realism; Objectivism

Definition

Objectivity – the quality of existing independently of a subject's beliefs or desires. Not dependent for its properties on any person's subjective

experience. Typically discoverable by publicly available and evaluable means.

Introduction

For purposes of this entry, a domain of facts is objective if those facts both (a) *exist* and (b) are *mind-independent*, meaning they do not depend for their existence on any human beliefs, attitudes, or desires (though for simplification, this article will only refer to beliefs in what follows). Accordingly, moral facts are objective just insofar as they both exist and are mind-independent. Here, the focus will be on how evolutionary considerations bear on the objectivity of morality. This article will not consider other ways in which evolutionary considerations bear on other moral phenomena, including how they might have shaped core moral emotions such as compassion or shame or widespread moral practices such as reciprocity and punishment.

For many philosophers, the objectivity of morality constitutes a “fundamental commitment” (Wong 2014, p. 337); the objective demands of morality are “nonnegotiable” (Joyce 2006, p. 117). Psychologists also discuss morality in objectivist terms, drawing clear distinctions between social or conventional norms on the one hand and moral norms on the other. According to one influential account, moral norms are distinguished in being universalizable and, more importantly, applicable independent of any authority or sanction (Turiel 1983).

Additionally, nearly all philosophers and psychologists also maintain that ordinary folk are committed to objectivism about morality, such that if two people disagree about the moral status of a moral claim – say, whether or not discriminating against someone on the basis of their sexual orientation is morally permissible – at most one of them can be correct (e.g., Smith 1994; Shafer-Landau 2003). The “philosopher's task,” according to one prominent account, is to make sense of precisely the puzzling objectivity of morality (Smith 1994). Philosophers predominantly base their claims by canvassing the nature of moral language and debate, by examining ordinary intuitions about the moral domain, and by

reflecting on the phenomenology or felt experience of moral life (Gill 2009). Psychologists, by contrast, have tested this claim using experimental methods, with several studies showing that individuals do, in fact, show objectivist tendencies (for a review, see Sarkissian 2016).

Evolutionary Arguments and Skepticism About Objectivity

Recently, some researchers have suggested that evolutionary theory can pose a serious threat to the purported objectivity of morality. Specifically, it can undermine the notion that most commonsense and widespread moral beliefs are justified by referring to mind-independent moral facts. Evolutionary explanations of commonsense moral beliefs do not, in themselves, lead us to deny or rule out the existence of mind-independent moral facts. Indeed, this is not the general strategy of such “debunking” explanations (Nichols 2014). Instead, evolutionary explanations are thought to undermine the warrant or justification of these beliefs. They can do so in several ways. Such explanations can provide a complete or convincing account of the causal processes giving rise to the belief in question without, at any point, having to say anything at all concerning whether or not that belief tracks any facts or truths about the world (Joyce 2006). Or, such explanations can show that the psychological processes that generate the belief in question are not the sorts of processes that could plausibly result in true, factual beliefs (Nichols 2014) or argue that whatever ends are supported by a theory of Darwinian natural selection – be they the flourishing of the gene, the individual, or the group – such ends cannot be moral ends (Sommers and Rosenberg 2003).

Regardless of these differences, all such accounts have the same strategy of arguing that the best evolutionary account of the origins of humans’ moral faculties and beliefs will refer to their fitness-enhancing properties, which have no bearing on whether or not the beliefs track mind-independent moral facts. Presumably ancestral humans gained adaptive advantages over their

rivals by cultivating or maintaining certain moral beliefs about themselves and others – whether in-group or out-group members. The differential reproductive success conferred on ancestral humans by adopting these beliefs would lead to their propagation. Humans inherit these beliefs today as part of their cognitive architecture. However, whatever moral beliefs they have as a result of such a process cannot be justified by claiming that they track mind-independent moral facts.

One widely cited account presents a dilemma for moral realists (Street 2006). If evolutionary forces played a pervasive role in the production and maintenance of moral beliefs, what could be the relation between these evolutionarily shaped beliefs and any mind-independent moral facts? There are two options, neither of which is attractive or acceptable, hence the dilemma. The first horn of the dilemma claims that mind-independent moral facts are not at all related to the evolutionary pressures on moral beliefs. But this implies an implausible general skepticism about the truth of many commonsense ethical claims, even intuitive claims such as that it is right to take care of one’s children. This is because even though this judgment seems obviously true – indeed, true in a way that does not require the endorsement of any particular person’s beliefs – ancestral humans would have not converged on this belief because it referred to a mind-independent fact. Instead, those who had such beliefs were simply more fit than others. The second horn of the dilemma claims that there is, indeed, some relation between mind-independent moral facts and the evolutionary pressures on moral beliefs. The ancestors of modern humans reaped adaptive advantage precisely by means of tracking independent moral truths. However, this leads to a different, but no less serious, problem: it requires some plausible “tracking” account, and, *any* such account seems otiose. It would be more parsimonious to leave out mind-independent moral facts and just focus on the adaptive links that ancestral humans forged between their circumstances and their responses to those circumstances. The latter account would also have greater explanatory power through its ability to describe how they had beliefs that

contemporary society now regards as false (like the tendency to prefer in-groups to out-groups; Street 2006, p. 134). By contrast, a tracking account fails to easily explain the origin or persistence of such false beliefs.

Joyce (2006, 2016) makes a similar argument, criticizing accounts of moral judgment that attempt to show that evolutionary forces produced in human minds a moral truth-tracking faculty. Joyce focused on the *function* of moral judgment in human beings: could it be to track mind-independent moral facts? Some faculties do appear to be truth-tracking in this sense: mathematical representations seem to track mathematical truth because an organism only derives adaptive advantage from true mathematical judgments and not from false ones. (E.g., a person that judged that $2 + 3 = 6$ would be at a significant disadvantage compared to another that judged that $2 + 3 = 5$). However, as Joyce argues, there is no comparable benefit to making true moral judgments. The moral faculty (such as it is and putting to one side the question of whether such a faculty even exists) does not appear to give its bearers advantage on the basis of its truth-tracking (Joyce 2006). Instead, to the extent that a moral faculty can be given an evolutionary explanation, it appears to have given ancestral humans an advantage in virtue of its other (non-truth-tracking) features, for example, signaling one's sincere commitment to social projects or maintaining one's reputation in the group (c.f. Miller 2007; Nesse 2009). Since one should not expect moral judgments to do anything other than what they were selected for, and since they were not selected for truth-tracking, this provides a plausible reason for doubting that moral judgments are formed by a reliable process.

Many theorists have argued that in the absence of good arguments against the justification of moral beliefs, those beliefs ought to be regarded as justified (Wielenberg 2010; Enoch 2011). However, the arguments above turn the tables on any such account when applied to the moral domain. Any account which claims that there exist moral faculties that in fact track objective moral facts must now present plausible explanations arguing for the existence of such facts and

their respective faculties. Given the success of evolutionary accounts to provide explanations for a range of phenomena, the burden of proof shifts to those who wish to defend mind-independent moral objectivism.

Evolution's Contribution to Perceived Moral Objectivity

However, even while maintaining that mind-independent moral facts are a fiction, Joyce (2006) nonetheless speculated that a tendency to see morality in objective terms is an evolutionary adaptation. Evolutionary forces selected for individuals who were highly motivated to act upon fitness-enhancing beliefs, including moral beliefs. Seeing morality as objective (independent of oneself) would be a much stronger motivator to act than seeing morality as mere subjective preference. For example, when one says that a person ought not to steal, one does not take oneself to be merely asserting that it is within the person's set of current desires that she not steal. Even if she does strongly desire to steal and thinks it a great idea, this has no impact on the fact that she *ought not steal*. The challenge for anyone who endorses moral objectivity is to show exactly how such "categorical imperatives" are possible. The standard approach is to show that every agent (or at least every *rational* agent) has some reason to be moral. This article will not be detained with the details of that discussion. The important point is that when one condemns those who commit atrocities such as genocide, coming to learn that the perpetrators are furthering their goals through genocide would not at all mitigate one's condemnation. It does not matter how the perpetrators feel about moral norms; moral norms apply to them *regardless* of what they feel. This seems a pervasive aspect of moral life.

As noted above, some take this objective categoricity to be a "nonnegotiable" part of the moral domain – a central tenet that any theory of morality must explain. Discovering that such a central tenet is false can reveal the discourse to be systematically flawed. If moral discourse is in fact committed to such categorical judgments,

then evolutionary debunking arguments (as discussed above) will imply moral skepticism. This leaves a question: Why do some philosophers take objectivity to be such a central part of moral discourse and practice to begin with? Why does it seem to be a feature of morality that moral facts exist? Whence comes the perception that morality is mind-independent in the first place?

Here, it may be instructive to separate two issues, following Edouard Machery and Ron Mallon (2010). The first concerns why one would be expected to adopt norms of behavior that, in general, come with costs and may serve to stifle or frustrate some of one's current desires. Call this "normative cognition," involving such concepts as "should" or "ought" or "ought not." It is rather uncontroversial that humans have evolved to pick up on prevailing norms in their groups (whether these norms are implicit/informal or explicit/formal), assimilate or internalize them, and feel motivated to adhere to them. Normative cognition also includes expectations that others comply with the same norms, along with a desire to sanction or punish those who do not. Finally, normative cognition can be accompanied with feelings of guilt and shame if individuals fail to adhere to norms that they have come to adopt or endorse. Indeed, people are, in general, adept at reasoning about norms (Cosmides and Tooby 2005).

However, any such account of normative cognition will not require anything like the sort of mind independence that moral objectivism entails. Normative cognition can include esthetic matters (e.g., how one ought to dress), prudential matters (e.g., how one ought to climb the mountain), or matters of propriety (e.g., how one ought to lay the dinner table). These all seem to depend, in some way, on the existence of contingent motivations in individuals to adopt them; *if* one wants to appear beautiful or be prudent or adhere to etiquette, then one ought to adopt certain norms of behavior. But, as just noted, moral norms seem to be different from these norms. Moral norms apply regardless of a person's contingent preferences or desires. How can one, then, explain the emergence of distinctively moral norms of this objective kind?

Some have speculated that *moral* cognition – that is, a form of cognition that sees certain norms as mind-independent, factual, inescapable, and nonnegotiable – was an evolutionary adaptation of our species to spur us to prosociality (Joyce 2006). Joyce (2006), for example, speculated that even though mind-independent moral facts are entirely fictional, it would have been beneficial for our species to have evolved a tendency to think they exist. A tendency to see the world as filled with such mind-independent moral facts would be a much stronger motivator to act prosocially. Thus, humans project objective moral facts into the world through our emotional reactions to morally relevant events. Goodness and badness, virtue and vice – these are not properties that exist in the world to be perceived by the mind. Instead, the mind *projects* these values into the world, which then motivates individuals to act according to moral norms. Thus, evolution selects for a capacity to objectify morality even while moral facts do not exist. This account, while speculative, merits further research.

Responses to Evolutionary Debunking

Those who aim to secure objectivity in ethics have responded to evolutionary debunking arguments in a number of different ways. On the one hand, some have offered *third-factor accounts* that purport to show that moral judgments do track moral facts even though they were not selected for this purpose. On the other hand, some have argued that the standards of reliability being invoked in debunking arguments are too strong; if they were adopted for other areas of common knowledge, this would lead to an untenable radical skepticism. These two approaches constitute well-developed contributions to the debate about the implications of evolution for moral objectivity, and they will be considered in turn.

Third-Factor Accounts

The most prominent response to evolutionary critiques of moral objectivity involves arguing that

moral judgments do track real moral facts. However, they do so as a by-product of some other epistemically respectable cognitive faculty. The strategy is straightforward: if a plausible evolutionary story can be told about how humans came to track objective moral facts in spite of the adaptive pressures which influenced ancestral humans' moral judgments, this might secure the reality of objective moral facts and maintain their objectivity at the same time. Different proponents of this type of response have different capacities in mind when they propose such "third-factor" accounts – accounts about some third factor that humans evolved to track that happens to also align with moral facts.

Enoch (2010) puts forward a quintessential third-factor account, which starts from the premise that survival is (on balance) a good thing. The advantage of such a starting point is that it is fairly obvious that adaptive pressures on ancestral humans did tend to favor their survival. He then argues that by making choices that assured their own survival – a good thing (on balance) – ancestral humans were in fact tracking moral facts indirectly. They developed the judgments they did because those judgments were adaptively advantageous, and it just so happened that such those judgments tracked moral facts as a by-product. Put another way, the capacity to track moral facts was not directly "selected for" by adaptive pressures but rather was merely "selected," because it was not adaptively advantageous to separate it from other faculties that were themselves selected for by adaptive pressures. It may be an accident that such an adaptation arose, but once it did, it conferred on ancestral humans a reliable way of making objective moral judgments. The capacity to perceive moral facts might be like the capacity to perceive stars (Huemer 2005); having the capacity to see stars did not itself give early humans any adaptive advantage but rather came about from other capacities that did confer such adaptive advantage. Other candidates for such third factors include the badness of pain (Skarsaune 2011), the importance of having personal boundaries that others cannot transgress (Wielenberg 2010), the goodness of altruism (de Lazari-Radek

and Singer 2012), cooperating with others (Brosnan 2011), or enhancing society's ability to meet its needs (Copp 2008). Each of these appeals to capacities or tendencies which enjoy better evolutionary pedigree than any purported faculty of moral judgment.

Nonetheless, Street (2006) objects to third-factor accounts on the grounds that these accounts are themselves vulnerable to a Darwinian dilemma: whatever capacity tracks this third factor must itself have been selected for as a result of adaptive pressures on ancestral humans. The question, then, is what the relation would obtain between objective moral facts and the evolution of this capacity. If there is no relation, Street says, this looks like an implausible and convenient coincidence. If there is some relation, then the realist must specify what that relation is. But, she argues, the capacity that allowed early humans to (indirectly) track moral truth would have to be fairly specialized and complex. It is implausible to think that such a specialized and complex capacity could have arisen as a by-product of some other cognitive capacity (Street 2006).

Proponents of third-factor responses generally deny the claim that grasping moral facts really requires a complex or specialized capacity in the first place. For instance, de Lazari-Radek and Singer (2012) argue that this capacity simply springs from our ability to reason in general, which is the same capacity involved in grasping other types of *a priori* truth (like truths of mathematics; see also FitzPatrick 2014). Similarly, the capacity to track facts about pain is not specialized or problematically complex (Skarsaune 2011). (For a more general defense of third-factor accounts, see Berker 2014.) If the capacity is suitably general, this allows the third-factor proponent to say that the relation between moral truths and the capacity which tracks them are unproblematic: humans track moral truths by their capacity to reason, and this capacity has an excellent evolutionary pedigree.

Finally, it should be noted that all third-factor responses invoke a moral assumption from the start, whether it be the goodness of survival, the badness of pain, or any of the other candidates. Thus, another prominent objection to third-factor

responses targets the legitimacy of this move. Street argues that any such assumption is “trivially question-begging,” because it simply assumes the reliability of our moral judgments, but those are the very judgements which the evolutionary critique is meant to undermine (Street 2008, pp. 216–217). This brings us to the second major response to evolutionary critiques: the overgeneralization response.

The Overgeneralization Response

The second response to evolutionary critiques of moral objectivity seeks to undermine the epistemic standards implicit in these critiques. This approach tries to show that if these standards were adopted universally, they would imply radical skepticism. This has also been dubbed “the containment problem” for evolutionary debunking arguments (Millhouse et al. 2016). In fact, some authors argue that the source of doubt implicit in these evolutionary critiques does not derive from evolution at all but rather an unjustified suspicion about the genealogy or causal history of any source of knowledge.

Evolutionary critiques of moral objectivity largely trade on a suspicion about the genealogy of certain beliefs, but the epistemic standards that lie behind this suspicion are not often well articulated. As was covered above, the problem introduced by evolution seems to be that adaptive pressures on the moral judgments of ancestral humans were not tracking mind-independent moral facts, and this seems to undermine their reliability. But one can further ask exactly what about this lack of truth tracking seems to undermine the objectivity of moral judgments. One possible thought is that if judgments are not tracking mind-independent moral facts, this means there is no good reason to believe they are true. In general, if one has no good reason to believe that a belief is true, one ought not to maintain it (Vavova 2014).

Though this standard looks quite reasonable at first glance, proponents of the overgeneralization

response think it goes too far. Crucially, it depends on whether a “good” reason is one that must come from outside the realm of moral judgments themselves. Street (2008) argues that “third-factor” accounts are trivially question-begging, because they rely on moral beliefs in the first place, which are themselves questionable on evolutionary grounds. However, proponents of the overgeneralization response think this argument implies far too exacting a standard. The reason is that if a “good” reason is one that must be independent of *all* moral judgments, a similar argument can be made about other sources of knowledge, for example, sense perception. Most people believe they are justified in believing the deliverances of their immediate sense perception, at least for medium-sized objects in conditions of sobriety and good lighting. But if they were asked to justify this judgment without reference to any beliefs gained from sense perception itself, they would come up empty-handed (Vavova 2014; Shafer 2012). This constitutes a clear *reductio ad absurdum*: if evolutionary critiques of moral objectivity rely on an epistemic standard that would also undermine perceptual beliefs, this is a good reason not to accept that standard and therefore also a good reason not to accept the critiques.

At this point, the proponent of an evolutionary debunking argument might grant that some judgments in the one domain can justify other judgments in the same domain (whether it be perceptual or moral). Relaxing epistemic standards in this way, however, risks allowing third-factor accounts a metaphorical foot in the door. If one is allowed to assume that one’s judgments about the objective badness of pain or the objective goodness of survival are justified (despite the adaptive pressures which caused early humans to make such judgments), many of one’s more substantive judgments can be justified on the basis of these judgments (Vavova 2014).

On a similar basis, some proponents of this response argue that evolutionary considerations can only fail to *vindicate* moral judgments but that they are not capable of producing any

independent *skepticism* about the reliability of moral judgments (Brosnan 2011; FitzPatrick 2014; White 2010). This can be shown by imagining a situation of total ignorance of the source of moral judgments. If one has no knowledge of evolution's influence on one's judgments, would this in any way improve the justification of one's moral beliefs? The answer seems to be "no." If total ignorance of the origins of one's moral beliefs does not improve one's epistemic lot, it is unclear how the truth of evolution's impact on one's beliefs could make it any worse, short of showing that these judgments are actually "anti-reliable." All that evolutionary debunking arguments can show is that moral judgments are made in a way that is independent of their truth, but this does not in itself imply that they are unreliable (see Brosnan 2011; White 2010).

A related point concerns the metaethical presuppositions inherent in evolutionary debunking arguments. In order to motivate the case against objectivism, these arguments take it to be the case that moral judgment is not truth-tracking. But in order to fail to be truth-tracking, there must be some truth to track in the first place. After all, if it turns out that nonobjectivist accounts of moral facts and concepts are correct, and these things depend in some way on human attitudes, it is not clear how evolutionary influences might undermine them (Kahane 2011).

As was covered in the section on "third factor" accounts above, determining the burden of proof in this disagreement is quite difficult. Joyce (2016) claims that given the fact that there is good reason to believe that humans' faculty of moral judgment was not selected for tracking mind-independent moral facts, the burden rests on the realist who wants to claim that it does so. But if the overgeneralization critique of this argument is correct, it is not clear that the burden of proof rests on the realist after all. It would seem that the proponent of an evolutionary critique must show how evolution's influences on moral judgments render them not just *independent* of moral facts but also *unreliable*.

The exact connection between these two claims constitutes an area of unfolding debate. Given the implications for a claim that many psychologists and philosophers take quite seriously – the objectivity of morality – quite a lot hangs in the balance.

Conclusion

The relation between moral objectivity and evolution is complex, depending on factors such as the function of moral judgment, what one takes moral judgment to be tracking, and the epistemic standard implicit in our evaluation of moral judgment. Though many philosophers, psychologists, and ordinary people perceive objectivity to be an integral part of morality, there is quite a healthy debate about whether moral objectivity can withstand an evolutionary account of human history. Though there is not yet a consensus, this article has laid out the main fault lines between proponents of evolutionary skepticism and their realist opponents.

Cross-References

- ▶ [Adaptations: Product of Evolution](#)
- ▶ [Altruism](#)
- ▶ [Altruism Norms](#)
- ▶ [Benefit Group Relative to Other Groups](#)
- ▶ [Biological Function](#)
- ▶ [Charitable Giving \(Peter Singer\)](#)
- ▶ [Cheater Detection](#)
- ▶ [Cross-Cultural Universality](#)
- ▶ [Cross-Cultural Variation](#)
- ▶ [Cultural Differences](#)
- ▶ [Cultural Evolution](#)
- ▶ [Cultural Universals](#)
- ▶ [Evolution of Culture](#)
- ▶ [Evolution of Morality](#)
- ▶ [Evolutionary Cultural Psychology](#)
- ▶ [Group Selection](#)
- ▶ [Indirect Benefits of Altruism](#)
- ▶ [Moral Development](#)

- [Moral Instincts](#)
- [Moral Instincts and Morality](#)
- [Morality](#)
- [Morality is Cooperation](#)
- [Naturalistic Fallacy, The](#)
- [Neuroethics](#)
- [Norms](#)
- [Observation of Altruism](#)
- [Problem of Altruism](#)
- [Reciprocal Altruism](#)

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Obligatory Investment

- [Differential Parental Investment](#)
- [Obligatory Parental Investment](#)

Obligatory Parental Investment

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Synonyms

Obligatory investment; Parental investment

Definition

Obligatory parental investment refers to the amount of time, energy, and resource expenditures that organisms are minimally required to make in order to ensure offspring survival.

Introduction

Throughout evolutionary history, offspring survival has posed a main adaptive challenge. In some species, this selection pressure has resulted in sex-differentiated forms of parental investment. This chapter describes obligatory parental investment, explores asymmetries in obligatory parental investment between males and females, describes examples of such differences across a range of species, and briefly highlights the implications of such differences in terms of human sexual strategies and conflicts.

Parental Investment Theory

Parental investment is defined as an expenditure of resources made by parents that increases their offspring's fitness at the expense of channeling their resources to other fitness avenues, such as their own survival or mating opportunities (Trivers 1972). Obligatory parental investment thus broadly refers to parental investment that is required in order for offspring to survive.

Differences in Minimum Obligatory Parental Investment

Trivers' (1972) seminal theory of parental investment provides a clear specification of two important components underlying Darwin's (1871) sexual selection theory. These components include intrasexual competition, where members of one sex compete for access to the sexual resources held by members of the opposite sex, and intersexual selection, where members of one sex exert preferential mate choice over members of the other sex. When the minimum obligatory investment is higher for one sex than the other, mating errors (e.g., mating with low-quality mates) tend to be more costly for the higher investing sex. Accordingly, the higher investing sex tends to evolve to be choosier, whereas the lesser investing sex tends to evolve to be more intrasexually competitive in order to gain access to the more reproductively valuable sex.

Offspring production and survival in mammals necessarily relies on internal gestation and postpartum suckling through the mother. These physiological requirements on the part of mammalian females, but not males, produce a typical sex difference in minimum obligatory parental investment for mammals (Trivers 1972). Mammalian females therefore typically invest significantly more in their offspring than males, and humans follow this general pattern of mammalian discrepancy in obligatory parental investment – women's minimum obligatory parental investment includes approximately 9 months of pregnancy and is often associated with years of lactation and nurturance during the child's formative years. In comparison, men's minimum obligatory investment is a single sperm and can end with a single act of sexual intercourse; additional paternal investment during the child's formative years is not essential for the survival of the child to reach adulthood (Goetz and Shackelford 2009; Trivers 1972).

For many species, including humans, females are the high-investing sex and, as such, have evolved to be more careful and discriminant compared to males in mate selection and are thus more likely to promote intersexual selection by exercising greater preferential choice over mates. This in

turn drives intrasexual competition in the low-investing males, because they need to contest against other males who are also eager to gain access to the discriminate and selective females (Buss and Schmitt 1993).

Examples of Parental Investment Theory

These sex differences in intersexual selection and intrasexual competition that arise from discrepancies in minimum obligatory parental investment can be observed in a wide variety of species. For instance, in elephant seals, pups are nursed solely by females; males do not partake in any paternal care and sometimes even kill their own pups by accident when they attempt to copulate with mates in the harem, underscoring the much larger parental effort and investment on the part of females. The value of the sexual and parental resources provided by females is matched by extreme male competitiveness – indeed, less than one third of males have a chance to copulate during any breeding season because the highest rank males secure at least half of all the matings (Le Boeuf 1974). As the desirability of a male as a mating partner is based on his standing in the social hierarchy, female intersexual selection of mates is facilitated by contests between rival males for dominance, and adult males arrive at the beach during breeding season and fight intensely with each other. The winners of the fights become the highest-ranked males, and females then choose these high-ranking dominant males to be their mates.

Intrasexual selection drives the evolution of exaggerated traits, displays, and behaviors in the males of various species, as can be observed from the large antlers of stags and tusks of elephants. Among the satin bowerbirds, males do not partake in any offspring care nor associate with females after mating. However, courtship is quite elaborate and competitive. Males build large, specialized, and highly decorative nest structures known as bowers in order to impress females, and females exercise selectivity based on the males' bower-building prowess (Borgia 1985).

In contrast, females in these species tend to be drab and are designed not to impress but to exercise choice. Interestingly, in insect species such as the water strider, females have evolved abdominal spines, which hinder the efforts of unwanted males and reduce the frequency of costly, unchosen matings.

Although heavier obligatory parental investment is more commonly observed in females than males, the pattern is reversed in some species. Consistent with parental investment theory, where males contribute a larger obligatory parental investment than females, the sex role is reversed and the males of those species are the more selective sex while the females intrasexually compete for the males (Trivers 1972). In a bird species known as the *Phalaropus lobatus*, the female phalarope's obligatory parental investment only consists of laying the eggs in the nest. The male phalarope, on the other hand, builds the nest himself, incubates the eggs, and looks after the young alone. As predicted by parental investment theory, the females aggressively court the males and compete with each other to be selected by the males (Johns 1969). Another example of a sex role reversal can be found in pipefish and seahorses. During mating, the females transfer their eggs onto specialized egg-brooding structures located on the males' tails, where they are nourished throughout the entire duration of gestation. As the lesser investing sex, the females evolved to be brightly colored in order to compete intrasexually to be selected by the higher investing males, who evolved to preferentially choose the most attractive and brightly colored females as their mates (Wilson et al. 2003).

Taken together, discrepancies in minimum obligatory parental investment between the sexes drive the operative components of sexual selection, with the higher investing sex (who faces greater mating costs) evolving to be choosier and the lower investing sex (with lesser mating costs) evolving to be more competitive with members of their own sex for mating opportunities and access to the more valuable high-investing sex.

Implications of Asymmetrical Obligatory Parental Investment for Human Sex Differences and Mating

In humans, differences in obligatory parental investment between males and females gave rise to a host of implications for sex-differentiated mating strategies. This section briefly highlights a few key sex differences between men's and women's mating strategies as predicted by their relative obligatory parental investment.

Sexual Strategies

Asymmetries in obligatory parental investment between the sexes present different constraints for the sexes and, accordingly, have led to the selection of sex-differentiated sexual strategies. In particular, offspring carry much higher costs to women than men if they result from uncommitted sex, particularly for ancestral females who lived without modern-day benefits such as easier access to food and social welfare. Thus, in reproductive terms, the costs of non-committed, casual sexual relationships typically outweigh the benefits for women more so than for men (Li and Kenrick 2006). As such, women, compared to men, have evolved to prefer a selective, long-term mating strategy in order to procure the commitment of a mate who can continually provide protection and resources. Men, on the other hand, do not face this constraint, and their reproductive success is largely constrained by the number of sexual partners to which they have access. As such, men, more than women, have evolved to pursue a short-term mating strategy in order to increase their access to a wider pool of sexual partners (Buss and Schmitt 1993). Consistent with these differences, a classic study found that when approached and propositioned for sex by an attractive member of the opposite sex, a large majority of college men agreed, whereas not one woman consented (Clark and Hatfield 1989).

Sexual Conflict

As a result of asymmetrical obligatory parental investment and the sexes pursuing different

optimal sexual strategies, men and women may often come into conflict. As men have a stronger preference for short-term relationships and stand to benefit more from multiple matings than women, men have a stronger desire for sexual variety and are more sexually persistent. Asymmetrical preferences between the sexes predict that men are more likely than women to pursue sex with partners who are reluctant or unwilling (Buss and Schmitt 1993). Studies have found that men are more likely than women to perceive that a woman is sexually interested based on minimal social cues such as a smile, a touch on the arm, or mere friendliness (Haselton and Buss 2000). This sex difference in perception has been proposed to reflect a male sexual overperception bias that evolved given the asymmetric reproductive costs to men of making inferential errors. That is, in judging whether a female is sexually interested in ambiguous situations, there is a greater reproductive cost associated with incorrectly inferring no interest and missing a potential sexual opportunity compared to mistakenly inferring sexual interest and wasting a bit of time and effort. As such, a male bias to overperceive sexual interest induces, on average, more instances of the less costly error while facilitating the enactment of a short-term mating strategy.

In contrast, women's higher obligatory parental investment, which leads to stronger preferences for committed long-term relationships, makes them more sexually restricted than men (Buss and Schmitt 1993). Women are therefore less eager and thus more likely than men to thwart the sexual advancements of the opposite sex. In line with evolutionary constraints favoring a choosy strategy, women may have evolved to be skeptical about a man's commitment even when it may be sincere, as the reproductive costs to women of wrongly inferring that a man is committed are large compared to the costs of requiring further signs of commitment before engaging in sexual relations (Haselton and Buss 2000). Further, as women value resources in a mate and seek mate quality over quantity, it is in their interest to "lead on" the other sex and entice further investments or induce intrasexual competition in the

opposite sex. For instance, a woman might dress provocatively and engage in flirtatious behavior despite having little or no sexual interest so as to attain more investments from interested suitors, or get them to compete so that she can enact a selective strategy and choose from the best competitor.

Together, these opposing interests arising from asymmetries in obligatory parental investment likely contribute to women's experience of unwanted sexual advances (Goetz and Shackelford 2009) and men's frustration with failed and protracted courtships. Indeed, it has been argued that differences in evolved mating strategy underlie historical and cross-cultural patterns whereby men are more likely than women to be the perpetrators of sexual coercion and rape, while women are more likely than men to be the targets (Goetz and Shackelford 2009).

Conclusion

Reproductively successful parents have enacted sexual strategies and mating behaviors that optimized their own reproductive fitness over evolutionary time, and these behaviors are a reflection of, as well as a response to, obligatory parental investment asymmetries. Across many species, including humans, females have a greater minimum obligatory investment than males to ensure offspring survival, which has tended to select for sexually choosy and discriminating females and sexually eager and competitive males. These sex differences in parental investment and mating costs have implications for men and women in terms of differences in their preferred sexual strategies, their judgments of potential mates, and the type of mating conflicts they experience.

Cross-References

- ▶ [Commitment Skepticism](#)
- ▶ [Error Management Theory](#)
- ▶ [Female Manipulation of Men](#)

- ▶ [Female Mate Choice](#)
- ▶ [Female-Female Competition](#)
- ▶ [Intersexual Selection](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Long-Term Mating.](#)
- ▶ [Male Mate Choice](#)
- ▶ [Male-Male Competition](#)
- ▶ [Maternal Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Paternal Investment](#)
- ▶ [Paternity Uncertainty.](#)
- ▶ [Preferences in Long- Versus Short-Term Mating](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Sexual Receptivity](#)
- ▶ [Sexual Selection](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Short-Term Mating](#)
- ▶ [Sociosexual Orientation](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)

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Definition

Altruism can generally be understood as voluntary behavior which benefits another organism(s) but that demands from the benefactor a certain sacrifice, that is, an action that increases the beneficiary's aptitude at the cost of the benefactor's aptitude. In this sense, self-sacrifice is a hallmark of altruism, given that it can sometimes involve risk, be unhealthy, or even be dangerous.

Introduction

More and more people are recognizing the importance of behaviors aimed at benefiting others (i.e., pro-social behaviors). This signals the importance of becoming aware of the implications of such actions for society as a whole. Of the different psychological phenomena, altruism stands out, this in view of the potentially high cost to the benefactor. This is true specifically in the case of human beings, which demonstrate their potential to act for the other in various ways, such as donating blood or organs or even giving money to unknown needy people in a recognizable situation.

However, the reader might now be wondering: How does evolutionary psychology understand altruism? Altruism is a complex phenomenon that has been discussed under differing conceptions such as *kinship selection*, *reciprocal altruism*, and *group selection*. *Altruism by kin selection* predicts the reproductive success of individuals who are genetically linked (i.e., kinship), even though it may risk the reproduction or survival of the helper. *Reciprocal altruism* refers to another perspective that defends the idea that the individual momentarily diminishes his own aptitude in order to favor another, in the hope of the latter returning the favor later. Finally, the *group selection* approach affirms that altruism has evolved because it increases the overall fitness of the group, affecting both group and individual outcomes. Aware of the existence of different notions about altruism, this entry aims not to resolve this

Obliterative Shading

- [Countershading](#)

Observation

- [Attention and Perception](#)
- [Play and Social Learning](#)

Observation Cues

- [Altruism and Watching Eyes](#)

Observation of Altruism

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Synonyms

[Altruism](#); [Expression of altruism](#); [Human and nonhuman behavior](#)

theoretical impasse but to seek a better understanding of how altruism comes to be expressed.

The evidence indicates that the origin of altruism in different species lies in the quality of the parent-child relationship (Batson 2012). However, in order to behave altruistically, it is first necessary to identify the goals of the other and the difficulties that exist toward achieving them (Warneken and Tomasello 2006, 2009). A particularly informative behavior for the study of altruism is that of instrumental aid, in which an individual performs an action in support of another, with the purpose of making him achieve a concrete goal (Warneken 2010). Based on this approach, the altruistic action is evaluated from observation of instrumental helping behavior; this form is configured as one of the first types of altruistic expression in human ontogenesis (Warneken and Tomasello 2009). Yet it remains essential to note that altruism is expressed in different ways, such as solidarity, comforting, sharing, cooperating, and caring for others, among others (Warneken and Tomasello 2009).

Study of this modality of behavior in nonhuman primates has been an enriching source of information for understanding the phylogenetic aspects of this construct. In this regard, the literature argues that nonhuman primates apparently have potentials, such as motivational and cognitive skills, which enable them to engage in altruistic acts (Tomasello 2010). Nevertheless, the results concerning the expression of altruistic behavior in nonhuman primates are still controversial (Warneken and Tomasello 2006). In view of this, one might ask the question: What causes nonhuman primates to engage in behavior favoring others in some situations, but not in others?

Evidence has shown that this may be conditioned upon a necessity for an expressive demonstration of wanting or needing help (Warneken and Tomasello 2008), such as the case of a nonhuman primate observing that an individual of his species is trying to reach food that is outside of their reach. Corroborating this perspective, the literature has pointed out that as with human primates, nonhuman primates are apparently also able to identify when another individual requires assistance (Warneken and Tomasello 2006).

Studies show that mechanisms and behaviors in human and nonhuman primates are similar

(Warneken and Tomasello 2006) until a certain age, but at some point (early in ontogenesis), they begin to differentiate, with humans showing greater diversity and sophistication in the expression of altruism (Warneken and Tomasello 2009). The literature has pointed out that nonhuman primates help one another in instrumental aid contexts (Warneken 2010), so it is admitted that they exhibit behaviors understood to be altruistic even though in a smaller variety of situations as compared to humans (Warneken et al. 2007).

In asking about the factors that may affect this differentiation as to the quantity and quality of altruistic behaviors, one notes the influence of cognitive factors. Indeed, cognitive ability plays a fundamental role in the performance of altruistic acts. This can be observed among other animal species (Stevens and Hauser 2004; Warneken and Tomasello 2009), even though other species engage in pro-social behavior less often than humans (Stevens and Hauser 2004). Also according to these latter authors, such situations can be understood in that altruistic actions can go well beyond simple problem identification and require resolution of complex problems to help the other. This would explain restrictions in altruistic behavior in nonhuman animals, since sometimes the aid demands notions involving estimation of time, learning, and memory.

In altruism, the physiological and hormonal influence of the hypothalamus, oxytocin, and peptide hormones on altruism has been increasingly observed. In this sense, there is now evidence of greater activation of these hormones and areas when individuals are involved in romantic and parental-offspring (caring) relationships. It is believed that such bonding modalities and the exercise of social roles have respective links to the construct in focus here, such that altruism influences them, contributing to the choice of romantic coupling (Stavrova and Ehlebracht 2015) or even affecting the quality of parental care (Swain et al. 2012).

In discussing aspects related to observations of altruism, one cannot fail to mention the influence of both culture and the magnitude of the force it exerts on psychological phenomena. Culture is part of the individual and acts as a guide for human behavior; it defines the traits and

behaviors which are valued in every social context. Despite the similarities among the most varied cultures as to altruistic behavior, Bowles, Choi, and Hopfensitz (2003) note the existence of differences in manifestations and cultural practice among various groups and contemporary societies, such that even neighboring groups present particularities in their forms of altruistic expression.

Conclusion

Evolutionary psychology has made important contributions to the understanding of the origins of altruism, and differing perspectives have contributed to understanding phylogenetic aspects, such as kinship selection, group selection or even reciprocal altruism. Indeed, altruism is a psychological phenomenon that, although controversial, has been increasingly recognized for being instrumental in increasing the fitness of various species. However, no consensus has yet been reached as to its motivations and evolutionary components.

This psychological phenomenon can be observed in human and nonhumans, and its primary or basic form of expression is instrumental aid. However, for an individual to engage in an altruistic action, it is necessary that he understands both the objectives of the subject in need and the obstacles that the individual needs to overcome. Thus, the cognitive component is a basic factor in the expression of altruism and is an important differentiating element both quantitatively and qualitatively in the various altruistic expressions found in humans and other animals. Despite relevant scientific advances, it seems that there remains a considerable distance to go until we fully understand this intriguing psychological behavior. In this field, more research is clearly needed.

Cross-References

- [Altruism](#)
- [Altruism and Watching Eyes](#)
- [Evolutionary Psychology](#)

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Observations of Sexual Dimorphism

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Synonyms

Cues; Honest signalling; Reproductive fitness; Reproductive value; Secondary sex characteristic; Sexual selection; Signals; Variation

Definition

Sexual dimorphism is the term used to describe when the two sexes of a species possess physical characteristics that differ from each other. These physical characteristics can include differences in height, weight, color, decoration, and pattern and can even include body parts unique to one sex or behaviors such as birdsong.

Introduction

Evolutionary psychologists are interested in human sexual dimorphism (the observation that men and women tend to have different physical qualities), and whether it constitutes an evolved signal of some kind. There is a large body of evidence that this is the case for nonhuman animals, for example, the peacock's tail which signals mate quality to the peahen; and the antlers of some deer species which signal to rivals the dominance of the deer. This chapter will report some of the evidence suggesting that similar signals occur in humans, as well as evidence that suggests they do not. Specifically, it will focus on two areas: *male ornamentation*, physical characteristics that males possess which seemingly do not help with survival chances but do help with reproduction chances, and *costly signalling*, the fact that signalling can use an animal's nutrients from food to grow an ornament at the cost of maintaining the animal's overall health or increase the risk of death by predation.

Male Ornamentation

When observing nonhuman animals, sometimes the two sexes of a species will look noticeably different from each other. When each sex of a species has physical qualities that are unique to that sex, or that differ quantitatively between the sexes, this is considered *sexual dimorphism* (from the Greek *dímorphos* meaning "having two shapes"). There are many types of sexual dimorphism in the animal kingdom. Sometimes, the two sexes are different sizes, such as with the blanket

octopus, whose females can be up to 40,000 times heavier than the males, or the colors of the animal can be quite different between the sexes, such as the many species of birds known for the stark difference between their brightly colored males and milder-colored females.

Although it is not always clear why these differences exist, evolutionary theorists have gathered evidence of the process behind their evolution, namely *sexual selection*. Instead of characteristics being selected because they help the animal survive (*natural selection*), some characteristics are selected because they help the animal gain access to mates, and this is what is called sexual selection. Sexual selection can lead to characteristics that help an animal in the mating market by giving it the means of winning the competition with its same-sex competitors, or by making it more attractive to the opposite sex.

This assessment is reinforced by the observation that some of the differences between the sexes appear to be purely decorative. Which is to say that it seems the specific characteristics have no use for the animal's survival, they just appear to be *ornamentation*. These ornaments appear far more often in the male of the species, rather than the female. This is driven by what is known as the males-compete/females-choose model of selection which most sexually reproducing animals follow. In such systems, males compete for access to females, and/or females choose which male to mate with. Under this model, ornaments do serve a function. They are communication devices or *signals* to other animals of the same species.

In order for a characteristic to be considered as an ornament, it needs to meet some criteria. First, it must be a *secondary sex characteristic*. Secondary sex characteristics are features that are used in the process of sexual selection but are not directly used for sexual reproduction. Second, it must correlate with some underlying quality of the animal. This could be an aspect of the animal's health or an aspect of the animal's behavioral temperament. And third, there needs to be evidence that the other members of the species actually use the signal as an indication of the underlying quality.

Ornaments can take on many forms. They can be qualities of the physical body, such as the

bright colors of the mandrill's face; elaborate patterns like those of the golden pheasant's feathers; or strangely shaped body parts like the hooked jaw of spawning salmon and trout. They can also be behaviors, such as the birdsong of the Australian whipbird; or the elaborate dances of the peacock spider.

The peacock is the most commonly used example of male ornamentation. It has elongated tail feathers with some of those feathers looking like large eyes (ocelli). Research has shown that the length of the male's tale feathers is positively correlated with overall body condition (Moller and Petrie 2002), so the peacocks with the longest tails are also generally the healthiest peacocks. Other research has discovered that during mating season, the peacocks with the most ocelli are the ones which mate with the most peahens (Petrie et al. 1991). With these two observations linked, it can be said that the peacocks with the longest tails are also more likely to have the most ocelli (more space on the larger tail to fit them in) and mate with the most peahens. So, we can see that the ornament is related to an underlying quality, and the opposite sex is using the ornament to make mating decisions, i.e., finding the healthiest peacocks in order to increase the chance that her chicks will be healthy too. This is an example of the ornament being used to communicate something to the opposite sex, but ornaments can be used to communicate to the same sex as well.

Ornaments can also communicate something about the animal's temperament or expected behavioral patterns. The fallow deer is a species found in many places around the world, due to its introduction from European origins. The mature bucks grow a new set of antlers every year before their mating season. The antlers are shovel-shaped, with some spike-like growths around the edges. Research has shown that the total number of these spikes and the dominant behavior of the bucks are positively correlated (Pélabon and Joly 2000). This finding, combined with the fact that, although the bucks do use the antlers for fighting, they are the main source of determining status in the male hierarchy *without* fighting (Lincoln 1972). Due to the likelihood of injury during a battle, it can be more effective to use the antlers as

a signal of which bucks to avoid. There has also been some conflicting evidence regarding the symmetry of the antlers, with Malyon and Healy (1994) finding that fluctuating asymmetry correlated with dominance, but Pélabon and Joly (2000) finding that it did not. It is also important to note at this point that the antlers are not strictly ornamental, as they do serve a function in fighting; therefore, the argument could be made that they are technically armaments.

Humans are dimorphic as well. There are differences in the average weight, height, bone density, muscle and fat distribution, and facial structure between the sexes (Burke and Sulikowski 2010; Gangestad and Scheyd 2005). Just as biologists and ethologists use theories of evolution to explain the function of dimorphism in nonhuman animals, evolutionary psychologists can use the same theories to explain the function of dimorphisms in humans. However, data to date suggest that humans are more complex than other animals in this regard, and it is not always clear what constitutes an ornament in humans. This may be because although they still exist, human ornamentations are less extreme than those seen in some other animals. While there are strong body shape dimorphisms in humans, which reflect greater muscle mass and strength in males, and differential fat distribution and pelvic structure in females, many of these differences might plausibly be related to being better able to perform sex-typical roles in traditional societies, and so, even though there is evidence to suggest that these differences may operate as signals/ornaments (e.g., hand-grip strength, Gallup and Fink 2018; waist-to-hip ratio, Singh 1993), the emphasis here will be on facial dimorphisms, since they are more likely to be pure ornamentation.

Facial masculinity is one possible ornament in human males. When the overall composition of the face, including the bones, fatty tissue, skin, and facial hair characteristics, aligns with those which are more likely to be found in men's faces, the face is considered to be masculine. Generally speaking, men will have wider jaws, larger chins, larger width-to-height ratio of the maxilla (the top section of the jaw), and a larger brow ridge relative to a woman of the same body size. Compared

to women, less fat is deposited in the cheek area, skin tone is generally darker, as are eyebrows, and of course, men are much more likely to be able to grow beards (Gangestad and Scheyd 2005).

Researchers have found that masculine facial characteristics are an indicator of underlying sex hormone ratios. Testosterone (found in greater quantities in men) is involved in the building of bone structures, while estrogens (found in greater quantities in women) suppress bone growth (Kung 2003; Neave et al. 2003). Additionally, masculine facial characteristics develop fully in structure during puberty, when there is an increase in sex hormone levels. This is another indication that facial masculinity is an ornament, as ornaments tend to develop in other animals as they reach reproductive maturity.

Based on these findings, it can be said that the level of facial masculinity seen in a man's face may be a signal of the measure of testosterone circulating in his system. This is important to prospective mothers and future children because testosterone promotes both morphological and behavioral differences.

A greater level of circulating testosterone has been found to lead to more aggressive behaviors and a reduction in pro-social behaviors. It has been shown that as circulating testosterone levels increase, so do levels of physical aggression, verbal aggression, anger, and hostility. Additionally, as levels of circulating testosterone increase, levels of altruistic and empathic behaviors decrease (Harris et al. 1996). As it would be in a prospective mother's best interest to provide a safe and nurturing environment for future offspring, it would be reasonable to assume that she would avoid those males signalling greater levels of aggression. However, in our ancestral past, a certain level of aggression would have been adaptive. An aggressive male would have stood a better chance of climbing the social hierarchy, thus making him more attractive; but he also would have stood a better chance protecting his family from other men wishing to take his mate and/or resources.

More evidence supporting this hypothesis is the fact that both women and men will judge images of highly masculine male faces as

belonging to a more dominant person, while less masculine faces are judged as less dominant (Windhager et al. 2011). However, although the relationships between testosterone and both aggression and physical dimorphism are well established; perceived dominance shows a relationship with testosterone which is not entirely clear. Neave et al. (2003) studied a group of males by taking measurements of both prenatal levels (2D:4D ratio) and current circulating levels of testosterone (salivary measure). They found that prenatal levels of testosterone are related to perceived levels of dominance, but the current circulating levels of testosterone are not. This indicates that greater levels of prenatal testosterone do indeed organize the bone structure of the face to make it appear more masculine and dominant. But, as the levels of prenatal testosterone and current circulating levels were also not related, this calls into question the relationship between facial masculinity and actual behavioral outcomes.

The males-compete/females-choose model has been cited as the reason behind ornamentation of males, but what if the roles were reversed? As predicted by Trivers (1972), when the parental care roles are the opposite of the norm, males can be choosy and females can evolve ornaments. For example, some female pipefish, seahorses, and seadragons are more ornate than the males. It is the males that carry, give "birth" to, and care for the young, and therefore, it is the females that work for the attention of the males.

A second model of sexual selection can also result in female ornamentation. The mutual mate choice model predicts that when both sexes compete intrasexually, and both sexes are choosy about mate selection, then both sexes could use ornamentation. This is the case in humans. Just as facial masculinity is considered an ornament in men, facial femininity is considered an ornament in women. As mentioned previously, testosterone is related to facial masculinity; but for facial femininity, there is a similar relationship with estrogen and progesterone (Law Smith et al. 2006). In women, these two sets of hormones are found in greater quantities, and they are responsible for maintaining and controlling the menstrual cycle.

In other words, they are related to a woman's fertility, and so the femininity of a woman's face is a potential signal of her fertility.

Costly Signalling

As has been explained, ornaments are a type of signal. In evolutionary theory, *signal* has a specific meaning. It is a characteristic of the animal that is used to communicate a specific message. It is done "intentionally" by the signaler (but rarely consciously), and its message is intended to be clear to the receiver, resulting in a behavioral change that is beneficial to both individuals. *Cues*, on the other hand, are unintentional, may be detrimental to the animal sending the cue, and may not always be clear in their message. However, if the cue turns out to be a useful communication device, there is the possibility that it evolves into a signal, which is known as the "signaler precursor route" (Laidre and Johnstone 2013). Take, for example, a wolf baring its teeth. This is a definite signal that the wolf is aggressive and about to attack. It is quite possible that this began as a cue, simply because a wolf needs to draw back its lips so it can bite. Those wolves that saw this cue and avoided conflict with the aggressive wolf would have lived longer, and thus reproduced more pups that tended to avoid other wolves when they saw teeth being bared. Additionally, those wolves that bared their teeth before attacking would have also avoided conflict, lived longer, and reproduced more pups that tended to bare their teeth when becoming aggressive. This is a simple example of a mutually beneficial signal, but signaler/receiver psychology can become more complex when the "cost" of the signal becomes high.

In line with the previous example, in order signal to evolve, the benefits must outweigh the costs. One "cost" of the signal is the amount of physical energy or nutrients/resources required to generate the signal, with ornament growth shown to decrease when food sources are low (Zeh and Zeh 1988). Costs are also associated with the increased risk of predation or being attacked by same-sex rivals due to the signal increasing the

visibility of the animal. Another potential cost is the opportunity cost of missing mating opportunities because of the signal. The "benefit" is defined as the increase in reproductive fitness – an increase in the number of offspring the animal produces. In short, if the development of any signal leads to a handicap for the animal's survival, then there must be a greater advantage to the animal's reproductive chances to warrant the cost; otherwise, the genes which guide development of the signal will never make it into the next generation (Zahavi 1975).

Returning to the wolf example, it is reasonable to believe that the cost of baring the teeth would be quite low. The energy cost would be minute, and the likelihood of attack from competitors would be low as well because the signal is expected to actually reduce the likelihood of violent conflict. However, consider the signal this sends to prospective mates. If the wolf were to bare its teeth excessively, then it may be seen as an overly aggressive individual, which puts the safety of future pups at risk. Therefore, the interpretation of the signal must be consistently reliable and accurate – an "honest" signal. That is, a signal must truly be signalling what it is "intended" to signal in order for the communication system to work; otherwise, the system would collapse. So, it can be seen that the cost of a signal needs to be finely tuned in accordance with the benefit to reproductive fitness. For female mammals especially, the cost of favoring a "dishonest" signal can be high from a mating perspective, as mating with the wrong individual can lead to the extremely high cost of gestating, giving birth to, and feeding young which have a lowered chance of going on to reproduce in the future.

For the facial masculinity of human males, one of the greatest costs comes from the negative effects of greater levels of testosterone. Exposure to high amounts of testosterone has been shown to impair the immune system and make it more difficult for the human body to fight off pathogens (Foo et al. 2017). According to the "good genes" theory of mate choice, the display of high levels of testosterone is seen to signal genetic quality (Penton-Voak et al. 2004). The theory predicts that for a male to be signalling his compromised

immune system, then his genes must be of a high quality in order to compensate for this disadvantage; and it is these genes that the female values to maintain health of future offspring. This theory was put to the test by Zaidi et al. (2018) who used a measurement of a genetic marker of immune system competence known as the *major histocompatibility complex*, and a measurement of facial masculinity in close to 2,000 participants. They found no relationship between the two measures. This means that the level of a man's facial masculinity may have nothing to do with his intrinsic levels of health. It is also worth noting that this finding and failures at explaining other mating behaviors (e.g., Jones et al. 2017) have led to the founders of the good gene theory to retract their support for the concept (Buss and Schmitt 2019).

There is another set of ornaments that is, as far as we know, unique to humans. Miller (2000) makes the argument that displays of intelligence such as those made through music, art, and humor are ornaments. He states that they have no other evolutionary function outside of mate attraction. In terms of costs involved in producing these signals, there is a massive resource cost in growing and maintaining the human brain, which is responsible for these displays. But there is also a social cost when these displays are delivered poorly. Take self-deprecating humor for example. This style of humor is received and interpreted through the context of the status of the person delivering the joke. When a higher status person makes a self-deprecating joke, it is seen as a mismatch with reality and the signaler's status is unaffected because it is believed they can "afford" the cost. However, if a lower status person uses self-deprecating humor, the results are different because they appear as self-defeatist or depressed (Greengross and Miller 2008).

Conclusion

Many sexually reproducing species exhibit sexual dimorphisms, including humans. Some of these dimorphisms are considered "ornaments" because they appear to serve no survival purpose; they are

purely for increasing access to mates. These ornaments are typically displayed by the male of the species, but there are exceptions such as humans. Ornaments can be body parts, or behaviors, and are in essence signals that advertise the quality of the individual who possesses them. Each signal presents a cost to the animal's ability to get its genes into the next generation, which must be weighed against the benefit to the animal's overall reproductive fitness.

Cross-References

- [Costly Signalling](#)
- [Female Mate Choice \(Intersexual Selection\)](#)
- [Intrasexual Male Competition](#)
- [Male Ornamentation](#)
- [Sexual Selection](#)
- [Sexual Signalling](#)

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Observed Mating Behavior and Women's Long-Term Mating

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Synonyms

Development; Mating competition; Reproduction; Sexuality

Definition

Women's mating behavior includes human female sexual development, mate preferences, and strategies to optimize reproduction and long-term mating. Each of these components of mating behavior has been shaped by selection to produce adaptive outcomes.

Introduction

A life history approach to evaluating human behavior can be fruitful for understanding the fundamentally unique nature of women's mating behavior (Luoto et al. 2018; Motta-Mena and Puts

2017). For example, early in development, puberty in humans marks a formative time during which changes in the visuoperceptual system can influence the ability to detect facial cues related to mating behavior and sexual relationships (e.g., sexual interest; Garcia and Scherf 2015; Motta-Mena and Scherf 2017), a crucial developmental transition that, thus far, appears to be exclusive to humans. As young women undergo puberty and begin menstruation, they begin to exhibit relatively cryptic fertile windows in their ovulatory cycle, report experiencing sexual desire and behavior outside of the fertile window, and engage in higher levels of mating competition compared to most female primates.

Following puberty, women compete for, choose, and engage in both short- and long-term relationships with mates during their reproductive lives. To do so, women must learn to navigate complex sexual relationships in adolescence (Motta-Mena and Scherf 2017), compete with other females for mates (Fink et al. 2014), and learn to provide reliable cues to their availability to potential mates, such as sexual ornaments that signal women's residual reproductive viability (Thornhill and Gangestad 2015). Importantly, women's sexual behavior is not constrained to the fertile phase (e.g., as in most primates; Thornhill and Gangestad 2015) and suggests that perhaps women's copulatory patterns across the cycle may reflect a mixed-mating strategy.

In what follows, this entry will discuss women's mating behavior from pubertal development through adulthood, as well as the evolutionary processes that have shaped women's modern mating behavior. While not exhaustive, this entry provides a broad overview of the emergence and development of women's mating behavior and mating strategies.

Pubertal Development

As a crucial life history transition, pubertal development involves the orchestration of anatomical as well as psychological changes associated with sexual maturation. Girls tend to enter puberty sooner than boys (Marshall and Tanner 1969,

1970) and experience a cascade of physical changes that include the emergence of secondary sex characteristics such as breasts, fat deposition on the buttocks and hips, and pubic hair growth, particularly as girls approach the onset of menarche (Grumbach and Styne 1998; Marshall and Tanner 1969, 1970). Estrogen inhibits the accumulation of fat in the abdominal region and stimulates fat deposits in the lower half of the body (Singh 1993), thereby producing a gynoid body shape (Singh 1993).

Fat around the midsection can be quantified with the waist-to-hip ratio (WHR), which is the ratio of the narrowest part of the waist relative to the widest part of the hips (Singh 1993). Before puberty, lower estrogen levels result in more even fat distribution across the hips and abdomen, resulting in a WHR closer to 1 (for review, see Singh 1993). Beginning in puberty and through the reproductive years, the typical range of WHR is 0.67–0.80 (Lanska et al. 1984). While some work suggests that WHR is related to levels of estradiol and progesterone (Jasińska et al. 2004; Zaadstra et al. 1993), other work has found no such association (Jones et al. 2017). The relationship between women's physical attractiveness and the underlying endocrinology thus remains ambiguous.

In addition to these complex physical changes, puberty also spurs profound changes in adolescent psychology (Dahl 2004; Motta-Mena and Scherf 2017). The transition from puberty into the autonomy of adulthood necessitates that typically developing adolescents learn to navigate increasingly complex social relationships in order to succeed in the competitive reproductive sphere. The complex interplay of hormones is simultaneously influenced by neuroendocrine feedback loops from the brain, which are believed to facilitate sexual behavior in adolescence (Schulz et al. 2004).

Further evidence suggests that adolescents are unable to detect facial expressions related to sexual interest until they have undergone puberty (Garcia and Scherf 2015; Motta-Mena and Scherf 2017), suggesting that perhaps puberty is fundamental for the development or onset of adult-like mating preferences. In short, the unique physical and psychological changes adolescents must

undergo during puberty raises compelling questions about changing social behavior, and how puberty impacts sex-typical social behaviors in adulthood.

Mate Preferences

Women experience greater levels of sexual desire and interest when fertile (Arslan et al. 2017; Jones et al. 2018a), but it remains unclear if shifts in mate preference also track with menstrual phase. Recent work has failed to find evidence in support of cycle shifts in preferences for masculine faces, bodies, and behavioral displays (Jones et al. 2018b; Jünger et al. 2018b) as well as for masculine voices (Junger et al. 2018).

Further inconsistencies in the literature are reflected in the results of two meta-analyses that reached opposite conclusions about whether women's judgments of men's attractiveness track with changes in women's cycle phase (Gildersleeve et al. 2014; Wood et al. 2014). On the one hand, Wood et al. (2014) reported little support, and on the other hand, Gildersleeve et al. (2014) concluded that cycle effects are robust and influence women's judgments of men's attractiveness in a systematic way. Critically, Wood et al. coded multiple studies for which effect sizes were unknown as "0.00" rather than as missing data, thereby categorizing them as potentially "null effects" and ultimately biasing the estimated overall effect toward zero. Gildersleeve et al. employed multilevel models to account for the nested nature of effects and aggregated across male traits in overall analyses. Differences in the statistical approaches for each meta-analysis may thus have contributed to the uniquely different conclusions.

To evaluate this ongoing question regarding cycle shifts in women's preferences for masculine features, a recent study employed masculine voices as the stimuli of interest in two large within-subjects experiments from different labs, using natural as well as manipulated voice recordings as stimuli, and also examined hormone concentrations and possible moderator variables (Junger et al. 2018). The results failed to support

cycle shifts in women's preferences for masculine voices.

Critically, while some researchers in this line of research argue that null results for cyclic shifts in mate preferences are likely specific to face preferences, this evidence as well as other recent studies evaluating cycle shifts for body or behavior preferences (Junger et al. 2018; Jünger et al. 2018a, b; Marcinkowska et al. 2016) indicate that it no longer appears to be the case that null results are peculiar to face preferences (Jones et al. 2018b; Muñoz-Reyes et al. 2014; Peters et al. 2009). Therefore, there is a strong need for continued work to elucidate the role (if any) of hormonal influences on cycle shifts in women's preferences across categories of stimuli (e.g., voices, faces, bodies).

Cognitively, several lines of research suggest that women in committed and satisfied relationships reportedly have poorer memory for attractive men's faces than women in low-commitment relationships (Wang et al. 2016; Watkins et al. 2017), presumably in the service of maintaining their current relationship by devaluing potential alternatives. Notably, however, partnered women were not significantly different from unpartnered women in memory for attractive male faces in the Wang et al. (2016) study. In a related study evaluating recognition memory for more and less attractive versions of male and female identities, Watkins et al. 2017 found that women in better quality relationships had greater false memories for attractive men. These findings suggest that women's memory for facial cues may vary systematically according to the factors that influence female mating competition and relationship maintenance (i.e., relationship status and male attractiveness).

Strategies to Optimize Mating and Reproduction

Female mate choice is a behavior that systematically biases a female's probability of mating with males having particular characteristics. Thus, female mate choice occurs when females exhibit behaviors such as selectively moving toward

and/or maintaining proximity to certain males, selectively soliciting copulation or attention from certain males, or selectively cooperating with certain males' solicitations, if these behaviors influence the probability of mating with these males (Puts 2010). Thus, differential acceptance of – or resistance to – male attempts at copulation appears to represent at least one form of female mate choice.

Evolutionary theories suggest that men and women are evolutionarily designed to solve different mating-related strategies (Trivers 1972), which lead to differences in mate preferences and competition. Such differences in mate preferences and competition are explained, at least in part, by sexual selection theory. Specifically, due to the relative asymmetry in parental investment between men and women, heterosexual women should theoretically compete with other women for mates that provide resources, while heterosexual men should compete with other men for mates that appear attractive, fertile, and healthy (Buss 1989; Conroy-Beam et al. 2015; Trivers 1972).

Women tend to compete with other women for mates by advertising qualities that are valued by men (e.g., beauty, clothing choice, and sexual exclusiveness; Durante et al. 2008) and by derogating rivals (e.g., through gossip and devaluing other women; Fisher 2004) rather than via direct displays of dominance, as in men. In addition, women tend to be influenced more by peer evaluations (i.e., from other women) than men are (Graziano et al. 1993), suggesting that intrasexual competition in women may elicit a uniquely different dynamic among women than intrasexual competition in men. Men tend to value those physical features in women that are related to *fertility* and *fecundability*, such as youthfulness, vitality, and an ideal body-shape (Conroy-Beam et al. 2015). In addition, when asked to spontaneously mention relevant characteristics about a rival that might attract their partner, women tend to report more jealousy when a rival is high in physical attractiveness (Dijkstra and Buunk 2002).

In most mammals, including primates (Nadler et al. 1983), female sexual activity is heightened during the fertile period of the reproductive cycle (Thornhill and Gangestad 2015). In contrast,

women's frequency of intercourse varies inconsistently (if at all) across the ovulatory cycle (Arslan et al. 2017). Nevertheless, there is a fertile phase increase in sexual motivation and desire, such that women report more in-pair and extra-pair desire as well as self-perceived desirability (Arslan et al. 2017). In addition, women have also reported more flirtation (Haselton and Gangestad 2006) as well as feeling less close to and more critical of their primary partner, particularly if the partner is less sexually attractive (Larson et al. 2013).

In short, women's sexual behavior and libido both appear to shift across the cycle, and evidence suggests that this shift tracks with ovarian hormones (for review, see Motta-Mena and Puts 2017). This raises intriguing questions about evolutionary causes and hints at roles of pair-bonding and extra-pair mating. If ovulation is concealed and copulation occurs throughout the cycle, then a mid-cycle rise in libido could promote extra-pair copulation in order to recruit good genes, while also being able to retain non-genetic benefits conferred by the pair-bond partner (Thornhill and Gangestad 2015). Ultimately, however, more work is necessary to evaluate and understand how women's sexual behavior throughout the cycle has evolved to produce adaptive outcomes.

Conclusion

Using a life history approach, this entry highlights the unique nature of women's mating behavior and cognition from puberty to young adulthood. While a clearer picture is emerging, many questions remain regarding how women select their mates throughout the lifespan, and particularly how they select and maintain long-term partners. While more fieldwork is ultimately necessary to understand the magnitude of effects outside of the laboratory in more naturalistic settings, recent work employing hormonal assays (Junger et al. 2018; Kordsmeyer et al. 2018; Shirazi et al. 2018a), large datasets with behavioral recordings (Arslan et al. 2017), as well as international samples (Shirazi et al. 2018b) provide robust evidence

and methodological rigor for elucidating women's mating behavior.

Cross-References

- [Female Mate Choice \(Intersexual Selection\)](#)
- [Mate Preferences](#)
- [Sex Differences in Long-Term Mating Preferences](#)

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Obsessive Fears

► Phobias

Obstetrical Dilemma

► Narrowing Birth Canal

Obstructed Labor

► Birthing Complications

Occipitotemporal Projection System

► Ventral Stream, The

Occlusion

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Synonyms

Interposition

Definition

Occlusion is a monocular depth cue produced by partially overlapping objects: Objects that partially block other parts of the scene are perceived to be closer to an observer than the blocked objects.

Introduction

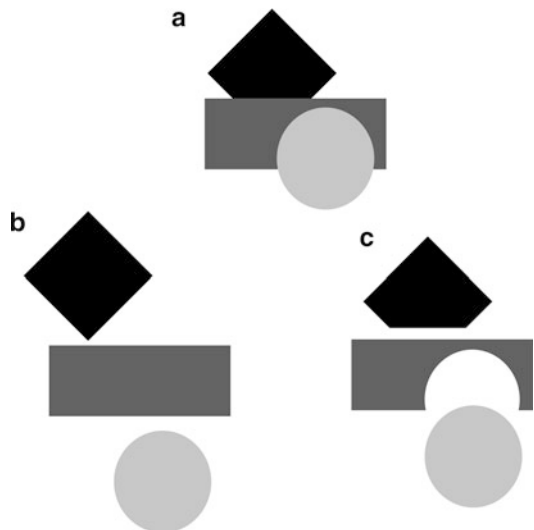
Like motion parallax, occlusion is a monocular depth cue that does not require integrating information from two retinas. Unlike motion parallax, however, occlusion is a pictorial depth cue that is available in static images. In addition to using occlusion for ordering objects in depth, human observers have a strong tendency to perceive partially occluded objects as being completed behind an occluded surface, a process called *visual completion* or *amodal completion*. However, the presence of amodal completion in non-

primate species is less explored and, in some cases, controversial.

Occlusion and Visual Completion in Humans and Nonhuman Animals

All organisms inhabit a world filled with opaque objects; thus, their visual systems must constantly deal with recognizing these objects on the basis of their visible parts and ordering them in depth. Human visual system handles these tasks by automatically completing partially occluded objects (Fig. 1); at 7 month of age, infants show both the ability to use occlusion for ordering objects in depth and to amodally complete them (Kavsek 2004).

In humans, amodal completion is normally demonstrated by using two-dimensional images similar to those shown in Fig. 1. The observers are asked, either directly or indirectly, to judge whether the occluded image (e.g., a rectangle, Fig. 1a) is more similar to the completed version of that image (e.g., a full rectangle, Fig. 1b) or an incomplete version that presents the portions not obscured by the occluded (Fig. 1c). Although this



Occlusion, Fig. 1 An illustration of amodal completion. When shown an image with overlapping objects (a), human observers assume that it consists of complete objects (b) rather than their visible parts (c)

approach has successfully been used for a number of mammalian species (reviewed by Fujita 2006), many other efforts to demonstrate amodal completion using such images were either unsuccessful (pigeons: Sekuler et al. 1996) or required additional contextual cues or experimental manipulations to induce amodal completion (baboons, Deruelle et al. 2000; pigeons, Nagasaka et al. 2007).

In contrast, experiments using real three-dimensional objects consistently revealed amodal completion in a variety of species (fish, Sovrano and Bisazza 2008; baboons, Deruelle et al. 2000). Moreover, pigeons have recently been shown to use occlusion for ordering two-dimensional objects in depth (Cavoto and Cook 2006), further suggesting that they may be capable of amodally completing objects in certain circumstances.

On the other hand, pigeons have also been shown to experience difficulties in recognizing pictures of occluded objects without additional experimental manipulations (Aust and Huber 2006; Lazareva et al. 2007). It is therefore possible that their depth perception in two-dimensional images is generally impaired unless motion-induced cues such as motion parallax are available. Unfortunately, there are no current studies exploring pigeons' (or any other bird species) amodal completion with static three-dimensional objects; thus, the conclusions about the generality of monocular depth cues in avian vision must await further comparative research. Finally, there is no current evidence to suggest that insects or other invertebrates either recognize partially occluded objects or amodally complete them (Baum et al. 2014).

Conclusion

Human observers experience little difficulty in navigating the world filled with partially occluded objects, possibly due to their ability to spontaneously perceive partially occluded surfaces as complete. Although animals must undoubtedly face the same problems, the evidence for the ability of vertebrate animals to recognize partially occluded objects and to amodally complete them

remains mixed; it is currently unknown whether invertebrates employ amodal completion or use occlusion as a depth cue.

Cross-References

- [Depth Perception](#)
- [Motion Parallax](#)

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Occurrence

- [Reaction Norms and Tokens](#)

Ocelli

- [Eyespots](#)
-

Ocellus

- [Eye, The](#)
 - [Eyespots](#)
-

Octave

- [Music and Hormones](#)
-

Odor and Memory

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Synonyms

[Odor expertise](#); [Odor familiarity](#); [Odor recognition](#); [Olfactory memory](#); [Olfactory perceptual learning](#)

Definition

The improvement through experience of the ability to detect and or/discriminate sensory stimuli.

Introduction

It is widely believed that the sense of smell has minimal impact on the critical aspects of existence. However, research has shown that olfaction is deeply involved in every aspect of our lives. Of all the forms of odor memory, odor recognition is the most common and direct measure of odor memory (Crowder et al. [1995](#)). Odor-evoked

memory is responsible for providing us a sense of self, who we are, where we are in time and place, present and past (Herz [2011](#)). The anatomy of olfaction seems to be tied to our emotions, motivations, and associations in a unique way which provides us with our personal and interpersonal experiences.

What Is Odor-Evoked Memory?

Odor memory is used to define both memory of odors and memory evoked by odors (Herz and Engen [1996](#)). Research in this field begun early in the twentieth century when early investigators compared verbal associations using images and odors as cues and found that odors were weaker reminders than images, described the emotions and associations odors evoked, and also described the characteristics of odor-evoked memories (Bolger and Titchener [1907](#); Kenneth [1927](#); Laird [1935](#)). Over the past decades, modern experimental methods have been used to investigate olfactory memory using cognitive experimentation such as the role of verbal mediation in olfactory processing, the duration of memory, olfactory recall and imagery, and neurological techniques that focused on impaired versus spared dissociation in clinical populations (Pelosi [1994](#)).

Most odors experienced in nature are a combination of many different odorant molecules. The ability to discriminate between these odors is one of the main functions of olfaction. This process involves initial analysis of the inhaled stimulus into its component molecular features which are then combined to provide a unitary odor object such as “chocolate” (Wilson et al. [2009](#)). The more familiar the odors become the more enhanced the encoding of the feature and their synthesis into objects becomes as well. This process leads to improvements in sensory discrimination in other words to determine whether two stimuli are different or the same. However, the ability to remember odors and the experience of memory evoked by an odor are two distinct cognitive-perceptual processes. Remembering odors refers to the ability to identify that you have smelled a specific smell before, and it does

not bring back any particular memory event (Herz 2011). On the contrary, memory evoked by an odor refers to the ability to recollect a specific event from one's life, but it does not have much to do with the odor itself. There is a possibility for the two processes to overlap in certain situations.

In the last 20 years, research concerning the special attributes of odor-evoked memory has been widely conducted. Herz et al. (2004) found left hemisphere dominance during episodic odor-evoked recall. Rubin et al. (1984) compared odor memories of participants with memories evoked by photographs or names and found that memories evoked by odors were reported as never having talked about prior to the experiments. They also suggested that odors might evoke more pleasant and emotional memories compare to other stimuli (Rubin et al. 1984). Hinton and Henley (1993) conducted a study to compare responses to stimuli that were resented in visual, lexical, and olfactory modalities. Their results indicated that the olfactory mode is significantly more emotionally arousing than verbal or visual stimuli and that odors can be more personally involving than those elicited by other sensory stimuli (Hinton and Henley 1993). However, odor-evoked memories do not elicit more accurate memories than other sensory cues (Hertz and Cupchik 1992). Research that followed suggested that memories triggered by olfactory information differ compared to memories evoked by verbal and visual information (Herz and Schooler 2002; Willander and Larsson 2006) in that they are more emotional. The results of Willander and Larson (2007) in their study of 72 older adults indicated that semantic knowledge of an odor's name significantly affects the age distribution of memories such that the memory peak in childhood observed for odors only was attenuated.

Characteristics of Odor-Evoked Memory

In order for an odor to be remembered, it needs to be encoded and stored in the olfactory system. This process is regulated by neuromodulators which store information in a way that maintains

the olfactory experience significant (Wilson and Stevenson 2006). The neurotransmitters nor-epinephrine and acetylcholine that affect both the implicit and explicit memory regulate these systems. Implicit odor memories do not require the deliberate recollection of an odor experience in order to form in the brain (Rouby et al. 2002). Previous exposure to a familiar stimulus seems to help the formation of implicit memories (de Wijk et al. 1995) through the process of habituation due to prolonged exposure to a stimulus (Wilson and Stevenson 2006). Jonesgotman and Zatorre (1993) studied odor memory in 121 patients with unilateral cerebral excision from temporal, frontal, frontotemporal, or centroparietal areas, and in 20 control subjects and found that participants showed impairment only after excision from the right temporal or right orbitofrontal cortex. All groups showed significant forgetting over time, and verbalized odors were recognized more efficiently than unlabeled ones. Rasch et al. (2007) in their study cued new memories in humans during sleep. They presented an odor that had been presented as context during prior learning. Their results showed that reactivation indeed causes memory consolidation during sleep and that reexposure to the odor during slow-wave sleep (SWS) improved the retention of hippocampus-dependent declarative memories but not of hippocampus-independent procedural memories. On the contrary explicit odor memories refer to memories that are consciously remembered, which in terms of olfaction refers to attribution of associative meaning to a specific odor (Radvansky 2006; Wilson and Stevenson 2006). By associating meaning to odors information is stored in a way that will aid in processing and comparing to other odors (Wilson and Stevenson 2006). Odor recognition and odor identification are probably the most commonly used tests to measure odor memory (de Wijk et al. 1995).

Several characteristics of odor-evoked memories contribute in distinguishing them from memories evoked by stimuli perceived through other sensory modalities (Herz 2011; Larsson et al. 2014). The most distinctive characteristic of these memories is their ability to evoke more emotional and evocative recollections than any

other stimuli (Herz 2016). This is due to the neuroanatomy of the olfactory cortex which includes the amygdala, the part of the brain that processes emotional experience and emotional memory as well as the hippocampus, which is responsible for associative learning (Aggleton and Mishkin 1986; Cahill et al. 1995; Eichenbaum 2001). The amygdala is a complex set of nuclei involved in the formation of memories of emotional experiences associated with defense, flight, and fear. The direct projections from the amygdala to the hippocampus involve integration of various sensations into memory which is extremely important for the development of olfactory memories (Buchanan et al. 2003). The olfactory system is the only one that makes direct and intense contact with neural substrates of emotion and memory, which may provide a better understanding of why odor-evoked memories are usually emotionally potent. Other sensory modalities are mediated by limbic projections which are connected to associational areas (Herz and Engen 1996).

Another unique characteristic of the olfactory system that is directly associated to odor memory is the fact that incoming information is not processed in the thalamus before it is projected directly to the cerebral cortex, it occurs in the primary olfactory cortex (Carmichael et al. 1994). Neural transduction in the olfactory system seems to be different than any other sensory modalities. The neurons are unmyelinated, thereby assisting the sensation of an odor to remain for a greater period of time than other sensations. These unique interconnections are responsible for the emotionally evoked memories.

Context-Dependent Memory

Based on the principle that environmental features encoded as part of a memory trace can contribute to memory for stored odors, context-dependent memory is formed. In other words, odors facilitate the retrieval of information already learned (Schab 1990; Smith et al. 1992). Ehrlichman and Halpern (1988) found that participants recalled significantly more positive memories

when presented with a pleasant odor than when they were presented with an unpleasant odor. Herz and Engen (1996) note that hedonic and emotional responses that maybe elicited from an odor depend on how the odor was first encountered. Hence, they seem to be based on learning principles.

It has been demonstrated in studies that hedonic and emotional responses an odor elicits are dependent on how the odor was first encountered. Jellinek (2004) notes that awareness of the emotions associated with an olfactory experience is prior to awareness of the presence of the sensory stimulus which elicits the experience. Almost all responses of odors have been shown to be based on associative learning principles (Davis and Ludvigson 1995). Therefore, if an odor is perceived as pleasant, it was first experienced in a pleasant context.

Herz and Cupchik (1992) proposed a theory based on the primacy of associative mechanisms in olfactory learning in order to explain autobiographical odor-evoked memories. He stated that if an odor is first experienced in an emotionally salient context, it will become a very effective trigger for the recollection of this memory. This is due to the higher level of activation in the amygdala which is critical for emotional memory (Cahill et al. 1995).

To examine the relationship between odor and emotion studies investigated whether heightened emotional states during the encoding of information relating to a new odor enhance the retrieval of that odor. The results indicated that word recall was higher when a specific odor was present at encoding and retrieval compare to no odor cue being available (Herz and Engen 1996). These findings support the theory that emotion is a vital variable in the formation of autobiographical odors.

Conclusion

Many studies have proved the existence of long-term odor memory and of previous experiences triggered by odors. Odors that are associated with emotion arousing events tend to be remembered

for years maybe even throughout the life span. The available data from various studies suggest that memories evoked by odors have several distinct characteristics related to their emotional quality such the fact that memories elicited by odors seem to be more emotionally potent than memories triggered by other sensory stimuli, and it seems this saliency produces the impression that odor memories are more real. Neuroanatomical evidence is consistent with this finding (Herz and Engen 1996).

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Odor Expertise

- [Odor and Memory](#)

Odor Familiarity

- [Odor and Memory](#)

Odor Recognition

- [Odor and Memory](#)

Offensive Sexual Advance

- [Sexual Harassment](#)

Offerings

- [Charity](#)

Offspring

- [Quantity Versus Quality of Offspring](#)

Offspring Defense

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Synonyms

[Brood defense](#); [Nest defense](#); [Offspring protection](#)

Definition

Protecting progeny against threats that may cause resource loss, bodily harm, or death

Introduction

In most species, the risk of extrinsic mortality (mortality due to external forces such as predation) is much higher for young than it is for adults. Young organisms are generally slower, smaller, and, due to inexperience, less skilled at navigating the world around them than adults are. While this is the case for nearly all species, it is particularly true for species which have altricial (as opposed to precocial) young. This includes humans, whose infants are considerably less neurologically and behaviorally developed at birth than the neonates of most other primates (Freedman 2016). They are entirely reliant on older caretakers for all of their basic needs, including protection.

In many species, there is considerable selective pressure on one or both parents to protect their offspring from threats of all kinds. By the time any young organism comes into the world, its parents have spent considerable energy getting it there. Both males and females have invested in gamete production and mating. For eutherian mammals, females have invested in internal gestation, and for all mammals, mothers continue using energy to lactate throughout their offsprings' infancy (Trivers 1972). In many birds and some fish, reptiles, amphibians, and invertebrates, both females

and/or males may have spent time incubating or guarding eggs (Clutton-Brock 1991). These investments in their direct fitness will only pay off if parents can keep their offspring alive long enough for them to reproduce.

While defense of young may come from a variety of sources, especially in highly social species such as humans, this entry is concerned specifically with offspring defense, that is, parents defending their young. In most cases, this means genetic parents, though depending on the specifics of the biological system, young may occasionally be raised by “social parents” who are not biologically related (e.g., human families with adopted children).

Defense Across Development

Depending on the ecology and life history of the species under consideration, offspring defense may take place within a small discrete window or continue across multiple stages of development. Some forms of defense begin at the moment of conception. For mammals, internal gestation provides the fetus with a considerable buffer against the outside world. While mothers are therefore a fetus’ first line of defense, in social species, a fetus can indirectly benefit from protection provided to its mothers by other group members, including the fetus’ father. In species that do not gestate internally, parents may protect vulnerable eggs from hungry predators by depositing them in places where they are hard to detect (e.g., Marquardt et al. 2016) or guarding their nests directly (e.g., Komdeur and Kats 1999). Some species that hide eggs leave immediately afterwards; their offspring defense begins and ends with finding a safe place for eggs to incubate. Others abandon offspring defense as soon as their progeny emerge (e.g., some nest-guarding reptiles; Gans 1996). After offspring hatch or are born, defense may occur in a variety of forms from infancy through early adulthood. In species with slow life histories such as primates (including humans) and cetaceans, offspring defense may continue over the course of many years (Clutton-Brock 1991, 2016).

Various models have been proposed to explain changes in parental defense behavior across offspring developmental stages. All fall within the basic theoretical framework of parental investment theory (Trivers 1972) and its associated cost/benefit analysis of the returns to various behavioral strategies (Montgomerie and Weatherhead 1988). One hypothesis is that parents will more vigorously defend offspring as their expected reproductive returns get closer to that of their parents (i.e., as they get closer to the end of the high-mortality infancy and/or juvenile period). Another proposes that parents will most vigorously defend infants who are most vulnerable to a given threat. Defense intensity or type may also vary as a function of offspring quality or number, parental experience, the confidence parents have that offspring are theirs, and/or the relative formidability of the threat, among other variables (reviewed in Montgomerie and Weatherhead 1988). The majority of empirical work testing such hypotheses has occurred in birds (but see also Koskela et al. 2000; e.g., Mahr et al. 2015; Thünken et al. 2010). However, there is little theoretical reason to believe that the underlying hypotheses are not equally applicable to most taxa, including humans.

What Do Parents Defend Offspring Against?

Predation: Most young organisms require protection from predation, which is a major source of extrinsic mortality in many species (Caro 2005). For many, parents’ deterrence and defense are the first and only form of protection against daunting odds. Even among apex predators (e.g., leopards, wolves) and species with adaptations (e.g., large body size) that make them functionally immune from predation in adulthood, predation is a meaningful risk during infancy. On land, young may be vulnerable to myriad terrestrial carnivores and omnivores, including felids, canids, snakes, raptors, and predatory arthropods. In the water, young animals have to contend with an equally daunting array of predatory fish, reptiles, amphibians, mammals, and even birds. Some social

species have sophisticated predator detection and warning systems that may benefit many social group members, including offspring (e.g., vervet monkeys: Seyfarth et al. 1980). Though many humans today do not incur any meaningful risk of predation, throughout humans' evolutionary history, predators – particularly large cats and caniform carnivores such as wolves – were likely an important threat to humans and their ancestors (Barrett 2015). Just as is true for other species, young humans were (and still are, in places where large predators remain in the ecosystem) likely an especially attractive target for predators.

Infanticide: In mammal species where the length of lactation exceeds the length of gestation, sexually selected infanticide (performed by males seeking mating opportunities with an infant's mother) is a common cause of infant mortality (Hrdy 1979). Defending offspring against infanticide may be an important driver of long-term male-female associations, since continual male presence means males not only have the ability to guard infants throughout development but also have higher paternity certainty, which incentivizes incurring the costs associated with infant protection (Palombit 2000). In many mammal species where infanticide is common, infanticide defense is likely the most evolutionarily consequential type of paternal care that fathers provide their offspring. Males' simple presence may be enough to deter many potentially infanticidal intruders, though they may also be forced to directly fight off threatening outside males (Palombit et al. 2000).

While males may be important infant defenders in some species, females have also evolved various counter strategies to mitigate infanticide risk. Depending on the specifics of the biological system, these may include grouping together to collectively defend against males; speeding up the weaning process, since infants that are still nursing are at far greater risk than infants who are weaned; changing behavioral patterns to avoid potentially infanticidal males; and deliberately sowing "paternity confusion" among multiple potential sires (Palombit 2012). These may all be viewed as forms of offspring defense.

Infanticide committed *by* females is far less common, though is well documented in certain taxa including mice, mongooses, and some social insects (Parmigiani and vom Saal 2016). Females may commit infanticide to curtail resource competition (e.g., food, paternal, or alloparental care) for their own offspring, or for the nutritive benefits, when it is accompanied by cannibalism. Unsurprisingly, in species where female infanticide is common, females also appear to have evolved behavioral or reproductive strategies to mitigate the risk other adult females pose to their offspring. These include territoriality, where females aggressively exclude others from the area(s) where they are raising their young (Wolff and Peterson 1998), and in species that breed communally, timing reproduction so that infants are less likely to be killed by allomaternal caretakers (Schmidt et al. 2015).

There is substantial evidence in the academic literature that patterns of infanticide in modern human populations meet predictions derived from an evolutionary framework. Young children are more likely to be abused or killed by step-parents than by biological parents, and when biological parents commit infanticide, it appears to be more often driven by instrumental concerns such as resource instability or offspring phenotypic quality (reviewed in Archer 2013). While absolute risk of infanticide is quite low in humans, parental presence may nonetheless be a form of offspring defense against infanticide as well as other threats.

Conspecific harassment: Finally, infants may also require defense against conspecific harassment. Both older animals and age mates may harass or bully infants, and parents can play an important role in defending them (Nguyen et al. 2009). Harassment can lead to injury, lack of access to prime resources, and considerable energy spent on self-defense, all of which are detrimental to a young organism's growth and development.

How Do Parents Defend Offspring?

Fighting: Depending on the relative size and formidability of an opponent, be it a predator or a

conspecific, parents may respond by threatening or directly attacking. Among social animals, group members will sometimes mob predators, which has protective advantages for all group members, including offspring. Direct attacks can carry considerable risk, as parents themselves may sustain injuries or be killed in the course of protecting their offspring (Alcock 2009).

Fleeing: When opponents are too large, formidable, or numerous to effectively fight off, parents may flee with their offspring. This tactic is most feasible in species that give birth to one offspring at a time (monotocous species), especially those that have physically precocial young. For example, young ungulates (hooved mammals) are able to run within a few hours of birth, an adaptation that is clearly beneficial to large herbivorous species which are vulnerable to multiple types of predators. Fleeing is far harder, or even impossible, in species that give birth to litters of young or in which infants must be carried. Carrying an infant may considerably slow down the carrier and thus increase the risk of injury or death for the parent(s). However, phylogenetic analyses suggest that carrying infants, rather than hiding them, decreases the risk of infant mortality in primates (Ross 2001). Thus, this appears to be a superior offspring defense strategy in some species.

Cryptic strategies: Some prey species rely heavily on stealth tactics, to avoid predator detection in the first place. For example, in cotton-top tamarins (a small-bodied species of New World monkey), adults carrying infants move less and spend more time concealed, perhaps to decrease their risk of predation for both adult and infant (Price 1992). While this is a useful strategy in species in which infants are regularly carried, the energetic costs of doing so are considerable. Not only is infant carrying itself metabolically expensive, it is also likely to hamper forging or hunting efforts (Price 1992). Unsurprisingly, then, there are many species in which females “park” or hide infants somewhere safe while they feed (Tecot et al. 2012).

Territoriality: While there are many reasons that animals, including humans, defend territories,

one may be to protect offspring (Hinsch and Komdeur 2017; Wolff and Peterson 1998). Owners may guard their territories against conspecifics or predators who threaten their offspring or important resources that their offspring need (e.g., food). Territoriality is a particularly useful offspring defense strategy when young are hard to transport and thus constantly directly guard. This may occur because there are too many of them to feasibly move, because morphological constraints prevent transport (e.g., an adult deer cannot carry its fawn) and/or because altricial characteristics prevent offspring themselves from moving about with their parents (Wolff and Peterson 1998).

Social learning: Human parents often teach children very early about how to spot dangers of all kinds and defend themselves against them. Active teaching about risk-mitigating behaviors constitutes a very important form of offspring defense in humans. Cross-cultural data suggest that humans have evolved a “danger learning system” that relies on multiple sensory cues to obtain and retain important information about sources of risk in the environment (Barrett 2015; Barrett and Broesch 2012). While this learning system is not parent-offspring specific, parents are a crucial source of information for their offspring, since they are important social partners who are often in close proximity. Of course, humans are not alone in their propensity for social learning. The young of most, if not all other, social species also use social cues to learn about dangers in their environment (Crane and Ferrari 2013). Just as for humans, nonhuman animal parent(s) may be a frequent source of social information, which is an important contribution to their offspring’s safety.

Technological and social innovations: In addition to the “fight-or-flight” responses employed by most animals, human innovations such as controlled use of fire, dog domestication, and sophisticated building practices (e.g., fences, alarm systems, and sturdy dwellings) serve as threat deterrence devices that allow parents to defend their offspring even while not physically present. In addition to such innovations, humans also use a wide variety of social institutions,

including law enforcement, courts, military, and social services, to help mitigate the need for individual direct protection under typical social conditions.

While such adaptations clearly occur in their most elaborate form in humans, many other vertebrates and invertebrates also build nests, dens, or burrows that protect their offspring (Alcock 2009; Clutton-Brock 1991). Other species also may employ innovative defensive techniques that do not slot neatly into fight-or-flight categories. For example, there is intriguing evidence that in species which use chemical defenses against predators, mothers may actively provision their offspring with the compounds needed to do so (Stynoski et al. 2014). Among birds, “broken wing displays,” where a parent feigns injury in order to lure an intruder away from their eggs or chicks, are a common form of offspring defense (Caro 2005). Most biological systems, especially invertebrates, are quite understudied relative to humans, with means that other species may have evolved additional forms of offspring defense that have yet to be described in the scientific literature.

Conclusion

Offspring defense is an important component of parental investment in many taxa. It can take diverse forms, including: direct defense either of offspring, or of territory and resources that they use; helping offspring to hide or flee from danger; providing them with information about danger and how to avoid it; and making use of technological or social innovations that provide protection. Offspring may face many different threats across the course of development, including but not limited to predation, infanticide, and conspecific harassment. While modern human societies have created myriad social institutions and technologies that dramatically reduce the need for routine direct offspring defense, parental defense of young was likely an important selective force in the evolutionary history of humans and their ancestors.

Cross-References

- Aggression
- Alarm Calling and Kinship
- Brood Care
- Dominance and Territory
- Grouping and Predation
- Parental Investment and Parenting
- Parental Investment and Sexual Selection
- Resource Defense
- Survival and Death
- Vigilance, Sentinels, and Alarms

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Offspring Diversity Hypothesis

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Synonyms

Genetic diversity hypothesis

Definition

Females mix sperm from different males in order to increase the genetic diversity of their offspring.

Introduction

If polyandry is a female strategy, it must benefit the reproductive success of females. By mating with more than one male, females may enhance

their fitness through direct or material benefit, such as increased provisioning. The payoff to fitness may also be genetically based. One possible explanation for these genetic benefits is the *offspring diversity hypothesis*, which states that females mix sperm from different males in order to increase the genetic diversity of their offspring (Williams 1975). Sexually reproducing parents produce genetically variable offspring because recombination of male and female genes produces novel gene combinations (Williams 1975). Genetic contributions from multiple males will result in more novel gene combinations and even greater offspring genetic diversity. Such diversity can improve female fitness either by reducing sibling competition or by serving as a hedge against environmental uncertainty (Loman et al. 1988; Watson 1991). Watson (1991) suggests that females who are employing this strategy should (1) have low quality of information on male viability and (2) choose to mate with the most phenotypically unique males, regardless of their viability.

Benefits of Offspring Diversity

In some species, more genetic diversity in a sibling set decreases between-sibling competition for resources and increases offspring survival (e.g., Aguirre and Marshall 2011). If genetic variation among offspring results in differences in morphology, physiology, or behavior, then genetic variation may also lead to variation in resource use, thus reducing competition for the same resources between members of the same clutch (Case and Taper 1986). Genetically diverse offspring may also result in increased fitness for their mother in unpredictable environments (Yasui 2001). Phenotypic differences will cause offspring to respond with variable success to changes in the environment, and a more diverse brood will increase the chance of at least some offspring surviving. Genetic and phenotypic diversity is less favorable in stable environments, however, which favor broods with the maximum number of individuals fit to the current environment (Yasui 2001).

Offspring Diversity Mechanisms

Some nonhuman females can obtain a diverse sperm pool by mating with multiple males within a short period of time, resulting in those males fertilizing the same clutch (e.g., Ridley 1993; Watson 1991). Other females – nonhuman and human – can also increase genetic diversity in offspring by mating with different males at longer intervals, resulting in subsequent pregnancies of which different males sire individual or clutches of offspring (Jennions and Petrie 2000). Humans achieve multiple mating in one of three ways: divorce and remarriage, extra-pair mating, or polyandry. The relationships between the men and women mate within subsequent marriages or extra-marital affairs have not been studied. However, we know it is very common for men in polyandrous relationships to be closely related to one another and for primary husbands to play a role in deciding who the subsequent husbands will be (Starkweather and Hames 2012). When a woman's multiple mates are brothers or first cousins, it is unlikely that her offspring will be very genetically diverse.

Conclusion

Evidence in support of the offspring diversity hypothesis is difficult to achieve for all animals, but particularly for humans given ethical constraints (Scelza 2013). So far, no studies have compared the genetic quality of in-pair and extra-pair offspring among humans. Some studies are using proxy measures for quality, such as facial symmetry and major histocompatibility complex (MHC) compatibility, in order to determine if and when these traits are preferred by women. Higher MHC similarity between partners indicates genetic incompatibility, and women report more extra-pair desires and mating when they have greater MHC similarity with their long-term partner (Garver-Apgar et al. 2006). A true test of the offspring diversity hypothesis does not yet exist, however, and would entail comparing the genetic diversity within sibling sets and determining the effect of stable versus unpredictable

environments. Given the nature of the husbands' relationships to one another in most polyandrous, it is unlikely that tests of the offspring diversity hypothesis would find support within polyandrous unions.

Cross-References

- [Inclusive Fitness](#)
- [Sexual Selection](#)
- [Sperm Competition Theory](#)
- [Women's Mate Preferences](#)

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Offspring Mating Behavior

- [Daughter Guarding](#)

Offspring Protection

- [Offspring Defense](#)

Offspring Sex

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Synonyms

[Male/female](#); [Sex of offspring](#); [Son/daughter](#)

Definition

Chromosomal composition of an individual's progeny

Introduction

Offspring sex refers to the chromosomal composition of an individual's progeny. In humans and most other mammals, this is determined by the joint contribution of either an X- or a Y -chromosome-bearing sperm from a father and the X chromosome-bearing ovum from a mother. Males possess both an X and a Y chromosome, whereas females possess two X chromosomes. Offspring sex can be influenced both pre- and postconception, and this is affected by many biological and environmental factors. Evolutionary theory predicts that parents may be able to adjust the sexes of their offspring. Although the exact mechanism for this remains unknown, several

physiological, psychological, and environmental factors have been implicated.

Facultative Adjustment of Offspring Sex

Sex ratio, or the ratio of the number of males to the number of females within a population, can be considered at both primary and secondary levels (tertiary sex ratio, or number of males to the number of females at sexual maturity in a population will not be discussed here). Primary sex ratio refers to the sex ratio at conception and secondary sex ratio refers to the sex ratio at birth. Although in humans the secondary sex ratio remains relatively stable at approximately 105–107 male births for every 100 female births, the primary sex ratio is more difficult to quantify.

Deviations from the typical male-biased secondary sex ratio have been observed in response to various large-scale events (e.g., wars) (reviewed in James 2009), but it was not until the Trivers-Willard hypothesis (Trivers and Willard 1973) was published that researchers began to untangle the potential mechanisms through which these changes might occur. Since then, parental manipulation of offspring sex has been studied from physiological, psychological, and environmental contexts, both pre- and postconception. However, in meta-analyses with ungulates and primates, respectively, both Sheldon and West (2004) and Cameron (2004) have demonstrated that facultative adjustment of offspring sex is most likely to occur close to conception rather than as a result of differential investment in offspring postconception. Thus, adjustment of sex ratios at conception may be the source of skewed secondary ratios in response to factors associated with the maternal environment.

The bulk of research involving facultative adjustment of offspring sex preconception involves maternal influences. Three physiological mechanisms have been proposed: stress, glucose availability, and testosterone levels (reviewed in Edwards et al. 2016). Maternal stress increases endogenous concentrations of glucocorticoids (e.g., cortisol), which may explain female-biased

sex ratios in chronically stressed women. Maternal glucose availability, which is indicative of energy store, is positively associated with the frequency of male offspring. Similarly, maternal testosterone levels may also increase the probability of conceiving a male (Grant et al. 2011). Paternal influences on offspring sex, such as changes in the proportions of X- and Y chromosome-bearing sperm in seminal fluid, may also occur, but this has not consistently demonstrated.

Interestingly, maternal stress, glucose availability, and testosterone level may all be interrelated and under the influence of psychological mechanisms. Maternal dominance, or a combination of inherent female traits (e.g., influential, authoritative), that facilitate the changing of another's view or actions, for example, has been associated with the production of male offspring in women (e.g., Grant 1990, 1994). It may also be associated with better access to resources (and thus, sources of glucose) and lowered feelings of stress, ultimately producing an intrauterine environment conducive to the conception of male offspring. Indeed, larger women as well as women with greater muscle mass in the upper arm – a possible proxy for nutritional status (i.e., resource acquisition ability) – also have more sons (Kanazawa 2005; Gibson and Mace 2003).

Conclusion

Offspring sex refers to whether an individual's progeny is chromosomally male (i.e., XY) or female (i.e., XX). Although offspring sex can be determined at both primary (i.e., at conception) and secondary (i.e., at birth) levels, the majority of human research involves analysis of the secondary sex ratio. Facultative adjustment of offspring sex has been proposed and likely takes place at conception under the combined influence of both physiological and behavioral influences.

Cross-References

► [Trivers-Willard Hypothesis](#)

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evolution as maintaining proximity to caregivers was associated with increased chances of survival and thus reproduction. Accordingly, children come into the world prepared to form attachments, doing so to individuals who are sufficiently available and responding to children's attachment behaviors. Offspring–parent attachment therefore denotes a hierarchical bond between children (the smaller and weaker part) and their caregiver(s) (the stronger and wiser part) and not the emotional bond that caregivers form to their offspring. Attachment bonds take time to form and are typically observable during the second half of children's first year of life, when attachment-related experiences with the caregiver(s) have become internalized in the child in the form of cognitive-affective representations of self and others (internal working models, [IWMs]) that organize the child's behavior and displays of affect in relation to the caregiver(s). Offspring–parent attachment varies in quality or organization depending on the caregiver's pattern of responding to the child's signals and is typically described using two dimensions (secure/insecure, organized/disorganized) subsuming four categories (secure, insecure-avoidant, insecure-resistant/ambivalent, insecure-disorganized/disoriented).

Introduction

Universally, human infants form strong bonds – attachments – to caregiver(s), seeking to maintain proximity to and protesting separations from the caregiver(s) and using the caregiver(s) as a “secure base” from which to explore the environment and a “safe haven” to return to for comfort and protection when distressed. John Bowlby, a psychoanalyst and child psychiatrist (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), was unsatisfied with the available explanations of attachment, with psychoanalytical and social learning theories deeming attachment a secondary result of children's drives and feeding (see ► [“Psychodynamic Foundations”](#)). Bowlby contested these “secondary drive theories,” arguing that attachment is a primary motivation, and sought an alternative explanation. He came to

Offspring–Parent Attachment

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Definition

Offspring–parent attachment denotes the strong bonds that children form to their caregiver(s), seeking to maintain proximity to and protesting separations from their caregiver(s) and using the caregiver(s) as a secure base to explore the environment and a safe haven to return to for comfort and protection. Children are endowed with an attachment behavioral system retained in

draw from multiple scientific traditions, most notably ethology and evolutionary theory, cognitive theory, and control systems theory as applied to ethology (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). The phenomenon of offspring–parent attachment, or to paraphrase Bowlby, “the nature of children’s ties to their caregivers” (Bowlby 1958/1982), is discussed below (see Cassidy 2008, for a thorough introduction).

The attachment system, attachment behaviors, and the relation between the attachment system and other behavioral systems. Bowlby (1982), following Darwin (1859), and drawing from ethology, argued that humans (and some other animals) are endowed with an attachment behavioral system that was retained through natural selection as it served an adaptive function in primate species’ typical ancestral environments (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). Specifically, Bowlby argued that the “predictable outcome” following activation of the attachment behavioral system is proximity to caregivers, which have served a biological “function” of increasing chances of survival against predators and other natural dangers (see ► [“Infant Survival”](#) for a discussion of alternative suggestions, such as facilitating learning from caregivers). As individuals endowed with an attachment behavioral system ultimately had more progeny, the attachment system became a stable characteristic of the human species.

Bowlby argued that the attachment system is interacting with other behavioral systems, most notably the fear system and the exploratory system. Regarding the fear system, Bowlby argued that the attachment system is activated by internal (e.g., illness, pain) and external (loud noises, darkness, strangers, separations from caregivers) signals of threat/danger and similarly terminated by signals that there is no more cause for alarm (as opposed to buildup and discharge of psychic energies, see ► [“Psychodynamic Foundations”](#)). For young infants, close (physical) proximity to the caregiver(s) is often paramount to terminating the activation, whereas older children, who, for example, have acquired language, can be soothed

by more elaborate means, such as talking to the child and conveying that there is no cause for alarm (psychological proximity). The attachment system is, however, also thought to affect the fear system, with children typically more able to explore their environments (i.e., less prone to fear), when a caregiver is available for comfort and protection (i.e., as a “secure base”; see ► [“Individual Variations in Attachment”](#)). Bowlby also argued that humans have an exploratory system (and an innate motivation to explore the environment) and that the attachment and exploratory systems are mutually inhibiting so that when one is activated the other is deactivated. Importantly, Bowlby argued that having a caregiver available as a secure base (or an internalized representation of the caregiver as available, called “felt security”) supports children’s ability to explore the environment (e.g., increasing their epistemic space). Children’s ability to balance flexibly between their attachment needs and need to explore the environment is therefore key in individual variations in attachment (see ► [“Individual Variations in Attachment”](#) for a further description). Moreover, variations in attachment are thought to partly affect children’s further development through effects on children’s ability to explore the environment (see ► [“Effects of Attachment Quality and Organization”](#)).

Children come into the world social and prepared to form attachments to caregivers who are (sufficiently) available and responding to their signals, particularly during times of distress when the attachment system is activated. Children are endowed with attachment behaviors, which are described by their evolutionary function of maintaining/increasing proximity to caregivers. Such behaviors include positive (e.g., vocalizing, smiling) and aversive (e.g., crying, screaming) signal behaviors and active behaviors such as following and clinging, with increased development of motor, language, and cognitive abilities expanding the repertoire of attachment behaviors as children grow older.

Bowlby also argued that caregivers are endowed with a complementary caregiving system, rendering them biased and responsive to their children’s signals, which possibly developed as

parents' genes are only passed on to future generations if their children survive and have progeny of their own (Simpson and Belsky 2008). Caregivers are, for example, usually monitoring their children's whereabouts and retrieving them (increasing proximity) upon cues of danger. Children's forming of attachments to their caregivers is thus a collaborative effort, and since children's environments typically include caregivers who are responding to their signals, almost all children form attachments (called "the universality principle"; van IJzendoorn and Sagi 1999), and the attachment system is hence considered a moderately environmentally stable system (but see ► ["Disorganized Attachment and Reactive Attachment Disorder"](#) for detrimental effects following severe social deprivation). The collaborative process between children and their caregiver(s) does however not mean that caregivers are attached to their children, a common misconception. Attachment denotes the bond that offspring form to their caregivers. That is, the nature of children's ties to their caregiver(s) is a hierarchical relationship between the child (the smaller, weaker part) and the caregiver (the stronger and wiser part), thought to stem from the evolutionary survival value of maintaining proximity to caregivers (see ► ["Attachment in Adulthood,"](#) for differences in functioning in adult relationships). With the words of Bowlby: "Because immature organisms are usually very vulnerable they are commonly endowed with behavioral equipment that produces behaviors specifically likely to minimize risk, e.g., behavior that maintains proximity to a parent" (Bowlby 1997/1982, p. 143).

Development of attachment, attachment representations, and individual variations in attachment. Attachment bonds develop slowly during children's first year of life and are typically first observable around 7–9 months of age, that is, when children are seen to monitor and maintain proximity to the caregiver(s) and to use the caregiver(s) as a "secure base" and a "safe haven" (Ainsworth et al. 1978; Bowlby 1982). Importantly, an attachment bond is denoted by an "organization" of attachment behavior in relation to one or more specific individuals, not in any single

behavior (see ► ["Individual Variations in Attachment"](#) and Sroufe and Waters 1977). Indeed, the behaviors shown in relation to the attachment figure(s) are typically in stark contrast to behaviors shown toward other persons. Attached children will, for example, typically not make do with comfort by another person when the attachment figure(s) is present.

The key facilitator of children's development of attachment is that a caregiver is being continuously available and responding to the child's attachment behaviors (not feeding, see ► ["Psychodynamic Foundations"](#)). Children can form attachments to multiple caregivers, and the caregiver's sex is unimportant (e.g., mothers are not by default more suited as attachment figures; Ainsworth et al. 1978; Bowlby 1982). Children are however thought to organize their attachment relationships in hierarchies (turning to the one highest in the hierarchy first if that person is present), and since mothers' are usually the primary caregiver (particularly early in children's lives), they are often at the top of children's attachment hierarchies.

The slow development of attachment is thought to be in part due to the immature state of the attachment system at birth (see ► ["Evolutionary Foundations of the Attachment System and Its Functions"](#)). The slow development is also due to the fact that children need repeated attachment-related experiences with their caregivers for an attachment bond to be formed. That is, organization of attachment behavior in relation to a specific person necessitates having formed representations of the other and what to expect from that person, particularly as regards availability for protection and support (i.e., as a secure base and safe haven). Indeed, drawing from cognitive psychology, Bowlby argued that experiences with caregivers lead to the development of cognitive-affective representations of self and others, which he termed "internal working models" (IWMs) and which he considered complementary in nature (Bowlby 1982; see ► ["Evolutionary Foundations of the Attachment System and Its Functions"](#)). Once formed, these IWMs, also termed "attachment representations," come to guide children's attention,

behavior, and displays of affect in relation to the caregiver, particularly in situations when the attachment system is activated.

The attachment system is also moderately environmentally labile, being open to learning and thereby permitting modifications to suit the child's environment. This openness is seen in the relation between the characteristic patterns (quality) of caregiving (e.g., sensitivity) that children receive and the different patterns of organization of attachment behaviors (i.e., quality of attachment) that children develop (see ► [“Individual Variations in Attachment”](#)). Briefly, Mary Ainsworth, who collaborated closely with Bowlby, found that children tend to show three different organized patterns of attachment, corresponding to the patterns of caregiving they have received during the first year of life (Ainsworth et al. 1978). Secure children, having received sensitive care, show a good ability to use their caregiver as a secure base and safe haven. Insecure-avoidant children, whose bids for proximity have been rejected, show an inability to turn to their caregiver when (mildly) distressed (i.e., a minimizing pattern). Insecure-ambivalent/resistant children, having received inconsistent sensitivity, show an inability to explore the environment, demanding comfort from their caregiver without being comforted by the contact (i.e., a maximizing pattern). Mary Main subsequently discovered a fourth group of children, termed insecure-disorganized/disoriented (Main and Solomon 1990). Disorganized children tend to have experienced frightening/frightened behaviors from their caregiver (Main and Hesse 1990) and show an inability to sustain an organized pattern of attachment behavior in relation to the caregiver. Variations in attachment are therefore generally described using two dimensions (secure-insecure, organized/disorganized-disoriented), subsuming four different patterns. Importantly, insecure children are attached to their caregivers. Profound difficulties forming attachments to others (i.e., reactive attachment disorder [RAD]; see ► [“Disorganized Attachment and Reactive Attachment Disorder”](#)) are typically reserved for children who have not had any caregiver consistently available (e.g., children growing up in some institutions).

Conclusion

As outlined by Bowlby, children are endowed with an attachment behavioral system and attachment behaviors and form strong bonds to caregivers that are (sufficiently) available and respond to their signals. The core function of attachment is maintaining proximity to caregivers, which have served an adaptive function of increasing chances of survival in primate species' typical ancestral environments. Offspring–parent attachment therefore denotes a hierarchical bond between children (the smaller and weaker part) and their caregiver(s) (the stronger and wiser part).

Cross-References

- [Attachment in Adulthood](#)
- [Charles Darwin: Theory of Natural Selection](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Individual Variations in Attachment](#)
- [Infant Survival](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Organized-Insecure Attachment](#)
- [Psychodynamic Foundations](#)
- [Robert Hinde](#)
- [Secure Attachment](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Old Age

► Senescence

Older Men

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Synonyms

[Age disparity](#)

Definition

The tendency on women to seek older partners

Introduction

As a general rule, heterosexual women like their male partners to be slightly older than they themselves are (Kenrick and Keefe 1992). The average age disparity between women and their male partners (real or imagined) has been consistently estimated at 2–6 years, but the preference for older men decreases slightly as women grow older, and at about 45 years of age, women no longer show a preference for older men (Antfolk et al. 2015; Kenrick and Keefe 1992). However, a lot of important information is lost when only looking at the mean population preference. A closer look at the distribution of age disparity from population-wide marriage data shows that approximately one-third of married women in the USA have a partner that is less than 1 year older (or younger) than they themselves are. Somewhat ironically, the most common “age disparity” is thus one where there hardly is any age disparity at all. The aforementioned mean disparity in the population therefore stems from the fact that whereas approximately 18 % of women have a male partner who is more than 6 years older, less than 4 % of women have a male partner who is more than 6 years younger (US census bureau 2013). More simply put, women tend to partner up with men of their same age, but when this is not the case, women more commonly partner up with an older man than with a younger man.

This general preference for men that are equally old or older has been explained as a consequence of the human bi-maturation process, by which women mature at a younger age than men (e.g., van den Berghe 1992). Accordingly, sexually mature women would look for sexually mature men, and because men tend to mature later, there would be more interesting older men than there would be interesting younger men. Although not explicitly mentioned in this type of reasoning, this model could also

explain why the preference for older men is more apparent in young women compared to older women: Women will at some given age find equally many interesting younger men as interesting older men, all of who are mature. It is, however, important to also note that age in itself is not likely a very important feature. Age is rather a proxy of other reproductively important features (e.g., fertility and/or maturity, available resources, social status). Whereas some of these features may be strongly associated with age and lead to a strong age-related preference (e.g., female age and fertility and men's preference for young women), other features show a weaker association with age and lead to less marked age-related preferences. With this in mind, it is a noteworthy finding that women put less emphasis on a partner's age than men do (e.g., Sprecher et al. 1994). The features that women cross-culturally tend to report as important in their choice of partner are, for example, social status, financial resources, and health (Buss 1989). These are all associated with age, but the association is not very strong and its strength will vary across time and cultural contexts (Buss et al. 2004). If older men (vs. younger men) usually have a higher social status and have more resources that can be directed to a child and its mother, the theory suggests that women would then for these reasons be attracted by older men. The same features in a young man would also make him attractive, but these features are simply less common among young men. Health, on the other hand, tends to decrease with age, but because some but not all men remain healthy even as they grow older, older men displaying signs of health and vitality might be particularly interesting to women (Boothroyd et al. 2005). Sean Connery (85 years old at the time of writing), Robert Redford (79), Harrison Ford (72), Dustin Hoffman (78), and Clint Eastwood (86) definitely have something most other men of their age do not – they are maybe not healthier than the average 25 year old man, but their health and vitality are unusually apparent given their age.

Any complete evolutionary model should not only attempt to explain the average preference but

also provide an explanation for several forms of variation. Concerning age preferences there is variation across cultural contexts, variation between individuals within the same cultural context, and even variation within the same individual over time. With respect to women's mate preferences, cross-cultural variation has, for example, shown that preferences for masculinity are stronger in areas with high pathogen stress (DeBruine et al. 2010) and that cultural empowerment of women (e.g., access to education) decreases the age disparity between married men and women (Casterline et al. 1986). A lot of research focusing on variation in mate preferences within the same female has focused on the variations across the menstrual cycle, and while there is some controversy regarding the robustness of these findings, women seem to increase their preference for high status and available resources during the fertile phase of the menstrual cycle but much less is known about whether age preferences also vary (Gildersleeve et al. 2014). Fewer studies have specifically investigated the between-individual variation in women's age preferences and the biological and environmental mechanisms behind them. One factor that has received some interest is whether the absence or presence of a biological father changes partner preferences. Although the absence of a father is associated with earlier menarche (Belsky et al. 1991), indicating earlier maturation – which according to the theory of bi-maturation would predict also a preference for older men – research results regarding age preferences are limited.

Conclusion

In sum, the variation in women's age preferences can be explained by multiple contextual, personal, and biological factors. The on-average preference for equally old or older men is also likely to be the result of several processes: Women reach maturity at a younger age than men, several features that are attractive to many women are more likely to be found in older (vs. younger) men, and some signals become more apparent in older (vs. younger) men. While all these processes contribute, a lot of

potentially important contributing factors need to be investigated in order to fully explain the variation in women's age preferences. It is also important to consider that most older men are interested in younger women (Antfolk et al. 2015; Kenrick and Keefe 1992) but that only some of these men display the features necessary to attract younger women. It is thus possible that relatively few women are interested in old men per se and that the observed age disparity is the result of many old men being attracted to relatively young women. Large age disparities could consequently be the result of preferences of men with above-average mate value.

Cross-References

► Age Differences in Marriage Partners

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Olduvai Gorge, The

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Synonyms

I am unaware of any synonyms for this place name.

Definition

Olduvai Gorge is a world famous paleoanthropological site in Tanzania that has yielded a series of important fossil remains of early humans.

Introduction

Olduvai Gorge, located on the Serengeti Plain in northern Tanzania, has been carved over the last 200,000 years by water erosion. The sediments within the gorge range in age from late Pliocene to late Pleistocene in age. While it became known to scientists in the early twentieth century, the work by Louis Leakey began in 1931 and eventually yielded a series of fossil remains and stone tools. These discoveries have made Olduvai Gorge one of the most famous sites for human fossil remains in the world.

Importance of the Site

A variety of important human fossil specimens have been recovered from Olduvai Gorge. The first, discovered in 1959, is OH (Olduvai Hominid) 5. OH 5 is the type specimen of *Paranthropus (Australopithecus) boisei*, a robust hominid with huge jaws, very large molars, and expansive chewing muscles as evidenced by broad attachment areas for those muscles on the skull. Though this specimen dates to the appropriate time period, Leakey did not consider OH 5 to represent the toolmakers at Olduvai Gorge. This role was later filled by a series of discoveries that Leakey and his colleagues Phillip Tobias and John Napier placed into the species *Homo habilis*. These fossils, which included the type specimen OH 7, plus OH 8, OH 13, and OH 24, have more lightly built faces with smaller teeth. OH 7 also included several hand bones, which were interpreted as enabling both a power grip and a precision grip necessary to manufacture stone tools. The species *Homo erectus* has also been found at Olduvai Gorge and is most famously represented by the specimen OH 9.

The “Zinj” site (FLK Zinj) at Olduvai Gorge, which produced the OH 5 specimen, also held a huge cache of animal bones. Many of these bones show signs of having been cut by stone tools, leading some to interpret the site as evidence of hunting by early humans. Some interpretations of the “Zinj” site suggested that it may have represented a home base for early humans, who were bringing meat back to provision a family or group who were camping at this site (see Bunn and Kroll 1986; Rose and Marshall 1996). Other work on these fossils is more strongly supportive of humans primarily scavenging carcasses at Olduvai (e.g., Blumenschine et al. 2012; Pante et al. 2012), but these interpretations remain somewhat controversial.

The oldest stone tool complex, known as the Oldowan, was defined based on artifacts discovered at Olduvai Gorge. The Oldowan is characterized by very simply made stone tools, manufactured by “hard hammer” (stone on stone) flaking. Choppers are the most common artifact type and are basically a stone that has

had flakes chipped from it to create a crudely sharpened edge. Flakes were also sometimes utilized by early hominids, but most commonly, the choppers were the primary focus. Oldowan tools are highly variable in their manufacture and lack the planning and skill evident in later stone tool technologies.

Conclusion

Olduvai Gorge is one of the most famous, and important, fossil sites in the world, and its importance to the study of human evolution cannot be overstated. It has provided key fossil evidence and crucial insights into aspects of early human behavior.

Cross-References

- [Paranthropus boisei](#)
- [Homo habilis](#)
- [Homo erectus](#)
- [Stone Hammers](#)

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Olfactory Brain

- [Olfactory Bulb, The](#)

Olfactory Bulb, The

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Synonyms

Neural Structure; Olfactory Brain; Rhinencephalon

Definition

A structure located in the forebrain of vertebrates that receives neural input about odors detected by cells in the nasal cavity.

Introduction

The environment, if filled with odorant molecules, and our emotions, moods, and behaviors may be controlled by olfactory stimuli. The first steps in processing olfactory signals are transducing and relaying odorant information centrally from olfactory receptor neurons (Purves et al. 2001). Receptor axons combine to form a large number of bundles making up the olfactory nerve. The target of the olfactory nerve on each side is the olfactory bulb. The olfactory bulb is an evaginated cortical structure that lies on the ventral anterior aspect of the ipsilateral forebrain and contains two main types of projection neurons and interneurons that receive primary afferent input from sensory neurons (Greer et al. 2008).

The Architecture of the Olfactory Bulb

The main olfactory bulb has a multilayered cellular architecture consisting of the glomerular layer, the external plexiform layer, the mitral cell layer, the internal plexiform layer, and the granule cell layer. In young adult humans, the olfactory bulb is connected by long olfactory stalk or peduncle and

is pulled forward from its point of attachment to the cerebral hemisphere (van Hartevelt and Kringelbach 2012). In most young adult humans, it is about 50–60 mm³ on each side (Turetsky et al. 2000). The olfactory nerve fibers make up the olfactory nerve layer and pass through the cribriform plate from the nasal cavity (van Hartevelt and Kringelbach 2012). This nerve layer appears to be thick where the nerves reach the olfactory bulb. The olfactory nerve fibers terminate in the glomerular formation.

Laminar Structure of the Olfactory Bulb

Every layer in the olfactory bulb is comprised of different types of neurons. The neurons in the olfactory bulb have been categorized according to the layers in which their cell bodies are found. According to this categorization, the juxtglomerular cells are found in the glomerular layer, tufted cells in the external plexiform layer, mitral cells in the mitral cell layer, and granule cells in the granule cell layer (Nagayama et al. 2014).

In the glomerular layer, neurons are morphologically heterogeneous and can be categorized in three types: Periglomerular cells (PG), superficial Short-Axon cells (sSA) and External Tufted cells (ET) (Pinching and Powell 1971). Most of these cells solely function within the olfactory bulb and do not innervate other brain regions. The most abundant type of neuron in this layer is the PG cell, which is the smallest in diameter, and most of the time they project their dendrites to a single glomerulus. These cells are thought to have an axon which terminates in the interglomerular space (Nagayama et al. 2014). Pinching and Powell (1971) were the first to report the sSA cell. These cells are found in the glomerular layer in a small percentage and are slightly larger than PG cells. They have dendrites that course exclusively in the interglomerular space, with an axon that extends as far as 1–2 glomeruli (Pinching and Powell 1971). The ET is the largest of the three types and has primary dendrites which are generally mono-glomerular. These

cells occupy a large volume of the glomerulus (Nagayama et al. 2014).

Mitral and tufted cells extend their dendrites within the glomerulus of the external plexiform layer (EPL), where they process odor signals. The odor signal reaches the cell body of tufted cells in the EPL and mitral cells in the mitral cell layer (MCL). The process by which back-propagation is conducted throughout the dendrites until it is blocked by local inhibition from granule cells is called lateral inhibition (Xiong and Chen 2002). The lateral inhibition mechanism by which activation of mitral and tufted cells occurs is associated with one glomerular molecule which is associated with neighboring glomerular molecules (Buonviso and Chaput 1990). This layer includes mostly dendritic fibers that are secondary dendrites. These dendrites are made up of mitral-tufted cells and apical dendrites of granule cells which are morphologically similar in that they both extend a single primary dendrite to one glomeruli from the thousands that are found in the olfactory bulb (Nagayama et al. 2014). This process signifies that each projection neuron receives odor information originating from only a single receptor. However, the lateral inhibition processes, which occurs through the dendrodendritic reciprocal synapses with granule cells, may enhance the contrast between strongly activated and faintly activated glomeruli. Thus, it may tune further the specificity of individual mitral and tufted cells to odor molecules. Therefore, it is possible that second-order mitral and tufted cells may be more tuned to specific features of certain molecules than sensory neurons (Yokoi et al. 1995).

The granule cell layer (GCL), of the olfactory bulb, is mostly occupied by granule cells. These cells are inhibitory interneurons with a small cell body, and they are divided into subgroups based on their morphological differences. Some granule cells can be found in other layers of the olfactory bulb, but they are generally found in the GCL. In order for the apical dendrite that they have to extend towards the surface of the olfactory bulb, it first has to ramify the EPL where granule cells have spines used to form synapses with the

secondary dendrites of mitral and or tufted cells (Nagayama et al. 2014). Because granule cells lack an axon, their output relies solely on dendrodendritic synapses. In addition to the granule cells, the GCL comprises of other interneurons called the short-axon cells (sSA). These short-axon cells have larger cell bodies than granule cells, and their dendrites rarely extend beyond the MCL. However, they have axons that extend to different layers of the olfactory bulb (Merrick et al. 2014).

The olfactory bulb is a complex system made up of various layers which interconnect in order to discriminate between thousands of odors (Bushdid et al. 2014). This is mostly due to the variety of odorant receptors that bid to different odorants with specific affinity profiles. The olfactory bulb is made up of multiple types of neurons that form a complex network in order to process information before it is transmitted to the olfactory cortex.

The Function of the Olfactory Bulb

The function of the olfactory bulb is mainly to recognize and discriminate a large number of different odors. In order to accomplish this, a series of information processing steps, at distinct anatomical sites of the olfactory system, take place. The initial recognition occurs in the olfactory receptor neurons which are located in the nasal epithelium (Ngai et al. 1993; Buck and Axel 1991). In the second step, the olfactory receptor neurons project axons to glomeruli in the main olfactory bulb, where synaptic connections with mitral and tufted cells take place (Kauer and Cinelli 1993). In the next layer, the external plexiform layer, mitral, and tufted cells form dendrodendritic synaptic contacts with the granule cells. These synapses undergo reciprocal regulation (Trombley and Shepherd 1993). Each granule cell shows divergent dendrodendritic synaptic contacts with a vast number of neighboring tufted and mitral cells, suggesting the induction of lateral inhibition of neighboring mitral and tufted cells (Rall et al. 1966; Scott et al. 1993). In the

following paragraphs, the function of each layer is further discussed.

The most distinctive characteristic of the olfactory bulb is probably an array of spherical accumulation of neuropil, signal processing molecules called glomeruli (Mori et al. 1999). Within glomeruli lie axons of olfactory sensory neurons from excitatory synaptic connections on dendrites of mitral and tufted cell which are the output neurons of the main olfactory system (Buck 1996). The odor molecule information enters the olfactory systems through the mitral and tufted cells and is then processed by the local neuronal circuits that mediate synaptic interactions within the molecule of the main olfactory system (Mori et al. 1999). The mammalian olfactory system can detect and discriminate a large variety of odor molecules. In order to distinguish between diverse odor molecules, mammals have developed approximately 1000 receptors (Axel 1995; Buck 1996; Yoshishara et al. 1997). These receptors are expressed on the ciliary membrane surface of sensory neurons in the olfactory epithelium. According to Maresh et al. (2008), the ratio from olfactory receptor neurons to glomeruli is 16:1 resulting in approximately 5500 glomeruli. Therefore, the initial distinction between different odors is based on specific glomeruli unit structures for olfactory discriminations (Mori et al. 1999).

Interneurons also called periglomerular cells send dendrites and axons close to glomeruli and receive synapses from the olfactory nerves. The periglomerular cell dendrites form reciprocal synapses with mitral and tufted dendrites (van Hartevelt and Kringelbach 2012). The external plexiform layer is located deep to the glomeruli and consists of dendrites of granule, mitral, and tufted cells along with the tufted cell somata which are also found scattered through this layer. At the border between of the external plexiform layer and the deeper granule layer, the mitral cell somata are located, which extend to the glomeruli (van Hartevelt and Kringelbach 2012). Approximately half of the volume of the bulb is made up of granule cells which are found

in much greater numbers than all other cells in the olfactory bulb (Bhatnagar et al. 1987). These interneurons do not possess an axon, and they form synapses with tufted and mitral cell dendrites. Studies regarding the morphometry of the olfactory bulb revealed approximately 5500 glomeruli and 40,000 mitral cells in young adults (Maresh et al. 2008; Meisami et al. 1998). These numbers were found to decline with age by about 10% each decade while the thickness of the glomerular layer was also found to be significantly reduced (Bhatnagar et al. 1987; Meisami et al. 1998; Maresh et al. 2008). This may account for the decline in the olfactory function with age (Murphy et al. 2000).

Studies on mice have shown that the olfactory epithelium contains more than two million sensory neurons which express only a single type of odorant receptor gene (Ressler et al. 1994). Although this suggests that individual sensory neurons may respond to specific odor ligands that bind to the expressed receptor, there is no indication as to which range of odor molecules individual sensory neurons tuned to (Bozza and Kauer 1998). The olfactory axon projection is based on two main principles: “zone-to-zone projection” and “glomerular convergence” (Mori et al. 1999).

Based on the expression patterns in the olfactory epithelium, the odorant receptors can be classified into four main spatial zones which are restricted in the olfactory epithelium (Sullivan et al. 1995). Within every zone neurons expressing different receptors intermingle. This type of zonal organization is also evident in the main olfactory bulb. Even though the molecular markers that distinguish glomeruli among zones are yet to be explored, studies of the main olfactory bulb suggest that their might be four spatially segregated zones similar to the zones in the olfactory epithelium (Vassar et al. 1994). Ressler et al. (1994) found that information highly distributed in the nose is transformed in the olfactory bulb of the brain into a highly organized spatial map. The spatial and numerical characteristics observed in their study indicate that in the olfactory bulb,

olfactory information is remarkably organized into a stereotyped map that makes discrimination between different odors possible. Therefore, odor information received by sensory neurons in a given zone of the olfactory epithelium is thought to be transmitted to glomeruli and then transferred to mitral and tufted cells in the corresponding zone of the main olfactory bulb (Ressler et al. 1994).

Glomerular convergence, the second type of olfactory projection, refers to the ability of the olfactory axons to bind their specific target glomeruli in the olfactory bulb. A glomerulus receives axonal inputs from thousands of olfactory receptor neurons that all express the same olfactory receptor (Al Yamani et al. 2012). In other words, as recent studies have shown, olfactory sensory neurons expressing a specific odor receptor converge their axons to defined glomeruli (Imamura et al. 1986; Katoh et al. 1993; Mori et al. 1999). The implications of glomerular convergence, in terms of coding, are believed to improve sensitivity so as to ensure detection and lead to a more compact odorant representation that available at the sensory level (Laurent 1999; Al Yamani et al. 2012).

Conclusion

Research has led to discovering a large multigene family of odorant receptors which in turn triggered rapid advances concerning the architecture and function of the mammalian olfactory bulb (Buck 1996). The olfactory bulb seems to be a complex structure made up of multiple neuronal layers which contribute individually to the olfactory process. One of the first areas that was researched was the functional roles of individual sensory neurons that can be found in the olfactory epithelium. This process triggered the elucidation of the axonal projection patterns of sensory neurons to the main olfactory bulb which in turn led to the glomerular convergence, in other words the pattern of olfactory axon connectivity to the main olfactory bulb. What has

been determined by research thus far is the vast amount of odorant receptors that the mammalian olfactory bulb consists of in order to be able to translate every odor. More recent studies have shown that individual glomerular modules function as a molecular feature and that local neuronal circuits mediate lateral inhibition and synchronized spike discharges among mitral and tufted cells that belong to different glomerular molecules (Mori et al. 1999).

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Olfactory Memory

► Odor and Memory

Olfactory Navigation

► Directional Smell

Olfactory Perceptual Learning

► Odor and Memory

Omega-3 Fatty Acids

► Docosahexaenoic Acid (DHA)

Omopagous

► Evolutionary Pressure on Meat Eating

On the Origin of Species

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Synonyms

► *An Abstract of an Essay on the Origin of Species and Varieties Through Natural Selection*;
► *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*; ► *The Origin of Species*

Definition

Unquestionably the most important book that was published in the nineteenth century and undoubtedly the most important duodecimo volume ever to be printed, Charles Darwin's *On the Origin of Species by Means of Natural Selection* is also a very good candidate for the most significant and influential book ever to be written (thus far) by a human being. The other two main candidates – Nicholas Copernicus's *De revolutionibus orbium coelestium* of 1543 and Isaac Newton's *Philosophiæ Naturalis Principia Mathematica* of 1687 – were of near-equal scientific value at the time of their first publication but were less immediately influential among the wider public than Darwin's *Origin*. A good indication of this is that in January 1860, there was an anecdotal report of a passenger enquiring about purchasing a copy of the *Origin* at a UK railway station bookseller, rather than a more usual potboiler novel.

The first edition of 1250 copies of the *Origin* published on 24 November 1859 was priced at 15 shillings and immediately sold its entire print run to booksellers, and a second edition of 3000 copies was then quickly printed on 7 January 1860. Across Darwin's lifetime, a total of six separate editions were eventually produced, the last printing of the sixth edition being in 1876 (18th thousand) and with a minor title change to *The Origin of Species* for the first printing of the

sixth edition (11th thousand) in 1872. The various editions contained significant modifications and elaborations on the original text.

For example, although it quickly became synonymous with the term “natural selection,” the phrase “survival of the fittest” was included for the first time only in the fifth edition (10th thousand) of 1869 (Browne 2003, p. 315), and a historical sketch of various precursors to the theory of evolution was first included in the third edition (7th thousand) of 1861. After nearly a decade, Darwin commented in 1868 that he had become “sick and tired of correcting” what he called the “everlasting *Origin*” (Freeman 1978, p. 221), the term “everlasting” here having multiple meanings. A centennial variorum text was eventually issued (Peckam 1959), while Darwin's two pre-*Origin* essays sketching the initial outlines of his theory of evolution from 1842 and 1844 were published together in book form in 1909 (Darwin 1909).

Introduction

Darwin had been busy working on a much larger work on “the transmutation of species” since 1837, after returning from his momentous 5-year H.M.S. *Beagle* voyage in 1836, this larger work from 1854 being provisionally titled *Natural Selection*. However, on 18 June 1858, he received a package from his fellow naturalist Alfred Russel Wallace that forced his hand into publishing a shorter “abstract” of the theory of evolution in book form: this became *On the Origin of Species by Means of Natural Selection* of 1859. Wallace had independently discovered many of the most important components of Darwin's theory of species origin, so it was decided that both naturalists should communicate short papers to a Linnean Society meeting (which were read on 1 July 1858) informing the public of the outlines of their theory, thereby sharing the credit for the new discovery equally between them (Darwin 1977 [1858]; Wallace 1977 [1858]).

Even so, it was Darwin's *Origin* that instantly became the definitive guide to the new scientific theory of evolution, with Wallace's various works

quickly taking second place in terms of both their scientific importance and their wider public impact (Cohen 1985, p. 603). Although the initial preeminence of Darwin's book over Wallace's works in the 1860s was in large part facilitated by Darwin's superior mustering of a wide variety of natural history data and his superior presentation of the theoretical arguments, it was also in part facilitated by the form and structure of *On the Origin of Species* as a book, and by the fact that in it, Darwin was first to controversially imply that "the origin of man and his history" could be explained by the same principles as the evolution of all other species and behaviors (Darwin 1872 [1859], p. 428).

Wallace had been much more hesitant on this issue than Darwin, positing that what Wallace called some "unknown cause or power," which had yet to be identified by naturalists, was required to explain the higher intellectual and moral aspects of human behavior, implying that they were too complex to explain by natural selection (Wallace 1889, pp. 463–464). Darwin's bulldog-advocate T.H. Huxley was quick off the block in expanding on precisely what "the origin of man" actually meant in its Darwinian meaning in his *Evidence of Man's Place in Nature*, with its opening chapter focusing directly on "the Man-Like Apes" and its subsequent search for "a Man more pithecoïd" than any yet known (Huxley 1863, p. 184). It was confirmed in 1904 that the closest primates to human beings were the apes (Nuttall 1904).

Although *On the Origin of Species* had been composed at a speedy rate over 14 months across 1858 and 1859, Darwin had based it in substantial part upon his previous two decades of study and composition for the proposed *Natural Selection* volume, so the *Origin* was a compact distillation of a very substantial research program. As has been explained: "Composed in bursts of furious activity separated by debilitating bouts of illness, it was a compromise between the compact, accessible essay he had written in 1844 and the all-inclusive, massively documented 'big book' that he hoped to write" (Van Riper 2008, p. 49). Much of Darwin's larger *Natural Selection* is now available for scholars to consult, so the exact relation

between it and the *Origin* can be traced in many instances: out of the 14 main chapters of the *Origin*, "nine had been preceded by extensive treatment in *Natural Selection*" (Stauffer 1975 [1856–58], p. 10). Unusually for such an important book, the *Origin* contained no formal references, but the real sources are often traceable by consulting *Natural Selection*.

Evolutionary Mechanisms in the *Origin*

Although the title of Darwin's book suggested that evolution occurred only "by means of natural selection," in fact, Darwin's theory of descent with modification posited that various different mechanisms of evolutionary change existed, these conventionally being cited as natural selection, sexual selection, and artificial selection. His theory of evolution is, therefore, perhaps most accurately described as the theory of evolution by selection mechanisms, instead of the more commonly encountered theory of evolution by natural selection.

All three of the outlined mechanisms were explicitly considered to varying degrees in *On the Origin of Species*, although only one chapter of the book (Chap. IV on "Natural Selection") was explicitly named after one of them. Within Chap. IV, Darwin also presented something called "the principle of divergence" as being of fundamental significance to his theory of evolution. Whether divergence can be conceived of as a separate fourth type of evolutionary mechanism – christened here as divergent selection – will be considered in what follows (Barnett 2019).

Natural selection is the process by which the slight variations that occur through descent with modification in species are either preserved or not preserved, depending on whether they are advantageous to the animal and thereby aid further reproduction. Or, as Darwin posited in the *Origin*: reproduction, inheritance, variability, the struggle for life, processes which then produces selection (Darwin 1872 [1859], p. 429). Sexual selection is the process by which (most commonly) females choose their mates based on some generally favored traits, features, or behaviors, thereby

selecting these traits for further enhancement, and males fight each other for this reproductive access, in what Darwin christened in the *Origin* as “the law of battle” (Darwin 1872 [1859], p. 69). Artificial selection is the process in which human beings consciously favor and develop particular species features and traits through selective breeding practices.

In the same spirit as these three forms of evolutionary selection but (arguably) conceptually distinct from them, divergent selection can be seen as the process by which local environments, or what Darwin termed “the same spot” in the economy of nature, will act to favor the evolution of what he called “very diverse forms” of animal and plant life (Darwin 1872 [1859], pp. 9–10). This evolutionary divergence takes place both in terms of the diversification of behavior and habit and also in terms of diversification of structure and constitution (Darwin 1872 [1859], p. 89). How divergent selection operates is that “the varying offspring of each species will try . . . to seize on as many and as diverse places in the economy of nature as possible” (Darwin 1872 [1859], p. 10).

This in turn means that the more varying in terms of utilizing resources in a specific local environment a given species can be, i.e., the more that they can use resources that the other existing species that occupy the same environment and ecosystem do not use or use to a lesser degree, the more likely they will be to prosper and propagate. Divergent selection thus provides one type of “directionality” to evolutionary change within specific local environments and ecosystems. Divergent selection can be conceived of as operating in a similar manner to sexual selection, but instead of female choice and male-male conflict being directing forces, the local environment and the local wildlife are (together) the directing forces. They act to channel evolutionary change into a more optimal use of local resources by “diverging” the existing forms of life so as to facilitate them in occupying different behavioral, structural, and resource using niches from those niches – or local ecosystems (Eldredge 1989, p. 129) – that have already been occupied by existing species.

That Darwin recognized a distinction between natural selection and divergent selection is evident from his statement that the “complex action of these several principles, namely, natural selection, divergence & extinction, may be best . . . illustrated by the following Diagram” (Darwin in Stauffer 1975 [1856–58], p. 238), this being the “tree of life” diagram illustrating the evolution of species from the *Origin* (Darwin 1872 [1859], pp. 90–91). At another point he specified “natural selection, extinction & divergence” as three distinct evolutionary processes that had been going on “since the dawn of Life” (Darwin in Stauffer 1975 [1856–58], p. 246). Hence, arguably, divergent selection is articulated as a separate fourth evolutionary mechanism within the *Origin*.

Speciation in the *Origin*

Although he did employ any strict definitional terminology in the *Origin*, it is evident that Darwin recognized that species could evolve in a number of different ways. For example, they could evolve in a very gradual linear manner while remaining in the same location (straight-line evolution); they could evolve more quickly upon reaching a new geographical area; they could evolve in response to large-scale geological and/or environmental changes; or they could evolve in response to the encroachment of their habitat by new species (Darwin 1872 [1859], pp. 282–289). Darwin provided a concise distillation of his approach to the different factors that contributed to the process of speciation in the *Origin* as follows:

The process of modification must be slow, and will generally affect only a few species at the same time . . . Whether such variations or individual differences as may arise will be accumulated through natural selection in a greater or less degree . . . will depend on many complex contingencies – on the variations being of a beneficial nature, on the freedom of intercrossing, on the slowly changing physical conditions of the country, on the immigration of new colonists, and on the nature of the other inhabitants with which the varying species come into competition. (Darwin 1872 [1859], p. 291)

Hence for Darwin, one species might remain unchanged over a very long period of time, while another might change very gradually, yet another at a much faster pace, depending on how the various factors identified above interacted, or how the “complex contingencies” played out in any given instance.

It is also evident from the *Origin* that Darwin, at least implicitly, distinguished between straight-line or phyletic evolution, in which a single species as a whole becomes modified over time in response to environmental or competitive pressures, and what is now called cladogenesis, where one parent species splits into two or more different resultant species in response to these pressures (Archibald 1997, p. 693; Darwin 1872 [1859], p. 293). The well-known hypothetical phylogeny figure (or fold-out illustration) in the *Origin*, inserted between pages 90 and 91 (of the sixth edition), illustrated the fates of 11 species, 9 of which undergo straight-line evolution and the remaining two experience cladogenesis.

Extinction in the *Origin*

Although Darwin is most commonly portrayed in the literature as an extinction gradualist, in fact both the gradualist and punctuated equilibrium approaches can be found outlined within the *Origin*. He accepted that, most commonly, background extinction of individual species occurred via natural selection, i.e., the gradual extinction of species occurred through interspecies competition (Sepkoski 2008, p. 225), species extinction usually being for Darwin “a slower process than their production” (Darwin 1872 [1859], p. 294). However, it is now known that near-instantaneous mass extinction events, defined as when more than 50% of all species disappear (Van Couvering 2000, p. 262), have sometimes occurred; as Darwin duly recognized in the *Origin*, “the process of extinction may have been rapid” in some cases of large-scale natural calamities such as the subsidence of an island or the eruption of a volcano (Darwin 1872 [1859], p. 294).

A key role allotted to extinction in the *Origin* was that it “played an important part in defining

and widening the intervals between the several groups in each class” of species (Darwin 1872 [1859], p. 380). As many ancient forms of life had now been lost, this has served to “thin out” the remaining set of species and accounted to a degree for the lack of closely intermediate forms between some of them, or, as Darwin phrased it, extinction has defined the animal groups. Finally, for Darwin, groups of species, or genera and families, followed the same general rules in their appearance and disappearance as individual species did (Darwin 1872 [1859], p. 292).

Classification in the *Origin*

Another key aspect of the *Origin* was Darwin’s use of the theory of evolution that was articulated within it to provide a foundation for a system of classification of the whole animal kingdom into sets as phylogeny, in a chapter (XIV) entitled “Mutual Affinities of Organic Beings.” In this chapter Darwin explained regarding the importance of descent with modification that:

... this element of descent is the hidden bond of connection which naturalists have sought under the term of the Natural System. On this idea of the natural system being . . . genealogical in its arrangement, with the grades of difference expressed by the terms genera, families, orders, &c., we can understand the rules which we are compelled to follow in our classification. We can understand why we value certain resemblances for more than others . . . and how the several members of each class are connected together by the most complex and radiating lines of affinities. (Darwin 1872 [1859], p. 381)

This system of classification can, for Darwin, also be used to assist in the understanding of animal morphology, defined by Darwin as the law of form independent of function, as “members of the same class . . . resemble each other in the general plan of their organisation,” or their overall body structure (Darwin 1872 [1859], p. 382).

Although the system of animal and plant classification in its basic outline nomenclature had been initially provided by Carolus Linnaeus in the eighteenth century, what Darwin added through the *Origin* was the correct framework

for understanding the links between the different members of the total animal set and of how the various members had been temporally connected. He consequently proposed a historical taxonomic methodology for classification that was based on an understanding of species evolution as a branching process (Richards 2008, pp. 164–165).

In relation to animal morphology and classification as revealed in the fossil record at it was understood at the time of the *Origin*, Darwin's resolute belief in the theory of evolution by selection mechanisms is demonstrated by his attitude to what was (arguably) the most significant obstacle to this theory when it was first proposed. This obstacle was that, according to the scientific understanding of the period, the earth was simply not old enough to have provided the length of time to facilitate the evolution of all the life that had been observed on it (and discovered in it within the fossil record), an obstacle that Darwin readily admitted to in the sixth edition of the book.

His response was that it was possible that the very early period of the earth's history had been subjected to more violent and rapid changes than those currently occurring, which would have increased the pace of evolution in this period (Darwin 1872 [1859], p. 286). This was not a particularly convincing proposition, but this defense was enough for Darwin to remain fully convinced of the accuracy of his theory. He should instead have argued that the theory of evolution by selection mechanisms itself provided sufficient evidence that the earth was older than the scientific theory of the time allowed.

Geographical Distribution in the *Origin*

According to Darwin, the theory of descent with modification in the *Origin* also assisted with an understanding of the leading facts in the observed patterns of species distribution across the globe. He explained on this issue that:

We can see why there should be so striking a parallelism in the distribution of organic beings throughout space, and in their geological succession throughout time; for in both cases the beings have been connected by the bond of ordinary generation,

and the means of modification have been the same ... On this view of migration, with subsequent modification, we see why oceanic islands are inhabited by only a few species, but of these, why many are peculiar or endemic forms. (Darwin 1872 [1859], p. 418)

In the chapter on “Geographical Distribution” (XII) in his book, Darwin listed what he called “three great facts” regarding distribution across the globe, the first being that neither the similarity nor the dissimilarity of the inhabitants of various regions could be wholly explained by climatic and other physical conditions. The second was that barriers or obstacles to free migration were clearly related to the observed differences between the productions of various regions. The third was that the observed affinity of the productions of the same continent or the same sea, even though the species themselves were distinct, was very noticeable (Darwin 1872 [1859], pp. 316–318).

According to Darwin, all of these three facts served to corroborate the theory of evolution by selection mechanisms or the veracity of descent with modification. Darwin also affirmed the idea that each species was initially produced in one area alone, with subsequent migrations then producing some degree of both straight-line evolution and cladogenesis (Darwin 1872 [1859], p. 321). Documenting the geographical distribution of animals across the planet was one of the few areas where Wallace's contribution to natural history eventually exceeded that of Darwin (Wallace 1876).

Instinct in the *Origin*

The chapter (VIII) on instinct is by far the most neglected chapter of the *Origin* among contemporary biologists, but many evolutionary psychologists trace the origin of their subject to this key section of Darwin's book. However, in the sixth edition of the *Origin*, Darwin gave precedence on the application of the evolutionary method within psychology to Herbert Spenser and his book *The Principles of Psychology* (Darwin 1872 [1859], p. 428), the first edition of which had been published 3 years prior to the first edition of the

Origin, Spenser's book containing a chapter-length account of instinct (Spencer 1855, pp. 539–553).

Darwin declared at the start of chap. VIII of the *Origin* that “instincts are as important as corporeal structures for the welfare of each species” (Darwin 1872 [1859], p. 206), and he then outlined his theory that most instincts had evolved by selection mechanisms acting on random variations in just the same way as organic corporeal structures had. As he explained: “why should not the brain, as well as all other parts of the body, sometimes vary in a slight degree,” with favorable mental variations then being preserved (Darwin 1873, p. 417). Darwin also allowed that some instincts could evolve or become modified by slow degrees through inherited habits (Darwin 1872 [1859], p. 206), which is not necessarily Lamarckian if the Baldwin effect – in which natural selection “lays down” the learnt habit as a form of instinct – is allowed (Weber and Deprew 2007).

Although Darwin did not explicitly define the concept of instinct in the *Origin*, elsewhere he defined an instinctive act as the “performance of any action without the aid of experience, or instruction or sufficient reasoning powers” (Stauffer (1975 [1856–58]), p. 468). He believed that a large number of instincts existed in both animals and human beings, and in addition to in the *Origin*, he also discussed them in detail in *The Descent of Man*. He categorized instincts into two basic types, individual and social instincts. Individual instincts such as imitation were seen by Darwin as more basic than social instincts such as community defense, but social instincts like the maternal instinct could override individual instincts like self-preservation (Darwin 1874 [1871], pp. 107–108). He also distinguished between simple and more complex instincts and between constantly operating instincts and those that only function at certain points in an animal's life.

Another key element of Darwin's theory of instincts was that different instincts had different strengths and persistence/endurance levels, as had been evolved by selection mechanisms, meaning

that when some instincts came into conflict with others, the stronger and more persistent instincts would usually win out. For example, he cited the migratory instinct in birds as conquering their maternal instinct in certain instances and the social instincts as a group being generally stronger than the less persistent instincts. He also asserted that individual animals of the same species possessed many of the same instincts but at varying strengths and persistence levels (Darwin 1874 [1871], pp. 99–110).

Darwin's work on instinct and animal intelligence was continued by George Romanes, who published Darwin's “Posthumous Essay on Instinct,” removed from the *Origin* “Instinct” chapter to save space (Romanes 1895, pp. 355–384). The first professional psychologist to take up Darwin's approach to instinct was William James, who first coined the now-familiar term “evolutionary psychology” in *The Principles of Psychology* with a memorable chapter subheading: “Evolutionary Psychology Demands a Mind-Dust,” or a mind-stuff theory of compound mental states (James 1891, 1: 146). James also discussed psychogenesis or the origin of instincts as an entirely natural process along Darwinian lines (James 1891, 2: 688). Although contemporary evolutionary psychologists have discarded James's mind-dust, they still employ – albeit in a much more sophisticated form – a modernized version of Darwin and James's formulation of the instinct concept as evolved psychological mechanisms.

The Initial Reception of the *Origin*

The initial reception of Darwin's book is best described as mixed. Some naturalists were very enthusiastic; Wallace, for example, characterized the *Origin* as immediately elevating Darwin to the exalted status of “the Newton of natural history” (Wallace 1889, p. 9), and Huxley was also very positive, writing a number of reviews defending Darwin's work as an important scientific advance. Others looked upon the book much less favorably. The astronomer John Herschel, for example,

gently mocked the theory of evolution by selection mechanisms as “the law of higgledy-piggledy” and implied that nature’s regularities could not conceivably be simply random variations (Hull 2002, p. E11). The geologist Adam Sedgwick wrote that to accept Darwin’s case for evolution would “sink the human race into a lower grade of degradation” than ever before (Browne 2003, p. 94). Darwin himself referred in 1860 to experiencing a “storm of hostile reviews” of the *Origin*, with one such reviewer asking if it was credible that “turnips are tending to become men” (Dorsey 1928, pp. 184–185).

However, some reviews raised more perceptive unresolved problems. For example, one reviewer pointed out that to finally demonstrate the reality of natural selection, a quantitative and precisely measurable account of key elements of it such as variation, advantage, rate of survival, and rate of reproduction would be required, something that Darwin had not really supplied (Gayon 2003, p. 250). As Huxley astutely judged, what Darwin had provided in the *Origin* was a brilliantly argued and very convincing interrelated set of hypotheses (Huxley 1863, pp. 125–128), but these required further empirical support before they could all be taken as proven fact.

It is also accurate to state that some parts of the theory were initially treated far more favorably than others. Many naturalists subsequently accepted that species could evolve in some general way; some accepted natural selection as a mechanism partly responsible for this evolution, but sexual selection as a mechanism was treated with far greater skepticism across the remainder of the nineteenth century. Even Wallace questioned the need for (and effect of) sexual selection, arguing (erroneously) that female preference in choosing ornamental traits would be neutralized by other selection mechanisms, as “the extremely rigid action of natural selection must render any attempt to select mere ornament utterly nugatory” (Wallace 1889, p. 295). And Darwin’s principle of divergence, here conceived of as divergent selection, was quickly subsumed within natural selection and lost its key separate place in his theory.

Conclusion

As others have already noted, the title of Darwin’s book – *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* – is actually misleading in various different ways. The book does not consider “the origin of species” at all, but rather only how species evolve; species evolve not “by means of natural selection” but by means of natural, sexual, artificial, and (arguably) divergent selection; “favored races” are not preserved in the struggle for life, but varieties and species well-adapted to their environments are. In the few instances where Darwin used the term “race” in the text of the book, he immediately clarified that what he really meant was “variety” (Darwin 1872 [1859], p. 12).

Despite being misleading in these literal senses, Darwin’s *Origin* title still works very effectively on both the metaphorical and conceptual levels at connoting the book’s central importance to the fields of natural history, evolutionary biology, and evolutionary psychology, and the book’s content – framed effectively by its author as “one long argument” designed to untangle the ever-branching bank of nature – has provided an inspirational foundation from which endless variant forms of understanding of the natural world have been and are being evolved.

Cross-References

- [Charles Darwin](#)
- [History of Natural Selection](#)
- [Principles of Geology](#)

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On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life

► On the Origin of Species

Onanism

► Coitus Interruptus

One Offspring

► Adaptation for Single Births

One Parent's Offspring Whose Other Parents Are Different

► Half-Siblings in Human Evolutionary History

One-Male Group

► Harems

One-Male Troop

- ▶ [Harems](#)

One-Male/Multi-female Group

- ▶ [Harems](#)

One-Male-Multi/Female Troop

- ▶ [Harems](#)

One-Night Stand

- ▶ [Costs of Short-Term Mating for Women](#)

One-Night Stands

- ▶ [Casual Sex](#)

Online Questionnaire

- ▶ [Online Survey](#)

Online Survey

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Synonyms

[Internet survey](#); [Internet questionnaire](#); [Online questionnaire](#); [Web-based survey](#); [Web-based questionnaire](#)

Definition

A Web-based survey used to collect information.

Introduction

As mentioned in the Surveys and Questionnaires section, data collection can occur online. Online methods can present unique benefits when compared with traditional survey methods, but they also come with a unique set of challenges. This section will discuss some of the advantages and disadvantages to using online methods, some ways to improve the quality of data collected online, and, finally, one commonly used source of online participants, Amazon Mechanical Turk.

Benefits of Online Surveys

Many of the positive aspects of online surveys revolve around the ease of creation and use, broad reach, low associated expense, and quick turnaround when compared to traditional survey methods. Online methods can be developed easily and quickly through software specifically designed for survey creation or through word-processing software. Often when using survey-specific software, a researcher can use methods that would not be possible with traditional methods, such as embedding multimedia (e.g., videos, pictures) or measuring reaction times. Additionally, these types of software often can automatize the process, allowing researchers to reuse previous questions without manually typing them, randomizing questions and answers, sending reminders to participants to complete the survey, and providing data in a format that is ready to analyze.

Another benefit to utilizing online surveys is the broad reach offered by the Internet. Researchers are easily able to contact people across the world with various demographic backgrounds. The Internet can also serve researchers looking to study relatively small populations through sites that specifically cater to those smaller populations. Sampling for surveys can

become easier through sites that provide samples, sometimes for a fee and sometimes just for the amount you wish to compensate your participants. Additionally, social media allows ease of contact for those looking to utilize snowball methods. Finally, there is less work involved for the participant, lowering the barriers to participation, as they can complete the survey on their own schedule, they do not have to travel to the research site, as with face-to-face methods, and they do not have to mail surveys back to the researcher, as with mailed surveys. These all serve to lower the costs associated with gathering a sample and compensating participants for their time.

Finally, the ease with which online surveys can be created and distributed combined with the readily available population lowers the turnaround time for online surveys. There is no longer a need to schedule times to speak with a participant, face-to-face or by telephone, or to stuff envelopes and wait for mailed responses.

Disadvantages of Online Surveys

Despite all of the potential advantages to using online surveys, there are also some potential disadvantages that need to be considered when choosing a method of survey distribution. One possible drawback is the typical user of the Internet. Often, those online are younger and more technologically savvy. This can eliminate, or greatly reduce, participation from those who are older or who do not have regular access to technology or Internet service. The self-selection of those willing to take online surveys presents a different population than those who may take telephone or written surveys. However, with the inundation of technology and the Internet into daily lives, this is becoming less and less of an issue, as even those without Internet service often have access through smartphones, and older populations are increasing online. The proliferation of technology and Internet action also presents an ethical challenge for researchers, as participants under the legal age to consent could

be participating without the knowledge of the researcher.

Another disadvantage to online methods is simply the changes in the cultural norms of the online environment. Participants are faced with a surplus of ads and information online, so capturing a participant's attention can be more difficult. A researcher has relatively little control of the environment in which a participant takes a survey; there is no way to ensure that a participant completed the survey in a distraction-free environment. Fortunately, this can be somewhat mitigated by including attention checks within the survey. Additionally, researchers face issues of attrition with online environments, especially with longer surveys. The Internet provides many distractions and with it the chance that a participant will simply not finish an entire survey, especially if they feel it is not worth their time.

Finally, technology itself can present a disadvantage. The online market is ripe with scams and phishing (i.e., malicious attempts to obtain private information), and thus the online participant may not trust the researcher with certain information. E-mail and spam filters often prevent mass e-mailing of participants, requiring researchers to find alternative methods of contacting potential participants. However, as stated above, there are services which can provide contact with willing participants.

One way to mitigate the disadvantages of online survey use, while still receiving the advantages, is to provide participants with the option to choose if they wish to complete the survey online or through alternative methods. While this may present more work for the researcher, it can result in improved response rates (Dillman et al. 2009). Another way to account for disadvantages is to mix the modes of data collection by including sections using online methods as well as sections using more traditional survey methods (see de Leeuw 2005, for review).

Mechanical Turk

With a large number of researchers utilizing the Internet to collect data, it is important to discuss a

participant recruitment method that is growing in popularity. Amazon Mechanical Turk (MTurk) provides a broad and diverse workforce that allows researchers to obtain data quickly and cheaply. MTurk users, known as “workers” or “turkers,” complete “human intelligence tasks” (HITs) that consist of various tasks for certain amounts of compensation as determined by the source (sometimes even as low as \$.10 per HIT). In order to receive compensation, workers must have their HITs validated such that they are rewarded for high-quality work and penalized for low-quality work. The average worker approximately earns only \$1.40 per hour, much lower than the national minimum wage, but will vary depending on the given task(s) (Horton and Chilton 2010; Ipeirotis 2010).

With such low wages, concerns have been raised in regards to the demographics of the workers on MTurk. Paolacci et al. (2010) collected demographics of approximately 1,000 MTurk workers. In general, workers tended to be more educated and have a lower average income than the general US population. Despite this, Paolacci et al. pointed out that the workers were still closer to the general population when compared to the convenience samples of college students. Other studies have shown that workers tend to be more ethnically diverse than traditional samples but still show a higher proportion of female users that is consistent with other methods (Berinsky et al. 2012). One major benefit of this diversity is the opportunity to recruit workers with particular demographics that may be more difficult to do in a less diverse local environment.

The characteristics of MTurk workers also tend to show a similarity to traditional samples of college students, but there are some important differences to note. In regards to personality traits, workers are less extroverted, have lower self-esteem, and are more socially unstable than traditional samples (Goodman et al. 2013). The cognitive capabilities of workers are more similar to traditional samples, but some evidence has shown that they may have a tendency to be more

risk averse, but the differences are slight (Paolacci et al. 2010; Goodman et al. 2013). In general, MTurk workers are seen as a valid recruitment method to study a variety of topics.

Tips for Conducting Online Studies

In general, online studies benefit from the same guidelines as surveys and questionnaires in regards to response bias (see the Surveys and Questionnaires and Response Bias sections in this book). Alternatively, there are certain aspects of online studies in particular that require careful consideration. First, the informed consent and debriefing information presented should have some method to ensure that the information has been read. For example, researchers could include a time delay before participants can continue the study. In relation, an important aspect of online studies is ensuring that the participants are attentive to the tasks given to them. Providing attention checks throughout the task(s) will allow for poor-quality participants to be parsed from the sample. Although MTurk workers tend to be more reliable in terms of attention, it is a necessary measure of participant quality for all online studies (Hauser and Schwarz 2016). It is also beneficial to record the time it takes a participant to complete the task(s) given to them. Specifically when using MTurk, researchers can set the percentage of HITs the workers have successfully completed in the past. This is often set at 90 % to ensure high-quality participants (Mason and Suri 2012). Lastly, checks should be in place to ensure that the target population is appropriately being sampled by excluding those that do not match the demographics of the target population (e.g., age, language, occupation).

Conclusion

Online studies provide a unique opportunity for researchers to obtain broader samples, conduct

quick and inexpensive research, and utilize unconventional stimuli compared to traditional survey methods. While they have unique benefits, researchers also need to account for the unique challenges associated with an online environment. When used correctly, online surveys provide a novel method which can benefit both the researcher and participant.

Cross-References

- [Response Bias](#)
- [Surveys and Questionnaires](#)

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Onomatopoeia

- [Bow-Wow](#)
- [Ding-Dong](#)

Onset of Menstruation

- [Menarche](#)

Ontogenetic Adaptations

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Synonyms

[Transient ontogenetic adaptation](#)

Definition

Ontogenetic adaptations are adaptations that serve an adaptive function at a specific time in development and disappear when they are no longer functional. Examples of ontogenetic adaptations are provided from the prenatal (e.g., placenta in mammals), infancy (e.g., nursing and rooting reflex; neonatal imitation), and childhood (e.g., overestimation of one's abilities, egocentricity) periods. Ontogenetic adaptations provide a mechanism for understanding how certain aspects of early life may have evolved to adapt the young organism to its particular time in development.

Introduction

Evolutionary developmental psychologists have identified three general types of adaptations characteristic of infancy and childhood.

Deferred adaptations serve to prepare infants and children for life as an adult or for the acquisition of important skills that will be useful throughout life. Related to deferred adaptations are *conditional adaptations*, in which current conditions serve as a cue to future environments, with children adjusting aspects of their development in anticipation of future context. Finally, *ontogenetic adaptations* (Bjorklund 1997; Oppenheim 1981) serve primarily to adapt the infant or child to their current developmental niche and are the focus of this entry.

Ontogenetic Adaptations of the Prenatal Period and Infancy

Ontogenetic adaptations are neurobehavioral characteristics that serve an adaptive function at a specific time in development, disappearing when they are no longer needed. Such adaptations are not simply incomplete versions of adult functions but evolved to deal with a specific problem associated with infancy or youth. The most easily identified ontogenetic adaptations are associated with prenatal development. For example, in mammals the placenta and the umbilical cord serve to transport nutrients to and rid waste from the fetus, but they are discarded after birth as infants' entire respiratory and consummatory systems become reorganized.

In humans, many infantile reflexes can be viewed as ontogenetic adaptations. For instance, the *sucking reflex*, activated when the lips or adjacent skin is touched, and the *rooting reflex*, which occurs when infants' cheeks are stroked and they turn their heads and open their mouths in the direction of the stimulation, are adaptive in nursing. The *swimming reflex*, the *palmar grasping reflex*, in which infants grasp objects pressed in the palms of their hands, and the *Moro reflex*, in which infants bring their arms forward as if to hold onto something in response to a loss of support, each have potential survival value and each disappear by 6 months of age or earlier, as control of motor behavior shifts from subcortical to cortical areas of the brain.

Neonatal imitation, in which infants match certain facial gestures of a model (e.g., tongue protrusion, lip pursing), has been proposed not to be a "true" form of social learning, as originally suggested by its discoverers Meltzoff and Moore (1977), but as an ontogenetic adaptation, designed to foster infant–mother interaction at a time in development when infants have little intentional control over their own behavior (Bjorklund 1987). Support for this interpretation comes from evidence that such matching behavior decreases to chance levels by 2 months of age, that infant–mother social interaction is positively associated with previous levels of neonatal imitation, and that such imitation is associated with subcortical brain areas, unlike the "true" imitation observed in children and adults (Nagy 2006).

Several researchers have proposed that infants' memory abilities are especially adapted to the niche of infancy (Bjorklund and Sellers 2014). For example, because of infants' nearly complete dependence on adults, they should be especially attentive to recurring events in their social world. Young infants' memories are also tightly tied to context, which, coupled with their poor inhibitory abilities, prevents babies from retrieving memories in "inappropriate" situations.

Another adaptive characteristic of infancy that promotes survival is "looking cute." The ethologist Konrad Lorenz (1943) long ago noted how immature facial features (e.g., large head relative to the rest of the body, large eyes, small flat nose) of many species promote caregiving. Adult humans find these features endearing and rate infants with these traits as more sociable, easier to care for, more likely to be adopted, and display greater empathy and careful fine-motor behavior as a result of viewing photos of "cute" infants. Adults tend to view infant- or child-like facial features positively relative to the faces of adults and older children until children are about 5 years of age. However, adults continue to view some types of children's *immature cognition* (e.g., "The sun's not out because it's mad") positively (more so than immature facial features; Hernández-Blasi et al. 2015), suggesting that ontogenetic adaptations are also found past infancy into childhood.

Ontogenetic Adaptations of Childhood

Another example of an ontogenetic adaptation in childhood is children's tendencies to overestimate their abilities. Preschool- and early school-age children have an overly positive impression of themselves – they believe they are stronger, smarter, better looking, and more popular than is typically warranted by more objective measures. Such optimistic impressions are not due to poor general cognitive skills. Children are usually able to provide accurate assessments of other children's abilities; their unrealistic assessments are typically limited to themselves (Bjorklund 1997). Such overestimation has been linked to enhanced *self-efficacy*. If young children were aware of how limited their abilities were, they would be less likely to persist at these task, which typically results in improved performance. Support for this comes from studies that report that 3- and 4-year-old preschool children who overestimated their imitation abilities had greater verbal IQ scores than more accurate children (the effect disappeared by age 5) (Bjorklund et al. 1993) and that kindergarten, first-, and second-grade children who overestimated how many words they had recalled on early trials of a memory task had higher levels of memory and strategy performance on later trials than more accurate children (Shin et al. 2007). With respect to memory, young children's tendency to spontaneously reference events and objects to themselves (egocentricity) may enhance their likelihood of later remembering information (Bjorklund and Sellers 2014).

Conclusion

Ontogenetic adaptations provide a mechanism for understanding how certain aspects of early life may have evolved to adapt the young organism to its particular time in development. The presence of such adaptations also causes one to consider that many aspects of infancy and childhood may not simply be unfinished forms of adult functions or as preparation for adult life. Rather, many of the characteristics of infancy and childhood that are considered “immature” may have specific,

evolved functions of their own, and we should be reluctant to speed children through a childhood that has important functions itself.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Adoption Preferences](#)
- [Deferred Adaptations](#)
- [Development](#)
- [Neonatal Imitation](#)

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Ontogenetic Versus Deferred Adaptations

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Synonyms

Transient vs. non-transient ontogenetic adaptations

Definition

An *ontogenetic adaptation* is a successful solution for a recurrent problem at a specific moment of development in the evolutionary history of a species that disappears once the problem has been solved. Examples are the placenta and umbilical cord in mammals. On the other hand, a *deferred adaptation* is a solution selected through the course of evolution, not just for solving a specific adaptive problem at a certain time in development, but also to prepare developing animals for their future life as adults. This would be the case of play in humans, and for many other species.

Introduction

An adaptation is a solution to a significant, recurrent problem of a species shaped by natural selection over time. As Darwin recognized (1868), adaptations have been shaped not only to solve problems of adult members of species (survival, mating, parenting and kinship, group living), but also problems of immature members of species at different stages of development. From an evolutionary developmental perspective, development can be compared with a bridge that connects two shores: conception and reproductive age (Bjorklund et al. 2016), whose length varies among species, and whose crossing is mandatory for adults aiming to reproduce themselves. In this context, ontogenetic and deferred adaptations are adaptations that respectively solve specific

problems of the developing members of a species (ontogenetic adaptations), and/or prepare them for adulthood (deferred adaptations).

Ontogenetic Adaptations

Immature developmental features in most species have been typically seen only as antecedents or basis for future adults' behaviors, and not as traits that can accomplish, by themselves, a certain function at a specific developmental moment (Hall and Oppenheim 1987). An ontogenetic adaptation is an evolutionary solution for a recurrent problem at a specific time in development that, once solved, disappears. In a sense, an ontogenetic adaptation is a disposable adaptation. This would be the case, for example, of hatching mechanisms in eggs-laying animals, placenta and umbilical cord in mammals, and many infantile reflexes, such as the sucking, rooting, and palmar-grasping reflexes. The first contemporary use of this concept in both developmental psychobiology and developmental psychology is attributable respectively to Oppenheim (1981) and Bjorklund (1997), although other authors (e.g., Baldwin, Werner) had referred to it, either explicitly or implicitly, earlier in the twentieth century.

Ontogenetic adaptations can be found at different levels (e.g., morphological, physiological, and behavioral) and at different developmental stages (e.g., prenatal period, infancy, and childhood in humans), although they are more easily seen when some drastic environmental changes take place. This would be the case, for example, of an amphibian metamorphosis, switching from living in an aquatic to a terrestrial environment, and therefore generating temporary adaptations for their temporary conditions (e.g., respiratory mechanisms such as gills while living in the aquatic milieu), or for a species whose prenatal and postnatal environments are quite different in nature, as in mammals and birds.

In humans, as well as in other altricial species (i.e., species whose offspring exhibit a high degree of motor, sensory, and/or social immaturity at birth or soon after hatching), many early postnatal ontogenetic adaptations have to do with catching adults' attention and/or guaranteeing

adult support at a time of extreme vulnerability and dependence. This would be the case, for example, of attachment behaviors such as smiling, crying, or raising arms toward an adult, or the “looking cute” *baby-schema* thoroughly described by ethologist Konrad Lorenz (1943). Importantly, these types of adaptation often require corresponding and simultaneous adaptations in adults: attachment behaviors or infants’ physical appearance would not have such effects if adults were not also notably sensitive and responsive to these kind of immaturity cues.

Deferred Adaptations

The concept of deferred adaptation was coined by Hernández Blasi and Bjorklund (2003), although it was already implicit in Oppenheim’s work, who pointed out that “in many cases ontogenetic events may serve immediate needs, as well as influence future goals” (Oppenheim 1981, p. 75), in a way that “the behavior exhibited by developing animals reflect a balance between meeting the needs of the moment and preparing for later life” (Hall and Oppenheim 1987, p. 95). This rationale seems to suggest that “in most instances ontogenetic adaptations may serve both immediate *and* future needs” (Oppenheim 1981, p. 99), and this is what deferred adaptations are all about. Namely, a deferred adaptation is an evolutionary efficient solution to a recurring significant problem of a species member at a certain time in development that *simultaneously* prepares the developing animal for adulthood.

Play is a good example of deferred adaptation in humans (as well as in other species), as it clearly helps children to both understand some critical issues of their immediate sociocognitive environment, and at the same time to understand the nuances of the world they will live in as adults (see e.g., Pellegrini and Bjorklund 2004, for an evolutionary analyses of both object and fantasy play in children). Theory of Mind might be also a good candidate for deferred adaptation. This is an important mechanism for social relationships, available when young children are approximately

about 4/5 years old (Perner et al. 1987), that makes it possible to “read others’ minds,” that is, to understand people as mental beings whose mental states (e.g., thoughts, beliefs, motives, feelings) can explain and predict their own and others’ behavior. This ability permits children to adapt to the increasingly out-of-family social world that follows in most of traditional societies after weaning (typically at 3 years, Dettwyler 1995), at the same time that it prepares them for their future social roles as adults by learning about other people’s mind and what motivates their actions.

It is important to note that deferred adaptations do not implicate the existence of an anticipated plan by natural selection, as, obviously, as far as we know, natural selection operates on the here-and-now basis. Quite probably, deferred adaptations functioned initially as ontogenetic adaptations, but instead of disappearing, as happens with *true* ontogenetic adaptations, they continue operating throughout life. This is more apt to occur when environmental characteristics during the developmental period in which they emerge and in adulthood are similar (Hernández Blasi and Bjorklund 2003).

Conclusion

Natural selection operates not only during adult life but also across development. Ontogenetic adaptations provide specific solutions to recurrent problems at specific moments in the development of a species and then disappear when they are no longer needed. In this sense, they are immediate, transient, and provisional adaptations. In contrast, deferred adaptations afford developing individuals not only immediate benefits in terms of skills and/or knowledge, but also delayed benefits that extend into adulthood. In this sense, they are nontransient, permanent, and anticipatory adaptations.

We do not have available a complete catalogue of ontogenetic and deferred adaptations in humans yet (nor a catalogue of epiphenomena, such as, for example, the belly button as

contrasted with the umbilical cord; not everything in development is an adaptation). Therefore, the determination of which behaviors contribute to adaptive outcomes (or might have contributed to adaptive outcomes in the *environment of evolutionary adaptedness*), and how – either to solve children’s adaptive problems at a specific time in development or to prepare children for their lives as adults – constitutes both a necessary and exciting challenge for understanding better the nature of human development and its evolution.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [Development](#)
- [Ontogenetic Adaptations](#)
- [Play](#)
- [Theory of Mind](#)

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Ontogeny

- [Development](#)
- [Fetus Development](#)

Open to Sex

- [Sexual Receptivity](#)

Openness to Experience

- [Five-Factor Model](#)

Operant Behavior

- [Selectionist Models: Implications for Behavior](#)

Operant Conditioning

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Synonyms

[Instrumental conditioning](#); [Negative punishment](#); [Negative reinforcement](#); [Positive punishment](#); [Positive reinforcement](#)

Definition

In behavioral learning theory, operant conditioning is defined as a learning process in which the likelihood of a specific voluntary behavior is strengthened (increases in frequency) or weakened (decreases in frequency) in response to consequences (reinforcement or punishment, respectively), occurring after the behavior is exhibited.

Introduction

Operant conditioning is a learning process appearing in behavioral learning theory. According to the theory, the likelihood of a specific voluntary behavior is strengthened (increases in frequency) or weakened (decreases in frequency) in response to the consequences (reinforcement or punishment, respectively) that follow the behavior. Whereas classical conditioning is used to re-train reflex behaviors (e.g., crying when we feel afraid, salivating when we smell food) so that they appear under new conditions (in the presence of a conditioned stimulus, not only of an unconditioned stimulus that requires no prior learning), operant conditioning is used to produce behaviors that are not part of one's repertoire of reflex behaviors (i.e., they are "new" behaviors). The major theorists in the area of operant conditioning are Edward Thorndike and B. F. Skinner, who maintained an experimental approach to the study of learning. Findings from learning experiments with animals in the laboratory were extrapolated to human learning as they maintained that fundamental principles of learning apply to learning across species (equipotentiality).

Overview of Operant Conditioning

Operant conditioning is based on Thorndike's Law of Effect (Thorndike 1898, 1911) that stated that responses to a situation that are followed by satisfaction are strengthened, whereas responses that are followed by discomfort are weakened

(Ormrod 2016). The term operant conditioning (Skinner 1937) derives from the idea that organisms learn to "operate" on their environment (i.e., produce a particular behavior) in order to receive or avoid a particular consequence (Snowman and McCown 2012). The term "conditioning" (as opposed to learning) is used by behaviorists to denote that learning happens in a way that is beyond one's control as it is dependent upon individual experience (i.e., an organism is conditioned to behave in a certain way as a response to environmental stimuli) and thus one might argue that it focuses on a deterministic nature of learning.

Learning in the context of operant conditioning has originally been described using a Response-Stimulus pattern. More recently, a three-term model (Stimulus-Response-Stimulus) has been used (Huitt and Hummel 1997). The main premise is that a response is preceded by an environmental event (also known as antecedent stimulus) and is also followed by a stimulus (also known as consequence), which determines whether the behavioral response is more or less likely to occur in the future. A pleasant consequence (reward) increases the probability of a behavior occurring in the future, while an aversive consequence (punishment) decreases the probability of the behavior being repeated.

The Work of B. F. Skinner

Skinner has been named as the most eminent psychologist of the twentieth century (American Psychological Association 2002) for his work on operant conditioning through which he showed that behavior can be shaped through reward and punishment. Animal behavior in the laboratory was studied using the operant conditioning chamber (also known as Skinner box), developed by Skinner himself. With this device, Skinner was able to observe and quantify the behavior of animals (e.g., rats, pigeons) interacting with the environment. Through his observations, he formulated the basic principle of operant conditioning: A behavior followed by a reinforcer is strengthened and is therefore more likely to occur again

(Skinner 1938) – in other words, reinforcement results in learning. Skinner was able to observe that an animal inside the Skinner box, initially through trial and error as they moved about the box, at some point engaged in a behavior that produces a pleasant consequence (i.e., is reinforcing) such as receiving a pellet of food when pressing a lever. Repetition of this pattern response-consequence pattern over time resulted in the animal forming an association between the behavior and its pleasurable consequence. The desire for receiving the reward acts as a motivator for the animal to continue to engage in that behavior and consequently the behavior increases in frequency (behavior strengthened). In an analogous manner, behavior that was followed by punishment (such as a mini electric shock) eventually decreased in frequency (behavior weakened). Some of his major contributions were: the investigation of intermittent patterns schedules of reinforcement and their effect on speed of learning and extinction of behavior (Ferster and Skinner (1957), the concept of behavior shaping through successive approximation (Skinner 1951), modification of behavior using principles of operant conditioning (Skinner 1938, 1953), the chaining of complex behavioral sequences via secondary reinforcers (Skinner 1938), and the development of superstitious behavior (Skinner 1948).

Necessary Conditions for Learning

Contiguity

Skinner highlighted the importance of *temporal contiguity* in forming the associations necessary for operant conditioning to take place. More specifically, he stated that “to say that a reinforcement is contingent upon a response may mean nothing more than that it follows the response. It may follow because of some mechanical connection or because of the mediation of another organism; but conditioning takes place presumably because of the temporal relation only, expressed in terms of the order and proximity of response and reinforcement” (Skinner 1948, p. 168).

The process of operant conditioning is very sensitive to temporal relations. For learning to

take place under the paradigm of operant conditioning, it is imperative that three conditions are met (Ormrod 2016):

- (i) The reinforcer must follow the response: The reward should appear after the target behavior takes place, it should not precede it as it is then less likely that the organism will associate the presence of the reinforcer with a specific behavior.
- (ii) The reinforcer must follow immediately: Delayed reinforcement is less effective because other environmental events or behavioral responses that may take place in between will constitute the formation of the association between the reinforcer and the target behavior more difficult as they intervene.
- (iii) The reinforcer must be contingent (conditional) on the response: A reward should only be presented when a desired behavior has occurred so that a direct link is made between the two.

Discrepancy

In order for an organism to make the association between environmental event (reinforcement) and action (behavior), the produced behavior must be discrete from already exhibited behaviors. *Behavioral discrepancy*, defined as the difference between an ongoing and an elicited behavior (Donahoe 2003; Donahoe and Palmer 1994) is a necessary condition. A reinforcer must not only be presented immediately after the behavior in order for the association to be made, but it must also induce a response that is not already occurring (Kamin 1969).

Principles of Operant Conditioning

In the laboratory, Skinner refined the concept of operant conditioning and the Law of Effect. Among his contributions were the investigation of how different forms of reinforcement and punishment affect evidenced behavior, a systematic exploration of intermittent schedules of reinforcement, the shaping of novel behavior through

successive approximations, the chaining of complex behavioral sequences via secondary (learned) reinforcers, and “superstitious” (accidentally reinforced) behavior. These major contributions are further discussed below.

Consequences and Contingencies in Operant Conditioning: Reinforcement and Punishment

Skinner (1938) identified three different types of operants that can affect behavior following conditioning: Neutral operants (no effect on frequency of exhibited behavior), reinforcers (increase frequency of behavior), and punishers (decrease frequency of behavior).

Reinforcement is defined as an environmental stimulus that results in an increase of the frequency of an exhibited behavior because the organism, after a number of contiguous presentations of behavior-reward, associates a specific behavioral action with a desired outcome. Reinforcement can be positive or negative, depending on whether a pleasant stimulus is added (positive) or an unpleasant one is removed (negative). Positive Reinforcement involves the presentation of a stimulus that increases the occurrence of a behavior (e.g., the presentation of food after the mouse presses the lever in Skinner’s experiments). Negative Reinforcement entails an increase of behavior because it results in the removal of an aversive stimulus (e.g., a person takes aspirin to treat their unpleasant headache).

Punishment has the opposite effect. A decrease in frequency of a particular behavior because it is associated with an unpleasant outcome. In Positive Punishment (also known as Punishment I), a particular behavior is followed by a presentation of an unpleasant stimulus (e.g., an electric shock in Skinner’s experiments). In Negative Punishment (also known as Punishment II or Response Cost), a pleasant stimulus is removed (e.g., a child is sent to bed without dinner following naughty behavior).

Schedules of Reinforcement

Continuous reinforcement (receiving reinforcement every time a particular behavior is exhibited) results in faster learning (fast response rate) as the organism can relatively quickly make the

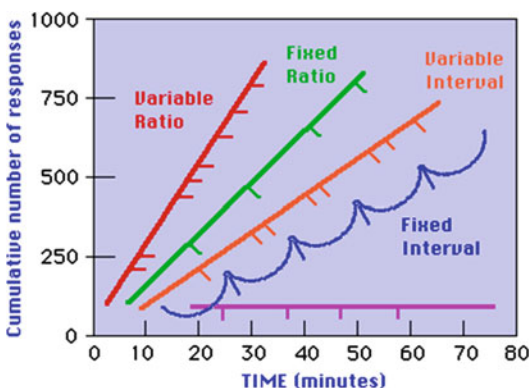
association between behavior and outcome when the reinforcement for a new behavior is given every time it is exhibited. What happens if reinforcement is not continuous, i.e., it is not given consistently? In the case of previously continuous reinforcement, removal of reinforcement results in fast extinction. Ferster and Skinner (1957) found that different schedules of reinforcement (continuous, ratio and interval) alter the speed of learning (response rate) and extinction (cease of a behavior). They experimented with fixed (regular) and variable (unpredictable) modes of presenting ratio and interval schedules of reinforcement.

In ratio reinforcement schedules, responses are reinforced on the basis of the number of responses exhibited by the organism. A *fixed ratio schedule* is one where a reinforcer is presented after a certain number of responses is displayed (e.g., after 10 responses). This type of schedule produces a high rate of response followed by a short postreinforcement pause (Ferster and Skinner 1957; Powell et al. 2017). The extinction rate following nonreinforcement of a previously reinforced response depends on the schedule of reinforcement applied to maintain that behavior. Resistance to extinction is higher the less frequent the reinforcement previously received, a phenomenon known as partial reinforcement effect (Mowrer and Jones 1945). More recent experiments have replicated these findings, as rats that were given continuous reinforcement extinguished the previously reinforced response of approaching a goal location in a water maze sooner than those previously given partial reinforcement (Prados et al. 2008). In a *variable ratio schedule*, reinforcement is presented after a varying and unpredictable number of responses and is determined by the average number of responses needed to receive a reward (e.g., a slot machine). This type of schedule results in a high response rate, with little or no postreinforcement pause (Powell et al. 2017) and is highly resistant to extinction following cease of reinforcement (Ormrod 2016) because the unpredictability of the reinforcement makes the realization of the cease of its presentation more difficult. When behavior has been maintained on a variable ratio schedule, it is usually more resistant to

extinction compared to a fixed ratio schedule (Reynolds 1975).

In interval schedules, the presentation of reinforcement depends on the time interval elapsed – the reward is presented following the exhibition of the first desired response after an amount of time has passed. A *fixed interval schedule* is one where reinforcement is contingent upon the first response after a predetermined and predictable time interval (e.g., after 5 min). Research shows that this type of reinforcement schedule results in a “scalloped” (curved upwards) response pattern. It involves a postreinforcement pause followed by a gradual response rate increase as the time interval is nearing completion (Powell et al. 2017). Response rate in this type of schedule is medium (a lower rate is observed compared to a fixed ratio schedule), and it is also less resistant to extinction (Ormrod 2016). In a *variable interval schedule*, the time interval elapsed for the presentation of reinforcement is less predictable as it depends on an average interval over a time period rather than a fixed one. This unpredictability results in a moderate and steady rate of response with little or no postreinforcement pause (Powell et al. 2017) and has greater resistance to extinction (Ormrod 2016).

Figure 1 summarizes response rates according to schedule of reinforcement applied (Huitt and Hummel 1997). The hatch marks on each line on the graph denote the presentation of a reinforcer.



Operant Conditioning, Fig. 1 Schedules of reinforcement and response rate (Huitt and Hummel 1997)

Shaping

Shaping (Skinner 1951) is a process where successive approximations of a behavior are reinforced, resulting in a gradual generation of the desired response (Powell et al. 2017). Successively closer approximations of a behavior are being rewarded until the organism succeeds in exhibiting the desired response (terminal behavior). This technique can be used to facilitate the demonstration of a particular response when an organism either lacks the skill or is not inclined to perform a desired behavior. Shaping can successfully be used in the process of learning a complex behavior or skill and has therefore useful applications in education (Snowman and McCown 2012). By reinforcing, gradually increasing in complexity behaviors that resemble the desired outcome and ignoring those that do not, a person gradually develops the necessary skills and moves closer to completing a complex task.

Chaining

A chain, according to Skinner (1953) is created when a response produces or alters some of the variables, which control another response. Complex behaviors, such as a sequence or chain, can be learned through the process of shaping. Chaining is a process where initially one response is reinforced, then two successive responses are reinforced, then a chain of three responses and so on (Ormrod 2016). Chaining establishes “*complex behaviors made up of discrete, simpler behaviours already known to the learner*” (Driscoll 2000). A *chained schedule* consists of a sequence of two or more simple schedules, each of which has its own discriminative stimulus, with the last in the sequence resulting in a terminal reinforcer (Powell et al. 2017). The majority of human endeavors consist of long response chains and in such cases where the terminal reinforcer is temporally distant (e.g., completing a Masters program), retaining the motivation to complete the chain can be quite a challenge. One way to deal with this is to identify the various links in the chain (e.g., the different courses) and the completion of each link to be made more prominent (for example, through self-reward, feelings of

satisfaction, etc.) so that it acts as a secondary reinforcer for the next part of the chain (Powell et al. 2017).

Superstitious Behavior

When a reinforcement is administered in a random fashion, it can result in superstitious behavior (Skinner 1948). When the organism receives reinforcement, it naturally assumes that it relates to its immediately preceding behavior, even though it may be unrelated. As a result, an incorrect connection between behavior and response is made (Ormrod 2016), and a behavior is “accidentally” reinforced. As stated by Skinner (1948, p. 168), “whenever we present a state of affairs which is known to be reinforcing at a given drive, we must suppose that conditioning takes place, even though we have paid no attention to the behavior of the organism in making the presentation.”

Applications of Operant Conditioning

Behavior Modification

Principles of operant conditioning have effectively been used in behavior modification for two main purposes: To *strengthen desired behaviors* (mainly through reinforcement) and to *weaken or eliminate undesired behaviors* (mainly through the ceasing of previous reinforcement or use of punishment).

Reinforcement, through rewards, has extensively been used to increase desired behaviors and is a particularly effective technique in educational settings. The methods of *shaping*, *token economy*, and *contingency contracting* have effectively been used.

According to Alberto and Troutman (2009) and Miltenberger (2008), the following steps should be followed in order to successfully achieve *shaping* of target behaviors in the classroom:

- (i) Identify target desired behavior
- (ii) Obtain baseline data by determining the anticipated frequency of target behavior’s occurrence
- (iii) Select reinforcers to be used

- (iv) Reinforce successive approximations of target behavior when it occurs
- (v) Reinforce target behavior when exhibited
- (vi) Reinforce target behavior using a variable reinforcement schedule

One of the major challenges of applying reinforcement in a classroom context that is comprised of a number of individuals is to identify a reward that will be reinforcing for every member of the group. What is reinforcing to one individual, may not be for someone else. For example, a piece of chocolate may be an effective reinforcer for one child but not for another who happens to be lactose intolerant. One method that can be used to overcome this challenge is the use of *token economy*. With this method, individuals “earn” tokens in the form of stars, coupons, plastic coins, etc. for evidencing desired behaviors, completing academic tasks, completing chores, etc. that can be accumulated and later be exchanged for “individualized” reinforcers (reinforcers individually chosen on the basis of interests and likes).

Drawing a *contingency contract*, a formal agreement specifying the target desired behaviors and the outcome of exhibiting those behaviors (i.e., the rewards to be received) is an effective way to communicate expectations and consequences concretely. Such contracts can be written or verbal and both parties (e.g., parent-child or teacher-child) should agree to it.

It is worth noting some challenges in the application of operant conditioning for the purposes of strengthening desired behaviors. Human learning is a complex process, and reinforcement alone may not always be effective when cognitive factors are not taken into account. For example, when the acquisition of a new skill is negatively affected by cognitive deficiencies, simple reinforcement will not produce the desired effects (Ormrod 2016). Furthermore, constantly reinforcing behavior can interfere with long-term learning and performance. Extrinsic reinforcement can make individuals susceptible to focus on the product and not on the process of learning (Ormrod 2016). Finally, extrinsic reinforcement of an enjoyable activity or task can weaken its

intrinsic value as individuals focus on the reward to be earned and are more likely to lose interest when it is taken away (Ormrod 2016).

Principles of operant conditioning can also be used to weaken or eliminate undesired behaviors, through the methods of extinction, negative punishment (time-out and response cost), and positive punishment.

Extinction is the elimination of an undesired behavior, and it is achieved through nonreinforcement of a previously reinforced response (Powell et al. 2017). At the initial stages of implementing this method, one may observe a variety of side effects, including extinction bursts (brief increase of the frequency of the undesired behavior; Lerman and Iwata 1995; McGill 1999), emotional behavior (Zeiler 1971), aggression (Azrin et al. 1966), and depression (Klinger et al. 1974).

Time-out and *response cost* are types of negative punishment as they consist of the loss of a privilege or a positive reinforcer for a brief period of time after the individual evidences undesired or problem behavior (Powell et al. 2017). *Time-out* involves asking the individual exhibiting problem behavior to stay in a specified setting that does not include reinforcers for a few minutes. This location should not include reinforcers and the time-out period should be brief. According to Miltenberger (2008), a time-out period of 1 min may be enough to effectively eliminate the undesired behavior. The key is to immediately reinforce more appropriate behaviors as soon as the individual returns to the normal setting. *Response cost*, involves the removal of a previously earned reinforce, following the occurrence of a problem behavior. According to Powell et al. (2017), an advantage of response cost is that one can easily adjust the severity of the punishment according to the degree of severity of the problem behavior.

Positive punishment consists of the presentation of a certain undesirable event to the individual (e.g., reprimanded by a parent, going to detention) following a problem behavior, which on the basis of operant conditioning principles leads to a decrease in frequency of the specific behavior. The use of punishment is advised when

the undesired behavior can harm oneself or others and can produce quick results (Ormrod 2016). In such context, it is imperative that the reasoning behind the specific behavior considered to be unacceptable and a justification of punishment is communicated clearly, as well as consistency in the delivery of punishment (Ormrod 2016). Various problems have been identified with the use of punishment, and so it should be used very cautiously. These include the elicitation of strong emotional responses, aggression, avoidance behavior, and the individual resorting in the use of punishment to modify others' behavior through the processes of modeling (Powell et al. 2017). Physical punishment should be avoided, as it provides the individual with a model of aggression that can be imitated at a later stage as it gives the message that aggression is an acceptable form of behavior (Landrum and Kauffman 2006). Psychological punishment, such as insulting comments or public humiliation, should also be avoided as it can have negative effects on emotional well-being and self-perceptions (Walker and Shea 1995).

Applied Behavior Analysis (ABA)

Applied Behavior Analysis (ABA) has been defined as a science in which systematic applications of principles of the analysis of behavior in order to improve socially significant behavior, using experimentation to identify the variables responsible for behavior change (Cooper et al. 2007). It is comprised of systematic description and implementation of a therapeutic intervention to change an undesirable or problem behavior, on the basis of the principles of behaviorism (Sulzer-Azaroff and Mayer 1991). According to Baer et al. (1968), an applied analysis of behavior highlights: the importance of the behavior changed, its quantitative characteristics, the experimental manipulations responsible for the change, the technologically exact description of the procedures leading to the observed change, the effectiveness of those procedures in making the change sufficiently valuable, and the generality of the change.

Skinner's operant conditioning theory contributed significantly to the birth of Applied Behavior

Analysis (Morris et al. 2005) and Skinner's (1938) three-term contingency model (S-R-S) can be a useful analytic tool. It is more commonly known in this context as the A-B-C model. In this process, the teacher or therapist collects information about (1) the target behavior and (2) the *Antecedents-Behavior-Consequences* (A-B-C). Antecedents include features of the environment immediately prior to a person producing a particular behavior. Behavior is the manifested response, and consequences are the events or outcomes that follow the behavior.

When the ABA method is applied in education contexts, it can be used to teach appropriate behaviors that involve breaking tasks into small, discrete "teachable" steps. At each step, appropriate behaviors are reinforced. Teaching targets are developmentally appropriate behaviors, and the child is given enough support to ensure success (thus ensuring the receipt of positive reinforcement). Gradually, the amount of support and reinforcement is reduced, while the behavior is monitored until the child is able to complete the task unaided. The behavior is closely observed, both before and during the intervention phase (Daly et al. 2009). ABA has been applied successfully in classroom settings for children with learning difficulties who evidence disruptive behavior (Jones and Kazdin 1975), as well as early intervention programs for children with learning difficulties. In such early intervention programs, parents are often trained to become the primary therapists (giving children one-to-one tuition at home), an approach that has been shown to be an effective intervention in helping children with autism to be more successful in mainstream schools (Keenan et al. 2000).

Evolutionary Perspectives on Operant Conditioning

Evolutionary psychology and behaviorism both attempt to understand human behavior in a scientific paradigm, and it has been argued that there is possibility of greater convergence than previously thought between the two theoretical orientations (Genovese 2007). Skinner, in fact, had considered the idea that genes and natural selection shape

behavior in his work (Skinner 1953) and had stated that "the behavior of organisms is a single field in which both phylogeny and ontogeny must be taken into account" (Skinner 1977, p. 1012). Learning could be considered as an evolutionary adaptive behavior, a capacity supporting the formation of predictions in unpredictable environments (Dawkins 1976), thus facilitating adaptation and survival. Skinner, had described operant conditioning as selection by consequences (Skinner 1981) and had stated that in a context where an organism adapts its behavior to a given environment and has therefore less need for an innate repertoire of behaviors, "operant conditioning could not only supplement the natural selection of behavior, it could replace it" (p. 501).

Skinner (1974, p. 41) acknowledged that "survival may be said to be contingent upon certain kinds of behavior." He used the examples of mating, protecting self from harm, and caring for one's child. While some of these behaviors are innate mechanisms facilitating survival, contingencies of reinforcement within the environment result in them being preserved through an operant conditioning process. And in cases where changes happen in the environment, operant conditioning principles guide organisms to develop new behaviors so that they continue to obtain reinforcers (Skinner 1974, 1981, 1984).

Conclusion

In behavioral learning theory, operant conditioning attempts to explain human behavior on the basis of a three-contingency model of stimulus-response-stimulus. It has succeeded in describing why some behaviors strengthen and others weaken in response to the consequences (reinforcement and punishment, respectively) that follow. It has a variety of applications in behavior modification, for example, in strengthening desired behaviors (mainly through reinforcement using methods such as shaping, token economy, and contingency contracting) and weakening or eliminating undesired behaviors (mainly through the extinction and punishment). It also has significant applications in educational settings and Applied Behavior Analysis. In the

context of evolutionary psychology, operant conditioning has been described as selection by consequences (Skinner 1981), facilitating adaptation in unpredictable environments.

Cross-References

- ▶ Classical Conditioning
- ▶ Conditioning and Association
- ▶ Positive and Negative Reinforcement and Punishment
- ▶ Reinforcement Schedule
- ▶ Shaping
- ▶ Skinner Box, the
- ▶ Thorndike's Law of Effect

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Operant Conditioning Chamber

► [Skinner Box](#), the

Operational Sex Ratio

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Synonyms

[Mating market](#)

Definition

The ratio of sexually available males to sexually available females in a population.

Introduction

The relative proportions of reproductive males and reproductive females in a population influence reproductive dynamics, including intersexual selection and intra-sexual competition. Across species, market influences of these proportions affect the intensity of mating competition and selectivity for partners. Female-biased (more available women than men) and male-biased (more available men than women) populations produce different outcomes because the reproductive strategies of men and women are somewhat divergent. Imbalanced sex ratios are associated with social and cultural trends in specific historical periods and populations. Male scarcity enhances male mating opportunities and decreases incentives for long-term commitment, facilitating serial and simultaneous polygyny. Female scarcity enhances the ability to secure commitment from partners and demand higher levels of resource investment. Male social power often constrains women's ability to leverage their market scarcity for serial or simultaneous polyandry.

Evolutionary Dynamics

Darwin (1871) recognized that a species' sex ratio was usually nearly balanced between males and females because on average, males and females in a population will have equivalent reproductive success. Each offspring has one female and one male parent. If there are more females in a population than males, a daughters' average reproductive success will be lower, favoring the production of sons. The advantageous production of the rare sex generates a stable equilibrium on an evolutionary time scale; human populations may exhibit imbalanced sex ratios at particular points in time (Darwin 1871). Düsing (1884) and Fisher (1930) created formal mathematical models based on these concepts.

Emlen and Oring (1977) originally defined the operational sex ratio (OSR) as the number of sexually active males per 100 sexually receptive females in a population. An OSR of 100 represents

a sex ratio with balanced proportions of males and females. An OSR below 100 is considered a low sex ratio representing a female-biased population (e.g., more available females than males). An OSR above 100 is considered a high sex ratio representing a male-biased population (e.g., more available males than females). Researchers have operationally defined the human OSR in terms of raw population counts (e.g., Barber 2000) and as the ratio of unmarried adult men to unmarried adult women (e.g., Kruger et al. 2010). Because the reproductive strategies of men and women are somewhat divergent, imbalances in the OSR exhibit directional effects consistent with the strategies of each sex.

Sex Roles in Reproduction

Following the economic patterns of supply and demand, the rare sex is more valuable in the mating market (Fisher 1958). Because men and women have somewhat divergent reproductive strategies, imbalances in the sex ratio have differential effects consistent with the strategies of each sex. Females are the limiting factor in reproduction in most animal and all mammalian species because they provide almost all of the physiological resources required for offspring production. Because of the larger necessary investment required for females, females have much lower potential reproductive capacities than males. Thus, females are more discriminating in selecting mates and males expend comparatively more effort in acquiring and retaining mates (Trivers 1972).

Human preferences for potential romantic or sexual partners in part reflect the differential roles and contributions made by men and women in successful reproduction. Both sexes prefer partners who exhibit characteristics such as kindness, understanding, and intelligence (Buss 1989; Kenrick and Simpson 1997). There is considerable overlap in men and women's criteria for potential partners; however, there is also divergence following reproductively relevant attributes. Although the nonphysiological parental investment that mothers provide is typically

higher than that of fathers, men's parental investment is much larger than that of other male primates (Buss and Schmitt 1993; Geary and Flinn 2001). The importance of father investment is indicated by the effects of their absence; children in foraging populations who grow up without a father present suffer higher mortality rates (Hill and Hurtado 1996). Paternal investment in offspring may enhance the offspring's reproductive success (Geary 2005). In modern populations, investment from fathers promotes positive child outcomes (Lamb 2004) and protects against negative outcomes such as delinquency (Harris 2002).

Women and men actively seek the resources related to reproductive value which men and women provide in reproductive relationships (Kruger 2008). Women provide physiological investment and men typically provide substantial material resource investment. Men seek women with cues of fecundity, the physiological potential for bearing offspring, whereas women prefer men with the ability and willingness to commit to long-term relationships and provide substantial paternal investment (Buss 1989). Men with higher social status and greater resource control have higher reproductive success across a wide variety of societies (Hopcroft 2006).

Male-Biased Sex Ratios

The economics of numerical supply and demand influences what individuals can demand from prospective mates. As the OSR becomes increasingly male biased, males compete more intensely for fewer females. The enhanced power of female choice raises the quality of valued male attributes necessary for securing female partners. There is more competition among men to demonstrate that they would be committed long-term relationship partners and resource providers (Pedersen 1991). Men offer more in a relationship, invest more time to wooing, are more romantic in dyadic interactions, and attempt to demonstrate more potential for resource investment (Guttentag and Secord 1983). Women will expect husbands to be of relatively higher social status, be kind, loving,

and generous and share the responsibilities of parental care (Guttentag and Secord 1983). Men with lower social status and fewer resources have an especially difficult time getting married (Pollet and Nettle 2007).

Women tend to marry at younger ages as they are able to secure male commitment earlier (Kruger et al. 2010). Some men also marry at younger ages as they have more motivation to secure a prospective partner before another man does. However, men also need to acquire greater social status and resources to be considered marriageable, and this can take considerable time and effort. Thus, as the population becomes increasingly male biased, the variance in male marital age increases (Kruger et al. 2010).

Male social power constrains potential female advantages, especially in societies where greater male social power is embedded in legal structures. High sex ratios are associated with greater emphasis on traditional sex roles and norms that both protect and constrain women, though women who can choose their own marriage partners have more power and control (Guttentag and Secord 1983).

Female-Biased Sex Ratios

In populations where women are more numerous than men, women compete more intensely for male partners. The forms of competition reflect attributes related to female mate value that men seek in partners, fecundity and sexual availability (Cunningham 1986; Tesser and Martin 1996). Sexuality and fecundity are emphasized in fashion trends for revealing clothing, such as shorter skirt lengths (Barber 1999; Time Out New York 2007). Women are more self-conscious about their physical appearance and the appearance of other women. Women wear revealing clothing, derogate other women who are wearing revealing clothing, and may even derogate other women for wearing the same fashions that they display themselves (Guttentag and Secord 1983; Time Out New York 2007).

When women are more numerous than men, men have less incentive to provide relationship

commitment and paternal investment (Pedersen 1991). Female-biased sex ratios are associated with higher divorce rates, more out-of-wedlock births and single mother households, and lower paternal investment (Guttentag and Secord 1983; Trent and South 1989). Greater proportions of females are associated with more promiscuous mating strategies across nations (Schmitt 2005).

Polygyny

The higher the degree of polygyny in a population, where high status men are better able to attract and/or retain multiple female partners, the higher the effective sex ratio will be. For every woman who is polygynously mated, there is one less woman available to other men. A polygynous population with a numerical balance of reproductive aged men and women may have an effectively male-biased sex ratio (Hendrix 1996). The degree of polygyny will constrain the effects of female numerical surplus, as well as accentuate male competition in balanced or male-biased populations. Higher degrees of polygyny are associated with greater consequences of male mating competition (Kruger 2010).

Conclusion

The operational sex ratio is a powerful influence on humans and other species. The more numerous sex faces greater intra-sexual competition for partners, and the scarce sex has greater power to select partners with desirable attributes, increasing the intensity of intersexual selection. Biased sex ratios exhibit patterns consistent with the divergent reproductive strategies of each sex. Men leverage their market scarcity for greater sexual access while avoiding long-term relationship commitments. Women are able to marry at earlier ages and obtain greater investment when scarce, although they are often constrained by social structures benefitting the reproductive interests of males.

Cross-References

- [Men's Mate Preferences](#)
- [Polygyny and Effective Population Sex Ratio](#)
- [Sex Ratio](#)
- [Sex Ratio and Men's Long-Term Mating](#)
- [Women's Mate Preferences](#)

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Opportunistic Mating

- [Sneak Copulation](#)

Opposing Reproductive Goals

- [Nonhuman Sexual Conflict](#)

Opposite-Gender Friend

► Opposite-Sex Friend

Opposite-Sex Friend

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Synonyms

Cross sex friend; Opposite-gender friend

Definition

Unrelated person of the opposite sex for whom one feels affection or esteem.

Introduction

Opposite-sex friendship is a historically novel relationship between a man and a woman that is supposed to be platonic and nonsexual. Evolutionary psychology considers opposite-sex friendships through two perspectives: as a specific type of friendship that has its own psychological adaptations and as a type of relationship “ruled” by mating strategies used in an evolutionary novel social situation. Considering sexual attraction is often experienced in this type of relationship, existing research mostly confirms the second perspective.

Historical and Social Context

Opposite-sex friendships are relationships between men and women that present a fairly new development in social relations and have only recently become a subject of research.

Additionally, opposite-sex friends are less common than same-sex friends. Historically, having an opposite-sex friend has been quite unusual, as men-women relationships have mostly been seen through the perspective of romantic partnership. For example, in the 1950s, it was extremely rare for men and women to have an opposite-sex friend, compared to now when people report having more than one opposite-sex friend. In that period, social structure and norms have separated women and men through different social roles they were fulfilling, and, aside from relatives and spouses, neither women nor men were able to develop more significant relationships with the opposite sex. The modern way of life has made it possible for men and women to spend time together, at work and in other social activities, which makes it possible to form opposite-sex relationships which are not focused solely on romantic motives or sex (Bleske-Rechek et al. 2012; Halatsis and Christakis 2009).

Evolutionary Psychology and Opposite-Sex Friends

Evolutionary psychology has viewed opposite-sex friendships as relationships that had existed in the evolutionary past and therefore caused the development of specific psychological adaptations, in order to manage such friendships (Bleske and Buss 2000; Buss 2008). As Bleske-Rechek et al. (2012) mention, this perspective would have required a regular interaction with opposite-sex friend(s) that would have helped our ancestors with two basic evolutionary problems: survival and reproduction. Essentially, that would mean opposite-sex friends helped our ancestors in their everyday survival, through sharing food and shelter and providing physical protection or sexual access, in such a way that enabled a higher survival rate and reproduction for individuals in such friendships.

A different perspective proposes that perceptions of the opposite-sex friend are by-products of mating strategies being used in a new evolutionary environment – the so-called by-product hypothesis (Bleske-Rechek et al. 2012). More specifically, the

attraction experienced in opposite-sex friendships is a manifestation of activated mating strategies applied to novel social situations, in which a person is in contact with numerous unrelated opposite-sex individuals. As previously mentioned, opposite-sex friendships are a historical novelty, as our ancestors were foragers and nomads that lived in small groups consisting of reproductive partners and kin, and it seems highly unlikely individuals had an opportunity to develop nonsexual supportive relationship with the opposite sex (Bleske-Rechek et al. 2012).

Mating strategies are psychological adaptations for partner selection which are sex specific due to the amount of resources invested in offspring, as proposed by Trivers (1972) in his well-known *Theory of parental investment*. Multiple research has proven the premises of the theory: men consider signals of fertility, youth, and health in a partner and have preferences toward a variety of partners, compared to women who are more discerning and looking for signals of good parenting and partnership, as well as efficient provision of food and other goods (Buss 2008). Considering opposite-sex friendship in this context, research has shown opposite-sex friendships follow the same patterns as is predicted by mating strategies: men consider their friends more sexually attractive; they over-perceive the females' sexual interest, while women value physical protection, as well as signs of "good mate" material in their male friends.

Sexual Attraction in Opposite-Sex Friendships

Sexual attraction is often experienced in opposite-sex friendships, and it can be considered as a benefit (e.g., "friends with benefits") or as a cost, when it negatively impacts the friendship. Research has shown attraction is often experienced in opposite-sex friendships (e.g., Reeder 2000), and if communicated, it can transform a friendship into a romantic relationship, end a friendship completely, continue it as a "friendship with benefits," or, in some cases, friends find a way to keep their relationship platonic (Halatsis

and Christakis 2009). For instance, Afifi and Faulkner (2000) reported that around 50% of their participants experienced sexual intercourse in an opposite-sex friendship, some of them even when involved in romantic relationships. This points us toward the potential cost and benefit of opposite-sex friendship: the threat it poses for the relationship with a romantic partner and a possible romantic relationship which can develop from a friendship.

Advantages and Disadvantages of Having Opposite-Sex Friends

Opposite-sex friends have certain benefits compared to same-sex friends: people learn more about the opposite sex and adequate ways to communicate, which can be beneficial in attracting and keeping a partner. Additionally, in opposite-sex friendships, men experience intimacy and emotional depth that is mostly lacking in friendships between men, while women can benefit from physical protection that a male friend can provide. Considering the fact that some friendships develop into romantic relationships, opposite-sex friends can be a pool of potential mates, which have already been evaluated and are considered compatible in some way. Opposite-sex friends will not become rivals during mating, which sometimes happens in same-sex friendships.

Partner's jealousy of an opposite-sex friend can be a potential disadvantage of this type of relationship, and men and women do consider attraction toward their opposite-sex friend as a cost of that relationship. Considering the fact that stronger attraction toward an opposite-sex friend is related to lower romantic relationship satisfaction (Bleske-Rechek et al. 2012), partner's jealousy seems evolutionarily justifiable.

Methodological Considerations in Researching Opposite-Sex Friendships

Opposite-sex friendship is considered as a platonic relationship between men and women; however, the previously mentioned findings signify a

need for a careful description of “friend” when opposite-sex friends are researched. Considering the frequently present attraction and sexual contact in opposite-sex friends, it is necessary for a researcher to carefully consider the possible “types” of friendships when choosing a sample and discussing their results.

Conclusion

Opposite-sex friends are essential members of a modern way of life and provide additional assets in one’s social context. Research results confirm the “by-product hypothesis”: the frequently present attraction in this type of friendship is a manifestation of mating strategies activated in a novel environment.

Cross-References

- [Friends with Benefits](#)
- [Friendship](#)
- [Gender of Friend](#)
- [Mating Strategies](#)
- [Sex Differences in Long-Term Mating Preferences](#)
- [Sex Differences in Short-Term Mating Preferences](#)
- [Sexual Access and Friendship](#)

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Opposite-Sex Friendships

- [Opposite-Sex Relationships](#)

Opposite-Sex Interpersonal Relationships

- [Opposite-Sex Relationships](#)

Opposite-Sex Peer Acceptance

- [Opposite-Sex Relationships](#)

Opposite-Sex Relationships

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Synonyms

[Opposite-sex friendships](#); [Opposite-sex interpersonal relationships](#); [Opposite-sex peer acceptance](#)

Definition

Interpersonal connections with peers of the opposite sex that are based on the quantity and quality of mutual respect, appreciation, and liking.

Introduction

Research clearly demonstrates the benefits of positive peer relationships for children's development (Martin and Dowson 2009). Findings show that children who have positive relationships with peers tend to be higher in academic outcomes (e.g., Martin et al. 2009) and personal well-being (e.g., Liem and Martin 2011). Research also shows that opposite-sex and same-sex peer relationships both positively impact children's development, but often in distinct ways (Liem and Martin 2011). Evolutionary psychology helps shed light on how peer relationships function in children's lives as well as some of the distinctive ways opposite-sex and same-sex peer relationships impact development. With a focus on opposite-sex peer relationships among children and the main contexts in which they interact (e.g., school), this discussion explores relevant research and theory through an evolutionary psychology lens.

Peer Relationships

Children's peer relationships and their effects on development have been explained from a variety of psychosocial and psychobiological perspectives. Under one such perspective – evolutionary psychology – it has been established that for individuals to coexist over time, they must balance their own interests with the interests of the group to which they belong. Thus, individuals are cooperative at key points in development (Barrett et al. 2002). Children coexist as peers in a group and adaptive intragroup synergies are developed through positive peer relationships. These positive peer relationships provide support and assistance for the child and the group to which he or she belongs.

Evolutionary educational psychology is particularly relevant to child development. Evolutionary educational psychology proposes two highly influential psychological systems. Biologically primary (folk) psychological systems that have an evolutionary basis and involve processing information related to self, others, and group

dynamics (Geary 2012). Biologically secondary psychological systems are acquired through individuals' interactions with their environment. Thus, biologically primary psychological factors and processes refer to pan-human phenomena such as social interaction and communication (Geary 2012). Thus, peer relationships (including their underlying mechanisms such as cooperation) are socially based phenomena that would be considered biologically primary knowledge and skill that humans are evolutionarily motivated to acquire and apply (Geary 2012).

Notably, however, at the same time as children are motivated to cooperate and socially interact, there are many contexts (e.g., classrooms) in which they must also compete to secure resources for survival and fitness (e.g., teacher's attention and support). Drawing on early work by Hamilton (1964) suggesting that there is "direct fitness" (producing one's own offspring) and "indirect fitness" (helping others to produce offspring that share one's genes), Martin (2017) has suggested that children can achieve by their own efforts ("direct achievement fitness") or they may also help other children achieve. In so doing, they may lift the group to a higher level of aggregate achievement that can assist their own capacity to achieve ("indirect achievement fitness"). This further establishes a potential evolutionary psychology basis for positive peer relationships in childhood.

Hamilton (1964) also argued that the more members in the group are connected to each other (referred to as the "coefficient of relatedness"), the less the benefits need to be for cooperative behavior to occur. In childhood, then, it might thus be argued that the higher the quality of peer relationships, the more cooperation is likely to occur. Indeed, a body of writing on cooperative contexts attests to the positive consequences of positive peer relationships in these contexts (e.g., Johnson and Johnson 2008).

The frequency of interactions among peers is also critical. The more peers interact, the more it makes sense for them to cooperate and assist each other. Moreover, to the extent they do, their academic and personal wellbeing outcomes are enhanced (Johnson and Johnson 2008).

Particularly in childhood, there is a greater frequency of peer interactions among same-sex peers and research has identified positive outcomes through these same-sex peer relationships (Liem and Martin 2011; Martin et al. 2009). Although ever-present, opposite-sex peer relationships are relatively less salient.

Opposite-Sex Peer Relationships

Studies on the relative effects of opposite-sex and same-sex peer relationships have identified similarities and differences in terms of academic and personal wellbeing outcomes (e.g., Liem and Martin 2011). There is agreement among researchers that both same-sex and opposite-sex peer relationships share functional importance by affording avenues for children to meet their psychosocial needs, such as providing sources of self-esteem, ego support, and affirmation of competence (Liem and Martin 2011).

It is also the case that opposite-sex peers represent a source of intragroup diversity. The potential for diversity to enhance children's outcomes is suggested in "niche partitioning," a term addressing the diverse roles and expertise of group members (Sulloway 2007). In the educational context, for example, niche partitioning suggests a need to optimally utilize children's different strengths and roles to increase the "fitness" of the class. In terms of opposite-sex peer relationships, because girls and boys have distinct motivational and achievement strengths (Liem and Martin 2011), each can make unique contributions to the class and to peers of the opposite sex.

Also in classroom contexts, opposite-sex diversity may have the potential to result in less intra-group conflict and competition and better ensure that students are equipped to deal with the diverse and fluid challenges characteristic of a changing world. That is, learning environments comprising a heterogeneous mix of students may evince less intragroup conflict because there are fewer students competing for the same spoils

(or more students striving for a diversity of spoils) (Martin 2017).

Although this discussion centers on children, it is worth noting related evolutionary theorizing on opposite-sex peer relationships among adults. Although much of this theorizing inevitably is about mating and genetic survival, it also articulates some ideas arising in this discussion with regard to niche partitioning (Sulloway 2007). For example, Lewis et al. (2011) describe how during human evolution men and women faced distinct adaptive problems (e.g., pregnancy, childcare, hunting, warfare, etc.). Natural selection would favor psychological mechanisms that orient men and women to developing friendships with others who possess characteristics valuable for solving distinct problems. Because many adaptive problems are sex-linked (i.e., men and women tend to face and solve different problems), opposite-sex peer relationships will develop accordingly.

Research Findings

Following from the above evolutionary theorizing, research has shown that the positive influences of opposite-sex peers may differ from those of same-sex peers (e.g., Liem and Martin 2011). This may not be surprising as children tend to interact and develop friendships with same-sex peers in their childhood, whereas opposite-sex friendships tend to emerge more saliently in later adolescence. As noted earlier, the frequency of interaction is an evolutionary-based factor that may inform the nature and effects of peer relationships. Importantly also, the opposite-sex peers that children interact with tend to be secondary friends more than best friends (Liem and Martin 2011) and so opposite-sex peers may be less influential in children's outcomes than friends of the same sex. Thus, it has been predicted that both opposite-sex and same-sex peer relationships are influential in childhood, but the extent to which this is the case will differ. Indeed,

research has found that same-sex peers, but not opposite-sex peers, directly predict children's academic performance; both same-sex and opposite-sex peers directly predict self-esteem; and, same-sex and opposite-sex peers both significantly predict school engagement – but to a greater extent for same-sex peers. Moreover, these findings tend to be invariant across gender and age groups (Liem and Martin 2011; see Martin et al. 2009 for aligned opposite-sex findings).

Conclusion

Positive peer relationships underpin key elements of children's development. Evolutionary psychology provides insights into how peer relationships function in children's lives. This perspective also sheds light on the distinctive ways opposite-sex and same-sex peer relationships impact development. With a focus on opposite-sex peer relationships in the present discussion, evolutionary psychology provides theoretical and empirical grounds for concluding that positive interactions with peers of the opposite sex are essential for academic development and psychological well-being during childhood.

Cross-References

- Friendship
- Peer Competition and Cooperation
- Peer Relationships In Childhood
- Peers
- Same-Sex Friendships

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Opposition to Economic Redistribution

- High SES Against Redistribution

Opposition to Human Sperm Competition

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Definitions

Human sperm competition: The competition, inside a woman, between sperms from two or more different men for the “prize” of fertilizing any egg the woman might produce.

Introduction

The potential evolutionary importance of sperm competition was first recognized for insects (Parker 1970), but within a little over a decade, the growing theoretical framework was being extended to a range of other animals, including humans (Smith 1984). Smith’s suggestion was seen as daring and thought-provoking, but triggered little opposition. However, when a series of papers by Baker and Bellis (see Baker and Bellis 1995) claimed evidence that sperm competition really had played a part in shaping human sexuality, resistance to the idea began to grow. Increasingly the view was expressed that even if sperm competition did occur occasionally in humans, its evolutionary significance was minimal. Some simply doubted that women behaved often enough in the way necessary for sperm competition to be a significant evolutionary force. Others reinforced their opposition with arguments based on the brevity of sperm fertility, variation in sperm biology, details of male anatomy, and most recently the genetics of ejaculates.

Female Infidelity and Levels of Extra-Pair Paternity

When first outlining the potential importance of sperm competition to human evolution, Smith

(1984) listed a range of situations in which such competition could occur: prostitution, group sex, rape, gang rape, and, on top of the list, female infidelity. Unfortunately, how often such behavior actually led to sperm competition could not be estimated. Although figures existed for all of the listed activities, not only for the USA but also for Europe, these figures could not simply be converted into rates of sperm competition nor, more importantly, how many children were conceived as a result.

When a woman conceives to a man other than her recognized partner, it is said to be a case of extra-pair paternity. Traditionally, based on a little more than hearsay and anecdotes, medical students had been taught that the level of extra-pair paternity in modern society was around 10–15%. This encouraged the belief that sperm competition led to conception often enough to be an evolutionary force.

The first direct attempt to estimate the frequency of sperm competition was made by Bellis and Baker (1990) based on a UK nationwide survey. From nearly 4000 replies, they separated out data for women being unfaithful “unprotected” by contraception during the fertile phase of their menstrual cycle and calculated that the proportion of children likely to be conceived via sperm competition was indeed likely to be of the order of 10%. On the basis of this figure, Baker and Bellis (1995), and later others, claimed that sperm competition had been common enough through human evolution to exert a significant selective pressure. Others, however, began to question this 10% figure and argue that the true value is considerably lower.

A debate over the matter springs from measures not of sperm competition but of extra-pair paternity. The earliest such investigations used blood-group analysis, the more recent DNA paternity testing, mainly in the USA and Europe. Nearly 70 studies have now been conducted, and various meta-analyses have been carried out. The most quoted figure is that obtained by Anderson (2006): only 1.7% of the assumed children of men with high paternity confidence had in reality been sired by other men.

Attempts have also been made to measure extra-pair paternity rates in the historical past using lineages stretching as far back as 700 years ago. This group of studies all involves obtaining samples of Y chromosomes from modern-day men linked by some feature that, like the Y chromosome itself, is passed from father to son through the generations. Examples are surnames, the right to participate in certain privileged land-use schemes, and discrete immigrant populations recorded through patrilineal descent. Mismatches between Y chromosome genes and, for example, surnames can indicate extra-pair paternity in the historical past. As a group, these studies generally seem to show per-generation rates of extra-pair paternity of around 1% (Larmuseau et al. 2016) and are all far lower than the 10% initially accepted by early authors.

Measures of extra-pair paternity are not in themselves measures of conception via sperm competition because, among other causes, not all cases of extra-pair paternity result from such a scenario. Nevertheless, the general impression given by so many extra-pair paternity figures of ~1% is that sperm competition may not be as important in human evolution as initially believed.

Sperm Fertility

Gomendio and Roldan (1993) were the first to question the contribution of sperm competition to human evolution that Baker and Bellis had been promoting in their papers. The formers' primary argument was that human sperm were fertile for such a short time that for sperm competition to occur a woman would have to mate with two men within only 2–3 days. Gomendio and Roldan thought it unlikely that such short-term "double-mating" happened often enough to be a selective force. Evidence that human sperm remained fertile inside a woman for longer than 2–3 days, such as the 5 days claimed by Barrett and Marshall (1969) or even longer by others, was dismissed by Gomendio and Roldan as unreliable. So too was the evidence published earlier by Bellis and Baker (1990) that short-term double-mating by

women did occur often enough to be evolutionarily significant.

Sperm Biology

Van der Horst and Maree (2014) investigated sperm biology for three animal species that they suspected evolved under very low levels of sperm competition. The species concerned were a passerine bird – the Eurasian bullfinch (*Pyrrhula pyrrhula*) – and two mammals, the greater bandicoot rat (*Bandicota indica*) and the naked mole-rat (*Heterocephalus glaber*). The authors noted that the sperm of all three of these species shared characteristics, such as low swimming speed and a high proportion of abnormal sperm, that they argued would evolve only under low levels of sperm competition. Van der Horst and Maree then compared the sperm biology of their three species with that of primates and claimed a greater similarity with the sperm of humans and gorillas, the latter evolving under low levels of sperm competition, than with the sperm biology of chimpanzees, evolving under high levels. In the authors' view, this similarity was evidence that humans evolved under low levels of sperm competition.

Male Genitalia

A variety of studies have compared the male genitalia of humans with the genitalia of other primates (see Dixson 2009). Length and diameter of the penis, presence and shape of the terminal coronal glans, presence and size of penile spines and internal penis bone, size of seminal vesicles, and size of testes (relative to body size) have all been analyzed across species. Although a range of primates are often included, the main question usually asked is whether human genitalia are more similar to those of low-sperm-competition gorillas or high-sperm-competition chimpanzees. Invariably, human genitalia emerge as intermediate between these two near relatives. Nevertheless, Dixson (2009) concluded that the weight of such evidence leans toward humans being more

similar to gorillas and hence toward sperm competition having played an insignificant part in the evolution of human sexuality.

Seminal Fluids

In recent years a number of investigations have estimated the rate of evolution of genes that encode aspects of primate ejaculates. Measured rates often correlate with the level of sperm competition in the different lineages. Not all conclusions concur, but one of the most quoted is from the study by Dorus et al. (2004). This showed that the evolution of *SEMG2*, the gene encoding a main structural component of coagulated semen, is accelerated under conditions of high sperm competition. The rate of evolution in humans, however, was much nearer to that of gorillas than chimpanzees, suggesting a low level of sperm competition in the human evolutionary past.

Conclusion

A range of evidence has been amassed that some authors claim show the human lineage evolving under low levels of sperm competition. It should be noted, however, that none of the streams of evidence are universally accepted. The measures of levels of extra-pair paternity all suffer from methodological quirks that could easily mask a population sperm competition level as high as 10% (Anderson 2006). The length of time the sperm stay fertile inside a woman and the frequency with which women double-mate during that time are also highly debatable (Baker and Bellis 1995). So are conclusions based on sperm biology (Baker and Bellis 1995) and male genitalia (Baker 1997; Gallup et al. 2006; Marczyk and Shackelford 2010), whereas those based on seminal fluids are simply contradictory (Leivers and Simmons 2014).

Essentially, interest in human sperm competition has divided authors into three main groups. The first (e.g., Baker and Bellis 1995; Gallup et al. 2006; Smith 1984) considers that

human sperm competition was very common in the past, is still moderately common today, and as such has been and still is a major selective pressure on human sexuality. The second (e.g., Birkhead 2000; Dixon 2009; Gomendio and Roldan 1993) proposes that sperm competition was minimal in the past, is trivial today, and has played either a minor or zero role in human evolution. The third (Marczyk and Shackelford 2010) maintains that, past or present, the actual level does not matter. As long as sperm competition occurs with some predictability and carries large fitness costs, even a relatively low frequency can act as a powerful selective pressure.

For the moment, the second (“low-level”) group appears to be in the ascendancy. However, the question of how important sperm competition has been in the evolution of human sexuality is still very far from settled.

Cross-References

- [Human Sperm Competition](#)
- [Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition](#)

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Oppressing

- [Child Abuse and Bullying](#)

Optical Flattening

- [Countershading](#)

Optical Illusions

- [Visual Illusions](#)

Optimal Clutch Size

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Synonyms

[Interbirth interval](#); [Lack clutch size](#); [Optimal litter size](#)

Definition

The number of offspring individual females are predicted to produce in a given breeding attempt (clutch) when there is a trade-off between the number of offspring in a clutch and the quality of each offspring.

Introduction

The study of life history evolution explores how species maximize fitness when traits directly linked with fitness (e.g., life span, fecundity, offspring quality and quantity) are negatively correlated with each other. One of the best-studied life history trade-offs is the relationship between offspring quantity and quality, in which additional investment in any one offspring will generally reduce the number of offspring a parent can produce. Economic models have been used to predict the clutch or litter size that will maximize evolutionary fitness. These predictions depend on shape of the relationship between offspring quality and fitness and offspring quality and quantity. In animals (and, in particular, birds), this predicted number of offspring is called the “optimal clutch size.”

Lack's Model

One of the first attempts to predict life history decisions using economic models was David

Lack's work predicting optimal clutch and litter size in birds and mammals (Lack 1947). Previous hypotheses about the determinants of clutch size posited that females would maximize fitness by producing the largest clutches possible given the species' physiological constraints. Lack hypothesized that a trade-off between clutch size and the per capita survival rate of clutch members might favor the production of smaller clutches than physiological possible. For example, while five eggs represent the potential for higher evolutionary fitness than four eggs, a per capita survival rate of 0.2 in a five-egg clutch will result in lower fitness at fledging (an estimated one surviving fledgling) than four eggs with a survival rate any higher than 0.25 (>1 surviving fledgling). Lack specifically suggested that food limitation might drive such a trade-off between clutch size and survival rate, but difficulty incubating or carrying large clutches and the potential for large clutches to attract predators are also potential sources of a trade-off between clutch size and offspring survival (Godfray et al. 1991).

Like any model in behavioral or evolutionary ecology, models of optimal clutch size serve to make testable predictions about behavior based on hypotheses about the relationship between those behaviors and evolutionary fitness. Lack's model hypothesized that the primary fitness trade-off of increased clutch size was the survival rate of fledglings within that clutch; this predicted clutch size is often referred to as the "Lack clutch size." Observational studies have revealed that clutches are typically smaller than the predicted Lack clutch size (Godfrey et al. 1991). Moreover, the experimental addition of offspring to clutches frequently demonstrates that animals can successfully produce more surviving offspring than they typically do (Van der Werf 1992). This suggests that either (1) estimates of the survival cost of increased clutch size are underestimated and/or (2) additional costs of increased clutch size need to be taken into account.

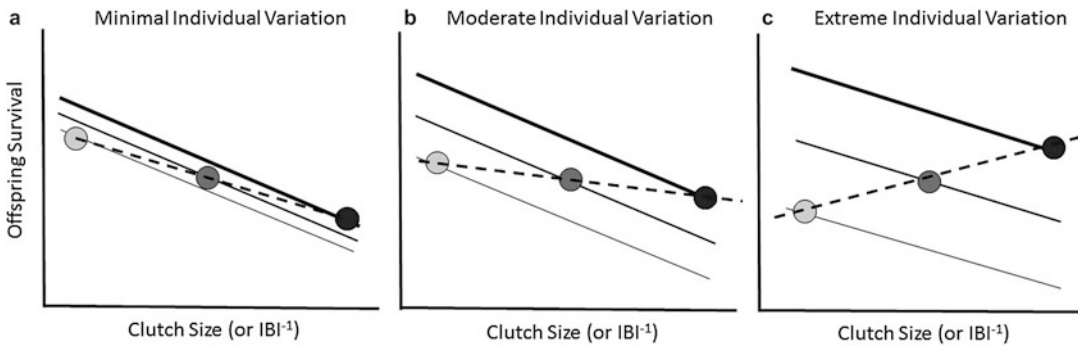
Individual Variation and the Underestimation of Fitness Trade-Offs

Observational studies used to assess the trade-off between clutch size and offspring survival are complicated by individual-level variation in the ability to successfully produce and rear clutches. The largest clutches in a population may be produced by females in particularly good condition or with access to particularly rich resources. These same females may also be better able to ensure the survival of offspring than low-quality females with smaller clutches. Such individual variation can mask the trade-off between clutch size and survival that likely occurs among individuals within a particular quality class. Therefore, in populations with interindividual variation, the cost of increased clutch size can be underestimated and the optimal clutch size thus overestimated (Fig. 1; Pettifor et al. 1988).

Additional Costs of Clutch Size

While Lack focused on the cost experienced by offspring within a given breeding season, increased clutch size may have fitness costs experienced in future breeding seasons by clutch members or their parents. The "cost-of-reproduction" hypothesis posits that large clutch sizes reduce the condition and survival of parents, thus reducing the production of future clutches. Moreover, large clutch size may influence the future reproductive capacity of clutch members. Both of these costs are reflected in the optimal clutch size of wrens: females whose clutches were experimentally increased produced smaller hatchlings during the experimental year, and themselves experience lower hatchling survival during the following year (Hodges et al. 2015).

Some hypotheses posit that females produce smaller clutches as a bet-hedging strategy against large costs that are only occasionally experienced. For example, the "bad years" hypothesis (Boyce and Perrins 1987) predicts that females maximize their geometric mean fitness by avoiding the



Optimal Clutch Size, Fig. 1 The influence of individual variation on estimates of the clutch size – survival trade-off. In all three plots, the actual relationship between clutch size (or interbirth interval [IBI]) and offspring survival is the same (*solid lines*). Where there is individual variation, females in better condition (*thick lines/dark circles*) can produce larger clutches (or shorter IBIs) and achieve higher

offspring survival than females in poor condition (*thin lines/light circles*). If females in better condition produce large clutches, estimates of the trade-off between clutch size and survival (*dotted line*, based on three hypothetical individuals) become increasingly inaccurate as individual variation in condition increases

production of large clutches that, while successful in times of plenty, lead to a catastrophic loss of fitness in “bad years,” when resources are scarce. The “parasitism insurance hypothesis” – another bet-hedging hypothesis – argues that birds may produce smaller clutches in order to accommodate the occasional additional offspring introduced via intra- or interspecific clutch parasitism. Bet hedging may also explain why some birds produce clutches of two eggs when only one offspring survives. While energy invested in the second egg typically represents wasted effort, the second egg insures against a total loss of fitness if the first egg is infertile or otherwise nonviable (Godfray et al. 1991).

Individual Optimization

The recognition that individuals can vary in their ability to successfully rear clutches led to the development of the “individual optimization hypothesis,” in which intrapopulation variation in clutch size is explained by each individual producing a clutch size that optimizes fitness given that individual’s particular “state” or “condition.” This hypothesis predicts a positive correlation between clutch size and some measure of

condition (e.g., size) and that removing or adding offspring to the females preferred clutch size will reduce her fitness. Both of these predictions have been met in studies on great tits (Pettifor et al. 1988) and Richardson’s ground squirrels (Risch et al. 2007) and thus potentially explain the extreme clutch size variation seen in these species.

Litter Size and Interbirth Interval in Humans

In humans, the optimal litter size is likely to be one. It is difficult for women to meet the nutritional requirements to support nursing more than one infant, and studies on hunter-gatherers indicate that women are typically unable to carry more than one infant (Hill and Kaplan 1999). Life history data collected in two Norwegian parishes from 1700 to 1900 indicates that the evolutionary fitness – measured as total grand offspring – of the mothers of twins was less than or equal to that of the mothers of singletons and the mothers of offspring made singleton via the death of their twin (Skjærvø et al. 2009).

A related life history trade-off more relevant to human variation is interbirth interval. Shorter interbirth intervals produce more infants but may

increase per offspring mortality rate. Research on the !Kung (Blurton-Jones 1987) and the Ache (Hill and Kaplan 1999) both revealed a negative relationship between interbirth interval and offspring mortality, supporting the expected trade-off between offspring quantity and quality. However, in the Ache, this mortality cost was not large enough to explain the length of IBI in this population (it was predicted to be shorter). As with animal studies, estimates of optimal IBI in these instances may underestimate optimal IBI because they do not take into account additional costs of reproduction or underestimate those costs by ignoring individual variation (Fig. 1). For example, a recent study on preindustrial Finns has demonstrated a negative genetic correlation between mean IBI and parent life span (Pettay et al. 2005), suggesting that increased mortality in parents is an additional cost of shorter IBIs.

Conclusion

Overall, clutch and litter sizes in vertebrates are smaller than individuals are physiologically capable of producing. This underproduction of offspring is most likely driven by a trade-off between offspring quantity and quality. In general, models that hypothesize that the cost of larger clutch size is only paid by clutch members and only experienced within a particular breeding season tend to overestimate optimal clutch size. Models that also include costs to parents, irregular but large costs, and individual variation tend to better predict the clutch sizes seen in nature.

Cross-References

- ▶ [Adaptation and Natural Selection](#)
- ▶ [Bird Clutch Size](#)
- ▶ [Birth Spacing and Birth Order](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Field of Behavioral Ecology, The](#)
- ▶ [Individual Differences](#)
- ▶ [Life History Theory](#)
- ▶ [Maternal and Offspring Condition](#)
- ▶ [Parental Investment and Parenting](#)
- ▶ [Variance in Female Reproductive Success](#)

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Optimal Designs

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Products and Byproducts of Natural Selection

What is the proper way to interpret the appearance of design in nature? Before 1859 and the publication of Darwin's *On the Origin of Species*, the answer seemed obvious – design means a designer. In *Natural Theology*, theologian

William Paley famously analogized the appearance of design in the living world to the appearance of design in a man-made object, a watch:

... [S]uppose I had found a watch upon the ground, and it should be inquired how the watch happened to be in that place ... There must have existed, at some time, and at some place or other, an artificer or artificers, who formed [the watch] for the purpose which we find it actually to answer; who comprehended its construction, and designed its use. ... Every indication of contrivance, every manifestation of design, which existed in the watch, exists in the works of nature; with the difference, on the side of nature, of being greater or more, and that in a degree which exceeds all computation. (Paley 1809)

In his book *The Blind Watchmaker* (Dawkins 1986), Richard Dawkins answers Paley's supposition:

The analogy ... between watch and living organism is false. All appearances to the contrary, the only watchmaker in nature is the blind forces of physics, albeit deployed in a very special way. A true watchmaker has foresight: he designs cogs and springs, and plans their interconnections, with future purpose in his mind's eye. Natural selection, the blind, unconscious, automatic process which Darwin discovered, and which we now know is the explanation for existence and apparently purposeful form of all life, has no purpose in mind. [...] If it can be said to play the role of watchmaker in nature, it is the *blind* watchmaker.

Paley's observation is still true today: we instinctively recognize purpose and intention in living things the same way that we recognize design in manmade artifacts. We now know that living things evolved into their present forms, and we look at how well organisms "fit" within the challenges of their environments in order to determine what selective pressures shaped them. But how well should we expect organisms to meet those challenges? What level of craftsmanship does the blind watchmaker employ? What does it mean when we see less than optimal designs in nature?

Case Study: The Spandrels of San Marco

We may have explained away the need for Paley's intelligent watchmaker, but the question remains, how good of a watchmaker is our blind watchmaker, natural selection? Are living things

particularly well designed? And does *everything* have to be the product of natural selection? Some living things have features that seem poorly adapted to their environments. It's also possible that some features that look like great designs to human minds might only appear that way in hindsight or through the lens of overly felicitous post-hoc reasoning. How many features are mere "spandrels" – byproducts of genuine adaptations? In their oft-touted 1979 paper, *The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme*, Stephen Jay Gould and Richard Lewontin compare the design of living things to that of the Cathedral of San Marco in Venice, which features beautiful mosaic portraits of the evangelists in its spandrels – the spaces between the cathedral's dome and the curved arches that support it:

The design is so elaborate, harmonious, and purposeful that we are tempted to view it as the starting point of any analysis, as the cause in some sense of the surrounding architecture. But this would invert the proper path of analysis. The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form. They provide a space in which the mosaicists worked; they set the quadripartite symmetry of the dome above.

... [E]volutionary biologists, in their tendency to focus exclusively on immediate adaptation to local conditions, do tend to ignore architectural constraints and perform just such an inversion of explanation. (Gould and Lewontin 1994)

The metaphorical spandrel here is what Gould would later term an exaptation – "a character, previously shaped by natural selection for a particular function (an adaptation), [coopted] for a new use" (Gould and Vrba 1982). This framing of exaptation can be misleading, as there are no raw evolutionary materials – every feature that is genuinely adapted for a given purpose must have begun as part of a different feature – but it is useful to consider whether the selection pressures an organism faces in a modern environment are the same as those that contributed the most to its design. "Spandrel" is still used interchangeably with "byproduct" in evolutionary biology and psychology, and the phrase "just a spandrel" has something of a pejorative connotation.

The concept of architectural constraints adds explanatory power to our story of the spandrels of San Marco. The spandrels do not exist simply to display mosaics of the evangelists, but, contra Gould and Lewontin, neither are the mosaics an afterthought entirely secondary to the architecture of the church. In *Darwin's Dangerous Idea* (1996), Dan Dennett shows that our understanding of the spandrel could benefit from an adaptationist analysis. He begins by pointing out that San Marco features only one kind of spandrel, more properly known as a “pendentive”:

Not only were the pendentives just one among many *imaginable* options; they were just one among the readily *available* options. Squinches had been a well-known solution to the problem of a dome over arches in Byzantine architecture since about the seventh century.

What the actual design of the San Marco spandrels—that is, pendentives—has going for it are mainly two things. First, it is (approximately) the “minimal-energy” surface (what you would get if you stretched a soap film in a wire model of the corner), and hence it is close to the minimal surface area (and hence might well be viewed as the optimal solution if, say, the number of costly mosaic tiles was to be minimized!). Second, this smooth surface is ideal for the mounting of mosaic images—and that is why the Basilica of San Marco was built: to provide a showcase for mosaic images.

The conclusion is inescapable: the spandrels of San Marco aren't spandrels even in Gould's extended sense. They are adaptations, chosen from a set of equipossible alternatives for largely aesthetic reasons. They were designed to have the shape they have precisely in order to provide suitable surfaces for the display of Christian iconography. (Dennett 1996)

Dennett advocates the intentional stance when approaching biological and, by extension, psychological phenomena, assuming that complex features are adaptations that evolved to serve a purpose. Though Gould and Lewontin rightly point out natural selection is not the direct cause of all characteristics, it *is* the only cause of complex adaptations. Even though the spandrels of San Marco are in some sense byproducts, they can also be viewed on their own terms as adaptations when compared to equally possible alternatives. It was by assuming the intentional stance that Dennett was able to find a possible adaptive purpose to the spandrels.

The debate over the appropriate perspective on possible adaptations may seem to come from the armchair – why should we care whether adaptation is more or less pervasive in shaping living beings than the genetic drift, developmental constraints, and genetic inertia that also play a role? Can't we just look at the evidence for any given case?

One reason that we must consider grand questions of causation is that the balance of the various evolutionary forces informs our null expectations. Any attempt to reverse engineer relies on the reasoning that complex, well-adapted features don't arise by chance alone, so the degree of their aptness for a given purpose is evidence that they evolved for that purpose.

More fundamentally, the intentional stance is often the only place to start when asking “why” questions about design in living beings. “Adaptationism” is a productive approach for generating hypotheses and making novel, testable predictions (Barkow et al. 1992). While any particular explanation of adaptive purpose is just a hypothesis until it is validated, it is important to have the intellectual warrant to proceed from the assumption that complexity has an adaptive explanation. In fact, the same instinctive recognition of design that led Paley to believe in an Intelligent Watchmaker sets today's evolutionary scientists on the course to investigating adaptations.

What Is Optimal?

A Note on Terminology

In common parlance, “optimal” is used interchangeably with “maximal,” but for our purposes, it is useful to distinguish the two. In engineering, optimal means “satisfactory, the best solution given all the constraints,” while maximal means “greatest possible,” and these are the definitions that I will adopt here. It is important to note that these terms are not always distinguished in biology or psychology, and their definitions may even be reversed.

There is a deeper philosophical issue that causes confusion between optimal and maximal

designs – actualism vs. possibilism. The *Stanford Encyclopedia of Philosophy* explains:

Actualism is the philosophical position that everything there is – everything that can in any sense be said to be – *exists*, or is *actual*. Put another way, actualism denies that there is any kind of being beyond actual existence; to be is to exist, and to exist is to be actual. Actualism therefore stands in stark contrast to possibilism, which [...] takes the things there are to include possible but non-actual objects. (Menzel 2016)

The disagreement boils down to what benchmark we are using to evaluate natural selection's designs. In our terms, adaptationists like Dawkins tend to be actualists – focused on how well natural selection solves a problem within its constraints and dismissing other possible sets of constraints as beside the point because those were not the constraints that *actually* impinged on natural selection in the given case. Those like Gould and Lewontin that focus on contingency and point out the inadequacy of nature's solutions often appeal to different possible, but not actual, circumstances under which the trait could have evolved to be better at solving the problems it now faces. Possibilists tend to see actual reality as just a subset of what could have been, whereas actualists tend to view what actually exists as all that could have been. I cannot resolve the actualism vs. possibilism debate in this chapter, but mention it in the hopes of empowering the reader to recognize sources of disagreement and misunderstanding around the concept of optimal designs.

I will henceforth use the word “optimal” to mean “best in the actualist sense” and “maximal” to mean “best in the possibilist sense.” The concept of the adaptive landscape illustrates how a solution can be optimal, a local peak on the landscape, but not maximal, a global peak with respect to fitness. [Define fitness?]

Optimal Designs Are Peaks on the Adaptive Landscape

Darwinism is not a theory of random chance. It is a theory of random mutation plus non-random cumulative natural selection. ... Natural selection ... is a non-random force, pushing towards improvement. ... Every generation has

its Darwinian failures but every individual is descended only from previous generations' successful minorities. ... [T]here can be no going downhill - species can't get worse as a prelude to getting better. – Richard Dawkins, *Climbing Mount Improbable*

Adaptive landscapes (also known as “fitness landscapes”) map genotype or phenotype to reproductive fitness. For any genotype or phenotype, all possible versions can be plotted as points on an adaptive landscape to show how fit each possible version of the phenotype or genotype is. Sewall Wright (1932) described an adaptive landscape as a n -dimensional space where “the entire field of possible gene combinations be graded with respect to adaptive value under a particular set of conditions.” For simplicity's sake, they are often rendered in two dimensions and only with respect to one genotype or phenotype as below:

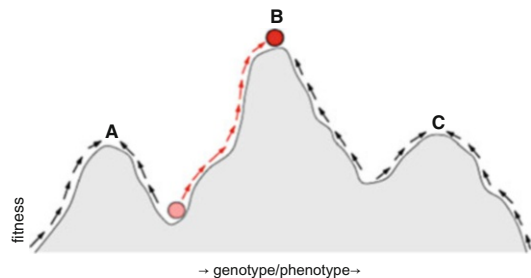


IMAGE adapted from: Public Domain, <https://commons.wikimedia.org/w/index.php?curid=193687>

Here we can clearly see how selection works given its constraints. Natural selection is a hill-climbing algorithm – it can only push a population up toward the nearest peak on the adaptive landscape. Theoretically, adaptive landscapes reflect all the constraints that shape them – the abiotic and biotic environment as well as the organism's other features. The constraints on a feature may be static or shift over time. When the constraints shift, the adaptive landscape reflects that shift, because the map of phenotype or genotype to fitness has changed. Even though it would be impossible to map every constraint, the metaphor of an adaptive landscape is useful because it shows us why only some paths are available for natural selection to climb. Natural selection

cannot tell which peak is highest (maximal); it can only tell which direction is up.

A change in the shape of the landscape does not change natural selection itself, but it can channel the action of natural selection into a new direction by introducing new selection *pressures*. In adaptive landscape terminology, a selection pressure is the incline of the peak. The stronger the selection pressure, the steeper the incline. There is a great deal of room for chance and contingency in traversing an adaptive landscape, particularly in what genetic variation becomes available (i.e., which spots individuals could occupy on the landscape), but chance of this kind is not chance in the action of natural selection. Natural selection is always an optimization algorithm that accumulates chance events, such as beneficial mutations, in a nonrandom way.

Individuals in a population occupy one point on the landscape at any given time, and the population evolves when its position on the landscape changes. Occupying a peak on the fitness landscape means the population has attained a local maximum in fitness, or an optimal design.

Natural Selection Cannot Cross a Fitness Valley

Natural selection increases the proportion of alleles in the population that lead to greater reproductive success. This principle is axiomatic. Therefore, natural selection cannot push a population to cross a valley in the fitness landscape. Populations can get stuck on a local maximum and rendered unable to access higher peaks, because doing so would require passing through generations in which individuals of lower fitness had higher reproductive success than those of higher fitness – which natural selection will not do by definition.

Just because natural selection cannot push a population across a valley doesn't mean it is impossible for populations to move from peak to peak. There are other evolutionary forces, particularly genetic drift, that can move a population across the landscape regardless of the fitness consequences. Wright (1932) referred to this

phenomenon as “shifting balance.” In effect, drift allows a population to sample a larger area of the fitness landscape. Usually, this simply means lower mean fitness in that population, but sometimes a subset of individuals strays far enough away from one peak to “shift the balance” so that natural selection begins to drive it up another peak.

Genetic Drift Gets in the Way of Natural Selection

When genetic drift is strong enough to overcome selection, you get stuck with features that were not chosen for any particular reason but also are within a range of acceptable harm or sub-optimality. Because genetic drift is essentially sampling error, the balance of selection and drift depends on the size of the population. In small populations, drift can be more influential relative to selection because the sampling of alleles with each new generation is less representative of the previous generation than it would be in a larger population. Response to selection is measured in generations, so the longer generation times of large animals like humans put a speed limit on natural selection while also increasing the role of genetic drift. This means that evolution happens very slowly for humans unless a selection pressure is very strong.

Natural selection is the only process that can lead to complex adaptations. Drift can sometimes lead to better designs, but only by accident. Drift cannot preferentially discover high ground on the adaptive landscape the way natural selection can. And since there are many more ways to fail to solve a problem than to solve it, drift is usually a drag on fitness.

What “Optimal” Means

In adaptive landscape terminology, optimal means a local peak. A local peak may also happen to be a global peak, or maximum. When speaking of natural selection, an optimal design can only mean one that achieves a local maximum on the fitness landscape with regard to selection pressures felt probabilistically throughout a lineage's past. There are no absolutely optimal designs.

A design can only be “optimal” with respect to its constraints. If there were no constraints on a design, there would be nothing to judge it by.

What “Optimal” Does Not Mean

Optimal designs are the best available, not the best possible. (Even designs that appear to occupy global maxima could still be made better if not for the physical constraints of our universe.) Nor does optimal mean inevitable or predetermined. How well a design feature performs a given task depends on the solutions available in design space, the genetic variation available to select on, and response to selection, which is not always strong or fast.

Also note that optimal designs may not be recognizably elegant – sometimes a “kluge,” a clumsy but effective design (Marcus 2008), is the optimal solution to a problem given the energy budget or developmental constraints.

Optimal for What Purpose? And for Whom?

The mind is what the brain does. – Marvin Minsky

The whole purpose of our search for a ‘unit of selection’ is to discover a suitable actor to play the leading role in our metaphors of purpose. – Richard Dawkins, *The Extended Phenotype*

The topic of optimal designs is contentious and confused enough when we’re talking about architecture and spandrels. It’s even more confusing to talk about the design of the mind because the mind doesn’t just follow whatever implicit goal natural selection moves it toward. The mind adopts its own goals. Failure to distinguish natural selection’s “goals” from the mind’s volition can make discussing the evolution of the mind nearly impossible.

The brain is the hardware from which the mind arises. Like a computer, the hardware was designed so that the machine could be applied to certain general purpose computations (Pinker 1997). Unlike a computer, the brain evolved by natural selection. When we use our on-board computer, we can adopt instrumental, shorter term

goals than natural selection. Mind and brain evolved so that we could adopt those short term goals, but natural selection cannot dictate what those instrumental goals should be. Is a mind optimal if it follows natural selection’s “goal,” or is it optimal if it does what it, the mind, wants?

Richard Dawkins refers to goals and purposes adopted by minds as “neo-purposes” to distinguish them from the “archeo-purpose” of natural selection (ref: https://www.youtube.com/watch?time_continue=1776&v=mT4EWCrfdUg).

Brains have evolved with various capacities that assist the survival of the genes that made them. Among these evolved capacities is the ability to set up goals, or purposes. [...] The brain is a kind of on-board computer used to control the body’s behavior in ways that are beneficial to the genes that built it. It can perceive the outside world. It remembers things. It learns the consequences of its actions—good and bad. It sets up simulated models in imagination [...] It sets up purposes or goals in the sense of neo-purpose. The capacity to have a mental goal, or neo-purpose, is an adaption with a survival value, or archeo-purpose.

The mind can easily adopt neo-purposes that are at odds with the archeo-purpose of the genes and the blind processes that created it, particularly as it finds itself in environments the genes haven’t “seen” yet through natural selection. Using contraception, for example, allows our brains to satisfy the desire for sex without ever producing the children sexual urges evolved to promote. The misgivings about children that lead us to use contraception have a long history as well – but the recent advent of highly effective birth control methods has changed the adaptive landscape by changing the consequences of these drives (Dawkins 2009). Philosopher Alan Gibbard (1990) points out that the implicit goals of the genes shouldn’t dictate our goals as their vehicles:

It is crucial to distinguish human goals from the Darwinian surrogate of purpose in the “design” of human beings [...] The Darwinian evolutionary surrogate for divine purpose is now seen to be the reproduction of one’s genes. That is not, as far as I know, been anyone’s goal, but the biological world looks as if someone quite resourceful had designed each living thing for that purpose [...] A like conclusion would hold if I knew that I was

created by a deity for some purpose of his: his goal need not be mine.

Our brains are much more optimal for an environment that has disappeared, one in which the desire for sex was enough to ensure the creation of offspring. John Tooby and Leda Cosmides argue that the most productive approach to evolutionary psychology considers the ancestral environment of modern humans, particularly the Paleolithic era during which anatomically modern humans evolved (Barkow et al. 1992). So what is being optimized when there are multiple competing interests at stake?

Game Theory and Evolutionary Stable Strategies

When multiple agents are in conflict, it no longer makes sense to speak of optimal designs because there is no one goal with respect to which the design *can* be optimal. What we get are Nash equilibria or evolutionarily stable strategies (ESS), strategies which are unbeatable by any newly introduced strategy (Maynard Smith 1972). Essentially, a stable design is reached when there is a stalemate among all the conflicting goals. These situations are the province of game theory.

Symbiosis and Parasitism

The same human individual can host a number of different organisms with different goals. Human gut microbes may have a range of psychological effects, including the ability to affect mood (De Palma et al. 2014). Humans may also host parasites that increase their own fitness by manipulating our bodies, such as when the influenza virus causes us to sneeze and spread viral particles. Parasites can also influence their own fitness by manipulating a host's mind, such as when *Toxoplasma gondii* makes mice more aggressive and willing to confront cats, who are the parasite's desired next host. *Toxoplasma gondii* cannot successfully complete its life cycle in humans, but infection with *T. gondii* can nonetheless affect human behavior (Flegr 2007). Here, a parasite employing very well designed host manipulation causes very suboptimal behavior for both intended and unintended hosts.

Intragenomic Conflict

Human genes can only successfully reproduce by making new humans, but that does not mean that all the genes in the human genome share the same goals. The genes within the genome have largely overlapping goals, but the fiercest battles are often fought over scraps. For instance, alleles that are marked as either coming from the mother or the father (imprinted) promote behavior in offspring that benefits that parent-of-origin's reproductive success (Moore and Haig 1991). Where mom and dad's genes disagree, there are evolutionary games.

The brain appears to be a major arena of conflict, judging by the fact that imprinted genes are disproportionately expressed in the brain compared to other tissues (Davies et al. 2005). The contested resource in this case may be how much support offspring can draw from relatives that are asymmetrically related to them at the causal locus. For example, babies with the imprinting disorder Angelmann's syndrome have only the father's imprinting. Angelmann's babies only sleep an hour or two a day and they want a lot of milk. This is very exhausting for the mother, who wants time to rest and recover. In the inverse disorder, Prader-Willi syndrome, which results from having only the mother's imprinting, babies sleep far more than usual and don't often want to breastfeed. There may be no one optimal amount of sleep for the baby – the amount of sleep we need may simply be a compromise between conflicting goals of the mother's genes and the father's genes (Haig 2014).

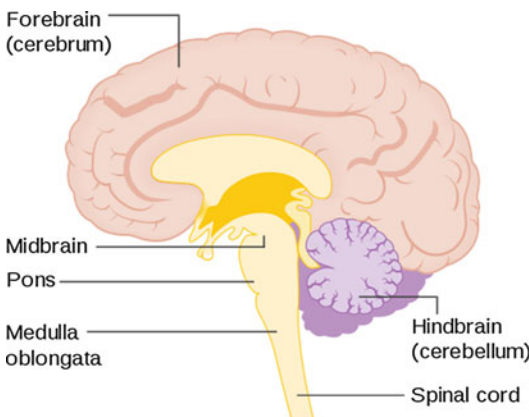
Examples of Optimal Designs and Suboptimal Equilibria in Psychology

The Regions of the Brain: Layers of a Kluge

Evolution often proceeds by piling new systems on top of old ones. The neuroscientist John Allman has captured this idea nicely with an analogy to a power plant he once visited, where at least three layers of technology were in simultaneous use, stacked on top of one another. The recent computer technology operated not directly, but rather by controlling

vacuum tubes (perhaps from the 1940s), which in turn controlled still older pneumatic mechanisms that relied on pressurized gases. If the power plant's engineers could afford the luxury of taking the whole system offline, they would no doubt prefer to start over, getting rid of the older systems altogether. But the continuous need for power precludes such an ambitious redesign. (Marcus 2008)

As Gary Marcus explains in his book *Kluge: the Haphazard Construction of the Human Mind*, a kluge is “a clumsy or inelegant – yet surprisingly effective – solution to a problem.” Marcus compares the construction of the human brain to the power plant control systems described above. The hindbrain is the most ancient part of the brain, shared by all mammals and reptiles, and controls our most basic reflexive functions such as breathing and alertness. The midbrain is involved in visual and auditory reflexes, and the forebrain is responsible for cognition, language, and judgment. Not only are higher functions like language dependent on more basic functions like breathing, higher regions of the brain are inextricably linked to the midbrain and the hindbrain (Bear et al. 2007).



The forebrain sits on top of the midbrain which sits on top of the hindbrain. The structures are arranged in descending order of evolutionary age. https://upload.wikimedia.org/wikipedia/commons/thumb/8/83/Diagram_showing_the_brain_stem_which_includes_the_medulla_oblongata%2C_the_pons_and_the_midbrain_%282%29_CRUK_294.svg/572px-Diagram_showing_the_brain_stem_which_includes_the_medulla_oblongata%2C_the_pons_and_the_midbrain_%282%29_CRUK_294.svg.png

[svg/572px-Diagram_showing_the_brain_stem_which_includes_the_medulla_oblongata%2C_the_pons_and_the_midbrain_%282%29_CRUK_294.svg.png](https://upload.wikimedia.org/wikipedia/commons/thumb/8/83/Diagram_showing_the_brain_stem_which_includes_the_medulla_oblongata%2C_the_pons_and_the_midbrain_%282%29_CRUK_294.svg/572px-Diagram_showing_the_brain_stem_which_includes_the_medulla_oblongata%2C_the_pons_and_the_midbrain_%282%29_CRUK_294.svg.png)

We have no reason to believe our brains are at a global maximum on the adaptive landscape. Ascending layers of updated systems in our brains indicate a history of updates on top of updates while the machine was still running. Evolution was constrained, in this case, by the existing brain's crucial job in survival and reproduction.

Optical Illusions: The Pitfalls of Solving an Impossible Problem

In *How the Mind Works* (Pinker 1997), Steven Pinker explains that from the perspective of light entering our eyes, there are no objects. There is just light of differing wavelengths. The mind processes that information to define objects, “the movable hunks of matter that we count, classify, and label with nouns” in our field of view. But defining objects is a difficult philosophical problem. Where does the nose end and the face begin? When does the head give way to the neck? Many objects lack clear boundaries, but the brain tries to find them all the same. The famous vase-face illusion shows that our brain can flip between entertaining one object (the vase interpretation) to another (the face interpretation) with the same visual information.



The face-vase illusion. <https://commons.wikimedia.org/wiki/File:Rubin2.jpg>

Optical illusions reveal the biases in our sensory processing. When our minds detect an object, that interpretation pops out and excludes others. In the case of the above vase-face illusion, the vase pops out and suddenly the faces are gone until the faces pop out and suddenly the vase is gone. As this illusion demonstrates, determining what it is we are seeing based on light alone is sometimes a hopelessly ambiguous problem, but the fact that optical illusions are reserved as parlor tricks shows a very robust and perhaps optimal mental design for perceiving objects.

Cognitive Biases: Optimized Shortcuts

Human cognition is subject to a long list of biases (https://en.wikipedia.org/wiki/List_of_cognitive_biases). These biases seem like suboptimal thinking because they don't always tell us the truth and occasionally fail to give accurate information. But when we view the purpose of human cognition more holistically, we see that time and processing power are limited, so in many cases shortcuts are the only way to get to an answer at all. Sometimes heuristics are better performers than slow and cumbersome solutions to those problems that aren't important to solve perfectly (Kahneman 2011).

To give a classic example, when the risks of ignoring a predator in the bushes are far greater than the risks of incorrectly interpreting the sound of a breeze as a predator in the bushes, overinterpreting noises can be an optimal solution. When our ancestors heard a sound, their minds jumped to the most emotionally salient possibility: a predator. This is called the availability heuristic – we judge the likelihood of an event by how easily it comes to mind, and emotionally salient things come to mind more easily. This is bad for accuracy, but very good for survival. A few minutes of panic and wasted time are much less costly than failing to avoid a real attack. With more time and resources, our predator detection could be even sharper, but when a heuristic works well enough, spending more resources on improving it would be gilding the lily. Those resources

could be better spent elsewhere if the cost of overreacting is small.

Summary

There is an on-going debate in evolutionary sciences about whether natural selection consistently provides optimal designs. The very idea of optimal designs hits a fault-line in biology and psychology between actualists and possibilists. The definition of optimal itself is disputed and a matter of perspective.

Natural selection can only climb hills on an adaptive landscape, and that landscape represents all the constraints on a feature's design. Genetic drift usually causes features to be suboptimal by overcoming the work of selection, but occasionally opens up the path for natural selection to climb a higher peak.

Optimal means the best design available, not the best design period. There are no absolutely optimal designs – they could always be better if some feature of the environment were better. You could almost say that the most perfect design is nothing, because then there's no problem!

Sometimes designs are not optimal with respect to their function because they are satisfying different and conflicting goals. Sometimes, as with freestanding arches and vision, conflict at one level is itself an optimal design at a higher level of function. Sometimes, as in the case of cognitive biases, a design is optimal even though it sometimes fails to perform its job because it's better to err in the right direction. Sometimes a design is suboptimal because other agents are working to exploit design weaknesses, as in the case of sensory bias.

Finally, it's important to remember that no matter how perfect or imperfect a feature appears to be, it always helps to consider what purpose it might have evolved to serve. What Stephen Jay Gould would call adaptationist thinking is a highly effective source of hypotheses, and sometimes hypotheses become part of evolutionary theory.

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Optimal Foraging Models

- [Currency and Constraint](#)

Optimal Imitation

- [Adaptive Learning](#)

Optimal Learning

- [Adaptive Learning](#)

Optimal Litter Size

- [Optimal Clutch Size](#)

Optimal Skew Theory

- ▶ [Skew Theory](#)

Optimal Versus Stable Group Size

- ▶ [Group Size Optimality and Stability](#)

Optimally Primed Stimulus

- ▶ [Supernormal Stimuli \(Konrad Lorenz\)](#)

Option Attributes

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Oral Sex

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Oral Sex and Human Sexual Behavior

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Definition

Sexual activity in which an individual uses their mouth to stimulate the genitals of a partner.

Introduction

Oral sex has been a prominent feature over human evolution. Oral sex occurs in many cultures, including preindustrial cultures, indicating that cunnilingus is not a culture-specific practice. Oral sex is depicted frequently in pornography, and the content of pornography is designed to appeal to evolved mechanisms (see ▶ [“Pornography as a Human Product and Source of Data”](#)). Oral sex is depicted in ancestral cave paintings. In fact, oral sex also occurs across many mammalian species, including dogs, hamsters, bovine, ring-tailed lemurs, pygmy marmosets, and Indian flying foxes. Thus, evidence suggests an evolutionary history of oral sex not only in humans but also in other mammals. Although we cannot directly

observe the human ancestral ecologies in which oral sex was adaptive, modern environments provide a useful starting point for investigation.

Oral sex is a common sexual activity in modern environments, and people report various reasons for practicing it. Men are equally likely to report their female partner performing oral sex on them (i.e., *fellatio*) and performing oral sex on their female partner (i.e., *cunnilingus*) at their most recent sexual encounter as women are to report performing fellatio and receiving cunnilingus. Most men and women report experiencing oral sex at least once in their life, and both desire to experience oral sex. Some reasons people report for engaging in oral sex include retaining virginity (because oral sex is sometimes not perceived as “real” sex; see ► [“Oral Sex and Sexual Debut”](#)), to increase their sexual reputation, to sexually satisfy their partner, to increase their own arousal, and to avoid the risk of pregnancy and diseases associated with penile-vaginal sex. However, the reasons people consciously report for a behavior, such as oral sex, may differ from that behavior’s evolutionary function.

Functional Hypotheses of Oral Sex in Humans

Several nonmutually exclusive hypotheses for the function of oral sex have been proposed, including: (1) mate retention, (2) infidelity-detection, (3) sperm-competition tactic of ejaculate adjustment, (4) fertility detection, and (5) paternal investment detection. First, oral sex may be performed as part of a benefit-provisioning mate retention strategy by both men and women (see ► [“Oral Sex as Mate Retention”](#)), because oral sex is most commonly performed within long-term relationships, is positively associated with relationship satisfaction, and women who receive cunnilingus are more likely to experience copulatory orgasm which increases their relationship satisfaction. Indeed, men and women’s performance of oral sex is positively associated with the frequency with which they provision their partner with benefits (Pham & Shackelford, 2013a; Sela et al. 2015).

Second, oral sex may function to detect infidelity because smelling and tasting a partner’s genitals may provide information about the presence of a sexual rival’s fluids in that area. Indeed, men at greater risk of a partner’s infidelity report greater interest in, and spend more time, performing cunnilingus on their partner (Pham & Shackelford, 2013b). In contrast, men do not typically perform cunnilingus on a woman during a casual, sexual encounter (i.e., “a one-night stand”), a mating context that presents no risk of a long-term partner’s infidelity. However, the infidelity-detection hypothesis has not been supported for fellatio (Pham, Shackelford, & Sela, 2013). Potential explanations for this sex-difference include asymmetries in the risk of contracting sexually transmitted diseases from fellatio versus cunnilingus and that more of rival male’s fluids are likely to linger on female genitals than female rival’s fluids are to linger on male genitals, influencing the effectiveness of, and motivation to use, oral sex as a means to detect infidelity.

Third, oral sex may function to increase men’s sexual arousal and consequent behaviors designed to increase the likelihood of fertilizing ova. Because men typically perform cunnilingus before they copulate and ejaculate, cunnilingus could influence sexual arousal and consequent sperm competition tactics such as copulatory thrusting and ejaculate adjustment (see ► [“Sperm Competition”](#) and ► [“Sperm Competition Tactics”](#)). Male sexual arousal is positively associated with ejaculate quality and volume. For example, men who report greater sexual arousal report more intense orgasm and more forceful ejaculation (Pham, Shackelford, Welling, Ehrke, Sela, & Goetz). Men experience greater arousal when the reproductive benefits outweigh the non-trivial costs of producing a higher quality, larger volume ejaculate. Men are sensitive to behavioral, visual, auditory, and olfactory cues to female fertility (Haselton and Gildersleeve 2011). Indeed, men who report spending more time performing cunnilingus report greater sexual arousal (Pham, Shackelford, Welling, et al. 2013), and time spent performing cunnilingus positively predicts ejaculate volume (Pham et al. 2016).

Fourth, oral sex (specifically, cunnilingus) may function as a sperm competition tactic to detect women's reproductive health and fertility status. Indirect evidence supporting this idea includes men's preference for smelling vaginal fluids produced during high (vs. low) fertility and men's surge of testosterone and greater copulatory interest after smelling such fluids (see also ► [“Female Orgasm and In-Pair Copulation”](#)). Additionally, common vaginal health problems (e.g., yeast infection) cause unpleasant odors which men could detect. Although both men and women desire to experience oral sex, men report a stronger, more frequent, desire for oral sex than women. This sex-difference is highlighted by the market demand for women's used underwear by men. In contrast, a much lesser demand exists for men's used underwear by women. Many male customers request that women wear underwear for a few days, and even masturbate while wearing them, to increase the amount of female fluids in the underwear before shipping them to the customer in a plastic bag to retain the genital scents. Furthermore, these customers prefer underwear worn by women who are young and attractive (i.e., fertile women). Potentially, men's desire to perform cunnilingus may be related to experiencing sexual arousal as a function of the information they gather about the woman's fertility. This hypothesized function of cunnilingus would be similar to its function in other species in which mucous from female genitals contain pheromones that elicit mounting behaviors in males.

Fifth, oral sex (specifically, fellatio) may function to assess paternal investment. Ancestral and modern mothers benefit from paternal commitment and investment (e.g., long-term resource provisioning, protection, and care for the mother and child by the father), and seem to adaptively respond to the absence of a committed partner, e.g., women are most likely to kill their newborn when they are unpartnered and lack resources – thus, avoiding the costs of raising a child under unfavorable conditions (see ► [“Filicide”](#)). It would have been potentially adaptive for women to spontaneously abort a pregnancy even earlier if they detected the absence of a committed

romantic partner. One way to assess the presence of a committed partner could be frequent exposure to his semen. Oral exposure to semen, compared to vaginal exposure to semen, is less risky (e.g., oral exposure will not lead to a second pregnancy which may jeopardize the first), and there is evidence that women who perform fellatio on their partner – especially those who ingest his semen – experience lower rates of preeclampsia (a leading cause of prenatal infant mortality) (e.g., Koelman et al. 2000).

Limitations and Future Directions

There are limitations of the few studies directly testing some of the functional hypotheses for oral sex. First, some studies relied on self-reports about oral sex and other behaviors. People may underreport the frequency with which they perform socially undesirable behaviors. Future research may benefit from securing data via other methods such as in-lab observations. Further, most studies rely on correlational data and, therefore, cannot determine causality. Future research may benefit from experimental designs with higher internal validity.

Research on the adaptive function of oral sex is in its early stages, and future research is needed to replicate current findings, test some of the hypotheses more directly, and expand this field into other areas of psychological research. For example, past studies have found that the oral sex performance is explained, in part, by individual differences such as men's agreeableness (Pham et al. 2015) and women's conscientiousness (Sela et al. 2015). Additionally, because oral sex is extremely common among other species, further investigation is needed to understand the function of oral sex among species that do not regularly participate in pair-bonding (i.e., mating systems in which mate retention has little adaptive value).

Conclusion

Oral sex is most common in long-term relationships and is linked to relationship satisfaction and

to partner's risk of infidelity. Several nonmutually exclusive functional hypotheses have been proposed and tested for oral sex: mate retention, infidelity-detection, sperm-competition tactic of ejaculate adjustment, fertility detection, and paternal investment detection. Given that each hypothesis has at least some supporting evidence, it is likely that more than one is needed to explain this common sexual behavior in humans. Further experiments are needed before causal statements can be made. The ubiquity of oral sex across cultures and across evolution warrant further investigation into its evolutionary significance.

Cross-References

- [Cunnilingus](#)
- [Fellatio](#)
- [Female Orgasm and In-Pair Copulation](#)
- [Oral Sex and Sexual Debut](#)
- [Oral Sex as Mate Retention](#)

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Oral Sex and Initiation

- [Oral Sex and Sexual Debut](#)

Oral Sex and Sexual Debut

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Synonyms

[Cunnilingus and fellatio](#); [Oral sex and initiation](#); [Sexual initiation](#)

Definition

STI sexually transmitted infection
HIV Human Immunodeficiency Virus

Introduction

Kyle, 16 years old, and Sasha, 17 years old, have been dating for 6 months. They have decided to become more intimate and are planning to have oral sex. Sasha remembers hearing about using

male condoms but doesn't think they need to use anything if she were to receive oral sex.

A few weeks later, Sasha sees her doctor for a check-up. Her doctor asks about whether Sasha has had sex yet. Sasha says no, since she doesn't think oral sex counts. Her doctor reviews types of birth control and encourages Sasha to make an appointment to discuss her options to avoid unintended pregnancy, before becoming sexually active.

Despite oral sex being the most common form of sexual behavior among adolescents, the scenario above is unfortunately very common. While associated with decreased risks of acquiring a sexually transmitted infection (STI) and pregnancy, oral sex is not risk free and can have negative consequences related to health, social, and emotional wellbeing; however, many youth do not understand the risks and don't seek advice or protection. In this chapter, we will review epidemiologic data on oral sex among adolescents and young adults overall and by demographic factors, discuss health and social factors associated with oral sex, and identify reasons why adolescents have oral sex. We end with an important discussion of the importance of health care providers, educators, and parents talking to adolescents and young adults about oral sex.

Rates of Oral Sex, Overall and by Demographic Factors

Based on the most recent data on oral sex, from 2012, 66% of females aged 15–24 years had ever engaged in oral sex with an opposite-sex partner (65% for males). In comparison, 67% of females in this same age group have had vaginal sex. There were variations by sex, with 49% of adolescent males (ages 15–19 years old) having ever had oral sex; 35% had given and 47% had received oral sex. Among adolescent females, 48% reported ever having oral sex with an opposite sex partner; 41% had given oral sex, and 43% had received oral sex. Prevalence of oral sex was higher among young adults (20–24 years old)

with 85% of females and 82% of males reporting having ever had oral sex. In comparison, national data from 2012 show that 47% of female and 44% of male adolescents had ever had vaginal intercourse. Prevalence was higher among young adult females and males (87% and 85%, respectively) (Copen et al. 2012). Similar trends were observed in other datasets (Halpern and Haydon 2012; Herbenick et al. 2010).

A more recent study on adolescent and young adult oral sex patterns found that the percent of females aged 15–24 years who ever engaged in oral sex was lower for both giving (59.6% from 2007 to 2010 compared to 58.6% from 2011 to 2015) and receiving (62.2% to 60.4%). Percentages increased for males for both ever having given (53.9% to 55.4%) and received (62.9% to 64.6%) oral sex. Racial and ethnic minorities were less likely to have given or received oral sex (Holway and Hernandez 2017).

Racial and ethnic variation in prevalence of any oral sex exist among 15–24-year-olds. White females reported ever having engaged in oral sex most often (69%), followed by black females (63%), and then Hispanic females (59%). There were no differences by race or ethnicity among 15–24-year-old males who had ever had oral sex. There were racial/ethnic differences among males who had reported giving oral sex, with white males having engaged most often (60%), followed by Hispanic males (51%) and black males (44%) (Copen et al. 2012).

Is there a relationship between initiation of oral sex and initiation of vaginal sex? The most recent data, from 2007 to 2010, show that 5.1% of females and 6.5% of males aged 15–24 years had oral sex but had not yet had vaginal sex. Of those who had both vaginal and oral sex within this same age group, percentages were nearly identical for females who had oral sex before having vaginal sex as vaginal sex before oral sex (26% and 27%, respectively). There were no differences in percentages reported among males, with 24% of males having oral sex first and 24% reporting having had vaginal sex first. Data from a longitudinal study of adolescents found that

18.3% of males and 11.0% of females reported initiating oral sex first, while 23.6% and 43.3% (males and females respectively) reported initiating vaginal sex first. Engaging in both behaviors within the same year was also common (38.4% among males, 26.6% among females) (Halpern and Haydon 2012). Another longitudinal study showed that adolescents who have had oral sex in the first 2 years of high school were significantly more likely to progress to vaginal sex than adolescents without oral sex experience or those who had oral sex later in their high school tenure (Song and Halpern-Felsher 2011).

How much should we worry about adolescent oral sex behaviors? While those who engage in oral sex avoid the risk of pregnancy, engaging in oral sex is not risk free. Transmission of sexually transmitted infections (STIs) including herpes, human papilloma virus (HPV), human immunodeficiency virus (HIV), gonorrhea, chlamydia, syphilis, and trichomoniasis have all been reported (Ballini et al. 2012; Edwards and Carne 1998; CDC 2017). Because of this risk, health care providers recommend using a barrier method (e.g., condoms or dental dams) when having oral sex.

Given the known health risks associated with oral sex, why do adolescents decide to have oral sex? Explanations of adolescent engagement in oral sex point to several factors, including social and attitudinal factors. These are described next.

One possible explanation for why so many adolescents have oral sex is that they often do not consider oral sex to be sex, and thus do not believe that oral sex confers the same health outcomes as those resulting from vaginal sex. Compared to vaginal sex, adolescents perceive oral sex as significantly less risky with respect to health risks such as STIs including HIV. Adolescents also believe that oral sex is less risky with respect to social and emotional outcomes. For example, adolescents report that having oral sex is less likely to get them into trouble, result in a bad reputation, produce feelings of guilt, or result in them feeling bad about themselves. Moreover, 14% of adolescents believe that there is zero chance of contracting chlamydia from oral sex, and 13%

believe there is zero chance of getting HIV from oral sex. In comparison, 1% perceive zero risk of contracting chlamydia and 2% perceive zero risk of getting HIV from having vaginal sex. Adolescents also believe that oral sex is more prevalent and more acceptable for people of their age, and doesn't impinge on moral or religious values as much as vaginal sex (Halpern-Felsher et al. 2005). Nevertheless, adolescents who indicate that religion is important to them are also less likely to have oral sex (Holway and Hernandez 2017).

A qualitative study of adolescents provided further insight into the reasons why they have oral sex. The main reasons adolescents cited were wanting pleasure, improving their relationship, gaining popularity, bettering their reputation, curiosity and wanting the experience, feeling it is less risky than vaginal sex, and peer pressure. Girls were more likely than boys to indicate personal benefits from having oral sex (e.g., it will improve my relationship, provide pleasure) and social factors (e.g., peer pressure), and to be concerned about fear or being forced to have oral sex (Cornell and Halpern-Felsher 2006). Oral sex is more common among adolescents who are in a committed relationship, which might explain in part why they don't use condoms during oral sex (Holway and Hernandez 2017).

These perceptions and misperceptions about oral sex, and oral compared to vaginal sex, are important given evidence that there is a strong link between perceptions and behavior. Perceptions of positive and beneficial outcomes resulting from oral sex are more likely to influence behavior than the threat of negative health outcomes. Interestingly, data on adolescents' actual reported consequences of having oral sex compared to vaginal sex mirror their perceptions. Adolescents who have had oral sex have indeed experienced fewer health consequences than those having had vaginal sex, including STIs, pregnancy, or HIV. Those with oral sex experience were also less likely to report feeling guilty, having their relationship worsen, or getting into trouble, compared to those with vaginal sex experience (Brady and Halpern-Felsher 2007).

Conclusion

Oral sex is the most common form of sexual behavior among adolescents, with adolescents having oral sex largely to avoid the health risks associated with vaginal sex, while still gaining pleasure and social benefits, such as maintaining or improving relationships. Despite the popularity of oral sex, most research, health messages, and prevention efforts in reproductive health focus predominately on vaginal intercourse including pregnancy and STI prevention. As such, adolescents receive limited education about oral sex, including the possible risk of STIs including HIV. Furthermore, they receive little information about the social and emotional outcomes that can result from engaging in oral sex.

Turning back to Kyle and Sasha, it is imperative that health care providers screen, counsel, and educate adolescents about oral sex specifically, not just sex in general or vaginal sex. Adolescents need anticipatory guidance around oral sex, and the progression from oral to vaginal sex. Further, parents and health educators should include discussions of oral sex when they talk to adolescents about sex, including information and discussion of related health, social, and emotional outcomes. Conversations must also go beyond a discussion of the health risks to also include guidance on how to navigate peers and partners as they make decisions about whether or not to have oral, or vaginal, sex.

Cross-References

- Abstinence
- Adolescent Parenthood
- Casual Sex
- Female Choice and Sexual Conflict Theory
- Human Sexuality
- Opposite-Sex Relationships
- Oral Sex and Human Sexual Behavior
- Oral Sex as Mate Retention
- Penile-Vaginal Sex
- Perceiving Sexual Intent
- Positive Sexual Development
- Predictors of Sexual Debut
- Sex Education In Schools
- Sexual Arousal

- Sexual Behavior
- Sexual Debut
- Sexual Outcomes
- Sex Ratio

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Oral Sex as Mate Retention

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Definition

Sexual activity in which an individual uses their mouth to stimulate the genitals of their long-term partner in an effort to retain that partner.

Introduction

People in long-term relationships perform a diverse array of behaviors, the motivation for which developed over evolutionary history, to minimize the likelihood of their partner's infidelity. Oral sex performed on a long-term partner may be one such behavior, as reviewed below.

Oral Sex as Mate Retention

Humans may have evolved psychological mechanisms that motivate the performance of "mate retention" – behaviors that lessen the risk of partner infidelity and desertion (see *Mate Retention*). Buss (1988) identified 104 acts of mate retention, and these were later grouped into two superordinate "domains": Cost-Inflicting mate retention behaviors and Benefit-Provisioning mate retention behaviors. Behaviors in the Cost-Inflicting domain reduce the risk of partner infidelity by lowering a partner's self-esteem, thereby causing that partner to feel unworthy of the current relationship, but especially of any other potential relationship. In contrast, behaviors in the Benefit-Provisioning domain reduce the risk of partner infidelity by increasing a partner's relationship satisfaction. The evidence that oral sex is a mate retention behavior, in general, and a Benefit-Provisioning behavior, in particular, is reviewed.

Oral sex is a common sexual activity (e.g., Santtila et al. 2008; Vannier and O'Sullivan

2012) that is linked with sexual satisfaction and relationship satisfaction. Men are equally likely to report their female partner performing oral sex on them (i.e., *fellatio*) and performing oral sex on their female partner (i.e., *cunnilingus*) at their most recent sexual encounter as women are to report performing fellatio and receiving cunnilingus (Vannier and O'Sullivan 2012). Most men and women report experiencing oral sex at least once in their life, and both desire to experience oral sex (Santtila et al. 2008). Men (relative to women) desire oral sex more often, and men's (but not women's) relationship satisfaction is positively correlated with their actual frequency of experiencing oral sex (e.g., Santtila et al. 2008). Notably, men's likelihood of orgasm at last copulation does *not* depend on the performance of fellatio, but women are more likely to experience an orgasm if they receive cunnilingus than if they do not receive cunnilingus (Richters et al. 2006), and female orgasm is positively associated with women's relationship satisfaction.

Oral Sex as Benefit-Provisioning Mate Retention

Men may perform cunnilingus as a means of mate retention. Men at greater risk of a partner's infidelity report greater interest in, and spend more time, performing cunnilingus on their partner (Pham and Shackelford 2013b). In contrast, men do not typically perform cunnilingus on a woman during a casual, sexual encounter (i.e. "a one-night stand"), a mating context that presents no risk of long-term partner infidelity. Men who report performing more mate retention behaviors, in general, also report greater interest in, and spend more time, performing cunnilingus on their partner (Pham et al. 2013b).

Men may perform oral sex as a Benefit-Provisioning (as opposed to Cost-Inflicting) mate retention behavior, in particular. Women who receive cunnilingus from their partner, relative to women who do not, report greater relationship satisfaction (e.g., Santtila et al. 2008). Because greater partner relationship satisfaction is an outcome of Benefit-Provisioning mate

retention, Pham and Shackelford (2013a) hypothesized and documented that men perform cunnilingus on their partner as part of a Benefit-Provisioning mate retention strategy. Specifically, men who report performing more frequent Benefit-Provisioning mate retention behaviors, but *not* more frequent Cost-Inflicting mate retention behaviors, also report greater interest in, and spend more time, performing cunnilingus on their partner. In fact, men who report performing more Cost-Inflicting mate retention behaviors also report less interest in performing cunnilingus on their partner.

Similar results have been documented in women. Women, like men, are more likely to engage in oral sex within a committed relationship (vs. casual sexual encounter; Vannier and O'Sullivan 2012), a mating context that would elicit mate retention behavior. Thus, Sela, Pham, Shackelford, and Euler (2015) hypothesized and documented that women who report performing more Benefit-Provisioning mate retention behaviors also report greater interest in, and spend more time, performing fellatio on their partner. However, women's interest in, and time spent, performing fellatio on their partner is not related to women's frequency of *overall* mate retention behaviors.

Limitations and Future Directions

There are limitations of the two main studies that directly test the hypothesis that oral sex is a mate retention behavior (Pham and Shackelford 2013a; Sela, Pham, Shackelford, & Euler, 2015). First, these studies relied on self-reported mate retention behaviors. People may underreport the frequency with which they perform socially undesirable behaviors (e.g., "I told others of my same sex that my partner might have a sexually transmitted disease"). However, both men's and women's self-reports of their mate retention behaviors have been shown to positively correlate with their partner's reports of these behaviors. Nevertheless, future research may benefit from securing reports from both partners. Further, the two main studies rely on

correlational data and, therefore, cannot determine causality.

Another limitation is that both studies explain just a small amount of variance in individuals' reports of their mate retention behaviors and oral sex behaviors. Although these studies have documented relationships between these behaviors in both men and women, they offer only a first step toward identifying a function for oral sex and only within a committed relationship.

Research on oral sex as a mate retention behavior is preliminary, and future research is needed to expand this field into other areas of psychological research. For example, past studies have found that the association between oral sex and mate retention behavior is explained, in part, by individual differences such as men's Agreeableness (Pham et al. 2015) and women's conscientiousness (Sela, Pham, Shackelford, & Zielger-Hill, 2015). Additionally, because oral sex is extremely common among other species, further investigation is needed to understand the function of oral sex among species that do not regularly participate in pair-bonding (i.e., mating systems in which mate retention has little adaptive value).

Conclusion

Preliminary evidence supports the notion that men and women perform oral sex on their partner as part of a Benefit-Provisioning mate retention strategy. Receiving oral sex from a partner is associated with increased satisfaction and thus may lessen the likelihood of partner infidelity or defection. Individual differences may help further explain why some people perform oral sex as part of a Benefit-Provisioning mate retention strategy, and this is one of several promising areas for future investigations.

Cross-References

- [Female Orgasm and In-Pair Copulation](#)
- [Mate Retention](#)
- [Oral Sex and Human Sexual Behavior](#)

- [Oral Sex and Sexual Debut](#)
- [Mate Retention Tactic](#)
- [Use of Mate Retention Strategies](#)
- [Mate Retention Strategies](#)

Acknowledgments This entry is based on Sela, Pham, and Shackelford (2015).

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Ordinal Position

- [Frank Sulloway \(1996\) On Birth Order](#)

Organ of Corti

- [Cochlea](#)

Organising Instruction

- [Instructional Design](#)

Organized

- [Strategic Aggression](#)

Organized-Insecure Attachment

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Definition

Organized-insecure attachment denotes patterns of attachment behavior in relation to the caregiver that are organized but which, in comparison to secure attachment, are inflexible and suboptimal (e.g., lower in quality). The less than optimal organization is seen in a decreased ability to use the caregiver as a secure base to explore the environment from and as a safe haven to return to for comfort and protection when distressed. The insecure-avoidant pattern is particularly characterized by a decreased ability to turn to the caregiver for support when distressed (e.g., as a safe haven), with these children showing avoidant

behaviors such as turning away from and/or ignoring their caregiver in the strange situation procedure (termed a “minimizing strategy”). The insecure-ambivalent/resistant pattern is characterized by a decreased ability to use the caregiver as a reference point for exploration of the environment (e.g., as a secure base), with these children showing high levels of negative affect and wanting comfort from the caregiver together with an inability to be soothed by the contact and rejections of the caregivers’ bids to soothe the child (termed a “maximizing strategy”). Although these patterns are considered insecure, the characteristic behavior in relation to the caregiver following activation of the attachment system is nonetheless predictable and considered functional in the sense that it typically results in maintenance of some level of proximity to the caregivers, hence the term organized-insecure. Organized-insecure attachment is reliably predicted by patterns of caregiving that are insensitive (e.g., rejecting and inconsistent caregiving) but not frightening.

Introduction

John Bowlby, a British psychoanalyst and child psychiatrist (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), was unsatisfied with the explanations of attachment available at the time, which deemed children’s attachments to their caregivers a secondary result of other mechanisms, such as children’s drives and/or feeding (see ► [“Psychodynamic Foundations”](#)). Seeking an alternative explanation for the phenomenon of attachment, Bowlby founded attachment theory by drawing from multiple scientific traditions, most notably ethology, cybernetics, and cognitive theory (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)).

Specifically, Bowlby (1982) argued that humans come into the world endowed with an attachment behavioral system (and attachment behaviors) which function is maintain proximity to caregivers and which was retained through natural selection as it was associated with increased chances of survival against predators and other natural dangers (see ► [“Infant](#)

[Survival”](#)). Thus, children (the weaker, smaller part) form attachment bonds to caregivers (the stronger, wiser part[s]) who are sufficiently available and responding to their signals (not the other way around; see ► [“Offspring–Parent Attachment”](#)).

Bowlby, having to contest the theories of attachment available at the time, and formulate a new, scientifically based explanation for the phenomenon of attachment, devoted a great deal of effort into delineating the normative aspects of attachment. Subsequently, although he believed that there are individual variations in the “quality” of children’s attachment, which he argued were manifested in cognitive affective representations of self and others (e.g., termed “internal working models” [IWMs]; see ► [“Individual Variations in Attachment”](#) and ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#); Bowlby 1982), formed from the history of interactions with the caregivers, he did not get around to systematizing these variations. Lacking an empirical method for examining inter-individual variations in quality of attachment, he instead focused his efforts on the need for a continuously available and responsive caregiver and the negative effects following separations and or loss of caregivers, which were readily observable in the post-world war era (e.g., Bowlby 1982).

Attachment theory therefore owes much to his close collaborator Mary Ainsworth and her colleagues and students, most notably Mary Main, for the subsequent mapping of systematic individual differences in attachment quality and organization (Ainsworth et al. 1978; Main and Solomon 1990). Drawing on Bowlby’s ideas about the interaction between the attachment system and other behavioral systems, most notably the exploratory system and the fear system, Ainsworth devised a semi-structured laboratory observation called the “strange situation procedure” (SSP), which enabled examination of the organization of behavior that children (aged 12–18 months) strike between their attachment needs and those of exploration. That is, the quality of children’s attachments to their caregivers cannot be indexed by any single behavior, but is rather seen in the organization of behavior in relation to

the caregiver (see ► [“Individual Variations in Attachment”](#)).

Ainsworth and her colleagues discovered three organized patterns of attachment. The first pattern, secure attachment, is considered the optimal organization of behavior (e.g., of highest quality) as observed in these children’s ability to use the caregiver as a secure base and a safe haven (see ► [“Secure Attachment”](#) and ► [“Individual Variations in Attachment”](#)). The other two organized patterns of attachment that Ainsworth discovered, which are considered less than optimal, yet organized, are described below (see ► [“Disorganized Attachment and Reactive Attachment Disorder”](#) for children who cannot maintain an organized strategy of attachment behavior and children showing profound difficulties forming attachments).

Insecure-Avoidant Attachment

Behavioral description. Avoidant children show a distinct pattern in the SSP which although viewed as insecure is nonetheless organized (“organized-insecure”). Although initially exploring the play material in the SSP, avoidant children’s play often lacks the complexity shown by secure children, being more stereotypic and shallow. Avoidant children also tend to share their experiences with the caregiver less often than secure children do, show less positive affect in relation to the caregiver, and do not involve their caregiver in play as often as secure children do. That is, avoidant children’s ability to use the caregiver as a secure base from which to explore the environment seems to be impaired.

Upon entry of the stranger, avoidant children are less often seen to retreat to their caregiver for protection and comfort. Avoidant children typically do not protest the separations and typically show only a little or no signaling behaviors such as crying and/or calling for the caregiver during the separations. In the reunion episodes, it is particularly characteristic of avoidant children to avert their gaze from the caregiver and/or turn and move away from the caregiver (e.g., avoidant behaviors). Indeed, they may actively ignore the

caregiver for an extended time, even if the caregiver is trying to gain the child’s attention. Their level of proximity-seeking and contact-maintaining behavior is thus typically low, and although some resistance may be present (particularly if the caregiver insists on interaction), it is not as characteristic as their avoidant behavior. In comparison to secure children, avoidant children do not show the same striking specificity of preference for the caregiver to the stranger.

Predictors of avoidant attachment and developmental correlates. Importantly, the avoidant pattern of behavior in relation to the caregiver in the SSP cannot be explained by stable dispositions such as temperament (Vaughn et al. 2008). Indeed, research examining physiological stress responses in children during and after the SSP has shown that avoidant children are stressed, as measured by galvanic skin response, heart rate, and cortisol level. Yet, they do not show an optimal ability to use their caregiver as a safe haven to return to for comfort when they are distressed. Ainsworth and her colleagues, and the research that subsequently followed (Isabella and Belsky 1991), have shown that avoidant children tend to have caregivers who are less sensitive than caregivers of secure children. Specifically, the caregivers of avoidant children more often “reject” their children’s bids for proximity and comfort when distressed and have difficulties being in close bodily contact with their children (Ainsworth et al. 1978).

Meta-analytical research has found that about 20 % of children in normative samples tend to be avoidant (van IJzendoorn and Sagi 1999). The avoidant pattern is often referred to as a “minimizing strategy,” denoting these children’s limited display of attachment behaviors and affect in relation to the caregivers (Cassidy 1994). However, although regarded as a suboptimal organization of behavior, it is important to note that avoidant children manage to maintain some proximity to their caregivers without risking further rejection and potential abandonment (Main 1981; Simpson and Belsky 2008). The avoidant strategy has, however, been found to constitute a risk factor for maladaptive development, for example, in

the form of higher levels of later behavior problems (see ► [“Effects of Attachment Quality and Organization”](#)) and suboptimal functioning in adult relationships (see ► [“Attachment in Adulthood”](#)).

Ambivalent/Resistant Attachment

Behavioral description. Ainsworth and colleagues (Ainsworth et al. 1978) identified a second pattern of organized-insecure attachment, which they termed ambivalent (or resistant) attachment. These children often have difficulties with exploration in the SSP, and it is not uncommon for them to show negative affect and distress even before the stranger enters the room, demanding attention by and proximity to the caregiver. These children often retreat to the caregiver when the stranger enters and show limited acceptance of interaction with the stranger. Thus, as avoidant children, these children also show an impairment in the ability to use the caregiver as a secure base for exploration. The ambivalent children typically show intense negative affect during the separation episodes and markedly reject the stranger’s efforts to comfort the child.

In the reunion episodes, they often show moderate to high levels of proximity-seeking and contact-maintaining behaviors together with low levels of avoidant behaviors. Their behavior is however particularly characterized by an inability to be soothed by the caregiver’s overtures, in combination with angry behaviors toward the caregiver (resistant behaviors). Such behaviors include temper tantrums, angrily arching the back when in close contact with the caregiver, wanting to be put down just to become more angry if put down and then wanting to be picked up again, batting away toys, etc. Thus, they often signal a desire to the caregiver for comfort, as do secure children, but they are not effective in being comforted by this contact, indicating that their caregiver is insufficient as a safe haven.

Predictors of ambivalent/resistant attachment and developmental correlates. Ainsworth and colleagues, and research that followed, have found that these children tend to have caregivers

who are inconsistent in their sensitivity, sometimes responding sensitively and sometimes not (Ainsworth et al. 1978; Cassidy and Berlin 1994). As for avoidant children, the pattern shown by ambivalent children is thought to be suboptimal yet an organized strategy that results in proximity to the caregiver. This strategy has been described as a “maximizing” strategy (Cassidy 1994). That is, due to the inconsistent responding by the attachment figure, these children may come to heighten the activation of the attachment system to increase the chances that the caregiver will respond should there be danger. Evolutionarily, this may have resulted in increased attention by and proximity to the caregiver, lowering the risk of being exposed to predators and other natural dangers (Main 1981; Simpson and Belsky 2008). Meta-analytical findings have indicated that about 5–10 % percent of children in normative samples are ambivalently attached (van IJzendoorn and Sagi 1999). As for avoidant children, this pattern is also associated with an increased risk for maladaptive development, including higher levels of behavior problems (see ► [“Effects of Attachment Quality and Organization”](#)) and lower functioning in adult relationships (see ► [“Attachment in Adulthood”](#)).

Missing pieces and current research. The significant but lower than expected correlation between sensitivity and attachment found in meta-analytical research (De Wollf and van IJzendoorn 1997) has yielded interest in other dimensions of caregiving besides sensitivity, such as mind-mindedness and reflective functioning (see ► [“Secure Attachment”](#)). Research is also trying to disambiguate the mediating factor (s) between insecure attachment and maladaptive development (see ► [“Effects of Attachment Quality and Organization”](#)). Lastly, research is also examining variations in attachment quality and organization in relation to adult functioning (see ► [“Adult Attachment”](#)).

Conclusion

Organized-insecure attachment denotes suboptimal yet organized patterns of attachment

behavior in relation to the caregiver (e.g., insecure-avoidant attachment, insecure-ambivalent/resistant attachment), wherein children's ability to use the caregiver as a secure base and a safe haven is impaired following insensitive caregiving on behalf of the caregiver. The organized-insecure patterns of attachment were discovered by Ainsworth using Bowlby's ethological approach, theoretically following Bowlby's ideas regarding the workings of the attachment system and its interaction with other behavioral systems.

Cross-References

- ▶ Attachment in Adulthood
- ▶ Disorganized Attachment and Reactive Attachment Disorder
- ▶ Effects of Attachment Quality and Organization
- ▶ Evolutionary Foundations of the Attachment System and Its Functions
- ▶ Individual Variations in Attachment
- ▶ Infant Survival
- ▶ John Bowlby: Pioneer of Attachment Theory
- ▶ Offspring-Parent Attachment
- ▶ Psychodynamic Foundations
- ▶ Secure Attachment

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Organizers

- ▶ Gender Schema Theory

Orgasm

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Synonyms

Climax; Sexual response

Definition

A sexual climax typically experienced as a result of sexual stimulation, accompanied by involuntary muscle contractions and endorphin release.

Introduction

Orgasm is typically experienced as a sexual climax between the plateau and resolution phases of the human sexual response cycle (Masters and Johnson 1966). Whether the stimulation experienced during solitary or paired sexual behavior is induced manually, orally, or through the use of an object, orgasm in men is most reliably achieved through direct penile stimulation and in women through direct clitoral stimulation. Though there exists substantial overlap in the physiological and psychological sequelae of orgasm between the sexes, copulatory orgasm may serve different evolutionary functions in men and women. While men's copulatory orgasm is necessary for reproductive success, it is unclear whether women's copulatory orgasm is an adaptive mate-choice mechanism or a by-product of developmental processes shared with males.

Physiological and Psychological Effects of Orgasm

The physiological changes accompanying orgasm include accelerated heart rate, increased blood pressure, and pelvic muscle contractions (Masters and Johnson 1966). In men, muscle contractions in the penis and anal sphincter are typically accompanied by ejaculation, which function in sperm transfer during copulation. Women experience muscle contractions in the uterus, vagina, and anal sphincter during orgasm, which may by several mechanisms increase sperm retention and facilitate conception (Levin 2011; Lloyd 2005; Puts et al. 2012). These perceptible physiological changes are accompanied by differential patterns of neuronal activation in the orbitofrontal cortex, cerebellum, and paraventricular nucleus (e.g., Georgiadis et al. 2009), the latter of which

modulates the release of oxytocin (OXT), a hormone implicated in human pair-bonding.

It may be because of these similar patterns of neuronal activation that the psychological experience of orgasm is similar for men and women. Written descriptions of orgasmic experiences do not differ significantly between men and women, though recent studies suggest that women may subjectively rate orgasms as more intense than do men. In both sexes, orgasm is described as satisfying and rewarding, which may encourage men and women to engage in behaviors that could result in orgasm and, in the case of copulation, to engage in copulation until orgasm is achieved.

As ejaculation is required for reproductive success in men, the ability to do so during intercourse has likely been under strong selective pressure throughout human evolution. More than 75 % of men report experiencing orgasm during every act of intercourse, and primary anorgasmia (never having experienced orgasm) in men is rare. By contrast, the prevalence of primary anorgasmia in women is much higher, with about 5–10 % of women never having experienced orgasm. Indeed, copulatory orgasm is experienced much less frequently in women than in men, with approximately 25 % of women always and 33 % never experiencing copulatory orgasm (Lloyd 2005).

Orgasm as an Adaptation

It has been suggested that orgasm serves a mate-choice function in women (Smith 1984). Orgasm may facilitate fertilization by high-quality mates by stimulating ejaculation, reinforcing copulation until ejaculation occurs, promoting repeated copulation with the same males, and inducing peristaltic contractions of the uterus and oviducts, which transport sperm toward the ovum (reviewed in Puts et al. 2012; Wheatley and Puts 2015).

Women may be more likely to experience orgasm during copulation with men possessing putative markers of genetic fitness (Smith 1984), such as facial attractiveness, facial masculinity, and low fluctuating asymmetry. Several studies

have found a positive association between these traits and women's frequency of copulatory orgasm, even when controlling for potential confounds such as relationship duration and relationship satisfaction (reviewed in Puts et al. 2012; Wheatley and Puts 2015). Women's frequency of copulatory orgasm may also be positively associated with the major histocompatibility complex (MHC) genetic compatibility of their male sexual partners, in that that conception with MHC-discordant men should produce offspring with strong adaptive immunity. Interestingly, this association was only found when women were in the fertile phase of the menstrual cycle (Garver-Apgar et al. 2006). Thus, there may exist a largely unexplored interaction between women's fertility and markers of men's genetic quality and compatibility in predicting the frequency of women's copulatory orgasm. More generally, women's greater difficulty in achieving orgasm may reflect their overall greater choosiness over sexual partners resulting from their greater investment in offspring (Symons 1979).

Women's copulatory orgasm may also serve a different adaptive purpose by facilitating long-term pair-bonding with men who are caring and would invest in offspring (Hamburg 1978). Some studies have found positive associations between women's frequency of copulatory orgasm and numerous indices of relationship satisfaction. More frequent copulatory orgasm, and concomitantly, more frequent OXT release, may facilitate women's desire to form pair-bonds with men who are perceived as caring, attentive, and investing. However, evidence for this hypothesis is mixed (for reviews, see Lloyd 2005; Puts et al. 2012; Wheatley and Puts 2015).

Orgasm as a By-Product

Alternatively, women's orgasm may be a by-product of developmental processes shared with men and devoid of any adaptive function in women. Prior to the tenth week of gestation, male and female embryos are physically indistinguishable (Hamburg 1978). Sexual differentiation of external reproductive structures begins around

the tenth week of gestation, when a previously undifferentiated structure called the genital tubercle develops into either the penis or the clitoris, both of which contain nerve and erectile tissues involved in sexual response. The presence of these tissues is patently adaptive in men, as they are required for ejaculation and sperm delivery. Such tissues implicated in orgasm in women, however, may not serve any adaptive function, but may remain present due to sexually antagonistic selection (Symons 1979).

Proponents of this by-product hypothesis have argued that if women's copulatory orgasm was under selective pressure and conferred a reproductive advantage, the frequency distribution of women's copulatory orgasm should look similar to that of men's: a distribution with little variability and with the majority of women reporting experiencing orgasm reliably and frequently during copulation. On the one hand, the frequency distribution of women's copulatory orgasm is almost flat and highly variable, suggesting a potential lack of selective pressure on a specific behavioral phenotype (Lloyd 2005). On the other hand, if female orgasm were selected to function in mate choice, then it should be less reliably induced on average compared to orgasm in men and exhibit greater variability due to its contingency on the quality of women's mates (Puts et al. 2012). In addition, because ejaculation is essential for reproduction whereas female orgasm is not, selection should favor the tendency for men to more quickly and easily achieve orgasm compared to women.

Conclusion

Despite the fact that "no other human sexual topic has been the focus of so much speculation and hypothesizing" (Levin 2011), it remains equivocal whether women's copulatory orgasm is an adaptation or simply a developmental by-product. Studies linking copulatory orgasm frequency to markers of relationship quality have necessarily been correlational. Consequently, causal relationships between these variables, as well as the directionality of any relationships,

have not been established. In addition to investigating causality, perhaps through longitudinal studies and path analysis, future work should continue to explore associations between women's copulatory orgasm and other markers of partner's genetic fitness and investment. Additionally, research should examine potential interactions between such markers and women's conception risk within the ovulatory cycle in modulating copulatory orgasm. Finally, future research should continue to investigate whether women's orgasm promotes sperm transport and whether the occurrence of orgasm contributes to the probability that coitus will result in conception during fertile days of the ovulatory cycle.

Cross-References

- [Copulatory Intrasexual Competition](#)
- [Female Choice and Sexual Conflict theory](#)
- [Female Copulatory Orgasm](#)
- [Female Mate Choice](#)
- [Female Orgasm](#)
- [Female Orgasm and In-Pair Copulation](#)
- [Human Sperm Competition](#)
- [Male Qualities and Likelihood of Orgasm](#)
- [Pair-Bonding](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Sexual Arousal](#)
- [Sexual Intercourse](#)

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Orgasm Triggered by Sexual Intercourse

- [Female Copulatory Orgasm](#)

Orgasmic Disorders

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Synonyms

[Anorgasmia](#); [Climax disorder](#); [Delayed ejaculation](#); [Female orgasmic disorder](#); [Inhibited ejaculation](#); [Premature ejaculation](#)

Definition

Difficulty reaching or controlling orgasm by a man or woman. The problem may be characterized by an early, delayed, or absence of orgasm.

Introduction

In both the four-stage model of sexual response first proposed by Masters and Johnson (excitement, plateau, orgasm, resolution) and the three-stage model later adapted by Kaplan (1995) (desire, arousal, orgasm), orgasm represents a reproductive and psycho-behavioral endpoint. In both models, orgasm follows variable periods of intensifying sexual arousal. Both sexes experience intense pleasure throughout the body during orgasm, a phenomenon mediated by brain regions involved with reward and pleasure. Although in men ejaculation nearly always occurs concomitantly with orgasm, women exhibit no comparable external genital response. Women's orgasm is signaled by, among other responses, pelvic and anogenital contractions, typically lasting two to three times longer than men's (Masters and Johnson 1970).

For men, the two most common orgasmic disorders are premature ejaculation (PE; ejaculating shortly after or prior to partner penetration, before the male wishes, and to the point of distress or disruption of his and/or his partner's sexual experiences) and delayed/inhibited ejaculation (IE; difficult or impossible ejaculation and orgasm). Women, by contrast, are characterized by only one orgasmic disorder called female orgasmic disorder (FOD), which is similar to men's IE, as it is characterized by the recurrent difficulty in reaching orgasm after becoming sexually aroused. Each of these disorders is sometimes further categorized as lifelong versus acquired (i.e., after some period of normal function) or situational (in specific circumstances or with a specific partner) versus global (across all circumstances) and may result from a variety of etiologies ranging from biological to psychological or their combination.

Premature Ejaculation

PE is characterized by ejaculation prior to expectation or desire and usually within a minute or two of penetration. Early studies suggested prevalence rates of 20–30%, but more recent studies using

dysfunction-based criteria suggest rates closer to 5–10%. A variety of theories surround the etiology of PE, spanning from physiological and psychological to relational – most likely all are involved, although to different degrees. Contrary to initial suppositions, PE does not appear to be age related (Binik and Hall 2014).

Various physiological or pathophysiological factors may contribute to PE, including a genetic predisposition, an anomalous sympathetic nervous system, a heightened penile sensitivity, medications, or a lower ejaculatory threshold. While all may contribute to PE, no single factor appears most relevant. Rather, an inherent range for ejaculatory latencies exists such that some men are predisposed to ejaculate rapidly after penetration (e.g., within 1–2 min), while others take longer (e.g., 5–10 min), with latency shaped further by contextual factors (e.g., lack of privacy) to better predict the actual timing of ejaculation. Psychological and relationship factors may also play a role in PE, such as social and emotional issues (including anxiety) that contribute to negative and distracting thought patterns during sex that might impair ejaculatory control or difficulties with the partner such as anxiety derived from sexual aversion or lack of interest.

Treatment for PE may involve pharmacological and/or psychosexual strategies, but in either case, as PE is considered a couple's issue, a team approach including the partner is preferred. Pharmacological treatment typically includes daily or on-demand use of low-dose selective serotonergic reuptake inhibitors, similar to antidepressant medications, where discontinuation marks the return of the condition. As an alternative, men could use a condom or apply a local anesthetic (e.g., lidocaine) to their penis, thus attenuating sensory input and increasing the latency to ejaculation. A possible side effect of using local anesthetics includes diminished vaginal sensitivity.

Psychosexual counseling such as cognitive-behavioral techniques (CBT), psychoeducation, and relationship counseling are alternate treatments, with a focus on lowering male sexual arousal and development of greater ejaculatory

control. Depending on the severity of the PE condition, these methods may be used in conjunction with pharmacological approaches. Combined psychosexual counseling with pharmacological treatments may improve overall efficacy, enabling couples to quickly gain sexual confidence while learning various psycho-behavioral techniques (Rowland 2012).

Delayed/Inhibited Ejaculation

Inhibited (IE) or delayed ejaculation refers to a man's persistent delay in or absence of orgasm despite adequate sexual stimulation. Normative data suggest that most men ejaculate within about 5–10 min after penetration, and therefore men who take significantly longer or simply give up due to frustration or fatigue may be considered for an IE diagnosis. The prevalence of this dysfunction is estimated to range from 5 to 15%, with an increasing prevalence associated with age (Laumann et al. 1999; Perelman and Rowland 2008).

A variety of pathophysiological and psychological explanations may account for men experiencing IE. Men who have recently acquired IE after some period of normal ejaculatory function may suffer from a pathophysiological origin such as surgical complication in the pelvic region, neuropathy, or endocrine dysfunction. Although pharmacological treatments have not proven effective in treating IE, should any of the man's ongoing medications interfere with ejaculatory response (and many do), the medication could be altered.

Psychological explanations, more relevant to lifelong IE or IE that has developed over a period of years, tend to focus more on attitudes toward sexuality (e.g., a high degree of religious orthodoxy and sexual guilt), inadequate sexual arousal, and anxiety surrounding sexual performance. For example, some men who masturbate frequently may develop a routine of rapid, stereotypical stimulation that does not replicate

stimulation during intercourse. Other men may worry about their ability to satisfy their partner, leading to distraction from erotic sensations that lead to sufficiently intense arousal for ejaculation.

IE may be particularly frustrating when it interferes with a couple's plan for procreation, yet a team (couple) approach carried out with the guidance of a psychosexual counselor can often alleviate the problem. Depending on its etiology, various treatments can be considered, but autoerotic patterns (e.g., masturbation, use of erotic materials), relationship issues (e.g., the man may no longer find his partner sexually attractive), and quality of the couple's communication about sexual stimulation preferences usually need to be assessed. Understanding relationship factors, such as underlying tension between the couple from fear of pregnancy or unresolved anger/resentment toward the partner, is an important precondition to treatment. In such situations the man may be mentally unable to allow himself to ejaculate, so such issues need resolution before other concerns are addressed.

Most IE treatments have the goal of increasing or reestablishing high levels of arousal and/or decreasing anxiety that may distract from erotic stimulation. For example, a man suffering from lifelong IE (fairly rare) must first learn his arousal and ejaculatory patterns and be comfortable communicating these to his partner. This process may include solo and/or mutual masturbation, exploring sexual fantasies together, and transferring the consequent arousal to situations involving intercourse. If the man has previously been able to reach orgasm or is able to do so during masturbation, treatment will likely focus on masturbatory retraining and underlying relational issues. Where, for example, current masturbatory patterns and/or use of erotic/arousing materials is not well aligned with partnered behaviors during intercourse, the clinician may recommend discontinuation or alteration in masturbation patterns in order to increase arousal during intercourse. Because such strategies often focus heavily on

providing and sustaining the man's arousal, the partner may sometimes feel that her/his needs are being neglected, but she/he can be counseled that the situation is a temporary strategy to improve sexual satisfaction for both of them. In addition to increasing the man's arousal, focus on anxiety and distraction reduction that typically interfere with arousal typically occurs throughout the treatment process.

Female Orgasmic Disorder

Female orgasmic disorder (FOD) is defined as a woman's difficulty or inability to reach orgasm following adequate sexual arousal. For this diagnosis, the woman must be bothered by the condition, and the inability must be abnormal for the woman's age, sexual experience, and adequacy of stimulation. Regarding this last criterion, as many women who have difficulty reaching orgasm are insufficiently sexually aroused, such women are generally regarded as having an arousal phase issue rather than an orgasm problem. FOD is thought to be the second most frequent female sexual dysfunction, estimated to affect 10–35% of women. Yet only about half of these women report concomitant concern about their condition (Meana 2012).

As with the men's orgasmic phase disorders, a myriad of possible etiologies exists for FOD. Importantly, no easily identifiable cause or causes can be invoked to explain the disorder. However, in contrast with men's sexual disorders, psychological and relationship factors tend to predominate, although biological and pathophysiological factors should not be discounted. Endocrine levels, medical conditions, medications, and surgical side effects all have the potential to affect women's overall health, their general sexual functioning, and the ability to reach orgasm. For example, extreme variation in testosterone levels (very high or very low), menopause status, orgasm-inhibiting medications (e.g., antidepressants), surgical interventions, and various illnesses can

affect women's sexual function. Furthermore, such physical conditions may impart psychological effects on mood, anxiety, and self-concept, all of which may reduce sexual interest, engagement, and the potential for sexual arousal. Such straightforward relationships between psychological issues and sexual functioning can often be identified through clinical investigation. Aging is another biological factor likely to affect sexual and orgasmic response in women, more through sociocultural expectation than the aging process itself. As menopausal changes occur, an agist view deems her reproductively spent, a view that impacts self-esteem, confidence, and a sense of self-efficacy, all of which are important to a sexually satisfying relationship. As with men with IE, no pharmacological treatments are available for FOD. However, if a medication is suspected of inhibiting orgasm, a substitute may be considered.

Aside from biomedical etiologies, a vast number of psychological factors have the potential to impact women's sexual arousal and orgasmic response, some already mentioned above. For example, a woman's self-concept, self-image, and response to general life stressors may affect her sexual functioning, distracting her focus from the erotic stimulation of the sexual experience. Socioculturally derived negative attitudes toward sexuality, depression, and anxiety – whether from sex-specific factors during sex (e.g., pain or discomfort during intercourse) or from broader life challenges – may inhibit women's sexual desire/interest and/or distract them from otherwise pleasurable stimulation during intercourse. Important to most women's sexual engagement and response is the quality of their relationship with their partner – whether they feel comfortable, desired, and a sense of emotional intimacy with him/her. Underlying tension in the relationship and/or feelings of anger toward the partner often act as strong inhibitors of arousal and orgasmic response. Overall, women may attribute their difficulty to a variety of etiologies. These attributions may be complex and sometimes vague, but they often provide an important starting point for treatment.

Psychosexual counseling is usually the most effective treatment for FOD. Clinicians typically use a combination of education, communication improvement, and cognitive-behavioral therapy (CBT), methods that enable the woman to learn more about bodily sensations and pleasure, to reduce anxiety, and to communicate effectively and comfortably with her partner. Effective methods for reducing anxiety – often an important first step – include a progression from pleasurable nonsexual touching to sexual intercourse (sensitive focus) or relaxation techniques to work through a hierarchy of anxiety-provoking sexual situations (systematic desensitization). In contrast, directed masturbation training is typically intended to increase sexual arousal by helping the woman identify her pleasure points. Initially done as an exploratory solo exercise, once able to reach an orgasm, the woman communicates with and assists her partner regarding effective ways to maximize arousal. Kegel exercises – the repeated 3-sec tensing and relaxing of the muscles used to stop urinating – can sometimes facilitate movement toward arousal and orgasm in women and so may be considered in conjunction with any of these methods.

Conclusion

Etiology of orgasmic problems may be different for men and women, but for each sex, a mix of physiological, psychological, and relationship factors are implicated. Psychosexual therapy approaches can be effective in ameliorating the condition, sometimes in conjunction with pharmacological treatment.

Cross-References

- [Cunnilingus](#)
- [Fellatio](#)
- [Female Orgasm and In-Pair Copulation](#)
- [Sexual Infidelity Versus Emotional Infidelity](#)
- [Victims of Violence](#)

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Orientation

- [Sexual Orientation](#)

Oriented Smell

- [Directional Smell](#)

Origin of Language

- [Bow-Wow](#)
- [Ding-Dong](#)
- [Early Theories of Language](#)
- [Müller's Language Hypotheses](#)
- [Spontaneous Language](#)
- [Yo-he-ho](#)

Origin of Species

- [Darwin on Speciation](#)

Origins of Patriarchy

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Synonyms

Male dominance; Patriarchy; Sexism; Sexual coercion; Sexual control

Definition

Explanatory hypotheses based on evolutionary theories on the process of submission of women with a view to the control of female sexuality and reproduction.

Introduction

Because of the different reproductive strategies (and biological configurations) of males and females, females would be more selective and therefore a rare resource in society, and males would face greater intrasexual competition. This scenario would be the basis of the male motivation to control female sexuality, and it is called patriarchy (Smuts 1992, 1995). Female sexuality coercion strategies involve various forms of violence such as physical assault, rape, threats, and other forms of intimidation that result in the creation of hierarchical cultures based on male domination (Appel 2016; Smuts 1992).

The biologist Barbara Smuts (1995) proposes, based on the integration of primatology findings, six hypotheses that would describe which cultural practices would be at the base of the patriarchal social organizations: (1) reduction of the females' ability to form alliances; (2) strengthening of

alliances between males; (3) male monopoly of resources; (4) inequality of resources between males; (5) female engagement in behaviors of submission to the control of their sexuality; and (6) use of language for the propagation of ideologies.

Mechanisms of Control of Female Sexuality

One of the common features of patriarchal societies is the limitation of females' ability to form alliances with other females or to maintain ties with their relatives. It is very common, for example, that when entering adolescence, females of nonhuman primates leave their group and become part of neighboring groups (Smuts 1995). Among humans, women leave their community and move into their husband's group. This isolation of the female favors the occurrence of sexual coercion, with the male forcing the female into intercourse and controlling the female's movements. In many species of primates, females are more frequently assaulted during their fertile period by males seeking intercourse (Smuts and Smuts 1993) or even by their own partner, in case she is very close to another male of the group during the fertile period (Kummer 1968). In social organizations in which females remain with their original troop and maintain alliances with relatives, such as in groups of *Rhesus* monkeys, Old World Monkeys, and Olive Baboons, or in groups in which there is an alliance between females, as among bonobos, there is a low frequency of male aggression and sexual coercion. Among humans, there is plenty of evidence that single women or those attempting to subvert this system end up becoming easier targets of violence and punishment (Appel 2016).

The formation of alliances between males is another important element in the constitution of the patriarchal organization. These alliances would have a dual function. Within the group itself, they can be used to coerce females and are more powerful than lone males. In the relationship between groups, they have the function of facing threats from other groups, which increases the

protection of the group and the status of the male in his group (Smuts 1995). Females of nonhuman primates copulate with males that kill their offspring because it is likely to be a male with a high status, which increases the chances that their baby will not perish (Watts 1989).

The advent of agriculture and husbandry is another important event for the exercise of control over females, as it had the effect of allowing the accumulation of goods and resources. Male monopolization of these resources forces females to submit to males to obtain means of survival and to compete for partners with more resources.

The male monopoly of resources is not enough to ensure the status of males. There must be inequality in the amount of resources monopolized by each male so that the "richest" can excel in sexual selection. Considering that the generations maintain these inequalities, females gradually became more vulnerable in relation to a small group of powerful males. If the more "peripheral" men cannot oppose the power of the more dominant, women also reduce the possibilities of establishing reciprocal and advantageous alliances with those men (Smuts 1995). Friendly relationships with more peripheral or younger males are advantageous for females as they may reduce the vulnerability or harassment received from males, as observed in baboons (Smuts 1985, 1995). Among these primates, females perform several activities with one or two males (such as feeding and hygiene), and in return, they receive protection for themselves and their offspring. This scheme is hampered if there is too much inequality among males, since the fighting or protective power that peripheral males could offer gradually gets smaller. In societies such as human society, this power could be illustrated by money or control of resources such as land, water, or food.

Patriarchal structures are not just products of male behavior. Some female reproductive strategies reinforce patriarchy. When isolated and dispossessed of resources, there is increased competition among females; preference for powerful male in resources; and preference towards male descendants (Smuts 1995). Dickemann (1979) points that behaviors that increase the control of males and the

certainty of paternity over the woman favor the obtaining of rich partners. These behaviors can range from imprisonment to genital mutilation (infibulation) and are often supported by women to obtain compensatory benefits. Chigbu (2019) noted that women in peri-rural communities in Nigeria exhibit behaviors that hinder women's access to land tenure. When they inherit land, these women often transfer ownership or management to their siblings, which is seen as a way to please them, but they do not do the same with sisters. Moreover, when women express an interest in buying land for themselves, they are intimidated and embarrassed by other women to pass on possession of the land bought to their siblings.

Lastly, the evolution of language allows the establishment of an ideological field of domination that reinforces previous structures (Smuts 1995). Through it, different beliefs that reinforce men's control over women are propagated, strengthening the maintenance of patriarchal practices. The belief that many societies have that men can physically punish females for adultery or that women who are alone invite harassment are examples of these ideologies. These mechanisms seem to contribute to the maintenance of female behaviors that can reinforce patriarchy and to alliances and agreements for male domination over women (Smuts 1992).

Conclusion

Patriarchy can be considered the product of a set of proximal contingencies related intimately to the advent of agriculture and husbandry, whose purpose is to control female sexuality and reproduction with a view to increasing male fitness. The variety of human organizations and evidence of primate social behavior make it possible to assert that although patriarchy is widespread among known social organizations, it is not inevitable, but rather the fruit of these proximal selection contingencies that may vary across cultures and throughout history. Evolutionary theory may contribute to enriching discussions of power relations in feminist theses on gender inequity, since these theses also consider power relations and the

control of female sexuality as bases of the patriarchal structure (Smuts 1995).

Cross-References

- [Coercive Control](#)
- [Contexts for Men's Aggression Against Women](#)
- [Men's Violence Against Female Partners: The Role of Culture](#)
- [Sexism](#)
- [Sexual Coercion](#)
- [Violence to Control Women's Sexuality](#)

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Ornamentation

- [Human Ornamentation](#)

Orrorin

- [Ardipithecus Group](#)

Orrorin tugenensis

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Definition

Orrorin tugenensis is the species name given in 2001 to fossils, from sites about six million years old in Tugen Hills in Kenya, that are thought to represent one of the very earliest members of the human lineage.

Introduction

At the turn of the millennium in 2000, a team led by French paleoanthropologists Brigitte Senut and Martin Pickford discovered a dozen fossil bones and jaw fragments of a previously unknown species in the Tugen Hills in central Kenya. The bones and teeth showed a combination of human and ape features not seen in any other species, leading them to name a new genus and species, *Orrorin tugenensis* (Senut et al. 2001). The name *Orrorin* means “original man” in the Tugen language, and Senut et al. noted that the pronunciation resembles the French word *aurore* meaning “dawn, daybreak,” both referring to the idea that this species lies at or near the beginning of the human family tree. The specific name *tugenensis* refers to the Tugen Hills where the fossils were discovered. Because it was discovered in 2000, it was nicknamed “Millennium Man” but this name is no longer widely used. At present, this is the only species placed in the genus *Orrorin*.

O. tugenensis remains one of two species (the other being *Sahelanthropus tchadensis*) that may be the oldest known species in the human family

tree (or “hominin,” the group describing all species that are more closely related to modern humans than to any other living species). Since its initial discovery, only a handful of additional fossils have been recovered, and more fieldwork is needed to expand what is known about this important species.

Sites: The fossils attributed to *O. tugenensis* came from four different sites in the Lukeino Formation, a geological formation spanning a time period from about 5.7–6.1 Ma (million years ago) (Pickford and Senut 2001). Most of the fossils were found at a site called Kapsomin; three other sites (Cheboit, Kapcheberek, and Aragai) each yielded one specimen attributed to *O. tugenensis*.

Key fossils: Every species has a “holotype” that represents the physical individual(s) on which the species name and definition are based. The holotype of *O. tugenensis* is specimen BAR 1000'00, consisting of left and right pieces of a mandible (lower jaw) preserving the back molars, or cheek teeth. Other fossils that are important to understanding the biology and behavior of *O. tugenensis* include BAR 1425'00, a right upper canine tooth; BAR1002'00, the top half of a femur (thigh bone; Fig. 1); BAR 1004'00, the lower portion of a right humerus (arm bone); BAR 349'00, a proximal phalanx (finger bone); and BAR 1901'01, a pollical distal phalanx (thumb tip bone).

Characteristic anatomy: Senut et al. (2001) make the case that *O. tugenensis* is distinct enough from other known hominins to justify the creation of a new genus and species name. The cheek teeth of *O. tugenensis* are smaller and less elongated than those of *Australopithecus* and have thicker enamel than those of *Ardipithecus*. The femur has a large head, long neck, and wide shaft similar to other hominins, but also shares primitive features with fossil Miocene apes (Sergio Almécija et al. 2013; Richmond and Jungers 2008). Its body size was similar to the size of a small chimpanzee (Grabowski et al. 2015).

Behavior: The anatomy of *O. tugenensis* sheds light on its biology and behavior. The low, rounded cusps on the cheek teeth suggest that,

***Orrorin tugenensis*,**

Fig. 1 Back view of BAR1002'00, the top half of a femur (thigh bone) belonging to *Orrorin tugenensis*. The long, narrow neck, large head, wide shaft, groove (for the *obturator externus* muscle) along the neck, and line (proto-*linea aspera*) on the back of the shaft are features related to upright, two-legged stance and linked to the human family tree



like other higher primates with similar tooth structure, *Orrorin*'s diet included fruit, nuts, seeds, leaves, insects, and occasional small animals. Its thicker enamel suggests that it was equipped to handle harder foods than those in the typical diets of most modern apes and monkeys.

O. tugenensis climbed trees but shows signs of walking upright on the ground more intensively than any living ape. Evidence for tree climbing comes from its humerus (arm) anatomy and curved finger bones (Richmond and Jungers 2008; Senut et al. 2001). Scholars agree that upright bipedalism (on two legs) was an important part of its posture and movement patterns, but it remains unknown exactly how well it was adapted to bipedalism. The thigh bone has a long, narrow neck, wide shaft, groove (for the *obturator externus* muscle) along the neck, line (proto-*linea aspera*) on the back of the shaft (Fig. 1), and aspects of internal bone anatomy; these point to similarities in function shared with later hominins such as *Australopithecus*, but some features are more ape-like (Sergio Almécija

et al. 2013; Galik et al. 2004; Richmond and Jungers 2008). A more complete picture of its bipedal behavior and adaptation is limited by the lack of evidence about other parts of its anatomy.

Surprisingly, the thumb tip bone (distal phalanx) appears more like a modern human thumb than the thumbs of *Australopithecus* that lived millions of years later in time (S. Almécija et al. 2010). At 6 Ma, *O. tugenensis* appeared to have better precision grasping capabilities than seen in any living ape and suggests that manual dexterity played an important role in the lives of the earliest hominins.

Clues about social behavior come from the canine teeth. In most higher primates, the upper canine teeth are long, sharpen against the lower teeth, and are used to communicate aggression and occasionally to fight, especially in male-male competition over social rank and access to females. *O. tugenensis*, like all later hominins, has a small canine that lacks a wear facet (Senut et al. 2001), showing that it was not “sharpened” against the lower teeth and probably not used, at least to the degree in most higher primates, in competitive social settings. There are many hypotheses regarding why, when, and how these social strategies changed during human evolution.

Conclusion

O. tugenensis has several important implications for our understanding of human origins, although these remain tentative until a more thorough body of fossil evidence is found. First, it suggests that the last common ancestor of humans and chimpanzees split into their separate lineages earlier than 6 Ma, consistent with other evidence from the fossil record and some studies of the genetic differences between humans and chimpanzees (Pozzi et al. 2014). Second, it supports Charles Darwin’s speculation that the human lineage began in Africa (Darwin 1871); in Darwin’s time, there was no known early human or African ape fossil record, so this idea was based on the observations that anatomy suggests a close relationship between humans and African apes and that Africa is the only place that humans,

chimpanzees, and gorillas inhabit today. However, this does not preclude the possibility that Eurasia was home to earlier ancestors of African apes and humans, where a diverse group of great apes lived in the Miocene and could have expanded into Africa during times when the connections between Africa and Eurasia were much more extensive than they are today. Finally, *O. tugenensis* shows that, at about 6 Ma, the earliest members of the human lineage had very few of the characteristics that make humans distinctive. Among them are features of the thigh bones related to upright posture and walking, canine teeth that are smaller and not sharpened against the lower teeth, thickly enameled teeth capable of resisting demanding foods, and a thumb capable of advanced precision handling. These fossils suggest that, at its earliest stages, the human lineage was set apart from our African ape ancestors by an increase in the importance of upright posture and walking as well as manual dexterity, possibly a shift in diet including harder or tougher foods, and a change in social strategy in which canine teeth were not used for social competition in the manner seen in other higher primates.

Cross-References

- [Ardipithecus Group](#)
- [Australopithecus Group](#)
- [Great Apes](#)
- [Male-Male Competition](#)
- [Sexual Dimorphism](#)

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Ostensive Communication

- [Understanding Human Points](#)

Ostentatious Consumption

- [Conspicuous Consumption](#)
- [Conspicuous Consumption \(Marketing and Economics\)](#)

Ostracism

- [Avoiding Stigmatization](#)
- [Peer Rejection, Gender Differences in Response to](#)

Othello Jealousy

- [Sex Differences in Morbid Jealousy](#)

Othello Syndrome

- [Jealousy: Psychiatric Diagnosis](#)

Other Children

- [Peers](#)

Other-Focused Emotions

- [Moral Emotions](#)

Otolith

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Synonyms

[Otolithic membrane](#); [Otolithic organs](#)

Definition

Small calcium carbonate particles that compose the otolithic membrane.

Introduction

The otoliths are small calcium carbonate particles that make up the otolithic membrane, which accommodates the utricle and the saccule inside the vestibule (Chang and Khana 2013; Seikel et al.

2010). Their function contribute to balance and motion (Clarke et al. 2003).

The Sacculle

The otolithic membrane covers the utricular macula which is a sensory organ endowed of hair cells and cilia (Seikel et al. 2010). The sacculle has a globular-shaped sac which is located near the scala vestibuli in the vestibule (Lee et al. 2016). It is connected anteriorly to the cochlear duct by the ductus reuniens and posteriorly to the endolymphatic duct through the utriculosaccular duct (Lee et al. 2016). The sacculle is connected with the cochlea through the miniscule ductus reuniens (Seikel et al. 2010).

The Utricle

The utricle is larger than the sacculle, and is located posterosuperiorly to the sacculle in the elliptical recess of the medial wall of the vestibule. It is connected anteriorly through the utriculosaccular duct to the endolymphatic duct. The three semicircular canals are opened into it through five openings. The posterior and the superior semicircular canals have a single opening at the crus commune. The macula of the utricle lies in the horizontal plane and located in the utricular recess, which is the anterior part of the utricle (Lee et al. 2016).

Both the sacculle and utricle are connected through the endolymphatic duct, which is implanted in the dura mater. Since otoliths are denser than endolymph, gravitational forces help to deflect the stereocilia of the hair cells when the head is not moving (Hain and Helminsky 2007). The linear motion or the tilting of the head creates inertial drag and cropping force between the otolithic membrane and the macular surface, having as a result the bending of the hair cells (Oghalai and Brownell 2012) which helps to keep a person balanced while moving or staying constant. In other words, the sacculle senses up and down movement and the utricle

senses forward and backward movement, left and right movement, or a combination of the two (Lee et al. 2016).

Functions of the Otoliths

The functions of the otolith organs vary. Clarke et al. (2003) have listed in their study a list with citations of researchers who have studied the functions of the otoliths. Firstly, they state that the otolith signals have a vestibulo-ocular function. Specifically, there is an ocular counterrolling when the head tilts; a linear vestibulo-ocular reflex (to stabilize the images in the eyes while the head moves) during the translation of the otolithic signals; a dynamic ocular-counterrolling; inertial processing of vestibulo-ocular signals; vergence control during linear movements; and a modulation of velocity storage that leads to interaction between the semicircular canals and the otolith organs.

Secondly, the otolithic organs serve a vestibulo-spinal function. Specifically, they help to the maintenance of postural tonus, and there is a vestibulo-spinal readaptation after spaceflight (Clarke et al. 2003).

Thirdly, the otolithic organs serve a vestibulo-autonomic function. Specifically, they help with vestibular autonomic regulation, post-spaceflight orthostatic intolerance, and vestibular control of the sympathetic activity (Clarke et al. 2003).

Fourthly, the otoliths serve a gravitational function, where they help with oculogravic illusion and determination of subjective vertical and horizontal axis. They, also, serve to the perception of spatial orientation and the cognitive aspects of it (Clarke et al. 2003).

Conclusion

Otoliths are the small calcium carbonate particles that compose the otolithic membrane. They are known as the sacculle and utricle, and they serve a

variety of functions that help with balance and posture.

Cross-References

► [Otolithic Membrane](#)

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Otolithic Membrane

► [Otolith](#)

Otolithic Organs

► [Otolith](#)

Outcomes of Homophobic Abuse

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Synonyms

[Homophobic bullying](#)

Definition

The harmful effects that are caused by the victimization of sexual minorities.

Introduction

Lesbian, gay, bisexual, and transgendered (LGBT) individuals are often the victims of abuse because of their sexual orientation. Victims of homophobic abuse may suffer several negative psychological outcomes, including difficulty maintaining scholastic achievement, drug abuse, depression, and suicidal thoughts and behaviors (Birkett et al. 2009; Poteat et al. 2011). These negative effects stem from a wide array of consequences, including fear of physical abuse, social stigmatization and exclusion, decreased school attendance and performance, and negative attitudes toward peers and schools.

Outcomes of Homophobic Abuse

Research has shown that LGBT high school students experience high levels of harassment from their heterosexual peers, which leads to truancy levels that are significantly higher than average (Birkett et al. 2014). In fact, the Massachusetts Department of Education (2004) found that LGBT students are over four times more likely than heterosexual

students to skip school because they feel unsafe. One study found that 40% of LGBT high school students had problems with truancy because they feared abuse at school (Elias et al. 1992).

This decrease in school attendance leads to decreased academic performance. Studies have shown that 80% of LGBT students display a steady decline in academic performance compared to their heterosexual peers, and 30% of LGBT students drop out of school altogether (Elias et al. 1992). LGBT students are also more likely to have lower GPAs, as well as greater negative attitudes toward school, than their heterosexual peers (Russell et al. 2001).

Not only does homophobic bullying decrease school attendance, but it also increases feelings of social exclusion (Poteat et al. 2011). LGBT students who are bullied often feel different from their peers, alone, and ostracized. These feelings are correlated with drug abuse, depression, and suicidal ideation (Poteat et al. 2011).

Possibly as a means of coping with the stress produced by being the victim of homophobic abuse, LGBT adolescents who experience homophobic bullying are significantly more likely to abuse marijuana and alcohol (Birkett et al. 2009). This increased usage of marijuana and alcohol among LGBT adolescents has been consistently documented across more than 20 peer-reviewed studies (Birkett et al. 2009; Marshal et al. 2008; Poteat et al. 2011).

Increased rates of depression have also been consistently documented within the LGBT community (Poteat et al. 2011). One study found that 41% of young LGBT males and 28% of young LGBT females indicate troublingly high levels of depression (D'Augelli and Hershberger 1993). LGBT individuals also possess significantly higher rates of suicidal thoughts and behaviors than heterosexual individuals. For instance, one study found that 60% of LGBT individuals had contemplated suicide (Hershberger and D'Augelli 1995). This increased risk of suicide has been found to be heavily influenced by homophobic bullying (Birkett et al. 2009; Poteat et al. 2011).

Conclusion

Although homophobic bullying produces a wide array of harmful outcomes for LGBT individuals, these effects are strongly mitigated by a positive school climate. If schools have preventative measures in place to decrease or eliminate homophobic bullying, the negative outcomes significantly decrease (Russell et al. 2001). In fact, in positive and supportive school environments, LGBT individuals' rates of truancy, drug abuse, depression, and suicidal thoughts and behaviors were at the same low level as their heterosexual peers (Birkett et al. 2009). Thus, providing an environment of acceptance for LGBT students in schools would likely dramatically decrease homophobic bullying and significantly improve LGBT students' quality of life as well as their future.

Cross-References

- [Cyberbullying](#)
- [Homophobic bullying](#)
- [Procedures for dealing with bullies](#)
- [School bullying](#)

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Outer (External) Ear

► Auditory System, The

Outer Ear, The

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Synonyms

External ear

Definition

The outer ear is responsible to capture sound in the environment.

Introduction

The outer parts of the ear are responsible for capturing sounds from the environment and transmitting them to the latter parts of the ear for further processing. The outer ear consists of the

pinna (auricle) and the ear canal (external auditory meatus).

The Pinna

The outer ear, otherwise called external ear, is consisted of the pinna, otherwise called the auricle (see Moller 2013; Seikel et al. 2010), the ear canal, otherwise called external auditory meatus, and the ear drum, which is the lateral portion of the tympanic membrane (Pickles 2012; Munir and Clarke 2013).

The pinna's main function is to collect sound to direct it to the area of the cochlea where the sound is further analyzed and processed. The pinna has many important functions, such as helping with the localization of sound in the environment (Seikel et al. 2010).

The Ear Canal

The sound arrives there through the ear canal (Seikel et al. 2010; Moller 2013). The ear canal has a length of roughly 2.5 cm and a diameter of roughly 0.6 cm, although its shape is enlarged over time – especially in men (Moller 2013). It is also covered by skin that secretes wax (cerumen) and has hairs on its surface. In the ear canal there are no sweat glands. There are two types of cells that help in the secretion of ear wax and are called sebaceous cells which are located close to the hair follicles and ceruminous glands. The wax has a minor antibacterial and antifungal function, and it can serve as an insect repellent (Moller 2013). However, if the wax is accumulated in the ear canal, it could lead to a hearing impairment, and if it covers the tympanic membrane, it could lead to a loss of hearing (Moller 2013).

Additionally, the outer layer of the skin (epidermis) in the ear canal together with the outer layer of the tympanic membrane migrates outwards, having as a result the healing of small injuries and the movement of cerumen. Failure of

this migration may cause inflammation of the ear canal (Moller 2013).

Furthermore, the skin of the ear canal is supplied with a variety of nerves. These are the sensory portion of the mandibular division of the trigeminal nerve, the facial nerve, the glossopharyngeal nerve, and the auricular branch of the vagus nerve which covers the posterior wall of the ear canal and the tympanic membrane (Moller 2013). These nerves explain why stimulation of the ear canal could affect heart rate, blood circulation, and fainting – especially in cases where the ear canal needed to be cleaned from wax (Moller 2013).

Furthermore, the ear drum forms a boundary between the outer and the middle ear, thus forming the beginning of the middle ear. The ear drum is divided into three bones called ossicles: the hammer, the anvil, and the stirrup (Balkany and Brown 2017).

Conclusion

The outer ear consists of the pinna, which serves as a sound collector, and the ear canal – or external auditory meatus. These structures contribute to capture the sound in the environment and transfer it to the deeper levels of the ear for processing.

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Out-Group

► Out-Group Members

Outgroup Derogation

► Prejudice

Out-Group Members

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Synonyms

[In-group](#); [Intergroup conflict](#); [Out-group](#); [Prejudice](#); [Stigma](#)

Definition

A member from a group of people that have either been excluded or do not form part of your own group.

Introduction

Throughout a lifespan, any one individual will be affiliated to a number of different groups. Some groups are assigned at birth, such as belonging to a family. Some groups are selected by the individual, such as supporting a local football team. Recognizing and being affiliated to a particular group is known as being an in-group member. In contrast, those who are outside of this group, particularly those who may affiliate to a rival group, are referred to as out-group members. This entry will explore some of the explanations for why in-group/out-group categorizations are

formed, what the consequences are this for out-group members, and what factors can be deployed to minimize the consequences of out-group categorization.

Social Identity Theory

Tajfel and Turner's (1979) social identity theory proposed that people's social identity is based on the group memberships that they affiliate to. These group affiliations provide us with a sense of pride, a sense of belonging, and reinforces who we are as an individual. In order to increase our self-standing, members of particular groups, also known as in-groups, will promote the status and importance of their group. On a cultural level, this can lead to racism that is prevalent, both historically and in modern times. In addition to discriminating against out-groups, stereotyping can occur, whereby negative attributes are disproportionately associated with out-group members. Furthermore, members of an out-group can all be perceived as having these negative attributes, rather than them being applied on an individual-by-individual basis.

Tajfel and Turner (1979) identified three different stages that are required in order to create an in-group and out-group belief. The first is *social categorization*, allowing us to group different people into different categories. For example, people could be categorized on their gender, nationality, religion, or team that they support. It is therefore also clear that no one person will just belong to one category, but will belong to several. The second stage is *social identification*, when we identify with a group, act in a way that would be perceived by members of the group, and adopt their norms. For example, this could be wearing a replica jersey of a local sports team and singing their songs at local games. The third stage is *social comparison*. Once we have categorized people into groups and decided our group memberships, active comparisons are then made with other groups. In line with the social identity theory, this involves promotion of one's own groups and

being derogatory towards other groups in order to maintain and increase self-worth.

Out-Group Homogeneity Bias

The concept of not being able to differentiate characteristics of out-group members is known as out-group homogeneity bias (Anthony et al. 1992). Humans have limited attentional resources and cannot encode all information in a social world (Todd et al. 2005). These limited attentional resources are allocated to those objects or people who have functional implications to the perceiver (Ackerman et al. 2006). Historically, many interactions that took place in an in-group (also known as a coalitional group) would benefit an individual's functional outcomes. For example, interactions could facilitate potential mate selection and subsequent reproduction. Other interactions could facilitate opportunities for reciprocal exchange. For example, these could be economic exchanges, such as food and clothing, or they could be less tangible exchanges, such as social support. From a social standing, interactions could facilitate potential negotiations for movement in a social hierarchy. For example, being affiliated with a more prominent member of the group could increase your social status within a group. Increased technology and infrastructure has meant that coalitional groups changed significantly in modern times. Despite this, many of the interpersonal interactions identified still take place within cultural and ethnic groups (Fiske 1992). As a result, contact with out-group members tends to be less frequent, meaning that the costs of interpersonal contact outweigh the functional benefits.

Not being able to distinguish between out-group members is based on the notion that individuals can gain more from interactions with in-group members when compared to out-group members. However, this idea ignores situations when an out-group member may be a source of threat. In this instance, that out-group individual is likely to become more functionally relevant and

have even greater functional importance. In this instance, homogeneity bias toward out-group members is likely to be eliminated. The emotion and facial expression associated with recognizing interpersonal threat is anger. Ackerman et al. (2006) proposed that it is functional to be able to distinguish angry out-group members and remember them in order to avoid them in the future. In their study, 192 white participants were shown white and black faces with either a neutral or angry expression. Participants were then shown a 5 min distraction video and recognition memory task. Recognition accuracy for black faces was lower, supporting out-group homogeneity bias. However, this bias was eliminated for angry black faces. Furthermore, recognition bias for angry black faces was higher than angry white faces, supporting out-group heterogeneity. The functional explanation of these findings is that all out-group members are considered as being potentially dangerous, supporting out-group homogeneity bias. However, additional mechanisms allow the perceiver to identify those out-group members who pose the most threat, supporting out-group heterogeneity.

Perceived Threat

Due to the prevalence of intergroup violence throughout human history, it has been hypothesized that humans have evolved a set of tribal instincts that specifically deal with antagonist group situations (Van Vugt and Park 2010). These instincts are designed to divide up the world to “us” and “them,” favoring in-group members and acting hostile toward out-group members. However, not all in-group-out-group categories are the same. Van Vugt and Park (2010) proposed a “tribal template” that differentiated those out-groups who could pose a threat (e.g., nations, ethnic groups) from those who do not (e.g., age, gender). Moreover, the level of hostility toward out-group member is increased when contextual cues suggest increased threat (e.g., being in the dark).

In addition to the threat of potential physical conflict, there is also the more subtle type of threat associated with disease. In ancestral times, it was likely that contact with an in-group member posed less risk of disease threat when compared to out-group members. This was because constant contact with in-group members would have allowed the body to build up the appropriate antibodies as an immunological defense for in-group members but not out-group ones. Furthermore, in-group members were more likely to have the aid necessary to deal with illnesses that were common to them (Navarrete and Fessler 2006). This therefore suggests that humans have evolved an intergroup bias that is associated with approach and avoidance motivations. On the one hand, humans are predisposed to avoid those who are categorized as out-group members, as they pose a higher risk of disease threat. On the other hand, humans are predisposed to approach in-group members as they offer less risk of disease threat as well as offering knowledge and support for disease threats that are known within the group (Navarrete and Fessler 2006).

Contact Hypothesis

Out-group homogeneity bias and prejudice can be fuelled, in part, by lack of contact between different groups. Addressing this point, Allport's (1954) *contact hypothesis*, drew upon the idea that contact may reduce negative evaluation of out-group members, providing participants were of equal status, shared the same goals, have an opportunity to get to know each other, and have the support of an authority (e.g., a school or the government). Thus, increasing contact with an out-group member(s) serves as an opportunity to work towards a common goal and create individual-level commonalities. Furthermore, Pettigrew and Tropp (2008) conducted a meta-analysis to look at the psychological factors associated with contact. They found that out-group prejudice is reduced by reducing anxiety towards out-group members, increasing the knowledge

about out-groups, and increasing empathy towards out-group members. Despite this intuitive intervention, the question still remains as to whether contact does actually work on a global scale? While contact with outgroup members in this particular setting seems to work, does it mean a global shift in someone's ideological beliefs? Put more simply, would all out-group members be treated fairly in the future? (Dixon et al. 2005).

From an evolutionary perspective, the conditions stated by Allport (1954) would result there being little to distinguish between in-group and out-group members; and with consistent contact between all members, there would be no "us" and "them." This would create a melting pot and has the potential to eliminate discrimination, prejudice, and stereotyping. Despite this being ideologically perfect, it is also practically impossible. We are prone to categorizing, and this is done in a functionally flexible way. In other words, consistent contact may have the potential to create new in-groups (e.g., those that you have completed an activity with), but this will just create new out-groups in place of existing ones. Therefore, it is much more likely that interventions, such as education, can motivate understanding of out-group members, reduce social categorization and subsequent negative evaluation of out-group members.

Conclusion

Humans are a social species and are affiliated to a number of different groups, such as family, religion, ethnicity, and supporting a particular sports team, this is just part of human nature. Drawing from our understanding of limited attentional resources and functional explanations, we can understand both why we favor those from in-groups and why it can come at the expense of others. We also understand that this is not so black and white and can be influenced by other factors, such as perceived threat and increased contact. Furthermore, we all belong to several groups and it is likely that what we constitute as an out-group member will be based on how we weight and perceive our social identity on a multidimensional continuum.

Cross-References

- [Competition for Resources Desired by Females](#)
- [Human Groups](#)

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Overconfidence

- [Information About Likely Combat Success](#)

Overimitation

- [Learning Versus Imitation](#)

Overweight

- [Body Reserves and Food Storage](#)
- [Obesity](#)

Ovulate

- [Ovulation](#)

Ovulation

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Synonyms

[Conception](#); [Fertility](#); [Menstrual cycle](#); [Mid-cycle](#); [Ovulate](#)

Definition

In humans, ovulation occurs around mid-menstrual cycle when an oocyte is released from an ovary and sex can result in conception.

Introduction

Several scholars have suggested that human females have evolved to conceal ovulation from males (e.g., Marlowe 2004). However, other scholars contend that cues to ovulation have not been entirely hidden, but rather have only been partially concealed (see Welling and Puts 2014).

Although there is evidence in favor of both perspectives, there is considerable recent evidence in favor of the latter hypothesis. This research falls into four related areas of research: (1) cyclic variation in female mate preferences, (2) changes in female sexual motivation, (3) changes in female attractiveness, and (4) male detection of ovulation.

There is supporting evidence for the claim that women have evolved to conceal ovulation, such as inaccurate beliefs surrounding the timing of conception among hunter-gatherers (Marlowe 2004). Ovulation may have been concealed for more than one purpose; concealed ovulation may have prevented women from selectively avoiding sex at certain times to avoid conception (Burley 1979), allowed women to better deceive their partners (e.g., Strassmann 1981), or enabled greater flexibility in choosing a mate (e.g., through cuckoldry; see Strassmann 1981). Similarly, the extended mating periods of humans coupled with concealment of cues to fertility may have evolved to make assessment of paternity more difficult, which may reduce rates of male-perpetrated infanticide if they are less likely to deduce nonpaternity (e.g., Heistermann et al. 2001). Certainly, degree of relatedness is related to violence toward children (Daly and Wilson 1985; Wilson and Daly 2002), suggesting that knowledge of nonpaternity could have severe negative impacts on children. Alternatively, concealed ovulation may have evolved to protect women from sexual attention from unwanted suitors when that attention could prove particularly devastating (i.e., result in unwanted pregnancy; discussed in Welling and Puts 2014).

Increasing research on physical and behavioral cues to women's fertility status has surfaced in recent years (e.g., Gildersleeve et al. 2014). Recent evidence suggests that cues to fertility status have not been entirely hidden, but rather have merely been partially concealed (Welling and Puts 2014). Evidence in favor of this hypothesis comes from four areas of research: (1) cyclic variation in female mate preferences, (2) changes in female sexual motivation, (3) changes in female attractiveness, and (4) male detection of ovulation. These subtle signs of conception risk

indicate that the previously accepted conclusion that ovulation is concealed in humans is not the whole story. Each of these areas is discussed in turn below.

Cyclic Variation in Female Mate Preferences

A variety of women's behaviors change as a function of menstrual cycle phase, such as increased creativity (e.g., Krug et al. 1996) and performance on cognitive tasks (e.g., Becker et al. 1982) near ovulation relative to other times. Importantly, these findings introduce the possibility that hormonal variation could have implications for women's mating-relevant behaviors. The ovulatory shift hypothesis states that systematic changes in female mating-related behavior and preferences should be expected over the course of the menstrual cycle (e.g., Gildersleeve et al. 2014). Should, for example, women's preferences shift toward cues to genetic immunocompetence, this would be quite adaptive because those women would reap the indirect genetic benefits whereby their offspring would be more likely to survive into adulthood and propagate their genetic line. Consistent with this view and in line with the ovulatory shift hypothesis, several studies report increases in women's preferences for putative cues to male mate quality, including preferences for the odor of men who are more dominant, symmetrical, and genetically compatible (e.g., Havlíček et al. 2005). Women also show increased preferences for masculine male faces, masculine male body shape, masculine vocal characteristics in men's voices, and facial symmetry around ovulation relative to other times in the menstrual cycle (reviewed in Welling and Puts 2014). It is likely that women's shifts in preferences across the menstrual cycle are driven by hormonal changes, although there is debate surrounding whether menstrual cycle preference shifts are driven by estradiol, progesterone, testosterone, cortisol, or some hormonal combination (reviewed in Welling and Puts 2014).

Other mate-choice relevant shifts occur across a woman's menstrual cycle. Preferences for male

dominant and competitive behavioral displays (e.g., Gangestad et al. 2004) and for courtship language (Rosen and López 2009) are highest near ovulation. When judging the attractiveness of video clips of men competing for a lunch date for a short-term (i.e., sexual) relationship, women rate men who display social presence and direct intrasexual competitiveness as more attractive on high- versus low-fertility days (Gangestad et al. 2004). Furthermore, women are more receptive to courtship in the late-follicular phase of the menstrual cycle (the fertile phase immediately preceding ovulation) compared to the luteal phase (the nonfertile phase following ovulation; e.g., Guéguen 2009). Women are even more accurate when classifying faces as male near ovulation (Macrae et al. 2002), especially when those faces are more masculine (Johnston et al. 2008). Interestingly, this finding is reversed among lesbian women, who categorize female faces more accurately around ovulation (Brinsmead-Stockham et al. 2008), suggesting that these findings are mate-choice specific.

Changes in Female Sexual Motivation

High conception risk is associated with increases in sexual desire, sexual fantasy, attention to attractive men, sexual self-stimulation, arousal in response to sexually explicit material, sexual activities, and desire for orgasm near ovulation (reviewed in Welling and Puts 2014). Sexual encounters increase (Wilcox et al. 2004) and are more likely to be female-initiated (e.g., Matteo and Rissman 1984) near ovulation. Women are more disgusted by incest around mid-cycle (Fessler and Navarrete 2003) and may decrease their risk-taking behaviors near ovulation (e.g., Bröder and Hohmann 2003). This latter finding may function to decrease chances of victimization, although sexual assault is no less frequent during high fertility (Fessler 2003). Thus, evidence suggests that sexual motivation increases with conception risk, whereas nonadaptive mating behaviors may simultaneously decrease.

Women are more sexually opportunistic (Gangestad et al. 2010), are less motivated toward sex for the purposes of intimacy (Sheldon et al. 2006), and are more interested in visiting singles nightclubs without their romantic partner (Grammer et al. 1997) near ovulation. They also demonstrate a greater interest in attending social gatherings, extra-pair men, extra-pair sexual activity, and extra-pair sexual fantasies when conception is more likely (reviewed in Welling and Puts 2014). Fertile-phase women report less commitment to, and relationship satisfaction with, their current partner. Perhaps as a consequence of an increase in mating motivation, female intrasexual competition increases near ovulation; women derogate same-sex competitors by downplaying their physical attractiveness (e.g., Fisher 2004), which effectively reduces men's attraction to their rivals (Fisher and Cox 2009). Women also report feeling more attractive (reviewed in Welling and Puts 2014) and are more willing to spend money on suggestive clothing (Hill and Durante 2009) around ovulation than at other times. Altogether, this research suggests that women are more mating motivated when they are more likely to conceive.

Changes in Female Attractiveness

Women modulate their appearance and clothing to enhance their attractiveness when they are most fertile, possibly as a reaction to a peri-ovulatory decrease in self-esteem (Hill and Durante 2009). Also, their faces, voices, and bodies are rated as more attractive around ovulation than at other times (reviewed in Welling and Puts 2014). Women have a more appealing body odor around ovulation (e.g., Miller and Maner 2010). Exotic dancers even receive more tips during peak fertility versus other points in the menstrual cycle (Miller et al. 2007). These studies suggest that men are maximally attracted to ovulating women and, by extension, that women are better able to attract men during the fertile phase of their cycles.

Male Detection of Ovulation

Given that attractive women receive more male attention (Buss and Barnes 1986) and that appear to be more attractive and sexually motivated around mid-cycle, increased attention from long-term partners would be expected near ovulation. Indeed, three studies have shown a relationship between female conception risk and their perceptions of jealous and possessive behaviors from their male partners (Gangestad et al. 2002; Haselton and Gangestad 2006; Pillsworth and Haselton 2006), and this relationship is strongest when the woman is particularly attractive (Haselton and Gangestad 2006) or interested in extra-pair mating (Gangestad et al. 2002). Similarly, women with less sexually attractive partners report receiving more attention from their partners around ovulation (Pillsworth and Haselton 2006). Overall, these findings suggest either that women's attention to extra-pair men may drive this increased attention or that men are sensitive to fertility-associated cues and become more responsive to the threat of cuckoldry.

There is evidence that women's ovulatory status influences male hormonal response. In a double-blind study, Miller and Maner (2010) investigated how the scents of women at peak fertility influence male endocrinological responses by having men smell T-shirts worn by women near ovulation or T-shirts worn by the same women during the luteal phase of the menstrual cycle. When controlling for baseline testosterone levels, testosterone was substantially higher in men exposed to the odor of a woman close to ovulation than in men exposed to the odor of a luteal-phase woman (Miller and Maner 2010). Additional research has shown that partnered men exposed to high-competitive rivals demonstrate significantly higher testosterone levels at high-relative to low-fertility, whereas men exposed to low-competitive rivals showed no such pattern (Fales et al. 2014). Moreover, men are also more likely to mimic a woman (a behavior thought to reflect attraction) and make risky decisions (a decision-making strategy men use to display desirable traits to women) when faced with a fertile-phase woman versus women in nonfertile

menstrual cycle phases (Miller and Maner 2011). Thus, men not only perceive cues to female conception risk but these cues may have a direct influence on their hormonal profile and their behavior.

Conclusion

That attractiveness and sexually motivated behavior appear to increase at ovulation contradicts the supposition that human ovulation is completely concealed (discussed in Welling and Puts 2014). These cues to fertility are quite subtle, however, possibly to avoid indiscriminate attention that may constrain or eliminate female choice. Although cues to ovulation and associated changes in male and female behavior and preferences are becoming increasingly well documented, additional research is needed to further tease apart the many complex mechanisms underlying human sexual selection.

Cross-References

- [Concealed Ovulation](#)
- [Concealed Ovulation and Pregnancy](#)
- [Cycle Variation](#)
- [Effect of Birth Control on Women's Preferences](#)
- [Mate Preferences](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Women's Mate Preferences](#)
- [Women's Mate Value](#)
- [Women's Preferences During Ovulation](#)

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Ovulation Suppression

► Birth Control

Ovulatory Cycle

- Menstrual Cycle
- Ovulatory Hormones
- Ovulatory Shifts in Psychology

Ovulatory Cycle Phase

► Problems of Assessing Fertility

Ovulatory Cycle Phases

► Cycle Variation

Ovulatory Hormones

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Synonyms

Hormones; Menstruation; Ovulation; Ovulatory cycle

Definition

Hormones that induce ovulation and regulate the ovulatory cycle.

Introduction

The key to the ovulatory cycle resides within the ovaries, and the primary hormone that regulates the ovulatory cycle is Estradiol. Every month, a follicle (egg) is randomly selected to release from the ovary. The first day of menstruation marks the beginning of the ovulatory cycle, and the start of the follicular phase. During the first 3–5 days of menstruation, Follicle-stimulating hormone (FSH) is triggering the growth of immature ovarian follicles. Estrogen is steadily increasing during this time; aiding in follicle development, thickening the endometrial lining in the uterus and in a general sense, promoting sociosexuality (Gray and Garcia 2013). A few days before the end of the follicular phase, estrogen surges as luteinizing hormone begins to rise, ultimately peaking when the follicle is released at the point of ovulation. When the follicle is released from the ovary, a lipid-rich substance referred to as the *corpus luteum* remains behind and stays active, steadily increasing the presence of progesterone (Gray

and Garcia 2013). The ovulatory cycle is then considered to be in the luteal phase and is characterized by the rising presence of progesterone. Progesterone continues to stimulate the endometrial lining in the uterus and prepare it for the potential arrival of a fertilized egg for the remainder of the luteal phase. If conception does not occur, the built-up uterine lining is shed and menstruation begins, marking the beginning of a new ovulatory cycle.

There are also changes in women's body odors that coincide with the hormones of her ovulatory cycle. Researchers asked women to wear a t-shirt to bed on various days throughout their cycle while avoiding practices that would mute their natural scent (no perfume, deodorant, etc.). Men were then asked to smell and rate numerous t-shirts for odor attractiveness. T-shirts that were worn when women were in their peak ovulatory phase were typically rated as smelling more attractive than t-shirts that were worn during the other phases of the cycle (Singh and Bronstad 2001). This was coined the "stinky T-shirt" paradigm. Kuukasjarvi et al. (2004) took this idea and added the extremely important mediating factor of oral contraceptives. Oral contraceptives (and really, any type of hormonal contraceptive) basically trick the female body into thinking that it is pregnant throughout the month, therefore never producing a peak in ovulatory hormones mid-cycle. When individuals were presented with various t-shirts to smell from various women in different phases of their ovulatory cycle, the same effect was found regarding ovulating women. What is fascinating is that there was no effect for women that were on the pill, supporting the idea that women's body odors are linked to the ebb and flow of hormones throughout the ovulatory cycle. Body odors oscillate slightly depending on where an individual is in their cycle *unless* they are on some sort of hormonal contraceptive.

Some researchers have proposed that, similar to other animals, humans possess pheromones. Pheromones are basically unseen chemical cues that our bodies use to interact with the physiology and behavior of others in our immediate environment. In particular, it is hypothesized

that two pheromones are typically released by women throughout their ovulatory cycle: a phase-advance and a phase-delay pheromone. Stern and McClintock (1998) demonstrated that when compounds from the armpits of women in the late follicular phase of their menstrual cycle were introduced to recipient women, it triggered a surge of luteinizing hormone and shortened their cycles. When the compounds from the armpits of the same women were collected at ovulation and introduced to recipient women, an opposite effect was found: luteinizing-hormone was delayed and menstrual cycles were lengthened.

Miller et al. (2007) found that (over the course of 3 months) women (exotic dancers) that were normally cycling (and were not on any type of hormonal contraceptive) received more money on average when they were ovulating. During a 5-h shift, ovulating women on average earned \$335, in comparison to an average of \$260 when they were in their luteal phase and \$185 when they were menstruating. So women who were normally cycling made the most money when they were in estrus (ovulating) compared to all other phases of the cycle – especially the women who were on hormonal contraceptives. Because hormonal contraceptives make it so that there is no peak in hormones (or fertility for that matter), the dancers that were on birth control made less on average (\$193 per shift vs. \$276 per shift). Due to these results, researchers claimed that unconscious cues were being shared to indicate where a female was in her ovulatory cycle.

Conclusion

Ovulatory hormones regulate much of the fluctuations within the female body, and they effect more than the subtle cyclic changes that happen throughout the month. As humans, we have come up with novel ways to manipulate the ovulatory cycle in order to avoid unwanted pregnancies, and in doing so, we have manipulated the subtle behavioral changes that have historically accompanied the cycle.

Cross-References

► [Ovulatory Shifts in Psychology](#)

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Ovulatory Shifts in Attraction

► [Attraction During Ovulation](#)

Ovulatory Shifts in Psychology

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Synonyms

[Hormones](#); [Menstruation](#); [Ovulation](#); [Ovulatory cycle](#); [Psychology of the ovulatory cycle](#)

Definition

Hormones that induce ovulation and the changes incurred in human behavior.

Introduction

Though the human ovulatory cycle is incredibly complex, it should come as no surprise that it shares striking similarities to other apes. The exact length varies depending on the individual, but the average ovulatory cycle lasts about 28 days. During the length of a cycle, a female goes through three distinct phases: menses, follicular, and luteal. Ovulation typically occurs halfway through the cycle, between the follicular and luteal phases (with the length of the follicular phase being the more variable of the two). The term *peak fertility* refers to a small window (usually thought to be anywhere between 2 and 6 days) when a female's conception rate goes up. In some species (including some distant ancestors like baboons), *sexual swelling* is a visual indicator that a female is approaching and/or in her peak fertility window (Gray and Garcia 2013). This visual cue is necessary to facilitate copulation, which in turn leads to reproduction, an essential outcome for evolutionary mechanisms to work.

Concealed Ovulation?

Humans obviously do not display this clear indicator when nearing ovulation, and therefore are considered to display *concealed* or *cryptic ovulation*. For millions of years, various evolutionary mechanisms shaped the ovulatory cycles of our distant ancestors, but as *homo sapiens* emerged as a distinct branch of great apes and became more specialized, so too did the behavior that evolved surrounding our ovulatory cycles. Though humans are thought to have *concealed ovulation*, females display (subtle) physiological, psychological, and behavioral indications when in their peak fertility phase. These behavioral adjustments, shaped by various evolutionary forces (like sexual selection), bolstered an individual's ability to conceive, and ultimately led to successful reproduction. Throughout each generation, the behaviors that increased an individual's ability to successfully reproduce were selected for, ultimately becoming indicators of reproductive fitness.

Attraction to an individual can also be affected by the ovulatory cycle. Physically, there are small adjustments to a female's appearance when she is nearing her peak fertility phase due to hormones. Soft tissue traits (ears, fingers, breasts) become more symmetrical; lips become fuller, and have a slightly deeper hue, and even the tone of a female's voice changes. Pipitone and Gallup (2008) demonstrated that women's voice attractiveness varies across the ovulatory cycle. The human larynx is (not surprisingly) affected by the hormones of the ovulatory cycle. When students were asked to rate how attractive a speaker's voice was, the highest ratings came from women that had the highest risk of conception probability. That is, when women were closer to ovulation, their voices were rated as more attractive than women that were at different phases in their cycle (Pipitone and Gallup 2008). From an evolutionary perspective, if a females' voice is perceived as more attractive during her peak fertility days, and increased attraction can lead to an increased potential for copulation, this can play out in terms of reproductive fitness.

Sexual Desire

Another important factor to consider when discussing peak fertility and conception probability is sexual desire. Sexual desire is an emotion that most likely evolved to coordinate a multitude of psychological mechanisms, ultimately working together to direct behavior toward increasing the odds of reproduction. Environmental cues play an important part in women's evolved psychology. For example, relationship satisfaction is extremely important when considering the effect of the ovulatory cycle on sexual desire: Women are more likely to feel increased sexual desire during peak fertility days for their partners if they are in happy, committed relationships. Interestingly, sexual desire for extra-pair copulations during peak fertility is positively correlated to the length of relationship (Pillsworth et al. 2004). This overall increase in desire in mated couples is compelling: The happier the couple is, the more likely the woman is to feel sexual desire (during her peak ovulatory days), but, as the length of the

relationship increases, the more likely she is to experience sexual desire for extra pair copulations during ovulation.

Attractiveness and Desire

Interestingly, partner attractiveness can moderate the psychological effects of the ovulatory cycle. When females rate their male partners as less sexually attractive, there is a significant shift at ovulation toward extra-pair sexual desire. A considerable portion of attraction lies in symmetrical features of the face. Fluctuating asymmetry moderates the effects of in-pair and extra-pair attraction in both directions: women with less symmetrical partners experience heightened extra-pair sexual desire when ovulating, and women with more symmetrical partners experience heightened in-pair sexual desire (Pillsworth and Haselton 2006). The degree to which a female's partner exhibits traits that are indicative of *high-fitness genes* is thought to be what drives this ovulatory shift in desire. Subtle genetic cues are essentially motivating a females' drive toward desire.

Indicators of *high-fitness genes* can be expressed *phenotypically*. Our *genotype* is the set of inherited instructions we receive from both parents that code for a multitude of attributes, including physical appearance. The physical manifestation of our genetic code (or, genotype) is referred to as *phenotype*. Specific phenotypic traits are thought to be linked to high indices of genetic fitness. In women, these traits include smooth skin, large eyes, full lips, and curved hips; in men, these traits include broad shoulders, strong jawlines, moderate muscles, and tallness. As mentioned earlier, when a female is in her peak ovulatory phase, the aforementioned phenotypic attributes become slightly more enhanced. So too, does the desire for specific phenotypic fitness indicators.

Dual Mating

The evolutionary push to find a good partner often creates friction. Sometimes, individuals are

presented with a weigh off: do they choose the individual that they are highly sexually attracted to, but doubt their fidelity and sincerity, or the individual that would be a good partner and has always been there for them, but, they are not as attractive as the other. . . When it comes down to it, most people would say the good partner, but when females are ovulating, this shift toward sexual attraction (and potentially "genes") is stressed slightly more. *Dual mating* is a strategy in which a female has a long-term committed partner, but unintentionally seeks out "good genes" through extra pair copulations.

Dressing During the Ovulatory Cycle

The ovulatory cycle can also affect the way in which a female chooses to dress. From an evolutionary perspective (under some circumstances), clothing choice may be evaluated as a courtship signal. Haselton et al. (2007) found that near ovulation, women's choice in dress became more provocative. Participants were brought in on a low fertility day and a high fertility day during the month, and their pictures were taken. When in their peak fertility days, women were more likely to wear skirts, wear more fashionable clothing, and show more skin on their upper body. In a similar study, participants were additionally asked to illustrate what they would wear to a social outing (during high fertility days), their illustrations showed more skin. In particular, this trend was strongest for women that were sexually unrestricted, meaning that single women were more likely to draw revealing clothing during their peak fertility days than women who were in committed relationships (Durante et al. 2008). Both of these studies seem to fit nicely into the idea that an increase in sexual desire was only found to peak in mated couples. Women who were in committed relationships experienced a peak in sexual desire during their peak fertility days, yet did not show a difference in dress choice, whereas single women did not experience a peak in sexual desire, and tended to dress in more revealing clothing at the onset of ovulation. Extending beyond that idea, a silhouette of women's body movements (specifically gaits and

dances) were recorded in the late follicular and mid-luteal phases of the cycle (Fink et al. 2012). Body movements during the late follicular phase of the cycle were considered more attractive than the mid-luteal, further supporting the idea that there are not only changes throughout the ovulatory cycle, but that individuals have a potential ability to detect subtle ovulatory cues.

Preferences for Partners

The ovulatory cycle can affect an individual's preference as well. Haselton and Miller (2006) found that when a woman was looking for a short-term partner and was in her peak fertility window, she tended to favor creativity (potentially high genetic fitness) over wealth (financial stability). This is based off of the general idea that human female sexuality is adaptively sensitive to trade-offs between “good genes” and “good dads.” In a general sense, *creative intelligence* is something that would be a valuable trait to pass on to future offspring. These evolutionary trade-offs seem to increase around ovulation: In general, women want a partner who will care for them, be trustworthy and offer financial stability, yet they also want an individual they are mentally and physically attracted to.

The level of estrogen in a woman's system seems to have a direct effect on preferences toward dominant personality traits. When searching for long-term mates, preferences for dominant personality traits seemed to positively correlate with levels of estrogen (which fluctuate throughout the cycle), but when searching for a short-term mate, these same preferences toward dominance seemed to positively correlate with luteinizing hormone and follicle-stimulating hormone (which peaks 1–3 days after ovulation). There is no peak in preference for dominant personality traits when a woman is rating a long-term mate, but, when rating a short-term mate, a preference for dominant personality traits began rising as the day of ovulation got closer, finally peaking 1–2 days after ovulation (Lukaszewski and Roney 2009). From an evolutionary point of view, this makes sense because the preference for

dominant personality traits steadily increases while a female approaches her peak fertility days, and if she is looking for a short-term mate (or extra pair copulation for that matter), she will be more likely to pursue a sexual encounter during this time.

Certain behaviors, like mate guarding, have evolved as a countermeasure in the evolutionary arms race. From an evolutionary standpoint, behaviors that will increase the likelihood of a partner spending time with you during peak fertility will increase the odds of conception. Interestingly, this seems to be moderated by indicators of genetic fitness: We only see an increase in mate guarding behavior during peak fertility days when female physical attractiveness is rated relatively low. When female physical attractiveness is rated as relatively high, mate guarding takes place throughout the cycle (Haselton and Gangestad 2006).

Conclusion

There are many factors that can affect a females' psychology, including the ovulatory cycle. The hormones that are responsible for regulating the inner-workings of the cycle can also play into the psychology of that individual. Though it is important to consider the ovulatory cycle when studying ovulatory shifts in psychology, it is equally important to understand the complex interplay that the ovulatory cycle has with an individual's immediate environment. This immediate environment includes potential partners and partners (including their relationship satisfaction).

Cross-References

► [Ovulatory Hormones](#)

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Oxidants

► Oxidative Stress and Free Radicals

Oxidative Stress and Free Radicals

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Synonyms

Oxidants

Definition

The outcome of disbalance between oxidants and antioxidants is known as oxidative stress (OS).

Introduction

Oxidation of substrates occurs during the process of aerobic metabolism, a crucial step towards efficient production of energy in the cells. There occurs a steady state balance between oxidation-reduction processes within the cell. During the process of substrate oxidation, free radicals particularly reactive oxygen agents with known toxicity are produced in low levels. Usually these free radicals are soon cleared by several antioxidant mechanisms preventing their accumulation. Oxidative stress is defined as “an imbalance between oxidants and antioxidants in favour of oxidants, potentially leading to damage” (Sies 2000). Various pathologic process disrupt this balance leading to oxidative stress which can occur both through the failure of the antioxidant mechanisms as well as the excessive production of prooxidants in the body (Kar and Choudhury 2016; Sies 2000).

Oxidative Stress

Oxidative stress is responsible for the generation of several reactive oxygen groups which are commonly referred as reactive oxygen species (ROS) too. In general, the molecular oxygen taken up by cells gets reduced to water by electron-transport mechanism during aerobic metabolism of substrates in mitochondria. Impairments of electron-transport mechanism in the respiratory chain lead to generation of partially reduced ROS. Apart from this, several intracellular enzymes such as xanthine oxidase, NADPH oxidase, cytochrome P450 monooxygenase, lipoxygenase, cyclooxygenase, and monoamine oxidase also play role in the production of ROS (Lee et al. 2013). The ROSs include superoxide, hydroxyl, hydrogen peroxide, and monovalent oxygen ion (Pizzino et al. 2017). They have roles in modulating

various cellular physiological processes (such as signalling, protein phosphorylation, activation of transcription factors, cellular differentiation, immunity, and apoptosis) (Pizzino et al. 2017; Rajendran et al. 2014).

Free Radicals

The free radicals are highly reactive moieties with unpaired electron that readily alter the structure and functioning of nucleic acids, proteins, carbohydrates, and lipids of the cell leading to injury and cell death (Ng et al. 2008). They have the potential to trigger apoptosis as well as necrosis. The major free radicals either belong to the reactive oxygen or nitrogen class of agents (e.g., hydroxyl radical, superoxide radical, peroxynitrite radical, and nitric oxide radical). Among these free radicals, hydroxyl radical is the most reactive. It rapidly reacts nonselectively with various compounds. In low to moderate concentrations, the free radicals deliver many physiological functions as well as provide immunity against infections (Valko et al. 2007). They are enzymatically produced as a by-product during cellular respiration, in activated leukocytes during inflammation, during metabolism of exogenous chemicals or drugs, as well as intracellular reaction involving transition metals like iron and copper (e.g., Fenton reaction). Ionizing radiations (e.g., ultraviolet light, x-rays) can nonenzymatically produce free radicals. Free radicals can be produced from endogenous or exogenous sources (Pizzino et al. 2017). Figure 1 enumerates the sources of free radicals.

Free radicals being highly reactive and unstable perish spontaneously. Body's natural antioxidant system attempts to neutralize the reactive oxygen agents. Several enzymes (such as superoxide dismutase, catalase, glutathione peroxidase, glutathione reductase, sulfiredoxin) and free radical scavenging molecules (such as vitamin E [tocopherols], vitamin C [ascorbic acid], vitamin A [retinol], polyphenols, flavonoids, glutathione, and uric acid) form the antioxidant reserve of the body (Pandya et al. 2013).

Mechanism of Action of Free Radicals

The free radicals target the lipids within plasma and organellar membranes, and produce damage to them by causing peroxidation. Peroxides formed this way used to be unstable and reactive and thus stems a chain of autocatalytic reaction leading to accumulation of oxidants. This results in widespread damage to organelles and cell membrane.

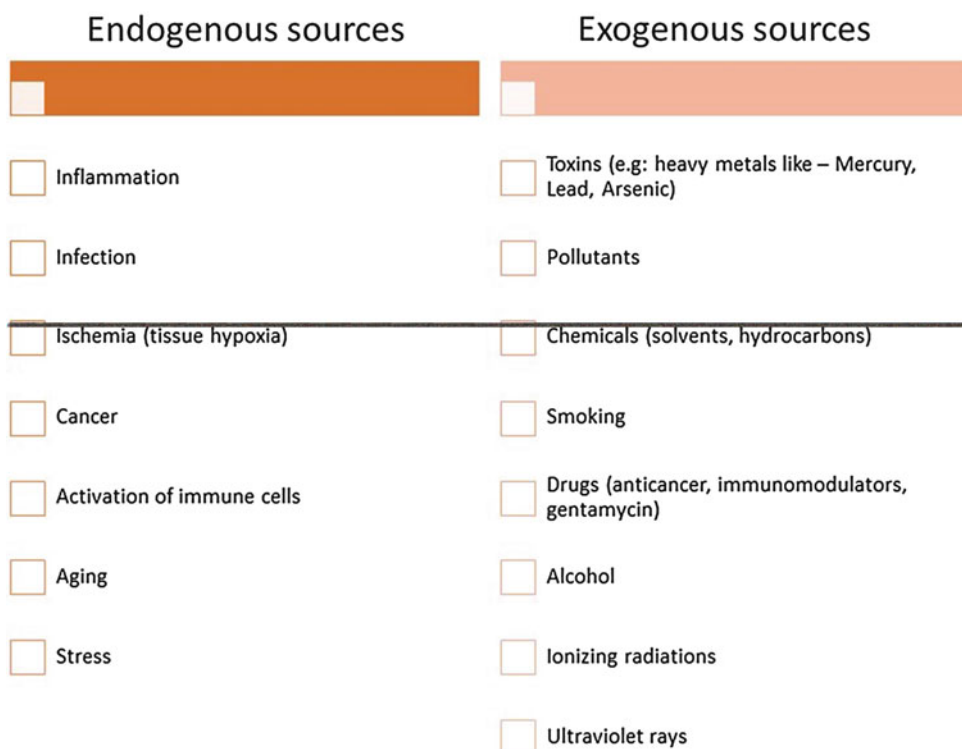
They also lead to alterations in protein structures by oxidizing amino acids, formation of covalent bonds (e.g., disulfide bonds) between proteins, and damaging the protein backbone. Oxidative damage to the proteins results in the alteration of enzyme binding sites, structural alteration of the proteins (receptors, transcription factors, and enzymes, etc.), as well as their proteosomal degradation.

Free radicals may target nitrogen-containing nucleobases or sugar residue leading to cross-linking of DNA strands, breaks in DNA strands, and formation of adducts. It thus damages cellular DNA.

Health Implications of Oxidative Stress and Free Radicals

During illness conditions, excessive unregulated production of oxidants occurs. The scavenging system (enzymes and nonenzymatic agents) fails to control the oxidants resulting in continuous tissue damage (Sies 1997). The oxidative stress and free radicals has been implicated in various illnesses like – inflammatory disorders, infections, diabetes mellitus, atherosclerosis, hypertension, cancer, metabolic disorders, and many other life style-related illnesses (Pizzino et al. 2017; Sies 2015). The inflammatory changes in atherosclerosis are due to increased formation of ROS. The ROS also damages the vascular endothelium (Kattoor et al. 2017). Medications like – statins, aspirin, angiotensin converting enzyme inhibitors reduce oxidative stress by their antioxidative effect (Kattoor et al. 2017). Oxidative stress produces epigenetic instability by damaging the DNA (e.g., producing oxidation and methylation

Sources of free radicals



Oxidative Stress and Free Radicals, Fig. 1 Endogenous and exogenous sources of free radicals

of DNA), which might lead to development of cancer (Nishida et al. 2013; Pizzino et al. 2017).

The brain is an organ with high energy demand and is reliant on aerobic respiration for efficient ATP production. It utilizes about 20% of total blood oxygen and is thus associated with an elevated risk of generation of free radicals and oxidative injury. Insufficient antioxidant defense mechanisms and high lipid content makes it further vulnerable. In addition, insufficient regenerative capabilities of neurons except for some stem-cell regions leave it susceptible to oxidative stress. Growing body of evidence has demonstrated disturbances of antioxidant defense mechanisms and increased oxidative stress in various neuropsychiatric disorders, including schizophrenia, bipolar disorder, autism depression, obsessive compulsive disorder (OCD), and anxiety disorders (Kar and Choudhury 2016). Oxidative

damage has also been a well-recognized phenomenon in the pathophysiology of various neurodegenerative disorders (e.g., Alzheimer's disease (AD), Parkinson's disease (PD), amyotrophic lateral sclerosis, and Huntington disease) (Niedzielska et al. 2016).

In Alzheimer's disease, there occurs increased production and accumulation of amyloid β and neurofibrillary tangles in the brain, which results in extensive oxidative damage. Oxidative damage has also been reported in PD. Significant lipid peroxidation in substantia nigra has been demonstrated. Oxidative protein damage was suggested to occur late during PD progression. Elevated markers of oxidative damage of DNA and RNA in brain has also been reported (Niedzielska et al. 2016).

In schizophrenia, various studies have reported oxidative stress; however, the results have been

variable with regard to the role of antioxidant enzymes with both reduced and elevated levels of superoxide dismutase (SOD) reported in an affected population. A meta-analysis evaluating the risk of oxidative stress in schizophrenia demonstrated that SOD activity was significantly decreased in the disorganized type of schizophrenia patients compared to healthy controls (Zhang et al. 2010). However, some recent studies also demonstrated increase or no significant difference in SOD levels and suggested the rise in levels as a compensatory response to oxidative stress. Oxidative stress markers upsurge may not be significant in the patients with first-episode psychosis (FEP). However, greater inflammation and oxidative stress indicate poor prognosis in this population (Fraguas et al. 2017). Oxidative stress parameters have also been suggested as the indicator of clinical status. The total antioxidant status, RBC catalase, and plasma nitrite are considered as the state markers for acute exacerbations of psychosis, whereas RBC superoxide dismutase to be a trait marker for schizophrenia (Flatow et al. 2013).

Patients with bipolar disorder exhibit significantly more lipid peroxidation, DNA/RNA damage, and nitric oxide compared to healthy controls. Lipid peroxidation was found consistently in both serum and postmortem brain samples and has been suggested as potential prognostic biomarker of bipolar disorder (Brown et al. 2014).

Major depression is associated with reduced plasma levels of antioxidants (uric acid, albumin, high-density lipoprotein cholesterol, vitamin E, zinc, and coenzyme Q10) and lower level of antioxidant enzymatic (serum paraoxonase and glutathione peroxidase) activity (Liu et al. 2015; Maes et al. 2011). Products of oxidative damage (such as red blood cell and serum malondialdehyde and 8-F₂-isoprostanes, 8-Hydroxy-2'-deoxyguanosine) are higher in depressed patients (Liu et al. 2015).

Evidences support that higher level of oxidative stress present in patients with OCD as well as their blood relatives who were healthy. This finding indicates to the possibility of oxidative

stress parameters as trait markers (Shrivastava et al. 2017).

Several pharmacological and non-pharmacological interventions have been shown to reduce oxidative stress. Antidepressant therapy was shown to enhance the levels of several antioxidant markers of oxidative stress (OS) in patients with depression (Liu et al. 2015). Drug treatment in bipolar patients also partly reduces the oxidative stress (Brown et al. 2014). Exercise during acute phase increases ROS production. However, in due course, antioxidant response compensates for this taking precedence. Exercise training regardless of the intensity, volume, type, and population tend to increase the antioxidant indicators and decrease prooxidants (de Sousa et al. 2017).

Conclusion

Oxidative stress and free radicals are important in a spectrum of health conditions. Life style modifications and appropriate therapeutic interventions can alter production of oxidative stress and free radical production to a greater extent. Preventing oxidative stress and generation of free radicals can prevent many neuropsychiatric disorders and life style-related disorders.

Cross-References

► Oxidants

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Oxytocine

► Music and Hormones

P

Pace of Life

- [Prototypical r-/K-Selected \(Fast/Slow\) Species](#)

Pacification

- [Decline of Violence](#)

Paddling

- [Spanking](#)

Pain/Absence of Pleasure

- [Consequentialism and Suffering](#)

Pair Bonding

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Synonyms

[Mating relationships](#)

Definition

Pair bonding addresses the role and function of the attachment system for long-term mating relationships. The attachment system is thought to have been co-opted by evolution to foster pair bonds because such bonds increased reproductive fitness for both infants and mates. Attachment-related variations are also thought to influence mating behavior and people's stance towards pair bonds.

Introduction

Attachment theory, as formulated by John Bowlby, seeks to explain how the human species has solved one main obstacle to reproductive fitness in the course of evolution – how to survive the dangers of infancy. Universally, human infants form strong affectional bonds – attachments – to their caregivers; seeking to maintain proximity to and protesting separations from their caregivers, using them as a secure base to explore the environment from, and a safe haven to return to for comfort and protection. According to Bowlby, the tendency to form such bonds evolved in response to the child's innate vulnerability. This is because a behavioral system functioning to secure proximity to caregivers would have implied increased chances of protection, which in turn increased chances of survival and reproduction, in the primeval environments most formative for our species' development (i.e., the environment of evolutionary adaptedness, EEA; see ► [“Infant Survival”](#)).

Bowlby also asserted that the attachment system is integral to human functioning throughout the life span (Bowlby 1969). This claim has been supported by a large body of evidence. For instance, child-caregiver and pair-bond relationships display unique phenomenological, behavioral, functional, neural, and endocrine similarities, indicating that the attachment system is operative in both kinds of relationships. Individuals' stance towards pair bonds (i.e., romantic attachment styles) has also been robustly linked to numerous aspects of relationship functioning (see ► [“Attachment in Adulthood”](#)).

However, while the adaptive benefits of attachment bonds in childhood are hard to dispute, the evolutionary functions of pair bonds are not as self-evident. This entry addresses the role of the attachment system in the evolution of pair bonding, and the evolutionary functions of such bonds. Moreover, in the course of development, the attachment system is thought to become integrated with the caregiving and sexual mating systems, making variations in adult attachment more complicated to interpret. Indeed, different views on the nature of such variations, as well as on the relative importance of these three systems for pair-bond functioning, have sparked a

controversy among researchers. The entry closes with a discussion of this controversy.

The Evolutionary Function of Pair-Bond Attachment

Increased Offspring Survival by Means of Strong Affectional Ties between Mates

Although exceptions exist both across and within cultures, human reproduction typically takes place within long-term pair bonds (Mellen 1981). This trend is thought to have followed a birthing crisis due to two opposing evolutionary pressures in our primeval environments. As humans developed bipedal locomotion, they also developed larger heads, housing more developed brains. This made it harder for infants to pass through the birth canal of our female ancestors. The pressure for bipedal locomotion, however, restricted the development of larger birth canals to accommodate this trend (i.e., the obstetrical dilemma). Prematurely born infants, with less developed brains and smaller and more flexible skulls, were then more likely to survive (Rosenberg and Trevathan 1995).

Decreased infant maturity at birth also resulted in a prolonged period of heightened neural plasticity. This may have been evolutionarily advantageous because it enabled behavioral systems that are not rigid but open for learning based on experience (cf. experience expectant and experience dependent learning; see also ► [“Evolutionary Foundations of the Attachment System and its Functions”](#)). The relative benefits of premature birth were, however, also accompanied by a protracted period of infant vulnerability. More extensive co-operative efforts by parents may therefore have increased children's chances of surviving this period.

According to attachment theorists Zeifman and Hazan (2016), the evolutionary function of adult attachment is likely to be found in this context. In a situation where increased joint parental investment in infants would be adaptive, the human species already possessed a highly specialized behavioral system for ensuring that an individual would be motivated to stay close to another and resist separations – the attachment system. Albeit

originally developed to ensure protection of infants, the attachment system may then have been co-opted by evolution (i.e., through exaptation) to foster strong affectional ties between mates, increasing the likelihood of cooperative parenting efforts (Zeifman and Hazan 2016).

Supporting this notion, a number of unique aspects of human sexuality seem to have evolved with the function of facilitating enduring ties between reproductive partners, rather than of genetic reproduction alone. For instance, in contrast to most mammals, human sexual activities are typically present at any phase of the female menstrual cycle, and frequently involve sexual behaviors not aimed at conception, especially in committed relationships. It has been argued that one function of this adaptation is to foster long-term pair bonds on the basis of sexual intimacy and reward. It has also been suggested that the development of largely concealed ovulation in human females would have fostered enduring pair bonds, by making it harder for males to detect fertile phases and hence making it reproductively advantageous for males to remain with the same partner for extended periods of time (see Zeifman and Hazan 2016).

Further Reproductive Advantages of Pair Bonds

The adaptive benefits of strong affectional ties between mates may also have extended their role in infant survival. According to Zeifman and Hazan (2016), enduring pair bonds would have facilitated survival of mates themselves, since they increased the likelihood of being protected and cared for in the case of danger or sickness. Evidence also indicates increased reproductive fitness for mates by means of pair bonding. For instance, women in long-term sexual relationships display more regular ovulation and typically reach menopause later. Long-term romantic partners typically also display more robust physical and mental health, which generally would make them better able to provide for themselves and their offspring (Zeifman and Hazan 2016).

Moreover, enduring pair bonds have been suggested to foster the intergenerational transmission of advantageous mating strategies, and to increase reproductive fitness for offspring, by

leaving them better equipped to attract and retain mates of their own. Supporting this line of thought, long-term pair bonds are associated with better physical and mental health in offspring, and children of cohabiting parents are also typically better able to maintain stable pair bonds themselves (Zeifman 2019). In contrast, adolescents from father-absent homes typically become sexually active earlier in their psychological development and display more negative attitudes toward mates. Children of divorced parents also typically display more fear of closeness and abandonment, and are more likely to abandon relationships themselves (Zeifman and Hazan 2016).

Pair-Bond Functioning and Romantic Attachment Styles

Numerous studies have linked variations in relational and reproductive behavior to variations in romantic attachment style (for a more detailed account of romantic attachment styles, see ► [“Attachment in Adulthood”](#)). Many of the aforementioned findings have thereby partly been translated into attachment terms. For instance, romantic attachment security has been associated with higher stability and commitment in pair bonds, less likelihood of engaging in extra-dyadic sex, and more enjoyment from romantic relationships. Avoidant individuals, in contrast, often display lower pair-bond stability, more short-term reproductive behavior, and report less commitment and intimacy in romantic relationships. Findings for romantic anxiety have been more inconsistent but have overall indicated lower relationship stability and increased risk for unwanted pregnancy and sexually transmitted diseases in anxious women, and less frequent sexual activity in anxious men (Mikulincer and Shaver 2016).

Individual Differences in Pair Bonding: Attachment or Reproductive Strategies?

In Zeifman’s and Hazan’s (2016) account, the attachment system is held to be operative in long-term pair bonds, due to exaptation of the

attachment system in the course of evolution. The proposed function of this exaptation is to facilitate long-term pair bond mating strategies, which are thought to have generally superior adaptive value compared to short-term mating strategies. Romantic attachment styles are also thought to reflect variations regarding the presumed availability and responsiveness of the mate (i.e., attachment-related dynamics), with secure attachment typically being the most efficient for maintaining pair bonds.

Some of these notions have been contested by other theorists. For instance, Kirkpatrick (1998) has argued that considering the many external threats of the EEA, it would have been maladaptive for our adult ancestors to be heavily influenced by a behavioral system that evolved to promote protection through reflexive proximity seeking in the face of danger. Kirkpatrick also finds it unlikely that an entire behavioral system would be retained through development and yet undergo a qualitative change in its function. Hence, he rejects the notion that the attachment system is central for pair-bond functioning. Instead, he argues that the sexual mating system should be regarded as the primary behavioral system in romantic relationships, and that features related to the caregiving system – especially love operating as a commitment device – were co-opted by evolution to cement such relationships. Kirkpatrick and others (e.g., Belsky 1999) have also questioned whether long-term pair bonds really are of superior adaptive value. While long-term, investing strategies – aimed at maximizing offspring quality – might have been evolutionarily advantageous in resourceful and reasonably harmonious rearing environments, short-term and less investing strategies, aimed at increased offspring quantity, might have been more beneficial in harsher and poorer environments. Thus, rather than reflecting attachment-related variations, romantic attachment styles might reflect the reproductive strategies learnt to be the most adaptive in the individual's childhood environment.

In response, it has been argued that Kirkpatrick's view relies on an overly narrow definition of protection that fails to acknowledge normative developmental changes in the protective aspects of attachment. It has also been pointed out that

although associations exist between romantic attachment styles (secure vs. insecure) and mating strategies (long-term vs. short-term), the variation with regard to mating behavior is far too widespread within the different attachment styles for them to simply be reduced to mating strategies. Moreover, even if different mating strategies are adaptive in different environments, their outcome might not be equal with regard to long-term reproductive success. Just as the organized insecure forms of childhood attachment could be considered optimal adaptations to particular caregiving environments, but are sub-optimal with regard to long-term outcomes compared to secure attachment, short-term mating strategies have been associated with less optimal outcomes for offspring in a number of subsequent life contexts (Zeifman and Hazan 2016).

Leaving this dispute unsettled, it nevertheless highlights an important gap in existing research on adult attachment. As noted by Mikulincer and Shaver (2016), little empirical work has investigated the mutual influence of attachment, sexual mating, and caregiving systems on pair bond dynamics, and the available evidence does little to verify the presumed superior influence of the attachment system. Furthermore, while largely focusing on the respective importance of the attachment and sexual mating systems, the possible role of the caregiving system in pair bonding has received less interest from researchers. However, as noted by George and Solomon (2008), the importance of the caregiving system in rearing contexts is not restricted to females. Although gender differences likely exist regarding the interaction among behavioral systems, males can also be sensitive and involved caregivers, and throughout evolutionary history males have often also served a function in caregiving (Hrdy 2009). Thus, it seems possible that the caregiving system – operating in both females and males – has played a role in the evolution of pair bonds, facilitating joint parental investment by means of mutual concern for shared offspring.

Conclusion

Following selection pressures in human's primeval environments, pair bonds are thought to have

enhanced reproductive fitness for both infants and mates. It has been suggested that the attachment system, originally developed to secure infant protection from dangers, was exploited by evolution to foster such bonds. As a result, it has been argued, attachment-related dynamics play an integral role in romantic relationship functioning. This view has been supported by various theoretical and empirical findings. However, as illustrated by contesting views on the nature of romantic attachment styles, important research questions – not least regarding the interrelations between the attachment, caregiving, and sexual mating systems – still largely remain open.

Cross-References

- [Attachment in Adulthood](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Infant Survival](#)
- [Marriage](#)
- [Mating Strategies](#)
- [Monogamy](#)
- [Special Friendships Among Baboons](#)

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Pair Bonds

- [Dyadic Relationships Versus Group Processes](#)

Pair-Bond Attachment

- [Romantic Attachment](#)

Pair-Bonding

- [Benefits of Commitment and Marriage](#)
- [Male Qualities and Likelihood of Orgasm](#)

Pair-Bonding in Other Mammals

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Synonyms

[Adult attachment](#); [Social bond](#)

Definition

Pair-bonding is an adult attachment relationship defined by a social preference for the pair-mate,

the distress upon separation, and the ability of the pair-mate to mitigate stressful situations.

Introduction

Pair-bonding is a behavioral construct central to adult human relationships and is also displayed in some other mammalian species (primarily ones which display monogamy as a social system). These other mammal species have given us the opportunity both to refine our definition of pair-bonding and to investigate its neurobiological substrates.

What is Pair-bonding and How do we Measure it?

Pair-bonding is a behavioral and psychological construct describing strong, enduring, selective social bonds between two adults. The concept is based on attachment theory as originated by Bowlby and Ainsworth (Bowlby 1969); however, they primarily applied this concept to infant-mother relationships, while pair-bonding is applied to adult dyadic relationships (Hazan and Shaver 1987). Pair-bonded adults (just like infants toward their mother) should display a preference for their familiar partner, distress upon separation, and lower responses to stress when in the company of their pair-mate (also known as “social buffering”) (Mason and Mendoza 1998).

Pair-bonding in nonhuman mammals has been well operationalized. The partner preference test was developed by Williams and Carter in the early 1990s (Williams et al. 1992). This test involves giving the test subject free access to three chambers: one which is empty, one containing the partner, and one containing a stranger of the same sex, and approximately the same age and weight as the partner. A partner preference is then defined as a statistically significant difference in the amount of time spent with the partner, higher than that spent with the stranger. The cohabitation time for the pair can be manipulated depending on whether you are experimentally testing a facilitation or an impairment of the bond. In other words, if you

want to know if your treatment increases the probability of forming a pair-bond, use a short cohabitation period; if you want to know if your treatment decreases the probability of forming a pair-bond, use a longer cohabitation period at least as long as the minimum time normally needed for bond formation.

Distress upon separation is typically measured by either distress vocalizations upon removal of the partner, increases in locomotion, or increases in the stress hormones cortisol or corticosterone. Finally, social buffering is measured by exposure to a stressor (e.g., handling) with and without the presence of the pair-mate. One caveat in these two measures is that experimenters rarely test the *specificity* of the social partner. For example, in order to really test whether an animal is distressed by removal of the pair-mate, the test animal should still have access to another familiar conspecific. This differentiates whether the distress is due to the missing pair-mate or social isolation. Other measures of pair-bonding have been suggested but not widely used, such as being willing to “work” to gain access to a pair-mate (Bardet et al. 2007).

What Other Mammals Pair-Bond?

In the animal world, pair-bonding is sometimes used interchangeably with the term “monogamous” or “socially monogamous,” or it is at least assumed that socially monogamous animals form pair-bonds. Social monogamy indicates a social system in which two adults and their offspring form basic groups. It is often, but not always, characterized by coordinated behavior between the pair-mates, defense of a mutual territory, mate-guarding behavior, and sometimes also male parenting. It differs from genetic monogamy, which is a mating system in which there are no extra-pair copulations, whereas most species branded as socially monogamous do display significant levels of extra-pair paternity. While most pair-bonds probably do occur in the context of socially monogamous species, social monogamy does not necessarily indicate the existence of a pair-bond. There is strong evidence for pair-bonding in remarkably few species, which we review below.

In the wild, titi monkeys (*Callicebus* spp.) live in nuclear family groups (a mated pair and their offspring) with coordinated activity, duetting of pair-mates, and mate-guarding (Mason 1968). Titi monkeys have also been well studied in captive settings. They display a preference for their partner in a classic partner preference test, although which pair-mate expresses a stronger preference may change over the course of pair-bonding (Carp et al. 2016). They display lower responses to stress when tested in the presence of the pair-mate (Hennessy et al. 1995), demonstrating stress-buffering effects. When the pair-mate is not present, they exhibit substantial distress (Mendoza and Mason 1986a), which is not attenuated by the presence of their infant (Mendoza and Mason 1986b) or an unfamiliar adult (Mendoza and Mason 1986a).

Prairie voles (*Microtus ochrogaster*), a classically monogamous species, in the wild display variations including monogamous families, communal groups, single female mothers with offspring, and wandering males (Getz and Hofmann 1986). It is unknown whether some of these variations are due to random circumstances (e.g., loss of a mate) or stable alternative reproductive strategies. Prairie voles do display all the hallmarks of pair-bonding in the lab, including a preference for the partner (Williams et al. 1992), distress upon separation (Resendez and Aragona 2013), and stress buffering (Smith and Wang 2014). While the specificity of the social buffering effects has not been well tested, “consolation” behavior is preferentially directed toward a pair-mate over an unfamiliar animal (Burkett et al. 2016).

Marmosets and tamarins, all members of the primate family Callitrichidae, display many interspecies similarities of social structure and behavior, with groups consisting of an adult pair, their offspring, and sometimes an additional reproductive unrelated or related adult (e.g., the brother or father of the breeding male, the mother or daughter of the breeding female) (Baker et al. 2002; Garber et al. 2016). Older offspring also help care for infants, making this a cooperatively breeding social system. Operational measures of pair-bonding have been tested in Wied’s

marmosets (*Callithrix penicillata*). During the first 3 weeks after pairing, these monkeys interacted more with strangers than with their partners during a preference test; however, by the end of 3 weeks, they interacted with both equally (Smith et al. 2010). After 8 weeks of cohabitation, females still spent more time in proximity with a stranger, while males spent equal amounts of time near their partner and a stranger (Cavanaugh et al. 2014). While it is possible that preference for the partner might increase over further development of the pair-bond, this cohabitation length was based on home-cage observations of affiliation (Agmo et al. 2012), suggesting that these may not always translate into a partner preference in a testing situation.

Marmosets show strong reactions to separation from their pair-mate. These separations are characterized by an increase in cortisol, which is attenuated by exposure to vocalizations from the pair-mate, but not by vocalizations from an unfamiliar animal (Rukstalis and French 2005). However, in male common marmosets (*Callithrix jacchus*), stress responses are buffered by familiar individuals such as a brother (Galvao-Coelho et al. 2012). Based on the evidence from this test and the partner preference testing described above, it seems less likely that marmosets have a strong, specific pair-bond.

Pair-bonds of other species which have been described as socially monogamous in the wild are less studied in captive settings, at least experimentally (e.g., the California mouse (*Peromyscus californicus*) and the owl monkey (*Aotus* spp.)). Mongolian gerbils (*Meriones unguiculatus*) do display the formation of a partner preference in females (only females were tested), whereas separation selectively affects males (Razzoli and Valsecchi 2006). Monogamous caviés (*Galea monasteriensis*) were similar; females developed a strong partner preference (only females were tested), while males displayed a separation response (only males were tested) (Adrian et al. 2008). In Siberian dwarf hamsters (*Phodopus sungorus*), males separated from their mates displayed a rise in cortisol as well as lower activity levels (only males were tested) (Castro and Matt 1997).

What Is the Neurobiological and Physiological Basis of Pair-Bonding in Other Mammals?

The neurobiology of pair-bonding is best studied in prairie voles. It is thought to involve co-activation of neurons for peptide hormones, oxytocin and vasopressin, and the neurotransmitter dopamine (Carter 1998; Gobrogge and Wang 2015). Briefly, oxytocin and vasopressin are involved in social memory, allowing for the selectivity of the pair-bond as far as which other individual is involved. During the formation of a bond, oxytocin acts on receptors in the nucleus accumbens in females, while vasopressin acts on V1a receptors in the ventral pallidum in males. Dopamine, a neurotransmitter involved in reward and addition processes, is also released into these areas. Its D2 receptors are present in the nucleus accumbens and ventral pallidum, and activation of those receptors facilitates the formation of the bond. Later, dopamine D1 receptors are upregulated and subserve the aggression which develops toward outsiders and functions to maintain the pair-bond. Mu opioid receptors facilitate the hedonic aspects of pair-bond formation, while kappa opioid receptors regulate the dysphoria of separation (Resendez and Aragona 2013).

The neural basis for pair-bonding in primates has been much less studied. Imaging of titi monkeys (*Callicebus cupreus*) indicates the involvement of the same neural areas implicated in rodent studies (Bales et al. 2007). In the same species, intranasal vasopressin in males increases contact with the female mate versus a strange female. In addition, agonism of mu opioid receptors and antagonism of kappa opioid receptors both decrease distress to separation from a mate (Ragen et al. 2015, 2013).

In common marmosets (*Callithrix jacchus*), oxytocin reduces interaction with an opposite-sex stranger, but only in females does it increase interactions with the mate (Cavanaugh et al. 2014). Treatment with oxytocin also made marmosets more attractive to their mates (Cavanaugh et al. 2015).

Conclusion

While arguments about whether or not humans are “monogamous” often take center stage, it is clear

that adult humans do develop strong, selective social bonds to each other. The study of pair-bonding in other mammals allows us to consider how experimental measures of pair-bonding would work in humans (without the use of questionnaires)! It also allows us to more fully investigate the neurobiological and physiological underpinnings of pair-bonding.

Cross-References

- ▶ [Attachment Theory](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Early Attachment Experiences and Romantic Attachment](#)
- ▶ [Evolution of Long-Term Pair-Bonding in Humans](#)
- ▶ [Exclusivity and Pair-Bonding Among Non-humans](#)
- ▶ [Helper at the Nest Among Nonhuman Primates](#)
- ▶ [John Bowlby](#)
- ▶ [Mating Strategies](#)
- ▶ [Mating Systems](#)
- ▶ [Monogamy](#)
- ▶ [Pair-Bonding](#)
- ▶ [Parental Effort Versus Mating Effort](#)
- ▶ [Parental Investment and Parenting](#)
- ▶ [Paternal Investment Relative to Maternal Investment](#)
- ▶ [Social Monogamy](#)

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Palatability

► Taste

Paleoanthropology

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Synonyms

[Human paleontology](#)

Definition

The study and interpretation of the fossil record of humans.

Introduction

Paleoanthropology is a subdiscipline within physical/biological anthropology that is devoted to the study and interpretation of the human fossil record. The fossil record includes not only the skeletal remains of human ancestors but other vestiges like fossilized footprints, endocasts (the natural or recreated casts of the brain), and stone tools or other artifacts. In the last decade, the study of ancient DNA (aDNA) has also progressed to become a significant contributor to paleoanthropological work.

Paleoanthropology

One of the primary goals of research in paleoanthropology is the reconstruction of evolutionary relationships, known as phylogenies, to better understand the relationships of various ancestor and descendant species throughout prehistory. This work has traditionally been accomplished through the study of various anatomical details found on the fossils themselves, which can provide clues to establish relationships between fossils and species. The addition of aDNA has enhanced our ability to understand relationships between more recent fossil groups, such as the Neandertals, and modern *Homo sapiens*.

Paleoanthropologists also examine the biology and behavior of human ancestors, and how hominins (humans and our ancestors) initially separated from the great apes. Bipedal locomotion has been recognized as the primary adaptation that separates a human ancestor from an ape. The origin of bipedality is quite controversial, with a variety of theories attempting to explain why humans would have adopted this posture and somewhat awkward form of movement. The earliest fossil humans include *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus ramidus*, and a variety of species of *Australopithecus*. Species joining us in the genus *Homo*, indicating similarities in body size, body proportions, and some behaviors, include *Homo habilis* and *Homo erectus*. Neandertals are typically referred to as either *Homo neanderthalensis* or *Homo sapiens neanderthalensis*, the latter suggesting a close relationship that would have allowed potential interbreeding with modern humans.

Paleoanthropology is a relatively young science, arguably tracing its origins to two key developments in the mid-nineteenth century. The first came in 1856 with the recognition of the first Neandertal fossil, discovered at Feldhofer's Cave in the Neander Valley in Germany (the word Neandertal refers to the location of this discovery, "tal" being the German word for valley). This first fossil skeleton forced scientists to confront the reality of ancient humanity, but at that time they lacked the theoretical basis to make sense of the find. In 1859, Charles Darwin provided that theoretical basis with the publication of *On the Origin of Species*. This seminal work laid the foundation for understanding the fossil record, and Darwin's 1871 book *The Descent of Man* addressed the evolution of humans specifically. The end of the nineteenth century brought a series of additional discoveries of fossil humans in Asia and Europe, further validating Darwin's predictions. The human fossil record now spans approximately seven million years, and includes dozens of fossil hominin species.

Advances in genetic sequencing technology, sampling, and computer processing have led to a revolution in the study of aDNA. The full nuclear

genome of the Neandertal has been sequenced and suggests that they may have interbred with humans (Green et al. 2010). These interpretations remain controversial, and more recent work casts some doubt on the potential for significant interbreeding (Fu et al. 2016; Mendez et al. 2016). Another exciting development has been the discovery of the Denisovans, the first human ancestor to be identified by its genetic sequence (Reich et al. 2010).

Conclusion

Paleoanthropology has illuminated many different aspects of our biological and intellectual evolution. The interpretation of fossil and archaeological evidence has been informed by a variety of scientists from different disciplines, with geneticists providing a series of important recent discoveries.

Cross-References

- ▶ [Australopithecus Group](#)
- ▶ [Charles Darwin](#)
- ▶ [Human Genome Project, The](#)
- ▶ [Neanderthals and Humans](#)

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Paleoneurology

- ▶ [Evolution of the Brain, The](#)

Pallium

- ▶ [Frontal Cortex](#)

Pan

- ▶ [Social Cognition and Communication in Chimpanzees and Bonobos](#)

Panhuman Manifestations of Genealogical Relationships

- ▶ [Universal Aspects of Kinship](#)

Pant Hoots

- ▶ [Vocal Grooming](#)

Paraaustralopithecus aethiopicus

- ▶ [Paranthropus aethiopicus](#)

Parable

- ▶ [Metaphor and Analogy](#)

Paranthropus

- ▶ [Australopithecus Group](#)

Paranthropus aethiopicus

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Synonyms

Australopithecus aethiopicus; *Paraaustralopithecus aethiopicus*

Definition

Early hominin species that lived in East Africa between 2.7 and 2.3 million years ago (mya) and is distinguished by its large teeth and jaws.

Introduction

Paranthropus aethiopicus is a species of early hominin that lived in East Africa approximately 2.7–2.3 million years ago (mya). Its designation as a hominin indicates that it is more closely related to modern humans than to any other living primate. However, this species lived alongside members of our own genus, *Homo*, and is thus believed to have gone extinct without contributing directly to the evolution of modern humans. Nonetheless, its study provides an important comparative context for our own evolutionary history.

Morphology and Evolutionary Relationships

Paranthropus aethiopicus is one of three hominin species distinguished by having more “robust” skulls than hominins of other genera. The “robust” traits of these skulls include large and thickly enameled postcanine teeth supported by deep and broad mandibles, zygomatic (cheek) bones extending both laterally and anteriorly, and the occasional presence of bony crests on the top and back of the skull, presumably for the

attachment of large jaw and neck muscles, respectively (Constantino 2013). Taken together, these traits suggest an animal that could both generate and dissipate high bite forces, and they imply that at least some portion of the *Paranthropus* diet was particularly difficult to break down (Rak 1983; Hylander 1988; Demes and Creel 1988). *P. aethiopicus* differs from the other members of its genus in having a more prognathic lower face (i.e., it projects further anteriorly), larger incisors, a shorter postcanine tooth row in a smaller mandible, a more posteriorly positioned sagittal crest, and a less flexed cranial base (Walker et al. 1986). These traits suggest a greater reliance on the anterior dentition, and along with features like a smaller cranial capacity (≈ 410 cc) suggest that *P. aethiopicus* may have evolved from the earlier *Australopithecus afarensis* (the species of the famous Lucy skeleton) (Skelton and McHenry 1992). Most paleoanthropologists agree that *P. aethiopicus* ultimately evolved into *Paranthropus boisei* (2.3–1.2 mya), which itself was broadly contemporaneous with the South African species *Paranthropus robustus* (1.8–1.2 mya).

Most paleoanthropologists recognize the distinctiveness of *Paranthropus* relative to other early hominin genera, but there is some debate about whether the species within this genus all evolved from a common ancestor to the exclusion of other hominin species (thus forming a monophyletic group) or whether the species from East and Southern Africa evolved from different ancestors in those areas. If they are not monophyletic, then the rules of taxonomic nomenclature state that they cannot be included in their own genus to the exclusion of others. Scientists who doubt their monophyly place them in the genus *Australopithecus*, along with approximately seven other species of less “robust” forms. Therefore, it is not uncommon to see this species listed as *Australopithecus aethiopicus*.

Key Specimens

Paranthropus aethiopicus is currently known from three sites including Laetoli in Tanzania, the Omo in Ethiopia, and West Turkana in

Kenya. Important specimens come from each of these sites, but the most well-known specimen is KNM-WT 17000 from West Turkana. It is a nearly complete cranium, though lacking in teeth. It is more commonly known as the “Black Skull” due to its dark color that reportedly resulted from high concentrations of manganese in the soil in which it was found. Other key specimens in the *P. aethiopicus* hypodigm include the mandible KNM-WT 16005, the mandible (and type specimen) Omo 18-18, and the maxilla EP 1500/01 (Arambourg and Coppens 1968; Walker et al. 1986; Harrison 2011). This latter specimen, from Laetoli, was the first of this species to be found outside of the Turkana Lake Basin. Moreover, it was found with a proximal tibia (EP 1000/98) – the first and only recognized postcranial element of this species (Harrison 2011).

Behavior

Most attempts to reconstruct the behavior of *Paranthropus* have focused on *P. boisei* and *P. robustus*, and with only one postcranial element confidently attributed to *P. aethiopicus*, we know virtually nothing about this species’ lifeways. There is even some lingering doubt about whether *P. aethiopicus* represents a valid species or whether it should be subsumed into *P. boisei*. Nearly all researchers accept there are differences between KNM-WT 17000 and the crania belonging to the *P. boisei sensu stricto* hypodigm, but there is less agreement about whether those differences justify a specific distinction between the two groups of fossils. The two studies that looked at this problem in detail have supported the validity of the species *P. aethiopicus* (Suwa 1988; Wood et al. 1994), but given the small size of the *P. aethiopicus* hypodigm, any solid conclusions about this species will need to await future discoveries.

Conclusion

Based on the evidence in the fossil record, *Paranthropus aethiopicus* originated at about

the same time as our own genus, *Homo*. Therefore, even though these hominins are not believed to be our direct ancestors, they may prove to be very useful for understanding our origins.

Cross-References

- ▶ [Homo habilis](#)
- ▶ [Paleoanthropology](#)
- ▶ [Paranthropus boisei](#)
- ▶ [Paranthropus robustus](#)

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Paranthropus boisei

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Synonyms

Australopithecus boisei; *Zinjanthropus boisei*

Definition

Early hominin species that lived in East Africa between 2.3 and 1.4 million years ago (mya) and is distinguished by its large teeth and jaws.

Introduction

Paranthropus boisei is a species of early hominin that lived in East Africa approximately 2.3–1.2 mya. Its designation as a hominin indicates that it is more closely related to modern humans than to any other living primate. However, this species lived alongside members of our own genus, *Homo*, and is thus believed to have gone extinct without contributing directly to the evolution of modern humans. Nonetheless, its study provides an important comparative context for our own evolutionary history.

Morphology and Evolutionary Relationships

Paranthropus boisei is currently known from at least eight sites in Ethiopia, Kenya, Tanzania, and Malawi. It is generally thought to have evolved from the earlier *Paranthropus aethiopicus* (2.7–2.3 mya) and been broadly contemporaneous with the South African *Paranthropus robustus* (1.8–1.2 mya). Together, these three species form a group that is distinguished by several morphological traits that give their skulls a more “robust” appearance than those of other hominins.

These traits include large and thickly enameled postcanine teeth supported by deep and broad mandibles, zygomatic (cheek) bones extending both laterally and anteriorly, and the occasional presence of bony crests on the top and back of the skull, presumably for the attachment of large jaw and neck muscles, respectively (Constantino 2013). *P. boisei* differs from the other members of its genus in being even more derived or “robust” in its skull features and having a more orthognathic (retracted) face (Rak 1983); the latter condition being one they share with members of our own genus *Homo* (Fig. 1).

Most paleoanthropologists recognize the distinctiveness of *Paranthropus* relative to other early hominin genera, but there is some debate about whether the species within this genus all evolved from a common ancestor to the exclusion of other hominin species (thus forming a monophyletic group) or whether the species from East and southern Africa evolved from different ancestors in those areas. If they are not monophyletic, then the rules of taxonomic nomenclature state that they cannot be included in their own genus to the exclusion of others. Scientists who doubt their monophyly place them in the genus *Australopithecus*, along with approximately seven other species of less “robust” forms. Therefore, it is not uncommon to see this species listed as *Australopithecus boisei*.

Key Specimens

The hypodigm of *P. boisei* consists of over 100 craniodental remains including the holotype subadult cranium OH 5 from Olduvai Gorge, the cranium KNM-ER 406 from Koobi Fora, and the mandible NMT-W64-160 from Peninj. Assigning postcranial fossils to this species has proven more challenging. A few have been attributed to *P. boisei* over the years (e.g., Grausz et al. 1988; Aiello and Porter 1990), but the only reported association of postcranial fossils with craniodental remains diagnostic of *P. boisei* comes from a single specimen from Olduvai Gorge (Domínguez-Rodrigo et al. 2013). The general picture that emerges from these limited



Paranthropus boisei, Fig. 1 Replica of a *Paranthropus boisei* skull (specimen OH 5) from Tanzania shown in (a) lateral, (b) anterior, and (c) inferior views

postcranial specimens is that of a muscular, terrestrially bipedal animal that may have continued to engage in arboreal behaviors. This behavioral reconstruction is not unlike those of other pre-*Homo* species, including members of the genus *Australopithecus*.

Behavior

When viewed as a functional unit, the “robust” skull traits of *P. boisei* suggest an animal that could both generate and dissipate high chewing forces, and they imply either that some portion of their diet was particularly difficult to break down or that they ate low-quality foods that required substantial chewing times. The latter hypothesis gained considerable support with the discoveries that *P. boisei*’s dental microwear shows no obvious evidence of hard food consumption (Ungar et al. 2008) and that this species had a carbon isotope signature consistent with extensive ingestion of tropical grasses and/or sedges (Cerling et al. 2011).

A lingering question about the behavior of *P. boisei* is whether or not they were capable of manufacturing and using stone tools. The dominant stone technology in existence during the time of *P. boisei* was called the Oldowan, and it

consisted mainly of hammerstones, cores (possibly used as choppers), and flakes used for cutting. However, most believe this stone culture was the product of the genus *Homo*, who was also around at this time and had larger brains than *Paranthropus*. Since all other great ape species and even capuchin monkeys use stone tools (Sanz et al. 2013), it is likely that *P. boisei* was capable of doing so as well. However, the question as to whether they could have intentionally modified and shaped stone to the extent that early *Homo* did remains open (Constantino and Wood 2007). Recent evidence of Oldowan tools at 3.3 million years ago (Harmand et al. 2015), prior to the appearance of both *Paranthropus* and *Homo*, is sure to reignite the debate.

Conclusion

Although *Paranthropus boisei* does not appear to be a direct ancestor of modern humans, knowledge of its paleobiology may prove critical in establishing the comparative context in which our genus evolved. Further discovery and study of these fossil remains may provide clues as to whether and how *Paranthropus* and *Homo* interacted, why the masticatory systems of *Paranthropus* enlarged while ours were becoming

smaller, and whether material culture was key in distinguishing the behavior of these two hominin groups. Ultimately, it may even help us to understand why *Paranthropus* went extinct while our own genus set off to inhabit almost the entire planet.

Cross-References

- [Homo habilis](#)
- [Paleoanthropology](#)
- [Paranthropus aethiopicus](#)
- [Paranthropus robustus](#)

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Paranthropus robustus

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Synonyms

[Australopithecus robustus](#)

Definition

An extinct species (*Paranthropus*, meaning “beside-human”; *robustus*, “strongly built”) of South African hominins – bipedal human relatives from the Pleistocene Epoch (ca. 2.2–1.5 million years ago), possessing a small brain, small incisors and canines, and large postcanine dentition, considered a side branch of the human phylogenetic tree.

Introduction

Early in the twentieth century (the 1920s–1930s), three important discoveries were made in Southern Africa: the Taung Child – the first known *Australopithecus*; an adult specimen from Sterkfontein (then named *Plesianthropus*); and *Paranthropus* from Kromdraai. The latter discovery, together with later found similar fossils from Swartkrans, led to the understanding that not all “ape-men” (as they were called) were ancestors of humans, i.e., early on in the evolutionary history of hominins, a branching event occurred, from which two evolutionary lineages arose: one leading to us, humans, the other becoming extinct without leaving descendants.

Discoveries

The history of the discoveries of *Paranthropus* (generally referred to as a “robust”

australopithecine) dates back to 1938 when Scottish-born medical doctor, Robert Broom, then working as a curator at the Transvaal Museum in Pretoria, obtained the first fossil remains from the Kromdraai site. The specimen (TM 1517: partial cranium and mandible) was designated as the holotype of a new genus and species – *Paranthropus robustus*. In 1948, other remains were discovered at nearby Swartkrans (SK 6: mandible with teeth). Broom recognized this as being related to *Paranthropus* from Kromdraai, but on the basis of tooth size differences, it was assigned a new species name – *Paranthropus crassidens* (meaning “thick tooth”). Since then many specimens have been unearthed from the Swartkrans cave (e.g., Sussman, Grine [in:] Grine 1988; Grine, Sussman [in:] Brain 2004), making it the second largest site (after Sterkfontein) for hominin remains in South Africa. Currently, at least five “robust” australopithecine-yielding fossil sites are known. All of these were once caves (e.g., Brain [in:] Brain 2004) formed in dolomitic limestone, located about 10 km from Krugersdorp (near Johannesburg and Pretoria), which have recently been incorporated into the “Cradle of Humankind” (South African National Heritage site). The key *Paranthropus* sites are Kromdraai (yielding a dozen or so individuals), Swartkrans (over a hundred individuals), and Drimolen (tens of individuals, including a female skull – DNH 7), as well as Cooper’s Cave (partial cranium) and Gondolin (lower molar).

Dating

Unfortunately, the South African early hominin fossils are difficult to date because the cave sediments in which they are found are not suitable for the most absolute dating techniques. Therefore, their temporal distribution is not precise, being based primarily on faunal comparisons with other – East African – sites, biostratigraphy, and paleomagnetism. The age of the remains of *Paranthropus robustus* is estimated at older than 2.2 (Bruxelles et al. 2018) to ca. 1.5 Mya.

Morphology

In his earliest descriptions of *Paranthropus robustus*, Broom compared the morphology of the new fossil to that of extant apes and humans, and the fossils from Sterkfontein (*Australopithecus africanus*), and noted the differences in shape and size of the teeth and features of the temporal bone, palate, and face. He was intrigued by the anterior position of the cheeks, writing: “if a ruler be placed on the two cheeks the rest of the face is behind the ruler.” Since then, a number of monographs describing various aspects of the morphology of the “robust” australopithecines (see Fig. 1) have been published, partially or entirely devoted to the subject (e.g., Broom and Schepers 1946; Broom and Robinson 1952; Rak 1983; Kaszycka 2002). For a list of characteristic, diagnostic *P. robustus* features, see Table 1.

Taxonomic Views

Broom was a “splitter” – for the fossils from each site he was inclined to assign a new genus. Robinson (1954) simplified the existing classification, placing the South African hominin fossils into two genera and species – *Australopithecus africanus* and *Paranthropus robustus*. The former was



Paranthropus robustus, Fig. 1 Frontal view of the Swartkrans *Paranthropus robustus* cranium SK 48 (Photo by KA Kaszycka)

***Paranthropus robustus*, Table 1** List of characteristic *Paranthropus robustus* morphological features

Cranium
– Short and broad face
– Anterior position of the cheeks (zygomatic bones) with posterior placement of the midface (so-called dished face)
– Thin, arched supraorbital tori
– Frequent bony crests at the top of the skull (sagittal crest)
– Zygomatic arches broad, sagittally oriented
– “Anterior pillars” of the face (vertical bony columns bordering the nasal aperture)
– “Maxillary trigon” (triangularly shaped concave area of the infraorbital region)
Mandible
– Usually thick and robust corpus
– Tall and wide ramus
Dentition
– Small anterior teeth (incisors and canines) relative to posterior teeth (especially second premolars and molars)
– Low-crowned canines
– Premolars: P4 larger than P3
– Maxillary molars: M1 < M2 < M3 (with larger disproportion between M2 and M1 than between M3 and M2); high incidence of a Carabelli trait
– Mandibular molars: M1 < M2 < M3; mostly 6-cusped (on M3s usually more); high frequency of C6; low frequency of C7; high frequency of protostylid
– Mandibular deciduous molars: dm1, mostly 5-cusped; dm2, mostly 6-cusped (with C6 present)

described as “gracile,” i.e., lightly built, while the latter as “robust,” i.e., strongly built. Robinson argued that the generic distinctiveness of *Paranthropus* be retained, as he postulated that both taxa show adaptive and ecological differences. The specific distinction between *P. robustus* from Kromdraai and *P. crassidens* from Swartkrans was then reduced to a subspecific one – the two samples were separated on the basis of subtle differences in their deciduous teeth. Although later some researchers, e.g., Grine (in Grine 1988), restored the species-level distinction between the Kromdraai and Swartkrans samples (the Kromdraai specimens being less specialized), most current opinions hold that they are not taxonomically distinct (e.g., Kaszycka 2002). Findings from Drimolen (a nearby hominin-bearing fossil site) support the

hypothesis that all South African “robust” australopithecines are a single, though variable, species: the deciduous teeth of these remains have a considerable amount of morphological and metrical variation, showing similarities with the Kromdraai sample in some features and with the Swartkrans sample in others.

Dietary Habits

Early hypotheses about dietary adaptations of the australopithecines were based on anatomical features – the analysis of the size and proportion of their front to back teeth, as described in John Robinson’s 1954 classic “Dietary Hypothesis.” *Paranthropus* was then seen to be a vegetarian, while *Australopithecus* – an omnivore. Since the 1980s, microwear patterns on the molar teeth have been used to reconstruct the australopithecines’ food habits. Differences in the proportion of scratches and pits on the enamel surface of the molar teeth were revealed: the “robusts” showing more pits, which led to the conclusion that *P. robustus* ate hard food objects (e.g., Kay and Grine [in:] Grine 1988). Subsequent reconstruction of the hominins’ diet was based on direct evidence – isotopic analyses of chemical signatures in their teeth and bones. According to A. Sillen, the strontium to calcium ratio for the Swartkrans fossils appeared inconsistent with a herbivorous diet, suggesting an eclectic omnivory of *P. robustus*. From the stable carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$) in tooth enamel, it was possible to determine the kind of plants that were predominantly consumed. Carbon isotope values have shown a broader *P. robustus* diet in their consumption of not only C3- but also C4-derived food (e.g., Lee-Thorp and van der Merwe [in:] Brain 2004). Thus, such savannah-based foods as seeds and roots of tropical grasses, pith and tubers of grass-like plants – sedges, and/or the animals and insects that themselves eat these plants made up an important part of its diet. Underground storage organs, such as bulbs and corms, were also a possible source of nutrition. Lastly, it is possible that insects could have supplemented their diet. Today, therefore, it is accepted that *P. robustus*



Paranthropus robustus, Fig. 2 Upper molars of the Swartkrans *Paranthropus robustus* specimen SK 831a (top) compared with those of a modern human (bottom) (Photo by KA Kaszycka)

was most probably an omnivore, inclined toward herbivory, feeding on diverse plant foods requiring intensive mastication (see Fig. 2). In terms of its diet *P. robustus* was more generalist than specialist.

Tool Use

Chimpanzees have been frequently observed using (and producing) simple tools, so there seems scant reason to assume that *P. robustus* could not have. Modified fossil bones have been found at Swartkrans, which, by some (Brain and Shipman [in:] Brain 2004), are assumed to be *P. robustus* digging tools for edible plants' bulbs and corms while, by others (Backwell and d'Errico [in:] Brain 2004), to have been used for digging into mounds to extract termites. Brain's excavations at Swartkrans led him to conclude that these hominins were obviously not hunters, but rather the hunted (Brain 1981), possibly being the victims of predators, such as leopards (see Fig. 3).



Paranthropus robustus, Fig. 3 Juvenile cranium of the Swartkrans *Paranthropus robustus* specimen SK 54 with puncture holes in the parietal bones that match the lower canines of a fossilized leopard (Photo by K.A. Kaszycka)

Sexual Dimorphism and Mating System

A significant part of arguments for the accuracy of the reconstruction of the reproductive strategy of fossil hominins is derived from data on their sexual dimorphism. Prior to the discovery of the Drimolen skull DNH 7 by A. Keyser, which was smaller than any other *P. robustus* skull, it was generally thought that, in terms of body size, the level of sexual dimorphism of this species was relatively low (similar to that of the chimpanzee), while, in terms of cranial size, there was no significant variation. Later, it became clear that in fact *P. robustus* possessed a large level of size dimorphism. Recently, a study was published suggesting evidence of a difference in duration of growth between *P. robustus* males and females (Lockwood et al. 2007) – males maturing and achieving full body weight later than females (and young adult males being smaller than older ones). Combining this with estimates of a high degree of sexual dimorphism, the authors hypothesized a polygynous social system of extinct *P. robustus* similar to that of extant gorillas (i.e., one-male harems). This hypothesis, although attractive, was challenged on several points (Kaszycka 2016) – above all, “sexing” individual specimens and the uneven sex ratio in the available *P. robustus* sample. In consequence, the evidence for extended male growth seems doubtful, while the difference in duration of growth between males and females does not necessarily

imply one-male social groups. Therefore, although *P. robustus* exhibited an almost gorilla-like level of size dimorphism, a multimale–multifemale social system for these hominins was more likely.

Conclusion

We now know quite a lot about these cousins of our ancestors, yet there is still also much which is not known. We know that their adaptive strategy was that of powerful chewing. We also know that they became extinct, although we are unsure why.

The species from which *Paranthropus robustus* is descended is still a matter of debate – was it *Australopithecus africanus* or *Paranthropus aethiopicus*? A further question is whether the South and East African “robust” australopithecines are a monophyletic group (which would mean that the separate generic name would be justified) or a paraphyletic one (meaning that similarities within the group are based on homoplasies – independent evolution, not homologies – common ancestry).

Cross-References

- [Australopithecus africanus](#)
- [Hominin Evolution](#)

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Paraphilia

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Synonyms

[Kinks](#); [Nonconforming sexuality](#); [Variant sexuality](#)

Definition

A paraphilia is a preferred sexual interest (philia: love) considered to be unusual (para: outside the norms).

Introduction

Descriptions of paraphilias are highly controversial. In this entry, the concepts of paraphilia and paraphilic disorder will be presented. Correlates of paraphilias will also be described, along with a

proposition for a novel definition based on evolutionary criteria.

Official Definitions of Paraphilias

According to psychiatric diagnosis manuals, certain sexual interests (fantasies, urges, and/or behaviors) are uncommon, atypical, or anomalous (e.g., APA 2013). Typical examples of atypical sexual interests include voyeurism (observing an unsuspecting person who is naked, disrobing, or engaging in sexual activity), exhibitionism (exposure of one's genitals to an unsuspecting person), frotteurism (touching or rubbing against a non-consenting person), sexual masochism (being humiliated, beaten, bound, or otherwise made to suffer), sexual sadism (the physical or psychological suffering of another person), pedophilia (sexual interest in prepubescents), fetishism (sexual focus on objects or nongenital body parts), transvestism (cross-dressing), telephone scatologia (obscene phone calls), necrophilia (corpses), zoophilia (animals), urophilia (urine), klismaphilia (enemas), and coprophilia (feces). If these sexual interests are "intense" and "persistent" or greater than or equal to "normophilic" interests (i.e., "normal" preference or "interest in genital stimulation or preparatory fondling with physically mature, phenotypically normal, consenting human partners"; APA 2013), they are defined as paraphilias. If the paraphilia involves an illegal behavior or induces distress or impairment to the practitioner, it is viewed as the manifestation of a mental disorder (i.e., a paraphilic disorder; APA 2013).

These definitions are controversial, as they are based on assumptions that have not been demonstrated empirically. A first concern is the supposed rarity of some paraphilic interests. For example, fantasies and behaviors associated with voyeurism, couple exhibitionism, fetishism, masochism, and sadism are not statistically uncommon among adults (Joyal and Carpentier 2017). Therefore, certain paraphilic interests do not meet the basic criterion of being atypical. Another concern is the notion of intensity and recurrence of the sexual interest, as more than half of a nonclinical adult

sample reported some paraphilic sexual fantasies of equal or higher intensity than their "normophilic" fantasies (Joyal 2015). Maybe fantasies should not constitute a sufficient criterion to define paraphilia. A third concern is the unproven validity of the diagnosis given that signs of psychopathology are difficult to find among many types of non-offender paraphilic persons. For instance, a growing number of data suggests that persons practicing BDSM (bondage–discipline/domination–submission/sadism–masochism) possess equal, if not superior, psychological balance, educational achievement, and socioeconomical levels than the general population (e.g., Wismeijer and Assen 2013).

In addition, psychological distress associated with paraphilic interest results much more commonly from social negative perception and stigmatization than personal, inner, self-originating discomfort. Therefore, any definition of mental disorder should also include the effect of (and to) society. A fifth concern is the blur existing between legal and psychiatric criteria of sexual mental disorders. An illegal act per se (i.e., involving a non-consenting person) is not necessarily the manifestation of a mental disorder. In addition, legal definitions are unstable as they vary substantially across eras (e.g., oral sex) and cultures (e.g., homosexuality). Finally, the necessity of identifying precise sexual behaviors as symptomatic is not clear. It could be argued that any sexual interest inducing psychological suffering to the person should be considered as problematic, no matter its nature. In the next section, an attempt to better define paraphilia is made.

Defining Paraphilia from an Evolutionary Perspective

In 1992, Wakefield proposed a definition of mental disorder within an evolutionary perspective that unites biological and social perspectives. According to his definition, a condition is a mental disorder if it results from *the failure of a mental mechanism to perform its natural function* (biological or functional criterion) and if *it causes harm or deprivation of benefit to the person as*

judged by the standards of the person's culture (sociocultural or value criterion). As for paraphilias, they are traditionally defined in the field of evolutionary psychology as *any sexual behavior that diminishes or abolishes the odds of having a coital relation with a fertile person of the opposite sex* (Quinsey 2012). As stressed by Wakefield (2011), however, a sexual preference should induce a negative, undesirable or harmful effect on the individual *or on society as judged by social values* to be considered as paraphilic.

It is worth noting that these definitions still view homosexual behaviors as paraphilic (no coital relation and harmful effects on societies disapproving homosexuality). However, another sex-related and crucial function for humanity survival (and society cohesion) is the capacity to take good care of offspring. Giving the lengthy period during which human offspring are dependent on adults, biparental (or bi-adults or several adults in cases of adoption, reconstituted couples, and community living) caregiving represents an adaptive reproductive (and society cohesive) strategy almost as important as pregnancy. Selection pressures have produced physiological (e.g., oxytocin and vasopressin secretion) and psychological (e.g., emotions and affection) mechanisms to induce interpersonal attachment generated by sexuality. In turn, interpersonal attachment ensures the presence of adults to raise children, which improve their chances of surviving, well-being, and eventually reproducing compared with children of no parental or monoparental environments. Therefore, the odds of having an interpersonal sexual relation seem as important as those of having a coital relation. For instance, adopted children raised by infertile or homosexual but happy couples have much higher odds of future psychological well-being and professional success, on average, than children conceived by the rape of a fertile adolescent in a socioeconomic underprivileged environment (even if the latter sexual behavior theoretically helps species survival).

Thus, any exclusive sexual preference for behaviors not involving an interpersonal relation should be considered as suboptimal or undesirable from an evolutionary point of view. Exclusive paraphilic behaviors such as exhibitionism,

fetishism limited to an object, partialism without interest for the person, frotteurism, voyeurism, telephone scatologia, zoophilia, necrophilia, but also exclusive (and preferential) non-paraphilic behaviors such as exclusive (and preferential) solitary masturbation could be considered as problematic. Therefore, the exclusive and solitary (a preference to avoid interpersonal relations) qualities of a sexual behavior seem more important than its precise nature (paraphilic or not) to define optimal sexuality from an evolutionary perspective. For this reason, it is suggested to use the more general terms "disorders of sexual preference" (typical or not) than any specific paraphilia to describe suboptimal or maladaptive sexuality.

Paraphilia and Sexual Drive

Another motive to put emphasis on exclusivity rather than on the nature of a behavior in the definition of suboptimal sexuality is the fact that most paraphilic behaviors are associated with *higher general sexual drive*. Thus, although paraphilic behaviors are not by themselves coital, they are usually associated with *higher odds of having a coital relation*. Paraphilic interests are associated with low cerebral serotonin level (Kafka 1997). Low serotonin level is causally linked with higher general sexual arousal, behavioral impulsivity, thrill seeking, mood instability, and anxiety, all conditions that are commonly observed in persons with paraphilia. Testosterone, also associated with greater aggressiveness and sex drive, interacts with serotonin availability. These links between low serotonin level, high testosterone concentration, and high sex drive might partially explain why much more men than women develop paraphilia. Certain men might be more prone to associate nonsexual targets (e.g., inanimate objects or emotional experiences) with sexual arousal because they are more frequently and easily aroused sexually.

Indeed, paraphilic behaviors are rarely exclusive, and they should be placed on a continuum (e.g., from no interest for the behavior to exclusive use of it). When persons with paraphilic experience are recruited among the general population,

they commonly report greater sexual arousal, more diverse sexual interests (paraphilic and not), higher sexual orientation fluidity, and higher general sexual activity than non-paraphilic individuals (e.g., Långström and Hanson 2006; Joyal 2015). Paraphilic behaviors such as voyeurism, exhibitionism, and sadomasochism are associated with more (not less) lifetime sexual partners – contradicting traditional theories associating paraphilia with arrested sexual development or courtship disorders. BDSM practices, for instance, are obligatory for only a minority of practitioners, whereas a majority of players also enjoy “normophilic” behaviors. Many BDSM practitioners also report being as satisfied with their typical sexual activities as they are with their BDSM practices. Using pain or exposing genitals to strangers for sexual arousal is also associated with significantly higher (not lower) frequency of intercourse within stable relationships. In fact, Langevin and Lang (1987) found that exhibitionists usually have typical dating and sexual experience, many are married, and they enjoy intercourse.

Ironically, then, certain paraphilic behaviors might be associated with above-average reproductive fitness (i.e., increased number of lifetime coital relations with fertile partners), which would be evolutionarily adaptive. A notable exception is pedophilia, which not only involves a sexual focus on individuals that are not yet fertile but also is associated with higher odds of being single, living alone, and having no or less children, even when the pedophilic interest is not exclusive or have never been acted out. Frotteurism might also indicate a less favorable picture (more research is needed on the odds of coital behaviors associated with each paraphilia).

Sexuality and Psychopathology

Another reason to use the general terms “disorders of sexual preference” to define maladaptive sexual interests instead of specific behaviors is the fact that most paraphilic persons are not intrinsically distressed by their preferences, whereas any typical sexual interests could induce distress (e.g., an elderly distressed by his interests in oral sex or

frequent masturbation). Although a consensus exists to define a *distressing, necessary, compulsive* (i.e., *acted on urge, following a tension and producing relief*) and/or *uncontrolled* behavior as a psychopathological symptom, it should apply to any sexual behaviors, not only those defined as “paraphilic.” This way, any sexually distressed individual would receive treatment for a problem that is not currently listed in psychiatric manuals (distress caused by a typical sexual behavior or fantasy is considered neither as a sexual dysfunction nor as a paraphilia).

Sexuality and the Law

As for sexual behaviors involving a non-consenting person, they should be considered as crimes, whether or not they are listed as paraphilias (e.g., rape vs. voyeurism).

How Can Disorders of Sexual Preference Be Defined?

It is suggested to put more emphasis on the exclusive (or preferential) or psychopathological qualities of sexual behaviors and less on their precise nature (or legal statute) to define disorders of sexual preference. Therefore, the manifestation of a sexual mental disorder would have to meet one of the two criteria, derived from Wakefield’s definition:

- (A) To be any exclusive (no other sexual behavior is practiced) or frankly preferential (chosen more often for sexual gratification, even when coital relationship is available), non-coital *and* non-interpersonal (solitary or involving an unsuspected stranger or a non-human partner) sexual (leading to sexual arousal and/or sexual gratification) behavior (not only fantasies)
- (B) Any sexual behavior or fantasy inducing psychological suffering, i.e., distressing, rigid, obligatory, or compulsive (provoked by an irrepressible need to act out to reduce an inner tension or anxiety, perhaps followed by remorse, usually accompanied by both a

relief and a distressing feeling of loss of control) or occupational impairment (e.g., time, energy, or resources spent to complete the behavior affect other areas of life) to the individual practicing the behavior or having the fantasy

Conclusion

With this definition of disorders of sexual preference, emphasis is put more on the result of a sexual behavior (i.e., exclusively non-interpersonal or producing psychological symptoms) than its nature (paraphilic or not). Homosexual or infertile couples are not considered as maladapted, but pedophiles and child sexual abusers are. Consistent and preferential solitary masturbation from persons in couple would also be considered as problematic. As for all non-exclusive sexual behaviors involving non-consenting persons, they would be simply considered as crimes.

Cross-References

- [Aggression for Sexual Access](#)
- [Attachment Theory](#)
- [Benefits of Commitment and Marriage](#)
- [Child Care](#)
- [Homosexuality Paradox, The](#)
- [Human Sexuality](#)
- [Penile-Vaginal Sex](#)
- [Sex as Bonding Mechanisms](#)
- [Sexual Behavior](#)

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Paraphilias

- [Sexual Pathology](#)

Parasite Adversity

- [Function of Pathogen Prevalence \(Thornhill and Fincher\)](#)

Parasite Avoidance

- [Disease Avoidance](#)

Parasites

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Synonyms

[Leech](#); [Sycophant](#)

Definition

An organism that can either live in or on a host organism, and draws nutrients from the host, at the expense of the host organism.

Introduction

Within evolutionary biology there are many forms of parasites. Parasitism, a form of symbiosis, also takes many different forms throughout nature. Almost all life including humans, animals, and even microscopic forms of life can be susceptible to parasites.

An Evolutionary Overview of Parasites

Famous entomologist E.O. Wilson stated that parasites are “predators that eat prey in units of less than one” (Wilson 2014). What he means by this is that parasites do not follow the same standard procedure of the typical predator. While most predators hunt, kill, and then consume the entirety of their prey, parasites instead infect and live within or on their host. It is important to remember that the parasite, while still causing some harm, does not kill their host organism. In most cases, if the parasite killed the host organism, the parasite that has infected it would die as well. This leads to a parasitic relationship, which is a form of symbiosis, where the parasite gains all the benefit, while the host is harmed as a result.

Parasites, and parasitic infection, reduce the host’s ability to survive, and as an extension, reduces the host’s fitness. This is demonstrated in many ways in nature. Some of the most common forms are parasitic castration, which renders the host unable to reproduce, and behavior modification, which can take many different forms depending on the species afflicted. However, parasites increase their own fitness by taking resources from the host. Parasites reproduce considerably faster than their hosts, and rely on either actions of the infected host, or actions of a secondary host, in order to help in their transmission.

According to Poulin and Randhawa, “Parasitism is widespread in the animal kingdom, and has evolved independently from free-living forms hundreds of times” (Poulin and Randhawa 2015). Parasitic organisms can be animals, plants, fungi, protozoa, bacteria, and viruses. Some of the more common types of parasitic organisms that target humans include protozoa and worms. Infections caused by protozoan parasites include Malaria, different forms of dysentery, and African Sleeping Sickness. Parasitic worms such as tapeworm, hookworm, and whipworm target and reside within the large intestine where they are able to sap nutrients from the host. Symptoms from these infections can include lethargy, various digestive issues, and constant hunger.

Conclusion

Parasites include a wide range of various organisms that all share a common pathology. Further, parasitic relationships across organisms also share a common theme of the parasite gaining a benefit, while the host organism suffers.

Cross-References

► [Evolution of Virulence](#)

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Parasite-Stress Theory

► [Function of Pathogen Prevalence \(Thornhill and Fincher\)](#)

Parasitic Male

► [Sneak Copulation as an Alternative Mating Strategy](#)

Parasympathetic Nervous System

► [Polyvagal Theory](#)

Parentecephalis

► [Cerebellum, The](#)

Parent Influences

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Synonyms

[Attachment](#); [Parental investment](#)

Introduction to Parental Influence

Parental influence refers to the effects that parental (or caregiver) behaviors have on the development of offsprings' future behavior, preferences, and personality traits.

There is little debate that parents have a profound effect on the development of their

offspring. Indeed, human infants are among the most helpless newborn species and their survival to maturity is categorically dependent upon the presence and investment of parental caregivers. The first 5–7 years of a child's life is a time of considerable neuroplasticity, thus, depending upon what the child is exposed to during this time, parents will have considerable influence on the child's development across a variety of domains. These include the language a child speaks, the child's food preferences, the child's future religious beliefs, and, indeed, enduring aspects of the child's personality (Maccoby 2000).

The Role of Parental Investment

Compared with other species, human infants are notably fragile and vulnerable and, thus, require significant time, energy, and resources from their parents in order to survive to maturity. Within evolutionary psychology, the term “parental investment” refers to the quality and quantity of parenting children receive. In mammals, females tend to provide a disproportionate share of parental investment during early development. Fertilization and gestation occur within the female and women provide the primary nutritional support for developing infants until they are weaned. Although paternal investment may be little as the sperm contributed toward fertilization, additional forms of paternal investment may include provision of food and protection from predators (Bjorklund and Pellegrini 2000). Parental investment behaviors vary across species, depending upon the level of vulnerability of the newborn, but are considered critical for the survival of human offspring. Accordingly, insufficient or protracted parental investment (either prenatally or postnatally) will have dire consequences for a child's development. For example, teratogenic exposure during pregnancy and insufficient prenatal care have been linked with a host of neurodevelopmental delays in human offspring (Kundakovic and Champagne 2015). In the postnatal period, variations in nutrition, exposure to toxins, stress, neglect, abuse, and other adverse experiences have been linked with reduced cognitive functioning, protracted social development,

and an increased risk of developing a personality disorder as an adult (Johnson et al. 1999). Thus, at the most fundamental level, adequate and ongoing parental investment is critical to a child's development.

Attachment Theory and Parental Influence

Beyond providing food, shelter, and safety for developing infants, the relationship or attachment children form with their parents is also critical to their development. Unlike attachment processes in primates, where the primary function appears is to reduce infant mortality risks by keeping the infant close by, early human attachment processes with parents provide essential socialization skills and a stable interface for language acquisition, both of which are critical for successful functioning in larger social groups and securing a mating partner later on. In addition, "attachment-related behaviors," including stranger anxiety and separation anxiety, tend to appear at about the same developmental age across human societies, suggesting a strong underlying evolutionary history in attachment processes (Geary and Bjorklund 2000).

To this end, Bowlby (1969) argued that the attachment with the primary caregiver (typically the mother) is not only universal, but also critical to survival. Stable attachments with primary caregivers are thought to provide a "working model" for the initiation and maintenance of future relationships. Bowlby postulated that continued disruption with the primary attachment figure during the first 2 years of life could result in long-term cognitive, social, and emotional difficulties. Extreme cases of disruption with primary attachment processes, including the severe neglect experienced by institutionalized infants, have been shown to result in significant developmental delays, impaired cognitive functioning, development of autism-like behaviors, and increased circulating stress hormones (Kundakovic and Champagne 2015). These sequelae, in turn, protract normal psychological and social development leading to reduced reproductive fitness in adulthood.

Personality development is also influenced not just by the presence of a primary attachment figure, but also the *quality* of the attachment. In a series of experiments with infants and mothers, Ainsworth (1970) identified three, qualitatively different, attachment styles: (1) secure attachment (i.e., feels attachment figure can meet their needs, attachment figure is a safe base from which to explore the environment, can be soothed by attachment figure when in distress); (2) insecure avoidant attachment (i.e., ignore attachment figure when investigating a new environment, do not seek comfort from the attachment figure when distressed); and (3) insecure ambivalent/resistant attachment (i.e., demonstrate clingy and dependent behavior, difficult to soothe, have difficulty exploring environment). A fourth attachment type, disorganized attachment (i.e., unpredictable, erratic behavior; Main and Solomon 1990), was identified later on.

Ainsworth argued that a child's attachment style is largely dependent upon the behavior of the primary attachment figure. Thus, caregivers who are sensitive to their child's cues and can accurately identify their child's emotions and needs are more likely to have a child with a secure attachment than caregivers who ignore, misread, or are otherwise impatient with their child's emotional cues and needs. These variations in attachment style, in turn, may have downstream consequences for the child's development and future reproductive fitness. For example, some studies have linked insecure attachments in childhood with the formation of short-term, unstable pair-bonds in adulthood. Unstable attachment bonds in early childhood have also been shown to be predictive of depression in adulthood which would also undermine adult reproductive fitness potential (Bjorklund and Pellegrini 2000). In contrast, other studies have linked more secure attachments in childhood with more stable relationships in adulthood and greater parental investment in a smaller number of offspring (Rutter and O'Connor 2004). With regard to specific attachment types, disorganized attachments in early childhood have been linked with an increased risk of developing a personality disorder as an adult, particularly Borderline Personality Disorder (Carlson et al. 2009).

Conclusion

Adequate and ongoing parental investment provides critical resources for survival and reproductive fitness. Parental behaviors influence a number of preferences and developmental milestones. The quality of the attachment between child and caregiver plays a pivotal role in shaping expectations and behaviors in future interpersonal relationships with further implications for mental health and reproductive fitness in later adulthood.

Cross-References

- ▶ [Attachment Theory](#)
- ▶ [Early Attachment Experiences and Romantic Attachment](#)
- ▶ [Evolutionary Foundations of the Attachment System and Its Functions](#)

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Parent(s)

- ▶ [Risk Variation with Parent Age](#)
- ▶ [Sex Differences in Death by Filicide](#)

Parental Behavior

- ▶ [Sex Differences](#)

Parental Care

- ▶ [Altruism in Kin Selection](#)
- ▶ [Brood Care](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Parental Investment as Mating Effort](#)

Parental Care, Parenting

- ▶ [Parental Investment Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)

Parental Choice

- ▶ [Arranged Marriages](#)

Parental Effort

- ▶ [Parental Investment and Parenting](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Parental Investment as Mating Effort](#)
- ▶ [Paternal Investment Relative to Maternal Investment](#)

Parental Effort Versus Mating Effort

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Synonyms

Parental investment vs. mating effort

Definition

Describes the trade-off between investing resources (e.g., time, money) in offspring already born or in mating to conceive more offspring. This is central to life history (LH) theory, where greater parental effort is associated with a slower LH strategy and greater mating effort is associated with a faster LH strategy.

Introduction

The distribution of resources into mating and parenting differs widely across species. But it may also vary within a species, subject to both genotypic, environmental, and situational influences. This variation is known as parental effort versus mating effort, here abbreviated as Parent/Mating. As predicted by parental investment theory (Trivers 1972), evolved sex differences are the most general and pervasive drivers of Parent/Mating within species (for humans see e.g., Galperin et al. 2013; Geary 2000; Verweij et al. 2016; Winking et al. 2007). Women are more selective in assenting to sex, are more agreeable and able to inhibit conflict-driving behaviors when required, and spend more time caring for offspring. These are but a few of an array of behavioral tendencies related to reproduction and attuned to interact with the social and physical environments. Cross-species and cross-cultural similarities as well as consistency with evolutionary theory indicate they are evolved mechanisms (see, e.g., Buss 2016 for humans). Another human universal is the tendency to engage in stable mating relationships,

which has important social, economic, and reproductive implications. Although the human pair-bond clearly confers advantages for the immature offspring compared to a single care-taker (see Geary 2000, pp. 61–65 for a review), the underlying selection pressures are not apparent. Prime candidates may be competition among males for mating opportunities, or fathers' parental investment. Some evidence is found for both, which suggests that the adaptive value of pair-bonds varies with the environmental context (Quinlan 2008).

Effort/investment is typically measured in terms of time, money, and other resources, either estimated or measured directly, or subjectively rated. Retrospective measures may also be applied. For example, parental investment could be indicated by the frequency of critical care activities across the first years of life. A general finding is that parents invest less in stepchildren than in biological children and that investment in stepchildren is more likely traded off for mating effort (Anderson et al. 1999; Marlowe 1999).

Many of the factors influencing Parent/Mating are addressed within the framework of life history (LH) theory, where greater parental effort approaches the slow (K) end of the LH continuum, and greater mating effort approaches the fast (r) end (Figueredo et al. 2005) (see Life History Theory for a detailed description). Specifically, persons at the K-end of the continuum seek to produce fewer offspring and provide more nurturing, whereas those at the r-end of the continuum produce many offspring without great investment in their welfare (Bjorklund and Shackelford 1999). These relations may of course be biased by evolutionarily novel environmental conditions, such as the incentives and subsidies provided by so-called welfare states (see Perkins 2016, for an example of such arguments). An early empirical study found a small association between an r/K dimension and Parent/Mating, consistent with LH theory predictions, based on measures of genitalia size, head circumference, strength of sex drive, intelligence, longevity, delinquency, sexual attitudes, and family size (Bogaert and Rushton 1989). However, parental investment in the current offspring may not always decrease the individual's ability to invest in future reproduction.

Male parental investment may function as a form of mating effort, by motivating females to have (additional) children (Anderson et al. 1999; Anderson 2011). For example, men will provide more care to their biological children as their mating opportunities decrease (Marlowe 1999). Theorizing in this area is constantly developing and becoming more complex, as more factors and their interactions are considered. Relevant factors for LH theory include caring and supportive, but also deceitful, delinquent, criminal, offensive, and violent behaviors, important for realizing adaptive tactics such as mate retention and competitor derogation (e.g., Figueredo et al. 2015). Nevertheless, it has been argued that individual variation, female investment, and interactions between the sexes are understudied in relation to Parent/Mating (Stiver and Alonzo 2009).

Studies of both sexes simultaneously find that maternal and paternal behaviors within the family vary between population subgroups and also across time. For both parents, larger family size is inversely related to the investment per offspring, even when high socioeconomic status would seem to allow for relaxing this trade-off (Lawson and Mace 2009). Considering female reproductive strategies, a study of 718 Western Australian women identified six dimensions: “short-term mating,” “early onset of sexual activity,” “reproductive output,” “timing of childbearing,” “breastfeeding,” and “child spacing.” The relationships between parental investment, reproductive timing, and overall reproductive success were consistent with LH theory. For example, women with a short-term mating strategy exhibited evidence for Parent/Mating between child quantity and child quality, but this was not the case for those with a long-term mating strategy (Milne and Judge 2012). Some women engage in short-term mating some of the time. Benefits that might be obtained from extra-pair liaisons include acquisition of resources, a better mate, mate skill, genetically diverse offspring, and mate manipulation. Greiling and Buss (2000) found the strongest support for mate switching and resource acquisition across a series of four studies. Similarly, women are more attracted to men high in Machiavellianism for short-term mating, but prefer men

low in this trait for long-term mating (Aitken et al. 2013).

Male reproductive strategies have been studied more extensively. Male Parent/Mating is affected by men’s self-perceived mate value and whether they are still in a relationship with the mother of their children. Men’s perception of their mates’ fidelity and their perceived resemblance to their offspring were also considered, both indicators of genetic kinship. Self-perceived mate value was positively associated with mating effort and negatively associated with paternal investment. Mating effort and paternal resemblance, but not mate fidelity, predicted investment for co-residing men. Mating effort and mate fidelity did not predict investment for separated men, but paternal resemblance was a strong predictor. Men with a low self-perceived mate value were less likely to reduce their investment in response to decreased mate fidelity than men with a high mate value (Apicella and Marlowe 2007). Similarly, facial attractiveness is positively related to mating effort, in terms of spending more time seeking sexual access and negatively related to spending it with kin. Less attractive men have more to gain by family involvement, either because it displays a potential for parental investment that is attractive to women for possible future relationships or because of so-called inclusive fitness, in which nepotism benefits shared genes (Waynforth 1999). The first of these explanations was supported by the finding that men of the Hadza foraging society in Tanzania trade off parenting effort for mating effort when facing better mating opportunities (Marlowe 1999). Evidence for male’s Parent/Mating is also found in the USA, in terms of a negative association between paying child support and having subsequent children. The fact that men who paid child support were more likely to remarry, however, suggests that child support payment functions as a display of parental commitment (Anderson 2011). A more specific test compared four classes of father-child relationships: (1) genetic offspring of current mates and (2) previous mates, and (3) step offspring of current mates and (4) of previous mates. Again, men invest more in their current mate’s children, regardless of whether the children lived

with him, suggesting that such investment functions as a mating effort (Anderson et al. 1999).

High mating effort is substantially associated with delinquency, promiscuity, and coercive sexual behavior. Offending is commonly used to gain and retain short-term mates, part of which includes fending off competitors. Self-reported delinquency and mating effort were correlated for both males and females, at about the same (0.5) magnitude (Charles and Egan 2005). Such behaviors are easier to perform if one is less empathic. The ability to recognize, manage, and appreciate emotions in oneself and others is sometimes called Emotional Intelligence. Accordingly, Emotional Intelligence was positively associated with slow (K) life history strategy, the end of the spectrum that correspond to high parenting effort and low mating effort (van der Linden et al. 2015).

Sex differences and individual variation in Parent/Mating presuppose a mediating mechanism. McGlothlin (2007) manipulated testosterone in wild birds and found that the level of this male sex hormone was positively associated with mating effort (aggressive response to a simulated territorial intrusion) and negatively associated with parental effort (nestling feeding). Thus, the bird model demonstrates how natural variation in testosterone or other androgens could mediate individual variation in Parent/Mating trade-off also for other species (McGlothlin 2007; Stiver and Alonzo 2009). The same effects of testosterone were found for human fathers, in a study also measuring the amount of caregiving, testicle volume, and neural activity related to nurturing. Caregiving was independently predicted by both testosterone and testicular size. When fathers were shown pictures of their own child, the activity in brain areas related to dopamine reward was negatively associated with testes volume (Mascaro et al. 2013).

LH theory also predicts that male Parent/Mating is affected by mate demand and supply, that is, the proportion of males to females in the population. On the one hand, a smaller number of males than females could enhance the males' short-term mating success and therefore make them less likely to commit by marrying. On the other hand, a larger proportion married of the scarcer

sex would confer the greatest overall mating success in terms of well-groomed and hence fertile offspring. However, males in industrialized societies tend to decrease their mating effort and increase their parental investment across the life course, presumably as a result of decreased circulating testosterone. Consistent with this, having a larger proportion of women in the population was associated with a lower proportion of men between 20 and 29 years of age being married, but a higher proportion of men between 35 and 74 being married (Kruger and Schlemmer 2009).

The nature and complexity of such dynamic interactions between the sexes can be addressed by computer simulation. Employing a game theoretic model, Dawson (1996) showed that Parent/Mating that was allowed to vary across the offspring (i.e., a realistic model) was evolutionarily stable only when one sex provides all parental effort. The inclusion of nonheritable variation in available resources to the individual made parental effort by both sexes an evolutionarily stable strategy (Dawson 1996).

Finally, Parent/Mating has been studied in relation to criminality. Two studies, one covering the Americas and one covering 39 countries across all continents, tried to determine whether regional variation in violent male criminality is explained by reduced parental investment of increased mating effort, in terms of mating competition (Barber 2006). Current crime incidences were analyzed in relation to the current single parenthood ratios and the historical single parenthood ratios 18 years earlier, allowing for the affected children to reach adulthood. Violent crime is best understood as a side effect of mating competition rather than an effect of reduced parental investment (Barber 2004, 2006).

Conclusion

Parental effort versus mating effort represents a fundamental adaptive problem for most animals. Although typically applied to differences across species, it has successfully been applied to study evolutionary mechanisms based on sex-, group-, and individual differences within the human

species. Situated in the midst of the nexus of human reproductive strategies, Parent/Mating constitutes an important tool that intersects with life history and parental investment theory. It is also powerful for understanding the behaviors of ourselves and others in everyday life.

Cross-References

- [Childcare](#)
- [Differential Parental Investment](#)
- [Grandparental Investment and Genetic Relatedness](#)
- [Life History Theory](#)
- [Maternal Investment](#)
- [Parental Investment](#)
- [Parent-offspring Conflict \(Trivers\)](#)
- [Paternal Investment relative to Maternal Investment](#)
- [Parental Investment and Parenting](#)
- [Parental Investment As Mating Effort](#)
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- [Reproductive Strategies](#)
- [Sex Differences](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Reproduction](#)

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Parental Filicide

- [Filial Infanticide in Humans and Other Primates](#)

Parental Infanticide

- [Filial Infanticide in Humans and Other Primates](#)

Parental Influence

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Parental Investment and Parenting

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Synonyms

Childcare; Childrearing; Parenthood; Parental effort

Definition

Traditional theories of developmental and family psychology such as family systems theory (FST;

Cox and Paley 1997) focus on interdependent and bidirectional interrelationships among members of the household by viewing the family as a system and the members of the family as parts. According to this approach, interactions between members occur in predictable and repetitive patterns that provide internal balance to the family system. Any perturbations to the system (such as inclusion of new members into the household or loss of old members of the household, major life stresses, or changes that alter one of the relationships within the household) result in loss of homeostasis, creating household dysfunction. Family systems theory would thus view parenting and parental investment as influenced by and products of such household perturbations.

Evolutionary approaches such as parental investment theory (PIT; Trivers 1972) posit that the optimal allocation of resources to a current offspring is critically dependent upon the cost assessed in any consequent reduction in the quality or quantity of future offspring. Differential parental solicitude theory (DPST; Daly and Wilson 1987), an elaboration of PIT, discusses that the optimal allocation of resources to a current offspring is critically dependent upon the relative likelihood of the future survival and reproduction of the current offspring in relation to those of its past or present siblings. These theories (and the other evolutionary theories discussed below) view parenting and parental investment as coordinated strategies that weight short- and long-term costs in a manner that maximizes resources toward reproduction.

Introduction

Standard Social Science Model Approach. Traditional approaches toward developmental research agnostic to evolutionary modes of explanation, typically labeled the standard social science model (SSSM), have investigated the nuances of parenting and its impact on child outcomes for many years. One such nuance is the clear division of labor that occurs between the sexes (Coltrane 2000). Across all stages of childhood, mothers are more likely to devote

considerable time toward caring for children than are fathers (Bianchi and Milkie 2010). While secular trends indicate an increase in paternal time and effort toward child-rearing – with legislation both perpetuating and facilitating this trend – the data reveals that moms do more than dads. Inequitable partitioning of child-rearing duties and low agreement between parents on parenting has been associated with poor romantic relationship functioning (Greenstein 1996; Suitor 1991) and poor child outcomes (Erel and Burman 1995; Grych and Fincham 1990). FST, (Cox and Paley 1997) a predominant theory in family psychology, would posit that this pattern of associations occurs when one or more relationships within the household are dysfunctional and/or produce poor coherence and homeostasis. The foundational premise of family systems theory is that, because members of the household are highly interdependent, the dynamics of these interdependent relationships will have mutual and bidirectional influence on other members of the family. The family systems approach thus has a clear perspective on what is conceptualized as a “good” or “functional” system versus a “bad” or “dysfunctional” system; in contrast, an evolutionary approach approaches parenting and household functioning as not “good or bad,” which are considered relativistic terms, but as what is appropriate or conditional given the context (Ellis et al. 2012a)

The fundamental goal for individual organisms, according to the tenets of natural selection, is to survive and successfully reproduce. This involves surviving to sexual maturity and successfully acquiring, retaining, and reproducing with a mate; however for an organism to ultimately be successful, an organism must also have descendants that survive and successfully reproduce as well. Across different species, the amount of parental effort needed to produce reproductively viable offspring varies. Additionally, the actors who provide the parental effort to offspring vary (Hrdy 1999). In 5% of mammals, for instance, there is evidence for direct paternal care of young (Geary 2000). While many factors exist that modulate the level of effort in men and women within and across human societies, a

degree of complementarity exists between the sexes in raising children (Kaplan et al. 2001). From this perspective, men and women attempt to increase their reproductive output (e.g., healthy and reproductive viable offspring) through parental alliances, linking their reproductive success and dividing parental labor to maximize productivity (Kaplan et al. 2001). An evolutionary perspective, in contrast to the family systems perspective, hypothesizes that the amount of effort allocated toward parenting, the dynamics of the household, and the outcomes of such parenting all reflect one coordinated and cohesive parental investment strategy.

Evolutionary Psychology Approach

Analytical Systems Approach (Interactions of Individual Traits)

Whereas the SSSM typically uses a top-down *holistic* approach toward understanding family systems, where participants within that system are considered subordinate to the emergent properties of the system, evolutionary psychology (EP) instead adopts a bottom-up *analytical* approach to understanding family systems, where the emergent properties of that system are considered to be generated by interactions among the potentially different traits possessed by the participants in that system. Put simply, the top-down holistic approach focuses more on household and family dynamics without fully considering the impact of individual and phenotypic differences between actors in the household that produce the emergent household and family dynamics. Accordingly, the typical conceptual causal model of the SSSM posits: Family Effects → Child Outcomes. For example, Trivers' (1974) parent-offspring conflict theory (POCT; Trivers 1974) is simply not comprehensible in terms of a top-down and holistic family systems theory. POCT contends that discrepancies between parents and their children in the optimal allocation of parental care and effort expended will result in conflicts between them. Whereas investment and care from parents to their children is often assumed to be unconditional and limitless, the

time, energy, and resources to produce and care for children are limited in reality. From a parent's perspective, it therefore makes more sense to withhold a certain proportion of parental care and effort from current offspring to ensure that a portion of those resources can be allocated toward future offspring. From the child's perspective, it makes more sense to attempt to maximize the amount of care and effort they receive from their parents in order to gain a fitness advantage over their siblings. Trivers used a genetic estimate to make his point about POCT. A child is 100% related to itself, and any resources it can acquire will help improve its chances for reproducing. Any additional child a parent produces is assumed to be related to the current child by 50% for full siblings or 25% for half-siblings, eliminating the relatedness and, thus, the shared genetic interests the current child has on its offspring. For parents, all their biological children will be related by 50% to them so should have an equal "chance" for investment.

POCT is critically dependent on a bottom-up understanding of the individual participants within the family system as well as the relations among them. Only by analyzing the genetic coefficients of relatedness among the siblings, as well as between each sibling and the parent, do the dynamics of POCT make any sense, especially where half-siblings are present as their presence predicted more conflict between the mother and the focal child in the study independently of other household characteristics (Schlomer et al. 2010). These effects persisted whether or not there was a stepfather present in the home, suggesting independent mechanisms for POCT conflict for mother-child and father-child relations.

Nevertheless, both family systems theory and more sophisticated versions of POCT than the Trivers (1974) version require genetically informed and controlled studies to make conclusive statements (Ellis et al. 2012b). One approach to remedy this issue has been to use a *sibling design* where data is collected on older/younger sibling pairs raised in a single household. By collecting data on siblings, genetics and environment are genetically controlled and could thus allow for examination of specific events such as

father absence and its impact of child outcomes such as risky sexual behavior (Ellis et al. 2012b). Similarly, the genetic coefficients of relatedness used in EP to compare full with half-siblings are typically estimated at one-half and one-quarter, respectively. Under conditions of assortative mating, however, these coefficients may be quite severe underestimates (Wolf and Figueredo 2011); moreover, if a woman assortatively mates with the fathers of both the full and half-siblings on genetic similarity, the genetic difference between the full and half-siblings will inevitably be attenuated due to the genetic similarity among the fathers.

These limitations are also related to the diminished emphasis by the SSSM of gene-environment (G-E) correlations. G-E correlations may be generated by various mechanisms, including (1) passive, (2) active, and (3) evocative (Scarr and McCartney 1983). The existence of such correlations makes it impossible to think of causal relations within family systems as being purely top-down. For example, in evocative G-E correlations, the heritable traits possessed by the child may alter the behavior of the parents toward the child and thus skew the outcome of the family system generated by their interaction.

Context-Dependent Parenting

The SSSM perspective of what is “good parenting” (Cabeza de Baca et al. 2012) is context independent and reflects the cultural ideals of WEIRD societies (Western, educated, industrialized, rich, and democratic societies; Henrich et al. 2010). This includes parenting that is sensitive, warm, and highly involved, which is a characteristic parenting style of slow life history strategists (Cabeza de Baca et al. 2012). As such, this type of parenting tends to occur in highly stable and controllable environments. In stressful environments characterized by external and uncontrollable sources of illness and mortality, investing in high-quality parenting may result in diminished returns to reproductive fitness. In such stressful environments, parents should instead invest little in parental effort and orient their resources toward mating to maximize reproductive dividends.

As human beings and private citizens, most researchers agree that no child should suffer from abuse or neglect and should instead grow up in safe, loving households; however, as researchers, placing value labels on parenting strategies and child outcomes may have unintended consequences when put into practice such as in interventions. As mentioned, EP focuses on behavior and development as it pertains to the ecological context. In some contexts, certain behaviors and developmental outcomes may confer a selective advantage on survival and reproduction but may be considered contrary to what typical social norms are. Interventions that seek to reduce aggression or risk-taking behavior in adolescents from dangerous environments neglect the functional aspects of socially unacceptable behavior and may actually be “declawing the cat” (Ellis et al. 2012a, p. 610) or stripping away psychological and behavioral mechanisms that allow individuals to cope with their environment and/or gain status and access to resources present in their environment. Declawing the cat does nothing to alter the environment or situation in which youth reside. Evolutionists thus caution that interventions should thus target the ecology as a way to alter risky behavior and deleterious outcomes.

Parental Condition Dependent

The SSSM perspective of what is “good parenting” (Cabeza de Baca et al. 2012) is also condition independent, usually failing to consider the phenotypic conditions of either the parent or the child. Parental condition is important according to Trivers’ (1972) parental investment theory (PIT). According to PIT, a woman near the end of her reproductive career will likely suffer less cost in future offspring by investing heavily in current offspring and dramatically less in mating effort than a woman at the beginning of her reproductive career. This would, in turn, decrease amount of conflict between mother and child that is present in the household (Schlomer and Belsky 2012). Research examining breastfeeding duration, an indicator of maternal effort, presented evidence indicating that older and educated mothers report breastfeeding

longer than their younger, less educated counterparts (Davis et al. 2007).

Similarly, offspring condition is also a critical factor in Daly and Wilson's (1987) differential parental solicitude theory (DPST). According to DPST, an offspring who is a poor "bet" or bad investment (i.e., least likely to successfully reproduce) will be neglected in favor of redirecting any parental resources toward its more fortunate or promising siblings. Differential parental solicitude, according to Hrdy (1999), is unique to humans, when compared to other primates. Maternal abandonment of offspring and infanticide (directly enacting it or passively allowing it) occurs in nonhuman primates, but these instances are less contingent on child attributes or quality and more on resource availability, rank, and maternal condition (Hrdy 1999). Nevertheless, Hrdy (1999) documents the widespread problem of resource allocation among offspring faced by human mothers in hunter-gatherer as well as primitive horticultural societies. While not as pronounced, evidence of differential parental solicitude is found in WEIRD societies. Much research focusing on this phenomenon has been examined in preterm children based on their high risk of poor developmental outcomes. Using high-risk children allowed for testing the *contingent model of parental investment* (Bugental and Beaulieu 2003).

The contingent model of parental investment builds upon prior theory (e.g., Daly and Wilson 1987; Trivers 1972) by highlighting the interaction between parental and child condition on parental effort. The theory proposes that parents with poor conditions and low resources will decrease parental effort toward their child if they have poor condition and, hence, low reproductive prospects. Conversely, if a child with poor condition has parents who have resources and are in good condition, the child will receive more attention to improve and bolster his health status and advantage in becoming a viable mate. In a WEIRD sample of mothers and their infants, preterm infants received decrease maternal investment if the mother had higher levels of depression. In full-term infants, women with higher levels of depression actually showed

increased investment in their children (Beaulieu and Bugental 2008).

The *Trivers-Willard hypothesis* (TWH; Trivers and Willard 1973) is a special case of differential parental solicitude, as it posits that the optimal allocation of resources to offspring will vary systematically by the offspring sex, depending on the current condition of the parents and the predominant mating system of the species. For example, in a polygynous species, a mother in good condition is expected to produce more male offspring, as they are more likely to benefit more than female offspring from the extra resources in terms of increased mating opportunities; a mother in poor condition is expected to produce more female offspring, as they are less likely to suffer from decreased mating opportunities than male offspring when resources are diminished.

According to the hypothesis, parents will prefer investing in male offspring in stable, predictable, and controllable environments; conversely, harsh, unpredictable, and uncontrollable environments would shift parental investment and preferences toward female offspring. The rationale behind this set of hypotheses was that in low-quality environments, reproductive success was more likely with female offspring, guaranteeing an increase in grandchildren for parents. Intensity of competition for high-quality mates would increase in high-quality environments, emphasizing phenotypic quality and costly signals of fitness (Zahavi 1975). In these environments, a parent's best "bet" would be to invest highly in male offspring. While the losses would be great, the reproductive gains of having a male mate with multiple females (siring many children) would be greater. Evidence for the Trivers-Willard hypothesis (1973) in humans has generally been mixed, with parents in some societies generally favoring male offspring, parents in some societies generally favoring female offspring, and parents in other societies generally favoring neither (e.g., Freese and Powell 1999; Guggenheim et al. 2007). An investigation of maternal condition in a sample of Tucson households found that women living below the poverty level reported a greater preference for large female babies than male babies (Davis et al. 2007).

Normative Cultural Value-Based Versus Functional Fitness-Based Approach

As has been mentioned, evolutionary theory does not define parenting behaviors as absolutely “good” or “bad,” as has been traditionally denoted by standard social science models. In contrast, evolutionary theory views parenting behaviors as responses to ecological context and hence strategic and functional. From this point of view, parenting and household dynamics are thus considered the conduits to the outside world and reflect the ecological conditions the children will likely face in adulthood (Belsky et al. 1991; Ellis et al. 2009). From this perspective, parenting acts as modulator that modifies the development, behavior, and reproductive strategies of the offspring.

Conclusion

Although FST represents a major advance in understanding family dynamics within the SSSM, it suffers from the limitations of a purely top-down and holistic approach in failing to analytically break down the different condition-dependent and context-dependent roles of the participants within the family system. The EP approach offers a bottom-up reconstruction of the interactions among the members of a family system to derive more specific and testable predictions regarding the particular dynamics that one would expect from different combinations of participants under different ecological conditions. Insights from the EP approach include those offered by parental investment theory, differential parental solicitude theory, contingent model of parental investment, parent-offspring conflict theory, and Trivers-Willard hypothesis.

Cross-References

- [Biparental Care](#)
- [Maternal Investment](#)
- [Maternal and Offspring Condition](#)
- [Maternal Sensitivity](#)
- [Parent-offspring Conflict \(Trivers\)](#)

- [Parental Effort Versus Mating Effort](#)
- [Paternal Investment Relative to Maternal Investment](#)

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Parental Investment and Sexual Selection

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Synonyms

Mate choice; Mate competition; Parental care; Parental effort

Definition

Parental investment, which occurs when parents provide costly investment that increases offspring survival, and sexual selection, which occurs when some individuals acquire more mates than others because of their traits, are highly connected. Differences in parental investment are often related to differences in sexual selection and can affect mate availability, competition, and choice. Here, we provide an overview of the link between parental investment and sexual selection.

Introduction

Parental investment (i.e., any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring; Trivers 1972) and sexual selection (i.e., covariation between mating success and the expression of sexually selected traits) are both major determinants of an individual's lifetime reproductive success. By investing into their offspring, an individual can improve the likelihood that offspring survive and reproduce, thereby improving the fitness (i.e., the relative lifetime reproductive success) of both the offspring and of the parent. Additionally, an individual can improve their own fitness by being selective about which individuals they mate with, in which case sexual selection can occur. Sexual

selection will act upon the traits that affect mating success, selecting for traits deemed as “attractive” by the choosy sex. This can span a variety of different traits including both physical attributes and behavior. Below, a brief overview of the link between parental investment and sexual selection is provided.

Parental Investment and Parental Care

Parental investment can occur in several different ways. In terms of prezygotic investment, gamete production is the primary form of parental investment, and both within and across species, females vary widely in the energy and resources that they invest into eggs. Post-zygotically, individuals can invest into their offspring via parental care. Parental care is often defined as parental behavior that occurs postfertilization, is directed at offspring, and appears to increase offspring lifetime reproductive success (Klug et al. 2012). Parental care is a form of parental investment when it is costly to the parent providing care, and the terms parental investment and parental care are often used interchangeably. Pre-zygotic and post-zygotic parental investment is incredibly diverse in nature (reviewed in Royle et al. 2012).

Sex Differences in Parental Investment, Mate Competition, and Sexual Selection

Sexual selection occurs when some individuals acquire more mates than others because of their traits, and sexual selection determines sex roles in a given system. Sex roles are considered to be (1) conventional when males are the mate-limited sex and compete more intensely for female mates and (2) reversed when females are the mate-limited sex and compete more intensely for male mates. Parental investment is a key driver of both sexual selection and the resulting sex roles in a given system, although we now know that sexual selection also influences the evolution of parental investment (reviewed in Kokko and Jennions 2008).

Parental investment differs in males and females, as females, by definition, produce larger

gametes than males and therefore contribute greater resources to eggs than males do for sperm. Because of this higher initial investment, a highly influential paper by Trivers (1972) suggested that females are more likely to provide parental care; however, more recent reexamination of this hypothesis has found that, from an adaptive perspective, current parental investment should not be based on previous investment and instead should be based only on the net benefits that a parent is likely to gain from that investment (see also discussion of the “Concorde fallacy” in Queller 1997 and Kokko and Jennions 2008). Thus, the differences in initial gametic investment between the sexes are not expected to directly determine the level of future parental investment that a parent provides. However, initial investment can influence a parent’s condition, for example, which will influence their likelihood of successful reproduction in the future, and the potential for future reproduction is expected to affect current investment in offspring. For example, if an individual has relatively little chance of reproducing in the future, we would expect them to invest heavily in current reproductive effort and current offspring.

If one sex initially provides greater parental investment in offspring (e.g., because of initial gametic investment, constraints, proximity to offspring, and/or reduced future reproductive potential), this can influence sexual selection. For instance, if providing parental care is associated with higher mortality than competing for new mates, the sex that provides parental care is likely to become rare in the population, and it will be difficult for the non-caring sex to find future mating opportunities. In such a case, coevolutionary feedback between providing parental care and competing for mates can lead to an evolutionary outcome in which sexual selection is relatively weak and both sexes provide parental care (Kokko and Jennions 2008). In contrast, if sexual selection is strong and mate competition is associated with greater mortality than providing parental care, the non-caring sex is expected to become relatively rare in the population. In such a situation, coevolutionary feedback between care and sexual selection would be expected to lead to

maternal care if females are the sex that initially provides care or paternal care if males are the sex that initially provides care (Kokko and Jennions 2008). Indeed, such scenarios highlight that (1) parental investment influences sexual selection and (2) sexual selection and the costs associated with mate competition can influence parental investment by males and females.

Multiple Mating and Parentage Can Affect Parental Investment and Sexual Selection

Another more recent study modeled the effect that parentage certainty can have on parental care. In some cases in which sexual selection is relatively strong on males, females might mate with multiple males, and this can lead to sperm competition and uncertain paternity. In cases where male paternity is likely to be uncertain due to multiple mating by females, males are expected to be less likely to provide parental care on a macroevolutionary scale (i.e., across species), creating a difference in parental investment between the sexes (Queller 1997; Alonzo 2010; Kokko and Jennions 2012).

In some cases, though, paternity certainty is unlikely to affect parental investment. For instance, within a species, males would only be expected to adjust parental investment in relation to paternity certainty if paternity certainty changes through a male's lifetime (i.e., if some reproductive episodes will be associated with greater paternity certainty; Alonzo 2010). Additionally, theoretical work suggests that when females are choosier, sexual selection will favor male parental care, regardless of paternity, such that females are more likely to mate with males who are better fathers (Alonzo 2012). This demonstrates that sexual selection alone does not explain the natural bias toward maternal care that is often observed in nature; rather, there are a variety of other factors that influence parental investment, including mate choice for parental care by fathers. Indeed, sexual selection in which females prefer mating with males who provide parental care has been observed in nature. For example, male care is sexually selected for in the sand goby (*Pomatoschistus*

minutus), such that females show a preference for males that provided more care (Lindstrom et al. 2006).

Time Out of the Mating Pool Post-Care Can Affect Investment and Sexual Selection

In addition to the above factors, the time in and out of the mating pool can also influence sexual selection and parental investment. For example, after mating, animals of many species cannot immediately remate because they (1) are providing parental care to current young and are unreceptive to additional mates and/or (2) are recouping energy or other resources required for mating. When some individuals are not able to immediately remate, the operational sex ratio (i.e., the ratio of males and females that are currently prepared to mate at a given time and place) can become biased. In such cases, biased sex ratios can either increase competition among members of the mate-limited sex or favor investment in parental care of current young (Parker and Simmons 1996; reviewed in Kokko and Jennions 2008).

Conclusion

Parental investment and sexual selection influence one another. In particular, parental care and mate choice and competition are expected to coevolve. Understanding why one sex might be choosier and why one sex might provide relatively more parental investment is complex and can be influenced by many factors, including parentage certainty, the costs of acquiring mates and providing parental care, constraints, proximity to offspring, sex ratio, and opportunities for future reproductive events. While much has been learned in the field of parental investment and sexual selection, there are still questions left to be expanded upon. In the future, it will be important to expand upon how these different factors interact with each other to lead to the origin and maintenance of different parental investment and mating strategies.

Cross-References

- [Differential Parental Investment](#)
- [Grandparental Investment and Genetic Relatedness](#)
- [Parental Investment](#)
- [Parental Investment and Parenting](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Parental Investment As Mating Effort](#)
- [Parental Investment Theory](#)
- [Paternity Uncertainty](#)
- [Robert Trivers](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Conflict In Mating Strategies](#)
- [Sexual Selection](#)

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Parental Investment and Sexual Selection (Trivers Foundational Theory)

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Synonyms

[Anisogamy](#); [Relative parental investment](#); [Reproductive success](#); [Sex differences](#); [Sexual dimorphism](#)

Definition

Where sex differences exist in relative investment in offspring, the sex that invests more is the limiting resource for the non-investing sex, resulting in differences in reproductive strategies and profound effects on morphology, physiology, and behavior between and within the sexes.

Introduction

Darwin's theory of sexual selection recognized that selective pressures could act differently on the sexes in ways that allowed individuals to effectively compete and pass on their genes. Darwin identified two main types of sexual selection: (1) competition within one sex for access to the other (e.g., male-male competition – weapons, large body size, aggressive behavior) and (2) differential choice by members of one sex for the

opposite sex (e.g., female choice – bright colors, elaborate plumage/pelage). What Darwin's theory lacked was a general framework that could explain and predict the interrelated variables and their consequences. Advances in evolutionary genetics, including Fisher's sex ratio theory (1958) and Bateman's (1948) work on variation in differential reproductive success (both within and between sexes) laid the groundwork for Robert Trivers' (1972) revolutionary work on parental investment and sexual selection. Trivers put forth an elegant model derived from basic economic principles to explain differences between the sexes based on reproductive effort. This theoretical framework can be used to explain a wide range of physical and behavioral differences between the sexes (Trivers 2002).

Trivers' Model

Trivers defined relative parental investment as “any investment by the parent of an individual offspring that increases that offspring's survival (and hence reproductive success) at the cost of the parent's ability to invest in other offspring.” (1972 pp. 139). Trivers concluded that the governing principle of sexual selection was the relative parental investment of the sexes in their offspring, beginning with the evolution of sexual reproduction and anisogamy (Trivers 1983). Anisogamy refers to the two distinct reproductive strategies within a species at the level of the gametes. One strategy is investing in fewer, larger, and relatively immobile gametes (e.g., eggs – quality over quantity). This strategy tends to involve extensive postconception investment (e.g., gestation, lactation, infant care in mammals) and is typically the female strategy. The second strategy is to produce massive numbers of small, inexpensive, mobile gametes (e.g., sperm – quantity over quality). This is most often the male strategy in mammals; there is usually little investment beyond insemination, and males mate often and with as many females as possible in order to maximize individual reproductive success. This creates intense competition for mates, typically between males, since fertile females are the limiting resource for individual

male reproductive success. This competition is compounded by variance in reproductive success observed among males in most species, where a few males father a disproportionate number of offspring in a given generation, while many males father none. Females typically benefit by being choosy because their return on investment is directly reflected in the genetic quality of the offspring.

Once Trivers established a coherent evolutionary logic, basic predictions of his theory could easily be tested by examining levels of parental investment by sex and associated behaviors and characteristics in insects, birds, fish, mammals, primates, and humans. Sex role reversed species, such as pipefish and spotted sandpipers, provided evidence confirming predictions based on investment strategy and not “sex” per se. In species, where males do the majority of parental investment, females are larger, more aggressive, more colorful, compete for access to males, and commit infanticide of rivals' offspring. Males in these species are choosy and only incubate and fledge offspring of certain females (Trivers 1985).

Conclusion

Trivers' theory of relative parental investment as the key variable controlling the operation of sexual selection has tremendous explanatory power for various physical and behavioral differences observed between and within the sexes. Some of these include differential mortality by sex, sexually dimorphic attributes such as brightly colored feathers and elaborate weaponry, sperm competition, different mortality by sex, and complex behaviors such as sexual jealousy, sexual coercion, infanticide, adultery, homicide, and cuckoldry.

Cross-References

- [Female Mate Choice](#)
- [Male-Male competition](#)
- [Male-Male Competition or Male Provisioning?](#)

- [Mate Choice](#)
- [Mate Guarding](#)
- [Parental Investment](#)
- [Reproductive Success](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)

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Parental Investment as Mating Effort

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Synonyms

[Mating strategy](#); [Parental care](#); [Parental effort](#); [Sexual selection](#)

Definition

Parental care is a strategy used to attract and select partners for mating.

Introduction

Parental investment can be understood as a mating strategy according to evolutionary theories. In some species belonging to animal kingdom, as well as in humans, the search for sexual partners considers characteristics such as sexual strategies, energy investment, and the chances of perpetuating genes. Thus, investment in parental care emerges as an effective strategy for attracting and selecting partners, primarily associated with long-term strategies.

Care for the Offspring as a Strategy of Sexual Competition

The human animal has primary goals for organizing their life, among them mating and genetic perpetuation. During the history of humankind, several parental and reproductive models were tested to reach more advantages and less disadvantages. The most perpetuated mating strategies are related to life history strategies, with short-term and long-term strategies. They would be characterized precisely by the emphasis given to the relationship, partner providing and fidelity (Giudice et al. 2015).

Sexual mating strategies are sets of adaptations that guide the investment and reproductive effort of an individual, defined as genetic programs or decision-making rules – conscious and unconscious – that individuals use to direct their efforts to behaviors that have specific objectives (Gangestad and Simpson 2000). Each sexual strategy influences how individuals choose and identify their sexual partners.

In a simplistic analysis, long-term strategies are usually associated with women, since they are the ones that need to invest more energy to carry and then ensure the survival of the offspring. While men are often associated with short-term strategies, they can quantitatively fertilize multiple partners simultaneously, without necessarily bearing the burden of women's energy investment, thus increasing their chances of reproductive success. However, men and women present short- and long-term strategies; gender differences

would only imply trends of more or less selectivity, not patterns. In addition, socio-environmental conditions, the search for good genes, and resources can influence the variability of the strategies adopted. It is in this context that the provision of parental care for the offspring, by men and women, presents itself as an important strategy for the effectiveness of procreation and genetic perpetuation. Both genders can benefit from this strategy; after all, parental care can contribute to offspring survival, success, and longevity (Gangestad and Simpson 2000; Shiramizu and Lopes 2013).

Parental investment comprises all forms of investment that parents offer in favor of offspring in a way that increases their chances of survival and reproduction (Gangestad and Simpson 2000; Manfroï et al. 2011). The provision of parental care is, on the one hand, a mating strategy and, on the other, a strategy for ensuring the generation of descendants. In species where there is a conflict of interest about reproductive strategies, as observed in mammal species, especially some species of primates, parental investment can serve as a way for males to conquer females. In the dispute between quality and quantity, offering care to the offspring can be an important success factor in the selection process of females (Smuts 1995).

There is a strong relationship between parental investment and sexual selection (intersexual attraction x intrasexual competition), which implies that the sex that invests more in the offspring tends to be more demanding in choosing sexual partners (intersexual attraction), while the sex that invests less would compete for the conquest of the opposite sex with more investor potential (intrasexual competition). Thus, the theory of sexual strategy considers that the choice of partners does not occur by what they may represent in the sexual act but by the role they may play as the father or mother of a future offspring (Borrione and Lordelo 2005).

It is possible to exemplify the relationship between intersexual attraction and intrasexual competition, with the fact that women necessarily invest more time and resources in the offspring, from the fertilization process to child care, which depends on the woman; thus, the female sex

would be more selective in the choice of possible sexual partners, which makes it the sex of greater intersexual attraction, whereas men are less discriminating and tend to exert greater intrasexual competitiveness (Buss and Schmitt 1993).

Despite there being a biological, evolutionary, and sociocultural justification for women to exert more parental investment on their offspring, men can also invest in their offspring from birth. When this occurs, it is possible that they are adopting parental investment as a mating effort and are also more selective in choosing their partners (Geary 2016).

Increased parental investment may be essential for the reproductive success of couples in diverse contexts, and it consists of multiple strategies of care, supply, and attention directed to the offspring. Some species depend on advanced levels of investment to achieve reproductive fitness, such as humans, who have prolonged gestational periods that result in an immature baby that relies on intensive and continuous care (Manfroï et al. 2011; Trivers 1972); however, other species of mammals and birds also require intensive care during and after birth.

Considering parental investment as part of a long-term sexual strategy, it is possible to identify advantages and disadvantages in its use, since it is a strategy that calls for monogamy and the choice of high-quality partners who invest in the offspring. For men the disadvantages are related to limited access to other partners, as well as the requirement for strict paternal care and investments; the advantages are linked to greater paternity certainty and the increase in the chances of the offspring to survive until reproductive age. For women, adopting the parental investment strategy has direct benefits, such as resources, protection, care, and transfer of status to the offspring; among the disadvantages faced by women is the fact that men with better genes are often not available for stable relationships (Gangestad and Simpson 2000).

Conclusion

Mating strategies differ slightly between the sexes. It is common for men to opt for short-

term strategies, while women are more likely to use long-term strategies. From an evolutionary perspective, it is possible to affirm that during the evolutionary process of human beings, men faced dilemmas between spending time and energy in raising children or in mating, while women are divided among the partners who offer parental care and have material resources or indications of good genes. Although the human species is characterized as a kind with high parental investment, the variability in the amount of parental investment offered to the offspring would be able to influence sexual selection of partners and the adopted mating strategy.

Cross-References

- [Differential Parental Investment](#)
- [Paternal Care](#)
- [Parental Effort Versus Mating Effort](#)
- [Parental Investment and Sexual Selection](#)
- [Sex Differences in Parenting and Parental Investment](#)

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Parental Investment Theory

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Synonyms

[Theory of asymmetric investment](#)

Definition

In most sexually reproducing species, the costs for reproduction are different for males and females.

Introduction

The great puzzle which Charles Darwin was bothered with but unable to find an answer to was why most animals reproduce sexually rather than asexually. In a publication on sexual selection in plants he states: “We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis . . . The whole subject is as yet hidden in darkness” (Darwin 1861, p. 94).

Antoinette Brown Blackwell (1875) put forward a reason for sexual reproduction in her book *The Sexes Throughout Nature* that was largely ignored by the scientific community, only to be formalized and popularized about a century later: She describes the advantages of asexual reproduction, as long as the

environmental conditions are stable, but explains that as soon as environmental conditions change, the more costly sexual reproduction becomes the better solution. It took almost a century for this idea to be integrated in modern evolutionary theory: Leigh van Valen (1973) coined the term Red Queen hypothesis to describe the necessity of organisms to maintain genetic variability in unstable environments. In a sheer radiation of theoretical papers and mathematical models published in the following decade, the idea of sexual reproduction having evolved from the necessity to cope with unpredictable selection pressures was firmly established (Maynard Smith 1971; Glesener 1979; Hamilton 1980; Hutson and Law 1981; Bell 1982). The scientific impact of the Red Queen on biological and evolutionary studies in general continues to be fundamental. A concise and detailed description of the concept was published in 1990 by William Hamilton and colleagues (Hamilton et al. 1990).

Sexual reproduction rarely occurs with gametes of similar size. In most species, small and large gametes are produced, the small gametes by the male and the large ones by the female. Other than many of her contemporaries, Brown Blackwell does not limit parental investment to energy provided through the gametes and direct nutrition. She outlines the different ways how “parental love” can manifest and benefit the offspring.

Forms of Parental Investment

Through provision of nutrients in the egg, but also through feeding, the offspring is provided with essential nutrients. Direct nutrition is in many species biased toward the female sex, i.e., the female parent is the one who provides more in terms of direct nutrition than the male parent. This is due to the female gametes’ larger size and resulting higher production costs and nutritional value. In mammals, direct nutrition is also provided during gestation and through lactation, which leads to a very pronounced sex difference in parental costs afforded through direct nutrition. The impact of direct nutrition on the fitness of the

offspring is crucial in early development, but in the course of individual development, the relevance of direct nutrition falls back behind other forms of parental investment.

Direct nutrition, such as lactation, is provided almost exclusively by female parents, whereas indirect nutrition can come from both fathers and mothers. In many bird species, both parents share the burden of providing their hatchlings with sufficient food. The feeding of the offspring is a highly demanding activity, resulting in a substantial drop in weight in feeding parents, often below the weight of fully developed fledglings. In elaborate forms of parenting, fathers can provide food to mothers that is then turned into direct nutrition for the offspring.

Male and female birds take turns in incubating the eggs, thus sharing the parental load of investment. This can involve building nests where the eggs are taken care of, the costs of which can be shared equally or unequally. There are a large number of species where nest building is exclusively the task of the males. Some male fish nurse the eggs within their mouths, sit on top of them, or carry them around in pouches. Also in birds, there are some species where the bulk of parental care in terms of incubation and feeding is carried out by the males. If the majority of parental care is provided by the males, other aspects of the male and female organisms are affected, too. That is, females might be larger in body size, more colorful, and more competitive.

How Are Asymmetries Determined?

Which of both sexes manifests as the main contributor in parental care depends on the interplay of a number of socio-ecological factors. Other than the size of the gametes and the amount of direct nutrition, indirect nutrition, protection, and care can be taken on by both sexes to varying degrees. As parental investment can go far beyond the size of gametes and direct nutrition, a more differentiated view on parental care is needed to understand the sex roles and sex differences in different species. This integral view of parental investment also provides a much more flexible

basis for the manifestation of systems of investment. Asymmetries might end up less pronounced, or even reversed, depending on the socio-ecological conditions.

Reproductive costs do not equal costs arising from parental investment. Behavioral, physiological, and physical characteristics serving the purpose to persevere in intra- and intersexual selection also add to the complexity of costs of reproduction. Neglecting those in terms of parental investment might skew the perception of reproductive costs and lead to an unjustified emphasis of sexual dimorphisms. That is, the substantial costs of developing features that allow an organism to persist in intrasexual competition and to be successfully chosen in intersexual selection should not be ignored when estimating the costs of parenthood. Also, the focus on the size of gametes might be misleading: Usually, male organisms produce a much larger amount of small gametes than the females produce large gametes. The surplus of male gametes is a necessity to ensure fertilization. Therefore, the ejaculate, rather than the single sperm, should be the unit taken into account as minimal direct nutrition. This shift of perspective has been suggested by a number of authors but has as yet failed to take hold in the theoretical discourse (Hubbard 1997; Fausto-Sterling 1992, 1995; Tang-Martinez 1997).

The argument often fails to appreciate the complexity of the matter, either overemphasizing the role of direct nutrition or negating it, as Sarah Hrdy (1999) states. Anisogamy, if used too deterministically, fails to acknowledge facts as nutrition provided by the males either directly in the ejaculate or as bridal gifts, as well as the often essential role of male care for the survival of the offspring. On the other hand, criticism of the theory of anisogamy often downplays the biological costs of reproduction.

Robert Trivers's parental investment theory, as based on the principle of anisogamy, makes two profound predictions. First, individuals of the sex with the larger reproductive costs will be more selective in with whom they mate. Second, individuals of the sex with the lower parental investment will compete among themselves for

reproductive access to the other sex (Trivers 1972). There exist animal species where males invest substantially more than females, i.e., because the males provide nutrients or incubate the eggs. In these species, the males are more discriminating about mating, and the females compete among themselves for access to males. The seahorse males are exclusively responsible for the parental care after fertilization, carrying the fertilized eggs around in a special pouch until they hatch (Hrdy 1999). The male mormon cricket produces a large spermatophore that is packed with nutrient, thus costly to produce and their means to attract females, who compete for access to the males with the largest spermatophores (Buss 1999). In a number of spider species, sexual cannibalism serves as a form of parental investment: The female eats the male in the course of the mating act, which enables her to properly equip the offspring with nutrients. While this form of parental investment seems to be rather extreme, the cost of cannibalism to males may, in fact, not be unduly high, especially when compared to the alternative: In redback spiders (*Latrodectus hasselti*), approximately 80% of males die without mating in the wild, suggesting that being cannibalized does not necessarily reduce male fitness. Not all males are consumed by the female during mating, but if they are, they sire more offspring than if they escape (Andrade 2003). Sexual cannibalism also highlights the adaptive plasticity of parental investment: In most species where sexual cannibalism occurs, it falls far short of happening at all mating events. Resource potential of the habitat is one of the factors predicting the likelihood of cannibalism to occur: The threshold to eat their sexual partner is lower for hungry females than for well-nourished ones.

As the political and societal implications of parental investment theory are substantial, the necessary nuance in the discourse is often lacking. Evolutionary approaches tend to downplay the environmental effects, and social scientists tend to negate biological factors. Both positions in their extreme are wrong. If parental care can be negotiated, and asymmetries are not predetermined, sex differences observed in human behavior might be resulting to a lesser

degree from biological constraints than generally assumed. As is the case for human capacities in general, *Homo sapiens* is a species that belongs to the group of generalist rather than specialist organisms. Humans are highly adaptive and can handle a large variety of environmental challenges. There is no reason why this behavioral plasticity should not apply to human sexuality and reproductive behavior. Quite the opposite: The existence of monogamy, polygyny, polyandry, and promiscuous systems in different cultures indicates that the behavior complex of human reproduction is rather flexible (Low 2005). Socialization and cultural influences might contribute to the establishment and maintenance of so-called traditional sex roles. A need for disentangling the biological and socio-cultural influences is being recognized by more and more scientists, but as the bidirectional influences are complexly interwoven, a definite answer is not within reach yet.

Conclusion

The elegance of parental investment theory has led to a fundamental impact of that line of thinking on the questions addressed in evolutionary studies of human behavior: The resulting focus on intrasexual competition and intersexual selection makes it hard for some scholars to acknowledge the possibility of general competition among individuals, irrespective of their sex, when it comes to resources equally coveted by all.

As the theoretical framework affects the research practice, an interdisciplinary exchange can contribute to fend against bias. In interactions across disciplinary boundaries, the concepts inherent to the disciplines are continually tested, which sheds light on weaknesses in the argument and broadens the approach.

While complete objectivity is beyond reach for science, it should be the foremost intention of scientists to strive to minimize potential sources of bias and to keep an open eye toward biases that cannot be eliminated.

Cross-References

- [Female Reproductive Variance](#)
- [Parental Investment and Parenting](#)
- [Parental Investment and Sexual Selection](#)
- [Paternal Investment](#)
- [Paternity Uncertainty and Father-Offspring Conflict](#)
- [Red Queen Hypothesis, The](#)
- [Reproductive Strategy](#)
- [Reproductive Variance](#)
- [Robert Trivers](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Dimorphism](#)

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Parental Investment Theory (Middle-Level Theory in Evolutionary Psychology)

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Synonyms

Parental care, parenting; Resource provision

Definition

Parental investment is referred to as any expenditure (time, energy, resources, etc.) that a parent incurs to benefit an offspring. *Parental investment theories* in evolutionary biology and evolutionary psychology explore mechanisms underlying parent-offspring relationships and investment. These theories examine adaptive functions and fitness dynamics of parent-offspring relationship, and how environmental conditions, sex differences in provision of reproductive resources regulate parental investment in sons and daughters.

Introduction

Throughout hominid evolution, our ancestors have always managed to do two things: survive to reproductive age and reproduce. Human survival and reproduction are characterized by internal fertilization, long-term gestation, lactation, and prolonged infancy that requires intense parental care and investment. *Parental investment*, in evolutionary biology and evolutionary psychology, is referred to as any expenditure (time, energy, resources, etc.) that a parent incurs to benefit an offspring (Trivers 1972).

From an evolutionary perspective, offspring are genetic vehicles for their parents. Without children, an individual's genes would perish. It is thus reasonable to expect that natural selection would favor powerful mechanisms in parents that ensure the survival and reproductive success of their children. Parental investment is thus pivotal for both offspring survival and perpetual reproductive success of the parents. Parental investment is viewed as a cost in parental fitness, via either direct physical or physiological expenditure or indirect opportunity cost in mating and reproduction.

Fisher's Principle

A pioneering analysis of parental investment can be traced back to Ronald Fisher. In his 1930 book *The Genetical Theory of Natural Selection*, Fisher developed an evolutionary model to explain why the sex ratio of most species that produce offspring through sexual reproduction is approximately 1:1 between males and females.

Fisher's model suggests that parental investment should also covary with this dynamic of evolutionary equilibrium. Fisher built his argument in terms of parental expenditure and predicted that parental expenditure may deviate from the 1:1 ratio but would be "corrected" back to an equal distribution by natural selection. Suppose females outnumber males in a population due to a war situation. A newborn male then receives more parental investment and would have better mating prospects than a newborn

female and therefore can expect to have more offspring. Therefore, parents who are genetically more disposed to producing males would have more than average numbers of offspring. As a result, male to female sex ratio becomes higher than 1:1. The demand and supply relationship thus is changed and then reversed: the shortage of males is replaced by a shortage of females. The male to female sex ratio is then downregulated toward the 1:1 equilibrium. Similarly, in situations that female births are less common than male births, the sex ratio would be regulated down toward the equilibrium (Hamilton 1967).

Regulated by natural selection, the total parental investment incurred will be equal across sex for children. This implication from Fisher's principle stands in contrast to persistent differential parental investment in sons and daughters. One way to understand the coexistence of the 1:1 sex ratio and differential parental investment is to view the former as population equilibrium and the latter as individual strategies that are dependent upon situational factors and the life-stage of the parents.

Sex ratio of an entire population is not as sensitive as operational sex ratio to natural selection and sexual selection. *Operational sex ratio* is a measure that is more sensitive to sexual selection. It is the ratio of sexually competing males that are ready to mate to sexually competing females that are ready to mate (Clutton-Brock 2007). This is a measure of how intense sexual competition is in a population and the potential rate of reproduction. This ratio reflects the severity of intrasexual mating competition and is controlled by relative parental investment (Gwynne 1990). For example, if females spend more time caring for young than mating, but males do the opposite, then more males would be ready to mate, thus creating a male-biased operational sex ratio.

Hamilton's Inclusive Fitness (Kin Selection) Theory

Parental investment theory can be viewed as a branch of kin selection theory. Building upon

Fisher's (1930) work, W. D. Hamilton (1964) proposed his inclusive fitness theory, which argues that altruistic acts toward neighbors who have copies of the helper genes would be favored by natural selection. Inclusive fitness theory holds the keys to understanding differential investment behaviors, including parental investment. The mathematical treatment of the theory ($C \leq rB$) is now often referred to as Hamilton's rule, which shows that an "altruistic design" can spread through the population if it causes an individual to help a kin member whenever the cost (C) to the helper's own reproduction is offset by the benefit (B) to the recipient's reproduction, weighted by the genetic relatedness between the two (r).

Hamilton's (1964) inclusive selection theory has been a powerful source for generating hypotheses about altruistic behaviors in social interactions, for which standard economic models fail to account. Hamilton (1964, p. 19) predicted that: "The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbor's fitness against his own according to the coefficients of relationship appropriate to that situation." For kin selection to work, a prerequisite is that "a suitable social object is available" in an interactive social context (Hamilton 1987, p. 420). Parent-offspring interaction thus might be the most typical case for kin selection.

Hamilton's rule also suggests *extended forms of parenting* from kin who are not biological parents. For example, Gorrell et al. (2010) showed that surrogate mothers of red squirrels adopt related orphaned squirrel pups but not unrelated orphans. The authors of this study calculated the cost of adoption by measuring a decrease in the survival probability of the entire litter after increasing the litter by one pup and the benefit of adoption as the increased chance of survival of the orphan. More precisely, females adopted orphans when $rB > C$ but never adopted when $rB < C$.

Another form of extended parenting can be seen in *eusociality* (true sociality) which is characterized by overlapping generations between parents and their offspring, cooperative brood care, and the specialized castes of non-reproductive individuals (Freeman and Herron

2007). Social insects provide good examples of extended parenting. The workers of some species are sterile, a trait that would not occur if individual selection was the only process at work. The relatedness coefficient r is abnormally high between the worker sisters due to *haplodiploidy*, whereby males are haploid and females are diploid. This ensures that sisters are more related to each other than they ever would be to their own offspring. Hamilton's rule readily accounts for such extended parenting behavior, though there are alternative explanations (see Nowak et al. 2010).

Humans also exhibit extended forms of parenting. A study of childcare practices among Canadian women found that respondents with children provide childcare reciprocally with nonkin. The cost of caring for nonkin was balanced by the benefit a woman received – having her own offspring cared for in return. However, for individuals without their own offspring, the inclusive fitness benefits of providing care to closely related children might outweigh the time and energy costs of childcare. Indeed, the respondents without children were significantly more likely to offer childcare to kin only (Davis and Daly 1997).

Trivers' Model of Parental Investment

Inspired by seminal work of Hamilton (1964), Robert Trivers, then a graduate student at Harvard University, developed a theory of parental investment as a result of sexual selection. In *iteroparous* species, where individuals may go through several reproductive bouts during their lifetime, a tradeoff may exist between investment in current offspring and future reproduction. The importance of parental investment can be seen especially in species in which the offspring are altricial (i.e., unable to fend for themselves from earliest ages). In many bird species and in modern humans, this leads to males spending more time caring for their offspring than do the male parents of precocial species, since reproductive success would otherwise suffer.

Based on this cost–benefit analysis, Trivers (1972) defined the term parental investment to mean any investment by the parent in an

individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring. Overall, parents maximize the difference between the benefits and the costs, and parental care will be likely to evolve when the benefits exceed the costs.

The evolution of sex differences in parental investment is widely attributed to anisogamy (i.e., sexual reproduction involving two types of gametes that differ in size). The initial asymmetry in premating parental investment (eggs vs. sperm) is assumed to promote even greater divergence in postmating parental investment (parental care). In such a situation, a male's reproductive success is limited by his ability to fertilize eggs with his sperm in the same-sex mating competition. A female's reproductive success is limited by her ability to produce eggs, which requires a large investment of metabolic energy (Trivers 1972, p. 138).

In humans, parental investment starts from the point when the sperm fertilizes the egg. Following fertilization, the minimal obligatory parental investment for the female is 9 months of pregnancy, followed by delivery. In contrast, the minimal obligatory parental investment for the male is almost zero. This difference of minimal obligatory investment between males and females suggests that the amount of investment and effort put into mating and parenting would also differ.

Trivers (1972) introduced two arguments to link premating and postmating investment. The first argument is that females are more committed than males to providing care because they stand to lose a greater initial investment. The second argument takes the reasonable premise that anisogamy produces a male-biased operational sex ratio leading to males competing for mates. Male care is then predicted to be less likely to evolve as it consumes resources that could otherwise be used to increase competitiveness.

These two arguments however are challenged by other scholars (see Kokko and Jennions 2008). The first argument has been criticized for committing the “Concorde fallacy” as optimal decisions should depend on future payoffs, rather than past costs. However, the argument can be made in

terms of residual reproductive value when past investment affects future payoffs. The second argument was challenged by the Fisher principle. Given each offspring has precisely two genetic parents, a biased operational sex ratio would generate frequency-dependent selection that favors increased parental investment by the sex facing more intense competition, in this case males.

Although facing some theoretical challenges, predictions from Trivers' (1972) model received ample empirical support. Using measures from time spent in vicinity, touching, and teaching children shows that women indeed care for their children more intensively than men do (Geary 2000).

Besides the mating opportunity costs hypothesis suggested above, another mechanism underlying the phenomenon that mothers invest more than fathers in offspring is the *paternity uncertainty* hypothesis. Mothers, consciously or not, are "sure" of their genetic contribution to their offspring (maternity certainty). When a female gives birth or lays a fertilized egg, there is no doubt that her offspring will contain 50 % of her genes. In contrast, from a male's perspective, there can always be some probability that the offspring was fathered by another male (paternity uncertainty).

Parent-Offspring Conflict

Given the importance of offspring, one of the astonishing facts about parental care is that many species do not engage in it at all (Alcock 2001). Part of the reason for the lack of universality of parental care is that it is so costly. By investing in offspring, parents lose out on resources that could be devoted to themselves or toward finding additional mates. Parents who protect their young risk their own survival. Thus, when fitness cost is higher than fitness benefit, a stopping mechanism becomes necessary.

From an evolutionary perspective, parents and children are predicted to have conflicts. Following his own work on parental investment and sexual selection, Trivers (1974) developed a model of parent-offspring conflict. In sexually reproducing species such as humans, parents and offspring are

genetically related by 50 %. This genetic relatedness between parent and child can exert selection pressure for parental care. But it also means that parents and children differ genetically by 50 %. Fitness benefit for one is not perfectly correlated with fitness benefit for the other. Specifically, parents and children will diverge in the ideal allocation of the parents' resources, the typical result being that children want more for themselves than parents want to give (Trivers 1974).

For a parent of two offspring with two units of food available, the optimal allocation would be to give one unit of food to each offspring. Considering that there is a diminishing return associated with each additional consumption, the value of the first unit of food consumed is higher than the value of the second unit of food. However, for each offspring, the ideal allocation is to get two units of food. The theory of parent-offspring conflict predicts that each child will generally desire a larger portion of the parents' resources than the parents want to give. In addition, parent-child conflict over the parents' resources is predicted to occur not merely at particular times such as adolescence, but at each stage of life.

Trivers' theory (1974) identified an important area of genetic conflict of interest between parents and children. Over evolutionary time, there will be an "arms race" between the genes expressed in parents and the genes expressed in children. Selection is therefore predicted to forge adaptations in children to manipulate parents toward the children's optimum resource allocation and counter-adaptations in parents to manage resource allocation toward their own optimum. This theory yields some surprising predictions. For example, mother-offspring conflict will sometimes occur in utero, such as over the blood supply to the fetus, the size of the fetus, and whether the fetus is spontaneously aborted. Empirical evidence supports these predictions (Haig 1993).

r/K Selection Hypothesis and Life-History Theory

The other overarching theory that is closely relevant to parental investment is the r/K selection

theory by MacArthur and Wilson (1967). According to the theory, when resources are sufficient to carry or support organisms living in an environment, organisms would be able to freely exploit rich resources for fast development and early reproduction that is characterized by a large number of offspring with little parental investment. This is known as *r* selection, with *r* representing the maximal reproductive rate of a species. In contrast, when resources become scarce, organisms adopt slow strategies, also known as *K* selection, with *K* representing the carrying capacity of the environment. *K* selection favors slow development and intense parental care and investment to reproduce few, high-quality offspring who can compete for and monopolize the depleting resources of the environment.

Species with *K*-selected traits, such as large body size, long life expectancy, and the production of fewer offspring, which often require extensive parental care until they mature, include elephants, humans, and whales. Although some organisms are identified as primarily *r*- or *K*-strategists, the majority of organisms do not follow this pattern (Hrdy 2000). The *r/K* dichotomy can be expressed as a continuous spectrum using the economic concept of discounted future returns, with *r*-selection corresponding to large discount rates and *K*-selection corresponding to small discount rates (Reluga et al. 2009).

The *r/K* selection theory has been challenged by its lack of empirical support and led to a newer paradigm of life-history theory that focuses on age-specific strategies and incorporates many of the themes important to the *r-K* paradigm (Reznick et al. 2002).

Life-history theory provides an evolutionary and psychobiological framework for studying parental investment. The theory primarily concerns tradeoffs among various survival and reproductive needs given finite energy and resources and infinite inter- and intra-species competition (Stearns 1992). The most essential tradeoffs are between somatic effort (growth, learning, and socialization) and reproductive effort. Reproductive effort itself involves the additional tradeoff between mating effort that results in offspring

quantity and parenting effort related to offspring quality.

Calibrated in terms of fitness or reproductive success, all tradeoffs can be summarized as the tradeoff between current or early reproduction and future or delayed reproduction. Varying along the fast-slow continuum, differences in life-history strategies result in the vast individual differences in observed behavior (Del Giudice and Belsky 2010). Variations in life-history strategies are the result of environmental conditions. Two overarching conditions relevant to life-history strategies are the extent of environmental harshness and unpredictability regarding mortality and mobility. High levels of extrinsic mortality and mobility lead to the adoption of fast life-history strategies with low parental investment because fitness is maximized by accelerating development and initiating early reproduction before extrinsic mortality or mobility hits. Conversely, low levels of environmental harshness and unpredictability do not necessarily predict slow life-history strategies but depend on other factors in the environment, such as resource levels and the extent of intraspecific competition over resources (Ellis et al. 2009). The most effective forms of signals in a child's environment are parental behavior and related information, such as the absence or change of parental figures (Ellis 2004). The mere experience of changes in parental and other adult figures has been found to be a robust predictor of fast life-history strategies (Tither and Ellis 2008).

Studies of life-history strategies suggest that quality of parental investment affects the adoption of fast or slow strategies by the offspring, which in turn determines the parental investment strategies of the offspring when s/he becomes a parent in the future.

Differential Parental Investment in Sons and Daughters

Trivers-Willard Hypothesis

Assuming an equal sex ratio in the population, sons and daughters, on average, have equal reproductive success. But the condition of the son or daughter might result in differential parental

investment in sons versus daughters. This is the core insight of the Trivers-Willard hypothesis (1973). According to this hypothesis, rich parents are more likely to have successful offspring and should favor sons since there is a greater opportunity for their sons to be rich and to have more offspring. Conversely, poor parents should prefer daughters to sons because daughters are not as likely to be reproductively unsuccessful as sons.

Stated differently, if being in “good” condition affects male reproductive success more than female reproductive success, as we would expect in a polygynous mating system, then parents should bias investment toward sons if the parents are in good condition and toward daughters if the parents are in poor condition.

Tests of the Trivers-Willard hypothesis in humans have proved inconclusive (Keller et al. 2001). A few studies find a Trivers-Willard effect. In one study, for example, using years of education as a proxy for parental investment, Rosemary Hopcroft (2005) found that sons of high-status men attained more years of education than daughters, whereas daughters of low-status men reached higher education levels than sons. She also found that high-status men sire more sons. Future studies are needed to determine whether the hypothesized Trivers-Willard effects are found among different populations of humans. Gaulin and Robbins (1991) found support for the Trivers-Willard hypothesis in their study of North American women. However, additional tests of this hypothesis have produced mixed results, particularly with human samples. In a study with larger data sets, Keller et al. (2001) reported that their results did not replicate the findings of Gaulin and Robbins (1991). Based on the analysis of the results from their own and other previous studies, these authors conclude that Trivers-Willard effects are at best tiny in the contemporary United States, where resources are too abundant compared to the typical conditions of hominid evolution.

Reproductive Variance Hypothesis

An alternative account of differential investment in sons and daughters focuses on the reproductive variance of sons versus daughters. The concept of

variance in reproductive payoffs has been pivotal in some recent evolutionary analyses of behavior (see, for example, Daly and Wilson 1997). The evolutionary logic for risk/variance sensitive strategies is that selection would favor a greater risk-proneness when risk avoidance promises not fitness but reproductive failure. Universally and throughout hominid evolution, men have a higher reproductive variance than women. That is, women tend to consistently produce a few children whereas men tend to have either a lot of offspring or zero offspring. From a Darwinian perspective, risks can be viewed as variance in reproductive fitness in terms of the number of offspring one has (Wang 2002). Thus, parental investment in daughters versus sons is like a risky choice between a safer bet and a gamble (a more probabilistic bet), respectively.

Following this line of thinking, parents from a contemporary US population whose wealth conditions are not clearly diversified tend to have comparable parental expectations (aspirations) for their children’s financial and reproductive prospects. Thus, what affects their differential investment in sons or daughters would be their psychologically perceived relative wealth compared to their neighbors instead of absolute wealth. When the perceived relative wealth is lower, the distance to parental expectations would be higher. Thus, sons would be favored since a higher variance in sons’ financial and reproductive success would increase the chance of reaching the parental expectations or goals. Conversely, daughters would be favored by parents who have a higher perceived wealth. Therefore, a reversed Trivers-Willard effect is likely to be found in a less stratified population as a result of the difference in perceived relative wealth. In contrast, a Trivers-Willard’s effect would be more likely to be found in a population with a stratified wealth structure. For instance, if a wealthy parent has a much higher than average expectation for his or her children’s financial and reproductive success, sons would be favored, thus a Trivers-Willard’s effect.

In a field study conducted in villages in north-west China, Wang (2002) found a reversed Trivers-Willard’s effect when perceived wealth

condition (rated on a 1–9 scale against families in the same local area) was taken into account. The interbirth interval as a measure of parental investment was significantly longer after having a son than after having a daughter for the families with lower perceived wealth but not the families with higher perceived wealth.

In another field study conducted in a Midwest U.S. rural community where the wealth structure was also unstratified, Wang (2007) found that actual household income affected overall parental investment in a child irrespective of the sex of the child, using breastfeeding and interbirth interval as the measurements of the degree of parental investment. In contrast, perceived wealth by parents relative to their neighborhood households affected differential investment in sons versus daughters. Independent of real income of the family, IBI was longer if the parents' perceived family wealth was lower. This effect of perceived wealth on IBI was evident both for daughters and sons. As predicted from sex-specific reproductive variance, a differential breastfeeding pattern in sons and daughters emerged. In the families of higher perceived wealth, the average percent of daughters being breast fed was significantly higher than that of sons (67 % vs. 36 %). In contrast, in the families of lower perceived wealth, the percent of daughters being breast fed decreased to 52 % and the percent of sons being breast fed increased to 49 % percent.

The results from these two studies suggest that investing in sons is riskier than investing in daughters. In terms of parental economics, sons can be viewed as a riskier prospect than daughters since men, on average, have a higher variance in wealth and reproduction than women.

Conclusion

Parental investment theories in evolutionary biology and evolutionary psychology have provided overarching frameworks and testable mechanisms that lead to novel predictions about parent-offspring relationships and investment. *Fisher's model* focuses on the natural selection mechanism that maintains the 1:1 equilibrium in sex ratio and

how parental investment covaries with the dynamic of the equilibrium. *Hamilton's inclusive fitness model* reveals the production rules for the evolution of cooperation between kin, including boundary conditions for parental investment. *Trivers' model* identifies a link between parental behavior and sexual selection, and sex-specific differences in reproductive resource provision before mating and post-reproduction. Since that parental investment is costly for the parents and that the genetic relatedness of a child to either of the parents is 50 %, the ideal resource allocation for a child does not coincide with the ideal resource allocation for the parents. Thus, parent-offspring conflict is inevitable and ubiquitous. *Parent-offspring conflict theory* thus provides unique predictions for parental investment related behaviors. The *r/K selection model* and *life-history theory* view parental investment as an adaptation to environmental harshness and unpredictability regarding mortality and mobility. Evolutionary analyses also help to understand *differential parental investment*. The concept of *paternity uncertainty* is used to account for one type of differential parental investment that mothers invest more in offspring than fathers. The *Trivers-Willard hypothesis* predicts another type of differential investment in sons versus daughters by the parents, contingent upon the wealth condition of the parents. An evolutionary analysis based upon *reproductive variance* in sons versus daughters offers an alternative mechanism for understanding differential parental investment.

Cross-References

- [Evolution of Cooperation](#)
- [Genetic Relatedness Affects Aid to Kin](#)
- [Hamilton's Rule and Theoretical Implications](#)
- [Kin Selection](#)
- [Life History Theory](#)
- [Operational Sex Ratio](#)
- [Parent-Offspring Conflict \(Trivers\)](#)
- [Paternity Uncertainty](#)
- [Reproductive Strategy](#)

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Parental Investment vs. Mating Effort

► Parental Effort Versus Mating Effort

Parental Mate Choice

► Arranged Marriages

Parental Monitoring

► Daughter Guarding

Parental Sensitivity

- ▶ [Maternal Sensitivity](#)

Parent-Child Resemblance

- ▶ [Promoting Paternity \(You Look Like Your Father Phenomenon\)](#)

Parenthood

- ▶ [Parental Investment and Parenting](#)

Parenting

- ▶ [Evolutionary Paradox: Adoption](#)
- ▶ [Paternal Care](#)
- ▶ [Paternity Uncertainty and Investment in Sons and Daughters](#)
- ▶ [Resemblance](#)
- ▶ [Sexual and Reproductive Development](#)
- ▶ [Socialization Processes](#)

Parenting Benefits

- ▶ [Evolutionary Paradox: Adoption](#)

Parenting Costs

- ▶ [Evolutionary Paradox: Adoption](#)

Parenting Decisions

- ▶ [Infant Abandonment](#)

Parenting Effort

- ▶ [Mate Preferences After Having Children](#)

Parent-Offspring Conflict

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Synonyms

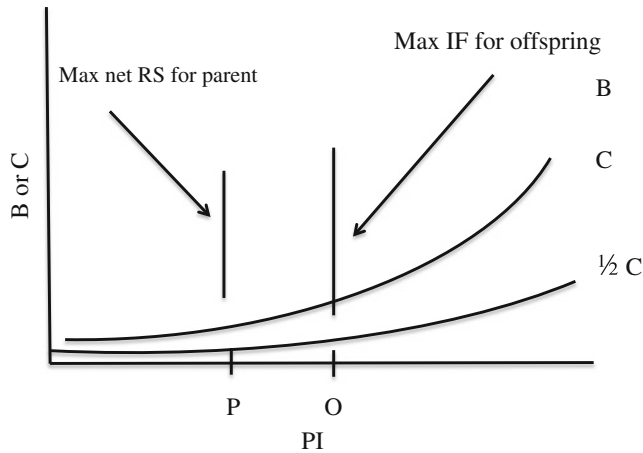
[Conflict over parental investment](#); [Maternal-fetal conflict](#); [Weaning conflict](#)

Definition

Using a gene level view of evolution, offspring and parent obtain equal status. The parent is related to each offspring equally with a 50 % probability that any gene in the parent is also found in a given offspring (e.g., degree of relatedness $r = .5$), while the offspring is related to itself by $r = 1$. This creates inherent levels of conflict over investment between parent and offspring, from conception in the form of maternal-fetal conflict to weaning conflict in early childhood as well as the molding of altruistic, egoistic, and reproductive tendencies of offspring into adulthood.

Introduction

In “parent-offspring conflict,” Trivers (1974) expanded on Hamilton’s kin selection logic of viewing relationships between individuals in terms of their genetic interests. In doing so, he recognized that the interests of offspring almost inevitably come into conflict with those of the individual parent. Parents share the same amount of their genes with each offspring ($r = .5$) and therefore should equally invest in their survival. Offspring, however, benefit by seeking to extract as much parental investment as possible for themselves, at least up to the point where the resulting



Parent-Offspring Conflict, Fig. 1 Conflict during the period of investment over the amount of investment. The benefit (B) or the cost (C) of investment at a given moment is plotted as a function of the amount of parental investment. The parent is selected to maximize the difference

between the two functions (B and C); that is, to invest P . The offspring maximizes ($B - rC$) (here $r = 1/2$); that is, it is selected to receive investment O . (RS reproductive success; IF inclusive fitness) (From Trivers 1985)

damage to their siblings begins to decrease their own inclusive fitness.

This was revolutionary in that classic evolutionary theory had traditionally viewed the parent-offspring relationship exclusively from the perspective of the parent. This interpretation assumed that parents would be selected to allocate their resources in ways that maximize their individual reproductive success, offspring serving merely as passive vessels into which this investment was deposited.

Recognizing offspring as active participants in the process of reproduction, the inherent conflict based on discrepancies of individual genetic interests, and key concepts of inclusive fitness allowed Trivers to generate a theoretical model of parent-offspring relations that could be used to explain the evolution of many complex interactions and behaviors within families (Trivers 1985, 2002).

Conflict Over Continuation of Parental Investment

Trivers made predictions based on economic modeling of when and where periods of conflict over resources between parent and offspring would occur. Weaning conflict in mammals and fledging conflict in birds were some obvious

examples. Trivers identified the period at which the mother would be selected to cut off investment to an individual offspring in terms of maximizing her own RS by ceasing investment in milk production so as to resume ovulating in order to conceive again. The offspring, however, being related to itself by $r = 1$, but to future siblings by $r = .5 - .25$ (depending on whether they share genes from a common father), devalues the cost of nursing and therefore would be selected to agree to be cut off at a date later in time when the costs to him in terms of inclusive fitness outweigh the direct benefits (Fig. 1).

Under this model, individual offspring would be expected to evolve a range of tactics to induce more investment from the parent, than the parent would be selected to give. This, Trivers argued, is why human babies throw tantrums, infant monkeys attack their mothers when they withhold breast milk, and bird chicks threaten to harm themselves when parents refuse to feed them (Trivers 1974, 1985, 2002).

Conclusion

Trivers' approach to the parent-offspring relationship from the view of genetic interests and

individual reproductive success is powerful in that it can be used to explain such diverse phenomenon as maternal-fetal conflict over resources in the womb (see Haig 1993), as well as the intricacies of social relationships within the family. Trivers argued that much of human socialization of children is influenced by conflicts of genetic interests where parents act in ways to increase altruistic tendencies in their offspring toward each other, while reducing selfish and egotistic behaviors that create conflict within the family. While this may decrease the individual offspring's reproductive success, it is selected for in the parent because it benefits them in terms of inclusive fitness (Trivers 2002).

Cross-References

- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Maternal-Fetal Conflict](#)
- ▶ [Reproductive Success](#)
- ▶ [Robert Trivers](#)
- ▶ [Violence from Women's Kin](#)

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Parent-Offspring Conflict (Trivers)

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Definition

The genetic interests of parents and their offspring are not identical. Offspring can be expected to

want more investment than their parents are selected to give them.

Introduction

Human infants cry. The noise seems louder than is necessary given the typical distance to a care giver and in the context of human evolution loud crying might attract predators. Crying has certain frequencies that are grating to adult ears. Crying expresses a need of the infant, but it seems that in a cooperative version of evolution these needs could be communicated with simpler, quieter signals. From weaning tantrums in primates to the loud begging of fledgling birds, parent-offspring communication often seems to reflect conflict rather than cooperation.

In 1974 Robert Trivers proposed an evolutionary framework within which to understand this conflict. Trivers' idea is rooted in the concept of kin selection. In this view, the evolutionary consequence of a behavior is affected not just by its impacts on the reproductive success of the actor, but also by the behavior's effects on the reproductive success of individuals sharing genes by common descent with the actor.

In the context of genetically monogamous family, a parent has a 50 % chance of sharing a given gene with an offspring and reciprocally an offspring has a 50 % chance of sharing any given gene with a parent. (Notated as a "degree of relatedness" of 0.5) Offspring (full sibs) are related to one another also by 50 %. A parent is equally related to all of his or her children. However, an offspring devalues benefits to siblings over benefits to itself. (It is perfectly related to itself but only 50 % related to a sibling). A parent's reproductive success is maximized if it feeds all offspring equally, but each offspring benefits from taking more than its share of the resources on offer. The conflict is usually seen when there are two or more competing siblings. However, the conflict exists if only one offspring is present. In this case, the parent is providing investment in relation to his or her lifetime reproductive effort, while the offspring devalues future offspring over its own benefits.

Benefits and costs are defined in terms of parental investment. Parental investment was defined by Trivers in 1972 as actions that increased the reproductive success of an offspring at the cost to the parent of producing future offspring. There can be an important difference between parental investment and the more general term parental care defined as any action directed at offspring that appears to benefit it. In the context of parent-offspring conflict, when food is abundant the offspring may not get any more benefit even with extra food being provided.

The differences in the degrees of relatedness in the family produce the conflict but at the same time constrains it. In true monogamy, an offspring is related to both parents by 0.5. It does not pay for an offspring to inflict costs on its parents greater than twice the benefit it receives. (Brood parasites, e.g., cuckoos are an exception where the chick is unrelated to the parents.)

The Status of the Theory

Some early critics argued that the parents were always in a position to impose their preference and conflict would not be seen. However, Trivers had already anticipated this idea and emphasized that offspring would be likely to be more likely to use psychological tactics, e.g., annoying crying than force. In the 1970s in a series of papers, Parker provided mathematical genetic underpinnings of the theory. More recently heritable genetic variation in begging behavior has been found in several species (e.g., Dor and Lotem 2009).

In 1995 Godfray produced an important modification to the theory. He argued that if begging (or any solicitation) is costly or risky to the offspring, there will come a point where the extra cost of solicitation will not be offset by the increased contributions of the parents. A costly signal becomes an honest signal. At this point, the offspring can no longer manipulate the parents and allocation of resources should follow the parents' optimum. The proposal requires solicitation to be costly. This has seldom been shown to be the case. The theory would also imply that offspring reach a stereotypical plateau of begging. However, there is evidence from several species that

begging animals alter their begging in relation to the target.

Parent-Offspring Conflict in Relation to Relatedness and Age

There are two variables that should vary with parent-offspring conflict, namely, the degree of relatedness within the family and parental age. With respect to degree of relatedness, Briskie et al. 1994 compared begging in species of bird where the female restricted her mating to her mate to species in which the female mated with several mates. In the latter case, young hatching in a brood may be half-siblings to one another. Begging was more intense in the less related broods. Boncoraglio et al. 2009 added eggs to the nests of barn swallows. Chicks in nests with unrelated eggs added begged more loudly than in normal nests. In humans, there are multiple studies showing that stepchildren (usually with a degree of relatedness of zero to the stepparent) are at greater risk of injury than natural children (Daly and Wilson 2007).

With respect to age, an older parent should hold back less for future offspring than a younger parent and should withhold little or nothing from the last child. There are a few results that show that older females invest more in their offspring. In red deer, older mothers give birth to calves in better physical condition, and the majority of human studies indicate that mothering improves with age (and this excludes the low level of maternal behavior seen in mothers under the age of 20). There are two problems studying the effects of age. First, senescence may reduce a female's ability to reproduce, and in most cases, an animal cannot know his or her chance of surviving to breed again.

For both relatedness and age, there is currently only spotty data in support parent-offspring conflict.

Who Wins Parent-Offspring Conflict?

It has proven very hard to collect data to determine whether parents or offspring are more likely to

distort benefits in their direction. The final fitness outcome of a relationship will be the sum of many individual interactions. In certain instances, e.g., when a mother chimp “gives in” and allows a screaming offspring access to the nipple, it appears that the offspring has its way. But integrating all such interactions has not been accomplished. (The only quantitative data on conflict resolution come from ants where Trivers and Hare (1976) could show that the conflict between the workers and the queen in a nest was usually resolved more in the workers favor).

David Haig (e.g., 1996) has analyzed examples of conflict over resources in pregnancy. Two medical conditions, preeclampsia and gestational diabetes, are probably the outcome of conflicts between the fetus attempting to garner resources and the mother countering. In the extreme but not unknown case of the mother dying from one of the two conditions, it seems clear that both parties in the conflict lose.

The Paradox

Our goal in this article was to illustrate how the theory [of parent-offspring conflict] can inform (and potentially revolutionize) both empirical and theoretical research. Schlomer et al. (2011)

We can certainly sympathize with these complaints having battled ourselves with designing empirical tests of parent-offspring conflict. Kilner and Hinde (2012)

These two quotes represent the paradox of parent-offspring studies. Schlomer et al. argue that parent-offspring conflict should be an important organizing principle for several branches of psychology notably all human developmental studies from infants onwards as well as topics such as mate choice particularly when parents and offspring differ. However, up to now only evolutionary psychologists have discussed the topic and then not very extensively.

Parent-offspring conflict is a powerful and interesting idea, but as the two excellent biologists from Cambridge lament, it has been very hard to go beyond the qualitative and produce good quantitative data.

Conclusion

Trivers theory of parent-offspring conflict provides a profound insight into family relationships. The biological interests of members of the family are not identical. Although supported by both theoretical and some empirical data, it has proven hard to collect good quantitative data on the topic.

Cross-References

- [Conflict Between Parents and Offspring](#)
- [Gestational Diabetes and Maternal-Fetal Conflict](#)
- [Paternity Uncertainty and Father-Offspring Conflict](#)
- [Weaning and Maternal-Fetal Conflict](#)

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Parent-Offspring Conflict in Mate Selection

- ▶ [Daughter Guarding](#)

Parents-as-Mediators

- ▶ [Grandparenting](#)

Parity

- ▶ [Implications for Pregnancy](#)

Parochial Altruism

- ▶ [Benefit Group Relative to Other Groups](#)
- ▶ [Tribalism](#)

Partial Migration

- ▶ [Alarm Callers Are Females with Greatest Genetic Representation](#)

Partner Abuse

- ▶ [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)

Partner Abuse and Homicide

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Synonyms

[Intimate partner violence](#); [Uxoricide](#)

Definition

Partner abuse is a form of domestic violence where any cruel or violent action is directed against an intimate partner, sometimes resulting in homicide.

Introduction

Partner abuse refers to a form of domestic violence where any cruel or violent action is directed against an intimate partner, sometimes resulting in homicide. These actions include, but are not limited to, physical and emotional abuse, sexual assault, and manipulation, each of which poses serious physical or psychological harm to the victim. Data show that women are at a higher risk than men for being abused or killed by a current or former partner, and that in many cases they are repeat offenses (Browne 1993; Garcia-Moreno et al. 2005; Stockl et al. 2013). An extensive literature exists to understand the ultimate causes and proximate risk factors associated with partner abuse and homicide.

Theoretical Overview

Wilson and Daly (1992) argued that various forms of partner abuse and homicide stem from men’s proprietary view of their intimate partners. According to Trivers’ (1972) parental investment theory, when the sexes differ in their minimal obligatory parental investment (i.e., minimal resources needed to produce offspring), mating

strategies also differ. The sex with higher obligatory investment, typically females, can increase their reproductive success from a mate's genetic quality and from investing resources in offspring development and growth. The sex with lower obligatory investment can increase their reproductive success by increasing the number of mateships with the high-investing sex. Thus, there is a greater degree of competitiveness among males – those who are successful in acquiring a mating partner take a proprietary view of their partner due to the potential risks of losing her to competitors. This theoretical model predicts that men evolved traits that minimize or alleviate factors that jeopardize the stability and fidelity of this relationship. Since abusive actions by men may be adaptive, and are costly to women, sexual conflict theory may also help explain its causes and consequences (see ► [“Sexual Conflict”](#) entry). Daly and Wilson argued that partner abuse functions as *coercive control*, by preventing the probability of extra-pair mating, and that partner homicide is not adaptive but is a by product of conditions that cause proprietary actions. There should be a male-bias in the degree to which partner abuse is perpetrated, but this does not suggest women do not engage in partner abuse or homicide. Factors motivating either sex should be different.

Risk Factors

The conditions or traits that impact the stability and fidelity of an intimate relationship can be understood as risk factors associated with partner abuse or homicide. Sex, age, jealousy and cuckoldry risk, relationship status, and psychopathy are important risk factors because they are theoretically relevant and have been consistently linked with partner abuse and homicide.

Sex

Though variation exists across nations, most studies find that men are more likely to commit intimate partner homicide than are women (Dobash et al. 1992; Sabri et al. 2016). Data from the USA have been used to demonstrate equivalence

between the sexes on intimate partner homicide, but the USA seems to be an exception, and more recent research found that the US data are now more consistent with other nations (Sabri et al. 2016). Globally, two-thirds of all intimate partner homicide victims are women (United Nations Office of Drugs and Crime 2013).

When considering non-lethal partner abuse, sex differences are not as evident, where some studies find very similar rates of partner aggression by either sex, some even showing a slight bias towards women aggressors (Archer 2000). Although these findings highlight the importance of considering men's victimization, it is possible that methodologies used to acquire them exaggerate such effects (Dobash et al. 1992). For example, much of the data showing sexual symmetry comes from using a self-report measure, the Conflict Tactics Scale (CTS), which has questionable validity. Some CTS items that qualify someone as an abuser can also be interpreted in a non-aggressive way, and the measure inaccurately treats items as equally as severe. For example, *grabbing* and *slapping* are treated as “minor,” and *trying to hit* and *stabbing* are both considered “severe.”

Women are more likely to be identified as victims of partner abuse when other sources of information are used, such as injury data, police reports, emergency departments, and data from armed forces (Archer 2000; Dobash et al. 1992). Considering sexual symmetry or even higher rates of women abusing men seem to be true only in younger, dating, and student samples, it is possible that such effects are due to younger men inhibiting their aggression and do not react to female aggression to improve their chances of establishing a long-term relationship (Archer 2000).

Age

Wilson and Daly (1993a) hypothesized that younger women are at a greater risk of partner abuse because they have higher reproductive value, eliciting stronger competition and sexual jealousy. Younger women also have a higher likelihood of finding another spouse, giving men additional risk to losing partner. The data

supports this hypothesis – not only are younger women victimized more frequently abused by an intimate partner, younger women are more likely to have partners with higher levels of sexual jealousy (Serran and Firestone 2004).

An alternative explanation for young women being at higher risk is that they also happen to be in a relationship with younger men, a group known to be violent (Peters et al. 2002). Daly and Wilson ruled out this explanation by showing that spousal homicide is more likely to occur when the male partner is older than the female (Wilson et al. 1993). They hypothesized that increased risk with higher age disparity could be due to men feeling more threatened and jealous, having previous partners that cause greater conflict in the current relationship, or some other third variable associated with conflict and interest in much older or younger partners.

Jealousy and Cuckoldry Risk

Sexual jealousy and cuckoldry risk are leading factors associated with intimate partner physical and sexual violence, and spousal homicide (Buss and Shackelford 1997a; Camilleri and Stiver 2014). Men faced distinct consequences due to a partner's sexual infidelity, the most salient being paternity uncertainty of their offspring (Serran and Firestone 2004). Considering women are always certain their offspring are genetically related to them, only men are at risk of being cuckolded (i.e., unknowingly raising unrelated offspring). This situation would have posed a strong selection pressure on men to identify and minimize this risk. To prevent such consequences from occurring, men attempt to control their partners' reproductive capacities, resulting in the use of coercive tactics, such as the use of violence, in an attempt to regain control (Serran and Firestone 2004). Spousal homicide is suggested to be a nonadaptive, unusual manifestation of similar conflict (Serran and Firestone 2004; Wilson et al. 1995).

Intimate partner sexual violence is also associated with risk of infidelity from one's partner. It has been hypothesized that sexual coercion reduces the risk of cuckoldry by engaging in sperm competition. Much of the literature has

found a robust link between infidelity risk and partner-directed sexual coercion and rape (Camilleri and Quinsey 2009b; Goetz and Shackelford 2006).

Other sexually coercive actions that qualify as partner abuse may function to prevent opportunities for extra-pair copulations from happening. These actions include: *herding*, which is when men aggressively separate women from other men; *sequestration*, which is when men aggressively remove women from their social group; and *harassment*, which is when men persist in their sexual pursuit until the female relents or escapes. Each of these abusive actions may function to prevent extra-pair copulations.

Women Who Abuse Men

Women also engage partner abuse and homicide. The motivations, however, appear to be different from men's: (i.e. women typically murder their husband out of self-defense or defending their offspring (Wilson et al. 1993). Interestingly, women show higher rates of abuse in studies that use younger, dating, and student samples, whereas men show higher rates of abuse in studies that use older, marital/cohabiting, and community samples, possibly because men are less prone to being aggressive in a situation where it would be easier for the female to leave the relationship (Archer 2000).

It is also possible that because women are more prone to emotional jealousy than are men, (i.e. women can increase reproductive success through mate quality, which includes having a mate with resources and/or spends time helping raise offspring) it is possible that women's response to emotional infidelity, in which time and resources are directed towards another mate, might motivate them to behave in ways that would minimize this risk (Buss et al. 1992). Consistent with this view, women do engage in some mate retention actions when their partner has a larger income, such as responding to an infidelity threat with punishment (Buss and Shackelford 1997b). Stieglitz et al. (2012) also found in a forage-farmer sample that 50% of spousal arguments are over the men diverting resources outside that relationship. (This measure of diverting resources outside the

relationship, however, included actions unrelated to infidelity, such as drinking) It is therefore possible that both men and women may respond to infidelity with coercive actions, but their function is slightly different – for men, it is to prevent a partner's sexual infidelity, whereas for women, it is to prevent a partner's emotional infidelity. More data specifically testing hypotheses about these possible sex differences are needed.

Relationship Status

Spousal homicide against both wives and husbands occurred more frequently in *de facto* (cohabitating) relationships than in registered marital unions. However, the youngest wives have been found to be at greatest risk in registered marital relationships, whereas in *de facto* unions, risk was found to be greatest among middle-aged wives (Wilson et al. 1993). Poverty and young adulthood are both associated with higher homicide rates and *de facto* unions are generally more prevalent among the young and impoverished. *De facto* unions are also generally childless, which could lead to the increased likelihood of estrangement as women in dating relationships can terminate the relationship more easily than women in marital relationships. Childless relationships are indeed associated with higher spousal conflict and divorce in registered marital unions (Wilson et al. 1993). *De facto* unions are also more likely to include stepchildren, which is a risk factor for spousal conflict and violence.

Many studies have shown that sexual jealousy and estrangement have been a common motive for intimate partner violence and homicide committed by men (Capaldi et al. 2012; Wilson and Daly 1998). In fact, there seems to be an elevated risk of partner homicides when couples are no longer residing together, possibly because such a scenario clearly indicates loss of a partner, leading to more coercive actions. Not only has estrangement been found to be a risk factor for uxoricide, but sublethal assaults have also been found to increase when separated. Women who had previously suffered from spousal abuse prior to separation are more likely to experience serious abuse following separation (Wilson and Daly 1993b). Research has shown that in the first few months

following separation, risk levels are at their highest; however, it has also been found that spousal homicide can occur months or even years later (Wilson and Daly 1993b).

Psychopathy

Although little attention has been paid to the consequences of being in an intimate relationship with a psychopath, some research has found that partner-psychopathy is associated with both intimate partner sexual and physical violence (Camilleri and Quinsey 2009a; Hilton et al. 2001). Psychopaths have been described as an obligate life-history strategy that includes, among other traits, high mating effort and coercive sexuality. It is therefore possible that such sexually coercive and aggressive actions continue even in a committed relationship.

Conclusion

Many of the risk variables associated with partner abuse and homicide stem from men's proprietary view of their intimate partners. Younger women are at risk of victimization because their higher reproductive value inspires greater competition for them, leading to greater jealousy and conflict in the relationship. Men are more likely to engage in partner abuse as a form of coercive control, sometimes leading to homicide. Jealousy, cuckoldry risk, and psychopathy are associated with both physical and sexual violence in relationships. These items do not represent all factors that are associated with partner abuse and homicide but are theoretically relevant and empirically robust. See Capaldi et al. (2012) for a systematic review on factors associated with intimate partner violence.

Cross-References

- [Forced Copulation](#)
- [Intimate Partner Violence](#)
- [Partner Homicide](#)
- [Partner Rape](#)

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Partner Abuse and Homicide: Victims and Perpetrators

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Partner abuse is defined as physical, emotional, and/or psychological abuse that occurs between partners (Caman et al. 2017). Partners include spouses, ex-spouses, and individuals who are or have dated and include couples who live together

and couples who do not. In the United States, incidents of partner abuse are estimated to occur between 4.8 and 5.3 million times a year (Sheehan et al. 2015). Approximately half as many men as women are victims of partner abuse and homicide. In 2010, 82% of victims of partner abuse and homicide were women (Sheehan et al. 2015). Though there is some national variation in the degree to which there are sex differences in spousal abuse, there are more men than women who are perpetrators across all locations (Wilson and Daly 1992).

Victims of partner abuse and partner homicide have similar characteristics. Many of these victims have lower socioeconomic status and less education, and female victims are generally younger than male victims (Kirkland Gillespie and Reckdenwald 2017; Swatt and He 2006). African-Americans are approximately 2.5 times more likely than Caucasians and others to be victimized (Caman et al. 2017), and individuals who live in more rural areas are more likely to be victimized (Jennings and Piquero 2008). Rurality presents higher exposure to risk variables, such as isolation from neighbors, higher rates of poverty, and lower levels of education (Kirkland Gillespie and Reckdenwald 2017).

Explaining Characteristics of Perpetrators and Victims

Evolutionary psychology may help explain patterns of partner abuse perpetration and victimology. Generally, intimate partner violence may be functional for men by using coercion to control the reproductive options of their intimate partner (Wilson et al. 1995). Since men have lower minimal obligatory parental investment, they can increase reproductive success through mate number, creating high competition between men for access to mating partners and placing men who are in intimate relationships at risk of cuckoldry. Wilson and Daly (1998) suggested that intimate partner violence decreases the probability of cuckoldry or loss of a partner to a rival. This theoretical model explains why men are typically the perpetrators and younger women

are typically the victims because there is greater competition between men for women with higher reproductive value. This does not mean women do not aggress against their partners. Much of women's aggression toward men is in response to being abused (Wilson and Daly 1992). A potentially unique characteristic of intimate partner homicide is the presence of "May–December" marriages, where men are much older than their partner (Wilson et al. 1995), though it remains unclear why such a pattern exists.

Though many evolutionary theorists agree that nonfatal IPV may be adaptive, there is some debate about intimate partner homicide, where some proposed that it is a byproduct of male sexual proprietariness (i.e., a belief of ownership and entitlement over intimate partners). Such a proprietary view would have aided men, who can increase reproductive success through mate number, to prevent competition for access to one's mate through coercive control. Sometimes, the coercive actions are so severe that they result in death (see ► ["Partner Abuse"](#) and ["Byproduct Theory \(Daly and Wilson\)"](#) entry). An alternative explanation is that uxoricide is an adaptation, because in the context of infidelity, it removes a mating opportunity from a rival and prevents gaining the reputation of a cuckold (see ► [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)"](#) and ► [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]"](#)). This explanation is problematic, however, because it is not clear whether these benefits outweigh the costs of losing a partner, losing a caregiver of any current offspring, reputation of being a murderer, and risk of retribution from the victim's family.

Cross-References

- [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)](#)
- [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)

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Partner Characteristics

- [Lowering Partner Standards in a Short-Term Mating Context](#)

Partner Choice

- [Cooperation Among Nonchimpanzee, Non-human Primates](#)

Partner Death as Designed Outcome

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Intimate partner violence is when a person uses physical or sexual violence, stalking, or psychological harm against an intimate partner (Center for Diseases and Control 2020), the most severe being homicide. Though there is some variation in the sex-ratio of perpetrators who kill an intimate partner. Across most regions, men to a large extent perpetrate intimate partner homicide more often than do women, with the USA being an exception (Wilson and Daly 1992). Female victims of homicide are disproportionately victimized by an intimate partner (39%) when compared to the proportion of male victims of homicide who were victimized by an intimate partner (6.28%). One of the first evolutionary explanations for this sex difference is that intimate partner homicide is a by-product of men's use of violence to coercively control their partner's mating options, thereby reducing the probability of cuckoldry (Wilson and Daly 1993). An alternative hypothesis suggests intimate partner homicide is an adaptation.

Duntley and Buss (2005, 2011) proposed Homicide Adaptation Theory, which suggests killing was advantageous for our ancestors because it provided solutions to problems of survival and reproduction. Homicide could function in different ways, such as using it to: remove a competitor who inflicts costs; get access to resources or protecting resources; or build a reputation to prevent being exploited. Applying this logic to intimate partner homicide, they proposed that homicide could be a response to partner infidelity to preserve one's status, because gaining a reputation of a cuckold may have repercussions in terms of being exploited by rivals or future mating partners. Such actions would also reduce a rival's reproductive benefits. These ideas are fully explored by Buss (2006), Duntley and Buss (2005, 2011), and Duntley (2015).

Research supporting these hypotheses come from data on intimate partner homicide, where many such cases involve sexual jealousy or infidelity (Shackelford et al. 2003; Wilson and Daly 1993), and from homicide fantasies where estrangement and partner infidelity are the most common reasons men give for having persistent thoughts of killing a partner (Buss 2006). Potential concerns with these lines of support is that associating homicide with jealousy and infidelity is consistent with both by-product and adaptation hypotheses, and homicide fantasies may not be a valid indicator of actual homicides. To identify which explanation is most accurate, researchers need to identify whether the possible fitness benefits of intimate partner homicide outweighs the various costs. These costs include loss of a mating partner, familial retribution, loss of a caregiver to one's offspring, and gaining a reputation of a murder which may scare off future mates.

Though men account for many intimate partner homicides, some women also kill their intimate partners. There is evidence to suggest that rather than being the aggressor, women kill in response to being abused or victimized by their intimate partner. Research on women who kill their intimate partners requires much more theoretical and empirical attention.

Cross-References

- [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)](#)

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Partner Desertion

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Synonyms

[Mate desertion](#)

Definition

Partner desertion occurs when one member of a mated pair absconds, leaving the remaining partner to care for any offspring alone.

Introduction

In systems with biparental care, parents are caught in a cooperative dilemma. Each partner could potentially benefit by deserting its mate and their young to begin a new breeding attempt with a different partner or to conserve energy for future reproduction, if the deserted partner rears the young alone. However, the costs of desertion can outweigh potential benefits if a deserted partner is incapable of raising young successfully alone, is itself likely to desert the young, or is selected to incompletely compensate for the loss of the partner's care (Trivers 1972; Dawkins 1976; Lazarus

1990). A variety of factors can influence whether a breeding individual gains fitness benefits from deserting its mate, and many questions remain about how these factors interact as well as which are most important in driving desertion in systems with multiple factors at play.

Theoretical models have identified several factors that can lead to either high benefits or low costs of desertion, favoring the expression of desertion behavior. The benefits of desertion can be high when, for example, the sex ratio is strongly biased, the deserting sex experiences higher mortality than the caring sex, or sexual selection is strong (Grafen and Sibly 1978; Queller 1997; Kokko and Jennions 2008; Alonzo 2012). All of these factors influence the benefits of desertion by influencing the likelihood that a deserting individual can find a new mate to initiate a new breeding attempt. If the adult sex ratio is biased, a deserting individual belonging to the rarer sex is expected to easily find a new mate, while the deserted partner is unlikely to find a new mate if it also abandons the offspring and thus is likely to remain and care for the offspring (Grafen and Sibly 1978; Queller 1997; Kokko and Jennions 2008). If the deserting sex suffers mortality at a rate significantly higher than the caring sex, desertion is (counter-intuitively) favored, because the deserting sex becomes the rare sex and thus deserters are likely to find new mates (Kokko and Jennions 2008). If sexual selection is strong, a high level of competition between members of one sex for mates implies that any individual of that sex who has a mate is a successful competitor, and thus is likely to succeed in gaining a second mate if it deserts its partner (Queller 1997; Kokko and Jennions 2008). However, this relationship can also be reversed, such that sexual selection disfavors desertion, if the target of mate choice by the choosy sex is investment in parental care (Alonzo 2012; Kokko and Jennions 2008), or if providing care yields greater fitness benefits than re-engaging in competition for a new mate (Kokko and Jennions 2008).

Factors that influence the costs of desertion often mediate the extent to which a single parent can successfully rear young alone. For example,

the costs of desertion may be reduced when food is abundant, as a single partner can feasibly collect enough food to provision the young (Emlen and Oring 1977). The costs of desertion can also be reduced by multiple mating: if one sex consistently has lower mean relatedness to its putative offspring, the sex with lower mean relatedness suffers a lower fitness cost of deserting that brood than does the sex with higher mean relatedness (Trivers 1972; Queller 1997). Another scenario in which the costs of desertion can be reduced is when partners are unspecialized in their care tasks, because each partner can perform all of the care necessary to raise offspring to independence: stable biparental care, without partner desertion, is more likely when males and females specialize on different care tasks than when carers are unspecialized (Grafen and Sibly 1978; Kokko and Johnstone 2002; Barta et al. 2014).

When comparing empirical evidence with theoretical models of partner desertion, it is important to remember that evolutionary models often make predictions that are testable with cross-species but not within-species comparisons (Kokko and Jennions 2008). For example, the prediction that the sex with lower mean relatedness to the offspring will be more likely to desert (Queller 1997) implies that species in which males have lower mean relatedness to offspring than do females will have a higher rate of male desertion than female desertion; the prediction does not imply that males will respond flexibly to their partners' extrapair mating by deserting offspring when their partners mate multiply. Socially monogamous birds show wide variation in partner desertion behavior, presenting opportunities for cross-species studies. While desertion by both males and females occurs in several species, female-only desertion is less common (Morton et al. 2010). Female desertion often occurs during the late nestling or postfledging care period (Tindle 1984; Wiktander et al. 2000; Griggio and Pilastro 2007; Szentirmai et al. 2007; Morton et al. 2010; Korpimäki et al. 2011); a factor contributing to this pattern may be that care necessary for early offspring development (e.g., incubating eggs and brooding young nestlings) is often provided primarily by females,

while the food required by older nestlings is provided by both males and females (Korpimäki et al. 2011). Although task specialization is beginning to be considered in models (Barta et al. 2014), specialization on care during certain developmental stages is not; incorporating this timing specialization into models could provide a stronger link between partner desertion theory and empirical results.

Conclusion

Two important future goals for research on partner desertion are comparing biparental and cooperative care systems, and the development of models that simultaneously examine multiple factors predicted to influence the fitness consequences of partner desertion. The first goal is important because, while the majority of partner desertion research to date has focused on systems in which care is provided solely by parents, the additional offspring care provided by at least one nonparent in cooperatively breeding systems has the potential to alter the fitness consequences of partner desertion. Models of the influence of nonparent carers on the likelihood of partner desertion are largely lacking, although several studies have investigated how carers respond to changes in each others' investments in care in multicarer systems (Härdling et al. 2003; Johnstone 2011; Savage et al. 2013). Both theoretical and empirical work on the characteristics of cooperative species in which partner desertion occurs are needed to understand how the conditions leading to partner desertion differ between biparental and cooperative care systems. The second goal, the development of models that incorporate multiple factors that can influence partner desertion, is crucial in order to determine the relative importance of different factors in predicting desertion behavior (Kokko and Jennions 2008). Recent examples of the power of this approach include work by Barta et al. (2014) showing that task specialization can prevent desertion even when sexual selection is strong, and by Alonzo (2012) showing that female choice for parental males can reduce male desertion even when mean relatedness between males and the offspring for which they provide care is low due to multiple mating. More investigations of the

interactions between factors are needed, both to resolve theoretical questions about which factors most strongly influence selection pressures and to derive empirically testable predictions.

Cross-References

- ▶ [Biparental Care](#)
- ▶ [Brood Care](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Differential Parental Investment](#)
- ▶ [Game Theory](#)
- ▶ [Helpers at the Nest](#)
- ▶ [Mating Systems](#)
- ▶ [Nonhuman Sexual Conflict](#)
- ▶ [Parental Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Reproductive Strategies](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Social Monogamy](#)

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Partner Exploitation

► Manipulation

Partner Homicide

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Synonyms

Femicide; Intimate partner homicide; Mariticide;
Uxoricide; Wife killing

Definition

Partner homicide, also listed in the scholarly literature as intimate partner homicide, refers to homicides where the victim and perpetrator are, or have previously been, in an intimate (romantic/sexual) relationship.

Introduction

Unlike most other homicide categories, the vast majority of victims of partner homicide are women. According to a report on the epidemiology of homicide worldwide, published by the United Nations Office on Drugs and Crime (2019), roughly 82% of the victims of partner homicide are women. This global sex difference in the rate of victimization has been stable since 2012. However, the specific rates at which the two sexes are victimized differ between societies. For instance, the victimization rate is four times higher for women than for men in Europe, and in Latin America, the rate is five times higher for women than for men. In contrast, the victimization rates for women and men in the USA have been remarkably even. For instance, for every 100 women killed by their husbands in the USA in the years 1976–1985, about 75 men were killed by their wives (Wilson and Daly 1992).

Although the victimization rates differ between societies, the characteristic traits of the perpetrators, victims, and circumstances of partner homicides appear to be cross-cultural. The cross-cultural similarities in characteristic traits of partner homicides undermine the notion that these homicides are solely driven by cultural norms or are random acts of individuals suffering some form of mental pathology. Rather, as will be detailed in the following, the cross-national similarities lend themselves to supporting the evolutionary psychological hypothesis that partner homicide is a behavioral manifestation of evolved psychological mechanisms that are triggered in the context of reproductive conflicts.

Hypothesis: Reproductive Conflicts Are at the Core of Partner Homicides

Evolutionary psychologists Martin Daly and Margo Wilson (1988) proposed that homicides, including partner homicides, should be understood as assays to reproductive conflicts. A reproductive conflict occurs when individuals have differing interests pertaining to their respective reproductive success, and the interests of one individual come at a cost to another individual. Daly and Wilson proposed that there are evolved psychological mechanisms that are triggered when individuals are confronted with reproductive conflicts. These psychological mechanisms have enabled the individual to react to the given conflict in ways that, on average, were beneficial toward reproduction or survival in our species' past. These mechanisms may elicit a range of behavioral responses, including lethal violence. According to Daly and Wilson, these psychological mechanisms are adaptations, the products of evolutionary selection processes. The range of potential behavioral outputs that may be performed on the basis of these mechanisms are then by-products. Thus they argued that adaptation must be sought at a psychological rather than behavioral level when studying homicide perpetration. They further argued that of the range of potential behavioral manifestations of the evolved psychological mechanisms that are triggered in the context of reproductive conflicts between intimate partners, homicide perpetration is an extreme and dysfunctional epiphenomenon, as it would not benefit the individual in any evolutionary significant way to perform such an act.

Evolutionary psychologists Joshua Duntley and David Buss (2008, 2011) have a somewhat different take on the benefits of homicide perpetration. They argue that the benefits of homicide perpetration, including partner homicide, were so significant to the individual in our evolutionary past that psychological mechanisms with the specific function of eliciting homicidal behaviors would have been selected for. What these two different perspectives have in common is the hypothesis that partner homicides occur in the context of reproductive conflicts.

Predicted Traits of Partner Homicide and Their Empirical Support

From their hypothesis that partner homicides occur in the context of reproductive conflicts within the couple, Daly and Wilson (1988) derived a list of risk factors for partner homicide – traits that they predicted would be characteristic for the perpetrators, victims, and circumstances for partner homicide, if their hypothesis were valid. This list, and the cross-cultural empirical support for them, will be detailed in the following.

Sex Differentiation in Motive for Partner Homicide Perpetration

The initiation and maintenance of long-term, intimate relationships is assumed to have had the evolutionary function of framing collaborations in fostering genetically shared children. Daly and Wilson (1988) proposed that the profoundly different physiological roles women and men have in reproduction would lead to sex-differentiated concerns regarding threats to this collaboration. These threats could be perceived as reproductive conflicts within the given couple. Daly and Wilson suggested that because the two sexes have such different physiological roles in reproduction, evolution would inevitably shape sex-differentiated psychological mechanisms for assessing cues for and acting on reproductive conflicts in intimate relationships. From this evolutionary informed reasoning, they predicted a list of characteristic traits for partner homicide perpetrated by women and men, respectively.

Sexual Proprietariness

A sex-specific reproductive challenge to ancestral men was the potential uncertainty as to whether or not a child in their care was their genetic offspring. This lack of certainty made them vulnerable to being cuckolded by a partner (i.e., unknowingly investing in the fostering of another man's offspring). Selection would favor men with psychological mechanisms that could protect against cuckoldry, as such mechanisms could increase the likelihood of that the individual man invested in his own genetic offspring, and not the offspring of his – in evolutionary

terms – competitors. Psychological mechanisms that would potentially protect against cuckoldry could be ones that made the individual man sensitive to cues of his partners' sexual infidelity, and that motivated him to take measures to reduce the likelihood of such infidelity. Men with such mechanisms could potentially outreproduce those men who did not have a sensitivity toward cues of and a concern with the sexual fidelity of their partners.

Daly and Wilson (1988) proposed that this male sensitivity to cues of and concern with the sexual infidelity of a partner could be described as underpinning a sexual proprietariness. This concept refers to a mind-set encompassing a presumption of ownership of and entitlement to an exclusive sexual access to a partner. This mind-set may motivate an inclination to exercise control over a partner's reproduction and reproductive options and taking measures to prevent losing that control. A range of behaviors may serve the function of preventing a partner from pursuing reproductive opportunities with other people (Buss and Shackelford 1997). Daly and Wilson noted that violence is among the effective behaviors a man could engage in to deter a partner from pursuing reproductive opportunities with other men and constraining her reproductive options to align with his interests. And at times, as a rare and extreme manifestation of the proposed evolved proprietary mind-set, the man might resort to lethal violence.

Daly and Wilson (1988) therefore predicted that male-perpetrated partner homicide would characteristically occur when the man experienced threats to an exclusive sexual access to his partner, such as in the context of suspected or actual adultery or the partner initiating a termination of their relationship.

There is empirical support for this prediction, as sexual jealousy and female-initiated relationship dissolution are the context in which male-perpetrated partner homicides most frequently occur. For instance, in a Canadian national sample, 1974–1983, 25.5% of the homicides perpetrated by husbands were after police investigations attributed to jealousy, whereas only 7.9% of those perpetrated by wives were

attributed to jealousy (Daly and Wilson 1988). This finding was replicated in a sample extending to 1990 (Wilson and Daly 1993) and in a local Canadian sample, from the city of Hamilton, 1974–1995, where male-perpetrated partner homicide characteristically occurred soon after the women initiated separation (Daly et al. 1997). Also in a sample from New South Wales, Australia, 1968–1986, and a Chicago sample, 1965–1990, the risk for female victimization was substantially elevated when the couples were estranged than when they were co-residing (Wilson and Daly 1993). Specifically, the risk of being killed was six times higher for women estranged from their husband than for women still living with their husband. In the Australian sample, about half the women were killed within 2 months of leaving their husband, and 91% were killed within a year. The data from the Chicago sample suggested that the male perpetrators were distressed at their victims initiating the dissolution of their relationship or having the intent to leave. In notable contrast, the risk for male victimization appeared to be considerably lowered in estranged couples.

Staying Alive

Evolutionary psychologist Anne Campbell (1999) noted that for ancestral women, staying alive was one of the more crucial requirements for reproductive success. Unlike men, who have no physiological obligation beyond their participation in conception, ancestral women were compelled to stay alive throughout the lengthy period of gestation and years of breastfeeding in order to achieve reproductive success. Campbell argued that this sex-differentiated selection pressure to stay alive has shaped a female psychology that motivates an avoidance of physical danger. Daly and Wilson (1988) also noted this crucial sex difference in the reproductive requirement to avoid physical danger and proposed that for a woman to nevertheless engage in the act of partner homicide, an act that might potentially be lethal to herself if her partner was to fend off her attack, her motivation had to be that her partner already endangered her survival. They therefore predicted that women who kill a current or former partner

would do so in the context of ensuring their own survival.

There are fewer studies on female than male-perpetrated partner homicides and fewer still that collect data on motives. However, existing studies collectively give empirical support to Daly and Wilson's prediction, as a majority of female-perpetrated partner homicides are reportedly motivated by self-defense (for a review of the empirical literature, see Campbell et al. 2007). For instance, in a sample from Denver in the USA, 1991–2009, the male victims of partner homicide had prior domestic violence arrests three times more often than female victims of partner homicide (Belknap et al. 2012). This sex difference increased to more than seven times for domestic violence convictions. Data on the motive for female-perpetrated partner homicides was available for only 12 cases in the sample. Of these, five perpetrators clearly killed their partner in self-defense. In two cases it was more complicated: Although there were elements suggesting the relationship had been “mutually combative,” the female perpetrators had records showing prior domestic violence victimization at the hands of their partners. Belknap and colleagues note, with surprise, that three cases were most consistent with being an artifact of the women acting on a sexual proprietariness. The last two cases were not categorized.

Age of Perpetrator and Victim

If the reproductive conflict that lies at the core of male-perpetrated partner homicide is one concerning the man losing his partner as a contributor to his fitness, the severity of his reaction to this loss may be expected to be dependent on his partner's fecundity (i.e., ability to produce offspring). Daly and Wilson (1988) therefore proposed that the age of the woman, which is a proxy for her residual fecundity, might have a significant impact on the man's response to losing her as a contributor to his fitness. The woman's age may therefore be a better predictor for the risk of partner homicide than the man's age (a man's age is otherwise a well-established predictor for the risk for homicide perpetration, as young men are overrepresented among perpetrators; see, e.g.,

the United Nations Office on Drugs and Crime 2019). This reasoning led to three predictions concerning age and the risk for partner homicide.

The Woman's Age as a Predictor for the Risk for Victimization

From the above reasoning, Daly and Wilson predicted that an increase in the woman's age would be associated with a decrease in her risk for partner homicide victimization. The empirical evidence supports their prediction. For instance, in a Canadian national sample, 1974–1983, the risk for partner homicide did indeed decrease with an increase of the woman's age for married couples (Daly and Wilson 1988). This finding was replicated in a sample extending to 1992 (Wilson et al. 1995b). In a US local sample from the city of Chicago, 1965–1996, 82.8% of the female victims were < 45 years old (Breitman et al. 2004).

However, the association between the woman's age and risk for partner homicide victimization appears to be dependent on the type of union the couple have. For cohabiting women, the risk for victimization increases until they are middle-aged, before dropping. This was identified in a Canadian national sample, 1974–1983 (Daly and Wilson 1988), and replicated in a sample extending to 1992 (Wilson et al. 1995a), and in US national samples for the years 1976–1994 (Shackelford and Mouzos 2005) and 1990–2005 (James and Daly 2012). However, this age difference in risk for victimization associated with type of union was not replicated in an Australian national sample, 1989–2002, where cohabiting women were, similarly to married women, at greatest risk when they were < 25 years old (Shackelford and Mouzos 2005).

Daly and Wilson (1988) suggested that the difference between married and cohabiting women in their apparently age-related risk for partner homicide victimization might be an artifact that cohabiting couples have children from previous relationships more frequently than married couples and that the likelihood of having children from previous relationships increases with the age of the woman. And, as will be returned to, having children from previous

relationships has been identified as a factor that increases the risk for female victimization.

The Woman's Age as a Predictor for the Risk for Perpetration

As the man may engage in more vigilant and coercive control, even to the extent of lethal violence, toward a young partner, Daly and Wilson (1988) predicted that a woman's young age would be associated with an increased risk for female-perpetrated partner homicide, as the woman reacts to her partner's threatening behavior (see section "[Staying Alive](#)" of this entry, concerning women's motivation for perpetrating partner homicide as self-defense). The empirical evidence supports their prediction, as a woman's young age does in fact increase the risk for male victimization. This was found in the Canadian national sample, 1974–1983 (Daly and Wilson 1988). In a Chicago sample, 1965–1996, women <45 years old constituted 82.9% of the female perpetrators (Breitman et al. 2004). Also in a US national sample, 1976–1994, and an Australian national sample, 1989–2000, of married perpetrators, the risk was highest for younger women (<25) and decreased with age (Mouzos and Shackelford 2004). For cohabiting women, however, the risk for perpetration peaked at a later age in both samples.

Age Disparity as a Predictor for the Risk to Both Sexes

It could be argued that more than a woman's absolute age, her age relative to her partner is a better proxy for her value to him as a contributor to his reproduction and thus a better predictor of risk for reproductive conflicts and partner homicide. Empirical evidence supports the prediction, and further the excess risk for victimization appears to be to the older individual in the couple, regardless of sex. For instance, Daly and Wilson (1988) found in a Canadian national sample, 1974–1983, that there was an increased risk for both female- and male-perpetrated partner homicide with increased age disparity. Further, a greater age disparity increased the risk regardless of what type of relationship the couples were in. These findings were replicated in a sample

extending to 1992 (Wilson et al. 1995), a national sample from England and Wales, 1977–1986 (Wilson and Daly 1992), a Scottish national sample, 1978–1987 (Wilson and Daly 1992); Australian national samples of female perpetrators, 1989–2000 (Mouzos and Shackelford 2004), and male perpetrators, 1989–2002 (Shackelford and Mouzos 2005); a regional sample from New South Wales in Australia, 1968–1986 (Wilson and Daly 1992); a US national sample, 1976–1994 (Mouzos and Shackelford 2004; Shackelford and Mouzos 2005); and a local US sample from the city of Detroit for the year 1972 (Wilson and Daly 1992).

Replicating the above-listed findings in a sample of partner homicides in Chicago, 1965–1996, Breitman et al. (2004) specifically identified that when the woman was older than her partner by 16 years or more, the rate of partner homicide was four times higher than for couples with no age difference. When the man was 16–20 years older than his partner, the rate of partner homicide was four and a half times higher than for couples with no age difference. The highest risk for partner homicide in this sample was for couples where the woman was 10 years older than her partner and for couples where the man was at least 16 years older than his partner. The perpetrator was older than the victim in near half of the incidents in the sample.

There has not yet been formulated an evolutionary informed reasoning and prediction concerning the increased risk for partner homicide in couples where the male is the younger party. But in line with the hypothesis that partner homicide occurs in the context of reproductive conflict, one may identify potential sources for such conflicts also in these couples. For instance, the young age of the man may be a proxy for the increased potential for him to produce healthy offspring (also see "sexy son theory"), which may be a significant reproductive cue for his partner. Also, an older woman might be a resourceful provider for a young man. The age disparity in these couples may then be a proxy for a disparity in mate value, which in turn could increase the vigilance and coercion with which the individual with the lower mate value reacts

to a potential loss of their partner as a contributor toward their own fitness.

Increased Risk Among Cohabiting Couples Compared to Married Couples

Cohabiting couples have a significantly increased risk for partner homicide compared to married couples. For instance, in a Canadian national sample, 1974–1983, cohabitating couples had an increased risk for both male and female victimization (Daly and Wilson 1988; Wilson and Daly 1992). This finding was replicated in a sample extending to 1992, where the rate of partner homicide was about eight times higher among cohabiting couples than among married couples (Wilson et al. 1995; see also Wilson et al. 1993). This finding has been replicated in England and Wales, 1977–1986 (Wilson and Daly 1992); the USA, 1976–1994 (Mouzos and Shackelford 2004; Shackelford and Mouzos 2005); Australia, 1989–2000 and 1989–2002 (Mouzos and Shackelford 2004; Shackelford and Mouzos 2005); and a local Australian sample from New South Wales, 1968–1986 (Wilson and Daly 1992).

Daly and Wilson had not sketched out any evolutionary informed reasoning and prediction concerning differentiated risk associated with type of relationship prior to identifying the increased risk for partner homicide among cohabiting couples compared to married couples. Upon discovering this characteristic trait for partner homicide, Daly and Wilson suggested that the increased risk might be an artifact of that commitment, and thus investment, is lower for cohabiting than married couples, and further considered whether cohabiting couples were more often poor, young, city dwellers. Such circumstances, they suggested, may in turn spur a more vigilant and coercive proprietariness in the relationship, and in turn this may lead to lethal violence.

However, findings from a US national sample, 1990–2005, have shown that cohabitation is not a static risk factor for partner homicide (James and Daly 2012). The respective rates of partner homicide among cohabiting and married couples converged over this time period in the USA, and by 2005 the risk was equal between the two types

of union. This change in risk occurred despite differences in demographic characteristics associated with married and cohabiting couples with regard to age distribution, and unemployment rates remained the same, and differences in level of education and income increased.

Children from Previous Relationships

In stepparental households the couples do not share the profound reproductive interest in investing in the children, as the couples do in households with two genetic parents. If the genetic parent wants more investment in the child than the stepparent is volunteering, this is a reproductive conflict that may be a major source of discord for the couple. Daly and Wilson (1988) therefore predicted that because of the increased potential for reproductive conflict with regard to the level of parental investment in stepparental households, such households might have an increased risk for partner homicide.

There is empirical evidence that supports their prediction. For instance, in a local Canadian sample from the city Hamilton, 1974–1995, the rates of partner homicide with female victims were substantially elevated in stepfather families (Daly et al. 1997). Half of the victimized mothers in the sample had children from previous relationships, compared to 7% of the population at large. Their risk for partner homicide victimization was thus 12.7 times higher than for women living in households with two genetic parents.

Familicide

Familicide is the killing of one or more children in addition to a current or former partner. From the same evolutionary informed reasoning as sketched out so far, it has been predicted that familicides will predominantly be perpetrated by men and occur in the context of the woman initiating a dissolution of the relationship (Wilson et al. 1995). There is empirical support for these two predictions. For instance, 93% of familicides in Canada, 1974–1990, and 96% of familicides in the UK, 1977–1990, had male perpetrators (Wilson et al. 1995). The available data also suggests that the familicides were elicited by the relationship dissolution initiated by the women.

Thus the victimized children do not appear to be the primary objects targeted by the perpetrators. Further, familicides appear to be more similar to partner homicide than child homicide with regard to perpetrators age, method of killing, and victim's age (Wilson and Daly 1992; Wilson et al. 1995a) and may therefore arguably be listed as a subcategory of partner homicide rather than a subcategory of child homicide (filicide).

Nonheterosexual Relationships and Partner Homicide

Both conventional social science and evolutionary psychological perspectives have given less theoretical and empirical attention to partner homicides in nonheterosexual relationships. However, some works that reference evolutionary psychological perspectives may form a foundation for a theoretical understanding of the underpinning psychology and thus improve identification of risk factors for partner homicide in nonheterosexual relationships. For instance, a study using a US national sample, 1976–2001, explored the methods and rates of partner homicide among heterosexual, gay, and lesbian relationships (Mize and Shackelford 2008). And a study using a sample from the Metropolitan Area of Buenos Aires City in Argentina (Aristegui et al. 2019) explored how transgendered people respond when confronted with romantic rivals. Assuming such confrontations will trigger psychological mechanisms evolved to detect and react to reproductive conflicts, such studies may be crucial to identifying the underpinning psychology and deriving predictions concerning characteristic traits of homicide perpetration among transgendered couples.

Cross-National Variance in Rates of Partner Homicide

In contrast to perspectives claiming that partner homicide is a product of, for instance, culturally driven gender roles or random acts caused by the perpetrators' psychopathology, evolutionary psychological perspectives argue that the psychological mechanisms underpinning the perpetration

of partner homicide are evolved adaptations, and as such are shared commonalities in our species. The variance that exists between and within nations in the extent to which partner homicide is perpetrated does not undermine the notion that the underpinning psychological mechanisms are species-typical. As with other evolved psychological mechanisms, the activation of mechanisms that may elicit lethal violence against a current or former partner is context dependent. And, further, the range of behavioral manifestations of the mechanisms is not limited lethal violence. Although Duntley and Buss (2008, 2011) argued that there are psychological mechanisms that specifically activate partner homicide, they also argued that the activation of these mechanisms is context dependent.

From an evolutionary psychological perspective, the variance in rates of partner homicide between and within societies is therefore expected to be largely attributable to the variance individuals in the given societies are exposed to the social factors and contexts that activate the relevant underpinning psychological mechanisms, and further what behavioral outlets are available for the manifestation of the mechanisms in the respective societies.

If this evolutionary psychological perspective on partner homicide is valid, variations within and between societies in the extent to which partner homicide is perpetrated should be predictable. So far the research performed with reference to this theoretical framework has emphasized identifying the commonalities in the patterns of characteristic traits of partner homicide across nations and cultures, rather than exploring the predictability of unique patterns in characteristic traits in a given society or culture (for one exception, see Daly and Wilson's (1992) study of the evenness in perpetration rates for women and men in the USA). The range of cultures where partner homicide has been studied from an evolutionary psychological perspective have been limited to Canada, the USA, the UK, and Australia. Future research would benefit from adding nations and cultures to this list to explore the robustness of the findings produced so far within this theoretical framework, by testing the predictive power of the framework

in non-Anglo nations and societies and the notion of partner homicide perpetration being contingent on environmental cues.

Conclusion

Benefitting from the theoretical guidance offered by an evolutionary informed understanding of how selection processes form social behaviors, evolutionary psychologists have derived the hypothesis that homicides, including partner homicides, are triggered by reproductive conflicts. From this hypothesis, they have been able to identify a list of characteristic traits of partner homicide – some of which were not identified by contemporary conventional approaches to studying partner homicide, such as the increased risk for couples with co-residing stepchildren and for couples with a significant age disparity.

Crucial to predicting what traits will be characteristic for partner homicides is the recognition of how profoundly different the physiological roles of women and men are in reproduction. This recognition entails appreciating that the respective physiological roles of women and men in reproduction give equally sex-differentiated challenges to reproductive success and that this in turn will inevitably spur the evolution of sex-differentiated cues to reproductive conflicts with an intimate partner and sex-differentiated ways of handling these conflicts. For men, the greatest concern would arguably be securing genetic paternity, whereas for women it would be to stay alive. The empirical support gained for the predictions derived from the hypothesis that reproductive conflicts lie at the core of partner homicide perpetration for over four decades testifies to the validity of the hypothesis.

The merits of the evolutionary psychological hypothesis that reproductive conflict lies at the core of homicides are not limited to explaining and predicting significant risk factors and characteristic traits of partner homicide. It has also proven its validity for other homicide categories, such as filicide (killing of a child by a caretaker), siblicide (the killing of a sibling), and parricide

(the killing of a parent) (for an introduction, see Daly and Wilson 1988). This makes evolutionary psychology singular among the theoretical perspectives within the scientific field of homicide studies as it succeeds in approaching the phenomenon in a comprehensive manner to both explain and predict a list of characteristic traits for a diverse list of homicide categories.

Cross-References

- [Famicide](#)
- [Filicide](#)
- [Homicide](#)
- [Homicide Fantasies and Evolved Homicide Module Theory](#)
- [Mate Retention](#)
- [Mate Value](#)
- [Partner Killing](#)

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Definition

Partner Killing – When one commits the act of killing their partner of whom they have a consensual relationship in the form of intimate, romantic, or sexual context. Partners may be identified within the following relationships: marriage, committed relationship (cohabitating and non-cohabitating), casual dating, “friends with benefits,” or strict sexual partners. Throughout this chapter, we will be discussing the topic of intimate partner killings (IPK) using the term “Paricide(s).” This term is not yet standardized but was derived from the root origins of “Partner-Par” and “Killing-Cide.” Related terms include Femicide – “deliberate killing of women and girls because they are female” (Campbell 2018); Matricide – killing of one’s mother (Heide 2013); Uxoricide – killing of wife by husband (Mize et al. 2011).

Introduction

This chapter aims to tackle the topic of intimate partner killings (IPK) and provide a comprehensive overview of the literature and research up to date. We will also be looking at many variables that have been discussed throughout different forms of literature and linking them together. Several of these variables include the timelines, national databases available, partner types, relationship types, relationship status, age discrepancies, location most likely to occur, and type of weapons used. Lastly, we will look at corollary victims, demographic data, motivation for killings, personality traits, neurological factors, evolutionary factors, and previous history data for intimate partner violence.

P

Partner Killing

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Synonyms

Matricide; Uxoricide

The Evolution of Paricide

Paricide is an act seen often in history due to motivations often driven by intense emotions, whether that be rage, jealousy, or fear (Mize et al. 2009). Dating back to the era of Cleopatra in 41 B.C., she was known for killing her husbands as a means to gain power or the upper hand in war (Andrews 2019). Another famous

historical figure that participated in paricide includes Queen Isabella, known as the “She-Wolf of France,” who executed her husband, motivated by revenge due to her husband’s affairs. In addition, Catherine the Great threw her husband in jail for execution due to the issues of power and relationship conflict (Meares 2017).

Considering Darwin’s sexual selection theory, Douglass et al. (2020) suggest, “The essence of Darwin’s theory of sexual selection pits males and females in competition, with each other (intersexual competition) and with themselves (intrasexual competition), in a way that is believed to have far-reaching consequences in how each sex has evolved.” Also, Baumeister et al. (2001), Ellis and Symons (1990), Jonason and Fisher (2009), and Mitchell et al. (2018) indicate men have evolved a stronger libido, various sexual partners, and desires for short-term mating. Douglass et al. (2020) acknowledge that these evolved attitudes lead to emotions such as jealousy, need for power, and control among female partners. Evolutionary explanations have also suggested intimidate partner violence as a defense mechanism when avoiding paternal uncertainty (Daly et al. 1982). Furthermore, explanations for females acting out aggressively are linked to scarcity of resources (Campbell 2015; Campbell et al. 1998), response to infidelity (de Weerth and Kalma 1993), competition for survival, and protection of offspring (Douglass et al. 2020).

Paricide Prevalence

This phenomenon is not isolated but a global issue across all countries as one in seven homicides and more than a third of female-related homicides are committed by an intimate partner (Stöckl et al. 2013). Shown below are more global statistics found by Stöckl and colleague (2013) (Table 1):

Adolescent Dating Violence as a Risk Factor

According to Knopf (2019), 7% of teen homicides are related to partner killing, and these killings are

typically a result of jealousy or breakups. Partner killings in teens typically involve gun violence and are femicide related (Knopf 2019). When exposed to maladaptive relationship patterns in adolescence, these patterns are likely to carry out into adulthood. Patriarchal culture holds views related to favoring violent behaviors in boys as a means of compensating when their virilities are threatened (Taquette and Monteiro 2019). Gender inequality is another risk factor among females within the adolescent population, yet there are instances where women are more likely to be physical and psychological aggressors as a result of developmental stage and hormonal changes (Taquette and Monteiro 2019).

Contributing to the evolution of paricide, virtual violence is now acknowledged as a risk factor associated with adolescent dating violence. It consists of “Monitoring, control, harassment, or verbal and emotional abuse of a partner through technology, cell phones, threatening text or voice messages, or online publications of insulting content” (Taquette and Monteiro 2019). This type of violence is associated with jealousy, an emotion mainly driven by love and anger, which is also identified as a risk factor for adolescents engaging in abusive behavior (Taquette and Monteiro 2019). There are various consequences of engaging in adolescent dating violence such as “Low self-esteem, depressive symptoms, psychiatric disorders, drug abuse, risky sexual behavior, and low academic performance” (Taquette and Monteiro 2019). Nevertheless, there is a lack of research among partner killing in adolescent populations (Taquette and Monteiro 2019).

LGBTQIA Community

According to Gaman and colleagues (2017), intimate partner violence is not anymore preventable within the LGBTQIA community than in the heterosexual community. When looking at paricide in this community, an individual has to notate the different roles each partner holds. Different roles and subcultures within this community include “bears, wolves, queens, princesses, butch, and lipstick (Biddle 1986).” Gaman and colleagues

Partner Killing, Table 1 Conservative, mid-level, and high-level estimates of the prevalence of intimate partner homicide among male and female homicides by region

	Total homicides of included studies	Conservative estimates (missing cases are regarded as non-partner homicides)	Mid-level estimate (missing cases are distributed as known cases)	High-level estimate (analysis is restricted to known cases)
Prevalence of intimate partner homicides among male and female homicides				
Worldwide (<i>n</i> = 32)	492,340	13.54% (9.24–18.23)	14.05% (12.97–20.43)	16.18% (14.07–20.73)
High-income countries (<i>n</i> = 18) ^a	476,537	14.92% (9.24–18.23)	18.38% (12.97–20.43)	19.42% (15.48–20.73)
Africa (<i>n</i> = 4)	4861	7.31% (5.65–18.31)	11.32% (8.61–18.58)	16.18% (12.62–18.57)
America (<i>n</i> = 3)	5112	0.72% (0.64–9.65)	1.33% (0.85–16.49)	4.68% (0.96–33.06)
Eastern Mediterranean (<i>n</i> = 0)	–	–	–	–
Low-income and middle-income Europe (<i>n</i> = 2)	419	10.98% (9.68–12.28)	11.16% (9.83–12.48)	11.16% (9.84–12.48)
Southeast Asia (<i>n</i> = 2)	601	18.75% (11.26–18.75)	22.04% (13.14–22.04)	22.74% (13.52–22.74)
Western Pacific (<i>n</i> = 3)	4810	4.82% (4.82–9.84)	5.55% (5.55–10.78)	5.68% (5.68–10.78)
Prevalence of intimate partner homicides among all female homicides				
Worldwide (<i>n</i> = 63)	133,691	38.55% (30.84–45.31)	42.71% (36.16–58.05)	47.36% (38.55–59.64)
High-income countries (<i>n</i> = 36)	115,515	41.19% (30.84–44.45)	44.95% (42.09–58.05)	48.56% (42.77–61.31)
Africa (<i>n</i> = 4)	6219	40.11% (38.55–41.67)	42.24% (31.93–45.72)	44.80% (42.25–47.36)
America (<i>n</i> = 15)	9658	40.54% (7.51–54.84)	42.54% (11.43–59.26)	42.60% (11.51–59.64)
Eastern Mediterranean (<i>n</i> = 2)	887	14.41% (5.26–23.56)	15.23% (5.56–24.90)	15.28% (5.58–24.98)
Low-income and middle-income Europe (<i>n</i> = 3)	200	20.00% (1.82–37.78)	20.40% (1.86–38.53)	20.41% (1.86–38.55)
Southeast Asia (<i>n</i> = 1)	80	58.75% (58.75–58.75)	62.10% (62.10–62.10)	62.30% (62.30–62.30)
Western Pacific (<i>n</i> = 2)	1132	19.12% (19.12–21.29)	20.22% (20.22–22.51)	20.28% (20.28–22.58)
Prevalence of intimate partner homicides among all male homicides				
Worldwide (<i>n</i> = 28)	373,077	6.28% (3.13–6.34)	6.47% (4.42–7.15)	6.48% (5.34–7.29)
High-income countries (<i>n</i> = 18)	364,410	6.28% (3.13–6.34)	6.59% (4.42, 7.15)	6.60% (5.34–7.29)
Africa (<i>n</i> = 3)	235	4.12% (1.55–6.38)	4.36% (1.56–6.47)	4.41% (1.80–6.48)
Americas (<i>n</i> = 2)	4580	0.43% (0.00–6.54)	0.81% (0.00–11.27)	4.00% (0.00–23.60)

(continued)

Partner Killing, Table 1 (continued)

	Total homicides of included studies	Conservative estimates (missing cases are regarded as non-partner homicides)	Mid-level estimate (missing cases are distributed as known cases)	High-level estimate (analysis is restricted to known cases)
Eastern Mediterranean (<i>n</i> = 0)	—	—	—	—
Low-income and middle-income Europe (<i>n</i> = 2)	226	3.59% (3.18–4.00)	3.66% (3.24–4.08)	3.66% (3.24–4.08)
Southeast Asia (<i>n</i> = 1)	334	0.87% (0.87–0.87)	1.01% (1.01–1.01)	1.04% (1.03–1.03)
Western Pacific (<i>n</i> = 2)	3292	1.33% (1.33–2.78)	1.54% (1.54–3.22)	1.58% (1.58–3.30)

Data are number of homicides or median (IQR). *n* = number of countries with existing data

Stöckl et al. (2013)

^aThe high-income countries (classified by the World Bank20) included Andorra, Australia, Austria, Canada, Croatia, Cyprus, Czech Republic, Denmark, England and Wales, Estonia, Finland, France, Germany, Hungary, Iceland, Ireland, Israel, Italy, Japan, Lichtenstein, Luxembourg, Malta, Monaco, Netherlands, New Zealand, Norway, Poland, Portugal, Scotland, Slovakia, Slovenia, Spain, Sweden, Switzerland, and the USA

(2017) noted patterns of violence included 64% of lesbians using their hands as a weapon in abuse vs. 47.7% gay males and 51% of lesbians and 43.8% of gay males engaging in destruction of property during abuse. In addition, it was found that children of lesbian couples are more often to be exposed to physical violence five times more often than gay couples (McClennen 2005). Below you will see a distribution of victim–abuser dyads based on gender orientation out of 214 participants (Table 2):

Emotional Factors

When looking at the emotional component for these killings, research has shown men are more often to report anger due to instances of infidelity as the main feeling leading up to the killing where women tend to report anxiety and fear leading up to the killing of an intimate partner (Mize et al. 2009). Women have also been found to score high on self-defeating personality scales in response to abuse often accounting for why they do not leave the relationship sooner (Pico-Alfonso et al. 2008). In many cases, the feeling of fear is not only for themselves but also for their children during IPV

Partner Killing, Table 2 Valid surveyed victim–abuser dyads based on gender orientation

Abuse dyad		Frequency (percent) (<i>N</i> = 214)
Gender of victim	Gender of abuser	
Female	Male	146 (68.2%)
Male	Female	19 (8.9%)
Female	Female	18 (8.4%)
Male	Male	17 (7.9%)
Transgender	Female	3 (1.4%)
Female	Transgender	2 (0.9%)
Transgender	Transgender	2 (0.9%)
Gender unidentified	Female	2 (0.9%)
Male	Transgender	1 (0.5%)
Male	Gender unidentified	1 (0.5%)
Female	Gender unidentified	1 (0.5%)
Transgender	Male	1 (0.5%)
Transgender	Gender unidentified	1 (0.5%)

McClennen (2005)

and during this episode of fear is when parricide is at a higher risk of occurring (Johnson and Hotton 2003). Daly et al. (1982) found that estrangement often leads to a higher risk of uxoricide (wife-killing by a man), but not matricide (husband-killing by a woman). Kimmel (2002) suggested

that men who engage in violent acts often do so because of a desire to control, and their loss of control is what often motivates that violence.

Means Used to Commit Paricide

Supplementary Homicide Reports (SHR) and covered cases from 1976–2001, as seen in Table 3:

Motives to Commit Paricide

The social learning theory was also applied to paricide, where the individual learns that violence helps achieve desired behaviors through observing violent behaviors, especially in childhood (Olowu et al. 2011). Children often learn through modeling, and when men witness such behavior from their father in childhood, their likelihood of abusing their wives in adulthood increases (Olowu et al. 2011). Traditional values of males being dominant and women being passive and

submissive can also result in abusive relationships. In Nigeria, beating wives and children is considered a socially acceptable form of discipline (Aihie 2016). “Traumatic bond theory offers explanation on factors that can make women remain in abusive relationship while victim precipitation theory account for the role that victims plays in falling prey to spousal homicide especially men that are killed by their wives” (Ghosh 2015; Olowu et al. 2011). Olowu et al. (2011) found most events leading to the death of a spouse were accidental, rather than premeditated.

Married or Cohabiting

Looking at the relationship status for victims of paricide, we will explore being married, cohabiting, or non-cohabiting. According to research, men are more likely to commit paricide in a dating or nonmarital cohabiting relationship vs. a legal marriage, men were also found to be ten times more likely to be killed in a cohabiting

Partner Killing, Table 3 Frequency and percentage of killings by murder weapon employed as a function of sex of offender

Weapon	Male	Female	Total (%)
Firearm, type not stated	602 (1.9)	283 (1.5)	885 (1.8)
Handgun – pistol, revolver, etc.	15,018 (47.0)	9,216(50.3)	24,234 (48.2)
Rifle	2,001 (6.3)	966(3.3)	2,967 (5.9)
Shotgun	3,047(9.5)	1,167(6.4)	4,214(8.4)
Other gun	36(0.1)	19(0.1)	55(0.1)
Knife or cutting instrument – ax, icepick, etc.	4,934(15.4)	5,915(32.3)	10,849(21.6)
Blunt object – hammer, club, etc.	1,464(4.6)	232(1.3)	1,696(3.4)
Personal weapon – hands, feet, teeth, etc.	2,695(8.4)	97(0.5)	2,792(5.6)
Poison	40(0.1)	27(0.1)	67(0.1)
Pushed or thrown out of window	25(0.1)	2(0.0)	27(0.1)
Explosives	8(0.0)	6(0.0)	14(0.0)
Fire	196(0.6)	78(0.4)	274(0.5)
Narcotics and drugs	74(0.2)	27(0.1)	101(0.2)
Drowning	50(0.2)	1 (0.0)	51(0.1)
Strangulation – choking, hanging, etc.	842(2.6)	30(0.2)	872(1.7)
Asphyxiation	210(0.7)	14(0.1)	224(0.4)
Unknown	728(2.3)	229(1.3)	957(1.9)
Total	31,970(100)	18,309(100)	50,279(100)

Mize et al. (2009)

relationship (Mize et al. 2009). Furthermore, previous research found that women ages 35–44 were at the greatest risk for murder in a cohabiting relationship, as age was found to be a strong predictor in paricide (Shackelford 2001). It was also found that opposite to cohabitation, women in marriages are at greater risk for paricide if they are below the age of 25 (Shackelford 2001). For men, research has shown that husbands are less likely to be the victim of paricide as age increases, serving as a protective factor and the patterns described above have been seen in multiple countries such as Australia and the United States (Mouzos and Shackelford 2004).

Neurological Factors and Intimate Partner Killings

The last section that will be reviewed on this topic is a brief overview of the interplay of neurocriminology and neuropsychology. We will look at current methods that are being used to determine not only abnormalities in the neuroanatomy of the brain leading to intimate partner killings but also psychological factors that play a role in this criminal behavior. Davidson et al. (2000) were able to identify with the use of PET scans that murderers who committed the crime of killing due to reactivity had not only reduced prefrontal cortex functioning but also reduced glucose metabolism in the prefrontal regions. The amygdala was also found to have lowered activity in murders according to Laurell and Daderman (2005). When looking at the hippocampus, temporal lobe, and cingulate cortex, several anatomical factors are noted. The temporal lobe, which houses the hippocampus, appears to function abnormally in murders leading to acts of violence that include murder (van der Gronde et al. 2014). The anterior cingulate cortex is shown to have low reactivity in individuals who commit murder (Aharoni et al. 2013). In addition, according to a review done by van der Gronde et al. (2014), the prefrontal cortex has a large impact on executive functioning, which controls attention control, behavioral flexibility, working memory, self-awareness, and abstract decision making.

According to van der Gronde et al. (2014), looking at neurotransmitters and hormones serotonin plays a particular role in aggressive acts. Metabolic enzymes such as monoamine oxidase A (MAO-A) when reduced can lead to higher levels of serotonin, eventually leading to aggressive acts (Nelson and Trainor 2007). MAO-A, when in deficiency, increases reactive aggression (Baum 2013), and inversely testosterone was found to be in high levels when MAO-A was showing deficiencies (Vaske et al. 2011). As shown above, there are many neurological factors that play an important role in determining why a partner might commit the act of paricide, and further research is needed to continue building the connection between intimate partner killings and the reason why it occurs.

Conclusion

As evidenced throughout the chapter, paricide has evolved with the inclusion of motivational, emotional, and physiological factors. Earlier eras throughout history suggest paricide as an act of gaining power or status, leading to paricide being driven by emotional factors such as protection of offspring, jealousy, or aggression. Themes throughout the chapter raise question on whether it is fair to conclude patriarchal norms have contributed to paricide throughout history. From a physiological perspective, it is acknowledged that neurological abnormalities such as reduced functioning in the prefrontal cortex, amygdala, and levels of glucose metabolism in prefrontal regions have been noted in homicidal behaviors (Davidson et al. 2000). It is also important to note a history of witnessing domestic violence in childhood and adulthood are precursors to paricide (Olowu et al. 2011).

Cross-References

- ▶ [Child Homicide](#)
- ▶ [Evidence of Intentional Killing](#)
- ▶ [Homicide](#)
- ▶ [Homicide Adaptation Theory](#)

- ▶ Infanticide
- ▶ Infanticide and Parenting
- ▶ Partner Abuse and Homicide
- ▶ Partner Homicide
- ▶ Same-Sex Homicide

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Partner or Acquaintance Rape

► Sexual Coercion and Dating

Partner Preference

► Hormonal Component of Homosexuality

Partner Preference Effects

► Mate Choice Effects

Partner Preferences

► Cultural Differences in Mate Preferences

► Men's Mate Preferences

Partner Rape

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Synonyms

Forced in-pair copulation; Intimate partner sexual violence; Partner sexual coercion

Definition

Partner rape refers to nonconsensual sex between intimate partners

Partner rape (also called *forced in-pair copulation*) refers to nonconsensual sex between intimate partners and is considered a form of *partner sexual coercion* and *intimate partner sexual violence*, which are broader terms that include all forms of harmful sexual acts or statements toward an intimate partner (Camilleri et al. 2009; Camilleri and Miele 2016).

Partner rape is not uncommon, where estimates of its prevalence vary anywhere from 7% to 34%, (summarized in Camilleri and Quinsey 2012), with one estimate reaching 51% (Black et al. 2011). Such variation is due to differences in operational definitions and methodologies. Despite the variation, even conservative estimates show how widespread this form of sexual violence is, where some studies have found that it is as prevalent as acquaintance rape (Spivak 2011).

There have been almost no studies around male victims or female perpetrators, likely due to their low base rates. Research on partner rape has also been limited due to social, cultural, and legal norms that minimize or deny that partner rape exists (e.g., Lynch et al. 2016).

Causes of Partner Rape

One approach to understanding partner rape is to see if characteristics of sexual offenders in general apply to partner rapists. Camilleri and Quinsey (2009b) tested whether three main paths to sexual offending (young male syndrome, competitive disadvantage, and psychopathy) were associated with partner sexual coercion. Of these three paths, only psychopathy was found to be related to partner sexual coercion, where 33% of convicted partner rapists were psychopaths, and among a non-forensic sample, only psychopathy significantly correlated with self-reported partner sexual coercion propensity. Psychopaths' coercive approach to reproduction, among other cheater strategies, is hypothesized to have evolved through frequency-dependent selection (Mealey 1995).

Cuckoldry risk appears to be another important risk factor for partner rape. Cuckoldry risk is defined as the risk of female-partner infidelity that may result in men raising offspring who are not genetically related to them. Since cuckoldry risk posed a serious threat to reproductive success, men may have evolved ways to detect and minimize this risk. Partner sexual coercion, which includes partner rape, may be one such mechanism. In situations where cuckoldry risk is high (e.g., partner engaged in an extra-pair copulation during the most recent ovulatory cycle), we expect men to be more prone to engaging in partner sexual coercion. Many studies have found associations between cuckoldry risk and partner sexual coercion, using both forensic and non-forensic samples (Camilleri and Quinsey 2009a; Goetz and Shackelford 2006; Starratt et al. 2008).

Camilleri and Quinsey (2012) reviewed how partner rape could be understood in the context of sexual conflict theory. This theory suggests that

sexual conflict occurs when a benefit to one sex comes at a cost to the other sex, creating a selection pressure for counter-adaptations to evolve. This cyclical process may explain various sex differences in behavior and morphology. In the context of partner rape, there may be conflict in how often to have intercourse – women's lower interest may signal infidelity or possible loss of a partner, and men's sexual coercion may be an adaptive response to such a scenario. Another possibility is that women's extra-pair mating may increase reproductive success by copulating with a male with "better genes," and so partner rape may be a counteradaptation to reduce the risk of cuckoldry by engaging in sperm competition. Though theoretical and empirical work on this topic is starting to emerge, partner rape remains an understudied area of sexual violence (Camilleri and Miele 2016).

Cross-References

► [Sexual Assault and Intimate Partner Violence](#)

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Partner Reproductive Value

- [Mate Value](#)

Partner Sexual Coercion

- [Partner Rape](#)

Partner Violence

- [Sex Differences in Intimate Partner Violence](#)
- [Unique Patterns in the United States](#)

Partner-Directed Violence

- [Evolutionary Psychology and Intimate Partner Violence](#)

Partnerships

- [Same-Sex Relationships](#)

Passive Coping

- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)

Pasture

- [Grasslands](#)

Paternal Assurance Tactics

- [Solution to Paternity Uncertainty](#)

Paternal Care

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Synonyms

[Mating effort](#); [Parenting](#); [Paternal investment](#); [Paternity certainty](#)

Definition

It is the care devoted, directly or indirectly, by the male to his offspring, increasing their chances of survival and social success.

Introduction

Paternal care directed to the offspring is not unanimous in the animal kingdom. Among mammals, for example, a small group of species presents this type of behavior, among which are humans.

Paternal care may take on different forms (e.g., protection and feeding) and is usually conditioned to the reproductive strategies adopted (short or long strategy). This parental investment offers the offspring more chances of survival (e.g., lower mortality rates) and social success (e.g., more access to resources) (Geary 2016).

Particularities and Predictors of Paternal Care

Paternal care is a set of behaviors performed by a male directed to a member of his offspring and which has a positive effect on their development, growth, well-being, or survival (Fernandez-Duque et al. 2009; Geary 2016; Manfroi et al. 2011). The first attempts to explain paternal care emphasized the cost-benefit relations of the fathers' investment. Among them, two hypotheses should be noted: (1) paternal care evolved from the fact that biparental care increases their offspring's chances of survival and success; and (2) paternal care evolved as a male mating strategy, allowing a better relationship with their partners and strengthening their position in the broad social network (Fernandez-Duque et al. 2009; McNamara and Wolf 2015). However, current research has emphasized that the differences in parental investment are due to differences and conflicts between the sexes, in a process of choice and control conducted by the females (McNamara and Wolf 2015). That is, the evolutionary differences between the sexes would lead to this distinction in the use of parental care as a form of sexual selection and in the type and intensity of parental investment. In this process, the females exert the choosing power.

The differences in parental care can be the result of evolutionary trajectories of development under different social and ecological conditions. Parental care is difficult, demanding an investment of resources, time, and energy. While females invest more in their offspring and are more sought after for care, most adult males support their offspring selectively. The females' internal fertilization leads to uncertainty regarding the males' paternity among all birds and mammals, which impacts the paternal care expression. In

some species, this care is common (e.g., birds, fish), while in others it is infrequent (e.g., amphibians, insects) or relatively rare (e.g., mammals) (Fernandez-Duque et al. 2009).

In the case of mammals, fathers' participation is especially important due to the long pregnancies and lactation period the females go through. Despite being a rare behavior among mammals, primates stand out. However, even among them, only a small number of males assume a distinct type of relationship with their offspring. In these cases, paternal care is common, clear, and direct, remaining over the years. Paternal care in a few species of primates and in human societies includes sharing resources (e.g., food, tools), transportation, safety, imparting survival skills (e.g., hunting, escaping), and affection, among others (McNamara and Wolf 2015).

Human beings are one of the species that requires the most parental care after birth, and this investment is vital for reproductive success. However, this care is usually associated with the maternal figure, who carries and nurses the offspring. The care given by males is present in human societies in different intensities and forms and is considered to be a peculiarity of the species, seen as this behavior is not so common among mammals. Nevertheless, motor, emotional, and adaptive skills may be impacted positively by paternal presence (Manfroi et al. 2011).

The expression of paternal care varies greatly between different societies, ranging from complete absence to intimate and direct care. This happens for both foraging societies and developed and developing societies. Intercultural variability seems to be linked to social and ecological aspects of the environment (e.g., family extension, availability of resources, exposure to pathogens, mortality rate) (Fernandez-Duque et al. 2009; Geary 2016).

In adverse contexts, paternal care can make the difference in guaranteeing the survival and development of offspring. Still, it can also be used as a mating strategy, a kind of differential that qualifies the male. Paternal investment may function as a mechanism for the male to decrease the female's resistance (Manfroi et al. 2011; Smuts 1995; Trivers 1972).

Another important element that is usually associated with paternal care is paternity certainty. Especially in species where fertilization is internal, as in humans, only the female can be sure that the offspring are her descendants. Aiming not to invest in offspring who are not their own, paternal care is usually conditioned to a guarantee of paternity (Geary 2016). In this sense, a greater facial similarity perceived by human parents between them and the child significantly impacts the paternal investment exercised, since this would be an indication of paternity certainty (Yu et al. 2019). According to Geary (2016), paternity uncertainty is related to paternal abandonment. When there is an increased paternity certainty, paternal care may take place if this increases the offspring's chances of success or even if the cost is lower than the benefits. To ensure this certainty, several mechanisms have been developed for female control: sexual coercion, monogamy, seclusion, and other forms of female control (Smuts 1992, 1995).

There seems to be a link between the existence of affective connections, monogamy, and paternal care. This is because these processes seem to be regulated by a common biological substrate, with similar neuroanatomical and neuroendocrine activities (Fernandez-Duque et al. 2009). It is hypothesized, then, that the evolutionary computational mechanisms connected to paternal care are related to the same ones that promote general social behavior. Thus, it is likely that changes in the mechanisms that regulate socialization may elicit paternal care. However, there should be more studies to identify precisely the cognitive mechanisms and the forms of activation that facilitate paternal care expression.

Conclusion

In some species, the involvement of parents in the care given to the offspring is need for the survival of the descendants. Despite the high cost of parental care, females invest more resources than males. Paternal care is rare but, when present, may positively impact the development, well-being, and survival of the offspring, through material and emotional investment, as well as through support given to females.

Cross-References

- [Ecology of Paternal Investment](#)
- [Paternal Investment](#)
- [Parental Investment As Mating Effort](#)
- [Paternity Certainty](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)

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Paternal Discrepancy

- [Paternity Uncertainty Hypothesis](#)

Paternal Disengagement

- [Children Without Paternal Investment](#)

Paternal Grandfather Invests Least

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Synonyms

Genetic relatedness; Grandparental investment; Investment in more certain kin; Parental investment; Paternity uncertainty; Pattern of biased grandparental investment; Relationship certainty

Definition

Grandparents can invest a large amount of time and resources in their grandchildren. However, all grandparents do not invest equally in their grandchildren and usually paternal grandfathers are the ones who invest the least of all grandparent types.

Introduction

Males in several species invest in offspring as a function of paternity certainty (Platek and Shackelford 2006). This applies to humans as well (e.g., Alvergne et al. 2009), although among mammals, humans are an exception. Human males typically invest in their offspring unlike 95% of males of mammalian species, but human males also have potential uncertainty in their relationship to their children. While women can be sure that the child they gave birth to is biologically related to them, men can never be 100% certain that the child is actually theirs. In terms of grandparents, this means that only the maternal grandmother has no relationship uncertainty because she can be certain that her daughter

and her daughter's children are genetically related to her. Maternal grandfathers and paternal grandmothers have one kinship link with paternity uncertainty, but the paternal grandfather has two. Therefore, according to paternity uncertainty, paternal grandfathers are assumed to invest the least in their grandchildren (Euler and Weitzel 1996).

Empirical Evidence

Previous studies from contemporary societies have shown that paternal grandfathers usually invest the least in their grandchildren and that maternal grandmothers invest the most (see Coall and Hertwig 2010 for review). This is consistent with the hypothesis derived from paternity uncertainty and occurs in countries with no explicit preference for matri- or patrilineal family relations (Danielsbacka et al. 2011). However, cultural variation in matri- and patrilocality is shown to mix the pattern. The most obvious way to show the significance of cultural variation is to study patrilocal cultures in which a woman becomes part of her husband's kin after marrying (Kaptijn et al. 2013). This usually means that grandchildren will live much nearer to their paternal kin than their maternal kin and will probably only see their maternal grandparents occasionally. This naturally affects which of the grandparents gets to become the closest to the grandchild (Pashos 2000).

In addition to the two links of paternity uncertainty, the paternal grandfather is usually the oldest of the grandparents and is most likely to be either in the worst condition in terms of health or to have already passed away (Coall and Hertwig 2010; Strassmann and Garrard 2011). Old age and poor health may also diminish the investment made by paternal grandfathers, but when the age of the grandparent is taken into account, the paternal grandfather still invests the least (Danielsbacka et al. 2011). Another factor that is detrimental to the investment made by the paternal grandfather is marital disruption (i.e., divorce, widowhood, or remarriage) in the parental or the grandparental generation. Marital disruption does not deteriorate women's

relationships or decrease their contacts with their children or grandchildren as much as it does in men (Danielsbacka and Tanskanen 2016).

Conclusion

The paternal grandfather is predicted to invest the least due to several evolutionary important factors, including sex, lineage, and paternity uncertainty. In addition, age, health, and marital disruption are important factors that may be associated with paternal grandfathers' investment. Several studies from contemporary Western societies are consistent with the prediction that paternal grandfathers invest the least, although cultural variations (patrilocality) may change the investment patterns. However, humans may be unique among other species because caring paternal grandfathers actually exist at all.

Cross-References

- [Father's Father Versus Mother's Mother](#)
- [Grandparents and Grandchildren](#)
- [Maternal Grandmother Invests Most](#)

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Paternal Grandfather Versus Maternal Grandmother

- [Father's Father Versus Mother's Mother](#)

Paternal Insecurity

- [Paternity Uncertainty and Father-Offspring Conflict](#)

Paternal Investment

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Synonyms

[Fatherhood](#); [Paternal care](#)

Definition

The provisioning of caregiving-related resources (e.g., money, time) from fathers to offspring that will influence the probability of offspring survival and reproductive success.

Introduction

Humans are among the very few mammals in which males invest in the well-being of their offspring. Substantive paternal care is only found in 5 % of mammals (Geary 2000). Human neonates are born exceptionally helpless in comparison to other primates and remain dependent on caregivers throughout a lengthy juvenile. The rearing of large brained children who experience long periods of dependency requires a significant commitment of resources from *multiple* caregivers. An offspring's prospect for survival is inextricably linked to the ability and willingness of mothers and fathers to provide critical resources throughout development. Ancestral fathers were recurrently confronted with tradeoffs in how to best allocate finite resources to their offspring. The solutions to this adaptive problem of resource allocation are embodied in the ways that fathers continue to manage these tradeoffs today in modern environments. Natural selection has equipped human males with the capacity to invest resources in offspring.

Background

Investment of resources (e.g., money, time) to enhance one child's chances of surviving and reproducing come at a direct cost to a parents' ability to invest these same resources in other individuals including other offspring, mates, kin, and self (Trivers 1974). Among humans, paternal investment is facultative: Observed levels of care and the amount of resources a father contributes to a child's welfare fluctuate due to a multitude of environmental factors (discussed below) that can vary both within and between cultures (Geary 2000). Paternal resources may be material (e.g., money in industrialized nations or basic provisions in subsistence societies), temporal, social, skill based, attentional, and emotional. Over the course of human evolution, fathers had to make tradeoff decisions in how best to allocate these resources to offspring.

Male parental resources can be partitioned into direct care and indirect care (Kleiman and

Malcolm 1981). Direct care includes any investment such as feeding, playing, grooming, and interacting with the child in ways that benefit that child's survival in their local environment. Indirect care is a more removed form of investment (i.e., harvesting resources from the environment). Across cultures, the levels of direct and indirect care from fathers can vary significantly. Despite agreement that paternal care is a key feature of human child-rearing, debate exists regarding how much and when direct and indirect care can be expected from males.

Empirical work has found a handful of consistent predictors of paternal investment across cultures. Evidence suggests that fathers demonstrate increased levels of investment in children based on perceived paternity. In ecologies where paternity uncertainty (the probability that a male's purported child is indeed his biological offspring) is high, males demonstrate lowered levels of paternal care (see Geary 2000 for review). A higher level of paternal investment has been shown by those males that report being in satisfactory romantic relationships with their child's mother. In review of the literature, Gray and Anderson (2010) found that the most consistent predictor of paternal involvement across cultures was the level of relationship satisfaction a male reported to have with his child's mother.

Early life experience in a male's own development can influence the degree of paternal investment he expresses as an adult. When mortality risks are high or resources are scarce in early development, investing in more (rather than fewer) offspring can help ensure that at least some offspring will survive to reproductive age. In harsh, unpredictable, and low-resource environments, the psychological and physiological stressors on fathers are high, resulting in decreased levels of paternal investment. In safer, high-resource environments, father-child relationships are warmer and reflect higher levels of investment. There is some evidence that a father's own early childhood environment does indeed predict the level of paternal investment expressed in adulthood but others found no such relationship (see Geary 2000 for an extensive review).

Testosterone and Paternal Investment

The endocrine system, together with its interactions with the genome, provides a method of integrating diverse sources of input into messages transmitted throughout the body. This system coordinates behavioral and physiological responses to the environment. Neuroendocrine hormones, such as testosterone (T) in human males, are designed to be responsive to environmental stimuli – conveying important information throughout a male's body and across the lifespan to facilitate adaptive responses. Across diverse taxa, male paternal investment is largely influenced by T. T stands out as a candidate hormone to explore how paternal investment tradeoffs are mediated on the neurohormonal level.

Low T found in fathers of young offspring may indicate a tradeoff from investment in mating toward investment in parenting. While T facilitates intrasexual (male-male) competition for mates through avenues such as aggression, status seeking, and dominance, these behaviors may compete with parenting. Thus, there has been selection for lowered T levels coincident with increased paternal investment in a range of species that feature varying degrees of male involvement specific to rearing offspring. Cross-sectional research on humans from a variety has indeed demonstrated a relationship between a father's lower T and increased paternal care (e.g., Berg and Wynne-Edwards 2001).

Studies looking at the role of T in human paternal behavior have received increased attention. Most published work on human males in industrialized nations does indeed report lower levels of T in human males that are partnered in committed relationships and further reductions in circulating T in those males that have recently become fathers (e.g., Storey et al. 2000). These reduced levels of T are most pronounced in the immediate postnatal period to facilitate paternal care and then steadily return to baseline levels as the offspring develop – this latter shift is proposed to help facilitate a transition from parental effort back to mating behavior once offspring are comparably less dependent.

Muller et al. (2009), when comparing neighboring Tanzanian groups, found that Hadza fathers (known for high levels of direct paternal care) had lower levels of T compared to non-fathers, while no such differences in T were observed for the Datoga fathers (who provide little direct care, but do provision their young). Taken together, human males appear to follow a pattern of T-mediated tradeoffs resembling that of the avian species reviewed above – where circulating T increases to facilitate mating behavior and decreases to allow for direct paternal care. These studies on human males, while numerous, have relied on cross-sectional data which made it difficult to assess the direction of causality regarding T declines and fatherhood behavior.

Gettler et al. (2011) conducted a longitudinal study to clarify whether fatherhood suppresses T or if men with low T are more likely to become fathers. These researchers found that men with higher waking T at intake had greater mating success as evidenced by being in a stable partnership and/or becoming a father at follow-up. The largest declines in T were of those males that were newly partnered or were recent fathers and these declines were significantly greater than the age-related declines in T found in those men who remained single nonfathers. These results did not differ when the researchers controlled for self-reported stress and sleep quality. Within the group of males that experienced this decline in T, it was those fathers that reported investing more time in direct childcare who had the lowest levels of T – indicating a possible effect of direct care with offspring suppressing levels of circulating T. This study supports a model of T mediated tradeoffs in human males whereby high T predicts mating success and then T is greatly reduced after a man enters a stable mateship and becomes a father.

Paternal Investment and Offspring Developmental Outcomes

Men who currently live in resource-scarce environments are significantly more likely to be low-investing fathers, have reduced contact with their children, and/or become wholly absent

fathers (Geary 2000). This lack of substantive paternal involvement has a damaging trans-generational impact. Across cultures, children that are recipients of low paternal investment are more likely to commit acts of violence, engage in early sexual activity, at greater risk of becoming teenage parents, and becoming low-investing parents to their own offspring (Coley 2001).

In developing societies, there is a relationship between paternal investment and offspring mortality rates (see Geary 2000). Those fathers that do provide care, food, and time have infants that are, on average, in better physical health and this is the case across traditional societies as well as industrialized nations. Among the hunter-gatherer Ache of Paraguay, there is a highly significant difference in mortality rates for father-present versus father-absent children (Hurtado and Hill 1992). Father absence triples the probability of death due to illness and doubles the risk of the child being killed by other Ache.

Receiving substantive paternal investment also provides social competitive advantages to offspring by increasing a child's ability to compete for resources in adulthood. In industrialized nations, the degree of one's social competitiveness can be indexed by their educational achievement. Paternal investment (both direct and indirect care) is correlated with better academic skills in children and higher SES when these children reach adulthood (Kaplan et al. 2000). Furthermore, paternal investment in play (direct care) is associated with children's skill at regulating their emotions and with their social competence as adults (Geary 2000). Those children who have fathers who engage them in physical play are more likely to be popular than those children who do not regularly engage in this type of play. This popularity in childhood is expected to lead to increased social competitiveness in adolescence and, eventually, in adulthood.

Conclusion

Human fathers exhibit a substantial amount of plasticity with regard to the level of investment provided to offspring. As ecological conditions

do vary widely both within and across cultures, one should not be surprised to see this phenotypic variation in the level of care provided by fathers. The endocrine substrates that have evolved to support this facultative paternal investment also demonstrates similar (and closely aligned) variation from one ecological context to the next. The nature of the specific ecological cues that a father's endocrine and behavioral systems rely on for developmental calibration has yet to be entirely elucidated. The downstream consequences of low (or absent) paternal investment are far-reaching. Combining research efforts from multiple fields (e.g., evolutionary psychology, behavioral endocrinology, biological anthropology, and developmental psychology) has the potential to advance our understanding of the predictors of paternal investment in humans and, in turn, improve societally undesirable developmental outcomes in children.

Cross-References

- ▶ [Life History Theory](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Paternal Care](#)
- ▶ [Paternity Certainty](#)
- ▶ [Paternity Uncertainty and Father-Offspring Conflict](#)
- ▶ [Sex Differences in Parenting and Parental Investment](#)

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Paternal Investment Relative to Maternal Investment

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Synonyms

Biparental care; Maternal investment; Parental effort; Parental investment; Sex differences in parenting

Definition

It is important to discriminate between two related but distinct constructs in evolutionary theory that

refer to parenting: (1) *Parental Effort* (PE) is the cost assessed in terms of *bioenergetic or material resources* of the production or maintenance of offspring, typically meaning that expended in behavioral parental care, but may also include biological gestation and lactation; (2) *Parental Investment* (PI), on the other hand, is the cost assessed in terms of the *production or maintenance of future offspring* of the parental effort presently expended upon *current offspring*. Presumably, the costs represented by parental investment are the direct consequences of the costs represented by parental effort, as the expenditure and depletion of available resources are the primary cause of limitations upon future offspring production or care, although not exclusively so. For example, Cabeza de Baca and colleagues (2016) provided a description of the additional costs of reproductive effort assessed in terms of physiological deterioration. Nevertheless, these additional physiological costs can be considered mostly indirect effects of the initial parental effort.

Technically speaking, the question of *maternal investment* versus *paternal investment* is therefore difficult to answer as the assessment of the cost in future offspring of resource expenditures upon the current offspring is rarely tractable and often inferential. In practice, the problem usually boils down to a comparison of the relative expenditures of *maternal effort* versus *paternal effort* as the relative *expenditures* of bioenergetic and material resources, which are more readily and directly measurable. A related question in many species that practice kin-selected alloparenting is that of the relative contributions of matrilineal alloparental effort versus patrilineal alloparental effort. Kin-selected alloparenting occurs when the genetic relatives of either the mother or the father assist in caring for the offspring, presumably to maximize their own inclusive fitness. The particular parent that is doing most of the parental care is therefore the most likely to recruit alloparental care from their own kin. In many human societies, for example, the mother typically contributes the bulk of the parental effort, and the maternal grandmother is often recruited to provide the bulk of the alloparental effort. Finally, further distinctions can be made within the matriline or

patriline providing alloparental effort, such as distinguishing between relative contributions of the collective female alloparental effort versus male alloparental effort. The case of the maternal grandmothers mentioned would then be classified as an instance of *female matrilineal alloparental effort*. Assistance from maternal aunts would also qualify within this category.

Introduction

Sex differences in parenting exist across many different animal taxa, most notably in mammals. These differences are posited to exist for many reasons that include anisogamy – differences in obligate parental investment based on gamete size (sperm vs. egg; Trivers 1972), ecological context, and sex ratio (Kokko and Jennions 2008), which modulates the intensity of intrasexual and intersexual competition. Under the assumption of anisogamy, the sex with the lower initial obligate investment in parenting – usually males – must compete to gain mating access to females. Females who typically have increased obligate investment must be more selective when choosing a mate, or risk mating with a low-investing partner that deflects on parental duties. In this scenario, females define the mating parameters of the ecology that emphasize choosing mates that are high-investing and/or physically attractive.

However, although anisogamy has been posited as the likely evolutionary *origin* of male–female differences in reproductive effort, about over a billion years ago in the “hot, thin soup” of the Precambrian seas where life arose, it is unlikely to be responsible for the subsequent *maintenance* of those traits in more complex multicellular organisms. What is more likely is that the ancestral anisogamy gave rise to a positive feedback loop in which females expended more and more parental effort to secure their initial reproductive investments and males did so to a lesser degree. In modern eutherian mammals, for example, the differential cost of an egg cell with respect to a sperm cell is trivial as compared with the physiological costs of gestation, lactation, and

parental care. These latter costs completely dwarf the initial cost of producing a single egg cell, however large it might be in comparison to a sperm cell. It should also be noted that male metazoans typically produce orders of magnitude more sperm cells than female metazoans do egg cells, and the relative costs of gamete production have rarely been considered in the aggregate. In summary, we need to go beyond the simple anisogamy model to correctly describe the relative selective pressures acting upon male and female metazoans with respect to their expenditures of parental effort.

According to *Sexual Strategies Theory* (Buss and Schmitt 1993), men as well as women have both short- and long-term sexual strategies, each with their own distinct tactics, which are strategically employed to maximize reproductive success in their respective environment. Because men and women differ physiologically, the adaptive problems they face vary. Acquiring resources to raise a child is an important problem women must face in selecting short- or long-term strategies and must weigh keeping a high-investing mate or limiting access to prospective mates. The primary adaptive problem men face is gaining sexual access to women. Thus, men are generally oriented toward investing more time and energy into mating than parenting.

Much within-species variation exists in parenting and mating behavior between the sexes. In species where both sexes are high-investing, such as in humans, the pattern of mating behavior resulting from anisogamy is altered, with competition for mate access increase in both sexes (Buss and Schmitt 1993). Contextual factors such as the sex ratio of males relative to females available to mate thus modulate intensity of intra- and intersexual competition. When the mating sex ratio is considered, the rarer sex controls the mating dynamics of the immediate environment. This means that in male-biased environments, male sexual behavior will be oriented toward parenting instead of mating; however, in environments where females are more abundant than males, sexual behavior of females and males will be oriented toward more mating and less parenting (Kokko and Jennions 2008).

The next section below briefly reviews between-species sex-differentiated mating and parenting behavior and focuses on the mating and parenting behavior in humans and nonhuman animals.

Evidences of PI Theory in Nonhuman Animals

Sex-role differentiation. According to parental investment theory, males are expected to allocate resources for the development of armaments and ornaments used during intra- and intersexual selection (Trivers 1972). Males are also predicted to destine a portion of their bioenergetic budget for searching and defending mates, whereas females are expected to be more selective (compared to males) when choosing a mate. This difference has been attributed to the costs accrued by females during reproduction including gamete production, incubation/gestation, nourishment, transport, and guarding behavior. Variations in parental effort then lead to differences in morphology, physiology, and behavior between males and females a phenomenon known as sex-role differentiation (SRD).

However, SRD is a continuum rather than a dichotomy, with ecological, social, and ontogenic factors moderating the degree of sexual differentiation on each species. Thus, even though a significant amount of evidence has been collected regarding sexual dimorphism, intrasexual competition and intersexual selection in fishes and amphibians, the absences of parental care in most the latter taxa (Reynolds et al. 2002), supports the fact that SRD is not fully reached. Furthermore, only 22 % of bony fishes (*Teleosts*) present some form of care (usually guarding the nest or the young). However, in those taxa where it has been found, male parental care is more widespread than female care. This phenomenon has been attributed to the fact that paternal care is correlated with external fertilization (89 % of bony fishes present external fertilization; Gross and Sargent 1985), whereas species displaying female guarding present internal fertilization.

In reptiles, SRD is also a heterogeneous phenomenon, where even though in most lizard (*Lacertilia*) species, males are larger than females, female-biased sexual dimorphism has been

described in turtles (*Testudinata*) and snakes (*Serpentes*; Cox et al. 2007). Furthermore different from other animal classes such as mammals or birds, parental care in reptiles is a rare phenomenon with only 4 % of lizards and snakes taking care of their young (Sinervo and Miles 2010). This reptilian pattern is not met by crocodilians, with most species displaying some form of parental care (~60 % of species present solely maternal care, whereas in 38 % of species males and females take care of their young; Grigg and Kirshner 2015) and with males usually being larger than females. Furthermore, in polygynous species, dominant males (i.e., “boss croc”) have been observed to copulate with multiple females, and defend their territory from invading rivals, while females protect the nest from predators and other conspecifics, assist the young when exiting the nest, carry their offspring to the water, and defend the crèche from predators and other adults (Grigg and Kirshner 2015).

In other clades, such as birds, some species do exhibit high levels of SRD, with males of numerous species being larger than females, as well as presenting armaments (e.g., spurs) and ornaments (e.g., plumages) lacked by females (Gill 2006). Moreover, behavioral differences have also been described, with males defending territories or performing complex displays during courtship rituals. However, since a main element of SRD is the level of parental effort expended by each sex, in birds 81 % of species exhibit biparental care (Cockburn 2006). Nevertheless, it is worth noting that most avian cooperative breeding species have altricial offspring (precocial: 4 %; altricial: 11 %), whereas the opposite is true for species relying exclusively of maternal care (precocial: 24 %; altricial: 7 %). Furthermore, in species where only one of the sexes invests in parental care, females more frequently take care of their young compared to males (females: 8 %; males: 1 %; Cockburn 2006). Consequently, in evolutionary terms, the degree of vulnerability of altricial hatchlings demands the attention of more than a single care taker, attenuating the degree of sex-role differentiation after fertilization but not before (e.g., intense males-male competition and female selection).

Evidence of SRD in extinct species remains a debated topic. However, descriptions of osteological, histological, and oological characteristics of nests, eggs, and remains may allow some degree of inference (Brusatte 2012). Thus, in clades such as *dinosauria*, evidence of sexual dimorphism has been attributed to differences in ornamentations as well as based on body size estimations. Furthermore adults dedicated a considerable amount of time to nest building (e.g., mounds or excavating holes), with nests of species such as *Maisaura peeblesorum* positioned adjacent to one another demonstrating a colony-type behavior (Brusatte 2012). The presence of multiple juveniles with poorly ossified bones also indicates that adults not only cared for several young simultaneously but that hatchlings were vulnerable and unable of an adult-type locomotion, requiring both active protection and provisioning. Additionally examinations of different types of parental care in relation to life history indicators (e.g., clutch volume and body mass) across 433 species of extant crocodilians and birds concluded that three extinct species of nonavian maniraptoran dinosaurs (*Troodon formosus*, *Oviraptor philoceratops*, and *Citipati osmolskae*) scaled better with respect to model including an avian paternal care model rather than with other forms of parental care (Varricchio et al. 2008).

Different from extant and extinct species of fishes, amphibians, reptiles, and birds with external fertilization, the internal fertilization and gestation of mammals not only increases the physiological costs accrued by females but it also releases males from directly investing in their offspring. Thus, across 1370 mammalian species, males have been found to be 10 % larger than females in 45 % of the taxa (Lindenfors et al. 2007). Furthermore, phylogenetic examinations have discovered significant differences in body size and canine size dimorphism across haplorrhine primates based on the level of intrasexual conflict (Plavcan 2004). Moreover, in most nonhuman primates males do not directly take care of their offspring, but rather females either on their own or with the assistance of kin not only protect the young from predators and

conspecifics but also carry and provide for their offspring (Gear 2000). Hence males allocate more resources to mating effort, whereas females to parenting effort.

Sex-role reversal. Parental investment theory is not restricted to predictions regarding circumstances where females choose mates and males compete for mating opportunities. Sex-role reversal (SRR), the occurrence of female-female competition and male choosiness over females, further has been described in fishes, amphibians, and birds.

In pipefishes and seahorses (*Syngnathidae*), for example, females have been found to deposit the eggs onto a brooding area located in either the tail or abdomen of the male (Foster and Vincent 2004). Moreover, male pregnancy (similar to female pregnancy in other species) has been found to be a costly endeavor. In seahorses (*Hippocampus* spp.) male gestation involves a considerable bioenergetic investment, including the osmoregulation of the brooding environment, transferring waste from the pouch into the blood stream, and synthesizing prolactin for the conversion of proteins to be consumed by the embryos (Foster and Vincent 2004). Although male brooding is considered a manifestation of SRR, the prevalence of female-female competition in *Syngnathidae* remains a highly controversial topic. Thus, whereas female intrasexual competition (and female ornamentation) has been observed in conjunction with male pregnancy in pipefishes, its occurrence is partial in seahorses (Wilson et al. 2003). Experiments with *Hippocampus fuscus* have found that female intrasexual competition is less intense compared to male-male aggression. The difference in female competition between pipefishes and seahorses has been attributed to the presence of social monogamy in former. This hypothesis has been supported by phylogenetic comparisons, where polygyny was found to be a better predictor of SRR in Syngnathids rather than social monogamy (Wilson et al. 2003). Even though further evidence is needed to determine the ubiquity of female-female competition in the genus *Hippocampus*, the co-occurrence of male pregnancy and female intrasexual aggression in other Syngnathids

supports the predictions made by parental investment theory.

SRR has also been described in amphibians. Paternal care (e.g., clutch attendance and carrying offspring) along with females' attraction to the vocalization of males in Poison-Dart Frogs (e.g., in *D. auratus*) support the occurrence of SRR (Eens and Pinxten 2000). This phenomenon was attributed to the time males were unreceptive while taking care of their young. The imbalance between the numbers of available males with respect to receptive females increased the competition among females for access to males (Wells 1978). However, similar to seahorses, observations with *D. auratus* have concluded that both males and females respond equally to competitive settings, despite the fact females are larger than males (Summers 1992). Thus SRR should be considered as partial in Dendrobatids. Additional studies with other Dendrobatid species could clarify the phylogenetic ubiquity of female intrasexual competition. In the meantime, more conclusive evidence of SRR in amphibians has been found in Midwife Toads (*Alytes obstetricans*; *A. muletensis*; Eens and Pinxten 2000), where males carry their young and females compete aggressively for copulation opportunities.

Similarly, instances of SRR have been observed in 35 species of five different avian families (*Scolopacidae*, *Centropodidae*, *Turnicidae*, *Charadriidae*, and *Jacanidae*; Eens and Pinxten 2000). In the Spotted Sandpipers (*Actitis macularia*), for example, not only males incubate, provide, and protect their young but females have been found to have more than one clutch per season with several mates. Females are also larger than males, a morphological trait associated to aggressive competitions for territories used to attract males (Emlen and Wrege 2004). Similarly, in Wattled Jacanas (*Jacana jacana*), males take care of their young, while females compete for copulations; moreover, sexual dimorphism is also reversed, with females presenting facial ornamentations and wing spurs, as well as being heavier than males (Emlen and Wrege 2004). Furthermore, in *Jacana jacana* SRR

extends beyond female intrasexual competition and male choosiness. After takeovers, females have been seen to destroy, evict, or kill the eggs or chicks of males who copulated with other females. Following the attack, targeted males not only copulate but also take care of the attacker's offspring.

Human Tests of PI Theory

The purpose of parenting is to raise viable, competitive, and reproductively successful offspring. Organisms must therefore decide how and where to allocate time and energy that best optimizes their level of reproductive effort allocated toward parenting and how much effort will be allocated toward different offspring (Ellis et al. 2009). While sex ratio matters, as discussed above, women face a unique burden that allocation of resources toward parenting is generally considered more vital to child survival than male parental effort (Hrdy 2009; Sear and Mace 2008). Because of this, human paternal care is highly variable and context-dependent, possibly facilitating transmission of status, quality, and social competency in offspring. Paternal effort in mammals is highly variable and rare. In Mammals, approximately 5 % of species have some form of paternal effort toward offspring (Geary 2000).

When do fathers invest in their children? According to Geary (2000), there are three things that must be considered when examining variation in paternal parental effort in mammals: (1) offspring survival, (2) mating opportunities, and (3) paternity certainty.

If male parental effort does not substantially increase offspring quality or survival, high-investing fathers will be selected against – the ecology will favor fathers who invest more in mating than parenting. Again, if paternal parental effort does not increase quality or survival of offspring, males will increase parental effort in mating than parenting. Only if there is a male-biased sex ratio will there be selection against low-investing fathers. In these situations, it may improve mating prospects to be mated to one female. Paternal effort and its impact is indeed highly variable. A classic example of

ecology-contingent fathering can be seen in the Aché and Hiwi hunter-gatherer tribes of South America (Hurtado and Hill 1992). Both tribes reside in areas where socioecological and environmental conditions differ. For instance, the Hiwi tribe live in an area of Venezuela where variable rainfall contributes to unreliable food and crop extraction; alternatively, Aché of Paraguay often experience constant rainfall that leads to abundant and reliable crops. According to Hurtado and Hill (1992), differences in resource extraction and male-male cooperation are essential among the Aché for group living. Male hunters within the Aché are in charge of hunting and collecting food for the entire tribe. Meat collected from group hunts is then communally shared, with no one in the tribe going hungry. Instead of focusing on male-male cooperation, Hiwi tribes emphasize spousal cooperation. For instance, during hunts, females assist males by helping collect carcasses or steering canoes, with food shared only among family members (Hurtado and Hill 1992).

Direct paternal involvement differs between males of both tribes. Hiwi fathers directly care for offspring and can be seen watching children while mothers are out gathering tubers. Paternal presence in Aché men involves little direct care. Instead, Aché males contribute protection for their offspring from unrelated males who may seek to harm or murder infants. Unstable pair-bonding contributes to higher male-male competition for mates that may include murdering the children of other males (Geary 2000; Hrdy 2009).

Both the Hiwi and Aché tribe demonstrate how socioecological factors may alter paternal involvement. Overall, Aché ecology is characterized by unstable pair-bonds, a male-biased sex ratio, and little parenting from fathers, while Hiwi ecology involves stable, long-term pair-bonding, more reproductive females than males, and direct care from fathers (Hurtado and Hill 1992). The effects of variable paternal presence on child mortality, as is expected, differ between both tribes; however, the effects are contrary to what is expected. For Hiwi children, paternal death and divorce had no impact on childhood mortality. Though it would be expected that

paternal death/divorce *should* matter in societies where fathers contribute direct care to their infants, it could be speculated that allomaternal bonds between the close-knit relatives living in the tribe could buffer against the effects of paternal death and divorce (Hurtado and Hill 1992). Additionally, divorce in Hiwi societies is extremely rare. Only 8 % of Hiwi children in the sample experienced pair-bond dissolution (Hurtado and Hill 1992).

While Aché males contribute mostly food provisioning and protection from unrelated males, paternal death and divorce (though common among the Aché) has an impact on child mortality. Specifically, father death and divorce has the most effect on mortality for children between the ages of 1 and 5 years old. Due to unstable pair-bonds and males seeking multiple mates, children from divorced families are more vulnerable to sickness, homicide, and capture in warfare (Hurtado and Hill 1992, p. 44).

The final factor to consider is paternity certainty. In environments where males have low paternity confidence in their offspring, it again makes most sense to invest time and effort mating. Investing time and energy raising children that are not biologically related to the male will result in net loss of resources and decrease inclusive fitness; however, in environments where paternity certainty is high, there would be an increase in paternal effort. Physiological differences between men and women, as was previously mentioned, affects reproductive strategies and affects the amount of investment the sexes contribute to parenting and mating (Trivers 1972). Additionally, paternal effort in children may also be affected by paternity certainty – fathers will seek to invest little in children if there is a chance that the offspring are *not* biologically related to the father (Geary 2000). The dilemma that males face in reproduction is that females do not display visible cues of estrus and, thus, are equipped with concealed ovulation. Thus, concealed ovulation presents an issue and a conflict of interest between the sexes with males seeking paternity certainty and females seeking male investment in their children (Geary 2000).

One possible mechanism that paternity certainty may work through is resemblance – whether the father believes the child resembles him. Phenotypic similarity (whether it is facial, physical, or behavioral) may be a proxy for genetic relatedness. Because investment in children is costly for males – with resources diverted from mating effort to support mothers in parenting – males must be highly discriminative and careful about investing in genetically unrelated children, which would be a waste of mating and parenting effort (Geary 2000). Paternal resemblance effects have also been noted in natural experiments involving fathers and their children. Fathers, whether presently in a relationship with the mother or not, reported higher levels of monetary investment toward their children if they reported increased paternal resemblance (Apicella and Marlowe 2004). Paternal resemblance has also been correlated between relationship quality of biological children and fathers, severity of injuries the mother received from the father, and amount of conflict between mother and father in a sample of males convicted of spousal abuse, with lower levels of perceived paternal resemblance increasing conflict and severity of injuries (Burch and Gallup 2000).

Competing Theories of Cooperative Breeding

There exists two broad set of theories regarding cooperative breeding in humans. The first focuses on the importance of mother-father cooperative breeding and the advantages the child incurs from this arrangement. The second set of theories posits that fathers are helpful, but grandmaternal alloparental care, care derived from someone other than the mother and father, is more important to child health and survival. According to embodied capital theory (Lancaster and Kaplan 2009), sexual specialization of labor evolved in primates, especially humans, due to a suite of adaptive traits called the human adaptive complex (Lancaster and Kaplan 2009) that advance brain development and long-term skill acquisition in young children. The human adaptive complex, which includes altricial young, long-term brain development, and delayed senescence, are

expensive traits that require large investments from mothers and fathers. Investment in somatic growth and reproduction, according to the theory, are investments in embodied “stocks,” where investment dividends are acquired through skill-acquisition and reproductive success (Lancaster and Kaplan 2009). In male-female cooperative breeding ecologies, sex-differentiated divisions of labor are vital for lower child mortality. When males and females focus on sex-specific tasks, the quality of childcare increases – while men are devoting long hours of hunting, which is a major source of calories in hunter-gatherer societies, females can allocate more energy in caring for dependent offspring without unnecessary exertion (Lancaster and Kaplan 2009). Hunting for women would be a source of unnecessary exertion if males did not participate in the task. Because women are caring for dependent offspring, hunting, which expends large amounts of calories, would not be ideal for women who are breastfeeding, since lactation is also a large caloric burden to the female, or seeking to get pregnant, which requires stored amounts of fat to maintain a pregnancy (Trivers 1972). Further, hunting is a skill-intensive task that requires long hours to master and long hours to perform and may be difficult with a dependent infant. If embodied capital is a long-term investment, it would be wise for a woman to complement a male in their skills than learn additional time-consuming skills. By allowing a spouse to hunt, women, aside from caring for young, can focus on harvesting foods that are high in carbohydrates (Lancaster and Kaplan 2009).

Other evolutionary theories postulate that male parental effort in children is expendable and can be replaced with allomaternal support from related females who can handle the burden of raising young (Hrdy 2009). In this view, parental effort from males will not necessarily matter in offspring survival or competency (Hrdy 2009; Sear and Mace 2008). The grandmothering hypothesis (Hawkes et al. 1998), a major hypothesis in this set of theories, posits that older, postmenopausal women are important to the survival and care of their grandchildren and increase their inclusive fitness by assisting in childcare versus

continuing their own reproductive capacity. Based on the principles of kin selection and paternity certainty, maternal grandmothers are hypothesized to be more investing toward their grandchildren than paternal grandmothers. A review of 45 studies found additional evidence suggesting the importance of maternal grandmothers in the survival of children and little evidence for the importance of fathers (Sear and Mace 2008). However, this analysis aggregated all natural fertility populations irrespective of subsistence economy, such as foraging versus farming, which might differ in the relative importance of male and female alloparents due to the different nature of their potential contributions.

Conclusion

The distribution of paternal to maternal investment across species is critically dependent upon a number of exogenous and endogenous factors, including the initial bioenergetic allocation of species-typical levels of parental effort, as governed by the dynamics of life history strategy, and the relative sex-typical bioenergetic allocations of parental effort, as governed by the dynamics of sexual strategies theory. These complex dynamics predict an entire continuous spectrum of partial reversals of the normative sex roles assigned by sexual strategies theory to males and females, respectively. These seeming anomalies do not count as either exceptions or objections to sexual strategies theory, as the specific circumstances under which these partial “sex-role reversals” occur is predicted by the basic dynamics that undergird parental investment theory.

Cross-References

- ▶ Biparental Care
- ▶ Helpers at the Nest
- ▶ Maternal Investment
- ▶ Parental Effort Versus Mating Effort
- ▶ Parental Investment and Parenting
- ▶ Parent-Offspring Conflict (Trivers)

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Paternal Resemblance

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Definition

Research indicates that men use child resemblance to make investment decisions as a strategy to prevent cuckoldry.

Introduction

Paternal resemblance based on shared features between the resident male and the child qualifies as a phenotypic indicator of shared genes. The literature overwhelmingly indicates that while both men and women can discern resemblance in others, there is a male specific effect of resemblance in child investment.

There are decades of studies stating the relationship between resemblance and male investment. Males who committed infanticide cited a lack of resemblance implying non-paternity as a reason (Daly and Wilson 1984). Resemblance has been implicated in the father/child relationship (Apicella and Marlowe 2004), with perceived child resemblance valued more highly by men (Volk and Quinsey 2002). Alvergne et al. (2010) found fathers reported the highest emotional proximity to children who displayed greater resemblance, but mothers did not. Alvergne and colleagues have also examined which facial features have the greatest effect on resemblance ratings by selectively showing parts of the face. Fathers were able to focus on specific resemblance cues even when the overall face was disrupted. Males also ignored facial features that fluctuated throughout development or failed to display resemblance cues.

Burch and Gallup (2000) examined this concept with 55 men in a domestic violence treatment program. The men answered several questions about the types of abuse they had committed toward partners, along with the relationships,

degree of relatedness, and perceived resemblance they shared with their children. Burch and Gallup (2000) also found that the presence of children that were explicitly unrelated to the male (e.g., children from a female's previous relationship or a stepchild) greatly increased the amount of violence in the home. In these instances, resemblance had no effect, as the men knew those children were not related to them. This indicates the underlying basis of paternal resemblance; the avoidance of cuckoldry. Cuckoldry, unwittingly investing in a child that is not your own, is a threat to fitness that is specific to males in species with internal fertilization (see ► [“Cuckoldry Risk”](#)). Because of this, men will avoid investing in children that are not their own, and decades of research (just as in the Burch and Gallup 2000 study) have shown that unrelated children are more at risk for abuse. Daly and Wilson conducted research in several cultures showing that non-biological parents are as much as 100 times more likely to kill their children than biological parents (Daly and Wilson 1985, 1996, 1998). Further, men have evolved strategies to determine if their children are their own. Phenotype matching, through paternal resemblance, is one strategy.

Burch and Gallup (2000) also found that these abusive males perpetrated more abuse, and showed increased severity of abuse directed toward their mates as the perceived paternal resemblance to the children decreased. That is, the more their children resembled them (in their own opinion), the better they treated, and the less they abused, their female partner. Their perceived resemblance to their children was also positively correlated to their relationship to and treatment of those children. The more the man thought a given child resembled him, the better he rated his relationship to that child, and the better he treated that child. As mentioned above, this effect was not seen with unrelated children, as the question of paternity with these children has already been answered.

Hypothetical Investment

Burch and Gallup (2000) show that the resident father's perception of resemblance plays a major

role in both partner and child treatment. However, there was no feasible or ethical way to experimentally alter child resemblance to examine differences in paternal investment. To do this, Platek et al. (2002) used imaginary children and hypothetical scenarios. Without the participants (undergraduate students) knowing, the faces of unknown children were digitally morphed with either images of the participants themselves or one of four other people of the same sex. Participants were then instructed to view a randomized array of children's faces, with one face resembling theirs. To measure the effect of shared facial features, the subjects were presented with hypothetical parental investment scenarios and asked to choose which child's picture they would invest in. Males chose their own morphed picture more often than females in almost every positive investment category (for example, which child they would spend time with, give money to, adopt, etc.) and less often in almost every negative investment category (which child they would physically punish, spend the least time with, etc.). The greatest difference between males and females occurred in response to the question, “Which one of these children would you be most likely to adopt?” with 90% of the males but only 35% of the females picking the child whose face had been morphed with their own. Likewise, none of the males picked children's faces that had been morphed with their own as the child they would be most likely to punish. In contrast, female participants reported having more difficulty choosing between hypothetical children, and several stated that they had tried to distribute positive and negative treatments as equitably as possible. In fact, two women halted their participation during the study, stating that the investment decisions were too difficult for them.

In a follow-up study, Platek et al. (2003) questioned whether these investment decisions were actually differences in the ability to detect resemblance; in other words, whether women would make the same decisions, but they could not accurately determine which child resembled them, or whether males were actually more likely to make decisions about child investment based on resemblance. The study showed no sex differences

in the ability to detect resemblance, but males were far more likely to make hypothetical investment decisions that favored children who looked like them.

Resemblance, Investment, and the Brain

To take this even further, Platek et al. (2004) used the same paradigm paired with magnetic resonance imaging to examine sex differences in neurological activation when viewing self-morphed baby pictures. Unlike females, males showed significant neural activation in the left frontal cortex (which is hypothesized to be involved in the inhibition of negative responses) when viewing children's faces that resembled them. Platek et al. (2005) also found that males showed greater cortical activity than females in response to children's faces that resembled them. Using a similar design, Wu et al. (2013) also showed that men showed higher detection of resembling child faces and self-referential processing in kin detection than did females. In total, these studies show a male advantage in resemblance and investment assessment that utilizes multiple areas of the brain and occurs at different stages of processing. Male brains may be designed to process children's faces and make investment decisions based on resemblance.

Adult Versus Child Faces

Differences in research methodologies illustrate how men and women may process faces in similar ways but differ significantly in how this affects decision making. DeBruine found a resemblance effect in cooperation and prosocial behaviors in adults but no gender difference (DeBruine 2002, 2005). However, she used adult faces, not child faces. Platek et al. (2004) found sex differences in brain activation to resembling child faces (Platek et al. 2004) but not adult faces (Platek and Kemp 2009). What is found throughout the literature is that gender differences are only found when children's faces are used. While Burch et al. (2006) imply this may be the case, Lewis (2011) makes it

clear: "The different contexts in which previous studies investigated resemblance effects may account for this apparent inconsistency. Platek et al. (2002, 2003) examined prosocial behavior toward children. Because of paternity uncertainty, facial resemblance would be expected to have a greater effect on men's than women's parental investment. DeBruine (2002, 2004, 2005), on the other hand, assessed prosocial behavior toward peer-aged individuals." (p.970). Therefore, both men and women have evolved to detect and utilize resemblance to make decisions like trust and cooperation, but men use this cue for child investment.

This resemblance, or phenotype matching, may extend to sensory modalities other than vision. Alvergne et al. (2009) found that paternal investment was positively related to both face (visual) and odor (olfactory) similarities between fathers and children. Research has yet to determine what neurological areas (or if the same neurological areas) may be implicated in olfactory phenotype matching processing. Gallup Jr et al. (2016) showed greater paternal investment in children based on shared psychological features (interests, attitudes, etc.). While both physical and psychological features made a difference, shared psychological features between fathers and adolescents and older children accounted for even more variance in measures of paternal investment than physical resemblance.

Maternal Strategies

Given these findings, it is understandable why mothers and their relatives often try to convince fathers of their child's resemblance. Daly and Wilson (1982) recorded spontaneous remarks in maternity wards about the appearance of the newborn child. Mothers, friends, and relatives were more likely to comment on how children resemble their fathers. When fathers voiced doubt, the mothers quickly reassured them of the child's resemblance. One father made it clear that if the child did not resemble him, he would leave the mother at that instant. Regalski and Gaulin (1993) also found that women consistently ascribed

resemblance to their current male partner, and Alvergne et al. (2007) found that mothers ascribed resemblance to the father, even when assessment by external judges revealed the opposite. Females consistently ascribe resemblance of their children to the resident father, because it may increase investment, decrease abuse, and ensure their child's survival.

Conclusions

Decades of research have shown that men use resemblance as a measurement for child investment decisions that male brains process resemblance cues differently specifically when making these decisions (and not when processing adult resemblance), and that women have developed counter strategies, attempting to convince fathers of resemblance where none may exist.

Cross-References

- [Paternal Investment](#)
- [Paternity Uncertainty and Father-Offspring Conflict](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)

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Paternal Role

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Synonyms

[Father responsibility](#)

Definition

Male parent of the child typically seen as a secondary role to the maternal position.

Introduction

It is clear times have changed in most societies when one looks at the role of the father from the primitive eras to the twenty-first century. Fathers typically are seen as a secondary caregiver in most societies around the world, while the woman is mainly responsible for the child, especially in the beginning critical stages of life. So, this begs the questions of what roles males typically have in the development of their offspring, and what happens when there is an absence of this?

Evolution of the Paternal Role

Various pieces have investigated the differences of maternal from paternal roles and what investment fathers have in their children. Typically, it was believed that men in order to maximize their reproductive success would attempt to reproduce with as many females as possible. Males were typically known to invest more in mating rather than supporting their child because doing such would waste resources that could otherwise be spent on spreading their genes (Geary 2000). This means only when they could not continue to mate with other females that males would support their children, but only if they were confident about their paternity to the child. When fathers did remain present in their children's lives, their main role was to provide protection to the family unit. Studies have looked at the likelihood of children and mammal offspring in general survival rates with and without a father present, and when there is the absence of a paternal role, the offspring usually suffer with those living – not being as healthy or large (Geary 2000). Animals differ greatly when it comes to the role of the father with predominantly carnivorous mammals, such as wolves and foxes; fathers aid the mother in hunting, protection, and are even seen playing with their young often. Yet, looking to our most closely related relatives such as chimpanzees, you will see that they are commonly uninvolved.

Recent investigation of the paternal role from Gray and Anderson's *Fatherhood: Evolution and Human Paternal Behavior* has shown a light on the assumption of past hunter-gathering tribes negating the view that men hunted for their children (Gray and Anderson 2010). Recent evidence they have done has suggested that men hunted for the entire tribe to share with other members, and their children were just included in the feasting. However, this sharing of food was mainly done in hopes of creating a reputation among other males in the tribe and attracting other women to mate with – feeding their children was just assumed to happen since they were part of the tribe. Not to say that they were uninvolved fathers, much of their time spent

hunting was to bring extra calories for the mother since they were less able to provide for themselves.

Family Dynamic

Typically, it is most usual for a male to have multiple wives, therefore a child to have more than one mother. Think of the old saying “it takes a village to raise a child” with many members of the tribe aiding in the infants’ survival. But in some Amazonian communities, it was and still is typically for a child to have multiple fathers (Hrdy 2009). “Partible paternity” was a concept Sarah Blaffer Hrdy coined in her book *Mothers and Others: The Evolutionary Origins of Mutual Understanding* which addresses a compelling topic for the idea that humans evolved the context of communal child care, where more than one father claims responsibility for the same child. Hrdy believes this arose as a result of extreme violence among rival tribes where many children lost their biological fathers so another male in the tribe stepped up. In a case such as this, having a strong male protector could mean life or death.

Conclusion

It’s clear that although shifts are happening between men and women caretaker roles, predominately we still see this being true in the twenty-first century where the mother is predominately responsible for the critical stages of the infant development, where the father will go out to work. Fathers can still be a valuable asset to a child’s well-being, and when it comes to healthy upbringing, the more positive bonds, the better.

Cross-References

- [Extended Kin Role](#)
- [Family](#)
- [Familial Violence](#)
- [Maternal Role](#)
- [Paternal Investment](#)

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Paternal Uncertainty

- [Cuckoldry Risk](#)
- [Paternity Confusion](#)

Paternal-Offspring Conflict

- [Paternity Uncertainty and Father-Offspring Conflict](#)

Paternity Certainty

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Synonyms

[Cuckoldry](#); [Paternal care](#); [Paternal investment](#)

Definition

It is the certainty perceived by the male parent that he is the biological father of the offspring.

Introduction

In most species of birds, mammals, and in some fish, extensive biparental care is observed (Safari and Goymann 2018). The amount of parental investment varies considerably, with females typically investing more than males (Safari and Goymann 2018). Caring for offspring demands an investment of time and resources, which competes with future reproductive success (Trivers 1972). Thus, certainty of paternity is, for many species, key for paternal investment. Mechanisms which may have developed to address this issue include the formation of monogamous couples, the sexual control of females, and different degrees of parental investment.

Paternity Certainty and Paternal Care

In species with internal fertilization like mammals, mothers are always completely sure about her relationship with her offspring. However, fathers never have total certainty. Thus, paternal care is usually subordinated to degrees of paternity certainty (Geary 2016). The essential uncertainty in paternal lineage affects even the amount of investment given by grandparents. Some research suggests that human maternal grandmothers show more investment in grandchildren than paternal grandfathers (or even paternal grandmothers). While the first group does not have any uncertainty about kinship, the second group has two uncertain events of kinship. Such findings enforce the relationship between relative degree of certainty of paternal kinship and differentiation in care (Bishop et al. 2009).

In a review of data concerning this issue, Geary (2016) points out some tendencies: (a) when there is low paternity certainty, selection favors paternal abandonment; (b) when there is high paternity certainty, selection favors paternal investment if its enhance chances of survival of the offspring or if the costs are lower than the benefits; and (c) when both certainty of paternity and associated costs are high, selection favors a mixed strategy influenced by ecological conditions. Despite all these factors, paternal care is a rare feature in nature. It is most commonly related to monogamy, although it is

observed in only 59% of monogamic species (Lukas and Clutton-Brock 2013).

Some male behaviors concerning the control of the sexual behavior of the female can be viewed as strategies to increase paternity certainty. Such control includes use of coercive force and aggressions as a way to internalize submission towards the male; demands of reclusion and proofs of non-promiscuity from the female; and subordination of the degree of paternal investment to the degree certainty offered by the female (Smuts 1992, 1995). Some group strategies include the formation of monogamous families through marriage and moral control over women, as laws of behavior or patriarchal ideologies (Smuts 1992, 1995).

Strategies to identify and deal with paternity uncertainty vary widely among species. Some species of fish rely on the visual detection of cuckolders to modulate their paternal investment (Gray et al. 2007). Depending on a combination of factors that also includes low prey availability, low energy reserves, and mate availability, the male may cannibalize the current brood in order to restore the energy lost in that brood and be ready for a new fertilization (Gray et al. 2007). In humans, researchers have shown that the perceived father-child facial resemblance influences the disposition to paternal care but has no effect on maternal investment, suggesting that perceived facial resemblance should be one of mechanisms underlying the verification of certainty paternity (Yu et al. 2019).

In species of birds, the temporary escape of the nest by the female is taken as an indicator of paternity uncertainty concerning the eggs delivered after her return. However, in some species of socially monogamic passerine birds, extra-pair paternity is a common feature, and investment in non-kin brood is also common. Even with experimental manipulations of the degree of uncertainty of paternity, these males expend the same amount of investment in paternal care towards the offspring (Kempnaers et al. 1998).

Conclusion

Certainty of paternity is a framework that synthesizes a set of variables to describe the conflict

between paternal investment and future reproductive success and thus interferes with the amount of investment that males can devote to offspring. This framework is related to evolutionary mechanisms such as the sexual control of females, monogamy and social control that, as a whole, can increase the male fitness. Insights concerning the evolutionary importance of paternity certainty can shed light on some cultural phenomena such as child neglect and male reluctance to support biological children.

Cross-References

- ▶ [Cuckoldry Risk](#)
- ▶ [Parental Investment As Mating Effort](#)
- ▶ [Paternal Care](#)
- ▶ [Paternal Investment](#)
- ▶ [Paternity Uncertainty](#)
- ▶ [Paternity Uncertainty Hypothesis](#)
- ▶ [Sex Differences in Parenting and Parental Investment](#)

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Paternity Confusion

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Synonyms

Cuckoldry; Paternal uncertainty

Definition

The uncertainty faced by males related to whether or not an offspring is his own. An adaptive hurdle that puts males at risk of raising offspring that do not share his genes.

Introduction

Males and females differ when it comes to parental investment (Trivers 1972). Given that females pay high costs to create one offspring, they tend to be more selective as to which mates they choose and typically pursue long-term mating strategies. Males, on the other hand, do not have to pay the costs of gestation and childbirth, and the cost of producing one offspring is only the time spent impregnating a female. As a result, males tend to be less selective as to whom they mate with, often pursuing short-term mating strategies. When a male does decide to stay and invest on a child, however, he is voluntarily sacrificing time and

resources that could be otherwise spent searching for additional mating opportunities. By increasing parental investment, both males and females increase the likelihood that their offspring will survive into adulthood and further reproduce. If an offspring is illegitimate, however, a male may spend crucial time and resources on an offspring that does not share his genetic lineage. As a result, paternity certainty is of uttermost importance. Whereas an individual female can be entirely sure that a child is hers, an individual male has no such insurance. Thus, males have evolved a set of mechanisms to avoid such cuckoldry and prevent rearing offspring that are not truly kin. Alternatively, women and other relatives have also evolved mechanisms meant to ensure that the male will believe the child is his and thus help in the rearing. These mechanisms are described in the following section.

Biological and Behavioral Adaptations Related to Paternal Confusion

While there is no questioning whether or not a child belongs to its mother, fathers cannot always be certain that an offspring is their own. As a result of paternal uncertainty and low parental investment in males, both males and females have evolved different adaptations to these adaptive hurdles.

For instance, Gallup et al. (2003) suggested that the penis has evolved morphologically in such a way that it can scoop the semen of competing males out. Over time, the male phallus has evolved from being flat, as seen in chimpanzees, to having a prominent coronal ridge for this purpose. In relation to this idea, the researchers also observed that deeper and rougher thrusting has been related to potential infidelities in heterosexual couples, with males that suspect infidelities in their relationship thrusting deeper and more frequently. This further suggests that the shape of the human penis has evolved to prevent cuckoldry, as harsher thrusting would possibly displace more semen.

While the shape of the penis is a biological adaptation to prevent cuckoldry, there are also

additional behavioral adaptations that can be seen in males to protect against paternal uncertainty, such as mate guarding. Buss (2002) defines mate guarding as strategies used to preserve access to a mate while preventing access to that mate from rivals and preventing a mate from defecting in the relationship. Examples of this include keeping a mate away from potential competitors, engaging in behaviors such as public displays of affection, feelings of jealousy, and male proprietariness behavior, which entails a man laying a claim over a particular woman and thus advertising and exercising the intention of defending this “property” (Wilson and Daly 1992).

Paternal resemblance is often another factor involved with male behavior and cuckoldry. Burch and Gallup (2000) observed that males reported lower quality relationships with their children when their perceived paternal resemblance was low (i.e., when, according to the male, his child does not resemble him all that much). Among male domestic violence perpetrators, the severity of abuse was reported to be more severe among men who reported lower levels of paternal resemblance in their children. Additionally, males were more likely to share resources with children who looked the most like them. In response to paternal uncertainty, paternal assurance tactics have evolved as well, mostly so that females who have cuckolded a man can convince him that the child is his, thus guaranteeing the man provides resources and aids in child-rearing. Research by Daly and Wilson (1982) states that suggesting paternal resemblance when a child is born is a paternal assurance tactic. After the birth of a child, the mother and the mother’s relatives are typically more likely to report that the baby looks more like the father, as opposed to looking like the mother.

Conclusion

As a result of females becoming pregnant and giving birth, there is no question as to whether or not an offspring is hers. Males, on the other hand, have no such insurance. In order to avoid

cuckoldry, males have evolved biological and behavioral adaptations to avoid rearing kin that is not their own. In response to these adaptations, women have evolved paternal assurance tactics. Typically, other relatives on the woman's side also engage in these tactics to ensure that a male will help raise the woman's child. Additionally, research has shown that paternal uncertainty has been related to relationship quality with one's kin, resource sharing, and abuse.

Cross-References

- [Conception](#)
- [Evolution of Adaptations](#)
- [How Evolutionary Psychology Can Still Explain Behavior](#)

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Paternity Uncertainty

- [Adaptive Benefits of Matriliney and “Walking Marriages” in Mosuo Culture](#)
- [Father's Father Versus Mother's Mother](#)
- [Grandparenting](#)
- [Level of Grandparental Investment](#)

- [Male Sexual Jealousy to Deter Partner Infidelity](#)
- [Maternal Grandmother Invests Most](#)
- [Men's Suspicions of Partner Infidelity and Women's Defection](#)
- [Paternal Grandfather Invests Least](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)

Paternity Uncertainty and Father-Offspring Conflict

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Synonyms

[Genetic conflict](#); [Paternal insecurity](#); [Paternal-offspring conflict](#)

Definition

The following entry discusses the concept of paternity uncertainty and the subsequent effects that it exerts on behavior, particularly in terms of offspring investment and conflict.

Introduction

Generally, parental certainty (how confident that an offspring produce by a partner is genetically related) differs between females and males. In humans, a female is certain that a child she has carried is genetically related to her (maternal certainty). In contrast, males cannot know for sure that his sperm, and not the sperm of another male, fertilized his partner's egg (paternal uncertainty). Hence, a human female is *completely certain* that her offspring are genetically related to her whereas a human male is not. Paternity

uncertainty sets the stage for conflicts between females and males as well as between males and putative offspring (i.e., father-offspring conflict).

Paternity Uncertainty and Father-Offspring Conflict

Because a mother and her offspring are unquestionably genetically related, a mother stands to gain greater genetic fitness (i.e., passing on her genes to future generations) through parental efforts (e.g., caring for, feeding, spending time and money, etc.) than through mating efforts (e.g., seeking and finding extra mating opportunities). She can be confident that her offspring and any offspring produced through the matrilineal line carry her genes. Any parental investment that she provides promotes their and, through them, her reproductive success. In contrast, a male stands to gain greater genetic fitness through mating rather than through parenting efforts *particularly if he is uncertain he is the biological father*: Investing in genetically unrelated offspring adds little or nothing to a male's direct genetic fitness. For a male, greater mating efforts increase the likelihood that at least some offspring are genetically related to him. Hence, paternity uncertainty places a male in a dilemma: Continue parental efforts (to invest in offspring that may be genetically unrelated) or reduce parental efforts and increase mating efforts (to increase the probability of producing genetically related offspring). Trivers (1972) was the first to propose that males, each of whom face paternal uncertainty, reduce parental investment for putative offspring relative to females who enjoy maternal certainty. Interestingly, a body of research demonstrates that maternal grandparents (certain of genetic-relatedness to distal offspring) invest more highly both financially and emotionally in grandchildren than do paternal grandparents (uncertain about genetic-relatedness to distal offspring; Michalski and Shackelford 2005; Bishop et al. 2009). The same finding has been documented in aunts and uncles, with both showing a matrilineal bias in terms of investments made (McBurney et al. 2002).

The sex-based asymmetry in parental certainty contributes to a variety of conflicts between males and females and to conflicts between males and putative offspring (Trivers 1974). Specifically, a male may come in conflict with offspring as he and the child attempt to further their own genetic success. As said, a male who is uncertain that the offspring shares his genes stands more to gain genetically by reducing investment in the child and increasing investment in mating and reproduction. In contrast, a child who receives continued investment from the male (regardless of genetic-relatedness) benefits in terms of its own reproductive success. This sets the stage for *father-offspring conflict*, a phrase that refers to any investment the male makes in the child (e.g., care, protection, provisioning, etc.) that detracts from the male's ability to produce and invest in additional offspring while simultaneously facilitating the reproduction and survival of genetically related offspring. Put differently, paternal uncertainty contributes to a propensity for a male to *reduce parental investment* (reduce parenting efforts) whereas the reproductive success of offspring contributes to a propensity for an offspring to *maximize parental investment* (induce increased parenting efforts) from the male.

There are strong empirical relations between paternal uncertainty and father-offspring conflict. For example, males are particularly sensitive to paternal resemblances. Physical similarities between the male and the offspring predict paternal investment: Fathers invest more in offspring that share a physical resemblance to him relative to less physically similar offspring. In one study, depictions of participant faces were morphed into photographs of children. Answering a series of hypothetical questions, males reported that they were more likely to adopt, spend time with, and spend money on the face best matching their own facial features (Platek et al. 2002). Similarly, men who perceive their offspring as physically similar to themselves and who report greater perceived partner fidelity provide the greatest parental investment (Apicella and Marlowe 2004). The same patterns of paternal investment are found in a polygynous population in rural Africa. In this sample, both facial and odor similarities between the father and offspring predict the extent

of paternal investment. Moreover, the extent of paternal investment predicts childhood health; children receiving more paternal investment showed superior growth and nutritional status (Alvergne et al. 2009). Finally, paternal resemblance appears to be an important predictor of the likelihood of domestic violence: The greater the perceived physical discrepancy between the father and offspring, the greater the probability of violence in the family (Burch and Gallup 2000). Taken as a whole, a growing body of evidence points toward positive relations between paternal uncertainty and parental efforts, suggesting that males use, among others, cues of offspring resemblance as indicators of genetic-relatedness and parental certainty.

Conclusion

Females enjoy absolute certainty that offspring they deliver are genetically related; males always run a risk of those offspring being genetically unrelated. This asymmetry anchors diverging patterns of parental investment on the part of females and males. A female's fitness is more likely to be enhanced through parental investment in offspring that she delivers. In contrast, a male must decide whether to continue parenting efforts (investing in the offspring with the risk that he is not genetically related to the offspring) or switch to mating efforts (investing in efforts to mate and reproduce which increase his chances of producing his own genetically related offspring). Signals that offspring are genetically unrelated to the male (e.g., perceived fidelity of the female, differences in child/male physical characteristics) increase the likelihood that the male will reduce parental efforts and increase mating efforts. Given that it is in the offspring's best genetic interest to extract as much investment from the parenting male as possible, a foundation is laid for father-offspring conflict.

- [Direct Guarding](#)
- [Human Mate Poaching](#)
- [Infanticide](#)

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Paternity Uncertainty and Investment in Sons and Daughters

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Cross-References

- [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)

Synonyms

[Adoption](#); [Cuckoldry](#); [Evolution](#); [Parental investment](#); [Parenting](#); [Paternity uncertainty](#)

Definition

Paternity uncertainty is when a putative father is uncertain of whether he is unknowingly investing in a genetically unrelated offspring.

Introduction

Parenting is an important evolutionary behavior that is associated with high costs such as reduced mating opportunities and somatic health and maintenance (Trivers 1972). However, these high evolutionary costs are offset by the investments in offspring that help to increase chances of offspring survival and reproduction. Thus, the benefits of parenting from an evolutionary perspective are strongly tied to parents investing in biologically related children. This is generally not a concern for women as the physiology of human reproduction means that mothers always know whether an offspring is genetically related to her or not. However, fathers do face the problem of paternity uncertainty, in which they could be unknowingly investing in a child that is not biologically related to them (Geary 2006).

Paternal Investment and Paternity Uncertainty

In order to reduce paternity uncertainty, men are theorized to initially engage in mate-guarding behaviors, in which they may conceal their mates from other rivals and/or physically prevent their mates from being taken over by rivals (Haselton and Gangestad 2006). However, as the prevalence rates of paternity uncertainty in humans are shown to average at 1.9 % (Anderson 2006), fathers may have predispositions to detect false paternity.

As such, father-child facial resemblance and offspring sex may function as proxies to determine genetic relatedness and levels of investment, respectively. Determining genetic relationship through facial resemblance is theorized to be a mechanism used by ancestral and present day fathers (Geary 2006). Studies have found that

fathers invest more into offspring which have higher levels of facial resemblance to themselves (see ► “**Resemblance**” chapter). Fathers may also be investing more in sons, compared to daughters, so that their sons can attract desirable and loyal mates (Bishop et al. 2009) and consequently reduce chances of cuckoldry. This may help to maximize genetic fitness for both fathers and their sons. In support of this theory, studies have found that boys, compared to girls, receive higher levels of paternal investment across cultures (Marlowe 2005), suggesting that paternal uncertainty may not only be a concern for fathers but also for grandfathers.

Grandparental Investment and Paternal Uncertainty

Investment in kin is strongly associated with the certainty of genetic relationship, even across generations (Trivers 1972). In terms of genetic certainty, maternal grandmothers (MoMo) have the highest genetic certainty of their grandchildren compared to paternal grandfathers (FaFa), because MoMo’s can be certain that their daughters are genetically related to them and that their grandchildren are genetically related to their daughters. However, FaFa’s do not have the same levels of certainty as they and/or their sons could be raising offspring that are not genetically related to them (Bishop et al. 2009). As a result, studies have found that grandchildren receive higher levels of investment from grandmothers, such as more frequent contact and emotional closeness with their grandmothers, compared to grandfathers.

Adoption and Paternal Investment

How do these findings compare to adoptive father-child relationships? From a kin selection perspective, adoptive parents should provide the least investment in adopted children due to lack of biological relatedness (Hamilton et al. 2007). However, studies have found that adoptive parents display similar or even higher levels of

parental investment. Researchers propose several explanations for these findings. First, adoptive parents do not have to worry about the presence of a rival (the biological father) who may steal the mate (Hamilton et al. 2007). Second, adoptive parents may be highly and intrinsically motivated by a strong desire to care for children (Hamilton et al. 2007; Volk 2011). Third, adoptive parents may be engaging in “kinning” (Howell 2003), where the investment in an unrelated child is an attempt to socially construct kin relatedness (a socially, but not genetically, viable strategy). Fourth, investing in an adopted child may allow for future support from grown-up adopted children if one lacks such support from one’s biological children (Volk 2011). Fifth, since humans today no longer frequently live in close-knit communities as they previously did, the parental care seen in adoptive parents may be derivative of a general predisposition to care for other’s children as a form of reciprocal altruism (Hamilton et al. 2007). Sixth, adoptive parents may be triggered by proxies of genetic relatedness as adoption agencies try to match adopted child based on facial resemblance with adoptive parents (Herring 2003). This is possibly because the adopted child is quite often a substitute for the lack of a biological child and therefore social and emotional mechanisms are required to help scaffold the lack of actual genetic relatedness (see ► “Resemblance” chapter).

There is currently less research regarding whether adoptive fathers invest more in adopted sons compared to adopted daughters. However, given the findings that (a) biological fathers may be investing more in sons to increase inclusive fitness, (b) adoptive parents may be influenced by cues of facial resemblance, and (c) fathers’ perceptions of genetic relatedness may be more strongly influenced by social and emotional cues (Volk 2011), it can be suggested that the predisposition of increasing level of investment for sons may also be triggered in adoptive fathers when facial resemblance to the adopted son is high. Put differently, facial resemblance may moderate the association between level of investment and sex of adopted child for adoptive fathers.

Conclusion

Evolutionary theories have generally theorized that paternal investment may be largely driven by perceptions of paternity (un)certainty for fathers and grandfathers. However, it is interesting that even though paternity uncertainty is highest for adoptive fathers compared to “biological” fathers, adoptive fathers are shown to provide moderate to high levels of investment in their adopted children. This is essential to understanding overall parenting, as nongenetic motivations may also be driving parenting behaviors (Volk 2011). However, few studies have investigated parenting in adopted families (Hamilton et al. 2007; Volk 2011) and even less have analyzed paternal caregiving in adopted families. As human evolution and parenting are suggested to be influenced by adoption practices (Volk 2011), additional empirical studies of adoptive families from evolutionary perspectives are important to advancing the parenting field.

Cross-References

- [Adoption Preferences](#)
- [Consolidating Familial Power](#)
- [Evolutionary Paradox: Adoption](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Resemblance](#)

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Paternity Uncertainty Hypothesis

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Synonyms

“Cads and dads”; Cuckoldry; Parental investment; Paternal discrepancy; Paternity certainty

Definitions

Imperfect probability that fathers are investing resources in offspring that carry their own genetic material, as compared to complete female certainty.

Introduction

Paternity uncertainty hypothesis is a construct in behavioral ecology and evolutionary psychology, used to explain differential investment in

offspring between the sexes. The hypothesis states that due to the nature of internal fertilization, a male inseminator cannot be fully assured (consciously or otherwise) of the genetic identity of what are seemingly his offspring. This lack of certainty will further extend to resource and time investment differences between maternal and paternal familial lineages (Buss 2012).

Paternity Uncertainty

Behaviors related to mating and offspring investment should be governed ecologically: an organism will invest energy, time, and resources to promote its own viability and ultimately the continuation of its own genetics. The paternity uncertainty hypothesis states that while the female member of any mating pair can always be 100% assured that her offspring are her own, males enjoy no such guarantee. This is the result of the possibility that the female has been fertilized by one or more *other* males, resulting in paternal, but not maternal, uncertainty. Behavioral strategies to mitigate this uncertainty are not necessarily conscious in nature and should work to diminish the amount of resources accidentally committed to another male's offspring.

The behavioral ecology of mating suggests that each the male and female within a mating pair must consider (in a behavioral sense) the relative costs and benefits of extra-pair copulations. As females stand to gain advantages in genetic material, parental or protective behaviors from alternate males, and other potential favors, multiple mating partners may confer a net gain to them in some circumstances. Conversely, the possibility of female extra-pair copulation confers a potential net loss to the male within the mating pair, namely, the threat that he will unwittingly invest time and resources toward the genetic product of another male. To defend against this, protective behaviors such as mate guarding (Trivers 1972) and offspring identification techniques (Chang et al. 2010) should be seen in species that practice shared offspring investment mixed with promiscuity.

The paternity uncertainty hypothesis further predicts that discrepancies should be seen

between sexes in regard to parental investment, which is the amount of energy and resources devoted by each parent to their offspring (Buss 2012). This should help account not only for the greater investment in resources by mothers but also for discrepancies extending through matrilineal and patrilineal investment rates. As predicted, research indicates that aunts and uncles from the mother's genetic line bestow a greater investment on average than equally distant relatives from the father's family (Gaulin et al. 1997).

These differences in investment represent an extension of Hamilton's rule, which predicts that the degree of relatedness between individuals should correlate with the amount of energy and resources that in individual will grant without expecting reciprocation, outside of benefits to one's own genetic legacy. In the case of paternity uncertainty, the degree of offspring relatedness that any individual on the father's side can assume is slightly diminished. These effects seem to extend to differences in investment by both matrilineal and patrilineal grandparents, where the amount of investment from a maternal grandmother is greater than the maternal grandfather's, paternal grandmother's, and paternal grandfather's, in diminishing order (Bishop et al. 2009).

Differences in behavioral strategies between the mother and father are described in theory and research. Buss et al. (1992) looked at self-reported differences in the causes and levels of jealousy between males and females. Males tended to react more strongly to acts of physical infidelity by their partner, while females were more reactive to emotional betrayal. The authors suggest that this difference is due to males being more threatened by the prospects of raising another male's offspring, while females could lose resources for herself and her offspring as a result of emotional betrayal by the male (i.e., abandonment).

As a result of these risks, researchers have suggested various mechanisms that exist to help reassure the putative father of his paternal certainty. One strategy would be for newborns take on physical characteristics of the birthfather, in order to allay any suspicion of cuckoldry (Daly and Wilson 1982). Others suggest that it is in the interest of newborns to display a nondeterminant

patrilineal identity, so as to avoid rejection behaviors (or worse) from unconvinced fathers. In this model, morphological indices would be replaced by paternity-affirming statements made by relatives, which should help assuage any doubt in the putative father (Bressan 2002). Costs may be incurred by other behaviors as well. Robert Trivers suggests in his book *The Folly of Fools* (2011) that the costs of being temporarily cuckolded may be minor when compared to the personal and social costs resulting from jealous or vengeful behaviors.

Conclusions

Paternity uncertainty is a useful framework for understanding differences between the sexes regarding offspring investment and mating strategies. Other social and cultural influences affect behaviors within individuals; however, unconscious motivations regarding individuals' investment in their own genetic legacy should be reflected in sexual differences in species-specific behaviors.

Cross-References

- ▶ [Differential Parental Investment](#)
- ▶ [Grandparental Investment](#)
- ▶ [Hamilton's Rule](#)
- ▶ [Kin Selection](#)

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Pathogen Avoidance

► Disease Avoidance

Pathogen Defense

► Pathogen Protection

Pathogen Disgust and Perceptions of Attractiveness

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Synonyms

Behavioral immune system; Disgust sensitivity;
Immunocompetence; Pathogen prevalence

Definition

In humans, pathogen disgust is associated with an increased attraction to phenotypic markers of health and genetic fitness.

Introduction

Health and the ability to resist pathogen infection are key to maximizing survival and reproductive fitness, thus humans have evolved to be particularly attracted to phenotypic markers of good health in potential mates (Buss and Schmitt 1993; Rhodes et al. 2005). Some scholars have argued that under conditions of higher pathogen load (real or imagined), attraction to ostensibly healthy potential mates should be amplified and health-connoting characteristics should be preferred (Gangestad and Buss 1993). Mounting recent evidence in support of this increased preference for phenotypic markers of health and immunocompetence has been found at three separate levels of analysis: (1) individual differences in pathogen disgust, (2) temporary salience of pathogen threat, and (3) environmental variation in local ecological pathogen prevalence.

Health and Perceptions of Attractiveness

A wealth of past research points to a link between health and indices of sexual attractiveness. Some studies have found that subjective ratings of attractiveness are associated with judgements of apparent health (e.g., Jones et al. 2004), and other studies have noted a preferential attraction to phenotypic markers of health and immunocompetence such as averageness, symmetry, and gender dimorphism. For example, facial averageness (population-level prototypicality of the face) is associated with strong genetic defenses to pathogens (Thornhill and Gangestad 1993), and average faces (vs. distinctive faces) are consistently rated as relatively attractive (Langlois and Roggman 1990). Similarly, bilateral symmetry, which is associated with fewer in utero infections, and gender dimorphism (i.e., masculinity in men, femininity in women) which is associated with immunocompetence, are two features consistently found to be physically attractive as well (see Rhodes 2006; see also Nedelec and Beaver 2014). This work suggests that perceptions of attractiveness may be guided in part by

phenotypic markers of good health and pathogen resistance.

The behavioral immune system is a suite of psychological mechanisms (including disgust) thought to have evolved in humans to inhibit the spread of disease by steering individuals away from parasitic infection (Schaller and Park 2011). For example, pathogen threat can lead to prejudicial responses against people who possess morphological abnormalities (who may be more vulnerable to pathogen infection), such as the obese (Park et al. 2007). These same cognitive processes may also lead to *approach*-oriented responses toward those who possess qualities of good health and immunocompetence. By seeking out and mating with a healthy partner, individuals may enjoy the direct fitness benefits of reduced risk of pathogen infection, as well as indirect fitness benefits of passing on immunocompetent genes to resultant offspring (Gangestad et al. 2006). Put together, this past work implies that the behavioral immune system may be a driving force guiding preferences for attractive faces and phenotypic markers of health and immunocompetence. If this is the case, then the extent to which perceivers feel vulnerable to pathogen transmission is likely to moderate these attitudinal preferences.

Researchers have investigated whether perceptions of attractiveness are influenced by pathogen disgust and threat of infection and evidence has been gathered at three separate levels of analysis: (1) individual differences in pathogen disgust, (2) temporary salience of pathogen threat, and (3) environmental variation in pathogen prevalence. This evidence is discussed in turn below.

Individual Differences in Pathogen Disgust

The behavioral immune system is not activated with identical frequency and intensity in all individuals; therefore, people vary in their sensitivity to pathogen disgust as well as their perceived susceptibility to infection; this can affect their perceptions of attractiveness and attitudinal preferences for ostensibly healthy individuals.

One prediction implied by this rationale then is that individuals who are more easily disgusted by

pathogens or chronically perceive themselves to be more vulnerable to parasitic infection should hold more negative attitudes against unattractive people. Indeed, correlational evidence suggests that those who are more chronically disgusted by pathogens (but not moral violations or sexual acts) tend to judge relatively unattractive faces as especially unattractive (Park et al. 2012) and those who are more susceptible to pathogen infection during childhood tend to exhibit an exaggerated preference for attractive opposite-sex faces as adults (de Barra et al. 2013).

In addition to an exaggerated preference for attractiveness more broadly, those who are dispositionally more sensitive to pathogen infection may also exhibit a heightened attraction to phenotypic markers of good health and immunocompetence. Indeed, perceived vulnerability to disease is associated with greater attraction to healthy-looking faces and an increased preference for symmetrical faces (Welling et al. 2007; Young et al. 2011). Similarly, trait-level sensitivity to pathogen disgust is positively associated with men's and women's preferences for gender dimorphism (DeBruine et al. 2010; Jones et al. 2013a, b) as well as preferences for lower waist-to-hip ratios and facial cues of lower weight (both indicative of good health; Singh and Singh 2006; Tinlin et al. 2013) in men rating women (Lee et al. 2015; Fisher et al. 2013).

Put together, research suggests that dispositional concerns about pathogens positively predict an exaggerated preference for attractive targets as well as a heightened attraction to health-connoting features more broadly.

Temporary Salience of Pathogen Threat

Perceptual cues indicating the presence of pathogens may temporarily trigger a heightened activation of the behavioral immune system and facilitate situation-specific behavioral avoidance or derogation of those perceived to possess phenotypic markers of poorer health and immunocompetence. Thus, the temporary salience of a parasitic threat or induced feelings of disgust may also affect preferences for attractive targets and phenotypic markers of good health and immunocompetence in ways similar to enduring

trait-level perceptions of pathogen load. Existing research largely supports this prediction.

Burgeoning experimental work suggests that a temporarily heightened concern about pathogens may lead individuals to prefer more attractive targets. Cantú (2013) experimentally manipulated the temporary salience of pathogens (e.g., by having participants read a narrative suggesting incidence of parasitic infection was on the rise vs. reading a pathogen-irrelevant narrative) and examined subsequent preferences for subjectively attractive potential mates. Two experiments revealed that women (but not men) in the “pathogen salience” condition exhibited a stronger preference for physically attractive potential mates. A third experiment revealed that women’s (but not men’s) temporarily heightened concerns about pathogens subsequently lead to faster approach-oriented muscle movements in response to highly physically attractive opposite-sex targets. The effect of temporary pathogen salience may also extend beyond mate preferences into other domains more broadly; for example, following a pathogen threat (vs. a no-threat and a predatory threat condition) individuals were more likely to express intentions to vote for physically attractive rather than relatively unattractive political candidates (White et al. 2013).

Temporary pathogen salience may also play a role in moderating preferences for phenotypic markers of good health and immunocompetence. For example, individuals primed with pathogen threat tend to exhibit preferential attraction to symmetrical and gender dimorphic faces (Young et al. 2011; Little et al. 2011). Other work focusing on women’s preferences has noted a similar pattern of results: The temporary salience of pathogen threat leads women to more strongly prefer masculine men and emphasize qualities indicative of “good genes” (including masculinity) in potential mates (Lee and Zietsch 2011; Watkins et al. 2012).

Put together, this experimental evidence furthers our understanding of how a heightened activation of the behavioral immune system affects perceptions of attractiveness and phenotypic markers of good health. Though these results suggest that temporarily heightened pathogen

concern leads to an exaggerated preference for attractiveness, it is important to note that some experimental investigations have failed to support this prediction (see Park et al. 2012), and more work is needed in this area before firm conclusions can be drawn. Still, when the threat of parasitic infection is salient, a growing body of work suggests that individuals tend to exhibit an exaggerated preference for attractive targets and perceive phenotypic markers of good health and immunocompetence as particularly attractive.

Environmental Variation in Pathogen Prevalence

Especially strong or especially frequent activation of the behavioral immune system among a population of individuals over time could eventually lead to population-level variability in related psychological tendencies and preferences (Schaller 2016). Thus, ecological variability in the actual prevalence of disease-causing pathogens may help to explain cross-cultural differences in perceptions of attractiveness. Specifically, in regions characterized by higher levels of pathogen prevalence, people inhabiting those regions may place a higher value on physical attractiveness or preferentially prefer phenotypic markers of good health and immunocompetence.

Gangestad and Buss (1993) analyzed data from thousands of participants in 29 countries worldwide and found a link between the importance placed on physical attractiveness (i.e., “good looks”) in potential mates and an index of parasite severity. Their results suggest that people in countries with a greater prevalence of pathogens value physical attractiveness in mates more than those in countries with lower pathogen prevalence. Recently this study was revisited, and, even when controlling for additional relevant variables (e.g., gender inequality), the same findings were noted (Gangestad et al. 2006). These results provide robust evidence that regional pathogen prevalence is positively associated with population-level emphasis on physical attractiveness in a mate. Regional variation in pathogen prevalence may also be associated with an exaggerated preference for attractive targets in domains irrelevant to mating as well. For example, during the 2010

US congressional elections, physically attractive political candidates enjoyed greater success in elections held in districts with relatively poorer health outcomes (White et al. 2013).

Regional variation in pathogen prevalence may also play a moderating role in individuals' preferential attraction to phenotypic markers of good health and immunocompetence. Much of this work has focused on women's masculinity preferences and found that women in regions characterized by higher parasite stress and poorer national health more strongly prefer masculine men (DeBruine et al. 2012; Penton-Voak et al. 2004; DeBruine et al. 2010).

Though more work is needed in this area, extant cross-cultural studies suggest that regional variations in pathogen prevalence may also moderate the importance individuals place on attractiveness, as well as phenotypic markers of good health and immunocompetence.

Conclusion

Preferential attraction to phenotypic markers of good health and parasitic resistance appear to be exaggerated under conditions of higher pathogen load (real or imagined). This effect has been noted in (a) individuals who are highly sensitive to pathogens, (b) situations when the threat of pathogen infection is temporarily salient, and (c) regions characterized by high pathogen prevalence and poorer health. Although evidence supporting the link between pathogen disgust and perceptions of attractiveness is becoming increasingly well documented, additional work is needed to further elucidate the intricacies of this relationship.

Cross-References

- ▶ [Disease Avoidance](#)
- ▶ [Disgust](#)
- ▶ [Facial Attractiveness](#)
- ▶ [Pathogen Load and Attractiveness](#)
- ▶ [Pathogen Resistance](#)
- ▶ [Pathogen Risk](#)

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Pathogen Load and Attractiveness

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Synonyms

Health cues; Immunocompetence handicap hypothesis; Sexual signalling

Definition

The influence of the amount of viruses, bacteria, and other pathogens present in the body on an individual's desirability as a mate.

Introduction

The dominant theory of attractiveness posits that attraction functions as a mechanism for identifying healthy, fertile, appropriate mates. By identifying such high-quality mates, individuals maximize the direct benefits (benefits that accrue

to the individual doing the choosing) and indirect benefits (benefits that accrue to the individual's offspring) available to them and their offspring (Trivers 1972). One such direct benefit is a reduced risk of infection with pathogens or parasites. While a number of studies have linked pathogen load (a measure of the amount of deleterious viruses, bacteria, parasites, and other pathogens in the body) to mate choice in non-human animals, evidence in support of this hypothesis in humans remains more indirect. Here, we define the pathogen load hypothesis, and briefly discuss the evidence.

Immunocompetence Handicap Hypothesis

The need to signal low pathogen load is thought to explain the evolution of extravagant sexual signals in a number of nonhuman species. In order to reliably signal mate quality, it is necessary for a signal to be costly so that it cannot be easily faked (costly signals would place too much of a burden on low-quality individuals). One way in which these ornaments are thought to inflict costs upon the bearer is by placing a burden on the immune system (Hamilton and Zuk 1982), thus ensuring that only individuals with good immunocompetence and low pathogen load can develop such ornaments and maintain good health. Individuals choosing to mate with individuals with more extravagant sexual ornaments may therefore be assured of a high-quality mate.

Male greenfinches with bigger, brighter, sexually selected carotenoid ornamentation show increased humoral immune responses to a novel antigen, more rapidly fight off viruses, and females prefer to mate with males with larger, brighter ornaments (Saks et al. 2003).

Increased pathogen load has also been shown to reduce costly behavioral sexual displays in nonhuman animals. Infection with greater numbers of nematode worms is associated with reduced frequency of courtship displays in male guppies, and females prefer to mate with males with fewer nematode worms (Kennedy et al. 1987).

Human Cues to Pathogen Load

While humans typically lack extravagant sexual ornaments, such as brightly colored feathers, there is evidence that human attractiveness may also partly depend on cues to pathogen load and immunocompetence. Individuals are able to identify sick people based on facial cues such as color of the skin and sclera, and swelling of the face (Axelsson et al. 2018), and on olfactory cues (Regenbogen et al. 2017), leading to avoidance behaviors (Regenbogen et al. 2017). Further, individuals with greater levels of pathogen disgust sensitivity show a stronger aversion to less attractive faces (Park et al. 2012), suggesting that facial attractiveness partly depends on cues to pathogen load.

Moreover, cues that may reflect better immunocompetence, such as facial and bodily symmetry in men and women, and more masculinized features in men (e.g., deeper voice), also seem to be associated with greater judgments of attractiveness (e.g., Feinberg et al. 2008).

There is also evidence that humans moderate their preferences for facial appearance in response to cues to pathogens, with observers showing increased preferences for symmetry and sexual dimorphism (cues thought to reflect immunocompetence and reduced pathogen load) following exposure to cues of high pathogen risk (Little et al. 2011).

Nonetheless, several studies of facial and bodily asymmetry have failed to demonstrate a relationship with health status measures, and even when such relationships are demonstrated, it is important to note that evidence for trait–health correlations now, may not reflect trait–health correlations in ancestral environments (Gangestad 2007).

Conclusion

In sum, pathogen load appears to play a role in mate choice and attractiveness in humans and nonhuman animals, though the precise mechanisms through which this operates are not known.

Cross-References

- ▶ [Costly Signaling Theory](#)
- ▶ [Disease Avoidance](#)
- ▶ [Disease Avoidance Hypothesis](#)
- ▶ [Facial Attractiveness](#)
- ▶ [Health Cues](#)
- ▶ [Mate Preferences](#)
- ▶ [Pathogen Disgust and Perceptions of Attractiveness](#)
- ▶ [The Handicap Principle](#)

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Pathogen Prevalence

- ▶ [Pathogen Disgust and Perceptions of Attractiveness](#)

Pathogen Protection

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Synonyms

[Immunologic protection](#); [Microbial defense](#);
[Pathogen defense](#); [Pathogen resistance](#)

Definition

The immunologic mechanisms that protect the human subject from microbial, viral, or other organism-derived antigen.

Introduction

In the field of immunology, the study of human pregnancy is perhaps one of the most perplexing topics. A tightly regulated and nuanced balancing act exists between the ability of the maternal host to accept specific foreign paternally derived alloantigens to allow fertilization and support ongoing pregnancy and her need to respond properly to pathogenic invaders, commensals, cell damage, and malignant transformation. The maternal immune system is repeatedly challenged with fetal/paternal alloantigens throughout the

reproductive process starting with exposure to semen, continuing through implantation and placenta-tion, and perhaps lasting several decades after delivery in the form of fetal microchimerism. Likewise, invasion of microorganisms or soluble microbial components into the gestational amniotic cavity can invoke a robust pro-inflammatory response in the fetal environment that can result in pregnancy loss, preterm birth, and neonatal organ damage such as necrotizing enterocolitis, bronchopulmonary dysplasia, retinopathy of prematurity, and cerebral palsy (Anders et al. 2017; Witkin et al. 2011). Inappropriate immune responses in the female regulatory and suppressive responses to both nonself antigens and pathogens could jeopardize the survival of the mother, the fetus, and ultimately the species.

Resistance and Tolerance: An Intricate Dance

Both complex and redundant mechanisms are essential to successfully promote acceptance of the fetal allograft and protect mother and child against pathogens and infection-related inflammation (Hyde and Schust 2016). Defined as the capacity to recognize and neutralize an invading organism, resistance is a means to *prevent* an adverse event. Conversely, tolerance is a mechanism that serves to *negate or minimize the consequences* of an event (Schneider and Ayres 2008).

The presence of circulating antipaternal antibodies in maternal sera at the time of fetal invasion into the maternal decidua was among the first pieces of evidence supporting the concept of maternal tolerance of the fetus (Hyde and Schust 2016). This was a shift from the historical perspective of maternal immune ignorance of paternally derived alloantigens that previously suggested the pregnant woman simply did not recognize the fetus as foreign and therefore did not mount an alloimmune response. In fact, both concepts are partially true, and the dominant response is almost certainly temporally dependent. The maternal immune system must undergo substantial deviations during pregnancy. This

involves mechanisms of at least local immune suppression but also periods of a predominately pro-inflammatory environment, including locally at the time of implantation and both locally and more systemically in the third trimester during preparation for labor (Dekel et al. 2014; Shynlova et al. 2013). To conclude that successful pregnancy is solely based on tolerance versus ignorance of paternal alloantigen or is characterized by an inflammatory versus immunosuppressed state would be an oversimplification. All likely play roles under the constraints of both time- and location-specific parameters.

The fetus must also balance the mechanisms of resistance and tolerance when faced with immunologic challenges. In utero, the fetus cultivates an ability to both recognize invading organisms and produce amplified immune responses to them. This must be balanced, however, by the evolutionary imperative to protect continued reproductive success. The fetal immune response must exhibit an essential capacity to generate tolerance mechanisms that downregulate the extent and duration of most pro-inflammatory states. This serves to both limit the extent of fetal damage and prevent early expulsion of the pregnancy from the uterine cavity whenever possible (Witkin et al. 2011). Some of the earliest evidence of fetal tolerance came from Billingham and colleagues in 1953 when they demonstrated that exposure to foreign antigens in fetal chicks and mice resulted in prolonged postnatal immune tolerance in offspring such that cells able to mount an immune response to these same antigens were absent after delivery.

Immune Structure and Interactions

The immune system is divided into a peripheral compartment, responsible for defense against blood-borne pathogens, and a mucosal compartment, responsible for defense against pathogens that access the body via mucosal surfaces. Not unlike other mucosal sites, the female genital tract acts as the initial barrier and assessor of all antigens, but it is also charged with the task of negatively discriminating against

pathogen-derived antigens while positively selecting tolerance toward seminal and fetal antigens (Hyde and Schust 2016). Strong hormonal control of the female genital tract aids in the tolerance of specific nonself antigens by affecting immunoglobulin transport, antigen presentation, cytokine levels, and distribution of immune cell populations. Estrogen, progesterone, and hCG have each been shown to promote immunologic changes that support maternal tolerance of fetally derived alloantigens, including the development of maternal T-helper 2 cell immune responses, the maintenance and expansion of maternal T regulatory cells, and the creation of anti-inflammatory cytokine environments, both locally and systemically (Hyde and Schust 2016).

Although far beyond the scope of this document, some of the most important immunologic mechanisms involved in fetal tolerance and pathogen protection are the unique immune cell types known to populate the female reproductive tract. In contrast to cells present in mucosae at other locations in the body, immune cells in the female reproductive tract are in contact with placental trophoblast cells singularly characterized by alterations in major histocompatibility complex (MHC) expression that allow prolonged and direct exposure of maternal immune cells to HLA-mismatched gestational tissues (Hyde and Schust 2016). Further, animal studies have demonstrated that there is a pregnancy-specific, local partial deletion of those maternal B cells that are directed against paternal antigens within the uterine decidua of the maternal-fetal interface. Significantly more antibody-producing cells can be found in the lower genital tract of the pregnant woman (endocervix > ectocervix > vagina) to maintain mucosal pathogen surveillance (Aït-Azzouzene et al. 1998). Decidual stromal cells are also immunologically unique and have recently been shown to respond to diverse bacterial and viral ligands that could cause placental inflammation (chorioamnionitis) and subsequent adverse outcomes such as preterm birth, neonatal sepsis, and cerebral palsy (Anders et al. 2017). In addition to their role in pathogen protection, decidual stromal cells are best known for their role in the immune acceptance of the allogeneic

fetus. They aid in the transformation of the uterine environment into a receptive implantation site, and they decrease the proliferation of certain natural killer (NK) cells and antigen-presenting cells that may stimulate attack of the implanting gestation. Other unusual immune cells specific to the female genital tract include decidual natural killer (NK) cells, decidual NKT cells (cells that exhibit characteristics of natural killer and T cells), decidual macrophages, T cell receptor (TCR) $\gamma\delta^+$ cells, and other less numerous innate lymphoid cells (Hyde and Schust 2016). Decidual NK cells differ from their peripheral counterparts in their cell surface receptor expression and in their poor killing activities. Unlike their peripheral and tissue-resident counterparts, decidual macrophages have cytokine secretory profiles that are skewed toward anti-inflammatory, M2-type activities.

Lastly, several contributions from the male partner have also been shown to be important for the success of fertilization and reproduction. One of these, termed “the leukocyte reaction,” is a semen-induced change in gene expression in the female reproductive tract that results in the presentation of pro-inflammatory antigens and recruitment and activation of immune cells necessary for fetal tolerance (Sharkey et al. 2012). Sperm lack major histocompatibility complex (MHC) class I and II molecules (transplantation alloantigens) on their surface. This allows them to avoid stimulation of specific histocompatibility-based adaptive responses in the female genital tract. Additionally, seminal fluid provides protection of sperm from reactive oxygen species that may be formed in response to an infectious agent (Hyde and Schust 2016).

The Fetal Role: An Active Player

Notably, it is now acknowledged that the fetus is an active participant in the immunologic interplay within the maternal reproductive tract, promoting tolerance of itself while simultaneously maintaining protection from microbial intruders. In early pregnancy, the main focus of the fetus is to promote tolerance. However, as the fetus nears delivery, an essential change from fetal

protolerogenic responses to pathogen-defensive, adult-type immune responses must take place so that the newborn is equipped to respond to outside invaders. This novel model of the fetal immune response across pregnancy has been called the layered immune system hypothesis (Burt 2013).

For example, although fetal immune cells can discern foreign pathogens, during the majority of pregnancy, there is a tendency for fetal T cells to differentiate toward T regulatory cells that promote a protolerogenic environment (Witkin et al. 2011). Further, a fetus challenged by pathogenic intruders appears to have an enhanced capacity to tolerate some level of local infectious stimuli, which diminishes its exposure to toxic immune by-products that would accompany microbe elimination and lessens the likelihood of premature delivery due to overly robust immune activation. One such mechanism involves the triggering of certain Toll-like receptor (TLR)-initiated pathways that promote the accumulation of specific lipopolysaccharide (LPS) – binding proteins and antimicrobial peptides (Witkin et al. 2011).

Later in gestation as the fetus matures and approaches delivery, its immune cells undergo transition to phenotypes more typical of adults, including the development of fetal memory T cells (Burt 2013; Zhivake and Lo-Man 2017). It is postulated that in this “layered immune system,” the *fetal tolerogenic* T cells are derived from *fetal* hematopoietic progenitor stem cells (HPSCs) and comprise the majority of the fetal immune system until late in the third trimester. At this point, fetal immune responses transition toward one dominated by *adult immunogenic* T cells derived from *adult* HPSC. This transition allows the fetus, and soon to be newborn, to have an adequate protective immune response to a wide variety of extra-uterine pathogens (Burt 2013).

Conclusions

The ability to fully understand and elucidate the immunologic nuances at the human maternal-fetal interface is hindered by the time- and location-specific nature of these interactions. Furthermore, many studies rely on evidence derived from

animal models due to logistical and ethical confines on human studies that are non-negotiable. Differences found in the human placenta, such as the high degree of placental invasion when compared to other species, limit the information that can be ascertained by even the most rigorous animal studies. The essential balance between pregnancy maintenance and pathogen protection involves numerous complex and overlapping immunologic mechanisms. It is only through a delicate interplay of alloantigen tolerance and maintenance of a robust ability to resist pathogen invasion that the human species is able to propagate into the future.

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Pathogen Resistance

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Synonyms

Microbial resistance

Definition

It is the resistance developed by the pathogen to survive in adverse host environment.

Introduction

Pathogens are microscopic organisms which can cause infectious diseases in other species. Pathogens that can cause human diseases are bacteria, viruses, fungi, and parasites (Janeway et al. 2001). There occurs continuous interaction of pathogens with their hosts in a given environment. As the host develops immunity to the pathogen (which is essential for host survival), the pathogen also parallelly develops resistance to overpower the host defenses. Evidences support that with the advent of chemical agents, intended to kill the pathogens and protect the host, there occurs emergence of resistant strains of pathogens (Narayanasamy 2008).

Pathogen Resistance: Evolutionary Perspectives

In the process of evolution, pathogens acquire features, which make them fit for their

environment. A survival need of any organism, is to remain fit in the adverse environment. Pathogens, for example, may develop mechanisms, to evade the immune system of the host and to resist the adverse effects of drugs in their vicinity. Thus, development of resistance gives an evolutionary advantage to the pathogens.

Evolutionary potential of pathogens may vary. Pathogens having high evolutionary potential are capable of overcoming genetic resistance quickly. They have higher mutation rates and have mixed reproductive system. Pathogens with low evolutionary potential have difficulty in overcoming genetic resistance. They have lower mutation rate and strict asexual reproduction (McDonald and Linde 2002).

In the environment, the pathogen and host evolve concurrently. The host also develops resistance to counter the spread of infection and tolerance to limit the after effects of infection (Roy and Kirchner 2000). Both the phenomenon of resistance and tolerance can propagate through genetic mechanisms.

Evasion of Host Immunity by Pathogens

Microbes have developed mechanisms to avoid or resist the action of host immune system. Some bacteria develop capsule (e.g., pneumococcus) which prevents adhesion to leukocytes, and some may produce exotoxins (e.g., diphtheria toxin) which are harmful for the leukocytes. Other examples include M-protein of *Streptococcus pyogenes* which reduces the complement activity. Certain bacteria (*Mycobacterium*) and fungi (*Histoplasma capsulatum*) survive intracellularly in macrophages, thus avoiding the humoral immune system (Delves et al. 2006). Fungi can inhibit intracellular killing by blocking intracellular respiratory burst. This is done by producing catalase, mannitol, and melanin. Fungal proteases can prevent the destruction of conidia inside macrophages. Viruses avoid the immune system by changing their surface antigens. Budding virions can laterally invade surrounding cells without becoming exposed to antibodies. Viruses can interfere with almost step in antigen

processing by host immune system. *Trypanosoma cruzi* the parasite responsible for Chagas disease has developed a DAF (decay-accelerating factor)-like molecule which breaks the complement factor C3b. *Trypanosoma brucei* releases decoy proteins to hide itself from the immune system. In malaria caused by *Plasmodium falciparum*, erythrocyte membrane protein 1 (PfEMP1) expressed on cell membrane of infected RBC helps the parasite to clump RBCs and spread without getting much exposed to the immune system. Some parasites avoid being recognized by the immune system by molecular mimicry with host tissues (e.g., *Ascaris* antigens mimic human collagen). Schistosomes cover their surface with host proteins like RBC glycoprotein and immunoglobulin G (Delves et al. 2006).

Resistance Against Antimicrobial Drugs

With the introduction of antibiotics, it was initially believed that infectious diseases would no longer pose a problem. Bacteria have, however,

gradually developed mechanisms to counter the effect of antibiotics on themselves. Due to injudicious use of these so-called magic drugs, multiple drug-resistant strains of almost all known bacterial pathogens have developed. Infections caused by these strains are very difficult to treat and responsible for very high mortality. Gradually there occurred emergence of “super-resistant bugs,” and dealing with them has become the biggest challenge for present medical science. Superbugs are strains of microbes with an increased level of resistance or resistant to multiple antibiotics. Table 1 shows common mechanisms by which bacteria generally acquire resistance to antibiotics.

β-Lactam antibiotics include penicillin and related drugs; cephalosporins, monobactams, carbapenems, etc. are the most widely used group of antibiotics. β-Lactam antibiotics act by inhibition of bacterial cell wall synthesis. Bacteria developed resistance to these antibiotics by producing β-lactamase enzymes, which dissociate β-lactam ring of the drug. For example, penicillinase enzyme was able to make the earlier

Pathogen Resistance, Table 1 Mechanism of drug resistance of bacteria against different antimicrobial agents

Mechanism of resistance	Example of antimicrobial class	Specific mechanism	Example
Efflux of the drug	Macrolides (erythromycin, azithromycin)	Efflux pumps pump the drug out of cell	Streptococci, staphylococci
Decreased uptake of the drug	Quinolones (ciprofloxacin, levofloxacin)	Altered outer membrane	Gram negative bacteria
	Aminoglycosides (amikacin, gentamicin)	Altered porin channels	Gram negative bacteria
Altered target of drug	β-lactam antibiotics (penicillin, piperacillin, cefuroxime, imipenem)	Altered PBP due to chromosomal mutation	MRSA
	Quinolones	Mutation in subunits of target DNA gyrase	Gram negative and gram positive bacteria
	Glycopeptides (vancomycin)	Production of altered cell wall precursors	VRE, VRSA
	Aminoglycosides	Mutations in ribosomal binding sites	Enterococcus
Enzymatic degradation of the drug	β-lactam antibiotics	Destruction of β-lactam ring	<i>S.aureus</i> resistance to penicillin, ESBL produces among gram negative bacteria
Enzymatic modification	Aminoglycosides	Aminoglycoside modifying enzymes	Gram negative and gram positive bacteria

PBP penicillin binding protein, MRSA methicillin resistant *S. aureus*, VRE vancomycin resistant enterococci, VRSA vancomycin resistant *S. aureus*, ESBL extended spectrum β-lactamase

generation of penicillin ineffective. Penicillinase-resistant β -lactams (e.g., methicillin, oxacillin) were developed. These drugs act by inhibiting the cross-linking between the peptidoglycan chains of bacterial cell wall. They bind and competitively inhibit the transpeptidase enzyme (penicillin-binding protein (PBP)). Bacteria have developed resistance to these antibiotics too. They have altered the target to form PBP2a, in place of its normal counterpart. PBP2a is coded by *mecA* gene carried on a mobile genetic element (*SCCmec*) (Peacock and Paterson 2015) in *Staphylococcus aureus*. PBP2a have low affinity for β -lactam antibiotics, and thus cell wall synthesis proceeds without much problem for the bacteria. Another very important mechanism of antibiotic resistance is production of extended spectrum β -lactamases (e.g., ESBLs) which are a group of plasmid-mediated enzymes (Rawat and Nair 2010). ESBLs are resistant to extended-spectrum (second- and third-generation) cephalosporins which include cefotaxime, ceftriaxone, and ceftazidime and monobactams like aztreonam. Multidrug-resistant *Salmonella enterica* is resistant to chloramphenicol, ampicillin, and sulfamethoxazole. Extensively drug resistant (XDR) in *Salmonella enterica*, serovar Typhi has been reported to show plasmid-encoded resistance to fluoroquinolones and third-generation cephalosporins (Klemm et al. 2018).

Polymyxin antibiotics (polymyxin B and colistin) are last-resort antibiotics for multidrug-resistant gram-negative bacteria. Bacteria like *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, and *Acinetobacter baumannii* have already developed resistance to these antibiotics, by various mechanisms like lipopolysaccharide modifications, efflux pumps, and overexpression of the outer membrane protein (Olaitan et al. 2014).

Resistance in hospital settings – infections that occur after 48 h of hospitalization – is referred to as nosocomial infections. Multidrug-resistant bacterial strains like MRSA and ESBL producers are common in hospital settings because of more environmental pressure. Transmission of the genes of resistance to sensitive bacteria also occurs. Three different mechanisms of horizontal

gene transfer, namely, conjugation, transformation, and transduction, are mainly responsible for transmissible drug resistance.

Intrinsic resistance to specific antibiotics is shown by certain bacteria. Intrinsic resistance is natural and predictable in bacteria like- *Klebsiella* to ampicillin, anaerobes to aminoglycosides, and *Burkholderia* to polymyxin B (Tille 2016). Keeping a track of the intrinsic resistance profile of causative bacterial pathogen is important to avoid development of resistant strains of other bacteria in the vicinity. Deciding the antibiotics after performing antibiotic susceptibility test, proper dosage and complete course of drug in the correct patient can help us to curb the spread of drug resistance.

Resistance Genes from Food

Sub-therapeutic levels of antibiotics like penicillin and tetracycline – are being given, since the mid-1950s, to animals to increase feed to weight ratio. They were then called antimicrobial growth promotants. Other reasons for which antibiotics are used in animals include disease treatment and prevention. These antibiotics were also used in agriculture industry (Marshall and Levy 2011; Verraes et al. 2013). Food processing can also add resistant bacteria to the food chain, i.e., certain bacteria that are intentionally added during the processing of food. Microbes added to foods requiring fermentation (e.g., *Lactobacillus*, *Leuconostoc*), addition of probiotics (e.g., *Saccharomyces*), and biopreservation where microorganisms are added to extend the shelf life and bacteriophages are used to kill foodborne pathogens (like *Salmonella enteritidis*, *Campylobacter jejuni*) (Verraes et al. 2013).

Antibiotic resistance in *Mycobacteria* occurs by vertical gene transfer, i.e., transmission of mutated gene to progeny. Mechanism of action of rifampicin, which is one of the most effective drugs against *Mycobacterium tuberculosis*, is binding to the β -subunit of the RNA polymerase enzyme, inhibiting the elongation of messenger RNA. β -Subunit of the RNA polymerase enzyme is coded by *rpoB* gene whose mutations lead to

rifampicin-resistant strains (Palomino and Martin 2014). Isoniazid, another common drug used in tuberculosis, is a prodrug. It requires activation by the catalase/peroxidase enzyme encoded by *katG* gene. It inhibits the synthesis of mycolic acids through the NADH-dependent enoyl-acyl carrier protein (ACP) reductase, encoded by *inhA*. Resistance to isoniazid occurs due to mutations in *katG* and *inhA* genes among other genes. Multidrug-resistant isolates of *M. tuberculosis* are resistant to both these drugs. Many other mutations causing resistance to different first- and second-line antimycobacterial agents are known. Newer drugs like bedaquiline and delamanid have also started showing resistance mutations (Palomino and Martin 2014).

Antiviral drugs are increasingly prescribed to counter viral infection due to immunosuppressive treatment in patients of transplantation, graft-versus-host disease, etc. Also, in PLHA (patients living with HIV and AIDS), antiviral drugs are to be taken for prolonged period. Prolonged exposure to antiviral drugs with continuing viral replication, owing to immunosuppressive state, is the key factor in the development of antiviral drug resistance in these patients (Strasfeld and Chou

2010). A major concern is treatment failures due to development of antiretroviral drug resistance in PLHA patients. Structural modification caused in antiretroviral target molecules of HIV occurs due to genomic mutation. Reverse transcription process is error-prone, and thus there is increased rate of mutation in HIV virus, leading to increased chances of survival of the virus in the patient.

Most common fungal pathogens encountered in clinical settings are *Candida* and *Aspergillus* species. A wide spectrum of antifungal agents is currently available including triazoles, echinocandins, polyenes, and allylamines. The choice of suitable antifungal agents however remains limited due to the emergence of resistant fungal species. There can be more than one mechanism of resistance development against a group of drugs, as shown in Table 2 (Chakrabarti 2011; Cowen et al. 2015; Ghannoum and Rice 1999; Peman et al. 2009).

Biofilm production by various bacteria, mycobacteria, and fungi imparts capability of drug resistance to the microbial colony (Donlan 2001; Esteban and García-Coca 2018). Recently, it has been seen that human T-cell leukemia virus-1 (HTLV-1) gets embedded in

Pathogen Resistance, Table 2 Mechanisms of resistance to antifungal agents

Group of antifungal examples	Mechanism of action	Most important mechanisms of resistance
Polyenes Amphotericin B Nystatin	Bind to ergosterol in the plasma membrane causing formation of large aqueous pores that disrupt cell	Altered membrane ergosterol synthesis ERG3 gene defects
Triazoles Fluconazole Itraconazole Voriconazole	Inhibition of ergosterol biosynthesis	Activation of efflux pumps Decreased affinity to target site <i>ERG11</i> and <i>Cyp51A</i> genes Overexpression of <i>ERG11</i> gene in <i>Candida</i> and <i>Cyp51A</i> in <i>Aspergillus</i> Impaired drug penetration
Echinocandins Caspofungin Micafungin	Inhibition of biosynthesis of β -1,3-D-glucan which is a major structural component of the fungal cell wall	Point mutations in <i>FKS</i> genes of target enzyme β -1,3-D-glucan synthase
Allylamines Terbinafine	Inhibition of ergosterol biosynthesis	Not yet documented, (cross-resistance with fluconazole reported)
Flucytosine 5-fluorocytosine	Inhibition of pyrimidine metabolism and DNA synthesis	Alteration of enzymes- Cytosine permease coded by <i>FCy2</i> gene Cytosine deaminase coded by <i>FCy1</i> gene

carbohydrate-rich adhesive extracellular “cocoon” (similar to biofilms) that helps efficient and protective transfer of virus between cells (Thoulouze and Alcover 2011).

It is difficult to develop immunity to parasitic infections because of their enormous variation in size, complex life cycle, and multiple hosts in different stages of life cycle. Parasite-causing malaria, *Plasmodium falciparum* species mainly, has evolved to develop several mutations to counter the antimalarial drugs. Drug resistance mutations in *P. falciparum* include point mutation in *Pfprt* gene, *Pfmdr1* gene, *Pfmrp* gene, *Pfdhps* gene, *Pfdhfr* gene, etc. To curb drug resistance due to antimalarial monotherapy, artemisinin-based combination therapies (ACTs) were started. Recent reports of resistance to artemisinin due to polymorphism in Kelch13 protein from Southeast Asia have raised alarm against successful treatment of malaria (Antony and Parija 2016).

Conclusion

Development of resistance by the pathogens is crucial for their survival. During the process of evolution, the host defense system develops against pathogens, and simultaneously the pathogens develop resistance to antimicrobial agents and host immune system. Understanding pathogen resistance gives insight about the evolution of the pathogens.

Cross-References

► Pathogen Protection

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Pathogen Resistance Theory

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Pathogen Risk

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Synonyms

Behavioral immune system; Disease; Disgust; Germs; Immunity; Infection

Definition

Pathogen risk refers to the danger presented by microorganisms that cause disease.

Introduction

There is a clear evolutionary opportunity for a pathogenic or parasitic existence, living at the expense of nutrient-rich, warm, renewable hosts. These advantages are reflected by the number and variety of infectious organisms that are pathogenic to humans alone, with a comprehensive literature review identifying 1415 species (Taylor et al. 2001). These pathogens can be divided into five major taxonomic divisions: 15% are viruses (including prions), 38% bacteria (including rickettsia), 22% are fungi, 5% are protozoa, and 20% are helminths (Taylor et al. 2001). To further illustrate the appeal of a host environment, nonpathogenic bacteria (distinguished from pathogens by lack of host-damage) far outnumber human cells within our bodies (Rohmer et al. 2011). While nonpathogenic bacteria are tolerated by hosts, pathogenic organisms are exploitative and so have to overcome host defenses. These include specific evolved mechanisms, such as toxic compounds, which can function defensively or offensively by manipulating or destroying rival microbes and host immune defenses (Rohmer et al. 2011; Rudkin et al. 2017). However, many of these mechanisms cause damage to and risk killing the host. This means there is an evolutionary trade off that every pathogen must contend with; just as there is no advantage to be unable to colonize or to be killed by the host’s defenses, it is of no advantage to be so lethal that you kill the host before you have a chance to benefit from the environment, replicate, and spread to other hosts. How each species contends with this trade-off is different, for example, lethality and host damage matter less for bacteria that are able to survive longer outside the host, or after the host has died, or can transmit to new hosts rapidly (Rudkin et al. 2017).

Just as there are clear evolutionary advantages for pathogens to live at our expense, it is equally advantageous for animals to develop systems to defend against pathogens. Communicable diseases caused by pathogens present a significant risk to human health and life and, despite deaths caused by certain communicable diseases having lessened in the past 100 years (recently, for

example, death by diarrheal diseases decreased by one million between 2000 and 2016), they remained as 3 out of the top 10 global causes of deaths in 2016 (diarrhea, tuberculosis, and lower respiratory infections). To illustrate the scale of this risk: the deadliest communicable diseases – lower respiratory infections – caused three million deaths worldwide in 2016 (WHO 2018). Further to the risk from existing pathogenic microorganisms, there is an ever-present risk of newly emerging pathogens, as 335 new infectious diseases have been reported since 1940 (Fumagalli et al. 2011; Taylor et al. 2001). These emerging infections are almost always caused by an existing pathogen that adapts to a new host. For example, the HIV virus previously infected chimpanzees and Ebola was previously found in bats (Sironi et al. 2015). There is also an evolutionary asymmetry to consider; humans have both far longer life spans and smaller populations than pathogens, meaning we evolve at a slower rate (Sironi et al. 2015). So, humans are faced with the threat of a wide variety of fast-evolving pathogens which are able to emerge as new threats from different host species.

Physiological and Behavioral Immune Systems

We are thought to manage the risks presented by pathogens first with our internal, physiological, immune system and second with a psychological, behavioral defense system. First, our physiological immune system uses two branches of defense, the innate immune system and the adaptive immune system. These two branches are primarily differentiated by mode of activation; the quicker but more primitive innate immune system relies on predetermined pattern recognition of abnormal, foreign bodies whereas the slower but more flexible adaptive immune system requires prior exposure and thus relies on specific recognition and immunological memory (Rohmer et al. 2011). Both systems are required for an effective response; emerging or unfamiliar pathogens must be dealt with quickly using the innate immune system, which can expel or hold the

pathogen at bay until the adaptive immune system can develop a more sophisticated, tailored response.

The second system for reducing pathogen risk, based around psychological and behavioral defenses, offers the advantageous outcome of avoiding infection completely. Aside from the obvious risk that our immune system could be bested by invaders, fighting off infection is debilitating (even if just temporarily) and metabolically costly (Schaller 2011). Therefore, it is thought that humans also possess what is termed the *behavioral immune system*, which was coined to capture the apparent unified functioning of specific behaviors and cognition that work to reduce the risk of infection (Schaller 2011). It is proposed that this system responds to various environmental cues, such as unpleasant odors, that tend to co-occur with pathogens, and triggers the disgust emotion. This disgust reaction encourages either withdrawal, for example, through feelings such as nausea, or pathogen-removal behaviors, such as vomiting, washing, and spitting. This helps us avoid objects, animals, and even people that may pose an infection risk. However, just as the physiological immune system has costs (such as metabolic expense) as well as benefits, as does the behavioral immune system. The avoidant responses of the behavioral immune system can stand in the way of other fitness relevant goals, for example, by encouraging avoidance of social or mating opportunities because of the possibility they carry some infection risk (Schaller 2011). As such, the individual sensitivity of our behavioral immune system is another trade off which we must contend with.

Psychological Consequences of Pathogen Risk

Although all humans are at risk from pathogens, it seems likely that there is variability in the sensitivity of the behavioral immune system between individuals, both at a trait level and dependent on current pathogen risk. First, we can infer trait level differences in an individual's behavioral immune system from measures of

disgust sensitivity (which measures our natural predisposition to feel disgusted). These individual differences can have far reaching consequences for our behavior, for example, those who are highly disgust sensitive are more likely to be politically conservative (Inbar et al. 2009), differ in mate choice (Gangestad et al. 2006), and display harsher moral judgments (Chapman and Anderson 2014). This pattern of behavior suggests that those who are more disgust sensitive are more avoidant of those who are perceived to be potentially infectious or harmful.

An interesting example of how disease burden has influenced our psychology is differences in disgust sensitivity and ingroup bias. Interpersonal contact with unknown others would expose an individual to unencountered, dangerous, pathogens. As such, it is clear that there is a connection between ingroup bias and disgust, for example, participants were less disgusted by clothing worn by a member of their University (Reicher et al. 2016) and disgust sensitivity predicts dehumanization of arbitrary outgroup (Buckels and Trapnell 2013). This effect can also be seen temporarily in those who are at greater risk of infection, for example, women in their third trimester of pregnancy displayed elevated levels of ethnocentrism (Navarrete et al. 2007).

We can also use the example of ingroup bias to show that some cultural differences could be linked to differences in disease burden between cultures. Pathogen risk varies across cultures, both historically and in the present day. When controlling for demography, selection pressures imposed by variation in pathogenic load explain much genetic variation between populations and is thus argued to be the primary driver of local adaptation (Fumagalli et al. 2011). Aside from genetic variation, it has also been demonstrated that countries with a historically high disease burden are more likely to be collectivist (Fincher et al. 2008). The reason for this difference is hypothesized to be due to collectivist cultures having a stronger ingroup-outgroup differentiation which, as discussed above, would limit exposure to new pathogens (Jetten et al. 2006). In further support of this, it seems that individualistic cultures were subjected to a higher

number of infectious disease outbreaks between 1950 and 2008 than collectivist cultures (Morand and Walther 2018). So, it seems that historically high pathogen risk may influence the psychology of a culture as well as providing some protection from infection.

Conclusion

It is not surprising that pathogens wish to benefit from the human body as it is an attractive ecosystem which at any time is home to thousands of microbial species, most of which rarely (if ever) cause us illness. Access to the rich diversity of nutrients within animal tissues is worth competing for, and as such dedicated pathogens have developed mechanisms that aid them in colonizing and replicating within host bodies. This is no easy task as humans have both psychological and immune defenses which exist to avoid, destroy, or expel viruses and infected somatic host cells. This competition to invade and avoid invasion exerts selection pressures on both organisms. As such, pathogen risk has far-reaching consequences for the virulence of the pathogens themselves, human biology, and both individual and cultural psychology.

Cross-References

- Disease Avoidance
- Disease Avoidance Hypothesis
- Disgust
- Immune Response to Disgust and Disease Cues

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Pathogens

- [Antimicrobial Hypothesis, The](#)
 - [Disease Avoidance Hypothesis](#)
-

Pathological Jealousy

- [Jealousy: Psychiatric Diagnosis](#)
 - [Morbid Jealousy](#)
 - [Sex Differences in Morbid Jealousy](#)
-

Patriarchy

- [Origins of Patriarchy](#)
 - [Sexism](#)
-

Patriarchy and Feminist Perspectives

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Synonyms

[Feminist waves](#); [Male social dominance](#)

Definition

A system of gender-based hierarchy in which men hold primary power. Feminist perspectives are related to the feminist movement based on the social, political, and economic equality of the sexes.

Introduction

During human evolutionary history, as also nowadays, most societies operate on a hierarchical system of organization. Patriarchy is an example of a hierarchical social system in which power is held by men based on male dominance in social, legal, religious, economic, and political organization (Sultana 2010).

The emergence of dominance hierarchies is not an aspect restricted to the human species but widely observed in nature (Buss 2015). Nonetheless, the environmental contexts of ancestral humans were far more hostile than in modern society. Therefore, ancestral contexts would create adaptive problems that could be successfully solved with conducts that are currently socially disapproved, such as aggressiveness and violence. For example, the use of force was a successful way of gaining social dominance by solving a conflict of interests and establishing a hierarchy (Buss 2015).

Denise Cummins (1998) developed the Dominance Theory, which primarily addresses the evolved ability to create strategies to reason about social norms (e.g., permissions, prohibitions, and obligations). The ability to strategize over social norms would enhance the reproductive fitness of the individual and, therefore, privilege those individuals that aspire to dominant status. Children in early life can already discriminate what is socially accepted, what is forbidden, and what is an obligation; acting accordantly with these social norms would consequently enhance the status quo of the individual in the group (Cummins 1998). For example, a woman adapted to a patriarchal context would behave accordantly with the obligation of being a good wife and mother, as well as the clear comprehension that she has not the permission to achieve an economic and political position of power designated for men. Due to the established adequate behavior, that woman would be a high-quality partner, and, hence, be able to access resources necessary for survival by mating with men of high status in hierarchies.

Male Dominance and the Origins of Patriarchy

Men and women present different mating strategies, however, they need each other to reproduce. Hence, survival and reproductive success are intrinsically affected by interpersonal relationships between men and women (Buss 2015; Parker 2006).

The conflict between the sexes over sexual strategies is a central topic in human social relations, and, therefore, human social organization. Males and females present different reproductive interests, which causes a conflict. Due to this conflict, men often gain access to females by coercive sexual strategies, which leads to the men's control over women.

The fundamental limitation in achieving reproductive success is access to a mate (Mesnick 1997). This limitation impacts directly on male mating strategies, creating a sexual conflict motivated by the asymmetry of interests between a man and a woman (Buss 2015). Historically, males have gained control of important resources to survival, such as food, shelter, and protection. This control forced women to submit to male mating interests so they could have access to resources for themselves and their offspring (Buss 2015). While coercive strategies were used by males to maintain control over women, the submissive position also had fundamental functions on the course of evolutionary human history, establishing survival and reproductive advantages for both sexes (Buss 2015). Nonetheless, the inflexibility of this social configuration and the coercive male dominance assumed an oppressive organization, thus preventing most women from achieving social, economic, and politic power that was not seen as proper for females. For example, male control over resource was maintained in society by legacies that neglected women and privileged male heirs, e.g., a direct son or a husband to a man's daughter (Alston 2012; Cooper 1976; Michaelson and Goldschmidt 1971). This control represents a system of gender-based hierarchy, in which men hold primary power – the Patriarchy. Therefore, over the centuries, women were socially

disadvantaged and mostly needed a male partner to be able to achieve some social power.

Therefore, Patriarchy established female biological inferiority, as well as evolved psychological mechanisms that would maintain male dominance. For example, the human species demonstrates an unusual male control over female sexuality, establishing a socially appropriate behavior for women (Smuts 1995). This moral stigmatization by men of adequate behavior for the female sex and what woman can do created a based-gender hierarchical organization in human society.

Feminist Perspectives: Female Resistance as a Threat to Patriarchy

Feminism movement represents the battle for the social, political, and economic equality of the sexes in a patriarchal society. However, this movement, despite posing gender as a central issue, does not have one singular and uniform perspective, but a wide variety of feminist perspectives, which impacts on science and, specifically, on evolutionary research (Rosser 1997). For example, the appearance of the Liberal Feminism, a theoretical perspective initiated in the eighteenth century and based on the scientific comprehension that human behavior is highly individualist and needs to be researched with a positivist approach (Jaggar 1983).

Moreover, this theoretical perspective assumes that women are socially oppressed by male dominance and, therefore, are victims of gender discrimination in the different fields of society (Rosser 1997). For example, studies suggest that the impact of the asymmetrical opportunities for men and women in modern society depends on lower access to resources for women to education and work opportunity (Arráiz 2018). In addition, Rosser (1997) indicates that the scientific field is mostly dominated by men, which represents that data interpretations are shaped by a subjective male point of view, despite the neutrality intrinsic to the scientific method.

The liberal feminism perspective also states that the opportunity gap has been legitimized

by science on the basis of research focusing primarily on the male perspective on evolutionary research, as well as excluding female subjects in experimental research or even by data interpretations based on patriarchal standards (Rosser 1997). Despite the relevance of questions elaborated by the liberal feminists, this perspective is committed to a capitalist economic structure and thus neglecting aspects of women's oppression not discussed at the time (Waites 2018). Therefore, postulations of liberal feminism only began to highlight the barriers that prevent women from having the same opportunities as that of men, enhancing the chances of overcoming those barriers, as well as questioning the objectivity of the scientific method on the matter of gender biases (Rosser 1997).

In contrast to Liberal Feminism, a perspective embedded in capitalist principles, Socialist Feminism rouses from Marxist ideology (Rosser 1997). Against the idea that scientific knowledge should be approached by individualistic and positivistic methods, Socialist Feminism assumes that knowledge is socially constructed and that the economic system of production influences how research is made (Rosser 1997). The socialist feminist theory states that female oppression should be addressed through an intersectional perspective, considering gender and economic class as social categories that due to their interaction form different configurations of oppression for women (Misra 2018). Therefore, patriarchy and capitalism would represent the social, political, and economic systems of a social organization responsible for maintaining a context of oppression for women (Burrell and Flood 2019).

However, this theory comprehends men and women differently in a biological and a social perspective, which would be explained by different evolved behaviors and psychological mechanisms (Arráiz 2018). Therefore, the socialist feminist perspective proposes the enhancement of female participation in science since the female point of view could reach a closer interpretation of reality, providing a contrast to the knowledge produced by a male scientist (Rosser 1997).

While Socialist Feminism assumes class as an intersectional category with impact on women's

oppression, African-American Feminism identifies race as a fundamental aspect that influences the approach to knowledge by science (Rosser 1997). Maintaining the intersectional perspective and the rejection of the individualism and the positivist approach to science, African-American Feminism began to gain force in the feminist movement and in science.

In addition, once the scientific knowledge is assumed incapable of complete objectivity and neutrality, it would be influenced by the white male scientists' point of view, representing the prevailing interests of the dominant race, class, and gender (Rosser 1997). Therefore, this perspective proposes not only the enhanced participation of black and Latina women in the scientific field, but a whole new configuration on the science discourse and methodology, providing a more critical decolonial data interpretation (Kelly and Jackson 2019).

Another feminist perspective is Radical Feminism, similar to the socialist feminist perspective on the critique to the social, economic, and political organization. This perspective does not rely on identity-specific aspects (e.g., race or class), but in the strong ideology that patriarchy and capitalism are the fundamental reason for women oppression (Waites 2018). Specifically, it emphasizes the more hostile and violent aspects of male oppression toward women, in which are more visible the asymmetrical relations of power between the sexes (Finlayson 2016), such as prostitution, rape, and pornography (Waites 2018).

In modern society, a discourse that the feminist movement was contributing to emasculate men began to gain activists using arguments based on deterministic social sex roles. Within the feminist movement, the diversity of approaches brought the fragmentation of feminism in plural discourses, emphasizing different aspects of women's oppression and dividing women (Cree and Phillips 2019). The postmodern feminist perspective emerged as a response to the propatriarchy movement, focusing on the critique of essentialist aspects of female and male identity categories, and, hence, breaking with a deterministic social sex role for men and women (Cree and Phillips 2019). Therefore, rejecting a discourse on

behalf of women, and collaborating to a more inclusive and non-fragmentized feminism, in which all women share gender as an identity aspect, but not neglecting individual traits that increase or minimize oppression, such as economic class and race (Rosser 1997).

The Darwinian Feminism

Evolutionary theory has been used for decades to legitimize a perspective of female inferiority, and therefore, creating biological arguments that maintained the subordination of women through human history (Vandermassen 2008). Those oppressive arguments were based mainly on the study of similarity between human and other primates behaviors' topography. However, the same perceived behavior in different species does not necessarily indicate the same function and the same genetic origin (Tang-Martinez 1997).

Thus, the feminist movement was severely harmed by false scientific arguments that postulate the patriarchy as inevitable. Due to a biological explanation, the evolutionary perspective was used to justify a genetic basis for the male dominance over the political and economic leadership, as well as the inherent female ability to be a caretaker and stay at home (Sork 1997).

Over human history, feminism obtained more visibility in society and collaborated to provide a new lens to research in a more ethical and accurate, scientific way (Rosser 1997). However, some feminists became strong oppositionists of evolutionary research, and some still are since the dialogue between feminism and evolutionary science demands the comprehension of evolutionary concepts, as well as a robust knowledge of the feminist cause (Vandermassen 2008). Although there are still many barriers that prevent the open dialogue on this topic, Darwinian Feminism emerges as a possible bridge.

Evolutionary psychology aims to comprehend how psychological mechanisms were selected and how they influence human behavior, while feminism advocates equal rights between the sexes (Wilson et al. 1997). Therefore, the Darwinian Feminism is the product of the last few decades

of the work of feminist researchers, who are also evolutionary biologists and evolutionary psychologists (Vandermassen 2008).

Despite the effort of researchers from the Darwinian Feminism perspective, evolutionary psychology is still targeted as sexist. This occurs when evolutionary analyses provide only biological explanations for oppressive behaviors seen nowadays, e.g., rape and male coercive sexual strategies (Wilson et al. 1997). The misunderstanding, however, lies in the necessity to acknowledge not only a holistic feminist point of view, but also how evolution and natural selection occur and its impacts on interpersonal relationships between men and women. From this point onward, it is possible to comprehend that explanations from an evolutionary perspective do not intend to justify oppressive male behaviors; rather, it aims to promote researches to improve understanding about the process involved in those mechanisms to possible future interventions.

For example, Eagly and Wood (1999) are evolutionary psychologists that proposed an explanation for the origin of sex difference in human behavior. To do so, they used the theory that different social roles between men and women would provide environmental pressures to select different psychological mechanisms between the sexes. Considering that research has shown that the human brain is highly sensitive to environmental change, once natural selection favored individuals with flexible responsiveness to extremely variable conditions (Smuts 1995), the human behavior can easily be modified in the short term if the environmental pressures change. Leadership ability, for example, taken as a masculine ability for centuries and even legitimized by science as an evolved mechanism for the male, could be observed in women that are put into high-hierarchy positions (e.g., Chief Executive Officer of a company).

Conclusion

In sum, based on social dominance and coercive strategies, men have been privileged within a gender-based hierarchical system entitled

Patriarchy. Although this social system has shown an evolutionary function for both men and women, the divergence of interests between the sexes has built an oppressive social structure for women.

Female resistance to male dominance created the Feminist Movement, in which plural perspectives were elaborated and had shown impacts on society as well as on the evolutionary research field. Nevertheless, the human species is highly responsive to environmental changes and, therefore, extremely capable of adapting to new social systems that do not represent an oppressive structure for either women or men.

Cross-References

- [Evolutionary Biology and Feminism](#)
- [Evolution of Female Resistance](#)
- [Feminism](#)
- [Sexism](#)
- [Sexual Conflict Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)
- [Social Dominance and Sexual Access](#)
- [Status Hierarchies](#)

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Patriline

► Maternal-Fetal Conflict

Pattern of Biased Grandparental Investment

- Father's Father Versus Mother's Mother
- Maternal Grandmother Invests Most
- Paternal Grandfather Invests Least

Patterns of Helping Behavior

► Altruism Norms

Paul Vasey

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Definition

Paul L. Vasey is a Professor and Board of Governors Research Chair at the University of Lethbridge in Lethbridge, Alberta, Canada. He conducts cross-cultural and cross-species research on the proximate and ultimate underpinnings of non-conceptive sex in humans and non-human animals.

Synonyms

Cross-cultural comparisons; evolutionary paradox of male same-sex sexual attraction; Cross-species comparisons; Evolutionary psychology research

Introduction

Early Life and Educational Background

Paul L. Vasey was born in Toronto, Canada, on January 30, 1966. Vasey was awarded his B.A. (Honors) from the University of Alberta in 1989. In 1991, he received his M.A. from Simon Fraser University. In 1997, he received his Ph.D. from the Université de Montréal. Dr. Vasey conducted postdoctoral research at the Université de Montréal, Concordia University, and York University.

Research Interests

Japanese Macaque Research

From 1995 to 2015, Paul L. Vasey conducted research on the development and evolution of same-sex sexual behavior among female Japanese macaques (*Macaca fuscata*). During this time, he observed captive and free-ranging Japanese macaque groups in Arashiyama (near Kyoto), Jigokudani (in the Japanese Alps near Nagano), and Minoo (near Osaka). This work has contributed to a greater understanding of the development and evolution of same-sex sexual behavior while challenging several assumptions common to the animal behavior literature.

Vasey and his research group demonstrated that same-sex sexual activity among female Japanese macaques does not serve a sociosexual function (e.g., aiding in alliance formation, communicating hierarchical position, or soothing conflict) (reviewed in Vasey 2006). Based on this evidence, Vasey proposed that it was possible for same-sex sexual behavior to exist as an evolutionary by-product, which is neither adaptive nor maladaptive for the species. This evidence-based claim challenged the predominant idea in the animal behavior literature that same-sex mounting is used to facilitate social goals. Further, he showed that the majority of female mounters stimulate their genitals, suggesting that this behavior is indeed sexual (reviewed in Vasey and VanderLaan 2012).

Vasey's group provided evidence countering the notion that females only engage in same-sex

behavior in the absence of sexually available males. They showed that female Japanese macaques actively reject soliciting males in favor of sexual consortships with females (Leca, Gunst, Huffman and Vasey 2015). Vasey also showed that females will, at times, engage in intersexual competition with males for female partners (Vasey 1998). Additionally, he and his research group found that juvenile females sexually debut earlier with females than with males (Leca, Gunst and Vasey 2015). They suggested that this developmental difference occurs because adult females solicit proceptive juvenile females for sex, whereas adult males act aggressively toward them.

Further, female mounting-posture patterns are flexible and arbitrary because they are unconstrained by penile-vaginal insertion (Leca et al. 2014). Female Japanese macaque same-sex mount postures vary between populations (Leca et al. 2014). This cross-population variation in an arbitrary behavioral expression suggests that, in this species, female-female mounting behavior is partially influenced by social processes.

Cross-cultural Research

In addition to his macaque research, Paul L. Vasey has carried out long-term research on the development and evolution of androphilia (i.e., sexual attraction and arousal to adult males) among human males. Vasey and his research group have studied this phenomenon in Independent Samoa, Canada, the Zapotec Istmo of Oaxaca (Mexico), and Japan. Because heritable traits that reduce reproduction are expected to become extinct, the persistence of male androphilia has been characterized as one of the major outstanding evolutionary paradoxes of evolutionary psychology. Vasey and his research group have made several important contributions toward resolving the paradox of male androphilia.

Male androphilia tends to manifest in either the masculine form (e.g., cisgender gay men) or the feminine form (e.g., gender nonbinary males). Both forms may be present within the same culture but one tends to predominate. Vasey and his research group have demonstrated that numerous developmental and psychobiological correlates

are common to masculine and feminine androphilic males alike. Namely, compared to gynephilic males (i.e., males who are attracted to adult females), both forms have more of older brothers, larger family sizes, more androphilic male relatives, similar population prevalence rates, little or no offspring production, increased gender nonconformity in childhood and adulthood, and elevated traits of childhood separation anxiety (reviewed in Vasey and VanderLaan 2014). As such, it is likely that the feminine and masculine forms are different behavioral expressions of the same underlying biological disposition.

In an award-winning paper, Vasey's research group found that conditions thought to typify the ancestral human sociocultural environment were more prevalent in cultures in which feminine androphilic males predominate compared to cultures in which masculine androphilic males predominate (VanderLaan et al. 2013). This suggests that the feminine form of male androphilia is evolutionarily ancestral to the masculine form. Consequently, the outcome of evolutionary processes may be obscured when using more derived forms of male androphilia (e.g., the masculine form), which may reflect historically recent cultural influences. As such, feminine androphilic males likely represent better models for understanding the evolution of male androphilia.

Vasey's group has repeatedly shown that feminine androphilic males in Samoa, known locally as *fa'afafine*, are more avuncular (uncle-like) than Samoan women and gynephilic men (reviewed in Vasey and VanderLaan 2014). Further, *fa'afafine* engage in avuncular behaviors in the absence of social pressure to do so. In childhood, *fa'afafine*'s altruistic tendencies appear to manifest as heightened anxiety related to concern about the well-being of kin (reviewed in VanderLaan et al. 2016).

Work by Vasey's group also indicates that *fa'afafine*'s avuncular tendencies could potentially increase their indirect fitness (reviewed in Vasey and VanderLaan 2014). Additionally, Vasey's group demonstrated that their avuncular cognition exhibits adaptive design features (e.g., *fa'afafine* are specifically interested in nieces/nephews and not kids generally; they are more

likely to invest in their sister's offspring than their brother's offspring) (reviewed in Vasey and VanderLaan 2014). This work furnishes support for the kin selection hypothesis, which states that genes for male androphilia could be maintained in a population if enhancing one's indirect fitness offset the cost of not reproducing directly. Theoretically speaking, androphilic males could increase their indirect fitness by investing in kin and, in doing so, facilitate the survival and reproduction of kin.

However, Vasey's research group has found virtually no support for the kin selection hypothesis in Canada or Japan, where the masculine form of male androphilia predominates (reviewed in Vasey and VanderLaan 2014). Consequently, they have proposed that a disposition toward investing in kin is contingent on feminine expression. Thus, gender expression may be relevant to the maintenance of genes underlying male androphilia via kin selection processes.

Vasey's group has also amassed some support for the Sexually Antagonistic Gene Hypothesis (SAGH). The SAGH posits that genes associated with the development of androphilia result in decreased reproductive output in male carriers, but the same genes result in increased fecundity in female carriers. A basic premise of this hypothesis is that androphilic male's maternal-line female relatives should produce more offspring than those of gynephilic males. Vasey's group repeatedly demonstrated that the mothers and maternal grandmothers of *fa'afafine* exhibit elevated reproductive outputs compared to those of gynephilic males (reviewed in Semenyna et al. 2017). However, to date, Vasey's group has failed to demonstrate elevated reproduction among *fa'afafine*'s maternal aunts. Because androphilic and gynephilic males share genes with their maternal aunts but not their aunt's reproductive partners, elevated reproduction by aunts would provide the clearest support for this hypothesis.

This body of work may be interpreted to suggest that male androphilia arose as an evolutionary by-product of sexually antagonistic selection for genes that promote elevated fecundity in females. The ancestral, feminine form of male androphilia tends to predominate in cultures with

maximally inclusive kinship systems and social tolerance of androphilic males (VanderLaan et al. 2013). These social conditions may have encouraged greater kin investment by androphilic males. Thus, feminine androphilic males may be particularly likely to behave in a manner that could facilitate greater offspring production by their female relatives. This, in turn, would have serendipitous effects on the sexually antagonistic genes in question even though androphilic male's heightened avuncularity was not originally selected for this purpose.

Androphilic male's elevated avuncularity might have resulted in greater offspring production by their kin. If heightened kin investment did, indeed, produce an indirect fitness advantage, kin selection processes may have acted to further refine androphilic male's avuncular cognitions to optimally facilitate reproduction among kin who share genes by virtue of common descent. This suggestion is consistent with the findings that *fa'afafine's* avuncular cognition exhibits adaptive design features (reviewed in Vasey and VanderLaan 2014).

Conclusion

Dr. Paul Vasey's cross-species and cross-cultural research has contributed to the field of evolutionary psychology by addressing the evolutionary puzzle of non-conceptive sexual behavior. Dr. Vasey and his research group have shown that social factors can influence the expression of same-sex sexual attraction. Additionally, he and his research group have made considerable strides toward understanding how male same-sex sexual attraction is maintained in the population despite lowering individuals' reproductive output.

Cross-References

- [Comparative Evidence](#)
- [Cross-Cultural Studies](#)
- [Evolutionary Cultural Psychology](#)
- [Fa'afafine](#)
- [Female Reproductive Variance](#)

- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Human Sexuality](#)
- [Kin Selection](#)
- [Kin Selection Hypothesis](#)
- [Male Reproductive Variance](#)
- [Non-Western Homosexuality](#)
- [Personality, Gender, and Culture](#)
- [Reproductive Strategy](#)
- [Sexually Antagonistic Hypothesis](#)

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Pavlovian Conditioning

- ▶ [Classical Conditioning](#)
- ▶ [Conditioning and Association](#)

Pay Equity

- ▶ [Women's Personal Resources](#)

PD

- ▶ [Iterated Prisoner's Dilemma Model](#)

Peck Order

- ▶ [Dominance Hierarchy](#)

Pecking Order

- ▶ [Hierarchical Climbing](#)
- ▶ [History of Dominance Theory](#)

Pedigree

- ▶ [Birthrights and Bloodlines](#)

Peer Acceptance

- ▶ [Peer Relationships in Childhood](#)
- ▶ [Popular Children](#)

Peer Competition and Cooperation

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Synonyms

[Competition](#); [Cooperation](#); [Intragroup competition](#); [Intragroup cooperation](#)

Definition

Peer competition is a form of social interaction in which at least two organisms of a peer group strive to obtain a limited resource or achieve a certain goal. Peer cooperation is the social interaction between at least two organisms of a peer group in which at least one of them acts in a way that fosters the benefit of other group members, regardless of whether those actions are beneficial or not to the actor herself.

Introduction

The study of peer competition and cooperation is essential for providing a theoretical account of human nature and its distinctive cognitive and motivational psychology. Research in these areas also has important practical implications. An accurate understanding of peer competition and cooperation is crucial, for instance, for understanding the factors that drive human conflict, as well as for overcoming the challenges that require collaborative effort, such as building and maintaining a large-scale irrigation system for agricultural production.

Peer competition and peer cooperation can be intuitively seen as opposing phenomena. However, depending on multiple factors, they might be complementary. In a population divided into groups, for instance, members of each group may cooperate with their peers in order to compete

with neighboring groups. Alternatively, they may compete with their peers as a means of choosing the best cooperative partners and demonstrate that they are reliable cooperative partners. For instance, if subjects can choose with whom they wish to interact, this may create competition to be more generous or loyal than others.

Drawing upon the developmental and comparative psychology literature, this article discusses the biological and cultural factors influencing the psychology of peer competition and peer cooperation in humans. Data from comparative psychology are useful to address questions about cognition from a broad evolutionary perspective. Developmental evidence, in turn, provides crucial information about how cognitive capacities emerge during the organism's life span, which will help to better illuminate how developmental trajectories are shaped by evolutionary processes. A special emphasis will be given to cooperative behavior, which, arguably, encompasses the most distinctive cognitive traits of the human species. The article ends by examining one of the most promising avenues of research on the psychology of peer cooperation: the *shared intentionality hypothesis*.

Evolutionary and Psychological Perspectives of Peer Competition and Cooperation

Peer competition and peer cooperation each possess a psychological and an evolutionary dimension. As such, research can focus on either the psychological mechanisms of competition and cooperation or the evolutionary explanations for them. For example, testosterone levels mediate competitive behavior when social challenges need to be confronted, and may also promote prosocial behaviors when this behavior enhances social status – e.g., when punishing norm violators brings reputational benefits to the punisher. The mechanisms involved in testosterone production are shaped by evolutionary forces that often have cascading effects on other traits. It has been argued, for example, that selection for increased social tolerance in the Middle Pleistocene led to a

decrease in testosterone levels (or perhaps reduced androgen receptor densities), which resulted in changes in human craniofacial morphology. The evolutionary trajectory of the hominin lineage seems to be characterized by both an overall decrease in aggressive behavior and an increase in social tolerance (Gonzalez-Cabrera 2017).

Much of the literature on the evolutionary dynamics of competition and cooperation focuses on formal mathematical models that apply insights from game theory. Models that focus exclusively on the ultimate explanation of cooperation (i.e., the reason why cooperation evolved), however, do not explain much about the psychological capacities or the specific neural systems that implement those cooperative behaviors. This is because cooperative behaviors could be implemented by different sets of psychological processes and neural structures that are functionally equivalent. As a result, a diverse range of mechanisms could evolve by natural selection to serve the same biological function. Many brain structures can serve the same purpose, for instance, in the same way that multiple morphological structures, such as wings in insects and birds, were selected for flying. Conversely, attention to the proximate mechanisms of cooperation (i.e., those psychological and biological substrates that explain how the organism reacts in the way that it does) helps to constrain evolutionary explanations, narrowing down the specific path by which cooperation could have emerged in a species. Thus, considerations about the proximate mechanisms of competition and cooperation are crucial for building more detailed models of the evolution of social behavior in humans and non-human animals.

For the most part, this article will set aside formal discussions in game theory and evolutionary game theory in order to focus on competition and cooperation primarily as psychological phenomena. This requires drawing a conceptual distinction between the evolutionary and the psychological variants of these phenomena. From a purely evolutionary point of view, competition and cooperation can be understood in terms of the *fitness consequences* that a certain behavior

has. Competitive behaviors are those that provide a fitness benefit for the actor and which are selected for because of their beneficial effect on the actor; cooperative behaviors, in contrast, are those that provide a benefit to other individuals and which are selected for because of their beneficial effect on those individuals who receive the fitness benefit. However, an organism need not have a mind for either competition or cooperation in the evolutionary sense. Viral and bacterial pathogens, for instance, cooperate in this sense when they cause human respiratory diseases. Psychological competition and cooperation, in contrast, are understood in terms of the *intention of the actor*. While competitive behaviors are those with which individuals intend to gain something (e.g., by establishing physical superiority over others), cooperative behaviors are those performed by individuals acting with the intention to benefit others, regardless of whether they intend to benefit themselves.

The rest of the article is organized into three sections. The first section outlines the conceptual framework of peer competition, its developmental trajectory, cultural differences, and the effect of both biological and cultural factors on those differences. The second section examines the psychological literature on peer cooperation. For theoretical purposes, the large body of empirical research on peer cooperation will be divided into two main lines of research: one focused on the mechanisms for generating the benefit of cooperation, and another focused on the mechanisms for distributing it. Generating and distributing the benefit are the two problems that individuals need to solve in order to achieve and maintain cooperation. Particular attention will be paid, to how the psychological mechanisms that deal with those problems emerge during human development and how they arose in evolutionary time. The third section focuses on the recent surge of psychological research on shared intentionality. The study of shared intentional psychology has provided a new and fruitful research program for understanding the distinctive nature of human cooperation. Competing accounts concerning the evolution and influence of shared intentionality on human cooperation will be analyzed.

Peer Competition

Understanding the phenomenon of peer competition not only requires conceptual clarity about what “competition” means but also some appreciation of the nature of peers and peer groups. Broadly construed, peers are those members of one’s social group with whom one shares certain social features such as age, interests, education, and social status. Overall, peers are psychologically relevant because they are likely to influence each other’s beliefs, values, and behavior. Depending on our explanatory interests, some features of social groups such as age and biological sex might be especially important in defining peer groups, while others such as spatial proximity might not. In many competitive sports, for instance, the age and biological sex of players are relevant to determining group membership, while their spatial distribution across the field is not. Careful attention to these defining features of peer groups is important because they make some patterns of social influence more salient than others and peer groups may display different forms of organization and social dynamics. For example, different forms of interaction can be observed among children of different ages, and further patterns of interpersonal relationships can be discovered when biological sex is taken into consideration.

Derivatively, peer competition can be roughly understood as the social interaction between at least two organisms within a peer group for a limited resource. Although, at a very general level, all species engage in biological competition to survive and reproduce, peer competition in humans is characterized by a set of distinctive psychological mechanisms. One salient difference is that competition in our species is significantly influenced by culture via implicit and explicit social norms. The effect of culture on competitive behavior is, of course, a function of different biological factors that can be shaped by evolutionary forces. For example, while some adaptations for peer competition emerge with age and enculturation, some others allegedly depend on biological sex. Understood as the systematic study of the biological basis of all social behavior, early

sociobiology tended to overemphasize the role of biological factors and the importance of biological evolution in shaping human social behavior. However, subsequent advances in evolutionary psychology have become more conscious of this limitation by paying more attention to the role of culture and evolution-like processes of cultural change. To the extent that distinctive forms of human peer competition are largely determined by cultural factors, the emergence of these special forms of competitive behavior deserves further discussion.

Developmental Trajectory of Peer Competition

While the relative impact of culture in human competition increases with age, adaptations for early peer competition seem to be strongly canalized in development: the emergence of those adaptations appears relatively impervious to variations in the environment or genotype of the organism. For example, human newborns have to compete for parental resources with both older and even yet-to-be-born siblings, because parents might continue to invest in their older children or invest in a new offspring as soon as the mother resumes ovulation. Thus, infants and toddlers need to appeal to others by engaging caregivers emotionally and, later in life, by monitoring their tastes and intentions using specialized cognitive mechanisms to secure adult attention (Hrdy 2009; Tomasello and Gonzalez-Cabrera 2017).

These adaptations for early competition are likely the result of concurrent processes of social selection in which conspecifics compete for access to resources other than mates. With the evolution of cooperative breeding in *Homo erectus* around 2–1.8 million years ago, hominin mothers could have babies at more closely spaced birth intervals than other apes due to the help received from others. Cooperative breeding is a social system in which offspring receive care not only from their parents but also from other group members, often called “alloparents.” Thus, in a cooperative breeding system, mothers had to divide their care and attention to offspring more

than other apes and to delegate responsibility for their offspring’s care to alloparents. Children would then have had to compete more actively for care and attention, and they would have had to learn to deal with different adults more flexibly.

During early (1–6 years of age) and middle childhood (6–12 years of age), children are still engaged in a process of competition with siblings and peers for the care and attention of adults. Children often obtain attention from adults by making themselves useful to them in everyday activities. This is especially clear in natural-fertility populations in which people make no conscious effort to control fertility and, therefore, population growth depends primarily on physiological and ecological factors affecting fecundity. Children who are situated in these populations help their parents and caregivers in various ways, such as harvesting, fishing, collecting shellfish, and foraging for fruit (for a review, see Kramer 2010). In doing so, they contribute significantly to their own consumption and the economic output of the group.

Around age 6, children increasingly display what is known as “interference competition.” Interference competition occurs when an individual’s actions prevent another individual from achieving a goal. This is a special form of competition since it requires physical interference – individuals may also compete with one another by capturing resources faster than their competitors without the need for physical interference. Peer interference competition is a highly debated topic in the literature, and this is due, in particular, to gender and cross-cultural differences in the way it is expressed. For example, it is commonly assumed that males who actively attempt to prevent others from achieving their goals may gain a reproductive advantage. In contrast, empirical evidence suggests that females engage in interference competition primarily when resources are scarce and that they avoid direct interference competition to reduce the probability of incurring physical harm through retaliation. The supposed biological rationale behind these differences, as one would expect from early sociobiological models of social behavior, is that females bear greater responsibility than males for their

offspring’s survival. Hence, they must avoid physical harm, including interference competition that might lead to retaliation.

This view is supported by some cross-cultural studies that indicate that female aggression is primarily directed toward other women and that physical aggression is typically used by a female when her own life or her children’s lives are at risk. Since elimination of direct competitors through coalitional support reduces the probability of harmful retaliation when the coalition outnumbered the victim, it is thought that social exclusion is a more effective strategy among females than males. Evidence from some Western samples seems to indicate that this strategy is indeed more common among women (Benenson et al. 2013). However, gender-based differences in interference competition can be alternatively explained as a response to male-dominated environments as research on gender inequality in the workplace in industrialized Western societies seems to indicate. Further cross-cultural data is therefore required to settle this debate.

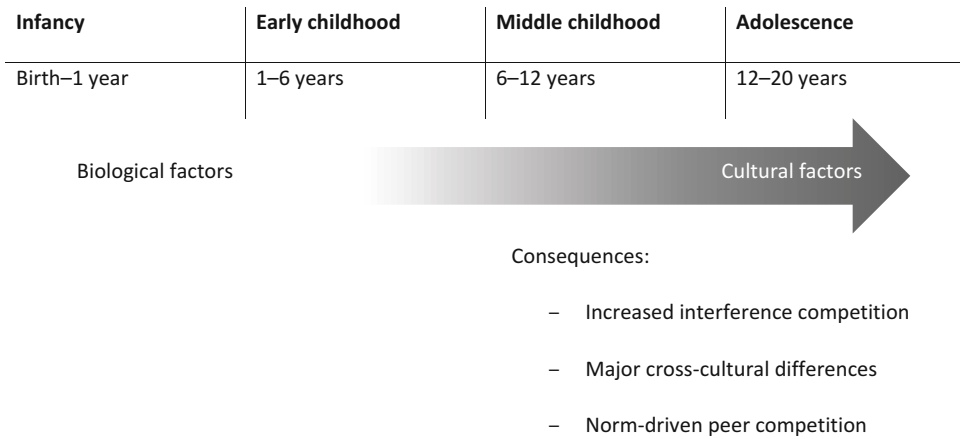
As children become more enculturated, role models and social norms begin to influence their competitive behavior (see Fig. 1). While there are few differences in children’s competitive behavior during early childhood, children from different cultural backgrounds begin to differ in their competitive behavior by middle childhood. For example, equal sharing is common among peers during

early childhood, especially when children collaborate to obtain a particular resource. However, as will be discussed in the section below, developmental trajectories for costly sharing diverge across cultures around middle childhood, in line with differences in the sociocultural niches that children experience (Callaghan and Corbit 2018).

Cross-Cultural Differences in Peer Competition

In general, the emergence of prosocial tendencies seems stable across developmental niches, when prosocial behavior is relatively low cost. Nonetheless, cross-cultural differences become salient under costly conditions in situations involving both helping and sharing (Blake et al. 2016). While disadvantageous inequity aversion (avoidance of receiving less than a peer) emerges by middle childhood across all populations studied, advantageous inequity aversion (avoidance of receiving more than a peer) has been shown to emerge only in some of the populations studied and only later in development. Overall, these results suggest that cross-cultural variation in adult norms of resource distribution shapes the acquisition of fairness behavior during childhood.

Adults influence children’s sharing behavior, but the nature and extent of this influence varies across populations. This variation might be



Peer Competition and Cooperation, Fig. 1 Consequences of cultural factors on peer competition through four developmental stages before adulthood

explained by differences in children's imitation of adult behavior in different cultural settings. Children in collectivist societies exhibit higher levels of imitation than children in individualist societies for instrumental tasks such as the retrieval of a prize from a puzzle box or a necklace-making activity (Clegg and Legare 2016). Collectivist societies typically emphasize obedience and conformity, especially children's obedience to authority figures such as parents and elders, whereas individualist societies emphasize children's autonomy and independence. Thus, it is thought that children in collectivist societies obey authority figures more than children in individualist societies, which results in increased imitation.

The influence of adults and cultural variation on competitive behavior often reduces potential conflict as interference competition becomes more common among children and adolescents. Cultural norms about the distribution of resources, for instance, shape social structures by regulating dominance hierarchies among peers. Dominance can be roughly understood as differential access to resources, territory, and relative power over others. Beginning in early childhood, implicit dominance hierarchies are established based on individual differences in physical prowess and social skills. But individual differences in dominance do not seem to significantly influence children's survival, as much of the necessary care and attention is already provided by parents and other adult caregivers. The importance of both dominance hierarchies and local cultural norms for the individual's fitness comes later in life.

Norm-Driven Peer Competition

As children progress into middle childhood, dominance is progressively determined by achievements in diverse cultural domains unique to humans, such as intellectual, musical, artistic, or athletic performance. Competition intensifies in adolescence as individuals begin to compete for reproductively attractive mates, which makes them increasingly aware of their place within the hierarchy. Most social interactions in children are regulated by models provided by adults or

straightforward norms that decrease the cost of competition among the young, facilitating them to compete for social status. This is in stark contrast with chimpanzees who, along with the bonobo, are one of the closest living relatives of humans. Juvenile male chimpanzees do not form a dominance hierarchy with their peers (Sandel et al. 2017). One possible explanation for this is that male chimpanzees begin to establish rank by dominating adult females, but adolescent males are often not physically prepared to face female retaliatory behaviors. This is also likely the case in bonobo populations in which there is no exclusive male dominance.

Social norms can regulate peer competition in a way that suppresses dominance hierarchies to a significant degree. This is evident in hunter-gatherer societies, which are consistently characterized as egalitarian, in the sense that political leadership is weak and ranking and stratification among adult males is relatively absent. Egalitarian behavior is found in a wide range of ecological settings, indicating that this feature of their social organization is the deliberate result of the group members' actions (Boehm et al. 1993). This egalitarian social structure, in particular, is considered a consequence of reverse dominance hierarchies in which leaders are dominated by subordinates who disapprove of hierarchical behavior. In this way, aggressive and competitive tendencies among humans are reoriented through cultural processes in a more prosocial direction.

These reverse dominance hierarchies are typically encoded in social norms that work as leveling mechanisms that prevent inequalities of wealth, power, and prestige. Among the !Kung, for instance, hunting success is known to be quite variable, but successful hunters are denied the opportunity to use their skills to build wealth and prestige. Rather than technical limitations, it is the value system of noncompetitive, egalitarian hunter-gatherers that seems to limit the development of agriculture. In these societies, sharing is imposed, and the accumulation of personal possessions such as clothing, tools, weapons, or bead ornaments is sanctioned. Hence, these rules restrict both the progressive accumulation of

wealth and the necessary investments that make agriculture possible.

Cross-cultural studies of behavior in experimental economics reveal that models based on self-interest often fail at predicting competitive behavior in small-scale societies (Henrich et al. 2005). Experimental economics uses experimental methods to study theoretical predictions of economic behavior. Research in this branch of economics has used a wide range of experimental paradigms including ultimatum, public goods, and dictator games to show that cultural, group-level differences such as degree of market integration (i.e., participation in wage labor and market exchange) and the relative importance of cooperation (i.e., the degree to which economic life depends on cooperation with non-immediate kin) significantly explain the level of prosociality expressed in these experimental games.

This cooperative behavior covaries with the costly punishment of noncooperative norm violators or, in other words, with the willingness of group members to pay the costs of punishing violators of prosocial group norms. Both evolutionary models and experimental research suggest that costly punishment is what allows norms of fairness and other prosocial behaviors to remain stable against invading defectors who behave in a selfish or antisocial manner. Yet, costly punishment is also able to stabilize arbitrary or even maladaptive norms within the group. These norms can spread in a population because, as the experimental evidence shows, children are able to imitate, for instance, the costly punishment of both equal and unequal offers in economic games from adult models, and the rates of imitation increase with age (Salali et al. 2015). That is, even when adults use costly punishment against those who make fair offers in experimental games, children imitate this behavior as if they were enforcing an antisocial norm of unfair behavior.

The above results illustrate how social norms not only curb competition as seen in societies with dominance hierarchies but can regulate competition in ways that favor increasingly hierarchical societies as well. Hierarchical organization is common in pre-state tribes headed by chiefs or “big men.” Social organization in large-scale

societies is also characterized by top-down power structures. Differences in social organization are fostered by variation in certain kinds of cultural practices and institutions. Storytelling, for instance, may help to broadcast social norms that coordinate prosocial behavior and promote cooperation (Smith et al. 2017). The so-called big gods and organized religion, in contrast, may foster the rise of increasingly stratified societies. Big gods are morally concerned deities who judge people’s behavior and exert supernatural punishment over norm transgressors. These moralizing gods are thought to play an important role in the emergence of complex societies by fostering prosocial behaviors such as cooperation and self-sacrifice (Norenzayan 2013). However, although there is a correlation between big gods and the rise of politically complex societies, the rise of big gods seems to have only played a causal role in maintaining and promoting social inequality (Watts et al. 2016).

In hierarchical social landscapes, individuals will compete intensely to climb the social ladder, which is not the case in societies with flatter social structures. If the social structure is hierarchical, individuals will try to optimize their position in the hierarchy based on an initial set of biological and culturally inherited conditions (such as education or inherited wealth) via individual within-group competition. This generates distinctive selective regimes that act on human populations. Egalitarian societies may have favored traits such as cooperation and low fertility, while inequality could have increased selection for within-group competition for social status, high fertility, and other selfish behaviors. Thus, individuals in the highest social classes within stratified societies may invest in cultural institutions that favor their own social status.

This investment in cultural institutions creates conditions for cultural group selection. Models of cultural selection extend the Darwinian account of evolution by natural selection in order to explain cultural change. Cultural group selection, in particular, accounts for the evolution of cultural traits as a function of the competitive advantage that these traits confer to social groups. Most evolutionary models assume that group-beneficial traits

are evolutionarily unstable. They are thought to be unstable because selfish individuals who do not collaborate with the group-beneficial traits can thrive within the group. But social interactions can result in multiple stable equilibria. This is because many different forms of social organization can become stable within a group if they are sufficiently supported by social norms and if there is concurrent punishment against norm violators (Boyd and Richerson 1992). Religious beliefs about big gods, for instance, are stable within the group because they are coupled with severe social sanctions and the threat of divine punishment, both of which deter free riding. Under these conditions, the costs and benefits of a specific behavior are transformed by the rewards and punishments that are associated with those social norms. With groups enforcing a variety of social norms that regulate within-group competition, selection can act upon different kinds of social behavior as well as the social norms that make them internally stable within the group.

On this view, an explanation of why stratified societies evolved could implicate group-level Darwinian processes. In other words, these societies evolved as a result of variation in norms that regulate within-group competition, as well as the selective advantage that more stratified societies obtain as a result of between-group competition. Simulation modeling suggests that stratified societies are more able to survive resource shortages in variable environments by secluding mortality in the lower classes and thus keeping the population low relative to carrying capacity (Rogers et al. 2011). In both variable and constant environmental conditions, the demographic instability that is generated by unequal access to resources also results in intense migration. This migration, in turn, drives the spread of such societies and the social norms that favor unequal resource distribution, even when population size is relatively small.

Moreover, since stratified agriculturalist societies were able to grow bigger by producing more food and resources, they were also more motivated, arguably, to expand and conquer neighboring territories, creating a strong incentive to invest in organized warfare. Evidence for warfare among prehistoric hunter-gatherers exists, but this

evidence becomes clearer in the archaeological record during the beginning of the agricultural revolution around 10,000 years ago, when humans transitioned from hunting and gathering to farming.

To sum up this section, the developmental trajectory of human peer cooperation is characterized by the increasing importance of culture. As children become more enculturated, cross-cultural differences in competitive behavior become more salient. These cultural differences owe primarily to social norms that regulate peer competition within the group – either by diminishing hierarchical social organization or by supporting it. The evolutionary stability of these norms depends on costly punishment, which can be transmitted early in childhood via imitation of adult models. As will be discussed in the next sections, social norms do not only regulate peer competition but depend on distinctive forms of peer cooperation for their existence. In the human lineage, the psychological mechanisms of peer competition and cooperation are highly intertwined.

Peer Cooperation

Norm-driven forms of peer competition are closely connected to human cooperative skills since they require norm compliance. The fact that people routinely comply with norms is genuinely puzzling since individuals frequently have selfish evolutionary interests in violating them. Certainly, norms can be enforced by costly forms of punishment. However, costly punishment is paradoxical precisely because it is an extreme form of cooperation that requires the agent to refrain from incentives to avoid carrying out punishment.

Peer cooperation can be roughly understood as a type of social interaction in which at least one individual acts with the intention to foster the benefit of other group members, regardless of whether those actions benefit the actors themselves. When individuals cooperate without regard to their own self-interest, their behavior is considered a case of *psychological altruism*. The form of costly punishment discussed in the previous section, for instance, is often considered

psychologically altruistic. However, not all cooperative behavior is altruistic in this sense. Mutualistic cooperation can be motivated by prudential reasons: an individual can cooperate with another because of the foreseen immediate or delayed returns of their cooperative behavior.

Understanding how cooperation evolves is not only a central issue in evolutionary biology but also in the psychological sciences. Various accounts of those cognitive abilities that are thought to be unique to humans often link the evolution of those features to the evolutionary history of cooperation in our lineage. From collective hunting to cooperative breeding, cooperation is a defining feature of human social life. For example, collaborative hunting, as observed among hunter-gatherers, seems to require the mastery of a set of special cooperative skills that go beyond those we see in our closest evolutionary relatives, the chimpanzee and the bonobo. This is because collaborative hunting relies on cognitive capacities such as role and task division, joint plans, and shared commitment, which are, arguably, uniquely human. To distinguish this psychologically rich form of cooperation from its less sophisticated counterparts, it will hereon be referred to as “collaboration.”

The Two Problems of Peer Cooperation

Explanations of the evolution of cooperation have primarily focused on what is sometimes called “the problem of distributing the benefit of cooperation”— namely, how cooperation can be maintained in the face of free riders that gradually undermine cooperative enterprises. This problem arises because cooperation requires groups to distribute the benefit of these ventures in ways that incentivize individuals to cooperate over time. But, as a rule of thumb, individuals have a strong incentive to free ride – i.e., to obtain the benefits of cooperation without paying the costs of generating it. As a result, free riding individuals become more successful than cooperators who bear the cost of cooperative activities, causing cooperation to progressively decline in the population. However, explaining the evolution of cooperation

demands not only an explanation of how the benefit is distributed but also of how it is *generated*. Successful cooperation sometimes requires skills for communication, division of labor, or task commitment that explain how the benefit is generated in a cooperative interaction. This problem is called “the problem of generating the benefit of cooperation” (Calcott 2008).

These two problems can be illustrated by a two-person “stag hunt” game, which involves a situation of social coordination. In this game, two hunters (or players) must decide simultaneously whether to hunt for stag or hare. Each player can successfully hunt a hare alone, which makes hare hunting the safer option. Hunting a stag, in contrast, requires cooperation from both players. If the two hunters agree to cooperate, they can successfully catch a stag, which is the preferred and more valuable game. If both players succeed in hunting a stag, the game is shared equally, as described in the payoff matrix in Table 1. This matrix defines, then, a solution to the problem of distributing the benefit of cooperative hunting: equal sharing. However, choosing to hunt a stag is risky since the other player may choose not to cooperate. If that is the case, the hunter who decides to go after the stag ends up empty-handed since the successful hunting of a stag requires both players. Thus, in order to generate the benefit of cooperative hunting, the two players need to coordinate their choices and to trust each other in their commitment to hunting a stag.

This distinction is psychologically relevant since mechanisms dealing with these two problems might be supported by two distinct sets of psychological mechanisms that are dissociated in

Peer Competition and Cooperation, Table 1 Payoff matrix of a generic two-person stag hunt game, where $a > b \geq c > d$. The payoff defined in the top-right corner cell describes a situation in which Player 1 decides to hunt a stag and Player 2 decides to hunt a hare. In this scenario, Player 1 obtains a payoff of c , and Player 2 obtains a payoff of b

		Player 1	
		Stag	Hare
Player 2	Stag	a, a	c, b
	Hare	b, c	d, d

both development (ontogeny) and evolution (phylogeny) (for a review, see Warneken 2018). On this view, while the capacity to *generate* the benefit of cooperation has evolutionary roots that we share, for the most part, with other great apes, there is little evidence that our ape relatives possess similar skills for *distributing* this benefit. This set of skills, furthermore, has a distinctive developmental onset. While many key skills for generating benefit through cooperation arise early in human development, the mechanisms responsible for distributing it in ways that protect cooperation against defection are acquired later, for they strongly depend on children’s acquisition of local social norms. For example, while basic capacities for helping, costly sharing, and collaborating arise relatively early during the first 2 years of age, mechanisms that help to distribute the benefit of cooperative activities – such as partner choice, partner fidelity, inequity aversion, and reputation management – begin to emerge at 3 years of age or later during middle childhood (see Table 2).

The Ontogeny of the Mechanisms for Generating and Distributing the Benefit of Peer Cooperation

There is significant evidence for the partial disassociation in ontogeny of the psychological

Peer Competition and Cooperation, Table 2 Time of onset of children’s skills for generating and distributing the benefit (see Warneken 2018)

Time of onset	Skills for generating the benefit	Skills for distributing the benefit
18 months	– Helping	
18 months	– Costly sharing	
14–18 months	– Collaborating	
21 months		– Partner choice
3 years		– Disadvantageous inequity aversion
3.5 years		– Partner fidelity
5 years		– Reputation management
7–8 years		– Advantageous inequity aversion

mechanisms responsible for generating and distributing the benefit of cooperation. Young children are not only able to identify cooperative partners but also seem to prefer them over uncooperative ones, as measured by their reaching behavior and preferential looking. By 2 years of age, children already possess context-sensitive expectations about equal resource distribution. At this age, for instance, children expect an experimenter to give a reward to each of two individuals who have worked together to complete a task, but not when only one of them has done all the work. It seems, however, that children’s evaluations are only able to regulate their social interactions in the cooperative direction later on in development. For example, 17- and 22-month-olds tend to help both antisocial and prosocial adult partners despite their preference for prosocial individuals, and 3-year-olds share indiscriminately in experimental tasks involving distribution of resources.

The best example of the delayed emergence of mechanisms for distributing the benefit of cooperation is children’s development of inequity aversion. Although children seem to expect an equal distribution of resources at a very young age, aversion to unexpected unequal distributions emerges significantly later. In fact, the two forms of inequity aversion discussed in the section on [Cross-Cultural Differences in Peer Competition](#) follow different developmental trajectories. While disadvantageous inequity aversion develops around 4 years, advantageous inequity aversion begins to emerge at around 8 years of age (McAuliffe et al. 2013).

The Phylogeny of the Mechanisms for Generating and Distributing the Benefit of Peer Cooperation

While chimpanzees and bonobos have basic capacities for generating the benefit of cooperation (such as skills for helping, sharing, and cooperating in mutualistic ways), they lack the distinctive machinery for solving the problem of distributing the benefit of cooperation. First, when a human or conspecific fails to retrieve an object that is out of reach, chimpanzees can engage in

instrumental helping and even select the correct tool from a set of options. Second, although only bonobos seem to be able to engage in active forms of food sharing, chimpanzees are also capable of sharing food with conspecifics in a passive way. They give food to others, for instance, when the food is difficult to monopolize or when they experience harassment from a beggar. Third, several studies with both species of African apes, chimpanzees and bonobos, indicate that they can cooperate with other conspecifics in a mutualistic fashion. For example, some studies have shown that chimpanzees will wait for a partner in a cooperative task, when the partner is necessary for solving the task and, therefore, for obtaining the food reward. They even actively solicit help from them or help them (e.g., by opening the door of the enclosure), so they can cooperate in the task.

Perhaps the most salient, but controversial, examples of the phylogenetic disassociation of the mechanisms for distributing the benefit between humans and other apes come from studies on partner choice and inequity aversion. While human children prefer helpers over mean partners, great apes prefer dominant individuals as these social relationships determine access to mating opportunities, food, and other resources. Even bonobos prefer individuals that hinder others over those that help. Yet, some researchers have argued that primates possess a sense of fairness. Their reason for doing so is that primates react aversely to experimenters when they see a conspecific receive better food than themselves (Brosnan and de Waal 2003). However, evidence for a sense of fairness in nonhuman animals have been somewhat difficult to replicate under more controlled conditions (Sheskin et al. 2014), leaving the phenomenon open to alternative explanations. A different account of these aversive reactions, for instance, is that seeing another individual receive high-quality food generates the expectation in the subject of receiving the same type of food. In fact, subsequent experiments in chimpanzees suggest that these reactions are better characterized as frustration for not getting the expected food, rather than aversive reactions based on a sense of fairness or some sort of social comparison with what conspecific partners obtain.

To summarize this section, explanations of peer cooperation require an account of how the benefit of cooperative ventures is distributed among group members, so that free riding does not undermine cooperation over time. Moreover, it needs an explanation of how the benefit of cooperation is generated. Psychological evidence indicates that humans possess specialized mechanisms for addressing these two problems. While basic capacities for generating the benefit of cooperation through helping, sharing, and collaborating arise relatively early in development, mechanisms for resolving the problem of distributing the benefit of cooperation – such as partner choice, partner fidelity, inequity aversion, and reputation management – only begin to emerge later during middle childhood.

Peer Cooperation and Shared Intentionality

Even though great apes and humans seem to share many of the skills required for generating the benefit of cooperation, there are still important differences in how humans and other apes address this problem. A significant body of research in developmental and comparative psychology shows that human cooperation is characterized by a set of unique skills that fall under the umbrella concept of shared intentionality. Shared intentionality is the capacity to coordinate social interactions through the sharing of mental states such as goals and beliefs. In the stag hunt game discussed in the previous section, for instance, both players could solve the problem of generating the benefit of cooperation by sharing their intention to create a committed partnership to hunt a stag.

Cooperative skills for shared intentionality seem to be in conflict with the idea that the mechanisms dealing with the two problems of peer cooperation explained in the previous section can be easily dissociated in both ontogeny and phylogeny. Indeed, skills of shared intentionality begin to emerge early in the context of child-adult interactions, but they continue to develop well into adulthood in the context of peer interactions.

One notable example is collaborative hunting in hunter-gatherers, which relies on joint goals and plans, task and role division, and shared commitment that begin to emerge during childhood. Moreover, skills of shared intentionality seem unique within the ape lineage, for comparative research has systematically shown that nonhuman great apes, with whom we share a common ancestor around 7 mya, systematically fail tests of shared intentionality (Call 2009). Thus, these skills are hypothesized to be adaptations for generating the benefit of cooperation that emerged, due to selective pressures unique to the hominin lineage, from an ape-like common ancestor who lacked these capacities.

Shared intentionality explains many of the features that make human cooperation different from great ape cooperation (Tomasello and Carpenter 2007). The *shared intentionality hypothesis* states that the distinctive nature of human cooperation is due to behavioral differences produced by the presence of these abilities in the human lineage. Different social and cooperative skills that were likely present in our ape ancestors seem to have been transformed by shared intentionality (see Table 3). First, great apes understand what other individuals see, but they simply follow another’s gaze to see if they are looking at something interesting, e.g., a piece of food. If they see nothing rewarding or valuable to them, they quickly stop looking. Human children are also able to see what others see, but they are also capable of sharing the attentional state in a way that involves mutual awareness that the experience is shared, as well as a shared interest in the object or event. From a

very young age, for instance, children are able to gaze at adults, point to an object, and then return their gaze back to the person with whom they are interacting. Children tend to focus their attention on objects and events that others are attending to because they seem to find it intrinsically rewarding to share those experiences with others. This facilitates the cooperative exchange of information. For example, children tend to show adults objects that are interesting to them and, in turn, follow an adult’s gaze to experience what is interesting for them. Adults can similarly bring objects in their surroundings to an infant’s attention solely by using eye gaze. This creates a psychological common ground that enables both cooperative communication and collaborative activities with joint goals.

Second, nonhuman apes use gestures and signals only to get what they want from one another, while young children also use gestural communication for cooperative purposes. Nine-month-old human infants often direct other people’s attention to objects through gestures aimed to initiate joint attentional interactions. Twelve-month-old infants use pointing to share interest and attention with adults as well as to inform others of things they might not have seen or know when there is no benefit for themselves (Liszkowski et al. 2006).

Third, while nonhuman great apes regularly engage in group activities such as hunting, these activities do not seem to involve individuals cooperating through shared goals to which they are all both committed and mutually aware of one another’s commitment. Group hunting may be cooperative, but not necessarily “collaborative” in the psychological sense specified at the beginning of the previous section. Experimental evidence suggests that 18- and 24-month-old children understand group activities around shared goals as involving commitment from all the parties involved. At this age, infants actively encourage an unresponsive adult to rejoin a game by communicating with them in various ways. In contrast, in the same experimental situation, chimpanzees never try to reengage their partners but rather focus on solving the task by themselves (Warneken et al. 2006).

Peer Competition and Cooperation, Table 3 Basic social and cooperative skills in great apes that are transformed by human-shared intentionality (see Tomasello and Carpenter 2007)

Individualistic (great apes: chimpanzees and bonobos)	Collaborative (humans: 1-year-olds and infants)
– Gaze following	– Shared attention
– Social manipulation	– Cooperative communication
– Group activity	– Collaboration
– Social learning	– Instructed learning

Fourth, while social learning in nonhuman great apes is mostly opportunistic (since individuals gather information from others unilaterally, copying only the actions that are relevant to achieve the desired result), human infants focus on causally irrelevant actions that they think are intentionally demonstrated by an adult. In other words, children *imitate* adult models in the sense that they learn the detailed actions that others perform (in a seemingly intentional way) to generate a certain outcome. If an adult demonstrator knocks a music box three times before making it work, children will tend to do the same, even if they know the action is instrumentally irrelevant for making the box play the music. Opportunistic learning in nonhuman apes, in contrast, biases learning toward the *emulation* of causally relevant actions. Moreover, as in the music box example, adults often demonstrate to children what they should do, which makes learning a cooperative activity. When adults provide communicative cues that they are demonstrating something (e.g., by saying “This is the way we do it” or “This is the way it works”), 14-month-old infants copy the specific actions adults use much more often than when they do not explicitly instruct. If adults do not provide those cues, young children tend to only copy the result the adult achieved (Gergely and Csibra 2006). Remarkably, older children around the age of 2 not only learn imitatively, but they also seem to understand group activities with peers as normatively grounded (Rakoczy and Schmidt 2013). For example, when they learn from a model that a certain activity is performed in a certain way, children enforce the conventional rules of the activity when others violate them.

The Cooperative Origins of Shared Intentionality

Traditionally, the evolutionary origins of shared intentionality have been linked to obligate cooperative foraging, especially collaborative hunting. According to the *interdependence hypothesis*, our early ancestors had none of the adaptations for vertical climbing, forelimb suspension, and knuckle-walking. This precluded them from

seeking protection by quickly climbing to the trees or engaging in the type of hunting that we sometimes see in chimpanzees. Given the local predatory fauna, foraging alone (seeds, tubers, or meat) would have been a very dangerous task. Foraging and scavenging in a group for safety then became necessary during the Middle Pleistocene around 780 kya. In order to face those challenges, hominins required new adaptations for collaborative foraging. When nonhuman great apes face situations in which they need to decide whether to forage alone or cooperate with others to obtain a food reward, they lack the skills of coordination and communication that facilitate the reliable coordination of action, especially in the context of risky coordination problems such as the aforementioned stag hunt game (see Table 1). Thus, on this view, hominin ancestors likely lacked these adaptations until the selective pressures for obligate cooperative foraging came into effect, creating the conditions for the gradual evolution of more planned and coordinated foraging in the human lineage.

One trouble with this traditional evolutionary account of shared intentionality is that it does not explain why many of these capacities emerge so early in ontogeny. According to an alternative account, the *cooperative breeding hypothesis*, the key selective pressures responsible for the development of shared intentionality were linked to cooperative breeding, which likely evolved in *H. erectus* around 1.9 mya. This new rearing environment allowed humans to wean infants relatively early and, in doing so, reduce the time periods between pregnancies. This situation, as explained earlier in the section on the [Developmental Trajectory of Peer Competition](#), increased competition between siblings and peers who must monitor the whereabouts and intentions of adults in order to secure their care and attention (Hrdy 2009).

Consistent with this scenario, it has been argued that cooperative breeding could have selected for skills of shared attention in infants. Shared attention is not simply *parallel* attention. Operationally, an infant is sharing attention with her caregiver when (i) the focus of the infant and caregiver’s attention is directed to the same object,

(ii) the infant is able to track the caregiver's focus of attention, and (iii) the infant engages caregivers just for the sake of sharing with them that attentional state. Unlike human infants, nonhuman great apes do not seem able to share attention or other experiences with members of their own species. Chimpanzees and bonobos are indeed able to meet a version of condition (i) by focusing their attention in parallel to the same object. They can even meet similar requirements to those stated in condition (ii) by tracking other individuals' attentional states in competitive contexts such as food seeking. However, since these species seem to be motivated to follow another's individual gaze only for instrumental and competitive purposes, they crucially fail to satisfy condition (iii). Thus, it has been claimed that cooperative breeding favored the emergence of shared attention in our lineage because gestures and eye contact would be crucial to direct adults' attention to objects, to events, and to themselves, just for the sake of sharing with them pleasurable experiences that foster attachment and care.

Similarly, basic forms of cooperative communication could have also been a consequence of the early emergence of these shared intentional skills, for they could have emerged prelinguistically in the form of pointing and pantomiming. Nonhuman great apes sometimes point for humans in an imperative way, e.g., when they want an out-of-reach object. In contrast, human infants across different cultures point declaratively from around their first birthday. At that crucial developmental stage, human infants become highly motivated to share their interest in different objects and events by offering, showing, and pointing declaratively to them.

Overall, all these uniquely human infant behaviors would have evolved in the context of sibling and peer competition. For in the context of cooperative breeding, infants compete with each other to provide adults with positive affective feedback in order to secure care and attention. As a result, they could have used these skills to reward adults by sharing emotions, interest, and attention with them. Shared intentionality would have begun as an ontogenetic adaptation, i.e., as part of a sequence of specialized changes that

enabled infants to survive the cooperative breeding environment created by their parents.

However, as it will be explained in the next section, it is also likely that these early mechanisms of shared attention and basic cooperative communication coevolved as mechanisms to facilitate social learning (and perhaps even teaching), when adult activities required skills that demanded prolonged periods of preparation and maturation. This view explains the developmental trajectory of human skills for peer cooperation as the result of selective pressures for both cooperative breeding and cooperative foraging. These selective pressures are thought to collapse into each other during middle childhood – a developmental period in which children's dependence extends from their parents and other caregivers to cooperative peers. Thus, although some capacities for shared intentionality emerge early in ontogeny, others appear relatively late to support the generation of benefits via peer cooperation.

The Role of Ontogeny in the Evolution of Human Peer Cooperation

Accounts of the evolution of human cooperation have started to pay increasing attention to theoretical work in evolutionary developmental biology or “evo-devo” for short. Evo-devo focuses on how developmental processes evolve. A key tenet of this research program is that many evolutionary processes result from changes in developmental timing. Building upon this program, a recent hypothesis about the role of ontogeny in the evolution of human cooperation considers the trade-offs that emerge during the different stages of human development in order to provide an evolutionary account of the ontogeny of human cooperative capacities (Tomasello and Gonzalez-Cabrera 2017). An advantage of this account is that it not only explains the *evolutionary emergence* of those traits but also their *distinctive developmental trajectory*.

The evo-devo hypothesis of the evolution of human cooperation integrates insights from both the interdependence hypothesis and the cooperative breeding hypothesis. As in the cooperative

breeding hypothesis, it maintains that shared intentional capacities were initially geared to dyadic interactions between infants and caregivers. As children grow older, the model similarly assumes that most of the attention of adults is redirected toward younger individuals, which makes engaging caregivers progressively more complex. Yet, as time progresses, children also become more physically capable of helping and collaborating. Learning how to make themselves useful to adults in their everyday activities would have been a possible way to gain such care and attention. This is a plausible assumption given how significant children's contribution is for the overall economy of extant natural-fertility populations. By the age of 5, for instance, Hadza children provide 50% of their own caloric intake. Among subsistence agriculturalists, Maya boys provide 50% of what they consume, while girls produce the same percentage by the age of 6, once subsistence work includes food processing and household tasks (see Kramer 2010). As a result, basic abilities for shared intentionality and collaboration in early human children could have subsequently extended into adjacent developmental periods. This is an expected result of the selective advantages these skills provide in adulthood, at the cost of little or no disruption in the overall cognitive development of the organism. For example, basic skills for shared attention, cooperative communication, helping, and collaboration would have presumably conferred a great selective advantage to hunting partners in a context in which cooperative foraging was necessary for subsistence.

Moreover, building upon the interdependence hypothesis, the evo-devo model of human cooperation assumes that selective pressures stemming from increased interdependence created demands for more complex adaptations for coordination, communication, and shared commitment. These adaptations progressively moved "upstream" into childhood as a preparation for adult activities, in the sense that they began to emerge earlier in development. Most of this preparation would have occurred during middle childhood as it is in this developmental period that children need to learn how to make decisions with others with little

or no adult supervision. They are typically low-risk decisions such as choosing those activities that interest them and match their level of competence. But these decisions must be fair and impartial as participation is voluntary rather than forced. Children must interiorize the social benefits of sharing resources with others and learn how to be reliable cooperative partners. Thus, the transition to middle childhood opened a window of opportunity to learn key cooperative skills in low-risk contexts where failure to cooperate was not lethal.

A prime example of this is children's early skills for reputation management and normatively grounded cooperation. Reputation management is the capacity to adjust one's behavior in order to be judged by others in a more positive light. Normatively grounded cooperation refers to one's capacity to understand cooperative activities as involving commitment and to enforce those commitments. These skills could have initially emerged in adult individuals as adaptations for cooperative foraging. Later in evolution, they could have begun to emerge progressively earlier in development. This is because longer periods of maturation for these skills would have given individuals an evolutionary advantage when collaborative foraging was necessary for human subsistence. The primary selective pressures would have proceeded mainly upstream from adulthood and adolescence to childhood, enhancing their sensitivity to shared commitment and to the reputational effects of their own cooperative behavior. Arguably, this capacity did not evolve in the context of child-adult interactions since these relationships are hierarchically structured and, therefore, much more sensitive to other factors such as authority and fear of punishment. In contrast, starting from adolescence, individuals must collaborate with others for basic subsistence. Individuals with enough time to develop complex skills of shared intentionality, such as a capacity to form shared commitments and enforce them normatively, would gain a selective advantage. Moreover, since the networks of allies and friends that children build during this period will endure into adulthood, investing in a progressively earlier onset of complex skills for peer collaboration would have made a nontrivial difference in their fitness.

Consistent with this hypothesis, human child development is longer when compared with any other great ape. It also includes the appearance of middle childhood as a developmental period between infancy and puberty that is distinct from the juvenile stage of other great apes (Thompson and Nelson 2011). Traces of this process can be observed in the increasing awareness of the child about their own social reputation and the norms that regulate their social environment. Unlike nonhuman great apes, human children seem to be concerned about others' evaluations of their cooperative and prosocial tendencies because they appear to adjust their behavior based on their prediction of how others will assess this behavior. Experimental results indicate that 5-year-old human children, but not chimpanzees, share more and steal less when they are being watched by a peer than when they are alone (Engelmann et al. 2012). Between 6 and 7 years of age, children begin to enact fairness norms against selfish individuals and exhibit a deeper understanding of the normativity of social rules as arising from social agreement and commitment (McAuliffe et al. 2017).

To conclude this section, a number of alternative hypotheses have been advanced to explain the evolution of human cooperative skills of shared intentionality. The *interdependence hypothesis* argues that cooperative skills of shared intentionality evolved due to the selective pressures of cooperative foraging in the hominin lineage, while the *cooperative breeding hypothesis* explains its emergence as a result of the selective demands of cooperative breeding. An alternative approach, grounded in theoretical insights from evolutionary developmental biology, explains the emergence of cooperative abilities for shared intentionality as a consequence of adaptive changes in developmental timing stemming from both selective pressures. Further research on the evolutionary basis of human cooperation should focus on refining and testing these alternative hypotheses.

Conclusion

Human peer competition is determined by several biological factors (e.g., age, gender, and

physiology) and cultural factors (e.g., social norms). The degree to which each of these factors drives human social behavior, however, is a matter of dispute. Arguably, the influence of cultural factors increases with age as children become increasingly aware of the customs, norms, and values of their groups. Peer competition starts early in development as children must strive for adult attention due to human rearing environments of cooperative breeding that are unique among other great apes. As time progresses, competition becomes increasingly regulated by norms that influence social behavior, including sharing and distributing resources. These norms likely explain cultural differences in peer competition. Some evolutionary models might, as illustrated by some accounts of the correlation between big gods and the rise of politically complex societies, overstate the role of social norms in thwarting within-group peer competition. However, social norms can also intensify resource and status competition by stabilizing hierarchical social organization through different forms of normatively driven punishment.

Competition and cooperation among peers are, as we have seen, interconnected phenomena. When human peers compete over resources, they often do so by cooperating with others. Similarly, norm-driven forms of peer competition are closely connected to human cooperation because they require norm compliance. From a theoretical point of view, cooperating with peers involves psychological mechanisms for generating and distributing the benefit of cooperative ventures. Extensive empirical research suggests that several psychological mechanisms that allow humans to deal with the problem of generating the benefit are shared with other nonhuman great apes. Mechanisms for distributing the benefit in humans are, in contrast, more distinctive: specifically, they are closely connected with norms that regulate within-group competition. Somewhat more controversially, some evolutionary-minded psychologists have recently argued that the distinctive trajectory of these two classes of mechanisms is evident in ontogeny as well as phylogeny. Controversy about this distinction in phylogeny comes mainly from the literature on fairness and

inequity aversion in nonhuman animals. The fact that capacities for shared intentionality are uniquely human, and that some of them, at least, begin to emerge relatively late in development, also provides grounds for skepticism concerning the notion of a distinctive ontogenetic and phylogenetic trajectory.

Humans are characterized by psychological mechanisms of shared intentionality that have helped to coordinate increasingly complex cooperative activities in the hominin lineage. In this sense, shared intentionality can be understood as a uniquely human capacity for generating the benefit of cooperation. Shared intentionality transforms several social skills that humans share with great apes such as chimpanzees and bonobos. Three basic accounts of the evolution of shared intentionality have been proposed in the literature: *the interdependence hypothesis*, *the cooperative breeding hypothesis*, and *the evo-devo hypothesis*. The first account explains the evolution of cooperative skills of shared intentionality as result of selection for collaborative foraging in adults. The second argues that these skills evolved due to the selective demands of cooperative breeding. The third approach explains the emergence of these abilities through a composite explanation: selective pressures for cooperative breeding in humans, in addition to changes in developmental timing in adult skills for collaborative foraging that required longer periods of maturation, jointly explain the evolution of cooperative skills. Evidence for this hypothesis can be found in the distinctive developmental pattern of middle childhood in humans. Choosing between these competing hypotheses, however, requires further investigation.

Cross-References

- [Competition Between Groups](#)
- [Competition for Resources Desired by Females](#)
- [Cooperation](#)
- [Cooperative Breeding](#)
- [Cooperative Foraging](#)
- [Dominance Hierarchies](#)
- [Evolution of Cooperation](#)

- [Fairness in Primates](#)
- [Female–Female Competition](#)
- [Fostering Values of Fairness](#)
- [Hunter-Gatherer Societies](#)
- [Male-Male Competition](#)
- [Peer Groups](#)
- [Peer Relationships in Childhood](#)
- [Primate Cooperation](#)
- [Resource Competition](#)
- [Social Hierarchies](#)
- [Status Competition](#)

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Peer Effect

► Peer Pressure

Peer Feedback and Norms

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Synonyms

Peer pressure

Definition

When members of one's social group respond positively and negatively to approved social behaviors and disapproved social behaviors, respectively.

Introduction

As children develop, their behavior becomes increasingly influenced by their peers. This is often due to the social acceptance and/or rejection that children receive from peers in response to particular behaviors – socially approved behaviors are met with social acceptance and positive feedback, while disapproved behaviors are met with social rejection and negative feedback. This peer feedback can also differentiate according to gender and age. The following entry reviews the literature on peer feedback and norms to display the possible age and gender differences regarding feedback within peer relationships. It will also discuss the impact that feedback can have on a child's social development.

Need to Belong Theory

Popular beliefs regarding human behavior have changed as new theorists have arisen and staked claims based on empirical evidence. Freud (1930) proposed that the two major driving forces behind humans' actions are sexuality and aggression. John Locke proposed that infants are born as "blank slates." Baumeister and Leary (1995) propose – with their *Need to Belong Theory* – that the actual driving force for humans is a biological need to establish and sustain interpersonal relationships. The interpersonal relationships that humans form have survival and reproductive benefits and are therefore believed to have developed as a result of evolutionary selection pressures.

Some of these evolutionary pressures are, metaphorically speaking, double-edged swords. For instance, researchers have examined how participants in need of social acceptance performed

certain tasks when offered incentives and when not (DeWall et al. 2008). Findings revealed that, when offered a social reward as an incentive, participants performed poorly on laboratory performance tasks and quickly provided excuses for their performance as a means of preventing or mitigating any peer rejection caused by their poor performance. When offered a monetary reward, the participants showed greater performance on the same task. The researchers concluded that, when there are no clear immediate benefits, humans would rather opt not to try than to experience social rejection due to personal failure.

Assimilation

Assimilation is the process of taking in and fully understanding information and/or ideas. Humans have a biological need to be assimilated into certain cliques/groups. As individuals find others who share many of the same attitudes and/or beliefs, this increases psychological comfort and subsequently the desire to be part of that group (Baumeister and Leary 1995). If this occurs at a young age, as individual ideas and concepts are being developed by individuals in the child's social environment, then peers can influence future decision-making as well as personality (Larsen and Buss 2010).

Gray and Rios (2012) conducted a study with students in a classroom setting where the students were primed for a need to assimilate or differentiate themselves from their peers. Focusing solely on the aspect of assimilation, students were asked to rate academic tasks based on how well the task would allow them to fit in with their peers. Therefore, students rated tasks higher based on how well the task would allow them to fit in with their peers. When participants were primed, the participants with the thought processes of wanting to assimilate into the group, performance on the highly rated tasks (i.e., tasks that allow individuals to assimilate into their peer group) dramatically increased. Primed participants were willing to go the extra mile, so to speak, in order to perform the task well, so that they would align with their

primed condition. This shows that individuals may choose to act in the interests of becoming one with the group.

This phenomenon is not novel, as it has been the theme of many films and television shows throughout the twentieth century. The movie *The Sandlot* (1993) – which is about the social relationships of a group of school-aged children in the 1960s – provides a depiction of assimilation and the positive effects that are a product of assimilation. *The Sandlot* (1993) begins when Scottie Smalls moves to a new neighborhood where he does not know any of his peers. He eventually meets the neighborhood boys and assimilates into their group while adopting their social and cultural practices (e.g., sleepovers, playing baseball, going to the local public pool, etc.). As his social acceptance grows, Scottie's self-esteem increases.

Breaking down the film in a more scientific approach, what we see in *The Sandlot* (1993) is that, young boys develop social relationships with individuals around the same age, same gender, and similar interests.

Failure to assimilate into a group, or society as a whole, can have adverse effects as well. Studies have found links between failure to socially assimilate and suicide (Baumeister and Leary 1995). Suicide has also been found to be prevalent for those who experience high rejection rates from groups they wish to join. This is one of the negative consequences of the process known as differentiation.

Differentiation

Differentiation is the process of creating distinctions between two objects. This can be both a beneficial and harmful concept. In the case of social relationships, differentiation refers to identifying oneself as separate – or excluded – from a particular social group. Differentiation can be harmful to individuals as it may lead them toward negative or depressive feelings (Stone et al. 2016). However, peers may pressure different peers to engage in harmful behaviors as a means of conforming to the group. For instance,

misconduct and antisocial activities are significantly correlated with peer pressure in adolescents (Gavazzi et al. 1993).

Differentiation, however, can also possess beneficial aspects. It can help individuals narrow down options for potential friends and allies, which can help them choose the social group (s) with which they wish to spend their time. Gavazzi et al. (1993) also found that high levels of peer support were associated with lower degrees of psychopathological symptoms and a greater degree of social competence.

A strong example of differentiation occurs in the novel *The Giver* (Lowry 1993). The main character Jonah is given the highest honor in the Utopian community in which he resides. He is chosen as the receiver of memories, which effectively and immediately sets him apart from everyone else in his community. As Jonah begins to receive memories and experience things that no one else in his community has been able to experience, the gap between himself and the rest of the community widens. Jonah begins to feel like an outsider because his peers share a much different viewpoint than he had come to know and understand. While this example starts off as an image of harmful differentiation, it reverses and becomes more of a beneficial tool as Jonah develops a unique mind and rejects his peers' black and white view of the world around them.

Positive Feedback

When individuals engage in a particular social behavior in the presence of their peers, the behavior is often met with a response from these peers. This response – which can be positive or negative – is referred to as *feedback* because individuals often utilize their peers' responses as a means of understanding which social behaviors are acceptable and which are unacceptable within their social group. Positive feedback refers to the approval and acceptance of a particular social behavior, which often comes in the form of some sort of reward (Salmivalli 2010). This reward may not always be a physical object – it may be

something as simple as smiling, laughter, encouraging statements (e.g., saying “good job!”) and positive physical contact from peers. Positive feedback operates as positive reinforcement – an individual engages in a particular behavior, his/her peers like the behavior so they subsequently reinforce that behavior by smiling and reacting happily and kindly toward the individual, which then encourages the individual to engage in that behavior again in the future.

However, positive feedback can have negative implications as well. Individuals may feel compelled to engage in negative, harmful, and even illegal behaviors because they are met with positive peer feedback. For instance, in one study, approximately 67% of participants aided and abetted fellow group members in lying, cheating, and stealing. This occurred even when the participants did not know the other individuals in their group (Geis and Moon 1981).

In addition, some individuals may find positive feedback through elevated social status among peers. For example, Salmivalli (2010) researched the structure of bullying in order to identify a way to weaken and eradicate such behavior. Her research concluded that most bullies committed aggressive acts as a means to establish dominance over their peers. This would give them the perception of being “cool” during certain times of the year. While the victim receives no positive feedback, the bully receives a lot of positive feedback via feeling powerful over his/her peers, which can reinforce the bullying behavior and cause it to continue or increase in frequency and severity (Salmivalli 2010).

Social popularity – a concept that is often associated with high levels of positive peer feedback – is also related to aggression and depression. Troop-Gordon and Ranney (2014) found that popular males tend to have a more aggressive demeanor to them, which is likely due to how males work their way up the social ladder, sometimes using aggression to assert. On the other hand, popular females are more affected by depressive symptoms (Troop-Gordon and Ranney 2014). This is likely due to females’ verbal aggression toward each other in order to climb their own social ladder (Geher 2014).

Negative Feedback

Although positive feedback can be utilized to reinforce negative behaviors within a social group, it must not be confused with negative feedback – which is the mechanism by which individuals illustrate which behaviors are disapproved within a social group. Negative feedback can come in the form of disapproving responses or social rejection. Stone et al. (2016) researched how rejection from peers influences depressive symptoms. In their study, they examined children previously diagnosed with major depressive disorder (MDD). A majority of these children were female. Researchers looked at pupil dilation and the retention of that dilation as a measure of how feedback affects and sticks with these young children. The researchers concluded that the effects of negative feedback and peer rejection were more pronounced in children with depressive symptoms. Specifically, pupil dilation lasted significantly longer than individuals without MDD. Furthermore, while positive feedback also had an effect on pupil dilation, the pupil returned to normal size at a much faster rate than those exposed to negative feedback.

There are two forms of negative feedback – representative negative feedback and non-representative negative feedback (Jansen et al. 2014). Representative negative feedback follows an incorrect decision, while nonrepresentative negative feedback follows a correct decision. Jansen et al. (2014) investigated children’s potential reactions to nonrepresentative negative feedback. Their findings revealed that children were more likely to change their answers to questions after receiving nonrepresentative negative feedback. This has been interpreted as a lack of understanding and differentiation of the two forms of negative feedback among children aged 6–12 years-old.

Conclusion

Human behavior and personality can be influenced by his/her peers in a variety of ways. When entering a peer group, the processes of

assimilation and differentiation often occur, which leads to acceptance or rejection from the peer group. As the research shows, assimilation tends to have positive effects for individuals, while differentiation tends to have negative effects (although differentiation can produce some positive effects as well). The processes of assimilation and differentiation occur via the mechanisms of positive and negative feedback from peers. While positive feedback often leads to social acceptance, it can also lead to some negative behaviors such as aggression, dominance, and bullying. Negative feedback, such as peer rejection, often leads to negative feelings and can even lead to depressive symptoms. Ultimately, the process of assimilation leads to positive and negative feedback (and sometimes differentiation), which can be a tumultuous time for individuals – especially children and adolescents who are beginning to develop their peer group and their sense of social belonging for the first time.

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Peer Groups

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Synonyms

Cliques; Coalitions; Crowds; Dyads; Friendship groups; Socialization

Definition

A group of people of approximately the same age who have similar interests, background, or social status. The members of this group are likely to influence an individual's beliefs and behaviors.

Introduction

For our ancestors, being a part of a group would have been critical for survival. Group membership would have offered benefits such as increased protection from predators, hostile out-group members, and challenging environmental conditions. Benefits such as these would be essential for reproductive fitness. As such, it is likely that the tendency to cohabitate, work, and play together in a group was favored by natural selection (Van Vugt and Schaller 2008).

In childhood, peer groups consist of individuals who spend time and interact with each other. In adolescence, peer groups are based increasingly around the reputation of its members. Therefore, peer groups play a particularly important role in socialization. Further, peer groups may not only provide a positive context for children and youth to be a part of beneficial relationships but can also have a large influence on the behaviors, beliefs, and attitudes of the individual members of the group. It is therefore important to consider that while there are often many benefits to being a part of such groups, it is also possible that aspects of these groups present certain risks to children and youth. The rest of this chapter will examine peer groups across the lifespan through an evolutionary lens by considering gender differences and potential costs and benefits of memberships in such groups.

Stratification of Peer Groups

The transition from childhood to adolescence marks a period of rapid stratification of individuals into peer group structures as adolescents move from elementary school to middle and high school. This period is characterized by increased levels of autonomy as peer relationships begin to supersede familial relationships. Further, during this period, adolescents experience new levels of reduced supervision (Volk et al. 2016). From a psychoanalytic perspective, this progression facilitates the process of *individuation*, which may be described as the manner in which adolescents restructure relationships with

parents and caregivers to accommodate new and different kinds of relationships with one's peers. This novel degree of independence from one's parents sparks feelings of vulnerability and anxiety in adolescents which, in turn, they attempt to quell through supportive and intimate relationships with their peers. Similarly, from a cognitive-developmental perspective, these new peer relationships are qualitatively different from previous relationships with adults, particularly in regard to the imbalance of power. The horizontal nature of friendships allows adolescents to explore opposing ideas and multiple perspectives, thus facilitating an advanced understanding of other persons as having independent thoughts and emotions.

During adolescence, the unified peer structure of childhood (i.e., elementary school) gives way to increasingly differentiated and stratified groups (i.e., middle and high school; Volk et al. 2016). General peer group structure changes to include various subcategories as individual's transition from childhood to adolescence. The broader level of peer group stratification is referred to as *crowds*, which describes large groups of individuals grouped together by common stereotypes or reputations who may, or may not, spend time together. Crowd membership is entirely dependent on assessment and consensus from one's peers (Rubin et al. 1998). Sussman et al. (2007) identified five major classes of crowds that are observable across many schools: (1) elites, the crowd with the highest social status; (2) athletes, the students who are known for their involvement in school sports and teams; (3) academics, the students who are both academically talented and socially accepted; (4) deviants, the students who are alienated from the larger student culture and are often involved in risky behaviors; and (5) others – students who, by in large, go unnoticed by most students. Stigmas and stereotypes associated with such crowds influence individual behavior and may constrain adolescents into relationship patterns and interests that are consistent with the crowd's reputation – for example, dating and sexual behavior. *Cliques* form within crowds, rather than across crowds. A clique is typically defined as 3–9 same-sex

adolescents, generally of the same race, that are linked together by friendship. Cliques are entirely voluntary and exist outside of the confounds of extraneous variables that may be imposed on adolescents by circumstance or by adults (Rubin et al. 1998). From an adaptive perspective, belonging to a group would have provided protection and safety from potentially threatening animals, persons, or other groups in the ancestral environment (Van Vugt and Schaller 2008).

Peer Groups as an Adaptation

Adolescence also marks a period of increased concern about one's reputation and acceptance from peers. These concerns are amplified by the increased stratification of peer groups and the resulting increased competition for social power and status (Juvonen and Graham 2014). From an evolutionary perspective, the benefits of group membership would not have been equally distributed among all members. Therefore, qualities that aided individuals in maximizing the social resources that were available to them through successful management of group dynamics would have been favored by natural selection (Van Vugt and Schaller 2008). As a result, adolescents may be compelled to use strategic tactics, some prosocial and others coercive, to obtain these limited social resources (Volk et al. 2016; Hawley 2003).

Social Dominance

Indeed, achieving high social status or dominance within one's peer group grants an adolescent access to adaptive advantages such as higher-quality mates and reputational benefits (e.g., Flinn and Ward 2005). Resource Control Theory predicts that children and adolescents use different strategies, consisting of different combinations of prosocial and antisocial behaviors, to attain social resources (Hawley et al. 2007). As such, popularity and being well-liked must be approached as two separate constructs. Being popular is associated with increased relational aggression, whereas being liked by one's peers is associated with decreased relational and overt

aggression in middle schoolers (see Hawley et al. 2007 for review). Similarly, children who have moderate levels of aggression, and who use that aggression instrumentally to achieve their goals, are perceived as more popular than children who are lower in aggression or children who use their aggression more recklessly (Hawley 2003).

While these adolescents may be regarded as popular and powerful within their peer network, they may not be guaranteed the benefits of altruism or affection from peers, especially if those peers do not readily accept this type of behavior. However, qualities such as forcefulness, assertiveness, strength, and Machiavellianism may be attributed to strong leadership skills by the group, thus granting individuals with these qualities enhanced social power and dominance. As such, high status, leadership, and aggression are often co-observed among adolescents (Hawley 2003). Both boys and girls compete for dominance in their peer groups, and the tactics used to attain such dominance reflect the differential reproductive pressures between the sexes.

Sex Differences in Peer Groups

Basic evolutionary theory predicts that reproductive pressures, such as the ones discussed below, will exert themselves differently between males and females. Furthermore, the social styles of boys and girls, influenced by everything from hormonal exposure in utero to culturally constructed gender role schemas, contribute to greater segregation.

Male Peer Groups

The structure of male peer groups evolved under selective pressures that made control over one's local environment (and the resources in it), control over mating opportunities, and influence within one's peer group adaptive. As such, boys will often organize into large male coalitions with dominance hierarchies (Geary 2010). From a sociocultural perspective, the emphasis in boys' culture on independence, autonomy, self-assertion, and competitiveness may exacerbate this tendency for boys to organize themselves

into large, loose-knit peer groups (Benenson et al. 2001). From an adaptive perspective, by developing coalitions among each other that emphasize status and dominance, boys may be more apt to compete against other groups of boys and protect their resources and kin (Geary 1998).

Within these loose-knit male peer groups, one-on-one and group-level competitive play among boys is ubiquitous across cultures and time periods. However, the degree to which play fighting is rough appears to depend on the degree to which male-on-male aggression is common within a particular cultural or historical context. For example, among the Yanomamö of South America, inter-group aggression is frequent in adulthood. Young Yanomamö boys are often given toys such as clubs, bows, and arrows, and play fighting often involves causing physical pain and harm to another. Furthermore, social norms dictate that pain not be expressed. As such, this culture emphasizes developing toughness, aggressiveness, and endurance and de-emphasizes sensitivity, thus preparing young boys for the life-or-death male-male conflict that they will encounter as adults (Geary 1998).

In the ancestral environment, men competed for social resources and capital within their groups, sometimes with deadly consequences (Geary 2010). To a lesser extent, this is still true of contemporary times. For example, according to Geary (2010), there is no significant difference between the motivations of a pastoral raider stealing another tribe's cattle or a white-collar criminal on Wall Street, as both examples reflect the desires of men to control resources relative to other men or groups of men. In these examples, men are not competing against one another simply for the purpose of amassing resources; rather, they are interested in attaining status in the dominance hierarchy and usurping the next person up in the ranks. This drive to attain resources makes male coalition forming adaptive – that is, forming coalitions would have provided benefits such as ability to control more territory, access to higher-quality mates, providing for family and kin through large-scale hunting efforts, and increased protection from other male coalitions. Furthermore, in the ancestral environment, the

dominance hierarchy would have facilitated coordinated group action, and the lack of emotional closeness would have facilitated building a larger coalition (discussed further in the next section; Geary 2010).

Female Peer Groups

Unlike boys and men, girls and women tend to organize into peer groups that consist of dyads or small groups of individuals who are of similar social status and are characterized by intimacy, personal disclosure, and support. Women tend to invest more heavily in the quality of their relationships rather than the quantity of relationships they maintain. For women, these peer group structures are also adaptive, as there are significant and immediate benefits in having a network of supportive friendships. In the ancestral environment, a female who maintained close friendships with other females would have increased her genetic fitness by attaining kin altruism and alloparenting of her own offspring from her female allies. Reciprocity (i.e., mutually beneficial exchanges), therefore, is an important characteristic of enduring female friendships. As such, women likely evolved psychological monitoring mechanisms that attune them to cues of nonreciprocal relationships and limit tolerance of such relationships (Geary 2010).

Therefore, while the intimate nature of female friendships is certainly beneficial, these same qualities may contribute to the swift undoing of female friendships. In the animal kingdom, research conducted by de Waal (1989) has demonstrated that female chimpanzees reconcile disagreements among themselves at a lower rate than their male counterparts. Similarly, research by Benenson and Christakos (2003) found that females, as compared to males, reported more fragility in their closest same-sex friendships. Further, females reported that their friendships lasted for shorter periods than males and were characterized by greater feelings of unease about the potential ending of their friendship. Moreover, while boys and men are more likely to engage in overt and physical aggression, it is well-established that girls and women are more likely to engage in relational or indirect aggression.

As such, the same personal disclosures that once formed the foundation for intimacy in a female friendship may leave an individual vulnerable to victimization in the event that the friendship dissolves (Geary 2010).

Potential Outcomes of Peer Group Membership

Well-Being and Health

Peer group involvement is associated with benefits to physical health, social development, and psychological well-being throughout the lifespan. As predicted by Abraham Maslow's hierarchy of needs, the inherent human need to belong is only superseded by other necessities such as food, water, and safety. Contemporary research has since highlighted the importance of belonging to a group, especially in adolescence. For example, Parker and Asher (1993) suggested that friendships within peer groups may fulfill specific needs for intimacy, social support, and instrumental aid. Furthermore, the intimate and accepting context of friendship may grant children and adolescents the significant benefit of a secure relationship in which they feel comfortable exploring different behaviors and attitudes (Parker and Asher 1993). Relationship strength in adolescence also predicts increases in self-worth and decreases in depressive symptoms in early adulthood (Narr et al. 2017). As such, it's not surprising that adolescents who report positive relationships within their peer groups often also report a strong sense of well-being.

Peer relationships also play a central role in the adolescent support system, offering youth encouragement to withstand emotionally challenging circumstances. In fact, research indicates that peer relationships may mitigate the harmful effects of environmental stress on adolescent mental health (Stanton-Salazar and Spina 2005). Moreover, the benefits of peer affiliation in adolescence include positive outcomes for future relationships. In this way, peer group membership and the relationships fostered within them provide individuals an important context for learning about the requirements of mature, respectful

interpersonal relationships (Stanton-Salazar and Spina 2005).

Into adulthood, peer groups continue to offer learning opportunities and social support networks. Peer group affiliation offers individuals the opportunity to observe and mimic the various coping strategies that others implement, therefore allowing the observer to evaluate the efficacy of such strategies and utilize them to cope with similar problems (Palmonari et al. 1991). In addition to offering social learning opportunities, peer groups fulfill important social support roles. This is particularly true following widowhood or divorce, where close peers take over the important functions that were previously provided by partners. Research suggests that after a spouse, older adults rank close friends as their most important source of support, ahead of adult children and other familial relations. The importance of peer relationships in filling that role may be attributed to secure attachment based on shared experience, reciprocity, and equality (Matt and Dean 1993).

Across the lifespan, peer group affiliation offers benefits to an individual's overall physical health as well as their emotional and psychological well-being. For example, greater social support and integration is associated with a decreased risk of morbidity and mortality. Specifically, research suggests that men who were more socially integrated with peers during childhood and adolescence reported lower blood pressure and body mass index 20 years later, both indicators of overall physical health (Cundiff and Matthews 2018). The benefits extend to women as well, with higher peer participation and encouragement being significantly related to a higher level of physical activity (Verloigne et al. 2016). These findings emphasize that the benefits belonging to peer group are not only social in nature but can extend to physical health benefits as well.

For some adolescents, peer groups may be a source of social stress. In particular, stress associated with peer groups is related to compromised emotional well-being, especially among young women. Furthermore, social stress appears to be strongly associated with lower self-esteem and higher depression for females but not for males,

while having social support through a peer group seems to have a stronger impact on males compared to females (Moran and Eckenrode 1991). Conversely, having strong social support fostered from a peer group was found to be associated with higher self-esteem and lower levels of depression more predominantly in males (Moran and Eckenrode 1991). It would therefore appear that the salience of the peer group context differs between the genders.

Academic Performance

Peer groups also have an important influence on youth achievement, beliefs, and behaviors in school contexts. As an inherently social space, the way that individuals engage with the school context is influenced by the attitudes of their peer group. For example, Ryan (2000) found that students with high-achieving friends have greater academic achievement over time as compared to students with lower-achieving friends. Similarly, this research also suggests that by associating with friends who have positive attitudes toward school, youth may enhance their own satisfaction with school, highlighting the influential role peers may be playing in adolescent academic achievement (Ryan 2000). Furthermore, associating with highly motivated peers may act as a protective factor during adolescence, a developmental stage typically characterized by heightened exposure to risk-taking behaviors.

Risk-Taking

The influence of peers has been found to play a large role in adolescents choosing to engage in risky behavior, as research demonstrates that when individuals are in peer groups, they tend to not consider the costs of risky behavior and, instead, focus on the benefits (Gardner and Steinberg 2005). This is evident in research by Gardner and Steinberg (2005), which found that adolescents were more likely to make riskier decisions when they were in peer groups compared to when they were alone. Further, this research found that the effect of peer groups to increase engagement in risky decision-making and behavior was stronger with adolescents than with adults. This emphasizes the influential role peer groups can

play, particularly during this stage of development. Considering these findings, adolescents within these types of peer groups may be more likely to engage in antisocial behavior, specifically bullying, as a means to attain resources such as increased social status.

Bullying and Victimization

The peer group may be an arena for antisocial or aggressive behavior. Aggressive behavior such as bullying may be considered a cost or benefit within a peer group, depending upon the role of the individual in the group (i.e., a bully versus a victim). From an adaptive perspective, bullying within a peer group may be a tool to attain resources such as higher social status within the group (e.g., Volk et al. 2014) and may therefore be considered as a benefit to the perpetrator. However, the overall cost may be that certain individuals in the peer group may be harmed (i.e., physically, emotionally). It is therefore important to take into account that membership of a peer group may produce benefits (e.g., may be a protective factor), but may also come with increased costs, particularly during adolescence. This may be particularly true if the individuals with the most status within the group are choosing to engage in antisocial behavior as a way of exerting control and attaining dominance over other members. Connected to this, reputation has been the most discussed benefit of engaging in bullying as it can be a means for both individual and group participation in dominance hierarchies (e.g., Volk et al. 2014; Salmivalli 2010). It may be a means to support in-group solidarity, as individuals have reported joining in with bullying as they did not want to be left out or as a way to emphasize their loyalty to the initial bully (e.g., Garandeau and Cillessen 2006). At the group level, this may also be another way to distinguish in-group versus out-group competition, as individuals who are members of particular groups may be encouraged to take part in bullying behavior to harm other groups. Further, bystanders to bullying behavior may choose to join in with bullying behavior as a way to try to attain membership into a more powerful (i.e., high social status) group (Salmivalli 2010).

Conclusion: Implications of Evolutionary Research on Peer Groups

Similarly, Spadafora et al. (2018) found that witnesses to bullying situations will choose to ignore the negative behavior when they perceive possible personal costs to them (i.e., loss of social status) and only consider intervening if there were direct benefits (i.e., it was a close friend being bullied or there was a potential for increased social status or to gain a friend). This research suggested that individuals within a peer group may make decisions, from an adaptive perspective, by considering personal costs and benefits to themselves. Furthermore, this research emphasizes the high value placed on social status by many adolescents who are involved in such groups. As such, future research should endeavor to use the adaptive perspective to achieve a better understanding of the social dynamics at play in peer groups and to use this information to create useful and effective interventions.

While peer groups can contribute to antisocial group behavior (such as bullying), they can also be instrumental in the success of anti-bullying intervention as seen through peer-based intervention programs such as KiVa (Salmivalli et al. 2012). Therefore, it may be important to further evaluate interventions that utilize both peers and the adaptive perspective such as the “Meaningful Roles” intervention as described by Ellis et al. (2016). This intervention focuses on offering alternative activities that can enhance an individual’s status, especially at the secondary school level as this is the time that social status seems to be most salient.

Cross-References

- [Cost of Same-Sex Friendships](#)
- [Peer Competition and Cooperation](#)
- [Peer Relationships in Childhood](#)
- [Peer Socialization](#)
- [Peers](#)
- [Same-Sex Friendships](#)
- [Status Competition and Peer Relationships in Childhood](#)

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Peer Networks

► Peer Relationships in Childhood

Peer Norm

► Peer Pressure

Peer Pressure

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Synonyms

Conformity; Peer effect; Peer norm

Definition

Peer pressure is the influence on people by peer-defined norms on how to behave, think, and feel.

Introduction

Living in social groups may enhance an individual's fitness. Throughout evolutionary history, humans have tended to live in large complex groups, and one of the reasons we evolved large brains was because having a large brain facilitates

interaction with a lot of people and the establishment and maintenance of a wide social network (Dunbar 2010). Because of the importance of group life humans are susceptible to peer pressure, in particular we are more susceptible to peer pressure than our closest living relatives, chimpanzees (Nettle et al. 2013).

Peer Pressure and Child Development

Peer pressure becomes apparent in early childhood, when children begin to explore the social world outside their own home. Group socialization theory of development (Harris 1995) asserts that parents do not play as big a role in their children's development as was once thought, because peer pressure plays a more important role that was first realized. A child is socialized outside the home through two processes: identification with a peer group and assimilation of group norms. Peer pressure functions less as an incentive to conform and more as an incentive to be involved in activities which are perceived to be relevant to one's identity within one's peer network.

Some seminal experiments showed that the presence of peers may induce behaviors approved of by the peer group. For example, adolescents make riskier decisions and to engage in greater risk behaviors when their peers are present (Gardner and Steinberg 2005). In addition, if adolescents have friends who show deviant behavior, they are more likely to display externalizing behavior themselves (Goodnight et al. 2006). The presence of peers may also induce prosocial behaviors (van Hoorn et al. 2016). In summary, peer-approved behaviors increase when peers are present. This peer-effect arose through natural selection and now all humans have an innate, subconscious response to peer pressure.

Peer Pressure and Mating

The sources of peer pressure vary over the lifespan. From middle childhood, individuals have to prepare to cope with the pressures

surrounding mating (Chen and Chang 2012; Del Giudice 2009). Furthermore, gender differences in peer pressure emerge during adolescence and adulthood. Men are more susceptible to peer pressure relating to social status and dominance, whereas women are more susceptible to peer pressure relating to physical appearance (e.g., clothing selection, body shape or size and hairstyle).

Men are more likely than women to experience the competitive pressure from the same-sex peers and also more likely to adopt dominance-relevant strategies (e.g., aggression) in intrasexual competition (Chen and Chang 2015). Women also compete for mates. Peer pressure applies in the digital world as well as in traditional face-to-face encounters. Social media can be used to exert pressure on peers in their daily life (Ferguson et al. 2011).

Conclusion

Peer pressure is part of human life. I briefly discussed the associations between peer pressure and child development and between peer pressure and mating. Children are vulnerable to peer pressure. There are sex differences in the effect of peer pressures on mating strategies that stem from sex difference in intrasexual competition.

Cross-References

- [Female-Female Competition](#)
- [Gang Affiliation](#)
- [Group Living](#)
- [Intrasexual Rivalry Among Women](#)
- [Male-Male Competition](#)
- [Peer Feedback and Norms](#)

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Peer Rejection

► Peer Relationships in Childhood

Peer Rejection, Gender Differences in Response to

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Synonyms

Gender; Ostracism; Social exclusion; Social rejection

Definition

Peer rejection Peer rejection is a negative social event in which an individual is deliberately excluded or isolated by his or her peers from social interaction or from social relationships.

Introduction

Human beings have an innate need to belong (Baumeister and Leary 1995). When an individual experiences rejection, he or she may therefore experience a variety of negative psychological, physiological, and/or behavioral outcomes. There are various forms of social rejection that lead to these negative outcomes, such as rejection by family members, rejection by potential or current romantic partners, and rejection by peers in which an individual is rejected by those who are theoretically the individual's social equals. This entry will focus exclusively on gender differences in responses to rejection by peers.

Although most people experience peer rejection as negative, responses to social rejection may differ based on dispositional traits of the rejected individual. One such moderating factor that has been examined in prior research is gender. Although most research examining gender as a moderating factor has not found statistically significant gender differences in participant responses to peer rejection (e.g., Forney et al. 2005; Flook et al. 2005; Nolan et al. 2003; Nesdale and Lambert 2007; Weiner and Handel 1985), a handful of studies have found significant differences between how males and females respond to rejection by peers. We discuss these differences below in relation to psychological detriments, physiological detriments, and behavioral outcomes.

Psychological Detriments

Several studies have examined gender differences in psychological reactions to peer rejection. One study found that although shy males reported significantly greater negative affect than

nonshy males following peer rejection, this difference was not found between shy and nonshy females (Howarth et al. 2013). Another study (Zimmer-Gembeck 2015) examined coping skills following peer rejection, such as avoidance of future social situations, rumination about the rejection incident, seeking social support post rejection, distraction from the social situation (e.g., engaging in a fun activity, reading a book, watching television), or opposition toward those who rejected the individual. After experiencing rejection, females reported more rumination, distraction, and social support seeking than did males. Males, however, reported greater opposition than females, specifically thinking about seeking revenge toward those who rejected them (Zimmer-Gembeck 2015). These findings could be explained by the work of Rose and Asher (1999), who found gender differences in how males and females cope with conflicts with their friends. Females were more likely to accommodate and compromise than males during a conflict, whereas males reported greater hostility and aggression than females during a conflict with a friend.

Other research conducted by Baldwin et al. (2003) suggests that peer rejection may be more psychologically detrimental to females than to males. Examining self-critique following peer rejection, rejected females reported increases in negative self-critique (e.g., using more words like “worthless,” “stupid,” or “inadequate” to describe themselves), decreased self-esteem, and increased negative affect. Rejected males, however, reported significantly more positive outcomes than rejected females, such as increased positive affect and increased self-esteem (Baldwin et al. 2003). Although this outcome was novel in terms of peer rejection, previous research shows that females tend to be more self-critical than males and that males tend to be more positive than females following negative events. For instance, one study reported that, in general, females are significantly more self-critical, exhibit greater interpersonal vulnerability (e.g., experiencing helplessness without social support), and report more internalizing problems (e.g., anxiety and depression) than males

following negative self-relevant events (Leadbeater et al. 1999). Furthermore, when examining other areas of stress (e.g., financial stress), men reported more optimism and positive affect than female participants (Jacobsen et al. 2014). Additionally, previous work has reported that males engage in significantly more self-compassion than females (Yarnell et al. 2015). The findings reported by Baldwin et al. (2003) are therefore consistent with other research examining gender differences in responses to negative events.

Moreover, females who experience ostracism or ambiguous exclusion from a group are more likely to believe the ostracism was in response to their own poor character than males, meaning they are more likely to believe that the ostracism was their fault (Williams and Sommer 1997). These findings relate to previous research examining gender differences in response to negative feedback. When interpreting negative feedback from a work assignment, females tend to view negative evaluations as accurate and serious, whereas males tend to view negative evaluations as inaccurate and unimportant, even going as far as to condemn the person evaluating them (Johnson and Helgeson 2002). Although rejection is not an overt negative evaluation, it can indicate that those rejecting the person do not value their relationship with that person. As a result, the way in which males and females respond to peer rejection is relatable to the findings reported by Johnson and Helgeson (2002) in the sense that rejection from a peer group may be an indication of a negative social evaluation.

Physiological Detriments

Although most research examining responses to peer rejection has focused on the psychological detriments of rejection, physiological detriments have also been examined in response to peer rejection. Furthermore, gender differences have been found in physiological responses to rejection. For instance, Stroud et al. (2002) found that females exhibit significant increases in salivary cortisol concentrations following peer

rejection whereas males do not (Stroud et al. 2002). To replicate the findings from Stroud et al. (2002) and to add additional physiological measurements of the hypothalamic pituitary adrenocortical (HPA) axis and of the autonomic nervous system (ANS) stress responses, Stroud et al. (2017) examined physiological responses to peer rejection in pre- and post-puberty males and females. They found that post-puberty females exhibited a significantly greater physiological stress response following peer rejection than pre-puberty females, pre-puberty males, and post-puberty males (Stroud et al. 2017). Peer rejection can, furthermore, affect heart rate reactivity. For women exposed to peer rejection in an online simulated game, heart rate reactivity significantly decreased from baseline measures (Sijtsema et al. 2011). This decrease, while also found in males, was more pronounced in females (Gunther Moor et al. 2014). Thus, research suggests that females may experience more detrimental physiological responses to peer rejection than males.

Behavioral Outcomes

Alongside psychological and physiological detriments, research has reported gender differences in behavioral responses to peer rejection as well. Females experiencing peer rejection reported engaging in more relational aggression than males (e.g., spreading gossip about peers, verbal bullying, not playing well with others; Sijtsema et al. 2011). Males, however, report engaging in more physical aggression after experiencing peer rejection (e.g., pushing, hitting, kicking, biting) than females (Kawabata 2016). Additionally, McEachern and Snyder (2012) found that peer rejection mediated the relationship between physical aggression of boys in kindergarten and covert antisocial behavior when those same boys were in the first grade. Moreover, individuals who experience peer rejection at an early age displayed significantly more teacher-reported aggression than individuals who did not experience peer rejection. Although rejected males and females were reported to be more aggressive than their

nonrejected peers, teacher evaluations revealed that rejected boys were rated significantly more aggressive than rejected girls (McEachern and Snyder 2012). Therefore, not only can peer rejection have immediate consequences on behavior outcomes, but also longitudinal consequences in the form of covert antisocial behavior, at least for males.

Conclusion

The studies summarized above have shown gender differences in psychological, physiological, and behavioral responses to rejection by peers. Although males and females may report or exhibit differences in the experience of rejection, both males and females experience potentially detrimental outcomes that could affect them long-term.

It is important to note, however, that not all studies observing psychological, physiological, and/or behavioral outcomes of peer rejection examine gender differences (e.g., Anderman 2002; Bishop and Inderbitzen 1995; Martin and Cole 2000; Schwartz 2000) and that the majority of studies examining gender as a moderating factor did not find significant evidence for gender differences in response to peer rejection (e.g., Forney et al. 2005; Flook et al. 2005; Nolan et al. 2003; Nesdale and Lambert 2007; Weiner and Handel 1985). Aspects such as gender and societal norms, as well as social desirability, may be a mechanism by which gender differences in self-report and observational measures occur. In regard to psychological detriments, it is often more socially acceptable for females to report psychological distress in response to peer rejection whereas males may perceive that it is less socially desirable and weak to report psychological distress in response to peer rejection (Chandra and Minkovitz 2006). For observational measures with behavioral outcomes, it is a social normative for males to be more physically aggressive, whereas, in females, physical aggression is neither a desired nor normative behavior (Baillargeon et al. 2007). Therefore, researchers should examine and be aware of this desirability when

examining their own or others' work in which gender differences are found in responses to peer rejection.

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and cooperated in social groups (Baumeister and Leary 1995). Yet competition for status and resources also exists within a group, and this can lead to hostility and exclusion. Research has found that peer rejection is likely to occur when a person deviates from prevailing group norms (Juvonen and Gross 2005). Individuals who are too boisterous, too shy, or too studious are at greater risk. This suggests that in addition to competitive motives within the status hierarchy, peer rejection may have the additional purpose of maintaining conformity and cohesiveness in the group. When rejection occurs, it can take a variety of forms, from passive avoidance to active, physical threats (Asher et al. 2001). Three general categories of aggressive rejection behaviors have received the most research attention. These consist of physical aggression, verbal aggression, and relational aggression. Sex differences have been found in each of these categories of behavior.

Peer Rejection, Sex Differences in Initiation of

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Synonyms

Interpersonal rejection; Social rejection

Definition

The deliberate exclusion of an individual from friendships, groups, or social interactions by peers of similar age and social position.

Introduction

Humans are social animals and have a fundamental need to be accepted by others. This need to belong may have evolved from advantages in survival and reproduction that would have been conferred upon ancestors that lived

Varieties of Rejection

Physical aggression consists of overt rejection behaviors involving potential physical harm (e.g., hitting, pushing), as well as damage to personal property. Studies have consistently found that across age groups and cultures, males exhibit more physical aggression than females (Archer 2004). This is one of the most robust sex differences to be documented in the research literature. Ironically, individuals who engage in highly aggressive behavior are often more likely to be rejected themselves. Verbal aggression, on the other hand, includes threats, name-calling, insulting remarks, taunting, and related behaviors. As in the case of physical aggression, males engage in more verbal aggression than females, but the difference is not as large (Archer 2004). These sex differences are consistent with sexual selection theory, which states that across many species, males have evolved to be larger and more aggressive in their behavior as a result of competition between rivals.

Physical and verbal aggression are relatively direct forms of social rejection. Relational aggression, however, is more indirect. Relational

aggression includes spreading rumors and gossip, ignoring or excluding individuals from activities, and otherwise undermining reputations and relationships. There is evidence that females are more likely to engage in relational aggression than males. For example, women are more likely to gossip about others, whereas men are more likely to talk about themselves (McAndrew 2014). Sex differences for relational aggression are less consistent than they are for the more direct approaches (McEachern and Snyder 2012), possibly because of the greater variation in behavior that falls under this category. Nevertheless, a tendency for females to be more likely to utilize indirect, relational aggression is consistent with the well-established finding that females have a lower tolerance for risk taking (Byrnes et al. 1999).

Cyber Rejection

Cyberbullying refers to activities such as threats, harassment, and rumor spreading that are carried out via cell phones, social media, and other electronic technologies. In terms of our previous distinctions, this form of peer rejection may involve either verbal or relational aggression. Cyberbullying is a growing problem in our ever more electronic world, yet it is less common than traditional bullying, and there is a substantial overlap among perpetrators of cyberbullying and other kinds of bullying (Modecki et al. 2014). Preliminary research has not found consistent gender differences in overall frequency of cyberbullying, but there is evidence that females who initiate rejection are more likely to turn to cyber bullying (Slonje et al. 2013).

Conclusion

Peer rejection is a universal human experience and an inevitable aspect of living in groups. Mechanisms for exclusion and ostracism likely evolved alongside of our tendency toward social affiliation (Leary and Cottrell 2013). Rejection occurs across age groups and gender, and nearly

everyone will suffer from a rejection experience at some point in life. Despite this prevalence, certain patterns of rejection behavior are more typical than others. Males are more likely to engage in direct aggression when initiating rejection, both physically and verbally. Females are more likely to initiate indirect or relational forms of rejection. These differences are consistent with evolutionary theory as well as traditional gender roles. Although potentially hurtful to individuals, peer rejection serves various group purposes, such as cohesiveness, resource management, and the delineation of relationships and status hierarchies.

Cross-References

- [Bullying](#)
- [Cyberbullying](#)
- [Peer Rejection](#)
- [School Bullying](#)
- [Sex Differences in Cyber Bullying](#)

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Peer Relationships

► Same-Sex Relationships

Peer Relationships in Childhood

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Synonyms

Friendships; Peer acceptance; Peer groups; Peer networks; Peer rejection

Definition

Peer relationships are the social bonds that tie together two or more individuals who are similar in age or social group.

Introduction

Relationships matter for youth. They matter for young people's well-being, impacting development, health, achievements, and overall life satisfaction. Relationships may take many forms, but

relationships with peers are among the most important and influential relationships in young people's lives. Relationships with peers, or others who are similar in age and/or social group, can be quite diverse. Some peer relationships are close and tightly knit, involving a small number of peers who form a strong bond with one another. Other relationships are more diffuse and involve many peers who share ties or connections to one another. Relationships can be positive – characterized by liking, support, and trust. They can also be negative – characterized by disliking and harm. Relationships can be hierarchical, with one or more members of the relationship leading or dominating others, and they can be egalitarian, in which leadership, power, and control are shared. Thus, a best friendship, in which two peers form a supportive, trusting bond with one another, a gang of youth who repeatedly come together to victimize others, and a classroom of children in which some set the norms for how to act and others follow those norms are all examples of peer relationships. As these examples hint, youth can have multiple peer relationships. Some relationships are embedded within others. For instance, close friends might be embedded within a larger social group. Others are distinct, as when a child is friends with one peer but enemies with another.

In this chapter, we explore peer relationships in childhood. In doing so, we consider their evolutionary significance and the ways in which peer relationships both change and remain the same as children grow up. We also address the fact that peer relationships are defined by the competencies and motivations that each child brings to the relationship as well as by the characteristics of the relationship as a whole. As we explain how relationships develop and evolve as a function of what individuals bring to the relationship and how the relationship as a whole entity is structured, we suggest that these factors can move relationships down more, healthy and effective pathways as well as down more unhealthy and ineffective pathways. We conclude by discussing the impacts of positive and negative peer relationships on children's lives and providing recommendations for ways to promote positive peer relationships among children.

The Evolutionary Significance of Peer Relationships

The fact that peer relationships are evident at all ages, even among the very young, hints that there may be evolutionary processes at play in the development of peer relationships. Indeed, evidence from animal studies shows that many species engage in social activities (such as play) and develop relationships with peers. Rhesus monkeys, feral pigeons, bottlenose dolphins, and whales are examples of animal species that, similar to humans, engage in social activities with peers (Amos et al. 1993; Connor et al. 2000; Giraldeau and Lefebvre 1987; Ruppenthal et al. 1974). Although peer relationships are common in many animal species, rhesus monkeys' peer relationships have received a great deal of attention because of the genetic, physiologic, and metabolic similarities between rhesus monkeys and humans (Roth et al. 2004). Thus, there is much to be learned about human behavior and functioning by studying rhesus monkeys. Several aspects of peer relationships that are evident in rhesus monkeys are also evident in humans. For instance, rhesus monkeys begin to engage in peer relationships early in life, just as young human children do. Moreover, like humans, rhesus monkeys continue to engage with peers at high rates into adolescence (Ruppenthal et al. 1974). Peer relationships can provide a forum for engaging in recreational activities as well as work activities that are needed to accomplish goals (Coolahan et al. 2000; Roseth et al. 2008). For both humans and monkeys, this could include, for example, playful interactions, grooming activities, collecting food and water, or exchanging goods (Bernstein 1970; Hassett et al. 2008; Suomi 2005). Further, like humans, rhesus monkeys' peer play becomes more gender specific and gender segregated, and involves more complex behavioral sequences as development occurs (Mehta and Strough 2010; Suomi 2005). That is, both rhesus monkeys and humans tend to play with same-gender peers, with males playing with other males and females playing with other females. They tend to engage in more social behaviors that are typical of their own gender,

and fewer social behaviors that are typical of the other gender (Berenbaum et al. 2008). And, with development, both rhesus monkeys and humans engage in increasingly sophisticated behaviors (Sackett 1972; Yang et al. 1995). The time spent with peers is useful because it provides a platform for learning valuable skills.

The fact that peer relationships are ubiquitous across species suggests that peer relationships are evolutionarily adaptive – or that they have evolved over time to promote the well-being of members of the species. Indeed, this is true. Peers are responsible for providing opportunities for individuals to develop skills that help to ensure their survival (Giraldeau and Lefebvre 1986; Suomi 2005). This is important for young individuals, as it is the primary job of youth to learn what is needed to live a healthy, successful, and well-adjusted life. This makes the development of peer relationships vital. For example, in young squirrel monkeys, play fighting, which involves dominant and subordinate monkeys wrestling with each other and attempting to pin each other to the ground, is common (Biben 1998). This supports the establishment of defense skills that are needed to protect the monkeys when they get older. Young children do the same thing; rough-and-tumble play, which is an active, physical play that can involve pretend fighting, is common, particularly for boys (Smith and Boulton 1990).

Not only is there an evolutionary basis for engaging in peer relationships, but there is also an evolutionary basis for how peer relationships may be structured and organized. Studies of domesticated pigs, for example, have shown that peer relationships are often hierarchically organized according to status or dominance (Meese and Ewbank 1973). When relationships with peers are hierarchically organized, those members of the peer group who are higher in status (e.g., strongest) have power over those who are lower in status. This power enables high status peers to obtain more resources or better resources (such as food, opportunities for potential mates) than their lower status peers. In this way, status within the peer group confers an advantage. To illustrate, studies of chimpanzees have shown that chimpanzees' status in the hierarchy is directly related

to food and reproductive success (Wittig and Boesch 2003). Similarly, dominance hierarchies can emerge among human youth. Youth may selectively use coercive and aggressive (e.g., talking about a peer behind his/her back; excluding a peer from a social activity) as well as pro-social behaviors (e.g., complimenting a peer or inviting him/her to an event) to maintain their own social status, to elevate their social power towards selfish goals, or to diminish another's social status (Hawley 1999, 2003). When targeted selectively at relatively high-status peers, this can increase one's own status. It is important to note, however, that even though having high status among peers can enable youth to obtain valued resources (such as invitations to social activities or preferred opportunities) it can also come at a cost. High status youth may be targeted for victimization by other high-status youth, and high-status youth are not necessarily well-liked by others (Andrews et al. 2017). Moreover, youth who find themselves lower in the hierarchy can suffer (Parker and Asher 1987). As we explain later in this chapter, social structures that enable youth to be more egalitarian and interconnected tend to produce adaptive outcomes for all children without significant costs (Cochran and Brassard 1979).

A Developmental Perspective on Peer Relationships

In humans, peer relationships begin to emerge in infancy and early childhood as very young children are first exposed to peers, and they extend across the lifespan into late adulthood. To be more specific, friendships are evident at all ages. Children at all ages can identify peers whom they like and those whom they dislike. Children at all ages form stronger social bonds with some peers and weaker ones with others. Thus, there is remarkable similarity across ages in the existence of peer relationships (Noller et al. 2001).

Beginning in the first years of life and continuing across the lifespan, individuals interact with one another. Interactions provide the building blocks upon which peer relationships develop.

Interactions can be simple, involving subtle non-verbal behaviors, such as eye contact or a smile. Although such subtle behaviors might seem insignificant, even a gaze can signal interest, engagement, and the potential for more in-depth interactions (Vaughn and Waters 1981). Similarly, behaviors such as parallel play – in which two or more peers participate in the same activity side-by-side – can provide a forum for more involved interactions to occur (Bakeman and Brownlee 1980). For instance, playing an electronic game next to another child who is playing the same game can lead to direct interaction, such as sharing of ideas. Interactions can be simple, such as brief exchanges (e.g., making and responding to a simple request), and they can be complex, rich, and reciprocal, such as extended conversations or participating in intricate, rule-based games (Fabes et al. 2009). Regardless of their complexity, each interaction sets the stage for the next, and over time, relationships are dynamically built. Thus, peer relationships can grow and change over time.

The complexity and sophistication of peer interactions changes with age. For infants and toddlers, whose physical, linguistic, cognitive, and social skills are still rudimentary, children begin to learn about peer relationships by observing others (Rubin et al. 2005). By watching social interactions, children develop a general understanding of peer relationships, soaking in information about how to interact and the effects of interactions (Bandura and Walters 1963). Moreover, by paying attention to how others respond to their own behaviors (e.g., gazing, smiling, crying, physical acts, statements, questions), young children begin to form relationships of their own. As children get older, new physical, linguistic, cognitive, and social developments allow children to become more and more sophisticated in how they communicate their emotions, desires, interests, and needs in social situations and in how they respond to others. This can be seen in the increasing complexity of children's interactions with peers – for example, nonverbal interactions that are characteristic of young children are augmented by verbal ones as children get older, simple statements or requests of peers are expanded by extended conversations, and the factors that

bring peers together develop from basic commonalities to include deeper and richer ones, such as mutual sharing, trust, and support (Fabes et al. 2009). Moreover, as children's interactional skills develop, so does the complexity of their relationships. Early relationships are fairly simple, typically involving straightforward interactions with a single peer. As children grow, their abilities to manage larger groups of peers and multiple peer groups also evolves (Strayer and Santos 1996).

The development of peer relationships is important because early relationship experiences set the stage for later relationship experiences. Thus, children's relationship experiences in early childhood – namely, the extent to which children have relationships with peers, the breadth of those relationships, and the nature and quality of these – impact their likely relationship experiences in middle childhood. In turn, these lay the foundation for the kinds of relationships that adolescents have with their peers. For this reason, one might see continuity in peer relationships, such that those who have many positive relationships early in life are also those who are well-connected with peers in positive ways later in life. Similarly, those who are withdrawn from peers and those who have conflictual peer relationships early on might continue to struggle in their peer relationships later (Hay et al. 2009). Yet, early relationships are not deterministic. Changes are certainly possible, and children can move from more challenging to more rewarding relationships as they learn and grow with practice, motivation, and support (Cairns et al. 1995; Coplan and Arbeau 2009). Indeed, we next consider factors that contribute to more and less effective relationships, and we conclude this chapter by providing suggestions for building effective peer relationships.

Determinants of Peer Relationships

What determines peer interactions and, consequently, peer relationships? This question has often been asked by children, the adults who work with them and support their development, and the scholars who study peer relationships. In answering this question, it is important to

remember that relationships are made up of multiple (two or more) individuals. Each individual brings his or her own competencies, motivations, and characteristics to the relationship and, in doing so, the relationship reflects aspects of each person while also being greater than the sum of its parts. In this way, the relationship is a unique entity and any one individual will have different relationships with different peers. In the sections that follow, we take a closer look at these two important factors: (1) the competencies and motivations that individual children bring to their relationships and (2) the relationship as an entity that exists among two or more peers.

Relationship Competencies and Motivations of Individual Children

The nature and quality of peer relationships are determined, at least in part, by the competencies and motivations that individual children bring to their peer experiences. This includes children's social and emotional skills. Social and emotional skills are those skills that contribute to effective (versus ineffective) peer interactions. Included in this list are such skills as emotion recognition and emotion display skills (the ability to accurately identify one's own and others' emotions and to present one's own emotions in ways that are modulated and appropriate for the situation); decision-making and problem-solving skills (the ability to identify and resolve problems, to make decisions about how to proceed in complex situations, and to evaluate the success of one's decisions); perspective taking and empathic skills (the ability to understand what another might think or feel and why he or she might think or feel a certain way); and communication skills (the ability to effectively listen to and respond to others' points of view and to express one's own) (Weissberg et al. 2013). Each of these skills is important to relationships because they enable individuals to understand their own needs, goals, and desires as well as those of others. They also enable members of the relationship to work toward establishing common goals that are shared by all. Thus, effective social and emotional skills contribute to effective peer interactions and, as a result, effective relationships. In contrast, ineffective social and

emotional skills contribute to ineffective peer interactions and, as a result, ineffective relationships (Rubin et al. 1998).

Also important are the attitudes and beliefs about relationships that each individual brings to the relationship. The behaviors that children exhibit when with their peers do not emerge out of a vacuum; rather, they are influenced by the perceptions that children have about relationships. For instance, some children feel efficacious or comfortable in their interactions with others, expecting that they will have positive and supportive experiences; others may feel inefficacious or uncomfortable, expecting negative experiences and outcomes (Zosuls et al. 2011). Children (like adults) hold attitudes, biases, and stereotypes about others, and these guide their interactions (Abrams et al. 2007). Children's interpretations of social experiences and explanations for their own and others' behavior (such as: "he did that on purpose" or "it was just an accident") can affect the tone of an interaction (Crick and Dodge 1994). Each of these attitudes and beliefs have the potential to promote either positive interactions and relationships or negative ones, thereby influencing the likelihood of a relationship forming as well as the nature and quality of that relationship.

The competencies and motivations that children bring to their relationships are important because they contribute to the affective tone of the relationship. Children vary in their relationship competencies and motivations. In other words, children who have more positive and effective skills and those who are more interested in and motivated toward building relationships tend to have more enjoyable, understanding, supportive, and trusting relationships than those whose skills are less well developed or who may be more reticent to engage with others. In the latter case, children may find themselves relatively isolated from their peers, challenged to connect with others, or in relationships marked by disliking, aggression, and mistrust. Importantly, relationship competencies and beliefs can be taught and learned. They can be learned in the context of interactions with other children, observing how others behave, practicing new skills, and receiving feedback about how their interactions are

perceived by others. Parents, teachers, and other supportive adults (e.g., grandparents, coaches) can also model relationship skills and beliefs and they can directly teach these to children. In fact, programs that teach relationship competencies (such as those implemented in schools) can be effective in building social and emotional skills and in expanding and improving relationships. Moreover, the positive effects of teaching effective relationship skills add up, leading to benefits in other areas, such as academic achievement and health (DeLay et al. 2016; Durlak et al. 2011; Miller et al. 2017).

Relationships as an Entity

Relationships can exist among two peers (known as a dyad) or more than two peers (known as a group). Groups can be small (made up of three or four peers) or large (for example, all of the students in a class). The size of the relationship is one indicator of how the relationship is structured. Another indicator of how the relationship is structured is the degree to which the members of the relationship are interconnected with one another. This becomes an increasingly important indicator of the structure of the relationship as groups get bigger in size. To illustrate what this means, consider a large group (for example, a class of students). If most of those students have strong ties to one another, that is, if most are friends with (or, at a minimum, friendly toward) most others then the group as a whole is likely to function well. In this case, few peers (if any) will feel left out of the large group peer relationship. And, the circumstances will be present to allow for egalitarian peer relationships, or those in which status, power, and leadership are relatively equally distributed and shared. In contrast, in a large group that is characterized by a lack of interconnectedness, the ties that bind peers together are weak. The large group is fractured, and many may feel disconnected and left out. When this happens, some may rise to the top of the group gaining more status and power than those who fall near the bottom of the hierarchy (Rodkin and Gest 2011). This type of relationship structure can be harmful because children jockey for position and status in a fractured peer network. This creates conditions

that are ripe for negative peer relationships to occur, such as those in which bullying and victimization are common (Ahn et al. 2010; Serdiouk et al. 2015). Thus, the structure of the peer relationship can impact the quality of children's peer experiences, just as can the individual competencies and motivations that children bring to their relationships.

Moving beyond the structure of the relationship, we also consider the constitution of the relationship. Often, relationships form among peers who are similar to one another. For instance, relationships may form among peers who are similar on gender, behavioral styles (such as aggressive or prosocial behaviors), interests, and even indicators of healthy functioning (such as depression or academic motivation) (Fabes et al. 2003; Kindermann 1993; Prinstein 2007). Thus, girls often form relationships with other girls, aggressive children spend time with other aggressive children, academically motivated youth connect with other academically motivated youth, and so on. This tendency is known as homophily. It is often driven by the children themselves, as they gravitate towards others who appear to be similar (Serbin et al. 1994). Homophily can also be reinforced by peers or adults as an appropriate basis for friendships, just as relationships with those who are different can be discouraged by peers and adults (McPherson et al. 2001).

Homophily is evident in peer relationships beginning in early childhood (Hanish et al. 2005). Thus, by the time children are aged 3–4 years, they tend to segregate themselves in relationships with other similar peers. Homophily does not disappear as children get older; this is a common feature of peer relationships across development, and it is demonstrable in middle childhood, adolescence, and into adulthood (Aboud and Mendelson 1996). Although we often think of homophily as relevant to positive relationships, such as friendships, it is important to note that homophily can just as readily occur in negative relationships, such as bully-victim relationships. Indeed, it is more likely that boys and girls aggress against same-gender peers than it is that they will aggress against other-gender peers (Russell and Owens 1999).

Such segregation in relationships is important to recognize when it occurs because it has effects on the relationship itself as well as on the individual participants in the relationship. Relationships with similar peers form readily. For instance, even when first meeting a new peer, those who are similar to one another tend to cooperate more and like each other more than those who are dissimilar (Andrews et al. *in preparation*). As relationships develop, children become more like one another over time via a process known as peer influence. Children model behaviors for one another and reinforce each other's behaviors (Prinstein 2008). When children are in relationships with similar peers, they tend to encourage one another to become even more alike. Thus, boys who spend more time with boys become even more masculine in their behaviors as compared to those boys who spend less time with other boys, and this is especially true for those boys who are most masculine at the beginning (Martin and Fabes 2001). Similarly, aggressive and delinquent children and adolescents who spend time interacting with other aggressive and delinquent peers become more aggressive and delinquent over time (Dishion et al. 1996; Hanish et al. 2005). And, children who behave prosocially become even more prosocial when they spend time with similar peers (Carlo et al. 1999). In other words, spending time with those who are similar to oneself increases the strength and impact of the factors that drew similar peers together in the first place.

Clearly, homophily is a common feature of peer relationships. But, is it the rule? In other words, might relationships form among youth who differ on key dimensions? For instance, might girls and boys form friendships? Might children of different racial and ethnic groups build relationships? Is it possible that aggressive and nonaggressive youth interact? These are important questions for those who want to broaden children's experiences and skills by encouraging a well-rounded set of peer relationships. The answer to all of these questions is *yes*. Although homophily is typical of peer relationships, relationships can also form among youth who might appear to be different from one

another. Take the example of gendered relationships. Children respond more positively to same-gender peers, they interact more with same-gender peers, and they are more likely to be friends with same-gender peers (Fabes et al. 2003; Hayden-Thomson et al. 1987; Howes et al. 1988; Kupersmidt et al. 1995). Yet, interactions and relationships can also occur among other-gender peers. The findings of one study, for instance, showed that interactions with only same-gender peers (girls interacting only with girls or boys interacting only with boys) occur about 60% of the time in preschool classes. For the remaining 40% of the time, children interacted with members of both genders simultaneously (30% of the time) or solely with those of the other gender (10% of the time) (Fabes et al. 2003). These data show that, despite a preference for same-gender peers, opportunities for interacting with and developing relationships with other-gender peers are readily available. The same can be said of other dimensions on which children might select peers.

Moreover, nonhomophilous relationships – or those in which members of the relationship differ in important ways – are valuable and should not be overlooked. In fact, they should be encouraged as such relationships are consistent with an inclusive attitude that is accepting of diversity and inconsistent with an attitude of exclusion. It is important to say that homophilous relationships are not necessarily problematic in and of themselves. Indeed, spending time with similar peers can have positive effects by, for example, increasing positive emotions (e.g., happiness, joy, satisfaction; Martin and Fabes 2001). The lack of relationships with those who are different from oneself, however, is problematic. This is because diversity in relationships provides opportunities for children to develop needed social competencies that are critical to effective interactions across the lifespan. Consider again the example of gendered relationships. When relationships are gender-segregated, children learn the interaction styles and skills that are most typical of their own gender, which leads to feelings of comfort with same-gender peers. Yet, children miss out on opportunities to learn the interaction styles and

skills that are more typical of the other gender, which can lead to feelings of discomfort with other-gender peers (Zosuls et al. 2014). And, over time, the lack of understanding of and comfort with other-gender peers can lead to more serious problems, such as biases against other-gender peers, stereotyping by gender, and harassment and bullying of others for gendered reasons (Fabes et al. 2013; Hunt and Gonsalkorale 2014). Similar problems can also arise when children's peer relationships are limited to homophilous peers on dimensions other than gender. Furthermore, when relationships are focused on others who are homophilous on behaviors that are generally problematic (such as aggressive behavior), the consequences that arise from the lack of exposure to others who encourage more positive interactional styles can be even more detrimental (Hanish et al. 2005).

Thus, providing children with opportunities and support for developing relationships with a wide array of peers is optimal for their development and well-being. That is, relationships with peers are good, having relationships with many peers is good, and having relationships with a variety of peers is good. In the next sections, we delve more deeply into relationships by considering the quality of relationships, how quality can vary, and why the quality of relationships matters. We conclude by providing simple suggestions that can help to build positive peer relationships among children.

Quality and Impact of Peer Relationships

Peer relationships can vary greatly. Some individuals have relationships with many other peers whereas others have a more limited set of peers in their social circles. For some, positive relationships (for example, characterized by mutual liking, support, sharing, and understanding) abound; for others, negatively toned relationships (for example, characterized by conflict, aggression, and distrust) are more common. When peer relationships are strong, plentiful, and positive, children typically flourish. When they are limited or

absent and when they are negative in tone and quality, children may struggle.

Positive peer relationships are defined by mutual liking and acceptance of one another. Often, liking leads to friendships, which are strong bonds between children that involve perceptions of compatibility, companionship, trust, and mutual affection (Brownell and Brown 1992; Hartup and Stevens 1997). These fundamental aspects of friendship provide children with a feeling of belongingness, or the feeling that one fits in with others and is part of a group (Newman et al. 2007). Belongingness is important to human's need for frequent positive interactions with others and to feel cared about (Baumeister and Leary 1995). When children feel like they belong, they flourish, demonstrating greater self-esteem, experiencing increased opportunities for positive social experiences, and achieving in school (Buhrmester 1990; Cauce 1986; Deci et al. 1991; McGuire and Weisz 1982).

Indeed, involvement in positive peer relationships promotes positive developmental outcomes. That is, good relationships lead to a good life. From a social and emotional standpoint, having positive peer relationships promotes social and relationship competencies, such as prosocial behaviors, perspective taking, empathy, emotional well-being and positive self-esteem (Rubin et al. 1998). For instance, a study found that positive peer relationships among preschoolers impacts the use of negotiation to find a solution that works for all parties, over and above ineffective techniques, like disengaging from the interaction (Hartup et al. 1988). There are also benefits of positive peer relationships outside of social situations. For example, studies show that positive peer relationships in middle school children support better classroom engagement and performance on academic tests (Furrer and Skinner 2003; Liem and Martin 2011). Other studies have shown similar findings, with positive peer relationships being related to children's motivation to achieve in the classroom in addition to enhanced academic achievement (Wentzel 2003). Positive peer relationships also have an impact on health. By engaging in positive, effective peer relationships, individuals may have the opportunity to

better their psychological and physical health (Cohen et al. 2000). For instance, a study on adolescents with Type I diabetes showed that supportive peer relationships are related to greater self-care for those with the disease (Skinner et al. 2000). These outcomes lead us to believe that positive, effective peer relationships are a fundamental part of development.

Not all peer relationships are positive and supportive experiences, however. Some children may be withdrawn from or rejected by others and feel disconnected from the larger peer group. Moreover, negatively toned relationships, like those characterized by conflict, aggression, disliking, and distrust, can occur among youth. Indeed, some children are disliked, rejected, and victimized by their peers. In fact, children who are socially isolated are more likely than those who are closely connected to peers to be involved in aggressive and victimizing relationships (Ladd and Burgess 1999; Laursen et al. 2007). Further, being victimized can lead to increased social isolation (Rubin et al. 2009). In other words, social isolation leaves children vulnerable to peers' attack and peers' attacks can further isolate children. In such cases, the very children whose relationships with peers are most challenged can also retaliate with aggression of their own. Children who have multiple relationship problems tend to also have the most challenges (Schwartz 2000).

Children's relationship problems breed problematic outcomes such as diminished social skills, emotional difficulties, academic struggles, and health problems. To illustrate, studies have shown that children who are victimized in their peer interactions are more likely to experience peer rejection and loneliness (Crick and Bigbee 1998). They are also prone to higher levels of depression as well as lower self-esteem (Crick and Grotpeter 1996; Olweus 1993). Other problematic outcomes could also include reduced participation in classroom activities, diminished academic performance, and, even, dropping out of school (Buhs and Ladd 2001; Coplan et al. 2001). For instance, studies show that experiencing negative peer relationships in childhood is associated with voluntarily leaving high school before graduation (Berston 1960; Elliott and Voss 1974). Further, children's mental and

physical health can be affected (Cacioppo and Hawkley 2003; Halle-Lande et al. 2007; Paxton 1996; Rigby 2000). For instance, children's experiences with obesity are directly related to their treatment by peers (Pearce et al. 2002).

Building Effective Peer Relationships

As we have suggested thus far, peer relationships can take many forms. Many children will experience positive relationships with peers. But, some will also experience negative ones. Often, people wonder whether it is possible to help youth who are experiencing problematic peer relationships to have more positive experiences and, if so, what can be done. It is important to note that peer relationships are, indeed, moldable. For youth who are struggling with peer relationships, and even for those who are not, it is possible to improve peer experiences. Here, we outline three considerations to keep in mind when working to enhance peer relationships. These are: (1) build relationship competencies and motivations; (2) provide opportunities for children to engage in fun, joint activities with diverse peers; and (3) create a supportive environment in which adults are on board with the plans.

As we noted previously, relationship competencies and motivations are not set in stone; rather, they are modifiable. Children can improve their skills for interacting with others. Even children who generally interact effectively might find opportunities to further shape and refine their skills, leading to even more successful interactions in the future. This can happen via instruction (or teaching children how to effectively communicate, understand and respect diversity, problem-solve, and work effectively with one another); modeling (or demonstrating positive interaction skills); reinforcement of positive interactions (or providing children with positive recognition for their efforts); and practice. Many schools have recognized the benefits of teaching such skills to children (Durlak et al. 2011). With this in mind, they have implemented social and emotional learning programs that help children to build the skills that underlie effective interactions.

Social and emotional learning programs are typically integrated into the school day and involve opportunities for children, with teacher support, to learn and practice the skills that contribute to healthy relationships. These programs have been shown to be effective (Miller et al. 2017). If such social and emotional learning programs are not readily available, children can still take opportunities to learn about relationship competencies from more knowledgeable adults or peers.

In addition to helping children to build relationship competencies, it is important to provide them with opportunities to engage with peers in enjoyable ways. These opportunities are most effective when they are structured equitably, so that all of the involved children are able to participate equally in an activity with shared goals. Indeed, for relationship-building to be successful, it is essential that the activities be ones that all peers agree with and are motivated for. These do not have to be complicated or demanding activities. They can be simple activities. For example, younger children might be given bubbles and asked to blow bubbles together or older children might try to work together to build a model. Activities can also be those that involve shared goals, such as group projects that provide each individual with opportunities to contribute. The point is that the participating children engage with one another in positive ways. Teachers, parents, or other adults can help support and guide children to ensure that the experiences are successful. To get the most out of this experience, it is important to pair or group children with a wide variety of peers, including those who are similar on key dimensions and those who are different. Peer partners can change over time, so that youth have opportunities to interact with multiple peers. Teachers, coaches, and other adults who work with youth can integrate these kinds of relationship-building opportunities in their everyday activities. Parents can also seek out opportunities to bring their children into contact with other peers in fun ways.

Finally, children will benefit from support in relationship-building from the adults in their lives. Relationship-building cannot happen, or, at least, it cannot happen effectively if adults are not on board. When adults value and prioritize positive

relationships, it communicates to children that relationships are important. Adults can let children know that they appreciate relationships by sharing this value and encouraging positive relationships. It is important to note that encouraging positive relationships is more effective than discouraging negative ones (Cialdini 2003). If adults direct most of their energy and attention to negative behaviors, even if they do so by telling children what not to do (e.g., “Do not hit”), they inadvertently put attention on problem behaviors. Instead, when adults focus on the positive and provide praise or other reinforcements when children interact well (e.g., “I liked how you listened when your friend was explaining what she wanted to do”), children are able to build a repertoire of skills. Adults can also communicate that they value positive relationships by using effective relationship competencies of their own when interacting with children and other adults.

Conclusion

The purpose of this chapter is to examine peer relationships in childhood. Children’s peer relationships are evolutionarily adaptive and important to their development and well-being. Children contribute to the nature and quality of their peer relationships by the competencies, skills, motivations, and expectations that they bring to their interactions with others. The resulting relationships, however, are also determined by the competencies, skills, motivations, and expectations that others bring. Many relationships are positive and healthy ones. These should be encouraged and supported. Although some relationship experiences can be problematic and challenging, children’s relationships with peers can be improved when caring adults support them in refining their social skills, provide opportunities to engage with others, and model and encourage effective relationships.

Cross-References

- [Bullying](#)
- [Dyadic Relationships Versus Group Processes](#)

- [Opposite-Sex Relationships](#)
- [Peer Feedback and Norms](#)
- [Peer Rejection, Sex Differences in Initiation of](#)
- [Peer Socialization](#)
- [Peers](#)
- [Play and Social Learning](#)
- [Same-Sex Relationships](#)
- [School Bullying](#)
- [Sex Differences in Social Development](#)
- [Social Development](#)
- [Social Withdrawal in Childhood](#)
- [Socialization Processes](#)
- [Specific Friendships](#)
- [Status Competition and Peer Relationships in Childhood](#)

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Peer Socialization

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Synonyms

Group socialization theory; Homophily; Peer groups; Peers; Social networks

Introduction to Peer Socialization

The presence of peers is essential to human life as socializing is inherent to human nature (Hogan and Roberts 2004). Peers can be classified as individuals who surround us in our daily lives such as classmates, colleagues, friends, etc. Due to the fact that humans are constantly surrounded by peers during their lifetime, it is likely that peer interactions influence personality psychology. The core elements of personality are such: how we see ourselves (identity), how others see us (reputation), how we interact in social roles, and how identity, reputation, and interaction influence how we get along with others and achieve goals (Hogan and Roberts 2004). The latter two consider the impact of socializing on oneself.

Defining Peer Socialization

Peer socialization is the process in which peers can help one another develop skills that allow him or her to cooperate and act within set norms. Merriam-Webster defines peer as “one that is of equal standing with another; *especially*: one belonging to the same societal group especially based on age, grade, or status.” Peer socialization is most readily studied in childhood and adolescent relations but is a pervasive feature across our lifespan. It is commonly believed that peer socialization during early adulthood is often deleterious to personality development due to the influence of maladaptive behaviors (Choukas-Bradley et al. 2015). This, however, is not always true. Peer socialization is integral to personality development, especially during childhood and adolescence. Although personality is not thought to undergo dramatic change during adulthood (McCrae 1993), personality changes related to prosocial behaviors have been observed in adulthood (Hoerger et al. 2014).

Homophily in Social Groups

Peers tend to form into social groups based on similarity in individual characteristics. This is the principle of homophily (McPherson et al. 2001).

When it comes to forming social network groups, race and ethnicity are an important factor. People are more likely to discuss important matters with members of the same race. Gender and sex also influence social group preferences. Children are taught that gender is a personal characteristic upon entering school (McPherson et al. 2001). Therefore, younger children tend to interact with members of the same gender. However, upon entering adulthood, relationships become more gender-integrated. On the other hand, adolescence marks a time where teenagers are more likely to associate with those who share similar behavior patterns (McPherson et al. 2001). During this time patterns of prosocial and antisocial behaviors may become clustered within social networks. The notion that peer socialization is deleterious to personality development stems from the fact that teenagers are often subject to peer pressure and antisocial behaviors (Choukas-Bradley et al. 2015). Behavioral homophily is also present among adults, as they tend to associate with those of the same political practice and orientation (McPherson et al. 2001).

Mate Selection

Humans generally exhibit assortative mating patterns. Individuals with similar personality traits often choose each other as mates. Research shows a positive correlation between personality variables between spouses (Buss 1985). Mating with someone who possesses similar genes results in offspring that is 50% related to each parent and further related by the amount of genes the parents shared in common (Buss 1985). Therefore, because peers usually share similar characteristics, and individuals are likely to find a mate within his or her peer group, this may increase likelihood that offspring will share common traits with parents.

Group Socialization Theory on Personality Development

Group socialization theory states that socializing within peer groups is critical to personality development. Children have many environments that

they must learn to function in. The at-home environment forces children to build relations with parents and siblings. These relationships are much different than the ones made outside the home. The theory posits that children learn to function outside of the home by partaking in social groups (Harris 1995). Within social groups, children learn assimilation and differentiation. Assimilation is the adoption of set social norms which results in peers becoming more similar to one another. Differentiation increases characteristic variability (make groups dissimilar from one another). Assimilation and differentiation show themselves depending on differing social context and are not mutually exclusive. Group socialization theory concludes that at-home relationships are not influential to personality development. In fact, Harris proposes that siblings differ in personality not only because of genetics, but because of socializing within different peer groups (1995).

Conclusion

Peer socialization is a critical aspect of personality development because it teaches one how to function in society. Children are first exposed to peer groups during school where they learn about gender and sex. These factors tend to drive the way peer groups are assembled until adolescence. Adolescents tend to socialize with peers who share similar behaviors. Adulthood is where peer groups become increasingly gender-inclusive but still dependent on homophily. In fact, all age groups build social networks on the basis of homophily, the tendency to associate with similar individuals. Personality development begins during childhood and is heavily influenced by peer social groups outside of the home, not by family. Peer groups exist in adulthood as well but are less impactful to personality at this stage (Harris 1995).

Cross-References

- [Peer Feedback and Norms](#)
- [Peer Groups](#)
- [Peer Relationships in Childhood](#)
- [Peers](#)

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Peer Victimization

- [Boys Physical Bullying](#)

Peers

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Synonyms

[Other children](#)

Definition

Peers are defined as individuals of the same age and status.

Introduction

Peers play a prominent role in adolescence, the time between the onset of puberty and achieving independence from one's family of origin, roughly mapping into the second decade of life. Compared to children and adults, adolescents spend more time with peers, enjoy peers' company more, and consider peer norms as more important. This heightened importance of peers is highly conserved across species. For example, adolescent rats spend more time investigating and interacting with peers, and peer behavior is instrumental in learning and practice of adaptive and adult-like behaviors. Although peer influences can be positive (e.g., academically successful friends can motivate youth to work harder at school), more prevalent are concerns about peers' role in adolescents' problem behaviors. Indeed, peer influence is a key contributor to a variety of risky behaviors occurring in adolescence, such as delinquency, risky driving, unsafe sex, and substance use. Some of these peer influences occur through direct modeling of specific behaviors and/or providing opportunities for the behaviors to occur (e.g., observing peers smoke cigarettes or going to a party where alcohol and drugs are available). Other times, peer influences occur indirectly through teens' perceptions of what behaviors are normative or valued within the larger peer group (e.g., believing that most other teens are having sex and not having sex makes one inferior). And sometimes the mere presence of peers is sufficient to increase adolescents' risky behavior. For example, in one study the presence of peers doubled risky driving among early adolescents, although it did not affect driving behavior among adults (Albert et al. 2013).

to become competitive for sex and reproduction. Peers, as prospective mates and competitors, play a key role in this process. Spending time with peers away from adult supervision allows youth to strive for status in the peer group, explore their mate preferences, and practice mate-attracting strategies. The underlying biological changes of puberty support this process by creating reproductive capacity and competitive competencies (e.g., making girls' and boys' bodies more attractive to the other sex); shifting the circadian rhythm to allow nighttime activities (when sexual behavior tends to occur); and increasing sexual desire, novelty seeking, and emotional responsiveness. Risky behaviors that signal dominance and maturity (e.g., rule breaking, substance use) suddenly become appealing and highly valued.

Orientation toward risky behavior is more prominent in youth who follow high-risk reproductive trajectories (also called fast life history), focusing on short-term vs. long-term reproductive benefits. These youth typically come from low-resource environments characterized by poverty, conflict, parent absence, or marginalization. With few prospects to achieve reproductive status over the long-term (e.g., through high education and prestigious employment), these adolescents are more likely to engage in risky behaviors that increase their social status and short-term reproductive benefits (e.g., violence, gang activity, early sexual debut, unprotected sex, teenage childbearing). Indeed, adolescent aggression and risk taking are linked with greater mating opportunities, and the prevalence of these risky and problem behaviors is increased through peer influence processes (competition for status, peer modeling, provision of opportunities, and social norms) (Ellis et al. 2012).

Evolutionary Perspectives on Peer Relationships in Adolescence

As a transition period between childhood and adulthood, adolescence is a time when individuals enter the reproductive period of their lifespan. From an evolutionary standpoint, a crucial task of adolescence is to achieve reproductive status –

Neurobiological Bases of Peer Influence in Adolescence

The profound social-emotional and cognitive changes of adolescence reflect major brain maturation processes triggered by puberty that may have been refined through the process of evolution to maximize reproductive fitness. These

changes include synaptic proliferation and pruning, increased myelination, and stronger connectivity among brain regions. As a result, adolescents gradually improve in their cognitive control, emotion regulation, and planning skills. However, puberty also triggers the proliferation of receptors for oxytocin in subcortical neural structures, which leads to enhanced social bonding and memory for social stimuli, and together with neural changes in reward processing circuits it increases sensitivity to social stimuli. This subcortical neural maturation occurs faster than neural maturation in the prefrontal cortex, which is responsible for cognitive control and executive functioning. As a result, adolescents are highly sensitive to peer stimuli but less able to regulate their behavior, leading to greater susceptibility to peer influences compared to other developmental periods. The neural remodeling that takes place during adolescence also enhances learning potential, so peer and other experiences during this time often carry profound, life-long effects (Crone et al. 2016; Steinberg 2014).

Implications for Interventions

Many interventions targeting adolescent peer processes have been ineffective or even harmful. Such interventions fail because they attempt to change adolescent problem behavior without understanding the benefits and functions of that behavior. To be effective, interventions need to create a context where social status is earned by prosocial behaviors, while minimizing peer dynamics that confer status and other rewards for antisocial behavior. In other words, the social environment needs to be modified so that problem behaviors are no longer adaptive. For example, classroom-based behavior modification systems typically provide points or tokens for children's positive behaviors and/or remove points for negative behaviors, with the points or tokens later exchanged for valuable rewards. Similarly, anti-bullying interventions that reduce the social status benefits of bullying (e.g., through empowering bystanders to intervene and changing the attitudes of principals, teachers, students, and parents) are

more effective than those that do not address the adaptive functions of bullying (e.g., zero-tolerance policies, working with peers to resolve bullying).

The potential for negative peer influence is enhanced in settings that aggregate at-risk youth (e.g., in school, community, or criminal justice programs). When deviant adolescents are grouped together, they tend to reinforce each other's problem behavior (termed deviancy training), which leads to escalation of problem behavior over time. In addition, they can also learn new and more severe forms of antisocial behavior from each other. In these settings, high structure and careful supervision are essential to prevent negative peer dynamics of deviancy training. Additionally, it is important to integrate high-risk youth into settings with low-risk adolescents where they would be exposed to prosocial peer norms, while engaging them in positive structured activities with the low-risk youth to ensure positive peer interactions and acceptance.

Many interventions targeting adolescents focus on the dangers of risky behaviors (e.g., substance use, having sex). By advertising the costs of these behaviors, such interventions may inadvertently make risky behaviors more appealing to adolescents. More successful interventions are those that instead create positive behavioral norms (e.g., not using substances or engaging in sex) by associating these positive behaviors with images and activities that adolescents value. For example, media campaigns that linked *not smoking* with fun and social acceptance were more effective than interventions that emphasized the harmful effects of smoking on health.

Interventions also need to be sensitive to sex differences in peer status and influence. From an evolutionary perspective, men show greater variation in reproductive success than women, with more variable numbers of offspring. Additionally, females are more selective than males in choosing sexual partners. Thus, males have more to gain from high-risk behaviors to improve their attractiveness and social status, and in turn their reproductive success. Indeed, adolescent males are more likely to engage in risky behavior when in the presence of male peers of similar social status,

but such effects have not been observed in adolescent females. In summary, boys are more sensitive to social and contextual cues for status than girls. The effectiveness of peer interventions may also be affected by the ratio of boys and girls in the group and the peer status of the individual members (Ellis et al. 2012).

Conclusion

In summary, peers play a critical role in adolescence, more so than at any other time in life. With the beginning of puberty, competition for social status and reproductive success arises and intensifies during adolescence, supported by complex neurobiological maturation processes that increase sensitivity to peer stimuli and rewards while cognitive and behavioral control is still developing. As a result, the value of social status is at an all-time high and adolescents are willing to take more risks than ever to improve their standing in the peer social hierarchy. This orientation to risky behavior is especially pronounced in youth growing up in deprived, dangerous, and unpredictable environments. However, a better understanding of the evolutionary bases of peer influence in adolescence can help interventions harness the power of social status and peer norms to support more positive youth development.

Cross-References

- [Adolescent Issues](#)
- [Aggression](#)
- [Friendship](#)
- [Peer Socialization](#)
- [Risky Behavior](#)

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Peer-to-Peer Aggression

- [School Bullying](#)
- [Social Aggression](#)

Peggy Mason

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Synonyms

[Author](#); [Neurobiologist](#); [Researcher](#)

Definition

Peggy Mason is a Professor in the neurobiology department at the University of Chicago. She received her Bachelors of Arts from Harvard University in 1983 and then continued on to earn her Ph.D. in 1987. Her early research interests examined cellular mechanisms of pain modulation. Such work in this area has focused on the role of serotonergic cells (Gao and Mason 1997; Mason et al. 2007) and pain modulation circuits in everyday life (Foo and Mason 2009).

Peggy Mason

Dr. Peggy Mason's research focus has recently switched from cellular mechanisms of pain

modulation to empathy and prosocial behavior in rats. In her current experiments, free rats are placed in an arena with a conspecific that is locked in a restrainer. Free rats are then able to open and release the restrained cage mate (Bartal et al. 2011). Dr. Mason and her colleagues found that the rats opened the cage more often when a trapped conspecific was present versus when the cage was empty or had an object in it (Bartal et al. 2011). Furthermore, the rats continued to open the cage door for trapped cage mates even when the social contact was prevented. In trials where rats had the option to open the doors for cages with chocolate or a cage mate inside, the rats would open both within minutes and share the chocolate (Bartal et al. 2011). Dr. Mason and her colleagues concluded that rats would prosocially respond to the distress of a conspecific (Bartal et al. 2011).

Dr. Mason also argues that this provides evidence for the biological roots of prosocial behavior (Bartal et al. 2014). Interestingly, while studying empathy in rats, Dr. Mason found that prosocial behavior is modulated by social experience (Bartal et al. 2014). First rats were tested to determine if they would help restrained unrelated individuals and strangers by releasing them from a cage. Results indicated that rats were willing to help both familiar cage mates and strangers, but only if the stranger was of the same strain (Bartal et al. 2014). Rats did not help strangers of a different strain. Dr. Mason and her colleagues conducted further tests where rats were housed with a rat of an unfamiliar strain for a short duration (Shan et al. 2016). After being housed with an unfamiliar strain, rats were more motivated to help that individual and release them from the restrained cage. The researchers indicated that this finding gives evidence that the social context matters when rats are choosing to help another individual or not and argue that prosocial motivation extends past the individual to group identity (Shan et al. 2016). As a final test, rats were raised with a different strain than their own from birth to determine if genetic relatedness is capable of influencing prosocial motivation. Dr. Mason and her colleagues found that when housed with a different strain, rats would not help individuals

of their own strain, but instead would act prosocially toward individuals of the strain that they were raised with (Shan et al. 2016).

Conclusion

Based on her work, Dr. Mason and colleagues have concluded that genetic relatedness is not enough to facilitate prosocial behavior. Her work provides more evidence that social context is an important factor when determining when to act prosocially toward another individual (Shan et al. 2016).

Cross-References

► [Empathy in Rats](#)

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Penalize

► [Ability and Willingness of Victim to Retaliate](#)

Penetrating Injury

► Specific Brain Damage

Penile Evolution

► Evolution of Genitalia, The

► Genital Evolution

Penile-Vaginal Sex

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Synonyms

Carnal knowledge; Coition; Coitus; Copulation; Fornication; Intromission; Sexual congress; Sexual intercourse

Definition

Human penile-vaginal sex occurs when the penis, usually erect, is thrust into the vagina.

Introduction

In consensual penile-vaginal sex or intercourse (PVI), where there is the agreement of both parties, the activity takes place for pleasure (recreation) or reproduction (procreation) or both, but if the female does not agree it becomes rape. Human penile-vaginal coitus with animals is usually classified as *bestiality (or zoophilia)* and is illegal in most countries. PVI or the coital act, the essential preliminary to the natural creation of another human being, has become invested for the female with attributes varying from the sacramental to psychological aspects far beyond its reproductive role. The coital act can also be used

to express motives as diverse as “to degrade, to punish and hurt, to overcome loneliness and boredom, to rebel against authority, to establish one’s sexuality, or one’s achieving sexual competence (adulthood), or to show that sexual access was possible (‘to score’), for duty, for adventure, to obtain favours such as a better position or role in life, or even for a livelihood” (Levin 1994).

Activating the Vagina for Coitus

The vagina is a potential space with a W or H cross-section, usually the anterior (upper) and posterior (lower) walls are collapsed. To prevent adhesions, their surfaces are kept just moist by transudation of a plasma filtrate from their capillary blood supply. The latter is under local control called “vasomotion” where only the minimum number of capillaries are kept open at anyone time to maintain the organ’s viability (Levin and Wiley 2008). This, however, does not allow pain-free penile penetration so sexual arousal increases the vaginal blood flow by neurally releasing the vasodilator neurotransmitter VIP (vasoactive intestinal peptide) and reducing the activity of its sympathetic innervation vasoconstriction of the blood vessels caused by noradrenaline. This alters the restriction on the vaginal microcirculation opening up the closed capillaries by reducing vasomotion. The increased capillary area and vasocongestion creates enhanced transudation of the plasma ultrafiltrate and greatly increases the lubrication of the surfaces facilitating penile penetration and thrusting. In the Western world, such enhanced lubrication is highly regarded as an index of successful female arousal but in a number of African states men prefer a dry, tight vagina for coitus influencing women to use methods of drying up their genital fluids.

During coitus, the male receives sexual pleasure from the friction generated by the thrusting of the penile glans (head) and shaft against the walls of the vagina and the vaginal entrance (introitus) and its surrounds (vestibule). The female’s pleasure comes from the dynamic friction and pressure of the thrusting penis against a number of genital structures containing various sensory end

organs innervated by the hypogastric nerve (uterus and cervix), the pelvic nerve (vagina and cervix), and the pudendal nerve (the clitoris). These genital structures can include the glans (head) of the clitoris, the introitus and the area of the vestibule around the urethral opening (periurethral glans), Halban's fascia (the vaginal/bladder septum), the vaginal walls especially the anterior (upper) with its inclusions of the urethra, internal aspects of the clitoris (crus and vestibular bulbs), and controversial G-Spot and, in a few women, the cervix (Levin 2015) but see the section on the cervix. Thus, for the female, PVI is a multisite stimulus and should excite the female rapidly and strongly, but in actuality most females find that stimulation of the clitoral glans brings about sexual arousal and orgasm more quickly and often with stronger force although not always as satisfying as that from coitus. The multisite nature of PVI creates difficulties for women's self-reporting of where the erotic stimulus comes from to create arousal to orgasm (Levin 2015). If the female is receptive and sensitive to the PVI it can lead to initiating the female orgasm per se, but this does not occur in all women many of whom need additional clitoral stimulation even during PVI to achieve orgasm (Levin 2014).

The Female Orgasm Problem

Freud (1905) suggested from his psychoanalytical work with female Austrian patients that "the development of female sexuality is complicated by the fact that the girl has the task of giving up what was originally her leading genital zone- the clitoris – in favor of a new zone – the vagina" and "if the clitoral zone refuses to abandon its excitability the young woman can become anesthetic at the vaginal orifice." This opinion later became transmuted by other Freudian psychoanalysts into the concept of a "clitoral orgasm" and a "vaginal orgasm" (attained from PVI alone) and that the "clitoris undermined healthy femininity." It was suggested that "investment in the clitoris is a barrier to the development of an adult femininity." While these concepts became outdated with the rise of feminism and

biologically based psychiatry recent ardent supporters of this "undermining healthy femininity" concept are Brody (2010) and a small coterie of co-workers who claim that clitoral stimulation in women leading to orgasm is not beneficial to their physical, psychological, interpersonal, or behavioral health and that only PVI with its induced orgasm (without clitoral stimulation) are able to create and maintain "normality" of the psychological and physical health of women. A major proposal of Brody (2010) is that PVI and its orgasm is the "one potentially reproductive sexual behavior" so that evolution "rewards" it while other sexual activities (fellatio, clitoral stimulation, masturbation, cunnilingus) are "punished" and lead to "noxious outcomes." Such an explanation is highly simplistic because any human sexual activity can always lead to the possibility of PVI thus no need to "punish" it. This stance of "demonizing the clitoris and sanctifying the vagina" has been extensively criticized (Levin 2014, 2015; Prause 2012; Laan and Rellini 2011).

The Anterior Vaginal Wall Complex

As mentioned previously, the anterior vaginal wall is the site for a number of structures that when stimulated generate erotic arousal (Levin 2015). The female urethra, running from the bladder exit to the urinary meatus (opening), is a short muscular tube containing a lining epithelium scattered with paracrine cells that secrete 5- hydroxytryptamine (serotonin) on activation. It is released from the stretching of the urethra by penile thrusting of the vaginal wall and sensitizes local nerves so facilitates turning the urinary conduit into an active sexual organ. Halban's fascia contains pressure sensitive end organs that also transmit impulses that activate arousal during coitus. The G-spot is a proposed structure that when stimulated by pressure activates sexual arousal. It has been the focus of a number of studies that have tried to identify it by a variety of techniques namely ultrasound, anatomical dissection, and most recently MRI. Unfortunately, some of the studies have identified structures that are different in size and position but none

have shown definitively that they are the functional G-spot (Levin 2015).

Is the Cervix Stimulated in PVI Causing Sexual Arousal?

Some misleading reports suggest that the cervix is stimulated by penile buffeting during PVI creating sexual arousal and even orgasm. These reports are not stringent in that they do not take into account a number of important factors, viz. (i) that when women are actively sexually aroused their utero-cervix complex is withdrawn up away from the penile thrusting axis (vaginal tenting) by striated and smooth muscle contractions into the false pelvis (Masters and Johnson 1966). It has been confirmed by direct observation, genital imaging (MRI), and electrical recording (Levin 2015). This expansion of the upper vagina gives many women during PVI the sensation that the “penis is lost in the vagina” (Masters and Johnson 1966), (ii) the sensory innervation of the cervix is so poor that some minor surgery can be accomplished without anesthesia (Levin 2015), (iii) anatomical and physiological conditions inhibiting vaginal tenting (obstetrical trauma from childbirth, especially long cervices, uterine prolapse), and (iv) poor sexual arousal leading to inadequate vaginal tenting.

Conclusion

Despite many studies of penile-vaginal sex in humans, there are still important functional issues that remain controversial and contentious; a number of these have been described in this entry. More stringent investigations and analyses are needed.

Cross-References

- [Female Orgasm and In-Pair Copulation](#)
- [Human Copulation](#)
- [Masters and Johnson](#)
- [Sexual Arousal](#)

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People's Responses to Personal Ads

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Synonyms

[Ad exposure](#); [Advertising effects](#); [Marketing influences](#)

Definition

The way people are influenced by advertisements appearing in magazines, newspapers, and other visual media outlets.

Introduction

Humans and human-like stimuli are used extremely frequently in advertising, given their ability to attract attention better than almost any other stimuli. As consumers, we are exposed to a wide array of marketing messages every day, many of which are shown to us visually through pictures or commercials featuring other humans. One group of humans that is hugely over-represented in advertising, and whose presence is presumed to produce profit, is aesthetically appealing and attractive humans. Pictures of such “hot” humans are often used with the implicit assumption that they will benefit the advertised products or brands through the beauty and sex appeal they convey. Even though meta-analytical research shows that sex does not sell particularly well in advertising (Lull and Bushman 2015), many companies still use sex cues and physically attractive individuals in their marketing campaigns. Recent studies also suggest that such “sexy” stimuli can have an impact on consumers’ financial decisions under certain circumstances.

Sex Sells Sometimes

Several studies have shown that appetitive stimuli, such as physically attractive individuals or sexually laden objects, exhibit cross-domain effects on impatient and impulsive responses, resulting in a generalized change in time preferences toward present pleasures and vices over virtues (e.g., Chiou et al. 2015; Otterbring and Sela 2017; Van den Bergh et al. 2008; Wilson and Daly 2004). In a classic study by Wilson and Daly (2004), participants were exposed to either “hot” or “not” stimuli (attractive vs. unattractive opposite-sex faces). After indicating how appealing they found the stimuli, participants were asked to choose between smaller-sooner and larger-later monetary rewards, for example, whether to receive \$15 tomorrow or \$50 in a week. Participants exposed to the “hot” stimuli were significantly more likely to favor the smaller-sooner monetary rewards; this effect was especially apparent among men, consistent with the view

that men tend to value a potential mate’s physical attractiveness more than women (Saad 2004).

Van den Bergh et al. (2008) exposed men to commercials with sexually laden (vs. neutral) content and examined whether type of exposure would influence participants’ financial decisions. Men in the sex-cue condition were shown physically attractive and alluringly dressed women, whereas men in the control condition were shown neutral stimuli. Mirroring the findings by Wilson and Daly (2004), men in the sex-cue (vs. control) condition were more inclined to choose smaller-sooner over larger-later monetary rewards. However, such sexy stimuli not only impaired men’s ability to make mature financial decisions. In a subsequent study, Van den Bergh et al. (2008) generalized their findings beyond the financial domain by showing that men who touched bikinis (vs. t-shirts) were more likely to prefer receiving fewer candy bars and soft drinks instantly instead of a larger number of these items at a later point in time. More recent research also shows that regardless of whether men are touching or only viewing sexually laden objects (such as lingerie), such stimuli make them willing to pay more for rewarding foods and beverages compared to if they are exposed to neutral stimuli (such as shirts) that lack a clear connection with sex (Festjens et al. 2014). Similarly, pictorial exposure to attractive (vs. less attractive) women makes male smokers significantly less likely to refrain from smoking during survey completion, with a more present-oriented mindset mediating this effect (Chiou et al. 2015).

Because both hunger and sexual desire have been shown to impair individuals’ ability to refrain from acting on impulse (e.g., Chiou et al. 2015; Orquin and Kurzban 2016), thereby shifting their preferences toward instant gratification and short-term goals, Otterbring and Sela (2017) examined the interactive effect of these drive states in an advertising context. Participating men and women were assigned to one of three advertisement conditions: neutral ads, sexy ads, or no ads. Participants in the neutral ads condition were shown six ads featuring nature motives, participants in the sexy ads condition were shown six ads with sexual content, and participants in the

control condition did not see any ads. Framed as a second part of the study, participants were presented with a series of binary choices between smaller-sooner and larger-later monetary rewards, after which they indicated their hunger. The results revealed that exposure to sexy (vs. neutral or no) ads made men significantly more financially impatient than women. This finding may be explained by the fact that men are more easily aroused by visual sexual stimuli than women and tend to have more positive attitudes towards explicit depictions of sex in advertising (e.g., Sengupta and Dahl 2008). However, hunger further moderated this effect, which only influenced hungry (vs. satiated) individuals: Hungry men made significantly more short-sighted financial decisions after viewing sexy (vs. neutral or no) ads, whereas women made significantly more future-focused monetary choices after similar exposure. Hence, the simultaneous activation of several distinct drive states seems to have interesting interactive effects on people's financial decisions, with sexual desire exerting a particularly powerful influence on monetary choices when another drive state is salient at the same time.

Apart from the above-stated findings, all of which focused on mate attraction motives or stimuli meant to induce a mating mindset, research also shows that mate competition motives (such as encountering a challenging same-sex rival) can influence people's purchase behavior.

Same-Sex Stimuli May also Sell

In a series of studies, Otterbring et al. (in press) examined how exposure to physically fit men, such as muscular male models featured in advertisements or the "handsome hunks" who work at stores like Abercrombie & Fitch, would influence male and female consumers' consumption patterns. Contrary to consumer lay beliefs, a field study demonstrated that the presence (vs. absence) of an athletic-looking male employee at the main entrance of a retail store made male consumers spend significantly more money than female consumers. However, this effect was not merely due to male consumers

purchasing a larger number of products than their female counterparts. Rather, the effect was driven by male consumers purchasing substantially more expensive products in the presence of the physically fit male employee, presumably in an attempt to signal status when encountering such an imposing same-sex rival, as status displays have resulted in reproductive success for men. Supporting such a status-signaling account, men and women in another related study were exposed to either a muscular or a nonmuscular male advertising model. After replying to a set of items related to the model, participants were presented with a blank shirt and asked to draw a brand logo on the shirt in a size they would prefer if they would buy the shirt themselves. Interestingly, whereas women's logo size drawings were not influenced by type of exposure, men exposed to the muscular (vs. nonmuscular) male model drew significantly larger logos, in line with the claim that status can be signaled through both price and size. Furthermore, consistent with the so-called Napoleon complex, this effect was even stronger among those men who lacked a bodily marker of dominance themselves (i.e., men with shorter stature or height). In yet another study, Otterbring et al. (in press) again exposed men and women to a muscular (vs. nonmuscular) male model, after which participants were asked to indicate how much money they were willing to spend on various products. Some products were strongly linked to status (such as a new car, jewelry), whereas others were not (e.g., household goods like batteries and light bulbs, or snacks). Similar to the findings on logo size drawings, women's willingness to spend money did not differ across conditions; however, men exposed to the muscular (vs. nonmuscular) male model were more motivated to spend money on the status-signaling products; this effect was again moderated by the men's own level of physical dominance, this time measured through the 2D:4D digit ratio. Thus, men with higher digit ratios (indicating lower levels of testosterone) were most likely to engage in status-signaling consumption after exposure to a muscular male advertising model, and their elevated feelings of intrasexual competitiveness drove this effect.

Conclusion

Consumers' decision making can be influenced by advertisements, commercials, and other marketing messages featuring sexually laden stimuli. Exposure to such stimuli typically results in more short-sighted decisions in men, but has weaker effects in women, and sometimes even evokes more future-focused female responses. Apart from advertising that aims to produce profits through mate attraction cues, recent research also suggests that mate competition cues can drive the dollars in the desired direction, as long as the products to be purchased signal status through price or size.

Cross-References

- [Advertising](#)
- [Conspicuous Consumption](#)
- [Conspicuous Consumption \(Marketing and Economics\)](#)
- [Geoffrey Miller on Conspicuous Consumption](#)
- [Greater Risk-Taking and Status](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Intrasexual Male Competition](#)
- [Intrasexual Rivalry Among Men](#)
- [Male-Male Competition or Male Provisioning?](#)
- [Men's Mate Preferences](#)
- [Physical Attractiveness](#)
- [Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?](#)
- [Sex Differences](#)
- [Social Status](#)
- [Status and Dominance Hierarchies](#)

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Perceived Control and Suicide from an Evolutionary Mismatch Perspective

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Synonyms

[Appraised helplessness and self-slaughter](#); [Perceived insurmountable problems and self-murder](#); [Sense of powerlessness/helplessness and self-destruction](#)

Definition

Individuals are at a greater risk of killing themselves when they have developed a sense of

powerlessness in relation to dealing with certain overwhelming problems in their lives. Such a drastic action, generally induced by one's judgment that he/she is incapable of influencing an outcome of vital importance, is believed to have been adaptive in some situations for the majority of prehistory from an evolutionary perspective. However, as a result of considerable familial/social transformations in the modern environment in comparison to the ancestral context, attempts at self-murder are conceived to be much less likely to serve any useful evolutionary function in the present day.

Introduction

Perceived control, the notion people hold regarding their ability to be in charge of their personal emotions/thoughts/actions and/or living conditions in engendering preferred consequences, has long been implicated as one of the core cognitive factors that could shape a person's well-being (Wallston et al. 1987). The worst possible impact perceived control (or the lack thereof) could have on one's welfare though pertains to its relationship with suicide – the act of terminating one's own existence. A vast body of empirical research has proffered the critical role a self-appraisal that one is incapable of influencing the outcomes of significant existential challenges can play in effecting suicidal acts (e.g., Gibbs et al. 2009). However, while the suggestion that a sense of powerlessness in dictating certain life events is instrumental in heightening one's suicide risk appears reasonable from the standpoint of logic, the idea that individuals would engage in self-murder in the wake of a perceived lack of control seems baffling from an evolutionary perspective (in which a continued existence is posited to be the primary objective of all living organisms) on the face of it (Nedelcu et al. 2011). What evolutionary function would self-destruction confer on an individual who has perceived that his/her problems are insurmountably beyond his/her control?

Evolutionary Underpinnings of Perceived Control-Suicide Link

Researchers have probed more deeply into this puzzle over the last few decades, and two persuasive explanations have arguably stood out from the rest to this end. One of them is deCatanzaro's (1980, 1991) inclusive fitness formulation. According to this approach, an individual could be at risk to kill oneself if he/she determines that his/her enduring survival might be detrimental to the evolutionary fitness of his/her biological relatives (deCatanzaro 1991). A terminally ill person, in this regard, would supposedly enhance his/her biological relatives' fitness through suicide by freeing up resources that would otherwise be directed to himself/herself if one has continued to exist (deCatanzaro 1991). Another prominent school of thought alternatively contends that an attempt at self-destruction is instead actually an intense cry for help to those who might stand to benefit evolutionarily from one's survival (e.g., Watson and Andrews 2002). Such a dangerous endeavor is believed to be necessary in order to elicit vital assistance/resources from close ones so as to resolve one's difficulties (Watson and Andrews 2002). A large proportion of empirical evidence to date has largely endorsed the cry for help formulation over that of the inclusive fitness approach (Syme et al. 2016). Regardless of the relative strength of their empirical validity however, a common thread that underlies both formulations is the assumption that one would initially perceive a lack of control in modifying his/her adverse situation which could in turn play a role in his/her eventual decision to attempt self-destruction (deCatanzaro 1981; Syme et al. 2016). Although such an undertaking might serve an adaptive function in the ancestral era, it might nonetheless be evolutionarily counterproductive in the present context.

Perceived Control-Suicide Link from an Evolutionary Mismatch Viewpoint

For instance, it is logical to assume that engaging in self-destruction might have enhanced one's

inclusive fitness (e.g., the fitness of one's kin) especially if the individual was faced with a perceived uncontrollable threat (e.g., being partially paralyzed from an accident), which might have required much attention and resources from kin for his/her continued survival in the prehistoric context (where one would generally reside together with kin in a closely knitted band) (Buss 2000). Such an extreme evolved strategy to enhance one's inclusive fitness in the present environment might be much less adaptive though in the evolutionarily novel present context, given that most people currently no longer reside in close proximity to their biological relatives (and hence would not have posed as much of a burden to them) (Buss 2000). By the same token, trying to obtain help from one's biological relatives by engaging in the potentially prehistorically adaptive dangerous strategy of attempted suicide when one has encountered a perceived uncontrollable threat could likewise be evolutionarily counter-productive in the modern environment – one's kin might not be physically close enough to render much-needed assistance and hence one could run the risk of actually completing the act (e.g., die) without obtaining the desired assistance on time. Furthermore, the provision of “social welfare” in an abundant of nations around the world in the present day has rendered self-destruction attempts evolutionarily superfluous, because such societal support has significantly alleviated the strain on family members and has widely broaden the options for help-seeking for those who might be in distress (Aubin et al. 2013, p. 6881).

Conclusion

In sum, the act of killing oneself, purportedly driven by a lack of a sense of control over one's negative circumstances in life, could conceivably have served some evolutionary functions in the ancestral period. In light of the considerable changes in the societal/familial make-up in the modern world (in juxtaposition to the prehistoric context) however, such an extreme stress-coping strategy is believed to be evolutionarily non-adaptive on the whole in the current environment.

Cross-References

- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
- [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)

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Perceived Income Inequality

- [Economic Hardship](#)

Perceived Insurmountable Problems and Self-Murder

- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)

Perceived Social Threat

► Extrinsic Mortality

Perceiving Sexual Intent

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Synonyms

Courting; Dating; Flirting; Mating

Definition

The phenomenon of perceiving another's behavior as sexual.

Introduction

In any one day, our activities often involve some sort of signaling to other individuals within our environment. Interactions with coworkers, friends, family members, partners, and even random strangers are a typical daily occurrence, yet the complexity of human interactions often leaves room for ambiguity. When it comes to interacting with potential mates, the ambiguity widens, sometimes resulting in the misinterpretation of signals between two individuals. A signal can be linguistic in nature, but it can also rest in body movement or a gesture at just the appropriate time. A smile and a touch on the leg can mean two very different things depending on the context. As humans, we have evolved behaviors to help us navigate the ambiguity of our complex behavioral signaling, but we will never be able to perfect a system by any means.

Error Management Theory and the Overperception Bias

Error management theory (EMT) is the idea that a bias should evolve due to an asymmetry in cost: the cost of a false positive versus a false negative (Haselton and Buss 2000). When in uncertain situations, the possibility of two errors exists: false positives (Type I errors), and false negatives (Type II errors). A Type I error is also sometimes referred to as a “false alarm” and a Type II error a “missed detection.” In a mating relevant context, a missed detection would be considered more costly than a false alarm due to the potential loss of a romantic partner. Sexual overperception bias is a solid example. Due to different selection pressures, especially the asymmetrical nature of Parental Investment (Trivers 1972), the overperception bias evolved via Error Management Theory. This can be understood in terms of costs versus benefits, where the costs of missing a sexual opportunity outweigh the costs of lost time. It is important to mention that this only applies to the sex with lower reproductive investment (males typify this category, but in some species this is not the case). If males regularly miss out on opportunities, they will be out-reproduced by other males that took opportunities. On the other hand, females face constraints due to reproductive efforts (i.e., gestation and offspring care) (Trivers 1972). Many research studies have found evidence in support of men over-perceiving women's sexual intent, supporting the idea that the asymmetrical nature of Parental Investment drives error management, resulting in the overperception bias in males. Of course, there is much research needed on the mediating factors of the overperception bias. For instance, though males do tend to over-perceive female's sexual intent, sociosexuality is a strong predictor of both men and women interpreting flirtatiousness.

The Influence of Alcohol on Overperception

Other factors can play into the overperception bias as well – especially situational factors. For

instance, alcohol use by a man or woman can greatly increase the overperception bias. At singles mixers, alcohol is almost always a must and is often used as an icebreaker when meeting potential partners. On the reality show, *The Millionaire Matchmaker*, the main character has a set of rules that all her potential clients must follow. One of the number one rules that is often broken is a limit on alcohol consumption when going on dates with one another. By sticking to a “two-drink maximum rule,” individuals avoid potentially embarrassing themselves. Simply put: The over consumption of alcohol leads to the overperception of sexual intent.

Conclusion

Human interactions can often be complex, but when considering the perception of sexual intent, a multitude of other variables come into play. Specifically, environmental factors and the individual’s sex play prominent roles when perceiving sexual intent from an individual. That being said, there are many questions left open-ended and unanswered before we can begin to fully understand the true nature behind the perception of sexual intent.

Cross-References

- [Casual Sex](#)
- [Human Courting](#)
- [Mate Choice](#)
- [Sex Differences](#)
- [Sexual Selection](#)

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Perception of One’s Capability and Extreme Fears of Some Creatures

- [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)

Perceptions of Infidelity

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Synonyms

[Assessment of unfaithfulness](#); [Judgment of cheating](#)

Definition

People’s attitudes toward different behaviors or information about their romantic partner that may constitute infidelity.

Perceptions of Infidelity

Researchers have come to the conclusion that there are two distinct forms of infidelity: sexual and emotional infidelity (Shackelford and Buss 1997). While sexual infidelity is considered as engaging in sexual behaviors (i.e., penile-vaginal intercourse, oral sex) with someone other than your primary partner, emotional infidelity refers to forming an emotional and intimate bond with someone else. However, despite this distinction, there is not much agreement on how to define infidelity and which behaviors might be perceived as a sign of sexual or emotional infidelity. The

same behavior might be sometimes considered as infidelity and sometimes not. A qualitative study states that even experienced couple counselors who worked with couples experiencing infidelity have conflicting definitions of infidelity (Moller and Vossler 2015). A descriptive study demonstrates that what people consider as infidelity varies based on their gender, attachment avoidance, and attachment anxiety (Kruger et al. 2013). Specifically, women gave higher ratings than men to several behaviors. Moreover, people high in attachment anxiety were more likely to consider many behaviors as infidelity, whereas attachment avoidance was related to decreases in the rating of behaviors as infidelity. Overall, sexual behaviors were rated as the most defining behavior of infidelity.

A seminal evolutionary psychology study showed major sex differences in response to different types of partner infidelity (Buss et al. 1992). Specifically, when participants were asked to choose which type of infidelity would make them more distressed (e.g., sad, jealous), males selected sexual infidelity as the most distressing type of infidelity, whereas it was emotional infidelity for women. Buss and his colleagues (1992) claim that men and women experience different reproductive challenges when their partners engage in different types of infidelity. For instance, men might experience paternity uncertainty when their partner engages in sexual infidelity, whereas women might lose their resources when their partner engages in emotional infidelity. Despite several replications of this hypothesized evolutionary sex difference, some researchers question the validity of this finding. For example, when a continuous scale was used instead of the previously used forced-choice question, no sex differences in response to partner infidelity were identified (DeSteno and Salovey 1996). Similarly, another study didn't also find this sex difference and showed that both men and women were more distressful in face of sexual infidelity as compared to emotional infidelity (Brogdon et al. 2006).

In another study, whether perceptions of infidelity could change based on the sex of the judge and the sex of the target individual, who was judged in terms of whether they engaged in infidelity or not, was investigated (Hackathorn and

Harvey 2011). Interestingly, they found that women were more likely to perceive infidelity when the target was a man, and similarly, men were more likely to perceive infidelity when the target was a woman. A factor that could contribute to this finding is same-sex protection, meaning that people might more easily empathize with members of their own sex, whereas they might become defensive when infidelity behaviors are enacted by the opposite sex.

Given the detrimental impacts of infidelity on individuals, it is important to be able to detect partner infidelity. From an evolutionary perspective, infidelity might be even considered as an adaptive mechanism since it gives the individual the chance to reevaluate their current relationship and even find a better mate after detecting partner infidelity. The literature suggests that it is possible to detect the presence of infidelity based on brief observations. For instance, researchers demonstrate that just seeing 3–4 min “thin slices” of couple interaction was enough for observers to accurately identify people who had cheated on their partners (Lambert et al. 2014). They also found that trustworthiness and commitment were two variables that mediate the relation between observers' ratings and targets' actual infidelity behaviors. Therefore, first impressions of trustworthiness might be one possible way to detect infidelity. Voice pitch is another factor that influences people's perceptions of infidelity (O'Connor et al. 2011). Specifically, men, but not women, are more likely to attribute infidelity to feminized women's voices (i.e., higher pitch). On the other hand, women, but not men, are more likely to attribute infidelity to masculinized men's voices (i.e., lower pitch). Moreover, another study showed that people accurately judged an unfamiliar target's past faithfulness from their voice (Hughes and Harrison 2017). Specifically, judges rated people who actually had cheated on their partners as more like to cheat after controlling for voice attractiveness and pitch.

Conclusion

While it is somewhat ambiguous how common infidelity is defined these days, research suggests

that its prevalence is somewhere between 1.2% and 85.5%, and this reported frequency depends on the way people define it and the sampling methods studies use (Moller and Vossler 2015). Despite this ongoing debate, there is no doubt that infidelity poses threats to both relationship and individuals, such as paternity uncertainty, divorce, or even abuse. Therefore, it is important to deter partner infidelity to decrease stress due to uncertainty and have long-lasting and satisfied relationship.

Cross-References

- ▶ [Cues to Infidelity](#)
- ▶ [Infidelity Risk](#)
- ▶ [Jealousy and Infidelity](#)
- ▶ [Perceptions of Infidelity Cues](#)
- ▶ [Sex Differences in Jealousy](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)
- ▶ [Voice Pitch](#)

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Perceptions of Infidelity Cues

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Synonyms

[Assessing faithfulness](#); [Detecting romantic cheating](#)

Definition

The assessment of visual or auditory information in relation to a potential mate's future likelihood of sexual unfaithfulness.

Introduction

Both men and women are vulnerable to the fitness risks of selecting an unfaithful long-term mate. Owing to this selection pressure, individuals who perceive and attend to infidelity cues during mate search may be better able to avoid the potential fitness costs of cuckoldry from unfaithful female mates, or reduced investment and protection from unfaithful male mates. Cues to infidelity stem from hormonally dependent traits, such as the degree of facial and vocal sexual dimorphism (male masculinity, female femininity). These cues contribute to perceptions of infidelity independently of their attractiveness and also have implications for mate selection.

Male Masculinity

Research suggests that women use markers of underlying testosterone to assess the risk of male infidelity. Relatively high levels of testosterone are necessary for the development of masculine male facial features, such as a broad jaw and prominent brow ridge (for review see [Feinberg 2008](#)). Similarly, the development of a lower-pitched voice (aka vocal masculinity) is dependent upon pubertal levels of testosterone (for review see [Feinberg 2008](#)). Among men, both vocal and facial masculinity vary with individual differences in levels of testosterone, and both traits have an influence on perceptions of infidelity.

In two separate studies, women listened to men's voices which were artificially manipulated to be higher or lower in pitch and were asked to select who was more likely to cheat on their romantic partner ([O'Connor et al. 2011, 2014](#)). Women were significantly more likely to select the lower-pitched male voice as presenting a greater risk of infidelity. Similarly, when asked to rate the likelihood of infidelity from men's faces which had been manipulated to appear more masculine or feminine, women rated masculinized male faces as more likely to cheat than feminized men's faces ([Kruger 2006](#)). When taken together, these studies demonstrate that women associate infidelity risk with the expression of testosterone both in men's voices and faces.

Male facial masculinity also has an important role in the accuracy of perceptions of infidelity risk. [Rhodes et al. \(2013\)](#) recorded men's history of infidelity and photographed their faces. Female participants then rated the likelihood of infidelity from photographs of the men's faces. Women were able to accurately assess the risk of infidelity from facial photographs alone, but only when viewing masculine men's faces. This suggests that perceptual associations between masculinity and infidelity risk have a role in women's ability to discriminate between faithful and unfaithful potential mates.

Women may perceive testosterone-dependent traits as associated with an increased risk of

infidelity owing to associations with unfaithful behavior. Among men, higher levels of testosterone are associated with higher reported rates of infidelity ([Booth and Dabbs 1993](#)). Men who possess other masculine, testosterone-dependent, traits, such as broad shoulders relative to narrow hips, also report a higher frequency of infidelity ([Hughes and Gallup 2003](#)). Therefore, men with relatively high testosterone are likely to possess masculine faces and voices, as well as engage in extra-pair sex, and are more likely to be perceived as romantic cheaters.

Female Femininity

Among women, relatively feminine facial and vocal traits influence perceptions of infidelity risk. Feminine women's faces are characterized by a small jaw and large eyes, whereas feminine women's voices are higher in pitch. Both vocal and facial femininity are associated with relatively higher levels of estrogen (for review see [Feinberg 2008](#)) and also have similar influences on perceptions of infidelity. Men perceive women with higher-pitched voices as presenting a greater risk of infidelity than women with lower-pitched voices ([O'Connor et al. 2011](#)). In comparison to masculine-looking women's faces, men perceive feminine-looking faces as more likely to be unfaithful ([Rhodes et al. 2013](#)). However, men appear to be unable to accurately assess the risk of infidelity from individual women's faces, regardless of the degree of facial sexual dimorphism ([Rhodes et al. 2013](#)).

Men's perceptions of increased infidelity risk from women possessing feminine traits may be owing to associations between estrogen levels and individual differences in the propensity for infidelity. Women with higher levels of estrogen report a greater future likelihood of adulterous behaviors ([Durante and Li 2009](#)). Women who possess other estrogen-dependent traits, such as wider hips and a smaller waist, also report higher rates of extra-pair sex ([Hughes and Gallup 2003](#)). This suggests that men's perceptions of increased infidelity risk from feminine women's faces and voices could be based on a kernel of truth.

The Role of Attractiveness in Perceptions of Infidelity

When examining perceptions of infidelity from sexually dimorphic faces and voices, the attractiveness of such traits could contribute to perceived infidelity risk. It is possible that female femininity and male masculinity are perceived as presenting a greater risk of infidelity because of differential sexual opportunity among attractive individuals. Furthermore, physical attractiveness in general has been linked with perceptions of infidelity risk (Rhodes et al. 2013; Waynforth 2001). Indeed, individuals with more attractive voices report higher rates of infidelity (Hughes et al. 2004). In order to examine this possibility, O'Connor et al. (2011) tested listener's perceptions of both infidelity and attractiveness. The results indicated that vocal attractiveness ratings were unrelated to perceptions of infidelity. In addition, Rhodes et al. (2013) found that men's facial attractiveness was not related to either women's perceptions of infidelity or the accuracy of their perceptions. Therefore, sexually dimorphic faces and voices function as a cue to infidelity risk, over and above any potential contributions of attractiveness.

Implications for Mate Choice

Given that the same traits that influence perceptions of infidelity also influence perceptions of attractiveness, it is important to consider the potential implications for mate choice. Both men and women value fidelity in a potential long-term mate, and disregarding cues to infidelity risk could increase the probability of future infidelity-related fitness costs. Consequently, cues to infidelity are likely to have a greater impact on mate preferences in the context of a long-term relationship. For instance, the more women attributed infidelity to lower-pitched voices, the weaker their preferences were for lower male voices for long-term versus short-term relationships (O'Connor et al. 2014). Thus, perceptions of infidelity risk from men's voices may function as an adaptive heuristic that helps

women avoid the potential fitness costs that could result from infidelity, such as the loss of resources and protection, yet allows the potential for women to obtain genetic benefits from short-term mating with high-testosterone males.

Conclusion

Facial and vocal sexual dimorphism provides a rich source of information when assessing potential mates for the probability of future infidelity. The influence of facial appearance and voice pitch on perceptions of infidelity is consistent with the associations between extra-pair behavior and the hormones underlying these traits. Individuals who attend to such cues may be better able to avoid the potential fitness costs stemming from partner infidelity.

Cross-References

- ▶ [Facial Attractiveness](#)
- ▶ [Infidelity](#)
- ▶ [Preferences in Long- Versus Short-Term Mating](#)
- ▶ [Secondary Sexual Characteristics](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Testosterone](#)
- ▶ [Voice Pitch](#)

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Perceptions of Race

- [Race as a Social Badge \(Kurzban\)](#)

Percussive Lithic Tools

- [Stone Hammers](#)

Performance

- [Play and Social Learning](#)

Performance Enhancement

- [Information About Likely Combat Success](#)

Perinatal Depression

- [Postpartum Depression](#)

Peripartum Depression

- [Postpartum Depression](#)

Peripheral Auditory System

- [Auditory System, The](#)

Permanent Marking

- [Scarification](#)

Permissibility of Reproduction

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Synonyms

[Antinatalism](#); [Natalism](#)

Definitions

The permissibility of reproduction refers to the debate over the morality and ethics of reproducing.

Introduction

Having a child is one of the most significant decisions a person can make within their lifetime. This decision has the potential to impact not only the parents but also the child and society at large. However, it is considered by some to be one of the most rewarding decisions that a person can make. Regardless, it is a decision that requires consideration of financial, physical, and emotional readiness. Much of the debate surrounding the ethics of procreation is centered around discussing the situations wherein procreation may or may not be

permissible. For example, if during pregnancy parents find out their child will have a debilitating congenital disease, would it be ethical to bring that child into the world knowing that it may not have a good quality of life? Natalists agree that there are situations, perhaps even most situations, wherein procreation is ethical. However, there is disagreement about the precise factors that may lead to procreation being unethical. Additionally, there is another academic group – the antinatalists – who also contribute to the debate on the ethics of procreation. The antinatalists assert that procreation is impermissible and, therefore, there are no situations wherein it may be ethical to procreate.

The Natalist Debate

Between natalists, there are some who find simply questioning the ethics of procreation to be offensive (Anscombe 1989). Others believe that, considering the personal nature of the decision, procreation cannot be subject to ethical debates or moral duty (Little 1999). However, many natalists concede that, given the high consequences, procreation does need a defense (DeGrazia 2012). There is disagreement towards how strong this defense must be. Some believe that it is sufficient for prospective parents to simply want to provide a good life for their child, whereas others believe that desire is insufficient and that there must be a reasonable expectation that the parents' will be able to provide the child with a good quality of life (e.g., financial stability). Still others believe that reasonable expectation is insufficient and it is necessary to select for children that have the best chance of a good life (i.e., genetic screening; Douglas and Devolder 2013; for further discussion on the natalist debates, see Hannan et al. 2015).

The Antinatalist Debate

Different versions of antinatalism have been proposed and defended based on different assumptions. For example, it has been proposed that procreation is unethical because of the lack of

consent from the child being brought into the world (Shiffrin 1999). Throughout an individual's life, he or she will experience a vast amount of pain and suffering, which arguable no one – not even a parent – has the moral right to force upon another without the person of interest's consent. Since consent cannot be attained prior to conception, procreation is thus never permissible (Shiffrin 1999). Others have argued that the worst outcome imaginable for an individual vastly outweighs the best outcome possible (Hayry 2004). This perspective contends that because it is impossible to know before procreation whether a child will have a good or a bad life, it is not morally permissible to bring a child into a world wherein they have a chance of their life having the worst outcome possible (Hayry 2004).

Another argument for antinatalism is that the suffering of sentient beings should always be avoided. Antinatalists extend this principle to state that there is harm in coming into existence and this harm greatly outweighs the benefits of existence. The asymmetry argument, proposed by David Benatar, a lead advocate of antinatalism, states that when coming into existence there are harms (–) and benefits (+) associated with existence. Alternatively, there is an absence of harm (+) and an absence of benefits (neutral) associated with nonexistence. Herein lays the asymmetry: whereas the harm (–) and benefit (+) may neutralize each other, the absence of harm (+) and the absence of benefit (neutral) results in a net positive for nonexistence (for a more detailed explanation and discussion of the asymmetry argument, see Benatar 2006).

Natalists often have one of two responses to the asymmetry argument. First, that suffering is not necessarily bad (e.g., Benatar and Wasserman 2015). They contend that suffering is what allows humans to appreciate the benefit, and that suffering can result in growth and actually improve life satisfaction and quality of life in the long term. The second response has to do with the asymmetry argument, whereby many natalists disagree with a fundamental tenant of the argument (see Smuts 2014). Specifically, natalists believe that the harm (–) and benefit (+) of coming into existence do not necessarily neutralize each other, nor do they believe that the harm (–) outweighs the benefit

(+). Rather, they contend that, in many cases, the benefit of existence far outweighs the harm. To support this claim, they point to the many joys of life (e.g., food, friends, and positive experiences) as well as self-reports from people. The vast majority of people, if asked, would report that their life contains more good than bad, and that they are happy to exist. How then, natalists ask, does the belief that one's life has more harm than benefit remain (Benatar and Wasserman 2015)?

The response from antinatalists originates from a phenomena discovered by psychological research called *the optimism bias*. The optimism bias describes the tendency for humans to believe their life is significantly better than it actually is. For example, researchers found that after a major accident that resulted in a loss of a limb or paralysis, participants had a decrease in perceived quality of life. However, within months, participants' reports of quality of life were back at their baseline without a significant change in their life circumstances. Furthermore, antinatalists point to the many harms and discomforts of life that are overlooked because they are shared among every human. These include hunger, thirst, exhaustion, and stress. Although it may seem unusual to count these as harms, Benatar asks his readers to imagine an alien species that never had any of these human harms. If this species were to come into contact with humans, would they view these daily annoyances as harm? Benatar contends that simply because a harm is shared by all members of a species does not make it less of a harm (Benatar and Wasserman 2015).

Conclusion

The debate over the permissibility of procreation is on an unorthodox topic that many believe should not even be subject to discussion. As outlined above, there is disagreement concerning not only the situations in which procreation is unethical but also whether there are any instances where procreation is ethical. Regardless of these differing theories, there is a general agreement between academics debating procreation that this is a topic that deserves careful and thoughtful consideration.

Cross-References

- [Better Never to Have Been](#)
- [David Benatar](#)
- [David Wasserman](#)

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Perpetrators Mostly men

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Synonyms

[Male aggression](#); [Male offenders](#); [Male violence](#);
[Males and crime](#)

Definition

Most crime, especially violent crime, is committed by males, which might be explained by mating efforts as well as exposure to specific androgens.

Introduction

It has been widely shown that males commit more crime than females and that males commit more violent crime than females. Several criminological explanations have been proposed as to why this happens. Evolutionary psychology provides a unique insight into human behavior that considers biological and genetic aspects, derived from the evolution of the species, that remain relevant and essential in the explanation of all human behavior, including criminal behavior.

Gender Differences in Criminal Involvement: Why are Perpetrators Mostly men?

Research has widely shown that males offend more and more violently than females, being that this relationship seems to hold for most crimes (except prostitution) and across different locations (Farrington and Painter 2004; Lancot and LeBlanc 2002; Moffitt et al. 2001).

According to Darwin, aggression, such as any other trait, exists to ensure survival. From an evolutionary standpoint, individuals had to fight for resources, survival, and mating opportunities, being that those who were more aggressive and competitive were more likely to survive, reproduce, and transmit their genes onto the next generations. Moreover, the fact that males are more aggressive than females is observed in all mammals and explained through sexual selection of partners. This sexual selection usually takes place when females select male partners, promoting inter-male competition for sexual selection and reproduction (Archer 2009; Darwin 1859, 1871; Lindenfors and Tullberg 2011).

Although the purely evolutionary perspective remains valid, research has evolved, incorporating psychological and social elements that helped explain why males remain more aggressive and more involved in crime than females (Archer 2009).

Evolutionary psychology asserts that human behavior, such as the behavior of any other animal, is a product of evolution processes that result from adaptations to ancestral environments, being that these adaptations occurred in a given cultural context and are activated by relevant environmental triggers (Walsh and Beaver 2008). These adaptations to ancestral environments developed to ensure reproduction and survival. In this way, it is reasonable to conclude that both prosocial and morally accepted behaviors and violent/criminal and morally unacceptable behaviors had a degree of usefulness in adapting to ancestral environments, increasing fitness, and ensuring sexual selection (Walsh and Beaver 2008). It is important, however, to note that these adaptations were to ancestral environments, not to the current modern society; thus even if considered maladaptive and morally condemnable nowadays, violent and aggressive behaviors provided some advantage in ancestral environments. Moreover, it is relevant to clarify that specific criminal behaviors are not actual adaptations (genes do not code for specific behaviors such as homicide or fraud) (Walsh and Beaver 2008).

There are several approaches to the evolutionary psychology's study of criminal and predatory behavior, being that most of these approaches focus on the reproductive strategies and behaviors that derive from these strategies. For the most part, research tends to focus on two types of behaviors that are directly related to reproductive strategies: parenting status and mating effort (Walsh and Beaver 2008). The behaviors and characteristics that have been associated to the mating effort are those more commonly associated with criminal behaviors, such as deceitfulness, impulsiveness, sensation seeking, and aggression, while behaviors that derive from parenting are more prosocial and cooperative, including empathy, altruism, and conscientiousness (Daly and Wilson 1988, 1990, 1997; Walsh and Beaver 2008; Wilson and Daly

1992, 1993). Other research has focused more on genetic (Y chromosome) and neurohormonal (testosterone) differences between males and females that account for differences in competition and aggression (e.g., Ellis 2003, 2005).

Matting Effort: Competition, Fitness, and Sexual Selection

Daly and Wilson (1988, 1990, 1997; Wilson and Daly 1992, 1993) applied the notion of sexual selection to studies of violent and criminal behaviors, specifically to homicide and intra-family violence. According to the authors, the sex differential observed in violent behavior reflects the evolution of the human male psyche to become more prone to accept risk-taking behaviors in situations of competition, specifically competition for resources and sexual partners by males (Daly and Wilson 1990, 1997; Wilson and Daly 1985).

Daly and Wilson (1988, 1990, 1997) strongly focused on the study of same-sex homicide, as they considered it to be the “best prototype of crime” (Daly and Wilson 1997, p.54), i.e., homicide is universally considered a serious crime, it is more reliably reported than other forms of crime, and finally it is an extreme form of conflict resolution, allowing to better explore the variety of factors that explain interpersonal conflict throughout the life course (Daly and Wilson 1997). Moreover, homicide rates are much higher among males than females. The authors observed that males had a significantly higher rate of same-sex homicides when compared to females, which is partially explained by intra-male competition for resources (Daly and Wilson 1988, 1990). This competition for resources is greater among males due to a greater variance in fitness among males, when compared to females, and thus a greater variability in sexual selection and reproductive success (Daly and Wilson 1997; Walsh and Beaver 2008). This reinforces the male’s need to focus on matting efforts, which are inherently more competitive and aggressive, while females are more focused on parenting efforts, i.e., on ensuring the survival of their offspring, which is more altruistic and collaborative (Walsh and Beaver 2008).

In line with this assumption, the authors observed that same-sex homicide is more

common among men that have fewer resources (Daly and Wilson 1988, 1990). Specifically, for males with lack of resources, an aggressive challenge of other males may be the only way to ensure successful sexual selection by females and consequent reproduction (Daly and Wilson 1988). This competition for resources, thus, allows to explain both instrumental/rational crimes as well as expressive/irrational crimes (Daly and Wilson 1997).

Although the authors strongly focused on same-sex competition and crimes, as individuals from the same sex tend to compete more as they desire the same type of resources, not all crimes, namely, homicide, are about sexual rivalry, being that many of the criminal actions observed are status crimes (Daly and Wilson 1997; Wilson and Daly 1985).

Daly and Wilson (1997) further propose that individuals are active agents in their behaviors, conducting a cost-benefit analysis. This cost-benefit analysis, which underlies evolutionary psychological explanations of behaviors, is not just a rational decision-making process but rather strongly determined by the process of natural selection (Archer 2009; Daly and Wilson 1997).

Finally, the authors approach the matter of violence against women. To this end, Wilson and Daly focused mostly on intra-family violence in the form of violence against wives (Daly and Wilson 1997; Wilson and Daly 1992, 1993). The authors propose that violence against wives could be explained as a way to deter these females from engaging in behaviors or courses of action that would threaten the male’s fitness and access to resources (e.g., infidelity) (Daly and Wilson 1997; Wilson and Daly 1992, 1993).

Other authors have proposed that rape or sexual violence of males against females might also be a way to overcome competition and ensure reproduction. Cashdan (1993) proposed that males can adopt one of the two reproductive strategies: (a) the Dad strategy, where males commit to a single female, complying to the female preference and helping raise the offspring, or (b) the Cad strategy, where males treat females as conquests, trying to trick or force them into sexual relationships, thus ensuring offspring, but not committing to the female (Cashdan 1993; Walsh and Beaver

2008). On the extreme of the Cad strategy are psychopaths, with reduced emotional responses, and reduced morality, although these tend to be a minority of males (Walsh and Beaver 2008).

Genetic and Neurohormonal Differences: Evolutionary Androgenic Theory

Other researchers have proposed that levels of testosterone may help explain the differences in aggression in males, as well as the increase in aggression that occurs during adolescence. Ellis has developed several studies on the influences of testosterone on behavior and aggression and proposed the evolutionary androgenic theory (ENA), which focuses on explaining offenses that cause harm to other individuals. ENA is based on two propositions: evolutionary and neuroandrogenic (Ellis 2004, 2005).

The *evolutionary proposition* posits that males engage in more violent crimes than females as a result of evolution, specifically due to the female choice, i.e., the selection of mates that were strong protectors and reliable providers, but who also tended to be more competitive. This preference led to a transmission of genes of more competitive males to future generations (Ellis 2004, 2005). This proposition closely matches what was proposed by other evolutionary scholars and studies on sexual selection.

The competitive behavior, nowadays, can be seen as placed along a continuum of competitive/victimization behavior, where the more sophisticated version of this behavior would be associated with profit- or nonprofit-making commerce and a cruder version of this behavior associated to more violent property offenses. Based on this, the author proposes that genes ought to be responsible for a great part of the phenotypic variation observed; also, given the clear differences in competitive and violent behavior between both sexes, it stands to reason that part of this variation would be caused by the Y chromosome (Ellis 2004, 2005). However, the theory does consider the possibility of female criminality; Ellis (2004) proposed that competition will exist in both sexes for resources to rear offspring; however, male competition and victimization behaviors will always surpass that of females. Moreover, females who are able to attract and select males that have access

to more resources will have less competitive tendencies (Ellis 2004).

The *neuroandrogenic proposition* states that testosterone plays a central role in the competitive/victimization behavior. During gestation, different testosterone levels are present in the womb, being these levels much higher for males than for females (produced after the development of the testes); these higher levels of testosterone will masculinize the fetus' brain. The presence of higher level of testosterone can promote the competitive/victimization behavior by causing sub-optimal arousal (decreased sensitivity to adverse consequences), by overstimulating the limbic system, or by leading to a greater neocortical function of the right hemisphere and decreased function of the left hemisphere associated with a less "empathy-based moral reasoning" (Ellis 2005, p. 293). There are two neurological processes that will further influence male competitive victimizing behavior, the individual's intelligence, i.e., their ability to learn, and their cognitive functioning, specifically ability to plan (Ellis 2004, 2005).

In this sense, individuals with more sophisticated behaviors usually present a more efficient cognitive functioning and higher intelligence, being able to better control their competitive expression in a more socially accepted manner, while those individuals with less efficient cognitive functioning and lower learning ability will resort to cruder competitive behaviors (Ellis 2004, 2005). Moreover, males who receive higher levels of exposure to testosterone during critical developmental periods are more likely to become offenders and more likely to remain offending over the life course than males that were exposed to low-moderate levels of testosterone (Ellis 2004).

Conclusion

Overall, evolutionary psychology has a unique perspective and contributions to the explanation of criminality and why it tends to be more prevalent in males. In short, this perspective proposes that males tend to exhibit more competitive and aggressive behaviors, which were evolutionary acquired as a response to ancestral environments

and a need to ensure reproduction and preservation of the species. In modern society, many of the criminal behaviors observed in males can still be explained by sexual and status completion in order to ensure reproduction. These innate tendencies observed in males, much more than in females, might be explained by a greater variability in access to resources observed in males, as well as by increased exposure to androgens, specifically testosterone, which will influence brain structures, specifically promoting the development of areas responsible for more aggressive and competitive behaviors. Taken to the extreme, these behaviors assume more violent and even criminal characteristics, which appear to be more common in males with lack of access to resources as well as those who have lower moral constraints.

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Persistence

► Object Permanence

Personal Distress

► Gratitude, Sympathy, and Empathy

Personal Memory

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Synonyms

Individual perception; Personalized experience; Self-recollection

Definition

Individual perception of intake information or events from a certain moment in time.

Introduction

If there is one proposition on which all psychologists seem to agree, it is that memory is useful. Memory allows organisms to adjust their behavior on the basis of information they acquire ontogenetically, through their experiences with the world. This connection between personal experience, memory, and behavior implies a close relationship between learning and memory. Memory in biological systems always entails learning as it constitutes acquisition of information and learning implies retention of such information (Tulving 1995). Recognizing this, psychologists have long exploited learning paradigms to study the properties of memory.

Self-Observation

Defining the self has challenged psychologists and philosophers for centuries. Self-observation can be defined as the ability to consider what is being observed about the self. It is the self-reflective function that allows one to marshal the resources of self-awareness to alter prediction errors. This ability provides a sense of agency in observing, planning, deciding, and evolving toward a future goal.

Self-Observation as a Social Process

Humans were provided with insightful and novel means of not only expressing but also observing their own experience. This would not be possible if experience was a purely individual and private matter. Instead, we live in an intersubjectively shared and immanently meaningful world. Humans exist as beings in constant communication with others, through which we come to develop shared perspectives on our experience. Introspective self-consciousness is derivative of consciousness of others and not vice versa.

Internal thought is a form of inner dramatization of social conduct and is thus necessarily bound up with social meanings.

Mead (1910) argued that “Other selves in a social environment logically antedate the consciousness of self which introspection analyzes.” In other words, the act of self-reflection presupposes social interaction with others. The introspection involves the incorporation of the other into the self. This conceptual move naturalizes the act of self-reflection by showing that it is an outgrowth of a social process. One’s own gesture does not initially have meaning for oneself. The gesture only has meaning for others, which is their response to the gesture. The establishment of shared meaning requires the existence of stable social institutions with interchangeable social positions – such as buying and selling. Since a vocal gesture can be heard from both sides of a social act in a social practice, it takes on a dual meaning and enables the movement from one social perspective to another. Introspective self-reflection is only possible through a history of interaction with others in social institutions.

Self-Observation and Consciousness

Self-observation results in cognizance of auto-information, such as intentions, expectations, feelings, cognitions, behaviors, and impact on others, and the ability to introspect on one’s own thoughts and to realize the relation of self to one’s social and cultural environment (Stuss and Benson 1983). It is associated with the capacities to distinguish inner from outer reality, pretend from “real” modes of functioning, and intrapersonal mental and emotional processes from interpersonal communications (Fonagy and Target 1997).

This transtheoretical process involves individuals becoming aware of and learning about their own functioning in order to change maladaptive responses and generate new responses for the future (Beitman et al. 2005). In helping the individual focus attention on their own self and idiosyncratic patterns, an external source, such as a psychotherapist, could assist in activating self-observation. This process serves as a tacit common thread woven among the different psychotherapies.

Activation of self-observation is collaboratively employed by practitioner and client within all psychotherapeutic orientations. Self-observation emerges from self-awareness, which, in turn, relies upon consciousness. Consciousness requires mobilizing functional brain structures, including the reticular activating system, and provides the platform for awareness. Awareness is the potential to be conscious of specific content such as objects, persons, and ideas. Self-awareness or “autoeotic consciousness” (Wheeler et al. 1997) is the potential to know the self and the self in context. Self-observation refers to actively scanning one’s inner landscape, mentalization, and the ideas in other people’s minds as well as what others think of the self (Baron-Cohen et al. 2000).

Self-Observation Within Psychotherapy

For many individuals seeking therapy, confusion, distraction, or troublesome symptoms may impede effective self-observation. Storms in the internal and external environment cloud vision, precluding accurate perception of one’s inner landscape. Although self-observation is a normal and adaptive capacity, it can be difficult to preoccupy oneself with such maladaptive thoughts, feelings, and behaviors. A safe and confiding therapeutic relationship offers a client the haven of an interpersonal relationship in which to observe the self, which is necessary to create new ideas and templates of expectations and actions to meet goals. Activation of self-observation thus empowers clients to make more informed decisions, alter prediction errors, create intentions, and plan courses of action (Pally 2004), resulting in increased freedom of choice, increased autonomy, and a wider scope of comprehension (Deikman 1982).

Inceptive and Derived Memory

It is useful to distinguish inceptive from derived memories as they serve survival. Inceptive memories are representations of external input stored in the way they were encoded at the time at which they were first experienced. Many episodic

memories appear to be inceptive; they often contain perceptual detail, proprioceptive information, emotion qualia, a sense of the self as present in the encoding situation, and the sense that the memory is very similar to the original experience. But not all inceptive memories are episodic. It is logically possible to have an inceptive memory about a specific event involving the self without its being episodic in character. It would not be episodic if it lacked the subjective sense of self in space and time that is diagnostic of episodic memory. A derived memory system together with its inferential machinery prepares answers or pre-processes information into usable and ready forms to facilitate decisions and judgments of a specific type that would otherwise be detrimental if they had to be computed from raw data on demand.

Human Memory and Computation

The computational operations that generate derived memory are not limited to mere extraction of information from inceptive memory. A derived memory can contain information not present in any of the inceptive memories on which it was based, generated by procedures that made inferences from the inceptive data. A derived memory may, in some cases, be the output of the same decision process that uses it at a later time. For instance, if one needs to decide at Time 1, on the basis of behavioral episodes, whether Person Y is honest, the conclusion might be stored as a derived memory for use at Time 2. A trait summary is a form of derived memory; a stored episode is an inceptive memory. Because of their advantages, human memory may be full of independent, derived memory stores linked to various inceptive memory stores (Nadel 1994). The linked memory stores of abstracted personality traits and behavioral episodes that exemplify those traits may prove to be a model system that can illustrate properties that are common to many memory stores.

Adaptive Function of Memory and Its Properties

The adaptive function of information storage is intrinsically prospective. It is used to support future decisions and judgments, which cannot be

known in advance with certainty. To the extent that the character of subsequent decisions and judgments can be predicted, the memory system can be tailored to flag relevant information and precompute variables that are required to make them – that is, it can develop a derived memory store. This set is indefinitely large and hence precluded by limitations on computational and memory resources. In functional terms, factors that should govern the number and type of derived memory stores include (a) predictability, the existence of factors, either ontogenetic or phylogenetic, that allows the successful anticipation of likely varieties of future judgment or decision types; (b) importance, the value of those judgments or decisions ought to justify the costs; (c) urgency, the requirement that such judgments be made quickly; and (d) economy, the number of judgments or decisions supported by a derived memory store should be proportionately large with respect to its size. The use of trait summaries in making decisions about social interactions meets all four criteria.

Benefits and Disadvantages

Storing semantic summaries has both advantages and drawbacks. Direct retrieval of precomputed representations (derived memory) economizes on online computation and is fast. But it takes up increasing amounts of memory the larger the set of representations that must be precomputed and on tap and may provide information that is no longer up to date. In contrast, procedures triggered online that take inceptive memories as input economize on derived memory and provide up-to-date information. But they are expensive computationally and increasingly slow, the more computational steps that are involved. An architecture designed functionally would be shaped by these trade-offs, using different mixes of memory versus computation for different types of adaptive problem (Pinker 1997, 1999). Decisions about personality traits provide a case in point.

Trait Summaries

Dynamically, when the data set of relevant events is small, judgments about personality traits appear

to be made predominantly based on retrieved behavioral episodes (Klein et al. 1997; Klein and Loftus 1990). As the behavioral evidence grows, judgments are increasingly made by accessing an emerging trait summary and decreasingly by accessing relevant episodes. When the amount of experience is high, the semantic summary is well developed, and trait judgments are made by accessing this knowledge (Klein et al. 1997; Klein and Loftus 1990). This process is faster than retrieving and considering individual instances (Klein et al. 1992), and it bypasses and inhibits this other judgment route. Evidence suggests that semantic trait summaries are constructed on the basis of the same set of behavioral episodes that are input into the episodic store (Sherman 1996), although supplementation from other sources of information has not been ruled out. Neurologically impaired individuals who exhibit an inability to retrieve individual events show no apparent impairment in their ability to make accurate trait judgments (Klein et al. 1999) and even maintain the ability to revise their trait judgments based on new episodes they cannot recall. This suggests retrieval of behavioral episodes for trait judgments lies outside conscious awareness. It further argues that either updating of semantic information occurs as each episode is experienced or else the procedures involved in updating do not require conscious access to the episodic store (Sherman and Klein 1994).

Stored Episodes

Trait summary is valuable in human evolution and survival as it fosters speedy access to information and avoidance of redundant and costly computation. Nevertheless, a summary lacks information present in the episodes from which it was derived. Retrieving a trait summary may be faster than constructing a judgment online from a database of episodes, but it is necessarily less accurate. Maintaining a database of inceptive, episodic memories solves several problems that a trait summary cannot. New information may cause previous episodes to be reinterpreted, drastically changing one's judgments of a person or a situation. Keeping a database of episodes is helpful even when a drastic reinterpretation of previous

events is not called for. Judgments can be revised in light of new information.

Scope Hypothesis

The scope hypothesis asserts that the function of priming inconsistent episodes is to place boundary conditions on the scope of a semantic summary. An excellent package of speed and accuracy can be engineered into a decision system by jointly activating a trait summary and episodic memories that are inconsistent with it. Trait self-descriptiveness judgments should activate trait-inconsistent, but not trait-consistent, behavioral episodes. In the event that scope hypothesis is supported, one would expect that trait-inconsistent episodic memories are primed by retrieval of a trait summary from semantic memory.

Boundary Conditions on the Scope of Generalizations

To rely on semantic memory alone is to sacrifice accuracy for speed as trait summaries lack the resolution of an episodic memory. Although trait judgments have predictive validity, the behavior of an individual manifests a great deal of situation specificity (Funder 1995). Episodic memories are situation-specificity incarnate. They are records of how particular people behaved in specific situations. A system engineered to retrieve, along with a generalization, episodes that place boundary conditions on its scope would achieve the best of both worlds: speed courtesy of semantic memory and accuracy courtesy of episodic memory.

Decision Context

The decision context should determine when boundary conditions are needed and which kinds of episodes would be relevant. Because decisions regarding personality traits are not amenable to all-or-none answers, it would be reasonable to assume that the trait summary takes a quasi-quantitative form. Thus, when the individual is asked if a certain trait describes them, possible answers might be “usually,” “sometimes,” or “rarely.” Boundary conditions would be episodes

in which the behavior did not meet the criteria for that trait. This should be true for any level the trait summary specifies, even “rarely.” This is because the decision context calls for a generalization about it; the function of activating episodes is to place boundary conditions on that generalization. The issue is “How often is Person Y friendly, and under what conditions is she or he not?” The decision rule activated is designed to make a judgment about the trait being asked about, whether the question originates with another person or with the individual making the judgment.

Different decision rules are designed to retrieve different kinds of information from memory. The type of decision being made matters, because that determines which search engine gets activated, which will determine which array of memory systems gets searched. When asked to trait-categorize their own behavior, subjects should retrieve a trait summary and episodes inconsistent with the trait they are being asked about.

The Self-Study

It was examined whether accessing a trait summary about the self would prime trait-inconsistent episodes but not trait-consistent ones (Klein et al. 2001). Subjects were presented with a list of trait adjectives and asked to perform one of three tasks with them. The describe task asked subjects to decide whether the stimulus trait describes them; the recall task asked subjects to retrieve a specific instance in which they manifested the stimulus trait; and the define task asked subjects to generate a definition for the stimulus trait. If the scope hypothesis is correct, then deciding whether a trait is self-descriptive will activate a summary representation and episodes inconsistent with the trait being asked about. Empirically, one should observe two things.

The results showed that deciding whether a trait describes oneself facilitates retrieval of trait-inconsistent episodes, which suggests that these judgments activate memories of behaviors inconsistent with the trait being judged (Klein et al. 2001). By contrast, there was no evidence that trait self-descriptiveness judgments

facilitated retrieval of trait-consistent episodes. Based on the outcome of the experiment, it is inferred that decisions about whether a trait describes oneself do not activate trait-consistent behavioral memories. That trait-inconsistent, but not trait-consistent, episodic memories are primed by retrieval of a trait summary from semantic memory is just what one would expect if the scope hypothesis were correct.

The Mother Study

This study had two primary objectives; first, it aimed to extend the generality of the scope hypothesis by testing whether judgments about a well-known other also conform to its predictions and, second, to address the finding that activation of trait-inconsistent behaviors occurred regardless of whether the trait judged fell in the high, medium, or low self-descriptiveness categories. This finding can be accommodated within the scope hypothesis by assuming that trait knowledge about the self is represented in summary form across levels of trait self-descriptiveness. According to the model of mental representation of trait knowledge about others, one's representation of a person's traits varies with the amount of experience one has had with that person. If the amount of experience is not sufficient to support abstraction, then trait knowledge will be represented only at the level of behavioral memories. Trait judgments about the person, therefore, must be based on inceptive behavioral memories, that is, on episodes. However, as the amount of experience becomes sufficiently large, trait knowledge is increasingly likely to be abstracted and represented in summary form.

The study results illustrated that for traits highly descriptive of one's mother, ones for which a summary should exist, trait-inconsistent episodes were primed, but trait-consistent ones were not. For traits only moderately descriptive of one's mother, ones for which there should be no summary, the opposite pattern was found. Trait-inconsistent episodes were not primed, but trait-consistent ones were.

The results of this study strongly support the scope hypothesis as they allow for comparisons in

priming when trait summaries are present versus absent. When a decision is made by accessing a trait summary, search engines should simultaneously retrieve inconsistent episodes to provide information about the conditions under which the summary ceases to be useful. Thus, trait-inconsistent behaviors were primed when a decision about one's mother was made by accessing summary representations of her traits. But when summary representations were absent, they could play no role in decision-making. This explains why trait-inconsistent behaviors were not primed in the medium-descriptive condition. According to the scope hypothesis, when no generalization has been accessed during a decision task, there is no representation whose scope needs to be delimited.

Summary Representation

Humans are sensitive to the summary statistics of the visual world. They derive this information from complex scenes, often without explicit awareness. The visual system is susceptible to summary statistical stimuli about group or ensemble characteristics in the natural world. The summary statistics are derived across a host of visual domains, ranging from average orientation to the average expression from crowds of faces. The ease with which people can detect an outlier suggests their representations of categories of objects incorporate some notion of what is average and of the upper and lower limits in the normal variability within the dimension in question. When viewing a set of objects, a particularly large or small member of the set will stand out and will be readily detected (Hodsoll and Humphreys 2001).

Summary Representation as a Function in Scope Hypothesis

It has been argued that generalizations from semantic memory allow speedy decisions, but at the cost of accuracy, whereas episodic memories provide accurate, situationally specific, information, but at the cost of speed. Nevertheless, both speed and accuracy can be engineered

into a decision-making system, if the system is designed to retrieve both kinds of information in the right combination. A generalization is most useful when its scope is delimited, that is, when it is accompanied by information specifying those situations in which it does not apply. Episodic memories that are inconsistent with the generalization can facilitate this function because they are broadband encodings of specific situations in which the generalization fails to predict the outcome. Interpretively, this task analysis constitutes the scope hypothesis. A decision rule needs a search engine that looks for summary information in semantic memory and, on retrieving it, looks for episodic memories that are inconsistent with that summary, ones that place boundary conditions on the summary's scope.

The Statistical Nature of Summary Representation

Research suggests that when subjects attend to a particular dimension of a set of items presented over an extended duration, they quickly learn about the central tendency of the set. However, it is unclear whether such learning can occur incidentally, when subjects are not attending to the relevant dimension of the set. Chris Oriet and Kadie Hozempa (2016) studied incidental summary representation over time exploring whether subjects could reproduce global statistical properties of a set presented over an extended duration when oriented to task-irrelevant properties of the set. Subjects were tested for their memory of its mean, its smallest and largest exemplars, the direction of its skew, and the relative distribution of the items. Subjects were able to accurately recall the average size circle, as well as the upper and lower boundaries of a set of 4200 circles displayed over an extended period. This suggests that even without intending to do so, they were encoding and updating a statistical summary representation of a task-irrelevant attribute of the circles over time. Such incidental encoding of statistical properties of sets is thus a plausible mechanism for establishing a representation of typically in category membership.

Change Blindness

The failure to notice differences in sequential scenes or images is a well-established phenomenon, suggesting that humans have a limited visual awareness from one moment to the next (Mitroff et al. 2002; Rensink et al. 1997). Although, on the surface, change blindness seems to suggest a sparse visual representation, an abundance of recent research has supported the notion that a failure to represent visual information is unlikely to drive this phenomenon. Much of the incoming visual input is preserved in spite of change detection failures (Beck and Levin 2003; Hollingworth 2003). For instance, Beck and Levin (2003) showed that observers could identify an object change in the absence of a durable representation of that object. Mitroff et al. (2004) demonstrated that this durable representation could potentially be used to aid in object identification. Hollingworth and Henderson (2004) found that visual scene information was preserved even when observers failed to detect a rotation in the scene. Research suggests that despite the limited conscious access revealed by change detection experiments, the "gist" of a scene remains accessible (Oliva and Torralba 2001; Potter 1976; Thorpe et al. 1996).

Given the fundamental and ubiquitous nature of summary statistical representation, Jason Haberman and David Whitney (2011) tested whether this kind of information is subject to the attentional constraints imposed by change blindness. They showed that information regarding the summary statistics of a scene is available despite limited conscious access. In a novel experiment, they found that while observers can suffer from change blindness (i.e., not localize where change occurred between two views of the same scene), observers could nevertheless accurately report changes in the summary statistics about the very same scene. In the experiment, observers saw two successively presented sets of 16 faces that varied in expression. Four of the faces in the first set changed from one emotional extreme to another in the second set. Observers performed poorly when asked to locate any of the faces that changed (changed blindness). However, when asked about the ensemble (which set was happier, on average),

observer performance remained high. Observers were sensitive to the average expression even when they failed to localize any specific object change. That is, even when observers could not locate the very faces driving the change in average expression between the two sets, they nonetheless derived a precise ensemble representation. Thus, the visual system may be optimized to process summary statistics in an efficient manner, allowing it to operate despite minimal conscious access to the information presented.

The Role of Attention

As the perceptual phenomenon occurs when a change in a visual stimulus is introduced, the observer does not notice it. Observers often fail to notice major differences introduced into an image, while it flickers off and on repeatedly. Researchers have found that shifting a person's attention, such as causing distraction, leads to increased change blindness. There is already evidence that summary statistical information operates beyond the focus of attention (Alvarez and Oliva 2008). Nonetheless, this has only been demonstrated with low-level features, such as features thought to be analyzed at the earliest stages of cortical visual processing, including orientation, contrast, and motion direction, which are expected to be processed in parallel (Watamaniuk and McKee 1998).

Conclusion

The aforementioned type of statistical summary learning appears to occur without conscious intent. Information taken in by the human visual system allows individuals to form statistical representations of sets of items. Memory evolved to supply useful, timely information to the organism's decision-making systems. Hence, decision rules, multiple memory systems, and the search engines that link them should have coevolved to mesh in a coadapted, functionally interlocking way. This adaptationist perspective suggested the scope hypothesis: When a generalization is retrieved from semantic memory, episodic memories that are inconsistent with it should be

retrieved in tandem to place boundary conditions on the scope of the generalization. Using a priming paradigm and a decision task involving person memory, the researchers tested and confirmed the scope hypothesis. The results support the view that priming is an evolved adaptation. They further show that dissociations between memory systems are not absolute and that independence exists for some tasks but not others.

Cross-References

- ▶ [Episodic Memory](#)
- ▶ [Inceptive and Derived memory](#)
- ▶ [Scope Hypothesis, The](#)
- ▶ [Self-Observation](#)
- ▶ [Summary Representation](#)

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Personal Protection

► [Defending Against Attack](#)

Personal Value

► [Self-Esteem as Manipulative Status Communication](#)

Personality

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Synonyms

[Big Five](#); [Temperament](#)

Definition

Certain personality features predict individuals' deployment of mate retention behaviors.

Introduction

Benefit-provisioning personality features (those associated with greater likelihood of providing benefits to one's partner) are significantly correlated with certain types of mate retention behaviors.

The popular Big Five Model of Personality describes a taxonomy of personality broken down into five factors: openness, conscientiousness, extraversion (or surgency), agreeableness, and emotional stability (or neuroticism) (Goldberg 1992; McCrae and Costa 1987; Norman 1963). Mate retention behaviors result from evolved psychological mechanisms in response to the adaptive problem of retaining a mate in a relationship (Buss 1988).

Mate retention behaviors are described in a taxonomy of five categories (*direct guarding*, *intersexual negative inducements*, *intrasexual negative inducements*, *public signals of possession*, and *positive inducements*) further broken down into 19 mate retention tactics. Miner et al. (2009) demonstrated that mate retention behaviors can usefully be divided into two domains: *cost inflicting* (consisting of direct guarding, intersexual negative inducements, and intrasexual negative inducements) and *benefit provisioning* (public signals of possession and positive inducements).

A limited but growing amount of research has begun to investigate the relationship between Big Five personality factors and mate retention behavior, including benefit-provisioning mate retention. For example, de Miguel and Buss (2011) investigated the relationship between Big Five personality factors and the 19 tactics of mate retention. They found that neuroticism was positively correlated with many (16 of 19) mate retention tactics, including some which fall under the Miner et al. (2009) domain of benefit provisioning (e.g., appearance enhancement and

submission/abasement). de Miguel and Buss (2011) also found a positive relationship between conscientiousness and appearance enhancement and a negative relationship between conscientiousness and cost-inflicting mate retention. Agreeableness was negatively correlated with cost-inflicting mate retention but was not related to benefit provisioning. Extraversion was associated with both cost-inflicting (e.g., jealousy induction, punishment of infidelity threats) and benefit-provisioning (e.g., sexual inducements, appearance enhancement) domains of mate retention behavior. Openness was found to be positively correlated with sexual inducements and the use of love and care, both benefit-provisioning tactics of mate retention.

McKibbin et al. (2014) examined the relationship between heterosexual men's mate retention and both men's personality and their partner's personality and found mixed results. As in de Miguel and Buss (2011), men's neuroticism was positively correlated with both domains of mate retention, based on men's and their partner's reports. However, their partner's neuroticism was not related to men's mate retention. Conscientiousness was generally not related to men's mate retention, although men's reports of their partner's conscientiousness were related to benefit provisioning. Men's reports on their own or their partner's agreeableness were not related to mate retention in either domain. However, women's reports of their partner's agreeableness were negatively associated with cost inflicting and positively associated with benefit provisioning.

Conclusion

Researchers have only recently begun to investigate how individuals' personality may affect their mate retention behavior. More work must be done before firm conclusions may be drawn regarding the relationship between these variables. Importantly, research highlights that men's and women's perceptions of themselves and each other differ, and these differences may affect the deployment of mate retention behavior. More work is needed to expand this domain of research.

Cross-References

- ▶ [Mate Retention](#)
- ▶ [Mate Retention Strategies](#)
- ▶ [Oral Sex](#)
- ▶ [Personality, Gender, and Culture](#)

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Personality and Mate Poaching

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Synonyms

[Extramarital affair](#); [Infidelity](#)

Definition

Mate poaching is a behavior intended to attract someone who is already in a romantic relationship in order to form a short- or long-term mating alliance with her/him.

Introduction

Mate poaching is a frequent and potent form of romantic attraction in humans throughout the world (Schmitt et al. 2004; Schmitt and Shackelford 2008). Research on the large sample of participants from 53 nations across the 10 world regions has found that around 60% of men and 40% of women admitted trying to poach someone else's partner for short-term sexual relationship or a new long-term mating alliance, while nearly 70% of participants reported that someone had tried to poach them either for short-term or long-term relationship (Schmitt et al. 2004). Identifying personal characteristics related to mate poaching is an important step in understanding its causes and consequences. Namely, personality traits are related to the creation of adaptive problems, as well as to their solution especially in socially relevant situations such as mateships (Buss 2010). Previous research have consistently shown that personality characteristics are related to different mate poaching experiences, such as trying to attract a person who was already in a romantic relationship, the success in poaching attempts, the experience of being a target of poaching, being successfully poached, and the experience of having others attempted to obtain someone's partner away (being the victim of poaching). These aspects of mate poaching are usually assessed by Anonymous Romantic Attraction Survey (ARAS; Schmitt and Buss 2001) and the most frequently examined personality characteristics related to mate poaching are Big-five personality traits, Dark Triad (DT) traits, and Sexy Seven personality attributes (Schmitt and Buss 2000).

We have identified only 12 studies dealing explicitly with the relationships between

personality characteristics and different mate poaching experiences. All of them are cross-sectional, mostly carried out on the samples of college or university students, and rarely community samples. They examined mate poaching for a short-term, and only three of them focused on mate poaching for both short- and long-term sexual relationship. The largest amount of data have been obtained from International Sexuality Description Project (ISDP; Schmitt et al. 2004, 2017; Schmitt and Jonason 2015; Schmitt and Shackelford 2008) that involved more than 30,000 participants from around 50 nations and 11 world regions.

Personality Correlates of Mate Poaching Attempts

Regarding five-factor personality traits, agreeableness and to a lesser degree conscientiousness were the most consistently negatively, while extraversion positively related to poaching attempts in both women and men (Kardum et al. 2015; Schmitt and Buss 2001; Schmitt et al. 2004; Schmitt and Shackelford 2008). Only one study found low positive correlations of openness and neuroticism with poaching attempts, and the latter only in women (Schmitt and Shackelford 2008). On the level of higher order factors, alpha (stability or general avoidance tendencies) and beta (flexibility or general approach tendencies) (Larsen and Augustine 2008), poaching attempts were positively related to beta factor in both women and men and negatively with alpha factor in men. Regarding DT traits, overall psychopathy was the most consistently related to poaching attempts in both women and men (Jonason et al. 2010b; Kardum et al. 2015; Williams et al. 2005). This trait as well as its specific components, egocentricity, antisocial behaviors (Centifanti et al. 2016), and primary psychopathy (Khan et al. 2017) have been found to be moderately related to poaching attempts. Narcissism was also positively related to poaching attempts on the whole sample (Jonason et al. 2010b), and Narcissism and Machiavellianism on the samples of women and

men separately (Kardum et al. 2015). Regarding the components of Narcissism, mate poaching attempts were across 11 world regions, the most strongly positively related to the socially maladaptive factor called Exhibitionism/Entitlement within the two-factor model of Corry et al. (2008) and with the relatively maladaptive facets of Exhibitionism, Exploitativeness, and Authority within the seven-factor structure of Raskin and Terry's (1988) model (Schmitt et al. 2017). DT traits composite was moderately positively related to poaching attempts on the whole sample (Jonason et al. 2010b) as well as on the samples of women and men, and it better predicted poaching attempts than alpha and beta factors (Kardum et al. 2015). Additionally, poaching attempts were moderately positively related to sociosexuality (Grundler et al. 2013), lowly positively to secure, dismissing, preoccupied and fearful attachment in both women and men (Schmitt and Jonason 2015), as well as to borderline personality disorder (Centifanti et al. 2016). Furthermore, poaching attempts were related to two of the Sexy Seven personality attributes (Schmitt and Buss 2000), negatively to relationship exclusivity (whether one is promiscuous and adulterous), and positively to erotophilic disposition (obscurity, indecency, and lust) in both women and men (Centifanti et al. 2016; Schmitt and Buss 2001; Schmitt et al. 2004).

To summarize, we could describe a person prone to mate poaching attempts as one with a callous affect, lower empathy and anxiety, interpersonally manipulative, antisocial, impulsive, egocentric, with feelings of superiority and entitlement, disagreeable, unreliable, extraverted, indecent, and promiscuous. It seems that psychopathy characteristics most strongly predict poaching attempts in women as well as in men probably because they include behaviors necessary to enact high mating effort strategy, like manipulateness, that helps initiating numerous shallow relationships, promiscuity that may increase the number of potential offspring, and low conscientiousness that enables leaving romantic relationships and ignoring parental responsibilities (Wiebe 2004).

Personality Correlates of Mate Poaching Success

From the five-factor personality traits, openness (Kardum et al. 2015; Schmitt et al. 2004), extraversion, and higher order beta factor were positively related, while agreeableness was negatively related to mate poaching success in both women and men (Kardum et al. 2015). Regarding DT traits, overall psychopathy (Jonason et al. 2010b; Kardum et al. 2015) as well as its components – erratic lifestyle, criminal tendencies, and interpersonal manipulation – correlated positively with poaching success in women, while erratic lifestyle, criminal tendencies, and cold affect with poaching success in men (Sunderani et al. 2013). Narcissism was also positively related to poaching success on the whole sample (Jonason et al. 2010b) as well as on women and men separately, while Machiavellianism was positively related to poaching success only in women (Kardum et al. 2015). Consequently, overall DT was positively related to poaching success on the whole sample (Jonason et al. 2010b) as well as on the samples of both women and men (Kardum et al. 2015). Additionally, self-esteem was found to be positively related to poaching success only in men (Sunderani et al. 2013). Four of Sexy Seven personality attributes were related to poaching success. Sexual attractiveness (facets of beauty and seduction) and erotophilic disposition were positively related, while relationship exclusivity and sexual restraint (abstinence and prudishness) were negatively related to poaching success in both women and men (Schmitt and Buss 2001; Schmitt et al. 2004). Therefore, personality characteristics of a person successful in mate poaching overlap with those who attempt poaching. However, successful poachers possess some distinctive characteristics that may signal their quality as potential partners, such as inventiveness, originality, curiosity, artistic interests (trait of openness), self-esteem as well as attractiveness, allurements, eroticism, amorousness, and seductiveness (sexual attractiveness factor of the Sexy Seven personality attributes).

Personality Correlates of Being a Target of Mate Poaching

Regarding five-factor personality traits, it has been found that extraversion, openness, and consequently higher order beta factor are the most consistently positively related to being a target of mate poaching in women as well as in men (Kardum et al. 2015; Schmitt and Buss 2001; Schmitt et al. 2004). Additionally, some studies found that neuroticism was positively related (Schmitt and Shackelford 2008) and agreeableness was negatively related to being a target of poaching in women and men (Kardum et al. 2015; Schmitt and Shackelford 2008). Conscientiousness was lowly and inconsistently related to this aspect of mate poaching, because some studies have found negative relationships in women and men (Schmitt and Shackelford 2008), and some positive, but only in men (Kardum et al. 2015). DT traits were more strongly related to being a target of poaching than five-factor personality traits. All DT traits as well as DT composite were positively related to this poaching experience in women and men separately (Kardum et al. 2015), while on the whole sample, Jonason et al. (2010b) found positive relationships for psychopathy, Narcissism, and DT composite, and Khan et al. (2017) for primary psychopathy. Furthermore, being the target of poaching was positively related to sociosexuality in women and men separately (Grundler et al. 2013). When the Sexy Seven sexuality attributes are concerned, sexual attractiveness and emotional investment (love and romance) were positively related, while relationship exclusivity negatively related to this aspect of mate poaching (Schmitt and Buss 2001). The results obtained from ISDP show that sexual attractiveness and erotophilic disposition were positively related, and relationship exclusivity negatively related to being a target of poaching in women as well as in men (Schmitt et al. 2004). Main characteristics of a person who has experience of being a target of poaching are those comprised in DT traits and those aspects of five-factor personality traits related to approach motivation, such as extraversion and openness as well as sexual attractiveness and generally higher interest in sexuality.

Personality Correlates of Being Successfully Poached

From the five-factor personality traits, this aspect of mate poaching experiences was the most strongly negatively related to agreeableness and conscientiousness in women and men (Schmitt and Buss 2001; Schmitt et al. 2004). Being successfully poached was also positively related to neuroticism (Schmitt and Buss 2001), extraversion, as well as higher order beta factor, but only in men (Kardum et al. 2015). DT traits, especially psychopathy, Narcissism, and DT composite, were more highly related to being successfully poached than five-factor personality traits (Jonason et al. 2010b). Similarly, the components of psychopathy, mostly interpersonal manipulation, and to a lesser degree cold affect and erratic lifestyle, were also positively related to being successfully poached in women (Sunderani et al. 2013). On the sample of women, psychopathy, Machiavellianism, and DT composite and on the sample of men, all DT traits and DT composite were positively related to being successfully poached (Kardum et al. 2015). Additionally, socio-sexuality was also positively related to this aspect of mate poaching experience in women as well as in men (Grundler et al. 2013). Regarding the Sexy Seven sexuality attributes, erotophilic disposition was positively related, while relationship exclusivity, gender orientation (masculinity) and emotional investment negatively related to being successfully poached (Schmitt and Buss 2001). The results obtained from ISDP show that relationship exclusivity was negatively related, while erotophilic disposition positively related to being successfully poached in women as well as in men, while it was negatively related to emotional investment only in women (Schmitt et al. 2004). To summarize, a person who is liable to be successfully poached could be described as disagreeable, unconscientious, psychopathic, narcissistic, and machiavellistic as well as having promiscuous and adulterous tendencies.

Personality Correlates of Being a Victim of Mate Poaching

Being the victim of poaching has been rarely explored in relation to personality characteristics.

This aspect of mate poaching was positively related to psychopathy, Narcissism, and DT composite (Jonason et al. 2010b). Although it was positively related to extraversion, higher order beta factor, psychopathy, Narcissism, and overall DT in women, while negatively to agreeableness, and positively to psychopathy, Narcissism, Machiavellianism, and overall DT in men, regression analyses show that only Narcissism is a positive predictor of this aspect of poaching in women, and DT composite in women and men (Kardum et al. 2015). Additionally, Khan et al. (2017) have found that being the victim of poaching was positively related to Borderline Personality Disorder. Notwithstanding that being a victim of poaching is the least predictable aspect of poaching experiences, personality characteristics that best describe victims of poaching are those comprised within DT traits. On the one hand, these personality characteristics are undesirable to their partners, and may facilitate their real sexual unfaithfulness, and, on the other hand, they may make them more suspicious to the faithfulness of their partners (Massar et al. 2017). Both of these processes could be facilitated by assortative mating in personality traits. Because people tend to match up with others on specific characteristics including DT traits (Kardum et al. 2017), being the victim of poaching may be driven by the choice of a partner whose characteristics facilitate their unfaithfulness.

Sex Differences in Personality Correlates of Poaching Experiences

Some sex differences in the relationships between personality and mate poaching experiences have been found. The results of aforementioned studies show that extraversion was somewhat more strongly related to poaching attempts in men (Kardum et al. 2015; Schmitt et al. 2004; Schmitt and Shackelford 2008), while Narcissism better predicted poaching attempts in women (Kardum et al. 2015). Men who experience more poaching success had higher scores on openness (Kardum et al. 2015; Schmitt et al. 2004) and self-esteem (Sunderani et al. 2013), while women had higher scores on DT traits and DT composite (Kardum

et al. 2015). Being the target of poaching was more highly linked to conscientiousness and openness in men, and DT traits and neuroticism in women (Kardum et al. 2015; Schmitt and Shackelford 2008), while being successfully poached was related more to extraversion and DT traits in men than in women (Kardum et al. 2015). Socially undesirable traits of disagreeableness, Machiavellianism, and sociosexuality were more highly associated with being the victim of poaching in men, while this aspect of mate poaching was related more to extraversion and Narcissism in women (Grundler et al. 2013; Kardum et al. 2015). Therefore, women and men have somewhat different set of characteristics related to all types of poaching experiences. Additionally, personality correlates of mate poaching experiences in women are more homogeneous across different types of experiences than those in men. They mostly include socially undesirable DT traits indicating sexual desire, a tendency toward recreational sex (Carter et al. 2014) and the lack of moral concerns (Arvan 2013).

Personality correlates of mate poaching experiences in men are more heterogeneous and depend more upon the type of experience. Approach motivation, sensation-seeking, sociability, and social visibility included in extraversion are more important for poaching attempts, while their poaching success is more determined by socially desirable traits such as openness and self-esteem, which indicate their higher mating quality. Similarly, highly valued traits of conscientiousness and openness are more strongly related to being a target of poaching, while the traits indicating approach motivation and a tendency toward the increase in reproductive success with minimal investment (DT traits) to being successfully poached. Personality traits related to poaching attempts and being successfully poached in men, both indicating their tendency to short-term sexual strategy, are those based on immediate rewards and gratification, enabling fast life-history strategy (Jonason et al. 2010a). Men's traits related to poaching success and being the target of poaching, two poaching

experiences that depend on how potential partners perceive their mating qualities, are highly valued traits, and are probably the consequences of women's choosy and discriminative nature regarding mate choice (Trivers 1972).

Cross-Cultural Universality of the Relationship Between Personality and Mate Poaching Experiences

It is important to identify whether personality characteristics related to mate poaching experiences are universal across cultures, i.e., features of human nature, or whether they are culturally unique, i.e., dependent upon specific sexual culture. The only source of information about this issue until now is data from ISDP and ISDP-2 (Schmitt et al. 2004, 2017; Schmitt and Jonason 2015; Schmitt and Shackelford 2008). Relationships of five-factor personality traits and Sexy Seven Sexuality Attributes with poaching attempts and success as well as being the target of poaching and being successfully poached were similar across most cultures and world regions (Schmitt et al. 2004). Furthermore, Narcissism (including two broad factors and seven traditional facets of NPI) was reliably linked to poaching attempts across all major world regions of the ISDP-2 – North America and Central/South America, Northern, Western, Eastern and Southern Europe, Middle East, Africa, Oceania, South/South East and East Asia (Schmitt et al. 2017). Additionally, culturally consistent relationships of short-term mate poaching and all forms of attachment insecurity were found in women, with preoccupied attachment demonstrating the most consistent links across different cultures. The relationships between attachment insecurity and mate poaching were much smaller and less consistent across world regions among men (Schmitt and Jonason 2015). In sum, although there are only few cross-cultural studies, the similar associations of personality and mate poaching experiences worldwide suggest that psychological mechanisms of mate poaching

are universal and not limited to any specific sexual culture.

Conclusion

It seems that personality characteristics are meaningfully related to various mate poaching experiences. These relationships are small to moderate, with poaching attempts, poaching success, and being the target of poaching more strongly related to personality characteristics than being successfully poached and being the victim of poaching. Personality characteristics that are the most strongly related to different poaching experiences are DT traits and sexuality attributes, followed by five-factor personality traits and attachment styles. Patterns of relationships between personality characteristics and mate poaching experiences are partly different in women and men, being more distinctive in men, which is probably the result of gender differences in evolved sexual strategies. Additionally, the links between mate poaching experiences and personality characteristics are largely cross-culturally universal and similar for mate poaching for short- as well as long-term relationships.

Cross-References

- [Costs and Benefits of Mate Poaching](#)
- [Human Mate Poaching](#)
- [Mate Poaching](#)
- [Sex Differences in Costs and Benefits of Mate Poaching](#)

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Personality Development

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Synonyms

Heritability; Personality traits; Sociogenomics

Introduction

Personality refers to stable patterns in the ways that an individual thinks, behaves, and emotes across situations and the passage of time. An appreciation of personality is central for understanding oneself and navigating the social world. McAdams and Pals (2006) have argued that an evolutionary perspective on psychology is a powerful approach to understanding personality as it sheds light on the origins of universals of human nature, the ways in which humans are similar to certain others, and the manner with which each human is distinct. An evolutionary approach to personality also draws attention to the impact of our nonhuman heritage: Aspects of our human genome, physiology, and behavioral phenotype are shared across species. Given the eusocial nature of the human species, many of our traits have been shaped by contingencies of cooperation and competition for survival resources with members of our own species and culture. Thus, an evolutionary perspective of personality takes into account that diverse classes of behavior are emitted by an organism, and certain behaviors are selected by environmental contingencies over

both phylogenic (ancestry) and ontogenic (personal lifetime) timeframes.

Evolutionary and genetic approaches to behavior have sometimes been construed as genetic essentialism, the belief that behavior and individual differences are determined by genes, and fatalistic viewpoints implying genetically influenced outcomes are immutable. Such views have troubling implications for behavioral health problems such as personality disorders as they may increase mental health stigma and deter individuals from seeking treatment (Kong et al. 2017). Emerging research, however, is revealing the epigenetic processes whereby DNA is modified by the environment. Thus, there is growing appreciation of malleable nature of personality (Kong et al. 2017; Roberts and Jackson 2008). As such, any momentary glimpse of personality is the result of the individual's ancestry, culture, and personal life experiences, with significant potential for development and modification into late adulthood.

Defining Personality

Merriam-Webster (2017) offers several definitions of personality including “the complex of characteristics that distinguishes an individual or a nation or group; *especially*: the totality of an individual's behavioral and emotional characteristics.” Although different situations present with different expectations of our behavior, many of us have an inherent or intuitive appreciation for our own stable sense of self. Our preferences, values, and ways may remain consistent over time, despite that our outward behavior may vary substantially across situations. Likewise, we are aware of the patterns, personalities, and traits of the individuals with whom we interact repeatedly. We may be aware of some colleagues and friends who are more dependable than others. Certain neighbors are reliably more gregarious, quick-tempered, or neurotic than others. When these individual differences in our own behavior or the behavior of others result in beneficial consequences such as friendship, affiliation, and cooperation they can be source of predictability and even comfort in an ever changing world. Whereas

patterns of ineffective behavior such as inattentive quirks may be source of bemusement, entrenched patterns of mistrust and aggressiveness may be a substantial source of misery for the individual or those around them.

Heritability and Behavior

Behavior and personality evolve when diversity exists in behavioral phenotypes and their underlying genotypes. Traits that increase reproductive fitness of the organism or their kin are more likely to be passed on to progeny. Traits that are passed on to progeny or offspring through reproduction are said to be inherited. The term heritability refers to the *proportion* of variability in a trait that is explained by genetic factors. A number of methods can be used to estimate heritability with varying degrees of complexity. For instance, significant correlations between personality traits of parents and offspring suggest that traits may be inherited. However, such methods are not able to discern the extent to which the shared variation in personality traits is explained by common a common underlying genotype versus common experiences in similar environments. Twin studies are useful paradigm for estimating heritability, as monozygotic twins share nearly identical DNA, and so differences in their personalities can be attributed to differences in their personal life experiences. Potential environmental impacts can be further parsed by comparing correlations in traits to correlations of traits of monozygotic twins who were reared apart, and with correlations of traits dizygotic twins who share similar environments but only roughly 50% of their DNA (Krueger et al. 2008). It has often been cited that approximately half of all variation in personality traits is accounted for by genetic differences (Turkheimer 2000).

Inheritance and heritability are often confused as identical constructs leaving some to believe that estimates of heritability indicate the degree to which a behavior or personality trait is *caused* by differences in genes. Hypothetically, if environments could be made to be identical for a group of individuals, then all differences in their

personalities would be explained by genetic differences. Inversely, if a group of individuals had identical DNA, then all differences in their personalities should be explained by their environments, or measurement error. Yet it would be erroneous to assume that the genome plays no causal role in this latter, as without a genome there would be no nervous system let alone any organism or individual. This realization has sparked considerable interest in gene–environment interactions, and several methodologies for probing these interactions will be described later.

A Brief History of Personality Psychology

Despite the intuitive appeal of the meaning of personality, a substantial amount of work was required to effectively operationalize personality in a manner that was reliable, valid, and broad enough in scope to be a useful construct in the behavioral sciences. As with many other foci of psychology, personality can be abstracted from discrete observations of public behavior, but also the subjective thoughts, and emotions and preferences of the individual. In 1953, in response to years of speculative analysis into Freudian personality dynamics and the failure of personality theory to inform psychotherapy of the time, B.F. Skinner eschewed personality as a causal factor in the explanation and control of behavior. Rather than an explanation for behavior, personality was viewed as a pattern of behavior to be explained in terms of its environmental antecedents and consequences. Whereas the early radical behavioral approach acknowledged the importance of evolutionary forces in shaping behavior, the research agenda emphasized the practical importance of studying operant and respondent control of behavior and intervening with the goal of addressing immediate problems in human behavior. Personality Psychology would face similar criticism in the 1970s as part of the “trait-situation” debate (McAdams and Pals 2006; Revelle 2016; Roberts and Jackson 2008). Personality psychology was the subject of further criticism in the person-situation debate when some psychologists questioned the utility of personality construct given that behavior varies so

widely based on situational demands. Additional work has since documented those independent ratings and cross-situations correlations in behavior. Meta-analyses and other reviews have consistently shown that personality is particularly useful for the scientific prediction personal and professional health and well-being.

Of the early leaders of personality psychology, Hans Eysenck remains the most impactful on the contemporary personality psychology field, and he is often recognized for his conceptualization of personality from a biological perspective (Revelle 2016). His approach to personality was unique in that it integrated methods from a number of fields of psychology including psychometrics, experimental psychology, and behavior genetics. The Eysenck Personality Questionnaire (EPQ) measured three dimensions of personality: extraversion – introversion, neuroticism – emotional stability, and psychoticism – superego control, which Eysenck (1990) argued had biological foundations. He offered as evidence that analogous behavioral systems had been documented in nonhuman species, and twin studies documenting stronger personality correlations among separated monozygotic twins compared to dizygotic twins reared together (Eysenck 1990). Eysenck’s integrative approach speculated that personality traits emerged via physiological structures in the nervous system that in turn had emerged from genes. Over the years behavioral genomics, behavioral neuroscience, and other fields have further vindicate Eysenck’s speculations by linking individual differences to physiology and specific genes and have begun to elucidate the ways that environment operates on the genome. Eysenck’s influence on contemporary personality psychology is also evident in the overlap of his model with contemporary models of personality (Draycott and Kline 1995).

Today, the Five-Factor Theory of Personality or The Big Five represents one of the most fruitful approaches to conceptualizing and assessing personality (McCrae and Costa 1999; McCrae et al. 2000; McAdams and Pals 2006). The theory is named for five factors that are commonly derived when sufficiently broad measures of traits and behaviors are assessed: (1) neuroticism, (2) extroversion, (3) openness, (4) agreeableness, and

(5) conscientiousness. Each of the traits falls along a continuum and is normally distributed. Neuroticism refers to a continuum that ranges from emotional stability and calmness to high levels of negative emotionality, pessimism, and avoidant coping. Extroversion refers to the tendency toward positive emotions, sensation seeking, and gregariousness. Openness refers to the tendency to take on new experiences, enjoy novelty, and to consider the perspectives of other individuals. Agreeableness refers to the tendency to trust, empathize, and affiliate with others. Conscientiousness refers to tendencies to be orderly and rule following. Aspects of the Big Five are applicable across cultures and even so across multiple species. The former finding is of interest from an evolutionary perspective as it suggests that phylogenetic contingencies have shaped behavior throughout biological history to produce a human nature that is observable across diverse geographies and cultures. The latter finding is of interest as it may suggest common and/or convergent evolution. The Big Five traits are reliable over time and are useful for predicting behavior in occupational and clinical settings.

Personality, Development, and Change

Given the definition of personality as stable patterns of cognition, emotion, and behavior across situations, high heritability of traits, and high reliabilities of traits over the lifespan, there may be an erroneous perception that maladaptive personality traits are immutable. While it is true that behavior modification may require specific and intensive interventions to address maladaptive personality traits, fatalism, genetic essentialism and other assumptions may raise strong emotions, elicit stigma and create self-fulfilling prophecies that interfere with the prevention and/or modification of maladaptive personality traits and even health behaviors.

A number of studies demonstrating that personality can be altered by early life experiences, major life transitions, and focused psychological intervention challenge assumptions of genetic essentialism and reveal that personality may be more malleable than previously expected.

Exposure to early life adversity moderates the associations of alleles with depressive behavior (Caspi et al. 2003). Following the loss of a loved one to lung cancer, caregivers reported significant increases in prosocial traits (Hoerger et al. 2014). Dialectical Behavior Therapy is considered an evidence-based treatment for Borderline Personality Disorder, a pattern of behavior marked by emotional dysregulation, unstable sense of self, and interpersonal conflict (Kliem et al. 2010).

Contextual Mechanisms of Change

Sociogenomic personality psychology challenges the misconception that behavior is only determined by genes and evolution (Roberts and Jackson 2008). The sociogenomic perspective expands the Eysenckian model through its emphasis on genes working in accordance with the environment. Genes are regulated by the cellular environment and are also influenced by the outside environment. It is reasonable to believe that personality is environmentally dependent, which also means that genes must also be at play in this process. Thus, from the sociogenomic perspective personality traits may be more malleable than previously expected.

The move towards a sociogenomic study of personality psychology targets the study of the genome, rather than solely studying humanity (Roberts and Jackson 2008). This is because the genome is highly conserved across species and is responsible for not only behaviors in human beings, but also in all life forms. The study of the genome in all species will provide a greater understanding of the interaction between genes and the environment. This new perspective will allow us to map the pathway from gene to behavior, thus, enhancing knowledge of personality psychology (Roberts and Jackson 2008).

Conclusion

Personality refers to the characteristics that distinguish an individual. Traits are heritable and differ from one person to the next by genetic and environmental differences. Hans Eysenck, an

impactful personality psychologist, argues that personality psychology is rooted in biological systems. His approach speculates that personality traits stem from physiological structures that themselves surface from genes. A reliable and popular way to conceptualize personality is through the Five-Factor Theory of Personality (McCrae and Costa 1999; McCrae et al. 2000). The theory includes five factors that can justly measure traits and behaviors: (1) neuroticism, (2) extroversion, (3) openness, (4) agreeableness, and (5) conscientiousness. These traits are useful for predicting behavior in social settings. A newer approach to personality psychology is sociogenomic biology. This theory counters Eysenk by stating that genes are heavily influenced by one's outside environment. This approach breaks down the misconception that biological mechanisms are immutable and will ultimately provide a better understanding of personality psychology by mapping the pathway from gene to behavior.

Cross-References

- [Evolutionary Personality Psychology](#)
- [Personality](#)
- [Personality Disorders](#)

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Personality Dimensions

- [Five-Factor Model](#)

Personality Disorders

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Synonyms

[Mental illness](#); [Psychological disorder](#); [Psychopathology](#)

Definition

A personality disorder is a pervasive and stable pattern of behavior that emerges in adolescence or early adulthood, in which distressing and impairing behaviors deviate from the expectations of the individual's society.

Introduction

The ten personality disorders (PDs) discussed in this chapter are divided into three clusters based on phenotypic similarity, according to the Diagnostic and Statistical Manual of Mental Disorders (5th ed.; DSM-5; American Psychiatric Association 2013). Cluster A PDs (paranoid, schizoid, and schizotypal) present with weak or nonexistent social attachments and odd/eccentric behavior, which may be an alternative expression of a schizophrenia predisposition (Miller et al. 2001). Cluster B PDs (antisocial, borderline, histrionic, and narcissistic) share common features with one another, such as impulsive acting out, unpredictable behaviors, and dramatic presentation (Sutker and Allain 2002). Finally, Cluster C PDs all have anxious, fearful, and inhibited traits in common (Miller et al. 2001).

Over time, the psychological field has held the perspective that PDs are not treatable; however, more recent research has shown benefits and a reduction of symptoms through various treatment approaches (Meloy and Yakeley 2014; Bateman and Tyrer 2004). Although there is mixed evidence for these findings, there is concrete support for treating borderline personality disorder (BPD) through dialectical behavioral therapy (DBT; Linehan 1993; Shearin and Linehan 1994). Aside from DBT, there are no other specialized treatment approaches for any of the remaining nine PDs. The author emphasizes the need for treatment of PDs as these are among the most frequent disorders diagnosed by psychiatrists (Zimmerman et al. 2005). Moreover, the majority of individuals with a PD have at least one other comorbid PD, along with additional disabling diagnoses (e.g., anxiety disorders, mood disorders, substance use disorders),

highlighting a greater need for treatment (Sutker and Allain 2002; Miller et al. 2001; Lieb et al. 2004; Bornstein 1995).

A huge problem in the psychological field is the lack of focus on Cluster A and C PDs, as Cluster B PDs (mainly antisocial and borderline) have dominated the academic literature. The majority of the Cluster A and C PDs discussed in this chapter have received few, if any, clinical trials, have limited information on their causes and etiology, and have no empirically supported treatment approaches. In this chapter, the author will discuss potential treatment methods, although there is limited empirical evidence supporting these approaches compared to the amplitude of literature supporting DBT. The goal of this chapter is to emphasize the lack of research on Cluster A and C PDs and raise awareness on the need for clinical trials and standardized treatment methods. Future researchers are encouraged to focus on Cluster A and C PDs to expand academic research and increase their knowledge concerning empirically supported treatment methods, while also striving to determine the evolutionary purpose of PD traits.

In order to understand the ten PDs, the author will outline the following key points for Cluster A, B, and C PDs: diagnostic criteria (see Tables 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10), prevalence rates, sex differences, comorbid conditions, causes and/or risk factors, and treatment approaches. Readers are encouraged to contemplate the evolutionary benefits of these “negative” behaviors, as they have continued through natural selection for a reason – one that may harm society as a whole, but may benefit the affected individual (Hashmani and Jonason 2017). It is important to note that all PDs yield some sort of adaptive benefit, although society often views these behaviors as harmful.

The Ten Personality Disorders

Cluster A

Paranoid personality disorder. Paranoid personality disorder (PPD) is a pattern of distrust and suspiciousness, where others' motives are

Personality Disorders, Table 1 DSM-5 Diagnostic criteria for paranoid personality disorder

A. A pervasive distrust and suspiciousness of others such that their motives are interpreted as malevolent, beginning by early adulthood and present in a variety of contexts, as indicated by four (or more) of the following:

1. Suspects, without sufficient basis, that others are exploiting, harming, or deceiving him or her
2. Is preoccupied with unjustified doubts about the loyalty or trustworthiness of friends or associates
3. Is reluctant to confide in others because of unwarranted fear that the information will be used maliciously against him or her
4. Reads hidden demeaning or threatening meanings into benign remarks or events
5. Persistently bears grudges (i.e., is unforgiving of insults, injuries, or slights)
6. Perceives attacks on his or her character or reputation that are not apparent to others and is quick to react angrily or to counterattack

7. Has recurrent suspicions, without justification, regarding fidelity of spouse or sexual partner

B. Does not occur exclusively during the course of schizophrenia, a bipolar disorder or depressive disorder with psychotic features, or another psychotic disorder and is not attributable to the physiological effects of another medical condition

5th ed.; DSM-5; American Psychiatric Association 2013

Personality Disorders, Table 2 DSM-5 Diagnostic criteria for schizoid personality disorder

A. A pervasive pattern of detachment from social relationships and a restricted range of expression of emotions in interpersonal settings, beginning by early adulthood and present in a variety of contexts, as indicated by four (or more) of the following:

1. Neither desires nor enjoys close relationships, including being part of a family
2. Almost always chooses solitary activities
3. Has little, if any, interest in having sexual experiences with another person
4. Takes pleasure in few, if any, activities
5. Lacks close friends or confidants other than first-degree relatives
6. Appears indifferent to the praise or criticism of others
7. Shows emotional coldness, detachment, or flattened affectivity

B. Does not occur exclusively during the course of schizophrenia, a bipolar disorder or depressive disorder with psychotic features, another psychotic disorder, or autism spectrum disorder and is not attributable to the physiological effects of another medical condition

5th ed.; DSM-5; American Psychiatric Association 2013

Personality Disorders, Table 3 Diagnostic criteria for schizotypal personality disorder

A. A pervasive pattern of social and interpersonal deficits marked by acute discomfort with, and reduced capacity for, close relationships as well as by cognitive or perceptual distortions and eccentricities of behavior, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:

1. Ideas of reference (excluding delusions of reference)
2. Odd beliefs or magical thinking that influences behavior and is inconsistent with subcultural norms (e.g., superstitiousness, belief in clairvoyance, telepathy, or “sixth sense”; in children and adolescents, bizarre fantasies, or preoccupations)
3. Unusual perceptual experiences, including bodily illusions
4. Odd thinking and speech (e.g., vague, circumstantial, metaphorical, overelaborate, or stereotyped)
5. Suspiciousness or paranoid ideation
6. Inappropriate or constricted affect
7. Behavior or appearance that is odd, eccentric, or peculiar

8. Lack of close friends or confidants other than first-degree relatives

9. Excessive social anxiety that does not diminish with familiarity and tends to be associated with paranoid fears rather than negative judgments about self

B. Does not occur exclusively during the course of schizophrenia, a bipolar disorder or depressive disorder with psychotic features, another psychotic disorder, or autism spectrum disorder

5th ed.; DSM-5; American Psychiatric Association 2013

consistently interpreted as malevolent (see Table 1; American Psychiatric Association 2013). Prevalence rates of PPD range from 1.21% to 4.41% of the general population, 10–30% of inpatient populations, and 2–10% of outpatient populations (Lee 2017; Vyas and Khan 2016; Miller et al. 2001). Regarding sex differences, research is mixed as epidemiological research finds higher rates in females, while clinical samples find higher rates in males (Lee 2017). Common comorbid PDs are antisocial, borderline, narcissistic, and avoidant, while other comorbid diagnoses are panic disorder and substance use disorders (Lee 2017; Vyas and Khan 2016).

Risk factors for PPD include childhood trauma (e.g., emotional, physical, and

Personality Disorders, Table 4 DSM-5 Diagnostic criteria for antisocial personality disorder

- A. A pervasive pattern of disregard for and violation of the rights of others, occurring since age 15 years, as indicated by three (or more) of the following:
1. Failure to conform to social norms with respect to lawful behaviors, as indicated by repeatedly performing acts that are grounds for arrest
 2. Deceitfulness, as indicated by repeated lying, use of aliases, or conning others for personal profit or pleasure
 3. Impulsivity or failure to plan ahead
 4. Irritability and aggressiveness, as indicated by repeated physical fights or assaults
 5. Reckless disregard for safety of self or others
 6. Consistent irresponsibility, as indicated by repeated failure to sustain consistent work behavior or honor financial obligations
 7. Lack of remorse, as indicated by being indifferent to or rationalizing having hurt, mistreated, or stolen from another
- B. The individual is at least aged 18 years
- C. There is evidence of conduct disorder with onset before age 15 years
- D. The occurrence of antisocial behavior is not exclusive during the course of schizophrenia or bipolar disorder

5th ed.; DSM-5; American Psychiatric Association 2013

supervision neglect), as well as physical abuse in childhood and adolescence (but not sexual abuse; Lee 2017). Additionally, disadvantaged backgrounds (e.g., African American, Native American, Hispanic), relationship history (i.e., widowed, divorced, separated, never married), low income, and social stress are all risk factors for PPD (Lee 2017). Individuals with PPD rarely seek treatment, perhaps due to their lack of trust in potential researchers, leading to no clinical trials, and thus no specialized treatment strategies (Lee 2017; Vyas and Khan 2016). Little is known about the effectiveness of PPD psychotherapeutic approaches, although cognitive behavioral therapy (CBT) and psychoanalysis are sometimes used (Lee 2017; Vyas and Khan 2016).

Schizoid personality disorder. Schizoid personality disorder (ScPD) is a pattern of detachment from social relationships and consists of a restricted range of emotional expressions (see Table 2; American Psychiatric Association 2013). Prevalence rates of ScPD are higher for males,

Personality Disorders, Table 5 DSM-5 Diagnostic criteria for borderline personality disorder

- A pervasive pattern of instability of interpersonal relationships, self-image, and affects, and marked impulsivity, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:
1. Frantic efforts to avoid real or imagined abandonment. (Note: Do not include suicidal or self-mutilating behavior covered in Criterion 5)
 2. A pattern of unstable and intense interpersonal relationships characterized by alternating between extremes of idealization and devaluation
 3. Identity disturbance: markedly and persistently unstable self-image or sense of self
 4. Impulsivity in at least two areas that are potentially self-damaging (e.g., spending, sex, substance abuse, reckless driving, binge eating). (Note: Do not include suicidal or self-mutilating behavior covered in Criterion 5)
 5. Recurrent suicidal behavior, gestures, or threats, or self-mutilating behavior
 6. Affective instability due to a marked reactivity of mood (e.g., intense episodic dysphoria, irritability, or anxiety usually lasting a few hours and only rarely more than a few days)
 7. Chronic feelings of emptiness
 8. Inappropriate, intense anger or difficulty controlling anger (e.g., frequent displays of temper, constant anger, recurrent physical fights)
 9. Transient, stress-related paranoid ideation or severe dissociative symptoms

5th ed.; DSM-5; American Psychiatric Association 2013

although they are still low rates (1–2%) for both sexes (Triebwasser et al. 2012). Common comorbid PDs are paranoid, schizotypal, and avoidant, and other comorbid diagnoses are anxiety disorders and depression (Ekleberry 2009; Pokos and Castle 2006; Bockian 2006).

Evidence indicates that childhood and adolescent major depressive disorder is a strong predictor of adult ScPD – an important factor to note, as this is not a prerequisite in any other PD (Triebwasser et al. 2012). Schizophrenia individuals often lose touch with reality, whereas Cluster A PD individuals do not experience this symptom – a key difference between the conditions. Additionally, having a family member with schizophrenia greatly increases the risk of developing ScPD (Triebwasser et al. 2012).

Personality Disorders, Table 6 DSM-5 Diagnostic criteria for histrionic personality disorder

- A pervasive pattern of excessive emotionality and attention seeking, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:
1. Is uncomfortable in situations in which he or she is not the center of attention
 2. Interaction with others is often characterized by inappropriate sexually seductive or provocative behavior
 3. Displays rapidly shifting and shallow expression of emotions
 4. Consistently uses physical appearance to draw attention to self
 5. Has a style of speech that is excessively impressionistic and lacking in detail
 6. Shows self-dramatization, theatricality, and exaggerated expression of emotion
 7. Is suggestible (i.e., easily influenced by others or circumstances)
 8. Considers relationships to be more intimate than they actually are

5th ed.; DSM-5; American Psychiatric Association 2013

Unfortunately, very little additional information is known about the genetic and environmental causes of ScPD. Regarding treatment, those with ScPD are often unresponsive and unwilling to engage in therapeutic relationships; however, research indicates that these individuals end up attending treatment more often when not pressured to engage (Ekleberry 2009). Furthermore, although lacking empirical evidence, the concept of “closer compromise” is a potential first step in treatment, where the individual is encouraged to experience an intermediate position between the states of unbearable anxiety regarding emotional closeness and permanent exile, such that they take risks to create less interpersonal distance, and instead, greater connection, communication, and sharing of ideas with others (Klein 2013). Next, longer-term therapy entails the concept of “working through,” where the goals are to change the old ways of feeling and thinking, and to free oneself from these negative vulnerabilities (Klein 2013).

Schizotypal personality disorder. Schizotypal personality disorder (SPD) is a pattern of acute discomfort in close relationships,

Personality Disorders, Table 7 DSM-5 Diagnostic criteria for narcissistic personality disorder

- A pervasive pattern of grandiosity (in fantasy or behavior), need for admiration, and lack of empathy, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:
1. Has a grandiose sense of self-importance (e.g., exaggerates achievements and talents, expects to be recognized as superior without commensurate achievements)
 2. Is preoccupied with fantasies of unlimited success, power, brilliance, beauty, or ideal love
 3. Believes that he or she is “special” and unique and can only be understood by, or should associate with, other special or high-status people (or institutions)
 4. Requires excessive admiration
 5. Has a sense of entitlement (i.e., unreasonable expectations of especially favorable treatment or automatic compliance with his or her expectations)
 6. Is interpersonally exploitative (i.e., takes advantage of others to achieve his or her own ends)
 7. Lacks empathy: is unwilling to recognize or identify with the feelings and needs of others
 8. Is often envious of others or believes that others are envious of him or her
 9. Shows arrogant, haughty behaviors or attitudes

5th ed.; DSM-5; American Psychiatric Association 2013

Personality Disorders, Table 8 DSM-5 Diagnostic criteria for avoidant personality disorder

- A pervasive pattern of social inhibition, feelings of inadequacy, and hypersensitivity to negative evaluation, beginning by early adulthood and present in a variety of contexts, as indicated by four (or more) of the following:
1. Avoids occupational activities that involve significant interpersonal contact because of fears of criticism, disapproval, or rejection
 2. Is unwilling to get involved with people unless certain of being liked
 3. Shows restraint within intimate relationships because of the fear of being shamed or ridiculed
 4. Is preoccupied with being criticized or rejected in social situations
 5. Is inhibited in new interpersonal situations because of feelings of inadequacy
 6. Views self as socially inept, personally unappealing, or inferior to others
 7. Is unusually reluctant to take personal risks or to engage in any new activities because they may prove embarrassing

5th ed.; DSM-5; American Psychiatric Association 2013

Personality Disorders, Table 9 DSM-5 Diagnostic criteria for dependent personality disorder

A pervasive and excessive need to be taken care of that leads to submissive and clinging behavior and fears of separation, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:
1. Has difficulty making everyday decisions without an excessive amount of advice and reassurance from others
2. Needs others to assume responsibility for most major areas of his or her life
3. Has difficulty expressing disagreement with others because of fear of loss of support or approval (Note: Do not include realistic fears of retribution)
4. Has difficulty initiating projects or doing things on his or her own (because of a lack of self-confidence in judgment or abilities rather than a lack of motivation or energy)
5. Goes to excessive lengths to obtain nurturance and support from others, to the point of volunteering to do things that are unpleasant
6. Feels uncomfortable or helpless when alone because of exaggerated fears of being unable to care for himself or herself
7. Urgently seeks another relationship as a source of care and support when a close relationship ends
8. Is unrealistically preoccupied with fears of being left to take care of himself or herself
5th ed.; DSM-5; American Psychiatric Association 2013

cognitive or perceptual distortions, and eccentric behavior (see Table 3; American Psychiatric Association 2013). Prevalence rates of SPD range from 1% to 5% of the general population, and are three times higher than schizophrenia (Kwapil and Barrantes-Vidal 2012). Rates on sex differences are mixed, although there is support for higher rates in males (Ryan et al. 2013). Moreover, females exhibit more *positive* symptoms (e.g., delusions), whereas males exhibit more *negative* symptoms (e.g., flattened affect; Kwapil and Barrantes-Vidal 2012). In clinical terms, positive symptoms are changes in thoughts/feelings that are added to one’s experience (e.g., delusions), whereas negative symptoms are thoughts/feelings that are removed from one’s experience (e.g., flattened affect). Comorbid PDs include paranoid and schizoid (paranoid encompasses suspiciousness, while schizoid

Personality Disorders, Table 10 DSM-5 Diagnostic criteria for obsessive-compulsive personality disorder

A pervasive pattern of preoccupation with orderliness, perfectionism, and mental and interpersonal control, at the expense of flexibility, openness, and efficiency, beginning by early adulthood and present in a variety of contexts, as indicated by four (or more) of the following:
1. Is preoccupied with details, rules, lists, order, organization, or schedules to the extent that the major point of the activity is lost
2. Shows perfectionism that interferes with task completion (e.g., is unable to complete a project because his or her own overly strict standards are not met)
3. Is excessively devoted to work and productivity to the exclusion of leisure activities and friendships (not accounted for by obvious economic necessity)
4. Is overconscientious, scrupulous, and inflexible about matters of morality, ethics, or values (not accounted for by cultural or religious identification)
5. Is unable to discard worn-out or worthless objects even when they have no sentimental value
6. Is reluctant to delegate tasks or to work with others unless they submit to exactly his or her way of doing things
7. Adopts a miserly spending style toward both self and others; money is viewed as something to be hoarded for future catastrophes
8. Shows rigidity and stubbornness
5th ed.; DSM-5; American Psychiatric Association 2013

encompasses social disinterest characteristics), while other comorbidities are mood disorders, anxiety disorders, and substance use disorders (Kwapil and Barrantes-Vidal 2012; Ryan et al. 2013). It is important to note that although SPD shares some similarities with other Cluster A PDs, this is the only one that involves magical beliefs or unusual perceptual experiences.

Similar to ScPD, risk factors for SPD include a relative with schizophrenia, indicating the importance of heritability, yet additional information on genetic factors is sparse (Kwapil and Barrantes-Vidal 2012). Furthermore, several environmental factors are associated with SPD, such as maternal smoking during pregnancy, maltreatment, early cannabis use, and childhood abuse, which all increase one’s vulnerability to schizotypy traits (Kwapil and Barrantes-Vidal 2012; Ryan et al. 2013). Currently, there are no randomized controlled trials for SPD, consistent

with the rest of the Cluster A PDs; however, the most promising treatment is derived from treating other schizophrenia spectrum disorders (Ryan et al. 2013). Examples of this include: CBT focused on alleviating positive and negative symptoms, Cognitive Training designed to address cognitive deficits, social skills training aimed to increase interpersonal functioning, family interventions, and last, interventions targeted at cannabis use (Ryan et al. 2013).

Cluster B

Antisocial personality disorder. Antisocial personality disorder (ASPD) is a pattern of disregard for, and violation of, the rights of others (see Table 4; American Psychiatric Association 2013). Additionally, the individual must be at least 18 years old, and must have presented with “conduct disorder with onset” before the age of 15 (American Psychiatric Association 2013). According to the DSM-5, children with conduct disorder must meet diagnostic criteria within the following categories: aggression to people and animals, destruction of property, deceitfulness or theft, and/or serious violations of rules (American Psychiatric Association 2013). Lifetime prevalence rates of ASPD are 4.5–6% in males and 0.8–1.9% in females, as ASPD is more common among males than females (De Brito and Hodgins 2009). Prevalence rates in the general population are low with 1% of males and 0.2% of females, but approximately 50% of prison inmates are diagnosed (De Brito and Hodgins 2009; Sutker and Allain 2002). Comorbid PDs include borderline and histrionic, and other comorbidities include substance use disorders, anxiety disorders, and depressive disorders (Meloy and Yakeley 2014; De Brito and Hodgins 2009; Sutker and Allain 2002).

Common risk factors stem from the prevalence of conduct disorder, as this is a prerequisite to ASPD. Risk factors for conduct disorder include family factors (e.g., psychiatric problems in parents, criminal behavior in fathers, inconsistent parenting), child factors (e.g., difficult temperament, early behavioral problems, low IQ), and community factors (e.g., socioeconomic disadvantage, delinquent peers, and a poor school

environment; Jain n.d.). Additionally, individuals with ASPD may have a higher threshold for stimulation and an underlying hypoarousal condition, which may drive them towards reckless, destructive, and impulsive activities (see Hashmani 2018). Unlike Cluster A PDs, researchers have conducted clinical trials on Cluster B PDs; however, evidence for effective treatments remain limited (Meloy and Yakeley 2014). Most treatment programs adhere to the risk-need-responsivity model, where the focus is on risk (targeting those at greatest risk of offending), need (criminological risk factors, i.e., criminal attitudes, substance abuse, impulsivity), and responsivity (maximizing offender engagement in the treatment process; Meloy and Yakeley 2014).

It is important to note that all PDs originally emerged and continue to persist through natural selection for a purpose – they present some sort of adaptive benefit or advantage. Although ASPD symptoms may be detrimental to society, they may yield benefits for the individual, at the cost of others (Hashmani and Jonason 2017). Moreover, life history theories (Frankenhuis and Giudice 2012) and an evolutionary developmental mismatch approach (Cameron et al. 2005) explain the emergence of these behaviors by suggesting that natural selection favors antisocial behaviors and increases fitness adaptability for individuals who engage in such a lifestyle (see Hashmani and Jonason 2017). Furthermore, psychopathy, for instance, consists of an inability to create close connections with others (negative trait); however, on the other hand, these individuals experience a lack of “normal” emotions (e.g., guilt, shame, empathy), which can be disabling and mentally exhausting (positive trait), and can assist in depersonalizing oneself from the victim in order to commit crime (positive trait; Hashmani and Jonason 2017; Hashmani 2018). The purpose of this chapter is to provide an understanding of the ten PDs and the need for standardized treatment; however, the author urges readers to consider the adaptive and beneficial aspects of PDs, rather than stigmatizing and pathologizing such conditions.

Borderline personality disorder. Borderline personality disorder (BPD) is a pattern of

impulsivity, as well as instability in interpersonal relationships, self-image, and affects (see Table 5; American Psychiatric Association 2013). Prevalence rates of BPD include 1–2% of the general population, 10% of outpatient populations, and 20% of inpatient populations (Lieb et al. 2004). Sex differences vary greatly, as BPD is more common in females than males (70–30%, respectively; Lieb et al. 2004). Comorbid PDs are paranoid, avoidant, and dependent, as well as other diagnoses, such as major depressive disorder, substance use disorders, post-traumatic stress disorder, anxiety disorders, eating disorders, and bipolar disorder (Lieb et al. 2004).

Causal factors for BPD follow a biosocial theory model (Linehan 1993) where the integration between biological/genetic factors and environmental factors leads to the development of BPD symptomology. Genetic factors illustrate abnormalities in the frontal limbic network, the prefrontal cortex, the hippocampus, the amygdala, and an inadequate role in serotonergic neurotransmission, which may be associated with disinhibited impulsive aggression (Lieb et al. 2004). Moreover, weak prefrontal inhibitory control could contribute to amygdala hyperactivity – a common factor in individuals with BPD (Lieb et al. 2004). Furthermore, adverse childhood experiences (e.g., neglect, sexual abuse) may cause emotional dysregulation and impulsivity, leading to harmful behaviors and psychosocial conflicts (Lieb et al. 2004).

Unlike the other PDs discussed in this chapter, BPD has a treatment method with empirical support proving benefits in those that follow the treatment plan (Shearin and Linehan 1994; Linehan 1993). This method, dialectical behavior therapy (DBT), aims to target individuals' interpersonal, self-regulation, and distress tolerance skills, while emphasizing the importance of mindfulness practices (Shearin and Linehan 1994; Lieb et al. 2004; Linehan 1993). Key areas that DBT targets include teaching individuals the skills needed to tolerate emotional distress, increasing effectiveness in interpersonal conflicts, improving motivation to change, and structuring the environment in order to reinforce skillful behavior (Lieb et al. 2004). The focus of DBT is to offer an explanation of the biosocial theory in order to facilitate an

understanding of why one may be presented with this diagnosis, while also providing numerous skills to reduce its destructive impact on individuals' daily functioning.

Histrionic personality disorder. Histrionic personality disorder (HPD) is a pattern of excessive emotionality and attention seeking (see Table 6; American Psychiatric Association 2013). Prevalence rates of HPD range from 1% to 3% of the general population, and similar to the other PDs discussed, HPD occurs more frequently among inpatient populations (Mullins-Sweatt et al. 2011). There is mixed evidence on sex differences within HPD literature, as most studies suggest that males and females receive the diagnosis at the same rate, while other studies support a higher prevalence rate for females (see Mullins-Sweatt et al. 2011). The latter perspective is not surprising, as expressing emotions is more widely accepted in females than in males, given social norms. Common comorbidities are with other Cluster B PDs (antisocial and borderline), and somatization disorder (i.e., hysteria); moreover, the association between ASPD and HPD may be sex-typed versions of the same condition, where males and females present with the same symptoms, but males receive the former diagnosis, whereas females receive the latter (Lilienfeld et al. 1986; Sutker and Allain 2002).

Regarding the etiology of HPD, research suggests that having a genetic predisposition towards impulsivity or sensation seeking (similar to the hypoarousal condition discussed for ASPD), in addition to a severe maladaptive variant of extraversion (e.g., excitement seeking) and neuroticism (e.g., angry hostility), may lead to HPD behaviors (Mullins-Sweatt et al. 2011). Aside from biological factors, the tendency for families to emphasize, value, or reinforce attention seeking in an individual with such a genetic predisposition may lead to the development of HPD (Mullins-Sweatt et al. 2011). Risk factors for HPD include flamboyant, flirtatious, and attention-seeking behaviors in adolescence (Mullins-Sweatt et al. 2011). Additionally, these individuals may fall in love quickly, but become attracted to another person just as fast (Mullins-Sweatt et al. 2011). Their employment histories are erratic, often

complicated by their tendency to become romantically or sexually involved with clients, as well as by their affective instability, suggestibility, and impulsive decisions (Mullins-Sweatt et al. 2011). Although there is no specialized treatment for HPD, CBT aims to counter the individual's assumptions surrounding their need for attention by focusing on current and past relationships (Mullins-Sweatt et al. 2011). Moreover, group therapy is often used for HPD in an attempt to reduce attention-seeking behaviors. More specifically, the HPD individual may want the exclusive attention of the therapist, and group members may confront the individual, promoting a reminder of appropriate behaviors (Mullins-Sweatt et al. 2011).

Narcissistic personality disorder. Narcissistic personality disorder (NPD) is a pattern of grandiosity, need for admiration, and lack of empathy (see Table 7; American Psychiatric Association 2013). Prevalence rates of NPD are relatively low, including less than 1% of the general population, but range from 2% to 16% of clinical samples, and ultimately, the majority of those diagnosed are male (Campbell and Baumeister 2006; Widiger and Bornstein 2002). Comorbid PDs include paranoid, antisocial, borderline, and histrionic (Widiger and Bornstein 2002). Other comorbid diagnoses include substance use disorders (as substances may enhance grandiose self-experiences), depression or dysthymia, eating disorders, and the bipolar disorder spectrum (Ronningstad 2011; Campbell and Baumeister 2006).

Research suggests that an unempathetic, neglectful, inconsistent, and devaluing parental style (where attention and love from parents are contingent on success) is a strong risk factor for the development of NPD (Widiger and Bornstein 2002). Here, the child may have believed the parents do not love them for who they are, but instead for their accomplishments, creating the perspective that their self-worth is dependent on continued recognition of achievements (Widiger and Bornstein 2002). Treatment of NPD is most strongly inhibited by individuals' reluctance, as the process may insult their self-esteem by bringing up problems, imperfections, and shortcomings

(Ronningstad 2011). If an individual seeks treatment, it is often due to an acute crisis caused by personal failures, in response to ultimatums from others, an increasing sense of meaninglessness in their own life, or a loss of outside sources for narcissistic gratification (Ronningstad 2011). Although there is no concrete treatment method, the most common approach is based on CBT insights (Campbell and Baumeister 2006). The goal of this approach is to moderate one's narcissistic cognitions that accompany current manifestations, such as grandiose self-views, lack of empathy, and reactance to negative feedback (Campbell and Baumeister 2006).

Cluster C

Avoidant personality disorder. Avoidant personality disorder (APD) is a pattern of social inhibition, feelings of inadequacy, and hypersensitivity to negative evaluation (see Table 8; American Psychiatric Association 2013). Prevalence rates of APD range from 2.1% to 2.6% in the general population and approximately 3.6% in outpatient populations (Rettew et al. 2015). In regards to sex differences, research on the rates of diagnoses between sexes are said to be equal (Rettew et al. 2015). Dependent PD is the most common comorbid PD; however, the majority of the literature (Turner et al. 1992; Holt et al. 1992) addresses APD in combination with various types of social phobias and social anxieties, as there is great overlap between these conditions. Therefore, anxiety disorders are the most common comorbid diagnoses, although mood disorders are also likely to be presented alongside APD (Holt et al. 1992; Widiger and Bornstein 2002).

Causes of APD include biological factors (e.g., heightened sympathetic reactivity to environmental change), as well as environmental factors (e.g., emotional or physical abuse) that transform the genetic predisposition into long-standing behavioral patterns (Alden 1989). Along with most PDs, there is no specific treatment protocol for APD. However, studies have demonstrated the use of skills training as a treatment approach, which focuses on the development of intimate relationships while teaching individuals to monitor

others' comments and emotions, to express empathetic concern, and to engage in appropriate self-disclosure (Alden and Capreol 1993). Additionally, graduated exposure, a regimen targeted towards mastering progressive relaxation techniques, increasing satisfaction with social activities, and facilitating individuals to approach social situations may yield benefits for those with APD (Alden and Capreol 1993).

Dependent personality disorder. Dependent personality disorder (DPD) is a pattern of submissive and clinging behavior related to an excessive need to be taken care of (see Table 9; American Psychiatric Association 2013). Prevalence rates of DPD range from 0% to 7% among outpatient populations, but are much higher among inpatient populations with approximately 15–25% diagnosed; moreover, females are diagnosed more often than males (Bornstein 1997). DPD has high rates of comorbidity with other PDs, such as schizoid, schizotypal, borderline, histrionic, narcissistic, and avoidant. Moreover, DPD is comorbid with many other diagnoses, such as eating disorders, anxiety disorders, and somatization disorder (Bornstein 1995).

Causes of DPD suggest that behaviors follow the onset of physical or physiological illnesses, as the illness causes the individual to feel vulnerable, frightened, and helpless, and seek the support of others; thus, showing an increase in overt dependent behavior (Bornstein 1995). Additionally, parental overprotectiveness and authoritarianism may reinforce dependent behaviors in childhood and prevent the child from developing independent, autonomous behaviors (Bornstein 1992; Faith 2009). Consistent with most PDs, there is limited research on treatment approaches; however, psychodynamic therapy attempts to help individuals better cope with object losses and/or previous separations (Faith 2009). Moreover, CBT is used to increase one's autonomy and self-efficacy while challenging dichotomous beliefs, such as the need to be either dependent or independent, with no in-between (Faith 2009).

Obsessive-compulsive personality disorder. Obsessive-compulsive personality disorder (OCPD) is a pattern of preoccupation with

orderliness, perfectionism, and control (see Table 10; American Psychiatric Association 2013). Prevalence rates of OCPD are approximately 2–8% of the general population, and it is considered to be the most common PD in the general population as well as among outpatients (Pinto 2016; Diedrich and Voderholzer 2015). Evidence on sex differences indicate mixed results, with some studies showing equal prevalence among males and females, while others demonstrate higher rates of OCPD in males (Diedrich and Voderholzer 2015). Common comorbid PDs include paranoid, schizotypal, and avoidant, while other comorbidities include obsessive-compulsive disorder (OCD), impulse control disorders, eating disorders, substance use disorders, and bipolar disorder (Abramowitz et al. 2008; Diedrich and Voderholzer 2015).

Causes of OCPD include biological factors, such as performance deficits in frontal executive functioning, resulting in obsessive-compulsive traits and impulsivity, as well as reduced gray matter volume in the limbic cingulate (Abramowitz et al. 2008; Diedrich and Voderholzer 2015). Additionally, research suggests that OCPD individuals never formed secure attachments, experienced more overprotection during childhood, and failed to develop emotionally and empathetically – all risk factors for the development of OCPD (Diedrich and Voderholzer 2015). There is very limited research on the treatment of OCPD; however, a case study showed potential benefits by using CBT to focus on clinical perfectionism, as well as skills training in emotion regulation and relationship flexibility (Pinto 2016). Other studies support the use of CBT models targeting dysfunctional cognitions, lack of appropriate contingencies, negative affective dispositions, and issues relating to attachment and identity (Kyrios 1998).

As a final note about OCPD, it is important to differentiate between obsessive-compulsive personality disorder (OCPD) and obsessive-compulsive disorder (OCD), an anxiety disorder. For instance, perfectionism is an OCPD criterion, but can be a symptom of OCD if it involves the need for order, symmetry, and arranging

(Abramowitz et al. 2008). Although there is great overlap between the symptoms of both disorders, there are qualitative differences in regards to the motivation to engage in such behaviors (Abramowitz et al. 2008). For example, if one's motive to complete a behavior is to avoid harm, they are likely presenting with OCD symptoms, whereas if one's motive is driven by feelings of incompleteness, they are likely presenting with OCPD symptoms (Abramowitz et al. 2008).

Conclusion

To conclude, the author has discussed the ten PDs according to the DSM-5 (American Psychiatric Association 2013). The purpose of this chapter is to raise awareness on the need for research on Cluster A and C PDs, and the need for empirically supported treatment methods. Thus far, Cluster B PDs (primarily antisocial and borderline) have received the majority of academic attention and research, while the remaining PDs have received scant attention, and very little is known about their etiology and treatment approaches. As clear support for this position, borderline personality disorder is the only PD with a specialized treatment plan – dialectical behavioral therapy. Additionally, the author encourages readers to consider the adaptive benefits of PD traits, rather than simply stigmatizing these behaviors and deeming them harmful. In order to outline the ten PDs, the author reviewed the following areas: diagnostic criteria (see Tables), prevalence rates, sex differences, comorbid conditions, causes and/or risk factors, and treatment approaches. Future researchers should target Cluster A and C PDs and strive to better understand these conditions and their reasons for emerging in evolution, while implementing clinical trials towards specialized treatment approaches.

Cross-References

- [Antisocial Behavior](#)
- [Psychopathy \(Mealey\)](#)

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Personality Models

► Evolutionary Personality Psychology

Personality Traits

► Evolutionary Personality Psychology

► Five-Factor Model

► Personality Development

Personality, Gender, and Culture

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Synonyms

[Behavioral syndromes](#); [Coping styles](#); [Personality](#); [Sociality](#); [Temperament](#); [Traits](#)

Definition

Research that uses perspectives from evolutionary biology to examine ultimate-level explanations for mean sex differences in personality traits, and whether the size of these sex differences vary according to cultural factors that are of interest to biologists (e.g., environmental harshness versus prosperity).

Introduction

There are biological differences between the sexes (Del Giudice et al. 2016; Hines 2011) and such differences, intertwined with culture, can account for mean-level differences in how men and women behave, their personality traits, cognitive and coping styles, and the ways in which they initiate and maintain relationships and form groups with others. Such differences can shape how men and women interact with the world and how people respond to them. In turn, although there are many similarities between men and women, sex differences have the potential to influence important social outcomes and may be particularly relevant to interactions between men and women in which one sex interacts with a member of the other sex at the extremes of a personality or behavioral trait. This entry consolidates knowledge on mean-level sex differences in personality traits and the extent to which these differences change across cultures and may be particularly

relevant at certain points in the lifespan. Evidence for differences between men and women in their social focus and coping styles are also discussed and the potential for these differences to influence important social outcomes (e.g., mental well-being). First, the entry outlines the importance of studying personality from a Darwinian perspective.

Personality and Darwinian Fitness

Differences between individuals in their personality and how they initiate and maintain relationships and form groups (i.e., their sociality) can have meaningful consequences for reproductive fitness in both humans and nonhuman animal species (reviewed in Nettle and Penke 2010; Seyfarth et al. 2012; Wolf et al. 2007). For example, personality traits related to risk-taking such as boldness and aggressiveness are measurable in nonhuman animals. Traits such as these are observed in nonhumans in environments in which low expectations for the future promote greater risk-taking (Wolf et al. 2007), which has parallels with evolutionary perspectives on human risk-taking in harsh environments (Daly and Wilson 2005). Other work has observed relationships between personality and reproductive fitness in human societies. For example, in polygynous societies in Senegal, female neuroticism and male extraversion are positively related to offspring quantity (Alvergne et al. 2010). Many Darwinian explanations are theorized for sex differences in temperament, personality, and sociality. To highlight one example, sex differences in direct (i.e., violent) aggression and risk-taking are explained in light of sexual selection theories. Here, sex differences both in physical strength and parental investment result in high cost and low reward from violent behavior or risk-taking by the sex that bears offspring (human females) in comparison to the sex that competes for access to mates (human males; Archer 2009; Campbell 2013). The following section consolidates knowledge on sex differences in personality at the trait level.

Sex Differences in Personality Traits

Although differences in traits and behaviors are more substantial *within* a given sex than between the sexes (i.e., the sexes still overlap on traits even when differences are observed between them), large-scale cross-cultural research suggests that there are reliable average differences in men’s and women’s responses to trait personality inventories such as the NEO-PI-R (Costa and McCrae 1992). For example, women, on average, score higher than men do on the trait dimensions of neuroticism (e.g., anxiety and vulnerability), agreeableness (e.g., altruism), warmth, and openness to feelings (Costa et al. 2001, see Table 1). Men, conversely, score higher than women do on the trait dimensions of assertiveness, openness to ideas, and excitement seeking (Costa et al. 2001). Meta-analytic reviews of the literature on impulsivity demonstrate that women are more sensitive to punishment than men are, whereas men are more prone to sensation-seeking both when measured via self-report and with behavioral measures of risk-taking (Cross et al. 2011). This same review also finds similarities between men and

women on other dimensions; whereas women are more sensitive to punishment than men are, there are no sex differences in sensitivity to potential reward (Cross et al. 2011). In other work, small but robust sex differences are observed on some dimensions of narcissism such as a tendency to exploit others and preferences for leadership or authority roles, where men score higher on these dimensions than women do (Grijalva et al. 2015). Collectively, there are reliable differences between men and women on some personality traits.

Sex differences in personality traits and temperament appear to emerge through early development. For example, among children between the ages of 3 months and 13 years, girls score higher than boys do on measures of inhibitory control and awareness of small changes in the environment (i.e., perceptual sensitivity), whereas boys score higher than girls do on measures of surgency, such as approach, laughter, impulsivity, and traits denoting extraversion, such as low shyness. Within these measures of surgency, boys score higher than girls do when reporting preferences for activity and high-intensity pleasure, which is consistent with active rough-and-tumble play styles observed more in boys than girls (reviewed in Else-Quest et al. 2006). Of note, these authors find no sex differences in measures of negative affect, which may point to the role of puberty and development in sex differences in neuroticism reported earlier. Sex differences in the personality traits discussed here, and their emergence during development, are of interest to scientists who formulate ideas about behavior with reference to an evolutionary perspective.

Although these analyses and reviews suggest evidence for sex differences in temperament and personality traits, other large-scale studies suggest that, in contrast to the small effect sizes for sex differences observed in the personality literature, more substantial sex differences are observed in men’s and women’s interests and proclivities (summarized in Table 1). For example, when analyzing large representative datasets of information collated from over four decades of interest inventories, which are used to inform an individual’s plans for their education and career, there are large

Personality, Gender, and Culture, Table 1 Snapshot of effect sizes for differences between men and women in interests, temperaments, and personality traits (Data from ^aCosta et al. 2001; ^bCross et al. 2011; ^cElse-Quest et al. 2006; ^dSu et al. 2009; ^eVoyer and Voyer 2014). Negative effect sizes indicate females score/perform higher than males do on the given dimension

Trait	Effect size (Cohen’s <i>d</i>)
Neuroticism (anxiety) ^a	−0.40
Neuroticism (vulnerability) ^a	−0.44
Agreeableness (altruism) ^a	−0.43
Assertiveness ^a	0.19
Openness to ideas ^a	0.32
Excitement seeking ^a	0.31
Sensitivity to punishment ^b	−0.33
Sensation seeking (self-reported) ^b	0.41
Inhibitory control (children) ^c	−0.41
Preference for activity (children) ^c	0.33
Interest in things versus people ^d	0.93
Educational advantage (languages) ^e	−0.73

sex differences in men's interest in "things" versus women's interest in people, whereas there are negligible sex differences in interests in working with data versus ideas (Su et al. 2009). To illustrate the former large *difference* and the latter *similarity* between men and women, the difference in interest in things versus people represents only a 46.9% overlap between men and women, whereas the similarity among men and women in their preference for data versus ideas represents a 92.3% overlap between the sexes. Consistent with the notion that sex differences are most apparent at the extremes or tails of a distribution, when Su and colleagues analyzed responses from the top 25% of individuals in the population, the ratio of females to males on the things-people dimension was 0.29. In other words, of those with a particularly *strong* interest in "things" nearly seven out of ten individuals within that population were male. These data demonstrate that men, on average, are more interested in things, gadgets, and environments, whereas women, on average, are more interested in conventional careers or careers with an artistic or social element to them. Sex differences in interests and proclivities may inform differences in social outcomes such as occupational choice, which is consistent with analyses that suggest that choice (whether free or constrained) plays a contribution in gendered occupational outcomes (Ceci and Williams 2011; Robertson et al. 2010). Interactions between temperament, environment, and interests may also inform other gendered social outcomes such as educational attainment. For example, girls have an average advantage in educational attainment that is large for language courses and negligible for maths courses (Voyer and Voyer 2014). The following section outlines some of the evidence for sex differences in sociality and associated relationships with important social outcomes such as well-being.

Sex Differences in Sociality and Social Outcomes

As men and women navigate their environment through time, sex differences in personality traits,

interests, and how we initiate and maintain relationships may contribute to sex differences in a variety of outcomes that are important from an evolutionary perspective. Indeed, the era of "big data" may play an important role for future research in this area. For example, researchers can analyze large "real-world" data sets from social networks and behavior online. To illustrate with one example, computer algorithms that analyze "likes" and "dislikes" expressed over social media can classify the sender of the like or dislike by their sex with a high degree of accuracy (93%, Kosinski et al. 2013). Moreover, analyses of behavioral displays online (e.g., self-selected profile pictures) suggest that women favor dyadic relationships with a few close friends, whereas men favor larger all-male groups or "cliques" (David-Barrett et al. 2015). These findings are interpreted as evidence that women favor quality in their social relationships (i.e., emotional closeness) over quantity of social relationships. Of note to evolutionary researchers, recent large-scale studies of this nature suggest that men's and women's social focus changes across the life course in ways that may influence reproductive fitness. Analyses of mobile phone datasets suggest that the sex difference in the quality versus quantity of relationships reverses around a person's late thirties, when women have more social contacts than men do. Presumably, these contacts function for gaining social or emotional support, whereas men's reduction in social contacts around this time may reflect a change in social focus from investment in attracting a mating partner to investment in paternity (Bhattacharya et al. 2016).

Consistent with differences in men's and women's social focus, and with the importance of emotional closeness in obtaining support from others, women are more likely than men to seek emotional support from others to cope with problems (Tamres et al. 2002). Sex differences in sociality may interact in complex ways with men's and women's temperament, cognitive styles, traits, and proclivities and with circumstances they encounter through the life course, to have cumulative effects on health or well-being. For example, the extent to which someone internalizes versus externalizes problems they

encounter is related to mental health concerns. Whereas internalizing is a predictor of the prevalence of mood and anxiety disorders, externalizing predicts the prevalence of antisocial personality traits such as substance use disorders (Eaton et al. 2012). Representative data from American samples demonstrate a sex difference in the lifetime prevalence of these disorders, such that being female reduces the odds of having an antisocial personality disorder ($OR = 0.63\text{--}0.84$) but increases the odds of having a mood disorder ($OR = 1.16\text{--}1.47$; Eaton et al. 2012). Potentially consistent with the sex differences discussed in risk-taking and social focus, in which males are greater risk-takers and less focused on emotional closeness and emotional support, being male is an important predictor of a suicide attempt compared to simply communicating suicidal ideation ($OR = 1.9$; Nock and Kessler 2006). As some researchers conceptualize suicidal ideation as a means to gain support from others in adverse circumstances, further work could examine the interplay between men's and women's sociality and important social outcomes related to health and mental well-being.

Culture, Development, and Caveats

Large-scale studies have examined the extent to which sex differences in personality are universal, or vary systematically according to various factors at the national or regional level. Some of these studies test evolutionary explanations for cultural variation in behavior against social role theories (see, e.g., Hyde 2014), according to which sex differences are theorized to be explained via socialization or exposure to culture (e.g., Western media) or structural factors that constrain opportunities for one sex to the advantage of another. In contrast to social role theories of behavior, the size of sex differences in personality traits measured via the NEO-PI-R (Costa and McCrae 1992) are *larger* in more prosperous countries in which females have greater educational opportunities (Costa et al. 2001). Other analyses of data from over 50 nations indicate that across nations, men and women score differently on extraversion,

agreeableness, neuroticism, and sex-typical occupational preferences. Moreover, women are more *variable* in extraversion than men are, and men are more *variable* in agreeableness than women are (i.e., the distribution of self-reported scores is wider; Lippa 2010). When examining national variation in sex differences in personality traits, measures of gender equality and economic development used by the United Nations are associated with larger sex differences in agreeableness, suggesting that sex differences on this trait dimension are greater in more prosperous nations (Lippa 2010). However, when Lippa examined trait means for each of the four traits at the national level, only biological sex predicted these trait means and did so more strongly than did measures of gender equality. Findings such as these suggest that although the size of sex differences in personality vary with national prosperity, sex remains a more powerful predictor of personality, which researchers suggest is evidence for universality in personality (Lippa 2010). These findings complement other cross-cultural work indicating that women in a majority of nations score higher than men on some of the Big-Five personality traits, but the size of these sex differences are *greater* in nations that are better developed, according to measures for national health and wealth, and have gender parity in access to education (Schmitt et al. 2008).

Evidence for sex differences in personality traits or proclivities at the population level does not rule out the possibility that individuals vary in how they develop these traits over time or the possibility that traits and temperaments are expressed differently in certain contexts or at different points in the lifespan. Further longitudinal work in this area that tests hypotheses from an evolutionary perspective is warranted. For example, measures of social dominance orientation (a facet of extraversion), conscientiousness, and emotional stability increase between 20 and 40 years of age (Roberts et al. 2006). The size of the change in measures such as social dominance orientation is much greater in young adulthood (ages 18–22; $d = 0.41$) than it is during adolescence ($d = 0.20$), whereas changes on this dimension are minimal around the fourth decade

of life. Changes in personality traits or lack thereof are interesting if they correspond to an age period where competition for mating partners is particularly intense (see, e.g., references to work by Daly and Wilson throughout this encyclopedia). Further work examining short-term and long-term changes to traits such as social dominance orientation and the relationships of these changes to sex is likely to advance knowledge, given the observed relationships between biological sex and both direct aggression (Archer 2009) and indirect aggression (Vaillancourt 2013).

Finally, research on sex differences is sometimes controversial, particularly when individuals (mistakenly) interpret or disseminate scientific findings through a political lens. If sex differences exist on certain dimensions, they are important to understand and to gain insight into the choices and tradeoffs that people make and the subtle differences in the ways that men and women perceive the world. Such knowledge may enable us to maximize well-being or flourishing for both men and women. Moreover, knowledge of behavior at the group level does not necessitate the conclusion that we should treat individuals unfairly based on such knowledge. For an excellent overview of the social implications of evolutionary research on sex differences, and the conclusions or fears that do not follow logically from knowing more about sex differences, Pinker (2003) is highly recommended. People may also view sex differences as controversial simply from viewing this term as implying 0% overlap between men and women on a given trait dimension, which is rarely the case, as demonstrated both by common sense observation and the research reviewed here. Finally, it is worth noting that in research which demonstrates (in large samples) small but significant differences between men and women according to conventional effect size measures, these differences are still important to understand (*contra* Hyde 2014). For example, if we form stereotypes (or mental shortcuts) about people based on minimal information about them, interactions between two groups may still reinforce firmly held stereotypes if we overgeneralize about the

other group based on interaction with a member of that group who lies at the extremes of a particular trait.

Conclusion

Personality and sociality are important topics for evolutionary-minded researchers. There are reliable differences between men and women on some personality trait dimensions, such as components of neuroticism and agreeableness. The size of sex differences in personality appear to be larger in environments in which men and women are better able to pursue their own interests and proclivities (i.e., prosperous environments). Effect sizes in this area are larger when examining men's and women's interests than when examining differences in trait-level personality, demonstrating that even when average differences are observed, there is still overlap between the sexes on these dimensions. Men's and women's temperament, their cognitive and coping styles, and how they initiate and maintain relationships and form groups may shape gendered outcomes related to health, well-being, educational attainment, and career pursuit.

Cross-References

- [Biology of Human Gender, The](#)
- [Development of Sex Differences](#)
- [Personality](#)
- [Personality Development](#)
- [Personality Disorders](#)
- [Sex Differences](#)
- [Sex Differences in Aggression](#)

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Personalized Experience

► Personal Memory

Perspective Taking

► [Gratitude, Sympathy, and Empathy](#)

Peter Kropotkin

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Synonyms

[Activist](#); [Author](#); [Evolutionary biologist](#)

Definition

Peter Kropotkin (9 December 1842 – 8 February 1921) was a Russian author, activist, scientist, and philosopher.

Introduction

Peter Kropotkin was one of the great thinkers of the late nineteenth and early twentieth centuries. He wrote incessantly and what he wrote was read by many, both in the East and the West. And when he wrote and how much he wrote is nothing short of remarkable. On the run from the Russian secret police, in between two multi-year jail stints, and when he was not talking to crowds numbering at times in the thousands, Kropotkin authored books on: (1) evolution, behavior, and natural history (*Mutual Aid: A Factor of Evolution*, 1902), (2) ethics (*Ethics: Origins and Development*, 1924), (3) anarchism, socialism, and communism (*Modern Science and Anarchism*, 1908, *The Conquest of Bread*, 1913, and *The State: Its Historic Role*, 1903), (4) the coming industrial revolution in the East (*Fields, Factories, and Workshops*, 1899), (5) penal systems (*In Russian and French Prisons* and *The Terror in Russia*, 1887), (6) The French Revolution (*The Great French Revolution*,

1909), and much more. At first glance these topics may seem unconnected, but in fact, a common thread – Kropotkin’s biological law of mutual aid, which he argued guided all living things from microorganisms to nonhuman animals to humans – tied all of these works together (Kropotkin 1899b; Dugatkin 2011). What Kropotkin then called mutual aid, we now call cooperation.

Early Life

Born in Moscow in 1842 to a family that once were princes, in his teenage years he was the personal page to Czar Alexander II. During that same stretch of time, he also read Darwin’s *On the Origin of Species*. He came to think that evolutionary principles explained the diversity and history of life. Over time he would argue that natural selection was the driving force that shaped life, but that Darwin’s ideas had been perverted. Kropotkin’s theory of mutual aid was born in the most unlikely of places. To follow in the footsteps of one his heroes, Alexander von Humboldt, in 1862 when he was 20 years old, Kropotkin began a five-year series of expeditions in Siberia. He was already an evolutionary biologist, but 50,000 miles and 5 years later, when he left Siberia, he thought very differently about how evolution worked.

Mutual Aid and Siberia

When Kropotkin began his journey through Siberia, just 3 years after *On The Origin of Species* was published, competition was thought to be the driving force producing evolutionary change. Kropotkin expected to confirm what he had read on this. He searched for competition, nature “red in tooth and claw.” But no luck:

Even in those few spots where animal life teemed in abundance, I failed to find—although I was eagerly looking for it—that bitter struggle for the means of existence, among animals belonging to the same species, which was considered by most Darwinists (though not always by Darwin himself) as the dominant characteristic of struggle for life, and the main factor of evolution. (Kropotkin 1902)

Instead, Kropotkin observed cooperation and altruism – what he called mutual aid. Animals grouped together to stay warm, emitted alarm calls warning of danger, and shared what food they had. “In all the scenes of animal lives which passed before my eyes,” he wrote, “I saw mutual aid and mutual support carried on to an extent which made me suspect in it a feature of the greatest importance for the maintenance of life, the preservation of each species and its further evolution” (Kropotkin 1902). Kropotkin studied the human populations of Siberia as well as the nonhuman. He spent much time in the small villages scattered across the harsh landscape, recording acts of mutual aid among the individuals in these places.

How then to align his observations with the predominant Darwinian theme of competition? Kropotkin’s solution was this: natural selection was indeed the primary force shaping life, but this process led to mutual aid, not competition, among individuals. Many years later, he would summarize these ideas in his classic book, *Mutual Aid*. Natural selection, he proposed, generally led to cooperation and altruism – what he called mutual aid – not to individual versus individual competition. He came to speak of *progressive evolution*, a term he used to describe how mutual aid became the *sine qua non* of all societal life – animal and human.

Conclusion

Kropotkin was at least a century ahead of his time. While Darwin introduced the world to the idea of descent with modification, it was Kropotkin that first made the detailed, cogent case that studying animals sheds light on the evolution of cooperation. And if animals could cooperate in small, leaderless groups, Kropotkin believed, then surely we can as well, if we would just open our eyes to the lessons that nature teaches. He devoted much of his life to this cause. His overarching goal was to understand cooperation in nature, so that he could promote cooperation in humans. Just like in the animals he watched for 5 years in Siberia, Kropotkin saw human cooperation as ultimately being driven not by government but by groups of individuals spontaneously uniting to do good,

even when they have to pay a cost to do so. Time will tell if he is correct.

Cross-References

- [Altruism Among NonKin](#)
- [Altruism](#)
- [Cooperation](#)

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Petroglyphs

- [Prehistoric Human Art](#)

Phantom Limbs

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Synonyms

[Amputated limbs](#); [Phantom pain](#); [Phantom sensations](#)

Definition

Phantom limb refers to a vivid sensation and a perception of the physical existence of a limb that has been amputated.

Introduction

It has been widely suggested that many people who lose a limb to amputation, they have continued to sense intensely and in a vivid manner the existence of the lost limb a phenomenon that has been widely termed as “phantom limb” (Pinel and Barnes 2017). Over the last century, there had been numerous attempts to analyze theoretically, operationally, and religiously this striking phenomenon, varying from psychoanalytic hypotheses related to unconscious wish fulfillment to the postulation of an immaterial psyche (Daroff 2015). However, in the last few decades, a substantial amount of researchers have proposed that these phenomena are the result of neuroplasticity (Ramachandran 2012). The most remarkable characteristic of those phenomena is the incredibly realistic sensation and perception of it by the individual who is experiencing it. Specifically, people who continue to feel the presence of a lost limb might attempt to walk onto a missing leg or to lift a glass of water, using a missing hand (Ramachandran 1998).

It has been consistently cited in the relevant literature that an amputated hand and/or a leg is perceived to operate in the same way as an existing limb. For instance, when a person who lost an arm is walking, he/she sense the phantom leg to move back and forth in perfect synchronization with the physically existed arm. Yet, from time to time an individual might sense his/her lost limb stacked in an atypical posture (Ramachandran and Rogers-Ramachandran 2000). For instance, a person might feel that her/his missing arm extends straight-out from the shoulder. Consequently, she/he feels that he must turn and as a result, he is turning sidelong every time she/he passes through a door. Moreover, approximately half of the people who experience the phenomenon of phantom limbs experience

long-term and intense pain in their missing limbs (Ramachandran 2012).

For a long period of time, neuroscientists presumed that the cortical area matching to an amputated limb will become dormant, as axons in different cortical areas cannot sprout as far as to get to the cortical area corresponding to the amputated limb (Zillmer et al. 2008). However, surprisingly researchers in a study of the cerebral cortices of monkeys whose sensorial neurons from either one of their front limbs were cut 12 years before detected that the stretch of cortex formerly reacting to a limb that had been cut was now reacting to the face (Ramachandran 2012). Following the loss of sensorial information by either one of their front limbs, the axons that were responsible for it were gradually degenerating. Consequently, there were left unoccupied synaptic areas at numerous dimensions of the central nervous system (Pinel and Barnes 2017). One hypothesis is that axons that are responsible for the face were sprout inside areas in the spinal cord, brain stem, and the thalamus. A further hypothesis is that axons that are accountable for the face and were there came to be more powerful due to denervation supersensitivity. A substantial amount of research using magnetic resonance imaging verified that human beings respond to an amputation of a limb in the same way (Pinel and Barnes 2017).

Pinel and Barnes (2017) propose that in cases in which some of the areas of the brain lose some of their incoming axons, it is expected to be observed as an increase in the reactivity of the axons that have survived and collateral sprouting by axons which have typically other functional qualities. Additionally, every limb has a specific set of nerve cells which receives sensorial information from it. As already has been mentioned, in a significant number of cases of limb-amputation, it has been hypothesized that this set of cells is now receiving sensorial info from the face (Pinel and Barnes 2017). That is, following the amputation of a limb, a significant number of patients experience a vivid sensation of the lost limb when a specific area of the face is stimulated. Specifically, the etiology of the striking phenomenon termed as phantom limb seems to lie in the

anatomical structures of the brain (Daroff 2015). The whole layer of tissue forming the natural outer part that covers the body's left side is charted onto the strip of cortex that is termed postcentral gyrus which is located on the brain's right side (Zillmer et al. 2008). This chart is usually demonstrated with the animation of a human male arranged on the brain's uppermost layer. Although this chart is mostly precise, some parts of it have been scrambled in comparison to the accurate design of the human body (Pinel and Barnes 2017). Therefore, in case of a leg amputation, the leg does not physically exist, yet a mapped leg still exists in the anatomical structures of the mind. The operational function of this chart is to represent its leg. Following the amputation of the leg, this map continues to represent the leg something that gives an explanation related to the etiology of phantom limbs phenomena (Ramachandran 2012).

Conclusion

Medical doctors have consistently observed that a significant amount of individuals who lose a limb continue to perceive a vivid sensation of the limb that they have lost. Yet this phenomenon is not a homogenous one. Specifically, the phenomenon of a phantom limb could be manifested in various ways. For instance, it can vary from a sporadic tingles to severe painful sensations and from an infrequent to a continuous manifestation (Pinel and Barnes 2017). Additionally, it has been consistently observed that people can experience this phenomenon in every part of the body that has been amputated. Moreover, the experience of a sensation of a lost limb may be manifested for few days, months, or for the whole duration of an individual's life (Ramachandran 1998). Recently, neuroscientists have suggested that this striking phenomenon manifests when the pertinent section of the somatosensory cortex alters in the way in which it is organized and grow to be responsible to other inputs (Pinel and Barnes 2017). For instance, axons reflecting the face acquire the capacity to stimulate the cortical area formerly responsible for a leg that has been amputated.

Furthermore, long-lasting plasticity consists of a central adaptive mechanism in the evolution of the human species. That is, through the process of natural selection, the human brain is considered to have acquired the capacity to use learning so that to operate and control the direction of cerebral as well as perceptual phase transitions (Ramachandran 2012).

Cross-References

- Cerebellum, The
- Primary and Secondary Auditory Cortex
- Proprioception

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Phantom Pain

- Phantom Limbs

Phantom Sensations

- Phantom Limbs

Pharynx

- Stereotyped Vocalizations

Phenomenological Self

► [Meaning Making and the Self](#)

Phenoptosis

► [Death](#)

Phenotype

- [Genetic Predispositions](#)
 - [Reaction Norms and Tokens](#)
-

Phenotype Linked Fertility Hypothesis, The

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Definition

Male secondary sexual (attractiveness or competitive) characters signal male fertility to potential female mates.

Introduction

The phenotype linked fertility hypothesis (PLFH) posits that male attractiveness traits, such as extravagant plumage, courtship, or weapon-like appendages, function as honest signals of male fertility. Robert Trivers (1972) reasoned that generally higher mating rates and the corresponding potential in males to become sperm depleted imposes selection on females to avoid sperm limited males. Males with the most vigorous courtship are indicating their sexual competence and adequate sperm supplies. Correspondingly, any

physical trait that males possess enhancing the appearance of this vigor would be exposed to strong sexual selection and quickly exaggerated through mate choice. The PLFH has also been invoked as an explanation for the observation that many bird species, which tend to exhibit social monogamy, have offspring sired by males other than primary social partners. If paired with a male that does not have adequate sperm supplies or possess nonfunctional ejaculates, selection would favor females to identify and mate with more fertile males outside the primary pair bond to avoid a reduction in fecundity (Sheldon 1994). This would result in two measurable effects: (1) a positive correlation between attractiveness and ejaculate quality and (2) extra-pair offspring should be sired by more attractive males. The PLFH invokes direct benefits of acquiring competent ejaculates to females, rather than the more controversial indirect genetic benefits of acquiring superior genes from more attractive mates (Sheldon 1994; Mautz et al. 2013).

Predictions, Assumptions and Evidence

Biologists are interested in the connection between pre- and postcopulatory sexual selection as both episodes interact and will determine net selection strength acting on male traits (Birkhead and Pizzari 2002). The PFLH predicts that there will be a positive correlation between male secondary sexual characters (SSCs) and (some aspect of) ejaculate quality. A positive relationship, as predicted by the PFLH, suggests that postcopulatory processes reinforce or strengthen precopulatory processes. If females can identify males by some phenotypic trait that indicates a functioning ejaculate, then this selection will generate a correlation between male traits and ejaculates and a direct link between pre- and postcopulatory processes. This prediction is connected to the “handicap hypothesis” that provides a general explanation for why male SSCs function as reliable indicators of male quality (Zahavi 1975). Secondary sexual characters increase male conspicuousness, divert resources away from other functions, and thus increase the

risk of mortality and other fitness costs. Only those males that are in the highest condition can invest in exaggerating SSCs without the corresponding mating gains being negated by greater costs of investment. Hence, condition is an indication of a male's ability to convert energetic resources into sexual signals and ejaculates.

Constraints on Investment

The relationship between SSC and functional ejaculates might not be as simple as a positive relationship. Resource, developmental, and evolutionary constraints might limit investment in either trait and alter the co-evolutionary dynamics. Life history theory predicts that there will be trade-offs between traits that depend on the same resources and that are closely related to fitness. Energy utilized to generate attractiveness traits might reduce the available resources that can be allocated to traits impacting the quality or size of an ejaculate (Mautz et al. 2013). In this case, a range of relationships can potentially be observed. For example, a negative relationship might be observed if the resources used to enhance attractiveness prevent investment into traits that might enhance fertility such as testis size or maintenance. Hence, the relationship will more broadly impact both variation in resource acquisition and allocation strategies. A negative relationship might also be found regardless of acquisition or allocation strategies. Selection tends to eliminate genetic variation in traits closely related to fitness, fixing those mutations that increase expression in both traits. The only standing genetic variation remaining then are deleterious alleles that have negative ("pleiotropic") effects on the focal traits.

Current Evidence

The current evidence to support the link between male traits and ejaculate quality is weak. Body size and a range of other male traits have been linked to female fertility, fecundity, and parental care, but most of the effects were relatively small (Møller and Jennions 2001). More recently a meta-analysis of 38 studies across a range of species found no relationship between exaggerated male SSCs and specific aspects of ejaculate

quality including sperm swimming speed, number, or size (Mautz et al. 2013). However, there was a weak positive correlation between SSCs and sperm viability (Mautz et al. 2013) which is, arguably, more important to female fertility over other sperm traits. Two subsequent meta-analyses specifically tested the prediction that longer sperm are correlated with larger weaponry used in intrasexual competition. One using ungulates (Ferrandiz-Rovira et al. 2014) found a negative relationship between weaponry and sperm length. Another comparing a broader range of animal taxa found no relationship (Lüpold et al. 2015). As with studies of other animals, studies in humans show mixed results. Humans show a range of sexually dimorphic traits that have been associated with sexual selection. A recent review has highlighted the potential for the PLFH to function in humans in a range of traits including facial symmetry/attractiveness, height, and intelligence. The data are mixed and issues with quantifying different sperm traits hamper the ability to make any judgment on whether the PLFH is supported in humans (Jeffery et al. 2015).

Assumptions of the PLFH

Apart from the differing predictions made by life history theory on the link between male attractiveness traits and ejaculate quality, the ability to detect these relationships is hampered by several issues (Mautz et al. 2013; Jeffery et al. 2015). These issues revolve around quantifying and defining both male quality and ejaculate quality. The definitions of "quality" and "condition" remain subject to much debate in the evolution literature (as in Mautz et al. 2013) which has made them difficult to measure in evolutionary ecology studies.

The problem when trying to infer if there is a general link between mate choice for particular SSCs and male fertility or sperm quality is that there is no current consensus on how to measure these traits across animal species. There is no standardized way of measuring sperm quality and typical measures might poorly correlate with actual fertility (Birkhead et al. 2009). Different fields have traditionally used different methods both to extract and analyze ejaculates, and

sampled populations might differ highly between species. For example, human fertility studies are generally based on men suffering from sterility issues, while studies from animal breeding programs typically involve highly fertile individuals only. Moreover, different techniques to measure aspects of fertility tend to yield highly different results (Jeffery et al. 2015). Despite decades of research on this subject, there is surprisingly no real consensus on the definition of sperm quality and different criteria are often used across studies. Important components of ejaculate quality generally include sperm morphology, swimming ability, longevity, and metabolic performance, though nonsperm related aspect of ejaculates such as seminal fluid components or chemical interactions between sperm and genital tract fluids might also play an important role (Mautz et al. 2013; Birkhead et al. 2009).

Finally, the phenotype linked fertility hypothesis relies on the assumption that females risk being sperm limited and need to ensure fertilization of their eggs, therefore needing external cues about a male's fertility. It is unclear how common infertility and sperm limitation actually are in the wild (Mautz et al. 2013). Sperm limitation and the need of external cues to evaluate males' fertility statuses might only be really relevant in truly monogamous species. Females that mate multiply (a very common phenomenon in nature) should be able to obtain sufficient quantities of sperm from different males and to rely on mechanisms of sperm competition to ensure the fertilization of their eggs by high-quality sperm. Mate-compatibility might be generally more important than fertility per se, in which case molecular mechanisms of sperm selection within the female reproductive tract, using specific chemical recognition cues on sperm cells, should be of particular relevance.

Conclusion

The PLFH currently lacks broad empirical support. Better definitions of quality and condition,

both for SSCs and ejaculates, might more clearly outline how researchers can measure the relationship between pre- and postcopulatory traits. Typical laboratory studies do not constrain resources available to their study organism. Performing studies under constraining environments might assist in measuring the relationship. Finally, determining if and when female fitness is constrained by access to ejaculates or some particular aspect of ejaculate quality will assist in defining the context that will generate a relationship between SSCs and fertility.

Cross References

- [Indirect Benefits of Altruism](#)
- [Mate Choice](#)
- [Precopulatory Intrasexual Competition](#)
- [Secondary Sexual Characters](#)
- [Sexual Selection](#)

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Phenotypic Resemblance and Kinship Detection

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Many types of cues can correlate with genetic relatedness. Contemporary researchers categorize potential kinship cues in two main classes: contextual and phenotypic (reviewed in Penn and Frommen 2010).

Contextual cues include information such as spatial location, timing of association, mating history, and state-dependent association (e.g., during the hormonal state that characterizes recent childbirth), as well as interactions between such factors. For example, co-residence duration is generally positively correlated with measures of altruism and incest avoidance between siblings (Lieberman et al. 2003). However, individuals who have experienced maternal perinatal association (i.e., the close association between your mother and a newborn potential sibling) show high levels of altruism and incest avoidance towards that sibling and do not show effects of co-residence duration (Lieberman et al. 2007).

Phenotypic cues are physical cues that correlate with genetic relatedness, such as odor, vocal, and facial resemblance. For example, facial resemblance is a strong candidate cue for phenotypic kin recognition in humans (DeBruine 2002, 2004a, b, 2005; DeBruine et al. 2005, 2008, 2011; Krupp et al. 2008, Krupp et al. 2012; Watkins et al. 2011).

Experimental approaches, such as computer-graphic manipulation (Tiddeman et al. 2001) of facial resemblance, have largely focused on behavior towards unfamiliar individuals (e.g., DeBruine et al. 2008). This research has established that these computer-generated “virtual siblings” elicit more cooperation in economic games (DeBruine 2002; Krupp et al. 2008) and are perceived as especially trustworthy (DeBruine 2005; DeBruine et al. 2011), but this resemblance

Phenotype Matching

- ▶ [Helping and Genetic Relatedness](#)
- ▶ [Holmes and Sherman \(1982\) on Ground Squirrels](#)

Phenotypic and Genotypic Plasticity

- ▶ [Reaction Norms and Tokens](#)

Phenotypic Cues

- ▶ [Kin Recognition and Classification in Humans](#)

Phenotypic Matching

- ▶ [Kin Recognition and Classification in Humans](#)

Phenotypic Quality Advertisement

- ▶ [Costly Signaling and Altruism](#)

does not enhance the attractiveness of other-sex faces as much as same-sex faces (DeBruine 2004a; DeBruine et al. 2011) and even decreases attractiveness in an explicitly sexual context (DeBruine 2005). However, some research using different computer-graphic techniques for creating resemblance has found that self-resemblance enhances the attractiveness of other-sex faces as much as own-sex faces (Saxton et al. 2009) or does not enhance cooperation (Giang et al. 2012).

Another area of work on facial resemblance focuses on the perceptual mechanisms for perceiving resemblance. For example, judgments of facial similarity map almost perfectly onto judgments of kinship (DeBruine et al. 2009; Maloney and Dal Martello 2006) and kinship judgments rely on information from the upper half of the face (Dal Martello and Maloney 2006). Additionally, inverting faces does not interfere with kinship judgments, suggesting kinship cues exist in featural but not configural information (Dal Martello et al. 2015).

Much research on phenotypic cues of parent-child kin recognition focuses on the theoretically compelling, but empirically controversial, extent to which children differentially resemble their parents and the extent to which such resemblance affects parental solicitude. Because mammalian paternity is always less certain than maternity, some have predicted that children should preferentially resemble their fathers (Johnstone 1997) or maintain an anonymous appearance (Pagel 1997). Although studies consistently find that people perceive newborns to resemble their fathers (Daly and Wilson 1982), early empirical evidence showing that young children did look more like their fathers than their mothers (Christenfeld and Hill 1995) was not supported by further studies (Alvergne et al. 2007; Bressan and Dal Martello 2002; McLain et al. 2000). Relatedly, the theoretically compelling hypothesis that men should have stronger responses than women do to phenotypic cues of relatedness has been supported by some correlational (Apicella and Marlowe 2004) and experimental work (Platek et al. 2002, 2003), but not by other experimental work (Bressan et al. 2009; DeBruine 2004b; Welling et al. 2011).

Research on odor cues to kinship has largely focused on odors associated with the major histocompatibility complex (MHC, a highly polymorphic region of the genome that codes for proteins involved in immune response, reviewed in Brown and Eklund 1994). In humans, almost all of this research has investigated mate choice or preference, rather than prosocial behavior (reviewed in Havlicek and Roberts 2009). Because of this limitation, it is difficult to determine whether MHC-related odors are associated with mate choice and preference because of their utility as a cue of kinship or because of their utility in signaling genetic compatibility (Roberts and Little 2008). Additionally, the findings for assortative versus disassortative preferences in this area are mixed, potentially because responses to MHC-related odors interact with other factors, such as facial appearance or relationship context (Havlicek and Roberts 2009).

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Phenotypic Similarity

► Facial Resemblance and Kinship Detection by Strangers

Phenotypic Variance

► Culture of Honor and Individual Differences ► Individual Differences

Philippa Foot

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Synonyms

[Author](#); [Ethics](#); [Philosopher](#)

Definitions

Philippa Foot was a British author and philosopher who is best known for her work in ethics, particularly her work developing *the trolley problem*. She died on her 90th birthday on October 3, 2010.

Introduction

Philippa Foot (née Bosanquet) was a British philosopher best known for her work on morality and ethics (Grimes 2010). She earned a bachelor's degree in philosophy, politics, and economics at Somerville College in Oxford, England, in 1942 and a Master's degree from the same institution in 1946. She worked as a researcher at the Royal Institute of International Affairs during the Second World War and began lecturing at Somerville College in 1947 (Grimes 2010). She became the first philosophy tutorial fellow at Somerville College in 1949 and vice-principal in 1967, a post which she later abandoned so that she could take up a variety of visiting professorships in the United States of America (O'Grady 2010). She became a professor of philosophy at the University of California, Los Angeles, in 1974 and retired in 1991 (Grimes 2010).

The Scholarship of Philippa Foot

In her early work, notably in the essays "Moral Beliefs" and "Moral Arguments" that were

published in the late 1950s, Foot argued that moral statements were essentially emotional expressions because they could not be assessed as correct or incorrect in the same way as factual statements (Grimes 2010). She also asserted that virtues like courage, wisdom, and restraint are essential to human existence and make up the building blocks of morality, a position known as virtue ethics (Grimes 2010). Virtue ethics is one of three major approaches in normative ethics (i.e., the study of ethical action), with the others being deontology (i.e., emphasizing rules as the foundation of morality) and consequentialism/utilitarianism (i.e., emphasizing the consequences of actions as the foundation of morality). Similarly, in her most recent book, *Natural Goodness* (published in 2001), she argued that morals are based in objective human needs that can be compared to the physical needs of plants and animals (Grimes 2010).

However, Foot is arguably best known for her 1967 essay "The Problem of Abortion and the Doctrine of the Double Effect," in which she discussed the moral distinctions between intended and unintended consequences and between the duty to do no harm versus the duty to help others, using a series of vexing examples (Grimes 2010). The ethical dilemma now known as *the Trolley Problem* was first outlined in this essay and has received the most attention of the examples Foot provided. The Trolley Problem involves a dilemma faced by the driver of a runaway trolley that is careering toward five workers. The driver faces the dilemma of whether to divert the trolley onto another track where only one worker is present, thus sacrificing one life to save five. Although the dilemma may seem an easy one – one life lost is preferable to five – Foot applied the same logic to a surgeon killing one patient to donate his organs and save five lives, which is considered morally reprehensible despite the result being the same. Later, Judith Jarvis Thomson created two variations of the Trolley Problem known as the loop variant, where a bystander must choose whether to throw a switch to divert the trolley (sacrificing one life to save five) or not to intervene at all, and the fat man variant, where a bystander must choose whether or not to throw an

obese man onto the tracks to derail the trolley and save five lives (Cathcart 2013).

Conclusions

The use of the trolley problem and its variants to study morality has become known as *trolleyology* (Cathcart 2013). The trolley problem has been used by many researchers from a diverse background of disciplines to show how moral reasoning changes according to slight variation in context (e.g., Bleske-Recheck et al. 2010). More broadly, the work by Philippa Foot has spawned into an important subdiscipline that informs the evolution of human morality through interdisciplinary research.

Cross-References

- [Development](#)
- [Judith Jarvis Thomson](#)
- [Trolley Problem, The](#)

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Philomachus pugnax

- [Ruff Shorebird, The](#)

Philopatry

- [Alarm Callers Are Females with Greatest Genetic Representation](#)
- [Females Remain with Natal Group](#)

Philosopher

- [Charitable Giving \(Peter Singer\)](#)
- [David Benatar](#)
- [David Edmonds](#)
- [Judith Jarvis Thomson](#)
- [Philippa Foot](#)
- [Thomas Cathcart](#)

Philosophical Antecedents of Darwin

- [Early Perspectives on Evolutionary Change](#)

Philosophical Foundations for a Modern Morality

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Synonyms

[Ethics](#); [Metaethics](#); [Morality](#); [Naturalism](#); [Substantive ethics](#); [Theories of morality](#)

Definition

Contrary to ancient ethics, which focusses on how to live a happy life, modern morality is the study of which actions are right or wrong.

Introduction

What Is “Modern Morality”?

In a sense, the phrase “modern morality” is an oxymoron, a bit like “weapons for peace.” Weapons cannot be for peace and morality cannot be modern. One does not speak of a modern geometry in the sense that Pythagoras’s theorem no longer holds, and one does not speak of a modern morality in the sense that one should no longer love one’s neighbor. But of course one does speak of a modern geometry in the sense that some geometries are not Euclidean and there all sorts of hitherto-accepted relationships that no longer hold. And one can speak of a modern morality in the sense that old moral norms no longer hold. Think of gay relationships, for instance, and how these were castigated and how far we – at least some of us – have come on these issues. Truly, there is not much of a paradox here, because it has been recognized at least since the Greeks that when one makes moral claims – treat gays and lesbians like you treat straight people – one is combining two things. First, *ultimate moral principles*, like the idea that you should love your neighbor as you do yourself. Second, *factual claims*, like the idea that sexual orientation is something conferred on us and not chosen, and does not in itself lead to degenerate behavior like pedophilia. An awful lot of the change in morality is change in beliefs about the nature of things. There are many reasons to criticize Freud, but let us never cease to praise him for bringing us from the Dark Ages of thinking about the supposed facts of sexuality.

Let us therefore never forget the empirical factual elements in making claims in the name of morality, and consequently let us not forget that, in one very important sense, in talking about “philosophical foundations” we are not directly talking about these factual elements. That is the job of the empirical scientist, although perhaps also of the novelist and the poet. Preachers will think it is their job too, but I will leave this as an exercise for the reader.

I have just said “in one very important sense.” Is there another important sense? One where factual issues are important? Generally, philosophers

divide moral questions into two categories: substantive or normative ethics and metaethics. *Substantive ethics* is concerned with what one should do. To take Christianity as a system with an ethical component, the Christian is told one should love one’s neighbor as oneself (i.e., what one should do). “Lord, when saw we thee an hungred, and fed thee? or thirsty, and gave thee drink? When saw we thee a stranger, and took thee in? or naked, and clothed thee? Or when saw we thee sick, or in prison, and came unto thee? And the King shall answer and say unto them, Verily I say unto you, Inasmuch as ye have done it unto one of the least of these my brethren, ye have done it unto me” (Matthew 25: 37–40). *Metaethics* is concerned with *why* one should do what one should do (i.e., foundations). For the Christian it is generally answered that one should do what one should do because that is the Will of God. It is what He wants. There are well-known problems with the so-called divine command theory, but these are not our problems here. For the Christian, it all stops with God.

Naturalism

We can take it that, in a system like Christianity, empirical factual elements do not really enter into the philosophical foundations. That God exists is presumably a fact – or not. Either way, it is not an empirical fact. You do not discover God under the microscope or through the telescope. And what God wills is what God wills. One often finds Christians wrestling with the Book of Job where God’s behavior is very un-Godlike in respects and where, when He is challenged on this, He basically tells people to mind their own business: “Where wast thou when I laid the foundations of the earth? declare, if thou hast understanding” (Job 38:4). However, to raise the other important sense about morality and the empirical world, there is an influential school of thought – probably David Hume (1739–40) was its most celebrated exponent – that thinks that philosophical foundations must begin with the empirical world. This is the “naturalistic” approach to philosophy. Hume was a century too early. He was not an evolutionist. But, thanks particularly to Charles Darwin (1859) – who was much influenced by Hume in

thinking about both morality and religion (Darwin 1871) – today we are evolutionists, and despite all of the newspaper chatter otherwise, the vast majority of serious evolutionists are Darwinian evolutionists. They think the key to understanding organisms – and this includes humans in their thinking and their behavior – is Darwin’s mechanism of natural selection (Ruse 2006). More organisms are born than can survive and reproduce. This leads to a struggle for existence. In the struggle, on average, those with features that help in the struggle will be successful – they will be the “fit” – and over generations this will lead to change, but change of a particular kind, namely in the direction of adaptive advantage. Organic features, characteristics – including human thought and behavior – will be as if designed for the benefit of their possessors.

Substantive Ethics

So how does evolutionary naturalism cashed out for human nature – more generally it used to be known as human sociobiology and now as evolutionary psychology – apply and yield insights when applied to morality (Ruse 1986, 1988, 2009, 2012)? Start at the substantive level. A common misconception – metaphors like the “selfish gene” have not exactly helped – is that Darwinism promotes strife and conflict and selfishness. After all, if the name of the game is survival and reproduction, then to use an old phrase, it is every man for himself. Every woman too, because one thing about Darwinism is that if women could not hold their own with men, very quickly we would all be men! One way out of this conundrum is to suppose that selection can act for the benefit of the group as well as for the individual. Hence, although groups may fight it out, within the group – which could well be a whole society – individuals are going to aid each other. Treat your neighbor like yourself. However, although there are some prominent supporters of “group selection” – notably ant-expert and sociobiologist Edward O. Wilson of Harvard – generally it is not thought a widespread and effective mechanism of change (Wilson and Wilson 2007). It is too open to cheating. I help you by giving you one of my two units of value (food or some such

thing), but you do not help me and keep both of your units to yourself. I end with one unit and you end with three, and pretty soon your selfish nature will spread through the population and all kinds of help – often known as altruism – will vanish (Williams 1966). However, there are several individual-selectionist mechanisms thought active and promoting behaviors that in the human we would describe as (substantively) moral. These are mechanisms that show that cooperation can have reproductive benefits. One may not get all of the cake, but half a real cake is better than all of a missed or nonexistent cake. One mechanism is so-called reciprocal altruism (Trivers 1971). You scratch my back and I will scratch yours, or in a bigger population you throw your unit of help into the general pool and draw on the pool as you need it, for instance, when young or old or sick. Another mechanism is so-called kin selection where one helps relatives because in so doing you are passing on your own genes – your units of heredity – that you share with relatives (Hamilton 1964; Maynard Smith 1982). Note that no one is saying that, in any of these cases, humans would be conscious of what they were doing. One would think slightly crazy someone who suddenly stopped helping someone else because they learnt that they were adopted and not really a blood sibling or cousin. As sexual behavior shows only too well, nature gets its way best when the actor is unconscious of the consequences.

Kin selection (as well as reciprocal altruism) points to one way in which modern science – modern Darwinian science – might make us reconsider our substantive moral norms. If we are more likely to help relatives, then moral sentiments – simple adaptations just like hands and teeth, penises and vaginas – are going to track this. We will feel a greater moral obligation to help relatives than strangers. And we will feel a great moral obligation to help those who might someday help us, or to help those whose position we might someday find ourselves in. So love your neighbor as yourself will not in fact be quite the simple norm that guides not just our actions, but our moral feelings about things. (This is an important caveat. We often do things that we do not

think are moral. What are being talked about now are things that we do think are moral.) How might the simple norm be modified? Well, you would think you have the greatest obligation to your closest relatives and in particular to those relatives who might still reproduce – children first, then siblings, and perhaps parents but probably not. After that, nephews and nieces, and cousins, and so forth. Then, real neighbors and friends, and so on out in your own society. It does not mean that you will not feel obligations to strangers in strange lands, but they will be down the list.

Note one very important thing about the naturalist approach to substantive morality. The naturalist is not a preacher, trying to get you to mend your ways. “Don’t waste your money on Oxfam. Your kid at private college needs another video game.” What the naturalist is trying to do is to get you to recognize fully and openly what you already really believe! I say I am going to quit smoking, but does anyone other than me think that I am really going to quit smoking? The naturalist is saying that we may preach a good line about loving our neighbors – and perhaps we do sometimes visit the sick or those in prison – but by and large we do not believe what we are saying. More than this, we don’t believe that we ought to believe what we are saying. If you heard a colleague being praised for his or her great contributions to charity, and then learnt that their kids have to eat at church food kitchens and their only clothing comes from Good Will, you would feel a lot less than admiring – even though, dollar for dollar their money is probably helping more people than otherwise. Charity begins at home.

The naturalist will back up these insights, showing that they are not merely self-justification by a selfish-philosopher by pointing to what others have said. Although he may not have been an evolutionist, Hume spotted what was happening and what should happen.

In like manner we always consider the natural and usual force of the passions, when we determine concerning vice and virtue; and if the passions depart very much from the common measures on either side, they are always disapproved as vicious. A man naturally loves his children better than his nephews, his nephews better than his cousins, his cousins better than strangers, where everything else

is equal. Hence arise our common measures of duty, in preferring the one to the other. Our sense of duty always follows the common and natural course of our passions. (Hume 1739–40, pp. 483–484)

In his great novel, *Bleak House*, Charles Dickens (1853 [1948]) makes a similar point. He is withering in his contempt for the philanthropist Mrs. Jellyby, who devotes all of her attention to the wellbeing of an African tribe – the “Borriboola-Gha venture.” In so doing, she ignores the needs of her own children and husband, not to mention the needy members of her own society, notably Jo the crossing-sweeper.

Metaethics

What of the naturalist approach to metaethics? There are those like Edward O. Wilson who think that in some ways nature is, if not living, then at least a thing of value in itself (Wilson 1992). This is the kind of thinking that inspires supporters of the so-called Gaia hypothesis, which states that the world is a living thing, and hence something of value that we should respect and cherish. This is a view with venerable roots, going back through the Romantics at least to Aristotle. For thinkers of this ilk, therefore, the fact that something is natural is itself value-conferring. Wilson, like others who belong to this tradition – notably the nineteenth-century English polymath Herbert Spencer (1857) – see life’s history as essentially progressive and humans as the apotheosis of this process. Hence, for them, moral norms center on human wellbeing. Anything that speaks positively to this is moral. Anything that does not, is not. Wilson himself has been much engaged in the biodiversity issue, arguing that the destruction of the Brazilian rainforests is devastating on species and hence – for our sake – should be stopped. Others, like the philosopher Holmes Rolleston III (1994), argue that value extends more broadly. He would be against the destruction of the rainforests not so much for our sake, but for the sake of the trees themselves. They have value and hence have rights.

Most naturalists do not buy into this line of argument. In this respect, they would be with Descartes (1964) in thinking that the natural

world is the world of inert substance – what Descartes called *res extension*, in contrast to the world of thought, *res cogitans*. (Most naturalists, starting with Hume, would not agree with Descartes that only we humans have *res cogitans*. They would deny that animals are pure *res extensa*.) The point is that if the world is inert then it has no value and we should not expect natural selection to produce it out of nothing. Evolution is not essentially progressive and what has evolved is not necessarily what is good. Darwin's great supporter Thomas Henry Huxley made this point: "Man, the animal, in fact, has worked his way to the headship of the sentient world, and has become the superb animal which he is, in virtue of his success in the struggle for existence" (Huxley 1893, p. 51). Continuing:

For his successful progress, throughout the savage state, man has been largely indebted to those qualities which he shares with the ape and the tiger; his exceptional physical organization; his cunning, his sociability, his curiosity, and his imitativeness; his ruthless and ferocious destructiveness when his anger is roused by opposition.

But, in proportion as men have passed from anarchy to social organization, and in proportion as civilization has grown in worth, these deeply ingrained serviceable qualities have become defects. After the manner of successful persons, civilized man would gladly kick down the ladder by which he has climbed. He would be only too pleased to see "the ape and tiger die."

So what is the naturalist to say about metaethics? The empirical world gives you no value and yet there is nowhere else to go but to the empirical world. The answer has to be that there is no value! Yet, this cannot be so, because we have values. Normal people feel strong obligations to look after their own children. People who do not do so are moral monsters. The solution has to be that we think we have values, we have sentiments that convey value, but there are no objective values out there in the world. Hume again. His analysis of causation did not deny that we have sentiments of causation. Of course a fire burns you. But his analysis of causation also said that there are no causes out there. There is no objective cause between the fire and the pain. It is all a matter of constant conjunction, giving rise to ideas – something we supply in our minds. The same with

morality: There is no morality out there. It is something we supply in our minds. So in a sense, just as thinking that there is an objective causality is an illusion – we post-Darwinians would say an illusion put in place by our biology to make us fear the fire – so there is no objective morality – we post-Darwinians would say an illusion put in place by our biology to make us good cooperators or altruists, because cooperation is a good reproductive strategy. One additional tweak, however: If we didn't think that causation and morality were objective, were really "out there," before long we would start to ignore them. Why should I help my neighbor if there is really no need to do so and if I can pretend to help but get away with doing nothing? So, to use an ugly word, we "objectify" causality and morality, because our biology makes us do so, and our biology acts as it does because those of our would be ancestors who were fooled and acted accordingly survived and reproduced and those that did not, did not.

One final point: Could not it be that there really is an objective morality and that natural selection tracks it? After all, because something is produced by natural selection, it does not follow that it is an illusion. I see and hear the approaching train and so get off the tracks. The train is no illusion. So why not morality? The point is that in the case of the train, if natural selection starts playing tricks and offers alternatives – it is no train but an alluring naked person (the sex and orientation of your choice) coming towards you – you are more likely to end up dead than reproducing. In the case of morality, natural selection could have gone another way. There is no necessary progress to one end. Morality is not like causation, dealing with the physical world. It is dealing with the world of relationships and that introduces a measure of freedom. Darwin knew the score.

It may be well first to premise that I do not wish to maintain that any strictly social animal, if its intellectual faculties were to become as active and as highly developed as in man, would acquire exactly the same moral sense as ours. In the same manner as various animals have some sense of beauty, though they admire widely different objects, so they might have a sense of right and wrong, though led by it to follow widely different lines of conduct. If, for

instance, to take an extreme case, men were reared under precisely the same conditions as hive-bees, there can hardly be a doubt that our unmarried females would, like the worker-bees, think it a sacred duty to kill their brothers, and mothers would strive to kill their fertile daughters; and no one would think of interfering. Nevertheless the bee, or any other social animal, would in our supposed case gain, as it appears to me, some feeling of right and wrong, or a conscience. For each individual would have an inward sense of possessing certain stronger or more enduring instincts, and other less strong or enduring; so that there would often be a struggle which impulse should be followed; and satisfaction or dissatisfaction would be felt, as past impressions were compared during their incessant passage through the mind. In this case an inward monitor would tell the animal that it would have been better to have followed the one impulse rather than the other. The one course ought to have been followed: the one would have been right and the other wrong; . . . (Darwin 1871, pp. 73–74)

If you want an example where you do not have to turn us into hymenoptera (ants, bees, and wasps), then consider what we might call the John Foster Dulles system of morality. Dulles, the secretary of state under Eisenhower in the 1950s, hated the Russians. He knew also that they hated him. It was not just a feeling. It was a sense of morality. But he knew that the mutual hate meant that they had to get along, otherwise they would start fighting. So they cooperated. Same ends, different moral system leading to them.

Conclusion

So now we can draw our discussion to an end. It is not so much that we have a modern morality, or if we do it is not because of its philosophical foundations. The modernity of morality comes from our better appreciation of the empirical facts. But modern science does support a newly empowered naturalistic approach to moral understanding, and that is what philosophy is all about. So perhaps our title is not really so misleading after all. Darwinian evolutionary theory – call it evolutionary psychology if you will – leads to renewed understanding of what we really hold as our moral norms and the same science leads to a fresh

understanding of the foundations, or perhaps the nonfoundations, of moral claims. In a way it is all in David Hume. But it is brought up to date by Charles Darwin.

Cross-References

- [Adaptation](#)
- [Cooperation](#)
- [Naturalistic Fallacy, The](#)
- [Science and Morality](#)
- [Social Darwinism](#)

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Philosophie Zoologique

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Synonyms

Zoological philosophy

Definition

Philosophie Zoologique, by early French biologist Jean-Baptiste Lamarck, was published in 1809. In this book, Lamarck developed the first complete theory of organic evolution, arguing that the incredible diversity of living material on the Earth came about through evolution and describing processes of evolutionary change that produced that diversity. Although the specific processes he proposed failed to find experimental confirmation in later years, the book has had considerable impact on the life sciences and social sciences.

Introduction

Fifty years before Darwin's *On the Origin of Species* was published, Lamarck developed the first complete theory of evolution of living organisms – the foundational “evolutionist thinking” step in biology (Mayr 1982; Hull 1988). Lamarck raised species transformation ideas first in an 1800 lecture and pursued them more extensively in his 1802 book *Hydrogéologie* (Corsi 1988), but their full development was not reached until the

Philosophie Zoologique (hereafter, *PZ: Zoological Philosophy* 1809/1963, translated by H. Elliot). Lamarck is widely known for the inheritance of acquired characters, the notion that offspring tend to inherit traits their parents acquired. Although the inheritance of acquired characters was central to his arguments, the view was not novel to him (Burkhardt 1977, 2013).

PZ had minor impacts on science and society upon its publication (Burkhardt 1977). It was criticized by Lamarck's contemporaries, most of whom advocated creationist/anti-evolutionary explanations (Gould 2002). Nonetheless, *PZ* soon had foundational influences on the development of evolutionary theory, particularly in England (Richards 1987). It was also the earliest major break from essentialist thinking that had dominated the life sciences for centuries, including Linnaean views of biological organization (Mayr 1982).

Zoological Philosophy: An Exposition with Regard to the Natural History of Animals

Lamarck's book comprised three parts. The first and longest part was on the natural history of animals. Across eight chapters, Lamarck described arrangement, classification, and characteristics of animal species and developed his evolutionary arguments to explain animal diversity. In Part II, Lamarck discussed the physical causes of life. These nine chapters covered key features of living material and notions of irritability and spontaneous generation on which his evolutionary theory was based. Part III dealt with the physical causes of feeling and behavior. In its eight chapters, Lamarck discussed the nervous systems of animals and notions related to animal behavior including sensibility, feeling, will, instinct, and intelligence.

In Part I, Lamarck described the classification schemes researchers used to understand the living world. He argued for a very old Earth and raised views that almost converged on Darwin's writings on species change 50 years later (though without introducing the idea of natural selection): “In the same climate, very different habitats and conditions at first merely cause variations in the individuals exposed to them; but in course of time the

continued change of habitat in the individuals of which I speak, living and reproducing in these new conditions, induces alterations in them which become more or less essential to their being; thus, after a long succession of generations these individuals, originally belonging to one species, become at length transformed into a new species distinct from the first" (PZ, pp 39). Lamarck explicitly ascribed evolutionary changes to naturalistic processes, ruling out supernatural explanations.

Lamarck then discussed classes of organisms (above the species level) increasing in complexity – this notion of an inherent tendency toward complexity was core to his evolutionary theory. Following this discussion, Lamarck raised his theory of evolution in detail, describing environmental change altering needs of organisms that cause them to change their behavior: "Now if the new needs become permanent, the animals then adopt new habits which last as long as the needs that evoked them" (PZ, pp 107). This argument stemmed from Lamarck's First and Second Laws of Nature. The First Law stated that the increased use of an organ leads to its strengthening whereas disuse leads to weakening. The Second Law stated that these use/disuse modifications of organs, if developed in both female and male parents, will be passed on to offspring – this was the inheritance of acquired characteristics. Thus, as long as environmental conditions modify the needs of organisms, those changed needs will drive changes in behavior, and these latter changes will drive changes in bodily structure. Over many generations and long time periods, the population gradually evolves, potentially becoming a new species. Part I concluded with classification and organization of extant groups of species, now viewed in light of evolutionary change. It interestingly described an evolutionary scenario by which humans evolved, including how that most complex human behavior – language – came to be.

Part II began with extended discussion about the material basis of living organisms, their organization and activity, and their evolutionary change over time. Although Lamarck made numerous references to "subtle," "vital," and

"nervous" fluids, it was clear that he viewed these as materially based, mechanical in their operation, and ultimately knowable to science. Later, Lamarck described the notion of *irritability* in the activity of animals, in which organs become primed to respond to environmental stimuli through natural buildup of fluids inside the tissues. When the right environmental conditions stimulate the animal, those organs contract in response. Rapid replenishment of fluids results in the irritability phenomenon, and these characteristics exemplify how animals become finely tuned to their local environments.

Late in Part II, Lamarck described the process of spontaneous generation, an essential plank in his evolutionary views. He argued that the simplest forms of animals and plants were continually being generated under the right environmental conditions. Spontaneous generation was coupled with the inherent tendency toward increased complexity that he argued characterized all living organisms. These processes, combined with the First and Second Laws (see above), were the material basis for the evolution of species over time. Toward the end of Part II, Lamarck began a discussion of features of "higher" animals that made complex behavior possible. These included a muscular system that generated sustained and repeated movements. Additionally, *feeling* was the product of nervous systems and approximated what we would now call an affective response to environmental stimuli. Part II ended with the notion of *intelligence* as distinct from, and less widely spread across animal species than, feeling. Intelligence was a central idea in Part III.

Part III of PZ was in some ways as important to the early development of behavioral and psychological theory as Part I was to the early development of evolutionary theory. Lamarck began with a continuation of his materialist view of behavior and action and the functions and structures of nervous systems. He developed ideas about instinct, intelligence, and volition that are still being debated today. For Lamarck, all animals with nervous systems possessed *physical sensibilities*, which were emotional responses to external stimuli. The evolution of nervous systems allowed greater adaptability to conditions, as nervous

systems released animals from the direct influence of environmental stimuli. Further, animals with more advanced nervous systems possessed *moral sensibilities* that stemmed from “ideas, thoughts, or acts of our intellect” (*PZ* pp 336). Lamarck viewed moral sensibility in animals, or an “intimate feeling of their existence” (*PZ* pp 346), as possibly having arisen in insects, but certainly occurring in birds and mammals.

Lamarck offered fairly sophisticated views of instinctive behavior as being “fixed tendencies displayed by animals in their actions” (*PZ* pp 350). Instinct was contrasted with will, found in any animals with nervous systems, and intelligence, found primarily in birds and mammals. Intelligence allowed animals to vary their habits in potentially adaptive ways, as it gave “them the faculty of calling up ideas” (*PZ* pp 359) independently of direct physical sensibility. Intelligence comprised four faculties: attention, thought (what today we would call representation, including creative use of ideas), memory, and judgment (today, reason). These ideas relate to views of Thomas Aquinas in the 1200s and were advanced six decades later by Darwin in his 1872 book, *The Expression of the Emotions in Man and Animals* (Malone 2009). Finally, Part III addressed ideas, signs, communication, and language, all topics Lamarck developed further in writings after *PZ*.

Conclusion

Beyond being the first complete theory of evolution, *PZ* was suffused with materialism, rather than the idealism that was then popular in philosophy and the early life sciences. His key evolutionary arguments included the following:

- Changes in the environment may elicit new needs in animals, causing animals to change their behavior.
- Continued use of a body part strengthens it; disuse weakens it. New habits over time can thus lead to heritable change in body structure.
- Changes in body structure can then generate new relationships with the environment and thus modify needs.

- There is spontaneous generation of the simplest living matter, and all living organisms have a tendency to increase in complexity over generational time.

In this framework, animals were in harmony with nature much of the time. However, once sufficient environmental change occurred, animals’ needs changed. Organisms “adapted” to the new needs through changes in habits, and use and disuse of organs related to those habits along with the inheritance of acquired characteristics reestablished harmony with nature (Mayr 1982; Corsi 1988). Lamarck had an awareness of deep time and argued for the centrality of gradual changes over geological time scales. Lamarck “replaced this static world picture by a dynamic one in which not only species but the whole chain of being and the entire balance of nature was constantly in flux” (Mayr 1982, pp 352).

There are major limitations to views raised in *PZ*, of course. Many of Lamarck’s arguments were insufficiently based on evidence (Hull 1988), unlike Darwin’s arguments 50 years later in *On the Origin of Species*. Lamarck also generated some clear predictions from his theory, but never tested them (Hull 1988). One reason he did not test his ideas likely stemmed from his deep history view – that evolutionary processes were so gradual there would be insufficient time to document them adequately (Gould 2002). He also believed the evidence for acquired characters was so obvious that no one doubted it. It was not until the late 1800s that the idea was seriously questioned and tested experimentally (and largely refuted). It is interesting, though, that by the 1990s, it became clear that the molecular and non-molecular bases of epigenetic inheritance were extending some of Lamarck’s ideas into new directions and deepening our understanding of development and evolution (Jablonka and Lamb 1995). Additionally, Lamarck’s idea of a tendency toward increasing complexity was long discounted, but recent empirical work lends some support to the notion (e.g., Adamowicz et al. 2008).

In terms of behavior, Lamarck raised several important ideas about motivation and emotion,

instinct, and intelligence, particularly in Part III of *PZ*. These ideas still have relevance to our science today. Lamarck viewed instincts as related to habits that evolved due to the needs of animals that depended upon environmental conditions, an ethological view preceding the field of ethology by over 100 years. His notion of intelligence providing animals the capability of varying their habits flexibly in the face of environmental problems suggests a cognitive view preceding the field of comparative cognition by over 150 years. His views regarding the use and disuse of organs (including the intellect) led him to argue for providing educational opportunities to all to decrease societal inequalities.

Will had no immediate role in evolutionary change for Lamarck, despite the caricature raised at his death by Georges Cuvier and carried down through the decades (Richards 1987; Gould 2002). Lamarck argued that animals lowest on the evolutionary scale, with minimal nervous systems and nothing resembling will, nonetheless faced the same tendency to increase in complexity and the same changes in needs with sufficient environmental change. Crucially, for Lamarck, all of biology and evolution was natural and so had a material basis, and this represented a sharp break with creationist and supernatural accounts (Burkhardt 1977). Lamarck was the “first to make a complete break with these essentialist impediments against evolution” (Mayr 1982, pp 328).

Cross-References

- [Charles Darwin](#)
- [Environmental Influences](#)
- [Evolution](#)
- [Jean-Baptiste Chevalier de Lamarck](#)
- [Nature Versus Nurture](#)
- [Problem Solving](#)

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Phobia

- [Universal Human Fears](#)

Phobias

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Synonyms

[Abnormal fears](#); [Irrational fears](#); [Obsessive fears](#)

Definition

Particular objects, places, situations, feelings, or animals that provoke extreme, overwhelming, and debilitating fear or anxiety out of proportion to, or in the absence of, any actual danger.

Introduction

Isaac Marks (1987) described phobias as an intense fear of objects or situations that is out of proportion to their danger, cannot be explained or reasoned away, is beyond voluntary control, and leads to avoidance of the feared stimuli. He distinguished phobias from typical fear, stating that phobias occur without any objective source of danger and can develop in response to nearly anything. Furthermore, he referred to the intense feeling of fear or anxiety experienced by phobic individuals when they encounter their feared stimuli as phobic anxiety. Therefore, unlike typically occurring fear, phobic fear is irrational and debilitating and is not adaptive. Most phobic or fear-relevant stimuli can be broadly classified into two categories: phylogenetic and ontogenetic stimuli. Phylogenetic fear stimuli are evolutionary-based stimuli that are typically common to all mammals and have posed threats throughout natural history, such as snakes, predators (e.g., tigers), and heights. Ontogenetic fear stimuli refers to feared objects or situations experienced during our life span that only recently emerged in our evolutionary history, such as guns, electric outlets, and flying. Phobias received their own diagnostic label as a mental disorder first in the International Classification of Diseases (ICD) in 1947 followed by the Diagnostic Statistical Manual of Mental Disorders (DSM) in 1952. Phobic disorders are classified among anxiety disorders, whose features include excessive fear and anxiety and related behavioral disturbances.

Phobic Disorders

Phobic disorders are the most prevalent of all the anxiety disorders and are among the most prevalent of all 12-month disorders (Kessler et al. 2005). These disorders, as classified in the DSM-5 (American Psychiatric Association 2013), consist of specific or simple phobia, social phobia (also known as social anxiety disorder), and agoraphobia. These disorders share a number of features and diagnostic criteria. To be diagnosed with a phobic disorder, the individual's fear or anxiety

must be intense or severe, these feelings must be evoked every time they come into contact with the phobic stimulus, and their response must differ from fears that commonly occur in the population. The individual's fear, anxiety, and avoidance behavior must interfere significantly with their daily routine and cause important impairment to their functioning. They will also show active avoidance to their phobic stimulus, where they behave in such a way to minimize or prevent contact with the specific phobic object or situation, otherwise enduring it with intense fear and anxiety. Finally, the individual's response must also be out of proportion to the actual danger that the object or situation poses. An important change in diagnostic criteria for phobic disorders in the DSM-5 is that an individual no longer has to recognize that their anxiety is excessive or unreasonable in order to receive one of these diagnoses. The following sections will briefly describe each disorder as specified in the DSM-5.

Specific Phobia

Specific or simple phobias are defined as intense and unreasonable or irrational fears of specific objects or situations. Approximately 75 % of individuals fear more than one situation or object, with the average individual fearing three or more objects or situations. The DSM-5 recognizes five categories of specific phobias: animal (e.g., spiders, insects, dogs), natural environment (e.g., heights, storms, water), blood-injection-injury (e.g., needles, invasive medical procedures), situational (e.g., airplanes, elevators, enclosed spaces), and other (e.g., situations that may lead to choking or vomiting; for children, loud sounds or costumed characters).

Social Phobia

Social phobia, also referred to as social anxiety disorder, involves the marked or intense fear of social situations where the individual may be scrutinized by other people. While up to a certain point social anxiety is normal and may facilitate functioning, moderate or severe levels result in impairment and dysfunction. The individual fears that their actions or behaviors will be negatively evaluated and that they may show

symptoms of anxiety such as blushing, trembling, or sweating. Individuals may also fear offending others, which may consequently lead to them being rejected. Individuals with social phobia may avoid feared situations where their symptoms may manifest themselves and cause them to be negatively evaluated.

Agoraphobia

Agoraphobia is characterized by intense fear or anxiety triggered by the real or anticipated exposure to a range of situations. To meet criteria for diagnosis, the individual must fear two or more situations. These include, but are not limited to, using public transportation, being in wide open spaces, being in enclosed spaces, standing in line or in a crowd, and being outside of the home alone. Fear or anxiety cued by the presence or anticipation of a phobic situation may include believing something terrible might happen, believing that help or escape from the situation is impossible, and experiencing panic-like, embarrassing, or incapacitating symptoms. Individuals with agoraphobia will actively avoid phobic situations both behaviorally (e.g., changing daily routines) and cognitively (e.g., using distraction to get through agoraphobic situations), sometimes resulting in the individual becoming homebound. Individuals with agoraphobia are likely to suffer from comorbid disorders and often experience panic attacks, with 30–50 % reporting panic attacks or panic disorder preceding the onset of agoraphobia. However, the DSM-5 no longer links panic disorder and agoraphobia, instead recognizing them as two separate disorders, as not all individuals with agoraphobia experience panic symptoms.

Developmental Theories of Phobias

One of the earliest theories of how individuals develop phobias was the preparedness theory proposed by Martin E. P. Seligman (1971). He suggested that evolution has helped shape an adaptive biological preparedness for humans and animals to learn to associate some stimuli with fear or threat more easily than other stimuli. He

specified that phobias comprise a relatively non-arbitrary and limited set of stimuli related to the survival of humans throughout the course of evolution, such as snakes, heights, and the dark. Seligman specified that phobias are instances of prepared conditioning of fear; that is, humans seem biologically prepared to easily acquire phobias to phylogenetic stimuli with biological and evolutionary relevance, compared to unprepared conditioned fears to fear-irrelevant or ontogenetic stimuli. In addition, he specified that phobias are selective and resistant to extinction and are non-cognitive or irrational.

However, empirical studies have offered mixed support for the preparedness theory (see McNally 2015). While studies did not find evidence of faster acquisition to biologically prepared fear cues, they did find that fear responses to these cues were both more resistant to extinction and noncognitive. Additionally, Seligman's interpretation of phobias faced some limitations. These included difficulty explaining phobias suffered by individuals who never had a negative conditioning experience (e.g., an individual suffering from a snake phobia who had never been bitten by a snake), that not all prepared stimuli for fear conditioning posed threats to humans historically (e.g., spiders), and that evolutionary significant fears may be sustained by the individual's avoidance of feared cues rather than being truly resistant to extinction (McNally 2015).

Since Seligman's classic theory, many others have emerged (see McNally 2015), with two recent theories briefly described here. Ohman and Mineka (2001) proposed an evolutionarily evolved fear module for fear learning and elicitation, a theoretical extension of the preparedness theory integrating findings from human, primate, and neuroscience studies. The module's characteristics are that it is activated by specific evolutionarily fear-relevant stimuli that often become the object of human phobias, it is automatically and involuntarily activated by such stimuli, it is encapsulated and therefore fear responses are impervious to cognitive control (contributing to the maintenance of phobic behavior), and it reflects the operation of a specialized neural circuitry for fear centered on the amygdala. Most

recently, Poulton and Menzies (2002) proposed a nonassociative theory of fear acquisition to account for fears to that are not acquired by conditioning. They claimed that members of a species will show fear to a set of biologically and evolutionary-relevant stimuli without requiring any direct or indirect associative learning experiences involving painful unlearned aversive stimuli. They suggested that the addition of a nonassociative pathway to classic conditioning models of fear acquisition contributes to understanding the nonrandom distribution of fears and phobias and helps account for failures to recall direct traumatic or conditioning events responsible for fear onset among phobic individuals.

Treatment

The most common treatment for phobias is exposure therapy. While this treatment can be delivered using approaches that vary across parameters such as duration, frequency, and context of exposure and degree of therapist involvement, exposure therapy has been shown to be effective across phobic disorders (Barlow 2002). The most common exposure approach is in vivo exposure. In vivo exposure involves systematic, repeated, and direct contact between individuals and their feared or avoided object or situation. Recent technological advances have introduced a new way to deliver exposure therapy using virtual reality (VR). VR integrates a number of systems including computer graphics, body tracking devices, and sensory input devices to immerse individuals in a real-time computer-generated virtual environment (Powers and Emmelkamp 2008). It can also be used to combine the real world with virtual elements (referred to as augmented reality [AR]). VR allows phobic individuals to confront virtual representations of their phobic stimuli. Advantages of VR over in vivo exposure include the ability to conduct exposure treatment in the therapist's office, the delivery of more tailored, personalized exposure, and potentially increased cost-effectiveness. Crucially, a meta-analysis found VR treatment to be as effective as in vivo exposure (Powers and Emmelkamp 2008), while

another study found individuals chose VR over in vivo exposure (Garcia-Palacios et al. 2007), suggesting using VR may help increase the low rates of individuals who seek treatment for phobias.

Conclusion

Phobias are objects, places, situations, feelings, or animals that invoke intense and crippling feelings of fear and anxiety. Unlike typical fear, phobic fear is always irrational and out of proportion to the danger posed by the stimulus, and thus is not adaptive. Phobic disorders, classified as anxiety disorders, consist of specific phobia, social phobia, and agoraphobia. Theories on the development of phobias suggest humans seem prepared to easily acquire phobias to stimuli with biological and evolutionary relevance, with or without a prepared conditioning experience pairing the stimulus with an aversive event. Exposure therapy is the most effective treatment for phobias, allowing phobic individuals to confront their feared stimuli and can be delivered in vivo or using virtual reality.

Cross-References

- Correlates of Fear
- Fear Affords Protection
- Fears
- Universal Human Fears

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Phonemes and Symbols

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Synonyms

[Consonants](#); [Segments](#); [Vowels](#)

Definition

Phonemes are the basic building blocks of speech sounds, which are symbolic in nature.

Introduction

Phonemes are perhaps the most intuitive of the units that constitute the speech sounds of language: They are essentially the consonants and

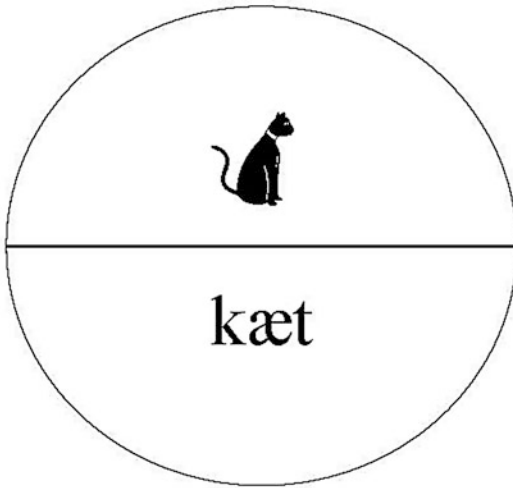
vowels that most people are familiar with. Besides being a product of vocalized speech, current phonological theory views phonemes as abstract mental representations of sounds. Linguistic overviews of the phoneme can be found in classic works such as Sapir (1925), Swadesh (1934), Twaddell (1935), Jones (1967), and a comprehensive modern overview is found in Dresher (2011).

Signs and Phonemes

The modern disciplines of semiotics and linguistics have their roots in Saussure's "Course in General Linguistics" (Saussure 1972). This important work introduced the notion of the linguistic *sign*. This idea has given rise to two important concepts that will be explored here: *symbols* and *phonemes*. These concepts have proven important for the way that researchers think about language today: as a system of symbolic representation, including in the domain of the sound system of a language.

Saussure envisioned language as a set of signs – a meaning coupled with a sound pattern. The representation of a sign, according to Saussure, would be the following, where the image of the cat is intended to represent its semantics and where the symbols (from the International Phonetic Alphabet, used for the phonetic values of sounds throughout this entry) are intended to represent the actual pronunciation of the word “cat” (Fig. 1).

For reference, Saussure terms the concept of the cat the *signification*, the sound pattern used to express the concept the *signal*, and the pairing of the two a sign. That this sign is an arbitrary pairing of sound and meaning is evidenced by the fact that other languages have different words for the same meaning (i.e., the concept “cat”): *chat* in French, *gato* in Spanish, and *duus* in Gitksan (an indigenous language of British Columbia, Canada), all of which have a different way of pronouncing the word. In this way, there is nothing inherent in the concept of “cat” that motivates the sound structure used for the word. The way humans use language involves arbitrary symbolic representation. Thus, while most of semiotics



Phonemes and Symbols, Fig. 1 Sign of “cat”

have focused on semantics and meaning, there is also the phonological aspects to be concerned with, which will be focused on here.

This discussion of semiotics also dovetails with the other remarkable fact about signs: that they constitute systems of contrast. The word “cat” is distinguishable from similar words such as “bat” “mat” “sat” “fat,” etc., by the fact that each of the initial sounds is contrastive: changing the initial sound triggers a difference in meaning. This characteristic of contrast is a hallmark of phonemes. Another fact worth mentioning is that speech is produced as a continuous acoustic stream of sounds; there are no breaks or pauses that naturally fall between speech sounds in a word. Despite this, humans are able to segment this continuous stream into categorical, isolable units. These units are symbolic in the sense that they are discrete and represent the content that is the basis for contrast. These symbols are abstract representations in the mind. There are also operations, as a part of grammar, that are able to operate on and manipulate these symbols, and this is what is considered a phonological grammar.

The abstract, symbolic nature of speech sounds is what leads to the core concept of the phoneme, a term first used in its current sense by Baudouin de Courtenay, who defined the phoneme as “the psychological equivalent of a speech sound” (1972,

p. 152). Phonemes provide a unified, abstract basis for speech sounds that appear in different contexts. Structural linguists such as Trubetzkoy (1969) and Sapir (1925) were among the first to consider the phoneme a psychological concept, i.e., a mental structure or representation, and it was Jakobson (1962) and Trubetzkoy (1969) who first discussed the phoneme in terms of its “contrasting properties.”

The idea of phonemes representing a unified sound among multiple sounds can be explored here further. Phonemes can be realized differently in different environments or distributions. Take for example the vowels of Mokilese, an Oceanic language spoken in Micronesia (data from Harrison 1976, p. 26). Mokilese has a set of voiced vowels, i.e., those which are produced with the vocal folds vibrating, as the vowels of English are produced. This set includes the vowels [i, u, e, o, ε, ɔ, a]. In addition to the voiced vowels, the language also makes use of voiceless versions of [i] and [u], which will be notated as [i̥] and [u̥]. Voiceless vowels are a typologically rare phenomenon (cf. Maddieson 1984), and in Mokilese, they have a very restricted distribution, occurring only between other voiceless consonants. For example, the vowels in *mine* “to be in a place” and *lujuk* “to tackle” are not devoiced; but between voiceless consonants, there are voiceless vowels, such as in the words *kisa* “we two” and *supwo* “pile of firewood.” It is likely that the environment between two voiceless consonants helps to facilitate the devoicing of the vowel. At some level of analysis, then, it becomes useful to think of the voiceless vowels and their voiced counterparts as being the same basic sound; the two variants just happen to surface in slightly different phonetic ways, depending on the environment in which each is found.

Phonemes and Allophones

A principal concept in phonology is the distinction between phonemes and *allophones*. Phonemes are sounds that are contrastive in a language, in the sense outlined above. For example, the two words “teen” and “keen” differ with

respect to one sound: the initial consonant [t] versus [k], respectively. These are the only sounds that are different when comparing these words, and they make these words contrast with each other, evidenced by their having different meanings. One way to conceptualize this is to say that phonemes are not predictable; in other words, there is no way of predicting ahead of time whether a word will have a word-initial [t] or [k] in English. As a principle, all unpredictable information for a given word must be packaged into the mental lexicon in the entry for that word. This idea will be relevant when different levels of representation are introduced.

While phonemes are the unified mental representations of sounds, *allophones* are the different surface variants, or expressions, of these phonemes. In the Mokilese case above, the voiced [i] and voiceless [i̥] would be allophones – surface variants of a single phoneme /i/ (where phonemic forms are placed between slashes, and allophones are placed in brackets). The same is true of [u] and [u̥]. Allophones are not contrastive in a given language. Instead, they are merely two different instantiations of a single phoneme in different contexts. Allophones are simply distributional variants. In Mokilese, the voiceless allophones of the vowels show up in contexts between voiceless consonants, whereas the voiced allophones are found in all other contexts. The distribution for these vowels in Mokilese is *complementary* in the sense that the distribution for each vowel type does not overlap with the other.

The contrasts that are available in a system differ across different languages. The net result is that languages have different phonemic inventories. Thus, the phonemes that are employed in different languages provide for a rich parameter of cross-linguistic variation. For example, the sounds /b/ and /m/ can be independently shown to be phonemic in English, as they are contrastive in words like “beat” and “bat” versus “meat” and “mat.” While they are phonemic in English, these consonants are not contrastive in Pirahã, a Muran language of Brazil (data from Sandalo 1989, p. 39). In this language, these consonants do not signal meaning differences. Observe the differential behavior of the word /mege/ when in different

environments (where // indicates a pause and where the relevant word is underlined):

a.	<u>mege</u> kaobée	“to fall on the floor”
b.	kapeega <u>bege</u> kaobée	“the notebook fell on the floor”
c.	kapeega // <u>mege</u> kaobée	“the notebook//fell on the floor”

This single word changes shape in different contexts: in utterance-initial position (a), the word begins with the nasal sound [m]. The same is true for the word when it follows directly after a pause (c). However, when the word is not in initial position, it surfaces as [bege] instead of [mege]. This is a case of an *alternation*. It can be assumed that there is a single underlying consonant sound in the word and that this sound is alternating between [b] and [m] when the word is in different environments. This alternation indicates that [b] and [m] in the language are allophones, because they are in a complementary distribution: [m] occurs utterance-initially, while [b] occurs in all other contexts. Because the sounds are not found in the same environments, they cannot possibly be used to distinguish different words or serve to trigger a contrast. Thus, the allophones of this b/m phoneme are predictable in the sense that given a particular environment, it is predictable which of the two sounds will surface:

Pirahã:	moopai “throat, neck”	(<u>m</u> only found word-initially)
	xísoobái “down”	(<u>b</u> only found word-medially)

In very much the same way, the voiceless alveolar stop [t] and the voiceless aspirated stop [tʰ] (which involves a short puff of air after the release of the consonant) are not contrastive in English: [tʰ] is found word-initially in words like “tea” and [t] occurs after the consonant [s] in words like “steep.” These two sounds do not have overlapping distributions, and therefore it is not possible to have *contrasts* between [tʰ] and [t] in English.

Minimal Pairs

The principle that allophones occur in complementary distribution leads to an empirical test for

phoneme-hood: the use of *minimal pairs*. True minimal pairs are pairs of words that differ only in a single sound. This difference determines that the sounds are contrastive (as nothing else in the word could trigger the difference, hence the descriptor *minimal*). The following constitutes a set of minimal pairs in English, where the only sound that is different in each case is the one in word-initial position (where all of these rhyme for West Coast American English speakers, and where some vowels will be subject to dialect variation): “hot,” “pot,” “tot,” “cot,” “lot,” “rot,” “yacht,” “watt,” “bought,” “got,” “not,” etc. The minimal pair test is not always possible, as many languages will conspire against having minimal pairs of sounds in particular contexts. In some cases, near-minimal pairs suffice as a test, so long as all environments can be controlled for (and demonstrably do not induce allophony). There are also possible gaps, such as “mot,” which is not a word for most English speakers, raising the question of whether /m/ is a phoneme of English. This is in fact a phoneme of English, as there are plenty of other contrasting pairs that can be observed, including “meat” versus “beat” versus “peat,” or “man” versus “ban” versus “pan.” Thus, it can be established that the sounds m/b/p all contrast in English, and since it was established above that h/p/t/k/l, etc. are all phonemes (by virtue of participating in other minimal pairs), then /m/ can be added to the list. The nonce word “mot” just happens to be an accidental gap of English, which is reinforced by the fact that “mot” is perceived to be a *possible* word in the language; one that could, for instance, be used for a new concept, product, or piece of technology.

Phonemic Inventories

Across languages, then, there are gross differences in the phonemes that exist. These phonemes that are used constitute the phonological *inventory* of a language. For instance, the inventory of consonantal phonemes in English (depending on the dialect) includes: /p, t, k, b, d, g, f, v, θ, ð, s, ʃ, ʒ, h, ʈ, ɖ, m, n, ŋ, l, ɹ, j, w/. In comparison, the inventory of consonantal phonemes of Urama, a language of Papua New Guinea (data from Brown et al. 2016),

includes only /p, b, t, d, k, g, v, h, m, n, r, w, j, ʔ/. On the face of it, Urama has fewer consonantal phonemes than English. There are, however, qualitative differences in that the Urama phonemic inventory has the consonant /ʔ/, which is a glottal stop (produced with a complete closure of the vocal folds), which English lacks in its phonemic inventory. Likewise, languages can differ in their vowel inventories. Some varieties of English have the vowels /i, ɪ, u, ʊ, e, ε, o, ɔ, æ, ɑ, ə/, while Urama has only /i, u, e, o, a/- a proper subset of the vowels of English. These differences yield a very simple and intuitive metric for comparing the sound systems of languages; an overview of the phonemic inventories of several hundred languages of the world is provided by Maddieson (1984).

In addition to the raw inventories of sounds in languages, there are combinatorial differences across languages. While two languages may have roughly the same phonemic inventories, the restrictions on how those phonemes can be combined into sequences can be different. Nasioi, a Papuan language of Bougainville, has a consonantal phonemic inventory that is very similar to Urama and a vowel inventory that is nearly identical. While vowels are freely sequenced in words in both languages, there are fairly tight restrictions on the sequencing of consonants. In Urama there is an absolute prohibition on consonant clusters, whereas in Nasioi a very small number of consonant cluster types are allowed. The sequencing of phonemes and the restrictions in languages are what is termed *phonotactics*. Data of this sort from over 1,000 languages is available in the World Phonotactics Database (Donohue et al. 2013).

Levels of Representation

While the nature of phonemes and allophones has been defined, what remains to be explained is the details of the *relationship* between phonemes and allophones. It might help to think of this in terms of different *levels*. One thing that was established early on is that the unpredictable, phonemic contrasts in languages must be encoded in the lexical entry for any given word. This lexical structure is what is termed the *underlying representation* of a

word. This is the level at which phonemic information is present, including which consonants and vowels make up the word and in which order they are sequenced (i.e., the information for “tip” must not only specify the consonants and vowels that are present but also the fact that they are ordered /t-i-p/, and not /p-i-t/, like the word “pit”). Since phonemes are not predictable, and not derivable by any principle, then this information must be stored for each word. In contrast, the surface or phonetic form is the level where all of the phonetic detail gets “implemented” by the articulators in the vocal tract, such as the tongue, lips, vocal folds, etc. The underlying form is an abstract representation – it is categorical and symbolic in nature. The surface form, on the other hand, is gradient and subject to the constraints that the vocal tract imposes on it.

Turning back to the Mokilese example, there are two things that can be noted about the vowel allophones. One is that cross-linguistically, voiceless vowels are extremely rare. The other is that the voiceless vowels are found in a very limited environment, i.e., only between two voiceless consonants. The voiced vowels, on the other hand, appear to be the forms occurring in the most widespread environments (i.e., everywhere *except* between voiceless consonants; this is termed the *elsewhere* case). This provides good reason, then, for the voiced vowels to be in the underlying representations of words in Mokilese, and the voiceless vowels are the forms that are derived on the surface. Since the underlying forms are inferred on the basis of this information and the surface forms can be observed in uttered words, the challenge is to get the phonological grammar to map the underlying forms to the surface forms. Another way of putting this is that the grammar must convert the voiced vowels of Mokilese to their voiceless counterparts only in contexts where they are between voiceless consonants. This process is termed a *derivation*.

Symbolic Operations and Rules

In order to *generate* a set of allophones from an underlying phoneme, there must be some sort of operation that maps the underlying form to the

surface form, i.e., an operation which is responsible for deriving the set of allophones for any given phoneme. This mapping can be formalized as a rewrite rule (see Chomsky and Halle 1968). A rewrite rule takes a string of symbols as input and returns a string of symbols as output. The process involves changing one (or more) of those symbols when it is in a specific environment. Taking the example of Mokilese vowels, a rewrite rule might take all instances of the set of phonemes {i, u} and change these symbols into {i̥, u̥} when the symbols are located between two voiceless consonants. Formalizing this statement would look something like: /i, u/ → [i̥, u̥]/C₁__C₂. Given that phonemes are abstract, symbolic mental units, they can be subject to rules of this type.

The resulting derivation from underlying to surface representation can be schematized as such:

Underlying Representation (Lexical Structure)

↓↓↓↓

Application of Rules

↓↓↓↓

Surface Representation (Phonetic Structure)

Distinctive Features

While phonemes are considered to be the atomic structures of phonology, they also have a rich internal structure. Because they are symbolic in nature and because they participate in contrasts in languages, phonemes have the appearance of basic, atomic units. They are, however, reducible to smaller, dependent units. As established above, phonemic distinctions can be characterized by oppositions. Each of the dimensions that can create these oppositions can then be expressed as a set of distinctive features (see Jakobson et al. 1952 and Chomsky and Halle 1968, which are classic works on early approaches to distinctive features). For instance, the contrast between “bat” and “mat” is only along one dimension: the soft palate is raised in the first sound of “bat,” keeping all of the airflow moving through the oral cavity, while

in “mat” the first sound involves a lowered soft palate, allowing airflow to move through the nasal cavity. Thus, the difference between /b/ and /m/ can be characterized as a difference in the feature [nasal], which can be characterized as an abstract motor command for the soft palate. Thus, /b/ is [−nasal] and /m/ is [+nasal]. Each possible contrast then constitutes a distinctive feature, which also presumably captures a natural class of speech sounds in languages. Each phoneme, in turn, consists of a bundle of values for each distinctive feature.

Recent theories about distinctive features view many features as being semi-independent of the phoneme, rather than an intrinsic component of it. This general approach is termed *nonlinear phonology* and assumes that phonological representation is not simply a linear string of phonemes such as consonants or vowels, each with their own bundle of distinctive features, but rather a loosely organized sequence of speech sounds, where distinctive features can potentially be shared across different sounds. This is the insight of Goldsmith (1976), who showed that in many languages where tone is contrastive, tones can exhibit behaviors that suggest they are somewhat independent of the vowels that they are realized on. A related idea adopts the notion that distinctive features are organized internally within the phoneme into phonetically motivated groupings such as place of articulation, manner of articulation, and voicing. This type of *feature geometric* model (Clements 1985; Sagey 1986) restricts the independence of features within a set of classes. The intuition is that in contexts of assimilation, there is a single gesture or distinctive feature that is being *spread* from one phoneme to another. In English this is illustrated with cases of voicing assimilation which affect the plural marker *-s* (phonologically, /-z/): cat/cat[s], dog/dog[z]. If it is assumed that /-z/ is the underlying representation of the plural marker, then it can be observed that when it follows voiceless consonants, it also becomes voiceless. In this case, since it is a single gesture involving a single articulator (the vocal folds) which is being held across two consonants in sequence, it makes sense to say that both consonants are specified with a single [−voice] distinctive feature. In this way, nonlinear phonology

is a radical departure from the classical view of the phoneme in that it prescribes a semi-autonomous existence for distinctive features and reduces the role of the phoneme in the linearization of speech sounds.

Conclusion

Much of modern phonology has placed a great deal of emphasis on the phonemic level of analysis; however, more contemporary approaches have explored nonlinear models that assume a more limited role for the phoneme. Despite these new developments, the phoneme remains a core area of investigation and is also assumed to be the “core” unit of phonology. In his contemporary in-depth overview of the phoneme, Drescher (2011, p. 241) states that despite the new areas of focus in phonological theory, “This does not mean that the phoneme plays no role in modern phonology; closer inspection reveals that the phoneme is far from dead.”

Cross-References

- [Field of Linguistics, The](#)
- [Language Modularity](#)
- [Physiology of Language](#)
- [Universal Grammar](#)

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Definition

The phonological loop is the subsystem of working memory that deals with auditory information. It consists of two parts: a short-term phonological store with auditory memory traces that are subject to rapid decay and an articulatory rehearsal process that can revive the memory traces.

Introduction

The multicomponent model of working memory (Baddeley and Hitch 1974) is considered to be one of the most influential models of working memory. According to this model, several components are involved in the execution of working memory: the central executive, the phonological loop, the visuospatial sketchpad, and a fourth component called episodic buffer (Baddeley 2000). Among these components, the phonological loop is specialized for the retention of verbal information over short periods of time. In addition, the phonological loop is comprised of two components, a phonological store which can hold memory traces for a few seconds before they fade, and an articulatory rehearsal process which helps to maintain decaying representations in the phonological store through subvocal rehearsal. Because of the relative tractability, the phonological loop has received more attention than other components in the model of working memory.

Phonological Loop and Rehearsal

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Synonyms

Articulatory loop; Phonological short-term memory; Phonological store and articulatory rehearsal

The Two-Component Model of Phonological Loop

In order to store phonological information for a short period and prevent its decay by continuously refreshing it, it was proposed that there should be two components in the phonological loop, and the two components are to some extent independent. Take memorizing a telephone number for example, the digits of the phone number are immediately entered into the phonological store, where they could be maintained for 1–2 s. And the articulatory rehearsal process helps maintain

the digits in the phonological store by repeating the phone number.

If the information is visually presented, for example, a telephone number printed on a paper, it can be transformed into phonological information by subvocal rehearsal and then be encoded into the phonological store. Therefore, the articulatory rehearsal process has two functions: to maintain the memory traces in the phonological store and to transform visual information into articulatory information.

Evidence for the Phonological Loop

A number of efforts have been paid to verify the existence of the phonological loop as well as the two components of it since the model was proposed by Baddeley. The followings are the most noticed phenomena found under laboratory manipulations that could support the existence of the phonological loop and could also be seen as the characteristics of it.

- (a) The phonological similarity effect, one of the most robust effects regarding the phonological loop, refers to the phenomenon that people tend to be much less accurate in recalling sequences of similar-sounding words (e.g., man, mad, map, mat) than recalling sequences of words that are phonologically distinct (e.g., day, sup, few, cow). Besides, the similarity of meaning has little effect on recall. The phonological similarity effect indicates that verbal information is mostly coded phonologically, and the phonological store indeed exists (Conrad and Hull 1964).
- (b) The articulatory suppression effect refers to the phenomenon that when participants are required to say something irrelevant aloud while memorizing lists of words, the performance of recall would be impaired, indicating the importance of articulatory rehearsal process (Richardson and Baddeley 1975).
- (c) The word-length effect refers to the tendency for participants to have more difficulty in an immediate serial-ordered recall of a sequence of long words (e.g., university, aluminum, hippopotamus, refrigerator) than in that of a sequence of short words (Baddeley et al. 1975).
- (d) The irrelevant sound effects refer to the research findings that immediate recall is impaired by the irrelevant spoken material presented at the same time or subsequently (Jones and Macken 1993). Notably, when the target materials are presented visually, the effect of irrelevant sound would be removed by articulatory suppression, but if the target materials are presented auditorily, the irrelevant sound could still reduce the recall performance under articulatory suppression (Hanley and Broadbent 1987).
- (e) Transfer of information between codes refers to the process where visual information is transformed into phonological codes by subvocal rehearsal, and such a process could be blocked by articulatory suppression (Murray 1968).

Besides the phenomenon mentioned above, neuropsychological and neurobiological findings also support the structure of the phonological loop. For example, with a deficiency of the articulatory rehearsal process, aphasic patients with dyspraxia are unable to set up the speech motor codes necessary for articulation (Waters et al. 1992). The phonological store has been found to be associated with left supramarginal gyrus, while articulatory rehearsal is associated with Broca's area, according to the evidence from fMRI and PET studies (Awh et al. 1996; Paulesu et al. 1993).

Evolutionary Functions of the Phonological Loop

Besides as a subsystem of working memory, the evolutionary role of the phonological loop (i.e., the reason why the phonological loop has evolved in human being) has also attracted much attention. Studies are mainly focused on the role of the phonological loop in advanced psychological processing such as reasoning

and reading comprehension. For example, research found that the phonological loop plays a role in syllogistic reasoning (Gilhooly et al. 1993) and analytic reasoning (Prabhakaran et al. 1997).

Evidence also shows that the phonological loop assists the process of reading comprehension. The articulatory suppression, which would disrupt the functioning of the phonological loop, was found to increase the accuracy of error-judgments of unacceptable sentences (Coltheart et al. 1990).

A more important function of the phonological loop, as proposed by Baddeley, is to facilitate the acquisition of language. The capacity of learning native vocabulary in children is assumed to depend on the phonological loop. Moreover, the ability to learn a second language of both children and adults could be directly predicted by the phonological loop (reviewed by Baddeley et al. 1998). Based on empirical studies, it is suggested that the phonological loop should facilitate language acquisition in two ways: the phonological store should provide relatively unconstrained temporary representation for new phoneme sequences, and the articulatory rehearsal process should facilitate learning.

Conclusion

The topic of phonological loop has proved to be more robust and productive than other components of Baddeley's model of working memory. The simple model of the phonological loop consists of two components, the phonological store and the articulatory rehearsal process. Series studies have explored the cognitive patterns that can prove the existence of the phonological loop and its components, such as the phonological similarity effect and the articulatory suppression effect, along with the neuropsychological evidence. Importantly, advanced psychological processing such as reasoning, reading comprehension, and language acquisition have been found related to the functioning of phonological loop.

Cross-References

- [Language Acquisition](#)
- [Neurobiology of Language](#)
- [Working Memory](#)

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Phonological Short-Term Memory

► [Phonological Loop and Rehearsal](#)

Phonological Store and Articulatory Rehearsal

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Phylogenetic

► [Polyvagal Theory](#)

Phylogenetic Analysis Within Comparative Psychology

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Synonyms

[Independent contrasts](#); [Model comparison](#); [Phylogenetic comparative methods](#); [Phylogenetic generalized least squares regression](#); [Phylogenetic](#)

[meta-analysis](#); [Phylogenetic path analysis](#); [Phylogenetic signal](#)

Definition

A class of statistical methods that incorporate information about phylogeny in order to test evolutionary hypotheses.

Introduction

Phylogenetic comparative methods are an array of statistical procedures developed to analyze evolutionary models including the reconstruction of ancestral traits; the coevolution of morphological, physiological, behavioral, and cognitive features; the effects of socioecological factors upon these characteristics; and the degree of evolutionary diversification and extinction, among others (Nunn 2011). The pertinence of their use is due to the fact that closely related species are expected to resemble more to each other than more distant taxa. This poses serious pseudo-replication issues at the time of conducting statistical analyses. However, phylogenetic comparative methods not only reduce the likelihood type I, but by meeting the required statistical assumptions, they also increase power and decrease type II errors (Macleán and Nunn 2017). This entry will briefly discuss some of the main diagnostic analytics used to determine the presence of phylogenetic dependencies, as well as some of phylogenetic methods currently employed in comparative psychology including phylogenetic independent contrasts, phylogenetic generalized least squares regression, phylogenetic logistic regression, phylogenetic generalized mixed model, phylogenetic path analysis, and phylogenetic meta-analysis. This review is an introduction to these approaches.

Phylogenetic Signal

This concept refers to the degree of phylogenetic dependence of a trait across species (Freckleton

et al. 2002), where phylogenetically close taxa are expected to be more similar to each other, relative to other species sampled at random from the tree (Nunn 2011). Over the years, various diagnostics destined to detect trait preservation had been proposed. Pagel (1999), for example, developed two scaling parameters to detect signatures of trait evolution in continuous data. The first parameter, δ (delta), was developed to distinguish the occurrence of fast and early trait evolution, followed by a period of stabilizations (as is observed in instances where δ is lower than one). Alternatively, instances when δ is equal or larger than one are associated with trait evolution occurring closer to the tips of the tree relative to more ancestral nodes (Nunn 2011).

Pagel also proposed λ (lambda) to determine if the evolutionary patterns in the phylogeny fit the degree of resemblance across species in the data (Pagel 1999). This approach rescales the tree structure as represented by variance-covariance matrix (Nunn 2011). According to Nunn (2011) when λ is close to one, the diagonal representing the variance will indicate if the model is equivalent to a model following Brownian motion evolution (the variation of traits occurs as a random walk in proportion to the passage of time represented by the length of the branches in the tree; Felsenstein 1985). Alternatively, if λ is zero, the covariance observed in the off-diagonal should also be zero, as well as the length of the branches (Nunn 2011). Consequently, λ values lower than one indicate that the trait of interest is less similar across species that it would be predicted based on the phylogeny, and a Brownian motion model of trait evolution (Pagel 1999). It is worth noting, however, likelihood ratio tests are required to determine whether λ is statistically significantly different from either one or zero (Freckleton et al. 2002; Nunn 2011). The precision of this diagnostic is dependent on sample size. Simulations indicate samples with fewer than 30 species compute equivocal λ values (Freckleton et al. 2002).

Another more recent metric K is also used to determine the level of phylogenetic signal in continuous traits (Blomberg et al. 2003). This procedure was based on the observed mean squared

error (MSE) and its corresponding expected value assuming the occurrence of Brownian motion, considering the structure and size of tree (Blomberg et al. 2003; Nunn 2011). One of the advantages of K is that in addition to examining the phylogenetic signal of a single trait, it can also be applied in analyses with multiple traits across more than one phylogenetic tree. This allows the analysis of trait change patterns across various evolutionary models (Blomberg et al. 2003). Similar to Pagel's λ (1999), K values lower than one indicate that the data and the tree structure do not suit a Brownian motion model (Nunn 2011). Some causes associated with a low K include the presence of homoplasies, where traits shared across species evolved in the absence of a common ancestors, or due to a high incidence of measurement error, either at the level of tips, at the length of the branches, or in the topology of the tree (Blomberg et al. 2003). Instances where K is greater than one indicate close species resemble each other, and trait evolution followed Brownian motion (Nunn 2011). Blomberg et al. (2003) observed the power to accurately estimate the phylogenetic signal, relied as well on the sample size. According to their simulations, samples with more than 20 species achieve adequate power levels (more than 0.8).

Abouheif (1999) also suggested adapting a test for serial independence (TSFI), developed by von Neumann et al. (1941) to determine the presence of nonrandom patterns in a series to a phylogenetic setting. This test examines whether the observations in the dataset followed an ordered sequence on the tips of the trees (Abouheif 1999). A positive autocorrelation is associated with similarity due to common descent, whereas negative values are product of convergent evolution (Abouheif 1999). TSFI allows the analysis of phylogenetic signal in binary discrete traits (Nunn 2011). Even though TSFI does not require any information on the length of the branches or the tree topology, it is a parametric test assuming the data is normally distributed. Other methods used to conclude the presence of phylogenetic signal in discrete traits are based on model comparison considering a null model with the characters reshuffled on a series of trees (Maddison and

Slatkin 1991). The series of randomized simulations create the distribution of s , the minimum number of transition from one state to the other and its reverse (Maddison and Slatkin 1991). Another approach, Moran's I (1950), relies on the computation of spatial autocorrelations to estimate phylogenetic dependencies. This diagnostic is estimated assuming a multidimensional matrix; however, as mentioned by Abouheif (1999), this procedure requires a previous knowledge of the branch lengths and the location and number of changes occurring in the phylogenetic tree.

Phylogenetic Independent Contrasts

Although alternative analyses for continuous variables had gained popularity in the last decade (see below), the use of phylogenetic independent contrasts (PIC) remains widespread. Felsenstein (1985) proposed this method as an alternative to nested analyses of variance, with the former considering genera or families rather than species as the unit of examination. PIC are calculated as the difference between the values of a trait in two closely related species, after taking into consideration the length of the branches in the phylogenetic tree (Swenson 2014). These computations are recursive, starting at the tip of the tree and progressing down to the root (Nunn 2011). However, branches are only used once in these computations (Felsenstein 1985; Nunn 2011). Consequently, the quantities used for the estimation of a contrast between two species, such as A and B, are excluded from further analyses. To circumvent this restriction, a subsequent step calculates the following contrast between the next phylogenetically close species, such as C, and the common ancestor of the previously used taxa (A and B). The value of the ancestral node is not the average of the daughter species, but rather it is extracted by weighing these quantities by the length of the branches (Nunn 2011).

Even though PIC is often used as an avenue to explore trait coevolution, this method calculates separately the contrasts for each trait, and in later stages, the researcher must compute a correlation or regression analysis to test hypothesized

associations between traits (Swenson 2014). It is relevant to mention that even though independent contrasts are frequently employed in bivariate correlations or other general linear model procedures, an advantage of this method is that it provides researchers with the flexibility of exporting contrasts and conducting more sophisticated analyses with them (e.g., factor analysis, principal components analysis, multilevel modeling, structural equation modeling). This method, however, relies on certain statistical assumptions. For example, outliers should be removed, residuals should indicate homogeneity of variance, and the variance observed should fit a Brownian motion model. Standardization is often used as a tool to solve heteroscedasticity issues. This approach divides the contrast, by the square root of the sum of branch lengths, allowing each value to display similar levels of expected variation (Nunn 2011).

Another recommendation at the time of running PIC analysis is forcing the regression line to go through the origin (Swenson 2014). This practice is due to the fact that the sign of the subtraction, positive or negative, is arbitrary (Nunn 2011). By forcing the intercept to zero, the regression line can go through the mean of X and Y (Nunn 2011). As mentioned by Nunn (2011), one of the advantages of this practice is that it allows the model to regain one degree of freedom. Although it may seem as an inconsequential difference, it is often the case sample sizes in this type of analysis that are considerably smaller, affecting the power of the test.

Phylogenetic Generalized Least Squares Regression

Although a variety of traits evolved under Brownian motion, an array of characteristics do not follow this evolutionary pattern. Consequently, analysis relying on PIC may not be adequate. Phylogenetic generalized least square regression (PGLS) is another method used to determine the association or prediction between two or more traits (Symonds and Blomberg 2014). Different from PIC, this approach is often

considered as more general and flexible. (Swenson 2014). For example, PGLS allows the implementation of the observed phylogenetic signal into the model (Nunn 2011; Symonds and Blomberg 2014). Therefore, if no significant phylogenetic dependency is observed across species, the output of the analysis is expected to be equivalent to a non-phylogenetic ordinary least squares regression (OLS; Symonds and Blomberg 2014). Alternatively, if the value of the signal is close to one (e.g., when using λ), the results of the bivariate analysis should be concordant to those of PIC (Nunn 2011). Hence, PGLS may be considered an extension of PIC (Blomberg et al. 2012). It is worth noting, however, the observed phylogenetic signal of the trait is not a statistical issue per se but rather whether the model's residuals exhibit phylogenetic covariance violating traditional statistical assumptions (Maclean and Nunn 2017).

Another advantage of this method is that it allows the implementation of models examining ordinal variables and dichotomous categorical predictors (Grafen 1989; Paradis 2006; Symonds and Blomberg 2014). Furthermore, as in ordinary least squares regression, PGLS enables the inclusion of multistate traits coded into binary predictive variables (e.g., dummy coding; Symonds and Blomberg 2014). The estimates of a PGLS analysis are unstandardized b coefficients with its corresponding p -value based on t -test statistic (Paradis 2006). Unfortunately, most phylogenetic packages do not provide standardized estimates. This issue, however, may be solved by standardizing the variables before conducting the phylogenetically informed examination. Therefore, the model's equation is similar to that of an OLS, $y = a + bx + e$. Due to its flexibility, PGLS tolerates the implementation of various evolutionary models for its subsequent comparison (Paradis 2006). Model fit indicators include the Akaike information criterion (AIC), the Bayesian information criterion (BIC), and the negative log likelihood (one employed in likelihood ratio tests).

Phylogenetic Path Analysis

Although exporting independent contrasts and using them in more sophisticated analyses have

been used as alternative approaches to test complex evolutionary models, more recent perspectives circumvent this additional step. The d -separation method (Gonzalez-Voyer and Von Hardenberg 2014), for example, is a tool that not only allows the computation of phylogenetic path analysis but it enables the examination of multiple competing models according to goodness of fit statistics. This procedure relies on the graphical representation of the variables, through a direct acyclic graph (DAG; Gonzalez-Voyer and Von Hardenberg 2014; Shipley 2000, 2013), where squares, also known as vertices, represent the variables in the model, and arrows, or edges, represent the paths between the vertices. Although this analysis shares some features with SEM or traditional path analysis (e.g., edges are not allowed to return to the previous variable but rather continue to next vertex), some significant differences exist between these methods. Whereas SEM directly estimates the path coefficients, the d -separation approach is based on the specification of a list of statements in which each one of these is comprised of a pair of variables statistically independent of each other (Gonzalez-Voyer and Von Hardenberg 2014).

To compute a phylogenetic path analysis, a minimum set of statements is required. This procedure relies on listing all pairs of non-connected variables and cataloguing all "parent" variables with a path oriented toward any of the non-connected pairs (Gonzalez-Voyer and Von Hardenberg 2014). The combination of these two lists is the basic set of statements corresponding to the conditional independencies in the model. To test these independencies, the statements are transformed into linear models such as multiple regressions. However, to account for the effects of phylogenetic closeness, these computations are often conducted through PGLS, with the parent variable and one of the independent pairs as predictors and the second component of the independent pair as a criterion. After estimating the significance tests, a Fisher's C is computed (see Shipley 2016; or Gonzalez-Voyer and Von Hardenberg 2014, for the corresponding formula). This C statistic is contrasted with a χ^2 distribution. The critical value corresponds to the degrees of freedom of

the model which are twice the number of parameters in the analysis (Gonzalez-Voyer and Von Hardenberg 2014). To be considered an adequate model, the significance of the C test is expected to be above the preselected alpha value.

For model comparison, the difference between C statistics is computed with a χ^2 distribution following the difference between the degrees of freedom of the first model minus the degrees of freedom of the second model (Shipley 2013). However, as pointed out by Gonzalez-Voyer and Von Hardenberg (2014), this procedure is restricted to nested models. For non-nested comparisons, the corrected C statistic information criterion (this statistic corrects for small sample sizes), a statistical analogue to the AIC, is required. After estimating the CICc for each model, a Δ CICc can be computed by subtracting the lowest CICc from the model of interest. Instances in which the Δ CICc is less than 3 are often considered to display adequate support (Gonzalez-Voyer and Von Hardenberg 2014; Shipley 2013). In addition to these metrics, it is recommendable to compute CICc weights to determine the probability of each model. Akin to model comparison in traditional statistics (AIC, BIC), goodness of fit indicators provides a guideline, but ultimately the researcher must decide which model exhibits adequate theoretical and statistical parsimony (Navarro 2013). Since multiple models may present similar CICc values and weights, model uncertainty is an issue. Alternative procedures, such as model averaging, which consists on averaging the standardized path estimates, had been found to solve these statistical difficulties (von Hardenberg and Gonzalez-Voyer 2013).

Phylogenetic Logistic Regression and Phylogenetic Generalized Linear Mixed Models

Inspired by the logic behind traditional logistic analysis, phylogenetic logistic regression (PLR) may be used when estimating the effects of a continuous predictor, or dummy-coded variable, for categorical factors with multiple levels, upon a dichotomous criterion (Ives and Garland 2010).

However, due to non-normality issues, these computations rely on the use of a logit function for the probability distribution (Ives and Garland 2014). The model's estimates are non-standardized coefficients, which may be transformed into β by previously standardizing the variables before the analysis. Different from traditional logistic regression, PLR takes into consideration the probability of a trait to change states (e.g., zero to one or one to zero). The switching rate is an indicator of phylogenetic signal (Ives and Garland 2014). Therefore, a low likelihood of change is associated with phylogenetically close species retaining the ancestral character (Ives and Garland 2014). In conjunction with other phylogenetic analysis (see Pagel's method for binary traits; 1994), this approach also takes into consideration the length of the branches between nodes in the phylogenetic tree, with a higher likelihood of change found in longer branches (Ives and Garland 2014). PLR estimates the effects of the predictors after accounting for the changes in the binary criterion.

Other methods destined to the analysis of binary criteria include phylogenetic generalized linear mixed models (PGLMM). This approach not only allows the implementation of statistical functions for nonlinear data, but it also enables the use of phylogenetically informed random variables (Ives and Garland 2010), as well as estimating the parameters through penalized quasi-likelihoods and restricted maximum likelihood (Ives and Garland 2014). According to Ives and Garland (Ives and Garland 2014), the proportion of σ^2 (estimated from the covariance matrix C) is not only an indicator of phylogenetic signal, but it also offers information regarding the underlying equality between PGLMM and PLR. For the authors, instances for a single predictor where $\sigma^2 = 0$ are equivalent to a logistic regression. Alternatively, when σ^2 is greater than zero, it indicates the presence of covariance parameter estimates in the random variable associated with covariances in the states of the criterion (Ives and Garland 2014). Since PGLMM are based on σ^2 values, which measures the level of phylogenetic signal, low σ^2 confounds the computation of accurate estimates.

Correlated Evolution with Categorical Traits

In 1994, Pagel proposed a method based on maximum likelihood estimations. The procedure compared a null model in which two traits evolved independently from each other, and an alternative model build on the assumption that both traits coevolved (Nunn 2011). The best model is determined after contrasting the likelihoods obtained for each model. If the dependent model presents a higher value, then the null hypothesis is rejected. Since the number of parameters ($k = 4$) of the independent model is nested within the dependent model ($k = 8$), a likelihood ratio test is often used to determine any statistically significant difference between the models. These computations, however, assume that the evolutionary modifications are independent on different branches, the change rate remains constant, and these alterations occur in small periods of time (Nunn 2011). Similarly, both traits are assumed to have two levels, or dichotomies, such as the presence or absence of the traits. The values for the independent model are calculated according to a transition matrix examining a trait changing from one of its two possible states (e.g., zero) to a different one (e.g., one). Based on these transition rates, a likelihood statistic is estimated for the states corresponding to each trait and summed over repeated reconstructions (Nunn 2011). In tandem, the same procedure is employed for the second trait.

Due to the fact that the dependent model assumes both traits coevolved, the number of parameters in the dependent model is larger relative to the independent model. The transition matrix considers the change from one state to next depending on the state of the second trait. Consequently, a change in trait A from zero to one requires estimating this change when B is zero and when B is one. The likelihood of the dependent model is estimated via a 4 by 4 matrix, with only one trait changing per time. Each transition between pairs (0,0 to 1,0) is contrasted with a similar transition, assuming the occurrence of an alternative state in one of the traits (0,1 to 1,1). The greater the difference and/or the number of

transition pairs differing among each other, the larger the likelihood. An advantage of this procedure is it allows the implementations of restrictions between the transitions, enabling researchers to test various models after considering the evolutionary evidence concerning the evolution of a trait before the other (Nunn 2011). In addition of estimating the correlated evolution of dichotomous traits through maximum likelihood, an extension of this procedure is often computed using a Bayesian approach in which the uncertainty of the model or the phylogenetic reconstruction is also taken into consideration (Nunn 2011).

Phylogenetic Meta-Analysis

A more recent method consists in estimating the consistency of the phenomena reported by independent studies examining various species, after accounting for phylogenetic closeness (Adams 2008). Traditionally this type of analysis requires collecting the variance, sample, and effect sizes corresponding to each study. Due to the use of different metrics, effects are standardized prior to the analysis (e.g., fisher's z transformation is one of the procedures used for standardization; Lajeunesse et al. 2013). The presence of study heterogeneity is estimated using a Q test (Lajeunesse 2009). However other analytics such as I^2 had been developed (Higgins et al. 2003). It is also advisable to run fail safe tests to conclude the presence of any publication bias. For example, Rosenthal's (1979) and Rosenberg's (2005) approaches are some of the available analytics.

According to Adams (2008) and Lajeunesse (2009), meta-analysis is amenable to a phylogenetic adaptation since both methods are based on generalized least squares calculations. PMA models compute a covariance matrix (Σ ; Adams 2008), considering the observed heteroscedasticity as well as the phylogenetic associations in the model. Hence, the heteroscedasticity is found on principal diagonal of the matrix, whereas the phylogenetic dependencies are in the off-diagonal (Lajeunesse 2009). After modeling the covariance matrix Σ , a weighted mean

effect size is computed. Confidence intervals (95% CI) can be calculated to determine if the average is different from zero. However, a significance test following a χ^2 distribution is also possible (Lajeunesse 2009). A second matrix (P) is comprised of the correlations among the effect sizes after considering the underlying phylogenetic dependencies. Lajeunesse concluded the strength of these correlations is based on the branch lengths of the phylogenetic tree. Consequently, the matrix structure resembles that observed in PGLS.

Even though, the methods proposed by Adams (2008) and Lajeunesse (2009) share some statistical features; the former takes into consideration whether the variation observed in the model is product of within-study error and bias. Lajeunesse (2009) suggested adapting the Q test to its phylogenetic homologue. PMA also allows the implementation of λ or K values in the model. Therefore, the correlation matrix P , comprised of these altered correlations, will be used in the rest of the meta-analytic procedure (Lajeunesse 2009; Lajeunesse et al. 2013). Model comparison not only between non-phylogenetic and phylogenetic models but also among various evolutionary assumptions is feasible. Moreover, models may not only include fixed but also random effects.

Although, akin to other phylogenetic analyses, likelihood ratio tests can be estimated, some authors recommend using AIC scores as indicators of model fit (Lajeunesse 2009). With respect of effect sizes, PMA usually yields lower estimates compared to traditional meta-analysis (Chamberlain et al. 2012). PMA with fixed effects is considerably sensitive to the degree of the phylogenetic signal as well as to the size of the phylogeny (Chamberlain et al. 2012). With respect to random effects PMA, Chamberlain et al. (2012) discovered that although these models are also dependent on its corresponding phylogenetic signal, phylogeny size was not statistically significant. This result, however, should not encourage researchers to disregard phylogeny size. On the contrary, Chamberlain et al. (2012) are emphatic regarding appropriate sample sizes (more than 20 species) for this type of analysis.

Models to Test and Compare Evolutionary Processes

While highly informative of evolutionary conservatism (as opposed to lability) of traits, measures of phylogenetic signal reflect only the *pattern* of conservatism but not the *process* behind it. It is impossible to determine, only with phylogenetic signal and analyses that rely on it, as the ones described above, *why* a trait exhibits high lability and another high conservatism in the phylogeny of interest. In other words, other indices are necessary to examine the evolutionary process, or processes, behind the evolution of a trait – has it been evolving toward an optimal value? Was there an early burst in evolutionary rates due to niche filling, which subsequently decelerated? Are evolutionary rates accelerating as ecological conditions have made the trait more salient to natural selection in recent evolutionary time? Below we summarize the main models that have been proposed to address these questions, which may be tested through a variety of R phylogenetic packages.

Ornstein-Uhlenbeck (OU): The OU model introduces an additional parameter relative to Brownian motion, for the strength of a constraint force, in other words, a selection pressure toward a certain value for all species in the clade being examined (Hansen 1997). While it is believed that this model describes “stabilizing selection,” that is a fallacious statement, as the pressure may drive species in directional selection toward the optimum or reflect adaptation to a fluctuating optimum that is itself constrained (Ingram et al. 2012). As species values are pushed toward the optimum, their earlier divergence is overwritten, with thus recent evolution under the OU model accounting for most of the total trait variance among species in a clade. Note that it is also possible to estimate whether different clades within a phylogenetic tree exhibit different optima (Butler and King 2004).

Early burst (EB): Like the OU model, EB also introduces a new parameter to the Brownian motion model. It describes how evolutionary rates increase *exponentially* through time (Harmon et al. 2010). When this parameter is 0,

Brownian motion can be assumed, as there is no consistent acceleration or deceleration of evolutionary rates. When negative, it reflects niche filling, suggesting that the clade experienced an early ecological opportunity and rapidly speciated, which was followed by exponential reductions in diversification rates as ecological space saturated (Simpson 1953). As such, branches closer to the tip are longer, indicating a period of considerable stasis.

Acceleration: Akin to the EB model, in a model examining evolutionary rate acceleration (commonly with Pagel's delta; Pagel 1999), rates may have decreased across evolutionary time. However, delta larger than 1 suggests accelerated evolution toward the tree tips and thus species-specific adaptations. This model differs from EB by not assuming *exponential* acceleration or deceleration and thus may serve as a good alternative to test similar hypotheses.

A variety of other, less common models also exist: for instance, a drift model permits examining the possibility that a trait has evolved with a directional component, consistently toward smaller or larger values (FitzJohn 2010); yet another model examines the hypothesis of punctuated evolution, with low values indicating that long tree branches reflect stasis, whereas rapid evolutionary changes were concentrated in short branches (Pagel 1994, 2002).

All these models exhibit one more parameter than the Brownian motion model, in addition to the same two parameters of the latter (although the OU model includes four parameters if the phylogenetic tree used for analysis is not ultra-metric; Hansen 1997). As such, they are modifications of the Brownian motion model, each with a different assumption. They may thus be compared through maximum likelihood tests either across themselves or to a Brownian motion model, with AIC comparisons taking into consideration the different numbers of parameters.

Conclusion

Phylogenetic methods include an array of analytics necessary for conducting comparisons and

reconstructions throughout the evolutionary history of a clade. These statistics provide a powerful control for any underlying effects due to phylogenetic closeness. Although PIC and PGLS are often considered as the main tools of phylogenetic comparative researchers, the last decade had seen a considerable expansion in the sophistication of these methods, including the adaptation of generalized linear mixed models, path analysis, and meta-analysis to its phylogenetic equivalent. It is worth to recall that statistical evidence is required prior to conducting these types of analyses. Furthermore, it is recommended to present the results of both traditional and phylogenetic examinations (Nunn 2011).

Cross-References

- [Comparative Evidence](#)
- [Field of Comparative Psychology, The](#)

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Phylogenetic Comparative Methods

► [Phylogenetic Analysis Within Comparative Psychology](#)

Phylogenetic Generalized Least Squares Regression

► [Phylogenetic Analysis Within Comparative Psychology](#)

Phylogenetic Meta-analysis

► [Phylogenetic Analysis Within Comparative Psychology](#)

Phylogenetic Path Analysis

► [Phylogenetic Analysis Within Comparative Psychology](#)

Phylogenetic Signal

► [Phylogenetic Analysis Within Comparative Psychology](#)

Phylogenetic Study of Homosexual Behavior

► [Comparative Evidence](#)

Phylogeny of Light Detection and Vision

► [Vision](#)

Phylogeny of Play Behavior

► [Evolution of Play](#)

Physical

► [Genetic Relatedness and Child Abuse](#)

Physical Activities

► [Physical Health](#)

Physical Activity

► [Exercise](#)

Physical Aggression

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Synonyms

[Abuse](#); [Physical Assault](#); [Physical Attacks](#)

Definition

Exhibiting behaviors that have the potential to cause tangible harm to another person.

Introduction

Physical aggression – an act that has the potential to cause tangible harm to another person or thing – has been displayed throughout human existence. Physical aggression can be used to achieve a goal such as securing resources (instrumental aggression) or in response to provocation from a potential threat (reactive aggression). Today’s culture has seen a drastic reduction in physical aggression when compared to human’s

hunter-gatherer ancestors, but the behavior is by no means sparse. Despite declines in violence, a recurrent pattern is the tendency for males to engage in more physical aggression than women.

The common assumption is that males possess a greater propensity toward acts of physical aggression than females do. There is significant data to support this claim; however, some experimental and meta-analytical studies show that the relationship between sex and physical aggression may be more complex. The following entry will review the classic view that males are naturally more physically aggressive than females; however, theoretical perspectives claiming that the discrepancy is less significant than commonly assumed will also be reviewed. The evidence concerning theories of sexually dimorphic expressions of aggression will also be examined from an evolutionary perspective. Finally, this entry will discuss the relationship between sex and aggression in a modern context.

Sex Differences in Physical Aggression

Sex differences in acts of physical aggression are present from as early as the first year of life and continue into maturity. Meta-analytic data of 27 studies sampling children with a mean age of 8 found that males engaged in significantly more physical aggression than females (Card et al. 2008). Debate exists over the initial age of detectable differences in aggression between the sexes. However, a recent longitudinal analysis of more than 2000 infants shows acts of toddler physical aggression (biting, kicking, slapping) are more commonly displayed by male infants than by female infants (Baillargeon et al. 2007). This difference is detectable within the first 17 months, refuting previous estimates that differences did not appear until children were 2–4 years old (Archer 2004). Other findings suggest that aggression in boys is most present in front of other boys (Maccoby and Jacklin 1980). Additionally girls too were found to be more aggressive in front of boys than in front of girls, but boys were less aggressive in the presence of girls (Maccoby and Jacklin 1980).

Sex differences in physical aggression persist into adolescence and adulthood. Males across all ages and multiple nations were more likely to self-report, have others report, or be observed displaying physical aggression according to a meta-analysis of 353 studies comprised of nearly 200,000 participants of various ages (Archer 2004). Additionally, this analysis determined self-reported sex differences were most prevalent between ages 18–30 and observed sex differences were most prominent between ages 12–17. Crime statistics also demonstrate that more physical aggression can be attributed to males than to females. Males are responsible for the overwhelming majority (approximately 85 %) of crimes involving physical assault and the vast majority (97 %) of same-sex homicides (Daly and Wilson 1990).

Despite this evidence, numerous researchers insist differences between physical aggressions are exaggerated and previous research is inconclusive or misguided (Frodi et al. 1977). This perspective claims women are equally likely to be physically aggressive, but the context in which females will display physical aggression varies. Additional explanations for reported differences in physical aggression may stem from the fact that males are more likely to cause harm when physically aggressive compared to women. Women may commit acts of aggression equally; however, the act may not cause severe enough harm to be observed or reported (Richardson 2005). Finally, females may act less physically aggressive as they are more often than not of lesser stature (based on size) to other physically aggressive people (Richardson 2005). The sum of these factors creates a context where reports of physical aggression may not reflect actual instances of aggression among each sex. While sex-based differences in expression of aggression is still a contentious debate, research on lifetime anger levels clearly shows both males and females demonstrate equal levels of anger throughout the lifespan (Archer 2004). The explanation for why the sexes may differ in their propensity to engage in physical aggression varies (Archer 2004). These differences between the sexes in

regards to aggression may be best explained by evolutionary theory.

Explanations of Sex Differences from an Evolutionary Perspective

Previous research has attempted to explain sex differences in aggression to differences in testosterone levels. Higher average testosterone levels in males were directly correlated to higher rates of physical aggression in males than in females. However, while this link between testosterone has been supported in primates (Maccoby and Jacklin 1980) there is limited support for this relationship in humans (Halpern et al. 1993). A more compelling argument, based in sexual selection theory (SST), posits the potential costs of being physically aggressive vary for each sex. For males, the benefits (increased resources, increased mating opportunities) gained through physically aggressive acts are more likely to outweigh the potential costs (serious injury or death) of those same acts. Males' obligatory investment in offspring is quite low, thereby making it possible for males to father hundreds of offspring in their lifetime, being hindered only by their ability to gain mating access to females. Thus, using physical aggression to deter rivals, compete for resources, or gain status can have large, positive, fitness consequences. And the alternative (i.e., not fighting) can lead to an evolutionary dead-end for one's genes. However, females potentially have more to lose from acts of physical aggression (Cross 2010). Females have a large obligatory investment in offspring that is time intensive and energetically costly. This substantially lowers their potential reproductive ceiling, compared to males. Moreover, given that females play a much larger role in parental care throughout a child's life, their absence due to injury or death is much more damaging to the wellbeing of the child than the absence of a male caregiver (Campbell 1999). For these reasons, there are far fewer incentives for females to engage in physical aggression to compete for mating opportunities; their reproductive success is better served by investing heavily in a few, high-quality offspring.

Aggression in a Modern Context

While there is plenty of research concerning physical aggression differences, other theories suggest that it is the physicality of aggression, not the aggression itself, which accounts for the differences between the sexes. One theory for the differences in aggression is that males tend to use direct aggression, such as physical aggression, while females prefer to use indirect or interpersonal aggression, a difference most drastic in adolescence, however adults demonstrate a preference for interpersonal aggression in both sexes (Bjorkqvist et al. 1994). This theory is also supported by evolutionary theory in that females may use indirect aggression because it is less likely to result in retaliatory harm. Moreover, females benefit from not using physical aggression, given the risks described above. This is consistent with the drop in its use for girls before menarche (i.e., when they are physically capable of bearing offspring) as males maintain usage into adolescence.

Conclusion

Regardless of whether females have an equal predisposition to physical aggression as males, evolutionary theory provides a solid theoretical framework in which to explain apparent sex differences in the use of physical aggression. In the context of caregiving, the costs associated with physical aggression greatly outweigh the benefits for females while the opposite is true for males. Modern society contributes to these evolutionary differences in the way anger maybe displayed by different sexes; however, as it stands males appear to demonstrate the majority of physical aggression both past and present.

Cross-References

- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Female Age as a Predictor of Men's Aggression Against Women](#)
- ▶ [Meta-analysis of Sex Differences in Aggression](#)

- [Patriarchy and Feminist Perspectives](#)
- [Play Fighting in Boys](#)
- [Self-Defense and Female-Perpetrated Violence](#)
- [Sex Differences in Aggression](#)
- [Violence as Coercive Control](#)

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Physical and Verbal Aggression

- [Women's Use of Direct Versus Disguised Social Aggression](#)

Physical Assault

- [Physical Aggression](#)

Physical Attacks

- [Physical Aggression](#)

Physical Attractiveness

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Synonyms

[Beauty](#); [Mate choice](#); [Sexual selection](#)

Definition

The visual cues used to judge mate quality.

Introduction

One of the most fundamental problems facing an individual is mate selection: how do we choose a partner? It is important that we are sensitive to the physical cues that honestly signal that one individual is more desirable (i.e., fitter and with a better reproductive potential) than another and use them to choose the partner which is most likely to enhance our chances of successful reproduction. The wrong choice will obviously have a negative impact on an individual's potential for reproduction, so one might expect very strong selective pressures for the development of mechanisms that accurately detect cues to health and

fertility in potential partners. In this context, attractiveness is based on features that accurately index health and reproductive potential.

Female Attractiveness

For female attractiveness, the two indices most widely researched are overall body fat (usually indexed by the body mass index or BMI) and the ratio of the circumference of the waist to the circumference of the hips (the waist-to-hip ratio, or WHR). BMI (weight scaled for height or $\text{kg}/\text{height in m}^2$) is a measure of total body fat and correlates well with more direct estimates of percentage body fat such as through densitometry or autopsy (e.g., Clarys et al. 2005). By contrast, WHR is an index of fat distribution, with a high WHR indicating a less curvaceous lower body shape with higher adipose deposition in the abdominal cavity as visceral fat and a low WHR indicating a more curvaceous lower body shape with low levels of visceral fat. WHR has been suggested to predict a range of health and fertility outcomes (Koning et al. 2007; Wang et al. 2005; Zaadstra et al. 1993).

As a result, Singh (1993) hypothesized that because WHR potentially provides information about youthfulness, reproductive status, and long-term health risks, WHR should be used in attractiveness judgments. This hypothesis is supported by studies that have asked observers to rate sets of either line-drawn figures of women's bodies (Furnham et al. 1997; Henss 1995; Singh 1993) or digitally manipulated photographic images (Henss 2000; Rozmus-Wrzesinska and Pawlowski 2005; Streeter and McBurney 2003). In these studies WHR is manipulated by altering the width of the waist of the figures, and their results suggest that a WHR of approximately 0.7 is most attractive with higher (i.e., less curvaceous) WHRs being rated less attractive. However, altering the width of the waist not only changes WHR but also apparent BMI. As WHR rises, so does apparent BMI, making it impossible to say whether changes in attractiveness are due to WHR, BMI, or both (Tovée et al. 1999; Tovée and Cornelissen 1999). An

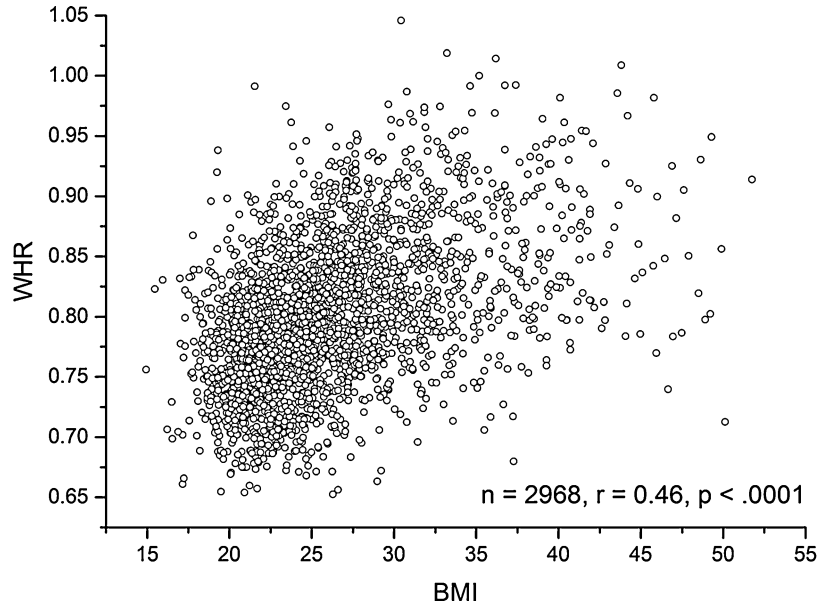
additional problem is that some of the manipulations may produce images outside the natural range of variation and so lack ecological validity (see Bateson et al. 2007).

To counter these criticisms, Singh and Randall (2007) asked observers to rate the attractiveness of pre- and postoperative photographs of women who had plastic surgery to redistribute fat from the abdomen to the hip and buttocks. This operation is suggested to reduce postoperative WHR without significantly changing BMI. Postoperative photographs were judged as more attractive than preoperative photographs, leading Singh and Randall to propose that WHR was a significant predictor of attractiveness independent of any overall body mass change indexed by BMI. However, the view of the women in the photographs was restricted to their lower torso and upper thighs. So it is not surprising that participants made judgments based on the WHR, when the waist and hips were all they could see (Cornelissen et al. 2009). It is quite possible that they might have rated them differently if they had seen the whole body.

A simple solution to the use of manipulated bodies is to use unaltered photographs of the whole bodies of real women (e.g., Smith et al. 2007a; Swami and Tovée 2007; Swami et al. 2006a, 2007). Results from these studies suggest that BMI is the principal determinant of attractiveness judgments (with a BMI of around 20 kg/m^2 being optimally attractive), with WHR playing only a very marginal role. However, these studies have the problem that BMI and WHR are often correlated, as has been demonstrated in large-scale health surveys. For example, the Health Survey for England (Health Survey for England 2003), which includes measurements from 2429 Caucasian women of reproductive age (16–45) ranging in BMI from around 15 to 50, shows a correlation between BMI and WHR of 0.46 (see Fig. 1). This correlation raises the problem of collinearity among explanatory variables in attractiveness studies, making it difficult to discriminate between the effects of BMI and WHR.

One approach to separating BMI from WHR is to model how fat is deposited on the female body

Physical Attractiveness,
Fig. 1 Scatterplot of waist-to-hip ratio (WHR) as a function of BMI from the Health Survey for England 2003 data set based on measurements from 2429 Caucasian women of reproductive age (16–45) ranging in BMI from around 15 to 50



as weight is gained or lost (Cornelissen et al. 2009). Understanding how fat deposition changes body shape allows an analysis which separates out lower body shape change based on changes in overall body fat versus estrogen-mediated change in WHR. This analysis shows that shape change due to overall body fat predicts attractiveness judgments but that shape change linked to estrogen plays no significant role. Another approach is to treat torso shape (i.e., moving from the shoulders to the hips) as a waveform and deconstruct the different components of the shape using principal component analysis (PCA). PC1 is highly correlated with both BMI and attractiveness ratings, but not significantly correlated with WHR. PCs 3 and 4 both correlate significantly with WHR, but neither explains significant variance in attractiveness ratings (Tovée et al. 2002; Smith et al. 2007b).

A final piece of evidence comes from eye-movement studies. The pattern of fixations made when judging body mass is significantly different from those made when judging WHR. When judging body mass, observers focus on the stomach, and deviations from this pattern of fixations reduce the accuracy of body mass judgments (George et al. 2012; Cornelissen et al. 2016). In contrast, when judging WHR

fixations are distributed on either side of the body at the level of the hips (Cornelissen et al. 2009). If these two fixation distributions are compared to the pattern of fixations made when judging attractiveness, it is clear that the fixations made to judge body mass are part of the fixations made to judge attractiveness suggesting a role for body mass in attractiveness judgments. However, the fixations made to judge WHR were not present in the distribution of fixations made when judging attractiveness, suggesting that WHR is not an important cue.

This does not preclude some role for WHR in mate selection, such as differentiating between genders or whether an individual has reached sexual maturity. But in discriminating between potential female partners, it does seem to play a negligible role. In addition to BMI and WHR, there are other features that may play a role in female physical attractiveness. Perhaps the best known of these is the degree of symmetry shown by a body. It is suggested that small deviations in bilateral symmetry (a phenomenon called fluctuating asymmetry (FA)) arise owing to developmental stress (such as from disease or parasites) and that these developmental stresses will have a negative impact on an individual's health and fitness. As when selecting a mate, one wishes to

choose an individual with good health and fertility; it is suggested that if one were sensitive to FA, it could be used as an index of a potential partner's suitability. Previous studies have suggested a weak effect of body FA (excluding the face) with its perceived attractiveness. (Tovee et al. 2000; Brown et al. 2008). This result suggests that although symmetry is a significant factor in determining physical attractiveness, it is a comparatively subtle cue compared with BMI or WHR.

Relative leg length (indexed by the leg-body ratio or LBR) seems to be relatively weak, but significant predictor of female attractiveness. The hormone surge during the first menstrual cycle at the onset of puberty causes the growing points in the long bones of the leg to fuse. The result of this is to halt growth in the legs, although growth in the torso continues until adulthood. Leg growth is very sensitive to diet and health. The increase in height in Western populations in the last century has been primarily driven by increased leg length. This means that relative leg length provides a potential measure of childhood health and nutrition, and relatively shorter legs predict a range of negative health outcomes including a high risk of cardiovascular disease (Gunnell et al. 2004), type II diabetes and insulin resistance (Lawlor et al., 2002), and an increased risk of certain types of cancer (Gunnell et al. 2003). Therefore preferring relatively longer legs should select a healthier partner, and a range of studies have suggested a positive relationship between relative leg length and attractiveness (e.g., Swami et al. 2006b; Frederick et al. 2010).

Male Attractiveness

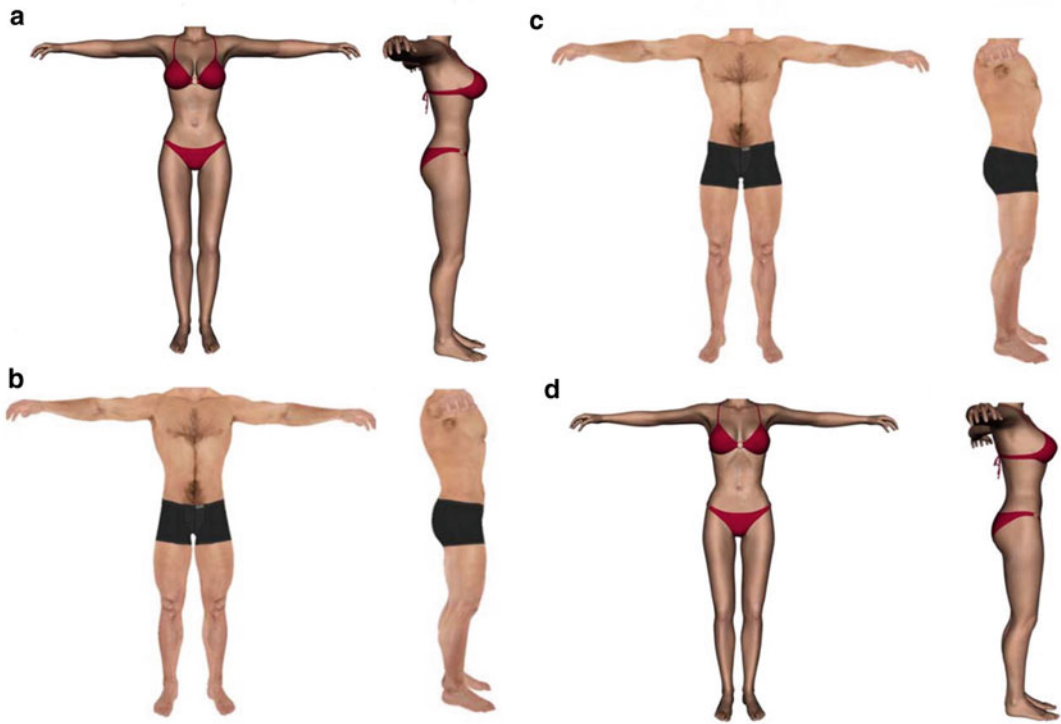
The primary determinant of male attractiveness seems to be upper body shape (a broad upper body and a narrow waist, the classic V shape). It has been suggested that this V-shaped torso represents a muscular, strong body type that would be an advantage in our ancestral environment and therefore be sexually selected (Frederick et al. 2005; Sell et al. 2008). Body fat is an important predictor of male health and mortality (Prospective studies Collaboration 2009; Emerging Risk Factor Collaboration 2011), and a narrow

waist circumference is also important in long-term health and so should also be associated with a low WHR (Lean et al. 1995; Zhu et al. 2002). However, unlike the female thin ideal body, the ideal male body is comparatively heavy, falling at the boundary of the normal to overweight categories of the BMI scale (Maisey et al. 1999; Crossley et al. 2012). As muscle is approximately 20 % denser than fat, more muscular bodies tend to have a higher BMI. Whereas there is a tendency for women to diet to achieve their ideal body, young men are more likely to be influenced by magazines to build up a bigger, more muscular body (Frederick et al. 2005; Cafri et al. 2005). So although the male ideal body is heavier, the additional weight is muscle rather than fat. As discussed above, BMI is a measure of body weight scaled for height and not a direct measure of percentage body fat. Its use in epidemiological studies is due to its ease of administration. The ideal male body is lean with high muscle definition (which requires a percentage body fat below 9–12 %). The male ideal is both muscular and low in body fat (Crossley et al. 2012) (Fig. 2).

There is also a weaker, but significant relationship between attractiveness judgments and height. For example, women prefer taller men in online dating, in questionnaire studies, and in speed dating (Kurzban and Weeden 2005; Fink et al. 2007; Salska et al. 2008). However, this is not a simple linear relationship. Being substantially taller or shorter than the average is linked to a range of negative health outcomes and to reduced reproductive success (Stulp et al. 2012). Additionally, there is the moderating effect of the female observer's own height. Women seem to prefer men taller than themselves, but not too much taller (Stulp et al. 2013). So the "ideal" height will vary dependent on the observers own height. However, the preference for a taller man may not be universal as there is some evidence that it does not extend across cultures (Sear and Marlowe 2009).

Physical Attractiveness Is Adaptive

Evolutionary psychology assumes that certain physical features honestly signal an individual's health and reproductive potential (Buss 2004;



Physical Attractiveness, Fig. 2 Examples of ideal bodies created by the female participants (**a** and **b**) and the male participants (**c** and **d**) using an interactive 3D computer program. Bodies **a** and **c** are the ideal female bodies set by the female and male participants, respectively, and

bodies **b** and **d** are the ideal male body set by the female and male participants, respectively. This illustrates that both men and women share a preference for a very slim but curvy female body and a muscular but lean, V-shaped male body (Modified from Crossley et al. 2012)

Symons 1980). Certain specific values of these features could signal optimal health and fertility; thus, an individual whose features correspond to these values would be regarded as optimally attractive. For attractiveness to be adaptive, it follows that in environments where the optimal values for these features differ due to differences in environmental pressures, the attractiveness preferences should also be different (Anderson et al. 1992; Ember et al. 2005). Moreover, as observers moved from one environment to another, it would be adaptive for them to alter their attractiveness preferences to those that accurately reflected optimal health and fertility in their new environment (Tovee et al. 2006).

This malleability of preferences may be partially based on an observer's physiological state (Swami and Tovee 2006), but the principal mechanism of recalibration seems to be based not on simple visual diet (i.e., the size and shape of the

bodies in an observer's visual environment), but on visual valency (i.e., the value a culture or society places on a particular body size and shape) (Boothroyd et al. 2012). For example, in the Nicaraguan rainforest, the introduction of TV whose content displays a high value on thinner bodies has led to a downward shift in ideal BMI, although the socioeconomic status of the local people has not changed (Boothroyd et al. 2016). This malleability of preferences in response to changing conditions is essential if the perception of physical attractiveness actually plays an adaptive role in human mate selection.

Conclusion

In Western countries a slim female body is preferred with overall body mass being the principal factor in attractiveness judgements, whereas for

the male body a muscular V-shaped body is preferred. However, the perception of physical attractiveness is a flexible ideal and subject to change based on environmental conditions. This allows attractiveness preferences to adapt to reflect changing conditions and so match mate selection preferences to the optimal body size and shape for health and fitness in a specific environment.

Cross-References

- [Body Fat Percent and Distribution](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Men's Mate Preferences](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)
- [Sexual Signalling](#)
- [Waist-to-Hip Ratio](#)
- [Women's Mate Value](#)

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Physical Bullying

► School Bullying

Physical Characteristics

► Anatomical Adaptations for Fighting

Physical Cognition

► Bird Tool Use

► Primate Tool Use

Physical Discipline

► Spanking

Physical Force

► Violence

Physical Health

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Synonyms

[Balance](#); [Cardiovascular metabolism](#); [Homeostasis](#); [Immune system](#); [Mood](#); [Physical activities](#); [Sports](#); [Welfare](#); [Wellbeing](#)

Definition

Physical health is a metabolic and cognitive state that involves the absence of any disease and it is obtained via sports, nutrition, and/or ergogenic aids that enable persons to have a suitable life with maximum functionality. *Sports* is defined as all forms of competitive physical activity, through causal or organized participation in teams, which aims to maintain or improve human physical abilities and skills, usually offering entertainment to participants and cheerfulness to winners (for review see Garcia-Falgueras 2015). *Ergogenic aid* is defined by the American governmental regulation and oversight as any training technique, mechanical device, nutritional ingredient or practice, pharmacological method or psychological technique that can improve exercise performance capacity or enhance training adaptations (Kerksick et al. 2018).

Introduction

Physical health is an individual and subjective dimension of each person, that can be reached by many different ways and they all are responsibility of the grown up person. Thus it implies an active approach. Consequently spectators or audiences of sports who watch a sportive competition but do not participate themselves with any physical activity are not improving their physical health. Competition in sport is a necessary but not

sufficient component to carry on with physical activities, because a systematic personal training and working out is a type of sport or physical activity which also achieves well-being similar as competitive team sports (for review see Garcia-Falgueras 2015).

Physical Activity for Mood, Cardiovascular Health and Body Concept

Cardiovascular exercises practiced regularly, which are aimed at increasing oxygen in the blood and changing the heart rhythm for higher metabolic demands (aerobic exercises), have been proved to improve cognitive functions and to have a positive effect on mental health and psychological well-being. Both individual sports such as fitness, jogging, weight lifting, equestrian, foot-ing, distance running, cycling, swimming, tennis, wrestling, and team-based sports such as soccer, football, rugby, etc. are having good effects over sleeping quality, working memory, long-term verbal memory, perceptual abilities, processing speed, cognitive inhibition, and flexibility (Gayda et al. 2017; Hartescu et al. 2015; Rice et al. 2016). Sedentary behaviors are related to cardiovascular and other diseases (Celis-Morales et al. 2018). Gender and age are variables of importance in order to choose which sport to practice (Eime et al. 2016). There are evidences that physical activity can create a better state for the person, because it is related to lower cholesterol levels, blood pressure, and blood lipids (for review see Ogden 2010). Exercises have been used for the treatment of obesity, weight loss, and weigh maintenance, because physical activity, increase of strength and fitness provide good benefits at reducing sedentary behaviors (Celis-Morales et al. 2018; Ogden 2010). With increase in physical activity and functions of the cardiovascular system, a reduction in cardiovascular diseases is obtained (Zheng et al. 2014) and regular exercise has been associated with a range of public health benefits (Hartescu et al. 2015).

Open air exercise practices had significant good effects on sleep quality for middle-aged

and older people (Hartescu et al. 2015), perhaps because of the sun light exposure. It was proved in a group of older adults that the amount of hours spent outside of the home was associated with better cognitive functions and improved physical and emotional abilities (Petersen et al. 2015). This study was performed during the period of one year and longitudinal data checked confirming that leaving home requires significant cognitive functions and resources: posture, way finding, navigation skills, gait, etc. Moreover, biodiversity and contact with the natural environment (parklands with scattered shrubs and trees) and a number of different species perceived (but no spiders or snakes which might raise phobias), provide many psychological and health benefits (van Heezik and Brymer 2018).

Even in minority groups, such as homeless people, in extreme social isolation conditions of risks and weakness (i.e., alcohol and drugs abuse, violence, sexual abuses, and infectious diseases), sports had a positive effect enabling them in building a new self-identity and starting a new life. After 8 weeks of regular sports and fitness, their well-being and reintegration into society were facilitated and improved (Sofija et al. 2018).

But cognitive and other disorders or even severe injuries do also occur in sports, elite athletes being the higher risk group: head injuries, concussions, limb injuries, including mental ill-health and substance use that can be attributed to the intense mental and physical demands of higher levels of competition (Rice et al. 2016). The vulnerability of physical injuries and risks for health are bigger for athletes involved in sports with a particular lean body-shape demand, such as ballerinas and gymnasts among female athletes. A collaborative team effort is required by different professional staff, such as medicine practitioners, psychiatrists, psychologists, etc., to care for the athletes' mental and physical health and assistance in overcoming barriers and stigmas in order to prevent damages, which are linked to the achievements in their chosen careers (Rice et al. 2016).

The endorphins hypothesis is the most popular explanation as to how a physical mechanism underlies the benefits of sports. In the brain, the

hypothalamus produces endorphins in the form of peptides and the pituitary gland releases them into blood circulation. Later, these endorphins act on their own receptors. It has been demonstrated *in vivo* (MRI) that professional runners release endogenous opioids in the fronto limbic areas of the brain after a sustained and intense physical exercise practice. That release is, in fact, closely correlated with perceived subjective euphoria (for review see Garcia-Falgueras 2015).

Anaerobic sports, such as Tai Chi, Yoga, or Pilates, have been shown to improve physical and mental health outcomes, such as proprioception, balance ability, flexibility, self-esteem, and in general, quality of life and sleep, through a controlled conscious diaphragmatic breathing for achieving body relaxation and a calmness of mind (Garcia-Falgueras 2016; Hartescu et al. 2015; Zheng et al. 2014).

Nutrients and Sports

Healthy eating has been recommended in relative quantities and appropriate consumption of food of different groups. They are: (1) fruit and vegetables; (2) bread, pasta, other cereals, and potatoes; (3) meat, fish, and alternatives; (4) milk and dairy products; and (5) fatty and sugary foods (Ogden 2010). However, there are many different combinations of these ingredients and kitchens in almost all homes have their very own personal and subjective concept of healthy food. There seems to be consensus on the effect of culture, ethnic group, history, and personal traits on diet and food consumption. According to Rozin (1980), “*there is no doubt that the best predictor of the food preferences, habits and attitudes of any particular human would be information about his ethnic group. . . . rather than any biological measure that one might imagine*” (for revision see Ogden 2010).

Several aspects do have a role in eating behavior: the hedonic, cognitive, and homeostatic systems are involved in food intake behavior. In obese people, the hedonic side is predominant (Hopkins et al. 2016; Ogden 2010). In metabolism and the body, satiety signals act as a cascade

(Cholecystokinin- CCK; Glucagon-like-peptide- GLP-1; Peptide YY₃₋₃₆ –PYY; Amylin). These substances are received and perceived in a cross-talk interaction by balancing metabolisms to stop the eating behavior (Hopkins et al. 2016). Obesity can be defined depending on the waist circumference; >88 cm in women and >102 cm in men is the measurement for obesity (Celis-Morales et al. 2018). However, this delicate cascade balance and metabolic and psychological equilibrium might be altered for extreme diets, or long periods of imposed starvation (Polivy 1996).

In recent years, an increased number of studies and publications have been done about supplements and complementary nutrients for athletes and sportive people. Exercise and other vital activities require extra energy and resource consumption; hence, many industries and companies are working on this goal to help sportive and active people. For instance, creatine supplementation intake, one of the most popular nutritional ergogenic aids for athletes, has been proved to have benefits in exercise, sport, and medicine for postexercise recovery, injury prevention, and thermoregulation (Kreider et al. 2017). Creatine is naturally found in meat and seafood, not always available in the right proportion for all those that practice sports. In animal experiments, it was tested and found that 5 days of creatine monohydrate administration might have a neuroprotective effect, ameliorating the extent of cortical damage. Its positive effects over specific diseases such as Huntington’s, Parkinson, and other neuromuscular dystrophies or diseases are currently under experimental evaluation (Kreider et al. 2017). Caffeine, beta-alanine, aminoacids, and nitric oxide agent in combination have been used for athletes to get synergistic effects in their intensity exercise performance and training adaptation. However, solid experimental conclusions in humans regarding gender difference in supplementation effects are premature and more robust controlled studies are required (Harty et al. 2018).

Proteins intake is also a very popular nutritional ergogenic aid for athletes and was initially recommended inside a range of grams per day depending on weight and age (children,

adolescents, or adults) (Kreider et al. 2017). Muscular temporal recovery in its function is improved after systematic whey protein supplementation. Proteins enhance strength and muscle mass in resistance training (isometric, isokinetic, torque or weight lifting, or isoinertial maximal voluntary contraction) and facilitate restoration of contractile function (Davies et al. 2018). Experimental comparison reported beneficial effects on the muscle function for the group who took proteins compared with the control who did not however, it is surprising that only eight high-quality studies have been published about protein and its effects, over a period of 10 years (Davies et al. 2018).

On the other hand, Magnesium (Mg), which is an essential mineral, is also good to enhance exercise performance. Animal studies have proved Mg might improve exercise performance because of facilitation of the glucose availability in the blood for brain, muscle, and heart. Glucose is converted to pyruvate during aerobic exercise and it is reduced to lactate during anaerobic exercise. Lactate might induce muscle fatigue or laces, and Mg reduces or delays lactate accumulation in the muscle. It also participates in energy metabolism, assisting muscle contraction and relaxation for muscle tissue recovery. In natural food it is found in nuts, seeds, fruits, vegetables, and whole grains. Mg is widely recommended to active and physical competitive athletes and for long-term strenuous exercise (Zhang et al. 2017).

Conclusion

The state of physical health, as the absence of disease, is reached through different cognitive and metabolic ways. Sports, exercise, and physical activities help to maintain the body in all its functions while nutrition, food, and supplements give the energy and compounds required to proper real performance capacities or enhance training adaptations. In this short chapter, we analyzed briefly some of the most interesting topics in the field.

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Physical Punishment

- [Spanking](#)

Physical Self-Similarity

- [Facial Resemblance and Kinship Detection by Strangers](#)

Physical Shape

- [Maternal and Offspring Condition](#)

Physician

- [Jack Kevorkian](#)

Physician-Assisted Death

- [Assisted Suicide](#)

Physiologic Processes

- [Physiological Mechanisms](#)

Physiological Evidence for Human Sperm Competition

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Synonyms

[Ejaculate adjustment](#); [Human sperm competition tactics](#); [Semen displacement](#)

Definition

Humans have experienced sperm competition in their mating history and men have evolved both physiological and psychological adaptations to prevent and correct it; the physiological ones are

focused on maximizing the chances of their own sperm winning the competition to fertilize an egg inside a woman's reproductive tract instead of a rival male.

Introduction

In mammals, paternity is not certain, creating the potential for unwitting paternal investment into genetically unrelated offspring; in humans, non-paternity rates for children that men believed they had sired with their regular partner range from 1.7 % to 29.8 % (Pham and Shackelford 2015). Because cuckoldry is costly in socially monogamous mating systems, men have evolved adaptations to thwart cuckoldry, including adaptations to sperm competition. Sperm competition occurs when a woman copulates with two or more men within a brief time period (about 3–5 days), resulting in the sperm of different males competing to fertilize ova (Pham and Shackelford 2015). These adaptations can be both physiological and psychological. The following discusses empirical evidence for physiological adaptations, namely ejaculate adjustment and semen displacement.

Ejaculate Adjustment

Given the nontrivial costs of producing high-quality ejaculates, one adaptation to sperm competition is strategic adjustment in ejaculate quality (also known as prudent sperm allocation) as a function of the risk of sperm competition (Pham and Shackelford 2015). Although widely studied in many species, investigations of ejaculate adjustment in humans have been limited and infrequent. Baker and Bellis (1993, 1995) collected copulatory ejaculates from heterosexual couples and documented a negative relationship between the proportion of time the couple spent together since their last copulation and the number of sperm ejaculated at the couple's next copulation, as predicted by sperm competition theory.

Ejaculate adjustment has also been documented using other measures of sperm competition risk. Men produce higher-quality masturbatory

ejaculates when viewing images of highly attractive women (indexing greater sperm competition risk) compared to men viewing images of unattractive women (indexing lesser sperm competition risk) (Leivers et al. 2014a). Kilgallon and Simmons (2005) documented that men produce masturbatory ejaculates with a greater percentage of motile sperm when viewing images of one woman and two men (cueing the presence of sperm competition) than when viewing images of three women (cueing absence of sperm competition). Pham et al. (2015) analyzed masturbatory ejaculates along several parameters (e.g., number of sperm, percentage of motile sperm, swimming velocity) and documented that men produce higher-quality ejaculates under a "sperm competition present" condition (men were instructed to imagine sex with their partner for the first time since she admitted to committing an infidelity) than under a "sperm competition absent" condition (men were instructed to imagine sex with their partner for the first time since she admitted to losing some of the couple's money from gambling).

Leivers et al. (2014b) documented that men in committed relationships who reported more "mate guarding" activities (e.g., monopolizing their partner's time) produced lower-quality masturbatory ejaculates compared to men who reported fewer mate guarding activities. Leivers et al. (2014b) argued that men who frequently engaged in mate guarding are at lesser sperm competition risk because they can better account for their partner's activities and, consequently, invest fewer resources into producing costly, higher-quality ejaculates.

Semen Displacement

It has been suggested that the length and shape of the human penis allows for it to displace semen from rival males that may already be present in a woman's reproductive tract and therefore give an advantage in sperm competition (Pham and Shackelford 2015). Consistent with this theorization, men who suspect their regular partner of infidelity or who have spent an extended period of time apart from their partners (another cue of

sperm competition risk) thrust deeper and more quickly during the couple's next copulation, as reported by both men and women (Gallup and Burch 2004). This deeper and quicker thrusting is intended to optimize the chances of displacement of any potential rival sperm that could be in their partner's reproductive tract. Similarly, prolonged duration of copulation has been reported as a semen-displacing tactic (Gallup and Burch 2004). Additionally, men who are at recurrent risk of sperm competition (as measured through their partner's personality traits and attractiveness) perform deeper and more frequent thrusts compared to men who are not at recurrent risk of sperm competition (Goetz et al. 2005).

Even at the commitment level of marriage, one study found that husbands performed more semen-displacing copulatory behaviors during their last sexual encounter when their wife spent more time with male coworkers and friends (i.e., potential rivals that may be a cue to sperm competition risk; Pham et al. 2017). This study also incorporated the variable of discrepancy in sexual interest between spouses as a cue to sperm competition. Specifically, when women engage in extra-pair copulations, they prefer to delay copulating with their regular partner to bias the outcome of sperm competition in favor of the rival male (Pham and Shackelford 2015). Accordingly, Pham et al. (2017) found that the bigger the discrepancy in sexual interest (e.g., wife's interest was much lower than the husband's) the more semen-displacing copulatory behaviors performed by husbands at the couple's last sexual intercourse.

Conclusion

Sperm competition has had a significant influence on the evolution of human mating strategies (Pham and Shackelford 2015). Physiological evidence of this influence is found in men's ability to adjust the quality of their ejaculates based on the risk of sperm competition at each copulation and their deployment of semen-displacing physical actions during copulation to reduce the risk of sperm competition. Compared to psychological

adaptations, men's physiological adaptations to sperm competition are not as well understood, and more research in this domain will improve the knowledge base of how methods to combat sperm competition function in humans.

Cross-References

- Ejaculate Adjustment
- History of Sperm Competition in Humans
- In-pair Copulation
- Psychological Evidence for Human Sperm Competition
- Sperm Competition Tactics

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Physiological Mechanisms

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Synonyms

[Physiologic processes](#); [Physiological responses](#)

Definition

The mechanism that carries out a physiological process is known as physiological mechanism.

Introduction

The healthy state of the body depends upon the integrity of various organ systems. The organ systems in the body function in a particular manner constantly. The mechanisms, by which the organ systems of the body function, are often referred to as “physiological mechanisms.” For example, “behavior” of an animal including human beings is one of the functional outcomes of the brain. In other words it can be said that certain neurophysiological mechanisms are responsible for particular behaviors of animals (Barnard 1983).

Physiological mechanisms explain any health-related events or outcomes. Physiological

mechanisms can be altered voluntarily. For example, exercise causes alteration in the cardiac physiology of resting state. A particular posture (e.g., cross-legged posture) may alter the physiological mechanism (increase in blood pressure) (van Groningen et al. 2008). Physiological mechanisms (reproduction, fertilization) are responsible for formation, development, as well as birth of an individual. Multiple physiological mechanisms are responsible for survival of an individual. Successful survival of an individual depends upon optimal functioning of all the organ systems of the body. Healthy state also requires successful combat of the pathogens and other harms that possess threat to the integrity of health. The individual must adapt with the environmental needs from time to time in order to remain healthy. Experiments among animals and lower organisms support that certain physiological mechanisms play pivotal role in acclimatization (Gates and Edmunds 1999). A similar pattern of physiological responses is seen among animals and human beings to adapt to stress (Martin et al. 2011).

Physiological mechanisms may operate in the subcellular (e.g., protein synthesis), cellular (e.g., nerve conduction), organ (e.g., detoxification of toxic metabolites in the liver), as well as inter-organ (e.g., neuroendocrine control of reproduction by hypothalamic-pituitary-adrenal axis) level. The physiological mechanisms operate to maintain the homeostasis in the body.

Physiological Mechanisms: Variations

Physiological mechanisms may vary within the species as well as across the species. For example, respiratory rates vary among mammals; within the species of mammals, respiratory rate also varies at different physiological states (resting state, exercise, during pregnancy). There are also variations in a particular physiological mechanism within a species for a particular physiological state. For example, lactation is a physiological mechanism that operates among mothers to meet the nutritional needs of their offspring; however there are individual variations in lactational physiology (breast development, milk production) among

mothers (Jonas and Woodside 2016). Many biological, psychological (personal), and social factors play crucial role for these variations in physiological mechanisms (Jonas and Woodside 2016). Sex of an individual too plays a role in determining the variations in physiological mechanisms. Evidences support that the experience of respiratory distress (e.g., exertional dyspnoea) differs among males and females (Schaefer et al. 2012). The physiological mechanisms differ between males and females, which specifically regulate the gonadal function and determine masculine and feminine characteristics (Miller 2014). Gender differences are also present in the physiological mechanisms operating to metabolize glucose and fatty acids in the skeletal muscles (Lundsgaard and Kiens 2014). Gender differences are also present in the physiological mechanisms associated with illnesses. For example, autoimmune disorders develop due to alterations in physiological mechanisms, and it is more common among females than males (Blair 2007). Similarly, calcium metabolism and bone mineral density are influenced by gonadal hormones (estrogen, testosterone). Deficiency state of estrogen (e.g., postmenopausal) predisposes to osteoporosis, which is more common in females than males (Blair 2007).

Variations in certain physiological mechanisms occur across the life span of an individual. The physiological mechanisms operating during fetal life change to a different type during infancy, childhood, adulthood, and late life (van Beek et al. 2016).

Physiological Mechanisms: Evolutionary Significance

Evolution brings change in the organism in totality. Various evolutionary processes like natural selection, drift, and sexual selection and various genetic changes are responsible for the changes in the organism. These factors may alter the physiological mechanisms (Feder et al. 2000). The changes in physiological mechanisms are capable of causing changes in the phenotype and genotype too.

Cell is the structural and functional unit of a living organism. The organ physiology depends upon the cellular architecture of the organ. Genes regulate the functioning of the cells to a greater extent. During the process of evolution, changes in the genetic elements happen. The genetic changes across the generations might be an important determinant of changes in the physiology and hence the physiological mechanisms (Ruiz-Mirazo et al. 2017).

Evidences support that social connectedness, bonding, and cooperativeness evolved with time. Certain physiological mechanisms (neuroendocrine and genetic) are responsible for the above social behaviors, which evolved with time to meet the needs of individuals (Taborsky and Taborsky 2015).

Physiological Mechanisms: Health Significance

Healthy state of an individual is determined by the optimal function of the organs of the body. Failure of the physiological mechanisms results in health hazards. Failure in regulation of physiological mechanisms results in development of physical illnesses as well as psychiatric disorders (McGuire and Troisi 1987). Postmortem brain studies suggest that alterations in brain physiological mechanisms result in development of certain psychiatric disorders (Berretta et al. 2015).

Restoration of the physiological parameters restores health, which is mediated through specific physiological mechanisms. For example, electrolyte imbalance (hyponatremia, hypokalemia, etc.) alters the cellular physiology, which in turn alters the electrophysiology of conducting tissues of the body (neurons and muscles), resulting in cardiac arrhythmia, seizure, and delirium. Correction of electrolyte imbalance restores the alterations in physiological parameters and corrects the adverse consequences associated with it.

Similarly, cerebral blood flow is regulated by certain physiological mechanisms (intracranial pressure, blood pressure, cerebrovascular physiology, etc.), failure of which may result in health

hazards or any pathological process that may alter the physiological mechanisms regulating cerebral blood flow (Mchedlishvili 1980).

At times the altered physiological response may indicate some ongoing harmful events. The increased intracranial hypertension secondary to head trauma or intracranial lesions manifests with hypertension, bradycardia, and respiratory irregularities called as “Cushing’s triad.” This altered physiological response may be considered as a clinical indicator for urgent surgical decompression in these patients.

Respiratory illnesses like bronchial asthma are related to failure of physiological mechanisms associated with autonomic regulation (cholinergic mechanism causes bronchospasm and adrenergic mechanism causes bronchodilatation) (Gazzola et al. 2018). This forms the basis of pharmacological management of bronchial asthma (either blocking the receptors producing bronchoconstriction or facilitating bronchodilatation).

Alterations in the physiological mechanisms at a particular stage of life may have association with experiences of earlier life events. Evidences support that early-life adversities have adverse consequences during adulthood. The physiological mechanisms involved in the association of childhood adversities to morbid illnesses in adult life are immune physiology, neuroendocrine physiology, as well as metabolic physiology. Alterations in physiological mechanisms may lead to development of psychiatric illnesses, cardiovascular disorders, metabolic abnormalities, and cancer, which can be traced back to childhood maltreatment and adversities (Berens et al. 2017). There is close association of physiological mechanisms with the psychological well-being. For example, during anxiety, there is heightened autonomic activity, which is manifested in the form of dryness of mouth, palpitation, tachycardia, increased sweating, and tightness of the muscles. Similarly, during depression there is activation of hypothalamic-pituitary-adrenal (HPA) axis. The relationship of physical and psychological well-beings is bidirectional, one affecting the other. It possibly explains long-standing medical conditions (e.g., most of the lifestyle-related disorders)

commonly have comorbid psychiatric disorders like depression and anxiety disorders. On the other way round, psychiatric disorders like depression, anxiety disorders, schizophrenia, and bipolar affective disorder are associated with metabolic syndrome and increased risk of diabetes, heart diseases, as well as stroke.

Physiological mechanisms are targeted in certain therapeutic interventions. Aerobic exercises, relaxation exercises, yoga, meditation, and related activities produce positive health effects by regulating the physiological mechanisms of the body. Biofeedback therapy uses the signals from various physiological parameters (heart rate, temperature, respiratory rate, skin conductivity, muscle contraction, electrophysiology of the brain) and gives feedback to the individual, who attempts to voluntarily control over the altered physiological mechanisms (Jung et al. 2012).

Conclusion

Many alterations in the physiological mechanisms of the body can be altered through lifestyle modifications. Hence, lifestyle-related disorders and many other noncommunicable diseases can be prevented by healthy lifestyles. Understanding the physiological mechanisms will help in the prevention of illness and restoration of wellness.

Cross-References

- Homeostasis
- Physiological Responses

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Physiological Responses

► Physiological Mechanisms

Physiology

► Evolved Physiological Reactions

Physiology of Language

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Synonyms

Physiology of reading processes; Physiology of speech articulation; Physiology of speech perception

Definition

Physiology of language refers to the organic processes and phenomena associated with speech perception, articulation, and reading.

Introduction

Comprehending and producing linguistic utterances relies on complex phonological, syntactic, and semantic representations that we incrementally and unconsciously build as the message unfolds in time. Behind these cognitive mechanisms there are physiological processes that drive visual and acoustic perception of linguistic stimuli and the production of sounds. In the following, the main principles underlying the physiology of speech perception and articulation as well as of reading abilities will be described.

Physiology of Speech Perception

Speech perception can be defined as a series of computations that take continuously varying acoustic waveforms as input and output discrete representations that are mapped onto lexical representations stored in long-term memory (Poeppel et al. 2008). It is known from linguistic research that mapping sound to meaning is a process that spans across several levels of representation and analysis. The smallest unit of analysis of the acoustic signal is represented by features, which reflect the articulatory basis of speech and encode independently controllable aspects of speech production, (e.g., $[\pm\text{voice}]$ indicates laryngeal involvement). Combinations of features make up segments, i.e., individual phones like $[p]$, $[s]$, or $[t]$. Segments that contrast with each other in nearly identical environments are called phonemes, such as $[t]$ and $[p]$ in *ten* and *pen*. In turn, phonemes are organized in syllables, the structure of which presents language-specific properties. Featural, segmental, and syllabic levels of analysis provide the infrastructure for prelexical phonological analysis and a prerequisite for mapping sound to meaning.

Central in speech perception research is the study of how listeners are able to identify and recover the sequence of phonetic segments that compose words and phrases, to ultimately comprehend a spoken utterance. Besides cognitive mechanisms, this engages complex processes at the physiological level. Thanks to modern

electrophysiological and neuroimaging techniques, much has been learned about the auditory areas and processing correlates associated with speech perception (see Friederici 2002, 2011 and Price 2012 for a review), but the understanding of the basic physiological and brain mechanisms of auditory processing still rests on animal (i.e., non-human primates) models.

Sound carries energy through the air at a speed of 340 m/s: ears capture this energy and transduce it into electrical signals that are analyzed by the nervous system. The first structure involved in this complex process is the external ear, which captures sound and channels it to the tympanum (or eardrum). The mechanical energy carried by air determines the motion of three small bones in the middle ear – the malleus (or hammer), the incus (or anvil), and the stapes (or stirrup). In particular, the stapes acts as a piston that pulls and pushes cyclically on the fluid-filled compartments of the cochlea in the inner ear.

Since the days of Helmholtz (1885) and Von Békésy (1960), it has been known that sound reaching the tympanic membrane triggers a traveling wave along the basilar membrane of the cochlea. This membrane acts as a mechanical frequency analyzer that distributes energy to hair cells arranged along the membrane length, based on the various tones that make up the acoustic stimulus. Low frequency sounds excite basilar membrane motion near the apex, where the membrane is thicker. Medium-frequency sounds excite the membrane in its middle, while high-frequency sounds excite the base of the membrane, where it is thinner.

Hair cells in the membrane transduce the basilar membrane oscillations into receptive potentials, and the neurochemicals that are released are picked up by the neurons of the eighth cranial nerve, which terminates in the cochlear nuclear complex in the brain stem. The complex auditory pathways of the brain stem mediate functions such as the localization of sound sources and the forwarding of auditory information to the primary auditory cortex (also called A1), in Heschl's gyrus. This region contains tonotopic maps, with neurons tuned to low frequencies arrayed in the rostral end of the area and those tuned to high frequencies at the caudal end.

The primary auditory cortex is surrounded by several distinct regions involved in the elaboration of specific types of acoustic information. Recent functional neuro-imaging studies have shown that auditory processing of speech and nonspeech stimuli activates the superior temporal gyrus bilaterally (Friederici 2011; Hickok and Poeppel 2007; Price 2012), including and surrounding Heschl's gyri. In contrast, selective activations to phonological analysis of speech sounds have been found both in the posterior portion of the left superior temporal gyrus and in the left inferior frontal and premotor areas, typically associated with articulatory processes, thus suggesting a tight interaction between acoustic and articulatory processes.

Successful mapping of familiar sounds to meanings (at the word and sentence level) has been shown to involve several left-lateralized areas. Recently, Hickok and Poeppel (2007) have proposed that mapping of sound to meaning involves a ventral stream that extends from the middle and posterior portion of the superior temporal sulcus bilaterally to the left anterior portion of the middle temporal gyrus. Moreover, anterior temporal areas appear to be recruited in accessing increasingly specific semantic associations, with activations for sentences and narratives extending to the temporal pole. In contrast, ventral inferior frontal regions, such as the pars orbitalis and triangularis, seem to be engaged in operations of selection and retrieval of semantic representations (Zhuang et al. 2011; Whitney et al. 2011).

Electrophysiological and magneto-encephalographic studies have shown that acoustic-phonological analysis of the input takes place as early as 100 ms after stimulus onset, as evidenced by two early negative components – the N1 and the mismatch negativity – associated with discrimination of vowel category perception (Näätäneiv et al. 1997; Obleser et al. 2006, see Luck 2014 for a review of auditory components). Their neural sources have been located in or close to the primary auditory cortex, suggesting that these processes occur at the earliest stages of speech perception.

Lexical analysis of the acoustic input is reflected by another electrophysiological

component peaking around 400 ms post-stimulus onset – the N400 (Kutas and Federmeier 2009 for a review) – the neural sources of which have been identified in the posterior portion of the temporal cortex (Lau et al. 2008). Moreover, the same component has been found to reflect processes of discourse integration at the sentence level (Halgren et al. 2002; Lau et al. 2008; Mancini et al. 2011; Tse et al. 2007).

The analysis of the syntactic structure underlying sentences has been associated with both early and late electrophysiological components. An influential model of auditory sentence comprehension (Friederici 2002, 2011) proposes that processes related to phrase-structure building are reflected in early left anterior negative (eLAN) effects, arising as early as 150 ms post-stimulus onset. Phrase-structure building mechanisms are followed by the establishment of grammatical relations, such as agreement between subject and verb, and would be reflected by anterior negative effects (left anterior negativity, LAN) between 300 and 500 ms. In the same temporal window, the elaboration of semantic relations among sentence parts would take place, as evidenced by N400 effects in response to thematic role assignment anomalies. Finally, the P600 component reflects the integration of formal and semantic information to assign an overall propositional meaning to a sentence. It should be noted that the functional interpretation of the P600 has changed over time. Initially thought to reflect processes of syntactic reanalysis, repair, and integration (see review in Hagoort et al. 1999), it has been more recently associated with a wider range of linguistic manipulations, ranging from conflicts in the semantic-thematic fit between predicates and arguments (the so-called semantic P600 effect, see Kuperberg 2007 for a review) to domain-general conflict monitoring operations (van den Meerendonk et al. 2009).

Physiology of Speech Articulation and Production

Articulation refers to the process by which speech sounds are formed and produced. From a

physiological point of view, articulation is the result of the coordination of muscles in the respiratory, laryngeal, and articulatory systems. These systems regulate three basic processes involved in sound production: the generation of air pressure in the lungs, the regulation of vocal folds vibrations in the larynx, and the control of resonance in the articulatory system.

Prior to initiation of speech, during *inhalation* (or inspiration), thorax and lungs expand, resulting in the pressure inside the lungs dropping below atmospheric pressure. It is through air inflow that the two pressures are maintained at equivalent levels. During speech, lungs pressure is maintained nearly constant thanks to the action of inspiratory muscles that prevent excessive airflow and keep a long expiratory phase. In contrast, during *exhalation* (or expiration), the thorax reduces its expansion, resulting in an increase of pressure inside the lungs. As lung pressure is higher than the atmospheric pressure, air flows out. Inspiration and expiration comprise a respiratory cycle. At rest, between 12 and 15 respiratory cycles per minute occur. During speech (also called phonic respiration), inhalation time is reduced while exhalation time is prolonged.

The air that is exhaled passes through several parts of the respiratory tract, such as the trachea and the larynx. The larynx is a sound producing organ that contains two pyramid-shaped muscles – the vocal folds – the vibration of which allows voice production. Four stages are involved in voice production, each of which comprises different positions of the vocal folds and different levels of air pressure in the larynx. During *closure*, vocal folds are brought together by laryngeal muscles. The accumulation of air below the folds (called subglottal pressure) produces a *compression* that forces vocal folds apart, leading air to flow out during the *release* stage. During speech, vocal folds vibration does not remain constant but is controlled by the speaker, based on his/her articulatory intentions. Increase in the frequency of vibrations determines voice pitch increase.

Speech articulation relies on processes carried out during the expiratory phase and consists of continuous changes in vocal fold vibration. Articulatory organs alter the resonance of the vocal

tract, making it possible to produce consonant sounds of different types. The most important articulator is the tongue, the deformation and movement of which determine vowel quality and the production of certain consonants: palatals (y in “yes”), velars (g in “guy”), and pharyngeals (typical of Arabic dialects). Dental (t in “time”), alveolar (s in “soap”), and retroflex consonants (r in “North America”) depend on the movement of the tongue blade and apex. Lips assist in the production of labial consonants (b in “beer”) and vowels (like u), while the velum controls opening and closing of the velo-pharyngeal port, allowing for the distinction between nasal and oral sounds. Articulation of vowels and back consonants (consonants articulated in the velum and farther back) engages pharyngeal muscles, which contract and thus adjust the width of the pharyngeal cavity.

As speech articulation involves the sequencing of a series of sound events, it often results in the articulation of one sound affecting that of another sound. This process is known as *coarticulation*. An example of coarticulation is represented by the production of the sound [k] before the vowel [i] in English, such as in *keys*, or the [k] sound articulated before [ow] in words like *cold*. In the first case, the place of articulation of [k] is palatal, while the second [k] is articulated farther back and gives rise to a velar sound. These adjustments are made before the articulation of the vowel in question and can extend across syllables and word boundaries.

A number of techniques have been developed to study speech articulation. One of these is palatography, which consists in recording contacts between the tongue and the palate to get articulatory records for the production of speech sounds (see Ladefoged 1997 for a description of the technique). Marker-tracking techniques include X-ray microbeam systems, which track small metal pellets attached on the articulatory organs, and magnetic sensing systems, which use small sensor coils to detect alternate magnetic fields with different frequencies.

Neuro-imaging studies have also been profitably employed in the study of speech articulation. The processes involved in speech production

largely overlaps with the mechanisms engaged in speech comprehension (Price 2012): sub-articulatory processing may be involved in discriminating auditory words, while auditory images may be automatically involved in articulation. In line with this, it has been suggested that a dorsal stream projecting from the superior temporal gyrus towards inferior parietal and posterior frontal lobe regions could be involved in auditory-motor integration, by mapping acoustic speech sounds to articulatory representations Hickok and Poeppel (2007). The overt articulation of speech sounds also involves sensorimotor activity in the pre- and post-central regions that control orofacial muscles as well as thalamic and left insula regions for the control of laryngeal activity, phonation, and breathing (Price 2012).

Physiology of Reading

For millions of years humans have spoken and understood language, but their ability to read has developed relatively recently (about 5000 years ago). From a psycholinguistic perspective, reading has been therefore considered as a secondary process that recruits neural circuits and mechanisms previously developed during the learning of auditory language. In line with this evolutionary view, results from a number of neuro-imaging studies have evidenced that there are no brain areas specific to reading. Rather, learning to read implies establishing associate connections between object processing areas in the visual cortex and speech processing areas in the temporal and frontal cortices (Price et al. 2001). Three specific processes are associated with reading that differentiates it from spoken language comprehension: the identification of visual features that are relevant to define letters, the subsequent identification of the whole word form, and the conversion of orthographic to phonological information.

Readers go through a text with rapid movements – *saccades* – that bring peripheral visual input onto the central part of the eye retina, the fovea. Between saccades, *fixations* occur, during which the eyes remain relatively still on a word for

about 200–300 ms. The average duration of a saccade during reading is about 30–50 ms, while the time it takes to plan and execute a saccade (latency) is about 150–175 ms (although both latency and duration can change depending on whether reading is silent or oral, see Rayner 1998 and Rayner and Castelhan 2007 for an overview), which suggests that saccade programming could be done in parallel with comprehension processes in reading (Rayner 1998). Eyes are never completely still, and other types of small movements occur during fixations. A constant tremor of the eyes (the *nystagmus*) serves to keep the nerve cells of the retina firing, while small and slow *drift* movements are thought to be due to an imperfect control on the oculomotor system by the central nervous system. To bring the eyes back to where they were before the drift, small and rapid eye movements, called micro-saccades, occur (a thorough review can be found in Gilchrist, 2011 and Martinez-Conde et al. 2009).

Visual processing begins in the retina. Light, focused by the cornea and the lens, traverses the vitreous humor that fills the eye cavity and finally reaches the retina and the fovea. Subsequently, it is absorbed by visual pigments in the photoreceptors, triggering a series of neurochemical reactions that lead to a change in the membrane potential of these cells.

The output of the retina is conveyed by ganglion cells, which depart from the optic disc and form bilateral optic nerves that project to the optic chiasm. Optic nerves project to three main subcortical areas: the pretectum and the superior colliculus in the midbrain, and the lateral geniculus nucleus in the thalamus, each of which has a specific function. The retinal projection to the pretectal area is important for pupillary reflexes: for example, when light shines in one eye, its pupil gets constricted, and so does the pupil of the other eye. Saccadic eye movements are controlled by projections to the superior colliculus, while the lateral geniculus nucleus represents the main subcortical structure that carries information to the primary visual cortex.

In the primary visual cortex (also called V1), located in the calcarine fissure of the occipital

lobe, low-level perceptual analysis is carried out: the outlines of a visual image are analyzed and decomposed into segments of various orientations, like horizontal or vertical lines.

Some authors have argued that visual information resulting from low-level sensory analysis carried out in the primary visual cortex enters the so-called Visual Word Form Area (VWFA, Cohen et al. 2000; McCandliss et al. 2003; see Price 2012 for a review) in the left occipitotemporal cortex. A wealth of studies agree that this area is consistently activated by visual word processing across languages and orthographies, that activation is higher for written than spoken words, and irrespective of case and font of the letters. However, more recent findings point to a functional parcellation of the ventral portion of occipitotemporal cortex, with more posterior areas involved in visual feature extraction, while more anterior ones would subserve lexico-semantic processing of whole words (Price 2012).

Electrophysiological studies on word reading report the presence of a series of early components typically related to the analysis of the features and parameters that characterize a visual stimulus, such as words, faces, and pictures in general (see Pratt et al. 2011 for a review of sensory electrophysiological components): the P1 (a positive component peaking about 110 ms after stimulus onset); the N1/N170 (a negative component peaking about 180 ms after stimulus onset, see Rossion and Jacques 2011), and the P2 (a positive component peaking about 280 ms post-stimulus onset). Of particular interest is the N170, typically associated with expert scrutiny of face (Carmel and Bentin 2002), which has been recently reported in studies comparing the effects of orthographic and nonorthographic processing (see Maurer and McCandliss 2008 for a review).

Conclusions

The study of language and of the mechanisms underlying its processing has advanced significantly and steadily over the last years, thanks to cutting-edge techniques and experimental paradigms that have made it possible to observe

physiological processes and neuro-anatomical substrates in controlled laboratory settings. Nevertheless, several challenges remain to be faced, the most important of which is arguably represented by the study of these mechanisms in the most ecologic and naturalistic setting, namely human-to-human interaction.

Cross-References

- [Auditory Neurobiology](#)
- [Auditory Perception](#)
- [Auditory System](#)
- [Human Visual Neurobiology](#)
- [Neurobiology of Language](#)
- [Physiological Mechanisms](#)
- [Vision](#)

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Physiology of Reading Processes

► Physiology of Language

Physiology of Speech Articulation

► Physiology of Language

Physiology of Speech Perception

► [Physiology of Language](#)

Physique

► [Strength and Anger-Proneness](#)

Picture Brides

► [Mail-Order Brides](#)

Pidgins and Creoles

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Synonyms

[Mixed languages](#)

Definition

A pidgin is a mixed language that emerges as a new medium of communication among speakers with distinct first languages.

A creole is a nativized mixed language.

Introduction

This chapter focuses on theories of creole genesis, elaborating on various scenarios accounting for the emergence and development of creole languages. First, we draw a distinction between pidgins and creoles and discuss the connections between the two, including the supposed pidgin-

to-creole cycle. Then, we introduce the superstratist, substratist, and universalist views of creole genesis and elaborate on the most recent theories that instantiate these different positions. We focus on processes of second language acquisition (Plag 2008), relexification (Lefebvre 1998), language creation (Baker 1994), and feature recombinations (Mufwene 2001; Aboh 2006).

On the Nature of Pidgins and Creoles

Pidgin and creole languages are considered “mixed” languages in the sense that they cannot be traced back to a single earlier language (Thomason 2008, p. 271), due to the multilingual context in which they emerge. These languages typically develop in plantation, trade, and other work settings where speakers with different first languages (henceforth, L1s) are in contact with each other for an extended period of time and create a new language for the purpose of communication.

It is often assumed that in the beginning stages of interaction between speakers with distinct L1s, they create a rudimentary pidgin that turns into a creole after it becomes nativized, meaning after it acquires native speakers. As with any natural language, creoles are elaborate, sophisticated, and complex linguistic systems, in comparison to pidgins. As a result, some creolists view adults as the original creators of pidgins and children as the creators of creole languages.

Things are not, however, that simple as the pidgin-to-creole cycle, and the nativization criterion are not generalizable to all cases of creole formation. On the one hand, there is indeed evidence that some creoles like Hawaiian creole first developed as a pidgin (Hawaiian Pidgin English) spoken by the Japanese, Portuguese, and Tagalog plantation workers (among others) before it became nativized and turned into Hawaiian Creole English (Bickerton 1984). On the other hand, there is no evidence that creoles in the Caribbean for instance (i.e., Jamaican) have been through a pidgin phase, suggesting that both children (in the Hawaiian case) and adults (in the Jamaican case) can be agents of creolization. Numerous factors

such as population demographics, settlement vs. plantation colonies, access to the dominant language, and power relations between the languages in contact may determine whether adults or children are the original contributors to creolization. In sum, this greatly depends on the socio-historical context in which a given creole emerges. Also, it is not always the case that pidgins are deprived of native speakers. Indeed, the extended pidgin Tok Pisin (in Papua New Guinea), which has been in use for a long period of time over a large territory, has now developed native speakers and can no longer be considered a pidgin by the strict definition of the term.

On the Superstratist, Substratist, and Universalist Views of Creole Genesis

As for the linguistic properties of creole languages, scholars agree that their lexicon is mostly derived from the superstrate (the socioeconomically dominant language). There is, however, no consensus as to the source of their grammatical structures. Some scholars argue that most of the grammatical structures found in a given creole derive from the superstrate that contributed to its genesis; this is the superstratist view. In contrast, other linguists believe that the original creolophones' first languages (substrates) mostly contributed to the grammatical structure of creoles; this is the substratist view. Finally, there are linguists who believe that it is not the source languages but rather language universals that are responsible for their most salient grammatical traits. This view rests on the assumption that creoles share similar properties and that children are the primary agents. Bickerton (1984) has proposed that due to the chaotic linguistic environment in which the original creolophone children are born, they cannot rely on consistent, stable input from a given language to proceed with a regular type of acquisition. Consequently, these children are dependent on a language bioprogram which is a biological blueprint consisting of unmarked settings. This is the universalist view. Bickerton offers a cluster of linguistic properties

that he argues are found in the most radical creoles. He claims for instance that tense, mood, and aspect markers (among other features), typically found in preverbal position (see the aspect marker *sta in* (1)), are signs of the bioprogram. Such markers convey temporal, modal, and aspectual meaning and appear just before the verb, rather than as inflections on the verb stem, as in Portuguese (2):

- (1) *N sta bai kaza.* (Cape Verdean Creole)
I ASP go home
"I am going home."
- (2) *Será que você iria para a sua casa.* (Portuguese)
be+Inflection that you go+Inflection for your house
"May be you would go home."

Similar views arguing for a creole prototype can be found in McWhorter (1998) and Bakker et al. (2011), among others.

Current Theories of Creole Formation: The Interlanguage Hypothesis, Relexification, Language Creation, and Feature Recombinations

We now delve into current theories, which build on the positions just discussed. For Plag (2008), the genesis of creoles is linked to processes of second language acquisition, as he views them as conventionalized interlanguages of an early developmental stage. According to this view, labeled the "interlanguage hypothesis," some creole properties such as SVO word order, preverbal negation, and sentence-initial *wh*-words can be best accounted for in light of processability. Plag backs this proposal by referring to developmental stages in English interlanguage syntax which typically displays the canonical word order SVO, as in "Bob kick ball", preverbal negation as in "he no like coffee" and the sentence-initial *wh*-word as in "where is John?". The fact that the set of creoles Plag examines shares the same features as interlanguage syntax led him to propose that

creoles are conventionalized interlanguages but this view is problematic on two fronts:

- (a) For processes of second language acquisition to be involved, one would have to assume that early creolophones had access to the superstrate. If this is the case, why don't we observe properties across creoles that reflect more consistently the features of their respective superstrate in the domains of word order, negation, or *wh*-words among others? What happens in the cases where the length of contact between early creolophones and colonists were fairly short due to massive influxes of slaves on sugar or cotton plantations? This would mean that the majority of the population would not have had access to the superstrate, hence second language acquisition would not have happened.
- (b) The "interlanguage hypothesis" also implies that interlanguage features can be found in the majority of creoles. This is not the case, based on the *Atlas of Pidgin and Creole Structures* (Michaelis et al. 2013) which reports a number of creoles as departing from the typical SVO word order and as displaying sentence-final *wh*-words, and sentence-initial or sentence-final negators, contrary to the predictions of the interlanguage hypothesis.

Another theory of creole genesis is relexification (Lefebvre 1998), which assumes that a creole lexicon originates from the superstrate but its syntax and semantics have their source in the creole substrates. This division of labor is represented in the schema in (3) which conveys that the lexicon (or phonology) of the original speakers' L1 was replaced by the lexicon of the superstrate but the semantics and syntax of their L1s were preserved.

- (3) /phonology/i/phonology/j
[semantic feature] i
[syntactic feature] i (Lefebvre 1998: 41)

This is illustrated in the Haitian "weather" expression in (4). The Haitian

weather construction is parallel to its Fongbe counterpart in (5) but distinct from its French equivalent in (6). Such examples allow Lefebvre to propose that the Haitian lexicon originates from French, whereas the syntax and semantics were derived from Fongbe:

- (4) *Lapli tonbe*. Haitian (Lefebvre 1998: 72)
Rain fall
"It is raining."
- (5) *Ji ja*. Fongbe (Lefebvre 1998: 73)
Rain fall
"It is raining."
- (6) *Il pleut*. French (Lefebvre 1998: 73)
It rain
"It is raining."

This theory has been criticized for granting too much importance to the grammar of the speakers' L1 at the expense of the superstrate's. It also postulates a clear-cut division of labor that is not always observable, as substrates can contribute to the lexicon of a creole and superstrates to its grammar and semantics. Relexification is considered a substratist theory.

The third theory we examine is language creation, as presented in Baker (1994). According to this theory, the original creole speakers were not motivated to target the superstrate, their main priority being to simply devise a "medium of interethnic communication" (Baker 1994). As the superstrate was not a target, this would account for the original speakers' creativity, as they did not replicate nor transferred faithfully the features in the source languages to the creole but instead fostered innovations that cannot be found in any of the languages in contact. For instance, speakers avoided homophony in Mauritian Creole by designing a lexicon where the use or absence of determiners helped distinguish between two words that would otherwise be homophonous in the language. For instance, in (7a), the word for "health" is distinguished from the word for "song" in (7b) by appending the definite determiner *la* to *santé*.

- (7) a. *lasanté* “health” (Fr. la santé) (Baker 1994: 72)
 b. *santé* “song” (Fr. chanter, v.)

Such innovations are not traceable to any of the source languages and led Baker (1994: 75) to argue that this is an evidence that original creolophones were more involved in creating a new language for the purpose of communication than in learning a second language.

We now turn to the theory of feature recombinations. Developed within a framework of competition and selection (Mufwene 2001), this theory is meant to illustrate the competition between features from distinct source languages, resulting in winners and losers. We consider below examples from Aboh (2006) in which he analyzes how features are recombined, proposing a modular view of feature transmission. According to this view, features from the languages in contact can recombine following a variety of paths. In some cases, the semantics and syntax of a given feature originate from the same source; in other cases, the semantics of a feature comes from the superstrate and the syntax from the substrate(s) or vice-versa. Specificity in Haitian Creole illustrates a case where the syntax and semantics of a feature come from a single source: Haitian uses a demonstrative realized as *a* or *la* to express specificity; such a marker appears to the right of the noun (8a). Gungbe (one of Haitian Creole’s substrate) also uses a specificity marker to the right of the noun (Aboh 2006), as in (8b). In both languages, the marker refers to an aforementioned entity. In contrast, the French determiner in (8c) appears in a pre-nominal position (to the left of the noun) and may refer to an aforementioned entity *or* to the entity the speaker and hearer know of (Aboh 2006: 225). Due to the exact parallelisms in syntax and semantics between Haitian and Gungbe, Aboh proposes that Gungbe is the source of both the semantics (marking specificity) and of the syntax (post-nominal position) of the marker *a/la* in Haitian Creole.

- (8) a. *Pè-a* (Haitian Creole)

Priest-Det

“The aforementioned priest”

*“The priest that we know of”

- b. *Mɔpɛ ɩ* (Gungbe)

Priest-Det

“The aforementioned priest”

*“The priest that we know of”

- c. *Le prêtre* (French)

“The aforementioned priest”

“The priest that we know of”

Conclusion

In conclusion, the different scenarios of creole genesis delineated above are tenable if one refrains from generalizing them to all creoles. For instance, the feature recombinations analysis seems quite valid in accounting for features of Haitian Creole but may find limitations in accounting for creoles that have remained in close contact with their lexifiers, resulting instead in a situation akin to second language acquisition (Chaudenson 2001). It is difficult to generalize a given scenario to all creoles because they have distinct demographics, histories, lengths of contact between the source languages, and different power relations between source languages. Scholars should therefore take such variables in consideration before proposing which of the scenarios presented above best accounts for the development of the creole they examine. In sum, the history of a given creole determines which scenario best fits its development.

Cross-References

- [Interactive Language Development](#)
- [Language](#)
- [Language Acquisition](#)
- [Language Development](#)
- [Spontaneous Language](#)

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Piercings

- [Body Modification](#)
- [Human Ornamentation](#)

Pinker and Chomsky

- [Language Instinct, The](#)

Pinker Evolutionary Psychology

- [How the Mind Works](#)

Pinker's (1994) The Language Instinct

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Synonyms

[Linguistic nativism](#); [Noam Chomsky](#); [Psycholinguistics](#); [Steven Pinker on language](#); [Steven Pinker on universal grammar](#)

Definition

A popular science text in evolutionary psycholinguistics asserting the innateness of language in humans and the theory that grammar reflects the linguistic organization of the mind.

Introduction

The Language Instinct is a wide-ranging book on language by cognitive psychologist Steven Pinker. The book gives an account of how the brain acquires and understands language and addresses various topics in linguistics and evolutionary psychology, such as the existence of universal features of language and the possible genetic basis of linguistic ability in humans. Throughout the book, Pinker asserts that the science of language can provide key insights into human cognition.

Pinker argues for a “nativist” view of language development, whereby the ability to acquire language is innate. On this view, humans possess a “mental module” specifically dedicated to learning language and understanding natural speech. Drawing on the theory developed by linguist Noam Chomsky, Pinker asserts that all humans are equipped with a Universal Grammar, which

explains how young children are able to extrapolate grammatical rules to form and understand novel sentences. The nativist position typically opposes the “blank slate” or “empiricist” thesis, which broadly states that people are born knowing nothing but are capable of learning anything.

Throughout *The Language Instinct*, Pinker refutes several common misconceptions about language, such as the belief that in general peoples' grammar is poor and language is deteriorating, that human thought is constrained by language, and that language must be explicitly taught to children.

Universal Grammar and Innateness of Language

Citing work done by Chomsky and experimental psycholinguists, Pinker argues for the universality of language and grammar in neurologically normal individuals. Pinker first notes that no mute civilization has ever been discovered; moreover, all languages, as well as dialects, exhibit complex grammatical structure.

Second, the phenomenon of creolization, or the standardization of a grammar-less pidgin language, suggests that children are able to “inject grammatical complexity where none existed before.” Pinker cites studies by Derek Bickerton on communities of immigrant laborers brought to work on Hawaiian sugar plantations. Having no shared language, the laborers developed a makeshift “pidgin” language, devoid of consistent word order, tense and logical markers, or complex structure. Yet children exposed to the pidgin used standardized grammatical markers in their speech that were both absent from the pidgin of their parents and distinct from the language of the colonizers, thus inventing Hawaiian Creole (1981, 1984). Grammatical standardization can also be observed in deaf children, as, for example, in the case of Nicaraguan Sign Language: younger children who were exposed to the pidgin signing of older children spontaneously introduced grammatical devices absent in the earlier version of the signing system (Kegl and Iwata 1989).

Third, the human brain must be using a mental algorithm to understand and construct new sentences, as opposed to building a “repertoire of responses” learned through rote memorization. Only the existence of a mental grammar explains why children are able to quickly learn the language of their parents, draw reliable conclusions about the meanings of new words, and generalize rules of grammar to produce new constructions which they have never heard (a line of reasoning which Chomsky called the “argument from the poverty of input”).

Pinker notes that the way mothers often speak to their infants, a style of speech he calls *motherese*, is devoid of constructions children are already able to grasp in early childhood, such as turning sentences with two auxiliaries into questions – for example, “A unicorn is in the garden” to “Is a unicorn the garden?” Therefore, these grammatical intuitions cannot have been learned from the child's environment.

The Myth of Degenerating Language

In the chapter titled *Language Mavens*, Pinker describes the arbitrary origins of many “rules” of style and syntax often promoted in writing manuals. Pinker demonstrates that the manipulations of language deplored by “legislators of ‘correct English’” are not only logical, but often serve to make language more rather than less complex. For example, converting nouns to verbs (i.e., *grandstand*, to *grandstand*) admits of an addition to the “mental dictionary,” since verbs constructed from nouns adopt regular conjugations, even when the verb base is itself an irregular verb (i.e., *he grandstanded*, not *he grandstood*). Meanwhile, the root noun retains its function as a noun.

Citing linguist William Labov (1969), Pinker also illustrates that dialects that deviate from the standard grammar of a language are no less grammatical, and they only employ modified grammatical rules. As an example, Black English Vernacular (BEV) possess a full inventory of rules for grammatical manipulations such as forming contractions, inverting sentences, and inventing subjects and auxiliaries (i.e., *Don't nobody know*).

Mentalese

In the chapter titled *Mentalese*, Pinker refutes the hypothesis that thought is identical to or constrained by language, a theory called “linguistic relativism,” or “linguistic determinism” and famously associated with linguists Edward Sapir and Benjamin L. Whorf (Carroll 1956; Kay and Kempton 1984). “People do not think in English or Chinese or Apache,” says Pinker, “they think in a language of thought,” which he calls *mentalese*. Pinker argues that this language of thought is a symbolic system, whose parts can be arranged and rearranged to produce intelligent conclusions, but that these symbols are not necessarily linguistic.

Pinker illustrates the distinction between language and thought by demonstrating that our ability to communicate or compute meaning from sentences is not constrained by the limitations of a given language: a speaker may use a phrase with an ambiguous word, but the underlying idea is *not* ambiguous. Similarly, readers are able to overcome ambiguities in speech or in written text, as in the headline “Drunk Gets Nine Months in Violin Case” (Seidenberg et al. 1982).

Design of Language

Pinker notes that a remarkable feature of grammar is that it allows an infinite number of possible sentences to be constructed from a finite set of symbols. Grammar can thus be described as a “discrete combinatorial system” (Chomsky 1991).

In the chapters *How Language Works* and *Words, Words, Words*, Pinker introduces theories of phrase structure and word structure, illustrating certain universal rules for forming sentences (Jackendoff 1977) and words. Pinker then discusses results from studies in psycholinguistics and cognitive neuroimaging that recommend these theories as models for the mental representation of language. Psycholinguist Peter Gordon, for example, showed that children intuitively reason that compound words can be formed from irregular plural nouns, but not from regular plurals

(i.e., *mice-infested* and *rat-infested*, but not *rats-infested*) (1986).

In another study, ambiguous words or parts-of-speech were shown to activate multiple meanings in the brains of listeners, suggesting that a “mental parser” searches through possible interpretations of words in real time before selecting the correct one for a given context (Swinney 1979).

Evolution and Language

Pinker deviates from Chomsky's position on the human language faculty in that he believes evolutionary theory can explain the development of the language instinct in modern humans.

Pinker applies concepts from Darwinian theory to address several questions about language, such as (i) why there exists a critical period for language acquisition, after which language acquisition becomes significantly more difficult or impaired; (ii) why language is unique to humans; and (iii) why there exists more than one language.

- (i) The critical period for language acquisition can be explained, Pinker says, by considering the benefits and costs of maintaining a mechanism for language acquisition: the skill confers an overwhelming benefit for a young individual, but incurs a great metabolic cost. Once language has been acquired, the skill becomes superfluous.
- (ii) Pinker argues that language, though not communication, is unique to humans in the modern animal kingdom. Despite the efforts of animal researchers to “translate” chimpanzee signing, for example, chimpanzee communication remains devoid of basic features of language such as syntax or vocabulary. (Terrace et al. 1979).
- (iii) According to Pinker, the proliferation of languages across the globe is explained by three major processes: linguistic innovation (the combinatorial creativity of language), the ability to learn, and migration (by which populations diverge over time). However, the similarities among different languages far outnumber, according to Pinker, the

differences between them. Paraphrasing Chomsky, he notes, “a visiting Martian scientist would surely conclude that aside from their mutually unintelligible vocabularies, Earthlings speak a single language.”

Conclusion

Pinker’s *The Language Instinct* has remained an influential work in popular psychology and is still among his best-known publications. Many of the concepts introduced in the book, including the innatist argument for language development, theories on word and phrase structure, and the fallacy of linguistic determinism are addressed in greater detail in subsequent books *Words and Rules: The Ingredients of Language* (1999) and *The Stuff of Thought: Language as a Window into Human Nature* (2007). Pinker’s opposition to the empiricist view of language development and the “Standard Social Science Model” of human nature is also a major focus of *The Blank Slate: The Modern Denial of Human Nature* (2002).

A recent edition of *The Language Instinct*, published in 2007, includes an additional section after the main text in which Pinker revisits each chapter and briefly discusses new research or addresses public and critical reception on the ideas presented.

Cross-References

- [Field of Linguistics, The](#)
- [Language Acquisition](#)
- [Language Development](#)
- [Nativism](#)
- [Noam Chomsky and Linguistics](#)
- [Steven Pinker](#)
- [Steven Pinker and Language Development](#)
- [Universal Grammar](#)

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Placental Proteins in Semen

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Definition

Seminal fluid contains dozens of compounds that affect male fertility, but may also affect female reproduction and physiology. Pregnancy related compounds have been discovered in seminal fluid

and appear to affect the female immune response and embryo implantation.

Introduction

Semen is a reproductive fluid, and as such it has been selected over generations to not only transport sperm, but also increase the probability of conception and maintain a resulting pregnancy (Burch and Gallup 2006). Researchers in the past 30 years have learned that seminal fluid contains ovulation induction factors, immunosuppressants, endogenous opioids, stress hormones, myotonia enhancing compounds, affiliative hormones, pregnancy maintaining hormones, and potential mood enhancing hormones and neurotransmitters (Burch and Gallup 2006; Gallup et al. 2002). Researchers have also administered many of these hormonal compounds through the vagina and determined high levels of absorption that elevated blood levels for hours after administration (Villanueva et al. 1981; Schiff et al. 1977).

Seppälä et al. (1985) found a number of pregnancy associated proteins in follicular fluid and seminal plasma. Since then, a variety of placental and pregnancy related proteins and compounds, including human chorionic gonadotropin (de Medeiros et al. 1992; Asch et al. 1984), human placental lactogen, pregnancy-specific beta 1-glycoprotein, placental proteins 5, 12, and 14 (Seppälä et al. 1985), pregnancy associated plasma protein (Bolton et al. 1986), relaxin (MacLennan 1991), vasopressin (Ney 1986), and ferritin (Brotherton 1990) have been found in human seminal plasma. In many cases their concentrations in follicular fluid and seminal plasma greatly exceeded those in the serum of non-pregnant women or men, and sometimes they even exceeded pregnancy levels (Seppälä et al. 1985). Concentrations of beta- human chorionic gonadotropin and luteinizing hormone were highly correlated with the numbers and motility of sperm in ejaculates (de Medeiros et al. 1992). The levels of placental protein 5 in seminal plasma showed an association with sperm motility, suggesting that placental protein 5 may have a significant biological function in the maintenance

of sperm motility (Lee et al. 1983). Clearly, researchers have concentrated on how these compounds affect male fertility, but it is also possible that levels of ovulatory hormones, human chorionic gonadotropin, pregnancy related proteins, and other compounds can increase the probability of conception and pregnancy maintenance in women.

Relaxin is a polypeptide hormone produced in the human female by the corpus luteum and decidua during pregnancy. In the male, it is produced in the prostate and is present in human semen (MacLennan 1991). According to Stewart et al. (1990), relaxin is significantly elevated 9–10 days following ovulation in women and also increases 1–2 days prior to the first detectable increase in plasma human chorionic gonadotropin during pregnancy. Relaxin may have significant roles in sperm motility, fertilization, implantation, uterine growth and accommodation, the control of myometrial activity to prevent preterm labor, cervical ripening and the facilitation of labor (MacLennan 1991; Weiss 1995). Its role in pregnancy maintenance has yet to be fully elucidated, but relaxin in seminal plasma may act to manipulate the female reproductive cycle or facilitate pregnancy.

Hamberg and Samuelsson (1966) isolated the presence of 13 different prostaglandins in human semen over 50 years ago, but little research has focused on each. The most notable prostaglandins have been shown to be absorbed vaginally, namely E1, E2, and F2 α and more rapidly than other methods of administration (Sandberg et al. 1968). Certain prostaglandins, F1 α and F2 α , are active in the dissolution of the corpora lutea and in ovulation and these compounds cause powerful contractions of the uterus (Mackenzie 1988). Based on this information, it is possible that prostaglandins in semen are used to assist in ovulation. Other studies have shown prostaglandins to have immunosuppressive capabilities (Kelly 1995), which would assist in conception. Skibinski et al. (1992) found that that prostaglandin E1 and E2 exerted a greater immunosuppressive effect than 19-OH prostaglandin E, but considerably higher levels of 19-OH prostaglandin E in semen might contribute the majority of immunosuppressive activity *in vivo*. Thus, with the

presence of prostaglandins, immunological reactions would be inhibited for a period of time after intercourse. This may be important in embryo implantation (see below). Other suppressive agents are also present in semen and may exert specific effects (Kelly 1995). Maegawa and colleagues (2002) reported a repertoire of cytokines in seminal plasma. Each of these immunosuppressants may act in the female to temporarily lessen her immunological reaction to the foreign bodies (sperm) invading her vagina and cervix.

There are other compounds in semen that appear to play a vital role in the initiation in pregnancy. T regulatory cells are essential mediators of the maternal immune changes necessary for embryo implantation. Deficiencies in T regulatory cells are linked to unexplained infertility, miscarriage, and pre-eclampsia in women and male seminal fluid is a potent source of the T regulatory cell-inducing agents Transforming Growth Factor- β and prostaglandin E (Robertson et al. 2013). T regulatory cell-inducing cytokine Transforming growth factor and male alloantigens present in seminal fluid may be sufficient to induce a state of active immune tolerance to paternal alloantigen. This seminal fluid priming impacts fetal survival in later gestation (Robertson et al. 2009). Transforming growth factor- β and other cytokines and prostaglandins result in improved endometrial receptivity to the implanting embryo. Cytokines have embryotrophic properties and also contribute directly to the optimal development of the early embryo (Robertson 2005). Researchers continue to identify both new seminal compounds and new roles for existing compounds in female reproduction, while at the same time fertility researchers and practitioners continue to see the effects of seminal fluid in pregnancy outcomes (Robertson and Sharkey 2016).

Pregnancy Outcomes

Compounds defined by their pregnancy maintaining effects are present in semen, implying that repeated insemination after conception may play a role in producing positive pregnancy outcomes (see Davis and Gallup 2006 for review). Live birth rates in couples undergoing in vitro fertilization are

significantly improved when they engage in intercourse prior to embryo transfer (Tremellen et al. 2000) and treating women who suffer recurrent miscarriages with seminal plasma also improves pregnancy success (Coulam and Stern 1993).

Preeclampsia is a contributing factor to maternal mortality and perinatal morbidity and mortality (Klonoff-Cohen et al. 1989) and is more likely in pregnancies that occur by artificial insemination, a procedure that sometimes requires the separation of spermatozoa from the seminal fluid (Koelman et al. 2000). One of the major protective factors against preeclampsia appears to be repeated exposure to the father's semen; women who have limited exposure to the father's semen are at an elevated risk (Robertson et al. 2003) and the risk of preeclampsia is reduced by repeated (paternal) semen exposure over time (Klonoff-Cohen et al. 1989).

Conclusion

Human semen biochemistry appears to have been selected to suppress the female immune system and increase female sexual interest, bonding, the potential for orgasm, the probability of conception and pregnancy maintenance. Researchers continue to discover seminal compounds that affect ovulation, conception, and in particular, implantation and early pregnancy survival.

Cross-References

- [Induced Ovulation](#)
- [Semen Familiarity](#)
- [Seminal Plasma](#)

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Plain

- ▶ [Grasslands](#)

Planned

- ▶ [Strategic Aggression](#)

Plant Hybridization

- ▶ [Mendel's Experiments](#)

Platonic Jealousy

- ▶ [Jealousy](#)

Play

- ▶ [Boredom as an Adaptation](#)
- ▶ [Play Fighting in Boys](#)

Play and Social Learning

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Synonyms

[Learning](#); [Observation](#); [Performance](#); [Practice](#);
[Recreation](#)

Definition

Observing others leads to recreational mimicry of witnessed behaviors; this mimicry (i.e., play) is a form of practice that allows children to develop a greater understanding of social norms, societal rules, and how these norms and rules influence social behavior.

Introduction

Social learning and play are of the utmost importance in the development of individuals, not only along the extent of a single lifespan but also for the development and evolution of a species. Social learning is imperative for transmitting information from one generation to the next. Play is vital for the practice and development of new methods for a species to grow and advance.

Development Through Social Learning

Social learning can be thought of as a way to transfer information, not through genetic inheritance, but rather from a learning process that comes from observing behavior of other individuals (Mesoudi and Whiten, 2004). In his early works with Social Learning Theory, Bandura (1977) stated that social learning is helpful for individuals “to acquire large, integrated patterns of behavior without having to form them gradually by tedious trial and error” (p. 12). From this, it is easy to see that children observing successful adults can learn certain societal roles and behaviors, techniques to hone specific skills, and acquire the morals adopted by the culture in which they live. Bandura et al. (1961) showed that children watching adults tended to imitate the behaviors that the adults modeled for them. In their studies, they had adults commit either violent acts or nonviolent acts. Children watching violent behavior had a tendency to act much more aggressively while the children watching

nonviolent behavior had a much stronger tendency to act in a less aggressive manner. From an evolutionary perspective, it is very beneficial for children to observe their adult counterparts to learn successful strategies to achieve a specific goal. An example of this would be a child following a hunter for food. By observing how the hunter successfully stalks and kills prey, the child can then learn how to become a successful hunter. The same could be said for farming techniques to be able to efficiently produce the greatest amount of crops possible. As for learning cultural norms, social learning comes into play with how societies view gender roles. Traditional agentic and communal gender roles are passed from generation to generation by social learning. Moral judgments about what is right and wrong can also be passed down from generation to generation via social learning. An example of this could be stealing. By observing the consequences of what happens to an individual when they break societal norms, children learn what is considered acceptable behavior and develop morals along the lines of what works best for their society.

Importance of Play

While social learning is paramount for learning specific behaviors, play is equally important for the development of these behaviors. Play is a very important resource for children. Play allows children to reenact behaviors that they have witnessed and expand on what they have seen. Bandura et al. (1961) found that after children viewed violent behavior from adults, they were more likely to generate new ways of violent behavior. While they never observed an adult use a doll as a weapon, children would make use of the doll as a tool that in a way was unintended. This shows that play allows for the creation of new ideas. Children need play to practice the behaviors that they have learned by observing adults, but also children may create a new idea that is similar, yet different than what was modeled for them. These new ideas may be more efficient or help solve a new problem. It is

easy to observe how predatory animals use play to practice hunting techniques. The same could be said for the development of survival as humans grew as a species. Developing new ways to hunt with projectile weapons made hunting a much safer endeavor. Play is essential for the development of these new techniques. Play is also crucial for practicing roles that a society deems as important. An example of this could be seen in how children play “house.” This game allows children to practice gender roles in the specific society for which they are a part. Play is also important for the practice of acceptable moral behavior. This can easily be seen in the game “cops and robbers.” Robbers are “punished” for pretend crimes once the cops catch them.

Conclusion

As we can see, social learning and play are very important for the development of children and the development of a species. One generation learns behaviors by virtue of social learning from the previous and pass what they have learned onto the next generation. Play allows for the practice of old techniques and development of new practices to help advance the species.

P

Cross-References

- [Learning Versus Imitation](#)
- [Play Fighting in Boys](#)
- [Social Learning and Social Cognition](#)

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Play and Tool Use

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Synonyms

Construction play; Playful behavior; Social play;
Tool play

Definition

Play is a pleasurable activity conducted with no apparent purpose; tool use refers to the use of different objects in the service of a goal.

Introduction

Children's play has held notable allure to child developmental psychologists and educationalists for a number of years, and since the time of Groos (1898, 1901), at least, play has been thought out as a hallmark of childhood. According to other numerous play theorists, too, such as Piaget (1962) and Vygotsky (1978), play during childhood gives the opportunity to children to learn the skills they need for a successful and healthy functioning in adulthood. This section considers different approaches in terms of defining play, explains what object play is, and finally addresses the concept of tool use in childhood.

What Is Play?

Although when we see play, we can recognize its occurrence, putting forward an operational definition has not been an easy task. Given the complexity of the phenomenon, it is universally agreed that no one definition of play is necessary or sufficient; thus definitions are usually multi-dimensional. According to the functional approach, play does not have a clear external

goal or an obvious end in itself, neither clear immediate benefits to the individual (Smith et al. 2015). In fact, a "functional" way of perceiving play is suggested – play is performed rather for its own sake and for enjoyment instead of for any other external purpose (Smith et al. 2015). Therefore, if an external goal exists such as a need to seek comfort or attention, then the behavior cannot be considered as play (Smith et al. 2015).

Similarly, the structural approach is primarily concerned with behaviors present only during play or the way these behaviors are organized during playful activities (Smith et al. 2015). These behaviors are usually called "play signals" and could, for example, take the form of laughter or the "open-mouth play face" which both signal play (Smith et al. 2015).

The two approaches, although logically different, could be considered to be theoretically in parallel and complementary to each other; after all, the child running up and down the slope has no clear, immediate goal except from enjoyment (Smith et al. 2015).

Finally, another approach suggests that play or playful behavior can be identified through a number of different criteria (Smith et al. 2015). No criterion is adequate enough to define playful behavior, but the more criteria are present, the higher the agreement will be on that a behavior is play (Smith et al. 2015). Based on this premise, Krasnor and Pepler (1980) proposed a model, which suggests that playful behaviors are characterized by a form of "flexibility," "positive affect," "nonliterality," and "intrinsic motivation."

Object Play

Jean Piaget's (1952) theory of cognitive development suggests that young children's perception and understanding of the surrounding world depend on their motor development – a fundamental skill necessary for the young child to associate visual, tactile, and motor representations of objects. Specifically, the infant has to understand that objects exist even when they cannot be seen, touched, heard, or sensed in any other way – what we call "object permanence" – and this

understanding comes through touching and handling objects in different ways (Siegler et al. 2017). Although initially this is best expressed as exploratory, as the child progresses through the sensorimotor stage, which usually lasts from birth until 2 years of age, exploratory behaviors are repeated and thus, perhaps enjoyed – two criteria for playful behavior to be present (Smith et al. 2015). These behaviors become also more flexible, such as that some of them would easily be characterized as playful (Smith et al. 2015).

As Piaget's theory further suggests, young children during their first 2 years of life are primarily focused on the activities of their own body (Siegler et al. 2017). Once their attention shifts from basic body reflexes to the events of the surrounding world, the stage is set for the appearance of object play (Hughes 2010). Except from the infant's interest in the world around them, however, there is another requirement for object play to occur: the motor skills needed to allow the infant to grasp and handle play objects (Hughes 2010).

Object play refers to playful behavior involving the use of different objects such as building blocks, jigsaw puzzles, cars, dolls, etc. (Smith and Pellegrini 2013). For instance, when babies engage in play with objects, they usually mouth objects and then they drop them down, while toddlers manipulate the objects such as assembling blocks, or sometimes they pretend play such as feeding a doll (Smith and Pellegrini 2013). Over time, young individuals learn how to use other, more abstract objects to portray other objects (Pellegrini 2016). Play with objects gives the opportunity to children to create new combinations of actions as well as to advance their problem-solving skills (Smith and Pellegrini 2013). Indeed, of all the possible uses of objects, play with objects is most highly akin to creativity (Pellegrini and Hou 2011).

In modern societies, object play typically involves toys which are made to favor children's play by being created based on mass media prototypes (Smith 2009). There is a huge production not only of simple toys and objects such as building blocks, jigsaw puzzles, cars, dolls, and toy animals but also of toys used for pretending and

fantasy activities, such as farm sets, castles, trains, action figures, and action objects based on either older but ongoing or current TV series or films such as Star Wars (Smith 2009).

As mentioned earlier, before babies, toddlers, and children engage in object play, they must explore the object first (Hutt 1966). In this initial exploration, young individuals extract characteristics of and uses for novel objects and individuals and then use this information as a basis for play bouts (Pellegrini et al. 2007). To illustrate, imagine a child entering the nursery school for the first time, being introduced to a completely new setting (Pellegrini et al. 2007). The child will allow substantial amount of time during the very first few weeks of their experience, to explore the physical and social environment of the nursery school – being a passive onlooker (Pellegrini and Goldsmith 2003). Exploration is used not only to become familiar with a new setting, but it is also needed to identify any potentially dangerous aspects of an environment and discover how to stay away from them (Spinka et al. 2001). Once a child determines that the novel environment is safe, then play can occur (Pellegrini and Goldsmith 2003).

Finally, it should be noted that any benefits of object play should be compared against those of instruction, keeping in mind different external influences such as the age of the child, the type of task, and whether learning is for particular skills or a more general developmental acquirement (Smith and Pellegrini 2013).

Tool Use

According to Bruner (1972), the design features that object play entails make it an appropriate and suitable way of developing tool-using skills. When considering the early development of tool use in infancy and childhood, the extent to which young children can indeed explore different objects' functions should be kept in mind (Deak 2014). Ideally, a common definition of "tool use" suggests that individuals make use of objects not attached to the environment or being part of individuals' bodies, in the service of a goal, for

example, getting food (Shumaker et al. 2011). To illustrate, using a fingernail to twist a screw would not be considered as an example of tool use, but using a screwdriver would (Pellegrini 2016). Tool use is an activity that encourages children's learning on how to use tools according to cultural conventions, such as using a fork (Pellegrini 2016).

Object functions depend on the physical layout and properties of objects such as their material, part configuration, and markings (Deak 2014). These object properties are related to tool use, and this is explained through the concept of *affordances* as suggested by Gibson (1982). An affordance is the extent to which an organism can interact with an object based on the object's properties (Gibson 1982). For example, to humans a cup affords containment of liquids or solids smaller than the mouth of the cup such as flour as well as tracing circles on paper (Deak 2014). Individual humans can achieve different affordances from the same object, too, of course such as a skilled player can exploit more affordances on a guitar when compared to an inexperienced person. This concept is relevant when we examine the early development of tool use, because in reality most objects or tools are designed to afford actions of adults and not of infants and young children (Deak 2014). As a result, infants must learn how to use tools and objects in a world with a setup engineered for adults (Deak 2014).

Unfortunately, infants and young children are not frequently, or sometimes not at all, allowed to explore object affordances or in other words to explore what they can do with a particular object. This is not only because of young children's physical limitations but also by the limited accessibility to these objects as adults usually design children's environments in such a way that they prohibit children's access (Deak 2014).

However, as infants grow and develop, so do their sensory and motor abilities, and these are the necessary skills needed for the development of tool use. Infants age 6–12 months old readily manipulate novel objects in order to explore their functions and properties – squeezing soft objects or banging hard objects (Bourgeois et al.

2005). As explained above, it is through exploration that children become familiar with novel objects, and once they do so, they enjoy their interaction with them. Exploration is a progressive, embodied, multimodal process that progressively allows children to adapt their reaching and refine their abilities to specific and similar novel objects, in other words, to detect new affordances (Deak 2014). Refinement can be gradual in the sense that younger infants learn how to use a type of tool, for example, a spoon, after a substantial amount of time of experience.

Further, as Tomasello (1999) suggested, tool use is supported by social interaction, with adults having an important role in children's tool-use learning. Specifically, infants and young children shift their attention to objects as a consequence of interaction or observation of adults using objects and tools (Deak 2014). For instance, when adults hold objects, children in turn become interested in those objects and reach out for them, to examine and learn about them (Tomasello 1999). Thus, it is suggested that social learning and sensorimotor development are combined in an attempt to favor tool-use learning in infants and young children.

In summary, as the young child moves from infancy to childhood, their tool-use skills are dependent on active, sensorimotor development. Through the acquisition of their sensory and motor abilities, infants and young children are able to explore novel objects and gradually learn how to use them in different ways, just like adults.

Cross-References

- [Newborn Behavior](#)
- [Object Play](#)
- [Social Play](#)

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Play as Adaptation

► Evolution of Play

Play Fighting in Boys

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Synonyms

Boys; Dominance; Physical aggression; Play;
Rough and tumble

Definition

Two or more prepubertal boys pretend as though they are fighting, without intentionally causing the harm associated with actual combat.

Introduction

Play can be very generally defined as a set of pleasurable activities, performed for the sake of the activity itself without a specific end point or goal. One category of play includes physically aggressive play fighting, in which young males participate in much more than young females, across practically every culture and mammalian species. The underlying reasons for play fighting include physiological, social, and evolutionary factors, from both ontogenetic and phylogenetic perspectives.

Definition of Play

Structurally, play is an activity marked by novel behavioral patterns that is exaggerated or discrepant, divertive, and orientated. Functionally, play has been viewed in many different ways: providing exercise and elaboration of skills needed for survival in adulthood, behaviors with immediate gratifications and no ulterior motives or benefits, and rehearsing social history by acting out instincts that characterized earlier phylogenetic evolution (Smith 2005). Play has important roles in socialization for many mammals; the more intelligent and social the species, the more elaborate the play, with humans displaying the most elaborate and differentiated types of play in the animal kingdom.

Mammals that are part of playful species begin to play as soon as they develop coordinated muscle movements. Play is most prominent during early development in most mammals, peaking during 2–9 years for wild chimpanzees, who have the most elaborate and free-ranging forms of play among nonhuman primates. Play can be separated from other early emerging behavioral activities like exploration, in which objects are manipulated to gain information, that dominate behavior for the first 9 months in humans. By 12 months, play and exploration co-occur, and by 18 months, play accounts for more of a child's interactions than exploration (Bjorklund and Pellegrini 2002). Involvement in playful activities generally follows an inverse U shaped curve, beginning and rising in infancy, peaking in the juvenile period, and fading during sexual maturation in early adolescence. In humans, however, play continues past adolescence and into adulthood, where the activity has become professionalized in many cultures.

Types of Play

Play can be broken into several categories, such as object play (involving nonfunctional manipulation of objects) or fantasy play (using mental representation of a situation as part of a

reenactment); however, play often has a vigorous physical component, which can be referred to as physical activity play, locomotor play, or exercise play. Robust sex and gender differences exist regarding physical types of play, with males participating in locomotor and exercise play to a much greater extent than females. Gross body movements observed beginning from birth, such as body rocking and feet kicking, are known as rhythmic stereotypies and have no apparent sex differences (Pellegrini and Smith 1998). By the end of the first year, however, solitary and social exercise play that involves physically vigorous gross locomotor movements, such as chasing, jumping, and climbing, begin to occur to a greater extent in boys than in girls. Exercise play peaks around 4–5 years of age, taking up approximately 20% of overall physical activity, and it occurs more often in open, spacious environments, with gender differences increasing throughout childhood to mid-adolescence (Pellegrini and Smith 1998).

Young girls not only engage in less exercise play than boys but they also report a significantly lower exercise self-schema (viewing self as less athletic), even though their social support is similar to that of boys for exercise, exercise models, exercise norms, the benefits/barriers differential, sedentary time, and access to exercise facilities and programs (Garcia et al. 1995). Exercise play begins to decline overall around 6 years of age in Western cultures, primarily due to restraints imposed by schools (Bjorklund and Pellegrini 2002).

R&T and Play Fighting

One type of physical play that males engage in to a much greater degree than females is referred to as Rough and Tumble (R&T) play, which is found in virtually all human cultures. R&T play is inherently social, as it involves either direct physical contact with others such as grappling, wrestling, holding, punching, pushing, shoving, or kicking (Smith and Boulton 1990). Additionally, R&T play can involve noncontact forms, such as

chasing or fleeing. Contact R&T looks very similar to actual fighting but has several distinct differences: it occurs in a playful context including the presence of a “play face,” does not commence with a threat, usually ends with continuing social activity between partners, often takes place between friends, and often involves self-handicapping and alternation of roles (Smith and Boulton 1990). R&T play emerges around 3 years of age and accounts for approximately 3–5% of play behavior in preschool children, 7–8% of recess behavior at ages 6–10, about 10% of activity at its peak from 7 to 11 years, and only 5% at 11–13 years at its initial decline, which is then followed by a mere 3% at 14 years (Bjorklund and Pellegrini 2002; Pellegrini and Smith 1998; Jordan 1995). During childhood, R&T is distinct from fighting, but around the adolescence period, R&T involves more cheating, manipulation, inflicting actual harm, and a focus on establishing dominance status. Late adolescence and early adulthood is the period in the lifespan where male–male competition becomes the most intense, with serious physical assaults and deadly physical aggression on the rise.

First documented in rhesus monkeys by Harlow and Harlow in 1965, R&T play occurs not just in humans but in most young mammals where it consumes approximately 10% of time and energy budgets. Participation in aggressive social encounters is also not restricted to only males. Across primate species, female-on-female physical aggression is just as common as male-on-male physical aggression; however, female aggression is less intense, less prolonged, and results in fewer injuries and fatalities than male aggression (Geary et al. 2003). In children, contact forms of R&T are more prevalent among boys, but noncontact forms tend to be similar for both genders (Geary et al. 2003). Preschool boys in the United States engage in playful physical assaults and other forms of R&T play 3–6 times more frequently than do same-age girls (Jordan 1995). Boys are also more likely to adopt goals of promoting their self-interest, controlling social situations, seeking revenge, and adopting hostile and dominance-related goals (Rose and Rudolph 2006).

Underlying Factors in Play Fighting

There are several underlying reasons for boys to engage in R&T and play fighting to a greater degree than girls. From an ontogenetic perspective, both nature and nurture exert significant pressures on males to encourage play fighting and aggression that are quite distinct from the pressures placed on females. Physiologically, the class of steroid hormones primarily responsible for the development and maintenance of male characteristics are androgens, which are produced by the testes. Androgens promote the enlargement of skeletal muscle cells, exert influences on the organization of brain circuits, change characteristics of play activities, and have regulatory effects on cognition, sexuality, emotion, and personality (Rubinow and Schmidt 1996). One clear effect of androgens observed in animal studies is increased aggression, which has been linked to testosterone in particular. For instance, adult groups selected for high levels of aggressiveness are found to have higher testosterone levels compared to control groups (Archer 1991). The relationship is bidirectional, however, between androgens and aggression. It is not just the case that testosterone influences aggression, as physical exercise and aggressive and competitive encounters also increase levels of testosterone. Both boys and girls possess androgens, but boys produce greater amounts overall; and the levels of androgens in boys dramatically increase during puberty and sexual maturation.

Socially, boys are exposed to greater social conflict and aggression compared to girls. Fathers spend more engaging in R&T play than mothers and also more time engaging sons in R&T play than daughters. In school environments, the activity of girls is more closely supervised than the activity of boys, which may have an inhibiting effect on female aggression (Bjorklund and Pellegrini 2002). Adults apply strong differential socialization pressures on boys and girls. Still, studies of children’s social preferences indicate that boys will independently seek out and interact with same-sex peers in groups more frequently than with girls, form large same-sex groups, and engage in coalitional competition once these

groups are formed (Geary et al. 2003). Both girls and boys interact with same-sex peers more frequently than opposite-sex peers throughout childhood, which results in the vast majority of children being exposed to same-sex peers far more than opposite-sex peers, leading to different relationship styles forming within same-sex peer groups than for opposite-sex peer groups. Boys from preschool to adolescence are more likely to have dense social networks and well-defined dominance hierarchies, engage in physical types of sports and games, and participate in physical contests over control of desired objects (Rose and Rudolph 2006). Additionally, boys are more likely than girls across childhood and adolescence to be victims of direct physical aggression, as well as verbal aggression or harassment by peers. In adulthood, male-on-male homicide is 30–40 times more common than female-on-female homicide (Geary et al. 2003).

Evolutionary Factors in Play Fighting

To understand why males are more physiologically and socially predisposed to play fighting and aggression, it is crucial to examine phylogenetic history for underlying evolutionary pressures on development. In most mammalian species, males invest little in parenting and much more in competition for mates, whereas females invest heavily in parenting and are the choosier sex. This pattern of male-on-male physical aggression, and associated sex differences, are expected for a species in which reproduction-related intrasexual competition has been more historically intense for one sex more than the other.

In all species of hominids, including the ancestors of modern humans, there is evidence of a male advantage in physical size, musculature, cardiovascular capacity, and bone density and architecture. The fossil record suggests at least 4 million years of evolutionary history of physical male–male competition in the human lineage (Geary et al. 2003). For males, one of the more common expressions of intrasexual competition involves one-on-one physical threats and fights for privileged access to resources and mating

opportunities. The advantage provided by aggressive play fighting in boys is to practice and hone the skills they have historically needed to acquire desired resources and sexual partners in adulthood.

One of the primary results of play fighting in boys is the establishment of a social dominance structure. Social groups are rarely structured equally, and within all human cultures there exists some form of social stratification. Dominance hierarchies created by alpha status individuals through unequal fighting ability (or inheritance) have deep evolutionary roots in many group-living animal species, including chimps, who display strong social inequality. Dominance hierarchies are prevalent (to different degrees) in modern hunter-gatherer societies, where physical dominance and skill as a warrior are related to social status among men. Play fighting can serve as an indicator of status in relationships, reaffirmation of friendships, and knowledge/establishment of the dominance hierarchy, with achievement of dominance in the peer group having both immediate and long-term effects (Geary et al. 2003). For example, longitudinal studies of children in middle school indicate that dominance-related strategies were more important for boys than girls in dating popularity with increases in dating being associated with decreases in segregation and increases in dominance (Pellegrini and Long 2003).

Conclusion

In summation, play fighting in boys is a result of increased overall physical activity and aggression in males due to various social and biological factors. There are immediate benefits to play fighting such as physical exercise and coordination, developing leadership abilities, emotional regulation (fear, aggression), greater tolerance for interpersonal conflict, self-efficacy, and opportunities for learning specific skills (Bjorklund and Pellegrini 2002; Geary et al. 2003). There are also delayed, long-term benefits for play fighting into adulthood, such as higher positions in a social hierarchy, which is directly related to access to desired

resources, preferential mates, and social dominance. It is not just in hunter-gatherer societies wherein social dominance established by physical prowess confers large benefits. In technologically developed cultures, aggressive physical competition can result in very high status in terms of professional sports and athletics.

Cross-References

- [Opposite-Sex Relationships](#)
- [Play and Social Learning](#)
- [Puberty in Boys](#)
- [Sex Differences in Cognitive Development](#)
- [Sex Differences in Social Development](#)
- [Social Roles](#)

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Play with Others

- [Social Play](#)

Playful Behavior

- [Object Play](#)
- [Play and Tool Use](#)

Pledge to Marry

- [Engagement Rings as Modern Commitment Cue](#)

Pleiotropy

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Definition

When a single gene has multiple phenotypic effects.

Introduction

The founder of genetics, Austrian friar Gregor Mendel, observed in his pea-plant experiments

that three phenotypic traits were inherited together in one of two sets: “brown seed coat, violet flowers, and axial spots or a white seed coat, white flowers, and lack of spots” (Stearns 2010, p. 767). Such strong covariation in phenotypic traits likely resulted from changes of a single gene. A single gene influencing multiple phenotypic traits is referred to as *pleiotropy*, a term introduced in 1910 by Ludwig Plate, a German geneticist (Stearns 2010). For evolutionary psychologists, pleiotropy has been especially important for the evolutionary explanation of aging and its role in human diseases and apparently fitness-reducing behaviors.

Evolutionary Theory of Aging

Medawar (1952) first suggested that pleiotropic genes could result in the evolution of senescence – increased mortality with advancing age – but he did so only in passing. In a highly influential paper, George C. Williams (1957) more fully explored this possibility. Williams developed the theory that aging evolved as a result of *antagonistic pleiotropy* – when a gene’s effects are beneficial early in life but harmful later in life. Natural selection would favor such pleiotropic genes, because the force of selection is stronger earlier in life than later in life. For example, a deleterious gene that results in death would be calamitous for fitness if expressed before reproduction, but not if expressed later in life after most lifetime reproduction has already occurred. The late-life harmful effects of various pleiotropic genes, Williams argued, would result in aging.

Molecular Genetics

The theoretical plausibility of pleiotropy assumed by Medawar and Williams has been transformed by technological advancements in molecular genetics into understanding of the mechanisms by which pleiotropy actually occurs. According to the modern theory of genetics, genes in DNA strands are read to produce mRNA, which in turn directs the production of proteins that act at the

cellular and intercellular level to affect phenotypes. Within this context, pleiotropy results when a single gene codes for a single multifunctional protein that, through one of at least seven different mechanisms, has multiple effects on the phenotype (Hodgkin 1998). Alternately, a single gene can result in the production of multiple proteins, each with different effects on the phenotype. This occurs in at least three ways (Stearns 2010). First, different proteins can be created if a gene is read by different start/stop codons, analogous to starting and stopping the reading of this sentence at the first and last word in one case or in another at the second and sixth word. Second, when mRNA is spliced to remove introns in preparation for protein production, the splicing can occur in different ways that produce different mRNA. Finally, cells can directly edit mRNA itself, changing the protein it produces.

Prevalence and Disease

Some early theorists suggested that all genes are pleiotropic, because their effects provide the context in which other genes work, but modern methods including experimental manipulations of genes suggest instead that most genes influence about four to eight traits (Stearns 2010). An analysis of data from genome-wide association studies found that about 17 % of human genes involved in diseases are pleiotropic, but this study might underestimate the prevalence of pleiotropy because it looked only for pleiotropy involving previously measured diseases and traits (Sivakumaran et al. 2011). One review identified numerous diseases whose underlying genetics result in antagonistic pleiotropy (Carter and Nguyen 2011), including the well-known example of sickle-cell anemia. This disease occurs for people who have two copies (homozygotes) of the autosomal recessive version of the gene. Their malformed red blood cells carry insufficient oxygen to the body and damage tissues. People with only one copy of the gene (heterozygotes), however, benefit from increased resistance to malaria and do not develop sickle-cell anemia.

Types of Pleiotropy Based on Effects

For people living in malaria-infested regions, the gene that causes sickle-cell anemia results in enhancement to fitness for people with one copy but a reduction in fitness for people with two copies. The gene has both beneficial and detrimental phenotypic effects and so is a type of antagonistic pleiotropy (Carter and Nguyen 2011). Evidence suggests homosexuality might also result from genes whose effects decrease fitness in some who carry them but increase fitness in other carriers (Zietsch et al. 2008). These divergent effects on fitness occur for different people, and so can be distinguished from the more commonly considered kind of antagonistic pleiotropy conceived by Williams (1957) in his theory of aging wherein the early life benefits and late-life costs were within-person. A prominent example of this is that higher levels of testosterone reduce longevity but increases mating success in human and nonhuman males (Hau 2007). Other distinctions among types of pleiotropic effects have also been proposed. Hamilton (1966) pointed out that “all genes which are age-specific in their action are pleiotropic, simply by the fact that they cause positive effects at some ages and null ones at others” (p. 35). This might be called *late-onset pleiotropy*. Rose and colleagues (Rose et al. 2007) noted that, “Morphological size characters often show ‘positive’ pleiotropy, whereby alleles that increase the size of one limb, for example, also tend to increase the size of other body parts” (italics added, p. 1267). Thus types of pleiotropy can be distinguished based on whether the multiple effects occur within an individual or between people and the fitness consequences of the effects: antagonistic, null-then-positive, or all positive. Pleiotropy can also be distinguished based on different molecular genetics mechanisms as described above.

Conclusion

The concept of antagonistic pleiotropy has played a large role in the evolutionary theory of aging. Modern molecular genetics research has substantially illuminated many of the mechanisms by

which pleiotropy can occur and demonstrated that it is fairly common. Pleiotropy can have opposing effects on fitness, consistent effects on fitness, or late-onset effects. The effects of pleiotropy can appear within a single individual or across individuals. Diseases and psychological traits that seem to reduce fitness are sometimes explained as resulting from selection pressure on the pleiotropic effects of related genes.

Cross-References

- ▶ [George C. Williams](#)
- ▶ [George Williams](#)
- ▶ [Selection Pressures as a Function of Age](#)
- ▶ [Senescence](#)

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Pointing

► [Communication and Developmental Milestones](#)

Political Affiliation

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Synonyms

[Political ideology](#); [Political orientation](#)

Definition

Where an individual falls on the political spectrum, usually a left-right continuum, which strongly determines their voting preferences.

Introduction

Political affiliation is where a person falls on the political spectrum, usually to the left or the right (Conover and Feldman 1981; Jost 2006). The right-wing and left-wing are usually defined along two spectrums: acceptance of inequality and favoritism toward the status quo (Jost et al. 2003). That is, in the first case, a preference or at least tolerance of some kind of societal injustice, either because it is inevitable or even preferable. In the second case, this means the extent to which someone prefers changing the current societal state of affairs versus changing society. Where someone falls on these two spectra will determine their political affiliation. If they prefer or tolerate inequality, they will tend to be more conservative; if they would like to assuage inequality, they will be more liberal. If they prefer to keep society the way it is or the way it has been, they will be more

conservative, whereas if they favor changing society, they will be more liberal.

What Is Evolutionary Political Psychology?

Evolutionary political psychology is the study of why political behaviors were beneficial in humanity's distant past. What made politics a beneficial adaptation? What advantages did politics give some groups of humans over others? How do these evolved adaptations continue to affect political behavior in the present day? And most importantly to the current discussion, what evolutionarily relevant variables influence people's political affiliation up to the present time? These are the kind of questions that this relatively young field tries to answer.

A helpful beginning point in explaining the evolutionary origins of political affiliation would be to decide what exactly politics is, at least in the context of humans' evolutionary past as hunter gatherers. According to Petersen (2015), politics probably developed as a way to coordinate the selfish desires of individuals in a group with the need to cooperate in order to survive. That is, each individual in the group would have wanted to maximize his or her own individual level of fitness; however, this sometimes conflicted with the fitness of the group as a whole. Thus, when an individual took down a great animal that they might have used for food, this was not political in and of itself. It became political when another individual or individuals claimed that they were entitled to a part of the food that the first individual had just acquired. It would have been in that first individual's best interest – the one who made the kill – to hold onto all of the meat they had just caught. But if they were a part of a group, those other individuals at least theoretically had a claim to some of it, because it was (and still is) generally accepted that one shares with one's ingroup members. This often put what was in the individual's best interests in conflict with what was in the group's best interest. Accordingly, a person's political preferences – policy preferences, political affiliation, etc. – would have been driven by the desire to have the group conduct its affairs in

such a way that promotes his or her best interest, as the individual himself or herself saw it. A person's perceptions, further, were determined by a number of measurable variables with evolutionary overtones (described below; e.g., Haidt and Graham 2009; Hirsch, DeYoung, Xu, & Peterson 2010). This is the case with modern political preferences as well.

Alford and Hibbing (2004) posited a similar hypothesis, but with some additions. They put forth the weary cooperator theory of politics. Similarly to Petersen (2015), they begin with the premise that humans are driven by a trade-off between the desire to act in their own self-interest and the desire to cooperate. Cooperation has clear survival benefits, but at the same time evolution should drive individuals to act in their own self-interest. Humans, being smart enough to realize that they must deal with this trade-off, therefore engage in altruistic punishment or sacrificing some potential gain for oneself for the sake of others in order to foster cooperation so that they can benefit from the protection of being in a group. However, they will also harshly punish those who do not reciprocate this cooperation, mainly because they themselves are making some sacrifice and do not like feeling as though others in their group are not doing likewise (e.g., Yamagishi and Kiyonari 2000).

Someone will make a sacrifice for the sake of the group insofar as they stand to gain from that sacrifice, and they will punish those ingroup members who do not reciprocate that sacrifice in some way, whether it be by stealing, not sharing, or committing a crime. Thus, the abovementioned individual who has just made a great kill will willingly give up some of the meat from their kill, because they know that doing so ensures their place in a group, which helps to promote their survival. This trade-off between altruistic punishment (i.e., willingly sharing with others) and selfishness, plus the desire to see those who do not reciprocate altruistic punishment, drives much of political behavior, according to Alford and Hibbing (2004). Thus, according to Alford and Hibbing, evolutionarily driven political behavior is not always entirely selfish, which stands in contrast to Petersen (2015).

Thus, a person's political preferences will be driven in part by their desire to promote their own best self-interest. If they see more liberal policies as being beneficial to them, then in the United States they are more likely to be a Democrat. If they see more conservative policies as being beneficial to them, then in the United States, they are more likely to be a Republican (but see Weeden and Kurzban 2016, for a counter-argument). But they also willingly make sacrifices of their self-interest to a degree for the sake of the group. This explains liberal individuals' willingness to invest in welfare programs – which often do not benefit them directly – and conservative individuals' willingness to sacrifice safety nets in order to promote spending on the military – which also does not tend to benefit them directly. In summary, there should be a number of evolutionarily driven variables – especially reproductive strategies (see below) – that predict whether someone will fall on the left or right of the political spectrum.

Evolutionary Predictors of Political Affiliation

What evolutionarily relevant variables predict political affiliation? This is a relatively new area of study, but some preliminary results suggest that evolutionary variables affect people's political affiliation. For example, Pinsof and Haselton (2016) found that participants with more of a short-term mating orientation (STMO) – meaning mating habits that require little investment over a long period (e.g., being promiscuous) – were more accepting of gays and lesbians, and that this was mediated by perceptions that gays and lesbians were promiscuous. That is, those who showed greater favorability for a long-term mating orientation (LTMO) perceived gays and lesbians as more promiscuous, and this accounted in large part for why they had negative attitudes toward homosexuals (also see Pinsof and Haselton 2017), attitudes that have obvious implications for political affiliation in the United States and many other countries. Those who have a LTMO will be more likely to be conservative, while those with a STMO will be more likely to be liberal.

Something similar has been found with regard to people's attitudes about recreational drugs, another issue with great implications for political affiliation in the United States. Kurzban et al. (2010) found that people with more of a LTMO showed more negative attitudes toward recreational drug use that remained significant even while controlling for political affiliation. This, they argue, is because people who use recreational drugs are perceived as more sexually promiscuous (i.e., have more of a STMO), because recreational drug use and promiscuity tend to be correlated (e.g., Whitaker et al. 2000). Thus, attitudes toward recreational drugs and homosexuals – which tend to be more negative among conservatives, who often oppose the legalization of drugs like marijuana, and tend to be more positive among liberals, who support the legalization of drugs like marijuana – are determined, at least in part, by mating orientation, a variable with heavy evolutionary overtones (Kaplan and Gangestad 2005).

Petersen (2012) also investigated a possible evolutionary origin of people's attitudes toward welfare. He performed a study on the deservingness heuristic. According to the deservingness heuristic, other members of one's ingroup who are perceived as cheaters (free-loaders, those who are not doing their part to support the group) will be perceived as undeserving of help, and those who are perceived as reciprocators (working or at least doing their best to help the group) are perceived as deserving of help. In theory, the deservingness heuristic is out-of-date in modern nation-states, which are much vaster than the hunter-gatherer bands in which humans evolved. However, the time from humans' hunter-gatherer past to the present was not long enough for humans to evolve new psychological mechanisms for judging the deservingness of others. Thus, it still influences the way people judge the extent to which welfare recipients are deserving of the assistance they receive. To that effect, Petersen ran a study where he found that participants tended to view people receiving help (whether it was welfare or help from a friend) and not putting effort into finding a job as cheaters in the sense of cheaters from humanity's hunter-gatherer days. Those who were being helped (whether it was welfare or help

from a friend) who were putting in effort were perceived as reciprocators. On the other hand, when no information was given about the effort they were putting in, the participants did not make this distinction. Thus, a deservingness heuristic that evolved to function in small bands of hunter-gatherers – in humanity's evolutionary past – continues to cause people's political attitudes today. When someone is perceived as a cheater, they will be perceived as undeserving of welfare assistance.

Interestingly, Petersen (2012) did not find that these effects were moderated by political affiliation. This would seem to be evidence contrary to the above contention that individual differences on variables such as the deservingness heuristic determine political affiliation. However, there is a possible counter argument to this, although it has yet to be explicitly tested. Skitka et al. (2002) put forth the motivated correction hypothesis of political affiliation. According to this, liberals and conservatives (this research was done in the United States) probably make similar attributions as to why poor people are poor, why criminals commit crimes, and other attributions important for determining political affiliation – but while they make the same attributions (e.g., poor people are poor because they are lazy; criminals commit crimes because they are horrible people) when they are made under cognitive load or under time pressure, when they are given more time to think about their views, liberals tend to change their attributions from the initial gut reaction (poor person is poor because he's lazy) to a view that is more in line with their ideology (poor person is poor because of economic inequality). Conservatives do not do this, because their immediate reaction tends to be more in line their ideology. It is possible that these effects would occur if cognitive load or time pressure were investigated as mediators in Petersen's (2012) study.

Moral Foundations and Motivated Social Cognition

Two further theories with evolutionary relevance have posited variables that predict political affiliation. According to the theory of political

conservatism as motivated social cognition (PCAMSC), political conservatism is heavily correlated with a number of epistemic (e.g., need for cognitive closure) and existential variables (e.g., fear of death; Jost et al. 2003). In this model, the need to perceive the world as simple, predictable, and knowable and the desire to see the world as meaningful are highly predictive of political conservatism (cf. Skitka et al. 2002). Indeed, they found support for this in an extensive meta-analysis of studies predicting political conservatism, finding variables such as fear of death, mortality salience, need for cognitive closure, need for cognition, and need for order across 88 different samples – and research since then has corroborated their findings (Jost and Amodio 2012).

Somewhat relatedly, Haidt and Graham (2009) put forth moral foundations theory (MFT). In their model, there are five moral foundations that were the basis for making decisions about what is right and what is wrong (i.e., shorthand for making moral decisions) in humanity's evolutionary past. They evolved according to natural selection because they helped humans in the evolutionary past to survive and pass on their genes more effectively. Different cultures at different times valued different foundations more or less than others, but each of them plays some part in every human culture, according to the authors. The five foundations are harm/care, to keep oneself safe and help others avoid being hurt and to relieve pain; fairness/reciprocity, help those who are good and harm those who are bad; ingroup/loyalty, need to belong to groups and punish traitors to the group; authority/respect, accord those of higher standing in the social order the respect they deserve (including, at times, obedience); and purity/sanctity, avoid being contaminated by dirty or immoral objects or people.

The harm/care and fairness/reciprocity foundations are categorized as individualizing foundations, because they place emphasis on the welfare of individuals. The other three, ingroup/loyalty, authority/respect, and purity/sanctity, are referred to as binding foundations, because they place more emphasis on loyalty, duty, and self-control in service of a group (Graham et al. 2009). Survey research measuring the five moral foundations has shown that liberals tend to rely on the

individualizing foundations, whereas conservatives tend to rely on all five (Haidt and Graham 2009).

Conclusion

Political affiliation, then, results from some combination of which moral foundations they value, where they fall on epistemic and existential variables, and other individual differences regarding mating strategy and their application of the deservingness heuristic. Future research is clearly needed, but this is where the field stands. It would seem that political affiliation – and by extension, political parties – evolved as a way for humans to serve their self-interest while maintaining the integrity of the group. Those who hope for a world where everyone gets married to their one true love and work together to raise happy children will *tend* to show homonegativity and to oppose recreational drug legalization. Those who are open to new experiences and open to ambiguity will tend to favor more racial, ethnic, religious, and sexual inclusion and so on. Political parties may be so ubiquitous across political systems because they helped people with differing temperaments and desires to have an outlet through which to try and further what they saw as best for the group they lived in while also promoting their own best interests.

Cross-References

- [Mating Strategies](#)
- [Moral Foundations Theory](#)
- [Political Orientation](#)

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Political Attitudes

- [Social Dominance Orientation \(SDO\)](#)

Political Bias

- [Politics in Science](#)

Political Ideologies

- [Politics in Science](#)

Political Ideology

- [Political Affiliation](#)

Political Interest

- [Civic Duty](#)

Political Left, The

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Synonyms

[American left](#); [Democratic party](#); [Leftist](#); [Left-of-center](#); [Left-wing](#); [Liberal](#); [Progressive](#)

Definition

The Political Left describes an orientation on the liberal-conservative/left-right political spectrum that describes individuals who tend to have greater concern for promoting social equality and protecting individual liberties and who are more likely to seek political reform as compared to political conservatives.

Introduction

Although political views are complex, the utility of a single continuum that ranges from liberal to conservative, or left to right, has been demonstrated to accurately predict individuals' voting behavior and opinions on a variety of issues (Jost 2003). People who fall more toward the left end of the spectrum, often colloquially referred to as *liberals*, are more likely to defend individual liberties from authorities, traditions, and institutions (Sowell 2002); express moral concerns about fairness/equality (Graham et al. 2009); and seek political reform as compared to political *conservatives* on the opposite end of the continuum (McCrae 1996). Conservatives, who prefer familiarity, stability, and predictability (McCrae 1996), have different perspectives about moral principles and behaviors compared to liberals. Conservatives are more inclined to endorse the view that moral values are objective and universal (i.e., notions of "right" and "wrong" do not and should not vary across cultures) and that behaviors are morally acceptable if they conform to these absolutes (e.g., Van Kenhove et al. 2001). In contrast, liberals are more likely to support *moral/ethical relativism*, or the related philosophy of *cultural relativism*, which holds that moral values are valid in different cultures and societies and are all equally deserving of tolerance and respect (e.g., Graham et al. 2009; Hunter 1991; Layman 2001). Liberals have historically supported policies based on this perspective (Layman 2001).

Relativism Versus Human Rights

The philosophy of cultural relativism rose to prominence in the twentieth-century by the

advancement of American anthropologists in opposition to Western imperialism, racism, and ethnocentrism (Lukes 2008). These left-leaning anthropologists were politically active both in their own country and abroad in their quest to promote tolerance of other societies' ways of life and cultural practices. Notably, the executive board of the American Anthropological Association issued a statement to the United Nations (UN) Commission on Human Rights in 1947 urging them to implement a relativist perspective in their forthcoming Universal Declaration of Human Rights (see Lukes 2008). Although the motion failed, it sparked a worldwide debate about human rights lasting decades. This debate, often framed as universal human rights vs. relativism, continues to influence the political tendencies of individuals today as evidenced by liberals' preference for policies that counter cultural imperialism and emphasize tolerance (Lukes 2008). Perhaps the most widely discussed and contentious issue from these discussions is the practice of female genital mutilation, which some argue is a violation of individuals' fundamental human rights (Danial 2013). This position has been criticized by others who believe such a stance is congruent with Western imperialism and argue that outlawing the practice represents a morally unjustified imposition on another culture (e.g., Shweder 2000).

Conclusion

In conclusion, efforts by the intellectual left (i.e., politically liberal academic social scientists) in opposition to Western imperialism gave rise to the philosophies of moral/ethical and cultural relativism (Danial 2013). This position is frequently expressed by political liberals, who are more likely than conservatives to hold that "right" and "wrong" are subjective and specific to cultural and religious contexts (Van Kenhove et al. 2001).

Cross-References

- [Cultural and Moral Relativism](#)
- [Modern Moral Relativism](#)

- [Moral Concerns](#)
- [Political Affiliation](#)

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Political Mechanisms

- [Politics in Science](#)

Political Orientation

- [Political Affiliation](#)

Political Psychology

- [Politics in Science](#)

Political Scientist

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Politics in Science

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Synonyms

[Political bias](#); [Political ideologies](#); [Political mechanisms](#); [Political psychology](#)

Definition

Politics involve the interpersonal negotiation among members of a group for power within a status hierarchy. Politics are involved in science in at least two ways. Evolutionary psychologists study the mechanisms involved in political behavior, and are subject to their own political biases which they bring to their work, which shapes both, the questions they ask and the inferences they make.

Introduction

Politics play multiple roles in science. First, as a field interested in human behavior, psychology as a field, including evolutionary psychology, has explored the mechanisms underlying variation in political ideologies. Second, like any community, the scientific community has its own norms and mores which are shaped by the prevailing zeitgeist of the cultures from which scientists come. Therefore, not only are the processes underlying variation in political ideologies studied by evolutionary psychologists and traditional psychologists, alike, but the field is often subject to the political biases of its members. In what follows, we will briefly explore

some of what evolutionary psychology has contributed to the study of political behavior and discuss the influence political ideologies have on field.

Psychological Mechanisms Involved in Political Ideologies

The approach to understanding human nature used in evolutionary psychology has contributed profoundly to the field of psychology, and the study of political ideologies is no exception. Here we will discuss several psychological mechanisms that have been used to understand variations in political ideologies. We will discuss the role of the pathogen aversion psychological mechanism in political ideology. Next, we will then discuss other psychological mechanisms proposed by Moral Foundations Theory. We begin, however, by discussing operational definitions of what it means to be conservative and liberal.

Being conservative versus being liberal has meant, and continues to mean, many things to many people. However, one distinction that has been made between conservatives and liberals is that concerning beliefs about individual liberties (Graham et al. 2013). Classic liberalism can be thought of as a belief system or set of values built on the fundamental belief that people are inherently good and benefit from greater liberty (i.e., liberal). This includes liberty from their groups and the expectations of those groups. Conservatism, on the other hand, can be thought of as a belief system or set of values built on the belief that assumes that people are not inherently good and benefit from greater restraint, whether that restraint be imposed by law or normative custom. Further, conservatism and liberalism are best thought of as existing along a continuum rather than as categorical distinctions. With these definitions in mind we now turn to the psychological mechanisms thought to produce variance in people's political ideologies.

Pathogen Aversion

Pathogens have historically presented, and continue to present, people with a selection pressure,

such that those best able to overcome disease survive longer. Certainly, our immune system plays a large role in meeting this demand. However, avoiding potential infectious agents and environments may be a preventative measure (Schaller 2006). Therefore, a pathogen avoidance mechanism that responds to inputs such as cues of potential high exposure to pathogens and parasites with outputs (e.g., the emotional response of disgust) that encourage people to avoid potentially infectious others would serve to stop infections before they even began. Schaller has proposed such a mechanism, with several other functionally similar mechanisms, in his behavioral immune system.

Researchers have argued that the psychological mechanisms that comprise the behavioral immune system can create differences in political ideologies. Specifically, research examining the behavioral immune system of political conservatives suggests that conservatives are more sensitive to disgust triggered by pathogens sexual acts and moral issues relevant to pathogen exposure and sexual acts (Tybur et al. 2013).

Moral Modules

Haidt and colleagues (Graham et al. 2013; Haidt 2012) have proposed that a suite of psychological mechanisms that process morally relevant issues is partially responsible for differences in political ideology. Namely, Haidt argues that conservatives and liberals differ in the extent to which they endorse five foundations of moral consideration and respond to cues of violations of these foundations with negative moral judgment. Haidt has organized these foundations into those that operate to benefit individuals (i.e., individuating foundations) and those that operate to benefit the groups people belong to (i.e., binding foundations). The individuating foundations include concerns with harm/care and fairness/reciprocity, while the binding foundations include concerns with loyalty/betrayal, authority/subversion, and purity/sanctity. Haidt and colleagues have suggested and found that conservatives endorse all five foundations equally, while liberals

principally endorse only the individuating foundations. It is for these reasons that conservative ideologies are thought to reflect concerns with disloyalty, subversion of authority and norms, and physical, sexual, and moral purity more so than are liberal ideologies. While liberal ideologies are thought to only reflect concern for preventing harm and ensuring fairness.

Haidt (2012) has further suggested a sixth foundation of moral concern, which he refers to as the liberty/oppression foundation. This foundation reflects a concern with the power wielded by governing individuals or entities. Specifically, those who endorse this foundation prefer weaker governing entities and greater individual liberties. Although, not much research has explored how this foundation might account for differences in political ideologies, what has been done suggests that liberals endorse this foundation more so than do conservatives (Hofmann et al. 2014).

Finally, research has begun to explore how these moral judgment mechanisms might explain libertarian ideologies. The limited work that has been done suggests that libertarians endorse the liberty/oppression foundation, but endorse all other foundations less than do liberals or conservatives (Iyer et al. 2010).

Thus far we have discussed some of the mechanisms thought to underlie variation in political ideologies. By no means have we provided or attempted to provide an exhaustive list. However, we now turn to the other important role politics plays in science, political bias.

Political Bias in Science

One of the defining qualities of the scientific endeavor is striving for objectivity. However, this is not always as easily done, as it is said. Recent commentaries and research have explored political bias in the field of psychology (Haidt 2011). Specifically, this work has revealed a strong liberal bias not only in psychology but in science in general (Honeycutt and Freberg 2017). This implicit bias is blatant when taking a bird's eye view at research examining variations in political ideologies.

While we will not provide a detailed discussion here, as such can be found elsewhere (Duarte et al. 2015), suffice it to say that a cursory glance at research examining variation in political ideologies may give the impression that the field of psychology views those with conservative ideologies negatively. Sadly, work suggests that psychologists with conservative ideologies feel as if their field views them negatively (Honeycutt and Freberg 2017; Inbar and Lammers 2012). Therefore, this suggests we must redouble our efforts to address our research questions with objectivity, putting our personal biases, political or otherwise, aside.

Conclusion

Here we have examined at least two of the roles, politics play in evolutionary psychology, a topic that has garnered great interest, and a biasing factor within the scientific community. It is ironic that those who study variations in these ideologies would be so led about by the biasing influences of these ideologies. However, given how interrelated these are, hopefully further exploration will lead our field to potential solutions.

Cross-References

► [Pathogen Avoidance](#)

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Poll

- [Surveys and Questionnaires](#)

Polyadic Aggression

- [Feelings of Excitement and Brotherhood](#)

Polyandry

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Synonyms

[Bigamy](#); [Polygamy](#)

Definition

Polyandry is the practice of having more than one husband or male mate simultaneously. It is among the rarest of human mating systems. Only 1.1 %

of cultures studied worldwide engage in polyandry.

Introduction

Polyandry has long puzzled the scholars who study it, particularly male scholars, according to Hrdy's comprehensive (1986) consideration of studies of human and nonhuman instances of this mating strategy. Its existence challenges many assumptions about human sexual and marital relationships and challenges evolutionary thinkers because of the assumption that it dramatically limits male reproductive success. Indeed when compared with polygyny and monogamy, it is relatively uncommon among humans and nonhuman primates. Demographically, among humans its most common form is fraternal polyandry, found almost exclusively among Tibetans and ethnic Tibetans of Nepal and India. Other mostly ephemeral instances of polyandry have been observed among egalitarian and primarily foraging peoples encountered in such diverse regions as the northern latitudes including among the Inuit, among some Plains tribes in North America, among some foraging populations of South America, in the Marquesas, and among the Nayar in Southern India. Aside from the Nayar, those forms of polyandry seen outside of the Tibetan culture area have typically been described as opportunistic and most likely to occur in instances of scarcity in environments characterized by patchy or temporally variable resource availability (Starkweather and Hames 2012 provide an excellent review). Among ethnic Tibetans, by contrast, polyandry is not ephemeral nor is it a temporary response to difficult environmental or economic circumstances. By contrast, it is the normative and most highly regarded marital form and typifies households considered by community members to be culturally successful.

Human evolutionary ecologists and other evolutionary thinkers use the theoretical and methodological tools from the nonhuman literature to understand human mating behavior, including polyandry. Studies from this perspective are important because they help precisely identify

the decision rules that people use in different cultural and environmental contexts as they make evolutionarily significant decisions. For instance, a number of studies have shown a positive association between a male's access to resources in various forms and their desirability to females. Others have identified the connections between female characteristics and their desirability to men as brides or mates. Studies of this kind illustrate the attention that human behavioral ecologists have focused on mate choice and on identifying and analyzing those characteristics which are most likely to ensure that a male or a female will be chosen as a mate. Our understanding of polyandry, particularly among fraternally polyandrous ethnic Tibetans, has been greatly enhanced by this theoretical lens.

Explanations for Polyandry

A primary focus of human evolutionary ecology research on polyandry has been on the timing and circumstances of marital events and the context in which they are made. Human behavioral ecological research into these questions seeks to identify the specific constraints that limit and shape marital decisions. Typically, the constraints that have been investigated by human behavioral ecologists have been factors like wealth or prior reproduction or marital histories.

This focus allows human behavioral ecologists to identify how marital decisions are affected, for instance, by economic conditions or opportunities, position in the sibling set and number of siblings, and prior marital and fertility histories. These factors have been shown to be influential in societies in which a mix of polygyny and monogamy prevails (Borgerhoff Mulder 1988; Strassman and Clarke 1996). Analyses of these issues by human behavioral ecologists rely heavily upon models borrowed from the nonhuman literature. The nonhuman models that examine flexible behavioral responses to environmental variability in nonhuman species are useful building blocks for predicting the organization of human social systems, including marriage systems, across environmental contexts. Like

analysts of mating systems in nonhumans, and based on evolutionary theory, behavioral ecologists predict that human beings will, on average, behave in ways that maximize fitness relative to other individuals in the population. Studies of mating systems across species typically test this prediction, looking at intraspecific variation in fitness as associated with mating strategy (Emlen and Oring 1977; Davies 1992; Searcy and Yasukawa 1989; Ryan and Causey 1989; Dunbar et al. 1990; Bradbury and Vehrencamp 1977).

The starting point for human behavioral ecology studies of polyandry was Emlen and Oring's seminal paper in which they argued that mating strategy will be influenced by the spatial distribution of resources and the temporal availability of mates (1977). In the same year Bradbury and Vehrencamp argued that parental care patterns also strongly influence mating systems (1977), and later studies showed that alternative mating strategies were affected by a number of other factors, for example, different strategies may be pursued by males and females depending upon age and current mating opportunities (e.g., Byers and Kitchen 1988 and Dunbar et al. 1990). The strengths of these studies lie mainly in their clarification of the importance of factors like age or position in the sibling set, as among communal breeders, as well as environmental factors such as the availability of the limiting sex (as among dunnocks after a harsh winter, when the sex ratio rose and polyandry became more common, [e.g., Davies 1991]), the availability of resources, and the importance of parental care (e.g., Beissinger 1987). Perhaps the most important conclusion to be drawn from these studies is that populations and even individuals rarely pursue the same mating strategy at all times. Populations are unlikely to be uniformly "polygynous" or "polyandrous," since individuals within a population may frequently shift from one mating strategy to the next depending on the factors listed above (e.g., Davies 1991).

The empirical studies inspired by the original models of Emlen and Oring and Bradbury and Vehrencamp have over the decades added considerable complexity to the way in which human behavioral ecologists think about marriage

strategies, including polyandry. Uniformly, individuals are regarded as active decision-makers facing specified costs and benefits and are assumed to be able to either consciously assess those or use advantageous “cultural” rules of thumb. Understanding marital strategies in polyandrous humans simply in terms of optimality or by using a small number of independent variables oversimplified the complex processes at play in these systems. Early studies suggested that polyandry resulted from a male-biased sex ratio – there were simply not enough women to go around – or suggested that polyandry was a response simply to resource scarcity. But neither of those hypotheses fit the ethnographic, demographic, and ecological realities in cultures where classical fraternal polyandry exists. Fortunately, a number of human behavioral ecological studies have taken a multidimensional approach to analyzing polyandrous systems, and these have shed light on the complexity and strategic considerations of decision-makers in these societies.

When Polyandrous Marriages Persist: A Multidimensional Conundrum

In a fraternally polyandrous society such as among ethnic Tibetans of Nepal and India, sets of brothers typically begin their marital trajectories polyandrously. Yet these systems show considerable flexibility, and communities often contain households comprised of polyandrous marriages, others with monogamous marriages, and much more rarely, households with polygynous or polygynandrous marriage. Individuals can phase out of the initial polyandrous phase of a marriage between brothers and their shared wife if and when members agree. So the question of interest has focused on those households in which polyandrous marriages persist, in comparison with those households in which polyandrous marriages partition.

Studies have shown that in a polyandrous system, the decision to stay or to leave the wife of one’s polyandrous brothers and marry monogamously cannot be simply understood, in terms of some of the variables traditionally studied by

human behavioral ecologists, like wealth or (prior or expected) reproduction. Decisions about first wives are typically made by the eldest brother together with his male kin and depend upon his age and the age of his parents, the number of brothers he has, the economic status of his fathers’ estate, his education, recommendations of local monastic authorities, and other factors related to the family system and the household economy. Similarly, the decision to partition a polyandrous marriage will depend upon age, number of children already produced, anticipated inheritance, familial monastic obligations, community sentiment, and other factors. A number of studies have shown that considering each of these factors allows a complete analysis of the strategies pursued and how individuals decide among them.

Durham’s (1991) synthesis of the competing hypotheses and evidence regarding the existence and maintenance of fraternal polyandry shows solid evidence from the earliest studies from Fischer (1952), von Fürer-Haimendorf (1975), Aziz (1978), Levine (1988), and Crook and Crook (1988), for what he termed the domestic economy theory of polyandry. These important early studies produced abundant ethnographic, economic, and demographic evidence supporting two hypotheses, including:

- a. The conservation of family property – the monomartial principle (one marriage per generation) kept estates together given the preference for and practice of partible patrilineal inheritance. In cases of partition, a per capita (male) inheritance rule would divide estates among separately marrying sons. Together, these principles serve to conserve family property across generations.
- b. The optimization of family labor – local ecological conditions set incentives for a diversified family economy, the consequence of which was an acute demand for labor and a domestic unit ratio that favored producers over dependents.

Human behavioral ecologists elaborate upon the findings from these classical studies.

Household wealth, or access to resources seemed particularly important, since most fraternally polyandrous people reside in harsh or unforgiving climates and/or topography and because wealth has been shown to predict marital decisions and reproductive success in many societies around the world. Among ethnic Tibetans practicing polyandry, it is very common for households to engage in a variety subsistence strategies, including agriculture, long distance pedestrian trade, and pastoralism. Levine and Silk (1997) showed the powerful effect of the size of the brother set and prior marital history on marriage decisions and reproductive success, where larger brother sets were less stable and the decision to partition a polyandrous marriage dramatically reduced reproductive success of active partitioners. Low socioeconomic status, long thought to be associated with the decision to marry and remain married polyandrously, did not in fact appear to be associated with the stability of polyandry among the Nyinba of northwest Nepal. But Haddix (2001) showed in her study of Panchapalli ethnic Tibetans in northern Humla District of Nepal that when the diversity of wealth holdings was analyzed, those families in households with higher economic diversity were more likely to remain polyandrous than those that were not economically diversified and for brothers to have higher reproductive success in comparison with men who opted to partition a marriage. Smith's (1998) meta-analysis established that in the most data-rich studies of polyandry that we have, even after considering the reduced coefficient of relatedness of brothers produced from a polyandrous marriage, polyandry conferred higher reproductive success upon men in certain economic circumstances and could be considered an evolutionarily adaptive response to those circumstances.

Conclusion

Polyandry represents a fascinating example of human mating strategy plasticity, and in its classical form among fraternally polyandrous ethnic Tibetans, it is a standout among marriage systems in terms of flexibility and community members'

acceptance of difference. The work of evolutionary thinkers has shed invaluable light by bringing analytical complexity to this fascinating topic.

Cross-References

- [Adaptation](#)
- [Marriage](#)
- [Mating Systems](#)
- [Multiple Matings](#)
- [Polygamy \(Behavioral Ecology\)](#)
- [Polygamy in Humans](#)
- [Social Status and Economic Resources](#)

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Polygamy

- [Mating Systems](#)
- [Polyandry](#)
- [Polygamy in Humans](#)

Polygamy (Behavioral Ecology)

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Synonyms

[Multiple mating](#); [Polyandry](#); [Polygynandry](#); [Polygyny](#)

Definition

A mating system in which one male mates with multiple females, or one female mates with multiple males, or both males and females have multiple mates.

Polygamy and Parental Investment

The concept of polygamy is at the heart of the study of mating system evolution. How many mates an individual has is likely to have a large effect on the reproductive contribution that individuals make to the next generation. However, there is an important difference between males and females with respect to polygamy that is related to the definitional distinction between the sexes (Trivers 1972). Females are defined by their production of large, nutrient rich gametes (eggs), whereas males are defined by the production of tiny, abundant gametes (sperm). The result of this dichotomy is that males in many species can profit reproductively from mating with multiple females. Developing ideas initially explored by Bateman (1948) and Williams (1966), Trivers (1972) argued convincingly that it is actually the difference in relative parental investment in offspring that is the key determinant of “sex roles,” with the sex that provides more parental investment in offspring becoming a “limiting resource” for which members of the opposite sex compete. Trivers (1972) also argued that the initial disparity in investment that defines males and females creates a bias in investment (gamete size disparity) that drives a bias in the tendency of females (as opposed to males) to invest in parental care.

This proposal met with considerable skepticism, leading to a long series of debates in the literature that are beyond the scope of this entry. However, Queller (1997) developed several theoretical arguments that supported two of Trivers’ main points concerning the influence of pre-existing investment disparities and stronger sexual selection on males on the probability of the evolution of male (as opposed to female) parental care. First, males that are likely to succeed in intrasexual competition for mates are selected to

invest in mating effort rather than parental care, and males that are not successful are rarely in a position to provide parental care to their own offspring. This does create a barrier to the evolution of male parental care. Second, differences in certainty of parentage between the sexes should strongly select against further investment by the sex experiencing lower certainty of paternity (typically males).

Although there have been some modifications to Trivers' (1972) original arguments, this seminal article developed several principles that remain cornerstones of sexual selection and mating systems theory (Kokko and Jennions 2008). Hence, in majority of animals that have been studied, males appear to be more inclined to aggressively compete for access to females. Trivers (1972) also argued that females should tend toward high selectivity in the context of mate choice. A vast literature confirms that this is typically the case (e.g., Andersson 1994). However, it does not necessarily follow that females will always avoid polyandry. In fact, with advent of the widespread use of molecular markers, it has become apparent that polyandry is relatively common in the animal kingdom. Even species with putatively monogamous mating systems were found to have frequent extra-pair copulation.

Environmental Influences on Mating Systems

The factors influencing the levels of polygamy in natural populations have been a focus of theoretical work for many years in the field of behavioral ecology. In fact, this area of study forms the main basis of mating systems theory (it is worth pointing out here that mating systems theory focused on social relationships, and did not necessarily accurately describe genetic relatedness to offspring). An early influential paper in this field was published by Emlen and Oring (1977). They focused on characterizing mating systems in terms of specific aspects of the environment and stressed the importance of environmental effects on the ability to acquire and maintain access to mates. Emlen and Oring (1977) incorporated the basic tenets of sexual selection theory

developed by Trivers (1972) into their arguments, and so focused on male access to females as mates (although they also considered sex-role reversed systems). In some cases, this would involve controlling access resources critical to females, whereas in others it would involve direct control of access to females.

They particularly emphasized the importance of spatial and temporal patterns of the dispersion of females in response to environmental heterogeneity. For example, if resources critical to females (e.g., food) are evenly and widely dispersed in patches that are not large enough to support more than a single female, then the best option for a male may be to defend access to an individual female. Conversely, if resources are distributed in patches, and each patch is enough to support several females, then males may be able to defend and mate with multiple females, resulting in polygyny (male polygamy). In the case of temporal variation, if females are ready and willing to mate (e.g., in estrus in mammals) in a staggered fashion, so that not all females in a group or area are receptive at once, then this provides the opportunity for sequential monopolization of mates by males (resulting in increasing levels of polygyny). Emlen and Oring (1977) developed several influential metrics that have commonly been used to describe mating systems, including the "Environmental Potential for Polygamy" or EPP, and the "Operational Sex Ratio," or OSR. The EPP refers to a combination of factors (e.g., the spatial distribution of crucial resources) that influence to what degree a small proportion of males in the local population (or females in sex-role reversed systems) are able to monopolize a large proportion of receptive females. Later this would be referred to as "reproductive skew" (see below). The OSR has been used as a measure of the intensity of sexual selection, although this has been controversial and a variety of other metrics have been developed (see, for example, Klug et al. 2010).

Mammalian Mating Systems

Following on Emlen and Oring (1977), a number of researchers tried to apply their logic to specific

taxonomic groups. Perhaps one of the most successful attempts in this regard was the application of these ideas to mammalian systems. Mammals have a long internal gestation, which means that beyond egg size differences, gestation time and effort impose an even higher disparity in initial male and female investment in offspring. This is probably responsible for the observation that very few mammals show paternal care. Because of this, classifications of mammalian mating systems have focused on different factors affecting polygyny. Clutton-Brock (1989) presented a classic classification of mammalian mating systems, in which he emphasized the extent to which female reproductive rate could be increased by male parental care, the size of female home ranges, the size and stability of female groups, and the density and distribution of females in space. Mating systems ranged from monogamy, to polyandry, to various forms of polygyny and polygynandry.

In obligate monogamy, one female defends a territory and is defended by a single male (e.g., some gibbons, prairie voles). In polymorphic monogamy/polygyny, females are solitary and dispersed, but sometimes one male can defend multiple females (e.g., galagos). In polyandry, females are solitary and defend a territory, but two or more males codefend the females territory (e.g., African wild dogs). In unimale polygyny, females form small groups (and are often territorial), and a single male is able to monopolize that group of females (e.g., yellow-bellied marmot). In multimale polygyny, females form relatively large groups (again, often territorial), and it generally requires groups of males to successfully defend the large female group (e.g., African lions). In some cases of multimale polygyny, males in a group of males defending the group of females are able to monopolize access to individual females within the group (e.g., Cape buffalo). In harem polygyny, females form non-territorial groups of small size, and one male defends the group (e.g., red deer), and in general polygyny, female groups are too mobile to be defendable, and so males defend resource-based territories in regions that females frequently pass through (e.g., zebra). Finally, in lek mating systems, females exist in large, unstable groups that move through

undefended ranges. In this situation, local female densities can be very high, and males defend small, non-resource-based territories where they can display to females. Females may sample multiple male display sites before choosing a particular male to mate with (e.g., Uganda kob).

Avian Mating Systems

In contrast to mammalian systems, most birds have biparental care, and social monogamy is the most common social mating system (e.g., Lack 1968). However, the advent of genetic fingerprinting analysis quickly revealed that genetic monogamy was actually quite rare (e.g., Gibbs et al. 1990). Hence, the actual mating system often involved both multiple mating (polygyny) on the part of males and on the part of females (polyandry). In spite of this, pair-bonding and biparental care does seem to provide important benefits to offspring (and to increase the reproductive success of parents) in many species.

With respect to the social mating system, initial efforts to classify avian mating systems focused on the polygyny threshold model (Verner and Willson 1966; Orians 1969). Under this model, females choose among males that vary in some aspect of quality (typically the quality of resources on the male's territory). Depending on the difference in reproductive success between mating with a low or high quality male, females may prefer to mate with a high quality male as a second mate (even if secondary females do not have equal access to the male's resources), rather than mate with a low quality male in a monogamous pair (this is the polygyny threshold). Some studies have provided evidence that supports the predictions of the polygyny threshold hypothesis for specific taxa. For example, in red-winged blackbirds (Pribil and Searcy 2001 and references therein), there is evidence that female settlement patterns are influenced by male mating status (females showed a preference for monogamous males when matched by quality against polygynous males). Removal experiments demonstrate that polygyny does impose a cost on females. Pribil and Searcy (2001) experimentally

manipulated variation in male territory quality to show that it influences female choice.

However, in other cases the predictions have not been supported, and researchers have proposed alternative hypotheses. For example, Altmann et al. (1977) proposed that female reproductive success might increase with harem size, especially if females engaged in cooperative territory defense. Evidence to support this hypothesis was found in yellow-rumped caciques.

Even when there is a cost of polygyny to females, the polygyny threshold hypothesis may not apply. For example, in pied flycatchers, Alatalo et al. (1982) proposed that females could not recognize whether a male had already mated or not (deception hypothesis). Alternatively, it was proposed that females were unable to find unmated males, or unable to drive off secondary females (Stenmark et al. 1988).

Mating Systems and Sexual Conflict

Davies (1989) proposed a synthetic hypothesis to explain levels of both polygyny and polyandry that focused on the costs and benefits of polygamy to both sexes when both sexes provide parental care (in addition to the effect of the dispersion of resources on male territory quality and female dispersion patterns). Davies (1989) used the example of the Dunnock, which shows extreme variation in mating systems within populations, to illustrate his arguments. Dunnock females and males attempt to extract parental investment from one or more members of the opposite sex. Polyandrous females that are able to attract two males to assist with offspring care have higher reproductive success than monogamous females. Polyandrous females maintain mating relationships with both males, but under some circumstances both males are better off tolerating this uncertainty of paternity rather than seeking a monogamous relationship. Symmetrically, polygynous males that can defend the territories of two females and mate exclusively with both females have higher reproductive success, but at some cost to the average reproductive success of his mates. Hence polyandry (polygyny) provides a benefit

to females (males), but a cost to males (females). Monogamous pairs also occur, as do polygynandrous groups (rarely) consisting of territorial groups of females and males. Variation in the mating system among groups appears to be controlled by a mix of different factors, including variation in individual competitive ability, the adult sex ratio, and environmental conditions such as the density of vegetation.

The argument that sexual conflict, and the resulting struggle over parental investment by males and females, strongly affects mating systems has become widely accepted. Brown et al. (Brown et al. 1997) developed a theory of mating system evolution that incorporated sexual conflict as a key component. They viewed mating systems as a set of adaptations designed to maximize the reproductive success of members of each sex, in the context of the resolution of sexual conflicts. They noted that conflict can occur at many different points in the sequence of intersexual interactions, including pair formation (e.g., signal reliability), courtship (e.g., persistence), copulation, and postcopulatory events (e.g., cryptic mate choice). They focused on several key aspects of manipulation in the context of sexual conflict, including persuasion (e.g., offering a fitness-enhancing incentive such as spermatophores), coercion (e.g., harassment), and forcing (e.g., traumatic insemination). They viewed mating systems as a series of key interactions: typically male-male conflict sorts out which males have the opportunity to mate, female-female conflict partly determines the effectiveness of different forms of male-male conflict, and determines which females have access to male resources (e.g., male parental care), and intersexual conflict affects the effectiveness of alternative forms of intrasexual competition. For example, female control of copulation favors male display and reduced male-male competition, whereas male control of sperm precedence (e.g., via sperm scoops) favors precopulatory mate guarding. They argued that the evolution of mating systems ultimately depends on three sets of variables: the distribution of resources and mates in the context of economic defensibility (as emphasized by Emlen and Oring (1977)), the presence and

availability of material and genetic benefits that are transferred between the sexes, and which sex controls events during the mating sequence (particularly the extent to which persuasion, coercion, or forcing are effective).

Other researchers have also attempted to paint the factors affecting mating systems with a broad brush. For example, Owens and Bennett (1997) emphasized the importance of life history constraints, ecological factors, and social conflicts as factors influencing the mating systems of birds. They used a broad, phylogenetically controlled comparative analysis to argue that these different factors were useful for explaining variation at different levels in the taxonomic hierarchy. Life history constraints appear to be most relevant to explaining variation across broad taxonomic groups (e.g., precociality vs. altriciality may explain differences at broad (family level and above) evolutionary scales). Differences in ecology are more likely to explain differences at lower taxonomic levels, such as variation among species. Finally, variation in the nature and level of social conflicts was more frequently associated with mating system variation among populations within a species.

The Evolution of Polyandry

While polygyny was the focus of mating systems theory early on, in the last several decades interest in polyandry has accelerated, and recent evidence suggests it is a widespread phenomenon, although variable in frequency among taxa (Taylor et al. 2014). In some systems, such as *Drosophila*, polyandry can impose severe costs on female fitness (e.g., Rice 1996). Even in this case, polyandry (promiscuity) is common. However, in other species females suffer no apparent costs and are likely to benefit from polyandry (Lemaitre and Gaillard 2013). For example, polyandry may enable females to acquire more male parental care than they would in a monogamous relationship, as in the Dunnocks described above (Davies 1989). Many other hypotheses concerning the evolution of polyandry have been proposed, and it is likely that different factors have favored its evolution in

different taxa. A recent meta-analysis of the genetic effects of polyandry provided some evidence (depending on assumptions) for both direct and indirect fitness effects of polyandry (Slayter et al. 2012). Other factors may favor the evolution of polyandry in specific taxa.

Beyond polyandry, some species have evolved what some call “Classical Polyandry,” which is associated with sex-role reversal, in which females are more aggressive than males in competition for mates, and males carry out most of the parental care provided to offspring (e.g., jacanas, pipefish). Andersson (2005) proposed a three step model to explain the evolution of classical polyandry: (1) the evolution of male parental care (possibly driven by different factors in different taxa), (2) females become capable of producing more eggs than a single male can care for, and (3) females evolve to compete to provide clutches to more than a single male. Although rare, this appears to have resulted in sex-role reversal in a number of species widely dispersed across the tree of life.

Lek Mating Systems

Another form of polygamy that has received considerable attention from theorists involves lek mating systems (Hoglund and Alatalo 1995). In these systems, males occupy and defend very small territories without resources valuable to females. Females typically observe and approach several males before mating and appear to be highly selective. Male mating success on leks is usually highly skewed, with a few males getting a large proportion of the matings. Lek mating systems are not common, but occur in mammals, birds, amphibians, and insects, so the system is widespread in nature. The factors which are key in the evolution of lek aggregations have been the subject of debate. Working on sage grouse, Gibson (1996) proposed that leks form when males settle on “hot spots,” where females are likely to encounter males during travel between their wintering and nesting ranges. Beehler and Foster (1988) proposed that some males may have especially attractive displays (“hotshots”), and other males may aggregate around these males to attempt to attract some of the many females

attracted to the hotshot male. Finally, others (reviewed in Hoglund and Alatalo 1995) have suggested that females may select for male aggregations because the aggregations allow them to select among a range of males of varying quality and select the best one. Another possibility is that females prefer to select mates in specific places that are safer for them in terms of risks of predation or parasitism. These different hypotheses are still being tested in a variety of taxa, and it is likely that different explanations apply to different species.

Human Polygamy

The mating system of early hominids is the subject of much debate, with some researchers arguing that pair-bonding and monogamy likely characterized the hominin lineage from early on (e.g., Reno et al. 2003), whereas others argue that early hominins were likely polygynous (e.g., Gordon et al. 2008). Early humans may also have been mainly monogamous, probably due to ecological constraints on the ability of a single male to support multiple females. There is some evidence from comparative studies of hunter-gatherers to support this idea (e.g., Walker et al. 2012).

Whatever the early human mating systems were like, the advent of sedentism and agriculture was associated with a major change in human mating systems across the world, with extreme polygyny developing in multiple societies in step with increasing levels of wealth accumulation, cross-generational transfer of wealth, and the size and complexity of social hierarchies (Betzig 2014). As Betzig describes, all of the major foci of civilization were characterized by having despotic reproductive hierarchies in which the (male) rulers had large numbers of mates (wives or concubines) and produced extraordinary numbers of offspring. In China, for example, emperors had access to literally thousands of women. Genetic evidence suggests that one in 200 men carry Y chromosome material inherited from the emperor Kublai Khan, who had a truly phenomenal number of offspring and descendants (Betzig

2014). Other civilizations, such as those in Egypt and India, showed similar levels of reproductive skew. Working down the hierarchy, males had progressively smaller numbers of mates. Given the roughly even sex ratio that characterizes human populations, this meant that there were vast numbers of males at the bottom of the hierarchy that had no mates, in many cases for life (Betzig 2014).

Many traditional cultures show some level of polygyny, and a number of researchers have focused on the causes and consequences of polygyny in traditional human societies, particularly in Africa (e.g., Strassmann 1997). While many cultures across the world still accept some level of polygyny, and some cultures even exhibit polyandry (e.g., Tibet), monogamous marriage has come to characterize the most populous cultures of the modern world. A variety of factors have been proposed to explain this trend, but that is beyond the scope of this entry (see entry on ► “monogamy”).

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Polygamy in Humans

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Synonyms

[Harems](#); [Polyandry](#); [Polygamy](#); [Polygyny](#)

Definition

Mating systems in which a member of one sex associates with multiple members of the other sex.

Introduction

There is little doubt that the “natural” mating system for human beings is polygamy, which includes two different reproductive arrangements: polygyny and polyandry. In polygyny, one man mates with more than one woman, a “harem” as traditionally understood. In polyandry, one woman mates with more than one man. Neither implies promiscuity, since both polygyny and polyandry involve establishing some sort of long-standing relationship.

Evidence for Polygyny

The evidence for human polygyny comes from several independent sources:

1. Sexual dimorphism, the pattern in which the sexes are phenotypically distinct, typically with males larger than females, and – in other animals – often outfitted with anatomical weaponry. Men are, on average, 20 % larger than women, with this difference greater yet with respect to muscle mass. Although such dimorphism does not in itself prove polygyny, it is consistent with male harem formation, since in such a system, male-male competition generally selects for traits leading to success, with greater size and strength often being positively favored. It is also noteworthy that there is a positive correlation between the degree of polygyny (average harem size) and degree of sexual dimorphism, when comparing closely related species this provides added confidence in the significance of sexual dimorphism as an indicator of polygyny.
2. Behavioral dimorphism, the nature of male–female differences in behavior. Physical dimorphism, in itself, would not enhance male fitness if it were not correlated with behavioral dimorphism, notably a greater male tendency toward aggressive behavior, since it is only in concert with behavior that physical endowment facilitates access to females. And in fact, boys and men are significantly more aggressive – even violent – than girls and women.
3. Sexual bimaturism, the difference in age at sexual maturation between girls and boys. Given that women (and female mammals in general) make a larger physiological and metabolic investment in pregnancy and lactation, it would seem that they would become sexually mature later than men, since the latter are required to make a much smaller investment in reproduction. But the pattern is reversed: girls become sexually and socially mature several years earlier than boys. As with evidence 1 and 2, this pattern is consistent with polygyny, since even though a male's biologically mandated investment in reproduction is much less than a female's, polygynous systems impose male-male competition, such that males are more fit if they delay entering the competitive arena until they are large, strong, and perhaps experienced enough to succeed.
4. Prior to the cultural homogenization imposed by Western colonialism, approximately 83 % of traditional societies endorsed polygyny. This does not mean that 83 % of men were harem keepers but that a small number of men would have been disproportionately represented as progenitors (Murdock 1967).
5. There is considerably more genetic variation in mitochondrial DNA (contributed through the maternal line, via egg cytoplasm) than in Y chromosome DNA (Dupanloup et al. 2003). This strongly suggests that the variance in women's reproductive success was less than the variance in its male counterpart – once again, strongly suggesting an important historical role of polygyny.

Evidence for Polyandry

By contrast, the biological evidence for polyandry is more diffuse but nonetheless suggestive.

1. Human beings are unusual among mammals in that females conceal their ovulation. In most species, ovulation is conspicuously advertised, but not in *Homo sapiens*. Although there is debate as the reason for this, one possibility is that whereas conspicuous ovulation would have led to sexual monopolization by one man, such “mate guarding” cannot be effective throughout the ovulatory cycle, so that concealed ovulation enabled ancestral women to mate on occasion with men other than their designated partner (Barash and Lipton 2009).
2. Women are also unusual among mammals in lacking a clear behavioral estrus (or “heat”) cycle. As a result, they are able to exert a remarkable degree of control over their choice of a mate, unlike most female mammals, who find themselves helplessly in thrall to their hormones. Absent such choice, polyandry

would be indistinguishable from literal promiscuity.

3. Recent studies by evolutionary psychologists have shown that during their ovulatory phase, women are attracted to men whose body build and facial features reflect high testosterone and basic good health (that is, good genes), whereas otherwise, they are more influenced by indications of intelligence, kindness, sense of humor, ambition, and personal responsibility. In other words, women follow a two-part reproductive strategy consistent with an evolutionary history of polyandry: mate, when possible, with partners carrying those good genes, but associate socially with those offering the prospect of being good collaborators and co-caretakers of children (Thornhill and Gangestad 2008).
4. The adaptive significance (evolutionary payoff) of female orgasm has long been debated. Among the possible explanations – all consistent with polyandry – is that orgasm enables women to assess the appropriateness of a short-term mating partner as a long-term prospect, while another suggests that female climax is not only rewarding for the woman in question but also reassuring for her partner, providing confidence that she will be sexually faithful while giving her the opportunity to be the opposite.
5. Given that polyandry among animals is predictably correlated with reversals in the “traditional” forms of sexual dimorphism, why has not human polyandry resulted in women being larger and more aggressive than men? For one thing, it is not possible for men to be larger than women (which is mostly a result of polygyny) and for women to be larger than men (because of polyandry). And for another, because of the higher variance in male fitness, the reproductive payoff to polygyny – and its associated male-male competition – is substantially greater than that of polyandry, which in turn has likely caused polygyny to be the more prominent driver of human sexual evolution. This is not to claim that polygyny (acting mostly on men) is any more real than is polyandry (acting mostly on women), but rather

that its effects are more dramatic and more readily identified.

6. Because of the negative fitness consequences for men resulting from polyandry on the part of “their” women, we can expect that men would have been selected to be quite intolerant of it. And indeed, sexual jealousy is a pronounced human trait – also widespread among animals – not uncommonly leading to physical violence. Such a powerful and potentially risky emotional response would not have been generated by evolution if women were not predisposed, at least on occasion, to behave in such a way that is adaptive for them.

Advantages of Monogamy

Although polygamy is more “natural” for human beings, monogamy has much to recommend it, mostly because it increases the likelihood of male involvement in child rearing, something that is otherwise rare in mammals because males, unlike females, lack evolutionary confidence in genetic relatedness to their purported offspring. Human beings also possess an array of proximate mechanisms that permit monogamy and even, under some circumstances, encourage it (Barash 2016). Moreover, a strong case can be made that human beings might be at their best when doing things that are “unnatural,” such as learning to play the violin, to speak multiple languages, and also, perhaps, when resisting their polygamous inclinations.

Conclusion

There is little doubt that human beings are “naturally” inclined to polygamy, apparent as both polygyny and polyandry. Although the impact of polygyny (male “harem” formation) is more immediately evident, there is strong evidence for simultaneous polyandry as well (in which a woman mates with more than one man). Worth emphasizing, however: the fact that polygamy is natural to *Homo sapiens* does not argue against the adaptive value, the desirability, or the

feasibility of monogamy. Human beings, perhaps alone among animals, are capable of consciously resisting their inclinations – and are empowered to do so in proportion as those inclinations are understood.

Cross-References

- ▶ [Female Mate Choice](#)
- ▶ [Female-Female Competition](#)
- ▶ [Harems](#)
- ▶ [Male Mate Choice](#)
- ▶ [Male-Male Competition](#)
- ▶ [Polygyny Threshold, The](#)
- ▶ [Sex Differences](#)
- ▶ [Sexual Conflict](#)

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Polygamy Threshold

- ▶ [Polygyny Threshold \(Behavioral Ecology\)](#)

Polygynandry

- ▶ [Polygamy \(Behavioral Ecology\)](#)

Polygyny

- ▶ [Polygamy \(Behavioral Ecology\)](#)
- ▶ [Polygamy in Humans](#)

Polygyny and Effective Population Sex Ratio

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Synonyms

[Mating market](#)

Definition

When men can have multiple female partners, the ratio of available women to available men in a population is reduced compared to the raw population proportions.

Introduction

Most mammalian species are polygynous, where a male can simultaneously have several female mates (Reichard and Boesch 2003). In polygynous species, male reproductive success is more highly skewed than female reproductive success, both because of high status males with multiple mates and because fewer potential partners are available to lower-status males.

Reproductive Dynamics

The operational sex ratio (OSR) was defined across species as the number of sexually active males per 100 sexually receptive females in a

particular population (Emlen and Oring 1977). Researchers have operationally defined the human sex ratio in terms of raw population counts (e.g., Barber 2000) and as an effective sex ratio in the mating market, e.g., the ratio of unmarried men to unmarried women (e.g., Kruger et al. 2010).

The economics of supply and demand give greater leverage and bargaining power to the rare sex (Fisher 1930); however, because the reproductive strategies of men and women are somewhat divergent, imbalances in the sex ratio exhibit directional effects consistent with the strategies of each sex. There is more competition among men to demonstrate that they are committed long-term relationship partners and providers when women are scarce (Pedersen 1991). Men with lower social status and less abundant resources are even less likely to be married when the sex ratio is male biased (Pollet and Nettle 2007).

In polygynous species, some males will have many offspring, while many others will have none, creating powerful selection pressure for traits that lead to success in mating competition at the expense of longevity (Plavcan 2000). Primates vary considerably in the degree of polygyny; humans have a moderate degree of polygyny (Betzig 1986). Still, men's reproductive success is more variable than women's reproductive success; resulting in male mating competition as a potent force of selection. Polygyny occurs in the vast majority of cultures (84%) documented by anthropologists (Ember et al. 2007).

The higher the degree of polygyny in a population, where high status men are better able to attract and/or retain multiple female partners, the higher the effective sex ratio will be. For every woman who is polygynously mated, there is one less woman available to other men. A polygynous population with a numerical balance of reproductive aged men and women may have an effectively male-biased sex ratio (Hendrix 1996). The degree of polygyny will constrain the effects of female numerical surplus, as well as accentuate male competition in balanced or male-biased populations. Higher degrees of polygyny are

associated with greater consequences of male mating competition (Kruger 2010).

Conclusion

Higher degrees of polygyny correspond to an effectively higher (more male biased) sex ratio, increasing the intensity of male mating competition.

Cross-References

► Operational Sex Ratio

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Polygyny and Male Risk-Taking for Status

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Synonyms

[Male mating competition](#)

Definition

When men can have multiple female partners, male reproductive success is more highly skewed, and male mating competition is more intense.

Introduction

Among mammals and most other animals, females are the limiting sex in reproduction because they provide almost all of the physiological resources required for offspring production. The larger investments allocated to offspring result in much lower potential reproductive capacities in females compared to males. Because of these factors, females are more discriminating in mate selection, and males exert comparatively more effort than females in attracting and retaining mates (Bateman 1948; Trivers 1972).

Although men provide less parental investment in offspring than women, human paternal investment is considerably larger than that of most other primate males (Buss and Schmitt 1993). Altricial human offspring require tremendous parental investment, and the value of the male contribution to this investment is indicated by the higher mortality rates (Hill and Hurtado 1996) and lower reproductive success (Geary 2005) among children who grow up without a father present.

Preferences for certain characteristics in selecting romantic partners are in part a reflection of the value that men and women provide in reproductive relationships (Buss 1989). Women

prefer men with cues of ability and willingness to commit to long-term relationships and substantial paternal investment (Buss 1989). Males with higher social status and greater economic power have higher reproductive success across a wide variety of societies (Hopcroft 2006). Thus, men compete for social status and resource control, and greater inequality leads to greater risk-taking in the service of this competition (Kruger and Nesse 2006). The degree of polygyny, related to the degree of male reproductive inequality, intensifies risk-taking related to male mating competition (Kruger 2010).

Human Reproductive Dynamics

Males compete more intensely for female sexual partners in most animal species because females usually invest more in offspring and are therefore selected to be more discriminating in selecting mates (Bateman 1948). Male mating competition can involve fights with other males for rank or territory; it can also involve competition over traits and displays that females prefer in their mates. Males succeeding in these competitions have more offspring, shaping traits that foster such success, even if those traits also have detrimental consequences (Darwin 1871). Thus, sexual selection helps explain sex differences in psychology and behavior, including greater male tendencies for risk-taking, competitiveness, and sensitivity to social hierarchy (Cronin 1991).

Both women and men share preferences for partner characteristics such as kindness, understanding, and intelligence (Buss 1989); however, male and female preferences also show divergence following reproductively relevant currencies. Human paternal investment is near the high end of the spectrum for mammals, especially for primates (Low 2003). Paternal investment may enhance offspring survival (Hill and Hurtado 1996) and reproductive success (Geary 2005). Thus women prefer males with higher social status and resource control as marriage partners, because of their high potential for investment (Buss 1989). Culturally appropriate indicators of male social status and economic power directly

predict reproductive success across a wide variety of societies (see Hopcroft 2006). Variance in male wealth and power increased over historical time through sociopolitical arrangements and intergenerational transfer (Smuts 1995).

Greater variation and skew in male social status and resource control produces greater competition for positions of power and status. This heightened degree of competition leads to higher levels of risk-taking, with resulting detrimental consequences for mortality (Kruger 2010). Socio-economic status has a stronger influence on mortality rates for men than for women (Kruger and Nesse 2006; Martikainen et al. 2001). Increasing uncertainty of economic opportunities and increasing variability in male social status and resource control within populations are also associated with elevated male mortality rates (Kruger and Nesse 2007).

Polygyny

Polygyny is the most common mammalian mating system, likely because of female specialization in infant nutritional provisioning and care and male specialization in mating effort (Low 2003; Reichard and Boesch 2003). The degree of polygyny is analogous to male reproductive inequality. In highly polygynous species, a few males will have many offspring, whereas many others will have none (Reichard and Boesch 2003). This highly skewed reproductive success creates powerful selection pressure for traits that lead to success in mating competition. Such selection pressure has produced elaborate ornaments (such as the peacock's tail) and armaments (such as a deer's antlers), all with substantial costs. The elephant seal is an archetypal example of a highly polygynous species. The disproportionately large males compete intensely for large harems of females, and most males die before reproducing.

The longevity gap between male and female vertebrates is highest among polygynous species (Clutton-Brock and Isvaran 2007). Most mammalian species are polygynous, where a male can simultaneously have several female mates (Reichard and Boesch 2003). In polygynous

species, male reproductive success is more highly skewed than female reproductive success, both because high status males can obtain multiple mates and because fewer potential partners are available to lower status males. Male elephant seals have over four times as much variance in reproductive success as females (Le Boeuf and Reiter 1988). The intense male mating competition in polygynous species selects for strategies that enhance competitive success at the cost of longevity (Williams 1957). Across species, higher degrees of polygyny correspond to greater male-male competition and higher levels of risky male behavior (Plavcan and van Schaik 1997), larger size and armor of males, and exaggerated male mortality rates compared to females (Leutenegger and Kelly 1977).

Human Polygyny and Risk-Taking

Humans are less polygynous than most other primates, but the variation in male reproductive success is still substantially higher than that for females (Betzig 1986). A small number of high status men have a disproportionately high number of mating partners, and the positively skewed distribution of male reproductive success makes mating competition a potent selection force (Betzig 1986).

Polygyny occurs in the vast majority of cultures (84%) documented by anthropologists (Ember et al. 2007). Human populations vary in their degree of polygyny, covarying with pathogen stress and male mortality in warfare (Ember et al. 2007). Polygyny is most prevalent in human societies when there is substantial inequality in resources and social status (Orians 1969). Increased sexual dimorphism, where males are larger than females, is directly and positively related to the level of male mating competition (Bribiescas 2006). Human females are on average 80% as large as males (Clutton-Brock 1985).

The degree of polygyny reflects the intensity of male mating competition, which in turn is associated with higher levels of risk-taking and greater male mortality rates (Kruger 2010). Some of this risk-taking is through physical violence, which is

a facet of human male mating competition both within and between groups (Chagnon 1992). Men can successfully use violence to elevate their social status and gain respect (Campbell 1993; Chagnon 1992; Hill and Hurtado 1996). Violence may result from competition over access to and control of resources, as well as position in the status hierarchy (Buss and Shackelford 1997). Greater nonviolent risk-taking, leading to higher numbers of accidents, results in greater male mortality rates. This is especially prevalent in young adulthood when males are entering into mating competition (Kruger and Nesse 2004, 2006).

Conclusion

The degree of polygyny in a population influences the intensity of male mating competition; greater competition for status leads to riskier behavioral and physiological strategies.

Cross-References

► Polygyny and Effective Population Sex Ratio

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Polygyny Threshold (Behavioral Ecology)

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Synonyms

[Polygamy threshold](#)

Definition

The polygyny threshold is the minimum difference in quality of male territories that is sufficient to make a female choose to mate with a male that is already mated, instead of mating with a male that has no mates.

Introduction

For decades, polygynous mating systems – in which a male is paired to two or more females – were seen as a reflection of the population sex ratio. Under this rationale, a 1:1 adult sex ratio (one male for each female in the population) would predict that males would mate, on average,

with one female during the breeding period, and females would behave the same way; i.e., the mating system would be monogamous. Following this rationale, in a biased sex ratio scenario of 1:3 (one male for three females), it would be expected that males would acquire more than one mating partner; i.e., a polygynous mating system would be predicted. However, through the accumulation of data on sex ratios and mating system characteristics, it was noted that there are cases that rebut the already mentioned rationale to explain the evolution and development of polygynous mating systems. For instance, there are monogamous species with biased sex ratios, and polygynous species with even sex ratios.

In the light of the inconsistency of the sex ratio hypothesis, in the 1950s, researchers started to develop hypotheses to explain the evolution of polygyny. Verner (1964) noticed that in a population of the long-billed marsh wren, *Telmatodytes palustris*, despite the even sex ratio, there were several cases in which females chose already mated males, while there were unmated males available. If females choose a mated male instead of a bachelor, they should gain fitness benefits from this behavior and, thus, there should be selection acting on females to mate polygynously. Given this scenario, Verner (1964), and Verner and Willson (1966) developed the hypothesis that when differences exist in the qualities of male territories, if the difference between two territories is large enough, females will choose the male in the better territory even if this territory already has a female and the other territory has no females. This led to the idea that there must be a threshold that determines whether a female must remain in monogamous relationships or join polygynous ones, i.e., the polygyny threshold.

From Monogamy to Polygyny

Every trait or behavior that enhances the fitness of an individual is expected to be selected. If a male acquires more offspring by mating with several females, one can expect the evolution of polygyny. However, if the male provides parental care to the offspring, the evolution of polygyny may be

disadvantageous to females, given that a polygynous male will have to share his parental effort among the offspring obtained with different females – each female receives less help than she would obtain in a monogamous relationship. If polygyny is disadvantageous to females (i.e., reduces their fitness), one can expect polygyny to be counter-selected.

If a female in a polygynous group receives less help in caring for her offspring, what could also make polygyny advantageous to females, to the point that polygyny would be selected? Mating with already mated males would be expected in situations in which the female may gain greater direct (e.g., food, protection, nest sites) and/or indirect (e.g., genes of higher quality to her offspring) benefits from polygyny. Given the potential benefits, females should choose among males basing their decision on: genetic male quality, potential paternal care, and the quality of the territory held by each male. Every time these benefits overcome the costs of polygyny (e.g., less help in caring for young, greater competition for resources), polygyny is expected to evolve. This evolution is likely to take place when there is variance in the distribution of a particular resource (e.g., food) in the environment. Such variance allows the existence of territories that contain greater amounts of resource than others. Once the territories are different in quality, if the male population is large enough, some males will occupy low-quality territories. Once males occupy territories that vary in quality, they cannot offer equivalent reproductive benefits to females.

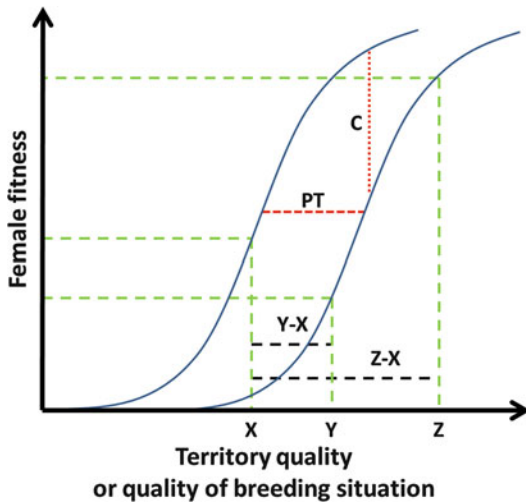
Hypothetically, the first female to choose a mate has all the n mature males available to her choice. If the territories held by these males differ in quality, the female is predicted to choose the male holding the best territory. The second female to make a choice faces a different situation; she may choose between a number of $n - 1$ unmated males, and one mated male holding the best territory. If this second female gains more offspring by choosing the male with the second best territory than mating with the mated male, she is expected to become monogamous. However, if despite the costs of sharing the best territory with another female, the second female gains more offspring

by choosing the mated male with the best territory instead of the bachelor holding the second best territory, she is expected to establish a polygynous relationship. This shift from monogamy to polygyny is created by the differences in quality between the males' territories. This polygyny threshold can only be crossed once a female joining a polygynous group can achieve reproductive success at least as high as if she would by mating with a bachelor. If the differences in territory quality are of great magnitude, it is possible that some males will be able to monopolize a larger proportion of females, leading some low-quality males with low-quality territories to stay unmated.

The Polygyny Threshold Model

The polygyny threshold model (PTM) was developed by Orians (1969) in order to propose a hypothesis for the evolution of mating systems in birds and mammals based on individual fitness, and in opposition to a hypothesis based on group selection. Through the analyses of female choice possibilities, the PTM provides theoretical basis to predict the development of mating systems, specifically the shift from monogamy to polygyny. Polygyny is always expected to be advantageous to males, thus to understand the evolution of polygyny, one should focus on benefits and costs to females. Hence, the PTM is based on female choice.

The PTM assumes that (a) females actively choose mates; (b) if a female chooses to mate with a particular male, this choice prevents her from choosing another male; (c) if a female rejects a particular male, there is no loss in fitness, on average, as there are other males available, and the female has a high probability of mating with at least one of them; (d) the population occupies a heterogeneous environment in relation to conditions or resources relevant to reproduction, such that territory quality, and reproductive success are correlated. The PTM is explained by graphical means and contains two curves: the left and right curves represent, respectively, females in monogamous and females in polygynous groups (Fig. 1). For a given territory quality value, the fitness



Polygyny Threshold (Behavioral Ecology), Fig. 1 The polygyny threshold model illustrates the relationship between the territorial quality (or any breeding situation related to a specific available male) and female fitness. X represents the quality of the territory held by an unmated male x . Y and Z represent the respective qualities of the territories held by two already mated males, y and z . C represents the fitness costs of mating polygynously, and PT represents the polygyny threshold. $Y-X$ represents the differences in quality of the territories held by males x and y , and $Z-X$ represents the differences in quality of the territories held by males x and z . Every time the difference in quality between territories exceeds the polygyny threshold, females are expected to mate polygynously

payoff of polygynous females is always less than the payoff that a monogamous female would gain, because polygyny tends to incur costs C that are absent or not as high as in monogamy (e.g., less paternal care, increased competition from higher density of individuals sharing higher quality habitats, increased predation risk from the agglomeration of individuals in higher quality habitats). Every time the differences in territory quality exceed the polygyny threshold, the female is predicted to mate polygynously (e.g., $Z-X$ in Fig. 1). However, when the threshold is not surpassed (e.g., $Y-X$ in Fig. 1), the female should mate monogamously.

The PTM promoted a great amount of empirical tests, and received support from different sources of data, for instance: polygynous females of great reed warblers, *Acrocephalus arundinaceus*, indigo buntings, *Passerina cyanea*,

and lark buntings, *Calamospiza melanocorys*, show similar reproductive success when compared to monogamous females; the majority of red-winged blackbird females chose polygyny when they were experimentally faced with mated males with territories containing more nest sites, and bachelors with territories containing fewer nest sites; by breeding in high-quality territories, these polygynous females gained fitness benefits that surpassed the costs of mating polygynously (Pribil and Searcy 2001), which makes the polygyny option adaptive.

Counter-Evidences and Criticism

The PTM was also refuted by other studies, which leads to the idea that the applicability of the PTM may be restricted to some contexts and systems, in a way that some species and even particular populations in generally polygynous species may not behave as predicted by the model. For example, in the work of Pleszczynska (1978), some females that could mate with a mated male with a better territory chose to mate with a bachelor. In red-winged blackbirds (different study from the mentioned above), females do not even pay a cost of polygyny. Moreover, other studies report that second females to mate with the male gain lower fitness than monogamous females. Given the difficulties in interpreting the contrasting evidence, alternative or complementary hypotheses to the PTM have been proposed. For instance, it has been argued that, if females settle asynchronously in a male territory, the overlap in urgency for paternal care by each brood may be reduced, which diminishes the polygyny threshold (Leonard 1990). The sexy son hypothesis has been proposed to explain cases of lower fitness of second females (Weatherhead and Robertson 1979). This hypothesis states that a second female to cross the polygyny threshold may gain less reproductive success than a monogamous female at a first moment. But, their young will be of higher quality – since the young received alleles from a high-quality polygynous father – thus, she will gain greater fitness in future generations through the offspring of her sons.

Another limitation of the PTM is that it assumes that females may choose mates freely (i.e., PTM is an ideal free model), but, in many cases, females are not free to choose partners. For instance, second females may not be allowed to settle by resident females of mated males (e.g., red-winged blackbirds), thus they may not be able to cross the polygyny threshold. Besides that, sometimes, females may mate with an already mated male just because it is difficult to find unmated males, distinguish mated from unmated males (Alatalo et al. 1981), and/or properly sample males and territories. Lastly, contrary to the PTM, sometimes it seems that females do not suffer costs from polygyny and just settle at random, which led to a neutral mate choice hypothesis (Lightbody and Weatherhead 1988).

Conclusion

The polygyny threshold is an important idea that helped to explain the evolution of polygynous mating systems. The concept led to the development of several theoretical models, especially the PTM. This model provided theoretical base and many predictions for empirical tests. The limitations of the PTM stressed in the last four decades are important and must be considered in the construction of the paradigm. Nevertheless, the PTM and, particularly, the concept of a polygyny threshold remain key points in the continuous effort to understand the evolution of mating systems.

Cross-References

- [Female Choice](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Female Mate Choice](#)
- [Female Mate Choice \(Intersexual Selection\)](#)
- [Harems](#)
- [Mate Choice Effects](#)
- [Mating Systems](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Polygyny](#)

- [Polygyny and Effective Population Sex Ratio](#)
- [Polygyny Threshold, The](#)

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Polygyny Threshold, The

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Synonyms

[Female choice polygyny](#); [Resource-defense polygyny](#)

Definition

The polygyny threshold model (PTM) provides an explanation for the occurrence of polygyny in the animal kingdom – the mating/marriage of one male with multiple females. This model is principally applied to species, including humans, in which males provide/defend resources to provision their mates and offspring. The *polygyny threshold* refers to the minimum level of inequality in male resource holding, such that a given female's reproductive success is enhanced by becoming the second mate of a resource-rich and already paired male, rather than the sole mate of a resource-poor unpaired male. Once this threshold is surpassed and there is sufficient inequality, polygyny is predicted to occur.

Introduction

Understanding the determinants of mating and marriage systems is vital to a complete understanding of humanity, since they have been demonstrated to have knock on effects at many levels of society. These tenants of social structure bear influence on parenting strategies and family dynamics, violence and crime rates, inheritance systems, and much more. In the case of polygynous societies – where one man mates/marries multiple women – such a system is associated with decreased paternal care for offspring (Strassmann 1981), increased male-male aggression (Schmitt and Rohde 2013), and patrilineal inheritance systems (Hartung et al. 1982). The socially imposed monogamy observed in many industrialized societies today is not representative of the majority of human populations. In fact, polygyny is estimated to be permitted in more than 80 % of human societies (Murdock 1967), and therefore it is still very relevant to our understanding of human behavior.

In order to understand the evolutionary explanation for the widespread occurrence of polygyny in human societies, it is necessary to comprehend the underlying mechanisms behind sex differences in mating behavior and mate choice. The following entry will have five sections:

(1) parental investment and female choice; (2) female mate preferences; (3) women's preference for resources; (4) the polygyny threshold model, theory; and (5) the polygyny threshold in humans – empirical evidence.

Parental Investment and Female Choice

Trivers defined parental investment as *any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring* (Trivers 1972, p. 139). These investments include energetic investments such as producing gametes, material investments such as provisioning an offspring with nutrients, and behavioral investments such as guarding offspring from predators. Males and females have different costs of reproduction, which begin with anisogamy – the fusion of two different gametes in sexual reproduction. The male sex cell is small and metabolically cheap to produce, whereas the female sex cell is larger and more costly. Usually the female is the sex which invests more in the offspring given the initial sunk investment of the more costly sex cell (Trivers 1972). Conversely, the extent of male parental investment (MPI) varies considerably between species, sometimes being limited to the contribution of sperm, e.g., in fish species with internal fertilization, males do not participate in any brood care (Perrone and Zaret 1979); and in other cases MPI includes considerable provisioning and protection for extended periods of time, as observed in many bird species (Møller and Cuervo 2000).

Given that the male gamete is cheap and that it is usually females who invest more in offspring, males have a fast potential reproductive rate; thus, the limiting factor of a male's reproductive success is access to opportunities to fertilize female sex cells (hence, polygyny is advantageous to males since it increases these opportunities). On the contrary, female reproductive rates tend to be restricted by the production of costly sex cells and considerable investments in rearing offspring; hence access to mates is not the primary limiting factor of female fitness (Clutton-Brock and

Vincent 1991). Therefore, it is typically females who are the more choosy sex in terms of mate selection, this phenomenon is referred to as “female choice” (Trivers 1972).

Female Mate Preferences

The traits valued by females of a particular species are largely determined by the necessity of MPI for the successful siring of offspring. Among species where MPI is low and unnecessary, females will predominantly select mates based on their genetic robustness (in terms of survival and reproduction prospects), and complementarity (in terms how well matched a male and female genome are for the production of robust offspring) (Trivers 1972). However, in other species where MPI is more necessary and biparental investment is more crucial to offspring survival, alongside purely genetic characteristics, females give consideration to the ability of a male to provide high-quality parental investment (Trivers 1972). This preference explains the ubiquity of the courting ritual in which males offer females nuptial gifts that serve as demonstrations of their willingness and ability to invest resources. Such behaviors are common in species where females rely substantially on MPI, including many species of bird, and indeed in our own – the diamond engagement ring is an appropriate signal of a man’s commitment to invest resources (Lack 1940; Miller and Kanazawa 2007).

Women’s Preference for Resources

Narrowing the focus to humans, compared to the rest of the mammalian class, our species are somewhat of an anomaly – in approximately 95 % of mammalian species, MPI is very limited (Geary 2000). In contrast, whether it is manifested in the form of hunting for the next meal or paying tuition fees, paternal investment is ubiquitous and extensive across much of the spectrum of human societies. This high MPI can be attributed to the combination of two factors – the restricted

reproductive rate of women and the highly dependent nature of human children.

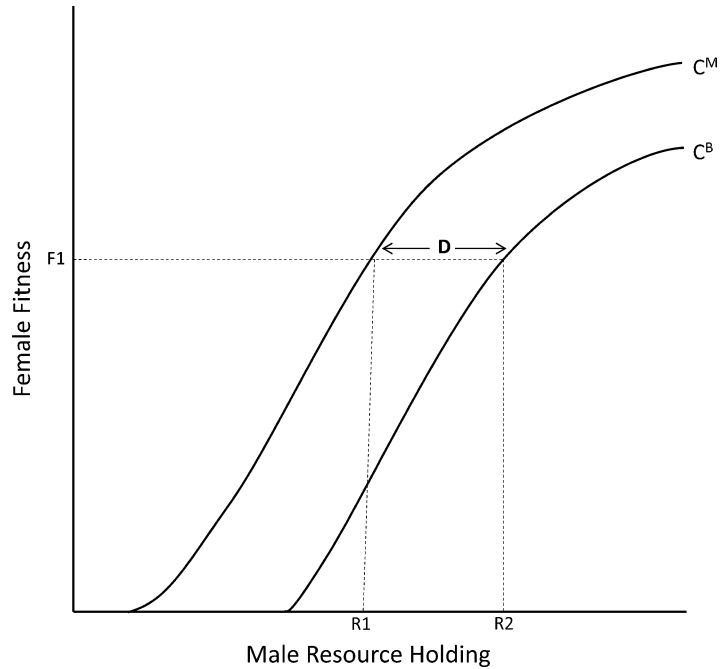
Due to the 9-month internal gestation period and the subsequent phase of lactational amenorrhea, women are very limited in the quantity of offspring they can produce over the course of their reproductive career. Additionally, the narrow female pelvic canal designed for bipedalism combined with strong selection for encephalization has resulted in the *obstetric dilemma* and human children being born altricial with a substantial proportion of brain growth having to occur postpartum (Rosenberg and Trevathan 2002). Thus children have an extended period of dependence, requiring extensive provisioning to support their metabolically expensive development (Kaplan et al. 2000). Therefore, women have been strongly selected to show mate preferences for men who demonstrate a capacity for high MPI and who can provide resources to maximize the quality of the limited quantity of (highly dependent) offspring they can produce. In a seminal study of 37 cultures across six continents, Buss (1989) showed that women consistently place high value on cues of male resource-holding potential.

Based on the information thus far, the evolutionary puzzle which emerges is deciphering why women would ever partake in polygyny. Polygyny provides an obvious evolutionary advantage to men since sperm is cheap and their potential reproductive rate is not restricted, and therefore access to more mates results in more potential fertilizations and higher fitness. However, for women, who are the choosy sex, it is resource access which is crucial to fitness. This begs the question of why a woman would choose to participate in a polygynous marriage given that such a system requires them to share their husband’s resources and parental investment with his other wives.

The Polygyny Threshold: Theory

As described above, in species such as humans where MPI is necessary, females require resource provisioning from their mates in order to maximize the quality of their limited quantity of

**Polygyny Threshold,
The, Fig. 1** Graphical
representation of the
polygyny threshold model
(Adapted from Orians
(1969))



offspring. Therefore, natural selection has shaped female mate preferences to place strong emphasis on male resource holding. This is the central premise of the *polygyny threshold model* (PTM) (Verner and Willson 1966; Orians 1969) – that a female’s evolutionary fitness is determined by the access to resources her mate can offer her; and her mating/marriage behavior should be shaped by natural selection to maximize her fitness. The model was first developed to explain mating systems in birds, and then latter applied explicitly to human polygyny (Borgerhoff Mulder 1988). It asserts that there is a level of inequality in male resource holding such that a female will achieve higher biological fitness being paired as the second partner of a resource-rich male than she would as the first partner of a resource-poor male. This is because with sufficient inequality, a fraction of a rich man’s resources, which are shared among multiple spouses, may be greater than the total of a poor man’s resources. This level of inequality is the *polygyny threshold*, and once it is surpassed, polygyny is predicted to occur. Therefore the PTM predicts that the incidence of polygyny in a society should be closely associated with the degree of stratification of male wealth.

Figure 1 provides a graphical representation of the PTM (modified version of the original figure from Orians (1969)). The curves reflect the relationship between a male’s resource holding and the fitness of a female pairing with him (a) monogamously (C^M) or (b) bigamously (C^B). For any given environmental quality, curve C^M is lower than curve C^B because resources must be shared if a female is paired to a male bigamously, and in turn her fitness is lower than if she was monogamously paired with him and had exclusive access to his resources. However, for each level of resources provided by an unpaired male, there is a corresponding higher level of resources provided by an already paired male which would result in a given female achieving the same fitness. For instance, a female would achieve the same fitness ($F1$) being paired monogamously to a male with resource holding $R1$ as she would being paired bigamously with a male with resource holding $R2$. Thus if this level of inequality (D) exists within a society, a female can achieve the same fitness via bigamous mating as monogamous mating and polygyny can emerge via female choice. Therefore, D represents the *polygyny threshold*.

The Polygyny Threshold in Humans: Empirical Evidence

The PTM makes three main predictions: (a) the incidence of polygyny across human societies should correlate with their relative levels of male inequality in resource holding; (b) in societies where polygyny does occur, it is resource-rich men who achieve polygyny; and (c) women marry polygynously when it is optimal for their fitness and therefore should not achieve lower fitness than monogamously paired women. All of these predictions have empirical support; however, the evidence for the final prediction is more mixed.

To begin with, there is strong support for the prediction that polygyny is more likely to occur in societies with greater male wealth inequality. At contact, Native American societies demonstrated a positive association between polygyny prevalence in a community and the extent to which males could monopolize food extraction sites, such as resource-rich fishing or hunting areas (Sellen and Hruschka 2004). This trend has even been applied at the macro level of nation-states. Schmitt and Rohde (2013) calculated a “human polygyny index” (HPI) for 38 nation-states based on the number of sexual partners reported by men and women and found a strong positive association between a nation’s HPI and their Gini index of income inequality.

Within societies with sufficient inequality, as predicted, it is the resource-rich males who marry polygynously. For instance, in Uganda, which is highly dependent on agriculture, ownership of land is a strong predictor of a man’s likelihood of having more than one wife (Pollet and Nettle 2009). Nettle and Pollet (2008) also analyzed selection gradients of wealth in 11 societies and found strikingly high selection on male wealth in the two polygynous societies from their sample, thus providing further evidence that it is indeed resource-rich males who benefit from increased mating access. Even more pronounced examples can be found in historical empires where male resource holding was extremely skewed, and emperors had access to immense wealth and in turn a vast number of mates. Dynastic leaders in

Asia had prolific concubines, and Y-chromosome research estimates that ~40 % of living Asian men may be descendants of just eleven powerful rulers from the last few thousand years (Balaesque et al. 2015).

Polygyny rates in extant hunter-gatherer societies, whose lifestyle reflects the way our species lived for the majority of human evolutionary history, are approximately 14 % (Marlowe 2005). The incidence of polygyny in this subsistence mode had previously posed a problem for the PTM since hunter-gatherers do not accumulate resources; hence, no inequality in male resource holding is assumed. However, recent research reconciles hunter-gatherer polygyny with the PTM, finding it is men with stronger social networks who marry polygynously in these groups, and these men may have superior resource access due to larger food sharing networks (Chaudhary et al. 2015).

With respect to the final prediction of the PTM, the evidence is less consistent. A woman’s evolutionary fitness is determined by both her fertility and offspring survival. There is some research indicating that polygyny can be detrimental to both of these components of female fitness and thus cannot be explained by the PTM, which asserts that it is an adaptive female choice. The polygyny-fertility hypothesis refers to the occurrence of lower fertility among polygynously married women than their monogamous counterparts, which is most likely caused by reduced coital frequency (Bean and Mineau 1986). In a review of 86 studies, 64 found evidence for the polygyny-fertility hypothesis (Josephson 2000). Moreover, the offspring of women married polygynously may also incur increased mortality risk since they have access to a smaller proportion of their father’s parental investment. The results concerning offspring mortality are inconsistent and vary cross-culturally. For instance, a study using demographic and health surveys from Ghana found that children whose fathers are married polygynously experience higher childhood mortality (Gyimah 2009); conversely, among the agropastoralist Kipsigis from Kenya, there is no significant effect of marital status on offspring survivorship (Borgerhoff Mulder 1989).

Despite considerable evidence for the polygyny-fertility hypothesis, which contradicts the PTM, the latter should not be disregarded. There are numerous potential confounding factors, which could result in the polygyny-fertility effect even if polygyny is an adaptive choice for women. For instance, women who marry polygynously are often older than those who marry monogamously, and men married to sterile wives will often marry polygynously (Pebbley et al. 1988). Additionally, Josephson (2002) found that although polygynously married women in the nineteenth-century Utah had fewer offspring than monogamously married women, they actually had the same number of grandchildren due to enhanced reproductive performance of their offspring. Thus the polygyny-fertility effect may fail to account for complex patterns governing the relationship between polygyny and women's long-term fitness.

Nevertheless, the possibility that polygyny may be detrimental to women's fitness in certain circumstances can certainly not be disregarded. Such cases may occur in settings where the rule of female choice is superseded by male coercion and thus the PTM is not applicable. In these contexts, dominant males are able to exert control over female reproductive behavior and monopolize multiple women. Among the Dogon of Mali, child mortality is a major determinant of female fitness, and the offspring of mothers married polygynously are 7–11 times more likely to die by the age of five (Strassmann 1997). Despite this, polygyny is extremely prevalent and has been attributed to the dominant position of men in Dogon society who are able to suppress female reproductive interests, i.e., male coercion rather than PTM/female choice explains polygyny (Strassmann 1997).

Conclusion

In humans, due to the restricted reproductive rate of women and the necessity of biparental care for altricial offspring, when selecting a mate, women are particularly concerned with a man's ability to provide resources. Therefore, the PTM

hypothesizes that in societies where there is sufficient inequality in men's resource holding, polygyny will emerge. This is because women will preferentially enter polygynous marriages with rich men than monogamous marriages with poor men.

The predictions of this model have mixed support from research on human populations. There is strong evidence that polygyny is more likely to occur in stratified populations and that it is rich men who marry polygynously within these societies. However, the PTM also predicts that women will choose polygyny when it is optimal for their fitness and therefore should not achieve lower reproductive success than monogamously paired women. Many studies indicate this may not be the case and that polygynously married women experience lower fertility or higher offspring mortality. These contradictory findings highlight that it is necessary to consider other models of polygyny, such as the male coercion model, in combination with the PTM for a full understanding of human marriage practices.

Cross-References

- [Female Choice](#)
- [Mate Preferences](#)
- [Mating Systems](#)
- [Parental Investment and Sexual Selection](#)

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Polyvagal Theory

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Synonyms

Autonomic nervous system; Heart rate; Parasympathetic nervous system; Phylogenetic; Respiratory sinus arrhythmia; Tenth cranial nerve; Vagal tone; Vagus nerve

Definition

The parasympathetic nervous system has two divisions affecting heart rate and general arousal, responding to novel stimuli/stressors. The older division causes freezing behaviors to novel stimuli. The evolutionarily newer division regulates social communication and self-soothing behaviors.

Introduction

Polyvagal theory was proposed by Stephen W. Porges (1995) to elucidate neurogenic control over the autonomic nervous system. Early related works assumed that the vagus nerve (tenth cranial nerve) was operated by only one neuronal control center in the brain, which is unable to explain some findings of parasympathetic functions on arousal, known as the vagal paradox, as well as being unable to explain how extreme stress can cause individuals to freeze. Polyvagal theory may overcome the vagal paradox and freezing issues by uniting under a neurogenic model of vagal regulation for orientation, attention, and emotion (Porges 1995) by assuming vagal control from multiple neuronal control centers.

In polyvagal theory, the parasympathetic system is composed of an evolutionarily older system and an evolutionarily newer system (Porges 1995). Multiple systems mean multiple neuronal nuclei feeding the vagus. Although only two systems are assumed in the model, several different nuclei in the medulla feed the vagus both afferently (receives signals from the body) and efferently (sends signals to the body) (Porges 1995). The evolutionarily older system causes freezing behavior common to lizards reacting to predators/prey; the evolutionarily newer system allows mammals to build social ties by dampening the effects of the sympathetic nervous system when no environmental threats are perceived (Porges 1995). The two systems in polyvagal theory are most noticeable in efferent pathways, showing a clear phylogenetic split between reptiles and mammals.

Vagal Tone

Vagal tone is the amount of activity traveling through the vagus nerve at any given time. The vagus, being part of the parasympathetic system, is used to measure the amount of parasympathetic activation (Porges 1995). Vagal activity is typically not measured directly, but because the vagus innervates the sinoatrial node of the heart (controls heart rhythm), heart rate and heart rate

variability have been the most widely used measures to assess vagal activity (Porges 1995). Heart rate can be viewed as tonic (producing muscular contraction) vagal control over the heart, whereas heart rate variability can be viewed as phasic (short-term step in the full tonic process) vagal control of the heart (Porges 1995). Decreases in overall heart rate are caused by high tonic vagal tone. In terms of heart rate variability, respiratory sinus arrhythmia (RSA) is used. Inhalation briefly suppresses vagal activity, causing a brief increase in heart rate, whereas exhalation resumes vagal activity, leading to a brief decrease in heart rate. The greater the difference in heart rate between inhalation versus exhalation, the greater the RSA and therefore higher vagal tone.

Vagal Paradox

The issue with taking heart rate or heart rate variability measurements is that they should both represent vagal activity, but within the interactions lie contradictions. The paradox is such that (1) increases in vagal tone are correlated with bradycardia (extreme slowing of heart rate) and (2) decreases in vagal tone are correlated with low RSA; (3) however, bradycardia can occur during periods of low RSA (Porges 1995). Therefore, if vagal activity was only controlled by one neural system, then bradycardia and RSA should happen in tandem, but they often do not.

Polyvagal Theory

Afferent Pathways: Neuroception

Because efferent pathways only make up 20 % of the vagus, 80 % are afferent fibers (Porges 2007). Although the brainstem is responsible for functions below conscious awareness (i.e., heartbeat and digestion), perceptions received at this level nonetheless cause the brain to react noticeably, through emotions and alertness. From this perspective, animals may not always know what has roused or relaxed them because this perception happens unconsciously. This unconscious perception of one's body and surroundings has been termed neuroception (Porges 2007).

Neuroception is vital for animals to quickly assess the amount of risk one is at, at any given time. Sympathetic and amygdalar pathways are also fed information via this route, causing neuroception in both arousal and emotional activation (Porges 2007), putting the body in the proper state of arousal given their unconscious assessment of the environment. Once risk is assessed, information is sent along efferent vagal pathways for immediate action, only inhibited by later, conscious, assessment of the environment.

Efferent Pathways: Phylogenic Differences

Polyvagal theory is based on the idea that there are several control centers on the medulla with projections on the vagus, giving the vagus multiple functions. The main idea is that there are two different efferent motor systems of the vagus that affect the body: one is evolutionarily older, common to all vertebrates, known as the dorsal vagal complex (DVC); the second is evolutionarily newer, mainly only distinguishable in mammals, known as the ventral vagal complex (VVC) (Porges 1995).

DVC The DVC originates in the dorsal motor nucleus of the medulla. It is the evolutionarily older system that is common to all vertebrates, innervating subdiaphragmatic organs (organs distal to the diaphragm, i.e., stomach and intestines) as well as the sinoatrial node of the heart. This system becomes active when orienting toward predators or prey, in order to slow down heart rate and conserve energy, tracked by measurements of bradycardia. However, it is unmyelinated, causing its signals to be slow and lingering (Porges 1995).

VVC The VVC originates in the nucleus ambiguus of the medulla. It is the evolutionarily newer system which is most observable in mammals. The VVC innervates supradiaphragmatic organs (superior to the diaphragm, i.e., lungs and esophagus), the sinoatrial node, as well as muscles related to vocalization and facial expression. This system becomes active during socially affiliative behaviors such as social communication and self-

soothing. It also acts as a vagal brake, keeping mammals from becoming overactive when inappropriate. This system's activity is tracked by RSA measurements (Porges 1995).

Vagal Brake

The VVC's inhibitory effects on the sinoatrial node of the heart inhibit the hypothalamic-pituitary-adrenal axis, effectively dampening the effects of the sympathetic nervous system when mammals are comfortable and relaxed (Porges 1995). Since the VVC is myelinated, its influence over the heart is immediate, versus the influence of the unmyelinated DVC. The fast-acting effects of the VVC allow it to quickly and repeatedly increase and decrease vagal tone. These rapid, instantaneous changes to heart rate are what characterize RSA (Cheng and Powley 2000). This also means rapid changes in sympathetic activation for mobilization. When the VVC is active, it creates a relaxed state for focusing on a particular stimulus; when the VVC is inactive, it allows for mobilization to change focus to another stimulus or engage with the stimuli in a different manner.

Phylogenetic Hierarchies

Because RSA is not observed in reptiles and other non-mammals, RSA is thought to be a phylogenetically evolved trait in mammals, giving RSA a separate control mechanism from bradycardia (Porges 1995). However, since both RSA and bradycardia are parasympathetic, that means the vagus has separate branches in mammals, a phylogenetically old tonic control branch and a phylogenetically newer phasic control branch. Different branches of the vagus also mean different parasympathetic control centers in the brain. In reptiles, the dorsal motor nucleus and the nucleus ambiguus are not separated, with efferent projections only coming from the dorsal portion (Porges 2007).

The phylogenetic development of the autonomic nervous system in vertebrates likely

happened in three stages. The primitive autonomic system, common to most vertebrates, is the DVC, responsible for immobilization behaviors by causing bradycardia. This is usually a fear response, causing an animal to freeze (death-feigning), or an orientation response to blend in with surroundings while stalking prey (more typical of reptilian “sit and wait” stalking than mammals stealthily tracking). Next is the sympathetic nervous system, present in all animals, but with phylogenetic increases in complexity up the evolutionary path. This system is operated by the spinal cord and endocrine system (i.e., adrenals in vertebrates); it is responsible for mobilization and fight-or-flight behaviors. The most phylogenetically evolved system, predominantly seen in mammals, is the myelinated VVC, responsible for vagal brake behaviors. Since the vagal brake allows for more rapid interactions between the sympathetic and parasympathetic systems, this catalyzes more complex behaviors typical of social interactions and self-soothing (Porges 2007). Recall that the VVC also innervates muscles related to vocalization and facial expression, as evidence of its relation to social behaviors.

From the polyvagal perspective, reptiles and mammals use opposing vagal strategies to survive. Reptiles, with low metabolic demands (low oxygen need from organs), typically have low vagal tone in order to traverse their environment (using the sympathetic system), only increasing vagal tone to novel stimuli, causing a freezing state, via bradycardia. This state is beneficial to them both defensively and offensively so that other animals cannot see them, be it predator or prey. Mammals, on the other hand, have high metabolic rates, so if the sympathetic system was given full control, then mammals would be in a constant state of high activity. Thus, mammals typically have high vagal tone, due to the vagal brake, in order to keep the sympathetic system dampened until needed. Reptiles can survive in prolonged bradycardic states, whereas mammals, with high metabolic demands, can only survive brief periods of bradycardia. Prolonged bradycardia in mammals would cause hypoxia, leading to

death. Alternatively, if reptiles did possess a vagal brake over the heart, their already low metabolic state plus the vagal brake would render them immobile, regardless of threat level (Porges 1995).

The Jacksonian principle states that phylogenetically newer systems inhibit older ones; however, older systems are not lost, but kept as backups in case the newer system fails (Porges 2007). Therefore, in mammals, when the VVC is found to be ineffective for survival, such as in situations of threat, the sympathetic system takes over. Further, one problem prior theories could not explain was why during *extreme* threat and trauma, mammals tend to freeze. Given the Jacksonian principle, this freezing behavior in *extreme* situations is the failure of both the VVC and the sympathetic system, leaving the DVC as the last resort (Porges 2007), causing a reptilian-like behavior to *extreme* threat or excitement.

Another relic of the reptilian brain in mammals can be seen in the orientation reflex. Both mammals and reptiles orient reflexively to novel stimuli, which is created by a sudden bradycardic state produced by the DVC. However, where reptiles tend to stay in this state when freezing from threat or waiting for prey to get close enough to attack, a mammal’s VVC quickly inhibits the DVC branch, given the Jacksonian principle (Porges 1995). This enables quick orientation changes typical of the vagal brake, as well as facial and vocalization responses distinctive of the VVC, allowing mammals to have a larger repertoire of actions to take when engaging with novel stimuli (Porges 1995).

Conclusion

Many phylogenetic insights from the theory have led to the idea that a need for more complex reactions to novel stimuli puts an emphasis on greater metabolic oxygen demands as the driving force behind the evolution of the VVC system (Porges 1995). However, numerous psychological and clinical disorders may be a function of

improper DVC and/or VVC activity (Porges 2007). Disorders such as sudden infant death syndrome and sleep apnea may be caused from overactive DVC or an underactive VVC. Disorders that compromise social behaviors, such as autism, may be facilitated by an underactive vagal brake, causing less social regulation and self-soothing behaviors. Other psychophysiological disorders, such as anxiety, may be mediated by overactive neuroception, causing otherwise safe environments to be assessed as threatening, leading to fight, flight, or freezing behaviors.

Cross-References

- Adaptations
- Adaptations: Product of Evolution
- Brain Size and Intelligence
- By-Products of Adaptations
- Carruthers on Massive Modularity
- Convergent Evolution of Intelligence
- Cortisol Affords Immediate Action and Alertness
- Error Management Theory
- Evidence of Brain Modularity
- Evolution of the Brain, The
- Evolved Physiological Reactions
- Heart Rate
- Mutation
- Parental Investment Theory
- Stress and Cortisol
- Tactics to Solve Adaptive Problems of Sperm Competition

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Pooh-Pooh

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Synonyms

[Expressions of emotions theory](#); [Expressive theory](#); [The interjectionist theory](#)

Definition

The *pooh-pooh theory* suggests that language has emerged from intuitive emotional cries, expressive, for example, of agony or joy.

Introduction

This early speculative language theory refers to the notion that language emerged from unintentional vocal responses to agony, fright, astonishment, enthusiasm, satisfaction, or other emotions (Barber 1965). Although animals produce sounds as well, yet language is unique only to humans. “Ouch!”, “Aaah!”, and “Wow!” are some examples of the unintentional vocal responses emerged from this hypothesis. This theory can be found in the literature as *the expressive theory*, *the interjectionist theory*, or *the expressions of emotions theory* (Barber 1965). Max Muller supported the pooh-pooh theory for a while, but later he abandoned it (Müller 1877).

The notion of the pooh-pooh theory that language has many emotional exclamations has been widely criticized by many reviewers. It has been argued that the explanations provided by this theory constitute a very limited part of the vocabulary of different languages. Further, the various languages worldwide have different interjections. For instance, in English pain is *ouch*, while in Greek it is *aou*. Therefore, it is indicated that

sounds could have been different if their origin was from interjections.

Conclusion

According to the *pooh-pooh theory*, the origin of language emerged from the sounds of our ancestors when they reacted to different emotional states or reactions. The cries and other vocal responses to pain, fright, astonishment, enthusiasm, satisfaction, and other emotions are considered to be the roots of speech. The interjections were of paramount importance to the beginning of communication through speech. To conclude, although early human beings could use words based on interjections, these may have been ultimately overruled by more sophisticated and abstract terms (Mandavilli 2016). Finally, it is important to emphasize that although animals react to the sudden feelings they experience using sounds, they didn't develop language as human beings did.

Cross-References

- Bow-Wow
- Ding-Dong
- Origin of language
- Ta-Ta

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Popular Children

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Synonyms

High status; Peer acceptance; Social dominance; Well-liked

Definition

Children or adolescents who are well-liked and/or admired by their peers.

Introduction

Status in the peer group is a central concept to be addressed when studying children and youth. Specifically, it is important to consider the distinction between a dyadic friendship and the greater overall acceptance of the broader peer group. A common method used to determine peer status is to ask children how much they like or dislike children in his/her class and then use this information to calculate an individual's sociometric status (or peer acceptance, in essence, how much they are liked or disliked by their peers as a whole). One of the groups children can be classified into is "popular children," and research has discussed this group in two categories. First, sociometric popularity is conceptualized by how liked an individual is by their peers and is generally associated with prosocial behaviors, whereas perceived popularity is often associated with social dominance and aggression, and not with prosociality. Children and adolescents who are high in sociometric popularity are viewed positively or liked by many peers, while being viewed negatively or disliked by few. Further, these children tend to have many positive characteristics

that contribute to well-adjusted development and positive experiences. They are generally nominated by their peers and the adults in their lives as being cooperative, sociable, and friendly. Children high in sociometric popularity are generally able to regulate their emotions well and have a substantial number of reciprocal friendships (Litwack et al. 2012). Research has demonstrated that there may be differences between children and youth who are high in sociometric popularity (i.e., well-liked) versus those who are high in perceived popularity (an individual's dominance within the social hierarchy). For example, whereas children who are high in sociometric popularity generally exhibit prosocial characteristics, it may be the case that children or youth who have high levels of perceived popularity may have similar prosocial traits, but may also display some negative traits and engage in antisocial behavior (Cillessen and Rose 2005). These individuals may choose to use both prosocial and coercive (e.g., aggressive) strategies to gain and/or maintain social status and power within the peer group.

Social Dominance: Aggression and Victimization

Children who choose to use aggression instrumentally to achieve their goals tend to be perceived as more popular than children who choose to use their aggression in a reckless fashion (Hawley 2003). From an adaptive perspective, gaining status can provide advantages to the individuals involved including higher levels of reputation or higher quality mates. Research demonstrates that early adolescents with high levels of perceived popularity are more likely to engage in bullying aggression, especially those with low levels of peer acceptance (de Bruyn et al. 2010). Although these adolescents may be disliked for their involvement in bullying aggression, it seems that engaging in these behaviors can provide certain benefits, including higher social status (Volk et al. 2014). This supports theories of evolutionary psychology, which suggest that bullying aggression may be an evolved adaptation and provides evolutionary advantages

to those who engage in the behavior. Specifically, adolescents may use bullying as a strategy to acquire certain benefits, such as social status, greater access to dating and sexual partners, material resources, and social dominance (Volk et al. 2014). Furthermore, longitudinal research demonstrates how popular adolescents are more likely to engage in future relational aggression, which allows them to maintain their high social status (Cillessen and Mayeux 2004). That is, these individuals are more likely to engage in aggression consisting of damaging another person's social relationships or social status, as this type of aggression is generally more effective when used by those already in a position of power.

Although popular adolescents are more likely than their less popular peers to engage in bullying aggression, there is also a small body of literature indicating that popular adolescents are at risk for victimization, specifically by reputational aggression (de Bruyn et al. 2010). High status peers tend to have admirable qualities and influence over their peers which may evoke envy by their lower status peers. Victimization of popular adolescents may arise from competition and rivalry. Reputational aggression consists of spreading rumors and gossip with the intention of ruining an individual's reputation. By derogating the reputation of a high-status peer, adolescents with lower social status have the opportunity to diminish the status of their target and ascend the social hierarchy themselves. Targeting peers with high status and power can be risky for the aggressor if their identity is revealed. Reputational aggression can be covert and anonymous which decreases the aggressor's risk of identification and subsequent retaliation. Popular adolescents who are characterized by aggressive behavior and low peer acceptance are at greater risk of victimization, suggesting that aggressors victimize high-status peers in the form of retaliation or perhaps they are being strategic in selecting their targets (de Bruyn et al. 2010). Targeting popular adolescents with low peer acceptance is a strategic move for the aggressor because these adolescents are less likely to have friends to protect them, and the

aggressor may even receive social approval by selecting an individual who is disliked by the peer group. In fact, research by Spadafora et al. (2018) found that adolescents were less likely to intervene in a bullying situation when they felt as though it may decrease his/her popularity, and more likely to intervene when they thought it could help them to gain popularity.

Risk-Taking Behaviors

During late childhood and adolescence, risk-taking behaviors seem more desirable as they are perceived to bridge the gap from adolescence to adulthood. At this stage, youth start to spend more time unsupervised by their parents and become more involved with their peers. The pressure to conform to peer norms and risk-taking behaviors becomes more common as adolescents feel the need to identify with peer groups (Steinberg and Monahan 2007). Popular individuals may feel this pressure at a greater level to maintain their social status and, therefore, are more likely to engage in risk-taking behaviors. Research has demonstrated that adolescents with greater levels of popularity are more likely to engage in risky behaviors, such as cigarette use, marijuana use, and risky sexual behavior (Prinstein et al. 2011). This greater involvement in risk-taking behaviors may be attributed to a stronger need to conform to peer norms to maintain social status; however, it may also suggest that popular adolescents have greater opportunities to engage in these behaviors. For example, popular individuals have a greater number of dating and sexual partners and are also invited to parties where substance use is common and easily accessible. The involvement of risky behaviors by popular peers is especially problematic because of the high level of influence these individuals have among their peers. Children and adolescents admire the attention that their popular peers receive and will emulate their behavior and preferences with the hope of receiving the same social approval from their peers. Despite the potential risk of greater involvement in risk-taking behaviors, there are also multiple potential benefits.

Positive Outcomes for Popular Children

Popularity in children has been associated with positive outcomes, such as academic competence, friendship quality, and psychosocial adjustment (Chen et al. 1997; Litwack et al. 2012). In regard to academics, research has found differences between popular and average children. In general, classmates tend to nominate popular students as being good students and are perceived by teachers to be more helpful than other students. Further, research supports a reciprocal relationship between academic achievement and peer acceptance, that is, while academic achievement may predict peer acceptance, children's adjustment (including their peer acceptance) is also significantly associated with their academic achievement (Chen et al. 1997). This highlights the importance of the positive adjustment and peer acceptance of children for strong academic achievement.

Moreover, children who are deemed as socio-metrically popular have more friendships with higher levels of intimacy and lower levels of conflict, compared to their rejected counterparts. This is likely due to having larger social network with higher levels of acceptance that allows for greater opportunities to build and develop friendships. Further, youth who have higher levels of perceived popularity, in general, had higher levels of friendship support and a greater number of friends than youth who were nominated as unpopular (Litwack et al. 2012). Lastly, higher levels of popularity have also found to be associated with higher levels of self-esteem and lower depressive affect, again highlighting some of the positive effects for popular children (Litwack et al. 2012).

Conclusion

Overall, it is important to consider children who are characterized as popular may have many positive attributes. Research has shown that these children not only feel more supported by their peers but may do better in school and have better overall psychosocial adjustment (Chen et al.

1997; Litwack et al. 2012). Moreover, having low levels of sociometric popularity has been found to predict depressive symptoms in early adolescence, further highlighting the importance of having status in the social hierarchy (Nolan et al. 2003). Since research also demonstrates negative associations with popularity, it is increasingly important for professionals working with children and youth to understand the importance of popularity and support these students to gain status through prosocial means. For example, Ellis et al. (2016) discuss the “meaningful roles” intervention, which focuses on giving youth alternate prosocial means to increase his/her status within the peer group, such as classroom roles and responsibilities reinforced by peers, to allow them to maintain status instead of resorting to antisocial methods, such as aggression.

Cross-References

- [Higher Status in Group](#)
- [Peers](#)
- [Status Competition and Peer Relationships in Childhood](#)
- [Status Hierarchies](#)

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Popularity

- [Status Competition and Peer Relationships in Childhood](#)

Population Bottleneck

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Synonyms

[Catastrophe](#); [Mass extinction](#)

Definition

An event that drastically reduces the size of a given population.

Introduction

Population bottleneck is the result of a catastrophic event that reduces the size of a population. The kind of event it is can vary considerably, and it can take many different forms as well. These can be climate or weather related (volcanos, earthquakes, hurricanes), things such as genocide (the Holocaust, genocide of Native Americans), biological destruction (the Black Plague), or even environmental destruction such as the deforestation of the Amazon. Essentially, any event that considerably reduces the size of a population of a living creature is considered to be a population bottleneck.

Population Bottleneck with Respect to Climate Fluctuations

Although population bottleneck results in the drastic reduction of a given population, there are times that the bottleneck can be advantageous. For instance, in the case of our ancestors in early hominids, they were likely pushed out of trees and onto the ground due to climate fluctuations (Hawks et al. 2000). With these climate fluctuations came many of these early hominids migrating from the tops of the trees onto the forest floor and begin changing their behavior to adapt to hunting and surviving in their new environment, as well as eventually the African grasslands. However, the vast majority of these early hominids did not make the transition to the forest floor, and likely decided to stay in the trees as they had done all of their lives. Given the nature of the climate fluctuations, staying in the trees was likely disadvantageous given the lack of vegetation and resources to be found. Without these resources, the organisms would die. Thus, it is most likely that the vast majority of these hominids died off and resulted in a population bottleneck, with a very small amount of the population being able

to actually adapt and survive on the ground floor. Of these that did survive, however, would have reproduced to have children adapt to the same lifestyle, and slowly build the population back up to reasonable proportions (Nei et al. 1975). When the population was large enough, the hominids began to migrate out of the forest and into the local grasslands that were also likely due to environmental change and deforestation. Those that were unable to survive on the African savannah did not, and failed to pass on their genes to their offspring due to either being hunted, being unable to survive and find resources, or being unable to find a viable mate in the conditions. Those that did survive were able to successfully adapt and pass on their genes, which long-term led evolutionarily to biological changes and mechanisms that ensured survival and adaptation to their new environment Wall and Przeworski (2000). These changes made what was once a population bottleneck slowly but surely into a flourishing community of hominids that gained skills such as weaponry and communication that their ancestors did not, and would eventually turn into the seven billion people we have on Earth today.

Conclusion

Population bottleneck is a severe decrease in a given population because of a catastrophic event. The name is given because of the shape of a bottle – round and broad at first, representing a large population, to which the “catastrophe” happens at the bottleneck. The population then severely decreases and eventually levels out at a level that was significantly less than its original figure. With respect to human evolution, our early ancestor hominids likely experienced population bottleneck in their transition from trees to the African savannah which most likely came as a result of climate fluctuations.

Cross-References

- [An Essay on the Principle of Population](#)
- [Evolutionary Arms Race](#)

- [Evolutionary Psychology, The Handbook of](#)
- [Genital Evolution](#)

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Population Ecology

- [Life History Theory](#)

Pornography and Women's Short-Term Mating

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Definition

Pornography is conventionally defined as imagery specifically designed to generate sexual arousal, although a related definition is imagery of sex acts themselves. Short-term mating relates to brief sexual encounters such as one-night stands, as opposed to stable long-term mating (pair bonding, either monogamous or polyandrous).

Introduction

It is a widely held misconception that the main function of pornography is to facilitate masturbation. In fact, the main function of pornography is to activate the pleasure circuitry of the brain that is naturally stimulated by sexual interactions in the

real world. This may or may not involve masturbation in any instance of porn usage. Examples of non-masturbatory usage are couples using it as part of their normal sexual activities and individuals viewing it in the same way that they watch non-porn content.

In making the benign suggestion that pornography has evolved, this could be meant in two senses. It could mean how pornography has developed over time, i.e., how the content of pornography has changed in response to cultural and technological trends. However, the evolution of pornography could also be meant in a Darwinian sense, that either pornography is in itself an adaptation or has evolved to fulfill an adaptive function or that the need/capacity for it has evolved by processes of natural/sexual selection: these are more controversial suggestions. The wider notion that narrative storytelling ability serves an adaptive function has previously been outlined (Tooby and Cosmides 2001).

Although it has not been highlighted, Charles Darwin explicitly placed pornography within his evolutionary framework for understanding the origin of animal instincts. While discussing the universal fact that human beings from across the globe have practiced various forms of artistic adornment for a very long period of time, he extended this to include the “almost universal habits of dancing, masquerading, and making rude pictures” (Darwin 1874 [1871], 577). If Darwin thought of “making rude pictures” as a type of artistic adornment, then their potential evolutionary function becomes evident.

Opposition to Pornography

Pornography is one of the most controversial areas of cultural production, eliciting strong feelings both in favor of it and against it, although some people are indifferent to it. Many but by no means all of the strong opponents of pornography are women, for example, the anti-porn radical feminists, but there is also a vocal group of female sex-positive pro-pornography activists. At the heart of the anti-porn attitude is the proposition that porn is exploitative, either of women in general or of the women who are involved in it as performers.

However, the fact that members of the anti-porn grouping only more rarely make the argument that porn also exploits the men that are involved, or that gay porn is exploitative, indicates that sex differences (and the associated evolved psychological mechanisms) are a key component of the controversy over the morality of porn. The contrast is highlighted by the fact that most (if not all) anti-porn advocates argue that pornography exploits women, some argue that porn exploits both the women and the men involved, but nobody has ever argued that porn exploits only the men involved but not the women. This latter argument seems absurd, but it is logically equivalent to stating that porn exploits only the women involved, indicating that there is something unequal at work when judging male versus female involvement in pornography.

A good summary of the calculative logic often at work when women choose to participate in pornography as a career has been provided by the editor of *Razzle* (a UK soft-core porn magazine):

Our would-be [nude] models weren't all desperate. Some of them ... were as bright as canaries, a-twitter with all kinds of daydreams [of fame]. Suzy, for instance. She had no CSEs [UK school exam qualifications], but God had compensated by blessing her with blonde curls, blue eyes and impossibly pointed tits ... She had it [all] planned. *Fiesta* [UK] today, *Penthouse* [UK] next month, and Hollywood [California] next year. (Whittaker 1997, 71)

A survey of US pornography actors/actresses revealed various different motivations for entering the porn industry, including the obvious ones – money, sex, and Suzy's shot at fame – but some less obvious ones too: work flexibility, freedom, and independence, sociability and interpersonal networking opportunities, and mobility across various branches of the sex industry (Abbot 2000, 19–31).

Short-Term Mating

As has been explained in the literature on evolutionary psychology:

In primates, short-term mating occurs in several of the prosimians (e.g., the ring-tailed lemur, *Lemur catta*), New World monkeys (e.g., the squirrel monkey, *Saimiri sciureus*), Old World monkeys (e.g., the rhesus monkey, *Macaca mulatta*), and great apes (e.g., the common chimpanzee, *Pan troglodytes*) ... numerous findings indicate humans are designed for at least some short-term mating. (Schmitt 2005, 264)

It is fairly uncontroversial to state that human females do engage in some degree of short-term mating, the evidence in part being the comparative degree of sexual dimorphism exhibited by *Homo sapiens* compared to other primates and other evolved behaviors such as the expression of jealousy and the prevalence of infidelity (Ibid., 260), but understanding the reasons why they do so is more controversial.

The most obvious reason – simply for pleasure – might sometimes apply, but there are a number of other potential explanations that have been advanced in the literature. These are, in exchange for resources, to obtain better/more diverse genes, to switch mates, to acquire mating skills, and to manipulate mates (Buss 2004, 176; Schmitt 2005). It seems likely that women may engage in short-term mating for a number of reasons in combination.

The hypothesis that ancestral women engaged in short-term mating in exchange for goods or other services is common in the evolutionary psychology literature, but it is more controversial outside of it. For example, some radical feminists have questioned this notion, claiming that it serves to legitimize contemporary prostitution. The link to pornography is less frequently considered, but the argument is similar: women have evolved psychological mechanisms relating to behavior exchanging sex (or pornographic imagery of sexual activity) for other goods, thereby allowing sex (and porn) to be conceived of as a service offered by them to men. This service can be in the form of exchange for money (prostitution and pornography) or other items (e.g., meals).

One problem with the radical feminist opposition to both prostitution and pornography is that the women involved often state that they are exercising their own free will in choosing to become pornography actresses, and they resent

anyone suggesting that they have been brainwashed into doing it. It is true that some pornography actresses later came to regret it, a classic case being Linda Boreman (a.k.a. Linda Lovelace) who starred in the 1972 film *Deep Throat* (Barnett 2018), but many other women have remained supportive of their career choice. Toward the end of Boreman's life, she worked in pornography again after previously rejecting it as exploitative. She then declared that some feminists had exploited her name in their publications on her pornography experiences: a case of all exploiters are equal, but some are more equal than others.

Two Human Natures

It seems reasonable to suggest that the different attitudes exhibited by some to female against male participation in pornography in part stems from the different evolved psychologies of men and women (Davies and Shackelford 2008; Salmon 2008). It is usually assumed that men will enjoy any and all short-term mating opportunities (e.g., porn sex, drunken night-club sex), but there is an implied assumption made by some that women will not, or at least not in the same quantity or to the same degree.

Reading through the memoir literature written by female porn stars leads to the conclusion that they do not enjoy some significant portion of the porn sex, but on some occasions, they do enjoy it very much (Jameson 2004). Compare this with the situation of female lavatory cleaners, who probably never or only very rarely actually enjoy the work of cleaning toilets as work.

Moreover, the proliferation of Internet porn has produced examples of female porn stars that only (or mainly) have heterosexual porn sex with their real-life male partners while also participating in other types of sex scene which do not involve other men, such as solo masturbation. For example, the Czech pornography actress Hedvika Makošová (a.k.a. Victoria Sweet) has performed in solo masturbation scenes, girl-girl scenes,

female-only water sports, and also straight and oral sex with her boyfriend.

In such cases the percentage of porn sex that female participants can be said to enjoy probably increases greatly, especially when it is recognized that many female porn stars identify as bisexual. It would be difficult to argue that a female lavatory cleaner has a better work experience than a partner-only bisexual porn star, especially when the comparative pay rates are included in the analysis.

Cleaners usually earn the minimum wage (around \$10 per h); female porn stars can earn up to \$1,000 for a 1-h scene, depending on the type of sex that is involved. In comparative terms, it would be difficult to maintain that the porn star's job is 100 times less fulfilling than the toilet cleaner's job, and therefore the comparative pay rates are commensurate with the nature of the work. It is true that the working life of porn stars is much shorter than that of cleaners, but the former can embark on new careers after leaving porn.

Conclusion

A key feature of pornography not often considered by feminists is that the women involved invariably receive much higher pay rates than the men involved in acting in the same scene. One position could be that this constitutes discrimination against men, but this argument is absent from the literature on pornography.

From an evolutionary perspective, pornography is just one variant of the long history of females employing their sexual capacity to obtain resources from males, as an extension of the short-term mating strategy deployed across various primate species. The different pay scale for male against female porn stars just reflects the fact that the males involved in porn are receiving part of their payment as sex, as against the women, who do not conceive of men having sex with them as any type of payment. This constitutes a classic example of the naturally evolved phenomenon of "two human natures."

For radical feminists, this sex-for-resources process is exploitative, but most other *Homo sapiens* accept it as a natural part of life as it has evolved on planet earth over millions of years. It is logically possible to conceive of a primate species evolving that exhibits different behavioral logic in this regard, for example, where females pay males for sex. Among contemporary *Homo sapiens*, male gigolos are not unknown, but these gigolos are rarely considered as objects for study in the literature on prostitution, which usually focuses only on female prostitutes and their male clients.

Cross-References

- [Catherine Salmon](#)
- [Patriarchy and Feminist Perspectives](#)
- [Sex Differences in Same-Sex Aggression](#)

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Pornography as a Human Product and Source of Data

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Synonyms

[Erotica](#); [Sexually explicit material](#)

Definition

Sexually explicit material primarily intended to sexually arouse the consumer.

Introduction

Evolutionary psychology (EP) contends that how people respond to current environmental stimuli is shaped by mental mechanisms that evolved in response to problems faced by our ancestors. EP perspectives seek to identify ultimate causes of behavior, complementing the focus on proximate causes characteristic of other psychological theorizing. By examining within the framework of evolutionary theories how people use pornography and differences between men and women in their consumption preferences, EP researchers have tested unique predictions and gained important insights about the evolved mechanisms of consumers.

Pornography refers to sexually explicit material primarily intended to sexually arouse the consumer. Such content is distinguished from a large proliferation of sexual material around this core in which continuous sexual stimulation and consequent arousal are not the primary motivation, such as movies in which some of the scenes include references to or actual portrayals of sexual interactions. It is clear that use of pornography is common and in recent years is primarily accessed on the Internet, a visual medium. For example, in 2015 people watched nearly 4.4 billion hours of

pornography on popular website *Pornhub*, which is the equivalent of spending more than 500,000 years watching online porn (“Pornhub’s 2015 year in review,” 2016).

Pornography and Environmental Mismatch

Put simply, EP theories on pornography suggest that it can be understood as the “parasitizing” of evolved mechanisms for sexual responses, particularly reflective of short-term sexual mating strategies. These mechanisms evolved to cause attraction and arousal to potential sexual mates. In ancestral environments, such attraction and arousal would have increased the likelihood of engaging in sexual acts contributing to reproductive success. Pornography use can activate the same evolved mechanisms for sexual responses. However, in current environments the activation of such evolved mechanisms in the context of pornography use does not typically lead to greater reproductive benefits. Indeed, although pornography may sometimes be used to stimulate sexual intercourse potentially resulting in reproduction, it typically elicits behaviors without clear reproductive consequences, namely, masturbation. The elicitation of such behaviors is due to a mismatch between modern and ancestral environments. Mismatch in this context indicates that a behavioral response that may have been adaptive in evolutionary environments and therefore became part of humans’ psychological mechanisms may not contribute to reproductive success in current environments.

From an EP standpoint, we are mechanism activators, not fitness strivers. Consider taste buds for sweetness, which evolved in ancestral environments as a way to increase the likelihood that we would eat scarce nutritious substances, for example, ripe fruit. Unfortunately, these taste buds respond as strongly or even more so to processed, artificially created sweets lacking in nutritional value, which were designed by modern technology to similarly activate our sweetness mechanisms. In a modern environment populated with an overabundance of such artificial sweets,

consuming them may be pleasurable because of the parasitizing of psychological mechanisms designed to discriminate between ripe fruit and other, less nutritious foods, even though in current environments the elicited behavior of eating may actually be harmful rather than beneficial to our health. In the same way, current use of pornography parasitizes an evolved tendency to become aroused by those sexually explicit stimuli that would appear to have had adaptive significance, despite the fact that such use may result in repeated behaviors, particularly masturbation, that may actually lessen the probability of reproductive success.

Evolutionary psychology’s unique contribution to understanding of and learning from the very wide use of pornography may be illustrated in three areas: (1) Content of Pornography Appealing Primarily to Men, (2) Content of Pornography Appealing to Women, and (3) Content Specifically Related to Increasing Reproductive Success.

Content of Pornography Appealing Primarily to Men

Importantly, by providing a window to our evolved psychological mechanisms, applying the EP paradigm can provide a framework for understanding gender differences in pornography consumption. According to sexual strategies theory (Buss and Schmitt 1993), the adaptive mating problems faced by ancestral men and women when pursuing long-term or short-term mating strategies differed in important ways. Those males who evolved mechanisms that increased their sexual mating with a larger number of fertile, sexually accessible women were more likely to become our ancestors who, in turn, transmitted such evolved mechanisms to subsequent generations of male offspring. Conversely, for those women who were equally attracted to short-term relationships involving copulations, more dire consequences would have ensued. Such a tendency would have “undermined female choice of partners and the circumstances of conception, reduced the likelihood of acquiring male parental

investment, increased the likelihood of being beaten, abandoned, or killed by a jealous husband (and also by angry brothers), and drastically impaired female fitness” (Ellis and Symons 1990, p. 457). Women today consequently are relatively selective about short-term partners, and when such mating does occur, they are particularly attracted to characteristics associated with “good genes” that in ancestral environments would have conferred competitive advantages for their offspring.

From an EP perspective, most pornography can be seen to conform to men’s rather than women’s short-term mating psychology or sexual fantasies. Indeed, much of it fits well with “solving” the main problems or challenges encountered by men over evolutionary time when pursuing short-term mating designed to produce the most offspring: identifying women who are willing to engage in casual sexual acts without a long-term commitment and who display a number of cues associated with reproductive fitness, such as young age, clear skin, good muscle tone, and facial symmetry. Studies show that men prefer content consistent with such a strategy for successful short-term mating, including female pornography actors with the ideal characteristics for reproductive success, pornography featuring many different women rather than the same women performing different sexual acts, and pornography devoid of any emotional attachments or nuances associated with encumbering commitments (Malamuth 1996).

Also consistent with EP theory, after viewing sexually explicit videos, men experience less negative affect than women do, which from an EP framework is associated with female hesitation to engage in unbridled sexual acts (Malamuth 1996). Furthermore, compared to women, men are generally more sexually aroused by pornography and are much more likely to use pornography on a regular basis as a masturbatory tool, whereas women are more likely to use pornography sporadically and seek it out primarily out of relatively fleeting curiosity (Hald and Malamuth 2008). All this helps to explain why men represent the greatest proportion of pornography viewers worldwide (e.g., 76% in 2015 according to

Pornhub’s latest statistics; in no country are women the majority of viewers; “Pornhub’s 2015 year in review,” 2016).

It is essential to note, however, that our psychological mechanisms are the result of an interactive blend of nature and nurture. They process and respond to the information from our social and physical environments and do not elicit rigid, fixed behaviors. Illustratively, a recent study of European Union countries found that while there are still considerable differences in many respects (Hald and Malamuth 2008), gender differences in the use of pornography are less pronounced in more liberal countries (Ševčíková et al. 2014).

Content of Pornography Appealing to Women

In contrast to male-oriented pornography, what does elicit more uniformly positive affect from women is erotic material that specifically targets women’s evolutionary psychological susceptibilities by conforming to the adaptive problems faced by our female ancestors. One example of this has been romance novels, which are written almost entirely for women and have been called a type of woman’s pornography. A heroine overcoming obstacles to secure a ruggedly handsome, physically imposing, intellectually gifted, often “dangerous” man who eventually desires and loves only her characterizes these works. Because the male character featured in these works is not only of high genetic quality but also, by the story’s end, turns kind and loving toward the heroine, romance novels may provide the best of both worlds in terms of women’s mating preferences. As Salmon and Symons (2004, p. 96) concluded, “We believe that genre romances are analogous to male-oriented porn in the sense that they are wish-fulfilling fantasies, well designed to pick the locks of the pleasure circuits in female brains. . .”

In addition to its descriptive power, evolutionary theory can help generate novel, testable predictions. For instance, Salmon and Symons (2004) have studied slash fiction, a brand of erotic fiction in which the lovers are both male. Slash fiction is typically very sexually explicit, although

the emphasis is on the emotional rather than physical elements of sex. They are essentially love stories, written primarily by and for women, in which the male characters suddenly find that they love one another. In their examination of slash fiction, these researchers asked who chooses to read or write such works. Two possibilities exist: (1) slash fiction should appeal to only a subset of psychosexually unusual women, or (2) it should appeal more broadly to mainstream romance novel readers. In view of the strong thematic correspondence between slash fiction and romance novels, they predicted the latter result. A study of members of a "romance readers club," in which 78% of members reported enjoying a slash fiction novel at least as much as other romances, generally supported their hypothesis (although there is some evidence that the female mating psychology of slash readers is a "little masculinized," as indexed, e.g., by reported tomboyism and frequency of fantasizing about sex with someone other than a current partner).

Content Specifically Related to Increasing Reproductive Success

Another example of using evolutionary psychology to inform predictions about pornography preferences comes from sperm competition theory. Sperm competition occurs when the female of a socially monogamous species engages in extra-pair copulations, resulting in some extra-pair fertilizations. To the extent that sperm competition was an important selection pressure for ancestral males, men may have evolved adaptations designed to reduce the risk of cuckoldry associated with female sexual infidelity. In fact, men at greater sperm competition risk do appear to possess indicators of adaptive mechanisms. One element of this concerns the role of sexual arousal responses. Greater sexual arousal to cues of sperm competition would have been a valuable strategy for dealing with paternity uncertainty by helping to elicit immediate copulation. This has led to the prediction that men should be more aroused by and prefer to view pornography that evokes the presence of male rivals. In support, researchers

have found that men often do prefer pornography depicting multiple males and a single female (MMF). For example, for pornographic DVDs, the frequency of scenes on the DVD covers showing two men interacting with one woman (i.e., simulating conditions of sperm competition) predicts the sales rank of the DVD, whereas this is not the case for covers depicting two or more women relating to one man (McKibbin et al. 2013). Others have discovered that for pornographic videos, photographs, and stories, men prefer MMF scene/image contents to other types of pornographic scenarios (Pound 2002). Relatedly, men have been found to produce a higher percentage of competitive (i.e., motile) sperm from viewing pornographic images of two men and one woman than from viewing depictions of three women. Higher ejaculate quality increases the likelihood of fertilization during intercourse (for a summary of these findings, see Pham and Shackelford 2015). These data taken together suggest that when men use MMF pornography, it is for its special arousal-inducing properties, which may in turn be the product of adaptations to sperm competition.

Conclusion

EP perspectives have provided unique and well-supported insights and predictions on the selection and use of pornography, which constitutes a large segment of the world's media. Scholars seeking to provide a comprehensive understanding of such topics as gender differences in the type of pornography consumed and the frequency of usage across cultures may include proximate factors including adherence to gender stereotypes and norms, but such explanations are complemented by incorporating knowledge about evolved mating strategies. In generating predictions specifically linked to reproductive success in ancestral environments, EP researchers have provided examples of how modern behaviors that appear at first glance to be contradictory to an evolutionary framework (e.g., males engaging in relatively frequent masturbatory behavior that has no clear reproductive benefits) are

actually highly supportive of evolutionary theory. Moreover, findings regarding sperm motility would not have been generated by any theory that only relies on proximate factors. Although the amount of currently available research on pornography derived from EP theories is not extensive, future work focusing on this controversial topic may benefit considerably from incorporating unique insights and predictions that may be derived from EP theories.

Cross-References

- [Differential Parental Investment](#)
- [Differential Reproductive Success](#)
- [Evolution of Desire, The](#)
- [Evolutionary Mismatch](#)
- [Problems of Assessing Fertility](#)
- [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- [Sex Differences in Long-Term Mating Preferences](#)
- [Sexual Fantasy](#)
- [Sperm Competition Theory](#)

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Positive and Negative Reinforcement and Punishment

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Synonyms

[Consequences](#); [Contingencies](#); [Operant conditioning](#); [Punishment I](#); [Punishment II](#); [Reward](#)

Definition

Consequences of behavior in operant conditioning that result in strengthening (reinforcement) or weakening (punishment) the frequency of that behavior.

Introduction

During the operant conditioning process, the consequences of behavior affect the probability of future demonstrations of that behavior. Thorndike (1898, 1911) and Skinner (1938) have shown that reinforcement (also known as reward) strengthens a behavior, i.e., increases its frequency, whereas punishment weakens a behavior, i.e., decreases its frequency. Reinforcement can also be distinguished as primary/secondary and intrinsic/extrinsic.

Positive and Negative Reinforcement

Reinforcement is an environmental stimulus whose presentation results in the strengthening (increase of the frequency) of an exhibited behavior. An organism, after a number of contiguous presentations of behavior-reward, associates a specific behavioral action with a desired outcome and is motivated to repeat it in the future. Reinforcement can be positive or negative. When pleasant consequences occur, the reinforcement is described as positive. When aversive consequences are removed, negative reinforcement takes place. Positive Reinforcement involves the presentation of a stimulus that increases the occurrence of a behavior (e.g., receiving food after pressing a lever in a Skinner box). Negative Reinforcement results in an increase of the frequency of a behavior because it results in the removal of an unpleasant stimulus (e.g., a person puts on their seat belt immediately upon entering the car, to stop the annoying sound of the buzzer).

Primary and Secondary Reinforcement

Primary reinforcers have the capacity to innately reinforce behavior (Powell et al. 2017), and they are sometimes also called unconditioned reinforcers. They satisfy a built-in, biology-related need or desire (e.g., food, water, oxygen, sexual contact), require no previous learning, and they are essential for our physiological and psychological well-being.

Secondary reinforcers, also known as conditioned reinforcers, are previously neutral stimuli that have become reinforcing through repeated association with another reinforcer (e.g., praise, good grades, money) (Powell et al. 2017). They become reinforcing through the process of classical conditioning, and they are not essential for physiological well-being. Positive experiences with these events serve as effective reinforcers that guide present behavior.

Intrinsic and Extrinsic Reinforcement

Reinforcement can be intrinsic if the act of performing the behavior is pleasant in itself for the organism. Early research has shown that monkeys engaged in solving mechanical puzzles (Harlow et al. 1950) without the need for additional incentives. In human learning, feelings of success, competence, and pride are intrinsically reinforcing (Ormrod 2016). Extrinsic reinforcement is reinforcement received by consequences external to the behavior. They may include material reinforcers (money, actual objects such as food or toys), social reinforcers (gestures received by others to communicate positive regard, such as a smile, attention, praise), activity reinforcers (engaging in a personally pleasurable activity such as watching TV or playing a favorite game), and positive feedback (positive messages about progress of learning such as grades). It has been argued in several studies that when extrinsic reinforcement is given for intrinsically motivating activities, this can decrease intrinsic interest (Deci and Ryan 1985; Lepper et al. 1973; Akin-Little et al. 2004; Deci et al. 1999, 2001). Dickinson (1989) claimed that this effect is transient and that it is less likely to occur if the extrinsic rewards are reinforcing, noncompetitive, based on rational performance standards, and when there is repetitive delivery of the reinforcers. Some meta-analyses (e.g., Cameron and Pierce 1994) have disputed the above and showed that extrinsic reinforcement has little or no effect on intrinsic motivation, although they acknowledged that external rewards can possibly undermine intrinsic motivation under certain conditions such as when the reward is expected, tangible and given only for the act of performing an activity.

Positive and Negative Punishment

Punishment results in a decrease in frequency of a particular behavior because it is associated with an unpleasant outcome (Powell et al. 2017). In positive punishment (also known as punishment I), a particular behavior is followed by a presentation of an unpleasant stimulus (e.g., a verbal reprimand

after a child breaks a vase). In negative punishment (also known as punishment II), a pleasant stimulus is removed (a child is not allowed to watch TV because they have not completed their homework). Various problems have been identified with the use of punishment, and it should be used very cautiously as it may elicit strong emotional responses, aggression, avoidance behavior, and resorting in the use of punishment to modify others' behavior through the processes of modeling (Powell et al. 2017).

Conclusion

In behavioral learning theory under the paradigm of operant conditioning, the consequences of behavior serve as guidance for future behavior. When behavior is followed by pleasurable consequences, reinforcement occurs and the behavior is strengthened in the future. When behavior is followed by aversive consequences, punishment occurs and the behavior is weakened. Reinforcement and punishment are further distinguished by whether a stimulus is added (resulting in positive reinforcement and positive punishment) or removed (resulting in negative reinforcement and negative punishment). Other identified forms of reinforcement include primary/secondary reinforcement and intrinsic/extrinsic reinforcement.

Cross-References

- [Classical Conditioning](#)
- [Operant Conditioning](#)
- [Thorndike's Law of Effect](#)

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Positive Frequency-Dependent Selection

- [Frequency-Dependent Selection](#)

Positive Impacts of Exposure to Nature on Human Health

- [Health Benefits of Nature](#)

Positive Parenting

- [Good Parenting Qualities](#)

Positive Psychology

- Stress Reduction and Mental Health

Positive Punishment

- Operant Conditioning

Positive Reinforcement

- Operant Conditioning

Positive Sexual Development

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Synonyms

Healthy sexual development; Normal sexual development

Definitions

It is an adaptive, harmonious, and healthy development of sexuality.

Introduction

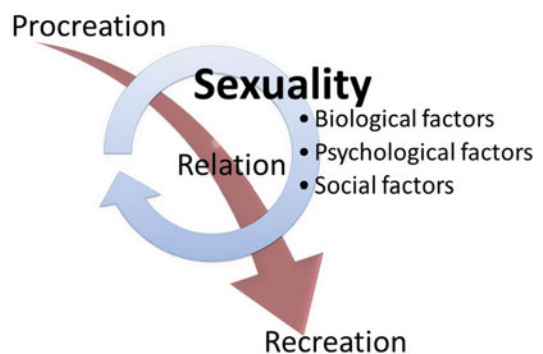
Development of humans is an ever evolving process. Sexuality is an essential element in the life of a human being. Its importance is not limited to procreation and survival of human race; rather it has many other significant roles. Sexuality adds to the identity of an individual. Sexuality needs to be understood beyond the boundaries of

health, as sexuality is also a social, cultural, economic, ethical, legal as well as spiritual phenomenon (Diamond 2014).

Development of sexuality can be understood from the aspects of physical, emotional, cognitive as well as social domains (Scott and Walsh 2014). Sexual development starts from the intrauterine life and continues throughout the life. Across the lifetime of an individual, many transitions come, during which sexual development gets different contours (Moshman 2014). Adolescence period is one of the major transition during which an individual's sexuality evolves into a mature form, physically as well as psychologically (Kar et al. 2015). Sex is a primitive behavior that serves to meet the basic needs (procreation) to the higher needs (recreation or pleasure) of life (Fig. 1). Sex also has an important function in holding the relation with the partner. Throughout the life time of the individual, a complex interaction between the sexual needs and sexual development goes on. Initiation of sexual activity varies across cultures. Developmental processes influence the thoughts, feelings, behaviors, and attitude towards relationship, other than the physical changes, which in turn direct the sexual activity (Arbeit 2014).

Factors Affecting Sexual Development

Sexual development can be manifested in the form of anatomical, physiological, as well as



Positive Sexual Development, Fig. 1 Spectrum of sexual behavior and factors influencing sexual development

psychological changes. There are various factors that influence the process of sexual development. Broadly they can be categorized as biological (physical), psychological (cognitive and affective), and social factors (Fig. 1).

The sex chromosomes determine the development of gender-specific sex characteristics. Gender-specific hormones facilitate the growth and development of sexual organs as well as gender-specific characteristics. Across the lifespan of an individual, under the influence of gender-specific hormones, development of sexual organs continues. Gender-specific hormones also influence the gender-specific thinking and behavior. Appropriate genetic makeup and neuroendocrinal integrity is responsible for positive sexual development. Similarly, psychological factors like individual's perception and attitude towards own sexuality to sexuality as a whole in broader sense also influence sexual development. Individuals, who perceive sexuality in a distressing and deformed way encounter difficulties in the sexual life. Social factors like parenting, peer relationship, life experiences, cultural values have significant influence in the sexual development (Moshman 2014).

These biological, psychological, and social (sociocultural) factors also influence each other (Halpern 2010). Moshman described development of sexuality as an extended (evolving across the lifespan), self-regulated (beyond the regulation of environment and genes), and qualitative (addition of newness time to time) process that occurs in a progressive fashion (Moshman 2014).

Positive Sexual Development

To be recognized as "positive sexual development," development of sexuality should follow certain norms as below.

1. It should be within the accepted norms (anatomical, physiological, and psychological).
2. It should be in harmony with self, family, and the sociocultural milieu.
3. Experience about sexual activity should be free from guilt and compulsiveness.

4. There should be respect for divergent view points and contrasting opinions about sexuality.
5. One should be able to understand and express one's sexuality appropriately without shame, guilt, and undue inhibitions.
6. One should have the ability to choose one's sexual partner as per mutual understanding without conflict and social bias.

An individual with positive sexual development perceives sex as a biologic function and should be free from myths and misconceptions. The individual should be able to express about sexuality without prejudices and biases. They should adopt safe sexual practices. Individuals with positive sexual development should be adopting socioculturally acceptable sexual behavior without any distress. As per Arbeit, certain skills like sexual selfhood (identity, desire, ethics); sexual empowerment (coping, setting boundaries); and sexual negotiation (consent, protection) help in positive development (Arbeit 2014).

It is also worthy to understand the range of sexual behavior on the basis of sexual preferences (exclusively heterosexual to exclusively homosexual). These ranges of sexual behaviors are in a continuum. An individual with positive sexual development has apparently no distress with own sexual preferences and is adaptable with the society without causing any social distress. But it is a debatable aspect of positive sexual development, as homosexuality is still not accepted as a normal sexual behavior in many cultures.

Implications

Lack of proper sexual development occurs in conditions that result from improper development of genital system (genetic disorders like – Turner syndrome, Fragile-X- syndrome; endocrinal disorders like – Cushing's syndrome, gonadal hormone insufficiency; trauma to the genitalia like - castration, amputation of genitalia; tumors involving the genitalia like - testicular tumor, ovarian tumor; toxic causes that impair gonadal

functioning like - heavy metal poisoning, chronic alcohol use). Sexually transmitted diseases also hamper positive sexual development. Difficulties of gender orientation and identity also produce significant distress.

Positive sexual development has a noticeable bearing on sex education, which needs to be congruent with respect to the sociocultural, moral, and ethical values as well as age appropriate for the individual.

Understanding positive sexual development will help the individual in promoting sexual health and preventing sexual dysfunctions, sexual abuses, teenage pregnancy, sexually transmitted diseases, and sexual conflicts. Better sexual health will obviously add to the betterment in global health.

Conclusion

Positive sexual development provides a positive identity to the individual. It makes an individual sexually acceptable as well as adaptable. An individual with positive sexual development possesses competence, confidence, and better scope for performance.

Cross-References

► [Sexual Behavior](#)

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Positive Sexual Imprinting

► [Sexual Imprinting](#)

Postcolonial Studies

► [Postcolonialism](#)

Postcolonialism

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Synonyms

[Colonization](#) effects; [Decolonialism](#); [Decoloniality](#); [Postcoloniality](#); [Postcolonial studies](#)

Definition

Set of studies that investigate the effects of colonization on colonized and colonizing peoples.

Introduction

Postcolonialism refers to a set of studies with an interdisciplinary approach that investigate the impacts of European colonization and imperialism on culture, identity, and knowledge production, among other aspects (Gandhi 1998). The historical marker of the postcolonial perspective is the struggle for the independence of African countries and the development of Indian subaltern studies (Ballestrin 2013). The authors of this approach criticize the dominant currents of knowledge, questioning the Western narrative on modernity that places Europe at the center of the historical, political, economic, and epistemological process. In the last decade, postcolonialism gained strength alongside theories such as poststructuralism, psychoanalysis, deconstructivism, and feminism, as an important critical discourse in the social sciences. The postcolonial intellectual constitution and formation of thought are marked by the influence of Marxism and poststructuralism/postmodernism.

Colonialism and Its Effects

Colonialism was a social, political, and economic phenomenon that consisted of the conquest, exploitation, and aggressive violation (e.g., slavery, genocide) of various peoples in the world by European civilizations, having extended for almost five centuries. To a large extent, the richness of WEIRD countries (Westernized, educated people from industrialized, rich democracies) is directly linked to this historical process. European dominion over the world has established frameworks of relationships between nations and between individuals that remain to this day (Grosfoguel 2016).

There is evidence that the psychological processes associated with colonialism remain long after the colonial relationship ends. Quijano (2005) conceived that coloniality would constitute subjectivities based on colonial parameters with the valorization of whiteness, the male gender, wealth, first world nations, and heterosexuality. As with other collective traumas, the traumatic

effects of colonial practices are passed down through generations. Researchers have been investigating the psychological effects of colonization (e.g., colonial mentality, internalized oppression) on colonized populations, such as a negative view of cultural identity, self-rejection, low self-esteem, and depression (Okazaki et al. 2008).

In addition, false beliefs about European superiority as the legitimate producer of truths and knowledge were created during this period. Thus, Europe was pretentiously placed as the culmination of human cultural evolution due to a premise of sociocultural evolutionism that says that cultures were selected in a manner analogous to biological species, a so-called conception of social Darwinism. Goff et al. (2008), when studying dehumanizing inferences arising from the beliefs of social Darwinism today, have found mental associations between Black people and monkeys to be linked to the biological explanations of racial hierarchies. Such associations affect human judgments by dehumanizing a portion of the population. For example, Black defendants are described in words associated with monkeys more often than White defendants in newspaper reports; and they are the ones who usually receive the most severe penalties in judgments.

Finally, perhaps one of the main points of convergence of postcolonial studies is the dominance over the production of knowledge. Seminal works question the formation of European knowledge within the Enlightenment tradition to the detriment of other possibilities of elaboration of concepts and ideas (e.g., Freire 1972; Martín-Baró 1986; Spivak 1988). For these authors, colonized and colonizers suffer the horrors of imperialism and need to be decolonized. They need to find ways of overcoming the historical relationship of exploitation and domination, not only in political-economic terms but also over their minds and bodies. In the field of knowledge production, they must decolonize knowledge (Grosfoguel 2016). Formerly subaltern peoples must have their voices recognized in their theories, methods, and ways of constructing knowledge, gaining space and thus composing other modernities (Gandhi 1998).

Postcolonialism and Mainstream Psychology

In this European imperialist colonial period, psychological science was influenced by current ideas and was also complicit in the colonizing process generated by scientific racism, which has segregated peoples in many parts of the world. Paulo Freire (1972) and Martín-Baró (1986) wrote about how psychology followed the interests of the powerful, strengthening oppressive and individualizing structures that were, actually, social. In this way, it served as an instrument of rationalization and justification of the oppression and exploitation of native peoples (Gandhi 1998). Evolutionary psychology in particular is criticized for supporting conservative political ideologies, such as economic neoliberalism or the naturalization of gender dichotomies (Pinker 2002). Evolutionary psychology has attempted to conduct multicultural studies in search of understanding human cognitive mechanisms shaped by evolution. The search for these explanations helps to create more accurate and affective intervention models to deal with major human problems, such as racism, inequality, and oppression. Such discoveries can be articulated to construct critical positions that confront the status quo.

Conclusion

In general terms, postcolonialism is an interdisciplinary movement that seeks to understand the effects of colonization. One of the main questions raised is the validity of the knowledge produced by the hegemonic way of thinking and producing knowledge (e.g., supposed scientific neutrality, restricted objectivity), as well as the extrapolation and universalization of the findings to other cultures. Many of the premises and discoveries made by evolutionary psychology in the quest for these universals can be used to question the status quo in society, with emancipatory potential. In addition, postcolonial studies could analyze discursive practices around the knowledge produced by evolutionary psychology and its impacts on everyday practices. These analyses can provide clues to the

relationship between power and subjectivity, as well as pointing out ways of resistance.

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Postcoloniality

► Postcolonialism

Post-Copulation Strategies in Oocyte Fertilization

► Non-primate Mammal Sperm Competition

Postcopulatory Conflict

- ▶ [Nonhuman Sexual Conflict](#)

Postcopulatory Sexual Selection

- ▶ [Sexual Conflict in Nonhumans](#)
- ▶ [Sperm Competition Theory](#)

Post-Copulatory Sexual Selection

- ▶ [Avian Sperm Competition](#)
- ▶ [Sperm Competition: Evidence in Nonhumans](#)

Postmenopausal Altruism

- ▶ [Grandmother Hypothesis](#)

Postmenopausal Somatic Maintenance Post-Reproductive Longevity

- ▶ [Extended Postmenopausal Lifespan](#)

Postnatal

- ▶ [Early Stage of Brain Development at Birth](#)

Postpartum Depression

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Synonyms

[Perinatal depression](#); [Peripartum depression](#)

Definition

Depressive episode of postpartum onset.

Introduction

Postpartum depression is one major psychiatric complication associated with child birth, which adversely affect the quality of life of mother as well as significant ones related to the mother. Postpartum depression negatively affects the parenting as well as relationship with the spouse (Moore Simas et al. [2018](#)).

Prevalence of postpartum depression among women ranges between 10% and 15% (Brummelte and Galea [2016](#); Couto et al. [2015](#)). The onset of symptoms in most patients is antepartum (~50%) (American Psychiatric Association [2013](#)). Postpartum depression becomes different from depressive episodes unrelated to childbirth by the heterogeneity in phenomenology of postpartum depression as well as diverse etiological factors attributing to it (Consortium [2015](#)).

Etiopathogenesis of Postpartum Depression

There are multiple causes of postpartum depression. Genetic basis of postpartum depression has been discussed in literature, which covers genetic susceptibility, epigenetic phenomena, as well as genetic polymorphism of mono-amine neurotransmitters; however, the currently available evidences

regarding genetic association with postpartum depression are insufficient (Couto et al. 2015). Many physiological changes occur in pregnancy and in the postpartum period. Perinatal depressive symptoms can be due to a hormonal imbalance involving the hypothalamo-pituitary adrenal axis (HPA axis) and hypothalamo-pituitary gonadal axis (HPG axis) (Brummelte and Galea 2016). This occurs rapidly in the first week after delivery. Women sensitive to rapid changes in the levels of these hormones might be at higher risk of developing postpartum depression (Schiller et al. 2015). These also lead to differential risk by affecting stress response and processing of emotions. A predictor can be elevated midgestational placental CRH. Also, density of monoamine oxidase A in prefrontal and anterior cingulate cortex is increased. Risk factors include firstly and foremost past history of postpartum depression, past history of unipolar depression, past history of anxiety disorder, family history of depression, and ongoing stressful events occurring and continuing through pregnancy and delivery. Along with these, history of sexual abuse, premenstrual dysphoric disorder, postpartum blues, young age (<25 years), single parenthood, marital conflicts, unwanted pregnancy, and birth of a female baby can predispose to the disease (Guintivano et al. 2018a, b). Perinatal anxiety disorders and sleep disturbances occurring during this period can act both as a risk factor and may exist as a comorbidity. Overlaps between the neurotic spectrum disorders are common; thus, sometimes it may be difficult to differentiate between them and take them as separate entities. Apart from these, psychosocial factors may also have a role to play. Socio-economic status, social position, employment status, income, migration, quality of marital relationship, psycho-social support, as well as expectations from pregnancy also considered to have determining role in postpartum depression (Guintivano et al. 2018a; Turkcapar et al. 2015).

Clinical Features of Postpartum Depression

The clinical features of postpartum depression are similar to that of a depressive episode independent

of pregnancy of postpartum (Turkcapar et al. 2015). Women suffering from postpartum depression often present with persistent sadness, lack of energy, and easy fatigability leading to difficulty completing her daily activities and inability to properly care for the infant along with loss of interest in previously pleasurable activities, which is commonly known as anhedonia. In addition to the above features, crying spells, lack of appetite, disturbed sleep, suicidal ideations, hopelessness, impairment of concentration, poor self-care, as well as poor care of the child may present, which significantly affects the quality of life and functioning. The patients may experience psychotic symptoms (e.g., delusions, hallucinations) and may have psychomotor disturbances as well. Risk of infanticide increases, if the mother develops psychotic symptoms during the course of postpartum depression. Women, who experience psychotic symptoms during postpartum depression, are more likely to develop similar symptoms in their subsequent pregnancies. Women suffering from postpartum (peripartum) depression often experience severe anxiety, which sometimes amount to panic attacks (American Psychiatric Association 2013). It is important to differentiate postpartum depression from postpartum blues ("baby blues"), which commonly characterized by repetitive crying spells, disturbed sleep, and weakness developing mostly within 2–3 days postdelivery. These symptoms are usually self-limiting and resolve within 2 weeks, hence, do not require any intervention (Sadock et al. 2015). In case, these symptoms do not resolve within the 2 week time period; a diagnosis of postpartum depression is much suited. Similarly, during postpartum many women report about altered appetite, sleep as well as energy level, which are self-limiting.

Nosological Status of Postpartum Depression

The ICD-10 classification of mental and behavioral disorders: diagnostic criteria for research classifies postpartum depression under "Mild mental and behavioural disorders associated with the puerperium, not elsewhere classified" and

denoted by code F53.0 (World Health Organization 1993). As per ICD -10, the onset of symptoms of depression should be within 6 weeks of childbirth. The Diagnostic and statistical manual of mental disorders (DSM-5) had kept “postpartum onset” as a specifier of the depressive disorder and considers the onset of symptoms within 4 weeks of childbirth (American Psychiatric Association 2013).

Management of Postpartum Depression

Postpartum depression is an undertreated clinical entity (Werner et al. 2015). Women with postpartum depression need to be evaluated in detail for confirmation of the diagnosis and association of co-morbid medical as well as psychiatric conditions. Detailed history taking, serial mental status examinations, physical examination, and appropriate blood investigations might be useful in ascertaining the diagnosis. Females at risk of developing postpartum depression can be screened using the Edinburgh Postnatal Depression Scale (Brockington 2004; Cox and Holden 2003). This can be applied even in pregnant women. Thus, this can form an important basis for diagnosis. Certain medical disorders (hypothyroidism and vitamin B12 deficiency) may increase the risk of postpartum depression, which need to be investigated for, if such suspicion arises. Apart from medical comorbidities occurring with postpartum depression, psychiatric disorders (obsessive compulsive disorder, panic disorder, generalized anxiety disorder and post-traumatic stress disorder) may coexist. Onset of the comorbid psychiatric conditions can be prepartum, antepartum, or postpartum.

The management plan depends on the nature of psychopathology, severity of episode, associated psychosocial stressors, family support, socioeconomic status and affordability, past history, family history, substance use, and response to medication in past (if any). Antidepressants are the mainstay of treatment. Selective serotonin reuptake inhibitors are commonly used antidepressants in the management of postpartum depression. Addition of antipsychotic agents may be required, if psychotic symptoms present during postpartum

depression. Benzodiazepines need to be used cautiously, as per the need. Caution need to be taken during use of psychotropic medications in lactating mothers as these are secreted in breast milk. Electroconvulsive therapy is another safe alternative to the pharmacological treatment. Psychological interventions (cognitive behavior therapy, interpersonal therapy, and supportive psychotherapy) are also found to have beneficial effect in postpartum depression.

Implications of Postpartum Depression

Maternal mental health is important for development of mother-child bonding. Compromised mental health of mother due to postpartum depression results in poor bonding with child and subsequently difficulties in development of social, behavioral, as well as cognitive skills (Brummelte and Galea 2016). Postpartum depression adversely affects the birth outcomes; hence, it is of utmost importance to conduct the mental health evaluation of mothers during perinatal period (Paschetta et al. 2014).

Conclusion

Postpartum depression is a common psychiatric disorder causing impairment to normal postpartum period and bonding between mother and infant. It can be screened on regular visits and managed early through interdisciplinary collaborative model of care. Sensitizing the obstetricians and midwives on common mental health issues associated with pregnancy and postpartum may be beneficial in early detection of postpartum depression and timely intervention.

Cross-References

► [Peripartum Depression](#)

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Post-Reproductive Life Span

► Menopause

Potential Mate or Partner Fitness Value

► Mate Value

Potential Mates

► Prospective Mates

Pounding Tools

► Stick Tools for Foraging

Power

- Dominance and Territory
- Dominance and Threat or Use of Force
- Dominant Acts Expressed (Buss 1981)
- Function of Dominance
- Higher Status in Group
- Individuals that Impose Costs
- Reputation as a Context for Men's Aggression Against Men
- Social Authority
- Status Competition and Peer Relationships in Childhood

Powerlessness

- ▶ [Learned Helplessness from an Evolutionary Mismatch Perspective](#)

Practical Reasoning

- ▶ [Emergence of Deontic Reasoning](#)

Practice

- ▶ [Play and Social Learning](#)

Practice Play

- ▶ [Sensorimotor Play](#)

Practices

- ▶ [Rituals](#)

Praeanthropus

- ▶ [Australopithecus Group](#)

Pragmatics

- ▶ [Interactive Language Development](#)
- ▶ [Social Learning and Social Cognition](#)

Prairie

- ▶ [Grasslands](#)

Precopulatory Conflict

- ▶ [Nonhuman Sexual Conflict](#)

Precopulatory Intrasexual Competition

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Synonyms

[Intrasexual selection](#); [Precopulatory sexual selection](#)

Definition

Precopulatory intrasexual competition occurs when individuals of the same sex compete directly for the opportunity to copulate with individuals of the opposite sex.

Introduction

Precopulatory intrasexual competition usually involves competition between males for the opportunity to copulate with receptive females. This phenomenon is thought to be responsible for the evolution of a variety of morphological traits, such as enlarged and elaborate male weaponry, and also behavioral traits, such as precopulatory mate guarding. When precopulatory intrasexual competition is particularly intense, it might also lead to the evolution of alternative reproductive tactics

among males, often resulting in male dimorphism (bimodality in the size of traits, such as horns, which creates two distinct male morphs). Precopulatory competition can also generate sexual conflict, where the evolutionary interests of the two sexes are not completely aligned. Finally, despite acting mostly on males, precopulatory intrasexual competition can also affect females under specific conditions.

Context, Causes and Consequences

Sexual selection results from the differential reproduction of individuals of the same sex due to their mating and fertilization success (Andersson 1994). This can result from: (1) individuals of one sex (typically females) choosing individuals of the other sex (typically males) with whom to mate and/or (2) direct competition between members of one sex (typically males) for reproductive access to receptive individuals of the other sex (typically females). The first mechanism is termed “intersexual selection” or “mate choice,” whereas the second mechanism is termed “intrasexual selection” or “male-male (more rarely female-female) competition” (Andersson 1994). Mate choice is the main driver of the evolution of sexual ornaments, whereas male-male/intrasexual competition is the main driver of the evolution of male weapons (Emlen 2008). Sexual selection is traditionally understood as acting in three different episodes, prior to mating (“precopulatory”), during mating (“pericopulatory”), and after mating (“postcopulatory”). Evidence for both processes of sexual selection, and across the three episodes, is ubiquitous in a wide range of animals, including humans.

Weapons and Fights

Throughout the animal kingdom, the reproductive success of females is primarily dependent on their fecundity, whereas that of males depends more heavily on their mating success. Greater variation in male reproductive success compared to female reproductive success is referred to as Bateman’s principle (Bateman 1948). Although still widely debated, the underlying cause for this discrepancy

is probably linked to the degree to which each sex invests in producing/rearing their shared offspring (“parental investment”; Trivers 1972). This phenomenon is thought to be as old as the evolution of sexual reproduction through anisogamy, i.e., the coexistence of a sex that produces large and generally immobile gametes (by definition females) and a sex that produces small and normally highly mobile gametes (by definition males). Because of anisogamy, females invest more in the offspring from the earliest reproductive stage. Indeed, their eggs, which are usually physiologically more costly to produce than sperm, begin to explain why females are limited by their fecundity and typically invest more in the offspring, while males, with their cheaper to produce sperm, are instead limited by their success in achieving matings. Recent mathematical models (Kokko and Jennions 2008), however, have criticized anisogamy and asymmetric parental investment as not sufficiently explaining traditional sex roles (females invest in the offspring more; males compete for females). Nevertheless, regardless of the causes for traditional sex roles, males are usually under stronger precopulatory intrasexual selection, the consequences of which are demonstrated by the evolution of male weaponry traits and combat (Andersson 1994).

Higher variation in the reproductive success of males, and their reliance on mating success, leads to males spending a great portion of their energy in producing and maintaining weapons that grow to seemingly exaggerated sizes, such as antlers, jaws, claws, highly elongated legs, and horns [on their heads or other parts of their bodies, including for instance thoracic horns in beetles (Emlen 2008)]. In certain groups both sexes bare weaponry that may serve a nonsexual function, for example, the naturally selected horns of male and female bovids (Bro-Jorgensen 2007), which are used as a defense against predators. However, for the majority of weapons in the animal kingdom, males are the only ones to produce them or produce them at a much greater degree of exaggeration than females. Interestingly, the nature of male-male fights can range from ritualized displays and sparring that involve mild physical

contact (Alvarez 1993) and no damage to brutal contests that cause severe damage to the contenders. Scenarios such as these are observed in Dawson's burrowing bees, for example, where fights between males often cause disabling injuries that lead to death (Alcock 1996).

Alternative Reproductive Tactics and Intrasexual Dimorphism

The production and maintenance of extravagant and exaggerated weapons can be extremely energetically costly to males, a cost that is often exacerbated by the long and sometimes brutal fights in which males engage. However, male combat theory predicts that weapons may function as assessment signals, and males will benefit if they are able to assess the potential of rival males and avoid fights with unbeatable opponents. In support, it is often observed that the most elaborate weapons rarely inflict real damage to opponents, but reveal and highlight subtle differences in male size, status, or physical condition [e.g., rhinoceros beetle horns (Eberhard 1979)], while unimpressive or inconspicuous weapons regularly inflict serious damage in male contests [e.g., spiders (Leimar et al. 1991)]. As a result of the high costs of producing or maintaining weapons and engaging in dangerous fights, small males of a variety of species have evolved tactics to completely avoid fighting (Oliveira et al. 2008). Instead, these males seek copulations through alternative means, such as sneaking undetected into a larger male's territory (Emlen 1997), searching for females that are not inside any territory (Alcock 1996), or pretending themselves to be females in order to get close to females without being chased away by larger males (Norman et al. 1999). Such alternative tactics are common within vertebrates, molluscs, arachnids, and especially insects.

Alternative reproductive tactics in males often consist of different mating behaviors that show high plasticity, so that the same individual can switch between tactics dynamically through the course of a breeding season, or even throughout the day, as in the butterfly *Lycaena hippothoe*, where the weather determines

whether a male defends a territory or actively patrols for females (Fischer and Fiedler 2001). In other cases, a male can only switch tactics a limited number of times, or only in one direction, as the damselfly *Calopteryx maculata*, where males switch from territoriality to a sneaking behavior as they age (Forsyth and Montgomerie 1987). Finally, alternative reproductive tactics can select for morphological specializations, leading to the evolution of dimorphic males, a phenomenon called male dimorphism or intrasexual dimorphism. In such cases, for example in many dung beetle species, the alternative tactics are irreversible, as fighter males develop enlarged horns that are absent in small sneaker males (Emlen 1997).

Precopulatory Mate Guarding

Intrasexual competition can also manifest through more subtle adaptations, such as mate guarding, where a male guards a female and directly prevents her from mating with rival males, a behavior that is particularly common in crustaceans when the period of female receptivity is short (Jormalainen 1998). In some butterfly species, males might even guard and fight for a chrysalis that contains an immature female going through metamorphosis, as a strategy to guarantee that they will be her first sexual partners (Mendoza-Cuenca and Macías-Ordóñez 2010). Interestingly, male birds that offer paternal care may guard their partner but only attempt to mate with them after being paired for several days, presumably to guarantee that the clutch is not sired by another male (Owens et al. 1995).

Mate guarding is also quite commonly observed after the mating has already occurred, but in these cases the behavior is regarded as a strategy to avoid postcopulatory competition processes, such as sperm competition. In fact, whether males guard the females prior or after copulation can be indicative of sperm precedence in the species: if the first male to mate fertilizes most of the eggs (first male sperm precedence), males tend to guard their mates prior to copulation; whereas if the last male to mate is the one who fertilizes most of the eggs (last male sperm

precedence), males tend to guard their mates after copulation. Evidence for this relationship, and its connection with the internal morphology of the female reproductive tract, which in itself predicts the pattern of sperm precedence mentioned above, came originally from studies of spiders (Eberhard et al. 1993).

As an example of “remote” mate guarding, and as an attempt to prevent or delay inseminations by rivals, the males of many taxa (e.g., insects, spiders, reptiles, mammals) deposit mating plugs to obstruct the female reproductive tract. When 100 % effective, mating plugs will prevent sperm competition and thus be beneficial to males by simultaneously providing paternity assurance while also allowing them to seek out and copulate with additional females (Sutter et al. 2015). As detailed in the following section, male prevention of postcopulatory sexual selection may not be beneficial to females.

Precopulatory Intrasexual Competition and Sexual Conflict

Sexual reproduction has historically been viewed as an act of cooperation. However, the complete alignment of male and female interests over reproduction is one extreme along a continuum for which the other extreme is complete conflict between the sexes (Arnqvist and Rowe 2005). Sexual conflict, which occurs when the evolutionary interests of the two sexes are not in accord, enforces opposing selection pressures on males and females. As mentioned previously, males and females often differ in their investment in reproduction, leading to distinct roles with different fitness optima for each sex. As both optima cannot be reached simultaneously, selection favors each sex to maximize its fitness at the expense of the fitness of the other sex. Cycles of adaptations and counteradaptations between the sexes can generate a perpetual tug-of-war, resulting in male–female coevolution and the rapid evolution of sexual traits (Arnqvist and Rowe 2005). Sexual conflict is ubiquitous in nature and can be observed at multiple levels, extending from courtship and mating to fertilization and parental investment.

Mechanisms and strategies of precopulatory intrasexual competition may not always align with the females’ best interest and thus generate sexual conflict (Bonduriansky and Rowe 2003). For example, dominant males that win intrasexual contests may increase their own mating opportunities by excluding rivals, but females in turn have reduced fitness when mating with dominant males (Wong 2004). Females may then discriminate against dominant males in favor of subordinates to increase their own fitness. Further, successful mate guarding attempts will prevent females from copulating with more than one male and therefore potentially hamper female fitness. Multiple-mating by females (polyandry) has been shown to be a profitable mating strategy when females gain either direct benefits from males (e.g., the nuptial gifts of insect species, Gwynne 2007) or via more indirect, subtle means that lead to the improved genetic quality of their offspring (i.e., the good and compatible genes models for the evolution of polyandry, reviewed by Jennions and Petrie 2000). In bird species in which females benefit from multiple-mating, and thus seek copulations with males other than their social partner (extra-pair copulations or EPCs), selection will favor traits that simultaneously enhance the male’s ability to guard his mate and the female’s ability to evade mate guarding. Female superb fairy-wrens have quite successfully adopted a tactic of acquiring EPCs by seeking out extra-pair males prior to dawn, presumably to avoid detection by their social partner (Double and Cockburn 2000).

Female-Female Competition

The ubiquity of the traditional mating roles, in which males fight over access to females or resources and females choose males, has led to studies of intrasexual competition focusing mainly on male-male competition. By contrast, precopulatory competition among females, which is not that rare and seems to act more commonly through male mate choice than female-female competition, has received considerably less attention.

A reversal of the typical mating roles might occur under specific conditions. For example, a

bias in the operational sex ratio (OSR) has been shown to predict which sex will compete for access to mates and how intense the competition might be (Kvarnemo and Anhesjö 1996). That is, mating competition is expected to become more intense as the OSR deviates further from equality, and the sex that is in “excess” (the sex predicted to become the predominant competitor for access to mating partners) will experience stronger sexual selection (Kvarnemo and Anhesjö 1996). When males are the limiting sex, females might compete directly for access to males, for resources that they acquire from them, including food and territories (e.g., nest sites), or for the protection they offer (Stockley and Bro-Jørgensen 2011 and references therein). When males vary in the quantity or quality of the resource/s they provide, females are expected to compete for mates as an indirect manifestation of resource competition. Consistent with this idea, women often compete for marriage partners in human societies that are characterized by monogamy and strong wealth differentials among males (Stockley and Bro-Jørgensen 2011). In food-stressed katydid populations, the low proportion of males able to produce a nuptial meal (the spermatophylax that envelops the spermatophore) leads hungry females to foraging for “mating meals” and consequently results in females competing for access to males (Gwynne and Simmons 1990). In the Chacma baboon, where sexually selected infanticide by unrelated males is a potential threat to offspring survival, females rely on support from male “friends” (with which they are more likely to mate) to help protect their offspring (Stockley and Bro-Jørgensen 2011).

In some cases it may not be the males or the resources that they provide that are limited, but instead sperm. Traditionally, limitations to male sperm supplies were not thought to influence the evolution of mating strategies. However, it is now known that this is not always the case, and sperm depletion among males may be promoted by several factors, such as a synchronization of female receptivity or breeding periods, high rates of polyandry, or unanimous female mate preferences that tips the OSR towards a female bias. The elicitation

of male sperm limitation and female-female competition for mates due to factors such as these are seen among ungulate species that experience strong breeding synchrony and high rates of female multiple-mating (Stockley and Bro-Jørgensen 2011). Whether females are competing for access to males, their resources or their sperm, precopulatory intrasexual female competition, in theory, could lead to the evolution of exaggerated traits used to outcompete rival females in contests, analogous to male sexually selected traits. However, in addition to survival costs, the development of female weapons seems to be limited by fecundity costs (Clutton-Brock 2009). Certainly, an absence of these traits in nature suggests that precopulatory intrasexual selection is not the same potent evolutionary force for females than it is for males.

Conclusion

Precopulatory intrasexual competition is a ubiquitous phenomenon that results from the competition between males for reproductive access to receptive females and more rarely between females for access to males or their resources. For males, this type of competition can be fierce and is recognized to have selected for a multitude of morphological (weapons) and behavioral (precopulatory mating guarding) traits. Often small males are unable to compete, and in such cases precopulatory intrasexual competition might select for alternative reproductive tactics that can even lead to the evolution of bimodality in the sizes of males and/or their weapons. If females benefit from mating with males that are not the winners of male-male fights, intrasexual competition can also lead to sexual conflict.

Cross-References

- ▶ [Copulatory Intrasexual Competition](#)
- ▶ [Female-Female Competition](#)
- ▶ [Intrasexual Competition Between Females](#)
- ▶ [Male-Male Competition](#)

- ▶ Male–Male Strategies
- ▶ Sexual Dimorphism and Sex-Biased Gene Expression
- ▶ Sexual Selection
- ▶ Sneak Copulation

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- [Precopulatory Intrasexual Competition](#)
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Predator Attraction

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Predator Confusion Hypothesis

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Synonyms

[Alarm call](#); [Alarm call confuses predator](#); [Antipredator vocalization](#); [Camouflage](#); [Decreased chance of predation](#); [Mobbing](#); [Pursuit deterrence hypothesis](#); [Reduction of predation](#); [Swarming](#); [Squirrel family *Sciuridae*](#)

Definition

The predator confusion hypothesis (Sherman 1977, 1981) predicts that group-living animals are adapted to make alarm calls that distract or confuse predators, thus lowering the predator's chances of consuming any prey individual. In birds and mammals, some species make anti-predator vocalizations that are thought to confound predators (Ficken 1989). When a single individual vocalizes in response to a predator, other group members will echo that call, creating disorder and preventing the predator from being successful.

Introduction

Animal species ranging from invertebrates to birds to mammals are targeted by predators for food. These prey species have evolved various behaviors to help them avoid predation, including crypsis, where animals hide or conceal themselves to escape predator attention; swarming, where animals move together while concentrated in a small space; mobbing, where animals approach a predator for the purposes of intimidating it; and/or alarm calling, where animals make loud vocalizations in response to the detection of threats (Charnov and Krebs 1975; Jeschke and Tollrian

2007). Alarm calls draw attention to the individuals who vocalize and can result in a higher chance of predation in some species, such as several Sciuridae rodents (Maynard Smith 1965; Sherman 1977). In other species, such as birds and primates, alarm calling may be one of several means by which prey animals reduce their chances of predation by confusing predators (Cresswell 1994b; Wheeler 2008). Alarm calls are adaptive if they drive predators away and/or enhance the survival rates of a caller's relatives (Maynard Smith 1965).

Several non-mutually exclusive hypotheses have been proposed in explanation for the adaptiveness of alarm-calling behavior, including the predator confusion hypothesis (Wheeler 2008). This hypothesis predicts that for group-living species, an alarm call by one individual that is echoed by other group members may distract the predator and also reduce the chance of single individuals being targeted through the dilution effect (Bertram 1978). Group members may approach and noisily vocalize toward a predator, which has the effect of confusing the predator and reducing its chances of prey consumption (Sherman 1977). The predator confusion hypothesis is one of several explanations for the evolution of antipredator vocalizations in group-living animals.

Alarm Call Creates Confusion

The predator confusion hypothesis is based on the idea that prey animal behaviors misdirect or confound predators, thus decreasing the likelihood of successful predation events (Charnov and Krebs 1975). This provides a survival advantage to the prey, stemming from predator confusion occurring in one of several forms. Prey may confuse predators through camouflage, swarming or aggregation, mobbing, and/or alarm calling.

While spiders are known to confuse predatory wasps through the camouflage provided by web decoration (Tseng and Tso 2009), and prey including invertebrates, fish, and birds are known to decrease their chances of predation by moving in swarms (Jeschke and Tollrian 2007), some mammals and birds confound predators through alarm

calling. When a predatory threat is seen, prey animals make alarm calls in response. Vocalizing reveals the caller's location to predators, and, for animals including various Sciuridae rodents, this causes the caller to be targeted by the predator (Sherman 1977, 1981). Because alarm calling does not increase the chance of survival for these prey species, other explanations are useful in understanding how alarm calling has persisted over evolutionary time (Maynard Smith 1965). For group-living prey animals, the predator confusion hypothesis predicts that when an individual makes an alarm call, other group members will also make alarm calls, in an attempt to confuse the predator and drive it away (Wheeler 2008). Group-wide alarm calling may divert a predator's attention, preventing it from being able to focus on a single prey animal for pursuit and generally causing disorder and confusion (Sherman 1985). The predator is thus less successful at killing and consuming prey as a result of the chaos caused by antipredator vocalizations (Sherman 1977).

Alarm calling has been theorized to create confusion for the predators of a number of animal species (Charnov and Krebs 1975). Whenever an alarm call is produced in a group-living species, this can create disorder as all group members echo this alarm vocalization and rush to escape from this threat. The unpredictable, erratic vocalization and movement behavior by the prey is thought to distract the predator, giving each animal in the group an increased chance of escaping (Jeschke and Tollrian 2007). Alarm calling has been proposed to cause confusion for the predators of rodents, birds, and primates (Sherman 1977, 1981; Ficken 1989; Bolt et al. 2015). For rodents including the Belding's ground squirrel (*Urocitellus beldingi*), individuals vocalized and moved to conceal themselves in response to predatory threats (Sherman 1977). These movements and calls were hypothesized to confuse predators and prevent predation, although empirical evidence does not support this and alternate hypotheses for the adaptive function of alarm calling in ground squirrels have received greater support (Sherman 1977, 1981). The predator confusion hypothesis has also been applied to other vocalizing animal species. Birds including black-capped

chickadees (*Poecile atricapillus*), Steller's jays (*Cyanocitta stelleri*), and Clark's nutcrackers (*Nucifraga columbiana*) engage in mobbing behavior by gathering around potentially dangerous predators while making group-wide alarm vocalizations at their own rates (Ficken 1989). These group-wide antipredator vocalizations were suggested as adaptations that add to predator confusion and reduce the chances of single animals being consumed (Ficken 1989). For primates such as the ring-tailed lemur (*Lemur catta*), antipredator vocalizations initiated by one group member are also made by other group members, which was suggested to cause confusion for predators (Bolt et al. 2015). However, although these prey species have alarm calls with the potential to cause predator confusion, it is unknown whether the calls of jays, chickadees, nutcrackers, and lemurs do confound predators. The alarm calls of these animal species have not been empirically tested for predator effects, and more direct observations of predator-prey interactions are needed to further evaluate this hypothesis.

Confusion Enables Escape

Group-wide alarm calling in a variety of prey species has been suggested to confuse predators, by distracting predators from targeting specific individuals and better allowing prey to flee and avoid consumption (Jeschke and Tollrian 2007). Although the predator confusion effect has been proposed for the alarm calls of various prey animals, few species have been tested for direct evidence that alarm calling causes predator confusion and better enables prey to escape. This stems from the difficulty of observing predation events in the wild and the difficulty in separating various non-mutually exclusive explanations for behavior (Bradbury and Vehrencamp 1998). A handful of alarm-calling rodents, primates, and birds have been tested experimentally or observationally for evidence of the predator confusion effect, with mixed results. For the redshank bird (*Tringa tetanus*), there was no higher chance of mortality for birds who alarm called while in flight, likely due to confusion for the predatory sparrow hawk

(Cresswell 1993). For the Belding's ground squirrel (*Urocitellus beldingi*), alarm calls showed no evidence of confusing predators since weasels and coyotes followed and killed the alarm callers at higher rates than non-callers (Sherman 1977, 1981). Tufted capuchin (*Cebus apella*) alarm-calling behavior was also tested for confounding effects and thought to be unlikely to confuse predators (Wheeler 2008).

The pursuit deterrence hypothesis (Sherman 1977) is a related and overlapping hypothesis which suggests that alarm calling is adaptive for prey because it discourages predatory targeting and leads to increased survival for the caller. Animal species ranging from birds to ungulates and primates have been found to have alarm calls that deter predators, although it is unknown whether predator confusion is a causative factor in this deterrence. Birds such as the Eurasian skylark (*Alauda arvensis*), ungulates such as the klipspringer antelope (*Oreotragus oreotragus*), and primates including the Diana monkey (*Cercopithecus diana*) are known to use alarm vocalizations to drive away stealth predators (Tilson and Norton 1981; Cresswell 1994b; Zuberbühler et al. 1997). In each of these cases, vocalizations are thought to deter predators through intimidation and/or the loss of the element of surprise, but there may also be some element of predator confusion involved, since the predator deterrence and predator confusion hypotheses are not mutually exclusive (Wheeler 2008). Further study is needed to elucidate whether alarm calls may deter predators through confusion in these species.

Although little direct evidence exists for predator confusion caused by alarm calling, the general phenomenon of predator confusion as a result of prey behavior is widespread and has support from a variety of taxa. Further evidence of confusion exists from prey species that confound predators through camouflage or swarming.

Camouflage is known to be used by spiders to confuse wasp predators, since those spiders who decorate their webs have a lower chance of being consumed (Tseng and Tso 2009). Web decoration is thought to divert predator attention by acting as a decoy, thus concealing the spider's actual

position on the web (Blackledge and Wenzel 2001). Swarming happens in various group-living animal species and has been found to confuse predators for many of these (Jeschke and Tollrian 2007). Swarming is when many conspecifics are in motion while in very close proximity, and it is the presence of many individuals moving together in an unpredictable way that is thought to make it difficult for predators to successfully attack (Olson et al. 2013). Predators are unable to focus on individual prey animals because they divide their attention between many visible members of a swarm, which results in a decreased chance of capturing a single individual (Dukas 2002).

Evidence of predator confusion through prey swarming behavior is widespread and exists for prey taxa including fish, birds, and invertebrates such as nematodes and common water fleas (*Daphnia* spp.) (Neill and Cullen 1974; Cresswell 1994a; Jensen and Larsson 2002; Jeschke and Tollrian 2007). The majority of predator-prey groups tested showed evidence of predator confusion (Jeschke and Tollrian 2007; Olson et al. 2013), revealing this as a widespread anti-predator adaptation for social prey organisms. Predators who detect prey based on both tactile and visual systems are affected, while prey species that move faster, move more erratically, and/or aggregate in larger groups are more likely to elude capture (Jeschke and Tollrian 2007). The predator confusion hypothesis is well supported by evidence from animal behavior in general, although alarm calling in particular has yielded little direct evidence of causing predator confusion to date.

Conclusions

A greater number of vocalizing and group-living prey species need to be studied for evidence of predator confusion. Although the predator confusion hypothesis is well supported with respect to swarming behavior in various animal taxa, evidence of alarm vocalizations causing predators to be less successful due to confusion is lacking (Ficken 1989; Olson et al. 2013). However, the predator confusion hypothesis stands alongside

the predator deterrence hypothesis as one of several cogent, non-mutually exclusive hypotheses for the evolution of alarm-calling behavior. In the absence of direct evidence for predator confusion, it remains a compelling and plausible theoretical explanation for the evolution of risky vocalization behaviors by group-living animal species.

Cross-References

- Alarm Calling
- Alarm Calling and Kinship
- Alarm Calling Predicted by Inclusive Fitness
- Alarm Calling upon Predator Detection
- Alarm Calls
- Deceptive Alarm Calls
- Prey Availability
- Prey Choice

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Predator Detection

- [Predators as Attention-Grabbing](#)

Predator Deterrence Hypothesis

- [Alarm Calling upon Predator Detection](#)

Predator Satiation

- [Predator Swamping](#)

Predator Saturation

- [Predator Swamping](#)

Predator Swamping

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Synonyms

[Predator satiation](#); [Predator saturation](#); [Safety in numbers](#)

In prey animals, it is widely accepted that living in groups reduces the risk of predation and that this occurs via a number of mechanisms, such as collective detection of predators (see “[Grouping and Predation](#)”). While this explains aggregation over space, *animals vulnerable to predators are often aggregated in time, where there is temporal synchrony in the period that individuals are exposed to predators*. This synchrony in timing “swamps” the response of predators, so that the overall rate of predation does not increase proportionally with the greater availability of prey. The result is a reduced risk of predation per individual prey, and predator swamping provides an evolutionary explanation for the collective emergence of mayfly larvae (Sweeney and Vannote 1982), cicadas (Williams et al. 1993), some species of sea turtle hatchlings (Santos et al. 2016), the young of some ungulates (Milner-Gulland 2001) and birds (Nisbet 1975) through synchronous breeding, and even mast seeding in plants, where large numbers of seeds are produced in some years within a population of plants and very few in

others (Kelly 1994). These examples demonstrate both the diversity of living organisms that show synchronous emergence, and also that this synchrony can occur within a set (clutch, brood) of related offspring (e.g., sea turtle hatchlings) and between individuals within a population (as occurs in mast seedings (Kelly 1994) and breeding aggregations (Milner-Gulland 2001; Nisbet 1975)). While predator swamping is often used to explain synchrony in reproductive contexts, it has also been used to explain behavioral synchrony, where individuals expose themselves to risk in a collective and coordinated manner. For example, the aquatic African clawed frog (*Xenopus laevis*) can breathe air at the water surface and increases the synchrony of this behavior after a disturbance, suggesting that this synchrony is a response to potential risk (Baird 1983).

A number of studies have shown that the risk of predation per prey individual decreases when the number of prey available increases (Nisbet 1975; Santos et al. 2016; Sweeney and Vannote 1982). A major explanation for this effect is handling times. All foragers are subject to a handling time, which is determined by the time required to capture, subdue, consume, and/or digest a food item. This places an upper limit on the rate that prey can be killed and consumed, and if the time that prey are available is limited (for example, as newborn individuals grow to be less vulnerable), the total number of prey consumed will be limited as well. The result is a “type II functional response,” where the consumption rate of predators increases with prey density but saturates at high densities (Holling 1959). If prey emergences are patchily distributed over space, the time required for predators to locate and move to the prey can have a similar effect, so that the spatial aggregation of predators to the prey patch is delayed relative to the time period that prey are available for capture. In a recent study, Santos et al. (2016) argued that both of these effects are likely to explain why individuals often hatch synchronously within nests of sea turtles. In their study system of green turtle (*Chelonia mydas*) hatchlings being preyed upon by the yellow crab (*Johnnarthia lagostoma*) as the hatchlings crawl to the sea, the large size of the hatchlings relative to the predators results in long handling times

where the prey are consumed and digested. Although crab densities were relatively high at the study site, the limited sensory range and mobility of the crabs searching for prey in the dark also makes it unlikely that the crabs could respond to a hatching event quickly enough for there to be a large increase in local predator density around a hatching nest. Once the crabs in the local vicinity have finished consuming their first captured prey, and those a further distance away could respond to the emergence, the hatchlings would have already reached the relative safety of the sea.

Although predator swamping is used to explain reproductive (Ims 1990) and behavioral (Baird 1983) synchrony, predator swamping through temporal synchrony can also occur via prey moving together in groups (see “[Grouping and Predation](#)”). If prey groups are mobile relative to their predators and do not show predictable patterns of movement, it is unlikely that predators will be able to track their location, so when prey are encountered, the time available to attack and consume prey is limited. With a handling time that limits the rate of capturing prey, this results in a predator swamping effect. In contrast, evenly or randomly distributed prey will be encountered more frequently, and the time between encounters will allow predators to handle prey and be more likely to be ready to consume prey in the next encounter. This is essentially attack abatement (Turner and Pitcher 1986), where the rate of attacks on a group is less than proportional to group size, and only a limited number of prey can be killed upon each encounter (also see “[Grouping and Predation](#)”). In general, the term predator swamping is applied to cases where prey can be either in a safe or vulnerable state, and the transition to the vulnerable state is synchronized with other individuals in time. Attack abatement is instead applied to prey aggregated in space, where being vulnerable depends on whether a group is detected by a predator. There is nonetheless a close link between mass emergences of prey and when prey are actively social and form groups.

While predator swamping is a simple and hence parsimonious explanation for synchronous emergence, alternatives have been suggested for

some systems. A high density of prey, even if they are not actively forming groups, can still result in antipredatory benefits similar to those documented for animals living in groups (see “[Grouping and Predation](#)”), such as the confusion effect (Baird 1983). Synchrony in emergence may be a direct response to variation in available resources rather than as a strategy to swamp predators. However, it is unlikely that environmental conditions will vary over time in such a punctuated manner that it can explain synchronous emergence in most systems, i.e., environmental variation will rarely perfectly match the variation in prey abundance over the appropriate temporal and spatial scales. Mast flowering in some plants can be explained by environmental prediction, where a cue triggers plants to respond by increasing reproductive effort to take advantage of favorable conditions that are expected to follow. This is likely to explain greater reproductive effort in some plants after fire, which releases nutrients into the soil and reduces competition for their offspring (Kelly 1994). The mast flowering of other plants can also be explained by wind pollination being more efficient where the probability of fertilization increases with the number of flowers, and this is well supported by empirical studies (Kelly 1994).

Synchronous emergence is not always beneficial for reducing predation risk, as predators can minimize handling times by storing killed prey, or aggregate around emergences if they are highly mobile. Where predators can switch between prey types or are mobile enough, synchronous emergence at a local scale can actually increase the risk of predation for synchronous rather than asynchronous prey (Ims 1990). For predator swamping to be effective, synchronous emergences of prey need to be difficult to predict by predators; if they are not, predators will move toward and aggregate around the emergence or even time their own reproductive effort so that the predator population size increases with the greater abundance of prey. As with understanding the antipredatory benefits of living in groups, the behavior of predators in response to mass emergences of prey needs to be studied, as well as the behavior of the prey, to fully understand predator swamping.

Cross-References

► [Grouping and Predation](#)

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Predators

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Synonyms

[Carnivore](#); [Hunter](#); [Killer](#)

Definition

An animal that preys on other animals for food.

Introduction

Bipedal locomotion introduced a number of profound changes for hominins. While ancestors of humans primarily lived in trees, it is believed that ancestors of hominins were the first to move out of trees and adjust to living in new terrains, such as savannahs. As a result, evolution took its due process and therefore induced changes in our ancestors to adapt to their new environment and accommodate to the new prey and means of killing them. As a result, hominins developed the ability to walk on two legs, also called *bipedal locomotion*. Bipedal locomotion changed a number of behaviors in hominins, but among them are their predatory instincts and especially the way they hunted (Lovejoy et al. 2009).

Effects on Hunting Behaviors

Given that bipedal locomotion frees up usage of the upper body and hands rather than using them to walk, this completely shaped the behavior of how these early hominins would hunt their prey. While prior to bipedal locomotion much of the hunting was executed in trees, these hominins now had entire savannahs to traverse using their two legs and therefore acquired the ability to run long distances. Running long distances was pivotal to hominin survival and therefore was a huge advantage in early human life. A key component to this was endurance rather than short sprints which were indicative of many preys that these hominin would hunt. While certain animals such as gazelles could quite easily outrun an early hominin, the hominin soon developed the ability with bipedal locomotion to be able to jog these distances for extended periods of time. The prey would eventually tire out from its short bursts of sprints and be forced to rest, to which the

hominin would then be able to execute its prey after its long distance chase. Behaviors like these were exclusively capable because of bipedal locomotion, as the change in body shape and posture allowed for longer, endurance-based runs rather than quick bursts of speed, as detected by footprints found of early hominids (Raichlen et al. 2010).

In addition to endurance-based running, bipedal locomotion had a profound effect on predatory behavior in hominins in many other ways, including vision. While living in trees, posture was developed to be able to climb trees and also typically had an arch in the spine as seen in many current primates in the wild. As a result, looking forward was quite difficult and led to a change in vision and the ability to perceive their surroundings. However, bipedal locomotion had the effect of forcing the spine into a straight, vertical orientation, not only changing the physiological structure of the hominin but also the way they looked out at their surroundings. Due to the lack of curvature in the spine, hominins now had access to a much wider horizon and field of view as compared to their previous orientation. As a result, this was extremely advantageous in a savannah-like environment, given the lack of structures such as trees blocking field of view. While living in forests required being able to climb to assess their surroundings, the move to savannahs meant wide stretches of flat land, to which being able to horizontally look around and assess one's environment was pivotal to survival, as well as to predatory behavior (Raichlen et al. 2008).

Lastly, bipedal locomotion also allocated two free limbs as compared to those limbs being used for locomotion. As a result, hominins developed the use of their arms, which allowed for countless behaviors that we can even see we use today. Behaviors such as picking up objects, grabbing, and even throwing became pivotal tools in our ability to hunt and survive on the savannah. As hominins continued to develop, they utilized the use of tools and weapons in their hunts, which they would not have been capable of doing had they not developed to bipedal locomotion. The

free use of their hands and arms then allowed them to create weapons in the first place, as well as develop throwing motions to be able to take down animals from a distance. Doing so allowed for hunting animals that prior to this development would have been faster than them or would have required a great deal of endurance and effort, thereby maximizing their resources while limiting expenditure of their energy.

Conclusion

These changes and adaptations made bipedal locomotion essential to the way we survived by hunting animals in our newfound savannah-like environment. Everything from increased endurance due to a change in physiological body shape, changes in vision due to the placement of the skull on top of the body, to the free usage of hands to create weapons and use them in throwing motions allowed these hominins to adjust to their change in environment and continue to survive and reproduce, eventually becoming the homo sapiens we see today.

Cross-References

- ▶ [Alarm Calling upon Predator Detection](#)
- ▶ [Bipedal Locomotion](#)

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Predators as Attention-Grabbing

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Synonyms

[Attentional capture](#); [Delayed disengagement](#); [Fitness-relevant](#); [Predator detection](#); [Survival-relevant](#); [Threat detection](#)

Definition

The fast, seemingly automatic detection of threatening words and images, coupled with delayed disengagement from their location and more durable memories of threat-relevant information.

Introduction

At the intersection between emotion and the evolutionary and cognitive psychology literatures lies a powerful adaptation: the seemingly automatic attentional capture of threatening stimuli in one's environment. For example, angry faces are quickly spotted among happy ones, and snakes and spiders are easily detected among neutral backgrounds of flowers, mushrooms, and non-threatening animals. The current review discusses common findings with these visual search and attentional cuing tasks, with a special emphasis on the mechanisms underlying attentional capture. Recent findings from the related adaptive memory literature also suggest that effects associated with threatening stimuli – faster detection, slower disengagement, and so on – can also

translate into more durable memories. Together, these findings support evolutionarily-derived hypotheses for cognitive processes and abilities.

Threats, Fears, and Attention

In the classic visual search paradigm, participants are presented with arrays of static images and asked to indicate whether the images belong to the same or different categories. As the images contain a variety of fear-relevant (e.g., snakes, spiders) and fear-irrelevant (e.g., flowers, mushrooms) stimuli, these investigations extend the typical visual search paradigm (i.e., assessing differences in search times as a function of varying array size) to consider whether search time also varies in accordance with the evolutionary significance of threat-detection. Öhman, Flykt, and colleagues (Flykt 2006; Öhman et al. 2001; Soares et al. 2009) have demonstrated a robust advantage for snake and spider detection, when presented among neutral backgrounds of flowers and mushrooms. These advantages in search times do not appear to be affected by grid size, nor do they rely on specific combinations or locations of images within the array. Furthermore, while some of their work has shown some additional sensitivity to images of snakes (Öhman et al. 2001), experiments sampling spider phobic individuals have shown comparable sensitivity to spider detection among neutral backgrounds (Soares et al. 2009).

Flykt (2006) has argued that search times involve a sequence of controlled searching for the target stimulus, automatic processing of the target, and action preparation in accordance with the target's associated level of threat. The more salient targets – those posing a potential threat – carry a great deal of emotional relevance and facilitate the search process, requiring shorter search times. Other, related work has shown that a *moving* threat (i.e., the more dynamic nature of a moving cockroach, relative to a moving ladybug) is particularly distracting in other attention-based tasks (Carretié et al. 2009). These findings have been replicated with face stimuli, with more efficient searches for moving threatening faces among moving friendly faces,

than vice versa (Hortsmann and Ansorge 2009). Thus, motion provides valuable information: a greater signal of imminent danger in one's environment. Simple procedural modifications have also shown that the advantages associated with threat detection in visual search can be observed among infants and young children, including those as young as 5 months old (LoBue 2010; Rakison and Derringer 2007). These findings indicate that attentional biases to spiders and related fears may originate from a stored template: one that may not rely on any prior experience with the threatening stimulus.

Researchers have also adapted attentional cuing paradigms for these threat-related investigations. Fox et al. (2001) have asked whether threatening stimuli automatically attract attention or whether they prevent disengagement of attention to other – positive or neutral – stimuli. They found that the presence of threatening words (e.g., fail) and angry faces delayed the disengagement component of visual attention, slowing participants' responses when these stimuli cued invalid locations (i.e., those other than the target location), relative to positive and neutral cued locations. Related findings with eye-tracker methodology have shown that participants are generally more distracted by dangerous stimuli (e.g., lions, snakes) than they are distracted by non-dangerous stimuli (e.g., impala, lizards), and these distractions are a function of both faster detection times (i.e., the time spent locating the lion) and increased fixation duration (i.e., the time spent looking at the lion) (Yorzinski et al. 2014). Thus, the delayed disengagement hypothesis is supported by both behavioral and eye movement data.

Additionally, Fox et al. (2001) have found that disengagement is particularly delayed among high-anxious participants, who in their fifth experiment took significantly longer to disengage from locations with threat-related words relative to low-anxious participants. Threatening faces provided similar results, with increased attentional dwell time to both real and schematic faces among high-anxious participants. Thus, an anxious individual's greater propensity to avoid dangerous situations is particularly apparent in these

experimental manipulations: an avoidance with adaptive value. Together, these adaptations help humans respond appropriately in times of threat, with findings from both the visual search and cuing paradigms supporting the notion that threatening stimuli in the foreground and background grab and maintain our attention.

Fox et al. (2007) have hypothesized a flexible, evolved fear module to account for this body of literature. In their visual search experiments, they compared search times for phylogenetic (i.e., ancestral fears of snakes and spiders) and ontogenetic (i.e., modern fears of guns and syringes) fears, with fear-relevant images presented among a variety of neutral backgrounds: flowers and mushrooms, as well as toasters and electric kettles. This particular comparison examines whether threat-detection varies as a function of the particular age of the threat: Were threats present at the time of mammalian evolution granted some priority or threat superiority? Their findings indicated a general threat-superiority effect, with images of snakes and guns attracting attention more effectively than neutral images, and no advantage of ancestral threat-detection. Supporting related work, their data indicate that stimuli appraised as highly relevant – threatening targets, moving objects, and so on – garner more attention in the present moment.

Related Findings and Conclusions

Recent findings have also shown that the attention-grabbing power of threatening stimuli can promote more lasting memories than neutral stimuli. The adaptive memory literature hypothesizes that the human memory system evolved to solve and remember fitness-relevant problems: those problems that engaged survival-relevant thought processing. In their seminal work, Nairne et al. (2007) found that participants' memory for neutral, concrete items (e.g., screwdriver, pan) was enhanced when considering how they might aid in locating survival materials and providing protection from nearby predators. This mnemonic improves upon other, well-known strategies, including those that engage deep, meaningful word processing (see Kazanas and

Altarriba 2015 for a recent review). Thus, the mere thought of predators – without needing to visualize them – may facilitate more efficient cognitive processing. In an interesting twist, researchers have also found that considering particularly salient predators – including demons and zombies embodying superior, supernatural capabilities – provides some additional memory benefit (Kazanas and Altarriba 2017; Soderstrom and McCabe 2011). Data collected at the intersection between emotion, evolution, and cognition, using a variety of tasks, have drawn similar conclusions: Engaging the predator-avoidance mechanism in times of threat is a combination of fast detection, slower disengagement, and durable memory formation.

Cross-References

- ▶ [Ability to Recognize Individuals](#)
- ▶ [Alarm Calling upon Predator Detection](#)
- ▶ [Development of Adaptations](#)
- ▶ [Emotions](#)
- ▶ [Environment of Evolutionary Adaptedness](#)
- ▶ [Episodic Memory](#)
- ▶ [Evolution of Adaptations](#)
- ▶ [Fears](#)
- ▶ [Fears and Phobias](#)
- ▶ [How Evolutionary Psychology Can Still Explain Behavior](#)
- ▶ [Phobias](#)
- ▶ [Predators](#)
- ▶ [Selective Attunement to Adaptive Problems](#)
- ▶ [Survival and Death](#)
- ▶ [Universal Human Fears](#)

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Predicting Events and Behavior

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Synonyms

Forecasting; Interactive decision-making;
Judgment and decision-making

Definition

Memory systems use the experience to expect what will happen in the present and future and decide how to behave in this circumstance.

Introduction

In 1989, researchers John R. Anderson and Robert Milson have stated that the basic principles of memory systems are to optimize the information retrieval to solve the current problems that memory systems encounter. Memory systems use their optimization algorithm to predict what kind of memory will be required to solve the current situation (Anderson and Milson 1989) and retrieve relevant and timely information to facilitate decision-making (Klein et al. 2002). This manageable number of previously stored information which people recall will be further utilized to predict what will happen in the future and frame the future behavior.

Predicting Events

Generally, the owner of memory systems is able to predict the event which will happen at a certain possibility based on the memory of a specific event or the summary knowledge which is abstracted from the repeated experience of similar episodes (Schank 1982). According to Schank (1982), this knowledge structure enables people to know what to expect and how to behave when facing an event of a similar situation. Researchers sometimes describe it as schema-driven memory (Graesser 2013) or script-based learning (Schank 1982). These predictions are not accurate all the time. They sometimes turn out to be wrong due to the complicated internal and external conditions. In these cases, people will remember these events with or without awareness in order to make a better prediction in the future (Klein et al. 2002).

Predicting Behaviors

Memory systems use the information required in the past to facilitate present and future behaviors

(Klein et al. 2002). With the experience, people can make an appropriate decision which people believe is the best solution to the current problems. The memory-based decision involves the retrieval of useful information which was stored in the past from memory and the construction of judgment based on this information. For example, the prediction of the forthcoming events plays an important role in how people behave now and next.

Memory produces transient or permanent long-term behavioral modifications by acquiring information about the past and current situation (Lorenzini et al. 1999). In some cases, these behavioral changes are performed without awareness. This kind of facilitation or change can contribute to habit learning, priming, or skill acquisition reliant on an unconscious recollection of prior learning episodes (Schacter et al. 1993).

Conclusion

Memory systems have undergone a long period of evolution to be capable to guide people behave appropriately in the present and future based on the information required in the past (Klein et al. 2002). However, little evidence has shown whether predicting events and behaviors are the designed function of memory systems or the functional product of evolved adaptations.

Cross-References

- [Forecasting](#)
- [Game Theory](#)
- [Judgment and Decision-Making](#)

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Predictors of Grandparental Investment

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Synonyms

[Grandparental care](#); [Grandparental involvement](#); [Grandparental solicitude](#)

Definition

Grandparental investment can be basically defined as any contribution directed toward grandchildren by grandparents. Grandparental investment can include emotional support, physical care, and financial aid, and may also be indirect (e.g., through supporting the grandchildren's parents). Typically, there are costs associated with grandparental investment (e.g., time or money), which are dependent on the nature of the investment. From an evolutionary perspective, grandparents are predicted to gain indirect fitness (i.e., ensuring the

proliferation of their genes) from grandparental investment, either through increasing the number of grandchildren by investing in their adult children to increase fertility or by increasing the well-being and survival of their grandchildren.

Introduction

Grandparental investment is determined by the length of time grandparents are simultaneously alive with their grandchildren, in the way that when shared lifetime between grandparents and grandchildren increases, so do the grandparents' possibilities to invest. During recent centuries, the shared lifetime between grandparents and grandchildren has increased substantially (Chapman et al. 2017), and in present-day societies, grandparents and grandchildren have more shared lifetime than ever before (Coall and Hertwig 2010).

Although the length of time grandparents and grandchildren share has increased, it does not alone drive the patterns of grandparental investment. Fertility and mortality declines mean that more grandparents are available to grandchildren, while there are fewer grandchildren to invest in, so there is less competition between siblings and cousins for grandparental investment. Grandparents today are also healthier and wealthier than before. Finally, technological advances and rapid long-distant travel mean that even distant grandparents can easily maintain contact with their grandchildren. Thus, grandparents today have great opportunities to invest time and other resources in their descendants.

Genetic Relatedness

Although grandparents are known to invest a large amount of time and resources in their grandchildren, all grandparents tend not to invest equally (Tanskanen and Danielsbacka 2018). The inclusive fitness theory (Hamilton 1964) predicts that biological grandparents should invest more in grandchildren compared to non-biological grandparents. The relatively scarce amount of studies

detecting differences between biological and non-biological grandparents has indicated that, in accordance with the theory, investments are more often made by biological than by non-biological grandparents. For instance, using data from 11 European countries, it was found that biological grandparents more likely provided childcare at least weekly to their grandchildren compared to non-biological grandparents (Coall et al. 2014). Moreover, two recent studies using data from the USA and Germany showed that biological grandparents invested more in grandchildren than step-grandparents (Gray and Brogdon 2017; Pashos et al. 2016). Finally, a US study detected the role of genetic relatedness in two-mother families and asked whether grandparents from the biological mothers' side invest more than grandparents from the non-biological mothers' side. More regular contact between children and grandparents from the biological mothers' side than from the non-biological mothers' side was detected (Patterson et al. 1998).

Sex and Lineage

In addition to genetic relatedness, grandparental investment in their grandchildren tends to vary by sex and lineage. One of the most common findings in grandparental investment studies conducted in contemporary Western societies is that maternal grandmothers invest the most, followed by maternal grandfathers, paternal grandmothers, and finally paternal grandfathers (Euler 2011). This biased grandparental investment pattern has been found in several societies and for many different grandparental investment variables, for instance, childcare, emotional support, and monetary transfers.

Perhaps the most important evolutionary theory explaining this biased investment pattern by grandparent types is based on paternity uncertainty (Daly and Perry 2017). Only maternal grandmothers can be 100% sure that they are related to their grandchildren, while maternal grandfathers (via themselves and their daughters) and paternal grandmothers (via their sons and sons' children) have one uncertain link of

paternity. Paternal grandfathers are in the most uncertain position and have two uncertain links of paternity (via themselves and their sons and via their sons and sons' children).

Nonetheless, the cultural context may remarkably shape the biased grandparental investment pattern. In patrilocal societies, where women become part of their husbands' family after marrying, it is observed that paternal grandparents invest more than maternal ones (Daly and Perry 2017; Pashos 2017). In patrilocal societies, grandchildren usually live nearer to the men's than the women's relatives, meaning that the grandchildren are likely to interact with their paternal grandparents constantly and may see their maternal grandparents only occasionally. This situation also means that paternal grandparents can become closer to the grandchildren than maternal grandparents. The opposite tends to be true in matrilineal societies, where children usually grow up with their maternal kin. It could also be argued that contemporary Western societies may provide a good base for the study of grandparental investment behavior because they lack clear patrilocal or matrilineal living arrangements (Tanskanen and Danielsbacka 2018). In these societies, individuals can commonly choose the relatives with whom they are willing to interact.

Sex of a Grandchild

During recent years, several evolutionary studies have asked, "Does the sex of grandchildren bias the investments by grandparents?" Genetic relatedness between biological grandparents and grandchildren is, on average, 25%. Because of the asymmetric inheritance of X and Y chromosome, the relatedness actually varies between 23% and 27% (Euler 2011). According to X chromosome relatedness, maternal grandmothers are 25% related to both grandsons and granddaughters, while paternal grandmothers are 0% related to grandsons and 50% related to granddaughters. Relative to Y chromosome relatedness, maternal grandfathers are 0% related to both granddaughters and grandsons, while paternal

grandfathers are 0% related to granddaughters and 100% related to grandsons.

According to the inclusive fitness theory (Hamilton 1964), increased genetic relatedness between kin is associated increased investment. According to this logic, there should be no differences based on the sex of grandchildren in the case of maternal grandparents. In contrast, it could be predicted that paternal grandmothers invest more in their granddaughters than grandsons, while paternal grandfathers invest more in their grandsons than granddaughters. A handful of studies have tested the X and Y chromosome relatedness predictions using data from contemporary societies (Chrastil et al. 2006; Tanskanen et al. 2011). These studies have not, however, found convincing support for the hypotheses. Thus, it could be that paternity uncertainty overrides any X or Y chromosome effect in present-day societies.

Outcomes of Grandparental Investment

Quantification of grandparental investment is not always easy, making it difficult to assess how the importance of grandparental investment has changed through time. In traditional and historical societies (i.e., natural fertility and mortality populations), the importance of grandparental investment in grandchildren is often harder to quantify than it is for contemporary societies. While current surveys can directly ask those giving and receiving care about the nature of investment, this is notably absent from historical records. In traditional and historical populations, the presence of older parents in the same household or in the same village as adult children has been used as a proxy for grandparental investment because when older parents live closer to their descendants, they also have a higher probability to invest (Sear and Coall 2011).

Existing research indicates that in traditional and historical populations, grandparental presence has often been associated with increased female fertility (Sear and Coall 2011). According to an extensive review, the presence of mothers was associated with increased female fertility in

7/12 studies, the presence of fathers in 5/8 studies, the presence of mothers-in-law in 4/6 studies, and the presence of fathers-in-law in 3/5 studies. Additionally, mother presence was associated with decreased female fertility in two studies. Overall, in nearly 90% of populations, the attendance of at least one parent or in-law was associated with fertility.

During recent years, an increasing number of studies have detected whether grandparental investment (e.g., childcare or emotional support grandparents provide to their adult children) is associated with parental fertility in contemporary Western societies. Although several studies have found that grandparental investment is associated with improved fertility, others have not detected such an association (Tanskanen and Danielsbacka 2018). These mixed results indicate that in contemporary affluent societies with public support to families, grandparental investment could not be as important for fertility compared to traditional and historical populations.

There is also evidence showing that, in traditional and historical populations, grandparental presence has been associated with improved child survival. Based on a review of the existing literature, maternal grandmother presence was associated with increased child survival in 9/13 studies, paternal grandmother presence in 9/17 studies, maternal grandfather presence in 2/12 studies, and paternal grandfather presence in 3/12 studies (Sear and Mace 2008). Furthermore, paternal grandfather presence was correlated with decreased child survival in 3/12 studies (Sear and Mace 2008).

In contemporary Western societies with low rates of childhood mortality, grandparents are not needed to keep their grandchildren alive compared to traditional and historical populations. However, it is argued that grandparents can still benefit their descendants when measured by “softer” outcomes, for instance, child development and psychological well-being (Sear and Coall 2011). Several studies have shown that grandparental investment is associated with increased grandchild well-being in particular, during family crises, such as parental divorce, severe illness, or even death, although it is unclear

whether grandparental investment causally improves child well-being in present-day societies (Tanskanen and Danielsbacka 2017). Hence, in traditional and historical populations, grandmaternal presence may have had a positive influence on child survival, while the presence of grandfathers may have no effect or may even have a negative effect.

Finally, it is assumed that the asymmetric inheritance of X chromosomes may bias the grandparental effect, meaning that granddaughters and grandsons survive differently with the presence of maternal and paternal grandmothers. According to a review of previous studies, in 7/7 studies, boys were found to survive more probably with maternal than paternal grandmothers, and in 6/7 studies, girls were detected to survive more likely than boys with paternal grandmothers (Fox et al. 2010). Nonetheless, in only 4/7 studies, girls were found to survive more probably with paternal grandmothers than maternal ones, which was in contrast with the theory (Fox et al. 2010). Additionally, a more recent study from historical Finland showed only limited support for the effect of X chromosome relatedness (Chapman et al. 2018). These findings indicate that an alternative explanation for the potential grandparental effect is needed.

Conclusion

Grandparental investment tends to vary according to genetic relatedness, sex, and lineage. Biological grandparents typically invest more than non-biological grandparents, and maternal grandmothers invest the most and paternal grandfathers the least. Studies concerning traditional and historical populations have used grandparental presence in the same household or village as a proxy for investment. Several studies have shown that in these populations, grandparental presence has been associated with both increased parental fertility and improved child survival. Studies from contemporary Western societies have shown that grandparental investment is often associated with child well-being, although it is unclear whether the association is causal. Studies detecting

associations between grandparental investment and parental fertility have provided mixed results. Although grandparents tend to be highly involved in their grandchildren's lives in different societies, the outcomes of grandparental investment may vary substantially.

Cross-References

- [Grandfather Investment Versus Grandmother Investment](#)
- [Grandparental Investment](#)
- [Grandparental Investment and Genetic Relatedness](#)
- [Grandparents and Grandchildren](#)
- [Importance of Grandparental Investment](#)
- [Level of Grandparental Investment](#)
- [Maternal Grandmother Invests Most](#)

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Predictors of Infanticide

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Synonyms

Filicide; Neonaticide; Progenicide

Definition

Infanticide is the intentional murder of a child under one year of age.

Introduction

One of the fundamental principles of evolution is that traits that enhance the survival and reproductive success of an individual are passed to offspring. Over time traits that have a selective advantage may become adaptations. These adaptations serve a special purpose and are designed to solve problems of survival and reproduction (Buss 2015). Infanticide is the intentional murder of a child under one year of age (Marks 2009). On the surface, murdering an infant seems like an evolutionary conundrum. That is, it seems to violate the idea that adaptations enhance reproductive success. The question becomes, can infanticide have an evolutionary function? Can it ever be beneficial to kill one's own child? This section will address predictors of infanticide and whether infanticide may be an adaptation.

Seminal research by Martin Daly and Margo Wilson (1980) addressed discriminative parental solicitude, the idea that parents vary in how much they invest in a particular child. There are circumstances in which parents benefit by investing heavily in offspring, but there are also circumstances in which parents do not benefit from heavy investment. The “payoffs” for investment vary for different individuals due to a number of factors, and investment can range from high levels to neglect, abuse, and sometimes murder (Daly and Wilson 1980). Evolutionary psychologists studying discriminative parental solicitude believe that low investment may be beneficial to some parents in terms of their overall survival and reproductive success, and it may even function as a form of intrasexual competition between women (Cousins and Porter 2017). As Martin Daly and Margo Wilson (1988) so elegantly put it, “Infanticide can be the desperate decision of a rational strategist allocating scarce resources” (p. 42).

Biological Parents vs. Stepparents

The first hours of a child's life are often the most precarious, partially because this is the most likely time when a child will be killed. In fact, research indicates that 45% of children that are murdered are less than 1 day old (d'Orban 1979). Historically this was also true. In Finland in the 1850s, 95% of infanticides involved children less than 24 h old (Koskivirta 2017). Canadian homicides records (1974–1983) indicate that younger children, especially those under 1 year of age, have a much higher risk of being killed by a biological parent. In comparison, when children are killed by individuals who are not related to them, the risk becomes higher as the child becomes older (Daly and Wilson 2008). From an evolutionary perspective, this makes sense. As parents invest more in a child, that child becomes more valuable to them. This occurs because the heavy investment in the child cannot be returned, so an evolutionary perspective predicts that parents should cease investment as soon as possible. During the first week of life, biological mothers are the most likely person to kill an infant (Marks 2009). Infanticide in this time period may be a function of the mother assessing whether she is capable of the high level of investment necessary to raise a child. Although fathers may invest heavily in children, their investment early on was less than women's due to women having to breast feed an infant (more on this later). Between 8 days old and 12 years old, biological mothers and fathers are equally likely to kill a child (Kunz and Bahr 1996).

Although biological parents are frequently the perpetrators of infanticide, stepparents are statistically even more likely to kill children. Compared to children living with two biological parents, children living with one biological and one non-biological parent – usually a stepparent – are up to 100 times more likely to be killed (Daly and Wilson 2008). The difference in rates of homicide between biological and non-biological parents makes sense in terms of evolution: biological parents reap much higher rewards for investment in children because those children share 50% of their genes. Stepparents, however, do not share any genes with their stepchildren, and therefore

the benefits for investing in them are lower. This is particularly true for the youngest children, who require much more care over a longer period of time. Research shows that the youngest children living with one non-biological parent face the highest risk of homicide, especially children under the age of two (Daly and Wilson 2008).

Discriminative Parental Solicitude, Life History, and Infanticide

For human females parenting is very costly in terms of time and resources needed to successfully raise a child. Due to internal fertilization and gestation, women can only produce one child every 9 months at a maximum. Figures from hunter gatherers show that fertility is surprisingly low despite not using contraceptives. Among the Hadza, the mean number of offspring is 6.1 (Blurton Jones 2016). The !Kung have even lower fertility with a mean of 4.7 offspring, while the Ache have slightly higher fertility at 8.0 offspring (as reported in Blurton Jones 2016). Although there is variability in these natural fertility populations, all these populations have very low numbers of children considering they do not use contraceptives. While a man's ability to produce offspring is only limited by the availability of fertile women willing to mate with him, menopause is a barrier to producing high numbers of offspring in women. By the time a woman reaches her mid-forties, her chance of conception is very low. Among the Hadza, the median age at last birth was 40 (Blurton Jones 2016). Prior to the modern invention of formula, women would have needed to breastfeed a baby for an extended period of time. Research shows that in traditional societies, women breastfed for just over 30 months on average (Kelly 1995). Based on this number, pregnancy and lactation may have required an additional 100,000 calories above what is normally necessary. Although some women may not choose to invest this heavily in each child, higher investment increased the odds that a child survived early childhood (Hrdy 1999). How much or little women breastfeed may be one indicator of the payoff for investment in offspring. For some women heavy investment in terms of maternal lactation and care had higher payoffs; other

women simply cannot afford the high price of this sort of investment (Hrdy 1999). There are a range of options these women may take. In some cases they kill their child, but sometimes they may simply wean their child early or neglect to care for their child. Discriminative parental solicitude predicts that parents do not always benefit to the same extent from investing in a particular child, and therefore both the quantity and quality of care will differ across predictable circumstances.

When biological parents kill their infants, a number of factors have been shown to reliably predict infanticide. The following sections explore the reasons biological parents sometimes kill their babies.

Low-Fitness Offspring

Across a wide range of cultures, one common reason for abuse and infanticide is a child that is born with an obvious problem (e.g., Lightcap et al. 1982). Twenty-one of 35 societies report infanticide or abandonment of deformed or sickly children (Daly and Wilson 2008). In Japan, disabled children are at higher risk of being killed by their parents (Taguchi 2007). While infanticide is the worst outcome for disabled and sick children, it is not the only potential hazard a child may face. For instance, disabled children are at higher risk for being abused (Hunter et al. 1978). In Brazil, impoverished mothers experience high infant mortality rates, which are partly due to these mothers neglecting infants who are in poor health (Scheper-Hughes 1984). Mothers with few resources may conclude that neglect or infanticide is the only option to save resources for other offspring or to wait and invest in a child born during better circumstances. In fact, across cultures, people often conclude that investing in sick or disabled children will be a hindrance to the parents (Scheper-Hughes 1984).

Mothers' Age

The age of the mother is an important factor in infanticide, with young mothers being the most likely to kill a child (Daly and Wilson 2008; Overpeck et al. 1998). Young motherhood was linked to the greatest risk of intentional fatal injury

in a large study of children in California (Putnam-Hornstein 2011). Research shows that the youngest mothers, those under age 15, had a rate of infanticide seven times higher than for mothers over the age of 25 (Overpeck et al. 1998). Other research shows that mothers under the age of 20 are more likely to kill their prematurely born infant compared to mothers older than 20 (Luke and Brown 2007) and that the median age of infanticidal mothers was 19 (Herman-Giddens et al. 2003).

Why does age of the mother matter? There are probably several reasons for this, including poverty and lack of paternal support, which are discussed further below. Another reason young mothers are particularly likely to kill their infants may have to do with differences in the costs and rewards of investment in children across a woman's lifespan. One such trade-off women face is between current and future reproduction. This is because energy is finite. Resources spent on reproduction cannot be used for maintenance, such as growth or staying healthy. This is called an opportunity cost (Kaplan and Gangestad 2005). What this means is that reproducing now may bring a cost to future reproduction. Reproducing during the teenage years may have extra costs if the woman is not yet fully matured. For example, a teenage girl may not be fully grown when she becomes pregnant. The pregnancy will hinder her growth, and she will never reach her full height. Young mothers have many more years to reproduce, so delaying reproduction may reap higher rewards compared to reproducing before full maturity. By delaying motherhood to a later time, women do not need to confront the competing demands of pregnancy and growth (Kramer and Greaves 2010). In assessing the Pumé, a South American hunter-gatherer group, researchers found that young women have a very early first reproduction (*Age* = 15.5), but Pumé women put more energy into early skeletal growth and reach full maturity earlier than women in some other hunter-gatherer groups. Therefore, Pumé women do not face trade-offs between growth and investment in pregnancy (Kramer and Greaves 2010). However, in most circumstances, teenage mothers are not fully physically

mature, and investing in a child therefore has a higher cost.

Older women have fewer years of future reproduction, so evolutionary psychology predicts that these women will be more apt to invest in children even when the circumstances are not optimal. This is expected to be especially true if they have no other children because women with other children should put more effort into existing children if circumstances limit a woman's ability to invest in a newborn. This is because older children have already received so much investment that a woman should prefer to invest in an older child, all other things being equal. In addition, older children have passed the very risky infancy, a time when, historically, many children succumbed to disease. Research supports the idea that older mothers should invest more in infants than younger mothers. Older mothers invest more in premature infants than younger mothers, especially when they have no other children (Beaulieu and Bugental 2008). When young women do become pregnant, infanticide may be the only mechanism left for them to limit investment in a child where the costs associated with investing in the infant may impede future reproduction. As stated earlier, infanticide is an action women take when they are in a dire situation and may find themselves in better circumstances in the future.

Paternal Support

Since human infants require so much investment by both parents, some evolutionary psychologists believe that marriage systems may have developed as ways to increase survival of children. It follows that a lack of paternal support decreases offspring survival and may favor lower investment and potentially infanticide, by mothers when they lack adequate help to raise a child alone. This may be particularly true when women are also facing resource scarcity, including living in poverty. Among premature infants, parental separation or other marital problems predicted abuse and neglect (Hunter et al. 1978). Marital problems or unhappiness may be linked with male desertion and therefore may be associated with infanticide. Unpartnered mothers seem

to be especially prone to infanticide. In the early 1800s in Finland, court records show that about a third of all filicides were perpetrated by single mothers, at least in part because of the dire economic circumstances in which these women lived (Koskivirta 2017). In nineteenth-century England, infanticide was particularly prevalent among unmarried women who wanted to maintain high social status; women from lower social groups did not have any social standing to begin with and were reportedly less ashamed by an illegitimate child (Sauer 1978). In Tibet, children often die after parental divorce or when the marriage is unstable. It is difficult to determine if infanticide occurred, but it is likely that even if the mother does not kill her child, her neglect essentially ensures the death of the infant, and this may ultimately increase her fitness by making her more able to marry again because Tibetan women with children from a previous union are not preferred as mates (Levine 1987). In all these cases, young and unpartnered women faced higher costs to raising a child, and therefore infanticide may have been beneficial for these women over a lifetime in terms of her fitness.

Resource Scarcity

Throughout human evolutionary history, resource scarcity was common and meant that women did not always find themselves in circumstances that permitted heavy investment in a child (Daly and Wilson 2008). Humans seem to have a built-in preparation for resource scarcity in the form of anovulation. Very lean women may not ovulate, and there is evidence that female athletes with low levels of fat, such as long-distance runners, are frequently anovulatory (Lunn 1985). Additionally, when women lose weight, they often do not ovulate for a time. Weight loss would have been a good marker of resource scarcity for our ancestors; not ovulating was the best way to prevent a pregnancy from occurring when the ability to invest heavily in a child would be too burdensome. In Nepal, women often lose weight during the monsoon season. Not surprisingly, women are much less likely to ovulate during the monsoon season (38% ovulate) than during the non-monsoon season (71% ovulate; Panter-Brick

et al. 1993). Anovulation is not the only effect of poor circumstances. Live births are also affected by poor environmental conditions. Among the Hadza, during years with extreme weather conditions (e.g., drought), there were significantly fewer live births (Blurton Jones 2016). Lactation has ovulatory suppressing effects even among Western women, and these effects are stronger among lean women and those that breastfeed at night, as is common in traditional societies (Lunn 1985). But what happens when a woman becomes pregnant despite poor conditions?

Resource scarcity is linked with child abuse and infanticide. Babies born prematurely were more likely to be abused if their parents were poor (Hunter et al. 1978). Poor Italian women are more likely to kill their children. Among these women, babies under 24 h old were at much higher risk than older infants and children (Ciani and Fontanesi 2012). To cease investment only for the youngest infants when conditions are not good makes sense because any investment by these women would be a waste of precious resources. In the United States, in those states that have more maternal poverty and lower per capita incomes, there are higher rates of infanticide (Gauthier et al. 2003). In the early 1800s in Finland, poverty was a leading reason for both infanticide and filicide, killing older children. In a study of court cases involving filicide, more than half of cases involved the most desperate parents with the lowest socioeconomic status, and rates of filicide were higher in years when crops failed and after war when there was little to eat (Koskivirta 2017). Poverty was a leading cause of infanticide in England from the sixteenth to nineteenth centuries, too. Not surprisingly, baptismal records indicate that fewer children were baptized when the economy was poor. This was probably due to several related factors: parents may have tried harder to prevent pregnancy, aborted pregnancies were higher, and children born during financial crises were more likely to be killed (Sauer 1978). In terms of fitness benefits to parents, those who ceased investment in children, especially infants, when resources were scarce and surviving childhood was unlikely, would have out-reproduced parents

who invested heavily in children even under poor circumstances.

Birth Spacing

Reliable contraception is a modern invention, although primitive condoms and other devices have been used for hundreds of years (Levay et al. 2015). The need for heavy investment in offspring should have necessitated adaptations that increased interbirth intervals without contraception. As discussed earlier, lactation can increase interbirth intervals by interfering with ovulation, but this is not a fail-safe method, and anovulation is more likely for women who are lean and breastfeed at night (Lunn 1985). Women who have births spaced too closely together may not have adequate resources for two young children. In some cases, it appears that insufficient birth spacing increases abuse and neglect of premature infants (Hunter et al. 1978). Mothers who had at least four other children were more likely to have an infant die, although this study did not show whether the death was due to infanticide (Puffer and Serrano 1973). As stated earlier, neglect is on the spectrum of parental investment and may be a way to divert resources from a child likely to die toward older children for whom the parents have already invested a great deal. There is evidence that among young mothers under age 20, infanticide was more likely if the mother had two children (Overpeck et al. 1998). At such a young age, birth spacing would be an important determinant of infanticide.

Can We Reduce Infanticide?

Although evolutionary theory predicts that a specific set of circumstances is associated with infanticide, can evolutionary psychology be used to reduce infanticide? I believe the answer is yes. Young mothers are more likely to kill their infants, especially when they are poor. Therefore, one suggestion would be to make reliable contraception readily available to these young women at no cost. Research supports that teen pregnancy rates are reduced when contraception is free and comprehensive sex education occurs. For instance, in a prospective cohort study of women who were at

high risk for repeated abortions, women were offered contraception (especially long-acting forms of contraception like implants and IUDs) free of charge. Women who entered this program were less likely to become pregnant as teens and were also half as likely to seek abortions compared to women regionally and nationally (Peipert et al. 2012). Reliable, free contraceptives may also reduce infanticide that is due to short interbirth intervals. Family planning is important in helping women improve the timing of births and access to contraception, especially forms that are long acting and reversible are an important part of making sure that women have children when they feel capable of successfully rearing those children.

Relatedly, comprehensive sex education should be taught in schools. Women need to be empowered to understand both how to use contraceptives and how to speak to partners about using contraception. Research comparing teen pregnancy rates between those who receive comprehensive sex education compared to those who receive abstinence-only education show that there is a reduction in teen pregnancy rates for those who receive comprehensive sex education, but the same is not true for those who participate in abstinence only programs (Kohler et al. 2008).

Resource scarcity is another predictor of infanticide. In industrialized countries resource scarcity is simply another word for poverty. One obvious way to reduce infanticide is to lift people out of poverty.

Finally, living with both a biological and non-biological parent increases infanticide over living with two biological parents. Does that mean a parent should not be allowed to live with someone not related to their child? I do not believe this automatically follows. Historical research assessing two regions during the seventeenth and eighteenth centuries show that after the death of a biological parent, having a stepparent did not necessarily increase child mortality; the environmental circumstances in the region mattered a great deal in determining whether having a stepparent was detrimental for a child after the death of a biological parent. In Québec where resources were plentiful and large families were better able to compete, having a stepfather was better than

having a widowed mother who did not remarry because a widowed mother would not have been able to adequately support a family in that region. Stepmothers had no effect on survival of children in Québec. However, this was not true when competition for resources was high. In the Krummhörn, where competition was high during this time period, having a stepmother increased child mortality. Stepmothers probably favored their own biological children at the expense of stepchildren living in the household and because resources were scarce, and competition was high, this meant that stepchildren were more likely to die. Overall stepfathers in the Krummhörn had no effect on child mortality (Willführ and Gagnon 2013). What this research shows is that investment in stepchildren is altered depending on environmental circumstances. Sometimes it is beneficial to have a stepparent, at least compared to having only one parent that has been widowed.

Conclusion

It is clear from cross-cultural, historical, and modern research that infanticide has been relatively common. Predictors of infanticide are young motherhood, lack of paternal support, resource scarcity, close birth spacing, and offspring that are sickly or have a clear physical problem. In addition, children living with non-biological parents are statistically more likely to be killed than those living with two biological parents. All these predictors of infanticide make evolutionary sense, and it appears that infanticide is an extreme solution for people facing poor outcomes; it may be an adaptation. However, evolutionary psychology may also be used to mold policies that, in particular, improve family planning and therefore could result in a reduction in infanticide.

Cross-References

- Discriminative Parental Solicitude
- Martin Daly and Margo Wilson (Founders of Evolutionary Psychology)
- Life History Theory

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Predictors of Sexual Debut

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Synonyms

First intercourse; Sexual initiation; Sexual onset

Definition

The age at which an individual initiates vaginal sexual intercourse.

Introduction

Human behaviors are regarded as either adaptive or maladaptive depending on the degree to which they promote or undermine health. Early sexual debut, typically defined as the initiation of vaginal intercourse before the age of 14, is associated with increased likelihood of multiple and risky sexual partners, as well as long-term negative health consequences like unintended pregnancies and sexually transmitted infections (Sandfort et al. 2008). Given the costs associated with these outcomes, most research has viewed early sexual debut as a problem behavior that should be prevented. This view, however, fails to account for evolutionary drives, such as reproductive success, that may be especially useful in understanding predictors of sexual debut in adolescents. Adolescent behaviors that are viewed as “risky” from a developmental psychopathology lens (Cicchetti 1989) can be adaptive for the individual if the anticipated benefits outweigh expected costs in relation to genetic fitness (i.e., reproductive success). Recognizing the adaptive functions of sexual behaviors across social contexts is crucial to understanding variations in sexual debut (i.e., early vs. late) and developing interventions that do not contradict individual’s goals and motivations for sexual activity (Ellis et al. 2012).

Theoretical Perspectives

Life History Theory (Roff 1992; Stearns 1992) posits that natural selection has favored biological mechanisms that allocate energy and resources to maximize potential benefits in relation to costs in differing ecological conditions. Thus, when individuals make decisions based on attaining a greater reward in one domain, it comes at the expense of missing out in another domain. For example, biological resources expended on growth and development cannot be invested on reproduction and child rearing. In the case of timing of sexual debut, individuals, given their ecological context, choose between a longer childhood and its associated costs and benefits versus early child rearing and its costs and benefits. These life decisions over time accumulate into differing trajectories, termed as life history strategies.

Building on the Life History Theory, the Psychosocial Acceleration Theory (Belsky et al. 1991) suggests that familial and ecological stressors (e.g., poverty, harsh parenting) can lead to an accelerated developmental trajectory in children, including a fast, quantity-oriented reproductive strategy with accelerated pubertal maturation, earlier sexual debut, and a tendency to form short-term, unstable social bonds. In contrast, children exposed to stable and supportive familial and ecological conditions develop quality-oriented reproductive strategies. Delayed pubertal and sexual onset, and eventually, formation of stable pair bonds, and increased parental investment (i.e., fewer offspring and more resources expended on children; Belsky 2012) are adaptive goals for children growing up in resourceful stable environments. In both cases, the development is adaptively adjusted based on local conditions.

Sex Differences

According to the Sexual Selection Theory (Trivers 1972), males and females need to solve different adaptive problems during development and therefore, are expected to have varying predictors of sexual debut leading to different adaptive reproductive strategies. For example,

earlier pubertal timing is a strong predictor of earlier reproductive strategies for females, whereas, peer status and intrasexual competition (e.g., possessing characteristics that make them attractive to mates and successful in same-sex competition) are more predictive of sexual debut for males. Sex differences in the role of perceived mate value was highlighted in a recent longitudinal study of 12–18 year olds which found that higher perceived mate value partially mediated the effect of early pubertal maturation on sexual debut, but only in case of males (James et al. 2012).

In case of females, fathers can play a unique role in predicting sexual debut that is separate from the effects of mothers or other environmental stressors. The quality of paternal investment in child rearing has varied across evolutionary history, and this variation has repeatedly influenced survival and reproductive success (Draper and Harpending 1982; Ellis 2004). A number of studies have found that females whose biological father was absent from the home during childhood tended to have earlier pubertal timing (Alvergne et al. 2008; Webster et al. 2014), and earlier sexual debut (Ellis et al. 2003; James et al. 2012), as compared to their female counterparts who grew up with their biological father present.

Family stressors also tend to have a larger effect on pubertal development and sexual debut in the case of females. In a prospective study of 120 children followed from infancy (12 months) to 5th grade (age 11), Ellis and Essex (2007) reported that for females, nonsupportiveness in the family during preschool was associated with earlier pubertal status at the age of seven, and subsequent earlier maturation of secondary sex characteristics in the fifth grade. Family stressors did not impact pubertal or sexual maturation in males. Others have found similar results with female adolescents (ages 9–16) with histories of maltreatment, who achieved pubertal maturation 8 months earlier than nonmaltreated females (Costello et al. 2007). Additionally, Belsky and The NICHD Early Child Care Research Network (2010) found that greater maternal harshness as early as 5 years of age predicted sexual risk-taking (i.e., frequency of oral and vaginal sex, sexually

transmitted infections, and pregnancies) at age 15 in females, and this effect was fully mediated through earlier pubertal timing. Relatedly, other longitudinal studies have found that the effect of childhood stress (i.e., parental absence, parental depression, low socioeconomic status) on sexual debut is partially mediated by pubertal timing for females, but not for males (James et al. 2012). These observed sex differences suggest that males and females may have differing evolutionary motivations and mechanisms for engaging in earlier or later sexual debut.

Environmental Predictors

Unpredictable and harsh environmental conditions have consistently been linked to faster life history strategies (Belsky 2012; Brumbach et al. 2009; Ellis and Bjorklund 2012). In harsh environments (e.g., heightened risk of dying), internal mechanisms have evolved to accelerate development in order to increase the chance of reproducing before death. Similar processes are at work in unpredictable environments. If an individual is unable to predict their future or foresees a bleak future, then having a slower, quality-focused reproductive trajectory may not pay off in the long run. Thus, exposure to harsh and unpredictable environments lead individuals to develop a “I need now – I can’t wait” attitude, and thus, increasing their likelihood of earlier sexual debut (Belsky 2012). Specifically, in terms of sexual initiation, some longitudinal studies have found that children who experience more harsh and unpredictable environments in early childhood (between ages 0–5) have an increased tendency for earlier sexual debut, for both males and females (Belsky et al. 2010; Ellis et al. 2012; Simpson et al. 2012).

Exposure to early stress is one mechanism by which early rearing environments can influence pubertal maturation and sexual debut. Developmental systems have evolved in order to adapt to the level of stress in the environment. Stressful environments do not necessarily interrupt development, but regulate it towards adaptive behavioral and functional processes that have been

successful in stressful conditions throughout evolutionary history (Ellis et al. 2012). Although these strategies may be evolutionarily adaptive in the moment, they can nonetheless be harmful to the individual in long run or damaging to the society (Ellis and Bjorklund 2012).

The effect of both supportive and stressful environments on life history strategies has been shown to be mediated by attachment security (Belsky 2012). Development of secure attachments during childhood has been linked to slower reproductive strategies (i.e., delayed sexual debut) (Miller and Fishkin 1997). According to Psychosocial Acceleration Theory, the main evolutionary function of the first 5–7 years of life is to instill a sense of understanding about the availability of resources, the trustworthiness of others, and the stability of close relationships – all of which affect an individual’s reproductive development and strategies. Attachment security plays a key role in the development of a child’s sense of trustworthiness and orientation towards others (i.e., manipulative vs. altruistic). The theory posits that exposure to adverse rearing environments (e.g., lack of resources, negative parenting styles) leads to the development of insecure attachments and mistrust in relationships, which accelerate pubertal development and results in earlier sexual debut (Belsky et al. 1991). Insecure infant attachment as early as 15 months of age has been associated with earlier pubertal timing (Belsky et al. 2010). Thus, attachment insecurity can influence early sexual debut both by impacting biological processes like pubertal timing but also by making it more challenging for individuals to develop and sustain long-term relationships that increase reproductive success.

Reproductive strategies (i.e., early vs. late sexual debut) are also differentially affected by the environmental contexts. Biological processes (e.g., genetics, physiological reactivity) function as susceptibility mechanisms that can moderate the effect of environmental influences on reproductive strategies (Ellis and Bjorklund 2012). Biologically susceptible individuals are more likely to experience lasting developmental changes resulting from positive (e.g., abundant resources and support) and negative environmental experiences (e.g., heightened stress and

adversity) as compared to less susceptible individuals (Belsky 1997). In an empirical test of this hypothesis, Ellis and colleagues found that in a sample of 120 children who were followed from preschool (ages 3–5) through grades 3–9 (ages 9–17), lower-quality parent-child relationships during the preschool years predicted earlier pubertal timing and quicker sexual maturation. However, these effects were only significant for children with heightened biological sensitivity to environmental contexts, as assessed through the child's physiological reactivity to standardized stressors (i.e., parasympathetic and sympathetic activation, and cortisol levels) (Ellis et al. 2011).

Conclusion

Human developmental processes are evolutionarily designed so that biological mechanisms are differentially expressed in response to environmental contexts. Female reproductive strategies seem to be more sensitive to familial and ecological factors, whereas male reproductive strategies tend to be more sensitive to peer influences (Belsky 2012). In both cases, environmental factors (e.g., stress, unpredictable and harsh conditions, and social status) adaptively calibrate biological mechanisms (e.g., pubertal timing), which subsequently leads to variation in sexual debut. Understanding the evolutionary function of sexual behavior is necessary to inform interventions that do not contradict individual's goals and motivations for sexual activity (Ellis et al. 2012).

Cross-References

- [Bruce J. Ellis](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
- [Fast Versus Slow Strategies](#)
- [Jay Belsky](#)
- [Life History Strategies](#)
- [Reproductive Strategies](#)
- [Reproductive Timing](#)
- [Sexual Debut](#)

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Predictors of Violent Intergroup Conflict

- [Evolved Psychology of Warfare](#)

Predisposing Factors

- [Risk Factors](#)

Predisposition

- [Genetic Predispositions](#)

Preference

- [Prejudice](#)

Preference by Mating Context

- [Preferences in Long- Versus Short-Term Mating](#)

Preference for Solitude

- [Social Withdrawal in Childhood](#)

Preferences in Long- Versus Short-Term Mating

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Synonyms

[Preference by mating context](#); [Short and long term preferences](#)

Definition

The physical and psychological traits that men prefer in their romantic partners and how these preferences differ between short-term romantic relationships and long-term romantic relationships.

Introduction

From an evolutionary perspective, men are expected to possess a set of mate preferences

that are adaptively adjusted and calibrated based on whether they are pursuing short-term or long-term mating. Evidence reveals that men's preferences do change in predictable directions based on their operative mating strategy: Preferences for cues of fertility and sexual accessibility take priority in short-term mating, whereas preferences for cues of reproductive value, health, and pleasant personality traits take priority in long-term mating. It is important to note that natural selection shapes motivational systems. Given that many of these motivational systems operate below conscious awareness, men may not be cognizant of their mate preferences nor their effects on men's fitness.

Men's Preference by Mating Context

Sexual Strategies Theory (SST) is the overarching theory that explains the adaptive significance of mating strategies in humans (Buss and Schmitt 1993). According to SST, a fundamental asymmetry in obligatory investment in reproduction (i.e., gestation) led men and women to evolve somewhat different mating psychologies: men are more interested than women in short-term mating, and women are more interested than men in long-term mating, on average. That said, most men and women pursue a range of mating strategies at some point in their lives. For example, many individuals might engage in short-term mating earlier in life, then transition to long-term mating later in life. The most common way to assess an individual's current mating strategy is to administer the revised sociosexual orientation inventory (SOI-R; Penke and Asendorpf 2008). Higher scores on the SOI-R indicate a stronger orientation toward short-term mating, and consistent with SST, men score significantly higher than women on this scale.

Short-term mating. Men who pursue short-term mating strategies increase their reproductive success by maximizing the number of fertile women to whom they gain sexual access. Men possess a number of psychological adaptations that facilitate this strategy, such as a desire for a variety of sexual partners, requiring less intimacy

before engaging in sexual contact, and erring on the side of false alarms rather than misses with regard to sexual approach behavior. In addition, men's mate preferences generally become relaxed in short-term mating to facilitate the accrual of additional mates; however, men increase their preferences for cues of sexual accessibility and fertility, traits that increase men's likelihood of reaping the reproductive benefits of short-term mating.

There are many factors that influence how selective a man will be in his mate choice (e.g., his mate-value, the local sex ratio), but pursuit of a short-term mating strategy is arguably one of the biggest influences. A successful short-term mating strategy rests on enlarging one's pool of potential mates, as each additional mate has the potential to increase a man's reproductive success. Less selective men, quite simply, have more options than choosy men. In many categories of mate preferences, such as intelligence and kindness, men show decreased selectivity specifically for sex partners but not for long-term mates (Kenrick et al. 1990).

As men pursuing short-term mating opportunities become less selective for many traits, they become more selective for certain traits that predict a woman's ability to increase their reproductive success. One such example is men's greater desire for sexual accessibility. Men pursuing short-term mating are more likely to find targets who display cues of easy sexual access to be desirable (Schmitt et al. 2001). Even if a woman does not show cues of overt accessibility, men might also look for signs that the woman is exploitable via persuasion or other means. Men do in fact find cues that a woman is exploitable to be sexually attractive, specifically as a short-term mate (Goetz et al. 2012).

Another set of traits that are particularly important for short-term oriented men are those predictive of a woman's underlying fertility. Because fertility is not directly observable, men rely on certain cues that have been recurrently correlated with women's fertility over evolutionary history. One of the clearest cues of fertility is a woman's waist-hip ratio (WHR; ► [Waist-to-Hip Ratio](#)) in that it tracks underlying estrogen levels and is

associated with ease of becoming pregnant, as well as a host of other positive health outcomes. The estrogen-dependent nature of WHR makes it a reliable indicator of whether a woman has reached sexual maturity (i.e., postpubescence) and is premenopausal. WHR also provides cues to whether a woman is pregnant – a condition of temporary infertility – as her WHR steadily increases as her pregnancy progresses. Finally, there is evidence that WHRs might slightly decrease at ovulation, the point in a woman's menstrual cycle at which she can become pregnant. Ovulating women are particularly attractive to short-term mating men for this reason (Men's Preference for Ovulation), whereas men pursuing long-term mating need not capitalize on a single ovulation given that they are likely to be with their partner for many future ovulations. Consistent with this body of research, studies show that women with relatively low WHRs (i.e., curvier women) are viewed as more attractive than their high WHR counterparts.

Given WHR's influential role in assessing fertility, it is perhaps unsurprising that men who are oriented more toward short-term mating tend to express greater interest in viewing a woman's body than her face. Several studies have now shown that men oriented toward short-term mating, and men experimentally assigned to consider a female target as a short-term mate, tend to pay more attention to a woman's body and spend more "mate dollars" improving a woman's bodily attractiveness than long-term mating men (for a review, see Cloud and Perilloux 2014).

Long-term mating. Men who pursue long-term mating strategies increase their reproductive success by committing themselves to (usually) one woman at a time and heavily investing in any resulting children. Research shows that in the pursuit of a long-term mate, men are just as selective as women (Kenrick et al. 1990). This follows from SST: In long-term mating, each partner's reproductive success is dependent upon the cooperation of another individual (e.g., providing reliable childcare, protection, and resources). Thus, poor mate choice in a long-term relationship can be extremely detrimental for both men and women. Consistent with this logic, cross-cultural

studies show that men (and women) prioritize traits such as kindness, intelligence, and an exciting personality in their long-term mates, probably because these characteristics help maximize compatibility and thus continued reproductive success with a single partner (Buss 1989). A related trait that becomes especially important for men in long-term relationships is a partner's faithfulness (Buss and Schmitt 1993).

One of the key adaptive problems faced by long-term mating men is to avoid accidentally investing in offspring that are not genetically related (i.e., cuckoldry). One solution to this adaptive problem appears to be the emotion of sexual jealousy (Buss 2000), but another solution is a preference for mates who are unlikely to engage in infidelity. This is clearly a probabilistic judgment, but one of the best predictors of extra-marital sexual permissiveness is premarital sexual permissiveness (Thompson 1983). Preferences for complete chastity before marriage, however, are highly variable across cultures (Buss 1989); therefore, men might rely more on cues to future faithfulness (e.g., ignoring advances from rival men, general sexual permissiveness) rather than chastity per se, when evaluating long-term mates.

Assuming fidelity on the part of his mate, one potential benefit for a man in a long-term relationship is continued sexual access. But this benefit only increases his reproductive success if his mate is capable of bearing children – ideally, for years to come. Thus, men in long-term relationships seek mates who have high reproductive value (i.e., those far from the end of their reproductive lifespan). Indeed, research shows that as men age, they prefer mates who are increasingly younger than they are (Kenrick and Keefe 1992), and the age gap tends to increase with each subsequent marriage (Low 1991). Men are also attracted to certain traits associated with youthfulness, such as a high energy level and a lively gait (for a review, see Sugiyama 2005).

Research on the relative importance of a potential mate's facial and bodily attractiveness reveals an interest in viewing a woman's face among men dispositionally orientated toward long-term mating and those experimentally assigned to consider

a female target as a long-term mate. This pattern of results is consistent with the premise that cues of youth – and hence, reproductive value – are more densely concentrated in a woman’s face (e.g., absence of wrinkles) than in her body.

Future directions. Even though much is known about how men’s mate preferences differ across mating strategies, less is known about the transitions many men make from a short-term mating strategy to a long-term mating strategy, or the reverse, over the lifespan. Relatedly, most researchers have focused on short-term and long-term mating as separable strategies, when in reality short-term and long-term mating motivations, if not behaviors, might exist on a continuum with some men pursuing both mating strategies simultaneously (e.g., having a short-term sexual encounter while married or searching for a life partner while having sex with many women along the way). Research designed to address these issues should provide evolutionarily minded scholars with a more nuanced understanding of men’s mating strategies.

Conclusion

Men’s mate preferences adaptively calibrate to short-term and long-term mating strategies. These changes reflect the output of evolved psychological mechanisms that adaptively motivated behavior, conditional on mating strategy, in ways that tended to increase men’s reproductive success over human evolutionary history. Men tend to possess high standards for long-term mates, revolving around personality, compatibility, and reproductive value, whereas men tend to lower their standards for short-term mates, with specific exceptions for traits indicative of sexual accessibility and fertility.

Cross-References

- [Evolutionary Standards of Female Attractiveness](#)
- [Mate Preferences](#)
- [Men’s Mate Preferences](#)
- [Waist-to-Hip Ratio](#)

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Preferential Investment Hypothesis

- [Grandparenting](#)

Preferential Investment in More Certain Kin

► Level of Grandparental Investment

Pre-frontal Cortex

► Frontal Cortex

Pregnancy

► Adaptation for Single Births

Pregnancy Brain

► Mother's Brain Size Decrease During Pregnancy

Pregnancy Complications

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Definition

According to CDC, the complications of Pregnancy are disorders and issues that impact the pregnancy in an adverse manner, leading to adverse outcomes of pregnancy for the mother and the fetus. These include, presence of anemia, previous C-section delivery, Cephalo-pelvic disproportion, advanced age, elderly or young primigravida, Rh-negativity, grand multi parity and other, hormonal disorders etc.

Introduction

Pregnancy is a life-changing experience. It is also considered as a very enthralling experience of women's life. Pregnancy brings about a lot of changes in physiology and psychology of the women. Usually pregnancies are predictable and progress according to a set pattern through the trimesters, but almost up to 15% of all pregnancies go through some or the other complications (WHO et al. 2017). This entry will briefly discuss the various complications that may arise and their management.

Objectives of the Chapter

pregnancy can be complicated in many cases and due to presence of various risk factors. There are various conditions which can predispose the women for those complications. The common complications of pregnancy with their management strategies are documented as follows.

Pregnancy with Previous Caesarean Section

Definition

Caesarean section is a common practice in modern obstetrics, as it is used in many deliveries for non-recurrent indications and often as a lifesaving procedure for both mother and child. A pregnancy after delivering by caesarean section is called post-caesarean pregnancy (Dutta 2004).

Impact of Complications on the Outcome

Usually a previous C-section (caesarean section) does not essentially change the course of pregnancy but heightens the risk of the developing some complications (O'Neill et al. 2014).

Complications During Pregnancy and Postpartum

The most common complications associated with previous C-sections include:

Preterm labor (delivery before the term, i.e., 37 weeks of gestation)

Abortion

Placental abnormal position and nature (*placenta previa* and *placenta accreta*) (*placenta previa*: attachment of the placenta in the lower uterine segment rather than the upper body of the uterus) (*placenta accreta*: infiltration of the chorionic villi deeper through the myometrium into serous and neighboring structures)

Increased operational interference and incidental morbidity

Postpartum hemorrhage (excessive bleeding after the birth of the baby more than 1500 ml)

Peripartum hysterectomy (removal of the uterus after the childbirth and related causes)

Effects on the Scar

The previous scarring of the uterus may impact the pregnancy in a unpredictable way. The risk or rupture of scar as there is about 0.2–0.5% chance for rupture of scar in the lower segment and usually may happen during labor, that can lead to life-threatening complications. In case of a classical hysterotomy, scar has a 4–9% chance for rupture in the late pregnancy and during Labour (Jacob 2012:68; Dutta 2004).

Effects on the Healing Wound

The previous caesarean section brings about the chances of difficulty in the wound healing as there may be chances of infection, excessive stretching of the lower uterine segment. The healing happens best when the tissues are apposed in the correct manner. Poor general health may lead to poor wound healing, leading to a weak scar (O'Neill et al. 2014).

Diagnosis

The risk for scar dehiscence can be determined by the following factors:

1. Type of scar: usually a lower segment scar is able to withstand better compared to the classical C-section scar. Due to factors such as angular pull during the growth of the uterus and during contractions of labor. In the

classical C-section, there are increased chances of trophoblastic infiltration (placental tissue) near the scar making it weaker.

Management

Elective C-Section

Previous C-section pregnancy complications can often be managed by delivering the baby by elective C-section in the following pregnancy. Pregnant woman should be admitted in the hospital in the 38th week and plan for surgery. Patient should not wait till the labor pains start.

Emergency C-Section

Whenever there is labor and risk for scar dehiscence, patient should be immediately prepared for OT, and emergency C-section should be done to prevent complications in the mother and the child.

Vaginal Birth After Caesarean Section

In about 70% cases, vaginal birth is successful after a previous C-section delivery (Dutta 2004), but in case of suspected maturity, a C-section delivery is advisable. There are a few benefits of having a vaginal birth after caesarean section. If done under supervision of a team of doctors and skilled professionals, one has lesser maternal mortality, lesser need for a blood transfusion, and better recovery time for mother and adequate care of newborn. There are also risks associated with this; they are risk for scar dehiscence and risk for fetal distress, postpartum hemorrhage, loss of baby, and maternal mortality (Dutta 2004).

Vaginal birth after caesarean section trial of labor (VBAC-TOL) should only be done if the pregnancy was uneventful, and onset of labor was spontaneous with good effacement and dilatation of the cervix, along with constant fetal monitoring. The hysterotomy scar dehiscence (breakage) has about 0.2-0.5% chance and the risk is greater in case of the scarring at the lower uterine segment. this may happen during precipitated labour (Dutta 2004; Myles et al. 1993; WHO et al. 2017).

Pregnancy in RH-Negative Women

Rh factor is an antigen found the RBC of humans and some other primates. This antigen determines the reaction of the blood to negative antibodies and can lead to a hemolytic reaction.

Incidence: Rh-negative people in Europe consist of 15–17%, and there is very less incidence of about 1% in China and almost nil in Japan. Among the Rh-positive, there are almost 40% homozygous and 60% heterozygous in the D locus. Overall chance for a Rh-negative mother to have a Rh-positive fetus is about 60% irrespective of partner's Rh type. The Indian incidence rate is 10% in northern India and 5% in the southern India.

Impact of RH Alloimmunization

The risk for women having pregnancies with Rh-positive partners can lead to the risk for fetal

Rh alloimmunization leading to fetal loss and death. The antibodies (anti-fetal antibodies) can remain in the mother's blood and can create complications for further pregnancies leading to spontaneous miscarriages and abortions (DONOHUE and WAKE 1964) (Fig. 1).

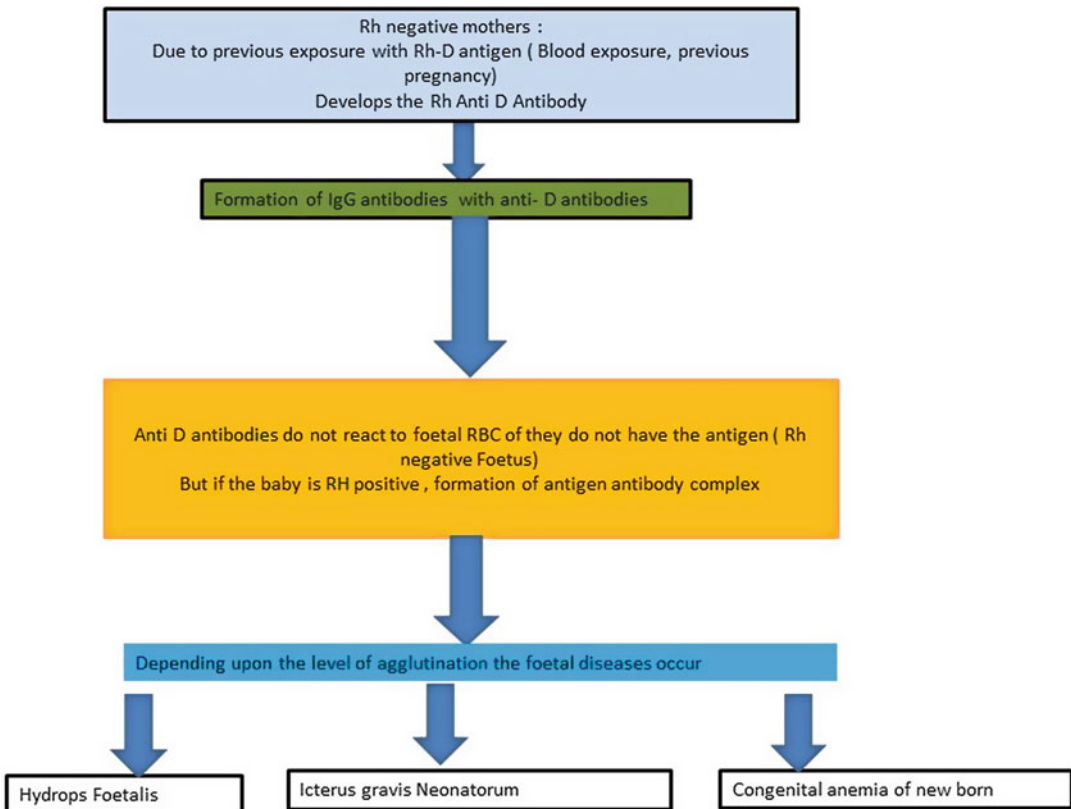
Diagnosis

A test to identify noninvasive fetal genotype (ffDNA) with the maternal blood for D, C, c, E, e, and K antigens could be done to determine the risk for the developing the fetal hydrops.

Management

Include the prevention of active immunization, avoidance of maternal and fetal blood contact, and avoid mismatched transfusion (Donohue and Wake 1964).

During the pregnancy, indirect coombs test every month till the 30 weeks and thereafter



Pregnancy Complications, Fig. 1 Diagram of pathogenesis of red cell alloimmunization

every 2 weeks of pregnancy. Injection Rh anti-D immunoglobulin in previously unimmunized women should be administered to prevent further active immunization; 300 µgm of antibody within 72 h of delivery should be administered at the earliest possible. Cord blood is collected and sent for testing direct coombs test, bilirubin, blood grouping, and cross-matching.

- Exchange transfusion of newborn (Dutta 2004) (the fetal blood is exchanged for unimmunized healthy RBCs for the better survival of the baby. This helps in maintaining the blood volume, preventing anemia, and improving icterus.)

Prognosis: the fetal prognosis depends on the level of maternal antibodies, paternal genotype and fetal genotype, availability of specialized services for care of such cases like NICU, exchange transfusion, etc.

Elderly Primigravida

This is a condition in which a woman usually gets pregnant after the age of 35 years (FIGO), which carries risk for the outcome of the pregnancy. This is a condition in which a woman usually gets pregnant after the age of 35 years (FIGO), which carries a risk for the outcome of the pregnancy. The current age limit of greater than 35 years has been decided arbitrarily by the outcome of pregnancy. It has been observed in the studies that pregnancy after the age of 35 years can lead to greater risk for fetal loss and anomaly. There are two types of elderly primigravida (WHO et al. 2017).

1. High Fecundity: Women who married late and got pregnant soon after marriage (prognosis is good for these women)
2. Low Fecundity: Women who married early on but could not conceive, for a long time, and had to use artificial reproductive techniques to conceive (prognosis is usually poor) (Myles et al. 1993).

Complication

During Pregnancy

The women more than 35 years of age have a higher risk for developing complications including the risk for abortion; deficiencies of folic acid; increased risk for hypertension and preeclampsia; risk for uterine fibroid and other medical complications like pregnancy-induced hypertension (PIH), gestational diabetes mellitus, cardiac the lesion, placenta praevia, and placental abruption due to hypertension; and risk for post-maturity and intrauterine growth retardation of the fetus (Dutta 2004; Jacob 2012; WHO et al. 2017).

During Labor and Delivery

During labor and delivery, there is an increased risk for malposition, malpresentation, preterm labor, prolonged labor, uterine inertia and impaired joint mobility, age-related stiffness in the soft tissue of the birth canal (Allanson et al. 2015) which can lead to poor outcome of the pregnancy, and increased maternal and perinatal mortality.

Fetal Risks

The fetus also has risk for developing congenital malformation, the risk for aneuploidy, and risk for neural tube defects in the fetus (Dutta 2004). This can complicate the pregnancy and impact the outcome adversely, resulting in polyhydramnios pregnancy induced Hypertension and Intra-Uterine death (IUD).

Puerperium

The puerperal period, i.e., the time from after the delivery of the baby to 6 weeks postpartum till the uterus becomes pelvic organ and extended up to 6 months after delivery. After the delivery, there is an increased risk for maternal morbidity as instrumentation and operations are more common and majorly women suffer from pregnancy-related health issues which complicate the outcome for both mother and the child (Jacob 2012).

Perinatal Outcome

Perinatal outcomes are adversely affected by the age factor in both mother and the partner, as with increasing the risk for trisomy 21 (Down's syndrome doubles) (James 2006). The advancing age of the parents and other pre-existing risk factors can increase the complications in the mother and fetus to multiple folds, and the risk for abortion and non-communicable diseases in the child for example; G6PD deficiency, congenital anomalies of internal organs, atrial septal defects, and ventricular septal defects became common giving the caregivers a tough time after the much-awaited childbirth (Myles et al. 1993).

Grand Multipara

Definition

The word grand multipara is a women with pregnancy who already has four or more viable births (Dutta 2004).

Parity

Means the to carry a baby till maturity in the uterus.

Incidence

Due to the small family norm adoption, the incidence of grand multipara has significantly reduced, but till date 1/10 women in the developing countries die due to the complications arising multiple child births. It is still a common cause of live long morbidity not if mortality of women (Allanson et al. 2015).

Complications of Grand Multipara

Pregnancy

Pregnancy of such condition can bring about the risks for:

1. Abortion
2. Iron deficiency anemia (due to draining of the iron reserve of the women due to multiple childbirths)
3. Malpresentation and malposition of the fetus
4. Lordosis loosening of the abdominal muscles

5. Herniation, cardiac disability, hemorrhoids
6. Multiple pregnancies, etc.

Labour and Delivery

Labour and delivery in the complicated cases of pregnancy, as the risk for uterine inertia, cord prolapse, and high-floating head at onset of labor may increase the risk for fetal loss. There is also chance for CPD due to secondary contracted fetus as a result of malnourishment of mothers (Dutta 2004; James 2006; WHO et al. 2017). Rupture uterus may happen as the uterus loses its elastic ability, postpartum hemorrhage, leading to shock and increased operative interference due to presence of complications (Myles et al. 1993).

Puerperium The puerperal period for these mothers becomes very important as they carry the burden of their own care plus the care for the family. The main issues during that period are subinvolution of the uterus, lactation failure, and several infections.

Long-term effects Grand multipara women suffer from some long-term morbidities due to child bearing, most commonly that is developing uterine prolapse and vesicovaginal fistula, recurrent UTI, sexual dissatisfaction, etc. Many women suffer from self-esteem issues due to these complications (Dutta 2004; Jacob 2012; Myles et al. 1993).

Management

Management of grand multipara is done with a few things in mind, the women are screened for the medical and other diseases and put into high risk, and close observation during the pregnancy can help in detecting and diagnosing a lot of problems early on, hence providing the women and her unborn child a way to be safe. There has to be a mandatory hospital delivery in order to prevent any complications (WHO et al. 2017).

Bad Obstetric History

Definition: bad obstetric history can be defined as a phenomenon when the women's current

outcome of pregnancy can be affected by the previous pregnancy disaster history in her life (Dutta 2004).

There are main three *principles of management* of such condition (Allanson et al. 2015; WHO et al. 2017)

1. Identifying the cause of previous related disasters
2. Treating the cause and managing the complications
3. Remaining vigilant till delivery

Etiological factors

1. Thyroid anomalies
2. Hormonal disturbances (PCOS)
3. Anti-phospholipid syndromes
4. Thrombotic disorders
5. Diabetes Mellitus
6. Hyperhomocysteinemia
7. Incompetence of the uterus and cervix
8. Structural anomalies of birth canal
9. Maternal systemic diseases. etc.

Manifestations

1. Recurrent abortions
2. Loss of fetus
3. Congenital anomalies of fetus
4. Weight gain
5. Spontaneous second trimester abortions
6. Cervical incompetence
7. Antepartum hemorrhage, etc.

Anti-phospholipid Syndrome

This condition is associated with the adverse outcome of pregnancy as the vasodilator mechanism occurring for the growth of the placenta and fetus is affected by the anti-phospholipids, leading to chronic placental insufficiency, PIH, placental hypoperfusion, IUGR, and growth failure of the baby (Dutta 2004; WHO et al. 2017).

Inherited Thrombophilia

They are conditions which lead to hyper-coagulability of blood within the blood vessels, and this leads to clotting of blood within the blood vessels.

Management

Assess the offending factor; prevent the factor to cause any more disruption. Provide the best therapy for the pregnant women to continue the pregnancy. Pre-pregnancy folic acid can reduce risk for congenital neural tube defects (Dutta 2004; Jacob 2012).

Vigilance

The care provider and the client have to be very vigilant in such cases, causes should be ruled out, and best practices according to govt. guidelines should be applied to save the mother.

High-Risk Pregnancy

This should be managed mainly by an interdisciplinary team and as an effort and obstetrician, endocrinologist, medical specialist, midwives, etc.

Obesity in Pregnancy

There is no defined criteria for obese in the world, but there is for normal weight, BMI (body mass index) helps us identify the level of obesity. People belonging to 18–24.9 kg/m² are normal and from 25 Kg/m² and above are overweight and people more than 29.9 kg/m². Obesity can bring about a lot of complications in the pregnancy like, gestational diabetes mellitus, HTN (hypertension), dyslipidemia, and many more complications (Murphy et al. 2010).

Effects on Pregnancy

1. Patients feel uncomfortable and have dyspnea on exertion.
2. Medical complications like hypertension, both essential and pregnancy induced, are increased and so also gestational diabetes.

3. There is difficulty in diagnosis of presentation and in hearing the FHS.
4. Macrosomic baby.

Effects on Labor

There is increased incidence of abnormal uterine contraction prolonged labor leading to operative interference and caesarean delivery. Pregnant women who are obese, There is increased incidence of abnormal uterine contraction prolonged labor leading to operative interference and caesarean delivery. There is higher chances of Shoulder dystocia macrosomia obstructed labor and increased risk for birth asphyxia and other foeto-maternal complications.

Puerperium

Postpartum hemorrhage, deep vein thrombosis, infections, fistula and delayed wound healing

Management

Use of planned diet and exercise in maintaining weight is a good way to avoid the complications (Alliance for Maternal and Newborn Health Improvement (AMANHI) mortality study group 2018). Heparin prophylaxis is given to prevent DVT, and mandatory hospital delivery and care in the months of pregnancy should be included. Woman should be counseled on the type of hazards and type of diet to be taken. Weight loss should not be aggressively attempted during pregnancy, but losing the weight and maintaining body weight has its own benefits.

Conclusion

Becoming pregnant and giving birth is a desire among most women. Complications frequently occurring during pregnancy can cause severe distress in them, as well as their immediate family. The knowledge about the pregnancy and related complications can save women their existing forthcoming children from crisis and burden. Timely medical attention can be instrumental in preventing certain complications and limiting their effect on the expecting mother and fetus. The awareness of the complications and their

management strategies can help people develop action plans for such complicated pregnancies. It is a non-negotiable role of the healthcare provider to educate and treat the women with the best practice evidence-based guidelines for a welcome outcome for the women and her forthcoming offspring.

Cross-References

► [Pregnancy](#)

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Pregnancy Prevention

► Abstinence

Pregnancy Sickness

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Synonyms

[Emesis gravidarum](#); [Morning sickness](#); [Nausea and vomiting in pregnancy](#)

Definition

A collection of symptoms, including food and odor aversions, experienced by pregnant women mostly within the first trimester of pregnancy.

Introduction

Until quite recently, nausea and vomiting in pregnancy (NVP) was viewed as an inconvenient by-product of the significant hormonal changes (hCG, estradiol, and progesterone) that take place during early pregnancy (Forbes 2002), with potential threats to the developing organism due to malnutrition (Pike 2000). However, more recently researchers have cited the adaptive function of pregnancy sickness (Sherman and

Flaxman 2000) on the basis of studies documenting favorable prognostic associations, including the aversions to and cravings of certain foods and improved pregnancy outcomes.

Is pregnancy sickness adaptive?

Pregnancy sickness is associated with approximately 60% of pregnancies (Flaxman and Sherman 2000). The high frequency of pregnancy sickness is puzzling from both a biomedical and evolutionary viewpoint. Given that a pregnant woman has to “eat for two,” why should a condition that limits food consumption take place simultaneously as this dramatic increase in nutritional and caloric demands? This question can be approached from two levels of analysis, proximate (the “how” question) and ultimate (the “why” question). The analysis of any behavior is complete only if both proximate and ultimate explanations are achieved. While most research effort in the field of pregnancy sickness has focused on the proximate mechanisms – that is, elucidating hormonal and psychological correlates of this phenomenon – more recently a discussion has been sparked about whether or not pregnancy sickness serves useful functions (Flaxman and Sherman 2000; Forbes 2002). The importance of this discussion is that it has the power to inform medical practice because it is beneficial to understand what (possibly non-pathological) symptoms were “designed” to do before trying to treat them. In particular, understanding the reasons of why NVP exist can inform us of whether or not it is categorically recommendable to suppress these symptoms (Flaxman and Sherman 2000).

Some researchers have argued that pregnancy sickness does not serve any function. Forbes (2002) has dismissed pregnancy sickness as a simple by-product of mother-embryo conflict over the degree of maternal investment. Women are immunocompromised during pregnancy to secure immune tolerance to the fetus, which the maternal immune system would otherwise reject as a foreign body. Because immunosuppression compromises the mother’s ability to resist

infection while immunoactivity puts the embryo at risk, it is plausible that the optimal level of immunosuppression may differ between the child-bearer and the developing organism. The theory predicts that maternal-fetal conflict will be most intense early in women's reproductive career, because the value of a given fetus depends on the mother's remaining reproductive potential (Forbes 2002). If pregnancy sickness is the result of maternal-fetal conflict, then its severity should be inversely related to maternal age. However, while some researchers report the predicted inverse relationship between NVP and maternal age, others find no association (see Fessler 2002).

Other researchers view pregnancy sickness as harmful. For example, Pike (2000) documented fitness costs (e.g., poorer pregnancy outcomes) associated with pregnancy sickness among a marginally nourished population in Kenya. She concluded that NVP may be maladaptive in resource-poor, low-income, and nutritionally compromised environments. In general, however, not many researchers argue that NVP is maladaptive. In fact, a growing body of evidence highlights the adaptive function of pregnancy sickness. There are two prominent functional theories about pregnancy sickness, the "maternal and embryo protection hypothesis" and the "compensatory placental growth hypothesis," which will both be discussed next.

The "maternal and embryo protection hypothesis" postulates that pregnancy sickness is an adaptation that prevents the intake of substances that could potentially be harmful to both the immunosuppressed mother and the fetus. In the initial formulation of this idea, pregnancy sickness was hypothesized to protect the fetus from embryotoxic substances, like caffeinated and alcoholic beverages. Building on this idea, Profet (1988) embedded the associated appetite changes and benefits into an evolutionary and adaptive framework. She listed the categories of foods that pregnant women might have avoided in our ancestral environment, emphasizing the risk of secondary compounds produced by plants to the fetus. More recently, Flaxman and Sherman (2000) and Fessler (2002) widened the scope to include meat-borne pathogens, fish and eggs. For

instance, *Toxoplasmosis* is an infection caused by a parasite called *Toxoplasma gondii* that can be caught via the consumption of raw or undercooked meat. The infection is typically only harmful to those who have a weakened immune system, as is the case for pregnant women. It can cause abortions or birth defects in pregnant women.

Sherman and Flaxman (2000) have put forward five critical predictions of the embryo protection hypothesis:

Prediction 1

The first prediction is that the NVP should be the greatest when the developing organism and the immunocompromised mother are most vulnerable to infections by pathogens. Organogenesis, the period when the embryo's organs are developing, occurs within the first trimester, and thus intake of harmful foodstuffs is most likely to be harmful at this time. Furthermore, a body of evidence suggests that maternal immunosuppression also peaks during the first trimester, which exacerbates the dangers inherent in this precarious phase. Consistent with prediction 1, several studies have found that, in Western subjects, symptoms of pregnancy sickness are concentrated during the first trimester. The same pattern is documented in numerous preindustrial societies (Fessler 2002).

Prediction 2

The second prediction of Sherman and Flauxman (2000) is that the food items women avoid during pregnancy should contain harmful substances, whereas food items that are craved should not. Sherman and Flaxman (2000), in a meta-analysis of studies examining food aversions and food cravings, discovered that pregnant women most often reported aversion towards food categorized as "meat, fish, poultry, and eggs"; "nonalcoholic beverages" (mostly caffeinated such as tea and coffee); and "vegetables." In line with prediction 2, these three most aversive food categories were the same categories that are high in levels of

potentially teratogenic and abortifacient agents. In contrast, the food categories that were the most craved – “fruit and fruit juice”; “sweets, desserts, and chocolate”; and “dairy” – were also the ones least likely to contain harmful substances. Another study found similar pattern of dietary taboos during pregnancy in many human societies (Fessler 2002). Interestingly, Mckerracher et al. (2015) reported that Yawasa women also developed aversions to their husband’s smell during pregnancy, which they interpreted as an aversive reaction to pathogens carried by their husbands and transmitted sexually.

A few inconsistent findings have been reported. One study of pregnancy sickness and aversions in Tanzania found that pregnant women actually developed food cravings for meat, the same food hypothesized to be principle target of aversions. Another study found olfactory cravings for noxious agents such as cigarettes, ammonia, and bleach (see Patil et al. 2012).

Prediction 3

The third prediction builds upon the second: Pregnancy-related aversions to potentially dangerous foodstuffs should be concentrated within the first trimester. Consistent with prediction 3, Flaxman and Sherman (2000) documented that, in a subsample of their meta-analysis, pregnancy-related aversions to foods peaked in this period and lessened or resolved after that. This finding is complemented by other research showing that pregnant women during their first trimester are significantly more aversive than non-pregnant women towards all food categories, particularly to “meat, fish, poultry, and eggs.”

Prediction 4

If NVP was “designed” as a maternal and fetus protection mechanism, then women who develop NVP should, on average, experience an improvement in pregnancy outcomes over those who do not develop these symptoms. A large body of evidence supports this prediction. Sherman and

Flaxman (2000), in a meta-analysis of nine studies involving 22,305 pregnancies, demonstrated that the risk of miscarriage was significantly reduced for women who developed NVP compared to women who experienced no symptoms. Tierson et al. (1986) divided pregnant women into three categories: (1) those who were asymptomatic, (2) those who only had nausea, and (3) those who developed both nausea and vomiting. The outcome results of this study demonstrated that asymptomatic women were significantly more likely to experience fetal death (20% experienced fetal death) compared to women with nausea only (10.3%) and those with both symptoms (4.3%).

A few researchers have found contradictory evidence. One reported no association between ingestion of certain food types that could cause adverse pregnancy outcomes and symptoms of NVP or pregnancy outcome. Another study did not show a relationship between lack of pregnancy sickness and an increase in the overall rates of major birth malformations (see Patil et al. 2012).

Prediction 5

The fifth prediction is that NVP should be observed less often when the diet consists of foods that rarely contained harmful substances historically. Sherman and Flaxman (2000) analyzed both the diet and frequency of pregnancy sickness in 27 traditional societies. The results of this analysis demonstrated that compared to societies in which NVP was documented, societies without pregnancy sickness were significantly more likely to have maize and/or corn as their main food staples and significantly less likely to consume meat. Consistent with prediction 5, domesticated corn tends to have minimal harmful compounds. Profet (1998) further noted that this corn-based diet is a good source for folic acid, which is a vitamin that reduces the occurrence of neural tube defect.

Taken together, the five predictions of the maternal and embryo protection hypothesis receive a great deal of empirical support, although contradictory findings are also occasionally

documented. Nevertheless, the question arises whether nowadays NVP is simply an evolutionary anachronism since the ingestion of potentially harmful foodstuffs has been significantly reduced through inventions such as the refrigeration and freezing of leftovers. Sherman and Flaxman (2000) argue otherwise. They postulate that the association between NVP and positive pregnancy outcomes in contemporary societies implies that pregnancy sickness remains an important maternal and embryo protection mechanism in the present-day world.

The other major hypothesis put forward to explain the function of pregnancy sickness is the “compensatory placental growth hypothesis” (Huxley 2000). According to this hypothesis, first-trimester nausea and vomiting are an adaptation that lowers maternal nutrient intake that, in turn, suppresses maternal tissues synthesis and promotes placental growth. The symptoms of pregnancy sickness may therefore aid to channel scarce nutrients to the developing placenta. Consistent with the theory, low maternal intake within the first trimester is associated with a larger placenta (Huxley 2000), at least for mild levels of dietary limitations. Based on this hypothesis, it is also predicted that NVP should be observed more frequently in women with high preconceptional body-mass index (BMI; Huxley 2000). However, the findings are inconsistent, with some reporting a higher frequency of NVP in heavier than light women, others finding no relationship, and still others reporting the opposite relationship (see Pepper and Roberts 2006). Overall then, the lack of studies examining or supporting the compensatory placental growth hypothesis makes it difficult to credit it at this stage.

Conclusion

In summary, until quite recently, most clinicians have considered pregnancy sickness as a psychological disturbance of pregnant women. However, recent research suggests that pregnancy sickness serves useful functions. Currently, the front-running functional explanation for pregnancy sickness is that it is an adaptive response that

protects fetal organ development and the immunosuppressed mother from the toxic effects of certain foods. This view has important clinical implications. Mckerracher et al. (2015) have argued that recognizing pregnancy as an adaptation rather than a pathology requires a change in language within the clinical literature: Rather than describing NVP as a “syndrome,” which suggests that it is pathological, they suggest using a more neutral vocabulary such as describing NVP as “the expression of one or more behavioral and physiological traits.” In addition, Sherman and Flaxman (2002) propose that viewing pregnancy sickness as adaptive may provide some comfort to women developing NVP and help health carers to develop new ways of reducing these symptoms (e.g., the removal of potentially triggering stimuli from the patient’s environment during the first trimester).

Cross-References

- [Concealed Ovulation and Pregnancy](#)
- [Darwinian Medicine](#)
- [Disgust](#)
- [Evolutionary By-Products](#)
- [Evolutionary Medicine](#)
- [Fetus Development](#)
- [Food Aversions and Cravings](#)
- [Low Birthweight and Preterm Infants](#)
- [Maladaptive By-Product Hypothesis](#)
- [Morning Sickness](#)

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Pregnancy-Induced Diabetes

► [Gestational Diabetes and Maternal-Fetal Conflict](#)

Prehistoric Human Art

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Synonyms

[Cave art](#); [Cave painting](#); [Petroglyphs](#)

Definition

Ancient products of human creative expression.

Introduction

Evidence for artistic expression is a relatively recent phenomenon in the evolution of humans. Prior to the Late Paleolithic, most human activity

was centered on subsistence with precious little time left for other pursuits. The oldest artwork currently recognized is a series of petroglyphs at the site of Bhimbetka, India, that have been dated to at least 290,000 years ago and could be somewhat older.

Prehistoric Human Art

Prehistoric art is generally placed into one of three categories: petroglyphs (carving or scratching into a stone surface), parietal art (cave paintings), or mobiliary art (small, portable items like figurines or other sculpture). Many of these forms can be quite difficult to obtain dates for, so the temporal context for many works of prehistoric art is highly subject to revision as new dating techniques are developed and existing techniques are improved.

Petroglyphs are made by pecking or scratching the surface of a stone face, often to reveal layers of lighter unweathered stone underneath. They have been found all over the world, with the most significant installations in parts of Africa, Scandinavia, Europe, and Australia.

Parietal art refers to any artwork made in caves, including cave paintings and engravings made on the walls, floors, or ceilings of caves. Such artwork may be produced using charcoal or a variety of pigments such as ochre or manganese. A number of dating techniques can be used to date materials involved in the production of such paintings to obtain an approximate age, and in some instances foreign substances like mineral deposits overlaying the artwork may also be used to estimate a minimum age of the artwork. Parietal artwork has also been found around the world, with noteworthy examples in Africa, North America, Australia, and Europe.

Mobiliary art is any small-scale artwork that is movable. This can include carvings, sculpture, or engraved tools. A number of different materials were used to create these works, including stone, bone, ivory, and ceramics. Perhaps the most famous mobiliary art is the Venus figurines that first appeared during the Late Paleolithic of Europe. These small statuettes depict rather exaggerated versions of the female body, with large

pendulous breasts and broad hips. Other forms of mobiliary art are seen in ornate bone tools like spearthrower handles and decorated harpoon heads.

Due to the relatively recent appearance of artwork in the archaeological record, it has often been cited as evidence for the appearance of the advanced intellect of modern *Homo sapiens*. However, there is a small but growing body of evidence that suggests that Neandertals were also capable of producing artwork. Eagle talons discovered among Neandertal remains in Krapina, Croatia, show signs of having been worn as jewelry (Radović et al. 2015). At Bruniquel Cave in France there is evidence that Neandertals created rings with broken stalagmites over 175,000 years ago, considerably older than the first appearance of modern humans in Europe (Jaubert et al. 2016). La Ferrassie, France, site of a series of seven Neandertal burials, also contains petroglyphs in the form of cupules in the cave walls and on a stone slab placed over the burial of a child. These discoveries, among others, highlight the behavioral complexity of Neandertals and the inherent difficulty in interpreting the significance of prehistoric artwork.

Conclusion

Prehistoric human art provides insights into the development of humans' capacity for symbolism, complex thought, and creativity. These types of expression are often considered hallmarks of humanity that separate *Homo sapiens* from our ancestors. Recent discoveries of artwork attributed to Neandertals may require us to either change our perception of the significance of this artwork or to alter our perceptions of the Neandertals and their relationship to *Homo sapiens*.

Cross-References

- [Evolution of Intelligence](#)
- [Human Ornamentation](#)
- [Neanderthals and Humans](#)

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Prejudice

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Synonyms

[Antipathy](#); [Attitude](#); [Bias](#); [Ingroup favoritism](#); [Outgroup derogation](#); [Preference](#)

Definition

Prejudice is an attitude, or an overall negative evaluation or devaluation, of a social group and its members. Prejudice entails affective reactions toward social groups (e.g., anger, fear, disgust, pity, guilt, envy, contempt).

Introduction

Advancing from Allport's (1954) definition of prejudice as "antipathy based upon a faulty and inflexible generalization" (p. 9), prejudice is defined as an overall unfavorable evaluation of, or attitude toward, a social group (Crandall and Eshleman 2003; Esses et al. 1993; see also Dovidio et al. 2005). Prejudice may include elements of outgroup derogation and ingroup favoritism, and can be understood in terms of direct antipathy toward outgroups as well as relative preference for ingroups (Brewer 1999). Thus, prejudice may not entail a strictly negative attitude toward a social group, but encompasses a

relative devaluation of one social group compared to another. In addition to prejudice as a general attitude or evaluation, prejudice is an affective state that entails emotional reactions toward social groups (Esses et al. 1993). In the United States, for example, African-Americans tend to elicit fear, whereas Native Americans tend to elicit pity, gay men tend to elicit disgust, and activist feminists tend to elicit anger (Cottrell and Neuberg 2005).

Overview

Prejudice is conceptually distinct from stereotypes (i.e., cognitive beliefs about the attributes and traits of a social group and its members) and discrimination (i.e., any negative, unfair, or unequal behavior or treatment accorded to others based on group membership), although these concepts are interrelated (Esses et al. 1993). Conceptualization of prejudice as an attitude necessitates consideration of prejudice in terms of propositional processes (e.g., explicit attitudes) and associative processes (e.g., implicit attitudes; Gawronski and Bodenhausen 2006). Considering the more automatic and spontaneous aspects of prejudice along with its more controlled aspects allows for a better understanding of the various ways in which prejudice is expressed, ranging from rather overt and blatant expressions (e.g., old-fashioned prejudice; McConahay 1986) to more subtle instantiations (e.g., modern prejudice and aversive prejudice; Dovidio and Gaertner 2004; McConahay 1986). Any conceptualization of prejudice would be remiss without acknowledging the functions that prejudice serves, which include the object-appraisal function, social expressive function, and value expressive function (Herek and McLemore 2013). Considering prejudice as an affective state allows for more nuanced understanding of how group stereotypes (Cuddy et al. 2007) and perceived group threats (Cottrell and Neuberg 2005; see also Stephan et al. 2016) differentially elicit intergroup emotions in predictable ways. Each of these areas forms a foundational basis in understanding prejudice and are elucidated below.

Implicit Versus Explicit Prejudice

Prejudicial attitudes may be implicit or explicit. Whereas implicit attitudes are automatic affective reactions toward a social group, explicit attitudes are controlled evaluative judgments (Gawronski and Bodenhausen 2006). Implicit attitudes are activated automatically upon encountering a social group, regardless of whether a person considers the associative evaluation to be accurate, and regardless of whether a person even intends to evaluate a group. Anecdotally, implicit attitudes are analogous to a “gut reaction” that may be experienced when approaching a shadowy stranger on a dark street. By contrast, explicit attitudes are evaluative judgments that a person endorses and believes to be true. Explicit attitudes are dependent on the assignment of truth values, intentional, and require cognitive resources to make syllogistic inferences. In other words, explicit attitudes are endorsed statements of people’s social group preferences. For example, prejudicial sentiment likely bases the statement “No fat chicks” recently seen on a bumper sticker.

People typically use their automatic affective reactions as the basis for their evaluative judgments (Gawronski and Bodenhausen 2006). However, prejudice is one domain in which implicit and explicit attitudes do not routinely match. For example, a person may have an automatic negative reaction toward African-Americans even though they may not personally endorse the negative associative evaluation (Devine 1989).

Forms of Prejudice Expression

Historically, prejudice has been studied in the form of direct, blatant expression of negativity toward social groups, which can be described as old-fashioned prejudice. Old-fashioned prejudice may be best conceptualized in terms of non-egalitarian beliefs, as it entails blatant antipathy toward social groups and the belief that some social groups are inferior to others (McConahay 1986). This form of prejudice is labeled old-fashioned because it is no longer acceptable in

most social circles. In fact, public opinion polls in North America have shown a steady decline in the negative evaluations of racial minority groups after World War II, mirrored by a steady increase in the endorsement of racial integration and equal treatment (Bobo 2001). Nevertheless, people vary in their endorsement of old-fashioned prejudicial attitudes. It depends on the social group in question as well. For example, some prejudices are relatively socially acceptable (e.g., negative attitudes toward illegal immigrants, ex-convicts, fat people) whereas others are socially unacceptable (e.g., negative attitudes toward blind people, Black Americans, Jews; Crandall et al. 2002).

Over the last few decades, researchers have proposed and refined theories of more subtle forms of prejudice, such as modern and aversive prejudice, due to observations of changing societal and personal norms regarding the overt expression of prejudice. Modern prejudice is exemplified in the case where people minimize diversity and group difference, deny the existence of discrimination, and thus do not support public policies aimed at reducing discrimination, such as affirmative action (McConahay 1986). From this perspective, prejudicial attitudes are expressed as concern over how group equality should be implemented. In this way, underlying negative attitudes toward particular social groups are justified on nonprejudicial grounds, thus allowing for the maintenance of an egalitarian and nonprejudiced self-image. For example, you may have heard someone make a statement like, “If I was Black, then I would have gotten that job.” This exemplifies modern prejudice as it denies discrimination, minimizes diversity issues, and communicates dissatisfaction with policies aimed to reduce discrimination.

Aversive prejudice is another subtle, often unintentional form of prejudice in which people hold strong egalitarian values, and, at the same time, harbor negative feelings and beliefs toward minority groups based on socialization and categorization processes (Dovidio and Gaertner 2004). From this perspective, people are socialized to be egalitarian and nonprejudiced, while also internalizing negative feelings and beliefs about stigmatized social groups. Aversive

prejudice focuses on the conflict between people’s denial of personal prejudice (i.e., explicit attitudes) and their underlying negative attitudes toward particular social groups (i.e., implicit attitudes). Notably, the theory of aversive prejudice argues that prejudice will only be expressed when people can justify it on nonprejudicial grounds, allowing people to maintain an egalitarian image. Otherwise, people may bend over backwards to demonstrate how nonprejudiced and accepting they are, especially if prejudice-related issues are salient.

The integrative prejudice framework (Brochu et al. 2008; Gawronski et al. 2012) specifies the conditions under which negative affective reactions toward social groups translates into negative evaluative judgments. It identifies egalitarian nonprejudicial goals (i.e., the extent to which one believes that negative evaluations of social groups are wrong) and perceptions of discrimination (i.e., the extent to which one believes that a specific social group is a target of discrimination) as central components that distinguish old-fashioned, modern, and aversive prejudice. Specifically, the correspondence between implicit and explicit prejudice is determined by the interplay between egalitarian nonprejudicial goals and perceptions of discrimination according to cognitive consistency principles. Research evidence indicates that explicit attitudes about a social group reflect implicit attitudes when nonprejudicial goals are weak and at the same time perceived discrimination is high, reflecting central components of old-fashioned prejudice (i.e., believing that discrimination of some groups is pervasive and that this discrimination is acceptable, even preferred). Further, explicit attitudes about a social group reflect implicit attitudes when nonprejudicial goals are strong and perceived discrimination is low, reflecting central components of modern prejudice (i.e., believing that discrimination is wrong but that discrimination is a thing of the past). Moreover, explicit attitudes about a social group do not reflect (or may even negatively reflect) implicit attitudes when nonprejudicial goals are strong and perceived discrimination is high, reflecting central components of aversive prejudice (i.e., believing that discrimination is

wrong but at the same time harboring negative underlying views about particular social groups).

More generally, the expression of prejudice can be understood from the perspective of the justification-suppression model of prejudice (Crandall and Eshleman 2003). In this model, genuine prejudice is distinct from expressed and experienced prejudice. Genuine prejudice is an authentically negative reaction toward social groups that develops from several social, cultural, cognitive, and developmental factors, including family influences, direct cultural learning, social categorization, group identity, intergroup contact, and intergroup conflict. Genuine prejudice undergoes a range of suppression and justification factors that shape how prejudice is expressed and experienced to the self and others. Suppression factors reduce the expression or awareness of prejudice and include social norms, empathy, personal standards, egalitarian beliefs, and values. Justification factors release the expression of prejudice without guilt or shame and include belief in a just world, Protestant work ethic, social dominance ideology, victim blaming, attributional scapegoating, situational ambiguity, shifting standards, and perceived threat, to name just a few.

Functions of Prejudice

A variety of motivations underlie prejudice, as attitudes can serve different functions. The basic assumption is that people hold and express attitudes because they fulfill psychological functions (Herek and McLemore 2013; see also Maio and Olson 2000). One function of attitudes, including prejudice, is object appraisal. Attitudes allow people to categorize objects into groups and then evaluate them accordingly. Applied to prejudice, attitudes allow people to recognize different social groups and label them as good or bad; having this knowledge assists people in making behavioral decisions, such as whether to approach or avoid a person who belongs to a particular social group. Importantly, object appraisal is the outcome of a normal cognitive process in which people automatically

categorize others into social groups to organize the world in a meaningful and consistent fashion. Social categorization into groups, like all categorization processes, highlights the similarities within groups and the differences between them (Brewer 1999). Intergroup conflict depends on the categorization of social groups into us versus them, as social categorization predisposes people to prefer ingroup members to outgroup members. This is remarkably easy to elicit: People prefer ingroup members even when they are assigned to groups temporarily according to arbitrary dimensions (e.g., minimal groups; Tajfel et al. 1971).

Another function of attitudes is that of social expression (Herek and McLemore 2013; Maio and Olson 2000). Attitudes allow people to express their sense of belonging to particular social groups, and assists people in gaining acceptance, approval, or love from others they consider important, such as family, friends, coworkers, and neighbors. In this way, the expression of prejudice is one way that may allow people to fulfill their affiliative needs. For example, Herek (1987) found that people's attitudes toward gay men and lesbians were at least partially based on their "perceptions of how the people I care about have responded to gay people as a group" and "learning how gay people are viewed by the people whose opinions I most respect" (p. 296). The self is defined largely in terms of group memberships, and as such, groups are an important source of identity for people (Tajfel and Turner 1986; Turner et al. 1987).

Attitudes also serve a value-expressive function, allowing attitudes to affirm people's belief in and adherence to important values that are closely related to their self-concept (Herek and McLemore 2013; Maio and Olson 2000). In this way, the expression of prejudice is one way that may allow people to display aspects of their identity that are based on moral, ethical, or political principles. For example, Herek (1987) found that people's attitudes toward gay men and lesbians were at least partially based on their "concern that we safeguard the civil liberties of all people in our society" and "moral beliefs about how things should be" (p. 296).

Prejudice as Affect

Simply conceptualizing prejudice as an overall negative attitude toward a social group and its members may obfuscate the nuanced complexity that different social groups elicit qualitatively different affective reactions. For example, people may report similar levels of prejudice toward two groups on an attitudinal measure, but may experience different emotional reactions to the two groups (e.g., fear versus anger; Cottrell and Neuberg 2005). This consideration is particularly important as emotions have motivational force; they serve as a spur to action (Crandall and Eshleman 2003; Cuddy et al. 2007).

According to the BIAS map (Cuddy et al. 2007), judgments of warmth and competence underlie social perceptions and drive our emotional and behavioral reactions to others. Upon encountering a person or a social group, people first seek to anticipate their intentions – do they intend to help me or harm me and my group? – and this leads to categorization based on warmth (e.g., trustworthy, kind, friendly). Then, people seek to know others' capability to pursue their intentions – are they able to help me or harm me and my group? – leading to categorization based on competence (e.g., creative, confident, intelligent). If a social group is perceived as lacking warmth, this tends to elicit dislike, whereas if a social group is perceived as lacking competence, this tends to elicit disrespect. Furthermore, judgments of social groups based on warmth and competence lead to predictable emotional reactions. Groups perceived as low on warmth and low on competence, such as the homeless and the poor, tend to elicit contempt. By contrast, groups perceived as low on warmth and high on competence, such as Asian Americans and the rich, tend to elicit envy. Furthermore, groups perceived as high on warmth and low on competence, such as the elderly and housewives, tend to elicit pity. And, groups perceived as high on warmth and high on competence, such as one's ingroups, tend to elicit admiration.

In Cottrell and Neuberg's (2005) sociofunctional approach to prejudice, specific feelings

that people have toward members of other groups are argued to depend on the specific tangible threats that these groups are perceived to pose. Qualitatively different group-based threats evoke qualitatively different affective reactions. For example, some groups are perceived to be threatening because they are viewed as a risk to physical safety, arousing fear. Other groups are perceived to be threatening because they are perceived as obstructing a desired outcome, such as threatening group economic resources or personal freedoms and rights of ingroup members, arousing anger. Some groups are perceived to be threatening because they are viewed as physical or moral contaminants, either through threat to group health via contagion or threat to group values, arousing disgust. Other groups are perceived to be threatening because they possess resources or opportunities that one lacks, arousing envy. Some groups are perceived to be threatening because they are disadvantaged for reasons beyond their control, eliciting distress and feelings of pity. Other groups are perceived to be threatening because they threaten the perception of the morality of one's ingroup, eliciting distress and feelings of guilt. It is clear that social groups pose multiple threats and elicit a variety of emotions.

Prejudice from an Evolutionary Perspective

Evolutionary processes can inform psychological research on prejudice (Schaller et al. 2010). From an evolutionary perspective, prejudice can serve meaningful purposes that benefit group outcomes. For instance, Neuberg et al. (2000) argue that prejudice is rooted in an inherent need to live in effective groups that promote survival. Human beings are social animals, and are greatly committed to group living. Interdependent and cooperative groups likely evolved to maximize survival; people are able to more easily secure fundamental resources like food, water, shelter, and mating partners that support child rearing and self-protection initiatives by living and working with others. Group living has its risks, however, and so

humans possess cognitive adaptations that alert them to others who may be likely to physically harm fellow group members, spread contagious disease, or free ride on the efforts of the group (Kurzban and Leary 2001; Schaller and Neuberg 2012). Thus, groups who are perceived to threaten the survival of one's ingroup will be the target of prejudice. Furthermore, the preference of some people to express domination over others may be understood from the adaptive utility of status hierarchies within social groups (Pratto et al. 1993). The process of prejudice can be considered a byproduct of evolutionary processes, in which prejudice functions to minimize threat by derogating others and maximize survival by aligning with strong ingroup members.

Even though the roots of prejudice may lie in the evolutionary past of humans, this does not imply biological determinism (Neuberg et al. 2000). Just because certain prejudices were adapted for the social and physical environments of the evolutionary past does not imply that they are adaptive today. Furthermore, even if some prejudices are adaptive, evolutionarily speaking, this does not mean that they are acceptable or justifiable.

Conclusion

In a time when the US government seeks to ban visitors from Muslim-majority countries and all refugees, and the nation is reeling from violence targeting stigmatized group members, including LGBT-identified people, Jews, and Blacks, prejudice remains an important social issue (Society for the Psychological Study of Social Issues 2017). Understanding prejudice, including its associative and propositional processes, forms of expression, functions, and affective aspects, allows researchers to better develop effective prejudice-reduction interventions. As Neuberg and Schaller (2016) point out, humans are *evolved* social animals, and research that considers prejudice from an evolutionary perspective has the potential to inform understanding of the nature of prejudice.

Cross-References

- [Avoiding Stigmatization](#)
- [Out-Group Members](#)
- [Prejudice as an Expression of Tribalism](#)
- [Racism](#)
- [Racism and Prejudice](#)
- [Sexism](#)
- [Sexual Prejudice \(Personality Correlates Of\)](#)
- [Social Dominance Orientation \(SDO\)](#)

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Prejudice as an Expression of Tribalism

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Synonyms

Racism and prejudice; Tribalism; Tribalism in moral tribes

Definition

People show a set of tribalistic tendencies such as ingroup favoritism and outgroup discrimination since they were adaptive in the past environmental conditions. In other words, groups that showed stronger ingroup favoritism and outgroup discrimination were more likely to survive in the past selective pressures. Therefore, prejudice can

be seen as a reflection of our evolved tribalist psychology.

Introduction

The finding that people cooperate more with members of their own group and thereby show tribal tendencies has been established in many different areas of research (Balliet et al. 2018; Fowler and Kam 2007; Yamagishi and Mifune 2016). For example, Ben-Ner et al. (2009) showed that when people share an identity (religious, political, etc.), they tend to make clear distinctions between ingroups and outgroups in their intended and actual social behavior. Other research shows that newborns show preferential behavior towards their own race and discriminate against those who do not speak their own language (Bar-Haim et al. 2006). Even in the minimal group paradigm, where groups are generated randomly, people show ingroup favoritism (Tajfel and Turner 1986). This tendency is observed in other primates as well. For example, capuchin monkeys can automatically distinguish the faces of ingroup and outgroup members (Mahajan et al. 2011). In fact, De Waal et al. (2008) showed that capuchin monkeys behaved prosocially toward their ingroup members but not toward the outgroup. In short, discrimination and prejudiced attitudes toward outgroups arise as a result of ingroup favoritism among both humans and our close relatives.

Prejudice is defined as preconceived opinions or attitudes, usually based not on a rational evaluation of evidence that a person has about another party (Allport 1954). Instead, prejudice is usually based on automatic judgments (Bargh 1999) and manifests itself implicitly at the perceptual and physiological level (Payne 2006). Likewise, as the human species evolved in intense intergroup conflicts involving coalition building (Geary 2005), cooperation was often only directed toward own group members. In general, it is thought that selective environmental pressures caused humans to acquire tribal characteristics including prejudice, since groups that showed stronger ingroup favoritism were more successful than others.

These coalitional conflicts manifest themselves in today's world as well. However, there is an ongoing debate as to whether all political groups have these tribal characteristics equally. In a meta-analysis by Jost et al. (2003), asymmetries between the liberals and the conservatives were found on many areas related to tribalism (e.g., ingroup favoritism, closed-mindedness, prejudice, etc.). For example, conservatives are more biased toward outgroups than liberals. However, these studies were later criticized on methodological grounds (i.e., Brandt et al. 2014). The most important of these criticisms is that past studies chose to study minority groups that the liberals favor (gays, atheists, etc.) as the target of prejudice. Interestingly, liberals reported more prejudiced attitudes than conservatives when minority groups favored by conservatives were selected, such as religious people (Brandt and Van Tongeren 2017; Brandt 2017). In other words, both ideological groups reported prejudice against groups that are not similar in value to themselves. This suggests that people tend to cooperate with ingroups – independent of political ideology – and support the argument that prejudice is a reflection of evolved tribalist intuitions.

In an attempt to explain the psychological differences found between liberals and conservatives, Haidt (2012) states that each political group originally has tribal characteristics, but that liberals spend cognitive effort to repress these tribal characteristics (such loyalty, authority, and sanctity). There is some evidence suggesting that liberals resemble conservatives when their cognitive resources are depleted through cognitive load or existential threat (e.g., Nail et al. 2009). Haidt's theoretical approach, therefore, supports the argument that everyone has a set of tribalistic tendencies and that favoring the ingroups and derogating the outgroups stem from our evolved psychology. Hence, prejudice reflects human nature, evolved due to function in past environmental conditions. One way to avoid such cognitive biases in general (Kahneman 2011) and prejudiced attitudes in particular (Yilmaz et al. 2016) is to promote the processes of effortful and analytical thinking.

Cross-References

► Evolution of Human Sociality

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Premarital Sexual Permissiveness

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Introduction

Sexuality colors the whole life of an individual, since the early childhood; the sexuality develops throughout individual life, leading to certain beliefs and attitudes about sexual relationships. Going toward adolescence, sexual relationships provoke interest among one and all. Sexual relationships can be comprehended as constant choices that one makes in their lives to engage in sexual activities. This is although a biological instinctual process in the beginning, but due to the complexity of human society, sexual permissiveness shows a great degree of variation throughout the world (Friedman 1992).

Marriage is a norm in all of the civilized human society which acknowledges the union of two human beings and grants them the permission to reproduce in a culturally accepted manner. In major cultures of the world, men and women are considered not to engage in sexual relationships before marriage which has been religiously governed majorly as chastity and strength of character (Zuo et al. 2012). Historically, men and women who engaged in premarital sexual acts were considered impure and unchaste which degraded their social status and also made them lose their honor (Ghaffari et al. 2016). These values color the sociocultural aspects of Christianity, Hinduism, Islamic, and Jewish societies majorly covering most of the human population (Gaje 1996; Reiss 1964a; Spercher and Hatfield 1996).

During the rapid urbanization and development of the western world with the insights of Sigmund Freud and liberalization of the society, premarital sexual permissiveness became an area of study, and during the 1960s, researches started happening in the United States of America followed by the rest of the world. It still remains an interesting area for research and study (Zuo et al. 2012).

Concept of Sexual Permissiveness

There are certain terms associated with sexual permissiveness:

- *Permissive society*: this is a type of society which is considered to be open to the ideas of sexual freedom. This type of society has existed in Europe, North America, and Australia. Here, people are allowed to engage in sexual activities before marriage (“Permissive society” 2018).
- *Liberalism*: liberal comes from the word liberty, which allows a person to think and hold varied and different philosophies. This liberty in the late 1960s in America and Europe not only remained as philosophical but also became broadened to accommodate with sexual freedom, which allowed the members of the society to enjoy the choice of choosing their own partners and engaging in sexual activities. But then this was considered as a bad label, as it meant high level of sexual promiscuity among the people of their society.
- *Secularism and permissiveness*: these two words are often related as permissiveness which was found to be closely related to secularism. As the secularism became more and more prominent in the western countries, their permissiveness increased.
- *Premarital sexual permissiveness*: literally means the mind-set of accepting sexual behavior before marriage.

The people of the Victorian era and the strong religious sentiments of Christianity started becoming more secular with the rise of Marxism and communism, leading to a more secular and irreligious societies during the 1960s, where mutual love preceded the religious rigor, and along with liberal philosophies, the sexual liberation also took place, and no longer the sexuality was something to be frowned upon, rather became acceptable in its all-pervading variants including the LGBTQ. Homosexuality was no longer considered a criminal offense. This type of change wave later rippled throughout the world and still affecting the global society (Reiss 1964a).

Factors Affecting Premarital Sexual Permissiveness

Gender: Gender has always played an important part in sexual preferences and activities as in all the cultures of the world, there are certain gender roles prevalent among the male and female gender. This in turn affects their sexuality significantly (Cheng et al. 2012). Sexual permissiveness among males are found to be more liberal, and their willingness to engage in sexual behaviors was much more prevalent and acceptable (Cheng et al. 2012; Zuo et al. 2012). According to a study in Eastern Asia where the “Confucian” beliefs prevail, it was found that male to female premarital sexual permissiveness was significantly different as the stigma related to sexual promiscuity was prominent and women were expected to be faithful to their husbands

completely during life and even after death, whereas among the western countries in the permissive societies, women and men both had a more acceptable outlook toward premarital sexual relationships (Debnam et al. 2017).

Age

Age has been a very important factor in deciding sexual permissiveness. In a study of African American population, it was found that adolescent girls would prefer to be in relationships with older boys belonging to racially, ethnically, and socio-demographically matched households (Carver et al. 2003). As the onset of puberty has reduced, sexual activities have become a greater interest among the younger age groups. Even though the premarital sexual relationships are majorly found among the age group of high-school students and above, a study from China and Vietnam showed that more number of adolescents are being exposed to sexual behaviors due to access of the Internet and pornography, so the average age of sexual involvement is continuously lowering for both boys and girls showing increase in premarital sexual permissiveness among younger age groups throughout the world (Zuo et al. 2012).

Religious Beliefs

Religious beliefs have a very important impact on the sexual permissiveness among the unmarried people. The regions of East Asia show that females most prominently abstained from premarital sexual relations as they would break religious taboos, which might affect their social status and marriage-related prospects (Zuo et al. 2012). A study from Iran (Ghaffari et al. 2016) stated that premarital sexual activities occurred rarely as it was considered to be un-Islamic and sin, which also provides evidence for the high impact of the religious sentiments on the premarital sexual behaviors. Although the European societies are considered permissive societies, it was found that their closeness with the religion often had restrictive mind-sets compared to the liberal ones (Spercher and Hatfield 1996).

Media: According to a study (Lou et al. 2012), media plays a very important part in development of the sexual attitudes. It was also found that the

concepts about sexuality were mainly influenced by the media content they were accessing which was instrumental in developing the concept of sexual permissiveness before marriage (L'Engle et al. 2006). A study among the black and white American adolescents from middle school was conducted regarding the sexual content from the Internet, books,, magazine, television, and mass media. The results showed that the sexual content in those platforms influenced their behavior and perception intention and variances in sexual behaviors. The rates of premarital sexual behaviors have been increasing continuously in the East (Lou et al. 2012). The role of media is associated with it. These videos and ease of access to pornography and sexual content through various methods have exposed the adolescents with premarital sexual behaviors, and study also found that sexual experiences have become more and more common at younger age group with the ease of access to various mass media and the Internet.

Social Belief Systems

Social belief system has always played an important role in shaping the sexuality, regarding the acceptable and unacceptable behaviors. A study among the unmarried college students of American, Russian, and Japanese nationalities found that American people were more acceptable in terms of premarital sexual relationships compared to their Russian and Japanese counterparts (Spercher and Hatfield 1996). A study from Hanoi, Taipei, and Shanghai found that the impact of confusion cultural values was prominent in Hanoi, but among the people of Shanghai, social beliefs were found to be inversely proportional with premarital sexual permissiveness and had more chances of being exposed to such activities. A study from the Middle East suggests that the prominent Islamic belief systems influence the sexual permissiveness and majorly the unmarried men and women were less likely to engage in premarital sexual activities (Ghaffari et al. 2016). A study from sub-Saharan Africa shows that there is a great impact of social beliefs in making early reproductive decisions and they have a great impact on the overall society (Gaje 1996).

Knowledge About Health Risks

The knowledge about the health risks has always impacted the premarital sexual behavior. A study from India (Naik et al. 2005) found that the Tribal population of India was migrating toward the cities and due to their permissive cultures posed a greater risk of HIV and AIDS compared to the other city counterparts. A study from the developing countries states that the awareness about the sexually transmitted diseases was directly related to sexual permissiveness of people (Friedman 1992). The similar pattern of association was also found among the college students of developed countries as well (Friedman 1992; Spercher and Hatfield 1996). Among the Far Eastern countries, the knowledge about the sexual and reproductive diseases remained an associated factor governing the premarital sexual permissive behaviors among both genders (Zuo et al. 2012).

Perceptions of Gender Role Expectations and Traditional Norms

The variations among sexuality are very prominent among the genders and so are their roles. Similarly there is a great variation among the premarital sexual permissiveness among both the genders concerned. Studies throughout the world show that males are comparatively more permissive of sexual behaviors comparatively to their women counterparts (Friedman 1992; Hipwell et al. 2013). The Asian cultures are comparatively less permissive compared to the western cultures; here the variations are more prominent as the role expectations here are mainly passive and recipient of sexual behaviors and are least likely to initiate as per the cultural norms expected from them. Different behaviors from their side would end them being labeled in a derogatory manner (Cheng et al. 2012). Similar findings were also from another Asian study (Zuo et al. 2012).

The other important factors that influence the premarital sexual permissiveness are availability of gender-sensitive sex education (Zuo et al. 2012). This gives the adolescents the right kind of knowledge about the sexual behaviors and the safe sexual practices which will not physically or mentally harm them. The access to right socially sensitive sexual education can have a protective

effect on the premarital sexual permissiveness and behavior (Cheng et al. 2012).

Stigma: Most of the cultures throughout the world have observed that women who had openly stated their sexual desires were often stigmatized, and in less permissive societies, chastity has been considered as an important virtue among women; thus this has been a very important psychological determinant throughout the world among women to refrain from premarital sexual relationships (Debnam et al. 2017; Ghaffari et al. 2016; Zuo et al. 2012).

Area of residence: It has been observed throughout the world that urban and rural cultures have differences in their social structures and also influence the patterns of perception premarital sexual behaviors. There has been a significant difference among the people residing in urban and rural areas (Cheng et al. 2012; L'Engle et al. 2006; Naik et al. 2005).

Scales for Measurement of Premarital Sexual Permissiveness

Guttman had developed scales for measuring premarital sexual permissiveness at Iowa University. These scales were found to be very effective in measuring permissiveness and differentiating high permissive and low permissive groups and have many subsections which can be used for studying separate topics of research (Reiss 1964b). These scales are validated and studied in further literature after the 1960s. The scale is divided into sections: standards for men containing 12 items and standards for women (12 items section) and a feedback section. This scale has been widely accepted and adapted for.

Premarital Sexual Permissiveness Among Various Ethnicities

The studies of the 1960s found that the sexual permissiveness among the blacks and the whites varied considerably (Friedman 1992). The main factors found in low permissive groups of whites were church attendance and belief in romantic

love, and the permissiveness increased more with the number of love relationships, whereas among blacks these associations were not significant (Debnam et al. 2017; Zuo et al. 2012). There have been gender differences among the adolescents and young adults regarding premarital sexual permissiveness all over the world. A study from Asia reports that there are various factors influencing the behavior, and the main associated factors presented in the studies are the “Confucian Beliefs” (Cheng et al. 2012; Zuo et al. 2012). The Middle Eastern communities have also shown to have more restrictions among women compared to men as sexual relationships before marriage are not permitted among the Islamic culture although there were gender differences, which were similar to other Asian region communities (Ghaffari et al. 2016).

Conclusion

Sexuality plays a very important part in human life and is a necessary aspect of life; it's a process where we preserve the progeny that exists in the world.

A systematic review of sexual practices among the adolescents (Friedman 1992) states that with sexuality is an inevitable part of human life and exists in our instincts, and it plays an important part in human growth, development, and maturity. It is already known that adolescence is a period of great storms in one's life; it also marks the beginning of sexual maturity. New dimensions are created during this time of life sexually; it is marked by intense feelings and emotional turmoil. Complexity of relationship increases, which leads to drastic outcomes and consequences in terms of sexual behavior. These changes affect not only the individual but also their societies at large (Carver et al. 2003). The contemporary times the lives of adolescents are confronted with a great deal of challenges which has changed very drastically in the previous few decades. This change brings about various patterns of sexual behavior. These changes are not only in the external world but also impacting their biology the changing world has

brought about changes in their biology as well like earlier puberty, delayed marriage, increased focus on individuality and less control by family and more autonomy these can be attributed as some significant factors. Intense exposure to sexual stimuli via the mass media and the Internet gives access to everything on fingertips (L'Engle et al. 2006). Increasing globalization and diminishing cultural boundaries have led to increased premarital adolescent sexual activity. This has only added to traditional existing problems of early marriage. Newer problems of like early pregnancy, childbirth, and induced abortion outside of marriage are sexually transmitted diseases and human immunodeficiency syndrome infection leading to acquired immunodeficiency syndrome (Naik et al. 2005). Various studies have strongly recommended age-appropriate sexual education in diminishing the high-risk behaviors pertaining to premarital sexual permissiveness, such as increased trust, and responsible sexual behavior among both the sexes will minimize the impacts of premarital sexual behaviors as it cannot be completely prevented, as well as can be handled in a way which promotes minimal harm and maximal maturity among the people.

Cross-References

- Relationship Choices and Sexuality
- Sex Differences for Pursuing
- Social Dominance and Sexual Access
- Sociosexuality

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Premature Birth

- Preterm Birth

Premature Ejaculation

- Orgasmic Disorders

Premature Infants

- Low Birthweight and Preterm Infants

Prematurity

- Preterm Birth

Premeditated Homicide

- Homicide by Design

Premeditated Murder

- Homicide by Design

Premodern Language Capacity

- Protosyntax

Prenatal

► Early Stage of Brain Development at Birth

Prenatal Androgens

► Biology of Human Gender, The

Prenatal Development

► Fetus Development

Prenatal Environment, The

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Synonyms

[Fetal programming](#)

Definition

The period of development extending from conception to delivery. The influence of this environment on the developing fetus can lead to permanent alterations in psychological and physiological outcomes.

Introduction

The flow of resources between parent and offspring is unidirectional. Across species, parents are the arbiter of resources – mothers determine the amount of resources (i.e., calories) allocated to offspring from the moment of conception.

Conventionally, psychological research has focused on environmental influences during infancy and early childhood as critical determinants of a child's later mental and physical health outcomes. However, converging evidence from a variety of disciplines – e.g., biology, anthropology, medicine, and epidemiology – has found that environmental input received by a developing fetus during the period extending from conception to infancy (i.e., the prenatal environment) can have permanent imprints on an organism's physiological and psychological development. The impact of this recent research interest in “fetal programming” is widespread and has implications for numerous fields including evolutionary psychology.

Within developmental biology, research on the “developmental origins of health and disease” (DOHaD) has recently benefitted from a more explicit focus on evolutionary principles (Gluckman et al. 2007). The core of the DOHaD hypothesis is simple: conditions early in development, including in utero, can have an enduring impact on one's developmental outcomes and these early influences may affect susceptibility to illnesses and diseases with onsets that occur much later in life. Many of these changes are associated with alterations in gene expression (epigenetics) affecting the hypothalamic-pituitary-adrenal (HPA) axis – a system responsible for the transduction of environmental information (e.g., nutritional status, psychosocial stressors) into signals that an organism can use to direct developmental timing and tempo. In animal studies, epigenetic changes in the HPA axis activity are associated with permanent changes in adult behavior and stress responsivity (see Turecki and Meaney 2016 for review). Using the guiding principles of evolutionary theory, researchers have started to look at such early “calibration” as *adaptive* responses to environmental input (as opposed to strictly pathological).

Background

Contemporary research on the sizeable impact of the prenatal environment on adult outcomes has

its origins in the work of Barker and colleagues who reported that rates of heart disease in the United Kingdom were more closely linked to environmental conditions when patients were born rather than to their current environment (Barker et al. 1989). It was clear that maternal conditions in the prenatal period had a lasting impact on the emergence of later developmental outcomes. This early work focused on size at birth as a proxy for prenatal conditions. A number of studies link small size at birth (a consequence of constrained prenatal energy availability) with adverse effects on the risk of chronic diseases later in life. The cluster of chronic diseases associated with metabolic alterations and modifications of glucose metabolism are particularly implicated.

Despite the clear detriment of increasing one's propensity for chronic disease in adulthood, these metabolic changes might also have adaptive value to the developing fetus in the short term. For example, a deprived prenatal environment (i.e., restricted calories) might help calibrate a fetus to permanently develop a "thrifty phenotype" by being small and insulin resistant through the early postnatal period and into adulthood (Turecki and Meaney 2016). In turn, as an adult, the individual would be well suited to an environment in which nutrient supplies were limited as their metabolic machinery "fits" with that of a resource-scarce environment. However, this individual would be more likely to become unhealthy in a nutritionally *rich* environment – a scenario in which the postnatal environment is at a mismatch with the environment predicted from the prenatal period.

Prenatal Environment as a Forecast

This adaptive calibration of one's phenotype in response to environmental signals received early in development (i.e., in utero) is a hallmark of the concept of developmental plasticity. From an evolutionary perspective, costly alterations in early development can be viewed as normal, adaptive responses to challenging prenatal environments. Postnatal pathology arises when the cost-benefit

trade-offs with other components of fitness calibrate developmental trajectories that increase short-term survival at the cost of increased health complications and shortened lifespan in the long term. These costs may include low birth weight, preterm birth, heightened stress reactivity, early reproductive development, and early mortality. However, if paying these costs would have led (on average and across ancestral development) to an increased probability of reproducing in the harsh or unpredictable environments that require them, the deleterious impact on longevity would have been a small price to pay from the perspective of natural selection (Harpending et al. 1990).

While in utero, the fetus "senses" its future environment via signals from its prenatal environment, and development proceeds as an integrated response to those signals. Gestation can be thought of as a 9-month assay of environmental conditions. This period allows the developing organism to make predictive adaptive responses (PAR) that can improve the fit between its own phenotype and the anticipated levels of challenge and threat in the postnatal environment (Gluckman et al. 2007). The mechanisms of fetal programming can only be adaptive, however, if in utero conditions are indeed predictive (more often than not) of characteristics of the postnatal environment.

There are now several lines of evidence (predominantly from non-humans) that support the idea that the prenatal environment does calibrate one's development in line with what would be expected of a PAR. For example, if signals in the developmental phase suggest limited nutrient availability, the prediction is that the organism should adjust its developmental trajectory such that the individual has a metabolic profile better suited for survival in a calorically scarce environment. Female rats subjected to undernutrition during pregnancy gave birth to offspring that developed a metabolic phenotype showing increased appetite, insulin resistance, and reduced physical activity, particularly if they are fed a high-fat diet after weaning (Vickers et al. 2003). In this example, poor prenatal nutrition led to a PAR of a poor postnatal environment. In response, a calorically thrifty phenotype developed but in

reality the postnatal environment was nutritionally rich leading to increases in chronic diseases and obesity later in life.

Toward the end of World War II, a German blockade cut off all supplies of food and fuel to Nazi-occupied regions of the Netherlands. The resulting famine devastated the region but provided a natural experiment for researchers to investigate some of the lasting effects of widespread caloric shortages – particularly the effects of famine on pregnant women and their children. Susser et al. (1998) investigated whether some of the destructive developmental effects on children of the Dutch Hunger Winter were a consequence of famine exposure in utero and not just postnatal environmental insults. They found a significant elevation of risk of psychiatric disorders such as schizophrenia among those whose mothers went through the peak of the famine during (specifically) their second trimester of pregnancy.

Forecasting Mismatch. As stated above, when an organism's PAR is correct, there will be a good match between the phenotype adopted and the environment in which the organism will later inhabit. However, when the prediction is inaccurate, there will be a mismatch between the adult environment experienced and the phenotype induced in earlier development. From the DOHaD perspective, the greater the mismatch itself, the greater the risk for adult disease. Specifically, pathologies later in life may not arise as result of poor environmental conditions in adulthood per se but are instead the result of a phenotype that did not accurately anticipate key features of the adult environment such as resource availability and the levels of harshness or unpredictability.

Because forecasting mismatches carry costs, some researchers have proposed that gestation should not be the sole assay of environmental conditions. Kuzawa's (2005) intergenerational phenotypic inertia model provided some rationale for expecting the effects of the prenatal environment to last more than one generation. Intergenerational phenotypic inertia provides the fetus with information, not only about the environment into which it will inherit but the environment into which its mother was born, and

(possibly) back a number of generations. Intergenerational phenotypic inertia may allow the fetus to cut through the "noise" of stochastic environmental conditions and, in turn, offset some of the costs of forecasting mismatches that may occur within a single generation.

Parent–offspring Conflict

The logic of Trivers' (1974) parent–offspring conflict theory states that any investment by the mother in an individual offspring that increases its chance of surviving come at a cost of the mother's ability to invest those resources in other (existing or future) offspring. A fetus' best interests are served when it can increase maternal investment in utero beyond that of what a mother may willingly provide. Conversely, a mother's best interests (in an evolutionary sense) are served when investment in an individual fetus can be decreased to levels more in line with levels that meet the minimum required for that specific fetus' survival – a strategy that would allow a mother to reallocate resources to existing offspring or future fetuses. This disagreement about the optimal levels of investment in utero is a source of great conflict.

Haig and Trivers (1995), using the logic of parent–offspring conflict theory, developed a model of maternal–fetal interaction that makes specific predictions regarding which prenatal environments might demonstrate the greatest sources of conflict. As one example, Haig observed that the genes for insulin-like growth factor 2 (IGF-2) and the IGF-2 clearance receptor (both implicated in growth regulation across species including humans) are imprinted – that is, their expression depends on which allele (that inherited paternally versus maternally) is expressed in utero. IGF-2 is expressed in the fetus from the paternal allele and the receptor is expressed from the maternal allele. The fetus drives fetal growth under paternal influences (i.e., paternal allele of the IGF-2 gene expressed). However, under maternal influences, mothers attempt to *limit* fetal growth by clearing IGF-2 from the prenatal environment.

Under conditions with low/predictable mortality rates, mother and fetus can resolve this conflict by cooperating (each can afford to give a little more). Resources available to the fetus are increased and subsequent fetal growth and postnatal health are improved. However, under harsh and/or unstable conditions, conflict can be lethal for mother and/or fetus. If the fetus survives, the reduced investment in utero may predict postnatal health complications much later in life. The application of parent–offspring conflict theory to understanding the adaptive trade-offs at work in the prenatal environment is in its nascence but will be a fruitful area of discovery.

Maternal Stress and the HPA Axis

A mother's HPA axis responds to stress with higher levels of glucocorticoid (GC) hormones (i.e., cortisol in humans). The influence of maternal stress on the prenatal environment has lasting effects on offspring physiological and psychological development, and thus, the HPA axis is a major target of inquiry in recent work. Psychosocial stress affects development of the HPA axis and does so in adaptive ways by calibrating a range of reproductive strategies mediated by HPA axis activity from infancy to adolescence and throughout adulthood (Belsky et al. 1991). Because of the involvement of the HPA axis in behavioral responses, one should expect that the prenatal environment, potentially through permanent epigenetic modification of HPA axis function in utero, influence temperament, stress responsivity, and psychiatric outcomes postnatally.

Fetal exposure to GCs are essential for development but excess levels can be harmful. Between 10 % and 20 % of maternal GCs cross the placenta to the fetus (Seckl and Meaney 2006). Maternal cortisol has an impact on fetal development of the brain and central nervous system and overexposure to GCs in utero leads to modifications in adult behavior in across species. In humans, prenatal exposure to elevated maternal cortisol is associated with behavioral and emotional disturbances

during both infancy and childhood (Seckl and Meaney 2006).

Conclusion

Evidence that prenatal conditions can be important determinants of one's adult phenotype is persuasive. In addition to the implications for research on adult-onset chronic diseases, emerging evidence supports the notion that understanding the impact of the prenatal environment on development can also offer insight into the development of specific emotional and behavioral outcomes. Animal models suggest that even moderate influence of the prenatal environment may permanently affect adult stress reactivity and can help predict some of the variation in HPA axis responsiveness. It is clear that the time scale for thinking about the influence of the "early" environment on an individual's development has been pushed back into gestation (and possibly further). Research on the prenatal environment continues to be increasingly multidisciplinary. The integration of research on the proximate mechanisms of fetal programming (e.g., endocrine and epigenetic) with the powerful theoretical lens of evolutionary biology will undoubtedly provide novel insights into how and why development unfolds as it does from conception to adulthood.

Cross-References

► [Life History Theory](#)

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Prenatal Hormones

► [John Manning](#)

Prenatal Sex Steroids

► [Digit Ratio](#)

Prepuberal Gonadectomy

► [Music and Hormones](#)

Presence of Children

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Synonyms

[Mate choice](#); [Mate selection](#); [Prior relationships](#); [Stepchildren](#)

Definition

How and why the presence of children influences parental mate preferences.

Introduction

This section covers the questions, how the presence of children affects parental mate selection in a subsequent partner for a new relationship and how children are expected to actively manipulate their parent in their mate preferences for a subsequent potential stepparent.

How Parent's Age Influences Their Mate Preferences in a Subsequent Partner

The presence of children from prior relationships affects the mate selection for a subsequent relationship. As studies have shown, women's parental status is a robust predictor of lower remarriage probability. This effect is likely to be an effect of age. Individuals who remarry are about 10 years older than the mean age of people who marry for the first time. As a consequence, there are fewer eligible (i.e., unmarried) partners, resulting in declining remarriage rates. This effect is stronger for women, as men prefer even younger women as they grow older (Schwarz and Hassebrauck

2012). Thus, the pool of eligible partners for women is reduced far more than is the case for men. From the perspective of the prospective male partner, the presence of children demonstrates the fertility of the woman, but men should be reluctant to invest their resources in someone else's children. Men's parental status, however, does not reduce probability of remarriage, because their reproductive lifespan is longer than women's. Men prefer younger women as spouses and are more likely to acquire resources as they age (Ganong and Coleman 2004).

What Characteristics are Important in a Subsequent Partner?

Regarding specific mate preferences, finding a suitable stepparent who will not abuse or kill their children is especially challenging for women. The single best predictor of child abuse is living with a stepparent, even after controlling for confounds such as socioeconomic status (Daly and Wilson 1988). Children, younger than 2 years old, are much more likely to be killed when living with one stepparent and one genetic parent compared to children living with two genetic parents. Therefore, women are expected to be especially sensitive to a variety of characteristics in a potential stepfather, and they should shift their mate preferences relative to women without children (reviewed in Weekes-Shackelford et al. 2008). For example, women with children might place greater importance than women without children on finding a partner who is willing to invest in them and prospective children. Further, women with children should prefer potential stepfathers with good parenting skills to avoid the abuse of the children. Thus, emotionally stable and kind men should be especially favored by women with versus without children. Women with children, relative to women without children, for example, should lower their expectations on men's health, and especially their physical size and strength, because these cues might be perceived as a risk of abuse.

How Children Actively Manipulate Mate Preferences of their Parents for Prospective Stepparents

Finally, children are expected to actively manipulate mating decisions of their parents in prospective stepparents. From the child's perspective, a half sister or brother is only genetically related to 25 %, while the biological parent is genetically related to 50 % with her/his new child in this family. Thus, the child is expected to manipulate their parent in her/his mating decisions, e.g., by devaluing the prospective stepparent. Another strategy for children is to sabotage this new relationship by inflicting costs on the stepparent or on themselves which could drive the stepparent away. Some of these strategies are drug use, delinquent behaviors, or suicide attempts. Correspondingly, empirically living in a stepfamily (vs. living with two genetic parents) doubles the child's risk of engaging in delinquent behavior (Duntley 2016). It is hypothesized that the costs of a delinquent stepchildren deter the potential stepparent from this new relationship.

Conclusion

Currently, there is very few research about how the presence of children alter mate preferences (see also Goetz, *Mate Preferences After Having Children*), and much of the evidence presented here is rather indirect. Preferences for partners who are willing to invest and not abusing the children are likely to be more important in the presence of children, especially in mothers. Further, it is possible that children actively manipulate mating decisions of their parents in prospective stepparents. However, most of these predictions should be investigated more directly in the future.

Cross-References

► [Mate Preferences After Having Children](#)

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Presence of Siblings

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Synonyms

[Alloparents](#); [Brothers and sisters](#); [Kin](#)

Definition: Alloparents

Introduction

In every century, promoting siblings and sibling relationships has been an integral part of families, societies, and cultures. The portrayal of siblings in folklore, mythology, religious texts and stories, books, cartoons, TV shows, and movies has suggested a standard message to siblings and families, “United we stand, divided we fall.” perhaps because sibling relationships can be the most intimate, yet conflictual relationships (Bank and Kahn 1982).

Over the years, depending on the cultural and family values, the definition of who is a sibling and who is not has changed. Therefore, siblings can include, but are not limited to, biological siblings, half/step-siblings, in-laws such as sisters/brothers-in-law, adopted siblings, foster

siblings, cousins, milk siblings, i.e., children nursed by the same female, God siblings, i.e., children of the Godfather or Godmother, friends who are like siblings, neighbors’ children who have grown together like siblings, coworkers, and more.

Despite the ambiguity in whether someone can be addressed as a sibling or not, there is ample evidence to conclude that siblings contribute tremendously in shaping one’s life trajectory. Hence, it is no surprise that sibling relationships are considered one of the closest and most long-lasting relationships (Bank and Kahn 1982; Cicirelli 1982), and sibling support is crucial at every stage of development (Whiteman et al. 2011). For example, evidence suggests that perceptions of positive sibling relationships are associated with higher self-esteem (Barnes and Austin 1995) and can be the most significant predictor of an individual’s adjustment in later life (Vaillant and Mukamal 2001). Overall, the sibling subsystem, “is the first social laboratory where children learn to negotiate, cooperate and compete with each other” (Minuchin, 1976 as cited in Perricone et al. 2014, p. 529).

Presence of Siblings and Life Span Development

In most cultures, especially with high maternal mortality rates, female kin members such as grandmothers, aunts, and sisters are often substituted as allomothers. In the absence of grandmothers and aunts, older sisters of newborn infants are intuitively considered “helpers at the nest” who assist their mothers in taking care of their younger siblings and household chores (Weisner et al. 1977). Notably, in cultures with high maternal and infant mortality rates, the presence of older sisters can significantly lower infant mortality rates (Sear et al. 2002).

Paradoxically, even in developed countries with lower maternal mortality rates, older siblings can be seen as an attachment figure (Ainsworth et al. 1978), a transitional object (siblings can use one another to make the transition away from the mother) or may help to support object relations (psychological processes that all people use early

in life to create internalized images of the self and other people) (Bank and Kahn 1982). Older children gain future life skills by interacting with their younger siblings, and younger siblings gain cognitive skills by imitating the older ones (Teti 1992). The mutual exchange of support and enhancement of skills in the early years may promote attachment, warmth, and the connection between siblings (Furman and Buhrmester 1985).

Over the adolescent years, sibling conflict increases (Brody et al. 1994), and sibling relationships may seem more autonomous, distant, and less emotionally intense (Cole and Kerns 2001; Scharf et al. 2005) as siblings try to act differently – aka sibling de-identification (Steinberg 2011). Nevertheless, positive sibling interactions still contribute to adolescents' academic competence, sociability, autonomy, and self-worth (Kim et al. 2007). In addition, higher perceptions of closeness with siblings were found to be linked with lower substance use (Samek and Rueter 2011). In minority families and collectivistic cultures, cultural norms may determine the implicit rules of the relationship and expectations (Cicirelli 1994) resulting in interdependence on each other. For instance, among African American families, reliance on siblings for support continues during the teenage years and caregiving responsibilities of younger brothers and sisters may promote resilience and the development of cultural identity (McHale et al. 2007).

In adulthood, siblings may serve as confidantes, teachers, role models, and friends and may provide help and support (Cicirelli 1982). Many adults continue to define themselves and measure their success in comparison to their siblings (Connidis and Campbell 1995; Milevsky 2005). Although professional and personal commitments may restrict frequent meetings with siblings, communication between siblings becomes meaningful and warm (Hamwey et al. 2019). Since the understanding between siblings grows stronger in comparison to the teenage years, sibling relationships are more intimate and less conflictual and can be a vital resource to fall back to at the time of traumatic life events such as divorce (Spitz and Trent 2018) or death of a parent (Kalmijn and Leopold 2019).

In older years, being the longest survivors of the family of origin, siblings become a valued repository of family memories and partners in shared reminiscence (Cicirelli 1982), and many may seek dependence on same-sex siblings for caregiving and support, with whom they have grown old with time (Mathur 2015). This dependence on siblings for caregiving and support during the older years may result in the resurfacing of any emotional conflict/emotional baggage from the early years carried by the caregiver (Bedford 1989).

It is important to state here that sibling caregiving is not limited to older years. Saxena et al. (2019), found that caregivers of individuals with disabilities were mostly younger adults, in their 20's, 30's and 40's. Moreover, the duration of caregiving provided by these sibling caregivers was reported to be equivalent to a part-time job.

Conclusion

The presence of siblings plays a vital role in the development of individual outcomes. Even though the definitions of siblings may vary in families and cultures, sibling relationships, for better or for worse, offer a unique opportunity to practice other relationships in a low-stake home environment. Besides, siblings shared history and environment, and lifelong commitment to supporting each other makes the relationship invaluable.

Cross-References

- [Full Siblings Versus Half Siblings](#)
- [Higher Survival with Older Siblings](#)
- [Siblings](#)

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Prestige

- Dominance and Health
- Dominance and Testosterone
- Dominance in Humans
- Facial Width to Height Ratio and Dominance
- Function of Dominance
- Higher Status in Group
- Indicators and Correlates of Status and Dominance
- Reputation
- Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?
- Status Competition and Peer Relationships in Childhood

Prestriate Visual Cortex

► Visual Association Cortex

Pretense

► False Beliefs

Preterm Birth

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Synonyms

Gestation; Premature birth; Prematurity; Preterm labor

Definition

Preterm birth is defined as babies born alive before the completion of 37 weeks of pregnancy.

Introduction

Preterm birth (PTB) is the leading cause of death in children under five worldwide and its complications are responsible for the deaths of approximately one million children annually. Babies born too soon are predisposed to suffer from neurodevelopmental, respiratory, gastrointestinal, and other complications throughout their lives. Both heritable and environmental risk factors contribute to PTB, and although PTB can be associated with medical disorders such as preeclampsia or intrauterine growth restriction, most cases of PTB occur spontaneously and lack an obvious

cause. Ultimately, why spontaneous PTB occurs in humans remains largely a mystery, but important clues can be found in the evolution of the traits and trade-offs that have shaped human pregnancy.

The Burden of Preterm Birth

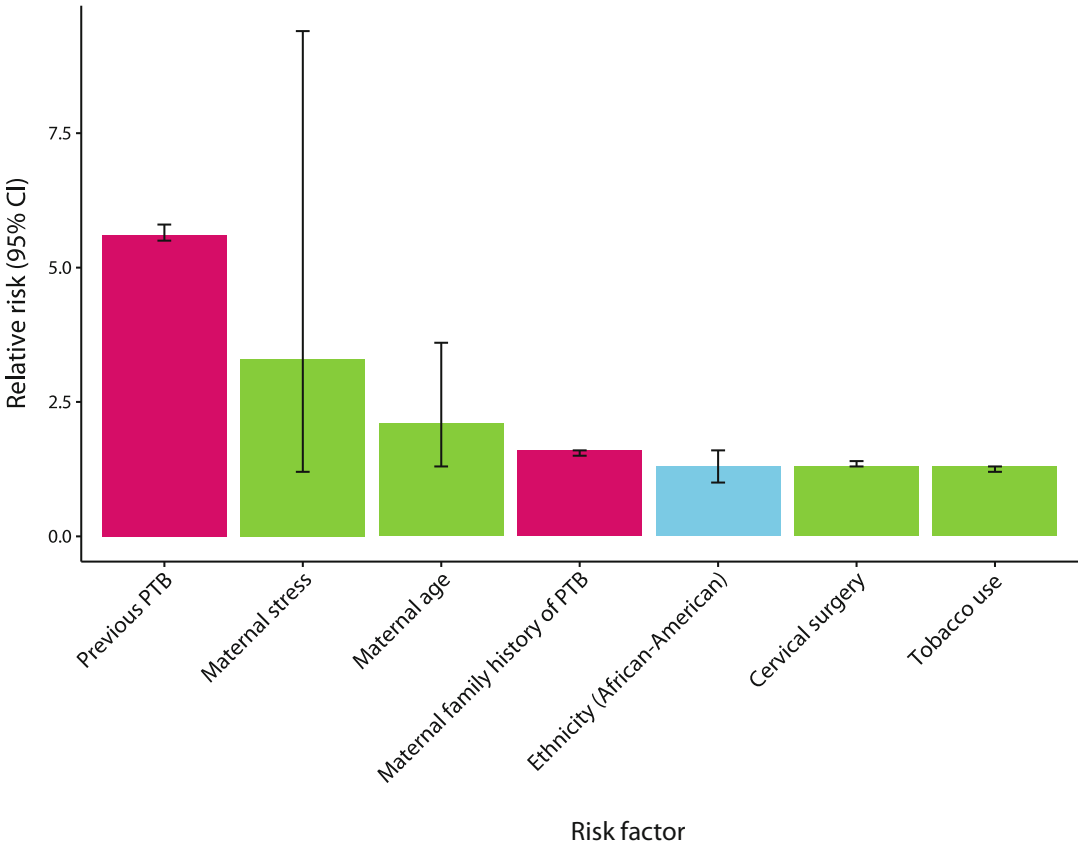
PTB is a complex, multifactorial syndrome associated with multiple mechanisms of disease and many causes (Goldenberg et al. 2008; Muglia and Katz 2010; Romero et al. 2014; Vogel et al. 2018). Generally defined as birth before 37 weeks of gestation or 259 days since a woman's last menstrual period (Vogel et al. 2018), PTB can be caused by: (1) the medically indicated induction of preterm delivery due to either maternal or fetal complications, (2) preterm premature rupture of membranes (PPROM), or (3) spontaneous, idiopathic preterm labor with intact fetal membranes (sPTB). Approximately, a third of all preterm births are medically indicated due to preeclampsia (PE), intrauterine growth restriction (IUGR), gestational diabetes mellitus (GDM), chorioamnionitis, or other complications. Of primary concern for reducing rates of prematurity is understanding the causes of the remaining two thirds of preterm births occur in the absence of any obvious risk factors (Goldenberg et al. 2008; Vogel et al. 2018). PTB is a global problem with rates that range as high as ~18% in low-income countries to lower rates in high-income countries (~5%) (Blencowe et al. 2013), and a global prevalence around 10% (Vogel et al. 2018).

Efforts to reduce the rates of PTB have only met with mixed success. In the United States, for example, the rate of preterm birth has increased by 30% since 1981, reaching its peak at 12.5% in 2006, with the rate currently reported at 9.6% (Blencowe et al. 2013). Recent estimates indicate that complications of PTB are the leading causes of death of children below 5 years of age globally (Vogel et al. 2018). In what follows, we summarize some of the risk factors associated with PTB, and then address more ultimate questions about why variation in birth timing might occur in the

first place, which requires that we take an evolutionary perspective on birth timing. There are many reviews that discuss what is known about preterm birth from more molecular, clinical, and obstetrical perspectives, such as Goldenberg et al. (2008), Romero et al. (2014), Swaggart et al. (2015), Di Renzo et al. (2018), Strauss et al. (2018), and Vogel et al. (2018).

In one comprehensive review, Romero et al. (2014) summarized the growing consensus that PTB does not represent a single disease, but a syndrome with many causes. The causes of the PTB syndrome are complex with multiple genetic and environmental risk factors at play (Fig. 1). Epidemiological studies have linked poverty, education, age, body mass index, marital status, prenatal care, rates of multiple births, tobacco use, and other factors with PTB incidence

(Goldenberg et al. 2008). A particularly important risk factor for PTB is intrauterine infection: about one out of every four pre-term births is associated with infection (Romero et al. 2001). Intrauterine infections can cause PTB by activating the innate immune system and triggering the release of inflammatory proteins, such as cytokines and chemokines, that can lead to premature labor (Goldenberg et al. 2008). Maternal medical conditions that have been shown to increase PTB risk include thyroid disease, asthma, hypertension, diabetes, periodontitis, a history of prior preterm birth or cervical loop procedures, and depression (Goldenberg et al. 2008; Cobb et al. 2017). Finally, PTB risk has also been shown to be associated with maternal age, and women under 20 and over 40 are more likely to deliver preterm (Boardman 2008).



Preterm Birth, Fig. 1 PTB risk factors. Risk factors for PTB stem from genetics (pink), environmental stress (green), and ethnicity (blue). Redrawn from Bezold et al.

(2013) where relative risk and confidence intervals were obtained from previous independent PTB risk studies applying a variety of methods

There is clearly a role for genetics and epigenetics in PTB risk (York et al. 2014; Monangi et al. 2015; Strauss et al. 2018). Twin studies have demonstrated both maternal and fetal genetic contributions to PTB risk, with heritability estimated between 15% and 40% (Clausson et al. 2000; Treloar et al. 2000; Kistka et al. 2008). More recently, York et al. (2014) summarized the contribution of fetal (11–35%) and maternal (13–20%) genetic factors based on European and European-American datasets. A woman's risk of delivering preterm is increased if her mother, full sisters, or maternal half-sisters have delivered preterm (Boyd et al. 2009). PTB risk also differs between ethnic groups. For example, the PTB rate among black women in the United States is twice as high as the rate among white women, even after adjusting for other confounding factors (Adams et al. 1993; Collins et al. 2007; Kistka et al. 2007). Conversely, East Asian and Hispanic women have relatively low rates of PTB, whereas South Asian women have increased risk of low birth weight with no connection to PTB risk (Goldenberg et al. 2008). The factors contributing to the observed racial disparities in PTB rates remain unresolved, and although some of the racial disparities in PTB rates are likely to be genetic, both novel environmental risks and epigenetic factors may play important roles (York et al. 2014; Barcelona de Mendoza et al. 2017).

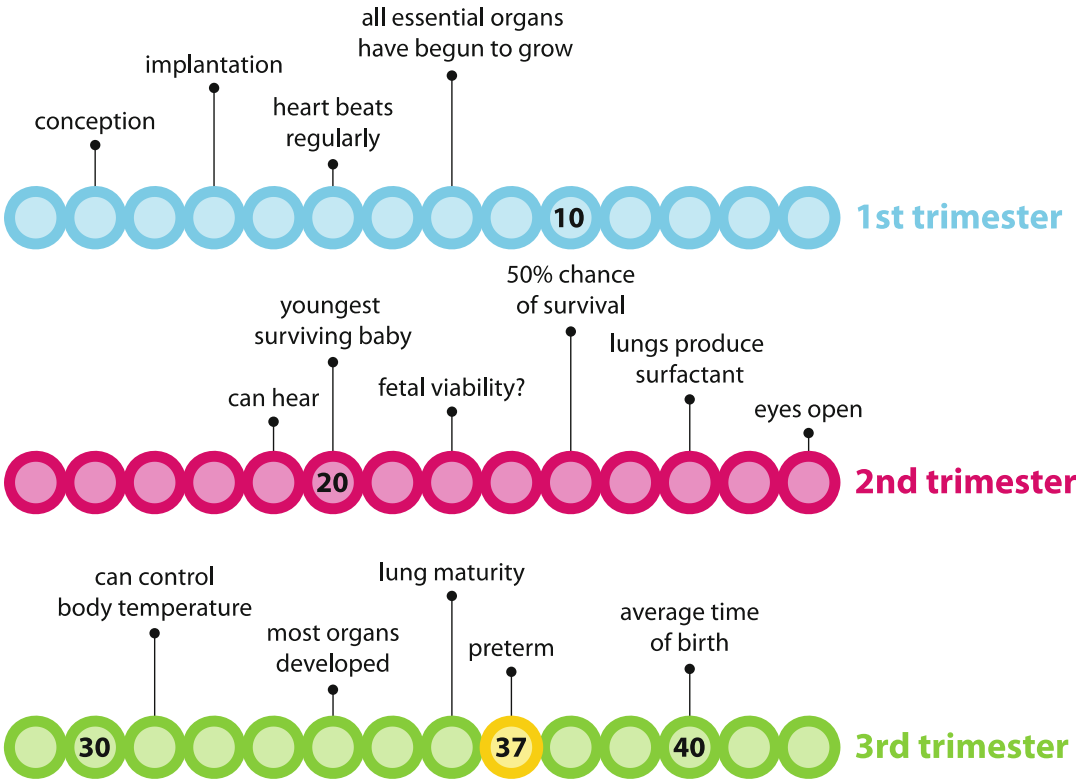
Not much is yet known about identifying the genetic variants that contribute to PTB risk, because most of the variants that have been discovered have either yielded conflicting results or have failed to be replicated (Strauss et al. 2018; Vogel et al. 2018). In a recent exciting development, Zhang et al. (2017) performed a genome-wide association study that led to the reliable identification of variants in six loci (*EBF1*, *EEFSEC*, *AGTR2*, *WNT4*, *ADCY5*, and *RAP2C*) that were significantly associated with gestation length and of variants in three loci (*EBF1*, *EEFSEC*, and *AGTR2*) that were significantly associated with PTB, opening the door for functional studies that shed light into the molecular mechanisms underlying PTB.

Long-term cohort studies have been particularly important in understanding the consequences of

low birth weight and preterm birth for adolescents and adults. An important longitudinal dataset known as the Helsinki Birth Cohort Study (HBCS) has provided many insights. The HBCS comprised 13,345 subjects from 1933 to 1944 with associated metrics that span prenatal to adult life. Another study that is beginning to yield results is the Born in Guangzhou Cohort Study, which has been tracking 33,000 Chinese babies and mothers since 2012. Data derived from the HBCS have provided important insights into the origins of disease in early life, including how low birth weight and premature birth increase risks of a variety of adolescent and adult diseases (Thornburg and Marshall 2015; Cyranoski 2018). Finally, some risk factors for PTB overlap with other inflammatory diseases such as inflammatory bowel disease or periodontitis, indicating strong gene x environment interactions that perturb general physiological and immunological processes involved in women's health (Strauss et al. 2018).

Clearly, many risk factors have been identified for PTB, but PTB remains disturbingly common. The majority of preterm births occur without any obvious risk factor and most risk factors are only weakly associated with PTB. Despite decades of effort, rates of PTB remain remarkably high or on the increase in many regions in the world, with variable patterns and etiologies that defy easy explanation (Byrnes et al. 2015; Vogel et al. 2018). One of the fundamental challenges in mitigating the risk of PTB is that the distinction between normal labor and prematurity is likely extremely subtle, and common pathways are at work in each (Romero et al. 2006). (Fig. 2). In the case of normal term labor, parturition is the result of complex uterine and extra-uterine factors (e.g., hormones) that physiologically activate “parturition complex cascade” (Di Renzo et al. 2018). In the case of premature labor, these same factors are disrupted, and as Romero et al. (2006) put it, are activated in a manner that can be described as “extemporaneous.”

This implies that understanding human gestation timing and PTB is tantamount to understanding not only human pregnancy but because pregnancy research involves animal models,



Preterm Birth, Fig. 2 Human pregnancy timeline. Normal human pregnancy lasts approximately 40 weeks. Delivery is considered preterm before 37 completed weeks of gestation

mammalian pregnancy more generally (Carter 2007; Phillips et al. 2015; Swaggart et al. 2015; Eidem et al. 2017). This is an enormous task, and the challenge of resolving PTB is entangled in the remarkable complexity of pregnancy itself. For example, pregnancy is the only physiological process where the cells of two genetically distinct individuals of the same species come into such prolonged and intimate proximity. In order to succeed, it requires elaborate physiological cooperation and coordination between mother and child, under conditions that range from the adverse to benign. Unexpectedly however, pregnancy is riddled with indications of difficulties and conflict. Less than 50% of conceptions result in pregnancy in humans, a rate higher than other mammals (Macklon and Brosens 2014). More dramatically, pregnancy remains one of the leading causes of female mortality worldwide. In

2013, the United Nations and World Health Organization estimated that a woman died about every 2 min from causes related to pregnancy or childbirth (Say et al. 2014). Although there are diverse causes, chief among them are excessive bleeding after childbirth, high blood pressure during pregnancy (pre-eclampsia and eclampsia), and difficult childbirth (Say et al. 2014), much of this can be pinned on (1) the deeply invasive nature of placentation in humans, and (2) the unusually large size of encephalized fetus at birth. As described in more depth below, both have important implications for understanding birth timing in humans (Rosenberg and Trevathan 2002; Dunsworth and Eccleston 2015). The common pathways that underlie pregnancy and PTB, and the unique features of human pregnancy, mean that understanding PTB requires a broad consideration of the evolution of pregnancy itself.

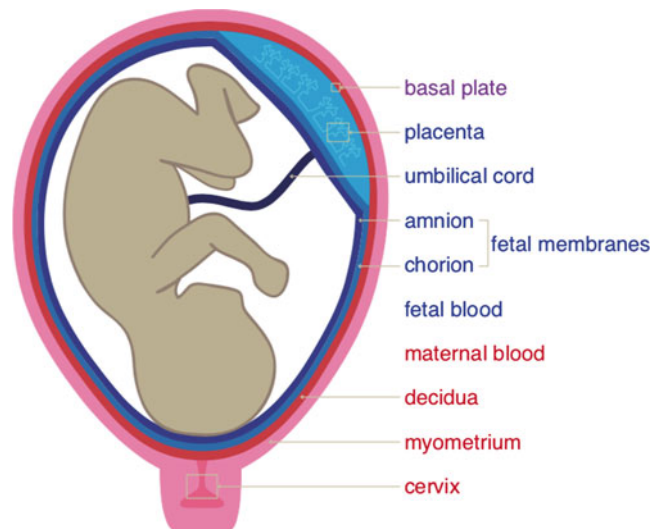
Human Pregnancy, in Brief

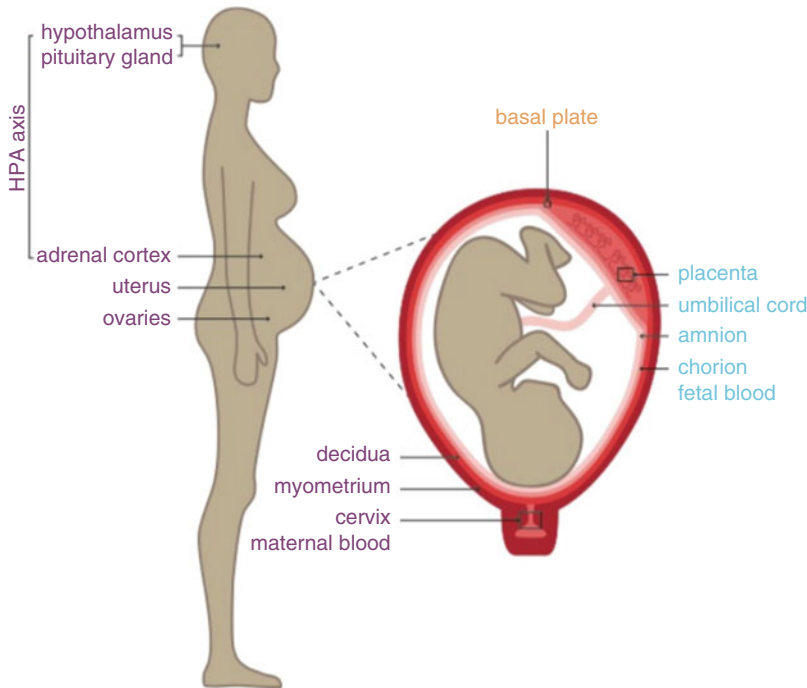
Humans are viviparous mammals – they have live birth. Live birth is not unique to humans or to mammals, however (Abbot and Rokas 2017). Viviparity has evolved over 150 times independently in vertebrates alone and occurs in invertebrates as well (Blackburn 2014; Wagner et al. 2014). Viviparity requires the development of means to nourish developing embryos and channel waste products away within the mother's body, and all eutherian mammals express *placental matrotrophy* – embryonic provisioning by maternal secretions by way of a transient, vascularized organ that attaches to the endometrial lining of the maternal uterus known as the placenta (Trexler and DeAngelis 2003; Fig. 3). In eutherian mammals, the placenta accomplishes many of the fetal functions performed by the major organs in newborns, including exchange of oxygen and carbon dioxide, the secretion of endocrine, growth factors, and cytokines, and the transport of nutrients and elimination of wastes (Burton and Fowden 2015; Nelson 2015). The eutherian placenta also has important endocrine functions as well, modulating maternal metabolism and the immunological response to pregnancy, while maintaining uterine quiescence (De Bonis et al. 2012). The centrality of the placenta is highlighted by the fact that, in the very

first days following fertilization, the majority of embryonic cells in the growing blastocyst are placental (Norwitz et al. 2001). The *chorioallantoic* placenta of eutherians is so-called because, soon after the blastocyst implants into the uterine wall, the fetal membrane that forms the embryonic bladder and stores fetal excretions, or allantois, fuses with and vascularizes the chorion, the outermost membrane involved in gas exchange that surrounds the embryo (Fig. 4).

Following conception, implantation of the blastocyst in the uterine endometrium involves penetration by the embryonic trophoblast (the precursor to the placenta) onto the uterine endothelial cells (Schlafke and Enders 1975). In most mammals, blastocyst implantation is shallow and superficial, and six tissue layers separate maternal and fetal blood (Gundling and Wildman 2015). In some however, including humans, the blastocyst embeds deeply and is engulfed interstitially by the maternal endometrium. Placental traits widely vary between mammalian groups (Martin 2008). In the *hemochorial* placenta of primates, rodents, and bats, the placental trophoblast cells invade the uterine lining, eroding and remodeling vascular tissues, facilitating the bathing of placental villi in maternal blood (Gundling and Wildman 2015; Burton et al. 2016). In humans, placentation is particularly invasive, and the remodeling of maternal blood vessels is exaggerated (Burton

Preterm Birth, Fig. 3 The tissues of pregnancy. Note that some tissues are of maternal origin (cervix, myometrium, decidua, and maternal blood; shown in red), others are of fetal origin (fetal blood, fetal membranes, umbilical cord, and placenta; shown in blue), and one is of mixed maternal and fetal origin (basal plate; shown in purple)





Preterm Birth, Fig. 4 Pregnancy uniquely requires communication and coordination across multiple tissues in two individuals. Multiple maternal tissues (written in purple font) and fetal tissues (blue) as well as tissues comprised of both maternal and fetal cells (orange) must interact to facilitate a healthy pregnancy. The placenta serves as the nexus of communication that links multiple tissues in the mother and fetus both locally and at a distance. For

example, interactions between NK cells in the decidua and fetal trophoblast cells in the placenta shape the degree of placental invasiveness and rate of the exchange of nutrients and oxygen. Similarly, the hypothalamic–pituitary–adrenocortical (HPA) axis communicates maternal and fetal stress levels across multiple tissues through cortisol shared through blood exchange in the placenta

et al. 2016). When maternal arterial remodeling is poor, reduced uteroplacental arterial flow to the placenta is followed by a cascade of potential consequences in response to fetal signals of distress, including inflammation, hypertension, kidney damage, and proteinuria in the mother, and an increase in oxidative stress and spontaneous PTB in the fetus, with a poor prognosis for both mother and fetus if untreated, and potentially life-long consequences for survivors (Redman and Sargent 2005; Thornburg and Marshall 2015). On the other end of the spectrum, the leading cause of maternal mortality is postpartum hemorrhaging (PPH), which results from improper separation of the placenta from the uterine wall, leading to massive maternal blood loss (Abrams and Rutherford 2011). PPH rarely occurs in mammals, and the degree with which it occurs appears

unique to humans (Abrams and Rutherford 2011). Abrams and Rutherford (2011) summarize evidence that suggests that PPH results from an overly aggressive placental invasion and vascular remodeling of maternal tissues, increasing the chances of impaired separation. Preeclampsia and PPH are but two of many disorders of pregnancy resulting from improper placentation, and as discussed further below, evolutionary perspectives provide unique insights into the factors that have led to the delicate maternal/fetal balance, and the complexities of birth timing (Abrams and Rutherford 2011; Thornburg and Marshall 2015).

Parturition involves a transition in the maternal myometrium from a state of anti-inflammatory quiescence to a pro-inflammatory contractile state. How this is accomplished varies

across mammals, but generally involves dynamic interactions between pro-inflammatory prostaglandins and the inflammation-suppressive effects of the steroid hormone progesterone (P4) (Swaggart et al. 2015). In humans, apes, and monkeys, P4 production is high throughout pregnancy and acts to repress pro-inflammatory genes. Towards the onset of parturition, increased expression of microRNAs (miR-200 family) induce functional progesterone withdrawal, the de-repression of inflammatory chemokine and cytokine pathways, and the production of contraction-associated proteins such as oxytocin and prostaglandin receptor (Di Renzo et al. 2018). Cervical ripening and changes in maternal inflammatory/proteolytic factors in decidual and uterine membrane mark the withdrawal of decidual support for pregnancy, culminating in membrane rupture and the onset of vaginal birth (Di Renzo et al. 2018). Preterm birth involves congenital or acquired agents that distort or disrupt this common template.

With respect to the evolution of pregnancy, there are two key trends. First, pregnancy-related genes and phenotypes have changed dramatically fast over evolutionary time and have often evolved independently, giving rise to convergence (Wildman et al. 2006; Wildman 2011; Wagner et al. 2014). The high evolutionary rate and convergence make studying the evolution of human pregnancy particularly challenging, because similarity in pregnancy phenotypes among distant relatives cannot be assumed to reflect the ancestral phenotype. For example, hyraxes, like humans, have highly invasive placentas, whereas elephants and lemurs have noninvasive ones, even though humans and lemurs are closer relatives to each other than to hyraxes and elephants (Wildman et al. 2006). Equally, there is variation in endocrine patterns as well. Levels of the hormone progesterone rise throughout gestation in humans and the great apes, but not in closely related Old World monkeys, nor in other mammals generally (Carter 2007; Grigsby 2016). What these patterns indicate is that even close evolutionary affinity cannot be used to infer similarity in phenotype (Swaggart et al. 2015).

Evolutionary Perspectives on Birth Timing in Humans

The persistence of complex heritable diseases like PTB that causes reproductive deficiencies or even untimely death is paradoxical, because these diseases seem to favor their own demise (Brown et al., 2013). Why is there heritable variation in birth timing in humans? Evolutionary perspectives on medicine are predicated on the idea that human diseases emerge out of the evolutionary challenges inherent to fitting complex biological systems to diverse and shifting optima (Gluckman and Hanson 2006; Nesse et al. 2012; Stearns and Medzhitov 2015). Nesse et al. (2012) outline six broad and interrelated categories of evolutionary explanations for traits that predispose humans to noncommunicable diseases. We highlight three of these for PTB. The first is **mismatch** between our biological legacy and our modern environments, as in the case of diaper rash (Gluckman and Hanson 2006; Corbett et al. 2018). Mismatch between our biological designs for ancestral environments and modern lifestyles accounts for many common diseases such as obesity, addiction, diabetes, or heart disease. Disruption of normal pregnancy may reflect a mismatch between our modern lifestyles and our biological designs. A second explanation, related to evolutionary constraints, is that of **trade-offs**, the idea that there are combinations of traits that cannot be simultaneously optimized by natural selection (Ricklefs and Wikelski 2002; Stearns and Medzhitov 2015). For example, many fitness-related traits draw on common energetic reserves, and investment in one comes at the expense of the other (Zera and Harshman 2001). An example is large body size, which may improve survival, but comes at the expense of numerical investment in reproduction. Finally, a third explanation is that of **evolutionary conflicts**. All multicellular organisms are aggregates of genes, cells, tissues, and organs; natural selection can act differently on any individual member or level, giving rise to evolutionary conflicts (e.g., a mutation that may favor cell division and propagation of the gene that carries it may not be advantageous for the tissue or organ, as in cancer) (Queller and Strassmann

2018). Conflicts over pregnancy may be particularly acute in humans, because of the invasive nature of placentation and that natural selection can act differently in parents versus offspring. Below, we consider each of these explanations in more depth.

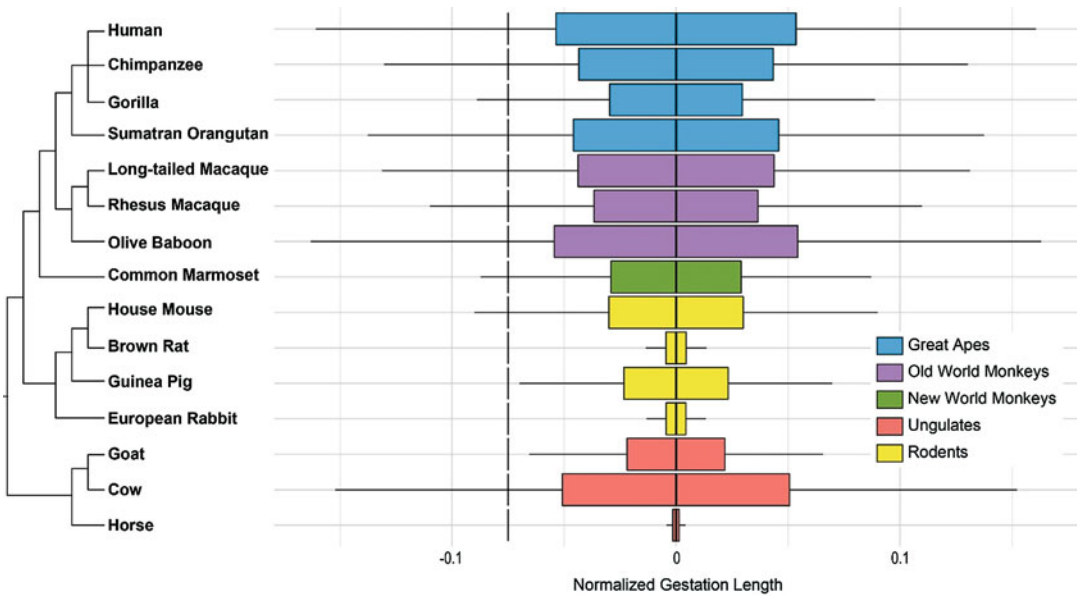
Mismatch and PTB

Some environmental influences on birth timing, such as tobacco use, represent modern causes of PTB that can be thought of as mismatches between the conditions our pregnant bodies were designed for, and the ones that our modern lives too often provide (Crump et al. 2011; Corbett et al. 2018). Many environmental risk factors probably fall in the category of causes that almost certainly emerged within modern times, and to which humans are poorly adapted. For mismatches that affect the outcome of normal pregnancy, there should be selection for traits that protect against maternal or fetal harm. Indeed, there is evidence not only that humans have experienced on-going natural selection on pregnancy-related traits but evidence of population-specific variation as well (Brown et al. 2013). An illustrative example can be found in preeclampsia (Ben et al. 2016). Modern changes in diet and nutrition may be a source of “mismatch” between contemporary diets and maternal physiological adaptations for pregnancy. Risk for preeclampsia varies inversely with salt intake, and paradoxically, rates of preeclampsia are low in countries such as Japan and Iran, where salt-intake is high (Brown et al. 2013). Brown et al. (2013) suggest that women in high salt-intake countries may have experienced selection for insensitivity to high-salt diets, conferring some protection against preeclampsia. In the absence of such insensitivity, the high-salt diets characteristic of Western societies represent evolutionary mismatches with potentially severe consequences for affected pregnant women. Like preeclampsia, PTB also exhibits population-specific, ethnic and racial variation similar to preeclampsia, raising the hypothesis that mismatches contribute to its high incidence.

One intriguing pattern is that it is not clear whether several of the known, important environmental risk factors for PTB, such as maternal

nutrition and stress, represent entirely modern perturbations of pregnancy. In a meta-analysis of 78 studies on maternal body mass index (BMI), Han et al. (2010) showed that low maternal BMI was associated with increased risk of both PTB and low birth weight. Likewise, in a systematic review of 39 studies, Staneva et al. (2015) concluded that psychosocial factors, such as maternal stress during pregnancy, can have a profound effect on birth outcomes. Glucocorticoids increase towards the end of pregnancy and are important for maturation of fetal organs. However, maternal stress can elevate glucocorticoids, which cross the placenta and result in reduced fetal growth rates (Thornburg and Marshall 2015). There is also evidence of racial differences in stress-induced inflammatory responses that are linked to PTB risk (Christian et al. 2013). In animal models, both nutrition and stress have adverse effects on birth outcomes. In rodents for example, various forms of stressors, from hypoxia to social stress via dominance interactions with conspecifics, can result in reduced litter sizes, smaller birth weights, selective reabsorption/abortion of fetuses, and various alterations of fetal developmental programs with adverse postnatal effects in offspring (Brunton 2013). While the mechanisms underlying these effects are not fully understood, conserved elements of the vertebrate neuroendocrine systems that regulate response to stress (e.g., the hypothalamo-pituitary-adrenal or HPA axis) are centrally involved.

That adverse pregnancy outcomes could display such sensitivity to environmental variation, mediated by broadly conserved vertebrate stress responses, has led to various evolutionary hypotheses that propose adaptive maternal/fetal mechanisms for inducible plasticity in birth timing (Gluckman and Hansen 2006). Plants and animals can alter phenotypic traits in response to environmental cues, a phenomenon known as *phenotypic plasticity*, and this can happen not only in adults but over the course of development as well (Via and Lande 1985). Crespi and Denver (2004) draw on abundant evidence for phenotypic plasticity in animals, encoded by conserved genetic and physiological mechanisms that predate modern human origins, to propose that at least some of the



Preterm Birth, Fig. 5 Within species variation in gestation length among representative primates and mammals. Boxes denote the range of values encompassed by 1 standard deviation from the mean in either direction; whiskers

extend to 3 standard deviations. The dotted line corresponds to 92.5% completed gestation time. (References for each species' data can be found in Phillips et al. (2015))

variation in birth timing in humans might reflect similar plastic responses to environmental input. Indeed, variation in birth timing is the rule, not the exception, in animals (Phillips et al. 2015) (Fig. 5). The mammalian HPA axis matures during the third trimester in humans, with a rise in stress hormones that regulate fetal development and prepare the maternal and fetal membranes for parturition (Crespi and Denver 2004). The months leading up to parturition are characterized increasingly by a finely-tuned period of stress sensitivity. In this view, both maternal and fetal fine-tuning of the rate of fetal development and/or parturition in response to such factors as nutrition or stress might reflect a form of adaptive plasticity in birth timing. To the extent that pregnancy is costly and that its costs vary with external conditions, maternal and fetal mechanisms may be present for navigating the course of pregnancy in a way that minimizes those costs, especially in conditions in which pregnancy outcomes are uncertain (McLean et al. 1995; Wells 2003; Pike 2004). Haig (2008) has suggested that mother and fetus may differ in plastic adjustments to gestation

length, depending on environmental conditions. Romero et al. (2014) make a similar point, that PTB in response to intra-amniotic infection likely has some survival value for both fetus and mother. Thus, it seems reasonable to hypothesize that some adverse birth outcomes, including some cases of PTB, may be due to mismatch between conditions that alter the maternal microbiome and birth outcomes (Chu et al. 2018). The major etiological roles of vaginal, intrauterine, and periodontal infections in PTB, and the organizing role of maternal inflammatory/immunological responses in pregnancy and labor, strongly implicate a microbial x environment interaction in pathologies of pregnancy. Indeed, four of the loci identified by Zhang et al. (2017) with variants conferring risk for gestation length or PTB, two (*EBF1* and *EEFSEC*) likely are involved in inflammatory pathways, albeit indirectly (Romero et al. 2006; Strauss et al. 2018).

In summary, an evolutionary restatement of the “common pathway” hypothesis for PTB could be as follows: PTB is the result of a mismatch between ancient, conserved biological

mechanisms for orchestrating of birth timing in viviparous mammals in response to once-reliable cues that are now absent or miscalibrated by modern lifestyles.

Trade-Offs and PTB

Evolutionary anthropologists have long hypothesized that two human traits interact to determine birth timing (Trevathan 2015). One is our big brain size, which has resulted in remarkably encephalized infants at birth relative to other primates. The other is our bipedalism, which has resulted in the remodeling of our pelvic girdles to accommodate our upright stance. Trade-offs and constraints lie at the root of a branch of evolutionary biology known as *life history theory* (Zera and Harshman 2001; Ricklefs and Wikelski 2002; Roff and Fairbairn 2007). Life history traits are those that characterize the patterns of organism survival and reproduction, such as age at first reproduction and body size. A tenet of life history theory is that these traits are interrelated and often negatively correlated. Large body size may increase offspring survival probabilities, for example, but it comes at the expense of risking dying before reproducing, since large bodies take longer to build. Natural selection is assumed to act on life history traits collectively, as if they each were constrained by the competing demands of the others, and the solution is a compromise.

With respect to birth timing in humans, one leading hypothesis, known as the *Obstetric Dilemma* (OD), is that gestation length is governed by a trade-off between brain size and pelvic proportions, and occurs at the point at which the head of a big brained fetus can barely fit through the narrow pelvic girdle of a bipedal-adapted female (Wells et al. 2012). This is proposed to account for the observation that, among primates, human neonates are particularly developmentally immature, with brain to body ratios the smallest among all primates (Rosenberg and Trevathan 2002). More recently, a competing hypothesis, known as *Energetics of Gestation and Growth* (EGG), argued that birth timing is set by the point at which it becomes metabolically inefficient for the mother to nurture the fetus

within her uterus relative to the provision she could accomplish after birth (Dunsworth et al. 2012). Both hypotheses invoke constraints and trade-offs in the ability of mothers to optimize neonate development in utero. The key point is that for any trait governed by trade-offs, outcomes can be precariously balanced between opposing demands, and changes to one demand can result in pathological over- or under-compensation in the others (Crespi 2010; Crespi and Go 2015; Queller and Strassmann 2018). If PTB is governed by trade-offs, the implication is phenotypic variation in birth-timing may be maintained because of how biotic and spatio-temporal variation affects the functional compromises required during pregnancy.

A particularly important trade-off in animals is between immunity and other energetically expensive traits, such as growth or reproduction. Maintaining or mounting immune and inflammatory responses comes at a cost to other physiologically demanding needs. Immunity trade-offs can have profound effects. For example, Urlacher et al. (2018) showed that in a population of Amazonian forager-horticulturalists, children who experience only mildly elevated immune responses can have as much as a 49% reduction in growth rate, resulting long-term differences in stature and likely other developmentally dependent traits. Such direct effects of immunity and inflammatory responses on human phenotypes may have particular relevance to pregnancy and birth timing.

As described above, mammalian reproduction has been superimposed on ancestral immune factors, which have been co-opted for key roles in the relatively more recent development of internal fertilization, placentation, and gestation (Abrams and Miller 2011; Bainbridge 2014). Early views on the role of immunity in pregnancy centered on the idea that the maternal immune responses must be suppressed in order to tolerate pregnancy, an observation that formed the rationale for Medawar's famous *allograft model* for mammalian pregnancy in which antigenically foreign fetal membranes are like grafts onto maternal tissues, requiring mechanisms for tolerance (Medawar 1953). While Medawar's model captured

elements of the immunological challenges posed by the particularly long gestation involved in human pregnancy (Bainbridge 2000), the modern view of the role of the maternal immune system in mammalian pregnancy is dramatically different. Inflammatory and immunological pathways are central to understanding the mechanisms that determine birth timing and parturition in humans (Moffett and Loke 2004; Trowsdale and Betz 2006; Abrams and Miller 2011; Mor et al. 2011; Romero et al. 2014). Maternal immunity first and foremost must protect against infections and pathogens. However, human reproduction involves cycles of up and down-regulation of immunological and inflammatory factors governed by reproductive hormones (Abrams and Miller 2011; Alvergne and Tabor 2018). Over the course of pregnancy, dynamic shifts in immunity are required for successful pregnancy (Abrams and Miller 2011). Fetal tolerance is promoted by the absence of MHC alloantigens on the fetal trophoblast cells. At the same time, the early stages of pregnancy bear many of the hallmarks of tissue injury, including a sustained maternal inflammatory response that underlies the all-too-familiar morning sickness (Macklon and Brosens 2014; Griffith et al. 2017; Ashary et al. 2018). Pro-inflammatory cytokines that induce cell-mediated immunity are down-regulated during pregnancy, leaving pregnant women more vulnerable to infectious diseases (Abrams and Miller 2011). Placental inflammatory responses vary with maternal body mass (Thornburg and Marshall 2015). With the onset of labor, increased catabolism of progesterone, which suppresses the inflammatory response, is associated with a dramatic increase in inflammation, including the invasion of leukocytes into the myometrium, cervix, and feto-placental membranes (Abrams and Miller 2011). These shifts in maternal immunity over the course of pregnancy underlie the critical role that trade-offs between the dual and sometimes competing roles that immunity plays in female health and reproduction (Romero et al. 2001). Little surprise then that inflammatory pathways, and genetic variants that disrupt the carefully choreographed involvement of inflammation in normal labor and birth, are emerging as prime

candidates for understanding the causes of spontaneous pre-term birth (Strauss et al. 2018).

Evolutionary Conflicts and PTB

Pregnancy should seem to be an entirely communal enterprise between mother and fetus. However, because of viviparity, placental traits reflect an evolutionary tug-of-war between parents and offspring over resources (Haig 1993). Matrotrophic nourishment in viviparous species implies that a developing fetus can negotiate with its mother over nutritive provisioning, something not possible in egg-laying species. An inevitable conflict arises in such cases, because in sexually reproducing species, the fetus only shares half of its genes with its mother, and in mammals that are not monogamous, less than half its genes with any future offspring that its mother may have. Mothers, on the other hand, are equally related to all of their offspring. Thus, the investment optima for mother and offspring can differ, with mothers maximizing total reproductive effort and each offspring favoring greater personal investment. The *viviparity conflict hypothesis* holds that many features of viviparity bear that signatures of parent-offspring conflict (Crespi and Semeniuk 2004). Indeed, as Crespi and Semeniuk (2004) point out, when the costs and benefits of matrotrophic viviparity are considered objectively, for offspring the benefits of starting out life nourished and sheltered within the uterus seem obvious, such as greater size and vigor at birth or avoidance of predation common to egg-laying species, and the costs few. But for mothers, the reverse is true. The direct apposition of maternal and fetal tissues over development thus seems designed for the benefit of offspring, by providing the most efficient means of resource transfer.

Conflicts of pregnancy are most easily recognized in live-bearing animals, where dramatic examples such as intrauterine cannibalism found in various amphibians, sharks, and fish or selective abortion of excess, small, or impaired embryos can be found in many animals, including primates (Forbes 1997; Crespi and Semeniuk 2004; Catalano et al. 2018). In the case of selective abortion, the data are so abundant due to

decades of selective breeding and work with laboratory models that it is known as *The Bruce Effect*, named after the researcher who first described adaptive reproductive suppression and selective abortion in pregnant females under conditions that signal declining prospects for gestating young (Catalano et al. 2017). Although controversial, the existence of a Bruce Effect in humans (spontaneous abortion of *perivable* infants before the 28th week of gestation) is supported by non-random patterns in spontaneous abortions, such as selection against morphologically, genetically, and chromosomally abnormal fetuses (Catalano et al. 2018). The larger implication is that gestation timing is not the result of a fixed program, but rather dynamic and highly sensitive to crosstalk between mother and infant informed by numerous inputs, including fetal health. As Catalano et al. (2018) put it, parturition in humans may be “strategic.”

Conflict theories of pregnancy thus hold that mothers and infants can have opposing strategies. Recognizing this sheds light on many puzzling features of pregnancy, each with implications for understanding gestation timing and PTB (Haig 1993, 2008; Crespi and Semeniuk 2004). Some of these include: (1) the placental production of fetal hormones and other factors that manipulate maternal physiology and nutrient transfer, in many cases seeming to wastefully duplicate those produced maternally (Haig 1993); (2) evidence of maternal inactivation of placentally secreted factors (Haig 1993); (3) a shift in the production of pregnancy-promoting progesterone at 5–7 weeks of pregnancy from maternal ovary to the placenta, which is uncommon in other mammals (Pavličev and Norwitz 2017); (4) evidence of maternal mechanisms to regulate placental invasiveness (Heap 1994; Moffett and Loke 2004); (5) the rapid evolution and multiple independent origins of placental traits, including multiple origins and evolutionary convergence of invasive placentae, implying strong and ubiquitous selection, fast and positive selection on placental or maternal genes and genome features involved in pregnancy, and the evolutionary reversion from invasive to less invasive placental types (Crespi and Semeniuk 2004; Wildman et al.

2006; Hannibal et al. 2014); and (5) the observation from many viviparous species that offspring size is governed in part by offspring genotype and is not solely under maternal control (Furness et al. 2015).

With respect to this last example, perhaps most convincing is the observation of *genomic imprinting* of genes expressed in the eutherian placenta, many of which are involved in nutrient transfer across the maternofetal interface (Frost et al. 2010; Monk 2015). Genomic imprinting is characterized by monoallelic, parent-of-origin gene expression, which is mediated by various epigenetic mechanisms acting both prior to and after fertilization (Peters 2014). In vertebrates, it occurs in therian mammals (marsupials and eutherian mammals) and is apparently absent in the oviparous monotremes (Renfree et al. 2009). Little more than a hundred genes are imprinted in humans, and many are associated with disease due to monoallelic expression or disruption of imprinting itself, implying strong countervailing selection (Peters 2014; Furness et al. 2015; Wilkins et al. 2016). Importantly, many imprinted loci are expressed early in development in tissues that are involved in nutrient transfer to developing offspring, and thus regulate growth (Babak et al. 2015; Wilkins et al. 2016). Numerous studies have demonstrated that paternally expressed alleles tend to promote fetal growth or other traits that promote maternal resource transfer, whereas maternally expressed alleles tend to inhibit growth (Furness et al. 2015; Wilkins et al. 2016). Interestingly, more genes are imprinted paternally than maternally, and in adult tissues, tend to be mostly expressed in the central nervous tissues, some of which affect maternal and social behaviors (Peters 2014; Furness et al. 2015). These patterns are consistent with the view of genomic imprinting as a form of genomic conflict (Wilkins et al. 2016). Alternative views, such as *co-adaptation theory*, hold that genomic imprinting coordinates the extraordinary complexity of sexual reproduction and fetal development between maternal, paternal, and fetal genomes (Wolf and Hager 2006).

The importance of genomic imprinting in pregnancy and early development bolsters the view

that birth timing is a delicately balanced compromise between genetic elements with competing strategic interests (Crespi 2010). In this tug-of-war view of pregnancy, the genomic background out of which birth timing emerges has the potential to greatly exacerbate the effects of environmental variation.

Conclusion

PTB is among the most serious and least understood challenges facing infant and adolescent health globally. Because of the singular complexity of pregnancy (Eidem et al. 2017), identifying the causes and remedies to PTB will require concerted efforts and close collaborations between scientists from diverse fields. The diverse perspectives offered by clinical, epidemiological, sociological, and evolutionary studies all shed light on the mysteries of human pregnancy, but it is evident that much more cross-talk will be required to understand the genetic and phenotypic causes of prematurity. A fundamental challenge will be developing opportunities for scientists from diverse fields to share perspectives, not all of which will have immediate clinical relevance.

Cross-References

- Birthing Complications
- Evolution of Live Birth in Mammals (140 MYA)
- Implications for Pregnancy
- Low Birthweight and Preterm Infants
- Maternal-Fetal Conflict
- Narrowing Birth Canal
- Parent-Offspring Conflict
- Prenatal Environment, The

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Preterm Labor

► Preterm Birth

Prevalence of Forced Copulation in Orangutans

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Synonyms

Forced matings; Resisted matings

Definition

The use of aggression or physical restraint by a male orangutan toward a female orangutan in the mating context.

Introduction

Before the 1980s, many orangutan researchers called forced copulations “rape”; however, this terminology has been replaced with the more accurate term “forced copulation.” Orangutans (*Pongo* spp.) are the only nonhuman primates who regularly exhibit forced copulations by males. Forced copulations have been observed in every study population of wild orangutans, as well as in rehabilitant and captive settings. Forced copulations are a form of sexual coercion, in which males use aggression to force a female to mate, when she is resistant to the mating attempt. Male orangutans are only physically aggressive toward females in the context of mating. When female orangutans resist matings, male orangutans may respond by pursuing, restraining, and attempting to force a female to mate.

Orangutan Background Information

Orangutans are semi-solitary, arboreal primates who live in tropical rainforests on the islands of Borneo and Sumatra in Indonesia and Malaysia. The primary social unit is an individual independent (adult or adolescent) orangutan or adult female with one accompanying dependent offspring. Offspring remain with their mother until they are 6–8 years old and start ranging independently around the time their mother gives birth to her next offspring. Orangutans form transient social groupings to forage together, to mate, or to travel together for a few hours or days. Male orangutans have two fully mature body morphs: flanged males and unflanged males. Flanged males are larger than unflanged males and exhibit secondary sexual characteristics: fatty cheek pads, enlarged throat sacs and the ability to produce long calls. The age at which males become

flanged is highly variable, and some males may never flange. Orangutans are sexually dimorphic in body mass. Flanged males are approximately twice the size of adult females, but unflanged males are approximately the same size as adult females.

Defining Forced Copulations

Forced copulations in orangutans are difficult to define because a single mating event may contain elements of both female proceptivity (active mating interest) or indifference, as well as female resistance and male aggression. Additionally, a single female may mate both cooperatively and resistantly with the same male in one day. Female orangutans display a variety of proceptive behaviors: approaching the male, spreading the legs of the male, inspecting male genitalia, and/or stimulation of penis manually or orally. Female resistance behaviors include vocalizing, running from a male, pulling away from a male, struggling against a male, and changing body positions to halt intromission. Female resistance behavior varies in degree, from a short push at the beginning of mating, to a prolonged struggle and the appearance of distress (vocalizations, defecation). Male aggressive behaviors in the context of mating include vocalizing, chasing, biting, hitting, pushing, pulling, or holding a female to force her into a mating body position. Interestingly, males are only aggressive in the mating context, and females never display injuries after a forced copulation.

Orangutan matings occur in trees and are often obscured from viewers by leaves and branches further complicating the characterization of matings. While many primate species have short matings characterized by stereotyped actions, orangutans mating events are prolonged, with male intromission lasting from 2 to 36 min (Knott 2009). The entire sexual encounter can last over an hour, and involve manual and/or oral stimulation by both male and female orangutans. Because of the orangutan’s large body size and their arboreality, there is often a lot of body repositioning required to

achieve intromission. Body position during mating often includes one or both individuals hanging from branches and may involve multiple body position (ventral-ventral, ventral-dorsal, and/or ventral-lateral). For all of these reasons, matings can be difficult to characterize as either solely forced or cooperative. However, it is clear that some orangutan matings do include elements of coercion or force.

Why Do Forced Copulations Occur?

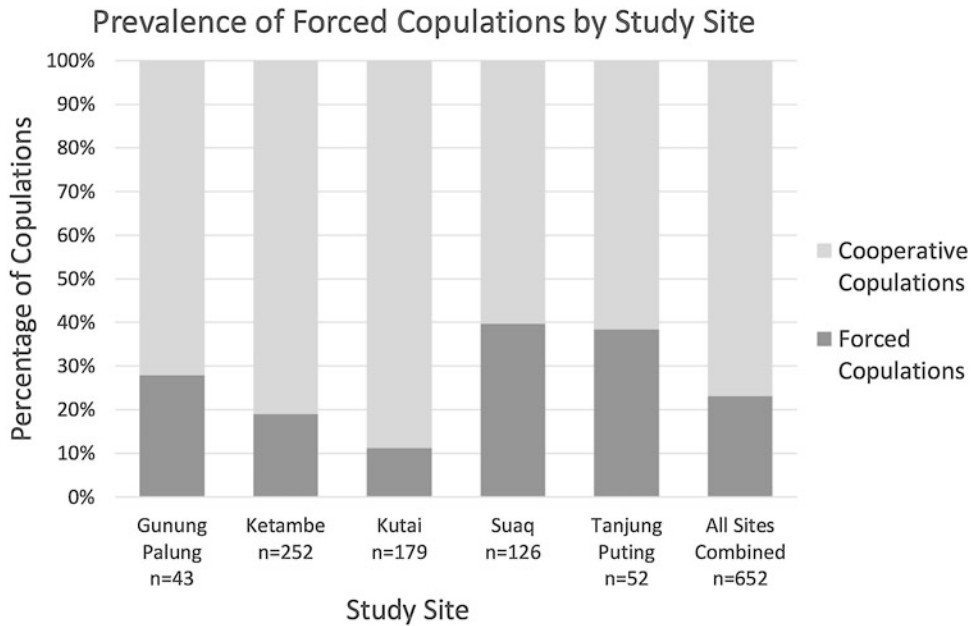
Female resistance to matings is negative mate choice, not an effort to assess mate quality (Fox 1998). Female resistance and proceptivity are affected by a variety of factors, including the length of social interaction, male morph, female ovulatory status, and male rank stability. Galdikas (1985a, b) found that females are less resistant to mating when the male and female pair have been traveling together for an extended period of 3 or more days. The length of the time a pair travels together and female proceptivity may both be indicative of female preference. Knott et al. (2010) found that male morph and female ovulatory status predict female proceptive and resistant matings. During the periovulatory period, when females are most likely to conceive, females are more resistant toward unflanged males and are proceptive toward flanged males, and outside the periovulatory period, females are more proceptive toward all males (Knott et al. 2010). This indicates that female resistance is negative choice against undesired paternity by unflanged males. Flanges and the accompanying secondary sexual characteristics may be an honest signal of male quality, which may be the reason for female preference. Utami et al. (2002) found that there were fewer forced copulations during a period of male rank instability, when flanged males were vying for dominance. This may be indicative of a female strategy to spread paternity certainty more broadly when the male hierarchy is in flux. Both of these findings indicate that female orangutans employ a mixed mating strategy, mating with multiple males to spread paternity certainty,

but focusing mating on desired males when the chance of ovulation is highest. However, if flanged males are preferred mates, the mixed mating strategy does not explain why females ever resist matings with flanged males. Perhaps females resist matings to reduce the possibility of disease transmission or to reduce energetic costs associated with mating (Knott 2009).

The costs of forced copulations for female orangutans have not yet been quantified. Females are never injured during forced copulations (Knott 2009). Fox (1998) found that females had reduced feeding efficiency on days when they were social compared to days when they were alone, but there was no further reduction in feeding efficiency on days with forced copulations. Disease transmission is another possible cost (Knott 2009), which may be more pronounced for orangutans than other gregarious primates, but this hypothesis remains to be tested. The most likely cost of forced copulations is undesired paternity, but this remains to be demonstrated. Female resistance to forced copulation attempts by males is effective in preventing intromission (Fox 1998; Mitani 1985). Female resistance behaviors also reduce the length of a copulation, which may prevent ejaculation and, in turn, undesired paternity (Knott et al. 2010).

Forced and Cooperative Matings, by the Numbers

The prevalence of forced copulations varies by study site. Figure 1 shows the percentage of orangutan matings that are forced and cooperative at five different orangutan study sites. The rate of forced copulations during a study period ranged from 19% to 40% of all matings. The variation is likely to be due in part to variation in the percentage of males that are flanged versus unflanged at each study site, whether the study was focused on collecting data from a certain class of males or females, male rank stability during the study period, and the number of cycling females in the study site during the study period. Individual and population variation may also play a role.



Prevalence of Forced Copulation in Orangutans, Fig. 1 The proportion of forced and cooperative copulations in five orangutan populations. (Data from Gunung Palung from Knott (2009). Data from Ketambe combined from two nonoverlapping studies Schurmann and van

Hooff (1986) and Utami (2000). Data from Kutai from Mitani (1985). Data from Suaq from Fox (1998). Data from Tanjung Puting from one study period by Galdikas (1985a, b))

Why Are Forced Copulations Prevalent in Orangutans

The reason why forced copulations are prevalent in orangutans is not well understood. Palombit (2010) discusses and refutes previously suggested reasons for the prevalence of orangutan forced copulations: sexual dimorphism, lack of female social support, and an alternative male mating strategy. It has been suggested that forced copulations occur due to sexual dimorphism in body size but this does not explain why unflanged males are able to employ forced copulations or the lack of forced copulations in other sexually dimorphic primates. It has also been posited that a lack of female social support due to orangutans' solitary social structure may contribute to the prevalence of forced copulations. However, this does not explain the lack of forced copulations in other solitary primates or why humans who are highly social are the only other primate who exhibit forced copulations. Based on early field observations, it was suggested that forced copulations were an alternative mating

strategy employed by unflanged males. However, this does not explain the use of force by flanged males that has since been observed in subsequent studies. Rather, the potential for sexual conflict is high in orangutans and forced copulations are a manifestation of sexual conflict. The potential for sexual conflict is high, in part, due to the extreme incongruence in parental investment by males and females, which in turn leads to conflicting reproductive strategies between males and females. However, it remains unclear as to why this results in mating conflict and forced copulations in orangutans, but no other nonhuman primate.

Conclusion

Combining all the published data on wild orangutan copulations reveals that approximately one quarter of all orangutan matings are forced copulations (Fig. 1). Forced copulations are a behavioral manifestation of sexual conflict. Forced copulations by male orangutans are in response to

resistance by females, which is negative female choice. Female resistance is affected by many factors: male morph, female ovulatory status, male rank stability, and likely more factors that are not yet understood.

Cross-References

- [Forced Copulation](#)
- [Sexual Coercion](#)
- [Sexual Coercion and Rape](#)
- [Sexual Conflict in Nonhumans](#)
- [Types of Sexual Coercion](#)

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Prevalence of STDs

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Synonyms

[Sexually communicable disease/infection](#); [Sexually transmitted infection](#); [Venereal disease](#)

Definition

Sexually transmitted diseases (STDs) are infections caused by viruses, bacteria, or parasites that are transmitted through sexual contact, especially vaginal, oral, and/or anal intercourse.

Introduction

STDs are a prevalent and significant public health threat affecting more than 20 million people in the USA yearly, with an associated economic burden exceeding 16 billion dollars in direct medical costs (Owusu-Edusei et al. 2013). STDs are associated with a number of signs and symptoms, potential subsequent morbidities, and even mortality. Preventive efforts are therefore needed to alleviate the burden of STDs, especially among higher-risk groups. This entry summarizes the prevalence and incidence trends of some of the most common STDs, as well as the most common morbidities associated with STDs. Human immunodeficiency virus (HIV) will not be included in this analysis given the special epidemiological factors and biological characteristics differentiating this condition from other STDs. Ultimately, through this entry, we aim to highlight the importance of STD prevention as a public health priority.

Scope of the Problem

According to the CDC annual STD surveillance report (CDC 2017), the three nationally reported STDs, i.e., chlamydia, gonorrhea, and syphilis, have reached an all-time high of two million new cases in 2016.

Chlamydia trachomatis was ranked as the most common notifiable condition in the USA in 2016, with more than 1.5 million cases reported. Between 2006 and 2016, the rate of chlamydial infections increased by 55%, though it remains 3.5 times lower than the historical peak of 464.1 per 100,000 population reached in 1975 (CDC 2017). This recent surge in incidence reflects potential changes in sexual behavior such as age at sexual debut and economic and sociodemographic factors such as decrease in marriage rate and delayed child-birth (Fenton and Lowndes 2004) as well as an improvement in screening. Chlamydia incidence is two times higher among women compared to men. Women aged 20–24 have the highest incidence rate of 3779 per 100,000 population. Similarly, the prevalence of the disease is highest among women (2.0% vs. 1.4% in men) and young people aged 20–24 (2.9% compared to 2.4% in age group 14–19 and 1.1% in age group 25–39) (Torrone et al. 2014). Considerable racial disparities exist in chlamydial infection with Black/African Americans having the highest rate of infection, more than five times greater than Whites (CDC 2017).

Gonorrhea is the second most common notifiable STD in the USA. Chlamydia and gonorrhea coinfection might explain the similar trend observed in both STD rates in the USA in recent years. Like Chlamydia, the rate of gonorrhea is increasing, mostly affecting young people and African Americans. After having reached a historic low of 98.1 per 100,000 population in 2009, the incidence rate of gonorrhea increased by 48.6% in 2016. Young people are at the highest risk for gonorrhea infection with an incidence rate of 510.2 per 100,000 persons for 20–24-year-old youth followed by 381.8 per 100,000 people aged 15–19 years old in 2016. Incidence of gonorrhea is highest among Black/African American people, particularly young African American men and women. For instance, the incidence among

African Americans is more than 17 times higher than that of Asians, the racial group with the lowest rate of gonorrhea infection (CDC 2017).

Non-congenital syphilis cases are medically classified into three main stages, primary syphilis characterized by the appearance of ulcers or chancre at the infection site, secondary syphilis with signs including skin rash and mucocutaneous lesions among others, and tertiary syphilis with more severe manifestations such as formation of gummas in vital organs, loss of coordination of movement, progressive dementia, paralysis, and even death. The incidence rate of primary and secondary syphilis increased by 17.6% in 2016 compared to the previous year to reach 8.7 cases per 100,000 population (CDC 2017). Young people aged 25–29 years old have the highest rate of reported primary and secondary syphilis infection (27.5 per 100,000 population). Primary and secondary syphilis are particularly concerning among men who have sex with men (MSM) who constitute the vast majority (80.6%) of cases while forming only 3.9% of the national population (Grey et al. 2016; CDC 2017).

With more than 40 distinct strains, human papillomavirus (HPV) is the most common sexually transmitted infection. Unlike other STDs, HPV prevention can be achieved through vaccine administration. In 2006, the Center for Disease Control and Prevention recommended vaccination of females under the age of 6 against HPV. Two main vaccines are used to target different numbers of high-risk HPV types, the quadrivalent and the 9-valent HPV vaccine. Comparing the pre-vaccine era (2003–2006) to the post-vaccine era (2009–2012), the prevalence of cervicovaginal HPV among women aged 14–19 years old declined by 64% (from 11.5% to 4.3%) and that of women aged 20–24 years old decreased by 34% (from 18.5% to 12.1%) (Markowitz et al. 2016). In light of its encouraging effectiveness in HPV prevention, there continues to be considerable opportunity for improving vaccine uptake nationwide. Trichomonas is a sexually transmitted infection caused by a protozoan called *Trichomonas vaginalis*. The prevalence of trichomonas infections in the USA remains relatively steady since the year 1990, with 139,000 physician office

visits in 2015. It is worth noting that since HPV and trichomonas are not nationally notifiable conditions, estimates of prevalence and incidence of these STDs are accompanied by a margin of error due to the methodological limitations of the studies yielding these figures.

Subsequent Morbidities of STDs

The clinical manifestations of STDs fall into a broad spectrum spanning from discomfort due to genital itching, odor, and discharge to life-threatening subsequent morbidities and comorbidities.

Chlamydia and gonorrhea are two preventable causes for infertility and ectopic pregnancy due to pelvic inflammatory disease (PID). When left untreated, chlamydial infection causes PID in 10–15% of infected women (CDC 2015). Most women who are infected with Chlamydia and gonorrhea are symptomatic, that is, they will show no symptoms, which underlines the need for routine testing for young women and women at high risk, as recommended by the CDC (CDC 2015).

Untreated cases of syphilis infection can progress into tertiary syphilis, a lethal condition that can affect the nervous, circulatory, and musculoskeletal systems. The invasion of the nervous system, called neurosyphilis, can cause paralysis and dementia among other neural symptoms. Ocular syphilis can cause a range of eye-related conditions ranging from vision changes to permanent blindness (CDC 2015). Untreated syphilis in pregnant women can be transmitted to the fetus through the placenta causing congenital syphilis. Congenital syphilis results in obstetric complications like premature birth, low birth weight of newborn and miscarriage, as well as fetal malformation and stillbirth (CDC 2015).

The oncogenic subtypes of human papillomavirus (HPV) cause virtually all cases of cervical cancer. Cervical cancer accounted for more than 12,500 new cases and 4,115 deaths among women in 2014 (US Cancer Statistics Working Group 2017; Walboomers et al. 1999).

Aside from the numerous subsequent morbidities related to STD infection, STDs increase the risk for acquiring HIV. HIV-negative heterosexual people and men who have sex with men who are infected with an STD are twice more likely to acquire HIV during sex with an HIV-positive heterosexual partner (Hughes et al. 2012). The association between STD infection and increased HIV susceptibility is biologically plausible due to the presence of STD-caused genital inflammation and ulcers that could facilitate HIV transmission (Fleming and Wasserheit 1999). The evidence supporting this relationship has led to a major shift in prevention interventions, now leaning toward incorporating mutually reinforcing STD and HIV preventive efforts (Fleming and Wasserheit 1999; Hayes et al. 2010).

STD Prevention

To reduce the burden of STD infections, it is important to understand the risk and protective factors involved and to implement targeted interventions for higher-risk groups (DiClemente et al. 2009). The risk of STD acquisition increases with sexual risk behaviors including having unprotected sexual vaginal, oral, or anal intercourse, having multiple sexual partners, having sex with an unfamiliar partner, and having sex under the influence of drugs or alcohol in addition to other risky behaviors like injecting drugs and binge drinking. Clinical and behavioral interventions are therefore crucial in targeting people at risk for STDs by enhancing awareness of STD prevention methods and associated risks. Evidence-based sex education in schools and clinical-based STD screening and risk-reduction programs can play a pivotal role in enabling youth and other high-risk groups to make better informed sexual decisions.

Conclusion

Despite the improvement in STD incidence rates at varying degrees over time, mainly in syphilis and HPV infections, STD infection remains a public health priority for three main reasons:

1. The increase in Chlamydia and gonorrhea rates nationwide.
2. The major health disparity concern due to the disproportional burden on racial and ethnic groups, particularly African Americans; young people and MSM find themselves to be at notably higher risk.
3. The robust association between STDs and HIV acquisition.

Increasing awareness about STD screening and treatment, and providing accessible health services to youth and high-risk groups, is a keystone for meeting the public health priority of STD prevention.

Cross-References

- [Oral Sex and Human Sexual Behavior](#)
- [Sexual and Reproductive Development](#)

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Prevention of Infidelity

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Synonyms

[Anti-cuckoldry](#); [Mate guarding](#); [Mate retention](#)

Definition

A suite of emotional, cognitive, and behavioral adaptations designed to prevent a relationship partner from engaging in sex with those outside of the pair-bonded relationship.

Introduction

One of the hallmarks of human (and primate) evolution relates specifically to brain evolution. Humans, compared to other primates, have a highly developed neocortex, which enhances the computational capacity for managing large social networks as well as facilitating self-regulation, both of which contribute to reaping the benefits of cooperating and living in social groups (Dunbar 1998). Nonetheless, humans also evolved bipedalism, and although this has resulted in selective advantages for our species (e.g., grasping, tool and weapon use), it has also generated potential costs as well, specifically the narrowing of the birth canal (Wittman and Wall 2007). Thus, as our brains evolved to be larger, the human birth canal simultaneously became much smaller in circumference relative to other primates. To address the incompatibility of increasing brain size and decreasing birth canal circumference, humans are born with a smaller portion of adult brain size (compared to other primates). Although this aids in the birthing process, it also means that human infants are relatively helpless for an extended period of time post-birth and a significant portion of development in human infants involves brain maturation (Martin 1983). Thus, much of human brain development occurs post-birth with human infants highly dependent upon investment from parents, relative to other primates.

Human infants have benefited from biparental investment (e.g., Quinlan and Quinlan 2007). That is, it has been selectively advantageous in terms of survival and reproduction for infants to receive investment (resources, protection) from both parents, and humans are characteristically more monogamous than many other primates. While biparental investment is advantageous for

offspring survival, infidelity by either partner can undermine these advantages. For example, infidelity by a female partner further undermines men's paternity certainty. Because men do not carry offspring via pregnancy, they never have absolute certainty that offspring birthed by their long-term partner are genetically theirs; sexual infidelity by a female partner exacerbates such paternity uncertainty concerns in men (Platek and Shackelford 2006). Nonetheless, a man's primary partner may be motivated to engage in extra-dyadic sex to produce an offspring with a genetically superior male, thereby increasing the health and survivability of her offspring (Gangestad and Simpson 2000). Additionally, because reproduction is more metabolically costly for women (pregnancy, lactation) than it is for men (the provisioning of a sperm), a female whose partner is unfaithful may experience a reduction in resources invested by the male in her and her offspring (due to resource diversion to females and offspring outside of the pair-bonded relationship; Buss 1988; Trivers 1972). Nonetheless, it can be evolutionarily advantageous for men to mate with numerous females to increase the absolute number of offspring he fathers (Buss and Schmitt 1993).

Although both men and women benefit through mutual investment in shared (genetically) offspring, both may also benefit from engaging in sexual behavior outside of the pair-bonded relationship. One partner's infidelity may be beneficial; the other partner likely incurs costs. As such, men and women have evolved adaptive mechanisms for preventing their partner's infidelity in the first place, detecting potential infidelity by their partner (should it occur) and responding to such infidelity in ways that reduce the reproductive costs associated with it. We summarize research on psychological and behavioral mechanisms for preventing, detecting, and responding to partner infidelity in this entry in terms of men and women's differential responses to that concern as well as burgeoning research on the role of individual differences (e.g., personality) in infidelity prevention behaviors (i.e., behaviors to prevent partner infidelity).

Preventing Infidelity

In the context of preventing infidelity in pair-bonded relationships, Ben Franklin (1735) could not have been more correct, from an evolutionary perspective: “An ounce of prevention is worth a pound of cure.” Human males risk investment in offspring who do not carry their genes if their long-term partner mates outside of the relationship and produces offspring. Although women do not to worry about “maternity uncertainty,” a woman whose partner mates outside of their relationship and produces offspring risks diversion of resources (protection, tangible resources) from her and her offspring. As such, humans have evolved numerous adaptive strategies for preventing infidelity.

Foremost, concern with partner infidelity elicits strong emotional reactions, specifically jealousy. For men, imagined partner sexual infidelity elicits greater anger than for women, whereas the reverse is true for imagined partner emotional infidelity (autonomic nervous system arousal confirms these differences; Buss et al. 1992). These sex differences to potential infidelity are sensible, given that men risk paternity uncertainty and women risk resource diversion. Men and women are highly motivated to enact different strategies to prevent infidelity, which are often referred to as mate retention tactics (Buss 1988). Below, we outline these sex-specific tactics to prevent partner infidelity as well as adaptations that reduce each sex’s propensity to be unfaithful to their partner.

Men’s Strategies to Prevent Female Infidelity

To prevent infidelity by their primary relationship partner, men engage in a variety of behaviors to appear more attractive to their partner as a long-term mate, thus potentially reducing their partner’s interest in extradyadic sex. For example, a common mate retention tactic men report using is benefit provisioning, such as buying gifts for their long-term partner (Buss 1988). Such a strategy is sensible; women’s reproduction is facilitated by

identifying a male partner with access to resources and a willingness to invest those resources in her and her offspring (Trivers 1972). Thus, a man who engages in benefit provisioning is likely to be more attractive as a long-term partner, which could reduce a woman’s motivation to be unfaithful with her current partner. Indeed, research finds that men are much more likely to engage in costly benefit-provisioning behaviors for a long-term partner than for a short-term partner, suggesting that this behavior is designed for infidelity prevention more so than courtship (e.g., Jonason et al. 2009).

Men report utilizing verbal compliments with their partner and sit closer to and act nicely to them as effective strategies. Complimenting and acting nicely toward one’s partner should reinforce the value of the relationship, whereas proximity-enhancing behaviors allow males to monitor and respond to potential mate poachers. Importantly, these strategies appear to be more effective mate retention/infidelity prevention strategies than cost-inflicting strategies, as they could dually communicate benevolence and paternal ability (Buss 1988). Men also use status displays to be attractive to a partner (e.g., Griskevicius et al. 2007), which could ultimately prevent infidelity. Given status’s association with greater access to resources, such displays may make men appear as more attractive long-term mates, thereby reducing their partner’s motivation for extradyadic sex (Buss and Shackelford 1997). Additionally, men increase their use of intrasexual threats (e.g., derogating or intimidating rival males) to reduce the likelihood that such males will try to initiate sex with their partner (Buss and Shackelford 1997).

Men’s infidelity prevention tactics also covary with the probability of partner infidelity and conception risk. For example, men who are concerned with infidelity report engaging in cunnilingus more frequently with their long-term partner for longer durations, which is positively correlated with their partner’s satisfaction with the relationship (Pham and Shackelford 2013a, b). Importantly, men’s cunnilingus provisioning is limited to long-term pair-bonds, suggesting the behavior’s utility in continuing commitment. Men may

use reinforcing sexual behavior to reduce their partner's interest in extradyadic sex (Sela et al. 2015a). Additionally, men's mate retention strategies are correlated with their partner's actual conception risk. Women report that their primary partner engages in more retention behaviors during days of peak fertility (Gangestad et al. 2002; Haselton and Gangestad 2006). Given the link between elevated conception risk and interest in extra-pair copulations (Gangestad et al. 2005), it would be sensible for infidelity prevention strategies to peak when women are most capable of conceiving to prevent extradyadic sex on these critical days.

Along with relationship-controlling and reinforcing behaviors directed toward women, men also display behaviors that reduce their own interest in extradyadic sex. By communicating disinterest in sex outside of the pair-bonded relationship, their primary partner may trust them more and reciprocate that trust via sexual fidelity. For example, men primed with romantic love demonstrate reduced visual attention to attractive female faces. Romantic love evolved to facilitate pair-bonding and biparental investment. By not attending to attractive relationship alternatives, men may be less likely to deviate sexually from their primary partner and, by avoiding their own infidelity, would be more attractive mates (Maner et al. 2008). Additionally, men in relationships, when implicitly primed with mating, demonstrate reduced attention to attractive females compared to single men (Maner et al. 2009; Miller et al. 2012), a potential analog in alternative derogation that would preclude subsequent attraction to alternatives from developing, as attractive individuals are perceived as more likely to be unfaithful (e.g., Thompson et al. 2016). Men also derogate faces of alternative women at peak fertility (Miller and Maner 2010). This derogation also appears more apparent when such alternatives are perceived as more attractive (Plant et al. 2010). By communicating that one is not attracted to females outside of their relationship that are at peak conception risk, men may be more attractive to their primary partner, thereby reducing the likelihood that their partner engages in infidelity.

Women's Strategies to Prevent Male Infidelity

Because paternity uncertainty would be more biologically problematic than resource diversion (in terms of genetic propagation), an asymmetry emerges in preventative strategies based on sex such that men utilize a greater variety of strategies. However, preventative strategies in women remain no less critical in their desire to ensure optimum access to resources. Costs of male partner infidelity include reduced protection, diversion of emotional and tangible resources away from her and her offspring, and potential desertion (e.g., Stieglitz et al. 2012). Women possess their own unique suite of infidelity prevention tactics. For example, to reduce infidelity likelihood, women report acting more affectionately toward their partner, enhancing their physical attractiveness, and using verbal possession displays toward their partners (Buss and Shackelford 1997). Additionally, both women's concern with partner infidelity and desire to maintain their current pair-bond are associated with increased performance of fellatio for longer durations, a behavior used to enhance her partner's attraction to her, rather than other women (Sela et al. 2015a, b). Additionally, women report faking orgasms more frequently when engaging in sex with their primary partner to facilitate their partner's sexual satisfaction (Kaighobadi et al. 2012).

Much like men, women also enact strategies to reduce their own likelihood of infidelity, thereby facilitating their partner's trust in them through such fidelity enhancement cues. Specifically, women visually attend less to attractive opposite-sex relational alternatives when primed with romantic love in a process similar to men (Maner et al. 2008). Partnered women, when primed with mating, also attend less to attractive opposite-sex relationship alternatives, compared to single women (Maner et al. 2009; Miller et al. 2012). Women's awareness of heightened interest in pluralistic mating strategies during peak conception risk also appears to influence their perception of prospective mates. Specifically, women in relationships who are ovulating may recognize the hormonal influence on their current motivational

state as potentially threatening to their current pair-bond, which may lead to greater derogation of potential relationship alternatives. Smith (2015) found that pair-bonded women derogated the attractiveness of male targets who served as alternatives to their current relationship, which would have served to buffer these women from engaging in extradyadic mating. Importantly, these effects were primarily seen among women who reported greater commitment to their current relationship partner.

Mechanisms to Detect Infidelity Cues in Partners and Interlopers

While the most ideal situation for men and women in pair-bonded long-term relationships would be to enact strategies to prevent infidelity altogether, both men and women have conflicting, yet adaptive motives for extradyadic sex. For men, sex with multiple females maximizes his reproductive rate and the absolute number of offspring sired, which increases his genetic lineage (Buss 1988). For women, according to strategic pluralism, extradyadic sex with a more attractive male (associated with good genes) can increase her production of healthy offspring while simultaneously retaining investment by her pair-bonded partner (Gangestad and Simpson 2000). As such, men and women may deviate from pair-bonded relationships, regardless of the infidelity prevention behaviors enacted by their partner. In such circumstances, it behooves men and women to be sensitive to cues in their partners' behavior indicative of potential infidelity or traits in same-sex conspecifics that might indicate an increased mate-poaching threat.

Men's Infidelity Detection Mechanisms

Given the high cost of an unfaithful female partner, men tend to have infidelity detection mechanisms that are oversensitive. That is, men are more likely than are women to overperceive that their partners have been sexually unfaithful. From an error management perspective (Haselton and Nettle 2006), such a bias is sensible.

Overassuming a partner's infidelity is an error (a false alarm), but underassuming infidelity (failing to assume a partner's infidelity when that partner has actually been sexually unfaithful) is a more costly error (a miss) because it increases the likelihood of a male to invest in genetically unrelated offspring (Goetz and Causey 2009). Men use several veridical cues of conspecifics in potentially identifying a partner's infidelity. For example, men tend to attribute greater infidelity risk to women who have highly feminized voices, since feminine voices are associated with youthfulness and attractiveness (O'Connor et al. 2011). Furthermore, men rate highly dominant male faces as even more dominant when their partner is ovulating; given the association of dominance to intrasexual competition and mate value, the presence of dominant male conspecifics might be an especially potent cue of a threat to one's pair-bonded relationship (Burris and Little 2006). Dijkstra and Buunk (2001) further implicate men possessing broader shoulders, an honest indicator of good genes, as evoking perceptions of dominance and subsequent jealousy from rivals.

Women's Infidelity Detection Mechanisms

Although infidelity by a male partner is costly for different reasons, women are nonetheless highly motivated to detect potential infidelity by their partner. Whereas men tend to overassume the likelihood of partner infidelity, women tend to be quite accurate at detecting a variety of infidelity cues. Women tend to attribute greater infidelity risk to men who have more masculine voices, which is sensible, given masculinized men's greater interest in pluralistic mating strategies (O'Connor et al. 2011). In terms of identifying potential rivals, women also utilize visual assessments to determine an individual's threat. Rival women with lower waist-to-hip ratios, a cue to fertility, are perceived as more attractive by men but also more intrasexually threatening by women (Dijkstra and Buunk 2001; Singh 1993). Another multimodal finding corroborates women's upregulation in intrasexual competitiveness

through olfaction. Women who smelled the scent of potential rivals at peak conception risk have heightened levels of testosterone, compared to those who smelled women's scent from luteal phases (Maner and McNulty 2013). This hormonal response may be adaptive to facilitate heightened vigilance against potential rivals. Additionally, women are rather vigilant with respect to rival women and in visual search tasks. That is, women demonstrate enhanced detection of scenarios connoting infidelity (Ein-Dor et al. 2015). These sex-specific acuties would be adaptive to ensure continued provision from a current partner.

Reducing Adaptive Costs of Infidelity

Despite the mechanisms and defenses employed by humans to prevent the occurrence of infidelity in their current relationships, the possibility of infidelity may still pose a threat. Gallup et al. (2005) indicated that 18% of women and 10% of men report having extra-pair copulations during committed relationships, suggesting that infidelity is a genuine threat to pair-bonded relationships. Upon identification, it becomes incumbent to limit costs posed by infidelity. Humans evolved several mechanisms assisting in mitigating costs posed by infidelity. Such techniques differ between men and women. Men's strategies favor frequent and rigorous sexual behaviors to displace potential rivals' sperm in favor of their own (e.g., Gallup et al. 2003). Conversely, women's strategies involve identification of reliable conspecifics who would assist in offsetting loss of resources that a long-term male partner may have typically provided (Miller and Maner 2008). Below, we provide sex-specific responses to genuine concerns of partner infidelity that run the gamut from benefit provisioning (e.g., Goetz et al. 2005) to intimate partner violence and coercion (e.g., Miller and Maner 2008; Goetz and Shackelford 2009).

Men's Mechanisms

Men's behavior in response to infidelity is best understood through the sexual movements to

eliminate potential competitors' sperm. Women can retain sperm from multiple partners with individual sperm having a life span of 5–7 days. Gallup and Burch (2004) posited the most recent male partner having greater chances in insemination. Thus, an adaptive response to double mating could include men's penis shape and behavior evolving to ensure own fertilization while mitigating potential threats posed by rival sperm in the vaginal tract from a previous sexual encounter. The human penis possesses a coronal ridge that operates as a "scooping" tool during copulation by drawing rival sperm from the cervical end of the vagina and replacing it with the current partner's sperm. Such "scooping" results in displacement of approximately 80% of semen already existing in a vaginal tract (Gallup et al. 2003). Successfully displacing sperm would also be contingent on men's ability to utilize their coronal ridge forcefully and attaining sufficient depth in the vagina to reach rival sperm. The required vigorous thrusting during copulation should also be greater, following concerns of infidelity (e.g., Goetz et al. 2005). Furthermore, following ejaculation, men enter a refractory period that precludes their own sperm from becoming displaced that involves loss of an erection and less vigorous thrusting, which would serve as a mechanism to prevent self-displacement (Gallup and Burch 2004; Gallup et al. 2005).

For this mechanical advantage to work, this would require increased copulatory behavior for more rival-displacement opportunities. However, copulatory opportunities may not always be plentiful. A greater degree of uncertainty surrounding potential rivals emerges when time between copulations increases that it would be adaptive for men to engage in sperm-displacing behaviors. For example, Gallup et al. (2003) found that increased time apart from one's sexual partner predicts men's engagement in more vigorous thrusting behavior to compensate for the possibility of double mating. Such displacement behaviors are also more apparent when infidelity risk appears higher (e.g., attractive partner; Goetz et al. 2005). Along with the actual sexual behavior corresponding to displacement, other behaviors emerge to facilitate eventual copulation. Greater time apart since the most recent copulation

predicts men's greater interest in sex with a long-term partner and perception of one's partner as more attractive (Shackelford et al. 2002, 2007). Further, rejection from a partner also elicits greater distress and persistence from men to eventually having sex, primarily if their partner has many male friends (Pham and Shackelford 2013c; Shackelford et al. 2007). Pham et al. (2017) further indicate that greater numbers of a wife's male friends and coworkers lead husbands to greater frequency of copulation.

Given the link between frequent in-pair copulations and mate guarding (Shackelford et al. 2006), infidelity risk also elicits more male mate-guarding strategies. Men at greater risk of mate guarding are more willing to engage in cunnilingus until their partner achieves orgasm (Pham et al. 2013b). Goetz et al. (2005) indicate that men experiencing greater infidelity risk engage in more mate-guarding behavior. Specifically, men utilize benefit-provisioning (e.g., love and care) and possessive strategies (e.g., verbal possession) more frequently as a function of competition risk. Benefit provisions and mate guarding also appear especially high when the woman is perceived as possessing a higher mate value (e.g., Pham et al. 2014; Starratt and Shackelford 2012). Starratt et al. (2007) have also found that men who perceive greater intrasexual competition have greater propensity to monopolize their partner's time to prevent contact with potential rivals and more aggression toward other rivals (Miller and Maner 2008; Starratt et al. 2007). The threat of cuckoldry predicts men's proclivity not only to coax women into sex but also predicts actual use of sexual coercion themselves (Camilleri and Quinsey 2009; Goetz and Shackelford 2009). Camilleri and Quinsey (2009) have also found that many rapists' concern over cuckoldry was a driving factor behind their crimes. These concerns have similarly been theorized as the basis of violence directed toward one's partner (for a review, see Kaighobadi et al. 2009). The increased spousal abuse in response to cuckoldry fears could be adaptive in potentially deterring women from considering infidelity in the future. For example, anxiety and accusations of infidelity predict partner-directed violence aggression (Armocky et al. 2015b; Kaighobadi et al. 2012).

Women's Mechanisms

Because women have complete certainty regarding the maternity of their offspring, their concerns following knowledge of their partner's infidelity are not centered around expending resources on another's child. Instead, given the investment often required of men in long-term relationships (Trivers 1972), learning of a partner's extra-pair relations appears to redirect women's desire for affiliation to those who are better able to provide for them. Women are more likely to incur greater costs from a single act of intercourse that puts them in a position to desire more resources. Miller and Maner (2008) found that women are more interested in seeking reaffiliation with others if they believe their partner to be unfaithful. While this desire for conspecifics should readily satisfy affiliative needs, access to more conspecifics would also ensure greater contact with potential resources that would offset the costs incurred from partner infidelity in women's committed long-term relationships.

Individual Differences in Infidelity Prevention

Given the within-species diversity exemplified by humans, individual differences in infidelity detection and mate retention behavior seem inevitable. For example, humans demonstrate varying levels of proclivity toward pluralistic mating strategies, with their successful utilization of pluralism being contingent on one's exhibition of good genes that would make them desirable mates. Those who do not exhibit good genes or those who may not adopt pluralistic mating strategy should thus be more averse to the thought of infidelity and may be more likely to perform more aggressive maintenance behaviors compared to those who may perceive themselves as having more mating opportunities. This section outlines both individual differences in physical appearance and personality in how either classification of traits influence responses to potential infidelity in an adaptive manner.

Physical Differences

Individual differences pertaining to phenotypic expression should leave some individuals more vulnerable to infidelity from a partner. Those who exhibit better genetic quality would likely feel more secure about their current pair-bond and thus not have to engage in aggressive mate-guarding or cost-inflicting behavior as frequently as those who may perceive themselves as not possessing commensurate fitness indicators in their own right. In fact, previous findings indicate high-mate value men engage in more benefit-provisioning tactics compared to lower-mate value men (Miner et al. 2009), particularly those whose partners have a perceived higher mate value (Sela et al. 2016).

Another desirable physical trait for men to possess is height (Stulp and Barrett 2014). Height is highly heritable trait that may also assist in benefit provisioning (e.g., Macgregor et al. 2006), which may suggest that taller men in committed pair-bonds may feel greater relationship satisfaction, as their height may serve as a buffer against their partner's interest in extra-pair copulations with taller individuals. Indeed, Brewer and Riley (2009) found that taller men report greater overall satisfaction with their relationships and ultimately report less jealousy toward prospective intrasexual rivals. These findings further suggest that those who exhibit objectively lower genetic quality compared to intrasexual rivals, however, should report greater jealousy in their relationships. Indeed, previous research indicates that individuals demonstrating worse overall fitness (e.g., health issues, fluctuating asymmetry) report greater concern of partner infidelity and ultimately greater jealousy within the context of their current relationship (Arnocky et al. 2015a; Brown and Moore 2003). Taken together, an individual who perceives to be of lower genetic quality would benefit from engaging in behaviors to affirm the established pair-bond, whereas those of higher quality may feel more afforded in not having to be vigilant of their partner or having to aggress against potential competition.

Personality and Infidelity Prevention Strategies

Personality appears to exert similar influence over infidelity prevention strategies. Individuals exhibiting higher levels of ostensibly prosocial traits are more willing to provision partners, whereas those low in such traits may demonstrate more aggressive mate-guarding behavior to continue established pair-bonds. When considering the HEXACO model, high-conscientiousness, high-agreeableness, and high-openness individuals are less likely to mate guard in their current relationship, whereas high-emotionality individuals appear more willing to mate guard (Holden et al. 2014). Importantly, individuals who are low in honesty-humility are more willing to manipulate and exploit their partners. Pham et al. (2016) have also found that low-honesty and low-conscientiousness individuals utilize coalitional mate guarding as a prevention strategy or the covert use of conspecifics to monitor one's relationship partner on behalf of that individual. Using the Big Five traits, de Miguel and Buss (2011) found greater vigilance toward partner's potential indiscretion as a function of neuroticism. Among more negative traits, Holden et al. (2015) have also found that pathological personality traits (as indexed by DSM-5 criteria) are associated with greater use of cost-inflicting mate-guarding strategies. In terms of attachment styles, men with an avoidant attachment are less willing to utilize benefit-provisioning infidelity prevention strategies compared to securely attached men (Barbaro et al. 2016).

In terms of benefit provisions, personality traits also correspond to various compensatory behaviors that seek to enhance one's partner. For example, individuals who score high in trait conscientiousness report greater use of resource displays (i.e., behavior indicating beneficence for the partner) as well as greater levels of appearance enhancement (de Miguel and Buss 2011). Importantly, these researchers also found that agreeableness predicted a reduction in cost-inflicting strategies, including punishment and derogation of one's mate. Individuals with an anxious attachment style are also more likely to engage in benefit

provisioning with a romantic partner (Barbaro et al. 2016). In terms of sexual behaviors employed to retain a partner, research has also found various personality traits correlate with proclivity to engage in oral sex. For example, Sela and colleagues (2015c) found that women's trait level of openness predicts their interest in performing fellatio in a long-term relationship while their conscientiousness predicts the duration of performing such an act. Similar findings have emerged for men such that agreeableness and conscientiousness predict their engagement in cunnilingus (Pham et al. 2015).

Conclusion

Given the heavy investment in child-rearing, it is crucial for humans to possess mechanisms to mitigate the likelihood of the dissolutions of necessary pair-bonds for offspring survival. Thus, humans appeared to have evolved various psychological and behavioral adaptations that would serve not only to facilitate individuals' identification of potential infidelity risks vis-à-vis their partner but also to encourage their own continuation of that pair-bond. Such adaptations manifest in several capacities ranging from benign gift-giving to coercion with various environmental and dispositional factors influencing preventative responses. This entry addressed several posited means of infidelity prevention.

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Previously Hominid Evolution

► Hominin Evolution

Prey Availability

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Synonyms

[Resource availability](#); [Resource selection](#)

Definition

Prey availability refers to the quantity and diversity of food items available to a predator.

Introduction

Prey availability determines what predators eat, and predators in turn influence prey availability. Considerable complexity underlies this axiomatic statement. Numerous ecological and evolutionary processes influence fluctuations in the relative abundance, and therefore availability, of prey. For example, life history factors, mortality, fecundity, disease, migration, and resources influence whether a species of prey is available to eat. Conversely, predators play a direct role in prey availability because their presence and activity may result in changes in prey population numbers.

Prey Availability and Foraging Decisions

Prey availability affects foraging behavior at both short- and long-term scales. It influences immediate decisions about what to eat and where, and it can also impact behavioral development and evolution. With regard to the former, prey availability may decline for an individual or group of foragers when a food patch becomes depleted or prey have taken evasive action. The prey choice model of optimal foraging theory predicts that a forager should pursue a particular prey item if the energy gained from consuming it exceeds that of an alternative type of prey. In the classical prey model, prey is chosen as a function of energy value divided by handling time (capture and consumption). The rate of intake is affected by this relationship as well as by predatory encounter rates with prey. For example, wolves prefer elk as their primary prey over bison. This is likely because elk are comparatively easier to capture and subdue than bison, providing a greater relative net energy gain. However, when elk populations decline, wolves will prey upon bison instead (Garrott et al. 2007).

Prey availability applies to models of foraging in patchy environments. The marginal value theorem predicts that organisms monitor depletion of

a given patch and balance current caloric availability with requirements to locate a new, replenished patch (Charnov 1976). Simply put, if prey become scarce in a predator's current foraging location, the predator will need to move to a new one. For example, organisms may alter their food and patch choices in accordance with seasonal changes. Biomass and abundance of fish in the Sylt-Rømø Bight vary throughout the year, with maximum values of each occurring during summer and minimums during winter. Harbor seals preferably feed on benthivorous fish in the summer when they become more available in the Sylt-Rømø Bight. During winter and fall, the seals switch their foraging location to the North Sea, where there is a greater abundance of benthivorous prey relative to the Sylt-Rømø Bight. However, seals in both the Sylt-Rømø Bight and the North Sea feed mainly on pelagic fish species in the spring when benthivorous species are smaller and less abundant (Vega et al. 2016). Changes in harbor seal foraging locations, and seasonal changes in diet, serve to increase energy efficiency across a spatiotemporal scale.

The loss or depletion of a particular food source in a patch may simply require that the predator alter its diet rather than search for prey in a new location. The generalist snake species *Thamnophis elegans* feeds opportunistically on metamorphic amphibians and fish inhabiting Eagle Lake in Lassen National Forest, CA. A 7-year period of lake recession saw plummeting amphibian populations, resulting in the near elimination of amphibians from snake diets (Kephart and Arnold 1982). Although fish were sufficiently available prior to and during the change in water level, the snakes prioritized toads because they offered a higher energy return owing to their lower capture cost in comparison to fish. Such ontogenetic shifts in prey choice in response to availability are not unusual among generalist feeders.

Prey Availability, Plasticity, and Evolution

Prey availability is an important ecological force influencing both ontogenetic and evolutionary processes. Food resource partitioning among

conspecifics in regions of sympatry may result in changes in behavior and trophic morphology that are mediated by phenotypic plasticity. Outcomes of food resource partitioning include increased foraging efficiency among conspecifics specializing on different available prey and, possibly, evolutionary divergence reinforced by assortative mating or further partitioning of habitat use. Indeed, competition for food is a primary mechanism of evolutionary divergence (West-Eberhard 1989).

Arctic charr (*Salvelinus alpinus*) are known to specialize on either benthic (macroinvertebrate) or pelagic (plankton) prey. These fish show high levels of phenotypic plasticity of trophic morphology, and different feeding experiences induce shape and size variation of the body and head. In the laboratory, captive born and reared Arctic charr with robust head and mouth morphology foraged for benthic prey, while charr with slender body and head shape fed on pelagic prey (Garduño-Paz and Adams 2010). Natural variation in head size and shape and correlated differences in diet have also been observed in wild-caught charr in regions of sympatry. These findings indicate that prey that are simultaneously available and abundant are not consumed equally by a natural predator. Resource partitioning among conspecifics, such as found in Arctic charr, can result in important microevolutionary changes (Skúlason and Smith 1995).

Further evidence for diet-induced microevolutionary change comes from studies of geographic variation in resource availability, morphology, and behavior (Foster and Endler 1999). Animals that consume different available food resources undergo both developmental and microevolutionary changes to adapt to local feeding conditions. Such locally adaptive responses, maintained by geographic isolation, play a major role in reinforcing reproductive isolation and, ultimately, speciation. For example, this pattern has been observed in coral feeding butterflyfish (*Chaetodon* spp.). Several different species of butterflyfish occur along coral reefs in the South Pacific Ocean. Three of these species are generalists, taking a relatively wide range of prey including soft and hard coral as well as motile invertebrates, and two are specialists, feeding

only on hard corals (Lawton and Pratchett 2012). It is important to note that prey availability is one of many factors influencing both micro- and macroevolutionary change, as is the case with butterflyfish. However, prey availability and dietary habits are of clear evolutionary importance, as they are related to species diversification. Phytophagous insects tend to be highly specialized on specific species of host plants, possibly as a strategy for responding to diverse mechanisms of defense employed by plants. In this case dietary specialism is favored. Indeed, among phytophagous insects, and probably other taxa, the evolutionary trend is to evolve from a dietary generalist into a specialist (Nosil 2002).

Predator-Prey Dynamics and Prey Availability

Intraspecific and interspecific interactions between predators are influenced by the availability as well as the behavior of prey. Male mountain lions (*Puma concolor*) in central California mainly feed in riparian woodlands where mule deer (*Odocoileus hemionus*) are abundant. Females, however, often feed closer to human-populated areas in order to avoid confrontations with males. Intraspecific aggression over prey carcasses, which can result in males attacking females and their offspring, may be the driving force behind this resource partitioning. Female mountain lions may feed in different locations in order to increase the safety of their young, despite the risks this brings via their encroachment on developed areas (Benson et al. 2016).

Curiously, when heterospecific predators hunt the same prey, the effort required to acquire that prey may be reduced for each predator when they both occupy the same patch. For example, the presence of horned vipers (*Cerastes cerastes*) facilitates barn owl (*Tyto alba*) predation on gerbils by forcing the prey into open areas where owls can more easily catch them. Conversely, when owls become an immediate danger to the gerbils, the latter will shift to a bush microhabitat where vipers prefer to hunt (Embar et al. 2014).

The dynamics that exist between predator and prey present a challenge to estimating prey

availability. Specifically, the activity patterns of prey species, and responses of prey to the presence of predators, influence estimates of prey availability conducted by researchers (and rates of prey capture by predators). For example, in the presence of various species of predatory shorebirds, fiddler crabs (*Uca* spp.) flee into their burrows to evade capture. Hiding in burrows reduces the amount of time crabs can engage in evolutionarily important behaviors such as courtship and foraging. Therefore, there are costs to either strategy – either the crabs miss out on opportunities to mate and eat because they are hiding or they increase their risk of being eaten because they are not (Backwell et al. 1998). Here, from the perspective of the prey species, availability is a function of how the animals respond to the evolutionary trade-offs they face.

Prey Availability and Human Foraging

A comparative framework for studying the effects of prey availability on human foraging is challenging because animal domestication and agriculture have fundamentally changed how humans acquire, store, and utilize their food. The most germane comparison comes from contemporary human groups that rely on hunting, gathering, and fishing for subsistence. Slobodkin's "prudent predator" hypothesis emphasized examples of predators focusing on younger or older prey rather than those in reproductive prime. This hypothesis fits with ideals we might hold for how humans hunt and forage, as we hope that our species has the intuitive foresight to avoid overharvesting in order to remain in harmonious equilibrium with prey. However, observations of the Mascho Piro people of Peru, an indigenous tribe of hunter-gatherers, do not suggest that this particular group adjusts its foraging tactics to maximize long-term prey availability (Alvard 1995).

In fact, large-scale work examining global impacts of hunting and fishing further raises doubt that humans are *sustainable exploiters*. Rather, from a comparative perspective, humans exploit prey populations at levels far outstripping

nonhuman predators, particularly large terrestrial carnivores and fishes (Darimont et al. 2015). Thus, reduced prey availability tends not to result in reduced consumption (e.g., conservation), and population sizes of large carnivores and fish are mitigated by constantly high kill rates, particularly of animals at their reproductive prime. These observations, however, do not mean that people who obtain their food through hunting and gathering are entirely free from the constraints of prey availability. Seasonal changes in prey activity, abundance, migratory patterns, and other factors are sources of variation in prey availability with which contemporary hunter-gatherers must cope (Bliege Bird and Bird 2005).

Conclusion

Prey availability is a constant constraint to which predators must respond in order to survive. Immediate foraging decisions involve weighing the costs and benefits associated with prey availability, as shown in models of optimal foraging. Even when organisms have adapted to particular, energy-maximizing diets available in their given environments, changes in the quantity and quality of preferred food items may lead to changes in prey choice, patch choice, and predatory tactics. Thus, on a long-term scale, prey availability is an ecological force affecting selection for successful foraging tactics. Phenotypic plasticity of behavioral and trophic morphology in response to dietary variation can in turn influence macroevolutionary events (speciation). It should be noted that prey availability is not a simple index of how much breeding has occurred in a given prey species. Rather, the activity patterns of prey and their responses to the presence of predators are two of many possible influences on how much prey is actually available to predators.

Cross-References

► [Prey Choice](#)

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Prey Choice

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Synonyms

Foraging decision; Prey preference; Prey selection

Definition

The term *prey* refers to an organism or part of an organism (e.g., eggs, seeds) that is consumed by a predator. *Prey choice* refers to the outcome of an organism's decision to seek, capture, and consume a specific type of prey. This may encompass a choice between alternative and available prey species, or opting for a specific characteristic of one particular prey species, such as a polymorphic variant or optimally sized prey item.

Introduction

In order to survive, and ultimately reproduce, animals must consume enough calories to meet their energetic requirements. Foraging involves balancing the benefits of consuming prey items that satisfy the energetic requirements of the predator with the costs and risks involved in finding and handling prey. Choice, therefore, plays an important role in predator behavior. Take, for example, crows foraging for clams along an intertidal zone. The crows actively search for and dig up clams of various sizes (and therefore caloric value). A crow then flies to a rocky surface where the clam can be dropped and broken and its contents made accessible. Large clams may require several flight-drop bouts before they break. The time and energy involved in searching for a large clam and possibly having to drop it multiple times are costs to the predator. The benefit (calories gained) of taking a single, large clam should

exceed that of taking multiple smaller clams. Thus, crows must make a choice about what size of clam they should seek out, and what size they should reject, in order to maximize net energy gain that is balanced against foraging costs. Being too finicky and ignoring small clams come at a cost, as does spending excess time trying to break large clams. Richardson and Verbeek (1986) measured the relationship between foraging effort and clam size in crows and estimated that the threshold for the optimal size clam is 28.5 mm. Thus, the *optimal decision rule* for a crow foraging for clams is to select one that is at least 28.5 mm and then expend the energy required to fly to a suitable location to break it open and consume it. As this classic example illustrates, there are trade-offs that determine what animals choose to eat.

Time and energy are key currencies influencing prey choice, but animals must also weigh other variables. For example, foraging may increase an animal's susceptibility to predation. A forager may need to leave a nesting area and therefore increase the vulnerability of its offspring. Furthermore, the quality, availability, and behavior of potential prey species influence prey choice. Choice of clam size by crows involves a decision rule encompassing variation of a single prey species. Predators may also follow decision rules that involve switching among alternative prey species. Canadian lynx (*Lynx canadensis*) shows a preference for snowshoe hare (*Lepus americanus*), but when population numbers of this prey decline, they opt for more abundant rodents (Stenseth et al. 1997). The switch from hare to rodents is an obligatory one, as it is attributable to declining availability of their preferred prey. Predators also actively seek ideal prey among several alternatives (Shulz and Finlayson 2010). Ecologists and animal behaviorists have long sought to model the complex dynamics between predators and their prey and, in doing so, predict and explain prey choice.

Modeling Prey Choice

Classic papers by Emlen (1966), MacArthur and Pianka (1966), and Schoener (1971) marked a

major surge of interest in modeling animal foraging behavior. Common elements across approaches to modeling animal feeding strategies include a currency that is maximized (calories), a cost-benefit function (e.g., reducing search time), and a solution toward an optimum (choosing the most profitable prey). Optimality modeling was integral to behavioral ecology through the 1990s, and although its popularity has waned, it continues to be a valuable approach to studying and understanding prey choice.

One useful concept is the *optimal diet model*, also referred to as the prey choice or contingency model, which predicts that animals should select the most profitable prey available (Krebs and Davies 1993). Larger prey may be more profitable because they afford greater net energy gain relative to smaller prey. However, subduing, transporting, and processing large prey require increased energy expenditure by predators. According to the optimal diet model, the ratio of energy gain (E) relative to handling time (h) determines the profitability of a prey item. Optimal foraging theory predicts that large prey will be chosen over small prey such that:

$$\frac{E_1}{h_1} > \frac{E_2}{h_2}$$

where E_1 is the energy value of the large prey item and h_1 is its handling time and E_2 is the energy value of the small prey item and h_2 its handling time. Based on this simple equation, the predator should choose to consume the larger prey₁ whenever it is encountered. What should the predator do if prey₂ is encountered? Prey₂ may be more profitable if the energy gain from eating it is greater than the gain from spending time (and energy) searching for larger prey₁ (see ► [Search Time](#) for further discussion on how this is modeled).

Work with numerous predator-prey systems supports the optimal diet model. Classic work by Elner and Hughes (1978) demonstrates optimal diet selection by shore crabs (*Carcinus maenas*) feeding on mussels (*Mytilus edulis*). Crabs position mussels using both major and minor chelae and then apply crushing force with the major chela to break open the shell and access the flesh. When

given unlimited access to mussels of different sizes, shore crabs choose the optimally sized ones (e.g., ones that are readily breakable and yield high calories). Crabs deviate from optimally sized prey if resources become depleted. Subsequent work showed that the presence of conspecific competition hastens the handling time of mussels and so actually increases the rate of energy intake (Chakravarti and Cotton 2014). Reduced handling time may be due to more rapid and forceful shell breakage, which results in quicker access to prey, but also carries increased risk of claw damage. Optimal diet selection is therefore influenced by the presence of conspecifics. Further examination of the optimal diet model suggests that it does well to account for prey choice in species that consume immobile prey but less so in predator-prey situations that involve active pursuit and capture (Sih and Christensen 2001).

Optimal foraging theory presumes that food is evenly dispersed, which may or may not be realistic. Food resources may exist in patches, with abundant resources in some areas and no food in other areas spanning a predator's home range. As a patch of food becomes depleted, the net energy gain from remaining at that patch drops below optimal and the organism may choose to locate a new patch. Charnov's (1976) *marginal value theorem* predicts that organisms will move to a new patch when net energy gain at the current one drops below gains that could be acquired by switching locations. Studies manipulating patch quality in laboratory simulations or seminatural situations suggest that the marginal value theorem accurately describes and predicts some aspects of foraging behavior (Lima 1984).

The marginal value theorem models individual foraging decisions, but group foraging presents an additional challenge. The decision to move to a different food patch may be influenced by the number of conspecifics currently utilizing a particular patch. Three-spined sticklebacks (*Gasterosteus aculeatus*) will congregate in foraging groups that are in proportion to food availability: When large quantities of food are at a patch, a large group of fish will forage at that location, and when small quantities are available,

a small group will forage at that location (Milinski 1979). Sticklebacks and other group foragers thus conform to the *ideal free distribution model*, which predicts that group size at a given patch of food will be in direct proportion to the amount of food at that patch.

Learning Processes

Laboratory-based operant learning paradigms have been used to study choice and foraging behavior in animals (Fantino and Abarca 1985). A general procedure for this type of work involves arranging concurrent schedules of reinforcement, where two schedules are simultaneously presented and free-operant responding by the subject (key pecking or lever pressing) to each schedule is monitored. For example, if a concurrent schedule is arranged such that one key is on a fixed ratio 3 (FR3) schedule, and the other is on an FR10 schedule, the organism should choose the FR3 schedule because the payoff is always better. Responding three times instead of ten times is always more efficient and profitable. However, concurrent schedules can be configured to more accurately represent the types of decisions that foraging animals must make. In nature food does not become available with the predictable regularity of an FR schedule. A concurrent schedule using variable ratios models how responding (e.g., searching for prey) is sometimes rewarded after many attempts or after very few attempts (Williams and Fantino 1994).

Furthermore, predators encounter prey that appear at different time intervals. Concurrent schedules of reinforcement using fixed-interval (FI) schedules model this facet of animal foraging (Fantino and Abarca 1985). For example, an FI-20s schedule and a FI-40s schedule give the subject the option of food reward after 20 s and 40 s have elapsed since the last response, respectively. The schedules are in effect regardless of whether the subject is responding, so the optimal choice is to respond to both keys. Of course, key presses will occur more frequently to the FI-20s schedule than to the FI-40s schedule, but the organism obtains the best payoff when it allocates its responses to each schedule.

The allocation of responses on concurrent reinforcement schedules tends to follow a pattern described by the *matching law*, which states that the relative rate of responding to alternative reinforcement schedules is directly proportional to (matches) the amount of reinforcement available for each (Herrnstein 1961). The matching law is expressed as:

$$\frac{BA}{BA + BA} = \frac{rA}{rA + rB}$$

where B represents behavior, such as a key peck, r is the rate of reinforcement, and A and B refer to the levers or keys that can be operated on two different schedules.

The use of concurrent reinforcement schedules and applications of the matching law has furthered our understanding of how animals make choices about feeding in the laboratory, and may apply to natural situations, though their ecological validity is questionable. Also, this approach is heavily focused on the process of choosing between alternatives of the same type of food. While this indeed does occur in nature, it does not directly address why or how organisms switch to different types of available prey.

Applications to Human Evolutionary Psychology

Studies of prey choice and modeling of foraging behavior have focused primarily on nonhuman species. Applying general principles of foraging behavior to humans is challenging because our species has harnessed considerable control over the food that is available for consumption: For most societies, agriculture and animal domestication obviate the need to actively hunt and gather for sustenance. There remain some exceptions comprising human populations that acquire food through hunting and gathering or subsistence foraging. These populations likely express how human populations foraged prior to agriculture and animal domestication.

An illustrative example comes from the Ache tribe of Eastern Paraguay. At the time of Hill

et al.'s (1987) observations, the Ache spent about a quarter of their days foraging in forested areas near the agricultural settlement they had inhabited since the 1970s. During these bouts of foraging the Ache hunt for animals such as peccaries, coatis, and capuchin monkeys and gather fruits, honey, and insects. Behavioral recordings and measures of returns on foraging bouts showed that optimal Ache hunting and gathering habits were dictated by the encounter rates and return rates of available food sources. Consistent with optimal foraging predictions, such as the optimal diet model, Ache foragers utilized food resources that offered significant returns in caloric value relative to efforts required to obtain them. This is why small prey such as insects, small fruits, and small birds were sometimes ignored so that foragers could pursue larger rewards such as peccaries. Furthermore, they did not exploit resources that would reduce returns from foraging bouts.

Based strictly on net caloric gain, foraging for and consuming plant matter is more profitable than hunted game. However, the protein provided by meat is highly valuable to the health status of humans, and optimal health is predicted to result in higher reproductive rates. Additionally, animal products are indispensable due to their lipid content, believed to be the most important nutritive component of animal tissue. This also justifies the pursuit of larger game as it provides a larger reserve of food with higher nutritional value to compensate for the fact that different hunting or gathering parties may acquire food at varying time periods and of different energy returns. As such, the models of optimal foraging theory in the context of the Ache must be modified to recognize the intrinsic health value of available food substances. There is also the matter of optimizing the time spent practicing different foraging strategies. Because there are so many different nutrients to be optimized, the Ache must recognize when the exploitation of one food source must be abandoned in place of another. Ultimately, any food type will have diminishing returns if over-exploited, reducing that food's caloric and nutritional payoff. Also, certain food sources, such as

armadillos, were only pursued during seasons in which they are large enough to be worth the effort (Hill et al. 1987).

Evolution, Plasticity, and Prey Choice

Prey choice has multiple determinants involving evolutionary, ecological, and behavioral factors. Evolved sensory capacities, such as search images or olfactory sensitivity, cue predators toward what type(s) of prey to pursue. Prey switching occurs when the relative abundance of potential prey species changes. Encounter rates between predator and prey will change due to a variety of factors, such as fluctuations in relative population numbers, migration, and defensive and evasive responses by prey. Ecological models predict that prey switching (or frequency-dependent predation) occurs in direct proportion to the abundance of a prey species, with high attack rates associated with elevated prey abundance and low attack rates with low abundance (van Leeuwen et al. 2013).

Evolutionary and ecological processes are major influences on predator-prey responses and dynamics. For example, predators that have evolved a resistance to the defensive mechanisms employed by potential prey offer compelling examples of the relationship between natural selection and prey choice. Garter snakes (*Thamnophis sirtalis*) consume a variety of amphibian species but express an aversion to newts (*Taricha granulosa*) that secrete a noxious chemical (tetrodotoxin) on their skin surface. Both species have a broad geographic distribution across North America, with regional “hotspots” where they share extensive habitat overlap. Garter snake populations inhabiting these hotspots have evolved a resistance to the toxicity of the newts and even incorporate them into their normal diet (Brodie et al. 2002). Thus, prey choice is controlled by both proximate factors such as abundance, migration, and learning, as well as ultimate factors involving evolutionary change. The predator-prey “arms-race” between garter snakes and newts nicely illustrates the relationship between natural selection and diet.

Prey choice is also influenced by rapid ecological disturbances. Bushmeat hunting in Congo basin rainforests influences prey choice by leopards. Cats inhabiting regions with high levels of bushmeat hunting feed on relatively small, less-desired prey in comparison to leopards that do not face such competition (Henschel et al. 2011). Species introductions into wild habitats can also influence both prey choice and avoidance. Cane toads (*Bufo marinus*) are lethally toxic to predators and were introduced in Australia in 1935. Populations of black snakes (*Pseudechis porphyriacus*) that have historical geographic overlap with cane toads actively avoid them when tested in the laboratory and instead choose to eat native frogs. Toad-naïve black snakes readily attempt to eat the toxic toads when tested in the laboratory. Laboratory experiments also show that aversion to toads is not the result of individual learning but rather to an evolved genetic disposition to avoid toads that has emerged over only about 23 generations among populations with historical overlap with cane toads (Phillips and Shine 2006).

Snakes are an ideal model for studying the mechanisms and evolution of prey choice. Snakes consume more than 2000 different species of prey, and what they eat is determined by jaw and body size, phylogenetic constraints, predatory tactics (e.g., envenomation or constriction), geographic distribution, and habitat (Burghardt 1993). The underlying genetic and experiential components of prey choice in snakes can be understood by examining geographical variation of a single species (Krause and Burghardt 2007) or by studying interspecific variation among species showing both shared and uniquely derived dietary preferences (Waters and Burghardt 2013). The genus *Thamnophis* includes several species with diverse, geographically variable diets. Neonatal common garter snakes (*Thamnophis sirtalis*) show chemoreceptive sensitivity to different prey species commonly consumed by adult snakes. Prior to their first feeding experience, neonates direct tongue flicking and predatory strikes toward chemical cues of species-typical prey (Burghardt 1993). While relatively strong responses are directed toward species-typical prey, feeding experience modifies chemoreceptive

responses and also prey choice. Predatory experience with a variety of prey species modifies the search, capture, and ingestion efficiency by garter snakes (Burghardt and Krause 1999; Krause and Burghardt 2001). Plasticity of predatory behavior is particularly important for a dietary generalist such as *T. sirtalis*, with neonates born into geographic locales with variable prey availability. Prey choice for garter snakes, and many other species with widespread geographic distributions, is largely determined (and constrained) by the populations into which they are born.

Genetic factors also interact with feeding experience to influence sensory responses and prey preference. Neonatal garter snakes born to mothers collected from a population that feeds almost exclusively on earthworms show strong and roughly equal chemoreceptive responses to both fish and worm chemical extracts prior to feeding experience (Burghardt et al. 2000). The heritability of these initial responses to both prey species is zero. However, after 12 feedings on fish, the relative change in chemosensory responding to fish (but not worm) odor was significant ($h^2 = 0.53$, $p < 0.0005$). Also, in simultaneous prey choice tests, the snakes showed significant, heritable ($h^2 = 0.26$, $p = 0.05$) preferences for fish over worms. These results demonstrate that genetic processes underlying prey choice change with predator experience. Also, prey choice is facilitated by ecological circumstances. Garter snakes are thought to have evolved from ancestral species that consumed mostly fish and amphibians, but not worms (Rossman et al. 1996). The snakes studied in Burghardt et al. (2000) showed a strong latent response and preference for fish, despite the worm-based diet consumed in natural conditions.

Prey choice in snakes and other organisms is influenced by intraspecific and intersexual morphological variation. Head size and mouth shape and size show considerable phenotypic variation in many vertebrate and invertebrate species, which may arise through evolutionary or epigenetic processes. Arctic charr (*Salvelinus alpinus*) reared on different diets of either large or small prey developed differently sized heads and mouthparts after 24 weeks of feeding experience (Adams et al. 2003). In wild situations, this type of feeding-induced plasticity could result in foraging

specializations and therefore differences in prey choice, within a single species. The foraging specializations in charr and other species could in turn reinforce differences in trophic morphology (Adams et al. 2003). Relatedly, female-biased size dimorphism of body and relative head size, present at parturition through adulthood, has been found in various snake species, including garter snakes (Krause et al. 2003). Among some species, female snakes have larger heads (adjusting for body size) than do male snakes, which may facilitate reduced resource competition between the sexes (Houston and Shine 1993). Wild-caught adult garter snakes show both intersexual and ontogenetic, diet-induced variation in body and head size. Adult females have larger heads than males, regardless of diet, and females from a geographic locale that feeds upon large-bodied vertebrates are significantly larger than are females that feed primarily on earthworms (Krause et al. 2003; Krause and Burghardt 2007). Such differences reflect both intersexual and intraspecific evolutionary and ecologically based dietary divergence, and they can further reinforce differences in prey choice.

Conclusion

Numerous variables influence prey choice. Optimal foraging models capture generalities such as relationships among profitability, handling, and search time: Predators alter their feeding behavior to maximize caloric profitability and minimize energy and time expenditure and predation risk to themselves and offspring. Decades of work in the field of behavioral ecology has shown the utility of optimality models in explaining and predicting prey choice. Agriculture and livestock production impose barriers to applying optimal foraging models to human prey choice, although some work on traditional hunter-gatherer groups has revealed some important insights. In addition to the variables modeled in optimal foraging theory, prey choice is determined by several proximate and ultimate factors. Prey availability certainly influences what predators choose to eat. Predators may switch to new prey via passive mechanisms, such as when a prey species

becomes more or less abundant. Or, a new species of prey may be incorporated into a predator's diet, which is especially likely among predatory generalists such as common garter snakes. Genetic, experiential, and epigenetic processes are also involved in alterations in prey choice. Feeding experience can influence the growth of body and trophic morphology, which can in turn reinforce ontogenetic changes and intraspecific differences in prey choice.

Cross-References

- [Prey Availability](#)
- [Search Time](#)

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Prey Preference

► Prey Choice

Prey Selection

► Prey Choice

Pride

► Culture of Honor ► Self-Esteem as Manipulative Status Communication

Primary and Secondary Auditory Cortex

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Synonyms

[Auditory cerebral cortex](#)

Definition

Parts of the auditory cerebral cortex.

Introduction

The auditory cortex involves a complex organization of connections between cells in order to process auditory information (Moller 2013). Based on an elaborate network of intrinsic and extrinsic connections, the auditory cortex is responsible for the conscious perception of sound and provides the foundation for the comprehension and production of meaningful sounds (Hackett 2015). Moreover, the auditory cortex is defined by the areas of the cerebral cortex that receive thalamic input from one or more divisions of the Medial Geniculate Complex (MGC) (Hackett 2011). The complete anatomy of the human auditory cortex is not completely known, and there is no common consensus amongst investigators regarding the names of the human auditory cortices. Furthermore, the exact anatomic location of the auditory components of the auditory cortex in humans varies from one person to another (Moller 2013). The primary and the secondary are briefly discussed next.

The Primary Auditory Cortex

The **primary auditory cortex (PAC)** occupies the cortex of the supratemporal plane (STP) and is bordered by auditory association areas in circular sulcus and superior temporal gyrus (STG) (Pandya 1995). Further evidence using structural MRI suggests that the location of the PAC is on a region on the medial two thirds of Heschl's gyrus corresponding to Brodmann's area 41 (Pickles 2012; Wasserthal et al. 2014; Moller 2013).

Creating a tonotopic mapping of the auditory cortex has been proven to be a challenging process. This is due to the small size of the auditory cortical fields relative to the spatial resolution of neuroimaging techniques, and the lack of a common consensus in regards to the specific architecture of the human auditory cortex

in terms of its areal borders and number of subdivisions (see Saenz and Langers 2014). Up to date, the only acoustic parameters that have been found to be topographically mapped are frequency (Isaa et al. 2017; Wolak et al. 2017) as well as other complementary maps such as modulation rate (Lithari and Weisz 2017), sensory tuning bandwidth (see Saenz and Langers 2014; Wang and Eliades 2017), and sound intensity (see Bilecen et al. 2002).

The Secondary Auditory Cortex

While neurons from the primary auditory cortex respond mainly to sound, some neurons in the area of the **secondary auditory cortex** respond to other somatosensory stimuli such as touch and vision (Moller 2013). Recent research has indeed shown a structural connectivity between visual cortex and auditory cortex (Chen et al. 2013) as well as multimodal sensory interactions between the sensory cortices (see Hosokawa et al. 2017). According to Moller (2013, p.103), the secondary cortex areas have specific roles such as connecting different parts of the brain. It is noteworthy that both primary and secondary auditory cortices take up only a small fraction of the neocortex. The largest part of the neocortex is composed of association cortices (see Moller 2013, p.103).

Conclusion

The anatomy and function of the primary and secondary auditory cortex was briefly discussed. There have been efforts to create a tonotopic mapping of the auditory cortex. However, the only acoustic parameters that have been successfully mapped are frequency, modulation rate, sensory tuning bandwidth, and sound intensity.

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Primary Circular Reactions

- Newborn Behavior
- Sensorimotor Play

Primary Language Acquisition

► [Language Acquisition](#)

Primate

► [Alarm Callers Are Females with Greatest Genetic Representation](#)

Primate Aggression

► [Nonhuman Primates: Within-Group Conflicts](#)

Primate Brain Size Evolution

► [Brain Size Growth in Humans and Nonhuman Primates](#)

Primate Cooperation

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Synonyms

[Altruism](#); [Collaboration](#); [Helping](#); [Mutualism](#);

Definition

One individual acting to benefit another individual. This includes mutualistic cooperation where two or more individuals act together to provide benefit for all.

Introduction

Cooperation is widespread and an integral part of primate life. Most primate species live in social groups providing many opportunities for cooperation, and this is reflected in the variety of cooperative behaviors observed such as grooming, alarm calls, and coalitionary support that pervade primate life. These behaviors vary in several aspects including how costly they are to individuals carrying them out, the benefits to the recipients, how many individuals are involved, and how frequently they occur. The following section will describe the main forms of primate cooperation and discuss proposed ultimate and proximate mechanisms involved in these behaviors.

Diversity of Primate Cooperation

By far the most common form of cooperation in primates is allogrooming. Individuals spend a large amount of time (up to 20 %) meticulously cleaning the fur and skin of others (Dunbar 1991), in doing so reducing their own vigilance and spending time that could be used for other activities. The time spent on this activity suggests that it has an important function. Part of this is likely hygienic, e.g., by removing parasites, but the major function is social. Grooming is an important aspect of establishing and maintaining social relationships (bonds); pairs that spend more time grooming each other are also more likely to cooperate in other contexts.

One of the correlates of grooming is coalitionary support. As well as cooperating, group members compete for resources, either directly or indirectly via positions in the hierarchy. This can lead to direct aggression between individuals; others may join in on either side of the fight, risking injury to themselves. Social bonds, measured by grooming or proximity, then influence who joins the fight in support of whom.

Food sharing is a further form of cooperation between individuals. Usually this refers to tolerated theft where one individual allows another to take some food from them, though there are also some cases of active transfer where food is given

to another. Food sharing is most common between adults and young, but in several species sharing also occurs between adults. In some cases this is between males and females, possibly related to mating opportunities, such as savannah baboons or rhesus macaques sharing with females on consortships. In other cases sharing can also be between same-sex partners: male chimpanzees will share meat, a highly valuable resource, after a hunt with both male and female group members (Jaeggi and Gurven 2013).

The examples of primate cooperation described thus far are cooperation on a dyadic or triadic level, but cooperation can also involve one individual helping many more individuals or several individuals working together. Alarm calls provide valuable information about a potential threat (including what type of predator) while possibly making the caller more vulnerable to the threat (by drawing attention to themselves). Evidence of audience effects, where individuals are more likely to call when others are present than when they are alone, indicates that this information is for other group members, and recent field experiments with chimpanzees have suggested that they also adjust calls according to whether recipients already know of the danger or not (Crockford et al. 2012).

In contrast to alarm calling, where one individual provides a benefit to many other group members, predator defense and intergroup conflict are two contexts in which several group members may act together in a way that benefits all group members. When neighboring groups of wild capuchin monkeys (*Cebus capucinus*) encounter each other, it can also result in aggression between the groups. Not all group members are involved in these encounters; rather some individuals will leave, presumably to avoid potential danger. Playback experiments have shown that the likelihood of individuals avoiding the intergroup conflict increases with the number of group members present (Crofoot and Gilby 2012). So we see that primates can be cooperative but not indiscriminately so; in some cases, they avoid cooperating to their own benefit.

Grooming, alarm calling, and territory defense are characteristic of primates living in groups.

However, there are also some forms of cooperation that are specific to only a small number of species. Two interesting examples are cooperative hunting and cooperative breeding. Hunting in groups is only seen in chimpanzees (and to a lesser extent in white-faced capuchins). Evidence from some chimpanzee populations suggests that group hunting is cooperative as hunts are more likely to be successful with increasing numbers of participants. The hunter that catches the prey (usually a colobus monkey) keeps possession of it, but will allow others to take pieces. This way a significant proportion of the group will benefit in some way from the hunt. Current research aims to identify whether and how hunters coordinate their actions with each other and how this may vary across populations.

Cooperative breeding is seen in callitrichids (tamarins and marmosets). In some species not only do fathers contribute to the care and provisioning of the infants but also nonparent helpers (often but not always previous offspring). This breeding system is of particular interest because it involves high levels of cooperation and the mature helpers generally do not breed while they are helpers, paying a seemingly high cost to fulfill their role (Digby et al. 2006). This brings us to the ultimate and proximate mechanisms of cooperation in primates.

Mechanisms of Primate Cooperation

The evolutionary puzzle of cooperation stems from the idea that during cooperation individuals are increasing the fitness of others while reducing their own. Therefore, the ultimate mechanisms of cooperation must explain how these behaviors evolved. The proximate mechanisms then aim to explain behavior on the individual level such as the motivational, cognitive, and physiological factors involved.

One important ultimate factor in primate cooperation is inclusive fitness or kin selection. This is particularly apparent in matrilineal species like vervet monkeys, macaques, and baboons; most cooperation (e.g., grooming and coalitionary support) occurs between members of the same matriline (Silk 2007). The proximate mechanisms that lead to preferential may not necessarily

involve individuals recognizing relatives (though there is some evidence that this may occur). Preferences for kin can also be achieved through contextual cues such as familiarity: by spending time with their mother individuals will be more familiar with their maternal siblings as well as other maternal relations such as aunts. Additionally, if there is male reproductive skew, in other words if the alpha male sires most offspring during his tenure, then a preference for same age peers will result in a preference for paternal siblings (Widdig 2007).

Cooperation also occurs regularly between unrelated individuals. In some cases cooperation is mutualistic: all parties benefit and there is no “evolutionary puzzle” to solve. An example may be cooperative hunting by chimpanzees as with increasing number of hunters, the likelihood of a successful hunt increases. While mutualistic cooperation is less of a puzzle from a theoretical perspective, the proximate challenges of coordinating behaviors remain. Experiments with captive populations have found great apes are able to coordinate their behavior for mutual gains by waiting for a partner when they need one (Melis et al. 2006).

When cooperation between unrelated individuals is not mutualistic, one individual pays a cost to benefit another. In this case the evolutionary assumption is that these benefits are reciprocated in some way (reciprocal altruism). There are several different accounts as to how this occurs differing in the time scales of reciprocation, the currencies exchanged. Long-term field observations show that grooming is reciprocated over medium to long time frames, but not short time frames. This is consistent with experimental studies that find little evidence for contingent reciprocity, suggesting that primates are not necessarily keeping track of each individual exchange (Amici et al. 2014). Rather, much cooperation is part of long-term stable relationships, termed social bonds or friendships (Silk 2007). These can be between kin and non-kin and within or between sexes (depending on the social structure of the species) and are characterized by spending more time in proximity, grooming more, and being more likely to support one another during aggressive interactions. The emotional bookkeeping

account proposes that these interactions result in an emotional response to another individual which then determines the quality of the relationship and the likelihood of further cooperation (Schino and Aureli 2010). This theory does not account for all instances of cooperation, but it does highlight that social bonds are a key aspect of primate life.

Conclusion

The examples of cooperation above are not exhaustive, but they should make it clear that primate cooperation is widespread and multifaceted; cooperation is integral to primate life. However, the examples should also make clear that cooperation is not separate from competition: the two are closely intertwined, and being able to cooperate with others is a part of successfully competing with group members. In summary, the variation in primate cooperation both within and between species reflects the complexity of primate social lives.

Cross-References

- [Cooperative Breeding](#)
- [Kin Selection](#)
- [Reciprocal Altruism](#)
- [Reciprocity](#)

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Primate Dominance Hierarchies

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Synonyms

[Agonistic interactions](#); [Despotism](#); [Dominance](#); [Group social structure](#); [Linearity](#); [Nepotism](#); [Submission](#); [Tolerance](#)

Definition

In nonhuman primates, dominance hierarchies represent one dimension of group social organization. The dominance hierarchy is a clearly discernible ranking order of group individuals, determined by the outcomes of aggressive and submissive (together, agonistic) social interactions that create asymmetrical dominance relationships between individuals.

Introduction

Nonhuman primates exhibit a wide range of social systems, from solitary living to large groups whose composition is fluid and changing;

however, the majority of species show a clear tendency to live in relatively stable, cohesive groups (Isbell and Young 2002). Indeed, numerous diverse animal species have evolved to live in groups, including hyenas, elephants, badgers, elephant seals, and sheep, among many others. A key feature of social organization that has repeatedly evolved in such group-living species is the dominance hierarchy (Lea et al. 2014; Sterck et al. 1997). Dominance hierarchies are an emergent property of asymmetrical agonistic (aggressive and submissive) interactions among group members in which some individuals consistently defeat others, leading to a discernible ranking order (Klass and Cords 2015). These agonistic interactions can take place in a variety of contexts, including access to important limited resources such as food, mates, high-quality habitat, or affiliative partners (Lea et al. 2014). An individual's dominance rank can thus be an important social variable that influences individual behavior and life history.

Describing and Quantifying Dominance Hierarchies

Researchers have developed a wide range of quantitative and descriptive measures to evaluate and compare primate dominance hierarchies. Some measures are indices which describe properties of the dominance hierarchy as a whole, and some refer to characteristics of individuals or subgroups within the hierarchy. Some of the main measures used to quantify dominance hierarchies in primates are described here.

Two widely used summary indices are linearity and steepness. Dominance hierarchies are often measured in terms of their *linearity*, i.e., the degree to which the rank order is transitive (de Vries 1995). In a completely transitive dominance hierarchy, there are no circular dominance relationships, in which, for example, A is dominant to B, B is dominant to C, and C is dominant to A. Rather, the rank order is entirely linear; in a group of six individuals, the top-ranked animal outranks five others, the second-ranked animal outranks four others, and so on. In a completely

nonlinear dominance hierarchy, all individuals will dominate the same number of group mates, and the dominance hierarchy will resemble a web, as opposed to a straight line. While *steepness* also describes the dominance hierarchy as a whole, unlike linearity this index quantifies the power differentials between adjacently ranked individuals, i.e., how certain dominant individuals are to win in interactions with subordinates (de Vries et al. 2006). The higher the steepness of a hierarchy is, the more asymmetrical the relationships within the group, and the more unlikely it is that subordinate individuals would win in agonistic encounters with individuals that are dominant. An additional aspect of the dominance hierarchy that is useful for descriptive and comparative purposes is *rank stability*, which refers to how stable (i.e., constant) the rank order is over time (Bergstrom and Fedigan 2010). Hierarchies in which individual animals frequently change position, moving up or down in rank, are less stable. Stable, and therefore predictable, dominance relationships and rank orders may be beneficial in that they may potentially reduce the risk, stress, and energy inherent in aggressive interactions (Perlman et al. 2016).

Dominance hierarchies are also characterized in terms of the *rates of aggressive or submissive behaviors*, or rates of agonistic interactions overall, experienced by different individuals within the group. Dominance hierarchies often differ in the frequency of agonistic interactions among individuals, and variation may also be seen between high-ranking and low-ranking individuals, who can display marked differences in the rates and types of interactions they experience and whether they display primarily aggressive or submissive behaviors (Klass and Cords 2015). The *severity of aggressive behavior* may also vary, from simply displacing a subordinate individual in space to threatening vocalizations and facial expressions and up to high-intensity physical attacks such as hitting or biting (Lu et al. 2008; Thierry et al. 2007).

An additional important aspect of a dominance hierarchy is the determinants of *rank acquisition*.

There are two main types: in one, dominance rank is determined largely by an individual's competitive ability, stemming, for example, from age, strength, or body size. In the second type of dominance hierarchy, rank is largely "inherited," meaning individuals acquire ranks similar to those of their close kin, which often result from relatives supporting each other in agonistic encounters with nonrelated individuals (Lea et al. 2014).

Three descriptive dimensions are commonly used to describe and differentiate among dominance hierarchies in primates, and the values of many of the above measures are considered indicative of these different types of dominance hierarchies (Isbell and Young 2002; Sterck et al. 1997). The *egalitarian-despotic* dimension describes how clearly established and formalized the dominance hierarchy is, with despotic hierarchies being highly linear and steep with clearly asymmetrical dominance relationships between dominant and subordinate individuals, whereas egalitarian hierarchies are nonlinear, shallow, and harder to detect. Despotic dominance hierarchies may also vary in terms of the *tolerant-intolerant* dimension, which describes how tolerant dominant individuals are of subordinate individuals. Tolerant hierarchies are characterized by decreased severity of aggression from dominants and an increase in challenges from subordinates, leading to overall more symmetrical dominance relationships and less steep dominance hierarchies. Conversely, intolerant hierarchies will display higher intensity aggression in agonistic interactions and highly asymmetrical interactions, as well as less frequent postconflict reconciliation and affiliative behavior. Lastly, the *nepotistic-individualistic* dimension describes the main determinants of rank order; in highly nepotistic dominance hierarchies individuals acquire ranks similar to their kin, and whole kin groups can be ranked relative to one another, whereas in individualistic hierarchies kin rank independently of one another and rank is determined by characteristics of the individual (Klass and Cords 2015; Thierry 2007).

Dominance Hierarchies in Primates: Variation and Phylogenetic Patterns

Primate groups differ in many ways. In terms of dominance hierarchies, two important types of variation that may shape the existence and type of hierarchy that develops are (Isbell and Young 2002):

- (i) Size of the basic social unit. Dominance hierarchies are not an important aspect of social organization in species that are largely solitary or pair-bonded; those that form stable groups can range in size from only a few individuals to hundreds (e.g., mandrills; Setchell and Wickings 2005).
- (ii) Group composition, i.e., single-male/multi-female, single-female/multi-male, or multi-male/multi-female. In species characterized by single-male groups, the dominance hierarchy describes relationships among the females only (and vice versa), whereas in multi-male/multi-female groups, all adults of one sex are usually dominant over the other (e.g., the more rare female dominance in ring-tailed lemurs; Koyama et al. 2005), and the dominance hierarchies of males and females are often analyzed separately, and may be quite different in terms of characteristics such as stability or determinants of rank.

Group composition is shaped by patterns of dispersal, the departure of juveniles or adults from their natal group (the group in which they were born) or current reproductive group to find and settle in a new group in which they attempt to reproduce (Lawson Handley and Perrin 2007). In many primates, dispersal is sex-biased, with mainly or only one sex dispersing and the other remaining in the natal group; the latter is termed the philopatric sex. Most Old World cercopithecines and many strepsirrhines display male dispersal and female philopatry, while this pattern is less common among apes and New World platyrrhines, which tend to have female-

biased dispersal (Lawson Handley and Perrin 2007; Printes and Strier 1999). Exceptions to these general phylogenetic patterns are however quite common, and in some species both sexes disperse at similar rates. A small number of species are characterized by the much rarer strict male philopatry, including chimpanzees, bonobos, spider monkeys, and marmosets (Silk 2009).

Dispersal patterns shape the type and longevity of relationships within the group, including dominance relationships. For example, in female-philopatric species where males disperse, females are able to form nepotistic dominance hierarchies that are stable over generations, where kin support each other in agonistic encounters and rank close together, as they remain in the same group with their female kin throughout their lives (e.g., yellow baboons; Silk et al. 1999).

Initial studies of female primate dominance hierarchies largely focused on a number of cercopithecines, a subfamily of Old World monkeys, many of which are terrestrial, living in open habitats that allow for easy observation. In these well-studied, female-philopatric taxa, such as Japanese and rhesus macaques, chacma baboons, and vervet monkeys, females display similarly stable, despotic, and nepotistic dominance hierarchies. However, while this type of dominance hierarchy has been shown to be quite common and indeed phylogenetically conserved among female-philopatric Old World monkeys (Di Fiore and Rendall 1994), subsequent studies of additional taxa from all primate radiations have uncovered a broad, diverse range of dominance hierarchies among female primates.

For example, the 22 species in the genus *Macaca* largely share the same basic group structure (multi-male/multi-female) and dispersal patterns (most males disperse to new groups at least once in their lifetime, and females are philopatric, permanently remaining in their natal group), leading to females with largely stable, nepotistic dominance rankings and males with dominance status that varies throughout their lifetimes. However, the dominance hierarchies of females in different macaque species vary

considerably in terms of despotism and tolerance, based on differences in the asymmetry in dominance relationships, severity and frequency of aggression, stability of dominance hierarchies, and numerous other attributes (Thierry 2007). Indeed, considerable variation in agonistic behavior and dominance hierarchies has been documented across populations of the same species (e.g., patas monkeys; Isbell and Pruettz 1998), and among groups within a single population (e.g., blue monkeys; Klass and Cords 2015).

The variation in female primate dominance hierarchies only increases when one looks beyond the cercopithecines. Female-philopatric, forest-dwelling Hanuman langurs have stable, linear dominance hierarchies in which rank correlates with physical condition (Koenig 2000). Female mountain gorillas have female dispersal and stable dominance relationships in their nonnatal groups, where rank is determined by age and group tenure (Robbins et al. 2005), and female chimpanzees disperse from their natal groups and have infrequent agonistic interactions and non-linear hierarchies (Pusey et al. 1997). Among female platyrrhines and lemurs, while some exceptions display dominance hierarchies that are similar to the above “typical cercopithecine” hierarchy (e.g., capuchins; Bergstrom and Fedigan 2010), rates of agonism are extremely low compared to cercopithecines (Wheeler et al. 2013) and clear dominance hierarchies are often difficult to detect (e.g., black howler monkeys; Van Belle et al. 2011).

Male primate dominance hierarchies have not been studied to the same extent as female dominance hierarchies (see “[Explaining the Evolution of Primate Dominance Hierarchies: Socioecological Models](#),” below), in terms of variation within and between species, and characterization of despotism, tolerance and nepotism, and their attendant numerical measures. However, several insights are available from existing research.

Linear hierarchies have been documented in many species with multi-male/multi-female groups where all males disperse from their natal groups to seek reproductive opportunities elsewhere, such as ring-tailed lemurs, olive baboons, mandrills, Nepal gray langurs, and crested black

macaques; by contrast, male white-faced capuchin dominance hierarchies have a clear alpha male but do not display a linear hierarchy among the rest of the group males (Perlman et al. 2016). In such species, adult male dominance rank is often determined by the shifting competitive abilities of each individual and the males he is competing against (Perlman et al. 2016; Thierry 2007). These types of male dominance hierarchies are thus often determined by individual attributes, such as fighting ability, size, or strength, which are often correlated with age, leading to an inverted U-shaped correlation curve between rank and age, with males achieving their highest ranks in their prime (Perlman et al. 2016).

In chimpanzees, a male-philopatric species, males compete aggressively for access to females and display linear dominance hierarchies (Muller 2002). They often also cooperate in agonistic coalitions to challenge rivals or maintain exclusive access to females, and agonism with fellow group males is often (but not always) less severe than that displayed in between-group encounters. In at least some populations, male chimpanzees show much higher rates of aggressive behavior, and more intense aggression, than female chimpanzees, and more dominant males show higher rates of aggressive behavior (Muller 2002). Chimpanzee social relationships have been compared to those of female baboons, although nepotism does not play as large a role in structuring relationships in male chimpanzees (Silk 2009). Much less is known about dominance hierarchies among male-philopatric New World species, such as marmosets and spider monkeys, although aggression between male spider monkeys is rare (Slater et al. 2009), male marmosets are known to maintain egalitarian dominance relationships, and males of both species show a considerable degree of affiliative and cooperative behavior (Silk 2009).

Explaining the Evolution of Primate Dominance Hierarchies: Socioecological Models

In some primates, a high dominance rank has been shown to provide fitness-related benefits such as

lower stress levels, reduced risk of aggression, or preferential access to food or mates, and ultimately, higher reproductive success, for both males and females (Majolo et al. 2012). While in studies of individual groups or populations this positive correlation between dominance rank and fitness benefits is not always apparent, a recent meta-analysis showed that broadly speaking, dominant males have significantly higher mating success and significantly higher fecundity (Majolo et al. 2012). A pattern of significantly higher female fecundity in some species, particularly in species with longer lifespans and significantly higher proportion of infants surviving, was also shown.

However, dominance hierarchies are important not only in terms of their consequences for the life history and fitness of individuals within the group but also for our understanding of social evolution: Why do dominance hierarchies form? Why are they such a ubiquitous feature of group living? What causes the enormous amount of variability seen in dominance hierarchies both across and within primate species? A number of ecological and social factors are considered to be the main variables that explain the evolution and variation in primate dominance hierarchies, and these have been combined in several socioecological models (Sterck et al. 1997).

The original socioecological model, developed by Wrangham (1980), focused on the effects of feeding behavior and competition on the formation of primate groups. Wrangham's (1980) model addressed only the "typical" diurnal cercopithecine primate group, with a core of related, philopatric females with a clearly discernible, stable dominance hierarchy, and is based on the fundamental hypothesis that females compete primarily for environmental resources, while males compete primarily for access to females.

This model was then modified by van Schaik (1989) to incorporate the effects of predation avoidance. In van Schaik's socioecological model, female primates form groups primarily as a mechanism of predation avoidance, owing to improved predator detection,

reduced per capita capture risk, and the potential for communal defense. Group living then leads to feeding competition among females, both within and between groups. The type and intensity of feeding competition is determined by the distribution, type, and abundance of food sources relative to group size, and this competition then shapes female social relationships, including agonistic interactions (which often occur in the context of feeding) and dominance hierarchies, similarly to Wrangham's (1980) original model. The distribution of males is then determined by the distribution of females.

van Schaik's (1989) model was further expanded by Sterck et al. (1997) to incorporate the effects of interactions between males and females on group structure and social behavior, specifically the effects of infanticide by males. Sterck et al. (1997) and subsequent studies (e.g., Isbell and Young 2002; Lu et al. 2008) also further developed model predictions regarding the specific effects of different types of feeding competition on agonistic relationships and the formation of dominance hierarchies among female primates, thereby expanding the applicability of the socioecological model to species that display dominance hierarchies that differ from the despotic, nepotistic hierarchy seen in many female-philopatric cercopithecines (e.g., spider monkeys; Slater et al. 2009). When individuals experience strong within-group resource competition, agonism should be frequent, leading to linear, steep, nepotistic, and stable dominance hierarchies, where kin support each other in agonistic encounters against nonkin. However, if competition over food resources occurs mainly between rather than within groups, females should benefit from forming group-wide alliances, which may lead to the formation of more egalitarian and tolerant dominance hierarchies that are less steep. When both types of resource competition are important, they may interact to produce clear dominance relationships and stable, linear, nepotistic hierarchies with a relatively high level of tolerance. Infanticide risk should also increase tolerance, similarly to competition between groups, because females benefit from defensive coalitions with

other group members against aggressive males. Thus when infanticide risk is high, shallower hierarchies with lower intensity aggression should be seen.

While many of the predictions of socio-ecological models are often and consistently borne out in studies of wild primates (see Isbell and Young 2002; Klass and Cords 2015; Sterck et al. 1997), a wide consensus has yet to be reached on the causes leading to the formation of primate dominance hierarchies and the considerable variation seen across and within species (Klass and Cords 2015). With their focus on proximate ecological and social factors, these models predict variation in social organization and behavior independent of any potential constraining effect of phylogeny (Isbell and Young 2002), and thus may only be able to provide partial explanations to observed patterns of dominance hierarchies across species (Clutton-Brock and Janson 2012; Klass and Cords 2015; Thierry 2007).

Conclusion

Dominance hierarchies are an important component of social behavior and organization among group-living primates. Primates display an impressive array of dominance hierarchies that differ in many ways, including between males and females of the same species. The evolution of this variety in dominance hierarchies is the result of a complex interplay of ecological, demographic, social, and phylogenetic variables, and while much remains to be discovered regarding the evolution of this aspect of social behavior among primates, it is clear that evolutionary history, resource competition, predation, dispersal patterns, infanticide, and group size all likely play important roles in shaping agonistic behavior and dominance hierarchies. Dominance hierarchies in turn shape individual primates' experiences within groups and their access to important resources, which may ultimately translate into differential effects on overall fitness and reproductive success.

Cross-References

- [Adaptation and Natural Selection](#)
- [Field of Behavioral Ecology, The](#)
- [Group Size](#)
- [Grouping and Predation](#)
- [Infanticide in Nonhumans](#)
- [Kin Selection](#)
- [Nonhuman Primates](#)
- [Nonhuman Sexual Conflict](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Richard Wrangham](#)
- [Status and Dominance Hierarchies](#)

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Primate Economic Strategies

► [Sarah Brosnan](#)

Primate Gesture

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Definition

Visual signals displayed behaviorally by members of the Primate order, which include lemurs, galagos, bushbabies, tarsiers, Old World monkeys, New World monkeys, great apes, and humans; manual gestures are visual signals displayed by the arms and hands.

Introduction

The most populous primate species, humans, displays rich gestural repertoires. Some human gestures seem universal, whereas many are culturally specific. For example, begging gestures are understood the world over, but the vertical extension of the index and middle fingers in a “V” configuration can mean “peace” (USA) or, depending on its

orientation to the recipient, either “victory” (UK, palm towards recipient) or an obscene expletive (UK, palm oriented away from the recipient). Long considered subsidiary to speech, human gestures have increasingly been characterized as a component in a language system that is inherently multimodal, displayed in multiple sensory channels. With this theoretical accretion of gesture into theories of the evolutionary origins of language has come a concomitant interest in the manual gestures of our nearest living relatives, the great apes.

Primate Gestures

Initial catalogues of primates’ communicative behaviors emphasized facial expressions, vocalizations, and whole-body postures. The first systematic description of apes’ manual gestures was by van Lawick-Goodall (1968), for chimpanzees at the Gombe Stream National Forest, in Tanzania. Fieldworkers subsequently applied functional analyses of apes’ gestural behavior, reporting language-like properties of manual gestures by chimpanzees, based on the theoretical framework of Bates et al. (1975). According to this view, human children begin life in an expressive mode (perlocutionary) and then develop an intentional mode of nonverbal communication (illocutionary) in which gestures and other signals are used to particular ends, culminating in the onset of speech (locutionary) near the end of the first year of life. This framework has been applied to the repertoires of chimpanzees at Gombe Stream; to free-ranging orangutans at the Tanjung Puting Reserve, in central Indonesia; and to numerous analyses of gestural communication in captive ape colonies. According to this framework, whereas locutionary communication is uniquely human, both perlocutionary (expressive signals not under volitional control) and illocutionary signals (intentional communication) are displayed by great apes and monkeys.

Apes display, both in the wild and in captivity, a number of different illocutionary signals. These include, primarily, proto-imperative gestures (requests, commands), for example, requests to be picked up, play solicits, and begging gestures. They also display what Bates and her colleagues

called proto-declarative gestures – the use of objects or the self to capture and manipulate the attention of an observer. Proto-declaratives include a number of overt displays, such as leaf-clipping, in which leaves are abruptly and ostensibly clipped by the signaller’s teeth, and running away with an object. In captivity, there are numerous examples of language-trained apes pointing declaratively, although at the time of this writing, this is disputed by a number of researchers who believe that proto-declarative communication is unique to the human species, that proto-declarative signaling signifies attempts to manipulate the mental states of the recipients of proto-declarative signals, which implies that the signaller has some ability to discern invisible psychological processes in others.

Intentional Communication

For many philosophers, to claim intentionality in the communication of an organism is to claim that the signaller represents the mental state of a recipient of a signal. This influential psychological process model entails that some mental state, an intent, in the signaller is encoded in communicative behavior, and then the original intent is reconstructed through an inferential process in the receiver. Recently, this model has been criticized on grounds that such claims are unverifiable. Most contemporary work in this area applies objective behavioral criteria developed in the study of human communicative development; thus, human babies are said to communicate intentionally when they use gestures to manipulate the behavior of their older caregivers in goal-directed sequences of behavior (Bates et al. 1975). Human babies after about a year of age are understood to communicate intentionally when they accommodate their gestural signals to the visual focus of an observer, alternate their gaze between an observer and the entity to which they are pointing, and they work to repair breakdowns in communication, by repeating their signals or elaborating upon them, when misunderstood (Leavens et al. 2005). All of these characteristics of intentional communication have been

documented in the great apes (chimpanzees, orangutans, gorillas, and bonobos), and subsequent work has demonstrated at least some of these characteristics of intentionality in the gestural communication of some monkey species. Chimpanzees and capuchin monkeys have even been reported to withhold pointing gestures and to point deceptively when a human experimenter establishes a pattern of taking food away when its location is indicated by the animal. At present, the state of the empirical evidence is that monkeys and apes communicate intentionally with gestures, where intentionality has been operationalized to conform with the objective behavioral criteria that establish the development of intentional communication in young humans. The metaphysical question as to whether intentional communication implicates mental state attribution remains open.

Relevance to the Origins of Language

Primate gestures are relevant to a number of contemporary theoretical debates. With respect to theories of the origins of language, scientists look to the manifest intentionality of gestures, which are directed to particular individuals, as evidence that the capacity for human speech was based on an evolutionary platform of intentional communication by gestures in our prehuman forebears (Arbib 2005; Corballis 2002). Subsequent work on captive ape populations established that apes choose the modality of signaling to accommodate the visual orientation of the recipients of their gestures, using audible signals to capture attention and visual signals (like gestures) when recipients are visually attending to the signallers – this implies that apes are sensitive to the behavioral markers of attentiveness in the recipients of their signals. Recent work with both Old World and New World monkeys demonstrates similar kinds of sensitivity to receiver status in the display of manual gestures. Thus, sensitivity to the attentional status of an observer when deploying manual gestures has been reported in Anthroidea (apes and monkeys).

The majority of humans are right handed (left-hemisphere dominant) for gesturing, and this asymmetry has been taken to support a theoretical model in which the left hemisphere dominance for speech was evolutionarily built on an existing left hemisphere specialization for manual gestures (Arbib 2005; Corballis 2002). Studies of handedness in primates reveal a right-hand population bias for manual gestures in great apes and some monkeys (Hopkins et al. 2012). Moreover, in accordance with Dunbar's (e.g., 1996) hypothesis that the origins of language lie in affiliative vocalizations that functionally replace manual grooming, it has been found that chimpanzees are primarily right handed for grooming, which constitutes a mode of tactile communication between individuals. These findings, collectively, are consistent with the idea of an anthropoid left-hemisphere cerebral bias for intentional communication with manual gestures.

Gesture Development and Social Cognition

Another contemporary theoretical debate to which primate gestures are relevant concerns the development of gestures. While many human gestures are conventional (e.g., the V-sign discussed above), some human gestures have been considered to be universal, such as begging and pointing. Among nonhuman primates, most researchers agree that some gestures seem to be biologically based and universal in some species. Examples include begging – which is displayed by the great apes and humans with an outstretched arm and a cupped, supinated palm – and species-specific gestures like the chest-beating display of male gorillas. Tomasello and his colleagues later developed the hypothesis of *ontogenetic ritualization*, the idea that intention movements, which represent whole actions, come to stand for the whole action within any given pair of individuals (e.g., Call and Tomasello 2007). An example of ontogenetic ritualization: when mothers offer their babies objects and the children reach for them, eventually, the children later use their reaching behaviors to instrumentally request object

delivery from their mothers. Chimpanzee juveniles, for example, develop a “tickle-me-here” gesture, involving the placement of their fingertips against the backs of their own necks, and another gesture involving presentation of the ventrum towards the interactive partner; this develops after experiences of being tickled in these spots by the caregiver. Thus, idiosyncratic gestures were taken to imply that individual pairs of primates conventionalize and abbreviate their gestural signaling through repeated interactions. Byrne and his colleagues (e.g., Genty et al. 2009) have criticized this interpretation of the development of ape gestures on several grounds, including (a) that rare gestures were misinterpreted as idiosyncratic based on too few observations, (b) that with large troops typical of wild apes, there becomes an upper limit to the available time to ritualize gesture meanings between all possible pairs of individuals, and (c) there are some gestures that clearly cannot be abbreviated – they give the example of drumming against a tree. On these grounds, they argue that the default hypothesis should be that ape gestures are mostly species typical and genetically canalized. Bard et al. (2014) recently examined the development of some chimpanzee gestures and found evidence for a multitude of developmental processes, including genetic canalization (gestures of submission), ontogenetic ritualization (tickling requests), and a dual-directional dyadic process that they term the “co-construction of meaning” in which both individuals actively construct conventional understandings of signals (grooming solicits).

Pointing and Other Nonverbal Deictic Signals

Finally, there is a contemporary concern with deictic gesturing among primates (use of gestures to indicate specific entities, e.g., pointing, Leavens et al. 2005). Long considered unique to humans, pointing and other such deictic gestures have now been demonstrated in representatives of the three genera of great apes, including orangutans, gorillas, chimpanzees, and bonobos, and

several monkey species, including rhesus macaques, capuchin monkeys, Japanese macaques, and baboons. Human pointing was previously viewed as depending on uniquely human and advanced cognitive capacities to refer to specific entities, and pointing by non-human primates poses a challenge to this erstwhile theoretical consensus. There are three theoretical responses to the emerging findings on primate pointing. In what we might term the Promethean perspective, pointing is viewed as cognitively complex when humans do it, but pointing by other animals is viewed as the consequence of simpler psychological mechanisms. In the Dionysian view, pointing by nonhuman primates heralds the same capacity for representing others’ mental states as it allegedly does when humans do it. Finally, in the socioecological view, pointing is seen as a relatively simple, problem-solving tactic that is adopted by humans and other primates when they are prevented from directly accessing desirable entities; pointing becomes a tool for the manipulation of others when barriers (e.g., cage mesh) prevent direct access to one’s environment. Pointing is frequent in captive populations of apes, but very rare in wild ape populations, although it does happen occasionally in wild habitats. Neither the Promethean nor the Dionysian views on pointing clearly predict this paucity of pointing in the wild, whereas the socioecological perspective predicts this pattern, based on the assumption that captivity imposes a problem space on captive apes that is not often encountered in the wild.

Conclusion

Primate gestures are used intentionally by a range of primate species, although clear evidence of the psychological mechanisms at play continues to elude us. Anthropoid primates use gestures to wide variety of ends; to solicit play, tickling, grooming; to request food and other items; to specify an entity of joint interest; to express subordination and dominance; to solicit sex; and to reposition sexual partners. Within different species, some gestures seem to be

genetically canalized, whereas others may be more conventionalized. There seems to be a right-hand bias for primate gestures, implicating a left-hemisphere specialization for intentional communication. Taken together, these findings support the idea that the common ancestor of humans and nonhuman primates had some of the cognitive bases on which humans later developed speech.

Cross-References

- [Communication and Social Cognition](#)
- [Language and Handedness](#)
- [Nonhuman Primates](#)
- [Primates](#)
- [Social Development in Nonhuman Primates](#)

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Primate Menopause

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Synonyms

[Great apes](#); [Humans](#); [Monkeys](#); [Reproductive aging](#)

Definition

The permanent, non-pathologic, age-associated cessation of ovulation.

Introduction

Menopause is fundamentally a physiological process, and the eventual cessation of female reproductive capacity is common to many primate species. Our understanding of this phenomenon is hindered by a paucity of data, especially in wild animals, and the differences that occur in wild versus captive animals that may obscure the full understanding of this physiological phenomenon.

Menopause is not a uniquely human life event; ample evidence suggests that this biological event occurs in a number of species, including non-human primates. Much of the confusion about the cessation of reproductive viability in non-human primates arises from the difficulty in confirming this phenomenon. Data arise from a variety of sources – field work, captive primate colonies, and from postmortem analyses of reproductive tissue. Evolutionary biologists take a different approach than do endocrinologists and reproductive physiologists, and these disparate

approaches often muddy the waters. Inferring reproductive senescence and postulating menopause based on data from the last live birth, a common approach in field biology and anthropology, provide interesting but inconclusive data. Evaluation of hormonal and histological data in aging nonhuman primates reveals a more compelling picture. It is clear that different methodological approaches to the issue of primate menopause can lead to vastly dissimilar conclusions (Walker and Herndon 2008; Alberts et al. 2013).

Definitional issues of menopause are problematic. Is it simply the “permanent cessation of menstruation” (Oxford English Dictionary 2006) or, more importantly from a biological perspective, the “cessation of ovarian steroid hormone secretion” (Johnson et al. 2004)? Perhaps the most appropriate approach is to view menses as a tangential marker and to focus on underlying physiology which more accurately reflects aging in the hypothalamic-hypophyseal-ovarian axis. Primate menopause, therefore, requires one to expand beyond the notion of menstrual bleeding to include follicular depletion, absence of perineal swelling (in some species), and hormonal changes indicative of permanent anovulation. Understanding of primate menopause can perhaps be more easily achieved if one understands that reproductive aging is not a singular event but rather a process. Falling birth rates, follicular depletion, and increased anovulatory cycles signal a system in decline.

In human females, where menopause occurs relatively early in life, a protracted post-reproductive period exists. The mean age of menopause in human females is approximately 50 years, whereas in rhesus monkeys, the average age is approximately 25 years (Vollman 1977). Humans can live upward of 120 years, so their postmenopausal period can represent nearly 60% of their life span. This contrasts with female rhesus monkeys who have a maximum life span of 40 years and a post-reproductive period reaching up to 40% of the life span. Chimpanzees, on the other hand, experience menopause late in life, occurring around 50 years of age (Lecreux et al. 2008; Herndon et al. 2012). The maximum lifespan for chimpanzees is estimated to be

60-plus years. In this species, only 15% of a female’s life is characterized as post-reproductive. Perhaps a more conservative picture of the post-menopausal period would emerge if average life span were used as the denominator instead of maximal life span. In all primate species studied, this period of age-related infertility would diminish considerably.

Perimenopause, or that transitional state preceding menopause, occurs in humans anywhere from the mid-30s until the early 50s. There are many explanations underlying the variability in the timing of this event, and compelling evidence suggests that nonhuman primates also exhibit perimenopausal signs, including decreased fertility, irregular perineal swelling, and acyclic menstrual bleeding (Santoro et al. 1996).

Great Apes

Among the great apes, most is known about chimpanzee reproductive senescence. Chimpanzees (*Pan* spp.) are not dissimilar to humans with regard to reproductive decline. For example, both species show a loss in follicular development and more frequent fetal loss with advancing age. Despite incongruence in the exact timing of these events, the trajectory is identical. A departure between the two species is evident; however, with regard to the precise timing, humans thrive for years postmenopausally, whereas the end of reproductive life coincides more tightly with end of life in chimpanzees (Herndon et al. 2012). Data from other great ape species is more sparse – in both orangutans (*Pongo* spp.) and gorillas (*Gorilla gorilla*); reproductive characteristics are similar to humans; however, few data exist to document the occurrence of menopause in these species (Caro et al. 1995; Margulis et al. 2007).

Baboons

Data regarding the occurrence of menopause in baboons (*Papio* spp.) are scarce, despite the similarities in the characteristics between human and baboon females with regard to reproductive physiology and pregnancy. The life span of baboons is approximately 25–30 years, and data suggest that irregular cycles and increases in infertility begin to occur in the mid-20s. Despite direct evidence

for menopause in baboons, age-related reduction in fertility and increased inter-birth intervals strongly suggest a gradual loss in reproductive function (Strum and Western 1982).

Macaques

Rhesus monkeys (*Macaca mulatta*) are, perhaps, the best characterized of all nonhuman primate species with regard to menopause. Most data come from captive animals, and evidence suggests that menopause does occur in this species beginning around the age of 26 (Walker 1995). Lack of ovarian reactivity and diminished responsiveness to gonadotropin stimulation has been reported in this species (Walker 1995; Nichols et al. 2005). Although data are sparse in other macaque species (e.g., *M. nemestrina*, *M. fuscata*, *M. sylvanus*), the picture as a whole suggests that all macaque species undergo a period of reproductive quiescence late in life (Paul et al. 1993; Pavelka and Fedigan 1999).

New-World Monkeys

In new-world monkeys, whose maximal life span reaches the late 20s, a reduction in fertility begins to appear in the late teens. Histological analysis of the ovaries of squirrel monkeys (*Saimiri sciureus*) reveals a marked change in folliculogenesis as a function of age, with a sharp, rapid decline in primordial follicles occurring early in life followed by ovarian reorganization later in life, consistent with a loss of ovulatory function (Walker et al. 2009). Tamarins (*Saguinus* spp.) have similarly been found to undergo a period of reduced fertility (Tardif and Ziegler 1992).

Conclusion

Among primates, menopause is not a uniquely human phenomenon. It appears that many (if not all) primate species experience a decline in reproductive function with increasing age. Species' differences exist with regard to the precise timing, vis-à-vis the loss of reproductive viability in the course of the life span, however. Humans appear to have a longer post-

reproductive lifespan than other primate species, although this may be due, in part, to human's increasing longevity. The underlying phenomenon in all primate species suggests a decline of reproductive capacity due to changes in the hypothalamic-hypophyseal-ovarian axis.

Cross-References

- Grandmother Hypothesis of Menopause
- Life Expectancy and Reproduction
- Menopause
- Non-Human Primates

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Primate Object Permanence

► In Nonhuman Primates

Primate Sexual Behavior

► Primate Sexuality

Primate Sexuality

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Synonyms

[Primate sexual behavior](#); [Sociosexual behavior in primates](#)

Definition

Primate sexuality pertains to all the behaviors and set of strategies that both male and female primates adopt to achieve reproduction and/or pleasure. It is influenced by biological and ecological constraints, mating systems, and social dynamics.

Introduction

Primate sexuality is an extremely diverse and complex topic, and notwithstanding many decades of research since the pioneering work of Carpenter in 1942, we still do not have a unified understanding of the complexity of sexual behavior and the factors that influence sexual behavior in our closest relatives (Dixon 1998).

Here the topic will be presented and illustrated with well-known examples, primarily addressing ecology and mating strategies but also the systematics of primate sexuality. The entry will first explore the sexuality of solitary prosimians, then pair bonding and polyandrous *callitrichids*, then the sexuality of uni-male and multi-male catharrines, ending with apes.

When reproductive strategies of primates are explored from a socio-ecological and comparative perspective, it appears that most primates respond to food distribution and predation risk in a predictable manner. This, in turn, influences reproductive strategies, which are often the result of conflicting interests and responses of males and females (Camperio Ciani and Chiarelli 1993).

Primate Socio-Sexual Ecology

Sexual Behavior of Solitary Species

Nocturnal small size prosimians generally feed on insects. Given the distribution of their food source, these species are widely dispersed and at relatively low density. Females do not gain much advantage by clustering in groups and prefer to be solitary. The female bushbaby (*Galago moholi*) has a sealed orifice, and the vagina is locked in a way that prevents copulation outside of estrus. It has been observed that this is a reproductive feature that more closely resembles non-primate mammals than simians (Lipschitz et al. 2001). The only possibility that males have to control them and copulate with them is to roam in larger territories than females and actively search for fertile females, eventually competing agonistically with other males for access to female mates. Some of the solitary nocturnal prosimians show the most divergent sexual behavior compared to other primates.

A long-term study was conducted on the mating behavior of the solitary nocturnal, gray mouse lemur (*Microcebus murinus*) from Madagascar, and once the genetic relationships among more than 300 study animals were determined, the reproductive success of each individual male was quantified. It was found that individuals differ substantially in sexual behavior. The most successful male mouse lemurs roamed extensively in search of mates, had superior fighting ability, and copulated as early as possible. During these searches, contest competitions to temporarily monopolize the females were observed. Traditionally, in nocturnal prosimians, the outcome of this intersexual conflict has been studied from the male perspective, but it also depends on female mating strategies, such as manipulating the temporal distribution of sexual activity, advertisement, and mate choice. In this study on the gray mouse lemur, the relative importance of female mating strategies for the outcome of the sexual conflict was also investigated. The dwarf gray lemur is a species where females are always solitary during their activity period, except for a single night of receptivity. The study found that most females were receptive asynchronously, thus

favoring the best males access to them, by competing with other males and copulate with them, one after the other when receptive. Females did not exhibit any direct mate choice, although they exercised indirect choice for multiple mating. It was observed that they could copulate with up to seven different males and up to 11 times during their only single night of receptivity. Males, on the other hand, exhibited different mating tactics, and heavier males mated more and had greater reproductive success. However, genetic paternity assessment confirmed that most litters had mixed paternities showing that alternative strategies such as having extra copulation hiding from the best males and sneakers, defined as alternative males stealing copulation from unaware best males, were also effective. Male gray lemurs who switched between tactics were influenced by a number of socio-ecological factors such as short-term monopolization potential, mating opportunities, and the operational sex ratio (Eberle and Kappeler 2004).

Sexual Behavior of Pair-Bonded Primates

Among New World monkeys, Callitrichids (marmosets and tamarins) are diurnal and frugivorous in large part, and they dwell in South and Central America. In general, they present mating strategies that are more flexible and span from pair-bonded monogamy, occasionally to polyandry, and even, albeit rarely, to polygyny. These are the first primates where twin births and paternal investment have been observed in the field.

Sexual Behavior of Polyandrous Primates

Studies of wild tamarins and marmosets have focused on understanding polyandry, which is rare in primates outside New World platyrrhine monkeys. Such studies have shown that these species exhibit variable mating patterns, including cooperative polyandry, monogamy, and, more rarely, polygyny. Polyandry is thought to occur in this species due to the very high frequency of twin births and relatively large weight of infants, but small size of adults; this makes infant rearing particularly difficult and need extra help from non parents. Nonreproductive helpers (older offspring) and polyandrous males may serve as

alternative sources of help with infant care. The apparent causes of facultative polyandry in saddle-back tamarins are however quite different from those of the cooperative polyandry that has been studied in some bird species (Goldizen 1988).

On the contrary, other studies suggest that twinning could not have evolved before pair bonding in these species. Further, if theoretically possible and all else equal, males would always increase their fitness with a polygamy strategy, which makes polyandry an evolutionary puzzle. It seems however that adult females in this species pursue a number of strategies designed to coerce the male into remaining monogamous or eventually polyandrous (Dunbar 1995).

As an example, in cohabiting families of common marmosets (*Callithrix jacchus jacchus*), high-ranking individuals of both sexes living within the nest suppress reproductive behavior of both sexes of low-ranking individuals. In this competitive way, these animals maintain a monogamous breeding system. In newly established peer group nests of common marmosets, one male and one female rapidly dominate all others and overtly inhibit sexual behavior in subordinates of their own sex. The highest-ranking dyad starts to copulate and exerts reciprocal sexual inhibition on subordinates: male subordinates are inhibited or restrained from showing sexual behavior influenced by the dominant male, while subordinate females suffer from complete ovarian failure due to dominant female suppression (Abbott 1984).

Old World Monkeys

Old world monkeys are the most widespread non-human primates. They range and prosper across a variety of ecosystems in Africa and Asia. A general socio-ecological classification suggests that females, depending on resource distribution, cluster more or less in different size groups. Consequently, males try to control them with aggressive behavior, without allowing other males into the harem (uni-male groups). If the group of females is too large to be defended, then more males are allowed into the troop. In this case, males will compete within the troop and maintain rank hierarchies to gain sexual access to the

resident female. Members of the multi-male multi-female troop are generally discriminatory and try to outcompete possible intruders (Camperio Ciani and Chiarelli 1993). Alternatively, a review of a number of Old World monkeys suggests that the presence of single- or multi-male troops is associated with the duration of the breeding season: harems are more common when the breeding season is long, whereas multi-male troops are more common when the breeding season is short. The sex ratio of adults in a troop is likewise correlated with the length of the breeding season (Ridley 1986). However there is not a large contradiction of the two perspectives which both rely on female control by males; the first one is based on female number and the second one on female sexual availability.

Sexual Behavior of Uni-male Groups

The hamadryas baboons, (*Papio hamadryas*), which are quite unique among Old World monkeys, are organized in a multilevel structure (harems, clans, troop). In this species, contrary to most nonhuman primates but not to chimpanzees and humans, males tend to remain in their natal clans whereas females tend to move between clans and bands. This creates special bonds that develop between adult males. Within the harem, males show jealousy and herding behavior to keep their harem females in close proximity and fight possible intruders. In the harem, the only adult male has exclusive sexual access to its females. However, uni-male harems of hamadryas baboons cluster overnight on cliffs and safe areas together with other harems. These night clusters generate larger multi-male troops where each single harem is well subdivided. During this crowded situation, extra harem copulations are possible. To apparently reduce the cost of extra harem copulations, it has been shown that closely related males within a troop cluster together in genetically related clans, and each clan is well subdivided within the troop night gathering (Colmenares 1992; Kummer 1968).

Sexual Behavior of Multi-male Groups

When the size of the female group is too large or the duration of the breeding season is too short for females to be controlled by a single male, primates

form multi male-groups. In multi-male groups, the mating system and sexual access is mediated by social rank. However, the relationship between social rank and male reproductive success is not always straightforward, and female choice cannot be overlooked. In many studies without genetic information, clear results cannot be obtained.

In a study on wild long-tailed macaques (*Macaca fascicularis*), a relatively strong correlation was found between rank and reproductive success which was attributable to selective mating by the highest-ranking male during female fertile periods. The relations between mating success (copulations), reproductive success (fertilization), and dominance rank suggest that mating competition is involved. This could be expressed in adult males by having different sexual partners at different phases of fertility, either through male contest competition or female choice (De Ruiter and Van Hooff 1993).

A large sexual behavior and rank review explored mating (copulation) data from 32 studies of primate behavior, totaling 75 study groups, and found, despite conflicting reports, a consistent relationship between male dominance rank and mating success at least among animals of the same age class. These findings suggest that the relationship between dominance rank and mating success appears to be a function of the level of competition that males face in the group for access to cycling females. Data on genetic paternity indicate that these results hold not only for the number of copulations but also for absolute measures of reproductive success (fertilization).

Protection of own offspring and defense from infanticide and the tendency to kill other males offspring also shape primate sexual behavior, and infanticide happens both in uni-male and multi-males troops.

Male parental care in primates is much more common than in other mammals. Adult males of many simians species provide care for infants and juveniles, but this is not observed in prosimians. Among prosimians, care is often observed in the form of grooming, carrying, support in agonistic interactions, and protection from infanticide. For these behaviors to be interpreted as true parental care, males must selectively direct care toward

their own offspring, and this care must result in fitness benefits.

In a wild population of savannah baboons (*Papio cynocephalus*) with genetically determined paternity for 75 juveniles, agonistic disputes by adult males in support of juveniles have been measured in order to examine male care in this species. The results suggest that these baboons show true parental care. Adult males differentiate their offspring from unrelated juveniles and selectively support their offspring in agonistic disputes. This seems to contribute to rank acquisition and protect juveniles from injury and stress (Buchan et al. 2003).

On the other hand, long-term research on wild Hanuman langurs (*Presbytis entellus*) in the southern Nepal forest demonstrates attack on immature juveniles by adult males and corresponding active defense by resident males on immatures. This study recorded in detail and identified all attacks on infants by males. These attacks were analyzed in connection with male residency, genetic paternity, and sexual behavior. Adult males played a major role in infant defense. Only the genetic father or males who were residents when the infant was conceived were observed to protect infants. Males who immigrated after a female had conceived may later attack her infant and were never observed to defend these infants. It seems that the males take only copulations with potentially fertile females but not with pregnant females as clues for paternity. It seems likely that the risk of infanticide is an important determinant in female-male associations even in anthropoid primate multi-male groups (Borries et al. 1999). It should be noted that no convincing evidences ever suggested that males actually could associate copulation and female estrus with infant paternity; hence, the causal explanation for infanticide cannot be the absence of previous copulation with the offspring mother. The infant appears several months after copulation. The physiological mechanism of paternity is a cognitive acquisition unique to humans, and all studies aimed to confirm paternity recognition in primates failed or were disproved. The occurrence of these affiliations between adult males and infants raises the question as to whether males really care for their own offspring

preferentially and, if so, how male paternity confidence is mediated. Recent field studies of baboons suggest that male-infant relationships are mediated through affiliations between the males and the infants' mothers. The male protects the infants of mothers whom they had an affiliative relationship with but attack infants whose mother is unfamiliar, which seems a more plausible proximal cause of paternal behavior rather than actual genetic paternity (Busse 1985; Camperio Ciani and Chiarelli 1993).

Apes' Sexuality

Ape sexuality is highly variable, as in other primate taxa. In general, their sexuality is not substantially different from monkeys, although there are a few interesting exceptions. Orangutan males rape females. Gorillas are not particularly interested in sexuality and have high risk of incest compared to other primates. However, the most peculiar species is the bonobo, a species of chimpanzee, where sex is used in exchange of almost anything, and with anyone, to the point where these animals have been defined as "hypersexualized apes."

Rape in Orangutans

Male orangutans are solitary primates, quite similar to the much smaller and primitive nocturnal prosimians, and like them, they tend to exploit larger territories than females and feed on sub-optimal fruit to attract females in their territory. Adult males keep other males at distance with specific loud calls that are intended to reduce male-male agonistic competition, which can be extremely violent but does not function to attract fertile females. In a long-term study in Tanjung Puting in Borneo, the large adult male indulged to copulate forcefully with the females found on their own territory. These observations suggested that orangutan might rape females. It is a form of rape more sexual than aggressive; in fact males who rape, beside obtaining a copulation, do not succeed in herd, lead, or coerce the raped female, as it happens in aggressive and dominant behavior in other primates (Galdikas 1981). Indeed, rape of females could occur on a daily basis, irrespective of female resistance (Nadler 1977).

Gorillas and Incest Behavior

The sexual behavior of free-ranging mountain gorillas (*Gorilla beringei beringei*) was studied at Karisoke Research Centre. In this ape species, immature males and females develop sociosexual relationships with both peers and adults, and these relationships often lead to mating between natal females and males who are "familiar" partners. This can cause incest with a possible risk of inbreeding. Immature males may copulate with both nulliparous and parous females. However, among adult males, a substantial level of within-group reproductive competition has been observed, which might counteract the risk of inbreeding. During field observations, it has been found that more than one unrelated silver-back male can reside in the same all-male group; however, if the female joins the group, these males become intolerant of each other. Female-female competition for opportunities to copulate with specific males, possibly the best ones, has also been observed. This female-female competition might also contribute to reduce the risk of inbreeding (Watts 1990).

Bonobo Sex for Resources and Sex as a "Social Vehicle"

The most peculiar habits in ape sexual behavior pertain to bonobos (*Pan paniscus*). In this species, sexuality is mostly non-conceptive and is used for a large variety of sociosexual interactions, such as appeasement, in exchange for food, and as a social bond within the group, and is frequently performed both in adult and juvenile relationships. Sexual behavior with non-fertile females, by same-sex partners, and adult-immature dyads is not a product of captivity and occurs both in wild and captive bonobos. Proposed functions of these wild sexual behaviors, in social primates generally, include practice for immatures, paternity confusion, exchange, and communication as well as appeasement (Manson et al. 1997). The evolution of non-conceptive sexuality in bonobos and chimpanzees (*Pan troglodytes*) can be examined from a functional perspective. Bonobos and chimpanzees have three functions of sexual activity in common (paternity confusion, practice sex, and exchange for favors), but only bonobos use

sex purely for communication about social relationships. Bonobo hypersexuality appears closely linked to the evolution of female-female alliances in other primate species. It has been suggested that these female alliances are made possible by relaxed feeding competition, favored through their effect on reducing sexual coercion, and a high level of sexual activity is ultimately responsible for the relaxed social conditions in bonobos. Perhaps female-female alliances allowed the evolution of this very peculiar form of communication through sexuality (Wrangham 1993).

Primate sexuality is not finished with this general classification from solitary prosimians to multi-male multi-female Old World monkeys. The sexual variety in primates is just started. Firstly, most or all apparently monogamous species show evidence of extra-pair copulations. Further, in most primates, sexuality does not finish with copulation, since sperm competition occurs, and sperm competition induces a variety of adaptations that originated in many species. Further, sexuality in primates is not limited to copulation for fertilization, as it has been shown for bonobos, but sex is also used for pleasure like masturbation, both in males and perhaps more rarely in females, sex with immatures, etc. Finally, even in a short exploration of primate sexuality, it is not possible to avoid mentioning primate homosexuality.

Other Relevant Aspects of Primate Sexuality

Consorting

First defined by Carpenter (1942) studying rhesus macaques (*Macaca mulatta*) in Cayo Santiago, “consortship” has a central role in the study of the mating behavior of multi-male group living primates. In general, among mammals, interactions between the sexes, particularly those of an affiliative nature, are associated with, and are often limited to, the period of copulation and only occur during female estrus. However, various species of primates exert their sexual behavior during the mating season by developing this special reciprocal bond between two individuals of the opposite sex of variable duration called

consorting. During this phase, the two partners groom each other, keep close proximity, and sometimes abandon the group crowd. The reason why such cohesive male-female bonds persist beyond estrus in nonhuman primates remains partly obscure. Protection from male infanticide has been offered as a potential benefit to females of bonds with males in a variety of primates, including mountain gorillas and gibbons (Palombit 1999). Primate consorting can be conceptually understood as a variation among male/estrous female dyads, which is characterized by three functionally relevant dimensions: mate assessment, courtship, and mate guarding. Here, a courtship component, but not a male mate-guarding component, predicts the rate of fertile mating (Manson 1997).

Copulation Dynamics

Primates generally copulate dorsoventrally, with the exception of orangutans and bonobo apes that indulge also in ventro-ventral copulation like in our species. The male penis is equipped with an internal bone called the *baculum* that assists with intromission during erection. Primate penis, testis morphology, and size are all extremely variable and species specific. In the case of macaques, as an example, the various species are possible to be classified exclusively on the morphology of their penis which is highly variable. The length of the penis and the size of the testis are good indicators of the presence of sperm competition and male-male competition in copulations. Even mounting behavior varies a lot in duration and sequence. In some case, copulatory dynamics reach complexities that have to be learned via trial and error during infancy, as in the case of the macaques, in which males have to climb and hold the rear legs of the female partner to achieve penetration. Among macaques, as an emblematic example, there are species which mount a single time and ejaculate very rapidly. Other species instead reach ejaculation after multiple mounts (e.g., more than ten mounts in sequence in some instances). In these last species, ejaculation takes longer and requires prolonged time of close proximity among partners. In these cases, consorting is more frequent (Camperio Ciani and Chiarelli 1993).

Sperm Competition

Sperm competition might be the inevitable consequence of polyandrous mating behavior or extra-pair copulations. It can happen if two or more males inseminate a single female. It has been demonstrated for a wide variety of animals that males adapt to sperm competition behaviorally, physiologically, and morphologically, e.g., by evolving relatively large testes size to produce more sperm. Sperm competition involves competition between the gametes of two or more males of a species for fertilization of a given set of ova. Sperm competition is widespread among mammals, as in many other groups of vertebrates. If the reproductive organs of male mammals are viewed as an integrated system for production and delivery of spermatozoa (and accessory glandular secretions) to females, then it is logical to assume that sperm competition might influence the evolution of all parts of the system, as well as associated physiological mechanisms (e.g., testicular endocrinology) and behavior (e.g., copulatory patterns). Comparative studies of genital anatomy and sexual behavior in male primates show that penile morphology, and copulatory patterns tend to be more specialized in species which have a multi-male or dispersed (nongregarious) mating system. The penis may be longer and more complex morphologically in such species. Copulatory patterns involving a series of intromissions or prolonged single intromissions are more common in multi-male systems than in species with a monogamous mating system. All pair-living primates investigated so far are found to have relatively small testes, suggesting a single male mating system (monogamy). Sexual selection may have favored the evolution of sperm competition in species where females mate with a number of males rather than with a single partner. Relative testis size is also greatest under such conditions and larger testes occur in some nongregarious or seasonally breeding prosimians, as well as in anthropoids with multi-male mating systems.

Data on interspecific variation in ejaculate quality further show that primate species with relatively large testes also produced ejaculates with relatively large volumes, high sperm counts,

high sperm motility, and more motile sperm. Hence testes size, after controlling for the effect of body size, can be related to breeding systems in primates, all circumstantial evidences of adaptations to sperm competition (Møller 1988).

Sperm Plugs

Adult males have evolved sperm plugs, another way to control fecundity of females. Sperm plugs are present in certain species of primates such as *Macaca fascicularis*. These sperm plugs are a clotted portion of the ejaculate that obstacle new intromission and copulation in the female's vagina. Moreover, sperm plug integrity informs the male that the female did not copulate after him. Sperm plugs can be manually or olfactory inspected, recognized, and removed by single males. Sperm plugs act as a lock or a signature to inform males about recent copulatory behavior of a female. Sperm plugs seem to be most frequent in those genera where females commonly mate with multiple partners and least frequent in genera where females are primarily monogamous or belong to polygynous units. Perhaps sexual selection has played an important role in the evolution of seminal coagulation and copulatory plug function in primates (Dixson and Anderson 2002).

Sneakers and Rape

Sneakers are those males that use an alternative sexual strategy to achieve copulation with females. These males do not compete to achieve a relevant rank and copulatory right, but rather sneak in proximity of a (willing) female to steal a copulation, and eventually a fertilization, unseen by other males. Rape instead happens if these sneakers approach an unwilling female and force her to copulate before the resident male(s) realize. A clear example of sneaker behavior has been studied in the mating behavior and paternity of offspring of patas monkeys (*Erythrocebus patas*). These primates were studied in wild conditions at Kala Maloue National Park, Cameroon. Sneaky mating occurred during both one-male and multi-male situations. If resident males could witness sneaker copulations, they would then perform compensatory mating with the female. This behavior might be effective for a dilution of

sneaker sperm. The presence of sneakers in wild patas monkeys explains the discrepancy found between observation of mating and paternity identification (Ohsawa et al. 1993).

Extra-Pair Copulation

Asian lesser apes are called gibbons and siamangs and live in strictly monogamous groups. These monkeys are very monogamous and there is no dimorphism at all among partners. Even the male sexual morphology of the penis resembles that of the clitoris and labia of the female. The absence of dimorphism has long been considered a clear evidence of strict monogamy. However, also in these strict monogamous species, not everything in their sexual behavior is clear and straightforward. In a study conducted in the rainforest of Thailand, it has been shown a clear evidence for extra-pair copulations in white-handed gibbons. Researchers found that extra-pair copulations constituted 12% of all recorded copulations. Extra-pair copulations were present among three free-ranging, well-habituated groups. These extra-pair matings involved one adult already-paired females and three adult already-paired males. Extra-pair copulations were explained by the researchers as an effort to breed with a partner of superior quality to the current mate and possibly as part of a strategy to forestall infanticide. In any case, in these highly monogamous primates, it has been shown that monogamy is not absolute, and extra-pair mating occurs (Reichard 1995).

Male Masturbation

Male and female nonhuman primates from all living taxa are known to perform auto-sexual behaviors (masturbation) implying that masturbation is a facet of the primate sexual repertoire. At a proximate level, masturbation satisfies sexual desires leading to a hormonal state of relaxation and reduced aggression in both sexes. This might be of importance above all in social living primate species. Ultimately, masturbation might be beneficial for males since it helps to discard old and low-quality sperm from the genital tract, allowing the production of new sperm with enhanced fitness. For example, in Japanese macaques (*Macaca fuscata*), masturbation occurred over

the whole year; however, it was more frequent during the mating than during the non-mating periods. Notably, masturbation with ejaculation is restricted to the mating period. In this species, male mating success correlates positively with social status. Both rate of masturbation only and masturbatory ejaculations increased as male social status and male mating success declined. Lower-ranking males had higher rates of masturbation, and they spend more time masturbating than higher-ranking males. Lower-ranking males also have higher proportions of ejaculates for masturbation, while higher-ranking males use most of their ejaculates for mating.

Female Masturbation

In bonobos, the species is characterized by a high frequency of ventro-ventral copulation, a prolonged period of female sexual responsivity and homosexual behavior, especially between females in the form of genito-genital rubbing, which can be considered a reciprocal masturbation. Both wild and captive female bonobos exhibit this form of non-copulatory sexual behavior called genito-genital (GG) rubbing – in which two females rub their genital regions together, producing a reciprocal masturbation. For female masturbation, however, an ultimate explanation is still lacking. It seems that GG-rubbing in bonobos occurs in several contexts and may serve several functions, including tension reduction and reconciliation. The hypothesis is that GG-rubbing reinforces or at least reflects social bonds. Bonobo females might GG-rub to generate pleasure rather than to reconcile conflicts, reduce tension during feeding, signal social status, or to attract mates (Manson et al. 1997).

Homosexual Behavior

Homosexual behavior is defined as genital contact, genital manipulation, or both between same-sex individuals. Available data indicate that this behavior is phylogenetically widespread among the anthropoid primates, but apparently absent among prosimians. There is a particular difference however from human homosexuality since in all primate studies with some evidence of homosexual behavior, no permanent homosexual

individuals have been observed, but on the contrary homosexuality is only occasional (Camperio Ciani et al. 2015; Vasey 1995). (See primate homosexuality for further information.)

Conclusion

This synthesis of variety in primate sexuality illustrates most of the possible primate strategies through which males tend to increase their reproductive fitness and how females exercise choice and partner selection. In primate sexual conflict, ecological and social variables suggest new solutions and strategies that sometimes favor females over males or vice versa but still select for optimal reproductive success. Primate sexuality should be an essential topic for anyone interested in the sociosexual behavior of our human species.

Cross-References

- ▶ [Aggression for Sexual Access](#)
- ▶ [Animal Signaling](#)
- ▶ [Bonobo Sexuality](#)
- ▶ [Breeding Systems](#)
- ▶ [Chimpanzee Sexuality](#)
- ▶ [Competition for Resources Desired by Females](#)
- ▶ [Conflict of Mating](#)
- ▶ [Copulatory Plugs](#)
- ▶ [Female Choice](#)
- ▶ [Helper at the Nest Among Nonhuman Primates](#)
- ▶ [Homosexuality](#)
- ▶ [Human Sexuality](#)
- ▶ [Infanticide](#)
- ▶ [Intersexual Selection](#)
- ▶ [Male-Male Competition](#)
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- ▶ [Paternity Confusion](#)
- ▶ [Polygamy](#)
- ▶ [Polygyny](#)
- ▶ [Primate Sperm Competition](#)
- ▶ [Promiscuity](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Resource Competition](#)

- ▶ [Sex Differences](#)
- ▶ [Sexual Behavior](#)
- ▶ [Sexual Selection](#)
- ▶ [Social Dominance and Sexual Access](#)
- ▶ [Sociosexuality](#)
- ▶ [Sperm Competition](#)
- ▶ [Status and Reproductive Success](#)

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Primate Sperm Competition

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Synonyms

[Competitive mating](#)

Definition

Competition between the sperm from two or more males for the fertilization of a given set of ova (Parker 1998).

Introduction

The definition given above can apply to all sexually reproducing animals. However, all primates have internal fertilization, meaning that the anatomy and physiology of the female reproductive tract are the only environment in which the sperm of the various males compete for access to the ova (Dixson and Anderson 2004). Furthermore, there are factors that affect the degree of competition among males to gain access to a female's reproductive tract, and this competition is played out at the physiological (e.g., testis histology, ejaculate output) as well as behavioral level.

Sperm Quality

There is a common assertion in animal behavior that sperm are “cheap” (relative to the “expensive” ova of females). While this comparison is superficially accurate, sperm do have a non-negligible physiological cost and are not an infinite resource. Competition among males to fertilize an egg involves physiological processes as well as behavior at both the individual and group levels. To understand sperm competition in nonhuman primates, then, it is necessary to explore all these factors.

Ejaculate Physiology and Frequency

In many species of primates, the ejaculate can be split into two fractions: a liquid and a coagulum (Wildt 1986). The degree to which the coagulum contracts and forms a solid barrier varies between species, but in many it forms at least a partial plug (e.g., rhesus macaques) or becomes a fully substantial plug (e.g., chimpanzees, ring-tailed lemurs). Regardless of the type of barrier this coagulum forms, as it hardens and contracts, it releases sperm into the reproductive tract. There

are two (not mutually exclusive) hypotheses about the function of these coagulates: (1) it helps males by preventing the loss of sperm via backflow out of vagina and/or (2) it might obstruct other males from depositing their own semen thus preventing direct sperm competition in the female reproductive tract (Dixon 2012). These plugs play a crucial role in primate sperm competition because they contribute a sizable portion of sperm to the overall ejaculate and may, in one way or another, increase the chances of fertilizing a female. However, unlike in many insect and bird species, the order in which male primates copulate with a female seems to play little role in the likelihood of fertilization. For example, in birds, the last male to mate with a female before she ovulates is most often the one to fertilize the egg due to sperm storage mechanisms in these species. Most mammals, including primates, do not store sperm in the reproductive tract. Therefore, the only “mating order” effects one would expect in primates relates to the role of the sperm plug. Specifically, the first male to form a plug with a female (and by extension, the longer his plug lasts) would increase his chances of fertilizing the egg. This phenomenon is not really an order effect, however, of the kind we see in birds and insects.

In addition to the physiology of the ejaculate, the frequency with which a male ejaculates can affect the quality of his semen. For example, in an experiment on captive chimpanzees, semen samples were collected hourly over a 5-h period. Over that time period, sperm count in the ejaculate declined by 54% (Marson et al. 1989). Therefore, it is not necessarily the most competitive strategy to constantly ejaculate with every female possible because sperm resources can become depleted. This is where male choice/behavior in concentrated mating effort can be very important in sperm competition (discussed below, see “[Male Behavior](#)”).

Social Organization

One of the biggest factors to affect the degree of sperm competition between males is the mating system of that species (or group). For example, males that live in multimale-multifemale groups with promiscuous mating systems have much more competition per reproductively active

female than relatively solitary monogamous pairs, who by definition should have exclusive access to a female and little to no competition from other males. Interestingly, relative testes size (the ratio of testes to body weight) is heavily predicted by mating system. Primates with multimale-multifemale mating systems have much larger relative testes size than those in polygynous (e.g., harems, one-male units) mating systems, which in turn have larger relative testes size than those of monogamous primates, who have the smallest relative testes (Dixon 2012). The relative size of the testes is important because it determines the seminal volume and amount of sperm an individual can produce. Therefore, if multiple males are competing to impregnate a single female, the male with the greatest seminal volume or highest sperm count has a better chance of fertilizing a given ova.

Male Behavior

As mentioned above, while sperm are “cheap” to produce, male ejaculate quality can decline from overuse. Males can engage in sperm competition by timing their ejaculations to coincide with the peak of female fertility. For example, many female primates advertise fertility through obvious and exaggerated signals such as swelling or skin color (e.g., baboons, rhesus macaques, Higham et al. 2011). Males who both correctly interpret these signals and concentrate mating effort at these times can reduce the number of ejaculations needed in order to fertilize an egg. By successfully concentrating mating effort at times of peak female fertility, males can not only increase their chances of fertilizing that particular female but they can also reduce the number of ejaculations spent per female. This reduction in number of ejaculations allows males to keep a larger reserve of sperm (i.e., nondepleted semen) for future mating opportunities.

Alternatively, males who do not ejaculate very often or at all can develop different problems with sperm quality. Specifically, if sperm are stored too long, they can degrade or develop abnormalities. A possible solution to this problem is masturbate to expel the degraded sperm in order to have only the best quality sperm available if a mating opportunity presents itself. However, this strategy is not

without risks because a male can never know when a future opportunity will arise. If a male masturbates too soon before a mating opportunity occurs he may suffer a cost such as being in a refractory period (i.e., the period of time it takes to recover and be able to ejaculate again after previously ejaculating) when a sudden mating opportunity arises. Males must make behavioral decisions based on likelihood of mating opportunity. One common proxy for mating success is male dominance rank, because the highest ranked males often mate much more often than lower ranked males. If this is the case, one would expect that lower ranked males (and/or less successful males) should masturbate more frequently, since they are mating less often, and are therefore more likely to have degraded or abnormal sperm. This phenomenon was confirmed in a study of Japanese macaques by Thomsen and Soltis (2004).

Conclusion

Despite the apparent “cheapness” of sperm, there is still fierce competition among males about how to “spend” this limited resource with females in order to maximize their chances of fertilizing a female’s ova. The degree to which males are forced to compete is heavily determined by the mating system of their group, with the highest rates of competition occurring in promiscuous multimale-multifemale groups. Quality and quantity of the sperm itself can vary, due to factors such as the effectiveness of sperm plugs or the rate of ejaculations. Male behavior can also affect sperm competition, in both positive (e.g., timing mating effort to coincide with female fertility) and negative (e.g., masturbating before a mating opportunity) ways. Therefore, due to the complex nature at which this competition plays out, it is important to consider all the potential factors that are working together.

Cross-References

- [Copulatory Plugs](#)
- [Intrasexual Competition](#)
- [Reproductive Strategies](#)

- [Sexual Selection via Direct Male-Male Interactions](#)
- [Sperm Competition](#)

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Primate Tool Use

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Synonyms

[Elementary technology](#); [Nonhuman primate tool use](#); [Physical cognition](#)

Definition

The use of an external object by a nonhuman primate to extend the function of its hand, foot, or mouth to help attain a desired outcome.

Introduction

Although one of the earliest scientific observations of tool use by a nonhuman primate (wild chimpanzees) was reported in the nineteenth century (see Savage and Wyman 1844), the modern study of primate tool use can trace its origins to Jane Goodall's (1968) fieldwork in Tanzania. It was there at Gombe National Reserve that her careful observations of chimpanzees using sticks to forage for termites helped change the view that tool use was a uniquely human ability (e.g., Oakley 1949). Today, reports of tool use among wild and captive primates are widespread and include the use of many objects for many purposes. Thus, in addition to using sticks to forage, primates use stone hammers to crack open nuts, folded leaves for drinking water, poles as ladders, and perhaps even branches and stones as weapons. What follows is an exemplar-based summary of primate tool use in these categories. For a comprehensive list of primate tool use and competencies, see Tomasello and Call (1997) and Shumaker et al. (2011).

Stick Tools and Foraging

Among all nonhuman primates, chimpanzees are the most reliable and frequent users of tools, and a chimpanzee fishing for termites is perhaps the most iconic image of a nonhuman primate using a tool (Povinelli 2000). To fish for termites, chimpanzees use tools that consist of a blade of grass, a strip of bark, or a twig stripped of its leaves. This last tool is of special interest because the chimpanzee modifies an object (a twig) to make it better suited for achieving a particular goal. Once the chimpanzee has an appropriate stick, it inserts the tool into a termite mound. Inside the mound, the termites bite the intruding stick. The chimpanzee then slowly withdraws the stick, pulling out masses of edible insects (Goodall 1968).

Blonde capuchin monkeys also use sticks to fish for termites (Souto et al. 2011). In contrast to chimpanzees who fish for this insect on the

ground, blonde capuchins fish for termites above the ground. With their bodies in a squatting position, these monkeys use their semi-prehensile tail to anchor themselves to a horizontal branch in a tree, which allows them to use both of their hands to fish for the termites. This activity begins with the capuchins firmly and quickly tapping the exterior walls of the termite nest, tearing off a small branch from the tree, inserting and rotating the branch into the nest, removing the stick and inspecting it, eating the termites attached to it, and then reinserting the stick into the nest with one hand and tapping the nest with the other hand. Tapping the walls of the nest and rotating the stick have not been reported for any other primate (Souto et al. 2011).

In addition to procuring insects, primates use tools to help them obtain and eat vertebrate prey. Forest-dwelling chimpanzees hunt and kill colobus monkeys and then use sticks to dig out marrow from these animals' bones and to clean out the orbits of the skulls after having eaten the eyes (Boesch and Boesch 1990). Savannah-dwelling chimpanzees hunt bush babies (small nocturnal prosimians) within tree cavities using a tree branch that they sometimes sharpen with their teeth. The method of capturing the prey varies. Sometimes a chimpanzee jabs the prey to rouse it from the tree hollow and then chases down and kills the prey (Pruetz et al. 2015). Other times, a chimpanzee forcefully jabs the stick multiple times into a tree hollow to injure the bush baby and then extracts the skewered prey (less often) or reaches into the tree cavity to extract the immobilized animal (more often). Used in this manner, these sticks function more like spears than rousing tools.

Orangutans use stick tools to extract honey from bees' nests (van Schaik et al. 1996). The orangutans begin by selecting a live branch from a tree near the nest and then remove the twigs and leaves from the branch. In some cases, orangutans use their teeth to strip the bark and to chew the tip of the branch to fray, split, or flatten it. The tool is sometimes held in the orangutan's teeth when it is being used; other times the branch is held in the primate's hand when it pokes at the nest, which prompts the

bees to exit. The orangutan then uses the stick to extract honey from the nest.

Orangutans also use sticks to pry open and remove the hairs of *Neesia* fruits (van Schaik et al. 2003). When these large fruits ripen, the hard and ridged husk partially splits open. The seeds inside the fruit are edible and desired by orangutans, but are difficult to obtain because they are surrounded by a mass of irritating hairs. To extract the seeds, orangutans select a twig about 12 cm long and use their teeth to strip it of the bark. While holding the stick in its mouth, an orangutan inserts the tool into the cracks of the split husk and scrapes out the hairs by moving them toward the fruit's apex. The orangutan then scoops out the exposed seeds using one of its fingers or the handheld tool (van Schaik et al. 1996).

Hammers and Anvils for Foraging

A New World monkey, the capuchin, uses hammers and anvils to crack open nuts and seeds. These hammers and anvils are often stones: rounded handheld stones for the hammer and flat larger boulders for the anvils. These tools are sometimes made of wood, such as when capuchins use a detached tree branch as a hammer and the roots of a tree as an anvil (Aguilar et al. 2014). Once a monkey finds an appropriate hammer and anvil, it places an object such as a palm nut on the anvil. While standing or sitting, the monkey holds the stone hammer in both hands and pounds the nut. This pounding involves lowering the hammer stone with arm and shoulder movements, but when more effort is required, the standing monkey lifts the stone to shoulder height before pounding the nut forcefully with the stone. After striking the nut, capuchins frequently inspect and reposition it (Fragaszy et al. 2004).

An Old World species, long-tailed macaques, uses stones and shells to detach or break oysters. One behavioral form, ax hammering, is used to crack open sessile rock oysters by chipping the oyster with the edge or point of the tool. A second behavioral form, pound hammering, is used to crack open an unattached food item that is placed

on an anvil (Tan et al. 2015). More specifically, ax hammering uses a tool's points, has a faster strike rate, uses a precision grip, has a wider range of motion, has a smooth strike recoil, and is performed using a variety of postures. In contrast, pound hammering uses a tool's face, starts from a seated posture, has a slower strike rate, uses a power grip, does not usually have a smooth strike recoil, and is performed toward the horizontal plane where the animal is seated (Gumert et al. 2009). Macaques select different stones suited to the different behavioral forms.

Ivory Coast chimpanzees also use stone hammers and anvils to crack open nuts. Like capuchin monkeys, chimpanzees select a smaller stone as a hammer and a larger flat stone as an anvil and may even transport these objects to preferred locations that over time form recognizable primate archaeological sites. One such site at Tai National Park unearthed 4,300-year-old collections of stone tools used by chimpanzees (Mercader et al. 2002). In addition to stone tools, chimpanzees have also been observed using a log as a hammer and the roots of trees as anvils to open nuts (Boesch and Boesch-Achermann 2000).

Fluid Transportation

Most examples of primate tool use are related to the procurement of food. It is perhaps not surprising then that primates also use tools to help them obtain water for drinking. Chimpanzees dip twigs, herb stems, and pieces of grass into water that collects in the recessed areas of a tree (Byrne et al. 2013). After they insert the twigs and stems into the cavities, chimpanzees withdraw these tools and suck the water that clings to them. Chimpanzees also use sponges made from masses of leaves in a similar manner (McGrew 2010). To manufacture these sponges, chimpanzees compress several fresh leaves into an absorbent mass (Sousa et al. 2009). Similarly, chimpanzees use leaf sponges to absorb residual liquids from fruit and the brain tissue from the skulls of vertebrate prey (Beck 1980). Wild bonobos also make sponges out of moss and use these similarly to how chimpanzees use leaf sponges (Hohmann

and Fruth 2003). Captive bonobos and chimpanzees use the shells of fruits as containers for water (Gruber et al. 2010).

Examples of sponging by wild orangutans are rare, though they do sometimes use crumbled leaves to absorb water and leafy branches to “scoop” water from holes in trees (van Schaik et al. 2006). Orangutans living in sanctuaries use cloth, plastic bags, and husks to absorb water (Galdikas 1982). Capuchin monkeys are also known to dip small branches with leaves into tree cavities that contain water (Aguilar et al. 2014). In an urban setting, these monkeys use bread seemingly as a sponge to absorb water (Aguilar et al. 2014). Wild capuchins also use leaves as cups to retrieve water from holes in trees (Phillips 1998).

Climbing and Other Motion Assists

Wild gorillas are not known to use tools. One exception was the observation of a Western lowland gorilla using a handheld detached tree branch seemingly as a walking stick to test the depth of the pool of water she was crossing (Breuer et al. 2005). In another observation of tool use by a wild gorilla, the animal used a detached tree trunk as an object for support. This gorilla held on to the trunk with one hand while outstretched and dredging for aquatic herbs with her other hand. After she finished dredging, the gorilla used the trunk as a bridge to cross a deep section of swamp (Breuer et al. 2005).

In a report of putative tool use by a wild gorilla, a female wild mountain gorilla was observed extending a bamboo pole to her infant who then climbed the pole so that it functioned as a ladder (Grueter et al. 2013). In this case, the observers could not rule out an alternative explanation based on happenstance: Perhaps the mother gorilla simply happened to have a pole in her hand when she looked down at her infant, who then began climbing the makeshift ladder.

Wild orangutans have been observed using tools to facilitate travel. One such report consisted of orangutans who first bit through the bottoms of vines to free them and then used the vines to swing

across a gap in the forest (van Schaik et al. 2006). There are also numerous reports of captive orangutans propping and climbing sticks to secure suspended food (e.g., Yerkes 1916) and captive chimpanzees behaving similarly when they vertically balance poles and then climb them to get bananas suspended overhead (e.g., Köhler 1927). Young chimpanzees will also use poles as ladders to clamber over a high fence (Menzel 1973) and will jam sticks into seams in a fence, creating pitons that they use to climb over the fence (McGrew et al. 1975).

Agonistic Encounters Using “Weapons”

Discussions of primates using tools during agonistic encounters are controversial. The core of the controversy is whether primates use tools as purposeful (goal-directed) weapons to ward off or disable conspecifics, humans, or even inanimate targets during these encounters or whether primates simply use objects as part of a display to make themselves look larger and noisier (Washburn and Jay 1967). The use of objects during agonistic encounters often appears purposeful (van Lawick-Goodall 1971). For example, wild chimpanzees wave and brandish large branches during aggressive interactions with other chimpanzees. During these interactions, chimpanzees adopt a bipedal position, hold the branch in one hand, raise it, and forcefully bring the branch down toward another chimpanzee. The stick-wielding chimpanzee often lets go of the stick before it contacts the target, though the attacking chimpanzee does sometimes continue to hold the stick when clubbing the other chimpanzee (van Lawick-Goodall 1971).

There are also reports of chimpanzees using objects to attack inanimate objects. One such report involved a captive chimpanzee who used a long branch (about 180 cm) to take down a camera-equipped drone. The attack sequence began with the chimpanzee collecting the stick and then climbing some scaffolding while holding the branch. As the drone came closer, the chimpanzee made two long sweeps with the branch she

held in her left hand, contacting and downing the drone with the second sweep. To the researchers who observed this event, the chimpanzee's chain of responses appeared purposeful (see van Hooff and Lukkenaar 2015).

Humans also have been the targets of apes using objects during agonistic encounters. For example, Cross River (Cameroon) gorillas have been observed throwing grass at humans. During other encounters, a gorilla threw a detached branch toward researchers, and a group of gorillas threw fistfuls of grass at a man who threw stones at them (Wittiger and Sunderland-Groves 2007). Whether these encounters reflect an understanding that a particular action produces a particular outcome or were simply a part of an unconditioned display is unclear.

Conclusion

Although there are numerous examples of tool use in nonhuman primates in the wild and in captivity and there are many studies of these animals' behavior both in their natural environments and in laboratory settings, it remains for future studies to answer three key questions about primates' tool use. The first question is: How does tool use develop? Despite an impressive range of tool use behavior (see Boesch and Boesch 1990; McGrew 2013), observations of primates using tools do not usually provide information about how this tool use came to be, particularly in terms of the prior experiences necessary for it. The interrelation between learning and developmental processes seems critical because, for example, capuchin monkeys less than 5 years old rarely manage to use a hammer and an anvil to crack open more resistant nuts (Fragaszy et al. 2013); chimpanzees may require almost 10 years to master this same behavior (Boesch 1993). What role learning plays in the formation of tool use remains to be investigated and debated (Machado and Silva 2003; Povinelli 2000; Tomasello and Call 1997).

The second question is: What do primates understand about their tool use? This is a difficult question to answer because "understand" is not a

well-defined scientific concept (Pear 2001). The answer depends on the definition of the term (see Machado and Silva 2003). For example, if understanding is demonstrated in the same way that concept learning is demonstrated – i.e., requiring that animals make a common response to a class of stimuli that have certain specifiable characteristics – then primates are demonstrating some degree of understanding when using tools in that they use different tools in different contexts (Boesch and Boesch 1990). If "understand" means "able to discriminate between tools on the basis of functionality," then the answer may depend on, among other factors, the species of primate and the testing conditions (cf., LeFauve and Margulis 2015; Povinelli 2000). If "understand" means being able to use the right tool at a particular moment across a range of problems in the absence of explicit training, then it is unlikely that primates understand their tool use (e.g., Povinelli 2000). If "understand" means "able to verbalize a cogent explanation," then primates do not understand their tool use. But if "understand" means simply "behaving in a goal-directed manner," then primates understand their tool use (Pear 2001).

The third question is: Why do some captive monkeys and apes use tools in ways that their wild conspecifics do not (Haslam 2013)? Examples involving gorillas are especially illustrative because these primates rarely use tools in the wild, but do use them in captivity and in laboratory studies. Animals bring to artificial environments what evolved in their natural environments (Timberlake 1990). In that sense, differences between captive and wild primates' tool use may reflect differences in performance rather than ability. The simplest explanation for differences in tool use between these two groups of primates relates to variation in the availability of materials for tools. In captivity, there are a greater variety of materials for tools than in an ecological niche. As such, opportunity more than necessity may underlie differences in primates' tool use in different environments (Koops et al. 2012). It remains for future studies to identify the variables that bring about tool use or constrain its expression.

Cross-References

- Bird Tool Use
- Cephalopod Tool Use
- Confounding Use of Tools on Physical Tasks
- Fish, Amphibian, and Reptile Tool Use
- Human Tool Making
- Role of Experience in Tool Use
- Sequential Tool Use
- Tool Manufacturing

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Primates

► [Social Development in Nonhuman Primates](#)

Priming Paradigm

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Primitively Eusocial

► [Cooperative Breeding](#)

Primogeniture

► [Birthrights and Bloodlines](#)

Principles of Geology

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The full title of this famous book is descriptive and informative: *Principles of Geology; being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation*. Underpinning everything is the concept of “deep time,” the idea that vast amounts of time were available in which geological activity shaped the world. Gradual processes could achieve the necessary shaping and construction; catastrophic events were not required.

John Murray in London published the first volume in 1830; the second volume appeared in 1832, and the third in 1833. Charles Darwin took

the first volume with him when he set off in the Beagle in 1831; the third volume reached him in Valparaíso in 1834.

The *Principles* was a very successful book; 11 editions were published in Lyell's lifetime and a 12th was in preparation at his death. A facsimile version of the first edition has been published by the Chicago University Press and this benefits from a bibliographical section by M. J. S. Rudwick. A successful one volume version has been published by Penguin. This has been edited by J. Secord and concentrates on the philosophical aspects of Lyell geology. The introduction by Secord is an excellent discussion of all aspects of the *Principles* from its conception and execution to its effects and reactions.

The *Principles of Geology* was a highly persuasive book. In clear, straightforward prose, Lyell described geological changes now at work and presented evidence of calm, undisturbed geological conditions on the earth's surface in the past. The book was read widely. By 1841, it was in its sixth edition. It won enthusiastic adherents, among whom was Charles Darwin.

Richard Holmes (2009), in his study of science and the romantic generation considered Charles Lyell and the *Principles of Geology*. He records that the initial publication would finally use scientific evidence to reject the Biblical account of short-scale creation of the earth, as maintained by every authority from Cuvier and Paley to Buffon and Buckland. Lyell's proposal of a "deep time" corresponded to the "deep space" cosmology of William Herschel. It would ultimately, wrote Holmes, provide the supportive authority for Charles Darwin, his great friend, to accept the deep time necessary for evolution by natural selection to take place.

The text was briefly summarized by Bailey (1962, pp. 81–94) and reviewed at greater length by Wilson (1972, pp. 262–339). In the first volume (1830), Lyell offers a history of geology; he wants geology to be separate from cosmogony in the same way that history is separate from theories of the creation of mankind. In chapters 2–4, he traces the history of the subject up to the founding of the Geological Society of London in 1807. He gives a full appreciation to the works of James

Hutton (he was born in the year, 1797, that Hutton died). In chapters 6–9, Lyell considers a theory to account for the life-succession in the rocks of Europe and North America. He suggests a correlation between changes of local climate and the geological distribution of the land and sea. Lyell explained his views on the changes in the organic world that would have followed on changes in the inorganic, he spends the rest of volume 1 discussing historical modifications of geography caused by rivers and springs and seas (chapters 10–17), volcanoes (chapters 18–22), and earthquakes (chapters 23–26).

In volume 2, chapters 1–4 are devoted to a statement and criticism of Lamarck's theory of evolution which proposed that variation of species, whether inborn, as "the effects of internal sentiment," or acquired as reactions to the environment, was inheritable, with results that knew no limit. Lyell argues that species are fixed in the sense that limits have been set to the variability of each and every one. Chapters 5–7 deal with the geographical distribution and means of dispersal of species, and chapters 12–18 consider burial of fossils and the influence that life has had upon the surface of the earth. Lyell is quite clear that the geological record proves that man is a very recent arrival.

The early material in volume 3 considers the parts played by earlier scholars in the consideration of European Tertiary successions after the first steps taken by Cuvier and Brongniart in their description of the Paris basin in 1811. Chapters 3 and 4 discuss unconformities and the probability of correlating fossil assemblages belonging to different zoological provinces, and chapters 5 and 6 present Lyell's scheme of Tertiary classification (based on the proportion of living species and genera to extinct) which he had developed with G. P. Deshayes. In 1839, he renamed the Late Pliocene as the Pleistocene. He introduced the term Pleistocene to describe strata in Sicily which had at least 70% of their molluscan fauna as current species. This distinguished it from the older Pliocene epoch, which Lyell originally thought to be the youngest fossil layer. Chapters 7–20 are devoted to marine, freshwater, and volcanic phenomena belonging

to the various divisions of Recent and Tertiary time. Chapters 21 and 22 discuss the denudation of the Weald of Kent and Sussex. Deshayes supplied a 52-page appendix consisting of tables of fossil shells. The appendix was repeated in the second edition of 1833, but was omitted from the third and subsequent editions. Lyell continued to revise the *Principles* for all of his life; it was always a work in progress so the history of geology from 1830 to 1870 is encapsulated in its pages, as well as Lyell's views on the important issues of the day.

volume 3 was dedicated to R. I. Murchison. "When we quitted England together for a tour on the continent, in May, 1828, the first sketch only of my '*Principles of Geology*' was finished. Since that time you have watched the progress of the work with friendly interest, and, as President of the Geological Society, have twice expressed in your Anniversary Addresses, your participation in many of my views." This sets the start of the *Principles* project; the completion was also commented on in volume 3, in the preface. "In the summer of 1831 I made a geological excursion to the volcanic district of the Eifel, and on my return I determined to extend my work to three volumes, the second of which appeared in January, 1832. The last volume has been delayed till now by many interruptions, among which I may mention a tour, in the summer of 1832, up the valley of the Rhine, when I examined the loess (vol. iii, p. 151)."

When volume 1 came out it was reviewed by Poulett Scrope (1830) for the *Quarterly Review*. This was, in some ways, a response by Scrope to Lyell's lengthy discussion in the Review of his book on the *Volcanic Formations of Auvergne*. The Lyell (1827) review was perhaps his first major piece of geological writing; it was the first small step towards the *Principles*.

Lyell wrote to Scrope on 9 November 1830: "Murray ought to send you £70 for the good you have done the review, to say nothing of probable aid to his book. I am going on now with vol.ii. It would sell, even if stupid (which it shall not be), so great is the excitement for and against, which vol.i and your article have together caused." Scrope later acknowledged the receipt of £100.

Charles Darwin wrote in his autobiography:

The investigation of the geology of all the places visited was far more important, as reasoning here comes into play. On first examining a new district nothing can appear more hopeless than the chaos of rocks; but by reading the stratification and nature of the rocks and fossils at many points, always reasoning and predicting what will be found elsewhere, light soon begins to dawn on the district, and the structure of the whole becomes more or less intelligible. I had brought with me the first volume of Lyell's '*Principles of Geology*' which I studied attentively; and the book was of the highest service to me in many ways.

Geology was important to Darwin and his main access to the ideas of geology was via the *Principles*, and of course via his friendship with Lyell himself. At a critical moment in his life, the copy of the *Principles* indicated a way forward, a process of thought, which led eventually to *The Origin of Species*.

Cross-References

- [Charles Lyell](#)
- [On the Origin of Species](#)
- [Life of Charles Darwin](#)

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Prior Relationships

- [Presence of Children](#)

Prisoner's Dilemma

- [Altruism](#)
- [Repeated or Iterated Prisoner's Dilemma](#)

Prisoner's Dilemma and Cooperation

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Synonyms

[Evolution of cooperation](#); [Evolutionary game theory](#); [Social dilemma](#); [Strategies for successful cooperation](#)

Brief Definition

The prisoner's dilemma (PD) is a two-player game where there is a conflict between individual and group interests. Overall, both players do better if they both cooperate, yet each individual player does better if they defect. However, if both players defect, then they do worse than if they both cooperate, hence the dilemma. This deceptively simple game has been used extensively to explore the conditions under which cooperation can evolve.

Introduction

The widespread evidence for cooperation in the natural world is often seen as an evolutionary

puzzle. This is because, all else being equal, it is fitness-enhancing to reap the rewards of others' cooperation without paying any of the costs. In a group of cooperators who freely help anyone else, selfish strategies possess increased fitness relative to cooperative strategies, and consequently spread through the population until only selfish types remain (West et al. 2007). The tragedy of this scenario is that all individuals would be better off (i.e., have greater absolute fitness) if everyone cooperated (Rand and Nowak 2013). However, natural selection is inherently myopic and only concerned with immediate relative fitness differences between phenotypes, hence this rather pessimistic conclusion. Nice guys, it would appear, do indeed finish last.

However, cooperation is widespread throughout the biological world, from aphids and bacteria to yeast and zebra finches. Meerkats teach young group-mates to hunt and handle prey by deweaponizing otherwise dangerous scorpions; bees will aggressively defend threats to their nest even if they sacrifice their own lives in the process; and slime molds, which are otherwise solitary, build communal structures when times are tough where only some individuals get the opportunity to spore and reproduce. Closer to home, our bodies are composed of highly-cooperative agents, with all our somatic cells facing no prospect of reproduction in order to pass on the germline. Even genomes and chromosomes can be thought of as collectives of cooperative individual genes.

Human beings are cooperative creatures *par excellence*, working together to build societies, engage in warfare (even at a high risk of mortality), and help strangers in need. We even extend this cooperation across the species barrier, by looking after pets who appear to give very little back in return. Even invisible deities or abstract ideological concepts frequently receive our cooperation. Given the ubiquity of cooperation, there must be some solution to the rather bleak conclusion that all life is destined toward selfishness. Without cooperation, the genes of our distant ancestors would not have collaborated, complex life would not have evolved, and the biological world would solely consist of short, microscopic,

strands of DNA. Of course, we should not be misled into viewing the widespread cooperation in nature through rose-tinted spectacles; exploitation is also rife in nature, with organisms frequently willing to manipulate, cheat, or deceive others, and this aspect of behavior should not be overlooked. Given this, the widespread cooperation we observe in the biological world must have evolved because these cooperative strategies outcompeted their less-cooperative counterparts. Using the framework of the PD, several such solutions will be discussed below.

First, the term “cooperation” needs to be defined, as different authors and different disciplines have different definitions of what constitutes “cooperation” (and associated terms such as “altruism”). Here, cooperation is defined as “a behaviour that provides a benefit to another individual (recipient), and the evolution of which has been dependent on its beneficial effect for the recipient” (West et al. 2007, p. 662). This includes behaviors which are both “mutually beneficial” (i.e., both the actor and recipient benefit from cooperation) and “altruistic” (i.e., the recipient benefits but the actor pays a cost). These “costs” and “benefits” are measured in terms of individual fitness, rather than short-term gains and losses (e.g., resources), meaning that behavior which is costly in the short term yet fitness-enhancing in the long term (e.g., reciprocity; see below) would be classed as mutually beneficial, rather than altruistic.

This definition also includes the important proviso that said behavior must have “evolved to benefit others,” meaning that behavior which helps others as a by-product of otherwise self-interested behavior does not count as cooperation, as defined here. For instance, imagine a scenario where a group of four organisms are being attacked; if none of the group retaliate, then the whole group perishes, while each individual who does retaliate increases their own probability of dying by 10%, while increasing the probability of group survival by 25%. In this scenario, the best strategy is for individuals to retaliate, regardless of the actions of others, as the costs to retaliation (a 10% increase in mortality risk) are outweighed by the benefits (a 25% decrease in mortality risk).

Thus, even though this retaliatory behavior may seem cooperative as it increases the survival of other group members, the benefits derived by others are an incidental by-product of otherwise self-interested behavior, so this should not be categorized as “cooperation” (Clutton-Brock 2009).

The Prisoner's Dilemma

The prisoner's dilemma (hereafter PD) is one of the most commonly used tools to explore the evolution of cooperation. The PD is an outgrowth of “game theory,” a branch of mathematics originated by John von Neumann and Oskar Morgenstern designed to analyze the best strategies when interacting with others, given different conditions. In its simplest one-shot version, the PD formalizes the scenario outlined above, where cooperation should not evolve. There are two players in the PD, both of which have to decide whether to cooperate or to defect. On average, both players do better if they both cooperate, yet there is always the incentive to defect as the fitness pay-offs are greater. Yet if both defect, both players earn less than if they both cooperated. These situations are known as “social dilemmas” (Rand and Nowak 2013), which pit individual and group interests against one another. The PD is by far the most common of these social dilemmas, but others are also possible (see below).

The canonical example of the PD (and where it gets its name) concerns two prisoners in the following scenario. Two suspected criminals are brought in for questioning regarding a serious crime and taken to separate rooms. The police have enough evidence to convict them of a minor crime, but not enough for conviction of a serious crime. Each prisoner is then offered a bargain and can either cooperate with the other prisoner (keep quiet) or defect (testify that the other prisoner committed the serious crime). The outcomes of these actions depend on the behavior of the other player. If both cooperate and keep quiet, then each gets charged with the minor offence and serves 1 year in jail. If one cooperates and the other defects, then the defector walks

		Player A	
		Cooperate	Defect
Player B	Cooperate	-1 / -1	0 / -10
	Defect	-10 / 0	-5 / -5

Prisoner's Dilemma and Cooperation, Fig. 1 A pay-off matrix for the PD. The behaviors at the top and the side of the matrix reflect the behavioral decisions made by each player (either cooperate or defect). Each cell represents the number of years spent in prison. The pay-offs for player A are shown in the top right of each cell (above the diagonal), while the pay-offs for player B are shown in the bottom left (below the diagonal). For each prisoner, regardless of how their partner acts, the highest pay-off is to defect, even though mutual defection is superior to mutual defection

away free while the cooperator spends 10 years in jail for the serious crime. While if they both defect then they both get 5 years in prison. These sentences (or pay-offs) are displayed in Fig. 1.

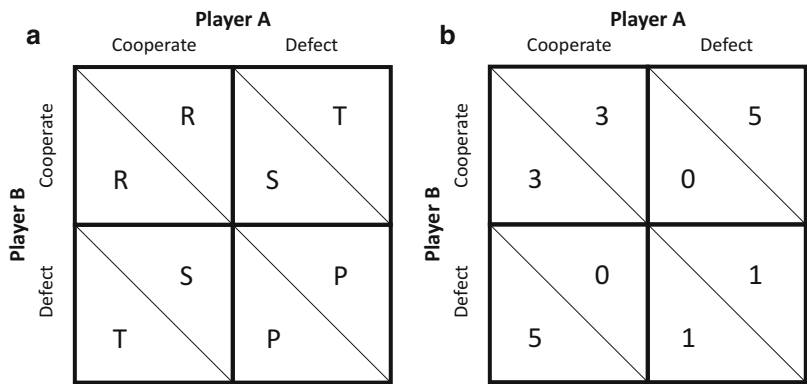
In this scenario, defection is the only rational decision. Even though mutual cooperation results in the highest average payoff for both prisoners (1 year in jail), there is always the temptation to defect if your partner cooperates, as then you would not spend any time in prison. Cooperation is therefore a risky decision because if you cooperate but your partner defects, then you spend 10 years in prison. Consequently, regardless of the behavior of your partner, defection is the only rational option: if your partner cooperates, you can do better by defecting; while if your partner defects, the best outcome is to also defect.

For generality, these outcomes can be displayed in an abstract pay-off matrix (Fig. 2a). There are four possible outcomes: Reward (R), where both parties cooperate; Temptation (T), where an individual defects on a cooperating partner; Punishment (P), where both parties defect; and the Sucker's pay-off (S), where an individual cooperates but their partner defects. These

outcomes can be ranked according to their pay-offs: $T > R > P > S$. This ordering of outcomes defines the PD scenario (other orderings of pay-offs are discussed below). In addition, for a PD scenario, two Rewards must be greater than a Temptation plus a Sucker's pay-off ($2 \cdot R > T + S$), otherwise in iterated games repeated turn-taking of Temptation then Sucker's pay-offs would lead to greater pay-offs than repeated mutual cooperation. The "classic" pay-offs for these outcomes are $T = 5$, $R = 3$, $P = 1$, and $S = 0$ (Fig. 2b). This formalizes the conclusion above that, regardless of the behavior of your partner, it is in your best interests to defect (as $T > R$ and $P > S$). As the same holds for the other player, they should also defect, regardless of the behavior of the first partner. In this one-shot situation, defection is an "evolutionary stable strategy" (ESS; Maynard Smith 1982), in that no other strategy can invade a population of defectors.

This situation seems to fit many of our intuitions regarding the fragility of cooperation and the benefits of reaping the rewards of others' cooperation. Take food-sharing among hunter-gatherers; it is always better to be the one who receives food without paying the costs of foraging (in terms of time, energy, or risk of injury), even if this reduces the overall amount of resources brought back into camp. Or take trench warfare during World War I; it is always better to attack first (defect), rather than abstain (cooperate), as the enemy might attack first, even if this increases the risk of mortality for both sides.

The PD can also be extended to an n -person game – the "tragedy of the commons" – where the same conclusion holds. To use an agricultural example, if farmers have cattle which graze on a plot of land, it would be optimal in the long run for individuals to only allow the cattle to graze as much as can be grown back (cooperate). This would mean that resources remain stable over time, sustaining the long-term future of the population. However, if one farmer purchases more cattle and allows them to graze on the land (defect), their short-term material pay-off will be higher than the other farmers. Therefore, other farmers must also obtain extra cattle in order to compete, causing the resources of the pasture to



Prisoner's Dilemma and Cooperation, Fig. 2 Pay-off matrices of the PD. The pay-offs for player A are shown in the top right of each cell (above the diagonal), while the pay-offs for player B are shown in the bottom left (below the diagonal). (a) This matrix displays the abstract pay-off structure in a PD. R = Reward (mutual cooperation); T = Temptation (defecting on a cooperative partner);

S = Sucker's pay-off (cooperating on a partner's defection); and P = Punishment (mutual defection). The ranking of these outcomes for a PD (from best to worst in terms of pay-offs) is: $T > R > P > S$. (b) This matrix displays the "classic" pay-offs applied in a PD. These pay-offs were used in Robert Axelrod's tournament

deplete past sustainable levels. Real-world illustrations of this "tragedy of the commons" abound: overexploitation of natural resources, man-made climate change, and tax avoidance are all obvious examples where short-term individual gain can have damaging long-term population-level consequences. As can be seen from these handful of examples, the PD can be an incredibly useful tool for modeling myriad different social dilemmas which pit individual and group interests against one another.

To summarize, in one-shot games defection is always the best strategy, which is why the evolution of cooperation is often seen as a puzzle. However, given that cooperation is widespread in the natural world, especially among humans, there must be solutions to this rather pessimistic conclusion. In particular, note that the main conclusion of the PD only holds under rather special circumstances: (i) partners will never meet again; (ii) partners are not related; and (iii) partners interact randomly with others in the population (i.e., individuals cannot choose their partners). If these conditions are not met, then cooperation can evolve, despite the short-term benefits of defection. Several such solutions will be discussed below.

Solution 1: Repeated Interactions

In a PD scenario, defection is the only optimal strategy if interactions are not repeated (and players are not related and cannot choose their partners; see sections "Solution 2: Kin Selection" and "Solution 3: Cooperative Assortment"). Clearly, however, in iterated games, the long-term pay-offs to cooperation are greater than the short-term benefits of defection. Imagine a PD with the pay-off structure in Fig. 2b, repeated for 10 rounds with the same partners. Now consider two sequences, X and Y. In sequence X, Player A cooperates first, while Player B defects; player A therefore receives 0 points, while player B receives 5. In sequence Y, both players cooperate, so both receive 3 points. So far, it appears that defectors have greater fitness. However, in sequence X, Player A now defects (as does player B); therefore, from rounds 2 to 10, each player only receives 1 point per round. For sequence Y, in contrast, both players continually cooperate, so earn 3 points per round. Both players in sequence Y earn 30 points, while in sequence X player A receives a total of 9 points, while player B receives a total of 14. Therefore, if the PD is iterated, cooperators can have higher fitness than defectors.

However, in a *finitely* repeated PD, there is a problem. If players know that the game will only last 10 rounds, then they have an incentive to defect on the last round, thereby increasing their overall pay-offs without harming their future interactions with the other player (because there are none). The other player of course also realizes this, so both players are likely to defect on the tenth round. This effectively means that the ninth round of the game becomes the “final” round, as players will expect their partner to defect on the tenth round, which encourages both players to defect in this preceding round. This vicious cycle repeats back until the first round, in which case the game simply returns to a one-shot PD and the only rational choice is to defect (Axelrod 1984).

Repeated interactions may not therefore solve the problem of cooperation unless the game is repeated for an *unknown* length of time (although note that experimental work has shown that even in finitely repeated games, levels of cooperation are sustained for longer than theoretically expected, although defection does increase as the known end-point approaches; Selten and Stoecker 1986). If players do not know when the final round will be, then the above issue does not arise. In this situation, players do not know with certainty when the final round will be, removing the temptation to defect on the final round; therefore, increasing overall levels of cooperation as long as the probability of repeated interactions is sufficiently high. This corresponds to the common-sense notion that it is better to cooperate with someone if you plan to meet them repeatedly in the future, compared to someone you probably will not meet again.

A test of these predictions was formalized in Robert Axelrod's infamous tournament competition, in which various strategies were pitted against one another in an iterated PD game (Axelrod 1984). There were two versions of this tournament. In the first version, 14 game theorists from fields of economics, psychology, political science, mathematics, and sociology submitted strategies which were paired against one another for five games of exactly 200 moves each (with the pay-offs in Fig. 2b). After this first tournament, a second tournament was staged, which

received 62 entries from six countries. In this second tournament, each strategy was paired for five games of varying length, with an average of 151 moves per game. Example strategies submitted to these tournaments include:

RANDOM: This program randomly cooperates and defects with equal frequency.

GRIM: This strategy cooperates until the other player defects, after which GRIM is unforgiving and always defects until the end of the game.

TFT (tit-for-tat): This program simply begins with “cooperate,” then repeats the previous move of its partner (i.e., if its partner defects, TFT will defect on the next round, while if its partner cooperates, so will TFT in the next round).

JOSS: Similar to TFT, but instead of always cooperating when the other player cooperates, 10% of the time JOSS will defect after its partner's cooperation.

TFTT (tit-for-two-tats): This strategy is equivalent to TFT, but rather than defecting after every partner's defection, it will only defect once its partner has defected twice in succession.

TRANQUILIZER: This rule attempts to build up mutually beneficial cooperative relationships with its partner, while also defecting if its partner defects too often. If a cooperative relationship is established, however, TRANQUILIZER attempts an occasional defection to try and exploit its partner, hoping that the partner will forgive the infrequent transgression. If the partner does not retaliate these defections, then the frequency of defections increases.

In both of these tournaments, rather surprisingly the simplest program came out on top: tit-for-tat (TFT). This strategy received the highest overall score in both tournaments and was shown to be robust in additional analyses against different compositions of other strategies. Additionally, in an iterated evolutionary simulation, where the strategies with the highest score in each generation produced more offspring in the next generation, TFT again outperformed all other strategies and left the most descendants. That is, TFT did

well against all manner of opponents, under a wide range of parameters. TFT was able to succeed against other cooperative strategies by reciprocating in kind, while at the same time was effective against “nasty” strategies as it could not be exploited easily (any defections were met by an immediate defection by TFT). More complex strategies which tried to exploit others were less successful as their defections were likely to set off chains of mutual punishment and defection.

In this iterated PD scenario, TFT was found to be an ESS, in that it is able to resist invasion from any other strategy, provided the PD is repeated enough times. This is because no other strategy can receive a greater pay-off – and therefore greater fitness – than TFT in an iterated PD (for additional details and formal proofs, see Axelrod 1984 and Maynard Smith 1982). The pay-off of TFT against itself is repeated mutual cooperation. The pay-off of TFT against any other cooperative strategy will also be sustained mutual cooperation (i.e., CCCC), so this strategy cannot have higher fitness than TFT, so cannot invade. The pay-off of TFT against an alternating strategy (e.g., DCDC) will always be lower than mutual cooperation (as $T + S < 2 \cdot R$), so this strategy cannot invade TFT. Similarly, a strategy of mutual defection (i.e., DDDD) will also have a lower pay-off than mutual cooperation, so also cannot invade. However, it is important to note that other cooperative strategies can do equally as well as TFT, and this point will be returned to below.

Given the success of this simple TFT strategy, from this tournament Axelrod devised four “guidelines” characteristic of successful strategies which are likely to be important in order to promote cooperation:

Be nice: Never be the first to defect. Of the 15 highest-ranked strategies, all but one was “nice,” in that they were never the first to defect (the highest-ranked “nasty” strategy finished eighth). Of the bottom-ranking 15 strategies, all were nasty.

Reciprocate both cooperation and defection: That is, be both retaliatory and forgiving. It is important to be retaliatory so that other strategies do not exploit you. TFT does this well by

punishing any defectors immediately. At the same time, it pays to be forgiving. If another player defects but then tries to cooperate afterward, it is better to forgive them and cooperate in the future rather than risk repeated mutual defection. It is this quality that enabled TFT to perform better in the tournament than GRIM (which never forgave an initial defection by its partner).

Don't be envious: Successful cooperation is not about obtaining a higher score than your opponent. A striking (although obvious, given some thought) fact is that TFT never beat any of its opponents; the best it could do was to draw (i.e., mutual cooperation), but in the process both partners could accrue a high score. Strategies which tried to beat their opponents were more likely to end up in cycles of defection and consequently earn lower scores.

Be clear: Don't be too clever. TFT is a simple strategy to understand, while more complex programs are difficult to figure out and therefore predict their behavior (such as TRANQUILIZER). For cooperation to be sustained, clarity is key.

This tournament highlights the importance of reciprocity and repeated interactions for the evolution of cooperation, supporting the conclusions presented a decade earlier by Robert Trivers (1971). However, despite the success of TFT, it is not an ESS under all circumstances. Firstly, in a population of ALLD (always defect), a lone TFT cannot succeed as there are no other cooperative strategies to interact with. Therefore, assuming that the mutation rate is not too high and that cooperative strategies enter the population one at a time, defectors will always have higher fitness (Axelrod 1984). As a concrete example, given five rounds of an iterated PD, a solitary TFT will only earn four points (TFT is a sucker once, then defects), while its ALLD partner will earn nine points. All other ALLD strategies in the population which only play against one another earn five points each. ALLD is therefore also an ESS, although TFT has a much wider basin of attraction once cooperative strategies have gained a foothold in the population. TFT therefore has trouble

explaining the initial evolution of cooperation from a noncooperative population, but it can explain its maintenance and spread once cooperation has crossed a certain threshold. However, from a population of defectors, cooperation can evolve if two cooperative strategies emerge at the same time and preferentially cooperate with one another (cooperative assortment; see section “[Solution 3: Cooperative Assortment](#)”), or if the two players are related (kin selection; see section “[Solution 2: Kin Selection](#)”).

Secondly, if there is “noise” in the model, either in terms of mutation and drift or mistakes by other players (e.g., a cooperative strategy may accidentally defect), then TFT is not necessarily an ESS. In a population of TFT, the pay-offs for TFT and other cooperative strategies are equivalent, meaning that given some mutation rate other strategies can invade by genetic drift (Nowak and Sigmund 1993). For instance, if ALLC (always cooperate) invades a population of TFT by drift, this will then trigger further evolutionary dynamics as “nasty” strategies can exploit ALLC. Additionally, Axelrod’s tournament is predicated on the assumption that strategies never make mistakes. This is clearly not the case in the real world as organisms may misinterpret or forget the behavior of their partner and subsequently defect when they should have cooperated. Indeed, after Axelrod’s tournament, it was found that TFT may not be the “best” strategy, as PAVLOV (or, “win-stay, lose-shift”) was found to do better than TFT if mutation and occasional mistakes were included in the model. PAVLOV simply repeats its own previous behavior if it wins (R or T pay-offs), while shifts to the alternative strategy if it loses (P or S pay-offs). PAVLOV’s success over TFT can be attributed to two factors. Firstly, it can exploit unconditional cooperators, while TFT only engages in mutual cooperation with these partners. This means that PAVLOV cannot be invaded by unconditionally cooperative strategies due to drift, unlike TFT. Secondly, PAVLOV can correct occasional mistakes, while for TFT any defection – even accidental – can result in repeated bouts of retaliation. There is therefore no single “best” rule in an iterated PD, independent of the environment of other strategies, but

rules such as TFT and PAVLOV do appear to be robust under a wide range of conditions.

Thirdly, these conclusions only hold in a simultaneous PD game, where both players make their decisions at the same time. While this situation may correspond to some types of cooperative behavior, other situations may reflect an “alternating” PD, where individuals take it in turn to decide whether to cooperate or not (Nowak and Sigmund 1994). For instance, bird parents often take turns obtaining food for their young, while bouts of animal grooming are generally alternating, as are food-sharing situations in human and nonhuman animals. TFT may not be the best strategy in these scenarios, especially if reciprocation is not immediate and there are disparities in need. Need is important as the value of receiving cooperation is greater for those in need compared to those with an abundance of resources (Trivers 1971). Take a monetary example; \$1,000 is more valuable to a person in poverty than to a millionaire. Similarly, the costs to sharing are greater for individuals in need compared to individuals with lots of resources. Using the \$1,000 example again, the cost of sharing this amount is obviously greater to the person in poverty compared to the millionaire. Many PD scenarios assume that the pay-offs are equivalent between the two players, yet these value asymmetries greatly change the cooperative dynamics, making cooperation more likely to evolve (Trivers 1971). For instance, in hunter-gatherer societies, a small number of highly-productive individuals tend to provision others much more than they receive in return. Although this behavior appears altruistic, the costs to sharing these resources are low, relative to the benefits to the needy individuals receiving the food. Importantly, when the tables are turned and these productive cooperative individuals find themselves in need, due to illness or injury, they are more likely to receive resources than less-productive foragers (Gurven et al. 2000). Similarly, among the Agta, a Filipino hunter-gatherer population, individuals in need were both less likely to share resources (Smith et al. 2016) and more likely to receive resources from others (Smith et al. 2018). Such need-based sharing may reflect reciprocal cooperation, but in

circumstances beyond those modeled by simultaneous PD games such as Axelrod's tournament.

Nonetheless, despite these caveats regarding TFT, the basic conclusion that reciprocity and nice strategies can facilitate the evolution of cooperation has been repeatedly supported, both theoretically (see above) and empirically. As a few additional case studies: repeated economic games in a lab are associated with greater levels of cooperation (Rand and Nowak 2013); stable hunter-gatherer camps with a high probability of repeated interactions are more cooperative than camps with a high turnover in membership (Smith et al. 2016); and truces in trench warfare in World War I were more probable when troops were stationed opposite one another for longer lengths of time (Axelrod 1984).

Solution 2: Kin Selection

The paradox of the PD can therefore be overcome by repeated reciprocal interactions. A further solution is through cooperating with those who you share genes with, meaning that by helping relatives you can indirectly pass on your own genes to future generations. Although evolutionary geneticists such as Sewall Wright and JBS Haldane had an intuitive understanding that shared ancestry was important in explaining cooperative behavior, this approach was formalized by William Hamilton (1964) with his theory of "inclusive fitness," often referred to as "kin selection." Hamilton demonstrated that genes for altruism could propagate through a population if these altruistic acts were directed toward genetic relatives. Thus, even though these altruistic acts harm the individual's own fitness (known as their "direct fitness"), they can still evolve if it increases their inclusive fitness by increasing the fitness of their relatives (an individual's "indirect fitness").

The likelihood of an altruistic trait spreading through the population depends on three factors: (i) the benefit to the individual receiving the altruistic act (b), in terms of lifetime reproductive success; (ii) the cost of the actor performing said altruistic act (c), in terms of lifetime reproductive success; and (iii) the coefficient of relatedness between the actor and the recipient (r), which is a measure of assortativity based on genetic

relatedness. If $r = 0$, then kin who share a trait are no more likely to interact with one another than randomly selected members of the population. As r increases, kin are more likely to interact with their genetic relatives (i.e., those who share the same trait), and less likely to interact with nonrelatives (i.e., those who do not share the trait). r frequently (although not always; West et al. 2007) reflects the proportion of genes shared by common ancestry (e.g., 0.5 for parents/offspring/full siblings, 0.25 for aunts/uncles/nieces/nephews, 0.125 for cousins, and so on). Altruism is therefore expected if the benefits to the recipient of a cooperative act, as a function of relatedness, outweigh the cost of the action. This is known as Hamilton's Rule, as is given by the simple formula: $br > c$. To take a simple example, if the cost of an altruistic act is a one-unit reduction in reproductive success for the actor, but a three-unit increase for the recipient, the actor is likely to cooperate if the recipient is a full sibling, but not a niece or nephew. This is because, for a full sibling, 3 (the benefit to the recipient) times 0.5 (relatedness between siblings) is 1.5, which is larger than 1 (the cost to the actor), so the benefits outweigh the costs. For a niece or nephew, however, the benefit is 3 times 0.25 (0.75), which is lower than the cost to the actor, so cooperation would not be expected to evolve in this instance.

As a more formal example, imagine a one-shot PD where $c = 1$ and $b = 3$, meaning that cooperative individuals give up one unit of fitness to increase the fitness of their partner by three units. Defectors pay no costs and help no one. Assuming that all individuals have a baseline unit of fitness (to avoid negative fitness outcomes), the PD pay-offs are: $T = 1 + b = 4$; $R = 1 + (b - c) = 3$; $P = 1 + 0 = 1$; $S = 1 + (-c) = 0$. If we assume random assortment (i.e., $r = 0$), then the inclusive fitness of cooperators is $1 + br - c = 1 + (3 \cdot 0) - 1 = 0$, while the inclusive fitness of defectors is just 1 (their baseline fitness). Given random assortment, defectors have higher inclusive fitness than cooperators. However, when individuals preferentially interact with kin (say, $r = 0.5$), then cooperators have higher inclusive fitness than selfish types, as now the inclusive fitness of cooperators is $1 + br - c = 1 + (3 \cdot 0.5) -$

1 = 1.5, while the inclusive fitness of defectors is still just 1 (their baseline fitness). Note also that from an inclusive fitness perspective the help received from others is ignored, as only the impact of the focal individual's behavior on themselves (c) and others (b , weighted by r) is counted.

Things become slightly more complicated from an inclusive fitness perspective when dealing with nonadditive pay-offs, meaning that the PD pay-off matrix cannot be described solely in terms of c and b . Take the matrix in Fig. 2b, where $T = 5$, $R = 3$, $P = 1$ and $S = 0$. To model this (again assuming a baseline unit of fitness): $T = 1 + b$; $R = 1 + (b - c + d)$; $P = 1 + 0$; $S = 1 + (-c)$, where $b = 4$, $c = 1$ and $d = -1$. Now a "synergistic" d term must be added to the Reward pay-off to satisfy the pay-off matrix. This addition makes deriving a simple " $br > c$ " type inequality – which partitions fitness into direct fitness (c) and indirect fitness (br) – more complicated, although not impossible (see Gardner et al. 2011).

A simpler method to model whether cooperation will evolve among kin when pay-offs are non-additive is to use the "personal fitness," rather than inclusive fitness, approach (also known as "neighbor-modulated fitness"). Personal fitness is calculated based on an individual's total reproductive success (i.e., costs to self of performing the cooperative behavior plus the help received from interacting with cooperative partners). This is in contrast to the inclusive fitness approach where fitness is based on the cost to self of performing the cooperative behavior plus the help given to others, weighted by relatedness. From this personal fitness perspective, the average fitness of each strategy is simply the pay-offs (R and S for cooperators; T and P for defectors), multiplied by the probability of different strategies interacting, which is determined by both r and the frequency of cooperators and defectors in the population (Maynard Smith 1982). Using this personal fitness approach, cooperators can invade a population of defectors if: $rR + (1-r)S > P$. P is the expected fitness of defectors (given that the population is composed primarily of defectors, defectors interact with cooperators so infrequently that the T pay-off is practically 0 so

can be ignored), rR is the pay-off to a cooperator meeting another cooperator (R) multiplied by the probability of a cooperator meeting another cooperator (r), while $(1-r)S$ is the pay-off to a cooperator meeting a defector (S) multiplied by the probability of a cooperator meeting a defector ($1-r$). By the same logic, defectors can invade a population of cooperators if: $rP + (1-r)T > C$. Therefore, given the PD matrix in Fig. 2b, cooperators can invade a population of defectors when $r = 0.5$, as $0.5*3 + (1-0.5)*0 = 1.5$, which is greater than P (1), while a population of cooperators can resist invasion by defectors, as $0.5*1 + (1-0.5)*5 = 3$, which is not greater than R (3). Note also that given the pay-offs in Fig. 2b, one-shot cooperation cannot evolve if $r < 0.33$, while a stable polymorphism of cooperators and selfish types will co-exist given values of $r < 0.5$ and $r > 0.33$.

Supporting these theoretical predictions, kin selection is a powerful explanation for the existence of cooperation in nature, with much seemingly altruistic behavior explicable in terms of increasing an organism's inclusive fitness, even if it damages their direct fitness (West et al. 2007). Organisms caring for their siblings, self-sacrifice in eusocial insects, somatic cells working in service for the germline, and numerous other examples highlight the importance of kin selection in explaining cooperative behavior. Although it can be difficult to dissociate indirect and direct fitness benefits in humans – e.g., we often reciprocally cooperate with our relatives (Rand and Nowak 2013) – kin selection appears to be a powerful force shaping human affairs: kin-based nepotism is rife in human societies, including inheritance rules and regal succession; fictive kinship terms, such as "brother" or "sister," are applied to non-kin as a sign of friendship; while food-sharing among foragers is often targeted toward kin, even when controlling for reciprocal sharing (Smith et al. 2016). Thus, kin selection demonstrates how relatedness can promote the evolution of cooperation, even in one-shot interactions.

Solution 3: Cooperative Assortment

The pessimistic conclusion of the PD also only holds in a well-mixed population, where

cooperators cannot choose who they interact with. If, however, organisms can “rig the game” and only interact and cooperate with other cooperative organisms, then cooperation can evolve much more readily. The previous two solutions above can also be thought of as solving the dilemma via similar assortative processes; repeated cooperative interactions with the same individual, rather than interacting randomly with the population (reciprocity; see section “[Solution 1: Repeated Interactions](#)”) and interacting with close kin, as opposed to nonrelatives (kin selection; see section “[Solution 2: Kin Selection](#)”). At a fundamental level, cooperation can evolve if there is positive assortment in cooperative phenotypes; in the words of William Hamilton, “kinship should be considered just one way of getting positive regression of genotype in the recipient, and that it is this positive regression that is vitally necessary for altruism. . . . it obviously makes no difference if altruists settle with altruists because they are related (perhaps never having parted from them) or because they recognize fellow altruists as such, or settle together because of some pleiotropic effect of the gene on habitat preference” (Hamilton 1975, p. 337). Thus, all theories for the evolution of cooperation are predicated on the principle of assortment.

However, while reciprocity and kin selection are theories of assortativity, they are not theories of *cooperative* assortativity as they do not require organisms to cooperate with others based solely on their partner’s level of cooperativeness. As will be described below, theories of cooperative assortativity can help explain the otherwise seemingly inexplicable cooperation between nonrelatives who may not interact again in the future. This type of cooperation is seen routinely in modern market-based economies, including giving to charity, volunteering, purchasing goods, and academic peer review.

At its most basic level, cooperative assortment occurs when cooperative phenotypes preferentially interact with other cooperative phenotypes. This is easier said than done, however, as mechanisms to establish and maintain this cooperative assortment are required to keep defectors at bay. The concept of “partner choice” is relevant here,

especially when compared to so-called “partner control” (Barclay 2013). Partner choice occurs when individuals can choose who to cooperate with (or to “walk away” from noncooperators), while under situations of partner control individuals cannot avoid noncooperators, but rather have to control the effects of their partner’s selfish behavior. In a repeated PD scenario like Axelrod’s tournament, partners cannot choose each other, so strategies which limit exploitative partners by conditional cooperation and punishment, such as TFT, are necessary; this is an example of a “partner control” situation. On the other hand, if individuals could choose their partners, or walk away from them when they wished, this would constitute a “partner choice” situation. Therefore, if individuals can avoid uncooperative others, rather than having to control them, cooperation can evolve more readily, even in one-shot interactions (Rand and Nowak 2013; Roberts 2015).

One method to promote this cooperative assortment is through the use of reputation. Indirect reciprocity is one such mechanism, which is based on the principle of “helping those who help others” (Nowak and Sigmund 1998). If individuals acquire a reputation for cooperation by being cooperative, and this reputation is known by others, those with a reputation for cooperation are more likely to be cooperated with, irrespective of a lack of previous encounters. Theoretical models have indicated that cooperation can evolve via this process (Nowak and Sigmund 1998), especially when combined with mechanisms of partner choice to avoid uncooperative individuals (Roberts 2015). Results from several empirical studies (reviewed in Milinski 2016) have found results consistent with indirect reciprocity. For example, noncooperative individuals are less likely to be cooperated with in the future, while individuals also appear to engage in “reputation management”; if their behavior will be made public to others, they are more likely to cooperate. Such behavior is particularly apparent in online marketplaces, such as eBay, where individuals who cultivate a reputation for outstanding customer service are more likely to attract new customers.

A related theory based on reputation and cooperative assortment is “competitive altruism” (also

known as “reputation-based partner choice”; Sylwester and Roberts 2013). According to this theory, individuals first signal their cooperativeness, after which these cooperative individuals are more likely to be chosen for mutually beneficial cooperative ventures. For instance, a forager may share their food widely with the camp in order to subsequently be chosen as a partner to share food with or to be chosen as a cooperative hunting partner. Although reputation-based partner choice and indirect reciprocity make similar predictions, such that seemingly costly displays of cooperation will be rewarded by cooperation in future encounters, the mechanisms are distinct. In reputation-based partner choice, individuals preferentially interact with cooperative individuals for future mutually beneficial cooperative interactions with said cooperator. In contrast, indirect reciprocity assumes that individuals help cooperative others solely to enhance their own cooperative reputation so that others will cooperate with them, irrespective of future mutually beneficial interactions with the same partner. Nonetheless, both are theories of cooperative assortment which can explain how one-shot cooperation among non-kin can evolve.

Theories of cooperative assortment are likely to have great relevance in understanding cooperation in modern market-based economies where much cooperation is between unrelated individuals and interactions may not be repeated. Note, however, that these theories based on cooperative assortment may not necessarily predict patterns of cooperation in small-scale societies, where cues other than cooperativeness, such as relatedness or reciprocity, can be used to select partners. For instance, among Agta hunter-gatherers, individuals were more likely to share with *less* cooperative camp-mates, potentially reflecting need-based sharing or the avoidance of being indebted to others. Instead, they were found to preferentially share with kin, reciprocal partners, and those in need (Smith et al. 2018).

Solution 4: Communication and Coordination

Communication and coordination between players does not change the logic of the PD in one-shot games. However, simply giving

strangers 30 min to interact before playing a one-shot PD is enough for participants to predict how cooperative their partner would be (Frank et al. 1993). This simple result highlights the importance of communication and coordination in shaping cooperative behavior. This is especially likely to be a factor in repeated games as individuals need to know that their partner will also cooperate. Unlike the “free-rider problem,” in iterated games, there is a “problem of coordination,” as the issue is not necessarily that of free riders having increased fitness relative to cooperators, but rather the difficulty in coordinating behavior for mutual benefit. In these situations, cooperation may be the best strategy for all parties, yet cooperation may not occur due to a lack of common knowledge over how others will behave.

The iterated PD can be thought of as a coordination game; individuals do best in repeated cooperative interactions, but in order to reap this benefit, they need to know that their partner will actually cooperate. These problems require “meta-knowledge” to solve. Put another way, the important point is not whether an individual knows that cooperation is the best course of action, but whether said individual knows that their partner also knows that cooperation is the best course of action and will act accordingly. Communication is therefore necessary to solve these problems of coordination, and numerous studies have shown that simply allowing players to communicate can promote cooperation (reviewed in Smith 2010).

These coordination games can be modeled in an abstract pay-off structure (Fig. 3), similar to the PD. In these scenarios, defection is not the optimal strategy, as the highest pay-off in these games is achieved by partners coordinating their behavior for mutual benefit (R). As a hypothetical example, imagine two hunter-gatherers having the option of either cooperating to hunt stag or foraging for berries by themselves (the equivalent of defecting in this scenario): If both individuals cooperate, then they are likely to successfully hunt a stag, which is a big haul for both partners (a pay-off of 5 each); if both players decide to forage individually for berries, then both receive a lower amount

		Player A	
		Cooperate	Defect
Player B	Cooperate	5 / 5	2 / 0
	Defect	0 / 2	1 / 1

Prisoner's Dilemma and Cooperation, Fig. 3 An example of a coordination game pay-off matrix. Here, in order to reap the most rewards, players need to coordinate their behavior. The pay-offs displayed here reflect a “stag-hunt” scenario (see text) where the player who cooperates does worse than the one who defects ($R > T > P > S$), although other coordination games exist where any non-matching behavior is inferior to mutual defection, in which case $R > P > T = S$. The pay-offs for player A are shown in the top right of each cell (above the diagonal), while the pay-offs for player B are shown in the bottom left (below the diagonal)

of food (a pay-off of 1 each); however, if an individual decides to hunt stag and their partner decides to pick berries, then the berry-picker still receives some resources (a pay-off of 2), while the stag-hunter has no chance of a successful hunt by themselves, so receives a pay-off of 0. Therefore, in order to reap the rewards of cooperation, individuals need to coordinate their behavior.

One real-world example of such a coordination game involves foraging strategies among the Lamalera from Indonesia (Alvard and Nolin 2002). In this society, individuals can either fish individually or collectively hunt whale (which has a greater pay-off than solitary fishing). In order to coordinate behavior and ensure that cooperation (collective whale hunting) is profitable for all involved, complex sets of social norms exist among the Lamalerans, including specific rules over distributing whale meat. These social norms ensure that all Lamalerans are aware of the “rules of the game,” thereby coordinating their behavior for mutual benefit. While language obviously serves this purpose of coordinating social behavior (Smith 2010), storytelling may be another such mechanism to broadcast this meta-knowledge,

therefore promoting cooperation (Smith et al. 2017). A large proportion of stories told in hunter-gatherer societies appear to concern social behavior, particularly regarding extolling the virtues of prosocial behavior (such as cooperation and equality) and the punishment meted-out to norm violators (such as selfish or lazy individuals). These stories also appear to enhance cooperation, as among the Agta (a Filipino hunter-gatherer population mentioned earlier) higher levels of cooperation in an experimental game were associated with a greater proportion of skilled storytellers in camp. Thus, the importance of mechanisms to coordinate behavior for mutual benefit should not be overlooked when exploring the evolution of cooperation.

Multilevel Selection and the Evolution of Cooperation

This chapter has focused on an “inclusive fitness” approach to understanding cooperative evolution (Hamilton 1964; West et al. 2007). An alternative conceptualization to understanding the evolution of cooperation is through “multilevel selection” (MLS; Hamilton 1975; Sober and Wilson 1998). MLS decomposes fitness into a “between-group” component and a “within-group” component (if the population is not structured into groups, then the between-group component is absent). Selection favors selfish behavior within groups (because altruists have lower fitness than selfish types within groups), while selection favors altruistic behavior between groups (because groups with altruists have greater fitness than groups with fewer or no altruists). If between-group selection outweighs within-group selection, then seemingly altruistic behavior can spread through the population.

However, there are two important points to note here. Firstly, MLS models are mathematically equivalent to inclusive fitness models; the only difference is how they decompose fitness. MLS decomposes fitness into within-group and between-group components, while inclusive fitness decomposes fitness into direct and indirect fitness components. From an inclusive fitness

perspective, the consequences of between-group interactions are part of an individual's inclusive fitness. Secondly, the MLS definition of altruism is different to the inclusive fitness definition of altruism. Altruism in an MLS framework is a behavior which lowers an individual's fitness within a group, regardless of the between-group benefits to cooperation (Sober and Wilson 1998). Altruism from an inclusive fitness perspective, as described above, is a behavior which decreases an individual's direct fitness, so can only evolve if cooperation increases an individual's indirect fitness (Hamilton 1964; West et al. 2007). It is important not to confuse the two: behavior may be altruistic from an MLS perspective, but not altruistic from an inclusive fitness perspective.

An example may make these points a little less abstract. Take between-group conflict. Imagine two groups in conflict over a limited resource (land, say), and individuals in each group can either cooperate (help in the conflict at a cost to self, relative to group-mates) or defect (not participate, so pay no cost, but reap the rewards of their group-mates' cooperation). From an MLS perspective, cooperative individuals obviously have lower fitness than selfish individuals within groups, so this behavior is altruistic (as defined by MLS). However, groups with more cooperators are more successful in between-group conflict, so cooperative behavior may spread in the population if the strength of between-group selection is great enough.

From an inclusive fitness perspective, however, if groups are composed of kin, then this cooperative behavior can be understood in terms of individuals maximizing their inclusive fitness by increasing their indirect fitness, even at a cost to their direct fitness. This behavior is therefore still altruistic, but this time from an inclusive fitness perspective. Alternatively, if groups are not composed of kin, then this cooperative behavior can still be understood from an inclusive fitness standpoint as individual fitness also depends on group fitness (i.e., individuals from cooperative groups have greater fitness than individuals from less cooperative groups). Cooperative individuals may therefore increase their direct fitness

by being part of a cooperative and successful group, even if said group contains some defectors who have even greater fitness than themselves. This behavior would therefore be altruistic from an MLS perspective, but not altruistic from an inclusive fitness perspective.

Each of the processes described above as solutions to the PD – repeated interactions, kin selection, and cooperative assortativity – can be described in a multilevel, as opposed to an inclusive fitness, framework (Sober and Wilson 1998). In each case, groups of cooperators propagate, even though individual cooperators have lower fitness than defectors within groups. However, it is essential to remember that MLS is not an alternative process to inclusive fitness, but rather is simply a different perspective on the evolutionary process and an alternative way of doing the math. The perspective one chooses to adopt will depend on the specifics of the system being studied: if groups act predominantly as unified wholes (such as whole organisms or, potentially, eusocial insect colonies), then an MLS perspective may be fruitful; if populations are not structured, then an inclusive fitness approach will be more appropriate; for cases in-between – where populations are structured into groups, but these groups do not act as unified wholes (such as human groups) – then it may be a matter of personal preference which perspective to adopt.

Limitations of the PD for Understanding Cooperation

While the PD has undoubtedly been a valuable tool for understanding the evolution of cooperation, it does possess some limitations. Firstly, not all cooperative behavior can be modeled as a PD. As discussed above, many cooperative situations resemble coordination game scenarios (Fig. 3), which do not suffer from the free-rider problem but rather suffer from problems of coordination. An alternative scenario, although still a social dilemma, is known as the “snowdrift game.” Imagine a situation where two drivers are stuck behind a snowdrift; as with the PD, individuals can either cooperate (dig through the

snowdrift) or defect (not dig). While joint cooperation would mean clearing the snow faster, defecting and letting the other dig would be a superior strategy as no energy would be expended. However, in this case, being the “sucker” (the individual who cooperates while the other defects) is superior to mutual defection, as they still benefit by clearing the snow and getting home. The pay-off structure for this scenario is therefore $T > R > S > P$ (Fig. 4). In the snowdrift game, defection is not the optimal strategy in one-shot interactions, resulting in a mixed population of cooperators and defectors (Doebeli and Hauert 2005). Accordingly, experimental findings have indicated that levels of cooperation are greater in an iterated snowdrift game compared to an iterated PD game (Kümmerli et al. 2007). Note also that this game is formally identical to the “Hawk-Dove” game (Maynard Smith 1982) or to the common childhood game of “chicken” (where the first to “blink” – or “chicken out” – is the cooperator).

When “cooperating” in this snowdrift game situation, the benefit to the partner may be incidental, meaning that behavior in these situations

		Player A	
		Cooperate	Defect
Player B	Cooperate	3 / 3	5 / 1
	Defect	1 / 5	0 / 0

Prisoner's Dilemma and Cooperation, Fig. 4 The pay-off matrix for a snowdrift scenario. As with the PD (Fig. 2), the Temptation pay-off is superior to mutual cooperation (Reward). However, in contrast to the PD, mutual defection (Punishment) is inferior to being the Sucker. The ranking of these outcomes for a snowdrift scenario (from best to worst, in terms of pay-offs) are: $T > R > S > P$. The pay-offs for player A are shown in the top right of each cell (above the diagonal), while the pay-offs for player B are shown in the bottom left (below the diagonal)

may not be strictly cooperative, but rather reflects self-interest (Clutton-Brock 2009; West et al. 2007). That is, players cooperate (dig through the snowdrift) in order to get themselves home because that is preferable to being stuck behind the snowdrift; the benefit to the other player is wholly incidental. Although cooperation in this scenario benefits others, it did not evolve to do so as the effect on the other player is an unintended by-product.

The snowdrift game appears to characterize several real-world circumstances, particularly regarding “producer-scuronger” dynamics. In these situations, some organisms produce resources, such as food, information, or cultural knowledge, which is then appropriated – or “scrounged” – by others in the group. To take a foraging example, while neither party may wish to forage and have food taken by others, the costs to not foraging are greater for some individuals. These individuals would therefore “blink” first in this game of chicken. For instance, compare an individual with multiple dependent offspring against another individual with no dependents. In this scenario, the second childless individual has less need to forage compared to the first as the costs to not foraging for the individual with multiple children are larger as their household is in greater need of resources. Consistent with this idea, men from Ifaluk atoll with more dependent offspring were more likely to fish compared to those with few dependents, as the costs to not foraging were greater for those with many mouths to feed (Sosis et al. 1998). These alternative pay-off structures have been under-researched compared to PD scenarios, despite their seeming applicability to several kinds of social interactions among a number of taxa (Alvard and Nolin 2002; Clutton-Brock 2009; Doebeli and Hauert 2005).

In addition to their theoretical utility, the PD and associated games, such as the Public Goods Game, Ultimatum Game, and Dictator Game, have been used extensively in experimental settings to empirically assess behavior in social dilemma scenarios (Camerer 2003). Although these experimental protocols offer conceptual simplicity and clarity, in practice there are many difficulties in interpreting behavior in these

games. Foremost among these are concerns over the ecological validity and interpretation of such experimental results.

Taking issues of external validity first, it is often not clear how, or even whether, behavior in these games reflects real-world cooperation. In these experimental games, initial levels of cooperation are generally quite high; in Public Goods Games players tend to share half of their endowment, while in Dictator Game situations (where individuals simply share some proportion of resources with an unknown recipient), individuals still often offer around 20% of the stake, despite no threat of punishment or future interactions (Camerer 2003). However, in the real world, such cooperative behavior is generally not observed; a recent field study based in Las Vegas found that individuals given a windfall of resources (casino chips) at a bus stop shared none of the chips with another individual waiting nearby, even after being instructed that they could share them with the other person if they wanted (Winking and Mizer 2013).

Additionally, there are difficulties concerning whether behavior in these experimental games reflects a single, stable, cooperative construct. For instance, it is not clear whether cooperation is a unitary phenomenon – and therefore stable from one context to the next – or whether it is more context-dependent – in which case experimental cooperation may not reflect real-world cooperation or cooperation in a different experimental game. Although some studies have attempted to overcome these criticisms, by demonstrating that game behavior predicts real-world cooperation and that cooperation in one context predicts cooperation in a different context (e.g., Peysakhovich et al. 2014), interpretation over the validity of these games is an area of active research and debate.

Conclusion

The PD has been widely used as a theoretical and empirical tool to explore the circumstances under which cooperation is likely to evolve. As of

August 2018, a Scopus search for the term “prisoner’s dilemma” in titles, abstracts, and keywords returned over 5,000 articles. It is likely that this fascination with this seemingly simple yet beguiling game will continue for years to come, offering insights into why humans and other animals both cooperate extensively with each other yet simultaneously aim to exploit one another when possible. The PD is an intuitive and fundamental insight into social behavior and the conflict between selfish and cooperative strategies; the dilemma is unlikely to be solved any time soon.

Cross-References

- [Evolution of Cooperation](#)
- [Evolution of Reciprocal Altruism](#)
- [Game Theory](#)
- [Group Selection](#)
- [Iterated Prisoner's Dilemma Model](#)
- [Kin Selection Hypothesis](#)
- [Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reputation and Altruism](#)
- [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)
- [Strategies for Successful Cooperation](#)

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Prisoner's Dilemma Outcomes

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Synonyms

Alliances; Being a sucker; Betrayal; Collusion; Noncooperation; Temptation

Definition

When two individuals are interacting, and their behaviors reward them in ways that depend on both their own actions and the actions of the other individual, one scenario that can occur is the “prisoner’s dilemma.” Four outcomes are possible in a prisoner’s dilemma: mutual cooperation (both parties cooperate), mutual defection (both parties’ defect), a sucker’s payoff (received by an individual who cooperates when the other player defects), and a temptation payoff (received by an individual who defects when the other player cooperates).

Introduction

How people interact with one another can involve a wide range of behaviors, intentions, and outcomes. There is a long history of philosophical positions about the fundamental nature of human interactions, including whether the nature of these interactions is fundamentally benevolent (e.g., Rousseau 1762), fundamentally aggressive (e.g., Hobbes 1651), or some combination thereof. As ideas about the nature of human interactions moved away from such a strict dichotomy and recognized the importance of context, other ways of characterizing human social interactions emerged. One approach, known as game theory, addresses how people interact with one another by simplifying the properties of those interactions to their most basic elements. Actors within a game play out strategies such that behavior can be cooperative or antagonistic depending on the costs and benefits of the situation (the payoffs). That is, the actions of one party have a direct effect, either positive or negative, on the outcome of others. Additionally, actors in a game can adjust their own strategies based on previous actions of other parties. For example, an actor who was previously disadvantaged by another player could choose to act antagonistically towards that player, or vice versa (Von Neumann and Morgenstern 1944).

Within game theory, one of the most well-known paradigms, or “games,” is called the prisoner’s dilemma. The prisoner’s dilemma

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	-2, -2	-10, 4
	Defect	4, -10	-6, -6

Prisoner’s Dilemma Outcomes, Fig. 1 Typical payoffs in a prisoner’s dilemma. Within each cell, the first payoff is for Player 1 and the second payoff is for Player 2. The blue-highlighted cell (top left) is the outcome of mutual cooperation, and the green-highlighted cell (bottom right) is the outcome of mutual defection. The orange-highlighted cell is the sucker’s pay off for player 2 and the yellow is temptation to defect for player 1, whereas those titles are reversed for the other player in those same cells

demonstrates why two completely rational individuals might not cooperate, even if it appears that it is in their best interests to do so. Formally, the prisoner’s dilemma involves two actors who each have a choice to either cooperate with or defect (not cooperate) from each other. The payoffs for these choices (see Fig. 1) are such that each actor would: (1) benefit the most from defecting when the other player cooperates (often called “temptation”); (2) benefit less from mutual cooperation; (3) benefit even less from mutual defection; and (4) benefit least from cooperating when the other player defects (often called the “sucker’s payoff”).

The individual choice of defection is the dominant choice in this version of the prisoner’s dilemma (i.e., the best outcome of temptation can occur, and the worst outcome of a sucker’s payoff is avoided for each party). However, if both parties in this situation understand the payoffs and choose defection, the result is the relatively unappealing outcome of mutual defection (−6/−6). Paradoxically, both people would almost certainly have preferred the mutual cooperation outcome (−2/−2), but that option seems to be unattainable because each player would assume the other player will rationally choose to defect.

Prisoner Dilemma Scenarios in the Repeated Prisoner’s Dilemma

The above prisoner’s dilemma is called a one-shot, or noniterated, situation because each player is allowed only one chance to cooperate or defect. In principle, cooperation should not occur

because both players have stronger incentives to defect. By not cooperating, however, both people come out worse than if they had worked together (mutual cooperation), hence the dilemma.

The prisoner's dilemma changes in important ways if it is a repeated, or iterated, situation. With multiple rounds of interaction, each player can use strategies that incorporate the other player's previous behaviors. One of the most well-known of the strategies for a repeated prisoner's dilemma is "tit for tat" (TFT), which uses a first move of cooperation but then all subsequent behaviors are based on copying the behavior of the other player during the previous iteration. Under many situations, the tit-for-tat strategy can generate stable mutual cooperation (Axelrod and Hamilton 1981).

Mutual Cooperation/Mutual Defection

These outcomes happen when both players either cooperate or both players defect. Mutual defection gives the worse outcome for both players. The existence of situations and strategies that can lead to mutual cooperation has been a long-standing focus of research with the prisoner's dilemma, because it is often seen as a way to potentially structure real-world environments in such a way that people will adopt cooperative rather than exploitative strategies. For a given environment, Axelrod (1984) offers four tips to foster mutual cooperation: (1) do not be envious; (2) do not be the first to defect; (3) reciprocate cooperation and defection; and (4) do not be too clever. For example, "tit for tat" (TFT) uses a simple algorithm to achieve these tips, whereas being too clever can reduce the clarity of your strategy, confuse the other player, and hinder willingness to cooperate.

Sucker's Payoff and Temptation to Defect

The sucker's payoff and temptation to defect payoff are inverses of each other, so the roles of the two players are inverses of each other. The defecting person is therefore identified as giving in to "temptation" and the cooperating person is identified as the "sucker." In an iterated situation, however, these are not viable long-term strategy options, because eventually the person who is the "sucker" will either "die" (run out of resources) or adjust by also defecting.

Conclusion

Subsequent research has explored many variations in how the prisoner's dilemma can be structured, the strategies that actors can employ within those situations, and the interactions between the prisoner's dilemma structure and player strategy (e.g., Axelrod and Hamilton 1981). Cooperative behavior (mutual cooperation) clearly can occur between people, and it can be a behavior that is rational within certain environmental contexts, but it is also not guaranteed to be stable or rationally proscribed as those contexts change. The effects of these subtle variations on individuals' behaviors are some of the most fascinating and fruitful areas of research within this paradigm.

Cross-References

- ▶ Iterated Prisoner's Dilemma Model
- ▶ Prisoner's Dilemma and Cooperation
- ▶ Robert Axelrod's (1984) *The Evolution of Cooperation*

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Prisoner's Dilemma, The

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Synonyms

Cooperation-defect; Logic game

Definition

A game in *Game Theory* involving a simultaneous choice between two players to either cooperate or defect, yielding four possible outcomes for each player based on the combination of choices between the players.

Introduction

The Prisoner's Dilemma game involves a simultaneous choice between two players – where each player makes a choice without knowing what the other player will do – to either cooperate or defect. In this game, defection yields a higher payoff than cooperation when paired with a cooperate choice from the other party, but if both defect they both do worse than if both had cooperated. In addition, the cost of being defected on, after providing a cooperate choice, is still greater. There is a total of four outcomes with the classic weighting of each being as follows: if both players cooperate they are awarded 3 points each, if they both defect they are awarded 1 point each, and if the first player chooses to cooperate and the other to defect then the one who has cooperated receives 0 points and the one who has defected receives 5. Receiving 0 points after being defected on is sometimes called the “sucker's payoff.” This point system is mirrored when framing the game around negative consequences rather than positive. Indeed, the classic framing of the game (giving it its name), the outcome is centered around prison terms of different lengths depending on outcome. The cover story involves a scenario where the police have arrested two suspects and are interrogating them in separate rooms. They are each offered a deal where they can go free if they confess, thereby implicating the other; the other option being to keep silent running the risk that if the other confesses then they (the cooperator) will receive the harsher punishment of 10 (or sometimes 5) years in prison for holding out. If both confess, each essentially trying to testify against the other, the deal is null and merely results in a standard sentence of 3 years each. If both remain silent however, the police only have evidence enough to charge them on minor offences

resulting in a 1 year prison term for each (see Axelrod 1984; Axelrod and Hamilton 1981). The basic structure of the game can be applied to a variety of scenarios such as arms races in international relations or business rivalries.

The Prisoner's Dilemma Game

At the core of the game as a one-time scenario is the logical solution that regardless of what the other suspect does, each can improve their own position by confessing. If the other remains silent, then the first can gain the most favorable outcome by confessing, taking the deal to walk free. If the other suspect confesses, then the first is still better off doing the same to avoid the largest sentence for a lone holdout. However, in a scenario of multiple rounds of the game, Robert Axelrod and William Hamilton (Axelrod 1984; Axelrod and Hamilton 1981) showed that an initial disposition toward cooperation paired with retaliatory defection if defected on the round before yields the most adaptive strategy. This strategy is dubbed the “tit-for-tat” strategy and shows how systems of cooperation may have evolved and are maintained (see entry on “The Evolution of Cooperation”). Essentially, one round of defecting on a cooperator yields an immediate 5-point payoff (or 0 year prison term). However, if this leads the other player defecting in the next round in retaliation, this will drop the initial defector's payoff to 1 point if they defect or 0 points if they shift to cooperation. Regardless, this leads to a lower or equivalent net payoff to mutual cooperation in both rounds (6 points total from 3 points per round). Continuing to defect and being defected on in return yields a much lower score than mutual cooperation across additional trials. Therefore, a tendency for cooperation – enforced when necessary by retaliatory defection – is the best strategy long term.

Conclusion

Within Game Theory, the Prisoner's Dilemma game involves a simultaneous choice between

two players to either cooperate or defect, yielding four possible outcomes for each player based on the combination of choices between the players. That is, each player makes a choice without knowing what the other will do – to either cooperate or defect – and each player’s outcome is dependent on the choice of the other player. The logical solution in a one-time scenario is that, regardless of what the other player does, each can improve their own position by defecting. However, in a scenario of multiple rounds of the game, an initial disposition toward cooperation paired with retaliatory defection if defected on the round before yields the most adaptive strategy.

Cross-References

- ▶ [Evolution and the Theory of Games](#)
- ▶ [Evolution of Punishment](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Game Theory](#)
- ▶ [Robert Axelrod](#)
- ▶ [Strategies for Successful Cooperation](#)
- ▶ [Theory of Reciprocal Altruism](#)
- ▶ [Robert Axelrod’s \(1984\) *The Evolution of Cooperation*](#)

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Privileges of the Human Brain

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Problem of Altruism

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Synonyms

Evolution of altruistic cooperation; Evolutionary altruism; Psychological altruism

Definition

We define two “problems of altruism.” The first is the classic problem of altruism, defined as the issue of how a behavior which decreases an individual’s lifetime reproductive success, while helping another individual (or individuals) increase their lifetime reproductive success, can evolve. We also define a “second-order problem of altruism,” where different authors have different conceptions of what does, and does not, constitute “altruism,” including approaches based on kin selection, multilevel selection theory, short-term altruism, and psychological altruism.

Introduction

Why would an organism help others at a cost to themselves, without any future reward or payoff? This, in essence, is the problem of altruism. Despite notions of “survival of the fittest” and “nature, red in tooth and claw,” seemingly altruistic acts abound in the natural world: meerkat sentinels famously forego feeding opportunities to guard the troop from predators; many species of mammals, birds, and fish engage in “cooperative breeding,” where subordinates sacrifice their own reproduction to help others breed; and humans regularly help others with no apparent benefit to themselves (e.g., giving blood, donating to charity, engaging in warfare). This altruistic behavior reaches its zenith in eusocial insects,

where huge swathes of the colony surrender reproduction altogether to help raise the offspring of a single queen (or handful of queens). Individual somatic cells within a body can also be thought of as altruistic, as only the germ line (sperm and eggs) is passed on to the next generation: all other somatic cells in the body therefore work altruistically in service of the germ line.

In all these cases, it would not appear to be in an individual’s interest to engage in such sacrificial behavior: for instance, a worker bee is not able to pass her genes down to future generations as they are unable to sire offspring of their own. Natural selection is generally believed to maximize individual fitness, yet the existence – and almost ubiquity – of altruism in nature clearly flouts this general rule and requires special explanation. Darwin appeared acutely aware of this issue, particularly regarding eusocial insects, and in *On the Origin of Species* Darwin (1859) wrote:

I...will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind.

Over the next 100 years, a solution to this conundrum of how such altruistic behavior can evolve was touched upon by some (including Sewall Wright, Ronald Fisher, and JBS Haldane), but was not comprehensively addressed until William Hamilton in the early 1960s published his concept of “inclusive fitness” (Hamilton 1964). Rather than taking an organism’s individual fitness in terms of personal reproductive success, inclusive fitness partitions fitness into the effect of the focal individual’s actions on their own fitness (so-called *direct fitness*) and the effect of the focal individual’s actions on others’ fitness (so-called *indirect fitness*), which is weighted by the coefficient of relatedness (r) between the individuals. r is the probability that individuals share altruistic genes, above baseline levels of the gene(s) in the population. Ignoring rare cases like greenbeards, r is primarily due to genealogical relatedness (so r approximates 0.5 for full siblings, 0.25 for

aunts/uncles, and so on). This focus on genealogical relatedness has earned Hamilton’s theory the name “kin selection.”

Hamilton’s formulation presents a simple rule for when altruism can evolve. If c is the direct fitness cost to performing an action and b is the benefit to others (in terms of increased reproductive success), altruism can evolve when: $br > c$. This is known as Hamilton’s rule and demonstrates how altruistic behaviors – such as sterile worker castes in eusocial insects – can evolve. As a simple example, imagine that individuals only interact with full siblings. Individuals with the altruistic gene increase their partner’s reproduction by three children at a cost of a decrease in their own reproduction by one child. Given these parameters, $b = 3$, $r = 0.5$, and $c = 1$. Therefore, as $br > c$ ($3 * 0.5 = 1.5$, which is greater than 1), this behavior can evolve, even though it involves a cost to the focal individual’s direct fitness. This concept was pithily summarized by Haldane, who quipped that he would lay down his life for two brothers ($r = 0.5$) or eight cousins ($r = 0.125$).

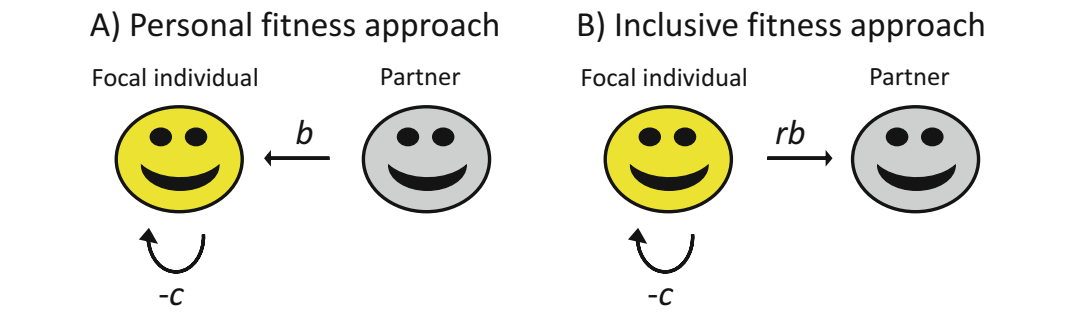
Formal Definition of Altruism

From this Hamiltonian perspective, altruism is defined as a behavior which causes a decrease in an individual’s lifetime direct fitness but increases the lifetime fitness of others. The lifetime direct fitness consequences to self are therefore negative, while the lifetime fitness consequences to recipients are positive ($-/+$; where the first term is the direct fitness effect of the behavior on the focal individual (c) and the second term is the indirect fitness effect of the behavior on recipient’s fitness (b)). This is in contrast to mutually beneficial behavior which has positive lifetime fitness consequences for both parties ($+/+$). Together, altruistic and mutually beneficial behavior can be grouped together as “cooperation” (West et al. 2007). Behavior can also be selfish, which means it increases an individual’s direct fitness at a fitness cost to others ($+/-$), or it may be spiteful, in which case behavior decreases both the direct fitness of the focal individual and the fitness of the recipient ($-/-$; Table 1).

Problem of Altruism, Table 1 A classification of social behaviors based on their direct fitness effects on the focal individual (actor) and the fitness consequences for the recipient

		Fitness effect on recipient (b)	
		+ (positive)	– (negative)
Direct fitness effect on actor (c)	+ (Positive)	Mutual benefit	Selfishness
	– (Negative)	Altruism	Spite

Note that altruistic behavior does not necessarily require a decrease in personal fitness relative to selfish behavior if interactions are assortative, which occurs when altruists preferentially interact with each other (i.e., $r > 0$). Rather, altruism is defined as a decrease in *direct fitness*, rather than a simple decrease in *personal fitness* (which is an individual’s total reproductive success, so it includes help received from others; note that personal fitness is also known as “neighbor-modulated fitness”). When $r = 0$, altruists will always have lower personal fitness than selfish types, but when $r > 0$, altruists may have greater personal fitness than selfish types, given that altruists preferentially interact with and help one another. Regardless of whether a personal fitness or inclusive fitness approach is adopted, for any value of r , altruists will have lower direct fitness than selfish types. As this is all rather abstract, the difference between personal fitness and inclusive fitness is presented in Fig. 1, while a worked example comparing the two approaches in a simple prisoner’s dilemma scenario is presented in Fig. 2. The essential difference between the two is that inclusive fitness only considers an individual’s actions on their own fitness (direct fitness) plus the fitness benefit *given to* others (weighted by relatedness; indirect fitness), while personal fitness considers an individual’s actions on their own fitness (direct fitness) plus the fitness benefits *received from* others (indirect fitness). In the personal fitness formulation, r is conceptualized as the probability of correlated interactions between individuals with altruistic genes (rather than strict



genetic relatedness), although in most species the main reason for correlated interactions is genetic relatedness (Birch and Okasha 2015). Despite different conceptualizations regarding whether indirect fitness is classified as help given to others weighted by genetic relatedness (the inclusive fitness approach) or as help received from others and r as the probability of correlated interactions (the personal fitness approach), both approaches are (by and large) mathematically equivalent as they both predict that altruism can evolve when $br > c$ (Birch and Okasha 2015). For additional details of how to measure inclusive fitness, and various pitfalls to avoid, see Grafen (1984).

Altruism in the Real World

As recognized by Darwin, the behavior of non-reproductive eusocial insects seems to fit this definition of altruism, where individuals help their relatives reproduce, even though they engage in no direct reproduction. Cooperative breeding in vertebrates (such as meerkats, callitrichids, and several bird species) also follows a similar pattern as it often occurs between relatives, so non-reproductive individuals appear to gain indirect fitness benefits by helping their kin. Additionally, as predicted by Hamilton's rule, in insects, birds, and mammals, monogamy (and therefore high levels of sibling relatedness) precedes the evolution of cooperative breeding (Lukas and Clutton-Brock 2012).

Despite the empirical and theoretical attention received by indirect benefits as explanations for such seemingly altruistic behavior, in many cases other potential explanations based on direct fitness benefits may have been overlooked (Clutton-Brock 2002). For instance, cooperation among kin is not necessarily evidence of altruism if both parties increase their direct fitness, as can occur with reciprocity between relatives. As another example, seemingly altruistic sentinel behavior among meerkats may in fact be less costly than often assumed, as sentinels are not at an increased risk of predation (Clutton-Brock et al. 1999). Additionally, relatedness to the group does not predict sentinel activity, suggesting that indirect benefits to kin may not

explain this behavior. Rather, the best-fed meerkats are more likely to take up guard duty if a sentinel is not present already, suggesting that this behavior may be largely for selfish reasons to avoid predation.

Furthermore, cooperative breeding in birds – where subordinates help dominants raise the brood – is again often claimed to be due to indirect fitness benefits, as the helpers are often siblings of the chicks. Although these indirect fitness benefits are likely to be important, subordinates may also gain direct fitness benefits by increasing the survival of both themselves and the nest, then subsequently inheriting the breeding rights of the nest after their parents. This appears to explain variation in helping behavior among birds, where the sex which is more likely to inherit the nest provides greater levels of help, despite equivalent levels of relatedness (Downing et al. 2018).

In long-lived animals where all individuals can reproduce, it can be especially difficult to determine whether an organism is acting altruistically, cooperating for mutual benefit, or behaving for purely selfish reasons. Nonreproductive eusocial insects are a rather simplified example as all fitness has to be indirect since reproduction is impossible, but it is much harder to determine whether behavior is altruistic in humans and other animals, as most adults are capable of reproduction and lifetime fitness consequences are hard to measure. Thus, although altruism is easy to define, it may be hard to spot in practice (Grafen 1984).

Alternative Definitions of Altruism

The discussion above can be thought of as the “first-order problem of altruism,” which explains the difficulties in altruistic behavior evolving. Next, we discuss the “second-order problem of altruism” (or “the problem of the problem of altruism”), in which different authors use different definitions of “altruism.” This is especially common in the human literature, which is often by necessity cross-disciplinary, meaning that terms common to various disciplines may have different meanings within each discipline. We discuss three common second-order problems of altruism

which are frequently found in the literature. The first concerns different definitions of altruism from a multilevel selection approach, the second concerns altruism measured on different time scales, while the third concerns conflating evolutionary and proximate definitions of altruism. Although we have presented a definition of altruism derived from inclusive fitness above (which was used as it is the most common definition employed in evolutionary biology; West et al. 2007), we are not advocating that this is the only or correct usage. Rather, we are advocating that whichever decisions authors make regarding the term “altruism,” they are clear on which definition they are using.

Altruism and Multilevel Selection

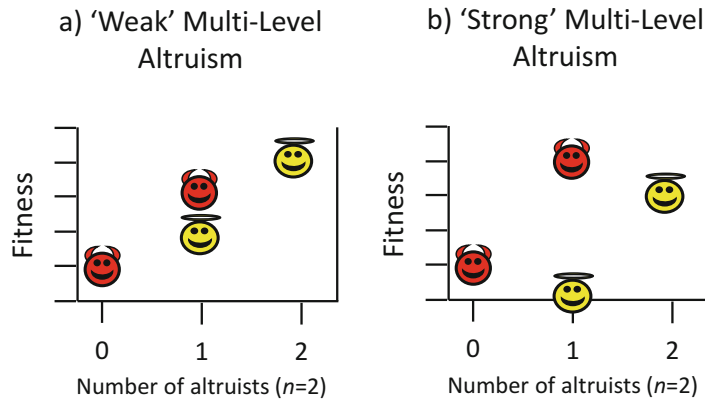
While the definition above based on a kin selection framework is a common definition of altruism in evolutionary biology, it is not the only one that exists in the literature (West et al. 2007). Proponents of a “multilevel selection” (MLS) perspective on evolutionary change define altruism as a behavior which decreases individual fitness within groups but increases the fitness of the entire group (Sober and Wilson 1998). The long-term evolutionary trajectory is then determined by the relative strengths of within-group selection (which acts against altruism, as selfish types have greater fitness than altruists within groups) and between-group selection (which favors the spread of altruism, as groups with more altruists have greater fitness than groups with fewer altruists). Note also that although kin selection and MLS approaches appear rather different, they are equivalent approaches mathematically (Birch and Okasha 2015); they just partition fitness in different ways (kin selection into direct and indirect fitness effects; MLS into within- and between-group components). One view is therefore not necessarily more correct than the other: the difference between these frameworks is in perspective, not process. While kin selection approaches define altruism in absolute terms over the entire population, from an MLS perspective altruism is defined relative to the group. As will be discussed below,

this can lead to different expectations of when altruism can evolve, depending on whether one adopts an inclusive/personal fitness or MLS perspective.

Within the MLS framework, there are two flavors of altruism: weak and strong (Wilson 1990). Weak altruism occurs when altruists have lower fitness than selfish types within groups, but have greater fitness than if they were not altruistic. An example is riding a tandem bike: if one person pedals and the other does not, then the lazy rider exerts less energy than the individual who pedals (i.e., selfish types have greater fitness within groups), but the altruist has greater fitness than if they did not pedal at all, as at least if one person pedals they will reach their destination (Kerr and Godfrey-Smith 2002). This scenario is presented abstractly in Fig. 3a. As the altruist increases their own fitness by cooperating, this behavior is not altruistic from a kin selection perspective but rather may be mutually beneficial to both parties, or simply self-interested, as the benefit derived by others is an incidental by-product. As such, weak altruism does not require assortment, so this behavior can evolve in randomly formed groups (i.e., if $r = 0$).

In contrast, strong altruism occurs when altruists possess both lower fitness than selfish types within groups and lower fitness than if they were not altruistic. The example presented in Fig. 2 of a classic prisoner’s dilemma is an example of strong altruism (see also Fig. 3b). If group formation is random, then altruists have lower fitness compared to if they did not cooperate. Thus, if a behavior is strongly altruistic from an MLS perspective, then it is also altruistic from a kin selection perspective and thus requires assortment to evolve (i.e., $r > 0$).

One must therefore be careful when converting between altruism as defined from an MLS perspective (which often uses the multilevel price equation, which partitions selection into between- and within-group components; Sober and Wilson 1998) and altruism as defined from a kin selection perspective (which uses Hamilton’s rule of $br > c$). Under conditions of weak altruism, behavior may be altruistic from an MLS perspective, but not altruistic from a kin selection approach, as acting “altruistically” increases an individual’s direct



Problem of Altruism, Fig. 3 Strong and weak altruism, as defined from a multilevel selection perspective. The population consists of altruists (smiley faces with a halo) and selfish types (smiley faces with devil horns). (A) “Weak” multilevel altruism: altruists have lower fitness than selfish types within groups (i.e., in a mixed group, selfish individuals have greater fitness than altruists). However, given the choice between being an altruist and being selfish, individuals have greater fitness if they decide to be an altruist (as the fitness of an altruist in a group of one altruist and one selfish type is greater than the fitness of a

selfish type in a group of no altruists). (B) “Strong” multilevel altruism: as with weak multilevel altruism, altruists have lower fitness than defectors within groups. However, given the choice between being an altruist and being selfish, individuals have greater fitness if they decide to be selfish (as the fitness of an altruist in a group of one altruist and one selfish type is lower than the fitness of a selfish type in a group of no altruists). Weak altruism does not require assortative group formation in order to occur, while strong altruism does

fitness. Of course, which definition people use is subjective – and a plurality of approaches can help to understand problems in greater detail (Kerr and Godfrey-Smith 2002). However, it can cause confusion if different definitions of “altruism” are used synonymously (West et al. 2007).

Short-Term Altruism

Some authors define altruism in terms of short-term costs, rather than in terms of lifetime direct fitness (e.g., Fehr and Fischbacher 2003). For instance, in reciprocal altruism, individuals pay a short-term cost to cooperating, but it is not necessarily altruistic in the Hamiltonian sense defined above, as they increase their direct fitness in repeated cooperative interactions. That is, the behavior is mutually beneficial (+/+), rather than altruistic (-/+; although note that reciprocity is weakly altruistic from an MLS perspective, as groups of reciprocators outcompete selfish groups, even though in mixed groups selfish types have greater fitness than reciprocators; Sober and Wilson 1998). Several models of

“altruistic punishment” or “strong reciprocity” also appear to share this feature, where altruism is defined in terms of short-term payoffs, rather than in terms of lifetime direct fitness (e.g., Gintis 2000). These features, combined with a focus on between-group competition to spread such “altruistic” behavior, can make it difficult to determine whether the behavior in these models is altruistic from a kin selection perspective or not (Lehmann and Keller, 2006).

Evolutionary and Psychological Altruism

Up until now, we have been dealing with why altruism might have evolved and how it may be adaptive in a social environment. However, as with everything else in biology, the study of a behavioral trait concerns two distinct questions – *why* a behavior evolved and *how* the behavior works, i.e., the ultimate and proximate explanations. It is crucial to maintain a separation between these explanations when attempting to understand and explain any trait. For instance, knowing that individuals feel rewarded when they punish

defectors is a proximate answer for why humans punish, but it does not answer why the behavior evolved. An answer to this question would be an ultimate explanation in terms of individuals who detect and punish free riders having greater fitness than those who do not detect and punish free riders. In the case of altruism, evolutionary explanations deal with fitness considerations of individuals and groups, while psychological explanations are largely based on the *motives* of the actor.

We now look at altruism from a psychological perspective. Hamilton's theory postulated that altruistic behavior can evolve due to the inclusive fitness benefits it bears for the actor via indirect reproduction in kin. For these benefits to play a mechanistic role in behavior, however, they need to be experienced by the actor in the form of feelings, motivational factors, or moral factors (Monroe 1994). Psychological altruism deals with the understanding of such motivations that can drive one to benefit others at a cost to self (although unless directed toward kin, such psychologically altruistic behavior is generally framed as being short-term altruistic, rather than evolutionarily altruistic). Empathy, for example, is an emotional mechanism that can propagate other-regarding behavior, by creating a feeling of connectedness (De Waal 2008). By the psychological mechanisms of emotion contagion and perspective-taking, individuals can "put themselves in other's shoes" and act in the interests of others and against narrow short-term self-interest. Morality forms a cultural norm, as well as part of one's conscience, that can promote such seemingly altruistic behavior by dictating that one must help others, sometimes even at a cost to themselves. To the extent that these norms become internalized, other-regarding preferences – and therefore psychological altruism – can emerge.

Though ultimate evolutionary explanations do not consider the internal motives of an actor to determine altruism – after all, eusocial insects are evolutionarily altruistic, yet it would be unlikely to ascribe to them altruistic motives – the literature largely persists in using terms that are reflective of these motives. Actions are called "selfish" or

"altruistic" based on whether the actor only seeks benefits for herself or intends to benefit another. This oftentimes ensues confusion between evolutionary and psychological altruism and leads to conflation of terms. Since these terms also have high vernacular use – which are mostly to do with one's motives – they can cause further confusion in the evolutionary understanding of altruism (Sober and Wilson 1998). Some authors use evidence of psychological altruism to claim that some human behavior is evolutionarily altruistic. For instance, Richerson and Boyd (2005, pages 216–221) review evidence for empathy and seemingly altruistic cooperation in one-shot economic games with strangers (to be discussed below) and conclude that humans possess other-regarding preferences. They then use this evidence for psychological altruism to argue that evolutionary altruism toward nonkin may also exist. However, as a general rule, there is no clear relationship between evolutionary and psychological definitions of altruism, and they should not be confused with one another or used interchangeably. Behaviors that are psychologically altruistic can be evolutionarily either selfish or altruistic and vice versa.

An example to demonstrate this is a man saving a drowning (unrelated) child. This behavior may decrease the man's lifetime direct fitness (and increase the fitness of the child) and therefore be evolutionarily altruistic. Alternatively, although this behavior involves a short-term cost, this behavior may increase his direct fitness if he is more likely to be chosen as a future reciprocal trading partner or as a mate, in which case this behavior is not evolutionarily altruistic. Similarly, the man's intentions may be psychologically altruistic if he genuinely cares about the child's welfare. However, his motives may not be altruistic if he perceives the scenario as a chance to enhance his reputation, rather than caring about the child. Thus, to classify an act as psychologically altruistic, the actor must *intend* to bring benefits to the recipients, even at a cost to themselves. But definitions of altruism based on intentions are separate from definitions of altruism based on whether behavior is detrimental to evolutionary fitness.

Does Psychological Altruism Exist?

While determining an actor's true intentions and motivations is a difficult task, many psychologists and economists often take a rather pessimistic view toward psychological altruism, in which altruistic acts are treated as a subtle variant of self-interest. For instance, altruistic acts have been explained from an egoistic perspective, in which actors help others solely in order to reap future benefits, for instance, by forming reciprocal relationships. Alternatively, these acts have been explained from an egocentric perspective, in which actors behave altruistically if watching the pleasure of her beneficiaries exceeds the satisfaction of consuming the commodity itself (Khalil 2004). According to both these views, no act is truly psychologically altruistic since the actor gets either reputational advantages or feels pleasure and internal gratification from their seemingly altruistic acts (altruistic hedonism). This pessimism has been well captured by Ghiselin (1974) in the following lines, "What passes for cooperation turns out to be a mixture of opportunism and exploitation... Scratch an altruist, and watch a hypocrite bleed." Based on these motivations, economists sometimes partition altruism into pure and impure altruism; in pure altruism, the only motive of the actor is the outcome of the altruistic act itself (e.g., aid being given to children in need), whereas in impure altruism, the impact on the recipient's welfare is not the primary motivator, as instead the actor gets a "warm glow" or feeling of goodness, which comprises a private benefit (Andreoni 1990).

However, despite these difficulties of determining whether an act is psychologically altruistic or not, some experiments have indicated that certain aspects of human behavior are indeed motivated by a concern for others' welfare. This optimistic view was endorsed by Adam Smith (1759) who wrote that,

How selfish soever man may be supposed, there are some principles in his nature, which interest him in the fortunes of others, and render their happiness necessary to him, though he derives nothing from it except the pleasure of seeing it.

The empathy-altruism hypothesis (Batson et al. 1987) claims that empathy evokes motivation to reduce the other's need, promoting altruism, and that self-benefits from such acts are simply unintended consequences of the ultimate goal (helping the other). In a series of experiments conducted by Piliavin et al. (1981), there were various degrees of emotional responses in reaction to seeing someone in need. Piliavin and colleagues quantitatively described a low magnitude emotional response to other's needs in non-emergency situations as empathy, such as feeling sympathetic, compassionate, or tender, and a high magnitude emotional response to other's needs in emergency situations as personal distress, such as feeling alarmed, upset, or disturbed. These emotional and psychological responses to other's needs are hypothesized to provide the motivation for other-regarding behavior in humans (Batson et al. 1987). These and other experiments suggest that humans, at least in part, are motivated by a concern for the welfare of others, indicating that psychological altruism may indeed exist.

Case Study of Human Altruism: Behavior in Economic Games

Numerous experiments have demonstrated that humans behave seemingly altruistically in experimental economic games, where the optimal strategy is to free ride on the cooperation of others: in all societies tested, humans frequently cooperate with strangers, contribute to public pools, punish selfish individuals at a personal cost in one-shot interactions, and even punish those who defect on others (so-called third-party punishment; Henrich et al. 2005; Bernhard et al. 2006). This behavior appears both evolutionarily altruistic – as individuals help others at a cost to self, despite a lack of repeated interactions or reputational effects – and psychologically altruistic, as individuals appear motivated to assist others and enhance their welfare.

However, leaving aside the question of whether behavior in these games is psychologically altruistic, the assumption that such behavior is detrimental to fitness, and therefore evolutionarily altruistic, has been questioned on several

fronts. First, although this behavior is seemingly altruistic in the context of the game (and is certainly short-term altruistic), the strategies adopted by players in these games may be mutually beneficial when applied outside the lab in real-world settings. The costs of mistaking repeated interactions for a one-shot interaction may be high, in which case seemingly irrational cooperation in one-shot encounters may evolve (Delton et al. 2011). Second, the design of these experimental games is likely to be unfamiliar to most participants, which means that individuals tend to use behavioral strategies from outside the lab (which are likely to be more cooperative than the optimal behavior in these games) when first playing these games. Supporting this interpretation are findings that individuals with greater experience in these games are less cooperative than “naive” participants, presumably because they have learned that it pays not to cooperate in these situations (Rand et al. 2014). Third, it is very difficult to know exactly what behavior in these games means in terms of real-world cooperation, as the external validity of behavior in these games is often low (Gurven and Winking 2008); although substantial levels of cooperation toward strangers are observed in these experiments, in the real-world unsolicited cooperation toward strangers is much rarer (Winking and Mizer 2013). Of course, perhaps behaviors in these games (and some behavior in the real world) are examples of evolutionary altruism, but it is very difficult to know definitively, and these alternative interpretations cast doubt on the conclusion that some cooperative behavior in humans (at least toward nonkin) is altruistic.

Conclusion

The concept of altruism has a fraught intellectual history, with numerous varying and conflicting definitions in use. With the term “altruism” being used across disciplines, like evolutionary biology, economics, psychology, and philosophy, it is impossible to classify altruism by a single agreed-upon definition. This plurality of approaches

means that authors – especially those engaging in cross-disciplinary work – need to clearly define what they mean by “altruism,” in order to forestall misunderstandings and unnecessary confusion. This is especially pertinent for the distinction between evolutionary and psychological altruism. In this chapter we have attempted to describe various definitions of altruism found in the literature, including Hamiltonian altruism, multilevel selection altruism (both weak and strong), short-term altruism, and psychological altruism, as well as the links – or lack thereof, in the case of evolutionary and psychological altruism – between these definitions. Given this multitude of definitions, it is no wonder that, despite being a topic of interest for centuries, we still do not have an established understanding and consensus on “what is altruism” and whether much human behavior is in fact altruistic (both from evolutionary and psychological perspectives). Clarifying one’s own meaning of altruism can go a long way to solve this second-order problem of altruism and allow coherent interaction between disciplines in order to understand whether, and under what circumstances, altruism may evolve.

Cross-References

- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism Norms](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [C < Rb](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
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- ▶ [Reputation and Altruism](#)

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Problem of Cheating

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Synonyms

Cheat; Defector; Free-rider; Manipulation

Definition

Cheating is a strategy or behavior that exploits social agreements of cooperation; from a genetic fitness perspective, cheating benefits the cheat while causing detriment to the cooperator.

Introduction

Cheats or free-riders are organisms that take advantage of the cooperative social behaviors of other organisms either within or outside of their species in order to obtain resources and/or mating opportunities while incurring less cost than would normally be associated with their acquisition. Ghoul et al. (2014, p. 319) define cheating as “(i) a trait that is beneficial to a cheat and costly to a cooperator in terms of inclusive fitness (ii) when these benefits and costs arise from the actor directing a cooperative behavior toward the cheat, rather than the intended recipient.” However, the term “cheat” has been used somewhat inconsistently throughout the evolutionary and ecological literature leading some researchers to suggest that the term is possibly inappropriate when applied to organisms other than humans. These researchers argue that the term “cheat” anthropomorphizes and implies a level of conscious intent that appears to be absent in many cases (Douglas 2008). Further, cheating has been defined in a multitude of ways (e.g., see Ghoul, Griffin, and West’s appendix). However, Ghoul et al. (2014) have since attempted to clarify the term by disambiguating the kind of cheating

occurring based on disentangling four important distinctions. Firstly, whether cooperation between the organisms is possible, if cooperation is not possible, then there would be no selection pressure for cheating; secondly, whether the behavior of the “cheat” involves deception, if deception is involved, then the cheat is exploiting a signaling system; thirdly, if the organisms are of the same or different species; and, finally, if the behavior is obligate or facultative. Facultative cheats use a strategy that is conditional on the behavior of their social partner, whereas obligate cheats use a fixed strategy such as always gathering less resources than the cooperators. Because cheating requires social cooperation, to discuss the problem of cheating, it is first important to discuss the prosocial or society promoting/maintaining cooperative behaviors that are performed by social organisms and exploited by cheaters. Secondly, we will discuss cheaters and the detection of cheaters by their social group. Finally, we will consider the idea that cheating and the detection of cheating are psychological mechanisms that evolved as part of an evolutionary arms race. For the purposes of this entry, we will discuss cheating as it applies to human cooperative groups. However, it is important to note that cheats have been reported in a diverse range of organisms including parasites, insects, fishes, reptiles, amphibians, birds, and mammals (see Ghoul et al. 2014, p. 319 for table of applicable sources).

Theory and Evidence

Initial research ideas surrounding behaviors that help another at a cost to the actor were discussed by social psychologists as being acts of “true” altruism, the idea of giving and receiving no benefit in return. However, like many theories of social behaviors with inherent biological consequences, the standard social science model fell short (for a good review of the ongoing argument between evolutionary theory and the standard social science model, see Burke 2014). The problem is that altruistic behaviors result in fitness benefits for both the actor and the receiver. Hamilton (1964) first posed the idea that altruism

passed between kin actually benefited the actor by way of inclusive fitness. That is, by helping family members, the actor is actually increasing the likelihood that some portion of their unique genetic makeup will persist in the species. Self-sacrificing behaviors between kin occur when the cost to the actor is lower than the benefit to the receiver. Hamilton's rule can be reduced to $c < rb$ where c is the cost, r the coefficient of relatedness, and b the benefit. Benefit passed to offspring is considered direct fitness, while benefit passed to other kin is indirect fitness. Direct and indirect fitness in combination equals inclusive fitness. Trivers (1971) extended on these ideas by introducing the theory of reciprocal altruism showing how behaviors associated with inclusive fitness when they occur between kin could have similar results when practiced reciprocally within social groups. Fitness benefits for the actor and receiver through reciprocal altruism (or reciprocity) in social groups only requires that the benefit to the receiver is greater than the cost to the actor, that the organisms are capable of recognizing individual members of the group, and that the organisms have a reasonably long life span. Trivers (1985) later stated that modern human societies fulfill the three prerequisites for reciprocity to occur, aid-giving between friends that is later reciprocated has been noted cross-culturally, and we have developed an emotional system that encourages cooperation. Because cooperation within the human species has resulted in the formation of societies, it has ultimately increased the fitness of those included within those societies. It is for this reason that we have evolved an emotion system that encourages cooperation, with positive emotions such as happiness and pride rewarding caring, cooperation, and reciprocation whereas punitive negative emotional experiences such as guilt and shame discouraging cheating, manipulation, and violence (Nesse 1990). The link between reciprocation and positive emotional and societal rewards can be seen in pre-industrialized societies such as the !Kung San of the Kalahari in Africa. The !Kung San have strong social traditions built around sharing the spoils of a successful hunt; failure to do so results in loss of social status. Sharing does not occur as an act of pure altruism;

reciprocation is expected when the fortunes are reversed. In this way reciprocal giving serves to increase inclusive fitness of all members of the !Kung (Harris 1998).

From a genetic point of view, Dawkins (1976) gave a strong argument for why "true" altruism could not exist. In *The Selfish Gene*, Dawkins outlines the argument that biological organisms are simply the vehicles of evolution, which for a brief period in time carry the replicators (genes). The replicator that most effectively promotes copies of itself (the selfish gene) will persist for an indeterminately large number of generations, whereas the replicator that promotes copies of other genes will fail to replicate as much and be removed from the gene pool more quickly. In other words, the genes for "true" altruism would not have persisted in the gene pool. The divide between "altruism" and reciprocity continues to be a contentious topic between researchers who follow the standard social science model and evolutionary theorists. Daly and Wilson (1983) give an illuminating explanation as to the source of this contention stating that altruism can exist as a proximate cause of behavior; organisms can display self-sacrificing behavior in order to benefit another. But using ultimate causation, if this altruism increases the fitness or inclusive fitness of the actor over a generational time scale, then it is ultimately a selfish behavior. So while making a large donation to charity may seem like an act of great altruism when viewed proximally, when viewed ultimately over the expanse of generations, the reputational benefits of making this donation will increase the actor and/or their kin's fitness.

Other forms of aid-giving between organisms have been identified. Clutton-Brock (2009) suggests that mutualism and manipulation are two ways in which aid can be given by conspecifics without reciprocation. Mutualism involves both parties benefiting at the time of the behavior, i.e., hunting in groups for shared food. Manipulation involves the use of coercion in order to receive aid with no intention of reciprocating. Both involve no cost-benefit asymmetry which must be repaid at a later time, differentiating them from reciprocation. However, both reciprocation and

mutualism involve a form of social contract or understanding of cooperation. Mutualism involves immediate cooperation, where the efforts of both individuals in combination allow them to obtain the resource successfully, whereas reciprocation involves the understanding that the giving of aid at one time will result in the receiving of aid at another. Both of these social strategies improve the fitness of the organisms and potentially their kin. However, both strategies are also vulnerable to exploitation through cheating. Due to this vulnerability, human cooperation is based on three evolved prepositions; firstly to seek cooperation that is of net benefit to both parties (whether in the long or short term), secondly to share cooperatively acquired resources with the group, and thirdly to punish free-riders and cheats. Because of the fitness benefits associated with successful cooperation, there would be evolutionary pressure to adapt ways of identifying and neutralizing cheats (Tooby et al. 2006).

Free-riders or cheats reap the benefits of cooperation without paying the costs, and this behavior places them at a competitive advantage (at least in the short term) (Tooby et al. 2006). Cheating also reduces the fitness of the victim as they either do not receive or receive less reciprocation or mutual benefit than the social rules would suggest. Social rules exist in order to maintain stability within the group. Cheating involves the violation of deontic social rules and is only considered nefarious (and subsequently detected) when three criteria are met. The cheater benefits, acted intentionally, and cheating was possible (Cosmides et al. 2010). Social predator phenotypes have been identified within the human species. Psychopathic individuals victimize others and are characterized by a callous disregard for others, lack of empathy, deception, lack of guilt, and impulsivity (Book et al. 2007). Although these characteristics appear to be detrimental as a long-term social strategy, they also result in short-term resource and mating opportunity benefits through the use of a cheater strategy. For example, impulsivity and a lack of empathy allow one to exploit the trust of another to obtain resources within a short window of opportunity, without guilt or thoughts of consequences hindering the act. This has been observed by Gervais et al. (2013) who found that

individuals high in psychopathic traits defect in prisoner's dilemma games when they perceive their relation to the other player as being of low value. Therefore, when opportunities arise to obtain resources from others that carry a low risk of consequences, individuals high in psychopathic traits are extremely likely to take advantage. Although socially predatory behavior within human societies often carries consequences, the immediate benefits of this predatory behavior suggest that psychopathy is an evolved adaptation related to use of a cheater strategy (among other things) and useful in resource-poor environments (Mealey 1995). An interesting question is if humans receive fitness benefits from social cooperation, how does a phenotype like psychopathy that is seemingly designed to optimize cheating behaviors evolve? Further, if cheating confers fitness benefits and discourages cooperation, how do genes that promote cooperative behaviors persist in the gene pool?

The evolutionary arms race theory may explain the evolution of both cheaters and mechanisms that promote cooperation and the detection of cheaters. According to this theory, a reciprocal relationship exists between predator and prey both within and between species. This relationship is referred to as an evolutionary arms race or coevolution and is the driving force of many evolutionary adaptations across both predators and their prey (Dawkins and Krebs 1979). An elementary example of an evolutionary arms race is the adaptation of speed shared between foxes and rabbits. Slow rabbits in a population are easily eaten by foxes, and thus natural selection favors faster rabbits. Consequently, there are fewer slow rabbits in the environment for slow foxes to eat, and therefore natural selection also favors the faster foxes. In this way, the slow rabbits effectively fuel an arms race that forces both species to adapt over generations and become progressively faster than their predecessors (Dawkins and Krebs 1979). Applying the same concept to humans, we can see that cooperation between individuals in society improves each individual's genetic fitness. However, cooperation is subject to cheating, and in comparison with cooperation, cheating results in increased benefits at a reduced cost. Because of this there

would be evolutionary pressure to cheat as well as evolutionary pressure to adapt ways of correctly identifying cheaters (Tooby et al. 2006). Those cooperators who are more successful at identification and avoidance of cheating would have increased likelihood of passing on their genes. However, when cooperators become aware that cheating is occurring, their natural response is a desire to punish the cheaters in order to either stop their cheating behavior or remove them from the group (Price et al. 2002). Being punished reduces the genetic fitness of the cheater as they then have reduced access to resources and mating opportunities. So individuals in society adapting to the presence of cheating by developing mechanisms of detection increases evolutionary pressure on cheaters to cheat more effectively, so that cheaters who remain undetected have a higher likelihood of passing on their genes. More effective cheating increases evolutionary pressure on cooperators to further enhance their cheater detection capabilities, and so the arms race continues.

Research on cheater detection has revealed much about our ability to identify and cope with those who seek to exploit us but little about the differences between those who successfully identify and avoid cheaters in comparison with those who become victims. For example, the vast majority of studies with the prisoner's dilemma game have focused on the dark triad personality traits – psychopathy, narcissism, and Machiavellianism – and how these factors influence the cooperativeness (or lack thereof) of players in the game (Gervais et al. 2013). Becoming a victim of cheating or exploitation is potentially a consequence of a reduced ability to detect cheaters or a lack of an ability to successfully alter behavior in order to avoid cheaters upon having detected them. The focus of research appears to be around understanding those who seek to cheat and fail to identify the evolutionary function of the victims themselves. This may be partly due to a societal taboo around the suggestion that individual differences may contribute to an increased likelihood of being victimized. This taboo takes the form of accusations of “victim-blaming.” However, understanding the individual differences between those who are victimized and those who successfully identify and avoid cheats is ultimately an area

of research seeking to enhance cooperative behaviors within society.

The general population has developed adaptive mechanisms like cheater detection to be sensitive to cues of predatory behavior (such as lying or not honoring agreements) in order to successfully navigate encounters with potential cheats without losing resources. If such an arms race does exist between cheaters and cooperators, individuals who are victimized may serve an evolutionary purpose – by losing one's resources to predatory behavior, the general population receives short-term benefit by way of an increased likelihood of discovering the presence of the predator and the predator's methods. The cooperators also receive long-term adaptive benefits in that those individuals who have not adapted effective cheater detection mechanisms have lower levels of inclusive fitness, and as a result, their genes will eventually be removed from the gene pool (Verplaetse et al. 2007).

A neural module has previously been suggested as the mechanism for detection of cheaters, fittingly called the cheater detection module (CDM). It has been theorized that the CDM indicates the presence of unequal exchange in the context of reasoning about social contracts (a social agreement where a cost is incurred and a benefit is received). Evidence for the CDM has been observed through an adapted version of the Wason selection task (Cosmides 1989).

The Wason selection task (Wason 1968) requires the use of logic to test a deontic rule (a conditional rule, i.e., if A occurs, B must also occur) in the most efficient way. For example, if the conditional rule is “if a card has the letter A on it, it must have an even number on the other side,” and there are four cards, marked “A,” “B,” “2,” and “3,” the most efficient way to test the rule would be to turn over the card marked “A” (to test if there is an even number on the other side) and the card marked “3” (to test if the letter A is not on the other side). Griggs and Cox (1982) found that when the Wason selection task was altered to place, the participant as a police officer looking for underage drinker participants did significantly better than normal. Manktelow and Evans (1979) suggested that increased success on the amended task was because the task was less abstract but

found that participants did not do as well when other concrete tasks that did not focus on the enforcement of social rules were developed. Simply removing the context of being a police officer enforcing a rule significantly decreased performance. Cosmides (1989) argued that the increase in performance is due to an adaptive cognitive module designed to identify cheating behaviors.

As a result Cosmides (1989) produced an adapted version of the Wason selection task (Wason 1968) that follows the same logic as the original task; however the deontic rule is framed in the context of a social exchange (e.g., if the car is borrowed, it must be returned with a full tank of fuel). While performance on the original Wason task is notably poor (average of approximately 30% correct), Cosmides (1989) discovered that when the task was framed in the context of breaking a social contract, performance increased dramatically (approximately 70% correct). Cosmides (1989) suggests that this is evidence of the existence of a neural module designed specifically to recognize when one has been cheated in a social exchange. As mentioned earlier social rules exist in order to maintain social stability. Cheating involves the violation of these rules and can be detected when the cheater benefits, acted intentionally, and cheating was possible. Cosmides et al. (2010) showed evidence for this in a series of experiments that manipulated the presence of a benefit, the possibility of cheating, and the cheaters intentions, finding that people were more accurate at identifying cheaters when all three conditions were met. Evidence for a cheater detection module has been replicated cross-culturally with Cosmides and Tooby (1992) replicating the effect using a sample of Ecuadorian foraging people. However, the existence of the CDM has been brought into question through criticism of Cosmides' interpretations and the integrity of the adapted Wason selection task itself (Buller 2005). Although this position has been refuted and potentially falsified (Cosmides et al. 2010), the topic remains controversial, and few alternative tasks have been designed to capture cheater detection. If there is a specifically evolved module, it makes sense that it would be activated in other experiments that utilize social contract violation situations.

One alternative task that has previously been used to capture cheater detection is the prisoner's dilemma game (Verplaetse et al. 2007). The original prisoner's dilemma places two theoretical co-conspirators in separate interrogation rooms where they must choose whether they will sell out their co-conspirator for a reduced sentence. Subsequently, the prisoner's dilemma has been developed into a game that can be played for money or points based on a payoff matrix (Verplaetse et al. 2007). In this game, players choose to either cooperate (share a reward with another player) or defect (take a reward for themselves). There are three possible outcomes in the game: (1) If both players choose to cooperate, they share a reward equally. (2) If one player chooses to cooperate and the other chooses to defect (cheat), the cooperator will not receive a reward, and the defector will receive a large reward (greater than if they had cooperated) for themselves. (3) If both players choose to defect (cheat), they will each receive the smallest possible reward. Much research has focused on the optimum strategy for this game, showing that the strategy that is most effective is dependent on whether it is a single game or an iteration of games. In an iterated prisoner's dilemma performance in the game relies upon the degree to which one player correctly determines the cooperative tendencies of the other player. Maynard Smith (1974) states that as long as most members of a group follow a tit-for-tat strategy (cooperate first and subsequently do what your partner did in the previous round), it is mutually beneficial for both parties. This strategy encourages future cooperation through an initial act of cooperation and allows for retaliation and forgiveness to defectors. Those who fail to follow this tit-for-tat strategy fall into two categories: cheaters and "suckers." If two people cheat, then they receive very little reward, so cheating is only a successful strategy when there are few other cheaters in the game. Further, if you fail to recognize the cheating behavior of your partner and cooperate with them, then you get no reward. In this way the iterative prisoner's dilemma game is seen as analogous to cooperation and cheating within human societies.

Interestingly, evidence shows that cooperators can identify cheaters by their facial expressions. Verplaetse et al. (2007) obtained photos of

participants' faces while playing the prisoners dilemma game for a real monetary reward. Photos were taken at the exact second the participant indicated their decision to cooperate or defect. These photos were shown to another participant pool, who were asked to discern if the person in each photo cooperated or defected. It was found that approximately 66% of defectors (or in other words cheaters) were successfully detected by participants based on facial cues alone. A memory bias was also present for defectors in a surprise memory test. This provides evidence that humans can utilize facial cues to successfully detect cheaters and may have specific mechanisms designed for remembering them. Perhaps those who fall victim to cheating do so partially because of an inability to detect facial expressions signaling that behavior.

However, if the cheater cannot be identified, then the cooperators may suspend cooperation (Price et al. 2002). The most impactful cost of the presence of cheaters is that it results in reduced or suspended cooperation within the group so that reciprocal behaviors that would have occurred previously cease to occur (Tooby et al. 2006). Fehr and Schmidt (1999) conducted a meta-analysis of studies using public good games. Public good games involve the depositing of some valuable into a shared pool, provided that all parties deposit something into the pool, a third party then increases the pool (usually $1.5\times$ the value of the pool) as a reward for cooperation. In this way all parties become richer on average. Fehr and Schmidt (1999) noted that parties are initially quite generous with their donations to the shared pool. However, after repeated iterations of the game, most parties contribute nothing. This is because they perceive others to be not contributing. Cheating in these public good games results in the suspension of cooperation. Another theory postulates that those who have experienced prior victimization may perform poorly in cheater detection tasks and cooperate less as they learn maladaptive strategies to avoid further victimization. Gollwitzer et al. (2012) discovered that individuals high in victim sensitivity (a personality trait that influences individuals' perceptions of unfairness) underestimate the trustworthiness of others and are less cooperative in ambiguous interactions as a result. As victim sensitivity is

predicted by prior experiences of actual victimization (Gollwitzer et al. 2015), it is possible that individuals who have previously experienced victimization may become wary of even well-intentioned individuals when making social judgments. This causes them to suspend cooperation and may contribute to poor performance in cheater detection tasks.

Conclusion

Cheating results in immediate consequences for the cooperator who failed to detect the cheating behavior until it was too late. These consequences, especially when incurred repeatedly, can result in decreased genetic fitness and ultimately a reduced chance of passing on your genes. However, the broader implications of cheating behavior are that it discourages cooperation and thus broadly affects the viability of the group. For the cheater this behavioral strategy can result in fitness benefits, provided that there are not a large number of other cheaters in the group and they remain undetected. The problem of intraspecies cheating in humans may have acted as the catalyst for an evolutionary arms race, serving to increase adaptations for both cheating and cheater detection.

Cross-References

- ▶ Altruism
- ▶ Coercion
- ▶ Free-Rider
- ▶ Game Theory
- ▶ Inclusive Fitness
- ▶ Manipulation
- ▶ Mutualism
- ▶ Prisoner's Dilemma
- ▶ Psychopathy
- ▶ Selfish Gene, The

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Problem of Genetic Inheritance, The

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Synonyms

Heritability; Missing heritability

Definition

Genetic inheritance refers to the transmission of genes from one generation to the next. In sexually reproducing species, offspring inherit 50% of their genes from each parent.

Introduction

Genetic inheritance is often defined in terms of heritability, which is the portion of phenotypic variance in a population that is attributed to “genetic differences” among individuals in that population (Plomin et al. 2013). We place genetic differences in quotes because genomic variation is only implied and not directly examined. Generally speaking, a trait is heritable to the extent that it is transmitted through biological mechanisms from one generation to the next. This includes genomic mechanisms of inheritance as well as other biological mechanisms such as passage of epigenetic marks and transmission of nutrients or bacteria from maternal circulation (Meaney 2010). In this article, the terms “genetic” and “heritable” are used to capture both genomic sequence variation and other biological mechanisms of familial transmission collectively.

There are two forms of heritability: (1) broad sense and (2) narrow sense. Broad sense heritability (H^2) includes all sources of biological inheritance that contribute to the familial transmission of a trait. These include additive genetic effects, gene-by-gene interactions (epistasis), gene-by-environment interactions (GxE), possible epigenetic inheritance, and several others (Barnes et al 2014; Meaney 2010). Narrow sense heritability (h^2) posits that only additive genetic effects contribute to trait heritability and therefore assume other sources of biological inheritance are zero, which is the standard twin model assumption (see Twin Models). This assumption may be problematic, however, the relative contributions of genes and environments inferred from these models may be systematically over- or underestimated when nonadditive genetic factors are left unaccounted (Barnes et al. 2014).

Narrow sense heritability is estimated by partitioning trait variance into additive genetic and environmental components via statistical modeling. This technique involves measuring neither genes nor environments and instead infers their relative contribution via latent variables. As such, heritability is a statistical characterization of genetic and environmental influences rather than a biological one. Because heritability describes the portion of differences between individuals in a given population that can be attributable to additive genetic effects, heritability cannot be applied to explain the phenotype of an individual. For example, height heritability in humans is approximately 80% (Yang et al. 2010), but it is not accurate to say that 80% of the reason a person grows to their given height is due to genetics and the rest is environment. Heritability is also population specific. That is, a given heritability estimate is specific to the population from which it was derived at the particular time and space it was measured. A heritability estimate derived from a given population can change over time within that population, and the heritability of a trait measured in one group does not necessarily translate to another group.

The problem of genetic inheritance in the life history context is an extension of broad and narrow sense heritability when viewed through the lens of alternative strategies and conditional adaptation (Rowe et al. 1997; Belsky 2000). When applied to human development, hypotheses derived from life history theorizing often take the form of conditional adaptations (or developmental plasticity more broadly), which can be conceptualized as gene-by-environment interactions (GxE; part of broad sense heritability). Alternative strategies resemble the sole influence of additive genetic effects (narrow sense heritability), which assume no environmental influences. The biological mechanism that entrains life history development via conditional adaptation in humans is not well known; however, research using animal models and some preliminary human research point to epigenetic modification as a key developmental life history strategy regulator (Ellis 2013). Gene-by-environment interactions, epigenetics, and other forms of

gene-environment interplay may help elucidate why research using measured genes have fallen short of explaining phenotypic variance of the magnitude typical of behavioral genetic models (i.e., missing heritability).

Alternative Strategies

Theory and research in evolutionary biology have converged on the conclusion that it is unlikely that a single “best” genetically underlain phenotype will evolve (at least for most species; see Boyce and Ellis 2005). Alternative strategies represent one way in which genetic diversity is maintained in a population. Alternative strategies refer to individual differences in phenotypic profiles that are strongly genetically regulated (i.e., alternative phenotypes are influenced by major genetic effects). The basic concept behind alternative strategies is that they are underlain by genetic polymorphisms, and different suites of genetic variation are strongly related to two or more phenotypes. Alternative strategies can evolve, for example, when the different phenotypes have equal fitness in the population as a result of the relative frequency of each alternative.

A classic example of frequency-dependent selection is the Hawk-Dove model, which describes in mathematical terms how two alternative antagonistic phenotypes can be maintained in a population (Maynard Smith 1982). Consider a circumscribed population where members have either a Hawk or a Dove phenotype. The Hawk phenotype is characterized by fighting and escalating aggression until injured or the opponent retreats. The Dove phenotype is characterized by aggressive display but will retreat if the fight escalates. If a Hawk encounters a Hawk they will fight until one is injured. If a Dove meets a Dove they display until one gets tired and quits. Importantly, neither phenotype alone can comprise a stable population. A population of all Doves could be infiltrated by a Hawk who would gain huge fitness benefits relative to Doves. Likewise, a population of all Hawks could be very costly for the Hawk members, and a Dove that enters this population could reap

disproportionate benefits by avoiding injury. Over evolutionary time, a stable ratio of Hawks and Doves could evolve based on the relative costs and benefits of each phenotype.

Alternative strategies may be evolutionary advantageous when the genetically regulated phenotype matches well to the developmental and/or adult reproductive environment. It would be evolutionarily advantageous for parents to produce some children with alternative strategies that are largely impervious to socialization from the parent or other sources and who would thrive in particular contexts that fit their proclivities (Belsky 1997). Alternative strategies may also be more advantageous in multination environments, where cues to future environments are unreliable (Ellis et al. 2006). However, highly penetrant genotypes are rare and, when applied to thinking about alternative strategies, should be considered probabilistic and encompassing a disposition range toward a phenotype that is malleable to environmental influences, although distinct from conditional adaptations. Most complex behavioral traits, such as life history strategies in humans, are multiply influenced by both genes and environments and both developmentally and concurrently.

Conditional Adaptation

It is important to keep in mind that evolutionary processes do not act on genes directly. Instead, selection pressures act on phenotypes that are genetically influenced. Alternative strategies are one way that phenotypic diversity is maintained in a population (predicated on corresponding genetic diversity). A second way is conditional adaptations. Conditional adaptations are: “evolved mechanisms that detect and respond to specific features of childhood environments, features that have proven reliable over evolutionary time in predicting the nature of the social and physical world into which children will mature, and entrain developmental pathways that reliably matched those features during a species’ natural selective history” (Boyce and Ellis 2005, p. 290). Due to environmental variation within the lifetime of an

organism, such as food availability and social and reproductive ecologies, selection should tend to favor phenotypic plasticity, where an organism can facultatively adapt their phenotype to better fit a changing and/or anticipated future environment. Individuals may be genetically identical in terms of neurobiological substrates but produce very different and environmentally contingent phenotypes (Rowe et al. 1997). Key to the idea of conditional adaptation is that contingent phenotypes are nonrandomly organized and are the result of selection pressures that favored one trajectory over another based on specific environmental information during development. Plasticity may not always be the best option, however, if the costs for maintaining plasticity mechanisms are high or if there are not reliable cues that can than entrain a developmental trajectory fit to a future environment. In such cases, alternative strategies would be favored by natural selection.

Gene-Environment Correlation

Gene-environment correlations are important to consider when evaluating conditional adaptation hypotheses since, in the absence of genetic controls, strictly environmental analyses cannot rule out this third variable confound (Ellis et al. 2012). Gene-environment correlations are another way heritability can obfuscate life history hypothesis that involves developmental plasticity. There are three types of gene-environment correlation: (1) passive, (2) active, and (3) evocative (Jaffee and Price 2007). Passive rGE occurs when the correlation between the gene and environment is the result of being born in that particular environment. For example, there is a correlation between father absence (the environment) and pubertal timing in girls. Multiple theories and mechanisms have been offered to explain this association (Ellis 2004), including passive rGE. In this case, the association between father absence and pubertal timing is hypothesized to result from daughters inheriting genes associated with earlier pubertal timing from fathers, which also dispose fathers toward parental absence. Active rGE involves niche selection. For example, adolescents who

have heritable characteristics that dispose them to deviance may self-select into deviant peer groups. The association between adolescent deviance and peer-group deviance would be the result of active rGE. Evocative rGEs result when heritable characteristics cause a systematic environmental response. For example, evocative rGE could explain the association between parental hostility and child behavior problems if the heritable component of child behavior problems evokes parental hostility.

Gene-Environment Interactions

Whereas the alternative strategy model focuses on heritable genetic variation, the conditional adaptation model emphasizes gene-environment interaction (Boyce and Ellis 2005). For example, the caterpillar *Nemoria arizonaria* demonstrates a diet-dependent phenotypic polymorphism (Greene 1989). Caterpillars born in the spring feed on oak catkins and develop an external phenotype that resembles the catkins, which provides evolutionarily advantageous camouflage. Caterpillars born in the summer feed on oak leaves instead of catkins since by summer the catkins have fallen from the tree. Caterpillars that eat the oak leaves phenotypically develop to look like oak twigs, which provides a similar camouflage advantage that reflects the seasonal change in the oak tree. Experimentally feeding the caterpillars the out-of-season food also produces the matching phenotype. These caterpillars have evolved a genetic structure designed to respond contingently to an environmental input, which adjusts their developmental trajectory in evolutionarily advantageous ways. In effect, conditional adaptations are gene-environment interactions.

The development of reproductive strategies in humans is another example of a conditional adaptation, although the GxE architecture is less well known. A substantial body of literature has demonstrated a reliable association between father absence and daughters' pubertal timing. Belsky et al. (1991) theorized that this association reflects a conditional adaptation that calibrates female reproductive strategies to match their future

reproductive ecology. Father absence and associated stresses serve as cues that the reproductive ecology is one where paternal investment is unreliable and/or unimportant. Earlier pubertal timing is a facet of an overall life history strategy that optimizes fitness through a phenotype characterized by early reproduction, unstable pair bonds, and relatively lower parental investment. It is important to note, however, that this association may actually represent a gene-environment correlation and not conditional adaptation, although some research has found fathering effects on girl's reproductive behavior using research designs that control for this confound (Tither and Ellis 2008; Ellis et al. 2012).

Epigenetic Modification

In order for a gene to influence cellular functioning, it must be expressed. Genetic expression involves a process where DNA segments in the cell nucleus – genes – are “read” by transcription factors, and a copy of the DNA segment is replicated into messenger RNA (mRNA). This process is called transcription. The mRNA carries the information out of the cell nucleus to the ribosomes where the protein encoded by the gene is created. This process is called translation. Epigenetic modifications alter the RNA transcription process, and the resulting epigenetic effect serves to turn up or turn down gene expression, upregulating or downregulating the gene like a dimmer switch turns up or down a light.

Epigenetic modification refers to changes *to* DNA (and its chromatin environment) as opposed to changes *in* DNA. The prefix “epi-” means above, on, or over, and epigenetic modifications mean changes to DNA that do not involve modifications to the actual DNA sequence. For example, the most commonly studied form of epigenetic change is DNA methylation, which occurs when a methyl group is added to a DNA sequence. When the methyl group is added in the promoter region of a gene, methylation turns down the gene by reducing, or even silencing, RNA transcription. There are no changes to the DNA sequence itself, only the gene's ability to

produce encoded proteins as well as non-protein-coding RNA (which do not encode proteins but are involved in many forms of genetic regulation).

Molecular Mechanisms for Conditional Adaptation. The hallmark of heritability studies is variance partitioning into genetic and environmental components. This approach assumes that genes and environments have independent main effects on a given phenotype (gene plus environment). This approach statistically quantifies the relative contributions of genotype and environment to phenotypic variation in a population. From a biological point of view, the separation between genome and environment is less well defined since the genome does not operate independently from the environment (Meaney 2010).

From the vantage of conditional adaptation, epigenetic DNA modification may serve as the mechanism through which conditional phenotypes are expressed. If humans have evolved to “detect and encode” relevant environmental information that adaptively entrain developmental trajectories, epigenetic change that results in differential gene expression across environments is a likely mechanism for the development of these phenotypes. Initial research in this area supports this idea. In particular a large body of research in animals (and emerging research in humans) indicates that early life adversity in the form of low maternal care, such as low maternal licking and grooming in rats and mice, increases methylation of the promoter region of the glucocorticoid receptor gene (*NR3C1*) in hippocampal neurons. This results in reduced glucocorticoid receptor expression in hippocampal neurons, stronger and more prolonged hypothalamic-pituitary-adrenal responses (glucocorticoids) to stress, and more fearfulness and defensive behavior against intruders (Meaney 2010). Variability in stress responsivity is hypothesized to be a conditional adaptation (Boyce and Ellis 2005).

Low licking and grooming also results in increased estrogen receptor alpha expression in the anteroventral periventricular nucleus of the hypothalamus and reduced estrogen receptor alpha expression in the medial preoptic area of the hypothalamus. These changes in gene expression regulate development toward faster life

history strategies: earlier onset of puberty in females, more play fighting in young males, greater sexual attractiveness/proceptivity in females, higher rates of pregnancy following mating, and less parental investment in their own offspring (reviewed in Ellis 2013).

The Missing Heritability Problem

Twin studies reveal that, across all traits, average heritability is approximately 50% (Polderman et al 2015). Although additive genetic effects inferred from latent variable models can account for approximately half the differences between individuals on a given trait, heritability estimates can vary substantially across traits. For example, as noted above, height heritability is approximately 80% whereas heritability for a complex trait like education attainment is approximately 20% (Okbay et al. 2016). These heritability estimates suggest that 80% and 20% of the variability in height and education attainment, respectively, can be explained by additive genetic effects (i.e., narrow sense heritability).

Advances in genomics have permitted researchers to examine associations between measured genetic polymorphisms and behavioral and psychological outcomes. The prevailing methodological approach to the study of genotype-phenotype relations are genome-wide association studies (GWAS). In GWA studies, hundreds of thousands to a million or more single-nucleotide polymorphisms (SNPs) are genotyped across chromosomes for every individual studied. Data are also collected on the phenotype of interest, often measured as a binary case/control (disease or no disease) outcome, such as depression diagnosis. A correlation is calculated between each SNP and the phenotype and a stringent multiple testing correction is applied to the statistical significance test, typically $p < .05 \times 10^{-8}$ ($p < .00000005$). The stringent p -value necessitates very large samples, on the order of tens of thousands, to achieve power high enough to meet this statistical criterion. Those SNPs with p -values below threshold, and which replicate, are considered meaningful for the phenotype, although the

GWAS approach is agnostic to the genomic function of a SNP or its causal relation to the phenotype.

GWA studies are a powerful method for gene discovery, however, they have fallen well short of identifying the magnitude of variance heritability studies attribute to genes. For example, GWA studies on height explain about 5% of the variance (Manolio et al. 2009). Similarly, a highly powered GWA study of education attainment explained only about 3% of the variance (Okbay et al. 2016). The discrepancy between variation explained by additive genetic effects in heritability studies and variance explained in molecular genetic studies is known as the missing heritability problem. If heritability studies suggest a large portion of phenotypic trait variation can be explained by genetics, why do molecular genetic studies fail to explain similar amounts of variance? Several explanations have been offered to account for the missing heritability. One class of explanations is methodological. These include imprecise phenotype measurement, questionable comparability between case and control groups, incomplete coverage of all phenotypically relevant polymorphisms, excluding rare variants (<1% frequency), excluding other DNA variations not captured by SNPs, failure to include causally related SNPs, and differences across genetic ancestry (e.g., European vs. non-European). Another set of explanations center on the accuracy of heritability estimates that assume only additive genetic variance contributes to a phenotype (i.e., narrow sense heritability). Heritability estimates may be inflated by nonadditive components, and omitting these sources of variability (i.e., broad sense) in molecular genetic studies may help to account for the missing heritability. More recently, a statistical technique called genome-wide complex trait analysis (GCTA) has been used to estimate heritability using genomic data. Heritability estimates of height, for example, using GCTA have come much closer to accounting for the missing heritability between molecular genetic studies and family studies. However, similar to family studies, this approach assumes nonadditive genetic variation is zero and statistically quantifies genetic variation as a percentage of variance explained. As a result, and similar to

family studies and GWAS, GCTA is limited in terms of identifying causal genetic variation. Importantly, the accuracy and reliability of heritability estimates using GCTA has been criticized based on mathematical and conceptual grounds and therefore may represent large overestimates of heritability (Kumar et al. 2016a, b; Yang et al. 2016).

Conclusion

Genetic inheritance can pose a problem for hypothesis testing from life history theory that posits adaptive phenotypic plasticity such as conditional adaption. In particular, alternative strategies and gene-environment correlations should be considered as possible explanation for conditional adaptation hypotheses and/or methodologically or statistically controlled. The issue of genetic inheritance in life history theory also has parallels with differences between broad and narrow sense heritability where the former captures conditional adaptations by virtue of gene-environment interactions. Because conditional adaptations are gene-environment interactions, this line of thinking and research could help explain the missing heritability problem by evaluating conditional gene-phenotype associations and potential underlying epigenetic mechanisms.

Cross-References

- [Genetic Influences of Puberty](#)
- [Sibling Studies](#)
- [Twin Studies](#)

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Problem Solving

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Synonyms

Complex problem solving; Problem solving ability; Social problem solving

Definition

A problem is a condition that needs to be resolved to achieve a desired goal. Problem-solving makes use of higher order cognitive processes that regulate lower order mental processes to achieve the

goal. Problem solving ability is a person's capability to transform the problematic condition to the goal state by using higher cognitive functions.

Introduction

The whole life involves problem solving from small scale to large scale problems, from simple to complex problems, and from personal and psychological to social, environmental, and collective problems. Problem solving in all problems involves three components: givens (facts or stimuli presented), goals (desired ending), and operations (methods or techniques to achieve the desired objective). Commonly, we engage in problem solving to overcome hindrances, to accomplish a goal, or to find a solution to a problem that has no readymade solution available. The mechanism of converting the given problem situation into the desired goal state is described as problem solving (Lovett 2002). Solutions to most of the problems are generally situation or context specific. Problem solving process usually starts with problem identification and representation, strategic planning and generating solutions, and then, enactment of the most suitable plan to solve the problem. Therefore, the way we understand a problem largely affects the way we solve the problem.

Historically, the early work on problem solving can be rooted back in experimental studies conducted by proponents of Gestalt school in early twentieth century (e.g., Duncker 1935). According to this approach, efficiency of problem solving depends on how much appropriately it is represented in mind. Effective problem solving in insight problems requires an individual to perceive the problem as a whole. Then, ultimately the success of problem solving depends on effective restructuring and reorganization of this representation. Gestaltists propose that problem solving involves closure of a problem because by appropriate representation and closure, an incomplete problem question is resolved towards a complete solution.

However, Behaviorists view problem solving as a process that develops gradually as a result of

positive and negative reinforcement mechanisms. The process also involves trial and error methods. Cognitive psychologists view problem solving as a process involving introspection, observation, and the development of heuristics. A subsequent approach is an information processing approach which proposes that problem solving is a process involving construction of a problem space and then, developing a path through the problem space to resolve the problem (Novick and Bassok 2005). A problem space according to this approach is a universe comprising an original state, all the possible actions and constraints applied to the solution, and an end state. This viewpoint has been quite successful in solving well-structured problems.

Types of Problems

Generally, the problems can be categorized into two categories: (i) *well-structured problems* and (ii) *ill-structured problems*. A well-structured problem is one which has a clear path to a specified solution, though not necessarily a simple and easy path. These problems commonly include formalized, formalized, analytical, and domain specific problems such as presented in disciplines including algorithms, mathematics, etc. They also include isomorphic problems, which have similar formal structure but different contents. Usually, such problems have clearly described given states, set of operations or rules, and goal states. Examples of such problems can be a chess game, a Rubik's cube, and towers of Hanoi game. As well-defined problems have clearly defined given and goal states as well as set of operations so these problems can be efficiently solved by computers. An ill-structured problem, on the other hand, is a problem that does not have a clear path to a solution. Such a problem also does not have a specified set of rules to solve the problem and a specified goal state. Problems involving creativity can be categorized as ill-defined problems. Nevertheless, such problems may involve subproblems that can be well structured.

Additionally, two related forms of problem solving can be described including complex problem solving and collective problem solving.

Complex problem solving involves a collection of creative abilities and knowledge, a broad set of strategies, and self-regulated cognitive processes to solve ill-defined problems. *Collective problem solving* can be described as a problem solving process that is accomplished collectively for problems which are of collective nature such as social and global issues. Such global and collective problems can only be solved at collective level because complexity of such problems exceeds the cognitive limits of a single individual requiring a variety of collaborative and collective but complementary efforts.

Problem Solving Strategies

Problem solving process involves a use of different problem solving strategies. A strategy is described as a plan of operations which can be performed to get a solution to a problem. Various strategies can utilize various actions plans in the way to achieve goal state. The following techniques are usually called strategies: (i) *Trial and Error*, a well-known and commonly used strategy, involves trying many possible plans until the correct solution is sought; (ii) *Algorithm* as a strategy is a formula or a set of step-by-step directions which can be used to solve usually analytical problems; (iii) *Analogy* involves applying an existing solution from an analogous problem to a problem at hand; (iv) *Abstraction* involves trying a solution of problem on similar models of a system before applying it to the real system such as doing psychological experiments on animals; (v) *Heuristic* is another strategy that provides a general framework to solve a problem. It may include mental short cuts or working backward starting from a desired goal. Using heuristics may save an individual's time, effort, and energy in problem solving, but it does not necessarily result in the best solution of a given problem; (vi) *Reduction* is converting a problem into another form for which existing solutions are available; (vii) *Hypothesis testing* involves proposing a probable solution to a problem and then trying to assess it; (viii) *Means-ends analysis* involves selecting and implementing an

appropriate action plan at each step to get closer to the goal; (ix) *Brainstorming* is an important strategy particularly important for collective problem solving which involves generating a large number of solutions by all or many members of a group and then, combining them until the best solution is developed; (x) *Divide and Win* is decomposing a large and complex problem into small, simple, and solvable tasks to get it done; and (xi) *Lateral thinking* involves developing a solution to a problem through indirect and creative means.

Specific use of a strategy varies according to type and importance of a problem, constraints, or the access of information. The problems that have only one specified solution such as mathematical and algebraic problems may involve algorithms and analogies. Other problems that can have multiple goal states and can be solved using multiple sets of operations in one or another combination may use different strategies. Still another category includes problems that can have solutions which change frequently depending on temporal personal, emotional, socioeconomic, and cultural factors, for example, choosing a favorite color on a festival or a present for someone for Christmas. Such problems may rely on heuristics of other logical strategies.

To understand problem solving skills, it is important to note that some problems, particularly analytical ones which are related to specific disciplines such as mathematics or natural sciences may require domain specific skills (Sugrue 1995), while other ones may require general but higher order mental capacities to for its solution (Funke 2001). However, the general complex mental capacities are more important than domain specific skills for a variety of problems in that they assist in better representation of a novel problem situation, which can be useful for generating solutions.

Problem Solving Methods

Problem solving always involves a cycle of step by step directions to solve problems. Generally, these steps include to identify the problem, to

define and represent the problem, to plan a solution, to implement the solution, to review the usefulness of solution, and to revise if needed. Still, many researchers have devised their own specific methods of problem solving. One of such models is a GROW model (Goal, Reality, Options, and Way forward) that is a four-step method to assist a problem solver in structuring problem solving process. Different variants of this model are now available including Goal, Current Reality, Options (or Obstacles), Will (or Way Forward). Another model is the OODA loop (Observe, Orient, Decide, and Act) which involves a decision-making approach to problem solving. The model guides to initially focus on accessible information, then, to filter the information and organize it, and finally, to make the most suitable decision regarding solution. Similarly, PDCA (Plan, Do, Check, and Act), a four-step procedure, is typically implemented in business and management disciplines for continuous improvement of products. Another model is Root Cause Analysis (RCA), which is a more systematic procedure to identify the causes of a problem and to eliminate these causes along with solving the problem. Finding and resolving a way to prevent the problem is the basis of this model. Additionally, a Hive Mind method or a group mind may refer to shared or collective intelligence to solve collective problems. The approach is most commonly used in social psychology and philosophy.

Additionally, there are other problem solving methods which are used in different disciplines including: (i) How to Solve It (understand, plan, carry out plan, and look back to review), which is used in solving mathematical problems; (ii) Eight Discipline Problem Solving (8Ds) is a model developed by a motor company and is typically used in engineering related disciplines; (iii) RPR (Rapid Problem Resolution) is a problem diagnosis model developed to determine the causes of IT related problems; (iv) a Structured A3 problem solving method that is commonly used by manufacturing workers to solve problems; and (v) System Dynamics is a computer-aided problem solving approach to policy analysis and design.

Obstacles and Aids in Problem Solving

There are many factors that can hamper or facilitate problem solving. First, a *mental set, entrenchment, or fixation* that describes an existing and fixed frame of mind to represent a problem, its context, or set of operations to solve it. If an individual has an entrenched mind set, he fixates on a commonly used problem solving strategy that may work well for many problems but may not work for a particular novel problem. Mental sets can also hamper problem solving for routine problems. Stereotypes, an aspect of social cognitions, are also a form of entrenched mental set which may impede generating novel ideas regarding a particular group of objects, persons, or functions. Stereotypes develop in childhood years (Seguino 2007) and usually develop in the same way as other entrenched mental sets develop.

Second, *functional fixedness* is another related hindrance in problem solving that can be described as fixation on a specific use of an object. More precisely, functional fixedness can be defined as an individual's inability to recognize that a particular object that is known to have a particular use can also be utilized for other functions (German and Barrett 2005; Rakoczy et al. 2009). Functional fixedness inhibits an individual from solving novel problems by using existing apparatuses in novel manners. By breaking the functional fixedness, people have become able to use coat hangers to open the locked car and credit cards to open spring locks.

Negative and Positive Transfer as a form of particular mental set may also impede or facilitate problem solving by carrying over already learned strategies to novel problems (Gentile 2000). Transfer of knowledge and skills can be positive or negative. Negative transfer happens when skills and strategies used to solve earlier problems may make it difficult to solve later problems. For example, an individual when presented with a new apparatus tries to operate it in a way he/she is already familiar with (Besnard and Cacitti 2005). Positive transfer occurs when a solution from an earlier problem facilitates solving a new problem (e.g., Campbell and Robert 2008). For example, car mechanics may generalize their

earlier strategies and skills to resolve related problems of different types of vehicles. Positive transfer also involves Transfer of Analogies where a solution from an analogous problem is applied on a new problem. However, transfer of analogies involves an *Intentional Transfer*, that is, the problem solver looks for analogies by recognizing the association between the earlier problem and the new one (Gentner 2000). It is important to note that similarity in content is less important than the similarity in structural systems between two problems in perceiving analogies.

Incubation is an aid to problem solving. For solving complex problems, what is important is to avoid obstacles due to negative transfer rather to look for analogies for positive transfer. Incubation means to set the problem aside for the time being and to take a break from problem solving process. During incubation, the problem solver does not consciously think about it to minimize interference due to negative transfer. However, problem solving process may occur at a subconscious level. Few early investigators have declared incubation to be an important stage of problem solving (e.g., Cattell 1971). However, a recent meta-analysis has reported that incubation is beneficial when individuals have more time for problem solving compared to the situation when individuals are occupied with highly cognitively taxing tasks. Also, incubation works well with divergent-thinking tasks compared to convergent thinking tasks (Sio and Ormerod 2009).

Neuropsychology of Problem Solving

Since the last few decades, neuropsychology has become a rapidly growing area of cognitive psychology focusing on neuropsychological abilities underlying all human behavior. Executive cognitive functions being very important components of neuropsychological abilities have been studied vastly. Executive cognitive functions are higher order cognitive and self-regulatory processes which control fundamental cognitive processes. Problem solving has been described to be one of these executive functions. These executive functions include inhibition, initiation, switching,

problem solving, planning, judgment, and decision making. These higher regulatory abilities are thought to be regulated by frontal areas of brain and particularly, by the prefrontal cortex.

Various studies have found that planning is an essential component of problem solving cycle (e.g., Gunzelmann and Anderson 2003). Planning makes problem solving an efficient and time saving process. As the frontal lobe and prefrontal cortex are described to regulate high regulatory processes, so these areas also play a crucial role in planning during problem solving process. Many brain imaging studies using functional MRI and positron emission tomography scans have reported activation in both the right and left prefrontal regions during the planning phase (Newman et al. 2003) and in frontal lobe during problem solving process (Unterrainer and Owen 2006). The same is described by other researchers studying patients with traumatic brain injury who described that the patients with least damage to the prefrontal areas performed best on problem solving tasks (Catroppa and Anderson 2006; Cazalis et al. 2006). On the other hand, patients with damage to prefrontal areas show difficulty switching from one problem solving strategy to another. Nevertheless, the detailed description of neuropsychology in problem solving is quite complicated and a single brain region cannot be attributed to this complex cognitive function. Rather, it is likely that several brain regions would work in coordination to perform a complex problem solving task.

Cross-References

- Cognitive Science
- Problem of Altruism

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Problem Solving Ability

► Problem Solving

Problems of Assessing Fertility

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Synonyms

Daily conception risk; Daily fecundability;
Menstrual cycle phase; Ovulatory cycle phase

Definition

A multitude of methods are used in evolutionary psychology research to assess women's menstrual cycle phase and/or fertility, each of which possesses advantages and disadvantages.

Introduction

Of long-standing interest for family planning purposes, the measurement and detection of women's fertility and ovulation have recently approached the forefront of evolutionary psychology research. According to the ovulatory shift hypothesis, women undergo a suite of adaptive physiological, behavioral, and cognitive changes across phases of the ovulatory cycle. While several recent meta-analyses have suggested the robustness of such ovulatory shifts (Gildersleeve et al. 2014a, b),

others have challenged their existence (Wood et al. 2014) and have attributed positive findings to imprecise and elastic procedures used to define fertility (Harris et al. 2014).

It is now well established that the probability of an act of intercourse resulting in conception is nonzero on the day of ovulation and on the 5 days prior (Masarotto and Romualdi 1997; Stirnemann et al. 2013; Wilcox et al. 1995). However, the best way to detect this “fertile window” remains equivocal. Transvaginal ultrasound affords a direct and unambiguous measure and is widely considered the gold standard for fertility assessment, but it is both time and cost intensive, rendering it impractical for many research purposes. Consequently, studies often employ indirect measurements of fertility using methods that fall broadly into three categories: measures relying on observable physiological changes, counting methods, and hormonal methods. Briefly reviewed here are the relative strengths and weaknesses of these different methods of fertility assessment, as well as how they have been applied in evolutionary psychology research, and conclude with methodological recommendations for future work on ovulatory shifts in behavior and cognition.

Physiological Measures

Basal Body Temperature (BBT)

Daily monitoring of BBT has long been used clinically to assess fertility and may be considered the oldest clinical method of fertility monitoring (Lynch et al. 2006). As the corpus luteum is formed after ovulation, it begins releasing large quantities of progesterone into the periphery, resulting in a concomitant increase in BBT of about 0.5 °C. As the increase in BBT is observed after ovulation, BBT monitoring can help retrospectively, though not prospectively, assess timing of ovulation. Epidemiological studies have found that, with little training, women are able to accurately measure their BBT, making BBT monitoring a feasible and valid method of fertility monitoring in large-scale studies. Though BBT monitoring is accurate, easy, and

inexpensive, BBT itself is influenced by many factors that may render BBT readings inconclusive. Psychological and behavioral variables such as stress, changes in sleep patterns, or alcohol use can all substantially affect BBT, leading to fluctuations unrelated to fertility status. Additionally, a small portion of women do not exhibit cyclic fluctuations in BBT during cycles when ovulation occurs.

Cervical Mucus Monitoring

The cervical mucus monitoring method of ovulation detection relies on observed changes in the frequency and consistency of vaginal discharge (Billings et al. 1972). Approximately 6 days before ovulation, rises in estrogen lead to increased cervical mucus secretion, with mucus being sticky or slippery in consistency. Cervical mucus monitoring has been shown to accurately estimate the fertile window when cross-validated with transvaginal ultrasound, LH surges, and plasma estrogen levels, and women can typically be trained to the method in about one cycle of teaching. However, women's hesitations about cervical mucus monitoring may yield it problematic for use in large-scale research studies. While women do not report discomfort or hesitation about BBT monitoring and urine collection for fertility assessment, a significant percent of women express such concerns about cervical mucus monitoring. Additionally, women have reported that the method is uncomfortable and difficult to use (Wright et al. 1992).

BBT and cervical mucus monitoring are often used concurrently for family planning purposes and are together referred to as the sympto-thermal method. Formal analyses have estimated the probability of unintended pregnancies using the sympto-thermal method to be around 2%, suggesting that women are able to accurately monitor their fertility in the great majority of cases (Frank-Herrmann et al. 2007). Nevertheless, due to the training required for such measures and the high drop-out rates associated with the discomfort or unwillingness to use them, these physiological measures are not ideal for fertility assessment in laboratory-based studies.

Counting Methods

Counting methods of assessing ovulation rely on inferences about the lengths of the follicular and luteal phases, as well as the length of complete cycles to determine the timing of the fertile window. To pinpoint this window, forward-counting methods use the starting date of a woman's last menstrual cycle and estimates of the length of the follicular phase, whereas backward-counting methods use the anticipated date of a woman's next menstrual cycle and estimates of the length of the luteal phase. While most studies have categorized women's fertility according to whether women were estimated to be in versus out of their fertile windows, some studies have used counting methods to assess fertility continuously. This is accomplished by assigning conception risk values according to estimated cycle day and published daily conception risk values from the medical literature. Continuous measures have been shown to be significantly more valid than discrete measures, affording greater statistical power (Gangestad et al. 2015). A third way in which counting methods have been utilized has been to assign hormone levels to each day based on estimated cycle day and published average daily hormone concentrations (Garver-Apgar et al. 2008; Puts 2006). Counting methods have been overwhelmingly the method of choice for estimating fertility in ovulatory shift research, with use in over 90% of studies published before 2010 (Gonzales and Ferrer 2015). While such methods are arguably the easiest and cheapest to employ in research, they rely on several assumptions that pose significant challenges to their accuracy.

Both forward and backward counting rely on women's self-reports of their average menstrual cycle length. Studies typically exclude women with reported average cycle lengths that deviate considerably from 28 days and women who report high variability in cycle lengths. Even with such exclusions, the accuracy of self-reported menstrual cycle length is uncertain. Almost half of women will have a cycle range of 7 days or more, and 20% will have a cycle range of 14 days or more across just four cycles (Creinin et al. 2004). It is unclear

whether women are able (Creinin et al. 2004) or unable (Small et al. 2007) to accurately report their average menstrual cycle length, but average cycle length correlates poorly with the length of any individual cycle (Creinin et al. 2004; Small et al. 2007). The accuracy of self-reports may also be moderated by age, such that women under 25 are almost three times as likely to be inaccurate in such reports compared to women 30 and above (Small et al. 2007). This is particularly problematic, as the majority of cycle shift studies are comprised of undergraduate women younger than 25. A second cause for concern is between-cycle variability in the lengths of menstrual cycle phases among regularly cycling women. Follicular phase length may be more variable than luteal phase length between cycles, with a third of women experiencing follicular phase length differences of 7 days or more across cycles, compared to about 9% of women exhibiting this variability in luteal phase length (Fehring et al. 2006).

A great deal of attention has recently been drawn to whether counting methods are accurate estimators of fertility. Two separate studies have reported that when using counting methods to define the 6-day fertile window, around 40% of the days in this presumptive fertile window are actually non-fertile (Blake et al. 2016; Eisenbruch et al. 2015). As much as 60% of the days in the fertile window may be misclassified if forward-counting methods are used (Blake et al. 2016). Such inaccuracies considerably weaken the power to detect true shifts in behavior and cognition during the fertile window. Backward-counting methods seem to outperform forward-counting methods (Gangestad et al. 2015; Gonzales and Ferrer 2015) and thus are associated with less dramatic reductions in statistical power, though when using a between-subjects design and expecting a moderate effect size, backward-counting methods may require 50% more subjects than hormonal methods to achieve the same power (Gangestad et al. 2015).

Hormonal Methods

Luteinizing Hormone (LH) Measurement

LH was first discovered as a valuable measure of fertility through a large-scale study led by the

World Health Organization with the goal of identifying urinary hormone markers of fertility (1983). Though estrogen and LH are typically part of a negative feedback loop during the early follicular phase, as ovulation approaches and levels of estrogen rise, this becomes a positive feedback loop, with increasing levels of LH accompanying increasing levels of estrogen (Hall 2004). During ovulatory cycles, a sharp urinary LH surge is observed between 24 h and 48 h prior to ovulation, making the LH surge a reliable marker of peak fertility and its absence a reliable marker of anovulatory cycles, which are typically observed in about 30% of cycles in undergraduate women (Cantu et al. 2014). As increasing levels of LH are limited to the 24–48 h before ovulation, LH levels can be used to detect earlier days in the fertile window only retrospectively.

Many tests measuring urinary LH are commercially available and are affordable (currently, about US\$0.50 per stick), accurate, and require little training to use, making such tests an attractive method for detecting fertility in research. It is then unsurprising that the majority of studies that have used hormonal measures of fertility in evolutionary psychology research have used LH tests rather than other hormonal measures (e.g., Cantu et al. 2014). While daily LH tests on each day of the menstrual cycle would identify virtually all LH surges, LH tests limited to 9–19 days prior to the anticipated start date of women's next menstrual cycles identify over 93% of all LH surges (Blake et al. 2016). Clear LH surges, however, are not always evident, even in cycles where ovulation does occur. Whereas about 5% of cycles in (non-undergraduate) women in their 20s and 30s are expected to be anovulatory cycles, 25–30% of such cycles lack a clear LH surge (Baird et al. 1991). Thus, while LH surge detection may be the most widely used hormonal biomarker of ovulation, its use in cycle phase studies, which are most often conducted with female undergraduate participants, may yield unacceptably many ambiguous data.

Estrogen-to-Progesterone (E/P) Ratio

The least common method of detecting fertility in recent cycle phase studies is E/P ratio

measurement – in one recent meta-analysis, only one study reviewed utilized E and P measurement to detect ovulation (Gonzales and Ferrer 2015), though several other studies not included in this meta-analysis have utilized E and P measurement as well (e.g., Puts et al. 2013; Bossio et al. 2014). Estrogen is released by the follicle during the late follicular phase, while progesterone levels stay low, resulting in a high E/P ratio. This ratio drops quickly after ovulation, when estrogen levels decrease and the corpus luteum releases progesterone into the periphery. An algorithm using the urinary E/P ratio was originally proposed by Baird et al. (1991) and was able to detect ovulation within 2 days of the LH surge in 88% of cases. Furthermore, the algorithm was able to detect ovulation for 90% of cycles that did not exhibit clear LH surges, suggesting the algorithm may yield more interpretable samples than would LH measurement alone.

Urinary measurement of steroid concentrations, however, has several limitations. First, urinary concentrations represent average concentrations over longer periods of time than salivary or blood concentrations. Second, urinary concentrations represent a combination of both SHBG-bound (i.e., not bioactive) and unbound steroid. Greater than 90% of estradiol and testosterone are SHBG bound, making the majority of the measured steroid in urinary samples of unclear relevance in determining the influence of hormone concentrations on behavior. By contrast, salivary steroid concentrations are more sensitive in that they represent concentrations at the time of measurement itself, rather than an average concentration over a longer period of time. Additionally, the amount measured is limited to bioactive, unbound steroid, affording researchers the ability to investigate relationships between changes in behavior and cognition and the amount of steroids that could be related to these changes (rather than the total amount of steroid).

Conclusion

Evolutionary psychology's increased interest in ovulatory shifts in behavior and cognition, as well as in the effects of ovarian hormones on

behavior and cognition more generally, have resulted in scrutiny of how fertility is assessed. Of the three recent large-scale studies tackling the issue of how fertility should best be defined (Blake et al. 2016; Gangestad et al. 2015; Gonzales and Ferrer 2015), all have provided a similar recommendation for the field moving forward: hormonal methods of fertility assessment should be favored as they are indisputably more precise than other physiological measures and counting methods in detecting women's fertile windows. Comparison of the percent of studies using hormonal methods of fertility assessments published before and after 2010 (7.5% and 11.1%, respectively; Gonzales and Ferrer 2015) suggests that researchers are increasingly perceiving the utility of such methods, and it is likely that this trend will continue in light of recent studies highlighting their advantages. Hormonal methods of fertility assessment that involve measuring ovarian steroids (estrogens and progestogens) afford a second significant advantage: any fluctuations in behavior and cognition across the menstrual cycle are likely to be driven by fluctuating ovarian steroid hormones; however, as so few studies have measured bioactive ovarian steroids, the contributions of individual hormones remain elusive despite over two decades of scientific interest in the topic.

Cross-References

- [Fertility](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Menstrual Cycle](#)

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Problems with Group Selection

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Synonyms

Multilevel selection theory

Definition

Arguments, examples, and alternative explanations that refute group selection theory.

Introduction

Group selectionists argue that it is possible for certain adaptations to evolve because they benefit the group as opposed to benefiting the individual or gene. This has led to arguments in favor of the notion that some cooperative behaviors may have evolved because they have led to the survival of the group. However, critics of this theory have provided many refuting arguments and examples against group selection, as well as alternative explanations for the evolution of cooperative behaviors. This entry discusses these arguments, examples, and alternative explanations.

Alternative Explanations for Group Selection

George Williams (1966) noted that although group selection is theoretically possible, it is unlikely to be a strong evolutionary influence in the natural world. This is because natural selection in favor of the individual will often supersede any selection in favor of the group. Buss (2012) provides the following example, “Imagine a bird species with two types of individuals – one that sacrifices itself by committing suicide so as not to deplete its food resources and another that selfishly continues to eat the food, even when supplies are low” (p. 14). The selfish birds are more likely to survive and reproduce than the suicidal birds who may die before ever passing on their genes. This illustrates that selfish behavior that favors individual selection will have a stronger evolutionary influence than the cooperative behaviors that favor group selection.

Although cooperative and altruistic behaviors are frequently observed in the animal kingdom – even behaviors in which an altruist sacrifices him-/herself to benefit the group – these behaviors are usually explained by theories of individual

selection and/or gene selection. For instance, one of the tenets of kin selection theory (Maynard Smith 1964) argues that individuals are more likely to risk their lives to rescue kin as opposed to nonkin. This is because altruistic behaviors may be caused by a particular gene, and although the altruist may perish during the altruistic action (such as saving a sibling from a burning building), that gene may still be passed onto the next generation through the reproduction of the surviving kin member – because the altruist had that particular gene, and the recipient is related to the altruist, there is a certain probability (depending on how closely related the altruist and recipient are to each other) that the recipient also has a copy of that altruism gene (Park 2007). Therefore, a sacrificially altruistic behavior, which appears to have been conducted for the benefit of someone else in the group, may actually have been performed for the benefit of the gene responsible for that behavior.

Similarly, just because an individual foregoes his/her own reproduction to benefit the overall group does not mean that his/her sacrifice is adequately explained by group selection. For example, some adult male jackals will stay with their parents to help raise future litters of their younger siblings. These jackals often do not reproduce, but their presence significantly increases the survival rate of the future litters, allowing for the male jackal’s genes to still be passed on indirectly via his siblings (Moehlman 1987). Although this cooperative behavior increases the survival of the group, it persists because it also increases the reproduction of the individual’s genes – indicating that this behavior is influenced by natural selection at the genetic level, not the group level.

Reciprocal altruism theory (Trivers 1971) is often another alternative explanation for cooperative behaviors that appear to be conducted for the good of the group – such as food sharing among unrelated individuals. Although humans and other animals will often share food with nonkin – indicating that this behavior is not influenced by kin selection – this sharing is frequently conducted between individuals who have a history of sharing. In other words, this sharing occurs on the basis of reciprocity. For instance, vampire

bats will share food with kin and nonkin; however, they will only share their food with the nonkin who have previously shared food with them (Wilkinson 1988). Humans possess similar food sharing behaviors, which have been studied extensively in modern-day hunter-gatherer tribes (Berte 1988; Gurven 2004; Gurven et al. 2001). In short, humans and other animals give food to unrelated individuals so that they may maintain reciprocal relations – allowing them to receive food in times of need. This allows for the successful survival of the individual.

Conclusion

Group selection has provided much controversy over the years with many great scientists each taking opposing sides. Although after Williams (1966) book, group selection was widely rejected in the scientific community. However, in recent years, group selection has seen a resurgence but is now called multilevel selection theory (see entry titled ► “Multilevel Selection Theory” for more information). Although these examples and alternative explanations continue to be used as arguments against group selection theory, proponents of group selection argue that not all cooperative behaviors can be explained by gene selection and individual selection.

Cross-References

- Altruism
- Cooperation
- Examples of Group Selection
- Group Selection
- Kin Selection Theory
- Multilevel Selection Theory
- Reciprocal Altruism

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Procedural Knowledge

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Synonyms

Automatic functioning; Habitual processing; Imperative knowledge; Schematic memory

Definition

Procedural knowledge is proposed as the system containing memories of how the human brain can proceed to do things.

Introduction

It is argued that physical activities as well as cognitive skills are the outcome result of

procedural knowledge, as they are not expressed through verbal communication but by means of performance. Procedural knowledge is relatively autonomous in relation to declarative memory. This can be argued by the expression of certain types of amnesia such as anterograde amnesia and Korsakoff's syndrome as individuals are no longer able to collect or recollect new declarative facts. Although painful and slower than normal, patients who suffer from amnesia are still able to acquire new procedural skills after the onset of the brain degeneration. Automatic functioning in procedural knowledge is also indicated by the learning procedures an amnesia patient's brain is able to accommodate. Examples of learning in amnesia patients are conditioning, word complementing, and the effect of priming on word recognition. These tasks render vivid implications that procedural skills are proceeded through performance and not by conscious recollection of the experience of the learning process.

Evolutionary Perspective of Procedural Knowledge

In animals the ventral stream of visual analysis is primarily concerned with object recognition. The dorsal stream is concerned not with seeing where but mainly with seeing how. This division bears a strong correspondence to the distinction between declarative and procedural memory (Baddeley 1990). Although the anatomical correlates of these divisions differ considerably, the functional correspondence is striking. These parallels unite a physiological approach with a psychological view on vision and its relation to action upon the environment (Goodale and Milner 1992).

Gibson's Theory

J.J. Gibson (1968, 1979) is the founder of what is canonically called "direct perception." Direct perception is the view that in perception it is not needed to assume that any higher-order processing and internal representations involved in perception. The environment contains sufficient information to give rise to visual perception. The theory of direct perception has been developed in response to serious problems that arose in the

traditional, physical, approach to vision. One of the core assumptions in Gibson's theory is the assumption that the most relevant features an animal perceives are what the world affords an animal to do. Accordingly, what affordances are perceived is unique for each animal. If what is perceived is meaningful, it is meaningful relative to an individual organism. Members of the same species more often perceive the same affordances of objects than individuals of different species. Gibson suggests that the ecological concept of "niche" is to be seen as the set of affordances for an individual member of a species. Because an affordance is not a phenomenal object, it changes as an animal changes, such as developing physical handicaps. However, it does not change as the need of an animal changes. Although Gibson avoided physiological or neurological considerations, it can be inferred that his theory refers to the dorsal stream of visual analysis, and it concerns animals with a cortex, since information stem from procedural memory and it concerns seeing "how" to do things.

Nonhuman Species and Evolvment of Knowledge

Phylogenetically, it can be argued that procedural knowledge is older than declarative knowledge. This can be shown by the fact that declarative learning only occurs in higher animals, if not human beings (Ornstein 1991). Ontogenetically, it is demonstrated by the fact that children begin to learn and remember procedures before they do facts (Bloom and Lazerson 1988). Also, procedural skills are more important for survival than declarative facts (Dudai 1989). Hence, it is not reasonable to assume that knowledge of facts evolved before the knowledge of skills. Another argument has to do with recent developments in the research on neural networks. By their very nature, neural networks are suited for the modeling of procedural knowledge. When an input is fed to a network, it "knows" how to react. This knowledge is implicit and can only be made explicit by the analysis of hidden units. Procedural knowledge is a concept of a dynamic process that cannot be

represented validly by means of a sequential rule system (Bechtel and Abrahamsen 1991). Networks have been designed in a way that are able to assimilate concepts which were traditionally considered to be propositional systems, for instance, certain rudimentary language structures and logical inferences (Bechtel and Abrahamsen 1991). In psychologically relatively plausible systems that operate on these classes of input, propositions are considered as a description of the outcome of a process, not as a description of the process itself.

Conclusion

It has been argued that declarative memory evolved from procedural memory and it constitutes a part of it. Some of its aspects might be reduced to procedural memory. It is both phylogenetically and ontogenetically younger than procedural memory, it is shown to be possible to model declarative knowledge in procedural systems and neural networks, and in some cases, one-trial learning can function within the procedural system. This notion suggests that declarative knowledge is made possible by procedural knowledge; interpretively, declarative knowledge could be considered a special case of procedural knowledge.

Cross-References

- [Declarative Knowledge](#)
- [Dorsal Stream, The](#)
- [Evolution of Teaching](#)
- [Ventral Stream, The](#)

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Procedural Learning

- [Non-associative Learning](#)

Procedures for Dealing with Bullies

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Synonyms

[Aggression](#); [Dominance](#); [Social sanctions](#); [Strategies](#)

Definition

Understanding and reducing the severity and frequency of aggressively dominant behavior.

Introduction

Bullying behavior is ubiquitous in human societies and appears to be a successful evolutionary strategy. However, the damage done by bullies in childhood can be severe. Along with a multitiered approach that involves the intervention of several adults, preventative measures should also encourage alternative prosocial strategies to achieve social goals.

Definition of Bullying

Bullying is a complex social behavior, loosely defined as the intentional use of physical and psychological force or power, threatened or actual, on a one-on-one or group basis against another person, group, or community that often results in injury, psychological harm, mal-development, deprivation, or even death (Krug et al. 2002). All bullying is aggression, but not all aggression is bullying (Hawley 1999). Bullying is a specific type of aggression that is intended to harm or disturb physically or psychologically, occurs repeatedly over time, and includes an imbalance of power with a more powerful person or group attacking a less powerful one (Nansel et al. 2001).

Forms of bullying include, verbal, physical, sexual, social, or racial/ethnic, each serving a particular function, but bullying is generally classified as direct or indirect (Juvonen and Graham 2014). *Direct physical bullying* is physically confrontational, which can involve hitting, tripping, pushing, poking, damaging property, physical threats, giving intimidating looks, stealing property, and touching and/or brushing up against (in a sexual nature). *Direct verbal bullying* can involve insults, name-calling, put downs, laughing at, threatening, sexual innuendo, and verbally abusing a name, family, religion, sexuality, disability, or other individual characteristic of a “target.” *Indirect bullying*, sometimes referred to as “social bullying,” harms someone’s social reputation and/or causes humiliation and is harder to recognize as it’s often carried out behind the targets’ backs (Juvonen and Graham 2014). Indirect bullying can entail lies, spreading rumors, playing nasty jokes to embarrass and humiliate, mimicking, deliberately excluding someone from activities, encouraging others to exclude someone, damaging social reputation acceptance, or deflating social status while concealing the identity of the perpetrator (Bernard and Milne 2008). A new form of bullying involving computers and social media, referred to as *cyberbullying*, consists of being cruel to others by sending or posting harmful material, or engaging in other forms of social

aggression using the Internet or other digital technologies.

Researchers have also identified other types of bullying, like *reactive bullying*, a defense reaction to a perceived threatening stimulus that’s accompanied by some visible form of anger; *proactive bullying*, an unprovoked aversive means of influencing or coercing another person (more goal-directed); *overt bullying*, a confrontational set of behaviors directed towards another individual or a group of individuals; *relational bullying*, a type of behavior that involves excluding someone from a social group, spreading rumors, keeping secrets, or humiliating someone in a social setting (indirect); and *punking*, a practice involving verbal and physical violence, humiliation, and shaming in public (Hong and Espelage 2012).

Prevalence of Bullying

Bullying has been observed in every human society, including modern hunter-gatherers. In a study of 79 different countries, approximately 30% of adolescents reported bullying victimization (Elgar et al. 2015). Multinational studies have found that the most intensive bullying was found in countries where violence and social intolerance are the most commonplace, with the lowest per-capita income (Bernard and Milne 2008; Elgar et al. 2015). In Western nations, an estimated 4–9% of youths frequently engage in bullying behaviors, and 9–25% of school age children are victims of bullying, with a smaller subgroup of bully-victims who both bully and are bullied (Nansel et al. 2001). Bystanders, referring to a viewer, observer, witness, or passerby, can also be indirectly involved in bullying incidents by encouraging fights, cheering the bully, and help the bully by warning them if an authority figure is coming (Hong and Espelage 2012).

Bullying begins in early childhood, where it emerges in almost any group of toddlers playing freely (Hay et al. 2004). Bullying increases over childhood, peaking around the age of 14 (Volk et al. 2012), with 85% of incidents occurring in the presence of peers (Bernard and Milne 2008). Girls are more likely to use teasing, rumors, and taking of personal belongings, while boys are

more likely to initiate bullying and use direct physically aggressive methods (Juvonen and Graham 2014; Nansel et al. 2001). While indirect bullying is more common for girls early on, during middle adolescence indirect bullying, specifically verbal aggression, becomes most frequently used by both genders (Juvonen and Graham 2014; Nansel et al. 2001).

Evolutionary History of Bullying

Dominance and submission are prominent underlying mechanisms that span all cultures (Boehm 2009). The universality of bullying across human societies indicates a species-typical human behavior, deeply rooted in our evolutionary history. Bullying-like behaviors are also found in many animals, including every major group of primates. The expression “establishing a pecking order” often represents dominance achieved through aggression and bullying, which is derived from birds (particularly chickens) that use repeated aggressive pecking to establish social hierarchies (Volk et al. 2012). In chimpanzees, our closest genetic relatives, direct physical aggression can be a strategic behavior, particularly for males who can achieve high social status through physical domination and intimidation that can lead to better access to food resources and mating opportunities.

Hunter-gatherer societies represent the oldest form of human culture, encompassing at least 90% of human evolutionary history (Lee and Daly 1999). The few remaining hunter-gatherers share some commonalities with chimpanzees, such as depending on foraging and living in flexible local groupings, but socially, they are vastly different. Hunter-gather cultures are quite egalitarian, with sharing being a central rule of social interaction, and community sanctions against bullies (Lee and Daly 1999). Social control in hunter-gathers is preemptive, with groups being vigilant about violators of cultural norms and ethics, and frequently using humor to cloak moralistic aggression (Boehm 2009). Bullying outside the family is considered unethical, since it brings about intergroup conflict, and adults line up against deviants who threaten the quality of social life (Boehm 2009). Deviants typically submit to

the group, but for those who don't, negative effects are being ridiculed and criticized, or more consequentially, ostracized and expelled (Lee and Daly 1999). If brain size is a measure of actuarial ability, then socially regulated behavior and moral sanctioning most likely began in the Middle Pleistocene, where notable increases in brain size exist in the fossil record (Boehm 2009).

Motivations for Bullying During Development

Humans have altered the impact of bullying through language and culture, but it is still used as a strategy to obtain valued resources and maintain social order in children and adults alike (Smith et al. 1999, p.16). According to *Resource Control Theory* (RCT), social dominance is a means of positioning oneself near the top of a social hierarchy for access to resources, either material, social, or informational (Hawley 1999). In support of RCT, commonly reported reasons that children and adolescents bully include displaying power, maintaining leadership status, gaining acceptance from or access to a desired peer group, strengthening self-identity, and getting what they want (Bernard and Milne 2008). Bullies can also shape social groups in that they often select out-group targets, which they perceive as unlike themselves in terms of social group and identity. Ultimately, the essential quality that bullies seek in a target is vulnerability, but they tend to focus on targets least like themselves (Bernard and Milne 2008).

There are psychological advantages to being a bully compared to victims and bully-victims. For example, those children who are classified as pure bullies generally report equal or better mental health than bully-victims and pure victims, and in adolescence, bullies are perceived as more popular, socially dominant, and likeable (Volk et al. 2012). Additionally, stronger adolescent boys (who are more likely to engage in bullying and also start dating at a younger age) report greater dating opportunities and likelihood of being in a dating relationship, and bullying behaviors in adolescence have been linked to high social status later in life (Volk et al. 2012).

Even though there are advantages to bullying, such behaviors are displayed overwhelmingly (approximately 90%) by students with low levels of social and emotional wellbeing (Bernard and Milne 2008). Several clinical factors have been associated with bullying (and victimization), including negative adult influences, low parental involvement, negative family interactions, childhood maltreatment, exposure to interparental violence, divorce, association with peers who bully, and neighborhood violence (Hong and Espelage 2012).

Psychological Effects of Bullying on Victims

Even though bullies may suffer from several clinical issues, victims suffer more immediate and long-term consequences, such as depression, loneliness, generalized and social anxiety, and lower self-worth (Volk et al. 2012). Rodent studies indicate that social stress, experienced when one rat repeatedly attacks or takes resources from another, results in heightened levels of anxiety and changes in brain chemistry lasting far after the stress alleviation (Kinsey et al. 2007; Vidal et al. 2011). With children, repeated exposure to bullying undermines their health and wellbeing, leading to anxiety, depression, and other psychosocial complaints. Victimized children and adolescents report ailments such as tiredness, sleep problems, abdominal pain, bedwetting, and suicidal ideation; with boys being four times more likely, and girls eight more times likely, to be suicidal because of bullying (Bernard and Milne 2008). Victims and bully-victims have elevated rates of psychiatric disorders in adulthood, such as generalized anxiety disorder, panic disorder, and agoraphobia, even when controlling for childhood psychiatric disorders and family hardships (Hong and Espelage 2012).

Procedures for Curbing Bullying

Given its prevalence in human cultures and animal species, bullying is a behavior that may never be completely removed from all social

interactions. From an evolutionary perspective, bullying can be seen as a successful strategy to obtain valued physical, social, and reproductive resources. In stable cooperative groups, however, an excess of bullying can lead to serious negative consequences for the social group, the bully, and particularly the victim. Ancient cultures dealt with in-group problems through cooperative efforts; bullying was not curbed simply by one individual, but through a collective reinforcement of social norms (Boehm 2009). Methods do exist to mitigate the frequency and severity of bullying incidents, but just like in older cultures, success depends on a collective and concentrated effort from many agents such as parents, teachers, mental health professionals, and peers.

Parents and extended family members can reduce bullying behaviors through fostering positive relationships with high parental warmth (listening and providing affection), employing authoritative parenting styles (clearly communicated expectations and calmly implemented discipline for poor behavior), and modeling appropriate behavior (displaying assertive skills and emotionally controlled responses) (Bernard and Milne 2008). Teachers can reduce bullying behaviors through behavioral contracts (plans of positive action that help students move towards acceptable behavior), socioemotional education (providing learning experiences in empathy and resilience), and nonpunitive problem-solving meetings (for bullies, victims, and parents) (Bernard and Milne 2008). Peers can be trained to mediate disputes, offer support and friendship, and assist bullying victims through the use of simple counselling skills like listening, showing understanding and support, and converting bullying bystanders to victim defenders (Bernard and Milne 2008; Volk et al. 2012).

While most antibullying programs are often successful in the short-term, they fail to address the root of the problem. Programs like “zero-tolerance” do not have long-term effects, considering they require bullies to stop advantageous behavior (Volk et al. 2012). Successful interventions should focus not just on punitive reactions to bullying, but proactive alternative, prosocial methods of attaining social dominance, as seen in many hunter-gatherer cultures (Hawley 1999;

Lee and Daly 1999; Volk et al. 2012). Although introducing prosocial strategies should be included in bullying prevention, a one-size-fits-all approach should not be used for every situation (Volk et al. 2012). The most effective methods have different tiers of response to children who bully, from teachers equipped with communication skills and interventions, to parents and principals who can employ more intensive interventions, to mental health professionals who can provide mentoring in social-emotional skills and more concentrated individual and family therapy (Bernard and Milne 2008; Volk et al. 2012).

Conclusion

Bullying is a successful evolutionary strategy for many animals, including humans. Dominance and submission are prominent underlying mechanisms that run across all cultures. However, all cultures, including hunter-gatherers, have social sanctions against killing, deceptive lying, theft, incest, and bullying by upstarts, coupled with positive views of altruism and cooperation for maintaining social order and consistency (Boehm 2009). By incorporating a deeper understanding of the evolutionary history of bullying, society can modify policies to increase the wellbeing of children, adolescents, and young adults.

Cross-References

- Child Abuse and Bullying
- Outcomes of Homophobic Abuse
- Peer Rejection, Sex Differences in Initiation of
- Peer Socialization
- Sex Differences in Cyber Bullying
- Specific Friendships

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Procreation

- Function of Reproductive Strategy (Kurzban)
- Sexual Reproduction

Procreative Ethics

- [Risk of a Lifetime, The](#)

Procryptic Resemblance

- [Masquerade](#)

Producing Young

- [Function of Reproductive Strategy \(Kurzban\)](#)

Production

- [Change in Male Hunting Returns](#)

Production of Eggs and Sperm

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Synonyms

[Eggs](#); [Gamete dimorphism](#); [Gametes](#); [Intersexual selection](#); [Intrasexual competition](#); [Sexual reproduction](#); [Sperm](#)

Definition

Males and females produce gametes that are differentially specialized to facilitate the sexes in reproduction.

Introduction

The production of gametes is a biological process occurring in organisms that sexually reproduce. Females make gametes called eggs, and males make gametes called sperm. Both egg and sperm cells begin as identical germ cells and are produced through a process of cell division called meiosis, which reduces the number of chromosomes in the germ cell from 46 (diploid) to 23 (haploid). In human males, meiosis begins after birth, and, upon reaching puberty, men produce sperm continuously for the rest of their lives. In human females, meiosis begins before birth and the raw materials for egg cell production are formed while the female fetus is still within the uterus of her mother. Every female is born into the world with a limited number of egg cells in her reproductive system. These eggs are released one by one (occasionally two at a time) into the uterus at each monthly cycle of ovulation when and after she has reached puberty, and this cycle ceases when she has reached menopause. Fertilization occurs when a sperm cell successfully combines with an egg cell inside the female reproductive system, and this restores the gametes to a diploid with 46 chromosomes in the form of a zygote. The process of gestation then begins and will likely result in pregnancy as the zygote develops into a fetus.

The Evolution of Sex-Differentiated Gametes

To understand the significance and implications of sex-differentiated gametes, it is important to consider how sexual reproduction evolved. This chapter covers the selection pressures that likely led to sperm and egg cells as highly specialized gametes each with their own reproductive interests and how these differences between gametes lead to intrasexual competition and intersexual selection on the part of males and females, respectively.

From Asexual to Sexual Reproduction

Before there was sexual reproduction or sex, organisms reproduced via asexual reproduction,

where all of a parent organism's genes are passed on to its offspring through a process of mitosis, or the division of the mother cell into two genetically identical daughter cells. In contrast, in sexual reproduction, two individual parent organisms are required and only half of each parent's genes are passed on to the next generation. A major constraint of sexual reproduction is that individual organisms must find and coordinate copulation with a conspecific mate in order to reproduce. Despite this significant cost, sexual reproduction dominates among multicellular forms of life, indicating that the gains in fitness to offspring produced sexually have, over evolutionary history, outweighed the costs of sex, especially for more complex life forms. The process of meiosis – recombination of genes from two genetically different parents from the same species – thus underlies the benefits of sex (Maynard Smith 1978).

The recombination of genes through sex provides another avenue besides random mutations for evolutionary adaptations to develop by allowing offspring of each generation to have genetic information and thus, phenotypic traits, that are different from what either parent has. A species that generates greater phenotypic variation can evolve faster in response to selection pressures because with greater variation, more advantageous phenotypes are likely to surface (Zimmer 2009). For instance, when new environmental parasites attack a population of asexually reproducing organisms, the organisms are unlikely to quickly adapt new defenses against these novel parasites as asexually reproducing organisms in the population share the same defense systems that only work against familiar (pre-existing) parasites. On the other hand, the genetic variation of sexually reproducing organisms enables offspring – from genetic recombination – to vary more greatly in their parasitic defense systems, thereby reducing the likelihood that an entire population would be rapidly wiped out from a single novel parasitic attack (Hamilton et al. 1990). Environmental factors therefore serve as useful selection pressures that eventually allow only the fittest organisms (i.e., those that have the most adaptive combination of genes) to survive and reproduce. Further, sexually

reproducing organisms tend to find mates with good genes attractive, leading to different recombinations that, on average, lead to better offspring fitness (Zimmer 2009). Sex therefore creates new gene combinations that can weed out bad genes and propagate good genes.

The Origins of Gamete Dimorphism, or Males and Females

Sexual reproduction occurs in two ways: either through isogamy, which refers to the fusion of gametes of *similar* shape and size, or anisogamy, which refers to the fusion of gametes that *differ* in shape and size. Among sexually reproducing organisms, isogamy is commonplace (but not universal) in unicellular organisms. As the gametes contributed by isogamous parents are similar, they cannot be differentiated as male or female. In contrast, anisogamy prevails exclusively in multicellular animals and plants (Zimmer 2009), and the smaller gamete is considered to be male while the larger gamete is considered to be female. In humans, an egg cell is 85,000 times larger than a sperm cell, and sperm are also produced in much larger quantities than eggs.

Ghiselin (1974) argued from an economic specialization standpoint that anisogamy could have originated from a physiological division of labor, whereby some gametes began specializing in nutritional and material resource provision, thus becoming larger, while other gametes specialized in motility, therefore maintaining a small size and growing tails for propulsion. Parker et al. (1972) also proposed that anisogamy evolved via individual-level selection and competition. Males that produce more (but smaller) gametes stand to gain a larger proportion of fertilizations because they produce a larger number of mobile gametes that can “seek out” the larger gametes. However, because zygotes formed from larger gametes have better survival prospects, this process can lead to the divergence and specialization of gamete sizes into large and small (female and male) gametes. The end result is one where numerous small gametes compete for access to large but scarce gametes that are tasked with providing maximal nutritional and material resources for the offspring (Parker et al. 1972). Males therefore tend toward

achieving “quantity,” while females tend toward achieving “quality” in a bid to increase reproductive success.

Intrasexual and Intersexual Selection Drives Production of Large Numbers of Tiny Sperm to Compete for Access to Valuable Female Gametes

In humans as well as many other anisogamic species, sperm are much cheaper than eggs. Men replenish their sperm at roughly 12 million per hour, while women only have a finite lifetime supply of approximately 400 eggs. This sex difference in the value of gametes is fundamental to psychological, behavioral, and physiological differences between males and females. Trivers’ (1972) theory of parental investment described how the sex with more resources (usually females) evolve to be more discriminant about having sex while the other sex (usually males) evolve to compete for access to the higher-investing sex. As there is an abundance of sperm, the selection pressure shifts for an egg producer to be prudent in choice as it is unlikely that her eggs will fail to find eager sperm. Conversely, the selection pressure shifts for a sperm producer to ensure that the sperm can reach the egg before it is fertilized by numerous other rival sperm. Evolution thus favors selectivity in females to ensure that their limited eggs get fertilized by the best sperm and greater sperm quantity production in males to increase their chances of winning during sperm competition.

In humans, men evolved to be more sexually persistent and have a stronger desire for sexual variety compared to women and to favor a short-term mating strategy in order to increase their access to more sexual partners. These adaptations serve to increase the chances that their sperm can fertilize as many eggs as possible. Women, on the other hand, evolved to be more sexually restricted than men and to prefer a selective, long-term mating strategy (e.g., Li and Kenrick 2006) in order to procure the qualities of one or a very limited few desirable mates (for their good genes, resources, etc.), since being wasteful with their limited eggs would be detrimental to reproductive success (Goetz and Shackelford 2009).

Females are also attracted to the victors of intrasexual contests, and thus men may have also evolved to be more aggressive and stronger than women in order to compete intrasexually with mating rivals (Buss and Duntley 2006).

Sperm competition is another form of intrasexual competition by males and intersexual selection by females for the best genes to be passed on to the offspring (Goetz and Shackelford 2009). As sperm quality and offspring quality may be correlated, a female’s reproductive fitness can be increased when more sperm competition is encouraged. Sperm quality (which pertains to how healthy and mobile the sperm are) and sperm quantity (which differs among males) both serve to signal the fertility of a male and the eventual differences in probability of successful conception. Indeed, in some species, females may mate with multiple males so that the sperm of these males can compete and only the best sperm will achieve successful fertilization of their eggs (Baker and Bellis 1995). Several studies have found that large testes size, hence greater sperm production capacity, is a feature of species that exhibit multi-male mating systems (Shackelford and Goetz 2006). Male reproductive fitness increases linearly with increasing mating encounters (with different females), whereas female fitness increases less rapidly with multiple matings (Trivers 1972; Goetz and Shackelford 2009). These circumstances create evolutionary pressures for males to produce the most and best-quality sperm within their own metabolic constraints to increase the odds that their sperm can fertilize the egg over rival sperm, while scarce and valuable eggs incentivize females to entice sperm competition so that they can be selective of mates with better quality sperm.

Among humans, women sometimes engage in multiple matings to generate sperm competition at some point in their lives, and women are also most likely to multi-mate when the chances of conception are high, indicating that women may (either consciously or unconsciously) schedule their copulation activities to allow the most competitive sperm to fertilize her egg (e.g., Baker and Bellis 1995). Women in contemporary human populations may therefore mate in a

polygamous manner to differing extents across cultures, potentially generating sperm competition in their reproductive tracts (Shackelford and Goetz 2006). Even in purportedly monogamous, committed, and long-term mating contexts, as the proportion of time a couple spends together since their last copulation decreases, the probability that the man's partner has been inseminated by another man also increases. Correspondingly, the longer a couple spends time apart, the greater the volume of sperm the man ejaculates at the couple's next copulation (Baker and Bellis 1995). Therefore, the pressures of sperm competition can further drive the dimorphism of gametes that were initially differentiated through the benefits of specialization.

Conclusion

The reproductive benefits of genetic variation gave rise to the evolution of sexual reproduction, where parents each share half of their genetic material to produce genetically different offspring through meiosis and fertilization of gametes. This process tends to eliminate bad genes and propagate good genes, thereby producing fitter offspring. Further benefits of gamete specialization drive the dimorphism of gametes such that males produce tiny and mobile sperm that specialize in seeking out eggs that specialize in carrying vital nutrients and resources. As eggs are more valuable than sperm, the reproductive success of a female hinges on the quality of the sperm that fertilizes her egg, while the reproductive success of a male depends on the quantity of sperm he can produce, which increases the likelihood that his sperm wins over rival sperm in fertilizing the egg. Reproductive success for anisogamous life forms therefore benefits from sperm competition (i.e., intrasexual competition between the quantity and quality of rival males' sperm and intersexual selection by females of the best sperm among rival males). Taken together, these factors drive the evolution of gametes such that males produce larger quantities of small sperm relative to the large and scarce eggs of females.

Cross-References

- ▶ [Concealed Ovulation](#)
- ▶ [Copulation](#)
- ▶ [Cultural Variation](#)
- ▶ [Ejaculate Adjustment](#)
- ▶ [Female Choice](#)
- ▶ [Female Mate Choice](#)
- ▶ [Female-Female Competition](#)
- ▶ [Gamete Size](#)
- ▶ [History of Sperm Competition in Humans](#)
- ▶ [Human Sperm Competition](#)
- ▶ [Infidelity](#)
- ▶ [In-Pair Copulation](#)
- ▶ [Intersexual Competition](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Male Mate Choice](#)
- ▶ [Male-Male Competition](#)
- ▶ [Mate Preferences](#)
- ▶ [Parental Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Reproductive Strategies](#)
- ▶ [Reproductive Variance](#)
- ▶ [Sexual Conflict After Conception](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Threats of Sperm Competition](#)
- ▶ [Women's Long-Term Strategies](#)

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Progenicide

► [Predictors of Infanticide](#)

Progression

► [Scaffolding in Learning](#)

Progressive

► [Political Left, The](#)

Progressive Learning

► [Evolution of Teaching](#)

Projected Confidence

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Synonyms

[Instil confidence](#); [Self-enhancement](#)

Definition

It is important to be clear on the meaning of projected confidence and how it differs from self-confidence. Self-confidence is personal assuredness in one's own ability or judgment. Projected confidence is the ability to ingrain that confidence onto others; in other words, have others believe in your competence.

Introduction

Following from the previous chapter, this entry focuses on how individuals may use manipulative communication with others via projected confidence in order to protect or enhance their self-esteem. It will also demonstrate how the specific personality construct, narcissism, may accentuate this from an evolutionary perspective.

Self-Enhancement

It could be argued that self-enhancement is the root of projecting confidence onto others. Self-enhancement involves a self-directed effort by an individual to increase the positivity of their public image (Wallace 2011). The personality construct that is most well known for chronic self-enhancement is narcissism. In accordance with the three key evolutionary perspectives discussed in the previous chapter (► [“Self-Esteem as Manipulative Status Communication”](#)), narcissists’ self-esteem is fragile and therefore, their continual self-enhancement is to preserve and protect it (Morf and Rhodewalt 2001).

It is believed that narcissism has evolved in accord with promiscuous mating strategies, or short-term mating, and that it has persisted through specific characteristics related to self-enhancement such as attractiveness and coercive tendencies (Holtzman and Strube 2011).

Attractiveness

Research has found that narcissism is associated with higher observer-rated physical attractiveness (Holtzman and Strube 2010). This is due to the types of behavior narcissists present and how they project this onto others. For example, the attention seeking style of behavior narcissists present may stimulate sexual desire among potential short-term mates. Holtzman et al. (2010) found that narcissists use more sexual words in everyday life, and importantly, this remained the case after excluding those swear words which have a sexual connotation. It seems that in relation to sexual language, narcissists are able to project this type of confidence on to others and that may be one explanation as to why others find them attractive. This is one example as to how a narcissistic individual has a higher chance of attracting a short-term mate. Another example is the exhibitionism they present, a core trait of narcissism. Research has found that narcissists take extra care in their appearance such as wearing expensive clothing (e.g., Back et al. 2010) and females in particular focus on their sexual appearance such as wearing

make-up (Vazire et al. 2008). Again, narcissists can project confidence, via exhibitionism, onto others which contributes to their chances of finding a short-term mate.

Coercion

Narcissism in both males and females has been found to be significantly related to sexually coercive strategies (e.g., Blinkhorn et al. 2015). It is believed that narcissists’ characteristics such as game-playing love styles (Campbell et al. 2002), musculature (Vazire et al. 2008), and disagreeableness (Paulhus 2001) all enhance their chances of successfully coercing another. Displaying this type of behavior is another way in which narcissists can project their confidence onto others. From an evolutionary perspective, it could be suggested that many years ago, narcissists who were less coercive had more difficulty reproducing (Holtzman and Strube 2011), and therefore, this trait has strengthened and evolved to facilitate higher chances of finding a short-term mate.

Conclusion

The personality construct, narcissism, is characterized by self-enhancing types of behaviors such as attractiveness and sexual coercion, in order to project confidence onto others. These behaviors are examples of manipulative communication with others in order to protect or enhance self-esteem. From an evolutionary perspective, it can be argued that narcissistic traits have adapted in order to increase the likeliness of short-term mating. The following chapter will discuss how narcissistic individuals may also manipulate others by the ► [“Derogation of Rivals.”](#)

Cross-References

- [Derogation of Rivals](#)
- [Self-Esteem as Manipulative Status Communication](#)
- [Self-Esteem Reflects Assessments of Valuation](#)
- [Sociometer Theory](#)

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Prolificacy

► Fertility

Promiscuity

- Multiple Matings
- Sociosexuality

Promoting Paternity (You Look Like Your Father Phenomenon)

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Synonyms

[Facial resemblance](#); [Kin recognition](#); [Parent-child resemblance](#)

Definition

The tendency for mothers and maternal relatives of infants to remark that a child looks like the father more often than commenting on resemblance to the mother.

Introduction

Paternity uncertainty is an adaptive challenge for males, but not for females (Buss 1996). Due to the risk of cuckoldry, a man is less likely to invest in his partner's child if he is less confident that the child is his own (Pagel 1997; Gaulin and Schlegel 1980). Children living with a step-father or adopted father are more likely to be abused or neglected than those who live in a home with their biological fathers (Daly and Wilson 1996). Similarly, women are at greater risk of being abused if some children in the home are not related to their male partners (Burch and Gallup 2000). Because of the potential risk to the health and safety of both women and children in the case of a father doubting his paternity, women may have an evolved tendency to assure their partners of paternity by making comments that attest to the children's resemblance to them. On the contrary, evolutionary pressure may have shaped the appearance of infants in favor of concealing the identity of their fathers, which would protect against abuse or abandonment in the case of cuckoldry (McLain et al. 2000).

Empirical Evidence

In a 1995 study on parent-child resemblance, Christenfeld and Hill found that photos of 1-year-old infants could be matched to photos of their fathers, but not to their mothers (as cited by Christenfeld and Hill 1995; McLain et al. 2000). These researchers suggested that infants may have evolved to closely resemble their fathers as a mechanism to afford paternity confidence and ensure paternal investment. However, other researchers report that infants are more accurately matched to their mothers than to their fathers (Nesse et al. 1990; Brédart and French 1999). Brédart and French (1999) failed to replicate the results found by Christenfeld and Hill (1995) and argued that if the appearance of infants had evolved to reveal paternity, the current degree to which babies resemble their fathers would be much higher than it is. They posited instead that babies conceal their father's identity by more closely resembling their mothers; this would afford protection to the child if the biological father was not the mother's partner. Further, the stronger mother-infant resemblance may be biologically significant; Moore and Haig (1991) provide evidence that genomic imprinting leads to preferential expression of maternal genes in order to allow greater control of resource flow from the mother to the fetus (as cited by McLain et al. 2000).

The pattern of results from these studies suggests that babies tend to resemble their mothers more closely than their fathers. However, as paternity confidence tends to promote greater paternal investment in offspring (Gaulin and Schlegel 1980; Alvergne et al. 2009), mothers and maternal relatives may have evolved a tendency to verbally attest to the likeness of infants to their domestic fathers. Indeed, Daly and Wilson (1982) found that comments on parent-child resemblance made by mothers in maternity wards were biased toward affirming father-child similarity. The comments made by fathers do not share the same bias. This difference suggests that women's comments about parent-child resemblance may have an ultimate purpose of promoting paternity certainty in order to secure resource investment from their male partners.

Conclusion

Though infants may have a tendency to more strongly resemble their mothers than their fathers, mothers may seek to ameliorate the problem of paternity uncertainty, as well as promote paternal investment in the child, by making comments about infants' resemblance to their domestic fathers.

Cross-References

- ▶ [Cuckoldry Risk](#)
- ▶ [Extended Kin Role](#)
- ▶ [Infant Survival](#)
- ▶ [Paternity Uncertainty](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)

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Propagation

- [Life Expectancy and Reproduction](#)

Proprietariness

- [As a Precursor to Partner Violence](#)

Proprietary Mate Retention Tactics

- [As a Precursor to Partner Violence](#)

Proprioception

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Synonyms

[Body parts awareness](#); [Somatosensory system](#)

Definition

Proprioception is considered the body’s perception and sensation of movement and awareness of tactile sensation.

Introduction

Proprioception is a general term that covers the somatosensory system. This tactile sensation is involved in the awareness of the limb per se and its movement – in other words, kinesthesia. The receptors that are in the muscles, joints, and under the skin inform the brain about the location and sensation of the specific body part. In the following headings, there will be an elaboration of what proprioception is and how it works as well as its function with rehabilitation programs and how it aids the physical recovery of an injury. Some techniques will be also introduced. Finally, there will be a very brief view of proprioception from O’Shaughnessy’s (2000) philosophical standpoint.

The Role of Proprioception

The word proprioception was first introduced by Charles Scott Sherrington in 1906 describing muscles as stretch proprioceptors (Hamant and Moulia 2016). Proprioception – often referred to as somatosensory system – is a general term that refers to a specialized component of tactile sensation that incorporates recognition of kinesthesia, i.e., the sense of joint movement, and the sense of joint position, i.e., the body’s sense of its position in terms of balance and movement (Saxby 2011; Johnsen and Agerskov 2009; Blackburn et al. 2000; Pincivero et al. 1998). It can be defined as a “special type of sensitivity that informs about the sensations of the deep organs and of the relationship between muscles and joints” (Iturri 2003, p. 274). In essence, it is the body’s awareness of the relative position of the body parts and is usually referred to as the body’s “sixth sense” (Saxby 2011; Hamant and Moulia 2016).

The proprioceptive system uses stretch and pressure receptors located in our muscles, joints, and skin, which inform the brain of the physical environment and the body’s interaction with it (Saxby 2011). Schafer (2006) described this process as a sensory feedback procedure, where mechanosensory neurons detect forces produced as an effect of the movement of the

body – such as membrane stretch – and use these data to control the activity of locomotor systems (Schafer 2006). The role of proprioceptive sensation is to receive information from the muscle-spindle receptors (see text below) and peripheral afferents such as Golgi tendon organs, the joint capsules, ligaments, and cutaneous receptors, as well as visual and vestibular receptors and convey this information to the Central Nervous System (CNS) through afferent neural pathways (Pincivero et al. 1998; Blackburn et al. 2000). Information taken from these mechanoreceptors is processed to produce a neural signal intended to facilitate neuromuscular control to compensate for any deviations in posture or gait. Joint stability and the strength of the muscles are important factors that contribute to balance (Blackburn et al. 2000).

Moreover, it has been proved that proprioception has a significant function in the skeletal muscles to regulate muscle length in response to stretch (Niechwiej-Szwedo and Steinbach 2008). These proprioceptors in the skeletal muscles are called muscle spindles and are found in the orbital layer of certain species such as humans, sheep, and some primates, but not in species such as rats, rabbits, horses, or cats (Niechwiej-Szwedo and Steinbach 2008). Muscle spindles are responsible for the sensation of position and movement, despite the fact that they are under fusimotor control as position sensors (for a review on fusimotor action see Prochazka and Hulliger 1998). An additional role of the muscle spindles is to provide peripheral feedback for the unconscious adjustments during posture and locomotion (Proske 2005). The role of tendons, ligaments, and joint capsules is not only to offer mechanical support and to induce movement but also carry mechanoreceptors which gather data on the position of the joints or the stretching of the tendons and ligaments, and send this information through the upper cord to the base of the encephalon to initiate an effective response and offer a dynamic stabilization and balanced reaction (Iturri 2003). Balance is the primary function of the vestibular system. Essentially, all these structures contain receptors that contribute to the monitoring of the body's actions through proprioception (see Proske

2005, for a review on the sense of static limb position and kinesthesia).

Besides the classical proprioceptors in the limb muscles of mammals (i.e., muscle spindles and Golgi tendon organs), it was also shown that Palisade endings are of functional proprioceptive importance. These endings are nervous end organs confined to the extraocular muscles of mammals and man and are immunoreactive for antibodies against choline acetyltransferase (Weir 2006; Blumer et al. 2006).

Regarding the case with mechanotransduction, there are still some gaps in the full understanding of the molecular and biophysical properties of these mechanoreceptors of proprioception. However, there are two ion channels families that best describe the molecular mechanisms of proprioceptor mechanotransduction. The first family is the DEG/ENaC/ASIC family of channels, which form heteromultimeric complexes with stomatins permeable to sodium and calcium. Several of these have been shown to play a significant role in mechanosensation, yet none has been reconstructed as a mechanically sensitive channel when expressed in heterologous cells (Schafer 2006). The second family is the transient receptor potential (TRP) cation channels, which are either known to play a role for in vivo mechanosensation or have been shown to be activated by mechanical forces in heterologous expression systems (Schafer 2006). Specifically, recent research suggests that TRP cation channel N1 – also known as NompC and TRP4 – are directly implicated in mechanosensation, based on a sample from fruitflies and nematode worms (Cheng et al. 2010). Cheng et al. (2010) suggested that TRPN1 plays a significant role for proprioception in *Drosophila melanogaster*. Specifically, they used a green fluorescent protein construct to show expression of the channel in subsets of peripheral sensory neurons responsible for locomotion coordination. For example, the TRPN1-null larvae crawled in less speed than the wild-type larvae, showing impaired proprioception based on the loss of TRPN1 in sensory neurons (Kingwell 2010). Additionally, TRP4 has been shown to function as an essential pore-forming subunit of a native mechanotransduction channel

(Kang et al. 2010). The authors, specifically showed that TRPN1 is responsible for the mechanoreceptor current by mutating key residues in the putative pore-forming domain of the channel protein, and they also showed that this changed the cation-selectivity of the current. Wilson and Corey (2010) further support this finding by describing the TRPN1 as the “bona fide” mechanoreceptor channel for nematode feeding behavior. It is noteworthy, however, that this specific channel (TRPN1) is not expressed in mammals, but several other TRP family members are expressed – a fact that shows promising research results in the future (Kingwell 2010).

Further research on the mechanotransduction channels of proprioception has shown that the mechanically activated nonselective cation channel Piezo2 is the major mechanotransducer of mammalian proprioceptors (Woo et al. 2015).

Proprioception and Rehabilitation

Before engaging in how proprioception can help with the coordination of muscles and rehabilitation, it is better to offer a definition of what coordination really means, as well as an explanation of relevant terms. Iturri (2003) defined coordination as “the capacity to perform movements in a smooth, precise and controlled manner” (p. 274). Therefore, in order for rehabilitation to work towards the coordination and strengthening of muscle movement, a certain re-education of neuromuscular and neuroarticular functions is needed. It is here where proprioception plays a crucial role (Iturri 2003).

In order to understand how proprioception plays this crucial role in sport, it is imperative to understand how it is different from other types of sensations. Based on Sherrington’s classification of sensitivity, proprioceptive sensation is the impressions on the functional state of the joints and muscles (Iturri 2003). These are divided in conscious proprioceptive sensation which is the awareness of passive and active movements, and the position of a somatic part of the body, in other words, kinesthesia. If the individual is not aware of these impressions, then these are called unconscious proprioceptive sensation and they relate to balance, tone, and muscular coordination (For a

full review of Sherrington’s classification see Iturri 2003, pp. 274–275). The difference between proprioceptive and exteroceptive sensation is that the latter is the sensation that is involved in the external surface, which includes touch, pressure, pain, and differences in temperatures. This type of sensation also involves other more specialized sensation such as sight, hearing, and smell. Proprioception is also different from interoceptive sensation, which is the type of sensation found in the viscera and vessels, and it can be divided in areas of gustatory and olfactory.

According to Lephart et al. (1997), rehabilitation programs should be designed to incorporate proprioception that addresses these three levels of motor control: spinal reflexes, cognitive programming, and brainstem activity. The main emphasis to this is to promote dynamic joint and functional stability not only in the rehabilitation programs but as a prevention program as well (Panics et al. 2008). Therefore there are specific ways to assess proprioception prior and post exercise or physical therapy.

Testing Proprioception at Sport

The assessment of joint proprioception is divided in two parts: kinesthesia and joint position. As Pincivero et al. (1998) suggest, kinesthesia is assessed by measuring the threshold to detect passive motion, and joint position sense is assessed by measuring the reproduction of passive positioning and the reproduction of active positioning. On the cognitive level, certain activities that require higher brain abilities are initiated; these activities could be to perform end range joint positioning activities, in order to stimulate the conversion of conscious to unconscious motor programming throughout repetitions. This conscious to unconscious transition is performed through dynamic balance rehabilitation activities by bringing awareness and concentration on the performed task in order to facilitate sensory input. The end result is to incorporate cognitive or psychomotor aspects to lead to unconscious motor programming (Pincivero et al. 1998).

Regarding the spinal level of motor control, rehabilitation activities that produce sudden changes in joint position must be included to the

unconscious processes of reflex joint stabilization. Certain activities such as training in unstable platforms and plyometric exercises enhance joint muscular contractions and reactive dynamic muscular stabilization which eventually address neuromuscular training at the spinal level of motor control (Pincivero et al. 1998).

Even by using specific psychophysical tests, the knowledge we have for proprioception is limited for the following reasons: (1) It is unknown how isolated proprioception mechanisms affect these tests; (2) it is impossible to measure proprioceptive function while the individual is under effort. Therefore, since the tests are performed while the individual is resting, the results are unreliable; (3) the results are not really understandable outside the individuals' awareness; (4) proprioceptive training has the paradoxical effect of influencing negatively the psychophysical test procedures. It has been shown, however, that electromyography can provide an orientated analysis of muscular function as the end-point of regulatory proprioceptive function (Iturri 2003).

It is noteworthy that the biggest challenge on using proprioception in sport is the lack of information about the proprioceptive situation prior to the injury. Nevertheless, it is possible to obtain epidemiological information from prior examinations based on the findings of both psychophysical and electromyographic examinations; the information gathered from minor injuries prior to a major injury that have been damaging the proprioceptive structures and directed proprioceptive training as a prognosis of injuries (Iturri 2003).

Proprioception Training Techniques

It has been demonstrated by several research studies that proprioception training reduces the injury rate in the lower extremities (Mandelbaum et al. 2005; Myklebust et al. 2003; Hewett et al. 1996; Halasi et al. 2005; Wedderkopp et al. 2003; Caraffa et al. 1996). Panics et al. (2008) have added to the existing literature that proprioception training improves the sensation of joint position in the knee joint, and that improvement in the joint position sense may be one explanation for the reduction in injury rate. It was also shown that proprioceptive training program produced

improvements in the ability to balance on a single-plane balance board and balance in general (Mattacola and Lloyd 1997; Hrysomallis 2011). Specific warm-up programs were also proven useful to increase the proprioceptive capabilities of athletes (Daneshjoo et al. 2012; Subasi et al. 2008).

Usually after an injury, kinesiotherapy and physiotherapy stimulate the exteroceptive and proprioceptive systems (Iturri 2003). Proprioceptive re-education aims to activate the muscular receptors to provide an immediate motor response (Scott and Fu 2000). Stretching, for example, has a significant proprioceptive effect on the injured area, and it gets the muscular receptors to work. Iturri (2003) suggested the following techniques for proprioceptive reprogramming: (i) balancing on unstable planes; (ii) balancing on one foot; (iii) balancing whilst sitting; (iv) sliding the foot along an unstable plane; (v) the Kabat method; (vi) semi-closed and open kinetic chain exercises. This way, individuals make integrated movements that use muscle groups that are used to work together following a set of rules: movement of the segments of the diagonal plane; a spiral component associated with each movement; and stretching stimuli which are used when applying physical resistance (Iturri 2003).

Proprioception and Consciousness

O'Shaughnessy (2000) in the last chapter of his book gives a comprehensive explanation of what proprioception is and what is not, mostly from a philosophical and psychological point of view. He specifically states that proprioception stands for:

"the familiar immediate experiential awareness of our own limbs and body... a distinctive sub-variety of perception... (proprioception) must be sharply distinguished from the attentively immediate awareness of bodily feelings like fatigue or warmth: the reason being, that these latter are mentalistically immediate perceptions of psychological objects" (p. 628).

He keeps on arguing that proprioception:

"...is an experience... whose content is caused non-deviantly by its object, and it can form the basis of an inference to the existence of that object... it is no kind of cognitive attitude, nor tendency to entertain a cognitive attitude. In short, we

have here an attentive experience in which a small sector of physical reality appears one way, which is to be sharply distinguished from cognitive attitudes of all kinds, even though it naturally sustains such” (p. 629).

O’Shaughnessy (2000) makes an interesting argument stating that in every example of tactile perception, a proprioceptive awareness of the individual’s body stands between him/her and the tactile object, and it is only if one perceives their own body he or she becomes cognizant of the objects to touch. Therefore, the sense of touch must depend upon proprioception and not the other way around. He adds that the major differences between proprioception and touch are the scope of the objects and the type of the properties, in particular the type of the spatial properties of the objects. For example, touch has no restriction in terms of surface and shape properties, whereas proprioception is limited to the sense of our limbs and body movement. In general terms, even though the sense of touch and proprioception are closely related and “body-oriented senses,” they are nevertheless not similar in a variety of levels, and neither could be reduced to the other (O’Shaughnessy 2000, p. 630).

Another curious fact O’Shaughnessy (2000) mentions in his book is what he has called “introspective proprioception,” where the limb is the focal point of attention. The difference here between introspection in general is that the attention is taken away from the outer objects and is turned inwardly towards the sensation and conscious movement of our lower and upper extremities. However, despite the fact that proprioception is needed for our normal physical interactions of the physical space around us, it stands merely by positing that it establishes no kind of distraction during any physical activity or, better yet, it stands lower in the attentional hierarchy need of a certain action.

Conclusion

In this chapter, a basic review of the role and function of proprioception was covered regarding the sensation of the physical world around us. In

essence, proprioceptive system uses stretch and pressure receptors located in our muscles, joints, and skin, which inform the brain of the physical environment and its interaction with it; a process called a sensory feedback procedure (Schafer 2006). There was also a brief overview of the specific ion channels families that best describe the molecular mechanisms of proprioceptor mechanotransduction: the DEG/ENaC/ASIC family of channels and the transient receptor potential (TRP) cation channels. Proprioception has also played a main role in the physical therapy of athletes during a rehabilitation program, as part of the re-education of neuromuscular and neuroarticular functions of the athletes and as a part of their training routine order to reduce injuries and improve balance. Lastly, as O’Shaughnessy (2000) stressed the importance of acknowledging our limbs and bodily movements as mediums of the tactile sensation we get from the physical environment, although this awareness stands true based of the level of our attention.

Cross-References

► [Somatosensory System](#)

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Prosocial

- [Altruism and Watching Eyes](#)
- [Altruism Defined by Benefits Conferred](#)

Prosocial Behavior

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Synonyms

Altruism; Cooperation; Donation; Helping; Sharing

Definition

Any action that benefits another organism regardless of intent or motivation.

Introduction

Prosocial behavior, as a voluntary action intended to benefit another (Eisenberg et al. 2006), is multidimensional in form, motivation, cause, and consequence (c.f. Padilla-Walker and Carlo 2014). Sharing, comforting, cooperating, helping, rescuing, and donating are among positive behaviors that benefit others. Motives may vary as a function of recipients (kin versus non-kin), contexts (relational, familial, cultural, or physical), and goals (other-oriented versus self-oriented). The term, “prosocial,” is distinguished from “altruistic” because the psychological motivation underlying their enactment differs (Carlo 2014). Whereas prosocial behavior includes both other-oriented motivations (empathic concern, internalized values) and self-oriented motivations (opportunism, reputation enhancement, good feelings about the self), altruism is exclusively motivated by other-oriented concerns and may include elements of self-sacrifice, risk-taking, or threat to the self (Batson and Shaw 1991; Carlo 2014). Scholars from an evolutionary tradition also discriminate between proximate and ultimate causes of altruism (Tinbergen 1963). Proximate causes are psychological, cognitive, physiological,

contextual, or ontological processes in the immediate environment, whereas ultimate causes address the survival function of a behavior (i.e., prosocial behavior) or its phylogenetic history. Proximate causes address *how* the behavior occurs and is the focus of many psychological theories. Ultimate causes postulate *why* the behavior evolved in the first place. Cooperation or cooperative behavior also is used as a term that falls within the dimensionality of prosocial behavior, as it is positive, coordinated behavior occurring among members of social groups to achieve a particular goal. Upon first glance, prosocial behavior seems to be a simple construct to conceptualize, yet its multidimensionality in form, motivation, consequences, and ultimate cause demonstrates its intriguing complexity.

Proximate Causes of Prosocial Behavior

Proximate causes of prosocial behaviors emphasize the psychological components of prosocial behaviors and their development. The processes involved in prosocial behavior are many and include such antecedents as genotypic predispositions, temperament, empathy and mentalizing, executive control, cognitive and social-cognitive abilities, preferences for self or other, affiliative and familial groups, and ecological niches, among many others (Carlo et al. 2016; Jensen and Silk 2014). Proximal causes also address ontogeny or the development of prosocial behavior and its correlates across the life span. Two proximal processes will be presented here, namely, the role of other-regarding preferences (consideration of the consequences of acting) and other-regarding concern (attunement to the emotions and welfare of others; Jensen and Silk 2014).

Other-Regarding Preferences: Helping and Sharing

The decision to benefit another through coordinated action or allocation of resources (e.g., food)

requires an actor to think about the consequences of their actions for others (Jensen and Silk 2014), which also requires the ability to ascertain the other's goal in order to provide assistance or share (Warneken and Melis 2012). Such preferences are considered prosocial when the choice of action enhances the welfare of another. Empirically, other-regarding preferences have been witnessed in chimpanzees using a variety of methods. Young chimpanzees were found to retrieve an object for a familiar caretaker, help a conspecific gain access to a room, and provide a needed tool to gain access to food (Warneken et al. 2007; Warneken and Tomasello 2006; Yamamoto et al. 2009). To date, chimpanzees do not give food prosocially to benefit a fellow conspecific (Jensen and Silk 2014). Using a modified prosocial game, where an actor has a choice between keeping food for the self and not giving food to a conspecific (1/0) or keeping food for the self *and* giving food with a conspecific (1/1), chimpanzees were indifferent in giving a partner food even when it did not incur any personal cost (Jensen and Silk 2014; Warneken and Melis 2012). Human toddlers do assist experimenters in a variety of ways by inferring cues from the person needing assistance and the environment (Warneken 2015; Warneken and Tomasello 2006, 2007). In contrast with chimpanzees, children share prosocially with adults and peers with increasing age as demonstrated through prosocial, dictator, and ultimatum games (Fehr et al. 2008; House et al. 2013a, b). Fairness or prosocial sharing appears to emerge in middle-childhood (ages 7–8 through puberty) when children become aware of social norms (House et al. 2013). Human children have a genuine and honest desire to help others from a very young age (Warneken 2015).

Other-Regarding Concern: The Role of Empathy

Other-regarding concern is witnessed when individuals are responsive to others' emotions and welfare motivating them to behave prosocially (Jensen and Silk 2014). Carlo et al. (2016)

distinguishes among empathy, sympathy (or empathic concern), and personal distress, as each play a different role in prosocial behavior (see also de Waal 2008; Eisenberg et al. 2006). Perspective-taking is the cognitive ability to understand the situations from another's point of view and may be implicated in particular types of prosocial behavior (Carlo 2014). Empathy, the apperception of and resonance with another's emotional state (Batson 1991; Eisenberg et al. 2006), can be positive or negative; that is, happiness is experienced when another is happy, or sadness is felt in connection with another's saddened state. Sympathy or empathic concern is felt as feelings of sorrow for another's circumstance and motivates individuals to alleviate the distress (Batson 1991). Personal distress is an overwhelming self-distress experienced by another's suffering and results in heightened physiological arousal undermining prosocial initiatives. Whereas empathy and sympathy are generally linked with prosocial behavior, personal distress is not (Eisenberg et al. 2006).

For scholars of evolutionary theory, the question is "Why has empathy evolved, and how is it linked with prosocial behavior?" According to de Waal (2008) "empathy evolved in animals as the main proximate mechanism for directed altruism. ... it causes altruism to be dispensed in accordance with predictions from kin selection and reciprocal altruism theory" (p. 282). Suggested to have evolved in parental care for their young among mammals (including humans) and birds, empathy is a selected trait because parents who were empathic and nurturing reared thriving offspring, whereas parents who were not empathically disposed left fewer descendants (Preston 2013). Evidence for the evolutionary roots of empathy comes from comparative and developmental psychology. Empathic responses to distress have been observed between and within species (Burkart et al. 2007; de Waal 2008). Ontogenetically, scholars propose the means by which empathy leads to prosocial actions among humans beginning with affective resonance followed by self-other distinction in the development of empathic concern (de Waal 2008; Jensen et al. 2014). Neonates, for example, have been shown

to affectively resonate with other infants' distress by crying themselves, suggesting an innate tendency to emotionally connect with others. Self-other distinction emerges around 18 months of age and allows toddlers to mentalize about the plight of the other within the situational parameters (de Waal 2008; Jensen et al. 2014). Once children experience empathic concern, understands others' point of view, and care about another's welfare (positive-other regard), then they are likely to act prosocially (de Waal 2008; Jensen et al. 2014). Recent evidence suggests that cultural or social context interacts with children's empathy and other-regarding tendencies to determine in what ways and how often they might intervene (Jensen et al. 2014). In other developmental research, temperament, defined as biologically based "individual differences in reactivity and regulation" (Rothbart et al. 2000), also is linked to more or less frequent prosocial activity (Carlo et al. 2016). Fear-proneness, negative emotionality, and executive control, in particular, may modulate the degree to which empathy might prompt prosocial behavior (Carlo et al. 2016). In sum, affective resonance or attunement appears to be shared across many species, but the capability of acting on empathy is a uniquely human quality (Tomasello 2014).

Ultimate Causes of Prosocial Behavior

Ultimate causes of prosocial behavior would identify the means by which lifetime fitness benefits are accrued and gene transmission is preserved through reproductive success. However, altruism is an act or set of actions that bestows a fitness benefit to another at an apparent cost to the actor. Several theories have worked to explain the presence of altruism in human evolution. Among those seminal ideas are (a) kin selection (Hamilton 1964), (b) reciprocal altruism (Trivers 1971), and (c) indirect reciprocity (Alexander 1987).

In the theory of kin selection, Hamilton (1964) demonstrated that altruistic behavior would be selected as a trait if the fitness costs to the benefactor were less than their recipients'

benefits multiplied by their degree of kinship ($[C < rB]$, where C = cost, r = relatedness, and B = benefit). That is, he measured "inclusive fitness" or the degree to which genetic material is shared with descendant kin versus non-descendent kin to determine the likelihood of acting altruistically toward another. From a genetic fitness standpoint, the more the benefactor and beneficiary are genetically related, the less costly the act becomes.

Empirical evidence for Hamilton's premise is abundant (Bourke 2014). Humans and members of many social species will behave altruistically for the sake of preserving their kin and genetic heritage (Hames 2016; Silk 2009). Cooperative and altruistic behavior has been explained through kin selection in amoeba, eusocial insects, and vertebrates (Mehdibadi et al. 2006; Russell et al. 2003). Empirically, kin selection explains the presence of cooperative courtship in *leks* (small groups of avian males that aggregate for the sole purpose of attracting females for mating) and helping networks among several species of birds (McDonald et al. 2016). Altruism among primates (e.g., in the form of grooming, food sharing, and alloparental care) consistently show favoritism toward close maternal kin (Silk 2009). Among humans, family members are more likely to foster kin than non-kin and do so in a way that is more beneficial to the children's growth and development; kin also are more likely to help fellow kin in high-risk or high-cost situations (c.f. Hames 2016). Yet, despite the wealth of evidence enjoyed for over four decades (see Hames 2016), kin selection theory is not without its critics (Nowak et al. 2010). The heart of criticism focuses on the puzzle of why individuals would behave altruistically or cooperatively toward non-kin when there appears to be no direct fitness benefit.

Reciprocal altruism complements kin selection to account for the presence of cooperative or altruistic behavior among unrelated individuals (Trivers 1971). Trivers (1971) proposed the notion of reciprocal exchange between conspecifics and cross-species cooperators. Often called "direct reciprocity," this form of altruism relies on the expectation that assistance bestowed will be assistance received in the long term. Thus, an

altruistic action would *not* ultimately be costly and, in fact, would be driven by genetic self-interest. The tit-for-tat exchange exemplified in the prisoner's dilemma demonstrated that direct reciprocity worked well as long as there were adequate numbers of members to ensure the cooperative strategies. Furthermore, when pitted against other social strategies in game theories, direct reciprocity gave way to more kind exchanges (forgiveness, in essence) during which periodic lapses are overlooked for longer term gain (win-stay; lose-switch approaches). Direct reciprocity has been observed primarily among humans and chimpanzees (Schnino and Aureli 2007) but rarely in other species (Clutton-Brock 2009).

Indirect reciprocity is another theory that addresses the presence of altruistic and cooperative behavior among non-kin (Alexander 1987). The basic premise of indirect reciprocity is the notion that individuals exist among a community of exchange partners, such that those who are observed to help others are the most likely to receive help themselves (Nowak and Sigmund 2005). A good reputation leads to direct fitness by receiving material resources long term as well as to genetic fitness through choice of potential mates. Those who are "freeloaders," that is, those who do not contribute their share, might gain in the immediate but lose in the long term by being ostracized, punished, or afforded diminished reproductive opportunities. Being able to distinguish between cooperators and freeloaders becomes a necessary and selective skill. The "partner choice" models in which cooperative partners are chosen over those who cheat are witnessed in cross-species and within-species partnerships (Baumard et al. 2013). Young children also selectively help others, provide resources, and give information to those who they witnessed acting prosocially toward others (Kuhlmeier et al. 2014). Even infants preferred *helpers* to *hinderers* in a series of experimental studies examining the early presence of social judgments (see Wynn and Bloom 2014 for a review). In sum, selecting those who act prosocially toward others not only aids the individual but benefits the survival fitness of a social group.

Conclusion

Prosocial behavior has multiple expressions and is multiply determined. Although rudimentary aspects appear in primates, many components seem to be uniquely evolved human capacities (Tomasello 2014). Innate tendencies, such as other-regarding preferences and concerns, are found in studies of early human ontogeny. Children demonstrate a genuine desire to help others, a sense of prosocial fairness through sharing, and an emotional sensitivity to promote another's welfare. Over time, these basic acts of kindness, generosity, and helpfulness led to coordinated and collaborative efforts that promoted interdependence and ultra-sociability (Tomasello 2014).

Cross-References

- ▶ [Altruism Advertises Cooperativeness](#)
- ▶ [Benefit to Another at Cost to Self](#)
- ▶ [Cooperation](#)
- ▶ [Empathy](#)
- ▶ [Empathy in Rats](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolved Moral Foundations](#)
- ▶ [Fairness in Primates](#)
- ▶ [Game Theory](#)
- ▶ [Michael Tomasello](#)
- ▶ [Selection for Cooperative Relationships](#)
- ▶ [Significance of Helping](#)

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Pro-social Behavior

- ▶ [Genuine Altruism](#)

Pro-social Emotions

- ▶ [Moral Emotions](#)

Prosocial Norms

- ▶ [Altruism Norms](#)

Prosociality

- ▶ [Emotional Closeness Predicted by Relatedness](#)
- ▶ [Evolution of Human Sociality, The](#)
- ▶ [Women's Prosocial Dominant Acts](#)

Prosodic Protolanguage

- ▶ [Musical Protolanguage](#)

Prosopagnosia

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Synonyms

[Face-blindness](#); [Facial apperception](#)

Definition

Prosopagnosia is characterized by impairment or inability in recognizing or distinguishing human faces.

Introduction

Prosopagnosia is a condition that inhibits the ability of individuals to recognize, remember, or distinguish human faces. Although this deficit can cause social distress, other sensory and cognitive functions are often unimpaired. Recognizing individuals is a crucial ability in social species, and face identification is the primary form of person recognition in humans. Face-specific areas of processing have also been identified in the brains of macaque monkeys (Tsao et al. 2006), suggesting that face recognition has been a persistent component of much of human evolutionary history. Because human facial recognition continues to be a ubiquitous feature of human social interactions, many prosopagnosics rely on other characteristics such as hairstyle or voice audio signatures to identify individuals and conduct social interactions.

Prosopagnosia and Modularity of the Mind

The term *prosopagnosia* was first used by Bodamer (1947) to describe a patient who exhibited difficulties in recognizing faces after suffering a head injury. Prosopagnosia can be acquired following a traumatic injury to the brain as in Bodamer's case but can also occur naturally. Prevalence for congenital (or developmental) prosopagnosia is estimated to be as high as 2.5% (Grüter et al. 2008) and has been observed to cluster in families, suggesting possible genetic contributions. Congenital prosopagnosia is also much more common than acquired prosopagnosia. Onset of prosopagnosia has been associated with abnormalities or damage of the fusiform gyri (e.g., Gainotti and Mara 2011), in particular the anterior fusiform gyrus

(Behrmann et al. 2007). In addition, bilateral gray matter loss has been noted in the temporal lobes of prosopagnosics, with greatest loss being in the right temporal lobe, particularly in the amygdala, hippocampus, parahippocampal gyrus, fusiform gyrus, and anterior temporal pole (Josephs et al. 2008). Prosopagnosia has been found to have a high comorbidity with cerebral achromatopsia (i.e., impairment of color vision acquired by trauma to the cerebral cortex; Bouvier and Engel 2006) and can co-occur with other identification impairments, such as semantic dementia (i.e., deficits in recognizing and naming objects; Josephs et al. 2008). Some brain injuries, such as right anterior temporal lesions, may produce inability to recognize faces, but are often not limited only to failures in facial identification, and are better understood as “multimodal people recognition disorders” (Gainotti and Marra 2011).

Disorders such as prosopagnosia and achromatopsia have been used to support the modularity of the visual perception system, as certain aspects of a sensory system may be dysfunctional (e.g., face perception), while other perceptual aspects remain intact (Celesia 2010). This modularity manifests in fairly independent functioning, such that various perceptual components of a perceptual system can function or falter relatively autonomously leaving other components relatively unaltered. For instance, prosopagnosics often have limited interruptions in other visual perceptions such as luminance discrimination, spatial resolution, and line and curvature orientation (Barton et al. 2004). Modularity of the visual field mirrors the proposed modularity of other perceptual systems in the brain and the mind in general (e.g., Cosmides and Tooby 1994). This modularity suggests that perceptual systems evolved rather independently to convey context specific advantages to ancestral humans and that even component parts retained a high degree of functional and structural integrity after integration into the perceptual systems of contemporary humans. This independence can also be observed in cognitive modules that rely on a shared perceptual system for information. For instance, the person-identity-recognition system and the emotion-recognition system of the brain are both

heavily reliant on visual input. However, they appear to be independent systems such that prosopagnosics have been shown to maintain the ability to distinguish and identify facial cues related to emotional states (Duchaine et al. 2003). This ability to recognize facial cues to emotion sans person-identification indicates that these seemingly related modules, both pertaining to recognizing facial cues, are differentially distributed in the neural cortex.

Deficits in recognizing spatial relations and contrast sensitivity have been proposed as the central apperceptive components of prosopagnosics' inability to distinguish faces, especially in acquired prosopagnosia (Barton et al. 2004). There have also been differences shown in the ability to perceive static versus dynamic faces (Steede et al. 2007), suggesting the importance of facial movements in conveying information and perceiving mental states. This finding also suggests that the difficulties in facial recognition stem more from recognizing idiosyncratic morphology rather than movement. Treatments for prosopagnosia tend to focus on developing and fostering these same compensatory strategies, such as recognizing other individual differences besides facial structure. Most success in treatment has come from improving the ability to attend to other distinguishing features such as voice pitch, clothing, hair style, and gait. Such treatment has been suggested for both congenital and acquired prosopagnosia (Cousins 2013).

Conclusion

Facial apperception can be a major impediment to intraspecies interactions, but prosopagnosics can still become adept at navigating social interactions without the use of facial recognition by relying on other identifying cues such as voice, clothing, and gait to discern the identity of individuals. Although prosopagnosia may be comorbid with other perceptual disorders such as achromatopsia and semantic dementia, it often does not inhibit most sensory functions. Impairment of one function of a perceptual system with maintenance of other functions in the same system, as is seen in

fairly stable performance of prosopagnosics in emotion recognition and curvature discrimination tasks, may suggest the independent evolution of functions of a particular perceptual system to solve particular ancestral problems. Thus, this divergent functioning fits with the modularity model of the evolved modern human mind.

Cross-References

- [Face and Object Recognition](#)
- [Face Recall](#)

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Prosopagnosia (Face Recognition)

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Synonyms

[Face blindness](#); [Visual agnosia for faces](#)

Definition

Prosopagnosia is a subtype of visual agnosia characterized by an impairment in the ability to recognize familiar faces, including one's own face.

Introduction

The word prosopagnosia comes from the Greek *prosopos* (face or person) and *gnosis* (knowledge). Although acquired disorders in face recognition have been described since the nineteenth century, Bodamer (1947) was the first researcher to use the term “prosopagnosia” to define the disorder in face recognition, isolated from other types of visual agnosia.

Clinical Characteristics

The patient who suffers from prosopagnosia loses the ability to recognize people by the face and has to resort to the recognition of accessory aspects to the face such as voice or clothing to achieve identification. It is a selective deficit of facial

identity, frequently (but not always) retaining the ability to interpret other types of facial information, such as emotional expression, age, and sex. In very serious cases, the patient loses the ability to determine the sex and age of the face (Lopera and Ardila 1992).

Patients with prosopagnosia recognize the differences between faces and are able to match similar faces, but cannot achieve their identity. Sometimes, the defect can extend to the patient's own face with impossible recognition in a mirror or a photograph, and the patient even indicates that he/she has forgotten what his/her face was like. The patient can, however, know that a face is a face and that it contains certain elements, such as eyes, nose, etc.

Prosopagnosia then seems to be a defect in recognizing individual members belonging to a specific visual category, and most patients also have difficulty recognizing the individual members of stimulus groups that belong to other visual categories (e.g., cars, flowers, animals, etc.). The patient can recognize the category ("it is a car") but be unable to determine what type of car it is, that is, the individual member of the category. So, in prosopagnosia, the recognition of the specific members belonging to a visual class is altered, despite the recognition of the class being achieved.

It has been observed, however, the presence of a covert recognition of faces in patients with prosopagnosia. Patients present a physiological response to familiar faces but not to the presentation of unfamiliar faces (Sergent and Poncet 1990). Likewise, better learning is achieved in tasks of associated pairs of faces if family faces are used for the patient. These findings suggest that despite not being aware of face recognition, the patient is performing a partial covert recognition, of which he/she is not aware.

Prosopagnosia is a relatively unusual neuropsychological syndrome and its anatomical correlates are still under discussion. From the initial descriptions it was considered that lesions of the right hemisphere were sufficient to produce prosopagnosia. This theory was maintained until 1980 when some pathological studies (Damasio et al. 1982) showed the presence of bilateral lesions in patients with prosopagnosia and described the temporal inferior and basal occipital

regions (fusiform and lingual gyri) as the determinants in the production of the syndrome, with all its clinical manifestations. Since 1985, however, new radiological studies have appeared with injuries exclusively in the right hemisphere (Vg., Landis et al. 1988) centering the anatomical location of prosopagnosia again toward the right hemisphere. The damage of the inferior temporal-occipital portion of the right hemisphere seems to be crucial but not sufficient in the production of prosopagnosia. Benton (1990) suggests that the production of prosopagnosia can be observed in cases of an exclusively right lesion, provided that it is associated with some abnormal condition of the left hemisphere, such as an atrophy associated with aging. De Renzi (1982) proposes that the production of prosopagnosia due to lesion of the right hemisphere depends on the size of the lesion. The lesion must reach a certain size that allows the appearance of the syndrome, but neither should it be very extensive since wider agnostic phenomena would opaque the defect in the recognition of faces.

More recently, it has been observed that prosopagnosia can appear as developmental disorders, usually referred as "developmental prosopagnosia." Developmental prosopagnosia can be defined as a severe impairment of visual face recognition in the absence of any apparent brain damage (Towler and Eimer 2012). These patients with developmental prosopagnosia usually report first experiencing face recognition problems in childhood or adolescence. Typical diagnostic criteria are that developmental prosopagnosia individuals must score below two standard deviations from the mean on a number of different face recognition tests (Towler et al. 2017). Developmental prosopagnosia has attracted special attention during recent years, and a significant number of papers exploring this developmental disorder have been published (Pennington et al. 2019).

Conclusion

Prosopagnosia represents a relatively unusual clinical syndrome observed in cases of the temporal inferior and basal occipital pathology. It is

characterized by inability to recognize familiar faces and, frequently, to recognize the individual member of a visual perceptual category. Some disagreement remains regarding the lateralization: where some authors state that right hemisphere lesions are sufficient to produce this syndrome, other authors consider that a bilateral pathology is required. Recently, it has been reported that face recognition difficulties can also appear as a developmental specific learning difficulty. The name of “developmental prosopagnosia” has been used to refer to this developmental abnormal condition.

Cross-References

- ▶ [Attention and Perception](#)
- ▶ [Brain Imaging](#)
- ▶ [Face and Object Recognition](#)
- ▶ [Face Recall](#)
- ▶ [Visual Association Cortex](#)

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Prospective Mates

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Synonyms

[Potential Mates](#)

Definition

Of all available mates, prospective mates are those that the individual has selected for further pursuit and may be investing time and resources in these individuals in an attempt to secure them as a long-term mate.

Introduction

As one of the most widely studied areas in psychology, self-esteem has been demonstrated to influence a number of outcomes. Most typically, differences emerge for individuals with high self-esteem and those with low self-esteem. The processes surrounding the selection of mates are no exception to this pattern of results. That is, individuals high in self-esteem score higher on self-reported attractiveness (Bale and Archer 2013). Additionally, it has been demonstrated that feedback from potential mates influences state self-esteem (i.e., feelings of self-worth in the moment; Kavanagh et al. 2010).

Self-Esteem and the Selection of Mates

As a species, we are motivated to seek high-quality mates, which in turn increase our reproductive success. There are a number of physical markers of attractiveness, as well as personality traits, such as self-esteem, that influence attractiveness. More specifically, it has been demonstrated that individuals with high self-esteem

report higher ratings of their own attractiveness (Bale and Archer 2013). Considering these findings in terms of sociometer theory, Leary et al. (1995) help to elucidate the nature of this relationship.

Sociometer theory (Leary et al. 1995) suggests that self-esteem acts as a status-tracking mechanism. That is, self-esteem functions to give us information about how valued we are by others. Therefore, individuals who are valued by others should have high levels of self-esteem (Leary et al. 1995). Understanding the degree to which we are valued and included by others would have had tremendous survival and reproductive benefit. Thus, it has been proposed that a “mating sociometer” exists, such that individuals are sensitive to how valued they are by potential mates (Kavanagh et al. 2010).

Multiple studies provide evidence for the mating sociometer. More specifically, it has been demonstrated that experiencing rejection from a potential mate significantly lowers state self-esteem (Kavanagh et al. 2010; Pass et al. 2010). Furthermore, this decrease in self-esteem influences mating aspirations (Kavanagh et al. 2010). That is, individuals who receive a rejection from a potential mate report a decrease in self-esteem and tend to pursue mates of lower attractiveness, while avoiding mates high in attractiveness (Kavanagh et al. 2010). Additional studies have demonstrated that this decrease in self-esteem following rejection is coupled by a decrease in self-perceived mate value (Zhang et al. 2015). Furthermore, individuals who experienced rejection reported a desire to evade situations wherein potential mates may be present, whereas individuals who experienced acceptance did not (Zhang et al. 2015). Therefore, decreased self-esteem may continue to influence mating decisions, as well as accessibility to quality mates.

Interestingly, this connection between rejection and decreased self-esteem is not observed in other domains, such as friendships, where individuals may face rejection (Kavanagh et al. 2010; Pass et al. 2010). Therefore, the sociometer may be particularly tuned to the domain of mating. This is further evidenced by research suggesting that self-perceived attractiveness, self-confidence

in appearance, and romantic self-confidence predict overall self-esteem (Bale and Archer 2013). These findings suggest that a large portion of self-esteem may be derived from the ability to attract a mate, which in turn suggests that self-esteem has an adaptive function for mating. If this is the case, it would then be expected that the cues to attractiveness for men and women would be different (i.e., status vs. physical attractiveness), and thus specific forms of rejection may be more impactful for men than women and vice versa. Indeed, it has been demonstrated that decreased state self-esteem in men only occurs after rejection stemming from their competence and status, whereas women only experienced decreased state self-esteem when the rejection was focused on their physical attractiveness (Pass et al. 2010). Therefore, the sociometer can be seen as particularly tuned to the domain of mating, but slightly differently tuned for men and women. Additionally, the findings discussed above suggest that individuals with low self-esteem are likely to be mated to individuals with similarly low levels of self-esteem, whereas individuals with high self-esteem seek out other high self-esteem individuals.

Narcissism and Prospective Mates

Thus far, it has been suggested that high self-esteem may reflect generally positive appraisals of one's attractiveness (i.e., from the self and from others), which in turn influences reproductive success. Therefore, it may be assumed that individuals who have particularly high self-esteem (i.e., narcissism) are more successful with prospective mates. However, this relationship may not be as clear-cut as assumed.

In many conceptualizations, narcissism is characterized by inflated feelings of self-worth (i.e., high self-esteem; Campbell and Foster 2007). As was previously discussed, individuals with high self-esteem have been deemed to be more attractive. It therefore stands to reason that narcissistic individuals would also be deemed more attractive. Indeed, it has been demonstrated that narcissistic individuals are reported to be more attractive (Dufner et al. 2013). However, this initial

attraction eventually fades, as partners of narcissists report lower relationship satisfaction, and these relationships are typically short-lived (Brunell and Campbell 2011). Additionally, narcissists have been found to be less committed to their ongoing romantic relationships (Campbell and Foster 2002) and more likely to be aggressive toward their partners (Keller et al. 2014). Therefore, narcissism may be somewhat beneficial in the initial selection of mates, and in short-term mating, but could be detrimental for long-term mating.

Conclusion

Self-esteem can be seen as a trait that influences attractiveness, and in turn the selection of mates. Typically, individuals who are high in self-esteem are deemed to be attractive and are motivated to seek out other attractive high-quality mates, whereas individuals with low self-esteem may avoid seeking out these mates. Put another way, self-esteem may be one of the many traits that play a role in assortative mating. Finally, although excessively high self-esteem may aide in early selection of mates, it appears to be detrimental to long-term mating efforts.

Cross-References

- [Aggression for Sexual Access](#)
- [Benefits of Short-Term Mating](#)
- [Casual Sex](#)
- [Costs of Short-Term Mating for Women](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Female Mate Choice](#)
- [Hookup Culture](#)
- [Human Courting](#)
- [Human Sexuality](#)
- [Kin Interest in Mating Relationships](#)
- [Long-Term Mating](#)
- [Lowering Partner Standards in a Short-Term Mating Context](#)
- [Male Mate Choice](#)
- [Mate Poaching](#)
- [Mate Choice Effects](#)
- [Mate Copying](#)
- [Mate Preferences](#)
- [Mate Selection Strategy](#)
- [Mate Value](#)
- [Men with Poor Mating Prospects](#)
- [Mating Strategy](#)
- [Mating Systems](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Opposite-Sex Relationships](#)
- [Personality and Mate Poaching](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Reproductive Strategy](#)
- [Reproductive Value](#)
- [Self-evaluations Track Perceived Mate Value](#)
- [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- [Sexual Contact and Sexual Disgust](#)
- [Sexual Strategies Theory](#)
- [Short-Term Mating](#)
- [Status and Reproductive Success](#)
- [Women's Long-Term Strategies](#)

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Prostitution

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Synonyms

Harlotry; Streetwalking; Whoredom

Definition

A sexual activity provided by women, men, and transsexuals in exchange for payment.

Introduction

Prostitution is sometimes called the “world’s oldest profession” and has been practiced throughout ancient and modern culture. The beginnings of this profession date back to ancient Mesopotamian civilization and expanded to ancient Greece, Rome, Japan, and China (Sanger 2015).

History of Prostitution

In antiquity, prostitution was connected with a secular rite (Sanger 2015). In the temple of the goddess of love, priestesses in exchange for donations for the goddess would offer up their bodies (Doufor 1902). Once a year in the Mylitty temple in ancient Babylon, each woman had to give herself to a foreigner, who would pay, in order to fulfill their sacred duty (Doufor 1902). In ancient Greece, the first brothels (*lupanarium*) were created in Athens by Solon in the sixth century BC. Prostitution was public and legal in ancient Rome (Sanger 2015). A special office was established in 260 BC, which was coordinated by an aedile. Aediles were responsible for guarding the peace in the *lupanarium* and controlling the taxes of income from prostitutes (Sanger 2015). Prostitution life was a concern in many public places. In the Roman baths, for example, special cabins existed, where erotic massages and oral and classic sex were performed by both female and male prostitutes (Sanger 2015). Prostitution practices from ancient Rome were uncovered on a fresco from Pompeii. Prostitution was common in many large cities during the Middle Ages. Professional prostitutes wore red bows on their arms as a sign of pride of guild membership, with the income from brothels feeding the municipal treasury. In the Middle Ages, the first similarity to red light districts was established, with the names of the streets referred to erotic or sex services (e.g., *Pousse-Penil* or *Puits d’amour*). Attitudes began to harden against prostitution in the sixteenth century. Syphilis transmitted to Europe from Columbian expeditions to America could have contributed to this (Harper et al. 2008). Practicing this profession became a crime, a transgression against human and divine laws. Together with this new type of crime, new ways of administering the penalty were created. Published by Charles V in 1530, *Norms and the Police Reform* severely prohibited prostitution with the penalties contained in them being extremely cruel. The eighteenth century was “The Golden Age of Prostitution,” and during this period, prostitution was widely popular. There were numerous places in Paris and London where prostitutes could receive

training in order to be professional and adaptable (Roberts 1992). Prostitution began to develop in the USA at the beginning of the nineteenth century, where bawdy houses were tolerated in American cities (D'Emilio and Freedman 1988). New Orleans is viewed by historians as the largest city brothel of all time. Various systems of regulating prostitutes and monitoring brothels were developed in Europe (Head 2009). Many prostitutes sexually served soldiers of both sides during World War I and World War II. Many soldiers were exposed to venereal diseases through these interpersonal contacts. In the Japanese war brothels, 200,000 women from China and Korea, called "comfort women," were forced into prostitution (Head 2009). Sex tourism, defined as travelling for sexual intercourse, emerged as a controversial aspect of Western tourism and globalization in the late twentieth century.

Regulation and Control

Prostitution functioned on the borderline of legality for centuries. The dynamic development of various erotic sectors was conducive to prostitution. Prostitution and the use of its services were socially stigmatized. Lack of control in many countries led to a different pathology, emerging as a profession whose cultivation was exposed to condemnation, violence, illness, and a breakdown of personal life. The prospect of quick earnings attracted women from different backgrounds, initially achieving success and then realizing the competition.

Prostitution is prohibited in 4 European Union countries, illegal in 16, and legal in 7 (Danna 2014). In the Netherlands, prostitution is legal and the most popular, especially in Amsterdam. Sex workers in the Netherlands, like in most European countries, were illegal prior to 1911 and considered criminals. New Dutch laws, however, legalized brothels, and sex workers began to be seen as any other business (Kilvington et al. 2001). Sex workers in the Netherlands have gained full social, legal, and employment rights but lost their anonymity (Kilvington et al. 2001).

Regulation and control of this profession could significantly contribute to reduction of the frequency of sexually transmitted diseases, reduce

crime on prostitutes and their clients, and eliminate prereproductive prostitution.

Service and Deviation

Individuals who work in the field of prostitution are called "sex workers." The term "sex workers" includes prostitutes who are streetwalkers, who work independently with clients, work through agencies, or who work in sex clubs or massage parlors (Clements 1996; DeCou 1998). Offering sex over special websites is particularly popular in the sex business (e.g., Prokop et al. 2018). Approximately 90 percent of sex workers are female, 10 percent male, and less than 1 percent transsexual (McGuire and Gruter 2003). The majority of prostitutes are of a reproductive age, ranging from 20 to 25 years old, which usually have the highest price per hour (Sohn 2016a; Prokop et al. 2018). A worrying phenomenon is present-day prereproductive prostitution (age 6–15), particularly in Asia. Berkman (1996) estimated that approximately a million child prostitutes are abused in India, Thailand, Vietnam, Sri Lanka, and the Philippines.

Sex workers provide not only classic sex but also sex massages and/or oral stimulation (sometimes for an additional fee). Moreover, different sexual deviations are also catered to anal penetration (client or prostitute), rimming, fisting, watersports, scat, sadomasochism (e.g., BDSM, sadistic personality disorder), and gangbangs (Pitts et al. 2004; Adriaenssens and Hendrickx 2012).

Customer Preferences

Males generally prefer younger and attractive females (Buss and Schmitt 1993). An individual who employs a prostitute's services uses the short-term pleasure without long-term effort. Additionally, engaging the services of a prostitute fulfills sexual desires not supported by regular partners (Pitts et al. 2004). Sohn (2016a) has demonstrated the price of sex with a prostitute as a good measurement of revealed male preferences. Sohn's (2016a) study, based on 8560 prostitutes from Indonesia, found that the price of sex decreased with the prostitute's age. The same results were found by Prokop et al. (2018) based on 2379

Polish prostitutes, where age and the body mass index negatively correlated with the price of sex. However, breast size (except for very large breasts) and the number of sexual offerings were positively associated with the price for sex (Prokop et al. 2018). Clients' preferences play an important role in unsafe sex with prostitutes, contributing to the transfer of venereal diseases (Adriaenssens and Hendrickx 2012). The first reason for unprotected sex is motivation for the additional price for sex without condom use (Adriaenssens and Hendrickx 2012). The second reason may be inspired for fear of violent reactions by clients (Willman 2008; Shannon et al. 2009). These two possibilities are, of course, not mutually exclusive.

Male Prostitution

Male prostitution has been found in almost all modern and ancient cultures (Dynes 1990) but has been studied far less by researchers. Male sex workers sell sexual services for women or men. Apart from money, heterosexual male prostitutes seek out sexual benefits and novel sexual practices. Females who make use of male prostitution often do not have time to get involved in relationships or have certain sexual requirements.

An Evolutionary Perspective

There is no evidence that prostitution has influenced the evolution of any aspects of human behavior, but we can use an evolutionary perspective to explain female engagement in prostitution and male (but not female) investment and cues of male preferences for female prostitutes. First, the parental investment theory suggests that females are reproductively more limited in terms of sex, and thus, females are choosier about sex than males and invest less in intrasexual competition (Trivers 1972). Indeed, females engage in prostitution more than males, and about 69% of American males have solicited a prostitute. In contrast, less than 1% of females solicited a male prostitute (Kinsey et al. 1948). This suggests that females can utilize male material investment as exchange for sexual intercourse. Secondly, the sexual selection theory (Darwin 1871) suggests that intersexual attractiveness is associated with preferences of

fertility and/or good genes. Male preferences for young females with low BMI and medium sized breasts, typical cues of female fertility (Jasienska et al. 2004), strongly support the idea that female prostitutes exploit men's ancestral preferences for fertile females. Females may further exploit men's preferences by means of plastic surgery, specific clothing, etc. Finally, the sperm competition theory (Parker 1970) posits that sperm from two or more males can compete for fertilization in the female reproductive tract. Males prefer cues of low sperm competition intensity (Prokop 2015), which ultimately increase paternity certainty. Young and less experienced female prostitutes are more attractive to males (Sohn 2016b), and popular media often provide information that young females can sometimes sell their virginity for hundreds of thousands of dollars. According to some evolutionists, sexually transmitted infections causing infertility and, in turn, divorcees can contribute to the prevalence of prostitution (Rózsa 2000; Apari et al. 2014).

Conclusion

All this information supports the idea that male preference for female prostitutes is a short-term mating strategy, ultimately influenced by the high probability of conception. These ancestral preferences still persist despite the frequent use of contraception in the modern world.

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Prostitution and Legal Regulation of Sex

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Synonyms

Sex trade; Sex work

Definition

The act or practice of engaging in sexual activity for economic or resources profit.

Introduction

Prostitution occurs in several countries, such as US, Japan, Poland, Germany, Ethiopia, among many others (Buss 2003). McGuire and Gruter (2003), from the analysis of the number of sex workers in the USA and in some countries of

Asian, estimate an increase in prostitution around the world, mainly child prostitution. Although there are other types of prostitution such as child, transgendered and male prostitutes, in general, it is a service exercised by women (Salmon 2008).

It is commonly known that prostitution involves payment for sex. However, others services may be offered, according to customer demand. Indeed, McGuire and Gruter (2003) affirm that over 50% of call girls attendances do not include sexual intercourse. Although prostitution includes a range of different services, such as escort and indoor attendance, the most known form of prostitution is street work. Therefore, these services have a variety of benefits and disadvantages. It is a fact that street work is the most dangerous and the worst paid compared to others forms of sex work. These women have very often lower socioeconomic conditions and suffer more attempts of physical and sexual violence at work. In turn, escorts and indoors forms a high class of prostitutes. They commonly come from a healthier family environment and are well paid (Salmon 2008).

Prostitution is considered a reflection of men's preference for casual sex and a women's choice or need to offer sex in exchange of money; hence it can be motivated by the lack of resources (Buss 2003). Although there have been reports of cases in which prostitution was carried out voluntarily, the reasons and motivations of these individuals are still poorly understood (McGuire and Gruter 2003).

Prostitution and Evolution

It is possible that an exchange of sex for resources and protection occurred between hominids since early societies and prostitution as we know it today may have derived from this behavior (Salmon 2008). Prostitution can also be understood as a product of within-species variance or evolutionary variance (Buss 2003). This process is responsible for many advantageous features and mechanisms; nonetheless, it can sometimes produce and select not so beneficial features to the

human species, such as the desire to engage in law-breaking behavior or some personal and sexual preferences related to prostitution.

Engaging in sexual intercourse with prostitutes offers for men the advantages of short-term relationship without the efforts of a long-term mating (McGuire and Gruter 2003). Evolutionarily, men are more oriented to seek short-term sexual relationships, since they pursue the largest number of partners possible and are the less-investing sex, in view of the low effort after copulation and during pregnancy. In other words, since they are imposed low obligatory parental investment, men tend to be more receptive to brief sexual encounters (Schmitt et al. 2001). Moreover, prostitutes represent an alternative to individuals that had not found or could not attract a mate or were not sexually satisfied in their relationship (McGuire and Gruter 2003). Thus, in several cases, prostitutes can fulfill the sexual satisfaction of these individuals.

Another point of view is that some women use prostitution consciously as a means to take advantage of men's sexual desire in exchange of resources. Female reproductive success is more linked to the quality of partners than quantity. Instead, short-term mating represents to women a chance to access high-quality genes, protection, or immediate resources (Schmitt et al. 2001).

Legal Regulation of Sex

Being a wide spread behavior and a way of living, for many women it has been tried, for many years, to eradicate or control prostitution. Even though the reasons for the regulation of prostitution often revolves around moral and religion matters, such as threatening marital institution and family, this practice also have imposed negative social consequences, such as facilitating the spread of sexually transmitted diseases (McGuire and Gruter 2003).

As a solution for this issue, three measures have been proposed, namely, criminalization, decriminalization, and legalization (Lutnick and Cohan 2009). Making prostitution a crime could be justified based on the presumption that the act of paying for sex would be suppressed if legal

consequences were imposed for those who practice it. In the other hand, decriminalization seeks to avoid the byproducts of coercive control of prostitution, which is the increase of criminal behavior or and prostitution itself (McGuire and Gruter 2003). Cunningham and Shah (2014) state that decriminalization in Rhode Island District in 2003 considerably reduced forcible rape offenses and gonorrhea occurrence in the region. Nonetheless, this measure does not insure, in every case, that the health risk commonly associated with prostitution is controlled.

That is the main goal of legalization. Registering, licensing, and checking up for health problems regularly would help in the control, mainly, of sexually transmitted diseases (Quast and Gonzalez 2016). However, this proposition falls short in the way that it does not contribute to other matters related to prostitution other than controlling for diseases, such as the risk of violence involved in the activity, which could lead to long-term physical and psychological complications.

In this sense, none of these public policies and regulations had been fully effective. Most legal approaches involve the control of streetworking, but services like social companionship performed by call girls and escorts are more difficult to control.

Conclusion

Prostitution is widely practiced, historically persistent, and resistant to control policies activity. Despite the moral judgment implied for those who sell sex for a living, this behavior have its roots founded in human evolutionary history. The way men tend to engage in short-term sexual activity have been selected throughout the ages and has probably contributed to the survival of our specie, as well the possibility of women benefiting from it (Buss 2003). It is also important to emphasize that, from the evolutionary perspective, sexual activity and resource acquisition and maintenance are key to motivate behavior and considering that prostitution, by definition, involves both of these elements, is

safe to say that this conduct will be still practiced for many years to come.

For that reason, it is possible that any attempts to regulate sexual behavior, including prostitution, will only bring partial and temporary results, insofar human species is predisposed to engage in sexual behavior (McGuire and Gruter 2003). Thus, Salmon (2008) states that any public policies on prostitution, to be truly effective, needs to be grounded on the knowledge of evolved specialized psychological mechanisms and environmental influences related to sexual behavior.

Cross-References

- ▶ [Benefits of Short-Term Mating](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
- ▶ [Prostitution](#)
- ▶ [Prostitution and Women's Short-Term Mating](#)

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Prostitution and Women's Short-Term Mating

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Synonyms

Escorting; Harlotry; Sex-work; Whoredom

Definition

The practice or occupation of engaging in sexual activity with someone for payment.

Introduction

Symons (1979) once said that “sex is something that women have, and men want.” It is a universal truism that men in every known culture and epoch are the sex that almost invariably pay for sex, with women offering this commodity as a service for cash or other resources (Salmon 2008). The opportunities that arise for women to engage in professions where sexual services are exchanged for money or resources reveal much about both men's cross-cultural and historical desire for sexual variety and women's decision to select men to mate with who possess wealth and a willingness to exchange this for sex (Monto 2000). Clearly there are circumstances where women are indeed coerced into prostitution; however, men do not, and never have, visited prostitutes under coercion, and women appear to be well aware of men's inclination to pay for sex. Offering sex for immediate resources may indeed be a short-term strategy that women strategically employ in specific, evolutionarily relevant contexts.

What's in it for the Woman?

Women engage in and enjoy uncommitted sex for a variety of nonfinancial reasons (Meston and

Buss 2009); however whereas male fitness can be enhanced by accessing multiple partners even in rapid succession (e.g., the Coolidge effect), with negligible costs, the same fitness benefits do not, at least superficially, accrue to females who seek sexual variety. With this in mind, why have so many women across historical time and cross-culturally offered sex for money? The frequent explanation as to why women offer sex for money (i.e., to address dire economic circumstances) is challenged in that many women choose to engage in this activity despite possessing financial stability and freedom (for a summary on the historical and demographic statistics pertaining to prostitution, see Salmon 2008). It is pointless denying the incontrovertible fact that many women engage in prostitution due to male coercion especially in certain sociocultural, demographic, and economic circumstances; however, in the absence of exploitation, what reasons do women give for becoming prostitutes? Rossler et al. (2010) asked a large sample of European and non-European prostitutes in Switzerland (where sex work is not illegal) to list the reasons they chose sex work as a profession. Those coerced into the profession and those citing drug addiction comprised only 2% and 22%, respectively. Even paying debts (24%), supporting family (26%) and being unable to find another job (29%) were considerably less than the percentage claiming that the reason for their involvement in prostitution was that they “liked the job” (37%). The universal existence of prostitution in the absence of a necessity to escape poverty suggests a more deep-rooted context triggering, strategic behavioral proclivity. How can women benefit from pursuing behavior when the associated costs would appear to outweigh any benefits, e.g., promiscuous reputation, rearing offspring in isolation, absence of partner protection, and increased likelihood of contracting sexually transmitted diseases?

Greiling and Buss (2000) listed five classes of benefits that may accrue to women who pursue short-term as opposed to long-term mating strategies. When comparing the five hypotheses, the authors concluded that women in addition to attempting to acquire resources also might

prioritize noncommitted sex as it facilitates current partnership dissolution, fine-tunes skills required for securing a long-term partner, and may secure good quality genes. Prostitution when viewed as a short-term mating strategy would appear to relate only directly to the first of the five classes of benefits outlined. Also, women more inclined toward adopting a short-term or *unrestricted* mating strategy as measured by, for example, the sociosexual orientation inventory (SOI) perceive the benefits of a more promiscuous strategy as being more positive compared to those who score lower (*restricted*). Such perceived benefits include expensive designer clothes, career advancement, jewellery, and access to sex partner's car (Greiling and Buss 2000). This "resource extraction" has long been documented in women, especially in cultures where promiscuous sexual activity has not been prohibited. Malinowski (1929, cited in Workman and Reader 2014) reported that women functioned as mistresses in the Trobriand Islands on the condition that their lover's *provision them with gifts*.

Daddy Issues

One factor that influences the likelihood of women pursuing short-term sexual strategies is the absence of a father during early development. According to Workman and Reader (2014, p.118), "the likelihood of a woman engaging in casual sex relates to whether or not her father was present during her childhood." Arguably, the non-availability of a resource investment role model may predispose women to abandon hope of finding a reliable long-term partner and to realize that archetypically men are only interested in pursuing short-term mating strategies. This may promote the adoption of a quantity over quality mind-set characterized by precocious sexual development and earlier engagement in sex. DelPriore and Hill (2013) found that even when employing experimental procedures (participants were invited to relive periods of "father absence"), college-aged women showed greater activation of sexual concepts, more sexually permissive attitudes, and greater willingness to engage in casual sex and to have more future sex than "father-present"

women. Arriving at firm conclusions regarding the identification of the proximate and ultimate triggers, propelling women to become sex workers is problematic. Father absence, for example, is often associated with a multitude of stress-inducing confounds (Rossler et al. 2010). Future studies may benefit from investigating the probability of "father absence" being evident in "high-class call girls" (sex workers who are more prone to choose sex work as a career).

Sex Ratios

Contemporary evolutionary theories of human mating emphasize the fact that age, contextual, and personality factors contribute flexibly and conditionally to influence the mating strategies adopted at a given time (Buss and Schmitt 2003). One demographic variable that may influence a tendency to adopt a short-term mating strategy is the local sex ratio. South and Trent (2011) found that Chinese men became less inclined to have intercourse with prostitutes and more inclined to engage in noncommercial sex when a high female-to-male ratio was evident. This suggests that opposite-sex partner abundance may increase early, frequent, and multi-partner noncommercial sex possibly restricting the opportunities normally available for women to pursue prostitution as a short-term mating strategy. Sexual dynamics inevitably change in contexts where women outnumber men (e.g., when warfare decimates male populations). Symons (1979) reported that in both the Ache and Yanomamo (cultures characterized by inter-tribal homicide), women appear to pursue short-term strategies in order to secure smaller amounts of resources from multiple partners.

How Much to Charge?

In a free market, the price a woman of one age charges in comparison to another age for sexual services reveals a great deal about both the value assigned to youth by men and the realization by women that they possess what men want. The Internet is an ideal medium to explore sexual behavior due to its nonintrusive method of data

collection. Dunn (2018) accessed an online escort website and sampled fees (incalls and outcalls) advertised by escorts for sexual services across various ages and age groups from five different cultures (the UK, Ireland, Australia, the USA, and Eastern Europe). Apart from Irish escorts advertising outcalls, differences were evident in all sampled countries with younger escorts indicating higher charges on their profile pages compared to older escorts. Female self-perceived short-term mate value appears to peak in mid 20s. The realization by women that this diminishes with age translates into a reduction in advertised fees by older women. A similar pattern was reported by Sohn (2016) with an Indonesian sample. Prices charged by prostitutes of peak age (late teens to early 20s) was more than twice that for prostitutes in their late 1930s. Griffith et al. (2016) found additional traits besides youth to be of importance. That said these were clearly all related to fertility. Lower weight and body mass index, breast and buttock nudity, and idealized 0.7 waist-to-hip ratios (WHR) were all associated with higher fees.

Conclusion

Traditional explanations for the existence of prostitution are challenged when adopting an evolutionary perspective. Differential sensitivity to resource acquisition benefits, demographic factors such as the sex ratio of a given cultural group, personality factors such as father absence, and perceived mate value may all contribute to the predisposition of women to pursue this perhaps most extreme manifestation of a short-term mating strategy.

Cross-References

► [Escorting](#)

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Protected Values

► [Sacred Values](#)

Protection and Evolution

► [Daughter Guarding](#)

Protective Resemblance

- [Butterfly Mimicry](#)

Protolanguage

- [Protosyntax](#)

Proto-Language

- [Mother Tongue Hypothesis](#)

Proto-Sapiens

- [Mother Tongue Hypothesis](#)

Protosyntax

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Synonyms

[Linear grammar](#); [Linguistic fossils](#); [Precursor to language](#); [Premodern language capacity](#); [Protolanguage](#)

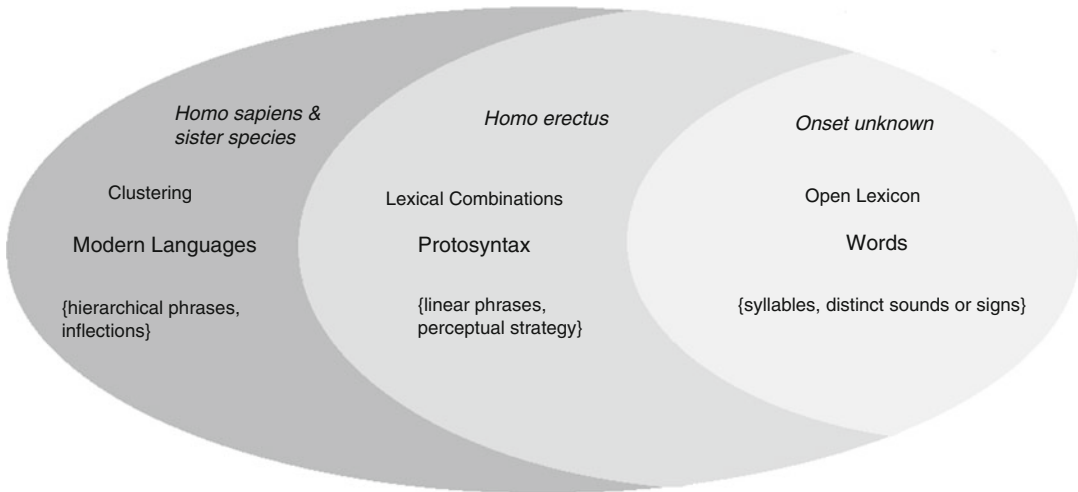
Definition

The term Protosyntax refers in cognitive science to a precursor stage of the human capacity for modern languages. It includes linear phrases with primarily uninflected nouns and verbs.

Introduction

The notion Protosyntax, also called protolanguage or linear grammar, is a possible window to our understanding of how the modern language capacity might have evolved from single words to complex syntactic structures. It typically refers to a hypothetical precursor stage in the language domain, but in principle, it can also refer to other cognitive capacities such as the Protosyntax of music. The linguistic notion implies that language evolved gradually in the hominid lineage from basic to more complex syntactic structures. Protosyntax uses a linear order of words, is non-hierarchical organized, and lacks inflectional morphology. For instance, it does not use inflections for Tense or Case, is based on semantic combinatory principles such as the perceptual strategy (Agent-First), does not form clusters (hierarchical phrases) to generate questions, passive voices, anaphors, or subclauses as found in fully-fledged modern languages.

Protosyntax, as assumed, is a linguistic fossil that mirrors a possible stage in the evolution of language (see for example Bickerton 1981, 1990; Jackendoff 1999; Progovac 2010; Hurford 2012). One possible implication is that our biological relatives such as *Homo erectus* (ca. 1.9–0.3 ma) were equipped with a basic language capacity scaffolding a linear word order but not the morphosyntactic complexity of modern languages. In contrast, the oldest fossils of anatomical modern humans more recently discovered in Morocco are about 300 ky old. Our extinct sister species, the Neanderthals (ca. 700–40 ka), had comparable genetic, neurological, and cultural parameters as modern humans, and thus their language capacity was presumably comparable to modern humans (Hillert 2015). One line of evidence finds these structures in emerging languages (e.g., pidgin or sign languages), another line in how children and adults acquire language, how language breaks down, or how these linear phrases resurface in modern languages. Although speculative, research on Protosyntax is highly relevant for the debate on the innateness and origin of the human language capacity (Fig. 1).



Protosyntax, Fig. 1 The Protosyntactic Stage in Language Evolution

Emerging Languages

Some languages emerge by the contact of speakers of different languages and who are unable to use a mediating language, a *lingua franca*, for communication. In Hawaii, for example, various ethnic groups such as Chinese, Japanese, Portuguese, Koreans, and Filipinos spoke at the end of the nineteenth century different pidgins to communicate with the English-speaking population, the Haole (Caucasians) and the native Hawaiians. Since pidgins are not fully-fledged languages but make use of linear syntactic structures, Bickerton (1990) assumes that a pidgin would reflect a protolanguage spoken of early humans or of other Homo species. The linguistic fossils found in pidgin are, however, sometimes less informative for identifying Protosyntax as pidgins are influenced by the speakers' native languages (e.g., flexibility of word order). Another example is Riau Indonesian, a Malayan dialect spoken by several million people. Virtually, no syntactic categories (nouns vs. verbs) and (almost) no morphology are used, and the word order is based on semantic principles (Gil 2005).

Several newly created sign languages are known, which use a perceptual strategy and lack morphology. One example is home signing. Deaf children create often home signs to communicate with their hearing but not signing parents.

Like spoken language, the children go through a two-gesture stage and their developed home sign system is more complex than speech-supporting gestures. Another example, which is well-known, is the Nicaraguan Sign Language, which previously isolated deaf children created in the 1970s from elements of their own diverse home sign systems. The first generation used signs to refer to objects they needed to talk about and stringed them together in phrases. To describe an event, they would sign each Agent followed by his or her role such as “girl push boy fall” or “boy give girl receive.” The next wave of deaf children elaborated on these structures (Senghas et al. 2004). The emerging sign language Sayyid Bedouin Sign Language (Sandler et al. 2005) and the isolated village sign language Central Taurus Sign Language (Caselli et al. 2014) are similar examples.

Modern Languages

Traces of Protosyntax, sometimes called “living fossils,” can be also identified in fully-fledged modern languages and how they are acquired and break down. Agrammatic aphasic patients, typical with lesions to Broca's area, fall back on a perceptual strategy, drop inflections and function words. Child language acquisition includes

always a two-word and a telegraphic stage, in which inflections and function words are rarely used. Again, second language adult learners without explicit language instructions show across all examined pairs of native and second languages a protosyntactic stage. Genie, a well-known victim of severe child abuse, who was not exposed to language until the age of 13 years, quickly acquired words after she was found, but her grammar remained behind even years after training.

Specific syntactic structures found in modern languages may also be traces of a protosyntactic stage (see Progovac 2010; Jackendoff 1999). For example, verb-noun compounds without a head (*pick-pocket*); noun-noun compounds based on concatenations are pragmatically interpretable (*cheesecake*); free placing of adverbial expressions (*apparently* or *in the morning*) can be in initial, medial, or final position of a clause; or small clauses (*problem solved!*).

The languages so far discussed do not fall all in the same category in terms of morphosyntactic complexity. Modern languages typically use more cognitive resources than creoles or indigenous languages such as Riau Indonesian, which in turn use more resources than emerging languages like pidgins or new sign languages. As we have seen, resources are used to various degrees, but all modern humans are equipped with the cognitive capacity to use these full resources associated with fully-fledged modern languages.

Conclusion

Protosyntax is typically considered as a linguistic fossil, which can be identified in emerging and modern languages, and possibly also in other cognitive domains such as music. This approach, although speculative, is highly intriguing for understanding the cognitive and neurobiological parameters of language processing and how these parameters might have evolved in the hominid lineage. The protosyntactic stage is certainly not the first stage of language evolution as a lexical stage with distinct sound units must precede a syntactic stage. Protosyntax might, however, mirror the premodern language capacity of our

biological ancestor *Homo erectus*. Although alternative scenarios are conceivable, the idea that the “language-ready brain” for fully-fledged modern languages coincides with the birth of anatomical modern humans and their sister species is plausible as is the idea that the “protosyntactic-ready brain” can be associated with *Homo erectus*. To what extent early modern humans or *Homo erectus* respectively used their genetically predetermined cognitive resources is a closely related but different issue. In conclusion, current evidence shows that the modern language capacity could not have evolved without the capacity for protosyntactic structures.

Cross-References

- [Darwin on the Origin of Language](#)
- [Grammar](#)
- [Homo erectus](#)
- [Language Acquisition](#)
- [Linguistic Evolution](#)
- [Musical Protolanguage](#)
- [Neanderthals and Humans](#)
- [Neurobiology of Language](#)
- [Pidgins and Creoles](#)

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Proto-tool

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Synonyms

Borderline tool

Definition

Proto-tools are functionally analogous to tools but are not held and directly manipulated during or prior to use. (Shumaker et al. 2011)

Introduction

An ancient prophecy once foretold that Aeschylus, the Greek playwright, would die by something falling on his head. He therefore spent the entirety of this cursed day in an open field, far from buildings, trees, and anything else that could fall on his head. Alas, he could not escape his destiny because an eagle dropped a tortoise on his head. If the eagle intended to kill him, this would be classified as tool use. However, it is possible she simply aimed for a nearby rock, or mistook the poet's shiny bald head for one, in order to crack the tortoise's hard shell. This would be classified as proto-tool use because the supposed tool (rock or head) was not held or manipulated by the eagle (Shumaker et al. 2011).

Defining tool use is an ongoing challenge that includes distinguishing it from similar behaviors

such as proto-tool use. An essential criterion of tool use is that the tool is manipulated by the user because otherwise the term would be too broad, encompassing behaviors such as climbing trees and living in burrows. Shumaker et al. (2011) emphasize that their distinction is logically rather than biologically meaningful, which others have argued to be arbitrary or anthropocentric (e.g., Shettleworth 2010).

Proto-tools are a subset of borderline tools, although some consider them synonyms. Constructions such as nests, bowers, and dams are made from numerous elements that are considered tools during construction. However, the construction itself is not a tool because it is not held or manipulated in its entirety. Constructions are classified as associative tool use because tools are involved during their creation, whereas tools are never involved in borderline cases. Examples of borderline behaviors are ingesting objects to aid digestion, self-medication, dust bathing, washing or soaking food in water, painting, object play, and pulling prepositioned strings or rakes. Borderline cases demonstrate that tool use is not always a clearly distinct behavioral category (Shumaker et al. 2011).

Fixed Anvils

Many species open encased or hard food items by dropping, throwing, or pounding them against fixed anvils, which is the archetype of proto-tool use (Cristol and Switzer 1999; Lefebvre et al. 2002; Shumaker et al. 2011). Birds such as gulls, crows, and raptors drop mollusks, nuts, eggs, bones, and – in line with the Greek tragedy – tortoises. Throwing or smashing encased foods is a more frequent use of fixed anvils in mammals, especially carnivores and primates.

The best documented type of proto-tool use is food dropping by crows. Mathematical models and dropping experiments predict that walnuts should be dropped from greater heights if the dropping surface is softer; the walnut species is harder; the walnut weight is lower, because heavier walnuts open slightly easier; the walnut has not been dropped before, because they

weaken with every drop; and the risk of theft is lower, when fewer conspecifics are present. American crows dropped walnuts in a manner consistent with these predictions, except that walnut weight did not influence dropping height. Attempted theft by others was frequent, so dropping from lower heights was highly advantageous (Cristol and Switzer 1999).

Similarly, hooded and carrion crows drop mussels onto rocks. Juveniles never succeeded on their initial attempts, probably because they dropped them over softer gravel or mud. On the other hand, adults dropped mussels onto rocky substrates and always succeeded on their first try, which suggests this proto-tool use has to be learnt during development. Adults might have dropped mussels from optimal heights to conserve energy and because there was no risk of theft during this study period. Dropping from greater heights might also shatter and disperse shell fragments farther, which would increase searching and handling time. Crows never selected small mussels. Approximately 22 medium-sized mussels are sufficient to fulfill the daily energy requirement of an adult crow, which illustrates the potential significance of proto-tool use (Davenport et al. 2014).

New Caledonian crows frequently use various tools in their natural habitat, and they crack nuts by placing them against a forked branch and then dropping them on rocks below. Certain nut-cracking sites are communally used, probably because exposed rocks are rare in their habitat. Dropping nuts from a branch might be more accurate than from flight, especially when the hard surface is relatively small. It also appears to facilitate finding a suitable dropping position in three-dimensional space, which reduces energy expenditure and risk of theft, although this was never observed. This technique may have originated from caching, because crows sometimes store nuts and tools in tree forks. Other possible explanations are that it is more effective in opening them, increases the predictability of success, or reduces time spent selecting and testing suitable locations (Hunt et al. 2002).

New Caledonian crows also secure nuts in crevices or holes and then force them open with

their beaks. These *vice-anvils* combine the properties of anvils (hammering support) and vices (restricting movement). After successfully opening nuts by dropping them on rocks below, they placed them in depressions on a fallen log to stabilize them while extracting kernels. Rooks, a crow species that does not naturally use tools, placed walnuts on fence posts or tree branches to open them. This occurred so frequently that the wood slowly eroded away, leaving clear walnut-sized depressions that presumably increase the efficiency of these vice-anvils (Hunt 2014). Vice-anvils are also used by other birds, such as woodpeckers and nuthatches. Shrikes and butcherbirds employ a different method: they secure prey by impaling it on thorns (Lefebvre et al. 2002; Shumaker et al. 2011).

It was often thought that the main reason why American crows drop walnuts on roads is so cars can crack them, but apparently they do so because the road surface is hard, and cars rarely drive directly over the walnuts. Crows also frequently dropped walnuts on other hard surfaces that vehicles could not reach, such as rooftops and sidewalks. Relying on cars as nutcrackers might even be disadvantageous because the resulting small food pieces cannot be monopolized, and bird species that do not drop walnuts might attempt to steal them (Cristol et al. 1997). Nonetheless, carrion crows in Japan put walnuts in front of cars waiting at traffic lights. This behavior seems to have originated at a driving school and spread over several kilometers the following 20 years (Nihei and Higuchi 2002). These roads had heavier traffic than the American study site, which may not have provided sufficient opportunity for the American crows to develop this behavior.

How Different Is Proto-Tool Use from True Tool Use?

Some species use both true and proto-tools. Sea otters, capuchin monkeys, and chimpanzees pound nuts and mollusks against stones and use stones to hammer them open (Shumaker

et al. 2011). Similarly, Egyptian vultures throw eggs onto rocks and rocks onto eggs. They throw pelican and flamingo eggs but they cannot easily grasp larger eggs so they use tools to break them. In one study, young vultures were not strongly interested in ostrich eggs until they fed from one. One juvenile spontaneously started to drop stones on an artificial ostrich egg after this experience without having seen others do so. Its accuracy quickly improved, but even experienced adults make direct hits in only half of their attempts. Neither is their tool selection optimal; both juvenile and adult vultures sometimes select ineffective objects such as wood, dung, or small stones (Thouless et al. 1989).

It has often been hypothesized that true tool use (dropping stones onto eggs) develops directly from proto-tool use (dropping eggs onto stones). Indeed, both wild and hand-raised Egyptian vultures prefer to drop round stones that resemble eggs. They select and manipulate stones as if they were pelican or flamingo eggs, and instead of throwing the object held in their beaks onto stones, they throw it at ostrich eggs, using identical movement patterns. Another explanation is that when vultures encounter an egg that is too large, they redirect their behavior to nearby stones as conflict behavior. The vulture might then accidentally break the egg, which would lead to an association that is repeated in the future and could eventually become a habitual species-wide behavior through social learning (Thouless et al. 1989).

Birds that use true tools have on average a relatively larger brain than those that only use proto-tools. This supports the idea that true tool use is more cognitively complex. The rate of feeding innovation is correlated with proto-tool use, and both are suggested to be an expression of behavioral flexibility. There is also a positive relationship between relative brain size and tool use in primates, but proto-tool use was not analyzed (Lefebvre et al. 2002). However, both true and proto-tool use are broad categories that might overlap, and some proto-tool users have relatively larger brains than true tool users (Shumaker et al. 2011).

Conclusion

The difference between proto-tools and true tools rests only in manipulation. Contrary to common assumptions, this does not necessarily mean that proto-tool use is more primitive, always arises earlier in development, or forms an evolutionary precursor to true tool use (Shumaker et al. 2011). Although they are sometimes viewed as identical categories based on associative instrumental learning (e.g., Shettleworth 2010), this should not be presumed without further study. The cognition, development, and evolution of proto-tool use should be investigated in its own right and not be merely inferred to be simpler or less important than true tool use. Dropping food onto hard surfaces is a complex functional behavior, and tool use might not increase its efficiency. After all, dropping food to open it is easier than aiming for someone's head for a killing blow.

Cross-References

- [Confounding Use of Tools on Physical Tasks](#)
- [Evolution of Tool Use](#)
- [Innate and Learned Tool Use](#)
- [Nonhuman Tool Use](#)
- [What Makes a Tool](#)

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Prototypical r-/K-Selected (Fast/Slow) Species

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Synonyms

[Pace of life](#)

Definition

Theoretical framework defining the major axes of variability of the life history strategies across the tree of life.

Introduction

The diversity of living forms on Earth is only paralleled by the heterogeneity of their life history traits, such as their longevity or growth rates, which can vary several orders of magnitude. From microscopic *Escherichia coli* to large blue whales (*Balaenoptera musculus*), species show a great

deal of variation in numerous traits that are inexorably linked to their success on earth's environments. Despite such a great diversity, all living creatures experience the same demographic processes of survival, development, and reproduction. The variation of these key demographic processes in timing, intensity, duration, and frequency defines important life history traits (e.g., age at maturity, net reproductive rate, etc.), and the combination of these life history traits results in life history strategies (Stearns 1992). Life history strategies ultimately determine the dynamics of the species, and they are the result of different evolutionary and ecological processes.

Why Is There So Much Life History Variation?

The course of evolution has sculpted a myriad of life history strategies, with planktonic organisms living for few years, while the Pando aspen clone in Utah (*Populus tremuloides*) can live up to 80,000 years. At first glance, one may wonder, why are all species not immortal and produce high numbers of progeny at a time? The response is the existence of “boundary conditions” (*sensu* Stearns 1992) that constrain the available combinations of life history traits. These constraints can be classified as *extrinsic* or *intrinsic*.

Extrinsic life history constraints are those imposed by the surrounding environment. Such life history constraints depict whether the extrinsic environment favors certain strategies but not others. For example, there are no strictly sessile animals on land, while this strategy is rather common in aquatic animals. In this case, the environment has likely enabled the evolution of sessile organisms that feed on the suspended material lying in the water column. Here, the surrounding environment not only refers to the physical one, but also the intra/interspecific interactions. For example, predation has a high influence on the life history of guppies (*Poecilia reticulata*) in Trinidad. Under high predation rates, guppies show higher densities, slower growth, with populations dominated by young, small individuals (Reznick 1982).

The *intrinsic constraints* to life history strategies, on the other hand, are related to the genetic material, as well as physiological, behavioral, and

demographic traits. Evolutionary history or phylogenetic ancestry plays a key role in determining the potential adaptations that a species has. Genetic material is transmitted from parents to descendants, and this nexus can determine the traits available to the latter ones. Heritable traits also set the limits to the evolutionary changes that can be achieved in the short term, and potentially at long term. For example, birds are more likely to have adaptations to optimize their flight than a mammal, with the exception of bats (order Chiroptera).

Intrinsic relationships between traits are commonly referred to as trade-offs. These budgetary compromises between investing resources in one trait/biological function at the expense of others are grounded on limiting resources (Stearns 1992). There are physiological constraints to the amount of energy that an organism is able to invest in one particular trait or biological function. The linkage between traits implies that the evolution of certain life history traits (e.g., high reproductive output) will have implications for others (e.g., adult survival). Thus, the fitness benefit through increasing a given trait must be balanced against the fitness cost of decreasing another trait. Overall, this means that not all life history components can be maximized simultaneously.

Life History Theory

The fascination for the vast diversity of living forms on earth has captivated many biologists. The quest of these scientists to reveal the causes and consequences of the variation in the life history strategies of species across the tree of life gave birth to the disciplines of evolutionary ecology and life history theory. Historically, life history evolution has been approached from the lens of problem optimization. That is, species are selected to evolve the life history strategy or strategies that maximize their fitness according to their evolutionary history and their surrounding environment. However, infinite combinations of strategies cannot evolve. This is, partly, due to the fact that life history traits covary, and it is possible to define major axes of life history variation. Thus, a given pool of traits characterizing different demographic processes can be reduced to fewer

n dimensions along which species can be classified.

There have been several attempts to unveil the major axis of life history variation. Pioneer Robert MacArthur proposed that species could be classified as organisms, type A or type B, in a similar way to the chemistry's periodic table of elements (MacArthur 1972). That is, to order species according to a set of life history attributes, as the chemical elements are classified by a combination of their atomic number (protons), configuration of electrons and certain chemical properties. Later on, Eric Pianka formalized the concept as "periodic table of ecological niches" (Pianka 1970), a scheme that organized species or organisms based on their similarity, as defined by a set of functional traits associated with various niche dimensions. During the consolidation of life history as an ecological discipline, the classification of life histories diverged into several schools, including plant scientists, animal scientists, and bacteriologists. Here we provide a subset of the main frameworks with relevant contributions to the development of life history theory.

r-*K* Strategies

One of the first attempts to classify species according to their life history strategies was the *r*-*K* strategies framework by Pianka (1970). In his seminal paper "On *r* and *K*-selection," Pianka suggested classifying organisms along a continuum of strategies with two extremes. The *r*-endpoint represents the extreme where species are highly reproductive, reproduce early in life, and have rapid development and small body sizes. On the other hand, at the *K*-endpoint, species are less reproductive, with late reproductive maturity and have slow development and large body sizes. For example, he suggested that vertebrates were *K*-selected species, while most insects were *r*-selected.

Pianka also developed the concept of *r*-*K* selection, relating species life history strategies with environmental conditions. This theory predicts that fluctuating environments with high environmental stochasticity and no density-dependence or limited competition (reduced population size), favor those species with traits maximizing productivity (here

population growth, *r*), *r*-strategies. In contrast, under conditions of high competition and density-dependence but with more environmental stability, species with traits that were more efficient in the use of resources and maximize the equilibrium population size were favored (*K*, carrying capacity), *K*-strategies. This principle was then linked to ecological succession. After a major disturbance, ecosystems experience a release of competition and new resources are available. Species colonizing such habitats will be favored when they have high values of *r*-traits. The “rapid” colonization of the habitat would be followed by its own saturation, increasing the number of individuals and then the competition. Under such saturated conditions, organisms that are more competitive at extracting energy from the habitat would then be favored. That is, phenotypes with a high *r* will be selectively favored at low densities/high resource conditions; while those with a high *K* at high densities/low resource conditions.

The dichotomous classification of species being either *r*- or *K*-selected gained both adepts and detractors. Perhaps one of the most insidious criticisms was provided by Stearns in extensive reviews about the life history theory (1992). One of his main critiques was that the *r*-*K* dichotomy did not provide an explanation for the underlying demographic mechanisms regulating populations. The lack of mechanistic explanations was indeed especially concerning, since different life cycle stages (e.g., young vs. adult) typically suffer differently the consequences of density-dependence. These, among other major flaws, caused a loss of popularity for the *r*-*K* paradigm. However, not much time elapsed till the empty niche was filled with newer life history frameworks.

Extending the *r*-*K* Dichotomy: The Fast–Slow Continuum

Following his critical essay to the *r*-*K* dichotomy, Stearns proposed a new life history framework (Stearns 1992). By empirically analyzing a set of life history traits from different mammal species, he showed that both body size and phylogeny had significant influences on life history strategies. In his framework, Stearns states that life history strategies vary according to how species invest

energy in maintenance, development, and/or reproduction. Accordingly, organisms may range between being *fast*, highly-reproductive but short-lived, to *slow*, long-lived, and rarely successful at recruiting. This axis of life history variation empirically evidenced an already known life history paradigm, the existence of a trade-off between survival and reproduction. The coined *fast–slow* continuum, opposed to the *r*-*K* framework, included the influence of body size and phylogenetic relationships on life histories (Stearns 1992). Importantly, this continuum also accounted for physiological limitations and trade-offs, a missing block in Pianka’s life history tenet.

The *fast–slow* continuum still has several limitations that remain to be resolved. First, the underlying ecological factors determining life history variation are still unclear. Besides, a rather controversial fact with the *fast–slow* continuum is that it only accounts for barely half of the life history variation. This flaw was indeed pointed in some early seminal works (e.g., Gaillard et al. 1989), which identified an important second axis related to reproductive traits in birds explaining additional rates of variation. His work suggested that species could be *fast* or *slow* in different ways, revealing that more axes of variation may be needed to fully capture the life history of species.

Beyond Dichotomies: The Fast–Slow and Reproductive Strategies

Despite the usefulness of the aforementioned frameworks, these classifications of life history strategies were limited in geographic, taxonomic, and phylogenetic scales and in the ability to differentiate life history trade-offs. However, these major drawbacks are currently being overcome with the growing body of demographic data. Salguero-Gómez (2017) recently analyzed the demographic trade-offs of 650 vascular plant species across biomes and accounting for the phylogenetic relationship of the species included. He identified two major dimensions of demographic variation: the well-established *fast–slow* continuum and a novel reproductive strategy dimension. The main achievement of this framework is that it reconciles the life history frameworks only focused on one single life

history axes of variation, such as the *r-K* or the *fast-slow*, with those begging for a “beyond K” axis of variation (Stearns 1992; Southwood 1988; Gaillard et al. 1989).

Another novelty of this framework is that it transgresses different ecological scales (Salguero-Gómez 2017) and kingdoms (Paniw et al. 2018). Because of the demographic basis of the *fast-slow* and reproductive strategies, and thus based in allocation strategies, this framework linked the population level demographic rates with the functional traits that constrain individual performance and fitness. That is, this framework shows connections between the position of species in the *fast-slow* and reproductive strategies to species’ functional traits (the leaf economics spectrum), biogeographical characteristics, to their rates of senescence and to their conservation status (Salguero-Gómez 2017). This establishes a nexus between the demographic trade-offs and the “real-world.”

Conclusions

Unlike other scientific disciplines like physics or chemistry, few universal laws have been formulated transcending all hierarchical levels in biology. MacArthur’s vision of a life history periodic table pointed the direction towards which a substantial fraction of life history theory has developed during the last decades. Despite the flaws of the *r-K* selection schema, this framework triggered the development of many different and complex life history tenets. Still, life history theory has only scratched the surface of what a “periodic table of life histories” framework may offer to subdisciplines like ecology, evolution, or conservation science. Life history theory should aim to provide a better understanding about the complex imbrications within different scales of biological organization. How can inter- and intraspecific variation in traits can be incorporated in such a periodic table? How do life history strategies determine the behavior of individuals? Are there other important axes of life history trait variation? How can we link the position within the periodic table to species’ responses to climate change? Despite all of the challenges that remain ahead, MacArthur’s dream is still pursued by many

scientists, aided by the increasing availability of high resolution demographic data across the tree of life.

Cross-References

- [Evolution of Adaptations](#)
- [Extrinsic Mortality](#)
- [Life Expectancy and Reproduction](#)
- [Life History Theory](#)

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Proto-World

- [Mother Tongue Hypothesis](#)

Provisioning

- [Feeding](#)

Proximate and Ultimate Explanations

- [Tinbergen's Four Questions](#)

Proximate Behavior

- [Alarm Calling upon Predator Detection](#)

Proximate Versus Ultimate Explanations

- [How Evolutionary Psychology Can Still Explain Behavior](#)

Psychiatric Darwinism

- [Darwinian Psychiatry](#)

Psychiatry of Nonhuman Apes

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Synonyms

[Comparative psychopathology](#); [Comparative psychopharmacology](#); [Evolutionary psychiatry](#); [Great ape psychiatry](#)

Definition

Interdisciplinary field of study based on evolutionary, comparative, and psychiatric principles employed for the assessment and treatment of behavioral disorders in nonhuman apes.

Introduction

There are currently eight living species of great apes (family Hominidae), classified in four genera, including chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla* and *G. beringei*), orangutans (*Pongo pygmaeus*, *P. abelii*, and *P. tapanuliensis*), and humans (*Homo sapiens*). Genetic analyses have revealed that *Homo* and the two species of *Pan* are the most closely related, collectively sharing more than 98% of their genomes, more than any of them share with *Gorilla*, the next most closely related taxon (Waterson et al. 2005). Given these extensive similarities and the shared phylogenetic history, there is a reason to believe that there are also continuities in the evolution of cognitive and emotional functioning between human and nonhuman apes, including the presence of homologous psychopathological conditions. However, without access to verbal reports of subjective distress, research efforts into psychopathologies in nonhuman primates have been restricted to a purely descriptive level, mainly stemming from observations and experiments conducted with captive individuals (Brüne et al. 2006). Insights from the results of early studies by Harlow on the devastating effects of social deprivation on monkeys (Harlow 1965) prompted adoption of policies to ensure avoidance of total isolation on primates raised in captivity, improving outcomes in many cases.

All great apes are characterized by long life-spans, relatively large body sizes, and complex cognitive abilities. Different species, however, exhibit widely different social organizations. Chimpanzees and bonobos exhibit high levels of fission-fusion dynamics; individuals belong to communities with stable memberships that collectively use and defend a territory but flexibly form

temporary subparties that differ in size, composition, and duration (Goodall 1986). Gorillas have stable multifemale groups with either a single or multiple adult males, Orangutans lead mostly semi-solitary lives but at the regional level can be described as having an individual-based fission-fusion system (Van Schaik 1999). Regardless of species and social organization, all great apes are obligatorily social, forming, at a minimum, a robust social relationship between mother and offspring during a prolonged period of infantile and juvenile dependency.

Inappropriate living conditions such as social, sensory, and/or motor deprivation, especially in barren and uncontrollable environments, appear to lead to a variety of behavioral abnormalities, including “an inability to copulate, incompetent maternal behavior, inappropriate emotional reactions—mainly fear and aggression—to companions, lack of species-typical communicatory signals, and generalized learned helplessness” (Brüne et al. 2006, p. 1249). Additionally, captive individuals have been observed to engage in numerous behavioral patterns that are abnormal in their frequency, severity, or gross anomaly, including bizarre postures, hand clapping, hair pulling, rocking, regurgitation, and re-ingestion of food, and many others (Brüne et al. 2006).

In free-living environments, away from overtly artificial contexts, manifestations of psychopathologies in apes have been limited to speculative anecdotes, primarily due to an incomplete knowledgebase of the full range of “behavioral normality” and a means of assessing distress or disorder. While reports abound of individuals appearing to behave more lethargically with a depressed appearance after experiencing the death of a close companion (typically one’s own offspring or mother), there is limited evidence of quantifiable distress.

Measurement Challenges and Potential Solutions

While a greater understanding of mental health in great apes could allow us to treat captive apes better and lend insight into the evolutionary

origins of psychopathology in humans, attempts to measure mental disorders in nonhuman primates face two significant challenges: (1) effectively defining “disorder” and (2) measuring the mental states of great apes. Finding a generally agreed-upon definition of pathology, especially for mental illnesses, has been a challenge which clinical psychologists and psychiatrists have still yet to remedy in humans. The problem of measuring the internal psychological states of apes is common to all approaches which seek to understand cognition in nonverbal animals.

Some researchers have attempted to adapt the American Psychological Association’s *Diagnostic and Statistical Manuals of Mental Disorders* (DSM) directly to assess the equivalents of mental disorders in apes, symptom by symptom (e.g., Ferdowsian et al. 2011). The DSM is currently on its fifth edition, and with each cycle of revision, the definitions of mental disorders are altered and often expanded. One issue with this is that expanding definitions could lead to “disorder creep,” increasing the proportion of individuals characterized as expressing pathological behavior.

Studies on comparative psychopathology are confronted with the issue of adequately defining concepts such as disorder and maladaptation. Clinical psychology and psychiatry employ these terms to describe an alternation of mechanisms regulating physiology, cognition, behavior, and affection, with treatment being aimed to restore the mechanism to its original state before the disruption. At the ultimate level, however, maladaptation refers to a fitness loss due to an organism’s phenotype (Del Giudice 2018). This distinction is crucial when considering behaviors that at first hand seem maladaptive but after further examination reveals the trait increases the organism’s fitness. The study of infanticide by males, for example, was at initially described as the outcome of pathological behavior. This position, however, has been abandoned and replaced with an adaptive hypothesis wherein the attacker attains fitness benefits by killing younglings (Troisi 2003).

One possible solution to the problem of defining disorder is to use Darwinian fitness as a metric, where evolutionarily adaptive traits are

considered “normal” and maladaptive traits are considered “abnormal” or pathological. In this scenario, ape behaviors which are associated with fitness losses compared to normative behavior would be considered as symptoms of a disorder, a breakdown of neural mechanisms which evolved to deal with specific scenarios but cease to function in other contexts.

While the evolutionary approach to defining “disorder” shows promise, adaptive significance can prove difficult to demonstrate for complex traits such as mental illnesses which are often characterized by a combination of many traits with varying heritability. The evolutionary definition also does not align with accepted human-specific definitions of disease which comprise sociocultural layers of meaning and often include context-specific definitions of “function” and “dysfunction.” Because of this misalignment, comparing across humans and other great apes using this approach could generate challenges. Nonetheless, taking an evolutionary perspective could be used in conjunction with definitions of pathology which include the statistical rarity of behavior, and the observation of stereotypes, especially given any individual’s known traumatic history. Because many human-specific definitions of psychopathology include a criterion of interference with daily life, applying a criterion related to function and disruption could create a useful area of overlap to compare humans and other apes.

Homologous Features in Individual Differences and Expression of Behavioral Symptoms

Although ethological research in individual differences had been conducted before the decade of the 1990s, few studies attempted to directly adapt instruments used for the assessment of individual differences to other species. King and Figueredo (1997) were among the first to hypothesize that chimpanzees would exhibit a personality structure akin to that of human participants. The authors generated a list of 43 adjectives associated with the personality traits described by the five-factor

model (i.e., conscientiousness, agreeableness, neuroticism, openness to experience, and extraversion). The factor analytical procedure not only extracted the hypothesized five personality factors but it also found a sixth dominance dimension, a trait absent, in the five-factor model of human personality (King and Figueredo 1997). Following this publication, psychometric research has consistently revealed parallels in the factorial structure of personality between human and great apes (Brüne et al. 2006).

The presence of similar, albeit not identical, personality dimensions in nonhuman primates, encouraged researchers to adapt several human self- and peer-report instruments used for the diagnosis of various psychopathologies. Researchers proceed to examine the validity, reliability, and factor structure of questionnaires employed for the assessment of personality disorders. Psychopathy inventories were developed to examine the degree of behavioral disinhibition, risk-prone, and antagonism. These measures presented adequate inter-rater reliabilities and were correlated with observed behaviors (Brüne et al. 2006). Furthermore, additional examinations of a triarchic model of psychopathy, based on dimensions such as boldness, meanness, and disinhibition, indicate these characteristics, has been found to that akin to human samples, display low to moderate heritabilities (ranging from 0.36 to 0.65; Latzman et al. 2017). Moreover, these analyses found evidence supporting the presence of a single higher order psychopathy factor, with a heritability of 0.64.

Behavioral and Psychopharmacological Interventions

Concerning treatment, studies examining the effectiveness of environmental enrichment concluded that enclosures facilitating cognitive stimulation, as well as encouraging physical activity decreases the frequency of stereotypes (Brüne et al. 2006). Similarly, behavioral intervention based on operant conditioning has also been found to decrease the frequency of regurgitation temporarily. However, there is still debate

concerning the long-term success of these procedures. In cases of regurgitation, for example, some evidence suggests this pathological behavior may reemerge months after the intervention stopped (Brüne et al. 2006). Even though compulsion, frequently observed in human patients suffering from OCD, could be hypothesized to share some features with stereotypies in nonhuman primates, it remains to be tested whether these aberrant behaviors are correlated with other manifestations of distress homologs to human psychopathologies (e.g., mood disorders or other anxiety disorders). It is relevant to notice that although most of these repetitive, functionless behaviors, have been observed in captive conditions, one must be cautioned against the oversimplification of equating “wild” with “normality” and “captive” with “pathology” (Brüne et al. 2006), particularly in light of the fact that not all captive individuals exhibit such aberrations.

Resocialization is also considered a potential avenue to assuage behavioral and affective disturbances, especially in cases where the individual grew in isolation of experienced trauma. The process can extend from weeks to months, with varying degrees of success depending on the type of pathological behavior and the temperament of the individual. Even though psychopharmacological interventions, for example, prescribing serotonin reuptake inhibitors, have been used to treat motor stereotypies, aggression, and self-mutilation, additional research is necessary to determine the level of effectiveness of these treatments. Future studies should also examine the degree to which the reduction of symptomatology is a product of each intervention or the interaction between treatments. Similarly, it remains to be seen whether these drugs produce similar side-effects, in great apes, as in humans. Some of the reported cases complemented the pharmacological treatment with behavioral interventions (Brüne et al. 2006).

Conclusions

Due to their phylogenetic proximity with modern humans, great apes had been hypothesized to display parallel manifestations of individual

differences, such as personality traits, and display similar signs of underlying pathologies. An array of methods had been employed to determine the presence of psychopathological features, from ethological observations to the adaptation of inventories. Although preliminary evidence suggests commonalities between human cognitive and behavioral disturbances, with that observed in disturbed individuals of other species, additional research is needed before concluding the presence of psychopathology. In addition to the challenges associated with diagnosis, a little research has been conducted on the efficacy of interventions such as psychopharmacological treatments have on behavioral abnormalities.

Cross-References

- [Anxiety Disorders](#)
- [Personality Disorders](#)
- [Psychopathy](#)
- [Psychopathology Versus Adaptation](#)

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Psychic Unity

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Synonyms

Cognitive universals; Human nature; Human universals

Definition

The “psychic unity” idea denotes the existence of a set of psychological and cognitive capacities universally shared by human beings and grounded in biological equality.

Introduction

The psychic unity idea assumes that all humans share cognitive and linguistic capacities that are grounded in biology and that uniformly underlie how we relate to one another and to the world we live in, regardless of differential cultural upbringing. This chapter is divided into three sections. In the first section, we detail how the idea originates in ancient Greek philosophy and how throughout the ages it has spread toward the different

sociocultural and linguistic disciplines. In the second part, we discuss how today, researchers in the cognitive, behavioral, and cultural sciences are providing a new biological foundation to the search for human universals. And in part three, we point toward current debates on the nature and tenability of the idea of a psychic unity.

History of the Concept

The psychic unity idea, or the idea that there exists an essential and uniform human nature made up of shared sensorial and reasoning capacities sometimes rendered with the notions of a “shared human nature” or “human universals,” has its roots in ancient Greek philosophy. Subsequently, it has spread throughout Western philosophical, religious, and humanist thought where it has been reinterpreted multiple times over. Common to all notions of a psychic unity is the adherence to assumptions on shared cognitive, cultural, and linguistic capacities which are contrasted from notions of particularity and relativity of such capacities.

The Philosophical Origins of the “Psychic Unity” Idea

Plato (428/427–348/347 BC) and Aristotle (384–322 BC) are among the first to argue that all beings have an essence that makes them into what they are. On their account, what makes humans “human” is their intellectual soul that enables them to reason (Gontier 2009). By making use of their reasoning skills, humans are able to distinguish truths from falsehoods, whereby falsehoods are “bad” judgments informed by the use of the senses and truths are “good” judgments that rely on the use of the intellect. At night, for example, we falsely “perceive” the objects around us as black or gray, but we “know” that in truth, they have colors. But although differences in judgment occur due to making judgments either based upon reason or upon the senses, these thinkers assume that all humans are equipped with the same reasoning and perceptual capacities enabling them to make judgments in the first place.

Early Judeo-Christian thinkers agree that all human beings are endowed with both intellectual and instinctive capacities. For them, the intellect is a divine gift, while instincts are inspired by evil. Following one's reason or one's instincts becomes a matter of "free will," and differences in judgment result from choice inspired by faith or lack thereof.

From the seventeenth century onward, rationalists such as René Descartes (1596–1650) continue to endorse that all humans share a "universal reason" that they receive from a benign god, while empiricists such as John Locke (1632–1704), George Berkeley (1685–1753), and David Hume (1711–1776) introduce the notion of a "common sense" grounded in a universal way of perceiving the world through the senses. In so far as differences in reason exist, these are now understood to be of a cultural rather than a psychological kind (Gontier 2006, 3).

The encounter of non-Western nations with different cultural traditions makes moral philosophers such as Thomas Hobbes (1588–1679), Jean-Jacques Rousseau (1712–1778), and Adam Smith (1723–1790) distinguish between an individual or natural state wherein all human beings are equal and a societal or cultural state wherein linguistic, social, economic, and political differences exist (discussed in Gontier 2009). Due to a growing awareness of natural history, differences between societies and cultures are subsequently understood as resulting from an "unequal development" of common capacities along a hypothesized gradient of stadial socio-cultural development that mimics the history of Western society, from hunter gathering over agricultural to industrial societies (Ingold 2006, 266).

Human Variation in Times of Biological Racism

In natural history studies and the early biological sciences, the encounter of non-Western cultural groups results in early attempts at explaining biological differences in terms of species variation. Carl Linnaeus (1707–1778) is one of the first scholars to divide the human species into five

varieties: "Americans," "Europeans," "Asians," "Africans," and "Monsters." For the last category, Linnaeus draws upon a combination of false mythical tales as well as more concrete reports of humans with birth defects. The first four categories are based upon variation in physical features and geographical location, as well as assumed cultural temperaments which corresponds to what we would call stereotypes (Gould 1981).

Differential psychological and cultural traits thus become understood as biologically innate. And together with the varied physical appearance of human groups and their differential geographical dispersal, these traits become a means to debate unity and variation within our species. Scholars are thereby split into two camps. Georges-Louis Leclerc, Comte de Buffon (1707–1788), Johann Blumenbach (1752–1840), and James Cowles Prichard (1786–1848) maintain that all humans share a single origin (monogenism), while Charles White (1728–1813), Christoph Meiners (1747–1810), Thomas Jefferson (1743–1826), and Georges Cuvier (1769–1832) assume that the human species can be divided into varieties or "races" that each have historical origins independent from one another (polygenism).

In this regard, Charles Darwin (1809–1882), the founder of evolution theory, claims that behavioral traits and variation thereof are the outcome of evolution and that all humans share common descent with modification (monogenesis). But Darwin (1871) also endorses the false view that human varieties can be divided into "races" with morphological, psychological, and cultural differences that Darwin (1871) differentiates "races" morphologically, by different bodily characteristics (what we today call phenotypic differences), but also psychologically, by assuming differences in mental capacities and character traits, and culturally, by assuming different levels of "civilization." He furthermore assumes that these traits can be classified along progressive scales that bear connotations as going from "inferior" to "superior"—an idea that is further developed by Ernst Haeckel (1834–1919) with his biogenetic law.

The Search for Universals in the Rising Psychological and Cultural Sciences

The biological racism of the eighteenth and nineteenth century becomes systematically countered by rising psychological and anthropological schools of thought that again reinforce the idea of a psychic or mental unity among mankind. Going back to Immanuel Kant's (1724–1804) concept of pure reason and Johann Gottfried Herder's (1744–1803) idea of historical particularism, Theodor Waitz (1821–1864), Edward B. Tylor (1832–1917), and the ethnologist Adolf Bastian (1826–1905) argue for the existence of universally shared mental capacities (cf. Shore 2000; Jahoda 2013). Bastian (1881), in particular, distinguishes *Elementargedanken* or “elementary ideas” which are universal, fundamental, and timeless psychological structures whereby all humans organize experiences, from *Völkergedanken* or “folk ideas” which are historically particular and culture-specific ideas shared only by members of the same group. The group therefore has a form of social group mind which he calls a *Gesellschaftsseele*.

Franz Boas (1856–1942), father of American Anthropology and student of Bastian, uses the idea of a psychic unity of humankind in his long battle against biological racism. Echoing Rousseau, Boas reintroduces the nature-culture divide and distinguishes between particular *cultural traditions* rooted in different histories and universal, biologically underpinned *mental endowment* brought about by biological evolution (Shore 2000, 91–92). Humans are assumed to be biologically equal in having evolved the same and universal mental capacities that enable them to become cultural beings, while particular cultural traditions result from historical particularities and contingencies.

Ideas of Psychic Unity in (Anthropological) Linguistics

Moving forward to the twentieth century, Edward Sapir (1884–1939) and Benjamin Lee Whorf (1897–1941), two linguistic anthropologists of the Boasian school, further couple the doctrine of psychic unity with ideas on cultural relativism, and they introduce the latter into the study of

language. While also retaining the idea of biological equality in psychological capacities, both Sapir (1929) and Whorf (1956) argue that the way wherein people conceptualize knowledge on the world is always relative to or even determined by the language they speak, so much so that languages underlie worldviews or specific views of the world, a view first introduced by Wilhelm von Humboldt (reviewed in Foley 1997, 197–201).

Sapir and Whorf's anthropological ideas on language also influence the general field of linguistics where, inspired by Eric Lenneberg's (1921–1975) notion of a “critical period” wherein language needs to be learned in order for it to be within the normal range, Noam Chomsky (1928–) subscribes to the existence of a biologically grounded faculty of language. This internal or I-language is characterized by a universal grammar (UG) and opposed to an external or E-language that is particular per individual and language. The former is grounded in biology and the latter in the language community where one forms part of.

In the beginning of the twentieth century, research on universal mental categories would furthermore start to include taboo concepts, kinship distinctions, color categories, etc. Regarding color categories, Brent Berlin (1936–) and Paul Kay (1934–), for example, and by continuing stage thinking and assuming the existence of ladders of complexity, famously argue that there are primary and universally shared color categories grounded in shared perception and that there is a nonrandom sequence in which cultures develop words to express these colors. Such research has nowadays evolved into the fields of folk psychology.

The Biological Foundations of the Idea of Psychic Unity

Today, we know that although humans vary phenotypically, we share the same genes, and the genetic distance between individuals, which is calculated to be 0.2%, is the same for everyone (Cavalli-Sforza 2001). In other words, genetic

differences are too minimal to divide the human species into races, and the different phenotypes we can distinguish are mere variations of the same kind of human. The neurological and cognitive sciences moreover demonstrate that all humans develop similar brain structures, and all normal individuals go through similar developmental stages.

Although there is general agreement on the fact that humans are endowed with alike cognitive structures, scholars are currently debating over which capacities are innate or instinctive and which are acquired or learned during development. On the one hand, *instructionists* maintain that our psychological and behavioral dispositions are acquired over the course of life through learning. On the other hand, *nativists* hold that both our basic physical-biological traits and our psychological structures are innate (Samet and Zaitchik 2017).

In the cognitive sciences, nativist and instructionist approaches go hand in hand with modular and anti-modular or domain-general conceptions of the mind. According to the modular or “mental organs approach,” introduced by Chomsky (1980) and further elaborated by Jerry Fodor (1983), the mind is made up of many genetically determined domain-specific modules or mental organs (Samuels 1998, 577–579; Samet and Zaitchik 2017, 7). On the other side of the spectrum, inspired by Jean Piaget, supporters of the anti-modular approach endorse that our innate cognitive capacities are general purpose (Samuels 1998, 575).

Today, from generative linguistics to universalist cognitive science, from evolutionary psychology to universalist cultural anthropology, a number of contemporary scholars work under the assumption of *evolved and therefore innate* mental competences to substantiate their universalist claims.

By drawing upon Chomsky’s work on UG, generative linguists seek to discover “the cognitive (and hence universal) foundations of language” (Haspelmath 2012, 92). In doing so, they maintain that human beings share a distinct “language faculty” or “innate specialization for language.” On this view, languages differ only

superficially from one another, while on a deeper and structural level, they share a common set of syntactic rules.

Contrary to Chomsky, Joseph Greenberg, the father of linguistic typology, maintains that the existence of linguistic universals can only be deduced from the comparative analysis of many languages. By analyzing the structure of 30 languages, Greenberg (1963) has demonstrated that there exist various types of universals, some “absolute” and some others “statistical.” Among the former, “unrestricted absolute universals” appear true of all languages (i.e., all languages have names and verbs, and all languages have vowels) and come close to the universals recognized by generative linguists (Evans and Levinson 2009, 437–438).

The idea of a psychic unity of humankind is also central to evolutionary psychology. Evolutionary psychology propounds a new “coherent framework for thinking about human nature and society” (Tooby and Cosmides 2005, 16), by maintaining that “a scientific definition of human nature” should focus on “the uniform architecture of the human mind and brain that reliably develops in every *normal human* just as do eyes, arms, a heart, and so on” (Tooby and Cosmides 1992, 209; quoted in Buller 2005, 428).

Examples are the study of *innate* or *evolved* mental competences in how we read other’s behavior (folk psychology) or how we cognitively classify biological species (folk biology). As Scott Atran (1998, 567), who studies folk biology, explains “taxonomies plausibly represent ‘modular habits’ of the mind, naturally selected to capture recurrent habits of the world relevant to hominid survival in ancestral environments.” Within this perspective, cognitive universalism and cultural particularism are ultimately reconciled: a universal system of classification is seen to underlie the development of different cultural classification systems. Evolutionary psychologists, such as David Buss, Leda Cosmides, Martin Daly, Steven Pinker, Todd Shackelford, Valerie Starratt, John Tooby, and Margo Wilson, identify human nature with the idea of a psychic unity of humankind which they define as “a set of psychological adaptations that are presumed to be

universal among, and unique to, human beings” (Downes 2018) (cf. Tooby and Cosmides 2005, 39). On this view, psychological adaptations are evolved psychological mechanisms (Starratt and Shackelford 2010, 235) or modules (reviewed in Downes 2010, 244) that originated between 1.8 million and 10,000 years ago during the Pleistocene Epoch and that helped our ancestors to deal with a number of adaptive problems (Starratt and Shackelford 2010, 231–235; cf. Downes 2018). As Starratt and Shackelford (2010, 232–238) point out, although such psychological mechanisms evolved to respond to inputs present in our ancestors’ environment and although such mechanisms are genetically hardwired and did not change over the last 10,000 years, their output is far from being “staunchly predetermined,” as our behavior is also variously influenced by the environments that we currently inhabit. Along these lines, by claiming that individual variation emerges from “a common nature” attending to different inputs or circumstances, evolutionary psychologists find a way to reconcile human diversity – whether it being cultural, linguistic, or behavioral – with the idea of a psychic unity of humankind, that is, the notion of a “universal human nature” (Buller 2005, 72).

Today, evolutionary psychologists propose various arguments for the universality of psychological mechanisms or adaptations. Among others, Cosmides and Tooby (1997) propose what David Buller dubs “the argument from *Gray’s Anatomy*” and “the argument from sexual recombination” (Buller 2005, 73). The former deduces the universality of “selection-designed psychological traits” from the universal character of “selection-designed morphological traits,” on the grounds of the fact that everything, from our bodies to our minds, has been drafted by selection (Buller 2005, 73). The latter, on the other hand, infers the universality of all complex adaptations, such as psychological adaptations, from the fact that the genetic basis of adaptation necessarily imposes “species universality” (Buller 2005, 424). Furthermore, informed by research in cultural anthropology, evolutionary psychologists reaffirm the intimate connection between the psychic unity idea and an antiracist attitude toward

the study of human behavior. As Tooby and Cosmides (1992, 38) explain “...models of a robust, universal human nature by their very character cannot participate in racist explanations of intergroup differences. (...) Human nature is everywhere the same.”

Contemporary Debate on the Idea of Psychic Unity

Contemporary claims on the existence of a psychic unity of humankind have not remained uncontested. Today, universalist theories about language, cognition, psychology, and culture face the criticisms of a number of linguists, cognitive scientists, evolutionary psychologists, as well as philosophers. Contrasting arguments about the possibility of delineating the universal traits of a supposed human nature fuel contemporary debates about the idea of psychic unity, while some universalist approaches are undergoing a massive reshaping following the emergence of new data which demonstrate the existence of considerable crosslinguistic and cross-cultural variation as well as the nonuniquely human character of some traits that were previously thought to be distinctive of our species (Everett 2013, 21).

Today, adherents of generative linguistics cautiously distinguish between a “faculty of language in the broad sense (FLB)” and a “faculty of language in the narrow sense (FLN)” (Hauser et al. 2002). On this view, whereas FLB can be found in humans and other species as well, the latter can be conceived as uniquely human (Hauser et al. 2002, 1578).

Linguistic typologists also use a more tempered language by understanding language universals as “tendencies,” rather than “strict universals” or “uncontroversial facts” (Evans and Levinson 2009, 429–431), i.e., as properties that are common to many languages and whose identification necessarily requires to be “non-aprioristic,” but based on the examination of “a sufficiently large and reasonably representative set of languages that have not influenced each other in recent times” (Haspelmath 2012, 91–99). Within linguistic typology, then language

diversity ceases to be a mere superficial appearance and becomes a fact with “long historico-cultural roots that explain the many divergences,” which should be accepted and studied as such (Evans and Levinson 2009, 432). Such diversity, as Evans and Levinson (2009, 431) notice, reveals the centrality of “cultural and technological adaptation in our species: language is a bio-cultural hybrid, a product of intensive gene-culture coevolution over perhaps the last 200,000 to 400,000 years.” In light of this, as language turns out to be not just a biological product, but also a cultural-historical artifact, language and its universal tendencies need to be studied from within “a coevolutionary model” (Evans and Levinson 2009, 446). In addition, according to scholars in linguistic typology, the acknowledgement of the importance of culture for the development of human language allows one to go beyond the threat of ethnocentrism and the limitations of nativism that appear intrinsic to the generativist approach to linguistic universals (cf. Haspelmath 2012, 99; Evans and Levinson 2009, 445).

According to Evans and Levinson (2009), the above arguments have fundamental implications for the universalist approach to cognitive research too. In their opinion, the increasing evidence of structural language differences should lead cognitive scientists to stop searching for cognitive universals in the wake of generative linguistics and to develop “a new approach to language and cognition that places diversity at center stage,” “a comparative psychology inside our own species in the central questions that drive cognitive science” (Evans and Levinson 2009, 429–432). Some cognitive scientists are already proposing such a comparative approach to cognitive research and point to the existence of cross-cultural variation to challenge nativist approaches to folk psychology and folk biology (Ravenscroft 2019).

Universalist arguments in evolutionary psychology too have not gone unopposed. David Buller (2005), Stephen Downes (2010), John Duprè (2001), David Hull (1986), and Tim Ingold (2006) have similarly argued that the evolutionary psychological notion of human nature is untenable as it conflicts with evolutionary biology and does not take human variation into consideration.

One for all, Buller (2005) puts forward five main critiques against such notion:

1. Both “the argument from sexual recombination” and “the argument from Gray’s Anatomy” that Cosmides and Tooby (1997) propose in support of the universality of psychological adaptations are unwarranted (424). According to Buller, whereas the former can be rejected on the grounds of the fact that “selection can, and frequently does, maintain polymorphism of complex adaptations within populations” (424), the latter appears unsustainable because it rests upon “a questionable analogy between anatomy and psychology,” among other things (425).
2. The notion of human nature relies on an arbitrary distinction between “normality” and “abnormality,” which finds no support in contemporary biological theories (428–438).
3. The idea of human nature is based upon an essentialist view of species, but Buller shows that species are individuals, rather than natural kinds, and hence there cannot be “species-specific psychological laws” that apply uniquely to human beings (439).
4. Buller shows that, contrary to what evolutionary psychologists hold, the existence of cultural universals does not necessarily corroborate the idea of a universal human nature consisting of psychological universals (471). This is because psychological universals are not the only possible mechanisms that lead to cultural universals. The latter could instead derive from a number of other processes (462–471). (In this regard, some of the classic examples of human universals – Jay Odenbaugh 2015 cites inbreeding avoidance and incest taboos, while Rafael Núñez 2017 refers to numerals – are demonstrably flawed: they are either too wide ranging to be uniquely human or too particular to represent universals of human nature (cf. Odenbaugh 2015, 9). Moreover, as Ingold 2006, Duprè 2001, and Núñez 2017 argue, many of such examples are fundamentally Western centric. In light of this, although the psychic unity idea has undoubtedly contributed to the affirmation of human

- equality against racist claims, such notion appears to have a fundamental “reverse ethical significance” (Job 2006), whereby it would back the West’s presumptions of superiority up by grounding human universals in Western principles and values (Ingold 2006, 262–279)).
5. For Buller, once we comprehend the true import of evolutionary theory, we will see that “our current adaptations” – whose roots evolutionary psychologists locate in the Pleistocene period – are “no more definitive of our ‘nature’ than past or future adaptations” (480) (cf. Downes 2010). In light of current evolutionary theory, it appears that our adaptations are “no more definitive of our ‘nature’ than nonuniversal adaptations and non-adaptations” (480).

Whereas Buller (2005), together with Hull (1986), Duprè (2001), Ingold (2006), and Odenbaugh (2015), remains skeptical about human nature, other scholars maintain that it is still possible to sensibly speak of human nature in biological terms (for an extensive review of some of the main arguments for and against the notion of human nature defended by evolutionary psychologists, see Downes (2018). Among others, Clark Barrett (2015) proposes to extend the evolutionary psychological notion of human nature to include human variation (reviewed in Downes 2018). Edouard Machery (2008), on the other hand, proposes a nomological notion of human nature, in opposition to an essentialist one. To Machery (2008, 322), Buller and Hull’s critiques to human nature invalidate only the essentialist notion of human nature, which has its roots in folk biology and which understands human nature as “the [distinctive] set of properties that are separately necessary and jointly sufficient for being human.” Machery (2008, 323; emphasis ours) thereby defends a nomological notion of human nature that interprets human nature as “the set of properties that humans *tend* to possess as a result of the evolution of their species.” According to Machery (2008, 328), such nomological notion, and not the essentialist one, corresponds to the idea of psychic unity espoused by evolutionary psychologists.

Both Barrett’s and Machery’s theories are not spared from criticism. Whereas Barrett’s view has been criticized for being a mere “big list of all the properties that humans have had and can have” (Downes 2018), Machery’s has been attacked for giving rise to a “far more permissive” notion of human nature than he intended, leaving us wondering whether, today, a concept of human nature is still at all useful (Lewens 2015, 78–79).

Conclusion

Over the centuries, scholars in various disciplines have contributed to refining the conceptual contours of the psychic unity idea onward and upward. In so doing, they have sometimes come to tie it with contrasting theories, such as relativist and universalist interpretations of human worldview formation. In spite of the diverse usages of the psychic unity concept, its advocates have generally agreed in regarding the existence of uniform cognitive capacities as a proof of human equality.

Contemporary accounts of human universals, whether they are cognitive, linguistic, psychological, or sociocultural, remain ideas defended by some and criticized by others in all fields, including philosophy, psychology, anthropology, and linguistics. Proponents newly back up the psychic unity idea and its inherent ethical dimension by pointing to a shared evolutionary history, similar genetic endowment, alike brain structures, and common sociocultural values. On the other hand, some scholars oppose such idea by citing the radicality of human variability, the threats of Western-centrism, the limitations of nativism, and the importance of considering gene/culture coevolution for understanding human evolutionary development.

Cross-References

- ▶ [Controversies in Evolutionary Psychology](#)
- ▶ [Cross-Cultural Universality](#)
- ▶ [Cross-Cultural Variation](#)
- ▶ [Evidence of Brain Modularity](#)
- ▶ [Genetic Predispositions](#)

- Groups and Categories
- Human Nature and Biocultural Evolution
- Individual Differences
- Language Acquisition
- Language Modularity
- Nativism
- Nature Versus Nurture
- Universal Aspects of Kinship
- Universal Grammar
- Universal Human Fears
- Why Humans Are Unique

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Psychodynamic Foundations

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Definition

Westen (1998) has defined psychodynamic theories with five postulates: (1) much of mental life is unconscious; (2) mental processes operate in parallel so that people can have conflicting feelings that motivate them in opposing ways; (3) stable personality patterns begin to form in childhood, and childhood experiences play an important role

in the developing personality, particularly in shaping social relationships; (4) mental representations of the self, others, and relationships guide people's interactions with others and influence psychological symptomatology; and (5) personality development involves learning to regulate sexual and aggressive feelings but also the move from an immature, socially dependent state to a mature, interdependent one. According to this definition, attachment theory is a psychodynamic theory. However, Bowlby explicitly demarcated his attachment theory from the drive principles.

Introduction

John Bowlby, a psychoanalyst and child psychiatrist, was interested in the close and continuous relationships – attachments – that children develop to their caregivers, the importance of children's actual experiences with their caregivers, and the potentially negative effects of early separations. Bowlby was dissatisfied with parts of the psychoanalytic metatheory, which he deemed unscientific. In particular, he could not accept the secondary drive theories that explained attachment as a secondary result of psychical energies and drives. Bowlby, who sought to reform psychoanalysis and provide a scientific theory for attachment, came to draw on evolutionary theory and ethology as well as cybernetics and cognitive psychology. The present discussion outlines the similarities and differences between attachment theory and psychoanalysis.

Psychodynamic Roots to Attachment Theory

Bowlby became interested in psychoanalysis while studying medicine at Cambridge University, and after becoming a psychoanalyst he remained a member of the British Psychoanalytical Association until his death. Bowlby thus had his roots in psychoanalysis. He also acknowledged Sigmund Freud for some of his contributions and accepted parts of the psychoanalytical metatheory; "Throughout this inquiry my frame of reference

has been that of psychoanalysis... the central concepts of my schema – object relations, separation anxiety, mourning, defence, trauma, sensitive periods in early life – are the stock-in-trade in psychoanalytical thinking” (Bowlby 1997, 1982, p. xv). Indeed, Bowlby argues at length in the first part of attachment and loss that many of his ideas are in accord with Freud’s, although formulated in modern scientific terms. Bowlby also argued that Freud – who himself reformulated important parts of psychoanalysis, treated its claims as preliminary, and sought a scientific basis for psychoanalysis – would likely have welcomed Bowlby’s ideas and scientific scrutiny.

Bowlby’s relationship with the psychoanalytic school of his time was, however, conflicted, as he viewed parts of the metatheory as unscientific. When Bowlby became a psychiatrist the British Psychoanalytical Association was territorial and ravaged with conflict. There were two main psychoanalytical schools, one revolving around Anna Freud who adhered to Sigmund Freud’s ideas and another revolving around Melanie Klein who had her own version of psychoanalysis. Despite their differences these schools nonetheless largely agreed on the basic tenets of the metatheory. In discussing psychoanalysis in relation to attachment theory, Bowlby used Rapaport and Gill’s (1959) description of the psychoanalytical metatheory as involving postulates regarding five principles: the dynamic (psychological forces), the economic (psychological energy), the structural (psychological structures), the genetic (psychological origin), and the adaptive (relationship to the environment).

Specifically, Bowlby contested the dynamic and economic, which in terms of a “psychical energy model” postulated that humans are endowed with a closed system containing distinct kinds of psychical energies that independently build up and need discharge in order to obtain homeostasis. These theories thus put a heavy emphasis on children’s drives (i.e., psychical energies), as primary motivational systems affecting psychological development through channeling of psychical energy. Along these lines it was argued that children’s attachments were a secondary result of psychical energies and feeding.

Bowlby called such theories “secondary drive theories,” and more sarcastically, “the cupboard theories of love.” Bowlby argued against the existence of any special type of energy beyond the energy of physics, deeming psychical energies as redundant. Bowlby, who thought that actual experiences with caregivers are important, sought to reform the psychoanalytic theory, the claims of which he argued should be aligned with scientific knowledge from other disciplines.

An Alternative Motivational Theory

Bowlby was part of a “third-wave” psychoanalytic school, often referred to as the British school of objects relations, and was particularly influenced by Donald Winnicott, who shared his view that children are sensitive to social interactions and in need of healthy interactions to develop well (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)). However, Bowlby thought that the other object relation theorists lacked an alternative to the instincts/drives proposed by Freud. Bowlby viewed attachment as a primary instinct/motivation and argued – drawing on evolutionary theory and ethology (i.e., imprinting and attachment behaviors in rhesus monkeys), and observations of human children’s behaviors – that the attachment system is a behavioral control system that has been retained because it served an adaptive function in our ancestral environments (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)). Specifically, Bowlby proposed that the function of the attachment system is seeking and maintaining proximity to caregivers as it has served an adaptive function for survival by protecting offspring from predators and other natural dangers (see ► [“Infant Survival”](#)). Another difference between attachment theory and psychoanalysis is thus the usage of animal data and observations of how other species respond to similar situations, regarding presence or absence of caregiver(s).

The attachment behavioral system, Bowlby argued, is open to and interacting with the environment, with attachment behaviors triggered and terminated by internal and/or external information

(e.g., changes in the environment). Bowlby argued that the better our understanding of the causal factors influencing the workings of behavior systems “the less useful the concept of drive becomes” (p. 136). With the words of Bowlby: “Termination is due not to a running down of some clockwork mechanism or to the running out of some psychical energy but to a specific signal” (Bowlby 1997, 1982, p. 94). Regarding the concept of homeostasis, Bowlby argued for a behavioral homeostasis as opposed to one based on psychical energies, and he attributed variations in the intensity and duration of attachment behaviors to variations in the activating conditions and the developmental state of the behavioral system (see ► [“Offspring–Parent Attachment”](#)).

An Alternative Method

Bowlby also sought to make the psychoanalytic theory more scientific by formulation of testable claims and usage of empirical hypothesis-driven methods for testing these claims; “There can be no doubt that if psychoanalysis is to attain full status as one of the behavioral sciences, it must add to its traditional method the tried methods of the natural sciences” (Bowlby 1997, 1982, p. 9). Psychoanalytic theory regarding children’s development was at the time largely based on reconstruction of case reports obtained from adults, which were debated in seminars. Direct observations of children were rare and theories about children’s development were thus largely based on hypotheses derived from an end product and backwards by means of historical reconstruction; “the events and processes inferred belong to a phase of life that is already passed” (Bowlby 1997, 1982, p. 3). Bowlby also argued that it was dangerous to overrate the data obtained in analytical sessions as the data (i.e., “free associations”) was likely restricted by the subject and selectively interpreted depending on the analyst’s theories.

In contrast, Bowlby advocated the usage of empirical methods, most notably careful observations of children in real-life situations, as he argued that young children’s behaviors are less restricted and thus more likely to reflect their

mental states. These observations, he proposed, should be conducted in prospective designs for forward extrapolation, wherein children’s development and the possible effects of presumed pathogens are followed over time. In Bowlby’s case, the presumed pathogen was early separations (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)).

Finally, attachment theory has a comparatively specific topical focus (i.e., on attachment) and may be understood as a “mid-level” psychological theory. In comparison, the topical focus of psychoanalysis is much broader.

Similarities Between Attachment Theory and Psychoanalysis

Bowlby accepted parts of psychoanalysis, although with some modifications (the adaptive, the structural, and the genetic). For example, Bowlby noted that many of Freud’s early ideas regarding factors causative of neurosis centered on the notion of trauma, and Bowlby perceived early separations and severely dysfunctional caregiving as potential traumatic agents. Bowlby was also, as Freud, convinced that we have psychological defenses that protect us against anxiety, but Bowlby formulated these defenses in terms of information processing and memory functions, following Dixon (1971) and Norman (1976). Instead of psychoanalytical defenses such as projection and denial, Bowlby argued for the development of cognitive-affective strategies that deal with threatening information regarding attachment (see Fonagy 1999). Specifically, Bowlby argued for two mutually dependent strategies: defensive exclusion and shifting of attention. Bowlby based defensive exclusion on the fact that organisms exclude irrelevant information to liberate processing capacity, and argued that the process of “defensive” exclusion is based on such processes, with the goal of shielding the organism from thoughts and feelings that would cause overwhelming anxiety and suffering as well as maladaptive behaviors. Shifting of attention is intimately connected to defensive exclusion and is, for example, seen when an individual shifts his/her attention away from attachment and

instead focuses on other aspects of a situation or on other persons than the attachment figure (e.g., Main 1991).

The development of psychological defenses was thought by Bowlby (e.g., 1973) to stem from early interactions with caregivers, with memories of these interactions organized as (implicit) internal working models (IWMs) of self and others. Insensitive caregiving was assumed to lead to the construction of incoherent (or multiple) IWMs whereby the later-emerging explicit layer of IWMs differ from the implicit layer. Thus, when asked about a caregiver, an adult may say that the caregiver was loving and sensitive (explicit/semantic processing) but fail to provide consonant examples (implicit/episodic processing). Bowlby argued that these defenses may be adaptive in the short run but maladaptive in the long run, as the attachment system may become deactivated or hyper-activated. Bowlby was careful to point out that the IWMs were “none other than the internal worlds of psychoanalysis seen in a new perspective” (Bowlby 1997, 1982, p. 82) and regarded psychopathology (cf. neurosis) as due to inadequate or inaccurate IWMs.

Attachment Theory and Psychoanalysis Today

As reviewed by Fonagy et al. (2008), there has been a rapprochement between attachment theory and psychoanalysis. This has several reasons. First, it has been increasingly acknowledged that the perspectives share common foundations (as Bowlby argued from the start), such as the central role given to the first object(s) (i.e., caregivers), the importance of nonconscious mental states, and the notion of psychological defenses. The rapprochement also stems from changes within the psychoanalytical field. Importantly, object relations theories (the psychoanalytical school to which Bowlby belonged) has become dominant in psychoanalysis. These theories, which are relational, share an assumption that development of subjectivity is interpersonal (cf. intersubjectivity), and hence emphasize early experiences in close relationships. Attachment

theory has been important and influential for several such theories, pertaining to both the theoretical postulates and the empirical approach advocated by attachment theorists. Indeed, psychoanalysts have increasingly accepted the need for systematic empirical examination, perhaps in part to counteract frequent charges of “pseudoscience.” The empirical approach advocated by Bowlby and other attachment theorists, and the empirical findings spurred by attachment theory, are now seen as an empirical foundation of psychoanalysis (Fonagy et al. 2008). The rapprochement was also facilitated by the linguistically based “representational” methods for examining attachment in older children, adolescents, and adults that were developed based on the concept of IWMs and their workings (Main et al. 1985). These methods ultimately opened the door to a closer examination of attachment in relation to psychoanalytical concepts, as well as to clinical usages of attachment theory with adults (Fonagy et al. 2008; Slade 1999).

Conclusion

Although Bowlby had his roots in psychoanalysis, and accepted some parts of the metatheory, there are important differences between attachment theory and psychoanalysis. Theoretically, Bowlby contested the psychical energy model which argued that children’s attachments were the secondary results of psychical energies and feeding. Bowlby instead argued that humans are endowed with a behavioral attachment control system that is activated and terminated by external and internal signals, and which has developed as it has had adaptive advantages in terms of survival in our evolutionary history. Methodologically, Bowlby also argued for scientifically formulated and testable psychological theories and usage of prospective methodology, naturalistic observations, and animal data. There has, however, been a rapprochement between attachment theory and psychoanalysis, in line with Bowlby’s quest to modernize psychoanalysis and give it an empirical foundation, as modern psychoanalytical approaches have often adopted both attachment theory and the empirical approach that Bowlby argued for.

Cross-References

- [Attachment in Adulthood](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Individual Variations in Attachment](#)
- [Infant Survival](#)
- [John Bowlby: Pioneer of Attachment Theory](#)

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Psychodynamic Theory

- [Freud's Psychoanalytic Theory](#)

Psycholinguistics

- [Pinker's \(1994\) The Language Instinct](#)
- [Steven Pinker and Language Development](#)

Psychological Altruism

- [Problem of Altruism](#)

Psychological Determinism

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Synonyms

[Bayes theorem](#); [Causation](#); [Evolution](#); [Free will](#);
[Information theory](#); [Probability](#); [Reductionism](#);
[Thermodynamics](#)

Definitions

Psychological, in this context, refers to patterns of thought and behavior across both individual and species-typical levels of description.

Determinism refers to the necessary and sufficient conditions of prior ascriptions of such patterns to the extent that they can provide causal indicators. The precise nature of what this means will be explored in more detail below.

Introduction

“Probability is the most important concept in modern science, especially as nobody has the slightest notion what it means,” so said Bertrand Russell, in 1929 (cited in Bell 1945). Chance and necessity, or, to put it differently, probability and determinism, lie at the heart of science. However, thinking about determinism is harder than it might initially appear, because thinking about probability is harder than is commonly supposed. Because scientists, naturally enough, draw on the most foundational science – namely, physics – for clarity and inspiration, it is very important to be clear about what is, and is not, implied by this, our most basic and predictively powerful science, if one wishes to understand what *determinism* could possibly mean at the levels that the behavioral sciences operate.

What is it to say that *x* caused *y*, or, perhaps, that the measurement of event *y*, was fully determined by the occurrence of cause *x*? Wilfred Sellars (1963) made a famous, and useful, distinction between the *manifest* and *scientific* images of the world. The manifest image is, essentially, the conception of things as it developed in human evolution, supplemented and clarified in various ways so as to bring it into line with modern knowledge. It thus contains such things as colors, living beings, and human relationships, together with more recent discoveries such as parliamentary democracy and fiat money. The scientific image is the modern scientific conception of the world. It thus contains such things as atoms, quarks, and the four fundamental forces.

In which of these two images – scientific or manifest – do *determinism*, and the attendant concept of *free will*, belong? Can the separate pictures be reconciled? The issue is pressing for psychologists, because elements of the scientific image – particularly those driven by particular understandings of physics – keep bleeding through from the scientific into the manifest image, allegedly rendering some concepts obsolete. There are many technical ways in which this can occur, but, broadly, these intrusions come in two varieties. They both derive from particular conceptions of the most basic and predictively powerful physical theory that humans have achieved – namely, quantum mechanics.

On the one hand, those (sometimes of a mystical bent) who think that quantum mechanics reveals a previously hidden universe of true randomness can hold out for a version of free will which owes a lot to the ancient concept of the Lucretian swerve. On this view, some events happen for (literally) no reason whatsoever, and, so the thought goes, if this sort of thing is happening in human brains – in microtubules perhaps – then humans are freed from the causal prison that the rest of the universe is trapped in.

It is not clear, however, how things happening for no reason whatsoever could lead to free choice as it features in the manifest image. In the manifest image, freedom isn't simply a pleasant feeling generated by reflections along the lines of “Hey! I'm free! So much nicer than being a robot.” Rather, free will is a concept intimately linked to the moral, legal, and social norms governing relations between individuals and the organization of society as a whole (see, e.g., Dennett 2004). It is also intimately connected to both psychological and commonsense understandings of humans as agents with intentions. To work in this way, as morally and socially foundational, choices have to meaningfully proceed from relevant personal features such as our characters and wishes, thus preserving agency. There are, in other words, reasons for our choices.

On the other hand, those who think that quantum mechanics can be interpreted in deterministic ways have been known to call for the abandonment of concepts of human free will entirely

and to (for reasons that are also not entirely clear) go on to call for the complete overhaul (or abandonment) of moral and legal systems in the light of this.

Psychology Studies That Appear to Undermine Human Agency, via Deterministic Forces

Often, this view of hard determinism, incompatible with free will, is buttressed by findings from social and neurocognitive sciences that appear to show that our human sense of free choice is demonstrably illusory. Examples abound, but the particularly popular go-to studies are of four kinds.

First are those where a person's moral sense does not prevent them from performing apparent atrocities under orders (e.g., Milgram 1963). Second are those where the sensation of an (arbitrary) choice is preceded by unconscious but measurable neural activation (e.g., Libet 1993). Then, there are experimental demonstrations of illusions of causal efficacy, when suitably pranked by a researcher (e.g., Wegner 2002). Finally, there is research into *ex post facto* rationalization – often taken to imply that so-called reason is a human conceit with no causal power.

These studies are all interesting and certainly help us understand, in sometimes excruciating and embarrassing (to a particular view of the human species) detail, the role of environmental forces, and *ex post facto* rationalizations, in human affairs. But it needs to be understood that such studies are interesting precisely *because* not all behavioral events are like them. It is because we usually, or in the case of rationality at least *sometimes*, behave in ways that make enactivist sense in our environment – sometimes emerging from a process of reasoning and education, sometimes from processes of training, that we can typically stand over and meaningfully own our actions. A brief survey of why this is, in each type of case, might be useful at this point.

Social Pressure

In the case of the social pressure studies – Milgram (1963) being the most well-known

example – it is a salutary lesson to realize that many of us can be led to do wicked things. Surprisingly little social pressure can be brought to bear to get people to carry out apparent atrocities (such as shocking an innocent stranger) against their consciences and against prior psychological predictions of the incidence of psychopathy in the population. The occasional attempts at debunking the validity of such studies (usually in terms of ecological validity or faux-naïveté of participants) are not our focus here.

History is, alas, replete with people who did not know what they were capable of, until it was too late, and perform far worse atrocities than in any social science lab experiment. And, history is neither ecologically invalid nor filled with participants only pretending to play along. The point is that not everyone succumbs to social pressure. Milgram reports (too little, alas) on some who refused to take part or who bailed early on the studies. Indeed, there is evidence that even learning about such studies makes people consider cases of obedience more thoroughly in the future. The fact that many of us are not as morally strong as our self-image proclaims is not a finding that we needed social psychology to teach us, although Milgram-style experiments should put paid to any complacent assumptions about what sorts (or nations) of people resist social pressure.

"It Was Not Me, It Was My Brain"

Libet (1985) was the first to show, via EEG, that a spreading neural activation pattern – readiness potentials – in a small brain region preceded the conscious experience of an arbitrary choice. Later studies, using fMRI technology, confirm that something like a prediction can be made to such choices, some seconds in advance of conscious experience (Soon et al. 2013). Some have concluded, from these sorts of findings, that consciousness is a mere epiphenomenon with no causal efficacy.

It is worth pointing out that some of the rhetorical work eroding free will done by such studies relies on not mentioning that these so-called predictions take hours of processing on the part of the brain scanners. This is not mere detail – a lot

of the force of such experiments in undermining a sense of agency comes from not drawing attention to such salient features.

More importantly, it is much less clear if such a dizzying loss of agency, which some report, would be felt if a decision actually mattered to the decider and could be shown to originate in a variety of coordinated brain states. As Marvin Minsky (1996) cheerfully puts it, “When someone says, ‘I just thought of something’, what they usually mean is that they just stopped thinking about that thing.” For instance, if someone points to my voting decision, as a target behavior outside of my conscious will, and traces that eventual decision to, variously, a part of my brain that processes empathy, and another part that processes arguments, another that...and so on...it is less clear that the fact of my action resulting “just from my brain” should trouble me in the slightest, in terms of agency. Where else could anyone want such a decision to issue from?

The fact that so much of the processing is unconscious should not worry anyone more than when a crossword answer just “pops” into the solver’s head after putting it aside for a while. They still solved the puzzle, in any meaningful sense. Indeed, many of the acts that are the most agentic in this sense are ones where we have trained ourselves so that our responses occur somewhat in advance of our conscious will. Emergency braking is a good example. We deliberately (and consciously) train ourselves to react without deliberation and no one seriously believes this undermines our agency.

The Illusion of Conscious Will?

Wegner produced some of the most famous of these studies of false control, where someone’s sense that an event is being controlled is pranked by the experimenter. Everyday instances of this – such as the ideomotor response that causes a pendulum swing or a Ouija board pointer to move – are familiar enough and raise the interesting point that the mere feeling (or absence of feeling) of conscious willing is neither necessary nor sufficient for causal ascription. But the existence of such phenomena are no more a general challenge to an everyday sense of control, than are optical

illusions to our sense of a generally informationally useful (which is not to say naively realist) sense of perception. Ideomotor automaticity, or the unconscious betrayal of our desires without conscious intention, is unsettling precisely because most of the time we have as much control as we need for everyday purposes. It is not clear what is to be gained by attempting to collapse complex cases into simple ones and then reading too much into the simple cases.

Well-controlled lab experiments (e.g., McConkie and Rayner 1975) that measure responses to stimuli presented with full conscious awareness, partial awareness, and absence of awareness show measurable differences in behavior. Thus, it is empirically inescapable that consciousness is no mere epiphenomenon. It is also plausible that it is not an all or nothing event but admits of degrees. Many, although by no means all, researchers are converging on a view that consciousness roughly corresponds to functionally important global access (e.g., Baars 2007).

Reasons and Causes

What is the causal efficacy of human reason? We will briefly consider two extreme versions before suggesting that a middle ground is sustainable and, furthermore, the sort of trait that could have reasonably evolved.

“One wants to be what tradition has it that Eve was when she bit the apple. Perfectly free to do otherwise. So perfectly free, in fact, that even God couldn’t tell which way she’d jump” (Fodor 2003). This is one extreme, namely, contra-causal free will that is somehow governed by reason. Such an extreme version seems to require a Cartesian separation of mind and body with all the attendant problems that has. That is one position on a continuum.

At the other extreme stands a variety of insights, from Freud onward, that a great deal of what humans produce as reason are, in fact, ex post facto *rationalizations*. That this is the case cannot be reasonably be in dispute. However, some might go further and claim that *all* reasons are of this kind and that reason acts merely as an advocate. In response to this, it should be pointed

out that this is, itself, only ever offered as a reasoned argument, intended to produce consequences in its listeners. If this, extreme, version of the rationalization argument were to be taken to its logical conclusion, then it would have the odd consequence that reasoned argument could only convince those outside of one's head, never oneself.

It is not just the circularity that means that this extreme position cannot be true. The logic here is similar to the frequency-dependent selection Umwelt that can be the only fertile ground for lying. If everyone lies, all the time, then lies could never be effective. It is only against a background of typical truth-telling that lies can function as manipulations. Similarly, if reason were only a manipulator and never had any independent force (such as appealing to checkable evidence), then it could not function in the way claimed. It is precisely because reason, at least sometimes, has independent checkability that it can have causal efficacy on others and on oneself.

Quantum Mechanics and Determinism

We noted above that our enlightened moral and legal concepts depend on personal qualities which are not generally associated with unpredictability. If anything, it is the other way round: for instance, a trustworthy person is someone who reliably delivers on her promises. So quantum indeterminism as such has no obvious bearing on the question. However, quantum mechanics is potentially relevant in other ways.

Bargh and Earp (2009) characterize the traditional concept of free will in a carefully written passage which is worth quoting in full:

Free will may be defined as an agent's ability to act on the world by its own volition, independently of purely physical (as opposed to metaphysical) causes and prior states of the world. The folk notion of free will is laden with the concept of a soul, a nonphysical, unfettered, internal source of choice-making—in other words, an uncaused causer. “The soul” may have gone out of fashion, and “the mind” taken over many of its functions and connotations, but the intuitive notion of free will has stayed much the same: there is something inside each of us that allows us to make “real” choices, choices that even

an omnipotent being, one who knew every environmental influence, and every physical fact leading up to the choice-making event, could not foretell with perfect confidence and accuracy.

Instead of complete indeterminism, the definition merely specifies that the agent's actions cannot be predicted “with perfect confidence and accuracy” – which is a much weaker requirement and one fully consistent with the concept of freedom as it features in the manifest image (consistent, in particular, with the idea that the trustworthy person, who has never let anyone down, nevertheless acts freely). The weakening of the indeterministic element is balanced by the introduction of the concepts of autonomy and spontaneity, i.e., the ability to generate choices internally, in a way which is partially (it need not be completely) independent of both the environment (autonomy) and the previous history of the individual concerned (spontaneity). From the standpoint of classical (i.e., pre-quantum) physics, this idea may seem highly implausible. But how does it seem when viewed from the standpoint of quantum mechanics?

Quantum mechanics is an extremely well-tested theory which underpins a large part of modern technology. On one level it is therefore hard to doubt. At the same time, the question, as to what the theory is actually telling us about nature, continues to be highly controversial. The reason is that while the theory makes clear and unambiguous statements about what we can expect to *observe* in a given situation (which is why we are able to test it and apply it to practical, technological problems), it is much more enigmatic about what is going on when we are *not* observing a system.

Classical physics purported to give a picture of the universe as a whole, *sub specie aeternitatis*, rather as God might be imagined to see it looking down from above: A tapestry with each particle position, and each field value, precisely specified at every moment of time. To someone attached to this picture, the observer dependence of standard quantum mechanics is deeply unsatisfactory. There have consequently been numerous attempts to fill in the gaps and construct a picture which agrees with quantum mechanics so far as the

experimental predictions are concerned while at the same time giving a description of the universe as a whole, including those bits which are not being observed. Pictures of this kind are called ontological interpretations of quantum mechanics. They include the well-known examples of Bohmian mechanics (Bohm and Hiley 1993) and the Many-Worlds Interpretation (Saunders et al. 2010). Related to this are collapse models, which make different empirical predictions from conventional quantum mechanics and which therefore, unlike ontological interpretations, are in principle empirically verifiable/falsifiable.

It may be questioned, however, whether the classical ambition is as reasonable, or even as desirable, as it may superficially seem. After all, there can be no doubt that our actual cognitive situation is that of agents embedded *in* the reality we seek to describe. In ordinary life, we are accustomed to the fact that we can only see an object from this or that particular perspective and that if we pay attention, we become aware of such details as the nose between our eyes or the spectacles through which we are looking. It may be thought that the observer dependence of quantum mechanical statements is similar to this. There accordingly exist a number of interpretations, such as the Copenhagen Interpretation (Faye 2019), in which the observer dependence of quantum mechanics, rather than being seen as a vice, is embraced as a positive virtue.

A detailed analysis of the interpretation problem would be far beyond the scope of this entry. Our aim here is simply to make a few points about the situation, as it bears on the question of psychological determinism.

The two schools of thought just identified are more-or-less evenly balanced. Schlosshauer, Kofler, and Zeilinger (2013) polled the attendees at a conference on their foundational beliefs. It might surprise non-specialists to learn that there was a roughly even split between those who did and those who did not believe that physical objects have well-defined properties prior to and independent of measurement. Related to this, a clear majority appeared to believe that an observer is *not* a complex quantum system. Of course,

science is not democratic, and physicists are as capable of error as anyone else.

It is likely that a similar poll conducted in the year 1900 would have revealed that a majority believed the Newtonian theory of gravity to be the last word on the subject. But, what these considerations do clearly reveal is the existence of some significant divergences between the actual position in physics and the position as many behavioral scientists believe it to be. In particular, those behavioral scientists who think that a human agent is a physical system like any other and therefore cannot exhibit the two properties of autonomy and spontaneity described above are basing themselves on something other than the consensus among physicists.

Dropping the idea that physics should adopt an imaginary position outside the physical fray and replacing it with the idea that physics should adopt the viewpoint of the agent herself, fully immersed in that fray, means that one is assigning some kind of distinguished position to the agent (not necessarily a distinguished *physical* position, but certainly a distinguished *conceptual* position). This has the interesting effect of undercutting all the usual arguments against free will. There are two interpretations which are particularly noteworthy in this regard, in that free will plays a central role: QBism (Fuchs 2017) and Stapp's (2011).

QBism is relevant to this issue for two other reasons. As we noted at the beginning, the free will question arises from a collision between the manifest image, where the concept of free will is of fundamental importance, and the scientific image, where the concept seems much more questionable. It is not the only such collision, another example being the problem of consciousness. The occurrence of these collisions is closely related to reductionism: One attempts to reduce all the properties of the human organism to neural firings and the like and then finds oneself left with a residue of phenomena like free will or consciousness which are certainly hard and arguably impossible to satisfactorily reduce. Fuchs (2010, 2017) has proposed, as an alternative to reductionism, an approach which might be called additivism: The idea being that, instead of trying to reduce old conceptions to new ones (as with

reductionism), one regards the new conceptions as *additions* to existing knowledge.

The situation might be compared with that of someone who has purchased a charming old farm and wants to introduce some new technology. The cheap and easy solution would be to surround the existing buildings with a collection of prefabricated sheds, thrown up any-old-how, without regard for aesthetics. But a more satisfactory solution, albeit one requiring a much greater input of time and effort, might be to try integrating the old with the new. Similarly here. Perhaps, we have been too ready to slam down the scientific image *alongside* the manifest one, as a completely independent structure. Perhaps, with more effort we could have melded the two together, to form a seamless whole.

The other reason QBism is relevant to this issue has to do with modes of inference. Determinists think of causal relationships as physically existent entities. However, as Hume (1978) noted long ago, this notion is questionable. A photograph of a murder will show the smoking gun and the victim lying on the ground, but it will not show the causal relationship between them. Of course, one is free to postulate that the cause, although it happens, like a ghost, not to reflect visible light, is still something that exists physically, out there in the world. But one is equally free to postulate that it is unphysical. Few people are tempted to think of logical connectives like “and” or “implies” as the names of actual entities. It is possible to think of causes in a way similar to this, as logical constructs playing an important role in our thinking about the world, without being a physical part of the world.

Conclusion

Similar considerations as these apply to probabilities. It is possible to adopt a frequentist or propensity interpretation, according to which a probability is a physical entity. But, it seems to many, the present authors included, that it is more reasonable to think of them in Bayesian terms, as logical constructs (Appleby 2005). This is the approach taken in QBism, which is thus able to

give a unified account of determinism and indeterminism alike. From this point of view, the only difference between a deterministic theory, like Newtonian mechanics, and an indeterministic one, like quantum mechanics, is that in the former one typically has, given sufficient control over the experimental conditions, a much higher degree of confidence in experimental outcomes.

It thus appears that one possible way through the conceptual difficulties in quantum mechanics is precisely the same as that which a growing body of mathematically minded behavioral scientists are advocating to explain causal determination in their field of research – namely, Bayesian reasoning.

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Psychological Disorder

► Personality Disorders

Psychological Evidence for Human Sperm Competition

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Synonyms

Anti-cuckoldry adaptations; Men's mating psychology

Definition

Humans have experienced sperm competition in their mating history, and men have evolved both physiological and psychological adaptations to prevent it, with the psychological ones focused on facilitating behavior toward achieving this goal.

Introduction

Sperm competition, in which sperm from more than one male are present simultaneously in a female's reproductive tract and therefore have to compete to fertilize an egg (Parker 1970), has been a recurring feature of humans' evolutionary past (Shackelford et al. 2015). Evolved psychological adaptations to avoid sperm competition are exhibited by men so that they do not suffer the costs associated with it (Shackelford et al. 2002). Specifically, as humans tend to form socially monogamous bonds, when females mate with another male other than her regular partner, the possibility arises that she may conceive offspring with the extra-pair male and trick her partner into raising genetically unrelated children (Shackelford et al. 2015). Because this can greatly reduce men's reproductive success, men's mating psychology is sensitive to female infidelity and ways of preventing or even correcting it.

Copulatory Desire Adjustment

When men are at greater sperm competition risk, it is argued that they inseminate more sperm when copulating with their partner than when they are at lesser risk (Baker and Bellis 1993). However, this is a physiological adaptation, and it could not successfully be executed without psychological adaptations to facilitate the appropriate behavioral and/or physiological response to sperm competition. Shackelford et al. (2002) proposed that, generally speaking, men would have increased copulatory desire toward their partner when they perceived a greater sperm competition risk to facilitate actual copulatory behavior.

More specifically, they found that for men who spend more time apart from their partner since the couple's most recent copulation rate their partner as more attractive, report that other men find their partner more attractive, report greater interest in copulating with their partner, and report that their partner is more interested in copulating with them. The authors thought this was due to the greater time spent apart since the couple's last copulation as time apart could be an opportunity for men's partners to copulate with other men. It is important to note that this finding was independent of total time elapsed since the couple's last copulation, which refutes the alternative explanation that men are just getting increasingly more sexually frustrated as time goes on. However, time spent apart since the couple's last copulation is not the only cue of sperm competition risk, and men are sensitive to multiple cues. This increased copulatory desire is also activated by the presence of potential rival males. Pham and Shackelford (2013) found that men whose regular partner spends more relative to less time with male friends (i.e., potential sexual rivals) express greater interest in copulating with her. Yet another cue is female attractiveness (as attractive women draw more male attention), as men who perceive their partner as particularly attractive report more desire and actual performance of in-pair copulations with her if she has a large number of male friends and coworkers (Pham et al. 2014).

Distress upon Sexual Refusal and Sexual Coercion

Another component of psychological adaptations to sperm competition is that men feel distress upon their partner's refusal of a request for copulation if they perceive themselves to be at high sperm competition risk (Pham and Shackelford 2013; Shackelford et al. 2002). When men's and women's sexual strategies are at odds with one another (known as intersexual conflict), male sexual coercion is more likely (Shackelford and Goetz 2012). Specifically, women are more interested in mating with an extra-pair male during the fertile phase of their ovulatory cycle if their

regular partner is relatively unattractive, and they are also more likely to postpone copulation with their regular partner if they actually follow through with such desires (theoretically to give the rival male an advantage in sperm competition; Shackelford et al. 2015). This conflicts with the in-pair man's reproductive goal of avoiding sperm competition, and under these circumstances, men are more likely to feel distress upon sexual refusal and subsequently coerce their partner into copulation to put their sperm into competition with that of the rival male (Shackelford and Goetz 2012).

Consistent with this reasoning, men who are at greater objective sperm competition risk are more likely to engage in sexual coercion, but only if they perceive a high likelihood that their regular partner engaged in an extra-pair copulation (McKibbin et al. 2011). Perhaps this is why men who report sexually coercing their partner are also more suspicious of her committing sexual infidelity and why women who report a greater interest in pursuing extra-pair copulations claim their partner is more sexually coercive (Goetz and Shackelford 2009).

Sexual Stimuli Preferences

Because increased and prolonged sexual arousal before ejaculation is associated with better sperm quality (Pound 2002), it is likely that men's increased sexual arousal to stimuli involving sperm competition is another psychological adaptation to increase reproductive success. Accordingly, investigations of pornographic videos and websites reveal that pornography featuring two men interacting with one woman (a scenario indicating sperm competition) is more popular than pornography featuring two women interacting with one man (a situation lacking sperm competition; Pound 2002). This finding also matches up with men's self-reported preferences (Pound 2002).

An alternative explanation unrelated to sperm competition for this preference was proposed, stating that men were reporting greater arousal from this type of pornography due to the presence of multiple and simultaneous sexual acts (e.g.,

vaginal sex, oral sex). To rule out this possibility of hypersexuality, pornography including multiple males and multiple females interacting were also included (as these should be the most super-stimulating), and the preference for the two-men and one-woman scenario remained (Pound 2002).

Conclusion

Sperm competition has had considerable influence not only on men's physiology but also on their mating psychology. It is related to men's sustained copulatory interest in a regular partner and what types of erotic stimuli they find the most arousing. Sperm competition even plays a role in morally controversial behavior, such as sexual coercion. All of these psychological adaptations work together with physiological ones to effectively reduce the chances of men's regular partner conceiving with a rival male and thus optimizing the chances of reproductive success.

Cross-References

- [Cues to Infidelity](#)
- [Infidelity](#)
- [In-Pair Copulation](#)
- [Psychological Mechanisms](#)
- [Sperm Competition Tactics](#)

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Psychological Mechanisms

- [Evidence for Modularity](#)

Psychological Reasoning

- [False Beliefs](#)

Psychologist

- [Douglas Kenrick](#)

Psychology

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Synonyms

[Moral philosophy](#); [Morality](#); [Social science](#);
[Trolley problem](#); [Trolleyology](#)

Definition

Psychology is the scientific study of the mind and its functions, including emotions and behaviors. The Trolley Problem has been used to study morality, particularly moral behavior, within psychology.

Introduction

The Trolley Problem is a moral dilemma first used by philosophers and then adopted by psychologists to examine moral thinking (Cathcart 2013). The original problem was created by Philippa Foot and involved deciding whether or not to switch a trolley that was speeding toward five people to a new track with only one person on it (i.e., whether you should sacrifice one life to save five; Foot 1967). Several variations of the Trolley Problem now exist, such as the Fat Man variant where the individual must decide whether or not to push a fat man on the tracks to save five people (Cathcart 2013).

The Psychology Behind the Trolley Problem

Psychologists have used the Trolley Problem and its variants to study the individual differences and other factors that influence moral behavior. For example, people are more likely to sacrifice one

person to save five if it involves less contact (i.e., pulling a lever versus pushing a person; Greene 2013; Singer 2005) and if they possess certain dark personality traits (Greene 2013). The characteristics of the would-be victim also influence moral decision-making, whereby younger, more closely related people, and current/potential romantic partners are less likely to be sacrificed to save the five people on the track (Bleske-Rechek et al. 2010). That people prioritize themselves, genetic relatives, younger individuals, and current or potential mates over others suggests that human moral thinking is rooted in our evolutionary history (e.g., reproductive drives; see Bleske-Rechek et al. 2010). Other evidence suggests that culture impacts moral decision-making, with people from collectivistic cultures being less likely to sacrifice one to save five than people from more individualistic cultures (Gold et al. 2014).

Conclusion

The Trolley Problem and its variants, although originally developed in the field of Philosophy, is a useful scenario for research into human behavior and can be used to investigate the psychology of moral decision-making. Moreover, these moral dilemmas can be used to test evolutionary theories surrounding aspects of human social behavior.

Cross-References

- ▶ [Fat Man, The](#)
- ▶ [Loop Variant, The](#)
- ▶ [Morality](#)
- ▶ [Philippa Foot](#)
- ▶ [Towards Methodological Pluralism in Psychological Sciences](#)
- ▶ [Trolley Problem](#)
- ▶ [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)
- ▶ [Utilitarianism](#)

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Psychology of Reciprocal Altruism

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Synonyms

[Reciprocity](#)

Definition

Different forms of reciprocal altruism – taking turns offering altruistic help – require different psychological building blocks.

Introduction

A pair of pied flycatchers busily snatch insects to bring back to their nest and feed to their young. Suddenly, an owl appears close to the nest, posing

a serious predation threat to their offspring. The pair fly straight to the owl, shrieking and dive bombing it to chase it away. A nearby pair of flycatchers detects the ruckus and also arrives to attack the predator. Another nearby pair, however, fails to help. An hour later, two owls appear, one at each of the neighboring nests. What should the original pair do? Krams et al. (2008) conducted this experiment and found that, out of 32 pairs of flycatchers, 2 stayed at the nest, 30 attacked the owl near the pair who helped them previously, and none attacked the owl near the pair who did not help them before. This willingness to pay a cost to cooperate or help another who has helped you before is called *reciprocal altruism* or *reciprocity*.

Natural selection favors genes that benefit the individual relative to others in the population. At first glance, it is unclear how altruistic cooperation could evolve since it benefits another individual at a cost to oneself. Hamilton (1964) proposed that costly acts could provide inclusive fitness benefits by helping individuals who share a proportion of your genes. Trivers (1971) removed the need for shared genes with reciprocal altruism. Trivers catalyzed the study of reciprocal altruism in his classic paper that formalized the concept, described its evolutionary preconditions, provided illustrative examples, and outlined the relevant psychological components. He proposed how natural selection could favor behavioral interactions in nonkin that yield overall net fitness benefits even if they produced immediate fitness costs. Reciprocal altruism recoups the immediate costs of altruism by emphasizing the long-term benefits of interacting repeatedly – you scratch my back, I'll scratch yours.

Trivers proposed evolutionary conditions needed for reciprocal altruism to evolve. First, the fitness benefits to the recipient of help must outweigh the costs to the cooperator. That is, after reversing roles helping has to result in a net fitness increase. Second, the probability of reciprocation must be high. Several factors may increase the probability of reciprocation, including (1) many opportunities for future altruistic situations, (2) repeated interactions with the same individuals, and (3) symmetrical exchanges in which the roles of donor and recipient reverse frequently

enough to result in roughly equal experiences at both roles.

Researchers have proposed a number of cases of reciprocal altruism across a broad range of species, from hermaphroditic worms to humans (Dugatkin 1997). Much of the data on reciprocal altruism involves correlations of altruistic behaviors between individuals. For example, vervet monkeys (*Chlorocebus pygerythrus*) are more likely to come to the aid of an individual who has previously groomed them (Seyfarth and Cheney 1984). There are, however, multiple types of reciprocal altruism. *Calculated reciprocity* involves tracking the precise actions of specific partners, along with the costs and benefits of those actions. Calculated reciprocity uses scorekeeping to ensure exact reciprocation, and this concept most closely matches the intuition behind “you scratch my back, I’ll scratch yours.” The first formal model of reciprocal altruism – tit-for-tat – is a strategy that exemplifies calculated reciprocity because cooperation is contingent on the partner’s cooperation in the last interaction (Axelrod and Hamilton 1981). Tit-for-tat strategists copy their partner’s last action: cooperate or defect (not cooperate).

Other, less precise mechanisms can also generate observed reciprocal correlations. *Attitudinal reciprocity* (Brosnan and de Waal 2002) and the similar notion of *emotional bookkeeping* (Schino and Aureli 2010) refer to situations in which altruism from a partner invokes positive attitudes/emotions toward that partner, which results in reciprocated altruism. Instead of precisely keeping track of previous actions, individuals track an overall emotional reaction to a partner. *Symmetry-based reciprocity* refers to reciprocal patterns of altruism that occur because of some symmetry in the relationship between two individuals (de Waal and Luttrell 1988). For example, if individual A and B often associate with one another but A and C rarely associate, A and B may be more likely to help each other due to their higher likelihood of interacting, whereas A and C will be less likely to help each other because they are rarely in contact. In symmetry-based reciprocity therefore, reciprocal altruism is a byproduct of some other symmetrical relationship, such as spatial proximity.

Researchers typically refer to these aforementioned types of reciprocity as cases of *direct reciprocity*, in which the reciprocal exchange occurs between two individuals. Other forms of reciprocity, however, involve more than just a pair of individuals. *Indirect reciprocity* refers to situations in which a third party tracks interactions between other individuals (Nowak and Sigmund 1998). If, for example, individual C observes that individual A helps individual B, then C would help A in a future interaction. Indirect reciprocity, therefore, uses third-party reputation rather than direct experience to reciprocate help. *Generalized reciprocity*, in contrast, does not track actions of specific partners. Donors help when they were helped in the previous interaction, irrespective of who helped them, thereby “paying it forward.” Thus, this form of reciprocity tracks only the actions of the last interaction regardless of partner (Pfeiffer et al. 2005).

These forms of reciprocal altruism have different psychological building blocks that are needed to implement reciprocal behaviors. For example, to use tit-for-tat, an individual must be able to recognize partners and remember their previous behaviors, which requires the building blocks of individual recognition and accurate memory. Understanding both cognitive and emotional building blocks is critical to the evolution of reciprocal altruism because the degree to which these building blocks are present can constrain what types of reciprocal altruism can evolve. Symmetry-based reciprocity may not require sophisticated psychological building blocks, because the reciprocity is a byproduct of other features of the relationship. Calculated reciprocity, in contrast, may require a number of building blocks to maintain the precise scorekeeping. Further, other psychological building blocks may not be required for reciprocity but may greatly facilitate its use.

Cognitive Building Blocks

Cognition refers to information processing, and cognitive building blocks are core cognitive abilities that process information. Though not all

cognitive building blocks are required for reciprocal altruism, several may be key, especially for calculated reciprocity.

Partner Identification

Reciprocal altruism involves reversing roles as donor and recipient with partners. Some mechanisms underlying reciprocity may require being able to identify partners. Both direct and indirect reciprocity, for example, require partner identification, though generalized reciprocity does not.

Individual Recognition

One cognitive building block that allows partner identification is individual recognition. Though humans take for granted the ability to recognize different individuals, other species may not be able to distinguish specific individuals from others. This may be especially true in species that do not have individually based repeated interactions, such as large swarms of invertebrates. Nevertheless, many species do recognize specific individuals. Social wasps, in particular, show remarkable abilities to use visual cues to recognize individuals: species that have complex social interactions also have highly identifiable physical features (Tibbetts and Dale 2007). Thus, the evolutionary pressures of social interactions may shape the degree of individual recognition that evolves.

Individual recognition may not be strictly required for all reciprocal interactions. Other cues such as location may act as a proxy for identity. Cleaner fish clients, for example, may return to the specific location to be serviced by the same cleaner fish (Trivers 1971). In this case, the clients do not have to recognize specific cleaners but simply remember a location.

Attributes of Payoffs

Though the ultimate currency of fitness is measured in terms of genes, animals make decisions about fitness proxies such as food, mates, predation risk, and habitat quality. Characteristics of these fitness payoffs have critical implications for processing information about them. For some payoffs, animals must be able to compare the quality of various options, or inhibit the impulse

to choose an immediately available, yet sub-optimal choice. Thus, certain cognitive building blocks are necessary to properly assess and decide between payoffs.

Quantification

Altruism involves a cost, which may require comparing two tangible fitness payoffs. These comparisons can be difficult since, across a wide range of species, large quantities are more difficult to discriminate than small quantities (Feigenson et al. 2004). In cooperative games, for example, Furlong and Opfer (2009) found that people cooperated more when the payoffs were described in U.S. cents (e.g., 300¢ vs. 500¢) compared to U.S. dollars (e.g., \$3 vs. \$5), even though the values were the same. When the values were larger and less discriminable, people cooperated more because it seemed less costly. Thus, the ability to quantify and compare the payoffs of various options can influence cooperation.

Inhibitory Control

After discriminating between fitness payoffs, individuals must choose between them. Since altruistic cooperation involves a cost and results in smaller payoffs compared to defecting, to cooperate, individuals must choose a smaller payoff over a larger one. Children and other species, however, have difficulty inhibiting a strong preference for larger rewards.

In the reverse-reward contingency task, individuals select between a small and large reward, but they must choose the smaller to receive the larger (Boysen and Berntson 1995). Young children and numerous species of primates fail at this task (Shifferman 2009), and special training is needed for them to override the strong preference for the larger payoff. Yet, the ability to forgo larger payoffs for smaller ones is exactly what altruism requires when given the choice between acting altruistically (and suffering a loss) or acting selfishly. Inhibitory control, an animal's ability to inhibit an immediately desirable response, can therefore facilitate reciprocal altruism. When fitness payoffs are presented sequentially instead of simultaneously, a lack of inhibitory control may not pose a problem for altruism.

Time Lag

By definition, reciprocal altruism involves a reversal of roles where an individual sometimes gives help and at other times receives help. In most cases of reciprocal altruism, a time lag exists between giving and receiving help. This time lag means that donors must wait before their help is reciprocated (Trivers 1971), which has critical implications for cognition because individuals may forget and have difficulty waiting for delayed payoffs.

Memory for Actions

Tracking the behavior of partners involves remembering either specific previous actions or overall summaries of actions for individuals. Tit-for-tat, for instance, requires remembering only the last action for a specific partner (Axelrod and Hamilton 1981). Though this is a rather simple memory problem for computers to solve, memory in humans and other species does not work like computer memory. Instead, natural memory systems are subject to error. Namely, they fall prey to two forms of interference: proactive and retroactive.

Proactive interference occurs when information already in memory interferes with the recall of new information. This is relevant for tit-for-tat because it requires recall of only of the last interaction with a partner. But it is possible that earlier interactions with that individual interfere with accurately recalling the most recent interaction. Retroactive interference occurs when new information interferes with the retrieval of older information. This is where the time lag between interactions becomes important, because often individuals have a number of social partners with whom they interact. Individuals likely interact with other partners between interactions with a particular partner. Therefore, these intervening interactions can interfere with accurately remembering the previous actions of a particular partner.

In a study of cooperative memory, Stevens et al. (2011) tested the impact of these two forms of interference on human memory. Though proactive interference did not impact memory, retroactive interference greatly reduced memory accuracy of previous partner actions. Increasing

both the overall number of partners as well as the number of intervening partner interactions degraded memory. Further, evolutionary simulations suggested that tit-for-tat and related strategies would have difficulty evolving with the memory errors rates demonstrated in the experiment. Thus, tit-for-tat's memory requirement of accurately recalling a partner's most recent action does not seem to match how human memory systems work. Importantly, other forms of reciprocal altruism are less subject to such memory constraints. Generalized reciprocity, for example, does not necessitate remembering what specific individuals do.

Memory for Individuals

Though calculated reciprocity requires tracking individual actions, other forms of reciprocal altruism do not. Attitudinal reciprocity and emotional bookkeeping require generating an overall impression of a partner and deciding to help based on that. Thus, rather than remembering individual actions, these forms of reciprocal altruism track a general impression of a partner, which seems much more amenable to actual memory systems (Bell and Buchner 2012).

One of the simplest forms of memory is recognition. Rather than remembering any content about an individual, recognition simply tracks whether the individual has been encountered previously. Aktipis (2006) demonstrated in a simulation that relatively simple memory strategies that simply recognized cooperators and only cooperated with individuals they recognized could maintain cooperation. So, simple recognition memory alone may allow cooperation to evolve.

In addition to recognition, individuals may remember an overall impression of a partner as a cooperator or defector. Cosmides and Tooby (1989) proposed that the costs of falling prey to defectors (cheaters) are so great that natural selection should favor individuals who can detect cheaters. Following this logic, researchers have tested whether people are better at remembering cheaters compared to cooperators, since, in general, missing out on the benefits of cooperation is not as costly as being cheated. In fact, evidence

suggests that people do have better memory for cheaters when the cheaters' misdeeds are described verbally, and this memory effect seems to be moderated by negative emotions associated with threatening information about the cheater (Bell and Buchner 2012).

In playing cooperative games against cooperators and cheaters, however, there does not seem to be a preference for remembering cheaters. Instead, people show a preference for remembering the rare type in the population (Barclay 2008). If there are many cheaters in the population, for example, remembering the cooperators provides a memory shortcut.

Patience

Another difficulty with time lags is that humans and other animals do not like to wait for delayed payoffs. Altruism requires forgoing larger, immediate payoffs, and reciprocity requires waiting to recoup the larger payoffs after a time delay. Reciprocal altruists, therefore, must be patient enough to wait for the reciprocated benefits. Waiting can be costly, however, because the future is uncertain – there is a risk that the partner might not reciprocate. This risk increases with the time delay for two reasons. First, the longer the delay, the more likely it is that something (e.g., death) interrupts the partner, preventing him/her from reciprocating. Second, the longer the delay, the more likely it is that the partner will forget to cooperate in return (see Memory for Actions). Therefore, the increased risk with time makes impatience evolutionarily rational as time delays increase.

When given choices between smaller, sooner and larger, later food options, nonhuman animals wait on the order of seconds or minutes for the delayed options, which is shorter than expected if they are maximizing the long-term rate of food intake per unit time (Hayden 2015). Humans also make short-sighted choices, preferring smaller, sooner options over larger, later ones, even when waiting provides better long-term payoffs, such as investing money in retirement funds (Frederick et al. 2002). Thus, humans and other animals have a difficult time waiting, which could constrain reciprocal strategies when long time intervals are involved.

Researchers have investigated this relationship between patience and cooperation by measuring them in the same individuals and correlating their responses. Human participants who can wait for delayed rewards also are more cooperative (Harris and Madden 2002), suggesting that patience is required for cooperation. To more directly test the effect of patience on cooperation, Stephens et al. (2002) directly manipulated patience in blue jays (*Cyanocitta cristata*) when playing a cooperative game. When the jays were experimentally induced to be more patient, they also cooperated reliably when paired with a reciprocating partner. Patience, therefore, is a key building block for reciprocal altruism.

Language

To avoid memory problems associated with the time lags inherent to reciprocal altruism, humans have evolved the ability to offload these transactions from memory onto physical objects via recordkeeping. In fact, archeologists propose that the earliest instances of symbolic writings are records of economic transactions rather than written transcriptions of language (Nissen et al. 1993). Basu et al. (2009) explored the effects of recordkeeping on individual economic behavior by demonstrating that allowing recordkeeping increases cooperative choices, reduces risky investments, and facilitates the formation of reputation in cooperative games. Thus, humans have evolved a workaround for the constraints of memory, and tracking cooperative interactions may have driven the evolution of written language.

Spoken language, though not a requirement, may greatly facilitate reciprocal altruism in a number of ways. First, it increases the precision of the altruistic exchange. In many cases, the fitness benefit and/or the time frame of a reciprocal exchange are rather abstract. Language allows more concrete exchanges because individuals can enumerate and describe benefits that may not be present at the time – for example, exchanging one goat now for 10 bushels of wheat after the harvest. It can also allow discussion of a future time frame, which is difficult to represent, otherwise. By specifying abstract concepts, language opens the possibility for formal contracts.

Language also provides a very flexible means to attempt to change the behavior of social partners through bargaining and coercion. Rather than requiring fixed exchanges, social partners can negotiate with language, describing multiple possible outcomes before settling on one. Moreover, a potential recipient can attempt to induce helping by imploring a potential donor with promises of future reciprocation or by cajoling the donor with warnings of withholding future help. The potential donor can, in turn, threaten the potential recipient with sanctions if the aid is not reciprocated. Language can allow for “cheap talk,” though; and enforcing the promises and threats can be difficult.

Language’s most powerful influence on reciprocal altruism is probably through indirect rather than direct reciprocity. Observing social interactions between others is a faster way to gain information about social partners than direct experience alone. Hearing about interactions that one did not directly observe opens the door to even more information about behaviors of social partners not witnessed by the focal individual. Thus, language greatly enhances the ability to track partner actions via gossip (Sommerfeld et al. 2007). In modern day social interactions, ratings provide an indispensable way for online sellers and buyers to trade goods for currency. With publicly visible ratings of their trustworthiness, sellers are forced to make good on their contract to provide good and services to buyers. For humans, language is an essential cognitive building block for multiple forms of reciprocal altruism.

Emotional Building Blocks

Emotional processes can also be important psychological building blocks for reciprocal altruism (Fessler and Haley 2003; Trivers 1971). In fact, attitudinal reciprocity and emotional bookkeeping critically depend on emotional building blocks. Though the emotional components are not well described for these forms of reciprocal altruism, they generally refer to a positive or negative affect directed toward individuals (Schino and Aureli 2010). These general emotional reactions are

akin to liking and disliking, and they facilitate the development of social bonds and friendships. Trivers (1971) suggested that, in humans, specific emotions may have evolved to facilitate reciprocal altruism, with different emotions associated with donating or receiving altruistic help.

Donor Emotions

Emotions experienced by donors help them detect a need for altruistic help in others and respond to instances of cheating.

Sympathy and Empathy

The first step a donor faces in an altruistic situation is to determine the degree to which a partner needs help. Sympathy and empathy are emotions that facilitate detecting partner need by attempting to understand others’ needs. Trivers (1971) suggested that these emotions motivate altruistic behavior based on need; the greater the need, the greater the sympathy or empathy. This emotional response may be necessary to overcome the cognitive impediments associated with strong preferences for maximizing current fitness payoffs for self (inhibitory control problems and impatience).

Trust and Betrayal

Donating help in a reciprocal way involves uncertainty since the partner may not reciprocate. This can occur in the time-dependent manner described previously (see Patience) or simply because the partner will choose not to reciprocate. Trust helps overcome an initial aversion to risk caused by the uncertainty associated with future reciprocation. When trust is validated by reciprocation, the level of trust will increase, and donors may be willing to accept greater altruistic costs. When trust is violated by cheating, donors experience the emotions associated with betrayal and withhold future altruism. Shackelford and Buss (1996) proposed that the emotion of trust betrayal serves two functions. First, betrayal motivates the donor to communicate the breach of trust to the partner, which may deter future cheating. Second, betrayal may prompt the donor to sever the relationship with the partner, preventing future exploitation. Betrayal can feed into the cognitive components of reciprocal altruism by highly weighting memories for

cheating by partners. Combined, trust and betrayal induce a donor to take a risk and help a partner – potentially reinforcing a strong positive relationship with that partner – but also track a partner's lack of reciprocation to minimize future cheating.

Anger and Moralistic Aggression

Though betrayal can motivate the rather mild response of communicating a breach of trust with a partner, it can also induce a stronger negative response by instigating anger or moralistic aggression. Trivers (1971) suggested that moralistic aggression protects against cheaters by (1) overriding positive emotions leading to continued altruism with that partner, (2) frightening the cheater into reciprocating, and (3) directly reducing the fitness of the cheater by injuring, exiling, or even killing him/her.

Anger can act as an honest signal of intention to punish and do harm. Sometimes the aggressive acts caused by anger seem out of proportion with the costs of cheating. If, however, there are many opportunities for future interactions, the benefits of inducing future cooperation may outweigh the costs of aggressive punishment (Trivers 1971). Moreover, anger can have strong reputational effects, such that third parties are induced to cooperate after observing or hearing about aggressive acts, even without direct experience with the angry donor. Thus, anger deters cheating in both direct and indirect reciprocity situations.

Recipient Emotions

Recipients have also evolved emotions associated with reciprocity, primarily to induce reciprocation.

Gratitude

Gratitude is appreciation for an altruistic act that serves three functions relevant to altruism (McCullough et al. 2001). First, it detects that a donor has provided a benefit to the recipient. This helps recipients track altruistic acts. Second, it motivates the recipient to pay back the altruistic debt in the future. Third, expressing gratitude toward a donor reinforces that donor's actions,

potentially increasing the likelihood of future altruistic behavior on his/her part. Trivers (1971) suggested that gratitude scales to the costs and benefits of altruism – the greater the costs and benefits, the greater the gratitude. This increases the motivation to reciprocate when the donor has accepted substantial costs or donated substantial benefits. Moreover, gratitude can overcome disliking individuals who have previously failed to reciprocate but have made amends (Trivers 1971). Gratitude, therefore, greatly facilitates reciprocal altruism by ensuring appropriately scaled reciprocation, inducing future altruism, and repairing damaged relationships.

Guilt

Guilt is the negative emotion that occurs when one has violated a moral or social standard (Kugler and Jones 1992). For reciprocal altruism, this occurs when a recipient has or is contemplating cheating rather than reciprocating. Following cheating, guilt may function to induce a cheater to correct the wrong either by immediately reciprocating or by compensating the donor in other ways (Trivers 1971). This allows the cheater to repair the relationship and avoid the long-term costs of never receiving altruistic support from the donor in the future. Anticipating the guilt associated with intended cheating also can motivate reciprocation. Guilt identifies, prevents, and repairs damage done to social partners, even if the damage was unintentional (Fessler and Haley 2003).

Conclusion

Psychology constrains the types of reciprocal altruism that can evolve, and models of reciprocal altruism without psychological constraints provide little predictive power. Species vary in what building blocks they possess, and, therefore, measuring these building blocks can focus attention on relevant types of reciprocal altruism. We cannot understand the evolution of reciprocal altruism without understanding the psychology underlying it.

Cross-References

- Alarm Calling Upon Predator Detection
- Altruism Among Nonkin
- Altruism Norms
- Altruistic Punishment and Strong Reciprocity
- Benefit Provisioning
- Benefit to Another at Cost to Self
- Blood Sharing by Vampire Bats
- Cheater Detection
- Cheater Detection Adaptations
- Coalitional Hunting
- Cooperation Among Fishes
- Cooperation Among Nonchimpanzee, Non-human primates
- Cooperation in Social Carnivores
- Cooperative Grooming
- Discounting of Future Returns
- Emotions
- Empathy in Rats
- Evolution of Cooperation
- Fairness in Primates
- Food Sharing
- Food Sharing and Nonhuman Reciprocal Altruism
- Frans De Waal
- Frans de Waal's (1982), *Chimpanzee Politics*
- Game Theory
- Helping and Genetic Relatedness
- Helping and Inclusive Fitness Benefits to Helper
- High-Cost Altruistic Helping
- Ingredients of Reciprocal Altruism
- Iterated Prisoner's Dilemma Model
- Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)
- Male Coalitions for Hunting
- Memory Enhanced for Cheaters Versus Non-cheaters
- Michael Tomasello
- Morality Is Cooperation
- Nonhuman Reciprocal Altruism
- Primate Cooperation
- Prisoner's Dilemma, The
- Reciprocal Altruism
- Reciprocal Altruism and Cooperation for Mutual Benefit
- Reciprocal Altruism and Group Living

- Reconciliation
- Repeated or Iterated Prisoner's Dilemma
- Reputation and Altruism
- Rescuing Friends and Relatives
- Rescuing Strangers
- Robert Axelrod's (1984) *The Evolution of Cooperation*
- Robert Trivers

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Psychology of the Ovulatory Cycle

► Ovulatory Shifts in Psychology

Psychoneuroimmunology

► Disease Avoidance

Psychopathology

► Personality Disorders

Psychopathology Versus Adaptation

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Synonyms

Neurodiversity

Definition

The potential reframing of psychological abnormalities and pathologies as having adaptive, evolutionary fitness-maximizing attributes.

The scientific conceptualization of psychological abnormalities and pathologies has been steadily refined through developments in cognitive science, neurobiology, and neuroendocrinology. The role that genetic and epigenetic influences play in undergirding the neural and biochemical activity that influences human cognitive development and function is now well-established in the literature. Indeed, many mental

health conditions that have typically been referred to as “diseases” or “ailments” are probably normal instances of within-species phenotypic variation with respect to differences in cognitive and affective processing and subsequent behavioral output. Rather than being disabilities, conditions such as autism, synesthesia, and even major depressive disorder – each of which have an enduring presence in the human genome – might have played a significant evolutionary role in helping to broaden and diversify the constellation of cognitive and affective traits of humankind (Reser 2011).

Furthermore, the trade-offs that accompany many of these conditions might only be considered to be disadvantages per se when considered in the light of the modern sociocultural milieu in which we currently find our species embedded. Autism and attention deficit hyperactivity disorder (ADHD) are two fulsome examples in this respect (Kapp et al. 2013). While the constrained social and interpersonal faculties that are typical of autism spectrum disorders are often highly disadvantageous to sufferers living in the modern world – globalized, socially expansive, and highly characterized by access to a massive breadth of potential social relationships – the propensity to automatically and rigidly engage in impersonal, systematic thinking might have proven highly advantageous in ancestral times, where cognition unbiased by social obligation and expectation might have conferred a level of cognitive clarity to the individual that proved highly valuable in hunting and foraging activity, environment navigation, weather pattern assessment, and so forth (Spikins et al. 2016).

Likewise, those people suffering from ADHD, though often tremendously hamstrung in many modern environmental contexts such as schooling (where the capacity for steadfastness and patience generally allow for greater ease of learning), might have, through an ancestral framing, possessed a level of unpredictability and behavioral variability that could have lent itself to maximizing evolutionary fitness (Brüne and Brüne-Cohrs 2006). A 2008 (Eisenberg et al. 2008) study of two separate tribes in Kenya found that a nomadic tribe possessing the DRD4 7R receptor gene –

which is strongly associated with ADHD, as well as novelty seeking and spontaneity – was better nourished overall than the members of a settled tribe who possessed the same allele. The authors of the study surmised that, for nomadic populations (which would have characterized ancestral humans), ADHD-like behaviors with more diffuse attentiveness might have lent themselves to greater advantages in environmental scanning and anticipation of predatory and other environmental threats (Jensen et al. 1997).

The major upshot here is that what may currently be referred to as an instance of psychopathology may in fact simply be an instance of an adaptation or byproduct whose evolutionary affordances have been blunted or attenuated due to the discordant influences of modern life. What is now considered a “disease” by the lights of modern psychological science may have been a highly advantageous trait for those possessing it during the vast majority of human history.

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Psychopathy

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Synonyms

Antisocial personality; Antisocial personality disorder (ASPD); Callous-unemotional traits; Fast life-history strategy; Sociopathy

Definition

Psychopathy is characterized by varying levels of four interrelated personality traits and behavioral tendencies: low levels of emotional reactivity (callous unemotionality, shallow affect, and boldness), glib interpersonal style (superficial charm, egocentricity, and deceitfulness), antisocial tendencies (poor behavioral control and aggression), and a parasitic lifestyle typified by impulsivity, irresponsibility, and a lack of long-term planning (Hare 2016).

Introduction

Psychopathy is of wide interest to clinicians, research psychologists, and the general public – likely as a result of human beings' vested interest in understanding (and guarding against) cheaters and social interlopers. While some unequivocally view the antisocial behavior and callous nature of psychopaths to be an obvious example of a human personality disorder (Crego and Widiger 2014), others note that these same traits can be thought of as adaptive (for the individual) inasmuch as they facilitate mining social groups for resources and opportunities (Krupp et al. 2013). A full understanding of whether psychopathy is disordered, adaptive, or neutral, is only possible after considering: (1) the way in which psychopathy manifests; (2) the development of psychopathy and whether or not it is indicative of normal

development gone awry or a suite of adaptive behaviors favored by natural selection; (3) the specific ways psychopathic traits are adaptive and confer either a survival or reproductive benefit to their carriers; and (4) whether selective forces could have favored and maintained traits associated with psychopathy across genealogical time.

Psychopathy in Context

Traditionally, psychopathy has been parsed into two distinct, yet somewhat overlapping, subtypes. *Primary psychopathy* is typified by a reduction (or absence) of social emotions, namely empathy, resulting in low emotional reactivity and a glib interpersonal style. *Secondary psychopathy*, which does not display the extreme shallow affect characteristic of primary psychopathy, is typified by impulsive actions, aggression, parasitic lifestyle, and the violation of other's rights – all of which are underpinned by callous-uncaring tendencies (Mealey 1995; Hare 2016). The uniting feature of both primary and secondary psychopathy is that both can lead to antisocial behavior and are underpinned by callous-unemotional traits.

The extreme (clinical) form of psychopathy occurs in roughly 1% of the general population, is more common among males, and is disproportionately represented among violent criminal offenders (Hare 2016). Although the concept of psychopathy initially grew out of psychiatry and clinical psychology (Crego and Widiger 2014; Mealey 1995), traits associated with psychopathy are normally distributed in the general population, often occurring at subclinical levels (e.g., Glenn et al. 2011). For this reason, it is often more useful to discuss psychopathic *traits*, which are somewhat normally distributed in the population, rather than psychopaths, who make up only a small percentage of humans. Because people with high levels of psychopathic traits tend to violate social norms, feel little to no guilt about their actions, engage in impulsive (sometimes reckless) behavior, and use deceptive charm and cunning to manipulate people to their own ends, their social strategies are necessarily short-term, often

resulting in volatile and short-lived personal and sexual relationships (Lalumière et al. 2009). Such a pattern of behavior is generally considered to be consistent with a “fast” life-history strategy that prioritizes immediate rewards over long-term stability, and employs short-term reproductive strategies focused on sexual relationships with low commitment and little to no parental investment (Glenn et al. 2011). Unsurprisingly, psychopathic traits are strongly related to low levels of agreeableness and conscientiousness, with the cardinal features of psychopathy being largely consistent across both adolescence and adulthood (Lynam and Gudonis 2005).

A Calloused Mind: How Does Psychopathy Develop?

Mealey (1995) suggested that primary psychopathic traits were predominantly the result of genetic and biological factors, whereas secondary psychopathic traits were the result of early life history experiences. This view holds that early childhood experiences serve as a relatively reliable indicator of the probable environmental conditions in adulthood. As such, it is hypothesized that early childhood experiences shift an individual's behavior to meet the demands of their environment. Negative early experiences purportedly shift an individual's behavioral tendencies to strategies that enable more successful navigation of a hostile, unpredictable environment. This would represent a “facultative,” or “contingent” shift toward a fast life-history strategy. Two decades of research have come to challenge this assumption, with two complimentary lines of evidence converging to suggest genetic and other biological factors are fundamental in mediating the expression of both primary and secondary psychopathic traits.

First, the callous-unemotional traits that underpin both primary *and* secondary psychopathy are substantially heritable, with 79% of the variance in unemotionality, and 70% of the variance in callous-uncaring tendencies being due to underlying variation in genetic factors (Henry et al. 2016), suggesting only minimal environmental impact.

Second, many characteristics commonly present among individuals who experienced negative childhood events – ineffective parenting, lower IQ, learning difficulties, higher fluctuating asymmetry, neurodevelopmental problems, etc. – are *not* found among psychopaths, making early environment an unlikely cause of psychopathic traits (Lalumière et al. 2009; Krupp et al. 2013). Given current evidence, it appears that the traits underpinning psychopathic tendencies and behaviors are largely heritable and not the result of negative childhood experience, thus calling into question why such antisocial traits would be tolerated by natural selection.

Adaptation or Disorder: Is Psychopathy and Advantage?

It is clear that psychopathic traits, and the behavioral outcomes they tend to produce, deviate from what is typical among humans. This difference, however, should not be taken as synonymous with disorder. Psychopathic traits appear to confer a selective advantage, or serve to increase Darwinian fitness, when demonstrated in the appropriate contexts. People with high levels of psychopathic traits (who we tend to think of as “true” psychopaths) rarely engage in actions that significantly harm their close kin, helping preserve their inclusive fitness (i.e., survival of close kin) (Krupp et al. 2013). Additionally, psychopaths have as many children as nonpsychopaths, and in many cases they reproduce *more* (Krupp et al. 2013). Indeed, psychopaths tend to be characterized by a unique pattern of sexuality involving early sexual debut, numerous short-term relationships, and the (false) signaling of mate-value and parental investment (Lalumière et al. 2009). Because of the obligate care-giving role that women have in rearing children, such a strategy would have been more successful (from a genetic point of view) among ancestral men than women, helping to account for the modern sex differences in psychopathic traits. That is not to say psychopathy doesn't exist among women, or that psychopathic women don't use their considerable charm and astute manipulations to beguile individuals in

their social environment (see Honey 2015; Verona and Vitale 2006). Simply put, psychopathic traits manifest differently across the sexes and likely result in differential behavioral (and genetic) outcomes. Given the advantages to the individual (at the expense of the group), the cluster of traits resulting in psychopathic tendencies has more in common with an adaptive suite of personality and behavioral predispositions than it does with a disorder in either socialization or neurodevelopment. Psychopathic individuals' tendency toward antisocial behavior, turbulent social relationships, and the harms of both on affected individuals are obviously problematic from a societal perspective. These same behaviors, however, are not inherently problematic from the standpoint of natural selection.

Callous by Design? Natural Selection and Psychopathic Traits

The exploitative and deceitful interpersonal style associated with psychopathic traits, and the subsequent lack of remorse, makes people high in psychopathy stand out among otherwise cooperative and social humans. There are two accounts for how human social groups could tolerate individuals with psychopathic traits across evolutionary time. The first holds that psychopathic traits emerge as a result of tumultuous, harsh, and unpredictable early environments, which serve to intensify underlying propensities toward callous social manipulation and result in a fast life-history strategy (see above). These traits would not be weeded out of the gene pool because they provide a selective advantage when elicited in response to these challenging environments. This account is plausible, but left unsupported by the data inasmuch as psychopathic traits are not associated with significant cognitive or developmental deficits, or abnormally adverse early life histories (Lalumière et al. 2009; Krupp et al. 2013).

The second explanation is balancing or frequency-dependent selection. Under these selection regimes, social species containing predominantly cooperative members can remain stable over time despite the presence of a small

number of habitual “cheaters” who only engage in self-interested behavior (Glenn et al. 2011). So long as cooperation is the dominant strategy, social relations in groups will remain stable, and the habitual cheaters will be able to take advantage of unsuspecting cooperators. Given the high heritability of psychopathic traits (Henry et al. 2016), and the fact that psychopathic traits confer an exploitative social advantage to their carriers (Krupp et al. 2013), balancing selection is a more likely mechanism for the maintenance of psychopathic traits in humans across evolutionary time. Additionally, psychopathic traits may become more or less common in certain human groups depending on the way various societal, geographic, and cultural milieus impact the relative success of these behavioral strategies (Glenn et al. 2011).

Conclusions

Psychopathy – characterized by charming, yet callous, unemotional, exploitative, and antagonistic interpersonal strategies, and impulsive, aggressive, and often reckless behavior – has garnered considerable attention from psychiatry, psychology, and the general public. While some may speciously consider psychopathic traits, and the social costs they impose on others, to be disordered behavior, it is more plausible that these traits are an example of an adaptive behavioral suite designed for the extraction of resources from social groups and the facilitation of short-term mating opportunities. This socially disruptive pattern of behavior has persisted in each generation because these few successful charlatans benefit from effectively cheating the predominantly cooperative human social system.

Cross-References

- ▶ [Antisocial](#)
- ▶ [Antisocial Behavior](#)
- ▶ [Sociosexuality](#)
- ▶ [Fast Versus Slow Strategies](#)

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where individuals engage in deviant, irresponsible, and egocentric behaviors, while maintaining an inability to establish successful connections with others.

Introduction

Dr. Linda Mealey, an evolutionary psychology researcher who passed away at the age of 46, contributed greatly to the scientific field through her work on psychopathy, evolution, and genetics. This chapter will discuss and review Mealey's work on psychopathy, with the majority of the chapter focused on her 1995 paper, *The Sociobiology of Sociopathy: An Integrated Evolutionary Model*.

The author will highlight psychopathy, a condition which encompasses 3–4% of the male population and less than 1% of the female population (Mealey 1995; see the Antisocial Behavior Chapter [Hashmani and Jonason 2017] for details on sex differences in antisocial behavior). Psychopaths, whether criminal or not, exhibit egocentrism, irresponsible and unpredictable behavior, impulsivity, deception, manipulation, superficial charm, and an inability to form concrete personal relationships (Mealey 1995). In 1941, Hervey Cleckley provided a list of personality-based criteria by which psychopaths could be identified (Cleckley 1941). Currently, psychopathy is assessed using an updated set of criteria – Hare's Psychopathy Checklist Revised (PCL-R; Hare 1991). Oftentimes, clinicians use the PCL-R along with the Diagnostic and Statistical Manual of Mental Disorders (5th ed.; DSM-5; American Psychiatric Association 2013) criteria when diagnosing psychopathy.

Based on Mealey's work, this chapter will begin by providing an explanation of the terminology used to understand psychopathy, while clarifying the two subcategories – *primary* and *secondary* psychopathy. Next, the author will outline six key distinctions between the aforementioned subcategories, including (1) differences in emotions experienced, (2) intellectual versus social deficits, (3) genetic versus environmental causes, (4) age that behaviors are first presented,

Psychopathy (Mealey)

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Synonyms

Antisocial personalities; Antisocial personality disorder; Sociopathy

Definition

Psychopathy is a mental disorder derived from either genetic or environmental risk factors,

(5) socioeconomic statuses, and (6) whether deviance is chronic or part of a fleeting lifestyle. Finally, the author will discuss preventative methods targeted at primary and secondary psychopathy, and suggest techniques to reduce their devastating impact on society.

Psychopaths in Society

Terminology

Clinicians, researchers, and the previous literature discuss psychopathy and its distinctions using varying terminology, portraying confusion and discrepancies across the psychological field. Such confusion results in a lack of consistency when labeling psychopathy, for instance, using the terms sociopathy, antisocial personalities, and antisocial personality disorder (ASPD) interchangeably or in replacement for psychopathy (Mealey 1995; Mealey and Kinner 2003; See the Personality Disorders Chapter [Hashmani 2018] for a detailed description of ASPD). Individual researchers may prefer one term to the other, as some may follow a categorical approach using the DSM-5 (e.g., ASPD; American Psychiatric Association 2013), while others may follow a typological approach, (e.g., a “psychopath” must have X traits, X socioeconomic status, and exhibit X behaviors, and a “sociopath” must have Y traits, Y socioeconomic status, and exhibit Y behaviors; Mealey 1995). For the purpose of consistency throughout the remainder of this chapter, the author will reserve the term “psychopath” for referring to primary and secondary psychopathic individuals and behaviors. In addition to the discrepancy regarding terminology when defining psychopaths, there is also a lack of clarity surrounding the distinctions and subcategories of such individuals. For example, in contrast to Mealey (1995) distinguishing between the subcategories of psychopathy as “primary” and “secondary” psychopaths, a portion of the literature refers to these distinctions as “simple” and “hostile” psychopaths. Thus, for the purpose of this chapter, the author will expand on Mealey’s work using the former terms.

What Is a Primary Psychopath?

According to Mealey, there are two main sub-sections/types of psychopaths – primary and secondary psychopaths. From the outside, these categories may present similarly (e.g., criminal behavior, manipulation); however, the author will outline six key distinctions throughout the following two sections. To begin, this section will examine traits of primary psychopaths, and will be contrasted in the following section by a discussion on secondary psychopaths. (1) Primary psychopaths are classified as individuals with a complete lack of social emotions. It is important to understand the two types of emotions – *primary* and *social* emotions. Primary emotions (e.g., fear, anger, disgust) are hard-wired, and directly related to survival and human evolution, while social emotions (e.g., guilt, shame, love) are more complex, cognitive interpretations of primary emotions, specific to humans (Mealey 1995). These social emotions (unlike primary emotions) are dependent on learning and socialization, and vary across cultures and individuals. Due to the fact that social emotions are not biological nor are they a prerequisite for survival, primary psychopaths are not equipped with the capacity to experience such sensations. Empathy, a common social emotion, is thought to develop through one’s theory of mind – a concept which psychopaths lack – leading to an inability to acquire this emotion (Mealey 1995, 1997; Mealey and Kinner 2003). (2) Although flawed at experiencing social emotions, primary psychopaths have no intellectual deficits, and endure pronounced social skills, an excellent ability to predict others’ behaviors, and an awareness of the discrepancy between their behaviors and societal expectations (Mealey 1995). (3) These individuals are genetically predisposed to psychopathy, and are less affected by environmental cues necessary for normal socialization and moral development – the opposite of secondary psychopaths. (4) Due to this genotype that leads them to an asocial lifestyle, primary psychopaths begin to present with deviant behaviors at an early age, since environmental risk factors (e.g., destructive social groups, poor childhood conditions) are not a requirement for the development of primary psychopathy. (5) Primary

psychopaths, due to their genetic predisposition, can come from all socioeconomic backgrounds, but in the absence of environmental risk factors, most psychopaths from the upper class will be classified as primary psychopaths. Mealey (1995) suggests that upper class children are less likely than lower class children to suffer harsh environmental conditions, and so when psychopaths come from upper class conditions, it is clear that there is a genetic predisposition rather than a poor environment contributing to psychopathy. (6) Finally, Mealey (1995) suggests that these individuals will likely present with asocial behaviors throughout their lives, since the genetic predisposition will remain constant, regardless of their environmental stressors.

What Is a Secondary Psychopath?

The above section outlined six key characteristics of primary psychopaths, which will be contrasted with secondary psychopaths. (1) Secondary psychopaths, unlike primary psychopaths, are capable of experiencing a spectrum of emotions, consisting of primary and social emotions. These individuals exhibit disruptive behaviors in the absence of emotional discrepancies; however (2), they demonstrate deficits in social skills, emotion-regulation, and problem-solving (Mealey 1995). Such deficits disadvantage children in relation to their peers, leading them to pursue alternative, destructive social groups where they can compete effectively, rather than pursuing prosocial counterparts who they may deem superior. (3) Secondary psychopaths are not equipped with a genotype that drives them towards disruptive behavior, but instead, their behavior is dependent on harsh environmental factors. Mealey (1995) suggests that children who experience events such as a disrupted family life, parental neglect, the use of punishment as opposed to rewards, and abuse have their development of appropriate social, emotional, and problem-solving skills disrupted. These children, with their poor skills, are then drawn to similarly rejected peers, leading to the formation of deviant groups, where asocial behavior is regularly reinforced, and thus, this pattern continues as a lifestyle. (4) Since a child's upbringing and social

groups are a huge factor in the development of secondary psychopathy, these individuals first present with disruptive behaviors later than their primary psychopath counterparts. (5) Due to psychopaths' poor upbringing, these individuals often come from lower socioeconomic statuses, where harsh conditions such as criminal parents, dangerous neighborhoods, and substance abuse are more common. Psychopaths from lower socioeconomic conditions are more likely to be classified as secondary psychopaths. (6) Lastly, these individuals may not exhibit chronic deviance, as their destructive goals and desires may fluctuate based on shifting life history patterns (e.g., age, statuses within groups, living situations, changing environmental contingencies; Mealey 1995, 1999).

Preventative Measures

Following a detailed review of what primary and secondary psychopathy entails, and the causes of these disruptive behaviors, the next question must examine: How can society prevent and minimize the impact of psychopathic tendencies? In order to address this question, recall that primary and secondary psychopaths present with six key distinctions, therefore, preventative measures may vary based on the individual's classification. Since primary psychopaths develop their asocial behaviors from a genetic predisposition, it is important to address their physiological arousal states, whereas for secondary psychopaths, it is important to target their environmental conditions, in an attempt to prevent psychopathic behaviors.

Primary psychopaths, with a physiotype encompassing a higher threshold for stimulation and an underlying hypoarousal condition, may require preventative measures targeted towards providing nonexploitative, thrill-seeking, and novel alternative experiences (Mealey 1995). When engaging in a disruptive act, these individuals look for a cost-benefit analysis of other alternatives in order to achieve their desired level of sensation seeking, while gaining high payoffs, and immediate gratification. If they are unable to find an alternative activity that may reap the aforementioned requirements, they may believe the disruptive act is their only option. If society were

to provide healthy alternatives that reach similar levels of stimulation and excitement, it is possible that primary psychopaths may turn to these activities instead of psychopathic behaviors. It is therefore important to ensure that positive alternatives are stimulating and rewarding enough to engage the psychopath and deter them from a similarly rewarding criminal act. Such alternatives include: stunt performing, racecar driving, and skydiving (Mealey 1995).

On the other hand, preventative methods for secondary psychopaths – individuals who are more responsive to environmental influences – should target early environmental risk factors, rather than physiological states. For example, parental training is a key intervention that may reduce the development of destructive patterns for secondary psychopaths. It is possible that asocial behaviors may be reduced, and prosocial behaviors may be reinforced by appropriate use of parental modeling, induction, and behavioral modification techniques (Mealey 1995). It is likely, however, that difficult children can elicit poor parenting, as exhausted parents may lose faith and become less effective. Mealey (1995) suggests that parents need assistance in identifying high-risk children, and instructions on how to approach such situations, which can be provided through parental training. Additionally, a second preventative strategy may be to increase the availability of rewarding, prosocial opportunities for at-risk youth from lower socioeconomic statuses. Such activities may include sports teams and extracurricular activities, where children can meet others and expand their social circles from similar at-risk youth to the general population.

Although this chapter has highlighted the contrasts between primary and secondary psychopaths, there is one preventative method that would support the reduction of asocial behaviors for both subcategories of psychopathy. Mealey (1995) suggests that when both primary and secondary psychopaths decide to engage in deception, they first and foremost take into account the past behavior of the victim (e.g., their likelihood of detecting deception or retaliating), rather than conducting a risk assessment from the fears and anxieties non-psychopaths feel in anticipation of

being caught. In order to tackle this concern, society must establish and enforce a reputation for high rates of detecting deception and a willingness to retaliate. In order to do so, Mealey (1995) recommends that society must deter crime by increasing the probability of detecting and identifying criminal behavior, while also establishing a reputation to retaliate by increasing the probability of incarceration. This strategy should effectively reduce psychopathy as a whole, since such individuals engage in disruptive actions based on the probability that they will not get caught or be retaliated against.

Conclusion

This chapter approached the topic of psychopathy from the evolutionary perspective of Dr. Linda Mealey's work. Psychopaths are individuals who present with deviant, irresponsible and egocentric behaviors, while engaging in asocial activities, such as criminal acts, deception, manipulation, and impulsivity. This chapter strives to provide an awareness of psychopathy and its causes, in order to facilitate treatment and preventative methods to reduce such behaviors. In doing so, the author began by providing clarification on the different terms associated with psychopathy, while defining the two subcategories – primary and secondary psychopathy. Next, the author discussed six key distinctions between these two subcategories (e.g., emotions experienced, genetic versus environmental causes, socioeconomic statuses) in an attempt to assist society in distinguishing between these deviant individuals. Finally, this chapter aimed to shine light on preventative measures that society can take in order to minimize the impact of these behaviors, such as providing stimulating alternatives to crime, early parental interventions, and increasing society's willingness to retaliate. By increasing our knowledge on psychopathy and strengthening the ability to differentiate between primary and secondary psychopaths, the hope of this chapter is to effectively target psychopathic behaviors and reduce their effect on society.

Cross-References

- [Antisocial Behavior](#)
- [Personality Disorders](#)

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Psychophysics

- [Cognitive Science](#)

Psychoses

- [Psychosis](#)

Psychosis

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Synonyms

[Psychoses](#); [Psychotic](#)

Definition

An absence of, or break in, reality contact.

Introduction

The term psychosis is used to refer to a severe form of mental illness which may include characteristic symptoms such as hallucination, delusions, and both thought and behavioral abnormalities. Diagnostically, psychosis is a primary aspect of psychiatric disorders including Schizophrenia and Delusional Disorder. Psychosis may result from various etiologies.

Psychosis

In general, psychosis denotes “a mental state characterized by a loss of contact with reality” (Klieger and Khadivi 2015, p. 9). Psychosis can be defined narrowly, in the case of the presentation of hallucinations and delusions, or more broadly as related to thought and behavioral abnormalities (Cardinal and Bullmore 2011). Historically, the term psychosis evolved a great deal, originally utilized to replace more stigmatizing terminology, then to refer to any form of serious mental illness, and currently as a reference to specific symptoms and expressed abnormalities in thought and behavior (McCarthy Jones 2015). Psychoanalytically, Sigmund Freud distinguished between neurosis and psychosis, theorizing that

psychosis represented a complete collapse of ego functioning.

According to the ICD-10 Classification of Mental and Behavioral Disorders (1992), psychosis refers to “the presence of hallucinations, delusions, or a limited number of severe abnormalities of behaviour, such as gross excitement and overactivity, marked psychomotor retardation, and catatonic behaviour” (p. 10). Diagnostically, psychotic disorders involve abnormalities in one or more areas including hallucinations, delusions, disorganized thinking, disorganized or abnormal motor behavior, and negative symptoms (American Psychiatric Association 2013). Hallucinations are defined as “perception-like experiences that occur without external stimulus” (American Psychiatric Association 2013, p. 87). Hallucination can occur through any of the five senses, with the most common being auditory and visual. Delusions are fixed beliefs that are unable to be dissuaded despite contradictory evidence (Minzenberg et al. 2008). Disorganized thinking, typically observed through an individual’s speech, may involve a variety of abnormalities including derailment or loose associations, tangentiality, or incoherence (American Psychiatric Association 2013). Disorganized or abnormal motor behavior may include catatonia, “repeated stereotyped movements, staring, grimacing, mutism, and the echoing of speech” (American Psychiatric Association 2013, p. 88). Negative symptoms represent an absence or restriction in typical cognitive and emotional functioning and/or expression and may include flat affect, deficits in communication, anhedonia, avolition, apathy, and asociality (Möller 2007). Disorders included in the DSM-5 (2013) classification *Schizophrenia and other Psychotic Disorders* include Schizophrenia, Delusional Disorder, Brief Psychotic Disorder, Schizophreniform Disorder, Schizoaffective Disorder, and Schizotypal Personality Disorder. Other diagnosed conditions such as major depressive disorder, bipolar disorder, and borderline personality disorder may also present with symptoms of psychosis.

Numerous organic and environmental etiologies have been identified for psychosis. Organic causes may include psychiatric illness described

above; neurological disorders or disease such as a cerebrovascular accident (CVA); delirium; endocrine disease, such as hypothyroidism; as well as immune and autoimmune disorders (Cardinal and Bullmore 2011). Environmentally, psychosis may result from severe stress, trauma, forms of deprivation, as well as the product of specific recreational and toxic substances (Cardinal and Bullmore 2011).

Conclusion

Psychosis is a form of severe mental illness that may present as altered perceptual experiences (hallucinations), irrational beliefs (delusions), thought and/or behavioral abnormalities, or negative symptoms including deficits in communication, socialization, and expression of affect. Psychosis may be present in various psychiatric conditions, organic illnesses, or as the result of environmental etiologies stress, trauma, or specific substance use.

Cross-References

- [Mental Illness](#)
- [Psychopathology](#)

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Psychotic

► Psychosis

Puberty

- Early Childhood and Adolescence
 - Fertility
 - Sexual and Reproductive Development
-

Puberty in Boys

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Synonyms

Development; Gonadarche; Maturation

Definition

“Stage of development during which secondary sexual characteristics appear and there is a transition from the sexually immature to the sexually mature stage” (Rosenfield et al. 2008, 531).

Introduction

Puberty is a critical period in an individual’s life history, characterized by the appearance of

secondary sexual characteristics and gonadal maturation, ultimately resulting in the ability to reproduce. This transition spans several domains, affecting growth, body composition, metabolism, reproductive function, and psychological development.

Aberrant pubertal timing and/or progression may herald underlying pathology and has the potential to cause significant psychosocial distress. However, it is important to note that there is a large natural variability in the onset and progression of pubertal maturation with some individuals maturing earlier or later or more rapidly or slowly than others. Although within the statistically normal range, earlier or later pubertal maturation may greatly affect an adolescent’s psychosocial development.

Puberty: Regulation, Variability and Pathology

The onset of puberty is closely regulated by an intricate network of neuroendocrine signals. Gonadotropin-releasing hormone (GnRH) produced in the hypothalamus acts on the pituitary gland to stimulate the release of gonadotropins, luteinizing hormone (LH) and follicle-stimulating hormone (FSH).

Luteinizing hormone is responsible for stimulating the testicles to produce testosterone, which travels to target organs to induce virilization and changes in body composition, bone density, and growth. Testosterone also acts indirectly to regulate its own secretion through peripheral conversion to estradiol, which, in turn, suppresses GnRH and gonadotropin secretion (Navarro 2012). Unlike LH or testosterone, FSH acts within the testicles to stimulate enlargement of seminiferous tubules and promote spermatogenesis, thereby inducing testicular enlargement (Abreu and Kaiser 2016).

The mechanism underlying pubertal induction was largely unknown until the 1960s. At that time, it was attributed to reduced sensitivity of a “gonadostat” to the negative feedback exerted by sex hormones. It is now widely accepted that pubertal onset is triggered by changes in the

frequency of GnRH pulses driven by the hypothalamic GnRH pulse generator (Rosenfield et al. 2008).

Subsequent discoveries have shed light on a complex network of integrated neuroendocrine signals that closely regulate puberty. These include proteins such as MKRN3, NKB, and kisspeptin, which mediate puberty via effects on hypothalamic GnRH secretion leading to downstream effects on gonadotropin and testosterone secretion (Navarro 2012; Abreu and Kaiser 2016).

This so-called hypothalamic-pituitary-gonadal (HPG) axis is active well before adolescence, both in utero and shortly after birth, during a period termed the “mini-puberty.” This is followed by the juvenile pause, a quiescent period characterized by small, irregular, widely spaced GnRH pulses and low gonadotropin levels (Sisk and Foster 2004). During late childhood, before physical evidence of pubertal maturation emerges, integrated inputs lead to a reactivation of the GnRH pulse generator. GnRH pulses increase in both amplitude and frequency as sensitivity to sex steroid decreases. This results in increased pulsatility at night with waxing and waning levels of gonadotropins and sex steroids during the day. As time progresses, GnRH pulses become more consistent, resulting in less variability in the level of sex steroids throughout the day. Interestingly, testosterone maintains a diurnal pattern with levels peaking in the morning and declining throughout the day but becomes less pronounced as maturation continues (Fuqua and Rogol 2013b).

Like testosterone, other hormones produced within the testes fluctuate during different phases of maturation. Anti-Müllerian hormone (AMH), for example, declines at the time of puberty as testosterone levels increase (Aksiglaede et al. 2010) but may remain high in boys with delayed puberty. On the other hand, AMH levels are low in gonadotropin deficiency and in patients with testicular dysfunction (Edelsztein et al. 2016). As with AMH, inhibin B is a glycoprotein produced within the testicles. It reflects testicular function via its feedback on the pituitary gland and effects on FSH secretion.

A comprehensive history and physical examination are critical for evaluating pubertal onset

and progression. When assessing pubertal maturation, it is important to differentiate pubarche from gonadarche. Pubarche refers to the development of pubic hair, which occurs in males at a mean age of 12 years, either before or after gonadarche. Gonadarche typically occurs at a mean age of 10 years. It may be identified clinically when testicular volume reaches >3 mLs, as assessed by a Prader orchidometer, a set of ellipsoid beads of known volume used to measure an individual’s testicular size. Pubertal stage is determined using a system developed by Marshall and Tanner in 1970, which incorporates age ranges at various stages of maturation (Marshall and Tanner 1970).

An accurate measurement of height is critical to a comprehensive physical assessment. Review of a child’s growth chart provides valuable insight into their pubertal maturation. The pubertal growth spurt is comprised of three phases. The first phase occurs prior to the onset of puberty and is characterized by a slight decline in the rate of height gain. This is followed by the most rapid growth or peak height velocity (PHV), which approximates 9.5 cm per year and occurs in mid to late puberty at a mean age of 13.5 years (Tanner and Davies 1985). Growth then slows significantly before fusion of the growth plates occurs and growth is complete.

Failure to demonstrate appropriate pubertal growth should raise suspicion for delayed puberty, defined as lack of testicular enlargement by age 14, and should prompt referral to a pediatric endocrinologist. However, children often present to medical attention well before they reach 14 years of age due to lack of secondary sexual characteristics or psychosocial concerns related to short stature and delayed development and their effects on quality of life.

Sports are often a major focus of preadolescent and adolescent males. It is at this time that there may be the greatest difference in size, strength, and power because of the physiologic alterations in pubertal maturation. Many small/slight boys know the distress of not being able to compete or being chosen “last” in pick-up games. Organized sports, except for those based on weight classifications (e.g., wrestling), are often formed

around age group categories. To paraphrase Dr. James Tanner (of the Tanner stages defining pubertal maturation and progression)...“to tell me that a boy is 14 years old is hopelessly vague” – is he a boy of 14, for example, with constitutional delay of growth and puberty or is he an emerging adolescent, virtually fully mature.

Young athletes are usually grouped by calendar age when considered for training or competition purposes. However, as noted above, it is well-known that youth of similar chronological age may differ greatly in biological maturity. A 14-year-old male may be completely prepubertal, but a 12-year-old may be fully mature with concomitantly much greater height, weight, and strength. Individual differences in growth and maturity may lead not only to competitive inequality but also to increased risk for injury due to overuse of structures (e.g., joints) not optimized for the training load or due to contact or collisions between athletes of vastly different body mass.

Bio-banding or the grouping of children based on physical attributes rather than chronological age is actually not a new concept – in the early twentieth century, for example, the development of pubic hair was considered an outward sign of readiness to do *adult* work (Cumming et al. 2017).

Bio-banding groups young athletes by maturity status, which may be based on secondary sexual characteristics (still subjective, in part, by physical examination), skeletal age (with the vagaries of standards and subjective interpretation) or by the percentage of predicted adult stature (estimate of maturity status), and the maturity offset (estimate of maturity timing, using peak height velocity as an estimate of status – either pre- or post-PHV, a reliable biological anchor of growth and maturation) (Malina and Cumming 2004).

Emerging evidence suggests that bio-banding, as an adjunct to age group competitions, can benefit both early and late maturers (Cumming et al. 2017). For a more complete discussion of this concept including some of the physical and psychological considerations, see Edge: Growth and Maturation <http://edge-growth-maturation.net.technion.ac.il/>.

When evaluating a child with delayed puberty, it is important to distinguish those with true pathology from those with “late blooming” or constitutional delay of growth and puberty (CDGP). Constitutional delay of growth and puberty is characterized by a *delay* in the timing and potentially tempo of maturation. Height velocity may appear slow as affected children continue to grow at a prepubertal rate as opposed to peers undergoing their pubertal growth spurt. Evaluation should include determination of a child’s bone age, as assessed by a radiograph of the left hand, which appears younger than chronological age (Styne and Grumbach 2016). When plotted against bone age rather than chronological age, the height of a child with CDGP appears normal and more consistent with parental heights. A family history of late blooming is not uncommon, and children often reach their genetic potential *without* intervention. Spontaneous puberty occurs by 18 years of age; however, testosterone therapy has the potential to reduce the psychosocial distress that frequently accompanies delayed puberty.

Although some studies have shown little effect of CDGP on psychosocial well-being (Zhu and Chan 2017), others demonstrate an association with poor psychological outcomes. In fact, many of these negative outcomes persist into adolescence and young adulthood. The Oakland Growth Study, for example, found that late-maturing boys were not only perceived as less mature and less attractive than peers but also had more feelings of inadequacy, which persisted into adulthood (Fuqua and Rogol 2013). Delayed pubertal timing has also been associated with higher rates of depression, anxiety, and substance use in adolescence and young adulthood. Academic achievement may be adversely affected as well (Zhu and Chan 2017).

Unlike CDGP, in which pubertal onset occurs spontaneously, delayed puberty may also occur in those with permanent hypogonadism, caused by failure to produce sufficient levels of testosterone, sperm, or both (Basaria 2014). Hypogonadism may be subdivided into hypo- or hypergonadotropic hypogonadism. Hypogonadotropic hypogonadism, also known as secondary

hypogonadism, occurs when there is a defect in the production or secretion of FSH and LH, resulting in small testicular size, insufficient sperm production, and low testosterone levels. Low testosterone may also occur in testicular dysfunction. Lack of feedback at the level of the pituitary gland results in elevated gonadotropin levels, leading to hypergonadotropic hypogonadism or primary hypogonadism.

Hypogonadotropic hypogonadism may occur in a variety of settings. It may develop in children with traumatic brain injury or other disorders of the CNS. Given that gonadotropins are produced within the pituitary gland, hypogonadotropic hypogonadism may be detected in hypopituitarism with multiple pituitary hormone deficiencies or in the absence of pituitary dysfunction, an entity termed isolated hypogonadotropic hypogonadism (IHH). Isolated hypogonadotropic hypogonadism is a heterogeneous disorder, characterized by insufficient production of FSH and LH resulting in a low testosterone state. Some feel that it may fall on a spectrum of delayed maturation, opposite from CDGP. Table 1 outlines notable distinctions between IHH and CDGP.

The term Kallmann syndrome is applied when IHH is associated with a defective sense of smell. It results from abnormal embryonic migration of

GnRH neurons from their origin in the olfactory placode to the hypothalamus, leading to both hypogonadism and anosmia. Normosmic IHH is thought to be due to a defect in one of the many genes involved in the regulation of GnRH secretion, such as those coding for kisspeptin, kisspeptin receptor, neurokinin B, leptin, or leptin receptor. Leptin is a cytokine produced by white adipose tissue that regulates satiety and conveys metabolic status to the CNS. Children with a defect in either leptin or its receptor develop severe hyperphagia and early-onset obesity and fail to enter puberty appropriately. Interestingly, maturation ensues with leptin replacement therapy, highlighting its role in both puberty (Farooqi and O’Rahilly 2005) and metabolism. As seen in females with calorie restriction, males also experience hypogonadotropic hypogonadism in response to relative energy deficiency, potentially due to alterations in leptin signaling (Fuqua and Rogol 2013a).

Hypogonadism associated with elevated gonadotropin levels (hypergonadotropic hypogonadism) may be detected in a variety of disorders, most notably Klinefelter syndrome. Klinefelter syndrome occurs in 1/500–1/1000 males and is the result of meiotic nondisjunction, resulting in excess X chromosomal material, most often 47, XXY. Classic features include tall

Puberty in Boys, Table 1 Clinical and laboratory findings in IHH and CDGP

Feature	IHH	CDGP
Hormonal profiling during “mini-puberty” at 4–8 weeks of life	Lack of appropriate rise in LH and testosterone	Elevated LH and testosterone levels
Pubertal onset	Absent or pubertal arrest (less common)	Delayed; spontaneous progressive maturation by age 18
Puberty pattern	Absent or arrested gonadarche	Delayed pubarche and gonadarche
Growth	Prepubertal growth; +/- euchanoidal proportions (delayed growth plate fusion)	Normal growth for bone age
FH of delayed puberty	+/-	+/-
Sense of smell	+/- anosmia (30–50%)	Normal
Testicular size	Small testes (1–2 mL); +/- history of cryptorchidism	Normal for bone age
Stretched penile length	+/- micropenis	Normal for bone age
Possible associations	Bilateral synkinesis (mirror movements), dental agenesis, renal anomalies, hearing impairment, midline defects (cleft lip/palate)	None

stature, behavioral disorders, motor dysfunction and mild-to-moderate deficits in language-based skills, and attention and auditory processing (Wosnitzer and Paduch 2013). The vast majority of males who are diagnosed postnatally present with developmental concerns (Visootsak et al. 2013) long before delayed puberty is detected. Parents often become concerned about their child’s development before children come to the attention of pediatricians, neurologists, and psychologists leading to a 2–5-year delay in diagnosis.

Appropriate care for individuals with Klinefelter syndrome should be multidisciplinary, as affected individuals require both medical and mental health services through every stage of their lives. Many children have ADHD, and up to 86% require special education services (Close et al. 2015). Furthermore, many children report poor quality of life, and it is estimated that nearly 70% of adults experience depressive symptoms (Close et al. 2015). The exact cause of the neurocognitive and psychosocial disorders that often accompany Klinefelter syndrome is unknown, though some speculate that the lack of androgen effect on early brain development may play a role. In fact, androgen therapy has been shown to improve visual-motor performance, anxiety/depression, and social functioning when administered to prepubertal boys (Ross et al. 2017). However, testosterone treatment is not typically initiated until early adolescence when pubertal arrest occurs.

Hypergonadotropic hypogonadism may also be detected in children with a history of malignancy arising from radiation directed to the gonads or pelvis or exposure to chemotherapy. Alkylating agents in particular have the highest rates of gonadal injury. Given the potential effects on future fertility and psychological implications, it is recommended that individuals undergoing cancer treatment be counseled on the risks of infertility and potential for fertility preservation prior to the onset of treatment (Rose et al. 2016).

Testosterone may be used in the treatment of boys with delayed or absent puberty to induce virilization, enhance linear growth, promote bone health, and improve psychosocial well-

being. A relatively low starting dose is used in young children with gradually escalating doses over approximately 24 months to mimic natural puberty. This allows for development of secondary sexual features while maximizing linear growth. It is important to note, however, that testosterone therapy does not improve fertility or stimulate testicular growth. Evidence of testicular enlargement during testosterone therapy suggests a diagnosis of CDGP or reversal of IHH (Boehm et al. 2015). Side effects occur rarely and include acne, gynecomastia, aggressiveness, dyslipidemia, and polycythemia.

As with delayed puberty, puberty that occurs too early may also have psychosocial implications. Precocious puberty is seen much less frequently in males than in females and is defined as maturation that occurs before the age of 9 (Herman-Giddens et al. 2001; Abreu and Kaiser 2016). It may be the result of a gonadotropin-dependent or gonadotropin-independent process. Gonadotropin-dependent precocious puberty may arise from a variety of CNS disorders, such as tumors, cerebral palsy, or traumatic brain injury. Table 2 lists potential causes of gonadotropin-dependent and gonadotropin-independent precocious puberty. In up to 50% of cases, however, no identifiable etiology is discovered. A portion of these cases may involve dysregulation within the complex network that regulates puberty. In fact, whole

Puberty in Boys, Table 2 Causes of gonadotropin-dependent (central) and gonadotropin-independent (peripheral) precocious puberty

Gonadotropin-dependent	Gonadotropin-independent
Genetic disorders	Genetic disorders (familial male-limited precocious puberty, McCune-Albright syndrome)
Previous exposure to chronic sex steroids	Severe chronic hypothyroidism (Van Wyk-Grumbach syndrome)
Tumors (hypothalamic hamartoma, optic gliomas)	Tumors (adrenal or testicular)
CNS malformations	
CNS infections/inflammation	

exome sequencing of several families with gonadotropin-dependent precocious puberty led to the discovery of MKRN3 (Abreu et al. 2013), a protein thought to play an important role in the inhibition of puberty (Macedo et al. 2014). The MKRN3 gene is maternally imprinted; thus mutations that alter protein function are paternally inherited and associated with precocious puberty in both males and females. While there are several studies on the psychosocial effects of female precocious puberty, data in males is limited.

Conclusion

Puberty is a unique period characterized by the development of secondary sexual characteristics, ultimately culminating in the ability to reproduce (Rosenfield et al. 2008). This critical transition impacts not only physical appearance but also social and psychological well-being (Zhu and Chan 2017).

Puberty is regulated by a complex network of neuroendocrine pathways with natural variability in onset (timing) and progression (tempo). Early or late puberty may indicate underlying pathology and has the potential to cause significant psychosocial distress. In fact, individuals with pubertal disorders frequently come to medical attention as a result of psychological or neurocognitive rather than pubertal concerns.

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Puberty in Girls

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Synonyms

Adolescence; Menarche; Reproductive maturation

Definition

Puberty in girls involves the maturation of the endocrine system resulting in the achievement of adult body size and proportions, secondary sexual characteristics, and development of the reproductive organs resulting in the capacity to reproduce.

Introduction

Puberty is a significant life history event marking the end of the prereproductive, juvenile phase of development, and entry into adulthood and reproductive life. Its characteristics, sequelae, and timing differ across species and between the sexes. Puberty in human females exhibits consistencies with the development of other mammals and primates, but unique qualities as well. Because puberty in girls is associated with a host of reproductive, medical, mental, and social changes, it has been the research focus of human biologists, physicians, psychologists, anthropologists, sociologists, demographers, and epidemiologists alike. Evolutionary theories and concepts, including life history theory, sexual selection, reproductive strategies, mate choice, conditional and alternative strategies, and parent-offspring conflict offer means to organize and synthesize the plethora of findings regarding puberty in girls.

Development and Puberty Within a Life History Approach

Development has been shaped by a long process of natural selection acting upon the developmental trajectories of individuals, resulting in species-specific life histories. Energetic resources available to organisms are finite and life history theory describes how fitness is optimized in different species through the nonrandom allocation of resources to maintenance, growth, and reproduction (Roff 2002; Stearns 1992). Typical life history traits include size at birth, growth pattern, age of sexual maturation, size at maturity, age of first reproduction, number and sex ratio of offspring, age- and size-specific reproductive investments and mortality schedules, and length of lifespan. Life history theory predicts trade-offs between energetic investment in growth, maintenance, and reproduction. Such adaptive patterns of allocation are referred to as life history strategies, whereas reproductive strategies describe the differential allocation of resources to mating and parental effort. Life history traits vary as a function of phylogenetic constraints and the different environmental selective pressures acting on male and female members of a species over their evolutionary history. From this perspective, puberty is envisaged as set of developmental processes nested within the overall species-specific human life history. As such its timing and characteristics are phylogenetically constrained, sexually differentiated, and intrinsically associated with other human life history traits.

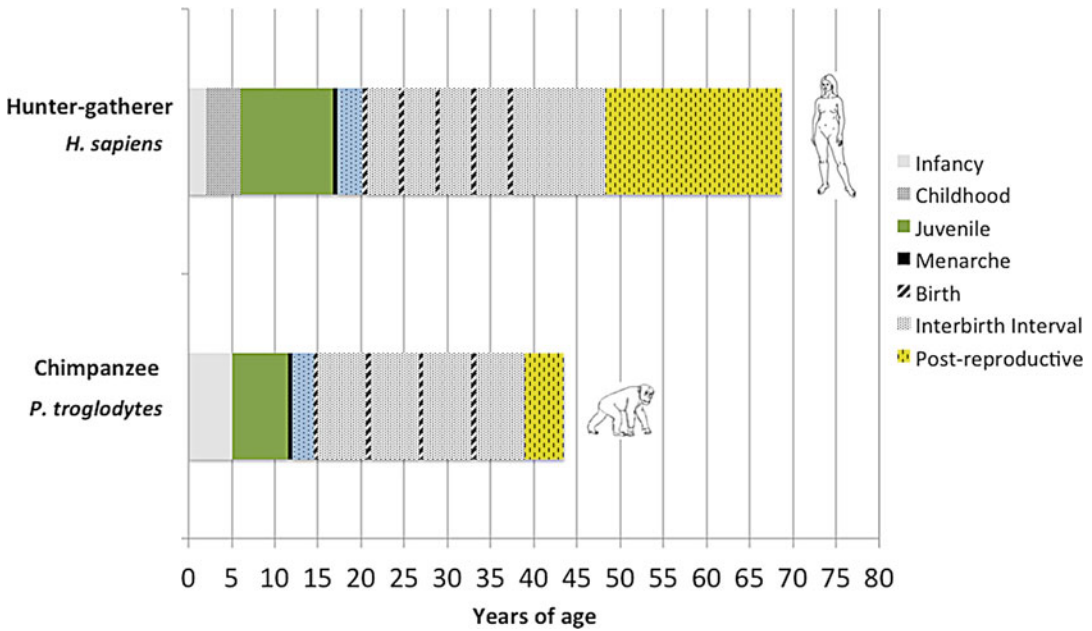
Typical Characteristics of the Human Life History and Sexual Differentiation During Puberty

Homo sapiens is a relatively long-lived, large bodied species with a slow tempo of development. Production of altricial (defenseless and dependent) young, a long period of dependency, late sexual maturity and first birth, wide birth spacing, low offspring number, and high levels of parental investment, including postreproductive investment (grandparenting), are typical of the human

life history. While infant, juvenile, and adult stages are shared with other social mammals and primates, humans uniquely exhibit an extended period of sociosexual maturation between the two latter stages, referred to as adolescence, and a distinct postreproductive phase. When the human life history emerged is not known, but fossilized dentition indicates that the life history of ancient members of the genus *Homo* was closer to that of African apes rather than modern humans. Converging evidence suggests that the prolonged life history of *H. sapiens* emerged at least 160,000 years ago, following the appearance of *Homo erectus* in the late Pleistocene era (Bogin and Smith 1996; Dean 2006; Smith et al. 2007).

Insofar as they invest differing amounts of energy in reproduction (Trivers 1972), the two sexes may be expected to exhibit different life histories. Female mammals invest greater energetically in offspring than males, and their smaller adult body size reflects a tradeoff that has occurred between reproduction and growth. Males, on the other hand, invest more in mating effort and male-male competition for which a larger body size is advantageous. Human females and males differ not only in the overall pattern of energetic investment in growth versus reproduction but also on other life history traits, including the relative timing of puberty, the onset of fertility, mortality rates, and life expectancy. The typical human female life history, as illustrated in extant hunter-gatherer populations, involves a long juvenile period leading up to a relatively late age at puberty (average age at menarche 16–17), followed by a period of adolescent subfertility and first birth around 19–20 years of age, wide birth spacing (3–4 years), production of an average of 5 offspring, last birth around 39 years of age, menopause around age 47, and a postmenopausal phase lasting up to 70 or more years of age (Howell 1979; Lancaster and Kaplan 2009) (Fig. 1).

Although producing relatively few offspring, human beings successfully raise about 60% of their infants to adulthood compared to around 35% for their nearest relative, the chimpanzee. (Lancaster and Kaplan 2009). Higher survivorship may be linked to the advantages provided by the evolution of bipedalism and increased



Puberty in Girls, Fig. 1 Life histories of female hunter-gatherers (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) (After Bogin and Smith 1996; Lancaster and Kaplan 2009; Walker et al. 2018)

brain size in hominins, in turn facilitated by later puberty and the unique growth pattern of human females. The evolution of bipedalism altered the pelvis, constraining the birth canal and restricting the somatic and brain size of human neonates. Human offspring are born altricial, but postnatal diversion of energy results in rapid expansion of the brain, while somatic growth slows. Once adult brain size is approached rapid skeletal growth and puberty occur. In most primate species, reproduction follows the onset of puberty within a few months to a year, but in humans a delay up to 5–10 years often occurs. This pattern of development suggests a unique trade-off between energy invested in body growth versus brain development (Bogin 2011) facilitating increased encephalization (ratio of brain volume to body size). Adult human brains are 3–4 times larger than those of our closest cousins, the chimpanzees. Achievement of adult body size before first pregnancy also means that maternal energy stores may benefit the neonate and its growing brain. Moreover, delayed puberty in girls and later first births permit a period of maternal psychological and social growth, and the acquisition of

parenting skills, together contributing to the enhanced survivorship of human offspring. Thus, the relatively slow life history of humans, with sexual maturity not occurring until late in the second decade of life, appears to be part of an adaptive suite of human traits, including an extended period of intense brain growth and learning, heightened parental care, increased adult brain size, enhanced cognitive abilities, and long lifespan distinguishing our species from other primates (Kaplan et al. 2000, 2007).

Sequence of Puberty in Girls in the Context of Mammalian and Primate Evolution

Girls' puberty involves a sequence of events emerging during primate evolution that transformed the juvenile phenotype (observable characteristics) into the adult form. Although humans do not undergo the spectacular metamorphoses observed in insects, the morphing of juvenile features into adult physical characteristics at puberty, especially in girls, is an overtly distinct phase, not

equally witnessed in other mammals or primates. Both girls and boys in industrialized nations undergo puberty earlier than typical for our species (see discussion of the secular trend), but the sequence of pubertal events remains invariant. Classic studies by Tanner and his colleagues (e.g., Eveleth and Tanner 1976; Tanner 1962) described the stages of pubertal development in modern girls according to the development of primary and secondary sexual characteristics:

1. Development of the breast bud (*thelarche*) is usually the first sign of puberty in girls and appears around 10–11 years of age. It takes 3–4 years for full breast development to occur. Development of breast buds is a noteworthy feature of human development, because other primate females do not develop breasts until the later stages of pregnancy. In those species, increased glandular tissue at pregnancy is resorbed again after weaning, while mature human breasts are continuously conspicuous and their size stable because they consist mainly of fat deposits.
2. Pubic hair begins to grow (*pubarche*) a little later under the influence of adrenal androgens as the adrenal cortex matures (*adrenarche*).
3. The ovaries, uterus, and vaginal canal then begin to increase in size.
4. An increase in height and weight, the growth spurt, begins around 10 years of age and intensifies.
5. *Menarche*, or first menstrual period, occurs fairly late the process, usually after the peak of height growth, with an average age of 12–13 year in North American girls, and a range of 9–18 years. At first menstrual cycles are irregular and many are anovular (an ovum is not produced). Apter and Vihko (1984) found over 50% of cycles were anovulatory in the first 2 years following menarche. During this period of adolescent subfertility, the probability of pregnancy is reduced.
6. The achievement of adult capacity of the pelvic inlet and birth canal, one of the most crucial features of reproduction, is not attained until the very end of the sequence of pubertal events, years after menarche. For example, in well-

nourished girls with menarche at 12–13 years, adult pelvic dimensions are not reached until 17–18 years of age.

The proximate trigger for the initiation of puberty is increases in the production of hormones (e.g., estrogen, testosterone, progesterone, growth hormone) as a result of changing activity in the hypothalamic-pituitary-gonadal (HPG) axis. In monitoring environmental and internal physiological conditions, the hypothalamus secretes releasing factors to the anterior pituitary, which in turn releases luteinizing hormone (LH), follicle-stimulating hormone (FSH), and growth hormone (GH). Growth hormone increases growth throughout the body, facilitating a rapid increase in height and weight. In girls, LH and FSH act on the ovaries, causing the release of estrogen and progesterone, which stimulate development of breasts, fat distribution, the uterus and its linings, and broadening of the hips. In boys, FSH and LH act primarily on the testes stimulating spermatogenesis and the production of testosterone. Testosterone is responsible for the development of male secondary sexual characteristics, including voice change, muscular and skeletal development (e.g., broadening of the shoulders), development of the seminal vesicles, penis and scrotum, and growth of hair on the chest, underarms, and pubic area.

In altering the timing of developmental events and the expression of somatic traits, the HPG axis is one of the physiological systems that has likely played an important role in the differential evolution of mammalian development and life histories. Ancestral selection pressures acting on the genetic substrate underlying the developmental inhibition and activation of the HPG axis have conserved some developmental features across species, but produced unique features in others. During human fetal development, a positive feedback loop in the HPG axis stimulates the production of FSH and LH and the hormones responsible for the initial development of the external genitalia. After birth, however, the HPG axis switches to a negative feedback loop. Detection of circulating steroid hormones by the hypothalamus inhibits the release of FSH and LH, and further sexual

development is paused until the onset of puberty. This pattern of activation followed by inhibition results in the long juvenile period of growth and development typical of humans and shared with many species of monkeys and all apes. However, as puberty is approached, the HPG axis switches back to a positive feedback loop and the completion of sexual development begins. As the HPG re-activates, the resulting heightened velocity of human growth contrasts with that of other mammals, including apes. While slow constant growth during the juvenile phase is conserved across these species, the acceleration of skeletal dimensions around the onset of human puberty, known as the growth spurt, is absent in other nonhuman primates whose growth decelerates around this time (Bogin and Smith 1996).

Sexual Bimaturism, Sexual Dimorphism in Size and Shape, and the “Fat Spurt”

Throughout childhood, boys and girls grow at a similar rate; however, prior to puberty their patterns of growth diverge. The growth spurt in height occurs a couple of years earlier in girls than in boys. In general, girls mature earlier than boys, a phenomenon referred to as *sexual bimaturism*, and this can be seen early in the first year of life as girls pass the developmental milestones before boys. Because boys grow slower, their long bones have an extra few years to grow before skeletal maturation is completed with the closing of the epiphyses (growth plates on the bones) (Tanner 1962; Limony et al. 2015). This results in men being on average taller and heavier than women, a phenomenon referred to as *sexual dimorphism* in size.

During childhood, girls and boys have a similar body shape and composition, but over puberty girls' and boys' body shapes and their distributions of fat and muscle undergo rapid transformation and divergence. One of the most obvious differences between girls and boys is the changing ratio of shoulders to hips. Girls reach the peak of their shoulder growth before their height spurt, but their hips begin to grow after the height spurt and the pelvis only reaches its adult growth in late

adolescence. Boys develop larger shoulders and torsos (upper body strength) over puberty, as a result of the laying down of muscle tissue in the chest and shoulder regions under the influence of male hormones (Winick 1981). Over puberty the proportion of muscle mass in boys increases significantly over that of girls. For example, in young adult males muscle tissue represents about 52% of body weight, whereas in girls it represents about 40%.

Fat tends to accumulate in children from 7 to 8 years old, but during the height spurt a loss in fat occurs in boys and the accumulation slows down in girls. Shortly after the height spurt ends, fat begins to accumulate again, especially in girls, who lay down twice as much fat as boys over adolescence. The increased deposition of fat or “fat spurt” occurs normally in girls during adolescence, regardless of their eating habits. The primary sites of fat accumulation include the thighs, hips, breasts, buttocks, and backs of the arms and this fat is very resistant to weight loss (Fig. 2). This deposition of fat is unique to human females and provides sufficient calories for gestation and the initial months of lactation (Frisch and McArthur 1974). It has been aptly termed “reproductive fat” for its functional value in maintaining a pregnancy and neonate (Lancaster 1986). Insufficient deposits of fat may both delay the onset of menstruation or result in its cessation if menarche has already occurred (Ellison 1990; Frisch and McArthur 1974). The accumulation of fat prior to puberty may contribute to the initiation of puberty, as leptin, a substance secreted by fat cells, appears to play a role in the activation of the HPG (Gueorguiev et al. 2001).

Girl's puberty further differs from that of boys as a result of the differential ordering of pubertal events. Although girls begin to go through puberty earlier than boys, they do not experience menarche and consistently ovulate until relatively late in the sequence of pubertal events. Girls must reach about 17–18 years of age before 80% of cycles are ovulatory, with maximal fertility not achieved until the mid-twenties (Apter and Vihko 1984; Bogin 2011). Boys, on the other hand, produce sperm relatively early (mean age = 13.3 years), even when they do not yet

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Fig. 2 Fat distribution in a mature human female following the “fat spurt” at adolescence (Based on Lancaster 1986, and other sources)



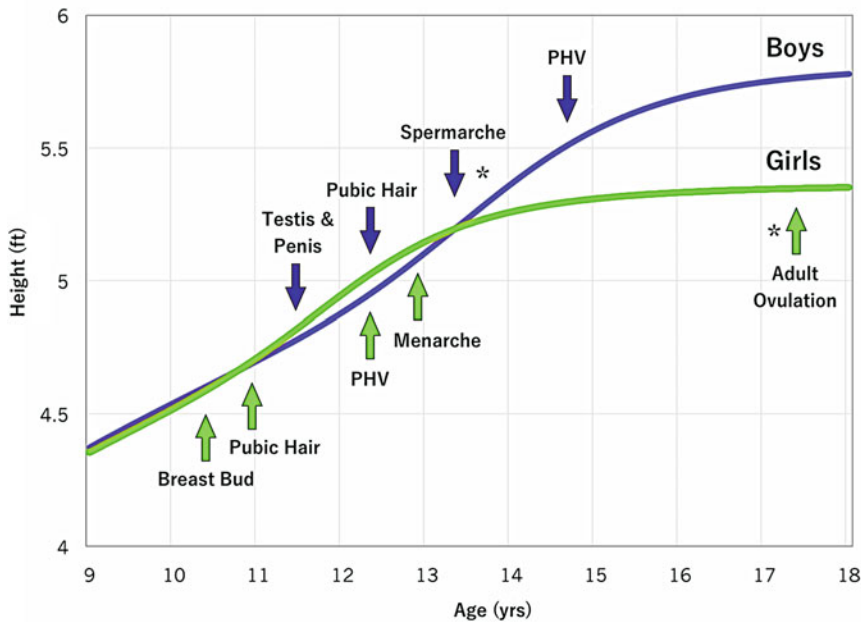
possess the mature morphological features generally necessary to compete for mates and have been described as “fertile eunuchs” (Richardson and Short 1978). Therefore, girls possess the outward signs of reproductive maturity before they can conceive, but the opposite prevails for boys (Fig. 3). Different selective pressures have acted upon the timing of external morphological changes and gametogenesis (production of ova and sperm) in boys and girls. Late external development and small size in boys protects them from male competition and aggression by older males. But an undeveloped boy could fertilize a female should the opportunity arise, so the relatively early onset of spermatogenesis may have been favored by sexual selection. Girls’ adolescent subfertility has been attributed to an immature reproductive system, but subfertility does not occur to the same degree in all mammals or primates and may be a uniquely human adaptation. The development of breasts and acquirement of a distinct, relatively lower waist-to-hip (WHR) ratio as the pelvis widens at puberty, appear to signal fertility

to prospective mates and attract male attention (Singh 1993). Appearing outwardly mature before the consistent occurrence of ovulation may provide a period for assessment and choice of the best possible mate. Early external signals of maturity, coupled with relative infertility, may also increase a girl’s time for social development, formation of a social network, and the learning of childcare skills vital for offspring survival. Cognitive development, especially the acquirement of higher cognitive processes, and empathy are also heightened during adolescence. Based on the life histories of extant hunter-gatherer populations, such as the !Kung (see Howell 1979), it is likely that throughout much of human evolutionary history, most women had approximately two decades to acquire advanced cognitive, survival, parenting, and mate selection skills before becoming mothers.

Sequelae of Puberty in Girls and Variation in its Timing

The outward signs of girls’ physical maturity result in changes in family and social relationships. In many traditional societies, puberty is attended by ceremony and initiation rites to mark a girl’s impending fertility and passage into adulthood. Parents begin to treat daughters as more adult-like and restrict their activities more than those of their sons. Parents and offspring do not have completely overlapping genetic interests, referred to as *parent-offspring conflict*, and mothers may direct their daughter’s behavior to their own reproductive advantage (a form of *parental manipulation*, Alexander 1974). For example, adolescent girls may be given the responsibility of helping raise siblings at the expense of their own reproduction. To ensure the choice of an appropriate mate and increase the probability of surviving grandchildren, parents may heighten the supervision of their daughters, behavior referred to as *daughter-guarding* (Flinn 1988).

Changes in girl’s self-concept and sociosexual behavior also occur at puberty. Beginning in the 1960s, an extensive literature revealed consistent differences in relatively early versus later



Puberty in Girls, Fig. 3 Sequence and relative timing of pubertal events in modern girls and boys. “Adult Ovulation” refers to the occurrence of 80% ovulatory cycles.

“Spermarche” refers to the first appearance of spermatozoa in urine. “PHV” signifies peak height velocity (After Tanner 1962, and other sources)

maturing girls. Early puberty is associated with increased risk of depression and anxiety, poor body-image, eating disorders, early and risky sexual behavior, poor school performance, alcohol and drug abuse, early (teenage) pregnancy, early marriage, and divorce (Graber 2013; Negri and Susman 2011; Udry and Cliquet 1982). Pubertal timing also has significant medical and health consequences with earlier menarche related to an increased risk for mortality from all causes, especially breast cancer, obesity, insulin resistance, cardiovascular disease, and polycystic ovarian syndrome. Later age at menarche is associated with fractures and lower bone mineral density (Jacobsen et al. 2007). Such consistent differences in early and late maturing girls have spurred interest in the causes of variation in pubertal timing.

Genetic and Environmental Influences on the Timing of Puberty in Girls

The wide variation in girls’ pubertal timing is accounted for by both genetic and environmental

factors. Early studies of the concordance between female relatives in the age at menarche showed the closer the genetic relationship, the higher the concordance. Estimates of the heritability (proportion of phenotypic variation attributable to genetic variation) of menarche suggest that anywhere from 40% to 95% of the phenotypic variance in menarcheal age is due to genetic variance (Towne et al. 2005). Discrepancies in estimates occur because heritability is higher when environmental variance is reduced (e.g., in wealthy societies with equitable living conditions). As with most complex human traits, girls’ puberty is polygenic with over 40 different candidate genes or loci identified as contributing to menarche and its correlates, including height, obesity, and mineral bone density (Dvornyk and Waqar ul 2012). For example, genetic variation in and adjacent to the gene *LIN28* on chromosome 6, a gene conserved across species, is associated with pubertal timing (Ong et al. 2009). The major allele of the SNP rs314276 is associated with a faster growth spurt in height and shorter adult height in both sexes. In girls it is associated

with an earlier age at menarche and breast development and in boys, earlier appearance of pubic hair and voice breaking and more advanced pubic hair development. In addition to predisposing girls to earlier or later puberty, genes and their expressed neurobiological processes affecting pubertal onset may interact with environmental factors or affect sensitivity to them (Ellis et al. 2011; Schlomer and Cho 2017).

Aside from hereditary factors, a number of naturally occurring and human-introduced environmental factors appear to influence the timing of puberty and correlated life history characteristics in girls. These include access to good nutrition and health care, disease, exposure to estrogen-disrupting chemicals, and psychosocial factors. That well-nourished, healthy girls, with higher socioeconomic status, achieve menarche earlier than others has been well established (e.g., Eveleth and Tanner 1976). Improvements in sanitation, living conditions, and medical advances reducing the prevalence of diseases are believed to be involved in the earlier onset of puberty and increased height and weight observed from the mid-1800s to the last half of the twentieth century, referred to as the *secular trend*. Between 1830 and 1960 the average age at menarche dropped in Great Britain, Scandinavia, Germany, and the United States by approximately 3–4 months per decade (Eveleth and Tanner 1976). Similar declines were seen in other industrialized and some developing countries. Although the trend stabilized by the late 1900s, there is evidence of a more recent resurgence. On average puberty in modern girls occurs 3–4 years earlier than in their ancestral hunter-gathers and has become somewhat decoupled from psychosocial development. Reversals of the secular trend have been noted in countries experiencing famine and food shortages during the Second World War and more recently in Bosnia (Eveleth and Tanner 1976; Tahirovic 1998). Menarche is usually delayed in underfed children as well as in athletes and dancers with intentionally lean body mass, but advanced in obese girls (Ellison 1990; Frisch and McArthur 1974).

Synthetic chemicals employed in pharmaceutical products, manufacturing and industry, pest

control, and other environmental contaminants that disrupt, mimic, alter the rate of synthesis or block endocrine hormones, especially estrogen, alter the timing of puberty in girls and carry health risks (Lee and Styne 2013). Inadvertent exposure to chemical flame-retardants containing polybrominated biphenyls (PBS) through breastmilk and the use of estrogen cream by mothers, some hair tonics, and DDT are associated with early and precocious puberty. On the other hand, lead contamination is associated with later puberty. Public concern about the developmental and long-term health effects of these chemicals have led to increased regulation of their use in consumer products, farming, and industry.

Girls' pubertal development appears to be sensitive to the social, as well as the physical environment, with a number of psychosocial factors reliably correlated with the timing of girl's puberty. Girls experiencing stressful environments, family dysfunction, lack of parental support, absence of their biological father or low paternal investment, presence of a stepfather, and sexual abuse experience early menarche and its associated sequelae (e.g., Ellis et al. 1999; Ellis and Garber 2000; Moffitt et al. 1991; Noll et al. 2017; Surbey 1990; Webster et al. 2014). In addition absence of both biological parents, occurring in domestic and international adoption, is also related to early and precocious menarche (Parent et al. 2003; Surbey 1990). What accounts for these consistent relationships is not yet clear, but the supposition that natural selection equipped offspring with means to adjust development to best adapt to the environment in which they find themselves has inspired a number of hypotheses. A corollary that parents or other adults may alter an offspring's development in their own genetic interests has also been explored. One widely advanced hypothesis uniting a number of findings is that early childhood stress and reduced paternal investment result in children adopting a "fast" versus "slow" reproductive strategy of early sexual development and reproduction, with a focus on offspring quantity rather than quality, so as to offset the deleterious effects of a poor rearing environment (Belsky et al. 1991; Chisholm 1993; Ellis 2004; Surbey 1990). Another

hypothesis, based on the finding that the mothers of father-absent girls are also early maturers, is that a behavior-genetic effect underlies the relationship between father absence, early menarche, and their sequelae (Barbaro et al. 2017; Rowe 2002; Surbey 1990). An additional possibility is that, as observed in other mammals, inhibition of reproductive development in girls living with their biological fathers may serve as a mechanism of inbreeding avoidance, whereas exposure to unrelated adult males, such as stepfathers, may accelerate puberty, possibly via a pheromonal cue (Ellis and Garber 2000; Surbey 1990). That mothers may suppress the development of their daughters and recruit their aid in raising additional offspring, a form of parental manipulation, was previously discussed. Adaptations for coping with environmental stress may also play a role. Stress, depending on its timing, and whether it is physical, psychological, chronic, or acute, appears to have paradoxical results on puberty (Boyce and Ellis 2005; Boynton-Jarrett et al. 2013; Surbey 1990). For example, nutritional stress in childhood may initially delay growth as an adaptation to low energetic resources, but later result in advanced catch-up growth and early menarche once food supplies improve (Proos et al. 1991). Moreover, while stress usually inhibits the HPG, suppressing development and reproduction, glucorticoids released from the adrenal glands may counteract this inhibition (Matsuwaki et al. 2006) protecting and enhancing reproductive development in some stressful conditions. This may explain why chronic nutritional stress does not delay menarche indefinitely and why psychological stress and childhood sexual abuse is related to an earlier age at menarche, whereas physical abuse is related to both early and late age at menarche (Boynton-Jarrett et al. 2013).

Significance of Variation in the Timing of Puberty in Girls and Its Sequelae

Like many other human traits, such as height or intelligence, the timing of puberty in girls exhibits continuous phenotypic variation and plasticity. Evolutionary biologists generally attribute

phenotypic variation in life history traits to (a) *noise or random variance* due to environmental or genetic variance, (b) *adaptive plasticity* whereby a given genotype (genetic constitution) maintains fitness by producing the phenotype best suited for a given environment or condition (referred to as a conditional strategy), (c) *maladaptive plasticity* where a phenotype is pushed outside of the species-typical reaction norm with negative fitness consequences, or (d) *alternative life history strategies* whereby two or more distinct phenotypes or *morphs* are produced by different genotypes maintained by frequency dependent selection (Stearns 1992). A proportion of the variation in the timing of girls' puberty is certainly due to genetic or environmental variation that presently has no adaptive value or is vestigial. Maladaptive plasticity, such as that producing extremely precocious menarche from exposure to environmental contaminants, estrogen mimics, or growth-hormone additives in meat, accounts for another portion of variation. Alternative life history strategies usually refer to differences between species and are uncommon within species. Much of the remaining variation in girls' pubertal timing and correlated traits likely reflects the combined results of adaptive plasticity or the conditional strategies of offspring (or adults in their environment) serving to functionally match development with environmental conditions (Belsky 2000; Ellis 2004; Surbey 1998). Conditional strategies are triggered in response to environmental conditions with their phenotypic expression not directly associated with genotypic differences. The resulting developmental plasticity serving to adapt individuals to their current environments, without altering the underlying genetic infrastructure of life history traits, would tend to preserve the late Pleistocene species-specific life history of *H. sapiens* through historical changes in living conditions, such as those experienced by modern girls.

Conclusion

The life history of *H. sapiens* was constrained by the preadaptation of bipedalism and directional

selection for larger brain size during hominin evolution. The unique pattern of the human life history involves production of altricial young, a long period of dependency, late sexual maturity and first birth, wide birth spacing, low offspring number, and high levels of parental and post-reproductive investment. The characteristics, timing, and sequelae of puberty in girls are one component of the human life history and exhibit similar, but also unique features compared to that of other female primates. Girls' puberty differs significantly in tempo, sequence, and expressed phenotypic characteristics to that of boys. The timing of puberty in girls shows considerable genetic and environmental variation and is related to girls' psychological, social, and reproductive development, and health. Application of a number of evolutionary theoretical concepts and models enhances our understanding of the significance of the unique characteristics and observed variation of pubertal timing in girls.

Cross-References

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- [Conditional Strategies](#)
- [Environmental Influences](#)
- [Father Absence](#)
- [Life History Theory](#)
- [Menarche](#)
- [Reproductive Strategies](#)

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Synonyms

[Civil archives](#); [Civil documents](#); [Civil records](#); [Federal public archives](#); [Federal public documents](#); [Federal records](#); [Governmental public archives](#); [Governmental public documents](#); [Governmental records](#); [Public archives](#); [Public documents](#); [Public register](#); [Public written material](#)

Definition

A public record is a document that has few restrictions on access. Public records are required by law to be created, stored, and available. Public records are created in the performance of duty from government officials.

Introduction

Public records such as census data and business records are available for access by the public. Online resources such as [Archives.gov](https://www.archives.gov) and [PACER.gov](https://www.pacer.gov) increase availability of access to the majority of people (for more, see section on Online Resources for Public Records). Not all public records are available online; however, there has been a recent increase in use of online records due to their accessibility. Social scientists are among the most frequent users of these public records databases. This entry details types of public data and availability in the United States, issues with public records, use of public records, and recommendations for future uses of public records in evolutionary psychology.

Availability and Use of Public Records

Some public records are available to only a small subset of individuals who spend hours searching physical archives for the information they are seeking. However, other public records are available online and are relatively easy to find with an online search.

Types of Public Records

Though state guidelines differ (Winkler and Byers 2010), under the federal Freedom of Information Act (FOIA, see section on FOIA below), the following types of information are considered public record:

- Birth Records
- Census Data
- Consumer Protection Information
- Copyrights and Patents
- Court Dockets
- Criminal Records
- Death Records
- Federal Legal Cases
- Government Publications
- Government Spending Reports
- National Health Statistics
- Professional and Business Licenses
- Real Estate Records

- Sex Offender Registry
- Voter Registration

Additionally, certain federally funded scientific research is also mandated to be publicly available (U.S. Department of Health and Human Services 2016; U. S. Government Publishing Office 2009). These publications are available through PubMed.

Online Resources for Public Records

There are an abundance of online resources of public record information. The National Archives and Records Administration (NARA; <https://www.archives.gov>) maintains the most comprehensive collection of public record data in the United States. NARA's website includes a searchable database of public record information. Some information is available online, and requests can be made for information that is not available online. Other national resources of public record data are listed below with the types of information you can find on those databases. Some of these databases have raw data, while other resources provide aggregated data and infographics.

- Environmental Protection Agency (<https://www.epa.gov>)
 - Toxic release inventory, hazardous waste sites
- Federal Bureau of Investigation (<https://www.fbi.gov>)
 - Crime statistics, sexual offender registry
- Federal Bureau of Prisons (<https://www.bop.gov>)
 - Inmate locator
- Federal Election Commission (<http://www.fec.gov>)
 - Campaign finance reports
- Government Publishing Office (<https://www.gpo.gov>)
 - Official information products of the US government such as official publications of Congress, the White House, and other federal agencies
- Internal Revenue Service (<https://www.irs.gov>)
 - Tax exempt organizations
- National Center for Health Statistics (<https://www.cdc.gov/nchs>)

- Data from national health surveys such as statistics on the prevalence and incidence of diseases, conditions, and health care
- Public Access to Court Electronic Records (<https://www.pacer.gov>)
 - A national index for the US district, bankruptcy, and appellate courts
- PubMed (<https://www.ncbi.nlm.nih.gov/pubmed>)
 - More than 26 million citations from MEDLINE and other science resources
- Securities and Exchange Commission (<http://www.sec.gov>)
 - Corporate filings
- Statue of Liberty – Ellis Island Foundation, Inc. (<http://www.libertyellisfoundation.org>)
 - Immigration records from Ellis Island
- United States Census Bureau (<https://www.census.gov>)
 - Index of data collected through the United States Census every 10 years
- United States Copyright Office (<http://www.copyright.gov>)
 - Records of copyrighted books, music, art, and periodicals
- United States Patent and Trademark Office (<https://www.uspto.gov>)
 - Index of existing and published patents

The Evolution of Societies and the Need for Public Records

During the majority of human evolution, we lived in small-scale societies where it was relatively easy to remember past interactions with your community. However, after the advent of agriculture some 10,000 years ago, humans were able to live in larger and larger settlements, including the megacities of today. During this transformation, it also became possible for people to specialize in a particular trade and have a division of labor. Once our communities became too large for us to remember all interactions with all people, particularly in the domain of resource exchanges, it became necessary to have some way of accounting for economic interactions with strangers (Basu and Waymire 2006). The earliest record keeping dates back to 8000 BC, when ancient Sumerians used tokens as an accounting tool. Since that time, all large-scale

human societies have kept records in some form or another.

In addition to keeping records for accounting purposes, we started keeping written records to keep track of other facets of large-scale society life including population growth and change, ownership of land, laws, marriages, and more. Some of these written records were kept for historical significance; other records were for book-keeping purposes. As we began recording more and more information, a significant challenge emerged in terms of organizing and archiving these records.

In the modern era, developing a central location for public records with a systematic method for maintaining documentation is still a concern. In the early 1900s, physical public records were often scattered in government buildings, making it difficult to access and secure them (Atherton 1979). Due to these challenges, a system of organizing and maintaining records was developed. The National Archives and Records Administration in the United States is responsible for maintaining public records.

Freedom of Information Act

In the United States, The Freedom of information Act was enacted on July 4, 1966, and was effective one year after the enactment ([FOIA.gov](https://www.foia.gov)):

Since 1967, the Freedom of Information Act (FOIA) has provided the public the right to request access to records from any federal agency. It is often described as the law that keeps citizens “in the know” about their government. Federal agencies are required to disclose any information requested under the FOIA unless it falls under one of nine exemptions which protect interests such as personal privacy, national security, and law enforcement ([FOIA.gov](https://www.foia.gov)).

Issues with Availability of Public Information

There are some concerns about the availability of public information. On one hand, transparency of information is important for public safety, law enforcement, and problem solving on a national level. On the other hand, privacy and restriction of access to individual data seem to be of most concern to the public (Munson et al. 2012). These concerns have been exacerbated by the

availability of public records online (Blankley 2004). Additionally, people seem to be divided on the issue of access: the slim majority believes availability should stay as is, with others believing in some form of reform. Availability of sensitive personal information increases risk of identity theft. For example, in 2015, a former Florida Governor released hundreds of thousands of emails that were considered public record; however, some documents contained sensitive data such as social security numbers, addresses, emails, and protected health information (Sottek 2015). According to Florida law, the social security numbers should have been redacted but were included due to human oversight. If criminals access sensitive information gathered from public records, they can steal and sell individual identities. However, those supporting the Freedom of Information Act, such as employers and lawyers, feel that transparency is needed for accountability in government (Munson et al. 2012).

Use of Public Records

Users of public records fall into a few distinct categories: individual information seekers and aggregate data for the purpose of diagnosing trends (Adams 2007). However, metadata or aggregated data is not considered public record in some states (Cockerham 2009). Individual use of NARA has resulted in an increase of requests for reproductions of archival records (Adams 2007). Other than personal inquiries, academics and researchers from public and private venues are among the most frequent users of public records for research with less use by historians than might be predicted. From 2001 to 2004, researchers accounted for nearly 90 % of fulfilled requests for reproduction of electronic records.

Since researchers are the most frequent users of archival data and public records, it has been suggested that collaboration between NARA and social science data archives would be valuable for productive research programs that could employ the use of both of these sources (Adams 2007). One archive of social science data is the International Association for Social Science Information Service and Technology (IASSIST). This professional organization aids in maintaining social science data records for uses in research and

education. Currently, the Library of Congress sponsors the Digital Preservation Program of the National Digital Information Infrastructure and Preservation Program that maintains several major social science data archives in the United States.

Evolutionary psychologists often turn to public records to test evolutionary hypotheses about human behavior that would be nearly impossible to explore without archival data. For example, Daly and Wilson (1988) used public records from thirteenth-century England and from modern Detroit to demonstrate that kinship plays a suppressive role in homicides. That is, people are far more likely to kill non-kin than kin. This suggests that even in the realm of criminal activity, the evolutionary pressure to support kin plays a role in shaping human behavior. Similarly, marriage records from nineteenth-century Sweden have been used to test predictions from behavioral ecology regarding resources and reproductive potential (Low 1991).

In another example, researchers used census and CDC data to calculate personalized estimates of risk. By dividing the number of people living with HIV by the population, the researchers calculated the base rate of HIV in the United States (Ellis and Brase 2015; Ellis et al. 2014). People largely ignore base rate information, and this can lead to errors in judgment and resulting decision-making (Kahneman et al. 1982). However, by tailoring base rate information to individuals, it is argued that individual models of risk will lead to more optimal outcomes (Gail et al. 1989).

Thus, public records can be a valuable resource for creating models of existing behaviors, testing evolutionary hypotheses, predicting behavior across contexts, and providing solutions for change toward optimizing behavior. Furthermore, using public records gives evolutionary psychologists the ability to study these patterns cross-culturally.

Future Research in Evolutionary Psychology Using Public Records

Regardless of the issues of privacy, researchers can benefit from the use of public records to answer research questions in evolutionary psychology. Evolutionary psychologists should

continue to use public records in the context of testing hypotheses from behavioral ecology and other evolutionary theories. Aside from the examples mentioned above, there are new uses and types of public records emerging with the aid of technology. For example, the CDC publishes the data from the annual Behavioral Risk Factor Surveillance System (BRFSS) that has been conducted since 1984 and is the largest continually collected health survey in the world (<http://www.cdc.gov/brfss/>). This will be a rich source for testing evolutionary hypotheses related to health. We expect that similar databases will become available in the coming years. Thus, evolutionary psychologists should stay abreast of the available resources for accessing public records.

Conclusion

Public records are available in digital and physical formats. The availability of public records varies by type and location. Multiple organizations and institutions were created to manage and maintain public records for use. Social scientists and other researchers comprise the majority of seekers of public records. There has been some use of public records in evolutionary psychology (e.g., census data, business archives). However, future research should focus on expanding its use and capitalizing on the wealth of information available through public records.

Cross-References

- [Census Data](#)
- [Online Survey](#)
- [Science and Morality](#)
- [Surveys and Questionnaires](#)

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Public Register

- [Public Records](#)

Public Written Material

- [Public Records](#)

Pulsastion of the Heart

- [Heart Rate](#)

Pulse Rate

- [Heart Rate](#)

Punish

- [Ability and Willingness of Victim to Retaliate](#)

Punishment

- [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- [Punitive Sentiment](#)
- [State-Sanctioned Punishment as Deterrent to Violence](#)
- [State-Sanctioned Punishment as Substitute for Tribal Vengeance](#)
- [Types of Sexual Coercion](#)

Punishment I

- [Positive and Negative Reinforcement and Punishment](#)

Punishment II

- [Positive and Negative Reinforcement and Punishment](#)

Punitive Sentiment

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Synonyms

[Negative reciprocity](#); [Punishment](#)

Definition

Punitive sentiment is the desire to harm someone because of their behavior or because of their relative status.

Introduction

Punitive sentiment is the desire to harm someone – even when doing so incurs a personal cost to the punisher (Clutton-Brock and Parker [1995](#); Raihani et al. [2012](#)). Punishment can be aimed at cheats in social interactions – this is typically called “responsible” or “justified” punishment. Punishment can also be aimed at cooperative, or helpful individuals, or meted out by the cheating individuals themselves – this is typically called “antisocial punishment” (Herrmann et al. [2008](#); Sylwester et al. [2013](#)). (Henceforth, the word “punishment” refers only to responsible or justified punishment.) Administering punishment is costly to the punisher as well as to the target. To understand how punitive sentiment could be favored by natural selection, one therefore has to ask how punishers ultimately derive benefits from these investments. I will outline the various

explanations that have been proposed to account for the adaptive significance of punishment.

How does Punishment Evolve?

Several possible solutions have been proposed to resolve the puzzle of how costly punishment can be favored by selection. In repeated two-player settings, punishment can theoretically evolve via direct-within interaction benefits to punishers, when targets behave more cooperatively with punishers after being punished (Clutton-Brock and Parker 1995; Price et al. 2002; Raihani et al. 2012). Nevertheless, in humans, this theoretical prediction lacks clear empirical support. Rather, many studies have shown that punishment does not necessarily induce targets to cooperate (Barclay and Raihani 2016; Bone et al. 2015, 2016b; Dreber et al. 2008; Nikiforakis and Engelmann 2011) and can even prompt counter-punishment (Balafoutas et al. 2014; Bone et al. 2015, 2016b; Dreber et al. 2008; Fehr et al. 2012; Nikiforakis 2008; Nikiforakis and Engelmann 2011), thereby further increasing the costs associated with punishment. Moreover, punishment in multiplayer settings and in one-shot interactions is harder to explain. In multiplayer interactions, non-punishing free-riders can reap the benefits of punishment without contributing to the cost, thereby creating a second-order social dilemma (Yamagishi 1986). In one-shot interactions, or in interactions where the punisher was not the victim of the cheat and does not expect to interact with the target in future, then punishers by definition cannot benefit from an improvement in the target's behavior in future interactions. How, then, does punishment evolve in these more puzzling scenarios?

Group-Selection Accounts of Punishment

In principle, punishment in multiplayer and/or one-shot settings could evolve via group level selection. Two different versions of the group selection explanation exist, which imply competition between genes and between cultural memes within a population, respectively. Both versions of group selection invoke the assumptions that

between-group competition is stronger than competition within groups, that groups with punishers outperform groups without punishers, and that variance among (genetic or cultural) groups is higher than variance within them (see Raihani and Bshary (2015c) for further discussion). These assumptions do not have unanimous empirical support (see, for example Lamba and Mace 2011; Yamagishi and Mifune 2016).

Under genetic group selection, punishment would be personally costly to punishers but could theoretically evolve via benefits to the punisher's kin, if these benefits depended on the success of the punisher's group in competition with other groups. The mathematics of evolution via kin selection and via genetic group selection are formally equivalent (Gardner 2008; West et al. 2011). Nevertheless, the circumstances under which genetic group selection could be an important force are thought to be extremely uncommon in human societies (see Bell et al. 2009; Seielstad et al. 1998), and theoretical models have shown that increasing relatedness among group members hinders the evolution of punishment via kin-based benefits (Gardner and West 2004), rather than increasing it as would be expected under a genetic group selection account.

A cultural group selection account assumes that individuals have higher cultural (rather than genetic) relatedness to members of their group than to outgroup members. This means that individuals have a higher probability of sharing the same memes with members of their cultural groups than they do with other randomly selected members of the population. High levels of cultural relatedness can be generated by predispositions to copy other group members – under the assumption that copying can be adaptive when the costs of information gathering are high (e.g., Boyd and Richerson 1982; but see Andre and Morin 2011). Selection acting on cultural, rather than genetic, variation between groups might in principle be more realistic since between-group differences in culture can be maintained if immigrating individuals adopt the norms and memes of their new group. Theoretical work has shown how punishment can be sustained in a population (via payoff-based imitation) when it is already common in

the population (Boyd et al. 2003). Note, however, that a high frequency of punishers in a population indicates that cooperation will also be high – and thus the costs associated with punishing are seldom incurred. It is far less clear how punishment could invade a similar population comprised mostly of nonpunishing defectors (Lehmann et al. 2007) – here punitive strategies would be (possibly prohibitively) expensive and, if rare, would not be expected to spread via imitation. Indeed, more recent theoretical work has shown that strategically nonconforming strategies are expected to dominate over strategies that blindly conform to payoff-reducing behaviors (e.g., Morin 2014; Mouden et al. 2014).

“Big-Mistake” Explanations of Punishment

An alternative explanation is that investment in costly punishment in one-shot interactions stems from the misfiring of psychological mechanisms that instead evolved in the context of repeated interactions, where punishment would have been under positive, individual-level selection. In other words, punishment in one-shot interactions can be viewed as a “big mistake” – the right behavior deployed in the wrong setting (see Raihani and Bshary (2015c) for description and critique). For instance, one recent study found that investment in third-party punishment was determined by the extent to which subjects inferred mistreatment of another individual predicted that the protagonist would also mistreat them (Krasnow et al. 2016). Thus, third-party punishment is predicated on an expectation that the punisher will interact with the target of punishment in future. The authors argue that this expectation would have been reasonable in the ancestral environment where these sentiments evolved, since one-shot interactions with unknown individuals would have been uncommon. The assumptions that one-shot interactions were indeed uncommon and that ancestral humans are unable to distinguish between interactions that are likely to be repeated or ones where there is no obvious future have been challenged, however (e.g., see Lamba and Mace (2010) and Raihani and Bshary (2015c) for a

review); as has the implicit assumption that we are unable to rapidly adapt to changing social circumstances (e.g., Rand 2016).

Individual-Level Benefits of Punishment

More recent studies have started to explore alternative explanations for the evolution of punishment in otherwise puzzling scenarios. One major route by which punishment could evolve without recourse to kin-selected benefits, spatial assortment, or between-group competition is by relaxing the assumption that the benefits of punishment are a linear function of investments (Raihani and Bshary 2011). Where the benefits of punishment scale nonlinearly with investments, then the dilemma more closely approximates an n-player snowdrift game (a volunteer’s dilemma, Diekmann 1993) than an n-player prisoner’s dilemma game. Relaxing the assumption of linearity has profound consequences for the evolution of costly social behavior – here, an evolutionarily stable strategy (ESS) can be to invest probabilistically rather than to always defect (the latter being the only ESS in a one-shot, n-player prisoner’s dilemma (Archetti and Scheuring 2012)). In nonlinear public goods games, the invasion of punishment does not depend on social learning and copying – punitive strategies can therefore invade when they are initially rare in a population (e.g., see Boyd et al. (2010), which is discussed in light of nonlinear payoffs in Raihani and Bshary (2011)).

Another, nonmutually exclusive possibility is that punishment yields direct reputation-based benefits to punishers (Barclay 2006; Raihani and Bshary 2015a). These benefits can arise if observers cooperate because they wish to avoid being targeted for punishment (e.g., Santos and Wedekind 2015; Santos et al. 2011, 2013) or because punishment acts as an honest signal of the punisher’s other-regarding preference or cooperative intent. In the latter scenario, punishers benefit because they are more likely to be trusted (Barclay 2006; Jordan et al. 2016), rewarded by others (Raihani and Bshary 2015b), or preferred as interaction partners (Raihani and Bshary 2015a). A signaling account of punishment can

explain the tendency to punish in seemingly anonymous one-shot encounters without invoking the assumption that punishers expect to interact with the target of punishment in the future. Rather, if the benefit of acquiring a punitive reputation outweighs the costs associated with punishing, then signaling punishment could in principle be favored by selection (Jordan and Rand 2017; Raihani and Bshary 2015a; Santos and Wedekind 2015).

A final possibility is that punishers benefit because they increase their fitness relative to that of targets. This is the case whenever it costs less to administer punishment than it does to receive it. Competition for status (in terms of payoffs not reputation) may indeed be an important function behind antisocial punitive sentiment (Bryson et al. 2014; Sylwester et al. 2013): previous studies have shown that when the fee to fine ratio of punishment is increased to 1:1 or greater, then antisocial punishment is markedly reduced (Falk et al. 2005). The extent to which competition for status (in terms of increased payoffs, rather than reputation) also explains some variation in justified punishment remains an open question.

How Is Punishment Studied in the Lab?

In lab studies, punishment is typically operationalized by allowing individuals to pay a (monetary) fee to exact a fine on a cheating individual (e.g., Fehr and Gächter 2002). Typically, the cost to the punisher is assumed to be lower than the cost to the target (the most commonly used ratio is 1: 3) although it is not obvious that this assumption would necessarily hold in real-world interactions, where players might often vary in their ability to mete out and sustain the costs of punishment (Raihani et al. 2012). Though humans are often willing to pay to impose costs on coplayers in these stylized experimental scenarios, it is unclear what behavior this captures in the real-world interactions (Guala 2012), particularly in industrialized societies, where punishment tends to be administered by legitimate centralized authorities, rather than by peers of the target (Baldassarri and Grossman 2011). Evidence for peer punishment has been

observed in smaller-scale societies (e.g., Mathew and Boyd 2011), but real-world evidence for peer punishment in industrialized societies is relatively scarce. Despite the uncertainty over the real-world behaviour that lab punishment maps onto, studying punishment in lab settings can be useful if it allows researchers to identify the situational or proximate factors which elicit punitive sentiment. By identifying the scenarios that reliably motivate punishment in the lab, we may be able to gain insights into the ultimate (evolved) function of punitive sentiment (Price et al. 2002).

Motives Underpinning Punishment

Previous studies have shown that interacting with a cheat produces feelings such as anger, disgust, and envy (Fehr and Gächter 2002; Pedersen et al. 2013), and that being allowed to punish the cheating individual (usually by paying a small fee to exact a larger fine on the cheat), individuals experience relief from these negative feelings and may even derive subjective pleasure from the punitive act (De Quervain et al. 2004). Investing in third-party punishment, where the punisher intervenes on behalf of another individual (Fehr and Fischbacher 2004), is also subjectively rewarding for punishers (Buckholtz et al. 2008).

Though interacting with cheats can elicit punitive sentiment, the precise cause of these feelings remains debated. In most laboratory settings, individuals that interact with cheats incur losses and experience disadvantageous inequity, in that they end up with lower payoffs than the cheat (Dawes et al. 2007; Raihani and McAuliffe 2012). Thus, punitive sentiment could feasibly arise from either the negative utility associated with experiencing losses (i.e., revenge-based motives) or from the negative utility of experiencing disadvantageous inequity (i.e., fairness concerns). These two potentially separate motives for punishment also suggest alternative evolved functions for punishment, with revenge-based motives being more consistent with a deterrent function of punishment and fairness concerns being more consistent with a fitness-levelling function of punishment (Bone and Raihani 2015; McCullough et al. 2013; Price et al. 2002).

Punitive Sentiment Reflects Fairness Concerns

Early attempts to tease these two possibilities apart found that when losses are held constant (see Bone and Raihani 2015; Bone et al. 2016a; Raihani and McAuliffe 2012), or are not a feature of the interaction (Dawes et al. 2007) then punishment is most common when the punisher has lower payoffs than the target. Preferences for equality are also a reliable predictor of investment in costly punishment in public goods games (Johnson et al. 2009) and that third-party punishment is more likely to reflect envy than moralistic anger on the part of the punisher (Leibbrandt and Lopez-Pérez 2011, 2014; Pedersen et al. 2013). When possible, punishers typically tailor their investment in punishment to equalize payoffs between themselves and the target (Bone and Raihani 2015) and will even invest in punishment when these actions will not be communicated to the target (thereby preventing any deterrence-based benefits (Crockett et al. 2014)). Finally, when given the option to compensate themselves or a third-party without additionally punishing a cheat, most subjects choose this option (Charness et al. 2008; Chavez and Bicchieri 2013; FeldmanHall et al. 2014; Lotz et al. 2011), suggesting that when alternative means to establish fairness are possible, then punitive sentiment decreases. Together, these many and varied findings suggest an important role of fairness concerns (synonymous with feelings of envy or disadvantageous inequality aversion) are an important proximate motive underpinning punishment decisions in humans.

Punitive Sentiment Reflects Desire for Revenge

Though the importance of fairness concerns is apparent, based on the empirical literature above, other studies have also emphasized the role of revenge in producing punitive sentiment. For instance, when individuals only have access to inefficient punishment (which doesn't allow punishers to redress disadvantageous inequity), they

still punish cheats (Bone and Raihani 2015), mitigating against fairness concerns as the sole underlying cause of punitive sentiment. Moreover, Marczyk (Marczyk 2017) showed that only inequality paired with losses motivated punishment – inequality that was produced without harming the other player did not motivate punishment (but see Dawes et al. (2007) for contrasting evidence).

Conclusion

Punishment has been well studied in laboratory games – where several studies have shown that people are willing to forfeit their own resources to take resources from another player. Punitive sentiment is apparently caused by a desire for revenge, fairness concerns, and a desire to elevate payoffs relative to that of the target. Enacting punishment yields subjective rewards. Despite the many lab-based studies, the prevalence of punishment in the real world seems scarce. Thus, a clear avenue for further research is to ask how the punitive sentiment we observe in the lab manifests in the real world.

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Purpose

► Biological Function

Pursuit Deterrence Hypothesis

► Predator Confusion Hypothesis

Puzzle of Altruism, The

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Synonyms

Mechanisms of altruism

Definition

There are different evolutionary mechanisms such as kin selection, reciprocal altruism, and cultural

group selection that explain the mechanisms of altruism commonly seen in human societies.

From an evolutionary perspective, a behavior is called social if it influences the fitness of both the actor and the recipient (West et al. 2007). William Hamilton (1964) classified social behaviors into four types: those that increase the fitness of both the actor and the recipient (mutual benefit), those that increase the fitness of the actor but decrease that of the recipient (selfishness), those that decrease the fitness of the actor but increase that of the recipient (altruism), and those that decrease the fitness of both the actor and the recipient (spite). The most puzzling seems to be altruism because even spite might have a relatively straightforward explanation: An actor might gain a foothold by a fitness decreasing behavior if it decreases the fitness of a rival even more. Therefore, most effort in social evolution theory in the last half-century went into developing evolutionary explanations of altruistic behavior.

Hamilton proposed kin selection as one mechanism through which natural selection can favor altruism over selfishness: If the actor and the recipient of the altruistic behavior are genetic relatives, the altruistic behavior is actually helping the survival of the altruist's genes. More precisely, altruistic behavior will evolve if the coefficient of genetic relatedness, r , exceeds the cost-benefit ratio of the altruistic behavior, c/b (see also Nowak 2006).

The first solution to altruism among nonrelatives was proposed by Trivers (1971) in his theory of reciprocal altruism: If the actor behaves altruistically toward the recipient in need at time t_1 , and the recipient returns the favor when the actor is in need at time t_2 , then both of them will be better off compared to the situation where neither behaved altruistically. The obvious threat to the evolution of altruism through reciprocal altruism is the possibility of cheating: taking the benefit at t_1 but never returning it. Since this is evolutionarily the most beneficial strategy, altruism cannot evolve unless cheating is prevented. For this reason, relatively complex cognitive skills, such as memory for past exchanges and mind reading skills for recognizing potential cheaters, must be in place before reciprocal altruism can lead to the

evolution of altruistic behavior (see Stevens and Hauser 2004).

In reciprocal altruism, reciprocity is direct: The same actor and recipient are involved in both interactions. Indirect reciprocity, on the other hand, involves the introduction of third parties at time t_2 and is based on the principle of reputation. By behaving altruistically at time t_1 , the actor gains a reputation in the population of being an altruist. This will increase his chances of receiving altruistic benefits from other members of the population at a later time because of his reputation of being a suitable cooperation partner (Nowak and Sigmund 1998).

One final mechanism proposed to solve the puzzle of the evolution of altruism is cultural group selection (Fehr and Fischbacher 2003). Economic exchange games played in the laboratory demonstrate that humans cooperate altruistically even when their game partners are nonrelatives (excluding kin selection as a mechanism), when the game is one shot with no future interactions (excluding reciprocal altruism), and when the game is played anonymously with no possibility of reputation building (excluding indirect reciprocity). Even under such conditions, at least some individuals display altruistic rewarding (rewarding fair and norm-compliant behavior even when the rewarding is costly to the actor) and altruistic punishment (punishing unfair behavior even when the punishment is costly to the actor). It has been claimed that stronger reciprocators, those who use altruistic rewarding and punishment, are at a disadvantage as individuals compared to selfish individuals; however, a group composed of strong reciprocators will be more likely to survive than a group composed of selfish individuals. Thus, altruism in the form of strong reciprocity has most likely evolved through the mechanism of cultural group selection. This proposal is controversial (see West et al. 2011), and it

remains to be seen whether individual selection mechanisms will suffice to explain strong reciprocity.

Cross-References

- [Evolution of Human Sociality](#)
- [Evolution of Reciprocal Altruism](#)
- [Indirect Benefits of Altruism](#)
- [Reciprocal Altruism](#)
- [Reciprocal Altruism and Group Living](#)

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Pyrexia

- [Fever](#)

Q

Qualitative Versus Quantitative in Evolutionary Science

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Quantitative data are analyzed using statistical techniques which summarize the data and supply inferential reports on the relationships between quantized variables. These can include such things as correlation coefficients, effect sizes, *p* values, odds ratios, and often (but not always) make use of the properties of the general linear model (Grafen and Hails 2002).

Synonyms

[Data analysis](#); [Research methods](#)

Definition

Qualitative data are necessarily subjective, being filtered through the medium of a human consciousness. Techniques for collecting these include interviews, ethnography, observations, or clinical reports. Resultant data are analyzed using techniques such as discourse analysis, thematic analysis, or interpretive phenomenological analysis. Goals of analysis include the triangulation of diverse viewpoints, and, arguably, aim at *saturation* – a state where enough iterative analysis has been performed, that the same themes now keep recurring (Willig 2013).

Quantitative data are numbers. They are collected through such activities as observations, questionnaires using numerical scales, and direct measurements of behavior, or physiology.

Introduction

Obviously, analysis of both sorts of data are searches for meaning, but meaning of rather different kinds. Qualitative data analyses expressly dig into the meanings that a person, or group, gives to events and experiences (e.g. Dempsey et al. 2019). Quantitative data try to go beyond mere numerical counts, to express confidence about the degree of relationship between variables. The ideal is to provide causal explanation, but this is rarely, if ever, achieved in behavioral science.

Quantitative data are often considered objective, but, once one appreciates that one can quantize subjective impressions, via Lickert scales, for example, then this cannot be the primary distinction between the two types of data. Quantitative data are numbers, and numbers, unless one is a mathematical Platonist, are *adjectives of quantity*, rather than reality itself. Thus, numbers (or rather, numerically operationalized behavioral data, or psychological constructs) can be compared with

degrees of rigor, and abstraction unavailable to qualitative data, but it does not follow that they are thereby more scientific. This may appear heretical to some people, but such people are confused by one of two things: Physics Envy or the Drunkards Search Principle.

The Art or The Real?

Physics Envy is a misplaced desire for elegance in explanation. In physics (but only here), elegance *is* one guide to truth. However, evolution is a series of messy kludges that maximizes fitness, without achieving perfection. Evolved solutions to fitness problems usually involve things like opponent processes that maximize fitness by achieving homeostasis or similar balances and trade-offs in an organism. Thus the ideal of elegant equations to explain human behavior is likely to be a wild goose chase (Minsky 1988).

The drunkard searches under a streetlight for his keys, not because they are there, but because the light is better there. Scientists also tend to search the data in places where their techniques work. However, theory, not technique, should govern what questions we ask of the data (Cronbach and Meehl 1955).

Subjectivity can appear messy, and unscientific, compared to counting. Is it true that qualitative research is synonymous with a postmodernist relativistic anti-science position? Although there is evidence of a specifically qualitative-based opposition to evolutionary principles (Jonason and Schmitt 2016), we argue that this antipathy is both misplaced and unnecessary. Both types of analysis can be done well or poorly, with rigor, or not. There is nothing unscientific about acknowledging that humans have minds. Deflationary accounts of psychology – such as extreme behaviorism – seek to downplay or eliminate consciousness from casual explanations. However, there is no compelling reason for evolutionary scholars to feel impelled down this path. Nature does not give free lunches, and subjective consciousness would be, if it were causally impotent, the most

lavish of all free lunches. Thus, evolutionary scholars should, on pain of incompleteness, find a place for causally efficacious consciousness in their science. There are various ways in which this heterophenomenology might be achieved (Dennett 2003). Two obvious illustrations are provided by the study of linguistic entities and self-report.

Language is a species-typical adaptation, and (arguably) our most direct window into the subjective human psyche. Its universality supports one evolutionary psychology foundational belief – that of the psychic unity of humanity. Humans use language to (among other things) generate social selves – centers of narrative gravity. Brains model worlds and any sufficiently advanced model contains a model of itself. Humans are good at this modelling – with the appropriate caveats of Freud (2018) and Trivers (2011) whose insights into self-deception are easily accommodated within evolutionary theory – particularly evolutionary game theory. Independent validations exist of our ability to access such things as personal history, attentional focus, sensations, and evaluations, but humans are poor at accessing their own motives (Nisbett and Wilson 1977). It does not follow that they are poor at assessing one another motives, however.

Self-reports of cognitive risk are more predictive of depression and schizophrenia in a non-clinical population than any extant brain scan (Haeffel 2010). The undoubted fact that humans fool themselves (Freud 2018; Trivers 2011) does not mean that these centers of narrative gravity are not legitimate foci of scientific analysis – on the contrary, they are part of the species-typical human signaling system, and rigor in analysis of meaning-making should therefore be part of the evolutionary toolkit.

Conclusion

Subjective meaning-making is a species typical trait and deserves to be treated as such by evolutionary scholars. Said meaning-making is not the final word on predictive or descriptive accounts

of human behavior, but it can be treated with appropriate rigor, as part of the complete picture of human behavior.

Cross-References

- [Objectivity](#)
- [Personality](#)
- [Subjectivity](#)

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Quality of a “Catch”

- [Women's Mate Value](#)

Quality of Attachment

- [Effect on Attachment](#)

Quality Versus Quantity

- [Quantity Versus Quality of Offspring](#)

Quantity Estimation

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Synonyms

[Approximate number system](#); [Number sense](#)

Definition

The ability to represent and manipulate the approximate quantities of collections of objects.

Introduction

The behavior of a very diverse range of nonhuman species and human infants and young children indicates that they can discriminate the relative quantity of both discrete collections of objects and continuous magnitudes, such as area (Feigenson et al. 2004). Research on these systems has intensified over the past decade, as has the study of the relation between these abilities and children's learning of formal, symbolic mathematics. The primary focus has been on the ancient approximate number system (ANS) that in turn may be part of a more general magnitude processing system. In primates the systems for

magnitude processing are situated in an area of the parietal cortex called the intraparietal sulcus (IPS) and functionally integrated with areas of the prefrontal cortex during quantity discriminations (Nieder et al. 2002; Piazza et al. 2004).

The selection pressures that drove the evolution of systems for processing discrete and continuous magnitudes likely involved foraging efficiency and evaluation of social signals associated with mating competition or mate choices (Geary et al. 2015). Foraging efficiency requires searching in locations that will provide the best payoff per unit of foraging time. The payoff will necessarily be dependent on the discrete number of prey and their size (i.e., magnitude) at a particular location, as well as the time needed to capture them and the number of conspecifics (others of the same species) foraging in the same place. Selection on foraging behaviors and decisions (e.g., when to switch to a new location) will thus favor the evolution of brain and cognitive systems that can represent and operate on the number and size of prey and integrate these with a representation of time and the number of competitors for the same prey.

Traits associated with mating competition or mate choices are often exaggerated and can only be expressed by fit individuals. These mating-related traits thus signal the health and overall fitness of the individual and can include traits based on discrete number, such as frequency of mating-song bouts, or continuous magnitudes, such as the area of colorful plumage patches on birds. Across species continuous magnitude traits (e.g., area) are more common than discrete traits in mating contexts, and computational simulations suggest that the systems for representing continuous magnitudes likely evolved prior to the evolution of the ability to discriminate discrete quantities. Nevertheless, most of the research on human quantity discrimination has focused on the ANS.

The signature feature of the ANS is that its representations are inherently “noisy” – resulting in approximate representations of quantity – and this noise increases with increasing set size,

following the Weber-Fechner law (Moyer and Landauer 1967). Behaviorally, the result is that accuracy in discriminating quantities is dependent on the ratio of the quantities and not the absolute difference between them. The ability to discriminate between collections of 4 and 8 (2 to 1 ratio) objects is much easier (faster and more accurate) than between 24 and 28 (1.16 to 1 ratio) objects, even though the absolute difference is the same. For humans, the acuity of the ANS undergoes substantial changes from infancy through adulthood. Neonates can discriminate between collections that differ by a 3 to 1 ratio, a ratio of 3 to 2 at 9 months of age, and up to a ratio of 11 to 10 in adulthood (Halberda and Feigenson 2008). The ANS may also support numerical intuitions related to arithmetical concepts and procedures. By 2 years of age, ANS representations are believed to support an intuitive understanding of ordinal relations of object sets (four objects > three objects > two objects) and possibly an implicit understanding of the effects of adding one object to or subtracting one from collections of a small (<4) number of objects.

In recent years, the neural signatures of these quantitative abilities have been studied in infants and young children (e.g., Ansari 2016), revealing both similarities to and differences from the brain systems that are engaged when adults process quantities. As with adults (and nonhuman primates), the engagement of the IPS and prefrontal regions is prominent during infants’ and young children’s processing of quantitative information, but with a strong right hemispheric bias, as contrasted with bilateral engagement in adults. Hyde et al. (2010), for instance, used near-infrared spectroscopy to identify the brain regions that are engaged when 6-month-olds discriminate between collections of objects (e.g., four vs. eight). They found increased activity in the right parietal lobe, localized in an area consistent with the adult IPS. Other studies suggest that the engagement of the IPS in both the left and right hemispheres of adults is due to their expertise with symbolic mathematics; that is, the engagement of the left IPS during the processing of quantities

associated with number symbols may only emerge with formal schooling.

On the basis of the numerical and potentially arithmetical competencies built into the ANS, it has been hypothesized that this system may be the foundation for children's learning of symbolic mathematics. Indeed, early studies found evidence that individual differences in ANS acuity were correlated with individual differences in children's mathematical achievement generally and perhaps to learning disabilities in mathematics. The results from subsequent studies have been more mixed, and there is now considerable debate regarding when during learning and how strongly ANS acuity contributes to symbolic mathematics. The primary alternative hypothesis is that young children's general mathematical achievement may be more strongly related to the speed and accuracy with which they can compare or manipulate (e.g., order) the magnitudes associated with Arabic numerals than to performance on measures of ANS acuity; in other words, the foundation for formal mathematical development may be children's learning of number symbols (number words and Arabic numerals) and the quantities they represent.

A recent meta-analysis found stronger associations between measures of number symbol processing (e.g., speed of determining which of two numerals is larger) and formal mathematical competencies (e.g., performance on achievement tests) ($r \sim 0.30$) than between measures of ANS acuity and these competencies ($r \sim 0.24$) (Schneider et al. 2016); the correlation between measures of ANS acuity and formal mathematical competencies is attenuated ($r \sim 0.16$) but still significant after controlling for domain general abilities, such as intelligence. One possibility is that fluency in processing number symbols and non-symbolic quantities independently contributes to different aspects of formal mathematical competencies. Another possibility is that ANS acuity has a time- and content-limited influence on the early learning of symbolic mathematics. Indeed, a series of studies revealed that the relation between measures of ANS acuity and young children's

mathematical achievement was fully mediated by their understanding of the cardinal value of number words, controlling for domain general cognitive abilities, preliteracy skills, and parental education (e.g., Chu et al. 2015). In this view, ANS acuity facilitates children's learning of the meaning of number words and Arabic numerals, but does not directly contribute to their formal mathematical development thereafter.

This cannot be the entire story, however; that is, it is not simply a mapping of number words or numerals to ANS representations. In nonhuman species, the development of mappings between the numerals (e.g., "3") and the quantities they represent (e.g., "●●●") takes thousands of trials to achieve, but once young children learn the first few ANS-number symbol mappings, they make a critical conceptual leap. They understand that all count words or numerals have a unique quantity associated with them and can infer these quantities once they learn the standard sequence of symbols (e.g., "one, two, three, ..."). Although the ANS embodies quantity information, nonhuman species do not make this conceptual jump. The ability to make these types of explicit, generalizable conceptual insights may be uniquely human, but exactly how this ability interacts with the ANS is not currently known.

Conclusion

Studies that span myriad species all point to the existence of an evolved system for representing and comparing the approximate quantities of discrete collections of objects and continuous quantities (e.g., area) and perhaps providing an intuitive understanding of aspects of arithmetic. In primates, magnitude representations are situated in the intraparietal sulcus and are co-activated with areas of the prefrontal cortex during quantity discriminations. Although much is now understood about the behavioral and brain signatures of this evolved system, its relation to competence with formal, symbolic mathematics is vigorously debated and not fully understood.

Cross-References

- [Cognitive Ethology](#)
- [Cognitive Science](#)
- [Development](#)
- [Sexual Selection](#)

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Quantity Representation

- [Space, Time, and Number](#)

Quantity Versus Quality of Offspring

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Synonyms

[Life history theory](#); [Offspring](#); [Quality versus quantity](#); [Reproductive strategies](#)

Definition

A key trade-off that organisms face concerning quantity versus quality in offspring: organisms that tend to invest heavily in offspring also tend to have lower numbers of offspring whereas organisms that invest little in offspring also tend to have higher numbers of lower quality offspring.

Introduction

Organisms continually face trade-offs for how to allocate limited energy and resources. One of the key trade-offs involves the quantity versus the quality of offspring. On the one hand, if organisms invest heavily in their offspring to better their developmental and survival outcomes, they tend to only have enough resources to produce a small number of “high-quality” offspring. On the other hand, if organisms make little parental investment per child, they can produce a large number of “low-quality” offspring – although each child has a lower chance of survival, there is a higher probability that at least some offspring will survive long enough to reproduce.

Ecological Conditions Affecting Reproductive Trade-Offs

According to life history theory (e.g., Stearns 1992), which concerns the allocation trade-offs

that organisms face throughout their lifespans between somatic investment (maintenance and growth) and reproductive expenditures, different species as well as organisms within species tend to evolve a reproductive strategy that favors quantity or quality based on various ecological conditions. As described below, such ecological conditions can be broadly classified into two types: environmental harshness and environmental unpredictability.

Environmental Harshness

A key factor that affects reproductive trade-offs is environmental harshness. Environmental harshness is indicated by the rates at which external factors result in the death or disability of organisms at each age in a population. External causes of disability and death, or extrinsic morbidity-mortality (Ellis et al. 2009), include predation, droughts, and disease and can occur regardless of organisms' allocation of resources between the competing life functions of maintenance, growth, and reproduction. When adults face high extrinsic morbidity-mortality (e.g., homicide, famines), offspring quantity is favored over quality. That is, if the environment imposes high rates of unavoidable mortality, an adult organism would benefit by quickly producing a larger number of offspring to increase the probability that some will survive into adulthood long enough to reproduce and propagate their genes. Heavily investing in a small number of high-quality offspring may not pay off in an environment with high risk of adult mortality, due to the higher likelihood of disability and death of the parent before the offspring receive the full benefits of their investment. For example, among the Ache, homicide, external warfare, and accidental deaths associated with food acquisition are some of the leading causes of death among adults. In turn, mating partnerships among the Ache are relatively short and women have children by several different fathers, reflecting a preference for offspring quantity over quality (Kruger and Nesse 2006). In contrast, when extrinsic morbidity-mortality affects the young, offspring quality is favored over quantity. An example of juvenile extrinsic morbidity-mortality can be found among red deer,

where male juveniles have high mortality rates as a result of their greater susceptibility to food shortages due to their faster growth rates and greater nutritional requirements (Clutton-Brock et al. 1985). In this case, adult red deers are better off investing more parental care into a small number of offspring to better ensure their survival in the face of environmental harshness rather than to produce a large number of offspring who are all unlikely to survive without sufficient parental investment. However, a high-investment strategy is only valid when parental investment has an effect on offspring survival. In contexts where offspring survival rates are independent of parental investment, offspring quantity would be favored over quality.

The effects of environmental harshness on the trade-off between quantity and quality of offspring also depend on population density (Pianka 1970), resource availability, and predation. For example, research on Trinidadian guppies has shown that environmental conditions such as high extrinsic morbidity-mortality (due to high predation) and high resource availability favored offspring quantity over quality. Although the costs of mortality are high and unavoidable in harsh environments, the strategy of producing a large number of offspring can only be sustained if there are enough resources in the environment for these offspring. In contrast, environmental conditions such as low predation, high population density, and lower resource availability favor offspring quality over quantity. High competition for resources as a result of high population density and limited resources leads to greater investment in offspring growth in order for offspring to be more competitive in such environments. Indeed, guppies in such environments invest more heavily in a small number of high-quality offspring to improve their chances of survival in a highly competitive environment.

Environmental Unpredictability

Environmental unpredictability refers to variation in environmental harshness over time and space (Ellis et al. 2009). Many organisms live in environments where resources and mortality rates vary in unpredictable ways due to factors such

as the behavior of predators or the weather. In unpredictable environments, morbidity-mortality risks are largely insensitive to the adaptive decisions and strategies of organisms and, therefore, are unavoidable. When there is high variation in adult mortality, adults are better off producing a large quantity of offspring rather than heavily investing in a small number of high-quality offspring due to their susceptibility to changing mortality rates.

However, when there is high variation in juvenile mortality, organisms may engage in one of two types of bet hedging: conservative and diversified (Einum and Fleming 2004). Conservative bet hedging corresponds to favoring offspring quality over quantity. In species where harsh environmental conditions affect an entire population over generations (e.g., years of drought), it is more beneficial to produce a small number of high-quality offspring who are equipped to handle the fluctuating conditions of the environment rather than a large number of low-quality offspring who are all unlikely to survive. In contrast, diversified bet hedging corresponds to favoring offspring quantity over quality. In species where environments vary substantially across individuals and within single generations, a large number of offspring (who have high phenotypic variance) would be preferred to increase the probability that at least some offspring would have a phenotype that would allow them to survive long enough in their environmental conditions to reproduce and propagate their genes.

Offspring Quality Versus Quantity Preferences in Humans

Human environments generally consist of low extrinsic morbidity-mortality (due to low predation pressures as a result of humans being at the top of the food chain), high population densities due to low extrinsic morbidity-mortality and efficient hunting-gathering practices, and high levels of competition for limited resources. These environmental conditions have resulted in humans evolving a general preference for offspring quality over offspring quantity. Low levels of extrinsic morbidity-mortality allow parental investment to have positive effects on offspring's

health, competitiveness, and reproduction; hence, it pays off for humans to invest heavily in their offspring to ensure their effectiveness in the highly competitive environment. In particular, it is adaptive in such environments for human males to produce only a few offspring, typically with the same mate, and to invest heavily in those offspring to ensure that they are of higher quality. As such, human paternal investment in children as well as monogamous marriage may reflect adaptive responses to morbidity, population density, and resource competition. Despite the fact that humans as a species are on the slow end of the life history continuum, however, there are key within-species differences in humans as a result of different environmental conditions.

Humans may evolve to favor either offspring quality or quantity depending on cues to extrinsic morbidity-mortality. When there are cues in the environment that extrinsic morbidity-mortality levels are high, humans tend to favor offspring quantity over quality. In these environments, heavy parental investment in offspring would not shield them from the dangers in the environment and would not enhance their fitness. Hence, parents would be better off producing a large number of offspring instead. One of the most important cues of extrinsic morbidity-mortality is low socioeconomic status (SES). Indeed, research has found that there is a negative correlation between SES and offspring number (Vining 1986) and a positive correlation between SES and levels of parental investment per child (Ellis et al. 1999). This could be because people living in low SES environments are more exposed to disability and death (thus cueing them to the harshness of their environment), but at the same time, they possess adequate resources to support the growth and reproduction of a large number of offspring.

Other important cues to extrinsic morbidity-mortality levels are personal knowledge of deaths among adolescents, exposure to violence, and environments characterized by short life expectancies. These cues inform individuals about their own and their offspring's probability of survival (which is likely to be relatively low) in their environment, thus causing them to favor offspring quantity over quality so that at least some of their offspring can survive. Harsh and

neglectful parenting styles can also indicate to offspring that a parent favors offspring quantity over quality, which signals to offspring that this is the appropriate strategy for their environment, thus propagating this strategy in future generations (Berezkei and Csanaky 2001).

Cues to the level of unpredictability in the environment are also informative. Interestingly, it is the level of unpredictability in the environment experienced during childhood that shapes preferences for offspring quantity versus quality. For instance, one indicator of childhood unpredictability is the number of parental changes as a result of divorce, death, remarriage, and adoption, among others. Frequent changes in parental figures indicate a high level of environmental instability and predict earlier age at first sexual intercourse, higher rates of premarital intercourse, teenage pregnancy, and premarital birth, which may all indicate a preference for offspring quantity over quality. Another indicator of childhood unpredictability is the frequency of residential change. Children who frequently move experience changes in social groups and may be more likely to join delinquent groups, who are more accepting of newcomers. Joining these delinquent groups may expose them to harsher environmental conditions which may prompt them to favor offspring quantity over quality. Indeed, frequent residential mobility is associated with earlier age at first sexual intercourse, multiple sex partners, and higher rates of premarital sex and pregnancy.

Conclusion

The application of life history theory to explain the reproductive behavior of organisms has been fruitful and has the potential to guide further research regarding the evolution and development of specific phenotypic traits and strategies associated with the trade-off between offspring quality and quantity. Understanding this important trade-off may provide insights into how organisms make reproductive decisions in not only the environments where they evolved but also in the modern world. In such evolutionarily novel contexts, offspring quality is so highly favored by humans

that the populations of many wealthy, industrialized societies – including all of Asia and parts of Europe – have been shrinking in recent decades. Researchers and policymakers who have been concerned with population growth rates and aging populations would benefit from a consideration of life history theory and, more generally, evolutionary biological perspectives.

Cross-References

- ▶ [Adolescent Parenthood](#)
- ▶ [Biparental Care](#)
- ▶ [Child Mortality](#)
- ▶ [Cost-Benefit Analysis](#)
- ▶ [Early Childhood and Adolescence](#)
- ▶ [Ecological Factors and Rape](#)
- ▶ [Ecological Influences](#)
- ▶ [Ecology of Paternal Investment](#)
- ▶ [Environmental Harshness](#)
- ▶ [Environmental Harshness/Mortality](#)
- ▶ [Environmental Influences](#)
- ▶ [Environmental Unpredictability](#)
- ▶ [Environmental Unpredictability and Bet-Hedging](#)
- ▶ [Fast Versus Slow Strategies](#)
- ▶ [Infant Survival](#)
- ▶ [Life Expectancy](#)
- ▶ [Prototypical r-/K-Selected \(Fast/Slow\) Species](#)
- ▶ [Prototypical r-/K-Selected \(Fast/Slow\) Species](#)
- ▶ [Paternal Investment](#)
- ▶ [Predictors of Sexual Debut](#)
- ▶ [Sexual Outcomes](#)

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Quasisocial

- [Cooperative Breeding](#)

Queasiness

- [Nausea](#)

Questionnaire

- [Self-Reports](#)

R

R = Coefficient of Relatedness

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Synonyms

Calculating relatedness; Kinship; Measure of relatedness

Definition

A measure of the probability that two individuals share a gene due to recent, common ancestry.

Introduction

Relatedness is a consequence of individuals sharing copies of particular genes or alleles. Alleles are variants of the same gene, for example, one of the genes for eye color has an allele for blue eye color and an allele for brown eye color. The coefficient of relatedness, denoted by the symbol r , is a measure of the probability that two individuals

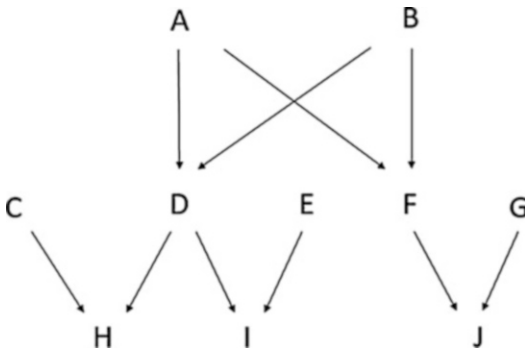
share the same allele via a recent, common ancestor, and thus it is “identical by descent” (Hamilton 1964). This measure excludes any identical alleles that are shared simply by being members of the same population or species.

Calculating the Coefficient of Relatedness: r

In diploid species like humans, and most other mammals, an egg and sperm, each containing half the normal number of chromosomes, fuse to form a single cell or zygote; therefore, each parent contributes 50 % of its genes. Half of a child’s genes come from their mother, and the other half of their genes come from their father, which means that the probability that the child shares an allele, identical by descent, with its mother is $1/2 = 0.5$ and with its father is also $1/2 = 0.5$.

R can be calculated for any pairs of relatives, for example, a grandparent and grandchild are related by one fourth. One parent received half its genes from the grandparent and then passed on half of these genes to their child. With distant relatives this becomes more difficult to follow, but there’s a simple method that can be used to calculate r , and it starts with the drawing of a family tree or pedigree (Fig. 1).

At each generation link (indicated by the arrows), 50 % of a parent’s genes are passed on, so there is a 0.5 probability that a particular allele



R = Coefficient of Relatedness, Fig. 1 Family tree. Letters refer to individuals, and the direction of an arrow indicates a parent-to-child relationship

is passed on. For n links, the probability is $(0.5)^n$. Thus to calculate r between any two individuals, we need to identify the shortest possible pathways or number of links between them, via any common ancestors. For direct relationships, this is straightforward. For example, A and D are parent and child with one link, so $r = (0.5)^1 = 0.5$; A and H are grandparent and grandchild with two links, so $r = (0.5)^2 = 0.25$.

D and F are full siblings with the same parents, and so to calculate r the links are counted via both parents (from D to A to F and also from D to B to F) so $r = (0.5)^2 + (0.5)^2 = 0.5$. H and I are also siblings, but with only one parent in common they are half-siblings, so $r = (0.5)^2 = 0.25$. H and J are cousins with two common ancestors, their grandparents, A and B. Thus $r = (0.5)^4 + (0.5)^4 = 0.125$. These calculations assume that incestuous inbreeding, which would increase the value of r , has not occurred within the family tree (Fig. 1).

Conclusion

The relatedness coefficient, denoted by r , is a measure of the likelihood that two individuals share a copy of the same allele, via a recent common ancestor (Hamilton 1964). It can be calculated for two individuals using a known pedigree or family tree, by identifying the common ancestors and counting the number of generational links between them.

Cross-References

- [Hamilton's Rule and Theoretical Implications](#)
- [Kin Recognition and Classification in Humans](#)

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R and K Strategies

- [Life History Strategies](#)

r Strategy

- [Semelparity](#)

r/K-Selection Strategies

- [Fast Versus Slow Strategies](#)

Race as a Social Badge (Kurzban)

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Synonyms

[Perceptions of race](#); [Race encoding](#); [Racial group relationships](#); [Social categorization by race](#)

Definition

Race encoding is a by-product of adaptive cognitive mechanisms to solve socialization and coalitional problems. Thus, phenotype and other traits work as a social badge for racial identification.

Introduction

Choosing a social interaction is an adaptive problem that would have favored cognitive mechanisms designed to make good decisions about socialization and group engagement (Kurzban and Leary 2001; Kurzban and Neuberg 2005; Kurzban et al. 2015). Just as there are evolutionary mechanisms prepared to associate fear with nonhuman predators, similar mechanisms exist to facilitate the association of fear with coalitional outgroup members (Cosmides et al. 2003). Such psychological mechanisms that enable individuals to distinguish quickly and efficiently between in-group and out-group are necessary to promote avoidance and caution with respect to out-group members. After eliciting these associations, they can be triggered immediately on the perception of out-groups.

Several characteristics are used by humans as clues or social badges to distinguish allies and rivals (e.g., dress, behavior, or language) (Cosmides et al. 2003). Among these, phenotypic traits (i.e., skin color, face shape, hair texture) that evoke the idea of race can be used to determine this categorization (Kurzban et al. 2001). Racial identification does not necessarily imply racism, it is just one way of categorizing people in groups. But racism requires such identification of people as being in or out of racial group. Thus, there is an important computational mechanism, since racial stereotypes are derived from this racial identification. And many of the discriminations and prejudices against minority groups stem from stereotypes.

Race Perception and Encoding: A Badge for Social Categorization

It seems very likely that natural selection has favored the development of a machinery encoding

sex and age automatically and mandatorily, but the same did not occur for race (Cosmides et al. 2003; Kurzban et al. 2001; Voorspoels et al. 2014). The reason is that no specific psychological mechanism was selected in the course of evolution for race encoding, since hardly our ancestors moved for great distances. Thus, it is unlikely that a mechanism for the identification of races has developed, since the individuals had no contact with populations of distinct phenotypic traits. In addition, our ancestors usually lived with individuals of different ages and sex, but not of other races. Therefore, selected cognitive adaptations for sex and age encoding allowed useful inferences, while there would be no reasons for a specific mechanism in relation to race.

In this regard, in social psychology prevails the perspective that people encode race automatically and mandatorily of all individuals. In an evolutionary perspective, categorizing individuals by race is not inevitable, but it occurs as a by-product of the adaptive mechanism for coalitions and alliances (Cosmides et al. 2003; Kurzban et al. 2001). Thus, phenotypic traits would be considered by the cognitive mechanisms for the in-group and out-group processes. Race would be a social badge of differences between groups arising from the alliance-building machinery. That is, there is no exclusive mechanism for race encoding. These operations are performed via nonautomatic or mandatory computational processes (Cosmides et al. 2003).

When individuals are categorized as in-group or out-group, there are many internal and external aspects that crosscut race, and it is possible for individuals to adopt one of these characteristics for group classifications rather than race. In addition, any clues (such as phenotypic characteristics) should only be significant insofar as they acquire predictive validity for the existence of a coalition. Indeed, people seem to have experiences that involve race in their lives, and that predict patterns of cooperation and conflict.

A research conducted by Kurzban et al. (2001) showed that an exposure of approximately 4 min to an alternative world weakened the tendency of racial categorization. This suggests that racism is maintained because of other systems of social

alliance and it can be eradicated. Moreover, when badges of coalition affiliation do not track race, subjects reduce the degree to which they categorize people by race, and may even stop to do so. Once the cognitive apparatus detects the relationship between apparent badges and loyalty, these can emerge in the cognitive system as reliable clues of an alliance (e.g., dress, language, posture). In this way, humans detect these shared clues – which may be the race – and infer social alliances. Thus, race would be one of the variables that indicates coalitions, but other alliance social badges can be used.

This identification, as well as other social clues, can precipitate the categorization “us versus they.” Social badges can be used as a criteria to discriminate in favor of the in-group and against groups considered to be rivals. This process immediately evokes negative perceptions, as well as hostile feelings and attitudes toward rivals (e.g., aversion, unfavorable opinion, denial of access to resources) (Cosmides et al. 2003). Such anticipation impedes cooperation and creates a predisposition for competitive interaction between groups.

Conclusion

Human relations of cooperation and competition between individuals and groups can be explained by many adaptive cognitive mechanisms selected during the evolution of the human species (Kurzban and Leary 2001; Kurzban and Neuberg 2005; Kurzban et al. 2015). The human cognitive architecture contains many functionally specialized computational systems, but race encoding is a by-product of coalitional psychology, not an independent system. In fact, coalition allegiance is what the mind is encoding when we identify race (Cosmides et al. 2003; Kurzban et al. 2001; Voorspoels et al. 2014). Researches highlight the dynamic nature of social categorization that indicate race is a badge for alliances and coalition, and other arbitrary clues can be linked with this process. Thus, contextual changes in the badges that indicate inclusion or exclusion of groups may mitigate racial encoding. If contextual

information can reduce racial stereotypes, this can help the development of new strategies to reduce racial prejudice and discrimination (Williams et al. 2016).

Cross-References

- [Prejudice](#)
- [Racism](#)
- [Racism and Prejudice](#)
- [Robert Kurzban on Group Processes](#)

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Race Encoding

- [Race as a Social Badge \(Kurzban\)](#)

Race Prejudice

- [Racism](#)

Racial Discrimination

- [Racism and Prejudice](#)

Racial Group Relationships

- [Race as a Social Badge \(Kurzban\)](#)

Racial Identity

- [Relationship Between Culture and Race](#)

Racism

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Synonyms

[Race prejudice](#)

Definition

Discrimination process based on race or ethnicity.

Introduction

Evolutionary psychology proposes the evolution of psychological mechanisms as part of the evolution of an organism, pointing out which contexts activate these mechanisms and the behaviors resulting from them; thus, the result of an evolved

psychological mechanism is related to the solution of a specific adaptive problem (Buss 2015). In this sense, many of these problems were solved by the natural selection of mechanisms that made social behavior possible (Neuberg and Schaller 2016). For example, living in communities facilitated protection against predators, nurturing of offspring, and maintenance of resources. Nevertheless, the proximity with others also had downsides. The possibility of nonreciprocal collaboration and mating competition, which in some cases would lead to violent and, sometimes lethal, encounters rank as relevant problematic issues in these contexts. Because of that, for this social living to work, some threat detection mechanisms had to evolve. This included the capability of recognizing members of the in-group and to respond to cues of possible harmful behavior of members of out-groups (Neuberg and Schaller 2016).

Social Categorization and Discrimination

Kinzler et al. (2010) point out the social categorization is a trait that is displayed early in the childhood, and despite having infinite arbitrary criteria for labeling later in life, some categories are especially influent in early life, namely, age, gender, and race. Child, by the age of 2–3, is already capable of distinguishing people and treating them differently based on sex, and by 4–5, they already can distinguish people by race. This mechanism of social categorization is believed to be naturally selected, once it appears consistently among humans in different contexts and cultures (Kinzler et al. 2010).

Through this categorization, one could perceive other people's characteristics similar to his own and recognize his in-group. Similar individuals are normally taken as in-group, even if they do not share a good portion of one's genes. This distinction is known to imply in cooperation and support in front of those perceived as in-group belonging (Efferson et al. 2008).

In the other hand, people tend to less cooperative and often defensive and/or aggressive to

out-group members (those that are not perceived as similar or related). That's because, historically, out-groups implied harm on contact, usually due to territorial and resource disputes. However, social categorization is not sufficient to support avoidance and hostility with out-group members; a cognitive association between some kind of specific negative emotional state, for example, fear or anger, or specific stereotypes and the out-groups should be present to promote behavioral avoidance and caution (Schaller and Neuberg 2008).

Schaller and Neuberg (2008) pointed out that some features are naturally conceived as cues of aggressive disposition. Angry face expressions, for example, tend to evoke avoidance or defensive responses. This type of stimuli is normally more prominently perceived in out-group members, and once one has been in harmful dispute with a member of an out-group, the whole group can be taken as a threat. Thus, it indicates that people may learn to associate danger stereotypes and fear with coalitional out-group members (Schaller and Neuberg 2008).

Notably, this threat detection system has evolved to be highly sensible, considering that danger imposed by a possible failure in this process. This fact, however, implies in the possibility of associating threat to harmless expressions or behaviors, which means that for defensive behavior to be triggered, threat doesn't have to be real, but some condition may have been linked somehow to an actual threat, making people perceive aggressive cues where there are none (Becker et al. 2010; Neuberg and Schaller 2016).

Moreover, it is known that the context largely influences these perceptions. Resource scarcity and harsh mating disputes or even environmental conditions could lead to misperceptions of cues of possible threats. In general, people who perceive themselves as in danger conditions tend to be more aggressive to out-groups (Neuberg and Schaller 2014). Throughout history, it is possible to observe that prejudice in general tends to be greater when social tensions arise, as it will be discussed later. Considering this, the concept of threat may have a central role in the understanding of contemporary prejudices. In fact, different

types of threats elicit different types of behavioral and emotional responses: escape, anger, and disgust, which implies different discriminatory responses.

In summary, racism consists in a discriminatory response that emerges from a process of social categorization, which groups all Black people within a same uniform group and associates them with depreciative stereotypes.

Evolution and Modern-Day Racism

In a sense, acts of behavioral discrimination, stereotypes, and contemporary prejudices can be viewed as results of psychological adaptations from natural selection mechanisms for managing threats and opportunities (Neuberg and Schaller 2016). Nevertheless, as already mentioned, the mere "us-them" distinction is not enough to elicit aggressive responses, especially in modern-day societies.

Besides the social categorization, the association of negative stereotypes is key to the expression of any kind of prejudice, including racism. These stereotypes, in turn, are culturally constructed and are directly influenced by political, economic, and social contexts. So, despite depending on a psychological mechanism that was selected by the environment in human evolutionary history, racial prejudice is also reliant on variables existing in human present environment.

Jackson Jr. (2016) defends that racism, at least as we know it today, has not emerged until the eighteenth century. The prejudice based on race bias, in this sense, could have emerged at a context in which White people, who had economic power and social privileges in hands, starts understanding Black and Latino people as out-groups. This would, by itself, favor discrimination. In addition, though, negative stereotypes are attributed to those groups. These people are seen as subservient, less-than-human kind, which culturally served the purpose of social dominance. That, in a context of scarcity and social instability, could significantly influence race discriminative behavior.

Conclusion

In sum, mechanisms of social categorization developed from an early age are important to understand racial prejudice; however, in addition to simple categorization, it is necessary to enhance the preponderant role of identifying out-group members as potential threats to the safety of in-group members, giving them negative stereotypes. These perceptions, although biased, are adaptive, since they induce aggressive or avoidant responses that facilitates the protection of the members of the same group and their offspring (Gilead and Liberman 2014), consequently increasing the individual's fitness.

It should be emphasized that the activation of threat management mechanisms does not necessarily require the out-group express, for example, aggressive cues, which may indicate that stereotypes are attributed arbitrarily and used to base the subjugation of a group by the other, justifying discriminatory behavior. In this sense, the cultural, social, economic, and political contexts are fundamental to understand the implications of modern-day racism in human's evolutionary history.

Finally, it is pointed out that evolutionary psychology does not manifest an attempt to naturalize any kind of prejudice but only to comprehend and systematize the possible mechanisms involved in discriminatory acts.

Cross-References

- [In-group](#)
- [Intergroup Conflict](#)
- [Out-Group](#)
- [Prejudice](#)
- [Racism and Prejudice](#)

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Racism and Prejudice

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Synonyms

[Ethnic prejudice](#); [Racial discrimination](#); [Xenophobia](#)

Definition

Discrimination elicited by negative stereotypes that highlights race/ethnicity as a social badge of threat and reduces subjects to a set of negative

characteristics, feelings, and behaviors associated with their race/ethnicity.

Introduction

Many contemporary social problems are related to processes of discrimination that lead to exclusion and conflicts. Human psychological processes emerged as adaptations to environmental pressures throughout evolution and so evolved sensitive psychological mechanisms that promote avoidance and caution in regard to out-group members (Kurzban and Leary 2001; Neuberg and Schaller 2016). In social psychology, the perspective that people automatically recognize and take into account someone's race is dominant (e.g., Devine 1989). From an evolutionary perspective, categorizing individuals by race is a by-product of the adaptive mechanism for coalitions and alliances and is not inevitable (e.g., Cosmides et al. 2003; Kurzban et al. 2001; Voorspoels et al. 2014).

Social Categorization and Prejudice

Throughout evolutionary history, humans have lived as hunter-gatherers in relatively small subsistence groups. Cognitive mechanisms designed to enhance socialization arose by natural selection in order to solve the adaptive problem of social interaction (Kurzban and Leary 2001; Kurzban et al. 2015). Group life in forage societies provided important advantages, such as facilitating mate or parental investment, protecting against predators, and assisting the achievement of mutual goals (Kurzban and Neuberg 2005). However, some threats may also emerge, such as competition for resources and sexual partners, disagreement that could culminate in physical aggression or death, exploitation of generosity without reciprocity (i.e., low-effort free riders), and contamination by infectious diseases (Kurzban and Neuberg 2005).

For survival reasons, it was necessary to develop a machinery sensitive to the social badges or behaviors that signalize threats. The perception

of threat clues automatically activates aversive cognitions and emotions (Cosmides et al. 2003; Kurzban and Leary 2001), such as feeling angry about low-effort free riders and disgusted about the ill aspects in sick people (Kurzban and Neuberg 2005). Thus, each specific threat is associated with a singular set of emotional, cognitive, and behavioral responses (i.e., prejudice syndrome, Schaller and Neuberg 2008). These psychological adaptations designed to reduce these threats include, for example, the tendency to stigmatize in-group members who violate social norms and to avoid those who are contaminated by infectious diseases (Kurzban and Neuberg 2005).

Race Encoding and Racial Identification

Many mechanisms regulate intergroup relations. Social categorization involves a complex set of computational separate systems designed for different types of sociality. For example, the encoding of age, gender, and coalitional in-group or out-group is an automatic process (Kurzban et al. 2001). Natural selection appears to have favored the development of a human cognitive machinery for sex and age encoding, but the same did not occur for race (Cosmides et al. 2003; Kurzban et al. 2001; Voorspoels et al. 2014). Our ancestors usually lived with individuals of different ages and sex, so that selected cognitive adaptations for sex and age encoding allowed useful inferences. In contrast, our ancestors hardly moved for great distances, so it is unlikely that they had contact with populations of distinct races. Therefore, it is likely that no specific psychological mechanism was developed in the course of evolution for race encoding and this process is thus a by-product of the adaptive mechanism for coalitions and alliances.

Several characteristics are used by humans as social badges to distinguish allies and rivals (e.g., clothing, behavior, or language; Cosmides et al. 2003). Among these, phenotypic traits (i.e., skin color, face shape, hair texture) that evoke the idea of race can be used to determine this categorization (Kurzban et al. 2001). Racial

identification does not necessarily imply racism, as it is just one way of categorizing people in groups, but racism requires such identification of others as being an in-group or an out-group member. It is thus an important computational mechanism, since racial stereotypes are derived from this racial identification and many of the discriminations and prejudices against minority groups stem from stereotypes.

Racial Discrimination

Categorizing an individual as an out-group member is not sufficient to promote belligerence. A cognitive association linking the out-group and its members to some sort of negative stereotype may provoke fear and avoidance, as the out-group members may be regarded as threatening and dangerous through a stereotyping process. Although it may elicit a discriminatory process, it is speculated that in some situations, emotional states such as fear might have promoted greater fitness advantages, as real threatening stimuli might have been avoided (Schaller and Neuberg 2008).

This threat detection system has evolved to be highly sensitive, and, consequently, a sense of threat is commonly elicited even in the presence of harmless social behaviors or badges (Neuberg and Schaller 2016). Therefore, avoidance is triggered regardless of whether the threat is real or not; it is only necessary that a stimulus is perceived as a real threat. This perception is influenced by contextual factors that may make individuals even more prone to aggressive reactions to non-real threats (e.g., resource scarcity, high mate competition; Neuberg and Schaller 2016), which is why prejudice might emerge strongly among intense social tensions. The perception of danger, insecurity, or fear might generate a more prejudiced, self-centered, and aggressive attitude so that people tend to associate aversive (cognitive and physiological) responses to out-group faces more quickly (e.g., Navarrete et al. 2012). Indeed, individuals tend to automatically perceive out-group members as sources of potential danger on account of these prejudice-

triggering cognitions (see, e.g., Neuberg and Schaller 2016).

Prejudice can be defined as an individual form of avoidance or a negative feeling linked to a social badge; racism can be described as prejudice aimed at individuals from racial minorities, notably black people (Cosmides et al. 2003; Kurzban et al. 2015; Neuberg and Schaller 2016). A set of negative stereotypes (i.e., racial prejudice at the institutional, structural, social level) link the subjects to degrading characteristics stereotypically associated with their race. Racism elicits discrimination by stereotypes that highlights race as a social badge of threat so that the subject racially identified is perceived as someone with a predisposition/disposition to emit/be characterized by negative characteristics, feelings, and behaviors (Schaller and Neuberg 2008).

We categorize people by race, even if biologically it does not exist. In fact, we use several characteristics as an alliance clue. However, how does this association occur between the traits that evoke race encoding and the subsequent association with danger? (And why does it not signal alliance?). This probably occurs because historical social processes maintain this negative association (Kurzban et al. 2001). Race is simply one historically contingent subtype of coalition. If other social badges were presented simultaneously to race markers, they would overlap with it (Kurzban et al. 2001; Voorspoels et al. 2014), and race could be a social badge of differences between groups arising from the alliance-building machinery, reducing its threat-triggering potential. As this process occurs mainly through the in-group/out-group categorization process, some contextual aspects that crosscut race could be used to modify the negative valence associated with it and thus reduce its avoidance-eliciting potential and, consequently, reduce racism. For example, Kurzban et al. (2001) have shown that a 4-minute exposure to an alternative world has weakened or stopped the trend of racial categorization. This suggests that racism is maintained because of other systems of social alliance and can be eradicated. So, racism, understood as the process of discrimination against different races elicited by prejudice syndrome (i.e., a suite of

thoughts, emotional responses, and behavioral inclinations designed to deal with a particular perceived threat), can be mitigated by the interruption, for example, of racial encoding (see Schaller and Neuberg 2008). An intervention that seeks to reduce racism could also target some other part of the process that leads to discrimination, namely, racial identification arising from race encoding, prejudice arising from stigmatization, and, finally, discrimination. Interventions could also address other badges that may signalize a threat, such as low socioeconomic status, poor access to resources, and diseases.

Negative stereotypes that elicit prejudice and, subsequently, racial discrimination must have emerged in a scenario where social power and privilege should be under the control of one group (such as white people) who have begun to harass another group (such as black people). That is, stereotypes are culturally constructed and influenced by political and socioeconomic contexts. In this sense, Moore (2012) argues that between 6000 and 12,000 years ago, when leukodermic (paler skinned) populations arose, racism would have arisen because of the conflicts and hostility generated by phenotypic differences between leukodermic and melanodermic (darker skinned) populations. This process has strengthened over time. For example, in more recent periods as in Greco-Roman antiquity, there was already proto-racism (i.e., attitudes and actions analogous to racism, but that predate the modern concept of race), as group-based slavery began between the seventh and ninth centuries among the Arabs.

Conclusion

Human relations of cooperation or exclusion can be explained by cognitive machinery selected in evolutionary human history. Human cognitive architecture consists of a set of separate systems designed to solve adaptive problems associated with sociality, which requires a dynamic performance in the management of these systems. Therefore, such processes are flexible and responsive to immediate contextual characteristics.

Understanding racial prejudice requires a comprehensive analysis. The computational processes that regulate social categorization involve several mechanisms to address threats, and each set of emotional responses, cognitions, and behavioral inclinations was designed to deal with a specific threat (i.e., prejudice syndrome; Schaller and Neuberg 2008). Some groups are victim of multiple forms of prejudice syndrome because they are perceived as multiple forms of threat. This is triggered by badges that signal threat, regardless of whether this threat is real or not. Negative stereotypes are then arbitrarily assigned and serve as a justification for discrimination, being thus important to address the socially constructed aspects of discrimination as illustrated by the fact that racism was established by the political, socioeconomic, and cultural domination of white people. Racism is therefore maintained because of other systems of social alliance, and it can be eradicated.

The evolutionary approach allows new ways of addressing the problem of prejudice. Because different racial beliefs can be generated by multiple inferential mechanisms, only research that links them can generate precise explanations. This ends up impacting the elaboration of interventions, since each prejudice syndrome must be separately addressed. As different prejudices can be linked to different mechanisms, this will require multiple strategies. Other potential implications for interventions include, for example, the possibility to act in processes prior to the elicitation of negative stereotypes, such as in race encoding through aspects that crosscut race or contextual changes that diminish the propensity of evoking prejudice (e.g., promote feelings of security and safety).

Cross-References

- [In-Group Versus Out-Group](#)
- [Intergroup Conflict](#)
- [Prejudice](#)
- [Prejudice as an Expression of Tribalism](#)
- [Race As A Social Badge \(Kurzban\)](#)
- [Racism](#)

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Radical Behaviorism

- [B. F. Skinner and Behaviorism](#)

Raiding

- [War](#)

Random Effects

- [Function Versus Capability](#)

Randy Thornhill

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Synonyms

[Disgust](#); [Mate retention](#); [Pathogen resistance theory](#); [Sociosexuality](#)

Definition

Randy Thornhill is an entomologist and evolutionary biologist at the University of New Mexico, especially noted for his applications of evolutionary biology and evolutionary psychology to human behavioral science. He attained fame beyond the academy for work with Craig Palmer on applying biological knowledge to the phenomenon of human rape (Thornhill and Palmer 2001). Although the book was specifically intended to help inform law enforcement in the identification and capture of criminals, and the prevention of crime, this was not deemed sufficient justification by many (Dreger 2016). However, Thornhill is more famous within the academy for work on insect mating, parasite-stress theory, and sociosexuality.

Introduction

Thornhill's early work (like that of sex researcher Alfred Kinsey) was in entomology (his MSc was in this discipline), and this may well be no

Professor of Biology at University of New Mexico.

coincidence. Studying insects allows for a degree of detachment from issues of human sentimentality and political commitment (Thornhill and Alcock 1983) focusing on the underlying nuts and bolts of the key drivers of mating success (or failure) rather than human rationalizations of same.

Thornhill brought this same detachment to the study of politics. Here a major insight was that the surface (proximate) rationalizations of political loves and hates may have underlying (ultimate) mechanisms driven by the need to associate with some and disassociate with others. Thus, the parasite-stress theory was born (Thornhill and Fincher 2014). Human immune systems are remarkably complex and, increasingly, being seen as drivers of human behavior in their own right. Thornhill was an early predictor of such mechanisms, realizing that traits such as religiosity, personality, and political leanings were non-accidentally linked to local adaptations to parasite loads). These traits are, in effect, part of the behavioral immune system.

Open vs Closed: Opportunities or Threats?

Thornhill has managed to link a number of behaviors, for example, to do with physical and moral disgust, attitudes toward strangers, and even food. For example, in the same way that regions of high temperatures tend toward spicy foods (because spices have antimicrobial properties), Thornhill hypothesized that visible signs of immunocompetence (such as low fluctuating asymmetry) may also be preferred in such regions. Fluctuating asymmetry is a marker that seems to hold across taxa as a visible honest advert of developmental stability and thus heritable resistance to parasites – making one an attractive partner. There also appear to be local and predictable responses to pathogens. Data from the Global Infectious Diseases and Epidemiology Network did indeed confirm that cultural groups that split along the collectivist-individualist axis showed a high covariance of collectivist (and thus xenophobic) attitudes and high pathogen stress. This work has

the interesting implication that the goal of making cultures more liberal would be best advanced through health care rather than argument – a conclusion that Thornhill appears happy to endorse.

Humans are obligate investors. Human babies are highly demanding in terms of both time spent in the womb and the aftercare required for them to be viable. Demands fall disproportionately on the females in our species – their minimum parental investment is considerably higher than the male minimum potential parental investment. What this means is that a suite of mating options are available to both sexes, but these are constrained in important ways.

Sociosexuality is a dimensional trait – which might also be appropriately termed an orientation. At one end of the dimension is restricted sociosexuality – characterized by an insistence on commitment in advance of engaging in sexual interactions. At this end of the scale, a typical person would answer positively to questions such as “I require a feeling of emotional closeness before engaging in sexual intercourse.” At the other end of the dimension is unrestricted sociosexuality – characterized by a willingness to engage in sex without commitment. Those at this end of the scale typically answer positively to questions asking whether they would be willing to have multiple sexual partners concurrently or to questions such as “sex without love is perfectly permissible between consenting partners.”

Within the general framework of life history theory, which models differential economic allocations of resources to key adaptive traits, sociosexuality describes a set of proximate markers of behaviors relating to mating and parenting effort. Organisms maximize their fitness by focusing resources on where they will have the most effect but, like an effective investment portfolio, bets are often hedged in various ways to achieve this fitness maximization. While both sexes benefit in similar ways from long-term mateships (e.g., through sharing resources and having reliable partnerships), there are predicted to be some sex differences in terms of what constitutes short-term mating opportunities – of which a major component is sociosexuality. This is what scholars have indeed found.

Given the obligate investiture of human females, it is predicted that willingness to engage in short-term matings will, for women, be mediated by said short-term partner's genetic quality. For example, Gangestad and Thornhill (1998) found that willingness to engage in short-term matings (especially extra-pair copulations) was highest when women were at the most fertile part of their cycle. Furthermore their preferences shifted, at these times, toward males who were more symmetrical.

It is likely that at least part of the measured sex differences in sociosexuality are mediated by testosterone. The relationship here is a complex one. In the trade-off between allocating resources to mating and parenting, testosterone facilitates mating effort. Men in long-term mateships tend to have lowered testosterone. McIntyre et al. (2006) used the sociosexuality index (SOI) focused on extra-pair interests to find support for the prediction that the relationship between testosterone and sexual partnership status would rest on extra-pair sexual interests.

Like all evolutionary scholars, Thornhill has had to contend with what appears to be a very human cognitive glitch that refuses to see evolutionary explanations as enhancing existing proximate ones rather than replacing them.

Critics who wish to emphasize that sex differences arise from local social structure (Eagly and Wood 2005) claim that the concept of patriarchy explains said differences. Patriarchy is a (proximate) descriptor of a cluster of local behaviors and dispositions rather than an ultimate explanation of the factors leading to fitness maximization; thus criticisms of this kind tend to miss the point of evolutionary explanations. For a behavior to be socially constructed, it must have pieces to be constructed from. An explanation like "patriarchy" is thus no explanation at all – it is merely a description which hangs in the air without visible means of support.

Indeed there is little evidence that critics are even aware of the logical distinction between proximate and ultimate explanations, relying instead on a folk-science understanding of "biological" as meaning "fixed action pattern" or similar. Evolutionary explanations are not

alternatives to proximate ones – they enlarge and compliment them. Therefore to the extent that "patriarchy" can be taken to be a meaningful designator (and this is not always clear), it should be the case that ultimate explanations will match with it. This is indeed what we find. For any meaningful cultural descriptor of "patriarchal" (meaning traditional male dominated official marriage systems), cross-cultural measures of the SOI match the predictions of evolutionary theory.

For example, when controlling for local markers of mating threats and opportunities that can be assumed to have occurred and re-occurred over evolved time, SOI measures track fitness maximization. Overall women are far more varied in their SOI than men are (mean $ds = 0.74$; Lippa 2009) and more variant in their sex drive across cultures (mean female to male variance ratio = 1.64, which also implies that SOI and sex drive are not identical).

Conclusion

Randy Thornhill still continues to publish widely and with a multitude of coauthors. If there has been any effect of a vocal (but one hopes minority) public unwilling to see their traits as having biological elements, then this has not had a visible effect on his investigations (Thornhill and Gangestad 2015).

Cross-References

- [Infidelity](#)
- [Jealousy](#)
- [Mate Retention](#)
- [Personality and Mate Poaching](#)

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Rank

- [Vocal Indicators of Dominance](#)

Rank Order

- [Alpha, Beta, and Gamma Males](#)
- [History of Dominance Theory](#)
- [Living in Groups](#)

Ranking

- [Hierarchical Climbing](#)

Rape

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Synonyms

[Forced sexual intercourse](#); [Sexual coercion](#)

Definition

The use of force or threat to achieve penile-vaginal sex without consent.

Introduction

Rape is more commonly defined as penile-vaginal penetration of a female without her consent by force or threat (McKibbin et al. [2008b](#)). However, definitions of rape vary, and rape laws have been reformed around the world leading to more broadened legal definitions. The main changes are related to the victim's gender, victim resistance, and the definition of consent (Tracy et al. [2013](#)).

Although legal standards regarding victim resistance have been excluded in most places, there are still stereotyped rape views that require visible marks of resistance (Tracy et al. [2013](#)). These stereotyped views consider, for example, that rape is only perpetrated by strange and violent men in an isolated street (Burt [1980](#)). In reality, estimates suggest that about 40% of reported rapes in the United States are committed by an acquaintance man and over 50% are perpetrated by an intimate partner (Black et al. [2011](#)).

Rapes are also often underreported, mainly due to its many negative consequences for the victims (McKibbin et al. [2008b](#)). These can include physical and psychological impacts, such as sexually transmitted infections, feelings of shame and fear, and the development of psychological disorders

(Chaudhury et al. 2017). In addition, Perilloux et al. (2012) identified social and mating-related costs, such as damage to a woman's sexual reputation and decreased self-perceived mate value. Rape also impacts female reproductive success, and, therefore, could be an adaptive problem to ancestral women.

Rape Costs

Research on rape has shown that forced sexual intercourse can be observed in many species including insects, birds, reptiles, and primates. For instance, some male animals presented anatomical features designed to facilitate forced copulation (e.g., scorpionflies; McKibbin et al. 2008b). Small males' orangutans presented reproductively disadvantaged compared to large males because they are considered less attractive for females. Thereat, they are likely to resort to rape more often (Malamuth et al. 2005). These pieces of evidence indicate that rape has been a recurrent adaptive problem for other species.

From an evolutionary approach, rape represents a circumvention of female choice (McKibbin et al. 2008b). In fact, rape can result in an unwanted pregnancy by a man she has not chosen and whose genes and resources are unknown (Buss 2015). In addition, human rape creates other risks for a woman's reproductive success. A raped women risks being blamed, being abandoned by her partner, and having their reputation and desirability affected. Therefore, women have evolved anti-rape mechanisms (Buss 2015).

This strategy has also possible costs for men. A man who raped a woman can face parental retaliation and woman's resistance which can result in physical injuries and even death (Apostolou 2013). Given these high costs, for rape to continuous occurring in the context of human evolution, the benefits must have outweighed the costs (McKibbin et al. 2008a). Conflicts between men and women regarding parental investment and mating strategies could contribute and increase the likelihood of male engagement in sexual coercion (Malamuth et al. 2005).

Theories of Rape

It is controversial if men have evolved specialized psychological mechanisms to rape, or if it is a byproduct of mechanisms selected to solve other adaptive problems (McKibbin et al. 2008a). These issues create two competing evolutionary perspectives: rape-as-adaptation theory and by-product theory of rape. The rape-as-adaptation theory assumes that rape has been selected as a useful behavior to male reproduction success and is the product of specialized psychological adaptations (Archer and Vaughan 2001). Human males do not present any anatomical feature designed to facilitate forced intercourse. However, if rape were an adaptive strategy, an ancestral man who raped must have gain reproductive advantages over a man who did not (McKibbin et al. 2008a). One hypothesis is that men of low mate value (i.e., a man with low status and few resources) are unlikely to be chosen by females; therefore, they might get reproductive benefits in using a forced-sex mating (Thornhill and Thornhill 1983). Rape allowed men to circumvent parental and female choice (Apostolou 2013) and enables them to access females of high mate value (Thornhill and Thornhill 1983). This hypothesis has been questioned mostly because evidence showed that rape is not restricted to men of low mate value and sexually coercive men have reported a greater number of sexual experiences than expected (Lalumière et al. 1996).

Rape-as-adaptation theory lists some supposed specialized mechanisms related to rape. For example, an ability to assess the vulnerability of potential victims, an increased sperm count in rape ejaculations compared to consensual sex ejaculations and a preference for fertile rape victims (Malamuth et al. 2005). These mechanisms have been used as supporting evidence of this hypothesis.

In addition, there are circumstances where rape holds minimum costs and could be adaptive. War-time is the most recurrent example, but other situations, such as when the victim is unprotected, when there are very few chances of the men being recognized or discovered, and when a victim is unlikely to disclose the rape, also indicate opportunities where the costs of following forced-sex mating are low (Apostolou 2013).

In contrast, the by-product theory does not admit that rape is a previously selected behavior. It suggests that rape derived from other evolved mechanisms, such as the desire for sexual variety, the willingness to engage in casual sex, and the general use of psychical aggression (Symons 1979). Men typically present some sexual proclivities, such as being more eager to copulate, being less selective about their sexual partner, and looking for a greater number of partners, and the combination of all these sexual proclivities may lead to rape (Vandermassen 2011). Therefore, this approach endorses that rape itself is not an adaptive feature and it is maintained indirectly due to other adaptive behaviors (Archer and Vaughan 2001).

Although these are the two main evolutionary hypotheses regarding rape, there are other hypotheses involving attempts to explain rape. Shields and Shields (1983) proposed that rape represents a conditional strategy, in other words, rape is only adaptive under certain conditions. They endorse that most males are capable of raping depending on the situation and that rape is not a behavior restricted to males of low status (Archer and Vaughan 2001). In this sense, McKibbin et al. (2008a) proposed five types of rapists, namely: (1) disadvantaged men who resort to rape, (2) men who are sexually aroused by violent sex, (3) men who rape opportunistically, (4) high-mating-effort rapist, and (5) partner-rapists motivated by assessments of increased risk of sperm competition. The first type refers to a mate deprivation hypothesis, which assumes that one motivation to men for rape is the absence of consensual sex opportunities. However, most researches have not found evidence to corroborate this type of rapist. An alternative motivation that has been pointed is a perceived relative deprivation, which refers to individual's expectations about their sex experience (Malamuth et al. 2005).

The second type indicated that some rapists possess different psychological profiles and can be considered "specialized" rapists. This type may be sexually aroused by violent sexual situations and may evaluate greater attractiveness to rape victims rather than consensual female partners.

Such men could also lack the inhibitory factors of sexual arousal to force that other men possess (Malamuth et al. 2005).

The next hypothesized type is the opportunistic rapist, a man that might shift for sexual coercion in low-costs circumstances. For example, a rape strategy can be used by some men in situations that a victim has high vulnerability and the risk of retaliation is low. The fourth type describes a man with dominant and psychopathic traits who pursue a great number of sexual partners with minimal investments, therefore, is more likely to engage in sexually coercive behaviors.

Finally, the last type includes men who commit partner rape in response to the risk of sperm competition (McKibbin et al. 2008a). In the animal world, forced-in pair copulation is rare, because typically there are not long-term pair bonds in most species. However, evidence that supports this hypothesized type is that men with unfaithful partners were more likely to perform sexual behaviors versus men with no suspect of partner's infidelities (Goetz and Shackelford 2006). That result indicated that sexual coercion may be a method to avoid cuckoldry. Although some data is consistent with this typology of rapists, future research should continue to investigate possible individual differences in men who committed rape as well as specific circumstances related to rape.

Conclusion

Nowadays, it is not clear if rape is the result of an adaptation mechanism favored by evolution selection or if it is a by-product of other adaptive behaviors. There are also unanswered questions regarding rapist's types and motivations. It is important to highlight that these evolutionary approaches do not justify sexual coercive behaviors and by no means promote rape. Therefore, evolutionary explanations do not imply that rape is inevitable. Men may have psychological mechanisms related to rape but that does mean that they cannot control their sexual desire or are not responsible for their behavior. Humans can control their tendency to eat fatty food, hints they also

can control any evolved mechanisms towards rape (McKibbin et al. 2008a).

In fact, an evolutionary perspective provides insights into why men rape, what are the costs and benefits of rape, and why rape is being maintained over human evolution. Finally, this evolutionary framework can set grounds for developing programs to reduce sexual violence (McKibbin 2014).

Cross-References

- [Aggression for Sexual Access](#)
- [Contexts for Men's Aggression Against Women](#)
- [Evolutionary Perspectives on Rape](#)
- [Female Age as a Predictor of Men's Aggression Against Women](#)
- [Female Counter-Adaptations to Rape](#)
- [Forced Copulation](#)
- [Rape and Dating](#)
- [Rape Avoidance](#)
- [Sex Differences in Aggression](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion](#)
- [Sexual Coercion and Dating](#)
- [Sexual Coercion and Rape](#)
- [Sexual Conflict in Mating Strategies](#)

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Rape and Dating

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Synonyms

[Acquaintance rape](#); [Date rape](#); [Forced copulation](#); [Sexual coercion](#)

Definition

Date rape is a subset of acquaintance rape; it is nonconsensual sex, defined as vaginal, oral, or anal penetration, through the use of force or threat of force, committed by someone with whom the victim has gone on a date.

Introduction

This chapter is a review of the research done on rape and dating from an evolutionary perspective. By no means does this review justify rape, rather it is meant to review the current research in the aforementioned field.

In this review, we will begin with a brief discussion on the premise of evolutionary psychology by examining sexual selection, gender roles, and aggressive behavior. The primary interest is to look into the reasons why male adolescents engage in date rape. Through reviewing the research on date rape in adolescents, we will examine data found in dating behaviors, patterns of violence, and sexual strategies of adolescents. The review will continue in describing the impact of status, and appreciating its relation to survival and reproductive success, both during our evolutionary past and in our present lives. Finally, this review will explain how adolescents may use date rape to climb the social hierarchy through attaining status via dominance.

Natural Selection, Sexual Selection, and the Ancestral Environment

Through an evolutionary lens, we are able to understand the underlying workings of the human mind and behaviors in the environmental context they were adaptive in (Buss 1995; Tooby and Cosmides 1990). The psychological mechanisms that work the human mind today are ones that were built in ancestral environments, at a time when certain behaviors addressed recurrent environmental pressures. Exploring the psychological mechanisms through this lens, researchers have been able to contextualize the human mind and behavior in the ancestral environment they were formed in (for a review, see Tooby and Cosmides 1990).

One specific challenge that our ancestors faced in regards to reproduction and one that we currently see today are the natural forces of sexual selection; men and women have different reproductive costs when it comes to mating. The cost for men to mate is the time spent having sex, while the cost for women is 9 months of pregnancy, health, and childbirth.

The structure of our past environment made survival and reproduction highly competitive due to social dynamics in such environments. As an accepted member of a group, one reaped the benefits of food, protection, and access to women (for a review, see Hagen 2008). In our ancestral past, groups were highly exclusive; if an individual was deemed unfit, their membership in the pack was highly detrimental to the group's survival.

The pressures from exclusivity of group-membership forced outsider ancestral men to find a different way to mate, one which would allow them to gain reproductive success despite their possible shortcomings in physical attractiveness, status, and resources. This brings the possibility that ancestral men not belonging to any group, and facing high exclusivity in group membership, may have used rape as a method for sexual access and passing on their genes.

Aggressive Behavior, Narcissism, and Social Hierarchy

Through an evolutionary perspective, Thornhill and Palmer (2000) argue that men who lack resources and status, rape in order to pass on their genes; however, there is little evidence to support this claim. In a similar argument and framework as evolutionary psychology, other researchers have argued that narcissistic men (similar to men who lack resources) share the aggressive responding attribute with rapists (Baumeister et al. 2002). Evolutionary metatheory has found that common attributes among males who commit rape, include being aggressive, more eager to mate, more sexually assertive, and less discriminating to choose a mate (Thornhill and Palmer 2000).

Laboratory findings have confirmed that distress and sexually aggressive behavior is more likely in narcissists who have received criticism, insults, and who have felt their pride threatened. Based on the narcissistic reactance theory, a narcissistic male's entitlement to sex by his partner roots from attempts to increase self-esteem through peer admiration and validation. Seeking peer validation has great importance to narcissists; therefore, obtaining sex, by any means necessary, is believed to give the narcissist peer validation for having sex that will help him maintain status among his peers (for a review, see Baumeister et al. 2002).

Date-Rape and Adolescents

In the majority of rapes that occur, the victim knows the perpetrator (Pedersen 1992). Young women are more likely to be raped by an acquaintance or a romantic partner than by a stranger. Adolescents and young adult women are four times more likely to be raped than women in any other groups (for a review, see Rickert and Wiemann 1998).

A large percentage of reported sexual offenses are committed by adolescents (Fehrenback et al.

1986). Adolescents are particularly vulnerable to being victims and perpetrators of date rape because of their young age and inexperience (Vicary et al. 1995). There are multiple risk factors that are linked to adolescents committing date rape. This is similar to how in our ancestral past a male who has been alienated from his group is more likely to engage in sexual assault. Furthermore, male college students who display high levels of hostile masculinity and engage in impersonal sex are at an increased risk for committing sexual assault (Wheeler et al. 2002).

One of the most prominent risk factors that is involved in adolescent date rape appears to be the use of alcohol (Rickert and Wiemann 1998; Muehlenhard and Linton 1987). Alcohol is closely linked with date rape as alcohol reduces men's restraints against committing violent behavior and offers an excuse for sexual assault, as well as reducing a woman's ability to withstand an assault (Muehlenhard and Linton 1987). It has also been seen that alcohol produces a boost in egotism in young men (for a review, see Baumeister 2002). Alcohol is also more likely to be involved in a case of date rape than a date where sexual assault did not occur (Muehlenhard and Linton 1987).

Conclusion

In the field of evolutionary psychology, researchers have examined the root of rape behavior through contextualizing rape in ancestral times and through examining the environment that the behavior may have been adaptive in. Environmental pressures are constantly changing; therefore, behaviors that may have been adaptive for our ancestors in previous environments are not adaptive in our current environment today (for a review, see Tooby and Cosmides 1990). Researchers propose that the purpose of investigating an issue such as rape through an evolutionary lens is invaluable as it provides a better understanding of where such behavior root from, with the ultimate goal of building new strategies

for preventing rape and implementing efficient antirape programs (McKibbin et al. 2008).

Cross-References

- [Rape](#)
- [Sexual Coercion and Rape](#)
- [Victims of Violence](#)

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Rape Avoidance

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Synonyms

[Female Counter-Adaptations to Rape](#)

Definition

Traits or behaviors evolved to reduce the risks of women being raped.

Introduction

Rape has occurred over time and across cultures (Buss 2015). It is responsible for inflicting severe psychological, physical, and reproductive costs on victims (Boyd 2011; Perilloux et al. 2012). The impacts on physical health can involve clinical conditions, sexually transmitted infections (Chaudhury et al. 2017), self-harm (Chen et al. 2010), and to a lesser extent even death (McKibbin 2014). The psychological effects can range from feelings of fear, shame, and anxiety to the development of psychological disorders (Tsai et al. 2016). Particularly in women, sexual violence can lead to gynecological complications and unwanted pregnancy (Krug et al. 2002).

In general, rape is a crime perpetrated mostly by men against women. Therefore, women more frequently tend to use some resistance strategies for avoiding rape. These strategies can be physical actions (e.g., scratching, hitting their attackers) or verbal resistance such as screaming, yelling, and pleading. In addition, women also tend to engage in rape prevention behaviors, for example, avoid wearing revealing clothing and going out alone at night (Ullman 2007). From an evolutionary perspective, women may have evolved psychological

mechanisms that motivate such rape avoidance behaviors (McKibbin et al. 2011).

Rape results in many negative consequences for women, including costs on reproductive success. A woman who has been raped risks: (a) being abandoned by her partner, (b) reducing their desirability to future mate, (c) losing offspring investment by the genetic father, and (d) an unwanted pregnancy with a sexual partner she had not chosen (McKibbin and Shackelford 2011). A forced-sex mating strategy could increase fitness by enabling men to circumvent parental and female choice (Apostolou 2013). Mate choice is a central step of women sexual strategies because it is what guarantees good genetic quality and the availability of protection and resources to their offspring (Buss 2015). Therefore, the greatest cost inflicted by rape on women may be the circumvention of their mate choice, since this can jeopardize their reproductive success (McKibbin et al. 2009).

Women are the sex that presents greater obligatory parental investment associated with pregnancy and lactation, and so they tend to be more selective of their sexual partners (Buss 2015). This fact constrains the amount of offspring a woman can successfully produce. In the rape context, women can entail high parental effort in an unwanted child with a man of unknown genetic quality and few resources. Considering these costs associated with rape, a strong selection pressure over evolutionary history may result in psychological mechanisms that motivate women behaviors toward avoid being raped by men (McKibbin et al. 2011).

Rape Avoidance Mechanisms

Rape has affected female reproductive success, representing a recurrent adaptive problem over human evolutionary history. Then, women may present evolved psychological mechanisms designed to motivate behaviors to avoid men's sexual coercion and rape. So far, it is not clear to evolutionary psychology if these behaviors reflect specialized evolved adaptations or by-products of more general mechanisms (Ellsworth and Palmer

2011). Despite that, several studies provide evidence suggesting the existence of specialized psychological mechanisms that motivate women to assess the risk of being raped or to evaluate the risk of a man being sexually coercive (McKibbin et al. 2009). For example, Gangestad et al. (2007) showed that women during the fertile phase tend to rate men as more sexually coercive. It can indicate that due to the greater risks of conception, women may be more attentive to signs of male sexual coerciveness, which might serve as a mechanism to prevent rape.

Several studies have cited some hypothetical strategies, such as the formation of alliances with other males and females to get protection from a rape threat (Smuts 1992), and the sensation of fear in face of risky situations of being raped (Chavanne and Gallup 1998). In addition, according to Wilson and Mesnick (1997), women's preference for physically and social dominant mates can reflect an anti-rape adaptation, because such partners would be more likely to defend them from a possible rapist. This notion is known as the bodyguard hypothesis. Another hypothetical mechanism is the psychological pain experienced by women after being raped. Thornhill and Thornhill (1990) argued that psychological pain works as an alert to the circumstances in which the rape occurred, leading women to avoid such circumstances and, thus, preventing revictimization. The authors found that reproductive-aged women (vs. post-reproductive-aged women) experience greater psychological pain after being raped, which may be because the former have a greater risk of pregnancy from rape.

Measuring Rape Avoidance Behavior

From an evolutionary perspective, it seems coherent that women have evolved mechanisms that motivate rape avoidance behaviors. However, there was still a need for an instrument that could capture the main behaviors emitted by women for preventing sexual assault. McKibbin et al. (2009) have addressed this gap by proposing the Rape Avoidance Inventory (RAI), a reliable

and valid measure composed of 69 behaviors. All the items were developed based on the reports of women about specific behaviors they had already performed or would perform in order to avoid being raped. Using an act nomination procedure, initially, McKibbin et al. (2009) collected 83 specific behaviors that formed the preliminary version of the scale. From this initial set, 14 items did not meet the validity and precision criteria and were excluded from the final version.

The final version is composed by 69 items related to four components: Avoid Strange Men, Avoid Appearing Sexually Receptive, Avoid Being Alone, and Awareness of Surroundings/Defensive Preparedness (McKibbin et al. 2009). The first component consists of behaviors with the purpose of avoiding unfamiliar men or those who represent a greater risk of being sexually coercive (e.g., Avoid taking rides with men I don't know). The Avoid Appearing Sexually Receptive component comprehends behaviors related to woman's clothes or appearance. For example, women tend to "avoid wearing revealing clothes" or "avoid attracting attention" as a way to reduce their physical attractiveness to a potential rapist. This component also includes behaviors that may diminish perceived sexual receptiveness (e.g., Avoid making out with a man I have just met). The Avoid Being Alone component includes behaviors to keep around others (e.g., "Avoid walking alone at night"). Finally, the Awareness of Surroundings/Defensive Preparedness encompasses behaviors that function to maintain a woman alert to possible signs and situations of danger (e.g., Look around before I get out of my car) and behaviors that can increase woman's ability to defend herself against a threat of rape (e.g., Carry a knife) (McKibbin et al. 2009, 2011).

The four components of the Rape Avoidance Inventory (RAI) conceptually converges to four guidelines for female defense against rape introduced by Judson (2002), which are: "avoid group of idle males," "do not attract attention," "do not leave home alone," and "do carry weapons." This may be evidence for the construct validity of RAI. The negative correlation between the performance of rape avoidance behavior and women's interest in and the pursuit of short-term sex found by

McKibbin et al. (2009) represents additional evidence of the validity of the RAI.

One possible limitation of this measure is that the majority of items are related to stranger rape over acquaintance rape, despite the greater numbers of the latter. However, it must be considered that the RAI was developed from women's report about their behaviors, and that, in general, women are more fearful of rape by an unknown person, which may indicate that stranger rape was the greater adaptive problem faced by ancestral women (McKibbin et al. 2008). The RAI contributed to the advancement of the research on individual differences related to rape avoidance behaviors.

Individual Differences in Rape Avoidance

Considering individual features and context variables involved in rape, individual differences of women rape avoidance behaviors that were evolutionarily selected become more evident as an adaptive mechanism for different environmental pressures. Evolutionary psychologists have been studying the existence of individual differences in rape avoidance behaviors in women (McKibbin and Shackelford 2011); therefore, evidence suggests that rape avoidance behaviors could vary when some women's individual variables are accountable (e.g., attractiveness, relationship status, kin living close by, and the age of the possible victim).

Theoretically, over evolutionary history, women that responded with rape avoidance behaviors to situations with rape-related risk could have shown more reproductive success (McKibbin and Shackelford 2011). However, evidence suggests that some individual traits could influence some women to be more targeted than others in rape-related situations. McKibbin and Shackelford (2011) gathered evidence that demonstrated that rape avoidance behavior is positively correlated to women's attractiveness, involvement in a relationship with a romantic partner, and the number of kin living close-by. However, despite previous

hypotheses, the age of women did not correlate negatively with rape avoidance behaviors as expected by the authors.

Although the mere presence of the described traits does not incur in a causal relation with rape avoidance behaviors, in an evolutionary perspective it is coherent that women with those characteristics were more targeted by would-be rapists or could be more harmed by the costs of a rape. For example, attractive women are the ideal standard in the men's preference to mate, once it is a feature related to immunocompetency, fertility, and an honest indicator of good genes, thus, more likely to generate healthy offspring (Buss 2015). Hence, those women would be more targeted by men for mating proposes. However, men with low mate value generally are not chosen by attractive women, turning rape as a coercive and successful copulation strategy to those men. Thus, attractive women would be more inclined to perform rape avoidance behaviors (McKibbin 2014).

In addition, women that are involved in a romantic relationship have reported more rape avoidance behaviors (McKibbin and Shackelford 2011). Evidence suggests that having a romantic partner is significantly and positively correlated to avoid appearing sexually receptive and being alone, intending to minimize the possibility of being courted by other men and, consequently, of being raped (McKibbin 2014). Also, significantly related to behaviors that aimed to avoid appearing sexually receptive, to maintain awareness of surroundings and to being defensively prepared were observed when the woman reported having male or female family members living nearby (McKibbin and Shackelford 2011). Having kin living in proximity could minimize eventual risk-related contexts (e.g., walking home alone at night; McKibbin 2014). Protection to family members is an inclusive fitness management provider, once protect a family female from rape, would be indirectly be protecting the family genetic fitness, and hence when the female has the possibility to select her preferable mate, her offspring have a higher chance of survival and parental support (McKibbin 2014; McKibbin and Shackelford 2011).

Conclusion

In sum, due to environmental pressures that humans were submitted in evolutionary history, rape became a sexual strategy that increased the pressure to female counter-adaptation to it, the rape avoidance behaviors. Due to physical, psychological, and evolutionary costs of being raped, behaviors that could minimize the possibility of being a victim of this crime were a constant necessity for women.

From the evolutionary perspective, it is possible to comprehend how these behaviors were selected in early human history. However, the transformation of society's laws has influenced more severe punishment to perpetrators of this crime but has not yet extinguished this harmful male behavior.

Despite the evolutionary explanation for counter-adaptations that are helpful to decrease risky contexts to rape, it is relevant to highlight that this is not a justification and do not intend to legitimize victim's blaming arguments. This crime is a product of coercive mating strategies. Modern society has a long way to go to extinguish coercive copulation and to rape avoidance behaviors not be a necessity to women worldwide anymore.

Cross-References

- Evolutionary Perspectives on Rape
- Female Counter-Adaptations to Rape
- Forced Copulation
- Rape
- Sexual Coercion
- Sexual Coercion and Rape

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Rape in Warfare

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Synonyms

Sexual assault; Sexual coercion; Sexual violence

Definition

Sexual aggression committed against women by outgroup men during times of intergroup conflict.

Introduction

Intergroup conflict is a ubiquitous feature of both modern and tribal human societies. In these conflicts, women are unlikely to be involved as warriors or members of raiding parties and are also less likely to be the deadly targets of warfare. Rather, women are the “resource” for which men are competing and consequently suffer as the victims of sexual aggression at the hands of the attacking group. We review the literature linking rape and warfare and present an evolutionary perspective positing that men’s propensity to engage in warfare serves as the function of increasing reproductive success through various mechanisms, of which the rape and capture of outgroup women is one.

Evolutionary Background

Males and females differ in the minimum level of investment that is required to produce viable offspring (Bateman 1948; Trivers 1972). The obligatory investment of males ends after ejaculation, but females bear the costs of a long gestational period and (among hunter-gatherers) up to 4 years of lactation. Even after weaning, women continue to play the role of the primary caregiver (Lancaster and Lancaster 1983).

For males, large investments in parenting are potentially risky given that males do not have paternal certainty. Furthermore, the relatively minimal paternal investment that is required to produce offspring means that males benefit to a greater extent than do females from large investments in mating. Consistent with this theorizing is evidence suggesting that early humans were mildly polygynous (Mitani et al. 1996; Symons 1979). In such a system, females are a limiting resource to men’s reproductive fitness, thereby creating an incentive for males to compete with other males for access to resources that will increase their ability to acquire mating opportunities. In this competition, some men will perform well and others will perform poorly, leading to larger variability in male’s reproductive outcomes than females (Andersson 1994).

Intrasexual competition among males for mating access occurs via multiple routes. Competition may include contests for territorial resources that provide the best protection from predators or access to nutrients, as well as more intangible resources such as social status, that can be converted into reproductive opportunities. This conversion occurs either because there is a direct appeal of the acquired resource to females or because the resource increases success in competition with rival males. Competition for such resources can occur among men within a group, as well as between groups in the context of warfare, when men form coalitions to usurp territory, resources, and mates from rival groups. It is this intergroup warfare that is the focus of this entry.

Reproductive Advantages in Warfare

Although there are risks involved in warfare, the potential benefits are to be accrued if victorious are substantial. Expansion of territory, acquisition of resources, increased social status as a warrior, and the rape and capture of the outgroup’s women all contribute to men’s mating success, indirectly or directly. Below, we focus on the direct reproductive benefits of warfare, in particular, reviewing evidence of the link between warfare and rape. The chaotic nature of conflict provides many affordances for sexual coercion to be used against women, especially by men of the invading group. These include the absence of consenting heterosexual mating options, antagonistic attitudes toward the victims’ group, and a reduced likelihood of punishment following acts of sexual violation (Smuts 1996). As a result, rape is a common feature of intergroup conflict. Below, we first review accounts of wartime rape among modern hunter-gatherers and tribal societies in order to provide insight into the probably patterns of behavior of our evolutionary ancestors. We then review modern warfare and the patterns of sexual aggression that continue to persist.

Rape in the context of tribal and nonstate warfare. Women are rarely involved in warfare as warriors or members of raiding parties and are less likely to be the deadly targets of warfare.

However, women often suffer as the victims of sexual aggression at the hands of the invading group. Indeed, the stated motivation for many intergroup conflicts is explicitly related to mating goals. In traditional lowland South American societies, jealousy over women and the desire to gain captive women are two of the top three motivations for intergroup killings (Walker and Bailey 2013). Along similar lines, Sanday (1981) examined correlates of rape frequency in 75 tribal societies. The research found that rape frequency across societies was predicted by the frequency with which the society raided other groups with an explicit purpose to take outgroup women for wives ($r = 0.29$) and was also predicted by whether the society could be characterized as engaging in frequent warfare ($r = 0.21$).

It is clear from many anthropological accounts that outgroup men are the targets of lethal intergroup violence. In contrast, the lives of outgroup women are typically preserved in intergroup conflict, but they instead suffer as the victims of sexual aggression. Meggitt (1962) describes the raiding, and counter-raiding, between the Walbiri and Warramunga of the Central Australian Desert; “Walbiri war parties would then invade the Warramunga country in retaliation. If they were able to surprise the enemy camps and kill or drive off the men, they carried away any women they found” (p. 38). Similarly, describing the fighting of the Kurnai tribe in Southern Australia, Fison and Howitt (1967) write that “they only speared the men, and perhaps some children. Whoever caught a women kept her himself” (p. 214). Based on the anthropological work of Chagnon (1988), Wrangham and Peterson (1996) describe the intergroup raids of the Yanomamö: “The stated object of a raid is to kill one or possibly two men and escape. If the raiders can do so without risking losses, however, they may abduct a woman from the enemy village. The abducted woman will be raped by all the raiders, taken to their village, raped by the remaining men in the village, and then given as a wife to one man. She can expect to spend the rest of her life with her new companions” (p. 67).

Synthesizing a large body of work examining nonstate warfare, Keeley writes:

It is extremely uncommon to find instances among nonstate groups of recognizing surrender or taking adult male prisoners. Adult males who fell into the hands of their enemies were usually immediately dispatched. . . . The capture of women was one of the spoils of victory – and occasionally one of the primary aims of warfare – for many tribal warriors. . . . In general, nonstate groups preserved the lives of captives only when some material benefit would accrue; this approach generally limited the persons spared to women and children. (1996, pp. 83–87)

Evidence that warfare and raids spared women can also be inferred on the basis of the sex composition of archaeological remains. For example, Kohler and Turner (2006) argue that the disproportionate absence of women and children in a burial population may indicate that a group had been attacked and the women and children taken captive and moved to a different location. Indeed, their own examination of the archaeological record from late pre-Hispanic northern US Southwest reveals a pattern suggestive of intergroup raiding for women.

Modern warfare and rape. The association between warfare and rape appears to be a constant force across time. Brownmiller (1975) reported that rape has been associated with religious wars dating back to the First Crusade. Sexual assault took place as knights and pilgrims made their way to Constantinople (Wilson 1969). Additional evidence suggests that wartime rape occurred in Medieval European warfare, including wars between the Ancient Greeks (reviewed in Gottschall 2004).

Moving forward in time and closer to present day, sexual assault in warfare was acknowledged by Brownmiller (1975) to have been committed by German troops in the First World War when proceeding through Belgium. Reviewing the historical record, Lalumière et al. (2005) conclude that “Mass rape has been perpetrated by American soldiers in Vietnam, Pakistani soldiers in Bengal, German soldiers on the Eastern front in the Second World War, [and] Soviet soldiers during the invasion of Germany. . .” (p. 25). In

some conflicts, the numbers of female victims number into the tens of thousands. During the Japanese occupation of the then capital of China, Nanking, historians have suggested that 20,000 women were raped (Chang 1998; Roland 1997). The Warburton Commission, established to investigate the treatment of Muslim women during the Bosnian War, estimated that between 10,000 and 60,000 Muslim women were raped (Buss 1998).

The prevalence of rape in the context of warfare is so pervasive that in 2008 the United Nations Security Council unanimously voted to pass a resolution that would classify acts of sexual violence as war crimes, crimes against humanity, and acts of genocide. The resolution was prompted by the fact that, during armed conflict, “women and girls are particularly targeted by the use of sexual violence” and that “such acts...in some situations have become systematic and widespread, reaching appalling levels of brutality” (UNSC Resolution 1820 2008, pp. 1–2).

Psychological Associations between Mating and Warring

A great deal of evidence suggests that rape of outgroup women is incredibly pervasive in the context of intergroup conflict and warfare. Underlying this behavior may be a strong psychological association between mating and warring. Crouthamel (2014) examined the inner life of German soldiers in the First World War through an analysis of archival documents including diaries, letters home, newspaper stories, and court records. Crouthamel draws many contrasts between what was expected of the male soldier and their actual behavior. The idea that male soldiers would dogmatically pursue their country’s military mission without interruption from base sexual drives was contradicted by a venereal disease crisis that spreads gonorrhea and syphilis to many thousands of soldiers.

Crouthamel also notes that many soldiers reported experiencing sexual arousal during

combat, as well as sexual dysfunction following their experiences in warfare. Indeed, Germany experienced a steep rise in sex crimes committed by soldiers on leave from the First World War, including sexual violence and rape of girls under 14. Moreover, reports from soldiers suggest that some males craved the sensation and arousal generated in warfare but found it difficult to achieve in postwar situations (Crouthamel 2014). This aligns with many PTSD veteran accounts documenting sexual dysfunction following participation in combat. For example, Cosgrove et al. (2002) reported that 85% of male veterans experienced erectile dysfunction.

Experimental work substantiates elements of Crouthamel’s historical analysis. Chang et al. (2011) sought to empirically demonstrate the association between mating and warring. In their research, participants were primed with either attractive or unattractive pictures of the opposite sex. Following this, the participants’ attitudes toward war-related behavior were examined. Results demonstrated that men (but not women) exposed to attractive women (but not unattractive) reported more positive attitudes toward war (but not more positive attitudes toward trade conflict). Similarly, men exposed to attractive women displayed faster visual processing of war scenes and faster lexical processing of war-related words (e.g., wars, fight) – even compared to other aggressive words unrelated to war. These findings are consistent with the idea that men’s motivation for warfare lies in the reproductive advantages it provides, or in the least, that for men mating and warring are tightly connected.

Conclusion

Though it is difficult to provide precise estimates of the frequency of rape during military and tribal conflicts, the weight of evidence suggests that, throughout human history, intergroup conflict has sharply increased a woman’s risk of becoming the victim of sexual aggression. The persistent and pervasive nature of this evidence implies that

there may be a deep psychological association for men between warfare and rape.

Cross-References

- [Coalition Leaders](#)
- [Gang Affiliation](#)
- [Reproductive Benefits Must Outweigh Costs](#)
- [Sexual Access](#)
- [Sexual Access as Benefit of Victory in War](#)
- [Unokais and the Headmen of the Yanomamö](#)
- [Yanomamo \(Chagnon, 1983\)](#)

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Rate of Death and Disability

- [Environmental Harshness](#)

Rate of Learning

- [Learning Curve](#)

Rational Actors

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Synonyms

Homo economicus

Definition

Economic model of individual decision-making formalized as utility maximization.

Introduction

The rational actor model is based on an individualist and consequentialist conception of optimal decision-making. The model posits that a rational actor will choose the course of action that maximizes expected individual net benefits. The formal framework of the rational actor model was developed in economics (Luce and Raiffa 1989; Ramsey 2016; Savage 1972; Von Neumann and Morgenstern 2007). Also known as *homo economicus*, the rational actor model became influential across the social and natural sciences – including evolutionary models of human and other animal behavior through game theoretic applications (Smith 1982).

Homo Economicus

The rational actor model is formally based on the axiomatic foundations of expected utility theory (Savage 1972; Von Neumann and Morgenstern 2007). This economic decision-making model gained wide scholarly use due to its powerful analytical capabilities derived from a small number of axioms – assumptions

viewed as self-evident. Most importantly, it is assumed that rational agents have pre-given (exogenous) preferences that are complete and transitive (Von Neumann and Morgenstern 2007).

Completeness means that the agent has a preference between any two possible alternative outcomes (A and B) such that either A is preferred to B, B is preferred to A, or A is seen as equally valuable as B. Transitivity means that, comparing any three alternative outcomes, if A is preferred to B and B is preferred to C, then A is preferred to C as well. The model predicts that the rational agent will implement the action that maximizes the highest possible difference expected between benefits earned from the outcome achieved and costs expended in achieving this outcome.

The term rationality in the model refers exclusively to the efficiency and consistency of decisions. On the one hand, the rational actor is motivated by the optimization goal of making the most use of available resources to achieve desired ends (Robbins 1932). On the other, efficiency requires that the rational actor behaves consistently in achieving these ends. In this sense, the model is focused on instrumental rationality in means-ends relationships and is therefore distinct from theories about procedural (Simon 1976) as well as substantive rationality (Sen 1977).

A common misperception of the model is that rational actors are necessarily selfish. Although it is a long-standing assumption in economics that individual behavior is governed exclusively by self-interest (Edgeworth 1881), the formal framework of the rational actor model does not make this assumption. Instead, the model implies that the substance of the goals that a hypothetical rational actor may pursue is independent of whether these goals are pursued in a consistent and efficient way. For example, a selfless altruist, a profit-driven executive, and a dangerous sociopath can in principle all be perfectly instrumentally rational in pursuing their individual goals. However, this formal flexibility of the model is also a methodological weakness since any behavior can be viewed as

rational as long as it is internally consistent and efficient.

Conclusion

Although the rational actor model has fundamentally shaped the behavioral sciences, it is increasingly seen as an inaccurate and inadequate description of human psychology and behavior (Sen 1977; see also entries on ► [“Bounded Rationality”](#) and ► [“Resource Scarcity”](#)). In particular, recent findings from economic and psychology experiments resulted in a long list of cognitive biases and heuristics in actual human decision-making that clearly contradict the assumptions underlying the rational actor model (e.g., Tversky et al. 1990). Nevertheless, the model continues to be widely used, but it remains particularly useful for studying when and how actual human behavior deviates from the normative benchmarks of optimal behavior.

Cross-References

- [Bounded Rationality](#)
- [Resource Scarcity](#)

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Rationality

- [Evolution of Free Will](#)

Reaction Norms and Tokens

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Synonyms

[Genotype](#); [Occurrence](#); [Phenotype](#); [Phenotypic and genotypic plasticity](#)

Definition

The range of environments that one phenotype has adapted to as a result of a genotype. Individual organisms or features that represent one type or the other are referred to as *tokens*.

Introduction

Organisms that are capable of adapting to their environment and reproducing successfully are selected over others that fail to do so. Adaptability or *plasticity* of an organism's inherited features, from an evolutionary perspective, would grant opportunities for the organism to travel and live across more diverse environments to obtain

resources essential for survival and reproduction. Evolutionary scientists recognize these ideas as *reaction norms and tokens*, which are responsible for the genetic and physical outcomes for all life forms, including humans.

Distinguishing Genotype and Phenotype from Reaction Norms

Each and every living specimen can be classified into groups based from its heritable material. Deoxyribonucleic acid (*DNA*), the molecule of life, accounts as the heritable material for the vast majority of contemporary life forms. The genetic composition of an organism is defined as its *genotype* (Lewontin 2011). Every organism has a unique genotype that ultimately characterizes its every quality.

Phenotype is exclusively the physical and behavioral features resulting from the genotype. Physical shape, size, movement patterns, cognition, etc. of every organism are examples of its overall phenotype (Lewontin 2011). Hair and skin color, body limbs and their locations, biological sex, and all other physical human universals compose the human phenotype. Each physically expressed feature is a product of the genotype and the general environment that the feature evolved from.

The general range of phenotypes that result from a single genotype is the *reaction norm* (Barrett 2012). The gills of a fish are an inherited adaptation to breathe oxygen from water; fish could not live outside their aquatic environments due to this physical attribute. A marine mammal, such as dolphin, lives in the sea and breathes oxygen in air when it surfaces; a dolphin's reaction norm is, therefore, more plastic than a fish's.

An organism's reaction norm may also be described as the interaction of its genotype and its evolutionary environments (Flatt 2014). Using the same example above, evolutionary environments of fish were likely to be less diverse relative to the evolutionary environments of dolphins whose ancestors lived on land before returning to the ocean. The reaction norm or a genotype's phenotypic plasticity can provide useful

information about the organism's evolutionary history. Every adaptation is a response to the selective pressures that constitute the organism's environments in the form of genotypic and phenotypic expression (Schlichting and Pigliucci 1995).

Tokens

Genotypes and phenotypes are classes in which an organism can be identified with. A *token* is the specific organism or trait(s) of a genotype or phenotype (Lewontin 2011). Tokens, in a more general biological context, are occurrences or examples of genotypic or phenotypic elements (Tibayrenc 2011). The fins of a fish, a phenotypic trait, would be tokens of an organism that swims in aquatic environments. A dolphin's unique genotype may be a token of the *Delphinus* genus, as a human's unique genotype may be a token of the *Homo* genus.

Significance of Human Reaction Norms to Evolutionary Psychology

Relative to the speed of biological evolution, the speed of environmental evolution is too fast. The survival of any species largely depended on the adaptability of their genotype's phenotypic expression (Wong and Candolin 2014). While inconsistent environmental conditions and environments are inevitable, the genotypes that produce the more versatile adaptations are naturally selected over less versatile adaptations (Rand 2016). The vast majority of contemporary life forms did not evolve in an environment containing uniform or fixed conditions. Relative to merely all other species that have ever existed, prehistoric humans encountered distinctive environmental forces that ultimately designed the adaptability of modern humans (Wong and Candolin 2014).

Like other species, humans demonstrate flexibility in their evolved traits. Physical features are conventionally conceived as adaptations; however, mental features, too, are human adaptations.

The central nervous system of humans is perhaps the most complex system ever created by biological evolution. More traditional psychologies describe the human mind as the product of only experiences and learned qualities, which is referred to as *the blank slate*.

It can be argued that the most significant adaptation that enabled the humans to dominate the globe is their higher intelligence. How to construct hunting tools; weave clothing; hunt various animals; harvest edible vegetables and fruit; build fires; raise healthy young; live in forests, woods, deserts, and frigid climates; and communicate these valuable skills and merits to human offspring required a nervous system of tremendous prowess. The organism most adaptable to change is selected over all others; the human brain and mind may be the adaptation that has granted humans the most flexible reaction norm achieved by any species.

Today, evolutionary psychologists are in close proximity to study the ultimate adaptations that formulate human reaction norms. Psychological mechanisms that engender emotions and behaviors that facilitated human survival and reproductive endeavors are the foundations of evolutionary psychological theories and hypotheses. The seemingly universal sense of disgust engendered by the notion of committing incest, for example, is hypothesized to prevent humans from conceiving young of poorer genetic quality. Incest avoidance, along with many other behaviors, is considered by evolutionary psychologists to be an adaptation that ultimately contributes to the reaction norm of humans.

Conclusion

Evolutionary psychology and psychology are descendants of biology. Biological principles underlie many psychological ones, and *reaction norms and tokens* are no exception to this perspective. All living organisms, especially humans, possess biological reaction norms that circumscribe their genotypic and phenotypic qualities. Like organisms, tokens of genotypes and phenotypes are selected for and against

based on their host's ability to adapt to its array of environments. With the human brain reaffirmed as a product of the human genotype and human evolutionary environments, evolutionary psychology is granted the opportunity to parse *higher intelligence*, the ultimate adaptation.

Cross-References

► Evolution of Adaptations

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Reactive Aggression

► Development of Aggression

Reality-Incongruent Beliefs

► False Beliefs

Reasoning About Social Norms

- [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)
-

Reasons to Punish Wrongdoers

- [Motivates Punishment](#)
-

Recalibration Theory of Anger

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Definition

The recalibrational theory of anger explains how natural selection designed anger to bargain for better treatment and how this can explain the major features of anger.

Introduction

The claim that anger has evolved via natural selection is not hotly contested. After all, anger bares many of the hallmark features of an evolved adaptation: it is a complex system instantiated in localized neural tissue (Potegal and Spielberger 2010), it shows early ontogenetic development (components of the adaptation are visible at 7 months, Stenberg et al. 1983), and it demonstrates many cross-cultural universals in basic design (Alonso-Arbiol et al. 2011; Ekman 1973; Wallbot and Scherer 1986). Furthermore, some features of anger are known to develop without exposure to the information that would be required to learn them through more general purpose systems, e.g., congenitally blind children produce normal anger

facial expressions (Galati et al. 2003). And so modern researchers generally conclude that anger is – at least in part – designed by natural selection (Potegal and Spielberger 2010).

The recalibrational theory, however, is the first theory of anger that (i) posits the precise selection pressure that evolved anger (i.e., animal conflict theory), (ii) derives the basic computational structure of anger from that selection pressure, and (iii) begins to catalogue the features of anger, each with reference to its evolved function. This leads to several advantages that the recalibrational theory has over other psychological theories of anger: (i) the theory is derived from well-established and validated models of conflict in evolutionary biology, (ii) the theory not only describes features of anger but can explain causally how those features evolved and what function they serve, (iii) the theory can be used to predict and explain multiple aspects of anger (e.g., aggression, negotiation, arguments, facial and vocal changes), and (iv) the theory does not rely on circular concepts that are often used to smuggle organized complexity under the umbrella of descriptive theories (e.g., “disrespect,” “frustration,” “bad treatment”).

The recalibrational theory was derived from the basic models of animal conflict that are used to explain the aggressive, threatening, and bargaining behavior of nonhuman animals. A review of this literature demonstrates that human anger has a kinship with these behavior systems and makes precise the selection pressures that – according to the recalibrational theory – designed human anger.

The Evolutionary Biology of Animal Conflict

There are striking parallels between human anger and bargaining aggression in nonhuman animals. These similarities include (Sell 2011; Sell et al. 2009b, 2014; Tooby et al. 2008):

- (i) Its triggering conditions (e.g., conflicts of interest, challenges to status)
- (ii) Individual differences in thresholds for anger (e.g., those with more bargaining power demand more deference)

- (iii) Patterns of aggression that can be triggered (e.g., low-cost demonstrations of formidability that escalate when neither individual backs down)
- (iv) Terminating conditions, e.g., submission of one's opponent
- (v) The body posturing preceding aggression
- (vi) The predictable sex differences in proneness to bargain with aggression
- (vii) Bodily and energetic shifts during bargain that prepare the organism for aggression
- (viii) The neurolocality of the bargaining systems that show continuity across mammals

These similarities suggest that the bargaining systems of other animals and the human anger system were designed by similar selection pressures, specifically resource conflict or "conflicts of interest."

So how do biologists explain animal conflicts? In short, animals have conflicts of interest because many reproductive benefits (e.g., food, mates) can only be acquired at another's expense. Aggression, then, is a tool that evolved to disrupt the functional complexity of another, rendering them incapable of contesting the aggressor's use of the resource (Huntingford and Turner 1987). Because of the potency of this selection pressure, animals evolved complex adaptations for governing their aggressive and bargaining behavior.

For any given conflict, an animal must determine whether to contest a resource or cede it to the other animal. Natural selection can be expected to design animals to attempt to take resources when the reproductive benefits of the resource outweigh the costs of seizing it (Maynard Smith and Price 1973). The benefit of winning a bout of aggression will be largely determined by the reproductive benefit of receiving the resource, e.g., the hunger level of the animal eyeing a piece of meat. The costs of seizing a resource are largely determined by how much one's opponent values the resource and a ratio variable that indicates the reproductive consequences for the actor of disregarding their opponent's welfare (Nowak 2006; Tooby et al. 2008). For example, the reproductive consequences for taking food from a relative will depend on how hungry the actor is

(benefit to $X = Bx$), how hungry her relative is (cost to $Y = Cy$), and the degree of relatedness between them (r), i.e., Hamilton's rule: $Bx > r * Cy$. Similarly, the selection pressures acting on a potential combatant who must decide whether to fight an opponent for food will look mathematically similar. The actor must weigh the benefit of the resource to themselves (benefit to X), how hungry his opponent is (cost to Y), and the relative ability of the organisms to impose costs on each other through aggression (i.e., relative resource holding power, RHP; see Hammerstein and Parker 1982; Maynard Smith and Price 1973). Similar mathematics underlies the selection pressures inherent in reciprocal altruism and other routes to cooperation (Nowak 2006).

In sum, for any given conflict, an animal will need to assess information relevant to the selective dynamics inherent in that situation, usually including the value of the resource to the self and other, kinship, and often other variables such as relative fighting ability, cooperative history, and so on. Many of these cues will vary across conflicts, e.g., how hungry each animal is, the presence of vulnerable offspring, and the organism's current energetic state. These cues must be reassessed – or estimated – during every conflict. Other cues are relatively stable, such as fighting ability, size, life stage, sex, estimated degree of relatedness, and so on. Because it is costly to reassess all of these variables for each conflict (particularly fighting ability – the more accurate assessments of which may require potentially lethal aggression), animals have evolved the capacity to store representations that correspond to relative bargaining power and use them as baselines for future conflicts with those individuals (Huntingford and Turner 1987). These stored variables give rise to dominance hierarchies on the group level but are in fact the output of information stored in each individual brain. Furthermore, these representations of relative bargaining power are – in a sense – resources that can be fought over. And thus animals will engage in aggressive tests with no resource at stake, in order to both demonstrate their formidability to their opponent and to learn the fighting ability of a future opponent (Huntingford and Turner 1987).

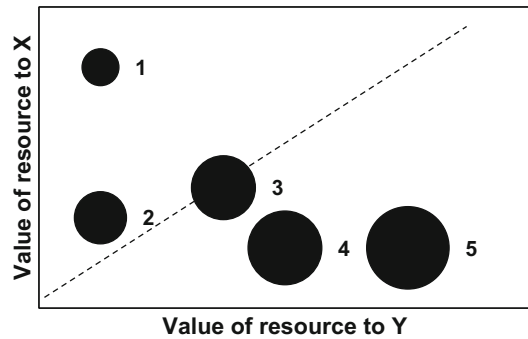
Bluntly averaging across many exceptions and unique species adaptations, animals are designed to assess their conspecifics to determine if they are afforded the appropriate “status” consistent with their bargaining power and recalibrate those individuals that do not afford them the status they are entitled to. This recalibration takes the form of aggressive posturing, escalating into bouts of communicative aggression and finally actual potentially lethal aggression if the target does not submit. According to the recalibrational theory, human anger is phylogenetically related to these bargaining systems.

Function of Anger

If, as the recalibrational theory suggests, anger evolved to navigate conflicts of interest, then one needs to understand how humans represent conflicts of interest and what kinds of mental structures evolved to decide a conflict in order to understand how anger can manipulate those mental structures (e.g., just as adaptations for bodily adornment must be understood by reference to adaptations for the assessment of attractiveness). In short, if anger evolved to recalibrate status-setting machinery in the minds of one’s conspecifics, then one needs a theory of that status-setting machinery in order to explain how anger works.

How Do Humans Represent Conflicts of Interests?

Just as with many other animals, humans faced conflicts of interest. During these conflicts, the individual human had to decide whether to take a benefit at another’s expense. Such a situation can be called a **cost-benefit transaction**. Cost-benefit transactions can be classified according to the ratio of cost to benefit (i.e., relative valuation of the contested resource) that results from the imposition of the cost on agent X for the benefit of agent Y. For example, in Fig. 1, there are five instances of cost-benefit transactions that differentially affect the welfare of agents Y and X. The size of the circle indicates the cost-benefit ratio (i.e., value (Y)/value (X)); the extent to which Y



Recalibration Theory of Anger, Fig. 1 Welfare trade-off ratio as a threshold of cost-benefit transactions

values the resource more than X). Such examples could be:

1. Person Y borrows X’s car and crashes it to avoid getting a \$20 speeding ticket (small benefit for Y, large cost to X).
2. A commercial pilot (Y) makes X wait for 30 min so that he can finish his birthday cake.
3. Y takes the last doughnut at a meeting between X and Y (equal value to both).
4. Y ruins X’s favorite sweater by using it to wrap a dog’s leg after it is caught in a bear trap.
5. A supermarket checkout employee (Y) makes X wait for 2 min, while Y takes a phone call to discover how his parent fared in open-heart surgery (benefit to Y much higher than cost to X).

In each case, Y must decide whether to impose that cost on X or not.

What kinds of factors should determine Y’s decision? In theory, these decisions will be informed by variables that relate to the ancestral costs and benefits of making these decisions. From the review of the animal literature above, one would predict that individuals become less likely to impose a cost on an individual as the size of the cost increases and as the size of the benefit one receives decreases, e.g., you become more likely to take a contested food item when you are hungry and when they are satiated. In addition to these transient variables, there are stable variables that are operative across many conflicts of interest,

e.g., kinship, bargaining power, and cooperative history (Nowak 2006). These variables would need to be integrated by the individual in order to make an actual decision, i.e., a man could not refrain from imposing the cost on his brother because of kinship, while simultaneously imposing that same cost because his brother is less formidable. Evolutionary psychologists have argued that humans evolved to compute and store a summary variable or function that integrates these factors for each individual that the person interacts with (Sell 2011; Tooby et al. 2008). In other words, this stored variable indicates the weight one person puts on the well-being of another; it answers the question, “Compared to myself, how much do I care about him?” This variable has been termed the *welfare trade-off ratio*.

The Welfare Trade-Off Ratio

The value one individual places on the welfare of another is indexed by their welfare trade-off ratio (WTR; see Sell et al. 2009b; Tooby et al. 2008). The WTR that Y has toward X (WTR_{yx}) indicates the extent to which Y will allow costs on themselves in order to benefit X and the extent to which Y will impose costs on X for Y’s own benefit, i.e., $WTR_{xy} = \text{benefit}(X)/\text{cost}(Y)$. The mathematics of the welfare trade-off ratio is identical to Hamilton’s rule, the asymmetric war of attrition, and other models of selection (Nowak 2006) that use ratio variables to delineate a limit on cost-benefit transactions. But there are key differences between these models and the welfare trade-off ratio. Hamilton’s rule, for example, is a model of how natural selection will act on genes, but the welfare trade-off ratio is a model of human cognition. Hamilton’s rule is not instantiated in the world but rather summarizes what happens to genes based on their effect on organism’s reproduction. Hamilton’s rule does not need to exist in the brain of any animal (Dawkins 1979). The WTR model, on the other hand, is theorized to exist in neural form in the brains of humans, and it regulates behavior in that individual.

An individual will have different welfare trade-off ratios for different individuals. For example, a person might be willing to ruin a stranger’s favorite sweater to dress their pet’s wound but

unwilling to ruin the dean’s sweater for a similar reason. An individual may be unwilling to give several thousand dollars to pay for a stranger’s education but willing to spend that amount on their own child’s education. This ratio can be seen as a threshold (the dotted line in Fig. 1), above which agent Y would relinquish the benefit rather than impose the cost on X and below which Y would impose the cost on X to receive the benefit. This ratio is Y’s welfare trade-off ratio with respect to X – as it indicates the extent to which Y is willing to trade off his own welfare in order to raise X’s and vice versa. In this case, he would not be willing to ruin X’s car to avoid paying a speeding ticket (1 is above the line), but he would be willing to make X wait in line while he called the hospital to check on a loved one (5 is below the line).

From a selective point of view, and ignoring cases of kin and the complicated nature of human cooperation, natural selection can be expected to have designed humans to adopt the lowest possible welfare trade-off ratio toward others (i.e., impose any cost in order to get even a meager benefit). But given the costs of contests and the nature of kin and competition, natural selection is predicted to have designed humans such that welfare trade-off ratios will be set higher based on numerous factors related to another’s ability to enforce their own welfare, just as with other animals. One set of factors is related to the ability to enforce WTRs by threatening to inflict harm: these include, e.g., greater physical strength and more coalitional support. Another set of factors is related to the ability to enforce WTRs by threatening to withdraw the benefits of cooperation: these include, e.g., the person’s status as a frequent and dependable reciprocation partner, their status as a friend who has a stake in your welfare, or their possession of special abilities that can be deployed to benefit others (Tooby and Cosmides 1996).

It is likely that there are at least two types of welfare trade-off ratios that govern cost-benefit transactions in different contexts: (1) extrinsic welfare trade-off ratios, which define the threshold of cost-benefit transactions when both parties are present or otherwise capable of defending their interests, and (2) intrinsic welfare trade-off ratios,

which define the threshold of cost-benefit transactions when the other individual is not present or unable to defend their interests. Intrinsic WTRs allowed individuals to adaptively partition cost-benefit transactions in a world where the welfare of other individuals was of adaptive significance for oneself. Although the full selection pressure analysis of intrinsic WTRs is beyond the scope of this entry, a quick starting point would be as follows: a subset of individuals in one's social world can improve one's welfare as a result of their existence, social power, and well-being (e.g., a devoted friend, a caretaker of one's children, a generous acquaintance, etc.). Benefits given to them, even without their knowledge, will correspond to benefits to oneself (see Tooby et al. 2008).

Those cases notwithstanding, an individual human is born into a world populated by others who, under most circumstances, are designed to give as little as necessary to the individual (i.e., to have low welfare trade-off ratios toward others, such that they would be willing to impose large costs on that individual for even small benefits). There would have been constant and powerful selection for an individual (X) to raise the WTRs that others used in their interactions so that the other would forgo some cost-benefit interactions that imposed costs on X and proceed with cost-benefit transactions that granted benefits to X. The higher the other's WTR can be pushed up, the more costs X can avoid. Thus, one could predict that natural selection would have designed a mechanism with the following design features:

- The mechanism should come online when there are indications that another individual does not value X's interests highly.
- That mechanism should gather the attention of the target and open a channel to the cognitive structures that calibrate WTRs.
- This mechanism should then feed information to these cognitive structures, information specifically designed to upregulate the target's WTR toward X.
- Such information could include threats or demonstrations of fighting ability, threats to withdrawal benefits or demonstrations of cooperative

value, indicators of kinship, and appeals to third-party judgment and coalitional support.

- The mechanism should turn off when there are indicators either that the target does indeed hold an appropriate WTR or that the target has recalibrated their WTR upward.

The recalibrational theory holds that this evolved mechanism is anger.

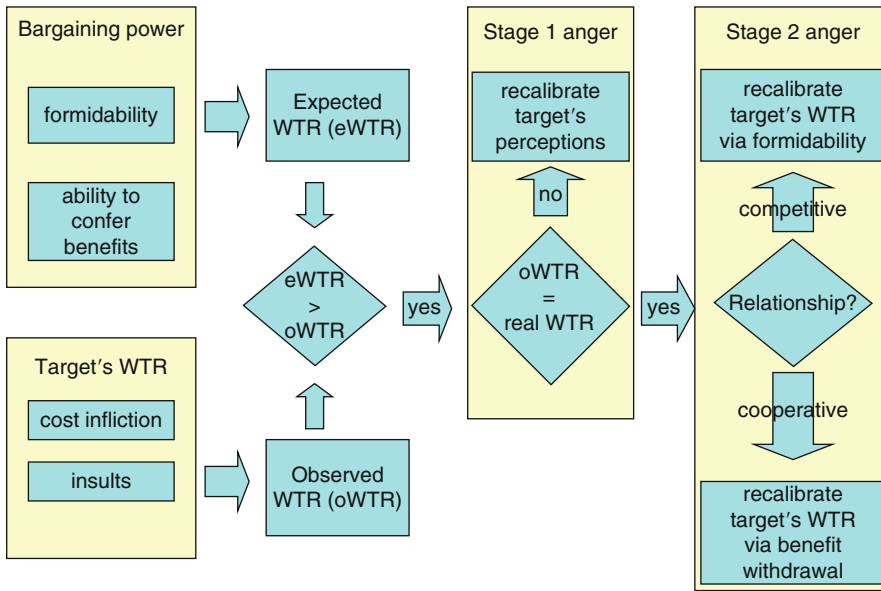
Computational Design of Anger

First, a quick sketch of the recalibrational theory will establish its primary components. This entry will then review how the recalibrational theory can explain the major features of human anger and then a more thorough description of how the model of anger can be used to explain the major features of the emotion.

Sketch of the Computational Structure of Anger

According to the recalibrational theory, anger is triggered when an individual perceives that another does not value their interests highly enough. The angered person feels entitled to a certain welfare trade-off ratio from the target ("expected WTR" or "eWTR") but observes evidence that the target holds a lower WTR ("observed WTR" or "oWTR"). When $eWTR > oWTR$, anger is triggered. See Fig. 2.

Expected WTRs correspond to intuitive notions such as entitlement and are believed to be calibrated to a large extent by the individual's bargaining power. Individuals with more bargaining power can demand better treatment from others and will thus become angry over a greater range of offenses (i.e., eWTR is more likely to exceed oWTR because eWTR is quite high). For example, because bargaining power in men was highly related to their personal fighting ability during our evolutionary history, physical strength and other indicators of fighting ability calibrate men's sense of entitlement and correspond to lower thresholds for anger (Lukaszewski 2013; Sell et al. 2016; Sell et al. 2009b; Salas-Wright and Vaughn 2016). Indeed, entitlement



Recalibration Theory of Anger, Fig. 2 The recalibrational theory of anger

generally is related to lower thresholds of anger (Bushman et al. 2009).

Observed WTRs are computed by the angry person from indicators that another individual does not value the angry person's welfare highly. The clearest case of this is when an individual imposes a large cost on another in order to receive a small benefit. Recall that WTRs relate to the maximum cost-benefit ratio an individual will impose on another (i.e., $WTR_{xy} = \text{benefit}(X)/\text{cost}(Y)$). So a low WTR_{xy} is indicated when $B(X)$ is small, e.g., your friend wastes your time to finish playing a video game, and when $C(Y)$ is large, e.g., you are waiting on him to take you to the hospital.

Once the anger system detects that the observed WTR is lower than the expected WTR, attention focuses on the incident, and a stream of mental computations is run that reevaluates the variables related to the observed WTR in order to determine if the observed WTR accurately represents the target's actual or real WTR toward the angry person. This is called *stage 1* anger (Sell 2011), which functions to bargain over a given conflict and determine if the target of anger actually holds a low WTR toward the angry person or if their actions reflect a misunderstanding and a temporary condition or are in fact consistent with

a higher acceptable WTR (i.e., does the observed WTR inherent in the target's actions accurately reflect their real WTR). Stage 1 anger is frequently characterized by an interrogation of the target of anger. For example, when the observed WTR is indicated by the prototypical imposition of a large cost for a small benefit (e.g., the angry woman's husband left her stranded at the airport while he was talking on the phone), the angry person will inquire about the magnitude of the cost imposed and the target's knowledge of that magnitude, e.g., "Did you know you were supposed to pick me up at the airport?", and the magnitude of the benefit, "You better have been talking to President Obama or the Pope!" The angry person will attempt to correct misperceptions of these variables to win the conflict (or similar conflicts in the future), e.g., "For the future. . . don't ever leave me stranded at the airport again! It's really disrespectful."

If the anger system determines that the observed WTR was not an accurate indicator of the target's actual WTR toward the angry individual, then anger will stay in stage 1 and may bargain over the conflict in particular, e.g., "Well next time let me know you'll be late at least." If, on the other hand, the target reveals that the observed WTR accurately indicates their true WTR toward the

angry person, then anger can escalate into stage 2, e.g., “I knew I was supposed to pick you up, but I felt like talking to Sue. And no, I won’t apologize for it.”

Stage 2 anger functions to recalibrate the target’s welfare trade-off ratio and is experienced as a more extreme form of anger. This recalibration is accomplished by feeding information to the WTR-setting machinery in the target. Specifically, anger recalibrates the target’s WTR by demonstrating the ability of the angry person to inflict costs (i.e., aggression) or the ability to withhold or curtail benefits (Sell 2011; Williams et al. 1998), because WTRs are calibrated by estimates of bargaining power such as physical formidability, cooperative value, coalitional support, and so on (Lukaszewski 2013; Sell et al. 2009b; Sell et al. 2016; Tooby et al. 2008). The strategies can “work” because the WTR-setting machinery in the mind of the target is designed to calibrate WTRs in response to the bargaining power of the other individuals. As with nonhuman animals demonstrating their fighting ability, these displays start with low-cost, presumably less accurate, demonstrations and escalate as needed to more accurate and dangerous behaviors.

The Recalibrational Theory and Features of Anger

This simple sketch of human anger serves as a framework for more specific subtheories about the features of anger, e.g., the triggering conditions of anger, the function of the universal anger face, and the calibration of thresholds for anger.

The Triggering Conditions of Anger

According to the theory, the primary activating conditions for anger will be cues that indicate another individual maintains a lower welfare trade-off ratio than is acceptable given their negotiated relationship. These cues exist in many formats because the WTR is likely to be used by many different cognitive mechanisms. That is, how much weight a person puts on another’s welfare may “leak” through many channels. This explains why anger can be triggered by so many computationally distinct indicators. For example, the degree to which one values the welfare of another

presumably regulates the fidelity of memory encoding such that information about an individual who is highly valued is more likely to be remembered. Thus, ignorance about a person can indicate a low WTR toward that person and activate anger in them. Ignorance is a less common trigger of anger though. The work by Averill (1982) identified the most common trigger of anger as that of a cost imposition.

By definition, cost-benefit transactions contain within them the implicit maximum WTR the cost imposer holds. Specifically, when actor X imposes a cost on Y in order to receive a benefit, the maximum WTR X has toward Y (i.e., WTR_{xy}) is (benefit to X)/(cost to Y). Thus, the maximum WTR that X has toward Y becomes lower as the cost imposed on Y increases and the benefit X receives as a result of that cost decreases. See Fig. 3.

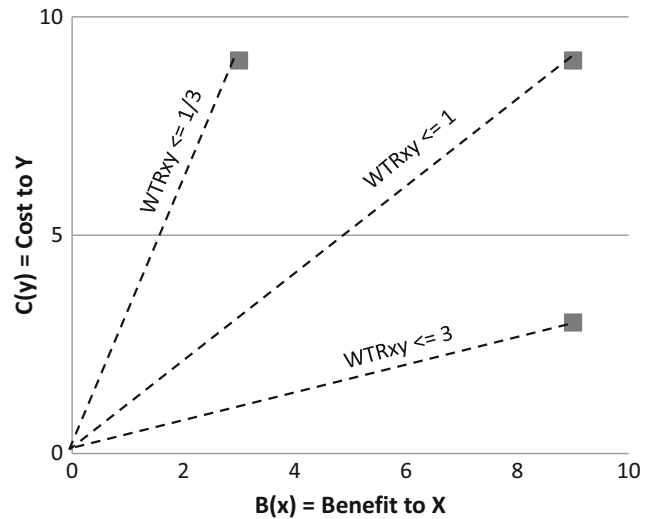
Consistent with these basic predictions, cross-cultural studies demonstrate that subjects become more angry as the cost imposed on them increases but less angry as the benefit to the other individual increases (Sell et al. *in press*). In other words, as the observed WTR lowers, anger becomes more active.

Welfare trade-off ratios can also be revealed when individuals refuse to grant benefits at a cost for themselves or impose costs on others to benefit third parties and so on. Furthermore, because humans have metacognitive abilities, a cost-benefit transaction does not need to actually be enacted in order to indicate a low WTR. If an individual attempts, plans, or in some cases even considers at some length, imposing a large cost on an individual for a low benefit, this can reveal one’s WTR. For example, imagine a medical swindler who approached a man and offered to buy his wife’s lungs. The swindler promised that she would be put down humanely. If the husband considered this proposal for more than a fraction of a second, one would assume that his valuation of his wife’s welfare was far too low, even if he did not ultimately decide to sacrifice her life.

Sell (2014) analyzed a large set of anger-based arguments and categorized them into 12 computationally distinct triggers of anger, each of which is a plausible (albeit currently unproven) predictor of holding a low WTR toward the angry person:

Recalibration Theory of

Anger, Fig. 3 A lower
WTR_{xy} is indicated as C
(y) increases and B
(x) decreases



1. Cost-benefit transactions (see above).
2. Insulting beliefs. The target of anger indicates that they evaluate the angry person low on a trait relevant to the setting of WTRs (e.g., “Do you think I’m stupid?!”). A prediction of this model is that anger-provoking insults will cluster largely around the two primary negotiative tools that are used to set WTRs: the ability to impose costs (e.g., being weak, cowardly, socially impotent) and the ability to confer benefits (e.g., unreliable, a cheat, unable to gather resources, low mate value, incompetent, sickly, a burden on others).
3. Co-opting decisions. The target of anger makes decisions for the angry person.
4. Social rejection and jealousy. The target of anger indicates a willingness to disengage from the angry person or indicates that such a disengagement would be low cost for the target, e.g., “I don’t really need you. . .”
5. Maintaining divergent goals. The target of anger indicates that they are seeking or will seek goals incompatible with the angry person, e.g., the target of anger could support the “wrong” political position or candidate.
6. Lack of inherent value in being together. The target of anger indicates that they do not sufficiently enjoy the angry person’s company.
7. Respecting rivals or disrespecting allies. The target of anger treats the angry person’s enemies too well or fails to value friends of the angry person.
8. Lack of empathy. The target of anger fails to exhibit concern over the suffering of the angry person. The target need not have caused the suffering, e.g., “Do you want to see the new Bond movie?” “I can’t; I just found out my mother has cancer!” “Oh. Maybe a comedy then?”
9. Lack of self-disclosure. The target of anger fails to “trust” the angry person with information about themselves.
10. Lack of memory. The target of anger fails to remember information about the angry person.
11. Deception used to win a conflict of interest. The target of anger lies to the angry person in ways that indicate that they do not “trust” the angry person, e.g., “I would have loaned him my car anyway. . .he didn’t have to lie!”
12. Arrogance. The target exaggerates (intentionally or unintentionally) their bargaining power or other trait that calibrates welfare trade-off ratios, e.g., “Sometimes I feel like the only intelligent person in the room.”

These triggers – in theory – all respond to different uses of the WTR, e.g., WTRs are used to make cost-benefit decisions (#1) but also regulate memory for important people (#10). Therefore, different variables will predict how high or

low the WTR is for different triggers of anger. For example, if you were to spill your colleagues' coffee on their pants, their anger system would respond much less aggressively if your actions were unintentional. But if your colleague was angry because you thought their latest paper was inept and stupid, their anger would not be assuaged if you indicate that you did not "intend" to think their paper was stupid. This is because anger triggered by cost-benefit interactions (e.g., spilling coffee on them for no real benefit) only indicates WTRs precisely if the target considered the cost and benefit and then decided to implement the cost. Their WTR toward the angry person is "leaked" accurately only when they knew these variables, weighted them, and then decided. But if you believe your colleague is unprofessional or incompetent, then saying that you did not "intend" to know they were terrible does not remove the accurate indicator of your WTR toward your colleague because believing that your colleague is deficient on a WTR-relevant factor (#2) would lower your WTR toward them whether it was intended or not.

Because there are multiple channels that leak information about WTRs, actions can sometimes indicate a high WTR through one channel but low WTR through another. For example, anger can be triggered by a cooperative partner's willingness to replace you (#4 above) because WTRs toward friends and romantic partners are indicated – in part – by one's estimated longevity of the relationship (Tooby and Cosmides 1996). Therefore, if a man were caught cheating on his wife, and she confronted him, her anger can be triggered by two simultaneous channels: one, she is angry because he indicated a willingness to replace her with another woman (#4), and two, she is angry because he engaged in an act that imposed a large cost on her for a relatively small benefit (#1). The other woman's attractiveness then modulates anger via both channels but in opposite directions. If the other woman was extremely attractive, this intensifies the signal through the jealousy channel, i.e., it indicates that he is more likely to replace his wife with the other woman. On the other hand, if the other woman was unattractive, it would intensify the cost-infliction channel by

indicating that her husband decided to impose this painful cost on his wife for a trivial and untempting benefit. This leaves the husband with two opposite arguments, both of which backfire by exacerbating anger via a second channel: "You don't understand; she was just so amazingly attractive!" or "She was ugly and smelled of garbage and bad judgment, but I threw our marriage away anyway..."

Factors that Trigger Escalation of Anger

Anger is expensive in both metabolic terms and social costs (e.g., retaliation, counter-bargaining by the target of anger). Furthermore, estimating another's WTR is fraught with error. Therefore, the first response of the anger system is usually to seek information from the target to refine the observed WTR estimate and give the target of anger a chance to explain why their actions do not indicate a low WTR. This is part of stage 1 anger in the recalibrational theory (Sell 2011). In addition to seeking confirmatory evidence of a low WTR, stage 1 anger can negotiate conflicts of interest in the short term without renegotiating the welfare trade-off ratio itself.

For example, in cost-benefit transactions, an individual in stage 1 anger can argue that the cost to them of the transaction is very high, and the benefit to be received by the target of anger is too low. Imagine two fraternity members arguing about which movie to watch in their dorm room. Arguments would include statements about the relative value of both movies (e.g., I've seen that already and my movie is rated 4 out of 5 on Rotten Tomatoes), turn-taking (e.g., we watched that train wreck of a movie you recommended last week), and other aspects of conflict negotiation. However, what will be absent in stage 1 anger are the kinds of negotiations used to recalibrate welfare trade-off ratios themselves. If during the fight one of them said, "You know I can kick your ass!" or "Nobody here even likes you" or "Fine, good luck driving yourself to the airport next week," both interlocutors would realize that the speaker's anger had escalated because those arguments are designed to illustrate bargaining power and are used to recalibrate welfare trade-off ratios (i.e., they are part of stage 2 anger).

During stage 2 anger, the angry individual will deploy strategies to recalibrate the target's WTR. To do this, the anger system must deliver information to the WTR-setting mental machinery of the target. This information must be in a format that is computationally intelligible to that system; in other words, the tools that anger can use to recalibrate WTRs are limited to the variables that set WTRs to begin with. WTRs are calibrated largely by bargaining power: the ability to impose costs and the ability to deny benefits. This means that anger could evolve at least two strategies to recalibrate the target's WTR, bargaining aggression, and cooperative withdrawal.

Bargaining Aggression

Anger-based aggression is distinct in form and function from other kinds of human aggression (e.g., warfare, hatred-based aggression, defensive aggression). According to the recalibrational theory, anger-based aggression is primarily designed to recalibrate the target's estimate of the angry individual's formidability (i.e., ability to impose costs). Such aggression is characterized by many features consistent with that function:

- (i) Anger-based aggression is frequently announced to the target with verbal threats, voice modifications, and a universal anger face (see below). Such announcements enable the target to direct attention to the angry individual and assess the demonstration of formidability, and they enable a low-cost means of success if the target immediately recalibrates under the threat.
- (ii) Anger motivates approach toward the target in an attempt to gather the target's attention for the same reason.
- (iii) An individual aggressing from anger will typically abstain from more lethal or damaging attacks, but instead focus on demonstrative actions, e.g., pushing, shoving, hitting, or throwing inanimate objects, slaps, strikes to less vulnerable parts of the body, and non-weaponized aggression. Retaliation may lead to escalation in the lethality of the fight (Luckenbill 1977), but the initial aggression is almost always

sublethal and only escalates if the target fails to capitulate (Luckenbill 1977).

- (iv) Anger-based aggression often allows for explicit turn-taking or "rules" (Romero et al. 2014) so as to allow for mutual assessment of formidability.
- (v) Aggression subsides (indeed anger subsides) when the target of anger recalibrates and apologizes, illustrating that the function of this aggression is to provoke recalibration not inflict harm itself.

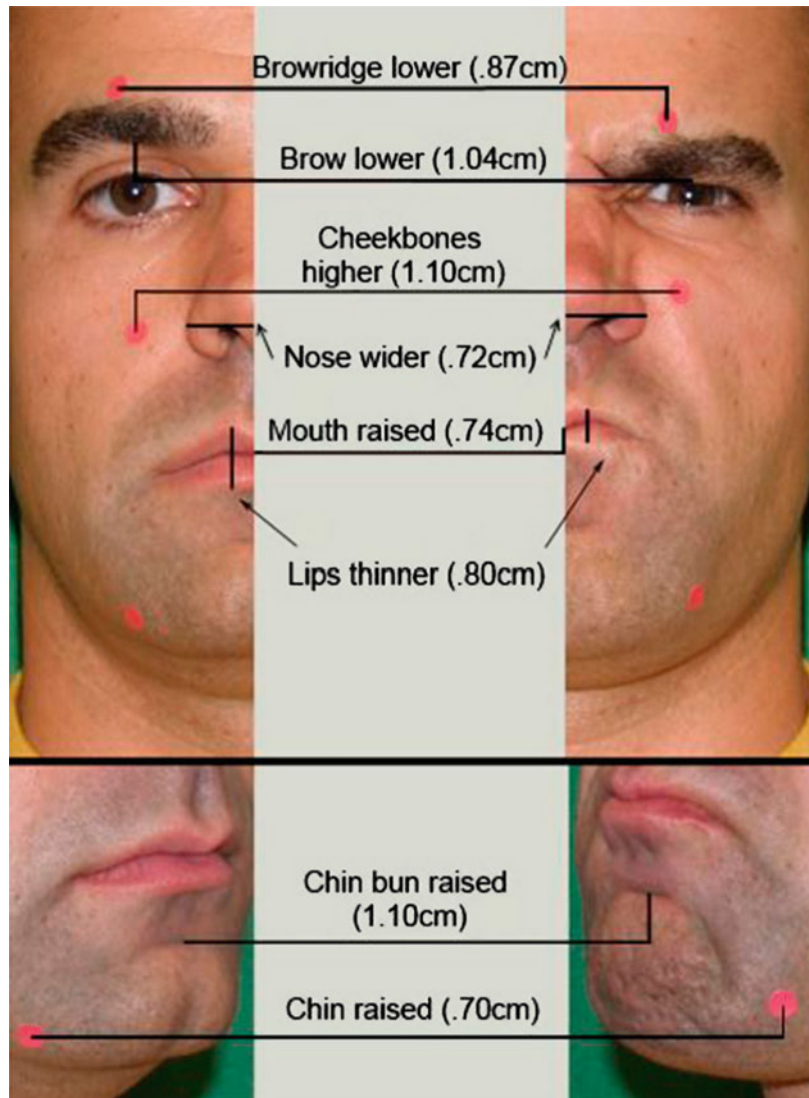
These features are consistent with ritualized aggression (or "escalating conflicts of assessment" or the "sequential assessment game") in nonhuman animals (Enquist et al. 1990; Huntingford and Turner 1987). Evolutionary biologists understand them as attempts to modify status calculators in the brains of their opponents. Both animals fight in a way that enables them to estimate the fighting ability of their opponents while minimizing the severity of injury. As with other nonhuman animals, these fights are frequently preceded by poses and body configurations that enhance cues of fighting ability in order to win conflicts of assessment early (e.g., dewlap inflation, bared fangs, piloerections). According to the recalibrational theory, the universal human anger facial expression evolved to perform this same function (see below).

The Function of the Anger Face

The universal human anger expression (Ekman 1973) is composed of distinct muscle movements that can be coded into facial action units (e.g., the brow lowers, the lips thin). The expression is cross-cultural, present in congenitally blind children, and distinct from chimpanzee expressions and shows other hallmarks of being an adaptation designed by natural selection (Sell et al. 2014).

The function of this adaptation, according to the recalibrational theory, is to enhance cues of physical strength that exist in the face. Previous research shows that such cues are readily apparent, e.g., humans can accurately estimate a man's upper body strength from photographs of his face (Sell et al. 2009a). The anger face modifies some of these cues of strength by a targeted flexing of

Recalibration Theory of Anger, Fig. 4 The anger face enhances cues of physical strength



the facial musculature. The result is a face that appears more physically strong. Sell et al. (2014) demonstrated this by showing that each component of the anger face – independently – increased the perceived strength of the face. In other words, the anger face itself is an evolved constellation of muscle movements that, like ritualized enhancement displays in other animals, enhances cues of physical strength during conflict (see Fig. 4.).

Cooperative Withdrawal

Although theories of anger have focused on aggressive behaviors as the primary action motivated

by anger (see Potegal and Spielberger 2010), the data suggest that aggression is rarely deployed during a bout of anger. Averil's survey, for example, showed that less than 10% of incidents of anger recalled by his subjects reported even the explicit threat of aggression (Averill 1982).

Why is anger so rarely aggressive? According to the recalibrational theory, anger-based aggression is designed to recalibrate the target's welfare trade-off ratio, and this can work because welfare trade-off ratios are responsive to estimates of another's fighting ability, i.e., one way to make an individual value your interests is to demonstrate

that you can hurt them if they do not. However, given the cooperative nature of human interactions, there will be many individuals who value your welfare for reasons that are unrelated to fighting ability, e.g., a couple with a child may value one another based on their commitment to the child's welfare, friends may value each other based on a history of reciprocity, and so on. If the nature of the relationship between the angry individual and the target of her anger is such that the target's welfare trade-off ratio is primarily calibrated by variables other than fighting ability, then aggression will be an inefficient means of recalibrating the target.

In such relationships, anger uses other behaviors to recalibrate the target. Most commonly, if the relationship is based on cooperative value, the angry individual can threaten or actually withdraw cooperation (Williams et al. 1998). Such a demonstration would work for the same reasons that demonstrations of formidability will work: by withdrawing cooperation, the angry individual demonstrates to the target that they will be worse off by continuing to treat the angry individual with such little regard.

As with conflicts of assessment and ritualized aggression, these bouts of cooperative withdraw are predicted to follow a pattern that enables individuals to demonstrate cooperative value in ways that minimize the damage done by the demonstration. In other words, just as two cichlid fish avoid biting but engage in tail-beating during a fight (Enquist et al. 1990), and two men punch and kick in a bar brawl but avoid eye-gouging (Romero et al. 2014), two feuding spouses may withhold chores and affection but would still rush to one another's aid if they were in a serious accident. These bouts of cooperative withdraw are predicted to be coupled with monitoring and other evaluations to determine changes in the mental state of the target of anger. This often leads to odd situations where an angry individual is abstaining from cooperative behavior and withholding attention, i.e., simulating to the target what it would be like if the cooperative pattern was ended, while actually focusing a great deal of attention on the target.

One prediction from this model is that individuals with greater cooperative value – those whose cooperation is of greater benefit to others – should

calibrate their expected welfare trade-off ratios higher. In other words, they should expect and demand better treatment from others, just as those with greater formidability are known to do. This has been confirmed empirically for several traits related to cooperative value, specifically physical attractiveness, wealth, and mate value (Lukaszewski 2013; Sell et al. 2016; Sell et al. 2009b).

The Content of Anger-Based Arguments

Though rarely empirically studied, arguments are, by far, the most common behavioral response to anger (Averill 1982), and any comprehensive theory of anger must ultimately explain the structure of such arguments. The recalibrational theory explains arguments as the mutual recalibration of variables that are relevant to the resolution of the conflict (e.g., relative value placed on the contested resource) and to the calibration of the individuals' welfare trade-off ratios. This information exchange has many evolutionary precedents, e.g., some species are known to send signals of their valuation of a contested resource. Bald eagles raise their crop to show the distention of their gullet to opponents when fighting over food (Hansen 1986). While eagles signal their hunger via a different channel than a human bargaining over whether he is allowed to take the day off of work, the cognitive grammar of the message is identical: "I value this highly, and therefore you should cede the conflict to me." Such an argument will sometimes recalibrate the opponent and lead to the resolution of the conflict in favor of the arguer, e.g., bald eagles that see the empty stomach of their opponent are more likely to relinquish the food (Hansen 1986).

Conclusion

According to mainstream evolutionary psychologists (Tooby and Cosmides 1990), emotions are evolved modes of operation that function to coordinate multiple systems of the body and orient them toward a temporary adaptive problem, e.g., fear coordinates attention, sensory input, and bodily responses and calibrates them toward the adaptive problem of imminent bodily

harm. The recalibrational theory of anger (Sell 2011; Sell et al. 2009b) is an evolutionary psychological theory that claims that anger evolved by natural selection to bargain for better treatment. This selection pressure has designed many bargaining systems in nonhuman animals, and these systems serve as phylogenetic precedents for anger.

The structure of anger itself appears well designed to bargain. Anger is triggered by indications that a target does not value the angry individual's welfare highly (i.e., the target has a low welfare trade-off ratio (WTR) toward the angry individual). These indications usually start in stage 1 anger where the angry person interrogates the target and bargains over the conflict itself. Anger can escalate into stage 2 anger when it is revealed that the target of anger does indeed hold a low WTR toward the angry individual. In stage 2 anger, the angry individual attempts to recalibrate the target's WTR by demonstrating an ability to harm the target by cost infliction (i.e., aggressive bargaining) or benefit withdraw (i.e., cooperative withdraw).

The recalibrational theory has many strengths. Specifically, it offers a specific computational analysis of human concepts like "status" and "disrespect." The theory is derived from well-understood and validated models of animal bargaining that have helped understand aggression in many other species. Furthermore, because it is a functional theory (rather than descriptive), it can be used to derive multiple subtheories about aspects of anger, such as the theory that the anger face is composed of muscle movements that enhance cues of strength. Finally, it has the potential to explain the largest unresolved issue in anger research: the computational design of anger-based arguments.

There are also limitations and weaknesses of the recalibrational theory. It cannot easily account for anger deployed at inanimate objects (e.g., a boy repeatedly fails to climb a tree and seemingly becomes angry at it) or anger at the self. Furthermore, the theory of anger depends on the computational structure of status-setting machinery (e.g., the welfare trade-off ratio and how it is calibrated) for many of its predictions. Until this status-setting machinery is well understood, the predictions about anger will be tentative.

Cross-References

- [Aggression](#)
- [Anger Proneness](#)
- [Attractiveness and Anger-Proneness](#)
- [Competition for Resources Desired by Females](#)
- [Dominance and Threat or Use of Force](#)
- [Emotions](#)
- [Facial Expressions](#)
- [Psychological Mechanisms](#)
- [Sex Differences in Anger Proneness](#)

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Recall

► Attention and Memory

Recall of Cheaters

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Synonyms

Memory; Reputational memory; Social cooperation; Social norm violation; Source memory

Definition

Memory for others is enhanced by details violating one's social expectations.

Introduction

All too often we encounter individuals engaging in behaviors that go against societal expectations. In a recent survey report, over one-third of graduate students, over two-thirds of college undergraduates, and over 90% of high school students admitted to knowingly cheating or plagiarizing academic work (McCabe 2017). As another example, we know that rates of cheating among married couples range between 2% and 4%, with infidelity being cited as the most common cause for divorce (Fincham and May 2017). Certainly, academia and romance are not the only examples in which deception can be encountered. Although engaging with individuals who have behaved in a socially deviant fashion may not always be avoidable, through evolution we have evolved mechanisms that assist in minimizing the potential negative impacts from these associations. Are such mechanisms specific to remembering socially deviant individuals, or are they more broadly employed?

Memory allows individuals to reflect upon and learn from information previously encountered. According to an evolutionary perspective, the skill of recollection has evolved as an adaptation that aids an individual in navigating his or her environment with the aim of genetic proliferation (see Confer et al. 2010; Cosmides and Tooby 1997, for primers). This idea of adaptive memory has gained momentum over the past decade with the underlying notion that information most relevant to survival (e.g., locating food and shelter, protection from predators, and identifying personal safety) demonstrates a prioritized place within memory (Nairne et al. 2007; Scofield et al. 2018). In this framework, the details of individuals who pose a threat have also been shown to induce efficient processing in observers. This efficiency encourages constructive social interactions to occur in the future, whether that means to engage with or retreat from such individuals.

As social beings, it is imperative for humans to have the ability to successfully recollect the faces of others. The results from early research (e.g., Mealey et al. 1996) on memory for others' reputations have focused on the presence of a processing system specifically adapted to detecting noncooperative individuals (e.g., cheaters). However, the extant literature instead suggests that superior memory recall for cheaters can be explained by a host of alternate variables.

A Memory Focused on Cheaters?

Socializing holds a possibility for immense rewards and severe costs. When interacting with others, we may mentally calculate the potential costs (e.g., losing resources, being harmed) and benefits (e.g., gaining resources, protection) to arrive at a decision as to whether or not we should engage and the degree of caution to take (Balliet et al. 2011). The act of cooperating with others can mean that an individual must accept a certain number of costs in order to help others and obtain a desired set of benefits.

While there may be a mental trade-off of potential outcomes, some have suggested that people

often behave in a way that is honest, fair, and beneficial to both parties (Axelrod and Hamilton 1981; Trivers 1971). One such highly-cited example comes from social contract theory (Cosmides 1989; Cosmides and Tooby 1992, 2005). This theory holds that unrelated persons engaging with each other hold an agreement to act in a moral and socially acceptable fashion. That is, we assume others will behave in a way that is honest, fair, and beneficial to both parties.

However, not all individuals encountered will act in such a cooperative fashion. When a person breaks a perceived contract, they may be acting with self-serving motives that disadvantages at least one party. Social cooperation is key when it comes to positive interactions with others (c.f., Gómez-Gardenes et al. 2012). Just as it can be advantageous to identify individuals with a history of cooperation, those with a history of non-cooperation should be detected and remembered with importance so as to minimize the chance of deception during future encounters. As such, one could identify individuals with a history of cheating or cooperative behaviors to appropriately avoid or seek out these individuals during social situations, respectively.

Aligning with the conceptual ideas of social contract theory, Cosmides and Tooby (1992, 2005) have posited a cheater detection module. This highly popularized account predicts that humans have adapted a particular attunement of attention and memory toward the cheaters within one's environment. This attunement is thought to occur whenever a situation involves social contracts, regardless of context. During a social exchange, it is predicted that other's reputations will be keenly remembered when a history of deception is perceived. When a person behaves in a way that goes against societal norms, such as cheating or acting noncooperatively, they may be particularly memorable due to the expectation violation (Kroneisen and Bell 2013).

It can be argued that unexpected events require one to utilize additional cognitive resources and effort in order to understand a situation that would otherwise be automated and simple. For example, stereotypes (a commonly held belief about a group of individuals) allow for information

about others to be processed quickly based on assumptions. However, instances that violate these biases can induce atypical and critical thinking (Rudman and Fairchild 2004; Sekaquaptewa and Espinoza 2004). In short, the prospect of being unfairly deprived of personal resources poses a specific threat that evolutionary pressures have selected for in shaping our modern cognitive abilities. The pillars of a cheater-detection module, generated from social contract theory, assume that human cognition developed to solve the specific adaptive problem of exploitation by cheaters.

Indeed, it is not difficult to imagine how recollection for those with a history of cheating could be advantageous from an evolutionary standpoint (Bell and Buchner 2009; Drigotas and Barta 2001; Mealey et al. 1996). Yet, if true, a question emerges as to why might memory for cheaters be enhanced, as compared to memory for cooperators?

A person who displays cooperative behaviors, such as fairly sharing resources or helping an ill family member, becomes associated with the notion that continued engagement with such an individual would be beneficial (Orbell and Dawes 1991). An individual who acts in a self-serving and noncooperative fashion, such as one who steals resources or does not follow through on an agreement, can be labeled as non-desirable or a “cheater.” The label of “cheater” can potentially frame future interactions with distrust. Such framing may even result in a decreased propensity to engage in future interactions.

While the label of “cheater” can dissuade people from future interactions, the label of “cooperator” may not be as diagnostic in indicating how to proceed. An individual who cheats in a given circumstance may have motivation to behave in a more socially desirable fashion in an alternative context (Axelrod and Hamilton 1981; Trivers 1971). For example, a person who unfairly trades resources with a stranger may choose to trade fairly with a friend who supplies a highly desirable item. A known cheater may act in an unpredictable fashion depending on situational context, but a known

cooperator is presumed to behave fairly regardless of circumstance.

Without an expectation of negative behavior, it seems we may assume others should behave cordially. Thus, cognitive resources may not be taxed by remembering cooperators: it is not harmful to interact with such individuals. However, additional effort could be required to remember unexpected deceptive behaviors, such as cheating. Moreover, the potential harm associated with forgetting a cheater (i.e., potential threat) is greater than is associated with forgetting a cooperator (i.e., potential help). In short, a reputation of cheating (displayed only by cheaters) is more diagnostic of future behavior than is a history of cooperation (can be displayed by both cheaters and cooperators). A memory tuned toward remembering cheaters and their reputations, as opposed to cooperators, is beneficial to avoid exploitation. Therefore, recognition (i.e., sense of familiarity) alone is not useful when engaging in social exchanges. Rather, the ability to recollect specific details of an encounter is essential for creating an association between a face and its behavioral history. Being aware of such an association can then be one component used to frame future interactions.

In summary, it has been argued that cheaters hold special value in evolving human cognition. Both the social contract theory and the cheater detection module predict that a superior memory for such noncooperative persons is the result of an evolutionary adaptation that allows for the detection of societal norm violations. If memory is indeed *not* specific for cheating behaviors, what more general mechanisms does it most readily process? The following sections will discuss how reputational memory is studied, followed by discussions of two main points of consideration: expectation violations and context relevancy.

Empirical Testing of Reputational Recall

Memory retrieval is typically studied in one of two methods: recognition (familiarity based) and

recall (recollection of details). The first instance of empirical examinations of memory for cheaters was provided by Mealey et al. (1996) using tests of recognition. Specifically, participants were asked to rate a series of photos of Caucasian males on their level of physical attractiveness. Importantly, descriptive information presented with each face indicated varied information about their social status (high or low) and general character (potential for cheating behaviors). A week later, the participants again viewed the images and were asked to indicate which faces they recognized from the previous session. Mealey and colleagues reported that participants were most accurate at identifying photos of individuals previously associated with cheating behaviors (e.g., caught embezzling money) than with trustworthy behaviors (e.g., returned a lost wallet). However, this pattern of results was mitigated for faces also associated with a high social status, who were viewed as more attractive overall: high-status individuals are well-recognized regardless of their behavioral history. The researchers concluded that faces associated with potential threat, particularly those of low-status individuals, produce a *recognition memory* attunement. This landmark research provided interest and evidence for understanding the influence of reputational status and character variables on memory prioritization.

However, such a memory advantage for cheaters has largely gone unreplicated (e.g., Barclay and Lalumière 2006; Bell and Buchner 2009; Bell et al. 2012; Mehl and Buchner 2008; Schaper et al. 2019). Recent experiments designed to assess reputational memory (i.e., remembering patterns of past behaviors) have employed variations of a face and description encoding task followed by a recognition and source memory test. One example of the common paradigm (Bell and Buchner 2009) tasked participants with rating the likability of faces presented together with behavioral descriptions that implied either positive (e.g., trustworthiness: a cheese monger who allows his customers to sample his products), negative (e.g., cheating: a used-car

dealer who conceals serious defects from his customers), or neutral (e.g., reputational irrelevant: a scaffolder who works where buildings are to be constructed) actions. Later, a standard recognition task was administered in which participants indicated if a given face had been previously presented or not, depicting a sense of familiarity with the individual. When a face was identified as previously rated, the participant also recalled the source memory by indicating the details of the associated behavior (i.e., cheating, trustworthy, or irrelevant).

The results of the *recognition* task indicated no difference for facial memory between those previously rated. Evidence supporting a lack of advantage in recognition memory based on cheater status has since been routinely found and is in contradiction to the conclusions reported by Mealey et al. (1996). However, patterns of differentiation emerge when asked to *recall* the nature of the specific behavioral description (source memory) associated with a previously rated face: faces associated with cheating behaviors were better remembered than those associated with trustworthy behaviors, which surpassed those associated with irrelevant behaviors.

The expansive literature regarding reputational memory challenges the merit of a true cheater detection module. Two main arguments have emerged against the presence of a cheater-specific cognitive adaptation. First, the mere identification of a cheater as having been previously encountered is not enough to avoid the possible repercussions of an interaction. Research has indicated that merely re-meeting an individual, regardless of their behavioral history, can increase trust and perceived importance due to a sense of familiarity with that person (Jacoby et al. 1989; Zajonc 1968). Therefore, it seems imperative that one cannot only detect a devious individual, but can also accurately associate that person with the correct behavioral history.

Second, it has been argued that a sole focus on the actions of cheating individuals does not produce a complete picture for successful interactions with others. That is, it is personally advantageous

to remember those who have demonstrated untrustworthy actions so as to avoid future deception. Similarly, there is a personal advantage to remembering people who demonstrate trustworthiness to continue engaging in reciprocal benefits (Bell et al. 2017). Indeed, after learning the likelihood that a given partner will cooperate with or act unfairly in a given task, individuals display a preference of willingness to engage with those who act in a mutually beneficial fashion (Schaper et al. 2019; Winke and Stevens 2017). Choosing to focus on cheaters or cooperators can be influenced by the contextual circumstances and present goals for the interaction.

While it is important to recognize an individual as having been previously encountered or not, this information alone is not sufficient in determining one's probability of acting in a cooperative or deceptive manner. Accordingly, when asked to indicate if an individual has been introduced before or is a novel stranger, the typical results indicate that there is no benefit to accuracy based on whether the individual was previously a cooperator or not: recognition is equivalent and better for cooperators and deceivers than previously unencountered individuals. However, when asked to identify the context (i.e., source memory) in which an individual was previously encountered (e.g., cooperator or deceiver), differences in *recall* tend to emerge. The variables influencing accurate recall memory for cheaters will be discussed in the next sections.

Violation of Social Expectations

While there is some reason to suspect that a unique base system for cognition has been enhanced to recollect the sources of cheating behavior (Bell and Buchner 2009; Mehl and Buchner 2008; Schaper et al. 2019), others have argued that the enhanced memory is driven by a violation of expectancy – or rather the presence of incongruent information. That is, the seemingly robust human ability to remember cheaters is a result of a more flexible cognitive

system that responds well to surprising information.

On a daily basis, we have expectations for how commonly encountered situations will proceed and for how others will behave in such circumstances. However, when these social norms are violated, the instance goes against our expectation and can produce a memory advantage for the individuals and details involved. For example, it is documented that we tend to quickly evaluate people possessing qualities associated with desirability (e.g., positive affect, physical attractiveness, and high social status) as trustworthy and memorable (Todorov, Pakrashi, and Oosterhof 2009). Such an understanding could, in part, account for the findings in Mealey et al. (1996) for improved *recognition* of high-status individuals, regardless of their cheater reputation: high-status trustworthy individuals were remembered for this desirability, while high-status cheaters behaved unexpectedly.

In the case of reputational memory, knowledge for individuals who violate societal expectations set by social contract rules are markedly perceived as a specific form of expectancy incongruence (Farrelly and Turnbull 2008). For example, Chiappe et al. (Experiment 2; 2004) presented participants with facial photographs accompanied by social contract rules in the form of logic problems that described either cheating (e.g., failed to repay a cost), cooperation (e.g., repaid a cost as agreed upon), or irrelevant (e.g., owes a business) behaviors. Each behavior involved either a relatively large or small sum of money as a means of identifying the influence of resource value. The results of a source memory test indicated that the cheating behaviors were most salient, regardless of the amount of resources involved. The researchers concluded that the threat to the social expectation that an agreement will be fulfilled led to cheaters standing out in memory.

In addition, the literature on memory has established a processing advantage for emotional (valenced) information (Bell et al. 2012; Kensinger and Schacter 2008). That is, events and stimuli that possess a positive or negative

connotation tend to be remembered with greater detail and accuracy than do non-emotional, neutral situations. Moreover, contexts eliciting negative emotions (e.g., sadness, fear) tend to be even more memorable than those eliciting positive emotions (e.g., happiness, trustworthiness; Ochsner 2000).

Encountering individuals with a history of cheating or deceptive behavior can be highly distressing, anger-provoking, and threatening to one's survival (but see Buss et al. 1992 for sex differences). Thus, such persons can constitute a negative context. By having selectively adapted for the ability to remember details of negative memories, humans should show enhanced success in remembering events that resulted in potentially dangerous social interactions. Indeed, faces encountered in a socially threatening context have been shown to be better remembered than faces associated with a cooperative or neutral context (Bell and Buchner 2010; Buchner et al. 2009).

However, not all negative events garner equal memory resources. The context of socially deceptive behavior plays a critical role on its memorability. For instance, consider the relevance that the deceptive action may have on the observer. One study (Bell et al. 2012; Experiment 2) exposed participants to individuals associated with a history of aggressive behavioral tendencies. Crucially, these behaviors were either directed at the observer (e.g., the person gets angry and throws things) or were directed toward the self (e.g., the person gets depressed). During a later memory test, the persons who were associated with behaviors posing a threat to the observer were better remembered as such than were the persons producing aggressive behaviors that only threatened themselves.

Similarly, some researchers have found that memory may be more likely to be enhanced for individuals committing acts of aggression, as compared to victims (Bell and Buchner 2011). In other words, a memory advantage may be most prominent when the act of cheating poses a potential threat to the observer, as opposed to a general bias toward cheating behaviors. The details of

negative events may be associated with threats to the self, enhancing memories for such contexts. As a result, how one recalls noncooperative behaviors could be context specific. The researchers concluded that the lack of equal memorability for threatening behaviors, regardless of the target, indicates a more generalized threat detection system than is posited by the cheater detection module. Rather, the degree to which other people's actions are perceived as threatening must be taken into consideration in creating a functional memory model.

The degree of surprise regarding an expectation violation can also be influenced by the relationship between the cheater and the cheated. That is, people who have a lot of trust in their partner may be most susceptible to the impact of having their expectations violated. For instance, some research has noted asymmetrical reputational memory for uncooperative individuals when they are thought to share group memberships (such as those based on interests and identities with oneself; e.g., common race, social status, teammates) relative to those perceived as outsiders (memberships wherein there is a lack of shared commonalities). Indeed recall memory accuracy was best for *uncooperative in-group members* even though participants assumed that their respective in-group members depicted more cooperative behaviors than did out-group members (Hechler et al. 2016). Thus, the act of deception was thought to be *most* surprising when completed by a trusted in-group member. The results indicated that people tend to trust those associated with having a shared group investment, situating actions that counter this expectation in the forefront of one's memory. The notion of a generalized cheating bias does not accurately encompass such nuanced patterns of results, providing further support for the notion of a more flexible, context-specific memory module.

Some faces inherently display a sense of trustworthiness (e.g., positive valence, attractive), providing that person with a more favorable perception, compared to those with an untrustworthy appearance. For instance, in one study researchers

(Mattarozzi et al. 2015) paired faces that had been rated as trustworthy, untrustworthy, and neutral with newspaper headlines depicting either a pleasant, unpleasant, or neutral action. Importantly, both the photograph and headline appeared simultaneously in an attempt to prevent a bias from the intrinsic appearance of the face. When asked to recall the details of the news article associated with a given face, participants were most accurate when the article elicited emotions (pleasant and unpleasant) than when it was emotionally neutral. In the case of pleasant articles, faces that were rated as either trustworthy or untrustworthy enhanced memory. For the unpleasant news articles, memory accuracy was best when it was associated with an untrustworthy face. This indicates that, without the chance to generate an expectation about others, the emotional context in which a face is encountered largely dictates its memorability. However, the initial interpretations based on facial appearance one has of others can influence memorability for both pro- and antisocial behaviors. Individuals with a threatening appearance are the most memorable, regardless of true behavioral actions. When preconceived expectations about a person are not available, the emotional context of a situation appears to drive memory recall particularly when facial details match the context valence.

When navigating the world and social interactions, it is clear that we are structured toward using mental shortcuts to minimize the amount of cognitive effort exerted. The instances and people that challenge such a shortcut, namely, by violating expectations, seem to cause unique memory processing. However, the degree to which a social violation affects memory is, in part, dependent on the individual observer.

Personal Relevance to Expectation Violations

The ability to recall the reputational history of others has been shown to be influenced in part by relevance to and characteristics of the observer (Kroneisen 2018). Individual differences in how

one interprets a situation based on personality traits – in addition to contextual information – can increase sensitivity toward known deceivers. Bell et al. (2014) predicted that individuals with a stronger sense of morality adherence would be particularly attentive to those who violated social norms. It was also hypothesized that memory for an indiscretion would be magnified if it violated *self-related* interests to a greater degree than self-unrelated actions.

Using a variation of the common cheater recall paradigm (described above), participants were shown facial photographs while listening to descriptions that indicated either moral or immoral behaviors (morality) and a personal benefit or cost as a result of the behavior (personal consequences). For example, an immoral behavior associated with a benefit would be, “He lied to another person to sell that person your useless products.” A moral behavior associated with a cost may constitute, “He gave the promotion to another person rather than you because the other person was most qualified.”

Accurate recall of behavior morality was facilitated when the acts were described in terms of personal consequences. Specifically, immoral behaviors were particularly remembered when they were associated with a negative consequence to the observer, relative to a benefit. This suggests that human memory is particularly salient for acts that violate morality, as well as possessing a self-serving bias. Furthermore, individuals who demonstrated a strong sensitivity to acts of immorality were *more likely* to accurately recall the behaviors associated with immorality when a personal cost, as opposed to a benefit, was implied. An individual’s personal understanding and adherence to what is colloquially defined as socially acceptable and moral behavior can dictate the degree to which cheaters are recalled during social situations. Specifically, negatively viewed behaviors that also result in negative consequences are particularly salient.

Factors altering one’s perception of exploitation can also influence memory processing (Baumert et al. 2012). Individuals who display certain traits, such as a heightened fear of

exploitation toward trustworthiness (victim sensitivity), tend to show superior face memory for people with negative labels (Süssenhach et al. 2016). For example, a person who has been labeled as an untrustworthy cheater but behaves in an unexpectedly kind fashion tends to be well-remembered by those scoring high in victim sensitivity. In this case, the expectation for a socially deviant behavior to occur by a person in the focus of attention is violated, rather than confirmed, producing a memory advantage. However, persons labeled and expected to act in a positive fashion do not influence memorability for those high in victim sensitivity, regardless of their actual behaviors. The lack of differentiation in memory for those expected to act in a cooperative fashion is due to the hyper-focused attention on expected wrongdoers. Thus, an analysis of persons with such a personality trait suggests that information that is prioritized in memory with regard to the reputations of others is based on what is relevant and seemingly important information to the individual observer. This provides further support for a flexible reputational memory module that is context dependent and highly susceptible to unexpected information (Bell and Buchner 2012).

In addition to our personal beliefs influencing memory, how others are perceived has also been shown to markedly alter the degree to which others are remembered. The way a new situation is presented can frame the cognitive response that is made toward it. For example, memory is markedly improved for individuals displaying pro-social, cooperative behavior when the meeting context is prefaced with a description of a negative, aggressive neighborhood (Kroneisen et al. 2015). However, those without a preconceived knowledge to the characteristics of a neighborhood displayed a typical source memory advantage for aggressive persons. This suggests that an attunement toward threat bias may only occur when a negative context is not anticipated.

The enhanced memory for cooperative individuals, as compared to threatening individuals, appears to be in direct violation of a cheater detection module. Yet, both findings correspond with

the notion of a more flexible expectation violation advantage. When a negative expectation for behavior is given, positive behaviors are not expected. However, when no behavioral expectation is provided, we assume persons to behave in a cooperative fashion in accordance with social contract theory. This flexibility allows us to appropriately respond to any social situation, as opposed to an exclusive focus on negativity and avoiding deception by cheaters.

Conclusion

It is a common assumption in evolutionary psychology that modern functions of humans developed to serve an adaptive need. In the case of human memory, we tend to display a bias toward recalling information pertaining to cheating behavior. The unexpected and negative nature of such socially deviant actions violates the terms of social contract theory and could thus constitute a need for greater memory for such behaviors. However, a more critical analysis of the extant literature provides an alternative explanation: a more flexible and general notion of expectation violation within the social realm enhances memory recall (Bell and Buchner 2012). Information that is relevant to an observer and comes as a surprise within a given context can be an indicator that one's schema may not be valid. Although memory appears to prioritize cheaters, the additional effort and cognitive resources needed to understand such situations could account for this pattern of results.

Human memory is capable of honing-in on information that has been adaptively relevant and most informative in social interactions, with a particular devotion to understanding the unexpected. Because we tend to encounter individuals who are agreeable and cooperative, the unexpected and socially deviant tend to stand out in our mind. By adaptively focusing memory on the select cases in which behavior is inconsistent with our expectations, we are able to selectively mark such individuals as unique cases deserving of recollection.

Cross-References

- [Attention and Memory](#)
- [Cheater Detection](#)
- [Cheater Detection Adaptations](#)
- [Face Recall](#)
- [Memory Enhanced for Cheaters Versus Non-cheaters](#)
- [Selective Attunement to Adaptive Problems](#)
- [Social Contract Rule Violation](#)
- [Theory of Reciprocal Altruism](#)

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Recessive Genes

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Definition

Alleles that are not expressed phenotypically, or are only partially expressed, in the presence of other alleles.

Introduction

Scientists have been conscious of the detrimental consequences of inbreeding for nearly 150 years, in large part due to Darwin’s (1891) experimentation with plant species. Indeed, across multiple plant and animals species it has been observed that the offspring of closely related parents or “inbred” individuals are more likely to suffer deleterious genetic effects than their “outbred” conspecifics (Roff 1997). It has become increasingly clear since the discovery of Mendelian genetics that inbreeding depression is the product of homozygous recessive alleles (Charlesworth and Willis 2009). However, the precise impact of recessive genes and their role in inbreeding depression has only been brought to light in recent decades (Charlesworth and Charlesworth 1999).

Recessive and Dominant Genes

In diploid organisms such as humans (and most mammals), for any given gene one allele is inherited from each parent. In Mendelian traits, only one allele will be expressed at the phenotypic level. This allele is dominant, while the other allele is said to be recessive. Dominant alleles will produce the dominant phenotype when only one copy of the allele is present (e.g., in the case of heterozygosis). In contrast, recessive phenotypes

are only expressed when two copies of the recessive allele are inherited (i.e., homozygosis). This is referred to as complete dominance, wherein the phenotype of a heterozygous dominant is no different from a homozygous dominant. However, the relationship between genotypes and phenotype is frequently more complicated than that described by Mendel. In the case of partial dominance, the phenotype may resemble a point along a continuum from homozygote dominant to homozygous recessive. Importantly, because of mutation in the population, some alleles will have harmful effects and how these effects manifest will be influenced by patterns of recessive and dominant gene expression.

Directional Dominance

In most populations, harmful alleles generally exist at a low frequency and are maintained by mutation-selection balance. This is the balance between natural selection against deleterious alleles and processes that introduce them into the population (i.e., mutation). Dominant alleles that manifest in harmful phenotypes are likely to be eradicated by natural selection, due to their negative impact on fitness-relevant characteristics. However, those that are recessive are less likely to be purified by selection, as they are less likely to manifest in the phenotype. This means that deleterious alleles are more likely to be recessive than dominant, a phenomenon called directional dominance (Charlesworth and Willis 2009). When two related individuals produce offspring, the likelihood of harmful alleles being homozygous, and therefore expressed phenotypically, increases (Charlesworth and Willis 2009).

The probability of inheriting the same allele (i.e., autozygosity) from separate parents is referred to as the inbreeding coefficient. The relationship between inbreeding depression and the magnitude of the inbreeding coefficient has been demonstrated in many animals (DeRose and Roff 1999). Likewise, inbreeding depression has been observed in humans relating to the increased probability of a range of mental illnesses including schizophrenia and bipolar disorder as well as cancer and heart disease.

Recent advances in access to large-scale genotyping data have allowed researchers to quantify the more subtle effects of inbreeding depression in the general population. This is possible because all members of a species are “inbred” to the extent that they are all related to each other, and even comparatively small inbreeding coefficients can be associated with inbreeding depression. For example, Verweij et al. (2014) investigated the relationship between runs of homozygous recessive genes throughout sections of the genome likely to be identical by descent (i.e., autozygosity) and inbreeding depression in a range of fitness-relevant traits. Genotype data was collected from over 5,000 “unrelated” Finnish individuals and analyzed with reference to 18 traits including birth length, body mass index, height as an adult, blood pressure, heart rate, and other measures of health, as well as educational attainment and marital status. As predicted by inbreeding depression effects, individuals with more of their genome in runs of homozygosity were more likely to have traits associated with lower fitness, such as lower height, income, educational attainment, and grip strength, and higher physical and social Anhedonia.

Subsequent work has shown similar relationships between inbreeding depression and homozygosity using a massive cross-national sample of over 350,000 individuals from four continental groups (Joshi et al. 2015). Four complex, fitness-relevant traits (height, a measure of lung volume, general cognitive ability, and educational attainment) were all negatively associated with increased homozygosity, providing further evidence of directional dominance in humans.

Overdominance

To a lesser extent, inbreeding depression may also be the result of overdominance; a situation that arises when a heterozygote results in an exaggerated phenotype compared to either dominant or recessive homozygotes. This is also known as heterozygote advantage (Charlesworth and Willis 2009). A classic example of overdominance in humans is the case of sickle cell anemia. Sickle

cell anemia is caused by homozygosity of a single recessive hemoglobin gene, which leads to disorder of the oxygen-transport protein hemoglobin causing numerous health complications and reducing life expectancy to around 50 years. However, the gene also confers some protection from the malaria parasite. As a result, it was hypothesized that the gene may be maintained in higher frequencies in malaria-dense environments as heterozygotes would possess a single, harmless recessive gene, which nonetheless provided some protection against the parasite. Consequently, heterozygotes would be at a selection advantage over both dominant and recessive homozygotes, hence the term heterozygote advantage.

Until recently, sickle cell heterozygote advantage was primarily theoretical or estimated indirectly. Cohort studies have since enabled the direct observation of the protective effects of the sickle gene. Aidoo et al. (2002) collected data from a Kenyan birth cohort in a malaria-dense region and analyzed sickle cell traits as a risk factor for mortality. While no differences in all-cause mortality emerged before 2 months and after 16 months of age, between this time period heterozygosity was associated with a significant reduction in mortality. This was also the developmental period during which severe malarial anemia was more likely to occur, suggesting specific heterozygote advantage (Aidoo et al. 2002).

While evidence suggests that heterozygotes may be better off in certain environments, they also increase the likelihood of inbreeding depression. As a consequence of their genetic advantage, heterozygotes may be more likely to survive and reproduce, thus sheltering the recessive allele from purifying selection. As a consequence, the probability of homozygous recessive alleles and therefore inbreeding depression is increased in offspring of heterozygotes.

Conclusion

The importance of recessive genes should not be understated given their role in both classical and modern genetic models (Charlesworth and Willis

2009). By their nature, recessive genes tend to be shielded from purifying selection and have profound implications for an organism's fitness. Until recently, these mechanisms were primarily theoretical, but with the advent of more advanced technology, empirical approaches to both classical and nascent models will become more frequent and more important (e.g., Zietsch et al. 2014).

Cross-References

- [Fluctuating Asymmetry](#)
- [Incest Avoidance](#)

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Reciprocal Altruism

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Synonyms

[Evolution of cooperation](#)

Definition

Behavioral strategy where the actor incurs a cost and the recipient receives a benefit in terms of reproductive success, where the return benefit may be reciprocated at a later time.

Introduction

An unresolved issue with Darwin's Theory of Evolution by Natural Selection was altruistic behavior in nature. Unrelated individuals engaging in behavior where the actor incurs a cost, and the recipient a benefit (in terms of reproductive success), appears counterintuitive to evolutionary logic, where individual organisms are expected to engage in behaviors that directly increase survival and the probability of genetic representation in future generations.

Background

In 1964, WD Hamilton laid out the logic for altruism being selected for in related individuals, based on kin selection and inclusive fitness theory. Hamilton utilized evolutionary logic acting at the level of the gene, and mathematical modeling to explain how altruistic behavior could have evolved within populations based on their degree of relatedness.

Trivers' Model

Intrigued by the logic and determined to solve the evolutionary problem of altruism between unrelated individuals, in 1971, Robert Trivers introduced a theoretical model to account for the natural selection of altruistic behavior between unrelated individuals in the first of a series of revolutionary papers that laid the groundwork for modern evolutionary psychology.

Trivers identified ecological conditions favoring reciprocal altruism as an adaptive strategy, inducing unrelated individuals to cooperate in order to increase their own survival and reproductive success. Within a population, individuals must be long-lived, have low dispersal rates, and live in small, mutually dependent stable social groups with parental care. This ensures individuals have many opportunities for reciprocity with known individuals. Crucial to the system is that the inherent cost to the altruist be less than the benefit to the recipient, in terms of reproductive success, and that individuals monitor and keep track of these interactions. The evolution of cooperation and selection for pro-social behavior would be adaptive in such a system and would spread quickly.

Cheater Detection and the Evolution of Human Emotional Systems

One obvious problem was the potential benefits to individuals within the system who adopted a cheating strategy, where they take the benefits but refuse to reciprocate (actual costs and benefits of reciprocal altruism were later brilliantly demonstrated in vampire bats by Wilkinson in 1984). For the system to work, Trivers argued cheaters must be identified and discriminated against immediately. Individuals must refuse to engage with nonreciprocators, and eventually cheaters suffer greater costs than if they originally reciprocated. Trivers proposed reciprocal altruism as the basis for development of human emotional systems that evolved to mediate social relationships. Friendship, loyalty, fairness, justice, gratitude,

sympathy, empathy, moralistic aggression, guilt, regret, remorse, and compassion were put forth as behavioral strategies that evolved to effectively monitor and participate in complex social environments (Trivers 1985).

Conclusion

While Trivers (2002) acknowledges that he should have taken Hamilton's advice and left out the "maths" in the 1971 paper, and that cleaner fish and bird alarm calls are better examples of return-effect altruism, the overall importance of this paper cannot be overstated. The use of evolutionary logic to model and explain the most basic social behavior – cooperation – led to a massive intellectual movement, to not only reorganize and reexamine data on behavior in existing disciplines, but the creation of entirely new areas of inquiry, such as economic game theory (Trivers 2005).

Cross-References

- [Absence of Events to Distinguish True Friends](#)
- [Altruism Defined by Benefits Conferred](#)
- [Contingent Reciprocity](#)
- [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- [Game Theory](#)
- [Gossip and Indirect Reciprocity](#)
- [Monetary](#)
- [Moralistic Aggression](#)
- [Rescuing Friends and Relatives](#)
- [Robert Trivers](#)

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Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)

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Synonyms

[Cooperative investments](#); [Cooperative returns](#); [Reciprocal rewards](#); [Reciprocity](#); [Sanctions](#); [Social partner choice](#)

Definition

Reciprocal altruism describes a situation in which an organism acts in a manner that temporarily reduces its fitness while increasing another organism's fitness. Underlying this behavior is the assumption that there is an ultimate fitness benefit based on an expectation that the other organism will act in a similar manner at a later time. It creates the obvious dilemma in which there is always a short-term benefit to cheating, which is why cooperating individuals must avoid being exploited by non-cooperating cheaters. Therefore, contingent cooperative investments that are based on the cooperative returns must be enforced through partner control and/or partner choice.

Introduction

It is relatively easy to explain altruism among relatives where kin selection causes genes to increase in frequency when the genetic

relatedness of a recipient to a donor multiplied by the benefit to the recipient exceeds the cost to the donor (Hamilton 1964; Carter 2014). How might an altruistic act be explained if the beneficiaries are not the organism's kin? Kinship selection works only when the individuals involved are closely related; it fails to explain the presence of altruism and cooperation between unrelated individuals, particularly across species. The theory of reciprocal altruism was originally developed by Trivers of Rutgers University in a landmark paper (1971) as an attempt to explain cases of (apparent) altruism among unrelated organisms, including different species. He argued that such altruism is advantageous to its practitioner if directed only toward those individuals who will reciprocate; given the right cost-benefit ratios, over time, each member of a reciprocal relationship will do better than by acting alone. As conceived by Trivers, reciprocal altruism is most likely to evolve in species with long lives, good memories, and viscous populations (those in which two individuals meet many times and remember each other's past behavior).

A major advancement of the theory of animal cooperation was the introduction of the concept of Prisoner's Dilemma. Initially invented in 1950 by Merrill Flood and Melvin Dresher who worked at the RAND company, the Prisoner's Dilemma was proposed as an instrument to model processes between conflict and cooperation and between selfishness and altruism. The Israeli mathematician Robert J. Aumann (1959) found that successful cooperation can emerge even between two competitors given they play a repeated Prisoner's Dilemma game called the "folk theorem." Aumann developed game theory with a special emphasis on the area of repeated games, the main topic for which Aumann was awarded the 2005 Nobel Memorial Prize in Economic Sciences. It was shown that if both players cooperate in the one-shot Prisoner's Dilemma, it is not a Nash equilibrium. For a game to be a Nash equilibrium, the number of interactions needs to be large or infinite. Anatol Rapoport, a Russian-born American mathematical psychologist, and his colleague Albert Chammah, a

Syrian-born American mathematical psychologist, further demonstrated the potential of the Prisoner's Dilemma when it is played repeatedly (1965). Trivers introduced the repeated Prisoner's Dilemma game to an analysis of animal behavior, and this Prisoner's Dilemma is known as the iterated Prisoner's Dilemma. However, it was not clear how to play the iterated Prisoner's Dilemma. The "folk theorem" did not define what is a good strategy here. Robert Axelrod, a political scientist from the University of Michigan, organized an unusual competition. He solicited computer programs containing different social strategies from other game theorists to be played against each other in repeated Prisoner's Dilemma tournaments. Across two tournaments, the winner was a short computer-based strategy submitted by Anatol Rapoport. This strategy is known as "tit-for-tat": it always cooperates on the first move and subsequently reciprocates what the social partner did on the previous move, betraying only when the partner betrays the cooperator. The development of the theory of reciprocity based on research of the Prisoner's Dilemma concept – the tit-for-tat and other strategies of cooperation and mechanisms of social control – has thrived since 1960s and 1970s. This has led to an important conclusion that social organisms use decision rules that are shaped by natural selection and that social processes can be expressed as mathematical equations and modeled with the help of evolutionary game theory.

Surprisingly, after hundreds of scientific papers published, the evolutionary and ecological importance of reciprocal altruism is still not clear, and there are serious questions arising on ecological/social/physiological conditions favorable for reciprocity to evolve. Evidence of reciprocal altruism in nonhuman species is largely denied based on, for example, an assumption that it requires sophisticated cognition. Although this restriction defines reciprocity out of existence, evidence shows that fungi, plants, fish, birds, rats, and primates enforce mutual benefit by contingently altering their cooperative investments based on the cooperative returns, just as predicted by the original

reciprocity theory. New evidence from vampire bats is of special interest because it shows that reciprocal exchange can indeed be more important for cooperation than relatedness (Carter and Wilkinson 2013, 2016). It is easy to understand skepticism related to the evolution of cooperation by reciprocity. Cooperation is costly to actors and beneficial to recipients; selection may favor cheaters accepting aid without reciprocation (Trivers 1971). However, reciprocity can generate evolutionarily stable cooperation if costly help sufficiently increases the likelihood that donors obtain fitness benefits in return for helping, provided that the benefits more than compensate for the costs of initial investment. This means that the benefit from being helped must on average exceed the cost of helping and that social interactions should be sufficiently frequent for social control to work (Taborsky 2013). This highlights the importance of considering information about the likelihood of getting adequate returns of any help provided to a social partner. Such information can be obtained from experience of previous interactions and can generate the following decision rules within evolutionary game theory: direct reciprocity (Axelrod and Hamilton 1981), indirect reciprocity (Nowak and Sigmund 1998; Rankin and Taborsky 2009), and network reciprocity (Nowak 2006) – the three directions which future research should focus on.

Prisoner's Dilemma

The Prisoner's Dilemma model shows how the rational pursuit of individual self-interest drives interacting organisms into an outcome that nobody prefers. To understand the Prisoner's Dilemma, one needs to imagine two partners in crime captured by police awaiting for a trial. Each person is faced with only two options: cooperating with the other one by refusing to confess or defecting from their criminal alliance by confessing. The prosecutor interrogates each crime partner separately and offers a deal to each person. If both cooperate by keeping silent, the

prosecutor cannot convict both partners of the more serious crime, and each criminal gets a light sentence (R, the reward for mutual cooperation). If one of them, the defector, incriminates the other partner, then the defector is rewarded with an even lighter sentence (T, the temptation to defect), while the other person gets the stiffest sentence (S, the sucker's payoff). If both partners defect each other, then each gets a lighter sentence than when only one goes for defection but still heavier than the sentence that each would have reaped from mutual cooperation (P, the punishment for defection). This is a nonzero game where all outcomes (T is the best; S is the worst) are relative and "my loss is not always your gain" as in a zero-sum game. This is because one partner can benefit without the other losing; they only need to cooperate. However, each prisoner has to make his decision without knowing what the other will do. In a non-repeated game, the prisoner should defect because defection pays better than cooperation. On the other hand, the dilemma has another solution given the social partners play the game repeatedly/indefinite number of times where "the future can cast a long shadow backwards onto the present," as noted by Robert Axelrod. The first experimental evidence of the iterated Prisoner's Dilemma in nature was presented by Manfred Milinski, the director of the Max Planck Institute for Evolutionary Biology in Germany (1987). Milinski studied the "predator inspection" in the three-spined sticklebacks (*Gasterosteus aculeatus*). This behavior is risky for the fish, but the information they obtain while inspecting an unknown object can benefit them. If the inspected is not a predator or it is not an active one, the group of sticklebacks does not need to move away. Milinski studied the behavior of sticklebacks when confronting a potential predator, because conflicts can arise within pairs of fish in these circumstances which resembled a series of games of Prisoner's Dilemma. Using a system of mirrors, Milinski provided single approaching a live predator with either a simulated cooperating partner or a simulated defecting companion. In both cases the test fish behaved according to tit-for-tat.

Tit-for-Tat and Related Strategies

Tit-for-tat won the famous Axelrod's tournament – a surprising outcome for such a simple strategy. Detailed analysis revealed that the simplicity accounted for the success of tit-for-tat either within the Prisoner's Dilemma game or in real-life situations. This is because a more complex strategy prevents the social partners from reading each other's intentions. Tit-for-tat has simple rules that are consistent and easy to figure out by the other player after a short set of interactions, thereby eliciting long-term cooperation (Axelrod 1984). Moreover, Axelrod found one more surprising property of tit-for-tat and other simple strategies such as tit for two tats submitted by John Maynard Smith, the British professor. The competition in each round of Axelrod's tournament became stronger as weaker computer programs were eliminated, while the remaining/dominating strategies were found to be all “nice” given they were also provokable – highly resistant against the occasional exploitation (Axelrod 1984). The property of being nice means never be the first to defect. Being nice is tightly linked to the property of “forgiving” because it only looks at the most recent move by the other player. All the rest of the history of interactions is not considered when deciding the current move, and this is why being nice and forgiving makes restoration of mutual cooperation possible.

Some other popular-related strategies are Pavlov, tit for two tats, generous tit-for-tat, contrite tit-for-tat, tit-for-tat empathic retaliator, and tit-for-tat sympathetic retaliator.

Pavlov (win-stay, lose-switch): Cooperates on the first move. If a reward or temptation payoff is received in the last round, then repeat the last choice; otherwise choose the opposite choice. It is relatively stable in a noisy environment. Similar to tit-for-tat but not forgiving, Pavlov will exploit altruistic strategies until it is punished by mutual defection (Kraines and Kraines 1989).

Tit for two tats: This strategy is same as tit-for-tat and cooperates on the first move. It is super forgiving and defects only when the opponent defects two times (Maynard Smith 1982).

Generous tit-for-tat: Similar to tit-for-tat, except that it cooperates with a probability q when the opponent defects (Komorita et al. 1968).

Contrite tit-for-tat: Same as tit-for-tat when an environment is not noisy and it is useful in a noisy environment. Social partners can be in good or bad standing: player A gets into bad standing if it defects when it should have cooperated. However, if A cooperates in the next round, it can restore its standing, and the pair (A, B) can recover from being stuck in mutual defection caused by a simple error in judgment or implementation (Sugden 1986).

Tit-for-tat empathic retaliator and tit-for-tat sympathetic retaliator strategies: Direct reciprocity is about repeated moves between a pair of social partners (Trivers 1971; Axelrod and Hamilton 1981), and indirect reciprocity deals with situations wherein cooperation is channeled toward the cooperative individuals within the group (Nowak and Sigmund 1998). Fishman (2006) considered the case of involuntary defection that is conceptually similar to an error in implementing a good intent, but in which case the reason for defection is the inability to cooperate given current circumstances. He concluded that the possibility of involuntary defection leads to the evolution of an “emphatic retaliator” but not of “sympathetic retaliator.” An emphatic retaliator is a rewording of contrite tit-for-tat, whereas the sympathetic retaliator differs from contrite tit-for-tat in which individual A refrains from punishing individual B after B has defected, if A assesses that B's defection was involuntary. However, “sympathetic retaliator” strategy has been recently found in nature where breeding birds used a tit-for-tat with an embedded “excuse principle” to forgive the neighbors that were perceived as unable to cooperate during mobbing of predators (Krams et al. 2013). The excuse principle dramatically increases the stability of tit-for-tat-like behavioral strategies within the Prisoner's Dilemma game and demonstrates the role of empathy in reciprocity since “sympathetic retaliator” strategy is also partially based on empathy.

Importantly, tit-for-tat's appetite for revenge proves self-destructive as it requires defection of a social partner even if the partner is unable to cooperate (Nowak 2006), while the "excuse principle" shows how this can be mitigated.

Direct Reciprocity

Briefly, direct reciprocity means that A helps B and B helps A. Direct reciprocity can be observed in cooperation between unrelated individuals or even between members of different species. Given that A and B can meet repeatedly during every encounter, each player has a choice between cooperation and defection. This game is known as the repeated/iterated Prisoner's Dilemma. The best strategy for playing the iterated Prisoner's Dilemma was found to be tit-for-tat. It is nice and never first to defect. Tit-for-tat is provokable: it returns defection for defection and cooperation for cooperation. It is not envious: it focuses on maximizing its own "score" instead of ensuring its own score is higher than that of the partner. Finally, tit-for-tat does not tend to be too clever because players need to figure out intentions of their partners. However, tit-for-tat is not resistant against mistakes which may cause the permanent breakdowns in cooperation. The substitutes of tit-for-tat, such as generous tit-for-tat and Pavlov strategy, are more flexible against defections and possible mistakes. Many other strategies have been suggested during recent decades, and the total number of these for the iterated Prisoner's Dilemma might even increase reflecting differences in the origin, evolutionary history, and ecological conditions of organisms under the study. Although strategies to reach reciprocity may be unlimited, Nowak (2006), a professor of Biology and Mathematics at Harvard University, proposes a general rule for direct reciprocity to become an important force in evolution of sociality: the probability w of another interaction between the same two unrelated players should exceed the cost (c)-to-benefit (b) ratio of the reciprocal act: $w > c/b$.

Indirect Reciprocity

Direct reciprocity is not capable of explaining many aspects of cooperation, especially when it comes to mechanisms for the evolution of cooperation in humans who often help strangers and donate to charities that never reciprocate back to the donors. Direct reciprocity needs the same individuals to meet again, while people often cooperate when they are not expected to see each other in the future. Some primitive forms of indirect reciprocity seem to be found in animals (Bshary and Gutter 2006). For example, Rutte and Taborsky (2007) of the University of Bern experimentally tested whether cooperative behavior of female wild-type Norway rats is influenced by prior receipt of help, irrespective of the identity of the partner. Rats that were trained in an instrumental cooperative task to pull a stick in order to produce food for a partner pulled more often for an unknown partner after they were helped than if they had not received help before. This reveals that nonhuman animals may show generalized reciprocity (Barta et al. 2011). However, this type of cooperation in full is a characteristic of human behavior only. Indirect reciprocity requires substantial cognitive demands because humans need to store in their memory information on hundreds and even thousands of other people and past interactions with those individuals and monitor information on interactions between members of our social networks. This often needs to be translated to/from other languages as a substantial part of our social information arrives from multiple often globalized channels. A good reputation is important, and humans take into account the possible consequences for their reputation before they decide to act. Theoretical and empirical studies of indirect reciprocity reveal that individuals who are more altruistic are more likely to gain reputation and receive help and other benefits (Leimar and Hammerstein 2001; Milinski et al. 2002; Fishman 2003; Hauser et al. 2003; Panchanathan and Boyd 2003; Nowak and Sigmund 2005). Several researchers have suggested that altruism is a costly signal of desirable qualities, which could have evolved by

sexual selection (McAndrew and Perilloux 2012). It has been recently shown that reciprocal altruism predicts mating success in humans so that altruists have higher mating success than non-altruists. This supports the idea that altruism is a sexually selected costly signal of difficult-to-observe qualities (Arnocky et al. 2016). The studies and calculations of indirect reciprocity may be complicated because humans often obscure their capabilities and reputation. Indirect reciprocity can lead to evolution of cooperation if the probability, q , of knowing someone's reputation exceeds the cost-to-benefit ratio of the altruistic act: $q > c/b$ (Nowak and Sigmund 1998).

Individual acts of indirect reciprocity may be classified as "upstream" or "downstream" (Nowak and Roch 2007). Upstream reciprocity is based on a recent positive experience which causes a person who receives a donation to feel motivated to act altruistically in turn. Individual A assists individual B, which then motivates individual B to help individual C. Downstream reciprocity is built on reputation, and it occurs when the performer of an act of altruism is more likely to be the recipient of a later act of altruism. In other words, A helps B, making it more likely that C will later help A.

Network Reciprocity

Network reciprocity is an interesting case of reciprocity which is based on the assumption that real populations are not well mixed and spatial structures of populations or social networks prevent individuals of random interactions. This means that some individuals may interact more often than others. Evolutionary graph theory is a useful approach to study such population effects (Lieberman et al. 2005). According to evolutionary graph theory, individuals occupy the vertices of a graph, and the edges determine who interacts with whom. Ohtsuki and coauthors (2006) show that if a cooperator pays a cost for each neighbor to receive a benefit, and defectors have no costs, and their neighbors receive no benefits, network reciprocity can favor cooperation. Research

shows that cooperators can prevail by forming network clusters, where they help each other. It has been suggested that the resulting "network reciprocity" is a generalization of "spatial reciprocity" (Nowak and May 1992).

Empathy-Altruism Hypothesis

Research in evolutionary biology has shown that altruistic behavior generally evolved for the return benefits it brings the actor. The empathy-altruism hypothesis by Daniel Batson and colleagues (Batson and Shaw 1991) postulates that for return benefits to play a motivational role in reciprocity or altruism, they need to be experienced by the social individual. Batson suggested empathy as the most potent candidate mechanism to underlie altruistic reactions in response to other individual's pain, need, or distress. The empathy-altruism hypothesis states that the decision of helping or not largely depends on whether the individual feels empathy for the person in need. Thus, altruistic behavior toward other including nonrelatives may be initiated when the individual feels empathy for another individual, that is, identifying with another individual and feeling and understanding what this individual is experiencing (Aronson et al. 1997; Gilovich et al. 2006; de Waal 2008). It is important to note that emotional response to another's suffering based on empathy has been shown to be different from aversive arousal or temporary depression-based egoistic responses to reduce aversive arousal or relieve negative emotions.

Empathy is a multifaceted phenomenon that is tightly linked to many psychological and physiological processes and thus provides a basis for other complex emotional and cognitive processes (Panksepp and Panksepp 2013; Palagi et al. 2014). Different levels of empathy are recognized according to neurobiological, psychological, and behavioral complexity (Hecht et al. 2012). The ability to react to the feelings of others appears early in life (Clay and de Waal 2013), and its neurobiological substrates have been documented in humans. Recently, it has

been shown that humans are instinctively prone to cooperate while selfishness comes with rational minds and experience that let people to decipher if they might occasionally gain more by acting selfishly (Rand et al. 2012; Jordan et al. 2016). Empathy is a well-documented phenomenon also in nonhuman primates (Palagi et al. 2014) and rodents (Langford et al. 2006; Bartal et al. 2011). Frans de Waal of Emory University, Atlanta, examines in *The Age of Empathy* (2010) how empathy comes naturally to a wide range of animals, including humans. Birds, for example, demonstrate some forms of reciprocal altruism while mobbing predators at nests of their nonrelative neighbors, a behavior which seems to be based on empathy (Krams et al. 2013).

Future research should test whether empathy is ubiquitous in cooperation and what is its role in shaping the decision rules and strategies of playing social games. It is also important to reveal physiological mechanisms of empathy. For example, recent research showed that reinforcement of adaptive social interactions in the brain requires coordinated activity of oxytocin and serotonin (Barraza and Zak 2009; Dölen et al. 2013) suggesting that important details of the mechanism of cooperation and reciprocity are still waiting to be revealed. Empathy might be also related to emotional disposition, i.e., tendencies to give, to cheat, and to respond to other's behaviors in which individuals significantly differ between each other, the evolution of which can be understood in terms of regulation of altruism as proposed by Trivers (1971).

Examples

Vampire Bats

Gerald Wilkinson of the University of Maryland showed that vampire bats (*Desmodus rotundus*) display reciprocal altruism (1980). The bats often feed each other by regurgitating blood. The bats only feed on blood and have to eat each second night – otherwise they will die. Therefore, food sharing is a great benefit to the receiver and a great

cost to the giver; food-sharing behavior was consequently explained in terms of direct reciprocity (Wilkinson 1984). It has been suggested that non-kin food sharing could have resulted from kin recognition errors, indiscriminate altruism within groups, or harassment. Gerald Carter and Gerald Wilkinson tested these alternatives and confirmed the role of reciprocity in the most excellent way (2013). Over a 2-year period, they fasted 20 individual vampire bats and induced food sharing on 48 days. It was found that donors initiated food sharing more often than recipients, a finding incompatible with the harassment hypothesis. Carter and Wilkinson found that food received was the best predictor of food given across dyads, and it was 8.5 times more important than relatedness of bats in dyads. Sixty-four percent of sharing dyads were unrelated. Consistent with social bonding, the food-sharing network was correlated with mutual allogrooming. Thus, these findings and past work published in 1980 in *Nature* support the hypothesis that food sharing in vampire bats provides mutual direct fitness benefits and can be explained in terms of direct reciprocity.

Primates

Grooming in primates can be explained as reciprocity (Stephens 1996) according to some studies. Robert Seyfarth and Dorothy Cheney (1984) found that in vervet monkeys (*Chlorocebus pygerythrus*) among unrelated individuals, grooming induces higher chances of attending to each other's calls for aid. However, vervet grooming behavior was also supported by kin selection because some part of this activity was observed between siblings (Lee 1987). Another study examined patterns of reciprocity in grooming among wild male chimpanzees (*Pan troglodytes*) where kin effects are negligible. It was found that some grooming was directed by lower- to higher-ranked individuals and that, on average, higher-ranked individuals groomed more reciprocally. However, reciprocity did not occur between

individuals close in their ranks. Thus, the results partly supported reciprocity and the current grooming trade within biological market model (Noë and Hammerstein 1994).

Mobbing Behavior and Nest Protection

Birds often help neighbors to defend their nests. Red-winged blackbirds (*Agelaius phoeniceus*), for instance, play a tit-for-tat strategy while helping their neighbors while mobbing nest predators (Olendorf et al. 2004). Additional experimental evidence has been obtained from mobbing behavior of the pied flycatcher (*Ficedula hypoleuca*). Krams et al. (2008) used stuffed owls to induce cooperative mobbing in triads of pied flycatcher mated pairs, with each triad consisting of three equidistant nest boxes (48–54 m apart) (A, B, and C). Pair A was exposed to a fake owl near their nest box to induce mobbing, pair B was held captive and prevented from mobbing, and pair C was left untreated, so that pair C always helped pair A with mobbing, but pair B could not. Pair B was released, and in 1 h pairs B and C were simultaneously presented with owls and tested at which nest box pair A would choose to assist during mobbing. In 30 of 32 trials, pair A assisted pair C. In an additional experiment, pair B was presented with an owl. In eight of nine trials, pair C, but not pair A, joined B in mobbing, as expected according to a tit-for-tat strategy. However, Russell and Wright (2008) objected that this strategy was cognitively unlikely for pied flycatchers. Connor (2010) stated that pair A did not assist pair B to avoid a potential parasite infestation. By showing that the degree of contingency was dependent on the costs and benefits, Krama et al. (2012) demonstrated in a follow-up experiment that reciprocal mobbing at nest boxes was not a by-product benefit. Subjects always helped neighbors mob regardless of past defections when nest boxes were placed only 20–24 m apart. This shows that when the predator is nearby, it is worth mobbing whether any benefit to others was incidental and not enforced. However, when the predator was farther away, the mobbing was more of a cooperative investment enforced by reciprocity. Therefore, reciprocity can involve both by-product mutualism benefits

and enforced benefits, while the difference between by-product mutualism and reciprocity is just the function of distance between the neighbors or the degree of perceived risk of predation.

Conclusion

Research on reciprocal altruism or reciprocity is an important part of modern evolutionary biology. Surprisingly, while mathematical part of research on reciprocal altruism may be viewed as extremely successful, there is less agreement about the importance of reciprocity for understanding interactions among nonrelatives and whether it occurs in nature at all. Indeed, experimental research on reciprocal altruism has so far received little attention, most likely because it is difficult to observe reciprocity in nature and to test its role and mechanisms within the framework of evolution of cooperative behavior. On the other hand, the most recent evidence from mobbing birds, Norway rats, and vampire bats indicates that reciprocal exchange can be more common in nature than previously thought and also more important for cooperation than relatedness, especially in social groups consisting mostly of non-kin members.

Cross-References

- Altruism
- Emotional Disposition
- Prisoner's Dilemma

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Reciprocal Altruism and Cooperation for Mutual Benefit

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Synonyms

Cooperation; Reciprocity; Reciprocal cooperation

Definition

Cooperation is a behavior that is adaptive because it provides a benefit to another individual. Reciprocal altruism, or reciprocity, is cooperation that is conditional on receiving help from the recipient.

Introduction

How can “helpful” traits evolve when natural selection rewards selfish replicators? Generally speaking, the answer is through mutual benefit. If genes for a cooperative or “nice” behavior reduced reproduction of the individuals bearing them, those genes would eventually disappear. Thus, for cooperative behaviors to exist, cooperative genes must persist through *direct fitness benefits* to the individual cooperators or through *indirect fitness benefits* via relatives of the cooperator who share copies of those genes. Given this, cooperative traits can be explained by asking the question: *how does a cooperator’s genes benefit from its actions?* Below is an outline of the ways in which benefits arise from cooperation (see also West et al. 2007; Bshary and Bergmüller 2008).

Indirect Fitness Benefits or Kin Selection

Rather than fitness only being measured by an individual’s production of offspring, fitness

should also take into account gene propagation through other genetic relatives. Natural selection will therefore favor organisms that maximize their *inclusive fitness*, which takes into account *direct fitness* from direct reproduction and *indirect fitness* through assisting the reproductive success of genetic relatives (Hamilton 1964). Hamilton’s rule ($rB > C$), a formulation of *kin selection*, predicts that cooperation will occur if the net direct fitness cost of helping (C) is less than the benefit to the recipient’s direct fitness (B) scaled by the relatedness between the helper and recipient (r).

Direct Fitness Benefits

The Free-Rider Problem

The fundamental evolutionary problem for cooperation among non-kin is that free riders or “cheats” can often gain the benefits of cooperation without suffering the costs. The free-rider problem is often illustrated by thought experiments such as the “Tragedy of the Commons” and “Prisoner’s Dilemma.” The costs and benefits of actions in these thought experiments are analogous to the fitness costs and benefits that determine whether or not a heritable cooperative trait is stable over evolutionary time.

In the Tragedy of the Commons, several individuals share a public good, such as a shared pasture for grazing. Each rancher benefits from grazing the pasture, but the costs of grazing are shared by all. If one rancher restricts his grazing of the commons, other ranchers can graze the area that he attempted to conserve. The ranchers would gain the highest long-term gain if they all restricted their grazing, but each rancher’s highest short-term gain is to graze as much as possible. The result is a breakdown in cooperation and exploitation of the commons that hurts everyone, hence “Tragedy of the Commons.” If only each rancher could somehow ensure that others would also conserve the commons (and vice versa), then mutual cooperation would be easier. In the absence of such enforcement, free riders that exploit the commons take advantage of cooperators that conserve the commons. Without enforcement to prevent free riding, cooperation is

Reciprocal Altruism and Cooperation for Mutual Benefit, Table 1 Example payoff matrix for A given B’s decision

A’s payoff if	B conserves the commons	B exploits the commons
A conserves the commons	15 units for A	1 units for A
A exploits the commons ^a	20 units for A	5 units for A

^aRegardless of B’s decision, A’s highest payoff is to exploit the commons

unstable. When the payoffs for the Tragedy of the Commons exist for two players, it is called a “Prisoner’s Dilemma” (Axelrod and Hamilton 1981) (Table 1).

By-Product Mutualisms

One solution to the free-rider problem is when cheating is impossible. Consider a scenario where two hunters are needed to kill a large prey. If either hunter invests less in the effort, the prey will escape. This is an example of a *by-product mutualism*, when a behavior that is selfish benefits another individual as a by-product. Of note, if cooperative traits are defined as only those that are selected for due to their benefits to a recipient (West et al. 2007), then by-product mutualisms are not always considered cooperative.

By-product mutualisms can only occur when there is no opportunity for *cheating*. Hence, in these scenarios, the best strategy and the selfish strategy is to cooperate. In some cases, the benefits of cooperating are immediate, for example, when predators increase success by hunting in coordinated packs or animals reduce predation risk by grouping together. However, the same mechanism can operate over the long term with delayed benefits giving the impression of “altruistic” behavior, for example, when individuals aid the survival of group members because it inevitably helps their own reproduction or the survival of their offspring (*group augmentation*, Kokko et al. 2001). Models of by-product benefits can be lumped together (Davies et al. 2012) or further divided based on whether one actor invests in the other (pseudo-reciprocity; Bshary and Bergmüller 2008).

Direct and Indirect Reciprocity

If cheating is possible, stable mutual benefit requires enforcement to reward cooperation, punish cheating, or both (West et al. 2007). Enforcement mechanisms include *direct reciprocity* where individuals prefer to help those who help them in return (also called “reciprocal altruism” Trivers 1971; Axelrod and Hamilton 1981; Carter 2014), *indirect reciprocity* where individuals help those that help others (also called “reputation-based reciprocity,” Nowak and Sigmund 1998), or the direct *punishment* of free riders. These mechanisms lead individuals to either punish or avoid individuals that do not provide returns on a cooperative investment. Enforcement mechanisms can be further divided into partner control (reward and punishment of a single partner) and partner choice (switching or choosing among partners, *biological market theory*, Noë and Hammerstein 1994, 1995). Depending on the supply and demand of cooperative partners, potential partners might compete to be chosen. This outbidding leads to scenarios of asymmetric helping, where individuals invest more in high-value helpers, and the value of these helpers depends on their relative frequency in the population.

Enforcement of cooperation is clearly important for humans. Experimental demonstrations of enforcement mechanisms are also common for interspecific mutualisms among simple organisms like plants, fungi, and fish, but they are more difficult **to study** in animals like nonhuman primates, because long-term social relationships are difficult to **experimentally** manipulate (Carter 2014). There are therefore many cases of non-kin cooperation among long-lived social vertebrates where the evolutionary explanation remains ambiguous (Carter 2014; Wilkinson et al. 2016). Faced with such cases, authors often disagree on whether the null hypothesis should be that cheating is inherently impossible or possible but prevented by enforcement (Carter 2014).

Conclusions

All cooperative behaviors are mutually beneficial at the genetic level, in the sense that they

will not evolve unless the inclusive fitness benefits of being “altruistic” outweigh the costs. These benefits may accrue via a variety of mechanisms. Indeed, it is important to remember that different mechanisms, from kin selection to by-product benefits to conditional rewards to partner choice, can occur simultaneously. This makes it difficult to classify cooperative behaviors simply. However, all evolutionary explanations of cooperation must explain what prevents the free-rider problem, where cheats outbreed cooperators by gaining the reproductive benefits of cooperation without paying the costs.

Cross-References

► Nonhuman Reciprocal Altruism

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Reciprocal Altruism and Group Living

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Synonyms

Direct reciprocity and group formation; Group living; Reciprocal cooperation; Reciprocity

Definition

Self-costly acts that confer benefits on others are reciprocated by the recipients such that a mutual benefit is gained. This reciprocal favoritism may be a mechanism relevant to the formation and persistence of group living.

Introduction

Group living is an elemental part of human life and is essential for the survival and replication of our species. Thanks to group living we have been more effective in hunting and protecting ourselves from predators through cooperation. One peculiar phenomenon observed in human group living is that individuals provide self-costly and seemingly altruistic benefits to other group members. For instance, someone might save a group member from drowning (benefit to the recipient) and thereby risking his/her own life (cost to the helper). Humans show such kind of behaviors even toward genetically unrelated others, such that inclusive fitness and kin selection (Hamilton 1964) cannot account for it. This kind of behavior

can be explained by reciprocal altruism, which may have played an important role in the evolution of human group living.

Reciprocal Altruism

In 1971, Trivers published his paper on reciprocal altruism where he explained how and why even nongenetically related individuals perform seemingly altruistic acts toward each other. He argued that natural selection favors performing altruistic acts as long as these acts are reciprocated and result in a net benefit for each of the involved parties. For instance, helping someone from drowning makes sense as long as this person reciprocates by performing a similar act of altruism at some point in the future (actor-reactor reciprocation). A considerable amount of research and theorizing has since been done that builds further on the ideas first posed by Trivers (1971).

One of the most influential papers was published by Axelrod and Hamilton (1981), which showed that in a repeated prisoner's dilemma (PD) game reciprocal altruism can emerge as an effective strategy. The PD game is a 2-player game in which one can either cooperate or defect (not cooperate). In this game mutual cooperation leads to the highest joint outcome (i.e., an altruistic act of both players), mutual defection leads to the lowest joint outcome (i.e., no altruistic act of both players), and if one player cooperates and the other defects, the cooperator will get the lowest possible outcome and the defector the highest possible outcome (i.e., an altruistic act of one player that is exploited by the other player). By letting different playing strategies compete against each other, Axelrod and Hamilton (1981) showed that a "tit-for-tat" strategy (suggested by Anatol Rapoport), in which one always starts with cooperation and then reciprocates the decision of the other player, is particularly effective. This can be seen as a demonstration of how reciprocal altruism may evolve, although it has been criticized for its appropriateness as a model of reciprocal altruism (for a discussion, see Boyd 1988).

Given that the standard repeated PD game is an oversimplification of real-life social interactions, others have since looked at additional factors that are often present in real life but ignored in the standard repeated PD game. For instance, it has been shown that forgiveness – modeled with a “generous tit-for-tat” strategy that proceeds cooperating despite facing defection some of the time – plays an important role in maintaining reciprocal relationships when the environment is noisy or error-prone (Nowak and Sigmund 1992).

One problem that arises when people perform reciprocal altruism is that it allows the recipient of the altruistic act to defect (not reciprocate), also known as cheating. Trivers (1971) already pointed out that a “complex, regulating system” must have evolved in order to detect or prevent cheating. For instance, it has been suggested that humans have developed adaptations to help recognize cheaters (Cosmides and Tooby 1992) and might use strategies like “raise the stakes,” in which one slowly increases the magnitude of the altruistic acts when it is reciprocated, so that the negative consequences of cheating by unknown interaction partners are minimized. Given that individuals are able to identify and distinguish cooperators and non-cooperators with whom they did not have prior interactions (e.g., by “cues” of an individual’s reputation), cooperators are able to help each other indirectly (i.e., indirect reciprocity; Nowak and Sigmund 1998).

The term reciprocal altruism has been criticized since its long-term consequences lead to a mutual benefit, therefore indicating that reciprocity actually does not involve individual costs, as it would be the case in “pure” (strong) altruism. Alternative terms that avoid this semantic problem are “reciprocity” or “reciprocal cooperation.”

Conclusion

There is convincing evidence that reciprocal altruism is an important predictor of human

cooperation. Yamagishi and colleagues have formulated the theory of bounded generalized reciprocity to describe how expectations of (direct or indirect) reciprocity account for behavior within and between groups. They argue that individuals expect greater reciprocity from in-group than from out-group members and that this in turn not only leads to within-group cooperation but also to in-group biased perceptions and behaviors (for a summary, see Yamagishi et al. 1999). Hence, reciprocal altruism may be an important mechanism for the formation, functioning, growth, and persistence of groups. For cooperation to remain in increasing group sizes, however, additional supportive mechanisms are required, e.g., retribution systems. Moreover, reciprocal altruism may also lead to the emergence of strong reciprocity among group members through group selection (Gintis 2000).

Cross-References

- ▶ [Altruism](#)
- ▶ [Cheating](#)
- ▶ [Cooperation](#)
- ▶ [Group Selection](#)
- ▶ [Inclusive Fitness Theory](#)
- ▶ [Indirect Reciprocity](#)
- ▶ [Kin Selection](#)
- ▶ [Prosociality](#)

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Reciprocal Altruism, Dyadic Cooperation Among Genetically Unrelated Individuals

- [Social Exchange Among Non-kin](#)

Reciprocal Cooperation

- [Adaptations for Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reciprocal Altruism and Group Living](#)

Reciprocal Grooming

- [Cooperative Grooming](#)

Reciprocal Rewards

- [Reciprocal Altruism \(Middle-Level Theory in Evolutionary Psychology\)](#)

Reciprocity

- [Adaptations for Reciprocal Altruism](#)
- [Altruism Advertises Generosity](#)
- [Cooperation Among Fishes](#)
- [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- [Enlarge Shadow of Future](#)
- [Evolution of Reciprocal Altruism](#)
- [Ingredients of Reciprocal Altruism](#)
- [Insist on No More than Equity](#)
- [Nonhuman Reciprocal Altruism](#)
- [Psychology of Reciprocal Altruism](#)
- [Reciprocal Altruism \(Middle-Level Theory in Evolutionary Psychology\)](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reciprocal Altruism and Group Living](#)
- [Sarah Brosnan](#)
- [Selection for Cooperative Relationships](#)

Recognition

- [Object Permanence](#)

Recollection

- [Attention and Memory](#)

Reconciliation

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Synonyms

Appeasement; Cease-fire; Resolution; Reunion; Settlement

Definition

Affiliative behaviors between a victim and an aggressor after a conflict (Emery et al. 2007).

Introduction

Reconciliation has not been observed in any corvids at this point. However, a related behavior, third-party post-conflict affiliation (also called consolation), is common in both rooks and ravens (Emery et al. 2007; Fraser and Bugnyar 2010, 2012; Seed et al. 2007).

Consolation

For rooks, consolation occurs as an affiliative behavior between a victim (or aggressor) and its partner, and it might reduce stress and strengthen alliances (Emery et al. 2007) (see the Social Systems subheading under the ► [Corvids](#) entry for information about affiliative behaviors in rooks and ravens). In particular for rooks, bill twining behavior appears between partners within a minute after a fight and almost exclusively in this context (Emery et al. 2007). Seed et al. (2007) discuss how consolation, but not reconciliation, makes sense in the context of the social system of rooks and matches what is seen in similar social system in primates. Rooks only form strong partnerships with one other rook, so there is no benefit to reconciling a “non-valuable” relationship, but there is a benefit in increasing the bond with one’s partner (Seed et al. 2007). Given that affiliative behaviors are often reciprocal, this could form a foundation for morals around exchange, as in humans (e.g., Stevens and Hauser 2004), but there are no reports of rooks punishing other rooks if affiliative behaviors are not reciprocated (Emery et al. 2007; Scheid et al. 2008; Seed et al. 2007), and indeed this kind of behavior is rare across all animal species (de Waal and Brosnan 2006; Stevens 2004; but see Bshary and Grutter 2005).

Ravens show consolation via affiliative behaviors toward other ravens that they associate with (not just mated partners), particularly those that they have a valuable relationship with (Fraser and

Bugnyar 2010, 2012). Consolation behaviors are correlated with social support (i.e., aiding another raven in an aggressive encounter); this social support is mostly given to aggressors in conflicts but also to victims (Fraser and Bugnyar 2012). Ravens are more likely to support group members that are dominant to them, suggesting that it functions to reinforce good relationships within groups of ravens, but they also supported kin and those who preened them (Fraser and Bugnyar 2012). There is no evidence that social support was reciprocal, so it seems to have more long-term functions relating to relationship stability within groups (Fraser and Bugnyar 2012).

Conclusion

Corvids do not show reconciliation, but they do show “consolation,” also known as “third-party post-conflict affiliation” in which a corvid will display affiliative behaviors toward a partner that had recently engaged in a conflict, either as the victim or the aggressor.

Cross-References

- [Be Forgiving](#)
- [Corvids](#)

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Recounting

► Human Storytelling

Recreation

► Play and Social Learning

Red Queen Hypothesis, The

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Synonyms

Red Queen's Race; The Red Queen Effect

Definition

The Red Queen hypothesis is an evolutionary hypothesis that states that all living beings

must constantly adjust, evolve, and reproduce while attempting to survive ever-evolving predators.

Introduction

This hypothesis was first proposed by Leigh Van Valen in 1973. The term “Red Queen” is a reference to a statement made by the Red Queen to Alice, characters in the popular 1871 novel *Through the Looking-Glass*, written by Lewis Carol.

The Red Queen Hypothesis and its Relevance

The statement that sparked this hypothesis is “Now, *here*, you see, it takes all the running you can do, to keep in the same place” (Carroll 1871). Van Valen's reference is essentially a metaphor for an evolutionary arms race. Predators that undergo a beneficial adaption may spark a change in selection pressure when it comes to a group of prey. This, in turn, would continue in a positive feedback loop, which gives rise to a form of antagonistic coevolution. Predators must attempt to compensate for better defensive adaptations that are being used by prey. For example, rabbits are considered prey, and foxes are considered predators. In this example, the only way the foxes can compensate for a better defensive adaption by the prey (e.g., rabbits are able to run faster than their parents) would be to adapt a better offensive adaption (e.g., foxes are able to run faster than their parents) (Vermeij 1987).

Further, the Red Queen hypothesis has other practical applications to humans outside of the predator/prey model. According to military researcher Azar Gat, evolutionary theory and the Red Queen hypothesis are instrumental in understanding some of the many aspects that can contribute to war. Gat states “The Red Queen effect arises when two competing groups find themselves in a security dilemma. The security dilemma results when a group takes defensive

measures (which possess inherent offensive capabilities) to improve their security, triggering a military arms race. This arms race, much like the example previously referenced, causes each side to consume ever increasing amounts of resources in order to outpace the other and to gain an advantage” (Gat 2009). An example of this occurrence was the nuclear arms race between the United States and the Soviet Union which began in 1945 and ended with the signature of the START I treaty in 1991. It is easy to see where the parallels exist between the evolutionary theory and the real-world application of this hypothesis.

Conclusion

In conclusion, the Red Queen hypothesis is rooted within evolutionary theory; however, it transcends theory and is able to be represented by several aspects of modern society, including war.

Cross-References

- [Evolutionary Arms Race](#)
- [Evolutionary Theory and the Causes of War](#)

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Red Queen's Race

- [Red Queen Hypothesis, The](#)

Redistribution of Resources

- [Redistribution Preferences and Low Socioeconomic Status](#)

Redistribution Preferences and Low Socioeconomic Status

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Synonyms

[Destitute](#); [Economically vulnerable](#); [Impoverish](#); [Income transfer](#); [Low social status](#); [Lower classes](#); [Redistribution of resources](#); [Socioeconomic flattening](#); [Status](#); [Undereducated](#); [Underemployed](#); [Uneducated](#); [Unemployed](#); [Voluntary redistribution](#); [Wealth reallocation](#); [Wealth transfers](#); [Working class](#); [Working poor](#)

Definition

Low SES. Socioeconomic status (SES) refers to a person's income, education, and occupation, some combination of which determines her overall social standing. The relevant markers of social standing will vary across communities and cultures, but researchers afford these three variables special attention given their centrality to the increasingly global market system. A person with low SES will rank toward the bottom of their community's income, education, and/or occupational prestige distributions.

Economic Redistribution. Although seemingly straightforward, economic redistribution – altering the prevailing allocation of some economic good or token among a population – is a

dangerously vague term, open to political exploitation, and the root of much jumbled thinking. Take, for example, the 2003 Bush tax cuts, which experts and most Americans recognized as a massive transfer of wealth from the poor to the rich. It was an economic redistribution, but not of the kind people usually mean when they talk about such efforts. Even if we limit the definition to those undertakings that give *from* them-that-have *to* them-that-don't (as is the case in this entry), we are still a long way from covering our bases. Private charitable donations and centrally run progressive tax schemes are worlds apart on the political spectrum and require totally different justifications and institutions. Experimentalists often record voluntary transfers of money between subjects, whereas public opinion scholars (on whose work we focus here) tend to measure survey respondents' self-reported attitudes toward government programs and tax policies. There are occasions when discussing economic redistribution *broadly* is reasonable, even preferable (review articles with strict word limits among them), but this should be done with great care in academic and policy settings. Whenever possible, specify: Redistribution of what, among whom and along what lines, facilitated how?

Introduction

Socioeconomic status has a clear-cut but surprisingly subdued relationship with redistributive preferences. Supporting economic redistribution stands to directly benefit people of low SES, and low SES individuals are empirically more supportive of and more likely to participate in redistributive measures, but not to the extent that most researchers would expect.

The Influence of SES on Redistributive Preferences

Individuals with less money, less education, and less work have clear incentives to be, and statistically are, more favorable toward redistributive efforts than those with more. Tied up with each

SES component are perceptions of socioeconomic mobility – the timing and apparent flexibility of SES. See Alesina and Giuliano (2011) for an extended introduction to the information provided in this section.

Income

The more money you take in, the less you support economic redistribution. (The language associated with income acquisition is tricky. I say 'take in' here because *earn* implies that wages are proportional to merit and secured through direct action on the part of the employee, and that automatically imbues the transaction with a moral quality. Such words identify the income as deserved *prima facie*, and that can influence people's willingness to redistribute it.) Income is a statistically dependable predictor of redistributive preferences and behavior, and its substantive influence is on par with that of education.

Education

The amount and pedigree of schooling serve simultaneously as markers of social prestige and determinants of economic mobility. In this light it is unsurprising that, all else equal, individuals with more formal education are consistently more opposed to economic redistribution. If schooling is (in part) an investment in future consumption, individuals making that investment will not want to part with its dividends. (This is not to say that all people are equally able to invest in their educations.) But this finding flies in the face of the popular conception of the socially progressive by-products of higher education. That is because schooling and ideology have an *interactive* relationship when it comes to redistribution, whereby "the effect of education reinforces that of political orientation" (Alesina and Giuliano 2011, p. 107). More years of schooling make self-identified left-wingers more supportive of redistribution, but taken by itself, education promises future economic and social prospects and therefore a disincentive to redistribute.

Employment

Unemployed individuals are more open to redistribution than are their employed compatriots,

though this relationship does not consistently achieve statistical significance. There is evidence that the American unemployed feel less defined by or trapped in their unemployment compared to the out-of-work in other nations, where unemployment can be a more dependable prognosticator of policy preferences. More reliably associated with support for redistribution is a *history* of unemployment and personal traumas of the kind that cause or directly result from trying financial situations, although the magnitudes of these explanatory variables are relatively meager. Individuals who experience and remember such negative shocks appear to learn from their ordeals, tempering their optimism about upward socioeconomic mobility and lessening their aversion to wealth reallocation in case the dice ever again roll against their favor.

Perceived Mobility and Personal Narrative

Personal SES trajectory is a double-edged sword. Whereas experiences earning a low income, being unemployed, and undergoing financial trauma as an adult induce an individual to favor redistribution, growing up in a family that experienced such trials may encourage a person to *disfavor* redistribution if they are relatively better off now. For example, individuals who enjoy higher occupational prestige than their parents are prone to oppose redistribution. The most prevalent explanation for this and related findings is that people who outpace the SES into which they were born are optimistic about upward socioeconomic mobility and will not want to threaten potential future economic gains by backing redistribution in the present. In addition to this strategic positioning, it may also be that someone who came from a low-SES household is invested in maintaining – both internally and in public – a personal narrative in which they overcame adversity and are therefore less willing to part with their hard-fought gains. That is, they may feel (and may need to feel) especially *deserving* of their improved SES and its attending financial benefits, and are therefore less willing to part with them (more on this later).

Explaining SES's Subdued Influence on Redistribution

While theoretically and statistically solid, the substantive connection between SES and distributive preferences is perplexingly meager. For example, a majority of the American poor deem the prevailing economic system “basically fair” (Jost et al. 2003) and back what they know to be self-harming, regressive economic policies (Bartels 2008). Why don't low-SES individuals support redistribution more vigorously and in greater numbers? There are several contending explanations, all of which need to better account for one another. See Bower-Bir (2014, appendix B) for an extended overview of prevailing explanations.

Greed and Optimism

The chattering class's favorite explanation holds that people on the lower rungs oppose shortening the socioeconomic ladder because they are confident that they will eventually climb it. That optimism, however, is neither excessive nor does it extend far into the future. Low-SES Americans, for example, have more-or-less reasonable definitions of and expectations regarding personal income and wealth. More to the point, they are not overly concerned with achieving wealth, focusing instead on financial stability. And however sanguine they are about their own financial futures, they are not overly so about their children's.

Neoliberal Intellection

Some economists posit that low-SES redistributive skepticism is farsighted. In wanting to grow the economic pie and their (relatively slender) slice of it, low-SES individuals may shun redistributive measures for fear they generate disincentives to work, save, and invest. This stance would be personally uncomfortable in the short term but might lead to widespread, long-term gains for everyone. But not only are such neoclassical arguments generally unpopular among low-SES populations, people of all socioeconomic backgrounds are decidedly myopic in appraising economic policies (Page and Shapiro 1992; Bartels 2008).

Confusion

Rather than economically, political scientists fear that the poor think incoherently. Scarcity of key dietary, social, and economic resources can temporarily, and in some cases permanently, impair a person's cognitive abilities (Mullainathan and Shafir 2013). Add to that redistribution's complexity, especially at the policy level where tax and welfare laws are negotiated outside of the public's view and in highly technically language. Low-SES citizens may not fully grasp issues like tax incidence, and their policy preferences are backward because of it. Moreover, low-SES populations may be hoodwinked into supporting regressive, self-detrimental policies through targeted, prolonged political and media promotions (Bartels 2008; Page and Shapiro 1992). Although powerful forces, ignorance and manipulation do not entirely account for people's puzzling redistribution preferences (Lupia et al. 2006).

Delusion

An influential set of psychological models known as "just world" or "system justification" theories postulate an automatic and near-universal human need to believe in the fairness of outcomes and/or processes: that people get what they deserve and vice versa. The basic notion is that "living in an unpredictable, uncontrollable, and capriciously unjust world would be unbearably threatening, and so we cling defensively to the illusion that the world is a just place" (Jost et al. 2003, p. 58). This reaction is apparently facilitated through conscious and non-conscious means and may persist whether the mentally insufferable transgression is directed at one's self or others.

Natural Justice

Combining insights from institutional economics and moral philosophy, researchers who study justice as a natural phenomenon find that people will tolerate psychologically troubling and financially detrimental economic distributions if they judge those distributions *deserved* (Bower-Bir 2014). Indeed, redistribution in such cases would be unjust, taking from the deserving and giving to the undeserving. People are not preoccupied with

justice because they are moral, *per se*, but because moral concepts like economic justice and deservingness are *social institutions*, (Binmore 2011) and violating institutional boundaries is expensive, inviting internally and externally inflicted costs such as guilt and ostracism. Rather than the universal, intuitive definition of fairness that psychologists often seek (e.g., Starmans et al. 2017), natural justice scholars treat desert as *emergent*, fashioned over repeated interactions among humans trying to allocate all manner of goods, treatments, and duties. Definitions of desert vary across communities and resources, but often with common elements. An individual's willingness to redistribute, then, depends on her definition of economic desert – which may preclude specific redistributive avenues – and the degree to which she thinks economic desert is currently rewarded (Bower-Bir 2014).

Conclusion

The above-detailed approaches likely complement one another, applying to specific situations and populations. Multiple researchers conclude, for example, that individuals must perceive inequality as undeserved before they are willing to combat it (e.g., Bower-Bir 2014; Starmans et al. 2017). The next question is not whether but *when* and *for whom* is this willingness driven by socially evolved norms, as the natural justice contingent contends, and when is it driven by a deep-seated aversion to inborn conceptions of injustice, as psychologists posit? Similarly, rather than wonder at and bemoan citizen ignorance and delusion, political scientists might uncover specific aspects of redistributive policy that confuse and frighten people. People of all backgrounds respond to social, psychological, and personal pressures, and plenty of parties peddle economic ignorance and fantasy. Rather than focusing on one angle of attack, researchers must cross disciplines to fully rectify the straightforward but empirically muted support for economic redistribution among the lower socioeconomic strata.

Finally, a warning: The theories introduced in this article use ancient and nuanced terms like

justice, fairness, and desert, often cavalierly. (For a preliminary untangling of these closely related terms, see Bower-Bir (2014, Chap. 2). Briefly, justice is getting what one deserves. Desert is the meriting of some treatment or resource, and the concept itself bridges the myriad and otherwise isolated notions of fairness.) Scholars from all disciplines are guilty, but those from the brain sciences – in their quest to uncover innate moral principles – are especially susceptible. For example, psychologists Starmans et al. (2017) acknowledge that their predecessors speciously equate *just* and *equal* outcomes, only to themselves conflate *fair* and *equitable* processes, the latter being one of many possible flavors of the former. Similarly, neuroscientists Decety et al. (2015) tacitly advance a definition of *just* behavior as *altruistic* behavior. Take care not to overreach, believing your favored definition of a moral concept to be *the* definition of that concept. Social scientists ignore one another and moral philosophers at their own peril (Binmore 2011).

Cross-References

- [Evolution and the Theory of Games](#)
- [Evolution of Morality](#)
- [Evolved Moral Foundations](#)
- [Game Theory](#)
- [High SES Against Redistribution](#)
- [Self-deception](#)
- [Social Status and Economic Resources](#)
- [Status and Redistribution of Resources](#)
- [Unemployed](#)

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Reduction of Predation

- [Predator Confusion Hypothesis](#)

Reductionism

- [Psychological Determinism](#)

Reeve (Female Ruff)

- [Ruff Shorebird, The](#)

Reflexive Conditioning

- [Classical Conditioning](#)

Reflexive Response

► Unconditioned Response

Regulation of Body Temperature

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Synonyms

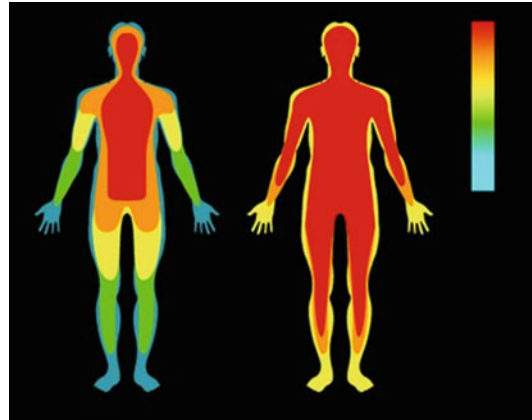
Balance; Degrees celsius; Degrees fahrenheit;
Hypothalamus; Thermometer; Temperature;
Thermoregulation

Definition

Thermoregulation is the maintenance of a relatively constant core body temperature that in humans is about 37 °C. Although there are normal fluctuations that occur during the day (circadian rhythm), month (menstrual cycle), and throughout the lifetime (aging), the maintenance of this temperature via physiological homeostasis is critical to human survival. The hypothalamus is the central integration center for thermoregulation (Tansey and Johnson 2015).

Introduction

Humans are homeothermic animals, which involve the pursuit of a homogeneous state for its thermodynamic temperatures and thermal inertia and the ability to adapt to fluctuation in the environment (Fig. 1) (Garcia-Falgueras 2017). However, in contemporary society, some humans have become too sedentary and physiologically unresponsive to the extent that some individuals might now require thermal therapeutic intervention for the lack of exercise or thermostatic



Regulation of Body Temperature, Fig. 1 Schematic representation of the human body with differences in color for temperatures. It is noticeable how in cold states (figure on the left) upper and lower extremities (i.e., hands and feet) are the first to get colder (color blue)

perturbations in their daily life (Tipton 2019). Both hot and cold water exposures have been reported to improve health and mood states (Naumann et al. 2017; Van Tulleken et al. 2018).

Autonomic hypothalamic disorders are accompanied by hypothermia. A case was described of a patient who, after a head injury, was unable to maintain core temperature during cold stress, unless he was capable of normal perspiration (for revision see Swaab 2004). Climacteric hot flushes are sudden vasodilatation episodes of the facial and upper abdominal skin, and they are accompanied by increased levels of luteinizing hormone (LH) and luteinizing hormone-releasing hormone (LHRH). Men with testicular insufficiency and woman after hypophysectomy also experience hot flushes (for revision see Swaab 2003).

The hypothalamus is composed of several nuclei populations interconnected to each other and to other brain areas, regulating the peripheral energy balance and expenditure. This process is controlled by the arcuate nucleus in the hypothalamus, the superior periaqueductal gray matter, the nucleus of the solitary tract structures, and the nucleus of superior septal area, via a multi-signaling cascade which includes GABAergic receptors, neuropeptide Y (NPY), leptin, insulin, agouti-related protein (AgRP), proopiomelanocortin

(POMC) neurons, orexin (OX), and other factors (Contreras et al. 2017; Griffin et al. 2001). They are released when the intestine detects the presence of nutrients, and they help to promote the feeling of satiation suppressing the behavior of eating or food intake (Hopkins and Blundell 2016). Norepinephrine is also involved in regulation of body temperature changes, and somatostatin from the periventricular nucleus potentiates the thyroid-stimulating hormone (TSH) response to cold in experimental animals (Swaab 2003, 2004).

The brain has specific neurons sensitive to temperature. In 2 μ m coronal tissue slices of rat preoptic area of the hypothalamus, it was described that different dendritic organizations exist depending on physiological characteristics: warm-sensitive neurons (receiving afferent input from spinal and skin-cutaneous thermal receptors) have a perpendicular orientation for its dendrites, whereas temperature-insensitive neurons are parallel to the third ventricle (Griffin et al. 2001).

Depression is one of the most common neuropsychiatric diseases, with sadness often being associated with the feeling of cold and the blue colors. Loneliness, marginalization, or isolated extreme states are also linked to cold and sadness. However, one-third of depressive patients fail to respond to conventional antidepressant medication. It is interesting that hyperthermic baths (water at 40 °C during 30 min) have recently been demonstrated in a pilot study to have a positive and consistent effect on mood, sleep quality, and treating severe depressive symptoms (Naumann et al. 2017).

Gender Differences in Human Thermoregulation

Structural differences between men and women have been found to relate to sweating or perspiration, but no substantial distinctions about effectiveness in thermoregulation were reported (Kaciuba-Uscilko and Gruzca 2001). A strategy for thermoregulation that implies evaporative cooling (sweating in humans, panting in dogs, salivation

in rodents) increases the heat loss (Morrison 2016) and is different among genders. Body size and surface area, adiposity, body mass and composition, working capacity or resting metabolic rates, and hormonal fluctuations in woman or menopause might all partly contribute to the overall thermal responses explaining those sex differences in thermoregulation. However, further studies would be necessary to tease these effects apart beyond (Kaciuba-Uscilko and Gruzca 2001).

The thyroid hormones (THs) in the brain act in the hypothalamus and its ventromedial nucleus to modulate energy balance. Central triiodothyronine (T3) regulates hepatic metabolism through the vagus nerve and brain adipose tissue (BAT) which increases lipid oxidation and thermogenesis in the whole-body level for central T3 and peripheral glucose homeostasis (Martínez-Sánchez et al. 2017). When patients present a thyroid dysfunction, hyperphagia is occurring, whereas weight loss is often found with hyperthyroidism (Martínez-Sánchez et al. 2017).

On the other hand, acute differences in temperature responses between men and women were measured, and they found in an experiment the existence of the difference related to sudomotor functions and skin blood flow, because of sex hormones or osmolality. But they did find no differences related to physical characteristics, for example, to the relative onset threshold of sweat production, but related to physiological functions, suggesting solid gender differences: women had a lower whole-body evaporative heat loss, higher requirements for heat loss employed, and bigger local sweat rate compared to men (Gagnon and Kenny 2012). It has been experimentally demonstrated that men and women respond differently to the same low temperatures: women feel less comfortable, feel colder by losing heat, and start shivering earlier as an indicator of cold stress to heat production, compared to men (Kaikaew et al. 2018).

During the lifespan differences in thermoregulation also occur: hot flushes affect millions of individuals, but the mechanism is not fully understood (Rance et al. 2013). Skin thermal afferent input reaches the hypothalamus

(preoptic, dorsomedial areas, and arcuate nucleus) to inhibit warm-sensitive output neurons (Morrison 2016). The hypothalamus plays an important role for this temperature process (regulation of systemic energy balance by regulation feeding behavior and energy expenditure), with dynorphin, LH and gonadotropin-releasing hormone (GnRH) neurons, and estrogen receptors being involved (Martínez-Sánchez et al. 2017; Rance et al. 2013).

Estradiol acts upon the ventromedial hypothalamus of rats and regulates brown fat thermogenesis and energy balance (González-García et al. 2018). The lateral and ventromedial hypothalamus regulates the thermogenesis and energy balance via brown adipose tissue and browning (described in the next section) of white adipose tissue (Contreras et al. 2017). Moreover, a wide array of nonthermal physiological parameters, disease processes, neurochemicals, or drugs can influence the natural circuit of thermoregulation (Morrison 2016).

Body Temperature in Obesity

There is a reciprocal and metabolic relationship between energy intake and energy expenditure, occurring in the hypothalamus as the calorimetric satiety center which regulates lipostasis (Hopkins and Blundell 2016) (Fig. 2). Brown adipose tissue in infants is located in the interscapular region and plays an important role in thermogenesis. This brown fat was thought to happen mainly in defenseless creatures (small mammals and human infants) exposed to hypothermia and to regress by adulthood, but brown fat tissue was “rediscovered” in adult humans, and it is activated robustly by cold (Cohen and Spiegelman 2015). Some investigators have suggested exposure to cold (19 °C for 2 h daily) might result in weight lost for brown and beige fat activation (Cohen and Spiegelman 2015).

A lower core body temperature has been suggested as a predisposing factor toward obesity; however, no general differences in the core body temperature were found between normal weight



Regulation of Body Temperature, Fig. 2 Thermographic picture of a sportive and thin person playing tennis. The image, taken with a special camera, shows how temperatures vary in different surfaces of the tennis player's body depending on the wavelengths

and obese individuals (Heikens et al. 2011). In a study performed on mice, a sex difference was found in their brains and saturated fatty acids, but not in plasma-free fatty acids. Male mice had an increase of saturated fatty acids (30%), while the amount of oleic acid and docosahexaenoic acid (DHA) was higher in female mice (Rodríguez-Navas et al. 2016).

Conclusion

Thermoregulation is the maintenance of a relative normal body temperature through fluctuations of temperature that occur during day (circadian rhythm), month (menstrual cycle), year (different seasons), and throughout the lifetime (aging). It occurs via physiological homeostasis regulated in the hypothalamus; it is critical to human survival. Body weight and energy consumption, expenditure, as well as feeding and satiation behavior are mainly regulated in the brain. Brown and beige fat seem to have therapeutical effects over body energy and its metabolism, while sex differences have been found in sweat, in adaptability to cold environments, and in brain-saturated fatty acids, but not in the plasma-free fatty acids.

Credits of Pictures

Photographs presented in this work come from files with free license in the public domain as Wikimedia Commons.

Cross-References

- [Body Fat Percent and Distribution](#)
- [Body Temperature Regulation](#)
- [Energy Consumption](#)

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Reichert-Gaupp Theory

► [Evolution of Auditory Perception, The](#)

Reichert-Gaupp Theory

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Synonyms

[Die Reichertsche Theorie](#); [Homology of ear ossicles to the reptilian jaw bones](#); [Middle ear first and second pharyngeal arches](#)

Definition

A theory from Karl Bogislaus Reichert and Ernst Gaupp regarding the homology of incus and malleus, with the quadrate and articular, respectively.

Introduction

Reichert and Gaupp's theory is credited for their thesis that mammalian middle ossicles are derivatives of the reptilian jaw bones. Despite some opposition to this theory, the contribution to the scientific knowledge is widely accepted.

What the Theory Postulates

This theory was firstly established by Karl Bogislaus Reichert (see Reichert's cartilage) and then further elaborated by Ernst Gaupp, founder of modern studies in craniogenesis. The theory is regarding the origin of the mammalian ossicles of the ear and the relationship between the reptilian jaw bones and mammalian middle ear bones in 1837 (World Heritage Encyclopedia 2017).

Specifically, the theory posits that the malleus and incus are the evolutionary products of the first pharyngeal arches of the skeletal features of the middle ear (Takechi and Shigeru 2010). Together with the stapes, without the dermal component called the goniale of Gaupp, it is suggested by Westoll (1944) to be homologous to the reptilian conumella auris, quadrate, and articular. Interestingly, the theory proposed by Reichert and Gaupp was established before Darwin's *Origins of Species* (Takechi and Shigeru 2010).

Modern histological developments have shown that the incus was developed from the posterior part of the palatoquadrate as a primordium associated with the basal part of the ascending process of the palatoquadrate by a fiber of connective tissue, therefore confirming Reichert's theory (Takechi and Shigeru 2010). Similarly, Reichert-Gaupp theory is supported based on molecular genetic evidence which supports the serial homology representation of the visceral arches (Prince and Hunter 2002).

There have been, however, other theories opposing Reichert's theory. Hanson et al. (1962) posited that the first and second arch contributed to the middle ear ossicles; Otto (1984) emphasized that human congenital abnormalities showed that the development of jaw and middle ear development are not related to each other and that the malleus and incus were derived from the extracolumella. Jarvik (1980, as cited in Takechi and Shigeru 2010) postulated that all the mammalian middle ear ossicles are derived from the second arch.

Furthermore, Reichert has mainly studied the embryogenesis of the second visceral arch, which was later named by him as the cartilage of Reichert (Maier and Ruf 2016). In essence, Reichert's cartilage is described as a continuous cartilaginous formation in the second pharyngeal arch, and this is where structures such as the styloid process of the temporal bone, the stylohyoid ligament, and the lesser horns of the hyoid bone are derived (Rodríguez-Vázquez et al. 2006). Specifically, as Rodrigued-Vazquez, et al. noted, the styloid process of the temporal bone is

created by the organic process of Reichert's cartilage.

Conclusion

Nevertheless, the theory posited by Ernst Gaupp and Karl Bogislaus Reichert was the first to present a comprehensive synthesis of embryological and paleontological information explaining the evolutionary process of the structures of the mammalian middle ear (see Maier and Ruf 2016). Based on the materials and methods used during their time, their scientific discovery is mostly accepted by the wider scientific community. The clarifications and additions Ernst Gaupp's has provided have significantly contributed to the Reichert-Gaupp theory.

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Reinforcement Delivery

► Reinforcement Schedule

Reinforcement Schedule

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Synonyms

Fixed-interval schedule; Fixed-ratio schedule; Reinforcement delivery; Variable-interval schedule; Variable-ratio schedule

Definition

The arrangement and rules of reinforcement delivery in operant conditioning, defined in terms of number of responses required (ratio schedule) or time elapsed (interval schedule), and in terms of consistency of reinforcement delivery (fixed/variable schedule).

Introduction

In operant conditioning, behavior followed by a reinforcer is strengthened and is more likely to occur again (Skinner 1938). Reinforcement can be continuous (consistently presented every time an organism exhibits a desired behavior) or intermittent (delivered irregularly, based on a predecided schedule). Reinforcement delivery schedules vary on the basis of whether the reinforcement is given on the basis of the number of responses required (ratio schedule) or the time elapsed (interval

schedule). Further distinctions are related to the consistency of reinforcement delivery, resulting in fixed schedules (where consistent reinforcement is given every time a behavior is observed) or variable schedules (where reinforcement is not dependent on raw data (number of exhibited behaviors or minutes elapsed) but on the average of number of observations or of time interval, resulting in an unpredictable mode of reinforcement delivery. Four schedules of reinforcement exist: fixed-ratio, variable-ratio, fixed-interval, and variable-interval.

Methodology for Measuring Responses Under Different Reinforcement Schedules

Skinner created a mechanical device known as a cumulative recorder, to investigate how the rate of responding changed on the basis of the reinforcement schedule applied. The device produced a cumulative record, i.e., a graph that measured the total number of responses since the beginning of the experiment (Skinner 1959). Each response by the animal (rat or pigeon, usually) moved a pen moving horizontally at a slow speed on a piece of paper one notch up, thus indicating vertically the number of cumulative responses recorded up to that point in time (measured in minutes and seconds horizontally). Ferster and Skinner (1957) experimented with fixed (regular) and variable (unpredictable) modes of presenting ratio and interval schedules of reinforcement and showed they can alter the speed of learning (response rate) and extinction (cease of a behavior).

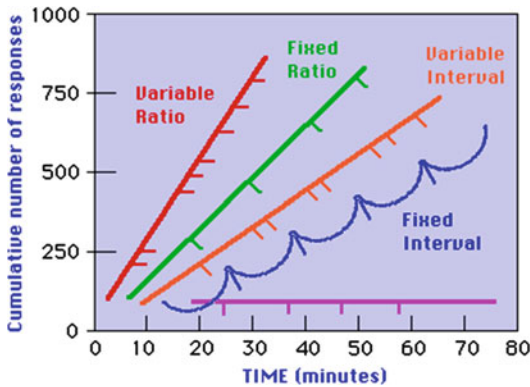
Ratio Reinforcement Schedules

In ratio reinforcement schedules, responses are reinforced on the basis of the number of responses exhibited by the organism. In a *fixed ratio schedule*, the reinforcer is presented after a predecided number of responses are exhibited (e.g., after five responses). Fixed ratio schedules produces high rates of response followed by a short post-reinforcement pause (Ferster and Skinner 1957;

Powell et al. 2017). Higher resistance to extinction is noted the less frequent the reinforcement previously received, a phenomenon known as the partial reinforcement effect (Mowrer and Jones 1945). More recent studies corroborate these findings. Rats previously given continuous reinforcement extinguished the previously reinforced response of approaching a goal location in a water maze sooner than those previously given partial reinforcement (Prados et al. 2008). In a *variable ratio schedule*, reinforcement delivery is based on the average number of responses needed to receive a reward (e.g., a slot machine), and it is thus unpredictable for the organism. This type of schedule results in a high response rate, with little or no post-reinforcement pause (Powell et al. 2017) and is highly resistant to extinction following cease of reinforcement (Ormrod 2016). Resistance to extinction in variable ratio schedules is high because the unpredictability of the reinforcement makes recognition of the cease of reinforcement more challenging compared to a fixed ratio schedule (Reynolds 1975).

Interval Reinforcement Schedules

In interval schedules, the presentation of reinforcement depends on the time interval elapsed. Reinforcement is delivered after the organism exhibits the first desired response following a predecided time lapse. In a *fixed interval schedule*, reinforcement depends on the exhibition of the first desired response after a predetermined and predictable time interval (e.g., after 8 min). A reinforcement schedule of this type results in a “scaloped” (curved upwards) response pattern, evidencing a post-reinforcement pause followed by a gradual response rate increase as the time interval is come close to completion (Powell et al. 2017). Response rate in this type of schedule is medium (a lower rate is observed compared to a fixed ratio schedule), and it is also less resistant to extinction (Ormrod 2016). In a *variable interval schedule*, the time interval elapsed for the presentation of reinforcement is less predictable as it depends on an average interval over a time period rather than a fixed one. This unpredictability



Reinforcement Schedule, Fig. 1 Schedules of reinforcement and response rate (Huitt and Hummel 1997)

results in a moderate and steady rate of response with little or no post-reinforcement pause (Powell et al. 2017) and has greater resistance to extinction (Ormrod 2016).

The figure below summarizes response rates according to schedule of reinforcement applied (Huitt and Hummel 1997). The hatch marks on each line on the graph denote the presentation of a reinforcer (Fig. 1).

Comparison of Different Reinforcement Schedules

More consistent reinforcement delivery (in fixed reinforcement schedules) results in a post-reinforcement pause, whereas less predictable reinforcement (in variable schedules) produces a steadier rate of responses.

Similarities between ratio and interval reinforcement schedules include a post-reinforcement pause is observed after each delivery of the reinforcer in both *fixed-interval* and *fixed-ratio* schedules, as well as a high rate of responding just before the delivery of the next reinforcer. Furthermore, both *variable-ratio* and *variable-interval* schedules maintain steady rates of responding with no predictable pauses. Major differences between ratio and interval reinforcement schedules include higher response rates in ratio schedules of reinforcement compared to interval schedules (Skinner 1938; Ferster and Skinner 1957; Zuriff 1970; Reynolds 1975) and the phenomenon of “ratio strain.” Whereas in interval

schedules responding is maintained even a very low rates of reinforcement, in ratio schedules responses become “strained” or irregular and eventually they cease (Ferster and Skinner 1957).

Baum (1993) suggested that theoretical accounts of reinforcement schedules should consider behavior as being dependent upon post-reinforcement activity, other unprogrammed activity, ratio-typical operant behavior, and interval-typical operant behavior.

Conclusion

The four different schedules of reinforcement (fixed-ratio, variable-ratio, fixed-interval, and variable-interval) produce distinctive operant behaviors. More consistent reinforcement delivery (in fixed reinforcement schedules) results in a post-reinforcement pause, whereas less predictable reinforcement (in variable schedules) produces more consistent performance, and behavior shows more resistance to extinction. Ratio reinforcement schedules produce higher response rates compared to interval schedules, although in interval schedules behavior can more easily be maintained at low reinforcement rates compared to ratio schedules.

Cross-References

- [Associative Learning](#)
- [Operant Conditioning](#)
- [Positive and Negative Reinforcement and Punishment](#)

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Rejected Children

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Synonyms

Disliked; Low social status; Unpopular

Definition

Children or adolescents who are disliked by many peers and liked by few peers.

Introduction

Sociometric status refers to how well-liked or disliked an individual is by their peers. Children who receive many positive nominations (e.g., nominations for being liked) and few negative nominations (e.g., nominations for being disliked) are classified as popular, whereas children who receive many negative nominations and few positive nominations are classified as rejected. A child's sociometric status can

influence their social interactions, psychosocial adjustment, and academic involvement. Rejection from peers has been associated with negative developmental outcomes, such as loneliness, victimization, internalizing and externalizing problems, and low academic performance (Ladd 2006; Veenstra et al. 2007; Zettergren 2003).

Characteristics of Rejected Children

In general, rejected children possess fewer peer-valued characteristics, such as physical attractiveness, style, athletic competence, and a sense of humor, when compared to their peers. They are also rated to be less socially competent than their other peers and tend to be left out of peer activities (Hymel et al. 1993). Rejected children can be classified into two categories: aggressive-rejected and withdrawn-rejected children. In addition to low social status, aggressive-rejected children exhibit aggressive tendencies and behaviors which may elicit dislike and exclusion from their peers. They are rated as uncooperative, less socially competent, and having difficulty getting along with adults. However, in terms of peer-valued characteristics, they were not rated as negatively as withdrawn-rejected children and were not always excluded from peer activities (Hymel et al. 1993). Children who experience peer rejection and exhibit aggressive behavior were more at risk of developing externalizing problems, such as disruption in classrooms, hyperactive and distractible behavior, and delinquency. This effect was stronger during early to middle childhood than late childhood (Ladd 2006).

Withdrawn-rejected children display a slightly different profile than aggressive-rejected children. In comparison to their aggressive-rejected peers, withdrawn-rejected children are nominated more negatively by their peers in regard to not possessing many peer-valued characteristics. However, their social and behavioral conduct does not fare as poorly as aggressive-rejected children. Despite being able to cooperate with their peers and get along well with adults, similar to their peers of average

status, they are still excluded from peer groups and activities (Hymel et al. 1993). Additionally, children who are withdrawn and rejected by their peers are more likely to also experience internalizing problems, such as anxious and depressive feelings. These children were more likely to experience these problems in middle to late childhood than early childhood (Ladd 2006).

Victimization

In addition to being disliked by their peers, rejected children are also at a greater risk of being mistreated by their peers. Their low acceptance and social status within the peer group increase their vulnerability to victimization, especially by bullying aggression (Veenstra et al. 2007). Bullying refers to a specific type of aggression in which the perpetrator has greater power than the victim. Considering this power imbalance, it is understandable that children with low status are more often targeted as a victim in bullying (Volk et al. 2014). From an adaptive perspective, bullying may be a strategy for children and adolescents to gain certain evolutionary advantages, such as social status (Volk et al. 2014). Children and adolescents who use aggression instrumentally may choose to target individuals who are easier to victimize. Rejected children are more likely to be targeted for victimization because of their low social status and emotional and social vulnerability (Veenstra et al. 2007). Further, research has found differences between the two categories of rejected children when it comes to victimization. For example, withdrawn-rejected children are more likely to be a target of bullying because they are socially vulnerable and less likely to retaliate (Veenstra et al. 2007). These characteristics can make it easier for a powerful bully to aggress toward the victim. By choosing a victim who is less likely to retaliate or does not have friends to protect them, bullies are able to use aggression to gain certain benefits, such as social status, while minimizing potential costs. On the other hand, aggressive-rejected children may be a target of bullying due to their tendency to provoke mistreatment from their peers due to their aggressive behaviors and hostile

attribution bias (Schwartz et al. 2001). In this instance, bullying may be a reactive action instigated by the victim. Overall, it is important to consider that rejected children are not only experiencing more victimization than their average or high status counterparts, but that this increase in victimization may also be associated with other negative outcomes or poor adjustment.

School Adjustment

Given the low social acceptance and likability that rejected children experience, there are also concerns of school adjustment and well-being. For instance, a study conducted by Buhs and Ladd (2001) found that rejected children were more likely to experience poor treatment from their peers, report loneliness, perform poorly academically, and participate less in school. In general, these students have a lowered desire to attend school and are more disliked by their teachers in comparison to their average status peers. Additionally, rejected children are typically perceived by their peers to be poor students and perceived by their teachers to have low self-confidence and be involved in more conflicts than children of average status (Wentzel and Asher 1995). Rejected children tend to have poorer academic performance and intelligence levels, in comparison to their popular peers, who tend to score above average (Zettergren 2003). Further, it seems that rejected girls have negative attitudes toward school in general, while the dropout rate for rejected boys was significantly higher than other boys, emphasizing the potential risk factor academically for rejected children (Zettergren 2003). Moreover, research by Wentzel and Asher (1995) also found academic differences between aggressive-rejected and submissive-rejected children, in that aggressive-rejected children tend to have more issues academically. Specifically, aggressive-rejected children reported being less interested in school, more impulsive learners, and less likely to be civil and compliant in class. Further, these students were perceived by teachers as being less independent and less likely to be nominated as liked by both teachers and students, while

these same characteristics were not found in the submissive-rejected subgroup (Wentzel and Asher 1995).

Psychosocial Adjustment

Aside from victimization and poor school adjustment, rejected children may also face psychosocial challenges. A study by Nesdale and Lambert (2007) found that peer-group rejection significantly increased anxiety in rejected children. Further, as children get older, peer rejection was found to increase the child's risk-taking behavior, while peer acceptance was found to decrease this behavior (Nesdale and Lambert 2007). Low levels of peer acceptance during adolescence were found to be associated with lower levels of self-regulation and were found to affect their decision-making. These adolescents were less able to tolerate distress and were more emotionally sensitive when dealing with negative loss in their life (King et al. 2018). Further, since we know that research has demonstrated that being a victim of bullying can be associated with higher levels of social isolation, anxiety, and depression (Veenstra et al. 2007), these rejected children who are also victimized may be more at risk for these outcomes.

Conclusion

In summary, children who face peer rejection are at greater risk of experiencing a myriad of other negative developmental outcomes. For decades, researchers and practitioners have worked on how to alleviate the difficulties and maladjustment associated with peer rejection. An emphasis has been put into providing these children with social skills training and opportunities to integrate with their peers, such as strategic seating plans and classroom activities (Bierman 2004). By providing children a safe classroom environment without the fear of mistreatment and rejection from peers, rejected children can participate more confidently in class and improve their scholastic adjustment and

academic competence (Buhs and Ladd 2001). Furthermore, research has found that rejected children who possessed more peer-valued characteristics were less likely to be targeted for victimization, suggesting that this may provide an avenue for intervention (Knack et al. 2012). For example, participating in sports and peer-valued activities may allow these children to better integrate with their peers, develop peer-valued characteristics, and experience less rejection. Overall, peer rejection has negative and persistent implications for children in many areas of their life, which highlights the importance of early intervention so that these children may experience more positive developmental outcomes.

Cross-References

- [Peer Rejection, Gender Differences in Response to](#)
- [Peer Rejection, Sex Differences in Initiation of](#)
- [Peer Relationships in Childhood](#)
- [Peers](#)
- [Status Competition and Peer Relationships in Childhood](#)
- [Status Hierarchies](#)

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Rejection

- [Avoiding Stigmatization](#)
- [Humor and Ostracism](#)
- [Loneliness in Modern Life](#)

Rejection Thresholds

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Synonyms

[Decision making](#); [Egg recognition](#); [Egg rejection](#)

Definitions

The threshold at which hosts of avian brood parasites reject a foreign egg, which can be adjusted according to their perceived risk of parasitism.

Introduction

The interactions between avian brood parasites, such as cuckoos or cowbirds, and their hosts have emerged as model systems to study coevolutionary processes under natural conditions. Instead of building a nest and tending their offspring, brood parasites lay their eggs in the nests of other birds and abandon the care of their young to the host. Adult parasites tend to remove or damage host eggs when depositing their own and parasite chicks generally eliminate the rest of the host's brood after hatching. Consequently, hosts evolve defenses against brood parasites, which select counteradaptations in parasites, further counteradaptations in hosts, and so on. While evidence of reciprocal adaptations and counteradaptations in hosts and brood parasites are evident at all stages of the host's nesting cycle (Feeney et al. 2014), interactions at the “egg-stage” of the nesting cycle, such as egg rejection by hosts, egg mimicry by parasites, and further discrimination abilities in hosts, are the best studied.

Rejection Thresholds in Hosts

The failure to successfully reject a parasite's egg, either through not rejecting an egg or mistakenly rejecting an own egg, can cost a host its nesting attempt as well as the time and effort it takes to raise the parasite's chick (see ► [Egg Rejection](#)). Studies across numerous host–parasite systems have demonstrated that the decision to reject an egg can be based on the egg color, pattern, and size of the foreign egg (Spottiswoode and Stevens 2010; Stoddard and Stevens 2010, 2011) and that rejection decisions are specifically tuned to biologically relevant stimuli (i.e., according to differences between naturally

produced egg colors), rather than simply total differentness in color (Hanley et al. 2017). However, mistaken rejection of own eggs can occur when own and foreign eggs closely resemble one another (Feeney et al. 2015), so hosts use cognitive mechanisms and additional information to increase their likelihood of correctly rejecting the parasite's egg(s).

When faced with the perception of being parasitized, several cognitive mechanisms have been identified in hosts that help them increase the likelihood of correctly discriminating the foreign egg(s) in their nest. For example, they can simply reject the odd egg in the clutch ("discordancy hypothesis") or reject an egg (or eggs) based upon comparison to a learned or innate template of what one's eggs should look like ("true recognition"). Most studied species appear to use a template-based recognition system; however, some have been reported to conform to simple discordancy mechanisms or use a combination of both (reviewed in: Stevens et al. 2013). While these mechanisms are intended to help identify foreign eggs, parasites can also exploit them: African tawny-flanked prinias (*Prinia subflava*) reject cuckoo finch (*Anomalospiza imberbis*) eggs according to an internal template; however, cuckoo finches regularly parasitize prinia nests, and as the number of foreign eggs in the nest increases, prinias require greater differences between foreign eggs compared to their internal template to reject the eggs, resulting in lower rejection rates in these nests (Stevens et al. 2013).

Hosts also weigh their decision to reject a foreign egg according to their perceived risk of parasitism. For example, Eurasian reed warblers (*Acrocephalus scirpaceus*), a primary host of the common cuckoo (*Cuculus canorus*), that live in areas with cuckoos more readily reject foreign eggs compared to those that live in areas without cuckoos (Lindholm and Thomas 2000) and the rate of egg rejection within populations varies according to parasitism rates across years (Thorogood and Davies 2013). Within a breeding attempt, individual reed warblers combine both personal (i.e., the sight of a cuckoo near

their nest) and social (i.e., the sight of a cuckoo near a neighbors nest, resulting from it being attracted by the neighbor's alarm vocalizations) information about the presence of adult cuckoos near their nest (Thorogood and Davies 2016) to inform their egg rejection decisions.

Conclusion

Egg rejection is among the commonest and best-studied defenses that hosts use to minimize the cost associated with brood parasitism. Rejection decisions are primarily based upon hosts being able to discriminate a foreign egg (or eggs) in their nest; however, they also employ cognitive mechanisms and weigh these decisions according to their perceived risk of parasitism to help ensure they correctly identify the foreign egg (or eggs).

Cross-References

- Egg Mimicry
- Egg Rejection

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Relatedness

- [Hamilton's Rule and Genetic Relatedness](#)

Relatedness Coefficient

- [Genetic Relatedness](#)

Relatedness Parameter

- [Genetic Relatedness](#)

Relational

- [Girls Psychological Bullying](#)

Relational Aggression

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Synonyms

[Covert aggression](#); [Indirect aggression](#)

Definition

Relational aggression is a form of aggression characterized by attempts to harm or threaten others through purposeful manipulation and damage to interpersonal relationships.

Introduction

Relational aggression is a form of aggression characterized by attempts to harm or threaten others through purposeful manipulation and damage to interpersonal relationships (Crick et al. 1999). Relational aggression is distinct from physical aggression in that it often occurs without physical force or the threat of it. Relational aggression can be considered a type of psychological aggression – a form of aggression that targets perceptions, feelings, or behaviors but is more specific in that it always targets relationships (Linder et al. 2002). Relational aggression may take direct forms (e.g., negative facial expressions) or more indirect forms that do not directly confront the target (e.g., rumor spreading). It can also be proactive (e.g., planned, purposeful, goal-directed) or reactive (i.e., impulsive or response to a perceived threat) and may be directed toward kin, peers, or romantic partners. Examples of relational aggression include humiliating the victim in front of others, excluding the victim from social activities, and flirting with others to make a romantic partner jealous. Below we discuss some correlates of relational aggression and its developmental trajectory.

Correlates of Relational Aggression

Although several individual differences relate to relational aggression, we focus our discussion on some of the most common ones, including gender, self-esteem, narcissism, the Big Five personality traits, and personality disorders.

Regarding gender differences, although men often show and report more direct and physical aggression, women often show and report more indirect and relational aggression (Archer 2004). These gender differences in relational (and physical) aggression are often socially and culturally reinforced over developmental time (see Development section below).

Although self-esteem tends to relate negatively to physical aggression, the link between self-esteem and relational aggression appears to be positive among adolescents (Golmaryami and Barry 2010). In addition, self-esteem may moderate the link between narcissism and relational aggression; adolescents with lower self-esteem have especially positive narcissism–aggression associations (Golmaryami and Barry 2010).

In contrast, although narcissism tends to relate positively to physical aggression, its link to relational aggression is more nuanced. For example, although some studies of adolescents have shown a positive link for narcissism (Golmaryami and Barry 2010), others have shown null effects or evidence suggesting mediation via dominance goals (Ojanen et al. 2012). As mentioned above, the simple narcissism–relational aggression link is more positive among adolescents with lower self-esteem (Golmaryami and Barry 2010).

The Big Five personality traits – extraversion, agreeableness, conscientiousness, neuroticism, and openness – are related to a host of behaviors, and relational aggression is no exception. For example, in a large sample of Greek adolescents, relational aggression related positively to neuroticism but negatively to – in descending order of magnitude – agreeableness, conscientiousness, openness, and extraversion (Kokkinos et al. 2017).

Relational aggression's links with personality disorders – particularly those in Cluster B (e.g., antisocial, borderline, histrionic, narcissistic, and

sadistic personality disorders) – have also been studied in normal populations of young adults. For example, relational aggression positively correlates with Cluster B (more so than Clusters A and C) disorders and, regarding specific personality disorders, correlates strongly with sadistic and antisocial personality disorders and moderately with borderline, histrionic, narcissistic personality disorders (Schmeelk et al. 2008); however, the links for antisocial and borderline appear to be stronger among women than men (Werner and Crick 1999). In addition, relational aggression in children has been linked to future social–psychological maladjustment in a longitudinal study (Crick et al. 2006). Relational aggression was moderately negatively related to perspective taking in college students (Loudin et al. 2003). Moreover, peer-rejected college students were more likely to score high on relational aggression than their more accepted peers (Werner and Crick 1999).

Development

Although relational aggression is common across the lifespan, people in different developmental stages display different forms and degrees of relational aggression. Below we provide an overview of the developmental trajectory of relational aggression from childhood to late adulthood.

Childhood

As social cognition skills develop, children exhibit more relationally aggressive behavior (Andreou 2006; Archer and Coyne 2005). Research has found that 3- and 4-year-old children display relational aggression (Ostrov et al. 2004). In addition, because preschool-age children have relatively immature social and cognitive skills, researchers posited that overt and direct forms of relational aggression (e.g., friendship withdrawal threats) are more common in early childhood, whereas covert and sophisticated forms of relational aggression (e.g., gossiping, spreading rumors) become more common in middle childhood (Crick et al. 1999). But because even preschool-age children can show complex

relationally aggressive strategies, young children may in fact possess the ability to display sophisticated relational aggression as well (Ostrov et al. 2004). Aside from maturation in social-cognitive abilities, developing strong social networks is also associated with higher relational aggression in children. Existing literature shows that children in middle to late childhood engage in relational aggression more than those in early childhood as social groups become more developed and exclusive at older ages (Archer and Coyne 2005).

How do children develop relationally aggressive behavior? Past studies found family environment and parenting, such as parenting styles, marital conflicts, and parent-child conflicts, play an important role in children's development of relational aggression (Hart et al. 1998; Ostrov and Bishop 2008).

Regarding gender differences, as children learn about gender roles, girls (vs. boys) engage more in relational aggression because this form is often considered more gender-appropriate. But prior research has produced mixed results. Although some studies showed that girls (vs. boys) displayed more relationally aggressive behavior (e.g., Ostrov et al. 2004), others found trivial gender differences (e.g., Card et al. 2008). Researchers posited that gender differences in relational aggression may not exist at early childhood but increase in middle to late childhood (Archer 2004; Archer and Coyne 2005).

Adolescence and Young Adulthood

Relational aggression often reaches its peak during adolescence as adolescents enhance their social-cognitive abilities and understandings of others' perspectives. Consequently, aggressive adolescents use more relationally aggressive behaviors to achieve social success (Voulgaridou and Kokkinos 2015). Moreover, as status and peer relationships become important to adolescents' self-identities, some adolescents – especially girls with negative self-images – may have greater motivations to control and manipulate peer relationships (Moretti et al. 2001). In young adults, involvement in relational aggression remains common but occurs more frequently between

romantic partners than among peers (Goldstein 2011), possibly because many young adults view establishing romantic relationships as an important goal.

Researchers have argued that adolescent girls (vs. boys) display more relationally aggressive behavior and that this gender difference is the most salient during this stage (Archer 2004; Moretti et al. 2001). In young adults, however, no gender difference in relational aggression was found (Goldstein et al. 2008; Linder et al. 2002; Murray-Close et al. 2010), even though women tend to use relational aggression with romantic partners, whereas men do so more with peers (Murray-Close et al. 2010). One possible explanation for the null gender difference in young adults is that rates of relational aggression are more stable for women over time, whereas men increase relational aggression during young adulthood (Archer 2004; Archer and Coyne 2005).

Adulthood and Older Adulthood

Although research on relational aggression after young adulthood is scarce, relationally aggressive behavior is not uncommon in adults and older adults (Murray-Close et al. 2010; Trompetter et al. 2011; Walker et al. 2000). In fact, in adulthood, rates of direct aggression decrease while rates of indirect aggression increase (Archer and Coyne 2005; Walker et al. 2000). This may be because overt and physical aggression might have too high a cost, especially in work settings (Archer and Coyne 2005). Thus, indirect, relational aggression can occur more frequently in middle-aged adults and older adults (i.e., ages ≥ 55 years; Walker et al. 2000).

Similar to young adults, research suggested few gender differences in adults or older adults (Archer 2004). Nevertheless, perceived gender roles relate to relational aggression in older adults (Walker et al. 2000). That is, people who perceived themselves as being more stereotypically masculine (e.g., assertive) were more inclined to engage in indirect, relational aggression. Because older adults are less able or willing to engage in overt aggressive behavior, they often use more

subtle and sophisticated forms of aggression to harm others relationally.

Consequences, Implications, and Applications

Relationally aggressive people often have or experience higher social intelligence, peer rejection (Andreou 2006), bulimia, and antisocial and borderline personality disorders, as well as lower levels of prosocial behavior (Werner and Crick 1999). In contrast, victims of relational aggression are more likely to be obese or overweight (Janssen et al. 2004), have mothers with less education (Jansen et al. 2012), and have chronic disabilities (Ung et al. 2016). Regarding romantic relational aggression, both perpetrators and victims are often more insecurely attached, socially anxious, and ruminative and have more depression and anxiety symptoms (Goldstein et al. 2008).

Relational aggression often negatively affects its victims. Targets of relational aggression are more likely to experience loneliness and depression and have lower self-worth (Prinstein et al. 2001). Furthermore, relational victimization can predict future social phobia symptoms (Storch et al. 2005).

Of course, relational aggression can also harm its perpetrators. Peer-directed relational aggression predicts depression and anxiety symptoms, whereas romantic relational aggression only predicts these symptoms in girls (Ellis et al. 2009). In addition, relationally aggressive adolescents are more likely to experience peer rejection themselves, which could then make them targets of relational aggression by others (Wang et al. 2015). Relational aggression also negatively affects romantic relationships; both relational aggression and victimization relate to lower relationship quality (Linder et al. 2002).

Conclusion

Limitations and Future Directions

One limitation of relational aggression is that it can be difficult to measure. Because relational aggression is typically a socially undesirable behavior, self-reports may be biased because

people underreport it. To address this concern, some researchers supplement self-reports with peer, parent, or teacher reports (Golmaryami and Barry 2010; Ojanen et al. 2012), which, because of self-report biases, are more likely to be accurate. Another measurement issue concerns using the same instrument (e.g., survey, behavioral checklist) over developmental time, because what may be considered relational aggression to a 5-year-old may have little relevance to a 15- or 25-year-old. Thus, it is imperative that researchers continue to improve and refine the assessment properties of relational aggression measures. In addition, because much of relational aggression is inherently clandestine – arguably the “best” perpetrators intimidate victims enough not to report it – researchers may wish to broaden their assessment to include multiple peer reports. One way to do this would be to use social network analysis to survey entire classrooms or peer groups about relational aggression. Such designs can yield dyadic assessments of relational aggression between each pair of students in a classroom.

Treatment and Intervention

Given the substantial psychosocial impact of relational aggression, researchers have sought interventions to assuage its harmful effects. In school settings, social support from both peers and teachers has been shown to buffer against some of the negative effects of relational victimization, and as such, programs that help build teacher–student and peer–peer relationships and encourage people to solicit social support may help to improve victims’ qualities of lives (Flaspohler et al. 2009). Similarly, intensive school-based anti-bullying programs can decrease bullying by 20–23% and decrease victimization by 17–20% (Ttofi and Farrington 2011). Although this was found when examining bullying more broadly, similar school-based programs may also be effective in decreasing instances of relational aggression. Research into interventions for relational aggression in romantic relationships is less established; working to understand and modify the power dynamics and communication patterns in romantic relationships could likely decrease

instances of relational aggression in these relationships (Coyne et al. 2017).

Cross-References

- Indirect Aggression
- School Bullying
- Social Aggression
- Verbal Derogation Among Women

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Relational Bullying

- School Bullying
- Social Aggression

Relational Uncertainty

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Synonyms

Uncertainty of biological kinship

Definition

The term relationship uncertainty here does not refer to uncertainty about the status of a current romantic relationship but to a biological kinship uncertainty due to paternity uncertainty. For example, how certain is the biological relationship between two cousins where maximally two links of doubted paternity (father, father's brother) can be involved?

Introduction

Already Roman law stated that only motherhood is certain, and paternity uncertainty was also dealt with in the new law introduced with the Code

Napoléon (for example, “Scrutiny as to paternity is forbidden.” Title VII. Of paternity and filiation, Chap. III. Of natural children). Maternity certainty has remained certain, except for occasional mix-ups in maternity wards, until in-vitro fertilization became possible several decades ago. But for the long natural history of humans, paternity uncertainty threatened males to misdirect their costly paternal investment into the descendants of rivals. The asymmetry between maternity and paternity certainty is assumed to be one of the reasons why fathers tend to invest less in their offspring than mothers do. This assumption is supported by the finding that the perceived facial similarity between father and offspring, which is one of several possible kinship recognition mechanisms, is associated with paternal investment and emotional closeness to the offspring (Alvergne et al. 2010).

From Paternity Uncertainty to Relationship Uncertainties

The asymmetry between maternal and paternal certainty can be extended to relationship (kinship) uncertainty, with the hypothesis that feelings of closeness and the tendency to behave altruistically towards kind depends on the number of kinship links where paternity certainty may enter. For example, grandparental investment into grandoffspring may have up to two paternity uncertainty links: none for the maternal grandmother, one each for the maternal grandfather and the paternal grandmother, and two for the paternal grandfather. Euler and Weitzel (1996) could show that the number of paternity uncertainty links, that is, the relationship uncertainty, correlated negatively with the amount of grandparental solicitude as rated by adult grandchildren.

The study of grandparental investment is complicated by the fact that grandparents usually come in pairs, and the within-pair mutual influence may confound the investment for each single grandparent. This problem of co-residence as a confound can be circumvented by the study of the investment by aunts and uncles because the

brothers and sisters of the parents, unlike grandmothers and grandfathers, typically do not live together and thus invest into nieces and nephews independently of each other. It has been shown that the investment by consanguineal aunts and uncles (relatives by blood as opposed to aunts and uncles by marriage) is influenced by links of paternity uncertainty: The offspring of sisters reported to have received more care than those of brothers (Gaulin et al. 1997; Hoier et al. 2001).

The logic of differential investment into kin as a function of relationship uncertainty can be extended to cousins as well. A person has no uncertainty link with the offspring of his or her mother’s sister, one uncertainly link each with the offspring of father’s sister and mother’s brother, and two uncertainty links with the offspring of brother’s brother. Jeon and Buss (2007) could show that emotional closeness, empathic concern, and contact frequency with these types of cousins varied accordingly.

The Prevalence of Paternity Discrepancy

So far we have not quantified the paternity uncertainty which may occur at each paternal link. Obviously, the individual paternity uncertainty varies with individual circumstances, for example, the possibility of contact of the mother with other men during the time of conception. But how much paternity discrepancy (assuming paternity incorrectly; paternity confusion) has occurred in the ancestral past, and how much occurs these days in our societies? The amount of paternity discrepancy in the ancestral past has been estimated from the magnitude of the differences of investments into relatives of the next generation (nephews, nieces, and grandchildren) between the female and the male line. These estimates are just rough ones due to metrical problems of quantifying the differences. Gaulin et al. (1997) and Hoier et al. (2001) suggested from their estimates that in the evolutionary past the misattributed paternity must have occurred somewhat over 10 % of the cases. How does this number compare with recent paternity discrepancies?

In an earlier review Macintyre and Sooman (1991) reported that paternity discrepancy prevalences from prenatal genetic screening data varied between 1.4 % and 30 %, depending on country, ethnicity, and social milieus, with an average of about 10 %, a number which has been reported up to date in both scientific and popular writings. However, later studies cast doubt on the present-day truth of this number, at least for Western industrialized countries. In a meta-analysis, Voracek et al. (2008) showed that during the last century the reported paternity discrepancy prevalences slightly declined over the decades, arriving at a number of about maximally 3 %. The most recent reliable study known to the author (Wolf et al. 2012) reports a prevalence of 1 % for Germany, a number which is in accordance with data reported from the United Kingdom and Switzerland. The reason for this decline can only be surmised, with increased availability of effective birth control and less restricted choice of long-term heterosexual partners being likely candidates. But this low prevalence of paternity discrepancy has not changed the motivational structure of humans. They execute ancestral adaptations and treat their kin as if misattributed paternity still occurred relatively frequently.

Conclusion

Paternity discrepancy is nowadays considerably lower than assumedly has been in the past, but humans still execute ancestral adaptations. Therefore, relatives with fewer paternity uncertainty links, like offspring of sister, are emotionally closer than relatives with more paternity uncertainty links, like offspring of brothers.

Cross-References

- Grandparental Investment
- Kinship and Emotional Closeness
- Paternity Confusion
- Paternity Uncertainty
- Resemblance

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Relational Understanding

- Concept Formation

Relational Value

- Self-Esteem Tracks Social Evaluation and Relational Value

Relation-Between-Relations

- Concept Formation

Relationship Between Culture and Race

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Synonyms

[Ethnic identity](#); [Ethnicity](#); [Racial identity](#)

Definition

Culture	The customs, beliefs, values, traditions, and knowledge shared by a society or community, which are transmitted from generation to generation
Race	A socially constructed concept that refers to a category or group of people that share a common ancestry, physical characteristics, and/or language

Introduction

Historically, the relationship between culture and race has been a source of debate. Although it was originally believed that race differed from culture in that race was a biological construct, findings from human genetics research have challenged the view that race is genetically determined. In particular, research showing that there is more within- than between-group variation in races led scholars to conceptualize race as a social, rather than biological, construct (Worrell 2015). The conceptualization of race as a social construct has increased uncertainty regarding the relationship between culture and race. That is, although scholars originally distinguished race from culture by viewing race as a biological construct,

establishing both race and culture as social constructs blurred the distinction between the two. Today, the distinction between race and culture is not completely clear, with some scholars arguing that culture and race are separate and different constructs (Phinney 1996), whereas others argue that the constructs are related and even refer to the same concept (Worrell 2015).

Race as a Social Rather than Biological Construct

For years it was believed that race was a biological construct that referred to a group of people who inherited certain physical characteristics (e.g., skin color; Worrell 2015). In science, race was used to describe the relationship between a person's ancestry and genes (Yudell et al. 2016). However, scientific research has consistently indicated that there is no gene or set of genes that are specific to one racial group. In addition, research has shown that there is great genetic heterogeneity within racial groups and more genetic variation within than between racial groups (Cosmides et al. 2003; Yudell et al. 2016; Worrell 2015). Research in social psychology has provided further support for the idea that race is a social construct through findings indicating that the conceptualization of race is different across cultures (Chen et al. 2017). Although scholars generally agree that race is a social construct, there continues to be a widespread use of race as a biological variable in scientific research, and some scientists have called for an end to the use of race as a biological variable given that it does not have a genetic basis (Yudell et al. 2016).

Evolutionary Explanations for Race

Despite the lack of biological support for distinct racial categories, the concept of race continues to be commonly accepted. Although research originally suggested that race was automatically encoded, it was determined that race was likely not built into our evolved cognitive machinery, since hunter-gatherers traveled primarily by foot,

making it highly unlikely that they would encounter individuals from different races (Cosmides et al. 2003). Other research findings also spoke against the automatic encoding of race by indicating that categorization by race may be dramatically reduced when presenting individuals with contexts in which race is irrelevant for determining coalitions (Kurzban et al. 2002). As a result, different evolutionary hypotheses have been proposed to explain the nature of race encoding (Cosmides et al. 2003). One particular theory proposed by Kurzban and colleagues (2002) suggests that race encoding results from an alliance detection system that evolved to identify coalitions and alliances. According to the theory, human cognition is not designed to automatically detect race. Instead, race signals coalitional alliances, thereby allowing individuals to successfully navigate the social world.

associated with race because both concepts refer to groups with a common ancestry. However, ethnicity may be distinguished from race in that it refers to groups of individuals with a common geographic origin or nationality, whereas race does not. Additionally, unlike ethnicity, race has been used to refer to groups of individuals with similar phenotypes. Nevertheless, there is confusion regarding the two concepts; for example, the term Latino/a refers to an ethnicity but is often perceived as a race because individuals from this ethnic group may share physical characteristics. The lack of clear-cut distinctions between race and ethnicity has resulted in discussions regarding the difference between the two concepts, with some scholars proposing that race and ethnicity should be conceptualized as a sole construct, such as “racial/ethnic identity” (Grosfoguel 2004).

Relationship Between Culture and Race

Culture and race are closely related in that they share several key characteristics (see Worrell 2015). First, both culture and race refer to an individual's membership in a particular social group. Additionally, both terms refer to groups of individuals with a common ancestry or history, as well as similar values and beliefs. In this way, culture and race are closely related constructs used to categorize social groups based on certain key characteristics. However, one clear distinction between culture and race is that, traditionally, culture has been applied more broadly to include groups of people who share a common nationality, art, and/or religion, whereas race does not usually include these characteristics.

Another way in which culture and race are related is through the concept of ethnicity. Ethnicity is a term used to refer to a group of individuals who identify with or belong to a particular cultural group (American Psychological Association 2018). Thus, according to this definition, culture is fundamental to the concept of ethnicity. Importantly, both ethnicity and culture may refer to groups of individuals with a common nationality. Ethnicity has also been closely

Conclusion

The conceptualization of race as a social, rather than biological, construct was important for eliminating misconceptions regarding innate differences between racial groups, but the new conceptualization also resulted in uncertainty regarding the relationship between culture and race. That is, the original view that culture and race were separate constructs became less clear once it was determined that there was no biological basis to race. The lack of clear-cut genetic differences between racial groups has led some to argue that culture and race refer to the same concept (Worrell 2015). However, others contend that the two terms should be considered separate concepts (Phinney 1996). From an evolutionary perspective, both race and culture serve similar social functions in that both may signal kinship or alliance. Overall, it can be said that culture has traditionally been used as a broader categorical concept based on factors such as ancestry, language, religion, or nationality, whereas race has a more limited categorical scope because it was mainly used to refer to groups of individuals with a common ancestry and/or common physical characteristics.

However, recent research highlighting the influence of culture on perceiving an individual as a member of a particular race (Chen et al. 2017) has further contributed to the uncertainty regarding the exact nature of the relationship between culture and race.

In general, the consensus is that both culture and race are related because they are social constructs used to categorize groups of individuals with a common ancestry (Worrell 2015). Additionally, research suggests that racial categorization is somewhat subjective (Chen et al. 2017). In general, relative to race, culture has been traditionally applied as a broader social categorization concept. Thus, the conceptual and functional similarities between culture and race (e.g., group of individuals who share a common ancestry) have led to debates regarding the relationship between the two. Continued research on culture, race, and ethnicity will likely contribute more information regarding the exact nature of the relationship between culture and race.

Cross-References

- [Evolution of Culture](#)
- [Race as a Social Badge \(Kurzban\)](#)

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Relationship Between Sexuality and Gender

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Synonyms

[Gender differences](#); [Sex](#); [Sexual behavior](#); [Sociosexuality](#)

Definition

Gender refers to the collection of psychological traits that differ between the male and female sexes. Often, the terms gender and sex are used interchangeably; however, sex may be used when discussing the biological or genetic differences between males and females, while gender may be used to refer to psychological traits. Sexuality is very broad and refers to feelings, behaviors, and identities associated with sex. Here, we discuss

the literature which has reviewed the relationship between sexuality and gender.

Introduction

Men and women differ in many aspects of sexuality. From an evolutionary psychology perspective, men and women faced different reproductive problems in evolutionary history and, thus, adapted different reproductive strategies. While men and women may have many adaptive similarities to solve many problems, mating and reproduction are two areas where several problem-solving strategies are dichotomized. Men's sexuality is often characterized as more open to sexual behaviors, thoughts, and experiences, while women's sexuality is characterized as less open to these arenas.

Causes of Gender Differences

Gender influences sexuality via the effects of sexual differentiation. This can include the impact of sexual and natural selection on sex differences, leading to differences in sexual behavior (see ► [Sex Differences in Long-Term Mating Preferences](#); ► [Sex Differences in Short-Term Mating Preferences](#)). For example, parental investment theory suggests women would be more selective regarding sexual encounters and partners because they risk committing to a pregnancy and subsequent child-rearing (see ► [Parental Investment Theory](#)). Biological variations, including hormonal influence, also appear to influence sexuality. For example, testosterone influences sex drive in both men and women, and a higher testosterone level in any individual is associated with higher sex drive. In men who are experiencing low testosterone, a common complaint is a lack of sex drive. While estrogens play an important role in women's sexuality (e.g., influencing vaginal lubrication and elasticity), clinical studies suggest that women's sex drive is improved by taking exogenous testosterone and estradiol, but not improved by taking solely estradiol (see ► [Ovulatory Hormones](#)). Regarding sex drive, Lippa

(2009) found that gender differences in this variable were very large and very stable across different cultures suggesting a strong biological determinant.

Some aspects of sexuality show gender difference patterns that suggest interacting biological and cultural influences. For example, gender differences in sociosexuality described by Lippa (2009) were moderated by several cultural variables including the relative level of gender equality and economic development within each culture tested. This is consistent with observations that women's sexuality appears to be more plastic and sensitive to cultural or social influence than men's sexuality (see ► [Female Homosexuality and Bisexuality](#)).

Gender and Sexual Behavior

In this section, we highlight some of the findings that find gender differences in sexuality. This section is not intended to be an exhaustive list of all findings that show gender differences in sexuality.

Men tend to masturbate more often than women and pay for sex more often than women, while women tend to get paid for sex more often than men, and men are more likely to report engaging in sexual fetishism (Baumeister 2000; Lippa 2009). Well-replicated, large effect gender differences in sex drive are often utilized to explain these behavioral differences (Peplau 2003; Lippa 2009). There are relatively fewer studies to draw from regarding the effects of sexual orientation, but it appears that homosexual men and homosexual women tend to exhibit male-typical and female-typical sexuality, respectively, in the domains described above (Peplau 2003) though of course with the exception of their preferred partner's gender.

Men tend to seek out sexual variety more so than women (see Baumeister 2000 for an overview). For example, women are less likely to seek out and engage in extra-pair sexual intercourse compared to men; and women are less likely to have multiple sexual partners at any one given time compared to men. Women are less likely to pay for sexual intercourse compared to men. Men

are more likely to seek out, or accept an invitation for, casual sex relationships compared to women, while women report more regret or negative associations with casual sex compared to men. In the USA, casual sex or “hook-ups,” particularly among college-age students, are more sought after by men than women, while women report feeling more regret and shame about casual hook-ups compared to men (Garcia et al. 2012).

Women’s sexuality appears to be more fluid than men’s sexuality (see ► [Female Homosexuality and Bisexuality](#)). Women report changing sexual orientations more so than men, and women report less stringent sexual proclivities for one sex over another compared to men.

Gender and Sociosexuality

Sociosexuality refers to attitudes, thoughts, and behaviors regarding non-committal sex (see ► [Sociosexuality](#)). Numerous studies find men and women to differ on all three domains of sociosexuality. Men tend to be far more permissive regarding attitudes toward casual sex and more likely to engage in casual sex compared to women (Schmitt 2005; Sprecher et al. 2013). This appears to be stable across cultural groups, though there is plenty of cross-cultural and interindividual variation.

There are additional findings which suggest that gender differences in sexuality are smaller than previously discussed (Baumeister and Twenge 2002) or at least decreasing over recent decades (Peterson and Hyde 2011), implicating an influence of social learning and/or societal structure influences on gender based behaviors, including sexuality. These theories suggest that if social or cultural “scripts” or norms are influencing the perceived gender differences in sexuality, then removal of these scripts or norms would result in more similarity between sexuality and genders. In one study, Jankowiak and Escasa-Dorne (2016) reviewed profiles of individuals on a popular casual sex dating website to see if gender differences emerged. Jankowiak and Escasa-Dorne

suggest that if sexual proclivities of men and women were influenced by social or cultural norms, then an outlier group of individuals who are open to casual sex should have diminishing differences in their online sexual personas. However, their findings suggest that men and women’s profile pages reflected the well-documented gender and sexuality findings such that men were more open to casual sex and variety than women. Yet, the use of women on casual sex websites is also a reminder that sexual behaviors or proclivities are still variable within genders and that cultural influence can influence the degree of difference seen between genders (see also Lippa 2009; Peterson and Hyde 2011).

Gender Variance and Diversity

While most studies dichotomize gender into men and women, many groups have third or multiple genders, androgenders, or transgender individuals whose gender categories may not be included in the research discussed in this entry. While little research has explored the relationship between gender diversity and sexuality directly, the Fa’afafine of Samoa (see entry Fa’afafine), Hijrahs of India, and the mātānū of Tahiti tend to prefer men as sexual partners. Sadhins of India typically remain celibate, likely due to culturally imposed expectations (Nanda 2000). In Brazil, three gender variations (travesty, viado, and bicha) are defined by whether an individual is penetrated, or penetrating, during sexual intercourse.

Conclusion

Evolutionary theory hypothesizes that men and women faced different reproductive strategies, selecting for variation in sexuality between men and women. Data on sexuality, including sociosexuality, psychological traits, and sexual behaviors, suggests that men and women differ in numerous areas of sexuality.

Cross-References

- ▶ [Female Homosexuality and Bisexuality](#)
- ▶ [Hormone Effects on Human Fetal Development](#)
- ▶ [Ovulatory Hormones](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- ▶ [Sex Differences in Long-Term Mating Preferences](#)
- ▶ [Sex Differences in Short-Term Mating Preferences](#)
- ▶ [Sex Differences Versus Gender Symmetry](#)
- ▶ [Sexual Orientation and Human Sexuality](#)
- ▶ [Sociosexuality](#)

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Relationship Certainty

- ▶ [Father's Father Versus Mother's Mother](#)
- ▶ [Maternal Grandmother Invests Most](#)
- ▶ [Paternal Grandfather Invests Least](#)

Relationship Choices and Sexuality

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Synonyms

[Casual sex](#); [Long-term mating strategy](#); [Short-term mating strategy](#); [Sociosexuality](#)

Definition

Sociosexuality was originally designed to capture individual differences in people's willingness to engage in sexual behavior outside a formally/informally committed relationship. Work on the construct has moved from simple one-dimensional models, to models that incorporate the behavioral, attitudinal, and behavioral intention aspects of motivations to engage in casual sex, to, finally, encompassing an expansive model that describes a two-dimensional coordinate system composed of short-term mating interest and long-term mating interest. This model is especially useful in examining the emergent nature of the variety of apparent relationships that characterize the sexual landscape today.

Introduction

Since Kinsey (circa 1953), it has been clear that there is a wide variety of sexual behaviors men

and women engage in. Despite this, there is a pervasive myth of heterosexual monogamy in laypeople and researchers. This myth implies that the only acceptable form of sexual behavior is when it occurs in a committed relationship. While there are various reasons individuals might disapprove of sex outside of this context (e.g., health, religious), it is clear that individuals do engage in such behaviors in various relationship contexts. A more complete and accurate picture of human sexuality demands researchers to consider the various forms of sexuality individuals engage in. Indeed, even a cursory look at the animal kingdom reveals an apparently infinite array of sexual variety.

In the early 1990s, there was a paradigm shift in scientific thinking about the variety of sexual behavior and attitudes. Up until then, sex out of the context of marriage (i.e., casual sex) was seen as a pathology warranting treatment. Evolutionary psychologists began pointing out that engaging in casual sex might be adaptive for men and women (Buss and Schmitt 1993). By no longer pathologizing casual sex, researchers opened the proverbial floodgates to scientific inquiry into various questions related to motivations and measurement of people's willingness to engage in casual sex (see Jonason and Balzarini 2016).

Relationship Choice

In efforts to try and account for individual differences in relationship choices, Simpson and Gangestad (1991) developed a construct called "sociosexuality." This construct is meant to describe individual differences in people's attitudes, behaviors, and desires for casual sex as a way to explain within – and between – sex relationship choices. For instance, items ask about willingness to have sex with someone sans feelings and how often individuals fantasize about someone other than their current partner. It has been quite useful in understanding broad-spectrum motivations to engage in casual sex, sex differences in such motivations, and is useful

in providing some insight into people's sexual psychology around the world.

However, there are a number of potential limitations with their conceptualization of sociosexuality. The one most attended to at present is its psychometric structure. For example, using the original scale's items, more advanced tests (i.e., confirmatory factor analysis) revealed that the scale was better described as a two-dimensional system of sociosexual attitudes and sociosexual behaviors, dimensions that differ in their associations with narcissism and hostility (Webster and Bryan 2007). This two-dimensional model was further improved in Penke and Asendorpf (2008) to include sociosexual desires. These researchers attempted to understand sociosexuality as a manifestation of the classic social psychological distinctions of attitudes, behaviors, and behavioral intentions.

Another limitation of the initial work on sociosexuality was that it treated human sexuality in a rather black and white, dichotomous manner with one-night stands and serious romantic relationships treated as the only relationships available to engage in. Partly, this may be the result of efforts to reduce cognitive effort and to simplify research. However, this is a suboptimal solution as between 25% and 75% (see Jonason et al. 2012) of sexual acts committed by adolescents and college students happen in the context of sexual relationships that lack formal commitment (in contrast to serious romantic relationships) but are recurring acts committed by those with more than a passing acquaintanceship (in contrast with one-night stands). In addition, individuals appear to engage in non-relational sex for reasons thought to be confined to serious romantic relationships (e.g., emotional intimacy; Jonason 2013). While prior research has treated all casual sex as the same, there is evidence that each has its own functions and characteristic types of sexual and emotional acts (Jonason et al. 2010; Jonason and Balzarini 2016).

If one takes a step back, however, the real problem with using the sociosexuality construct to account for variance in relationship choice is that it treats motivations to engage in casual sex

and motivations to engage in committed relationships as opposite ends of the same spectrum when there are likely multiple competing interests at once (see Jonason and Balzarini 2016). In a third conceptualization of sociosexuality (Jackson and Kirkpatrick 2007), researchers highlighted the theoretically important dimensions of long-term mating interest, short-term mating interest, and past sexual experiences. Such an attempt better highlights the multidimensional nature of human mating strategies and may better allow researchers to capture the range of potential relationships people may engage in. Despite this theoretically relevant dimensional structure, researchers have not taken a fully evolutionary approach to relationship choice.

Importantly, evolutionary theory, as applied to all manner of human existence including, but not limited to, relationship choice, suggests observable patterns in the world emerge from the competitive interactions of lower-order agents/factors without any overarching plan/planner, that is, relationships, as seen from our day-to-day lives, are not natural kinds but, instead, are the result of processes going on within people, societies, and couples. Relationships are likely the result of negotiations or, in other words, responses to numerous socioecological constraints imposed by those within (e.g., the partners) and outside relationships (e.g., society), but also ecological conditions like the availability of quality mates and resources (Jonason and Balzarini 2016). To treat relationships as distinct phenomena fails to deal with the fact that every relationship is different over a person's lifetime but also across individual relationships.

Emergent Relationships

In hopes of convincing the reader that relationships are emergent solutions to conditions, a review of some (but not all) relationship types is presented next (see Jonason and Balzarini 2016). For instance, polyandry tends to occur in locations where the means by which resources are extracted from the earth are so labor-intensive that it takes

multiple men to work their farm. Alternatively, polygyny is an option made available by a localization of resources. And last, polyamory might be a function of an interaction of individual differences in jealousy responsivity, the cobbling together of one's sexual and security needs from multiple sources, and the desire to seek secondary benefits like excitement. While these options represent "extreme" solutions to the psychosocial and reproductive tasks organisms, including humans, face, they are expressions of a mating system that is flexible to "cultural" conditions. Less extreme solutions might be found in booty-call relationships or friends-with-benefits where latent mating systems interact with technologies (e.g., mobile phones) to enable mating success (Jonason et al. 2009, 2010).

An important aspect of this emergent solution hypothesis (see Jonason and Balzarini 2016; Jonason et al. 2012) is that there are winners and losers in the battle of the sexes as would be expected from sexual strategies theory or a parental investment theory (Buss and Schmitt 1993). In terms of the present discussion, in serious romantic relationships, women may gain more than men do as the former have secured the dedicated resources of a single man. In contrast, in one-night stands, men may gain more than women in that they gain access to low-investment sex. However, most research assumes stark zero-sum solutions in relationships. Instead, in negotiations, middle-ground or hybrid relationships may emerge in the form of mildly positive-sum relationships where both partners win something when they compromise a little. If we assume that people have ideal standards in their partners, any willingness to deviate from those ideals acts as a compromise (Li et al. 2002). While a woman engaging in a one-night stand may have to fully compromise what she wants (excepting sexual pleasure), a woman who engages in a booty-call relationship may get some of what she wants. In an idealized world, people would not need to compromise, but as the alternative to not doing so is potential reproductive oblivion, evolution would have fashioned flexibility into the system.

Conclusion

In conclusion, the utility of sociosexuality in hopes of accounting for individual differences in relationship choices has progressed like most good science, starting with simplicity and advancing to a more complicated, comprehensive conceptualization known as strategic pluralism (Gangestad and Simpson 2000). This hypothesis suggests that flexibility in mating systems is in-built as over generations individuals who could be flexible in their relationship choices had increased reproductive fitness. For instance, the purely short-term maters would have had trouble securing a partner, and their offspring would have not fared well, whereas the purely long-term maters would be overly invested in a single partner and unable to switch if the need emerged. Indeed, even gibbons (sp. *Hylobates*), the most “monogamish” (lesser) ape, are not fixed into monogamy. Instead, humans, like gibbons, may be able to swing from one mating strategy to another as the need arises. That is, the sexual variety observed in the world is the solution, not the problem to life’s greatest task: reproduction.

Cross-References

- [Condition-dependent Mating Tactic](#)
- [Impersonal Sex](#)
- [Individual Differences](#)
- [Infidelity](#)
- [Sex Differences](#)

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Relationship Closeness

- [Emotional Closeness Predicted by Relatedness](#)

Relationship Dissolution

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Synonyms

[Breakup](#); [Conjugal dissolution](#); [Divorce](#)

Definition

The process of ending a relationship by the voluntary action of at least one partner.

Introduction

Most ancestral mammalian species didn't form long-term male-female pair bonds. Males mated with estrous females, and when the female went out of estrus, the relationship ended. Dissolution only became an issue when the human species came into existence, at which time males and females began living together in long-term relationships. During the hunting and gathering era, the dissolution of these relationships was apparently simple and without serious consequences, either for the couple or their offspring. However, following the development of agriculture, dissolution became more problematic. Children needed paternal investment from a biological father, accumulated wealth made inheritance possible and paternity important, and rising religions condemned adultery and divorce.

Currently, in many societies, relationship dissolution is once again becoming easier, due to changes in mores and technological developments such as birth control, with consequences that are still becoming apparent (see, e.g., Draper and Harpending 1982).

Human Evolution and Relationship Dissolution

For the most part, mammals don't engage in long-term male-female relationships. Beach (1976) estimates that "perhaps 90% of all mammals are seasonal breeders" (quoted in Symons 1979, p. 79). Even in mammalian species that live in social groups (herds, packs, and troops), long-term male-female dyads are rare.

Some of our distant primate relatives, marmosets and tamarins, do engage in male-female pair bonding (e.g., Dunbar 1995). Gibbons live in "small groups which superficially resemble the

human family because they are composed of a mated pair and their immature offspring", but, according to Lancaster, the "gibbon 'family' is a common pattern for . . . mammals in the tropics and does not represent a predecessor to the human family" (Lancaster 1975, p. 34). The Hamadryas baboon "harem" is another primate social arrangement that seems to be a precursor of a version of the human family (Kummer 1968), but it is "not so much a unit adapted for mating as it is for foraging in an environment of scarce and scattered food resources" (Lancaster 1975, p. 33).

Among our closest primate relatives, the chimpanzees, males are usually interested in bonding with females only when females are in estrus (e.g., Van Lawick-Goodall 1971; De Waal 1989), although recent observations indicate that "male chimpanzees living in an exceptionally large community display long-term tendencies to associate with particular females" (Langergraber et al. 2013).

With some exceptions, the basic reproductive strategy of mammalian males is to impregnate as many females as possible, while the female strategy is to nurture a relatively small number of offspring. The male strategy is perpetuated by basic psycho-physiological mechanisms common to all mammals (Gray 1971). These include the following:

Pursuit of Novelty

Every mammal responds to novelty with excitement and interest, an aspect of mammalian psychology that is well substantiated. In laboratory studies, a male "typically copulates with an estrous female several times and then stops. When the original female is replaced with a new estrous female, the male begins to copulate with the novel female" (Morton and Gorzalka 2015, p. 493). See also Schmitt et al. 2001.

Habituation and Sensitization

Every mammal is subject to habituation – a decrease of interest in, or attention to, a stimulus once it becomes familiar. It's what causes a stimulus that was once salient to fade into the background. Habituation enables animals to ignore

repeated stimuli once they prove not to be dangerous. Sensitization is the opposite of habituation. Animals become increasingly sensitive to repeated stimuli instead of tuning them out (Plaud and Gaither 1997).

Hunter-Gatherer Innovations: Marriage, Father, and Family

At some point, perhaps even before *Homo sapiens* came into existence, males and females began living together in dyads, with males hunting and females gathering. They shared the work of subsistence and raised their offspring more or less together, thus giving rise to the family. A group of related families formed the foraging band. Meat was shared with the entire band, while vegetables, fruits, and nuts were usually shared among the immediate family (Lee 1979; Lee and Devore 1976; Tonkinson 1978; Turnbull 1961.)

The institution of marriage arose, and males became *fathers* who provided significant paternal investment to the children of the band. Striving for dominance among males was muted because virtually every male could have a wife. The family and the band replaced the dominance hierarchy.

With the advent of long-term male-female pair bonds, reproductive strategies took a new turn. Females lost the obvious estrus of ancestral species and became receptive to sex during times when they weren't ovulating. Males developed a new set of emotions, reinforced by the members of the extended family, which urged them to stay with a female partner (or partners) and invest in the care of offspring, while females sought a relationship – a marriage – with a male who could be expected to invest, often an older man, preferably a successful hunter.

However, if contemporary hunter-gatherer practices are any indication of what went on in ancestral bands, divorce and extramarital sex were common. The new male desire to stay with a partner coexisted with the ancient drive to impregnate many females. As Symons notes:

a male hunter/gatherer with one wife (who will probably produce four or five children during her lifetime) may increase his reproductive success an

enormous 20 to 25 percent if he sires a single child by another woman during his lifetime. If he can obtain (and support) a second wife, he may double his reproductive success. The reproductive realities facing his wife are very different. She will bear four or five children during her lifetime whether she copulates with one, ten, or a thousand. (Symons 1979, p. 161)

Married males didn't stop trying to have sex with other women. In all hunter-gatherer bands that have been studied, illicit trysts were common. For example, anthropologist Asen Balikci writes that some Netsilik Inuit men "...were well known for their sexual enterprise..." (Balikci 1970, p. 160). Although their behavior sometimes caused quarrels and was disapproved of, it was tolerated.

A small percentage of contemporary hunters had more than one wife in addition to the extramarital sex (Turnbull 1961; Tonkinson 1978; Lee 1979; Balikci 1970), and it is likely that polygamy existed in ancestral bands.

Although the female strategy remained focused on nurturing offspring, now with a male partner in a band, women participated willingly in extramarital relationships. Shostak describes such affairs from the perspective of Kung women:

To succeed at and to benefit from extramarital affairs, one must accept that one's feeling for one's husband—"the important one," "the one from inside the hut"—and for one's lover—"the little one," "the one from the bush"—are necessarily different. One is rich, warm and secure. The other is passionate and exciting, although often fleeting and undependable. (Shostak 1981, p. 267)

Relationship Dissolution in Foraging Societies

First marriages are usually between a young woman who has recently entered puberty and an older man. Sometimes these first marriages last, but often they break up rather quickly. According to Shostak, most! Kung

experience one long-term marriage, although most are also married more than once. Dissolution of marriages by divorce is quite common. It usually occurs during the first few years of a marriage, before the couple has had children, and is usually initiated by the woman... No formalities or legal procedures are necessary, but emotions often run high. Arguments for and against termination may

go on for days or even weeks, as everyone in the village expresses a point of view. Eventually, a decision is made, and if the choice is separation, it ends there... The divorced girl or woman simply re-enters the category of highly desirable potential wives, to be sought after by eligible men. (Shostak 1981, pp. 130–131)

Among the Netsilik Inuit, the custom of wife exchange could precipitate the dissolution of the original marriage. Wife exchange often

...led to permanent separations. After temporary arrangements had been organized, the exchanges increased, and the men lost interest in their wives and decided to settle down permanently with their partner's wife. A new marital situation was thereby created, with the children following their mothers to their new houses. (Balikci 1970, p. 143)

Women in most hunter-gatherer societies could initiate breakups and have affairs without dire consequences, for themselves or for their children, because (1) they were equal partners with men in the work of survival and (2) the band as a whole was responsible for raising the children, not just the parents. For example, among the Mbuti:

...as far as the child is concerned, all adults are his parents or grandparents... He knows his real mother and father, of course, and has a special affection for them and they for him, but from an early age he learns that he is the child of them all, for they are all children of the forest. (Turnbull 1961, p. 128)

Extramarital sexual relationships and relationship dissolution no doubt produced jealousy, anger, resentment, and sometimes violence in the bands of our ancestors, as they do today. However, it's important to note that a male's drive to have sex with many females did not necessarily dissolve his marital relationship. Nor did it have to cost him reproductive success – or damage his children – because paternal investment was provided by all the males in the band. Nor were women who engaged in extramarital affairs ostracized or condemned. The survival of children was not dependent on long-term conjugal relationships.

In general, when marriages ended, both males and females could find new partners, and the new arrangements were eventually accepted, or at least tolerated, by the other members of the band.

Although “sexually enterprising” males and females often caused tension and trouble, they weren't destructive of the social system.

Relationship Dissolution After the Agricultural Revolution

Once our species abandoned nomadism and settled down to farm, often with a husband and wife sharing all the labor and raising the children by themselves, things changed dramatically. Without the band to raise the children, the parental investment of the biological father became critical to their survival. Children without fathers tended not to do as well as children who did have fathers. In agricultural societies, if a male abandoned the mother of his children, they might not survive, and his own fitness would be compromised.

With agriculture came the ability to accumulate wealth – property and, eventually, money. These could be passed on to one's children. For people with something to pass on, paternity was a crucial issue. Wealth, inheritance, and the need for parental investment from a father turned the dissolution of a conjugal relationship into a far more serious issue than it had been in foraging bands. Breaking up could result in the loss of the support children were dependent on. This in turn could be a serious blow to a man's fitness. It could also mean financial loss for men, such as return of a dowry or payments to the wife's family. Staying with one's wife (and perhaps having affairs on the side) was often a better economic decision for males than divorce.

In addition, rising religions enshrined monogamy and faithfulness in many societies. “Thou shalt not commit adultery” became a centerpiece of morality in Judaism, Christianity, and Islam. For hundreds of years in Europe, divorce was a sin, and for hundreds of years, more women couldn't initiate it. Men's extramarital affairs were frowned upon, but women's affairs were punishable by death (and still are in some societies). Religious prohibitions put enormous pressure on both males and females to stay with the family despite their personal feelings and desires.

The Coolidge Effect

In societies where adultery was a sin and fidelity was expected, the mechanisms that served to break up relationships could cause serious trouble for couples and the society. Primary among them was the male drive to have sex with multiple partners, often referred to as the Coolidge Effect (Symons 1979; Wilson 1982; Morton and Gorzalka 2015).

The Coolidge Effect is the progressive decline in a male's interest in mating again and again with the same female combined with a heightened interest in new females. It is, essentially, the old mammalian male reproductive strategy that hasn't gone away. The persistence of the Effect in human males has been documented in a great many studies (e.g., Kinsey et al. 1961; Masters and Johnson 1966; Bermant 1976; Symons 1979; Dewsbury 1981; Wilson 1982; Schmitt et al. 2001; Morton and Gorzalka 2015). Thus, it is not surprising that in her cross-cultural study of conjugal relationship dissolution in many societies around the world, Betzig found that adultery was the most common cause of relationship dissolution. She also found that the "double standard" was also a common cross-cultural phenomenon:

In 25 societies, divorce follows from adultery by either partner; in 54 it follows only from adultery on the wife's part and in 2 only from adultery on the husband's. If marriage qualifies as near universal, so must the double standard. Almost every one of the causes of conjugal dissolution that might be related to infidelity is ascribed significantly more often to one sex than to the other. (Betzig 1989, p. 658)

The Coolidge Effect in Therapeutic Practice

Therapists who deal with sexual issues sometimes encounter men who may love their wives/partners but are forced either to give up sex or to look elsewhere for it, a situation which can begin to undermine the relationship. Men are often reluctant to admit that they aren't sexually interested in the woman that they love any longer. It's too frightening an admission for them to make and too painful to communicate to their partners. So they don't say anything and begin avoiding sex.

Then, often, a wall of silence arises between the man and his mate.

At first, many men in this situation begin to worry about their own potency. When they find that they are attracted to other women, they often experience a sense of relief that they're not impotent. At that point, a Coolidge-affected man may become sensitized to some aspect of his partner's behavior that didn't bother him before. Something negative about his partner sticks in his mind and can't be driven out: "She's such a nitpicker," "She's nagging me all the time." He may manufacture reasons to engage in an extramarital relationship or initiate a breakup.

Another way the Coolidge Effect leads to relationship dissolution is via the female response to it. Faced with a male's loss of sexual desire, women are likely to feel neglected and unloved. They begin to look around and are more likely to have affairs or to initiate a breakup themselves. Wilson notes that when women:

...are questioned about why they have extramarital sex, it usually turns out that their relationships with their husbands were in some way unsatisfactory at the time or that they saw other men as being in some sense superior to their husbands. . . . Another fairly common reason . . . is that they hoped to create some effect on their husbands, for example, getting revenge on them for similar behavior. (Wilson 1982, p. 51)

See also Greiling and Buss (1999).

The mechanisms noted above – the pursuit of novelty, habituation, and sensitization – can become very troublesome when long-term relationships are the goal. For example, humans in long-term relationships can become sensitized to nonsexual stimuli that were initially tolerated or tuned out. Humans can also habituate to sexual stimulation over time (Plaud and Gaither 1997). In the novelty phase, a partner's every move can be intensely rewarding, but as time goes by, the excitement and the charm fade.

For much of civilized history, economic necessity, social pressure, and fear of damnation kept many couples together who didn't want to be. Staying together may have maintained parental investment in children and kept the couple socially acceptable, but both the male and female

often led what Thoreau called “lives of quiet desperation.”

Relationship Dissolution Today

In many contemporary societies, relationship dissolution is once again becoming relatively easy, but new social and technological complications have been added. Among these new features are birth control, no-fault divorce, prenuptial agreements, financial independence of women, legal and governmental support for single mothers, decline in the power of religious prohibitions, social acceptance of long-term cohabitation without marriage, and custody arrangements.

Birth Control

The ability to have sex without pregnancy is an extraordinary development in human history (Critchlow 1996). Control of reproduction allows women to have sex with males who are attractive but unlikely to invest in children, leaving women free to pursue individual gratification without fear of harming children. It also allows men to have sex with women without fear that they will incur a paternal obligation.

Birth control tends to increase the likelihood that women will dissolve a relationship (Marcen 2015).

No-Fault Divorce

In many states in the USA today, divorces may be obtained without providing a particular reason for the breakup. Couples can simply agree to part, and the dissolution of the relationship is sanctioned by the state. In a study of the impact of no-fault divorce on divorce rates in all 50 states in the USA, Nakonezny et al. (1995) found that the number of divorces increased in all but six states after no-fault legislation was enacted. Of course, no-fault divorce is easiest when there are no disagreements over assets such as money and property or custody of children.

Prenuptial Agreements

Such agreements are common where one partner, usually the man, is wealthy. In effect, they

constitute an agreement in advance to dissolve the relationship under certain conditions. They provide some protection for the wealthier party and generally guarantee that if the less wealthy party, usually the woman, wants to dissolve the relationship, she and any children will not be exposed to poverty. Prenuptial agreements have commonly been initiated by the rich, but Marston (1997) makes the case for extending prenuptial agreements to all couples, regardless of their wealth.

Financial Independence of Women

Today many women can dispense with the need for investment by the biological father. The ability of women to make enough money to support their children gives them a vastly increased ability to leave unsuccessful marriages and an incentive to do so. According to a 2005 study (Milligan 2005), single women were the second largest group of home buyers in the USA in 2004. Divorce, delayed marriage, and financial independence are fueling this trend.

Alimony and Child Support

The availability of alimony and child support is another factor that contributes to the rise in relationship dissolution. These supports not only provide a source of income for the woman, but they may also serve to reduce a male's sense of guilt about initiating a breakup. On the other hand, fear of living in reduced circumstances due to alimony payments can deter men from dissolving a relationship (Zagorsky 2005).

Welfare for Women and Their Children

Women whose spouses don't or can't provide alimony and/or child support are eligible for government support. Welfare makes it possible for a poor married woman to initiate divorce without fear of penury. In the USA today, there is little reason to think that a fatherless child won't survive.

Decline in the Power of Religious Prohibitions

In many modern societies today, religious prohibitions against divorce and adultery have less force as a constraint on people's willingness to

abandon a marriage and on the propensity of both males and females to act on their desire to pursue extramarital sexual opportunities (Stokes & Ellison 2010).

Social Acceptance of Cohabitation

Possibly because of the decline in the power of religious prohibitions, living together without being married is increasingly accepted in many societies. Cohabitation was once thought to be a way of strengthening relationships because it allowed couples to get to know each other without the legal and social trappings of marriage, but Axinn and Thornton (1992) found that not only are there a high number of relationship dissolutions among cohabiting couples but those who married after a period of cohabitation also had a high divorce rate.

Unmarried couples in long-term relationships who break up don't get the advantages that have been built into the law to support and encourage marriage (e.g., custody, alimony, child support), but, as Axinn and Thornton's research demonstrates, there is more freedom for both partners in a nonmarital relationship, particularly if there are no children, and it's much easier for either partner to dissolve the relationship.

Custody

Some of the most bitter battles in the breakup of relationships today are fought over who gets the children for how much time (Ayoub et al. 1999). According to Wolman and Taylor:

...the contested child is faced with an extremely complicated set of conflicts and stresses arising from the interparental battle. Some of these problems include: (1) inadvertent or conscious involvement in marital hostilities; (2) parent-child role confusion and role reversals; (3) the stress of living in a highly volatile emotional climate in which one has little control over the outcome of events and a great deal at stake; (4) cognitive dissonance resulting from parents' presentations of radically different, competing views of reality; and (5) disillusionment, or dissonance between what children have generally been socialized to believe and what they learn to expect on the basis of their own experience. (Wolman and Taylor 1991, p. 406)

Conclusion

Human males and females, like most other mammals, have different reproductive strategies, and those differences can create tension, resentment, and anger that often lead to the dissolution of long-term relationships. Our hunter-gatherer ancestors evolved a social structure that gave individuals both the security of long-term relationships and a considerable amount of sexual freedom. Relationship dissolution was common and relatively easy. Children were cared for by the entire band, so parental breakups did not compromise their physical or psychological health.

Today, after thousands of years during which relationship dissolution was fraught with many difficulties and dangers, it has again become relatively easy. Modern societies provide fairly well for the survival and physical well-being of children but often less well for their psychological welfare when their parents break up (Wolman and Taylor 1991).

Reliance on the nuclear family – a unit that is subject to dissolution due to the vagaries of sexual attraction, love, and social and religious mores – puts many children at risk today, sometimes physically, often psychologically. The risk would be minimized if children were raised by a “band,” as they were throughout most of our existence as a species. Unfortunately, although many contemporary societies have made it easier for people to dissolve long-term relationships, they haven't fostered communities that can offer the broad adult support that the children of breakups often need.

Cross-References

- [Circumventing Mate Choice](#)
- [Cues To Infidelity](#)
- [Frequency of Infidelity](#)
- [Human Mate Poaching \(Schmitt And Buss, 2001\)](#)
- [Reproductive Strategy](#)

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Relationship Longevity

► Relationship Satisfaction and Commitment

Relationship of Evolutionary Behavioral Sciences and Social Sciences

► [Crisis in Sociology](#)

Relationship Outcomes

► [Relationship Satisfaction and Commitment](#)

Relationship Pattern

► [History of Attachment Theory](#)

Relationship Satisfaction and Commitment

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Synonyms

[Relationship longevity](#); [Relationship outcomes](#)

Definition

Relationship satisfaction and commitment refer to the extent to which people are happy with and intend to maintain their intimate relationships.

Introduction

Throughout evolutionary history, humans evolved various cognitions, emotions, and behaviors that helped them to overcome the numerous adaptive challenges that they faced. Those cognitions, emotions, and behaviors, in turn, functioned to increase survival and future gene propagation.

Not only did such adaptive challenges include those associated with producing offspring, ancestral men and women also faced challenges associated with the ability to successfully rear offspring to reproductive age. Traditional evolutionary perspectives argue that one way humans overcame this challenge was by forming lasting pair bonds, or long-term, romantic relationships, which functioned to provide offspring with biparental care (Kokko and Jennions 2003). Indeed, individuals who were able to form lasting pair bonds likely produced higher quality offspring and experienced lower childhood mortality. This entry highlights the role of relationship satisfaction and commitment to the maintenance of such romantic relationships.

Relationship Satisfaction

Not all romantic relationships are ideally suited for successfully rearing offspring. There are numerous costs and benefits associated with every partnership, and relationships in which the costs outweigh the benefits may be reproductively maladaptive – that is, they may have negative consequences for offspring. Scholars have argued that relationship satisfaction may serve as a barometer of the ratio of costs and benefits associated with a given pair bond and thus the extent to which that pair bond meets evolutionary-based mating needs and desires (Shackelford and Buss 1997; Meltzer et al. 2014a; see also Kelley and Thibaut 1978). Indeed, evolutionary perspectives posit that positive emotions evolved to promote and maintain reproductively adaptive behaviors (Nesse and Ellsworth 2009), and relationship satisfaction may reflect the accumulation of those emotions in response to the relationship. Consistent with this perspective, recent evidence suggests that relationship satisfaction reflects the extent to which people associate their partner with positive versus negative affect (McNulty et al. 2013). Accordingly, partnerships in which the costs outweigh the benefits (and thus do not meet people's evolutionary-based needs) should be characterized by relationship dissatisfaction whereas partnerships in which the benefits

outweigh the costs (and thus meet people's evolutionary-based needs) should be characterized by relationship satisfaction.

Factors Influencing Relationship Satisfaction

Many factors can influence people's perceptions of their relationship costs and benefits. For example, the quality of people's relationship partners and the extent to which those qualities match their ideal partner qualities can influence relationship satisfaction. Although some rewards and costs likely involve evolutionarily novel partner qualities, many qualities likely reflect those associated with effectively producing and rearing offspring (Fletcher et al. 1999). For instance, both men and women are more satisfied with romantic relationships in which they have partners who meet the evolved desires of both sexes, such as sexual intimacy and physical health. Yet, the implications of other partner qualities are more sex differentiated. For instance, consistent with the notion that there are sex-differentiated preferences in long-term romantic relationships, women's relationship satisfaction appears to be particularly sensitive to the extent to which their partner provides enough resources (Rogers and DeBoer 2001), and men's relationship satisfaction appears to be particularly sensitive to the extent to which their partner is physically attractive (Meltzer et al. 2014b).

But relationship satisfaction also depends on people's own mate value, particularly as it relates to their partners' mate value. The mate values of long-term relationship partners are often positively associated due to assortative mating (see Shackelford and Buss 1997), and partners whose mate values are similar report higher levels of relationship satisfaction. When there are discrepancies across partners' mate values (that is, when one partner has a higher mate value than the other partner), in contrast both partners may be at risk for decreased relationship satisfaction (Shackelford and Buss 1997). Whereas the relatively lower mate-value individual may experience anxiety due to concerns that their partner may leave them for another potential partner of higher mate value, the relatively higher mate-value individual may perceive that they could

obtain more benefits from an alternative relationship with a higher mate-value partner.

Relationship Commitment

But satisfaction alone does not determine whether one remains in a relationship; the alternatives to the relationship also matter. Taken together, satisfaction and alternatives predict relationship commitment, which directly predicts remaining in a relationship (Kelley and Thibaut 1978). Specifically, people should remain committed to their relationships to the extent that they (a) are satisfied with their current relationships and (b) perceive that their current relationships provide more benefits (relative to costs) than their alternatives outside of those relationships might provide (Kelley and Thibaut 1978). Indeed, individuals who perceive that their relationship costs outweigh their relationship benefits, and thus experience lower relationship satisfaction, are typically less committed to maintaining their relationships; and individuals who perceive that the benefits associated with their relationship alternatives (e.g., other potential long-term partners, short-term relationships) exceed the benefits (relative to costs) associated with their current relationship are typically less committed to maintaining their relationships.

Not only does commitment directly predict remaining in a relationship, it can also motivate intimates to improve the quality of their relationships (see Rusbult et al. 2001). Accordingly, both men and women benefit to the extent that they and their relationship partners remain committed to quality relationships. Indeed, compared to less committed intimates, more committed intimates invest more resources in their relationships – resources that benefit their partners and their potential offspring – and attend less to attractive alternative partners, which reduces the likelihood of sexual infidelity.

Conclusion

Ancestral men and women would have benefited to the extent that they could maintain satisfying,

committed romantic relationships. Throughout evolutionary history, not only did those individuals who remained happily committed to long-term partners have increased sexual access that would have been associated with an increased likelihood of conception, they also invested more time and resources into their relationships that would have increased the likelihood of biparental care and thus offspring's future reproductive success. That is, relationship satisfaction and long-term commitment likely evolved to help people meet the needs associated with reproductive success.

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Relationship Status

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Synonyms

[Marital status](#)

Definition

It refers to the current position of a romantic relationship (preferably marital).

Introduction

Relationship is defined as “the state of being related” or “the state of affair between an individual with another individual(s) or environment” (Dictionary 2006). Similarly, status is defined as “position or hierarchical rank of an individual in relation to others” (Dictionary 2006). Relationship status often refers to the marital status (*state of being married or not married*) (Dictionary 2006). The relationship status can be single or married. Single relationship status refers to individuals who are either never married, socially separated, divorced, widower, or widow. Other relationship statuses refer to individuals who are neither single nor married. Often individuals who are living together (cohabiting) or committed for marriage but not married yet come in this category of relationship status. Certain individuals are not willing to disclose their relationship status due to personal reasons and prefer not to specify their relationship status. Relationship status also tells the sexual orientation of the individuals. Individuals often mention their sexual orientation (straight, gay/lesbian, bisexual) along with their relationship status. Individuals with casual relationships often refer to their status as single, but those in committed or long-term relationships seldom label their status as single. Men with “single”

relationship status are found to have higher testosterone level than those in long-term relationships (van Anders and Goldey 2010).

In a romantic relationship (particularly among the opposite genders), the concerns are usually gender specific. The relationship status might have a role in determining the concerns of men and women. The sexual behavior of men and women in a relationship too differs. Men often have willingness toward casual sex, whereas women often offer resistance for casual sex (Roese et al. 2006). Often, men in a relationship regret their inaction (i.e., not advancing in romantic relationships or losing romantic opportunities outside the current relationship) (Roese et al. 2006). In a romantic relationship, retaining the mate is an important and challenging task. Mate poaching is a threat to the relationship and people adopt various mate retention tactics to save the relationship (de Miguel and Buss 2011).

Relationship Status: Online Activities

With the advent of the digital revolution, people tend to focus more on online social networks. Association of online social networks has popularized the term “relationship status.” People often post their relationship status online. Relationship status has various personal as well as social implications. Posting the relationship status publicly (in social media), or discussing it publicly, too has many psychosocial implications. Evidences support that relationship status has huge influence on the activity of males on Facebook; however, it has little influence on the Facebook activity of females (McAndrew and Jeong 2012). Posting relationship status online is a form of self-portrayal as well as self-disclosure in public. Neuroticism, extraversion, and agreeableness direct an individual to disclose self, online (Seidman 2013). Relationship status of the individual influences online sexual behavior. Evidence supports that men and homosexuals (gays/lesbians) are found to be involved more in online sexual activities than women and straights (Albright 2008). Loneliness is found to have a positive association with various parameters of

Internet use (Matsuba 2006). Individuals, who are never married, separated, divorced, and in unstable relationships are more likely to experience loneliness and hence have higher probability of Internet use and online activities. Self-portrayal of relationship status online can be one determinant of intimacy seeking or avoiding behavior. Many people quote their relationship status to be “single” in the online social networking platforms to invite potential romantic relationships (Young et al. 2009). Similarly, nondisclosing relationship status online might have multiple implications like avoiding invites from opposite genders for a romantic relationship, hiding the ongoing relationship, doubt about current relationship or it may be due to social concerns.

Implications of Relationship Status

Evidence supports that stable relationship status is associated with better subjective well-being and greater life satisfaction (Dush and Amato 2005). As individuals move from an unstable relationship to a stable and committed one, the life satisfaction becomes better too (Dush and Amato 2005). Individuals who are single, are found to have lesser subjective well-being than those who are dating or in a stable relationship (Soons and Liefbroer 2008).

Relationship status not only influences the life of young individuals; elderly people are affected equally as well. A study attempted to evaluate the association of relationship status in elderly population with hospitalization in long-term care facilities and it was found that single (widowed, divorced, or never married) individuals possess the highest risk of hospitalization in long-term care facilities. Again, relationship status was found to be an important determinant of long-term hospitalization more so for men than women (Thomeer et al. 2016). It is seen that relationship status determines the likelihood of postretirement work. Men with a relationship often work in their postretirement period, whereas the reverse happens in cases of women (Settels and McMullin 2017). Relationship status not only influences the interpersonal relationship and

quality of life between spouses, it has impact on the mental well-being of their children. Children of mothers in unstable relationships have more than 8 times higher risk of development of mental health issues than those children whose mothers are in stable relationships (Hannighofer et al. 2017). Relationship status of pregnant mothers too influences the fetal well-being. It was reported that pregnant mothers, who have an unstable current relationship are more likely to have babies with small gestational age than those mothers with current stable relationship status (Steinberg et al. 2016).

Relationship status has a positive impact on life satisfaction as well as achieving remission from stress by causing structural brain changes in specific brain regions (left superior frontal gyrus and bilateral middle frontal gyrus) (Zhu et al. 2018). Relationship status seems to influence mortality risk. Individuals who are single have higher risk of mortality than those in a relationship (Scafato et al. 2008).

Individuals in a stable relationship often perceive their sexual relationship to be safe, secure, and stable. Stable relationship possibly gives rise to the belief of low risk of acquiring sexually transmitted disease. This reason might be responsible for low perceived risk of human papillomavirus (HPV) infection in women, who are in monogamous stable sexual relationships (or have fewer sexual partners). These women often resist or avoid HPV vaccination (Thompson et al. 2017). All these evidences support that relationship quality and stability are more important than relationship status for subjective well-being.

Evolution and Relationship

Relationship status can be seen from an evolutionary angle as well. It has been seen that pair bonding and romantic love has played a role in the evolution of the human race. Romantic love serves as a mode for commitment, which in turn helps in pair bonding of humans. The life history of humans says that this commitment gives an investment to rear children. These long-term pair bonds have helped in the evolution of social

intelligence and large brains. It was seen that romantic love is universal and it suppresses the need for search of other mates and also promotes better health. This leads to successful pair bonding. Phylogenetics suggests that monogamy goes back to the *Homo erectus*. The societal structure of modern humans has been dependent on this pair bonding. Even the metabolic requirements of large brains were dependent on pair bonding. Though there have been challenges to this proposition in the form of polygamy, divorce, infidelity, and arranged marriages, it has been seen that in the vast majority of the human culture the concept of romantic love and pair bonding remains true (Fletcher et al. 2015).

Understanding evolutionary background, enables us to conceptualize the factors that influence “stability of relationship”. Relationship alternatives that can be tempting can pose a threat to the commitment of the relationship. It has been suggested that not only do overt characteristics play an important role but also that hidden cues have a role as well. Evolutionary psychology gives new predictions regarding processes in the mind about increasing reproductive success. Research shows that levels of fertility in women have helped in describing characteristics that can be alluring for a prospective male partner and thus can also be a threat to long-lasting relationships. Thus, evolutionary theories of mating are also important in understanding the maintenance of long and stable relationships (Miller and Maner 2010).

Conclusion

Relationship status of an individual gives an idea about his/her social as well as psychological well-being. Relationship status can be better understood by knowing the quality and stability of the relationship.

Cross-References

► [Vigilance over Kin's Romantic Relationships](#)

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Relationship Violence

- **Men’s Violence Against Female Partners: The Role of Culture**

Relationships

► Dyadic Processes

Relative Brain Size, Encephalization Quotient

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Definition

The encephalization quotient is a between-species measure of relative brain size, operationalized as the ratio of actual to predicted brain mass for a given species relative to body mass. This indicator is used in comparative analyses involving different species as an index of cognitive ability.

Introduction

The comparative study of the neural substrates of cognition has demonstrated to be more elusive than previously thought, with epistemological and methodological caveats that create the conditions for tireless disagreements among researchers within and between fields of study for which neuroanatomical or brain activity measures are central variables or potential correlates. This entry will deal one such neuroanatomical measure, specifically the encephalization quotient.

Review

Overview

As neurological data that permit comparing across species or populations are difficult to collect at the physiological level (Striedter 2005), most studies use neuroanatomical measures instead of brain activity indicators. However, confounding factors such as body size have forced researchers to spend more time studying the relative validity and accuracy of diverse measurement approaches rather than analyzing the connection between neuroanatomical measures and cognitive and behavioral traits. Other confounds also exist: for example, even though such traits have been found to be evolutionarily labile, the distribution of neuroanatomical traits in primates and other mammals appears to have been highly conserved through phylogenetic history (i.e., with little lability within clades; Kamilar and Cooper 2013). Thus, it is argued that analyses to test hypotheses of coevolutionary ties between neuroanatomical and other variables should be conducted only after controls for the confound of phylogenetic history. This is a realization that has been increasingly taken into account in the last two decades, with findings from earlier evolutionary studies of the brain being more likely to be confounded with phylogenetic inertia.

Brain Size, Brain-Body Size Ratio, and Encephalization Quotient

Big brains do not necessarily mean complex cognition (e.g., such as in the case of blue whales, *Balaenoptera musculus*). Thus, brain size on its own is an inaccurate estimate of psychological processes. Brain-body mass ratio was proposed as a solution to the conundrum by endorsing the notion that the *proportion* of the volume of the brain in comparison to the rest of the body was the actual predictor of behavioral and mental traits (Kappelman 1996). Nevertheless, this ratio also created new problems; for example, it was found that smaller species exhibited larger brains in proportion to their body mass.

Jerison and Barlow (1985) proposed the encephalization quotient (EQ) as an alternative for estimating brain size while taking into account

body mass. The EQ was conceived as the observed brain volume divided by the expected brain size for a species of a particular body mass. Furthermore, it took into account the estimated surface of allometric growth of the animal studied (i.e., $2/3$ in the case of mammals) permitting the construction of the following formula:

$$EQ = \frac{\text{brain mass}}{(0.12 \times \text{body mass}^{(2/3)})}$$

Here, 0.12 is a constant of average growth. Thus, the emphasis of the measure lied neither on the actual brain volume nor in the ratio between brain and body size but rather on the brain size that was *expected* for an animal of a particular body mass. With this, animals of disparate sizes such as mice, rats, and baleen whales displayed expected EQ values in accordance with the mammalian regression line.

EQ exhibits important limitations however. Chief among them are the drastic differences on the steepness of the regression line after including few species in some analyses and removing them from others. Humans are arguably the clearest example of this, suggesting that the evolutionary pressures on brain size in the human lineage differed starkly from the average pressures that occurred throughout primate history. By settling on a regression line in the estimation of EQ, one is assuming that all taxa included have been subjected to similar regimes of selection for brain size evolution. Outliers (such as humans among extant primates) are eliminated in order to meet the assumptions of traditional statistical analyses and must therefore be considered separately. Running an analysis for an outlying datapoint, such as *Homo sapiens*, is by definition impossible. A solution, in order to examine humans' place in the EQ scale, is to consider it in the context of data from closely related extinct species such as *hominins* (Falk et al. 2000).

EQ is further limited by the fact that close taxa have similar body sizes. As a consequence, distantly related species will exhibit different scaling exponents. Thus by including or removing a clade, the computations of EQ and its correlation

to other variables can be altered depending on the degree of relatedness among the clades in question. To address this, Jerison and Barlow (1985) encouraged the construction of multiple regressions lines, where each line corresponds to a specific clade in the sample.

The Size of Specific Brain Regions as Alternative Neuroanatomical Measures of Cognition

Some researchers have endorsed the use of alternative neuroanatomical volume indicators and statistical techniques as proxies for intelligence (e.g., Shultz and Dunbar 2010), rather than simply using the suggested post hoc solutions to EQ. A current and popular option is to collect size data from a specific brain region hypothesized to be involved in complex cognition. Any confounding effects produced by the size of other areas can be removed when studying a single area of interest, either before or during analyses, for example, by creating a ratio of their sizes or entering the sizes of the other variables as control variables in a regression model. It is important to note that, if nonlinear relations are expected, the ratio approach should be avoided. It is important to note that in this approach, an assumption is made that brain evolution occurs in a modular fashion, where each region is hypothesized to be subjected to different selective pressures in the ecological conditions of each taxon (Barton and Harvey 2000). Hence, for example, studies interested in the neuroanatomical correlates of executive functioning and cognitive complexity have analyzed the volume of the neocortex across species.

Even though measures based on region size in comparison to overall brain volume have the benefit of automatically also controlling for the confounding effects of body size, using a raw estimate of the region's volume and residualizing the region's volume against body size itself (rather than against the size of the rest of the brain or of other regions) has also been proposed as an alternative (Deaner et al. 2007). A less strict alternative involves including body size as another predictor in the regression equation, achieving to control for allometric effects without restricting the proportion of variance in the sample.

Conclusion

The difficulty in comparing the predictive validity of these different methods of neuroanatomical measurement stems in part from the lack of reliable indices of nonhuman animal intelligence. In other words, there is no established standard measure of cognition to compare the neuroanatomical measures against. Major disagreements exist on what laboratory tasks or naturalistic observations of behavior to use as indicators of cognitive abilities (Reader et al. 2011), and debates still exist on whether such abilities should be conceptualized as independent or aggregated under a general intelligence factor (Burkart et al. 2016).

Alternatives to neuroanatomical volume measures exist for explaining cognitive evolution; however, they are comparatively underexplored, and testing their validity also suffers from this same limitation. Possibilities include gyrification of the cortex (i.e., the formation of circumvolutions that compact more gray matter in less volume), neuronal myelination and the associated speed of transmission, and neuronal and glial cell densities throughout the brain. While these variables are unlikely to fully explain interspecies variation in cognitive abilities, they should be considered *in addition to* neuroanatomical volume measures.

Cross-References

- Brain Size and Intelligence
- Convergent Evolution of Intelligence
- Convergent Evolution of Intelligence Between Corvids and Primates
- Evolution of Intelligence, The
- General Intelligence Factor *G* (Reader, Hager, and Laland, 2011)
- Intelligence Testing
- Intelligence Versus Natural Selection
- Nonhuman Intelligence

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Relative Parental Investment

- Parental Investment and Sexual Selection (Trivers Foundational Theory)

Relative Sex Distinction

- Kinship Distinctions According to Sex

Relatives

► [Family](#)

Relativism

► [Standard Social Science Model](#)

Relevance of Evolved Interests to Modern Morality

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Synonyms

[Metaethics](#); [Motivational states promoting survival and reproduction](#); [Normative ethics](#)

Definition

Evolved interests are attitudinal states that motivate us to act in ways that typically enhance the prospects for survival and reproduction. Modern moral systems and the state-sponsored legal institutions of enforcement to which they give rise suppress the fitness-diminishing instinctual interests that may have served to amplify the individual fitness of our hominid ancestors.

Introduction

Our behavior is rooted in motivational psychological states such as wanting or desiring. Such content-bearing attitudinal states, although quite

specific for each individual, can be more generally described under the rubric “evolved interests.” These seemingly ubiquitous interests include, but are not limited to, amicable relations with others (cooperation), aversion to harm (flight or fight), finding someone with whom to have and raise children (mating), acquisition of the resources required for survival (food), and a buffer against unforeseen or intolerable environmental conditions (shelter).

Now it is obvious (but important to note) that for one to want or desire something, such as decadent pastries or someone else’s spouse, it does not thereby entail that one has a genuine interest in indulging such appetites. Noshing on copious amounts of sweets is known to have deleterious effects on one’s health, and compromising otherwise good health is typically considered wrong. This is, for instance, why parents give out sweets to their children only on special occasions. Similarly, the revelation of an extramarital affair can have dire consequences ranging from costly divorce proceedings or social stigmatization to physical violence and even murder.

The Explanatory Promise of Evolutionary Psychology

The allure of a neo-Darwinian picture of human evolution is that it promises the conceptual resources with which to explain not only the alignment of motivational states and evolved interests but also the disconnect between them. Some stage-setting is in order here. It is necessary to state at the outset that *evolved* interests are determined as such only by way of reference to the fitness-bearing individuals that comprise a population in a particular environment. What is ultimately of interest to individual members of a population (or the genes that they carry), from the evolutionary perspective, is survival and reproduction. Any behavior or behavioral capacity that enhances prospects for survival or is conducive to increased fecundity is an evolutionary adaptation insofar as it has been naturally selected

for fitness-enhancement. Notice that the psychological motivations that prompt adaptive behavior can exhibit significant variation. It matters not whether one does the right (adaptive) thing for the wrong reason; consequences measured in terms of relative inclusive fitness are the evolutionary metric of importance.

How, then, can the occasional disconnect between currently held beliefs or desires and evolved interests be explained? Evolutionary explanations typically proceed by distinguishing between the selective pressures at work on our hominin ancestors during the Pleistocene and those facing modern humans. Small heterogeneous tribes of hunter-gatherers have given way to large stratified societies. These diachronic changes have placed very different demands upon human decision-makers. When our desires happen to contravene what is actually in our best interests, the mismatch is accordingly attributed to the dissimilarities in these environments. A well-worn example involves our craving for sugary or fatty foods. Such foods were rare or difficult to attain in ancestral environments and thus highly prized sources of energy. The brains of our hominin predecessors associated strong positive sensory responses with the intake of fatty or sweet foods, which promoted and reinforced the expenditure of additional effort to acquire them. In the developed world, however, calorie-rich culinary delights abound. Only with painstaking effort are we able to avoid overindulgence and many tragically succumb. This evolved interest is a critical factor in the causal story behind epidemic levels of obesity in First World Nations.

Morality as an Adaptation

Morality presents a particularly interesting and perplexing case for this evolutionary narrative about our evolved interests. With language comes a heightened ability to coordinate collective action, and there are undoubtedly great benefits (e.g., division of labor) that accrue from robust social organization. But, as evolutionary game theorists are fond of reminding us, there remains incentive to behave selfishly when it comes to

collective endeavors, the rewards of which are equally distributed (Maynard Smith 1982). If one's duplicity can go unnoticed, it pays to be a "free rider." Moral codes are deployed to encourage cooperation and license the punishment of those who would attempt to cheat a social system. Hunter-gatherer life was such that tribal members were often closely related to and quite familiar with one another. This type of social arrangement makes the evolution of cooperation more likely than it would otherwise be since there are repeated encounters among the members of a tribe and expectations of reciprocation remain fairly reliable. It is, in short, exceedingly difficult to shirk one's interpersonal duties and have such behavior repeatedly go unnoticed or unremembered. There would be a strong intergenerational incentive to teach, learn, and abide by moral codes for the group and individuals alike. In such an environment natural selection would tend to favor psychological capacities and neurophysiological mechanisms that function to encourage cooperation and other prosocial behaviors. Mechanisms like kin selection and reciprocal altruism could work in tandem with cultural transmission to effectively suppress selfish incentives.

As group size increases, however, a rational agent will become less likely to cooperate to secure the benefits of repeated direct reciprocation. Interaction between any two agents will on average be less likely and information regarding the character of any particular individual, whether attained via hearsay or recalled from memory, typically more unreliable. Furthermore, the extent to which individuals are genetically related dwindles. Large stratified societies are now commonplace. Accounts of genuine moral disagreement regarding what we should do and how we ought to live abound in these modern social arrangements. Whereas it was once in our evolved interest to abide by tribal morality because doing so increased the inclusive fitness of individuals, changing social environments since the Pleistocene apparently enable a decoupling of fitness and utility (Sterelny 2003). Competing normative prescriptions now proliferate among — *as well as within* — societies and the specter of rampant moral relativism looms large.

One way to restore social cohesion and resist defection from a moral code is of course to codify normative prescriptions in the garb of religious tradition. In many religious traditions, there is reference to the existence of deities. These supernatural figures often have the role of punishing, whether in this life or the next, those who would transgress religious mores. The prospect of such divine reckoning presumably provided yet another way to ensure social cooperation in accordance with accepted norms. Even if one's self-interested (free riding) behavior could escape the notice of neighbors and their retributive practices, eluding the ire of an omnipotent and omniscient deity is another feat altogether. A propensity to reify the divine might in this sense be depicted as a social adaptation insofar as it strengthens the tendency to cooperate among those who share beliefs. As an unfortunate but telling corollary, it also lends to more fervent disagreement when groups with dissimilar belief systems begin to cohabit, since they are all the more committed to the objective authority of their moral beliefs.

There are seemingly insuperable problems with invoking a deity to bolster the efficacy of a moral system. Most notable, perhaps, is a dilemma introduced by Plato in his dialogue the *Euthyphro*. He therein asks whether what is good (or right) is so merely because it is willed by the gods or whether the gods will it because they have some sort of insight into its being good. On the former horn, even what appear to be morally reprehensible acts would have been good had the gods seen fit to stipulate them. The good is thus by definition equivalent to what the gods will. If so, however, a believer must accept a tautology in place of a substantive theory of morality: If the good is that which the gods will and that which the gods will is good, then that which the gods will is that which is willed by the gods. This is an empty truism. The will of the gods becomes arbitrary rather than beneficent; the doctrine of the goodness of god is reduced to nonsense. Recourse to the latter horn of the dilemma fares no better. If the gods somehow determine what is good by way of divine reason or omniscient insight, morality must be independent from, and exist prior to, the will of the gods. Believers are damned to ponder why the

gods have chosen the moral principles that they have (Rachels 1986).

Somewhat surprisingly, an evolutionary account of morality faces a similar dilemma. Plato's query resurfaces in something like the following manner: Is morality as we know it the result of natural selection on a highly contingent species-specific set of conventions for ensuring social cooperation, or has natural selection endowed human cognition with the capacity to grasp objective moral truths? Even thinkers quite sympathetic to evolutionary moral psychology are split on the answer. Those who find the idea of objective moral truth suspect hold to the former alternative. Moral skeptics, for example, begin by pointing out that human origins are entirely neo-Darwinian and materialistic (i.e., explicable solely by reference to physical-chemical processes and other naturalistic phenomena). They contend that our moral standards and intuitions, even our consciences, evolved because they were effective survival devices. Morality helped to ensure cooperation, which tended to enhance the prospects for survival and reproduction. Survival devices are not, however, reliable indicators of the truth. Cognitive and perceptual mechanisms and the behaviors which issue thereupon need not be perfect. Even highly unreliable indicators of external circumstances can sometimes suffice for avoiding detrimental outcomes. Moreover, it seems as though humans have no other characteristics that can help in the discovery of moral truth. As a consequence of the foregoing argument, it is impossible for humans to discover or even make reliable progress towards moral truth (see discussion in Richards 2000, pp. 203–211).

Moral antirealists urge an even stronger claim that flatly rejects the existence of any objective moral truths. The most contentious premises are those which claim that (i) survival devices are not reliable indicators of truth and (ii) that humans have no other means by which to discover moral truths. For the moral realist who is sympathetic to a story of human origins along neo-Darwinian lines, it is not obvious that the opportunistic character of selective explanation should make us cynical about the prospect of moral truth (Fitzpatrick 2015). While traits or characteristics

are often selected for one purpose, traits might well be retained for other purposes or even changed during the evolutionary process. Perhaps we have the moral capacities that we do because they are conducive to truth, despite the historically contingent origins of such prosocial capacities. Natural selection accordingly “tracks the truth,” and being true (or closer to the truth) is what makes one moral scheme “better” or “more fit” than another. Those who hold true beliefs and theories are more likely to thrive. So, argues the moral realist, it is not out of the question that we have capacities that at least allow for the perception of moral truths.

Do moral standards or personal intuitions about right and wrong exhaust our moral insight? Here, too, naturalistically inclined moral realists think otherwise (Shafer-Landau 2012). At minimum, humans have the ability to reason. Evolution via natural selection has left us with certain cognitive inadequacies that systematically lead us astray. Research in behavioral economics under the heading “biases and heuristics” has revealed many of these. Among the best known is the susceptibility to confirmation bias (e.g., Wason’s selection task). We tend to search for, interpret, and preferentially recall information that favors preexisting beliefs, while neglecting relevant information that can undermine the veracity of our beliefs. More important to the moral realist, however, is that we have been able to discover such species-wide unreliability through the use of reason. Much of a formal education consists of alerting students to such biases and teaching them how to reason correctly in spite of these tendencies. Why should matters be any different in the moral domain? We clearly appeal to metaethical (justificatory) standards when assessing competing ethical claims. When moral intuitions give rise to unsavory or inconsistent implications, we recognize that something is amiss. If this does not qualify as a resort to reason, it is unclear what would.

Conclusion

While metaethical debate still rages, it is well worth reminding readers that it does so more

than ever within neo-Darwinian confines (e.g., under the auspices of evolutionary psychology or behavioral ecology). Inquiry into moral disagreement and potential resolutions must at least acknowledge evolutionary cognitive endowment. Perhaps the most promising aspect of this approach is that it includes an empirically testable element: the search for gene networks (or mental modules) associated with the propensity to believe in the objectivity of morality. That both an avowed moral skeptic/antirealist and an agent without so much as an inkling of metaethical commitment share the sentiment that physically harming an infant is morally repugnant and worthy of severe punishment makes it plausible that this propensity is “a collective illusion of the genes” (Ruse 2002; Joyce 2006). Metaethical views apparently make no difference to actual moral behavior in such a case. It is compelling testimony to the power of the propensity to objectify moral truth that even a moral skeptic/antirealist should instinctively feel this way (Stamos 2008, pp.168–175).

Common to the adherents of conflicting moral systems is the devout belief that their normative principles are the right or true ones. Most cling to the idea that moral truth is a matter of discovery rather than social construction. In the end, their (evolved) interest in doing so may prove to be more telling than the contents of their various axiological commitments.

Cross-References

- ▶ [Cheater Detection](#)
- ▶ [Cooperation](#)
- ▶ [Cultural and Moral Relativism](#)
- ▶ [Cultural Transmission](#)
- ▶ [Dangers of Evolutionary Ethics](#)
- ▶ [Evolution and the Theory of Games](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolution of Morality](#)
- ▶ [Evolved Moral Foundations](#)
- ▶ [Genetic Influences of Puberty](#)
- ▶ [Genuine Altruism](#)
- ▶ [Kin Selection](#)
- ▶ [Mismatch Between Evolved Morality and Modern World](#)

- [Nonhuman Reciprocal Altruism](#)
- [Philosophical Foundations for a Modern Morality](#)
- [Wason \(1966\) Selection Task](#)

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Reliability and Deception in Language

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Synonyms

[Costly signalling](#); [Deceit](#); [Honest signalling](#);
[Honesty](#); [Reputation](#)

Definition

In general terms, honest signalling theory seeks to explain what keeps animal communication an

honest and reliable indicator of health, condition, and genetic quality in the face of many incentives for deception.

Introduction

Many commentators on animal communication and human language evolution have suggested that several aspects of language can be characterized in terms of honest signalling theory. Granted, although the complexity of language and human social interactions make plausible the suggestion that human utterances may have many parameters that could conceivably be assessed by receivers, I nonetheless selectively focus here on the most evidence-based proposals current to the honest signalling literature. Namely, the particular honest signals to be reviewed here include three related areas of research: (1) voice pitch, (2) vocabulary size, and (3) unfavorable social reputation.

Human Language and Honest Signalling Theory

In human social interactions, there are many motivations for deception, as people want to make the best possible impression (to appear important, dominant, intelligent and trustworthy) while others want to know if they accurately and reliably signal and possess these qualities. As language is perhaps the most salient and elaborate of human signalling systems, many recent attempts have been made to characterize aspects of language according to honest signalling theory. In general terms, honest signalling theory seeks to explain what keeps animal communication an honest and reliable indicator of health, condition, and genetic quality in the face of so many incentives for deception (Searcy and Nowicki 2005). Although honest signalling will be described in fuller detail in the following discussion, for present purposes, I firstly define language here as the uniquely human biological capacity for complex vocal imitation – the ability to imitate complex multi-syllabic vocalizations – including the cognitive, anatomical, physiological, and genetic systems that underpin human speech (Fitch 2010).

Honest signalling is ubiquitous throughout the animal kingdom in many different competitive, and occasionally cooperative, social interactions. For instance, in animal mating competitions, males of the most superior genetic quality, health, or physical condition also tend to display the most exaggerated sexual ornaments and weaponry (Andersson 1994). The female peahen's affinity for the male peacock's large and showy tail is often cited as the prototypical exemplar of sexual advertisement, as the male pays a cost as an assurance of its honesty: only those peacocks of adequately high health, vitality, and genetic quality can afford the most exuberant, burdensome tails in the face of mating competition, female choice, and predation (Andersson 1986). Sexual advertisement, in this sense, is defined as an honest signal of genetic quality or social status which increases the probability of reproductive success (Searcy and Nowicki 2005).

That said, though honest signals are often found in cases of sexual advertisement, they need not necessarily be found solely within this context. By definition, the primary criterion for honest signals in animal communication is cases in which the interests of signallers and receivers conflict (Searcy and Nowicki 2005). Accordingly, evolutionary biologists typically associate honest signals with particular costs which ensure their reliability, generally grouped into two basic categories: receiver-dependent costs (i.e., those that reflect agonistic, mating, and social costs) and receiver-independent costs (i.e., those that reflect underlying physiology including production, development, and maintenance costs) (Searcy and Nowicki 2005). Although some have argued that the latter type of honest signal – sometimes referred to as an index – is a special case that can be explained without reference to a particular cost, other studies have suggested that index signals fit squarely within the conventional framework of honest signalling theory. For example, receiver-independent production costs would include the considerable time, energy, and increased predation risk of many vocalizations (e.g., calling frogs, singing birds, or roaring red deer as an indicator of body size, health, or genetic fitness) (Searcy and Nowicki 2005), while receiver-dependent social

costs would include the increased aggression due to badges of status (e.g., variable facial patterns in wasps as an indicator of social dominance) (Tibbetts and Dale 2004). For present purposes, I adopt this more conventional definition of honest signalling theory and presume that honest signals can often be associated with a detectable cost.

With respect to human language, many commentators have suggested that several aspects of language can be similarly characterized in terms of honest signalling theory. Granted, although the incredible complexity of both human language and human social interactions make plausible the suggestion that human utterances may have *many* parameters that could conceivably be assessed by receivers, perhaps more than most animal calls, I nonetheless selectively focus here on the most theoretically-sound, evidence-based proposals current to the honest signalling literature. Namely, the particular honest signals to be reviewed here will include the associated receiver-independent development, production and physiological costs of (1) voice pitch and (2) vocabulary size, as well as the receiver-dependent social cost of (3) unfavorable reputation.

More specifically, some have suggested that many suprasegmental features of language, such as voice pitch, may have evolved as an honest signal of sexual attractiveness, social dominance and genetic fitness, with concurrent costs including suppressed immune function as well as risky social and sexual behavior, due to the masculinizing effects of testosterone (Puts et al. 2016). Alternatively, others have proposed that vocabulary size may have evolved as an honest signal of human intelligence and should therefore be attractive to prospective mates, with concurrent costs including the effort necessary to amass a large vocabulary as well as the cognition required to store and retrieve words in memory – as a receiver-independent cost (Miller 2000; Lange et al. 2014; Oesch *in revision*). Lastly, others have argued that human honest signalling theory should emphasize social status and influence, with the concurrent cost including the risk of unfavorable social reputation in an information-based society – as a receiver-dependent cost (Silk et al. 2000).

According to this honest signalling proposal, reliable indicators of biological condition and genetic fitness may have evolved once a rudimentary system of protolanguage was already in place (Dunbar 2009). Although the original biological function of human language remains hotly debated, most authorities are nonetheless in general agreement that honest signalling is thought to be a secondary function – as it is for most animal communication – which evolved at a later stage in the evolution of language (Dunbar 2009; Oesch 2016; Oesch *in revision*). By analogy to a previous example, the original biological function of feathers was and likely continues to be for thermoregulation (and flight) (Bock 2000), in spite of the fact that iridescent peacock plumage nonetheless secondarily functions as sexual advertisement in mating contexts (Andersson 1986). The original biological function of language, it has been argued at least by some authorities, is that language initially evolved for social bonding in large human communities (Dunbar 2009; Oesch and Dunbar *in revision*). In the context of human language evolution, this distinction is often more technically referred to as the difference between *direct* and *derived* functions (Millikan 1984). In simple terms, the direct function generally refers to the primary adaptive significance of language (e.g., social bonding, cooperation, cultural learning), having deep ancestral origin and which thereby directly aided the survival and reproduction of the human species, relative to other ancestral hominids which did not evolve language (Oesch and Dunbar *in revision*). By contrast, the derived function refers to any secondary, more specialized adaptive function(s) of language (e.g., voice pitch, vocabulary size), having more recent ancestral origin (once some form of language was already in place), but which also contributed to the survival and reproduction of the human species (Oesch 2016; Oesch and Dunbar *in revision*).

Voice Pitch as an Honest Signal

The human voice is a rich and nuanced source of information for listeners. In addition to

functioning as the primary medium of communication in spoken language, in its nonlinguistic role, the human voice has the ability to convey biological information like sex, age, height and weight, emotional states, social dominance, and even social categorizations such as race (Puts et al. 2016). For example, the primary perceptual correlate of voice pitch, also known as the fundamental frequency (F_0), is approximately half as high in men as it is in women, thereby providing information relevant to sex determination (Titze 2000). Moreover, the sexual attractiveness of a particular voice may be related to a number of speaker-specific physical and social assessments. Human voice pitch, similar to other phenotypic traits relevant to mating, such as facial symmetry, may be a reliable indicator of condition and biological quality in humans (Puts et al. 2016). Attractiveness, as a general topic, is of further interest for many reasons, and one major perspective is that human physical attraction drives the selection of mate partners. For vocal, as opposed to physical, attractiveness, this theory is supported by a body of research linking vocal traits to human sexual dimorphism that have likely undergone intense sexual selection in humans (Puts et al. 2016). For instance, vocal attractiveness has been shown to be correlated with both body attractiveness and facial attractiveness in both men and women (Puts et al. 2016). That said, active debate and research currently exists as to whether the most important influence on such sexual dimorphism was due to intersexual selection (male and female choice of the opposite sex) or intrasexual selection (competition between members of the same sex for access to the opposite sex) (Puts et al. 2016).

Nonetheless, at a proximate physiological level of explanation, this consistent relationship between facial and vocal attractiveness, at least in men, is likely mediated by the masculinizing effect of testosterone across many dimensions of human genetics, development, anatomy, and behavior (Puts et al. 2016). Moreover, producing a low-pitched voice in men – due to differences in length and tension in the vocal folds of the larynx – is believed to be costly, since testosterone, which lowers male voice pitch during puberty, is

associated with suppressed immune function as well as risky social and sexual behavior (Puts et al. 2016). Low-pitched voice in men, due to its association with testosterone, may provide a reliable signal of immunocompetence and genetic quality, long-term health, physical strength, reproductive potential, and in traditional societies, reproductive success (Puts et al. 2016). In addition, both men and women use lowered voice pitch in order to assess social dominance and leadership behavior, as well as trustworthiness (Puts et al. 2016). For example, male corporate chief executive officers (CEOs) with deeper voices often manage larger, wealthier companies, while male candidates for elected public office with low-pitched voices also appear to have better election outcomes. Given these findings, it is perhaps not surprising that women generally prefer men with more masculine, lower pitched voices especially near ovulation, and when evaluating short-term, sexual relationships (Puts et al. 2016).

In women, high voice pitch may signal low testosterone and/or high estrogen levels. Moreover, women's voices are judged more attractive by men mid-cycle and voice pitch increases as women near ovulation when estrogen levels are high. Higher pitched female voices are further associated with attributions of femininity and youth, though they apparently seem to be more closely tied to femininity (Puts et al. 2016). In general, current research on men's preferences for vocal dimorphism in women has found that men prefer more feminine or higher pitched voices (Puts et al. 2016).

Apart from these relatively straightforward features of human mate choice, there is at least some suggestion that voice pitch may also be a reliable indicator of even more complex aspects of human sexual behavior, including conformity to community speech norms. For instance, at least one recent study has found that men may attribute high infidelity risk to overly feminized women's voices, whereas women may attribute high infidelity risk to overly masculinized men's voices (O'Connor et al. 2011). This suggests that voice pitch may be used as an indicator of sexual strategy in addition to underlying mate value. Accordingly, the aforementioned attributions may be

adaptive if they prevent cuckoldry and/or loss of parental and relationship investment through the avoidance of partners who may be more likely to be unfaithful (O'Connor et al. 2011).

That said, although some voice pitch features of masculine or feminine traits may reliably indicate positive attributions in the speaker, they may also, at times, reliably indicate negative attributions. For instance, masculine men are more likely to be attributed potentially antisocial traits, such as dominance and dishonesty. Men with masculine traits are also generally more interested in pursuing short-term than long-term relationships. In addition, men with high levels of testosterone have been shown to invest fewer resources in their partners and offspring. Taken together, these findings suggest that although some masculine characteristics are associated with traits that are desirable in a mate, such as long-term health, immunocompetence, and genetic fitness, other features may be associated with traits that are not so desirable in a mate, such as low parental and relationship investment.

Lastly, recent investigations to determine whether men and women can intentionally manipulate vocal attractiveness have produced equivocal findings, but unquestionably indicate that both sexes often modulate their voices when speaking to attractive members of the opposite sex. Both men and women often appear to intentionally raise their voice pitch in order to express confidence and intelligence. At a perceptual level, listeners should be further selected and/or learn to detect vocal modification, given that misattribution of speaker traits such as attractiveness, dominance, and intelligence can be costly to the listener. Evidence for this proposal is also equivocal: as listeners can often accurately discern deliberately modified speech, such vocalizations nevertheless also seem to positively affect listeners' evaluations of these traits, suggesting that even when detectable, vocal modulation can often remain effectual, at least in some contexts.

Such intentional modification of voice pitch has clear potential benefits. For instance, individual variation in voice pitch can potentially influence the mate choice decisions and social attributions made by others in the local

environment, such as success in a job interview and political voting behavior. That said, although humans may be able to intentionally modify vocal pitch to emphasize or deemphasize various acoustic traits with meaningful variation in some limited contexts, such modifications nevertheless fit squarely within the constraints imposed by the many mechanical and anatomical limits on coherent vocal production (Pisanski et al. 2016). In other words, while some deliberate modification may be possible at the margins, the consistent and reliable wholesale “faking” of these traits, universally across most contexts, seems unlikely.

Vocabulary Size as an Honest Signal

Although many current hypotheses have attempted to explain the evolution of language (Fitch 2010; Oesch and Dunbar *in revision*), few proposals are able to explain why humans have such large, expressive vocabularies. De facto, no other species apart from humans are able to take a finite series of elements – conservatively between 15,000 and 30,000 word families for an educated, native adult speaker of English – and combine them into an enormous pattern of possible arrangements, all of which carry well-defined meanings. Curiously, this quality is a puzzling feature of human language, as natural selection does not usually favor costly, wasteful, exuberant traits. In general, nonhuman primate societies typically manage complex social interactions with comparatively fewer distinct calls. Nonetheless, a plausible explanation of this apparent redundancy is that large vocabularies could be used to demonstrate intelligence, and by approximation, biological fitness to potential mates (Miller 2000). By comparison, female birds have been shown to respond to greater song production, song rate, and repertoire size produced by males of the same species, which also have greater lifetime reproductive success. Bird song repertoire size has been further suggested to be reliable indicator of age, learning ability, brain size, health, nutritional condition, intelligence, and general fitness. In humans, a large body of psychological literature has similarly found that intelligence has the

highest heritability of any adult cognitive ability and that positive correlations exist between general intelligence, symmetry, and developmental stability, suggesting that intelligence could be a reliable indicator of heritable fitness.

Moreover, both twin and genetic analyses have shown that expressive vocabulary at ~24 months is modestly heritable ($h^2 = 0.16\text{--}0.38$), while large twin studies have reported a steady increase in the heritability of language-related factors during development from adolescence ($h^2 = 0.55\text{--}0.66$) through middle adulthood ($h^2 = 0.70\text{--}0.80$) (Spinath and Gottschling 2015). In particular, adult vocabulary size has been noted to differ quite dramatically among people, is at least 60% genetically heritable (even though every word in an individual’s vocabulary is learned) (van den Berg et al. 2004), and has about an 80% correlation with general intelligence (Trzaskowski et al. 2013). Moreover, intelligence has been established as one of the single most important traits desired in a long-term partner for both men and women (Plomin et al. 2013). Studies have also found that people in long-term relationships usually have vocabularies of similar sizes (Plomin and Deary 2015). Further evidence for this hypothesis has shown that men do indeed use more low-frequency vocabulary in the presence of attractive women (Rosenberg and Tunney 2008) and that the display of low-frequency vocabulary is attractive to both sexes, especially in the context of long-term relationships, suggesting that vocabulary size is in fact a reliable indicator of heritable mental fitness (Lange et al. 2014; Oesch *in revision*). On the other hand, as few studies have been done to determine if low-frequency vocabulary can be modified in the same way as volitional vocal pitch manipulation, (i.e., whether or not low-frequency vocabulary can be “faked,” as a deceptive proxy of intelligence in the same way as vocal modulation), the potential context-specific nature of this trait remains an open question. Clearly, the answer to this question would be contingent on whether the manipulator was aware of the potential benefits from using low-frequency vocabulary, “knowing of” a particular word while being simultaneously unfamiliar with its actual meaning, and the listener being

savvy enough to recognize its out-of-context usage. In this case, deceptive use of low-frequency vocabulary could be effectual as a context-specific signalling device.

Reputational Consequences of Dishonest Signalling

In the animal communication literature, deception refers to the act in which the signaller (or speaker) may benefit from the breakdown of the normative relationship between the signaller attribute or referent and the actual nature of the external world, while the receiver (or listener) may incur a significant cost from this misrepresentation (Searcy and Nowicki 2005). In more informal terms, deception has been defined elsewhere as “the projection, to one’s own advantage, of an inaccurate or false image of knowledge, intentions, or motivations” (deWaal 2005, p. 86). Chimpanzees, for instance, have been observed using deceptive nonverbal signals in the wild, as well as deceitful sign-language mimicry in trained conditions (deWaal 2005). Of course, whether any such acts of deceit constitute deliberate or intentional deception remains an open question (deWaal 2005). Nonetheless, punishment and the enforcement of sanctions against uncooperative or deceitful behavior have further been reported to occur in several social species; for example, in social insects in social dominance contexts (Tibbetts and Dale 2004), in rhesus macaques who find food covertly and withhold calls of the discovery (Hauser 1992), and in geladas from cuckolded males (le Roux et al. 2013).

In humans, other commentators have similarly suggested that human honest signalling theory should emphasize social status and influence, with concurrent costs including the risk of unfavorable reputation in an information-based society (Silk et al. 2000). More specifically, some have argued that nowhere would this phenomenon be more salient among traditional and modern societies than in the context of honest linguistic communication, given the potential costs of unfavorable social reputation and implementation of

strict social sanctions against lying and deception (Oesch 2016; Oesch *in revision*). Indeed, given so many clear incentives to deceive, often in the interest of manipulating rivals, many investigating the evolution of language have questioned how linguistic communication can remain primarily honest in the everyday use of language (Fitch 2010). One possible explanation, as noted above, is the risk of negative reputation and/or social sanctions against lying and deception (Oesch 2016; Oesch *in revision*; Silk et al. 2000).

Some indirect support for this proposal seems to suggest individuals could be wary of the potentially unfavorable social consequences of lying. For example, research has revealed that individuals seem to be much more inclined to deceive when the potential stakes are quite high, as for example when attempting to advertise to prospective mates, suggesting a context-sensitive signalling device (Toma et al. 2008). For instance, one study of online daters in New York City found that 87% of men and 76% of women lied about at least one attribute in their personal profiles; men tended to increase their height, whereas women tended to lower their weights (Toma et al. 2008). Deviations from truth were generally quite small in magnitude, however, suggesting that individuals were at least partially aware of the possible social repercussions from being discovered as deceitful (Toma et al. 2008).

Furthermore, previous findings have also revealed that lying and deception are relatively rare occurrences in the general population (Serota et al. 2010). For example, Serota et al. (2010) found, in a sample of 1000 Americans, the average number of lies told per day was 1.65. Moreover, the distribution was highly skewed; 22.7% of all lies were told by 1% of the sample, and half of all lies were told by 5.3% of the sample. Studies conducted in controlled laboratory environments have obtained similar results (Abeler et al. 2012). Granted, although the finding that lying is infrequent does not necessarily imply concern over negative reputational consequences, it would certainly be consistent with this argument.

Moreover, recent experimental work has shown that dishonesty can and often does indeed have unfavorable consequences on a person's social reputation (Oesch [in revision](#)). For instance, in a recent vignette-based study of dishonest protagonists in a hypothetical courtship scenario, dishonest protagonists were rated significantly lower on a 7-point Likert scale on the personality dimension of reputation, in addition to the dimensions of intelligence, pleasance, warmth, sexual attractiveness, dating desirability, relevance, and prestige. In effect, deception was shown to be ineffective strategy, insofar as the lies are made public, due to lower ratings on reputation as well as various personality dimensions included in the study. Accordingly, the findings supported the hypothesis that the high prevalence of linguistically honest information, in the everyday use of language, may have emerged as a socially or sexually selected handicap. In other words, truth-telling may be an honest signal of prosociality, trustworthiness, and social status with respect to alliances as well as mate choice, with concurrent costs including the risk of unfavorable social reputation.

Finally, social psychologists typically characterize human deception according to four different types of lying: (1) *prosocial*, lying to protect someone, or to benefit or help others; (2) *self-enhancement*, lying to save face, avoid embarrassment, disapproval or gain an advantage; (3) *selfish*, lying to protect oneself at the expense of another and/or to conceal a misdeed; and (4) *antisocial*, lying to hurt someone else intentionally (Iñiguez et al. 2014). In many cases, it is often useful to distinguish between two general types of lies: prosocial lies of type 1 and antisocial lies of types 2–4. Of these two general types, it is widely recognized that antisocial lies are destructive of relationships, whereas prosocial lies often help to keep relations in good condition (Oesch 2016). Therefore, as with voice pitch, while some intentional acts of deception may be possible, and even adaptive, in certain contexts, the normative and successful application of this strategy across many different circumstances seems less likely (Oesch 2016).

Conclusion

In conclusion, current research indicates that language can be aptly characterized in terms of honest signalling theory and further described by reliable and deceptive approaches to human social interaction. First, it seems clear that many supra-segmental features of language, such as voice pitch, may have evolved as an honest signal of sexual attractiveness, social dominance, and genetic fitness, with concurrent costs including suppressed immune function as well as risky social and sexual behavior, due to the masculinizing effects of testosterone (Puts et al. 2016), as a receiver-independent cost. Second, there is also emerging evidence that vocabulary size may have evolved as an honest signal of human intelligence and is thereby attractive to prospective mates, with concurrent costs including the effort necessary to amass a large vocabulary as well as the cognition required to store and retrieve words in memory, as a receiver-independent cost (Lange et al. 2014; Oesch [in revision](#); Rosenberg and Tunney 2008). Third, it seems further clear that honest signalling theory may alternatively emphasize social status and trustworthiness, while simultaneously discouraging widespread deception, with the concurrent cost including the risk of unfavorable social reputation in an information-based society, as a receiver-dependent cost (Silk et al. 2000).

There also remains the open question of whether voice pitch, large vocabularies, and other fitness indicators can be used to deceive others into inferring an individual has better fitness than they do in actual fact. For example, it is certainly conceivable that dishonest individuals might attempt to exaggerate others' impressions of their intelligence by intentionally using large vocabularies in the presence of those that they want to impress. However, apart from the fact that adult vocabulary size is largely heritable (van den Berg et al. 2004), and therefore difficult to convincingly fake, the deceiver would have to: (1) be aware of the fact that low-frequency vocabulary is attractive in the first place and (2) convincingly use the words correctly and appropriately to

the situation. Given that most potential acts of deception probably do not consistently satisfy both these criteria appears to make this possibility unlikely (Oesch [in revision](#)). In addition, if deceivers do attempt to manipulate potential romantic prospect's assessments of their fitness through deception, we should expect individuals to have evolved some effective countermeasures against these misleading displays (Cosmides and Tooby 1992). Furthermore, as we have seen here, the potential reputational impacts, coming from any discovered acts of deception, make this possibility even more unlikely. Consequently, though it is conceivable such deception may be an effective strategy within short-term interactions, it is unlikely to be convincing over long-term relationships.

Cross-References

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Reliability, Efficiency, and Economy

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Definition

Reliability, efficiency, and economy are criteria for adaptations attributed to George C. Williams.

Introduction

In the classic textbook *Adaptation and Natural Selection* (and to some extent in his *Natural Selection*), George C. Williams (1992) provides an account for when a biological trait is an adaptation. Establishing such an account, for Williams, is a “matter of basic importance” (Williams 1966, p. 8), as it would help to properly distinguish between traits that constitute bona fide adaptations from traits that just happen to be advantageous to the organism.

(This was an important distinction for Williams, as he thought traits should be classified as adaptations only once all other credible alternative explanations have been ruled out (Williams 1966, p. 11).) This entry sketches the three criteria for adaptations – reliability, efficiency, and economy – that are generally attributed to Williams and then presents one way in which these criteria have been further discussed in the literature.

Criteria for Adaptations

For Williams, an adaptation is best understood as a “function,” designed for bringing about some “goal” (Williams 1966, p. 9). The goal, in this case, is to “promote the success of an individual organism” (Williams 1966, pp. 96–97). It is generally thought that Williams puts forward three criteria for when a given trait can be classified as an adaptation: reliability, efficiency, and economy (Cosmides and Tooby 1997; Buss 2015). Consider these in turn.

Efficiency refers to the idea that adaptations achieve their effects in a (near) optimal manner. So, if a given trait increases an organism’s chances of survival and reproduction, but does so in a (significantly) less than optimal manner, it is not to be classified as an adaptation: only if the trait is (near) optimal in the production of its effects should it be seen as an adaptation. For an example, consider the length of time male dung flies mate (about 35 min – Parker 1978). It is not unreasonable to think that this length of time maximizes the males’ expected reproductive success (Parker 1978). Given this, the dispositions that cause male dung flies to mate for about 35 min qualify as possible adaptations. By contrast, if the mating time of the males were significantly different from 35 min (i.e., significantly different from its optimal value), the mating dispositions of males should not be classified as adaptations.

Not only must a trait be efficient to count as an adaptation, the trait must also promote survival in a way that is *reliable*. A trait is reliable if it is found in most organisms within the population and performs “dependably in the contexts in which it is designed to function” (Buss 2015,

p. 16). Consider a scenario in which fleetness develops only in a small subset of springboks and does not effectively provide a means of escape from cheetahs; in other words, suppose cheetahs pose a significant threat to springboks as they can outrun most of the latter – and even those that could run faster than the cheetah often fail to do so (e.g., for lack of energy or agility). In this case, we should not regard this trait as an adaptation. However, if fleetness were to regularly develop in most springboks and provide a reliable means for evading predators, then it would satisfy the reliability criterion.

Lastly, for a given trait to count as an adaptation, it must be *economical*. That is to say, the trait in question must solve an adaptive problem in such a way that the benefits outweigh the costs. For instance, fleetness does not constitute an adaptation if springboks exert so much energy that they die of starvation every time they successfully escape from cheetahs. Note that this is not to say that adaptations must be *perfectly* economical (e.g., that springboks incur no cost whatsoever from evading predators) (Williams 1966, p. 204). All that matters is that these costs are *minimized* – not that they are zero.

At this point, a quick note of caution is in order. While the criteria of reliability, efficiency, and economy are often attributed to Williams (1966) (see e.g., Buss 2015; Cosmides and Tooby 1997), it is not clear that Williams actually subscribed to them (at least as they are commonly understood). Williams himself is mostly concerned with assessing the extent to which a given trait can be seen as designed, and he uses the above criteria (or related ones, such as precision) merely in an informal manner (Williams 1966, pp. 10–11). So, for example, he writes: “In this book I will rely on informal arguments as to whether a presumed function is served with sufficient precision, economy, efficiency, etc. to rule out pure chance as an adequate explanation” (Williams 1966, p. 10).

Given this, it may be better to see the criteria of reliability, efficiency, and economy as *inspired* by the work of Williams, rather than as actually *defended* by the latter. However, be that as it may, there can be no doubt that these criteria have proven extremely influential in the

evolutionary biological and evolutionary psychological literature. Furthermore, since it is the content of the criteria that is important, rather than who (first?) defended them, historical questions concerning the formulation and defense of these criteria will not be discussed further here. Instead, what is of more interest is to consider one of the ways in which these criteria have been further developed and analyzed.

Further Developments

One of the most important ways in which Williams’s criteria have been further developed concerns the literature surrounding optimality models as methods for identifying adaptations. For example, Orzack and Sober (1994) accept the outlines of the above remarks concerning efficiency, economy, and reliability, but then go on to refine and expand these criteria. Roughly, they argue that a given trait can be seen to be an adaptation only if a model *restricted to the operation of natural selection alone* (a) accurately (in a standard statistical sense) predicts the value of the trait, and (b) there are no significant phenotypic differences in individual organisms in this population (Orzack and Sober 1994, p. 370). In other words, Orzack and Sober (1994) are notable for making precise Williams’s idea that genuine adaptations should be seen to be traits that are (near) optimal in terms of efficiency and economy of operation and which reliably develop in the relevant population of organisms.

However, it is also important to note that Orzack and Sober’s (1994) account is not without its detractors. In particular, Brandon and Rauscher (1996) have argued that Orzack and Sober’s (1994) account does not take into account the possibility that *other restricted models* (e.g., ones restricted to the operation of drift) can also accurately predict the value of the relevant trait. Similarly, Godfrey-Smith (2001) has argued that a trait can be seen to be an adaptation even if not all members of a given population have it. For these reasons, the status of Orzack and Sober’s (1994) account – and of Williams’s criteria more

generally – must be seen as a matter of current debate. However, what also needs to be noted is that there can be no doubt that these criteria have sparked much important discussion and that they continue to be taken very seriously in evolutionary biology and evolutionary psychology (see, e.g., Buss 2015).

Conclusion

George C. Williams's criteria of adaptations sparked an ongoing discussion about the nature of adaptations and their role in evolutionary biology and related fields. While not uncontroversial, the criteria of adaptations generally attributed to Williams – efficiency, reliability, and economy – have undoubtedly contributed significantly to our understanding of adaptations and the nature of natural selection.

Cross-References

- [Adaptation and Natural Selection](#)
- [George Williams](#)

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Religion

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Synonyms

[Belief](#); [Faith](#); [Religiosity](#); [Worship](#)

Definition

A system of faith and worship typically composed of animism of inanimate objects and sometimes of a superhuman controlling power that may or may not be a personal God or gods and with its own set of moral injunctions.

Introduction

Despite the wide array of both past and present cultures and the incredible variety among them, religion seems to be part of our evolutionary heritage (Schmitt and Fuller 2015; Wilson 2002). Granted, some religions are monotheistic whereas others are polytheistic, and some religions, although not all, believe in a high god creator of the universe. Nevertheless, despite this apparent variability, religions do share some near universal features. Explaining the existence of these beliefs has been a goal of the interdisciplinary field known as the cognitive science of religion, a field that encompasses both the evolutionary psychology and evolutionary anthropology of religion. The major question regarding the field is whether religion itself is a mechanism selected by natural selection to solve a particular adaptive problem, or if it is merely a by-product of a lion of different psychological mechanisms such as agency detection. This section will explore the main theories regarding the evolutionary origins of religion. It is important to bear in mind that specifics of different religions will not be

addressed. Instead, only near universal features of religion will be discussed.

Near Universal Features of Religion

When one hears the word “religion,” it is instinctive to think about Christianity, Islam, Judaism, Hinduism, or other of the most well-known religions. These are known as world religions, and they actually have more in common than meets the eye. Most cultures and their respective religions share a common narrative about the origins of humanity, invoke supernatural agents, signal in-group loyalty through organized public affirmation of religious beliefs, ascribe animistic agency to nonhuman, mysterious sources, and distinguish between morally sacred and morally profane thoughts, beliefs, and actions (Schmitt and Fuller 2015). Nevertheless, it seems not all of these near universal characteristics evolved simultaneously. We do not know if some of these are sufficiently ancient for biological evolution to have shaped them for a particular purpose. In other words, some religion-related adaptations may have evolved before the emergence of organized religion as we know it, whereas others are modern inventions (Kirkpatrick 1999). For instance, Peoples et al. (2016) found that animism was the oldest trait of religion across a wide sample of hunter-gatherer societies. Other traits such as belief in the afterlife followed by shamanism emerged shortly after and were still present in most societies. Ancestor worship, which appeared later, was no longer found in many of the societies studied. Finally, belief in high gods was the most recent and least common characteristic, suggesting that these were absent in early humans. This emergence of religious characteristics over different periods of time makes it even harder to distinguish whether some aspects of religion are indeed adaptations selected through natural selection to solve a particular problem, or if they are by-products of other psychological mechanisms. Given that the debate is still ongoing, this section will describe both stands on religion, that which argues

religious belief is an adaptation and that which argues it is a by-product.

Religion as an Adaptation: Society as Organismic

The main theory arguing for religion as an adaptation views religion as organismic (Wilson 2002). Religious believers often compare their communities to a single organism that can work similar to individuals in the harmony and cooperation of their parts. Simply put, religious groups may work like social insect colonies. Organisms are a product of natural selection that acquires properties that enable them to survive and reproduce through variation. If religious groups are organismic in this sense, particular groups may have evolved because their properties proved more adaptive than the properties from other groups.

For instance, imagine a flock of birds. Selection at the level of the gene would involve birds varying in the degree to which they alert other birds of approaching predators. An individual bird does not gain anything by alerting other birds of danger, unless the surrounding birds are kin and share genes with the caller. Instead, a hypervigilant bird may be detracted from feeding by spending more time scanning the horizon, and by drawing attention from predators. As a result, these callers are less likely to survive and reproduce than non-caller birds. Generations later, the remaining birds are the descendants of non-callers.

An organismic theory, on the other hand, would argue that a group composed of mostly non-caller birds could face possible extinction and that natural selection would favor groups of *callers* over groups of non-callers. In this case, suppose there are two different flocks. The first flock is the one described above, in which the new generation is mostly composed of selfish birds that will not alert others of predators. The second flock is formed of mostly callers, with a few non-callers. When danger comes, the first group will have few or no birds alerting. Even if there are a

few callers, chances are predators will get these birds first since raising an alarm makes them an easy, conspicuous target. At one point, the group will be out of callers to raise alarms, and the unsuspecting birds will become another animal's meals and go extinct. The second flock, however, has better odds at surviving as a group. Because most birds are callers, some will die when alerting others, but some will also survive and further reproduce. The "caller" genes will be passed on to future generations, and the flock will likely live on.

But how do flocks of callers and non-caller birds compare to humans and religion? First and foremost, it is important to remember that humans are social animals. Our ancestors would not have lived long had they not realized that cooperation was a reliable method to survive. To support this idea, Wilson (2002) mentions how current hunter-gatherer societies are strong units of selection and egalitarianism. Meat is usually shared among all members of the community, with the best hunter and his family getting no more meat than others. Additionally, it appears many hunter-gatherer societies do not have leaders, aside from those who have earned the respect of other members by being models of good conduct and advise. Such egalitarian utopia seems counterintuitive to the concept of the selfish gene, yet even members in these societies are likely to have selfish impulses. The reason why they do not act on these impulses is because they are effectively controlled by other members of the group, a form of guarded egalitarianism known as *reverse dominance*. In many animal groups, the strongest individual is usually capable of dominating any rivals, but in hunter-gatherer tribes, any individual who attempts to dominate the rest is likely to encounter combined resistance. Even the strongest individual would be no match for the collective strength of the group and could instead be punished for these dominance attempts. Examples of reverse domination range from gossip and ridicule to ostracism and assassination. With such costly consequences, individuals are better off by simply cooperating and following the group's social norms.

Mechanisms that promote the welfare of the group as whole without demanding extreme sacrifice from its members would further reinforce adherence to social norms. It is here where religion and superstitious beliefs come into place. Wilson (2002) describes the case of the Chewong, a hunter-gatherer tribe that resides in the rainforest of the Malay Peninsula and that functions on egalitarianism like many other hunter-gatherer societies. Equal distribution of food and resources is governed by a system of superstitions known as *punen* in which not satisfying an urgent desire results in calamity. Actions that may result in a state of *punen* include not inviting someone to share food brought back from the hunt, and not sharing gathered goods when these were obtained from far away regions or when these are scarce.

Belief in the *punen* system conveys great advantages, and it is probably not by mere coincidence that the actions that may result in calamity have to do with food sharing. If a gatherer had to go very far to obtain a resource, then such resource must be shared with everyone, whereas if the resource is close to the settlement, individuals are allowed to keep whatever amounts they gather on their own. Such rules make perfect sense from an evolutionary perspective; forcing others to share resources that can easily be acquired would not convey any advantages because anyone would be able to gather these anyway, whereas sharing resources that were hard to obtain increases the chances of survival for those individuals who would have never been able to acquire these goods by themselves. Additionally, if all members truly believe that calamity will befall those who do not share, then they are more likely to obey any injunctions imposed by the group.

Overall, fear in a higher, punishing force or entity ensures compliance and obedience. Groups with such altruistic beliefs like the Chewong would have been more likely to cooperate and aid each other than groups with selfish beliefs, and because cooperation in a hostile environment is essential for survival, tribes with selfish systems would have disappeared. In this sense, like a beehive that works as one single organism because all

its parts work together to ensure survival, religion serves as an adaptation that allows humans to function as a coherent whole.

Religion as a By-product: From Hyperactive Agency Detection to Mating and Attachment

Though an interesting theory, Wilson's (2002) proposal of viewing society as organismic and religion as an adaptation that allows groups to function as a whole is not an idea that goes unchallenged. Selection at the level of the gene rather than within-group selection is a major key idea in evolutionary studies. Furthermore, one must consider other possible explanations and assess which one can do a better job at explaining the wider array of phenomena that religion has to offer. As Buss (2002) states, "Explanations for some religious phenomena, such as rituals and rites, may fail to account for other phenomena such as piousness or prayer." In order for a religion-specific mechanism to have evolved, it would have had to solve a particular adaptive problem faced by our ancestors, yet religion encompasses such a diverse amalgamation of beliefs and behaviors that is highly unlikely that it is the product of a single adaptation. Additionally, as discussed previously, many features of religion are too recent to have been shaped by natural selection and thus work as an adaptation. Finally, any hypothesis on the evolutionary origins of religion should not assume the existence of yet other unexplained mechanisms. An argument that religion evolved to ameliorate fear of death begs the question as to why humans would be built to even fear death in the first place (Kirkpatrick 1999). Finally, as Tooby and Cosmides (1992) state, our cognition resembles a confederation of hundreds of functionally dedicated computers, each designed to solve one particular problem faced during our evolutionary history. There is not one single general purpose computer capable of solving several adaptive problems at once. It is unlikely that religion is *the* computer in charge of creating cooperative behaviors among social groups, solving humans'

fear of death, monitoring sexual conduct and reducing promiscuity, preventing immoral actions, and so forth. Instead, the idea that religion is a by-product resulting from numerous domain-specific psychological mechanisms is perhaps more plausible and could help explain the myriad near universals that were described at the beginning of this section.

Because our minds evolved to process the world in ways that are adaptive rather than truthful, our cognition is prone to the occasional systematic error. For instance, it seems humans come equipped with mechanisms for categorizing and reasoning about the natural world (Kirkpatrick 1999). These include reliably distinguishing animate from inanimate objects, invoking different principles of inference such as causal reasoning, and ascribing goals, desires, and motives to people and objects displaying certain patterns of motion. Sometimes, these mechanisms may be misapplied beyond their intended domains. For instance, humans tend to have what is known as a hyperactive agency detection device. This device allows us to assume agency in inanimate objects, which may have been adaptive during our Pleistocene years, as confusing a rattling branch for a snake and avoiding it did not present costs to survival, whereas ignoring a rattling sound could lead to death if such sound did, in fact, turn out to be a snake. It is generally safer to mistake an inanimate object for an animate one, yet when these mechanisms are taken a step too far, an individual may ascribe agency and even anthropomorphize inanimate objects. As mentioned previously Peoples et al. (2016) found that animism or attributing a soul to plants, inanimate objects and natural phenomena was the oldest and most common religious characteristic found across a wide sample of current hunter-gatherer societies. These findings suggest humans are particularly prone to assign some form of life or essence to objects.

Social exchange and kin-related mechanisms are also manifested in religious beliefs and practices. Ancestor worship, reciprocal altruism, promotion of social cohesion and cooperation, and subordination of individuals' self-interest to that of the group are other common characteristics of

religions (Kirkpatrick 1999). Worshipping dead ancestors reflects kin altruism, as the living attempt to help the dead in the afterlife by burying artifacts and possessions while asking for help and guidance with their own worldly affairs. Attempts to enforce altruism do not end there, as many religions promote prosocial behavior beyond blood ties through the widespread use of kinship terms such as calling other members “brothers and sisters” or calling a priest “father.” Promoting deities that monitor cooperation and altruism and punish those who do not abide by these rules may also be an encouraging method for promoting prosocial behavior.

Additionally, altruistic and kin mechanisms can be observed not only in how people interact with each other and with their ancestors, but also in how they interact with the supernatural forces that they believe control nature, be it a high god or other entity. If a deity is perceived as kin, then attachment mechanisms may become activated. Perceiving God as a fatherly figure or as a caretaker plays on the attachment system by which the caregiver is sought as a haven of safety, particularly during times of danger. If a deity is not perceived as kin, interaction with it should be guided by the same principles of reciprocal altruism. Such seems to be the case given practices in which individuals offer deities different forms of offerings (e.g., impressive and massive monuments, works of art, and a variety of sacrifices) with the intention of gaining favors (e.g., good harvests, military victory, a place in heaven) from these high-status forces. In general, supernatural beings across religions tend to resemble humans, albeit with some “super” characteristics added. Deities may be ubiquitous or have the power to control some aspect of nature, but they otherwise display the full range of standard human emotions, desires, and motives, which is why interactions between humans and deities operate under the same psychological mechanisms as interaction amongst humans.

One final mechanism worth mentioning that seems to come into play in religion relates to mating and controlling others’ sexual behavior. As Buss (2002) points out, religious doctrines

frequently target mating and sexual behavior. When it comes to sociosexuality, religion has tried to regulate aspects such as when conception should take place, the age at which intercourse should begin, how many sexual partners an individual is allowed to have, the moral standing of premarital sex, and so on (Schmitt and Fuller 2015). According to the reproductive religiosity model (Weeden et al. 2008), heightened religiosity is often adaptively used by religious groups to discourage sexual permissiveness. Discouraging unrestricted sex is beneficial for males in that it decreases the chances of being cuckolded, and it is also beneficial for females in that it helps ensure their husbands will not abandon their long-term commitments to themselves and their offspring. Several studies suggest a link between religiosity and measures of permissive sexuality. For instance, Strassman et al. (2012) found that religions that were stricter in forcing females to signal menstruation and had higher levels of mate guarding had higher chances of paternity certainty.

Another aspect of religion as a device for mating is that religious leaders are often males who hold power and resources, which are important for females when looking for mates. Buss (2002) explains that religious leaders use their power to gain preferential access to fertile women. In native Greenland, for example, a woman would be considered fortunate if the Angekokk or prophet offered his sexual caresses. Similarly, the religious leaders among the Tachtadshys in Lycia could have sexual intercourse with any women they fancied during the yearly religious assemblies, and virgins among the Zikris were believed to be cleansed if they had intercourse with the high priest. These examples show how religious leaders had better access to females than the average man, which in turn increased their reproductive success.

Conclusion

The evolutionary origins of religion are still unknown, and religion is composed of such a plethora of phenomena that it is hard to separate

one aspect from the other. Although it is tempting to believe religion is an adaptation, it seems to be involved in one too many aspects of the human psyche to have evolved to solve a particular adaptive problem. Additionally, several aspects of religion seem to have evolved across time, with some practices such as burying the dead emerging before others such as belief in high gods or injunctions on moral sexual behavior. If religion did evolve as an adaptation, it could be possible that later components (e.g., belief in a punishing deity to ensure compliance to norms imposed by the group) were added to it because humans realized the value in them.

Cross-References

- [Adaptation](#)
- [John Hartung \(1995\) Love Thy Neighbor](#)
- [Joseph Henrich on Religion](#)
- [Moral Instincts and Morality](#)
- [Religion and Religious Beliefs](#)
- [Religious Teachings](#)

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Religion and Development of Civilization

- [Moralizing Gods and the Rise of Civilization](#)

Religion and Religious Beliefs

- [Religious Teachings](#)

Religion and Sexuality

- [Religious Teachings](#)

Religiosity

- [Joseph Henrich on Religion](#)
- [Religion](#)
- [Religious Beliefs](#)

Religious Beliefs

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Synonyms

[Religiosity](#); [Sacred values](#); [Spirituality](#); [Superstition](#)

Definition

Mental representations of rites, tenets, and supernatural agent concepts derived from psychological processes and cultural inputs.

Introduction

Religious beliefs are both a product of natural selection and cultural evolutionary processes. Aspects of our evolved psychology, including certain cognitive by-products, underlie counterintuitive beliefs and supernatural agent concepts. Combinations of religious beliefs spread through competition between groups over the course of human history. Gradually, combinations of supernatural beliefs, tenets, and rituals that were increasingly effective at instilling deep commitment, reinforcing group solidarity, and sustaining large-scale cooperation became prominent among human societies (Atran and Henrich 2010).

Supernatural Agents and Counterintuitive Beliefs

Belief in supernatural agents plays a central role in both religion and religious ritual. Religions often invoke supernatural agents to reinforce values and moral principles, and to deal with distressing existential anxieties, such as loneliness, calamity, and death. Supernatural agents come in many shapes and sizes; there are malevolent and predatory deities as well as benevolent and protective ones. The cognitive mechanisms underlying the perception of agency act as a precursor for supernatural agent concepts, which are then modified by cultural transmission (Atran and Norenzayan 2004). Yet, what makes certain religious beliefs so memorable, especially beliefs concerning supernatural agents, is that they are *minimally counterintuitive* – they subtly violate our expectations about the world (Atran 2002; Atran and Henrich 2010).

Religious beliefs are counterintuitive because they violate universal expectations about how the natural world works. Counterintuitive concepts facilitate the recall and transmission of cultural information and also reinforce the underlying knowledge that can be inferred from them (Atran and Henrich 2010; Atran and Norenzayan 2004). The inclusion of a few minimally counterintuitive elements gives a story an advantage over other stories with either no counterintuitive elements or an overabundance of counterintuitive elements by

making the story more memorable for the learner (Atran and Norenzayan 2004). For example, the presence of a few counterintuitive concepts in a narrative, even within a list of otherwise ordinary concepts, improves memory recall for the entire narrative or list (Norenzayan et al. 2006). This suggests the existence of a “sweet spot” for the inclusion of counterintuitive concepts; there is an optimal balance of how much these concepts conform to and violate our intuitive assumptions about physical, biological, and psychological phenomena. That is, the presence of an optimal amount of such concepts can confer a mnemonic advantage to a set of beliefs – increasing their transmissibility. As far as *minimally counterintuitive* supernatural beliefs are concerned (e.g., belief in supernatural agents), they must be outlandish enough to capture attention, but natural enough to still make sense. Religions further propagate counterintuitive beliefs through ritualistic behavior, music, dancing, and other rhythmic coordinations of affective body states.

Cognitive mechanisms underlie supernatural agent beliefs (gods, ghosts, ancestor spirits) as evolutionary by-products. Natural selection did not, in all likelihood, select for the capacity for supernatural beliefs per se, but rather selected the underlying psychological processes involved with the perception of agency. Agency-detection mechanisms once served other adaptive functions (e.g., predator avoidance, identifying other humans) and have been repurposed by cultural inputs to incite supernatural concepts. Because of its utility in helping ancestral humans to overcome recurrent evolutionary obstacles, such as the threat of predation, agency-detection is a prominent psychological mechanism and is biased toward over-detection (Sanderson 2008). As a result, humans have a strong tendency to over-perceive agency and extend these intuitions about agency to many features of the natural world, such as the sun, elements, and other aspects of the environment. That is, humans often infer agency in natural processes where natural explanations are not available or not understood (e.g., weather patterns, lunar cycles, shifting tides; Atran and Norenzayan 2004; Sanderson 2008). Counterintuitive beliefs in supernatural agents (i.e.,

by-products of psychological adaptations and folklore) set the stage for the creation of powerful deities and moralizing high gods.

Moralizing High Gods

Beliefs in *moralizing high gods* are the product of psychological processes that facilitate belief in supernatural agents, coupled with cultural evolutionary processes that favored cooperation-enhancing beliefs. By the end of the Pleistocene (roughly 13,000 years ago), humans began transitioning away from seminomadic hunter-gatherer groups, coalescing into larger, sedentary populations in response to the advent of agriculture, population growth, intergroup competition, and warfare. These developments introduced somewhat evolutionarily novel challenges to humans living in large-scale groups, who now faced difficulties in coordinating behaviors among participating individuals, monitoring the actions of group members, preventing free riders from exploiting other group members, and facilitating large-scale group cohesion. For civilization to accommodate these new population constraints, it was necessary to invent and enforce beliefs in moralizing high gods that punished noncooperation and defectors within groups (Shariff et al. 2011). The central features of religions, such as moral guidelines, traditions, and the belief in one particular god or a specific pantheon of gods, have proliferated due to competition between different cultural groups, who each spread their respective religious beliefs and practices concerning moralizing high gods.

Costly Displays and Rituals

Rituals are a form of costly display that facilitates commitment to group ideologies, religious beliefs (e.g., belief in moralizing high gods), and shared values that promote solidarity and cooperation within groups (Atran and Henrich 2010; Atran and Norenzayan 2004; Henrich 2009). Costly displays can encompass a wide variety of complex, coordinated behaviors – from music and dance to

body modification, self-mutilation, and sacrifice. Such behaviors are “costly” because they are often time consuming, energy intensive, or dangerous. Though these behaviors may seem wasteful, harmful, or superfluous to an outsider, engaging in costly ritual displays confers an overall benefit to both the individual and the group by signifying commitment to a belief system and promoting group cohesion between individuals. These honest signals of commitment also encourage the adoption of supernatural beliefs, values, and customs that define a group’s culture.

Rituals both encourage and require the involvement of other group members and facilitate commitment to beliefs that promote group benefits, resulting in large-scale cooperation and group solidarity. Rituals promoted success in competition between other religious groups, because religious groups that engage in costly ritual behaviors bolster group cohesion. Religious groups with more costly rituals were more likely to survive over time than religious groups with fewer costly rituals (Henrich 2009). Differential group survival yielded a greater number of costly rituals across different competing religious groups. Rituals reinforce religious beliefs that manipulate our psychology to facilitate solidarity and commitment to the group, which in turn encourages group success (Atran and Henrich 2010; Henrich 2009).

Conclusion

Religious beliefs arise from a combination of evolved cognitive mechanisms, commitment-inducing rituals, and cultural evolutionary forces driven by competition between groups. Minimally counterintuitive beliefs in supernatural agents are by-products of our evolved cognitive mechanisms that create expectations about the natural world and cognitive adaptations devoted to the perception of agency. Cultural evolution, driven by competition among groups, spread such counterintuitive beliefs, rituals, and norms that ancestrally conferred an advantage to groups that adopted them. Civilization emerged with both commitment-

inducing rituals and the belief in powerful supernatural agents, such as moralizing high gods. Large-scale societies tend to incorporate beliefs in omnipotent supernatural agents that monitor and incentivize behaviors (e.g., rituals) that promote cooperation, strengthen faith, and facilitate solidarity in response to external threats. The wide variety of religious beliefs, rituals, practices, and institutions that we see today spread over time due to their ability to surmount the challenges posed by competition with other cultural groups and to sustain large-scale cooperation.

Cross-References

- [Credibility Displays](#)
- [Religion](#)
- [Sacred Values](#)
- [Scott Atran](#)

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Religious Building Design

- [Cathedral Acoustics](#)

Religious Teachings

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Synonyms

[Religion](#); [Religion and religious beliefs](#); [Religion and sexuality](#); [Reproduction](#)

Definition

Different religions have provided their followers with advices regarding reproduction, advertising both quality and quantity strategies in producing offspring.

Introduction

“The only purpose, the real purpose of every communion in love is the procreation, the birth of a child, although people who are in love are unable to conceive the nature’s treacherous way, casting over the actual act a shining veil”

Arthur Schopenhauer

Why do religions tend to “teach”? Irrespective of religions’ ecological origin or their philosophical foundations, almost all religions have specific teachings. Evolutionary psychology of religion may provide an insightful analysis of religious teachings and their social function in different settings. The universal tendency toward religious beliefs has remained a genuine puzzle for evolutionary scientists. The current consensus among many evolutionary psychologists is that religion originated, as a by-product, from the interaction of several evolved psychological mechanisms

(Atran 2002). This explanation may be applied to all religions and reflects an inherent component of human nature. All religions have specific (and sometimes quite strict) rules and teachings ranging from food taboos to sexual advices.

One of the universal aspects of religious teachings is reproduction. Almost all religions have sets of rules about reproductive behavior. Aside from exceptions and special circumstances, the religious rule of thumb is “the more, the better.” There are various verses in religious texts that encourage heterosexual marriage and subsequent reproduction in large quantities (e.g., Bible, 1:28). As a result, most religions are said to take a pronatalist standpoint (i.e., promoting human reproduction). Religions would promote child-bearing and parenthood as desirable for social reasons and to ensure the continuance of that very religion. There are numerous teachings and incentives for religious people to reproduce, for example, children are considered *a gift from God*. There are controversies regarding different religions’ stands on abortion and contraception (Ekmekci 2016); however, most religions limit or prohibit these practices, which is consistent with pronatalism.

In many traditional African religions, bearing a large number of children fulfills one’s mandatory duty to ancestors and indicates that those who produce large numbers of children have been favored by their ancestors (Caldwell and Caldwell 1987). Strong stigma is attached to childlessness, which is viewed as a punishment imposed by the gods or their ancestors on evildoers. Since women would be primarily blamed for the failure to produce offspring, mothers, in these cultures, might be privileged with particular status for giving birth to a large number of offspring. However, large numbers of children would lead to individually less buttressed offspring who are at higher risk of survival, so religions do not always encourage a large number of children, that is, fewer children with higher quality are also important for a religion to flourish and prosper (Atari and Chegeni 2016). In other words, religions teach both “quantity” and “quality” strategies in reproduction. In

terms of life history theory (see Del Giudice 2009), organisms have evolved to apportion their metabolic resources in an adaptive manner across the lifespan. For example, some species (e.g., humans) apportion most of their metabolic resources toward a few offspring that abundantly receive parental care; however, other species (e.g., cockroaches) allocate most of their resources toward the production of many offspring that receive little parental care. This trade-off, often operationalized as *number* versus *survival* of offspring, arises because parents have limited amount of resources to invest in reproduction. Neither strategy is better or worse than the other, as each has its own advantages and costs.

Evaluation of the impact of religious teachings on reproductive behavior may be better understood if classified into two levels of analysis: (1) the societal level and (2) the individual level. Religious teachings’ influences at a societal level are usually examined by demographers. At this level of analysis, religiosity of a society is linked to its fertility pattern and population. At the individual level, however, one’s extent of religiosity and its intrapersonal manifestations on reproductive behavior is analyzed, usually by psychologists.

Religious Teachings Regarding Reproduction at Societal Level

Generally, specific teachings to directly influence the proximate determinants of fertility are most typical of *the religions of the book*: Christianity, Judaism, and Islam (also known as *Abrahamic religions*). Research attention has largely focused on the teachings of these religions regarding contraception and abortion, the most notable proximate determinants of fertility in many modern societies. In short, these religions take a pronatalist standpoint and set restrictions on at least some of these fertility-related practices. The Roman Catholic Church took the clearest stand in forbidding most forms of contraception and any recourse to abortion (Noonan 1986). Yet, other

Christian denominations have gradually moved toward more relaxed perspectives on the issue of contraception while maintaining strong opposition to the practice of abortion. In Judaism, a somewhat similar process has occurred. Yet, Orthodox groups still uphold strict regulations on these issues. Abortion is considered sinful as it interferes with the *creationistic* ideology of monotheist religions.

The reproductive teachings of Islam seem a bit more complicated than those of Christianity and Judaism. Opposition to abortion and to at least some forms of contraception, particularly sterilization, has been expressed by many Islamic leaders (Hoodfar and Assadpour 2000). A baffling aspect of the Islamic teachings corresponds to the differences between the teachings of Islamic leaders and the lay perceptions of the Muslim (Underwood 2000). While analyses of religious writings and even surveys of religious leaders suggest general approval of fertility control, several Muslim populations have reported religious reasons for not practicing contraception (McQuillan 2004; Wusu 2015). These seemingly paradoxical findings point to the importance of examining the official position of Islam on such controversial topics.

Frequent emphasis on the importance of the family and a positive representation of large families may perpetuate higher fertility and lead religious individuals to believe that the practice of family limitation is contrary to God's will (McQuillan 2004). Islamic Revolution of Iran in 1979 showcases the manipulation of religious teachings and religious fertility policy by religious leaders. Just after the revolution, religious leaders strongly encouraged fertility by referring to religious texts and postulated that "the generation of the Islamic Revolution" should be multiplied; however, concerns with overpopulation stimulated the leaders to discourage large families in 1990s and early 2000s (see Atari and Jamali 2016).

Many religions have articulated other guidelines that have the potential to increase or limit fertility rates (i.e., stimulate "quantity" or

"quality" strategies). One example involves teachings regarding entry into sexual mateships. Limitations on minimum age of entry into mateships, number of spouses, and entry into subsequent sexual relationships after widowhood or divorce are typical of many religions. The second example involves prohibitions regarding sexual activity outside the officially recognized mateships. A third, less frequently discussed, example (McQuillan 2004) involves issues of sexuality within marriage. A number of religions have detailed rules concerning the timing and frequency of sexual relations between spouses.

Religious Teachings Regarding Reproduction at Individual Level

How can one's religiosity affect his or her reproductive behavior? Actually, that is a good research question which has received less attention than it really deserves, particularly from an evolutionary theoretical perspective. The relationship between reproductive strategy and religious beliefs is a vibrant field of investigation (Gorelik and Shackelford 2016; also see Fieder and Huber 2016). In very general words, individuals more strongly affiliated to religion have, on average, more children than less religious ones. One of the most notable evolutionary theoretical works on the association between religiosity and reproductive behavior is the reproductive religiosity model (Weeden et al. 2008).

A central claim of the reproductive religiosity model is that one of the primary functions of religious groups is to help tip the balance of the risks associated with monogamous sexual relationships (e.g., cuckoldry for men) in favor of high-fertility strategies. Individuals who pursue such monogamous strategies need increased assurances of commitment from their marriage partners. Religious individuals seek honest assurances by embedding themselves within sexually conservative communities that increase the social costs of, and reduce opportunities for, promiscuity. Religious groups do not simply show

disapproval for promiscuity; they express moral condemnation. Moralizations of this sort impose social costs on those who are noncompliant, damaging their reputations and ostracizing them. Moralizations of this kind serve not only to manipulate the cost–benefit equations for followers of the religion but also to discourage those with competing, disruptive strategies from affiliating with the group. Moreover, religious groups usually do not limit their moral enforcement to their own members but work to impose sexually conservative norms on their society, sometimes by organized political efforts (Weeden et al. 2008).

The reproductive religiosity model is consistent with suggestions by Buss (2002), in that they raise the possibility that people may be attracted to or repelled from religious affiliations by the fit between long-term reproductive strategies and traditional family morals and by the social support provided by religious groups. Atari and Chegeni (2016) found that religiosity is positively correlated with the desired number of children in a sample of young Muslim women, which is line with empirical findings of Fieder and Huber (2016) and Weeden et al. (2008).

Conclusion

Religions have provided their followers with a set of pronatalist teachings on why, when, and how of producing offspring. Importantly, religions seem to advertise both “quantity” and “quality” strategies because these strategies are responsive to different evolutionary problems and are required for a population to be fruitful and multiply. Two levels of analyses were discussed: societal and individual. At a societal level of analysis, demographers examine the role religiosity on fertility patterns of large populations. *Abrahamic religions* present specific pronatalist teachings regarding high fertility, in addition to restrictions on contraception and abortion. At an individual level of analysis, psychological mechanisms linking religious beliefs and reproductive behaviors are investigated. Individuals who score higher

on religiosity often desire (and produce) larger numbers of children.

Cross-References

- [Quantity Versus Quality of Offspring](#)
- [Religion](#)
- [Religion and Religious Beliefs](#)
- [Reproductive Strategies](#)

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Religious Terrorism

► [Suicide Terrorism](#)

Religious Views

► [Joseph Henrich on Religion](#)

Remating

► [Luring Hypothesis](#)
 ► [Mate Preferences After Having Children](#)

Reminiscence

► [Attention and Memory](#)

Repeated or Iterated Prisoner's Dilemma

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Synonyms

[Behavioral game theory](#); [Evolutionary psychology](#); [Human computer interaction](#); [Prisoner's dilemma](#)

Definition

Formalizing Strategic Interactions.

Introduction

In prisoner's dilemma, and its group-level version – public goods – players face a nearly identical problem of exploitation by free riders or defectors. Product-services like TripAdvisor, Airbnb, Uber, etc., all rely on continued feedback from their users to produce and share vital information in a game-theoretic format. These businesses are somehow able to dodge the free-rider problem that has puzzled economists for decades. While they may seem like commonplace practices to a customer, the underbellies of these large markets reveal subtle and sophisticated architectures interacting with behavioral research. A quick step back into the theory may help formalize why this is worth investigating.

Game Theory and Its Behavioral Ally

Game theory presents a set of powerful mathematical frameworks that has wide-ranging formal applications from genetic strategy, couples' dating scenarios, to international commerce and warfare. For example, game theory explains nuclear warfare where two equally armed players achieve a state of Nash Equilibrium preventing confrontation as well as disarmament (Lakoff 2007).

However, one common criticism of game theory (despite producing 12 Nobel laureates) is that it does not fully predict real-world observations, especially those involving human players. One potential explanation for this weak predictive power may be that most mathematical models assume “rationality” of players, whereas human players systematically violate mathematical and economic rationality in game-theoretic decisions (see Camerer and Lowenstein 2004).

Behavioral game theory examines human players' decisions in game-theoretic interactions, attempting to unlock psychological factors that

may explain the apparent disconnect between purely mathematical game-theoretic models and real-world human interactions (Camerer 2003).

Prisoner's Dilemma and Public Goods

Prisoner's dilemma (PD) was one of the first games to reveal the power of game theory in explaining seemingly puzzling phenomena (Davis and Holt 1993). PD formulaically explained why individuals and/or groups of individuals would actively make decisions that made them ultimately worse off. Alternatively, PD can also be applied to analyses of choices between selfish and socially desirable behaviors and conditions that influence individuals to choose in a specific direction.

In the basic form of PD, two individuals decide whether to cooperate or defect, leading to specific and known outcomes (C, D, W, and S; see below). Each individual decides independently and is blind to the other's choice. However, final payoff for each individual is ultimately contingent on other player's choice. If both players cooperate, each is better-off (C) than if both defect (D). If both players choose differently, the defector gains significantly more (W, winner's payoff) than the cooperator (S, sucker's payoff) (Table 1).

Outlining the mutual payoff matrix makes it clear that assuming player rationality (a common assumption in economics), it is always better for individuals to adopt a "selfish" strategy (Nash Equilibrium), therefore foregoing the mutually beneficial outcome. This discovery was quickly used as a justification for both rational and pure selfish behaviors in social life (for review, see Caporael et al. 1989), ignoring both the structural and generalizable qualities of in-game choice.

Repeated or Iterated Prisoner's Dilemma,
Table 1 Simple PD outcomes matrix

Player 1	Player 2		
		Cooperate	Defect
	Cooperate	C, C	S, W
	Defect	W, S	D, D

Note: $W > C > D > S$

Dawkins' selfish gene theory (1976) was and is often incorrectly implicated in these justifications despite his clear discouragement of it. On the other hand, opponents of this view often cite the thousands of experiments with actual human players that consistently defy rational self-interest (Camerer 2003). Current academic debate explores the reasons why humans seemingly violate expected rationality.

An extension of PD to a group-level interaction with N players is the public goods game (PG) (for other interpretations, see Kuhn 2014). PG is arguably more directly social as it formally models several real-life social interactions such as a group of individuals acting to conserve a visibly exhaustible resource or groups facing a trade-off between resource consumption and environmental conservation, etc.

Of the N players, each (i) has assets worth a_i from which they can contribute resource r_i ($r < a$) toward a shared good valued at v_i . Thus, any given player i 's payoff can be calculated as

$$a_i - r_i + v \left(\sum_k r_k \right) / N$$

This reveals that the economically rational strategy (payoff maximizing) for any player is to not contribute anything, regardless of what others do $r_i = 0$ (when $v < 1/N$). But does this translate to real life?

Evolutionary Mechanisms May Explain Game-Theoretic Violations

Individual user payoffs for services like TripAdvisor resemble PG. Individuals who use the service can leave feedback and tips for other users. This is the resource (r_i) they contribute for others to benefit from which includes their time and effort which are limited assets (a_i) in writing the review into the pool of reviews (v) which is a shared good. It is important to note that while individual expends time and effort, no promise of payback is given. Such a scenario dictates that no individual should ever leave a review ($r_i = 0$) and the survival and success of such a system

should therefore be very difficult if not impossible to achieve as it heavily depends on group-level cooperation between independently operating individuals.

So far, the TripAdvisor comparison shares the structure of formal interactions and the outcomes with PG, but there is one important difference. TripAdvisor offers subtle yet powerful *socio-evolutionarily salient rewards* to individuals who provide reviews, namely, individuals receive *peer appreciation* in return for reviews and tips that others find useful. Reviewers also build *reputation* and *social status* by accumulating reviews and continuing to build their profile. It is therefore theoretically arguable that traditional PD and PG analysis suffers from a lack of incentives that are present in the real world. Specifically evolutionarily salient incentives can be particularly powerful in shaping decisions. This could be one possible explanation behind the theoretically unlikely success of TripAdvisor, especially since various other services like Yelp and Wikipedia use a similar model. Evolutionarily salient incentives then can foster cooperation in PD and PG.

To Cooperate with Humans, Computers Need to Integrate Evolutionarily Salient Variables

An important application of evolutionarily salient factors in game-theoretic modeling is direct interaction between humans and computers. For instance, in traditional Indian culture, friends and families arrange a marriage between a couple (Ghimire et al. 2006); in modern Western and Indian societies, this function is more frequently performed by interactive computer systems such as online dating websites and mobile apps. As computers become more involved in human social life, it may become more important to design more socio-cognitively aware computer systems. Game theory provides an important framework to study how human players interact with computers.

As PD models essential aspects of human cooperative behavior (Axelrod and Hamilton 1981), it is interesting to note that several PD studies report that humans use socio-evolutionary

behavioral cues in decision-making (e.g., see Eckel and Wilson 2003). In the PD framework (also in other games), fMRI studies report that humans use specific brain regions to anticipate opponent mental states (theory of mind) when making interactive social decisions but use the same regions to a lesser degree when interacting with computers (Rilling et al. 2004). This is likely to have grave consequences for automation and robotics as humans cooperate less with computer players, reciprocate less, and tend to perceive them as less open and agreeable, compared to other human players (Rilling et al. 2004; Sandoval et al. 2015).

Humans are wired to be social, and we seem to use several social-cognitive mechanisms such as theory of mind to navigate through life. When computers are implored to take over a function, they are usually economical and accurate, but currently they lack social-cognitive efficiency. For computers to be smarter, they need to account for evolved social-cognitive functions.

Conclusion

Humans exhibit peculiar patterns in prisoner's dilemma gameplay, which models social behavior. Several socio-evolutionary factors are likely explanations for these peculiarities. In order for computational systems to better interact with humans, it may be important to acknowledge and integrate evolutionarily salient mechanisms.

Cross-References

- [Iterated Prisoner's Dilemma Model](#)
- [Theory of Mind](#)

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Replicating Entities of Culture

- [Memes](#)

Replication

- [Function of Reproductive Strategy \(Kurzban\)](#)

Representational Mental States

- [False Beliefs](#)

Reproduction

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Synonyms

[Asexual reproduction](#); [Sex](#); [Sexual reproduction](#)

Definitions

The process by which offspring are produced by their parents; in humans, reproduction is the combination of genetic material from two sexes, male and female, to produce offspring.

Introduction

While many of us may feel that we have a personal understanding of sex and reproduction, we rarely stop to consider how important the process of reproduction is to all life on earth. Reproduction is the method by which genetic material contained within an organism, whether it be within single-celled protozoa or in multicellular humans, is passed from one generation to the next. This movement of genetic material through generations is how evolution occurs; natural selection acts upon heritable differences between individuals and favors some genetic combinations over others. This makes how, when, where, and in many cases with whom you reproduce an especially significant question in evolutionary terms.

When we think about the concept of reproduction, we are usually thinking specifically about sexual reproduction. Sexual reproduction is ubiquitous, occurs in a large variety of taxa, and can be observed in single-celled organisms, plants, and animals. Sexual reproduction is the combination of genetic material from two different, distinct individuals that come together to create offspring that contain a full complement of that species’ DNA. Most organisms who sexually reproduce are diploid, meaning they carry two copies of

every chromosome in their somatic, or body, cells: one set they got from their mother and one set they got from their father. In humans, for example, all of our cells (excluding sperm and eggs) contain two sets of every chromosome; we have 23 pairs of chromosomes for a total of 46. For viable zygotes to be created, haploid cells (containing only one set of chromosomes from each parent) fuse together during fertilization to create a single diploid cell, which contains two complete sets of chromosomes (i.e., 23 pairs). These haploid sex cells are known as gametes, and in sexually reproducing species we define sexes based upon the size of an individual's gametes. The individuals in a species which produce larger, usually immobile gametes are referred to as females, and those who create smaller, motile gametes are referred to as males. For example, human females produce eggs that are many times larger than the sperm created by males.

Advantages of Sexual Reproduction

Sexual reproduction is ubiquitous in the natural world, which means that it must confer evolutionary advantages. One of the rather large benefits of sexual reproduction is a result of sharing genetic information between individuals, referred to as genetic recombination or simply recombination. Because each parent contributes a portion of the DNA needed to create a zygote, their offspring have a novel combination of genes that neither of their parents had. While this genetic shuffling may not seem very impressive on the surface, it opens the doors for many evolutionary benefits by creating new allele combinations and increasing genetic variety in populations (for a review of current hypotheses on the evolution of sex and genetic recombination, see Hartfield and Keightley 2012).

One benefit of sexual reproduction is the constant creation of genetic variety through recombination, which the Fisher-Muller hypothesis argues is better able to bring together favorable combinations of alleles than asexual reproduction (Hartfield and Keightley 2012). Sexual reproducers can combine beneficial genes into the same genomes through recombination, but for asexual reproducers to have two beneficial alleles

occur in the same line, each mutation has to arise independently in that line (which would take considerably more time and is also much less likely an occurrence). Sex can therefore create new combinations of genes and new phenotypes faster than asexual reproduction. Because recombination mixes genetic material, it can produce novel genetic combinations that may be more adapted to the environment than either of the parental genomes were.

Another benefit of sexual reproduction is that recombination purges deleterious mutations from a population. If one parent has many deleterious mutations and they mate with someone who does not, then it is possible due to recombination that their offspring will only carry some of the negative mutations they carried. Purging deleterious mutations from populations is important, as the higher a deleterious mutational load a population has, the more likely it is to go extinct (Hartfield and Keightley 2012).

Finally, sexual reproduction can also result in the complementation of negative recessive alleles (Hartfield and Keightley 2012). Complementation is the masking of a deleterious recessive allele by a dominant allele. For example, if a man who has cystic fibrosis, meaning he is homozygous recessive for the gene that causes the disease, has a child with a woman who is homozygous dominant for the allele which causes cystic fibrosis, then her functional copies of the gene will mask the dysfunctional copies in all of their children. None of their children will have cystic fibrosis because the dominant, functional allele compensates for the dysfunctional recessive allele.

Disadvantages of Sexual Reproduction

Although sexual reproduction appears to have many genetic and evolutionary benefits, it is not without cost. These costs become more apparent when we consider the case of asexual reproduction or parthenogenesis. In contrast to sexual reproduction, where two distinct gametes from two parents fuse together to create a new organism, asexual reproduction occurs in females whose offspring arise from an embryo where no fertilization occurs. In asexual species, male gametes are not necessary to produce viable offspring,

and therefore in asexual reproduction all of a female's offspring are genetically identical to her. In this system, females can avoid costs associated with sexual reproduction. Because asexual females do not need a partner to create offspring, they do not have to invest time and energy into acquiring and mating with partners, ventures that are quite dangerous and costly in some species as any time not spent devoted to maintenance of self and survival can greatly reduce life span.

In addition to skipping the costs of finding and acquiring mates, asexual females also enjoy avoiding what is referred to as the twofold cost of sex. The twofold cost of sex is based upon the theoretical ability of asexual populations to outreproduce sexual populations (Kodric-Brown and Brown 1987). Consider a population composed of a single asexual female and a single female-male pair, and suppose that each will contribute the same number of offspring to the next generation. This means that the asexual female will produce two offspring, and the male-female pair will produce two offspring (a male and female). In the next generation, there are now two asexual females who will produce four asexual daughters, but there is only one female-male pair, which will only produce two offspring (again). Because the female-male pair must share genetic information to produce offspring, the sexual population size remains the same in each generation, whereas the asexual population doubles in size each generation. In this simplified scenario, the twofold cost of sex should stipulate that asexual reproducers outcompete sexual reproducers in terms of sheer numbers.

The Evolution of Sexual Reproduction

There are clearly many costs associated with sexual reproduction, and considering the twofold cost of sex, it would seem that asexual populations are intrinsically able to outreproduce sexually reproducing populations (Kodric-Brown and Brown 1987). However, we frequently see the exact opposite occurs in nature, which suggests that the benefits of sexual reproduction in some way compensate for its costs.

One theory for the evolution and maintenance of sexual reproduction suggests that sexual

reproduction has been selected for so strongly because it provides better protection against rapidly evolving parasites when compared to asexual reproduction (Hamilton et al. 1990; Hartfield and Keightley 2012). This hypothesis is known as the Red Queen effect (also called the Red Queen hypothesis). It is named after a line in Lewis Carroll's *Through the Looking Glass* where the Red Queen says to Alice, "Now, here, you see, it takes all the running you can do, to keep in the same place" (Van Valen 1973). According to the Red Queen effect, species must very rapidly adapt and evolve to keep pace with parasites so that they are not driven to extinction; they must evolve or "run" very quickly only to stay in the same (extant) state. Parasites pose an evolutionary challenge to more long-lived species because they have a much smaller generation time compared to their hosts. This means that parasites can very rapidly evolve novel adaptations that allow them to better take advantage of their hosts within the host's lifetime. This is difficult for the hosts, whose longer generation time means they take longer to adapt reciprocal changes to fend off their parasites. It is this coevolutionary arms race between parasite and host, according to Hamilton et al. (1990) that has selected for and maintained sexual reproduction in populations despite its numerous costs. Thus, sexual reproduction is selected for over asexual reproduction because it generates more genetic variety in populations. Genetic variety is favored in the scenario between host and parasite because the more genetic variety the host population has, the harder it is for a parasite to infect all individuals.

Another major theory of the selection pressures that led to sexual reproduction is known as the mutational deterministic hypothesis, and it suggests that sexual reproduction evolved because it allows populations to purge deleterious mutations from a population (Kondrashov 1998; Hartfield and Keightley 2012). In all populations, sexual and asexual, mutations will occur due to inherent error rates in DNA replication and DNA maintenance and because of environmental factors that disturb these processes. An important aspect of new mutations is that they are much more likely to be deleterious than beneficial to organisms. In

asexual populations, if a deleterious mutation arises, all of the offspring from individuals carrying that mutation will also have it. In this scenario, deleterious mutations will continue to accumulate over generations, because the only way to purge negative mutations from asexual populations is for the organisms carrying them to stop reproducing or for another mutation to occur that reverses the effect of the initial deleterious mutation (an unlikely event). Because of this inability to purge deleterious mutations, these asexual populations will eventually accrue too many negative mutations and will most likely go extinct, a process referred to as Muller's ratchet (Kondrashov 1988). However, genetic recombination allows sexually reproducing populations to purge deleterious mutations at significant rates by mixing genetic material between parents to create offspring, which may help sexually reproducing species outcompete asexual reproducers (Hartfield and Keightley 2012).

Evolution of Two Biological Sexes

Although a few sexually reproducing species, such as slime molds, have evolved more than two distinct "mating types," most diploid, multicellular taxa that sexually reproduce have only two distinct biological sexes: male and female. This is theorized to be the result of differential selective pressures that gametes underwent very early on in the evolution of sex. These differential pressures on gametes started the cascade of evolution that has led to the differences we observe between males and females in all sexually reproducing species today (Kodric-Brown and Brown 1987).

To consider the pressures that early gametes may have experienced, we have to look back to when sexual reproduction was new to the evolutionary scene. Very early on in the evolution of sexual reproduction, the haploid gamete cells that organisms produced were isogamous, meaning that all gametes were the same size. Because isogamous gametes do not differ in terms of morphology, they are not classified as either male or female. Rather, the compatibility of gametes is determined by genes at specific mating-type regions in the genome. These isogamous

individuals are assigned mating types such as "+" and "−." Although isogamy was the ancestral condition of sexually reproducing species, most extant plant and animal species have subsequently evolved anisogamy (Matsuda and Abrams 1999). Anisogamy is the production of two morphologically distinct gametes and is the foundation of sexual dimorphism. Although males and females can vary greatly in terms of appearance and behavior in different species, the origin of that variance is rooted in differences in gamete size. In order to understand the evolutionary switch from isogamy to anisogamy, we need to consider how exactly gamete size is important for successful reproduction and what selective pressures may have led to the deviation away from similarly sized gametes between mating types.

Gamete size is important for successful reproduction because it is linked to the viability of future offspring; the larger the gametes that parents contribute to a zygote, the more cellular resources that zygote will have to successfully develop (Parker et al. 1972). Parker et al. (1972) contend that this relationship between gamete size and zygote viability is a continuum, wherein the more resources gametes contribute to a zygote, the more viable that zygote will be. However, parents cannot invest infinite amounts of energy in generating large gametes. Therefore, there is a fixed amount of resources that any parent can contribute to gamete production, and the more gametes they produce, the smaller the allotted resources will be. Because of this, there is a trade-off between how many gametes an organism can generate and how much those gametes can contribute to the viability of zygotes. Parker, Baker, and Smith used these parameters to generate a computer simulation to model isogamous populations. In this model, gamete sizes varied slightly between individuals in the parent population, gamete size was heritable, and gamete size responded to selection pressure. Gametes in this simulation were released and mated randomly, meaning they fused with the first gamete they encountered.

Interestingly, this model always generated populations that were eventually anisogamous. The authors concluded that this was because "proto-females" (i.e., individuals who produced

slightly larger gametes on average) had zygotes that survived well regardless of the size of the gametes they were fertilized with, which meant that producing larger than average gametes was a stable, successful strategy. On the other hand, “proto-males” (i.e., those who make more but smaller gametes) were more able to capture and fertilize those larger gametes produced by “proto-females” than intermediate gamete sizes because there were more of the smaller gametes. In other words, the smaller gametes were better able to parasitize the investment of larger gametes made by proto-females than intermediate gametes were and were more reproductively successful (Parker et al. 1972). This phenomenon is referred to as gamete competition, because as soon as a proto-male arises in a population, they can fertilize more gametes than gametes of an intermediate size and will outcompete the intermediate gametes (Parker et al. 1972). This places a selective pressure on other members of the population to either produce small competitive gametes or nutritive large gametes. This disruptive selection on gamete size has resulted in two distinct sexes among sexually reproducing species (Hartfield and Keightley 2012), although there can be more than one morphological type within a given sex (e.g., plainfin midshipman fish males have two types: sneaker and guarder males).

Sex Differences in Early Development

As time passed, differences in more than just gamete size began to evolve between males and females in anisogamous species. Today, in large, multicellular, anisogamous species females and males have evolved complex differences in gonads, internal genitalia, and external genitalia that impact how each biological sex develops, reproduces, and behaves. Although the development of the stereotypical set of human male and female gonads, internal genitalia, and external genitalia is considered below, there are many intermediates that arise between the male and female developmental pathways, and up to 2% of live births in the United States result in individuals who deviate from the stereotypical male or female reproductive tracts (MacLaughlin and

Donahoe 2004). This results in a spectrum of possible outcomes between the typical male and female phenotypes (for a review of intersex phenotypes, see MacLaughlin and Donahoe 2004).

All zygotes, regardless of chromosomal sex, begin as a bipotential embryo, meaning that they are capable of taking both the male and female developmental routes, a process that is known as sexual differentiation. At this point in development, zygotes have both Wolffian ducts (proto-male internal genitalia) and Müllerian ducts (proto-female internal genitalia; Hughes 2001). In humans, whether or not a zygote develops into a stereotypical male or female is determined by the presence of a gene known as the sex-determining region on the Y chromosome (SRY) gene, which is located on the Y chromosome (Hughes 2001). When a functional copy of this gene is present, it codes for a protein that activates other genes that begin the cascade of male-specific development. If this gene is absent or dysfunctional, then these male-specific genes are not expressed, and the female developmental pathway is undertaken.

The typical male pathway is initiated when the SRY gene induces the development of testes from bipotential gonad tissue (Wilhelm and Koopman 2006). The testes then secrete three key hormones: testosterone, anti-Müllerian hormone (AMH), and dihydrotestosterone (DHT). Testosterone is responsible for the development of internal genitalia, including the epididymis, seminal vesicle, and vas deferens, whereas AMH causes the proto-structures of the female-typical reproductive tract to regress (Wilhelm and Koopman 2006). DHT causes the development of male external genitalia. In contrast, the typical female developmental pathway is undertaken in the absence of a functional SRY gene. In this case, testis never begins to develop from the bipotential gonad tissue. This means that testosterone and AMH will not be produced, and in their absence the bipotential gonad tissue develops into ovaries, the Wolffian ducts regress, and the Müllerian ducts develop into the uterus, cervix, and part of the vagina (Wilson and Davies 2007).

Sex Differences in Later Development

Hormones play an integral part not only in the development of the reproductive tract but also in the psychosexual behavioral differentiation of males and females later in life. This phenomenon is referred to as the Organizational-Activational Hypothesis of hormones (Phoenix et al. 1959). It states that steroid hormones have two modes of action; first, during a critical window in the animal's early development, steroid hormones organize neural systems that are later responsible for generating sex-typical behavior. Then, upon sexual maturation, these same steroid hormones activate the neural pathways organized during development, which results in the organism performing sex-typical behavior when appropriately stimulated and in some cases developing secondary sex traits (such as facial hair in men or development of breasts in women).

The Organizational-Activational Hypothesis of hormones appears to be at play in the development as humans as well; prenatal exposure to testosterone and estradiol selectively prunes specific areas of the brain in a sexually dimorphic manner, which influences sex-typical behavior in later life (for a review of sexually dimorphic regions of the human brain, see Wilson and Davies 2007). For example, among those with congenital adrenal hyperplasia (CAH), where fetuses are exposed to abnormally high levels of testosterone due to a problem with an adrenal enzyme, female children will display more male-typical behaviors throughout their lives. As children, these females exhibit more rough-and-tumble play, less nurturing behavior, are more interested in male-typical toys and male playmates, as adults are more likely to enter a male-typical field, and are perhaps more likely to identify as bisexual or lesbian as adults (Hines et al. 2004). This suggests that early exposure to high levels of testosterone during their gestation may have masculinized some of their female sex-typical neural pathways.

Another line of evidence that early exposure to hormones can alter sex-typical behavior later in life comes from individuals with complete androgen insensitivity syndrome (CAIS). When CAIS

occurs in genetic males who have a mutated copy of the androgen receptor gene which makes them completely unresponsive to the androgens (testosterone and DHT) that their testes produce (Hughes et al. 2012), these males develop as female. Specifically, because their bodies cannot react to androgens during development, their phenotypic development follows the female-typical pathway, and although they lack a uterus and have internal testes, they also exhibit female-typical, sexually dimorphic behavior and have a female gender identity (Wilson and Davies 2007). This suggests that the absence of the effect of androgens early in development not only caused the development of a physical female phenotype, but it also prevented male-typical behavioral pathways from developing.

Ultimate Explanations for Sexual Dimorphism in Humans

Men and women clearly differ when it comes to their physiology and, in some cases, their psychology (Wilson and Davies 2007; Collaer and Hines 1995). The proximate cause of these psychological differences is due in part to the differential developmental pathways that typical males and females undergo during development and the hormones that influence their behavior and secondary development later in life. Why then, ultimately, do men and women seek different qualities in mates? Why are they different behaviorally and psychologically in some romantic and sexual aspects, but not in others? Two theories that seek to explain the evolutionary pressures that differentially shaped men and women's development and behavior in relation to reproduction are (1) Buss and Schmitt's (1993) sexual strategies theory (SST) and (2) Gangestad and Simpson's (2000) strategic pluralism theory (SPT).

Sexual Strategies Theory

The SST posits that throughout our evolutionary history, humans have sought specific mates to solve specific adaptive problems. The choices men and women made were contingent upon the context and the temporal nature of the relationship (i.e., short- vs. long-term relationships). In some

cases, because men and women faced different adaptive problems, they have evolved different strategies when it comes to finding and pursuing relationships with the opposite sex.

A major asymmetry between the sexes that has influenced the evolution of sexual differences is the amount of parental investment that each sex must contribute to offspring (Trivers 1972). If both sexes were to invest the minimal amount of time and energy possible into an offspring, the male would spend only the amount of time and energy it took to generate sperm and fertilize a woman's egg. The female, however, must generate a much larger gamete, gestate the fertilized egg for 9–10 months, and then give birth. This difference in minimal investment sets up a dichotomy in terms of the most beneficial reproductive strategy for men and women. According to Buss and Schmitt, although both sexes benefit from long-term relationships wherein each parent contributes substantially to the success of their offspring, men benefit more from having conditional short-term engagements than women do and will therefore seek more short-term relationships, on average, than women. It is this discrepancy in what optimizes each sex's reproductive success that has led to the evolution of different reproductive behavior in men and women.

When it comes to short-term relationships, men, who are limited by the number of eggs they can gain access to and fertilize, are most benefited by factors such as finding more partners and identifying partners that are potentially fertile. Buss and Schmitt (1993) found that men do appear to desire more short-term relationships than women and express a greater desire for more partners in the immediate and distant future than women express. Additionally, there is evidence that men may be able to detect the fertility status of women based off of subtle changes in their physiology, such as in the pitch of their voice or in body odor, which change in response to where women are during their menstrual cycle (reviewed in Haselton and Gildersleeve 2011). On the other hand, women's short-term concerns deal more with gaining resources, such as increased social status, because they are not restricted by the number of partners they can

accrue. Li and Kenrick (2006) found that when women were tasked with spending a budget of "mate dollars" to buy characteristics to create an ideal short-term mate, they spent a significantly higher amount of their restricted budget on a partner with higher social status and resources than men did when given the same task and budget.

In terms of longer relationships, both men and women must solve the problem of finding mates with good parenting skills and a willingness to commit to long-term partnerships. Men, however, must also be concerned with paternity certainty and attaining mates who have high reproductive value, whereas women are constrained by attaining partners who are able and willing to invest time and resources into their offspring in the long-term. It appears as though men place value on traits in partners such as faithfulness and sexual loyalty and also have psychological adaptations such as jealousy for detecting sexual infidelity threat, which may help solve the problem of paternity certainty (Buss and Schmitt 1993). Additionally, it appears that cross-culturally men prefer long-term partners who are younger than they are (about 2–3 years younger), whereas women prefer men who are older than they are (3.5 years older; Buss 1989). This may be a psychological adaptation for both sexes; preference for younger women may help men find highly fertile partners, and preference for older men may help women find men who have more resources to invest in them and their potential offspring.

Strategic Pluralism Theory

It is important to note that there is no one "best" strategy that all men or all women adopt all of the time. Although the SST does propose that both men and women have evolved mixed strategies wherein both sexes can and do choose to pursue both short- and long-term relationships, the SPT proposed by Gangestad and Simpson (2000) proposes that the strategy either sex pursues is dependent on cues from the environment. Although differences in minimal parental investment still influence the mating choices men and women make, SPT posits that there is also considerable

intrasexual variation in strategy choice. What strategy an individual adopts is contingent upon environmental cues that allow them to make cost-benefit decisions when it comes to mating strategy. These cues include many conditional extrinsic factors, such as the availability of mates, number of competitors, and quantity of available resources, in addition to intrinsic factors, such as how attractive one is and how able they are to obtain short-term mating partners (Gangestad and Simpson 2000).

Interestingly, these conditional factors may better explain women's short-term mating strategies. SPT contends that, in addition to extracting resources from partners, women also take into account access to good genes when making short-term mating decisions and may have evolved to seek good genes for their offspring from short-term relationships. In the same study using "mate dollars" described above, the authors found that both sexes highly prioritized attractiveness for short-term partners. However, Li and Kenrick (2006) note that what constitutes physical attractiveness differs between the two sexes, whereas men prefer estrogen-linked traits, such as breast symmetry, which are associated with fertility in women, and women prefer testosterone-linked traits like facial masculinity (at least, for a short-term relationship), which may be markers of good, immunocompetent genes (see, e.g., Pillsworth and Haselton 2006). Women, therefore, also prioritize attractiveness for short-term partners (but not long-term partners), which may indicate that access to good genes is a contributing factor in women's choices to pursue short-term partnerships (Pillsworth and Haselton 2006).

Pair-Bonding as an Adaptation for Reproduction

Another key component of the reproductive strategies of both men and women has been the evolution of pair-bonding. Pair-bonding is the long-term formation of a very close social and sexual bond to another human being that exists outside of the typical relationship shared with an acquaintance (Quinlan 2008). Not only is the formation and maintenance of pair-bonds facilitated by

complex neurological and hormonal networks in our bodies and brains (Young and Wang 2004), pair-bonding also occupies a large portion of the collective mental energy of our species. Pair-bonding and the experience of being in love have inspired countless creations of music, poetry, literature, and art among other manifestations, all of which are an integral part of human culture. The formation of long-term social partnerships, be it inside or outside of a marriage, appears to be culturally universal as does romantic love, both of which have significant implications for human reproduction (Jankowiak and Fischer 1992).

Two explanations for the evolution of pair-bonding in humans consider selection pressures for parental investment and male-male competition. Because newborns require so much nourishment and rearing to ensure survivorship, it is in the father's best interest to sacrifice some potential mating opportunities to help provision their offspring to increase its likelihood of survival (Trivers 1972; Quinlan 2008). Pair-bonding may therefore have evolved as a mechanism to increase biparental and cooperative care for offspring from both parents. On the other hand, it is also possible that pair-bonding could have evolved as a consequence of male-male mating competition. Because of the operational sex ratio in humans, at any time there are many fewer fertile, ovulating women than there are men who can fertilize their eggs. This means that males must compete with one another to gain access to females. From this perspective, pair-bonding may have evolved as a mechanism to prevent other males from gaining access to a pair-bonded female by facilitating mate guarding by her partner (Quinlan 2008).

Philosophy and Reproduction

As such an integral part of our existence, the act of reproduction itself has garnered its fair share of intrigue and evaluation from philosophical minds. Is it always the most ethically and morally correct decision to reproduce? When is it appropriate to reproduce and when to refrain from reproducing? Two viewpoints regarding reproduction that have been articulated in part since ancient times are natalism and antinatalism. Natalism is a belief

that human reproduction should be encouraged and encompasses a range of viewpoints, such as the idea that human reproduction is of the ultimate importance and philosophical considerations of the value of bringing another human into the world. On the other hand, antinatalism views reproduction in a negative light and considers the suffering associated with being brought into existence, the impact of humans on other species on our planet, and the impact of humans on our environment, among other factors arguing that birth is unfavorable.

Two prominent pro-natalism thinkers are David Wasserman and Rivka Weinberg. When it comes to whether or not it is morally permissible to have children, Wasserman argues that in many cases it is permissible but that this is only the case when the rights of the future child to live a life with a minimal standard of well-being are considered and met (Benatar and Wasserman 2015). Although this argument is permissive of reproduction, it also heavily rests on the moral stature of the parents, as Wasserman argues that for reproduction to be permissible parents must bring children into the world with the intent of giving those children lives worth living (Benatar and Wasserman 2015). Rivka Weinberg proposes that giving birth is an imposition of risk on an unborn child. In this light, it is only morally permissible to procreate when the risk imposed on a child is a risk you would have accepted as a condition of your own birth and that parental motivation to have children should be driven by the want and intention to love and care for those children (Weinberg 2015).

On the other hand, a prominent antinatalist, David Benatar, proposes that to bring someone into the world always does that person irreparable harm (Benatar and Wasserman 2015). His argument is based off of two lines of reasoning: (1) that by having a child you cause all of the good and bad that that child will experience during their lifetime and (2) that even when one accounts for all of the good and bad in a life, the bad far outweighs the good. When one considers the case of nonexistence, the absence of pain is good, and the

absence of pleasure is not bad, because there is no one there to deprive pleasure of (Benatar and Wasserman 2015). From this perspective, it is better to never have existed, because there is nothing bad about not having come into existence, whereas coming into existence necessitates that you experience painful things.

Is Modern Life Changing Reproduction?

Modern medical technologies such as in vitro fertilization have emerged in the last few decades, which now allow couples to conceive when previously they would have been unable to. These technologies, collectively known as assisted reproduction technology (ART), are a hope for the estimated 80 million individual worldwide who experience infertility or subfertility (Vayena et al. 2002). Although ART has been a boon to many, it has been a concern to some because ART may be bypassing some important biological filters that otherwise do not allow for two individuals to conceive (Niemitz and Feinberg 2004). Although developmental pathways have evolved to withstand or buffer a certain amount of changes in genotype and environment, it is possible that ART in some cases may be causing that buffer to break down. For example, ART might be interfering with embryo imprinting and epigenetic maintenance of fetal gene expression, which both may lead to problems with development (Niemitz and Feinberg 2004).

Another aspect of modern life that is influencing how individuals choose to reproduce is concerns with overpopulation. An important example of this is China's one-child family policy, which was enacted in 1979 amidst concerns that a booming population would cause a large sacrifice in living standards (Hesketh et al. 2005). This policy was meant to create a shift toward small-family culture and has been more strongly enforced in urban, highly populated areas than in rural sectors. However, an unintended consequence of this policy has been a change in the sex ratio in China toward male children, as traditionally boys are preferred to girls. Preimplantation genetic diagnosis (PGD) and early fetal sexing in combination

with sex-selective abortions have decreased the number of female children born in China. This, in combination with poor medical treatment of female children resulting in a higher female mortality rate, has significantly altered the sex ratio in China. This shift in the sex ratio has been associated with a doubling of crime rates, an increase in demands for sex workers, and an increase in the transmission of HIV (Tucker et al. 2005). From an evolutionary perspective, artificially altering the operational sex ratio and the availability of mates may alter the intensity of competition for mates, changing human mating dynamics, behavior, and preferences.

Conclusions

How, when, and with whom we choose to mate are a complicated process that has been influenced by many factors: by the earliest evolution of sex, how our brains and bodies develop pre- and post-natally and into later life, what evolutionary pressures have shaped our species over time, the culture we are surrounded by, and the intrinsic values and characteristics that are unique to each of us. Although humans exist in a vast range of geographical locations and our cultures vary across them, the mating preferences we have evolved over our species' history are still at play, and how these preferences interact with modern technology and culture will have significant impacts on the evolutionary future of our species.

Cross-References

- [Anti-natalism](#)
- [Conception](#)
- [Concealed Ovulation and Pregnancy](#)
- [Development of Sex Differences](#)
- [Female Mate Choice](#)
- [Male Mate Choice](#)
- [Medically Assisted Reproduction](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)

- [Ovulation](#)
- [Religious Teachings](#)
- [Reproduction, Suicide, Euthanasia](#)
- [Sex Differences](#)
- [Sex Differences in Same-Sex Aggression](#)

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Reproduction, Suicide, Euthanasia

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Synonyms

[Death](#); [Death by suicide](#); [Medical definitions of death](#); [Reproduction](#); [Survival and reproduction](#)

Definition

Reproduction, suicide, and euthanasia are existence-related moral phenomena with the mutual component of decision-making regarding life and death.

Introduction

Natural selection will never produce in a being any structure more injurious than beneficial to that being, for natural selection acts solely by and for the good of each. No organ will be formed for the purpose of causing pain or for doing an injury to its possessor.

Charles Darwin

Does life stink? There is, obviously, no simple answer to this philosophical question. David Benatar (1997, 2006) argues that life stinks, and even if it does not stink so badly, there is a good chance that it will begin to do so. Existence may be painful and frustrating; however, nonexistence cannot be painful or frustrating. Back to the first fundamental question of this entry, nonexistence is completely “odor-free.” Benatar (2016) further argues that since it is better never to exist, one is harmed by being brought into existence. This author concludes that procreation is “always” wrong and morally problematic (for a discussion see Weinberg 2012). This philosophical idea is not new in philosophical writings and has inspired many noble writers and thinkers (e.g., Sadegh Hedayat; see Fadaei 2009).

The line between existence and nonexistence and its moral factors have been the center of heated debates over the centuries. Psychologically speaking, morality is tightly associated with *decision-making*. There are three important, existence-related phenomena that are tied to the concept of decision-making: reproduction, suicide, and euthanasia. In the former, two persons usually make a conscious decision to produce offspring. The other two concepts entail deliberately putting an end to one's life. These three phenomena and their related factors have been largely discussed in philosophical, sociological, psychological, and bioethical texts.

In evolutionary psychology, *survival* and *reproduction* are probably among the most widely mentioned keywords. Both keywords are associated with the "line between existence and nonexistence." Evolutionary psychologists argue that humans, over deep evolutionary history, have developed psychological mechanisms in order to reproduce and guard their offspring at least until they become sexually mature to be able to reproduce. The evolutionary psychology of suicide and euthanasia is, however, more puzzling because individuals consciously hinder survival. While evolutionary psychological understanding of suicide and euthanasia seems complicated or puzzling, evolutionary psychologists have adequately addressed these issues. In what follows, a short description is given for each behavior (i.e., reproduction, suicide, and euthanasia). Of note, there are other existence-related phenomena which are greatly influenced by moral decisions (e.g., abortion) that are discussed at length in other entries.

Reproduction

As an empirical science, evolutionary psychology has successfully described, explained, and predicted human reproductive behavior; however, maybe it has remained neutral on "badness" or "goodness" of reproduction. Existence may be either pleasing or frustrating, and much of this attribution is formed through the quality of parental care which is an evolved psychological

mechanism. Consistently, research suggests that insecure attachment is strongly associated with depressive symptoms (Burnette et al. 2009). A considerable proportion of the literature in evolutionary psychology has focused on mating whose primary purpose is successful reproduction. In different cultures, and depending on environmental features, people deploy various reproductive strategies in mating context, and there are culture-specific values and religious teachings that promote reproduction.

From an evolutionary viewpoint, offspring are a sort of vehicle for their parents (Buss 2008). Parents' genes may get transported to succeeding generations through successful reproduction. Without children, an individual's genes may perish forever, and again, to a typical evolutionary psychological scientist, this is neither "bad" nor "good." Considering the paramount importance of offspring as genetic vehicles, it stands to reason to expect that natural selection would particularly favor powerful mechanisms in parents (e.g., parental care) to ensure the survival and reproductive success of their offspring. Of course, without the success of offspring in reproduction, all the effort that was previously invested in mating would be reproductively meaningless. By investing in offspring, parents miss resources that could be potentially devoted to themselves. Parents who protect their young children risk their own survival. In some cases, some parents become wounded or even die while protecting offspring from predators. Given the costs associated with parental care, it is reasonable to expect that reproductive benefits of parental care are large enough to outweigh the abovementioned costs.

Suicide

To someone who commits suicide, existence truly stinks! Life is a frustrating and "bad" experience for such persons. In fact, there is a well-developed research literature on the relationship between depression and suicide. There are a number of philosophers and writers who actually committed suicide after writing brilliant literary works on life

and death (Fadai 2009). Existing evidence shows that suicide has occurred throughout history and across the world. Something that is not bound to a specific place or era and happens in high rates should be fundamentally traced back to human nature. Suicide is, as worded by David Buss (2008), a genuine evolutionary mystery. At first sight, it seems so contrary to anything that evolution would favor. Evolutionary theory suggests that differential reproduction is the engine of the evolutionary process and survival is obviously necessary for reproduction. So how can evolutionary theory account for suicidal ideation and behavior?

An evolutionary psychological theory of suicide has been postulated by de Catanzaro (1991, 1995). According to this theory, suicide would be most likely to occur when an individual has a considerably reduced ability to contribute to his or her own inclusive fitness. This reduced capacity consists of indicators such as poor health, poor prospects for heterosexual mating, chronic illnesses, and perceptions of being a burden on one's genetic kin. Importantly, all these conditions are subjective and are not necessarily accurate in reality. Under these conditions, it is at least plausible that the replication of an individual's genes would have a better chance without his or her physical presence. For example, if an individual perceives that he is being a burden to his family, then kin's successful reproduction, and consequently the person's own fitness, might suffer as a result of his physical, fruitless presence. To empirically test this evolutionary theory of suicide, de Catanzaro (1995) collected self-reports of suicidal ideation (i.e., thoughts about how to kill oneself, which can range from a detailed plan to a fleeting consideration and does not include the final act of killing oneself) and the fitness-related variables (i.e., perceived burdensome to family, perceived significance of contribution to society and family, success with heterosexual mating, homosexuality, sexual activity, financial welfare, number of friends, social status and approbation, and physical health condition). Findings of de Catanzaro (1995) supported the outlined theory. The evolved suicide adaptation

hypothesis has also successfully explained sex differences in suicidal ideation (Buss 2008).

In conclusion, suicidal ideation and behavior have been, to some extent, explained by evolutionary theory. Yet, more research is warranted to explore evolutionary adaptations behind suicidal ideation and behavior. There are other sorts of suicidal behavior and suicide-related analyses that were not addressed in this entry (e.g., bargaining suicidal behavior, parasite manipulation; for a review of different evolutionary hypotheses regarding suicidal behavior, see Aubin et al. 2013; for a review of evolutionary psychology of suicide terrorism, see Liddle et al. 2011).

Euthanasia

Broadly, euthanasia is succinctly defined as the practice of intentionally ending a life in order to relieve pain or suffering. Euthanasia, meaning "good" or painless death (from the Greek *eu*, "good," and *thanatos*, "death"), was used in the last decade of the twentieth century to mean a death that is perpetrated or accelerated with the help of medicine. There are at least two classifications for euthanasia, one on the *decision-making* process and the other on the form of death. The first classification suggests that three types of euthanasia can be practiced: voluntary, involuntary, and non-voluntary. *Voluntary euthanasia* is that which is requested or agreed to by the subject. *Involuntary euthanasia* is practiced when the agreement of the subject could be obtained, but is not. *Non-voluntary euthanasia* is that in which the agreement of the subject cannot be obtained because of his or her physical or mental state. The second classification suggests that euthanasia could be active or passive. The former is where death is produced deliberately and actively, while the latter applies where death is purposely produced by withholding or withdrawing of the medical means of nutrition or the treatment of the subject's condition. Physicians assist suicide when they intentionally help a person commit suicide by providing lethal drugs for self-administration.

Voluntary euthanasia and physician-assisted suicide are quite similar to regular suicide in terms of decision-making, that is, one consciously decides to end his or her own life. However, the distinction between voluntary euthanasia and suicide rests upon the presence or absence of an incurable and progressive disease that is inevitably drawing the patient toward death. Therefore, voluntary euthanasia and physician-assisted suicide can be adequately explained by de Catanzaro's (1995) evolutionary model of suicide. Involuntary and non-voluntary euthanasia may be explained by the notion that ending patient's life could enable the family members and genetic relatives to redirect their resources (e.g., time, energy, and money) from keeping the patient alive to other domains. Generally, treatment of end-stage patients is very costly for the family or the society and limits family's ability to invest in other potentially reproductive domains.

Conclusion

Reproduction, suicide, and euthanasia are important concepts with the mutual factor of decision-making with regard to life and death. Reproduction is a crucial behavior in human evolution as offspring are the vehicles through which parental genes get transported into future generations. Suicide has been referred to as a "puzzle" because it seems paradoxical to every adaptation in evolutionary history for survival. However, evolutionary psychologists have documented explanatory theories and hypotheses regarding different types of suicide. Euthanasia is also a moral dilemma which has been investigated in different disciplines from bioethics to personality psychology. Evolutionary foundations of different types of euthanasia were also discussed. In sum, evolutionary psychology may inform different fields of study regarding the mentioned phenomena that are closely associated with existence and nonexistence. Of note, evolutionary psychology, as an empirical science, is more involved in explaining *functions* of each behavior rather than judging it as either "good" or "bad."

Cross-References

- [Evolution of Morality](#)
- [Medically Assisted Reproduction](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Reproduction](#)
- [Science and Morality](#)
- [Survival and Reproduction](#)

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Reproduction+

- [Fitness Benefits of Costly Signalling](#)

Reproductive Aging

- ▶ [Primate Menopause](#)

Reproductive Benefits Must Outweigh Costs

- ▶ [Altruism and Costs to Altruist](#)

Reproductive Cell Size

- ▶ [Gamete Size](#)

Reproductive Coercion

- ▶ [Sexual Coercion and Dating](#)

Reproductive Competition

- ▶ [Female-Female Strategies](#)

Reproductive Competition Among Members of the Same Sex

- ▶ [Copulatory Intrasexual Competition](#)

Reproductive Costs

- ▶ [Cost of Same-Sex Friendships](#)

Reproductive Development

- ▶ [Life History Theory](#)

Reproductive Fitness

- ▶ [Decreased Reproductive Success](#)
- ▶ [Evolutionary Paradox: Women Choosing Not to Have Children](#)
- ▶ [Observations of Sexual Dimorphism](#)
- ▶ [Variance in Female Reproductive Success](#)

Reproductive Frequency

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Definition

High frequency sex is an adaptation to the loss of cues needed to synchronize insemination with ovulation, and it promotes conception in species with low reproductive rates. Moreover, high frequency sex promotes semen tolerance and semen sampling. It also serves as an algorithm for paternal commitment, functions as an anti-cuckoldry strategy, and reduces the risk of prostate cancer.

Introduction

Some species engage in high frequency sex (*iteroparous* species); others only have sex once in a lifetime (*semelparous* species), if they are lucky. Species differences in reproductive frequency evolved to promote their *replacement value*. For sexually reproducing species where each individual has two parents, the replacement value of two offspring for the parents is the

equilibrium point for that population. An average replacement value that exceeds 2 means the size of the population will increase, while a value of less than 2 will cause the population to shrink and if it remains in effect long enough eventually the species will go extinct.

Variation in one of two evolved strategies can be used to promote replacement values of 2 or more. Species that rely on *r-selection* produce large numbers of offspring but invest little time or effort in any of them. In salmon spawn, for example, the female releases thousands of eggs. As a result, salmon can produce hundreds of fry on a single reproductive occasion, and spawning in Pacific salmon triggers mechanisms that lead to the death of the parents within a matter of days. As a result, when the baby salmon hatch they will have to fend for themselves and many will perish, but the production of a lot of baby fish increases the odds that at least two will survive to complete the cycle and spawn thereby numerically replacing their parents in the next generation.

Species that are *K-selected* produce a small number of offspring but in terms of time and resources invest heavily in each of their progeny. Humans anchor the reproductive strategy at the end of this continuum. Women typically only produce one child at a time and they provision, protect, and care for their offspring for as long as several decades. Reproduction for women puts their capacity to be re-impregnated on hold for 3 or more years. That is because pregnancy lasts for nine months and breastfeeding (which until recently was the only option) typically lasted in the environment of evolutionary adaptiveness for 2–3 years. Breastfeeding produces hormonal changes which serve to suppress or inhibit ovulation. This is referred to as *lactational anovulation*. Because the biological costs of pregnancy and lactation are so high, lactational anovulation evolved as a birth spacing mechanism to afford the uterus a chance to recover from the previous pregnancy before being impregnated again (Gallup and Hobbs 2011; Gallup et al. 2016). As a consequence, humans have an unusually low reproductive rate.

Another factor that may contribute to the frequency of sex involves timing. Because humans

no longer engage in prominent patterns of seasonal breeding and human females no longer produce salient ovulatory cues, patterns of high frequency sex and continuous breeding represent an adaptation to the loss of ovulatory cues (see Gallup and Stolz [in press](#), this volume).

Orgasm and High Frequency Sex

Other things being equal, you would expect the frequency of sex to be proportional to the pleasure that the participants derive from sex. Consistent with this view, orgasm frequency in female college students is highly correlated ($r=.82$) with orgasm intensity (Gallup et al. 2014). The capacity to experience an orgasm is a byproduct of neurological mechanisms that evolved to promote the reoccurrence of the reproductive act in species with low reproductive rates (Gallup et al. [under review](#)).

There is also reason to believe that high frequency sex may be used by some men to keep their female partner sexually satiated and thereby less likely to engage in sex with other men (Kaighobadi and Shackelford 2008). Thus, an insistence on high frequency sex may also function as an evolved anti-cuckoldry strategy (for a review see Gallup and Burch [in press](#)). High frequency sex also promotes semen tolerance and semen familiarity which serves to facilitate healthier pregnancies by reducing the risk of preeclampsia and spontaneous abortion (Davis and Gallup 2006). Indeed, some people have theorized that being inseminated by a range of prospective mates during courtship may enable women to make more biologically informed mate choices (Gallup and Reynolds 2014).

Finally, there is evidence that high frequency sex and ejaculation also reduce the risk of prostate cancer (Leitzmann et al. 2004).

Cross-References

- [Breastfeeding Benefits](#)
- [Mate Choice](#)
- [Orgasm](#)
- [Semen Familiarity](#)

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Reproductive Limitations

- [Helping and Reproductive Value of the Recipient](#)

Reproductive Maturation

- [Absence Prior to Puberty](#)
- [Puberty in Girls](#)

Reproductive Parasite

- [Female Mimics](#)

Reproductive Potential

- [Children Have Greater Reproductive Value than Sibs](#)

Reproductive Roles

- [Sex Differences in Navigation](#)

Reproductive Skew

- [Mating Systems](#)
- [Social Dominance and Sexual Access](#)
- [Status and Reproductive Success](#)

Reproductive Skew Theory

- [Skew Theory](#)

Reproductive Strategies

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Synonyms

Life history strategies; Mating strategies

Definition

A cluster of interrelated physical, psychological, and behavioral characteristics that reflect selective allocation of time and energy toward propagation. The term “strategy” does not imply conscious decisions on the part of the organism, but rather refers to the nonrandomly organized set of characteristics that make up a reproductive phenotype.

Introduction

Reproductive strategy is an often used term in the evolutionary psychology literature that is rarely formally defined. It is generally used to refer to aspects of a reproductive phenotype along “fast” and “slow” dimensions, such as slow versus fast reproductive traits and behaviors or short-term versus long-term mating strategies. These fast and slow reproductive strategies are typified by quantitatively different clusters of characteristics that serve different reproductive goals. A fast strategy favors earlier reproduction, multiple offspring, and low parental investment. In contrast, a slow strategy favors delayed reproduction, fewer offspring, and high parental investment. Reproductive strategies are not necessarily fixed for either a population or an individual. In fact, humans often use a mixed strategy that includes aspects of both fast and slow strategies. Sex differences in reproductive strategies are well documented and are related to variability in attachment security.

Development of Reproductive Strategies

Early thinking on the development of reproductive strategies in humans can be found in Draper and Harpending (1982) and subsequently Belsky et al. (1991), both of which are based in life history models of development. Generally speaking, psychosocial acceleration theory (also sometimes termed the BSD model; Belsky et al., 1991) posits that early developmental

experiences, in particular parent–child relations and processes, serve to entrain developmental trajectories toward phenotypes that will ultimately match adult reproductive ecologies. Relevant parent–child relations/processes include harsh parenting, parental rejection, inconsistent parenting, and/or unpredictability and are hypothesized to foster a general reproductive strategy characterized by early pubertal timing, earlier onset of sex and reproduction, less stable pair-bonds, more offspring, and lower investment in each. In contrast, parent–child relations/processes that are more warm, supportive, and consistent should foster a reproductive strategy characterized by later pubertal development, later age at first sex and reproduction, more stable pair-bonds, and greater investment in fewer offspring.

Sex Differences in Reproductive Strategies

Sex differences in reproductive strategies can be traced back to anisogamy in humans. Anisogamy refers to sexual reproduction that involves the fusion gametes of unequal size. In humans, the larger gamete is female (ovum) while the smaller gamete is male (sperm). The larger gamete is more energetically costly to produce and the sex with the larger gamete must invest more in its production and, consequently, will produce fewer. The sex that produces the smaller gamete invest less in their production and can thereby produce more and increase their reproductive success via multiple fertilizations. Evolutionary processes, such as disruptive or diversifying selection, can select for the tails of the gamete-size distribution and lead to a population divided by two distinct sexes. Reproductive strategies and sex differences in reproductive strategies derive from these gamete-size differences and evolutionary processes. Because of the larger investment needed for larger gametes, females should be selected (on average) to be more discriminating when choosing reproductive partners. Males, however, should be less discriminating due to the inexpensiveness of the gamete and their ability to produce many. One

consequence of lower discretion is higher male conspecific competition for reproductive opportunities.

Extending from anisogamy are differing environmental influences on reproductive strategies. Women are relatively constrained by the resources they can extract from the environment, reproductive partners, and relatives to produce and rear offspring. As a result, women should be more attuned to the local ecology and cues to the availability of resources. One such source of information is parenting experiences, as described in the BSD model. Thus, girls' reproductive strategies should be relatively more influenced by these experiences compared to boys. Similarly, because men's reproductive success is constrained by their ability to attract and retain mates, male reproductive strategies should be more greatly influenced by their relative standing among other male competitors (James et al., 2012).

Additional research links sex differences in attachment to differences in reproductive strategies. For example, Del Giudice (2009) suggests sex differences in attachment security emerge during middle childhood as part of a sex specific reorganization of the attachment system. Differences in attachment patterns and reorganization in middle childhood consequently result in different reproductive strategies in adulthood. Insecurely attached boys and girls develop different attachment patterns during middle childhood that reflect sex-specific characteristics needed to enact reproductive strategies geared toward faster reproduction. Boys tend to develop an avoidant attachment style, which is characterized by higher aggression, self-reliance, and self-esteem, which are potentially beneficial in the context of high male conspecific competition. Girls, on the other hand, tend to develop ambivalent attachment styles that facilitate faster reproductive strategies (avoidant attachment) that may include tactics aimed to elicit investment from partners (anxious attachment). Securely attached individuals of either sex are expected to develop reproductive strategies based on more stable pair bonds, fewer offspring, and higher parental investment (i.e., slow reproductive strategy).

Conclusion

Reproductive strategies are defined by clusters of characteristics that are nonrandomly organized and that facilitate optimal propagation. On one end, a reproductive strategy is characterized by fast/short-term reproductive features that include earlier pubertal timing, earlier reproduction, multiple offspring, and low parental investment. On the other end, a reproductive strategy that can be characterized by slow/long-term reproductive features includes later pubertal timing, delayed reproduction, fewer offspring, and high parental investment. Research and theory point to early developmental experiences as a key factor for regulating reproductive strategies, although this may be more so for girls than for boys. Boys' reproductive strategies may be more influenced by competition among peers. Reproductive strategies are thought to be mediated by attachment security, which may explain some additional sex differences (Sung et al., 2016).

Cross-References

- [Early Attachment Experiences and Romantic Attachment](#)
- [Evolutionary Personality Psychology](#)
- [Long-Term Mating](#)
- [Quantity Versus Quality of Offspring](#)
- [Sex Differences in Long-Term Mating Preferences](#)
- [Sex Differences in Short-Term Mating Preferences](#)
- [Sexual Conflict in Mating Strategies](#)
- [Short-Term Mating](#)
- [Sociosexuality and Sexual Conflict in Mating Strategies](#)

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Reproductive Strategy

- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)
- ▶ [Sexual and Reproductive Development](#)

Reproductive Success

- ▶ [Charles Darwin: Theory of Sexual Selection](#)
- ▶ [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)

Reproductive Suppression and Sexual Conflict During Mating

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Definition

Competition takes place during coitus between males and females to control fertilization and reproduction. Research indicates that males may use seminal fluid chemistry to influence female

reproduction in response to females concealing their ovulation.

Introduction

Female mammals and other species are normally sexually receptive around ovulation, and the ovulatory period is advertised to males by distinct visual, behavioral, or pheromonal signals. Most species possess slight or overt ovulation, showing vulval swelling or reddening, while others have marked sexual swellings including perineal skin (Sillen Tullberg and Moller 1993). The contrasting pattern of damped or concealed ovulatory signals accompanied by sexual receptivity outside of the ovulatory period is frequently referred to as concealed ovulation (Andelman 1987).

There is consensus in the literature that mating system and signs of ovulation are strongly correlated, if not involved in a causal relationship (Alexander and Noonan 1979). Sillen Tullberg and Moller in 1993 completed a phylogenetic analysis using two behavioral characters: the presence of ovulatory signals and type of mating system (monogamous, multi-male, or uni-male). They concluded that in the majority of instances, when ovulatory signs have been lost, it has been in a nonmonogamous context. They go on to state that of the extant monogamous taxa, none possess sexual swellings and most have no visual ovulatory signs, which would indicate a connection between monogamy and lack of ovulatory signals. The absence of signs is much more tightly coupled with monogamy than with any other mating system and the absence of ovulatory signs could be an important, though not necessary prerequisite for the evolution of monogamy if concealed ovulation evolved first. The most cited hypothesis regarding the evolution and adaptivity of concealed ovulation was put forth by Alexander and Noonan (1979). This stated that females concealed ovulation as a strategy to obtain male aid for females and children.

Given this information, it is not extraordinary to suspect that concealed ovulation has created a selection pressure in human males to either better

detect ovulation or develop counter strategies. Research indicates that one possible counter strategy to concealed ovulation is the chemical composition of human semen (Burch and Gallup 2006).

Many induced ovulation species do not show ovulatory signals. Research in induced/spontaneously ovulating species shows that not only is it the seminal fluid that induces ovulation but also it is a factor that is a potent stimulator of luteinizing hormone (Adams and Ratto 2013). These “ovulation induction factors” (bioactive prohormone forms) are absorbed through the female reproductive tissue into the bloodstream and have been shown in rats, Bactrian camels, alpacas, koalas, llamas, cows, mice, and rabbits.

Human seminal plasma contains estrone, estradiol, follicle stimulating hormone, luteinizing hormone (Ney 1986), and luteinizing hormone releasing hormone. Of these, luteinizing hormone releasing hormone is the most appropriate as an OIF candidate, acting in physiologically similar ways to the OIFs listed above. However, human males also have five times more LH in their semen than circulating blood levels (Ney 1986). OIFs may not be needed when luteinizing hormone is in such high levels. Induced ovulation in humans could be due to luteinizing hormone, luteinizing hormone releasing hormone, or another OIF.

Cutler et al. (1979) first investigated this when seven of the eight women studied who experienced extreme cycle lengths also had sporadic sexual behavior. These authors in 1980 showed that there were no aberrant short menstrual cycles and relatively fewer cycles that lasted over 33 days among the regular sexually active women. Veith et al. (1983) investigated the effect of exposure to males (sexually or sleeping) to ovulation. Ninety-two percent of the women who spent two or more nights with a male ovulated, as compared to only 56% of the women who only spent one night or less with a male. However, no relationship was found between sex and ovulation. It was suggested that it was not the number of sexual encounters, but the consistency that had an effect on ovulation.

In 1985, Cutler et al. found that women who maintained a weekly coital frequency had no incidence of short cycles and no very long cycles. Women who reported regular weekly sex with men had a greater incidence of fertile menstrual cycles. Finally, 1991, Burleson et al. studied the effect of heterosexual activity on menstrual cycle variability. Celibate women had more variable cycles than regular women, even when gynecological maturity was controlled for. This is similar to the Whitten effect in rodents where females isolated from males display irregular cycles.

It is important to note that all studies found that sex had to be consistent to have an effect on the menstrual cycle. This is very interesting in light of the effect of concealed ovulation on the human mating system. It is possible that not only did concealed ovulation demand greater male investment but also the female reproductive system functions better with consistent male physiological “investment.” For example, preeclampsia studies show a cumulative benefit of semen exposure over time; limited sex or condom use is linked with increased risk (Klonoff-Cohen et al. 1989), and the effect is partner-specific (Dekker et al. 1998).

Conclusion

In summary, males and females throughout human history have created selection pressures upon each other, as they competed to meet their reproductive goals. For women, ovulation became concealed, which resulted in greater paternal investment and more positive child outcomes. For men, semen chemistry evolved to better synchronize insemination with ovulation, increasing (among other things) fertilization rates.

Cross-References

- [Copulatory Intrasexual Competition](#)
- [Evolutionary Arms Race](#)
- [Intrasexual Competition](#)

- [Placental Proteins in Semen](#)
- [Semen and Vaginal Chemistry](#)
- [Semen Familiarity](#)
- [Seminal Plasma](#)

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Reproductive Timing

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Synonyms

[Continuous breeding](#); [Cyclical breeding](#); [Induced ovulation](#); [Seasonal breeding](#); [Sexual timing](#)

Definition

For conception to occur, both temporal and spatial proximity are required for the release of male and female gametes.

Introduction

Sex alone will not suffice when it comes to reproduction. Among most sexually reproducing species, insemination (the deposit of male gametes) must be proximate to ovulation in both time and space in order for conception to occur. Because sperm viability is short-lived in humans (Gallup et al. 2009), insemination and ovulation must be tightly coupled in time; certainly no more than ± 24 h and probably closer to ± 12 h. While sperm may be capable of staying alive in the female reproductive tract for longer periods of time, once activation occurs with the introduction of sperm into the vagina, they rapidly lose the ability to achieve capacitation (a sudden increase in vigorous activity when sperm encounter an egg in the fallopian tubes that is needed to penetrate and fertilize the egg) and are no longer reproductively viable.

Temporal Synchronization

Temporally synchronizing insemination with ovulation among different species has been achieved through the evolution of four different breeding patterns: seasonal breeding, cyclical breeding, induced ovulation, and continuous breeding.

Seasonal Breeding

Patterns of *seasonal breeding* are triggered by changes in the photoperiod (i.e., changes in the amount of light relative to the amount of dark in a 24 h period) which trigger the release of sex hormones, and as a consequence, breeding only occurs during a relatively narrow seasonally specific period of time. Seasonal breeding evolved not only to synchronize insemination with ovulation, but among species that are displaced to the north or south of the equator it serves to synchronize the production of offspring with a period of time during the year that will give offspring enough time to acquire the necessary resources to survive their first winter (see Gallup et al. [in press](#)). Although humans are no longer seasonal breeders, a disproportionate number of human babies are born in the spring and if you count back in time by 9 months to determine when they were conceived, humans show a vestigial tendency toward summer breeding (Timonen and Carpen [1968](#)). With the invention of artificial illumination, humans have unwittingly created a “continuous summer” where they are exposed to ± 16 h of light day in and day out, 365 days a year (Gallup et al. [in press](#)).

Cyclical Breeding

Other species employ patterns of *cyclical breeding* where breeding proclivity is under the control of endogenous mechanisms that trigger the release of hormones on a recurring cyclical

basis. Among many species that are affected by cyclical breeding, female sexual receptivity is usually restricted to the fertile/ovulatory phase of the cycle which serves to synchronize insemination with ovulation. Among many species that engage in cyclical breeding, females produce ovulatory cues (visual, auditory, or olfactory) that signal ovulation and have a powerful effect on males by triggering sexual arousal. Cyclical breeding in humans is expressed as the menstrual cycle. Even though humans can engage in sex at any point in the menstrual cycle, growing evidence shows that women are still unwittingly subject to important menstrual cycle effects that often operate below the radar (i.e., at a subconscious level).

A classic and compelling case in point is a study conducted by Miller et al. ([2007](#)) where they tracked the tips earned on a daily basis by lap dancers as a function of where they were in their menstrual cycle and whether they were using hormonal contraceptives. Those who were naturally cycling almost doubled their tips when they were in the fertile phase as compared to the menstrual phase. Equally interesting was that naturally cycling lap dancers earned more money in tips during all phases of their menstrual cycle than those on hormonal contraceptives. While all the lap dancers were acutely aware of day-to-day variation in their tips, none had any idea that where they were in their cycle or that using hormonal contraceptives made a difference.

Taking hormonal contraceptives not only diminishes your attractiveness and your libido, it also puts many evolved and otherwise adaptive choice mechanisms on hold. Couples who met when the woman was on the pill are far more likely to have children who are immunocompromised, i.e., at greater risk of a variety of common ailments (Birnbaum et al. [2016](#)). Moreover, women who discontinue using hormonal contraceptives to get pregnant often discover that they are living with a man they feel they no longer know and who they find less sexually attractive (Roberts et al. [2012](#)).

Induced Ovulation

A relatively small number of cyclical breeders also exhibit *induced ovulation*. Cats and rabbits, for example, are induced ovulators. As anyone with an adult female cat that has not been neutered can testify, when cats go into heat (which means they are in the fertile phase of their cycle), their behavior changes dramatically. But unless your cat has sex with another cat while she is in heat, she will not ovulate. Among induced ovulators, vaginal stimulation is required for ovulation to occur. Induced ovulation provides for the more efficient use of eggs.

Continuous Breeding

Although humans are still affected by subtle effects of seasons and cycles, women no longer produce vivid, easily discernable ovulatory cues. As a consequence, human sexual behavior is no longer driven solely by such considerations and humans approximate what are called *continuous breeders*. In the absence of ovulatory cues, the problems posed by synchronizing insemination with ovulation become more acute. Engaging in high-frequency sex that is independent of seasons and cycles represents an evolved statistical solution to this problem, i.e., high-frequency sex that occurs over an extended period of time will eventually lead to instances in which insemination and ovulation will be coincidental. Thus, patterns of continuous breeding represent an evolved solution in humans to the problem posed by the loss of ovulatory cues.

Spatial Proximity

In addition to the need for temporally synchronizing the release of male and female gametes, spatial proximity is also important.

Internal Versus External Fertilization

The problem of achieving proximity in space for gamete release can be illustrated by the distinction between external versus internal fertilization. Among many species of fish, the male and female simply release their genetic material into the environment in sufficiently close proximity to one another that the sperm from the male will intermingle with and fertilize some of the female's eggs. For species that live in moving water (i.e., rivers and streams), the male must position himself immediately upstream from the female for spawning so that his sperm will drift downstream to come into close proximity to the eggs being released by the female. With the emergence of internal fertilization, sperm are deposited inside the female's reproductive tract where it is in much closer proximity to her eggs. This represents a more efficient use of sperm and eggs. The penis evolved primarily as an internal fertilization device (but see Gallup et al. ([in press](#)) for other derived functions that the human penis serves).

Spatial Proximity and Insemination

Most people do not realize that human evolution has also put a premium on spatial proximity when it comes to insemination. With the assumption of an upright posture and bipedal locomotion, the woman's reproductive tract has changed from what used to be a parallel orientation with respect to gravity when we were quadrupeds to what is now a perpendicular orientation where it is poorly suited for sperm retention (Gallup and Suarez [1983](#)). Under such conditions, natural selection may have operated to put a premium on penis length as a means of depositing sperm deep in the vagina in close proximity to the cervix as a means of promoting sperm retention. Consistent with this analysis, the human penis is largest among the great apes, which are our closest living relatives (Short [1979](#)).

Conclusion

Sexual reproduction requires the release of male gametes to occur in both temporal and spatial proximity to the release of female gametes in order for conception to occur. Temporal contiguity has been achieved by the evolution of four distinct breeding patterns: seasonal breeding, cyclical breeding, induced ovulation, and continuous breeding. Along with restrictions on timing, spatial constraints have led to the evolution of internal fertilization, and in the case of bipedal, humans may have contributed to a reproductive advantage associated with a longer penis. When it comes to reproduction, it is not simply a question of whether to breed or not to breed, it is a question of when and where.

Cross-References

- [Orgasm](#)
- [Reproductive Frequency](#)

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Reproductive Value

- [Fitness Benefits of Costly Signalling](#)
- [Helping and Reproductive Value of the Recipient](#)
- [Observations of Sexual Dimorphism](#)

Reproductive Value and the Evolution of Aggression

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Synonyms

[Fitness](#); [Harming](#); [Homicide](#); [Lifetime reproductive success](#); [Long-term growth rate](#); [Violence](#)

Definition

Reproductive value is defined as the contribution of an individual to the future gene pool of a population. Because reproductive value mediates the fitness costs and benefits of social behavior, it plays a key role in the adaptive value of aggression.

Introduction

Most populations are structured into classes. Classes are features of organisms and their environment that influence the portion of their lifetime reproductive success that is not directly ascribed to the action of genes associated with the trait of interest. In such populations, individuals can transition between different classes over the course of their lifespan, and, while in each class, they generate fitness that contributes to their lifetime reproductive success (Frank 1998). The relative weight of each class on the lifetime reproductive success of an organism is given by its reproductive value, which measures the contribution of individuals in any given class to the future gene pool of a population (Frank 1998). Class structure and reproductive value influence the evolution of traits. The impact of traits on lifetime reproductive success depends on their effect on the fitness of each class, with each of these effects being weighted by the reproductive value of the corresponding class. Thus, classes with high reproductive value will in general contribute more to the action of natural selection than classes with lower reproductive value (Frank 1998).

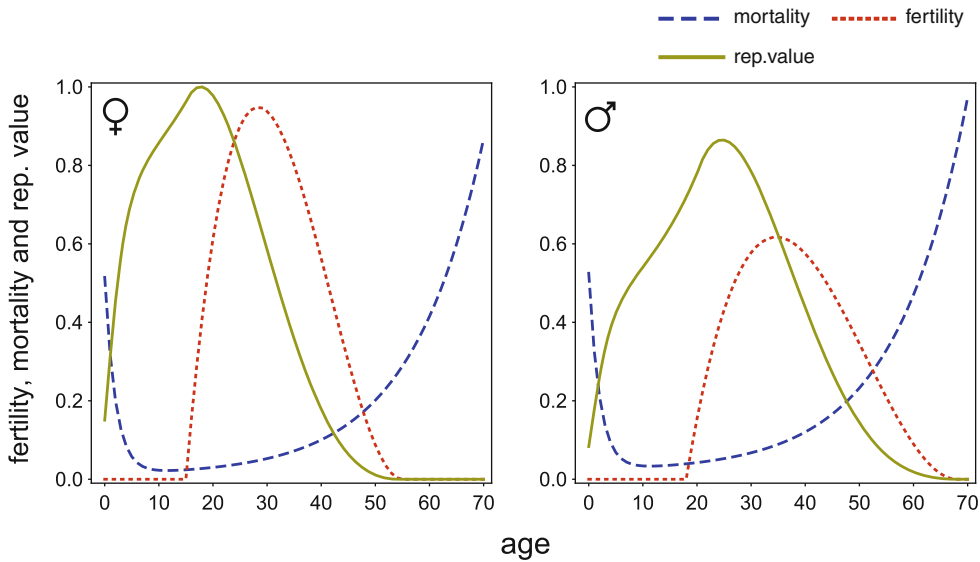
Class structure and reproductive value mediate the evolution of social traits, including aggression (Rodrigues and Gardner 2013). In populations without class structure, Hamilton's rule, the condition governing the evolution of social behaviors, is given by $-c + rb > 0$, where c is the cost of the social behavior to the actor, r is the coefficient of relatedness between the actor and the recipient, and b is the benefit enjoyed by the recipient of the behavior (Hamilton 1964). Hamilton's rule tells us that an altruistic act will evolve if the cost to the actor is sufficiently low and the benefit – depreciated by the coefficient of relatedness – is sufficiently high. Although Hamilton's rule is often described in terms of an altruistic act, it explains the evolution of any type of social behavior. These behaviors can be classified into four main types, depending on the sign of the fitness costs and benefits: when $c > 0$ and $b > 0$, the behavior is denominated altruistic; when $c < 0$ and $b > 0$, the behavior is

denominated cooperative (or mutually beneficial); when $c < 0$ and $b < 0$, the behavior is denominated selfish; and when $c > 0$ and $b < 0$, the behavior is denominated spiteful. Most often aggression is a selfish strategy because it benefits the aggressor and imposes a cost on the victim, but it can also be a spiteful behavior in which both the aggressor and victim suffer costs.

This classical formulation of Hamilton's rule assumes that the actor and recipient belong to the same "class." That is, the only difference between actor and recipient lies in their genes, a difference that is encapsulated in the coefficient of relatedness, r . More generally, actor and recipient can differ in many respects, including age, state, and/or sex (Rodrigues and Gardner 2015, 2016; Rodrigues 2018). These differences matter for the evolution of social behavior, and they are partially captured by reproductive value. When social partners are in different classes, Hamilton's rule can be written as $v_A C + r v_R B > 0$, where C is the survival (or fecundity) cost to the actor; B is the survival (or fecundity) benefit enjoyed by the recipient; v_A is the reproductive value of the actor (or actor's offspring); and v_R is the reproductive value of the recipient (or recipient's offspring; Rodrigues 2018). This form of Hamilton's rule highlights that reproductive value mediates both the costs experienced by the actor and the benefits enjoyed by the recipient.

Reproductive value is typically measured as age- and sex-specific averages at the population level and is calculated from age-specific fertility and mortality rate curves. If we assume a stationary population, reproductive value at age x is given by $v_x = \sum_{y=x}^{\infty} (l_y/l_x) m_y$, where m_y is the fertility rate at age y and l_x (or l_y) is the probability that an individual survives to age x (or y), with $l_x = \prod_{a=1}^x (1 - \mu_a)$, in which μ_a is the mortality rate at age a (Fig. 1).

While the reproductive value curves of men and women are similar, there are important differences that have an impact on sex-specific patterns of aggression. In men, reproductive value rises and peaks later in life, and once it attains its peak, it slowly decreases as men enter old age. In women, the pattern is different: they achieve



Reproductive Value and the Evolution of Aggression, Fig. 1 Hypothetical fertility, mortality, and reproductive value curves for women and men as a function of age. Age of peak reproductive value is less than age of peak

fertility. Typically, the reproductive period of women starts earlier than the reproductive period of men, while the reproductive period of women finishes earlier than the reproductive period of men

peak reproductive value earlier in life, and unlike men they experience menopause – i.e., the early cessation of reproductive function – which is characterized by a sharp decline in reproductive value after they reach their 40s or early 50s (illustrated in Fig. 1).

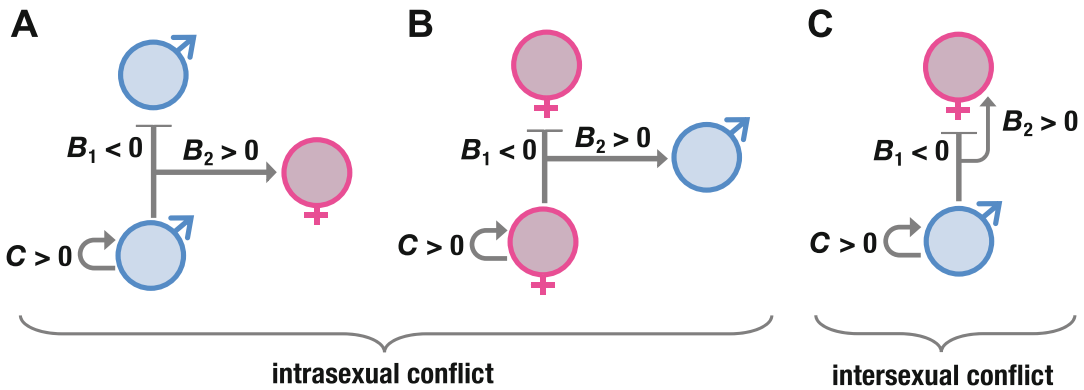
The total reproductive value in a population is shared between the sexes. In humans, an offspring receives half of their genes from her father and half from her mother, and therefore 50% of the gene pool of the population is composed of paternally derived genes and 50% of maternally derived genes. As a result, approximately half of the total reproductive value in a population is accrued to males (i.e., = 0.5), while the other half is accrued to females (i.e., = 0.5). This introduces intra-sexual competition for reproductive shares within each sex but also intersexual competition over control of fertility shares and breeding resources (Fig. 2).

Natural selection favors the evolution of aggression when it increases mating opportunities or breeding resources or, more generally, when it increases the reproductive value of the aggressor. Because many forms of aggression affect multiple individuals, it is helpful to consider a form of

Hamilton's rule that reflects such scenario. In particular, if we consider that the behavior involves an actor and n recipients, we can then write $-Cv_0 + \sum_{i=1}^n B_i v_i r_i > 0$, where v_0 is the reproductive value of the actor, B_i is the effect of the behavior on the fitness of the recipient "i," v_i is the reproductive value of the recipient "i," and r_i is the relatedness between the actor and the recipient "i."

Hamilton's rule and the reproductive value curves of humans allow us to make several predictions. First, when resources are limited, those with lower reproductive value are at higher risk of being victims of aggression. Second, individuals with high reproductive value are at risk of experiencing aggression that targets their reproductive potential. Finally, those with more future reproductive value weigh less their current fertility. Here, we explore some examples of how these and other general predictions can generate some insights into the evolution of aggression in human societies.

Aggression by males – In humans, mothers devote a large share of their time and resources to caring for their dependent young (Sear and Mace 2008). While the absence of any other family member has relatively little effect on the



Reproductive Value and the Evolution of Aggression, Fig. 2 Costly aggression, in which an actor pays a cost $C (> 0)$ to inflict a cost $B_1 (< 0)$, may evolve if this gives access to additional mating opportunities and/or reproductive resources $B_2 (> 0)$. Competition for breeding resources can occur against individuals of the same sex

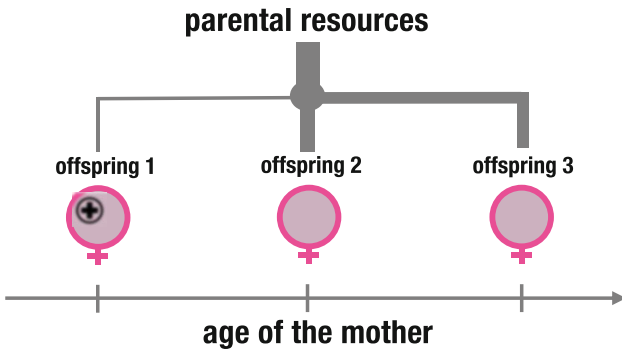
(intra-sexual competition, panels A and B) or against individuals of the opposite sex (intersexual competition, panel C). Males (or females) usually compete with other males (or females) for breeding opportunities. The benefits of aggression (B_2) tend to increase with the reproductive value of the individual of the opposite sex

survival of young, without a mother offspring survival drops significantly (Sear and Mace 2008). Because birth is followed by this intensive period of maternal care, it often takes 4–5 years between births. Under monogamy, this period of parental care can be harmonious: the genetic interests of both mother and father are closely aligned, and, therefore, they have a shared interest in the survival and well-being of current offspring. However, human societies are often characterized by serial monogamy and/or some degree of promiscuity. In such cases, a stepfather may be present, while a mother is still caring for the dependent young of a previous relationship. Because stepchildren and stepfathers are normally unrelated, the dependent young can represent a cost to the fitness of stepfathers. Further, the younger the offspring, the longer the period of maternal care before mothers can conceive again and therefore the longer the period before stepfathers can sire offspring of their own. Thus, the young age of stepchildren can increase the probability of abuse by stepfathers.

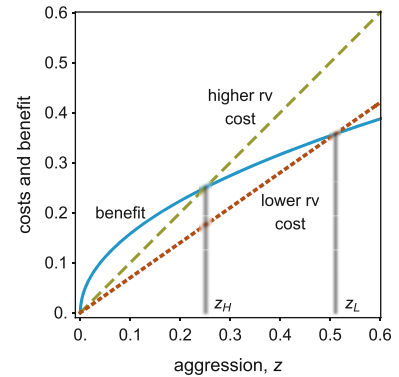
The age of the mother also influences the probability of abuse by stepfathers, which is higher when mothers are relatively young. First, younger mothers have higher future reproductive value. Second, reproductive value of infants (and children) can be low. Thus, the loss of a young

offspring may have a marginal impact on the lifetime reproductive success of a younger mother. Some evidence supports these predictions. First, the presence of a stepfather in the household increases the probability of child abuse. In a Canadian population, for instance, less than 1 in 1,000 children were victims of child abuse if they lived with their natural parents, but more than 12 in 1,000 were victims if they lived with one stepparent (Daly and Wilson 1988). Second, the risk of infanticide by a stepparent is significantly higher when children are within the 0–5 age range but drops significantly among older children (Daly and Wilson 1988). Finally, children of younger mothers are most at risk of violence (Daly and Wilson 1985; Nobes et al. 2019).

Aggression by females – In general, high relatedness between mother and offspring reduces the potential for maternal-offspring conflict. However, as we have seen above, other factors also play a role in mother-offspring interactions, and under some social and environmental conditions, maternal neglect of offspring – and other forms of aggression – is more likely to occur. For instance, whenever future reproductive opportunities are lost because of ongoing investment in current offspring, neglect of current offspring may allow parents to redirect resources to future offspring. This tendency may increase when current



Reproductive Value and the Evolution of Aggression, Fig. 3 The fitness costs of aggression are lower when directed toward a lower-reproductive value (lower-rv) offspring (i.e. offspring 1), and therefore lower-rv offspring are at risk of experiencing higher levels of



aggression ($z_L > z_H$). Mothers may decide to allocate more resources to future children when a current child has low reproductive value, for instance, due to a congenital disorder

offspring are of lower quality (i.e., lower reproductive value) owing to genetic factors, such as heritable diseases, or to nongenetic factors, such as chronic diseases caused by parasite infections (Fig. 3). Second, postponing childbearing may allow parents to accumulate social and economic capital, which they can invest in future offspring. Older women, by contrast, may not have this option.

As menopause approaches, pregnancies become increasingly unlikely, and therefore current offspring are relatively more valuable for older mothers. As a result, we expect older mothers to be less likely to neglect their current children than younger mothers. Evidence that supports these predictions is diverse. Infanticide rates are highest among mothers that give birth before their 20s; and infanticide rates among mothers that give birth in their early 20s are higher than those of mothers that give birth in their late 20s or early 30s (Daly and Wilson 1988). Further, older primiparous mothers are more likely to invest in high-risk (i.e., premature) children than younger or multiparous older mothers (Beaulieu and Bugental 2008).

Sexual coercion – While in most cases there is mutual consent between sexual partners, in others some degree of sexual coercion may occur. There are certainly costs associated with such violent behavior but – from an evolutionary perspective –

there are also potential fitness benefits. For instance, the benefits of sexual coercion increase with the fertility and reproductive value of the victim. Coercion of infertile victims renders zero benefits, but the potential costs will still be large, and therefore such behavior can seriously compromise the fitness of aggressors. Because fertility and reproductive value tend to be higher among younger women, they are at a higher risk of being the target of aggressors. Some evidence supports these predictions. First, the age group that is more at risk of rape is the 20–24 age group (Thornhill and Thornhill 1983). Second, in a study among forager-farmers, a key predictor of wife abuse was the young age of the wife (Stieglitz et al. 2012). Wives in their early 20s are almost twice as likely to be abused than wives in their mid-30s (Stieglitz et al. 2012). Finally, a statistical analysis has found that of those women that were victims of robberies, younger women were also more likely to be victims of rape (Felson and Cundiff 2012).

Neglect of elders – If reproductive value was the only measure of value, then elders would have little or no value for societies. Elders are users of a community's resources, and this can create a tension between elders and other members of the community. Despite this tension, in many societies, elders are revered and therefore there must be factors that promote a positive view of old age.

Naturally, how societies perceive old age depends on culture. However, biological considerations may also contribute to a positive perception of old age. While the reproductive value of elders is zero, their behavior often increases the reproductive value of daughters, sons, and grandchildren. For instance, the survival and well-being of young depend on to a certain extent on the care provided by grandparents (Sear and Mace 2008). Despite this, the lower reproductive value of elders, the fragmentation of extended families in contemporary societies, and the societal cost of old age may sometimes contribute to the neglect of elders, which, in some cases, can lead to self-harming behaviors among this age group. Old age seems to be especially taxing in males. While men are more likely than women to commit suicide across all age groups, the difference is highest at older ages, when men are more than seven times more likely to commit suicide (Kruger and Nesse 2006). Moreover, a cross-cultural study found that male suicide rates increase significantly at old age, especially in harsh environments (Syme et al. 2016).

Male-male aggression – As we have seen above, the reproductive value of males and females follow similar patterns: they increase rapidly after maturity, peak during middle age, and decrease as men and women approach older age (Fig. 1). There is, however, an important contrast: variance in reproductive value is greater among males. High variance in male reproductive value occurs because some men father many offspring, while others father few or none, a discrepancy that is less pronounced among women. Variance in reproductive value emerges because of the hierarchical structure of human societies: those men that attain higher status tend to father more offspring (Chagnon 1988). Because of the correlation between status and reproductive success, competition for status, which can take the form of aggression, can be fierce. Males are willing to pay the cost of aggression – as aggressors risk injury and even death – if aggression increases their status and consequently their mating success. Naturally, mating success can only be translated into reproductive success if the male is fertile. Thus, it is perhaps not surprising that aggression

is more prevalent among younger men, when male fertility is at its peak. A statistical analysis of contemporary societies shows that homicide among men increases rapidly after sexual maturity and is significantly larger among men than among women (Daly and Wilson 1990). In tribal societies, aggression can be positively correlated with number of wives and children (Chagnon 1988; Glowacki and Wrangham 2015), which suggests that male-male aggression may have been adaptive in our ancestral environment.

Female-female aggression – While intra-sexual competition is more salient among men, female-female competition is also widespread, with women competing for resources as well as mates. Intra-sexual competition among women can be indirect, which is usually manifested in the form of displays or gossip, but it can also be direct, as women may resort to verbal abuse and even physical aggression (Campbell 2013; Stockley and Campbell 2013). The proclivity for indirect aggression is similar between men and women (Hess and Hagen 2006), but women tend to target features of other women that are correlated with fertility and/or reproductive value. For instance, women tend to derogate more the appearance and promiscuity of other women than men do (Buss and Dedden 1990). Sometimes, male preferences may mediate competition among women. For instance, because younger women have higher fertility rate and reproductive value, men tend to prefer younger women. As such, younger women can be at higher risk of aggression from older women (Campbell 2013).

Conclusion

Reproductive value provides a measure of an organism's value to the evolutionary process, and therefore it mediates the costs and benefits of social behavior, including aggression. Reproductive value can explain and predict a vast number of human behaviors. It can predict the intensity of aggression that occurs within each sex, between the sexes, and between individuals in different condition and of different age. While

aggression may have an evolutionary basis, human societies have undergone major transformations over the past few millennia, and therefore contemporary expressions of aggression may not be adaptive. Ultimately, to prove adaptation we must find correlations between behavior and fitness that are consistent across a wide range of cultures (Stearns and Rodrigues 2020). Finally, aggression is not an inevitable outcome hardwired in the genes of organisms. Aggression is often a context-dependent behavior, and it depends on multiple cultural and biological factors, which include reproductive value. Understanding the biological factors that mediate aggression can ultimately be used to reduce aggression both within and between societies.

Cross-References

- [Adaptation](#)
- [Aggression](#)
- [Contexts for Men's Aggression Against Women](#)
- [Evolutionary Psychology](#)
- [Female Age as a Predictor of Men's Aggression Against Women](#)
- [Inclusive Fitness](#)

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Reproductive Variance

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Synonyms

Bateman's principle; Parental investment theory;
Sexual selection

Definition

The degree of success that individuals of a species are able to achieve by producing offspring. Male reproductive success tends to be limited to the number of matings one can achieve, while female reproductive success tends to be limited by the number of eggs that can be produced.

Introduction

The term reproductive variance in biology refers to the distribution of reproductive success that characterizes a species or sex within a species. Among most vertebrate species, the reproductive variance of males is higher than the reproductive variance of females. Robert Trivers' proposed parental investment theory, according to which anisogamy and internal gestation result in a higher minimum obligate investment in offspring on the part of females. According to Trivers, a host of mating-related behaviors are the result of the disproportion in obligate investment between males and females. Angus Bateman investigated the difference in reproductive variance between males and females while studying *Drosophila melanogaster* (fruit fly). Bateman observed that very few females failed to reproduce, while a much larger proportion of males failed to reproduce. Additionally, the amount of copulations was a stronger predictor of reproductive success for

males than for females. From these observations, Bateman's principle was formulated which states that reproductive variance is greater for males than for females. Finally, modern research has found this relationship to hold constant among the majority of animal species; however, there has also been research on a few species in which these sex roles are reversed. Additionally, the field of evolutionary psychology has utilized the theoretical contributions of Bateman and Trivers to explain a range of human mating-related behaviors, such as sex differences in responses to an infidelity.

Sexual Selection

Charles Darwin proposed natural selection as the mechanism by which evolution occurs in his work *On the Origin of Species by Means of Natural Selection* (Darwin 1859). However, Darwin noted that some features found in nature did not appear to confer an advantage to an organism's survival. According to his theory of natural selection, the plumage on a male peacock should not be selected for it is metabolically costly and likely to attract predators while not conferring any benefits to survival. Darwin followed his first work on evolution with *The Descent of Man, and Selection in Relation to Sex* in which Darwin proposed a second mechanism by which traits are selected, sexual selection (Darwin 1871). According to Darwin, certain features, such as the peacock's tail, evolved because they conferred benefits to mating rather than survival. There are two complementary processes by which sexual selection occurs: intrasexual competition and intersexual selection. Intrasexual competition is the direct or indirect competition between conspecifics of the same sex in which the result of the competition leads to differential access to mating opportunities. These competitions can take the form of direct aggression, production of ornamental features, etc. For intersexual selection to occur, individuals of one sex must have a general consensus on the traits that are preferable in members of the opposite sex and will choose those members differentially based on those preferences. For

example, the bright plumage that male peacocks display is selected because female peacocks are more likely to choose males based on the number and arrangements of eyespots on their train (Petrie and Halliday 1994).

Bateman's Principle

Angus Bateman (1919–1996) was an English geneticist who received his B.S., Ph.D., and D. Sc. from King's College, London (Dewsbury 2005). In 1948, Bateman reported a study investigating the reproductive success of *Drosophila melanogaster* (fruit fly) males and females (Bateman 1948). The principal report of Bateman's 1948 study would later be defined as Bateman's principle by E.O. Wilson (1975) to mean that "the variance of reproductive success is greater in males than in females" (Wilson 1975, p. 325).

In Bateman's 1948 study, he set out to provide what he referred to as more systematic and statistical support for sexual selection as described by Charles Darwin. Bateman put groups of equal numbers of males and females from different strains of the *D. melanogaster* into small bottles and then allowed them to mate and lay eggs for several days. Bateman tracked the success rates of males and females by mixing different strains of the fly who had distinctly different chromosomal markers that would allow for him to identify the fertility (or reproductive success) of the males and females in the groups. First, Bateman identified that there was a greater variance in the reproductive success of males compared to females. For example, only 4% of all of the female flies failed to reproduce contrasted with 21% of the males failing to reproduce. Bateman identified this as a "sign of intra-masculine selection" being that sexual selection is working primarily on males. Second, Bateman found a positive linear relationship between male fertility and the number of copulations achieved, while female fertility and number of copulations were very weakly correlated. Bateman referred to this second phenomenon as the "cause of intra-masculine selection" since the success rate of

males to produce offspring is limited by the number of copulations (and inseminations) that occur, while the limiting factor of female reproductive success is the number of her own sex gametes that are available to be inseminated. Bateman argued that the existence of these two pieces of evidence, (1) the differential of males who are able to successfully copulate compared to the number of females who are able to copulate and (2) the number of copulations with novel sex partners that predicts greater success in males than in females, indicates that the pressures of sexual selection will have a stronger effect on males than on females. For example, in many species of polyandrous elephant seals, females usually have at least one pup in their lifetime, while the majority of male elephant seals father zero pups in their lifetime, while a small number of alpha-male seals father the majority of offspring (Hoelzel et al. 1999).

Parental Investment Theory

A parent's investment of resources in an offspring often comes at the expense in the investment in oneself, other offspring, or potential mating opportunities. Robert Trivers (1972) proposed parental investment theory. According to Trivers, the sex that has the higher minimum obligate investment in offspring will be more selective in their mating. As a corollary, the sex that has the lower minimum obligate investment will tend to engage in more intersexual competition for mates. Investment in offspring occurs at several levels. Most sexually reproducing species are characterized by anisogamy, meaning the gametes produced are not equivalent. In humans, females produce of relatively large, expensive eggs, whereas male sperm is far cheaper to produce (a male will produce hundreds of billions of sperm over the course of his life). In addition to the production of gametes, females must endure 9 months of internal gestation and then breastfeeding in order to produce viable offspring. Males, however, need only to minimally invest in the act of copulation in order to produce viable offspring. According to

Trivers, this difference in gamete size and gestation begets further differences in investment as the offspring continues to age. This difference in investment between the sexes is predicted to lead to a mating pattern that is different for males and females. Females, due to their higher investment, will tend to be more selective with their mating opportunities in order to prevent the costs of making a poor mate choice. Because females will be more selective with their mating decisions, males are expected to be more likely to compete among themselves in order to gain mating opportunities. This pattern of mating strategies between the sexes is referred to as the ardent male-coy female hypothesis.

Modern Research

Bateman's principle, the theory of sexual selection, and reproductive variance have been demonstrated and explored in a number of different species, ranging from humans (McKean and Nunney 2005; Brown et al. 2009), the sex-reversed pipefish (Jones et al. 2000, 2005), the rough-skinned newt (Jones et al. 2002), redback spiders (Andrade and Kasumovic 2005), bank voles (Mills et al. 2007), wild turkeys (Krakauer 2008), red jungle fowl (Collett et al. 2014), seed beetles (Fritzsche and Arnqvist 2013), and hermaphroditic freshwater snails (Pelissie et al. 2012) to name a few.

Bateman's principle has been expanded to explain a diverse number of species ranging from plants and hermaphroditic species (Arnold 1994) as well as to different mating systems and sex roles among humans (Brown et al. 2009) and to species where the sex roles are reversed (Jones et al. 2000, 2005). In all of these unique circumstances, male and female psychology and behavior tend to follow trends where males have more variability in their access to females and in their ability to successfully reproduce. Mating frequency and control over their partner's mating availability (in applicable species) are significantly better predictors of male success than female success. Sex-reversed species are seen as exceptions that prove the rule in that pregnant

males tend to become choosier and rely less on access to mating than their female counterparts (Jones et al. 2000, 2005) who compete mating access at a similar rate to the non-sex-reversed species.

Bateman's principle has contributed to a significant line of research in human evolutionary psychology, especially when taken into consideration in concert with parental investment theory, for example, men being less discriminatory in choosing mates than women (Buss 1989; Buss and Barnes 1986) and women having the most intense discrimination when choosing potential long-term partners (Buss 1994; Townsend et al. 1995). Miner and Shackelford (2010) review many of the aspects of sex-predicted behavior related to reproductive variance. Men's preference for younger, more attractive partners, women's preference for partners with resources and partners who are willing to invest, and men engaging in behaviors to prevent, correct, and anticipate their partner's potential infidelities are examples of men and women utilizing strategies that are consistent with the predictions laid out by Bateman's principle. Men are, in general, likely to be more upset by the prospect of their partner committing a sexual infidelity (increasing the risk of cuckoldry and their partner's fertility), while women are generally more upset by the prospect of their partner committing an emotional infidelity (increasing the risk of partner defection and a loss of investment) (reviewed in Bjorklund and Shackelford 1999). Relationships are more likely to be dissolved over issues of infidelity and infertility (reviewed in Miner and Shackelford 2010). Bateman's principle predicts that males are more likely to be concerned with having access to females, while females will be more interested in discriminating high- and low-quality males. Indeed, men tend to most attuned to the issues of their partner's fertility state and are reflected in how they pursue, maintain, and end relationships as well as how they become emotionally distraught and where they place their attention. Women tend to place more of their attention to the ability of their partner to invest in long-term relationships and provide for a family.

Conclusion

The reproductive variance of a species and sex within a species is an important component in determining the mating strategies that the organisms within that group adopt. Bateman's principle outlines a pattern in which males tend to experience greater reproductive variance than females do. Indeed, this pattern has been found in the majority, but not all, of the animal species that have been studied. In addition to Bateman's theoretical contribution, Robert Trivers explained the reason why the sexes within most species demonstrate differences in reproductive variance: obligate minimum investment. According to Trivers, the obligate minimum investment in offspring is much higher for female. Among humans, females produce a much larger, more costly gamete, are required to endure 9 months of internal gestation, and then must continue to breastfeed and care for the offspring after birth. Due to the difference in reproductive variance and obligate minimum investment, males and females display differences in their mating behaviors and strategies. These sex differences have been studied across a range of species and, in the field of evolutionary psychology, have been documented in humans as well. For example, human females tend to be more discriminant when selecting potential long-term mates than human males do (Buss 1994).

Cross-References

- [Female Reproductive Variance](#)
- [Male Reproductive Variance](#)

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Repulsion

► Disgust

Reputation

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Synonyms

High status; Prestige

Definition

The families of suicide attackers might benefit reproductively from the increased reputation associated with having a family member celebrated as a martyr, suggesting a potential evolutionary motivation for suicide attack.

Introduction

Suicide terrorism might yield heightened family reputation and status within local communities, providing an avenue through which suicide terrorists might generate benefits to their genetic kin. Though this is an interesting hypothesis, there are currently no studies that measure the mating or reproductive outcomes of the kin of suicide terrorists as a function of increased reputation.

Theoretical Overview: Suicide Terrorism and Reputational Benefits to Kin

Research conducted in several Muslim nations indicates that identity based on collectivism as opposed to individualism is associated with greater support for terrorism (Kruglanski and Orehek 2011). The cultures of the Middle East and circum-Mediterranean region are often deemed honor cultures where many social norms and priorities are constructed around reputation maintenance and shame-avoidance (Peristiany 1965). Employing agent-based modeling, Nowak et al. (2016) demonstrated that honor cultures could be adaptive under conditions wherein institutional authority is weak and resources are scarce. Thus, honor-based strategies, i.e., retaliation against aggressors in defense of one's own and family's reputation and honor, might be an effective and evolutionarily stable strategy. An abundance of evidence suggests that suicide is used in a geographical array of "honor cultures" to reestablish one's own or one's family's honor (Osterman and Brown 2011). Likewise, motivations for suicide terrorism include the defense of honor of one's people and homeland; moreover, suicide terrorists are often celebrated as "martyrs" (Hafez 2006). The reputational benefits obtained by the deceased in these instances appear to extend to their kin, and theoretically, the kin might receive reproductive benefits (e.g., greater access to high status mates) as a result of the death of their loved one as a perpetrator of a suicide attack.

Hafez (2006) contends that in a rational-choice approach to suicide terrorism, the honor afforded the families of martyrs might factor into cost-benefit calculations, noting that in this perspective the social benefits for the suicide terrorist alone cannot be considered “rational” since he or she will not survive to see those benefits. In this sense, the reputational argument of suicide terrorism must factor culture into consideration. The veneration of martyrs, Hafez (2006) argues, will occur in a society when the following conditions are met: (1) the justification and celebration of martyrdom through tradition and symbolic representations; (2) the promotion of violence and martyrdom by recognized cultural authorities (e.g., local leaders or institutions); and (3) the society feels victimized or threatened by an outside aggressor.

Conclusion

Numerous studies demonstrate that high status correlates with reproductive success. Though reputational benefits are anecdotally cited as a potential motivator for suicide attack, there are currently no studies that even quantify reputation, nor measure how those might translate into reproductive benefits for the kin of suicide attackers.

Cross-References

- [Benefits to Kin](#)
- [Culture of Honor](#)
- [Denis Decatanzaro](#)
- [Indirect Benefits of Altruism](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)
- [Reliability and Deception in Language](#)
- [Sexual Access Manipulation](#)
- [Status Competition and Peer Relationships in Childhood](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Reputation and Altruism

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Synonyms

[Cooperation](#); [Helping](#)

Definitions

Reputation is used to mean a publicly available index of past behavior.

Altruism is used to mean a behavior that is costly to the individual and benefits another individual or group of individuals. Here it is taken to include behaviors that have some cost, but which may have a net benefit due to the responses of others.

Introduction

Why might individuals help others? Evolutionary psychologists seek adaptive answers to this question by investigating how helpers get something

back. This becomes most challenging when individuals are not kin and do not get a return through direct reciprocation. One way in which helping might actually be self-interested is if others learn about the helpful behavior and in consequence act preferentially toward you. Thus it may pay to care about reputation – about behavior not just with a partner but in a social setting where others may have access to some index of past behavior. It is apparent that people act more altruistically when they are being observed, e.g., people are more charitable in the presence of group mates (Bereczkei et al. 2007). This tendency is found even when the “observer” is simply an image of “watching eyes” (Bateson et al. 2006). Furthermore, people are viewed in a better light when they act altruistically, gaining in reputation (Hardy and Van Vugt 2006). Research has then focused on what benefits individuals get from this boost to reputation.

Altruistic Reputations

Individuals who have been seen to be altruistic might be less likely to be punished for contributing little, or may be more likely to be rewarded. Focusing here on the possible rewards, these may come through indirect reciprocity or through reputation-based partner choice. Indirect reciprocity is where people are more likely to help those who help others. Through this mechanism, altruism pays when it leads to an increase in altruism received. The best known models of this process invoke what is termed “image scoring,” a simple index of past donation behaviors (Nowak and Sigmund 2005). Laboratory experiments show that people do indeed tend to give more to those with higher image scores (Wedekind and Milinski 2000).

Theories of reputation-based partner choice consider instead that when someone is altruistic, they are not just helping another individual; they are displaying something about themselves. Costly signaling theory shows how being altruistic can honestly indicate high quality to an observer since the costs of altruism can make it pay off for high-quality individuals but not for

those with fewer resources (Gintis et al. 2001). Economic experimental games show that people will display greater altruism in order to make themselves more attractive partners and that this pays off in the long term from engaging in profitable partnerships (Sylwester and Roberts 2010). The increase in altruism associated with competition for partners has been called competitive altruism (Roberts 1998). Using an altruistic reputation to signal to potential social partners may explain phenomena such as charitable giving and willingness to contribute to public goods games.

An altruistic reputation may also be driven by sexual selection. For example, people are more likely to be altruistic to attractive members of the opposite sex in economic games (Farrelly et al. 2007) and also when giving to women seeking sponsorship for charities (Raihani and Smith 2015).

Conclusion

It is apparent that being seen to be altruistic can be in an individual’s own interests, and the benefits of reputation building may be a powerful explanation for altruism in humans.

Cross-References

- ▶ [Altruism](#)
- ▶ [Altruism Advertises Cooperativeness](#)
- ▶ [Altruism Advertises Generosity](#)
- ▶ [Altruism Among Nonkin](#)
- ▶ [Altruism and Costs to Altruist](#)
- ▶ [Altruism and Watching Eyes](#)
- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Altruism Displays Cooperative Potential](#)
- ▶ [Altruism in Kin Selection](#)
- ▶ [Altruism Norms](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Altruistic Punishment Enhances Reputation](#)
- ▶ [Cooperation](#)
- ▶ [Cooperation Among Fishes](#)
- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation and Social Cognition](#)

- Cooperation in Social Carnivores
- Cooperation in Social Insects
- Cooperation Varies with Genetic Relatedness
- Cooperative Alliances
- Cooperative Breeding
- Cooperative Foraging
- Cooperative Grooming
- Cooperative Hunting
- Evolution of Reciprocal Altruism
- Food Sharing and Nonhuman Reciprocal Altruism
- Genuine Altruism
- Helping
- Heroic Rescue in Humans
- High-Cost Altruistic Helping
- Indirect Benefits of Altruism
- Nonhuman Reciprocal Altruism
- Observation of Altruism
- Prisoner's Dilemma and Cooperation
- Problem of Altruism
- Puzzle of Altruism, The
- Reputation
- Social Reputation

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Reputation as a Context for Men's Aggression Against Men

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Synonyms

Culture of honor; Dominance; Formidability; Hierarchy; Intergroup conflict; Power; Sexual selection; Status

Definition

An individual's reputation refers to knowledge others share about that individual. Aggression can be used to manage one's reputation or influence the reputation of others.

Introduction

Research suggests that people are generally concerned with how aggressive other individuals are. For example, researchers have shown that people are good at detecting angry facial expressions (Hansen and Hansen 1988), can form first impressions of an individual's aggressiveness after looking at their face for 0.01 s (Willis and Todorov 2006), and usually judge people on warmth before judging them on other traits

(Fiske et al. 2007). Furthermore, people (especially men) also seem interested in displaying their own aggressive tendencies. For instance, experiments illustrate that men may act aggressively to assert their manhood when it is challenged (Bosson et al. 2009). Also, in cultures of honor, aggression is often used by men as retaliation after being offended (Nisbett and Cohen 1996). The propensity to track how violent other individuals are, as well as the drive to show one's aggressiveness, sets the stage for the emergence of reputations for aggression in human societies. This entry will use an evolutionary perspective to explore why people care about aggressive reputations and why men seem keener on being viewed as aggressive, relative to women.

Status, Hierarchy, and Other Related Constructs

Before answering those questions, it is worthwhile to distinguish reputations from other related concepts. As previously defined, reputation refers to knowledge that others possess concerning an individual. Some of the concepts often confused with reputation include those of status, hierarchy, power, and dominance. Cummins (2005) defines status as the priority one has over access to resources. To be high status, other people must know that one has priority over resources – i.e., one must have a specific reputation. The concept of hierarchy is directly related to status, but is at a higher level of analysis. A hierarchy refers to how a group is organized in terms of the individuals' statuses. A group has a hierarchy if some individuals in the group have a higher status than others. Finally, power and dominance are associated with how people interact as opposed to their standing in a group. Keltner et al. (2003) define power as an individual's ability to influence other individuals' states by granting or withholding resources or administering punishments. Dominance refers to the power relationship between two people. A person is dominant if they have more power than the other person.

Aggression is often used to negotiate or enforce dominance, power, or status. For example, individuals can increase their status by demonstrating their aggression publically and signaling that they have more power and dominance. In this way, people can use aggression to shape their reputations. Studies on the aggressive behaviors of men from cultures of honor exemplify this: Nisbett and Cohen (1996) report how men from the South of the United States (which has a stronger culture of honor than other regions of the United States) are more likely to respond aggressively when insulted by another man. Furthermore, people in these cultures usually give more weight to hierarchies, and men strive to maintain their status through demonstrations of power and dominance. While status or power afforded by aggressive reputations may seem intrinsically beneficial, their importance throughout (and before) human history was not due to intrinsic benefit but because of the consequences they had for an individual's fitness. Below, some adaptive functions of aggressive reputations are examined.

Accessing Resources for Survival

In hunter-gatherer tribes, which were the most common form of social organization during human evolution, labor was often divided among tribe members (Villotte et al. 2010). Although most of these societies were relatively egalitarian (primarily the nomadic tribes) and the fruits of their labor may have been shared throughout the tribe, those who had the means to occasionally access a larger share of that food (especially in times of scarcity) would be more likely to survive and provide resources to their kin. Aggressive interactions might have been an effective strategy to take food from others, and reputations may play an important role in these interactions.

From the perspective of those who are not aggressive, keeping track of who has a reputation for aggression can be extremely beneficial. One can avoid losing food by hiding it from them; one

can also choose to forfeit food preemptively to avoid getting injured in a confrontation or to gain an aggressive individual's favor. Those who are known to be aggressive also benefit from keeping track of other's reputations. They can target their efforts toward less aggressive individuals and be vigilant of those who are more aggressive than them. In addition to tracking reputations, those who are aggressive benefit from managing their own reputations. Directly attacking others in public may be an effective way of achieving this; however, merely threatening others (especially those who already have reputations for being aggressive) may also create a reputation for aggression while reducing the risks of injury associated with actual violence.

Accessing Mates

A notable feature of aggressive reputations is that men are generally more concerned with them than women. While this sex difference is pronounced in cultures of honor (Nisbett and Cohen 1996), men tend to be more aggressive than women across cultures. Daly and Wilson (1988), for example, famously showed that men are much more likely than women to commit homicide. Archer (2004) extended this result to other measures of aggression in real-world contexts. He also found that the sex difference in aggression occurred from early childhood on.

Evolutionary psychologists commonly explain this sex difference using sexual selection theory (Buss and Duntley 2006). The theory describes the different adaptive problems faced by the sexes due to a differential energy investment in reproduction. For example, women are required to bear the energetic costs of internal fertilization, placentalation, and gestation – much steeper physiological costs than those for men. A consequence of this is that men are able to have more offspring throughout their lifetimes than women. This pushes them to invest more time and energy into mating frequently, while females devote more resources to selecting mates that will be worth their

investment. The men who are more frequently chosen as mates are more likely to pass on the genes for their reproductive strategies. Because of the competition to access as many females as they can, a fruitful reproductive strategy for men is to use aggression to increase their potential for successful competition, for example, by stealing their resources, stealing their mates, physically injuring them to deter attempts to compete for a mate, or injuring them to demonstrate strength to a potential mate. Thus, men have more incentives to be aggressive (especially among each other) than do women.

The sexual selection of aggression in men increases the value of having a reputation for aggression. Men who are known to be more aggressive (or have more capacity for aggression, such as physical formidability) are seen by women to be more suitable reproductive partners (e.g., Snyder et al. 2011). Aggressive men can also deter competitors from trying to mate with their partners, their own partners from mating with other men, and are more likely to regain former mates (Buss and Duntley 2006).

Aggression Between Groups

While the sections above focused on aggression between individuals as a means to manage reputation, the same reasoning can be applied to aggression between groups. Assaulting groups can grant similar benefits as attacking other individuals – i.e., access to resources and mates. In fact, intergroup conflicts are common among human hunter-gatherer societies and other species of primates (Wrangham and Peterson 1996). This highlights the adaptive benefits that intergroup conflicts had during human evolutionary history.

Just as individuals manage their reputations for aggression, groups can also use coordinated attacks to create a reputation for themselves. This aids groups in maintaining control over subordinate groups which are less likely to offer counterattacks and will often surrender resources at the other group's will. As argued by Sidanius

and Pratto (2001), intergroup hierarchies are an important aspect of social behavior, and people strive to justify and maintain them. Yet, as in interpersonal competition, men stand to gain more than women do by using aggressive tactics to maintain a hierarchical order of groups (Navarrete and McDonald 2014). Indeed, substantial research has shown that men more strongly prefer systems of group-based hierarchy, relative to women (Lee et al. 2011), and therefore likely have a stronger interest in maintaining their group's reputation for toughness.

Building a Reputation

As has been argued in previous sections, having a reputation for being aggressive can confer many benefits, especially to men. Given this advantage, it can be worthwhile to trick others into believing that one is more aggressive or formidable than one actually is. This way, people who would otherwise be unable to forcefully steal resources can convince others to surrender resources. However, adaptations for deception will create selection pressures for counteradaptations to detect deception. Those who detect liars do not forfeit resources unnecessarily. The end result of these selection pressures is that people only believe someone is aggressive if there are reliable indicators of aggression. These indicators are referred to as honest signals (Van Rhijn and Vodegel 1980).

Aside from actual conflict, there are many honest signals of aggression (or at least the capacity for aggression) that people use. One of them is physical formidability. Sell et al. (2009) demonstrated that people have specialized mechanisms to determine an individual's fighting ability merely by observing their face and body. Carré et al. (2009) extended these findings by showing that a person's facial width-height ratio is related to that person's aggressive behavior. In addition to physical characteristics, a person's risk-taking behavior can also indicate his/her propensity toward aggression. Fessler et al. (2014) found

that men who took more risks were estimated to be physically larger than men who did not take risks. It is likely that more physical characteristics and behavioral patterns associated with aggression are also used as honest signals. These help individuals maintain accurate reputations of their and other people's aggressiveness without engaging in costly conflicts.

Conclusion

Managing reputations for aggression has been an important activity in men's lives throughout human evolutionary history. Such reputations can confer power and status, which may lead to more material resources and access to mates. The strategy to use aggression to influence other individuals' behavior likely extends to how groups interact. Lastly, an important aspect of this strategy is that the signals of aggressiveness men send must be reliable indicators of their actual aggressiveness.

Cross-References

- ▶ [Aggression](#)
- ▶ [Culture of Honor](#)
- ▶ [Culture of Honor and Retaliation](#)
- ▶ [Information About Likely Combat Success](#)
- ▶ [Reputation as a Context for Men's Aggression Against Men](#)
- ▶ [Sexual Selection](#)
- ▶ [Sexual Selection via Direct Male-Male Interactions](#)

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Reputational Memory

- [Memory Enhanced for Cheaters Versus Non-cheaters](#)
- [Recall of Cheaters](#)

Rescue

- [Rescuing Strangers](#)

Rescuing Friends and Relatives

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Synonyms

[Heroism](#); [High-cost altruism](#); [Inclusive fitness](#); [Reciprocal altruism](#)

Definition

High-cost altruistic behavior, which is directed towards kin, friends, or acquaintances, and could have evolutionary origins in kin selection and/or reciprocal altruism.

Introduction

High-cost altruistic behavior takes place when the altruistic donor incurs substantial fitness costs (e.g., in terms of time, energy, resources, risking injury) when helping the recipient. The cost of altruistic helping seems to be directly associated with relatedness – we are willing to engage in higher cost help when it is directed towards close kin (Stewart-Williams 2007). The highest possible costs are paid when the altruist is risking her own life. Especially in those circumstances, we are more likely to help closely related individuals rather than friends or more distant relatives (Fitzgerald and Whitaker 2009). This kind of high-cost altruistic help is best explained by the theory of inclusive fitness, suggesting that by helping our close relatives, we are also helping our own genes.

However, people are willing to engage in high-cost altruistic acts directed towards unrelated individuals, especially to those who are considered as friends. Altruism within friendships could potentially be explained by reciprocal altruism, the idea that favors will be returned over a larger period of time. Nevertheless, when helping puts the altruist's life in danger, the likelihood of returning the favor at a later stage is reduced. In situations of heroic rescue, reciprocal altruism becomes a nonviable evolutionary explanation. It is important to understand the evolutionary roots of friendships in order to understand why high cost helping takes place between acquainted, but unrelated individuals.

Helping Relatives

According to the idea of inclusive fitness, it makes sense to help relatives if it increases their reproductive success, as by doing this, the altruist is benefitting his own genes. Research on many different species has shown that group members are more likely to emit alarm calls when closely related individuals are present.

Alarm calling is a form of a costly altruistic action, as the callers may be more easily spotted by predators, and as a consequence, could lose their lives. This kind of behavior could have been chosen for if it saves the lives of relatives. Indeed, nepotistic alarm calling is prevalent across a wide variety of species (Hollen and Radford 2009). In humans, kin may be favored over unrelated individuals in high-risk rescuing situations. A famous study by Burnstein et al. (1994) demonstrated that in hypothetical situations, humans are more willing to run to a burning house to rescue a close relative, suggesting that these kind of altruistic actions are guided by a kinship heuristic.

Helping Friends

High-cost altruistic help among friends is not based on kin selection, but possibly on the quality of the relationship, which could be a key factor in the maintenance of reciprocal altruism (Curry et al. 2013). Research has suggested that people expect reciprocation more when helping friends rather than siblings (Rotkirch et al. 2014). In extreme situations, such as in those where people are putting their lives to risk in order to rescue a friend, reciprocal altruism does not make sense as a theoretical explanation. If there is an increased likelihood of serious injury, or death, the benefits from future reciprocation are not sufficient for offsetting the costs. It has been suggested that especially women treat friends as if they were kin (Ackerman et al. 2007). If friendship is akin to kinship, high-cost altruistic rescuing behavior may not be adaptive at all, but rather, a by-product of a kinship heuristic that is applied to friendships.

Conclusion

High-cost altruistic behavior, where an individual incurs substantial fitness costs, is best explained by kin-selection. By helping closely related

individuals, direct fitness costs are offset by the increase in inclusive fitness. Research has shown that helping that involves physical pain, injury, or death is more likely to be directed towards close relatives. However, occasionally, individuals do put their lives to risk for their friends. This could be potentially explained by a kinship heuristic that is applied to friends, and may not serve an adaptive function.

Cross-References

- ▶ [Alarm Callers are Females with Greatest Genetic Representation](#)
- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)
- ▶ [Helping and Genetic Relatedness](#)
- ▶ [Helping and Inclusive Fitness Benefits to Helper](#)
- ▶ [Heroic Rescue in Humans](#)
- ▶ [High-Cost Altruistic Helping](#)
- ▶ [Rescuing Strangers](#)

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Rescuing Strangers

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Synonyms

[Altruism](#); [Hero](#); [Heroism](#); [High-cost](#); [Rescue](#)

Definition

Heroic rescue of strangers is an event where the rescuer puts hers/his life into risk in order to save the life on an unrelated person who the rescuer is unfamiliar with.

Introduction

Heroic rescue is a high-cost altruistic behavior that puts the life of the donor into danger while saving the life of the recipient. As such, it is an extreme form of high-cost altruism, where the ultimate cost is death (i.e., complete loss of fitness). Rescuing relatives and friends can be understood in terms of kin selection and reciprocal altruism. However, rescuing strangers is harder to explain in evolutionary terms, as this is something that has no association with future returns in terms of inclusive fitness, or returning a favor. One of the theories that has been used in trying to explain heroic rescuing of strangers is the Costly Signaling Theory, which will be briefly reviewed below.

Costly Signaling Theory and Rescuing Strangers

According to the Costly Signaling Theory, some aspects of behavior may have a function in signaling the quality of the individual to others, with the ultimate goal of changing the behavior of the receiver of the signal. Strength, stamina, and physical risk-taking have all been considered as

honest signals of quality as a sexual partner. Physical risk-taking is more typical to men than it is to women, and women prefer risk-taking men in short-term mating contexts (Sylwester and Pawlowski 2011). This indicates that risk-taking is an indicator of genetic fitness, and risk-takers are preferred by women who are shopping for good genes for their offspring.

Heroic actions often (but not always) include significant physical risk. Heroic risk-taking has been proposed as a costly signal, indicating the underlying genetic quality of the rescuer. Heroic risk includes both the elements of physical prowess and altruism, both of which are attractive to women, and have been proposed as costly signals of mate quality. Research has found that men are more likely to engage in physically risky rescues of strangers than women are (Lyons 2005), especially when their mating interests are activated (Griskevicius et al. 2007). Interestingly, some of my earlier work found that especially men from lower socio-economic backgrounds were more likely to rescue a stranger than wealthier men were (Lyons 2005). It is possible that poorer men have less to lose and more to gain in if they put their life in danger in order to rescue a stranger.

There is some evidence to suggest that women have a mating preference for heroic men. Farthing (2007) found that women perceived heroic (but not nonheroic) risk-takers as “sexy,” possibly due to genetic benefits coupled with possible status, resources, and protection that may have an association with high-cost altruistic acts. Thus, if a male engages in a dangerous rescue and survives, they may have increased mating opportunities, leading to enhanced reproductive success. Indeed, research on war veteran has found that heroic rescuers had later more offspring than nonheroic veterans (Rusch et al. 2015), pointing at the possibility that heroism has evolved through female choice for heroic males.

Conclusion

Heroic rescuing of strangers is more typical to men than for women, and women have a preference for men who risk their lives in order to rescue

another person. Evolutionarily speaking, the ultimate causes for heroic rescue of strangers could be explained by the Costly Signaling Theory, and female choice for heroic males. If a male can “afford” a heroic rescue, and survive, they may have underlying genetic quality that will be transferred to the woman’s offspring.

Cross-References

- [Heroic Rescue in Humans](#)
- [High-Cost Altruistic Helping](#)

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Research Methods

- [Advertising](#)
- [Qualitative Versus Quantitative in Evolutionary Science](#)

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Resemblance

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Synonyms

[Adoption](#); [Evolution](#); [Facial cues](#); [Parenting](#)

Definition

How similar in appearance or behavior an individual is to another, often used as a proxy for genetic relatedness.

Introduction

An important evolutionary benefit which might offset the high costs of parental investment is the opportunity for parents to maximize their genetic fitness through offspring survival (Trivers 1972). However, while women can always be certain that the offspring is genetically related to them, men risk chances of being cuckolded and mistakenly investing in biologically unrelated offspring (see ► [“Paternity Uncertainty and](#)

[Investment in Sons and Daughters”](#) chapter). In fact, the rates of paternity uncertainty are found to be approximately 1.9%. Therefore, evolutionary theories suggest that men may have adapted mechanisms to mitigate this possibility. In addition to limiting their mates’ opportunities for extra-pair copulations through mate guarding and jealousy behaviors (see ► [“Paternity Uncertainty and Investment in Sons and Daughters”](#) chapter), men may be predisposed to detecting paternity uncertainty before and after the birth of offspring. Prior to the advent of modern genetic testing, men were not able to accurately determine the paternity of a child and relied on behavioral, social, and physical cues. For behavior, fathers are theorized to evaluate mates’ behavior around the time of conception (Gray and Anderson 2010). If the father is physically away for a long period before conception, other potential mates show interest in mother, and/or if the mother seems less enthusiastic about the birth of the child, fathers may be suspicious of cuckoldry. Similarly, fathers may rely on information from other individuals about the fidelity of their mate (see below). Finally, fathers may rely on resemblance as a proxy for genetic relatedness (Volk and Quinsey 2002). In particular, fathers evaluate genetic relatedness after birth of the offspring by assessing the degree of facial resemblance with offspring (Daly and Wilson 1982; Gray and Anderson 2010).

Detecting genetic relatedness through facial resemblance is found to have modest levels of accuracy in humans (Alvergne et al. 2007). This mechanism of detecting cuckoldry and paternity uncertainty is shown to be used across cultures. For example, in polyandrous societies, such as Nepal, father-child facial resemblance is used to detect the actual father of the child (Gray and Anderson 2010). Similarly, in Sierra Leone, father-child facial resemblance is used to detect adultery. In addition to determining rates of paternity uncertainty, cues of facial resemblance to offspring are also shown to influence the degree of paternal investment.

Facial Resemblance and Paternal Investment

Mothers may also be showing positive parental behavior based on the degree of facial resemblance due to a general association between genetic resemblance and altruistic behaviors (Hamilton 1964); however, fathers have found to be more strongly influenced by cues of facial resemblance to offspring across cultures. Men are shown to emphasize cues of facial resemblance when making hypothetical investment decisions (Platek et al. 2004; Volk and Quinsey 2002). In addition, studies on actual paternal investment have found that father-child resemblance is associated with higher levels of emotional bonding and investment (Alvergne et al. 2007). Further, neurological studies have found greater activations in brain areas associated with the inhibition of negative responses when men view children's faces that are morphed with their own faces compared to non-morphed faces (Platek et al. 2004).

Adoption and Facial Resemblance

Although adoptive parents are aware of the non-genetic relationship to adoptive children, studies show that facial resemblance between adopted parents and children is still shown to be an important factor for adoption agencies and for adoptive parents (Indekeu 2015). In fact, studies have shown that the successful adoptions are more likely to occur for families with high facial resemblance between adoptive parents and children. One explanation could be that adoptive parents require social and emotional mechanisms to help support the lack of genetic relatedness to the adoptive children. Therefore, cues of high facial resemblance to adopted children may generate recognition of genetic similarity and influence altruistic behaviors in order to increase inclusive fitness (Hamilton 1964). In addition, high levels of parent-child facial resemblance may help with kinning, in which the adoptive parents make a

deliberate effort to frequently expose the adopted child to the immediate and extended family in order to increase perceptions of kinship (Volk 2011). In this case, high levels of facial resemblance between adoptive parents and adopted children may reduce social disconnections between the adopted child and the immediate and extended family. Finally, cues of facial resemblance may increase adoptive parents' investment as it may increase the appearance of genetic relatedness to others and consequently reduce social stigma associated with adopting.

Perhaps as a consequence of this, men's perceptions of facial resemblance are more strongly influenced by social factors. For example, biological mothers and maternal family are shown to ascribe paternal facial resemblance to the offspring more in the presence of the putative biological father (Daly and Wilson 1982) possibly to increase perceptions of relatedness and investment. In addition, unrelated men provide higher facial resemblance ratings between a child and a male when they are informed that an unknown man is the biological father of an unknown child (Bressan and Martello 2002). Thus, social indicators of facial resemblance may similarly influence adoptive fathers' perceptions and responses to the adopted children.

Conclusion

Children in adopted families are shown to form healthy attachments to their adopted families at similar levels to children with parents in biological families (Gray and Anderson 2010). However, high facial resemblance between the adoptive parent, especially the adoptive father, and children may increase attachment and investment. Although evolutionary theories explain why adoptive parents invest in adopted children, there is still less empirical research regarding why adoptive parents sometimes provide higher levels of investment compared to biological parents (Volk 2011). Therefore, future studies should further investigate the influence of facial

resemblance on parental investment in adoptive parents by examining individual factors, such as personality differences, in order to shed light into why some adoptive parents may be emphasizing cues of facial resemblance more than others.

Cross-References

- [Adoption Preferences](#)
- [Consolidating Familial Power](#)
- [Evolutionary Paradox: Adoption](#)
- [Forms of Adoption](#)
- [Function of Adoption](#)
- [Paternity Uncertainty and Investment in Sons and Daughters](#)

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Resentment

- [Downfall of “Tall Poppies”](#)

Residual Reproductive Value

- [Helping and Reproductive Value of the Recipient](#)

Resistance to Welfare Policies

- [High SES Against Redistribution](#)

Resisted Mating

- [Forced Copulation](#)

Resisted Matings

- [Prevalence of Forced Copulation in Orangutans](#)

Resolution

- [Reconciliation](#)

Resource Availability

- [Access to Resources](#)
- [Prey Availability](#)

Resource Competition

- [Self-Assessment of Fighting Ability](#)

Resource Control

► Resource Defense

Resource Defense

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Synonyms

Resource control; Territoriality

Definitions

Resource defense consists of controlling or denying others' access to resources, including territoriality.

Introduction

Resource defense is a broad category covering all the means by which individuals or groups actively attempt to control or deny access of others to resources, using agonistic or display behavior. This entry focuses on defense of material resources located within spatially circumscribed territories by humans, particularly in non-state societies documented ethnographically and archaeologically.

The Logic of Economic Defensibility

Half a century ago, the biologist Jerram Brown published a short paper entitled "The Evolution of Diversity in Avian Territorial Systems" (Brown 1964). Brown's immediate goal was to explain why some bird species are strongly territorial, others are not, and some species in fact alternate between territorial and open-access regimes. Further variation exists in the immediate benefits of

controlling a resource; for many species, it is local patches of food that are defended, while for others, nesting sites or roosts are the object. Brown pointed out that controlling the resources in a territory has benefits, but comes at a cost: time and energy (and potentially risk of injury) spent monitoring an area, advertising one's presence, and deterring intruders. His simple but profound argument was that natural selection would only favor defending territories if the benefits of doing so exceeded these costs – if the net benefits (measured in fitness or its correlates) were positive. This principle has since been labeled *economic defensibility*. Brown gave this principle empirical meaning by linking it to the spatiotemporal distribution of resources – specifically, their density and their predictability.

Dense resources are more defensible (are more likely to repay the costs of territorial defense) because the area the territory holder must defend to control access to a given resource is smaller, thus requiring less time and effort to monitor. Predictable resources are more defensible for two reasons: the area that must be defended to encompass them is easier to locate (spatial predictability) and the income from them is higher and more reliable (temporal predictability). Note that this argument does not entail environmental determinism, since the costs and benefits of both territory defense and resource acquisition also depend on the resource consumer's capabilities (e.g., birds can fly, can advertise territory residence with song, and so on); in the human case, consumer capabilities include technology and other culturally variable attributes.

Although dated in its particulars, Brown's simple argument has greatly helped biologists explain the diversity of animal territorial systems, just as his title had promised. It harnessed the logic of natural selection (i.e., the trade-offs involved in gaining some benefit at some cost and their effects on fitness) to ecological variation. The economic defensibility model has proved remarkably durable and has been validated in hundreds of studies of spatial behavior in a wide variety of species (Davies and Houston 1984; Dubois and Giraldeau 2005). Dyson-Hudson and Smith (1978) published the first anthropological application of

the model. That paper employed qualitative assessments of the economic defensibility model in various ethnographic and ethnohistoric contexts to draw three broad conclusions: (1) territorial behavior (exercise of spatial ownership claims, controlling access to resources) is facultative and varies strategically (demonstrating that people are at least as clever and flexible as birds); (2) this strategic behavior corresponds to variation in resource density and predictability across space and over time, as predicted by the economic defensibility model; and (3) within the same social system (even the same household), territorial strategies may be applied to some resources but not to others. The following section expands on these points, citing relevant ethnographic and archaeological data.

Variation in Human Resource Defense

The basic expectations derived from the economic defensibility model are summarized in Table 1 (after Dyson-Hudson and Smith 1978; see also Cashdan 1992). Note that these expectations and their predictors are stated in ordinal terms (e.g., low versus high density, intermediate defensibility); rigorous tests would require precise quantitative measures rarely found in the ethnographic and archaeological data (for a recent effort to estimate such values, plus a formalization of the economic defensibility model, see Baker (2003)). Nevertheless, the qualitative evidence is quite extensive.

Variation Across Space

The economic defensibility model predicts that, if density and predictability are high enough, territorial systems (property rights in land) will be

favorable. There are many cases in which steep gradients in resource density or predictability correlate with marked shifts in land use. For example, over a vast stretch of the Pacific coast of North America, dense and predictably located runs of salmon fostered permanent villages, territorial claims to salmon streams by corporate kin groups (Donald and Mitchell 1994), and chronic warfare (focused not only on control of resource sites but also on seizing property and slaves). Yet a short distance inland, across the coastal ranges in the Columbian Plateau and Subarctic regions, where resources were much lower in density and also generally less predictable, the indigenous societies had traditional land use patterns stressing communal access rights (the exceptions being favored salmon-fishing spots at falls and rapids, which were sometimes owned by kin groups).

Finer-scale variation in land use within ethnolinguistic areas is perhaps even more convincing. The Eskimoan (Yup'ik and Iñupiat) peoples of coastal Alaska had permanent (winter) villages and strongly defended discrete territorial boundaries (Andrews 1994; Burch 1980). Yet when some Iñupiat spread eastward across the Canadian arctic about one millennium ago, the much lower resource density encountered there led to greatly relaxed boundaries approaching open-access land use. Similar variation in territoriality and related aspects of land use are found in the ethnolinguistically homogenous Great Basin. Most of the Great Basin is very arid, resulting in low resource density and predictability. The indigenous Shoshone and Paiute were highly mobile and had few controls over land use. Yet in well-watered areas such as the Owens Valley, relatively dense and predictable resources were associated with decreased mobility and forms of land ownership that were clearly territorial (Steward 1938;

Resource Defense, Table 1 Resource density, predictability, defensibility, and resultant land use (Modified from Dyson-Hudson and Smith 1978)

	Resource density	Resource predictability	Economic defensibility	Predicted land use
A.	Low	Low	Low	High mobility, dispersed population
B.	Low	High	Intermediate	Home range system
C.	High	Low	Intermediate	Mobility, information sharing
D.	High	High	High	Geographically stable territoriality

Thomas 1981). Archaeological analyses of variation in territorial strategies too numerous to cite here detail similar patterns in varied locations worldwide.

Steep gradients in resource density and predictability can have profound implications for broad aspects of political economy. Many scholars have pointed out that stratified social systems have initially arisen in areas with such gradients, such as fertile floodplain valleys surrounded by arid regions and rainforests with patchily distributed potable water resources. The link to economic defensibility can be quite direct: where kin groups or other coalitions are able to control key resource patches, subordinates have few options, and stable levels of exploitation can increase (Boone 1992; Smith et al. 2010). Again, note that this is not environmental determinism: resource density and predictability are in part functions of social and technological variables (e.g., agricultural techniques, labor division, social stratification), and social agency (in seeking or resisting political and economic domination) is central to the process.

Variation Over Time

A theory of spatial behavior that did not allow rapid change over time would be falsified by the historical record. In fact, the economic defensibility principle leads one to expect such change whenever there are sufficient large shifts in resource density or predictability. These shifts can arise from exogenous factors, such as environmental change that alters these parameters for key resources; or it can be generated by endogenous shifts in resource utilization due to technological, demographic, economic, or political variables.

Examples of both exogenously and endogenously driven shifts in defensibility parameters are evident at various temporal scales. Ethnohistoric data on Algonquian peoples in the North American eastern subarctic document a shift from hunting focused on caribou to semi-sedentary settlement patterns focused on trapping of furbearers and foraging for moose and small game (Bishop 1986). The former pattern was characterized by high mobility, extreme flux in

group composition, and open access to resources, the most adaptive configuration for harvesting caribou with indigenous technology, as these preys clump together and move rapidly and unpredictably across the landscape. In contrast, fish, hare, furbearers, and even moose are dispersed and relatively sedentary prey, most efficiently harvested by foragers in small family-based groups who can economically defend hunting territories and coterminous traplines. The shift from the caribou-hunting economy to the fish/hare/moose/trapping economy was a complex process driven by economic factors (particularly the fur trade) as well as technological (steel traps, guns, etc.) and environmental ones (e.g., caribou declines).

On intermediate time scales, the intensification of agriculture is generally associated with higher labor inputs and shortened fallow, which increase both resource density and predictability. Such intensification is also associated with increased formalization of property rights and wealth inheritance (Shenk et al. 2010), thereby institutionalizing resource defense across multiple generations. On an even broader time scale, it has been argued that the dramatic increase in environmental stability (and thus resource predictability) with the transition from Pleistocene to Holocene climates, coupled with suitable local ecological and social conditions, was necessary for agriculture to develop and spread over much of the globe in the last five to ten millennia (Richerson et al. 2001).

Differential Defense Across Resources

There are many cases in which actors (individuals, households, or larger groups) exhibit territorial behavior with some resources but not others. This can be fully consistent with the economic defensibility model: if resource X is dense and predictable enough to be economically defensible, but resource Y is not, the simplest expectation is territorial defense of X but not Y. An example is the pattern of land use and property rights found among many East African cattle herders, where garden plots and livestock are claimed as property by individuals or households, but grazing land is communally owned by the “tribe” (ethnic group).

This is clearly expected from defensibility logic, as good grazing areas are dependent on patchy and highly unpredictable rainfall distribution, whereas gardens are dense and predictable resources due to direct management. Livestock are even denser and predictable to the extent that people control their movements (Dyson-Hudson and Smith 1978). Extension of this argument to pastoralists in other areas has found broad support for economic defensibility predictions (Casimir 1992).

Group-Level Territoriality and Collective Action Problems

The previous section explained how the spatio-temporal scale of a resource is critical to its defensibility. This logic applies to the demographic scale as well. Suppose a resource is indefensible at the individual level because monitoring and defense costs are too high relative to the benefits of resource control. The resource may become defensible if individuals cooperate in monitoring and defense, and the economy of scale lowers per capita cost sufficiently. For example, East African pastoralists generally do not defend grazing land against members of their own “tribe” (ethnolinguistic group) but violently defended it against encroachment by other tribes. Dyson-Hudson and Smith (1978) admit their model does not explicitly treat intergroup conflict of this scale, focusing analysis of territory defense on the household level. The question then is how to secure the cooperation necessary to defend agricultural plots at the household level and grazing land at the ethnic group level. More generally, how and under what circumstances do individuals solve the problem of cooperative resource defense?

A collective action problem (CAP) arises when members of a collective (e.g., a household, village, voluntary association, etc.) must pay costs to produce a collective good – a resource available to all members of the collective (Olson 1965). Some theorists define CAPs more stringently as any case in which increasing the number of cooperators in a

group increases the average group payoff but any given member of the group is always better off defecting no matter the actions of other members (McElreath and Boyd 2007). The structure of the payoffs to collective action matters. For example, if group members benefit from cooperating whatever their social partners do, there is no CAP to solve (Clutton-Brock 2002). If group members can share the benefits or costs of cooperation and the benefit-to-cost ratio is high enough, a stable mixture of cooperators and defectors (or a stable mixed strategy employing both cooperation and defection) is expected to emerge (Doebeli et al. 2004; Maynard Smith 1982). Even if cooperation is mutually beneficial to all, complications may remain if group members must coordinate their cooperative investments (e.g., in organizing territorial monitoring). The linguistic capabilities of humans certainly facilitate complex coordination and communication of social norms (Smith 2010).

In sum, at least two types of CAPs may occur in territory defense: when it is impossible for a group member to defend the territory alone, and when the loss of territory is not costly enough to a single group member to deter a positive fraction of group members from shirking (Boone 1992). Even in fairly small groups, the mechanisms that potentially ensure cooperation in dyads such as direct reciprocity (Axelrod and Hamilton 1981; Trivers 1971) and kinship (Hamilton 1964) are insufficient (Boyd and Richerson 1988). If enforcement (punishment of free riders) is also costly to group members, a second-order collective action problem must be solved.

One class of solutions emphasizes private (individual) gains linked to collective action. Models of indirect reciprocity posit that individual reputations for cooperation become known through observation or gossip and then cooperators can avoid helping defectors even if they will not have the repeated interactions required for direct “tit-for-tat” reciprocity (Leimar and Hammerstein 2001; Panchanathan and Boyd 2003). Linking this to collective action requires that reputations be determined by contributions to collective action and then subsequent dyadic interactions allow cooperators to withhold aid

from defectors (Panchanathan and Boyd 2004); for example, if B knows A avoids contributing to territory defense, B can then withhold aid from A when A is sick or hungry or wants to arrange a marriage for his son.

Alternatively, contributions to collective action can constitute a signal of individual qualities (such as health, fighting ability, social network size and quality, etc.) that are difficult to observe directly (Gintis et al. 2001), and observers can use the signal to make mutually beneficial “side deals” with above-average signalers by allying with or deferring to them in other contexts (Lyle and Smith 2014).

Another class of CAP solutions involves inter-demic group selection, which involves selection among partially isolated and competing groups in a population. Under this framework, selection occurs both within and among groups. Within-group evolution selects against altruism because altruism is by definition costly to a given group member (e.g., those who vigorously monitor and defend group boundaries may suffer increased mortality risk). Selection among groups favors altruistic participation in group resource defense (collective action) because this increases the average payoff, thus the rate at which the group proliferates at the expense of other groups. Because within group variation is usually much greater than variation among groups, selection must be weaker within groups than between them for group selection to work (Boyd and Richerson 2007). Inter-demic group selection may be more likely in cultural species like humans because cultural transmission occurs on one-to-many and many-to-one bases, which, coupled with conformist bias within groups (“When in Rome, do as the Romans”), will decrease variation within groups and increase variation between them (Henrich and Boyd 2001), paving the way for culturally transmitted group-beneficial traits to proliferate at the expense of individuals. There is some empirical support for group selection involving territorial defense. Soltis et al. (1995) found that cultural group selection among warring territorial groups in New Guinea could have favored group-beneficial traits through the

extinction of groups by assimilation, though at a quite slow rate. Mathew and Boyd (2011) analyze ethnographic data on Turkana cattle raiding as reflecting the effects of cultural group selection.

To sum up this section, territoriality occurring in larger groups requires cooperation among the individuals and smaller social units that make up the group. The cooperation requirement introduces possible collective action problems (CAPs). Solutions to such CAPs might involve complex conditional strategies, interactions between genetic and cultural inheritance, selection occurring at multiple levels, or a combination of these. Regardless of mechanisms, as long as groups do find a way to cooperatively defend territories, the basic predictions of economic defensibility models apply.

Conclusions

This article summarizes the evolutionary ecological approach to resource defense known as the economic defensibility model and application of this model to explain variation in human territorial behavior that demonstrates its robust support in light of ethnographic and archaeological research. It highlights the importance of assessing model validity relative to the appropriate spatio-temporal as well as social and demographic scales. In addition, the economic defensibility principle of territoriality models can be applied to a broad range of resource types, including social networks (Chabot-Hanowell and Smith 2013).

Three main conclusions follow. First, ecological approaches to territoriality developed in biology and anthropology provide a flexible and robust framework for analyzing resource defense in a variety of species, including humans. Second, the net benefits of territorial resource defense are a function of variation in resource density and predictability, as specified in the economic defensibility model, as well as the specific capabilities of the competing individuals or groups. Finally, human territoriality involves a complex set of practices that vary within and across societies

and thus requires nuanced understanding and application of evolutionary ecological models.

Cross-References

► Body Fat Percent and Distribution

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Resource Holding Potential

- [Social Dominance and Sexual Access](#)
- [Social Dominance Reduces Fighting](#)

Resource Limitation

- [Resource Scarcity](#)

Resource Provision

- [Parental Investment Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)

Resource Scarcity

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Synonyms

[Resource limitation](#)

Definition

The economic problem of having inadequate resources to fully satisfy needs.

Introduction

While the psychology of resource scarcity is a new research area, the universality of resource scarcity has been a foundational assumption in modern economic analysis. Accordingly, limited resources required for satisfying our needs (e.g., labor, capital, and time for production or food for consumption) are always limited, which forces any rational individual to prioritize efficiency concerns (i.e., how to make the best use of resources at hand). This combines with the idea of diminishing marginal utility – another foundational concept in modern economics – to suggest that the economic value of a good, as reflected on its market price, increases with its level of scarcity. Despite its critical role in defining economics as the science of efficient use of scarce resources, however, effects of scarcity on the psychology of decision-making have been ignored until recently. It remains an implicit assumption in modern economic theory that the motivation for efficiency gains is independent of the level of scarcity (Isler 2009). Recent findings on the cognitive aspects of scarcity suggest that this assumption can be misleading (Shah et al. 2015), thereby directly linking the

foundations of economic science with evolutionary psychology.

Literature Review

Isler (2009) provided an early philosophical criticism of the “dominance of scarcity” in mainstream economics, hypothesizing that the formal framework of rational choice misleadingly results in the implicit assumption that humans are always fully motivated to efficiently use scarce resources. This assumption has over the past decade been subjected to serious empirical questioning, which resulted in promising findings that can guide both evolutionary psychology and experimental and behavioral economics towards new directions (Mullainathan and Shafir 2013).

Shah et al. (2015) showed in a series of experiments that low levels of income are associated with increased concern with opportunity costs and with making trade-offs, reflecting a focus on efficiency. The authors also showed value judgments of low-income participants to be less open to the influence of irrelevant contextual cues. Separately, Salerno and Sevilla (2019) found that people perceive scarce foods as having more calories. Together, these results suggest that scarcity increases expected utility for the goods in question and induces people to prioritize efficiency concerns for the task at hand, thereby moving people closer to the ideal of *homo economicus* presumed by rational choice theory.

This attentional focus, however, is also found to come at a high cost. Shah et al. (2012) devised a series of economic experiments for studying the undesirable cognitive effects of scarcity. Participants were assigned to scarce or abundant resource conditions (number of attempts available) in various tasks such as solving puzzles, some of whom were allowed to borrow resources from future rounds at high interest. Among resource-poor but not resource-rich participants, the ability to borrow improved short-term performance at the expense of worsened overall scores. Similarly, Tamm and Zhao (2016) showed

resource scarcity to improve memory of information about the scarce resource, while increasing attentional neglect of unexpected opportunities as well as weakening memory of abundant resources. These results highlight the main cognitive side effect of resource scarcity: increased focus on the current task results in attentional neglect of more distant opportunities through cognitive fatigue.

The finding that scarcity impedes cognitive function has substantial policy relevance, since it implies that poverty can in part be self-fulfilling. For example, Mani et al. (2013) found that Indian farmers experiencing seasonal income fluctuations exhibit improved fluid intelligence and cognitive control after harvest, when incomes are at peak levels. This and similar findings strongly suggest that poverty can breed more poverty through attentional neglect and cognitive impairment of economic decisions.

The link between resource scarcity and cognitive scarcity is likely to be a fundamental part of human psychology. For instance, Huijsmans et al. (2019) found in an fMRI study that the inducement of scarcity vs. abundance mindsets activated different neural networks associated with valuation and goal-directed choice. Given its underlying neurological basis, attentional focus and neglect due to scarcity are likely to shape heterogeneous domains of behavior. For example, Krosch and Amodio (2014) found economic scarcity to enhance biased perception of race, indicating that scarcity increases out-group discrimination. Similarly, scarcity manipulations have been shown to increase selfishness, deceptiveness, and antisocial behavior at the expense of cooperation (Prediger et al. 2014; Roux et al. 2015).

Conclusion

These findings directly link the economic concept of resource scarcity with the dual-process model of cognitive processes. Given that resource scarcity was – although varying in extent – a predominant feature of our evolutionary past and a critical determinant of our evolutionary success, it is perhaps not surprising that resource scarcity has

fundamentally shaped how our minds work. Research on the cognitive effects of resource scarcity is in its infancy, and the study of scarcity's relationship with intuitive cognitive processes promise to shape economics and evolutionary psychology.

Cross-References

- [Bounded Rationality](#)
- [Rational Actors](#)

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Resource Selection

- [Prey Availability](#)

Resource-Defense Polygyny

- [Competition for Resources Desired by Females](#)
- [Polygyny Threshold, The](#)

Resource-Holding Potential

- [Vocal Indicators of Dominance](#)

Resources

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Synonyms

[Food](#); [Male provision](#); [Material extrinsic investments](#); [Shelter and protection](#); [Status and wealth](#)

Definition

Male resource provision plays an important role in parental care and offspring survival; as a consequence it can act as a signal that is important in female mate choice. Male resource provision involves providing material extrinsic investments in the form of food, shelter, and protection and can be signaled through wealth and status.

Introduction

Because human babies require a longer period of parental care compared to other mammals,

parental investment by both sexes can have implications for offspring survival (Hill and Hurtado 1996; Nettle 2008). Since males invest in parental care through extrinsic material investments, through resources in the form of food, shelter, and protection, it pays for women to select mates that have the ability to make these provisions (Symons 1979). Males show off (signal) resources through wealth and status because females have marked preferences for those who do (Buss 1989; Pawlowski and Dunbar 1999). Resources may therefore act as a signal of mate quality that is important in female mate choice.

Resources as a Signal of Parental Investment

We contribute to offspring survival in two ways: one, through passing on our genetic code (good gene quality) and, two, through parental care (good provider quality) (Trivers 1972). Human babies are relatively costly to produce and raise. The increased size of the prenatal brain in humans means that to allow for the large head to pass through the birth canal, birth at 9 months is relatively premature compared to that of other primates (Portmann 1990). This means that human babies are more helpless than other mammals; they are more dependable and require a longer period of parental care. Because of the demands of raising human babies, both female and male parental care contributions (as well as their good gene contributions) are important for offspring survival. Whereas female parental care typically involves biological intrinsic investments, in the form of pregnancy and nursing, male parental care involves the provision of material extrinsic investments, through resources in the form of food, shelter, and protection (Symons 1979). Male status and level of resources therefore can influence offspring survival. Children without a father face greater mortality risks, especially in preindustrial societies without predictable and accessible food production and modern health care (Hill and Hurtado 1996). Even in Western societies with access to government social and health care, the lack of paternal involvement

could have negative impacts on offspring in terms of IQ and social mobility (Nettle 2008). Females therefore who seek males with high resources would gain fitness advantages for doing so, and males who signal resources may be selected over those who do not.

Males' Signal Resources to Attract Mates

Signaling theory highlights underlying attributes that cannot be directly observed, but can be communicated to others through signals (Bliege Bird and Smith 2005). By showing off resources (through wealth and status), males can signal to females their underlying mate quality as a good parental investor. By engaging in conspicuous consumption (driving an expensive car, wearing a designer suit), an individual can indicate their underlying wealth or status and therefore their ability to provide for offspring. Veblen's (1973) theory of "conspicuous consumption" suggests that consumption of luxury goods signals a person's underlying financial quality. Males therefore gain reproductive advantages by "showing off" (signaling) these traits in the presence of a potential female mate. Females gain reproductive advantages by choosing males who display traits that help them to produce and rear better quality offspring. In humans, men competitively show off their quality through status and resources. In restaurants, groups of men leave much better tips for waitresses than groups of women, and men on dates with women leave especially good tips (Miller 2001). Even mobile phones have been shown as a resource status symbol. Lycett and Dunbar (2000) found that in social situations, males tended to be more visual with their mobile phone use; in particular, males tended to show off and play with their mobile phones more as the ratio of males to females increased. They argue that males competitively display their mobile phones as indicators of wealth and status. Showing off resources has real fitness implications; among hunter-gatherer societies, men who regularly provide large animal meat have more sexual partners (Hawkes and Bliege Bird 2002). In more contemporary settings, such as lonely heart

adverts, males, when seeking a mate, will highlight their luxury consumption (cars, houses, holidays) significantly more than females. Pawlowski and Dunbar (1999) compared the lonely heart adverts of 454 males and 445 females (aged 18–59) in a UK newspaper (*The Observer*) in the late 1990s. They found that while women tended to offer signs of fertility (physical attractiveness) and seek resources (cues of wealth and status), males tended to seek physical qualities of fertility and offer resources (through referring to themselves as a house owner and professional or suggesting a lavish lifestyle: holidays abroad and expensive cars). Resources however may be used as a bargaining power to access high-quality mates. Male advertisers who did not mention cues of status/wealth in lonely heart adverts were less demanding of the qualities they sought in the opposite sex (Waynforth and Dunbar 1995). However, when men are primed with feelings of financial wealth, they raise their minimum requirements for a date. Yong and Li (2012) exposed male and female participants to either stacks of paper, a small sum of money, or a large sum of money. After handling large sums of money, men, but not women, raised their minimum requirement for a dating partner, particularly the attractiveness of that date partner. Similarly, Li et al. (2016) tested how feelings of having more or less money influenced long- and short-term mating strategies among Chinese college students. They found when men were primed to feel they had more money, they were less satisfied with their long-term partner's physical attractiveness. This same finding was not found for women.

Females Are Attracted to Signals of Resources in Mates

Women seek men who are good providers and select males who display cues of high social status and wealth. Because of higher reproductive and parental costs (Bateman 1948; Trivers 1972), females are more strongly influenced by non-physical factors than males. For example, Townsend and Levy (1990) found that social status could enhance females' existing perception of

physical attractiveness in prospective mates. Whereas both sexes value physical attractiveness in a potential partner, women value social status more in long-term relationships, across both Western (American) and Eastern (Singaporean) sample populations (Li et al. 2011). In a seminal paper, David Buss (1989) confirms that these sex differences are universal. He found that across 37 cultures, women place greater emphasis on status and wealth, and males place emphasis on sexual fidelity and physical attraction. Even resource potential is valued by women. Through analysis of lonely heart adverts (taken from the "Eye Love" section of the fortnightly UK magazine *Private Eye* between January and June 1991), Greenlees and McGrew (1994) found that women, more than men, sought cues that revealed resource potential (ability to acquire resources in the future) as well as actual resources. Qualities such as intelligence and education signal a male's resource potential and are consequently considered attractive mate qualities by females (Miller 2001). Education can act as a measure of socioeconomic status, because education correlates with personal income and occupational position. For example, Bereczkei and Csanaky (1996) found that Hungarian women preferred males with either the same or higher education than themselves. Women however may make a trade-off between a mate's parental investment and genetic benefits. When women have less need for men's resources, for example, when they possess their own resources to take care of their children, they place greater emphasis on physical attractiveness of a mate over good financial prospects (Moore et al. 2006). The desire for resources in a mate can depend on the economic environment in which women are selecting mates. McGraw (2002) analyzed lonely heart adverts published in the United States in 1999 and found that as the costs of living increased, the desire for a mate with the capacity for better financial resources increased also. Women were adopting conditional mating strategies depending on specific environmental factors to optimize their reproductive opportunities. Anderson and Klofstad (2012) sampled 2944 Internet dating profiles in the United States, and found that

women in high-cost living areas increased their desire for mates with resources. However, when women's own resource status was taken into account, no significant relationship in local resource pressure and resource seeking was found. Nevertheless, even in environments that have faced dramatic cultural change, women more than men value resources in potential mates. Souza et al. (2016) compared the Brazilian mate preference scale answers from 1984 (as presented in Buss' 1989 Culture Mate selection project) and 2014. They found that even through industrial and economic transformations, males still place greater emphasis on signals of fertility (health, youth), whereas women place greater emphasis on "good earning capacity" and "good financial prospects" – highlighting social status, education, intelligence, ambition, and industriousness as important mate qualities.

Females Are Attracted to Signals of Willingness to Share Resources

Although females may be attracted to males who signal resources, the extent to which males invest their resources in offspring should also be of concern for women. Signals of disposition toward parental investment as well as level of resources should be attractive traits for women. For example, it would not be an advantage for a woman to mate with a man with high resources but who spent these resources on other women and offspring. Kruger et al. (2003) found that women's expectations of having a short-term versus long-term relationship depended on whether males displayed qualities of "dads" or "cads." They found that "dads" were preferred as long-term relationships, but "cads" were preferred as short-term relationships. They argue that, due to risk of mate defection, women discount males with "cad" features for long-term relationships, even if they also display suitable resources. In contrast, men who signal compassion, kindness, and romantic qualities (or "dads") were valued by females as long-term partners. By showing willingness to share

resources, males can signal good "dad" qualities. This may explain why males, more than females, are more likely to show off financial generosity by donating more money to charity if they are knowingly observed by an attractive member of the opposite sex (Iredale et al. 2008). It may also explain why females, when selecting for long-term relationships, have marked preferences toward males who cooperate and share their resources (Farrelly 2013). So important is this signal of willingness to share resources that males compete to show off financial generosity (Roberts 1998). For example, males have been seen to sequentially increase their public good donations when observed by a female in both Western and non-Western populations (Tognetti et al. 2012; Van Vugt and Iredale 2012).

Conclusion

Male parental investment through resource provision can have significant implications for offspring survival (Hill and Hurtado 1996; Nettle 2008). Females therefore have marked preference for males who display resources, and males show off resources (through wealth and status) to attract a mate (Buss 1989). Female preferences for mates with resources however can depend on their own financial wealth and the wealth of the environment (Anderson and Klofstad 2012; Moore et al. 2006). Similarly, males may vary their mating demands depending on their own wealth and status (Waynforth and Dunbar 1995; Yong and Li 2012). Although, for females, there are fitness benefits for mating with males with good resources, willingness to share these resources may be a more important signal of mate quality than resource acquisition alone (Kruger et al. 2003).

Cross-References

- ▶ [Adaptive Benefits of Matriliny and "Walking Marriages" in Mosuo Culture](#)
- ▶ [Female Mate Choice](#)
- ▶ [Parental Investment](#)

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Resources for Brain Development

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Synonyms

Brain fitness; Brain growth; Cognitive development; Neural development; Neurogenesis

Definition

A source of supply, support, wealth, or revenue; a natural feature or phenomenon that could increase human brain size, efficiency, or health.

Introduction

Throughout the process of evolution, human development has been tied to the need to adapt to our environments and compete for resources. Traits such as bipedalism, manual dexterity, and vocalization are among the many characteristics that have allowed for humans to proliferate (Jabr and Quanta Magazine [n.d.](#)). Of all the adaptations that make our species unique, none are more important than the human brain. The brain is one of the largest, most sophisticated and vital organs of the body, and all of its astounding complexity is the product of millions of years of evolution (“Evolution of the Human Brain” [2019](#)). Its success and development have been very much connected to the resources it has been exposed to. Although identifying and describing each resource that has been vital to brain evolution and development would be too expansive, for this article we will seek to identify some of the main resources complicit in human brain evolution.

Resources and Experience

The development of the brain is based on a collaboration of nature with nurture. However, the percentage inherited vs. the percentage created by experience is still unknown (Siegler et al. [2017](#)). And while the importance of genetic predisposition cannot be discounted, experience and exposure are paramount for development. This process of experience can be described as being experience-expectant or experience-dependent (Prado and Dewey [2014](#)).

Experience-expectant refers to the process in which brain development occurs secondary to experiences that are expected to occur (Prado and Dewey [2014](#)). An example would be “visual

input through the optic nerve for normal development of the visual cortex (Prado and Dewey [2014](#)).” Experience-dependent refers to the ongoing process of brain development resulting from an individual’s unique experiences (Prado and Dewey [2014](#)). Woollett reported that London taxi drivers were shown to have increased volume in the hippocampus secondary to the experience driving the city streets. The role of the environment and nurture on development is therefore a consequence of expected milestones during sensitive periods as well as a continuing process in which our everyday occurrences modify our anatomy and physiology.

Resources in Development

The first environment all humans experience is in utero. There, the fetus is dependent upon the mother not only for access to nutrients but also for maintaining an environment that can facilitate proper development. These factors include proper prenatal nutrition facilitated by the mother and minimal exposure to toxins, infections, or external elements. On the other hand, some agents can negatively impact brain development if mothers are exposed to them at critical junctures during pregnancy. Teratogens are agents that can provoke or increase the risk of a baby being born with a birth defect. These agents could be street drugs, alcohol, tobacco, chemicals, and some viruses and bacteria.

Severe acute malnutrition, chronic undernutrition, iron deficiency, and iodine deficiency can significantly impair brain development. Therefore, resources such as proper nutrition of the expectant mother may have to include supplementation to ensure nutrients are being attained. Prado and Dewey ([2014](#)) stated that research has demonstrated that nutritional supplementation can have influence to brain development and that *recovery is plausible* if the nutrients are made available while the developmental process is still occurring. Development can also be inhibited in certain situations, such as when we are going through a significant amount of stress in our daily life. This means that the brain has very

sophisticated adaptive functions where, depending on the experience the person is going through, it can either regenerate more neurons or decrease neurogenesis according to the current external situation (Siegler et al. 2017).

Once the baby is born, the environment becomes much more expansive. This continues to increase as we grow and begin to ambulate independently. Because babies can neither read nor fully speak until more advanced stages of development, they usually learn from observing others, connecting with their parents and caregivers, and exploring the environment. One of the most important factors for a healthy brain development is nurturing and taking care of the child (“Early Brain Development” n.d). Proper care and exposure of children to different experiences, from when they are born until the end of their childhood, ensures that the child’s brain will develop appropriately; therefore, positive and negative experiences will affect the child’s development and can portray enduring effects. Exposing the child to stressful or traumatic situations could possibly exhibit long-lasting negative effects in the brain of the child, whereas other constructive activities such as reading and playing can instead stimulate their brain growth (Allen 2015).

As soon as children are born, they are ready to learn; however, they depend on their family and caregivers to help them develop the competencies that will allow them to become independent and manage a healthy life in their future. The level of development that the child’s brain reaches is strongly linked to their experiences with the world that they encounter while growing up. Children exhibit better learning abilities when they grow under conditions of social support and emotional well-being, which are derived from constructive relationships held inside and outside their homes. Parents and other caregivers can sustain the children’s healthy brain development by incentivizing positive learning. The most efficient way to achieve this is by speaking and playing with the kids, exposing them to books, and telling them stories that would help the children develop their curiosity, self-confidence, and moral understandings.

Moreover, the experiences children go through when they are growing up can directly affect their future mental health and brain development. Mental health affects how people think, feel, and act; therefore, growing up in a safe and healthy environment would shape our brains to be able to cope with different life challenges. Two common recommendations for child mental health and brain development are to “use it or lose it” and to perform regular exercise. Stimulating our nerve cells by reading, learning, and thinking improves mental fitness and even leads to the development of new brain cells. However, if we stop stimulating our brain, we could lose some crucial abilities that help us overcome daily challenges while keeping a healthy lifestyle (Pendick 2012). On the other hand, doing regular exercise helps the stimulation of blood flow through our body, therefore, assisting our brain to obtain the nutrients and oxygen we need to maintain a good brain functioning. Additionally, exercise can improve mood and activates the release of hormones and chemical substances that enhance brain health.

Nutrition as a Lifelong Resource for Brain Development

A shortage of nutrients in utero and during early stages of life could lead to impairments in the functions of the brain, negative effects in brain development, and cognitive deficits through and after the developmental process (Cusick and Georgieff 2016). Through the development of the brain, the effects of nutritional deficiency are determined by the nutrient’s specific metabolic physiology (what processes are impacted during brain development and whether the insufficiency takes place during a critical or sensitive period). Even though the brain undergoes plasticity throughout our lifetime, and it is able to recover from a nutrition deficiency, during development, there are critical periods where parts of the brain have greater nutritional needs (“What to Feed Your Child to Support Healthy Brain Development” 2019). Deficiency in crucial nutrients over a critical period results in long-lasting negative effects (Cusick and Georgieff 2016).

Children who undergo malnourishment suffer the risk of not being able to reach the maximum potential of development in crucial aptitudes such as cognition, socioemotional abilities, and motor skills. Studies have shown that providing supplements to pregnant mothers and children throughout the first few years of life has provided long-lasting positive effects in the child's cognition as they develop (Prado and Dewey 2014). On the other hand, research suggests that breastfeeding may improve cognitive development due to the plethora of nutrients, hormones, and important growth factors that are found in the breast milk. Additionally, the mere act of breastfeeding strengthens the mother-infant relationship, which is considered crucial for healthy brain development (Prado and Dewey 2014).

Brain-Derived Neurotrophic Factor (BDNF)

BDNF is a protein encoded by specific genes that facilitates important functions in neural development, survival, and regeneration (Marosi and Mattson 2019). It is defined as a potent small protein that stimulates new brain cell's production and reinforces the existing ones. Therefore, it is scientifically proven that increased levels of BDNF upsurge the ability of faster learning, more efficient memory, slower aging, and a quicker rewiring of the brain (Marosi and Mattson 2019). Additionally, it is also known that BDNF participates in boosting the **plasticity** of the brain – the power of the brain to adapt to positive or negative changes at any age (Kolb et al. n.d.). During a stressful situation when the brain cells suffer damage, plasticity takes place by increasing the flexibility in the neural pathways instead of shutting down the connections in the brain (Marosi and Mattson 2019).

Moreover, BDNF is a very important protein in sustaining homeostasis. It regulates patterns of feeding and physical activity and stimulates glucose transport to strengthen cellular bioenergy while protecting neurons against possible damage and illnesses (Marosi and Mattson 2019). Our

body releases the protein fibronectin type-III domain (FNDC5), which contains proteins that increases BDNF, by doing exercise (Rasmussen et al. 2009), and, simultaneously, releases BDNF throughout the deep stages of sleep. On the contrary, two main blockers of this protein are stress and sugar. As stress remarkably inhibits BDNF, it has also been proven that the intake of sugar (especially fructose) tends to curb BDNF production in rats (Stranahan, et al. 2008) and links to a cognitive decline in humans (Barnes and Joyner 2012). Mutations of the human BDNF gene are usually associated with cognitive and behavioral disturbances (Narayanan et al. n.d.).

Research indicates that BDNF is fundamental to postnatal survival due to the fact that in experiments where mice have lacked this protein, they exhibit critical deficiencies in the development of the peripheral nervous system and mild defects in the development of the central nervous system (Murray and Holmes 2011). Lastly, exercising positively affects BDNF even during homeostatic disturbances such as stress or disruptions in energy metabolism. Research studies indicate that exercise in reasonable intensity and frequency has been shown to upsurge the BDNF expression after each exercise session in humans (Liu and Nusslock 2018).

Conclusion

Throughout human evolution, we can conclude that the brain has endured a diverse set of changes. Continued research is important to understand these ancestral evolutionary changes, such as genetic abnormalities and modifications and to also find new resources that help us improve our performance and skills throughout our lives. It is important to emphasize how the initial periods of the children's lives are vital for their further development. The brain of a child produces more than a million neural connections each second from the time they are born until the age of three ("Brain Development" n.d.); therefore, proper stimulation and enhancement are crucial for their development. As it was previously discussed in this

article, throughout evolution, the development of the brain has been influenced by many factors, including the children's interactions, experiences, and environment where they are raised. Factors such as exercise and deep sleep can aid in the release of BDNF, a resource that enhances the development of a healthy brain, but a greater benefit can be achieved when these factors are combined with a proper nutrition.

Cross-References

- Brain Development
- Brain Size and Intelligence
- Development

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Respect

- Culture of Honor

Respiratory Sinus Arrhythmia

- Polyvagal Theory

Respondent Bias

► [Response Bias](#)

Respondent Conditioning

- [Classical Conditioning](#)
 - [Conditioning and Association](#)
-

Response Bias

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Synonyms

[Dissimulation](#); [Respondent bias](#)

Definition

A group of cognitive processes that prevent participants from providing accurate responses or cause them to alter their behavior in a given situation.

Introduction

Response biases are a group of cognitive processes that prevent participants from providing honest or accurate responses to questions or cause them to alter their behavior from what they would normally do in a given situation. These response biases act as a source of error in data collection, sometimes obfuscating data slightly, sometimes completely invalidating them. As such, it is incredibly important to account for response biases as much as possible when constructing measures for studies and during the actual collection of data.

Response biases can stem from several sources. Sometimes participants intentionally alter their responses in order to deceive the researcher in some way. This can occur when participants wish to alter how they appear to the researcher, such as when a participant responds in such a way as to appear “better” than they truly are. In other circumstances, participants may actively deceive the researcher in order to hide information, such as illegal activities. Other times something about the study itself may influence the participants’ behavior without their being aware of it. This can occur when questions in a survey are unclear or confusing, making it difficult for respondents to provide accurate answers despite a desire to do so. Lastly, bias can result from a lack of attention on the part of the participant. This is especially common when participants are not adequately compensated for their time and when participation in research is strongly encouraged (as is the case in most undergraduate introductory psychology courses). This also occurs when participants become fatigued during long or demanding studies. Addition of attention-check items can mitigate this effect. Examples of common response biases are discussed below. Regardless of their source, however, all response biases lessen the ability of the researcher to confidently interpret the data and can sometimes render the data useless.

Types of Common Response Biases

Social desirability. Social desirability is the tendency for an individual to deny traits and behaviors deemed unacceptable by society and to claim traits and behaviors deemed acceptable by society, casting themselves in a favorable light (Nederhof 1985). Participants answering in socially desirable ways can change the mean levels to the response (Podsakoff et al. 2003), as well as conceal the relationships between variables (Ganster et al. 1983). Social desirability can be managed by the researcher using techniques to measure and control for the effects of social desirability or by using methods to reduce or prevent social desirability (Nederhof 1985).

Acquiescence bias. Acquiescence bias (i.e., yea-saying) is the tendency for participants to agree with statements. This tendency can cause spurious relationships between variables, capturing an artifactual relationship rather than the true relationship between variables (Podsakoff et al. 2003). Acquiescence is positively correlated with age and negatively correlated with both education and income worldwide (Meisenberg and Williams 2008). Acquiescence bias can be managed by including reverse-coded items so that affirmative responses do not indicate the same response for each item. The opposite of acquiescence bias, nay-saying, is also managed by reverse-coding items.

Extreme response style and “fence-sitting.” Extreme response style is the tendency for participants to use the end-points of a scale. This tendency may be due to a desire to appear more sincere or answer with more conviction (Cheung and Rensvold 2000). Alternatively, the opposite of an extreme response style, sometimes known as fence-sitting, is the tendency to select the midpoints of a scale. This may be due to participants attempting to appear modest or nonjudgmental (Cheung and Rensvold 2000). Extreme response style can be managed by including a greater number of points on a scale (e.g., going from a 5-point scale to a 10-point or continuous scale). Both extreme response styles and fence-sitting can be managed by utilizing other methods of questionnaires, such as binary choice or open-ended questions.

Conclusion

While this entry only discusses a subset of the possible response biases, it illustrates some of the possible artifacts which can be present in a researcher’s data, and how to account for and prevent their effects. For additional information on possible data artifacts, see Podsakoff et al. (2003).

Cross-References

► [Surveys and Questionnaires](#)

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Response Inhibition

► [Inhibition](#)

Responsibility for Child Suffering

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Synonyms

[Ethics of conception](#); [Morality of creating new life](#)

Definition

The moral debate surrounding the ethics of reproducing and responsibility for any subsequent suffering that the individual experiences.

Introduction

Responsibility for child suffering is the foundation to the anti-natalist claim that it is morally wrong to create new life. In line with anti-natalism, the ultimate responsibility for any suffering a person endures in their life is attributable to their parents, as a nonexistent person cannot consent to be born and as all individuals can be expected to experience some degree of suffering. On the other hand, pronatalists argue that holding parents responsible for all of their child's suffering typically ignores an extensive chain of more direct and immediate possible causes of suffering rendering the ultimate responsibility with the parents as a reduction to absurdity.

Responsibility for Harm

Although it could be argued that causing a person harm *with* their consent is not necessarily immoral, few would argue that causing a person harm *without* their consent is immoral. The cause – and thus responsibility – for harm is therefore central to the ethical debate on reproduction. Pronatalists argue that parents can't be held responsible for the suffering of their children as long as they did not cause it directly. The causal chain of responsibility ends once an adequate source of fault is found. This may not be the immediate source of the harm, but in all but the most extreme cases (e.g., known and certain genetic disorders that cause great suffering), the chain of responsibility is regressed to insignificance before reaching the individuals' very conception. For example, it may not be fair to solely blame a soldier for killing or maiming an enemy soldier in a war between their respective countries, but (assuming the soldiers were acting on orders) the countries, governments, or those involved in starting the war can more appropriately be blamed before the enemy soldiers' parents for conceiving him or her in the first place. Similarly, responsibility does not necessarily need to be placed with anyone at all. For example, parents are arguably not responsible for the suffering if their child gets cancer, assuming they did

not intentionally cause the cancer and did not know that their child would get cancer before he or she was born. In this way, pronatalists would argue that, when suffering is not inevitable and not predictable before birth, responsibility can be placed elsewhere. However, anti-natalists would argue that at least some suffering is inevitable and predictable from before birth and therefore responsibility can and should be placed with the parents.

Anti-natalism asserts that we can and should be held accountable for not taking all the possibilities into account when we make them possible and thus parents are responsible for creating the *possibility* and *inevitability* of suffering where none before existed. People can be accountable for negligence, which is making a choice to do a thing knowing that a bad outcome is possible and not taking all the necessary precautions. From this view, procreation would only be morally justified if there was some method for acquiring consent from the person to be born, and, as this is impossible, procreation is thus immoral (Licon 2012). That is, if a person imposes life without consent and without control of the outcome, they are responsible for the suffering and death that life will experience.

According to philosopher David Benatar (2006), the infliction of harm is morally wrong and to be avoided, and therefore, as procreation always entails the infliction of harm to some extent, procreation is always morally wrong. Benatar's argument is based on the following premises:

1. The presence of pain is bad.
2. The presence of pleasure is good.
3. The absence of pain is good, even if that good is not enjoyed by anyone.
4. The absence of pleasure is only bad if there is somebody for whom this absence is a deprivation.

From these premises, it is argued that if someone exists, there is the presence of pain and the presence of pleasure, whereas if that person had not come into existence, the pain is avoided which is good and the absence of pleasure is not bad (i.e.,

neutral) as the individual does not exist to be deprived of it. For Benatar, the harm that coming into existence creates is avoidable and pointless, and therefore, as it is always good to avoid harm whenever possible, it is always good not to come into existence.

Conclusion

In summary, from the combination of the predictability and inevitability of harm and the lack of prior consent from the individual who will experience this harm, anti-natalists argue that the responsibility for any and all suffering that a child experiences is with the individuals who brought them into existence. From this stance, biological parents are ultimately responsible for all the harm their child experiences, regardless of any more immediate or direct specific sources of harm, as it would have been avoided if the child had never been born in the first place.

Cross-References

- [Anti-natalism](#)
- [Better Never to Have Been](#)
- [Child Abuse](#)
- [Child Homicide](#)
- [David Benatar](#)

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Restricted Reproductive Potential

- [Limited Reproductive Potential](#)

Retaliation

- [Self-Defense and Female-Perpetrated Violence](#)
- [State-Sanctioned Punishment as Substitute for Tribal Vengeance](#)

Retina, The

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Definition

The retina is the tissue that undertakes the initial steps of image formation in the visual system, being the tissue within the eye formed of photo-receptors and other cells.

Introduction

In vertebrates, the focus herein, the retina lines the inside of the globe of the eye, whereas in invertebrates the eye takes on many forms and the retina is often exposed more directly to the environment.

The Vertebrate Retina

By way of analogy, the vertebrate eye is often described as being “camera-like” in that it has lenses and apertures that focus light onto a thin detection layer. In this analogy, the retina is the *film* of the analog camera – the component that is sensitive to light – and the signals thus generated are interpreted by the brain. Research over many decades has revealed that this analogy is very limited: the retina does much more than detect light but instead is a complex network of neurons that processes these signals to simultaneously compute and encode information about a stimulus’ shape, color, movement, intensity and contrast, among several other characters. Thus, if we are to portray the eye as analogous to a camera, the

retina is more akin to a contemporary smart phone: detecting light towards image formation is a required and impressive function of this tissue or device, but merely the beginning of a complex conversion of immense information that is translated, computed, refined, and transmitted to produce remarkable outcomes. Despite ocular structures having long been celebrated for their elegance and efficiency (Darwin described this an “inimitable contrivance” in a chapter titled “Organs of Extreme Perfection”) (Darwin 1858), they are indeed typically still underestimated in how marvelous they are.

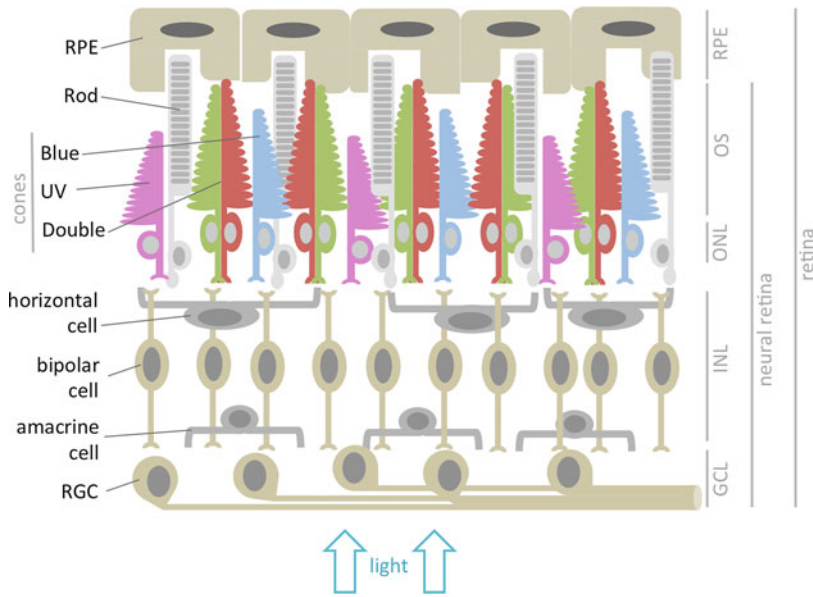
Akin to film in an analog camera, the retina is a sensitive and precise component whose operation is critical to vision, and disruptions to the retina structure or function are causal of many types of visual impairment and blindness.

For many researchers, the retina is considered “an accessible part of the brain,” e.g., as asserted by John Dowling (2012). Unambiguously, the retina is part of the central nervous system, formed during embryonic development as a lateral out-pocketing of the forebrain. Like the brain, the retina is made up of a complex suite of neurons and supporting cells (such as vasculature and microglia, radial glia forming a blood retina barrier akin to the blood brain barrier). The retina is experimentally “accessible” compared to other vertebrate CNS tissues in many synergistic ways, including being readily examined for health by instruments of ophthalmology and optometry. The morphology of the retina lends itself to study due to its regularly layered structure created by consistent connectivity of identifiable neuron subclasses (Fig. 1). Functional measures are relatively tractable, because the retina is comparatively easy to record from, e.g., via electroretinogram, and easy to stimulate because light as a stimulus can be precisely controlled in both its quality and quantity. Experimentally, the retina is accessible to treatment delivery via intraocular injection into the globe of the eye. These sum to retina being highly amenable to comparative sensory ecology and fundamental neuroscience, as well as to being an attractive target for development of emerging CNS treatment modalities designed to ameliorate neurodegeneration (such

as gene therapy, stem cell therapy, and neural prostheses) because outcomes can be elegantly and powerfully measured in longitudinal study designs and safety of the interventions can be carefully monitored using the ophthalmologist’s toolkit.

The retina tissue is formed from diverse cells including many subtypes of photoreceptors, support cells, and neurons (Fig. 1). Photoreceptors and downstream neurons are distributed in three layers and make up the “neural retina,” whereas the broader term “retina” often is used to describe both the neural retina and the retinal pigmented epithelium (RPE). The RPE lines the back of the eye and interdigitates its processes with the rod and cone photoreceptors. The RPE plays several roles, including impeding off-axis light from reaching the photoreceptors, and supporting photoreceptor metabolism by phagocytosing photoreceptor outer segments and recycling visual pigments. Such support roles are critical because photoreceptors are highly metabolically active cells, producing much protein to support absorption and transduction of light.

The photoreceptors in the retina are the cells that perform phototransduction, i.e., they convert light stimuli into biochemical and electrical signals that eventually are computed in the brain to manifest as vision. The vertebrate retina is considered to be “duplex” because vision is accomplished by two classes of photoreceptors: the rods and the cones. A third class of photoreceptor, the intrinsically photosensitive ganglion cell, does not participate in vision but instead communicates about light levels to regulate the size of the pupil and to entrain circadian rhythms, i.e., simply these ipRGCs help to tune the master biological clock that adjusts day/night biological rhythms. The ipRGCs are rhabdomeric photoreceptors and have distinct physiology as compared to rods and cones that are ciliary photoreceptors, in that ipRGCs express distinct opsin (melanopsin) and phototransduction machinery (Fain et al. 2010). Rhabdomeric photoreceptors underpin vision in many most invertebrate species; thus, ipRGCs share similarities with invertebrate visual receptors. The last common ancestor of vertebrates and invertebrates perhaps then had both rhabdomeric



Retina, The, Fig. 1 Schematic of typical vertebrate retina. The vertebrate neural retina has several distinct layers, beginning closest to the eye's vitreous is the ganglion cell layer (GCL) – this layer is closest to the pupil and faces the arrival of environmental light. Behind this are the inner and outer nuclear layers (INL and ONL), and photoreceptor outer segments (OS) form a distinct compartment. Photoreceptor outer segments interdigitate into the retinal pigmented epithelium (RPE), a darkly pigmented layer of support cells. Photoreceptors underpinning the first steps of vision are rods and cones. Vertebrates typically have four types of cones maximally sensitive to different wavelengths of light: the example here is cones maximally

sensitive to blue and ultraviolet (UV) light (both with a single cone morphology) and a double-cone morphology maximally sensitive to red and green light (wherein two independent cone photoreceptors are fused). Mammals have less complexity in their complement of cones (see text). The cones synapse onto cells of the INL, wherein photoreceptor outputs are compared and calculated by horizontal cells and amacrine cells. Bipolar cells transmit these signals to the RGCs. The RGC axons form bundles running along the inner surface of the eye and coalesce into the optic nerve that transmits retinal outputs to the brain. Not represented in this schematic is the diversity of glia and vasculature that is also critical to retinal function

and ciliary photoreceptors, and this state is observed in extant annelids (Fain et al. 2010). We will not consider ipRGCs further but go on to consider rod and cone photoreceptors as the cellular instigators of vertebrate vision.

Rod and cone photoreceptors have much in common, expressing opsin in the apical end of the cell called the outer segment that is engulfed by the RPE. These photoreceptors are highly polarized cells, with inner segments dense with mitochondria to feed their high metabolism, below which are the nucleus and active perinuclear protein production and trafficking machinery, and extending synapses basal direction, towards the center of the eye where they connect to downstream neurons (see Fig. 1). The photoreceptor outer segment elaborates much

bilipid membrane to maximize the abundance of opsin. Opsins are proteins that begin the process of vision – they absorb photons of light and, via changing their shape and signaling to other proteins, convert the light signal into electrochemical nerve pulses.

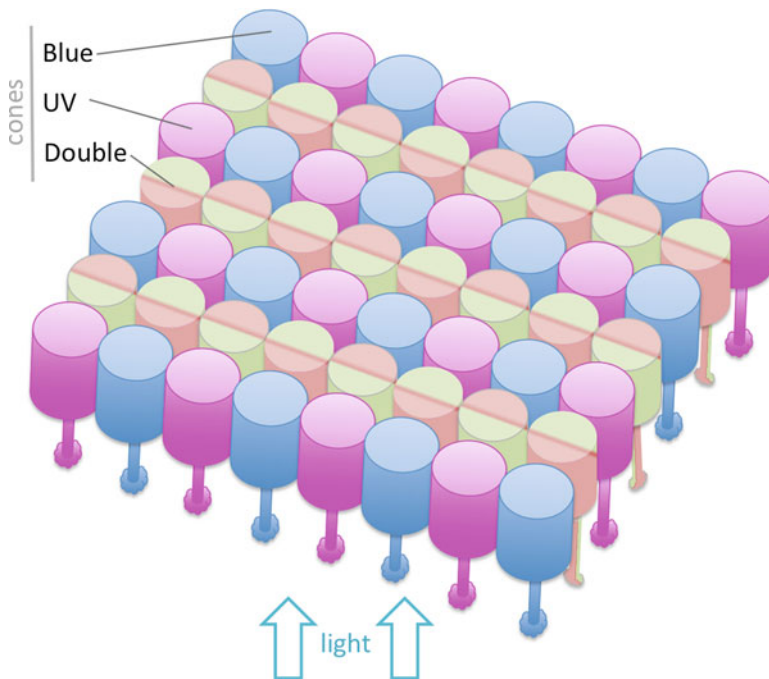
Rod and cone photoreceptors differ in their functions and are named for differences in their namesake morphology: Rods have outer segments that are shaped like rods, whereas the outer segments of cones typically are more conical (Fig. 1). Vertebrate vision in very low light environments begins with rods. Rods are very sensitive and famous for being able to respond experimentally to a single photon of light. Rods are quenched by moderate light levels, e.g., during crepuscular times of day (dawn or dusk), such that they are

of most utility under light levels provided by starlight or moon light. Rod photoreceptors typically express an opsin that maximally absorbs photons of 500 nm wavelength (green light).

Cone photoreceptors are active in moderate light levels and brighter, and are responsible for high-acuity vision. Cone photoreceptors mediate color vision by having multiple spectral subtypes – e.g., humans have populations of cones maximally sensitive to red, green, or blue light. Thus, each cone typically expresses a single opsin type and responds maximally to certain wavelengths of light. Color perception begins in the retina when the outputs of the various cone photoreceptors are compared. Vertebrates typically have four cone spectral subtypes that are maximally sensitive to ultraviolet, blue, green, and red photons. Mammals lost much of this array of photoreceptor complexity during the nocturnal bottleneck, a phase of early mammalian evolution wherein

adaptation to nocturnal lifestyle was perhaps enabled by changes in the retinal photoreceptors and led to evolution of thermoregulation (Kim et al. 2016). Thus mammals, including those that have subsequently evolved diurnal (daytime active) habits, often have only two cone photoreceptor types. Primates including humans typically have duplicated long-wavelength cone opsin gene and thus have trichromatic vision.

The proportion and density of cones varies among different species. An extreme example is in some primates, where cones are dense in the macula and fovea, wherein few rods are present. In many vertebrates, a similar condensation of cones such as a “visual streak” or “area centralis” is observed and presumably allows that area of the retina to maximize its resolution of shapes and colors. Cone photoreceptors of most vertebrates, e.g., fishes, are arranged in a crystalline lattice (Allison et al. 2010) where cones of different



Retina, The, Fig. 2 Cone photoreceptors are typically patterned into crystalline mosaics. Though lost during evolution of tetrapods, most vertebrates have their cone photoreceptors organized into elaborate array of reiterated spacing and neighbor relationships. The view schematized here is an oblique angle relative to Fig. 1 and presents a “row mosaic” typical of many fish including zebrafish,

though other variations on this pattern are also common. Cones maximally sensitive to blue or ultraviolet (UV) light have a single cone morphology and alternate to form rows. Double cones are a fusion of cones maximally sensitive to red or green light and establish elaborate rows between the single cones

identities are regularly positioned in an elaborate spatial array (Fig. 2).

Cone photoreceptors are also arbiters of sensory modalities that not generally part of the human experience. For example, cones are the arbiters of polarized light vision in vertebrates, and this ability has various functions in detecting predators and prey, detecting celestial cues for navigation, and for social communication (Kamermans and Hawryshyn 2011). Cones also are responsible for light-dependent magnetoreception in vertebrates (Niessner et al. 2011), which is thought to play various roles especially including long-distance migrations.

Conclusion

Thus the retina, enabling the first steps in vision (Rodieck 1998), is remarkable in its ability to disambiguate various environmental energy signals, including not only specialization for magnetic fields and polarization of light but also simultaneously allowing complex perceptions of the environment by encoding movement, intensity, shape, flicker, and colors.

Cross-References

► [Eye, The](#)

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Retribution

► [Cross-Cultural Punishment](#)

Rett Syndrome

► [Social Disabilities](#)

Reunion

► [Reconciliation](#)

Revenge

► [Ability and Willingness of Victim to Retaliate](#)
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 ► [State-Sanctioned Punishment as Substitute for Tribal Vengeance](#)

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- [Positive and Negative Reinforcement and Punishment](#)
-

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- [Olfactory Bulb, The](#)
-

Rhodesian Man

- [Homo heidelbergensis](#)
-

Ribonucleic Acid

- [RNA](#)
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Richard Dawkins on Constraints on Natural Selection

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Introduction

Richard Dawkins presents a nuanced take on optimality in his seminal work *The Extended Phenotype*. Dawkins's central argument is that optimality is *not* attainable in nature because of constraints on the process of natural selection. His discussion focuses on six key constraints: time lags, historical

constraints, trade-offs (which he calls constraints of costs and materials), constraints due to available genetic variation, imperfection due to selection operating at different levels, and constraints due to environmental unpredictability.

Together, these six constraints on optimality offer a deeper understanding of how natural selection works and the kinds of outcomes it produces. They also help lay to rest the erroneous view that evolutionists endorse a Panglossian, pan-adaptationist view in which every aspect of animals' bodies and brains is optimally designed. No credible evolutionist thinks this. Instead, it is widely understood that natural selection builds suboptimal adaptations because of the following key constraints.

Time Lags

Evolution by natural selection is a gradual, step-by-step process. As a consequence, organisms are adapted to *past* circumstances, not present circumstances. If it so happens that the environment has not changed much, then organisms may be well adapted to their current environment. But if the environment they inhabit has changed, organisms can exhibit maladaptive behaviors simply because environmental change has taken place faster than the slow, cumulative process of evolution by natural selection.

For example, humans are adapted to a time in which food was scarce. As such, our species has evolved taste preferences for calorie-dense foods, fat, and sugar (Buss 2015). In the calorie- and nutrient-scarce environments in which we evolved, these preferences were adaptive. By contrast, in modern environments with an overabundance of fast food, these evolved taste preferences lead to obesity, type II diabetes, and cardiovascular disease. They are no longer adaptive because of the discrepancy between the environment in which we evolved and the one we currently inhabit (Nesse and Williams 1994). Stated differently, the environment has changed too fast for selection to keep up: time lags have rendered our adaptive taste preferences maladaptive in modern environments.

Historical Constraints

History provides a second key constraint on the power of natural selection. When an engineer sets out to build something, she can always start over if something goes wrong in the process. By contrast, natural selection is constrained by millions of years of history. Once a certain body plan or nervous system is in place, certain areas of evolutionary “design space” are closed off for that lineage, and others are rendered less “evolvable” (Dennett 1996). In other words, the phylogenetic background of a species affects what it is capable of evolving next: history constrains evolution.

Consider the case of how jet engines superseded propeller engines (Dawkins 1999). Designers of the first jet engine had a blank canvas from which to construct prototypes. This meant that they were not forced to stick with any initial mistakes or missteps they made – they were free to start from scratch if needed. Moreover, in the case of humanly engineered machines, there is no need for each new step in the process to be an improvement on its predecessor: our foresight enables us to add or change parts that have no immediate effect, but that will eventually improve the machine’s functioning when the design is complete.

Natural selection has neither of these luxuries. It cannot start from scratch; it can only build upon what is already there – and every single intermediate step must function better than its predecessor. These constraints limit the power of natural selection to produce optimally designed mechanisms. The consequence is suboptimal designs such as the vertebrate eye, which has a blind spot and appears to be installed backward (Dawkins 1999). Such a design is suboptimal by engineering standards – but there are limits on natural selection that do not exist in engineering.

Trade-offs

Every adaptation comes with a cost, and this makes trade-offs inevitable. For example, gazelles under predation pressure from wolves may evolve

longer legs, enabling them to run faster and increase their likelihood of escape. But longer leg bones are more brittle and more likely to break. The gazelle thus faces a cost either way: more robust bones but diminished capacity to flee or enhanced capacity to flee but more vulnerable bones. Some trade-offs are simply unavoidable.

The blind Mexican cavefish (*Astyanax mexicanus*) illustrates the same point. Over millions of years, this fish has lost its sight. One hypothesis for how this happened involves trade-offs: the Mexican cavefish may have lost its eyes because vision requires energy-hungry neurons, and in a pitch-black cave it is a waste of metabolic resources to build and maintain a visual system. In such an environment, those physiological resources can be more profitably channeled toward something else – cell repair, immune function, or a stronger tailfin, for example.

The key point is that every adaptation imposes a cost. These costs lead to unavoidable trade-offs – and if the trade-off is truly unavoidable, then it is impossible to optimize the traits being traded off against one another. Because of this, trade-offs lead inexorably to suboptimal designs.

Available Genetic Variation

Natural selection cannot make new genes arise out of thin air; it can only work with whatever genetic material happens to be available in a population at a given time. As a result, the availability of genetic variation is a key constraint on natural selection. To put it differently, it is impossible for natural selection to produce an adaptation – let alone an optimally designed one – if the relevant genes are simply not present in the population.

It is difficult to exaggerate the importance of this point. The selection pressure for a particular trait may be exceedingly strong, but this will not matter at all if there is no genetic variation underlying that trait. No matter what other factors are in place, the trait in question will not evolve unless there happens to be genetic variation for it in the population. An analogous constraint in human engineering would be the following: it is

impossible to build something – no matter how badly we need it – if we simply do not have the raw materials with which to build it.

Artificial selection on cattle illustrates this point. Researchers carried out experiments in an attempt to produce more heifer (female) calves rather than bull calves, as only heifers produce milk. However, it turned out that the genetic variation required for this outcome (producing more female offspring) did not exist, so the experimenters were unable to produce the desired sex ratio (Dawkins 1999). The key point is this: if the relevant genetic variation does not exist, the trait will not evolve – no matter how long natural selection operates and how strong the selection pressure is. Natural selection is unavoidably constrained by the raw material that happens to be available in the population at the time.

Imperfections at One Level Due to Selection at Another Level

Optimality in nature is also constrained by the fact that selection at one level can lead to maladaptive effects at another level. Dawkins describes this in the following way: “selection at the level of the gene can give rise to apparent imperfections at the level of the individual” (Dawkins 1999).

Heterozygous advantage provides an illustrative example. In such cases, a gene may be positively selected because of its beneficial effects when in a heterozygous state. But when in a homozygous state, the effects of such a gene are harmful. For example, the allele for sickle-cell anemia has been selected for because it is protective against malaria in a heterozygous state. However, if a person inherits *two* copies of this allele, he or she will develop sickle-cell anemia, which can be fatal (Allison 1954). It is thus possible for selection at the genic level to have detrimental effects on an organism’s health. And because it is impossible to optimize two conflicting levels (genic and individual) simultaneously, suboptimal outcomes are unavoidable.

Mistakes Due to Environmental Unpredictability

Dawkins’s final constraint is that of environmental unpredictability. Animals may be exceedingly well adapted to their environments, but since some environmental events are inherently unpredictable, mistakes and missteps are inevitable.

For example, a bird may be well adapted to fly in conditions that are, on average, favorable to flight. But it would not be surprising for the mechanism of flight to fail in a severe hurricane. Unpredictable catastrophes can kill even the most well-adapted organisms. As Dawkins puts it, “it will usually be impossible to cater to every conceivable contingency of detail, and any given animal will therefore frequently be observed to make ‘mistakes’, which can be fatal” (Dawkins 1999).

Stated differently, organisms are adapted, on average, to the statistical conditions of their environments. But no matter how well designed an animal’s flight or vision or bipedalism might be, some environmental events are anomalous and unpredictable. Natural selection is constrained by this unpredictability and cannot build biological mechanisms that are somehow immune to random environmental accidents. Environmental unpredictability thus acts as a sixth key constraint on the power of natural selection.

Further Constraints: Antagonistic Pleiotropy and the Conflict Between Survival and Reproduction

These six limits on the power of natural selection to produce optimally designed mechanisms are not exhaustive, but space considerations prohibit us from offering a comprehensive account of all the constraints on natural selection. We briefly mention two others here: (a) conflicts between survival and reproduction and (b) antagonistic pleiotropy.

Survival and reproduction often come into conflict in nature. Because differential *reproduction*, not survival, is the bottom line of evolution, when they do conflict, reproduction inevitably trumps survival (Alcock 2009; Dawkins 1976;

Williams 1966). The peacock's tail illustrates this well. It is a burden to survival: cumbersome, metabolically expensive, and a hindrance when it comes to escaping from predators. But peacock genes build these tails anyway because peahens are attracted to them – such is the power of sexual selection. The key point regarding the conflict between survival and reproduction is this: because it is impossible to simultaneously optimize two conflicting outcomes (survival and reproduction), suboptimal outcomes are inevitable. And because differential reproductive success – not survival – is the currency of evolution by natural selection, design for reproduction takes precedence. This often leads to suboptimal design for survival (see, e.g., Al-Shawaf et al. 2015).

Antagonistic pleiotropy – a phenomenon in which a single gene may have conflicting effects (Nesse and Williams 1994; Williams 1957) – provides another constraint on optimality. For example, some genes have beneficial effects in early adulthood but detrimental effects in later adulthood. This is the case with genes for testosterone production, as testosterone enhances male reproductive success in early adulthood but increases susceptibility to a wide variety of diseases in later years (Trivers 1985; Williams and Nesse 1991). And because selection is more powerful earlier in the life span and weaker later in the life span (after reproduction has already occurred; Nesse and Williams 1994; Williams 1957), it will favor genes that help the organism early in the life span even if they hurt it later on. In this way, antagonistic pleiotropy – combined with the waning strength of selection across the life span – constitutes another key driver of suboptimal design in nature.

Conclusion

Richard Dawkins's seminal account of the limits of natural selection focused on six key constraints: time lags, historical constraints, constraints due to available genetic variation, trade-offs, imperfection due to selection operating at different levels, and constraints due to environmental unpredictability. To these six key constraints, we

briefly added two more: antagonistic pleiotropy and the conflict between survival and reproduction.

One more theoretical point bears mentioning. Natural selection should not be understood as an optimizing process at all – instead, it is a “meliorizing” process (Dawkins 1999). That is, natural selection does not produce the best design possible by engineering standards – rather, it produces designs that are *better*, on average, than the other available designs in the population at the time.

This definition of natural selection, together with the eight constraints discussed above, explains why natural selection cannot produce optimally designed mechanisms in nature.

We hope this entry helps elucidate the nature of these constraints on natural selection, why they exist, and the important role Dawkins has played in highlighting them. We also hope this entry underscores the erroneousness of the oft-repeated criticism that evolutionary scientists think adaptations are optimally designed. They are not, of course – for all the above reasons.

Cross-References

- [Adaptations: Product of Evolution](#)
- [Natural Selection](#)
- [Optimal Designs](#)
- [Sexual Selection](#)
- [Survival and Reproduction](#)
- [Thirteen Misunderstandings About Natural Selection](#)

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Richard Lewontin and Stephen Jay Gould

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Stephen Jay Gould was (he died in 2002) a celebrated evolutionist and writer, someone who was called a Living Legend by the US Library of Congress in honor of his many literary achievements. Richard Lewontin, a fellow Harvard Professor when Gould was alive, is known for his pioneering research into the genetics of variation within populations as demonstrated by gel electrophoresis, a technique that shows just how much hereditary variation there is in the populations of living things.

Both men deeply opposed the work of sociobiologists and evolutionary psychologists, two groups of researchers who use the adaptationist approach, which involves employing natural selection theory as the basis for investigations into the possible adaptive value of behavior. One expression of their resistance to this approach came in an extremely influential paper published in the Proceedings of the Royal Society B (Gould and Lewontin 1979) on the supposed failures of adaptationism. This paper has been cited nearly

3000 times according to the Web of Science. In their piece, Gould and Lewontin argued that the “adaptationist program” involved faith in the ability of natural selection to produce adaptations without consideration for other likely influences on evolution. Further, adaptationists were, according to Gould and Lewontin, prone to produce “adaptive stories,” generally of a speculative nature, that they accepted on the basis of plausibility alone, which is to say without the rigorous testing against alternative explanations that is the hallmark of a truly scientific approach (see The Just-So Story, also by Alcock). The ignored alternatives included those that focused on the origin rather than the current utility of a trait of interest as well as the power of such things as genetic drift in addition to natural selection in affecting the course of evolution.

In their paper, they introduced the concept of a spandrel, namely, a significant structural component of a building or body that was later co-opted for some other additional purpose in the course of building an edifice or developing a body as in the decorations on the supports of arches in cathedrals. The argument here was that the decorations on spandrels are not adaptations per se, but instead are mere by-products of an object that originated for other reasons altogether.

Gould elaborated on his opposition to the “adaptationist program” in many of his broadly read monthly contributions to *Natural History* magazine, 300 in all, thereby enlarging the effect of his views on the utility of natural selection theory (as well as its modern addendum, kin selection theory) as the foundation for research into possible adaptations. He was a productive writer with frequent pieces in the *New York Review of Books* as well, where he once wrote (Gould 1997) that evolutionary psychology and its adherents were fatuous, foolish, and pathetic, among other things.

The assault by Gould (and Lewontin) on evolutionary psychology and the like failed ultimately although the intensity of the attack disconcerted some adaptationists in some fields as seen in the reluctance of sociobiologists to employ the word “sociobiology.” But natural selection theory (in conjunction with its modern

modifications) is without doubt the most important tool ever devised for sociobiological and psychological researchers interested in the evolution of the complex behavioral traits of living things, including humans. The record of exploration of the adaptive value of these traits by natural selectionists is breath-taking in its scope as can be seen in any textbook on animal behavior or evolutionary psychology (Alcock 2013; Buss 2015; Gaulin and McBurney 2003).

Among the many counters to Gould and Lewontin's arguments were responses written by other evolutionary biologists, like Borgia (1994), who pointed out that among other things the adaptationist program involves the use of natural selection theory to produce hypotheses about the possible adaptive value of a trait of interest so that one or more of these hypotheses might be *tested*, a point that Gould never acknowledged. The scientific literature is filled with examples of tested hypotheses on the adaptive value of this or that characteristic. So *contra* Gould and Lewontin, adaptationists do not settle for plausibility as the criterion for acceptance of a hypothesis. Scientific journals do not either, which is why selectionists must and do test their ideas before submitting them to the scrutiny of a journal and its reviewers.

Moreover, Gould and Lewontin blurred the difference between adaptationist research on the possible adaptive significance of traits and studies of the origin and evolution of these traits. In reality, there are two different kinds of evolutionary studies, one that focuses on adaptation (i.e., current and past reproductive or genetic value of the attribute) and another that focuses on the historical sequence of changes that have occurred during the evolution of a characteristic. These are related areas of research but they are different in that one (adaptationism) relies heavily on Darwinian natural selection as the underlying hypothetical cause of the trait in question, while the other focuses on the role of preceding changes in shaping the attribute in question.

Furthermore, evolutionary studies, whether on the possible adaptive value of a trait or on the history of modifications of the trait over time, differ profoundly from research into the

proximate causes of the trait of interest. So when Gould and Lewontin state that adaptationists are at fault for not analyzing the role of development in the production of a trait, they are confounding the proximate (immediate developmental) and ultimate (evolutionary) causes of the character under investigation. This error is a fundamental one that has long been known to cause many misunderstandings and unnecessary arguments (Mayr 1961). The developmental biologist and the geneticist have interesting and valuable roles to play in understanding how a trait comes into being but they are under no obligation to expand their studies to include the possible adaptive value of the trait. Likewise, the adaptationist is not obliged to consider the proximate foundation of a trait if he or she is more interested in testing why the trait has been shaped and maintained by natural or kin selection.

Although Gould and Lewontin tried to argue that Darwin was a pluralist who even-handedly dealt with all manner of causes in his efforts to explain how and why a trait came to be the way it was, a pluralist of this sort he was not (Queller 1995). Darwin's *On the Origin of Species* is almost entirely about the role of natural selection in producing the adaptations of living things. Indeed, Darwin was the first adaptationist who realized how powerful selection could be in shaping the attributes of all animals, plants, bacteria, and fungi. Here is what he actually said about the nature of adaptation with all three quotes coming from his book on orchid adaptations (Darwin 1862), which he wrote in the years immediately after publishing *On the Origin of Species*:

When this or that part has been spoken of as adapted for some special purpose, it must not be supposed that it was originally always formed for this sole purpose. The regular course of events seems to be, that a part which originally served for one purpose, becomes adapted by slow changes for widely different purposes. (p. 282.)

Although an organ may not have been originally formed for some special purpose, if it now serves for this end, we are justified in saying that it is specially adapted for it. (p. 283.)

On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly

altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes... (pp. 283–284)

I would not quote Darwin on these matters except that Gould and Lewontin claim, irresponsibly, that the author of *On the Origin of Species* was in their corner, when he most definitely was not.

So why were Gould and Lewontin so eager to downplay the role of Darwinian natural selection in the evolution of adaptations? Here I rely on Trivers (2015), who in his review of the two biologists, notes that both were ideologues of the Marxist variety, believers in the ability of cultural pressures to shape human behavior in ways that made all behavioral possibilities equally likely. Lewontin (1976) wrote, “As working scientists in the field of evolutionary genetics and ecology, we have been attempting with some success to guide our own research by a conscious application of Marxist philosophy.” Ironically for persons who were eager to attribute ideological bias to their opponents, both Gould and Lewontin permitted their own political views to profoundly affect their conclusions about adaptationism (Borgia 1994; Queller 1995; Trivers 2015). Their ideological biases also caused them to argue against what they portrayed (inaccurately) as the genetic determinism of adaptationists. In fact, Gould and Lewontin tried to equate adaptationism (an evolutionary approach) with genetic determinism (a proximate claim about the nature of development) in order to assert that the adaptationist approach is obviously wrong, since human behavior is indisputably variable, a point known to all.

Why does it matter? After all, Gould died long ago in 2002. Since his demise, sociobiology (broadly defined to include behavioral ecology) and evolutionary psychology have flourished. Durant and Ellis (2003) found that the number of papers in evolutionary psychology had increased from 4 to 231 per 4-year blocks beginning in 1985 and ending in 2000. The field has expanded even more vigorously since 2000 (Webster & Jonason, 2009). If we examine the frequency of the use of

“evolutionary psychology” as a keyword in 2211 papers covered by the Web of Science starting in 1973, 1424 or 64% have occurred in the last decade (beginning in January 2007). So a great many researchers have in recent years come to make use of the adaptationist program despite the complaints of Gould and Lewontin.

However many of us realize that Gould is still accepted as an evolutionary authority by those who are not evolutionary researchers themselves. As Borgia (1994) noted, evolutionary biologists may have a strongly negative view of Gould and his anti-adaptationist stance, but non-evolutionary types are far more accepting. Non-evolutionary commentators often repeat the points made by Gould and Lewontin as if they were novel and had never been rebutted by scientists who disagreed with these arguments (e.g., Gottlieb 2012; Slater 2013). Indeed, many philosophers of science, social scientists, and economists, even non-evolutionary psychologists, believe that evolutionary theory is completely irrelevant for their studies of human behavior. Gould and Lewontin provided a reason for these individuals to ignore natural selection theory and to the extent that they influence the thinking of their students and the general public, the evolutionists among us need to keep trying to explain why the adaptationist program is not only viable but essential if we are to fully understand human behavior.

This effort is all the more necessary to the extent that creationists continue to have a strong influence in the United States where over 40% of respondents accept the creationist account of the origins of human beings (Gallup Poll 2014). Gould’s critique of adaptationism, despite his many anti-creationist activities, was used by creationists in their ongoing efforts to attack evolutionary thinking. Creationists need to be countered to the extent possible by showing why Gould (and Lewontin) were mistaken in their anti-adaptationism.

There are therefore several reasons why Gould and Lewontin’s spandrels paper deserves continuing rebuttals from evolutionary biologists and psychologists who are aware that adaptationism is the foundation for the success of behavioral

ecology and evolutionary psychology in making sense of animal behavior.

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Richard Wrangham

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Definition

Richard Wrangham, Ruth B. Moore Professor of Biological Anthropology at Harvard University, founder of Kibale Chimpanzee Project, and Co-founder of the Kasiisi Project.

Introduction

Richard Wrangham was born 1948 in Britain and earned his PhD at Cambridge University in 1975 and is a Ruth B. Moore Professor of Biological Anthropology at Harvard University. Dr. Wrangham researches primate ecology and human nutrition and social behaviors. He has authored or co-authored many books such as *Science and Conservation in African Forests: The Benefits of Longterm Research*, *Demonic Males: apes and the Origins of Human Violence*, and *Catching Fire: How Cooking Made Us Human*. Dr. Wrangham is a board member, co-founder, and co-director of the Kasiisi Project. Dr. Wrangham is also the founder of the Kibale Chimpanzee Project.

Kasiisi Project and Kibale Chimpanzee Project

The Kasiisi Project, located in Uganda, was founded in 1997 in order to aid in educating in tangent with the Kibale National Park. The Kasiisi Project serves as a link between locals and the Kibale Chimpanzee Project (Kasiisi Project 2017). The Kibale Chimpanzee Project, founded to study the behavior, ecology, and physiology of wild chimpanzees in 1987 (Kibale Chimpanzee Project 2017), has been dedicated to the survival, welfare, and understanding of chimpanzees

(kibalechimpanzees 2013). Some recent research by Dr. Wrangham done with the Kibale Chimpanzee Project involves social customs, reproduction, hormones, and disease in chimpanzees (The Kibale Chimpanzee Project 2017).

Recent Research

Listing some of Dr. Wrangham's work, he has completed research on social constructs within chimpanzee groups that has examined grooming behaviors and learning, foraging, and hunting calls. Chimpanzees' have unique grooming styles per group in and out; how these styles developed were unknown. Wrangham et al. found that individuals keep their mother's style and are not influenced by other chimpanzees, impacting community traditions for generations (Wrangham et al. 2016). Foraging in chimpanzees is primarily done by females; however their ability to forage is affected by their group, particularly how many males are in the group and if they have children. In a recent article, Thompson et al. determine that having many males in a group has long-term costs associated with reproduction via negative effect on C-peptide levels and foraging capabilities (Thompson et al. 2014). Hunting initiative of chimpanzees has also been examined, finding that groups of male chimpanzees often have constant initiators that spur on the group to hunt, including non-common hunting participants within the group. After the removal or death of the common initiators fewer hunts are enacted (Gilby et al. 2015).

Books

Dr. Wrangham has extended some of his work to humans; two primary examples being his books *Demonic Males* and *Catching Fire*. In *Demonic Males*, Dr. Wrangham examines the great apes in his travels in Africa, detailing violent behaviors in both humans and nonhuman great apes. In his book, he looks at the common ancestry of great apes to today discussing the differences in how humans have developed opposed to the other

great apes (Wrangham & Peterson, *Demonic Males: Apes and the Origins of Human Violence*, Wrangham and Peterson 1996). In his book *Catching Fire*, Dr. Wrangham covers the possibility that humans evolved to what humans are today because of cooking. In that cooking made digesting and eating more efficient allowing the brain to develop further (Wrangham 2009).

Conclusion

Dr. Richard Wrangham studies a variety of subjects in relation to chimpanzees and humans. He is a distinguished author and publicist, co-founder and co-director of the Kasiisi Project, and the founder of the Kibale Chimpanzee Project. His recent work has examined behaviors in chimpanzees such as grooming behaviors and learning, foraging, hunting calls, and more. He has extended some of his work to humans, one example being his book *Demonic Males* comparing common ancestry and violent behaviors. In another book, *Catching Fire*, he examines how humans may have gained the ability to evolve the brain to how the human brain is today.

Cross-References

► [Chimpanzee Raiding](#)

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Riddoch-Syndrome

- [Blindsight](#)

Right and Wrong

- [Function of Morality \(Haidt\)](#)

Right and Wrongs

- [Evolution of Morality](#)

Righteousness

- [Evolution of Morality](#)

Rising Life Expectancy

- [Increasing Longevity](#)

Risk

- [Environmental Harshness](#)
- [Genetic Predispositions](#)

Risk Attitude

- [Risky Behavior](#)

Risk Aversion

- [Environmental Unpredictability and Bet-Hedging](#)

Risk Contract of War

- [Members of Coalition Must Believe They Will Win](#)

Risk Factors

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Synonyms

[Predisposing factors](#); [Vulnerability factors](#)

Definitions

Risk factors are factors that increase the chances of an untoward event.

Introduction

Understanding of health and illness remains incomplete without the consideration of risk factors. As risk factors are present much before the outcome, their understanding will help in promoting health and preventing development of illness. Outcome of the risk factors in the context of health refers to illness, disease, or disorder. For a given health-related adverse outcome in different individuals, the profile of risk factors in those individuals is not the same. This is because multiple risk factors interact among each other, as well as with the protective factors, in a highly complex manner to cause disease. The strength of association of risk factors with the index individual is also very important for understanding a particular outcome. For example, positive family history of schizophrenia increases the risk of development of schizophrenia in an individual; however, the risk of development of schizophrenia in that individual depends upon the number of family members affected with schizophrenia and the degree of genetic relationship (first-degree, second-degree, or third-degree blood relative) with the affected individual(s). Similarly, if a twin is affected, the risk of development of schizophrenia in the other twin sibling depends upon whether they are monozygotic or dizygotic twins.

Therefore, within a category of risk factors (e.g., family history of an illness), many risk-determining variables exist. The complex permutation and combination of multiple such variables within multiple risk factor categories combine to influence a particular health outcome.

Types of Risk Factors

Risk factors can be broadly divided into two subtypes (modifiable risk factors and non-modifiable risk factors). Modifiable risk factors are those which can be prevented, altered, and manipulated. Non-modifiable risk factors cannot be altered or manipulated. For example, stress is a risk factor for depression, which is modifiable; however, female sex, which is also a risk factor for depression, is non-modifiable. The risk factors that

cannot be modified are also called as fixed risk factors. The modifiable risk factors are also known as variable risk factors. Risk factors can take the form of biological, psychological, as well as sociocultural variables, according to their constituents. For example, in the causation of depression, “positive family history of depression among the first degree relative” can be a biological risk factor, whereas “poor coping skills” is a psychological risk factor and “isolation,” and “cultural taboo” can be sociocultural risk factors (Bernard and Krupat 1994).

Evolution of Risk Factors

Association between risk factors and disease are well-established. The nature of risk, however, changes with time. In modern society, there are several emerging risk factors that significantly influence global health, including mental health. The major emerging risk factors currently are pollution, relational difficulties, exposure to radiations, exposure to toxins (pesticides), maladaptive lifestyles, technology, war and terrorism, and epigenetic changes. Over several decades, there has been a significant change in the intensity and extent of exposure to the above risk factors, which is likely to affect the risk of physical as well as mental illnesses. Similarly, stress has also evolved significantly over time, which is a potential risk factor for ill health. The causes of stress, nature of stress, intensity, and frequency of exposure to stress have changed over time. These evolving risk factors affect health significantly.

Globally five major health-related risk factors have been identified, which attributes to mortality by increasing the risks of chronic diseases (World Health Organization 2009). These risk factors are:

1. Hypertension
2. Diabetes
3. Overweight and obesity
4. Tobacco use
5. Lack of physical activity

Similarly, several risk factors that contribute to global burden of diseases are being underweight,

unsafe sexual activity, unsafe (unhygienic) water, and alcohol use, of which the first three factors are commonly reported in underdeveloped and developing countries (World Health Organization 2009).

Distribution of Risk Factors

Risk factors vary across different socioeconomic strata. Evidence suggests that people from low socioeconomic strata often suffer from nutritional deprivation in comparison to people from higher socioeconomic status (James et al. 1997). The risk factors also change with sociodemographic variables like age, gender, and occupation. Old age, being female, and having a stressful job can be considered as risk factors of depression. Certain religion (e.g., Islam) can be instrumental in protecting from suicide as it is considered as a sin in various religious texts. Similarly, poor social support can be a risk factor for onset and maintenance of psychiatric illnesses. Geographic and climatic conditions also influence health; hence they can also be considered as potential risk factors. Stress-related disorders like acute stress reaction and post-traumatic stress disorder are common in regions where war, terrorism, natural calamities, and disasters are common. Similarly, seasonal affective disorder is commonly reported among people living far away from the equator region.

Risk Factors: Clinical Implications

Every illness has certain risk factors. During evaluation of clients in therapeutic settings, the risk factors that might have contributed to the development of the illness as well as progression of illness, or which might impede treatment, need to be identified. Identification of risk factors help in understanding the etiopathogenesis of an illness. It contributes to the explanatory model of illness. Identifying the modifiable risk factors and targeting their alteration are the mainstay treatment goals for most noncommunicable as well as infectious diseases. Risk factors segregate the population into two halves on the basis of its

degree of association with an outcome: one segment of the population who are at high risk of developing a health ailment and the other segment being at a relatively lower risk (Offord and Kraemer 2000). Minimizing the risk factors in order to restore the well-being of the individual is an important goal of treatment.

Risk Factors: Implications in Prevention

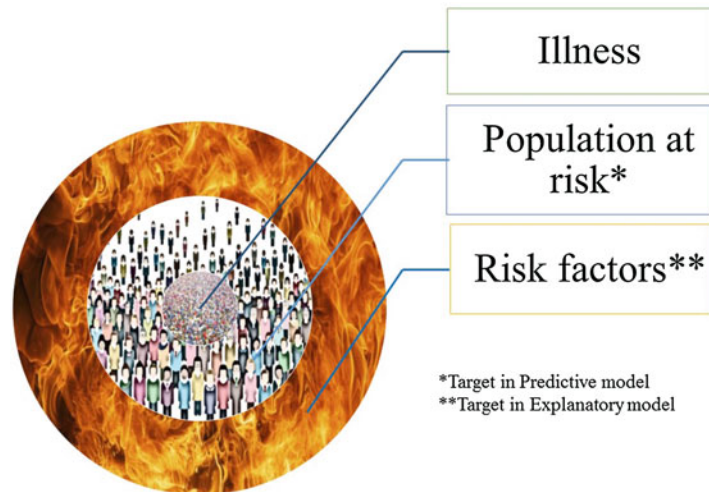
Identification of risk factors for health conditions helps in prevention of development or progression of a disorder. For example, unprotected sex is a potential risk factor for transmission of HIV infection. Understanding this risk factor helps in prevention of transmission of HIV infection. There are two models (predictive model and explanatory model) which operate on the basis of understanding of the risk factors in prevention programs (Fig. 1). The predictive model is built on the basis of various risk factors attributing to a health condition and often target the population at risk. The explanatory model targets to risk factors (causal factors), rather than the population (Schooling and Jones 2018). For example, air pollution causes respiratory illness; the predictive model will target the population at risk of respiratory illness (those with asthma or other chronic obstructive pulmonary diseases), whereas the explanatory model will emphasize on control of pollution.

Risk Factors: Research Implications

Various research designs have been implemented in the study of risk factors. Longitudinal studies usually evaluate the temporal association of risk factor (s), with development of disease and removal of risk factor to examine the alteration in the course of disease (Burt 2001). Cohort studies follow groups of a population over a period of time to examine the adverse outcome among the population group exposed to a risk factor in comparison to a population group not exposed to the risk factor. Similarly, retrospective studies also examine the association of risk factor(s) with a disease/disorder by evaluating the population from outcome back to cause. The

Risk Factors,

Fig. 1 Targeting risk factors in therapeutic interventions



population who developed a disease are examined for previous exposure to risk factors in the past and are sometimes compared to healthy individuals exposed to those risk factor(s).

Risk Factors: Statistical Relevance

Risk is always a probability that predicts the occurrence of an event (Burt 2001). Probability estimation of an event (e.g., disease) in epidemiology is also known as risk estimation. Estimation of risk factors provides insight for planning the therapeutic interventions. Risk factors are considered as a clinical correlate of health whereby their prevalence increases the probability of an adverse health outcome (Offord and Kraemer 2000).

Statistical techniques are useful in estimation of risk for a health condition among the broader population (Schooling and Jones 2018). Studies predict the risk, as well as attempt to establish a biological or psychological link with the etiological factors of a health condition. Significance in a statistical test depends upon the sample size. Estimating the risk factor in a larger sample may show some statistical significance; however, it always does not establish a significant association (Offord and Kraemer 2000). Hence, the nature of risk factor and outcome need to be evaluated before interpreting the statistical findings.

Conclusion

Understanding risk factors fosters a better understanding of health and illness. Risk factors play a pivotal role in the etiopathogenesis of illness and limiting the risk factors help in restoration of health. Given the growing emphasis on prevention of illness and promotion of health, studying and remediating risk factors will help in achieving greater population health.

Cross-References

- Risk
- Vulnerability Factors

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Risk of a Lifetime, The

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Synonyms

Book; Procreative ethics; Rivka Weinberg

Definition

The Risk of a Lifetime: How, When, and Why Procreation May Be Permissible is a book written by Rivka Weinberg, originally published in 2016 by Oxford University Press. This book discusses procreative ethics and how a contractualist approach can be applied in the context of procreative ethics.

Introduction

Rivka Weinberg is Professor of Philosophy at Scripps College, Claremont (located in California, USA), who received her Ph.D. from the University of Michigan. She is a philosopher and bioethicist who specializes in ethical and metaphysical concerns regarding birth and death (Oxford University Press 2018). She is the author of the book *The Risk of a Lifetime: How, When, and Why Procreation May Be Permissible* (Weinberg 2016), which discusses procreative ethics generally and the application of a contractualist approach (i.e., the view that morality is based on a contract or agreement; see also, e.g., Baumard and Sheskin 2015) to the study of procreative ethics.

The Risk of a Lifetime

In *The Risk of a Lifetime: How, When, and Why Procreation May Be Permissible*, Rivka Weinberg (2016) discusses the importance of carefully considering procreation. She begins with an analysis of the justifiable motivation behind procreation and argues that humans are ultimately individually responsible for the risks we take with our gametes and for the offspring that may develop. Weinberg contends that procreation may be permissible if it is done respectfully and when the child's chances of thriving and living a prosperous, full life are high. Moreover, she asserts that the view that procreation is never permissible because life results in suffering and is imposed on people without their consent is flawed. However, she nonetheless concedes that procreation is a risk from welfare and moral perspectives, even when it occurs under permissible conditions.

In order to assess whether or not procreation is permissible, Weinberg argues that contractualist principles should be applied. Contractualism broadly refers to the view that morality is based on a contract or agreement. Within this view, any act "is wrong if its performance under the circumstances would be disallowed by any set of principles for the general regulation of behaviour that no one could reasonably reject as a basis for informed, unforced, general agreement" (Scanlon 1998, p. 153). In other words, an act is moral when it conveys equal advantage to all involved members of a group. Contractualist principles can be imposed, Weinberg (2016) argues, to fairly take into account both the interests of the prospective parents in procreating and the interests future generations have in prospering in life.

Conclusion

In her book *The Risk of a Lifetime: How, When, and Why Procreation May Be Permissible*, Rivka Weinberg (2016) maintains that life is a risk rather than a gift, but that the risk can be permissible under the right circumstances. She outlines conditions under which she believes procreation is permissible and in so doing takes a middle

position in the debate, arguing against both the view that procreation is never (or almost never) permissible and the view that it is always (or almost always) permissible.

Cross-References

- [Euthanasia](#)
- [Reproduction](#)
- [Rivka Weinberg](#)
- [Suicide](#)

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Risk of Conception

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Synonyms

[Daily fecundability](#); [Probability of fertilization](#)

Definition

The day-specific probability that a single act of intercourse will result in conception.

Introduction

Conception risk refers to the probability that a single act of unprotected coitus will result in conception. A woman's conception risk varies as a function of life's historical, contextual, and cyclical factors, all of which are accompanied by different hormonal milieus that modulate conception risk (Motta-Mena and Puts 2017). Researchers have drawn on evolutionary theory to posit that women's mating psychology may change in relation to conception risk in adaptive ways. Further, women may adjust their attitudes and behaviors toward men and other women – and be perceived differently by other men and women – as a function of conception risk. Here, we briefly review work suggesting that mating psychology, intrasexual competition, and perceptions by men and other women vary with conception risk.

Although conception risk changes across the 6-day “fertile window” of the ovulatory cycle, peaking approximately the day prior to ovulation (Wilcox et al. 1995), many studies in evolutionary psychology do not treat conception risk as a continuous variable and instead dichotomize it as either nonzero (during the late follicular phase) or zero (during all other cycle phases). Cycle phase and conception risk are frequently assessed through the use of urinary luteinizing hormone (LH) test kits, self-reports of menses dates, or hormone values, with hormonal (including LH) methods being more precise (Gangestad et al. 2016).

Mating Psychology

Women's self-reported desire for sexual behavior rises throughout the follicular phase, peaks around ovulation, and falls during the luteal and menstrual phases (reviewed in Motta-Mena and Puts 2017), and is likely influenced by concentrations of estradiol and progesterone (Roney and Simmons 2013). Increases in general sexual desire concomitant with increases in conception risk may serve as the mechanism by which energy and effort are concentrated on reproductive

behavior, when reproduction is most likely or when the benefit–cost ratio of engaging in sexual behavior is high (Roney and Simmons 2013). Increases in the desire for uncommitted sex or extra-pair sex specifically may also track conception risk, perhaps functioning to recruit genetic benefits for offspring when conception is possible (Thornhill and Gangestad 2008).

Shifts in women's mate preferences as a function of conception risk are comparably less robust. Whereas some meta-analyses suggest that women express heightened preferences for partners with putative markers of genetic quality, such as facial symmetry, vocal masculinity, and behavioral dominance, when fertile (Gildersleeve et al. 2014); others do not (Wood et al. 2014). Moreover, recent large, within-subjects studies have failed to find support for the predicted patterns of association between changes in women's ovarian hormone levels and their preferences for masculine characteristics (e.g., Jones et al. 2018). As such, additional work using large samples and confirmed ovulatory cycle phase or hormonal measures is necessary to detect where shifts in women's mate preferences exist and, if they do, their magnitude.

Intrasexual Competition

Intrasexual competition may increase during periods of heightened conception risk, with observational and lab-based studies suggesting differences in women's clothing and make-up use across the ovulatory cycle. Testosterone is the primary endocrine mediator of changes in self-reported competitiveness, suggesting that increases in intrasexual competition around ovulation may be driven by mid-cycle peaks in testosterone. Levels of intrasexual competition may be predicted not just by a woman's own conception risk, but by the conception risk of same-sex rivals. For example, when partnered women were exposed to photographs of other women taken during ovulatory and non-ovulatory cycle phases, women consistently reported intentions to socially avoid women in the ovulatory (but not non-ovulatory) phase, and only when

their own partners were highly desirable (Krems et al. 2016).

Perceptions

Studies examining participant ratings of women's voices, odors, faces, and bodies generally suggest that heightened conception risk is accompanied by subtle but perceptible cues. For example, increases in progesterone across laboratory sessions (indicating decreases in conception risk) negatively predicted women's facial and vocal attractiveness to both men and other women (Puts et al. 2013). Hormone-driven changes in phenotypes such as complexion, skin color, and facial expression (reviewed in Motta-Mena and Puts 2017) are likely the more proximate causes of differences in perceived attractiveness across the ovulatory cycle. It is possible that such changes function to increase women's attractiveness when they are most fertile, perhaps especially to long-term mates, who might most easily detect such subtle intraindividual changes. Alternatively, changes in observable cues may reflect imperfect suppression of ovulatory cues tied to fluctuating hormones, coupled with strong selection on competitors and potential mates to detect these cues.

Conclusion

Relative to the pronounced genital swellings observed in many other primate species around estrus, physical changes that track conception risk in women are subtle, though likely perceptible by potential mates and same-sex competitors. Cyclic changes in women's mating psychology may function to adaptively allocate mating effort in relation to expected costs and benefits. Future work should continue to draw upon evolutionary theory to identify in which psychological and behavioral domains cyclic shifts may be reliably observed. Such work, and work on shifts concomitant with conception risk more generally, will significantly benefit from a sustained methodological emphasis on

large samples, within-subjects designs, and hormone-confirmed cycle phase.

Cross-References

- [Human Courting](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Perceiving Sexual Intent](#)
- [Sexual Selection in Evolutionary Psychology](#)

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Risk of Illness

- [Darwinian Medicine](#)

Risk Propensity

- [Men Riskier, More Aggressive](#)
- [Risk Behavior](#)

Risk Spread

- [Environmental Unpredictability and Bet-Hedging](#)

Risk Variation

- [Risk Variation with Parent Age](#)

Risk Variation with Parent Age

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Synonyms

[Age](#); [Child abuse](#); [Child murder](#); [Filicide](#); [Homicide](#); [Parent\(s\)](#); [Risk variation](#); [Victim](#)

Definition

Filicide is defined as the deliberate act of a parent, stepparent, or parental figure killing their own child. Subcategories of filicide include neonaticide, when the child is killed within the first 24 h of its life by his or her parents, and infant homicide, sometimes infanticide, although in some countries, infanticide only applies to the mother and the term infanticide has medicolegal implications.

Introduction

Filicide is a phenomenon with many causes and characteristics that are often difficult to isolate. This article looks at the variation of the risk of filicide with parent age: how much the age of the parent influences the likelihood of filicide.

Although a large body of literature exists on filicide, not much of the research focuses on the risk variation with age, as it is often mentioned, but the element of risk variation is not studied. Therefore, most statements in this article regarding risk variation are made based on inferences from the literature, unless stated otherwise.

Many classification systems have been created in an attempt to organize filicide, depending on the perpetrator's gender and the type of crime that is committed. Resnick was the first to attempt to classify filicide with five categories: altruistic filicide, acutely psychotic filicide, unwanted child filicide, accidental filicide, and spouse revenge filicide (1969). However, many other classification systems have been created in addition to Resnick's, for example, Bourget and Bradford (1990), which includes paternal filicide as a separate category. Unfortunately, many of the categories within the different classification systems overlap. In this article, the most commonly recurring categories will be used to organize the information, which are as follows: altruistic filicide, filicide due to mental illness, unwanted child filicide, accidental/fatal abuse filicide, retaliation/spouse revenge filicide, and other/unknown. One section will also cover risk variation with parent age for infanticide and neonaticide.

Altruistic Filicide

A large majority of cases of filicide fall under the category of altruistic filicide (49 % of cases when reviewed by Resnick 1969). This type of crime is generally caused by the parent killing the child because they believe it to be in the best interest of the child. The parent either believes the world is too cruel to leave the child in after their own death or they believe they will relieve the suffering of the child, for example, if the child had a disability (whether real or imagined by the parent) that the parent cannot tolerate. No specific research has covered parent age in altruistic filicide, but it is safe to assume that the parent might either be much younger or much older, as they might be incapable of safely taking care of the child or lack the necessary support (Daly and Wilson 2013).

Filicide Due to Mental Illness

Mental illness is one of the main causes of filicide. A sample of 6144 people convicted of child homicide showed that fathers were more likely than mothers to be convicted of filicide (male to female ratio 2:1) but mental illness was more common in mothers (66 % vs. 27 %) (Flynn et al. 2013). The study found the average age of the perpetrator to be 27 years old, with 16 % of them being teenagers when the child was born. Lewis and Bunce showed that psychotic women who had committed filicide were generally older than non-psychotic women (2003).

Unwanted Child Filicide

This can be compared to infanticide and neonaticide (which will be covered later in the article) as the child is regarded as a hindrance. This category also includes parents who benefit from the death of the child, for example, by receiving insurance money or marrying a partner who does not want stepchildren. Because of its similarity to neonaticides and infanticides, we can infer that the risk of unwanted child filicide would increase the younger the parent is.

Accidental/Fatal Abuse Filicide

Accidental filicide and fatal abuse filicide is often linked with mental illness. One study suggested that the younger the parent, the higher the risk of fatal abuse or accidental filicide, as the parent does not know how to take care of the child or has other children to take care of (Connelly and Straus 1992).

Retaliation/Spouse Revenge Filicide

This is the rarest type of filicide (Friedman and Resnick 2007). Because this depends on the relationship between the parents, the parents' age is not very relevant and it's therefore possible to assume the risk of filicide does not vary much with the parent's age.

Infanticide and Neonaticide

The classification systems of filicide do not generally include infanticide and neonaticide. The risk of filicide varies between filicide, infanticide, and neonaticide. The average parent age for filicide is 29 years old, on the other hand, the average parent age for infanticide is 23.8 years old (Brewster et al. 1998), and the average parent age for neonaticide is 21.2 years old. We can therefore conclude that from this study the younger the parent, the higher the risk for neonaticide, infanticide, and filicide, respectively. This study, specifically looking at risk factors for infant homicide in the United States, found that one of the strongest predictive factors of filicide was a maternal age of 15 years (relative risk, 6.8 as compared with 25 or more years) (Overpeck et al. 1998).

Conclusion

The research on risk variation of filicide with parent age remains a topic with limited research. The current literature seems to suggest a higher risk of filicide for young parents, generally

mothers who are in difficult and deprived circumstances. However, Flynn, Shaw, and Abel argue that because young mothers have a lack of education, economic opportunities, and marriage stability, they are at a greater risk of hurting themselves than they are of hurting their infants (2013). Therefore, more research on the parent age in filicide needs to be done in order have a clearer picture of the risks associated with it.

Cross-References

- [Child Abuse](#)
- [Child Homicide](#)
- [Child Mortality](#)
- [Methods of Filicide](#)
- [Sex Differences in Death by Filicide](#)

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Risk-Taking

- [Men Riskier, More Aggressive](#)
- [Risky Behavior](#)

Risky Behavior

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Synonyms

[Risk attitude](#); [Risk propensity](#); [Risk-taking](#)

Introduction

The study of risk propensity has a long and rich history of inquiry in various disciplines such as biology, economics, and psychology (see Mishra 2014 for a recent overview). In the evolutionary psychological sciences, currently, the main debates mostly revolve around the role that life-history variables and the early living environment have on risk propensity, what part sexual selection may have played in shaping risk-seeking behavior, and how risk-taking can be operationalized and measured when researchers are interested in studying risky behavior from a functional perspective.

Exploring Risky Behavior in a Life-History Framework

Life-history theory, a theory subset of evolutionary biology and behavioral ecology, argues that biological aspects of the life course result from trade-offs when allocating finite effort among survival, current reproduction, and future reproduction (Chisholm 1993). The underlying logic is that patterns of birth, growth, and death (i.e., life-histories) result from competing costs and benefits of different allocations at different times in the life cycle. At any given point, organisms can decide

whether to spend energy on their own bodies (i.e., somatic effort) or to spend energy in reproduction, which can be through attracting a mate (i.e., mating effort) or in caring for offspring (i.e., parental effort). Which patterns of expenditure are most effective for survival and reproduction depends on the environment the organism is facing: In environments with longer life expectancy (often including high environmental stability and low mortality rates), it might pay to invest effort in growth and development, whereas in an environment with shorter life expectancy (often including high instability and high mortality rates), it might be advantageous to reproduce earlier. Thus, variables in decision-makers' personal and ecological environment can determine adaptive individual differences in risky behavior due to differences in how we discount the future and which reproductive strategies are selected. Including such concepts from life-history theory has been shown to improve existing models of risk-taking. In a classic paper, Hill et al. (1997), for instance, could show that people with higher future unpredictability beliefs and shorter lifespan assessments were found to be more risk prone in their behaviors, even after accounting for classic statistical predictors of risk-taking (e.g., sex, age). Similarly, Sherman et al. (2016) showed that humans can internalize environmental cues of mortality risk (e.g., prevalence of violent and property crimes, registered sex offenders) already at an early age during childhood and that those cues can have an effect on subsequent risk perceptions and behaviors later in life during adolescence and adulthood.

There is good evidence that patterns of risk-taking are also linked to variables which are important life-history variables in and of themselves, such as sex, age, marital status, and parenting. Wang et al. (2009), for example, examined the effect of life-history variables on risk-taking propensity, as measured by the likelihood of engaging in risky behaviors in multiple evolutionary domains of risk. The effects of life-history variables on risky behavior were domain-specific, and there was support for the common observed sex difference, in which men showed greater risk-seeking tendencies than women. Older age,

parenthood, and a higher reproductive goal setting all reduced risk propensity in some of the studied evolutionary domains, but not others. Shorter subjective life expectancy was associated with an increased willingness to take risks in the mating and reproductive domain.

Understanding the Role of Risky Behavior in Mate Attraction

Viewed in the framework of evolutionary theory, human risk-taking shows some remarkable sex differences. This raises the possibility that risky behavior is a sexually selected trait. Typically, males in their teens and twenties not only are more prone than females of the same age to take risks of many different kinds (e.g., unprotected sex, extreme sports, binge drinking) but also suffer from the higher mortality rates associated with this behavior (Kruger and Nesse 2004). From a decision point of view, many of these risks not only involve an increased variance in payoff but also typically lead to a lower mean payoff than not taking the risk at all.

Sexual selection provides two rationales for why males engage in these risky behaviors, especially at ages of high fertility and high intersexual competition. First, the variance and skew in male mating success may favor risk-taking when there are high potential gains that outweigh high risks (e.g., via an increased likelihood of partner acquisition). Second, males might take risks as a form of advertisement of their genetic quality to both females and rival males. Here, the argument for why risk-taking might be an honest indicator of quality follows the logic of the handicap principle: Risky behaviors are less of a danger to high-quality males than to low-quality males, high-quality males can afford to take such risks more often, and thus rivals and potential mates should use risk-taking as a cue to partner quality.

Wilke et al. (2006) tested some of these ideas by recruiting both singles and individuals in stable relationships. Young men and women rated how attractive they would find it if a potential partner engaged in various risky activities. Interestingly, not only men but also women reported that they found recreational and social risks as attractive

and other forms of risk-taking (e.g., gambling, health) as unattractive. This indicates that risk-taking is attractive to the opposite sex in some domains but unattractive in others. Both sexes were relatively accurate in predicting what kind of risky behavior would be attractive to a potential opposite sex partner if they themselves would engage in this activity, and individuals in stable long-term relationships showed positive assortment for risk-taking behaviors. This indicates that people with similar risk attitudes might have a greater likelihood of encountering each other or that there is generally higher mate compatibility between such mates.

Measuring Risky Behaviors Within Evolutionary Content Domains

Is someone who takes high financial risks (e.g., investing money in a speculative stock) also more likely to risk harm to his/her own health (e.g., smoking) or more prone to engage in dangerous sport activities? Not necessarily. The old conception that individuals differ in a situation-consistent and domain general level of risk propensity has been largely abandoned in the behavioral decision sciences (see, for instance, Hanoch et al. 2006). New methodologies have been developed that can not only distinguish the propensity to take risks in different domains but also construct integrated risk attitudes based on peoples' risk perceptions and levels of perceived benefit regarding a particular behavioral activity that involves risk.

From an evolutionary point of view, risk-taking behavior should be viewed as domain-specific due to the recurrent and enduring risks in the environment of evolutionary adaptedness that shaped human risk propensity, and risky behavior itself should be conceptualized as variations in payoff distributions within specific domains of adaptation. To test this, Wilke et al. (2014) created a large set of risky modern-day analogues of qualitatively similar actions in recurring problem domains of the ancestral environment that were potentially beneficial but also costly to survival and reproductive success. Multiple risk behavior questionnaire items were

pooled into individual risk domains that were generated from a textbook analysis of the fields of biological anthropology and evolutionary psychology. Each evolutionary risk domain was covered by various diverse activities and subdomains within this area. The psychometric analyses from Wilke et al. (2014) resulted in an evolutionary domain-specific risk scale that assesses risky behaviors in a total of ten content domains: between-group competition, within-group competition, status-power, environmental exploration, food selection, food acquisition, parent-offspring conflict, kinship, mate attraction, and mate retention. The authors found that respondents' degree of self-reported risk-taking was indeed not consistently risk-seeking or risk-averse across evolutionary content domains and additionally surveyed life-history variables had domain-specific effects too. Overall, men were more risk-seeking than women, but interestingly not in all domains. Women were more risk prone in the domains of food selection and kinship. Study participants that reported not being in stable long-term relationships had higher risk propensity in the domains of mate attraction and mate retention. As supported by other studies, age, reproductive goal setting, parental status, number of siblings, and birth order all affected reported risk propensity.

In subsequent research, Jarecki and Wilke (in press) investigated the cognitive processes with which such different risk-taking tendencies across content domains can be reliably produced. Such work is necessary to close the existing gap between proximate (mechanistic) and ultimate (functional) considerations of decision-making under risk and uncertainty. Specifically, Jarecki and Wilke (in press) compared three cognitive process models with regard to how attributes retrieved from memory could account for the found domain differences and how specific types of informational risk cues and their respective frequencies are associated with peoples' domain-specific risk behaviors. Results suggested that specific types of situational attributes are most relevant for the found domain differences in risk-taking propensity.

Conclusion

The evolutionary psychological sciences provide a rich framework for studying risky behavior as they highlight what risk domains should be studied, what influence life-history variables have on risk propensity, and why young men, typically, are more risk-seeking than women.

Cross-References

- ▶ [Greater Risk-Taking and Status](#)
- ▶ [Judgment and Decision-Making](#)
- ▶ [Life History Theory](#)
- ▶ [Life History Strategies](#)
- ▶ [Men Riskier, More Aggressive](#)
- ▶ [Risk Variation with Parent Age](#)

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Rite of Passage

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Synonyms

[Social change](#); [Stages of life](#); [Transition](#)

Definition

A ceremony known as the rite of passage denotes a person's leap in life. It marks all important or milestone events, or it is used to pronounce the tumultuous transition from adolescence to adulthood and includes essential transitions in one's life such as births and beginnings, initiations, partnering, and endings or death.

Theoretical Framework

A number of models have been devised to define the process of shift in boundaries while maintaining various aspects of organizational regulation and social strength (Lewin 1951). Considered together, these models tend to provide an explanation to the shift of individuals or groups, at important stages of life and assuming new roles and responsibilities. Therefore, crossing social boundaries is a considered unavoidable outcome of social change, and such boundary transitions, if unfettered and unconfined, tend to challenge a person's social status.

It has been asserted by Van Gennep (1960) at the start of the twentieth century that even

though every society had distinct content of social transformations, an attribute of social transformation is that their form or pattern remained universal. Those societies that were entirely distinct from each other had almost the same formal rites of passage that allowed individuals or groups of individuals to adjust their personal status. A rite of passage refers to an event in which an individual moves from a certain condition of life experience to another, from a certain phase in life or a state of social status, to a more sophisticated one (Van Gennep 1960). A rite of passage essentially signifies significant personal life experiences or life crises. These include, for instance, life-changing events like marriage, parenthood, or demise of a closed one. In addition, a rite of passage may also be present in other critical life experiences, like academic accomplishment or becoming an official member of an occupational group or profession.

A three-staged model of social transition was put forward by Van Gennep (1960). The model was formulated using a separation stage (when the person or group is eliminated from an earlier state), a transition stage (the liminal stage, a social limbo in which the person may establish a close relationship with other group members), and an incorporation stage (which involves integrating back into the society in a novel state). Henceforth, a rite of passage signified variations in social status, which involved intricate symbolic ceremonies and/or simple practical occurrences, determined by the nature and situation of the transition (Draper 2003). For example, it was observed by Froggatt (1997) that certain stages of a rite of passage may be more noticeable depending on the kind of life event being experienced. The separation stage would be more obvious while mourning, the transition stage would be more obvious while experiencing parenthood, and the incorporation stage would be obvious in the early period of marriage. The purpose of rite of passage related to these life events was to decrease their possible adverse effects on the individual and on social order and solidity.

Conclusion

The ceremonies, rules of society, and culture enable transitions in one’s life. These transitions also authenticate the stability and direction of social groups by allowing the acceptance of social and cultural transition and by evading interpersonal or group conflicts. It is established that both groups and individuals change with the passing time, the level of their status and wisdom changes and they also acquire new skills and abilities. The formation of new social groups means new transitions. Therefore, negotiation has emerged as a necessary element of an effective transitional procedure.

Cross-References

- ▶ [Honor Code](#)
- ▶ [Human Enculturation](#)
- ▶ [Morality](#)
- ▶ [Social Values](#)
- ▶ [Spiritualism](#)

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Rites

- ▶ [Rituals](#)

Ritual

- ▶ [Nonhuman Reactions to Death](#)

Ritual and Speech Coevolution

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Synonyms

[Conventionalization](#); [Metaphor](#); [Mimesis](#); [Symbolic culture](#)

Definition

Thesis originally developed by anthropologist Chris Knight on the important consideration of novel forms of group cooperation, and corresponding conflict, in the emergence of human language, analogous to signaling in other species.

Introduction

In this entry, I discuss the ritual/speech coevolution hypothesis for the evolutionary emergence of spoken language. This brings the main theory on the evolution of animal signals to bear on the question of language origins. Our closest primate relatives are fundamentally constrained in their ability to mimic or produce novel vocalizations, under pressure to maintain reliability in their signals. The ritual/speech coevolution theory explains how those selection pressures were relaxed in the case of human evolution through the generation of novel levels of in-group trust.

The Problem of Cooperation in Communication

Ritual/speech coevolution is a hypothesis explaining the evolutionary emergence of spoken language. It rests on the assumption that language can only evolve given novel conditions of social

cooperation widespread across human communities – effectively cooperation between strangers. In the contexts of human evolution, the only medium for securing such cooperation within and between groups was costly ritual (cf Durkheim 1912; Knight et al. 1995; Maynard Smith and Szathmari 1995; Deacon 1997; Rappaport 1999; Irons 2001; Alcorta and Sosis 2005; Knight and Lewis 2017).

Ritual/speech coevolution brings to the problem of language origins the main body of theory applied to the evolution of animal signals. Signal evolution theory deals with the emergence, function, and design of animal signals (Maynard Smith and Harper 2003). Focused on social interaction and behavior in the world, signal evolution is necessarily political in its approach. Central debates concern the honesty and reliability of signals (Zahavi and Zahavi 1997), manipulation and mindreading (Krebs and Dawkins 1984), and the effects of shared versus conflicting interests in outcomes (Maynard Smith and Harper 2003).

Among primates generally, tactical use of deception is predicted by neocortex volume (Byrne and Corp 2004), a finding consistent with the Machiavellian intelligence hypothesis – the idea that intelligence evolves under pressure to deal with social challenges. Humans are clearly Machiavellian in terms of political alliance formation and capacities for deception. Issues of trust and reliability are critical to any understanding of language origins.

While apes and monkeys have rich repertoires of calls, they seem to be severely restricted in their ability to mimick or to produce novel vocalizations (Fitch and Zuberbühler 2013). In particular, when phonating, they lack neural control over articulators such as the lips, tongue, soft palate, etc. This means that our closest relatives are unable to manipulate vocalizations at will. No monkey or ape has an inflexible tongue, but when communicating it leaves the tongue out. Knight and Lewis (2017) draw on signal evolution theory to explain why. While sound – unlike visible gesture – carries over distances, goes around corners, and works in the dark, in these contexts listeners lack corroborating evidence of reliability. It makes sense then that vocalizations

tied to bodily and emotional states will be perceived as more reliable than those which can be altered at will. Mistrusting one another's scheming, Machiavellian minds, primates ignore the all too-flexible tongue, preferring to rely on the evidence of their own eyes and ears. In this view, apes are “too clever for words” (Knight 1998: 72).

So the conundrum of speech and language evolution is to explain how and why natural selection, in the human case, switched from quarantining the primate tongue – excluding it from all but a marginal communicative role – to developing and fine-tuning that same tongue's role as the most important speech articulator of all.

Signal evolution theory contrasts two divergent trajectories depending on the degree to which signaler and receiver share interest in the same outcomes. Where we find high-cost, repetitive, multimedia displays, we may infer a function in terms of social manipulation, conflict, and exploitation. Resistance by receivers sets up selection pressures acting on signal design. Signalers who encounter “sales resistance” are driven to respond by prolonging and repeating signals, increasing amplitude, and resorting to costly multimedia displays. Such extravagant advertisers include peacocks displaying to would-be mates or caribou bulls bellowing in the rut. Zahavi (1987) shows how the discernible costs of such displays enhance their credibility by tapping and hence testing the very reservoirs of quality that signalers are attempting to advertise. The evolution of high-cost signaling is driven by skeptical receivers pushing signalers to ever greater competitive effort to prove their quality.

By contrast, where we find low-cost, quiet, and efficient signals, a cooperative audience can be inferred. If signalers can afford to cut their emission costs, it is only because listeners are investing corresponding effort in receiving, decoding, and acting on signals. This implies that signalers and receivers significantly share interests. For such “conspiratorial whispering” (Krebs and Dawkins 1984) to evolve, signalers must be imparting useful information to receivers and those receivers are not expecting to be deceived.

The ultimate cost-cutting strategy would be to resort to purely tokenistic, wholly conventional

signals that can be processed categorically at speed – relieving listeners of the need to evaluate gradations in physical performance and signalers of such costly performance. According to Zahavi (1993), however, animal “conspiracies” are never sufficiently cooperative. Internal conflict and skepticism precludes selection for reliance on tokenistic “paper money.” Nowhere in the living world do we find purely conventional signaling – with the puzzling exception of human speech.

Turning to human symbolic communication, Knight (1998, 1999) argued that our ancestors developed divergent, formally contrastive types of communication along these two “high-cost” and “low-cost” trajectories: ritual and speech. Table 1 shows the diametric opposition of characteristics of each. On the basis of signal evolution theory, we can infer that speech emerged in a cooperative context while ritual did not. For speech to have evolved, “conspiratorial whispering” in the human case must have been anomalously trusting. By contrast, ritual – with its costly, inefficient features of redundancy and display – can only have emerged from a dynamic of conflict, manipulation, and exploitation.

The paradox here, in the light of nonhuman primate vocalization, is that the extremely low-cost, conventional codes of speech can easily leave listeners vulnerable to deception. With no

intrinsic link between sounds and their purely arbitrary meanings, words are routinely decoupled from emotional veracity or real-world stimuli. Despite speech having no intrinsic reliability, human conversation works on Grice’s “cooperative principle” (Grice 1969), with participants, even where they may be in some degree of social conflict, cooperating at the level of mutual conversational ends. If humans are on “speaking terms,” they expect intentional honesty. Somehow this new default of honesty – honesty in the deployment of volitional, conventional signals – became established. In the course of human evolution what were once frequency-dependent tactical deceptions became increasingly harnessed to a reversed social function: group-wide sharing of socially useful information.

This paradox can be unraveled if we consider that whereas speech is fundamentally interpersonal, ritual operates group-on-group and may function to demarcate boundaries of those groups (Cohen 1985; Harrison 1993). Experience of the high-cost, multimedia signals involved in ritual will differ according to whether the receiver is outside or inside the performing group. For outsiders, the costly signals are manipulative and exploitative, needing to overcome “sales-resistance” by impressing observers with the quality of performance. Among insiders, the “collective effervescence” (Durkheim 1912), aroused by singing, dancing, and musicking together, will intensify in-group trust and generate a sense of group identity as “We” (Rappaport 1999). Focusing on the emotional responses of individuals to ritual experience, Alcorta and Sosis (2005) show that the very costliness of undergoing ritual enables those individuals to demonstrate in hard-to-fake terms their commitment to the group.

There are two major emergent effects from such proto-ritual experience. First, the novel levels of in-group trust can now permit conventionalization and shorthand reference – volitional, conventional signals – in communicating among group members, now on the way to becoming a speech community. Secondly, in representing their coherent and enduring solidarity, ritual performers generate sacred, supernatural, and counter-intuitive concepts – the first gods

Ritual and Speech Coevolution, Table 1 Speech versus ritual (After Knight 1999: 231)

Speech	Ritual
Cheap signals	Costly signals
Interpersonal	Group-on-group
Two-way communication	One-way signals
Low amplitude	High amplitude
Dispassionate	Emotive
Vocal-auditory	Multi-media
Digital	Analog
Discrete-combinatorial	Holistic
Productivity/creativity	Repetition/redundancy
Stress on novelty	Stress on conservatism
Conventionally coded	Iconic and indexical
Focus on underlying intentions	Focus on body-boundaries and surfaces

(Durkheim 1912; Knight et al. 1995; Rappaport 1999; Alcorta and Sosis 2005).

Roy Rappaport analyzes the form and features of ritual that make it “the social act basic to humanity” (Rappaport 1999: 31). Ritual overcomes the divisiveness of individually held beliefs. Defining ritual as “the performance of more or less invariant sequences of formal acts and utterances not entirely encoded by the performers” (Rappaport 1999: 24), Rappaport focuses on the unique conjunction of features in ritual. Ritual form permits the intersection of the symbolic with what is not purely symbolic. Ritual combines formal canonical messages – encoded by other than the performers – with the indexical signals, the current state, mood, and emotions of the flesh and blood performers. This “substantiation of form and ...informing of substance” mean that the establishment of convention is intrinsic to ritual. Without this, no social contract, moral order, or language could exist.

The function of ritual is not to differentiate between lexical meanings but to establish, for everyone, an overarching meaning – a meta-performative or Word – from whose subsequent fragmentation a limitless multiplicity of subsidiary meanings can be derived. Rappaport explains how apparently irrational nonsense – perhaps the endless repetition of just a few meaningless sounds – may “provide the ground, deeper than logic and beyond logic’s reach” upon which to establish sufficient collective authority and mutual trust to build up “the usages and rules of social life,” in turn enabling words to make sense.

While Rappaport did not have any very satisfactory model for the evolution of ritual (hence speech), Knight and Lewis (2017), within the ritual/speech coevolution paradigm, provide a specific evolutionary account. Words and grammar, they claim (Knight and Lewis 2017: 435), are “means of navigating within a shared virtual world. Singing, dancing, and other forms of communal ritual are necessary to join people together in such ideal or imagined worlds.” Language then will not even begin to evolve unless ritual action has already begun to establish intensified levels of community-wide trust in association with a shared virtual domain. This explains why nonhuman

primates, confined as they are to the brute world of physical facts, have no need of it.

Knight and Lewis explain how the generative principle for both words and grammar is the ostensive-inferential process underlying metaphor. In this view, symbolic communication “rests on the ability of listeners to infer relevant communicative intentions from expressions that, interpreted literally, are inadequate or untrue” (Knight and Lewis 2017: 436). Not only does language comprise zero or very low-cost volitional vocal signals, but at the level of both words and rules, lexicon and grammar, these amount to conventionally agreed “lies” or deceptions. Whereas nonhuman primates would simply reject these sound sequences, we humans instead search out the hidden implications and communicative intentions.

Knight and Lewis draw on hunter-gatherer ethnography to work out a model for the emergence of such socially agreed “deceptions.” Human abilities to manipulate pitch were first exercised in fooling outsiders: animals, whether these were prey being hunted (by men) or predators being evaded (by women and children). Song first – a communal polyphony of meaningless sounds – used to confuse and deter predators regarding numbers of hominins in groups, would have developed capacities for intentionally varying pitch. In such a context, the emotional solidarity among chorusing groups would override any dangers of deceptive use. Shorthand snatches of song, animal-sound mimicry, or pantomime dance steps could now begin to take on specific shared meaning. From there, a fully grammaticalized language could emerge with extraordinary speed, as long as the freedom to innovate – freedom to “say” one thing while “meaning” another – was maintained. What had blocked earlier hominins and hominids from any such grammaticalization process was “the burden imposed on all signals to incorporate some costly component to demonstrate reliability” (Knight and Lewis 2017: 445). Grammaticalization is based on a tendency to efficiency, but requirement of reliability in signals demands the opposite, increased cost. The release from this constraint frees the tongue and other articulators so they can be recruited to

increasingly efficient, conventionalized communication: speech.

Knight and Lewis (2017) aim to make their model testable by specifying, in detail, the “world’s first metaphor,” identifying it as a gendered ritual performance in which the core principles of primate politics are overturned. They argue that as female hominin ancestors faced increasing reproductive costs with very large-brained offspring, critical points of conflict occurred whenever an alpha male attempted to monopolize an imminently fertile (menstruating) female. This would have conflicted sharply with reproductive interests of both other females and other males. Ritual display developed as female coalitions mounted resistance to any would-be alpha, with the whole female group signaling their nonavailability to males through song and pantomime dance: we are the wrong species (animals); we are the wrong sex (males); and this is the wrong time (blood). By identifying their own “menstrual” blood as the blood of the game animals they wanted the men to hunt, women’s first morally authoritative ritual construct established categorical rules encompassing sex, kinship, and economics.

The specific model proposed here has the merit of testability. But the general ritual/speech coevolution paradigm has advantages (Power 2014). Firstly it offers a coherent basis for continuity with animal communication systems through theory of ritualized behavior. Secondly, regarding the archaeological record, it makes the clear prediction that the origins of language will be marked by evidence for ritual behavior (Watts 2014).

Cross-References

- ▶ [Communication, Cues, and Signals](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolution of Female Resistance](#)
- ▶ [Grammaticalization](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Reliability and Deception in Language](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Signal Reliability](#)

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debate as to the evolutionary origins of religion is mostly divided between whether religions emerged over time as an adaptation selected through natural selection or that they are by-products of other psychological mechanisms, this section will specifically address some of those religious rituals considered by both theories to have plausible universal salience in the general development and maintenance of religious cultures worldwide.

Rituals

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Synonyms

[Ceremonies](#); [Customs](#); [Practices](#); [Rites](#)

Definition

Established rites, ceremonies, and customs performed publically and/or privately by individuals or groups as prescribed by religions.

Introduction

Religious and cultural rituals represent those observable activities and series of actions or behaviors requiring recitations, gestures, and the manipulation of objects as expressed by groups or individuals to demonstrate commitment to and in compliance with the accepted religious traditions and customs of specific communities. Religious scholars and social scientists agree that religious rituals are significant features of most world religions, influencing the cohesion of the cultural groups that practice them, providing practical benefits for individuals, and informing the practitioners' beliefs about life after death (Durkheim 1912, 2008; Wilson 2003). Although the ongoing

In-Group Functionality of Religious and Cultural Rituals

Religions, whether monotheistic or polytheistic, animistic or naturalistic, have throughout human history been expressed in remarkable varieties (Schmitt and Fuller 2015; Wilson 2003). Despite their tremendous diversity, religions share many common ritualistic activities. Religious rituals are seen as providing opportunities for community members to cooperatively and publically manifest shared beliefs, thus strengthening individual personal commitments to the group as well as substantiating and maintaining in-group bonds. Among the vast array of rituals practiced from the earliest religions through to the present day, certain key evolutionary benefits of ritualism emerge as essential such as the promotion of social cohesion and cooperation, unified beliefs in life after death via ancestor veneration, and the subordination of individuals' self-interest for the benefit of the group (altruism), among others. These represent common characteristics of religions and are all seen in various individual and group rituals to varying degrees of import (Kirkpatrick 1999).

Commonly practiced religious rituals are shown to increase the ability to bind groups together, engender trust and cooperation among practitioners, and allow for public demonstrations of allegiance and commitment to the group (Whitehouse 2012). According to Whitehouse, during human prehistory, group identity was based primarily on shared experiences and rituals,

which had the effect of producing greater levels of intragroup member confidence and trust. Ritualized eating or avoiding of certain foods or wearing of specific items of clothing or hairstyles allowed for inferences of common beliefs and trustworthiness even in strangers, which had the effect of spreading group cohesion and therefore religious cultures, more widely. Victor Turner theorized that traditional and modern religious rituals could be understood in terms of the two separate concepts of structure and *communitas* with the latter referring to an egalitarian community of individuals sharing moral claims and the former referring to a systematized set of roles community members occupied, differentiated by age, sex, and status (Wilson 2003). In this light, religious rituals provide communal, visceral, and emotional experiences that help communities and social structures to remain united, especially during those times when adherents transition between social status roles such as from adolescent to adult (coming of age), unmarried to married, married to widowed, and elder community member to deceased ancestor. In these universal life experiences, rituals enable religious community members to cooperatively and publically express mutual beliefs, share grief and joy, commiserate about the rigors and goals of the rituals, and create cherished group memories, in addition to strengthening in-group bonds. Historically, religions successfully unify communities under common sets of customs, institutions, and organizations when the majority of the people in the population are members of the predominant religious community (Richerson and Newson 1987).

Coming-Of-Age Rituals

Coming-of-age religious rituals vary considerably from religion to religion, from era to era, and geographically but all are meant to signify to the adolescents, their families, and the religious community at large that they are willing participants in the physical, emotional, and spiritual

journey from being a child of the group to an adult within the group and, when successful, assume their newly acquired and specific rights and responsibilities. These coming-of-age or initiation rituals often include extended periods of fasting, going without sleep, venturing into the wilderness alone, sequestration, memorizing and performing elaborate chants and dances, as well as physical alteration of the body such as scarification of the skin, shaving of the head, and piercing of body parts, among many others (Gennup 1960, 2004). For girls, religious rituals for coming of age often pertain to the onset of menses, with the community acknowledgment of their fertility and an increased set of expectations and responsibilities to keep sacred the sexual and reproductive customs of the group (Gennup 1960, 2004). For boys, acts of bravery and courage are required such as the hunting of predator animals, exposure to stinging insects or plants, and feats of strength and endurance including long runs or carrying heavy objects over great distances. There is the universal expectation that the successful adolescent initiate not only pleases their parents and religious community by completing the initiation rites but also pleases the god or transcendent power honored at the center of the religion's belief system.

Religious Burial Rituals

From the perspective of most of the world's religions, ritual disposal of the human dead brings closure for the surviving family and friends of the deceased, confers respect on the departed, and is believed to assist in their transition to the next life. The earliest evidence of human religious sentiments is the treatment of the dead. Early human behavior as demonstrated in ritual burial is thought to represent cognition of the states of life and death. Ritual burials of modern humans at the site of Qafzeh, Israel, contained 100,000-year-old skeletons that were stained with red ocher and whose graves included the mandible of a wild boar. The

placement of corpses in shallow graves along with common stone tools and animal bones indicates an emotional connection to the deceased and reveals a belief in an afterlife. These types of ritual burials are believed to have served a number of different goals, including honoring the dead and communing with gods and spirits (Whitehouse 2012). Human remains found in Turkey revealed evidence of funerary practices 8000 years ago in that the bodies were elaborately manipulated before burial (Whitehouse 2012). With respect to the further development of religious sentiments in mortuary practices, it is likely that funereal rituals developed over time, becoming clearer and more complex as the various religious beliefs in a hereafter expanded.

Gennep developed the theory that funereal rites accompanying life transitions consist of three structural elements: rites of separation, preparing the dying person and giving the last rite; rites of transition, such as the final burial of the corpse in the cemetery or the group; and the rites of incorporation, a prayer service offered with the intention of praying for the salvation of the deceased person's soul. As in the performance of other religious rituals, there seems to be an attenuated tendency during burial rites wherein the community members conducting the rituals summon or invite the god(s) and spirits to assist. It is as if the mystery of physical death and the yearning for the assurance of afterlife are issues the living cannot understand or attend to without supernatural assistance and only when the living adherents offer obeisance to their god figures can there be an expectation of the burial rituals succeeding.

Rituals and Health

Among the potential evolutionary benefits of religious rituals is increased physical health. There have been numerous studies showing that religious beliefs and practices increase individual health and other aspects of well-being. According to the researchers at Duke University,

religious rituals can function as anti-stress mechanisms (Paul-Labrador et al. 2006). They were able to demonstrate that individual prayer and meditation, as well as attending church services, reduces blood pressure, high blood pressure being a reliable index of psychological stress. As elevated blood pressure causes heart disease and heart disease is the number 1 killer in many developed countries, the scientists determined that prayers and rituals have the capacity to enhance health and lengthen life. If the individual benefits of ritual prayers and meditation are enhanced by the ritual activities of communal religious practices and by the culture as a whole, then the rituals can be seen as positive manifestations of group-level adaptations. However, some religious behaviors such as dangerous initiation and coming-of-age rituals involve potentially significant costs to individual members' health as well as to their religious communities writ large, suggesting that unless potentially dangerous and risky rituals provided significant advantages, natural selection should act against them.

Conclusion

Throughout human history, religious and cultural rituals have been used to promote in-group functionality, to challenge adolescents in coming-of-age rituals, and to provide solace and closure for loved ones with burial rituals and have been shown to positively promote physical and emotional health. While there may yet be no definitive answer to the question as to whether religion evolved as adaption through natural selection or emerged as psychological by-products, it is clear that the multiplicity of religious rituals throughout the world's religions attempts to address universal human concerns of life, death, and beyond.

Cross-References

► [Joseph Henrich on Religion](#)

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Rivalry

- [Contexts for Men's Aggression Against Women](#)
- [Female-Female Competition](#)

Rivka Weinberg

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Definition

Rivka Weinberg is a Professor of Philosophy at Scripps College in Claremont, California.

Weinberg received her Bachelor of Arts degree from Brooklyn College, City University of New York, and her Philosophical Doctorate degree from the University of Michigan, Ann Arbor.

Introduction

Rivka Weinberg's main areas of interest are ethics and metaphysics. Her areas of expertise include reproductive ethics, bioethics, theories of moral obligation, and the metaphysics of life and death. In December 2015, Weinberg published a book, entitled *The Risk of a Lifetime*, which incorporates much of her previous work in these areas and presents a cohesive argument for a new way of thinking about the permissibility of procreation. In this entry, Weinberg's early work that led to the development of her arguments in *The Risk of a Lifetime* will be highlighted, beginning with Weinberg's contributions to metaphysics. Her metaphysical views lay the foundation for her work in reproductive ethics, which will be reviewed in the second section, touching upon her theories of procreative justice and parental responsibility.

Part One: Metaphysics of Life and Death

The Nonidentity Problem

The nonidentity problem was posed by Derek Parfit (1984, Part 4) and picks up on three seemingly opposed intuitions about personal identity. The first intuition is that an act can be wrong only if it harms an existent or future person. The second intuition is that an act that confers a flawed existence upon someone, but existence that is still worth having, is not a wrong act (does not harm that person) compared to a world in which this person did not exist. That is to say that where a person's existence has some flawed qualities, if the person's life is preferable to the option of not existing, then they were not harmed by being brought into existence. The third intuition is that some acts that confer existence are wrong, even if they do not cause harm to the person they cause to exist or any other future person (for a full

explanation of the nonidentity problem, see Roberts 2015).

Weinberg is interested in this question because the nonidentity problem makes it difficult to discover who might be harmed by a reproductive act. In this case, philosophers have theorized that it might always be permissible to procreate as long as a person's life is likely to be worth living (Weinberg 2015). Weinberg thinks, however, that the nonidentity problem makes a mistake, which is the assumption that existence is "a good bequeathed by our ancestors" (2015). Instead, she argues, existence is simply a state of affairs, something everyone has and nobody needs, as she puts it (Weinberg 2013, 2015).

Existence as a Precondition for Interests

Thus, contrary to a common intuition and line of argumentation, Weinberg sees existence as neither a gift nor a benefit. She aims to break away from the idea that existence is itself a good thing and to encourage others to stop thinking of it this way as well. Instead, existence is a precondition to having interests of any kind (Weinberg 2013, 2015). One cannot receive a benefit unless one exists. So, existence is just the state of affairs of being able to receive benefits (or harms). Existence is the state of having interests in doing well or not doing badly.

Common Moral Principle

The view that existence is a prerequisite for having interests is in line with what Weinberg considers to be a common principle of morality, which is that one may have obligations to those who do or will exist, but not to hypothetical entities. Weinberg thinks this moral principle fits with intuitions about whom we might have duties or responsibilities to. Existence, she says, is required for being a subject and having interests. If one does not exist, one is of no moral importance even to oneself (Weinberg 2015). So, one may have moral obligations to those persons who exist, and one may have obligations to those persons who will exist, but we do not have obligations to those who may exist, but may not.

Weinberg's metaphysical positions are important because they frame her views on questions

of reproductive ethics. That existence is not a benefit, that it is merely a condition in which one is subject to having interests, and that hypothetical persons have no interests are main premises upon which many of her arguments about procreation stand. For example, in arguing against David Benatar's (457, 462) anti-natalism (2912) position against procreation, Weinberg (2012) posits that since only existent persons have interests, a person must exist for them to be benefitted or harmed. Nonexistence cannot benefit anyone; there is no subject to receive the benefit. Without a subject to receive the benefit, Benatar's argument that nonexistence is better than existence because it is a state of no harm should not be granted and the anti-natalist position rejected (Weinberg 2012).

Part Two: Reproductive Ethics

Procreative Justice

Weinberg is interested in questions about the morality of creating a child, rather than the morality of raising a child. In order to discover a principle of procreative justice, she attempts to redevelop John Rawls' original position (Rawls 2003; Weinberg 2002). This principle of procreative justice, she thinks, will shed light on which conditions may morally permit procreation. The reason that such a principle is needed, Weinberg argues, is that procreation actually involves a conflict of interests.

Procreative Conflict of Interest

Weinberg argues that procreative justice is primarily concerned with a distributive conflict of interests between parents and the children they will have (Weinberg 2002). Parents, she says, have an interest in procreating at the best time, from their perspective. This might mean being younger when procreating, for their personal health and lifestyle reasons. However, their child may have interests that conflict with these; a child may have an interest in being born later in their parents' lives, when they are more financially stable, for example. Weinberg thinks that this conflict of interest requires a principle by which the benefits

and burdens of procreation are justly distributed (Weinberg 2002).

Rawlsian Contractualism

John Rawls' contractualism is a theory formulated to address questions of distributive justice. Everyone that will be party to the result of a social contract enters into what Rawls (2003) called the original position, which is a position of undifferentiated vulnerability to social, economic, environmental, and other uncertainties. Rawls argued that in the original position, everyone would step behind a "veil of ignorance" about what their life conditions would be when the contract was created and the veil lifted. One would thus not know their race, religion, gender, sexual orientation, nationality, or any other differentiating quality that may lead to distributive injustices (and does in the real world). Therefore, everyone in the original position would need to assume that they might be the worst off in society and so have an interest in making sure that the worst off were still doing well enough to make such a position acceptable if one found oneself in it (this is known as the Maxi Min principle) (Rawls 2003).

Applying this method of arriving at distributive justice is challenging for questions of procreation. Parfit (1984), for one, does not think that Rawlsian contractualism can be applied to questions of procreation, because it is implausible for any of us to enter the original position and suppose that in the real history of the world we did not exist. He argues that questions of distributive justice in procreation will affect how many people exist, because some people who would have otherwise procreated may not be permitted to procreate under the resulting principle. If we assume that we will exist, this is like assuming that we will be the beneficiaries of a racist or sexist principle of distribution. Thus, the purpose of the original position would be thwarted, and the principle that resulted would be unjust.

Weinberg (2002) does not fully address these objections, but defends her use of Rawlsian contractualism by arguing that it does not require one to imagine one's own nonexistence, because issues of justice in procreation are restricted to

birth conditions and procreative liberty. Weinberg does not think that contractualism involves questions of justice in existence. She further argues that existence is not a distributable benefit. There can be no issues of justice between those who will exist and those who may exist, since those who may exist have no interests. There cannot be justice issues in not being created, because there is no subject of injustice.

A number of modifications to Rawls' contractualism are required to apply it to questions of procreation. Briefly, the nature of the parties to the contract will be "hypothetical future participants": those people who would exist and those who would be subject to the resulting procreative rules (Weinberg 2002). The veil of ignorance, for Weinberg, results in indeterminate identity, but not indeterminate existential status. Thus, Weinberg's original position includes only and all participants who will exist once the procreative rule is applied. In taking this approach, Weinberg attempts to sidestep Parfit's objection, but we can see how it poses a problem for her view. There are people who currently exist who may not exist if the procreative rule was applied prior to their birth, and there are people like them who may not exist in the future once the rule is in place. Each possible principle of procreative justice will include and exclude different groups of people who would exist under it. Weinberg does not address how these people would participate in the original position, but says it includes only the participants who will exist once the rule is in place and those who will be subject to procreating according to the rule. As Parfit pointed out, this may prioritize those who will exist in a similar fashion to prioritizing those who would benefit from being male in a sexist society and thus not reveal a just principle after all.

Setting this aside, however, when behind the veil of ignorance, participants will not know whether they are a prospective parent or a child (Weinberg 2002). Interestingly, because children are also future prospective parents, everyone behind the veil of ignorance will occupy both positions in the conflict of interests. While Rawls thought that information about probabilities should be veiled from the parties in the

original position, Weinberg (2002) thinks that probabilistic information is crucial to a procreative contract. She therefore argues that while individual information should be veiled, information about social and cultural norms, species information (i.e., “normal” human functioning), and other details must be known.

Finally, Weinberg (2002) thinks that for procreative justice, the concept of what is Good in life that participants in the original position should use needs to be specific and comprehensive, while also allowing a plurality of visions of a worthwhile life. The capability conception of the Good, under which certain conditions that permit the development and exercise of important human functionings are guaranteed or promoted, is the most appropriate choice, she thinks (Weinberg 2002; also see Nussbaum 1990). The capability conception of the Good, then, will inform a decision principle for the participants behind the veil of ignorance. This decision principle is a tool of self-interested and prudential reasoning, which directs participants in the original position to the principle of justice that will help to make their lives better, overall. Since participants will be using capability theory as their idea of a Good life, Weinberg (2002) reasons that the procreative decision principle they decide upon will be “maximizing capability” or “MaxC.”

In the procreative original position, children and prospective parents are represented and, Weinberg thinks, interchangeable in the sense that each participant will occupy both positions to her procreative conflict of interest. As such, MaxC is not just interested in the maximization of the child’s capabilities from birth; the parents must also enjoy a maximization of capabilities through procreation. Weinberg (2002) thinks that MaxC leads to interesting answers to important procreative questions. For example, she thinks that MaxC shows that the first-born child increases parental capability in a way that no subsequent child can (Weinberg 2002). With each additional child, parental procreative interest and the maximization of parental capabilities decrease. Thus, MaxC seems to encourage procreation, but perhaps places a limit on how many

children parents could have and still experience capability maximization.

However, taking this position indicates that Weinberg has placed special emphasis on parenting as a capability enhancer without providing an argument to support this value judgment. She states that not procreating inflicts “all kinds of losses” on a person, of a biological, emotional, and social nature (Weinberg 2002). Not procreating, she says, takes “a sharp, deep bite out of one’s capability to achieve a life of human flourishing” (Weinberg 2002). Weinberg presents this statement as factual, which indicates that she may not have considered that the participants in the procreative original position might severely restrict procreation (to only some individuals, say) or rule it out entirely. It also indicates that she may not have considered that parenting even one child may decrease capability, rather than maximize it. By assuming that parenting will be recognized as a significant contributor to human flourishing by participants in the original position, Weinberg begs the question of procreative permissibility.

Leaving this challenge for Weinberg’s account to the side, the principles of procreative justice that she thinks MaxC would yield from hypothetical future participants in the procreative original position are as follows:

i. *The obvious principle*

The obvious principle prohibits procreation that undermines everyone’s interests, such as teenage pregnancy (Weinberg 2002).

ii. *Procreative balance*

The balance principle permits procreation when it is not irrational for a parent to accept the risks their procreation imposes upon their prospective children in exchange for permission to procreate (Weinberg 2002).

iii. *Motivation restriction*

The motivation restriction requires that procreation be partially, yet prominently, motivated by a desire to raise, nurture, love, and care for the child once it is born (Weinberg 2002).

These three principles of procreative justice derived from MaxC are central to Weinberg’s

position on procreative permissibility and figure prominently in *The Risk of a Lifetime*.

Theories of Parental Responsibility

Another issue central to Weinberg's work is the source of parental responsibility. She considers many prominent theories of parental responsibility and rejects them, before presenting her own hazardous materials (HazMat) theory (Weinberg 2008). Briefly, these accounts are as follows:

Voluntary Commitments

The voluntary commitments theory states that parental responsibility is bestowed upon people who voluntarily decide to become parents. This would include people who become intentionally pregnant, people who adopt, and people who accidentally conceive but opt to continue the pregnancy and become the child's parent. However, because some conceptions are accidental and unwanted, it is possible for some children to be born without anyone being parentally responsible for them according to the voluntary theory. While some philosophers would accept this result as not particularly problematic (because, e.g., the State assumes responsibility until such a time as another voluntary [adoptive] parent comes forward), Weinberg (2008) thinks this result is unintuitive and an insurmountable problem with the voluntary commitments theory.

Intent to Raise

On this theory, parental responsibility is bestowed upon those people who intend, often before a child is conceived, to raise the child. This would include people who become intentionally pregnant, people who adopt, people who conceive accidentally but decide to keep the child, and people who conceive with the assistance of a gestational surrogate, for example. Weinberg thinks that, like the voluntary commitments theory, the intent to raise theory is problematic because it allows some children to be born without anyone being parentally responsible for them. Additionally, this theory is vulnerable to problems with knowing and discerning people's intentions (Weinberg 2008).

Genetics/Gestation

On the genetic and gestational theories, parental responsibility falls upon whoever's genetic material is used in the creation of the child or whoever gestates the fetus, respectively. The genetic theory of parental responsibility would include anyone genetically related to the child, which might be two parents involved in unassisted procreation, one parent plus an egg or sperm donor, or up to three people, in the case of one assisted reproductive technology in which an older woman's ovum is injected with cytoplasm from a younger woman's ovum; once inseminated, the resulting embryo contains three strains of DNA (see Connor 2014). Weinberg (2008) does not fully reject the genetic theory of parental responsibility, drawing on it heavily in her HazMat theory, though she finds it problematically simplistic.

The gestational theory bestows parental responsibility upon whoever has gestated the child. Though the gestational theory has been applied in some custody contests involving gestational surrogates, it does not capture the entirety of parental responsibility, even intuitively. Since only females can currently gestate a child, this theory would leave the male contributor to a child's existence without parental responsibility.

The HazMat Theory

Weinberg's (2008) hazardous materials (HazMat) theory bestows parental responsibility upon all people, by virtue of our possession and high degree of control over our own gametes. She considers gametes to be hazardous material because they can join with other gametes and grow into "extremely needy, innocent persons with full moral status" (Weinberg 2008). These dangerous possessions, she acknowledges, are not ours by choice; we have gametes as a biological function of our species. However, she argues that our risky actions involving our gametes, such as sexual intercourse, are under our control (most of the time), and therefore we are parentally responsible for the results of our gametes meeting with others. Weinberg (2008) thinks that the HazMat theory is in tune with many of our intuitions about parental responsibility, such as holding people

responsible for a pregnancy or child resulting from a failure of birth control.

The HazMat theory is similar to the genetic theory because it follows genetic relatedness to discover parental responsibility. Weinberg provides a different and more nuanced justification for her HazMat theory, by focusing on our risk behaviors, but the result is the same: whoever is genetically related to the child bears (non-transferable) responsibility for the child's existence.

Transfer of Parental Responsibility

Weinberg finds the transfer of parental responsibility to be particularly problematic and potentially impossible. Since the HazMat theory tracks genetic relatedness to discover parental responsibility, it seems that Weinberg would reject the notion of a transfer of responsibility because genetic relations cannot be altered. She does not acknowledge this similarity, however, and because her argument against the transfer of parental responsibility may betray a prior commitment to the importance of biological relatedness, her arguments may again be question begging.

Gamete Selling and Donation

In considering whether parental responsibility can be transferred, Weinberg (2008) presents two cases (Joe Blow and Joe Spermdonor) that she thinks are morally equivalent; if we find parental responsibility in one of these cases, then we must find it in the other. The case of Joe Blow involves accidental conception resulting from a broken condom. The case of Joe Spermdonor involves the donation or sale (though these may not be equivalent acts) of sperm. According to Weinberg's (2008) HazMat theory, both Joes are responsible because of the risky activities they engaged in. Since the HazMat theory states a child that results from our (voluntary) risky behavior involving our gametes, no further argument is required to establish Joe Blow's responsibility. If one disagrees that Joe Blow is parentally responsible, it must be that one does not accept the HazMat theory. Further argument is required, however, for the justification of Joe Spermdonor's

responsibility, because on some notions of risky behavior involving gametes, Joe Spermdonor would not qualify. This is because Joe S. gives his gametes to an agency that undertakes to secure and preserve them and make decisions about when they may be used.

Weinberg uses an argument from analogy to try to defend her view that Joe S. is responsible: if a company has enriched uranium to dispose of and gives this uranium to another company for safe-keeping and something goes wrong in that company causing a major explosion, we would not absolve the first company from their responsibility for the uranium. This, however, may be counterintuitive. When a company manufactures a gun, and a person purchases that gun and uses it to murder someone else, we do not hold the company that manufactured the gun responsible for the murder. There are many instances where we permit the transfer of responsibility for dangerous materials or weapons; our gametes may be no different.

However, if we accept Weinberg's argument that giving sperm to a donation facility does not absolve Joe S. of responsibility for his hazardous material, then we may also conclude that Joe S. has parental responsibility for a child that is produced using his sperm. Weinberg (2008) argues that Joe S. knew, or had good reason to think, that his sperm would be used to create a child, and so by giving his gametes away, he voluntarily permitted his gametes to potentially come into contact with others. This result, Weinberg allows, may be too counterintuitive to accept (or unwelcome, given that many people using assisted reproductive technologies like sperm or egg donation do not want the donor to have responsibility for the resulting child and vice versa). However, she challenges that if a sperm donor was the only match to a child needing a bone marrow transplant, we may not be willing to absolve the donor of responsibility toward the person created from their gametes (Weinberg 2008). In this case, we can see that Weinberg finds genetic relatedness, more than risk behavior, to be an important factor in determining responsibility.

The Love Obligation

In addition, Weinberg presents the argument that responsibility is non-transferrable partly because love is a parental obligation, and the people whose gametes were used to create the child can provide a special kind of love that others cannot provide. Weinberg (2008) thinks that we can assume that love is one of a child's basic needs and that this creates an obligation upon the parent to form a relational bond of loving and caring. It is unclear, she says, that the responsibility to relate with a particular feeling toward another person can be coherently transferred; the parental responsibility to love one's child, she argues, must involve *one's* love – not anybody's love (Weinberg 2008). Passing responsibility to stand in a particular emotional relation toward another person may be impossible.

However, Weinberg's argument that the love given to a child must be the love of the people whose hazardous materials were used in its creation seems to assume a special value in genetic relatedness. That there is something special about being someone's biological parent (or child) is a common bias. There are many reasons to be suspicious of the assumption that the love of a person who is genetically related is obviously or naturally superior to the love of a person who is not genetically related; cases of abuse, neglect, or abandonment make this clear. Thus, it seems that while children require love, this requirement may be satisfied by the love of people of various kinds, genetically related or not.

Weinberg (2008) is interested in arguing that Joe Spermdonor has an obligation to love the children who are created as a result of his sperm donation and that he cannot transfer this love obligation to others, such as the parents who request and utilize his sperm to create children. One may wonder whether, even if one agrees that Joe Spermdonor holds parental responsibility toward the children created from his gametes, love can be an obligation. As Weinberg (2008) describes it, the love obligation requires one to stand in a particular emotional relation to another. This may not be a coherent understanding of love, nor of obligation. Love seems to be something significantly different from the kind of action

that can be made obligatory, as it is an emotional state. One may be obliged to perform acts that look like love: taking care, providing for needs, giving support, etc. However, as Harry Frankfurt (1988, p. 85) says, "it certainly cannot be assumed that what a person cares about is generally under [their] immediate voluntary control." Thus, it is not clear that one could be obliged to give the feeling of love (or create the feeling in oneself).

Conclusion

Weinberg's work covers many important questions about reproduction and parenting, which have only been touched upon here. The ideas that have been covered form the basis of the arguments she presents in *The Risk of a Lifetime* and elsewhere. Weinberg's theories present new, though not uncontroversial, ways of thinking about and understanding the metaphysical nature of existence, procreative justice, and parental responsibility.

Cross-References

- Adolescent Parenthood
- Debating Procreation (With David Benatar)
- Reproduction
- Risk of a Lifetime, The

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RNA

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Synonyms

Ribonucleic acid

Definition

RNA is one of the two nucleic acids produced by cells.

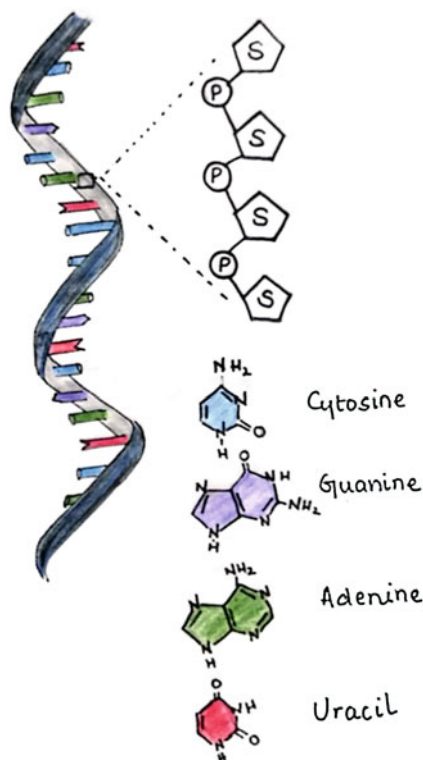
Introduction

Friedrich Miescher first discovered nucleic acid in 1868. There are two types of nucleic acids. Deoxyribonucleic acid (DNA) has the blueprint to encode all the proteins in the biological world. DNA does this via another set of nucleic acid called RNA (Crick 1970). RNA plays essential roles in protein synthesis, gene regulation (by various noncoding

RNAs), rRNA processing (by snoRNA, i.e., small nucleolar RNA), and catalytic functions (by ribozymes).

RNA Structure

RNA is a single-stranded polymer of ribonucleotides. Ribonucleotides have three components: ribose sugar, one of the four nitrogenous bases (adenine, uracil, guanine, and cytosine), and a phosphate group (Fig. 1). The 1' carbon molecule of the ribose sugar (ring structure made of five carbons and one oxygen atom) attaches to the nitrogenous base and 5' carbon molecule to the phosphate group. The phosphate group forms a phosphodiester bond with the 3' hydroxyl group of the next nucleotide. Thus, backbone of the RNA molecule is formed by ribose sugar and phosphate in succession. Typically, RNA is single-stranded; however, there is extensive



RNA, Fig. 1 Structure of RNA (S-ribose sugar, P-phosphate group)

pairing between the complementary bases within a RNA strand. So, RNA has the ability to fold and form three-dimensional structure. This folding is essential for certain functional aspects. RNAs form highly organized complexes with various RNA-binding proteins to form ribonucleoproteins (RNPs) which are the functional forms of RNA.

Functions

Protein Synthesis

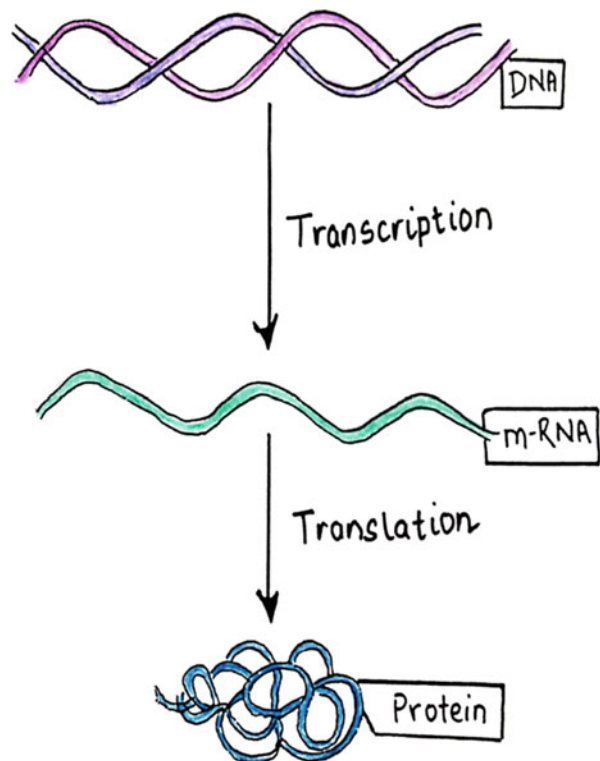
Protein synthesis requires two important steps, namely (Fig. 2):

- (a) Transcription involves transfer of information from DNA in the form of a genetic code into a new molecule of mRNA.
- (b) Translation where the nucleotide sequence on the mRNA is translated (language changed) to amino acid sequence of protein.

Three kinds of RNAs, namely, mRNA, rRNA, and tRNA, play important roles in protein synthesis. mRNA (messenger RNA) carries the message for protein synthesis in the form of series of “three base codes” (codon), from DNA to the cytoplasm. rRNAs (ribosomal RNAs) form the molecular machines called ribosomes, which, after attaching to mRNAs, start protein synthesis. tRNA (transfer RNA) recognizes the transcribed code and adds appropriate amino acid (building block of protein) according to the code (Chapeville et al. 1962).

During transcription, RNA polymerase II reads one particular gene of the DNA and complementary base addition generates pre-mRNA. Pre-mRNA is then edited by addition of methylguanosine in its 5' end and polyadenylates in its 3' end, called as capping and tailing, respectively. Capping protects the mRNA from attack by ribonucleases, and tailing is important for its transport from nucleus to cytoplasm for translation. The noncoding parts of pre-mRNA (known as introns) are removed by a process called splicing. This process is executed by a

RNA, Fig. 2 Overview of protein synthesis



large complex called spliceosome, which comprises of snRNAs, splicing factors, and numerous RNPs. A single gene can give rise to multiple protein types by the process of alternative splicing, where different set of introns are removed (Early 1980). After splicing, only the coding segments (exons) remain to form the mature mRNA. This mature mRNA is transported to the cytoplasm via their binding with cap-binding proteins (CBP) and transcription export complex (TREX), present in the nuclear pores.

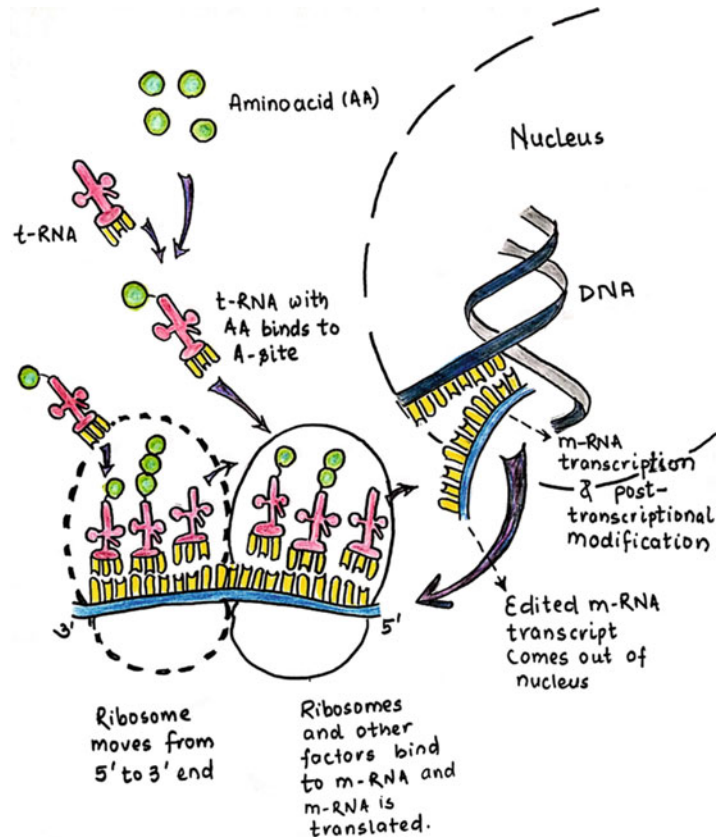
Once the mRNA is in cytoplasm, ribosomes bind to it and translation begins. This process is divided into three broad phases: initiation, elongation, and termination (Crick 1958). In eukaryotes, first there is formation of an initiation complex comprising of the 40s subunit of ribosome, eukaryotic initiation factors (eIFs), and nucleoside triphosphates. This initiation complex recognizes the 7-methylguanosine cap at the 5'

end of mRNA. With the help of CBP and eIFs, the ribosome binds to the mRNA.

A charged initiator tRNA carrying the amino acid methionine (Met-tRNA_i) binds the IF. tRNA becomes charged by binding with the amino acids (methionine, etc.) by the help of enzymes aminoacyl tRNA synthetases. After binding of the Met-tRNA_i to the IF, the ribosome moves from 5' to 3' end of the mRNA in search of the start codon AUG. Once the AUG is identified, the accessory proteins (like CBP and IF) dissociate, and the 60s subunit of ribosome binds to the smaller subunit and Met-tRNA_i. This step is the beginning of the next step (elongation) of the translation process (Fig. 3).

The larger subunit of ribosome has three compartments, A site (aminoacyl site for binding of aminoacyl tRNA), P site (peptidyl site binds tRNA with amino acid that has formed peptide bond with growing chain however is

RNA, Fig. 3 Detail process of protein synthesis showing different types of RNA. mRNA transcribed from DNA undergoes posttranscriptional modification in nucleus and then is transported through the nuclear membrane to cytoplasm, where the translation process is carried out. tRNA binds with the amino acid by the help of enzymes aminoacyl tRNA synthetase. tRNA carrying the amino acid binds to mRNA (by codon-anticodon interaction) at the A site on the ribosome (except Met-tRNA_i which binds to P site directly) and then sequentially at P and E sites (see text), gradually increasing the length of the peptide chain. The dotted ribosome shows the future position of ribosome as the translation process proceeds



not dissociated from the tRNA), and E site (exit site releases the dissociated tRNA). These compartments also extend to the smaller subunit. The charged tRNAs bind sequentially to A, P, and E sites and in turn add amino acids to the growing polypeptide chain (Fig. 3). Exception to this is, first charged tRNA (Met-tRNA_i) that binds directly to the P site. As the ribosome moves on the mRNA, the three base codons are matched with the corresponding anticodons in the tRNAs. A peptide bond is formed between amino group of A site amino acid and carboxy group of P site amino acid by the enzyme peptidyl transferase (Fig. 3). When the ribosome encounters one of the three codons (UAA, UGA, and UAG), the synthesis of protein terminates as there are no corresponding tRNAs for these codons.

Gene Regulation

A diverse group of noncoding RNAs (ncRNAs) are involved in gene regulation at transcriptional and translational levels. These regulations may include heterochromatin formation, histone and DNA modification, and gene silencing. Important examples of ncRNAs are miRNA, siRNA, piRNA, and lncRNA.

miRNA (microRNA): These are of about 22 nucleotide long. They bind to specific complementary target sequence in the mRNAs and promote its degradation (in case of strong binding) or blocking of translation (in relatively weak binding). miRNA is formed as a primary transcript (pri-miRNA), which is broken down by ribonuclease called Drosha to form double-stranded pre-miRNA. RNA-induced silencing complex (RISC) is a multiprotein complex having a single-stranded miRNA guide, Dicer enzyme (endoribonuclease) and Argonaute proteins. Pre-miRNA is cleaved by the enzyme Dicer to form functional single-stranded miRNA which on binding to mRNA is cleaved by Argonaute (Bernstein et al. 2001). This process called RNA interference (RNAi) (Anandalakshmi et al. 1998) is one of the essential processes in gene silencing (Bass 2000).

siRNA (small interfering RNA): It is a double-stranded RNA and very similar to miRNA. It can

be introduced from outside of the cell. Function is through the RNAi pathway (Hamilton 1999).

piRNA (piwi-interacting RNA): They too are involved in gene silencing via RISC. piRNAs interact with piwi proteins of Argonaute protein family. piRNAs direct these proteins to the transposon targets and induce gene silencing (Klenov et al. 2011).

lncRNA (long noncoding RNA): These are more than 200 nucleotides long. They recruit chromatin remodeling complexes, thus actively involved in epigenetic modifications.

Evolutionary significance of RNA: Earlier RNA was considered as a poor cousin of DNA, but research in last 50 years show that life's origins on Earth started with RNA. The RNA Tie Club was formed by Francis Crick and some other scientists in 1955. This group seriously considered the important roles that played by RNA in evolution of life on the Earth.

According to the RNA World Hypothesis, RNA was the first self-replicating molecule during evolution (Scott et al. 2014). Thomas Cech and Sidney Altman independently discovered that RNA molecules could serve as enzymes by catalyzing chemical reactions in the cell. RNA adaptation (including RNPs, RNA editing, and RNAi) to a changing environment is thought to be responsible for subsequent diversification of life. Scott and his coworkers suggested 2',3'-cyclic phosphate version of nucleotides to be the prebiotic monomer to form polymer RNA abiotically (Lehman 2010).

Several attempts have been made for synthesis of RNA in abiotic environment. Experiment of Miller and Urey showed the synthesis of amino acids when mixture of gases was treated with electric current (Ferus et al. 2017). In 1960, Oró and his colleagues reported the abiotic synthesis of adenine (which is an important constituent of nucleic acids) from a hydrogen cyanide and ammonia (Roy et al. 2007).

In organisms, RNA evolves by undergoing certain processes (point mutation, insertions, deletions, recombination) that alter its sequence. Alterations in the RNA result in changes in the structural and functional dimensions of the organism (Lehman 2010).

Significance in Diseases

As RNAs have great impact over the function and regulation of cellular processes, their dysfunction give rise to many diseases including cancers.

Diseases Involving mRNA Metabolism

Mutation in splicing-associated proteins and regulatory RNAs causes numerous diseases, particularly neuromuscular and neurodegenerative diseases and cancers. Cis-acting mutations (involving the transcript from which protein is synthesized) at exon intron junction can disrupt normal splicing, because this region has the spliceosome binding site. Mutations in trans-acting (set of proteins having origin from different genetic loci) splicing components or the regulators can interfere with expression of several genes. Table 1 shows examples of diseases due to altered mRNA metabolism (Naryshkin et al. 2014; Sironi et al. 2002; Friedman et al. 1999; Růžicková and Staněk 2017).

Modification in alternative splicing events causes development of isoforms which promote tumorigenesis, including proliferation, invasion, and neovascularization. Mutations in core spliceosome components (SF3B1, U2AF1, SRSF2) have been studied extensively in hematological malignancies like myelodysplastic

syndrome, various myeloid neoplasms, and chronic lymphocytic leukemia (Malcovati et al. 2011).

Diseases Involving miRNA and siRNA

1. Neoplasms: miRNA is found to be associated with cancers like gastric carcinoma and pancreatic carcinoma (Sand et al. 2012). miRNA expression profiles are different in tumors from those in normal tissues. They differ among various tumor types. miRNAs can be oncogenic or tumor suppressors, depending upon their target mRNAs.
2. Neurological diseases: miRNA is mainly involved in neural developmental processes. Disruption of miRNA machinery in different neuronal and non-neuronal cells can cause neurological diseases. Examples include Purkinje cell in ataxia, oligodendrocyte in multiple sclerosis, and alpha calcium-dependent protein kinase type II expressing neurons in Alzheimer’s disease. Table 2 shows examples of mutation in central miRNA processing complexes causing neurological diseases in humans (Ling et al. 2010; Sunamura et al. 2018; Brás et al. 2017).

Particular miRNAs have also been linked to distinct disease processes like miR-206 in speeding development of ALS, miR-9 in spinal

RNA, Table 1 Diseases due to altered mRNA metabolism

Type of mutation	Disease	Alteration in RNA function
Cis-acting mutations	Spinal muscular atrophy	Single nucleotide substitution mutation in <i>SMN2</i> gene, which plays critical role in snRNP biogenesis
	Duchenne muscular dystrophy	Single nucleotide substitution
	Cystic fibrosis	Difference in nucleotide length a particular region in 3' splicing areas
Trans-acting mutations	Autosomal dominant form of retinitis pigmentosa	Mutation PRPF proteins, cause disruption of basal spliceosome function

RNA, Table 2 Neurological diseases due to altered miRNA function

Human disease	Alteration in RNA function
Amyotrophic lateral sclerosis (ALS)	Drosha microprocessor complex mutation
Fragile X syndrome	Fragile X mental retardation 1 protein (FMRP) (RISC component)
Alzheimer’s disease in Down’s syndrome	miRNA dosage alteration (magnitude of expression)

motor neuron diseases, and miR-19 in pene-
trance of spinocerebellar ataxia type1.

3. Cardiovascular diseases: miR-1 is involved in the development of heart during embryonic life. It downregulates certain ion channels and has been linked to arrhythmias. Myocardial tissue in heart failure shows different miRNA expression profile from that of normal myocardium. Many of the vascular diseases are also caused by miRNA-related molecular changes.

Diseases Involving lncRNA

Correlation of lncRNA with various diseases has been observed, as suggested by its differential expression. It is particularly involved in patients of Alzheimer's disease, Huntington's disease, and Parkinson's disease. It is also seen to be associated with cardiovascular diseases.

Conclusion

RNA is vital for cell function and is dependent on countless mechanisms for its production, processing, and regulation. This involves plethora of sequence elements, RNA-binding proteins, and regulatory RNA species. All these complexities provide fertile ground for potential errors, which give rise to many disease processes; however, it also provides miscellaneous targets for possible therapeutic intervention.

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Definition

Robert Axelrod is an American political scientist and professor of political science and public policy at the University of Michigan, USA. He is best known for his work on cooperation.

Education and Awards

Robert Axelrod received his bachelor of arts degree in mathematics in 1964 from the University of Chicago. He received his M.A. in political science in 1966 and his Ph.D. in political science in 1969, both from Yale University. He taught at the University of California, Berkeley, from 1968 to 1974, before joining the Department of Political Science and the Gerald R. Ford School of Public Policy at the University of Michigan (Axelrod 2018). For his academic contributions, he was awarded the 1980–1981 Newcomb Cleveland Prize of the American Association for the Advancement of Sciences for an outstanding contribution to science, the 1990 National Academy of Sciences Award for behavioral research relevant to the prevention of nuclear war, and the 2014 National Medal of Science (Axelrod 2018). He is also a member of the National Academy of Sciences, the recipient of a five-year MacArthur Prize fellowship (1987–1992), and the former president of the American Political Science Association (2006–2007). He was awarded an honorary Doctor of Laws degree by Harvard University, in 2015.

Research and Publications

Professor Axelrod's interdisciplinary research focuses on topics like international security and cyber-security (Axelrod 2018), with a particular interest in international peace and the threat of nuclear war, but he is best known for his work on the evolution of cooperation (Ostrom 2007). Axelrod has contributed to several areas of research, including public policy analysis (Axelrod and Cohen 2001), the sustainability of cooperation in various settings (e.g., Axelrod 1981, 1984),

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international relations (e.g., Axelrod 1979; Axelrod and Keohane 1985), the use of simulation and agent-based modeling (e.g., Axelrod 1997a, 2006), and biological and sexual evolution (Axelrod et al. 2006; Axelrod and Hamilton 1981; Axelrod et al. 2004; Hamilton et al. 1990). In addition to numerous research articles, chapters, and commentaries, Professor Axelrod has published six books, including *Conflict of Interest: A Theory of Divergent Goals with Applications to Politics* (Axelrod 1970), *Framework for a General Theory of Cognition and Choice* (Axelrod 1972), *Structure of Decision: The Cognitive Map of Political Elites* (Axelrod 1976), *The Evolution of Cooperation* (Axelrod 1984, revised in 2006), *The Complexity of Cooperation: Agent-Based Models of Competition and Collaboration* (Axelrod 1997b), and *Harnessing Complexity: Organizational Implications of a Scientific Frontier* (Axelrod and Cohen 2001). Collectively, his work has been cited more than 98,000 times.

Axelrod's best known book is *The Evolution of Cooperation* (Axelrod 1984), which expands on an earlier paper by Axelrod and Hamilton (1981). This book drew on Game Theory, which refers to the investigation of strategy. Briefly, there are three broad categories of games within Game Theory: zero-sum games (i.e., where one player's gain always equals the other player's loss), positive-sum games (i.e., where there is the potential for mutual gain and conflict with respect to the division of gain), and negative-sum games (i.e., where there is the potential for mutual loss and conflict with respect to the degree of loss; see also the "Game Theory" entry in this volume). Axelrod (1984) used the game *The Prisoner's Dilemma* to investigate the conditions necessary for cooperation to occur. *The Prisoner's Dilemma* game involves a simultaneous choice where each player must decide to either cooperate or defect (i.e., betray) without knowing what the other player has decided. The basic premise is that both players are members of a criminal group who have been arrested and are being questioned separately by the police. Both players are offered a deal, whereby they can betray the other player (i.e., testify that the other committed the crime). If both players cooperate with each other (i.e.,

neither testifies), they will both serve a lesser sentence. If both betray the other (i.e., both defect), both players will serve the original sentence. However, if only one betrays the other, the betrayer will go free and the other player will serve a harsher sentence (see also "The Prisoner's Dilemma" entry in this volume). Axelrod (1984) found that the "tit-for-tat" strategy, where the player cooperates in the first round and then mimics the other player's first-round choice in all subsequent rounds, was the most successful strategy when playing a series of rounds against the same player, although defection was the most successful strategy in a single encounter. Axelrod (1984) makes inferences about how cooperation has evolved in complex social groups, noting that a cooperative disposition followed by reciprocation is adaptive when faced with repeat encounters with others.

In a later work, *Harnessing Complexity: Organizational Implications of a Scientific Frontier* (Axelrod and Cohen 2001), Axelrod and Cohen extend Axelrod's previous work on cooperation by examining cooperative processes in more complex settings, such as military personnel systems, contemporary information systems, and fighting the AIDS virus. The authors develop a framework that highlights the importance of comprehension with respect to system variations, interactions, and selection, and make eight specific recommendations to those looking to harness complex systems (see also Ostrom 2007): (1) Arrange organization routines to generate balance between exploitation and exploration, (2) build systems of reciprocal interaction that encourage trust and cooperation, (3) link processes that generate high variation to processes that select with few mistakes in ascribing credit, (4) assess strategies with respect to the spread of their consequences, (5) promote effective "neighborhoods" of systems, (6) do not propagate sizeable failures when only deriving small efficiencies, (7) proliferate valued criteria using social activity, and (8) look for shorter-term measures of success that can usefully stand in for broader long-term goals (Axelrod and Cohen 2001). Importantly, these recommendations differ markedly from more typical policy analysis that emphasizes "top-down control" by leaders who

then delegate to subordinates (Ostrom 2007). This and other work has provided a solid foundation that Axelrod and other researchers can build upon to investigate cooperation, complex intergroup relations, and various systems.

Conclusion

Robert Axelrod is an important figure in political science and public policy. His work is well cited and respected within the social sciences. He has had a tremendous, positive impact in advancing knowledge and theory in political, social, biological, psychological, and other fields, particularly with reference to public policy and the evolution of cooperation. His contributions will undoubtedly continue to prove invaluable as work in these areas advances.

Cross-References

- [Cooperation](#)
- [Game Theory](#)
- [Prisoner's Dilemma](#)
- [Robert Axelrod's \(1984\) *The Evolution of Cooperation*](#)

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Robert Axelrod's (1984) *The Evolution of Cooperation*

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Definition

The Evolution of Cooperation (1984), by political scientist Robert Axelrod, is a book for a non-specialist audience based on four of the author's papers. The book's central question is: "Under what conditions will cooperation emerge in a world of egoists without central authority?" Axelrod answers this question using a computer tournament and simulations of the iterated prisoner's dilemma game, where a tit-for-tat strategy was successful. Based on these results, he

proposes general characteristics of strategies and interactions that promote long-term stable cooperation and discusses their societal and biological applicability.

Introduction

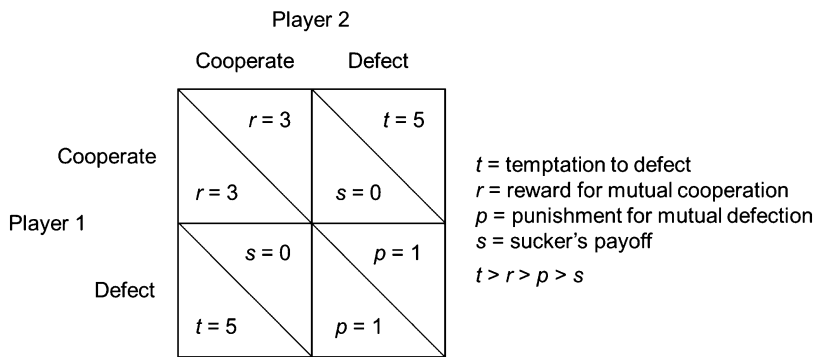
“When should a person cooperate, and when should a person be selfish, in an ongoing interaction with another person?” (p.vii), specifically “in a world of egoists without central authority” (p.3). This is the question that motivates *The Evolution of Cooperation* (Axelrod 1984). The book is based on a single, appealingly simple idea applied to different sociopolitical and biological contexts (Courtney 1985): many interactions take the form of a two-player iterated prisoner’s dilemma (IPD; Fig. 1) and the best strategy in such a game for both individual success and mutually beneficial long-term mutual cooperation is one of reciprocity, such as Tit-for-Tat (TFT). *The Evolution of Cooperation* summarizes and popularizes four of Axelrod’s papers that contain these findings: the results of computer tournaments (Axelrod 1980a, b), the supporting theory (Axelrod 1981), and the implications for evolutionary biology (Axelrod and Hamilton 1981). Axelrod uses these findings to assess what characteristics successful strategies share, describe how stable cooperation can

become established in an IPD, and suggest how to design interactions in the real world in order to promote cooperation.

Theoretical and Empirical Basis

The book’s argument is built around the two-player prisoner’s dilemma, a game whose key requirement is that payoffs follow the pattern $t > r > p > s$ (Fig. 1). That is, although the two players are better off collectively when both cooperate, the best strategy for any individual player in a single round is to defect. Axelrod’s insight is that the game can be continued over multiple rounds, i.e., an iterated prisoner’s dilemma (IPD), and that the probability w of playing another round with the same partner is key for the emergence of cooperation. In fact, when w is high, a player can do well by cooperating in the IPD.

Axelrod arrived at this result through two pioneering computer tournaments. Contestants submitted programs to play the IPD, accruing points each round according to the payoff matrix in Fig. 1. Each tournament consisted of five IPD games; each game lasted 200 rounds, and each strategy played each other strategy (including itself). To Axelrod’s surprise, the winner of the 14 programs in the first tournament was one of the simplest: Tit-for-Tat (TFT). A player using this strategy cooperates in the first round and thereafter copies its partner’s move from the previous round. In a second tournament with 62 programs,



Robert Axelrod's (1984) *The Evolution of Cooperation*, Fig. 1 A typical payoff matrix for a 2-player prisoner’s dilemma. The bottom triangle in each cell is the payoff to Player 1, the top to Player 2. The numerical payoff values are examples (those used in Axelrod’s

computer tournament), but the key criterion is that $t > r > p > s$. In the iterated prisoner’s dilemma (IPD), there is a probability w that the players interact in the next round, giving a probability $1/(1-w)$ of a sequence of interactions

where contestants knew the results of the first tournament, TFT also won.

But was TFT just successful in the particular “environment” of strategies in the two tournaments? That is, is it a *robust* strategy? To investigate a wider range of environments, Axelrod simulated the IPD over 1000 generations. Each generation represented one computer tournament, and the set of strategies was those that had competed in the tournament. A strategy's tournament score in generation i determined the number of copies of the strategy in generation $i + 1$, so strategies with proportionally higher scores gained proportionally more representation in the population. Once again, TFT was the winner. What features, then, facilitate TFT's robust success?

Characteristics of Robust Successful Strategies

Axelrod identifies four characteristics of TFT that allowed it to do well over a range of environments and that were shared by other successful strategies:

1. Niceness

Nice strategies are never the first to defect, i.e., they cooperate on the first move. Nice strategies are successful playing against each other, because they reap the gains from repeated mutual cooperation (but on the other hand, they suffer when playing against not-nice strategies).

2. Forgiveness

Forgiving strategies have a propensity to cooperate after being defected against. This allows them to avoid becoming locked into mutually destructive mutual defection.

3. Retaliation

Retaliatory strategies are provokable, i.e., they defect on their partner after their partner has defected on them. Retaliation has the potential to prevent further defection by the partner and thus to prevent exploitation of the retaliatory strategy.

4. Clarity

Clear strategies are easy for others to recognize. Other strategies do well by cooperating with

TFT and so benefit from recognizing it; this in turn helps TFT do well.

While successful strategies in Axelrod's tournaments and simulations undoubtedly had these characteristics, their universality has been shown to be sensitive to assumptions Axelrod made, such as the initial population composition in the simulation and the potential for strategies to make mistakes (Hoffmann 2000). These have been explored extensively in the subsequent literature, including by Axelrod himself (Axelrod and Dion 1988; Hoffmann 2000). In games with relaxed assumptions, TFT was no longer as dominant: for example, the potential for errors favored “Contrite TFT,” while a different starting population favored “Grim” (Binmore 1998).

Spatiotemporal Patterns of Cooperation

Axelrod recognizes that to understand when cooperation is a successful strategy, we need to examine its “chronology” by considering three separate questions about the sequence over which cooperation emerges. First, we can ask what makes strategies robust across environments, as I have discussed in the two sections above. Second, we examine initial viability: how can a strategy become established (i.e., invade a population) in the first place, particularly in a noncooperative environment? Third, we consider stability: how can an established strategy resist new strategies invading the population? I discuss the latter two points here.

Under what conditions can TFT invade a population (i.e., be initially viable)? Axelrod shows that the strategy always defect (All-D) cannot be invaded by TFT, so in a population of All-D, there must be some additional mechanism to allow TFT to become established. One mechanism familiar to evolutionary researchers is kinship (Hamilton 1964). In a population of related individuals, a cooperative strategy could do better than All-D and invade.

A second mechanism is spatial structure. One major inroad for TFT is that it does better playing against itself (due to mutual cooperation) than does All-D playing against itself (due to mutual defection). This means that if the probability that an invading TFT player interacted with another

invading TFT player were high, TFT could invade. This can occur if TFT players form clusters, making them more likely to interact with each other than with other strategies. Such spatial structure in a population may be physical or geographical (such that neighbors interact with each other more than do non-neighbors), or it can be more abstract, as in Axelrod's example of a cluster of companies producing the same products in a population where others' production is different.

Last in the chronology, under what conditions can a population of TFT be resistant to invasion by other strategies (i.e., be stable)? Axelrod demonstrates mathematically that neither a single player or nor a cluster of players using another strategy can invade TFT if w is sufficiently high, and that the threshold value of w depends on the IPD payoffs t , r , s , and p . That is, once cooperation is established, TFT can be stable even in a not completely cooperative environment.

Note that the conditions for "collective stability" that Axelrod uses are less restrictive than those for "evolutionary stability" (Maynard Smith 1982) and that if evolutionary stability is considered instead, then no pure strategy can be stable, and TFT can be invaded by "Suspicious TFT" (Boyd and Lorberbaum 1987). This underscores Axelrod's point that when w is high, there is no single best strategy in the IPD independent of the other player's strategy.

Implications for Promoting Cooperation

How can the principles from Axelrod's computer tournaments and simulations be applied, and in what situations are they relevant? Axelrod approaches this question from two angles.

First, given an IPD, what should a player do in order to be individually successful? Axelrod offers four suggestions:

1. Don't be envious

Many interactions are not zero-sum: instead of comparing yourself to the other player, compare yourself to how another strategy would be doing in your position. For example, a business buying from a supplier should not be envious of the supplier, since both parties can do well, and retaliation against each other would harm both.

2. Don't be the first to defect

The best predictor of success in Axelrod's tournaments was niceness.

3. Reciprocate both cooperation and defection

TFT and its variants are successful in a range of environments, because they elicit cooperation and are not readily exploited. To avoid retaliation leading to long-term feuding, "limited provokability" may be beneficial, i.e., a reciprocal defection of lesser magnitude than the first.

4. Don't be too clever

Does the other player know that you know that they know that you know what they will do? Chains of contingent behavior reduce a strategy's clarity, making suboptimal responses by the other player more likely. In an IPD, players do not benefit from hiding their intentions. For example, in the trenches of the First World War, truces emerged between British and German troops, but they nonetheless gave firing displays to indicate their willingness to retaliate if necessary.

Second, how can interactions be structured (the "strategic setting") in order to promote cooperation? Axelrod offers five suggestions:

1. Enlarge the "shadow of the future."

To increase w , interactions should be made more durable and more frequent. This could be achieved by spatiotemporal structure, e.g., clustering of small groups in space, having specialization on different roles, or decomposing larger interactions or goals (such as signing an arms control treaty) into smaller time steps. Conversely, reducing w can be destructive, exemplified by First World War troops being moved to different trenches, companies who are about to be bankrupted, employees about to be transferred, or politicians about to be defeated have little incentive to cooperate.

2. Change the payoffs.

The goal is to make long-term mutual cooperation more attractive than short-term defection. Restructuring the payoffs, for example, through creating institutions, can shift the interaction from

an IPD to a different game where cooperation is easier to achieve. The challenge is to determine effective payoffs: for example, if a government sets tough pollution limits, companies have an incentive to defect, but if the limits are not high enough, the payoff from companies' cooperation is low.

Axelrod summarizes the last three suggestions as "teaching values, facts and skills that will promote cooperation" (p.126):

3. Teach people to care about each other.
4. Teach reciprocity.
5. Improve recognition abilities.

These are all proximate mechanisms (Tinbergen 1963) that promote cooperation via TFT and that strengthen the four characteristics of successful strategies (niceness, forgiveness, retaliation, and clarity). As an example of teaching, Axelrod points out that in the First World War trenches, rotating troops passed on information to each other necessary to maintain cooperation. Feelings of caring can motivate nice and forgiving behavior, and better recognition abilities can facilitate both retaliation and clarity. Indeed, in the First World War, "the cooperative exchanges of mutual restraint actually changed the nature of the interaction. They tended to make the two sides care about each other's welfare" (p.85).

To what extent can these suggestions be applied to the real world (particularly politics, business, and international relations), as Axelrod proposes? One issue is that Axelrod's results are based on a simple IPD, and it is not always clear which real-world interactions do indeed take this form (Gowa 1986). For example, the First World War trench warfare may be a collaboration game instead of an IPD, and in many interactions there may not be a lack of central authority, as Axelrod supposes (Gowa 1986). A second issue is whether, for real-world interactions that are unambiguously IPDs, Axelrod's suggestions are actually feasible. For example, players must be able to demonstrate credible threats and respond flexibly, rapidly, and accurately to each other's behavior,

which may not be possible in international negotiations (Gowa 1986; Homans 1985).

Implications for Evolutionary Biology

Following a "strategic rather than genetic" (p.x) approach, Axelrod's concept of evolution is not restricted to true biological evolution (changes in gene frequency). His concept has two components: (1) "differential growth of the successful" and (2) "a source of variety" (p.170); the first of these suggests that he conflates evolution with natural selection. Regardless, Axelrod uses this "evolutionary" approach to investigate the invasion and stability of cooperation (discussed above), which were not taken into account in the original computer tournaments or simulations. In addition, despite the disclaimer avoiding genetics, Axelrod uses "evolution" as an opportunity to discuss cooperation in nonhuman organisms, in a book otherwise focused on human cooperation. The question, then, is how applicable to non-human organisms are (1) the IPD game and (2) the TFT strategy?

Axelrod argues that an IPD is possible whenever players can recognize and remember previous interactants, which is possible in many nonhuman organisms. However, this requirement can be bypassed if there are other mechanisms that facilitate repeated interactions, for example, if at least one of the players has a fixed location, as do many symbiotic mutualisms and territorial animals. Subsequent empirical work has shown that limiting spatial range as a way of increasing w may indeed promote cooperation in cleaner fish mutualisms (Oates et al. 2010). Future interactions are also more likely when an organism has a longer expected lifespan. Axelrod uses this principle to explain patterns of disease: for example, chronic infections become acute when hosts are likely to die, and genetic defects due to "cheating" chromosomes are more common when mothers are older.

However, others argue that there is limited empirical evidence for the IPD in nature, with many interactions not meeting the game's assumptions. For example, the IPD precludes

any sharing of information, but most interacting animals monitor each other's behavior (Dugatkin et al. 1992). In addition, the players' decisions may not simply be a binary choice to cooperate or defect: there may be a continuum, or there may be additional strategies such as choosing alternative partners (Raihani and Bshary 2011). Other interactions that appear IPD-like may not meet the payoff assumptions ($t > r > p > s$; Fig. 1): for example, in many cases there may in fact be no temptation to cheat (Riehl and Frederickson 2016). Measuring the values of the payoffs is a key challenge in assessing the validity of the IPD in nature (Raihani and Bshary 2011).

In cases where interactions do constitute an IPD, is there evidence that TFT has evolved and is successful? A handful of studies have demonstrated reciprocity in nonhuman animals, but are controversial because of the difficulty of measuring payoffs and demonstrating conditionality on others' behavior (Dugatkin et al. 1992; Raihani and Bshary 2011). Regardless, TFT appears to be uncommon in nature. Reasons for this include: (1) TFT requires a relatively high degree of cognitive complexity; (2) given such complexity, strict bookkeeping strategies like TFT may be less successful than other strategies for conditional cooperation, such as those based on emotional bookkeeping over a longer term; this may particularly be the case when payoffs are in different currencies for different players (Cheney 2011; Raihani and Bshary 2011).

Conclusion

Axelrod concludes that "the two key requisites for cooperation to thrive are that the cooperation be based on reciprocity, and that the shadow of the future is important enough to make this reciprocity stable" (p.173), and furthermore that "key to doing well lies not in overcoming others, but in eliciting their cooperation" (p.190). The concept of reciprocity has become so well incorporated into the literature on human behavior that can be difficult to appreciate its original impact.

Although Axelrod was not the first to put forward the concept of reciprocity in cooperative interactions (Trivers 1971), he made a major contribution by generalizing and popularizing it (Hoffmann 2000). *The Evolution of Cooperation* also made novel contributions in terms of considering the iterated game (Homans 1985), Axelrod's point that confrontation can be damaging (Courtney 1985), and his pioneering use of the computer simulation (Hoffmann 2000).

Much of the book's impact comes from its clear and straightforward message and simple game structure, helping make it a highly transmittable meme (Dawkins 1976). However, calling this message "Cooperation Theory," as Axelrod does, is somewhat misleading in its scope (Gowa 1986). The IPD models only one of many types of cooperative interactions (Dugatkin et al. 1992), and the extent to which the IPD accurately represents real interactions is under debate (Gowa 1986; Raihani and Bshary 2011). In other game structures, a diversity of mechanisms exist for maintaining cooperation among non-kin "in a world of egoists without central control" (p.69), such as indirect reciprocity and enforcement (West et al. 2007).

The book's reductionist approach also means that it has raised many issues for future research (Courtney 1985). One key assumption is that the IPD has two players, whereas an n -player game may better represent many real interactions; an implication is that the importance of direct retaliation is overstated (Binmore 1998). Another assumption is that the two players are equal, for example, in their perceptions of w as well as in the payoffs from a given action. Taking Axelrod's Cold War case study, the United States may be harmed less by its own spending on the military than would Russia (Courtney 1985) and may have different assumptions about how long the two countries will be opponents (Homans 1985). Unequal payoffs could lead to one player dominating the other, which could change the game such that that player acts as a central authority, which may be more common than Axelrod assumes (Gowa 1986).

The Evolution of Cooperation has an optimistic message: Axelrod claims that “the machinery for the evolution of cooperation contains a ratchet” (p.177), citing increasing norms of reciprocity in the US Senate as evidence. Judging this in January 2017, his conclusion seems naïve – but perhaps it is a question of choosing the appropriate timescale, and whether cooperation and conflict increase over time is an issue debated elsewhere (Pinker 2011). In addition, a major point the book makes is that many interactions or comparisons are not zero-sum, because both parties do well from cooperation (Courtney 1985; Gowa 1986). While this may be true in some scenarios, more recent research on the scale of competition shows that in many cases, individuals compete locally with potential cooperative partners and this hinders cooperation (Taylor 1992; West et al. 2006). Fitness is measured relative to others, and people have a tendency to compare their own payoffs to their neighbors’, which can lead to outcomes worse for all (Frank 2007).

Assuming, though, as Axelrod does, that players are in an IPD, to what extent should we follow his suggestions for promoting cooperation? A first concern is their effectiveness, which I have discussed above: relaxing Axelrod’s assumptions introduces complications, and in fact many other strategies in addition to TFT are successful (Raihani and Bshary 2011). A second concern is their morality, which, as Axelrod points out, may be in conflict with their effectiveness. For example, Axelrod shows how labels can be favorable for promoting cooperation, but can also lead to harmful stereotypes – and cooperation could also be promoted by forming a reputation as a bully. Importantly, Axelrod points out that many people may feel a strategy following the “Golden Rule” (“do unto others as you would have them do unto you”) is more moral than the “rough justice” (p.137) of TFT, but the former is less likely to promote mutually beneficial cooperation in the long run. This tension is intriguing and unresolved and would benefit from further attention.

In sum, despite these caveats, *The Evolution of Cooperation* offers suggestions for promoting cooperation that do apply to many scenarios. Axelrod’s interdisciplinary book is accessible and thought-provoking. Both its successes and limitations have stimulated continuing research on the evolution of cooperation.

Cross-References

- [Evolution of Cooperation](#)
- [Prisoner’s Dilemma and Cooperation](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Robert Axelrod](#)
- [Strategies for Successful Cooperation](#)

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Robert Hinde

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Robert Hinde (October 26, 1923–December 23, 2016) was a British behavioral biologist who studied the behavioral development and social relationships of birds, monkeys, and humans. He was the primary influence on a generation of behavioral biologists.

From 1940 to 1945, during World War II, Hinde was in the Royal Air Force, an experience that contributed to a lifelong disdain for war and concern to promote an ethos of peace. In 1948 he obtained a 1st class BA in Natural Sciences at the University of Cambridge, as well as a B.Sc. from the University of London. From 1948 to 1950, he conducted research for his D. Phil. in zoology at the University of Oxford, where he worked as a research assistant at the Edward Grey Institute, was advised by the ornithologist David Lack, and was influenced by the ethologist Niko Tinbergen. In 1950 he returned to the University of Cambridge to become the initial Curator of the Ornithological Field Station, designed by William H. Thorpe to integrate studies on instinct and learning (Hinde 1987). The station was established at Madingley, three miles from Cambridge, under the auspices of the Department of Zoology. Later it became the Sub-Department of Animal Behaviour, where from 1970 onwards it housed the Medical Research Council Unit on the Development and Integration of Behaviour, a focus of primate research. Hinde continued to work there as Honorary Director until his retirement in 1989. From 1950 to 1989 Hinde also taught in the Department of Zoology at the University of Cambridge, where in 1963 he became the Royal Society Research Professor of Zoology. In 1989 he retired from teaching and began a 5-year term as Master of St. John's College.

During his career, including almost three decades following retirement, Hinde wrote more than 15 books and 300 scientific articles and edited or co-edited a further 19 books. He won awards or medals in ethology, primatology, developmental psychology, social psychology, psychiatry, and anthropology, including becoming a Fellow of the Royal Society in 1974 and a Foreign Associate of the USA National Academy of Sciences in 1978. His students included Richard Andrew, Neil Chalmers, Dorothy Cheney, Tim Clutton-Brock, John Crook, Dian Fossey, Jane Goodall, Sandy Harcourt, Phyllis Lee, Patrick McGinnis, Robert Seyfarth, Kelly Stewart, and Richard Wrangham (Kelley and Sussman 2007).

Hinde's doctoral dissertation was a year-long study of the behavior of wild great tits (*Parus major*) in Marley Wood (Hinde 1952). He followed with a series of studies analyzing the causation of behavior, including courtship and predator-mobbing in captive birds (chaffinches *Fringilla coelebs* and greenfinches *Chloris chloris*), at the same time becoming increasingly involved in behavioral endocrinology. During this early work, Hinde was concerned with integrating the concepts of instinct, as analyzed by Konrad Lorenz and Niko Tinbergen, and learning and development, as emphasized by Daniel Lehrman. This effort culminated in his path-breaking 1966 textbook, *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology* (second edition 1970).

An important shift in Hinde's research interests began in 1953 after the ethologist Konrad Lorenz heard him distinguish a series of processes involved in the waning of the mobbing reactions of chaffinches to owls. Lorenz was deeply impressed and recommended Hinde's work to the developmental psychiatrist John Bowlby. In February 1954, Bowlby and Hinde talked together for the first time at a scientific meeting on ethology and psychiatry organized by the Royal Medico-Psychological Association (RMPA) in London (van der Horst et al. 2007). Their relationship became one of strong mutual influence. Bowlby credited Hinde as a crucial source of advice in his scientific development of attachment

theory, including asking Hinde to comment on his draft manuscripts. Hinde became fascinated with the potential to use behavioral studies to solve human problems. In 1959, in order to study the effects of separation of infants from their mothers, he added a colony of rhesus monkeys to the Madingley field station. Hinde's monkey studies, conducted with Yvette Spencer-Booth, Lynne Davies and others, led him to an increasing focus on human behavior and research on children, represented by his 1974 book *Biological Bases of Human Social Behaviour* (McGraw Hill, New York). It also led him to becoming the advisor for a series of primatologists working in the wild, beginning with Jane Goodall in the 1960s. Hinde helped to systematize the study of primates by insisting on rigorous methods. Among other contributions, he developed the Hinde index, which operationalized the responsibility taken by individuals for maintaining proximity within a dyadic relationship, and he provided an empirical concept of social relationships as the nature, frequency, and patterning of social interactions.

After retiring from teaching in 1989, Hinde was an active Emeritus Royal Society Research Professor based in St. John's College, Cambridge. He devoted much of his writing to papers and books on eliminating the causes of war, including *War No More* (Hinde and Rotblat 2003). He was Chair and President of the British Pugwash Group and President of the Movement for the Abolition of War. He was convinced that "changing the popular view of war as heroic, inevitable, or a solution to disputes, must be an important strategy for peace."

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Robert Kurzban

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Definition

Professor of psychology and evolutionary psychologist, at the University of Pennsylvania.

Introduction

Dr. Robert Kurzban, Ph.D., is a professor of psychology at the University of Pennsylvania who specializes in evolutionary psychology. He attended graduate school at the University of California, Santa Barbara (UCSB), where he studied under evolutionary psychologists Dr. Leda Cosmides and Dr. John Tooby. Kurzban earned his Ph.D. from UCSB in 1998. After earning his Ph.D., Kurzban accepted a postdoctoral fellowship in the Economic Science Laboratory at the University of Arizona (1998–2000) followed by a postdoctoral fellowship in the Department of Anthropology at the University of California, Los Angeles (2000–2002). He joined the Department of Psychology at the University of Pennsylvania in 2002. Shortly after joining the University of Pennsylvania, he founded the Pennsylvania Laboratory for Experimental Evolutionary Psychology. He has also served as a Visiting Research Associate at the Economic Science Institute at Chapman University and the Rasmuson Chair of Economics at the University of Alaska Anchorage.

Career

Dr. Kurzban is an evolutionary psychologist who has researched many facets of human behavior but is arguably known best for his work on the modularity of the mind. Dr. Kurzban's work has posited that different behaviors may be controlled by different mental mechanisms (Kurzban 2010). At times, these mechanisms may have conflicting goals, which may result in internal decision-making conflicts for individuals. For example, one mechanism may motivate an individual to eat some cookies, while a second mechanism may motivate that same individual to be healthy and therefore eat a salad instead of the cookies. The stronger mechanism will “win” this conflict, which leads the individual to engage in the behavior of that mechanism (i.e., either the individual will adhere to the first mechanism and therefore eat the cookies, or they will adhere to the second mechanism and eat a salad). This modularity may also give the illusion of free will, as individuals believe they are making a free choice when they are adhering to the stronger mechanism. In 2010, Kurzban published a book titled *Why Everyone (Else) Is a Hypocrite*, which focuses on this theory of modularity within the mind.

In 2014, Dr. Kurzban published a second book – coauthored with Jason Weeden – on self-interest in politics. The book, titled *The Hidden Agenda of the Political Mind: How Self-Interest Shapes our Opinions and Why We Won't Admit It*, covers a range of controversial and politically charged topics such as the legalization of marijuana, gay marriage, abortion, affirmative action, and many others. The books take a nonpartisan stance and illustrate how and why people take the political stances they do, as well as how and why people – both liberal and conservative – believe their political stance is the just and sensible viewpoint, while their opponents' political stance is ignorant (Weeden and Kurzban 2014).

Conclusion

Kurzban is an active writer who continues to publish new psychological research. Besides his

two popular press books mentioned above, Kurzban is the editor of five academic books on evolutionary psychology (see references), and he has published a combined total of over 100 peer-reviewed articles, book chapters, and book reviews. He has also consistently written blogs covering a range of topics in evolutionary psychology and popular culture and serves on numerous editorial boards for different peer-reviewed evolutionary psychology journals. As of 2016, he is the editor in chief of *Evolution and Human Behavior* – a peer-reviewed scientific journal that publishes research in the field of evolutionary psychology and the official journal of the Human Behavior and Evolution Society. He is also the editor of five new volumes of texts covering a wide range of topics within evolutionary psychology (Kurzban, 2016a, b, c, d, e)

Cross-References

- [Evidence of Brain Modularity](#)
- [Modularity of Mind](#)
- [Theory of Mind](#)

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Robert Kurzban on Group Processes

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Synonyms

[Adaptive solutions to socialization](#); [Choice of sides](#); [Evolution of morality](#); [Group relationships](#)

Definition

Dynamic operation of several cognitive mechanisms adapted throughout evolution to solve socialization problems.

Introduction

The majority of other species' individuals only cooperate for common goals when they are genetically close. Humans commonly cooperate with one another for the common good. This happens at a level from individual–individual interactions such as mother–child relationships or friendship, to individual–group interactions, for example, people who sacrifice their lives in defense of a nation in a war. These behaviors can be explained from some cognitive mechanisms adapted by the evolution of the human species (Kurzban and Leary 2001; Kurzban and Neuberg 2005; Kurzban et al. 2015).

Cognitive Mechanisms and Group Processes

The interactions among individuals to form and maintain groups are limited by the costs of establishing a social network, and choosing a

social interaction imply excludes some others (Kurzban and Neuberg 2005). Therefore, this choice represents an adaptive problem that would have favored cognitive mechanisms designed to make good decisions about social interaction. Group processes involve some opportunities and costs. These opportunities can include benefits such as parental investment and cooperation to achieve mutual goals. Besides, the costs can include direct conflict and violence, competition for scarce resources, transmission of infectious diseases, and so on.

Kurzban and many collaborators have investigated computational mechanisms in humans designed to group processes. These researches involve different adaptation of cognitive mechanisms that make up the dynamics of human group relations. First, Kurzban contributed to the evolutionary game theory, researching individual differences in group cooperation processes through experimental methods, such as social dilemma game and public goods game (Kurzban and Houser 2001; Houser and Kurzban 2002). For example, investigating the influence of individual differences on group contexts, Kurzban and Houser (2005) reinforced the evidences that the reciprocity is an important motivator in group contexts because groups composed of mostly cooperative types enjoyed improved group cooperation and tend to earn more. Second, their researches demonstrated that the human cognitive mechanisms explain relationships of cooperation or competition and the management of ingroup and outgroup engagement. Concomitantly, many others process directly or indirectly involved in these phenomena were researched, such as morality (DeScioli and Kurzban 2009a, 2013), stigmatization (Kurzban and Leary 2001), altruism (Kurzban et al. 2015), social exclusion, prejudice and discrimination (Kurzban and Neuberg 2005), alliance and friendship (DeScioli and Kurzban 2009b), revenge and forgiveness (McCullough et al. 2013), among others.

As an example of these researches, DeScioli and Kurzban (2009a) realized an adaptationist analysis of morality, highlighting three evolutionary mysteries of moral condemnation: third-party judgment, moralistic punishment, and moral

impartiality, concluding that these processes are performed by different cognitive mechanisms. As a possible solution to explain a variety of mysterious moral phenomena, DeScioli and Kurzban (2013) proposes that moral condemnation functions to guide of choosing sides in conflicts. Thus, moral cognition would be designed to manage two coping strategies when conflicts occur: choice based on the high status of the disputant or on the preexisting relationships. The decision comes through the implementation of a dynamic coordination strategy in which bystanders coordinate the choice of side by focusing on the contestants' actions rather than their identities. These researches proposed the dynamic coordination theory based on mind computational theory. It regards the human mind as an advanced computational control system. Therefore, moral cognition, as part of these systems, is a cognitive mechanism designed to execute highly sophisticated processes in the computations and strategies of many our social interactions and particular reflections.

Finally, DeScioli and Kurzban (2009b) proposes human friendship would be based on cognitive mechanisms designed to bring together support groups for potential conflicts. Grounded on the computational theory of games, the alliance hypothesis for human friendship recognizes that human friendship results from a system of alliance similar to the alliance between countries, not based on proximity or exchange of benefits. Thus, the friendship would occur through a self-reinforcing process initiated when individuals value each other because their partners value them. All researches presented indicate the existence of various systems operating in the same organism dynamically; all these processes derive from a set of cognitive mechanisms adaptations throughout evolution to solve problems related to socialization.

Conclusion

Kurzban and scholars suggest that there are different adaptations for the different types of sociality. Thus, the human cognitive adaptations will

probably consist of a set of shared systems designed for the personal choice of interaction partners, as well as the entry and stay in groups, and also for group processes of cooperation and competition (Kurzban and Leary 2001; Kurzban and Neuberg 2005; Kurzban et al. 2015). Human beings have cognitive mechanisms adapted to discriminatory sociality and have psychological mechanisms designed to maintain and maximize the benefits and to limit and minimize the costs derived from it (Kurzban and Leary 2001; Kurzban and Houser 2005). Advances in cognitive mechanisms and group processes researches have led to new challenges on human cooperation's studies. Issues such as development, punishment, and parents and offspring demand special attention (Kurzban et al. 2015).

Cross-References

- [Moral Concerns](#)
- [Racism and Prejudice](#)
- [Science and Morality](#)
- [Social Exclusion](#)

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Robert Trivers

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Synonyms

[Deceit and self-deception](#); [Fluctuating asymmetry](#); [Genomic imprinting](#); [Jamaican symmetry project](#); [Moralistic aggression](#); [Parental investment and sexual selection](#); [Parent-offspring conflict](#); [Reciprocal altruism](#); [Selfish genetic elements](#); [Trivers-Willard effect](#); [Variance in reproductive success](#)

Definition

One of the most influential contributors to modern evolutionary theory, Trivers' work utilizes

selection acting at the level of the gene to understand the adaptive function of complex human behaviors such as cooperation, conflict, self-deception, homosexuality, and the evolution of morality.

Introduction

Robert Trivers is undoubtedly one of the most important and influential thinkers in modern history. His work inspired and revolutionized entire disciplines including sociobiology, evolutionary psychology, behavioral ecology, evolutionary genetics, and economics. His series of papers published in the early 1970s resulted in an explosion of empirical work on a diversity of species from insects to humans. Trivers introduced evolutionary theory to economic thinking, by embracing selection acting at the level of the gene; he sought to understand the adaptive function of behavior as well as the constant selective pressures that result in increased efficiencies. Trivers recognized the power of viewing social behavior as a co-evolutionary struggle between constant conflict and cooperation – within the individual, relationships, and groups. Trivers presented an eloquent and simple underlying logic that explains the complexity of social interactions in terms of the partial overlap of genetic interests between and within different groups of organisms.

Early Life and Education 1943–1966

Robert Ludlow Trivers was born on February 19, 1943, in Washington, D.C., the second of seven children of Mildred Reynolds Trivers, an accomplished poet, and Howard Trivers, a diplomat and philosopher. Throughout his life, Trivers' academic interests have been varied and intensely studied, at 12 he became obsessed with astronomy, and by 13 he had moved on to math and mastered differential calculus in 2 months using only textbooks. After graduating from Phillips Academy in Andover Massachusetts, Trivers enrolled at Harvard University in the fall of 1961 as a math major. His interest in math soon waned

and he decided to focus on becoming a lawyer to fight for justice and equal rights. In 1965, Trivers graduated from Harvard with a degree in history and, after recovering from the first in a series of mental breakdowns, found a job writing fifth grade science textbooks, which included teaching evolution. Having never taken a course in biology nor any particular interest in or experience with animals, Trivers was assigned Bill Drury, an ornithologist to mentor him.

Drury's wealth of knowledge in animal behavior and ecology, and passion for the emerging field of evolutionary biology, exposed Trivers to the principles of evolutionary theory and invaluable fieldwork experience. Trivers describes the moment he comprehended the power of viewing the world from the perspective of natural selection acting at the level of individual genes as "I felt a sense of religious awe (Trivers 2002)."

Academic Career at Harvard 1966–1978

In the spring of 1966, Bill Drury introduced Trivers to Ernst Mayr who encouraged him to enroll at Harvard to earn a PhD in evolutionary biology. Observing pigeon behavior on the roof of his Cambridge apartment led Trivers to describe behavior we now refer to as extra pair copulations, mate guarding, male-male aggression, and sexual coercion – all present in what was thought to be a relatively conflict-free "monogamous" mating system. He began to think of these interactions as strategies, with economic costs and benefits measured in genetic contribution to the next generation, based on context-specific ecological conditions.

Trivers conducted his dissertation research on *Anolis* lizards in Jamaica under Harvard's curator of herpetology, Ernest Williams. Trivers was one of the first to study how a single parameter (body size) affected reproductive success differently in the two sexes in nature (Trivers 1976).

Trivers spent the late 1960s until 1978 at Harvard, first as a graduate student, then as a postdoc under Irvan DeVore, and eventually as an instructor, assistant professor, and associate professor. He married his first wife Lorna Staple in 1974.

During this time, he published a series of remarkable papers that revolutionized the field and evolutionary biology and generated entire fields of inquiry on social behavior.

Reciprocal Altruism

After attending a talk by Richard Lewontin at Harvard in the spring of 1969, Trivers realized that theoretical ecology was not something he would enjoy. He decided to put his intellectual energy into solving important questions in the field that had yet to be resolved. He set his sights on reciprocal altruism. Darwin's theory of evolution by natural selection was based on the premise that individual organisms are expected to engage in behaviors that directly increase survival and the probability of their genes being passed on to future generations. The presence of altruistic behavior in nature was a puzzle that Darwin had been unable to solve. Unrelated individuals engaging in behavior, where the actor incurs a cost and the recipient a benefit (in terms of reproductive success), appear counterintuitive to Darwin's theory. In 1964, WD Hamilton laid out logic for altruism being selected for in related individuals, based on kin selection and inclusive fitness theory. Hamilton utilized evolutionary logic acting at the level of the gene and mathematical modeling to explain how altruistic behavior could have evolved within populations based on their degree of relatedness (Hamilton 1964). Trivers introduced the concept of reciprocity to explain how altruism between unrelated individuals could have evolved based on economic principles. He created a testable hypothesis regarding repeated interactions between unrelated individuals and identified the ecological conditions that would favor the evolution of reciprocal altruism as an adaptive strategy for individuals to cooperate in order to increase individual survival and reproductive success. Trivers argued that repeated opportunities to engage in altruistic behaviors with the same individuals, in order to build up reciprocal relationships and maximize long-term benefits, were a key factor in the evolution of reciprocal altruism. Trivers predicted that

biological parameters such as long life spans, low dispersal rates, a need to interact for mutual dependence, and parental care would allow for many repeated interactions between individuals over a lifetime. The promise of delayed return over time confers benefits to individuals who participate by conforming to rules of the social system based on reciprocity – low cost to actor and high benefit to recipient. Over time, Trivers argued, these conditions select for the evolution of cooperation. One issue Trivers kept coming back to was cheaters – individuals who take benefits but do not incur costs, by not reciprocating. Under specific circumstances, this would be adaptive. Trivers argued that given the unstable nature of the system, evolution would rapidly favor complex psychological mechanisms in individuals to regulate both their altruistic and cheating tendencies. He viewed relationships between individuals as complicated interactions involving costs and benefits associated with conflict and cooperation determined by patterns of overlap and nonoverlap of long-term genetic interests. Trivers argued that the evolution of reciprocal altruism led to the development of complex human emotions to maximize survival and reproductive success within a wide variety of social relationships. Emotions such as friendship, loyalty, fairness, justice, gratitude, sympathy, empathy, moralistic aggression, guilt, regret, remorse, and compassion are examples (Trivers 1971).

Trivers' work on reciprocal altruism led to the evolution of entire disciplines including economic game theory. EO Wilson had encouraged Trivers to expand his theory in mathematical terms; WD Hamilton and Axelrod accomplished this in 1981 in the development of an evolutionary stable rule of action, elegant in its simplicity – tit for tat.

Parental Investment Theory 1972

After reciprocal altruism was published, unlike most academics that may have chosen to build a career around this important topic, Trivers immediately moved on to a subject where he felt there was progress to be made – sexual selection. While Darwin had identified the two basic types of

sexual selection, male-male competition and female choice, Trivers felt that Darwin's treatment lacked a general framework within which important variables could be related. At the insistence of Ernst Mayr, Trivers read Bateman (1948) in *Heredity* and rediscovered the concept variance in reproductive success analyzed by sex. Trivers also reviewed behavioral data on sex role reversed species from George Williams and developed a theory to explain details of the male-female relationship in terms of the amount each sex invested in individual offspring. Trivers formulated an objective and unbiased system for thinking about evolution of the two sexes that emphasizes equality of parents – each receiving 50% genetic representation in offspring. His theory was sex-blind, based on parental investment strategies not biological sex and could be applied everywhere. This theoretical framework could be used to explain a wide range of sexually dimorphic features and behaviors, from body size and shape to sex differences in complex psychological behaviors such as sexual jealousy and homicide (Trivers 1972).

Trivers-Willard Effect 1973

In 1970, Trivers was a teaching assistant in Irven DeVore's Primate Behavior course when he met Dan Willard, a graduate student in mathematics. After attending his lectures on sex ratio at birth and the evolutionary logic of mate choice, Willard approached Trivers with an interesting question – wouldn't it make sense for humans to adjust the sex ratio of their offspring based on socioeconomic status? Fleshed out and published in 1973, the theory was simple and based on return on investment based on gender of offspring, dependent on maternal condition and differences in potential reproductive success in offspring by sex (Trivers 2002). The theory predicted in species with extreme variance in reproductive success between males (e.g., where a few males father the vast majority of offspring and most males father none); females of low rank or in poor condition should invest more in daughters, while dominant females with access to plentiful resources should invest more in sons. In most

species, the difference in reproductive output between females is much less variable than males, where each fertile female produces on average the same overall number of offspring. Females in good condition benefit in terms of inclusive fitness by investing in sons who have a better chance of becoming dominant and more often chosen as a mate, resulting in a much larger payoff for her investment in terms of potential reproductive success compared to daughters whose RS is less variable based on dominance and condition. Empirical evidence from mammals such as red deer and human populations supports the model. In human societies, because daughters tend to marry up the socioeconomic ladder and males do not, parental investment in daughters is favored at the lower end, where males often remain unable to afford mates and therefore have decreased prospects of obtaining RS. Male offspring born into high socioeconomic status have access to resources and can often afford multiple mates, therefore exponentially increasing the number of potential offspring and hence reproductive success (Trivers and Willard 1973).

Parent-Offspring Conflict 1974

In early 1971, Trivers began to develop a biological theory of the family based on natural selection. He determined that degree of relatedness (r) was the key parameter and decided to focus on the parent-offspring relationship. Trivers viewed the relationship in economic terms as a competing series of interactions involving cooperation and conflict based on overlapping genetic interests resulting in conflict over parental investment. Parents share 50% of their genes with each individual offspring ($r = 0.5$) and should therefore invest in each equally. Each offspring is related to itself by $r = 1$ but to the parent by $r = 0.5$, resulting in the offspring being selected to desire to continue extracting parental investment longer than the parent is selected to continue providing it.

Trivers utilized weaning conflict to mathematically model how parent-offspring conflict over length of the period of parental investment manifests, including specific behavioral tendencies that

would result in both parent and offspring in order to maximize their own individual RS (Trivers 1974). This line of reasoning eventually led Trivers to pursue conflict within the individual at the level of the gene via maternal and paternal imprinting and other forms of intergenomic conflict (Trivers 1995, 1997; Trivers Burt 1999).

Haplodiploidy and the Evolution of Social Insects

Irv DeVore arranged for Trivers to work as an anthropology instructor at Harvard in 1971. After lecturing on Hamilton's kinship theory (1974), Trivers decided to apply the logic of Hamilton's kinship and Fisher's sex ratio theory to understand the evolution of haplodiploidy in social insects. In the Hymenoptera (ants, bees, and wasps), unfertilized eggs develop into males and have only one set of chromosomes (haploid) and fertilized eggs are female (diploid), the majority of which are nonreproductives. Colonies in these species usually have a single reproductive queen and castes of nonreproductives that forgo reproducing themselves and instead invest in raising the offspring of the queen. This system is referred to eusocial and is relatively rare in nature, yet common within the Hymenoptera. Trivers was interested in developing the evolutionary logic explaining the complex interactions between the varying degrees of relatedness of individuals, overall sex ratio, and ratio of investment bias in eusocial colonies (Trivers and Hare 1976).

With the help of EO Wilson and Bert Holldobler, Trivers tested his hypothesis in over 20 species of ants and showed that once eusocial colonies appeared, the ratio of investment should be biased toward females and stabilize at a sex ratio of one male to three females.

Deceit and Self-Deception

Trivers was conscious of self-deception from an early age and recognized the pervasive and confounding use of deception in humans. Some

examples included biblical passages, the pervasive practice of purposefully misrepresenting prices (e.g., \$4.99), American history, and politics. After learning evolutionary biology, the mechanisms of self-deception appeared counter-intuitive to Trivers. After observing intense psychological warfare in baboons while in East Africa with Irv DeVore in 1972, it became clear to Trivers that the complex social nature of humans could easily select for self-deception because it allows for better deception of others. While working on parent-offspring conflict, Trivers' thoughts on the topic began to coalesce as he hypothesized that parents might be selected to induce self-deception in offspring to alter their behavior in ways that disproportionately benefit the genetic interests of the parent. This began a 40-year process of developing a cohesive theory on the evolution of deceit and self-deception (Trivers 1985, 1991, 2002, 2011).

University of California, Santa Cruz, 1978–1994

After being overlooked for tenure at Harvard, Trivers moved his family west to the University of California at Santa Cruz in 1978. Here he would raise his four young children, meet Huey P. Newton, and become a member of the Black Panther Party. He continued his exploration of self-deception, coauthoring a paper in 1982 with Huey Newton on the crash of Air Florida Flight 90. Cockpit voice recordings were analyzed to demonstrate the real cost of self-deception – an impaired ability to deal with reality (Trivers and Newton 1982). In 1991, Trivers formally presented the evolutionary logic for deceit and self-deception, exploring the connection between communication and consciousness (Trivers 1991).

Social Evolution 1985

In 1985, Trivers' long-awaited textbook on evolutionary social theory was published. It was

written for both general readers with no background in evolutionary theory and introductory undergraduate college courses in anthropology, animal behavior, or related disciplines. The book began with chapters that systematically laid out the theory of evolution by natural selection and basic genetics. The heart of the book introduced an interconnected body of theory and supporting evidence on the principles underlying social evolution including kinship, parent-offspring relationships, reproductive altruism, sexual selection, sex ratio, and the evolution of sexual reproduction. The final chapters covered social interactions in general, such as the evolution of cooperation and deceit and self-deception (Trivers 1985).

Mate Choice

Trivers viewed mate choice as an area ripe for investigation. After finishing his work on parental investment and sexual selection, he felt strongly that there needed to be a theory of mate choice based on genetic quality. He began in earnest in 1977 to solve this question and addressed it in 1985 in *Social Evolution* where he suggested that there was sexual selection pressure acting on females resulting in female-biased female choice (Trivers 1985). Trivers argued that this had been a neglected form of female choice but that it may be important in nature. Since the limiting reproductive factor for any population is fertile females, the species that improves daughters would have a competitive advantage. Collaborating with Jon Seger, they published a paper on asymmetry in the evolution of female mating preferences in 1986 using population genetic modeling to demonstrate that a female choice gene harming daughters was inhibited by its spread compared to female choice harming sons. This was the first work to explicitly show how female choice could have evolved to place special emphasis on traits that promote female fitness. Trivers views this as important work that has gone relatively unnoticed and an area still ripe for further research (Seger and Trivers 1986).

Fluctuating Asymmetry

In 1990, WD Hamilton gave a talk at UC Santa Cruz. Trivers asked him what was new in sexual selection and Hamilton replied “fluctuating asymmetry (FA).” Trivers interest in FA deepened after reading work on mate preferences and symmetry in birds and discoveries on correlates of fluctuating asymmetry in scorpion flies. FA refers to small deviations from perfect symmetry ($L-R = 0$) that fluctuate around zero. Levels of FA are measures of developmental stability and genetic quality. There was already a significant literature from biology with associations between FA and mate choice, reproductive success, body size, and fighting ability (Trivers 2002).

Rutgers University 1994–2017

Having divorced his first wife in 1988, Trivers moved back east in 1994 to teach in the ecology and evolution and anthropology departments at Rutgers University and be closer to his children. He remarried in 1997 to Debra Dixon and together they had a son in 1999. They divorced in 2004.

In 1994, Trivers coauthored a review paper on the science of symmetry in biology with coauthor Michal Polak (Polak and Trivers 1994). Trivers recognized the power of having an observable measure of genetic quality. Symmetry was not only easy to measure but had become recognized as a major variable in the study of humans including mate choice and attractiveness preferences. In 1996, Trivers led an international team of researchers including Devandra Singh, Randy Thornhill, and John Manning to Jamaica where they collected behavioral data and measured fluctuating asymmetry, waist-to-hip ratio (WHR), and second to the fourth digit ratio (2D:4D) on 285 Jamaican school children. Some initial findings revealed boys were more symmetrical than girls; Jamaican children were more symmetrical than European children; symmetry decreases as children age; the lower body is more symmetrical than the upper body; symmetry in one feature may

correlate with some behavioral traits, while others do not; and boys with symmetrical lower bodies were more aggressive (Trivers et al. 1999). Data was also collected from the subjects' mothers on 2D:4D and WHR, leading to the discovery by John Manning that 2D:4D ratio is positively correlated with the number of offspring in females, mothers with higher WHR gave birth to more sons, and low 2D:4D is associated with left handedness (Manning et al. 2000a, b). The project has resulted in numerous publications on topics including the ultimatum game, FA and running speed, mate choice, and 2D:4D (Trivers et al. 2004, 2013a, b). The initial subjects have been followed for over 20 years and are periodically remeasured, providing valuable longitudinal data on fluctuating asymmetry, reproductive success, and mortality (Trivers 2002).

Genetics

After completing *Social Evolution*, Trivers began pursuing his interest in the evolutionary dynamics of within-individual conflict in earnest. He underestimated the vast and complicated nature of genetics but found willing collaborators in Austin Burt and David Haig. Trivers coauthored several papers on B chromosomes in plants and insects, selfish DNA and breeding systems in flowering plants, the logic of kinship theory applied to genomic imprinting, and the genetic basis of intrapsychic conflict (Burt and Trivers 1998; Trivers et al. 2004). After 15 years of research on genetic conflict within various organisms, Trivers and Burt published a comprehensive book on the topic in 2006, *Genes in Conflict: The Biology of Selfish Genetic Elements* (Burt and Trivers 2006).

Self-Deception

In 2011, Trivers published a book on deceit and self-deception. It was a culmination of a lifetime of personal observations and extensive research and delivered a general theory of deceit and self-

deception based on evolutionary logic. In typical Trivers fashion, the book takes a comprehensive, interdisciplinary, and functional approach, providing supporting evidence from neurophysiology, immunology, evolutionary genetics, sexuality and reproduction, and psychology. Trivers uses his theoretical framework to examine self-deception in real life from the role it plays in space disasters and the stock market to the complex way it manifests in humans from confirmation bias and religious belief in individuals to genocide and war between groups (Trivers 2011).

Current Research Interests

Trivers, along with Bernhard Fink and John Manning, published a series of papers on symmetry, 2D:4D, and FA in elite Jamaican sprinters (Trivers et al. 2013b, 2014). Following up on his research on self-deception, Trivers collaborated with Bill von Hippel on the aging positivity effects and function of the immune system (Kaloerinos et al. 2014). He is still interested in trying to provide evolutionary logic to explain behavioral phenomenon that appear to contradict expectations. Some areas he intends to make progress on include homosexuality, where same-sex attraction decreases individual reproductive success, honor killings, where family members kill closely related individuals in order to restore honor to the family, and the evolutionary genetics involved in cancer.

Honors and Awards

Trivers has been recognized and honored for his contributions to science by diverse organizations around the world. His work was recognized by *Time Magazine* when he was featured as one of the top 100 thinkers of the twentieth century. He is an honorary distinguished fellow at the University of the West Indies, received a regents fellowship at the Smithsonian Institution, has been a fellow at the Institute of Advanced Studies in Berlin, received the distinguished Animal Behaviorist

Award from the Animal Behavior Society, is a member of the American Academy of Arts and Sciences, and received fellowships from the John Simon Guggenheim Foundation and Smithkline-Beecham. In 2007, Trivers was awarded the prestigious 25th Crafoord Prize by the Royal Swedish Academy of Sciences for his seminal contribution to understanding the evolution of complex social behaviors by introducing evolutionary logic to view life in terms of selection acting at the level of the gene in a series of conflicting and cooperative strategies.

Wild Life

In 2015, Trivers' autobiography *Wild Life: Adventures of an Evolutionary Biologist* was published. In it he describes his unconventional life, from literally stumbling upon evolutionary theory to death-defying adventures in the field; Trivers reflects on his life with unusual candor and brutal honesty. A full-length feature documentary *Wild Life* is scheduled for release in 2017 (Trivers 2015).

Conclusion

Robert Trivers has had a profound influence on our understanding of the human condition. His unique ability to master literature and make connections between the economics of efficiency based on degrees of relatedness and complex social behavior has had a profound effect across multiple disciplines. By taking a functional approach to genes and behavior, Trivers' work has allowed for a depth and breadth of knowledge on the biology of social behavior that has enhanced our ability to better comprehend life itself.

Cross-References

- [Fluctuating Asymmetry](#)
- [Genomic Imprinting](#)

- [Jamaican Symmetry Project](#)
- [Moralistic Aggression](#)
- [Parental Investment and Sexual Selection](#)
- [Parent-Offspring Conflict](#)
- [Reciprocal Altruism](#)
- [Selfish Genetic Elements](#)
- [Variance in Reproductive Success](#)

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Robin Baker and Mark Bellis

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Synonyms

Female orgasm; Human sperm competition

Definition

Robin Baker and Mark Bellis are two British researchers who carried out a series of pioneering and controversial studies into human sperm competition and female orgasm in the late 1980s and early 1990s.

Introduction

Robin R. Baker was an evolutionary ecologist at the University of Manchester, where he was best known for his work on the evolution of reproductive strategies in humans and other animals. In the late 1980s and early 1990s, he and his student Mark A. Bellis carried out a series of groundbreaking studies on intrasexual competition in humans. The chief results from this research were published in four prominent papers in the journal *Animal Behaviour* (Baker and Bellis 1989, 1990, 1993a, b) and in a 1995 book (Baker and Bellis 1995). Although their studies received criticism (Schilthuizen 2014; see below), these five publications jointly have been cited in the scientific literature more than 1,500 times.

Baker and Bellis Studies

Using data from women interviewed in three UK cities, Baker and Bellis first showed that human “double mating” (i.e., copulation while fertile sperm from a previous, different partner is still present in the woman’s reproductive system)

takes place at a frequency of c. 0.1 % of all copulations (Baker and Bellis 1989). This is a rate high enough to allow the evolution of competitive traits in ejaculates. They then collected ejaculates (resulting from either copulation or masturbation) from volunteers and counted sperm content. They discovered that the proportion of time a couple had been separated since their previous copulation (and, hence, the likelihood of male intrasexual competition) was a strong predictor for the number of sperm in a copulation-derived ejaculate. Ejaculates collected after masturbation, however, did not show such a relationship. This indicated that, as theory predicted, human males are able to adjust the competitive ability of their ejaculate in response to the likelihood of sperm competition.

In a separate study, based on a large questionnaire returned by over 3,700 female readers of the magazine *Company*, Baker and Bellis showed that the women's sexual activity patterns also played a role in this: extra-pair copulations (the ones that would potentially generate such double matings) took place at peak fertility more often than expected by chance (Baker and Bellis 1990).

In 1993, Baker and Bellis published two back-to-back papers (Baker and Bellis 1993a, b) with a much larger analysis of the data from their *Company* questionnaire, as well as data from an experiment with an extended set of volunteers: not only men who were asked to return condoms with copulation/masturbation ejaculates but also women who were asked to collect "flowback," the semen that emerges from the vagina after unprotected sex – often interpreted as a form of sperm dumping (Schilthuisen 2014). In total, the study involved 278 ejaculates. In addition, the volunteer couples filled out detailed questionnaires on their sexual activities during the experimental period.

These larger analyses showed several things. First, they confirmed the earlier results that their male volunteers ejaculated larger numbers of sperm during copulation (but not during masturbation) if they had been separated from their partners for longer. Moreover, the numbers of sperm that men ejaculated were consistent with a "topping-up" model, where men manage their

ejaculations such that an optimal number of sperm cells are always present in the reproductive system of their partners.

Second, they showed that, although the concentration of sperm cells in an in-copula ejaculate decreased if there had been a recent masturbation, this did not negatively affect the number of sperm retained by the woman. Baker and Bellis interpreted this as an indication that masturbation serves to prevent the accumulation of senescent sperm cells and thus to maintain the quality and fitness of the next in-copula ejaculate.

Finally, they showed that there is great variability in the amount of flowback, ranging from full retention of the entire ejaculate to its full ejection. More importantly, the amount of retained sperm cells was largely dependent on female orgasm. Without orgasm or if orgasm took place more than a minute before male ejaculation, few sperm cells were retained. Baker and Bellis interpreted this as a sign that female orgasm serves a role in cryptic female choice, by enhancing (perhaps via the negative pressure created inside the uterus during climactic spasms; Baker and Bellis 1993b; Schilthuisen 2014) the uptake of ejaculated sperm.

Conclusion

The publications by Baker and Bellis form a classic set of studies, since they were the first to test, in an experimental setting, hypotheses about sperm competition in humans. However, they were also criticized because of small sample sizes, questionable methodologies, and overinterpretation of the results. One claim specifically, namely, that some sperm cells ("kamikaze sperm") in human ejaculates serve to physically interfere with competitors' sperm cells in double-mating situations, could not be replicated later (Moore et al. 1999). In 1996, Baker moved out of academia and became a free-lance author of popular science books (of which the 1996 *Sperm Wars* is the best known; Baker 1996) and novels, in which he continued to use the intrasexual competition themes of his research work. He was attacked by his academic colleagues for promulgating

unsubstantiated evolutionary interpretations of various human sexual behaviors in these books.

Since retiring from academia, Robin Baker has been a science communicator and novelist. Mark Bellis is currently Director of Policy, Research and International Development at Public Health Wales.

Cross-References

- ▶ [Cryptic Female Choice](#)
- ▶ [Ejaculate Adjustment](#)
- ▶ [Genital Evolution](#)
- ▶ [History of Sperm Competition in Humans](#)
- ▶ [Human Copulation](#)
- ▶ [Human Sperm Competition](#)
- ▶ [Infidelity Risk](#)
- ▶ [Opposition to Human Sperm Competition](#)
- ▶ [Penile-Vaginal Sex](#)
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- ▶ [Sexual Behavior](#)
- ▶ [Sperm Competition](#)
- ▶ [Sperm Competition Risk and Partner Abuse](#)
- ▶ [Sperm Competition Tactics](#)
- ▶ [Sperm Competition Theory](#)
- ▶ [Threats of Sperm Competition](#)

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Robin Baker and Mark Bellis: Pioneers of Research on Human Sperm Competition

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Definitions

Human sperm competition: the competition to fertilize a woman's egg that takes place inside a woman between sperm from two or more different men.

Introduction

From 1962–1970, Robin Baker studied zoology at the University of Bristol, UK. One of his contemporaries, both as an undergraduate and postgraduate, was Geoffrey Parker who, around 1965, was the first person to recognize the phenomenon of sperm competition. Parker's focus was on insects, but from the beginning, according to Baker (2015; p. iv), Parker envisaged a wider relevance for his theory. During the winter of 1965–1966, the pair shared an apartment, and there, Baker writes, they would sit “talking about sex – as postgraduates do.” Mainly, their conversations revolved around dung flies, but from time to time, they mused

Robin Baker has retired

over whether sperm competition might also occur in humans. Their conclusion was always the same: maybe it did, but study would be impossible. A further 20 years were to pass before Baker revised that conclusion.

Parker eventually published his groundbreaking ideas for insects in 1970 (Parker 1970). Slowly at first, then faster, sperm competition became recognized as a major evolutionary force for a range of animals. The first collection of papers on the subject was organized by Robert Smith, University of Arizona, USA, who dared to end the volume by proposing that sperm competition really could have been an evolutionary force on humans (Smith 1984).

A year after this collection of papers was published, a chance meeting triggered the transformation of Smith's speculations into an experimental investigation. Robin Baker had by then been a lecturer in zoology at the University of Manchester, UK, for a decade. In Baker's (2015) account of those years, he describes (p. viii) how in his Behavioral Ecology lectures he annually proclaimed that human sperm competition would be a "fantastic" subject area. "Totally impossible to study, of course," he would say, "unless one of you..." and he would wave his hand around the class "...can think of how it could be done." Baker had made that gesture and spoken those words 6 or 7 years in succession before a student came to his room to say that he thought he did know how it could be done. His name was Mark Bellis.

So began a 10-year collaboration that on the one hand developed the latent field of human sperm competition into a serious scientific study but, on the other, greatly divided academic opinion. To some, Baker and Bellis were "heroes" (Gowaty 1996) and their papers eventually "classic" (Shackelford and Pound 2006; p. xix). To others, their work was mere fantasy. According to Tim Birkhead (2000; p. 29), quoting the title of the 1992 cult film by GWR, "Robin Baker and Mark Bellis may see themselves as pioneers in the study of human sexuality, but ... the view of human sperm competition they have perpetuated is little more than sexual fantasy – phallus in wonderland."

The Collaborative Decade (1985–1995)

Kamikaze Sperm (1988)

Baker and Bellis's first publication (1988) was to be their most notorious. Entitled '*Kamikaze Sperm in Mammals?*', the paper hypothesized that not all sperm in mammalian ejaculates were present to fertilize eggs.

It had long been known that mammalian ejaculates, including those of humans, always contained a proportion of strangely shaped sperm. Head shape, for example, varied hugely, some being small, others large, and yet others pear shaped, cigar shaped, or simply oddly shaped. Some even had two heads or more. Tails varied too: short, bent, coiled, or double. The proportions differed consistently between species: in gorillas and humans, up to 40% of sperm could look very different from "normal," whereas in chimpanzees, the proportion was nearer 5%. Traditionally, such sperm had been interpreted as abnormalities: mistakes during sperm formation (Cohen 1977). Baker and Bellis (B&B, for short) suggested instead that they were adaptations to sperm competition. Some were even present specifically to die – a "kamikaze" role – a suggestion inspired by B&B's study of rats.

During mating, a male rat leaves a hard plug of coagulated semen in the female's vagina. This hinders mating by later males. The plugs are reinforced by the intertwined bodies of countless dead sperm (Baker and Bellis 1988) perhaps making them stronger and more difficult to remove. B&B proposed that such large-scale sacrifice of sperm could increase, not decrease, the plug producer's chances of fertilizing the female's eggs.

Although the "Kamikaze Sperm Hypothesis" was B&B's first joint publication, it was to remain a purely theoretical concept until their very last joint publication 7 years later. Only then did they formulate the hypothesis fully and provide experimental support.

Ejaculate Adjustment During Copulation (1989)

By the mid-1980s, Geoff Parker had produced a number of testable sperm competition hypotheses, one being that the greater the risk of sperm

competition, the more sperm a male should inseminate.

To test this prediction for humans, B&B began recruiting volunteer couples to collect ejaculates from copulation and masturbation during their normal sexual activity (using condoms) and to return these to the Manchester laboratory for analysis. A questionnaire was also completed for each ejaculate, one of the questions being the percentage of time the pair had spent together since their last copulation. Nobody had carried out such a study before.

B&B reasoned that the less time a pair spent together, the more likely was the female to mate with a different male between matings with her partner. They suggested, therefore, that percentage time together between copulations could be used as a proxy for risk of sperm competition. Their resulting prediction, based on Parker's hypothesis, was that the lower the percentage of time a couple had spent together since their last copulation, the more sperm the male should inseminate at the couple's next copulation. Such a trend should not be present for masturbatory ejaculates.

The paper eventually published (Baker and Bellis 1989), entitled "*Number of sperm in human ejaculates varies in accordance with sperm competition theory*," supported this prediction. Perhaps even more importantly, it provided the first demonstration that humans could be used to test the predictions of sperm competition theory.

Frequency of Human Sperm Competition (1989–1990)

Robert Smith (1984) listed a range of situations in which human sperm competition should occur: prostitution, group sex, gang rape, rape, and, top of the list, female infidelity. Figures existed for all of these activities, not only for the USA but also for Europe. None, however, could be converted into rates of sperm competition nor, more importantly, how many children were conceived as a result.

When a woman conceives to a man other than her recognized partner, it is said to be an example of extra-pair paternity. Traditionally, based on

little more than hearsay and anecdotes, medical students had been taught that the level of extra-pair paternity in modern society was around 10–15%. This was the figure still being quoted in medical textbooks when B&B began their collaboration. However, even this figure could not be used as a frequency for conception via sperm competition because not all cases of extra-pair paternity are the result of sperm competition.

In April 1989, in collaboration with the UK woman's magazine *Company*, B&B circulated a questionnaire nationwide which would enable them to calculate the figure needed. From nearly 4,000 replies, they separated out data for women being unfaithful "unprotected" by contraception during the fertile phase of their menstrual cycle. From these, they calculated that the proportion of UK children likely to be conceived via sperm competition was indeed likely to be of the order of 10% (Bellis and Baker 1990).

In order to make this calculation, an assumption had to be made about how long sperm stayed fertile once inside the female. Robert Smith (1984) had argued that for a woman to contain live sperm from two different men in her reproductive tract and to generate sperm competition, she would need to mate with a second male no more than 7–9 days after the first. B&B adopted a more conservative 5-day gap.

On the basis of a 10% figure for conception via sperm competition, B&B claimed that sperm competition had indeed been common enough through human evolution to exert a significant selective pressure on the shaping of human sexuality.

Female Promotion of Sperm Competition (1990)

Sperm competition theory focussed first on the behavior of males. However, as Robert Smith (1984) had noted, females could also gain benefits. If sperm competitiveness is heritable, females fertilized by the most competitive sperm will gain through the greater reproductive success of their sons. So, if a female is unable to judge ejaculate quality from a male's appearance, her best strategy is to promote sperm competition via *double matings* (matings that lead to a woman having

sperm from more than one male inside her reproductive tract) around times of peak fertility.

The *Company* dataset allowed B&B to test this hypothesis (Bellis and Baker 1990). Although female infidelity in general showed no pattern with respect to the menstrual cycle, double matings “unprotected” by contraception were most likely during the fertile phase. B&B concluded that women are most likely to promote sperm competition when the probability of conception is highest.

Ejaculate Adjustment During Copulation and the Function of Male Masturbation (1993)

Armed with their *Company* data plus further copulatory and masturbatory ejaculates collected by more couples, B&B were now in a position to use humans to test a much greater variety of hypotheses from Parker’s sperm competition theory (Baker and Bellis 1993a).

B&B began by providing evidence that the percentage of time couples spent together really was a good proxy for risk of sperm competition. They then demonstrated that from intercourse to intercourse, even individual males would adjust the number of sperm inseminated into a long-term partner according to the risk that she might contain sperm from another male. Another of Parker’s predictions, that males should inseminate more sperm into women of higher reproductive value, in B&B’s case larger women (within the normal healthy weight range), was also tested and supported. Finally, B&B evaluated the prediction that a male should optimize his partitioning of sperm across successive copulations with his long-term partner. In this last case, however, they rejected existing models in favor of their own “top-up” optimization model.

The 1993a paper was also notable because, for the first time, B&B cast doubts over an existing tenet of sperm competition theory. Most early predictions had assumed that the number of sperm inseminated is a trade-off between two opposing pressures: (1) risk that sperm may find themselves in competition with sperm from another male, favoring more sperm, and (2) the cost of sperm production, favoring fewer. However, for male mammals, B&B noted that this

trade-off ignores the apparent wastage from self-masturbation and spontaneous emission which runs counter to sperm cost being a critical factor.

The data presented in their 1993a paper showed that a recent (<72 h) masturbation did reduce the number of sperm inseminated at the next copulation but had no effect on the number retained (see section “**Female Orgasm (1993)**”) by the female. B&B concluded that male masturbation functions to increase mean sperm fitness by reducing sperm numbers. This in turn suggested that, in the absence of sperm competition, the probability of fertilization actually decreases if too many sperm are inseminated, a factor that B&B claimed could be more important than sperm cost in favoring male restraint over the number inseminated.

Female Orgasm (1993)

Three explanations for the female orgasm existed in the early 1990s: (1) it was functionless and, like nipples on males, existed only because its functional counterpart existed in the other sex; (2) it disinclined a woman to walk around after intercourse, thus reducing loss of the ejaculate; and (3) it sucked semen from the vagina into the uterus.

According to Baker (2015; p. ix), he and Mark Bellis had mused over the female orgasm from the beginning of their collaboration. Although believing it to be part of the sperm competition story, they were unable to see a role, the main problem being their suspicion that most female climaxes occurred outside of copulation.

The eventual “game changer,” Baker (2015; p. ix) writes, was a chance remark by a female collaborator who questioned why men should bother making fine adjustments to sperm number when so much of the ejaculate comes back out of the woman within the hour. She was immediately press-ganged into pioneering a collection technique for what B&B chose to call the “flowback,” thus beginning a whole new branch of study never attempted before.

In B&B’s eventual publication (Baker and Bellis 1993b), the flowback was transformed from a medically undesirable “sperm loss” into a very positive “sperm ejection.” In this ejection,

B&B saw a cryptic but powerful means for female influence on the outcome of sperm competition. They hypothesized that the female orgasm, both associated and not associated with copulation, was a central player in this influence.

B&B's studies of copulatory ejaculates (Baker and Bellis 1993a) were now sufficiently advanced to allow prediction of the number of sperm inseminated on any occasion. So, after counting the number of sperm in a flowback, B&B could estimate how many sperm had been retained by the female on that occasion. The female's orgasm history in the days, hours, and minutes preceding, during, and immediately after the copulation was provided, thus allowing the study of any link between retention and orgasm.

Both the occurrence/nonoccurrence and the timing (relative to copulation and moment of male ejaculation) of female orgasm influenced sperm retention. Orgasms at any time between 1 min before the male ejaculated up to 45 min after led to a higher level of sperm retention. Lack of climax or alternatively a climax during foreplay led to a lower level. So, too, for up to 8 days before the intercourse did "inter-copulatory" female orgasms (either spontaneous/nocturnal or masturbatory).

B&B concluded that the female orgasm generates a blow-suck mechanism that draws the contents of the upper vagina just a little way into the cervix, there to interface with the cervical mucus. These contents include sperm and seminal fluid if present, acidic vaginal fluids if not. Hence, inter-copulatory orgasms lower the pH of the cervical mucus and either slow down or kill any sperm that later attempt to penetrate. Inter-copulatory orgasms may also serve an antibiotic function.

With regard to sperm competition, B&B's main conclusion was that copulatory and inter-copulatory orgasms endow females with considerable flexibility in the manipulation of inseminates. In a single male "faithful" situation, a female's orgasm pattern is such that it reduces the number of sperm retained. During periods of infidelity, however, females change their orgasm pattern. These changes favor the sperm from the "lover" rather than the long-term partner and are cryptic to both male partners.

Final Joint Publication (1995)

After 1993, B&B never again published jointly in a peer-reviewed journal. Baker (2015) opines that because ethical committee dictates and health and safety restrictions (driven by the specter of AIDS) were by then beginning to bite, he and Mark Bellis may not have been allowed to continue in the cavalier way that suited them anyway. He adds, though, that in the end, this looming threat made no difference. Both researchers had already decided it was time to move on to new and different challenges. Before finally disbanding, however, they produced a book, *Human Sperm Competition*, published in 1995.

Primarily, B&B's book detailed their view that all aspects of human sexuality had been shaped in part or in whole by sperm competition. Further data were presented for all subject areas covered previously in their papers. In addition, however, they took the opportunity to address a few aspects of human sexuality for the first time. One of these, rape, was analyzed from the literature. Another, male and female homosexuality, they hypothesized, was adaptive. Data were presented from their *Company* survey which B&B claimed showed that bisexual women produced fewer children in their lifetime than heterosexuals but at an earlier age, thereby gaining a shorter generation interval.

Two further new hypotheses concerned male genitalia. One addressed the shape of the penis, in particular the fact that the erect human organ is straight and piston shaped with a smooth terminal protuberance (= glans). To B&B, this shape, the fit of the penis in the vagina, and the pumping/thrusting action during copulation all suggested a role in the removal of semen potentially inseminated previously by a different male. As the penis pulls back, sperm, seminal fluid, and cervical mucus are sucked down the vagina. On the next forward thrust, the glans pushes through this material and then on the next backward pull, the back edge of the glans scrapes the material further down the vagina. They summarized the process (Baker and Bellis 1995; p. 171) as "push-pull-suck-push-suck-push-pull-scrape."

The other new hypothesis addressed the testes, particularly size and variation. Testes size is

heritable. It is also extremely variable: in B&B's UK sample, the volume of the left testis ranged from 7–31 ml, a variability that they hypothesized reflected an evolved balanced polymorphism. On their hypothesis, men with larger testes are, in effect, sperm competition specialists, whereas men with smaller testes are mate-guarding specialists. Between the two extremes, individuals pursue a mixed strategy. In support of their hypothesis, they showed that men with larger testes (1) spend less time with their long-term female partner, (2) copulate more frequently, (3) ejaculate more frequently, and (4) are more likely to become involved in sperm competition.

The culmination of B&B's book was a detailed formulation of the Kamikaze Sperm Hypothesis along with a presentation of the first supporting evidence. Three categories of sperm were recognized: "egg-getters," to move through the female tract and fertilize any egg the female produces; "seek-and-destroy," to find, recognize, and destroy any sperm present from rival males; and "blockers," to settle and maybe agglutinate in numbers in any constricted passageway. The most likely of these constrictions, B&B suggested, were channels through the cervical mucus and the openings from the uterus into the oviduct. Speed, straightness of track, and other characteristics of the different sperm morphs were described, likely membership in one of the three categories assessed, and a range of supporting experimental evidence presented.

It was already known that fewer than 1% of sperm in mammalian, including human, ejaculates showed any "interest" in fertilizing an egg (Cohen and Massey 1984). B&B suggested, therefore, that egg-getters were a tiny (<1%) subset of the commonest morph (oval headed with single straight tail), a subset that appeared at a particular physiological age or stage. The heads of this most common morph vary in size along a continuum but, in B&B's studies, the mean size gradually increased as if growing with time after ejaculation. For descriptive convenience, B&B divided oval-headed sperm into three visual stages: micro, modal, and macro.

B&B's hypothesis, for which they offered supporting data, was that these micros, modals,

and macros represent different phases in development and behavior: while in micro form, the oval-headed sperm are in waiting; while in modal form, they behave as seek-and-destroy sperm; and while in macro form, some at least go in search of an egg. At any one time, therefore, there are around 1% of oval-headed egg-getters in the ejaculate, whereas the bulk of oval-headed sperm fulfil a seek-and-destroy role, this being the function that requires the greatest numbers.

Evidence for seek-and-destroy behavior was obtained through "mixing" experiments. On the assumption that such behavior would not be triggered until sperm had left the seminal fluid and were at least in the cervical mucus or even higher in the female tract, sperm were separated from the semen of two different men and mixed together in an appropriate medium. As a control, two subsamples of sperm from each man were also mixed self-with-self. The data collected included how many sperm die, how many form dyads (pairs of sperm joined at the head), and how many are swimming around without an acrosome (the "bomb on the head" that B&B suggested was the weapon sperm used to kill each other). More seek-and-destroy traces were predicted to be seen in "self-other" than "self-self" mixes. Over a long series of such experiments, B&B reported that the first signs of seek-and-destroy activity appear after 6 h, peak after 12 h, and are still evident, despite the sperm becoming generally less active, after 24 h.

With regard to blocker sperm, although B&B considered several of the less common morphs to be candidates, the one that attracted their attention most was the coiled-tail sperm. Once again, this was an "age" morph, essentially a slow old sperm (with normal tail) that when it settles in a channel of cervical mucus, it then coils its tail and, even if it dies, becomes obstructive enough to bar passage to any later sperm. B&B showed that self-self mixes of sperm formed frequent and sometimes large agglutinations of sperm. They also showed from their study of flowbacks that the more soon-to-be coiled-tail sperm that were inseminated at one copulation, the fewer sperm in total were retained by the female at her next copulation.

After publication of their book, B&B disbanded. Robin Baker left academia to become a full-time writer and to migrate with his family to southern Spain. Mark Bellis became a professor and director of the Centre for Public Health at John Moores University, Liverpool, UK, and was eventually awarded an OBE (Order of the British Empire) for “services to healthcare.”

Post-collaborative Publications

Although B&B never coauthored anything new after 1995, three further publications stemmed from the collaborative decade.

The book *Sperm Wars* (Baker 1996) was Robin Baker’s attempt to bring his and Mark Bellis’s work to a wider audience. As a collection of 37 short stories, the book shows people engaged in all aspects of sexual behavior. Each story is followed by an explanation of the role of sperm competition in the evolution of the behavior portrayed. Although primarily a popularization of the coauthored *Human Sperm Competition*, Baker did expand certain aspects. He also renamed seek-and-destroy sperm as “killer” sperm. The book has so far been translated into 25 different languages.

In 1997, Baker published a paper entitled *Copulation, masturbation, and infidelity: State-of-the-Art* based on his keynote lecture to the International Society for Human Ethology in Vienna in 1996. Baker used the opportunity to address criticisms B&B had received since the collaborative era and also presented three new analyses based on expanded B&B data. One showed that female strategy over contraceptive use, orgasm pattern, and infidelity changed over the transition from younger courtship to older reproductive phases of female lives. Another presented sperm counts from bisexual males alongside a data-based discussion of bisexuality as a reproductive strategy. A third, using the first ever ejaculates collected during acts of infidelity, showed that substantially fewer sperm were inseminated than sperm competition theory predicted. A new interpretation was offered.

Nearly 20 years after ending their original collaboration, B&B again worked together briefly to produce a digital version of their book *Human Sperm Competition* (Baker and Bellis 2014). In the preface to the new edition, they corrected a misunderstanding (see section “[Legacy: Growth of a Field, Support, and Opposition](#)”) that had arisen over egg-getter sperm.

Legacy: Growth of a Field, Support, and Opposition

The experimental methods developed by B&B were rooted in an era before health, safety, and ethical concerns were paramount. However, even by the time they disbanded, no other author had published an experimental paper on human sperm competition.

The delay meant that when other workers did at last begin to appraise B&B’s results and hypotheses, they had to confine themselves to less direct protocols. Early workers in the United States found ingenious ways to use and assess B&B’s work without actually collecting sperm, and later this approach was hugely and successfully expanded in many different ways by Todd Shackelford and the team he assembled at Oakland University, Michigan (Shackelford et al. 2016). Not until a decade after B&B’s departure were the first studies of whole ejaculates performed, and even these were restricted to collection during masturbation (ejaculates which B&B had shown could differ markedly from copulatory ejaculates: Baker (1997); Baker and Bellis (1989, 1993a)). The first studies involving copulatory ejaculates and flowbacks were delayed until 2016, though no results have yet been published.

B&B had pioneered several study areas within the broader field of human sperm competition. Levels of human sperm competition, male adjustment of ejaculates, function of the female orgasm, penis shape, variation in testes size, female behavior through the menstrual cycle, and sperm polymorphism have all since grown into subjects in their own right. As would be expected, some of B&B’s early hypotheses and results have been supported, and others have been questioned

(compare Birkhead 2000; Dixon 2009; Gallup and Burch 2004; Grammer et al. 2004; Kura and Nakashima 2000; Leivers and Simmons 2014; Pound et al. 2006; Shackelford et al. 2016; Thornhill 2006). Moreover, a few have been vigorously opposed.

The evolutionary approach to the female orgasm spearheaded by B&B was strongly attacked by Elisabeth Lloyd in her book, *The Case of the Female Orgasm: Bias in the Science of Evolution* (Lloyd 2005). After making clear her anti-evolutionary views, she then set about refuting B&B's work. Her attack was almost entirely statistical and concluded with the pronouncement that B&B's work on the female orgasm was "worthless."

B&B's hypothesis that men with large testes are "sperm competition specialists" has also aroused strong feelings. In his book *Promiscuity*, Tim Birkhead (2000; p. 25) describes the occasion that Baker first presented the hypothesis publicly. According to Birkhead, the lecture caused "sniggering incredulity" and "downright indignation" among some members of the academic audience. In his opinion, the work presented was "difficult to defend" and "naïve" and caused him to lose faith in Baker as a scientist. A few years later, Baker (1997) addressed the more constructive criticisms from that meeting and claimed that the hypothesis was still robust. At present, despite a "no evidence" paper by Simmons et al. (2004), all of B&B's testes size predictions have supporting evidence. The most recent such support comes from Mascaro et al. (2013) who demonstrate that men with larger testes show reduced parenting effort.

Of all B&B's hypotheses, the most contentious has been that of kamikaze sperm. Indeed, B&B have been attacked for this suggestion at a level far more personal than is usual in the academic literature. Tim Birkhead's "sexual fantasy" and "phallus in wonderland" comments are two examples, and Roger Short (1998; p. 22) provides another. He dismissed B&B's evidence that egg-getter sperm were an age category (macros) of oval-headed sperm by saying that they were no more likely to be egg-getters than they were "to contain little men." Such put-downs appear to

have been accepted by the field without question. Birkhead's assertion (Birkhead 1996; p. 29) that the kamikaze sperm hypothesis had been "repeatedly squashed" has led subsequent authors to accept, without any direct appraisal, that the hypothesis has been discredited.

The grounds for such categoric dismissals of the kamikaze sperm hypothesis are obscure. According to Baker and Bellis (2014), Short's "little men" comment was misplaced, a mistake based on his misinterpretation of their use of the descriptor "macro." No direct test of their egg-getter hypothesis has been attempted. Similarly, blocker sperm in humans have not yet been investigated. Although Moore et al. (1999) briefly mentioned that they may have found hints of such sperm, they chose to dismiss the possibility on the grounds that they were not searching for such evidence. Moore et al.'s paper also reports the only mixing experiments performed to date. Ostensibly the intention was to test for the presence of killer sperm, but the methodology rather suggests otherwise. B&B had shown that the first signs of killer activity appeared after sperm from two men had been mixed for 6 h and peaked after 12 h. Moore et al. stopped their experiments after only 3 h and, consistent with B&B's results, found no sign of killer activity up to this time. Why these researchers did not continue longer remains unexplained, and to date, no study has checked B&B's claims over what happens after 6–12 h. It is difficult, then, to see on what evidence B&B's kamikaze sperm hypothesis has been discredited even once, let alone repeatedly.

Exactly why B&B's work and ideas proved so divisive and generated such antagonism has never been made clear. Unless, that is, Tim Birkhead (2000; p. 29) intended the following as an explanation: "Baker's and Bellis's claims regarding human sperm competition were momentous and caught the public imagination almost to the same extent as Stephen Hawking's *A Brief History of Time*." Birkhead then asks "Why?" given that results from studies of sperm competition in other animals are "equally exciting, equally bizarre and far better substantiated, (yet) hardly ever make the press or television."

Conclusion

When Baker and Bellis first began their collaboration in 1985, the field of human sperm competition was no more than a daringly speculative paper by Robert Smith and a 20-year-old “impossible” fantasy for Robin Baker. Mark Bellis, though, could see how that fantasy could be developed into a scientific enterprise, and by the time B&B finished, they had created a whole field of study with many questions asked, a number provisionally answered, and a range of new experimental methods devised. Since then, through a mixture of support, questioning, and often caustic criticism, others have built on B&B’s foundations to turn human sperm competition into a major arena for biological, psychological, medical, physiological, anatomical, and most of all evolutionary study.

Cross-References

- [Human Sperm Competition](#)
- [Opposition to Human Sperm Competition](#)

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Role

► Social Roles

Role of Experience in Tool Use

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Synonyms

Insight; Learning; Spontaneous problem-solving

Definition

Cognitive mechanisms (e.g., previous experience, learning) that play a role in tool-use contexts.

Introduction

In one of Köhler's classical problem-solving experiments, chimpanzees were presented with an out-of-reach banana suspended from the ceiling (Köhler 1925). Importantly, the only available “tools” in the room to solve the problem were some boxes. Chimpanzees' first reaction was to try to directly reach the banana. After a few initial unsuccessful attempts, several chimpanzees *suddenly* started to stack the boxes and eventually obtained the reward. When explaining their performance, Köhler stressed the *insightful* nature of chimpanzees' responses and argued that his chimpanzees solved the problem by an *immediate* reasoning process that reorganized their previous individual experiences (e.g., moving boxes, box in relation to reward) into a mental representation that allowed them to find the solution (Köhler 1925). However, Köhler's explanations were criticized since little was known about chimpanzees' previous learning history with boxes.

In this regard, Epstein et al. (1984) study with pigeons helped to shed light on the role that learning plays in problem-solving situations. In their experiment, Epstein and colleagues used operant conditioning to train pigeons to perform two different behaviors: (1) to push a box toward a target location on the floor and (2) to stand on a box and peck at an out-of-reach target (i.e., a toy banana) that was hanging over the box. Next, pigeons were presented with a new situation, in which the box was placed some distance away from the target toy. After a brief “confusion” period (approximately 2 min long), the three pigeons started to push the box toward the toy banana to finally climb up and peck the target. Importantly, those pigeons who were trained to perform only one of the two actions – either to push the box or to stand on the box and peck the target – failed to find the solution to the problem. What is significant about Epstein et al.' study is that pigeons' behavior seemed superficially as insightful as chimpanzees' behavior in Köhler's experiments. In fact, since pigeons were trained to perform the two separate actions and never to execute the combined sequence of actions, Epstein

et al. (1984) suggested that performing the two actions was an instance of insightful behavior. On the other hand, it is also possible that the actual mechanism underlying pigeons' performance is a synthesis of the previously trained behaviors (Epstein et al. 1984). In fact from an associative-learning approach, pigeons' behavior can be explained as follows: when the first response – orientation toward the target – is extinguished, the most coherent response to appear next is the previously trained “pushing the box” behavior. Once the distance between the box and the target has been reduced, the second previously trained behavior – peck the target – is performed.

Previous Experience vs. Training

The question is how chimpanzees and pigeons are solving the problem. Are they using the same cognitive mechanism? While it is true that little was known about chimpanzees' previous experience with the boxes, an obvious difference between the two studies is that whereas pigeons were shaped to reach the successful response, chimpanzees were not. As such, Call (2013) argued that while chimpanzees were able to *spontaneously* chain the two actions in order to solve the problem, pigeons' behavior was missing the *spontaneity* component. In this regard, those pigeons who were trained only to perform one of the two actions are informative because they failed to *spontaneously* solve the problem. However, the lack of training does not equate to the lack of experience (Call 2013). In fact, Birch (1945) found that previous experience with the distinct elements of the problems was required in order for chimpanzees to solve the Köhler's (1925) box problem. Importantly, this experience was acquired spontaneously – young chimpanzees pile boxes on top of each other while playing – rather than from an operant training program. Thus, “acquiring and using this information is quite different from training the pigeon to move the box under the target” (Call 2013 pp. 9). Along the same lines, Emery (2013) claims that insight does not underlie pigeons' performance. Based on Thorpe's (1964) definition of

insight – “the sudden production of a new adaptive response not arrive at by trial behavior or as the solution of a problem by the sudden adaptive reorganization of experience” (pp. 110) – Emery (2013) argues that pigeons' responses were trained (and therefore, not sudden or spontaneous), were not new, and were not restructured from *similar* previous behavior – but from the *same* previous behavior.

Regardless of how one interprets Köhler's (1925) and Epstein et al.' (1984) findings, everyone would agree that both studies highlight the importance of understanding how animals solve problems – particularly, if we are to understand the evolution of tool use. In the recent years, birds (e.g., New Caledonian crows, ravens, keas) and nonhuman primates (e.g., capuchin monkeys, chimpanzees, orangutans) have been shown not only to avoid traps, pull strings, use tools to release a platform, or use tools in sequence to obtain food but also to manufacture tools or to save and transport them for future use (e.g., Povinelli 2000; Shettleworth 2010a). However, despite the increasing number of studies, the question that still remains under heated debate is which cognitive mechanism underlies animals' performance in these tool-use tasks. While some researchers have argued that undoubtedly “insight” or “reasoning” can explain animals' behavior (e.g., Emery 2013), others have argued that simpler mechanisms – learning and associations – can account for their performance (e.g., Shettleworth 2010b).

Cognitive Mechanisms Involved in Tool Use

Why does the role of experience and learning *still* remain such a controversial issue in the context of problem-solving and tool use? As mentioned above, insightful solutions have been described as those solutions that appear *suddenly*, *after initial unsuccessful attempts*, and also involve certain *reorganization* of previous behaviors (e.g., Köhler 1925; Thorpe 1964). Importantly, in the human literature, insightful solutions have also been associated with a phenomenological and

subjective experience of a sudden realization of the solution to the problem – so-called “aha” moments (e.g., Bowden et al. 2005). Assessing subjective experiences – such as “aha” moment, mental time travel, or causal understanding – is extremely difficult when the subjects undergoing such an experience lack verbal abilities to express and share them (e.g., Shettleworth 2010b, 2012). On this point, Call (2013; see also Shettleworth 2012) argues that comparative research has tended to identify psychological process with the phenomenological experience associated with them. As such, the debate has been polarized into the two conflicting views – those arguing that (associative) learning is behind problem-solving and those arguing that (causal) understanding is behind problem-solving (e.g., Shettleworth 2012). While this debate has contributed enormously to the increase in the number of empirical studies on problem-solving and tool use, research has reached a point in which new theoretical and empirical approaches might be needed if we are to move the field forward.

In this regard, Call (2013) proposes three mechanisms to identify a “creative” problem solver: (1) acquisition of information, for example, through a trial-and-error process (e.g., reinforcement program) or exploration (e.g., during play), (2) organization of the information (i.e., recombining and restructuring previously acquired information), and (3) object manipulation (i.e., predisposition to explore and manipulate objects). By stepping out of the “associative learning vs. reasoning” debate, Call (2013) suggests a framework based on animals’ abilities to acquire, store, and use information in problem-solving situations. His proposal allows assessing animals’ performance in terms of “how much information (or what type) they need to solve a task and how separate different pieces of information have to be to still be able to produce a viable solution” (pp. 16). Thus, if problem solving is seen as a creative process in which different psychological processes are involved (Call 2013), methodologies will focus, for example, on how manipulating previous experience with a particular problem will affect animals’ abilities to generalize to new problem-solving contexts –

as opposed to investigate how animals solve entirely new problems.

Conclusions

While approaches like Call’s (2013) approach could shed light on which cognitive mechanisms underlie animals’ problem-solving skills, the question of insight might still remain open. This is particularly true since neuroimaging research with humans has shown that insight is a distinct cognitive process that is associated with specific brain areas (e.g., anterior superior temporal gyrus) (Bowden et al. 2005). Thus, new experimental paradigms will still be needed if we are to fully understand the role of experience in problem solving, in general, and tool use, in particular. Although challenging, the future of the study of problem solving looks bright. There is no doubt that there is still plenty of room for more research on the cognitive processes involved in tool-use contexts and the role that experience might play in them.

Cross-References

- [Associative Learning](#)
- [Insight](#)
- [Nonhuman Tool Use](#)
- [Tool Use](#)

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Roles

► Social Roles

Romantic Attachment

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Synonyms

Adult attachment; Pair-bond attachment

Definition

Romantic attachment is a deep emotional, and often sexual, bond with another person. This idea of romantic love is believed to be the integration of the attachment system along with the caregiving system and the mating system (Hazan and Shaver 1987). Romantic attachment is comprised of two independent dimensions: avoidance of intimacy, or generalized beliefs that others are not

dependable and trustworthy, and anxiety about abandonment, or generalized beliefs about one's self, believing that one is valuable and worthy of affection. A romantic attachment characterized by low feelings of avoidance and anxiety is considered to be secure.

Introduction

When John Bowlby (1969/1982, 1988) originally proposed attachment theory, he conceived of attachment as extending over the entire lifespan and reasoned that our desire for attachment figures extends from “cradle to grave” (p. 62). In short, Bowlby argued that because of our vulnerability upon birth, humans have an attachment behavioral system or an evolved set of behaviors and reactions that ensure survival by keeping children close to their caregivers (Bowlby 1969/1982). Early work primarily focused on attachment in children and the bidirectional effects with caregiver interactions. In some of the earliest empirical work, Mary Ainsworth and her colleagues proposed three categories of attachment: secure, avoidant, or anxious/ambivalent (Ainsworth et al. 1978) – based on observed interactions between infants and caregivers in what has come to be known as the “Strange Situation” interaction. She and her colleagues found that when children were temporarily left with a stranger (i.e., researcher) in an unfamiliar room, they tended to respond in one of three distinct ways: (1) In the face of threat, some children feel secure, (2) others adopt an anxious/ambivalent hyperactivated strategy and demonstrate a strong desire to connect with and be reassured by their caregiver, and (3) others adopt an avoidant deactivated strategy, demonstrating a diminished desire to connect with or be reassured by their caregiver.

Cindy Hazan and Phillip Shaver (1987) were the first researchers to propose that the attachment system witnessed in the infant-caregiver relationship might be a reasonable explanation for adult romantic love. They proposed that using an attachment framework as a means to explain romantic love posed several advantages over then-existing models:

- (a) Given that love relationships may differ from couple to couple, a model of romantic love must be able to accommodate these and attachment allows for such differences.
- (b) Attachment theory explains how both healthy and unhealthy forms of love can develop as reasonable responses or adaptations to particular social circumstances.
- (c) Attachment theory explains the importance of separation and loss in infant-caregiver relationships and thus can explain why loneliness and love are related.
- (d) Attachment theory allows love to fit squarely within an evolutionary context.

In a series of two studies examining both community (Study 1) and student (Study 2) samples, Hazan and Shaver found evidence that the proportion of people endorsing each attachment style originally proposed by Ainsworth (secure, avoidant, and anxious/ambivalent) when considering their romantic relationships would match those found in infant-caregiver relationships (Hypothesis 1), the emotional experiences in one's romantic relationships (e.g., happiness, jealousy) differed based on one's attachment style (Hypothesis 2), people's working models for relationships correlated in predictable ways with their attachment styles (Hypothesis 3), and people's recollections of their parental relationships mirrored those of their current romantic attachment styles (Hypothesis 4). Study 2 also tested and found evidence that attachment styles were meaningful predictors of both state and trait loneliness (Hypothesis 5). Further, they concluded that their results provide evidence that romantic attachment and love, rather than being historical-cultural inventions, are biological and social processes with evolutionary roots.

Conceptualizing romantic love as an attachment relationship has become one of the major theoretical approaches in the study of romantic relationships (Fraley and Shaver 2000). The original Hazan and Shaver (1987) paper has been cited in PsycINFO 2940 times. In their review, Farley and Shaver (2000) propose that the idea of romantic love as an attachment relationship has become so popular because it provides a unifying

framework for understanding multiple aspects of relationship, including formation, maintenance, and dissolution, and does so by integrating findings from multiple fields such as psychology (including physiological, developmental, social, clinical), cognitive science, ethology, and even, psychodynamic thought.

Currently, romantic attachment theory proposes that based on experiences with a primary caregiver, people develop *internal working models of attachment* that they use in their romantic relationships (Bretherton and Munholland 1999). Adults whose caregivers were consistent and reliable in their support provision go on to form secure romantic attachments, characterized by low avoidance and low anxiety. They have positive views of themselves, believing that they are worthy of love, and have positive views of others, believing that close others can be relied up for effective support and help should they need it. This allows for a great deal of flexibility and openness to dealing with relationship stresses and threats. Adults whose caregivers were more inconsistent develop insecure romantic attachments. Those who have negative views of themselves as worthy of affection but see others as a possible source of care and comfort adopt *hyper-activating strategies*, clinging to and trying to control their romantic partners in an attempt to ensure support when needed. This is consistent with a more anxious romantic attachment. By contrast, those who have positive views of themselves, seeing themselves and valuable and worthy of affection, but have negative view of others as being able and willing to provide comfort and support, adopt *deactivating strategies*. These strategies involve denying one's attachment needs and prioritizing independence in an attempt to ensure that one is self-reliant and will not need support. This is consistent with a more avoidant romantic attachment.

How Romantic Attachment Differs and Develops from Infant-Caregiver Attachment

Although derived from the infant-caregiver attachment system developed in early life, there are important distinctions between romantic attachment and this earlier attachment system.

Primarily, the difference lies in the symmetrical, or mutual, nature of adult romantic relationships, meaning that both romantic partners seek each other out and provide support to one another. This is different than the asymmetrical nature of the earlier attachment with a caregiver, with support provision being provided solely by the caregiver. In addition, romantic relationships frequently serve a sexual, or mating, function which is absent in the infant-caregiver relationship.

According to Bowlby's original conceptualization (1988), attachment relationships are characterized by four distinct features. First, individuals want to be physically close to their attachment figure and are motivated to maintain this closeness (*proximity maintenance*). Second, when individuals are upset or face uncertainty or stress, they turn to their attachment figure for consolation and reassurance (*safe haven*). Third, individuals protest separation from their attachment figure and show distress during prolonged and/or unanticipated absences (*separation distress*). Finally, individuals use their attachment figure as a foundation, or base, from which they explore their environments and engage in new activities (*secure base*). (Conceptualizations of proximity maintenance frequently include the separation distress component, and therefore, some works discuss three components of attachment.) Attachment theory proposes that in adulthood, one redirects the attachment initially experienced with one's caregiver to a romantic partner and in turn, it is the romantic partner who becomes the primary attachment figure. Although peers or other close others (e.g., siblings) may fulfill some of these attachment functions, it is unlikely that they will possess all of the necessary characteristics, making romantic pair bonds actual attachment figures (Hazan and Diamond 2000).

Hazan and Zeifman (1994) discovered that these components are transferred to one's romantic partner in a specified order – one's proximity maintenance, followed by safe haven, and ending with secure base. Further, they found that 80% of their sample relied on their romantic partner for all three of these attachment functions by two years into their romantic relationship. Subsequent work by Farley and Davis (1997) and Fagundes and

Schindler (2012) has confirmed this two-year time span for romantic partners to be seen as full attachment figures. Fagundes and Schindler (2012) also found that at time of formal commitment to a relationship, people perceived their romantic partners as the primary attachment target for proximity seeking and secondary attachment targets for safe haven, suggesting that attachment formation had its origination during more casual dating phases of a relationship. Seeing one's partner as a secure base did not increase during casual dating and was the last attachment function to be transferred to the romantic partner. Of note, these authors also point out that although individual differences in the speed of attachment transfer did emerge from people of different attachment orientations (e.g., anxious romantic attachment was associated with seeking proximity from a romantic partner earlier in the relationship), attachment transference to romantic partners does follow a normative pattern of proximity seeking, safe haven, and secure base.

If romantic attachment stems from infant-caregiver attachment, then there should be some correlation between the two attachment experiences. The original work done by Hazan and Shaver (1987) made connections between the current romantic attachments people reported and their concurrent recollections of parent attachments. Subsequent research has adopted longitudinal methods to better assess this potential connection. Roisman et al. (2005) found a 61% correspondence between participant's current romantic attachment (assessed at age 20–21 with a semi-structured interview) and infant-caregiver attachment assessed at 12 months and 18 months of age with the Strange Situation. Pascuzzo et al. (2013) found a link between parental insecure attachment (assessed in adolescence with a self-report measure) and anxious romantic attachment (assessed 8 years later with a self-report measure) but did not find a link with avoidant romantic attachment.

Romantic Attachment as Evolved Mechanism

In the original conceptualization of romantic love as romantic attachment, Hazan and Shaver (1987) noted a benefit of their conceptualization as being

grounded in evolutionary theory. The similarities between romantic attachment in adulthood and infant-caregiver attachment (proximity seeking, safe haven, secure base) are regarded as “behavioral homologues,” meaning that they foster the same goals and are affected by the same types of conditions (Fraley and Shaver 2000). In considering the integration of the attachment, caregiving, and mating systems, Shaver et al. (1988) suggested that pair-bonding, or romantic attachment, may have evolved to enhance offspring survival. This idea was further discussed by Fraley and Shaver (2000), whose review of the literature suggested that romantic attachment/pair-bonding is beneficial as it prevents issues related to paternal certainty for men by keeping partners close together and it provides additional protection for vulnerable offspring, increasing the likelihood that they reach maturity. However, their review also pointed out that this account may be insufficient as pair-bonding is relatively rare in other species, which seems unlikely if it is uniformly advantageous. Further, pair-bonding does not automatically guarantee increased investment in one’s offspring.

Several studies have examined the evolved nature of pair-bonding specifically. Research by Fraley et al. (2005) examined archival data of a variety of animals (Study 1) and primates exclusively (Study 2) and concluded that pair-bonding and parental care appear to have co-evolved and are homologous/functional (rather than simply analogous). Further, parental care appears to emerge first, followed by pair bonding. By way of example, they mention a study’s finding that oxytocin is released both when people mate and when they take care of their offspring. This suggests that the same biological outcomes are occurring in both behaviors, thereby facilitating romantic attachment. The issue of romantic attachment being an adaptation to address the unique human challenge of concealed ovulation has also been discussed. Eastwick and Finkel (2011) note in their literature review that infant-caregiver bond evolved approximately 35 million years ago, but the romantic attachment bond probably evolved much more recently, at roughly the time of the appearance of the genus *Homo*,

approximately 1.5–2 million years ago. Their research further found that naturally cycling women (i.e., those not taking hormonal contraceptives) who reported a strong romantic attachment bond to their current partner and were at increased likelihood of conception reported stronger sexual motives than women who did not report such romantic attachment. They concluded that “attachment processes appear to capitalize on the ovulatory motivation to desire sex with particular men and re-channel that motivation in a manner that potentially strengthens the attachment bond” (p. 180).

Measurement of Romantic Attachment

Alongside the theoretical development of adult attachment theory, there has also been considerable development in how attachment is measured. In the seminal article by Hazan and Shaver in 1987, the approach was to use the three attachment types/styles originally identified by Ainsworth’s work on infant-mother attachment (see Ainsworth et al. 1978) to categorize adults in terms of their attachment to romantic partners in general. In this original approach, Hazan and Shaver (1987) provided three type-descriptions in the realm of romantic relationships that were analogous to the three infant categories: secure, avoidant, and anxious/ambivalent. For instance, secure attachment was described as, “I find it relatively easy to get close to others and am comfortable depending on them and having them depend on me. I don’t often worry about being abandoned or about someone getting too close to me.”

Since this initial approach to measuring attachment, researchers have developed more sophisticated tools. One of the early major developments in measurement was introduced by Bartholomew and Horowitz (1991) with a scale called the Relationships Questionnaire (RQ). The RQ, and the associated theoretical model, were defined by two changes. First, the RQ introduced a conceptualization of adult attachment that argued for a fourth style that reflected a second kind of avoidance known as dismissing-avoidance. Second, the RQ shifted toward a continuous measurement of attachment that reflects the consensus that

individuals are not necessarily in one category or another, but rather fall somewhere along a continuum. At the center of this model were two dimensions: Anxious Attachment and Avoidant Attachment.

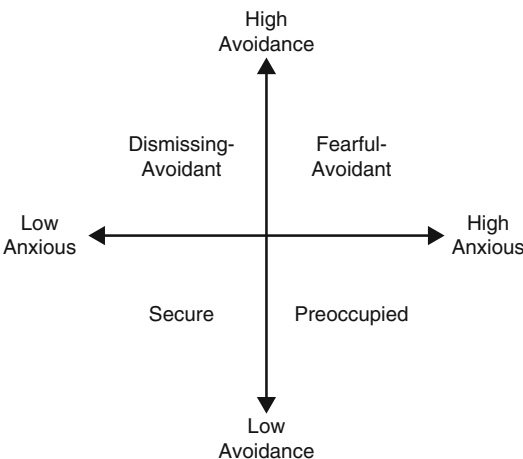
By measuring people along these two continuums, researchers are able to conceptualize the four attachment styles as essentially different levels of anxious and avoidant attachment (see Fig. 1). In this approach to measurement, secure attachment is denoted by being relatively low on both dimensions of anxious and avoidant attachment, indicating relatively few insecurities. Relatively high scores on both anxious and avoidant attachment dimensions denote fearful-avoidant attachment. A relatively high score on the anxious dimension and low score on the avoidant dimension reflect preoccupied attachment. Finally, dismissing-avoidant attachment reflects being relatively high on the avoidant attachment dimension and low on the anxious attachment dimension. This two-dimension approach to measuring attachment – anxious and avoidant – continues to be used by modern scales.

A few years later, Brennan et al. (1998) put forth a new 36-item scale called the Experiences in Close Relationships (ECR) scale. To do so, they conducted a large-sample factor analysis that included all self-report measures of attachment at the time. This factor analysis revealed 12 specific-

construct factors that formed higher-order factors that reflected anxiety and avoidance. This scale was later revised into the ECR-Revised (ECR-R; Fraley et al. 2000), which is composed of 36 items, including two 18-item subscales that measure anxious attachment and avoidant attachment. To date, the ECR-R is the recommend scale for self-reports of general adult attachment.

As theoretical perspectives on attachment continued to develop, researchers have attempted to update and modernize the ECR-R. One trend among researchers is to develop shorter scales. Because participants have limited attention spans and researchers have limited resources, there is a constant push to develop faster and less burdensome measures. This has led to several shorter versions of the ECR, which include a 12-item version referred to so the ECR-Short Form (Wei et al. 2007) and a 9-item version known as the ECR-Relationship Structures scale (ECR-RS; Fraley et al. 2011). In general, both of these scales can be used as abbreviated versions of the ECR-R and retain the same factor structure, including both anxious and avoidant dimensions.

Another important recent development teasing apart differences between global working models of relationships and working models of specific attachment figures. Specifically, these scales allow researchers to identify a specific target for the questions, such as a current romantic partner, best friend, or a family member. This approach is exemplified by ECR-Relationship Structures scale (ECR-RS; Fraley et al. 2011). As noted above, the first measure developed by Hazan and Shaver (1987) focused on how people generally feel about relying on close others. This was also the approach used in developing the RQ, ECR, and the ECR-R. In general, these approaches have the strength of applying to people regardless of who their current attachment figures are. However, this may also serve as a weakness in some research contexts. Using the traditional scales is potentially problematic, as most self-report measures are designed to assess romantic attachment and thus contain items that do not translate to nonromantic partners (e.g., “When my partner is out of sight, I worry that he or she might become interested in someone else”). For instance,



Romantic Attachment, Fig. 1 Two-dimension model of attachment

La Guardia et al. (2000) were interested in within-person variability in attachments across relations (romantic partners, friends, and family members) as a function of various relationship qualities. This type of research question is dependent upon the ability to conceptualize and measure attachment as a relationship-specific variable.

Finally, there is considerable interest among modern adult attachment researchers in assessing attachment as a state, rather than a trait variable. That is, rather than conceptualizing attachment as “locked in” and stable over time or across relationships, that it is sensitive to situational and contextual factors. From this perspective, although attachment may generally exhibit stability over time, it is also a function of continued experiences. For instance, recent work has shown that there is considerable variability in attachment over time within relationships, which has subsequent implications for relationship functioning (Girme et al. 2018). Further, recent theoretical advances in attachment theory propose short-term and long-term mechanisms for how individuals’ attachment changes over time in adulthood (Arriaga et al. 2018). Although a full description of these works is beyond the scope of this entry, as our understanding of how attachment fluctuates across time, situations, and relationships continues to advance, there will be a need for increasingly sophisticated tools for measurement.

Linking Romantic Attachment and Relationship Outcomes

Variations in romantic attachment have long been thought to predict relationship outcomes. Specifically, secure romantic attachments are thought to be more beneficial for relationships compared to insecure romantic attachments. In their original study, Hazan and Shaver (1987) found that secure romantic attachments were generally associated with more positive and less negative relationship outcomes. (The specific pattern of results depended on whether the sample was drawn from a community or undergraduate population.)

Two meta-analyses have since been conducted to examine the subsequent research that has since been produced. Li and Chan (2012) examined the two dimensions of attachment (avoidance of

intimacy and anxiety over abandonment) and their prediction of several indices of relationship quality (including positive and negative cognitive, emotional, and behavioral outcomes) in 73 studies, including 118 separate samples and 21,602 participants. Most measures of relationship quality (with the notable exception of negative cognitive indicators) were weakly to moderately associated with avoidant and anxious romantic attachment; these insecure attachments were linked to increased negative relationship quality indices and decreased positive relationship quality indices. In addition, avoidant romantic attachments were more negatively associated with the positive relationship qualities when compared to anxious romantic attachments.

Hadden et al. (2014) examined the same two dimensions of attachment but focused exclusively on relationship satisfaction as the indicator of relationship quality and relationship commitment as the indicator of relationship strength/stability. Their meta-analysis included 57 independent effect sizes including a total of 14,340 participants. Both anxious romantic attachment and avoidant romantic attachment were negative predictors of relationship satisfaction, with the avoidant-satisfaction association being stronger than the anxious-satisfaction association. The same pattern of results was found for relationship commitment. The authors also examined whether the above relationships were moderated by relationship duration. The link between relationship satisfaction and both anxious romantic attachment and avoidant romantic attachment became more negative as relationships progressed. In other words, insecure romantic attachment’s correlation with relationship satisfaction was more negative for people whose relationships were of a longer duration when compared to people who were in shorter relationships. Due to an insufficient number of studies, the analyses examining insecure attachment and commitment were underpowered, but results suggested a similar pattern of results. Although not statistically significant, the correlation between avoidant romantic attachment and anxious romantic attachment and relationship commitment became more negative as relationship duration increased.

Individual Differences in Romantic Attachment

Researchers have been curious whether there are individual differences in people's experiences of romantic attachment.

Age Differences

An interesting line of research has considered whether romantic attachment changes over the lifespan. In their literature review, Chopik and Edelstein (2014) propose that in response to changing reproductive strategies and adoption of new roles and then later lack of such changes, anxious and avoidant romantic attachments are likely to be more or less stable as people age. In a sample of 90,904 adults aged 18–64 from 11 world regions, they found that anxious romantic attachments were highest among young adults and were lower in middle-aged and older adults, whereas avoidant romantic attachment showed the opposite pattern, with younger adults having the lowest levels and middle-aged and older adults having higher levels. However, the trajectory of age-related changes was flatter (i.e., smaller) for avoidance when compared to anxiety. The authors also note that the size of the changes across the lifespan are relatively small, supporting the contention that one's romantic attachment is relatively stable in adulthood.

Sex Differences

In the original work on romantic attachment, Hazan and Shaver (1987) did not propose theoretical reasons for or predict sex differences in people's romantic attachments. In his meta-analysis of sex differences in romantic attachment, Del Giudice (2011) discusses this "tacit consensus in the field that sex differences do not exist, or at least can be safely ignored" (p. 193) but also reviews work that proposes that romantic attachment may also reflect different mating strategies, which are reliably associated with sex differences (e.g., males report being more comfortable with short-term mating arrangements than females do). Further, he makes the argument that attachment mechanisms are but one behavioral manifestation of a larger factor, life history

strategies. In his analysis of 112 independent samples from 100 published and unpublished studies resulting in data from 65,047 participants, females reported higher anxious romantic attachments than males and males reported higher avoidant romantic attachments than females, but the overall effect sizes were very small ($-.04$ and $.02$ respectively). However, significant variability existed between sample types, with substantially larger sex differences emerging in community samples compared to student and web-based samples. Closer analysis of the distribution of scores using relative density plots found that sex differences were more substantial at the upper and lower levels of avoidant romantic attachment and at the extremes of anxious romantic attachment.

Both meta-analyses discussed earlier examined whether the links between romantic attachment and relationship outcomes were moderated by gender. Li and Chan (2012) found that gender was a weak moderator of the associations between romantic attachment and positive and negative relationship qualities. Hadden et al. (2014) found that gender did significantly moderate the negative relationship between satisfaction and avoidant romantic attachment (with the relationship between the variables being more negative for women) but did not moderate the satisfaction-anxious romantic attachment relationship. Gender did not significantly moderate the avoidant romantic attachment-commitment relationship and was only a marginally significant moderator of the anxious romantic attachment-commitment relationship.

In sum, it seems that Del Giudice (2011) may have been correct in concluding that "a strictly sex-neutral view of romantic attachment does not seem tenable any longer" (p. 204) and it seems prudent that future research should pay closer attention to the size and nature of sex differences.

Cultural Differences

Despite its grounding in evolutionary theory and the universality that can imply, there may be cultural differences in romantic attachment given that fact that there is little argument that cultural

differences in both parenting practices and romantic relationship dynamics exist (Schmitt 2010). It appears that the internal working models of attachment are similar across cultures, but they degree to which they are endorsed does differ. In his review of data from the International Sexuality Description Project (ISDP-2) which assessed people from 58 countries in 11 world regions, Schmitt found substantial differences in the proportion of people in each region who endorsed a secure romantic attachment. Although secure romantic attachment (low feelings of attachment anxiety and avoidance) is associated with better relationship outcomes, only one world region of the 11 assessed (Northern Europe) had over 50% of its population reporting this type of romantic attachment. Six of the 11 world regions reported less than 40% of its population endorsing a secure romantic attachment. In addition, substantial variations exist between world regions in the discrepancy between internal working models of the self and internal working models of the other. Further, cultural factors such as individualism/collectivism and ecological stress significantly predicted differential patterns of romantic attachment.

In the meta-analysis of sex differences discussed above (Del Giudice 2011), significant variability in sex differences was also seen when samples were separated into geographic region, with the largest differences emerging in Europe and the Middle East and the smallest differences seen in North America. Of note, there was cultural similarity in the direction of effects, such that males scored higher in avoidant romantic attachment and females scored higher in anxious romantic attachment (with the exception of East Asia where no significant sex differences in anxious attachment emerged). In their study of 11 world regions, Chopik and Edelstein (2014) did not find evidence of collectivism-individualism moderating the relationship between age and romantic attachment.

Sexual Orientation

Although research has suggested that there are more similarities between same-sex and

heterosexual couples than differences, the question of whether romantic attachment is related to sexual orientation was addressed by Ridge and Feeney (1998). The results of their study concluded that gay and lesbian participants reported similar patterns of romantic attachment when compared to a control sample of heterosexual participants. Consistent with studies focusing on heterosexual couples, Mohr et al. (2013) found that their partnered gay and lesbian participants who reported more avoidant and anxious romantic attachments also reported relationship experiences that were less positive (e.g., less satisfaction, less trust). The link between romantic attachment and relationship outcomes was in the same direction for both gay and lesbian participants although some relationships were stronger for gay men than lesbian women, suggesting some gender moderation.

Conclusion

The concept of romantic attachment has provided one of the most generative frameworks over the past 30 years for understanding adult romantic relationships and pair-bonding. Originally proposed by Bowlby as a way to understand processes underlying caregiving, researchers have expanded this work to develop a deeper understanding of adult romantic relationships. Some of the most important principles surround the development of enduring insecurities regarding working models of romantic partners, and how those insecurities affect our approaches to handling stressful situations, to seek and provide support, and ultimately our ability to maintain our romantic bonds. Ultimately, this field of work provides one of the most valuable theoretical frameworks for understanding social relationships across the life span.

Cross-References

- [Attachment in Adulthood](#)
- [Attachment Theory](#)
- [Individual Variations in Attachment](#)

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Romantic Attachment and the Prototype Hypothesis

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Synonyms

Developmental correspondence between childhood and romantic attachment

Definition

In the normative course of development, individuals gradually transfer attachment functions

from the child-caregiver relationship to peer relationships, principally to romantic relationships. According to the prototype hypothesis, early attachment experiences influence the development and quality of subsequent close relationships. Drawing on this hypothesis, it has commonly been thought that individual variations in romantic attachment partly reflect individual variations in early caregiving experiences.

Introduction

Romantic attachment denotes an individual's stance regarding attachment-related aspects of romantic relationships, as manifest, for example, in the ways in which one uses the partner, and allows the partner to use oneself, as a safe haven for regulating distress, and as a base of security when exploring. Individual variations in romantic attachment have been found to exert significant influence over important aspects of relationship functioning, including relationship intimacy, communicative strategies, and emotion regulation (see ► [“Attachment in Adulthood”](#)).

In trying to explain these variations, researchers have commonly drawn on what has been termed “the prototype hypothesis” (Bowlby 1973). According to this hypothesis, early attachment experiences influence the development and quality of subsequent relationships over the life span. Thus, variations in romantic attachment have been thought to be rooted in individual differences in early caregiving (e.g., Hazan and Shaver 1987). This entry begins with a brief description of important similarities and differences between childhood and romantic attachment, followed by the theoretical rationale for assuming a correspondence between the quality of the early child-caregiver relationship and subsequent romantic attachment style. Finally, the entry reviews existing evidence for the prototype hypothesis with regard to romantic relationships.

Childhood and Romantic Attachment: Similarities and Differences

Attachment in childhood denotes the affectional bond that children form to their caregiver(s), seeking to maintain proximity to and protesting separations from their caregiver(s), using the caregiver(s) as a secure base to explore the environment from and a safe haven to return to for comfort and protection (see ► [“Offspring–Parent Attachment”](#)). In the course of development, these attachment functions are typically transferred to the relationships of adult life, principally to romantic relationships. This is thought to occur via a gradual process, starting in middle childhood and ending in late adolescence or early adulthood. A large body of evidence supports the notion of long-term romantic bonds as the normative instantiation of attachment in adulthood. For instance, child-caregiver and romantic relationships display unique similarities regarding the sequence of relationship formation, verbal and nonverbal communication, reactions to separation and loss, and the use of the caregiver/partner as a safe haven for emotion regulation. Moreover, the respective relationships have a similar and uniquely powerful impact on physical and psychological well-being, and are underpinned by a number of uniquely shared neural and endocrine features (for a more detailed account, see ► [“Attachment in Adulthood”](#)).

Importantly, although the individual functions of attachment bonds largely remain unaltered in the process from childhood to adulthood, a number of important changes are, however, also thought to occur. First, the increased cognitive and emotional maturity of adulthood leads to important differences between child and adult attachment dynamics, not least regarding the capacity to tolerate separations. Second, in romantic relationships, the attachment system is thought to become integrated with the sexual mating and caregiving systems. As a result, sexual attraction is usually the precipitating force that brings adult partners into close contact, rather than need for comfort and protection. Third, the asymmetrical nature of child attachment relationships becomes substituted for more symmetrical

relationships, with adult partners mutually seeking and providing security (Mikulincer and Shaver 2016).

Theoretical Background of the Prototype Hypothesis

The prototype hypothesis is based on Bowlby’s (1973) notion that early experiences with primary caregivers gradually become internalized, forming internal working models of self and others (IWMs; cognitive-affective representations; see ► [“Effects of Attachment Quality and Organization”](#)). The IWMs are thought to display a relatively high degree of continuity under stable environmental conditions, and to become generalized to other close relationships later in life, where they (mainly unconsciously) guide the individual’s expectations on and behavior towards others in attachment-relevant situations. Thus, it makes theoretical sense to hypothesize that early attachment experiences affect how the developing individual relates to subsequent romantic partners.

It should, however, be noted that the prototype hypothesis entails no full correspondence between childhood and romantic attachment. Bowlby carefully stated that the main function of IWMs is to foster adaptive behavior in the individual’s actual environment. Hence, changes in the environment, for example, in the form of new interpersonal experiences, might require the IWMs to be updated. Moreover, most scholars today regard IWMs to be organized hierarchically, with generalized models of self and others at the top, models for classes of relationships (e.g., caregivers, romantic partners) at an intermediate level, and models for specific relationships (e.g., mother, present partner) at the bottom (see ► [“Attachment in Adulthood”](#)). While the generalized models are thought to inform perceptions of self and others on the lower levels in a top-down manner, new relationship experiences with a specific partner could also, in a bottom-up manner, affect the models for the class of romantic partners, without altering the models for caregivers. However, since the generalized models

derived from relationships with caregivers are thought to found the basis for subsequent models on other levels, some degree of correspondence is still expected.

Empirical Evidence for the Prototype Hypothesis with Regard to Romantic Attachment

Romantic Attachment and Retrospective Measures of Childhood Attachment

Early investigations of the prototype hypothesis mainly relied on adults' self-reported memories of attachment-related experiences in childhood. A number of these studies supported the hypothesis. For instance, Hazan and Shaver (1987) found secure romantic attachment to be associated with memories of warmer and more caring relationships with parents. Avoidant individuals were more likely to remember their mothers as cold and rejecting, while anxious individuals tended to remember their fathers as unfair. The results are, however, weakened by notable methodological limitations, not least the obvious risk for reconstructive memory biases inherent in retrospective self-reports.

A number of studies have also examined the prototype hypothesis, by relating self-reported romantic attachment to concurrent classifications on the Adult Attachment Interview (AAI; see ► [“Attachment in Adulthood”](#)). The AAI is an in-depth interview measure, shown to possess psychometrical robustness with regard to parent-related working models in adults. If parent-related IWMs serve as prototypes for subsequent romantic relationship IWMs, the working models captured by the AAI should be associated with measures of romantic attachment (given that the measures employed in romantic attachment research are valid with regard to romantic IWMs). Studies based on this line of reasoning have, however, shown inconsistent results, typically demonstrating weak and at best moderate associations (e.g., Shaver et al. 2000).

There is, however, reason to believe that this inconsistency is partly a result of measurement issues. For instance, the self-reports

predominantly used when assessing romantic attachment likely capture limited, conscious parts of an individual's IWMs. In reality, IWMs are to a large extent unconscious, due, for example, to defensive exclusion of painful information from awareness (see ► [“Psychodynamic Foundations”](#)). This might cause trouble for researchers employing self-reports – especially when studying insecure forms of attachment, because insecurity is characterized by incoherent IWMs, as manifest, for instance, in conscious self-perceptions that are incompatible with the individual's actual (unconsciously motivated) organization of behavior in attachment-relevant situations. Supporting this line of thought, a tendency has been found in individuals classified as dismissing/avoidant on the AAI to report themselves as secure on self-report measures (DeHaas et al. 1994).

Romantic Attachment and Prospective Studies of Attachment Beginning in Early Childhood

Due to the children from some extensive studies of the 1970s to the 1990s now having reached adult age, it has become increasingly possible for researchers to examine the prototype hypothesis prospectively. In one such study, secure infant attachment was prospectively associated with secure romantic attachment representations in young adults, as measured by an in-depth interview measure. Secure infant attachment was also associated with higher observed relationship quality and more positive self-reported perceptions of the partner (Roisman et al. 2005).

Associations between early attachment and young adults' self-reported romantic attachment have also been reported. For instance, high quality maternal caregiving at 18 months has been associated with lower self-rated avoidance and anxiety in young adults' romantic relationships (Zayas et al. 2011). Partly in line with these findings, higher maternal nurturance, as measured by emotional openness, responsiveness, and control, has also been linked to lower levels of self-reported romantic avoidance – but not anxiety – in young adults (Chopik et al. 2014). Genetically based differences regarding the

susceptibility to environmental influence on subsequent romantic attachment have also been suggested. In a study following over 1000 participants, higher maternal sensitivity in childhood was linked to lower self-reported avoidance in adult relationships, but only among carriers of a certain variant of a serotonin receptor gene (Salo et al. 2011).

In the most ambitious longitudinal study to date, Fraley and colleagues (2013) investigated a large number of potential antecedents to self-reported global (i.e., across all relationships) and romantic adult attachment. This study found no substantial correlation between childhood attachment classifications and subsequent romantic attachment. However, lower maternal sensitivity, maternal depression, and father absence in childhood were predictive of higher global avoidance in late adolescence. Individuals reporting avoidance in romantic relationships were also more likely to have experienced decreases in maternal sensitivity over time. Few caregiving-related antecedents were found with regard to attachment anxiety, except that anxious individuals were more likely to have experienced increases in maternal depression during childhood. In examining potential genetic contributions to romantic attachment, this study largely failed to replicate the findings obtained by Salo and colleagues (2011). Interestingly though, the findings by Fraley and colleagues (2013) emphasized the importance of extra-familial relationships for romantic attachment, with social competence and the quality of close friendships over time being more robustly linked to subsequent global and romantic avoidance, than changes in family of origin variables.

In sum, the reported associations have not been strong and consistent enough to offer a reliable set of predictors for romantic attachment. Conclusions are also hampered by methodological limitations, not least the inconsistency with regard to the measurements used for assessing aspects of caregiving in childhood. Future research will be important to illuminate some of the present unclarity. It has, however, been

pointed out that, due to the enormous number of factors involved in shaping an individual's interpersonal development, weak associations should perhaps be expected (e.g., Fraley et al. 2013). In line with the mentioned association between romantic attachment and extrafamilial relationships, romantic attachment styles have been shown to be influenced by a number of factors beyond early caregiving experiences, including more recent and ongoing relationship experiences, and major life events such as the transition to parenthood (see Mikulincer and Shaver 2016). The explanatory power of any specific factor relative to the others will therefore likely be diminished. Thus, even if early experiences are important for maintaining a lifespan perspective on attachment and subsequent interpersonal functioning, they might not be essential for answering proximal questions about romantic attachment.

Conclusion

Partly supporting the prototype hypothesis, individual variations in romantic attachment are associated with attachment-related experiences in childhood. However, associations are neither strong nor consistent enough to offer a reliable set of predictors for romantic attachment. Findings also indicate that a number of factors beyond early caregiving are involved in shaping romantic attachment styles. This complexity underscores the importance of including a broad set of developmentally relevant factors, in future research attempting to shed further light on the etiology of romantic attachment.

Cross-References

- ▶ [Attachment in Adulthood](#)
- ▶ [Effects of Attachment Quality and Organization](#)
- ▶ [Individual Variations in Attachment](#)
- ▶ [Offspring–Parent Attachment](#)
- ▶ [Psychodynamic Foundations](#)

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Romantic Desirability

- ▶ [Self-Esteem Tracks Mate Value](#)
- ▶ [Self-Evaluations Track Perceived Mate Value](#)
- ▶ [Sex-Specific Link Between Self-Esteem and Mate Value](#)

Romantic Identity

- ▶ [Sexual Identity](#)

Romantic Kissing

- ▶ [Kissing](#)

Romantic Love

- ▶ [Mate Retention and Romantic Attachment](#)

Romantic Rejection

- ▶ [Circumventing Mate Choice](#)

Ronald Aylmer Fisher

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Sir Ronald A. Fisher was born on February 17, 1890, in East Finchley, England, and died on July 28, 1962, in Adelaide, Australia (Yates and Mather 1963). It was a life full of high accomplishments. Fisher built an enduring foundation for the advancement of multiple scientific fields. In evolutionary biology, Fisher is one of the three architects of the Modern Synthesis – theoretical work which elicited the genetic mechanisms and consequences of natural selection. Fisher (1999), Sewall Wright (1981), and J. B. S. Haldane (1993) each made unique insights on the genetic processes that lead to the evolution of phenotypes. Fisher (1999) introduced the concepts of life history, reproductive value, and runaway selection –

all of which have been central to theoretical advancements in fields such as evolutionary developmental biology, animal signaling, behavioral ecology, and evolutionary psychology. Fisher and Wright founded the field of population genetics. Their independent contributions to understanding genetic drift have been synthesized into the Wright-Fisher model of genetic drift (Crow 2002). Fisher is more famous for his work in statistics. Volumes of published scientific research have relied upon Fisher's methods of estimation and tests of statistical significance. Fisher's life and his enormously invaluable contributions to science have been thoroughly documented (Box 1978; Crow 1990; Edwards 2014; Moore 2007; Skipper 2007; Yates and Mather 1963). However, his sociological analyses have received scant attention. Yet, his ideas could serve well as a foundation for the development of evolutionary social sciences.

Fisher's "Sociological Views"

From one perspective, Fisher's interest in what he called "man's sociological development" was bound to occur (Fisher 1999, p. 184). Throughout most of his life, Great Britain was at the height of its power and global domination. In its rise to dominance, British forces effectively ended the Dutch, Portuguese, French, and Spanish empires. British archaeologists and historians continued to compile a vast wealth of knowledge about the rise and fall of ancient empires. British anthropologists were compiling an equal amount of data on the characteristics of indigenous peoples around the world. At home, sociologists were addressing questions about the rise and fall of European ruling classes and proffering teleological models of societal evolution. Perhaps most important of all was rapidly growing eugenics movement in England. Much like Darwin sought to elicit the mechanisms of natural selection, Fisher sought the mechanisms of social selection. The subject of social evolution was a major theme in his book, *The Genetical Theory of Natural Selection*. He devoted the second half of it to social evolution. He wrote:

While genetic knowledge is essential for the clarity it introduces to the subject, the causes of the evolutionary changes in progress can only be resolved by an appeal to sociological, and even historical facts. (Fisher 1999, p. 174)

In his view, the evolutionary success of a society depended upon the degree of the inversion in the relationship between social position and fertility. He proposed that the longevity of a social system ultimately depends upon the degree to which social position facilitates adaptive fertility behaviors (Fisher 1932). If social organization is the product of the optimizing tendencies of natural selection, positions higher up in the hierarchy should yield conditions most favorable to fertility. In this way the characteristics of higher-ranking members would be reproduced via biological and sociological mechanisms in offspring. Fertility rates would scale upward with position in a social hierarchy (Fisher 1932, 1999). Fisher (1999) pointed to the fact that in "savage" and "barbarous" societies (Fisher's references to "savage" and "barbarous" societies reflect European ideologies of racial supremacy and global dominance. Fisher seemed to make the following distinctions. A "savage" society lacks spatial and temporal stability and operates with minimal social control systems. A "barbarous" society has more formal social control systems that are strongly aligned with kinship. Social divisions are maintained by "blood feuds." Its language system is more complex, and its cultural knowledge is accumulated. "Civilized" societies operate formal systems of social control and cultural knowledge accumulation. Darwin and Fisher seemed to reject the moral sentiments normally attached to "savage," "barbarous," and "civilized." Darwin (1871/1998) argued that all civilized societies evolved from savage states of existence. Fisher (1999) argued that "civilized" societies were no less susceptible to natural forces.) reproductive opportunities were organized collectively and were allocated to individuals who have made demonstrable contributions to the survival of the group. Judgments of worthiness of higher social rank were often based on ritual tests of skills. The outcome determined an individual's local status and access to reproductive opportunities (Fisher 1999). In contrast,

Fisher pointed out European societies were marked by an inversion of the relationship between social position and fertility. Although the wealthy could afford larger families, their genetic lineages were frequently extinguished as a result of low fertility. Among the poor, fertility levels were much higher but economically unsustainable. Moreover, fertility rates were closely scaled with social position. Individuals striving for higher social ranks delayed reproduction much later into their lives or invested more in the well-being of close genetic relatives rather than themselves. Fisher (1999) argued that sociological factors, not genetic factors, were pushing reproductive efforts of higher-status individuals to levels below an adaptive threshold.

Naturally, Fisher approached his model of the social selection and the inversion process in the same way he approached his model of natural selection. He decomposed fitness into two components: *directed agencies* and *undirected agencies* of evolution. Directed agencies include both genetic and environmental factors whose cumulative effects create optimal conditions for genetic evolution and, hence, maximize variation of fit genotypes within a population. Undirected agencies deteriorate the environment of genetic evolution and reduce the reproductive value of the individual and, over time, the population (Fisher 1999). Undirected agencies include harmful mutations, increased competition from internal and external groups, and temporal and spatial changes which bring about scarcity in available resources. Fisher stated that even if an organism is highly adapted to its environment undirected agencies will persistently challenge the fitness of the organism.

Social structures can function as directed or undirected agencies. According to Fisher, elements of “savage” and “barbarous” societies functioned as directed agencies of evolution. These societies had their share of problems. However, they achieved organizational forms and practices that tended toward optimization of the connections between genetic qualities, social rank, and fertility. On the other hand, modern European societies lost this quality at some point in their industrial evolution. Industrialization had

overcome some problems inherent in collectively oriented societies, but it presented a different set of “sociological difficulties” which threaten individual and population fitness. Inversion of the relationship between social rank and fertility resulted from three factors: (1) the economic organization of industrialization increased the cost of parenting; (2) the value of wealth as an indicator of fitness became greatly exaggerated; and (3) individual reproductive and mating preferences adapted to local cultural conditions.

Industrialization has increased the costs of parenting as a result of the individuation of property and wealth accumulation. This, in turn, generated resource scarcity to the degree that an individual must make tradeoffs between time invested in wealth accumulation and time invested in offspring. Since industrialized societies lacked ritual tests of an individual’s biological qualities, fitness indicators had become more subject to cultural manipulation. Cultural indicators might impose minimal or no genetic costs to the individual displaying the indicator. In a speech to the Eugenics Education Society, Fisher argued that the wealth had become greatly exaggerated in its value as an indicator of an individual’s true genetic fitness. Wealth, like many other cultural indicators, can be easily acquired through non-genetic inheritance. Individuals can simply imitate or mimic the behaviors of the wealthy. Hence, possession of the indicator (wealth), because of biasing cultural influences, became decoupled from the gold standard of genetic fitness. Fisher likened the process to runaway sexual selection:

[This form of social selection] has, however, all of the dangers noted in the case of sexual selection, of running into extravagance; for the standards of taste will necessarily be modified, step by step, with the qualities to which preference is given, and it may indeed, be that some of the virtues which appeal most to our imagination are more of the nature of ornaments than serviceable moral ideals. (Fisher 1999, p. 251)

Eugenics and the Question of Race

Fisher had professional ties to eugenics movement of the early twentieth century. His published

comments were mostly in broad agreement with philosophy of eugenics and seemed sympathetic, at least, to nationalist agenda it embodied. In a speech given to the Eugenics Education Society, Fisher stated:

Eugenics is not inherently associated with nationalism; but in the world of nations, as we see it, nationalism may perform a valuable eugenic function. The modern nation is a genetic, a territorial, and an economic organism, and the modern tendency is to emphasise its essential unity, the community of interests of its individual members; European nations are grouping themselves along ethnic lines, and the individual finds himself more and more closely engaged in serving the greater interests of his race. (Fisher 1914, p. 310)

But there is also a complexity in his views (Louçã 2009). While Fisher saw the virtues of a eugenics program, he also recognized its limitations. In the same speech, he presented the “specialization problem.” Fisher believed a eugenics program should strive to improve environmental conditions as much as it might focus on improvement of the genetic stock in a population. He proposed that any effort to build stock must consider that the expression of traits is the result of an interaction between genes and environment (Fisher 1914). But this, Fisher explained, begged the question of what type of an environment should be built. Should a eugenics program strive to create an environment which leads to the rapid evolution of individuals with highly specialized skill sets as seen in other cooperative species? Or, should a eugenics program strive to evolve individuals with generalized skills? Fisher did not provide a resolution, but he clearly believed the optimal strategy to ensure the long-term survival of any civilization would encourage “versatility” in traits in the same way evolution favors biological diversity in populations of species.

In a similar way, Fisher held views on race which, on the one hand, aligned with eugenicist arguments but also stood in stark contrast to them. In 1952, the United Nations’ Educational, Scientific and Cultural Organization (UNESCO) wrote a statement on race which would drive policy. The statement was intended as a response to destructive consequences of racial prejudice wrought in Nazi Germany and elsewhere. UNESCO sought

to “launch a campaign against race prejudice and extirpate this most dangerous of doctrines” (UNESCO 1952, p. 5). UNESCO proclaimed the idea of race is essentially a social construction with very little biological significance. Furthermore, intelligence and other desirable traits varied within groups as much as between racial groups. Before publishing the statement, UNESCO invited criticisms from 96 scientists representing various disciplines in the natural and social sciences. Fisher was among them. He agreed with the intentions of UNESCO but was critical of the denial of the genetic basis of racial group differences in behaviors and intelligence. He believed part of the UNESCO statement should be revised to read:

Available scientific knowledge provides a firm basis for believing that the groups of mankind differ in their innate capacity for intellectual and emotional development. (UNESCO 1952, p. 55)

Fisher’s criticisms are placed in the same group of scientists such as Carleton Coon, whose work was heartily embraced by white supremacy groups in the United States (Jackson 2001). However, Fisher’s earlier writings clearly show he did not support the core tenets of white supremacists’ philosophy. Sixteen years prior to the publication of the UNESCO report, Fisher was critical of studies of racial group differences because researchers would exaggerate the meaning of the concept of statistically significant difference. He wrote:

It must be stressed that the test of significance calculates a probability; it does not calculate a racial difference. (Fisher 1936, p. 4)

In *The Genetical Theory of Natural Selection*, Fisher countered prevailing theory that miscegenation would lead to the erosion of civilized societies in Europe. He aimed his critique specifically at a theory proposed by Arthur Gobineau (Gobineau and Collins 1915), which stated: (1) there are three races; (2) the white race is superior among them; (3) inequalities between races were unrelated to social factors; and (4) racial differences in intellectual capacity were entirely due to biological factors (Gobineau and Collins 1915). Gobineau reasoned racial mixing would deplete the genetic stock of the

white race and, thereby, cause the decline of white civilization. Fisher (1999) criticized Gobineau on logical and genetic grounds. Logically, Fisher argued it does not make sense that a supposedly “biologically superior” race can be so easily taken out of existence by a supposedly “biologically inferior” race. On genetics, Gobineau’s argument ignored Mendelian effects of racial mixing and failed to consider the vital importance of biological diversity within a population. Fisher wrote:

The general consequences of race mixture can be predicted with confidence. . . . If the races and their descendants intermarry freely, the factors which are inherited independently will be recombined at random; each person if mixed race will resemble one parental stock in respect of some factors, and the other stock in respect to others. Their general characteristics will therefore be intermediate, but their variability will be better than that of the original races. . . . [T]he ultimate effect of mixture will be the production of a race, not inferior to those from which it sprang, but rather superior to both, in so far as the advantages of both can be combined. (Fisher 1999, p. 238)

Fisher firmly believed that the lessons of science and the knowledge acquired through science should be used toward building healthier environments and healthier populations. In part of his speech to the Eugenics Education Society, he offered this appeal:

From the individual point of view our duty is, I think, clear; like all healthy philosophies, eugenics urges us to simplify our lives, and to simplify our needs; the only luxury worth having is that of a worthy human environment. We must be ready to sacrifice social success, at the call of nobler instincts. And, even as regards happiness, has any better way of life been found than to combine high endeavour with good fellowship? We require a new pride of birth, in that whatever valuable quality we show really goes to establish the quality of the family; and a new confidence in our instinctive judgments of human worth. (Fisher 1914, p. 313)

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Room-Sharing

- Co-sleeping

Rotation Injury

► Specific Brain Damage

Rough and Tumble

► Play Fighting in Boys

Roy Baumeister

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Overview

Roy F. Baumeister is one of the most widely published and highly cited social psychologists in the world. He is known for his work on many aspects of the self and human nature. As of 2018, he is currently a professor of psychology at the University of Queensland, in Brisbane, Australia.

Honors and Awards

Although a comprehensive list of honors and awards is not practical in this space, a few of Baumeister's most noteworthy honors are included. In 2015, Baumeister was inducted into the American Academy of Arts and Sciences. That same year, he and his co-author Mark Leary were awarded the Scientific Impact Award from the Society of Experimental Social Psychology for a paper they had written titled "The Need to Belong" (Baumeister and Leary 1995). In 2013, Baumeister was awarded the highly prestigious William James Fellow Award for lifetime contributions to psychological science from the Association for Psychological Science. This is the highest honor that the Association for Psychological Science bestows. Also in 2013, the Association for Psychological Science announced

that the Baumeister et al. (2003) article on self-esteem that was published in *Psychological Science in the Public Interest* was the most frequently cited article in the entire history of all journals published by the Association for Psychological Science. In 2012, Baumeister was awarded the Distinguished Lifetime Career Contribution Award from the International Society for Self and Identity, and in 2011 he was awarded the Jack Block Award for Distinguished Contributions to Personality Psychology by the Society for Personality and Social Psychology. In 2007 he was awarded the Distinguished Service Award for the Society for Personality and Social Psychology and in 2008 the Lifetime Achievement Award from the International Network on Personal Meaning.

Research Activity

Baumeister has published a wide variety of topics in the fields of social psychology, personality, evolutionary psychology, developmental psychology, social clinical psychology, social cognitive psychology, sport psychology, and many others. A sampling of the topics covered in Baumeister's research includes the self, belongingness and rejection, consciousness, human sexuality, human nature, suicide, psychometrics, economics, gender issues, emotion, motivation, free will, choking under pressure, UFO abductions, and sex, drugs, and rock and roll.

As can be seen from the partial list of topics that he has researched, Baumeister has always had a strong interest in interdisciplinary research and has often focused on the interpersonal perspective in his work. He has been a strong proponent of the importance of studying behavior in the behavioral sciences, rather than relying solely or even mainly on self-reports and responses to computerized stimuli to dominate our view of the human psyche.

Much of his work has centered on the psychology of the self, identity, and human nature. As of 2017, he has a total of over 630 publications, with over 300 peer-reviewed journal articles and 35 books. Twelve of his articles have

appeared in the highly esteemed journals *Psychological Review* and *Psychological Bulletin* (e.g., Baumeister and Masicampo 2010; Baumeister et al. 1996), and over 50 of his articles have appeared in the *Journal of Personality and Social Psychology* (e.g., Baumeister 1984; Baumeister et al. 1990, 2002).

In addition to being highly prolific, Baumeister's work has had a huge impact on the fields in which he publishes, as demonstrated by the numerous citations of his work. As of the end of 2017, Baumeister's work has been cited over 143,000 times. In 2017 alone, his work was cited 15,214 times. Put another way, every day there is new scientific work published that lists some of his publications in its References section – indeed that happens on average over 41 times each and every day of the year. Baumeister has 29 papers that have been cited at least 1000 times as of 2017.

In recent years scientific productivity has increasingly been measured by the h-statistic, which is the highest number (H) for which the scientist has H publications that have each been cited H times. Note that doubling the statistic requires far more than doubling one's success. An H of 20 signifies 20 articles cited 20 times each, while an H of 40 indicates 40 articles cited 40 times each. Baumeister's h-index in 2017 was 157, and his i10-index is 446, making him one of the most cited and influential social psychologists in the world.

Areas of Research of Special Interest to Evolutionary Scientists

Although Baumeister has published in many different areas of psychology over the course of his career, a few of the topics he has covered may be of special interest to evolutionary psychologists. These topics include human sexuality, the need to belong, the cultural animal, self-regulation, suicide, and the idea that bad things have a stronger impact on us than good things.

Baumeister's human sexuality contributions that have had the greatest impact (in terms of citation rates) include his review and theory

papers on the topics of gender differences in sex drive, erotic plasticity, and sexual economics.

In 2001, in collaboration with Kathleen Catanese and Kathleen Vohs, Baumeister published an article reviewing the literature on gender differences in strength of sexual motivation (Baumeister et al. 2001b). After reviewing a large number of papers with different studies and different measures of sexual motivation, the authors observed that men showed stronger sexual motivation, as demonstrated by findings that men are more likely than women to have spontaneous thoughts about sex, greater frequency and variety of sexual fantasies, greater desired frequency of intercourse, greater desired number of partners, more masturbation, and greater liking for various sexual practices. They also observed that men were more likely to initiate (and less likely to refuse) sex, were more likely to make sacrifices for sex, and in other ways seemed to display more frequent and more intense sexual desires than women. In their review of the literature, they found no evidence from any measure indicating that women had stronger sexual motivation than men, although they cautioned that their findings should not be generalized to other constructs such as sexual or orgasmic capacity, enjoyment of sex, or extrinsically motivated sex. The authors concluded from their review that the male sex drive is stronger than the female sex drive. As of the end of 2017, this article has been cited over 780 times, indicating that it is a classic article in the field.

Drawing on the idea that men have a stronger sexual motivation than women, Baumeister (2000) suggested that the strength of men's motivation for sex would decrease the plasticity or flexibility of the sex drive in men as compared to women. Baumeister coined the term "erotic plasticity" (Baumeister 2000) to refer to the idea that the female sex drive is more malleable and flexible than the male sex drive in response to socio-cultural and situational factors. After reviewing the literature, Baumeister (2000) concluded that female sexuality exhibited more flexibility than male sexuality across three dimensions. Firstly, individual females exhibited more variation across time in their sexual behavior than did males. Secondly, female sexuality was more

responsive than male sexuality to sociocultural variables. Thirdly, women showed a lower level of consistency between their sexual attitudes and their sexual behavior than men did, suggesting that outside influences could lead to greater sexual flexibility in females compared to males. Baumeister (2000) discussed possible explanations for this greater erotic plasticity in women compared to men, including the idea that women have a milder innate sex drive, allowing women's sexual behaviors to be more responsive to sociocultural and situational factors. As of the end of 2017, this article has been cited over 850 times, indicating that it is also a classic article in the field.

A third paper on human sexuality with almost 400 citations by the end of 2017 is the paper Baumeister authored with Kathleen Vohs on sexual economics (Baumeister and Vohs 2004). In this paper, the authors compared the heterosexual community to a marketplace in which men seek to acquire sex from women by offering other resources in exchange for sex. In other words, sexuality was compared to an economic market in which men are buyers and women are sellers of sexuality. The paper examines many behaviors that are consistent with such a view of sexuality as an economy, such the fact that most societies place higher value on women's sexuality in issues such as virginity, fidelity, and chastity than they do on men's sexuality. In Baumeister and Vohs's (2004) interpretation, economic principles such as supply and demand, competition and collusion among sellers, and other economic factors will affect the "price" that women can ask and that men will pay for sex. In their explanation, price refers not only to the price of prostitution but also the price that must be paid for marriage or divorce, courtship, or infidelity and the finding that women's sexuality has what economists refer to as value but men's sexuality has no such marketplace value. The authors discuss how describing human sexual exchanges as economic exchanges with men as buyers and women as sellers can help explain various factors including the repression of women, the suppression of female sexuality, abusive relationships, rape, and changing norms and sexual attitudes.

In addition to work on human sexuality, other works by Baumeister may hold special interest to evolutionary psychologists. In conjunction with the eminent social psychologist Mark R. Leary, the paper published on the need to belong (Baumeister and Leary 1995) is Baumeister's most highly cited and influential paper, with over 15,000 citations by the end of 2017. The authors described the universal human need to belong, expanding and differentiating it from the older, simpler notion of need for affiliation. They reviewed the existing literature, developed the theory, and determined that the need to belong was a powerful, fundamental, and extremely pervasive human motivation. In addition to proposing the universal need to belong, the authors also developed an exhaustive description and criteria for what is required for something to be classified as a fundamental human motivation, and it is this description and classification that is of special interest to many evolutionary scientists.

One of Baumeister's publications most directly relevant to evolutionary science is his book *The Cultural Animal: Human Nature, Meaning, and Social Life* (Baumeister 2005). In *The Cultural Animal*, Baumeister makes the case that humans evolved for culture. Rather than being merely "the social animal," a better sobriquet for humans is "the cultural animal." Although the idea of humans as social animals is correct, humans are not the only, nor perhaps even the most, social animal. What may be much more distinctive about humans and account for our evolutionary success is the fact that we evolved to take advantage of the ability to create and participate in culture. Other animals may show rudiments of culture, but we are the only species to use culture to such an extent as an evolutionary strategy. The main idea of the book is that human nature, and the individual human psyche, was designed by evolution to enable humans to create and sustain culture.

In another area of research of interest to evolutionary scientists, Baumeister has published numerous articles and books on self-control with his colleagues (e.g., Baumeister et al. 1998). Self-control has been shown to be important to evolutionary success in a variety of species

including humans. Baumeister and colleagues' work on willpower, ego depletion, the mechanisms underlying self-control, and other aspects of self-control have added extensively to the literature on self-control and its importance to human nature. Many of these books and articles on self-control have very high citation counts, and his book *Willpower: Rediscovering the Greatest Human Strength*, written with John Tierney, became a *New York Times* bestseller and spent over a month on Amazon's top 100 list.

Suicide has often posed somewhat of a problem for evolutionary researchers seeking to explain human behavior because most evolutionary accounts emphasizing survival and reproduction have difficulty explaining evolutionary benefits or even explanations for suicide. Baumeister's (1990) theory of suicide as an escape from self-awareness (as part of his research on escape-from-self mechanisms including binge eating, sexual masochism, alcoholism, and other behaviors as escape from self-awareness) can explain some elements of a behavior that runs contrary to our usual motivations to survive and reproduce. Baumeister's (1990) article on suicide as an escape from the self has had over 1500 citations as of the end of 2017.

Baumeister coined the term "bad is stronger than good" to describe the work published with colleagues (Baumeister et al. 2001a) on the idea that bad things exert a stronger influence on us than good things. Their paper examined the evolutionary advantage of bad being stronger than good. This paper has over 4900 citations as of the end of 2017. Baumeister is currently (2018) working on a book on this topic with his co-author John Tierney.

Protégés

One estimate of a scholar's impact is the protégés that he or she has mentored. Baumeister has an impressive list of graduate and postdoctoral students that he has mentored that have gone on to have made significant contributions to the field of psychology. As of 2017, his full list of protégés comprises 19 postdoctoral fellows and 27 Ph.D.

students in social psychology, as well as a couple of additional students in clinical and industrial psychology. Thus far, every single one of Baumeister's protégés has gone on to an academic job after working with him.

A sampling of some of his protégés, as of 2017, includes:

Postdoctoral Fellows

Todd Heatherton
 Len Newman
 Astrid Schütz
 Kristin Sommer
 Keith Campbell
 Julie Exline
 Jean Twenge
 Kathleen Vohs
 Catrin Finkenauer
 Sander Koole
 Liad Uziel
 Jill Lobbestael
 Isabelle Bauer (clinical)
 Andrew Monroe
 Jina Park
 Stephan Lau
 Cory Clark

Graduate Students

Jim Hamilton
 Arlene Stillwell
 Joseph Boden
 Karen Leith
 Jen Butler
 Harry Wallace
 Natalie Ciarocco
 Ellen Bratslavsky
 (Mark Muraven)
 Kathleen Catanese
 Liqing Zhang
 Brandon Schmeichel
 Matt Gailliot
 C. Nathan DeWall
 Tyler Stillman
 Nicole Mead
 E.J. Masicampo
 Lauren Brewer
 Jessica Alquist
 Jina Park

Sarah Ainsworth (McPherson)
 Andrew Vonasch
 Michael Ent
 Michael MacKenzie
 Bo Winegard
 Tania Reynolds
 Heather Maranges

Visiting Graduate Students

Michael Daly
 Hallgeir Sjøstad

Educational Background

Baumeister received his bachelor's degree in 1974 from Princeton University, where he worked with Joel Cooper. During his undergraduate years, he spent a year abroad at the University of Heidelberg where he studied philosophy. After receiving his M.A. from Duke University in 1976, he moved back to Princeton when his graduate advisor, Edward E. Jones, accepted a job there. He received his Ph.D. from Princeton University in 1978.

Employment History

After receiving his Ph.D., Baumeister moved to the University of California at Berkeley for a 1-year postdoc in sociology. In 1979 he moved to Case Western Reserve University where he held a faculty position until 2003. From 2003 to 2016, he was the Eppes Eminent Professor of Psychology at Florida State University and in 2016 moved to the University of Queensland in Australia.

Baumeister has traveled extensively during his career, taking advantage of sabbaticals and leaves of absence to work as a visiting professor in numerous locations. In 1986–1987, he had a visiting position at the University of Texas at Austin, and in 1991 he was a Visiting Professor at the Max Planck Institute in Munich, Germany. In 1993 he spent his sabbatical at the University of Virginia, in 2001 as a Fellow at the Center for Advanced Study in the Behavioral Sciences at Stanford

University, and in 2009 at the University of California, Santa Barbara. From 2010 to 2015, he served as a Special Professor at the VU University, Amsterdam, Netherlands, where he taught graduate classes every year. In 2013 he spent a year as a Research Fellow at the Russell Sage Foundation in New York City, and in 2014 he served as a Distinguished Adjunct Professor at the King Abdulaziz University in Saudi Arabia.

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Royal Lineages

- [Birthrights and Bloodlines](#)

Ruff Sandpiper

- [Ruff Shorebird, The](#)

Ruff Shorebird, The

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Synonyms

Calidris pugnax; *Philomachus pugnax*; Reeve (female Ruff); Ruff Sandpiper

Definition

Paleartic lekking sandpiper that breeds across Northern Eurasia and winters in Europe, Africa, South Asia, and Australia.

Introduction

The Ruff is a member of the *Scolopacidae* family representing the genus *Philomachus*. The genus name means “combative battle lover” reflecting the aggressive male-male competition during the breeding season in this lekking bird. Some taxonomic authorities have assigned the species to the genus *Calidris* (Van Gils et al. 2016). Ruffs breed in coastal and inland wetlands and tundra habitat across Northern Eurasia (Bird Life 2015; Van Gils et al. 2016).

General Biology

The Ruff is a sexually dimorphic species; males are 10–70 % larger than females (Van Gils et al. 2016). Ruffs have a strongly female-biased sex ratio that is already apparent in juveniles; males only comprise 34–40 % of the population (Jaatinen et al. 2010). This sex bias may have contributed to the evolution of the highly polygynous mating system. The oldest known Ruff in the wild reached an age of more than 10 years based on banding data (Van Gils et al. 2016). Ruffs are insectivorous during the breeding season but may also feed on plants including rice seeds during wintering.

Total population is estimated to be above two million individuals. The conservation status is “least concern” although the range is contracting because of habitat degradation caused by intensified agriculture meaning that populations especially in Europe are likely declining (Bird Life 2015).

Ruffs are migratory birds. Migration schedules are different for males and females. Adult males generally migrate earlier than adult females and juveniles leave the breeding grounds last. Females overwinter further south than males, probably

because males need to arrive early on the breeding grounds to obtain a position on the lek. Some Ruffs overwinter in Western Europe, although the majority of Ruffs will winter in Africa (Van Gils et al. 2016). Other significant wintering locations are in Southeast Asia and Australia.

Adult Ruffs molt up to three times a year. After the breeding season they will acquire a dull grey brown winter plumage through a complete post-breeding molt that lasts until mid-autumn (van Rhijn 1991). Within 2 months of completing the postbreeding molt Ruffs molt into more variable high contrast plumage that serves as a breeding plumage for females and prenuptial plumage for males. Males gain their breeding ornaments during a nuptial moult on the late stages of spring migration. The full breeding plumage of males includes the characteristic a neck ruff of extended feathers, which gave the species the name, colored head tufts, and facial wattles. The legs of males and females will take up a vibrant orange coloration during the breeding season whereas during the nonbreeding season they are green to brown.

Breeding

From April to July, Ruffs breed in open areas in Arctic, subarctic, and temperate zones of Eurasia. Ruffs are able to breed in the second calendar year in captivity although young males will rarely be able to obtain a place on a lek and search for vacant lek positions as marginal males. Ruffs are polygynous and males gather in leks consisting of typically 4–9 displaying males who compete aggressively for matings (van Rhijn 1991). The male breeding plumage is highly variable; barely two males will resemble each other. Ornament feathers of ruff and head tufts can take up a range of colors from white, ivory, straw, rusty brown to black with regular, irregular barring or spots of different size. Plumage is not associated with reproductive success, rather it may aid individual recognition replacing acoustic communication, since Ruffs are barely vocal (Lank and Dale 2001). This recognition is thought to reduce repeated exhaustive fights between males on leks once a dominance hierarchy has been established.

The reproductive success is heavily skewed among males, the dominant male on the lek will mate with most females (van Rhijn 1991). Females frequently mate with more than one male and provide all parental care whereas the male only contributes the sperm to the joint offspring. Females will often nest near leks in a well-concealed nest where they usually lay four eggs that hatch after 20–23 days. Chicks usually fledge with 25–28 days although the female may leave the young a few days before fledging (Van Gils et al. 2016).

Alternative Reproductive Tactics

Ruffs exhibit one of three discrete alternative mating strategies, which have the strongest impact on male appearance and behavior. The majority of male Ruffs (~85 %) are “Independents” (also called “Residents”). They try to obtain a place on a lek where they then display aggressively and fight other independent males to mate with visiting females. Independents are characterized by darker breeding plumage ornaments (van Rhijn 1991). They also comprise the largest morph (Lank et al. 2013). By contrast, “Satellite” males (~14 %) are nonterritorial, paler ornamented birds of intermediate size. They show submissive behavior towards lekking independents and do not fight aggressively for matings (van Rhijn 1991). However, they are the “kingmakers”: by forming an alliance with an independent territory owner, they make this male more attractive to females. Satellites themselves receive no obvious direct reward from their ally, but they use the confusion that arises during frequent fights on leks to mate with visiting females. The third morph (“Fæders”) has no male breeding ornaments and does not display (Jukema and Piersma 2006; Küpper et al. 2016). It is the smallest and rarest morph (~1 %). Fæder males travel with females and, like Satellites, they are nonterritorial and nonagonistic. They remain proximal to displaying males and use their female mimicry to rapidly sneak copulations when females solicit. Avian studies demonstrated that the differences between morphs are irreversible and encoded by a

Ruff Shorebird, The,

Fig. 1 Independent (*left*) and Satellite (*right*) Ruff males displaying on a lek. Ruff males show a large range of variation in breeding plumage color and ornamentation (Photo Credit: Clemens Küpper)



simple genetic dominant/recessive mechanism (Lank et al. 1995, 2013). Fæders and Satellites carry specific variants of a large dominant chromosomal inversion that corresponds to ~20 % of chromosome 11 (Küpper et al. 2016; Lamichhaney et al. 2016). The inversion is lethal when homozygous meaning that Fæders and Satellites require a copy of the ancestral Independent variant to survive. It contains 90–125 genes among them several candidate for differences in aggressive behavior and plumage ornaments (Küpper et al. 2016; Lamichhaney et al. 2016). The inversion has probably arisen first in Fæders about four million years ago whereas the Satellite variant has arisen through subsequent rare hybridization event between Independent and Fæder chromosomal variants about 500,000 years ago (Lamichhaney et al. 2016) (Fig. 1).

Conclusion

The Ruff is a classic ecological model system of sexual selection characterized by high intraspecific diversity in morphology, plumage, and behavior. Ruff populations have three discrete morphs that are strongest expressed in males although both males and females carry morph-defining genetic variants. The currently large populations of this migratory shorebird are declining and may be further impacted by ongoing habitat changes caused by global warming.

Cross-References

- [Female Mimics](#)
- [Lekking](#)
- [Male-Male Competition](#)
- [Sexual Selection](#)

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Rule

► Norms

Rule Extraction

► Insight

Rule of Law

► Moral Language Regulation

Rule Violations Checked If High Status

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Synonyms

Cheating; Dominance theory; Rules violations; Status

Definition

The idea that individuals of high standing in a social hierarchy check for and remember rule violations of relatively lower-status individuals.

Introduction

The ability to detect rule violations is often seen as necessary to the development of social contracts. Specifically, cooperation and reciprocity are typically understood to depend on the ability of group members to identify and penalize social rule violations. In this regard, it is crucial to detect and remember cheaters, those who (intentionally) violate social rules. Importantly, in communal species such as our own, the social environment is governed, in part, by a social hierarchy wherein some members occupy higher levels of status. In this context, higher-status individuals have been hypothesized to maintain their priority access to resources (e.g., food, mates) by increased detection and memory of lower-status cheaters (Cummins 1999). Evidence in support of this claim is reviewed as well as investigations indicating that social status may not have an impact on cheater detection. In addition, insights from the broader domain of cheater detection, unconcerned with social status, are detailed, indicating that identification, memory, and penalization of cheaters is a complex process in need of continued study. Finally, the various methods of measuring social status in humans are noted, providing avenues for future exploration into the role of social status in cheater detection.

High-Status Individuals and Cheaters

While there are numerous accounts in social animals, such as primates, investigating and supporting the idea that high-status individuals are more likely to check for and detect cheaters of lower-status there have been relatively few empirical investigations in humans. Indeed, it appears the oft-cited Cummins' (1999) is the only published work empirically and explicitly investigating the effect of social status on checking for and detecting cheaters in humans (although see Fiddick and Cummins 2001 for discussion of conceptually similar studies demonstrating mixed results). In specific, Cummins conducted two experiments wherein the relative

status of subjects was manipulated in a Wason Card Selection Task. In the first experiment, subjects had to test compliance with a college dormitory rule (i.e., if someone is assigned to tutor a study session, that person is required to tape record the session) and were split into four conditions:

High-status: Subjects engage the task as a high-status individual (Resident Assistant) checking on lower-status individuals (Students).

Low-status: Subjects engage the task as a Student checking on Resident Assistants.

High-status Equal: Subjects engage the task as a Resident Assistant checking on fellow Resident Assistants.

Low-status Equal: Subjects engage the task as a Student checking on fellow Students.

In all conditions, save for the High-status condition, 15–20 % of subjects used a cheater detection strategy. In contrast, 65 % used a cheater detection strategy when engaging the task as a high-status individual checking on lower-status individuals. Thus, subjects were significantly more likely to look for cheaters when checking on individuals who were of relatively lower status. The second experiment was identical to the first with one important change: in this version, subjects were initially asked to engage the task from a high-status perspective and then switch to a low-status perspective. This ordering was reversed for half the participants and a distraction task was used between perspectives to decrease the chance of carry-over effects. When subjects engaged the task as a low-status individual first, 41 % used a cheater detection strategy. After switching to a high-status position, this percentage increased significantly to 65 %. Thus, in the same person a cheater detection strategy was more likely to be employed when they were a high-status person investigating low-status individuals. When taking the High-status perspective first, 50 % used a cheater detection strategy and 40 % continued to use this strategy even after being placed in the lower-status position. This was a nonsignificant decrease and was taken to indicate that once cheater detection is engaged in a high-

status position, it is difficult to disengage regardless of any change in relative social status.

In contrast to Cummins, which directly assessed checking for cheaters by high-status individuals, most investigations into this effect have relied on memory paradigms focused on pictures of people's faces. In these tasks, subjects are typically presented with pictures of faces alongside descriptions of cheating, trustworthy, or neutral acts and tested for their memory of these faces after a time interval (e.g., a few minutes to a week). The central idea being that individuals using a cheater detection strategy should have better memory for faces matched with descriptions of cheating (i.e., cheaters). When social status is manipulated in these tasks, it is typically done via the job title given in the character descriptions (e.g., low-status job: baseball game vendor, high-status job: bishop). Using this technique, Mealey and colleagues (1996) found, in line with Cummins' results, significantly better memory for faces of low-status cheaters compared to high-status or noncheaters. These results, along with Cummins', are typically cited as evidence that high-status individuals are more likely to detect and remember low-status cheaters.

Despite the widespread citation of Cummins and Mealey et al.'s findings, recent investigations have noted areas of concern and have failed to replicate key status-related results. In this regard, Mealey and colleague's findings have been the main focus of examination, with apparently no studies attempting to replicate Cummins' findings. For example, Mehl and Buchner (2008) detail several areas of concern regarding the methods reported by Mealey et al. noting that the behavior and character description stimuli were not fully reported and that those descriptions that were reported differed in length and amount of detail, which may make some stimuli easier to remember. In a similar vein, Barclay and Lalumière (2006) comment that cheaters in Mealey et al.'s stimuli may be more salient, and thus more memorable, because their actions, in comparison to cooperators', are more intense, with cheaters not only breaking small social rules but also engaging in more threatening or

physically dangerous behaviors such as robbery or child molestation.

Beyond these concerns, and more importantly, six experiments across three studies have failed to replicated Mealey et al.'s results regarding high-status individuals (i.e., experiments 1 and 2 in Barclay and Lalumière 2006; experiment 4 in Buchner et al. 2009; experiments 1, 2, and 3 in Mehl and Buchner 2008 – experiment 3 did find better memory for faces associated with high-status professions, but there was no interaction with cheating or trustworthy behavior). These studies not only attempted replications they also sought to control for and assess potentially confounding variables such as sex of participant, sex of the face used in the stimuli, attractiveness and likability of the faces used, and time interval between initial display of the stimuli and memory testing. Overall, these results indicate that Mealey et al.'s findings may be singular or that there are influences in the original finding that are currently unaccounted for. Given this, and the lack of replication of Cummins findings, evidence to-date is equivocal that higher-status individuals preferentially check for or have greater memory for lower-status cheaters.

Complexities in Cheater Detection

The discussion of whether social status impacts cheater detection is necessarily couched within the much larger and historic debate on whether humans possess a cognitive mechanism specifically for detecting cheaters. While not able to engage this broader debate in full, the studies using the memory paradigm detailed in Mealey et al., although unable to confirm the impact of social status on cheater detection, do indicate that detecting cheaters is a highly complex process. For example, Chiappe et al. (2004) found that people see it as subjectively more important to remember cheaters than cooperators and that this was more evident when there were larger amounts of resources involved. They also noted that cheaters were looked at longer than cooperators,

that subjects were more likely to remember the faces of cheaters, and that cheating behavior was more likely to be remembered. Put another way, Chiappe and colleagues found that cheaters are remembered more and that individual (i.e., subjective importance and visual attention) and contextual variables (i.e., amount of resources involved) may moderate this effect.

In contrast to these results, Buchner and colleagues (2009), across four separate experiments, were unable to detect evidence of improved memory for cheaters despite also investigating the impact of various stimuli features such as attractiveness, likability, different intervals of memory retention, and whether the behavior described in the stimuli was exceptional or ordinary. They did, however, find evidence of improved memory for the conditions or features under which people did cheat, also known as source memory. In other words, people did not show improved memory for cheaters, but did show improved memory for the situations or context the cheaters acted in. Lastly, and importantly, Barclay (2008) demonstrated that the ability to remember cheaters or cooperators may be related to their rarity. Specifically, in this study, cheaters were remembered best when they were rare but worst when they were common, with the same being true of cooperators. These results suggest that people remember whatever behavior is rarest regardless of whether that behavior is cheating or cooperating. Overall, this collection of results demonstrates that cheater detection is shaped and dictated by a host of individual and situational variables.

Moreover, the often implicit but sometimes explicit assumption is that cheaters, especially lower-status cheaters, will be punished or penalized when detected. In stark contrast to this, Fiddick et al. (2013) has documented the cross-cultural presence of *noblesse oblige*, the tendency or obligation of higher-status individuals to be more tolerant of and generous to lower-status individual's, even if they cheat. Thus, even if status does not impact the detection of cheaters, it may effect the actions taken once they are detected.

The Many Faces of Status

The evidence so far indicates, in a somewhat contradictory fashion, that cheater detection may not be influenced by social status in humans but that it may be influenced by a host of other individual and situational variables. In this context, it is important to note the way social status has been manipulated or investigated up to this point. Specifically, in all of the studies described here status was manipulated via occupation or income. In contrast to this, literature and research on social status in humans indicates that an individual's position in the social hierarchy is determined by a variety of connected, yet independent, constructs, such as power, socioeconomic status, dominance, prestige, influence, and leadership (Blader and Chen 2014). Adding to the complexity of this picture is the fact that while social status is often discussed as a dispositional trait, it is also highly situational, such that an individual may be of high status in one environment (e.g., friend group or family) but low status in another (e.g., occupation). In this regard, the concepts and methods used to assess the impact of status have been relatively narrow.

Conclusion

Evidence in humans is currently equivocal as to whether high-status individuals display an increased detection or memory of lower-status cheaters. At the same time, the methods used to investigate the effect of status have been relatively narrow and numerous studies have demonstrated the impact of various individual and situational variables on cheater detection. Further clarity on the influence of status on cheater detection could be achieved through boarder investigation into the numerous ways social status is determined in human hierarchies and by more diverse methods of inquiry.

Cross-References

- [Higher Status in Group](#)
- [Rule Violations Not Checked If Low Status](#)
- [Social Contract Rule Violation](#)
- [Social Reasoning Affected by Rank \(Mealey, Daoood, Krage, 1996\)](#)
- [Status and Dominance Hierarchies](#)
- [Status Competition](#)

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Rule Violations Not Checked If Low Status

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Synonyms

Cheating; Dominance theory; Rules violations; Status

Definition

The idea that individuals of low standing in a social hierarchy do not check for or remember rule violations of relatively higher status individuals.

Introduction

The development of social exchanges, such as cooperation and reciprocity, is typically seen to be dependent, in part, on the ability to detect and remember the violation of social contracts. In this regard, it is crucial to be able to discover and identify cheaters, those who (intentionally) violate social contracts. Importantly, by their very nature social exchanges and cheating operate within social systems created by social species. Like many social species, ours has developed a social hierarchy wherein some members hold higher standing than others. In this context, it has been suggested that lower status individuals are less likely to detect, remember, and penalize cheaters of relatively higher status (Cummins 1999). Evidence in support of this claim is presented as well as results from recent studies which call this account into question. In addition, the definition of social status in humans is explored, providing ways of further clarifying the role of status in cheater detection. Finally, the ability of lower status individuals to enforce social rules is explored as a potentially important variable to

consider when exploring social status and cheater detection in humans.

Low-Status Individuals and Cheaters

In nonhuman animals, there is a wealth of literature supporting the idea that lower status individuals are less likely to detect, or at least penalize, cheating in higher status individuals. In humans however, empirical data are sparse. Indeed, it appears that the oft cited Cummins' (1999) is the only published work to empirically, and directly, investigate this effect in humans (although see Fiddick and Cummins 2001 for discussion of conceptually similar studies demonstrating mixed results). In this work, Cummins, using the Wason Card Selection Task, had participants test compliance with a college dormitory role (i.e., if someone is assigned to tutor a study session, that person is required to tape record the session), with relative status manipulated via four groups:

High-Status: Subjects engage the task as a high-status individual (Resident Assistant) checking on lower status individuals (Students).

Low-Status: Subjects engage the task as a Student checking on Resident Assistants.

High-Status Equal: Subjects engage the task as a Resident Assistant checking on fellow Resident Assistants.

Low-Status Equal: Subjects engage the task as a Student checking on fellow Students.

In the first experiment, participants were simply placed into one of the four groups and their actions were tallied. Here, Cummins found that participants in the high-status group used a cheater detection strategy about 65 % of the time. In contrast, those in the remaining conditions, including the low-status condition, used a cheater detection strategy only 15–20 % of the time. In other words, low-status individuals were unlikely to engage in detection of cheaters when checking on higher status individuals, at least relative to high-status individuals checking on those of lower status. In the second experiment, Cummins employed the same task but had

participants answer from both a high- and low-status position, with the order reversed for half the sample and a distraction task between perspectives. In this version of the task, participants starting from the low-status position used a cheater detection strategy 41 % of the time, which increased significantly to 65 % after switching to the high-status position. In contrast, 50 % of participants used a detection strategy when starting from the high-status position, with this dropping a nonsignificant amount to 40 % after switching to the lower status position. Like the first experiment, these results were taken to indicate that lower status individuals were less likely to detect cheaters of higher status.

In contrast to Cummins investigation, which directly evaluated the impact of social status on cheater detection, most investigations into this effect use tasks focused on whether individuals can remember the faces of cheaters. In these tasks, participants are typically presented with pictures of people faces along with descriptions of cheating, trustworthy, or neutral behaviors. Then, after a predetermined time interval, usually ranging from a few minutes to a week, participant's memory is tested, with the key idea being that individuals using a cheater detection strategy should have better memory for cheaters' faces. When social status is manipulated in these tasks, it is typically done via the job title given in the character descriptions (e.g., low-status job: baseball game vendor, high-status job: bishop). The most well-cited study using this technique is Mealey et al. (1996), which found, after a week-long interval, better memory for *low-status* cheaters in comparison to high-status or non-cheaters. These results mirror Cummins' and can be seen as providing evidence that low-status individuals are less likely to attend to or remember cheating by relatively higher-status individuals.

Despite being widely cited, however, recent investigations have noted areas of concern and have failed to replicate Mealey and colleague's results (there do not appear to be published attempts to replicate Cummins findings). Specifically, Barclay and Lalumière (2006) note that the cheating behavior in Mealey et al.'s stimuli includes instances of more threatening or

physically dangerous behaviors, such as robbery and child molestation, which may make cheaters easier to remember compared to cooperators. In a similar vein, Mehl and Buchner (2008) note that the behavior and character descriptions used in Mealey et al. were not fully reported and that those descriptions that were reported differed in length and amount of detail which may make some easier to remember. Moreover, six experiments across three studies (i.e., experiments 1 and 2 in Barclay and Lalumière 2006; experiments 1, 2, and 3 in Mehl and Buchner 2008; and experiment 4 in Buchner et al. 2009) have failed to replicate Mealey et al.'s results regarding status, despite also investigating the impact of potentially confounding variables such as sex of participant, sex of the face used in the stimuli, attractiveness and likability of the faces used, and time interval between initial display of the stimuli and memory testing (experiment 3 in Mehl and Buchner 2008 did find better memory for faces associated with high-status professions but there was no interaction with cheating or trustworthy behavior). The data from each of these suggest, in contrast to Mealey and Cummins results, that status does not impact detection or memory of cheaters, and thus, that low-status individuals are just as likely to detect and remember high-status cheaters.

Complexities in Cheater Detection, Defining Status, and Enforcing Rules

Current data are equivocal as to whether social status has a meaningful impact on cheater detection in humans. In contrast, a wealth of data suggest that there are other individual and situational variables that may impact cheater detection. For example, Chiappe et al. (2004) found that participants saw it as subjectively more important to remember cheaters compared to cooperators, that this effect was greater when larger amounts of resources were involved, and that subjects were more likely to remember cheaters. In turn, Barclay (2008) demonstrated that the rarity of behavior may play a crucial role in detection and memory by showing that people tend to remember whatever behavior is rarest, regardless of whether that

behavior is cheating or cooperating. In this context, it is important to note that to-date, studies specifically looking at the impact of social status on cheater detection have manipulated relative status via descriptions of occupation or income. In contrast to this, literature and research on social status in humans indicates that social hierarchy is determined by a variety of connected, yet independent, constructs, such as power, socioeconomic status, dominance, prestige, influence, and leadership (Blader and Chen 2014). Furthermore, while social status is often seen as a dispositional characteristic, it is also highly situational, such that someone may be of high status in one environment (e.g., friend group or family) but low status in another (e.g., occupation). In this regard, the constructs used to measure status so far have been relatively narrow and are unable to speak to the broad definition of status in humans.

Moreover, there is typically an important caveat to the idea that low-status individuals should be less likely to notice, remember, and penalize social rule violations by individuals of relatively higher status. Specifically, this should occur to the extent that there is no advantage to detecting cheaters of higher status (Cummins 1999). This situation is believed to appear when lower-status individuals are unable to force high-status individuals to follow social rules. In many nonhuman animals, this appears to be the case. There are reasons to believe, however, that in humans this represents only a subset of possible situations. Specifically, in humans, there are many mechanisms that can be used to enforce social rules, regardless of status. For example, contracts, laws, and courts provide sanctioned and thus official methods of enforcing social rules. Outside of official channels, gossip, exclusion, and public media (e.g., news, social media) provide broader avenues for compelling or penalizing individuals or groups. Of course, an argument can be made that these mechanisms may be more accessible or effective for individuals of higher status. At the same time, it is clear from grassroots campaigns and social movements that lower-status individuals, broadly defined, can also leverage these mechanisms to coerce and punish those of higher

status. Regardless of these specifics, research in humans is currently unable to fully explicate the role of status-based rule enforcement in the relationship between social status and cheater detection.

Conclusion

Evidence to-date is equivocal as to whether lower-status individuals are less likely to detect, remember, and penalize rule violations from higher-status individuals. However, there is a wealth of evidence to suggest that cheater detection is moderated by a host of individual and situational variables. In this respect, investigations into the impact of status have relied on relatively narrow conceptualizations of human status and have not explicitly explored the role of status-based rule enforcement. Future research can clarify the influence of status on cheater detection through boarder investigation into the numerous ways social status is determined in human hierarchies and by considering the role status plays in enforcing social rules.

Cross-References

- [Higher Status in Group](#)
- [Rule Violations Checked If High Status](#)
- [Social Contract Rule Violation](#)
- [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)
- [Status and Dominance Hierarchies](#)
- [Status Competition](#)

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Rules Violations

- ▶ Rule Violations Checked If High Status
- ▶ Rule Violations Not Checked If Low Status

Rule-Utilitarianism

- ▶ Utilitarianism

Ruling Class

- ▶ Birthrights and Bloodlines

Rumination

- ▶ Sexual Regret

Rumor Spreading

- ▶ Verbal Derogation

Runaway Selection

- ▶ Fisherian Runaway Selection

Runaway Sexual Selection

- ▶ Fisherian Runaway Selection

Runaway Tram

- ▶ Trolley Problem, The

Running

- ▶ Nonhuman Primates: Species Typical Movement

Rushton, J. Philippe

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John Philippe Rushton (known as “Phil”) was born on 3rd December 1943 in Bournemouth, a coastal resort in southwest England. He was the eldest of two sons of a Methodist couple: decorating contractor John Rushton (1911–1997) and Andrea Adou alias Adamson (1916–1991). Rushton’s mother was the daughter of a British conscript stationed in France during World War I, John Adamson, and his girlfriend, a French farmer’s daughter, Marguerite Adou; hence

Rushton's Gallic middle name. In 1919, the Anglo-French couple moved to the industrial town of Bolton, near Manchester, where they married (Dutton 2018, p. 121).

In 1948, Rushton's family migrated to Durban in South Africa where Rushton began school. However, they returned to Poole, near Bournemouth, in 1952. Passing an IQ test called the "11-Plus," Rushton attended grammar school (academically focused high school) in Bournemouth. However, in 1956 the family emigrated to Toronto, because Phil's father had got a job as a set artist for the Canadian Broadcasting Company. Aged 15, Rushton became fascinated by both psychology – voraciously reading the works of Hans Eysenck – and politics. He joined the small, libertarian Social Credit Party and sent off for pamphlets published by the International Association for the Advancement of Ethnology and Eugenics (Dutton 2018, p. 121).

Aged 17, Rushton fell in love with his friend's sister, Nina Sack. Dropping out of high school, he took a bookkeeping job for the Canadian railway. Sack became pregnant, the couple married, and in November 1962 they had a son, Stephen Rushton. The couple split up, eventually divorcing, and Rushton became a single father. He began a relationship with Margaret Von Klein (c.1943–2011) and the couple moved to England with dreams of becoming writers, taking Rushton's son with them. Settling in Streatham, in South London, Rushton took a job as a bus conductor. In 1965, Rushton and Von Klein moved to Hackney in the "East End" where their daughter Katherine Marguerite was born in the same year. With two children, Rushton decided he needed a more lucrative job. He did his A-Levels (English school leaving certificate) via a correspondence course. However, during this period Rushton and Margaret split up and Margaret returned to Canada with Katherine from whom Rushton became estranged.

Having completed his A-Levels, in 1967 Rushton began a Psychology degree at Birkbeck College, London, living mainly off the means tested grant that was available to all students at the time, there being no tuition fees. Rushton

graduated with a first class degree in 1970 and transferred to the London School of Economics to pursue a doctorate on altruism in children. In 1973, Hans Eysenck (1916–1997) came to speak at the London School of Economics and Rushton attended. Due to Eysenck's 1971 book on race differences in intelligence, *Race, Intelligence and Education* (Eysenck 1971), this meeting was interrupted by protesters wielding such placards as "No Free Speech For Fascists." Just as Eysenck began to speak, protestors pulled away his microphone, the podium collapsed, and fighting broke out. Believing Eysenck was under a pile of these violent demonstrators; Rushton intervened and was punched in the face (Nyborg 2013).

Rushton spent 1974 as a postdoc at Oxford University before returning to Canada to begin a career as an academic psychologist first at York University and then at the University of Toronto before settling at the University of Western Ontario in London, Ontario, in 1977. He became a tenured professor in 1985. In 1983, Rushton took a sabbatical year working under Hans Eysenck at the University of London's Institute for Psychiatry. As a consequence, he started to become fascinated by race differences and to develop his "Differential K" theory (Dutton 2018, p. 131). According to this model, due to differences in the stability and harshness of their ancestral ecologies, the three main races – Sub-Saharan African, Caucasian, and East Asian – consistently differ in life history speed, with Sub-Saharan Africans the fastest (the most r-strategist); East Asians the slowest (the most K-strategist); and Caucasians intermediate, though closer to East Asians. Rushton presented a large number of measures on which this was the case including twinning, gestation length, age at menarche, intelligence, personality, relationship stability, sexual promiscuity, and longevity (Rushton 1995). In 1988, he first published on this subject and also took up a year-long fellowship with the Guggenheim Foundation. Around this time, Rushton married his second wife, Serpil Kocabayik, a Turkish researcher who completed her PhD in Mathematics at Western Ontario in 1987 (Dutton 2018, p. 138).

In January 1989, Rushton presented *Differential K* at a San Francisco conference at which media were in attendance. This resulted in a media storm, newspaper cartoons of Rushton in Ku Klux Klan robes (over which he sued), Ontario's premier calling for Rushton to be fired because his views were "morally offensive to the way Ontario thinks," left-wing campaigners invading Rushton's department and scrawling "Racists [*sic.*] pig lives here" on his office door, a panicked Rushton being hospitalized with a suspected heart attack, a police investigation into whether he could be prosecuted for inciting racial hatred, his department head grading his research "unsatisfactory" due to its "insensitivity" (against which he successfully appealed), and the Attorney General of Ontario ultimately declaring that Rushton was "loony but not criminal." Until 1991, Rushton's lectures had to be given via video link to avoid student riots, and when he returned to lecturing in person he required security to protect him from protestors (Dutton 2018, pp. 133–134). *Differential K* was divisive in psychology with some condemning it as "racist," immoral, cherry-picked, and based on poor data and others regarding it as a work of near genius (Dutton 2018, Chap. 1). Rushton went on various talk shows to defend his theory and became famous within Canada. While researching *Differential K*, Rushton also accrued data for his "Genetic Similarity Theory": that people tend to be attracted to those who are more genetically similar to themselves, as seen in marital partners and even friends being more genetically similar than two random coethnics, thus allowing people to maximize their genetic fitness via indirect means (see Rushton 2005).

Differential K had been criticized for data it drew upon to supposedly prove race differences in penis size. So, in 1994, Rushton went to the Eaton Mall in Toronto to collect data on this and related matters from males of different races. He paid his subjects with money from the Pioneer Fund, which has been criticized for its alleged association with white supremacism and eugenics, and of which Rushton became president in 2002. In 1995, Rushton published, with a US publisher, his book on *Differential K – Race, Evolution and*

Behavior: A Life History Perspective. Copies were held by Canadian customs officers for 6 months as they investigated whether the book broke Canada's race hate laws.

In 1999, Rushton sent out 40,000 copies of an abridged version of the *Race, Evolution and Behavior* to academics. This led to a furor about its contents with some scholars insisting on returning it to the publisher and the publisher, Transaction, withdrawing the book and the book-proper's second edition, which was published in 2000 (Dutton 2018, p. 137). In the year 2000, Rushton divorced his second wife and married American physical anthropology researcher Elizabeth Weiss (b. 1973), also producing a third edition of *Race, Evolution and Behavior*, which he published via his Charles Darwin Institute (Dutton 2018, pp. 127–138).

Around 2001, Rushton's estranged daughter, who had been raised in care, got in touch with him and in 2003 his third marriage broke down. In the same year, Rushton was diagnosed with the rare condition Addison's disease (Dutton 2018, pp. 140–141). He also became particularly interested in a "General Factor of Personality" (GFP); the idea that the Big 5 personality traits can be reduced to one essential factor of social effectiveness (see Nyborg 2015).

In 2005, Rushton became involved in another controversy when he told *The Ottawa Citizen* that black immigration into the city would precipitate its decline and lead to the death of "Toronto the Good" due to supposed low black IQ. By this time, Rushton was regularly speaking at far right-wing conferences, such as those run by *American Renaissance*, and writing for related magazines, such as *V-Dare* and *Right Now!*. In 2008, Rushton was door-stepped by a TV reporter asking, "Are you a racist?" Clearly irked, Rushton made his way to his car and lifted his wheeled suitcase in such a way that the reporter's microphone hit the reporter in the face, cracking the reporter's tooth (Dutton 2018, p. 142). Between 2010 and 2012, Rushton transferred half of the Pioneer Fund's money to his Charles Darwin Institute. He then bequeathed this to his son who changed its name to JSP and used it to establish a scholarship fund at the university where he

works in Florida. Accordingly, half the Pioneer Fund could no longer be used for the kind of research – on such areas as race – for which the fund was established (Dutton 2018, pp. 143–144).

Rushton, by that time a great grandfather, died of cancer in the palliative ward of Victoria Hospital in London, Ontario, on 2nd October 2012. An opinion piece, 2 days later in the *London Free Press* (Gilespie 4th October 2012), was headlined “Rushton’s Ideas Died With Him.” By contrast, an obituary in *The Big Think* by psychologist Satoshi Kanazawa (10th October 2012) compared Rushton to Galileo, as the exemplar of the scientist persecuted for telling the truth, stating that “Unlike Galileo, he never recanted.” In 2013, the journal *Personality and Individual Differences* published a special issue on J. Philippe Rushton and his work which was subsequently republished in book form (Nyborg 2015).

Cross-References

- [Controversies in Evolutionary Psychology](#)
- [Genetic Relatedness Affects Aid to Kin](#)

- [Helping and Genetic Relatedness](#)
- [Life History Strategies](#)
- [Life History Theory](#)

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Sacred Values

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Synonyms

Protected values

Definition

Those values that a moral community treats as possessing transcendental significance that precludes comparisons, trade-offs, or any mingling with secular values.

Introduction

The use of sacred values by humans to enforce cooperation has been seen throughout human history, as demonstrated by philosophers like Marx and Aristotle observing that humans are more likely to follow rules when framed from a sacred view of “don’t do x because God says so” versus a secular view of “don’t do x because I say so” (Tetlock 2003). As these types of rules are common across all cultures, anthropologists began noticing that, although the value being upheld was vastly different between cultures, the presence of sacredness was near ubiquitous. This led to research into the psychology of sacred values.

Sacred Values

Sacred values are those values which humans attribute a priceless value to. This means that, regardless of what the costs of upholding the value are, these costs will not typically outweigh the costs of giving up the value. However, because there is only a limited amount of resources available to us, humans will give up their sacred values if the cost to maintain them is too high. This belief that a sacred value is priceless, yet a willingness to give it up given the right circumstance, has led psychologists and political scientists to study sacred values further (Tetlock et al. 2000).

The major area of research on sacred values has focused on its application to international conflicts (e.g., Atran and Axelrod 2008). Given that many of these conflicts are caused by perceived transgressions, understanding the mechanisms behind these values is important. To understand how these values operate, Atran and Axelrod (2008) argue that sacred values may not be cultural, but evolutionary. Sacred values likely evolved to counter evolutionarily recurrent problems that posed long-term threats to our ancestors. One example is the presence of children. Indeed, a consistent sacred value across cultures is the importance of children to parents. For the parents, their children’s safety is frequently presented as a priceless condition, not to be compromised even if offered large amounts of resources (e.g., time, money, health) or great sacrifice (e.g., giving up one’s career or even life).

Conclusion

Sacred values are a ubiquitous part of everyday life, and although the specific content of a value may shift across cultures, the presence of values with sacred beliefs attached is cross-culturally consistent. As these types of values can be charged with violence when transgressed, they are frequently the cause of many international conflicts (e.g., religious wars). Because of this, much research has been devoted to understanding their presence from an evolutionary perspective to better negotiate peaceful resolutions.

Cross-References

- [Religious Beliefs](#)
- [Scott Atran](#)

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Sacredness/Purity/Disgust

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Synonyms

[Behavioral immune system](#); [Contamination vulnerability](#); [Moral foundation](#); [Sanctity](#); [Sociomoral emotion](#)

Definition

Disgust is a sociomoral emotion elicited by moral violations against sacredness and purity of body and spirituality.

Disgust is one of the fundamental and universal human emotions like fear, anger, sadness, and joy (Ekman et al. 1969). In broader terms, disgust is a defense mechanism against purity and sacredness of body and soul. Common behavioral responses of disgust are gape face, feeling of nausea, physical avoidance from the disgusting stimulus, and the stimuli contaminated by the source stimulus. In addition to behavioral responses, common cognitive responses are a sense of being offended and contaminated. Two kinds of disgust have been defined in the literature: a nonmoral form of disgust defined as visceral disgust, which guards the body against threats to its integrity, and sociomoral disgust as a reaction to moral transgressions of others (Rozin et al. 1993).

Core disgust is thought to be an evolutionary adaptation to protect the gastrointestinal system (Schaller and Park 2011). Accordingly, disgust sensitivity generally operating as an orally based aversion prevents digestion of toxic and poisonous food. Behavioral responses like nausea also help us avoid harmful foods via preventing immediate digestion. Another function of core disgust as an evolved mechanism is to protect the body against pathogens. Accordingly, disgust leads to avoid physical contact with infected and contagious stimuli as well as avoiding places where pathogens can be carried (Rozin et al. 2008). Reflex-like withdrawal behaviors and purity concerns are also other behavioral mechanisms protecting the organism.

Aside from being a response to harmful foods and pathogens, disgust is a response to a number of moral violations as hypocrisy, betrayal, and cruelty (Miller 1997). A theoretical framework to understand disgust as a sociomoral emotion is provided by contempt, anger, disgust (CAD) triad hypothesis (Rozin et al. 1999) which is then incorporated to the Moral Foundations Theory (MFT; Haidt 2007). This line of research highlights the importance of emotions and unintentional gut reactions in terms

of moral judgement unlike the cognitive developmental tradition (e.g., Piaget 1932/1965; Kohlberg 1969) which focuses on rational thought processes to explain the cognitive roots of morality. According to this view, there are several moral emotion clusters such as “self-conscious” emotions including shame, embarrassment, and guilt, whereas disgust is one of the “other-critical” moral emotions along with contempt and anger. Those “other-critical” emotions are triggered by specific ethical violations. Those violations are, that derived from the work of Shweder et al. (1997) work on Hindu Indians, autonomy (individual freedom and rights), community (social hierarchy), and divinity (sacredness and purity regarding God, oneself, and others). Ethical violations to one of those concerns elicit anger, contempt, and disgust, respectively. The link between disgust and divinity further explained by MFT which proposes evolutionary rooted five universal moral foundations. Those foundations are care/harm, fairness/cheating, loyalty/betrayal, authority/subversion, and sanctity/degradation foundations. Accordingly, human beings use those five moral intuitions, which are emotion-based and partially unconscious, to make moral judgments. Sanctity/degradation is associated with controlling bodily desires and protecting and preserving sacredness and purity of body and soul. Since sanctity foundation is assumed to be unique to human considering the exclusiveness of disgust and fear of contamination among species (Rozin and Fallon 1987), it is assumed that sanctity evolved most recently among other moral foundations in line with religious beliefs commonly seen in human societies.

As a result of this evolutionary process, it is thought that behavioral immune system to protect organism is generalized to moral issues which are not directly linked to survival instincts manifested by disgust sensitivity (Schaller and Park 2011). Accordingly, during the evolution of the moral domain which defines oughts and things to be avoided, at some point it is converged with the evolution of disgust as an immune system. Therefore, disgust became a response mechanism for social and abstract issues as religious views and political ideologies. In other words, disgust

became a way to differentiate what is pure and sacred against impure and immoral at the individual level. For instance, it was found that higher levels of disgust sensitivity are related to higher levels of motivation to maintain physical and spiritual purity (Horberg et al. 2009). Likewise, reminders of physical purity increased political conservatism and condemnation of incest and masturbation (Helzer and Pizarro 2011). Further, disgust helps to foster cooperation and group cohesion by creating powerful negative emotions against out-group members. For instance, triggering disgust with noxious odor is related to negative attitudes towards gay people (Inbar et al. 2011). Similarly, reminders of the contagious disease led to an increase in negative attitudes toward immigrant people (Faulkner et al. 2004).

Disgust is an emotional reaction to protect organism against harmful food and pathogens, and it is also an emotional reaction to protect and preserve sacredness and purity against threats to moral values. This sociomoral function of disgust plays role in forming social attitudes and relevant behaviors.

Cross-References

- Disgust
- Sacred Values
- Moral Instincts
- Evolution of Morality

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Sadism

- [Victims of Violence](#)

Sadness

- [Depression \(Randolph Nesse\)](#)

Safety in Numbers

- [Predator Swamping](#)

Sahelanthropus

- [Ardipithecus Group](#)

Salience of Category

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Synonyms

[Category salience](#); [Salience of social categorizations](#)

Definition

A person's social category is salient when he or she is perceived, or perceives himself or herself, as a group member rather than as a unique individual. Category salience implies that the impression of and the behavior towards the person shift from the interpersonal level to the intergroup level.

Introduction

Psychological theory and research has extensively focused on the process of social categorization, its antecedents, and consequences. A person's social category is salient when he or she is perceived, or perceives himself or herself, as a group member (e.g., a “woman” or a “manager”) rather than as a unique individual. Category salience implies that the impression of and the behavior towards the person shift from the interpersonal level to the intergroup level. Without category salience, intergroup behavior is not possible – behavior between groups can only be shown if people categorize each other into groups. Therefore, social category salience is the most fundamental

foundation of stereotyping, social identity formation, and intergroup relations. According to self-categorization theory (Turner et al. 1987), category salience is determined by the interaction between the relative accessibility of the category for the perceiver and the fit between stimulus input and stored category specifications. Accessibility means how readily a given category becomes cognitively activated and it reflects the goals, motives, and circumstances of the perceiver. In contrast, fit refers to the extent to which a distinction between social categories matches reality in both its comparative and normative aspects (Bruner 1957; Oakes 1987). In situations in which people's social categorizations of themselves and others become salient, they are more likely to define themselves and others as group members and thus to engage in stereotyping, intergroup behavior, and conflict. Intergroup bias in return is likely to affect team performance in work settings.

Salience of Social Categories and Stereotyping

Research has consistently demonstrated that variations in the salience of social categories influence self-perception, impressions of others, attitudes, and behavior (Fiske and Neuberg 1990; Oakes 1987). Stereotypes are cognitive representations of prominent attributes of group members, which result from the cognitive process of categorizing social groups. While categorizing others might be beneficial for the person who engages in the process (e.g., it reduces the complexity of our world; Macrae et al. 1994), perceiving and treating others as group members, rather than unique individuals, can foster stereotyping and prejudice, which in turn may create discrimination.

Social categories such as a person's sex, ethnicity, or age are particularly likely to affect perceptions and judgments of others as they are readily visible and immediately evident. In contrast, categories such as a person's personality or values are less likely to impact immediate impression formation and judgments of others, as they are not so immediately apparent to people.

Research has further shown that any social category can become salient as a function of the social environment in which the individual is perceived. For example, in an experiment in which the salience of gender in the classroom was manipulated, via frequent exposure of children to gender classifications (e.g., lining up children by sex or not), teachers in the high gender salience classroom produced stronger gender stereotypes among their pupils and less positive attitudes toward peers of the other sex and less willingness to play with them (Hilliard and Liben 2010). Similarly, Retelsdorf et al. (2015) found, in a time-lagged study, that teachers' beliefs about reading favoring girls at time 1 were negatively associated with boys' (but not girls') reading self-concept at time 2. Exploring the role of salience in age stereotyping in simulated employment settings, one meta-analysis found that younger workers have higher mean job qualification ratings than older workers when age is salient (Finkelstein et al. 1995), i.e., when raters judged old and young workers concurrently, than when age was not salient, i.e., in a between-subjects condition design. Additionally, when individuals are distinctive, unique, or "token" members of their social categories, that category becomes contextually more salient and guides observers' impression of these individuals or the individual's own perception and judgment. Indeed, numerically rare group members are perceived more stereotypically (Kanter 1977; Oakes et al. 1991; Taylor et al. 1978). In particular, several studies have documented how rarity of women negatively impacts others' perceptions of and behavior toward women in work settings (e.g., Heilman 1980; Sackett et al. 1991; Taylor et al. 1978). For example, in her hiring study with MBA students, Heilman (1980) varied the sex composition of the applicant pool and found that raters evaluated female applicants as less favorable and as more stereotypical when the applicant pool included only 25% women or less. These rarity effects bear even more important implications as women rise in organizational hierarchies. Women will be increasingly in a minority position and their female-stereotypical qualities will become more salient, which – due to their incongruity

with stereotypical male qualities perceived in leaders – might produce disadvantages for women (see Eagly and Karau 2002). In general, in organizational settings compared to other settings, people's behavior is less stereotypic because organizational roles (e.g., based on occupation or status in the organizational hierarchy) tend to be more salient and therefore more impactful than diffuse roles (e.g., based on gender, age, or ethnicity), consistent with social role theory (Eagly et al. 2000). Demonstrating the powerful impact of *social roles*, experiments showed that gender-stereotypical trait judgments were reduced, or even eliminated, when men and women were portrayed as occupying the same role (e.g., nurse, firefighter) than without role information (Bosak et al. 2008, 2012).

Social category salience however does not only impact others but also individuals' self-perception and behavior. People learn the content of stereotypes (e.g., gender stereotypes) and can internalize stereotypes into their *self-concept*. Thus, if a stereotype is cognitively activated following a process of social categorization, *self-stereotyping* can occur and have individuals act in a way consistent with their stereotype. One area in which the powerful effect of self-stereotyping can be observed is career aspirations and choices. Bosak and Sczesny (2008), for example, found that women, compared to men, judged themselves as less suitable for an advertised leadership position because they perceived themselves as possessing fewer of the agentic traits (e.g., assertive, competitive) typically ascribed to leaders and men. Another area in which self-stereotyping and its negative impact on the behavior of group members can be observed is stereotype threat (see Hoyt and Murphy 2016). Demonstrating the powerful influence of social-cultural stereotypes on individual performance, Shih et al. (1999) made one of two social-cultural identities to which participants belonged salient. Specifically, these researchers found that Asian women, whose gender identity was made salient, underperformed in a math test, whereas those who were subtly reminded of their Asian identity performed better than participants in the control condition. Thus, the salient identity can hinder or facilitate performance. This

finding applies even to members of traditionally advantaged groups in certain situations. For example, in another stereotype threat experiment, White men underperformed on a math test when beliefs about Asian superiority were made salient (Aronson et al. 1998). Finally, salient role models have been found to buffer the negative effect of stereotype threat on performance (see, for example, the “Obama effect” for African-Americans; Marx et al. 2009).

A powerful demonstration that socio-cultural stereotypes ascribed to salient categories fulfil a function is given by the stereotype content model (SCM; Fiske et al. 2002). Stereotypes in terms of warmth (“Are they friend or foe?”) and competence (“Are they capable of reaching their goals?”) provide fast and the most fundamental information about outgroups. Stereotypes based on these fundamental dimensions (e.g., physically disabled people as warm and incompetent; business women as cold and competent) have been shown to appear across cultures (e.g., Asbrock 2010; Cuddy et al. 2009) and to predict specific emotional and behavioral reactions toward the respective outgroups (e.g., Becker and Asbrock 2012; Cuddy et al. 2007).

Salience of Social Categories and Intergroup Behavior

A social identity refers to membership of a social group and a certain emotional value attached to this group (Tajfel and Turner 1979). According to the social identity approach (Tajfel and Turner 1979; Turner et al. 1987; see Abrams and Hogg 2010, for a review), social identities rely on the conceptualization of *social categories as groups*, that is, on the salience of a social category and one's awareness of being connected with this category. The sufficiency of these two factors for intergroup behavior has been shown in research applying the *minimal group paradigm* (MGP; Tajfel et al. 1971). Individuals are assigned to one of two groups based on a random or trivial criterion. Subsequently, the individuals allocate money or tokens to others, only knowing the other person's group membership and a code

number. Hundreds of MGP experiments have shown that minimal group information was sufficient to elicit a preference for the ingroup (ingroup bias) in the distribution (Diehl 1990).

Social identity is an important part of the *self*, and individuals strive for enhancing or maintaining a positive social identity by positively distinguishing their ingroup from relevant outgroups. According to social identity theory (SIT, Tajfel and Turner 1979), group members can adopt several strategies for this purpose, depending on the permeability, legitimacy, and stability of the respective group boundaries. While permeable group boundaries allow for leaving a low-status group and moving into a group with higher status, low permeability calls for social creativity or social competition measures. Social creativity allows for regaining a positive social identity when group boundaries are perceived as stable and legitimate, for example, by downward comparison with a lower status group instead of unfavorable upward comparison with a higher status group (e.g., Blanton et al. 2001). Other social creativity strategies are a positive reevaluation of the value of the comparison dimension (e.g., “black is beautiful”) or a comparison with the outgroup on an alternative, more ingroup-beneficial dimension (but see Martiny and Rubin 2016, for a critical review).

If group boundaries are perceived as illegitimate, group members adopt social competition strategies and directly confront the status relations in order to change them or to maintain the social hierarchy. Low-status groups can engage in collective action to improve their status (Van Zomeren et al. 2008), and high-status groups can discriminate against outgroup members to maintain their status (Sachdev and Bourhis 1991). However, different strategies to regain positive social identity can interfere with each other. In a series of experimental studies, Becker (2012) tested if engaging in social creativity, (e.g., gaining a positive social identity by comparing one’s group with a lower status group), enhanced social identity for low-status groups but simultaneously undermined collective action intentions. As predicted, participants from different samples

(women, students, and unemployed people) showed fewer intentions to engage in collective action and change the status quo of the ingroup after engaging in social creativity strategies.

Individuals possess many group identities (Tajfel and Turner 1979) and these identities can change with goals, motives, experiences, or perceptions. According to the common ingroup identity model (Gaertner and Dovidio 2000), recategorization of in- and outgroup members elicits changes in ingroup bias. Recategorization of outgroup members into a common superordinate ingroup makes them members of the ingroup and, therefore, provides them with those positive emotions, beliefs, and behaviors directed towards ingroup members. Recategorization does not necessarily lead to the abandonment of the less inclusive ingroup identity. Group members can develop dual identities, and superordinate identities can include subgroups. Gonzáles and Brown (2003, 2006) showed that dual identities are effective in facilitating intergroup contact effects relative to a one-group representation. Recently, Hehmann et al. (2012) provided evidence that group status moderates the preference for single or dual identities of common ingroups. Both, minority and majority group members strive for a common ingroup identity that is most beneficial for their group. For majority groups, this is a one-group representation, as it draws attention from disparities between the subgroups and therefore reduces subgroup identification and collective action in the minority subgroup. Minorities, however, prefer dual identities, because subgroup identification increases the likelihood of detecting injustice between the subgroups and confronting it via collective action (Gaertner et al. 2016). Ufkes et al. (2016) recently confirmed the advantage of a dual identity over a single-group identity for minority group members. They showed that increasing the salience of a common US identity for categorizing Blacks and Latinos in the USA undermined their collective action intentions, while salient dual identities did not. Simon and Ruhs (2008) found evidence that Turkish migrants in Germany holding a dual identity as Turks and Germans engaged in normative but not nonnormative political behavior.

Despite these benefits, dual identities can harm intergroup relations. Subgroups can perceive their ingroup as more prototypical for the superordinate group (e.g., people from West Germany might perceive themselves as more prototypical of Germans than people from East Germany) and perceive the outgroup as substandard or inferior, leading to more bias (Mummendey and Wenzel 1999; Wenzel et al. 2008). Whether dual identity increases or decreases intergroup conflict depends on perceived prototypicality, relevance, and diversity of the superordinate category, as well as on the outgroup status (Hall and Crisp 2005; Steffens et al. 2017; Verkuyten and Martinovic 2016).

Salience of Social Categories, Diversity, and Team Performance

The salience of social categories plays an important role in many applied contexts. One prominent application of research on social category salience is organizational research on the effects of (team) *diversity*. This research employs social categorization approaches (see Meyer 2017; Williams and O'Reilly 1998, for reviews) to propose negative effects of team diversity. (To be clear, this research also proposes a competing positive effect of team diversity on team performance.: Information processing advantages of heterogeneous groups are likely to increase creativity and problem-solving performance of diverse groups (e.g., Williams and O'Reilly 1998; van Knippenberg and Schippers 2007).) If team members perceive each other as belonging to different social categories on the basis of salient social categories, *intergroup bias* ensues among employees who are supposed to collaborate towards a common goal, with detrimental consequences for inter-category communication and trust (van Knippenberg et al. 2004; van Knippenberg and Schippers 2007). Consequently, if colleagues construe their interpersonal demographic differences in terms of different social categories that signal identities, negative consequences are likely to ensue (Shemla et al. 2016; Carton and Cummings 2012).

However, empiric evidence for these arguments is mixed. Several meta analyses on the

effects of team diversity (Bell et al. 2011; Horwitz and Horwitz 2007; van Dijk et al. 2012) did not identify a consistent negative main effect of team diversity on team processes and performance. This indicates that interpersonal differences are not automatically associated with social categorization processes and intergroup bias on the basis of salient social attributes. Indeed, the effects of team diversity appear to be largely context-dependent (Joshi and Roh 2009). However, the negative consequences of demographic differences among members of a social unit are more likely to materialize if multiple differences with regard to several potential social categories are aligned in the same way. *Faultlines*, hypothetical dividing lines splitting a group into relatively homogeneous subgroups on the basis of several attributes (Lau and Murnighan 1998), are associated with more conflict and decreased performance in teams, as a meta-analysis indicates (Thatcher and Patel 2012). This is likely to be the case because faultline strength – which researchers can quantify with different algorithms (Meyer et al. 2014) – constitutes an applied operationalization of the meta-contrast from self-categorization theory (Meyer et al. 2011; Meyer 2017). Self-categorization theory (Turner et al. 1987) posits that social categories become salient on the basis of stimuli, which are grouped together into a category in such a way that within-category homogeneity of stimuli is maximized and between-category heterogeneity of stimuli is maximized. This ratio of within-and-between category heterogeneity, i.e., the average difference between categories divided by the average differences within a category, is the meta-contrast (Turner et al. 1987). Faultline researchers typically operationalize faultlines in the same way. The two most frequent measures of faultline strength, Thatcher's Fau (Thatcher et al. 2003) and Average Silhouette Width (ASW, Meyer and Glenz 2013), deliver the ratio of within-subgroup heterogeneity of several demographic attributes to between-subgroup heterogeneity of these attributes, where larger values indicate that the differences lie between subgroups, not within subgroups. In sum, applied organizational measures of faultline strength offer a quantification of

the meta-contrast of self-categorization theory. Perceiving the faultline – in other words, if the categories that are distinguished by the faultlines become salient – results in comparative fit, “the extent to which observed similarities and differences between people or their actions are perceived as correlated with a division into social categories (Turner et al. 1987)” (Meyer et al. 2011, p. 261). Accordingly, if team members subjectively perceive a faultline within their social unit, i.e., if faultlines become active in contrast to being dormant (cf. Jehn and Bezrukova 2010), the negative effects of faultlines intensify (Thatcher and Patel 2012). Thus, in sum, the findings from applied research on team diversity and faultlines is very much in line with the predictions of the self-categorization theory with regard to the salience of social categories.

However, some findings of this line of research also extend classic theories and knowledge surrounding category salience. Research on team and societal diversity (Kauff and Wagner 2012; Kauff et al. 2013) indicates that perceived interindividual differences on the basis of salient social categories do not entail outgroup devaluation if perceivers see value in diversity. The same is true for faultlines – teams consisting of members who see value in interpersonal differences are not negatively affected by team faultlines (Homan et al. 2007).

Conclusion

Social category salience is fundamental to intergroup perception and behavior. Category salience is a function of the Fit $\times$ Accessibility interaction. In situations in which individuals perceive themselves and others as belonging to different social categories based on salient features, they tend to engage in (self-) stereotyping and intergroup bias. While stereotyping and intergroup bias can yield detrimental consequences for individual group members as well as teams (e.g., discrimination, intergroup conflict, lower team performance), salient positive identities and dual identities can also bring positive consequences and advantages with them (e.g.,

invulnerability to stereotype threat, absence of harmful collective action).

Cross-References

- [Self-Concept](#)
- [Self-Stereotyping](#)
- [Social Roles](#)

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Salience of Social Categorizations

► [Salience of Category](#)

Salter, Grammer, and Rokowski (2005)

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Synonyms

[Maintaining rank in dominance hierarchy](#); [Subordinate behavioral tactics](#)

Definition

Individuals who have lower status in the dominance hierarchy use elements of a behavior repertoire which help reduce the aggression of dominant group members.

Introduction

Throughout our lives, we are part of many different groups: school, sport club, book club, pet lovers' club, knitting club, and so on and so forth. In all these different groups, we all have our own role and position which might very well be different in each of them. And that is because humans, just like other animals, form hierarchies. Depending on the social context, people may have different ranks in different groups. In some cases, rank is achieved via aggression – the dominant individual defeating the subordinates. Leadership characteristics can also lift someone to dominant status.

The advantages of being dominant seem rather obvious: better access to resources and possible mates. At the same time, however, protecting

members of the group might expose them to danger. On the other hand, a subordinate enjoys certain advantages as well, mainly those coming from being a member in the group: safety, knowledge and information, and not having to solve in-group conflicts. This natural order is advantageous to all parties and is a means for minimizing aggression within the group (Eibl-Eibesfeldt 1989).

Tactics to Rise in the Hierarchy

Aggression, as it is, is more of a characteristic of male dominance negotiation: open fights for the top rank (Buss and Shackelford 1997). This, of course, would put a continuous strain on the opponents and the chance of suffering major injuries. For this reason, humans and animals alike use expressive movements such as facial expressions and other ritualized attack movements. One very common example of ritualized fighting is verbal conflict (Eibl-Eibesfeldt 1989). This, as opposed to physical aggression, shows no sex difference: females use verbal aggression just as much as men do. The difference between the two sexes regarding the type of aggression they are likely to use is in part the consequence of sex-specific intra-sexual strategies (Buss and Shackelford 1997), just as it is the consequence of childhood experiences (Lauer 1992).

Tactics of Subordinates

So far, research has accumulated many pieces of information on what negotiating dominance is like, but we do not know quite as much about the other side, namely, the tactics subordinates use. From animal studies it has been gathered that strategies of submission, such as nod of the head, making oneself seem “smaller,” prostrating oneself, and adopting a childlike manner, help block aggression of dominant individuals (Eibl-Eibesfeldt 1989). Smiles, humor, self-deprecation, and breaking eye contact are also appeasements that are meant to reduce others' agonistic motivations. It has also been observed that between sexes, flirtation is an affiliative tactic (Salter et al. 2005). For example, young women use physical attractiveness as a tactic to persuade opposite-sex strangers to do favors (Davies

et al. 2008). Sexual stimuli have been said to lower aggression in males (Salter et al. 2005).

Sex Differences in Subordinate Tactics

In their study, Salter et al. (2005) observed whether courtship signals serve as appeasement techniques when facing aggressive authority. For this purpose they observed the behavior of would-be patrons (i.e., people who wanted to enter) and doormen outside of a German nightclub.

The researchers analyzed video footages of patrons approaching a nightclub in Munich and their interactions with doormen. From the videos various behavioral categories were constructed. Doorman threat behavior included watching patron, turning and moving toward them. Greeting doormen, nodding, smiling, talking to doormen, touching their face or hair, putting their hands in pocket, parading, and swaying were considered patron behavior categories. Patrons' appearance was also rated, namely, their "sexiness": the tightness of clothing and the proportion of skin showing over the legs, torso, and arms.

There was a significant difference in attention and threat male and female patrons received from doormen when there was only one doorman. The average duration of threat from a single doorman was higher for men than it was for women. This difference, however, was not significant when there was more than one doorman.

As hypothesized by the authors, the behavioral repertoire used by the two sexes differed significantly. They also differed in approach speed, showing that men accelerated while women slowed down when there were three or more doormen present. The authors interpreted this strategy as "fleeing through the threat" when males try to minimize exposure in face of threat. This strategy also included minimizing anxiety by masking agonistic affects. On the other hand, women slowed down, the authors reason, to give themselves time to execute an appeasement strategy that involved mannerisms (i.e., behaviors performed predominantly by one sex) like parading, stroking their hair, smiling, and touching their face. Moreover, females' clothing style and their behavior showed a correlation which supports the notion that women's mannerisms are qualitatively

different from those of men. Women who were wearing clothes that were tight and left their legs bare also tended to show more mannerisms. The authors interpret clothing style as an interpersonal tool in appeasing male aggression and at the same time attracting mates, by releasing sexual motivation in them. An alternative to this is that stereotypical female dress and gestures enhance attractiveness (apart from being a tool for appeasement), which doormen use for judging whether to admit a female into the club or not. Using one's attractiveness has been also said to increase the chances of persuading an opposite-sex person to do a favor (Davies et al. 2008).

Conclusions

Belonging to a group with a stable hierarchy is advantageous for both dominant and subordinate individuals. Depending on the sex of the individual and the actual rank in the hierarchy, the behavioral repertoire used to maintain the status, and to avoid unnecessary collisions, may vary. Salter et al. (2005) presented data from real-life observations illustrating this assumption. Females seem to use sexually releasing behaviors to lower male aggression, whereas males try to mask their anxiety and minimize exposure time to threatening males.

Cross-References

- [Dominance Hierarchies](#)
- [Dominance in Humans](#)
- [Nonverbal Indicators of Dominance](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Social Dominance Reduces Fighting](#)
- [Status and Dominance Hierarchies](#)

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Salty

► Taste

Same Sex Aggression

► Intrasexual Violence and Aggression

Same-Different Categorization

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Synonyms

Difference judgements; First order relational reasoning; Sameness judgements

Definition

Same-different categorization refers to the ability to judge two or more objects or events as sharing an attribute or as being dissimilar with regard to an attribute.

Introduction

It is unequivocally accepted that humans have the capacity to reason about sameness and difference. It is also apparent that many animals share the capacity to generalize responses between items that are the same or different. Reasoning about sameness and difference at a more abstract level is more difficult to ascertain, however, and is important because it reflects an ability to think about relations between objects, rather than simply representing the perceptually apparent properties of the stimuli – a feat that many animals can easily perform. Scientists have acknowledged the importance of this ability from the dawn of the study of psychology.

Demonstrating Sameness/Difference Concepts in Nonhumans

Being able to detect similarities and differences amongst natural stimuli is critical for survival in any environment as this ability allows an organism to generalize what it has learned to other members of the same categories. For instance, an animal could learn that it is safe to eat fruits and vegetables but that it is not safe to eat other kinds of vegetation, such as poison ivy. The same animal can learn to avoid predators while not being alarmed by other prey species. Animals may make such generalizations by attending to perceptual features and learning to respond in similar ways to stimuli that possess a similar attribute, such as eating a fruit with a faintly sweet odor and bright color. However, to truly represent concepts for sameness and difference, it must be possible to show that animals can respond to items based on the relation of sameness or difference between these items regardless of whether specific attributes are the same or different. For example, an animal might know that the relation between a red grape and a purple grape is the same as the relation between a green pear and a yellow pear – both are sameness relations, but the actual colors differ. To make this assessment, the animal must attend to relational features, rather than absolute perceptual features of the stimuli.

In order to demonstrate same-different categorization at a conceptual level, it might also be useful to show that animals can classify items together based on a nonperceptually evident common feature. For instance, humans can categorize people based on qualities of introversion or extroversion and employment positions and can categorize various disparate objects into functional categories such as “household, decorative, tool, toy, etc.” Little empirical work has been done thus far to investigate these more abstract sameness judgements in nonhumans.

It is relatively easy to assess same-different categorization in most humans because researchers can ask individuals to indicate verbally which items are similar or different, what makes them similar or different, and which items should be classified together. Most animals cannot respond in such tasks, with the possible exception of Alex, the grey parrot, who answered questions such as “What is same” with responses such as “color, shape, and matter” (Pepperberg 1987). Despite this limitation, it is still relatively easy to assess same-different categorization at a purely perceptual level using a variety of paradigms that have been applied to nonverbal infants and extended to nonhumans ranging from honeybees (Giurfa et al. 2001) to chimpanzees (Parr and de Waal 1999).

With infants, researchers use habituation/dishabituation tests in which the infant is shown an image until looking time to the image declines (i.e., habituation). When researchers present a novel image, looking time increases, indicating that the infant recognizes the change in the stimulus. If researchers present the same stimulus after a short interval, infants do not look at it for very long, indicating familiarity, but after longer intervals, looking time increases again. This procedure tells researchers when an infant can perceive a stimulus as the same, even when it is presented at different time intervals. When children are old enough to make operant responses, but too young to verbalize similarities and differences, they may be presented with tasks such as sorting, in which objects of one type (e.g., based on shape, color) are placed in one container, while objects of another type are placed in a different container.

Nonhuman primates can be trained to perform sorting tasks as well. Sorting tasks can also be performed on the computer using the well-known Wisconsin card sorting task. A broader range of species have been trained in match-to-sample tasks where they are shown a sample (either a real object or a two-dimensional depiction) along with two or more comparison stimuli (either simultaneously or successively) and they are tasked with selecting the stimulus that matches the sample. Matches can be perceptually identical to the stimulus (as in identity matching) or share some attributes, such as shape or color (Vonk 2003), or match based on an underlying construct, such as numerosity (Vonk 2014), taxonomic category (Vonk 2013), relatedness (Parr and de Waal 1999), or emotional valence (Parr 2001). The perception of sameness can also be assessed by allowing subjects to indicate particular responses for members of the same category. For example, in many of Wasserman’s classic categorization tasks, pigeons are trained to select one key for flowers and different keys for cars, chairs, and people (e.g., Lazareva et al. 2004). Pigeons are successful at this task, indicating that they perceive the similarity between different members of the same class/category. Most of these tasks are presented on touch-screens where animals can directly contact the correct stimuli or response keys.

A more abstract concept of sameness and difference is tested when animals must respond based on the sameness relation between stimuli that are not themselves identical. That is, they must determine that the relationship between a group of items that are the same is the same relationship depicted by a different group of same items. Whereas many animals, including pigeons and rhesus macaques, can learn to match arrays of stimuli based on whether all of the items in the array are similar or different, their accuracy declines as the number of items in the array declines. Performance when only two items are depicted falls to chance (Wasserman and Young 2010). Orangutans and gorillas, on the other hand, successfully matched items based on shared shape or color when only two items appeared in the arrays (Vonk 2003). Although some researchers

have concluded that the ability to perceive abstract relations is unique to humans (Penn et al. 2008), these results from other great apes suggest that the capacity may be shared at least within the apes. These same apes were also able to match stimuli based on second-order relations (e.g., two items of the same shape were matched to two other items of a different shape when compared to two items of different shapes; Vonk 2003). Although insects, fish, birds, and mammals may share the capacity to match based on sameness, these results may be due to perception of variability or entropy, thus explaining why performance declines with fewer items in the arrays. Thus, although it is clear that many different species wield the capacity to respond to variability, it is not clear whether the underlying mechanisms for such behavior are the same as those that underlie understanding of sameness and difference as abstract concepts, as in humans (e.g., Wasserman and Young 2010).

Conclusion

Although the extent to which nonhumans truly represent sameness and difference at the same level of abstraction as humans do is debatable (Penn et al. 2008), it is clear that they are able to perceive similarities and differences and to use these judgements to inform responses.

Cross-References

- [Concept Formation](#)
- [Learning](#)
- [Non-Human Primates](#)

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Same-Different Concepts

- [Concept Formation](#)

Same-Gender Parents

- [Two-Parent Families](#)

Sameness Judgements

- [Same-Different Categorization](#)

Same-Sex Behavior

- [Alloparenting and Female Same-Sex Behavior](#)

Same-Sex Coalitions That Exclude Women

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Synonyms

Male coalitional psychology; Male-warrior hypothesis; Social dominance

Definition

Males show a preference for forming and maintaining large social groups composed of same-sex peers. This tendency is argued to be a mechanism for forming coalitions to engage in intergroup warfare.

Introduction

From a young age, males show a proclivity for forming large same-sex social groups. This is contrasted by the dyadic relationships generally preferred by females. One explanation for this preference among men to form large groups of same-sex peers is that it is an evolved mechanism for building and maintaining coalitions that function to protect the group from attack by outsiders and that can be used to attack outgroups. This entry will describe the evolutionary evidence for why such a mechanism should be restricted to men rather than women and review evidence from the literature providing support for the idea that these same-sex male coalitions serve the function of facilitating success in intergroup warfare.

Evolutionary Background

Observation and study of human history show that human aggression is typically perpetrated against

and by males (Daly and Wilson 1983). Differences in male and female reproductive physiology incentivize greater competition among males to secure access to mating opportunities. This includes competition among men within a group but also the banding together of men to protect the group and its resources from attack by outsiders, as well as the acquisition of resources from other groups via preemptive attacks.

These ideas are built on the foundation provided by parental investment theory which states that the sex that invests fewer resources into offspring (i.e., males) will compete more aggressively for mating opportunities (Trivers 1972). In other words, given their reduced obligatory investment to offspring, males can optimize reproductive success by increasing the number of females with whom they mate. However, this strategy requires a high level of competition with other males for mating access. In contrast, owing to their reproductive biology, females have a highly constrained reproductive ceiling and therefore benefit most from finding mates who will invest heavily in their offspring. As a result, female preference drives competition among males. A man's failure to compete can lead to the end of his lineage.

Given the male reproductive strategy, gaining access to reproductive resources is incredibly important. These resources can be direct (i.e., mating access to women) or indirect, such as in the form of financial resources or social status that attract women. Thus, engaging in intergroup conflict can be a highly beneficial endeavor as victory allows males of one group to acquire the resources of the defeated group (both direct and indirect). Although there are risks involved in one's participation in intergroup conflict, certain conditions can shift the balance of risk and reward. For example, Tooby and Cosmides (1988) have argued that warfare is most likely to be initiated when the chance of victory is high, when the risk of bodily harm is distributed equally across all members of the coalition, and when it is believed that any resources gained from conflict will be split equally among victors. Consequently, if warfare is only initiated when the

potential risk of a defeat is quite low, then the cost-benefit ratio may often favor warfare among males.

Building on these ideas, the male-warrior hypothesis (Van Vugt 2012) suggests that, owing to the reproductive advantages gained by men who engage in intergroup conflict under favorable conditions, men's psychology will be equipped with psychological mechanisms that function to motivate men to engage in warfare and that increase their probability of success. One such mechanism is the tendency to build large same-sex coalitions of males. Indeed, group size is a key predictor of warfare in tribal societies (Wrangham and Glowacki 2012). Along these lines, tribal warfare produces very few casualties on the side of the attackers, primarily owing to the asymmetric group size and the strategic advantage it affords. If large coalition size can function to deter attack from outsiders and nearly assure victory in asymmetric attacks on an outgroup, then men's preferences to form large coalitions of same-sex males should be quite strong.

Male Coalition Building

From a young age, males report larger peer groups as compared to the peer groups reported by females (Benenson 1990). Males are also significantly less likely than women to ostracize same-sex peers over an internal conflict, choosing instead to "bury the hatchet" (Benenson et al. 2013). This phenomenon is also exemplified by research examining post-conflict affiliation among competitors (Benenson and Wrangham 2016). The authors examined same-sex competitors, both male and female, and observed their behavior following competition to determine how long the competitors interacted with each other after the contest. Relative to females, males were significantly more likely to engage in post-conflict affiliation for extended periods of time. Men's willingness to move past the competitive interaction may function to promote coalitional solidarity. This solidarity is essential for helping a group pursue a focused goal in which group size is a key determinant of success.

Studies have also found a strong preference among young adolescent males to prefer same-sex peers with attributes associated with status within the peer group (Benenson 1990). Such attributes include a respect for authority, quality of work habits, athletic ability, academic ability, and whether they are a "fighter." Preference for such attributes may indicate a stronger proclivity for hierarchical systems of organization within groups that would enable greater efficiency while working toward a particular cause (i.e., war, competition, etc.).

Coalitional Functionality

When men form a coalition, group consensus/agreement reduces discontinuity and increases cooperation, which facilitates progress toward the coalition's agreed upon goals. Evidence that men seek to minimize the potential for disagreement can be seen in the behavior of men on the night before a war raid. At this time, men have been observed to banish women from the group to minimize whatever sexual conflicts might exist among the men in the coalition. Brown argues that females will inevitably create competition between the males of the group, thereby breaking down the trust within the group. Thus, excluding females may increase cohesion and cooperation among male members and therefore increase the probability of success in warfare.

Another driving force of men's behavior within a coalition is the fear of acting with cowardice, thus shaming themselves in the eyes of their comrades in arms (Browne 2001). This shame is an emotional tool used to encourage loyalty to the group. It also encourages risk-taking behaviors that increase trust among comrades. One's fear of cowardice may be particularly motivating given that perceived cowardice by one's group may carry severe costs. For example, refusal to participate in warfare may result in punishment, including ostracism from one's group (Boyd et al. 2003; Boyd and Richerson 1992). Similarly, when asked to judge the actions of unskilled versus cowardly male warriors, members of a nomadic pastoral society in Kenya

reported greater willingness to punish cowardice than lack of skill, including refusal to lend an animal or marriage to their daughters (Matthew and Boyd 2014).

Goldschmidt (1988) reviewed cultural influences on men's participation in raids and warfare in 27 non-state societies and concluded that there are strong systems of social rewards, and punishments, in place for warriors. Indeed, successful male warriors are often awarded high social status within one's group. For example, among the South American Yanomamö, men who kill another man in warfare are given the high honor of being labeled a "Unokai" and earn greater mating access as a reward (Chagnon 2013). Ultimately, risk taking and loyalty to a group in the context of intergroup conflict have tremendous potential for reproductive benefits, which motivates cooperation within a group under a variety of circumstances.

Conclusion

Males prefer large, cohesive, social groups of same-sex peers, whereas females generally prefer dyadic relationships. This preference among men may be best construed as a coalition-building mechanism that functions to promote men's success in intergroup warfare. When intergroup conflict occurs, men form coalitions that exclude women and fight to protect or gain reproductive resources. Such coalitions have served a significant evolutionary function in creating cohesive bands to fight and defend against outgroups in the struggle to advance the group's status in the social dominance hierarchy.

Cross-References

- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Feelings of Excitement and Brotherhood](#)
- [Information About Likely Combat Success](#)
- [Male Adaptations That Facilitate Success in War](#)
- [Mechanisms to Detect and Punish Cheaters](#)

- [Mechanisms to Prefer Traits in Coalition Members](#)
- [Members of Coalition Must Believe They Will Win](#)
- [Men but Not Women Will Have Adaptations for War](#)
- [Reproductive Benefits Must Outweigh Costs](#)
- [War More Likely with Higher Likelihood of Success](#)

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Same-Sex Friend

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Synonyms

Affiliative bonds; Associations; Coalitions; Female-female; Male-male; Social relationships

Definition

Same-sex friendships are lasting coalitions between individuals who are the same biological sex.

Introduction

Friendships are intriguing cross-species phenomena that clearly contribute to both fitness and survival. Friendships involve coalitions based on altruistic interactions over a long period of time. Unlike opposite-sex friendships, same-sex friendships are less likely to include sexual motives. Although affiliative bonding is common in a large number of species, humans may be unique in the extent to which this happens among unrelated individuals. The theories that have been used to explain same-sex friendships are mainly reciprocal altruism and kin selection, which will be reviewed briefly below.

Kin Selection and Same-Sex Friendships

Research that investigates proximate determinants of friendships has found that friends are genetically similar (Christakis and Fowler 2014), suggesting that friends are viewed as extended kin

(Brent et al. 2014). Women especially have the tendency to treat close friends as kin (Ackerman et al. 2007), which could be part of an evolved mechanism for establishing and maintaining close social bonds. During human evolution, ancestral women had high rates of migration from their natal groups, which could explain the importance of friends for women as a kind of a functional kin. When emotional closeness is high, altruism in friendships can be as strong as between genetically related kin. However, in order to flourish, friendships need more maintenance than kinships do. Therefore, friendships are not based on the same behavioral principles as relationships with kin are, and kin selection alone is insufficient in explaining evolution of same-sex friendships.

Reciprocity and Same-Sex Friendships

Although long-term collaborative relationships with non-kin can be explained by the theory of reciprocal altruism, friendships do not form a straightforward case. Friendships do not seem to involve keeping a tally of whether favors are reciprocated, which leaves room for cheaters to flourish (Silk 2003). On the other hand, an expectation of reciprocation in friends is higher than among siblings (Rotkirch et al. 2014). This suggests that friends are not completely exempt from the rules of reciprocation. In order to maintain reciprocation and deter cheating, friendships are characterized by high levels of trust and emotional closeness. Trust plays an important role in friendships not only in humans but also in our closest relatives, chimpanzees (Engelmann and Herrmann 2016). Thus, reciprocity in friendships requires high levels of trust and emotional closeness, and when these are lacking, there may be more “bookkeeping” in reciprocation of favors.

Conclusion

Friendships are a widely spread phenomenon in the animal kingdom, and the ability to form affiliative long-term bonds with unrelated individuals clearly has evolutionary benefits. Same-sex friendships can be explained by the theories of kin

selection and reciprocal altruism. Friendship selection may have a base in assortative choice for genetic similarity, which suggests that friends could be viewed as extended kin. Although close friendships do not involve conscious counting of favors, it is possible that reciprocity is maintained via high levels of trust and emotional closeness.

Cross-References

- [Altruism](#)
- [Altruism Among Nonkin](#)
- [Friendship](#)
- [Gender of Friend](#)
- [Kin Selection](#)
- [Reciprocal Altruism](#)

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Same-Sex Friendships

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Synonyms

[Cooperative alliances](#); [Friendships](#)

Definition

Same-sex friendship is a nonsexual and nonfamilial communal bond characterized by voluntary independence between two same-sex individuals.

Introduction

Friendship is a unique dyadic relationship that is not only cherished but also sought after for a variety of reasons in almost every culture studied. Not surprisingly, there is a word describing a relationship established outside the kin environment in nearly all cultures and languages. Even though some of these words share a common root with kin-relation words, they over time became uniquely associated with the idea of friendship (Krappman 1996).

One critical issue in defining friendship concerns the possible overlap with other relationships. The theorized lack of sexual relations between friends differentiates it from relationships specifically formed to address mate attraction and retention. Also, the idea of voluntary interdependence as one of the defining feature of friendship is essential for distinguishing relationships with kin from those involving nonkin. That friendship is psychologically, objectively, and subjectively different from kinship and that it is a nonfamilial bond is a critical distinction. The importance of this distinction is sometimes highlighted at the theoretical level (Park and Ackerman 2011) and frequently encouraged at the methodological level (Demir et al. 2015). Yet, our ancestors were likely to call friends those who were genetically related (Hruschka 2010), a tendency, albeit to a lesser degree, still observed in modern times. Also, when the friendship between two unrelated individuals exceeds a certain level of closeness, people consider the friend as part of the family by calling each other brothers or sisters. This prompted some scholars to postulate that people can be both kin and friends. From an empirical point of view, however, not differentiating friendship as a bond between nonrelatives from other relationships could hinder scientific progress in the understanding of the benefits and costs associated with this

cherished bond and create a problem in testing the utility of various theories explaining why and how we form and maintain friendships. Without proper definitions and differentiation, we might be studying the “friendships” between uncles, mothers and their offspring, and nonrelatives at the same time, while it is clear that these relationships serve different functions and roles.

Same-sex Friendships

One could generate a synthesis to define friendship from the myriad definitions reflecting the perspective of the Western world. Accordingly, friendship is defined as a nonsexual and non-familial communal bond characterized by voluntary interdependence between two individuals. The continuity of this voluntary independence promotes an unrestricted closeness that facilitates and promotes the experience and satisfaction of various provisions such as intimacy, affection, in/tangible mutual aid, companionship, self-validation, emotional security, and comfort to varying degrees. An evolutionary perspective would make a meaningful contribution to this list by highlighting some critical functions friends serve such as providing help to address mating-related issues and forming cooperative alliances. Yet, while some of the indispensable notions and provisions of Western conceptualization of friendship such as mutual aid is similar in every culture studied (Cohen 1966), the eloquent work by Hruschka (2010) showed that some of these features such as voluntariness of the bond, frequent socializing, and self-disclosure display significant variety across cultures and in some cases are absent.

Notably, there are different types and forms of friendships observed in various cultures such as inalienable, expedient, casual, and close friendships (Cohen 1966). These different forms of friendships vary on the level of closeness and support provided or received in the relationship. Inalienable friendship, for instance, concerns the institutionalization of the bond via rituals that serve the goal of conversion to a fictive kin. The conceptualization of same-sex friendship that

represents varying degrees of interdependence is similar to Cohen’s close friendship form.

Much of the literature has treated friendship as a same-sex phenomenon, specifically a bond between two males. This emphasis, sometimes romanticized, was evident in ancient societies and cultures and dominated the writings of classical philosophers. Although females were establishing and incurring the many benefits of friendships with other females, the empirical and literary attention to this unique dyadic experience is relatively recent.

Friendship usually involves same-sex peers, with the majority of adults’ friendship networks, and overwhelmingly best and closest friends, consisting of same-sex peers (Demir et al. 2015). Although people establish and maintain platonic opposite-sex friendships (OSFs), and incur benefits not available in same-sex friendships (e.g., the provision of insider perspective that entails learning about how the other sex feels and thinks), OSFs are perceived as gateways to sexual and romantic experiences, usually for heterosexual men. Indeed, the preferences for and selection of OSFs overlap considerably with mating strategies and preferences (Lewis et al. 2011).

Benefits and Costs of Same-Sex Friendships

In pursuing an understanding of same-sex friendships, an evolutionary perspective would address the puzzle of why friendships evolved in the first place and what functions they served. Hruschka (2010) argued that friendships served to address the “common adaptive problems of cooperation and mutual aid in uncertain contexts” (p. 10). Forming cooperative alliances with nonkin would have provided direct and indirect benefits linked to survival, adaptive problem solving (i.e., finding mates and retaining them, alloparenting), and well-being. Previous research has theorized friendships to be governed by reciprocal altruism, which is the expectation that each friend is contributing equally to the friendship. This involves keeping track of the other’s contribution, with failure to put in equal contributions resulting in conflict.

However, this view may not be useful to understand friendships. Specifically, in an interdependent bond where people show sincere concern for each other's well-being, a tit-for-tat exchange would not only be destructive and but also almost impossible to maintain. Besides, males and females do not generally report monitoring their friends' inputs and consider doing that as a violation of friendship (Park and Ackerman 2011). Instead, friendships have been viewed as being communal in nature and are governed by cooperative coalitions where support is provided on a need-by-need basis. Engaging in this communal relationship highlights the importance of being selective who one chooses as a friend (Tooby and Cosmides 1996). Given that costs arise in any given relationship (i.e., cheaters, freeloaders), individuals thus must limit their friendships to people who display deep engagement and are worthy of both tangible and intangible investments. The benefits of same-sex friendships, however, appear to balance or offset the costs, especially when one becomes irreplaceable (Tooby and Cosmides 1996). Becoming irreplaceable ensures that friends will be concerned with and invested in each other's well-being.

One benefit of same-sex friendships for both sexes concerns finding and retaining mates. Men and women appear to prefer establishing friendships with people who are desirable to the opposite gender; forming this relationship gives them access to more potential mates. This may explain why men tend to value instrumental characteristics (i.e., attractiveness, athleticism) in friendships (Lewis et al. 2011), while women seem to value physical attractiveness and interpersonal traits such as kindness (Vigil 2007). The benefit of gaining a larger mating pool from friendships does come at a cost: rivalry over mates. Both men and women experience feelings of rivalry with their friends over potential mates, with the less attractive friend reporting a higher amount of perceived rivalry. Furthermore, both sexes not only report more negative emotions when rivalry comes from a friend rather than a stranger, but they also will downplay their sexual promiscuity to avoid scaring off potential friends, with women being slightly more sensitive in these domains

than men (Bleske and Shackelford 2001). In terms of how these issues are addressed in friendships, it has been argued that men and women evolved to favor people who are not perceived as mating rivals for friends, and when these issues do arise in friendships, individuals may be forced to reevaluate whether the friendship is truly beneficial to them. Thus, being selective in friendships not only produces the benefit of mate selection but also minimizes the cost of mating rivalry.

Similarities and Differences in Males' and Females' Same-Sex Friendships

Given the universality of same-sex friendships, it is not surprising that men and women are similar to each other in terms of certain aspects of friendships (Hall 2016). For instance, propinquity, or mere proximity, is one factor contributing to the development of a friendship for both sexes. Also, both males and females value similarity in their same-sex friendships, and they are similar to their friends in a number of domains ranging from age to interests, personality, and physical attractiveness. Another domain in which males and females do not differ concerns the social meaning of the friendship, referred to as the deep friendship structure (Hartup and Stevens 1997). This is contrasted with the surface structure capturing the actual social exchanges in the friendship. Accordingly, males and females are on the same page about what friendship is, the rules governing friendship, and the value of having friends. Yet, differences arise in the way friendships are experienced between males and females, some of which could be explained by the fact that historically they were required to perform different tasks within their communities (i.e., hunting vs. gathering) and had different adaptive problems to address.

Male and female same-sex friendships differ on a number of domains, including intimacy and self-disclosure, friendship expectations, and stability. These differences can be prefaced with the common notion that female same-sex friendships are "face-to-face" relationships, while male same-sex friendships are characterized by "side-by-side" interactions (Wright 1982). In essence, women opt

to engage in more emotional experiences, while men strive for more shared experiences.

One well-established pattern in same-sex friendships is that males tend to have lower levels of intimacy and self-disclosure than females. Men spend less time talking with their best friends and more time engaging in activities with friends. Furthering this idea, men not only display less intimacy but also appear to sacrifice intimacy for a greater number of friendships. Furthermore, men report higher numbers of close and best friends, along with a desire to have more friends with less intimate behaviors (i.e., support). In contrast, females display the opposite trend: they opt for fewer, but more intimate, friends. Similarly, they also tend to engage in more self-disclosure and relational maintenance behaviors (i.e., tending to and being aware of each other's needs) than their male counterparts in their same-sex friendships.

Notably, sex differences in intimacy were observed across studies relying on different assessments of intimacy. Of course, one is not referring to an all-or-none issue here such that males do experience intimacy in their same-sex friendships but not to the extent females do. This suggests that males and females have a similar understanding of what intimacy is and how to achieve it in same-sex friendships. Rather, males do not prefer to engage in intimacy promoting behaviors in their same-sex friendships as much as females do. Males' avoidance of intimacy might be evolutionarily functional such that intimate disclosures to a same-sex friend might hurt their reproductive success in the case of the termination of the friendship (Shackelford and Buss 1996). Also, cultural norms and gender roles such as encouraging emotional restraint for men and homophobia toward gay men explain why same-sex friendships are less intimate and supportive among men than women (Bank and Hansford 2000). Although these constraints and concerns reinforce the belief that males might prefer to have less intimate friendships, they might not be content with this preference as research has shown that males ideally want to experience more intimacy and support in their same-sex friendships (Demir and Orthel 2011).

Despite lower levels of observable intimacy, male friendship persists. Male friendships not only display less reciprocity and intimacy than female friendships but also they appear to be more tolerant of their same-sex peers (Benenson et al. 2009). Also, these friendships appear to last longer and be more resistant to deterioration after conflict. These trends make sense, as research has found men to be less affected by aggression committed by their same-sex peers and are more likely to move past the conflict than women (Benenson et al. 2014). On the other hand, female friendships have been characterized not only by higher expectations of reciprocity and intimacy but also by shorter durations and more emotional conflict. The connection is clear; higher standards are more difficult to live up to, and thus failing to meet them might be more common. When expectations are not met, conflict may ensue.

Explaining Sex Differences in Same-Sex Friendships

From an evolutionary perspective, sex differences in same-sex friendships can be explained in number of ways. Evolutionary psychologists have theorized that the trends in male relationships evolved to better suit them for survival (Buss 2015), and one useful framework in which functions of male friendships can be understood is the structure of cooperative coalitions, or the alliance hypothesis (DeScioli and Kurzban 2009). This hypothesis, in essence, states that when three or more parties are competing for resources, forming an alliance with one of the other parties would mean that the members of the alliance have a better chance of getting more resources than the lone third party. This hypothesis differs from other exchange theory models in one important way: it is not based on equal reciprocity, but rather the expectation that one will provide support in a time of need. This may explain why in general men tend to have lower expectations of reciprocity and intimacy than women.

Early human groups followed the hunter-gatherer model, where men typically did the hunting of big game and fighting with other groups.

Although researchers have described sex differences in expectations of reciprocity as slight (Hall 2016), it is possible they served an important role. Considering that male relationships tend to have high levels of competition (Buss 2015), forming a social structure in which competition is replaced with cooperation would have been adaptive to acquiring more food and security. These slight differences in expectations, which promote stable relationships, may have played an influential role in ensuring the continuity of friendships and social structures in ancestral communities. This is coupled with the findings of Vigil (2007), who found men to report higher levels of cooperation. These lower expectations and greater willingness to cooperate with nonkin may explain why men report a larger network of friendships. This idea is corroborated by a recent study that found that men prefer to form larger coalitions with other males, while females prefer intimate, dyadic relationships (David-Barrett et al. 2015). This may serve to explain why males not only have larger friend groups (i.e., more allies) but also why they value traits like athleticism and power. Befriending individuals with these traits would have increased their collective strength and status.

Female friendships are theorized to have functioned as a means of developing supportive networks and protection. The slightly higher expectations of reciprocity from females may have evolved to facilitate survival. Historically, females mated outside of their kin networks, throwing them into a community of strangers. In stressful and harsh situations like this, they needed to be skilled in establishing supportive relationships with other nonkin, which would have provided them and children with safe and supportive environments. When presented with stress or conflict, males typically exhibit a fight-or-flight response; females, however, opt for a “tend-and-befriend” strategy (Taylor et al. 2000). Considering females were typically assigned the role of caring for children, choosing to engage a threat or uncertain situation with a fight-or-flight response could have endangered their children or other children they were caring for. Thus, creating a strategy to manage stress that involves both tending to their children and befriending other

women to create a protective social network would have been a more adaptive survival strategy for females and their children. This strategy may also explain why they have higher expectations in reciprocity and self-disclosure; women who were able to live up to these higher expectations would have been more likely to reliably provide support in times of need.

Establishing these relationships and meeting high expectations would have created an environment where they both supported and were supported by other women in domains such as child care and would have had a protective network from other males. The practice of alloparenting would have provided the benefit of shared parenting responsibilities between women; however, this placed children in a position to be harmed by other women. These stricter standards for friendships would have ensured that the women they invested personal trust and resources in would be able to provide support and safety for them. While men formed alliances to gather resources, women tended to rely much more on each other for their well-being. Thus, higher expectations of friendship behaviors may have allowed them to parse out which individuals were both beneficial and willing to engage in reciprocal support for them. This may explain why these friendships tend to display more conflict and early termination, because not meeting expectations may have alluded to unreliability in times of need or a lack of investment in each other’s well-being.

Same-Sex Friendship and Well-Being

From an evolutionary perspective, another function of same-sex friendship would be its contribution to survival by promoting the mental and physical health of the individuals. To the extent that the paradox created by modern living is addressed by establishing deeply engaged friendships as opposed to ambivalent friendships (Tooby and Cosmides 1996), males and females likely incur additional benefits from their same-sex friendships. For instance, positive same-sex friendships might be the antidote to feelings of loneliness and alienation, concerns prevalent in modern life. Although social integration and diversity of relationships have been

shown to predict health, longevity, and survival (Holt-Lunstad 2016), the specific role of same-sex friendships is not clear. However, since same-sex friendship experiences are robust correlates of happiness, and happiness promotes longevity and physical health (Diener and Chan 2011), it is possible that same-sex friendships add to the prediction of survival and physical health. As for happiness, although it is argued that social relationships would be more important for females than males, research on adult same-sex friendships has found that both sexes benefit similarly from the quality of their same-sex friendships (Demir et al. 2015).

Conclusion

The existence of same-sex friendships in every culture studied suggests that it is a valuable relationship. Ostensibly one should be careful in choosing a same-sex friend for it entails costs related to reproductive success. Yet both sexes establish and maintain interdependent same-sex friendships and reap the many benefits this cherished bond entails. Although the internal constitution of the friendships might be different for males and females, the ultimate beneficial impact is the same. Future research has the potential to enhance our understanding of how, when, and why same-sex friendships are beneficial.

Cross-References

- Cooperative Alliances
- Cost of Same-Sex Friendships
- Friendships
- Mating Rivalry
- Reciprocal Altruism
- Specific Friendships

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Same-Sex Homicide

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Synonyms

Intrasexual homicide; Intrasexual killing; Same-sex murder

Definition

The intentional killing of someone in which the perpetrator and victim are the same-sex, that is, both are male, or both are female.

Introduction

There are four combinations of perpetrator-victim relations by sex: men killing men, men killing women, women killing men, and women killing women. The proportion of homicides that occur in each of these categories is not equal, contrary to the expectation when random occurrence is hypothesized in large populations. Rather, the majority of homicide cases consist of men killing other men. When you look specifically at same-sex homicide, male-male homicide occurs much more frequently than female-female homicide, especially between unrelated persons, across many different societies and cultures, and spanning long periods of time (Daly and Wilson 1988). This entry will discuss an evolutionary explanation for this phenomenon.

Violence and Sexual Selection

Most homicides occur as a result of a conflict between individuals. Homicide cases where victims were randomly chosen without any particular personal conflict are very rare. The nature of conflict is variable, depending on the relationship among the people involved: whether they are families, lovers, or unrelated acquaintances. Common motives of men killing unrelated men are predominantly competition over social status, face, pride, and reputation, as well as conflict over more tangible material resources. Despite the seeming triviality of these motivations, more than half of male-male homicides across many different societies are precipitated by a conflict over status or reputation. Evolutionary psychology provides a functional explanation for why this behavior occurs and why it is most common among men.

Key to understanding the sex differences in the rates of same-sex homicide are the theories of parental investment and sexual selection (Trivers 1972). Male's obligatory investment of time and energetic resources in offspring is quite minimal, whereas the required investment of females is extensive. As a result, men are capable of having many more offspring in their lifetime than are

women. Women are therefore the limiting resource that constrains men's reproductive success. The consequence of this is that there will be greater variability in the reproductive success of men compared to women. This is amplified by the fact that most small-scale, traditional societies practice polygyny. Moreover, many hunter-gatherer societies that are regarded to be "egalitarian" permit men to have extra-wives. Thus, men must compete with other men for access to mating opportunities or risk reproductive oblivion.

This competition may take the form of direct competition for access to a female or competition for resources, status, and prestige that will indirectly increase reproductive success by increasing one's appeal to females. Therefore, winning competition should have been a critical issue for men during the long history of human evolution. Material resources such as cattle or land are not necessarily the purpose of gain per se but ultimately a means to increase reproductive success. Under these conditions, men will be willing to take large risks in competitive situations because the alternative strategy of opting out of competition drastically reduces one's chances of acquiring reproductive opportunities (Daly and Wilson 1990). From this perspective, homicide can be viewed either as a by-product of adaptations for engaging in competition or as a direct adaptation for removing intrasexual rivals competing for the same mates.

Cases in women killing other, unrelated women are quite rare. However, this does not mean that women do not engage in intrasexual competition. Given women's large investment in offspring and their limited lifetime reproductive output, there is less incentive for women to compete with each other in order to increase the quantity of mating opportunities. Rather, women are likely to compete with one another in order to gain and maintain access to the highest quality mates, for example, those best able to ensure the survival of the mother and her offspring, those with high genetic quality, and those with ample resources to help provision of offspring.

However, because their own survival is essential and more important to infant survival than father's survival, women have lower threshold

for fear in situations that pose bodily injuries and higher threshold for employing physical violence in a competitive situation than men. Engaging in high-risk violent competition poses a serious threat to their reproductive fitness (Campbell 1999; Sear and Mace 2008).

Consequently, women adopt more subtle, indirect tactics such as gossip and social exclusion, thereby attacking the competitor without the danger of physical violence. Because a woman's own survival is critically important for her reproductive success, it is reasonable to assume that there has been a strong selection for women to use indirect tactics for intrasexual competition that would unlikely to result in personal injury or death (Campbell 2006). Considering this, the relative rarity of same-sex homicide among women is consistent with evolutionary theorizing.

Conclusion

Male-male homicide occurs much more frequently than female-female homicide, especially among unrelated individuals. This is fundamentally due to the sex difference in parental investment, leading to that male-male competition for the access to females being much more stronger than female-female competition. From this perspective, homicide can be viewed either as a by-product of adaptations for engaging in competition or as a direct adaptation for removing intrasexual rivals competing for the same mates. This does not mean that there is no competition among women; rather, there is a great deal of competition among women for access to high-quality men who are willing and able to provide parental investment. However, because women's own survival is critical for their reproductive success, women tend to avoid risking bodily injury, resulting in lower occurrence of female-female homicide.

Cross-References

- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Contexts for Women's Aggression Against Women](#)

- [Meta-Analysis of Sex Differences in Aggression](#)
- [Sex Differences in Same-Sex Aggression](#)

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Same-Sex Murder

- [Same-Sex Homicide](#)

Same-Sex Relationships

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Synonyms

[Coalition members](#); [Companionships](#); [Fellowships](#); [Friendships](#); [Partnerships](#); [Peer relationships](#)

Definition

Same-sex relationships are intimate affiliations between individuals of the same chromosomal

sex and/or gender that typically share homogeneous characteristics such as age and social status.

Introduction

The formation of same-sex relationships evolved to provide a context for humans to engage in reciprocal interchanges of resources with and learn sexually specialized behaviors from conspecifics. Same-sex relationships also serve as the ecological context in which *intrasexually* selected characteristics are expressed and moderate certain social fitness outcomes.

Evolutionary Origins

The social nature of humans consists of sexually specialized cognitive and behavioral adaptations that are developed and expressed in the context of and ultimately function for regulating same-sex relationships. These relationships evolved in humans and other socially dependent animals for extracting reproductively indirect resources, such as protection, shared effort, and sociopolitical opportunities, from the types of conspecifics that are most likely to reciprocate such resources.

Adaptive Significance

Formation of same-sex relationships in humans enhances survival and reproductive success by providing the ecological context in which characteristics that have been selected by intrasexual (within-sex) fitness pressures are learned and refined. Same-sex relationships also enable individuals to extract ecologically valid resources from the types of social affiliates that are most likely to reciprocate such resources.

Homophilic Peer Preferences

Same-sex relationships are usually formed among people that share similar characteristics such as

age, physical features, and social status. Homophilic peer preferences ultimately facilitate the formation of alliances between individuals with similar *reciprocity potential*, or perceived value to other people, by creating an opportunity in which both social agents can reciprocally benefit through mutual exploitation (Vigil 2007).

Sex Differences in Communication Styles

Humans engage in specialized communication styles for interacting with either males or females. These differences reflect the disproportionate use of behavioral advertisements of the capacity and trustworthiness components of human reciprocity potential for regulating different types of peer network structures (Vigil 2009). While men tend to form larger and more fluid peer networks and express higher levels of behaviors that demonstrate *immediate* capabilities, females tend to form smaller, more intimate networks and express higher levels of behaviors that demonstrate *continuous* reliability. These distinct sociorelational styles are comprised of what are conventionally referred to as “dominant” and “submissive” social behaviors, respectively.

Conclusion

Formation of same-sex relationships facilitates fitness and reproductive success in humans by exposing individuals to other social agents that are most likely to engage in reciprocal altruism. These specialized and functional forms of affiliation also provide the context in which certain sexually selected characteristics are developed and expressed. To date, the form and function of same-sex relationships have been linked to the development and expression of numerous life history traits, physical traits (Vigil et al. 2015), perceptual responses (Vigil et al. 2014), social behaviors (Vigil 2008), self-descriptions (e.g., self-esteem; Vigil et al. 2011), and medicine, including the expression of disease, pain (Vigil and Coulombe 2011; Vigil et al. 2013), health promotion behaviors, and the manner in which

people are evaluated and treated by health care professionals (Vigil and Alcock 2014).

Cross-References

- [Biology of Human Gender, The](#)
- [Emotional Disposition](#)
- [Evolution of Cooperation](#)
- [Intersexual Selection](#)
- [Intrasexual Selection](#)
- [Male Coalitions for Hunting](#)
- [Masculinity and Femininity](#)
- [Peer Socialization](#)
- [Reciprocal Altruism](#)
- [Sex Differences](#)
- [Sex Differences in Social Development](#)
- [Sexual Selection in Evolutionary Psychology](#)

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Same-Sex School Bullying

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Synonyms

Aggression; Direct bullying; Indirect bullying; Intersexual selection; Intrasexual competition; Victimization

Definition

Bullying is a behavior used to intentionally cause harm on less powerful individuals to obtain tangible, social, and reproductive resources (Volk et al. 2014). Same-sex school bullying includes intrasexual bullying, when boys bully boys and girls bully girls in order to achieve these goals. Often, same-sex bullying behaviors occur outside of the classroom setting, including school hallways, washrooms, and lunchrooms, where there may be less adult supervision (Kasen et al. 2004). Under specific school ecologies, same-sex school bullying may be more adaptive for children and adolescents.

Introduction

Same-sex school bullying may serve adaptive functions for children and adolescents. This may be why a significant proportion of youth, anywhere from 30 % to 40 %, are involved in school

bullying as the perpetrator (15 %), victim (14 %), or bully-victim (i.e., individuals who are both perpetrators and victims; 4.4 %; e.g., Espelage and Holt 2007; Hymel and Swearer 2015). School bullying peaks during the transition from middle to high school (Juvonen and Graham 2014), suggesting that bullying may serve more benefits than costs during this time period. The benefits of bullying during this developmental period may be a result of two key social changes. First, there are many new peers at the start of high school, which encourages the reformation of peer networks (Juvonen and Graham 2014; Pellegrini and Long 2002). Second, adolescence coincides with sexual development, which may heighten the desire for dating and mating relationships. Therefore, school bullying may serve adaptive purposes during these two important social changes.

Goals of Same-Sex School Bullying

Adolescents may strategically use same-sex school bullying for three primary goals: (1) obtain material resources, (2) establish dominance among same-sex peers, and (3) attract opposite-sex peers for reproductive opportunities (Volk et al. 2014). Several studies support these goals of same-sex school bullying. For instance, adolescent bullies often are high in social status with same-sex peers, especially when targeting victims who were disliked by other same-sex peers (e.g., Veenstra et al. 2010), demonstrating dominance and status goals. In addition, bullies often start dating and have more sexual partners during adolescence than nonbullies (e.g., Volk et al. 2015), demonstrating reproductive opportunities. While these studies demonstrate that the functions of same-sex school bullying may be the same for both sexes, the mechanisms and behaviors used by boys and girls to achieve these resources, status, and mates may differ. For example, Dijkstra et al. (2007) found adolescents have different criteria for same-sex peer acceptance and rejection in comparison to cross-sex peer acceptance and rejection. Boys are more accepting of boys and girls who show prototypical “boy” behaviors, while girls are more accepting of girls and boys

show prototypical “girl” behaviors. However, within both sexes, same-sex peers who showed prototypical cross-sex behaviors were more likely to be rejected. Thus, at a developmental period when status with same- and cross-sex peers is significant, the criteria to achieve acceptance and status may differ intrasexually. Evolutionary theory may help explain sex differences in the way adolescents use same-sex bullying as a tool to achieve material, social, and sexual resources.

Parental Investment and Sexual Selection

Differences in reproductive variability may explain why there may be intrasexual variation in school bullying strategies for adolescent boys and girls. According to the parental investment theory (Trivers 1972), females are the higher investing sex when it comes to parenting and offspring survival. Since females are often the primary caregivers for human offspring, they directly invest more resources per offspring including feeding and guarding, in comparison to males. As a result of the unequal parental investment, the sexual selection theory (Archer 2009; Daly and Wilson 1998) explains that there are different selection pressures for males and females. While males’ reproductive success is dependent on access to willing females, females’ reproductive success is dependent on choosing the best suiting male (Trivers 1972). Therefore, although the goals of bullying may ultimately be the same for all adolescents, given the differences in reproductive roles, it is logical for same-sex bullying to differ in behavior and strategies in adolescent boys when compared to girls.

Same-Sex School Bullying in Boys

Since boys have to compete with other boys for access to girls, boys may have more benefits when engaging in overt competition in comparison to girls. Indeed, sex differences in forms of bullying peak during early adolescence (Archer and Coyne 2005). When compared to other forms of aggression, the largest sex difference is for physical aggression (e.g., hitting, punching) in favor of boys (Archer 2004). Moreover, multiple studies on adolescent bullying found support for this sex difference in physical bullying (Hong and

Espelage 2012; Hymel and Swearer 2015). Overt physical bullying may be adaptive to boys as it may increase reproductive fitness through two key methods.

First, physical behaviors allow boys to compete with other boys to establish status among same-sex peers (Archer 1996). By targeting a weaker victim through the use of physical bullying, boys can secure a high, powerful role in their peer hierarchy (Ellis et al. 2012). Physical bullying behaviors can eliminate same-sex rivals who are competing for the same resources, while deterring future rivals by signaling costs to engaging in physical conflict (Volk et al. 2014). Rodkin and Berger (2008) support this idea when they found adolescent boys who bully weaker boys were more popular by their peers. Moreover, Sijtsema et al. (2009) found that boys who bully had high status goals. As a result of establishing status, boys may then have increased access to material resources, such as food, money, or school territory (Volk et al. 2014). Therefore, the first way physical bullying increases reproductive success for boys is by enhancing one’s own status and access to material resources at the expense of other same-sex peers.

The second way physical bullying can increase reproductive success is by demonstrating features that may be attractive to opposite-sex peers (Archer 1996). Given that girls are the selective sex when it comes to picking mates, boys may use physical bullying as a method to demonstrate toughness and bravery (Archer 2009; Benenson 2009; Ellis et al. 2012). For example, Rodkin et al. (2006) found that adolescent girls were more likely to nominate boys they thought were tough as being cool in comparison to nontough boys. Exhibiting physical strength may signal the ability to provide material resources and protection to offspring, which may encourage girls to pick them as a mate (Ellis et al. 2012). Thus, boys may use physical bullying to both display their resources and seek girls as a specific type of resource. Pellegrini and Bartini (2001) support this idea in a study on bullying among adolescent boys. As these boys aged, physical bullying was associated with increased dominance, popularity, and dating. Similar results were found by Veenstra

and colleagues (2010) as boys who bullied other boys were rated in high acceptance by girls. Therefore, the second way physical bullying increases boys' reproductive success is by attracting girls who may select them as a mate. Bullying may also increase reproductive success for girls, but the mechanisms and behaviors may differ from boys.

Same-Sex School Bullying in Girls

Girls engage in less overt competition when compared to boys. This may be due in part to different selective pressures. According to the parental investment and sexual selection theories, females are more discriminating than males when selecting a mate (Trivers 1972). This may be because reproduction is a costly event both biologically during pregnancy but also after birth. Human offspring are born dependent on mothers as primary caregivers for resources including safety, warmth, and food (Hrdy 1999). In fact, survival for the first 2 years of an infant's life is often dependent on the survival of their mother as documented in multiple societies (Sear and Mace 2008). Thus, it is in a female and her offspring's best interest to expend resources on parenting as opposed to overt sexual competition (Trivers 1972; Hrdy 1999). As a result, females are more selective than males in choosing a mate who demonstrates not only his ability to contribute healthy genes but also his ability to provide material resources that could aid maternal care (Hrdy 1999). However, this does not mean that adolescent girls do not engage in bullying at all. Instead, girls may strategically use covert bullying behaviors through two important methods.

First, indirect bullying behaviors such as social exclusion and rumor spreading may be advantageous to adolescent girls, because they can reduce the attractiveness of competitors, without expending physical resources. While boys may use physical bullying to demonstrate their own ability to provide resources, girls may strategically use indirect bullying as a way to show how rivals may not be able to provide maternal resources (Archer and Coyne 2005). Girls' indirect behaviors often denigrate features that are ideal to boys, such as an attractive physical

appearance and lower sexual promiscuity (Geary 1999). These qualities are often targeted since they signal reproductive health to boys. Thus, girls who allow sexual access to boys would threaten and reduce other girls' power to be selective when choosing a mate (Benenson 2013; Campbell 2004). For example, in a study by Vaillancourt and Sharma (2011), undergraduate women perceived other women who dressed attractively as more negative and threatening. Therefore, these individuals may make for a logical target to bully among girls. Leenaars et al. (2008) support this idea when they found that adolescent girls who were more physically attractive and had more dating and sexual partners were at a higher risk for indirect victimization from other girls. Similarly, Rodkin and Berger (2008) found that victimized girls were rated higher in peer-valued characteristics such as physical competence and social preference, in comparison to victimized boys. This suggests that while boys victimize weaker boys, girls victimize girls that may have some resources and pose a threat. Consequently, strategically excluding or gossiping about girls' appearance and sexuality within girls' close peer networks may subtly reduce the mate value of rivals to boys, while increasing their own status, dominance, and value.

Thus, similar to boys, the second way engaging in same-sex school bullying may increase reproductive success for girls to enhance one's own status and dominance in same-sex peer networks. However, the way girls establish dominance may be different than that of boys. While boys use physical behaviors to establish dominance, girls use social knowledge such as personal information and stories about their peers, as demonstrated through indirect bullying to establish status. For example, indirect bullying was associated with social knowledge, which reinforced girls' membership in a powerful social group (Owens et al. 2000). Moreover, Coyne et al. (2006) found that when compared to boys, girls reported indirect forms of bullying as more harmful to their social relationships. Therefore, appearing to have a lot of social resources may boost status and social power among other girls.

In turn, being a member of a powerful girl social group may lead to accessing additional material resources, as well as high-status boys who girls can then choose as a dating or mating partner. Pellegrini and Long (2003) and Sijtsema and colleagues (2009) support this idea as they found higher levels of aggression and bullying in adolescent girls were associated with dating and popularity, respectively. Additionally, covert bullying has the benefit of potentially remaining anonymous to the victim, thereby decreasing opportunities for the victim to retaliate (Campbell 2004). Therefore, indirect bullying may be adaptive for adolescent girls since they tarnish the reputation of competitors, allow girls to remain anonymous to the victim, and indirectly enhance their own status and mate value.

Conclusion

Taken together, it is evident that adolescents use same-sex school bullying during times of social transition and uncertainty as an adaptive tool to increase status, power, and access to resources. Adolescents may use same-sex bullying to increase access to resources, secure a position within their same-sex peer networks, and also attract high-status opposite-sex peers. However, the specific behavior and mechanism may vary within each sex in order to maximize benefits and minimize costs. Boys may benefit from using overt bullying behaviors to appear tough and strong to both rivals and prospective mates. However, girls may benefit from covert indirect bullying behaviors that degrade rivals while increasing their own status and value. The evolutionary underpinnings reveal an important aspect that should be targeted in anti-bullying school initiatives.

Few studies and interventions focus on the heterogeneity of bullying, including sex differences in bullying behaviors and peer network dynamics (Volk et al. 2012). Interventions might affect intra- versus intersexual bullying differentially. Therefore, when targeting intrasexual bullying, interventions targeting a school's ecology should also take sex dynamics into consideration, such as the ratio of boys and girls in a classroom, grade, or school

(Ellis et al. 2012). Moreover, by focusing on the evolutionary sources of bullying behaviors, interventions may focus on altering the cost-benefit ratio for a given bullying behavior for both boys and girls, where bullying behaviors are not rewarded with any resources (Ellis et al. 2012). Therefore, existing interventions may want to incorporate methods to counter intrasexual competition. For instance, the KiVa intervention focuses on bystander interventions so that bullies are not provided with social rewards from peers (Salmivalli et al. 2010). In addition, the Meaningful Roles intervention provides prosocial strategies for adolescents to achieve their goals, without resorting to bullying (Ellis et al. 2015). Therefore, by including ways for bystanders to intervene in same-sex school bullying or providing alternative prosocial methods for adolescents to achieve status among same- and opposite-sex peers may help reduce bullying. In conclusion, school antibullying initiatives should be mindful of the motivations, costs, and benefits behind same-sex bullying, as well as intrasexual peer-network dynamics, in order to effectively intervene.

Cross-References

- [Boys Bully More Than Girls](#)
- [Boys Physical Bullying](#)
- [Girls Psychological Bullying](#)

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Same-Sex Sexual Behavior

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Synonyms

[Bisexual behavior](#); [Homosexual behavior](#)

Definition

Sexual behavior between individuals of the same sex.

Introduction

An estimated 3.5 % of adults in the United States (US) identify as lesbian, gay, or bisexual (LGB), which amounts to more than 8 million people (Gates 2011). An even larger percentage reports that they have engaged in same-sex sexual behavior (8.2 %) or acknowledges at least some same-sex attraction (11 %) (Gates 2011). Further, studies have demonstrated that sexual attractions, behaviors, and identities can change over time and across situations, especially for women (e.g., Diamond 2008). This indicates that same-sex sexual behavior transcends self-identification as LGB, and it underscores the widespread relevance of same-sex sexual behavior. This entry describes sexual behavior between individuals of the same sex, including the specific sexual behaviors that they engage in, the prevalence rates of these behaviors, and their relative risks for HIV. Given the brief nature of this entry, the focus is on cisgender individuals (those whose current gender identity is consistent with their sex assigned at birth). Less is known about the sexual behaviors of transgender individuals (those whose current gender identity is not consistent with their sex assigned at birth), and most research on this topic is focused on sexual risk behavior (e.g., Feldman et al. 2014).

Types of Same-Sex Sexual Behavior

In order to describe the types of sex that same-sex partners engage in, it is first necessary to define sex. To do so presents a challenge, as there is not unanimous agreement about what constitutes sex. Since 1999, researchers have studied people's definitions of sex by asking them if they consider various behaviors to be sex. Across studies, people generally agree that vaginal and anal intercourse are sex (for a review, see Horowitz and Spicer 2013). Horowitz and Spicer (2013) provided evidence for a hierarchy of sex acts (from most to least constitutive of sex), which included intercourse (vaginal and anal), other genital contact (oral and manual stimulation, stimulation by a sex aid), breast/nipple contact (oral and manual stimulation), and kissing. There is also some evidence that lesbians and gay men think differently about what constitutes sex, such that lesbians consider genital stimulation to be more constitutive of sex than heterosexuals do (Horowitz and Spicer 2013) and gay men consider anal intercourse to be the behavior that constitutes sex the most (Hill et al. 2010). Given disagreement about what constitutes sex, behavioral definitions of sexual acts have the greatest potential to facilitate clear communication about sex.

Most of the sexual behaviors that same-sex partners can engage in are the same as those that different-sex partners can engage in. However, certain sexual behaviors are exclusive to either same-sex or different-sex partners, and others are commonly associated with same-sex partners even though different-sex partners can engage in them as well. Vaginal intercourse is the one behavior that is exclusive to different-sex partners, and it involves one person inserting their penis into another person's vagina. In contrast to vaginal intercourse, most sexual behaviors are not exclusive to same-sex or different-sex partners (e.g., manual and oral stimulation, anal intercourse). Manual stimulation can be a solo or partnered activity. When it is engaged in as a solo activity, it involves one individual stimulating their own genitals (penis, vagina, or anus) using their fingers or hand and it is referred to as masturbation. When it is engaged in as a partnered

activity, it can take the form of masturbating in the presence of a partner or one person using their fingers or hand to simulate another person's genitals. Manual stimulation is colloquially referred to as jerking/jacking off or a hand job (when performed on a man) and fingering (when performed on a woman). A specific type of manual stimulation is fisting (anal or vaginal), which involves inserting four or more fingers into the anus or vagina. Although men and women can both engage in fisting, it is commonly thought of as a behavior that gay men engage in.

Oral sex involves one person using their mouth to stimulate another person's genitals. It is referred to as fellatio when performed on a man and cunnilingus when performed on a woman. Colloquially, it is referred to as giving a blow job (when performed on a man), eating someone out (when performed on a woman), and going down on someone or giving head (when performed on either a man or a woman). Anilingus (or rimming) is a specific type of oral sex, which involves one person using their mouth to stimulate another person's anus. Anal sex involves one person inserting their penis into another person's anus. Similar to fisting, anal sex is typically thought of as a behavior that gay men engage in, even though men and women can engage in it with each other as well. Scissoring is the one behavior that is exclusive to female same-sex sexual partners, and it involves one person rubbing their own genitals against another person's genitals. Finally, many people use sex toys (e.g., vibrators, dildos) to stimulate their own or their partner's genitals.

Prevalence Rates Among Men

It is challenging to estimate how common it is to engage in specific sexual behaviors, especially to do so for different sexual orientation groups, for several reasons. First, few population-based surveys assess sexual behaviors and the ones that do vary in how they define the behaviors and the time frames in which they are measured. Second, sexual orientation is operationalized differently across studies, with some studies comparing

individuals who self-identify as heterosexual versus LGB (e.g., Dodge et al. 2016) and others comparing individuals who report sex exclusively with men, sex with men and women, and sex exclusively with women (e.g., Mercer et al. 2007).

Dodge et al. (2016) reported rates of sexual behaviors among men in the USA using data from the 2012 National Survey of Sexual Health and Behavior. All of the rates reported in this section are based on those data unless otherwise noted. They found that sexual behavior was concordant with self-identified sexual orientation for most people. Most heterosexual men reported past-year sex with women only (75.1 %) compared to men only (1.0 %), both women and men (0.3 %), or not being sexually active (23.6 %). Similarly, most gay men reported past-year sex with men only (84.9 %) compared to both women and men (2.4 %) or not being sexually active (12.7 %). Although most bisexual men reported not being sexually active in the past year (39.7 %), a slight majority of those who were sexually active reported past-year sex with both women and men (24.8 %) compared to women only (22.2 %) or men only (12.4 %).

Self-stimulation, or masturbation, was common among men, regardless of sexual orientation (Dodge et al. 2016). The majority of men reported solo masturbation in their lifetime (91.5 % of heterosexual men, 99.7 % of gay men, and 100.0 % of bisexual men). Further, most gay and bisexual men reported solo masturbation in the past month (85.5 % of gay men and 93.6 % of bisexual men), whereas only 56.9 % of heterosexual men reported solo masturbation in the past month. Lifetime masturbation with a partner was also common among gay and bisexual men (94.0 % of gay men and 79.5 % of bisexual men), but it was less common among heterosexual men (51.9 %).

The majority of gay and bisexual men reported lifetime oral sex with a male partner (99.2 % of gay men and 90.3 % of bisexual men), whereas only 5.4 % of heterosexual men reported lifetime oral sex with a male partner. The majority of heterosexual and bisexual men reported lifetime oral sex with a female partner (86.8 % of heterosexual men and 92.5 % of

bisexual men), whereas only 34.8 % of gay men reported lifetime oral sex with a female partner. Most heterosexual and bisexual men reported lifetime vaginal intercourse (87.9 % of heterosexual men and 78.1 % of bisexual men), whereas only 28.4 % of gay men report lifetime vaginal intercourse. Most gay and bisexual men reported lifetime insertive anal intercourse (83.3 % of gay men and 74.8 % of bisexual men) as well as lifetime receptive anal intercourse (90.0 % of gay men and 65.7 % of bisexual men). In contrast, 32.7 % of heterosexual men reported lifetime insertive anal intercourse and 2.8 % of heterosexual men reported lifetime receptive anal intercourse. Finally, most gay and bisexual men report lifetime sex toy use either during solo or partnered masturbation (Rosenberger et al. 2012). In a large sample of gay and bisexual men, the most commonly used sex toys were dildos and butt plugs (62.1 %), which refer to objects designed to be inserted into the vagina or anus for sexual stimulation. Among those who had used dildos or butt plugs, most reported use during solo masturbation (89.4 %) followed by use during sexual foreplay with a male partner (69.4 %) and use during sexual intercourse with a male partner (66.5 %).

Prevalence Rates Among Women

While the prevalence rates of sexual behaviors among men in the USA have been reported separately for different sexual orientation groups (Dodge et al. 2012), the same data have not been reported for women. However, using data from the National Survey of Sexual Attitudes and Lifestyles, Mercer et al. (2007) reported rates of sexual behaviors among women in Great Britain. They compared the rates of sexual behaviors among women who reported sex exclusively with men (heterosexual), women who reported sex with men and women (bisexual), and women who reported sex exclusively with women (lesbian). Of note, this entry uses the terms “heterosexual,” “bisexual,” and “lesbian” to refer to these groups for convenience, but the groups were based on the sexual behavior that the women had engaged

in. All of the rates reported in this section are based on those data unless otherwise noted.

In this sample, 9.7 % of the women reported same-sex sexual experiences and 11.2 % reported sexual attraction, at least in part, to women. Past-month masturbation was most common among bisexual women (68.9 %), followed by lesbians (59.7 %) and heterosexual women (36.6 %). Among women who reported past-year sex with a man, most had engaged in vaginal sex (98.3 % of heterosexual women and 96.2 % of bisexual women), oral sex (85.4 % of heterosexual women and 94.8 % of bisexual women), and other genital contact (e.g., stimulation by hand) (81.5 % of heterosexual women and 95.2 % of bisexual women). In contrast, fewer had engaged in anal sex (12.1 % of heterosexual women and 26.9 % of bisexual women). Among women who reported past-year sex with a woman, most lesbians had engaged in oral sex (80.3 %) and other genital contact (92.7 %), whereas approximately half of bisexual women had engaged in oral sex (53.5 %) and other genital contact (60.9 %). Similar to gay and bisexual men, the majority of lesbians and bisexual women report lifetime vibrator use (86.0 %), including use during solo masturbation (80.9 %) or with a female partner (76.3 %) (Schick et al. 2011).

Risk for HIV

According to the Centers for Disease Control and Prevention (CDC 2016), the primary methods of HIV transmission in the USA are anal or vaginal sex (with someone who has HIV without using a condom or taking medicines to prevent or treat HIV) and injection drug use. In regard to sexual transmission, anal sex is the highest-risk behavior and vaginal sex is the second-highest-risk behavior. Of note, receptive anal sex is higher risk than insertive anal sex, but transmission can occur in either position. The risk of HIV transmission through oral sex is extremely low, with risk being highest for fellatio. Gay and bisexual men have the highest rates of HIV in the USA, whereas female-to-female transmission of HIV is rare.

Conclusion

People generally agree that vaginal and anal intercourse are sex, but there is disagreement about whether other behaviors constitute sex. Given that different behaviors are associated with different degrees of risk for HIV, definitional precision is of utmost importance. This may be especially true for same-sex sexual behavior, because LGB individuals think somewhat differently about sex compared to heterosexuals. Although sexual behavior is largely concordant with self-identified sexual orientation, there are more people who engage in same-sex sexual behavior or who report same-sex attractions than people who identify as LGB. As such, same-sex sexual behavior is relevant to individuals regardless of their self-identified sexual orientation.

Cross-References

- [Alloparenting and Female Same-Sex Behavior](#)
- [Ancient Homosexuality](#)
- [Female Homosexuality and Bisexuality](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexual Receptivity](#)
- [Homosexuality](#)
- [Hormonal Component of Homosexuality](#)
- [Human Sexuality](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Non-Western Homosexuality](#)
- [Relationship Between Sexuality and Gender](#)
- [Same-Sex Relationships](#)
- [Sexual Behavior](#)
- [Sexual Identity](#)
- [Sexual Orientation and Human Sexuality](#)
- [Sexual Orientation](#)
- [Sexuality](#)

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Same-Sex Sexuality

- [Female Homosexuality and Bisexuality](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Sexual Orientation and Human Sexuality](#)

Sanctions

- [Reciprocal Altruism \(Middle-Level Theory in Evolutionary Psychology\)](#)

Sanctity

- [Sacredness/Purity/Disgust](#)

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Definition

An influential anthropologist working across multiple disciplines to contribute to our evolutionary understanding of female human and nonhuman primate behavior. Author of *The Woman That Never Evolved*; *Mother Nature: A History of Mothers, Infants and Natural Selection*; and *Mother and Others: The Evolutionary Origins of Mutual Understanding*.

Introduction

Sarah Blaffer Hrdy is a leading evolutionary anthropologist and primatologist who has significantly influenced numerous disciplines including evolutionary psychology, evolutionary biology, anthropology, primatology, developmental psychology, and women's studies. Her groundbreaking theorizing is based on systematic observations, comparative studies, historical documentation, and people's lived experiences, such that it bridges traditional disciplinary boundaries. Her work spans many topics that collectively remind scholars that individual fitness is key when understanding behavior. She is an award-winning scholar; her most notable achievement to date is being the recipient of the National Academy of science Award 2014 for Scientific Reviewing. With this award, she was recognized "for her insightful and visionary synthesis of a broad range of data and concepts from across the social and biological sciences to illuminate the importance of biosocial processes among mothers, infants, and other social actors in forming the evolutionary crucible of human societies." She is most noted for her meticulously researched books, which are also written "with the grace of a novelist" (van Schaik and Silk 2013).

Personal Biographical History

Sarah Blaffer Hrdy completed her undergraduate degree with *summa cum laude* distinction at Radcliffe College (at that time, the woman's part of Harvard) with a major in anthropology. Her undergraduate thesis was on h'ik'al, a bat-like demon of the Maya-speaking Zinacantan. H'ik'al had a tendency toward mischief and unrestrained sexuality, and the thesis was published in 1972 (and in paperback in 2012). In this cultural anthropological study, she explored other myths as well, ultimately leading to an analysis of regulation and enforcement of cultural norms, and specifically sex roles.

From here, Hrdy went on to Stanford and audited a course by biologist Paul Ehrlich, where he discussed challenges resulting from human population growth and problems associated with overpopulation. This material called to her mind a comment during one of her undergraduate primate behavior courses by Irven Devore at Harvard. Devore had mentioned that among Hanuman langur monkeys (*Semnopithecus entellus*) in India, males commit infanticide when living in high population densities (Sridhar 2016). She transferred to Harvard where she studied male langur infanticide in various habitats. From there, she became interested in other facets of langur behaviors such as female intrasexual competition, bonding, and shared care of infants (Sridhar 2016). These were exciting moments for Life Sciences at Harvard. While being supervised by Devore for her doctoral research, her committee member Edward Wilson had recently published *The Insect Societies* (1971) and was working on *Sociobiology: The New Synthesis* (1975), and her other committee member, Robert Trivers, was working on his papers pertaining to altruism (1971), parent-offspring conflict 1974 and parental investment theory 1972 (see also Sridhar 2016). Hrdy received her doctoral degree from Harvard, followed by a stint as a lecturer at Harvard, more fieldwork, a visiting professorship at Rice University near Baylor where her husband Dan was doing his medical residency, followed by time as a volunteer assistant at her children's daycare center back in Cambridge while Dan completed

his MD-PhD program at Harvard and MIT. In 1984, she and her husband both accepted jobs at the University of California at Davis, where she is now Professor Emerita.

Hrdy reports that this era was challenging in that it became marked by “science wars” against sociobiology. Her own work on infanticide as a reproductive strategy became controversial (see Rees 2009), and her publication in *American Scientist* (1977) resulted in letters to the editor and follow-up articles.

Her initial research on infanticide as a male reproductive strategy paralleled significant developments and paradigm changes in evolutionary biology, anthropology, and psychology, where these fields became influenced by models around the selfish gene and individual fitness. After her work on langurs, she widened her research focus to include topics that were previously understudied, including female intrasexual competition, female sexuality, alloparenting, and infant sharing.

Hrdy is a former Guggenheim fellow, member of the National Academy of Sciences, a fellow in the American Academy of Arts and Sciences, the California Academy of Sciences, Animal Behavior Society, and the American Philosophical Society. She was listed among the “50 Most Important Women in Science” by Discovery Magazine in 2001. In 2013, she received the Lifetime Achievement Award from the Human Behavior and Evolution Society, and in 2014, received the National Academy of Sciences Award for Scientific Reviewing. In addition to being Professor Emerita at the University of California-Davis, she is an Associate in the Peabody Museum of Archeology and Ethnology at Harvard. She and her husband have three children and combine growing walnuts with habitat restoration on their farm in Northern California (<http://www.citrona.com>).

Infanticide

In *The Langurs of Abu: Female and Male Strategies of Reproduction* (1977; paperback edition 1980), Hrdy chronicles five years of research. The work that she published on Hanuman langurs

provided a foundation for a shift in how the scientific community came to view infanticide in primates (including humans) but also female and male mating strategies more generally.

Originally, Hrdy undertook the study of langurs with the hypothesis that high population density among those living in Mount Abu, India, caused males to commit infanticide as a maladaptive behavior. However, she noted that males who are likely to be the fathers of infants born in their group are quite tolerant of infants. Further, overcrowding did not influence whether langur males committed infanticide or not. Instead, she discovered infants were only being attacked when males entered from outside the breeding system. The only plausible explanation was Darwin’s theory of sexual selection, and in particular, male intrasexual competition for access to mates.

Langur troops typically consist of one male and several females, with additional males who remain external to the core group. One of these outside males ousts the troop leader approximately every 2 years and, in the process, takes over the harem and often kills young infants. She documented that only un-weaned infants were attacked and proposed that by eliminating the source of lactational suppression of ovulation, the new leader could compress the mother’s fertility into the period he was likely to have reproductive access to her before another male replaced him. In other words, in killing the infants, the new leader increases the sexual receptivity of the females which results in a higher probability of him siring offspring with those females.

The arguments put forth by Hrdy were groundbreaking, as she posited that infanticidal behavior by male langurs was an adaptive reproductive strategy. Her research went one step further though, as she proposed that males relied on the mothers, not the infants, when deciding whether to attack or tolerate an infant, in that it depended on whether he had previously mated with the mother. In the paperback version of *The Langurs of Abu*, Hrdy cites evidence of infanticide as a heritable trait among rodents, and then almost two decades later, DNA analyses support that langur males only attack infants that are genetically unrelated (Borries et al. 1999).

The controversy that emerged in response to her arguments on the adaptive nature of infanticide lead her to complete an edited volume (Hausfater and Hrdy 1984, republished in 2008) entitled *Infanticide: Comparative and Evolutionary Perspectives*.

The Woman That Never Evolved

After studying langur monkeys, Hrdy began to consider sources of variation in female reproductive success. She had documented that the females mated with the new troop leader, but also with the old leader, and with males who were peripheral to the core group, even when they were already pregnant. She argued that females' promiscuity was an effective strategy to decrease the probability of their infant becoming a victim to infanticide by a male, given that he would likely not kill a related infant. In other words, females had evolved counterstrategies that were effective in working around males' strategies, including opportunistic promiscuity, which had previously been unexplored in the literature. Her interest in female primates, including women, and issues such as variation in their mating strategies and reproductive success, led to the publication of *The Woman That Never Evolved* (1981, revised paperback 1999). It was selected by the *New York Times* as a notable book for 1981.

At this point in her research, she began to argue that females were not coy or passive in the manner described by Darwin, as well as by others. She writes that "a handful of partially true assumptions were permitted to shape the construction of general evolutionary theories about sexual selection" (1986, p. 119). She questioned assumptions such as how sexual selection theory had been used to explain females' choosiness about mates (while males were argued to be indiscriminating), which led to views of males providing little, if any, parental support to offspring, females as having minimal reproductive variance relative to high variance among males, and females engaging in mating only for reproductive purposes.

In his conceptualization of sexual selection, Darwin (1871) had written that females are

relatively passive in the mating process but show some activity by selecting the best mate from an array of contenders. These narrow views of females remained over time and were strongly reinforced by the work of Angus Bateman (1948), leading to the dominant way of perceiving female and male sexuality. He had published work on fruit flies (*Drosophila melanogaster*), where he had altered some individuals and then determined how many offspring displayed each individual's genetic trademarks. His results (based entirely on looking at phenotypes, not behavior) showed more males than females did not have offspring, while some males had far more offspring than any female. He extrapolated these findings to suggest males had higher reproductive variance than females, but also that males are ardent and sexually indiscriminating, whereas females are sexually restrictive and coy. This view largely remains today in evolutionary psychology, despite repeated calls for it to be re-examined (e.g., Fisher and Burch, [in press](#)).

In *The Woman That Never Evolved*, Hrdy elaborated on female mating strategies in primates, including women. She argued that females are not passive, but instead are able to manipulate male reproductive strategies while simultaneously competing and cooperating with other females in areas that are relevant to them. She suggested that the reason women's competition has been largely neglected is because researchers have not developed the ability to adequately document it due to its subtle and covert nature. Her work clearly indicated that primate females were active strategists, seeking to increase their fitness using a variety of tactics. Female competition, Hrdy proposed, was key in shaping relationships among females, and used to respond to challenges in the local environment, including social context. Her work largely inspired the tremendous growth of research on female competition, resulting in compendiums such as Fisher (2017).

Further, at this point, males were considered essentially polygynous while females were thought to be monandrous. Her own research, supplemented with re-examination of the primate literature, caused her to realize that polyandrous

mating was common across primates. Therefore, not only was the ardent male-coy female perspective flawed, but so too were the underlying theories regarding mating systems.

On Mothering

After the work summarized in *The Woman That Never Evolved*, Hrdy continued to explore mothering in two books. The first of these, *Mother Nature: A History of Mothers, Infants and Natural Selection*, was published in 1999 and awarded the 2000 Howells Prize, among other considerations. It was also selected as one of the best books of 1999 by Publisher's Weekly and Library Journal. In this body of work, Hrdy departs from primarily focusing on nonhuman primates to begin to explore modern humans. However, she continued to rely on comparative work of nonhuman primates to inform her arguments.

Hrdy outlined how selective forces have shaped maternal behaviors and strategies, and in particular, how they involve trade-offs. She continued to challenge the long-held assumptions that pervade modern theorizing that are already noted (i.e., higher variance in reproductive success among males, males but not females are active in mating and compete to gain access to mates, females mating only as much as is needed to conceive offspring). The result of this limited view is that maternal success is seen as automatic, with little variance in mothering abilities or interest. Instead, she contended, mothering for humans means deciding whether one has the social support to raise infants and children before committing to having children. If the support is absent or weak, women may decide to abandon or kill their offspring. This decision is at least partially based on a mother without support realizing that she needs to reduce her current costs of caring for her young, in the hopes of being able to have future children with stronger support, and hence, better fitness.

Struggling to reconcile maternal love with ambivalence, Hrdy was struck by just how much help human mothers need, increasingly convinced that unlike other apes, mothers in

the line leading to the genus *Homo* must have evolved as cooperative breeders. "It's time then to ask," she wrote in *Mother Nature* "just who beside mothers subsidized the long, slow development that is the hallmark of the human species, the very late maturation that distinguishes us from every other primate?" (p. 265). Hunter-gatherers have short inter-birth intervals, with an average 2–3 years between children compared to six for other great apes. This interval produces overlapping nutritionally dependent altricial young. It means that mothers need to provide care for dependent young (e.g., toddlers) and infants while possibly being pregnant with the next child. This reproductive pattern is only possible if mothers receive assistance from others; their children would fare better, and the mother herself would be healthier. In this way, she drew a parallel reliance on allomaternal care in langurs and in humans which in both cases allowed mothers to breed faster after shorter intervals and still raise surviving offspring. Hrdy also discussed partible paternity, similar to polyandry, which exists among some cultures such that mothers have multiple mates to help provide and protect her children in the event that her primary mate deserts her or dies. In *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (2009), she explored the implications of having to rely on alloparental care and provisioning of immatures for mothers and especially on infants.

Throughout these books, Hrdy highlights women as strategists, actively seeking to improve their individual and inclusive fitness. Consequences of striving to improve one's fitness can include child abandonment, neglect, and infanticide, where especially young women facing a less than desirable future may kill their offspring to increase their prospects. Further, infants who are likely to decrease the fitness of their siblings are often the victims; infants who are weak, display a disability, the wrong sex, or born too soon after the last child are typically victims. Collectively, Hrdy's research clearly indicates that the popular and common idea of a "maternal instinct" is simply flawed, given that mothers must remain evolved strategists.

On the Importance of Others

Hrdy's second book pertaining to mothering was *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (2009). It was awarded the 2012 J. I. Staley Prize from the School for Advanced Research, which is awarded to a living author for a book that "exemplifies outstanding scholarship and writing in anthropology, but also goes beyond the discipline's traditional frontiers" (2020). It was also awarded the 2012 Howells Prize, given by the biological anthropology section of the American Anthropological Association, for informing "a wider audience of the significance of physical or biological anthropology in the social and biological sciences, and demonstrate a biocultural perspective" (2020).

At the end of working on *Mother Nature*, Hrdy realized that the traits associated with the life history of humans meant that our evolutionary history involved cooperative breeding (Johnson 2012). Human young are extremely dependent, and until the age of 18–20, they do not generate as many calories as they consume (Johnson 2012). Compared to other great apes, humans have the largest neonates, and their infants are costly in terms of requiring nutrition and protection, and overall, human children are the latest to mature. Alloparents (i.e., individuals other than parents) provide care and help by providing provisions for infants and children. These individuals include an impressive array of individuals: grandmothers, post-reproductive females, fathers and men who may be fathers, patrilineal relatives, matrilineal relatives, older siblings, aunts, uncles, and unrelated individuals in the group who help rear offspring in exchange for group membership. Further, Hrdy contended that mothers accept this help from others in an opportunistic fashion, based on the benefits such assistance brings to her and her children.

One point worth emphasizing is how Hrdy views children as active in helping to maintain their own survival and are not simply immature adults (a line of thought that helped to propel evolutionary developmental psychology forward as a sub-discipline). Humans rely extensively on wide social networks to successfully raise infants

and children. Humans, unlike other great apes, care for and pay attention to each others' children and engage in food sharing and share other scarce resources. Natural selection has thus favored the survival of children who are more easily monitored and receptive to being cared for by individuals other than the mother. Children who are able to engage socially with other individuals solicit their help and positive attention, determining whether someone may help or hurt them, and have a distinct advantage over those who are not able to do so. The importance of children as being able to solicit help from others must be noted, given that among hunter-gatherer societies (from which we may model our evolutionary heritage), infant mortality is approximately 50% (Volk and Atkinson 2013).

The ability of infants and children to engage with people other than their biological mother has led to several critical developments for humans, and indeed, it is these uniquely human adaptations that are truly astounding. Hrdy argued that these adaptations include our unique (compared to other great apes) ability to care about others and their intentions, anticipate other's needs, use empathy and have a theory of mind, to use language and gestures, and be able to coordinate action toward a common goal. Indeed, cooperation is a key feature to highlight; humans frequently help each other, including unrelated others, and anticipate their needs. However, it also involves complexity, in terms of worrying about other's views of us, or attempting to maintaining status, (see Pridmore-Brown 2009). Hrdy proposed that women's tendency toward tend-and-befriend (Taylor et al. 2000) to help create alloparents would have led to higher infant survival, and that those individuals with better skills for cooperating may have had better fitness.

Hrdy has researched a multitude of other related issues, which collectively serve to further the point that mothers are strategic, and that the relative contributions of people other than the biological mother can be critical for a cooperative breeding species such as humans. Individuals such as the maternal grandmother had long been overlooked, yet it is this relative who particularly improved infant survival, by providing food,

resources, and childcare. Fathers, too, play a role, albeit a much more conditional one, depending on issues such as paternity certainty, but also cultural context and individual variation.

Conclusions

Hrdy is an influential scholar who has shaped how we view topics such as strategies to promote inclusive fitness, parenting behavior, maternal love, competition, infanticide, the importance of non-related individuals in raising children, cooperation, and mating strategies. Ultimately, her work serves as a strong reminder that it is important to question past assumptions, and consider individuals as actively strategizing to increasing their fitness.

Cross-References

- [Alloparenting](#)
- [Childcare](#)
- [Cooperation](#)
- [Evolutionary Biology and Feminism](#)
- [Female-Female Alliances](#)
- [Feminism](#)
- [Infanticide](#)
- [Maternal Age](#)
- [Parenting](#)
- [Peer Competition and Cooperation](#)
- [Polyandry](#)
- [Primate](#)
- [Status](#)
- [Variance in Female Reproductive Success](#)
- [Women](#)

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Sarah Brosnan

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Synonyms

Evolution of cooperation; Fairness; Primate economic strategies; Reciprocity

Definition

Dr. Sarah Brosnan is a researcher investigating the ontogeny of reciprocity and cooperation in primates. To date, she is best known for her work showing that primates detect and react to unequal pay for the same tasks (Brosnan and de Waal 2003).

Introduction

Dr. Sarah Brosnan researches mechanisms underlying cooperation, reciprocity, inequity, and other economic decision-making strategies from an

evolutionary perspective. She uses both human participants and nonhuman subjects in her investigation of the decisions individuals make and how they make them, how their social or ecological environments affect their decisions and interactions, and under what circumstances they alter their behaviors in line with these conditions (Brosnan 2014). Sarah Brosnan received her B.A. in Biology from Baylor University and went on to work with Dr. Frans de Waal at Emory University to complete her Ph.D. in their *Population, Biology, Ecology, and Evolution* program. Her research focuses on the evolution of economic decision-making strategies, with a particular focus on animal perceptions of the value of exchanged goods and services (Brosnan 2014).

Monkeys React to Unequal Pay

In 2003, Sarah Brosnan and Frans de Waal published a study showing that monkeys detect and react to unequal pay, which was previously believed to be an exclusively human trait. In the study, five capuchin female monkeys were trained to exchange tokens with a human researcher to receive food rewards. Each subject then experienced each of four conditions: (1) “equality,” in which two monkeys exchanged for a cucumber reward; (2) “inequality,” in which the test monkey exchanged for a cucumber while its partner exchanged for a grape (a higher quality food); (3) “effort control” in which a grape was simply handed to the partner without exchanging a token and then the subject herself exchanged a token for a cucumber; and (4) “food controls” in which the partner was absent, yet the subject witnessed a grape being placed in the location where the partner normally sat, followed by the subject herself exchanging for a cucumber. Researchers measured the female subject’s latency to successfully exchange the token for the food reward, and assessed situations in which she did not exchange the token, or refused the given reward. It was found that subjects were less likely to exchange for low-value rewards (i.e., cucumber) when high-value rewards were present, and even less likely to exchange if the partner received the high-value

reward with no effort. Because refusals were more likely when the partner was present, Brosnan and de Waal concluded that capuchins must be assessing the value of their reward by comparing them to visible conspecifics. Results shed light on the evolution of adaptations for group living, such as cooperation, fairness, and value estimation (Brosnan and de Waal 2003).

This study provided the first evidence that, like humans, capuchin monkeys comparatively estimate the value of rewards, evaluating both availability and effort compared to others. Furthermore, these monkeys display an emotional response to unfairness, such as throwing away lower-value rewards after seeing a partner receive a higher-value reward for the same or relatively little effort. These reactions are integral to long-term human cooperation and influence how we form expectations about resource value, work effort, and ethical treatment of others and how resources should be divided (Brosnan and de Waal 2003).

Conclusion

Dr. Brosnan continues to research primate cognition, including the evolution of cooperation, fairness, property, prosocial behavior, comparative economics, social learning, and social and ecological influences on decision-making. She is currently an associate professor of psychology at Georgia State University (GSU) in Atlanta, GA (USA). She is a research associate in GSU's Neuroscience Institute and is also a member of the *Brains and Behavior* program and the *Center for Behavioral Neuroscience*. She directs the *Comparative Economics and Behavioral Studies Laboratory* (CEBUS Lab) and does research with nonhuman primates at both the *Language Research Center* at Georgia State University and the *Michale E. Keeling Center for Comparative Medicine and Research* at UT/MD Anderson Cancer Center (Brosnan 2014).

Cross-References

- [Comparative Evidence](#)
- [Cooperation](#)

- [Fairness](#)
- [Prosocial Behavior](#)
- [Reciprocity](#)
- [Social Learning](#)

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SAS

- [Sexually Antagonistic Hypothesis](#)

Satisfaction with Life

- [Measuring Well-Being](#)

Savagery

- [Victims of Violence](#)

Savanna Hypothesis and Landscape Preferences, The

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Definition

According to the savanna hypothesis (Orians 1980, 1986), current habitat biases were shaped by selection pressures in our ancestral past. The theory argues that natural selection favored preferences, motivations, and decision rules that

attract us to resource rich environments over resource poor environments.

Introduction

Current habitat preferences were shaped by selection pressures in our ancestral past, according to the *savanna hypothesis* (Orians 1980). The theory argues that selection favored preferences, motivations, and decision rules that attract us to resource rich environments while avoiding environments populated with survival threats and lacking resources. The African savanna, widely believed to be the site in which humans originated, fulfills these requirements.

Two perspectives are helpful in addressing evolved responses to landscapes, one spatial and the other temporal. The spatial frame of reference points out particular stages of exploration in novel landscapes. The temporal dimension concerns short-term and long-term habitat variation in critical survival factors (e.g., weather patterns and seasonal transitions).

Stages of Exploration

The details of the savanna hypothesis can be unfolded to include three stages of habitat selection: *selection*, *information gathering*, and *exploitation* (Orians and Heerwagen 1992). The primary decision faced in stage 1 is whether to canvass or flee a landscape upon initial encounter. Completely closed forest canopies are rejected because they inhibit viewing and mobility. Wide-open environments lacking cover and protection are also abandoned. Initial preferences and choices made during the selection stage are often emotional rather than intellectual. They do not usually involve an exhaustive cognitive evaluation of all the benefits and disadvantages of the landscape. It is something closer to sensing a vibe or having a hunch.

Assuming the experience in first stage is decent, individuals begin exploring the environment for resources and possible hazards. Stage 2, *information gathering*, involves mentally mapping the area for hidden places to harbor oneself,

family, and allies. One can also evaluate possible routes for escape in the event of danger. At this stage, people show a preference for hills and pathways that change elevation and wind around, hinting at the potential of something promising around the corner. One study found that people have an affection for mystery and intrigue at this stage (Kaplan 1992). In sum, great effort is put into risk assessment and resource estimation at this stage.

The decision of whether to stay or leave is at the heart of stage 3, *exploitation*. This final stage involves elaborate mental calculations that help to determine if one should stay long enough to enjoy the full bounty of resources available in the habitat. All humans face decisions about how much time and energy to allocate to competing demands. The solutions to these decisions involve trade-offs. A lofty rock ridge brings benefits (e.g., easy observation of competitors below), but they may not outweigh the risk of death that comes from falling. Likewise, a clear and exposed area good for foraging may open the door to predators (Orians and Heerwagen 1992).

Weather Patterns and Seasonal Transitions

An additional layer of the savanna hypothesis involves decision-making over different time frames (Orians and Heerwagen 1992). Light availability and weather patterns are two time-related factors that impact choices. Long shadows at the end of the day may elicit the desire to set up campsite instead of continuing to move through the environment in darkness. Likewise, daily weather issues can force one to seek shelter quickly. Dark clouds, winds, thunder, and lightning are cues that may initiate the decision-making process.

Along with daily fluctuations, humans are sensitive to environmental changes on a seasonal scale. In general, natural selection favors traits that maximize benefits and minimize costs. People will show preferences for long-term signs of robust prosperity because the algorithms that make habitat-related decisions were shaped

over time in response to specific positive and negative features of the environment. Indicators of harvest, such as fruit, budding flowers, and verdure, are favored over bare trees and impoverished fields.

Landscape Preferences

Support for the savanna hypothesis can be found in studies of landscape preferences. One such study asked subjects to rate a series of standardized photographs of trees taken in Kenya. Pictures were taken under similar daylight and weather conditions. Each photo focused on a single tree and varied along four dimensions – canopy shape, canopy density, trunk height, and branching pattern. Subjects from Australia, Argentina, and the United States all showed similar taste in the photos depicting trees. The trees that made a moderately dense canopy with trunks that separated in two near the ground – the savanna-like trees – were preferred by participants across the three cultures (Orians and Heerwagen 1992).

Modern technology, structural designs, and construction materials allow us to comfortably inhabit climates that would have required intense effort just a few generations ago. Still, we carry with us the psychological preferences shaped by generations of ancestors living in a much different world and often customize our environments to resemble that ancient habitat. Most of us prefer physical spaces that offer views of green vistas over windowless basements. Looking at trees might even have a tangible health benefit: Patients who viewed trees outside the window recovered more quickly from hospital stays (Ulrich 1984). Flowers also appear to have a positive impact on hospital patients. Bringing flowers increases optimism and actually improves the rate of recovery (Watson and Burlingame 1960).

The relationship between stress and uncultivated outdoor settings may play a role in this. When placed in uncertain and stressful situations, individuals who viewed pictures of nature scenery showed less physiological distress (Ulrich 1986). Contact with vegetation need not be active, such as gardening, to provide health benefits. Passively viewing

vegetation through a window can produce desirable effects as well. Studies in biophilic design demonstrate that people living and working in spaces with vegetation compared to those without vegetation show improved performance on mental tasks, more positive moods, greater ability to refocus attention, stress reduction, and diminished perceptions of pain in health-care settings (Kellert et al. 2008).

Additional support for the savanna hypothesis comes from the body of evidence showing that humans often prefer natural environments over built environments (Kaplan and Kaplan 1982). Using data from 30 studies, Kaplan (1992) summarized the results of participant ratings of photographed scenes of Western Australia, Egypt, Korea, British Columbia, and the United States. Across these varied geographic regions, participants preferred natural environments over built environments. Other data suggest that the addition of trees and vegetation increases positive evaluations of built environments, thus demonstrating the transformative power of foliage (Ulrich 1983).

One of the earliest studies to test the idea that people have a generalized bias toward savanna-like environments hypothesized that “innate predispositions” for the savanna should be more likely to be revealed in children than in adults, given that adults have had greater opportunity to experience non-savanna ecosystems (Balling and Falk 1982). In a study that included six age groups (8, 11, 15, 18, 35, and 70 or over), subjects were asked to rate photos from five natural biomes on scales that measured how much they would like to “live in” and “visit” each one. The researchers found that the youngest group (8-year-old children) preferred the savanna over the other habitats on both scales. The deciduous forest, coniferous forest, and savanna were equally liked among ages 15–70, with ratings for the desert and rainforest coming in lower at all ages. The study also implies that people have an aversion to drought conditions and arid landscapes. Photos depicting greener savanna were rated higher than similar savanna photos taken during the dry season. Finally, all age groups gave the lowest ratings to the desert environment (Balling and Falk 1982).

Conclusion

In a broad sense, the savanna hypothesis addresses the issue of how we select places to live and why we find some landscapes more beautiful than others. The central argument is that our preferences in this domain were shaped over evolutionary time *through the repeated selection of safe and healthy environments over dangerous and resource poor landscapes*.

Cross-References

- [Ancestral Threats Versus Modern Threats](#)
- [Gordon Orians](#)
- [Landscape Preferences: Climate and Weather](#)
- [Natural Versus Artificial Environments](#)

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Savanna Hypothesis, The

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Synonyms

[Habitat selection](#); [Landscape aesthetics](#)

Definition

The Savanna Hypothesis states that we retain genetically based preferences for features of high-quality African savannas where our ancestors lived when their brains and bodies evolved into their modern forms.

Introduction

Selection of a place to live is a crucial step in the lives of most animals. Selection depends on the recognition of objects, sounds, and odors to which an animal, molded by natural selection, responds *as if* it understood their significance for its future survival and reproductive success. Evolutionary theory suggests that the ability of a landscape to evoke positive emotional states should be positively correlated with the expected survival and reproductive success of individuals of that species in it. In other words, good habitats should evoke strong positive responses; poor habitats should evoke weak or negative responses (Orians and Heerwagen 1992). Habitat selection has served as a conceptual basis for many studies on human responses to landscape features (Orians 1980;

Heerwagen and Orians 1993, see Orians 2014 for a synthesis).

Rarely did habitats occupied by humans during most of our evolutionary history provide reliable resources long enough to enable our ancestors to settle in permanent sites. Frequent moves through the landscape were the rule even though traditional sites might be revisited on an annual basis (Campbell 1985). We have lived in mechanized and urban environments for relatively few generations. Unless there has been strong counter-selection against them, not enough time has elapsed for our evolutionarily based response patterns to landscapes to have been substantially modified in the dramatically new and different environments in which we live today.

People's initial emotional responses to an unfamiliar environment are almost instantaneous and noncognitive. The strength of these emotional responses strongly influences immediate decisions about where to stop and explore. Although no direct evidence yet exists for genetic influences on these responses, a number of investigators have used an evolutionary perspective to generate testable predictions about human responses to environmental features. Among the hypotheses, they have generated is the **savanna hypothesis** (Orians 1980).

The Savanna Hypothesis

The savanna hypothesis is based on a large body of evidence showing that our ancestors lived in African savannas during the time when our brains tripled in size and we became human. Tropical savannas are characterized by relatively low and highly seasonal rainfall. They have widely spaced trees interspersed with areas of treeless grassland. The open canopy allows sufficient light to reach the ground to support a vibrant herbaceous layer consisting primarily of grasses. In some regions, especially Africa, the scattered trees and rich herbaceous understory support large populations of grazing and browsing herbivores and their predators. In tropical savannas, most resource production takes place within a few meters of the ground where people and grazing and browsing mammals

can easily harvest it. Meat production is higher in savannas than in forests, where much primary production goes to wood, and in deserts, where overall productivity is low. In addition, many savanna plants have underground storage organs that a person can harvest with a simple digging stick.

During their long occupancy of African savannas, our ancestors lived in small social groups; many members were close genetic relatives. They had few material possessions that they carried with them as they moved their seasonal campsites to follow changes in food and water availability. Bipedal locomotion, which reduced both heat stress and water loss, and loss of body hair, enabled our ancestors to travel great distances across savanna landscapes in search of carcasses at times of day when competing and dangerous carnivores would have been resting in the shade.

We have strong reasons to expect that contemporary human behavior should reflect adaptations of our ancestors to African savannas. A relatively small number of generations separate us from our ancestral "mother-Eve," who lived some five million years ago in East Africa. Evidence from a number of species demonstrates that behavioral patterns may persist long after selection continued to influence them (Coss and Goldthwaite 1995). Even though traits can persist for many generations in the absence of selection against them, some human traits, such as evolved responses to the chemical characteristics of the foods that people encountered as they occupied new geographical regions (Nabhan 2004), have evolved relatively rapidly during recent millennia.

The savanna hypothesis has generated a variety of predictions about how people may respond today to the environment. At a large scale, people respond to features of the broad landscape, that is, scattered trees with an herbaceous understory and signs of water. They also respond to the shapes of the trees that dominate the highest quality savannas. At a still smaller scale, because most savanna trees and shrubs have either small simple leaves or highly divided compound leaves with small leaflets, such leaves should also be attractive to us today.

When our ancestors descended from the trees and become primarily terrestrial, they increasingly added animal flesh to their diets. Evidence of the presence of medium-sized and large animals should enhance the attractiveness of a landscape. In addition, perhaps by sampling animals killed by savanna fires, our ancestors discovered that cooked meat was tasty as well as being much easier to chew, swallow, and digest. They also discovered that many inedible raw things were good to eat when cooked. Cooking greatly expanded the range of things they could eat; it outsourced to fire a major part of the cost of digestion. Energy previously expended in chewing food and breaking down complex molecules to more easily digested smaller ones was available for other functions, most notably for supporting an energy-demanding larger brain. Major morphological changes among our ancestors – reduction in the length of the digestive tract, reduction in the mass of the jaws – were probably made possible by cooking (Wrangham 2009).

Humans are not desert-adapted animals. Our ancestors would have needed to drink every day; dehydration was probably a constant risk. Their home ranges were probably determined by the greatly restricted distribution of water during the dry season and location of safe sleeping sites. Although water is present in all environments in which humans can survive, evidence of the presence of this vital and scarce resource in savannas should have a special appeal for us today.

Landscape Features

Predictions about which landscape features are most attractive to people today have been tested by observing people's responses to photographs and paintings of landscapes and by studying the features of "aesthetic environments," that is, environments, such as parks and gardens, that are designed to be places in which people would like to spend time (Orians 1980, 2014). These experiments are appropriate because people respond similarly to photographs and real settings (Shuttleworth 1980).

Responses to paintings and photographs of landscapes. Landscapes first appeared in paintings as background to other actions and events, usually religious. Only later did they become the direct subjects of paintings. Psychologists have tested predictions about landscape preferences by asking participants to evaluate paintings and photographs of landscapes that differ in structure, composition, social information, number and kinds of objects, and colors. Two artists, Vitaly Komar and Alexander Melamid (1997), asked a marketing research firm to conduct a survey to assess the attitudes and preferences of adult Americans about landscapes. Pollsters asked people about their favorite color and the criteria they would use to select pictures, photographs, or other pieces of art for their homes; whether they preferred natural or portrait settings, indoor or outdoor scenes, geometric or random patterns, flat or richly texture surfaces, and sharp angles or soft curves.

Komar and Melamid incorporated the most preferred features into a single landscape painting, *America's Most Wanted*. The savanna-like landscape features a lake, gently sloping hills in the background, and a wooded cliff. The most prominent trees would be easy to climb in the event of sudden danger. The scene features two deer, three young people in their reproductive prime plus an older man. Komar and Melamid got similar results from comparative surveys in nine other countries. All people preferred savannas with water, easily climbed trees, happy people, and large mammals. Overwhelmingly they also preferred painted outdoor scenes that looked "real."

The kinds of changes landscape architects have recommended to their prospective customers have also been used to test predictions from the savanna hypothesis. Humphrey Repton, an eighteenth century British landscape architect, drew "before" and "after" pictures of the landscapes he proposed to modify and bound them in red covers together with prose that explained why he suggested those changes (Repton 1907). Based on the savanna hypothesis, Heerwagen and Orians (1993) correctly predicted that Repton would propose changes that created more savanna-like scenes,

increased visual access, fragmented closed woods, opened up distant views to the horizon, added refuges and cues that signaled ease of movement, and added evidence of resource availability, particularly large mammals.

Parks and Gardens. People probably designed gardens long before they invented agriculture, but prior to the Medieval Period we know little about the forms of ancient gardens. Medieval gardens were either herb gardens designed for growing food plants or places set aside for recreation. Which species of plants were available, what societal ideals and symbols plants or structures represented, and societal attitudes towards nature, influenced the forms of gardens and parks (Tuan 1974). Nonetheless, habitat preferences that evolved while our ancestors lived in African savannas should continue to influence how we design parks and gardens.

If our aesthetic preferences today reflect our savanna origins, parks and gardens should be designed to be more similar to African savanna vegetation than to either closed forests or deserts. Trees similar to those that dominate resource-rich savannas should be preferentially planted. Japanese gardens are savanna-like in that trees are scattered and are pruned or genetically modified to resemble savanna trees. Water is emphasized, in the form of ponds or as rocks and gravel molded to simulate waves (Orians 2014).

Western gardening began in the Middle East, a dry region with brutally hot summers. Persian gardens were designed as places to sit and escape from the sun's heat. They were models for Islamic gardens, which spread east to India and west to Turkey, North Africa, and Spain. We have only indirect evidence of the forms of those ancient Persian gardens. One source is carpets. Gardens portrayed on surviving Persian carpets have a small border of flowers, followed by a wider one of trees. The main part of the garden is divided into four sections, separated by rivers with fish. Each of the four sections is divided into six squares where flowerbeds alternate with beds containing plane and cypress trees. Marco Polo's descriptions of gardens he observed during the 1260s accord with those patterns. No ancient Persian gardens remain

today, but the Moorish gardens of southern Spain retain some of those features.

Political stability in eighteenth century England, combined with great wealth of the upper classes, favored expansive landscape gardens. The most famous ones, designed by Lancelot Brown (1716–1783), closely resembled tropical savannas in having scattered trees, often in clumps. Unlike in Japanese gardens, trees in English gardens were not pruned; only much more recently were mutants with different shapes incorporated into them.

British geographer Jay Appleton (1975) developed prospect/refuge theory to predict which features of a landscape increase the likelihood that the individual will find a scene attractive or unattractive. Appleton proposed that *prospect* should be attractive because it offered a good view or vista from which an individual could learn valuable things about the area. *Refuge* should enhance a scene by providing cover from which to observe and assess the environment. The presence of *hazards*, risks an individual would face while exploring an environment, should make an environment less attractive (see Orians 2014 for details).

In combination, the savanna hypothesis and prospect-refuge theory predict that garden designers should provide visitors with a succession of refuges, each one offering a view (prospect) of a different part of the garden. Views should feature areas that have water, appear resource-rich, and offer safe walking routes. Aesthetic experiences would be enhanced if walkers followed a specific route of travel indicated by clearly marked paths.

Japanese gardens fit these predictions. Paths curve; rocks, trees, or shrubs frequently hide their courses. A walker emerges from one refuge with a new prospect view. After a short walk through an open area, another refuge (a group of trees and shrubs that obscures other parts of the garden) is encountered. Multiple prospect views also foster an impression that a garden is much larger than it actually is.

The most famous of eighteenth century English gardens – Wickenham, Stowe, and Stourhead – were also designed with prescribed routes. Guidebooks informed walkers where to

go and how to interpret what they saw (Ross 1998). Controversy exists about which interpretations were really intended by the designers of the gardens, but visitors were expected to understand that the views, sculptures, and structures distributed around the gardens had classical, religious, or sexual significance. Whatever the interpretations, visitors experienced a sequence of prospect/refuge events. The most elaborate formal garden designed around a specified route of travel is the largest – Versailles. Louis XIV wrote an itinerary for viewing Versailles that prescribed the route and commanded visitors to look at views in a specific way. A visitor that followed Louis' itinerary moved through the garden from one fountain to another, never losing sight of water, as long as helpers raced along hidden parallel passages to turn on and off fountains as needed.

Tree Shapes

Trees are dominant features of most environments historically used by people. They are sources of food, shade, and safety. The trees that dominate resource-rich tropical savannas are typically broader than they are tall, have canopies wider than they are deep, and have trunks that are short relative to their total height. In drier, less productive habitats, most trees are short; many have multiple trunks. Thus, tree growth forms signal the resource potential of the area.

Early gardeners should have preferred trees with shapes similar to species common in high-quality savannas. Subsequent modifications of those trees should have made them even more like trees of resource-rich savannas than their wild ancestors. These predictions have been tested in Japanese gardens where gardeners prune many woody plants to alter their shapes and have selected and used genetically modified types of woody plants. The three Japanese maple species that dominate gardens naturally grow sideways to seek patches of brighter light in the forest understory. Japanese gardeners do not need to prune them extensively; they already have savanna-like shapes (Orians 2014). Most rarely planted species

are taller relative to their breadth than the commonly planted ones.

The natural growth forms of conifers commonly planted in Japanese gardens are not savanna-like, but Japanese red pines that grow in windswept locations, such as seashores and mountain ridges, resemble tropical savanna trees. Their growth-form flexibility may have attracted Japanese gardeners. Red pines and other species of conifers in gardens are pruned so that they are broader than tall, have trunks that divide close to the ground, and have canopy layering similar to that of African savanna trees (Orians 2014).

Heerwagen and Orians (1993) recorded people's responses to photographs of *Acacia tortilis*, the species that dominates resource-rich East African savannas. They tested four hypotheses: (1) Trees whose trunks bifurcate closer to the ground should be more attractive than trees whose trunks divide higher up. (2) Trees with moderate canopy density should be more attractive than trees with low or high canopy density. (3) Trees with a high canopy layering should be more attractive than trees with low or moderate layering. (4) The broader a tree's canopy relative to its height, the more attractive it should be. As predicted, people on three continents preferred *Acacia tortilis* trees that had highly or moderately layered canopies, low-bifurcating trunks, and higher canopy width/tree height ratios than trees with narrow canopies and trunks that split higher above the ground. Contrary to predictions, the canopy width/canopy height ratio did not influence a tree's attractiveness.

College students in Australia, Brazil, Canada, Israel, Japan, and the United States all rated spreading and globular trees higher than conical and columnar ones (Sommer and Summit 1996). College students from Zimbabwe, South Africa, Estonia, Italy, Switzerland, and the US-Mexico border also preferred trees with an acacia-like shape (Sommer 1997). Participants also scored trees more highly if they were common where they had grown up, indicating that early exposure to tree shapes also increases their attractiveness. In laboratory experiments, people have lower blood pressure when they view pictures of trees with

spreading rather than rounded canopies (Lohr and Pearson-Mims 2006).

Most experiments have been conducted with adults. Children should respond differently to trees; their responses should change with age as their ability to climb improves. Coss and Moore (2002) tested whether young children with little or no tree-climbing experience understood that trees could be antipredator refuges and sources of shade by asking them where they would seek refuge from a predator. Because our female ancestors were better climbers than males during most of human evolution, Coss and Moore predicted that preschool girls would value trees as antipredator refuges more highly than preschool boys did. As predicted, girls selected the acacia tree more often than either a crevice or top of a boulder in an imaginary landscape. The boys, on the other hand, did not favor any one of the three.

Leaves

Because the dominant trees of high-quality African savannas have small compound leaves, the savanna hypothesis predicts that trees commonly planted in gardens should have smaller, more deeply divided leaves than rarely planted ones. As expected, the maples commonly planted in Japanese gardens have simple leaves, but they have from five to seven lobes that penetrate at least to the middle of the blade, giving them a compound-like appearance (Orians 2014). Maple cultivars commonly planted in gardens have leaves that are much smaller than those of wild individuals. The leaves of very few cultivars are as shallowly lobed as wild-type *Acer palmatum*. More than half are lobed to the base, rendering them compound.

Cliffs

A prime requirement of a suitable residence is protection from the dangers posed by the physical environment – wind, rain, and extreme temperatures – and from dangerous animals and other humans. The most important predators on our

ancestors and tropical people today hunt primarily at night. Humans probably were unable to sleep on the ground until they domesticated fire and learned how to build structures that predators could not penetrate. Simple protections, such as fire, thorn bushes, or animal bones, would have been sufficient to repel predators, but they would have offered little protection from hostile humans. A cliffside cave with difficult access and a fire at its entrance would have been effective against both. Early humans made extensive use of caves as living quarters; some of them were occupied for thousands of years.

Cliffs and bluffs attract us today, an attraction often associated with a strong desire to climb to the top. Climbing cliffs, which requires physical effort that is normally shunned, is intrinsically rewarding. It is engaged in enthusiastically by well-fed, unthreatened persons with no immediate intention of hunting or pursuing or escaping from hostile humans.

Water. In seasonally dry African savannas, our ancestors needed to drink every day. Dehydration would have been a constant risk. Their home ranges were probably determined by the distribution of dry-season water and safe sleeping sites. A legacy of that intimate relationship is that water is prominent in myths, such as flood myths, which are found throughout Africa, Australia, Eurasia, and the Americas (Witzel 2015).

Yet, water offers both positive and negative affordances. We need water for drinking, washing, and cooking. Aquatic environments have greater variety and density of foods than drier places, but many serious diseases are water-borne. Water may form barriers to movement (lakes and rivers) and pose hazards (cascades, rapids, and waves), particularly during stormy weather. Which of these features is most relevant varies with distance between the viewer and the water and a viewer's physiological needs.

Water nearly always enhances the quality of a scene (Ulrich 1981). People rank natural scenes containing water higher than scenes without water. Swedish college students ranked natural scenes with water higher than natural scenes without water on scales of ugly-beautiful and unpleasant-pleasant (Ulrich 1981). College students in North Carolina,

viewing colored slides depicting different types of waterscapes (waterfalls, rushing mountain streams, rivers, lakes, ponds, swampy areas), ranked swampy areas with stagnant, slime-covered water lower than other types of scenes (Herzog 1985). Water is prominent in most of Turner's "Picturesque Views in England and Wales." Most of them show people boating, fishing, hunting, watering livestock, or simply relaxing near water (Shanes 1979).

In the most definitive study of people's responses to water, investigators electronically manipulated photographs to delete features in otherwise identical pictures. Evidence that water was dirty or polluted, such as scum or detritus, greatly reduced the desirability of the scene for recreation (Wilson et al. 1995). People find scenes depicting water, or lush vegetation that grows near water, more attractive than strictly arid scenes (Balling and Falk 1982; Lyons 1983). Amplitudes of participants' EEG, which measures physiological arousal, were consistently higher when individuals viewed vegetation scenes rather than urban scenes. Amplitudes were lower when they viewed scenes with water than scenes without water (Ulrich 1981). Scenes with water evoked the strongest positive ratings as well as the greatest amount of "wakefully relaxed" cortical activity, measured as recordings of alpha wave amplitude (Ulrich 1981).

Children also prefer scenes with water (Zube et al. 1987; Bernáldez et al. 1987). They also find savanna pictures taken during the wet season, when grasses are green, more appealing than those taken during the dry season, when grasses are brown, even though no water is apparent (Lyons 1983). Desert scenes are the least attractive to children among an array of slides showing African savannas and relatively dense coniferous and deciduous North American forests (Balling and Falk 1982; Lyons 1983).

Our strong attraction to water also expresses itself in our choices of the surface finishes of art works and consumer products (Coss 2003). Bone artifacts older than 70,000 years of age in Blombos Cave, South Africa, were ground and polished to transform them into shining awls and symmetrical points (Henshilwood et al. 2001). The appeal of luster may have influenced choice

of materials for decorative objects, beginning with malleable copper for jewelry in the early Neolithic (Mellaart 1968), followed by gold and silver. Our attraction to gold, silver, and diamonds may be the result of our attraction to the glitter of water, a truly valuable substance.

Conclusion

The Savanna Hypothesis has proven highly successful in generating a variety of testable hypotheses that have extended, refined, and altered its original formulation and conceptual foundation. A rich and expanding literature shows that many of our immediate and unconscious responses to landscapes, in photos and paintings as well as real environments, accord with predictions generated by the hypothesis. We have stronger positive responses to the shapes of trees that dominate high-quality savannas, both as indicators of habitat quality and as providers of immediate benefits such as shade and safety. Water, which was scarce during the dry season in African savannas, enhances our appreciation of landscapes. The experiments conducted to date indicate that we have immediate and strong responses, both positive and negative, to landscapes, but that we are generally unable to explain our reactions. An evolutionary perspective suggests that we should expect responses that had to be made quickly, without time for reflection and evaluation, to be unconscious. Although the existing experimental evidence is highly suggestive, much more research is needed to determine which of these responses are truly universal and to assess how much our evolved responses to landscapes can be modified by the specific experiences individuals have as they grow up and experience a wide variety of environments.

Cross-References

- [Emotions](#)
- [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)
- [Landscape Preferences](#)

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Savannah

► Grasslands

Savoriness

► Taste

Savory

► Taste

Scaffolding in Learning

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Synonyms

Instruction; Learning process; Modeling; Progression; Zone of proximal development

Definition

A process in which more competent people provide a temporary framework that supports children's thinking at a higher level than children could manage on their own.

Introduction

Scaffolding is a method of teaching, where a more knowledgeable individual provides a framework that allows a less knowledgeable individual to be able to think at a higher level than they would have been able to on their own. The goal is for the less knowledgeable individual to eventually be able to think at that level or complete a specific task on their own. Giving this framework can include demonstrating how the task is done, explaining the overall goal, and helping with the most complex parts of the task. In general, this is how most parents teach their children throughout their lives, and this type of teaching has also been adopted into educational settings. Through scaffolding, the learner may start by requiring extensive help and then less and less support until they are able to complete the task on their own. It is vital for the more knowledgeable individual to instruct, model appropriately, and use questions to assist and to provide feedback (Sanders and Welk 2005).

Development of Scaffolding

Over the last century, the concept of scaffolding has been defined, strategized, and implemented both organically and purposefully into many learning environments. Historically, scaffolding derived from the work of tutors, whose main focus was to deliver information as well as content, to assist the learner in understanding a topic (Wood et al. 1976). Child development theorists, Albert Bandura and Lev Vygotsky, explored this process of learning through scaffolding using two different frameworks.

First, Bandura (1989), using social cognitive theories, believed that the environment was a crucial aspect in the way people learn, as we use attention, retention, repetition, and motivation to observe our surroundings, behaviors, and information in front of us. We observe learning in several types of environments: a classroom, at home, or on a playground. It is through the abovementioned learning processes that we pay particular attention to the information we observe and retain what we are interested in or what connects to us. Through repetition, the information moves from our working memory to our long-term memory, and finally, intrinsic and extrinsic motivation to succeed and achieve, allows us to push into more difficult learning scenarios (Bandura 1989).

On the other hand, Vygotsky theorized that our learning derives from exchanges we have with our own cultural groups and when we learn information, we need it to connect to our pre-existing knowledge and social experiences to make better sense of it (Vygotsky et al. 1980). Vygotsky believed that knowledge construction happens when the individual learner interacts with others around them. According to Vygotsky, the basis of learning is in interacting with other people with a focus on social interaction, the more knowledgeable other, and the zone of proximal development. The zone of proximal development is the difference between what a learner can do without help and what the learner can do with guidance from a more knowledgeable individual. Through guidance and collaboration, this is where students learn to build on

what they already know to achieve a higher level of understanding or further knowledge (Black and Allen 2018). This is where scaffolding comes in, as it is the process of teachers demonstrating how to solve a problem and then taking a step back and offering support when needed. In other words, the basis of higher-order learning is when a child or person interacts with someone who has more knowledge than him or her (Sanders and Welk 2005). The learner must master tasks in stages and expand on prior knowledge with each stage progression. This is often seen from early on in development, with children from a young age being shown how to complete basic tasks from their parents or caregivers.

Parental Scaffolding

Scaffolding is often the way in which parents teach their children from a very young age. Adults tend to model behavior, helping children with tasks a lot at first, assisting them less and less until they are able to complete the task on his or her own. Research has consistently found positive effects between parental scaffolding and the abilities of the child. For example, a study by Hammond and Cappendale (2015) found that parental scaffolding of children's participation in chores was significantly correlated with that child's willingness to help. It is therefore important to consider that the role of parents when it comes to scaffolding is not only for academic tasks (e.g., helping with homework) but also daily tasks and chores. With these social frameworks in mind, parents should consider the impact of modeling positive actions and instructing children step by step. Further, research has also found significant effects with parental scaffolding and improved executive functioning and problem-solving abilities of the child (Hammond et al. 2012). Parents who effectively used scaffolding tended to have children with improved problem-solving abilities. Moreover, a study by Neitzel and Stright (2003) concluded that parental scaffolding is the basis for the self-regulatory competence of the child and is associated with both problem-solving skills and

academic self-regulation. In other words, children were found to have improved self-regulatory abilities when their parents effectively used scaffolding when teaching them how to do things. Overall, research seems to support that parental scaffolding is not only important for tasks at home but can also impact the child's behavior in an academic setting.

Scaffolding in the Classroom

Scaffolding is an important skill for educators to utilize within a classroom setting. Mercer (2013) argues that the best strategies for scaffolding are through appropriation of information, co-construction of information, and transformation of an individual's reasoning or understanding. While these strategies are within the framework discussed, these newer strategies also tend to focus on the collaborative aspects of scaffolding, rather than the individual retention and delivery of knowledge (Mercer 2013). Further, Black and Allen (2018) explain that the best type of information to work with when scaffolding are real-life problems, as students need to be able to relate to the information. When students collaborate with information from real-world experiences or events, they are able to engage and apply that knowledge to different scenarios and the knowledge and skills can therefore become more transferable (Black and Allen 2018). The use of strong questioning can help the student move between zones of development (i.e., progressing from what they don't know to having said knowledge) as students begin to think about what they know, the perspective they want to take, and how to apply that knowledge to other problems or experiences (Black and Allen 2018). It is also important to randomly assign students to different groups to work together. If students are not placed in groups with differing perspectives, it is unlikely that the questions will challenge their pre-existing way of thinking and allow them to build from their prior knowledge to transform their learning, ultimately enhancing their ability to transfer higher-level information from one environment to another (Black and Allen 2018).

As scaffolding has moved from tutoring to being integrated into classrooms, teachers and researchers have developed several strategies as to best implement a scaffolded learning environment. Strategies for scaffolding range from the process of implementation to the specific content, to reflection, and to questioning afterwards. According to Wood et al. (1976), there are six keys strategies to effective scaffolding:

- (1) Recruit interest in and adherence to requirements of the task.
- (2) Simplify the task by reducing the number of actions.
- (3) Maintain direction by motivating the learner to stay on task.
- (4) Mark critical features by accentuating the most important parts.
- (5) Control frustration while keeping the learning responsible for the task.
- (6) Demonstrate or model solutions.

(Wood et al. 1976 as cited in Black and Allen 2018, p. 82).

Limitations of Scaffolding and Recommendations to Use It Effectively

It is important to consider that while scaffolding can have many positive effects to children, the results of scaffolding in an educational setting are only as good as the delivery of the model. For as many scaffolding strategies as there are, there are equally as many drawbacks to the process ranging from interactions with groups to the delivery of the scaffolding process. First, collaboration and group work are skills that need to be taught, as most students do not have the natural ability to effectively communicate ideas to reach a higher level of learning or to push through the next circle of the zone of proximal development (Black and Allen 2018). Mercer (2013) argues that argumentation is a key skill in collaborative scaffolding, and if students are not taught to critically discuss perspectives and opinions, they will not develop the transformative process necessary for true scaffolding to occur. Next, adults choosing to use

scaffolding should be aware that placing students in homogeneous groups to collaborate is not necessarily the most effective, as students tend to share similar perspectives and experiences; they likely will not formulate higher-order ideas or be challenged by multiple perspectives (Black and Allen 2018). Lastly, modeling is a large component of successful scaffolding. If modeling is rushed or not personalized by being simplified for each learner, students will likely not reach their potential for expanding their knowledge and building the transferable skills necessary for successful collaboration and application of their learning in multiple contexts (Black and Allen 2018).

Conclusion

Overall, scaffolding is an important concept for individuals working with children and youth to foster and utilize. From a young age, scaffolding can have positive effects on child development, particularly as children learn about the world around them and how to complete tasks in everyday life. Educationally, it is important that educators are effectively executing scaffolding in classroom settings, as Fischer (2018) explains that when students are learning through scaffolding, there is a natural phasing out of direction given by the teacher. However, if the students have not successfully been challenged to think more critically and advance their knowledge base, the likelihood that the students will be able to successfully transition the information and skills outside of the individual scenario is limited. Children naturally learn through social interactions around them, and therefore it is important to ensure that these interactions are positive and helpful in the learning of the child.

Cross-References

- [Child-Centered Learning](#)
- [Learning](#)
- [Learning Versus Imitation](#)
- [Social Learning](#)
- [Social Learning and Social Cognition](#)

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Scaling Factors

- Selection Pressures as a Function of Age

Scares

- Fears

Scarification

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Synonyms

Carving; Laceration; Cutting; Permanent marking

Definition

Burning/Branding/Scratching/Images or designs into the skin

Introduction

A subsection of body modification that signifies complex costly signaling is scarification. Today ornate scarification is an integral part of the body ornamentation community, yet it has historic roots reaching far back into our evolutionary history. Before individuals began using scarification to systematically ornament their body, scars were the outcome of (sometimes battle) wounds. They were maps to an individuals' past, each telling a story of past hardships. Some particularly large scars can indicate near death experiences in which an individual overcame great odds to remain alive. Humans quickly realized that the momentary pain of cutting the skin in an artistic fashion resulted in permanent ornate designs in the skin via scarification.

Scarification as a Right of Passage

In Australia, scarification practices are practiced among Aboriginal individuals as a right of passage. Between the ages of 16 and 17, women and

men are intentionally scarred on their chests, shoulders, and bellies. Without these scars, members of the tribes are not allowed to partake in cultural customs and other tribal activities. In the Sepik region of Papua New Guinea, the people believe that crocodiles created humans. Bamboo is cut into sharp slivers and used to cut slices into a young man's chest and the entirety of his back down to his buttocks. These cultural practices are more instances of costly signaling; especially since the cultures that scarification practices originated in did not have access to modern medical interventions (so having open wounds was particularly risky).

Badges of Honor

Another form of scarification is a byproduct of a slightly different form of body modification: suspension. Suspension practices would be categorized as multiple semi-permanent deep tissue piercings strung together used to suspend an individual's body off the ground. People who practice suspension often start with hovering off the ground for a few minutes and then eventually escalate to basically being able to swing in the air weightlessly for long periods of time. Historically, suspension practices are originated in both Hindu and Mandan religious life. The Mandan are a native tribe that was located along the Missouri River that explicitly practiced suspension. During their *Okipa* ceremony, individuals were pierced and suspended as part of a story about the creation of the earth and as a rite of passage for their warriors. Though suspension would qualify as deep tissue piercing, individuals who practice this regularly wear their suspension scars as badges of honor – not necessarily as a form of ornate art, but as an indicator of an ability to do something that only a small portion of the population would dare do.

During the Hindu festival of *Thaipusam*, individuals take part in a practice referred to as *vel kavadi* in which some type of hardship must be endured. Some pierce their face with skewers, while others pierce their backs with hooks and attach ropes to them to tow various size objects:

The size of the object and amount of pain endured is supposed to indicate the amount of devotion that individual has for their worship. Though these practices are not always explicitly about suspending one's body, the repeated piercing year after year to indicate devotion leaves lasting scars that indicate many things about an individual depending on their culture.

Conclusion

Today, culture is a melting pot of many other cultures and time periods, allowing many westernized societies the luxury of sampling various practices with the assurance of modern medicine to back them up. Tattooing and piercing are nearly commonplace, and scarification is gaining some popularity within various social groups. Some tattoo and piercing shops actually specialize in precise scarification with the use of a scalpel and medical cutting techniques. Across cultures, we see scarification practices as considerably well received if it is based in historical practice and individuals are taking precaution against blood born pathogens and disease.

Cross-References

- ▶ [Advertising](#)
- ▶ [Ancestor Worship](#)
- ▶ [Appearance/Beauty in Girls](#)
- ▶ [Art](#)
- ▶ [Beneficial Side Effects](#)
- ▶ [Body Modification](#)
- ▶ [Burials](#)
- ▶ [Camouflage](#)
- ▶ [Carving](#)
- ▶ [Competition Between Groups](#)
- ▶ [Culture of Honor and Individual Differences](#)
- ▶ [Emotions](#)
- ▶ [Facial Attractiveness](#)
- ▶ [Facial Disfigurement](#)
- ▶ [Good Genes](#)
- ▶ [Greater Risk-Taking and Status](#)
- ▶ [Health Cues](#)
- ▶ [Human Ornamentation](#)

- [Individual Differences](#)
- [Male Ornamentation](#)
- [Manipulation and Dishonest Signals](#)
- [Peer Groups](#)
- [Peers](#)

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Scavenge Hunting

- [Extractive Foraging Hypothesis, The \(Parker and Gibson 1997, 2015\)](#)

Schadenfreude

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Synonyms

[Fall of “tall poppies”](#); [Malicious joy](#)

Definition

Pleasure felt in response to learning of another person or group's misfortune.

Introduction

Schadenfreude is a portmanteau of the German words *schaden*, harm, and *freude*, joy. Although

the word “schadenfreude” has no English language equivalent, there is a word for it in many other languages, including Dutch, Greek, Chinese, and Russian (van Dijk and Ouwerkerk 2014). Children as young as 24 months old have expressed schadenfreude when a minor misfortune has befallen a preschool friend with the seemingly unfair advantage of their mother's exclusive attention (Shamay-Tsoory et al. 2014). Thus, there is linguistic evidence for schadenfreude's cross-cultural universality and empirical evidence for its emergence early in social development. In addition, Buss (2000) has noted that schadenfreude may be an evolved psychological mechanism designed for successful competition, and research on schadenfreude has supported this notion. Schadenfreude occurs because it should feel good when competitors suffer, as such suffering often directly or indirectly leads to increases in one's relative status. As would be expected given that few competitive contexts are more consequential than the competition for desirable mates, recent evolutionary social psychological research has shown that gender-based differences in schadenfreude may reflect that one of its functions is as an indicator of positive change in one's relative mate value (Colyn and Gordon 2013; van Dijk et al. 2015). In addition to its adaptive role in competitive interpersonal contexts, schadenfreude also figures powerfully in competitive intergroup contexts, especially when the stakes are high, and the pleasing benefits are keen (Cikara et al. 2011).

Origins of Schadenfreude

By definition, schadenfreude's antecedent is the perception of another person or group's misfortune. The underlying reasons for that happiness will vary widely, as schadenfreude occurs as a result of an appraisal that a negative event that has befallen another has simultaneously advanced one or more important personal concerns, be they specific motives or broad goals (Frijda 1988; van Dijk and Ouwerkerk 2014). Not surprisingly, research shows that, for example, schadenfreude is especially likely when another one envies

suffers a misfortune, as that misfortune will often reduce the painful gap in status between the self and the other (Floyd et al. [in press](#); see entry “Fall of ‘Tall Poppies’” for a review).

Enjoying Potential Romantic Rivals’ Downfalls

As noted, schadenfreude often flourishes in the crucially important context of mating. Men and women tend to pursue somewhat different mating strategies and place different degrees of emphasis on a number of qualities of their mates as a result of differences in parental investment and different needs for maximal reproductive success (Colyn and Gordon [2013](#); Trivers [1972](#)). Among the qualities that same-sex individuals compete on in the struggle to attract the highest-quality long-term mate possible are physical attractiveness and social status, and thus Colyn and Gordon ([2013](#)) reasoned that schadenfreude might occur when a local competitor suffers a setback in those and other areas (e.g., interpersonal popularity), signaling the potential that the schadenfroh person might indirectly benefit as a result. A widespread tendency among people to experience schadenfreude in the context of mating-relevant events, they reasoned, might therefore have evolved as a result of increased fitness among those who experienced schadenfreude following a potential rival’s downfall, signaling to them that their relative mate value has increased, creating opportunities to pursue “new, additional, or better mates” (Colyn and Gordon [2013](#), p. 525). The degree of that schadenfreude, they further reasoned, should be greater among females when a close, same-sex friend suffers a decline in physical attractiveness than in social status, with the opposite being the case among males, who should feel greater schadenfreude when a close, same-sex friend’s social status declines. That is, gender-based differences in schadenfreude should emerge on the basis of the degree to which one’s mate value has increased.

Responses to both recalled and hypothetical misfortunes happening to participants’ close friends of the same sex supported Colyn and

Gordon’s predictions consistently for females and substantially less consistently for males across two studies. Subsequent work by van Dijk et al. ([2015](#)), in which schadenfreude targets were acquaintances (rather than close friends), replicated Colyn and Gordon’s results for females (e.g., that schadenfreude was greater when a same-sex acquaintance suffered a decline in physical attractiveness than when her social status declined). However, they also found *consistent* evidence that males do indeed feel happier when a same-sex acquaintance loses social status than physical attractiveness. Moreover, schadenfreude differed among neither females nor males on the basis of whether declines were in looks or social status when such misfortunes were suffered by *opposite-gender* acquaintances. Taken together, Colyn and Gordon’s and van Dijk et al.’s results suggest that schadenfreude facilitates successful competition for mates in sex-specific ways consonant with evolutionary psychological theory.

Enjoying Out-Group Misfortunes

Schadenfreude at the intergroup level entails some of the same competitive processes as those in interpersonal contexts. Naturally, people feel good when an out-group suffers because one’s own group is likely to gain as a result. However, social neuroscience research suggests schadenfreude following out-group mishaps may actually encourage a desire to take direct action against members of hated out-groups. For example, in an fMRI study assessing avid major league baseball fans’ responses to a hated rival team’s simulated misfortunes (i.e., bad plays), greater activation of the ventral striatum, a neural structure implicated in both rewarding feelings and approach motivation, was associated with greater self-reported willingness to aggress against fans of a rival team weeks later (Cikara et al. [2011](#)). In line with such findings, schadenfreude may play an especially powerful role in motivating aggression in intergroup contexts. Such contexts often weaken moral prohibitions against harming others, perhaps as a result, in part, of evolved “tribal instincts” encouraging the acquisition of

valued, reproductively relevant resources, such as territory or mates, via coalitional acts of intergroup violence (Cikara et al. 2011; Van Vugt 2009).

Conclusion

Schadenfreude is an “opportunistic” emotion not only in the sense that one has not personally brought about the competing party’s misfortune. At a deeper level, schadenfreude indicates an opportunity has presented itself to adaptively recalibrate one’s behavior, such as through seeking out better mates or striking while the enemy group is down.

Cross-References

- [Downfall of “Tall Poppies”](#)
- [Fall of “Tall Poppies”](#)
- [Intrasexual Competition Between Females](#)
- [Intrasexual Male Competition](#)
- [Long-Term Mating](#)
- [Male Warrior Hypothesis](#)
- [Parental Investment](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Self-Enhancement Relative to Others](#)
- [Sexual Strategies Theory](#)
- [Status and Reproductive Success](#)

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Schematic Memory

- [Procedural Knowledge](#)

Schizophrenia

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Synonyms

[Bleuler’s syndrome \(obsolete\)](#)

Definition

Psychiatric condition characterized by delusions, hallucinations, and/or disorganized speech, as well as by grossly disorganized or catatonic behavior and/or negative symptoms. The symptoms must have persisted for at least 6 months and affect interpersonal, academic, or occupational functioning.

Introduction

The term “schizophrenia” refers to a group of disorders characterized by severe cognitive, emotional, and behavioral symptoms, which typically include the presence of delusions, hallucinations, disorganized speech or behavior, and the development of negative symptoms such as abulia, apathy, or social withdrawal (American Psychiatric Association 2013). Schizophrenia becomes usually clinically apparent in late adolescence or early adulthood. However, in many cases there are precursor symptoms in childhood, and attenuated psychotic symptoms or brief self-limiting psychotic episodes may precede the onset of the disorder. Research suggests that schizophrenia is phenotypically similar across cultures, though a more malignant course and outcome is more frequent in first-world societies. The dogma of cross-culturally equal prevalence and incidence rates of schizophrenia has recently been challenged and may need to be revised (McGrath 2006). Twin and adoption studies clearly demonstrate that genetic factors play a significant role in the trans-generational transmission of schizophrenia; however, there are important environmental risk factors contributing to the manifestation of schizophrenia, including male sex, migration, urbanicity, areas with a lower ethnic density of a minority population, and abuse or neglect during childhood (reviewed in Abed and Abbas 2011). Diathesis-stress models of schizophrenia suggest that prenatal conditions also affect the risk of developing schizophrenia, among which intra-uterine virus infections, poor nutritional status, or exposure to toxic substances during the fetal period are commonly accepted. Early disruption of neural development caused by these adverse events may be followed by a second (possibly social) incidence around puberty, when the brain undergoes dramatic reorganization (Insel 2010).

Aside from the fact that even a conservative estimate of 1% prevalence rate of schizophrenia in the general population exceeds what one would expect to occur by chance due to a high mutation rate, there is evidence to suggest that the fecundity of people with schizophrenia, particularly men, is reduced by about 50% compared to unaffected

individuals. These findings create an evolutionary enigma, because it is unclear why genes that are associated with an increased risk for schizophrenia are maintained in the genepool of a population in spite of the dramatic reproductive disadvantage associated with the condition.

Evolutionary Accounts of Schizophrenia

A plausible explanation for this puzzle is that genes associated with the condition, though increasing the risk for schizophrenia, convey advantages in terms of survival or reproduction (balanced polymorphism), or that these genes interact with other fitness-promoting genes in beneficial ways (epistasis). Following this approach, an almost countless number of hypotheses exist regarding possible advantages of genes carried by affected individuals, by nonaffected kin of index patients, or advantages for the social group (group selection approaches; overview in Polimeni and Reiss 2004). These hypotheses comprise ideas concerning adaptive properties of schizotypal traits in relation to group selection, schizophrenia as a trade-off of human language acquisition or creativity, reduced risk of cancer in relatives of schizophrenia patients, schizophrenia as an extreme phenotype produced by variation of sexually selected traits, and effects of maternally imprinted genes (reviewed in Brüne 2016). A problem of these approaches is that many of them implicitly assume that schizophrenia is a homogenous “disease entity,” or that the risk for schizophrenia is conveyed by a single gene or a few genes with large effect size, which is currently not supported by empirical evidence (Keller and Miller 2006). However, there is some evidence for positive selection in the human lineage at several loci including those coding for DISC1, dysbindin, and neuregulin, which are known to be involved in neurodevelopment (Crespi et al. 2007).

As space is limited, two plausible scenarios are highlighted in the following paragraphs, one concerning a genetic approach and the other a more environmental slant.

With regard to a possible role of sexual selection in schizophrenia, an interesting hypothesis

posits that these disorders represent “low-fitness variants” of sexually selected traits (Shaner et al. 2004), which may explain why patients with schizophrenia have reproduction rates below average. It could also account for recent reports about a relationship of age at onset of schizophrenia varies and latitude suggesting that onset is earlier in populations living closer to the equator. For example, it could be that increased exposure to pathogens and higher levels of polygyny create pressure on shifting mating to a younger age. Consequently, a dopamine overshoot in the ventral striatum may lead to earlier expression of schizophrenia-associated signs and symptoms, when the need for premature courtship behavior serves as nonspecific stressor. Moreover, since stabilizing selection tends to reduce deleterious mutations, it could be that an individual’s higher than average number of fitness-reducing alleles leads to the expression of a schizophrenia phenotype, though many of these alleles may be evolutionarily transient. Thus, the emergence of new fitness-decreasing mutations may contribute to an equilibrium through which the average prevalence of schizophrenia in a population is maintained. Such a scenario may also explain why the replicability of findings concerning genes conferring risk for schizophrenia is difficult (Shaner et al. 2004).

Consistent with the hypothesis of schizophrenia as maladaptive extreme of variation of sexually selected traits, there is some evidence for genomic imprinting in schizophrenia. For instance, maternal imprinting could be associated with a general undergrowth and “femaleness” of the brain in schizophrenia, indicated by lower gray matter volume, diminished lateralization, and hyperactive social cognition producing delusions of reference – the opposite of what is typical for autism in which paternal imprinting may prevail (Crespi and Badcock 2008).

Aside from these genetics-oriented hypotheses, approaches taking into account environmental risk factors suggest that schizophrenia may arise from a mismatch between ancestral and current environments, whereby schizophrenia (foremost those phenotypes associated with

paranoid ideation) could be the extreme of variation concerning the intolerance of outgroup membership (Abed and Abbas 2011). In support of this idea, the anthropological record of *Homo sapiens* indicates that, for the most part of their evolutionary history, humans have lived in small-scale communities associated with xenophobic attitudes towards strangers. Culturally determined interaction with large numbers of people who are personally unknown may produce heightened vigilance, fear of being assaulted by others, and suspiciousness with regard to others’ malicious intentions. In vulnerable individuals, exposure to novel environmental conditions brought about by migration, urbanicity, poverty, or ostracism may then culminate in psychosis (Abed and Abbas 2011). Predictions derived from this hypothesis include higher rates of schizophrenia in males, in people who migrated to other countries or social systems (extending to the second generation), in those who have experienced exclusion from the community or social defeat, and in young people during adolescence (i.e., changing role models and social expectations). Consistent with the “outgroup intolerance hypothesis,” the content of persecutory delusions has been found to differ between men and women regarding the number and sex of persecutors, as well as regarding the degree of familiarity with the perceived persecutor. That is, whereas men usually feel more often threatened by groups of strange males, women more often feel persecuted by individuals from their personal environment. Both deluded men and women primarily report fears of being physically injured or assaulted. Indeed, in stone-age conditions, the main threat for men was presumably being assaulted by men from other tribes; women, by contrast, were more threatened by exclusion from the community (reviewed in Brüne 2016).

Conclusion

Evolutionary hypotheses about schizophrenia are abundant, but many are difficult to test empirically. Potential pitfalls concern the heterogeneity

of the phenotypic picture, shaky boundaries between psychosis and “normalcy,” and uncertain diagnostic validity of “core” symptoms of schizophrenia (Brüne 2016). There is clearly a need for addressing open genetic questions to resolve the question of why schizophrenia is associated with high heritability, high prevalence, and low reproductive fitness, and what the role of immune function of “risk” genes for schizophrenia might be (Flint and Munafò 2014).

Cross-References

► [Darwinian Psychiatry](#)

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School Bullying

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Synonyms

[Cyberbullying](#); [Peer-to-peer aggression](#); [Physical bullying](#); [Relational aggression](#); [Relational bullying](#)

Definition

Bullying is most commonly defined based on Olweus's (1993) definition that includes three elements: (a) an imbalance of power, (b) intent to harm, and (c) is repeated over time. Recently, an alternative definition that integrates recent theory and empirical data has been proposed: “Bullying is aggressive goal-directed behavior that harms another individual within the context of a power imbalance” (Volk et al. 2014, p. 328).

Introduction

Bullying, a subset of aggressive behaviors, is a construct that often elicits strong opinions. Some people believe that bullying is a part of growing up or a *rite of passage* that “builds character,” while others view it as a severe problem that can be harmful, even detrimental, to those involved. Bullying can be understood as a “unique but complex form of interpersonal aggression, which takes many forms, serves different functions, and is manifested in different patterns of relationships” (Swearer and Hymel 2015, p. 344). Olweus's (1993) definition illustrates bullying as intentional versus accidental; this is generally agreed upon by bullying researchers. Further, some researchers have linked bullying to proactive aggression, which is consistent with the idea that bullying is goal-oriented (Volk et al. 2014). To understand the complexity of school bullying,

the following factors are discussed: common theoretical perspectives, who is involved in bullying, types of bullying and prevalence rates, the impact of school bullying on youth, and prevention and intervention services.

Theoretical Perspectives on Bullying

The importance of theoretical perspectives in bullying is that they provide a means to understand the underlying causes of bullying – specifically why some youth bully others and why some youth are bullied or victimized – and that they can be applied to guide the development of interventions. Several theoretical perspectives have been used in research to understanding bullying, ranging from theories that explore individual characteristics that contribute to bullying behaviors to ones that examine the broader context – the systems within which the bullying takes place – and the relationship between the context, the individual, and the bullying behaviors. Three theoretical perspectives are discussed below.

Social Ecological Theory

Social ecological theory, more commonly referred to as ecological theory (Bronfenbrenner 1979), has been applied extensively throughout the aggression literature and has also been used throughout the bullying literature. The social-ecological framework has been used to understand systems (i.e., micro-, meso-, exo-, macro-, and chronosystems) that impact bullying and to create prevention and intervention programs effectively relevant to various settings (Espelage 2014). From this theoretical perspective, bullying is construed as an event that is influenced by multiple factors, including: individual characteristics, interactions with others (e.g., peers, families, teachers), and the influence of the varying contexts within which they exist (Swearer and Hymel 2015). This framework has been used to examine concepts such as school climate, peer-to-peer relationships, family dynamics, and bystander roles as they relate to bullying. More recently, technology has been viewed as a subsystem and proposed as an addition to the social

ecological model as the techno-subsystem (Johnson and Pupilampu 2008) that is a “...dimension of the microsystem...[and] includes child interaction with both living (e.g., peers) and nonliving (e.g., hardware) elements of communication, information, and recreation technologies in immediate or direct environments (p. 23).” The techno-subsystem is purported to influence the relationship between the child and the microsystem by acting as a mediator. It is likely that, as research evolves to support the techno-subsystem, this element of the social ecological framework will be applied the bullying literature, particularly in the examination of cyberbullying.

Evolutionary Theory

Some researchers have applied evolutionary theory to understanding aggression, which has been useful and suggests the utility of this theoretical approach for understanding bullying (Volk et al. 2014). This is not surprising as bullying is functionally adaptive across several social animals (Volk et al. 2016). Evolutionary theory posits that bullying serves certain functions that lead to positive outcomes, such as resources and reputation, implying that bullying is a goal-directed behavior (Volk et al. 2014). This theoretical perspective posits that there are benefits tied to bullying others. For example, the bully may be viewed as more attractive by others and may be perceived as popular or having social status (Volk et al. 2016). In this case, evolutionary theory suggests that the bullying persists because it continues to be adaptive (Volk et al. 2014). This is not meant to imply that bullying is without consequences, but rather that the underlying goals may outweigh potential negative consequences. This further illustrates the complex nature of bullying.

General Strain Theory

General strain theory (GST) is a theory that is popular in contemporary criminology and is a newer theoretical framework that is being applied to understanding traditional bullying and cyberbullying (Patchin and Hinduja 2011). GST suggests that when individuals experience strain, it

can lead to a range of negative emotions (e.g., frustration, anger), which increases the likelihood of engaging in delinquent behavior (Agnew 1992). Patchin and Hinduja (2011) argue that two of Agnew's (1992) major types of strain have potential relevancy for understanding bullying: (a) threat or actual presence of a negative stimuli, and (b) the loss or threat of loss of a positive-valued stimuli. A few studies have examined traditional bullying and/or cyberbullying as potential outcomes of strain (type a) and found a direct relationship between strain and both types of bullying (e.g., Keith 2017; Patchin and Hinduja 2011). Other researchers have found support for peer victimization (or experiencing bullying) as the source of strain (type b) that leads to delinquent or problematic behaviors (e.g., Baker and Pelfrey 2016).

Who Is Involved in School Bullying?

When considering bullying as a dyad, most people identify the victim (or target) and the bully (or perpetrator). Researchers have also identified bully-victims and bystanders as having substantial roles in the bullying dyad.

Bully

The *bully*, also referred to as a perpetrator, is the individual who harms another person or group of people through use of aggressive behaviors (e.g., physically hurting, calling names, excluding). There are several myths about who the bully is, such as the stereotype perpetuated by the social skills deficit model that suggests a bully may have power over others, but is socially incompetent (Hymel and Swearer 2015; Sutton et al. 1999). Sutton et al. (1999) suggest that while social-emotional deficits can contribute to aggression, contextual factors such as peer group and environmental influences also need to be considered. Sutton and colleagues (1999) defined two different roles for the bully: the ringleader and the follower (one who accompanies the ringleader). The ringleader bully may have power over the supporter bullies, and by imitating the leader's behavior, supporters may feel a sense of

belonging to a clique. Another common stereotype that research has clarified is that a bully has low social status and is not liked at all by peers. Volk and colleagues (2014) noted that several research studies have demonstrated that peers perceive bullies as being dominant and popular even though they are rated lower on likeability. In short, the myths about bullies cannot be accepted as facts, and inferences ought not to be made over these myths.

Victim

Victims, also called targets, are individuals who are on the receiving end of bullying from others. Researchers have identified different types of victims such as passive victims and provocative victims (whose offensive behaviors may elicit bullying from others; Olweus 1997). Victims are often described as having low self-esteem, poor interpersonal skills, and difficulty in building friendships (Olweus 2003). Further, researchers have found that victims of bullying often experience loneliness and internalizing issues (e.g., anxiety, depression), and low self-esteem (Swearer and Hymel 2015).

Bully-Victim

Bully-victims are students who both bully others and are victimized by others; this group has been identified as distinct from bullies (Olweus 1993). Bully-victims are often considered a subtype of bullies, sometimes called reactive bullies, and are seldom discussed under the characteristics of victims (Volk et al. 2012). However, the literature shows that there are substantial differences between nonvictimized bullies and bully-victims. It is hypothesized that bully-victims are more likely to engage in reactive bullying, whereas nonvictimized bullies are more likely to use proactive aggression (i.e., aggression that serves a purpose; Volk et al. 2012). Research has consistently demonstrated that bully-victims tend to experience poorer outcomes in comparison to victims and bullies (Volk et al. 2012).

Bystander

Bystanders are the individuals who observe bullying, are present in the vast majority (around

85%) of bullying incidents, and can often have an effect on bullying incidents (Swearer and Hymel 2015). The main roles of bystanders include reinforcer, assistant, outsider, and defender (Salmivalli et al. 1996). *Reinforcers* mostly support the aggressive and offensive behavior of the bully by laughing at the victim and/or cheering on the bullying. *Assistants* actively engage in the bullying incident and take part in harassment. The *defenders* attempt to protect the victim and stop the bullying. Lastly, a bystander may take the role of *outsider*; in this role, the bystander has no direct involvement in the bullying incident but acts as a silent approver through inaction. Interestingly, Salmivalli and colleagues (1996) found that girls were more likely to assume defender and outsider roles, while boys were more likely to be reinforcers or assistants.

Prevalence Rates

No child or adolescent is necessarily immune to school bullying, though there are some factors that increase the risk and/or likelihood for some individuals to be more likely to be involved in bullying. Some of these factors include age or grade level, gender, and individual characteristics. School bullying is observed as early as in pre-school and generally peaks during middle school (around ages 11 through 14) and somewhat decreases toward the end of high school (Hymel and Swearer 2015; Nansel et al. 2001). Youth in middle school are likely to be at the greatest risk for involvement in bullying. Prevalence rates can vary widely dependent upon how it is defined and measured. In general, overall prevalence rates range from about 30% to 35% of youth reporting involvement in bullying in some capacity (Currie et al. 2012; Hymel and Swearer 2015; Nansel et al. 2001). Hymel and Swearer (2015) conducted a review of the past four decades of research and found that 10%–33% of students reported being bullied by others (victims and bully-victims) and 5%–13% reported bullying others (bullies and bully-victims). A study by the World Health Organization (WHO; Currie et al. 2012) examined bullying across 43 countries and reported

prevalence rates ranging from 2% to 32% for victimization and 1%–36% for bullying others. These prevalence rates of victimization and bullying are inclusive of victims, bullies, and bully-victims. Bully-victims are often a smaller group with prevalence rates ranging from 1% to 12% (Hymel and Swearer 2015). Prevalence rates can vary based on several factors such as how bullying is defined, how bullying is assessed (e.g., self-report, peer nominations, teacher report), the specific type of bullying, and sample characteristics.

Types of School Bullying

Olweus (1993) classifies the types of bullying as direct and indirect forms; they have also been referred to as overt (e.g., physical) and covert (e.g., relational). As the terms imply, direct bullying refers to visible attacks against the victim and indirect bullying refers to covert actions that are less easily seen (e.g., exclusion from a group, rumor spreading, and gossiping). Recent literature suggests four common types of bullying that are classified as: physical bullying, verbal bullying, relational aggression/bullying, and cyberbullying.

Physical Bullying

Physical bullying is defined as harming others and their property in a repeated way via the use of physical force and includes the threat of physical damage such as kicking, hitting, hair pulling, stealing, and attacking with a weapon (McGrath 2007). This type of bullying is considered easier to detect because physical attacks are overt and observable. Victims of physical bullying are usually weaker physically and have less power. Researchers have found that male students are much more likely to engage in physical bullying compared to female students, while females *may be* more likely to engage in relational, verbal, and cyberbullying, though gender differences are not always evident across these types of bullying (e.g., Hymel and Swearer 2015).

Verbal Bullying

In contrast to physical bullies, verbal bullies seek victims who are weaker in terms of their social

status (e.g., unpopular, new in the school, having low SES; Sonneborn 2013). Verbal bullying includes behaviors such as name-calling, insults, and threats. Students might perceive name-calling or insults as a part of childhood or adolescence rather than a serious form of bullying. Distinguishing teasing from verbal bullying can sometimes be a challenge for youth and for researchers. In past studies, threatening other's physical health has also been included in the definition of verbal bullying. According to Rivkin (2013), verbal bullying happens two times more than physical bullying – regardless of age, SES, gender, and ethnic status.

Relational Aggression

Various terms are used throughout the bullying literature interchangeably with relational aggression, including social aggression and indirect aggression, though researchers may define these constructs somewhat differently. *Relational aggression* is defined as harming others through damage, or the threat of damage to end relationships, to exclude from the group, or to lose feelings of acceptance (Crick et al. 1999). Relational aggression differs from the previous forms of bullying in that its main focal point is to harm interpersonal relationships (Crick et al. 1999). As the name implies by *indirect aggression*, the victim is not confronted by the hostile behavior in an explicit way. For instance, rumor spreading and ignoring are the most frequently used forms of indirect aggression. However, relational aggression conveys all hostile behaviors, including both indirect and direct actions (Crick et al. 1999). Crick and colleagues (1999) suggest that *social aggression* is a broader term than relational aggression and the difference between these terms is that while relational aggression includes the intention of harming relationships, social aggression does not require this intention. This includes verbal insults, rumor spreading, negative facial and body expressions, and physical aggression.

Cyberbullying

Cyberbullying refers to bullying that occurs through electronic devices (e.g., computers, cell

phones, etc.) with the goal of hurting someone else (Peterson 2013). Other terms (e.g., online bullying, internet bullying) have also been used; however, cyberbullying is the most commonly used term. Cyber-bullies mostly harm their targets through rumor spreading in online platforms, threats of harm via text messages, sending sexualized posts, racist rhetoric comments on the social media channels, or leaving out from a group chat (McGrath 2007). Cyberbullying is different from traditional forms of bullying in that bullies have anonymity – they can hide behind their screen. This anonymity and distance from the victim contributes to the bully feeling emboldened and engaging in more insulting and hurtful language than they might use when face to face (McGrath 2007).

Instant messages, social media sites, pictures or videos, phone calls, emails, weblogs, and so forth are most commonly used to cyberbully (McGrath 2007). Cyber-bullies may possess multiple accounts on social media sites or apps (e.g., Snap Chat, Facebook, Twitter, YouTube, etc.) and use their fake accounts as a tool for bullying, soliciting personal information, pictures, etc. from potential victims. Cyber-victims are not as easily able to escape from these stimuli and can be exposed to this bullying regardless of place or time (McGrath 2007). Though some have noted that youth can disconnect from technology to escape the bullying, technology has become an aspect of life that is often heavily integrated both socially and academically.

Impact of Bullying on Youth

Extensive literature has examined the impact of bullying on youth involved and found that all individuals are negatively impacted by the experience, with bully-victims experiencing the worst outcomes (Swearer and Hymel 2015). Bully-victims experience greater risk for several issues such as internalizing issues, low self-esteem, suicidality, and substance abuse. Swearer and Hymel's (2015) review of the literature found that victimization is related to a host of problems including poor physical health, poor social

adjustment, peer rejection, and internalizing (e.g., anxiety, loneliness) and externalizing (e.g., hyperactivity, delinquency) issues. The authors note that while these issues can result from victimization, some of these may be antecedents to the bullying. Bullying perpetration is also related to several problems such as further aggressive behavior, conduct problems, and internalizing issues (Swearer and Hymel 2015).

Effective Prevention and Intervention

There are numerous school-based prevention and intervention programs that have been developed to address bullying. These programs typically address school-wide populations, small groups of students, or individuals. Some programs also promote parent/caregiver or familial involvement and include community partners. In addition to formal prevention and intervention programs, many schools adopt anti-bullying policies or integrate anti-bullying information into existing policies.

School-Wide Bullying Prevention

Although there is a wide variety of programs that claim to decrease bullying behaviors, few programs have been researched thoroughly enough to be considered empirically supported. Programs such as *Bully Busters*, *Expect Respect*, *KiVa*, *Olweus Bullying Prevention Program*, and *Bully-Proofing Your School* are commonly implemented programs that have undergone sufficient research to be considered evidence-based. Two of these programs will be discussed in greater detail, followed by a discussion of anti-bullying policies.

Bully Busters. The Bully Busters program has demonstrated effectiveness in addressing the issue of bullying. The overarching goal of Bully Busters is to promote a safe and healthy learning environment for students through enhanced social environments and decreases in bullying behaviors. This program increases awareness of bullying among educators and teaches students to reject bullying as an acceptable behavior. Bully Busters also includes a parent and family guide which

promotes bullying awareness and provides additional information for how to support children who may be affected by bullying behaviors.

Several published studies have evaluated the effectiveness of Bully Busters at the elementary and middle school levels and found positive teacher and student outcomes (e.g., Browning et al. 2005; Newman-Carlson and Horne 2004). For example, Newman-Carlson and Horne (2004) evaluated a treatment and control group of middle school teachers to evaluate the effectiveness of the Bully Busters training curriculum for teachers. Results revealed a significant increase in teachers' bullying knowledge and an increase in use of bullying intervention skills. Furthermore, an examination of disciplinary referrals demonstrated a significant decrease in students' bullying behaviors.

Bully-Proofing Your School. Bully-Proofing Your School (BPYS) is an empirically supported program that includes teacher training and a student curriculum. Teacher training is comprised of disseminating important information, including: (1) definitions, (2) understanding the roles and characteristics of bullying, (3) recognizing the impact of bullying on learning and social-emotional outcomes, and (4) reviewing the student curriculum and practicing teaching it. The student curriculum includes explicit instruction of definitions, establishing anti-bullying rules, learning techniques for protecting against bullying, and learning how to stand up against bullying. Role plays, recognition, and rewards are three tangible steps to student understanding and buy-in.

Empirical literature measuring the effectiveness of the BPYS Program demonstrates positive outcomes, which includes decreases in bullying behaviors and increased perceptions of school safety, particularly at the elementary level (e.g., Beran and Tutty 2002; Menard and Grottpeter 2014). Menard and Grottpeter (2014) surveyed nearly 3,500 elementary-age students across six elementary schools to measure the effectiveness of the BPYS Program. Results indicated that the schools which implemented the BPYS Program treatment had significantly reduced bullying behaviors and increased perceived school safety as compared to the control group.

School-Wide Bullying Policies. One popular approach to addressing disruptive behaviors is the implementation of zero tolerance policies. The literature regarding this authoritarian approach to discipline suggests that zero tolerance policies are ineffective methods of addressing bullying and may increase negative mental health outcomes for students (American Psychological Association Zero Tolerance Task Force 2008). More effective approaches may include: (1) the implementation of school-wide positive behavioral interventions and supports (PBIS), (2) small group interventions that enhance social skills and/or teach students healthy coping skills, or (3) cognitive-behavioral therapy for at-risk students.

Although zero tolerance policies are not appropriate for addressing bullying prevention and intervention, whole-school policies related to bullying may be beneficial. Olweus (1997) suggests that developing school-wide goals for decreasing bullying behaviors and creating standardized guidelines for addressing these behaviors is helpful. To the greatest extent possible, the development of these policies should be collaborative in nature, including educators, families, community members, and students (when appropriate).

Targeted Prevention and Intervention

Unfortunately, no school-wide prevention program or policy is 100% effective. Therefore, more targeted prevention and intervention strategies are necessary to address the needs of children who are at risk for or engaged in bullying behaviors. Two effective evidence-based targeted prevention and intervention strategies are the *Method of Shared Concern* and social skills group interventions (Rigby and Griffiths 2011).

Method of Shared Concern highlights the social dynamics of bullying behaviors. This targeted intervention is appropriate for small groups of youth who have been identified as having involvement in bullying either as bullies or victims. A qualified and trained professional individually interviews the suspected bullies and explicitly shares concern for the student who is a target of bullying. After these interviews, the same practitioner will meet with the student who is a target of the bullying behaviors to provide support

and talk through the situation. A final meeting, known as a summit meeting, is held in which the target student(s) and the suspected bully or bullies come together with the trained professional to resolve the problem.

Intensive School-Based Intervention

The existing literature on bullying and school-based prevention and intervention is limited with regards to intensive intervention. Felix et al. (2014) suggest that no literature is available that supports the explicit, intensive intervention of chronic bullying and bullying victims. However, individuals who may require intensive intervention for bullying may display additional concerns related to depression, anxiety, or aggression. In these circumstances, a school-based mental health professional such as the school psychologist may conduct an assessment and/or refer the student for appropriate school or community services that can provide adequate, evidence-based treatment(s).

Additional Considerations

Educators and other professionals who work with youth at risk for or engaged in bullying should be knowledgeable about issues of diversity, including the social and political climates that can contribute to bullying behaviors in schools. In an effort to create safe and positive learning environments for all students, school-based bullying prevention and intervention programs should take into consideration the unique strengths and needs of the student body. In particular, minority students may be at an increased risk for victimization due to race, sexual orientation, special education status, or immigration status (among many other variables).

Conclusion

School bullying is a problem for many youth and it does not appear that bullying will cease to exist in schools any time soon, or possibly ever if it is to be believed that this construct serves an evolutionary purpose. Regardless, given the impact that school bullying has on many youth involved – either directly or indirectly – it is important that

schools address bullying through both prevention and intervention efforts.

Cross-References

- [Bullying](#)
- [Cyberbullying](#)

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School Climate

► [School Environment](#)

School Context

► [School Environment](#)

School Culture

► [School Environment](#)

School Environment

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Synonyms

[School climate](#); [School context](#); [School culture](#)

Definition

The school environment encompasses institutional and structural features (e.g., size, space, structural organization, availability of resources), social relations (e.g., teacher-student relationships, relations between students), teaching and learning (e.g., quality of instruction), physical and social-emotional safety, as well as shared beliefs, values, and attitudes (that are often referred to as school culture or school climate).

Introduction

The school is an important microsystem that affects the personality development of students, in general, and their development of academic skills in particular. Students spend more time at school than at any other place outside their homes. For example, adolescents from Europe and the USA spend about 37% of their waking hours at school (Alsaker and Flammer 1999). While scholars agree upon the important role that the school environment plays in student development, they differ in the use of terminology. For example, while many researchers use the terms *school environment* and *school climate* interchangeably (e.g., McGiboney 2016; Wang and Degol 2016), others define school climate narrowly as the shared beliefs, values, attitudes, or perceptions held by students, teachers, and administrators, in contrast to more objective characteristics of the school environment, such as instructional practices and leadership (e.g., Rudasill et al. *in press*). In most cases, both views will not conflict with one another as the large majority of studies assessed the school environment via self-reports of students and/or teachers (Fraser 2012; McGiboney 2016; Wang and Degol 2016).

Aspects of the School Environment

While researchers and practitioners agree that the school environment is multidimensional, scholars have proposed different typologies for describing the school environment. Nonetheless, the majority of researchers agrees that the following four

aspects are major areas of the school environment or school climate, respectively: (a) the academic climate (such as academic tasks and instruction, leadership, and professional development), (b) relationships (teacher-student relations, peer relations, and relations between teachers in terms of level of support and connectedness), (c) physical and social-emotional safety (e.g., concepts and measures for addressing violence in the school), and (d) the institutional environment (such as environmental adequacy, structural organization, and availability of resources) (e.g., Ramelow et al. 2015; Wang and Degol 2016). These four dimensions could also be assessed at the classroom level, although contents must be adapted (e.g., school rules for misbehavior vs. behavior management practices in the classroom). In general, assessments of the school environment and of the classroom environment tend to be only weakly correlated, as related measures address different dimensions and as classrooms are somewhat insulated from the school as a whole (Fraser 2012).

Assessment

A number of measures have been developed for assessing the school environment, such as the “What’s Happening in This School?” questionnaire and the Inventory of School Climate (see McGiboney 2016; Ramelow et al. 2015), although none of them includes all of the four main domains that have been proposed. While most of these measures show satisfactory reliability, support for their validity tends to be limited. An overview of measures of the classroom environment – such as the “What is Happening in this Class?” questionnaire, the Classroom Environment Scale, and the My Class Inventory – has been provided by Fraser (2012). There is high variability in the assessed dimensions of the classroom environment, with quality of the social relationships (e.g., cohesiveness, teacher support), task orientation (e.g., class level of achievement motivation), differentiation (e.g., different students work with different materials), and organization (e.g., rule clarity) being measured most often. Some of these measures do not only assess the actual classroom environment as it is

experienced but also the preferred or ideal classroom environment. Differences between the actual and preferred environment can be a starting point for interventions.

Studies that collected data from more than one group of respondents (students, teachers, parents) indicated that the perspectives of these respondents on the school environment differ: Students tend to give less favorable reports on safety and connectedness than teachers and parents do (e.g., Ramsey et al. 2016); this is most likely an indication of the fact that adults are not aware of some existing problems the students face in their school. In addition, Ramsey et al. (2016) observed that, compared to students, teachers gave lower ratings of academic emphasis (such as teachers setting high standards for teaching) and parents rated parental involvement lower. Thus, informants may give lower ratings of dimensions of climate which are most directly related to their own behaviors. Correlations between the views of students and teachers tend to be in the moderate range (Brand et al. 2008). Ratings of students and parents on the school environment tend to be less congruent if schools have more ethnically diverse student populations and more newcomers (McGiboney 2016). These results indicate that data should be collected from more than one source in order to get a balanced picture of the school environment.

Given the fact that self-report data on the school environment are nested (students attend an individual class which is, again, part of an individual school, which is located in a particular school district), multilevel modeling is the preferred method for statistical analysis, although very few available studies have included more than two levels in the analysis. For example, Koth et al. (2008) observed that the majority of variance in student perceptions of school climate occurs at the individual level, while 8–9% of the total variance was based on classroom membership, and an additional 5–27% of the total variance of perceptions of the school environment occurred between schools. Perceptions of school safety showed stronger variations between schools than perceptions of students’ achievement orientation, such as their willingness to learn.

These results indicate important variability of perceptions of the school environment within classrooms, with male students and those from ethnic minorities tending to perceive the school less favorably.

Variations in the School and Classroom Environment

In many countries, formal education is divided into a number of distinct educational stages, such as elementary school, middle school, and high school, which differ in the school environment. In elementary school, students are typically assigned to one teacher and spend much of the day in that teacher's classroom with the same group of students. In middle and high school, students are typically assigned to a team of teachers and move from classroom to classroom over the course of the school day, in part with somewhat different groups of students in each. Compared to elementary schools, middle schools place greater emphasis on discipline and academic accomplishment and provide less opportunity for close relationships to specific teachers. High schools provide a larger, more impersonal, teacher-centered, academically demanding, and competitive school environment than elementary and middle schools, although they often allow students to make more choices in terms of academic and extracurricular activities. Research by Eccles and coworkers (for overview, Eccles and Roeser 2012) indicates that students moving from primary schools to secondary schools leads to a deterioration of the perceived classroom environment through, for example, the use of more control-oriented strategies and provision of fewer opportunities for student autonomy and decision-making in the classroom. These environmental changes are associated with an increasing mismatch between the classroom environment and students' growing needs for autonomy, competence, and relatedness. The fit or misfit between students' psychological needs and their school environment influences their motivation for academic success.

Changes in perceptions of the school environment are not limited to school transitions, as a number of studies also described a decline in school climate perceptions while students

attended the same school, such as perceptions of teacher support or clarity of school rules (e.g., Wang and Dishion 2012). It is not clear whether school climate deteriorates because of age-associated behavioral changes of the students (such as declines in seeking support from adults or increasing rates of delinquency) or changing academic demands, or whether students become increasingly dissatisfied with their schools, irrespective of a school environment which is actually rather stable.

In many countries, students of secondary schools are placed into different types of schools, hierarchically structured by performance (ability grouping or tracking). The quality of the school environment tends to vary by school track, in particular in the field of teaching and learning, as well as safety. Cognitively activating teaching is more often found in the highest track (college-bound), while teacher support tends to be highest in the lowest track (vocational-bound) (Kunter et al. 2005). Students in schools that offer academically oriented tracks also report a school climate with fewer disciplinary problems (e.g., classroom disruption, student victimizations) (van de Werfhorst et al. 2012). Low track placement has been related to poor attitudes toward school and low academic achievement, although academic self-concept may benefit due to better opportunities to compare oneself with peers with similar or worse academic achievements. There is an ongoing debate whether differences in achievement result from academic tracking or reflect pre-existing disparities (Eccles and Roeser 2012).

Association of the School Environment with Student and Teacher Outcomes

"School effects research" originally analyzed how the school environment shapes students' academic attainment and social behavior. Subsequent research examined how school factors relate to the psychological well-being and physical health of students and teachers. Up to now, the empirical evidence on effects of the school environment is limited because most available studies are cross-sectional and do not allow for drawing causal

conclusions: Academic achievement, behavior problems, or mental health of the student may also affect aspects of the school environment, such as teachers' behavior toward the individual students or the risk of being bullied. Although few cross-lagged studies have found stronger effects of the perceived school environment on changes in students' outcomes compared to students' effects on changed perceptions of the school environment (e.g., Košir and Tement 2014), Benbenishty et al. (2016) observed that a sum measure of school climate (belongingness, adult support, school participation) did not predict changes in academic achievement, while initial levels of academic achievement predicted improvements in perceived school climate. In addition, many available studies have not controlled for potentially confounding effects of family and neighborhood characteristics, as families with lower socioeconomic backgrounds and those from deprived living areas may send their children to lower-quality schools.

The following paragraphs summarize research on the associations of the four major areas of the school environment (academic climate, safety, relationships, the institutional environment) with academic achievement, problem behavior, and psychological well-being of students, based on the systematic review by Wang and Degol (2016). As studies on associations of the school environment with student health behaviors and teacher outcomes addressed only few environmental dimensions, related results will be presented in a more condensed form.

Academic Outcomes

Academic outcomes have long been examined as a consequence of variation in the school environment. A meta-analysis by Karadağ et al. (2016) found a moderate correlation between indicators of a positive school climate and academic achievement ($r = 0.36$). When focusing on individual dimensions of the school environment, the most consistent results have been found with regard to the *academic climate* and the quality of social relations. Higher academic achievement is found in schools which emphasize the importance of commitment to high academic standards and

that are characterized by effective leadership from teachers and principals, who believe in their ability to improve student outcomes. For example, students from schools that maintain higher academic standards and encourage students to do their best tend to show stronger growth in math and science achievement than other students (Hoy et al. 2006; Ma and Wilkins 2002).

A positive *relationship between teachers and students* has also consistently been related to better academic outcomes (e.g., student motivation, school attendance, grade point average). A meta-analysis by Roorda et al. (2011) identified small to moderate positive associations of teacher support and caring with student engagement ($r = 0.34$) and academic achievement ($r = 0.16$). Košir and Tement (2014) found that (student-rated) teacher support and (teacher-rated) teacher acceptance predicted improvement in grade point average over time. Studies indicated that the association between positive student-teacher relationships and academic achievement is mediated by students' classroom engagement (Wang and Degol 2016).

Higher levels of school *safety* were associated with positive changes in academic achievement in a cross-lagged study by McCoy et al. (2013). In that study, higher initial school levels of academic achievement also predicted improved perceptions of school safety over time. However, some other studies found no association between safety and academic achievement or indicated that the association between both variables disappeared when other dimensions of the school environment were controlled for (Wang and Degol 2016).

Structural/institutional characteristics of the school do not seem to directly affect student achievement, but may alter classroom processes, which could affect achievement. Studies consistently indicate that students perform better in schools where more children come from families of high socioeconomic status (SES), regardless of their individual SES; this effect is mediated through the quality of the learning environment, such as quality of curriculum and instruction and level of support within the teacher-student relations (Perry 2012). Meta-analyses have found small to moderate positive associations between school resources, such as per pupil expenditure,

and student achievement (e.g., Greenwald et al. 1996), although translating resources to student academic performance depends on how these resources are used for improving more proximal processes in the classroom, such as instructional quality (Archibald 2006). Results on associations of other institutional/structural aspects (e.g., school size, private vs. public schools, location in urban, suburban, or rural areas) with academic achievement are inconsistent and tend to disappear when more proximal processes are controlled for (Wang and Degol 2016).

Externalizing Problem Behavior

A meta-analysis by Steffgen et al. (2013) found a small to moderate negative association between sum measures of school climate and school violence ($r = -0.26$), with the size of the correlation varying between studies. As externalizing behavior refers to delinquent and aggressive behavior, one could expect that social relations (between teachers and students, as well as between students), as well as the physical and social-emotional safety at school, should show the most consistent relations with the levels of externalizing behavior of the individual student. Nonetheless, few studies indicated that a high-quality *academic environment* is also related with lower levels of externalizing behavior of the individual student in the classroom. For example, Wang (2009) found lower levels of externalizing behavior if schools/teachers emphasized mastery goals (i.e., focusing on self-improvement, effort, and true understanding) rather than achievement goals (i.e., focusing on the attainment high grades and outperforming others). The statistical effects of mastery goal orientation might be based on the promotion of more positive relations with peers within the classroom and the investment of more time for learning after school rather than misbehaving.

Associations between the *quality of interpersonal relationships* within the school and experiences of bullying, aggression, and delinquency have been observed in many studies. For example, a meta-analysis by Ali et al. (2015) revealed a small negative correlation between perceived

teacher acceptance and students' conduct problems at school ($r = -0.22$). Nonetheless, evidence for causal effects of teacher support/acceptance on externalizing problems still has to be established. For example, Leflot et al. (2011) did not find effects of teacher support on change in students' externalizing behavior over time. With regard to social relations between students, the meta-analysis by Cook et al. (2010) indicates that students who are less accepted by their peers are more likely to bully their classmates and to be bullied by them. Longitudinal studies on bidirectional associations between aggression and peer status have found that physical aggression predicts peer rejection, which in turn, predicts subsequent increases in aggression (e.g., Lansford et al. 2010).

The *safety* of the school environment shows negative associations with aggressive behavior and bullying victimization of the individual student. Schools in which safety rules are effectively enforced, and schools with better discipline management, have lower rates of student victimization and delinquency, but available results are mainly based on cross-sectional data (e.g., Gottfredson et al. 2005).

Associations of *institutional/structural variables* – such as student-teacher ratios, poverty concentration, and suspension rates – with externalizing problem behavior at school may be indirect, by influencing the opportunities for aggressive and delinquent behavior at schools and the consequences of these behaviors (Wang and Degol 2016).

Students' Psychological Well-Being

There is very limited research on the association of *academic climate* with psychological well-being of children and adolescents. Nonetheless, Wang (2009) observed that school endorsement of a mastery goal structure (emphasis of effort; expectations that all students can improve their skills) was related to lower levels of depression, most likely due to the focus on individual progress. In contrast, school endorsement of achievement goals (such as pressuring students to acquire high grades and outperform others) was associated with higher levels of depressive symptoms,

as low-achieving students receive consistent negative feedback about their performance.

Most available research on the association of the school environment with psychological well-being has focused on *social relationships* between students and teachers, or between students. More concretely, supportive teacher-student relationships, respect for students' opinions, and measures that promote feelings of school belonging are robust predictors of students' emotional health (Wang and Degol 2016). Changes in perceptions of teachers' support have also been found to reliably predict changes in students' self-esteem and depression (Reddy et al. 2003).

Positive associations of *school safety* with psychological well-being have been identified in a few studies, for example, because students from safe schools are protected against negative feelings associated with peer harassment (see Wang and Degol 2016).

Structural/institutional characteristics, such as school size or urban versus rural location, tend to show no relationship with students' psychological well-being (Anderman 2002).

Students' Health Behaviors

Schools are a popular area for health promotion among children and adolescents, as they can target a large population in an efficient manner. Selected aspects of the school environment have been linked with substance use, eating habits, and levels of physical activity. Lower rates of *substance use* are found in schools with higher educational attainment and attendance than would be expected from the social profile of the students, although the mechanisms that explain this result have not yet been assessed (Bonell et al. 2013). Studies on restrictive school policies (such as a smoking ban) showed mixed associations with substance use, probably indicating the difficulties that accompany putting such rules into practice (Bonell et al. 2013). In line with this, higher numbers of unobservable and unsupervised places in and around schools are associated with higher substance use (Kumar et al. 2008). In general, associations of the school environment with substance use tend to be small or very small because most substance use occurs outside the school.

A review by Morton et al. (2016) indicates that a larger total campus size is associated with higher levels of *physical activity* at school. In contrast, availability of physical activity facilities, such as baseball fields or sports equipment, was not consistently related to higher physical activity, thus indicating that not all available opportunities are frequently used. Regarding teacher behavior, support for student autonomy (e.g., provision of choice), a mastery-oriented motivational climate, and, in part, physical activity promoting teaching behaviors were related with higher levels of physical activity among the students. Studies on schools' policies about "intramural versus interscholastic sports participation" indicated that intramural sports were consistently associated with more physical activity, whereas interscholastic sports showed no association.

Studies addressing school effects on students' healthy *eating* have found no significant school-level effects of the availability of healthy/unhealthy food on eating habits after controlling for student-level characteristics. However, there is some evidence for an independent statistical effect of school organization factors related to food choice (e.g., quality of information provision, related campaigns) which explained up to 12% of the variance of students' food choices (Townsend and Foster 2013).

Teacher Stress and Burnout

A positive teacher-rated school climate has been consistently linked to lower levels of stress, lower burnout scores, and lower attrition among teachers (McGiboney 2016). For example, teachers who report that they openly discuss issues of teaching quality with their colleagues and who perceive low levels of competitiveness between staff members report lower levels of burnout (Lim and Eo 2014). Teachers' negative perceptions of their students (e.g., low motivation), of the teacher-student relationships, and of the school administration (e.g., failure to set clear standards) have also been found to correlate with higher burnout scores (Grayson and Alvarez 2008). A meta-analysis by Aloe et al. (2014) found that high levels of student misbehavior are related to higher teacher burnout with mean

correlations varying between $r = 0.31$ and 0.44 . Associations of student problem behavior with teacher burnout tended to be stronger in younger and female as compared to male teachers.

Up to now, the causal role that the school climate plays in regard to teacher burnouts has been difficult to evaluate as studies are lacking that test the associations between the two variables either experimentally or longitudinally with cross-lagged analyses.

Intervention Research

Although the majority of work on the school environment has been correlational, a number of interventions have been developed for improving the school environment. Intervention effects from randomized controlled trials on academic achievement, behavior problems, psychological well-being, or other variables can provide more compelling evidence for a causal link between school environment and student outcomes. For example, a randomized controlled intervention study aimed at enhancing teachers' capacity to create a caring, well-managed classroom environment (the Responsive Classroom approach) showed that the use of responsive classroom practices mediated the effect of treatment assignment on academic achievement (Rimm-Kaufman et al. 2014). Nonetheless, similar to other studies, the size of the observed intervention effect tended to be small. Most intervention studies tried to change more than one aspect of the school environment, and many of them combined attempts to change the school environment with student-focused interventions (e.g., training of life-skills), thus precluding the identification of causal relations between individual aspects of the school environment and student outcomes.

Relating Genetic Dispositions and the School Environment

The View of Evolutionary Psychology on the School Environment

Schools are a relatively new cultural innovation, as places of active teaching did not exist in traditional hunter/gathering societies. The oldest

known classroom and pedagogical materials were found in Mesopotamia from the third millennium before the current era (Lancy 2016). There is some controversy whether active teaching has been relatively uncommon in our species' history and whether children have traditionally acquired their culture only through "self-guided learning" (e.g., observation, imitation) or whether there were some formal teaching processes through demonstration, intervention, and collaboration of experienced adults because complex skills are difficult to learn via self-guided learning. As the human mind and behavior have been shaped by natural selection for life in the hunting/gathering groups of our ancestors, we are not genetically prepared for today's typical school environment, i.e., sitting in classrooms with same-age peers, seated in chairs or at tables while performing "seatwork," or listening to instruction from a teacher (Bjorklund and Bering 2002). The misfit between evolved learning (and evolved learning contexts) and the modern-day demands of formal schooling (and characteristics of the present school environment) may cause common problems, such as lack of students' motivation or restless behavior in the classroom (Bjorklund and Bering 2002; Gray 2011).

Based on our phylogenetic history and data from extant traditional societies, Gray (2011) argued that an ideal educational environment would, for example, permit unlimited free time and an abundance of space in which to play and explore, provide opportunities for interacting with children of all ages, and allow freedom of expression and debate of any idea. A few schools that have adopted such a traditional approach to pedagogy found positive effects on students, in particular with regard to their motivation (e.g., Gray 2011). In contrast, other proponents of evolutionary psychology have explicitly stated that this theoretical approach should not be taken in order to adopt a "back-to-nature" approach to schooling (Bjorklund and Bering 2002), as socializing with one's peers and discovery-based experiential learning may not be beneficial for mastering abstract, evolutionarily novel information. Thus, teacher-directed instruction should be most effective when acquiring evolutionarily novel concepts

and skills that are remote from the folk domains of knowledge (e.g., solving linear algebra problems), and the goal is oriented toward acquiring knowledge for its own sake (Geary and Berch 2016). This view is consistent with empirical studies showing that sufficient external guidance is needed for effective learning, in particular if there is no prior student knowledge on the given content (Kirschner et al. 2006).

Up to now, evolutionary theory and evolutionary psychology did not play an important role for designing the school environment, as the basic assumptions on the evolution of species are very general, and as some debates (e.g., on direct instruction vs. experience-based learning; Kirschner et al. 2006) and concepts about learning environments had already come up independently of evolutionary psychology. For example, starting from 1907, Montessori education practices included mixed-age classrooms, students' choice of activity (from a prescribed range of options), and discovery-based learning.

Gene-Environment Correlations and Interactions

While evolutionary psychology has stated theoretical assumptions on genetic dispositions that affect learning of today's students, behavior-genetic and molecular-genetic studies have provided some empirical data on the role that genetic factors play within teaching and learning.

Genetic effects have been found on many aspects of the family environment as parents create a family environment that fits their own and their children's genetic disposition and as parents react to behavioral manifestations of the genes of their children (gene-environment correlations). In contrast, fewer genetic effects on the school environment could be expected as this environment is not child-specific. Nonetheless, genetic effects come into play when particular schools are actively chosen by the parents and/or children, when dyadic aspects of the school environment are assessed (e.g., teacher warmth toward the individual child), and when the individual perception of the school environment, rather than the objective environment, is analyzed. Up to now, very few studies have tested genetic effects on the

school environment. The behavior-genetic study by Brendgen et al. (2011) did not find an effect of student's genotypes on teacher ratings of his or her relationship with the individual student. Thus, teachers may try to show rather similar behavior (e.g., warmth, openness of communication) toward all students, regardless of their genetic dispositions. In contrast, Coon et al. (1993) found that associations of boys' academic achievement with attending a private school and with students' and parents' perceptions of competitiveness of the school environment were, in part, genetically mediated.

A number of studies on the school environment have identified gene $\times$ environment interaction effects. The biological sensitivity to context model suggests that variation in susceptibility to environmental influence has been maintained by natural selection because this variation promotes success and failure in different ecological contexts. While focusing on the school environment, Essex et al. (2011) showed that biological sensitivity to context moderated the effects of the early teacher-child relationship on the development of mental health by adolescence: The association of the teacher-child relationship with adolescent mental health was stronger for more reactive children. Differential sensitivity to context is associated with variations in dopaminergic genes. A study showed that the size of associations of student-reported teacher-student affiliation with parental reports on school engagement, and of associations between students' dissatisfaction with their teacher and rule-breaking behavior, was moderated by the dopamine transporter DAT1 and the dopamine receptor DRD4 genes, respectively (De Laet et al. 2016).

Some behavior-genetic studies addressed whether the size of genetic influences on student outcomes varies by the quality of the school environment. Stronger genetic influences on reading comprehension were found in the case of lower school-level SES (Hart et al. 2014), probably indicating that poorer school environments are less capable of compensating for the effects of less than optimal genetic achievement-related dispositions. In contrast, heritability estimates of aggression levels and levels of other forms of

externalizing problem behaviors were found to be higher in better school environments, such as those characterized by programs aimed at reducing violence (Boutwell 2010). While many students show some externalizing behaviors irrespectively of their genetic disposition in poorer school environments (e.g., because of social learning or peer pressure), these behaviors are more specific to students with genetic risks in the better schools.

Conclusion

The school environment is an important developmental context for children and adolescents which affects not only academic skills but also the development of social behavior, health behavior, and psychological well-being. Interventions aimed at improving the school environment have been shown to promote student development, although most effects tend to be small. These interventions should not only strive to improve the school environment but also the interplay with other environments, such as parental involvement in schooling (home-school linkage) and school-community linkages (e.g., provision of community service learning opportunities). Given the heterogeneity in definitions of the school environment and related aspects, in the proposed dimensional structure, and in the dimensions assessed with individual instruments, more unifying concepts are needed that increase the comparability of results across studies. Because students, parents, and teachers tend to perceive the school environment differently, it is recommended that researchers collect data from more than one source. As the quality of the school environment may vary by characteristics of the students' families (due to selection effects) and the neighborhood, careful research designs are needed that control for these confounding influences when searching for school effects. Given the possibility of bidirectional associations between aspects of the (perceived) school environment and student's feelings and behaviors, more experimental and cross-lagged longitudinal studies are needed for identifying the direction of effects. More

behavior-genetic and molecular-genetic research is also needed for getting a differentiated picture on the interplay of genetic dispositions with the aspects of the school environment.

While research on the school environment has been conducted based on a larger number of theoretical approaches (such as the Bronfenbrenner's bioecological model; Bronfenbrenner 2001), evolutionary psychology has not yet played an important role in that field. In order to gain importance, evolutionary educational psychology would have to provide more specific, testable hypotheses on the school environment and on environmental effects that go beyond common assumptions from other theoretical approaches. For example, the discussions on effective forms of learning (Geary and Berch 2016) could inspire systematic research that tests differential effects of teaching/learning strategies (direct instruction vs. discovery-based learning) for different kinds of materials and different groups of students.

Cross-References

- [Evolution of the Brain, The](#)
- [School Bullying](#)

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Science and Morality

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Synonyms

[Alliances](#); [Condemnation](#); [Fairness](#); [Morality](#)

Definition

The scientific study of morality has increasingly revealed its underlying psychological processes and features.

Introduction

Presently, there is no unified definition of morality (Krebs 2011). From a lay perspective, morality is

one's sense of the difference between right and wrong. It is a system of personal attitudes and beliefs about what actions are socially permissible, which behaviors should be morally condemned, and what degree of punishment is appropriate for various social transgressions; it is a collection of conventional rules that guide how individuals navigate and solve ethical dilemmas. In lieu of offering definitions of morality, current scientific research on morality attempts to identify the underlying psychology of moral intuitions by organizing aspects of morality into universal processes or features (Graham et al. 2013; Haidt and Joseph 2004); identifying the evolved, mechanistic design of moral cognitions and behaviors (e.g., Baumard 2010; Asao & Buss. 2016; DeScioli and Kurzban 2009; Kurzban et al. 2012); and detailing the neurobiological, computational, and social cognitive mechanisms of moral judgment and decision-making (Cosmides and Tooby 1996, 2006; Tooby and Cosmides 2010; Tooby et al. 2006; Gigerenzer 2008; Greene 2004). Collectively, this research has led to the development of several prominent theories of morality (Cosmides and Tooby 1996, 2006; DeScioli and Kurzban 2009; Mikhail 2007; Graham et al. 2013) as well as several relatively younger theories and ideas that elaborate on earlier models (Baumard et al. 2013; Asao and Buss 2016; Marczyk 2015). However, each is guided by the same underlying philosophy: morality is housed within a physical entity of the natural world (i.e., the brain) and can therefore be studied as a product of natural events.

The scientific method has been integral in identifying the processes and component features of natural phenomena within various areas of human inquiry (e.g., physics, biology, chemistry, psychology). In turn, this work has facilitated the development of technologies and ideas that have fundamentally shaped human societies. Using the scientific method to likewise examine the psychological structure and function of morality promises to reveal the underlying principles and processes of moral intuition and judgment. Current evidence suggests that morality can be understood as the result of biological processes and neurocognitive decision-making rules (Cosmides and Tooby 1996, 2006; Greene 2004; Gigerenzer

2008) whose design and development has been fundamentally shaped by natural selection (DeScioli and Kurzban 2009) and refined by experiences (Graham et al. 2013; Mikhail 2007). A complete scientific understanding of the structure and function of this moral machinery will be valuable insofar as it has the potential to inform ways of optimizing various features of modern human life that have traditionally been developed from folk understandings of morality, such as law (e.g., Cosmides and Tooby 2006; Stake, 2016 resource distribution (e.g., Greene 2014), values (e.g., Harris 2011), and treatment of social deviance (e.g., Kurzban et al. 2010; Glenn et al. 2009).

This section reviews current literature on the scientific study of morality. Given the complexity of this topic, a more exhaustive and detailed account of extant literature is forgone and may be found elsewhere (see Krebs 2011). Instead, several current scientific theories of morality are summarized and the practical applications of these ideas are discussed. To this end, this entry serves as a primer for those who are interested in contemporary scientific research on human morality.

Computational Heuristic Models

Several theorists detail computational heuristic models of morality (Cosmides and Tooby 2006; Gigerenzer 2008). Generally, these models outline how complex networks of heuristic decision-making rules guide moral reasoning and how these cognitive mechanisms may have been shaped by natural selection to address recurrent adaptive issues. In this respect, these models may be considered the foundation of other contemporary theories of moral psychology insofar as they identify and elaborate on the cognitive machinery underlying human morality. Heuristics are “fast” (i.e., require little time) and “frugal” (i.e., require little information) solutions to complex problems. They comprise solutions that address problems quickly and efficiently, but with potential for error, and are currently understood to be the building blocks of a heritable, modular psychology (Barrett and Kurzban 2006; Cosmides and Tooby 1996; Gigerenzer 2008). Moral heuristics

are therefore “rules of thumb” that underlie moral intuitions and judgment.

As an example, Tooby and Cosmides (2010) propose that adaptations for morality were born, in part, out of heuristics for coalitional living. Coalitional living is particularly complex in humans compared to other species and involves environmentally and socially responsive decision-making rules that guide how individuals form and maintain alliances, recruit allies, evaluate those allies, and motivate those allies into taking actions that are beneficial to the individual. These features of coalitional living are accompanied by unique adaptive challenges such as dealing with free-riders, negotiating social dominance hierarchies, distributing resources, coordinating group effort, and mapping alliance networks. They argue that the evolution of language, negotiation, and situation evaluation, in conjunction with adaptations to coalitional living, allowed for dynamically complex social games and thereby introduced novel adaptive issues (i.e., second-order moral games), and selection pressures (e.g., exploitation) from which moral heuristics evolved. Several lines of research support and elaborate on computational heuristic models, including several contemporary theories (see Asao and Buss 2016; DeScioli and Kurzban 2009, 2013; Greene 2004; Marczyk 2015; Mikhail 2007).

Moral Condemnation by Third Parties

DeScioli and Kurzban (2009, 2013) highlight the importance of third-party condemnation in understanding the design of evolved moral psychology. Whereas other evolutionary accounts of morality have focused on kin selection and reciprocal altruism as key pathways in the evolution of morality (e.g., de Waal 1996; Wright 1994); they propose the idea that adaptations underlying moral judgment function to strategically levy and avoid third-party condemnation. They differentiate between two subsystems of moral cognition: moral conscience and moral condemnation. Moral conscience refers to adaptations that regulate one’s own moral behavior whereas moral condemnation refers to adaptations that specialize

in judging another’s moral behavior. They use models of three-player games to demonstrate how actors (player 1) may perpetrate moral violations against victims (player 2) and be condemned for these behaviors by third parties (players 3+). Third-party condemners face the problems of detecting, judging, and punishing these violations while recruiting others’ support and avoiding counteraccusation (i.e., becoming targets of moral judgment). This condemnation thereby presents a different set of problems for actors who must weigh potential costs (e.g., victim revenge; third-party sanctions) and benefits when choosing to perform certain actions (i.e., moral conscience). Likewise, second parties should be expected to have evolved adaptations for avoiding costs (e.g., exploitation) and recruiting help from third-party condemners.

This view is consistent with computational heuristic models of morality (e.g., Tooby and Cosmides 2010) and has received support in subsequent studies. For example, DeScioli et al. (2011) found that people are more willing to take money from another person by omission than by commission when threatened by third-party punishment. This suggests that omission is a strategy for reducing the probability of third-party condemnation and punishment. Kurzban et al. (2012) also present evidence that the heuristics underlying moral judgment cannot be entirely explained by kin selection, reciprocity, or other altruism theories. Instead, they argue that adaptations for altruism (i.e., kin selection and reciprocity) and moral judgment are separate systems, and can, at times, be in opposition. Their evidence supports the idea that moral judgment is impartial (i.e., activated in response to an individual’s behavior rather than the outcome of that behavior) (DeScioli and Kurzban 2009). Indeed, impartial moral judgment based on behavior rather than an individual’s identity permits third-party condemners to change which parties (i.e., actors versus victims) they support depending on the potential costs and benefits of choosing one side over the other (DeScioli and Kurzban 2013). This suggests that humans may possess cognitive adaptations that motivate vigilance of moral disagreement (e.g., belief systems and development of

shared moral commitments) which allow individuals to adaptively prevent problems of coordination (i.e., increased partisan conflict and fight costs from siding with others based on preexisting relationships) and exploitation (i.e., empowering individuals to be able to exploit others).

Tripartite Theory of Machiavellian Morality

The tripartite theory of Machiavellian morality (Asao and Buss 2016) expands the moral condemnation and moral conscience distinction (DeScioli and Kurzban 2009) to include a third classification: moral influence. Under this conceptualization, moral judgment, moral influence, and moral conscience are functionally discrete collections of adaptations which strategically guide moral decision-making. Moral judgment adaptations allow an individual to identify whether a conspecific affords either a net cost (i.e., is exploitative) or a net benefit (i.e., is prosocial) to one's inclusive fitness. Moral influence consists of heuristics which evolved to efficiently and cost-effectively alter another's behavior so as to be less costly and more beneficial to one's fitness. Moral conscience heuristics evolved as counteradaptations to others' moral judgment and influence mechanisms, and thereby motivate an individual to avoid fitness consequences that arise from them.

The Evolution of Fairness by Partner Choice

Baumard et al. (2013) present a theory that elaborates on how partner choice may have been a key selective pressure from which fairness, a key feature of morality, evolved. Their theory rests on conclusions from game theory and models of mutualism which show that mutually beneficial cooperative exchanges permit individuals to accrue benefits that would otherwise be unavailable through solitary effort. Given these advantages, individuals are motivated to attract and invest in allies with whom cooperation will produce a better quality of life. However, because

people differ in their opinion of how mutually accrued resources should be ideally distributed, individuals should be selective about with whom they cooperate. Therefore individuals whose cooperation provides a net benefit will be favored as partners over those whose cooperation provides fewer benefits (or inflicts costs). They contend that moral conscience, as developed by DeScioli and Kurzban (2009), evolved to regulate one's reputation as a cooperator. Individuals who successfully monitored their moral reputation as a reliable cooperator would have been more frequently chosen for mutually beneficial exchanges, and therefore would have experienced greater reproductive success.

Moral Alliance Strategies Theory

Moral alliance strategies theory (Marczyk 2015) builds upon other work (Baumard et al. 2013; DeScioli and Kurzban 2009, 2013) by elaborating on why observable behavior, rather than identity, acts as input for moral cognitive mechanisms. Its central premise is that third-party condemners use actors' behavior to decide with whom to form alliances because these behaviors signal an actor's need for coalitional support. This need provides an opportunity for third parties to either invest in an alliance that is personally beneficially (i.e., provide support to the actor) or dissolve an alliance if it is too costly (i.e., condemn the actor). This implies that an actor's relational value influences third party condemnation decisions. Compared to other models, this theory reaches conclusions about the role of impartiality, proportionality, harm, omission, and moral praiseworthiness in moral cognition that are compatible with earlier models but offers additional insights into how these features may be influenced by an actor's relational value and shared interests.

Universal Moral Grammar

Universal moral grammar (Mikhail 2007) models human morality by drawing parallels between moral cognition and concepts used in the study

of linguistics. Like other theories, it emphasizes the importance of nativist intuition, modularity, and computational heuristics in moral judgment but elaborates these ideas using terminology endemic to Chomsky's program in linguistics. It rests on two fundamental arguments. First, the mind contains a moral grammar of complex and possibly domain-specific sets of rules, concepts, and principles that individuals apply to an infinite variety of moral acts and omissions. Second, this moral grammar is generated by the innate structure of the mind but is also developmentally shaped and refined by individual experiences.

Moral Foundations Theory

One of the more prolific contemporary theories of human morality is Jonathan Haidt's moral foundations theory (Graham et al. 2013). This theory posits that collections of universal and functionally distinct moral intuitions underlie individuals' moral judgments. These intuitions (i.e., foundations) precede moral reasoning, which is constructed after an intuitive judgment has already been made. Consistent with other perspectives, these foundations have been shaped by evolution by natural selection and are hypothesized to operate modularly. Each foundation describes a functionally distinct set of psychological modules which specialize in processing information that has been relevant to solving ancestrally recurrent adaptive problems inherent to group living. The care/harm foundation refers to psychological mechanisms which permit individuals to easily and automatically process cues of suffering in another individual. These mechanisms are hypothesized to have originated from mechanisms that motivate kin and reciprocal altruism and are sensitive to signs of distress and neediness that trigger feelings of compassion for victims. The fairness/cheating foundation comprises heuristics for identifying and reacting to evidence of cheating within nonzero-sum cooperative exchanges and relationships. In any social interaction, individuals attempting to establish a mutualistic exchange of resources with another individual may be cheated out of those resources. Individuals have therefore evolved mechanisms for identifying and judging

trustworthiness in cooperative interaction to avoid exploitation. The loyalty/betrayal foundation entails adaptations which facilitate in-group loyalty and condemn in-group betrayal, thereby increasing individual fitness via enhanced cohesion and effectiveness of the groups to which an individual belongs. The authority/subversion foundation consists of modules which permit individuals to effectively navigate social dominance hierarchies (e.g., via obedience and deference), thereby facilitating the formation of useful social alliances that provide material and reproductive benefits. The sanctity/degradation foundation includes modules that function as a "behavioral immune system" which motivates avoidance of stimuli that signal actual or moral pathogen risk (e.g., immigrants, sexual promiscuity). Each of these foundations is hypothesized to underlie cross-cultural variation in moral judgment and practices and give rise to these variations insofar as they supply the initial blueprint from which culturally nuanced variations in moral practices are subsequently developed and refined.

Conclusion

In a recent news article, Jonathan Haidt and Steven Pinker (2016, para. 13) explain the importance of a scientific understanding of morality:

Recent discoveries in moral psychology [reveal that]... many ethical convictions are underpinned by strongly felt intuitions that some action is inherently good or bad. Sometimes those intuitions can be justified by philosophical reflection and analysis. But sometimes they can be debunked and shown to be indefensible gut reactions, without moral warrant. Historical examples include outrage over heresy, blasphemy, and *lèse-majesté*, revulsion against homosexuality and racial mixing, squeamishness about medical advances like vaccination and blood transfusions, callousness toward slaves and animals, and indifference or hatred toward foreigners. Any news reader will confirm that some of these historical examples are all too modern.

Psychology, neuroscience, and evolutionary biology, though they cannot by themselves debunk moral intuitions, are highly relevant to evaluating them, since our naive intuitions about the ethical warrant of our gut feelings might themselves be gut feelings and cannot be taken at face value.

This passage highlights the advantages of deconstructing human moral psychology using

theoretical and methodological ideas from other sciences (i.e., neuroscience and evolutionary biology) whose work has fundamentally shaped our understanding of how humans process information, respond to their environment, and respond to each other. The theories of morality outlined above have been applied in understanding various social issues, including mental illness (Glenn et al. 2009), procedural fairness (Bøggild, and Petersen 2016), law (Cosmides and Tooby 2006), illicit drug use (Kurzban et al. 2010), and moral aggression (Benavidez et al. 2016). These types of practical applications of the science of morality promise to expand descriptive understandings of human morality and may have profound implications for the way that humans deal with moral transgressions. In the words of Sam Harris (2014, para 31):

We should admit that a person is unlucky to be given the genes and life experience that doom him to psychopathy. Again, that doesn't mean we can't lock him up. But hating him is not rational, given a complete understanding of how he came to be who he is. Natural, yes; rational, no. Feeling compassion for him could be rational, however—in the same way that we could feel compassion for the six-year-old boy who was destined to become Jeffrey Dahmer. And while you [may] scoff at “medicalizing” human evil, a complete understanding of the brain would do just that. Punishment is an extraordinarily blunt instrument. We need it because we understand so little about the brain, and our ability to influence it is limited. However, imagine that two hundred years in the future we really know what makes a person tick; procrustean punishments won't make practical sense, and they won't make moral sense either.

Cross-References

- ▶ [Evolution of Cooperation](#)
- ▶ [Evolved Moral Foundations](#)
- ▶ [Fairness in Corvids](#)
- ▶ [Fairness in Primates](#)
- ▶ [Game Theory](#)
- ▶ [Harris' Moral Landscape](#)
- ▶ [Jonathan Haidt](#)
- ▶ [Moral Concerns](#)
- ▶ [Moral Instincts](#)
- ▶ [Morality Is Cooperation](#)
- ▶ [Trolley Problem, The](#)

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Science and Religion Compatibility

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Definition

Science and religion are two fundamental ways that we have of understanding ourselves and the universe

within which we exist. Both science and religion assert authority in the world. That is, both have – and utilize – “the power to influence or command thought, opinion, or behavior” (Merriam-Webster) in their respective areas of purview.

Science is the systematic study of the physical and natural world.

Religion is defined in a number of ways. For the purpose of this discussion, we will define religion as a shared system of beliefs, moral code, faith, and worship, with a focus on a god or similar supernatural forces. It is relevant to highlight the distinction between the *practice* of religion as the perspectives and actions of groups of people in regard to their faith (i.e., praxis) and the *tenets* of a particular faith (i.e., theology). While the *practice* of faith can be studied using quantitative and qualitative research methods, the *tenets* of faith are difficult, if not impossible, to investigate empirically, as they are not bound by the laws of the physical and natural world.

Science and religion compatibility refers to the degree to which beliefs about science have been viewed as being consistent – or inconsistent – with religious views and practices and the degree to which beliefs about religion may be consistent or inconsistent with the tenets and practices of science.

Introduction

The relationship between Western science and religion is one that has been discussed and debated among European scholars at least since the seventeenth century, which is when the scientific approach began to emerge, and be perceived, as a legitimate method for understanding the world in which we live (Barbour 1997). This relationship continues to be an active area of scholarly interest, as demonstrated by the number of academic journal articles being published on the topic. A search of the JSTOR digital archive of academic works that were published in English between January 2000 and August 2018 using the keywords *science* and *religion* yielded 25,453 entries. In fact, the convergence and divergence of science and religion is a topic of interest across

all three of the major monotheistic religions. Using the same search criteria as above with the keywords *Christianity* and *science* yielded 5,485 articles, *Islam* and *science* yielded 5,391 articles, and *Judaism* and *science* yielded 1,418 articles. The purpose of this work is to provide a general framework for understanding the intersection between science and religion in modern Western thought with reference to some of the more notable people, places, and organizations associated with this topic.

Perspectives, History, Studies, and Resources

One way to achieve a sense of the relationship between science and religion is to assess the perceptions of individuals. One's perception, of course, will be influenced by the respective roles that science and religion serve in the life of that individual. Perhaps the best starting point is to describe the ways in which taxonomies or categorization strategies have been used to facilitate understanding of the various ways in which people think about/describe the relationship between science and religion. For example, in an investigation of the contemporary philosophical and educational literature, Yasari et al. (2013) synthesized a number of existing taxonomies and proposed an empirically based taxonomy focused upon people's views of the relationship between science and religion. These authors ultimately proposed and investigated seven views that they believe capture the main perspectives on the relationship between science and religion.

- Although some aspects of science and religion appear to conflict, it is difficult to understand the conflicts.
- When science and religion conflict, science is correct.
- When science and religion conflict, religion is correct.
- There is no conflict because science addresses questions of the physical universe, while religion addresses questions of ethics, values, and purpose.

- There is no conflict because science constructs knowledge through the scientific method and religion constructs knowledge through interpreting religious writings.
- Science and religion answer the same questions, so it is possible to combine them.
- Science and religion are both useful to understand life, so they are complementary.

These perspectives can inform the development of a list of major questions that underlie the discussion of the compatibility of science and religion. The most productive conversations tend to revolve around the following questions, many of which are rooted in the scholarly writings from the seventeenth century to today.

- How has the perception of the relationship between science and religion developed over time?
- What are some of the ways in which science and religion intersect?
- What are the conditions under which science and religion can operate or function in a compatible way?
- What are the events, conditions, and circumstances in which science and religion cannot be viewed as being compatible?
- To what degree do science and religion – respectively and together – help us to deepen our understanding about the truth of human nature?
- In what ways have empirical methods been used to study religion and spirituality?
- To what extent is the discussion about intellectual reasoning or moral reasoning?

In order to provide a broad perspective on science and religion compatibility, we address a sampling of these questions below.

How Has the Perception of the Relationship Between Science and Religion Developed Over Time?

Within Western thought, religion predates science. The advent of scientific methods of investigation during the sixteenth and seventeenth centuries began to change the way we think

about the world and our understanding of the world. During this period, there was no serious competition or conflict between what we consider today as science and religion. Early men of Western science (e.g., Kepler and Newton) were religious men who saw no inherent incompatibility between their religious beliefs and their systematic exploration of the natural world. They viewed science as a procedure that helped us understand the Creator.

For example, the study and writings of Rene Descartes during the first half of the sixteenth century represent a movement toward a greater distinction between natural and theological understanding of the world. Descartes proposed a dualistic representation of persons as having both a physical presence (body) and a nonphysical presence (mind/soul). One consequence of this philosophical perspective during his time was a justification for systematic study of the body. At that time, the body was viewed as the temple of the soul (i.e., the spiritual essence of the individual), which did not allow for the human body to be violated for any purpose, including study. Descartes' dualistic theory broached the idea that the soul could, in fact, be separated from the body at death, thus opening the door to the study of human anatomy without fear of violation of the soul. This idea of the possibility of separation of the essence of the person from the body also signaled an increasing bifurcation between study of the natural world and the spiritual world. Eventually science became increasingly reified as the source of knowledge about who, what, and why we are in the world, which had previously been the purview of religion. This elevation of science became a source of contention among religious thinkers.

More recently, the popular notion of irreconcilable differences between science and religion is most commonly exemplified by debates between the two groups that have been described as *atheist scientists* and *religious fundamentalists*. These debates often center on issues related to the nature of the creation of the universe and the establishment of human existence, especially questions regarding the authoritative sources of such facts. Scholars have suggested that, in some ways, this discussion has evolved as a debate over

knowledge and which group holds the greater authority over knowledge generation, dissemination, and validation. In contrast, among those who view science and religion as authorities of different aspects of human experience (e.g., understanding the *what* of the physical universe, compared to the *why* of human moral behavior), there is less conflict and greater room for cooperation and collaboration.

What Are Some Ways in Which Science and Religion Intersect?

Science and religion are both institutions with the shared goal of increasing our understanding of the human condition. However, science and religion have divergent premises, beliefs, and strategies that underlie and serve that goal. As noted above, it is sometimes said that science is about *how* humans came to be here, while religion is about *why* humans came to be here. Therefore, beliefs about the creation of the earth and the beginnings of human life on this planet represent an inherent point of intersection. As an example of divergent viewpoints, a creationist view holds that life was created by a single divine creator at a specific moment in time (e.g., Ham 1987). In contrast, an atheistic scientific view is that life on earth evolved through a purely biological process that is spurred by natural selection, sexual selection, and genetic mutation (e.g., Dawkins 1986). These two exclusionary views would represent a point of contention between beliefs in religion and science that are irreconcilable. Any number of views that fall at midpoints between these creation-evolution endpoints suggest that there exists at least the possibility that there are scenarios that would allow both to be true (e.g., Haisch 2006).

In What Ways Have Empirical Methods Been Used to Study Religion and Spirituality?

Both quantitative and qualitative methods have been used to study various aspects of religion and spirituality. Quantitative studies of religion have been conducted within both experimental and nonexperimental paradigms. The following provide examples of different types of studies that one might find in the academic literature across diverse disciplines.

- Psychology is the study of human behavior. Consequently, studies of religion as a *psychological* phenomenon might address questions such as the following.
 - What are the personal characteristics of individuals who choose to be religious?
 - What are health outcomes for individuals who practice a religion, compared to those who do not practice a religion?
- Sociology is the study of human relationships in society. Consequently, studies of religion as a *sociological* phenomenon (a social institution) address questions such as the following.
 - What is the relationship between religiosity and civic engagement?
 - Are health (or religious, or psychology) outcomes related to religious affiliation?
- In any discipline (e.g., psychology, sociology, social work, nursing, education) studies of religion or spirituality as an experiential phenomenon address questions such as the following.
 - How do people feel about talking about God with people of different religions?
 - What is the experience of health or social service practitioners who provide services that are antithetical to their religion?

Experimental studies that attempt to bridge the gap between science, religion, and spirituality attempt to apply the tools of the scientific method to the investigation of the nonphysical aspects of religion, faith, and spirituality. Some classic studies are noted here as examples of research questions and methodologies that have been employed. To our knowledge, no study has yielded findings that provide support for any metaphysical aspects of religion. However, it is also relevant to note that, according to the tenets of the scientific method, the inability to demonstrate a phenomenon under experimental conditions (i.e., a null finding) is not the same as evidence that the research hypothesis is not true. However, repeated null findings in studies that use rigorous methodology can cast doubt on a hypothesis. One of the major obstacles to the scientific study of metaphysics is, of course, that the tools of science are designed to study physical – not metaphysical – phenomena. The following are

representative examples of historical and contemporary studies of spirituality related to religion.

In a now classic study that has been come to be called the *21 Grams* study, MacDougall (1907) attempted to demonstrate the soul as an entity separate from the body by documenting the weight of the soul as it leaves the body upon death. MacDougall used the simple but effective method of comparing the weight of the live body (ostensibly with its soul) against the weight of the body immediately after death (ostensibly after the soul has left), imposing logically appropriate experimental controls. In the *21 Grams* study, MacDougall reported a change in weight of 21 grams following the death of one subject, surmising that the human soul weighs exactly that. However, a number of follow up studies failed to confirm these findings and the studies have been widely criticized over time (Park 2010).

Similarly, a number of studies have been conducted over the years regarding the impact of intercessory prayer. For example, Galton (1872) wrote about a study by a contemporary in which he also recorded his own musings about the statistical evidence regarding the efficacy of prayer. More recently, Harvard researchers (Benson et al. 2006) conducted a randomized control trial to study the efficacy of intercessory prayer. In addition, Hodge (2007) conducted a meta-analysis of a large number of investigations of intercessory prayer.

Despite a lack of findings in these particular empirical studies, they serve as examples of historical and continued attempts to bridge the gap between science and religion in an effort to better understand our experience of the world. In fact, religious and lay academics and scientists the world over are engaged in this discussion through sites and programs such as the Vatican Observatory (<http://www.vaticanobservatory.va/>) and the Smithsonian's Human Origins Initiative Broader Social Impacts Committee (<http://humanorigins.si.edu/>).

A Representative List of Resources with a Focus on Science and Religion

The following are examples of academic resources, academic journals, and academic

centers that focus on science and religion. The list is representative, not exhaustive.

Academic Resources with a Focus on Religion and Science Although studies on religion are prevalent in the journals of any number of academic disciplines (e.g., psychology, sociology, and education), the following are examples of academic resources devoted entirely to the study of the relationship between religion and science.

- Journal for the Scientific Study of Religion (Wiley; <https://onlinelibrary.wiley.com/journal/14685906>)
- Stanford Encyclopedia of Philosophy: Religion and Science (2017)
- Theology and Science (Center for Theology and the Natural Sciences; http://www.ctns.org/theology_science.html)

Academic Journals with a Focus on Religion that Publish Empirical (in addition to philosophical) Studies About Religion. This is not a comprehensive list.

- Journal of Religion and Health (Springer; <https://www.springer.com/public+health/journal/10943>)
- Journal of Contemporary Religion (Routledge/Taylor & Francis; <https://www.tandfonline.com/toc/cjcr20/33/1?nav=tocList>)
- Journal of Religion and Society (Creighton University; <http://moses.creighton.edu/JRS/>)

Academic Centers Centers for the study of science and religion exist around the world. This is a representative (not comprehensive) list.

- Center for Theology and the Natural Sciences (CTNS; <http://www.ctns.org/about.html>)
- Ian Ramsey Center (Oxford; <http://www.ianramseycentre.info/aboutus.html>)
- International Association for the Cognitive Science of Religion (http://www.iacsr.com/iacsr/CSR_Links.html): Includes a list of resources that includes Journals and Reviews, Centers and Websites, Programs, and Associations under the headings of both “Science and Religion” and “Science of Religion.”

- Society for the Scientific Study of Religion (SSSR; <http://www.sssrweb.org/About.cfm>)
- Smithsonian’s Human Origins Initiative Broader Social Impacts Committee (<http://humanorigins.si.edu/>)
- Templeton Foundation (<https://www.templeton.org/>)
- Vatican Observatory (<http://www.vaticanobservatory.va/>)
- Zygon Center for Religion and Science (Lutheran School of Theology at Chicago; <http://zygoncenter.org/resources/>)

Conclusion

Although the dialogue about the relationship between science and religion is larger than evolution, what we typically read in the press are stories of large and irreconcilable differences between a religious view of the origin of human life and a scientific view of the origin of human life. However, it is also possible to find scholarly and general writing in which theologians take a less literal approach to the Bible that easily accommodates an evolutionary theory of the origin and development of the universe, including humans’ place in that universe. Similarly, there are scientists who accede to the possibility of some divine action that cannot be explored using the scientific method. Stories of scientists’ rationalization of their work with their faith also abound (e.g., Consolmagno 2007) and add perspective to the discussion. Among some, there is optimism that ongoing dialogue can foster a richer and fuller understanding of the universe and our place in it.

Cross-References

- Religion
- Religious Beliefs
- Religious Teachings

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Scientific

► Falsifiability

Scope Hypothesis, The

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Synonyms

Episodic and semantic counteraction; Joint activation of derived and inceptive memories; Priming paradigm; Tandem memory retrieval

Definition

The scope hypothesis proposes when a generalization is retrieved from semantic memory; episodic memories that are inconsistent with it should be retrieved in tandem to place boundary conditions on the scope of the generalization.

Introduction

The scope hypothesis asserts that the function of priming inconsistent episodes is to place boundary conditions on the scope of a semantic summary. An excellent package of speed and accuracy can be engineered into a decision system by jointly activating a trait summary and episodic memories that are inconsistent with it. Trait self-descriptiveness judgments should activate trait-inconsistent, but not trait-consistent, behavioral episodes. In the event that scope hypothesis is supported, one would expect that trait-inconsistent episodic memories are primed by retrieval of a trait summary from semantic memory.

Boundary Conditions on the Scope of Generalizations

To rely on semantic memory alone is to sacrifice accuracy for speed as trait summaries lack the resolution of an episodic memory. Although trait judgments have predictive validity, the behavior of an individual manifests a great deal of situation specificity (Funder 1995). Episodic memories are situation specificity incarnate. They are records of how particular people behaved in specific situations. A system engineered to retrieve, along with a generalization, episodes that place boundary conditions on its scope would achieve the best of both worlds: speed courtesy of semantic memory and accuracy courtesy of episodic memory.

Decision Context

The decision context should determine when boundary conditions are needed, and which kinds of episodes would be relevant. Because decisions regarding personality traits are not amenable to all-or-none answers, it would be reasonable to assume that the trait summary takes a

quasi-quantitative form. Thus, when the individual is asked if a certain trait describes them possible answers might be “usually,” “sometimes,” or “rarely.” Boundary conditions would be episodes in which the behavior did not meet the criteria for that trait. This should be true for any level the trait summary specifies, even “rarely.” This is because the decision context calls for a generalization about it; the function of activating episodes is to place boundary conditions on that generalization. The issue is, “How often is Person Y friendly, and under what conditions is she or he not?” The decision rule activated is designed to make a judgment about the trait being asked about, whether the question originates with another person or with the individual making the judgment.

Different decision rules are designed to retrieve different kinds of information from memory. The type of decision being made matters, because that determines which search engine gets activated, which will determine which array of memory systems gets searched. When asked to trait-categorize their own behavior, subjects should retrieve a trait summary and episodes inconsistent with the trait they are being asked about.

Research Studies on Scope Hypothesis

On the basis of the scope hypothesis, it was predicted that retrieving a trait summary to answer a described question would prime trait-inconsistent episodes, but not trait-consistent ones. The first experiment probed knowledge about one’s own traits, because it is fairly certain that the typical adult already has formed a database of trait summaries about themselves. The second experiment probed knowledge about another person’s traits, the subject’s mother, to see whether the same results pertain when trait summaries are lacking.

The Self-Study

It was examined whether accessing a trait summary about the self would prime trait-inconsistent episodes but not trait-consistent ones (Klein et al. 2001). Subjects were presented with a list of trait adjectives and asked to perform one of three tasks with them. The describe task asked subjects to

decide whether the stimulus trait describes them; the recall task asked subjects to retrieve a specific instance in which they manifested the stimulus trait; and the define task asked subjects to generate a definition for the stimulus trait. If the scope hypothesis is correct, then deciding whether a trait is self-descriptive will activate a summary representation and episodes inconsistent with the trait being asked about. Empirically, one should observe two things.

The results showed that deciding whether a trait describes oneself facilitates retrieval of trait-inconsistent episodes, which suggests that these judgments activate memories of behaviors inconsistent with the trait being judged (Klein et al. 2001). By contrast, there was no evidence that trait self-descriptiveness judgments facilitated retrieval of trait-consistent episodes. Based on the outcome of the experiment, it is inferred that decisions about whether a trait describes oneself do not activate trait-consistent behavioral memories. That trait-inconsistent, but not trait-consistent, episodic memories are primed by retrieval of a trait summary from semantic memory is just what one would expect if the scope hypothesis were correct.

The Mother Study

This study had two primary objectives; first, it aimed to extend the generality of the scope hypothesis by testing whether judgements about a well-known other also conform to its predictions and, second, to address the finding that activation of trait-inconsistent behaviors occurred regardless of whether the trait judged fell in the high, medium, or low self-descriptiveness categories. This finding can be accommodated within the scope hypothesis by assuming that trait knowledge about the self is represented in summary form across levels of trait self-descriptiveness. According to the model of mental representation of trait knowledge about others, one’s representation of a person’s traits varies with the amount of experience one has had with that person. If the amount of experience is not sufficient to support abstraction, then trait knowledge will be represented only at the level of behavioral memories. Trait judgments about the person, therefore, must be

based on inceptive behavioral memories, that is, on episodes. However, as the amount of experience becomes sufficiently large, trait knowledge is increasingly likely to be abstracted and represented in summary form.

The study results illustrated that for traits highly descriptive of one's mother, ones for which a summary should exist, trait-inconsistent episodes were primed, but trait-consistent ones were not. For traits only moderately descriptive of one's mother, ones for which there should be no summary, the opposite pattern was found. Trait-inconsistent episodes were not primed, but trait-consistent ones were.

The results of this study strongly support the scope hypothesis as they allow for comparisons in priming when trait summaries are present versus absent. When a decision is made by accessing a trait summary, search engines should simultaneously retrieve inconsistent episodes to provide information about the conditions under which the summary ceases to be useful. Thus, trait-inconsistent behaviors were primed when a decision about one's mother was made by accessing summary representations of her traits. But when summary representations were absent, they could play no role in decision-making. This explains why trait-inconsistent behaviors were not primed in the medium-descriptive condition. According to the scope hypothesis, when no generalization has been accessed during a decision task, there is no representation whose scope needs to be delimited.

Conclusion

It has been argued that generalizations from semantic memory allow speedy decisions, but at the cost of accuracy, whereas episodic memories provide accurate, situationally specific, information, but at the cost of speed. Nevertheless, both speed and accuracy can be engineered into a decision-making system, if the system is designed to retrieve both kinds of information in the right combination. A generalization is most useful when its scope is delimited, that is, when

it is accompanied by information specifying those situations in which it does not apply. Episodic memories that are inconsistent with the generalization can facilitate this function because they are broadband encodings of specific situations in which the generalization fails to predict the outcome. Interpretively, this task analysis constitutes the scope hypothesis; a decision rule needs a search engine that looks for summary information in semantic memory and on retrieving it and looks for episodic memories that are inconsistent with that summary, ones that place boundary conditions on the summary's scope.

Cross-References

- [Episodic Memory](#)
- [Inceptive and Derived Memory](#)

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Scott Atran

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Synonyms

[Author](#); [Researcher](#)

Definition

Scott Atran is an anthropologist and psychologists whose area of study focuses on values, conflict

negotiation, and the evolutionary psychology of religion.

Introduction

Much of Scott Atran's work has focused on values, conflict negotiation, and the evolutionary psychology of religion. Most of his work combines two or more of these areas to produce theories with real-world applications. For example, he studied how individuals hold and react to value violations (Atran and Axelrod 2008), applied this theory by asking Zionists and Palestinians living in the West Bank how they would react to different peace offerings were they to be proposed (Ginges et al. 2007), and summarized his data to be used by international organizations (Pinker 2011). Other notable contributions include his work on transnational terrorism, where he argues that terrorist ideology stems from nepotism, not psychopathy, with findings drawn from field work internationally (Pinker 2011).

Sacred Values and Conflict Resolution

Sacred values are moral imperatives that drive behavior in the absence of any specific goal (Atran and Axelrod 2008). These values are frequently the reported cause of many international conflicts. This can be problematic, as holding sacred values is a largely irrational behavior, and many international peace efforts approach conflicts as if adversaries will always make the rational choice. This is demonstrated through the rhetoric used by US foreign policy, where they state policy decisions should be informed by taking into consideration the goals of both parties through the use of results-oriented planning (Atran and Axelrod 2008). Because of this, many attempts at peace are met with outrage not because the offer was unreasonable, but because the offer did not take into account the sacred values of the other side (Ginges et al. 2007).

These sacred values may be the product of recurrent evolutionary problems, specifically those problems that posed a long-term threat to our ancestors. If so, this would explain why they can override our short-term self-interest to the point that it can cause death (Atran and Axelrod 2008). One such evolutionary recurrent problem may be the presence of children, as this value appears sacred across most cultures. Seeing the health of one's children as a sacred value would have been a struggle shared across all ancestors and one that would have had strong selection pressure for it. Furthermore, the presence of sacred values on non-evolutionarily recurrent problems may be the result of a selection pressure to promote cooperation. For example, the presence of sacred forests may represent a collective resolve to resist the temporary, immediate benefit of firewood for a shared access to renewable resources.

Although there are some examples of potentially beneficial sacred values, other examples such as sacred honor display a sacrifice far greater than any potential payoff. For example, many instances of desire for revenge are held so deeply it can result in death of the individual seeking revenge. In these cases, had the individual lived, there still would have been no payoff to their actions from a resource standpoint. In these cases, it is likely that a sacred honor represents a collective, rather than individual payoff. For example, consistent willingness to avenge regardless of the cost can deter stronger, less committed enemies from engaging in combat as the potential cost for them may be far larger than the benefit. This, it is argued, is a likely reason for seemingly irrational conflict (Atran and Axelrod 2008; Ginges et al. 2007). Further evidence for this was demonstrated by Atran et al. (2007) where interviews with families of Palestinian suicide bombers showed less willingness to accept compensation for a family member's death as the amount of compensation increased. This means that the more money offered, the less likely they would be to accept the money. They said that willingness to accept large amounts of compensation points to a focus on materialism and a disregard for their sacred value.

Symbolic Concessions

All of this points to a strong need to appeal to each side's sacred values in order to come to a peaceful resolution. One way of doing this is through symbolic concessions. Symbolic concessions are gestures that are weighty to one or both parties involved, but may seem trivial to an outside source. Symbolic concessions are, more often than other forms of negotiation, a quick and peaceful way of coming to a resolution. A problem with these acts is that policymakers are rarely able to implement this strategy as they are unable to see the other side's sacred values as sacred (Atran and Axelrod 2008).

A major problem with ignoring the sacred values of either side in a negotiation is that it can lead to violent escalation in a short period of time. For example, a large number of international negotiations involve presenting one side with resource in response to asking for a concession. In many affairs this works fine, but if the concession violates the other side's sacred values, then the results are problematic. Ginges et al. (2007) interviewed multiple groups in the West Bank and Gaza asking individuals for their responses to multiple proposals. The participants actually responded with more outrage when offered material compensation for violation of a sacred value than if they were simply asked to give up their sacred value with no compensation.

A successful method of resolving these issues is to offer a symbolic concession rather than a material one. Symbolic concessions are displays of a willingness to give up one side's sacred values as a concession to the other side giving up their own. As both sides are giving up something they believe to be priceless, the offer appears to be balanced for both. An example of this can be found between Zionist leaders and Germany post-WWII (Lustick 2006). Israel was in dire need of economic support and knew it could receive much of what it needed from Germany as compensation for the destruction of property inflicted on European Jews. However, at that time a sacred value held by Israel was a public boycott of anything German, including potential aid. To overcome

this, German leadership declared to the world that Germany was aware of the untold suffering brought upon the Jews of Germany and elsewhere and that most German citizens held in contempt any who had participated in the genocide. This declaration functioned as a sacred concession, with Germany giving up what had previously been a sacred value of supporting Nazism, while the Jews gave up their sacred value of boycotting Germany. In this example, the sacred concession did not complete negotiations, but it opened the way for further negotiations and the allowance of resources to be transferred without the violation of sacred values.

Real-World Applications

Atran has addressed the UN Security Council on multiple occasions to advise on matters of violent extremism in international terrorism. Unlike most of the research on this topic, Atran approaches many of these extremists from a sympathetic viewpoint, allowing him to better understand their operations and motives. His main focus in these discussions is to demonstrate the impact of youth and social bonds in the presence and spread of terrorism.

While performing field research, Atran discovered that roughly three out of every four people who join ISIS or Al Qaeda outside of the Middle East do so through friends, with the fourth being recruited through family or travelers. A large reason for this is that the parents in groups of Muslim refugees refuse to discuss the problems going on in their homeland with their children, leading to intense desire from their children to understand. This leads to uninformed youth actively seeking out and, subsequently joining, extremist groups (Atran, as cited in Downey 2015).

The goal of these discussions is to reframe the perception of violent extremists from inhuman psychopaths to disgruntled youth desperately trying to find a place for themselves. Atran puts it best in his address to UN Security Council: "Violent extremism represents not the resurgence of traditional cultures, but their collapse, as young

people unmoored from millennial traditions flail about in search of a social identity. . . They radicalize to find a firm identity in a flattened world” (see Downey 2015, para. 12). In these groups, their primary sacred value is a need to belong, and any attempts at stopping them without first granting them sympathy violates these values, leading to subsequent retaliation and failure to negotiate. To prevent this, Atran presents three conditions that must be met before any resolution can be met.

First, Atran argues that to counter terrorist groups, the youth which may potentially join them must be offered something that makes them idolize “a life of significance through struggle and sacrifice in comradeship” (see Downey 2015, para. 18). The reason such a grand sounding offer must be presented is because this is what is being presented by terrorist groups. The youth that join these groups do so because they are offered a chance to be a part of something bigger than themselves. When you compare this to the many countries they are forced to flee to, where racism and institutional prejudice isolate and alienate these youth, it is clear why they join violent extremists (Atran, as cited in Downey 2015).

The second condition is that youth must be offered a positive personal dream with a solid chance of it being realized. Atran fails to offer direct suggestions for this condition other than critiques of current practices (Atran, as cited in Downey 2015). Although terrorist groups will recruit youth through appeals to moral crusades, governments frequently do no more than fan these flames. By providing outlets for youth who have a desire to be passionate, governments may be able to redirect some of the youth attracted to these groups.

The final condition presented by Atran is the need to allow youth to create their own local initiatives. By engaging youth in projects that provide meaningful ways to alter the world around them, governments will simultaneously be providing an outlet for the youth’s passion while allowing them to fix the local problems that may cause transitions to violent extremism. As the most frequent recruitment tool of radical

extremism is to elicit moral outrage over a shared negative circumstance (Atran, as cited in Downey 2015), allowing the youth to fix the negative circumstance would provide a solid solution.

Conclusion

Scott Atran has studied a wide range of topics with a focus on minimizing violence between groups. Starting with work on sacred values, Atran began to develop models of conflict negotiation rooted in the evolved psychology of humans. From here, he developed a model of sacred concessions that multiple international organizations have used to smooth out negotiations between conflicting sides. Finally, Atran is currently investigating details of terrorist groups from an anthropological perspective to better understand and inform international groups on how to peacefully resolve future hostile situations.

Cross-References

► [Sacred Values](#)

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Sea Slug

► [Aplysia](#)

Search Latency

► [Search Time](#)

Search Time

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Synonyms

[Search latency](#)

Definition

The search phase of foraging refers to movements or strategic waiting that increases an animal's chances of finding food, and *search time* is the interval between the onset of those activities and prey capture.

In ethological terms, searching is a part of the appetitive phase of a motivated behavior, such as seeking food, water, or a mate. With regard to predatory behavior, searching may involve active, directed movement within areas where prey have previously been encountered, waiting in ambush for prey, or increased movement within the predator's home range where prey *may* be present. Both endogenous (hunger) and exogenous (movement, sound) cues can elicit search behavior. Once a food item or source has been secured, the predator engages in handling and ingestion responses (*consummatory responses* in ethological terms).

The time spent searching for prey represents a cost to the forager in terms of energy spent, time

away from other survival and fitness relevant activities, and increased vulnerability to predation because the forager is away from refuge sites or is distracted. However, since food does not land in the lap of the forager, it must endure these costs. Adopting an optimal search strategy can outweigh the costs of foraging with the benefits of finding an adequate food source.

Search time varies by characteristics that are both inherent to the predator, such as species-typical foraging behaviors, and the environment in which it forages. Active search mode (referred to as cruising) involves maximizing coverage of a search area where prey are likely to occur during a given time period. Ambush searching involves remaining still in order to minimize detection by prey and maximize the ability to detect moving prey (Schoener 1971; Alpern et al. 2011). Search time will be influenced by which of the strategies is adopted or how they are used in combination while foraging. Foraging bats remain in active search mode and therefore allocate far less, if any, time to ambushing prey compared to vipers. In contrast to both, lions might spend considerable time traveling to areas where prey are likely to be encountered and then switch to stealth mode as prey searching becomes more targeted.

Learning impacts search time. The *search image*, a topic of ethological study, refers to a perceptual fine tuning that allows the predator to increase the likelihood of detecting prey. Acquiring a search image to prey that use cryptic coloration as a mechanism of defense is an example. Thus, perceptual learning may influence search time. The role of learning in search time is also integrated into *behavior systems theory* (Timberlake 1994). Behavior systems theory describes how learned responses interact with the mechanisms and processes of unconditioned, biologically essential responses involved in feeding, reproduction, and other adaptive behaviors. The feeding system involves different responses occurring on the continuum of locating and ingesting food. Predation can be divided into a sequence of modes, or motivational substates, which function to bring the predator closer to its prey. Feeding begins with a general search

mode, progresses to focal search, then to handling and consuming prey. If the predator is not satiated, it will return to focal search mode and then to either handling-consuming if new prey are secured, or to general search, depending on the immediate availability of additional food. General and focal search modes are both elements of total search time but are behaviorally distinct. For example, general search may involve moving and tracking the strength of olfactory cues and then transitioning to focal search responses such as visual tracking, running, and prey capture.

The effects of learning processes on search time have also been examined in instrumental conditioning procedures. As described in prey choice, concurrent chain reinforcement schedules are used to study how organisms allocate responses in proportion to available reinforcement. Two salient properties of reinforcement learning are the amount of work needed to acquire the reward and the delay to receiving the reward. Behavioral ecological models of optimal foraging encompass both of these properties, with search time relevant to the delay aspect: Longer delays to reward are analogous to increased search times during natural foraging situations. Williams and Fantino (1994) tested the relative roles of rate maximization of reinforcement and delay to reinforcement in pigeons and found that the animals were particularly responsive to conditioned reinforcers that signaled shorter waiting times for food. Thus, although food profitability is a crucial factor in optimality modeling (and in real feeding behavior), reducing the delay, and therefore search time, is also important.

As described in ► [prey choice](#), the optimal diet model

$$\frac{E_2}{h_1} > \frac{E_2}{h_2}$$

predicts that larger, more energy profitable (E) prey₁ will be chosen over prey₂ unless handling time h justifies reversing the preference. If

handling times are equal, the choice should always be the larger prey₁. However, if smaller prey₂ is encountered, the forager must compute whether it is worthwhile to pursue and consume the smaller prey or continue searching for a larger item. Search time can be integrated here as

$$\frac{E_2}{h_2} > \frac{E_1}{S_1 + h_1}$$

with S_1 representing the search time for the larger prey item. Thus, prey₂ should be chosen if:

$$S_1 > \frac{E_1 h_2}{E_2} - h_1$$

Search time is an important component of both behavioral ecological and psychological perspectives of feeding behavior. For behavior systems theory, the amount of time predators spend finding prey will be a function of behavioral, motivational, and perceptual constraints. Instrumental analogs to natural foraging behavior emphasize the relative contributions of rate maximization of reinforcement and delay reduction, with the latter emphasizing the saliency of anticipated search time in foraging decisions. Behavioral ecological models mathematically incorporate search time by factoring it in with other critical variables such as energetic profitability and handling time.

Cross-References

► [Prey Choice](#)

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Seasonal Breeding

► Reproductive Timing

Second Language Acquisition

► Critical Period of Acquisition

Second Sexism

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Synonyms

Male wrongful discrimination; Sexism against male; Unfair male disadvantage

Definition

Sex discrimination against male.

Introduction

In 2003, David Benatar published an essay on a phenomenon he called the second sexism. It received harsh criticism in proposing

recognition about the existence of another sexism's facet, but this time against males. In 2012, David Benatar's book *The Second Sexism: Discrimination Against Men and Boys* was published, in which he abstracts this discussion, reinforces arguments, and presents more evidence of wrongful discrimination against males based on sex. The book exposes several situations where males are disadvantaged compared to women, such as, are more likely to military conscription, to be victims of violent crimes, to receive more frequently and intense corporal punishment, to their sexual assault be taken less seriously, to lose custody of their children in the context of divorce, and so on.

The Second Sexism

Sexism is defined by Benatar (2012) as a wrongful discrimination based on sex. Thus, the second sexism is another facet of sexism, whose primary victims of unfair discrimination are males. It presents sexism as a continuum composed of two facets and only one of its forms is taken seriously and studied; in other words, the second sexism is an unrecognized form of sexism. Benatar's position is that men and boys are victims of sexism, but this wrongful discrimination is not widely recognized as those against women. It endorses the existence and the seriousness of the first sexism (when females are the primary victims). However, there is a predominance of the scientific literature about the first sexism and a lack of knowledge and denial about the second sexism. It claims that discrimination against men undermines the fight against sexual discrimination in general. His first effort to systematize the second sexism (Benatar 2003) received objections mainly focused on cultural factors and in defense of the first sexism rather than the second sexism (e.g., Quinn and Tong 2003; Digby 2003). The main issues of his first essay and the second sexism's book remain without academic attention, particularly the implications about sex differences on the male disadvantages' explanations. Only cultural aspects were considered, but

to a lesser extent (Kelland 2014, 2015), even so Benatar (2015) considered these researches as an ideological opposition.

Sex Differences and Second Sexism

One of the central issues of the book is the claim that beliefs about men, based on the discussion of sex differences, allow us to understand and justify second sexism. Benatar enquires about the existence of a biological basis for the differences between the sexes and the extent, if any, of their influence. Although, he is ambiguous in considering the psychological differences between men and women to be appropriate. Sometimes the author assumes these differences, as when he endorses the statement that women tend to have smaller standard deviations in intelligence, but also fewer geniuses. In another moment, he minimizes it when he questions whether men are more aggressive than women. And finally, underestimates evidence of sex differences, for example, ignoring why men are predominantly the perpetrators of wrongful discrimination against men and women. The author usually recognizes the influences of biology in a general sense (e.g., environmental influences, nutrition) but underestimates or disregards sociobiology and evolutionary psychology contributions about the effects of evolution on human psychology and behavior. This ambiguous position reflects in his argument on the sex differences, so he recognizes that the basis for distinctions is primarily biological but accuses evolutionary psychologists of overestimating them.

Sociobiologists and evolutionary psychologists present empirical data on sex differences and similarities, provide an evolutionary account of sex selection, and present the psychological and behavioral consequences of different reproductive strategies of men and women. In this way, these contributions can facilitate the understanding of the issues raised. For instance, in presenting the beliefs about males, Benatar argues that commonly the lives of adult male

seem to be less valuable than adult female lives. It is because female lives are more important for procreative efficiency and population survival than the male lives. While a man has the potential to fertilize a large number of women, ensuring continuity of the population, a woman can only become pregnant and have a baby approximately once a year, regardless of the number of partners available. Despite of the capacity of societies to survive with higher rates of female mortality or the individual desire to preserve the human species through reproduction, it has been in the evolutionary history of our species that attitudes toward the male and female lives had been constituted. The preservation of women's and children's lives is a priority over the preservation of adult male lives because it increases the chances of a population's survival. Therefore, in the face of a disaster, men, to protect these other lives, are most likely to be sacrificed or put at risk. This factor, as well as intrasexual competition, helps to understand why there is predominance in male victimization by other males in genocides. Intrasexual competition seems to have the function of stimulating the search for resources and mates rather than the complete population's genocide. Intrasexual competition helps to understand why violence against men is more common and socially accepted. The intrasexual competitiveness of males, as part of evolution, influences human behavior and psychology. That's because while women have a high degree of certainty that their descendants are theirs, men can never have the same degree of certainty. In this competition, some traits are more adaptable for the male. According to Buss and Shackelford (2008) women want good genes indicators, good investment indicators, good parenting indicators, and good partner indicators, it all from the same men, only limited to their own mate value. Thus, there is a desired pattern that involves features such as masculinity, muscularity, "confrontativeness" (Gangestad et al. 2007), current and potential acquisition of resources (Buss and Schmitt 1993) among others.

Conclusion

The second sexism proposes the existence of wrongfully discrimination against men and boys, unfair disadvantages that male experiences for the fact of being a male. Rigorous arguments and empirical data are presented to support a second sexism, situations in which males are the primary victims of unfair discrimination. Even if evolutionary mechanisms explain the devaluation of male lives, this does not justify doing so, since there are no relevant sex differences to justify an intrinsic value of one life over another. Also, one may choose to morally reject the view that boys and men should be more resilient, aggressive, assertive, sexually assertive, and greedy than women. However, the selected adaptive differences remain. The more valuable lives of women and children compared to the lives of males because of the importance for population survival. Males' vulnerability in suffering violence is due, among other things, to competition for mate and resources, and the acquisition of desirable characteristics such as masculinity and "confrontativeness." It is necessary to expand the knowledge on the subject, considering the researches of evolutionary psychology and the extension of the influence of biological factors in extent of the second sexism.

Cross-References

- [Male Warrior Hypothesis](#)
- [Racism and Prejudice](#)
- [Sexism](#)

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Secondary Adaptation

- [By-Products of Adaptations](#)
- [Evolutionary By-Products](#)

Secondary Sex Characteristic

- [Observations of Sexual Dimorphism](#)

Secondary Sex Characteristics

- [Secondary Sexual Characteristics](#)

Secondary Sex Traits

- [Secondary Sexual Characteristics](#)

Secondary Sexual Characteristics

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Synonyms

Epigamic traits; Secondary sex characteristics; Secondary sex traits; Secondary sexual characters

Definition

A secondary sexual characteristic is defined as a sex-specific trait that appears at the onset of sexual maturity and plays a role in sexual selection but is not directly involved in, or essential for, the act of reproduction (Darwin 1871).

Introduction

In the animal kingdom, an extraordinary diversity of structures exists that cannot be explained by natural selection (Darwin 1871). Consider, for instance, the elaborate antlers in a male deer (Fig. 1a; family Cervidae; Emlen 2008) or the wonderfully extravagant feathers of the peacock (Fig. 1b; *Pavo cristatus*; Petrie et al., 1991). These remarkable structures, referred to as secondary sexual characteristics, are most commonly observed in males and are thought to have evolved by means of sexual selection (Andersson 1994). These sexual characteristics may be energetically costly to produce and maintain and may be conspicuous, potentially subjecting the bearer to an increased risk of predation (Andersson 1994). Moreover, the use of such structures as advanced “weaponry” during combat with rival males while striving for the attention of females can lead to

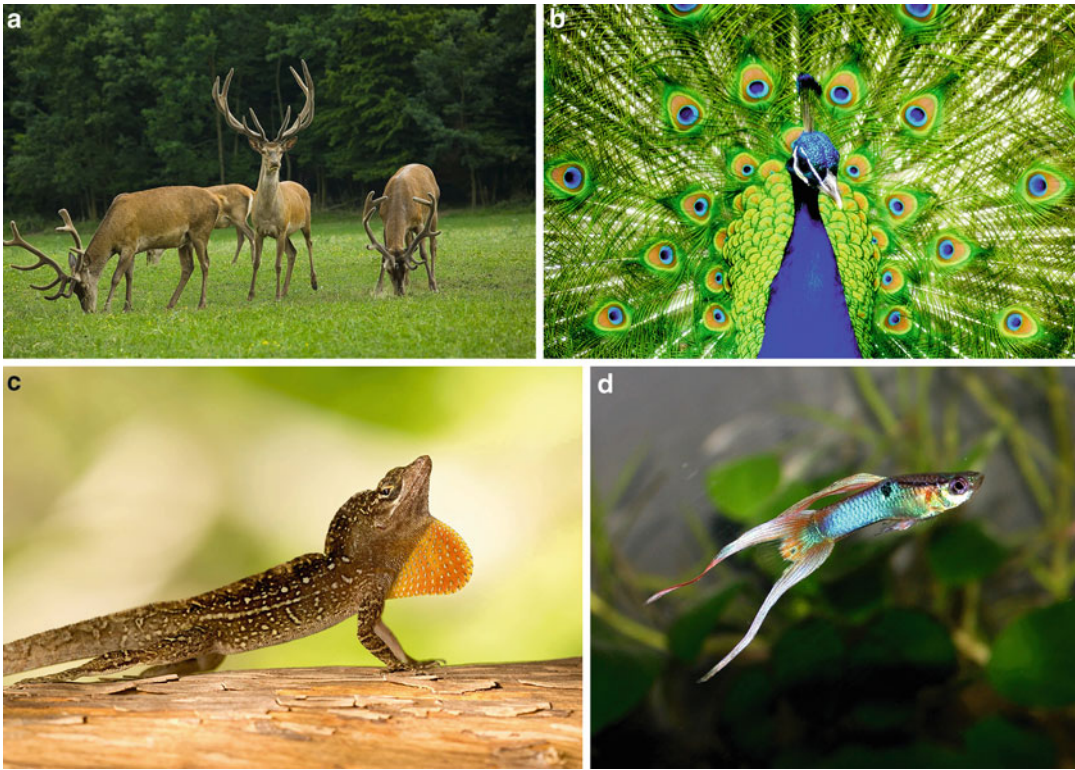
injury or, in extreme cases, even death (Miller 2013). This raises the question: if these characteristics are so costly, why have they evolved in the first place? In *The Descent of Man, and Selection in Relation to Sex* (1871), Charles Darwin laid the foundation for the two main theories on sexual selection that still persist to this day:

There are many other structures and instincts which must have been developed through sexual selection - such as the weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals - their courage and pugnacity - their ornaments of many kinds - their organs for producing vocal or instrumental music - and their glands for emitting odours; most of these latter structures serving only to allure or excite the female. (1st Edition, volume 1, p.p. 257–258)

In this seminal book, Darwin posits that secondary sexual characters may evolve either as “weapons” that enhance a male’s competitive ability in male-to-male competition for access to females or as “ornaments” that enhance a male’s attractiveness to females (Fig. 1a–d).

The Evolution of Sexual Characters as Weapons by Means of Male-Male Competition

In many species male-male competition is known to play a pivotal role during sexual selection. It is generally accepted that male-male competition can drive the evolution of secondary sexual characteristics by improving a male’s success in competition for mates with rival males (Darwin 1871; Miller 2013). Secondary characters involved in male-male competition can include songs, colors, ornaments, as well as characters involved in direct combat. In systems where males engage in fierce struggles for access to females, traits that enhance a male’s competitive success (either directly by overpowering rivals with weapons during combat or indirectly by deterring rivals with powerful songs or impressive displays) will also directly increase their chance of reproduction. Here, secondary sexual characteristics convey a clear fitness advantage, because the male with the most impressive song or most advanced weapon will chase away its rival and get the chance to mate



Secondary Sexual Characteristics, Fig. 1 Photographs showing secondary sexual characters: (a) a male red deer (*Cervus elaphus*) showing off its antlers (Source: Wageningen University), (b) a peacock (*Pavo cristatus*) presenting its extravagant tail (Source: Wageningen

University), (c) a male brown anole lizard (*Anolis sagrei*) displaying its dewlap (Photo: Thijs van den Burg), and (d) a male guppy (*Poecilia reticulata*) with beautiful body coloration and ornamental fins (Photo: Leo van der Meer)

with the female and produce offspring (Miller 2013). Theory predicts that such secondary sexually selected characters will evolve when the benefits of increased reproductive success outweigh the potential costs of producing and maintaining such structures, and an increasing body of literature on this topic indicates that male-male competition is indeed responsible for the striking diversity of weapons (i.e., antlers, horns, and tusks; Fig. 1a) in the animal kingdom (Emlen 2008; Miller 2013; Panhuis and Wilkinson 1999).

The Evolution of Secondary Sexual Characteristics as Ornaments by Means of Female Choice

Secondary sexual ornaments can also be selected because they facilitate female mate choice

(Andersson 1994). If females show a preference for a particular male character, then males having that character will have a greater fitness. Male ornaments are thought to have evolved in a variety of animal species, but the most famous examples come from birds, for instance, the extravagant plumage of male birds-of-paradise (family Paradisaeidae), the long tails of long-tailed widowbirds (*Euplectes prognus*; Andersson 1982), and, of course, the ornamented tail of peacocks (Petrie et al. 1991). There are two main hypotheses explaining the evolution of male ornaments by female choice:

- (i) Fisher's (1930) runaway model of sexual selection (also known as Fisher's "sexy son" hypothesis) proposes a correlation between the expression of a male trait (ornament) and female preference for that ornament.

Such genetic correlations between ornament and preference arise when females with a preference for a particular ornament mate with males that have that ornament, leading to the production of offspring that have both the genes for the ornament from the father and genes for the preference of the ornament from the mother (Fisher 1930). Fisher argued that, initially, a “primitive form” of the male trait might have evolved because it was favored by natural selection and that it subsequently evolved into an exaggerated ornament via a self-reinforcing runaway process of trait elaboration (while females simultaneously evolved an enhanced preference for that ornament) that continues until the fitness costs (e.g., reduced survival) of having that ornament outweighs the fitness benefit of increased reproductive success. Houde and Endler (1990) tested this hypothesis in natural populations of the Trinidadian guppy (*Poecilia reticulata*) that varied in the amount of orange coloration on males. They showed that in populations where males had a more pronounced orange coloration, the females also had a stronger preference for this trait, suggesting a genetic correlation between the male trait and female preference consistent with Fisher’s hypothesis (Houde and Endler 1990).

- (ii) Zahavi’s (1975) “handicap” hypothesis (also referred to as the “good genes” or “condition-dependent indicator” hypothesis) proposes that females choose males with exaggerated ornaments, because these represent a reliable indicator of the male’s genetic quality. The presence of a large elaborate ornament is costly and can severely impair a male’s chance of survival. The ability to survive despite bearing such a costly feature (or “handicap”) provides an honest signal of the condition of the male and, hence, the overall fitness of the male’s genotype (Zahavi 1975). Females that mate with males that have exaggerated ornaments will thus produce

offspring with a higher fitness, because they pass these “good male genes” on to their offspring. One of the most famous examples is the extraordinary tail of the male peafowl (*P. cristatus*). A study by Petrie et al. (1991) on a peafowl population from England shows that the number of eyespots of a peacock predicted its mating success, i.e., more eyespots significantly led to more matings. This increased mating success was attributed to female choice (rather than male-male competition), because females always chose from more than one male. Furthermore, offspring sired by males with more eyespots survived better, which supports the “good genes” theory (Petrie et al. 1991). Another classic study was done by Andersson (1982) on long-tailed widowbirds. Male widowbirds can have remarkably long tails: up to half a meter. Andersson experimentally modified the length of the tail: elongating the tail of some males and shortening it in others. Males with elongated tails attracted significantly more females than males with shortened tails (Andersson 1982). Moreover, males with shortened tails performed better at flying and, hence, presumably were better at escaping from predators, indicating that long tails represent a handicap to males (Andersson 1982). This suggests that female choice can lead to the evolution of costly male traits.

Conclusion

There are two main hypotheses explaining the evolution of secondary sexual characters by sexual selection. The first states that these characters have evolved as “weapons” to improve a male’s success in combat with rival males. The second hypothesis states that these characters have evolved as attractive “ornaments” by means of female’s choice.

Cross-References

- [Cryptic Female Choice](#)
- [Lekking](#)
- [Multiple Matings](#)
- [Self-Stereotyping](#)
- [Sneak Copulation](#)
- [Sperm Competition](#)
- [Vocal Competition](#)

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Secondary Sexual Characters

- [Secondary Sexual Characteristics](#)

Secondary Sexual Traits

- [Male Ornamentation](#)

Secure Attachment

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Definition

Secure attachment denotes a flexible and balanced (“optimal”) organization of attachment behavior in relation to the caregiver, which is observable in these children’s ability to use their caregiver as a secure base from which to explore the environment freely when there are no signs of danger, and as a safe haven to turn to for comfort and protection when distressed. Secure attachment is reliably predicted by having a consistently available caregiver who is responding sensitively to the child’s signals, supporting the child’s exploration and providing comfort and protection when the child is distressed.

Introduction

John Bowlby, a British psychoanalyst and child psychiatrist (see ► [“John Bowlby: Pioneer of Attachment Theory”](#)), was unsatisfied with the explanations of attachment available at the time, which deemed children’s attachments to their caregivers a secondary result of other mechanisms, such as children’s drives and/or feeding (see ► [“Psychodynamic Foundations”](#)). Seeking an alternative explanation for the phenomenon of attachment, Bowlby founded attachment theory by drawing from multiple scientific traditions, most notably ethology, cybernetics, and cognitive theory (see ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#)).

Specifically, Bowlby (1982) argued that humans come into the world endowed with an attachment behavioral system (and attachment behaviors), which function is to maintain proximity to caregivers and which was retained through

natural selection as it was associated with increased chances of survival against predators and other natural dangers (see ► [“Infant Survival”](#)). Thus, children (the weaker, smaller part) form attachment bonds to caregivers (the stronger, wiser part) who are sufficiently available and responding to children’s signals (not the other way around; see ► [“Offspring–Parent Attachment”](#)).

Bowlby, having to contest the theories of attachment available at the time, and formulate a new, scientifically based explanation for the phenomenon of attachment, devoted a great deal of effort into the normative aspects of attachment. Subsequently, although he believed that there are interindividual variations in the “quality” of children’s attachment, manifested in cognitive affective representations of self and others formed from the history of interactions with the caregivers (e.g., “internal working models” [IWMs]; see ► [“Individual Variations in Attachment”](#) and ► [“Evolutionary Foundations of the Attachment System and Its Functions”](#); Bowlby 1982), he did not get around to systematizing these variations. Lacking an empirical method for examining variation in the quality of attachment, he instead focused his efforts on the need for a continuously available and responsive caregiver and the negative effects following separations and or loss of caregivers, which were readily observable in the post-world war era (e.g., Bowlby 1982; Robertson and Bowlby 1952).

Attachment theory therefore owes much to his close collaborator Mary Ainsworth and her colleagues and students, most notably Mary Main, for the subsequent mapping of systematic individual differences in attachment quality and organization (Ainsworth et al. 1978; Main and Solomon 1990). Drawing on Bowlby’s ideas about the interaction between the attachment system and other behavioral systems, most notably the exploratory system, Ainsworth devised a semi-structured laboratory observation method, called the “strange situation procedure” (SSP), which enabled examination of the organization of behavior that infant toddlers (aged 12–18 months) strike between their attachment needs and those of exploration. That is, the quality of children’s

attachments to their caregivers cannot be indexed by any single behavior, but is rather seen in the organization of behavior in relation to the caregiver (see ► [“Individual Variations in Attachment”](#)).

Ainsworth and her colleagues discovered three organized patterns of attachment. The first pattern, secure attachment, which is considered the optimal organization of behavior (e.g., highest quality) and which is shown by about two thirds of children from low risk contexts, is discussed below (see ► [“Organized-Insecure Attachment”](#) for the other two organized patterns and ► [“Disorganized Attachment and Reactive Attachment Disorder”](#) for children who cannot maintain an organized strategy of attachment behavior and children showing profound difficulties forming attachments).

Secure Attachment

Behavioral description. What is meant by secure attachment, or “a secure organization of behavior,” is best described with the (varied) behavior these children show in the SSP, where their behavior is typically characterized by a flexible balance between attachment behavior and exploratory behavior. In the SSP, secure children typically use their caregiver as a secure base from which they explore the room and the play material in the initial pre-separation episodes. Their play is typically elaborate and complex, and they tend to check back and share their experiences with the caregiver, holding up toys, smiling and vocalizing, and often seeking to involve their caregiver in their play.

Upon the entry of the stranger, secure children show varying reactions, with some children retreating to their caregiver as a safe haven, whereas others are more immediately responsive to and interested in the stranger. Indeed, four sub-patterns of secure attachment have been identified (Ainsworth et al. 1978), possibly in part reflecting differences in temperament (Belsky and Rovine 1987; Vaughn et al. 2008). Indeed, whereas secure children at one extreme can be described as “happy with distance interaction,”

at the other extreme, some secure children can be described as “happy playing on the caregiver’s lap.” However, as long as they are allowed to be in close proximity with their caregiver, most secure children eventually accept interaction with the stranger.

When the caregiver leaves the child with the stranger during the first separation, secure children again show varying reactions, with some children being happy to play with the stranger or playing independently, some children becoming distressed after a while and showing aversive signaling behavior (crying, screaming), and other children immediately displaying signaling behavior and protesting the separation, calling for the caregiver to come back.

In the two reunions with the caregiver, particularly in the second reunion episode wherein the stress is typically more pronounced, secure children who have become distressed by the separation typically approach the caregiver and/or signal to the caregiver that they want proximity and/or comfort (proximity-seeking behavior). Importantly, secure children who have become distressed are successfully soothed by this contact, so that they can eventually go back to exploring the play material. They also show that they are effective in maintaining the contact with the caregiver for as long as they need in order for the attachment system to become inactive (contact-maintaining behavior). For example, secure children protest effectively if the caregiver should try to put the child down too soon (e.g., clinging to the caregiver, turning to make closer contact), prolonging the contact to get what they need. That is, they show an ability to use the caregiver as a safe haven when their attachment system is activated. Secure children who have not become particularly distressed by the short separations tend to greet the caregiver happily, try to involve the caregiver in play, and share their experiences with the play material. That is, and addressing a common misconception, children do not have to cry following short separations (in the SSP, maximum 3 min) in order to be judged securely attached.

Secure children typically do not show marked avoidant behavior, such as turning away from and

ignoring the caregiver for a substantial amount of time in the reunion episodes (a hallmark of avoidant attachment). Moreover, secure children show limited ambivalence and resistance in relation to the caregiver in the reunion episodes (a hallmark of resistant attachment), although some secure children, particularly if distressed, can show some initial resistance. Secure children also tend to show a marked specificity in their preference for the caregiver. Even if they can be partly soothed by the stranger for a while, the caregiver is much more effective in soothing the child. Moreover, secure children who have not been particularly distressed by the separations and have played with the stranger during the separation episodes tend to interact more with and share more emotions with the caregiver than the stranger. Importantly, this description of variations in “specific” behaviors shown by secure children underscores the need to examine the “organization” or patterning of behavior and not focus solely on any individual behavior.

Predictors of secure attachment and developmental correlates. Ainsworth and colleagues found that secure children tend to have caregivers who, during the home observations, were sensitive to the children’s signals. That is, they perceived their children’s signals and responded to them in a timely and appropriate fashion. They both acted as a secure base, supporting children’s exploration, and as a safe haven, effectively comforting the children when distressed. The link between sensitivity and attachment has subsequently been supported by multiple scientific studies around the world, as well as in meta-analyses (De Wolff and Ijzendoorn 1997). Interestingly, although secure children often protest during separations in the SSP, secure children were more able to endure short separations in the home, such as if the caregiver switched rooms, and showed less negative affect during the home visits than children who were subsequently classified as insecure (including avoidant). Meta-analytical research has indicated that about two thirds of children tend to be securely attached in normative samples, with lower rates in children from high-risk groups (van IJzendoorn and Sagi 1999).

Secure attachment should not be mistaken for “dependency.” All children are dependent; what matters is if children are effectively or ineffectively dependent. Secure children, being effective in getting what they need from others, having their emotions accepted, and being taught flexible emotion regulation through constructive dyadic regulation with their caregiver(s), tend to develop many positive characteristics. Securely attached children, as a group, have, for example, been shown to be more independent in preschool, to become well-liked by their peers, to be rated as having high social competence, to be empathic, to show less behavior problems of both an internalizing and externalizing kind, and to have low levels of anxiety (see ► [“Effects of Attachment Quality and Organization”](#)).

Missing pieces and current research. Although the correlation between sensitivity and attachment is well established, meta-analytical research has failed to replicate the strong association that Ainsworth initially found, a phenomenon called the “transmission gap” (De Wolff and Ijzendoorn 1997). This may have several reasons. First, both attachment and sensitivity are hard to examine, and few studies have examined sensitivity as thoroughly as Ainsworth did, often settling for a few minutes of observation of play in a laboratory or naturalistic environment. However, the transmission gap has also yielded an interest in other dimensions of caregiving besides sensitivity. Caregiving attributes such as mind-mindedness and reflective functioning in relation to the child’s mind have been shown to predict child security over and above the effects of sensitivity (e.g., Fonagy et al. 2008). Another issue pertains to the mechanism(s) mediating the association between variations in attachment quality and subsequent development. That is, although secure attachment is consistently associated with a multitude of positive developmental outcomes (such as high social functioning), there are several hypotheses regarding the mechanism(s) mediating these associations, and it is currently unclear whether any mechanism is particularly important or if attachment quality and organization should be seen as a factor having broad effects on a multitude of such mechanisms

(see ► [“Effects of Attachment Quality and Organization”](#)). Lastly, although Bowlby argued that the attachment system is active and functional throughout life, he did not devote as much effort into its functioning in adult relationships, which are typically symmetrical (see ► [“Attachment in Adulthood”](#)).

Conclusion

Secure attachment is predicted by sensitive caregiving and is the pattern of attachment that is considered optimal (e.g., of highest quality), as seen in these children’s flexible and balanced organization of behavior in relation to the caregiver. That is, having internalized secure affective-cognitive representations of self and others (IWMs), secure children are able to use their caregiver both as a secure base from which to explore the environment and as a safe haven to return for comfort when distressed. Secure attachment is associated with positive socio-emotional and cognitive development.

Cross-References

- [Attachment in Adulthood](#)
- [Disorganized Attachment and Reactive Attachment Disorder](#)
- [Effects of Attachment Quality and Organization](#)
- [Evolutionary Foundations of the Attachment System and Its Functions](#)
- [Individual Variations in Attachment](#)
- [Infant Survival](#)
- [John Bowlby: Pioneer of Attachment Theory](#)
- [Offspring–Parent Attachment](#)
- [Organized-Insecure Attachment](#)
- [Psychodynamic Foundations](#)

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Seeking Extra-Pair Partners

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Synonyms

Adultery; Extra-Pair Copulations (EPCs); Infidelity; Non-paternity

Definition

The phenomenon whereby individuals in a socially monogamous union pursue additional sexual partners

Introduction

Biologists have long known that monogamy is rare in the animal world, especially among our fellow mammals. But biologists didn't have any idea how truly rare it is until DNA fingerprinting was applied to animals, in the 1990s. For decades it has been the received wisdom among ornithologists that 92 % of bird species were monogamous. With the advent of DNA fingerprinting, however, along with extended field studies, it became evident that social monogamy is not equivalent to sexual monogamy, i.e., that many animals seek extra-pair sexual partners while retaining their social partner.

Extra-Pair Copulations

Over time, however, a new realization dawned: social monogamy – in which a male and a female court, spend time together, and set up joint house-keeping – is not the same as sexual monogamy, i.e., limiting copulation to one's social partner. Hence the term extra-pair copulations (EPCs) was born, now a standard concept in animal behavior research, as studies employing DNA fingerprinting have revealed, time and again, that even those species that seemed devotedly monogamous were only socially so. Depending on the species, it is common to find that from 10 % to 60 % of avian offspring are not fathered by the mother's social partner (Barash and Lipton 2002).

Biologists were not surprised to find evidence that males are prone to sexual gallivanting. After all, even though the basic biology of sperm makers doesn't quite mandate searching for and when possible indulging in multiple sexual partners, it clearly inclines males of most species in that direction, simply because for males – including male *Homo sapiens* – additional mating partners means additional opportunities for fitness enhancement. What was perplexing, however, was the finding that females – even those in apparently stable domestic unions – were similarly disposed. It's just that they are more secretive about it. As a result, biologists would spend hundreds of hours carefully watching the behavior of

a mated pair without seeing any indication of sexual infidelity by the female – not necessarily because she was sexually faithful to her mate, but because she was hiding her EPCs, not from researchers, but from her social partner. Why was she doing this? For reasons not dissimilar from why socially monogamous human beings are comparably secretive when it comes to their own EPCs.

Downsides of EPCs

Evidence has accumulated from a variety of animal species that if and when the male finds evidence that “his” female has been associating with other males, he is prone to do the animal equivalent of refusing to provide child support, no longer provisioning or defending the offspring, presumably because they might not be genetically his. This pattern has been found in certain mammals (Richardson and Coetzee 1988) as well as birds (Cezilly and Nager 1995). And although there do not seem to be any data dealing explicitly with the effect of suspected adultery on divorce in human beings, common sense suggests a very close relationship.

There are remarkably little reliable DNA data on the actual frequency of human extra-pair paternity, despite the fact that such testing is now widely available. Maybe this paucity shouldn’t be surprising, because of possible reluctance on the part of most men to publicly question their wife’s fidelity. As a result, the available information tends to be biased toward circumstances (such as divorce proceedings, when child support is in dispute) in which there is liable to be higher than average extra-pair paternity. In any event, the frequency of human marriages in which the husband is not the genetic father of the mother’s children ranges from as low as 0.03 to 11.8 % (Simmons et al 2004).

Reasons for EPCs

It is one thing to understand why females – of pretty much all species – hide their EPCs from

their social partners, especially if biparental cooperation is expected when it comes to rearing offspring. More mysterious is this: given the potential costs of being caught, why do females engage in any EPCs at all? Since eggs are produced in very small numbers whereas sperm are astoundingly abundant, females very rarely need to copulate with more than one male in order to be fertilized. Biologists have identified a number of potential benefits accruing to a “cheating” female, with the specifics varying with the species and, sometimes, with individual circumstances.

Here are a few of the major fitness payoffs thus far recognized:

- Increase the genetic variety of their offspring.
- Obtain more desirable (i.e., fitness-enhancing) genes for their offspring than can be provided by their social mate.
- Obtain additional resources, notably food, from their “lovers.”
- Enhance their social status by affiliating with a male who is more dominant than their current partner.
- Purchase “infanticide insurance” by inducing other males to behave parentally toward the females’ offspring.
- Explore the potential of switching from a less desirable to a more desirable partner.

There is no reason why similar considerations (obtaining additional resources, better genes, and so forth) couldn’t motivate human females, too, although in the case of women, other factors could be involved as well – which typically are not assumed to operate among animals. These causes are all “proximate,” although they each have straightforward ultimate (evolutionary) underpinnings. Moreover, although biologists have had less reason to seek explanations for EPCs by men than by women (since the biology of sperm-making provides more than enough evolutionary rationale), the following considerations could apply to both sexes:

- Retaliating for infidelity by one’s partner
- Responding to other sources of anger with one’s partner

- Short- or long-term fascination or interest in a lover
- Seeking sexual or social gratification not otherwise available in the primary relationship

Male–Female Differences

A bottom-line message is that when sexual infidelity occurs among human beings – and whether the “infidel” is a woman or man – it is because a fundamental, biologically generated polygamous inclination (polygyny in the case of men, polyandry in the case of women) has broken through the existing monogamous social structure (Barash 2016). Not surprisingly, men consistently report higher levels of sexual infidelity in marriage than do women. This, in turn, conforms to the biology of maleness versus femaleness, and with such findings as a study that encompassed 52 different countries and about 16,000 respondents, and found that men consistently expressed interest in having more sexual partners than did women (Schmitt 2003). But a male–female difference in adultery could also be due, at least in part, to the near-universal double standard, in which men are socially encouraged to be more sexually adventurous and to seek multiple partners, in order to be seen as “real men,” whereas women who are acknowledged to be similarly inclined are often denigrated as “sluts.” Some men, as well, may be liable to exaggerate their number of infidelities, just as some women may be inclined to understate theirs.

It is pretty much a cross-cultural universal that men intimidate their spouses to refrain from extra-marital sex, punishing them – often severely and, not uncommonly, lethally – should they do so. Aside from their internal motivations, women may be most prone to “cheating” under the following circumstances:

1. When they have the support of their own relatives, which is especially likely in societies that are “matrilocal” – that is, when women live near their extended families – as opposed to “patrilocal” societies, in which following marriage, the bride moves in with her husband’s

family. Most human societies are patrilocal, which means that a wife is surrounded by her husband’s kin. This makes it easier for a man to keep tabs on her and itself facilitates a double standard (it is quite possible that patrilocality became the most common marital living arrangement precisely because it serves to discourage a wife’s infidelity, thereby reassuring husbands).

2. When wives don’t rely very heavily on their husbands for material support, protection, and assistance in child-rearing. Cross-cultural studies have found that among societies in which women get most of their sustenance from relatives, rather than from their husbands, they are more likely to have extramarital affairs and are also more prone to divorce (Flinn and Low 1986).
3. When their husband is less “desirable” than others who are sexually available, with “desirability” assessed either biologically or socioeconomically.

There is a growing body of experimental evidence suggesting that women partake of a “dual-mating strategy,” consisting of both long-term and short-term tactics. The former involves establishing a bonded relationship with a consistent partner, typically someone able to invest sufficiently in offspring and also predisposed to do so, whereas the latter calls for responding positively – especially when ovulating – to men who are literally perceived as “sexy,” which is to say, possessing good genes. Evidence for this dual strategy comes largely from a diversity of studies showing that when they are most fertile, women are especially predisposed to prefer images, sounds, and even smells arising from men who are higher in testosterone and who possess greater body symmetry – in short, who are likely to offer “good genes” (Gangestad et al. 2005).

Even though advances in contraception have enabled women to free themselves from the reproductive tyranny that had previously restricted their sexuality, it is safe to say that the great majority of women are less liberated than basic fairness would prescribe.

Change and the Future

Nonetheless, change is, ironically, the most reliable human constant, if not in our biology, then in its cultural accompaniments. In February, 2015, South Korea's Constitutional Court – citing the country's changing sexual mores and a growing emphasis on individual rights – struck down a law that for more than six decades had made adultery a criminal offense, punishable by up to 2 years in prison. Share prices for a leading Korean condom manufacturer, *Unidus*, immediately rose by nearly 15 %, and *Hyundai Pharmaceutical*, which markets so-called morning-after birth control pills, rose in value by nearly 10 %.

Conclusion

Individuals – whether male or female – who are part of a socially monogamous relationship not uncommonly seek extra-pair partners. The adaptive significance of this behavior differs for males and females, with the fitness payoff for males primarily involving additional opportunities for fathering offspring, whereas for females, the evolutionary payoffs are more diffuse but nonetheless real, notably including access to resources and seeking “better” genes for one's offspring.

Cross-References

- [Sex Differences](#)
- [Sexual Conflict](#)

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Segments

- [Phonemes and Symbols](#)

Selected Effect

- [Biological Function](#)

Selection

- [Attention and Memory](#)

Selection by Consequences

- [Selectionist Models: Implications for Behavior](#)

Selection for Cooperative Relationships

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Synonyms

Altruism; Collaboration; Helping; Prosocial behavior; Reciprocity

Definition

Individuals (or groups) working together for a mutual benefit.

Introduction

“Many of the benefits sought by living things are disproportionately available to cooperating groups” (Axelrod and Hamilton 1981, p. 1391)

Cooperation involves individuals (or groups) working together for a mutual benefit, often at an initial cost to each participant, although the benefits from cooperation ultimately outweigh the costs to individuals. Cooperation is associated (conceptually and empirically) with altruism – behavior in which an individual forgoes a benefit to assist another. Some degree of altruism is necessary (at least initially) for cooperation to occur. To cooperate, an individual must initially give up a benefit. Altruism becomes cooperation when two or more individuals join in giving up benefits for a common goal, which they typically perceive as greater than the cost of the benefits they gave up. Our focus here is on cooperation among humans – in particular, the selection pressures (ultimate causes) that stimulated cooperation among our ancestors, the mechanisms (proximate causes) that enable cooperation to occur, and the cues people use to select other individuals as cooperative partners. What is

unique about human cooperation is that humans cooperate *widely* with other humans to whom they are *not related*. This ability to cooperate with non-kin has been critical to the complex division of labor, the widespread growth of civilizations and nation-states, large organizations, and national and international economic systems.

Selection Pressures for Cooperation

Throughout the course of human evolution, people faced selection pressures favoring interdependence and cooperation (Tomasello et al. 2012). Climate change in Africa about 2.5 to 3 million years ago likely created resource pressures on early hominids by reducing jungle and increasing savannah areas (Handwerk 2014). The capacity to cooperate probably became instrumental in helping hominids adapt to these patchier resource environments (e.g., by making foraging more successful). As humans left Africa and began to populate the globe, they encountered different environments than they had grown accustomed to, again requiring increased cooperation to survive. With the spread of humans, there was undoubtedly greater competition from other groups, adding further adaptive pressure for cooperative traits and institutions. These pressures most likely created feedback loops reinforcing cooperative behavior for both individual and group survival.

Mechanisms for Cooperation

Many species engage in cooperation among kin, which is commonly known as *kin selection* (Hamilton 1964). An allele promoting helpful behavior toward kin, even at a cost to one's self, could readily evolve and remain evolutionally stable. By helping relatives (who share one's genes), an individual can get more of his or her genes into the future. Thus, individuals should be motivated to cooperate with kin to maximize their inclusive fitness.

Cooperation among non-kin has been more difficult to explain, because it is usually in the actor's best interest to behave selfishly when interacting with non-kin. *Reciprocal altruism* (Trivers 1971) provided a plausible mechanism to explain helping behavior among unrelated individuals: People help one another when they expect that the behavior will be returned in kind. Two basic forms of reciprocity have been described. The simplest form, direct reciprocity, is a tit-for-tat cooperative strategy in which two individuals exchange cooperative acts and cease cooperating if either party defects (Axelrod and Hamilton 1981). In contrast, indirect reciprocity involves cooperation based on reputation (Nowak and Sigmund 2005). Reciprocation is indirect when it is given by someone other than the initial beneficiary. In this case, individuals help those who are known to have been helpful to others. Thus, individuals must cultivate a reputation for being cooperative if they hope to receive the benefits of cooperation.

Circumstances in which cooperation is most critical (e.g., natural disasters, wars, and famines) are those where reciprocity-based cooperation is least likely to occur. Why help someone in these circumstances, because it is unlikely that he or she will be around to return the favor? To address this problem, the theory of *strong reciprocity* suggests that humans are predisposed to cooperate and punish non-cooperators even at their own personal cost (Gintis 2000). Thus, a trait of "cooperativeness" must have evolved and been selected for so that humans are inclined (some more than others) to be cooperative.

Cooperators could have been taken advantage of by selfish individuals within their groups, making selection for cooperativeness unlikely at the individual level. Therefore, prosocial traits and behaviors must have been beneficial at the group level. Although cooperativeness can be costly to *individuals* and may be disadvantageous within groups (i.e., individual selection), cooperation increases the fitness of *groups* relative to other groups (i.e., group selection). This is the logic of *multilevel selection* theory (Wilson and Wilson 2007). Cooperation allows groups to outcompete less cooperative groups, making

cooperative individuals more likely to survive and reproduce. Integrating the perspectives of strong reciprocity and multilevel selection, Bowles and Gintis (2011) suggest that a genetically based predisposition to cooperate most likely coevolved alongside social institutions and cultural norms that reduce within-group competition (e.g., food sharing, monogamy) and help maintain cooperation, making groups that adopted those institutions and norms more successful than those who did not.

The transition from kin selection to reciprocal altruism to large-scale cooperation among non-kin is not well understood, although probable paths have been proposed (e.g., Tomasello et al. 2012). One possibility is that as kin-selection consolidated among early humans, associated cognitive and emotional mechanisms facilitating cooperation developed apace (e.g., prosocial emotions). These psychological mechanisms then might have generalized to small-scale cooperative practices among non-kin (e.g., cooperative breeding). As cultural learning and institutions (e.g., religion) became more widespread, these too reinforced cooperative sentiments and practices.

Identifying and Selecting Cooperative Partners

Cues signaling trustworthiness are important in selecting partners who are likely to cooperate. Trust cues can be categorized as personal or situational (Thielmann and Hilbig 2015). *Personal trust cues* are characteristics of a potential partner that may provide information about his or her trustworthiness. These include aspects of outward appearance, reputational information, and social category information (e.g., ingroup versus outgroup). *Situational trust cues* are features of the situation that may make someone more or less trustworthy (e.g., temptation to betray, sanctions for betrayal).

People use readily accessible verbal and non-verbal cues to judge others' trustworthiness (i.e., personal trust cues). For example, people readily infer others' (un)trustworthiness based on aspects of their faces, including its basic features or

structure, emotional expressions, and similarity to the judge's own face. Altogether, research suggests that faces are judged more trustworthy when they look happy (rather than angry), feminine (rather than masculine), mature (rather than young), and similar to the target's own face (Todorov et al. 2015). All of these facial cues appear to have adaptive significance. For example, a similar face may be a cue of kinship, a happy face may suggest that someone is approachable, an angry face may suggest that someone has harmful intentions, and a wide, masculine face may suggest that someone has the physical stature necessary to carry out their ill-intentions. Although people make trustworthiness judgments based on facial cues quickly and show high agreement in their judgments, these judgments tend to be inaccurate (Todorov et al. 2015).

People may also use reputational and social category information as personal trust cues. Individuals are more trusting of people with positive reputations than those with negative reputations (Thielmann and Hilbig 2015). Reputational information about someone can be acquired directly by observing their behavior as well as indirectly via gossip. Additionally, people are more trusting and cooperative toward strangers who are ingroup members. Thus, cues that signal ingroup membership should make someone a more attractive cooperative partner (e.g., clothing, tattoos, tribal scars).

When selecting a cooperative partner, it is wise to consider not only characteristics of the partner, but also features of the situation that may impact his or her trustworthiness. Thus, *situational trust cues* include characteristics of the social context that may make someone more or less trustworthy. The two most well-studied situational trust cues are temptation to betray and sanctions for betrayal (Thielmann and Hilbig 2015). Temptation to pursue selfish interest at the expense of mutual interest is inherent in cooperative situations, and cooperation becomes less likely the more the benefits of betrayal outweigh the benefits of cooperation. On the other hand, sanctions for betrayal (e.g., punishment or diminished reputation) can be expected to elicit more trustworthy behavior and cooperation.

Conclusion

Cooperation helped our ancestors overcome threats to survival and is a large part of the reason why *Homo sapiens* has flourished as a species. Researchers have proposed several complementary reasons why cooperation may be so widespread in humans. Ultimately, we cooperate to promote our own genes, and we do so by helping our kin, cultivating mutually beneficial social exchanges, enhancing our reputations, and because the momentum of genetic and cultural evolution compels us to. These mechanisms bear on our everyday psychological tools for identifying and selecting cooperative partners who are likely to help us achieve our goals.

Cross-References

- [Cooperation](#)
- [Evolution of Cooperation](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)

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Selection in Relation to Sex

► Charles Darwin: Theory of Sexual Selection

Selection Pressures as a Function of Age

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Synonyms

Hamilton's forces; Scaling factors

Definition

The strength of natural selection on mortality and fecundity varies across ages.

Introduction

The insight that natural selection should be weaker with age was originally proposed by Ronald A. Fisher (1930) in *A Genetical Theory of Natural Selection*. In this groundbreaking book, Fisher fused Charles Darwin's theory of natural selection with Gregor Mendel's theory of particulate inheritance – a fundamental insight in the modern synthesis in biology. Fisher, however, did not fully explore how the force of selection differs across ages. That exploration would have

to wait for decades, when biological theorists (Medawar 1952; Williams 1957) realized that weakening in the force of selection with age could explain how evolution not only could – but should – result in aging: the decrease of fecundity or increase in mortality with age. Soon thereafter, William D. Hamilton (1966) provided theoretical clarity on the issue by explaining mathematically how the strength of selection varies across age groups. Age-dependent selection continues to be a topic of considerable interest, largely in research on aging and life-history theory, which addresses how organisms adapt to unpredictable versus stable environments.

Historical Origins

Ronald A. Fisher (1930) and John B. S. Haldane (1941) first proposed that the strength of selection should vary depending upon age, and more specifically that it should be weaker as adults get older. Fisher (1930) suggested that the reduction of strength of natural selection with increasing age results from the related reduction in reproductive value – the number of offspring an organism is likely to have summed across the current age and all later ages. Reproductive value is at its maximum value until reproduction begins, at which point it reduces throughout adulthood.

Age-Related Selection and Aging

Inspired by Fisher's insight about change in reproductive value over the lifespan, the biologist Peter B. Medawar (1952) made an early attempt to explain the evolution of aging in which he argued that selection should act less at later ages because of the cumulative effect of mortality across ages. That is, by assuming that death rates and reproduction rates are constant across age, a population will have a demographic structure that is comprised of more younger than older adults, with smaller and smaller proportions for older and older age groups. In this demographic structure, younger adults will produce a larger proportion of offspring each year than older members of the

population – and therefore younger individuals will contribute more genes to the next generation – resulting in stronger evolutionary selection upon younger than older individuals. Medawar therefore argued that genes whose effects were expressed earlier in life would experience stronger selection, whereas genes expressed very late in life would experience little to no selection. Medawar observed that wild animals infrequently live so long as to suffer from aging, so selection would be unable to eliminate harmful mutations that would be expressed at ages later than death usually occurs in the wild (see also Haldane 1941). The resulting buildup of deleterious mutations would cause aging when expressed in individuals living in safe environments, such as in a lab or a zoo.

George C. Williams (1957) also attempted to explain aging based on age-specific strength of selection. He argued, in particular, that strong selection early in life but weaker selection later in life would result in populations carrying pleiotropic genes – specifically genes with beneficial effects early in life but detrimental effects later in life. The harmful effects of pleiotropic genes in late life, Williams argued, would result in aging.

Building largely on the work of Fisher (1930) and Williams (1957), William D. Hamilton (1966) made explicit the mathematics underlying the intuitions of others about how the strength of selection varies across ages and therefore results in aging. In particular, Hamilton improved upon Fisher's proposal that evolutionary forces work on reproductive value. For example, Hamilton showed that a population that is decreasing in size fast enough has stronger selection on older than younger individuals (Charlesworth 1980). Hamilton demonstrated mathematically how the strength of natural selection on survival and fecundity varied across ages during the life cycle.

Hamilton's Forces of Natural Selection

Hamilton's (1966) analysis identified two scaling factors for how the strength of selection changes across the lifespan: a survival factor and a

fecundity factor. Rose and colleagues (Rose et al. 2007, p. 1265) referred to these factors as "Hamilton's Forces of Natural Selection," equating their importance for biology with Einstein's contributions for physics. The survival factor looks at "the fitness impact of an individual's future reproduction" across different ages (Rose et al. 2007, p. 1266). Its value is at its maximum of 1 before sexual maturity, 0 once reproduction ends, and decreases with age between those values. This factor looks at how much of an effect natural selection can have on the survival probability of an age group. For example, natural selection has a strong effect on the survival probability of prereproductive ages and no effect on the survival probability of ages after the cessation of reproduction (the 0 value once reproduction ceases), should such ages exist in a species. As per Rose and colleagues (2007), this force "has to decline throughout adult life until the last age of reproduction, after which the force of natural selection is zero for all remaining ages" (p. 1272). The second factor is age-specific fecundity. As per Rose and colleagues (2007), "the force of natural selection acting on fecundity . . . declines with age until the last age of survival in the population's evolutionary history" (p. 1272). That is, the second factor evaluates how much natural selection can influence the fecundity of different age groups. A common result is that selection can strongly influence the fecundity of younger age groups but has less effect on the fecundity of older age groups.

Hamilton's forces have some notable limitations and implications. When describing the death rates of humans, Hamilton (1966) suggested that the death rates should asymptote as the curve approaches the end of reproductive years. However, in humans the curve goes too far to the right (people live too long), especially for women. Hamilton agreed with Williams (1957) that the most likely explanation is parental care provided by mothers and grandmothers. This explanation is now referred to as the "grandmother hypothesis" and is also used to explain human menopause (Lahdenperä et al. 2004). By helping the survival and reproduction of kin in late life, selection would continue to work on mortality late in life

and thereby increase the lifespan. Thus, although he did not incorporate parental care (or grandparental care) into his formulas for the strength of selection across ages, Hamilton acknowledged such care as another potential way for selection to act on different age groups.

Hamilton also addressed why infant mortality is so high in humans. He suggested that in general selection should drive deleterious effects to be expressed later in life (when they are less detrimental to fitness). The exception in the human case arises because offspring with deleterious genetic effects prohibit parents' fitness and the children's own inclusive fitness (the genes it shares with relatives, another idea for which Hamilton provided the definitive mathematical statement; Hamilton 1964). For example, Hamilton suggests that a child who dies at 10 years of age wastes more parental effort than one that dies soon after birth or even soon after conception. For children with a gene that is likely to result in death, by dying earlier in life the child can be replaced by another sibling and thereby increase inclusive fitness.

Finally, note that both forces of natural selection can have declined to the point of being zero, but that survival and fecundity rates themselves need not also be zero. This means that at sufficiently old age, aging itself stops – that is, mortality rates no longer increase – and fecundity rates no longer decrease (Rose et al. 2007). Given that both forces of natural selection are strong only in early life and eventually reduce to zero, natural selection should only result in somatic adaptations that are beneficial either for young individuals or for individuals across all ages; that is, bodily adaptations for late life are not expected (Rose et al. 2007).

Evidence

Charlesworth's (1980) review found substantial evidence supporting age-specific effects of genes that are consistent with Hamilton's forces, but some anomalous findings as well. He considered five aspects of cross-species comparisons. First, strong supporting evidence is found for the

presence of aging in species which separate soma and germ cells. Second, correlational evidence supports Hamilton's scaling factors, such as species with greater external mortality – death due to uncontrollable dangers such as predators and disease – also aging faster. Third, species such as large reptiles, amphibians, and fish in which fecundity increases with age can live very long lives, as Hamilton's theory predicts. Fourth, aging should begin immediately after reproductive maturity because of one of Hamilton's scaling factors is constant before that point then decline. This is consistent with the reduced survivorship of humans immediately after puberty, the point in the lifespan of humans with the lowest mortality. However, the high juvenile mortality rates in many species are not anticipated by this theory. Fifth, for species in which reproduction ends before death, selection should allow deleterious genes to build up, but human females live after menopause. As mentioned above, Hamilton suggested this might be because they gain inclusive fitness by caring for children and grandchildren.

Implications

Diverse consequences result from the unequal strengths of selection across the lifespan and its relation to change in population size. One of the most important is that natural selection results in aging (e.g., Williams 1957). Another set of consequences are embodied in life-history theory, the idea that species (and individuals) that face relatively high rates of external mortality emphasize earlier-life reproduction at the cost of investing in growth, bodily maintenance, and parental investment (Del Giudice et al. 2015). This shorter-term strategy makes sense in unstable environments where long-term investments are unlikely to pay off.

Conclusion

Although Fisher (1930) had the insight that selection weakens as adults age, a full understanding of

how natural selection on mortality and fecundity varies across ages did not arise until theorists attempted to explain how evolution would result in aging (Medawar 1952; Williams 1957). In particular, Hamilton's (1966) mathematical treatment of the strength of selection not only provided a firm ground for addressing the evolution of aging, but laid the foundation for the major evolutionary perspective provided by life-history theory.

Cross-References

- Age
- Fisher's Reproductive Value
- George C. Williams
- Life History Theory
- Ronald Aylmer Fisher
- Senescence
- Theory of Senescence
- William Hamilton

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Selectionist Models: Implications for Behavior

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Synonyms

Action; Consequent; Context, Instrumental Behavior; Contextual Behavioral Science; Evolutionary Behavioral Psychology; Functional Behaviorism; Movement; Operant Behavior; Selection by Consequences

Definitions

Instrumental Behavior	Coordinated movement of a whole living organism that, in the genetic and/or experiential history of the organism and the presence of cues correlated with the presence of a specific class of adaptive problem, caused systematic (predictable) environmental change.
Behavior	The “coordinated responses of whole living organisms to . . . stimuli” (Dugatkin 2014, p. 7).

Introduction

“If you root yourself to the ground, you can afford to be stupid. But if you move, you must have mechanisms for moving, and mechanisms to ensure that the movement is not utterly arbitrary and independent of what is going on outside.” So opens Patricia Churchland's classic (Churchland 1989) (p. 13) *Neurophilosophy*. Although the

truth of this is obvious, all too often Psychologists forget it. In seeking the short-term gains of a science of the mind, the field pays long-term costs of isolating Psychology from the well-established natural and life sciences and from factors driving evolution both in phylogenetic and ontogenetic time. Consider the following exchange between Endel Tulving and Henry L. Roediger, III (Roediger III 2004),

It is quite clear in 2004 that the term ‘psychology’ now designates at least two rather different sciences, one of behavior and the other of the mind. They both deal with living creatures, like a number of other behavioral sciences, but their overlap is slim, probably no greater than psychology or sociology used to be when the world was young. No one will ever put the two psychologies together again, because their subject matter is different, interests are different, and their understanding of the kind of science they deal with is different [We are aware that this is an argumentum ad ignorantiam]. Most telling is the fact that the two species have moved to occupy different territories, they do not talk to each other (any more), and the members do not interbreed. This is exactly as it should be. (Passage quoted in Roediger 2004)

The purpose of this chapter is to highlight a long-term cost Evolutionary Psychology pays by isolating itself from Behavioral Psychology and the long-term benefit obtained by embracing it.

We can say, like primitive man, that the existence of the mind is to be inferred from human (or animal) activity; we can say, strange as it may appear to the Behaviorist, that mind is itself, and always has been, simply a theory of behavior (Hebb 1934).

Solving adaptive problems requires functional action. Those actions include both private (observable only by the actor) and public (observable by others) behaviors. In a sexually reproducing species, taking action is necessary for genes to pass from one generation to the next. Given that fact, it is obvious that selection pressures operate *directly* on the *functional efficacy* of behavior when an organism faces adaptive problems. It is equally obvious that evolution by Natural or Sexual Selection does not occur without differences (variation) in how well behaviors solve specific classes of adaptive problems. Finally, because behavior is necessary to realize differential reproductive success, understanding

the organization of behavior and the forces that shape it is an essential component of understanding biological evolution.

In light of the facts above, a separate entry on the “implications for behavior” is somewhat baffling because, properly structured, Evolutionary Psychology (EP) focuses equally on the brain, cognition, the organization of behavior, and proximate/ultimate models of the relations among them. Orthodox Evolutionary Psychology, however, has married itself to a cognitive psychology that, while investigating matters of mind, ignores the organization of behavior.

This marriage of Evolutionary Psychology to this form of cognitive psychology rests on the assumption that “Natural selection does not operate on behavior per se” (Tooby and Cosmides 2016, p. 15). The marriage additionally assumes the existence of (physically-instantiated) cognitive-developmental *programs*, best characterized through information-processing theory, that generate unspecified but flexible and plastic adaptive behaviors. These assumptions lead Evolutionary Psychologists to focus on descriptions of the algorithmic structure of hypothetical *adaptive programs* composed of complex sets of instructions and to consider behavioral-level descriptions inadequate to capture species-typical adaptations (Tooby and Cosmides 1992).

In contrast, following James’ (1907/2013) and Peirce’s (1905) *pragmatic* approach to scientific psychology (see Baum 2017), we argue that (1) the information-processing approach to cognition is at best an awkward way to describe adaptive behavior as functionally contingent on ecological contexts (see Gladden and Jacobs 2019), (2) an information-processing approach to cognition, which is based on what philosophers call *naïve realism*, awkwardly assumes the (predesigned) “...existence of informational categories in the environment” (Edelman 1987, p. 43), independent of a receiver that has “...computational programs in the brain that can produce a broad range of plastic adaptive behavior” (Edelman 1987, p. 43) in response to those hypothetical (fictional?) informational categories. In so doing, current Orthodox EP overtly

rejects (and even disparages) a “natural” theoretical partner, a partner based on thoroughgoing *selectionist* theory.

Orthodox EP has, at its core, Darwin’s three fundamental principles: Trait variation, differential reproductive success, and trait inheritance. The theory does not specify mechanical cause-and-effect relations that occur in proximate time. Instead, the theory is pragmatic and statistical, noting trends that occur typically over many generations (i.e., the aggregate effects of many instances of mechanical causes).

Our current understanding of the organization of specific behavioral types (classes) makes use of the same principles. According to Orthodox Behavioral Theory, the organization of instrumental behavior rests on constrained behavioral variability (base rates), differential success (e.g., reinforcement; punishment), and inheritance (changes in probability of the behavioral variant exhibited resulting from experiential history). As with Darwinian Theory, the principles operate pragmatically and statistically (probabilistically), not mechanically. Although the theory may serve to guide those interested in proximate interactions that produce variability, differential success, and inheritance, the mechanisms governing them remain outside of the current domain of the theory.

Adopting such a view opens Evolutionary Psychologists to a much broader perspective. For example, examining the basis of “decision making” (exhibiting one form of behavior over another) in terms of experience with ultimate *and* proximate adaptive problems or the degree to which a specific form of instrumental behavior “solves” a complex of adaptive problems (bringing the behaving organism closer to differential reproductive success) or the proximate/ultimate adaptive costs and benefits of exhibiting one form of behavior over another. Answers to questions such as these, of course, will be found in the phylogenetic history of the organism and some within its ontogenetic history, all of which can be done without dulling Occam’s Razor by importing extraneous ill-specified theoretical terms or structures.

As with orthodox EP, orthodox (radical) Behavioral Psychology does not attempt to specify hypothetical “internal” or “external” proximate *mechanisms* because each is a descriptive science, one that does not make distinctions between internal (private) and external (public) events. Both Behavioral and Evolutionary Psychology reject dichotomies that divide the causes of behavior as if those located in the organism’s internal environment differ in some fundamental way from those located in the organism’s external environment. Both recognize that all well-organized behavior results from interactions of organisms with environments. Both acknowledge that extant behavior results from a relatively long evolutionary history and a relatively short developmental history of successfully dealing with adaptive problems.

It is of some interest that critics accuse both of attributing behavior solely to internal causes (EP) OR external causes (Behavioral Psychology). Characterizing a behavioral approach as blank-slate like because it, “. . .proposes conditioning mechanisms that apply to all situations” (Tooby and Cosmides 1992, p. 37) or asking, “Does the mind consist of a few, general-purpose mechanisms, like operant conditioning, social learning, and trial-and-error induction. . .?” is a mischaracterization.

The orthodox study of behavior qua behavior makes no assumptions about “general purpose” or “content independent” mechanisms *at all*. Instead, it studies how the organization of behavior changes in light of available behavioral variation, differential behavioral success, and inheritance of “successful” behavioral organization relative to the suite of extant adaptive problems. In short, Behavioral Psychology studies behavioral evolution in ontogenetic time (Skinner 1981).

Deconstructing a Common Misconception

B.F. Skinner (1966, 1981) was a pragmatic evolutionary-selectionist thinker who rejected the blank slate view and equipotentiality assumptions:

No reputable student of animal behavior has ever taken the position that the animal comes to the laboratory as a virtual tabula rasa, that species' differences are insignificant, and that all responses are about equally conditionable to all stimuli. (Skinner 1966, p. 1205)

From a pragmatic perspective, useful descriptions are done at various levels of analysis, without being “incoherent” about the (currently unknown) neuro-cognitive mechanisms. Baum (2017) answered a common complaint about the modern Behaviorists' assertion that many mentalistic terms are both fictional and failures as explanatory constructs:

A common response to this argument is to suggest that attitudes, beliefs, wishes, and the like exist as things in the brain. The present level of understanding of the brain, however, allows no such assertion. Perhaps someday the working of the brain will be well enough understood to shed light on the mechanisms underlying studying for an examination or robbing a store, but that day appears to lie far in the future, if it will ever arrive at all. Behavior analysis needs to wait on discoveries about the nervous system no more than physiology needed to wait on discoveries about biochemistry. Nowadays cell function is often explained with biochemistry, but physiologists understood cell function with concepts like membrane, osmosis, metabolism, and mitosis before chemists were any help at all. Similarly, behavior analysis can understand behavior at the level of interaction with the environment without any help from neurophysiologists. Indeed, when help from neurophysiologists is forthcoming, behavior analysts will have described the phenomena that could be explained further by reference to bodily mechanisms.

By the same argument, behavioral analysts understand behavioral organization at the level of interaction with functional classes of adaptive problems without necessary help from information-processing theorists. Much like Evolutionary Psychologists, modern Behavioral Psychologists focus on creating theoretically useful descriptive concepts that serve as elements in a descriptive, predictive, and useful scientific description of behavioral organization and how it evolves.

A Natural Relation Between Modern Behavioral and Evolutionary Theory

Accepting a Darwinian/selectionist view permits both modern Behavioral and Evolutionary

Psychologists to consider overt (e.g., instrumental) and covert (e.g., remembering, planning) behavior as plastic phenotypes subject to pressures exhibited by short- or long-term adaptive problems. In so doing, a whole array of selectionist theory and technique becomes available to study the full gamut of behavioral, physiological, cognitive, and emotional traits from a common and well-integrated perspective. Moreover, the apparently natural relation between Modern Behaviorism and Evolutionary Psychology provides the EP with a view that permits these plastic phenotypes to lead evolution – as factors that contribute to the variability so necessary for the development of novel traits, to new directions of change, and thereby to influence the course of evolution (see West-Eberhard (2003), for a comprehensive review).

For Evolutionary Psychologists interested in either short- or long-term evolution, modern Behavioral Psychology offers a relatively well-integrated set of descriptive theories that permit deep thinking about the evolutionary history and significance of processes influenced by extant adaptive problems presented by the environment. Indeed, Pontes et al. (2020) have provided a striking demonstration of this principle. They began with self-replicating, nonlearning, immobile digital organisms within environments that contained adaptive problems (trail nutrients) promoting the evolution of (1) navigation and (2) associative learning. The “organisms” were equipped with three familiar characteristics: they reproduce passing on any evolved traits to their offspring (trait inheritance); the process of passing on these traits could involve random mutations (variability), and individual fitness depends on how well the organism solves extant adaptive problems (differential reproductive success). Assuming that associative learning is a *phenotypic* characteristic of behavior that may be described or implemented independent of a specific set of mechanisms, these authors demonstrated that the original sessile ancestors evolved to use trail nutrients as cues, that behavior evolved from preexisting behaviors in a predictable sequence, and that a specific cognitive structure evolved depending on the stability of

adaptive problems (and solutions) that the digital organisms could exploit. Adaptive problems that remain stable across generations produced reflexive (“instinctual”) behaviors; adaptive problems that varied across phylogenetic time but remained stable in ontogenetic time built upon such reflexes and led to the evolution of two forms of associative learning. In addition, a basic “value system” appeared to evolve that permitted associative learning by gauging experience as positive (reinforcement or benefit) or negative (punishment/penalty or cost) feedback for instrumental behavior. In each case, behavior was a fundamental part of the evolution of higher-level cognitive traits.

But What About the Brain and Information Processing?

The late Gerald Edelman (1987, 1992) argued that selectionist approaches to brain development and function (“Neural Darwinism”) outperform information-processing (IP) approaches at both proximate (mechanistic) and ultimate (statistical) levels. Edelman sees information-processing approaches as failing to account for perceptual categorization, in part, because they implicitly assume an organism is *instructed* by *preexisting* categories of information that necessarily exist external to the individual and independently of its perceptual machinery. “Processors of information,” Edelman (1987) writes, “...must have information defined for them *a priori*” (p. 43), just as computers demand clarity, precision, and explicitness (Pinker 1997/2009) to process information reliably. In other words, if the brain works by processing external information, that external information must already be organized for objectively “meaningful” perceptual categorization, independent of the individual interpreter.

Assumptions that divide the hypothetical causes of behavior into classes that exist external to the organism (“information”) and those that exist internally (algorithmic “programs”), information-processing is based in philosophical realism rather philosophical pragmatism (Miller 2016). Evolutionary psychologists might imagine

that selection processes created a complex set of internal “programs” that enable organisms’ brains to respond to adaptively relevant categories of information effortlessly. But “At one stage or another of such models...,” Edelman writes, “...one sees evidence of typological thinking or essentialism – the positing of prior categories either in the environment or in the brain or in both” (p. 43).

Having identified information-processing models of brain function as instructionist and essentialist, Edelman (1987) uses evidence drawn from cognitive psychology to argue that perceptual categories are neither fixed nor closed, and, given that information-processing models of brain function require both, these models must be wrong. He notes three major features of perceptual categorization that he regards as incompatible with information-processing models: First, he describes evidence that perceptual categories are not veridical, but rather are adaptive and modifiable by context. “The very same object,” he notes, “may be classified differently at different times [e.g., a table may be used for eating in one context and as a dance floor in another], and an animal may use different means to classify that object at different times [e.g., the table may be used as a bedding area at another time]” (p. 30). Second, Edelman notes that perception involves the capacity to generalize category membership on the basis of only a few examples. Referring to Herrnstein’s (1979, 1985) work demonstrating such an ability in pigeons, Edelman argues this capacity must be independent of language. A third feature of perceptual categorization that Edelman claims is incompatible with an information processing view of perception is that, for most perceptual categories, the classical view of category “representations,” as defined by a precise list of necessary and sufficient features (e.g., a grandmother must be a female and be a parent of a parent), does not account for how people classify entities or events. Most perceptual categories are polymorphous sets, where context affects the contents of the categories. To qualify for membership in such a set, an element must satisfy a specified number, but not all, of the rules governing membership in the category.

Edelman concludes that these three features of perception "...together strongly challenge any logic-based or 'information driven' explanation of the data" (p. 30). He argues that the evidence shows that perceptual categories are created only *after* environmental signals are received, because of evolutionary selection and/or because of experience. Therefore, he concludes, the necessary a priori code assumed by information-processing models cannot exist.

Edelman sees a clear analogy between perceptual categories and the Darwinian view that species are changing and adaptable entities rather than the fixed categories of the essentialist. Noting that computers and other electronic devices must be precisely wired to function properly, he argues this variation "...would doom any equivalent parallel computer to produce meaningless output even with the best of error correcting codes" (p. 42). In other words, due to the environment being "unlabeled" (undifferentiated), contextualized, and because of variable and novel environmental changes, an organism with evolved information processing machinery would not produce appropriately flexible adaptive behavior. Instead, Edelman sees this variability as precisely what would indicate a machine that is, through behavior, tightly tied to both recurrent and variable adaptive demands, operating through processes governing differential reproductive success rather than that of an information processing machine.

But What About Cognitive Psychology and Information-Processing?

In his concern for with what goes on in the [organism's] mind, Tolman has neglected to predict what the [organism] will do. So far as the theory is concerned, the [organism] is left buried in thought. Guthrie (1935), p. 72
...it behooves a so-called 'cognitive theorist'...to explain how his intervening cognitive and motivational variables ever issue into actual behavior... Tolman (1955), p. 315

Information processing is a useful tool that may well describe important characteristics of actions such as remembering, perceiving, or feeling,

which, in the cognitive literature, bear category names like memory, perception, or emotion. The user of such a tool, however, runs a risk of reaping small short-term benefits of popular description at the large cost of theoretical coherence, scientific integration, and the benefits of cross-boundary scientific cooperation. Put another way, information processing may provide cognitive psychology with a parochial view, a light that shines brightly on specific modes of description but a light that fails to illuminate the whole contextualized broader picture: the coordinated organization of behavior, cognition, brain, and the evolutionary history of the species under study.

One problem with light shone on a specific target is that it produces biases, leaving too much in the dark. There is a large cognitive literature on implicit biases, for example, almost none of which asks, "How would a system of this form improve the differential reproductive success of our ancestors?" Likewise, the massive cognitive literature examining remembering fails to ask, "How does remembering, acting in these ways, enable organisms to out-reproduce their neighbors?" Without an overarching guidance and constraint both from the statistical properties of a central theory (i.e., selectionist theory) *and* mechanical properties of the theory underpinning it (Anatomical and Physiological theory), cognitive psychologists remain free to characterize or mischaracterize the systems that evolved to in response to selective pressures and that organize behavior in a way that permits evolution to proceed.

Among Evolutionary, Behavioral, and Cognitive psychology, modern Cognitive Psychology appears to be the odd man out. Both Evolutionary and Behavioral Psychologists use deeply related selectionist models to account for the organization of directly measurable (e.g., instrumental) and indirectly measurable (e.g., cognitive) behavior. In contrast, modern Cognitive Psychology uses an informal version of "information" processing theory to account for the behavioral organization they infer (e.g., reasoning, acquiring, consolidating, storing, retrieving "information," etc.) and appear to reify at least some of these hypothetical constructs (e.g., memory, acquisition, consolidation, storage of information).

Conclusion

EP and modern Behavioral Psychology are both pragmatic approaches that rely on descriptive selectionist models to account for behavior. Contrary to claims, both approaches reject a “blank slate” view of organisms’ inheritance. Both approaches reject the false dichotomies of nativism versus environmentalism and of internal versus external causes of behavior. In contrast, modern Cognitive Psychology embraces an instructionist (antiselectionist) information-processing approach and is grounded in a philosophical realism that assumes we can meaningfully divide the proximate causes of behavior between “prearranged” external informational categories and internal information-processing programs (complex sets of instructions instantiated in the brain) that enable the brain to interpret those hypothetical environmental categories reliably and correctly. EP needs to bring a most necessary ingredient of reproductive success-behavior-back to the center of the field to have a selectionist partner at the proximate-ontogenetic level to complement its selectionist approach at the ultimate-phylogenetic level. It is time for a productive reconciliation between two selectionist approaches EP and contextual Behavioral Psychology to create an Evolutionary Behavioral Psychology that includes an essential component of evolution, that of behavior.

Cross-References

- [Blank Slate, The](#)
- [Information Processing and the Interdisciplinary Perspective](#)

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Selective Attending

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Synonyms

Alternating attention; Controlled attention;
Directed attention; Divided attention;
Executive attention; Sustained attention

Definition

Concentration on certain stimuli in the environment and not on others, enabling important stimuli to be distinguished from peripheral or incidental ones (APA [n.d.](#))

Introduction

Theories and models of attention differ in a number of ways, as they attempt to explain how and when an individual processes the physical and semantic aspects of their environment. Early selection models of attention suggest that stimuli pass through a filter before they can be attended to and processed for meaning. Broadbent (1958) investigated this idea of early selection by using a split-span, or dichotic listening paradigm. In the dichotic-listening paradigm, participants are presented with two different auditory stimuli (one in each ear) at the same time and are instructed to attend to one or both of the stimuli. Afterward, they are asked about the content of either the message they were asked to attend to or the message that they were told to ignore. Broadbent found that participants had increased accuracy when asked to recall stimuli presented in the same ear than when asked to recall stimuli presented in each ear, suggesting that the information was filtered based on physical characteristics of the stimuli (such as pitch, direction, or the

ear in which the information was presented). According to this model, stimuli that are presented are held in a preattentive state and must be either selected for relevance and processed for meaning, or filtered out as irrelevant. All semantic processing of the stimuli takes place after being filtered and selected for attending. In essence, the information selected has no meaning during the selection process.

However, this model must be an incomplete explanation. Cherry's (1953) work found that participants receiving stimuli in both ears, attending to one message in one ear, were able to detect their name from the unattended ear. This is defined as the "cocktail party effect": the ability to detect significant stimuli in a multi-talker situation. This unattended-to information gained attention and was processed for meaning, which contradicts the idea of selection based on basic characteristics, rather than by meaning.

Late selection models of attending indicate that information is selected after processing for meaning. Gray and Wedderburn (1960) hypothesized that if early selection models were correct, then the presence of other, conflicting information presented at the same time in the same ear would be able to disrupt recall of information. In their study, participants were given a mixture of words and numbers presented in each ear. For example, in the left ear, participants heard *mice – 5 – cheese* and in the right ear, *3 – eat – 4*. If the early selection model was correct, then participants should have reported all stimuli presented, grouped by ear. However, they found that participants reported information grouped by type: *mice, eat, cheese* and *5, 3, 4*. This suggests that stimuli were selected according to meaning, not basic characteristics.

Memory selection models of attending merge the early and late selection models. They follow the principle of early selection that stimuli are selected based on physical characteristics, but also that of late selection: that attended and unattended information both pass through the filter to be processed for selection based on meaning. Meaning, not the filter, decides the focus of attention. Deutsch and Deutsch (1963) suggested that meaning is assigned based on importance,

and that important stimuli will be processed, placed into memory, and then on to awareness thus, only important stimuli will be remembered. In this model, all information is processed, but only information deemed important will be available for later recall.

The attenuation model of attention disagrees with the idea that stimuli must pass through a filter and that the filter decides what stimuli pass into awareness. Treisman (1969) proposed that while an early selection filter exists, the filter attenuates, or weakens, stimuli that are unattended. If stimuli are to be attended to, they must surpass a threshold to leak through the filter. This threshold itself acts as a filter, in that important words (such as an individual's name) pass through relatively easily, whereas unimportant words (such as *chair*) have greater difficulty in passing through the filter.

The multimode model of attention adheres to the notion of a flexible filter, whereby what kind of selective attending is used is dependent on what is needed at the time. In this model, both physical features and meaning can be used for selection, based on their costs and benefits. Johnston and Heinz (1978) found that as the perceptual-processing system shifts from early to late, it collects more information from unattended sources but requires more capacity to focus on an attended source. In their study, participants performed a listening task and a reaction-time (RT) task at the same time. The listening task required participants to either attend to a single list or to a target list of two or three lists. The RT task required the detection of light signals and was used to measure the amount of capacity devoted to the listening task. Longer RTs implied more capacity expended on listening. In the first condition, the target and nontarget lists differed in voice (a male or a female), but were similar in meaning. In this condition, faster response times were recorded than those in the second group, implying that early selection was able to be used due to processing based on physical characteristics (i.e., voice, direction). In the second condition, the two lists were spoken in the same voice but differed in meaning. In this condition, response time was longer, implying that early selection could not be used and late selection was necessary due to the difference in meaning.

Conclusion

Each of these models differs slightly in when exactly meaning is derived and attending occurs. To review, in early selection models, information must pass through a filter before either meaning or attending. In late selection models, information is processed for meaning and then attending may follow. Memory selection models hold that all information, regardless of attention, will pass through the filter to be processed for selection based on meaning. In the attenuation model, information is filtered, but is attenuated instead of completely filtered in or out. If information is perceived despite being attenuated, then it may be attended to and continue to have meaning extracted. In the multimode model, selective attention varies according to the individual's needs at the time, and can use the processes outlined in early, late, memory, and attenuation models of selective attention. Each of these models, however, retains the idea that some mechanism restricts the flow of all information being attending to at the same time. In addition, regardless of when meaning is eventually attached, all information requires meaning to differentiate it and activate perceptual processing.

Cross-References

- [Attention](#)
- [Attention and Memory](#)
- [Predators as Attention-Grabbing](#)

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Selective Attention

► Selective Attunement to Adaptive Problems

Selective Attunement to Adaptive Problems

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Synonyms

Allocation of attention; Cognitive biases; Emotion detection; Fitness-relevant; Mate selection; Negativity engagement bias; Selective attention; Survival-relevant; Threat detection

Definition

The tendency for individuals to readily process and focus on information pertaining to survival and successful reproductive practices.

Introduction

In today's world, individuals are constantly faced with numerous avenues where cognitive resources can be distributed. However, our cognition remains peculiarly attuned toward processing the types of problems our Pleistocene ancestors faced. While individuals in modern society do not often experience the specific issues of our grassland ancestors, our memory and attention systems

evolved under this context and thus seem to demonstrate superior processing for these types of adaptive problems. Adaptive problems are those that provide challenges to an individual's survival or ability to reproduce. For example, the possibility of starvation, presence of predators and disease, and competition in procuring a mate are all threats to an individual's well-being or opportunity to produce offspring. The current review explores research on memory, attention, and emotions, providing support for the notion that human cognition is attuned to the adaptations developed to aid in survival under the earliest human conditions.

Human Cognition and Survival Threat

Inspiring a field of research combining evolutionary and cognitive psychology, Nairne et al.'s (2007) research on the survival processing effect demonstrated the memory advantage for processing items according to their grassland survival relevance. In a typical experimental evaluation of this mnemonic effect, participants are asked to rate a list of words for their relevance to the individual's ability to survive in a foreign grassland – including the need to find food, water, and protection from predators – or for their relevance to a control condition (e.g., moving homes to a foreign land where a house and transportation must be obtained). A surprise recall test is then completed where participants attempt to remember as many words as possible from the rating task. Furthermore, the survival processing conditions have been pitted against intentional learning conditions, in which participants are specifically instructed to remember words for a later memory test. Even when compared to intentional learning, words processed in an ancestral survival context are remembered to the greatest extent (e.g., Nairne et al. 2008).

This robust adaptive memory advantage has been well-established. A heightened memory for survival related concepts has been shown to occur when considering survival in isolation (e.g., stranded alone in a foreign land) or within a group (e.g., stranded with others in a foreign

land), as well as in both ancestral contexts (e.g., lost in a jungle) and unfamiliar scenarios (e.g., lost in outer space) (Kostic et al. 2012). While the underlying mechanisms of the effect are not yet fully understood, other known mnemonic devices such as self-reference, semantic relatedness, and elaboration have all been shown to play key parts (see Kazanas and Altarriba 2015 for a recent review). Once the concept of survival is activated, it appears to recruit a slew of memory mechanisms to achieve an adaptive end of preparing and reacting to potential threats (Nairne and Pandeirada 2016). Through an increased memory for adaptive problems, an individual is better able to seek out solutions that perpetuate life and avoid death. For example, it would be beneficial to remember where to find potable water and which color of berries is poisonous. The benefit of a memory that is keen for promoting survival by engaging various other mnemonic mechanisms allows the individual to actively maintain his or her life.

While remembering has its obvious advantages, the ability to selectively forget information is also beneficial. A healthy memory is naturally attuned to retaining positive, self-affirming information while disregarding instances that threaten the self-concept (Nørby 2015). Human memory has developed to be self-protecting as a means to ignore information that cannot be changed and could otherwise cause personal distress (e.g., maintaining an embarrassing childhood experience). Positivity is associated with comfort and is most often an indication of a safe environment. By selectively creating memories that fit the characteristics of a preferred environment, cognitive resources are able to be spent on true threats, such as avoiding predators and starvation, which can be planned for and dealt with accordingly.

To encode information into memory, attention must first be paid to the stimulus in question. What type of information best captures attention? As discussed, stimuli that allows for the detection and processing of potential danger and benefit is given a high priority in human cognition. Emotional stimuli often have a high adaptive value because they provide a large amount of information about the environment. In a recent study by

Fernández-Martín et al. (2017), participants viewed pairs of scenes while their eye movements were recorded. As compared to neutral scenes (e.g., flowers or mushrooms), individuals tended to look at pleasant visual scenes (e.g., babies and families) first. This inclination toward pleasant stimuli indicates a positive orientation bias. However, negative visual scenes (e.g., mutilation or weapons) were more often assessed for a longer period of time than either positive or neutral scenes. This indicates a negativity engagement bias such that negative information is harder to withdraw or disengage from. Furthermore, when images were presented centrally in front of the participant, males were more likely to orient their vision toward scenes depicting opposite-sex and couple erotica (i.e., reproductive focus) while women more readily looked at images of illness and loss (i.e., nurturer and caregiver roles). The authors concluded that visual attention is automatically drawn toward emotional images, particularly those that coincide with an individual's domain-specific or sex-specific goals. The heightened attention toward emotion, particularly negative emotion, serves as a mechanism for individuals to readily identify and extract information that will most benefit the individual within his or her adaptive roles.

From an evolutionary perspective, emotions have evolved to assist in solving a range of problems to include: signaling danger and disgust; indicating levels of mood, energy, and effort allocation; and prioritizing motivations (Al-Shawaf et al. 2016). Memories from experiences that elicited a negative emotion are indicative of situations that should be avoided in the present and future. However, positive emotions tend to motivate approach behaviors, as individuals tend to seek feelings of safety and comfort (see Elliot and Covington 2001, for a review of approach-avoidance motivation).

Directing attention toward emotionally arousing stimuli can serve adaptive purposes for self-survival, but also for procreation. From an evolutionary perspective, humans have an innate drive to not only preserve their life, but reproduce and maintain their genes through offspring. For both sexes, there is an attunement toward attractive

individuals. Maner et al. (2007) showed participants images of male and female faces and recorded their eye-movements. When presented images of highly attractive persons and neutral-attractive persons, individuals of both sexes not only looked at the attractive faces longer, but they had the most difficulty disengaging their attention from the attractive female faces. The authors argued that for men, this attunement serves the purpose of identifying prospective mates. For women, detecting potential threats to their current or future partner is an important component of securing and maintaining a mate. In this case, the potential concern for mate poaching is at hand, where individuals seek to engage with individuals known to already be in a romantic relationship (see Davies and Shackelford 2015 but see also Buss et al. 2017 for a discussion on mate switching). The ability to quickly recognize individuals who may be potential mates or competitors is an adaptive strategy to improve one's chance of reproductive success.

Conclusion

As discussed, the systems composing human cognition have developed to readily process information pertaining to survival. This ability to quickly identify possible sources of threat and procure safety and mates allows the individual a greater chance at maintaining life and passing on their genes. By allocating cognitive resources to survival, individuals have evolved memory, attention, and emotional systems that coordinate to be best fitted for solving adaptive problems.

Cross-References

- ▶ [Adapted Mind, The](#)
- ▶ [Adaptive Problems](#)
- ▶ [Attention and Memory](#)
- ▶ [Costs and Benefits of Mate Poaching](#)
- ▶ [Environment of Evolutionary Adaptedness](#)
- ▶ [Evolution of Memory, The](#)
- ▶ [How Evolutionary Psychology Can Still Explain Behavior](#)

- ▶ [Human Mate Poaching](#)
- ▶ [Mate Preferences](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
- ▶ [Predators as Attention-Grabbing](#)
- ▶ [Survival and Death](#)

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Selective Breeding

- ▶ [Breeding Systems](#)
-

Selective Focus

- ▶ [Attention and Perception](#)
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Selective Imitation

- ▶ [Neonatal Imitation](#)
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Self Determination

- ▶ [Daniel Dennett on Free Will](#)
-

Self-Agency

- ▶ [Meaning Making and the Self](#)
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Self-Aggrandizement

- ▶ [Narcissism](#)
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Self-Annihilation

- ▶ [Death by Suicide](#)
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Self-Assessment

- ▶ [Self-Assessment of Fighting Ability](#)

Self-Assessment of Fighting Ability

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Synonyms

[Aggression](#); [Fighting Ability](#); [Resource Competition](#); [Self-Assessment](#); [Sexual Selection](#)

Definition

Males are likely to be equipped with psychological mechanisms for estimating their own fighting ability, thereby enabling them to compare their own ability to that of competitors and to opt out of interpersonal conflicts in which their likelihood of success is low.

Introduction

Interpersonal conflict, particularly among males, can be quite costly in terms of risk of injury. Individuals are likely to be equipped with psychological mechanisms for self-assessment of fighting ability in order to determine whether to participate in the conflict as a function of their predicted likelihood of success. The likelihood of success is estimated by combatants through the approximations of one's own strength relative to those with whom they are in competition. The strategies that are employed in order to gauge the fighting prowess of the self and competitors have been observed and documented by a number of studies. This entry will describe how humans, particularly males, estimate their own strength and fighting ability.

Evolutionary Foundation

Human aggression is most commonly deployed against and by males (Daly and Wilson [1983](#)). In

this way, humans conform to a widespread mammalian pattern in which the sex that invests less in offspring competes more aggressively for access to mates and the resources used to keep and acquire them (Daly and Wilson 1983). This prediction is borne out of parental investment theory (Trivers 1972). Parental investment refers to any expenditure by the parents that is meant to aid the offspring at the cost of the parents' own potential reproductive opportunity. Given the inherent time and energetic costs of reproduction undertaken by females during the gestational and postnatal periods, large constraints are placed on females' reproductive capacity. This shifts women's mating strategy to one that prioritizes long-term mating and investment, rather than short-term. Conversely, males' obligatory investment in offspring is fulfilled at the time of conception, thereby creating a reproductive ceiling that is limited only by their ability to access mating opportunities. This shifts men's mating strategy to one that prioritizes short-term mating with minimal investment in each offspring.

This dimorphism between the sexes is the precursor to sexual selection. Females, being the primary investors in offspring, are discriminating in their mate selection, thereby evoking intrasexual competition among men who seek to gain reproductive access to many females. This competition creates large variability in the reproductive success among men, such that a few men may monopolize many females, leaving other men with few to no mating opportunities. The potential for reproductive oblivion escalates the intensity of intrasexual competition among men, often turning the competition into violent conflict. Such mating contests present the potential for a highly valued benefit, but also carry very real costs in the form of the risk of injury or death.

Minimizing Costs of Competition

The risk entailed in violent conflict is amplified when males compete with men to whom they are vastly outmatched. Even among the most formidable men, there are costs of suffering physical injury which can impair their ability to fend off

future attacks, hunt, build shelters, etc. Moreover, any interpersonal conflict carries opportunity costs, in that individuals who are spending time fighting or healing from injury are not using that time to promote their fitness through other activities. It would have therefore behooved males to be able to accurately estimate their probability of winning such a contest. Lower probabilities of winning may be tolerated by men who are most in danger of reproductive failure. This is consistent with data presented by Daly and Wilson (1985) showing that rates of male-male homicide are particularly elevated among men who are unmarried and/or unemployed. Men may therefore be equipped with psychological mechanisms that calculate the expected utility of engaging in an interpersonal conflict. A key element of this calculation is an estimation of the likelihood of winning the contest which requires the ability to compare one's own fighting ability to that of a competitor.

Perceived fighting ability is used as a gauge in order to determine the likelihood of emerging victorious in a potential fight. As males are the primary combatants in physical confrontations, it logically follows that they would have adapted methods for estimating the formidability of their competitors in relation to their own in order to properly gauge risks and rewards of confrontation.

Due to the nature of prediction, there is a trade-off between the accuracy and cost of the assessment. For example, one can estimate fighting ability very well by fighting someone to the death, but that comes at a great price. On the other side of the trade-off are perceptual estimates of fighting ability that are energetically cheap and do not risk injury but provide less precise assessments. Although not perfect, research suggests that these assessments are valid indicators of fighting ability (Sell 2016) and may therefore serve as a primary source of information in the decision of whether or not to engage in a physical contest.

Characteristics of Rival Assessment

Information about the physical capabilities of an adversary is useful in that it can inform one's self-

assessment of fighting ability. An essential aspect of self-assessment lies in rival-assessment. For example, early in childhood, young boys engage in a great deal of rough-and-tumble play (Daly 1994) that establishes a status hierarchy among boys and provides each individual with information about how their own fighting prowess compares to that of their peers. This hierarchy persists into adolescence and adulthood, changing as members become more or less formidable. Research suggests that the reason for this could be that this preference helped ancient hominids to estimate the costs, rewards, and outcome potentials of ingroup and outgroup aggressive conflicts.

A number of cues are perceived that can aid in the assessment of physical prowess. These cues are read as indicators of formidability of an opponent with regard to potential future altercations. Most definitive among perceived cues are those that provide information about an individual's upper body strength. This is because upper body strength is the single best predictor of someone's fighting prowess. Most human fighting requires several techniques for hitting or grappling, all of which rely primarily upon upper body strength. Upper body strength can be inferred from a number of traits that provide cues to observers to help them approximate the strength of a rival. For example, facial features predict a quarter of the variance in upper body strength, particularly among male raters, when rating male targets (Sell 2016). The structure of the face has been formed through evolutionary processes and carries with it indicators of upper body strength. These facial clues include roundness of the face, eyebrow width, and the prominence of the jaw (Windhager et al. 2011). Another cue that is predictive of upper body strength is the acoustics of the voice. According to Sell et al. (2010) listeners consistently attribute higher estimates of size and strength to men with lower pitched voices. Despite this, the pitch of a person's voice is very limited in its predictive capability. It is thought that the vocal pitch is influenced by the vocal folds that are highly reactive to testosterone and therefore highly sexually dimorphic, which leads people to infer that more dramatically dimorphic voices must also be physically dimorphic and stronger.

Characteristics of Self-Assessment

Research investigating the mechanisms that make self-assessment of fighting ability possible is still in early stages. However, high correlations between self-assessments and objective measures of strength have shown that humans can store and update a representation of their own formidability (Sell et al. 2009). This representation is updated whenever new experience or knowledge is gained pertaining to one's prowess. A lost fight, for example, can lead to a more modest estimate of one's prowess. It is this estimate, the estimate of one's own fighting ability, which allows costs and benefits to be compared through a visual assessment of a rival. Because men are significantly more likely than women to assess their own fighting ability without provocation (Buss 2016), it is inferred that they maintain a hierarchy and acknowledge their place within it. These unprovoked assessments are common because men are regularly updating their hierarchical positioning. Cues that are observed to assess the formidability of an opponent presumably could play a role in the self-assessment of formidability. However, such cues would not have been as readily accessible to ancestral humans, owing to a lack of modern technology (e.g., mirrors for self-reflection). Thus, cues to their own upper body strength would need to be indirectly inferred.

Evidence of self-assessment must be inferred through observation of conflict and pre-conflict behaviors. Males will attempt to appear larger than they are when facing rivals in order to intimidate them. When a competitor knows that they are outmatched by a rival, they will back down rather than escalating conflict. Nonhuman animals have been observed engaging in "conflicts of assessment" (Huntingford and Turner 1987; Alcock 2005) that allow the animals to ritually size up their competition before engaging in physical confrontation. This leads to a reduced chance of injury for both parties. Other animals have also been observed to win perceived contests with dummy rivals and thus perceived themselves as more capable. This led to them being more likely to challenge a real rival in future confrontations (Sell 2016). What this tells us is that animals are

not only estimating their own prowess, but they can also update these estimates as they gather more information and experience much the same way that humans do.

This sizing up has also been observed to allow individuals to assert their fighting prowess and avoid conflict by driving a foe to submission before any escalation of conflict. For example, red deer have been observed to employ roaring contests before engaging in conflict (Clutton-Brock et al. 1979). These rituals provide an extra gauge for the rivals to finalize their assessment of each other in reference to their own self-assessments and make a final determination regarding the risk and rewards of contest.

Conclusion

Homo sapiens have adapted numerous ways of determining the likely outcome of confrontation before ever engaging in said confrontation. This ability is greatly beneficial, as it allows them to estimate both the risks of confrontation as well as the likelihood of gaining access to potential benefits (i.e., resources, access to mates, etc.). This is particularly prominent among males as they are known to be the primary instigators of conflict as they engage in competition for resources. Knowing this, it can be extrapolated that males in particular have adaptations for assessing their own fighting ability and updating this assessment as new information and experience are introduced. Further research will most likely be directed at estimating aggression based on perceptions of the physical characteristics of the self and rival alike.

Cross-References

- Contexts for Men's Aggression Against Men
- Evolution of Fighting Assessment Abilities
- Feelings of Excitement and Brotherhood
- Information About Likely Combat Success
- Size and Dominance

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Self-Awareness

- Accuracy of Self-View
- Evolution of Self
- Mirror Self-Recognition
- Self-Monitoring
- Self-Observation

Self-Beneficial Political Attitudes

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Synonyms

Fitness-related goals; Fundamental motives; Self-interest

Definition

Across a range of evolutionary relevant political domains, humans seek to advance tangible fitness-related goals.

Introduction

Politics is about “who gets what, when and how” (Lasswell 1950). At the heart of politics is the regulation of access to resources and the distribution of them (Easton 1965). Politics can take place in species where individuals have interest conflicts about the rules regulating the distribution of resources and have cognitive capacities for a sense of social regularity (Petersen and Aarøe 2015). This article focuses on self-beneficial political attitudes in humans.

From an evolutionary perspective, the existence of politics across species suggests that biologically instantiated psychological mechanisms evolved through natural selection underlie political behavior. Evolutionary psychologists have mapped a wide range of domain-specific cognitive mechanisms designed to assess the distribution of costs and benefits “within and between groups from the perspective of the self” (Petersen and Aarøe 2012, p. 804). To the extent that modern political issues reflect evolutionary recurrent problems such as resource sharing with needy individuals, deterrence of exploiters, relationships with outgroups, and

warfare, evolved cognitive mechanisms should be expected to shape modern political attitudes (Petersen and Aarøe 2012, p. 804). An evolutionary perspective highlights that humans are equipped with a political psychology that is *ecologically rational*, i.e., optimized to operate efficiently in the face of recurrent adaptive problems and maximize reproductive fitness in the ecology of ancestral life (Petersen et al. 2014).

The Classic Puzzle About the Influence of Self-Interest on Political Attitudes

In the political science literature, Thomas Hobbes, one of the founders of modern political philosophy, identified self-interest as a fundamental human motive shaping political behavior (1651/1950). The notion that individuals are self-interested optimizers is also the cardinal assumption in modern rational choice theory on political preference formation (see Chong 2013 for an overview). Importantly, in a number of studies, the influence of self-interest on policy preferences has often been relatively weak (e.g., Sears and Funk 1991). Outlining the state-of-the-art view in the political science literature, Haidt (2012, p. 100) sums up: “Many political scientists used to assume that people vote selfishly, choosing the candidate or policy that will benefit them most.” But decades of research on public opinion have led to the conclusion that self-interest is a weak predictor of policy preferences (see also Weeden and Kurzban 2014, p. 28). The limited influence of self-interest in empirical studies of political attitudes represents an important puzzle in the public opinion literature.

An Evolutionary Approach to the Concept of Self-Interest and Political Attitudes

In the political science literature, self-interest has often been defined in relatively narrow, short-term economic terms as “the tangible, relatively

immediate, personal or family benefits of a policy” to avoid conceptual challenges of separating different sources of interests (Chong 2013, p. 101; see also Sears and Funk 1991). In the political science literature, scholars often emphasize this narrow conceptualization and measurement of self-interest as part of the explanation for the limited influence of self-interest found in many public opinion surveys (Chong 2013).

An evolutionary approach to the study of public opinion and preference formation highlights the relevance of a wider conceptualization and a biologically informed understanding of self-interest. From an evolutionary perspective, self-serving goals can go beyond the short-term and economic benefits (e.g., Kenrick et al. 2010; Kenrick and Griskevicius 2013; Weeden and Kurzban 2014, 2017). An evolutionary approach to political attitude formation views humans as political animals equipped with psychological mechanisms designed to solve adaptive problems and pursue tangible goals that ultimately increase survival and reproductive fitness (e.g., Weeden and Kurzban 2017, p. 75; Petersen and Aarøe 2015; Kenrick et al. 2010). As explained by Kenrick and Griskevicius (2013, p. 9), “as in the case of all other animals, natural selection has endowed modern humans with brains designed to make decisions in various domains in ways that consistently enhanced our ancestors’ odds of passing their genes to the next generation.”

Humans can increase their reproductive success by achieving a range of subsidiary typical goals representing distinct domains of adaptive behavior. The human mind is equipped with multiple domain-specific motivational systems designed by natural selection to solve adaptive problems that have been recurrent over human evolutionary history and in this way advance evolved strategic goals. Typical subsidiary fitness-enhancing goals include social status, resources, affiliation, mates, and parenting (Kenrick et al. 2010; Weeden and Kurzban 2017). In this view, self-serving political attitudes include not only positions that are consistent with short-term economic interests. Rather they can reflect “a range of people’s typical goals, whether directly involving material gain or not, whether involving immediate gain or something that

advances someone’s progress over the longer term” (Weeden and Kurzban 2014, p. 37).

Genetically Selfish Goals and Inclusive Interests

An evolutionary perspective highlights that organisms are ultimately motivated by genetically selfish goals (Dawkins 1989; see also Weeden and Kurzban 2017, p. 75). Organisms seek genetic reproduction either through their own reproductive success or through the reproductive success of individuals carrying the same genes. From this perspective, “self-interest” can be understood to include both the self and close kin. Drawing on the concept of “inclusive fitness” (Hamilton 1964) which in evolutionary biology refers to the combined gene-level reproductive success of an organism and its relatives, some scholars have therefore suggested to “jettison the term self-interest altogether” and replace it with the notion of “inclusive interests” (Weeden and Kurzban 2014, p. 38).

The Debate Over Self-Interest and Political Attitudes Continues

Weeden and Kurzban’s (2014, 2017) wider definition of self-interest and their concept of inclusive interests have been criticized for being too broad. Critics argue that the wider definition lacks clarity with respect to what would count against the argument that self-interest is often a major determinant of political attitudes (e.g., Caplan 2015). In response, Weeden and Kurzban (2015) have highlighted that their point is not that self-interest is the only factor in public opinion but that there is no reason to reserve the term self-interest to short-term economic interests. Thus, Weeden and Kurzban (2015) explain: “An evolutionary perspective can help highlight various strategic conflicts within societies that go beyond income redistribution, including fights over in-group preferences and conflicting reproductive lifestyles. We don’t think there’s any clear reason to call it ‘self-interest’ when one of these domains is at issue but *not* self-interest for the others.”

Conclusion

In the political science literature, self-interest has often been defined in relatively narrow, short-term economic terms as “the tangible, relatively immediate, personal or family benefits of a policy” to circumvent conceptual challenges of separating different sources of interests (Chong 2013, p. 101; see also Sears and Funk 1991). In the political science literature, the standard view is that self-interest has limited effect on political attitudes. An evolutionary approach to the study of public opinion emphasizes that self-serving goals can go beyond short-term economic interests. Humans are equipped with a political psychology that is *ecologically rational*, i.e., optimized to operate efficiently in the face of recurrent adaptive problems and maximize reproductive fitness in the ecology of ancestral life (Petersen et al. 2014).

Cross-References

- Adaptive Problems
- Goals
- Jonathan Haidt
- Moral Concerns
- Robert Kurzban
- Political Left, the

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Self-Concept

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Synonyms

Identity formation; Fluidity in self perception and expression; Social identity formation; Context-dependent self-conceptualization

Definition

Self-categorization theory posits that self-conception is formed through the process of *categorizing* or cognitively grouping the self, as either similar to or different from another class of stimuli. Contextual salience of various categories, ranging from personal (self-concept in terms of idiosyncratic attributes) to social (self-concept in terms of social category membership), and their relative influential strength at a given moment underlie the possibility for categorization at different levels of inclusiveness. The theory posits that different levels of self-conception are not only distinct from each other but also represent equally valid and authentic expressions of the self. Self-concept is characterized as an on-the-spot reflexive categorizing of the self in relation to an ever-changing and contextually-dependent frame of reference, which gives coherence to fluidity of the self and variation in human behavior.

Introduction

Self-categorization theory (SCT; Turner et al. 1987) has been characterized as the as “the social identity theory of the group” (Turner et al. 1987, p. 42), as it provides a social-cognitive account of *intragroup* process (e.g., group identification and behavior) through group-based construal of self and others. Self-categorization theory holds that the cognitive mechanism that gives rise to group-level processes, such as group cohesion and solidarity, is embedded in the shifting of self-concept from *personal* to *social* identity. This entry is a brief delineation of self-categorization theory’s view on self-concept, underlying factors that generate shared social identity, and how the ability to experience a subjectively *shared* self-concept could have an evolutionary advantage.

Fluidity in Self-Concept

The theory assumes that through the process of self-categorizing, one’s self-concept is generated.

Categorizing refers to the grouping of the self as identical to some class of stimuli in contrast to another. As with all natural categories, categorization can operate at varying levels of abstraction based on the process of class inclusion. Self-categorizing can occur at levels more inclusive than that of the individual level, as “we” and “us,” or at levels less inclusive than the individual, as “the real me,” or “the me I was yesterday as opposed to today.” Cognitive representations of the self are proposed to operate on three main levels of inclusiveness: the superordinate category of the self as human being (or *human identity*), a level that differentiated the self from other species; the intermediate social level of self as an ingroup member, a level that differentiated the self from outgroup members (*social identity*); and the subordinate personal level, which defines the individual as a unique person, distinct from other ingroup members (*personal identity*). The theory emphasizes that each level of self-conception is representative of a distinct, yet equally valid, and authentic expression of the self.

The process of self-categorizing is considered to vary in relation to contextual factors, as perceived similarities and differences operate in parallel to the perceiver’s self-appraisal in relation to an ever-changing frame of reference. Individuals that are perceived and categorized as different in one context (e.g., biologists vs. physicists in the science department) can be perceived as similar in a different context (science faculty vs. art faculty in a university) without any actual change in an individual’s own position. Simply put, the extension of a perceiver’s frame of reference also extends the degree to which a target person is seen to share a common categorical identity with the perceiver, in a manner predicted by the meta-contrast principle, which proposes that category formation and distinction are contingent on maximized perception of intercategory differences relative to intracategory differences (Turner et al. 1987). The perception of the self or others, as either similar or different, is therefore not fixed or based on absolute relationships, but rather determined by the level of inclusiveness that one categorizes themselves in a given context. The theory explains that as the content of self-concept

varies across levels of categorization, so will the meaning of a particular stimulus to the perceiver and subsequently their behavioral response to it. This is corroborated with evidence showing that the same information may be accepted or rejected by the same person in different social contexts, depending on how they have categorized themselves and others at the time. For example, group polarization studies have shown that the same information is rejected when it comes from an outgroup member, but accepted when it is received from an ingroup member (Turner et al. 1987).

It is noteworthy that the abovementioned fluid and variable process of self-conception contrasted with the dominant view of the self, which was portrayed as a unique and relatively fixed mental structure, stored in memory in an invariant state until activated by a specific circumstance, leading to consistent behavior despite situational variability (e.g., Markus and Wurf 1987). Turner and colleagues challenged this characterization and argued that rather than being preconceived and in a ready-to-be-activated state, self-concept is generated *reflexively* and on the spot to fit the perceiver's relationship to an ever-changing social context and reality. Context-driven category formation was posited to rely on an on-the-spot self-appraisal made possible by the recruitment of cognitive resources (e.g., long-term knowledge, implicit theories, cultural beliefs, social representations) that interacted with the specific set of instances being represented (Turner et al. 1994).

Formation of self-concept, at any instance, is proposed to be subjected to multiple salient categories that reinforce or conflict each other. Self-perception is thought to be influenced and shifted based on the relative strengths of competing self-categorizations at the personal and group level (Turner and Oakes 1989). The self-concept that emerges is therefore noted to reflect the compromise in self-perception made when choosing among several competing and alternative ways of categorizing the self in any given situation. Category salience is considered to be dependent largely on the interaction between accessibility (the readiness of a perceiver to use a particular category) and fit (the match between the category

and reality) within a given situation (Oakes 1987) and is thought to be reflective of an individual's past experiences, present expectations, and current motives, values, and needs (Turner et al. 1994). Accessibility of categorizations can be due to their frequent use (chronic accessibility) or relevancy to a particular situation (situational accessibility). Fit, which has two aspects, refers to whether categorization accounts for relevant similarities and differences between individuals or stimuli in a particular context as defined by the principle of meta-contrast (comparative fit) and whether categorization is based on beliefs and theories about the meaning of the category (normative fit).

Social Identity

Self-categorization theory substantially revised the conception of *social* identity. This was done by differentiating it from *personal* identity, stating that it can sometimes function to the relative exclusion of personal identity, and generated through a different level (of inclusiveness) of self-categorization. Prior to SCT, "social" selves and "social identities" were not regarded as selves that were in a subjective sense psychologically *shared* with others. Rather, "social" identity was considered to mean an outward impression that was perceived by others, whether or not it corresponded to the inner, private self. Terminology such as "global," "collective," "public," "interdependent," or "relational self" that existed in mainstream self-literature all referred to the *personal* self, meaning the self-concept as a representation or collection of representations of the perceiver as an *individual* person, understood to be different from other individuals (for a review, see Tyler et al. 2014). In sum, there was no self outside of the private, inner, idiosyncratic self.

Self-categorization theory postulates that perceiving ourselves through the lens of our social identity (e.g., in terms of "we" and "us"), as opposed to our personal identity (e.g., in terms of "I" and "me"), is a normal and authentic variation of the self, arising from the same general processes that give rise to personal self. Self-

conception at the social level is thought of as defining and experiencing the subjective self as similar or equivalent to a social group in contrast to another. When an individual experiences themselves through their social identity (as opposed to their personal identity), at that moment “the self is defined in terms of *others who exist outside the individual person doing the experiencing* and therefore cannot be reduced to personal identity. The self can be defined and experienced *subjectively* as a social collectivity (Turner et al. 1994, p. 454). The social collectivity becomes self, through a process known as *depersonalization*, which refers to individuals perceiving or defining themselves, and other members of primed social group, less as differing individual persons and more as interchangeable exemplars of the group prototype. Turner and colleagues argue that depersonalization is the psychological process underlying group behavior. Previous research has shown depersonalization as an explanatory variable for major group phenomena, specifically group formation and cohesiveness, cooperation, competition, social influence, social stereotyping, and crowd behavior (for a review, see Turner and Onorato 1999).

The notion of group *prototype* is important when considering group processes, as it represents fuzzy sets of attributes that define a group and its members and distinguish them from other groups by maximizing ingroup similarities and intergroup differences. Prototypes describe and prescribe group attitudes, beliefs, feelings, and behaviors that are appropriate in a given context, thereby generating stereotypical expectations and encouraging stereotype-consistent interpretation of ambiguous behavior. By accentuating intragroup similarities and intergroup differences, prototypes serve to define groups as distinct entities. Categories are however not defined by a fixed but rather *context-dependent* prototype, driven by the particular outgroup that is contextually salient and serving as a comparative point of reference or vary based on what dimension or attribute of the group gains importance. For example, as groups become more polarized (i.e., a group becomes more extreme in an intergroup setting), the more extreme members of that group will gain relative

prototypicality (Turner 1991), which in turn will shift the meaning of a self-category based on the contextually dependent change in its representative members. The fluidity of prototypes is yet another element that contributes to the variability of self-concept.

Conclusion

A shared social identity implies a shared mental representation of the self – a shift in self-concept from personal to social identity – which transforms and aligns thoughts, feelings, perceptions, and behaviors to group prototype, thereby engendering a sense of solidarity and connectedness which enables collective and unified behavior. From an evolutionary perspective, the transition of the self-concept, from personal to social (group persona), has many adaptive benefits that include, but are not limited to, positive ingroup attitudes and cohesion, cooperation, altruism, emotional contagion and empathy, collective behavior, and mutual influence (Hogg and Terry 2000). Group identification and group-related processes may have been fostered by our early evolutionary environment, in which individuals relied on group formation in order to gain greater access to resources, heightened defense against predators, and greater reproductive success (Buss and Kenrick 1998), all of which enhance survival and fitness. Given that individual survival is directly linked to group survival, the well-being and progress of any group are dependent on the engagement of its members in pro-social and cooperative behavior, in other words, the ability to compromise self-interest for the benefit of the group. Forgoing self-interest is conceivably contingent upon the ability to expand the sense of self – to be able to depersonalize and experience a sense of oneness with others – or the ability to see ourselves as interchangeable members of a social category. In this way, serving the group can be experienced as serving the self. The theory’s conceptualization of the self-concept, as variable, and able to operate at social or higher levels of inclusiveness, captures the psychological prerequisite for non-selfish mentality and

behavior. It may be our ability to shift our self-concept from personal to social that enables the generation of emotion such as *empathy* for strangers or non-kin members, as one can identify with or share a sense of self with any target, to the degree that merging point of relatedness can be conceived of.

Cross-References

- ▶ [John Turner](#)
- ▶ [Meaning Making and the Self](#)
- ▶ [Salience of Category](#)
- ▶ [Social Neuroscience of Self-Categorization](#)

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Self-Concept and Family

- ▶ [Kinship Is Central to Self-Concept](#)

Self-Concept Determined by Relatives

- ▶ [Kinship Is Central to Self-Concept](#)

Self-Consciousness

- ▶ [Evolution and Self-Awareness](#)
- ▶ [Evolution of Self](#)

Self-Control

- ▶ [Inhibition](#)

Self-Deception

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Synonyms

[Deceit](#); [Deception](#)

Definition

The active misrepresentation of reality to the conscious mind in order to better deceive others

Introduction

After being introduced to evolutionary theory, Robert Trivers became interested in the

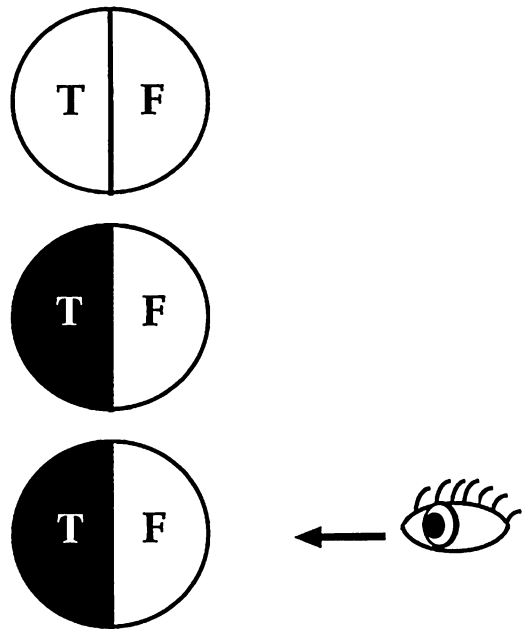
counterintuitive paradox of self-deception. How could natural selection simultaneously favor the evolution of complex sensory organs and fine-tuned detection mechanisms while also selecting for the systematic distortion of information once received by the brain. The more he learned about social evolution, the more he was convinced that the driving force behind the evolution to deceive oneself was selection pressure to be better able to deceive others (Trivers 1985). Given the intense psychological warfare observed in social creatures, Trivers argued that selection could act to favor various forms of reality manipulation that would benefit the individual. One result of this coevolutionary arms race Trivers suggests was the evolution of human intelligence; a very real cost, however, is the impaired ability to deal with reality (Cashdan and Trivers 2002, Trivers 1991, 1997, 2000, 2010, Trivers and Newton 1982).

Early Interest in Self-Deception

Trivers refers to self-deception as an important factor in human social interactions in early papers on reciprocal altruism and parent-offspring conflict, but it was in the forward to Richard Dawkins's *The Selfish Gene* that he first formalized his theory. Dawkins wrote extensively on the adaptive function of deception in nature, from avoiding predation via crypsis to frightening off predators using visually mimicry. If deception is an important part of animal communication, Trivers argued that humans, with their complex communication systems and big brains, must be under intense selection pressure to develop mechanisms to detect it, and therefore counterselection for self-deception as a strategy to avoid detection by rendering some facts unconscious, and thus less likely to betray the truth via subtle unconscious signals (e.g., sweat, increased heartbeat, galvanic skin response, change in micro-expressions, etc.) (Trivers 2011).

Development of an Evolutionary Theory of Self-Deception

Trivers developed a scientific theory of deceit and self-deception using evolutionary biology over



Self-Deception, Fig. 1 True (*T*) and false (*F*) information are simultaneously stored within an organism, but with a bias: the true is stored in the unconscious mind (*shaded area*), the better to deceive an onlooker (eye).

the next 40 years. He described fragmentation and conflict where true and false information are simultaneously stored in the brain with a bias toward the true information being stored in the unconscious and the false information in the conscious (Fig. 1) (Trivers 2002).

Trivers identified situations in which self-deception in the service of deceiving others would evolve as an adaptive strategy. Denying ongoing deception reduces the physiological costs of stress and cognitive load that are associated with deception, such as reduced immune function (Von Hippell and Trivers 2011). Being literally unaware that you are doing something, not only makes you less likely to be detected but also more sympathetic if you are caught. Self-promotion is also a major source of self-deception, where individuals tend to emphasize positive qualities and deemphasize their negative qualities. Humans are especially prone to self-deception in the construction of biased social theory and tend to view everything from personal relationships to the state of world

affairs from perspectives that portray themselves and their perspective in favorable ways (Trivers 2011).

Conclusion

Trivers' 2011 book *The Folly of Fools* provides a comprehensive overview of evidence in support of Trivers' theory of deceit and self-deception based on evolutionary logic. The functional view of lying to ourselves to more fluidly deceive others is supported with diverse lines of evidence from neurophysiology, immunology, parent-offspring relationships, genomic imprinting, sexuality and reproduction, and psychological studies on cognitive dissonance, confirmation bias, and aggression. Trivers provides many examples of self-deception in everyday life from the stock market to drug addiction and lie detector tests. He investigates the role of self-deception in air and space disasters and the use of false historical narratives to explore complex behaviors in groups and societies such as genocide, war, and religion (Trivers 2011).

Cross-References

- [Deceit](#)
- [Deception](#)

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Self-Defense

- [Defending Against Attack](#)
- [Defending Against Predator](#)
- [Defense Against Attack](#)
- [Self-Defense and Female-Perpetrated Violence](#)

Self-Defense and Female-Perpetrated Violence

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Synonyms

[Intimate partner violence](#); [Male sexual jealousy](#);
[Physical aggression](#); [Retaliation](#); [Self-defense](#)

Definition

Whereas men use physical aggression against women to control women's sexual behavior, women typically use physical aggression against men to defend themselves from male attacks or to retaliate for long-term abuse.

Introduction

In many samples, men and women inflict physical aggression against one another with relatively equal frequency (Archer 2000). However, Archer (2000) reports that female-perpetrated violence against men is primarily nonlethal, whereas men's aggression against women is more likely to be lethal. A woman uses physical aggression against a man in self-defense and in response to her partner's violence, as retaliation for prolonged abuse, or because the woman does not see an alternative method to escape the abusive relationship (Buss 2006; Daly and Wilson 1988). Women are less likely than men to inflict physical aggression against a partner in retribution for that partner's infidelity (Wilson and Daly 1985).

Motivation for Violence

Women experience and respond to fear differently than men (Cross and Campbell 2011). Although fear sometimes motivates competitiveness and combativeness in men, women's fear more often inhibits aggression. Women respond to danger or threats more sensitively and carefully than men, although both sexes may have evolved psychological anti-homicide mechanisms to avoid physical injury and death (Buss 2006). Women are less prone to engage in physical violence, perhaps because the majority of child-rearing responsibilities fall to women, who therefore may have more to lose as a consequence of debilitating physical injury (Campbell 2013). Engaging in violent behavior and subsequently dying might be especially devastating for the survival prospects of a woman's offspring. Additionally, avoiding physical violence would be advantageous for women because fertilization and gestation occurs within women. Safeguarding the ability to successfully rear offspring may have been particularly important for women's ancestral reproductive success. Given strong selection pressures for women to avoid physical injury, female-perpetrated violence primarily occurs in situations in which women must protect themselves from extreme bodily harm or death.

Self-Defense

Female-perpetrated violence is often initiated in response to a male intimate partner's aggression against the woman. *Male* sexual jealousy is the primary reason women defend themselves from or kill their mates (Daly and Wilson 1988). Male sexual jealousy motivates men to use aggression against women to manipulate female sexual behavior (e.g., to dissuade the woman from committing infidelity or abandoning the relationship; Buss 2000; Smuts 1992). In response to physical aggression and the threat of homicide motivated by male sexual jealousy, women use violence to protect themselves, their current offspring, and their future reproductive opportunities. In fact, women's aggression is greater against intimate partners than against other targets and is typically associated with a disinhibiting situation that evokes aggression (Cross and Campbell 2011), such as contexts in which the woman is defending herself from a violent intimate partner. Additionally, Cross and Campbell (2011) reported that female-perpetrated aggression against men peaks between the woman's ages 15–19 years. Women within this age range have maximum reproductive value or expected future reproduction. Given the importance men place on fertility and youth in a long-term partner, men are more likely to respond violently to a younger (and therefore more reproductively valuable) partner's desertion or infidelity (Buss 2006; Daly and Wilson 1988). Thus, younger women are more likely to use violence to defend themselves against sexually jealous male partners.

Retaliation

Outside the context of defense from a partner's violent attacks, it may have been ancestrally beneficial for a woman to kill or to use violence against her partner. A woman who kills her partner after experiencing his violence over an extended period may eventually kill him to permanently end the abuse or to protect her children. For example, Daly and Wilson (1988) report that wives kill their husbands after prolonged and severe intimate partner abuse, when they reside closer to their genetic relatives, and when their children are threatened or abused. Women retaliate when

they are not able to identify an alternate strategy to escape their abusive partner. Unlike men, who often use partner-directed violence to coerce and control a partner, women use partner-directed violence (including homicide) to escape a dangerous partner or to seek retribution for previous and ongoing physical violence against them or their children.

Additionally, in rare instances, women kill their partner for suspected or actual infidelity. Although jealousy-motivated partner-killing is more often committed by men against women, some women cite jealousy as the primary motivator for killing their partner (Daly and Wilson 1988). For example, of all homicides in Detroit in 1982, 58 were related to marital conflicts and 20 of these were completed by women (Wilson and Daly 1985). Of these 20 homicides, six women killed their husband because of his infidelity. Women may be less likely than men to kill their partners in response to a real or suspected infidelity because women cannot be duped into investing in a genetically unrelated offspring – that is, a partner's infidelity may be less reproductively costly for women than for men. However, partner-killing may be beneficial for women in cases in which killing the husband would halt allocation of his resources to a female rival and her offspring.

Conclusion

Women perform most child-rearing duties and invest more heavily in offspring than do men. Thus, women may have more to lose by engaging in or experiencing physical violence. Although women benefit less by perpetrating violence than do men, women use aggression strategically to physically defend themselves from jealous mates, to escape abusive relationships, to retaliate for prolonged abuse, to protect offspring, and, occasionally, to punish or prevent a partner's infidelity.

Cross-References

- [Contexts for Women's Aggression Against Men](#)
- [Female-Perpetrated Violence](#)

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Self-Destruction

- [Death by Suicide](#)
- [Factors Associated with Suicide](#)
- [Suicide](#)

Self-Domestication

- [Decline of Violence](#)

Self-Efficacy, Animal Phobias, and Evolutionary Mismatch

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Synonyms

[Interpretation about one's competence and aversions of certain living organisms; Perception of one's capability and extreme fears of some creatures](#)

Definition

The judgment one has about his/her own competence to cope with certain feared animals is believed to have been an adaptive psychological mechanism that has assisted humans in their attempts to avoid serious harm (and therefore enhancing their survival chances) throughout evolutionary history. Nevertheless, such an evolved psychological mechanism is conceivably less relevant in the modern, largely urbanized and medically progressive environment whereby the risk of being severely injured by the dreaded creatures is relatively more modest.

Introduction

Self-efficacy, the perception of one's proficiency in accomplishing tasks that are related to the achievement of a specific goal (Bandura 1977), is a concept that has garnered considerable empirical endorsement and has been successfully utilized in elucidating an extensive range of phenomena over the years (Pajares 1997). One of the most intriguing of these applications pertained to the topic of phobias (e.g., the extreme distress associated with encountering some dreaded situations/objects) in humans (Bandura 1977). A phobia, or more specifically an animal phobia in this case, was contended to develop when one has appraised that he/she would not have the competence to ensure his/her own well-being in the presence of the specific animal (Williams 1992). For instance, if an individual has reached the conclusion that he/she would not have the agility to dodge an attack by a nearby snake or the strength to prevent being grievously harmed by it, then he/she is likely to be immensely afraid of it.

Self-Efficacy: An Adaptive Mechanism Against Animal Threats

Taking into account the apparent ubiquitousness of both self-efficacy and the extreme apprehension toward certain creatures around the world

(Davey et al. 1998; Scholz et al. 2002), it is logical to assume that self-efficacy must have evolved in humans as a psychological mechanism which has provided useful information for an individual about his/her own capability to deal successfully with any possible threat (e.g., any likely danger that might have been posed by a particular animal in this case) and how to react accordingly across prehistory. On occasions (or even possibly quite regularly), although such a mechanism (when utilized specifically in the domain of animal threats) might result in undue fears and unnecessary avoidance (e.g., when an animal is actually harmless), the price that one might pay (e.g., death) for making a careless mistake (e.g., being self-assured, and therefore calm, about one's competence to handle a venomous snake) is so high that it would have been adaptive for humans to develop more generalized phobias about certain creatures (e.g., an excessive fear toward all snakes just to be safe) (Nesse 1994). Indeed, empirical data to date have broadly supported the suggested role of self-efficacy in the manifestation of zoophobia symptoms (e.g., Johnstone and Page 2004), and the notion that such apprehensive reactions were typically excessive (e.g., Jones and Menzies 2000).

Evolved Self-Efficacy and Zoophobias in the Modern World

The utility of self-efficacy as an evolved psychological mechanism in coping specifically with animal threats has largely dwindled in the present world however, as a result of massive societal/technological and medical transformations in the recent era. For instance, a huge proportion of the human race is presently located in urban settings (as opposed to more natural surroundings), which are environments whereby encounters with potentially dangerous animals are considerably much more uncommon (United Nations 2014). In addition, significant advances in medical research and treatment have likewise greatly reduced the lethality of an attack by any feared animal (e.g., Dart et al. 2001). In fact, humans are much more likely to die under

modern technology-related circumstances (e.g., in a vehicular accident) as compared to an attack by a feared creature in the current world, although most are still likely to be more apprehensive of the latter due to the vast amount of time psychological mechanisms (e.g., animal coping self-efficacy) would generally require to adapt to evolutionarily novel objects/conditions (Nesse 1994).

Conclusion

Self-efficacy is interpreted to be an evolved psychological adaptation that has played a pivotal role in influencing relevant coping reactions (e.g., be extremely fearful or remain relatively calm) toward a diverse array of potential threats (e.g., animals) across prehistory by virtue of a pertinent assessment about one's survival risk (if threatened by a particular creature) in relation to his/her own capability. Such an adaptation, specifically in the context of zoophobias, might nonetheless be considered excessive in the current environment given the radical introduction of evolutionarily-novel technologies and medical treatments in the modern, predominantly urbanized world.

Cross-References

- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)

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Self-Enhancement

- [Projected Confidence](#)

Self-Enhancement Relative to Others

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Synonyms

[Group-serving biases](#); [Self-other bias](#); [Valuation motive](#)

Definition

Self-enhancement refers to a group of psychological phenomena whose common feature is holding a tendentiously favorable view of oneself. Given the fact that an individual's self-view is largely socially constituted, one's relationships with others greatly influence self-evaluation. This interpersonal aspect of self-esteem regulation can be observed especially well in phenomena such as the better-than-average effect and in-group favoritism and in various self-evaluation maintenance strategies specified by Tesser's (1988) self-evaluation maintenance model.

Introduction

The idea that people strive to feel good about themselves is a part of folk psychology. Scientific evidence accumulated over the past decades attests to the prevalence and cross-cultural universality of this need. This entry is a brief delineation of the main themes emerging from the literature on self-enhancement in relational context, including the possible evolutionary bases of the self-enhancement motive.

Self-Enhancement and Relationships with Others

People's desire to sustain or enhance a positive self-view has been widely documented and suggested as determining a broad range of human behavior. For example, individuals tend to see themselves as better than most other people, and they tend to evaluate more favorably members of their own group than the out-group. The former effect, known as the better-than-average effect (also referred to as the self-other bias), was first identified over four decades ago (e.g., Codol 1975) and is regarded as the most robust of all self-enhancement phenomena. Further studies have revealed four general types of moderating factors that alter the effect's strength: the scales on which the effect is measured (i.e., the effect is stronger when ratings come from direct scales

than when they are derived from separate scales for the self and an average peer), the nature of the judgment dimension (i.e., the effect is stronger when the attributes being compared are controllable or ambiguous rather than uncontrollable or unambiguous), the nature of the comparison target (i.e., the effect is stronger when comparisons involve specific and real individuals rather than hypothetical targets such as an average peer), and characteristics of the judge (i.e., individual differences such as depression affect the tendency to evaluate oneself more favorably than others) (Alicke and Govorun 2005). It is also worth noting that the perception of being better than the average person can be achieved either by overestimating one's own positive traits or by underestimating one's negative traits. A preference for these strategies differs among narcissists and individuals with genuine high self-esteem: whereas narcissists tend to self-enhance by augmenting their positive aspects, those with genuine high self-esteem are more prone to bolster self-worth through the more socially accepted discounting of negative traits (Hovrath and Morf 2010).

The latter effect, that is, the in-group favoritism (otherwise known as the in-group superiority), can be thought of as an extension of the self-other bias to social self. In-group favoritism has been shown to occur in naturalistic groups (e.g., one's ethnic or religious group) as well as in experimentally manufactured groups (e.g., Masuda and Fu 2015). Indeed, the so-called mere categorization effect, where the mere labeling of people as "us" and "them" results in an in-group favoritism, has been one of the most reliable findings in social psychology (e.g., Brewer 1979).

Both the self-other bias and the in-group favoritism represent direct forms of self-enhancement, since individuals are directly claiming a superior status for the self. Such forms of self-enhancing biases are exhibited to a greater extent by people with high self-esteem than by people with low self-esteem. Low self-esteem individuals, who doubt their capacities in many areas, tend to engage in indirect forms of self-enhancement, which means they use their relationships with

others to promote feelings of self-worth (Brown et al. 1988). Indirect self-enhancement strategies include connection-focused tactics of boasting (i.e., proclaiming a positive link to a favorable other), burying (i.e., disclaiming a positive link to an unfavorable other), blaring (i.e., proclaiming a negative link to an unfavorable other), and blurring (i.e., disclaiming a negative link to a favorable other) and other-focused tactics of burnishing (i.e., enhancing the favorable features of a positively linked other), boosting (i.e., minimizing the unfavorable features of a positively linked other), blasting (i.e., exaggerating the unfavorable features of a negatively linked other), and belittling (i.e., minimizing the favorable features of a negatively linked other; Cialdini 1989). Favorable self-other and in-group/out-group comparisons may also be considered as examples of comparative self-enhancement strategies that are generally more prevalent among narcissists than among nonnarcissists. Non-comparative techniques (e.g., strategically evaluating the importance of the task) do not distinguish as readily narcissists from non-narcissists (Campbell et al. 2000).

An interpretive mechanism for understanding how others affect an individual's self-evaluation is provided by Tesser's (1988) self-evaluation maintenance model. The model assumes that people's self-evaluation is determined by two antagonistic processes: a reflection process and a comparison process, both of which have as component variables the closeness of the relationship with the comparison other, the quality of the comparison other's performance, and the self-relevance of the performance domain. The better the other's performance and the closer the psychological relationship, the more one can gain in self-evaluation through the reflection process (this is the basking in the reflected glory effect mentioned earlier), yet, at the same time, the more one can lose in self-evaluation through the comparison process. The relative importance of the reflection and comparison process is dependent upon the self-relevance of the performance domain: when relevance is high, individuals are likely to engage in comparison and suffer decreases in self-evaluation. To

prevent the loss in self-evaluation, one can either alter the closeness of the relationship with the comparison other (e.g., distance oneself from that other), alter the importance of the performance domain to one's self-definition (e.g., decide that the domain is simply no longer self-relevant), or alter own or the other's performance (e.g., sabotage the other's efforts). All these strategies have been extensively explored in the context of social interactions and close relationships (e.g., Tesser 1988). Also, previous studies found support for the role of several factors, including chronic self-esteem, as moderators of the responses to social comparisons (e.g., Beach and Tesser 1995).

It has been long debated whether a robust self-enhancing tendency fosters or hinders psychological well-being. Paulhus (1998) attempted to empirically reconcile the divergent findings in the literature and provided evidence that self-enhancement is adaptive with regard to intrapersonal functioning (e.g., having a positive self-attitude), but not interpersonal functioning, at least in the long run. Initial positive impressions self-enhancers generate wear off after increased acquaintance.

Self-Enhancement in an Evolutionary Context

Self-enhancement is thought by many to be a universal force of human behavior (e.g., Sedikides et al. 2004). Its prevalence and cross-cultural occurrence suggest the possibility that the motive has been evolutionarily selected because it conferred a survival advantage. Sedikides et al. (2004) describe ecological (e.g., food acquisition) and social (e.g., intragroup interactions) pressures that likely facilitated the capacity to make self-evaluative judgments and to use tactics of impression management and led to the evolution of self-enhancement. The potential evolutionary utility of self-enhancement strivings is to promote the adaptiveness of an individual's self-system (e.g., by leading one to select tasks with a high probability of success), improve an individual's ability to interact with others (e.g., by increasing one's

perceived mate value), and benefit an individual's standing in the group as well as the group itself (e.g., by promoting one's chances to attain a leadership position; Sedikides et al. 2004). The notion that self-enhancement evolved as a psychological solution to the adaptive problem of tracing one's position within a group hierarchy and one's relational value to others is reflected in Barkow's (1989) and Leary et al.'s (1995) works. Apart from these social advantages, self-evaluation maintenance processes could also be seen as helping individuals to identify and create relatively unique spheres of competence within the primary social group (Beach and Tesser 2000). The evolution of self-enhancement has also been explained by Pyszczynski and colleagues' (2004) terror management theory to be due to the buffering effect of self-esteem on the fear of death.

Several authors have studied the evolution of in-group favoritism, widely observed in non-humans as well (e.g., Masuda and Fu 2015). Evolutionary models of in-group favoritism typically rely on mechanisms of cooperation, which implicitly assume material payoff maximization and affective empathy. Of particular interest in this context are processes of cultural group selection, which explain why groups composed of altruists outcompete groups of selfish individuals (Mesoudi and Jensen 2012). As suggested by Habermacher (2015), self-enhancement may function to direct and restrict altruism and compassion. That is, humans could have evolved to have depersonalized and generalized altruistic motivations, but self-enhancing biases – as ad hoc adaptations – helped to contain within the group their beneficial effect.

Conclusion

Self-enhancement has received much theoretical attention, and the empirical evidence that people strive for self-esteem is voluminous and compelling. In evolutionary context, various manifestations of self-enhancement might have promoted successful adaptation to group life and offered considerable survival and reproductive advantages.

Cross-References

- ▶ [Changes in Self-Esteem Motivate Behavioral Changes](#)
- ▶ [Self-Concept](#)
- ▶ [Self-Esteem as Manipulative Status Communication](#)
- ▶ [Self-Esteem Increase Motivates Similar Behavior](#)
- ▶ [Self-Esteem Reflects Assessments of Valuation](#)
- ▶ [Self-Esteem Tracks Mate Value](#)
- ▶ [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- ▶ [Self-Evaluations Track Perceived Mate Value](#)

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Self-Esteem

- [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- [Sociometer Theory](#)

Self-Esteem and Perceived Social Value

- [Self-Esteem Increase Motivates Similar Behavior](#)
- [Self-Esteem Reflects Assessments of Valuation](#)

Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?

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Synonyms

[Narcissism](#); [Prestige](#); [Self-regard](#); [Social rank](#)

Definitions

Self-esteem denotes the positivity of one's overall self-evaluation. Status denotes the social prestige one gains in virtue of being respected and admired. Dominance theory and hierometer theory, drawing on evolutionary theory, specify how self-esteem and status might interrelate.

Introduction

Human beings, as self-conscious animals, evaluate themselves positively or negatively. In addition, as social animals, they also evaluate one another positively or negatively. The former type of evaluation, when positive, is commonly known as *self-esteem* (Rosenberg 1965). The latter type of evaluation, when positive, might be labeled “social esteem.” One important question is how the two are linked.

Everyday intuition suggests, and classic theories propose, that self-esteem derives from social esteem (Cooley 1902). However, people do not absorb social information passively, but actively process it in a manner that protects their self-esteem (Sedikides and Gregg 2008). In addition, whereas self-esteem is inherently unitary – the self as a whole being a singularity – social esteem is inherently complex. Three fundamental dimensions stand out. First, people may be accorded

respect and admiration, in virtue of being competent or powerful (*social status*; Fiske 2010). Second, people may be liked and appreciated, in virtue of being cooperative and caring (*social inclusion*; DeWall et al. 2011). Third, people may be fancied and pursued, in virtue of being fertile or rich (*reproductive fitness*; Shackelford et al. 2005).

Several theories address the link between social esteem and self-esteem and the evolutionary function that this link might serve. However, the theories differ in focusing on one or another of these three fundamental dimensions of value. For example, *sociometer theory* (Leary et al. 1995) in its original form focuses on social inclusion, but later extensions of the theory to romantic relationships focus on reproductive fitness (Bale and Archer 2013). Here, we discuss two theories that focus on social status as a fundamental dimension of value: *dominance theory* and *hierometer theory*. Both theories claim to identify aspects of mind and behavior that have arisen in response to recurrent adaptive challenges present in the human ancestral environment.

Dominance Theory

Dominance theory (Barkow 1980) seeks to explain the striving for self-esteem in human beings as an elaboration of the more primitive strivings for social ascendancy in nonhuman animals. Most animal societies are hierarchically organized (Pusey and Packer 1997); that is, conspecifics spontaneously rank order themselves in ways that determine their priority of access to resources and mates. Doing so permits members of those societies, whatever their rank, to avail of the adaptive advantages of reduced aggression (Kaufmann 1983). Human societies are likewise stratified (Fiske 2010). However, given the greater cognitive sophistication of human beings (Gregg and Sedikides 2018), the mental mechanisms underlying their social stratification, although still shaped by evolutionary forces, are also liable to contain novel elements.

Dominance theory starts with the observation that rank order in animals can be largely characterized in terms of behavioral *dominance* or *submission*. Whether through differences in ability, motivation, or personality (Hurd 2006), some animals succeed in asserting themselves over others, often through ritualized signaling instead of overt aggression. Accordingly, each animal's rank order comes to reflect their level of comparative success in asserting themselves over time. Moreover, given the overall adaptive advantages of occupying a higher rank, it is plausible that some dedicated drive evolved to motivate animals toward seizing opportunities, when available, to attain this rank. Human beings should be no exception to this rule – and indeed, there is ample evidence of a universal desire for social status among them (Anderson et al. 2015). However, given that human beings are also self-conscious organisms, who contemplate themselves as well as their environment, dominance theory postulates that the impulse to physically prevail over other animals has been largely transformed into an impulse to *symbolically evaluate oneself as better than other people* – which dominance theory characterizes as self-esteem. However, it should be noted that this definition of self-esteem – perceived relative superiority – differs from standard definitions of self-esteem, which involving seeing oneself as individually possessing adequate worth (Rosenberg 1965).

Dominance theory also specifies likely antecedents of self-esteem. Given that human beings are cultural animals (Baumeister 2005), their capacity to please real or imagined others (including, in aboriginal societies, ancestors and gods), by meeting expectations that are normative in their societies, is likely to be one key antecedent. Doing so can be understood as a means of gaining *prestige* in the eyes of others, as opposed to attempting to achieve dominance over them using raw power (De Waal-Andrews et al. 2015). Thus, whereas for most nonhuman animals (with possible exceptions among higher primates such as chimpanzees or bonobos), their rank in the social hierarchy is *only* the result of power-mediated dominance; in humans it can *also* be

the result of consensus-mediated prestige. For this reason, indeed, dominance theory might be better labeled “prestige theory.” The drive for dominance is what human self-esteem evolved out of, not what currently underlies it.

Hierometer Theory

Like dominance theory, hierometer theory (Mahadevan et al. 2016) also postulates that self-esteem rises and falls in tandem with higher or lower social status. However, it differs from dominance theory in the account it gives of the adaptive function of self-esteem and of the motivational goals being pursued. In general, whereas dominance theory invokes an absolute drive toward social status, hierometer theory invokes a contingent one.

Hierometer theory starts from the premise that, although higher social status may be generally more conducive to survival and reproduction than lower social status, it is nonetheless *not* generally adaptive for people to strive perpetually for higher social status, by invariably and inflexibly seizing opportunities to contest their place in the hierarchy. The simple reason is that such contests can be lost as well as won; and with one’s survival potentially at stake, the avoidance of catastrophic defeats is no less imperative as the securing of profitable victories. Accordingly, the decision as to whether or not to enter such a contest, if it is to be optimally adaptive, must depend on people’s actual competitive prospects, as best they can be determined. The situation is analogous to that arising in poker: all else equal, it makes more sense to raise when in possession of a relatively good hand and to fold when in possession of a relatively poor one. Hierometer theory postulates that the quality of one’s poker hand corresponds to one’s *existing* social status. Specifically, when one’s social status is high, it makes more sense to escalate an incipient conflict assertively, whereas, when it is low, it makes more sense to de-escalate it acquiescently. This is because being already respected and admired (in a prestige hierarchy; or alternatively, being feared and

obeyed in a dominance hierarchy) is a reliable sign that one has at one’s disposal sufficient material and social resources to compete successfully. Accordingly, behavioral assertiveness should covary with social status. How does self-esteem fit into this picture? Hierometer theory postulates that self-esteem evolved at least in part as a psychological variable to mediate between the two – by reflecting social status on the one hand, and by regulating behavioral assertiveness on the other.

Note that, unlike dominance theory, hierometer does not specify the achievement of higher self-esteem per se as the motivational goal (although it does not deny the possibility). Rather, hierometer theory postulates that self-esteem *moderates* levels of motivation to escalate conflict so as to optimize people’s chances of navigating social hierarchies. Another way of putting this point is to say that, whereas dominance theory characterizes the achievement of self-esteem as a symbolic proxy for the achievement of behavioral dominance, hierometer theory characterizes the achievement of self-esteem as the result of having previously attained higher social status, which in turn facilitates the expression of assertive or “dominant” behaviors. A further implication is that, whereas dominance theory implies a *compensatory* dynamic – people will strive for self-esteem or prestige if they perceive one or the other to be too low (sociometer theory makes similar claims in respect of social inclusion; Leary et al. 1995), hierometer theory implies a *consolidatory* dynamic – people will strive for social status (via assertive behavior) to the extent that they already possess it.

Hierometer also goes further in postulating a role, not only for self-esteem but also for a variant form of self-regard, namely, *narcissism*, conceived of as normally distributed trait as opposed to a discrete clinical condition (Foster and Campbell 2007). Narcissism is characterized by grandiose self-views and exhibitionistic displays, an interest in exercising power and authority, and a tendency to feel entitled and to exploit others (Ackerman et al. 2011). As such, it is nonetheless potentially suited to mediating the impact of social status on competitive behavior.

Empirical Evidence for the Link Between Social Status and Self-Esteem

Despite the differences between dominance theory and hierometer theory, they make an identical prediction with respect to the link between social status and self-esteem (or narcissism): levels of the former should covary with levels of the latter. Moreover, this prediction should be borne out whether both variables are measured as traits or states as well as when confounding factors are taken into account.

Across diverse literatures and samples, the predicted positive correlation between social status and self-esteem emerges. For example, Faunce (1984) found that the social status of high-school students in their class, as reflected in peer rankings, especially when given by best friends, strongly predicted their self-esteem. Similarly, Smith et al. (1998, Study 3) found that, among university students, the belief that they were accorded respect by most members of their university community strongly predicted their self-esteem.

Nevertheless, given that social status covaries with other antecedents of self-esteem – in particular with social inclusion – such zero-order positive correlations are open to alternative interpretation. However, several studies have also confirmed that social status predicts self-esteem more specifically. For example, Fournier (2009) found that, among high-school students, peer ratings of respect, prominence, and influence predicted self-esteem even after controlling for peer ratings of likability and personal ratings of social support. In addition, Huo et al. (2010) found, in a similar populations, that social status (bundled with peer approval) predicted self-esteem (bundled with mental health) independently of social inclusion. Using cleaner operationalizations, Mahadevan et al. (2016) likewise found that social status predicted self-esteem independently of social inclusion. Furthermore, the link persisted even after controlling for the clinical confounds of depression and anxiety. Finally, only higher social status, but not higher social inclusion, independently predicted higher narcissism, thereby highlighting the value of

operationalizing self-regard in more than one way and pointing to a unique functional role for social status and narcissism.

Although dominance theory and hierometer theory imply that social status – again, defined as the respect and admiration afforded by others (Anderson et al. 2015) – should predict self-esteem, they also imply that the objective foundations of social status, in particular, factors such as income, education, and occupation, often termed *socioeconomic status* (SES), should also predict self-esteem. A meta-analysis by Twenge and Campbell (2002) indeed established that SES exhibits a small positive correlation on self-esteem. More recently, Kraus and Park (2014) reported that family income and personal education weakly predicted self-esteem but also that the effect was wholly mediated by subjective perceptions of one's social standing.

The best evidence for the impact of social status on self-esteem is experimental.

Wojciszke and Struzynska-Kujalowicz (2007, Study 2) showed that participants, assigned the group task of deciding which of several candidates should be hired for a job, ended up with higher state self-esteem after being randomly assigned to the role of a supervisor as opposed to a subordinate. Similarly, Leary et al. (2001, Studies 1 and 2) orthogonally manipulated social status and social inclusion by providing lab participants with false feedback about how many of their groupmates had nominated them as a group leader or as group member, respectively. Both manipulations exerted roughly equal effects on state self-esteem, in the expected directions. Finally, Mahadevan et al. (2018) conducted two experiments in which college students were led to anticipate, on the basis of credible but bogus tests of intellectual and emotional competence, that their future social status and social inclusion would be markedly either high or low relative to most of their peers. Care was taken to otherwise match the format and content of feedback delivered. Again, both manipulations exerted roughly equivalent effects on self-esteem. However, raising perceptions of future social status lead to a greater increase in narcissism than raising perceptions of future social inclusion did. This again

suggests that narcissism may be a more specific tracker of social status.

Hence, on the basis of converging evidence of varying methodological strength, social status and self-esteem, as well as narcissism, are linked in the manner predicted by both dominance and hierometer theory.

Conclusion

Within limits, how individuals are regarded by others affects how they regard themselves. Among other things, being respected and admired – enjoying social status – leads individuals to like themselves more, to have higher self-esteem, or even narcissism. Two theories, dominance theory and hierometer theory, both make this prediction, each offering an evolutionary rationale for it. However, they differ on the precise role they ascribe to self-esteem or narcissism, and how levels of status striving might be subsequently affected. Nonetheless, the initial prediction they make enjoys good empirical support. Most compellingly, experiments indicate that manipulations of social status exert a unique impact on self-esteem and narcissism and find that the effects observed are comparable in size to those observed for manipulations of social inclusion (which concurrently support sociometer theory). Accordingly, there are solid grounds to propose that the function of self-esteem and narcissism might be, at least in part, to track levels of social status and possibly as a prelude to regulating subsequent status-seeking behavior.

Cross-References

- [Biosociology of Dominance and Deference](#)
- [Changes in Self-Esteem Motivate Behavioral Changes](#)
- [Dominance and Territory](#)
- [Dominance Hierarchies](#)
- [Dominance Hierarchy](#)
- [Dominance in Humans](#)
- [Dominance Theory \(Cummins\)](#)
- [Function of Dominance](#)

- [Indicators and Correlates of Status and Dominance](#)
- [Male Dominance Hierarchies](#)
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- [Social Dominance Orientation \(SDO\)](#)
- [Social Dominance Reduces Fighting](#)
- [Sociometer Theory](#)
- [Status and Dominance Hierarchies](#)

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Self-Esteem as a Status-Tracking Mechanism

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Synonyms

Sociometer; Sociometer theory

Definition

Sociometer theory suggests that self-esteem functions as a mechanism by which individuals track

their relational value (i.e., status) to others. Therefore, individuals who are high in self-esteem tend to be held in high regard.

Introduction

As a species, it is vital for an individual to have a good understanding of where he or she stands in relation to one's peers and to be able to accurately assess his or her status in a social hierarchy. This understanding allows the individual to reap the benefits of increased cooperation and opportunities for reciprocal altruism, along with increased mating opportunities. Alternatively, a misunderstanding of one's status would be detrimental. Therefore, it seems likely that not only would individuals be motivated to accurately assess their social status but that there would also be evolved mechanisms to facilitate this process. Indeed, it has been proposed that self-esteem acts as a status-tracking mechanism such that high self-esteem is indicative of higher status and inclusion among peers, whereas low self-esteem would reflect lower status in the group (Leary et al. 1995). A historical perspective on sociometer theory will be provided, followed by a discussion of the connections between sociometer theory and various outcomes (e.g., romantic relationships), and will close with a discussion of new developments in sociometer theory.

Perspectives on Self-Esteem

In the current research literature, self-esteem is often defined as the evaluative aspect of the self that is concerned with the degree to which people like themselves (Brown and Marshall 2006). In other words, self-esteem reflects the amount of worth and value an individual places on himself or herself. Thus, individuals with higher levels of self-esteem are more likely to view themselves in a relatively favorable light, whereas individuals with lower levels of self-esteem will tend to view themselves more negatively or at least be uncertain about their self-

views. High self-esteem has been found to be associated with a variety of important life outcomes (e.g., psychological well-being). In contrast, low levels of self-esteem have been shown to be associated with an array of negative outcomes (e.g., criminal behaviors; see Zeigler-Hill 2013, for a review). Despite the associations linking self-esteem with various important life outcomes, there has been a great deal of debate in recent years concerning the value of self-esteem with some researchers continuing to argue that self-esteem is an important construct (e.g., Zeigler-Hill 2013), whereas other researchers have adopted a much more negative view of self-esteem and consider it to be an epiphenomenon that has – at best – limited value (e.g., Baumeister et al. 2003).

This conflict over the importance of self-esteem can be resolved when a more nuanced approach to self-esteem is taken. More specifically, researchers have recognized that it may be important to account for aspects of self-esteem beyond its level because individuals with high levels of self-esteem appear to be a heterogeneous group consisting of those with *secure* high self-esteem and those with *fragile* high self-esteem (see Jordan and Zeigler-Hill 2013, for a review). Secure high self-esteem reflects positive attitudes about the self that are realistic and resistant to threat, whereas fragile high self-esteem refers to feelings of self-worth that are vulnerable to challenge and require constant validation. This distinction between secure and fragile forms of self-esteem adds depth to our understanding of self-esteem in that it helps us to understand how self-esteem level might fluctuate in the short term following different types of feedback. In turn, this has helped to elucidate previously conflicting findings. However, understanding secure and fragile self-esteem does not address the function and purpose of self-esteem. The question of the purpose of self-esteem is at the core of sociometer theory (Leary et al. 1995). The central premise of sociometer theory is that self-esteem functions as a status-tracking mechanism which provides important insights into the purpose and development of self-esteem.

Introduction to Sociometer Theory

The sociometer theory was developed in an attempt to provide an explanation about the purpose of self-esteem (Leary et al. 1995). More specifically, the concept of affiliation has an evolutionary foundation because relationships with other people have been important for human survival, reproduction, and the survival of offspring over the course of evolutionary history. For example, maintaining close proximity to other people has offered individuals with protection and opportunities to effectively solve social issues (Leary 2010). The driving force behind the self-esteem system is the fundamental need to associate with other people and build relationships that are strong and lasting (Stinson et al. 2015). This perspective states that the self-esteem system is developed in order to protect people from the negative consequences of social exclusion by monitoring the social environment for signals concerning social acceptance and social rejection (Leary 1999, 2010).

According to sociometer theory, self-esteem has a *status-tracking property* such that an individual's level of self-esteem depends on his or her relational value. Sociometer theory argues that self-esteem is an evolved regulatory system and adaptation that helps people establish and sustain meaningful relationships (Leary et al. 1995; Stinson et al. 2015) by allowing individuals to monitor the degree to which they are valued by others. In essence, self-esteem serves as a gauge that alerts individuals to either gains in their relational value (accompanied by increases in self-esteem) or losses in their relational value (accompanied by decreases in self-esteem). An important element of the sociometer theory is that changes in self-esteem may trigger compensatory mechanisms. For example, individuals who perceive a decrease in their state self-esteem should be motivated to engage in compensatory behaviors – such as being nicer to other people – in an effort to increase their relational value. A central tenet of sociometer theory is that people do not actually care about self-esteem for its own sake. Rather, self-esteem is only important because it indicates the degree to which

individuals are valued by others in their social environments (Leary et al. 1995). Sociometer theory provides a reason for self-esteem and moved away from previous approaches that simply suggested that individuals have an inherent need to feel good about themselves. Sociometer theory suggests that self-esteem functions as a means to motivate individuals to act in ways that increase their acceptance and decrease the likelihood of rejection within their social groups. That is, boosting self-esteem is not the ultimate objective but is simply a consequence of increasing relational value and avoiding rejection (Leary 1999, 2010).

Consistent with sociometer theory, a large number of studies have shown that self-esteem is responsive to social acceptance and rejection (e.g., Leary et al. 2001). The majority of sociometer research has focused on the consequences that acceptance and rejection have on mood and state self-esteem (e.g., Leary et al. 2001), but there have been attempts to expand sociometer theory in various ways such as by examining the implications of this perspective for social decision-making (Anthony et al. 2007). When making a social decision, people calculate the probability of social rewards (e.g., developing a new friendship) versus social costs (e.g., experiencing a rejection). People either engage in self-enhancing behaviors (e.g., seek social experiences) in order to achieve social awards or self-protecting behaviors (e.g., avoiding social experiences) in order to limit social costs (Baumeister et al. 1989). The sociometer monitors relational value in one's environment, but the resting point of the sociometer (i.e., self-esteem level) may impact one's relational value. For example, people with high self-esteem are more secure with their relational value and have a higher threshold for acceptance. As a result, people with higher levels of self-esteem are more likely to exhibit self-enhancing behaviors by forming new relationships regardless if there is a direct sign of group acceptance (Anthony et al. 2007). In contrast, people with low self-esteem are more likely to display self-protection behaviors because they anticipate rejection. As a consequence, people with lower levels of self-esteem avoid forming new

relationships unless there is a direct sign that the group will accept them (Anthony et al. 2007). It appears that people with low self-esteem are more reluctant to form relationships because of their fear of rejection. However, this need to protect one's empty relational value can be disregarded with unambiguous proof of acceptance. In sum, these findings support that the calibration of the sociometer is derived from acceptance and rejection in one's environment and directs one's social behavior (Anthony et al. 2007).

Multiple Domains

Individuals are able to function in a wide variety of environments that have different adaptive problems and these problems entail different solutions. A single sociometer or gauge may be ineffective at detecting an individual's relational value in different social environments. For example, a sociometer that monitors relational value in romantic relationships may be helpful for assisting a person's mate-selection strategies, but not for indicating a person's relational value in his or her workplace (Kirkpatrick and Ellis 2001). As a result, Kirkpatrick and Ellis (2001) proposed that self-esteem is not a unitary construct and that natural selection may have designed multiple psychological mechanisms for monitoring relational value in different social environments (i.e., domain-specific sociometers). However, the question regarding how many different sociometers in fact exist remains unanswered, but any interpersonal relationship that is important for survival may have a distinct sociometer (e.g., instrumental coalitions, mating relationships, familial relationships; Kirkpatrick and Ellis 2001).

Hill and Buss (2006) argue that self-esteem is not a unitary construct because it may be too limited to capture the numerous adaptive problems that individuals are likely to encounter. Rather, they suggest that self-esteem consists of a number of psychological components (e.g., internal representations, monitoring mechanisms, updating mechanisms, evaluative mechanisms, motivational mechanisms, mechanisms to generate output). More specifically, the first

psychological element to self-esteem is the ability to maintain *internal representations* of one's own capabilities. Maintaining an awareness of one's abilities allows the individual to compare oneself to other people during ambiguous situations and to make careful behavioral decisions. The ability to have *monitoring mechanisms* that are domain-specific provides an individual with cues about potential changes in one's relational value in different environments. This is important because an individual's ability to solve adaptive problems may change over time due to past experiences (e.g., the birth of a child). When the monitoring mechanisms detect a success or failure, it informs the *updating mechanisms* component of this new information which results in changes of internal representations. The fourth aspect of self-esteem is *affective evaluation* and this component is designed to evaluate internal representations. For example, trait self-esteem occurs when the affective evaluation consists of stable repetitions, as opposed to state self-esteem, which is an evaluation of updates or fluctuations. According to Hill and Buss (2006), none of these psychological mechanisms would exist without some motivational aspect. The affective evaluation component of self-esteem motivates people to engage in behaviors regarding their newly updated internal representations. The last component of self-esteem is the specific behavioral output and this underpinning takes into account that behavioral solutions are expected to change.

In addition, Hill and Buss (2006) further extended the theory regarding domain-specific sociometers by suggesting that attributes in one domain may contribute to successes in different domains. For example, good health increases an individual's value as a mate but may also have implications for perceptions of that individual as a friend and family member. If an attribute is specific to a domain, then it will be positively correlated with that domain and weakly correlated with other domains (Kavanagh and Scrutton 2015). An example is the attribute of physical attractiveness which plays an important role in the mating domain, but is not viewed as essential in other domains (e.g., coalitional domain; Cottrell et al. 2007). Attributes that contribute to multiple

domains may explain why self-esteem level has been found to be positively associated with different facets, and this approach may serve as a way to distinguish between domain-specific and domain-general attributes (Hill and Buss 2006).

The Mating Sociometer

From an evolutionary standpoint, selecting and retaining a mate is a primary concern (Buss 1988). Socially speaking, entire holidays and rituals have developed around mating. Furthermore, a large number of studies have been conducted to examine the factors that influence the selection and retention of mates (e.g., Buss 1988). These studies have revealed that individual differences – such as self-esteem – play a role in these processes. Furthermore, in accordance to sociometer theory, self-esteem level can be seen as an indicator of mate value (Holden et al. 2014).

After a mate has been selected, the next challenge for successfully rearing offspring is in retaining that mate. A variety of mate retention behaviors have been documented. That is, an entire taxonomy of behaviors that are intended to prevent the defection of a mate has been developed (Buss 1988). There are a large number of mate retention behaviors but they can be classified along the broader domains of benefit-provisioning and cost-inflicting behaviors. Benefit-provisioning behaviors are designed to make the relationship more positive and decrease the likelihood of defection by bestowing gifts and affection on the partner. Conversely, cost-inflicting behaviors are designed to make defection costly to the partner through manipulation and abuse. Furthermore, these two domains differ in terms of the costs and risks faced by the individual using these mate retention behaviors. More specifically, benefit-provisioning behaviors can be seen as low risk in that they have a low likelihood of having negative consequences for the relationship, but these behaviors are also high cost in that they involve the investment of time and resources in the partner. The opposite is true of cost-inflicting behaviors. These mate retention behaviors can be considered to be high risk, but

low cost. Therefore, individuals may essentially be choosing between these two sets of tactics. A number of individual differences and situational factors may play a role in the decision between benefit-provisioning and cost-inflicting behaviors. However, self-esteem level has been demonstrated to have a profound impact on the use of mate retention behavior.

As mentioned above, self-esteem level, through the lens of sociometer theory, can be seen as an indicator of mate value (Holden et al. 2014). In turn, individuals partnered to someone of high mate value should be more motivated to retain that partner. Indeed, it has been demonstrated that individuals who are partnered with someone who is high mate value tend to engage in more mate retention behaviors (Starratt and Shackelford 2012). In other words, these individuals are motivated to hold on to this valuable reproductive resource. However, not all individuals can invest in these mate retention behaviors equally. That is, some individuals may be more prone to engage in benefit-provisioning behaviors, whereas others may be more prone to engage in cost-inflicting behaviors.

Indeed, it has been demonstrated that self-esteem level influences mate retention behavior, such that individuals who report high levels of self-esteem tend to engage in benefit-provisioning behaviors, whereas individuals who are low in self-esteem tend to engage in cost-inflicting behaviors (Holden et al. 2014). Furthermore, individuals who are held in a higher regard by their partner report less use of cost-inflicting behaviors and are perceived to engage in more benefit-provisioning behaviors (Holden et al. 2014). Put in terms of sociometer theory, this suggests that information about an individual's perceived relational value influences their decisions concerning how they manage their relationships.

Previous work has demonstrated that assortative mating occurs in humans as it does in other species. For example, individuals tend to select partners who are similar in physical attractiveness and personality characteristics as mates (e.g., Buss 1985). The mating sociometer suggests the

mechanism behind this process. Namely, the information that individuals receive through rejection influences their decisions with regard to mate selection. That is, the sociometer may function in this domain to tell individuals about their probability of obtaining particular mates. Indeed, it has been demonstrated through research using dating paradigms that rejections from potential mates are followed by a decrease in self-esteem and, in turn, a decrease in mating aspirations (i.e., selection of less-attractive mates, avoiding potential mates; Kavanagh et al. 2010). Furthermore, this mating sociometer may be differently tuned between the sexes (Bale and Archer 2013). Therefore, it appears as though the sociometer is particularly well-suited for the domain of mating and may be quite helpful in guiding the mating efforts of individuals.

Attachment Theory

Sociometer theory can also help us to better understand attachment perspectives. It has been found that attachment perspectives vary between individuals and as a result different strategies are used to regulate and detect relational value (Bowlby 1969). Also, sociometer theory and attachment theory have similar aspects (e.g., a need to belong) which support the idea that there is an interpersonal purpose for the affective and behavioral regulation system (Srivastava and Beer 2005).

Attachment theory has two dimensions which include an *avoidance* and an *anxiety* dimension. These attachment dimensions explain differences in regulatory systems of adults (Srivastava and Beer 2005). Individual differences in anxious attachment are explained by *hyperactivating strategies* which occur when a person uses extreme measures in order to receive support from others (Mikulincer and Shaver 2003). In contrast, individual differences in avoidant attachment are explained by *deactivating strategies* which are used when an individual needs to protect himself or herself from rejection and does so by avoiding others (Mikulincer and Shaver 2003). These

hyperactivating and deactivating strategies may have implications for the sensitivity or regulation of the sociometer (Mikulincer and Shaver 2003). For example, high-anxious individuals have been found to have a sensitive sociometer, whereas avoidant individuals have been found to have a sociometer that is less responsive to certain situations (e.g., Srivastava and Beer 2005).

Numerous studies have found a relationship between attachment perspectives and the sociometer (e.g., Foster et al. 2006; Srivastava and Beer 2005). For example, it has been found that perceived likability in one's social environment resulted in more positive self-evaluations, which provides support for the sociometer theory (Srivastava and Beer 2005). In addition, Foster and his colleagues (2007) found that unstable self-esteem was associated with less secure attachment, which validates the reason for the sociometer (i.e., state self-esteem fluctuates in response to acceptance and rejection). In sum, the impact that anxiety has on self-esteem shows support for a relationship between attachment perspectives and sociometer theory (Srivastava and Beer 2005).

The Extended Informational Model of Self-Esteem

Sociometer theory indicates that self-esteem has a status-tracking property which measures an individual's relational value in his or her social environment. This status-tracking property of self-esteem is an important addition to the self-esteem literature because it explains the function of self-esteem. However, the status-tracking model does not take into consideration other ways in which information is exchanged between an individual and other people in his or her social environment (Zeigler-Hill 2012). For example, the status-tracking property of self-esteem does not address how an individual's level of self-esteem may impact how he or she is perceived by another person. This is the focus of the *status-signaling* model of self-esteem (Zeigler-Hill et al. 2013) which focuses on the possibility that an individual's self-

esteem level may affect how that individual is perceived by other people in his or her social environment. For example, self-esteem may influence how one is perceived on various dimensions (e.g., romantic desirability, social dominance) such that individuals who convey high levels of self-esteem may generally be viewed more positively than those who express low self-esteem. This suggests that people may be motivated to maintain or improve their self-worth because their self-esteem may influence how they are viewed by other people (Zeigler-Hill 2012). The status-signaling model of self-esteem is believed to complement the status-tracking properties of self-esteem captured by sociometer theory and provide a more comprehensive understanding of self-esteem.

Conclusion

Sociometer theory is an important addition to self-esteem research because it provides a possible function for self-esteem. This is important because questions concerning what self-esteem actually does had largely been ignored prior to the introduction of sociometer theory (Leary 1999). There is a tremendous amount of research concerning the correlates and consequences of self-esteem, and sociometer theory is helpful for integrating much of that work by providing a clear function for self-esteem (i.e., monitoring relational value in the current social environment). Sociometer theory has been supported by numerous studies and provides an explanation for the intimate connections that have been observed between self-esteem and social acceptance. Also, sociometer theory provides a rationale as to how individuals monitor their relational value in a specific domain. However, future research should focus on important issues such as whether there is a single domain-general sociometer or several domain-specific sociometers (e.g., position in a social hierarchy; Mahadevan et al. 2016). Continued research concerning sociometer theory will help to clarify the purpose and functioning of self-esteem from an evolutionary perspective.

Cross-References

- ▶ [Changes in Self-Esteem Motivate Behavioral Changes](#)
- ▶ [Mate Value](#)
- ▶ [Reproductive Value](#)
- ▶ [Roy Baumeister](#)
- ▶ [Self-Concept](#)
- ▶ [Self-Esteem as Manipulative Status Communication](#)
- ▶ [Self-Esteem Increase Motivates Similar Behavior](#)
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Self-Esteem as Manipulative Status Communication

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Synonyms

Confidence; Dignity; Personal value; Pride; Self-regard; Self-worth

Definition

Self-esteem is a widely used concept in psychology and has been defined in numerous ways. Self-esteem can be described as an individual's overall sense of self-worth or personal value. It is generally accepted that self-esteem is the evaluative component of the self-concept. The self-concept is an extensive representation of the self that also includes cognitive and behavioral characteristics (Blascovich and Tomaka 1991). Within psychological research, self-esteem has been linked to a

variety of domains, from personality, clinical, and behavioral concepts to eating disorders, aggression, and criminality. Almost all psychology theory refers to self-esteem, and as such, it is widely agreed that the need to maintain and enhance self-esteem is central to human behavior (Leary et al. 1995).

Introduction

This entry focuses on three key evolutionary perspectives of self-esteem; sociometer theory, ethological perspective, and terror management theory. Each perspective will be discussed in relation to how they present the function of self-esteem and how this may contribute to an individual's manipulative communication with others.

Sociometer Theory

Many theories have difficulties when attempting to fully explain the purpose of self-esteem. Sociometer theory was offered as a new perspective, in order to help answer the questions other theories found problematic. Sociometer theory was developed by Leary et al. (1995) who proposed that self-esteem is an adaptation in the form of a gauge that monitors interactions an individual has with others. This gauge sends signals to the individual informing them as to how socially acceptable their behaviors are. According to this theory, all humans have an innate desire to have interpersonal relationships and to maintain these in a productive way. The desire for interpersonal relationships has been evolving since the beginning of the human species, as those who were part of formed groups had the highest chances of survival and, subsequently, reproduction. Individuals have evolved to have the ability to sense signals from this psychological gauge which alerts them to how much they are accepted or rejected by others and how well their overall behavior is aiding their integration into society (Anthony et al. 2007). The importance of an individual's relationship with others is often dependant on the reactions they receive from them. The sociometer is very

sensitive to even the slightest change in these perceptions, and as such, when an individual's behavior is initiating a decrease in their evaluation, the sociometer makes them aware that there is a threat to their social acceptance, which then drives them to confront the problem. According to Leary et al. (1995), there are two variations of self-esteem: state self-esteem and trait self-esteem. State self-esteem refers to the perception of changes in an individual's level of social inclusion, given a particular setting. Self-esteem increases or decreases based on positive or negative feedback. Trait self-esteem refers to an individual's accumulated lifelong perception of social inclusion and exclusion. This is sometimes considered the resting position for the sociometer as this is how an individual feels when interpersonal information is absent (Leary et al. 1995).

Sociometer theory explains much human behavior and addresses important questions concerning self-esteem (Anthony et al. 2007). A common belief is that self-esteem is to be maintained or increased; however, the sociometer theory explains that its exact function is to reduce the chances of social rejection (Leary et al. 1995). Research has suggested that low self-esteem is related to a variety of issues such as academic failure, substance abuse, depression, anxiety, and criminal behavior; however, according to Leary et al. (1995), these relationships are typically overemphasized. From the perspective of the sociometer theory, these issues are actually due to low interpersonal evaluations and sometimes social rejection. In other words, low self-esteem is not the cause of these issues, but rather, levels of self-esteem and the psychological behavioral problems co-occur. When this happens, further issues may develop and maladaptive behaviors become more common.

As sociometers monitor individuals' current standing in order to guide them toward adaptive strategic choices, it could be expected that they are designed to do this accurately. However, interestingly, there is a substantial amount of literature suggesting that most individuals have modestly inflated views of themselves and, as a result, display a variety of "positive illusions" (Taylor and Brown 1988). Krebs and Denton

(1997) explain that positive illusions to in-group and out-group biases reflect the adaptive design of these cognitive systems rather than malfunctions. In other words, sociometers may be regulated by an adaptive, built-in, positive bias. This may have implications on the behavior of individuals, specifically when interacting with others. As an individual's value or current standing in interpersonal environments is the function of how others evaluate them, the main way to increase their value could be to deceive others using manipulative communication. However, the effectiveness of impression management strategies is limited when the individual is not convinced of their levels of worth they are promoting to others, as all humans are skilled at detecting this form of deception in self-presentation (Zahavi and Zahavi 1997). "Positive illusions" may therefore denote a form of self-deception designed to increase the effectiveness of an individual's attempt to convince others to overvalue them, primarily due to their built-in positive bias or, in other words, because they believe in the level of worth they present (Kirkpatrick and Ellis 2003).

Ethological Theory

Ethology regards the adaptive value of behavior and its evolutionary history. The origins of ethology can be traced back to Darwin, the very first ethologist. His key belief was that behavioral traits are part of organisms' evolved phenotypes. During the 1960s, its application to research began; however, it has become more influential in recent years.

In relation to self-esteem, the ethological perspective proposes that it is an adaptation that has evolved in order to maintain dominance in relationships (Barkow 1980). According to this theory, human beings have evolved specific mechanisms to monitor dominance, as this is what facilitated the attainment of a mate. Favorable reactions and attention from others were associated with being dominant; thus, feelings of self-esteem became attached to social approval and respect. From this perspective, the motive an

individual has to enhance themselves positively, in evolutionary terms, is to enhance their relative dominance (Leary 1999). As this perspective deems an individual's dominance as crucially important in order to form relationships and reproduce, it's probable that humans will do anything they can to maintain this dominance. This could include using forms of manipulative communication such as telling lies, blackmailing, cheating, and seducing. More specific forms of this will be discussed in the following two short chapters, "Projected Confidence" and "Derogation of Rivals."

Terror Management Theory

Terror management theory is based on the writings of Becker (e.g., 1962) and Rank (e.g., 1941) and proposes that human beings continuously seek out ways to improve their self-esteem in order to protect them from the fear of death (Greenberg et al. 1986). According to this theory, the fear of death creates an instinct for self-preservation, just like other species. However, despite it being the same instinct, only humans are conscious that eventual death is unavoidable, and therefore, the self-preservation instinct will inevitably fail. This combination of an instinctive drive for self-preservation and the knowledge that eventual death is unavoidable can create debilitating terror (Harmon-Jones et al. 1997). The possibility of experiencing this terror is managed by a cultural anxiety buffer consisting of the cultural worldview and self-esteem. "The cultural worldview is defined as a set of beliefs about the nature of reality shared by groups of individuals that provides meaning, order, permanence, stability, and the promise of literal and/or symbolic immortality to those who live up to the standards of value set by the worldview" (Harmon-Jones et al. 1997, p. 24). Due to the cultural anxiety buffer being a social creation, humans are dependent on others to validate and maintain it. As a result, the terror management theory proposes that a large percentage of behavior, both on an individual and social level, is specifically carried out to protect the cultural worldview and self-esteem.

Similar to the other theories already discussed, within the terror management theory, self-esteem provides protection against anxiety. Therefore, the higher the self-esteem one has, the less prone they are to experience anxiety and thus display anxiety-related behaviors. For example, various studies have demonstrated that the higher the self-esteem one has, the less they are to experience death anxiety (e.g., Templer 1971). In addition, any threats which may reduce self-esteem may cause one to behave defensively in response, for example, making excuses (Mehlman and Snyder 1985) and ego-defensive attributions (Gollwitzer et al. 1982). This behavior would involve one manipulating others in order to enhance their perceived social value and, as a result, protect their anxiety buffer.

Conclusion

It is clear that the three key evolutionary perspectives of self-esteem discussed above share common themes in terms of the functions of self-esteem. Firstly, they are all concerned with protecting and preserving self-esteem. The reasoning behind this differs with each theory; however, the general principle is the same that self-esteem is important in order for individuals to live a fruitful life. Secondly, due to this importance, when their levels of self-esteem are threatened in any way, individuals will behave, sometimes undesirably, in order to protect it. As a result, various forms of manipulative communication with others can occur such as deception, telling lies, blackmail, and cheating, in order to maintain their perceived social value and self-esteem. In the next two short chapters, there will be a discussion into how individuals may manipulate others in specific ways, by “Projected Confidence” and the “Derogation of Rivals” and how specific personality constructs may accentuate this.

Cross-References

- [Derogation of Rivals](#)
- [Projected Confidence](#)

- [Self-Esteem Reflects Assessments of Valuation](#)
- [Sociometer Theory](#)

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Self-Esteem as Self-Perceptions of Social Worth

- [Self-Esteem Increase Motivates Similar Behavior](#)
- [Self-Esteem Reflects Assessments of Valuation](#)

Self-Esteem Feelings

- [Sociometer Theory](#)

Self-Esteem Increase Motivates Similar Behavior

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Synonyms

[Self-esteem and perceived social value](#); [Self-esteem as self-perceptions of social worth](#)

Definition

Self-esteem is a theory that addresses an individual's overall affective feeling of self-worth. Individuals differ both in their stable sense of self-esteem and in their self-esteem responsive to stimuli. Humans are highly motivated to increase

self-esteem and thus experience motivation to engage in similar behavior as that which previously boosted these feelings of self-worth.

Introduction

Self-esteem describes an individual's overall sense of self-worth or value based on an affective evaluation regarding the self. This evaluation encompasses both feelings about the self (e.g., "I am worthy") and emotional states, such as pride or shame. This differs from the self-concept in that one's self-concept encompasses thoughts and beliefs about the self. Self-esteem may be global (i.e., "I'm a good person"), or it may be domain specific (i.e., "I'm great at basketball"). Some individuals tend to have higher self-esteem than others on a consistent basis. This is *trait self-esteem*, as it reflects an individual's general tendency. While trait self-esteem is fairly stable across time, it is subject to short-term fluctuations based on individual experiences. For example, should something positive occur, such as receiving a promotion at work, an increase in self-esteem is likely to occur. Known as *state self-esteem*, these fluctuations influence both perception and behavior (Cihangir et al. 2010).

Rationale for Self-Esteem

Historically, approaches to self-esteem have been contradictory, arguing that it is a self-evaluation largely based on the perceived evaluations of others. Edward Higgins attempted to address this paradox through the theory of self-discrepancy. He theorized that individuals have multiple representations of the self, such as the ideal self and the actual self (1987). Self-discrepancy refers to the gap between these representations; as this gap grows, self-esteem becomes increasingly lower (Moretti and Higgins 1990). A large gap between the actual self and the ideal self is associated with low self-esteem and vice versa.

More recent work has produced two predominant explanations for the development of self-esteem in humans. Sociometer theory suggests

that humans are inherently social creatures that seek out the support and approval of others (Leary et al. 1995). As such, humans have developed a “sociometer” that allows one to detect social acceptance or rejection and translate these as increased or decreased self-esteem. The second primary theory is terror management, which argues that humans are uniquely aware among animals, of one’s impending death (Greenberg et al. 1986). To protect oneself from this paralyzing fear, humans construct beliefs, such as religion or patriotism, which provide them a sense of meaning and purpose. This sense of purpose is what one experiences as self-esteem, thereby reducing anxiety regarding one’s own mortality. Although there are conceptual variations among the current models of self-esteem, all posit that humans have an inherent drive to increase self-esteem.

We see that humans high in self-esteem tend to experience more success in life as they often approach challenges more confidently, viewing them as a way to demonstrate their abilities (Baumeister et al. 2003). Conversely, those lower in self-esteem are often simply hoping to avoid failure. Individuals high in self-esteem tend to be happier compared to people lower in self-esteem. Self-esteem is positively correlated with both life satisfaction and personal relationship satisfaction. Thus, people high in self-esteem tend to report both more stable dating relationships and more happiness within those relationships. Self-esteem is negatively correlated with a variety of mental health issues, such as depression and anxiety.

Learning, Motivation, and Behavior

Broadly, learning can be defined as the alteration of behavior resulting from individual experience. Although learning theory has advanced a great deal since the seminal works of Pavlov and Skinner, most human learning is considered associative in nature, entailing a process in which a new response becomes associated with a particular stimulus. While operant conditioning accounts for voluntary behavior, it is important to note that one need not be consciously aware of the rewards and punishments that shape one’s action (Esteves et al. 1994).

Motivation is simply our drive to do things. Thus, motivation involves goal-directed behavior, such as choosing between completing a homework assignment or napping on the couch instead. Although there are competing models of motivation, most distinguish between extrinsic motivation (doing something for an external reward) and intrinsic (doing something for an internal reward). Despite the traditional view that these two motives are at odds, more recent work has suggested that at times they may operate in tandem (Covington and Müeller 2001). This is consistent with the perspective that self-esteem fluctuations motivate behavior, as self-esteem relies on a view of the self processed through the eyes of others. Therefore, motivational drive is intrinsically linked with self-esteem. A high level of self-esteem often provides one with the motivation to take on multiple tasks. Equally important, due to the negative consequences of low self-esteem (e.g., depression), humans have strong motivation to engage in self-esteem-bolstering tasks. Fortunately, this proves effective, as humans have the capacity to learn (both consciously and nonconsciously) what behaviors result in higher levels of state self-esteem (Leary et al. 1995).

Indeed, we see that when humans experience an increase in state self-esteem driven by behavior, there is a learned response to engage in the same, or similar, behavior in the future. This has been documented for a wide range of human behavior, encompassing activities societally endorsed (e.g., athletic motivation and academic performance) as well as those in which society tends to take a harsher view (e.g., substance abuse and promiscuity). Beyond personal activities, self-esteem motivates human behavior in interpersonal settings. For example, state self-esteem predicts whether one is motivated to engage in a playful or an aggressive style of teasing others (Honeycutt and Wright 2017). Similar results have been found in such diverse domains as human interaction in online video gaming and motivation to self-disclose with others on social media. Much like a rat pressing a lever, humans will intuitively seek out the same behavior that bolstered self-esteem previously. In instances when the same opportunity is not available, such as the lack of a previous sexual partner or psychotropic chemical, humans are also

very adept at finding similar substitutes. Drug substitution is a common phenomenon encountered in therapeutic settings. Substitutive behavior is seen in a variety of domains, however, squashing the notion that it is simply the result of drug addiction. Rather, it can be likened to a self-esteem addiction, with individuals seeking other methods to achieve their self-esteem needs. Despite sounding extreme, humans have demonstrated that they are willing to forgo such pleasant activities as sex, eating, consuming alcohol, and even receiving a paycheck if they can receive a self-esteem boost instead (Bushman et al. 2011).

Conclusion

There are many sources of motivation for human behavior. Perhaps none is as powerful, though, as the need to feel a sense of personal worth. Through both conscious and nonconscious processes, humans learn what behaviors bolster self-esteem, as well as those that hamper it. In a variety of settings, humans demonstrate motivation to repeat behavior that has improved self-esteem previously. As self-esteem is crucial to an adaptive existence, humans are highly motivated to identify those actions that increase feelings of self-worth and to engage in similar behavior, even when that involves maladaptive behavior.

Cross-References

- [Changes in Self-Esteem Motivate Behavioral Changes](#)
- [Evolution of Self](#)
- [Self-Esteem as a Status-Tracking Mechanism](#)
- [Sociometer Theory](#)

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Self-Esteem Reflects Assessments of Valuation

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Synonyms

Self-esteem and perceived social value; Self-esteem as self-perceptions of social worth

Definition

The self-esteem system is a psychological adaptation that services the need to belong by regulating social thinking, feeling, and behavior. It functions in part by monitoring, and eventually internalizing, one's perceived value as a relational partner, both globally and in specific social domains.

Introduction

Human beings rely on their social bonds to survive and to thrive. In the early ancestral environment, a lone individual would not have fared well against predators or the natural elements. To survive and successfully reproduce, people needed to establish strong bonds with others and then work to maintain those bonds over time. Thus, natural and sexual selection shaped humans into a uniquely social species, possessing psychobiological adaptations designed to help them navigate the complexities of social interaction. Such adaptations include a powerful need to belong, which functions in part by rewarding social need fulfillment and punishing those who fail to nurture their social bonds (Baumeister and Leary 1995). For example, over and above the effects of satisfying the basic physical needs for survival, forming and maintaining high-quality social bonds brings rewards like feelings of life satisfaction, security, and general well-being, whereas failing to form such bonds results in costs like depression, intense loneliness, poor physical health, and even premature death (e.g., Cohen 2004; Uchino 2006). To service the need to belong, humans developed additional adaptations aimed at helping them to form and maintain high-quality social bonds. One such adaptation is the self-esteem system, which functions in part by monitoring, and eventually internalizing, one's perceived relational value.

Global Self-Esteem Reflects Perceived Global Relational Value

To understand how the self-esteem system services the need to belong, it is first necessary to

understand how social relationships shape the development of the self. Cooley (1902) and Mead (1934) were among the early theorists to acknowledge and document the relational nature of the self. Cooley coined the phrase “the looking glass self” to refer to the process whereby people learn to see themselves as others do. From this perspective, people's interactions with others and their perceptions of how others view the self play a significant role in shaping their sense of self and identity. For example, when a mother compliments her young daughter's artistic efforts and proudly displays her daughter's artwork on the fridge, the young girl may internalize that positive impression of her artistry, and, with time, she may come to identify as creative and artistic. As part of this broader process of self-concept development, self-esteem is also formed. Self-esteem is a core aspect of the self and reflects one's feelings of worth or value as a person. Although self-esteem is influenced by genetics and temperament (Niess et al. 2002), it is also intimately tied to the quality of one's social relationships. People infer their worth from the way they are treated by others. If they feel cared for and respected in their social relationships, they will develop the sense that they are a worthy and valued relational partner. In contrast, if they feel rejected and neglected or if they feel that others are simply unresponsive to their needs, they will develop the sense that they are not a worthy or valued relational partner. Over time, these social messages and experiences become internalized and manifest as one's sense of global self-esteem. Thus, global self-esteem is intimately twined to one's *perceived relational value*, which is one's perceived worth and value as a social partner. Indeed, some theorists have even gone so far as to propose that the two constructs are virtually synonymous.

According to sociometer theory, global self-esteem is a person's internalized sense of their perceived relational value (Leary 2004). Thus, self-esteem is proposed to be a *sociometer*, a barometer that indexes one's perceived relational value. Over time, repeated experiences of being valued by others, being treated with respect and kindness, and enjoying responsive care from loved ones create feelings of high perceived

relational value, which are then internalized into a feeling of high self-esteem. In essence, “other people value me,” becomes “I am valuable.” In contrast, repeated experiences of being devalued by others, being treated with disrespect and disregard, and experiencing unresponsive or neglectful care from loved ones create feelings of low perceived relational value, which are then internalized into a feeling of low self-esteem. In this situation, “other people do not value me,” becomes “I am not valuable.”

In turn, these self-views become an important compass for helping people to navigate their social worlds. People rely on their self-esteem to make sense of their past, present, and anticipated future social experiences. In short, higher self-esteem imbues a confidence in others’ regard and acceptance, whereas lower self-esteem does not. This confidence subsequently influences how individuals interpret their social world. For example, when people are asked to imagine interacting with a romantic partner whose negative mood has no obvious cause, lower self-esteem individuals (LSEs) and higher self-esteem individuals (HSEs) make very different attributions for their partner’s bad mood (Bellavia and Murray 2003). Because HSEs are confident about their partner’s positive regard, they are unlikely to blame themselves for their partner’s negative mood. In contrast, because LSEs are less confident about their partner’s positive regard, LSEs are more likely to feel responsible for their partners’ negative mood. Moreover, when individuals are uncertain of their likelihood of being accepted, LSEs’ social insecurity leads them to feel anxious and motivated to protect themselves from the rejection they anticipate (Stinson et al. 2009). Yet in the same ambiguous social situation, HSEs’ social confidence leads them to feel optimistic and motivated to pursue the acceptance they anticipate. In this way, self-esteem helps people make sense of, and learn from, what can often be ambiguous or confusing social experiences.

People also use their self-esteem to regulate their social behavior. For example, when they interact with a new social partner for the first time, LSEs self-protectively engage in more inhibited behaviors such as closed posture and

averted gaze, whereas HSEs promote new relationships by decreasing their use of inhibited behaviors and increasing their use of warm behaviors such as smiling and eye contact (Stinson et al. 2015). As this example attests, LSEs’ and HSEs’ social behaviors can look quite different in the same social situation. Yet the underlying motivation remains constant: People are motivated to maximize their belongingness and minimize the risk of rejection. How to go about achieving that goal will necessarily depend on one’s relational value and, relatedly, on the perceived probability of acceptance or rejection in a given situation. Because this relational calculation will be different for people of varying levels of self-esteem, people of varying levels of self-esteem will often behave quite differently in the same social situation. Thus, although LSEs may typically focus on avoiding rejection and HSEs may typically focus on achieving belonging, both types of behavior ultimately service the paramount need to belong.

In all of these examples, self-esteem is able to perform these adaptive functions specifically because it reflects people’s assessment of their relational value. But these examples have focussed on global self-esteem and global perceptions of relational value. In fact, the self-esteem system also includes *domain-specific* components that also help service the need to belong as well as other closely related social goals. That is, in addition to internalizing a global perception of their relational value, people also internalize a sense of their relational value within specific social contexts, or *domains*, resulting in domain-specific self-esteem (sometimes also called *self-evaluations*; Brown & Marshall, 2006).

Domain-Specific Self-Esteem Reflects Perceived Domain-Specific Relational Value

Social relationships are complex and varied, and so it is improbable that people possess just one psychological adaptation to help them navigate the varied social dilemmas they will face (Kirkpatrick and Ellis 2001). Romantic relationships, friendships, family relationships, and

workplace relationships each pose their own unique set of demands, and the qualities and behaviors that make one a valuable relational partner in one type of relationship are not necessarily the same qualities and behaviors that make one a valuable relational partner in another type of relationship. For example, a man's modest and sensitive nature may make him a valuable friend and confidant, but these same qualities may hinder his likelihood of advancing to a management position within a workplace that strongly values dominance in their employees (Moss-Racusin et al. 2010). Because people's skills and talents vary widely and few people are likely to possess the myriad traits necessary to succeed in every social domain, it is possible that the same person can have relatively positive social experiences in one domain, but relatively negative social experiences in another domain. Because such experiences will be internalized over time, it is also possible that the same person can have relatively high self-esteem in one domain, but relatively low self-esteem in another domain.

In turn, just as global self-esteem helps people to navigate their social relationships in general, domain-specific self-esteem helps people to navigate their social relationships within the specific, relevant domain (Kirkpatrick and Ellis 2001). So people rely on their domain-specific self-esteem to make sense of their past, present, and anticipated future social experiences in that specific domain. For example, if two women are decorated athletes on their university's swim team and have similarly high levels of athletic self-esteem, then both women will expect to succeed at the upcoming swim meet and feel optimistic and energized about the challenge of competition. However, if one has low academic self-esteem whereas the other has high academic self-esteem, they will have very different feelings and motivations about their upcoming calculus exam. People will also use their domain-specific self-esteem to regulate their behavior in that specific domain (Kirkpatrick and Ellis 2001). In general, the goal of such behavior is to meet the need to belong, but the behaviors that will best achieve that goal will vary by situation. For example, securing a stable and valued place in an organization may require

an employee to demonstrate competence and skill, whereas securing a stable and valued place in a romantic relationship may require a partner to demonstrate responsiveness and kindness. Different domains may also activate goals that are related to, but not the same as, the need to belong, including romantic and sexual goals and dominance goals, and the self-esteem system includes adaptations to facilitate the attainment of those goals as well.

Domain-specific self-esteem reflects perceived romantic and sexual value. Obtaining and maintaining high-quality romantic and sexual relationships is a fundamental part of human life and critical to the success of the human animal. Therefore, if the self-esteem system includes domain-specific adaptations, it is highly likely that one would be specialized for romantic and sexual relationships (Kirkpatrick and Ellis 2001). So it is not surprising that people do internalize their perceived value to others in these domains, forming domain-specific self-esteem concerning their attractiveness and value as an intimate partner (Messer and Harter 1986).

In turn, romantic and sexual self-esteem may also help people to successfully navigate the rocky waters of intimate relationships. For example, romantic and sexual self-esteem may facilitate adaptive relationship choices by motivating individuals to form relationships with the highest-value romantic and sexual partners that they can attain, given the limitations imposed by their own romantic and sexual value and by the norms of the "mating marketplace" (Kirkpatrick and Ellis 2001). Consistent with this account, although everyone desires to obtain the most attractive mate possible, in reality, people target their romantic overtures toward potential partners who are "in their league" when it comes to physical attractiveness (e.g., Lee et al. 2008). Such targeted pursuit is thought to simultaneously maximize the rewards that one can obtain from a partner, while also minimizing the possibility of rejection by one's love interest. Furthermore, experiencing rejection from a potential romantic or sexual partner lowers people's romantic and sexual aspirations, but leaves their friendship aspirations unchanged (Kavanagh et al. 2010), further

demonstrating the domain specificity of this adaptation.

Romantic and sexual self-esteem may also help people to calibrate their investment in ongoing relationships by monitoring both their own and their partner's relative romantic and sexual value over time. For example, because weight affects people's romantic and sexual value, and because women are expected to weigh less than men, newlywed heterosexual couples monitor their own and their partner's weight, and couples are more satisfied when wives remain thinner than their husbands over time (Meltzer et al. 2011). More generally, when one partner perceives that they have higher romantic and sexual value than their partner, they will feel less satisfied with their relationship and reduce their efforts to maintain such a relationship (Hatfield et al. 1978). So husbands who perceive that they are more attractive than their wives behave more negatively toward their wives and report lower relationship satisfaction (McNulty et al. 2008). In these ways, romantic and sexual self-esteem may function to alert an individual to inequities in their relationships and motivate responses aimed at correcting that inequity, including reducing one's investments or even ending the relationship.

Domain-specific self-esteem reflects social dominance. Another consequence of being a social animal is humans' propensity for group living and the subsequent development of status hierarchies (Anderson et al. 2015). Individuals who are ranked highly on these social hierarchies, and thus enjoy *social dominance*, receive a wide range of social benefits. For example, socially dominant individuals have greater access to resources, greater influence within their social groups, and greater success in attracting desirable mates (Sadalla et al. 1987). So once again, it is not surprising that people internalize their perceived rank on various status hierarchies, forming domain-specific self-esteem concerning their social dominance (Leary et al. 2001).

Social dominance self-esteem may also help people regulate their social behavior and, in particular, their place within the group (Barkow 1975; Kirkpatrick and Ellis 2001). For example, when people believe that they are low in social

dominance, they are more willing to accept a position of lower status within their group, whereas people who believe they are high in social dominance are less willing to accept subordinate roles (Anderson et al. 2012). Indeed, men with high dominance self-esteem report that they would react to a threat to their dominance with direct aggression, including violence (Wyckoff and Kirkpatrick 2016). In contrast, men with low dominance self-esteem report that they would respond with indirect aggression, including talking behind the offender's back. In these ways, individuals use their dominance self-esteem to guide their social decisions and behavior in an effort to optimize their inclusion and status within their social groups. Yet if an individual strives for a social rank that is higher than others believe they deserve, the group will react negatively and may even attempt to exclude that person (Anderson et al. 2006). Thus, to fulfill the higher-order need to belong or to benefit from one's actual level of dominance, people need to develop a relatively accurate understanding of their social status and dominance within their groups.

Social dominance self-esteem may also help people to negotiate dominance and status hierarchies by assessing their status relative to others and then using that information to regulate their social behavior. Although men who are high in social dominance self-esteem generally prefer to use direct aggression tactics to preserve their social status, if their rank is threatened by a higher-ranked provocateur, such men will nevertheless adapt their response and retaliate with more submissive, indirect aggression tactics (Wyckoff and Kirkpatrick 2016). Thus, people will track the relative dominance of their interaction partners and use this information to make sense of their own place in the broader status hierarchy and to guide their dominant and submissive behavior toward others.

The Attunement of Global Self-Esteem to Domain-Specific Self-Esteem

Although global self-esteem and domain-specific self-esteem are theoretically and empirically

distinguishable, they are not completely independent. This is because both types of self-esteem are internalized from the same life experiences. Perceived relational value *within* specific domains is internalized to form self-esteem that is specific to those domains, but perceived relational value *across* domains is internalized to form global self-esteem. However, the association between global and domain-specific self-esteem can vary quite widely across domains. For example, physical appearance self-esteem is very strongly related to global self-esteem, whereas friendship self-esteem is only moderately associated with global self-esteem (von Soest et al. 2016). Thus, the degree to which global self-esteem is *attuned* to domain-specific self-esteem – that is, the degree to which global self-esteem overlaps with domain-specific self-esteem – varies widely across domains (Anthony et al. 2007). But this variation is not random. A person's relational value in some domains is more consequential to their overall social value than is their relational value in other domains. Thus, a person's perceived relational value in some domains is more likely to be internalized and generalized to form global self-esteem than is their perceived relational value in other domains. As a result, global self-esteem is more attuned to specific self-esteem in some domains than to other domains.

Domain-specific self-esteem is often assessed by asking people to evaluate their possession of various skills, talents, and abilities in various domains (see Brown 2006). Therefore, the clearest way to observe the differential attunement of self-esteem to various domains is to observe the association between global self-esteem and specific self-evaluations, either for specific traits or for specific domains of traits (Anthony et al. 2007). For global self-esteem to be evolutionarily adaptive, it should be most strongly attuned to traits that are the most universally valued across social contexts, such as likeability, competence, social influence, attractiveness, and morality (Baumeister 2012). Both throughout our ancestral history and today, these traits were and are indicative of an individual's genetic fitness, ability to bear and raise offspring, and status within social groups. Sure enough, global self-

esteem is most strongly attuned to traits and qualities that are most highly prized in relational partners and less strongly attuned to traits and qualities that are less highly prized in relational partners. The attunement of self-esteem to highly valued qualities is evident in the correlation between self-esteem and specific self-views, in self-esteem differences, in self-concept clarity, and in the impact of social feedback on social decision-making (Anthony et al. 2007; Stinson et al. 2008).

Moreover, global self-esteem will attune itself to the traits that are most essential for acceptance within a particular social environment (Anthony et al. 2007). Although some traits seem to be universally valued in relational partners, the value of other traits is much more context dependent. In particular, the attunement of self-esteem to specific traits appears to depend on cultural norms and expectations. For example, for people who have an independent cultural identity (e.g., people raised in the United States or Canada), self-esteem is most strongly attuned to easy-to-observe *social commodities* like popularity, social skills, and physical attractiveness that quickly and easily distinguish among individuals (Anthony et al. 2007). In contrast, for people who have an interdependent cultural identity (e.g., people raised in Japan or Korea), self-esteem is most strongly attuned to difficult-to-assess *communal qualities* like kindness, warmth, and responsiveness that facilitate harmonious long-term relationships. Self-esteem will also attune itself to the demands of the particular social roles that people occupy. For example, in Western societies, women's social role demands that they are warm and nurturing of their social bonds, whereas men's social role demands that they cater to their individuality. Consistent with these roles, Western women's self-esteem is more strongly attuned to communal qualities than to individualistic social commodities, whereas men's self-esteem is more attuned to social commodities than to communal qualities. Such sensitive attunement of global self-esteem to cultural and social demands suggests that the self-esteem system may fine-tune itself to the requirements of the individual's specific social milieu. Ultimately, possessing such a responsive

system should benefit survival and reproductive goals by allowing individuals to effectively minimize the risk of exclusion across a variety of situations and roles.

Conclusion

The self-esteem system evolved to facilitate the acquisition and maintenance of high-quality social bonds. To fulfill these belongingness needs, the self-esteem system monitors and internalizes one's perceived relational value, forming global self-esteem. In turn, global self-esteem helps people to make sense of their past, present, and future social experiences and regulates social behavior aimed at maximizing belongingness. However, social relationships are complex and varied, and so too are people's social goals. As a result, domain-specific self-esteem also evolved to help people navigate their social relationships within specific domains, most notably, within their romantic and sexual relationships and within status hierarchies. In this way, global and domain-specific self-esteem function as a system to enable people to successfully navigate the full breadth of interpersonal relationships and social environments that they may encounter.

Cross-References

- [Self-Esteem Tracks Mate Value](#)
- [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- [Sociometer Theory](#)
- [Self-Evaluations Track Perceived Mate Value](#)

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Self-Esteem Tracks Mate Value

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Synonyms

Romantic desirability; Self-worth

Definition

Self-esteem is an individual's overall evaluation of their worth. It includes both attitudinal and affective components.

Mate value refers to the desirability of an individual as a long- or short-term sexual partner, relative to intrasexual competitors.

Introduction

Sociometer theory (Leary and Baumeister 2000) proposes that self-esteem is an evolved adaptation which functions to monitor the quality and quantity of individuals' interpersonal relationships, together with their perceived desirability as a relational partner. Kirkpatrick and Ellis (2004) extended this theory, arguing that since different types of relationships present different adaptive challenges, there may be multiple sociometers, each functioning to monitor individuals' status and desirability in a specific domain. Given that successfully reproducing is a primary adaptive challenge in humans, it is likely that the sociometer system, and thus self-esteem, should be especially sensitive to assessments of individuals' sexual or romantic desirability, and accordingly, Kirkpatrick and Ellis (2004) suggest that there are specific long- and short-term mating sociometers. This perspective predicts that individuals' self-esteem should reflect both their romantic relational status and their perceived eligibility as a long- or short-term partner, which is termed their *mate value*.

Self-Esteem and Romantic Relationships

The prediction that self-esteem should be sensitive to individuals' relational status and evaluations of their romantic relationships has found empirical support. For example, in an analysis of narrative accounts of various relationship experiences, it was found that romantic rejection strongly undermines self-esteem (Baumeister et al. 1993). Similarly, individuals who have divorced experience lower self-esteem than those in intact marriages (MacDonald et al. 1987). Furthermore, individuals who report higher satisfaction with their romantic relationships (Hendrick et al. 1988), and who perceive a greater level of commitment from their current partners (Rill et al. 2009), experience higher levels of self-esteem, and men who doubt the fidelity of their spouses have lower levels of self-esteem (Shackelford 2001). Such findings suggest that self-esteem is sensitive to both individuals' relational status and their evaluations of the quality and stability of their current relationships, supporting a mating sociometer perspective on the romantic relational monitoring function of self-esteem.

Self-Perceived Mate Value

In addition to responding to individuals' assessments of their existing relationships, a mating sociometer perspective suggests that self-esteem should also reflect individuals' assessments of their eligibility for such relationships: their self-perceived mate value. A wealth of empirical evidence supports this prediction by demonstrating that individuals' self-perceptions in domains relevant to mate value predict their levels of self-esteem.

For example, Feingold (1992) conducted a meta-analysis of both published and unpublished studies which measured physical attractiveness, which forms an important component of mate value in both sexes (Buss 1989), and self-esteem. In this analysis of 38 samples, with a total of 4942 participants, Feingold found a significant

moderate positive average correlation ($r = .32$) between self-rated attractiveness and self-esteem. The analysis also found that the correlation was significantly stronger in women ($r = .32$) than in men ($r = .27$).

Historically, this sex difference in the relationship between self-perceived attractiveness and self-esteem has been explained in terms of cultural values that emphasize women's physical attractiveness over men's (e.g., Mathes and Kahn 1975). However, the mating sociometer perspective predicts that since physical attractiveness contributes more to mate value in women than in men (Buss 1989), women's self-esteem should be more strongly related to their self-perceived attractiveness than is men's.

Bale and Archer (2013) reasoned that if individuals' perceptions of their physical attractiveness influence their self-esteem because they reflect their mate value, the relationship between self-perceived attractiveness and self-esteem should be mediated by romantic self-confidence. Specifically, they argued that individuals who believe that they are highly physically attractive should have greater confidence in their ability to establish and maintain romantic relationships, and this in turn should increase their self-esteem. Bale and Archer (2013) found support for these predictions by demonstrating that in both men and women, romantic self-confidence significantly mediated relationships between a variety of measures of self-perceived facial and bodily attractiveness, and self-esteem.

In addition to research indicating that self-perceptions in domains of specific relevance to mate value, such as physical attractiveness, predict self-esteem, studies have examined relationships between global evaluations of mate value and self-esteem. For example, Brase and Guy (2004) asked participants to rate themselves on a single item measuring their overall desirability, which described a range of attributes which contribute to mate value, including physical attractiveness, social status, and intelligence. They found that participants' ratings on this item significantly and positively correlated with their self-esteem. Similarly, Penke and Dennisen (2008)

found strong significant positive correlations between a multiple-item measure of mate value and self-esteem in both men and women.

Experimental Studies

In addition to the correlational studies described above, recent experimental studies have demonstrated that manipulating participants' self-perceived mate value, and leading them to believe that they have either been accepted or rejected by potential mates, influences their self-esteem.

Pass et al. (2010) asked participants of both sexes to complete fake personality inventories and then provided them with false feedback relating to either their capacity as a romantic partner, which was designed to influence their self-perceived mate value, or their capacity as a friendship partner. Participants who received negative feedback regarding their mate value reported lower subsequent levels of self-esteem than those who had received negative feedback regarding their friendship capacity, and controls (who received no feedback). These results suggest that influencing individuals' beliefs about their desirability as romantic partners, and hence their mate value, has particularly strong effects on their self-esteem, supporting a mating sociometer perspective.

Kavanagh et al. (2010) examined the effects of perceived romantic acceptance or rejection on self-esteem in a study which was ostensibly concerned with people's perceptions of potential dating partners. Participants who indicated their relationship status as single responded to questions posed by attractive members of the opposite sex who were in fact confederates in the study. They were then provided with false feedback indicating whether these individuals would be interested in meeting up with and dating them. Participants who received positive (accepting) feedback showed increases in self-esteem compared with their pretest scores on this, and also higher levels of self-esteem than those who received negative (rejecting) feedback, who experienced decrements in self-esteem compared to their pretest scores.

These results were subsequently replicated by Kavanagh et al. (2014) who used the same experimental paradigm in a sample of men and women who were involved in ongoing romantic relationships and found similar increases or decreases in self-esteem following false mate value feedback.

Further support for the finding that inducing participants to experience either romantic acceptance or rejection influences their self-esteem was provided by a study by Zhang et al. (2015). This study involved men and women being presented with descriptions of social scenarios involving romantic acceptance or rejection, and then asked to imagine how they would feel in that situation, and recall and describe their own similar previous experiences. Participants who had been presented with romantic rejection scenarios subsequently reported lower levels of self-esteem than those who had considered accepting scenarios.

Thus, the available evidence from experimental studies supports the mating sociometer perspective by demonstrating that self-esteem is sensitive to experimentally induced manipulations of self-perceived mate value.

Other-Rated Mate Value

In comparison to studies examining relationships between self-perceived mate value and its constituents and self-esteem, there are fewer studies of how others' perceptions of attributes relevant to mate value relate to individuals' sense of self-worth, perhaps due to the relatively greater complexity of employing this method. These studies typically find much lower correlations between other-rated mate value and self-esteem than self-report studies. For example, in his meta-analysis of the literature, Feingold (1992) found only a very weak, albeit significant average correlation ($r = .06$) between other-rated physical attractiveness and self-esteem. Such findings accord with other research which suggests that in general, people are not very good at accurately appraising their own level of physical attractiveness (e.g., Santor and Walker 1999) and present a challenge for a mating sociometer perspective on self-esteem.

The sociometer system is supposed to take relevant self-evaluations of mate value as its input, and use these to produce an overall level of self-esteem, which subsequently guides adaptive relational behavior. However, if these initial self-evaluations are inaccurate, this could potentially lead to maladaptive behavioral responses, and so further research into the discrepancy between self- and other-evaluated mate value is needed to address the conditions and variables which might influence the accuracy of self-evaluations.

Conclusion

The evidence presented here supports a mating sociometer perspective by demonstrating that self-esteem relates to self-evaluations of mate value and related attributes, and is sensitive to experimental manipulations of these. However, there may be discrepancies between self- and other-rated mate value in this regard, and this warrants further investigation. Moreover, given that it is proposed that the sociometer system adaptively regulates interpersonal behavior in response to self-evaluations and self-esteem, differences in self-esteem should predict differences in the strategies individuals employ to establish and maintain mating relationships. At present, there is a lack of research which directly examines this prediction, and so future studies are needed to address this and examine whether and how self-evaluations of mate value and self-esteem influence interpersonal behavior in mating relationships.

Cross-References

- [Mate Value](#)
- [Self-Concept](#)
- [Self-Esteem Reflects Assessments of Valuation](#)
- [Self-Evaluations Track Perceived Mate Value](#)
- [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- [Sociometer Theory](#)
- [Women's Mate Value](#)

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Self-Esteem Tracks Social Evaluation and Relational Value

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Synonyms

Evolutionary mismatch; Relational value; Self-esteem; Social value; Sociometer hypothesis

Definition

Self-esteem is an individual's perception of self-worth, reflecting both self-evaluations and perceived evaluations from others, which may have evolved to alert and motivate individuals toward behaviors that avoid social exclusion and disapproval.

Introduction

Self-esteem is commonly understood as an individual's appraisal of self-worth as an overall judgment of the value of one's entire self or one's standing in a specific domain (Rosenberg 1965). Self-esteem is subjective, may not always tally with objective truths about the self, and is connected to what the individual considers to be

interpersonal evaluations of him or her (Leary and Baumeister 2000).

The foundations of an evolutionary perspective of self-esteem are rooted in studies that demonstrate variance in self-esteem (Twenge and Campbell 2002; Twenge and Crocker 2002), the heritability of self-esteem (Neiss et al. 2002), and the potential fitness advantages conferred by high self-esteem (Campbell and Foster 2013). Evolutionary scholars have argued that self-esteem serves an informational function in signaling how the self is evaluated by others. Such evaluations serve as a proxy for social acceptance or rejection, which then prompt behaviors aimed at improving social affiliation and increasing associated survival and reproductive benefits (Campbell and Foster 2013, p. 341). Among the various informational models of self-esteem that have been proposed in contemporary social psychology, the sociometer model stands out as one of the most important (Leary and Baumeister 2000; Leary et al. 1995).

Self-Esteem: The Sociometer Hypothesis

According to the sociometer hypothesis (Leary et al. 1995), self-esteem is regarded as an internal index of an individual's relational value to others, which is defined as “the degree to which a person regards his or her relationship with another individual as valuable or important” (Leary 2005, p. 82). Because humans evolved to live in groups and depend on the cooperation of others, relational value serves as an indicator of the likelihood of social inclusion and receiving support from others (Baumeister and Leary 1995). Thus, humans evolved to be sensitive to relational value in order to manage their inclusionary levels and avoid social expulsion or rejection (Leary 2005).

In framing self-esteem as a warning and guidance system, self-esteem departs from its traditional conceptualization as a desired end state and becomes, instead, a functional mechanism that motivates adaptive behavior based on social monitoring and self-evaluations (Hill and Buss 2006). For example, individuals detecting cues indicating social disapproval or rejection from

others, such as frowning or a decline in interest level, may experience negative feelings. This aversive state motivates compensatory behaviors aimed at restoring social acceptance and relational value, such as self-enhancement efforts (Leary 2005). Over evolutionary time, individuals who were sensitive to their relational value and managed their inclusionary status better gained an edge and outreproduced others, resulting in the sociometer mechanism being passed down the generations and establishing itself in our psychological repertoire.

Domain-Specific Sociometers

Studies have also revealed that self-esteem tracks value in specific life and social domains (von Soest et al. 2016). For example, a sports athlete's overall self-esteem may be unaffected by his academic performances because the evaluations placed on him by the sporting community, from which validation and approval are pertinent, depend more on his athletic prowess. This further demonstrates that self-esteem ultimately serves a social function – the influence of domain-specific sociometers on overall self-esteem depends on how much the relational value within these social domains matter to the self.

By extension, self-perceived mate value may also be indexed by fluctuations in self-esteem to the extent that social inclusion is linked with mate value (Brase and Guy 2004). For instance, social acceptability and popularity may contribute to an individual's mating desirability and produce a correlation between mate value and self-esteem. However, research has also found evidence for a distinction between mate value and other domains of self-esteem (Kavanagh et al. 2010). Findings reveal that although evaluations from the opposite sex affected mating aspirations and was reflected by changes in overall self-esteem, this did not generalize to effects on self-worth in terms of same-sex friendship formation. Taken together, domain-specific factors underlie self-esteem and the impact of success or failure in each domain on self-esteem depends on their significance to relational value.

Evolutionary Mismatch and Self-Esteem

In ancestral environments characterized by small population sizes and social networks with relatively few degrees of separation, any social information was likely to be self-relevant and important. Given the huge survival and reproductive costs of social rejection and expulsion, humans evolved to be highly sensitive to information that may have a bearing on the inclusionary status of both themselves and others (Lim and Yong 2019). This heightened sensitivity was likely adaptive in ancestral contexts as it enabled our predecessors to protect and manage their inclusionary status within a dynamic social environment.

Unlike the early environments that humans evolved in, modern social environments (both physical and online) present information that impacts self-esteem in far more variable and excessive ways, leading to a mismatch between the sociometer mechanism of self-esteem and the social information it evolved to process. For instance, online social networks (e.g., Facebook, Instagram, Snapchat) are laden with public displays of opinions, beautified photographs, and accomplishments accompanied by evaluations from other users (e.g., followership, likes/dislikes, shares). Modern mass media also frequently showcases idealized images of thin and fit individuals as benchmarks of beauty and mate value (Yong et al. 2017). As early humans evolved in an environment where all persons encountered were real and all social information was likely to be important, our information detection systems are not well-equipped to distinguish between virtual images of people and real persons (Yong et al. 2017) and to disregard surplus social information (Lim and Yong 2019). Therefore, perceptions of seemingly perfect individuals on social and mass media and receiving dislikes (or not receiving likes) can significantly harm our self-perceptions, as if we were in the presence of formidable individuals or had received public disapproval from others in an ancestral tribe.

When the sociometer fails to discriminate between various sources of information and processes them all as important, such overexposure to

stimulus that induces negative self-evaluations can decrease self-esteem and prompt detrimental compensatory behaviors. For instance, individuals who are exposed to attractive mating rivals online may be motivated to respond in an intrasexually competitive manner, such as by posting photographs of themselves in a sexually revealing manner to garner more likes. Extended exposure to media stimuli overrepresenting desirable mating rivals may produce an obsession with competition, leading to maladaptive self-cognitions such as body dissatisfaction and behavioral problems such as eating disorders (Yong et al. 2017). The prospect of gaining social approval via positive comments, likes, and followership may also induce hypervigilance over others' opinions, evaluations, and validation, resulting in an obsession with social media usage, dissatisfaction with the self, and heightened negative affectivity including depression (Lim and Yong 2019).

Conclusion

Research suggests that self-esteem serves an adaptive social function by helping humans detect evaluative cues that signal social standing in important life domains. This sociometer function facilitates the enactment of behaviors that increase affiliation and relational value, thereby improving survival and reproduction in ancient environments by managing the threat of social exclusion and preserving crucial social relationships. Modern social and mass media technologies, however, create a mismatch between the sociometer and the stimuli it evolved to handle. In particular, the heightened social information available today, such as the numerous idealized images of attractive individuals and social evaluations in the form of likes and followership, may overload the sociometer with negative social evaluation and undermine mental well-being. Thus, understanding the factors that trigger our evolved sociometer and how to mitigate them, such as the harmful evaluative effects of social media use, is a research area that carries both importance and urgency.

Cross-References

- [Evolutionary Mismatch](#)
- [Intrasexual Competition](#)
- [Relational Value](#)
- [Self-Esteem](#)
- [Sociometer](#)

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Self-Evaluation

► Sociometer Theory

Self-Evaluations Track Perceived Mate Value

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Synonyms

Romantic desirability, Self-perceptions

Definition

Self-evaluations are defined as the subjective judgments individuals make about their personal qualities.

Mate value refers to the desirability of an individual as a long- or short-term sexual partner, relative to intrasexual competitors.

Introduction

Since successfully producing offspring is critical from an evolutionary point of view, men and women should be especially concerned with monitoring their status in intrasexual competition for mates (Buss and Schmitt 1993). Relative desirability as a long- or short-term sexual partner is defined as mate value, and individuals are expected to track this in order to help guide adaptive decision-making in mating contexts. Thus, individual's self-evaluations should reflect relevant social feedback regarding their mate value. Furthermore, assessments of mate value are also expected to predict self-esteem, since this is defined as a global evaluation of the self.

Social Comparison and Mate Value

Mate value is an inherently relative, zero-sum construct (Brase and Guy 2004) such that in order for some individuals to be highly desirable (have high mate value) others must be less so (have low mate value). Since mate value is defined as an individuals' desirability relative to intrasexual competitors, individuals' judgments about their mate value should be influenced by social comparisons with others.

Gutierrez et al. (1999) provided strong experimental support for the contention that social comparisons influence individuals' self-perceived mate value. They exposed men and women to images, which were either high or low in physical attractiveness, and short descriptions, which contained cues to either high or low social dominance, of individuals and asked them to subsequently rate their self-perceived attractiveness and dominance, together with their desirability as a date, sexual, and marriage partner. Women, but not men, who were exposed to highly physically attractive images subsequently rated themselves as being less desirable as marriage partners than those who were presented with unattractive images. Conversely, men, but not women, who were exposed to high-dominance descriptions subsequently rated themselves as less desirable

as marriage partners than those who had read low-dominance descriptions.

Gutierrez et al. (1999) suggested that these results can be understood from an evolutionary perspective emphasizing intrasexual competition for mates. Since physical attractiveness is a more important determinant of mate value in women, and social dominance is more important for men (Buss and Schmitt 1993), these results can be interpreted as demonstrating that individuals are sensitive to social comparisons on dimensions most relevant to their mate value and adjust their self-evaluations of their desirability according to their perceived relative standing.

Further support for this analysis was provided by a more recent study by Castro et al. (2014). These authors exposed participants to pictures and short descriptions of same-sex individuals which varied in their perceived physical attractiveness and desirability as a romantic partner. Participants who were exposed to more attractive and desirable individuals subsequently reported more negative self-evaluations, and lower overall desirability (i.e., mate value) than those exposed to less attractive and desirable individuals, suggesting that social comparisons influenced their subsequent judgments about their own personal qualities.

Self-Esteem as a Global Self-Evaluation

Self-esteem can be defined as a global self-evaluation, which includes both attitudinal and affective components. A number of correlational studies have demonstrated that self-assessments of overall mate value (Brase and Guy 2004), and its specific determinants, such as physical attractiveness (Bale and Archer 2013) and social status (Twenge and Campbell 2002), significantly predict self-esteem.

Furthermore experimental studies have demonstrated that directly influencing participants' self-perceived mate value by providing false social feedback regarding this influences their subsequent self-esteem (Kavanagh et al. 2014). Such studies support the finding that self-

esteem, as a global self-evaluation, tracks perceived mate value.

Conclusion

The prediction, derived from evolutionary theory, that individuals' self-evaluations track their perceived mate value has received empirical support from a range of experimental and correlational studies. A number of evolutionary theorists have suggested that self-evaluative systems serve to regulate relational behavior in humans (Buss and Schmitt 1993). Accordingly, studies have begun to examine how self-perceived mate value and self-evaluations influence aspects of individuals' relational behavior, such as their mating aspirations (Kavanagh et al. 2014). Future research could profitably further explore whether self-perceived mate value and self-evaluations predict other aspects of mating behavior such as mate attraction and retention tactics (Buss 1988a, b) and investment in romantic partners (Ellis 1998).

Cross-References

- ▶ [Mate Value](#)
- ▶ [Self-Concept](#)
- ▶ [Self-Esteem Reflects Assessments of Valuation](#)
- ▶ [Self-Esteem Tracks Mate Value](#)
- ▶ [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- ▶ [Women's Mate Value](#)

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Self-Examination

- [Self-Observation](#)

Self-Harm

- [Suicide \(Evolutionary Clinical Psychology\)](#)

Selfhood

- [Object Permanence](#)

Self-Inflicted Suicide

- [Assisted Suicide](#)

Self-Injury

- [Suicide \(Evolutionary Clinical Psychology\)](#)

Self-Insight

- [Accuracy of Self-View](#)

Self-Interest

- [Self-Beneficial Political Attitudes](#)

Selfish

- [Defection](#)

Selfish Gene, The

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Synonyms

[Evolution of selfishness and altruism](#); [Gene-centered theory of evolution by natural selection](#)

Definition

A seminal text in evolutionary biology that articulates the gene-centered view of evolution by natural selection, explains how self-interested genes can give rise to altruism, and introduces the meme.

Introduction

The Selfish Gene (1976) was English ethologist and evolutionary biologist Richard Dawkins's first book. Drawing on the theory developed by G. C. Williams (1966), Dawkins asserts that the gene is the primary unit of natural selection and criticizes group selection accounts. Another goal of the book was to "examine the biology of selfishness and altruism" (p. 1) by combining theories of inclusive fitness, such as kin selection, with the gene-centered view of natural selection. Dawkins also coined the meme as a unit of human cultural evolution. *The Selfish Gene*, now in its fourth edition, has remained an influential articulation of evolutionary theory and has been employed by evolutionary psychological science as a foundational theoretical perspective (e.g., Tooby and Cosmides 1992).

The Gene-Centered View of Life: Replicators and Gene Machines

Biologists since Darwin have agreed that evolution by natural selection occurs by the differential survival and reproduction of self-replicating entities. However, as explained early in *The Selfish Gene*, there has been debate as to the level(s) on which selection acts, with some advancing the possibility of selection between groups in addition to selection between individual organisms. Dawkins expresses skepticism toward group selection accounts, arguing groups lack "longevity, fecundity, and copying-fidelity" (p. 35), the key attributes of a replicator. The gene, by contrast, exemplifies those properties. Defined as a given stretch of DNA, genes are capable of persisting across generations, exist in duplicate copies found across individuals of a species, and self-replicate with a high degree of accuracy. Such attributes allow Dawkins to conclude that the gene is the "largest practical unit of natural selection" (p. 36): it is the fittest gene which outcompetes its rivals (alleles) and differentially propagates into the next generation.

All successful genes are then necessarily selfish in the sense that they seek replication at the expense of their competitors. A gene may gain an advantage over another should it code for proteins that compose what Dawkins terms survival machines, or vehicles, that enhance that gene's capacity to exploit the environment and reproduce. Early in the evolution of life, these vehicles consisted of relatively simple chemical barriers, but eventually "both animals and plants evolved into many-celled bodies" as "selection has favored genes that cooperate together" (p. 46). Central to Dawkins's thesis, therefore, is that a successful gene is "compatible with, and complementary to, the other genes with whom it has to share a long succession of bodies" (p. 84). In brief, genes are replicators that cooperate to create machines, living bodies, which enhance their individual reproduction. Selection then favors the fittest set of genes based on their phenotypic, expressed, effects on the world.

The Evolution of Altruism

Next, Dawkins references the work of W. D. Hamilton (1964) to illustrate how altruism may arise between individual organisms. Altruism is defined as a behavior which confers a fitness benefit to another at a cost to one's own fitness. For example, a honeybee may launch a suicide attack on an intruder in support of her hive mates. The selfish gene theory, Dawkins argues, best predicts such phenomena because a given gene exists as duplicates found across individuals of a species. As a consequence, selection would favor a gene that was able to promote its duplicate's fitness in another body, and "this would appear as individual altruism but it would be brought about by gene selfishness" (p. 87). Genes therefore may be selected to promote their inclusive fitness, all copies, in addition to their personal fitness, a particular copy.

This is observed in kin selection. First note that there is a comparatively higher probability that close relatives, such as bees from the same hive,

share a particular gene. Altruistic behavior may evolve should an action result in a net gain in gene replication, even at the expense of a particular individual's genes: a honeybee's costly defense of her relatives is ultimately an act that benefits the survival and reproduction of her genes across bodies. Kin-directed altruism extends into parent-offspring relations as well. Indeed, a parent can invest in its offspring at an expense to itself, but to the net benefit of the genes shared between the two (although conflict may arise between parent and child concerning the optimal distribution of investment; see Trivers (1972)).

In a later chapter of *The Selfish Gene*, Dawkins also connects the gene's-eye view of natural selection with work from economics, political science, and psychology to explain the evolution of reciprocal altruism. This is where an individual behaves altruistically toward a non-kin other, given that the roles are reversed at some point in the future. Such situations are often modeled after the prisoner's dilemma, where two agents both have the option to cooperate or defect. Typically the payout structure of the different outcomes favors the decision to defect. However, should the scenario be played out repeatedly over an indefinite period of evolutionary time, with offspring as the payoff, selection may favor the evolution of mutual cooperation. Under such conditions, simulation studies reveal that a simple "tit for tat" strategy of default cooperation coupled with punitive recrimination of defectors evolves as a stable evolutionary strategy in iterated games of prisoner's dilemma. Empirical examples that Dawkins cites include the regurgitation of blood from a successful vampire bat to a less fortunate conspecific after a hunt. Recent laboratory evidence additionally suggests humans have a host of evolved psychological mechanisms regulating reciprocal exchange relationships (Kaplan et al. 2012).

Memes: The Cultural Replicators

The Selfish Gene also devotes a chapter to human cultural transmission and evolution. Change over

time in human language and technology, Dawkins notes, exhibits parallels to genetic evolution. Indeed he writes that an evolutionary process is inevitable given the existence of any self-replicating entity. Genes are one such replicator, and in the domain of human culture Dawkins proposes the existence of a replicator he calls the meme. These are ideas or beliefs that "propagate themselves. . . by leaping from brain to brain" (p. 192) and constitute the unit of cultural evolution. Like in genetic natural selection, the meme that is most fit to its environment, in this case by appealing to human psychology, differentially reproduces across the minds of individuals. Successful memes then band together, forming clusters that mutually reinforce their transmission. Examples of such meme complexes may include religious doctrine, a symphony, or scientific theory. Dawkins's meme spawned its own field of study, memetics, whose proponents include philosopher of mind Daniel C. Dennett. Critics, however, argue that memes do not replicate from mind to mind with the requisite accuracy (e.g., Richerson and Boyd 2005).

Conclusion

Richard Dawkins's *The Selfish Gene* greatly popularized the gene-centered view of evolution and has remained influential across disciplines. In biology, Dawkins expands on several of the book's arguments in his follow-up, *The Extended Phenotype* (1982). Here, he describes how genes have consequences that extend far outside the body they inhabit, for instance, in the creation of artifacts like a bird nest or in the actions of parasites. Furthermore, *The Selfish Gene* bridged the life and behavioral sciences, foreshadowing the development of evolutionary psychological science. Specifically Dawkins provides early speculation that "our basic psychological attributes and tendencies" (p. 192) are the product of evolution, including kin selection and selection for reciprocal altruism, assertions later supported by entire literatures. Highly focused yet wide-ranging, the

selfish gene theory continues to inform research connected to the life, brain, and behavioral sciences.

Cross-References

- [Evolution of Cooperation](#)
- [Extended Phenotype, The](#)
- [Memes](#)
- [Richard Dawkins on Constraints on Natural Selection](#)

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Selfish Genetic Elements

- [Robert Trivers](#)

Selflessness

- [Benefit to Another at Cost to Self](#)

Self-Monitoring

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Synonyms

[Conscious experience](#); [Consciousness](#); [Metacognition](#); [Self-awareness](#)

Definitions and Conclusions

Consciousness research is today one of the cornerstones in neuroscience. Almost all studies in the field have focused on identifying neural events accompanying appearances in the outer world, the “qualia,” like the redness of wine. These attempts have typically neglected the issue of the “Self.” Obviously, the self and qualia are two sides of the same coin. As formulated by Ramachandran (2004, p. 96): “You cannot have free-floating sensations, with no one to experience them.” Self-awareness is the essential tool for conscious metacognition. Metacognition monitors and controls behavior, the “self,” and thereby adjusts our beliefs of the world, essential for learning by conscious experience. This occurs not only within ourselves, but, importantly, also between individuals. Self-awareness is a primordial human capacity and is of decisive importance by giving humans an upper hand in phylogenetic development of culture and society (Frith 2012).

Self-awareness, or conscious self-monitoring, is the focus of this entry, based on a recent review (Lou et al. 2016a). It was until recently considered off-limits for the natural sciences. Neurobiological research shunned the “hard question of how consciousness and self-awareness arise from a physical basis,” influenced by the philosopher David Chalmers in the late 1990s (referenced by Lou et al. 2016a). Therefore, it has been fashionable to limit the quest for understanding the workings of the brain in consciousness and self-awareness to the task of identifying neural

“correlates” of these mental functions. The limitation clearly involves the risk of arriving at two parallel worlds: a mental and a physical, without understanding how they interact. The consequence of this would be severe impediment of our understanding of the biological function of self-awareness and how it may account for disease in default.

However, using electrophysiological and pharmacological manipulations we have discovered that highly connected “hubs” of medial prefrontal and parietal are associated with self-awareness. They are not only linked to that function but indeed instrumental in its generation: Transcranial magnetic stimulation (TMS) targeting the hubs impedes specific aspects of self-awareness (Lou et al. 2004; Luber et al. 2012). Conversely, self-awareness is increased by dopaminergic challenge, primarily via GABA neurotransmission directly in the medial prefrontal cortex (Joensson et al. 2015; Lou et al. 2016b). The hubs are provided by an exceptionally rich assembly of fast-spiking parvalbumin interneurons assuring synchronization of their pyramidal cells for generation of self-awareness. The exceedingly high metabolic rate of these hubs makes them vulnerable in penuria of oxygen and/or glucose as a common final path in the pathophysiology of the many disorders with deficient self-awareness, like autism, attention deficit disorder, schizophrenia, and dementia.

Investigating Self-Awareness

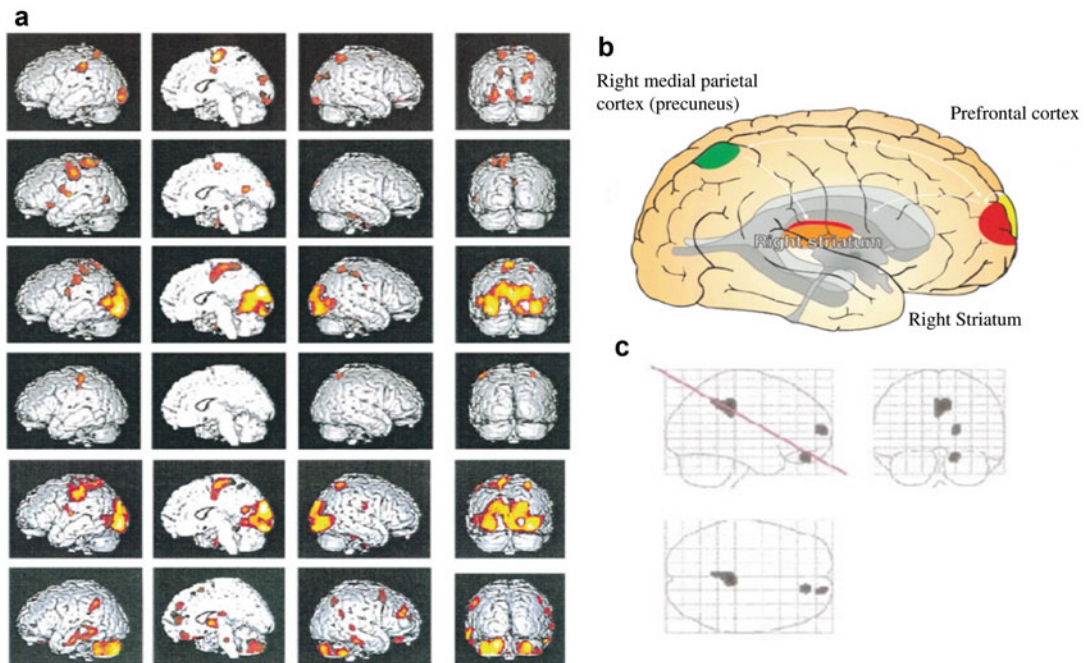
Gallagher (2000), following Wittgenstein and the phenomenologists, claims that we are self-aware whenever we are conscious. Accordingly, self-awareness is an indispensable part of our experience of the world, whether it is minimal self-awareness (pre-reflective, with an automatic sense of ownership of the experience) or narrative (extended and reflective, based on retrieval of episodic (personal) memory). Minimal self-awareness may be investigated using rapidly presented stimuli, which become aware to the observer when presentation time exceeds a certain threshold (Weiskrantz et al. 1995; Kjaer et al.

2001) or by comparing first person perspective with third person perspective (Vogeley et al. 2004). Narrative (extended) self-awareness may be investigated using retrieval of episodic memory of previous judgment of self versus another person (Lou et al. 2004). Both minimal and narrative self-awareness may be ranked according to the degree of self-reference (Craig et al. 1999).

The Paralimbic Network as a Signature of Self-Awareness and Conscious Self-Monitoring

“Mind wandering,” where the person is shifting his attention to changing states and objects, is associated with shifting patterns of brain activation (Lou et al. 1999). In spite of this variability, a set of medial paralimbic regions, including medial parietal (precuneus) and medial prefrontal regions, are continuously active as measured by principal component analysis (Fig. 1) (Kjaer and Lou 2000). The network is similar to the network activated by focusing on one-self versus another person in a dark room without intended sensory stimulation or motor activity (Fig. 2) (Kjaer et al. 2002). This medial paralimbic network has proved to be a common neural signature for widely different aspects of self-awareness and conscious experiences in all functional domains examined. This was evident in a large meta-analysis of investigations using ^{15}O -H $_2$ O positron emission tomography or functional magnetic resonance imaging (fMRI) (Northoff et al. 2006).

The midline cortical “hubs” of the paralimbic network are usually linked with activity in the angular gyri, right insula, and subcortical regions (e.g., Joensson et al. 2015). The two midline hubs interact by means of recurrent oscillations in the entire frequency range measured, i.e., from less than 5 Hz to 100 Hz, with a maximum at 40 Hz. The network is active at rest without intended sensory or motor activity. That condition is characterized by a fairly large proportion of spontaneous self-referential thinking (Kjaer et al. 2002). When self-referential thinking becomes dominant, for instance, during relevant tasks in an experimental setting, a large



Self-Monitoring, Fig. 1 Cerebral activation patterns vary with shifting contents of consciousness. All conditions include a paralimbic network. The four *upper rows* represent cerebral blood flow patterns measured with ^{15}O - H_2O -positron emission tomography (PET) during yoga nidra meditation on weight of own body part (*upper row*) abstract perception of joy (*second row*) visual imagery of landscape (*third row*), and symbolic representation of self (*lower row*) (Lou et al. 1999) (a) (With permission). The

right medial parietal cortex (precuneus), prefrontal cortex, and right striatum are coactivated in all meditative states and the control state (Lou and Kjaer 2005) (b) (With permission). Visual presentation of single words long enough to be perceived consciously activates medial orbital, medial prefrontal, and medial parietal cortices when compared to subliminal presentation (c) (Kjaer et al. 2001) (With permission)

increment is seen in the entire frequency spectrum (Fig. 3) (Lou et al. 2011).

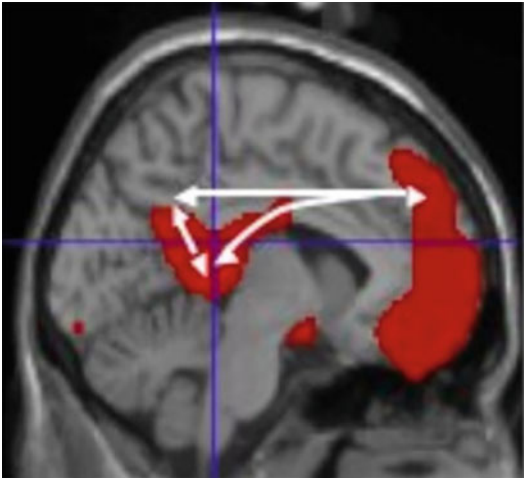
From Association to Causality

The ascription of the medial paralimbic network to self-awareness is essentially based on imaging data and can, as such, only be correlative. Accordingly, the significance of these findings for self-awareness has been disputed (e.g., Smith 2012). To test whether the paralimbic network is indeed instrumental in the generation of self-awareness, a series of intervention studies has been carried out. The investigations included behavioral consequences of electromagnetic as well as neurotransmitter manipulation of the network: Directly targeting the medial parietal and medial prefrontal region with TMS showed unequivocally that the former region is

instrumental in retrieval of self-related episodic memory (narrative self-awareness), while the latter region is instrumental in self-evaluation (Lou et al. 2004; Luber et al. 2012). The effect was simultaneous at the two disparate sites, with a latency of 160 ms after sensory stimulation (Fig. 4). This confirmed the global neuronal network hypothesis for access to consciousness and the simultaneous “ignition” of separate brain regions in the course of conscious processing (for review, see Lou et al. 2016a). Magnetoencephalography and Granger causality computation show that interaction between the prefrontal and parietal “hubs” occurs with oscillations mainly in the gamma range. Causality of lower gamma oscillations in the frontal regions for self-awareness has subsequently been confirmed by application of synchronous oscillations around

25 and 40 Hz over the frontal skull, showing stimulation induced self-reflective awareness in dreams during REM sleep (Voss et al. 2014).

Generation of gamma frequency oscillations depends on fast-spiking parvalbumin GABA-ergic interneurons. Experiments with transgenic mice deficient in these interneurons have shown

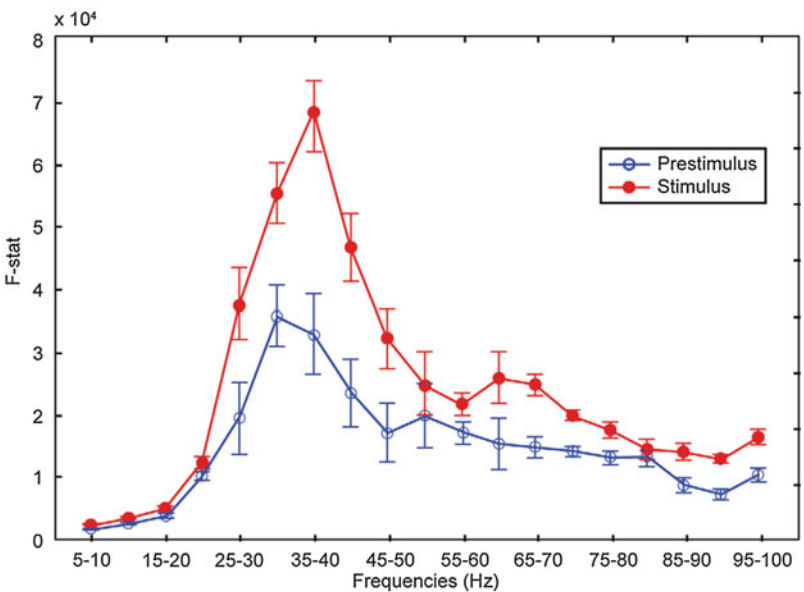


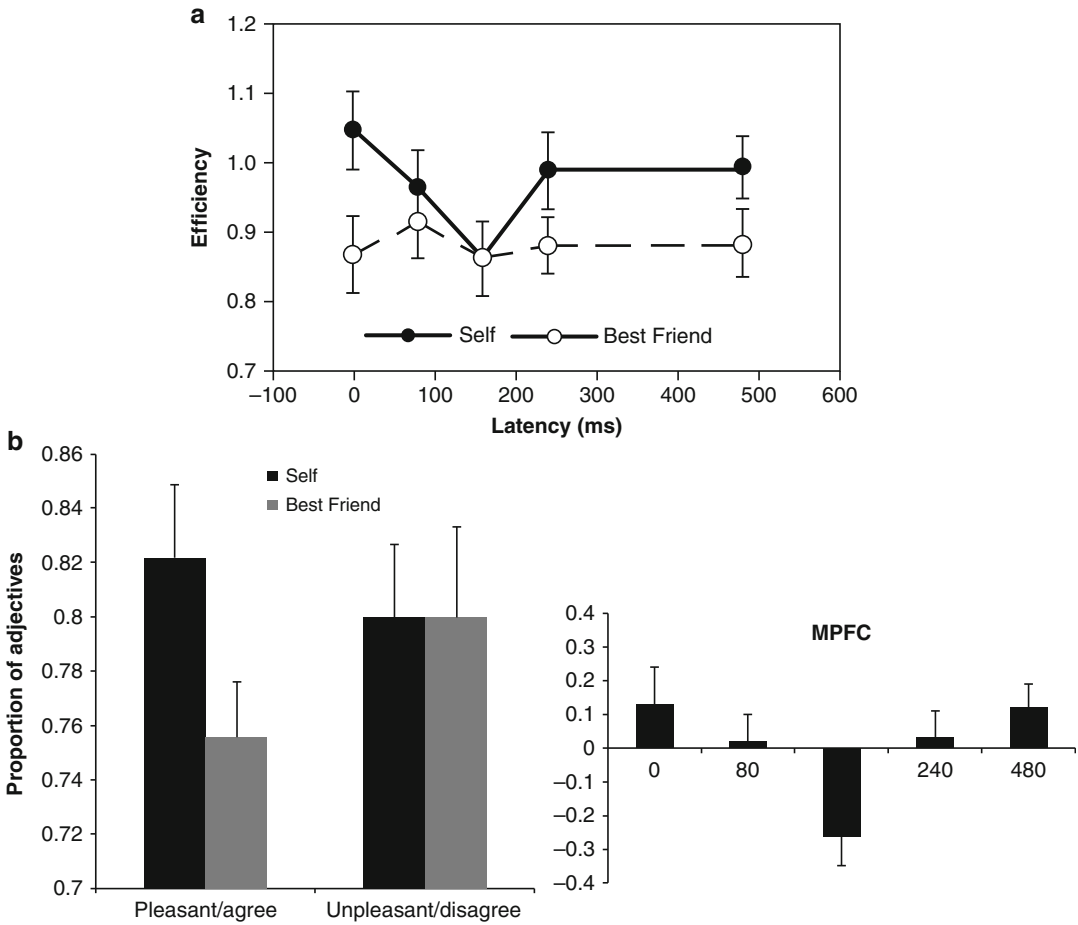
Self-Monitoring, Fig. 2 The paralimbic network in self-awareness. Retrieval of previous judgment of oneself activates dramatically the paralimbic network of medial prefrontal (anterior “hub”) and medial parietal cortices (posterior hub), together with thalamus ($^{15}\text{O}\text{-H}_2\text{O}$ PET) (Lou et al. 2004; Changeux and Lou 2011) (With permission)

deficient gamma oscillations and behavioral defects, which may be restored by optogenetically stimulating prefrontal cortical interneurons. In humans, Hall et al. (2010) found that GABA-ergic stimulation induces power increase predominantly in pyramidal cells of the prefrontal cortex. Such power increase depends on synchronization of pyramidal cell output. Recently, we have demonstrated that dopamine increases self-awareness in humans (Joensson et al. 2015) (Fig. 5) via increased GABA activity (Lou et al. 2016b) (Figs. 6 and 7). This occurs mainly in the medial prefrontal/anterior cingulate cortex, and, as a trend, in the right insula, explaining our previous finding that dopamine regulates self-awareness via medial prefrontal cortex (Fig. 5). It also explains that self-awareness is preferentially dependent on right hemisphere activity, as demonstrated by Keenan et al. by carotid infusion of anesthetics (see Lou et al. 2016a).

Also acetylcholine, an agonist of dopamine activity, may directly activate subsets of inhibitory interneurons, with synchronization of pyramidal cells as a result. This has recently been demonstrated at the cellular level in layer II/III in prefrontal cortex of mice using in vivo two-photon imaging (Koukoulis et al. 2016). Figure 8 schematically illustrates the transmitter regulation of self-awareness.

Self-Monitoring, Fig. 3 Recurrent information flow between medial prefrontal and parietal hubs. Granger causality [magnetic encephalographic (MEG) amplitudes] is seen in the entire frequency range (5–100 Hz, maximal at 40 Hz) in the prestimulus state (rest), a condition characterized by mind-wandering and self-referential thoughts (see Fig. 1). During retrieval of episodic memory (previous self-judgment), power is increased throughout the frequency spectrum (Lou et al. 2011) (With permission)





Self-Monitoring, Fig. 4 Causality of paralimbic network evidenced by transcranial magnetic stimulation (TMS). Efficiency of retrieval of self-judgment is selectively impaired at medial parietal (Lou et al. 2004) and both angular gyri, while preference for allocating positively

rated adjectives to one-self rather than best friend is selectively impaired with TMS targeting the medial prefrontal cortex (Luber et al. 2012) (With permission). The results demonstrate that the different aspects of self-awareness “ignite” access simultaneous at a latency of 160 ms

Thus neural system, cellular, electromagnetic, and transmitter physiology all testify that the paralimbic system is instrumental in self-awareness. It is tantalizing how closely this discovery, based on experimental data, fits with suggestions based on bedside clinical observations by Ramachandran (2004, p. 112).

Ontogenesis of Self-Awareness and Metacognition

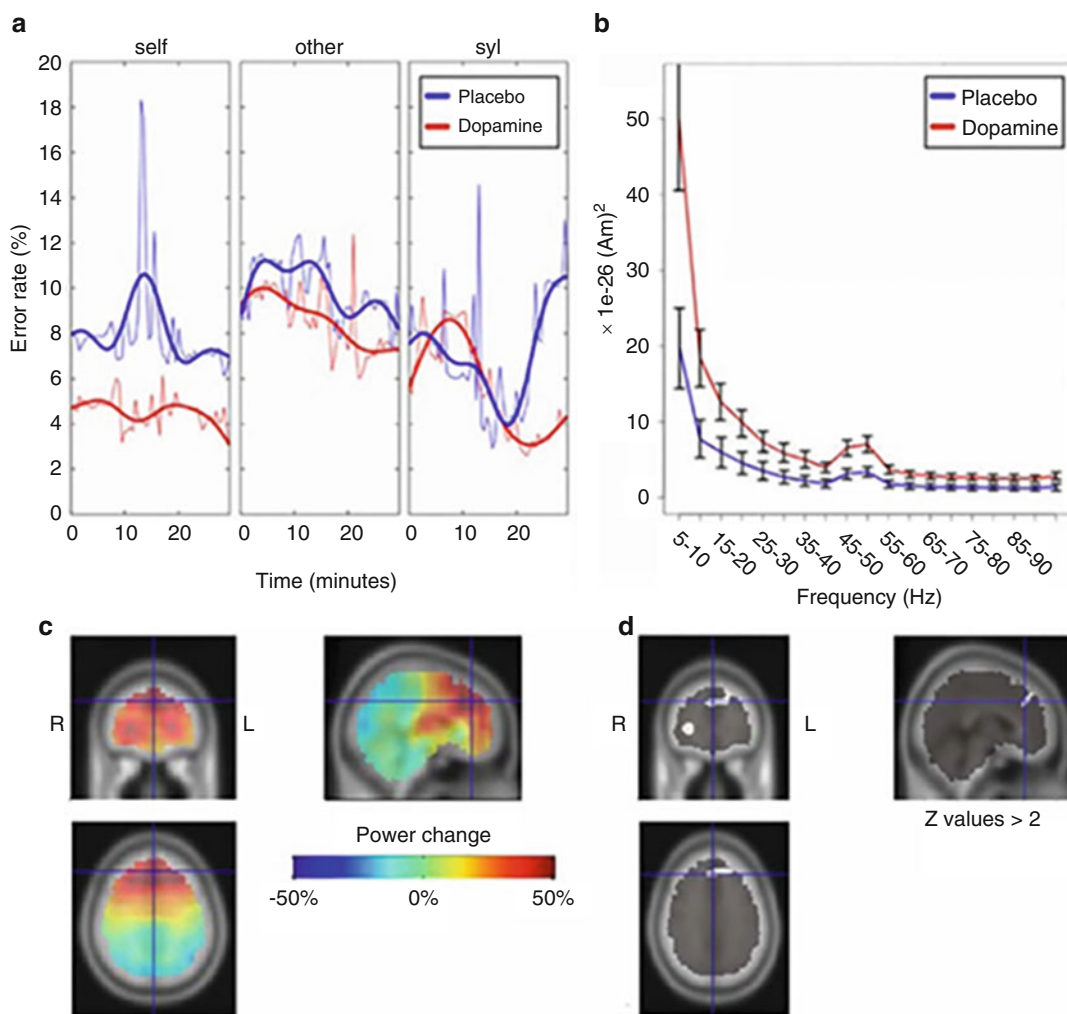
The infant is probably aware only of events in the present time, while the adult capacity to put these sensations into a time perspective, with ability to

plan for the future, has to await later development (Lagercrantz and Changeux 2009). Similarly, the development of metacognition does not seem to occur until after 3 years of age.

This development occurs concomitantly with the development of resting state activity in the medial prefrontal and medial parietal hubs and insula, i.e., the paralimbic network (Fransson et al. 2011).

Pathophysiology

Due to the fundamental biological importance for the individual and society of self-awareness, self-



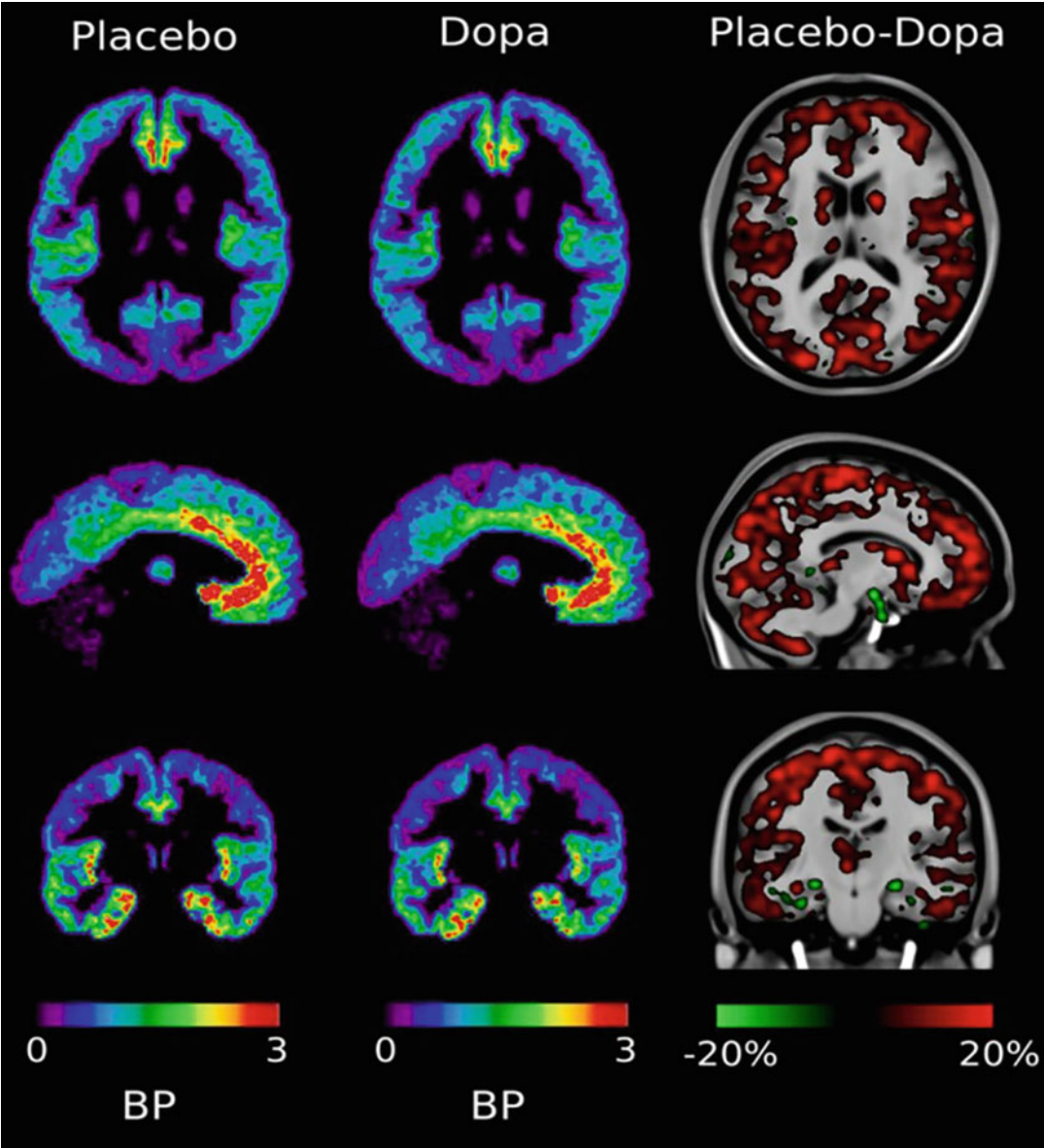
Self-Monitoring, Fig. 5 Dopamine increases self-awareness and gamma power. Dopamine challenge (sinemet 100 mg) decreases error rate in retrieval of previous judgment on whether adjectives fitted one-self or not compared to placebo (**a**), while retrieval of judgment of a control person is not changed significantly (**b**). (**c**) Whole brain MEG showing distribution of dopamine-induced power increase (gamma range (30–100 Hz). Preferential

power increase in prefrontal region is documented and is likely due to the distribution of dopamine receptors in the brain (Joansson et al. 2015) (With permission). The blue cross shows location of peak increase with dopamine at the MNI coordinates (0, 36, 36 mm). (**d**) Z - values > 2 (Monte Carlo simulation of the difference between placebo and dopamine medication groups)

monitoring, and metacognition, their disturbance is likely to be linked to severe pathology. Thus, frontal and medial parietal cortices are dysfunctional in a monosymptomatic condition with deficient conscious self-monitoring such as behavioral addiction (Rømer Thomsen et al. 2013) (Fig. 9). It is also the case for more complex disorders involving poor self-awareness and self-monitoring such as substance abuse, ADHD,

autism spectrum disorder, schizophrenia, and the dementias, and also traumatic brain injury. Even in a pervasive dysfunctional state such as the vegetative state, recovery of the paralimbic network is tightly linked to clinical recovery (For review see Lou et al. 2016a).

The widespread dysfunction of self-awareness in pathology is the result of the exceedingly high oxygen demand of the paralimbic default network

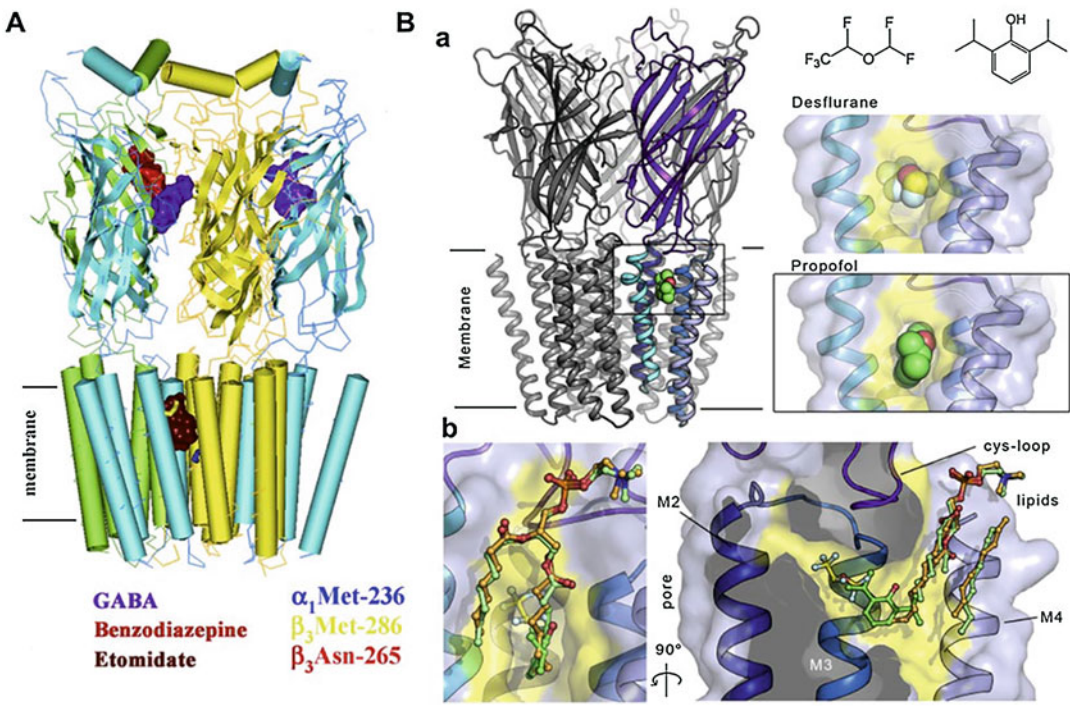


Self-Monitoring, Fig. 6 Dopamine activates the GABA system in paralimbic network. The distribution of the GABA receptor PET ligand [^{11}C]Ro15-4513 binding, with placebo, dopamine challenge, and placebo minus dopamine. With placebo, the ligand is bound primarily in the medial prefrontal/anterior cingulate region, and in left

and right insula. After L-dopa, the binding is reduced, seen clearly by subtraction. There is a reduction of between 5% and 20% throughout most of gray matter, indicating widespread cortical activation of the GABA-ergic interneurons. (Lou et al. 2016b) (With permission)

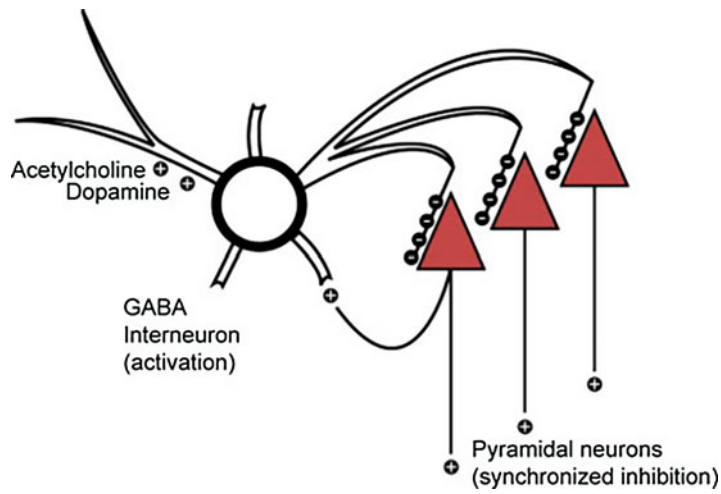
(Kann 2016). This makes self-awareness, conscious self-monitoring, and metacognition particularly vulnerable to deficient oxygen and glucose supply. The high metabolic requirement is mainly due to dense concentrations of interneurons in the

richly connected “hubs” of the paralimbic default network, their GABA-ergic synapses being instrumental for pyramidal cell synchronization in the paralimbic network. In particular, gamma oscillations are vulnerable to metabolic



Self-Monitoring, Fig. 7 GABA-receptor molecule at pyramidal cell membrane. Molecular model of the GABA-A receptor on pyramidal cell and of the main categories of binding sites for pharmacological agents. The GABA binds to defined subunit interfaces in the

extracellular domain (*violet region*). Activation of this molecule is the final common path for generating gamma synchrony and self-awareness (With permission). For details, see (Li et al. 2006; Nury et al. 2011; Bocquet et al. 2009; Changeux and Lou 2011)

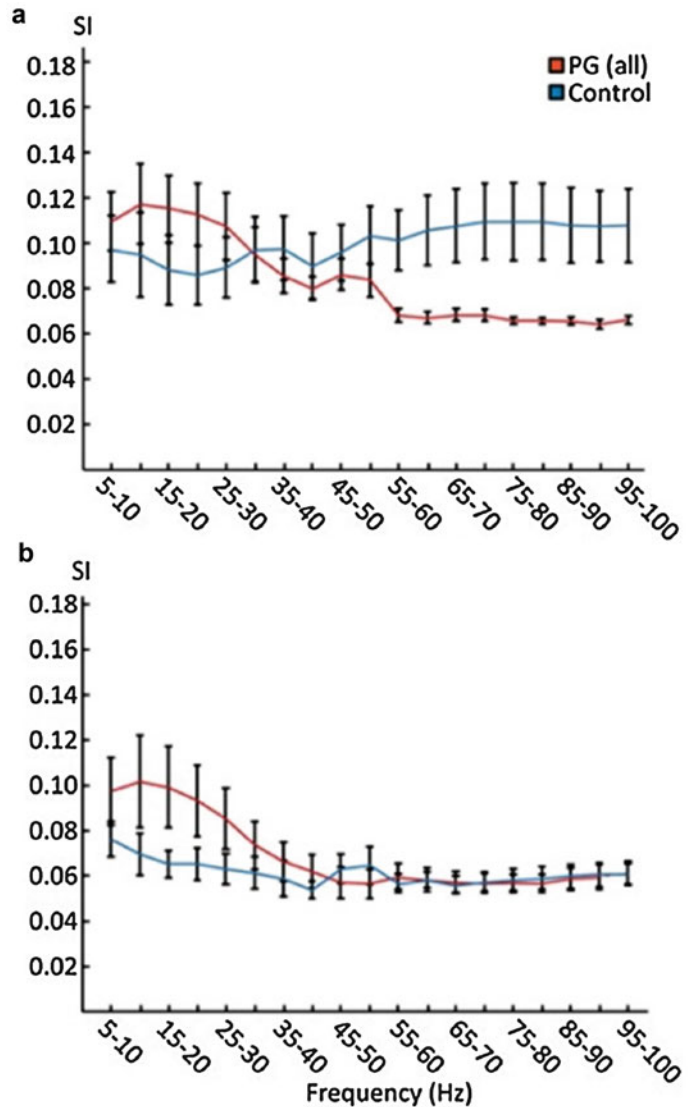


Self-Monitoring, Fig. 8 Overview of neurotransmitter regulation of self-awareness. Fast spiking GABA-ergic interneurons are activated by dopamine and acetylcholine and quite possibly other neurotransmitters at receptors located at or near the soma. Via GABA receptors in the

pyramidal cell membrane dopamine enhances paralimbic synchrony for self-reference, a crucial constituent of any conscious experience (Changeux and Lou 2011) (With permission)

Self-Monitoring,

Fig. 9 Abnormal gamma synchronization (SI) in pathological gamblers. At rest, pathological gamblers have lower synchronization than controls in gamma band (30–100 Hz) (b vs a). (Subgroup analysis showed that this difference was present both for gamblers with and without a history of comorbid stimulant addiction (both $P < 0.05$)) (a) (Rømer Thomsen et al. 2013). This illustrates abnormal function in the paralimbic network of self-reference linked to abnormal conscious self-monitoring and metacognition in individuals susceptible to pathological gambling (With permission)



disruptions, a promising venue in the treatment and prevention of disorders of self-awareness.

Perspectives for Prevention and Treatment

The new understanding of the physiology and pathophysiology may lead to the application of novel or recently developed therapeutical strategies to increase dopaminergic activity and to improve neural interactions. These strategies may include meditation, which in independent

studies have been shown to increase dopaminergic tone and induce growth in paralimbic structure, and targeted training aiming at increasing the availability of dopaminergic receptor. Also improvement of sensory input may be an important venue to increase dopaminergic tone and induce growth in relevant structures. Likewise frontal electromagnetic stimulation of oscillations may have a role. More generally, the new discoveries provide impetus to efforts to maintain oxygen homeostasis in neural tissue ranging from decreasing oxygen demand by cooling, for instance, in distressed neonates, to controlling

cerebral perfusion pressure and autoregulation of cerebral blood flow, and obtaining optimal cerebral blood flow distribution via the capillary network (for review, see Lou et al. 2016a).

Cross-References

- [Brain Imaging](#)
- [Consciousness](#)
- [Evolution and Self-awareness](#)
- [Metacognition](#)
- [Mirror Self-recognition](#)
- [Neurons in the Cerebral Cortex](#)
- [Personality Disorders](#)
- [Reciprocal Altruism and Group Living](#)
- [Social Cognition](#)
- [Status and Dominance Hierarchies](#)

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Self-Murder

► Death by Suicide

Self-Observation

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Synonyms

Consciousness; Inner-directed phase; Mindfulness; Self-awareness; Self-examination; Self-reflection; Self-scrutiny

Definition

The ability to consider what is being observed about the self, the self-reflective function that allows one to marshal the resources of self-awareness to alter prediction errors. This ability provides a sense of agency in observing, planning, deciding, and evolving toward a future goal.

Introduction

Defining the self has challenged psychologists and philosophers for centuries. The phenomenon to which the word self applies derives from four domains of experience: thought, feeling, functional capacity, and the observing center. Experience in each of these realms is evidence of one's locality in space and unique psychological identity (Deikman 1982). The thinking self refers to one's engagement in controlling immediate activities and planning, such as problem solving, worrying, and imagining. The emotive self consists of affective states such as anxiety, joy, anger, and sadness, whereas the functional self is indicative of the experience of "doing." This self is aware of acting and one's capacity to affect the environment in a concrete way. The observing self is "the transparent center, that which is aware. This fourth self is most personal of all, prior to thought, feeling, and action, for it experiences all of these functions" (Deikman 1982). Self-observation refers to the active scan of these former three "selves" of inner environment and landscape.

Self-Observation as a Social Process

Humans were provided with insightful and novel means of not only expressing but also observing their own experience. This would not be possible if experience was a purely individual and private matter. Instead, we live in an inter-subjectively shared and immanently meaningful world. Humans exist as beings in constant communication with others, through which we come to develop shared perspectives on our experience.

Introspective self-consciousness is derivative of consciousness of others and not vice versa. Internal thought is a form of inner dramatization of social conduct and is thus necessarily bound up with social meanings.

Mead (1910) argued that “Other selves in a social environment logically antedate the consciousness of self which introspection analyzes.” In other words, the act of self-reflection presupposes social interaction with others. The introspection involves the incorporation of the other into the self. This conceptual move naturalizes the act of self-reflection by showing that it is an outgrowth of a social process. One’s own gesture does not initially have meaning for oneself. The gesture only has meaning for others, which is their response to the gesture. The establishment of shared meaning requires the existence of stable social institutions with interchangeable social positions – such as buying and selling. Since a vocal gesture can be heard from both sides of a social act in a social practice, it takes on a dual meaning and enables the movement from one social perspective to another. Introspective self-reflection is only possible through a history of interaction with others in social institutions.

Self-Observation and Consciousness

Self-observation results in cognizance of auto-information, such as intentions, expectations, feelings, cognitions, behaviors, and impact on others, and the ability to introspect on one’s own thoughts and to realize the relation of self to one’s social and cultural environment (Stuss and Benson 1983). It is associated with the capacities to distinguish inner from outer reality and pretend from “real” modes of functioning and intrapersonal mental and emotional processes from interpersonal communications (Fonagy and Target 1997).

This transtheoretical process involves individuals becoming aware of and learning about their own functioning in order to change maladaptive responses and generate new responses for the future (Beitman et al. 2005). In helping the individual focus attention on their own self and

idiosyncratic patterns, an external source, such as a psychotherapist, could assist in activating self-observation. This process serves as a tacit common thread woven among the different psychotherapies.

Activation of self-observation is collaboratively employed by practitioner and client within all psychotherapeutic orientations. Self-observation emerges from self-awareness, which, in turn, relies upon consciousness. Consciousness requires mobilizing functional brain structures, including the reticular activating system, and provides the platform for awareness. Awareness is the potential to be conscious of specific content such as objects, persons, and ideas. Self-awareness or “autonoetic consciousness” (Wheeler et al. 1997) is the potential to know the self and the self-in-context. Self-observation refers to actively scanning one’s inner landscape, mentalization, and the ideas in other people’s minds as well as what others think of the self (Baron-Cohen et al. 2000).

Self-Observation Within Psychotherapy

For many individuals seeking therapy, confusion, distraction, or troublesome symptoms may impede effective self-observation. Storms in the internal and external environment cloud vision, precluding accurate perception of one’s inner landscape. Although self-observation is a normal and adaptive capacity, it can be difficult to preoccupy oneself with such maladaptive thoughts, feelings, and behaviors. A safe and confiding therapeutic relationship offers a client the haven of an interpersonal relationship in which to observe the self, which is necessary to create new ideas and templates of expectations and actions to meet goals. Activation of self-observation thus empowers clients to make more informed decisions, alter prediction errors, create intentions, and plan courses of action (Pally 2004), resulting in increased freedom of choice, increased autonomy, and a wider scope of comprehension (Deikman 1982).

Conclusion

Highlighting self-observation as a core process common to all theoretical orientations simplifies

the complex dynamics of it. Although there are many techniques and interventions that may be used to activate self-observation, helping individuals become more aware and reflective of their subjective experience is a central and important theme. The recent surge of literature on mindfulness (Wylie and Simon 2004) and on the neurobiology of interpersonal learning in psychotherapy (Siegel 1999) drives the need to elucidate self-observation.

Cross-References

- [Consciousness](#)

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Self-Other Bias

- [Self-Enhancement Relative to Others](#)

Self-Perceptions

- [Self-Evaluations Track Perceived Mate Value](#)

Self-Recollection

- [Personal Memory](#)

Self-Referent Processing

- [Kin Detection by Odor](#)

Self-Reflection

- [Evolution of Self](#)
- [Self-Observation](#)

Self-Regard

- [Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?](#)
- [Self-Esteem as Manipulative Status Communication](#)

Self-Reinforcing Choice

- [Fisherian Runaway Selection](#)

Self-Reported Data

► Self-Reports

Self-Reports

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Synonyms

[Interview](#); [Questionnaire](#); [Self-reported data](#);
[Survey](#)

Definition

Self-reports are data that are sourced from written or verbal representation of individuals' cognitions, emotions, attitudes, experiences, behavioral intentions, and/or beliefs about the self.

Introduction

Self-reports have been widely used in evolutionary psychology research targeting many domains (e.g., mate preference, tactics of deception, cooperation, and helping). While researchers using self-reports have been able to collect and examine data that would otherwise be unobtainable (e.g., sexual fantasies), the use of self-reports in evolutionary psychology has been challenged and criticized (see Shields and Steinke 2003). Although there are valid criticisms of the self-report method, such as the potential for respondents to provide deceptive answers or to have their answers be influenced by social desirability concerns, there is strong evidence to support the use of self-

reports as a valid methodological tool in evolutionary psychology research (Allen and Yen 2001; Crocker and Algina 1986; Simpson and Campbell 2005). The following examines the uses, strengths, and criticisms of self-reports in evolutionary psychology research and offers suggestions for using self-reports in evolutionary psychology research effectively.

The Value of Self-Reports in Evolutionary Psychology

Self-reports exist in various forms, from verbal and written responses to open-ended questions, to numeric responses that indicate individuals' levels of agreement with statements that characterize a latent construct. As such, self-reports intend to measure what individuals believe to be true about themselves, their behavior, and their experiences. The greatest contribution to the literature that self-reports can make then is the obtainment of data (e.g., preferences, motivations, self-perceptions, reports of past behavior) that could not otherwise be obtained, or not as easily obtained, through other research methods. Thus, the self-report method is especially useful to evolutionary psychology research which often focuses on topics (e.g., mate preferences, violence against spouses) that, researched in any other way, could be deemed inappropriate, unethical, and/or overly intrusive.

Self-report research has been prevalent in evolutionary psychology and has in many ways provided important bases of knowledge for the field. Important, and even seminal, research using self-reports has tested evolutionary hypotheses pertaining to human mate preferences (e.g., Buss 1989), mate retention (e.g., Buss 1988), mating desires (e.g., Regan and Dreyer 1999), tactics of deception (e.g., Tooke and Camire 1991), violence against spouses (e.g., Buss and Shackelford 1997), strategies for elevating your status within a social hierarchy (e.g., Cummins 2005), familial helping (e.g., Burnstein et al. 1994), and many other relevant and important evolutionary

psychology research topics (see Buss 2015 for a comprehensive review). This research employing self-report measures has been heavily cited, creating important foundations for testing further evolutionary psychology hypotheses to expand the understanding of human cognition and behavior.

One of the major strengths of self-report research is that it is a time- and cost-effective method for doing research, reducing the necessary expenses in time, money, and labor to conduct. Self-reports often do not come with the drawbacks of other research methods that may be more expensive, laborious, and obtrusive (e.g., studies employing behavioral observations of individual participants). When beginning a new research program or exploring a new research question, it may be unwise to choose other, more arduous research methods because these efforts may be unfruitful and the invested resources (e.g., time, money) may then be wasted. Thus, self-reports are a practical methodological tool and a sensible first step in a research program.

One particular strength is the predictive power of self-report measures. Self-reported emotions and beliefs have been shown to predict important attitudes and behavior in testing hypotheses derived from evolutionary psychology. For example, using a sociofunctional theory of intergroup prejudice, researchers have used self-reported perceptions of the specific threats posed by different groups to predict specific emotional profiles evoked by these groups (Cottrell and Neuberg 2005), thus demonstrating that there may be many different functionally relevant kinds of prejudices as opposed to one generalized prejudice. Similarly, researchers have used self-report measures to test hypotheses about the adaptive functions of disgust sensitivity and their relationship to fundamental moral values (e.g., van Leeuwen et al. 2016) and voting behavior (Inbar et al. 2012). As another example, self-reports have also been successfully used to predict cost-inflicting mate retention behaviors. Men's partner-directed insults were found to be related to women's reports of their partners' mate value, such that women's decreased

assessments of their male partners' mate value were associated with more frequent insults from their partners (Miner et al. 2009a, b). These are but a few prominent examples of the value of self-report measures in conducting research in evolutionary psychology.

An additional benefit of self-report methods is that they can be designed to measure opinions or preferences that allude even the participants' own conscious knowledge, for instance, when the participants may not be aware of, or able to explain, how the variables at play influence their perceptions and behaviors. For example, male participants may not be able to articulate, or even be consciously aware of, their preferences for female romantic partners as a function of the women's waist-to-hip ratio (WHR). However, by systematically manipulating the size of a woman's figure using line drawings, Singh (1993) was able to conclude that women's distribution of body fat (i.e., WHR) played a critical role in men's judgment of females as healthy and attractive. Similarly, if asking participants whether or not they prefer unique or average faces, participants are likely to mistakenly report they prefer unique faces. This may at first appear to be a limitation of the self-report method. However, by designing self-report methods in which participants can rate their preferences for faces that are manipulated or chosen based on key features, such as their representing a composite "average" face of varying numbers of individual faces (e.g., Grammer and Thornhill 1994; Jones 1996), researchers can gather important data about individuals' preferences, even when the factors that influence these preferences may be outside of the participants' own conscious awareness.

Self-reports have thus far played an important role in building the foundation of many psychological fields, including the field of evolutionary psychology. Innovative researchers have used creative methods in which to test their hypotheses and make significant contributions to the knowledge bases of their fields. It should be noted that the above strengths are in no way an exhaustive list of the strengths of self-report methods; however, these strengths do provide evidence that self-reports are a versatile methodological tool that

researchers may adapt to fit their needs in the pursuit of important research objectives.

Criticisms and Limitations of Self-Report Methods

The uses of self-reports, particularly with college student populations, have been criticized and challenged in the literature (see Shields and Steinke 2003; Silvers 2011). One particular limitation noted among these criticisms is that participants may be deceptive when reporting their attitudes, preferences, and behaviors. This criticism is not necessarily specific to evolutionary psychology, but the topics examined in evolutionary psychology research may make this a particularly important concern. Evolutionary psychology often examines sensitive topics (e.g., extramarital affairs, unusual sexual fantasies), and thus participants may be especially hesitant to report thoughts or experiences they fear will result in negative judgment by others. Alternatively, participants may not be reporting the information “truthfully” because they have limited self-knowledge or because they themselves have been deceived by their own lies (Paulhus 1988). Thus, the issues of self- or other-focused deception are particularly worrying limitations of the self-report method.

Another criticism leveled at self-report methods is that they are a fallible source of data because seemingly insignificant variations in the wording, format, or content of the items or questions to which participants respond may have significant unintended effects on how participants respond (Schwarz 1999). To illustrate this point, the self-report research that has examined individuals’ responses to infidelity has yielded contradictory results. Early work found sex differences that supported the *jealousy as a specific innate module* (JSIM) hypotheses through hypothetical forced choice self-reports (Buss et al. 1992). However, alternative methods, such as using rating scales or self-reports of individuals’ actual experiences, revealed evidence that was contrary to the JSIM (see Harris 2003 for a comprehensive review). Again, while this is not a concern unique to

research conducted only in evolutionary psychology, it is a concern that evolutionary psychology researchers must consider when employing self-report measures.

Perhaps the biggest limitation that self-reports must overcome is that self-report measures are not direct or exact records of an individual’s actual behavior. As such, because self-report data are dependent on individuals’ perceptions and interpretations of events, collected data may be subject to bias. Further, various cultural norms or stereotypes may taint the data. And because human memory is fallible and often unreliable, researchers must be careful when asking questions that pertain to the past frequency of behaviors or to the recollection of past experiences.

As discussed above, data collected by self-report measures may also be unreliable due to participants’ desire to be viewed as favorable. For instance, participants may knowingly report their preferences dishonestly or be motivated to exaggerate their experiences (e.g., embellished accounts of sexual experiences), especially when they believe that their responses may be publically evaluated. Social desirability concerns (Crowne and Marlowe 1960; Paulhus 1988) have long been a problem in self-report data. Researchers must be aware of this issue and take reasonable steps to reduce their participants’ desires to respond to self-report measures in ways that enhance their own social impressions, such as by ensuring the anonymity and confidentiality of the participants’ responses.

Addressing the Limitations of Self-Report Methods

While the criticisms of self-reports discussed above are valid, it is important to remember that all research methods are imperfect. All research methods bring with them some degree of measurement error in their failure to completely and accurately assess the constructs they operationally define. Researchers must be cognizant of the limitations of the research methods they employ and make informed decisions about designs and procedures. Further, although it may be impossible to

eliminate measurement error, researchers may implement methods that reduce it. A preferable method for the reduction of measurement error in self-reports is triangulation (Buss 2015; Kenrick and Keefe 1992). By pairing self-reports with a multi-method, multi-measure approach, researchers can obtain more robust and ideally converging results, providing them with more confidence in their conclusions.

Because seemingly trivial variations in the wording or format of self-report materials can strongly influence participants' answers (Schwarz 1999), researchers should take particular care in wording their self-report measures. Making sure that the participants' understanding of the items or questions match what the researchers intend is crucial to the interpretation of their results. Thus, researchers are encouraged to pilot test their materials (see Schwarz and Sudman 1996) to assess their reliability and validity before large amounts of data are collected.

Finally, with new technological advances, researchers can collect large amounts of data while eliminating various sources of measurement error (Miller 2012). For example, to help reduce problems associated with memory or lack of self-knowledge, researchers may employ text messaging as a method in order to receive immediate, or near-immediate, data that do not rely on the individual to recall past events or count the frequency of past behaviors. Furthermore, with the now ubiquitous use of smartphones, researchers can create interactive surveys and experiments to collect data from real-world behaviors, experiences, and emotions in real time, rather than later in a lab room (Miller 2012).

Conclusion

All research methods have strengths and limitations. When designing studies, researchers should be aware of the particular, potential limitations of each research method and take the necessary steps in reducing measurement error and avoiding unnecessary pitfalls. The criticisms associated

with self-report measures are real; however, researchers aware of these criticisms may still use self-report methods in their research to obtain reliable and valid results. In the absence of infinite resources, self-reports are valuable, practical, and cost-effective measurement tools that can be employed by researchers in their investigations of fascinating research questions in evolutionary psychology.

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Self-Sacrifice

► Factors Associated with Suicide

Self-Scrutiny

► Self-Observation

Self-Stereotyping

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Synonyms

Sex-differentiated behavior; Gender self-stereotyping; Secondary sexual characteristics; Mating strategies

Definition

According to self-categorization theory (Turner et al. 1987), self-perception is influenced by salient self-categories, and the ascription of ingroup-defining characteristics to the self is defined as self-stereotyping.

Introduction

Self-categorization theory (Turner et al. 1987) posits that group-level processes occur through the process of categorizing or cognitively grouping the self as either similar to or distinct from another class of stimuli. One can categorize the self on a *personal* level, as a unique individual, different from other individuals (based on idiosyncratic attributes), or conversely, categorization can be done on a *social* level, in terms of identification with social groups, which would render

one's cognition to be filtered through a salient social identity. The operation of self-concept on a personal or social level is thought to be dependent on the perceiver's contextually driven frame of reference and the subsequent categories that may become salient (Turner et al. 1987; Oakes 1987).

Self-categorization theory explains that social identity emerges by way of *depersonalization*, whereby the self is perceived less as a distinct idiosyncratic individual and more as an interchangeable member of a social group. It is through awareness of ingroup norm or prototype that ingroup assimilation and the sense of interchangeability can occur, as prototypes serve to describe and prescribe group appropriate ways to think, feel, and behave, thereby establishing normative behavior among members. Group-based self-construal, and in general intragroup processes, is fostered through the process of *self-stereotyping*, which involves ascribing ingroup-defining traits to the self, and in doing so enhancing the similarity between self and ingroup members, while augmenting the contrast between the ingroup self and outgroup members. The objective of this entry is to discuss self-stereotyping when sex is a salient category (i.e., me, as a woman, versus you, as a man), while deliberating on how gender-based self-stereotyping can be understood from an evolutionary perspective.

Self-Stereotyping by Sex

Group identification entails the incorporation of an external social category into internal self-definition, thereby transforming self-perception and behavior to become consistent with ingroup stereotypic characteristics and norms. Self-categorization can be based on a novel, never-before encountered social category, such as arbitrarily assigned group, or a preexisting one, such as sex (or gender). In instances when sex category becomes primed or salient, *general knowledge about gender stereotypes may become activated*, which may momentarily shape an individual's self-concept based on the sex-category membership they identify with. This leads to gender-based

self-stereotyping. For example, simply put, if an individual woman categorizes herself as a woman in contrast to a man, through her sex-based social category identification ("us women"), her self-perception and behavior will become depersonalized to accentuate her similarities to other women, and attenuate her idiosyncratic personal differences from other women, thereby enhancing perceptually her stereotypical difference from men (Hogg and Turner 1987).

As Hogg and Turner (1987) explained, it is important to note that while social stereotypes are *shared* representations of the defining features of a particular social category, they are nonetheless still cognitively represented by individuals, who possess their own individual idiosyncrasies shaped by personal experiences; in other words, the social stereotype can be thought of as superimposed on the individual stereotype, and for that reason social stereotypes, while shared, are not necessarily rigidly invariant across individuals. With that said, the individual idiosyncratic self-concept will be significantly overshadowed by the similarities embedded in the social, shared self-concept, leading to stereotypical behavior among members of an ingroup (Hogg and Turner 1987).

Evolutionary Reasoning on Own-Sex/Gender Self-Stereotyping

It is well known that there are different beliefs about the characteristics associated with women and men. These differential attributes are the basis for gender-based categories that distinguish the male social group from the female group. When sex category becomes salient, identification with a gender/sex category engenders alignment of self-perception and behavior to match one's own-sex group, leading to stereotypic behavior that ultimately highlights one's similarity to the prototype of their gender ingroup, while simultaneously augmenting stereotypical differences from the gender-outgroup. It is conceivable to link the content of gender-based stereotypes to adaptive traits that have been favored through sexual selection, and to also conceive of engagement in gender-

based stereotypic behavior (self-stereotyping) as a way of propagating evolved mating strategies. As it will be elaborated on, the different sex or reproductive roles of men and women point to differential adaptive challenges in the context of reproduction and mating. The different adaptive problems may have engendered differences in the psychologies of men and women that contribute to gender stereotypes, and the engagement in gender-based stereotypical behavior may serve as a means for easily identifying whether a particular individual is a man or a woman in order to facilitate sexual selection. Gender-based self-stereotyping can therefore be thought of as a form of secondary sexual characteristic that taps into our evolved mating preferences and strategies.

Sexual selection refers to the processes associated with any aspects of breeding behavior, such as competition with members of the same sex and species over mates, as well as the process of mate selection (Darwin 1871). The dynamics associated with sexual selection are thought to be influenced by the degree to which each sex focuses their reproductive effort on parenting or on mating (for a review, see Geary 2002). For a woman, a 9-month pregnancy is the minimum obligatory investment to produce a child, whereas for a man, one act of sexual intercourse is the minimum investment required to produce that same child. Given a woman's larger parental investment (e.g., nine months gestation, post-birth nurturing via lactation and breastfeeding), they are predicted to desire certain characteristics in men that would lead to an increase in reproductive success. A woman's sexual selection is predicted to include competition for men who are willing and able to make the most parental investment – such as willingness and ability to invest economically in raising their offspring and high social standing or dominance, which are typically correlated with resource acquisition – in order to ensure that the offspring reaches reproductive age; while for men who do parentally invest, mate selection criteria includes health, fertility, and sexual fidelity (Davies and Shackelford 2008), which are cues linked to probability of either immediate or future reproductive potential.

Women, cross-culturally, place a greater importance on good financial prospects of a marriage partner than do men and value qualities linked to resource acquisition, such as ambition, industriousness, and social status (for a review, see Buss 2007); similarly, female American undergraduate students were found to prefer, far more than men, mates who show ambition and industriousness, which are qualities linked to securing higher salaries and occupational status (for a review, see Davies and Shackelford 2008). Women's greater preference for mates who are able to economically invest in their offspring may have produced sexual selection pressure for men to have an evolved psychology that motivates meeting these preferences (Shackelford and Davies 2008). Indeed, this may have been the case, as women's universal mate selection criteria resemble the characteristics found in male-specific gender stereotypes, which include attributes such as strong, controlling, assertive, and achievement-oriented (for a review, see Burgess and Borgida 1999). Interestingly, previous studies of the behavioral tactics that men use to attract or retain mates have demonstrated that “men tend to display and bestow resources on the women they are trying to attract and retain. They tend to denigrate their rivals by impugning the rival's professional prospects, such as mentioning that the rival is lazy, lacks ambition, or lacks clear goals in life” (for a review, see Buss 2007). Men's engagement in tactics that involve displaying their own resources, ambitiousness, and physical and social dominance can be conceived of as a demonstration of men's engagement in sex-based self-stereotyping that has roots in evolutionarily adaptive sexual selection endeavors.

Cross-culturally, men place a greater importance on a marriage partner's physical attractiveness than do women, by showing preference for cues to youth and physical appearance (e.g., full lips, smooth and clear skin, lustrous hair, and low ratio of hips to waist). These cues are valued, as they have previously been shown to have a robust link to a woman's health and fertility, and serve as strong predictive factors in either immediate or future reproductive success. Men's greater

preference placed on physical attractiveness is hypothesized to have resulted in women evolving a psychology that motivates them to use strategies that facilitates meeting this preference (Davies and Shackelford 2008). Women are indeed found to have success with tactics involving appearance enhancement more so than men, and behavioral strategies used by females to attract or retain mates include not only putting more effort into appearance enhancement but derogating rival's by pointing out their physical flaws (for a review, see Buss 2007). With respect to parental investment, the greatest threat to the reproductive success of a man is being cuckolded into raising children and directing economic investment toward children that are not genetically related to him. This may have led to men having evolved a psychology that causes them to prefer women who are not sexually promiscuous and are likely to be sexually faithful to them. Cross-culturally, men do place a greater importance on the chastity or virginity of a potential marriage partner (for a review, see Buss 2007), and indeed females have been shown to have success with mating tactics that involve displaying their own sexual fidelity and impugning rivals as being sexually promiscuous (for a review, see Davies and Shackelford 2008). Other female stereotypical traits include attributes such as being warm, caring, deferential, and interpersonally skilled (for a review, see Burgess and Borgida 1999), which are agreeable and nurturing traits that have been adaptive due to promoting the survival of their children. Thus, gender-specific self-stereotyping may reflect the inherited strategies that our ancestors have relied on as they faced many different sex-specific adaptive problems in the context of reproduction and mating. Gender-based self-stereotyping may therefore serve as behavioral signals of an individual's ability to successfully fulfill their respective sex roles based on strategies that maximize reproductive success.

Conclusion

Reproductive success, or the passing of genes to the next generation, involves not only producing

offspring but also ensuring that at least some of these offspring survive to reproductive maturity. Two different sexual strategies can accomplish this: one is the "quality" strategy which consists of heavily investing in a few offspring to increase their individual chances of reaching reproductive maturity, and the other is a "quantity" strategy, which consists of producing as many offspring as possible, in the hope that some will survive to adulthood (Cunningham and Russell 2004). Based on the aforementioned parental investment theory (Trivers 1972), evolutionary psychologists have argued that the "quantity" strategy would primarily benefit men, whereas the "quality" strategy would benefit women. The differing reproductive roles and beneficial strategies (quantity versus quality) may have created divergent selection pressures for each sex, paving the way for the evolution of differential secondary sexual characteristics to meet sex-specific challenges. Examples of these secondary sexual characteristics are competition and aggression among males over limited fertile females, or nurturing qualities that would promote child bearing and care in females. These evolved traits and behaviors are attributes that parallel the content of gender stereotypes, and may therefore reflect characteristics that have been selected and inherited based on the sexual selection pressures expressed by preferred mates. Exhibiting gender-specific characteristics that are valued by a potential mate through gender-based self-stereotyping may be an inherited strategy that facilitates sexual and reproductive success via expressing increased potential in these domains.

Gender-stereotypes could be conceived of as sex-specific attributes that have enhanced the mating strategy and success of our ancestor, and self-stereotyping, when gender is salient, may be a way of behaviorally displaying evolved features that signal a promise for reproductive success.

Cross-References

- ▶ [Salience of Category](#)
- ▶ [Social Neuroscience of Self-Categorization](#)

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Self-Thought

- [Evolution of Self](#)

Self-Worth

- [Self-Esteem as Manipulative Status Communication](#)
- [Self-Esteem Tracks Mate Value](#)
- [Sex-Specific Link Between Self-Esteem and Mate Value](#)

Semantic Content

- [Meaning \(Philosophy\)](#)

Semantic Memory

- [Declarative Knowledge](#)

Semelparity

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Synonyms

[r strategy](#)

Definition

A reproductive strategy characterized by a single reproductive episode over the course of a lifetime.

Introduction

The term *semelparity* refers to a reproductive strategy characterized by a single reproductive episode over the course of a lifetime and contrasts with *iteroparity* (see ► [“Iteroparity”](#)). Semelparous species have only one reproductive episode in a lifetime; thus they invest all reproductive efforts into optimizing one reproductive episode (e.g., by having a single litter with several offspring; Ricklefs and Miller 1999), at the expense of losing future mating opportunities. This risk, however, pays off to some species. Previous research and theoretical models have shown that semelparous species have higher expected adult mortality; thus it is more optimal for semelparous species to invest all resources into

a single reproductive episode (e.g., Young 1990). Nonetheless, both reproductive strategies are observed in plants and animals. Semelparity is uncommon in vertebrates – exceptions include a few fish (e.g., bony fish, Osteichthyes), lizards (e.g., Labord's chameleon, *Furcifer labordi*), amphibians (e.g., gladiator frog, *Hypsiboas rosenbergi*), and a few mammals (e.g., marsupials) (e.g., Braithwaite and Lee 1979). Among invertebrates, most cephalopods and some insects (e.g., butterflies, arachnids) present a semelparous reproductive strategy (e.g., Schneider and Lubin 1997; Fritz et al. 1982). Most annual plants reproduce a single time during their life span, thus are considered semelparous species (Young 1990).

The Evolution of Semelparity

The evolution of semelparity (and iteroparity) has been subject of several theoretical models. One set of models attempts to explain the differential evolution of semelparity by examining the trade-offs between reproductive effort involved in offspring produced and offspring forgone (for a review, see Roff 1993). According to the trade-off models, the reproductive effort of an organism occurs optimally when the benefits of offspring produced outweigh the costs of offspring forgone. That is, the greatest distance states the optimal reproductive strategy for a given species. Semelparous (vs. iteroparous) species usually have higher expected adult mortality (e.g., Schneider and Lubin 1997). Accordingly, for species with high forgone offspring rate (i.e., high mortality rates), the optimal reproductive strategy is to invest all reproductive efforts into a single reproductive episode in a lifetime.

In a classic paper, Cole (1954) proposed a demographic model for the evolution of semelparous and iteroparous reproductive strategies. Cole's model resulted in a semelparous species that has one litter of four and dies afterward having the same rate of population growth than a iteroparous species bearing annual litters of an average of three offspring. This suggested that an advantage of just one offspring would select for semelparity. Charnov and Schaffer (1973) then identified that sensible

variances in adult and infantile mortality were responsible for costs of a semelparous reproductive strategy that were not accounted by Cole's model. These demographic models have been successful when tested with real-world systems. That is, according to these models, the risks involved in semelparity pay off to species in which the benefits of devoting reproductive efforts to a single reproductive episode outweigh the costs of losing future mating opportunities.

Semelparity and K-Selection

Semelparity should not to be confused with a *K*-selection strategy. The former regards to a reproductive strategy in which a single reproductive episode occurs in a lifetime (vs. multiple reproductive episodes; see ► “Iteroparity”), and the latter refers to selected traits that cause a species to have fewer but higher-quality offspring (compared to a *r*-selection strategy; see Pianka 1970). For example, the North Atlantic right whale (*Eubalaena glacialis*) has limited offspring, costly gestation, and high parental investment (Knowlton et al. 1994). Despite the high costs of bearing an offspring, this particular type of whale can still produce more than one offspring in a lifetime. Therefore, it cannot be considered a semelparous species, even though it clearly follows a *K*-selection strategy.

Conclusion

Semelparous species incur in a single reproductive episode over the course of a lifetime (Cole 1954). Numerous semelparous species produce more than one offspring in a single litter (Young 1990). Optimal reproductive strategies differ between species within species, and the semelparity reproductive strategy played a key role in the evolution of several species' reproduction and parenting systems (Roff 1993).

Cross-References

- Iteroparity
- Reproductive Strategies

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Semen

► Seminal Plasma

Semen and Vaginal Chemistry

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Definition

Seminal fluid possesses more than just a transport medium for spermatozoa. Seminal fluid also contains dozens of compounds, including ovulatory- and pregnancy-related hormones. Many of these compounds can also be absorbed through the vaginal wall.

Introduction

Semen is a reproductive fluid. Seminal fluid has been selected over generations to be composed in such a way that it not only houses sperm but also increases probability of conception and pregnancy maintenance (coagulates to retain sperm in the vagina, decreases acidity for sperm survival, etc.). This has a direct effect on the fitness of the human male.

Ney (1986) suggested that the high concentrations of estrone and estradiol, testosterone, dihydrotestosterone, follicle stimulating hormone and luteinizing hormone, prolactin, and 13 different prostaglandins in semen could be biologically active if absorbed by the vagina. Researchers have administered many of these hormonal compounds through the vagina and determined high levels of absorption that elevated blood levels for hours after administration (Schiff et al. 1977; Villanueva et al. 1981).

What is in seminal fluid? Glucocorticoids that aid in the stress response and reaction to pain, androgens that increase sexual desire, endogenous opiates that increase pain relief and pleasure, immunomodulators which increase sperm longevity and appear to have significant effects on the launching of pregnancy, and myotonia enhancing compounds that aid in orgasm. Seminal fluid also contains a host of ovulatory compounds (including estrogens, luteinizing hormone, luteinizing hormone releasing hormone, and follicle stimulating hormone) and over a dozen compounds that aid in the initiation and maintenance of pregnancy. Beyond these, there are also several affiliative and psychotropic hormones and neurotransmitters (see Burch and Gallup 2006 for review).

The major question when faced with these findings is why: why do humans have such elaborate and unique seminal fluid? The answer lies in the evolutionary history of human females. Women are concealed ovulators. Males cannot synchronize insemination with ovulation if they cannot detect ovulatory signals. The chief male strategy then becomes surveillance and support of the female along with consistent coitus, ensuring paternity. In fact, Sillén-Tullberg and Moller (1993) found that this shift from ovulatory signals to concealed

ovulation emerged and then triggered a shift in the human mating system, pushing humans to become monogamous. This placed a significant pressure on males, forcing them to choose between monogamy (with its paternal certainty) and promiscuity (with its high reproductive pay off). Males that could, through semen chemistry, better synchronize insemination with ovulation would have a reproductive advantage. Research has shown that other parameters of ejaculate (volume and sperm counts, for example) vary with context of ejaculation (masturbatory/coital) and are greater during coitus. It is possible the same is true for seminal compounds.

Strategies such as this have been found in other species, with “ovulation induction factors” found in several species, and in many, this factor is a potent stimulator of luteinizing hormone (Adams and Ratto 2013). Human males have five times more luteinizing hormone in their semen than circulating blood levels (and also Luteinizing hormone releasing hormone) and researchers have long argued that coitus-induced ovulation occurs in humans as well (Jöchle 1973). If concealed ovulation led to ovulation induction strategies in humans, how does seminal fluid compare in other primates who do not possess concealed ovulation? Chimpanzees, our closest living primate relatives, are conspicuous ovulators. If the composition of human semen has evolved to compensate for the loss of ovulatory signals, then levels of luteinizing hormone and follicle stimulating hormone should differ between human and chimpanzee semen. Levels of luteinizing hormone were lower (and more variable) in chimp than human semen and follicle stimulating hormone was completely absent (Burch and Gallup 2006).

The effect of seminal compounds on female physiology does not end there. The triggering of ovulation does not guarantee conception, and conception does not guarantee pregnancy. Human seminal fluid also contains a host of pregnancy inducing and maintaining compounds that actually assist the zygote in implantation and the formation of the pregnancy (Relaxin; Human Chorionic Gonadotropin; Human Placental Lactogen; Pregnancy-Specific β 1-Glycoprotein; Placental proteins 5, 12, and 14; and Pregnancy-associated

plasma protein). Several fertility studies have shown that seminal fluid exposure effects positive outcomes. Live birth rates in couples undergoing In Vitro Fertilization are significantly improved when women engage in intercourse circa embryo transfer (Bellinge et al. 1986; Tremellen et al. 2000). Treating women who suffer recurrent miscarriages with seminal plasma pessaries improves pregnancy success (Coulam and Stern 1993). Preeclampsia studies show a cumulative benefit of semen exposure over time: limited sex or condom use is linked with increased risk (Klonoff-Cohen et al. 1989; Robillard et al. 1995) and the effect is partner-specific (Dekker et al. 1998).

Some of these effects might also be result of a variety of cytokines and growth factors that culminate in improved endometrial receptivity to the implanting embryo. Cytokines have embryotrophic properties and also contribute directly to the optimal development of the early embryo (Robertson 2005). Cytokines and male alloantigens in seminal fluid are sufficient to induce a state of “active immune tolerance” to paternal alloantigen and this priming positively influences fetal survival in later gestation (Robertson et al. 2009).

Perhaps the most fascinating (or at least the most publicized) effect of seminal fluid is that on female psychological functioning. Seminal fluid contains a variety of neurotransmitters and mood regulators; Tyrosine, DOPA, Norepinephrine, Serotonin, Melatonin, and Thyrotropin-Releasing-Hormone. Very little research has been done on the effects of these compounds on the female psyche.

Gallup et al. (2002) reported that females who engaged in intercourse but never used condoms showed significantly lower scores on the Beck Depression Inventory than those who used condoms more frequently and those who never engaged in intercourse. Depression scores between females who used condoms and those who did not engage in intercourse were not significantly different. In then “no condom” and “little condom use” groups, time since last sexual intercourse and depressive symptoms were positively correlated. Being in a relationship, length of that relationship, use of oral contraceptives, and frequency of sex did not affect depressive symptoms.

Conclusion

In short, human semen biochemistry appears to have been selected to suppress the female immune system and increase female sexual interest, bonding, the potential for orgasm, the probability of conception and pregnancy maintenance, partially in response to concealed ovulation. This process also appears to have the byproduct of affecting female physiological and psychological functioning.

Cross-References

- Semen Familiarity
- Seminal Plasma

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Semen Displacement

- Physiological Evidence for Human Sperm Competition

Semen Familiarity

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Definition

The effect of one man's semen on the physiological state of a female and patterns of reproduction related to a consistent partner's seminal fluid versus a new partner's.

Introduction

It has already been established that seminal fluid contains several compounds that may assist in

pregnancy maintenance and prevent spontaneous abortion (see [Cross-References](#) below). Roberts and Lowe (1975) estimated that about 78% of all human conceptions do not make it full term, so spontaneous abortion is a major factor in human reproduction.

Some researchers have determined that semen familiarity, repeated exposure to the father's semen, may be a factor in pregnancy maintenance. Live birth rates in couples undergoing in vitro fertilization are significantly improved when women engage in intercourse circa embryo transfer (Tremellen et al. 2000). Treating women who suffer recurrent miscarriages with seminal plasma pessaries improves pregnancy success (Coulam and Stern 1993), and preeclampsia studies show a cumulative benefit of semen exposure over time: limited sex or condom use is linked with increased risk (Klonoff-Cohen et al. 1989). This "cumulative benefit" also implies that this exposure is to seminal fluid of the same male.

Preeclampsia, a cluster of symptoms (including high blood pressure and protein release), is a contributing factor to maternal mortality in the USA and a major cause of perinatal morbidity and mortality (Einarsson et al. 2003; Klonoff-Cohen et al. 1989). One of the major protective factors against preeclampsia appears to be repeated exposure to the father's semen. Women who have limited exposure to the father's semen are at increased risk for preeclampsia (Robertson et al. 2003). Preeclampsia also is more likely in pregnancies that occur by artificial insemination, a procedure that sometimes requires the separation of spermatozoa from the seminal fluid (Koelman et al. 2000).

Because the likelihood of preeclampsia is higher for women who are not cohabitating with the child's father, for women who conceive as a result of artificial insemination, for women who use condoms, and for successive pregnancies that involve a change in paternity, there may be biochemical differences that distinguish one man's semen from another's. Dekker et al. (1998) identified changes in "paternity," the female's sexual partner, as a predictor in preeclampsia. This implies that it is not only exposure to semen that aids in pregnancy maintenance but the consistent

exposure to the father's semen. Although not all of the factors that distinguish one male's seminal fluid from another's have been identified, Doss and Louca (1991) showed that the ratio between testosterone and dihydrotestosterone is different from one man to another due to the heterogeneity of seminal plasma. They hypothesized that this ratio may be useful in identifying a particular man's semen.

Conclusion

Davis and Gallup (2006) argue that the absence of semen familiarity may be a cue that triggers female mechanisms that evolved to terminate pregnancies that were not in a woman's reproductive best interests. Making a judicious mate choice and being in a committed relationship with the child's father are two markers of reproductive success for women. Not only do females have a vested interest in the other 50% of the genes being carried by each of their children in ancestral environments the chances of her children surviving to reproductive age would have depended on the presence of a committed, protective, and provisioning mate.

Cross-References

- [Copulatory Intrasexual Competition](#)
- [Evolutionary Arms Race](#)
- [Intrasexual Competition](#)
- [Placental Proteins In Semen](#)
- [Reproductive Suppression and Sexual Conflict During Mating](#)
- [Semen And Vaginal Chemistry](#)
- [Seminal Plasma](#)

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Semen from In-Pair Partner

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Synonyms

In-pair copulation; Sperm competition

Definition

Semen from in-pair partner describes the psychological and adaptive functions of semen during copulation between individuals in a relationship.

Introduction

Aside from its main role in aiding fertilization, semen production can be influenced by psychological, physical, and social factors that promote its quantity and quality in sexual behaviors. These influences play an adaptive role in increasing the probability that fertilization may occur and aid in reducing the probability of another man fertilizing the ova of their partner. For instance, men have cognitive mechanisms that are sensitive to specific contexts that may doubt their paternity, and this may influence their sexual behavior with their current partner. Additionally, there is evidence to suggest that semen has psychological and biological effects, such as reducing emotional distress (Gallup et al. 2002) and reducing prenatal complications (Koelman et al. 2000). Semen from in-pair partner provides an insight on how human relationships are affected by the perception of infidelity and on the interdependent relationship between copulation and psychological health. Taken together, semen from in-pair partners may suggest the important role of long-term pair bonds where ingestion of semen ejaculate would be most common.

Sperm Competition

Sperm competition is when females engage in sexual intercourse with different men which results in sperm from different partners occupying the reproductive tract (Parker 1970). Although this implies an act of infidelity in a relationship, the thought of unfaithfulness in a relationship can cause changes in semen production and sexual behavior. A man who is at risk of his partner engaging in extra-pair sex may end up investing resources in offspring that are not genetically related (Pham and Shackelford 2015). This may result in psychological and physical changes in a relationship to counter that risk, such as increased semen production, or methods to remove a possible partner's semen, known as semen displacement. There is a body of research that has looked into time spent away from a current partner and the effects it has on semen quantity in men. Time

spent away from a partner puts a man at risk for cuckoldry, as there is no certainty that his partner has been faithful. When away from their partner, men ejaculate more and produce more sperm until their next copulation (Baker and Bellis 1993). This suggests a strategy of sperm competition as an attempt to counter the possibility of another man's semen in the female's reproductive tract.

Another tactic that men incorporate when perceiving that their partner have been unfaithful is semen displacement. Semen displacement refers to sexual intercourse where there is deep thrusting to remove semen from a rival male. This can be accomplished by long copulation, where there is more time to remove semen from intercourse, or by quickly ejaculating following an assumption of infidelity. If this strategy is to be effective, then it should be used in situations where there is a likelihood of partner infidelity or where there has been an amount of time of separation where extra-pair copulation may have occurred. In situations where women have male coworkers or male friends that they spend time with, men have reported more semen displacing behaviors, such as increased and deep thrusting (Barbaro et al. 2015). Deep thrusting may be an effective strategy if copulation with another male has been short, where the rival male's semen is still in the vagina. However, if time between an extra-pair copulation and in-pair copulation has been longer, a shorter copulation with an in-pair partner may be more effective as displacement would not be effective once sperm has entered the reproductive tract and away from the vagina (Barbaro et al. 2015). Semen displacement behaviors are also prevalent in committed relationships (e.g., marriage). It has been reported that men engage in semen displacing behaviors at their next copulation with their partner if their wives spend more time with male friends or male coworkers (Pham et al. 2017). This suggests that sperm competition is not independent of relationship status, but dependent on psychological and environmental factors where one is at risk of cuckoldry.

Perceptions of infidelity may be mediated by mate guarding behaviors. Mate guarding is a costly behavior, but it is effective if it can ascertain faithfulness and paternity certainty. However, this may be determined by the quality of the male that is

utilizing mate guarding, such as his level of attractiveness and dominance. It has been found that men who engage in more mate guarding behaviors display lower quality of ejaculate and less quality of sperm than men who engage in less mate guarding behaviors (Leivers et al. 2014). It could be argued that this may be influenced by mate value, where high quality males may not engage in mate guarding behaviors because their high quality traits prevent women from leaving them. Men of low mate value may engage in more mate guarding behaviors because they are at greater risk of their partners leaving them (Leivers et al. 2014).

Psychological Effects of Semen

It has been suggested that semen can have psychological effects when absorbed through the vaginal wall due to the many hormones in the seminal plasma, such as testosterone, prolactin, follicular stimulating hormone, estrogen, and luteinizing hormone (Gallup et al. 2002). Known as Ney's hypothesis, the effects that seminal plasma has on female behavior is through the modulating effects that prostaglandins have on neurotransmitters. Estrogen can have mood-elevating properties in postmenopausal women and younger women who take estrogen-based contraceptives (Gallup et al. 2002). If semen does have psychological effects, then women who have intercourse without condoms, where semen would be in the reproductive tract, should report less emotional distress, such as depression. Research investigating the role of semen and emotional distress has shown that women who have sex without condoms have fewer depressive symptoms compared to women who use condoms and women who abstain from sexual intercourse. Although it can be argued that this association may be due to sexual frequency, women who have frequent sex with condoms report similar depressive symptoms to women who abstain from sexual intercourse. These effects also carry over to lower suicide attempts in women who do not use condoms when compared to women who use condoms and women who abstain from sexual activity (Gallup et al. 2002).

Preeclampsia Risk and Semen Ingestion

There are many other functions that semen may provide an in-pair partner, whether it is semen obtained through oral or vaginal sex. Although there are many different reasons why couples engage in oral sex (i.e., arousal, pleasure, rival detection), the benefits of fellatio on women has not been fully explored. There seems to be an important role that semen plays in couples who are expecting children, which may highlight a function of oral sex where it is dependent that the female swallows the semen. In women who are pregnant, preeclampsia is a complication that results in hypertension and can lead to severe consequences in pregnancy. Research has shown semen may be beneficial in women who are at risk for preeclampsia (Koelman et al. 2000). Prior to gestation, semen has been found to induce immunological responses in women who ingest their partner's semen through oral sex resulting in a reduce likelihood of preeclampsia. This is through the result of molecules in semen that aid in inducing immunological tolerance in women.

Are the benefits of semen ingestion dependent on relationship context? Research has investigated if these effects can be explained by women who receive semen through their own partner (in-pair) or semen received through an out-pair, such as donor sperm. There are many reasons why women would want to receive donor sperm, such as issues related to infertility, or lesbian couples who are trying to conceive. In looking at the risk of preeclampsia, it has been shown that women who receive semen from a donor are at a significant increase from developing preeclampsia compared to receiving semen from their partner (Gonzalez-Comadran et al. 2014). Although the findings are unclear as to why donor semen would increase preeclampsia, it points to the important role that relationship context may have on semen ingestion in developing preeclampsia.

Conclusion

Semen serves as an important vehicle for transporting sperm in an attempt to fertilize an ova.

This process can be modulated by environmental and psychological factors where a male may feel compromised as to his certainty in paternity. This discrepancy may influence the amount of semen produced, as well as the behaviors utilized to combat the possibility of a rival's sperm inside the reproductive tract of a partner, as is seen in semen displacement. Although sperm competition has received a lot of attention in the literature, semen's influential role to mental health and prenatal care is equally important. It is noteworthy to point that these influences may be the result of relationship context, where semen ingestion may be dependent upon semen obtained from a committed relationship (in-pair partner).

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Semen Toxicity

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Synonyms

[Semen-based cost of mating](#); [Toxic molecules in seminal fluid](#)

Definition

In some taxa, molecules in the ejaculate can lower the longevity of females that receive them.

Introduction

Mating requires cooperation between the sexes. In species in which there are separate sexes, females and males of the same species must communicate to find each other, and sperm and eggs need to be united in the correct manner to achieve fertilization. And, at least in some organisms with parental care, cooperation between parents continues after the progeny are produced. Yet, against this background of cooperation, there are less salutary interactions. For example, in some taxa, males transfer in their seminal fluid molecules that result in premature death of their mates (e.g., in the fruit fly *Drosophila melanogaster*, nematode worm *Caenorhabditis elegans*, bean beetle *Callosobruchus maculatus*, Colorado potato beetle *Leptinotarsa decemlineata* (see Chapman et al. 1995; Shi and Murphy 2014 for examples)) or interfere with the function of other males' sperm (a point that even merited mention in an episode of the TV series *House*). How and why would this occur?

Males and Females Have Different Reproductive Strategies

Males and females have a shared reproductive interest in passing on their genetic material to as many high-quality offspring as possible. But strategies to best achieve this may often differ between the sexes (e.g., see Chapman et al. 2003 for review). Egg production requires a large energetic investment that may outweigh investment in sperm or seminal fluids. In some organisms, progeny care and feeding are also disproportionately performed by females, requiring additional energy expenditure. Thus, it is often advantageous to females to mate selectively and use the sperm from the highest-quality males to fertilize their gametes. Phenomena such as limiting the extent of multiple mating, or increasing pair-bonding, may be useful strategies in this regard. Males, in contrast, may often benefit from adopting a very different strategy. With gametes that are energetically cheap to produce and can be made in very large numbers, males can benefit from mating multiply and frequently, with less regard to mate quality – it is a numbers game. When males are abundant, this can manifest as polyandry (more than one male mating with a given female), provided that this is not diluted by male social dominance strategies. When more than one male has mated with a female there is competition among the males' sperm/ejaculates for fertilization opportunities. In a competitive situation such as this, any modification that can increase a male's access to fertilization opportunities will increase his reproductive success and that of his male descendants who display it. Thus, over evolutionary time strategies such as increased sperm numbers and faster, "better," sperm may be selected for.

Seminal Proteins Are Critical Contributors to Reproductive Success

A very important contributor to male reproductive success is the set of molecules that males make and transfer (along with sperm) to females during

mating. These molecules include seminal proteins, whose effects can promote the success of their “own” sperm by harming the sperm of rival males. This was demonstrated in Hymenoptera (bees and ants; den Boer et al. 2010) in which sperm viability is decreased when sperm are incubated in seminal fluid of a different male (relative to within their own seminal fluid).

Seminal proteins also affect females in important, reproduction-enhancing ways, in all animals thus far examined (e.g., Avila et al. 2011 for insects). Within the female, seminal proteins access and act upon the neuroendocrine and reproductive systems, resulting in physiological changes that impact the female’s reproductive efficiency. For example, beta-NGF in the seminal fluid triggers female camelids to ovulate (Ratto et al. 2012), and an unrelated seminal protein, ovulin (Rubinstein and Wolfner 2013), does so in *Drosophila melanogaster* fruit flies. These actions ensure that eggs are quickly available to be fertilized by the male’s sperm, an outcome that is advantageous to the reproductive success of both the male and the female.

Differences in Reproductive Strategies Impact Seminal Protein Evolution

It is thought that seminal fluid proteins may have been selected initially in order to coordinate the many complex reproductive processes that need to be initiated following mating. Hence, seminal fluid proteins allow the matching of the timing of the cascade of reproductive changes in females that must occur in order to achieve successful fertilization. Such effects would be mutually beneficial for both sexes. For example, the female could “use” the male’s provision of seminal fluid to regulate her physiology to increase energy-demanding egg production only after mating has occurred and thus not “waste” energy on producing and ovulating eggs that cannot be fertilized and will die.

However, once there was the opportunity for males to influence the reproductive investment of

females, particularly in polyandrous species, the stage was set for males to potentially “manipulate” female physiology and benefit male fertility or competitive success even if exacting costs in females. The different optimal reproductive strategies for males and females means that seminal proteins can be selected for that are advantageous to males, even if their effects might not benefit females. For example, seminal fluid of insect males contains molecules that decrease their mates’ propensity to remate (Avila et al. 2011). This effect can increase a male’s relative reproductive success by decreasing the likelihood that his sperm will be usurped by a rival’s or that his progeny will be in competition with half siblings from subsequent reproductive episodes by the same mother. Although this remating inhibition can potentially provide some benefit to the female (giving her more time to lay eggs and avoiding any negative physical consequences of mating itself), this effect of seminal proteins also decreases the female’s likelihood of mating with a “better” second male. In this sense, the interests of males and females are in conflict, with the seminal protein benefitting the male to the potential detriment of the female.

As long as a strategy benefits a male relative to his rivals, it can be selected for even if it causes harm to the female. If the negative effects of a seminal protein are large enough, female resistance can evolve, for example, by selection for mutations that make receptors for the seminal protein less abundant or less active or by increasing the amount or activity of seminal-protein degrading enzymes. This in turn can favor the emergence of new mechanisms in males to circumvent resistance, such as alternative strategies to prevent remating. An interesting example in this regard is the *Drosophila* “sex peptide” seminal protein. One function of this peptide is to decrease the female’s propensity to remate (Chen et al. 1988). Decreased remating propensity is most effective for the male if it persists as long as his sperm are available in the female to fertilize eggs. Interestingly, the sex peptide becomes attached to sperm, which maintains it in the

female as long as sperm are present while protecting it from degradation by proteases in her circulatory system. Kubli and colleagues suggest that the development of sperm binding as a way to retain and protect sex peptide in the female may have led to the evolution of very long *Drosophila* sperm: males can retain more sex peptide in females this way. A number of studies have provided evidence for such an “arms race” of evolution of molecules and strategies by males, followed by counter-evolution of the females to resist harm, leading to new male strategies.

Semen Toxicity Occurs in Some Taxa and Likely Relates to the Sexes’ Differing Reproductive Strategies

A striking example of a situation in which males benefit at a clear cost to females is that seminal proteins decrease the longevity of females in some taxa (e.g., Chapman et al. 1995; Shi and Murphy 2014). Some decrease in female longevity as a cost of mating seems unsurprising. The energetic cost of producing eggs and progeny can trade off against somatic maintenance and health. However, if such earlier death is balanced by the benefits of having more progeny, especially early in life, then there is no overall net fitness cost. In order to attribute costs of mating to the receipt of seminal fluids, it is therefore important to consider the net outcomes of lifespan versus reproductive success. For example, when the source of the cost of mating (Fowler and Partridge 1989) was probed genetically in *Drosophila melanogaster*, it was found that there were additional costs besides increased egg production. In particular, a component of seminal fluid caused premature death of the female (Chapman et al. 1995). In experiments in which egg production and male exposure/harassment levels were controlled, females that mated repeatedly with males that supplied seminal proteins died sooner than females that had mated with males that did not supply seminal proteins. Thus, a seminal protein(s) decreased female longevity. Subsequent experiments showed that a particular seminal protein, the *Drosophila*-specific sex peptide, caused decreased female

longevity (Wigby and Chapman 2005), although overexpression assays suggested that several other seminal proteins might also have a negative effect on female lifespan.

How and why can a seminal protein, like the sex peptide, result in significant harm to females? The reasons are as yet unknown but we can make some guesses. One possibility is that the sex peptide’s negative effects on female lifespan could be an “intended” and directly selected function that is actively selected for. Such an explanation would suggest that it is advantageous to the male to cause his mate to die soon after mating, either so that she would rapidly produce progeny as a terminal investment or so that her death would decrease the chances of her producing subsequent offspring with a rival. Although this is a formal possibility, there is as yet no experimental support for it.

An alternative hypothesis is that the female’s longevity decrease is not a direct consequence of the effect of sex peptide but is instead a side effect of some other, beneficial, effect. In this model, there would have been selection for the effects of sex peptide and the female response system to be tuned to balance the fertility-enhancing benefits of the male peptide with females being sufficiently resistant to its negative effects on longevity so as to have minimal impact on net fitness. Consistent with this interpretation, the effects of mating on female longevity in *Drosophila* are small – multiple matings are needed before a statistically significant longevity decrease is observed – and the increase in female death rate occurs after at least the initial burst of progeny production is completed. At the moment, we do not know which of the sex peptide’s many effects could result in this indirect but negative effect on female longevity, but there are several possibilities. First, the sex peptide increases feeding by females. Increased feeding is also required to provide increased nutrition to meet the energy expenditure of egg production. However, since increased caloric intake is also associated with decreased longevity in many organisms including *Drosophila*, feeding stimulation by sex peptide could have negative consequences on longevity. A second possibility is that sex peptide also decreases siesta sleep in mated females, improving their chance of finding egg-laying sites but also perhaps resulting in

increased energy expenditure that could lead to earlier death. The sex peptide also induces immune gene expression in females, and it is possible, but is not yet demonstrated, that a high level of immune-gene expression could reduce female viability either due to increased energy expenditure on immune proteins or perhaps due to deleterious effects on the female's microbiome. Finally, sex peptide changes hormone levels (juvenile hormone) in mated females; the shift in hormonal milieu could potentially be costly. In all cases, the positive effects of sex peptide on reproduction would have outweighed these negative side effects.

Although costs of semen receipt have been reported in a number of invertebrate taxa (e.g., Chapman et al. 1995; Shi and Murphy 2014) (it has not been searched for systematically in vertebrates), this phenomenon is not universal and is even context dependent in some taxa. Moreover, the one well-characterized inducer of early death in mated females – the sex peptide (Wigby and Chapman 2005) – is not found outside the genus *Drosophila*. And, not all *Drosophila* species show post-mating longevity decreases. For example, polyandry is reported as beneficial to female lifespan in *D. simulans* and in *D. mojavensis* increased mating confers resistance to desiccation stress. Hence different molecules and mechanisms may underlie costs observed in different taxa. This is consistent with our argument above that semen toxicity is not a directly selected effect. Rather, we suggest that in some taxa, a male-benefitting effect of a seminal protein may exact costs in females. Counterselection will keep the level of cost expressed in those taxa at a level that does not unduly impact upon net fitness, though some cost may be expressed as a pleiotropic effect of the beneficial reproductive effects of the seminal protein. Consistent with this, the toxicity of proteins that cause costs, and potentially even the type of toxicity they cause, are not expected to be conserved.

Conclusion

Semen toxicity represents a fascinating reflection of the fact that males and females use different

strategies for optimal reproductive success. It will be intriguing to examine what has led to the evolution, and retention, of semen toxicity in some taxa but not in others.

Cross-References

- [Evolution](#)
- [Intralocus Sexual Conflict](#)
- [Reproduction](#)
- [Sexual Conflict Theory](#)
- [Sperm Competition](#)

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Semen-Based Cost of Mating

► Semen Toxicity

Semicircular Canals

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Synonyms

Inner ear structure

Definition

The superior, posterior, and lateral semicircular canals of the inner ear responsible for balance and the movement of the head

Introduction

The semicircular canals are part of the structures of the inner ear, specifically the bony labyrinth. (Munir and Clarke 2013). The canals are filled with perilymph (Hain and Helminsky 2007). Their neurosensory elements are known as the crista and cupula, and the neurosensory elements of the canals' otolithic organs are known as the macule and the striole. The semicircular canals are responsible for keeping the person's balance and posture; they are also responsible for the movement of the head with the help of the otolithic organs.

Structure of Semicircular Canals

The semicircular canals are part of the bony labyrinth of the inner ear (Munir and Clarke 2013). The bony labyrinth consists not only of the semicircular canals but of the cochlea as well. The canals are filled with a fluid similar

to the cerebral fluid, called the perilymph (Hain and Helminsky 2007), which is contained in the perilymphatic duct in the subarachnoid space (Chang and Khana 2013). There is perilymph also between the membranous and the bony labyrinth (Pickles 2012).

Each semicircular canal is perpendicular to the other canals on the ipsilateral side and coplanar with the contralateral canals (Chandrasekhar 2013). Each canal forms two thirds of a circle with a diameter of roughly 6.5 mm and a cross-sectional diameter of 0.4 mm (Lee et al. 2016). The neurosensory elements of each canal are called the crista and cupula and are perpendicular to the plane of the canal (Chandrasekhar 2013). Each otolithic organ has a curvilinear shape at right angles with each other. Their neurosensory elements are called the macule and the striola; the macule is located around a central dividing line, and the hair cells of the striola are located either toward the line in the utricle or away in the saccule (Chandrasekhar 2013).

Function

The three semicircular canals of the inner ear (superior, posterior, and lateral) perceive the turning motion of the head (Munir and Clarke 2013). They are oriented at right angles to each other. Each canal is responsive to angular motion and is paired with a canal on the contralateral side so that what is an excitatory stimulus to the one, to be inhibitory to the other (Lee et al. 2016).

Otoliths

The utricle and saccule respond to the pull of gravity rather than the motion. These two otoliths provide mass to the balance system hair cells, and when the head is moved into new positions, gravity pulls on that mass and pressures the tips of the hair cells. Consequently, this sends a nerve signal to the brain which indicates movement (Munir and Clarke 2013). A structure called semicircular ducts has the same structure as the bony semicircular canals where they are contained

(Chang and Khana 2013). They compose the kinetic labyrinth that senses the acceleration or rotation of the head. The semicircular ducts are attached to the utricle, and at the end of each duct there is a structure called the ampulla, which contains the sensory neuroepithelium on the crista ampullaris. This is covered by the cupula; a gelatinous substance entrenched with hair cells (Chang and Khana 2013). The cupula is displaced by the endolymph motion based on the rotational acceleration of the head, which bends the hair cells in the opposite direction of the rotation, subsequently opening the ion channels and depolarization of the hair cells, which in turn increases the firing of its afferent fibers (Chang and Khana 2013). Rotational deceleration of the movement of the head displaces the cupula in the same direction of the head movement, which subsequently closes the ion channels of the hair cell which causes it to become hyperpolarized, having the result of a reduction in afferent nerve firing (Chang and Khana 2013).

Conclusion

The structure and function of the semicircular canals were reviewed as well as a brief discussion of how the otolithic organs contribute to keep a person's posture and balance in check was provided.

Cross-References

► [Otolith](#)

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Seminal Fluid

► [Seminal Plasma](#)

Seminal Plasma

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Synonyms

[Ejaculate](#); [Semen](#); [Seminal fluid](#)

Definition

Human male reproductive fluid, separate from spermatozoa (sperm)

Introduction

Only 5 % of an ejaculation consists of sperm. The remaining 95 % is called “seminal plasma” which consists of a bewildering array of different ingredients, including various hormones, neurotransmitters, endogenous opiates, and immunosuppressants. Burch and Gallup (2006) have theorized that many of the different components in seminal plasma may have evolved to commandeer the female reproductive system in

such way as to promote the reproductive best interests of males (Burch and Gallup 2006; Gallup and Burch 2006; Gallup et al. 2012).

Compounds in Seminal Plasma

Just as there appear to be context-specific mechanisms that promote sperm competition by adjusting the number of sperm in the ejaculate to take into account the probability of rival male sperm in the female reproductive tract, Burch and Gallup have championed the view that similar mechanisms operating at the level of the testicles may modify or adjust the composition of seminal plasma to fit the particular situation or setting in which ejaculation occurs. Gallup et al. (2012) refer to this as the “Topping off Hypothesis.”

For example, although it may appear counter-intuitive, the chance of conception as a consequence of nonconsensual sex or rape is 2–6 times higher than is true for consensual sex (see Gallup et al. 2012 for a review). Contained in human seminal plasma are several compounds necessary for female reproduction, including follicle stimulating hormone (FSH) and luteinizing hormone (LH). During the ovulatory phase of the menstrual cycle, changes in FSH and LH serve to prompt the maturation and release of an egg. Researchers have theorized that during sexual assault, evolved mechanisms may operate to adjust the levels of these hormones in seminal plasma to increase the likelihood of induced ovulation and conception as a consequence. At least in principle, this hypothesis could be easily tested by assaying semen from victims of sexual assault or by collecting and assaying semen from sperm donors who watch either consensual or non-consensual pornography while masturbating.

Conclusion

It is entirely possible that evolved mechanisms may exist that also function to adjust different aspects of the chemistry of seminal plasma to fit other reproductive contexts as well (Gallup et al. 2012).

Cross-References

- ▶ [Placental Proteins in Semen](#)
- ▶ [Semen and Vaginal Chemistry](#)
- ▶ [Semen Familiarity](#)

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Semiotic Constraints

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Definition

Semiotic constraints refer to the notion that the behavior of animals (including humans) is organized at least in part by what the things that they encounter in the world signify, or “mean,” to them. In the context of evolutionary psychology, such “meanings” do not refer to self-conscious mental processes but to naturally evolved patterns of behavior wherein a given stimulus has come to indicate, or point to, something other than itself for the members of a species. The term “semiotic constraints” has thus been used to refer both to those signs in the environment that productively constrain, and thus give shape to, an organism’s behavior, as well as to the conditions under which such stimuli have become meaningful for an organism to begin with.

Introduction

“Semiosis” comes from the Greek terms *sēma* “sign” and *-ōsis* (“process”). Biosemiotics is thus the study of sign-processes in living systems, and “semiotic constraints,” in this context, refer to the evolutionary and material constraints that shape those sign processes and that, in turn, shape the behavior of organisms in response to them.

The Danish molecular biologist and biosemiotician Jesper Hoffmeyer explains the need for this concept well, when he notes that “every organism is tossed at birth into a [world of] sounds, smells, movements, colours, shapes, electrical fields, thermal radiation, waves of all kinds, chemical signals, touching, and so on . . . to which it must adapt correctly, if it is to survive” (1996: vii).

The question from the evolutionary biologists’ point of view, then, is: What are the processes by which any given naturally occurring phenomenon – the vibrations in the air made by the setting down of a paw in the forest, for example – can come to reorganize organisms’ biology evolutionarily such that an appropriate stimulus-response is reliably produced in the presence of this “sign” of danger (e.g., a twig snapping) that is not dangerous in itself? And even more fundamentally: By what evolutionary processes have the intrinsically nonmeaningful aspects of the natural world – air vibrations, light wavelengths, molecular structure, etc. – become the meaning-laden sights, sounds, smells, and colors of living creature’s phenomenal experience?

Semiotic Constraints on the Population Level

Twentieth-century physiologist and experimental biologist Jakob von Uexküll (1864–1944) coined the term *Umwelt* to refer to the perceptual surround specific to each species as a result of its own particular biological constitution. The wavelengths of light that constitute the colors of the human world do not all appear in the *umwelt* of bats, just as the ultrasonic sounds by which bats

navigate the world are undetectable to humans. Biology thus constrains which “signs” of the external world each species can detect, and thus act upon, in order to accomplish its survival needs of hunting, fleeing, mating, etc.

Within this semiotic niche, the detections and responses of other animals – particularly a species’ conspecifics, predators, and prey – to such signals exert evolutionary selection pressure, such that the evolved capabilities of one species result in the evolved counter-capabilities of another (e.g., the tiger moth’s evolved ability to “jam” the sonar that the bat has evolved to detect the tiger moth). The differential success and failure of such signal-using strategies and behaviors for a population, too, form part of the ever-present semiotic constraints shaping animal evolution.

Semiotic Constraints on the Biological Level

For physicist and systems scientist Howard Pattee (1926–), the notion of “biological information” can best be thought of as those material constraints upon a living system’s *internal dynamics* that have been selected over evolutionary time in order to preserve and enhance an organism’s survival. Building upon mathematician John von Neumann (1903–1957) pioneering work on self-reproducing automata, or systems that contain within them the encoded instructions for copying and maintaining themselves, Pattee (1972, 1997) distinguishes between the laws governing the physical dynamics of a living system, which are universal and time-reversible, and the informational control mechanisms acting upon those dynamics, which are species-specific and the product of each species’ history of natural selection.

The same molecule, for example, can and will trigger different processes to take place in different organisms (and even in different parts of the same organism). “What makes a molecule a message (i.e., endows it with the power of physically harnessing the dynamics [of a living system]),” writes Pattee’s biographer Joanna Rączaszek-Leonardi, “is not its particular physical or

chemical properties, but its evolutionary history within a system: i.e., its being selected for bringing about a particular phenotypic effect" (2012).

Such dynamics-controlling mechanisms are informational, or semiotic, in two senses: (1) they are "constraints that, while obeying laws [governing all physical structures], can also implement arbitrary syntactic and formal rules" specific to the cohesive functioning of each species' particular bodily organization, and (2) they have, again, become organized as such as a result of a species' history of successful and unsuccessful interactions with the world via the recursive feedback processes of natural selection.

Semiotic relationships are understood above as involving processes that are broader than, and evolutionarily prior to, the much later evolution of human language and meaning, for here "semiotics" denotes "the study of how meaning is built, but the word 'meaning' is taken in its original non-textual and non-linguistic interpretation: [i.e.,] how one privileged trajectory is built, out of an indefinite number of possibilities; in that sense, semiotics is the study of order building" (Akrich and Latour 1992).

Semiotic Constraints on the Evolutionary Level

Similar, though nonidentical, dynamic systems approaches to the role of semiotic constraints in the evolution and functioning of biological organization have been taken by biochemist and complexity theorist Stuart Kauffman and colleagues, who write that:

The typical requirement for work itself is to construct those very constraints on the release of energy that then constitute further work. Information creation, we argue, arises in two ways: first information as natural selection assembling the very constraints on the release of energy that then constitutes work and the propagation of organization. Second, information in a more extended sense is "semiotic," that is, about the world (or internal state of the organism) and that requires an appropriate response. (2008)

and by the neuroscientist and biological anthropologist Terrence Deacon (2011), who

argues that biological "information" is a relational property that emerges from the interplay of three nested and recursive sets of constraints: (1) the set of purely physical constraints on signal dynamics, (2) the set of mathematical likelihood constraints on signal probability, and (3) the set of Darwinian fitness constraints required for the self-maintenance of the signal-using living system. By "generalizing the insight of Claude Shannon's equation of *information* with *entropy-reduction* and tracing its linkage [with] thermodynamic and evolutionary domains," Deacon hopes to show how physical constraints become informational (or semiotic) constraints by virtue of how they delimit certain systemic possibilities in the ways that an organism senses and responds to inputs from the environment.

Semiotic Constraints on the Human Sociological Level

The term "semiotic constraints" was first used in the humanities by the linguist and semiotician Algirdas Julien Greimas (1917–1962) to denote how the use of any given sign is always embedded in a larger system of signs, wherein the meaning possibilities that any given sign-user can assign to it are productively (and also prohibitively) constrained. These constraints intersect to form a "semiotic square" (or closed "phase space") of permitted meaning combinations.

Robotacist and Artificial Intelligence researcher Luc Steels and his colleagues have employed modified versions of Greimas' semiotic square as part of their experimental design for modeling the evolution of language using artificial agents (2004), while linguist and psychologist Joanna Rączaszek-Leonardi (2012) employs Howard Pattee's notion of semiotic constraints as material structures evolved for the use of controlling dynamics in her own rethinking of what it is that constitutes human language use.

"It is useless to search for meaning in symbols without complementary knowledge of the dynamics being constrained by the symbols" wrote Pattee in regards to the informational controls

that have evolved in biological systems (Pattee 1997). Likewise, argues Rączaszek-Leonardi, we should stop thinking of language as a set of formal, immaterial, rules and signs that speakers manipulate in the privacy of their minds, and start seeing it instead as a way that human beings deploy “soundwaves with a history” in order to constrain the dynamics of human interaction in particular goal-oriented directions.

“In order for those soundwaves to have acquired functionality, i.e., to have a meaningful history” so as to act reliably as effective semiotic constraints, writes Rączaszek-Leonardi:

they have to be stable and reliable under the laws of physics and principles of perception, and they have to have the power to evoke the desired effect. . . . Thus, what makes a natural language symbol a message, i.e., what makes it different from any other soundwave produced by a human, is that it has been selected and stabilized in the process of cultural evolution; these are, to paraphrase Pattee (1972) the ‘integrated constraints that endow what otherwise would indeed be ordinary [sounds] with their symbolic properties.’ (Rączaszek-Leonardi 2012)

Finally, in line with both his earlier work on brain/language coevolution (Deacon 1997) and his work on the nested nature of informational entropy-reduction processes discussed above, Terrence Deacon posits that the systemic requirements inherent to the avoidance of equivocation “about who did what to whom, when, with what [and] in which way” in any given system of symbolic communication constrains the variety of forms that informational entropy reduction systems such as languages can take. “Such semiotic constraints can be conceived as selection pressures,” argues Deacon, “and language origins and evolution in the larger sense must also have proceeded within these constraints at every stage” (2003).

Conclusion

The move towards investigating the informational and sign-processing (semiotic) dynamics produced by, and relevant to future, evolution has been growing steadily in the last two decades,

informed by ideas that were only partially sketched out by previous thinkers. Common to almost all of these approaches is the move away from a reified, mentalistic, and anthropocentric understanding of “signs and symbols” as creations of human language in the first instance, and towards a more naturalized understanding of the role that semiotic controls and processes play in the fundamental organization and evolution of living systems.

Cross-References

- [Biosemiotics](#)
- [Evolution of Language](#)
- [Information Theory](#)
- [Semiotic Square](#)

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Semiotic Square

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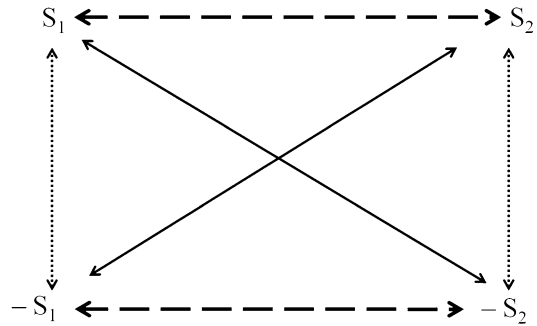
Definition

The semiotic square is a conceptual tool that was first developed within the field of semiotics to depict the logical relations of opposition and implication inherent in any given sign or sign system. It has more recently been refashioned for use in the study of the evolution of language.

Introduction

The Semiotic Square is an analytic tool developed by linguist and semiotician Algirdas Julien Greimas (1917–1962) to depict how complex, nuanced, and even contradictory meanings can emerge from more primitive sets of oppositions (e.g., prescribed/forbidden) and their logical negations (e.g., not prescribed/not forbidden) in any given sign or sign system.

A graphic representation of the “possibility space of meaning” bounded by the four corners of opposition and implication as depicted below, the semiotic square is intended by Greimas to reveal “the elementary structure” of signification whereby terms and values are defined at least in part with respect to what they are not (Greimas [1966] 1983). For Greimas, this system of logical oppositions and their implications constitutes the “deep structure” of any coherent system of meaning, from the rules of a society to the narrative logic of a literary text. Accordingly, cultural



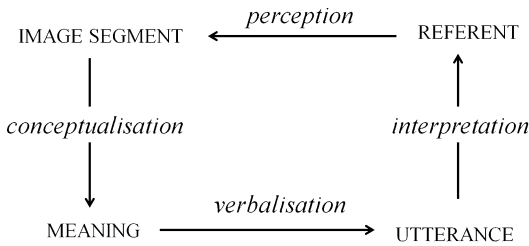
Semiotic Square, Fig. 1 A simplified version of Greimas' semiotic square, wherein any given “meaning” that can be assigned to a sign can be plotted along the coordinates of these axes (adapted from Greimas and Rastier 1968). In this framework, S_1 and S_2 represent a pair of signs holding contrary meanings (such as male/female or happy/sad) that necessarily imply the existence of their logical negations, $-S_1$ and $-S_2$. The resulting square depicts the field of meanings which can then be derived from logical relations of contrariety (dashed arrows), contradiction (solid arrows), and implication (dotted arrows)

theorist Fredric Jameson describes Greimas' semiotic square as “a virtual map of conceptual closure, or better still, of the closure of ideology itself” (Jameson 1976) (Fig. 1).

According to Greimas, individual actions, ideas, and identities arise from, and can only be meaningfully understood in relation to, the possibilities defined by the enclosing logical structure (Greimas and Rastier 1968) – and it is this insight that several researchers in the fields of Artificial Intelligence and Evolution of Language studies have been recently trying to operationalize.

The Relevance of the Semiotic Square in Language Evolution Studies

Roboticist Luc Steels and his collaborators have developed a modified version of Greimas's semiotic square in their experiments designed to have robotic agents create and “evolve” a shared language based on their interactions with the environment, which are then further codified by their interactions with one another (Gantelluci and Steels 2008; Steels 2011, 2015). In Steels' conceptualization, the four corners of the square



Semiotic Square, Fig. 2 Luc Steels and colleagues' version of semiotic square (adapted from Steels 2015), depicting the process by which any given sign derives its meaning, as explained in the text below

represent what he claims are the four mutually “scaffolded” linguistic entities through which shared meaning emerges and is sustained in a community of symbol users. These conceptual entities he calls the REFERENT, the IMAGE SEGMENT, the MEANING, and the UTTERANCE, all of which mutually influence each other in an ever on-going dynamic of perception, conceptualization, verbalization, and interpretation, as illustrated below.

Steels' version of the semiotic square differs in several important aspects from Greimas'. For whereas Greimas's square is a structuralist and formalist attempt at diagramming the topography of logical relations inherent in a given sign or sign system, Steels' square is an attempt to diagram the *evolutionary process* by which a sign's “meaning” is first bestowed and then recursively fine-tuned and employed within a group of interacting agents (Fig. 2).

As part of the “4E” (embodied, embedded, extended, and enactive) turn in cognitive science, Steels' model finds agents' initial perceptions of the world “grounded” in their embodied, sensorimotor interactions within the world. No objects in the external world are pregiven REFERENCES per se in Steels' semiotic processing framework. Rather, the plenum of available sensory input enabled by the agent's biology (or machinery, in the case of artificial agents) must be selectively organized by the agent (or by the agent's evolutionary history) so as to result in reliably successful interaction in an as-yet unlabeled world. The resulting *perceptual* IMAGE SEGMENT is so named to acknowledge that cognition deals with

only relevant and actively selected *aspects* of external objects, as those aspects are implicated in action sequences relevant to the agent, and not to a pictorial “representation” of the fullness of the external world per se (Steels 2006, 2011, 2015).

These perceptual IMAGE SEGMENTS then become *conceptualized* and given meaning within contexts of interaction via a *selectionist* dynamic. Categorical groupings and the acquisition of task-appropriate distinctions to be preserved for use in future similar interactions are the result of exuberant possibility-testing in the assignment of image segments to action repertoires, followed by the Darwinian pruning and “entrenchment of particular solutions by positive [and negative] feedback loops” not only over evolutionary time, but ontogenetically, as well (Steels 2015).

Both the *verbalization* and the *interpretation* of linguistic signals, likewise, are fine-tuned by the feedback based on the successful and unsuccessful interactions with other agents in using those symbols – and as these feedback cycles are ever-ongoing, generative, and recursive “semiotic networks” grow in the space defined by the interaction of these four mutually scaffolded processes of meaning (Steels 2004, 2006, 2011).

Conclusion

The disciplines of semiotics and of evolutionary psychology use term “semiotic square” somewhat differently. In semiotics, the square is used as an analytical tool to depict “the elementary structure of signification, marking off the oppositional logic that is at the heart of both narrative progression and semantic, thematic, or symbolic content” (Felluga 2015). In evolutionary psychology, the semiotic square is used to examine the real-world conditions under which sign-based meanings are created and evolve among a community of agents.

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Senescence

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Synonyms

Advanced age; Aging; Old age

Definition

Senescence is a multifactorial, deleterious, progressive, and cumulative alteration of cells and somatic structures that occurs in an age-related, but not age-determined, fashion, thereby decreasing individual probabilities of survival and reproduction with increasing age.

Senescence is a soma-wide process of functional losses secondary to decreased replicative capacity in dividing cells and accumulated exposures to stressors and related damage in both

dividing and nondividing cells as their time of survival increases. Senescent biology progresses as age-related declines in cellular, tissue, and organ fidelity and function lead to decreased reproductive potential, physiological and psychological dysregulation, and increased probability of death.

Introduction

Currently, across multiple populations, average life spans exceed 80 years (e.g., Italy, Japan, Sweden, women in the USA), and the verified maximum human life span has exceeded 121 years (France). Many factors have contributed to achieving these demographic landmarks. Primary among these have been social and political changes leading to improved public health, hygiene, and population nutrition. These, along with advancements in biotechnology, improved the understanding of the biological and social basis of disease, and applications of evidence-based medicine have contributed to large portions of many populations surviving past their 65th year. In Europe, improvements in average life span began during the nineteenth century as their current economies and social systems emerged and developed. Over the twentieth century, similar demographic trends have affected most of the world's populations (The World Bank 2013). In 1930, the average age at death was 60 years (men 58, women 61 years) in the USA, and only 50% of men and 57% of women survived to age 65 (Bell and Miller 2002). Across nations worldwide, age 65 years is a common criterion for retirement and social security programs, which provides a standard age for internal and cross-national comparisons and health evaluations. Eighty years later, life expectancy was 75 years among men and 80 years among women, with 80% and 88%, respectively, surviving to their 65th year (Bell and Miller 2002). Elsewhere average life spans are lower. In Kuwait life span averages 70 years and in Madagascar 64 years, with only 3% and 2%, respectively, surviving to age 65 years. Average life spans exceeding 70 years with maxima of 13 decades are a new

frontier for humankind. Just 40 kya (kiloyears ago), few individuals appeared to have survived past their 40th year (see Caspari and Lee 2004).

Today, those aged 65+ years are an increasing proportion of most national populations. During the 1920s, less than 5% of the US population was aged 65+ years; in 1950–1960, they exceeded 8% of the total; today they make up 14% (see Bell and Miller 2002; The World Bank 2013). Exceeding the USA, Japan's population includes 24% who are over 65 years and Sweden 21%, while Poland ties the USA at about 14%. Over the nineteenth and twentieth centuries, continued development of built environments, new agriculture methods, advances in medical treatment, and improved diets have reduced multiple stressors that limited human growth, development, and life span in previous environmental settings. These changes allowed today's elders (persons aged 65+ years) to escape many external hazards while receiving better nutritional and energetic intakes and medical care during their growth, development, and reproductive adulthood than did their ancestors.

Today, in high-income industrialized settings, over 80% of people survive to age 65, and 1 of every 4 persons who do so may expect to survive into their 90th year. Such long lives do not characterize our closest primate relatives, gorillas and chimpanzees. Even when housed in well-maintained zoological settings with healthcare, immunizations, balanced nutrition, and free from predation and most parasites, the oldest documented age for a gorilla is 60 years (Colo was born December 1956 at the Columbus Zoo and Aquarium and died there in 2017). Among humans, average life spans of women commonly exceed their reproductive spans by decades. Broad differences in the timing and pattern of life history events between humans and other large-bodied apes throughout life, particularly during the latter decades of life, did not arise solely due to long-term sociocultural developments. More likely, new patterns of sexuality, gestation, somatic growth and development, neurological and physiological systems, psychological structures, and sociality arose as humans and their immediate ancestors (hominins) exploited and adapted to prevailing conditions of

the late Pliocene, through the Pleistocene and Holocene. Humankind's ancestors exploited and adapted to niches significantly different from those exploited by competing hominins and other species. Among these divergent adaptations were upper limbs freed from weight-bearing and bipedalism. These were followed, several million years later, by a long-term trend toward brain expansion, suggesting not only increasing dependence on cognition and evolution of integrated physiological and psychological systems but also evolution of the theory of mind and intentionality (see Dunbar 1998). This evolutionary trend toward dependence on cognition required evolving hominins to allocate additional time and energy to neocortical tissues during their growth and development. This shift in resource allocation also initiated a trend toward secondarily altricial offspring, i.e., neurologically and physically immature at birth compared to other large-bodied apes. Eventually, evolutionary trends in hominin growth and development would require over a decade and a half of relatively high and constant parental investment before they were reproductively mature and socially capable of birthing or siring their own offspring (see Crews 2003; Crews and Bogin 2010).

By decreasing the rate of development and maturation from conception to reproductive adulthood, slow-maturing secondarily altricial offspring reshaped the hominin and human life history pattern compared to other large-bodied apes (see Crews 2003; Crews and Bogin 2010). As this life history pattern evolved over the last 2-plus million years, hominins showed an increasing life span potential (illustrated in Carey and Judge 2000, Fig. 8, p. B207). This long-term evolutionary trend, in conjunction with the development of language, sociocultural systems, built environments, and agriculture, produced the 80+ year average and 120+ year maximum life spans observed today. This contribution explores the evolutionary bases for extended human life spans and their concomitants, senescence and aging. The first focus is on the evolutionary basis of senescent biology being an indirect consequence of surviving and reproducing in a stressful world since the beginning of life. At its most

basic, senescence reflects a compromise between countervailing evolutionary pressures to survive and maintain the soma while also being reproductively successful. The model followed here is that stressor-related damage to cells, tissues, organs, and somatic systems along with their internal fragility produces the senescent phenotype (see also Kim and Jazwinski 2015). This is not a review of the biology of senescence, which would fill an encyclopedia of its own. Rather, it is an evolutionary perspective on how humans came to survive a century and more.

Evolution and Stressors

To survive and reproduce, early life (likely RNA-based replicators) responded to Earth's challenges by evolving multiple stressor-limiting adaptations (e.g., DNA, membranes, cells, multicellularity, mobility). To maintain fidelity and reproduction of its hereditary material, life evolved many forms, none of which escapes environmental and internal stressors. All life-forms evolved their current phenotypes and life history patterns, periods of growth, development, somatic maintenance, and reproductive effort as adaptations to stressors their ancestors experienced. As adaptive responses accumulated, new phenotypes emerged, including offspring who required extended time to grow, develop, and mature. As these increasingly complex phenotypes evolved, early phases of human life history were altered. Among these were, "secondarily altricial offspring" birthed at an earlier stage of development than other apes, extended periods of growth and development including addition of childhood and adolescence phases, and parental provisioning over 1.5-plus decades. To accommodate these evolutionary adaptations, later life history phases necessarily were delayed, and achievable life spans extended (see Carey and Judge 2000; Crews 2003; Crews and Bogin 2010). Across species, longevity (length of life) increased as successive generations evolved increasingly efficient adaptive responses to life's stressors. As more complex stress-limiting adaptations evolved (e.g., digestive and nervous systems, neurological

integration, skeletons, cognitive processing), they required longer periods of growth and development to fully mature. Among humans, these processes extended the premature stage of life leading to our current altricial offspring and delaying commencement of reproductive effort. Evolution of altricial offspring extended the time needed for parental investment and, apparently, also slowed the pace of human cellular senescence. By extending growth and development and delaying the onset of reproductive effort, this suite of adaptations altered human life history, slowed phenotypic aging, and extended human survival.

Although all organisms show deleterious cellular and somatic alterations with increasing survival, senescence is not viewed as an outcome of positive natural selection for cellular dysfunction, organismal frailty, decrepitude, or death in most organisms (see Williams 1957; Kirkwood and Austad 2000; Crews 2003; Arking 2006; Crews and Bogin 2010; Crews and Ice 2012). Rather, biological dysfunction likely developed as a by-product of natural selection for improved defenses against stressors limiting survival and reproductive success (see Williams 1957; Kirkwood and Austad 2000; Arking 2006). Senescence is an inherent by-product of life's fragility. As structural, somatic, physiological, psychological, and behavioral responses to senescent-promoting stressors improved, species' life span potential increased apace. These evolved responses to ancient and more recent stressors continue to mold human phenotypes, senescent biology, and life history. Senescence results from progressive, deleterious, cumulative, and age-related, but not age-determined, alterations associated with decreasing probabilities of reproduction and survival (Arking 2006; Crews and Ice 2012). Biological senescence is an ancient and universal cellular process associated with the loss of cellular integrity that proceeds at a biological, not a chronological, pace (Arking 2006). In dividing cells, senescence is paced by cycles of DNA replication and mitosis. Aging, or organismal senescence, is paced by losses of terminally differentiated (nondividing) cells, physiological function, strength, agility, and endurance and

increased somatic, physiological, and psychological dysregulation, frailty, morbidity, and mortality.

An introduction to life's evolution is necessary to review the evolutionary basis of senescence. Among life's earliest ancestors, individual existence likely was short and replication rapid. Eventually, these short-lived ancestors of life evolved adaptive responses to environmental stressors they encountered (see Hoeppner et al. 2012). One major adaptation was DNA to replace error-prone RNA as a hereditary molecule. More stable than RNA, DNA was a major evolutionary leap. As early replicators evolved internal processes and structures to protect themselves and their hereditary molecules (e.g., membranes, organelles, multicellularity), they increased their survival time (longevity). Eventually, these accumulated adaptive responses led to integrated vascular and neurophysiological systems, skin and skeletons, brains, and complex minds. The latter eventually provided humankind the ability to conceptualize and engage in intentional niche construction and build environments in which to better survive and reproduce. All extinct and existing species evolved as their progenitors responded adaptively to experienced environmental stressors. As biotic evolution continued, organisms capable of slowing their own demise lived sufficiently long to experience senescent biology as a by-product of their evolutionary success. Eventually an array of life-forms evolved, some that today survive only hours before reproducing and perishing, others that live a few days, and still others showing 100+ year life spans. Such differences in longevity and senescence are evolved products of life's continuing struggle to halt damage from stressors while surviving and reproducing in stressful environments.

Stressors and Senescent Biology

Although specifics differ, damage to life from environmental challenges continues today. For many ancient stressors (e.g., UV radiation, nonenzymatic glycation, reactive oxygen species, mutagens), life continues to evolve protective

responses. Still, damage to nuclear DNA (nDNA) and mitochondrial DNA (mtDNA), long-lived proteins and cells, and housekeeping systems increases with age. Many environmental stressors challenging human survival have declined or been altered in modern settings, for example, mega predators (e.g., leopards, tigers, bears) and infectious and parasitic organisms (e.g., bacteria, viruses, worms). At the same time, new stressors have emerged, exposures to pollution, human and animal wastes, built environments, artificial lighting, noise, and sociocultural stressors related to living in groups with high population density. Although all life-forms evolved because of their ancestors' adaptive responses, they still are not able to halt all related damage and losses. As a result, senescent processes are common to all biotic life, and different phenotypes and divergent LH patterns have evolved as populations and species followed their unique adaptive paths to survive and reproduce.

Multiple life history commonalities exist across species, including, for instance, a period of growth and development that culminates in a mature reproductive adult, who eventually succumbs to life's stressors. Commonly, this adult stage coincides with a period of maximum reproductive potential and effort when somatic and physiological function, psychological balance, and somatic resilience are at their maxima. Whether species' survival potential is days or decades, during immature life all organisms must possess sufficient resources, response systems, and/or social support to delay current stressors sufficiently long to mature and engage in reproductive effort. As survival time increases, progressive and cumulative damage to cells and tissues disrupts organismal function producing deleterious changes throughout the system; concurrently, organ and somatic damage secondary to external and internal stressors accumulate. Among multicellular life-forms, some long-lived (nondividing) cells senesce and lose their integrity, while others die as damage to their DNA, proteins, organelles, and membranes accumulates, leading to systemic physiological and psychological dysregulation. Similarly, as dividing cells

sustain damage over time, their replication time increases, and, eventually, they cease proliferating.

Stress-Limiting Systems

The multiple stress responses cells eventually evolved (e.g., multicellularity, organs and organ systems, defensive and repair systems, and psychological structures) constitute sets of overlapping survival and senescence-delaying mechanisms. Many previously evolved defensive adaptations likely have been lost as species went extinct. Other successful adaptations have been conserved and remain observable today as anti-stressor/anti-senescence responses, mechanisms, structures, and modules across species. Such features include the skin, fur, shells, tree bark, slime, vision, neurological structures, theory of mind, introspection, behavioral flexibility, verbal communication, and social systems. These anti-stressor adaptations continue to aid species survival and reproduction. Our cells, organs, and internal structures, whether skeletal, muscular, cardiovascular, neural, or psychological, evolved as adaptations to preserve life and reproduce in ecological settings where resources were scarce, stressors were immediate, life was short, built environments were nonexistent, and hominins were not a dominant species. In today's physically secure and nutritionally adequate settings, humans grow and develop sufficient organ and somatic capacity to exceed that necessary to survive and reproduce (see Crews 2003; Crews and Bogin 2010). Some organs (e.g., kidneys, liver, heart, bone) significantly exceed their minimal capacity to sustain life through the period of reproductive effort, including fledging of offspring. Among these, humans have an innate ability to use available energy in excess of what is needed for growth, development, and reproductive effort to build cellular, organ, somatic, and structural reserve capacity. In many of today's environmental settings, humans are able to accumulate energetic, somatic, physiological, and psychological capacities exceeding what they need to survive and reproduce. This accumulated

reserve capacity helps support somatic function during later decades of human post-reproductive life (see Crews 2003; Crews and Bogin 2010).

Human Evolution and Variation

Aspects of modern biology and senescence separating humans from other modern apes are based upon adaptive responses and peculiarities hominins evolved as their phylogenetic branch led to modern humans through the Pleistocene (approximately the past 2.6 million years, ending with commencement of the Holocene about 12,000 years ago). Humankind's current somatic, physiological, and psychological capacities coevolved as hominins responded to environments that stretched their adaptive limits, somatic reserves, and mental capacities to survive and reproduce in stressful environments (see Dunbar 1998; Crews 2003; Crews and Bogin 2010). Settings wherein, the hominin adaptive repertoire likely provided sufficient capacity for growth, development, survival, and reproductive effort, but little for late-life survival. In built environments of the twenty-first century, phenotypes based on this adaptive repertoire are able to exceed somatic and energetic capacities required to complete their growth, development, reproduction, and fledge offspring. In high-income settings today, this trend toward building reserve capacity continues into reproductive adulthood, providing a physiological reserve to support average life spans far exceeding those of our hominin ancestors. Today, a similar trend is observed among cats and dogs humans have domesticated as pets within built environments.

As living systems evolved, they faced not only old and new external challenges but also internal stressors generated by the processes evolved to defend themselves against external stressors. While responding to life's stressors over their 160 million years of existence, mammals evolved finely tuned and highly interactive neuroendocrine, immune, physiological, and psychological networks to modulate their internal milieu, behaviors, and external environment. Still, over their life spans, terminally differentiated and dividing

cells; the tissues, organs, and physiological and psychological systems they form; and somas they comprise lose their functional capabilities as maintenance, defense, and structural systems fail. Because the genomes of well-adapted organisms change slowly, some somatic structures, physiological and psychological capacities that evolved during earlier phases of hominin evolution, to then stressful environments, may not be ideal adaptations in current environmental and sociocultural settings. The Pleistocene is conceived by some as humankind's environment of evolutionary adaptedness, a time when our current biology and physiological and psychological systems evolved (see Foley 1995). Rapid improvements in life spans across not only high-income, industrialized, and wealthy nations but most populations have occurred in recent centuries, *prima facie* evidence that environmental and social stressors during earlier phases of evolution significantly constrained human somatic maintenance and life span. A doubling of life expectancy in the USA from the eighteenth to twentieth centuries, along with a current life expectancy 30% higher than in 1900, additionally attests to the severity of environmental and sociocultural influences affecting human survival as recently as a century ago.

Assessing Senescence

Gerontologists and geriatricians have proposed a variety of overlapping definitions for senescence and aging (reviewed in Crews 2003; Crews and Ice 2012). However, they have not agreed upon any specific quantitative measure for assessing the senescent phenotype that predicts mortality more accurately than age alone. Because senescence is a multifactorial outcome of innumerable interacting traits, no simple scale for assessing an individual's senescent phenotype is available. Rather, combinations of multiple physiological and somatic biomarkers currently are the best estimators of senescent dysregulation. Alterations in DNA expression patterns, mRNA and protein profiles, losses of mitochondria, and instability across the genome, including telomeres and

epigenetic markers, pace cellular senescence (see Arking 2006; López-Otín et al. 2013). At the organismal level, following growth and development, humans generally experience a period of health and somatic maintenance during their period of maximum reproductive effort. This commonly is followed by a period of somatic decline, physical and mental losses, and increasing frailty and chronic diseases, described as somatic aging.

Theoretically, aggregate biomarker indices integrate and reflect aspects of systems biology shared across all populations by tapping into individual variability secondary to genetic, familial, local, historical, cultural, and ecological backgrounds and current circumstances. These indices are proposed to assess clinical, and even subclinical, aspects of somatic, physiological, and psychological dysfunction. The main phenotypic assessments in current use to determine senescent losses are activities of daily living (ADLs; see Katz et al. 1963) and its secondary derivative, independent activities of daily living (IADLs). Others include biological age (see Levine and Crimmins 2014); metabolic syndrome (Camus 1966); the Framingham index (Wilson et al. 1998); allostatic load, a measure of physiological dysregulation (McEwen 2003); and frailty, a measure of somatic dysfunction (Walston 2005). Theoretically, when based on groupings of age-related biomarkers of functional and physical losses, stress response, and physiological dysregulation, these indices should assess current morbidity and predict future morbidity and mortality risks, cognitive and physical declines, and life span across populations. All are known to assess to at least some degree somatic and physiological losses over the life span. Two of the most recently proposed indices, allostatic load and frailty, are reviewed here.

Physiological Dysregulation and Senescence

Stressor exposures are a constant of life. Throughout growth and development and during adult life, exposures to persistent non-life-threatening stressors (e.g., hypoxia, cold, toxins) may improve somatic function and limit negative response in that specific setting, a process

of adaptability known as hormesis. Still, following a lifetime of stressors and stress responses (allostasis), our inability to halt all related damage leads to physiological dysregulation and increases risks for noncommunicable diseases and mortality (see Sterling and Eyer 1988; McEwen 1998, 2003; McEwen and Seeman 1999; Edes and Crews 2017). Jointly stressors and responses produce senescence (see Crews 2003; Kim and Jazwinski 2015), a multifactorial phenotype uniquely expressed by each individual.

By combining soma-wide sensory neurons, neurotransmitters, and hormones to modulate human physiology, the mammalian hypothalamic-pituitary-adrenal axis (HPA) regulates human allostasis (stress response) (see Sterling and Eyer 1988; McEwen 2003). Allostasis occurs in response to observable, quantifiable stressors (e.g., heat, hypoxia) and stressful situations (e.g., predator avoidance, antagonistic interactions, lack of food or water), along with individual mental states, including anticipated, perceived, and not quantifiable stressors, even when these do not occur. Allostasis alters hormonal and physiological set points (e.g., cortisol, epinephrine, blood pressure, glycemia, body temperature) in response to cognitive dissonance (Sterling and Eyer 1988; McEwen 1998, 2003) as external or internal stressors alter one's mindscape from moment to moment (discussed by Peters et al. 2017). Following allostasis, system components reset to their current optima. As a dynamic neurophysiological response to stressors, allostasis evolved to promote current survival by limiting systemic perturbations secondary to external and internal stressors (see Sterling and Eyer 1988; McEwen 1998; Peters et al. 2017). Over time, stressor exposures may overwhelm response systems, attenuating, over-activating, or halting allostasis, thereby promoting progressive physiological dysregulation, a hallmark of senescence (see Crews 2003; Austad 1997; Rose 1994; Arking 2010).

Allostatic load indices combine neuroendocrine and physiological biomarkers of stress response to assess cumulative somatic dysregulation theoretically attributed to stressors (see Sterling and Eyer 1988; McEwen 1998; Edes and Crews 2017). When stressful events occur,

they induce cognitive dissonance (Peters et al. 2017). When this signal reaches the hypothalamus, it promotes the release of corticotrophin-releasing hormone (CRH) to the anterior pituitary, stimulating the release of adrenocorticotrophic hormone (ACTH) to the circulation. ACTH activates the sympathetic-adrenal system to release cortisol, adrenaline, and noradrenaline, promoting behavioral and psychological (e.g., aggression, agitation, attentiveness, fear, fight-or-flight) and physiological responses (e.g., increased blood pressure and heart rate, reduced visceral blood flow) (see Sterling and Eyer 1988; McEwen 1998; Peters et al. 2017; Edes and Crews 2017). Excessive, constant, and lifelong allostatic responses tend to damage cells and organs, alter systemic regulation, and lead to progressive physiological dysregulation and increased allostatic load. This system can neither sustain its function indefinitely nor halt all stressor-related damage (Sterling and Eyer 1988).

Frailty, a Clinical Syndrome of Functional Losses

Since humans first recorded their ailments, they have remarked on losses of physiological function and physical abilities with increasing age (frailty). Frailty is a clinical phenotype of declining somatic function secondary to physical losses, including sarcopenia (loss or death of muscle cells) and osteoporosis (reduced bone matrix leading to fragility). Loss of function and the physical changes associated with frailty include unintended weight loss; declining strength, endurance, and walking speed; and reduced physical activity. Frailty indices are based upon tabulations of accumulated somatic deficits and losses that correlate significantly with age and tend to increase exponentially during the later years of human life (see Studenski et al. 2004; Walston 2005; Kim and Jazwinski 2015). Illustrating the likely genetic basis of frailty, offspring of short-lived parents show more rapid increases in frailty than do children of long-lived parents (Kim and Jazwinski 2015).

As a clinical phenotype, frailty increases with age and predicts future morbidity and mortality across samples (Walston 2005). Frailty

differs from allostatic load in that it measures current functional abilities, not physiology. Losses of functionality lead to reduced physical activity, less activity-related energy expenditure, poorer nutrition, weight loss, muscle weakness, and exhaustion. Various combinations of biomarkers, from as few as 5 to over 100, have been amalgamated into frailty indices (see Studenski et al. 2004; Walston 2005). Across multiple samples, frailty indices predict future losses of mobility, inability to complete ADLs/IADLs, more frequent falls and injuries, and higher morbidity and mortality, particularly among those aged over 65 years (Walston 2005, 2005; Studenski et al. 2004). Increased frailty and allostatic load over the life span are not solely a consequence of senescent biology; illness, trauma, accidents, social support, and psychological factors also contribute.

Senescence: An Evolutionary Trade-Off

Once growth and development are complete and reproductive effort commences, with increasing survival time, an evolutionary trade-off between somatic maintenance-survival and reproductive effort reduces investments in the former to support the latter. With increasing age post-maturity, cellular senescence and somatic wear and tear promote physiological dysregulation and reduce resilience leaving organisms more vulnerable to stressors. Given the variety of processes involved, human senescent phenotypes are as heterogeneous and similar as are fingerprints, facial features, and disease risks. Senescence is a change in systemic biology, not a process unique to a specific organ, physiological system, or psychological construct. Among most life-forms, alterations reflecting changes in systemic allocations of somatic resources from growth, development, and maintenance to investments in reproductive effort follow attainment of reproductive maturity. Switches in resource allocation usually are not as obvious among humans and nonhuman primates as they may be among other species. Still, age-related alterations in phenotypes and underlying genetic and molecular

regulators are fundamental to species life histories. An interesting example is a senescent-promoting genetic switch observed in nematodes, *C. elegans*. Following gamete production, germline stem cells produce a molecule halting production of heat-shock proteins, thereby limiting stress response and promoting somatic decline within 8 h of maturity (see Labbadia and Morimoto 2015). When this gene is blocked, heat-shock proteins remain active, stress resistance is maintained, and life is extended (Labbadia and Morimoto 2015). Likely, many early life-forms evolved gene-based single-locus switches and responses over their evolution. Some likely went extinct, while others likely have been passed on in evolutionarily modified forms.

Ancient adaptations, more recently evolved genetic propensities, and variable environmental settings continue to interact, modulating senescent biology across organisms. Among modern humans, growth, development, and reproductive and post-reproductive adulthood occur in environmental, ecological, and sociocultural settings differing significantly from conditions proposed for the “environment of evolutionary adaptedness.” In modern environments, humans experience variable stressor exposures and show broad variation in age-associated physical and psychological decrements and average life spans. Differences in familial disease risks and longevity attest to influences of shared genes and environments on life span. Across human samples, few specific SNPs, alleles, or haplotypes have shown consistent associations with life span, although distributions of multiple SNPs, candidate alleles, and haplotypes differ between younger and older cohorts within populations. Variants enriched among older cohorts in one population usually are not in others. Variability in genomic associations with longevity across populations suggests that strong gene-environment along with gene-environment-sociocultural interactions influence late-life survival. They also illustrate the need to apply evolutionary, systems biology, and social-ecological approaches and models to aid understanding of variability in human senescence and longevity.

As age increases, somatic and behavioral stress points that prime the soma for higher allostatic load, frailty, morbidity, and mortality reveal evolutionary compromises in basic physiological, immune, neural, and psychological functions. These stress points reflect evolutionary trade-offs related to competing needs for somatic growth, development, maintenance, defense, and reproductive effort (see Ellison 2014). Age-related processes of physiological dysregulation, fragility, and frailty simply reflect the inability of living systems to optimize their physiology, protect themselves from all internal and environmental insults, and show long-term reproductive success via evolutionary mechanisms. Given multiple trade-offs and evolutionary constraints (inertia) on the metabolism and structure of organisms, the individual cells of which they are composed likely are as optimized as possible for maintaining their function and reproducing their somas (see Vijg 2007). This applies equally to neurons and the cells composing our neurological structures, the brain, amygdala, hypothalamus, pituitary, and endocrine system. Similarly, continuing selective processes over hominid, hominin, and human evolution likely have optimized human neurological structures, along with their systemic connectivity, including the hypothalamus-pituitary-adrenal axis and the human mind. Theoretically, human neurological structures and the theory of mind they maintain also are adapted and optimized to receive and process selected sensory information, assess its survival and reproductive consequences, and produce as optimal a response as is currently possible.

Internal metabolism is another evolutionary stable trade-off, one between providing energy for cellular respiration and function while also generating reactive oxygen species (ROS) that damage DNA, membranes, and other cellular organelles, leading to cellular dysfunction, senescence, and death. Across the spectrum of life, organismal biology depends on evolutionary compromises (see Ellison 2014). At the DNA level, alleles conferring a net survival advantage during early life and reproductive ages, while also promoting detrimental phenotypes at later ages, are evolutionary advantaged because of their early

life effects (see Williams 1957). Due to early benefits, alleles showing such antagonistic pleiotropy increase in population gene pools despite their late-life ill effects. Williams (1957) articulated two associated hypotheses about evolution and senescence. First, later-life ill effects of alleles showing antagonistic pleiotropy will accumulate at ages just beyond those required to maintain their selective advantages. Second, as the late-acting detrimental effects of alleles exhibiting antagonistic pleiotropy reduce the relative reproductive success of their carriers, selection will push any associated ill effects to later ages. Observed in experimental settings with worms and fruit flies, antagonistic pleiotropy is a fitness trade-off that also affects humans. Proposed examples include testosterone levels in men, apolipoprotein variants across populations, reactive oxygen species (ROS) created during oxidative phosphorylation, and multiple late-life penetrant chronic and genetic conditions. Cellular senescence and somatic aging reflect multiple long-term evolutionary trade-offs across the spectrum of life. For most species, senescence follows periods of growth, development, and reproductive adulthood and effort associated with a relatively well-maintained soma. In humans, following about two decades of life to attain maximum somatic and reproductive function and 30+ additional years of reproductive effort, output, and parental investment, the soma shows a LH trade-off, increasing internal and external signs of dysfunction and physiological dysregulation.

Stressors and Life Span

In general, the evolved physiological and psychological propensities and systems of humans are the same across all people and populations. However, variable genes, along with their combinations, and developmental processes influence individual response, reactivity, resistance, and resilience to stressors. Stressor exposures of parents, grandparents, and more remote ancestors that marked their DNA or personalities (e.g., epigenetic markers, historical trauma) also may contribute to individual stressor responses. Variation

in life span also is affected by developmental processes and differential exposures to early life stressors and life events. As each individual lives postmaturity, their unique genetic endowment, developmental processes, stressor exposures, and related responses during life produce variability in their somatic function and dysregulation as their age increases.

Those experiencing greater adversity (e.g., undernutrition, malnutrition, infections, trauma, psychosocial, physical abuse) during early life, whether prenatal or postnatal, expend a larger proportion of their total lifetime energetic and physiological capacity resisting current stressors leaving little opportunity to accumulate reserve capacity (see Crews 2003; Crews and Bogin 2010). Conversely, those whose social and physical environments limit their exposures to early life stressors experience more opportunities to build reserve capacity, thereby promoting resilience and resistance to stressors and longer lives. Unfortunately, as age increases, defense and maintenance costs increase and reserve capacity declines as it is expended to meet current needs. Total daily energy expenditure (TDEE) is an ideal example of a physiological trade-off and decline with age. TDEE has three components, resting metabolic rate (RMR ~ 60–70%), activity energy expenditure (AEE ~ 20–30%), and diet-induced thermogenesis (DIT ~ 10%) (see Kim and Jazwinski 2015, Fig. 4). On average, all three components decrease with age among older adults. In the Louisiana Healthy Aging Study among participants aged 60+ years, RMR was higher at older ages but remained inversely associated with age (Kim and Jazwinski 2015). In one interpretation, as age increases and health declines, additional energy is required to maintain the soma, leaving less available for physical activity. Supporting this interpretation, in the Louisiana study, TDEE remained stable over the age span examined, suggesting physical activity decreased and additional energy for survival (RMR) was derived from AEE (Kim and Jazwinski 2015).

At all ages, but particularly among the aged, reduced physical activity sets the stage for sarcopenia and bone loss, components of

the frailty syndrome. Decreased physical activity begins a cycle of bone and muscle loss, reduced activity, and increasing frailty. Disrupted growth during early life is associated with poor somatic and neurological development, impaired physiological and psychological function, increased risk for chronic conditions, more rapid progress of allostatic load and frailty during adulthood, and early senescence (Crews 2003; Walston 2005; Crews and Ice 2012). Physiological and psychological processes by which early life insults, trauma, and mental abuse influence adult and late-life physical and mental morbidity and mortality are open questions. Long-term research across the biological and psychological sciences, including evolutionary psychology and biological anthropology, will be necessary to identify and untangle them.

Physiological Losses

After completion of reproduction, multiple age-correlated vulnerabilities appear in all life-forms. Over the human life span, physiological and psychological stress responses decline, and stress-related physiological dysregulation increases. Although all show age-related physiological losses, these vary between individuals and families and across local and regional settings. Within individuals, functional and physical losses do not pace chronological age; rather they occur at variable rates. Bone biology, biomechanical stability, and skeletal function provide a specific example. Many species evolved bony skeletons and structures for support and mobility, to encase their fragile organs, and to promote their long-term survival and reproductive success. Over its long evolutionary history, bone has been optimized to perform these functions. Among humans, bone and muscle loss, impaired mobility, and subsequent frailty are differentially distributed by age and sex and differ across samples of the same age and sex across settings and nationalities (Walston 2005; Kim and Jazwinski 2015). Variation occurs because genetic interactions and propensities, developmental insults/benefits, hormonal variability, lifestyles, environmental

stressor exposures, and individual patterns of genetic endowment and wear and tear influence muscle and bone biology and structure. The aging skeleton clearly illustrates cellular senescence and losses. Mobility is a major adaptation supporting organismal health and survival across species. Human mobility is dependent on more than a functioning skeleton to support the body with muscles and tendons to move it. Mobility also is dependent on physiological and psychological mechanisms that allow cognitive processing and produce the abilities to walk with a steady gait while moving with balance and agility. Impairment of these components increases with use, as do risks for accidents, injuries, and fractures. Concurrently, as age increases, injuries take longer to heal and may lead to additional gait and mobility problems, producing a cycle of functional losses and increased frailty. Sarcopenia, osteoporosis, and loss of strength with age correlate with psychosocial stress, allostatic load, frailty, and the onset and progression of noncommunicable diseases. As in past populations, wear and tear occurs on the joints of modern people, along with injury- and osteoporosis-related lesions and fractures, impairing mobility and leading to frailty. Even with available medical remedies and interventions, among Medicare-eligible beneficiaries ages 65+ years in the USA in 1999–2005, 25% had osteoporosis, while 42% of women and 10% of men who received benefits for 6–7 years had osteoporosis (Cheng et al. 2009).

Male-Female Mortality Differentials

Across all current sociocultural setting, women outlive men. However, over their longer life spans, women experience higher risks not only for osteoporosis but also other illnesses (e.g., urinary tract infections, depression, arthritis), morbidity (e.g., stroke, fatal heart attack), and disability than do same-aged men. Still, across all age groups, men die more frequently and earlier in life than do women. Longer life spans among women reflect evolved differences from men in their patterns of growth, development, reproductive effort, and reproductive output that

have differentially patterned their LH schedules and, thus, their senescent biology. Observed differences in disability, morbidity, and mortality, among men and women, represent a morbidity-mortality paradox. A tendency for females to outlive males is observed across diverse species from insects and birds to primates (see Oksuzyan et al. 2008). Data suggest that among humans, patterns of frailty and disability reflect physiological and psychological processes differing from those that increase risks for morbidity, disease, and death. This further suggests frailty may not directly predict mortality. Over their shorter lives, males generally show higher risks for congenital, chronic, and genetic conditions, more frequently engage in competition with conspecifics, engage in more risky behaviors, are more susceptible to environmental stressors, and expend greater proportions of their time and available energy on growth, development, and somatic maintenance and repair earlier in life than do women.

Conclusion

Multiple stressors challenge human somatic integrity over their finite life spans, underlying senescent biology and somatic aging. Our major response system to life's constant external and internal stressors is allostasis, a cognitively based, neurophysiological, and systemic response. Allostasis evolved to modulate, delay, and halt adverse physiological outcomes arising from stressor exposures. Human cells and the somas they build did not evolve to be immortal, nor did single-celled organisms. Immortal individual organisms are an evolutionary impossibility, but long life is not. As previously stated, biological life cannot optimize somatic growth, maintenance, reproduction, and reproductive effort via evolutionary processes. Eventually, all life succumbs to stressor exposures that promote cellular senescence and somatic aging. Across long-lived animal species, survival depends on genetic propensities that slow molecular damage and cellular losses while maintaining somatic integrity. Animals, not able to promote their own resilience and maintain their systemic biology

via genetic, physiological, psychological, and allostatic processes, show more rapid senescence; sarcopenia; bone loss; fraying of their tendons, ligaments, and supporting structures; cardiovascular and metabolic dysfunction; physiological dysregulation; allostatic load; frailty; and mortality.

During the late Pliocene, through the Pleistocene and Holocene, and into the Anthropocene, humans have experienced continually changing ecological settings and social/cultural systems. Adaptive responses to earlier unconstructed environments, from alleles to genotypes and epigenetic marks, may not be as “fit” (in the Darwinian sense) in current ecological and sociocultural settings including newly emerged and emerging stressors. Current human life history, including growth, development, adulthood, reproductive effort, and senescence, along with our stressor responses is based on 160MY of mammalian, 65+MY of primate, and 7+MY of evolution among bipedal hominins to modern humans. Multiple adaptations and physiological functions that enhanced survival and reproductive success of our ancestors during these earlier periods remain beneficial today. Other adaptations likely limit organismal survival and later-life reproductive effort. Given the premise that no organism is immortal, senescence and aging result from two major processes, exposures to environmental and internal stressors and the quality of their genome-based somatic resilience to stressors. Somatic structures, physiological allostasis, and psychological constructs evolved, and even sociocultural systems developed, in response to life’s pervasive stressors. Concurrently, systemic biological interactions across cells and tissues evolved to repair damage sustained from stressors, while psychological modules, constructs, and processes evolved to promote behaviors that enhance organismal resilience and slow, delay, or halt stressors.

Evolutionarily, a key component of success among humans has been their adaptive flexibility. Over hominin evolution, multiple genetically programed phenotypes and behaviors adaptive among our ancestral species likely became less able to track rapidly changing ecological

settings, particularly as the pace of sociocultural developments increased exponentially. Adaptive flexibility allowed humans to rapidly alter their behaviors as they experienced new challenges and environments. Most species show genetically programed responses to their common environmental stressors. Likely, humankind’s earlier ancestors did also. Today, some human behavioral responses likely are highly evolved gene-based propensities for responding to current informational inputs, acting like switches for turning on allostasis, e. g., jumping away from a snake, or detecting falsehoods. Among humans much of this genetic programming appears to have been overlain and to variable degrees replaced by flexible responses to environmental input at a variety of phenotypic levels. This flexibility includes fetal programming, developmentally variable responses to experienced environments, and individual and genomic epigenetic modulation of DNA expression. Physiological systems and psychological mechanisms attuned to environmental inputs during growth and development provide greater opportunity for phenotypic flexibility and rapid responses to changing environments than does the slower process of genetic change, perhaps even at so fine a level as generation-to-generation. Changing selective pressures over hominin evolution produced a trend toward secondarily altricial offspring with slower cellular senescence and promoted humankind to evolve a slower LH pattern than other apes. One based on a growth strategy of developmental responses to experienced environments over an extended period of maturation, rather than specific genetic adaptations to relatively constant environmental pressures. Today, genetic structures underlying human physiological and psychological responses to stressors continue to evolve, and life span continues to increase across human populations as developmental processes during growth occur in ever more secure constructed environments. At the same time, elders now survive sufficiently long to invest not only in their offspring but also their grand-offspring and kindred’s survival and reproduction, thereby enhancing selective pressures to extend human life.

Cross-References

- [Adaptation](#)
- [Adaptation and Natural Selection](#)
- [By-Products of Adaptations](#)
- [Death](#)
- [Environment of Evolutionary Adaptedness](#)
- [Environmental Influences](#)
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- [Life Expectancy and Reproduction](#)
- [Life History Theory](#)
- [Parental Investment](#)
- [Reproductive Value](#)
- [Theory of Senescence](#)

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Sense of Powerlessness/ Helplessness and Self-Destruction

- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)

Sensitive Mothering

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Sensitization

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Synonyms

[Sensitizing](#)

Definition

The increase in responsiveness due to a strong, usually painful stimulus.

Introduction

Sensitization is a non-associative learning process that leads to increased responsiveness to a stimulus and is considered complementary to habituation. The increase in responsiveness or behavior is due to the exposure of a strong, most commonly noxious, stimulus that is causing pain. It is therefore logical to infer that sensitization's adaptive value is high, as it protects an organism from predators and other potential dangers Eisenstein, Eisenstein, Smith (2001).

Theoretical Background

The most prominent non-associative learning theory was composed by Groves and Thompson

(1970). Neurophysiological concepts were combined with concerns of human ethology and evolution to create the “dual process” theory. The dual process theory was the one which took into consideration both sensitization and habituation. This theory advocated that repeated stimulation would produce two independent processes that could both be active at the same time: decreased responsiveness (habituation) or increased responsiveness (sensitization). The authors believed that the two processes take place in different parts of the nervous system. Habituation is believed to take place in the so-called S-R system (reflex arc) that controls reflexes, whereas sensitization is believed to occur in the “state system” which is responsible for the level of readiness to respond. The state system requires arousal to become activated, while the S-R system is activated with the presentation of an eliciting stimulus. Further, habituation is thought to be stimulus-specific and involves learning, in contrast to sensitization which is not highly specific and does not require learning. However both are of relative permanence; they are expected to decay at the absence of stimulation. More characteristics of sensitization are presented below.

Characteristics of Sensitization

During sensitization an organism will only respond to high- or strong-intensity stimulus rather to low-intensity stimulus as it happens in the case of habituation. This constitutes a fundamental difference between the two processes, but it is not limited to that; sensitization can occur without necessarily having continual stimulation (a single, strong stimulus can sensitize the organism). Further, sensitization has a limited time course and relatively short-term effects; however that depends on the intensity of the stimulus Eisenstein, Eisenstein, Smith (2001). Petrinovich (1984), based on the “dual process” theory, outlines eight basic assumptions in relation to sensitization and are listed as follows:

1. Sensitization occurs in the “state” system and not in the “S-R” system.

2. During habituation training, sensitization appears initially but then deteriorates.
3. The amount and duration of sensitization are directly related to stimulus intensity. At high intensities, sensitization is directly related to stimulus intensity and frequency. However, at low intensities there may be little or no sensitization.
4. Sensitization decays spontaneously as soon as the sensitizing stimulus has stopped.
5. Repeated presentations of a sensitization stimulus result in gradual reduction of sensitization.
6. Response sensitization displays generalization.
7. Dishabituation is considered as an instance of sensitization.
8. Temporal conditioning of sensitization may occur.

Sensitization has not received as much attention as habituation did; however especially enlightening was the study of the neurophysiological basis of sensitization, in laboratory settings, with the mollusk *Aplysia* and the work of Kandel, as well as with the work of others scholars on *kindling* and *long-term potentiation*.

Long-Term Potentiation

Sensitization and long-term potentiation are similar processes but differ in their site of application. Sensitization occurs in specific pathways (state), while long-term potentiation occurs in synapses. However, the process of sensitization involves the mechanism of long-term potentiation.

Long-term potentiation of synaptic transmission is a major mechanism for investigating learning and memory in the synaptic level. Long-term potentiation is found in several regions of the brain, with the most prominent being the hippocampus thus its obvious involvement in the neural basis of some forms of memory Cooke & Bliss (2006). It is a form of synaptic plasticity and is defined as a persistent increase in synaptic strength following high-frequency stimulation of a chemical synapse.

High-frequency stimulation causes an increase in the efficiency of synaptic transmission, therefore enhancing the efficiency of the signal. For the induction of long-term potentiation, the activation of excitatory receptors is required Cooke & Bliss (2006). Bliss and Collingridge (1993) reported on the properties of long-term potentiation that differentiates it from other forms of synaptic plasticity: *input specificity* (it does not spread to other synapses), *associativity* (when a weak input of a single pathway is insufficient for the induction of long-term potentiation, simultaneous strong stimulation of another pathway can potentiate the weak stimulation), and *cooperativity* (apart from strong stimulation, long-term potentiation can be induced by the cooperation of many yet weaker stimulations). Since long-term potentiation occurs when a neuron shows an increased excitability over time due to a repeated behavior and the heightened synaptic transmission leads to the amplification of responses (i.e., pain), its involvement with the process of sensitization is high.

While the long-term potentiation of synapses in localized cell tissues seems to provide an elegant substrate for learning and memory, researchers turn their attention into experimentations with the whole living organism (in vivo experiments). Morris and colleagues (1986) provided for the first time some data from in vivo experiments in which it was indicated that long-term potentiation was essential for the construction of memories. Using rats, Morris and colleagues were able to examine their spatial memory by inserting an N-methyl-D-aspartate (NMDA) blocker drug in their hippocampus, a brain structure implicated in learning. NMDA is a glutamate receptor and an ion channel protein within nerve cells, and it is responsible for the control of synaptic plasticity and memory function. Initially rats were trained to swim in a water maze, in order to find the platform hidden beneath (in the center and the sides of the pool) and escape. As soon as the rats were able to locate the platform, they were separated in two groups. One group constituted the control group, while rats of the second group received the drug that blocks NMDA. Then both groups of rats were exposed to

the water maze spatial memory task with the rats of the control group being successful in locating the platform and escaping the pool. Contrary, the second group of rats exhibited impaired performance, as long-term potentiation could not be induced indicating thus damage in the hippocampus. This series of experiments indicated that long-term potentiation is implicated in learning and memory processes. Finally, dysfunctions in the process of long-term potentiation are thought to be implicated in mood disorders Post (2007) and neurodegenerative diseases as Parkinson's Cooke & Bliss (2006). Long-term potentiation is a fundamental process in a cellular level with implications in the process of learning.

Kindling

Both sensitization and kindling are forms of learning occurring in some parts of the nervous system, and the common characteristic they exhibit is the increase in responsiveness. Kindling can be thought of as a specific type of sensitization.

Kindling became known to the scientific world in the late 1960s through the published work of Goddard (1967) on the neurobiology of learning and later after the application of Goddard's model on the study of epilepsy. Goddard (1967) runs a series of experiments on rats where, in order to investigate their abilities to learn tasks, he administered electrical stimulations in various regions of their brains. With daily repetition of the electrical stimuli, the rats began seizing. That response, however, was astonishing, as the administered stimuli were too low to induce seizures. Even more surprising was the final observation of the rats having unprovoked seizures, that is, seizing without stimulation. In sensitization repetitive stimulation produces a full response. A full response can be elicited even with lower stimulus levels than the original stimulus. It appears that a decrease in the threshold of excitability develops leading to the automatic occurrence of the response, without external stimulation. Eventually, with further repetition, the response occurs spontaneously, in the absence of any stimulus demonstrating thus the phenomenon of kindling.

The changes caused by kindling seem to be long-term, but they are not permanent.

Kindling is universal across species (from frogs to humans) and throughout the brain, and it was the first neuroplasticity phenomenon suggested to give information on memory processes. At a first glance, it may seem awkward to imply that epileptic seizure activity could be interconnected learning; yet, it is plausible that the diverse mechanisms constituting kindling and learning interconnect and share several common mechanisms. In effect, under this conceptualization, both kindling and learning can potentially be considered as phenomena of neuroplasticity. However when kindling was compared to long-term potentiation as to which neuroplasticity phenomenon was more appropriate for modelling memory processes, long-term potentiation appeared to dominate, mostly because long-term potentiation was observed under normal neural activity contrary to kindling that was observed under seizures.

Further, kindling constitutes the model for the development or recurrence of medical (epilepsy) and psychiatric illnesses such as addictions and mood disorders, in which pathologies' recurrence is inherent Post (2007). Goddard's model has been referred to as the "kindling model for epileptogenesis" as it is the most frequently used model for temporal lobe epilepsy with complex partial seizures. It is used by scientists to study the effects of repeated seizures on the brain. What was demonstrated in the experiments with rats, the same applies for humans; a seizure may raise the possibility that more seizures will occur since repeated stimulation "lowers the threshold" and paves the way for seizures to reoccur (Dennison, Teskey, Cain, 1995, Racine, 1978). In an attempt to better understand the occurrence of epileptic seizures, many scientists including Racine (1978) have turned their attention to the underlying mechanisms of kindling, in neurotransmitter systems and intracellular mechanisms, as well as genes.

Goddard's experiments suggest that the processes underlying kindling and learning interconnect and possibly have similar underlying mechanisms. Kindling is of particular importance

in disorders where recurrence is involved, in addictions (relapse) and mood disorders (recurrent episodes), but its underlying mechanisms are yet to be refined by empirical investigations.

Drug Sensitization

Drug sensitization is a process frequently encountered in the literature of the field of addictions and pharmacology, and it is an essential process toward the understanding of drug action and use. Drug sensitization is a type of sensitization, and it refers to an increase in drug effect upon continual exposure to a drug in the organism, which was previously exposed to the drug. With repeated drug administration, gradual and incremental neuroadaptations are produced, which make animals hypersensitive to the specific drugs. Even though users or abusers will be keeping the same dosage levels, drug effects will be greater and greater; therefore they would become intoxicated even in small doses. Using repeatedly a drug but with some pauses in between causes greater sensitization compared to taking a single dosage or even taking repetitively the drug. Moreover, sensitization is promoted if periods of use are alternated with periods of abstinence. When a person who is sensitized let's say to cocaine and abstains from use for some time, he/she is at risk of fatal overdosing at reuse (Steketee & Kalivas, 2011, Robinson & Berridge, 2008). Known addictive substances, where sensitization has been observed in, are cocaine, amphetamines, morphine, nicotine, and even alcohol; importantly not all drugs are subject to sensitization, mostly stimulants. In addition, the selected route of drug administration as sensitization is influenced by the speed or the time it takes for a drug to reach the brain. Sensitization in the case of drugs is long lasting with its effects on behavior and cognition lasting for years even with abstinence; however factors such as the time lapse between dosages, the choice of drug, the age and sex of the user, and genetics influence the strength of sensitization. Due to these factors, vulnerability to sensitization differs between individuals Steketee & Kalivas (2011). That provides

an insight into the long-asked question of why some users become addicts while others do not get addicted. The sensitization of behavior and other psychological or psychomotor functions implies neural sensitization. Drugs seem to alter or reorganize neural systems and neurotransmitters, and even though causal relationships are yet to be established, neuroadaptations seem permanent. The permanency of changes in neurotransmitter circuits has crucial implications on the matter of cravings and relapse. Of special importance is the sensitization of the mesolimbic pathway of the mesotelencephalic dopamine system. Since dopamine is responsible for the motivation to go after pleasure and happiness and fulfill our “wants,” drugs come to jeopardize this process by making dopamine hyper-reactive, consequently increasing the prominence of drug cues, hence the intense cravings Robinson & Berridge (2008). In the matter of cravings and relapse, kindling is thought to be implicated. The aforementioned comprise the “incentive sensitization” theory of addiction developed by Berridge and Robinson (1998) and is noteworthy of further reading.

Drug sensitization is a complex process influencing drug users in a cellular level and in consequence in a behavioral level.

Conclusion

Sensitization is one of the simplest forms of non-associative learning, and it is of significant value as it has helped organisms to adapt in potentially dangerous situations and evolve. While sensitization's underlying mechanisms are still under investigation, research thus far has been able to provide data for the better understanding of learning phenomena and the appearance and treatment of pathologies.

Cross-References

- [Aplysia](#)
- [Drug Sensitization](#)
- [Habituation](#)

- [Kindling](#)
- [Long-Term Potentiation](#)
- [Non-associative Learning](#)
- [Spontaneous Recovery](#)

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Sensitizing

► Sensitization

Sensorimotor Play

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Synonyms

Functional play; Practice play; Primary circular reactions; Sensorimotor stage

Definition

During the first year of life, much of children's playtime involves, mainly, the exploration of the world through the repetition of already assimilated sensory and motor activities, for the sheer pleasure of doing so.

Introduction

Child development is such a diverse and complex subject; no single theory sufficiently meets all of it. The most common theories focus primarily on cognitive development or on social development. Providing a good theoretical ground of development in either of these theoretical fields is an endless challenge, as each of them accounts for an enormous range of topics. Cognitive development entails the growth of various capabilities such as perception, language, attention, reasoning, conceptual understanding, problem-solving, and intelligence (Siegler et al. 2011). This chapter focuses on cognitive development and more specifically during the sensorimotor period, where according to the Piagetian perspective, the young infant explores its roots of adult intelligence (Siegler et al. 2011). We consider each stage's

fundamental assumptions about how young infants develop conceptually through play behaviors during the sensorimotor period.

An Evolutionary Perspective

Applying evolutionary theories on human condition to gain a better understanding has a long history in psychology. According to Groos (1901), play during animals' periods of immaturity, such as the juvenile period, was "critical" in shaping later development. This view was later incorporated into Piaget's (1962) theory of play in human development. Play is considered to be a central component for the immature child; in fact, an extended period of immaturity is common when play occurs in most species (Pellegrini et al. 2007).

According to the evolutionary biology perspective, there is a desire to play in specific ways and at specific points in life, common to a variety of mammals (LaFreniere 2011). Evolutionary biologists have long been intrigued to the origins and functions of play. In the evolutionary biology dictionary, the term "functions" with regard to play refers to when a behavior has typically added to the survival or reproductive success of an individual (genes) over many succeeding generations (Pellegrini and Smith 1998). Functions can also be defined in the context of beneficial outcomes during the life cycle of the individual player (Pellegrini and Smith 1998). As mentioned earlier, evolutionary biologists interested in the study of animal behavior (hereafter, ethologists) have suggested that play has been acquired by our species through the process of natural selection, in order to provide deferred benefits to the individual (LaFreniere 2011). In other words, through play a child develops and practices skills crucial to survival and reproduction in adulthood (Smith 2009).

Life history theory is a worldwide accepted analytical framework, used mainly in biology and evolutionary psychology since the 1970s (LaFreniere 2011). It considers an organism as an ever-changing life cycle – not as a static adult – suggesting that certain species-typical

characteristics evolve to favor somatic and reproductive efforts throughout life-span (LaFreniere 2011). Accordingly, Bogin (1999) postulated that because of a finite amount of time, energy, and resources available, individuals must make choices regarding their behavioral priorities and allocation of resources with respect to developmental periods and life goals suitable to those periods. For example, despite its clear costs, during the early-juvenile period, play is prioritized in all social primates, while social play takes up most of the time not spent eating and sleeping (LaFreniere 2011). This fact is considered to be crucial as the main basis for concluding an adaptive function of play, because natural selection favors only behaviors whose benefits clearly outweigh the associated costs (LaFreniere 2011). Play can be costly in terms of time and energy devoted to it as it diminishes the time, effort, and energy spent on other activities.

Despite such costs, there is a natural tendency of young mammals to engage in play as long as and as often as ecological constraints and opportunities afford (LaFreniere 2011); it is, in fact, indispensable to the development and good functioning of a healthy adult.

Jean Piaget's Theory

It wasn't until Jean Piaget's work appeared in the 1920s for the world to have a recognizable field of cognitive development. Jean Piaget (1896–1980) began his journey from an early age. It was his keen interest in observing animals in their natural environment and his enthusiasm in philosophy that led him into his studies of clinical psychology. While in Paris, he became more interested in the mistakes children make in response to intelligence tests and came to suggest that exploring children's errors could offer an insight into their cognitive processes. By integrating the disciplines of psychology, biology, and epistemology – a branch of philosophy concerned with knowledge – Piaget aimed to establish a scientific approach into understanding how humans acquire and understand knowledge. Almost a century later, Piaget's theory remains one of the most influential and

best-known cognitive developmental theories in the field. Yet, it is notable that current reinterpretations of Piaget's theory came to suggest that children might have more capabilities at a younger age than Piaget thought (Smith et al. 2015).

According to the cognitive theorist, children are active mentally from birth onward as they are physically and that their experiences and activities indeed contribute to their own development. His proposition has been labeled as *constructivist*, as it represents children as constructing knowledge for themselves through their own experiences (Siegler et al. 2011). Piaget further explains that children use – mainly – three constructive processes including generating hypotheses, performing experiments, and drawing conclusions from observations (Siegler et al. 2011). This description depicts the process of scientific problem-solving and this in fact, the dominant metaphor in Piaget's theory: the “child as scientist” (Siegler et al. 2011) where children do not depend on instructions from adults or others, but they rather learn on their own.

Central Developmental Ideas

In addition to the above, Piaget suggested significant insights into the roles of nature and nurture and of continuities and discontinuities in development (Siegler et al. 2011). For instance, he believed that nature and nurture interact to favor human cognitive development. Nurture includes every experience the child encounters in the environment (Siegler et al. 2011). Nature includes the child's maturing brain and body and the ability to perceive, act, and, learn from their activities as well as meeting the two basic functions that are essential components of cognitive growth: *adaptation* and *organization* (Siegler et al. 2011). Adaptation is when children are able to respond to environmental demands in ways that meet their own goals, while organization is when they are able to accommodate specific observations into coherent knowledge (Siegler et al. 2011). It has been suggested that because both of these functions involve children's reaction to experience or otherwise nurture, it can be further said that part of

children's nature is to respond to their nurture (Siegler et al. 2011).

As mentioned previously, Piaget also offered important insights into the roles of continuity and discontinuity in development. Three processes form the main sources of continuity – *assimilation*, *accommodation*, and *equilibrium* – and work together to favor development (Siegler et al. 2011). Assimilation refers to the process by which people integrate new incoming information into conceptual ideas they already understand, while accommodation refers to the process by which they apply their current knowledge in response to new experiences (Siegler et al. 2011). Equilibrium is the process by which people balance assimilation and accommodation to create stable understanding (Siegler et al. 2011). In fact, this process happens in three phases. First, young children feel contended with their current knowledge about a phenomenon; Piaget named this a state of equilibrium, as children do not face any gaps between what they see and their understanding (Siegler et al. 2011). Once new information is encountered, children face a stage of disequilibrium as their understanding about a phenomenon is not sufficient, and thus they fail to generate a superior alternative (Siegler et al. 2011). Finally, children develop a more mature, inclusive understanding, which provides a more stable equilibrium, in terms of being able to understand a broader range of observations in the surrounding environment.

Although Piaget emphasized elements of continuity in cognitive development, the most well-known part of his work concerns discontinuous aspects, which he presented as distinct *stages* of cognitive development. Each stage represents a meaningful way of getting an insight into one's experiences, and each transition between stages represents a discontinuous thoughtful leap from one meaningful way of understanding to the next, higher one (Siegler et al. 2011).

Piaget suggested a number of central properties, which define as well as underlie the four cognitive developmental stages. He believed that children at different ages think qualitatively different, and he named this property *qualitative change*. For instance, he explains that children in

early stages of their cognitive development perceive the concept of morality in terms of the consequences of a person's behavior, whereas older children perceive it in terms of the person's intent (Siegler et al. 2011). A 5-year old would believe that someone who, by accident, broke a jar of cookies is naughtier than somebody who deliberately stole a single cookie; an 8-year old would have the opposite judgment. This difference suggests a qualitative change as the two children are basing their moral assessments on different criteria (Siegler et al. 2011). Then, Piaget suggested that the type of thinking characteristic children acquire from each stage influences their thinking across varied topics and contexts; Piaget named this property *broad applicability* (Siegler et al. 2011). Additionally, before entering a new stage, children engage into a brief transitional period (Siegler et al. 2011). During this period children fluctuate between the type of thinking characteristic of the new, more advanced stage and the type of thinking characteristic of the old, less advanced one (Siegler et al. 2011). This property has been labeled as *brief transitions*. Lastly, Piaget suggested that everyone progresses through the four stages with the same order and cannot skip a stage, what we call *invariant sequence* (Siegler et al. 2011).

Stages of Cognitive Development

As Piaget suggested people progress through four cognitive developmental stages: the *sensorimotor* stage, the *preoperational* stage, the *concrete operational* stage, and the *formal operational* stage. In each stage, children demonstrate new abilities, which allow them to experience and understand the world in qualitatively different ways than they had before (Siegler et al. 2011).

1. In the sensorimotor stage – from birth to 2 years of age – infants experience basic sensory and motor abilities through which adult intelligence develops. Through these abilities young children explore the world and gain information about the objects and people in it (Siegler et al. 2011). In this stage, young

- children live mainly in the here and now, while their intelligence levels are based on their immediate actions and perceptions (Siegler et al. 2011).
2. In the preoperational stage – from 2 to 7 years of age – preschoolers can remember their experiences for longer periods of time and develop more sophisticated ideas as they can now represent their experiences in language and mental imagery (Siegler et al. 2011). Yet, according to Piaget, they still lack the ability to form *mental operations*, that is, forms of reasoning as part of an organized system of mental activities. For example, during the preoperational stage, a young child would be unable to form the idea that pouring a liquid from one glass into a different-shaped glass does not change the amount of liquid (Siegler et al. 2011).
 3. In the concrete operational stage – from 7 to 12 years of age – children can reason logically about concrete objects and events (Siegler et al. 2011). For example, they can now understand that the amount of liquid is unchanged when it is poured from one glass to a differently shaped one. Yet, they still cannot think in abstract terms, neither to test out their beliefs through scientific experiments.
 4. In the last stage of cognitive development, known as the formal operational stage – age 12 and beyond – children can think sophisticatedly about abstract ideas as well as hypothetical scenarios (Siegler et al. 2011). They can also test out their beliefs and gain appropriate conclusions by forming scientific experiments.

With this overview of Piaget's cognitive development theory, we can examine in greater extent the changes that occur during the sensorimotor period. Specifically, we consider how newborn children behave during this stage in terms of sensorimotor play and exploration.

Sensorimotor Play

During their first year of life, children engage mainly, in what Piaget called sensorimotor play

or practice play (Piaget 1962). This consists mainly of already experienced, sensory and motor activities, which are repeated for the absolute pleasure of doing so (Hughes 2010). Piaget (1962) suggested that this form of play is integral for the child's intellectual development and that the young child moves through a number of different substages of sensorimotor progression. Sensorimotor play is acquired gradually during the first 18 months of life before the newborn child moves to symbolic or make-believe play (Hughes 2010). In fact, Piaget gave a detailed description of the process by which children develop their own capacity for thinking by carefully observing how his own children were behaving (Smith et al. 2015). Based on these observations, he divided the sensorimotor play period into three behaviors, which he called circular reactions (Hughes 2010).

Primary Circular Reactions

This is the earliest form of sensorimotor play – the *primary circular reaction*. During this period, which begins from birth and usually lasts up to 4 months of age, an infant accidentally discovers a pleasing sensory or motor reflex activity that is related to its own body (Hughes 2010). The infant experiences enjoyment and, thus, repeats the activity (Hughes 2010). Piaget used the term “circular” to emphasize the way that children repeat newly reflex experiences, notably the ones that are pleasing such as scratching or grasping (Smith et al. 2015). The term “primary” relates to basic behaviors that the child learns to exhibit, from the reflexes of the initial period (Smith et al. 2015). Based on his own 8-week-old son's behavior, Piaget illustrated the concept of primary circular reaction by explaining: “Laurent ‘scratches and tries to grasp, let's go, scratches and grasps again, etc. . . . At first, this can only be observed during feeding. Laurent gently scratches his mother bare shoulder. [The next day] . . . Laurent scratches the sheet which is folded over the blankets, then grasps and hold it for a moment, then lets it go, scratches it again, and recommences without interruption” (Piaget 1963, p. 191).

In behaving as he did, Laurent's actions could be perceived, as play with objects rather than play

centered on his own body (Hughes 2010). Yet, according to Piaget this is not the case as he explains that the play is the physical action such as the grasping or scratching (Hughes 2010). According to this idea, an infant is interested in the action itself, rather than being interested in the object they are performing the action on (Hughes 2010). For example, the same action is performed on any object that happens to be around the infant. In this matter, we can appreciate that children, even early on in their life, can manipulate objects once they are given to them. Indeed, such reflex behaviors are purposeless and lack intellectual awareness – two essential elements that characterize object play (Hughes 2010).

Secondary Circular Reactions

From the age of 4 until the age of 10 months, children move to the next stage of circular reactions that is distinctly different (Piaget 1962). They are now interested on objects and the consequences of their actions, instead of being focused on their own body and repeating actions based on early reflexes (Smith et al. 2015). They engage in what Piaget called *secondary circular reactions*, the intentional alteration in their surroundings by making interesting things happen such as moving a hanging object by hitting it (Smith et al. 2015). Particularly, secondary circular reactions refer to the young infant's enthusiasm to repeat newly initiated actions, aiming to influence their surrounding environment.

To illustrate the difference between primary and secondary circular reactions, Piaget described the behavior of his daughter, Jacqueline, at 5 months of age. He describes: "Jacqueline looks at a doll attached to a string, which is stretched from the hood to the handle of the cradle. The doll is at approximately the same level as the child's feet. Jacqueline moves her feet and finally strikes the doll, whose movement she immediately notices. . . The activity of the feet grows increasingly regular whereas Jacqueline's eyes are fixed on the doll. Moreover, when I remove the doll Jacqueline occupies herself quite differently; when I replace it, after a moment, she immediately starts to move her leg again" (Piaget 1936/1952, p. 182). Thus, we can see that Jacqueline's interest

has moved from her own body toward her surrounding environment and the consequences of her actions. In behaving as she did, the young girl seemed to have detected a relation between her movement and the doll's and was involved in secondary circular reaction.

During secondary circular reaction substage, as children continue to grow, they also start to combine different behavioral schemas, what Piaget called *coordination of secondary circular reactions* (Smith et al. 2015). In the following example, we can see how Jacqueline combined different schemas such as "sucking" or "grasping" an object in a series of coordinated actions when a new toy is introduced to her at 8 months of age: "Jacqueline grasps an unfamiliar cigarette case which I present to her. At first, she examines it very attentively, turns it over, then holds it in both hands while making the sound 'apff' (a kind of hiss which she usually makes in the presence of people). After that she rubs it against the wicker of her cradle then draws herself up while looking at it, then swings it above her and finally puts into her mouth" (Piaget 1936/1952, p. 284). Jacqueline's behavior illustrates how children begin to combine several schemas to achieve goals or get through new situations.

Tertiary Circular Reactions

While the newborn child between 8 and 12 months of age would engage in a repetition of their actions in order to enjoy an interesting outcome, the young 1-year old progresses to the next level. Although children would still repeat the previous stage, they are not repeating it precisely, but instead, they try to vary the activity, a new behavior known as a *tertiary circular reaction* (Hughes 2010). Children's behaviors are now more flexible, and this could lead to new results (Smith et al. 2015). By repeating actions in alternative ways young children are, essentially, applying already-established schema to new situations and needs (Smith et al. 2015).

Consider the example of Piaget's daughter Jacqueline – now 13 months old – in her bath: "Jacqueline engages in many experiments with celluloid toys floating on the water. . . Not only does she drop her toys from a height to see the water splash or displace them with her hand in order to

make them swim, but, she pushes them halfway down in order to see them rise to the surface. Between the ages of a year and a year and a half, she amuses herself by filling her sponge with water and pressing it against her chest, by running water from the faucet. . . along her arm, etc.” (Piaget 1936, p. 273). The playful element in this form of circular reaction is evident, as the child seems to enjoy their time with novel objects as well as actively trying to create new interesting experiences.

As the young child progresses through the previous stages of sensorimotor play, they learn to act directly on their surrounding environment via their sensory and motor schemas. According to Piaget, the sensorimotor play period ends when children finally achieve what we call *internal representation* (Smith et al. 2015). Internal representation refers to the child’s ability to act indirectly on the world because they have now a mental representation of the world, and this ability is not acquired until the newborn child reaches the age of 18–24 months (Smith et al. 2015). This means that children are able to manipulate their mental representation of the world such as being able to think and plan.

Object Permanence

Piaget (1954) made an interesting, yet controversial, claim suggesting that children through the age of 8 months experience a deficiency in their thinking or, in other words, lacking *object permanence*. Object permanence refers to the knowledge that objects continue to exist even when we cannot see them (Siegler et al. 2011), and according to the cognitive theorist, very young infants ignore any object that was out of sight. For instance, if an infant was reaching for a doll but then the doll was covered with a cloth, the infant would immediately lose interest in it and look away. This claim was based on Piaget’s observations of his own son Laurent, and he explains the young child’s behavior in the following account: “At age 7 months, 28 days, I offer him a little bell behind a cushion. So long as he sees the little bell, however small it may be, he tries to grasp it. But if the little bell disappears

completely he stops all searching. I then resume the experiment using my hand as a screen. Laurent’s arm is outstretched and about to grasp the little bell at the moment I make it disappear behind my hand that is open and at a distance about 15 cm. from him. He immediately withdraws his arm, as though the little bell no longer existed” (Piaget 1954, p. 39). Therefore, it has been suggested that infants younger than 8 months can only represent objects they can perceive at the moment (Siegler et al. 2011). The adage “out of sight, out of mind” is literally true.

According to Piaget (1954), it was only through the last substages of the sensorimotor play period that children demonstrated an awareness that the object continued to exist even when it was out of sight (Smith et al. 2015). Looking for an object that cannot be seen directly suggests that the child has a mental representation of the object. In fact, the idea of object permanence supports Piaget’s claim that by 18–24 months of age, young children are able to manipulate their mental representation of the world, known as internal representation.

By the end of their first year of life, infants explore for hidden objects rather than behave as if they had disappeared, indicating that they can mentally represent the object’s enduring existence even when they are out of sight. These first object representations are sensitive, however, as reflected by the *A – not – B error* (Siegler et al. 2011). In this error, once the young child reaches the age of 8–12 months and learn to reach for and find a hidden object several times in one place (location A), when they see the object hidden at a different place (location B) and they are restricted from immediately searching for it, they usually reach where the object was originally found (location A) (Siegler et al. 2011). Not until around the first year of life do young children initially explore at the object’s current location.

At around 1 year of age, infants begin to actively explore their surrounding environment including the potential ways in which objects can be used (Siegler et al. 2011). Piaget described young children as “scientists” and suggested that their own activity greatly contributes to their development (Siegler et al. 2011). To illustrate this emerging competency, Piaget described how

his son Laurent would vary the positions from which he dropped different objects to observe what would happen. Consider this description: “Laurent is lying on his back... He grasps in succession a celluloid swan, a box, etc..., stretches out his arm and lets them fall. He distinctly varies the position of the fall. When the object falls in a new position (for example, on this pillow), he lets it fall two or three more times on the same place, as though to study the spatial relation” (Piaget 1963, pp. 268–269). Piaget viewed such actions as the beginnings of scientific experimentation rather than as bad behavior.

By the end of the sensorimotor stage (18–24 months of age) as the young child develops, according to Piaget, they are now able to form enduring mental representations (Siegler et al. 2011). The evidence for this new mental capability is what Piaget called *deferred imitation*. This is when young children carry out a behavior they observed other people doing, minutes, hours, or even days after it occurred (Siegler et al. 2011). Piaget provides a good example of this by illustrating an observation of 1-year-old Jacqueline: “Jacqueline had a visit from a little boy... who, in the course of the afternoon, got into a terrible temper. He screamed as he tried to get out of a playpen and pushed it backward, stamping his feet... The next day, she herself screamed in her playpen and tried to move it, stamping her foot lightly several times in succession” (Piaget 1951, p. 63). According to Piaget, Jacqueline had never before shown such a temper. The reason for doing so, probably, is because she had watched and remembered the boy’s behavior, retained a representation of it overnight, and imitated it the next day; in other words, she had a mental representation of what she had observed the previous day (Smith et al. 2015).

Conclusion

When we consider Piaget’s account of cognitive development during the sensorimotor period or otherwise infancy, the infant progresses from very simple and basic reflex actions at birth, to more complex behaviors at the end of the stage. At

first, infants’ motor or sensory activities are related to their own bodies with concrete goals being the ultimate outcome, such as shaking a rattle and listening to the sound it makes. Later, infants’ activities are mainly focused on the surrounding world with more abstract goals such as differing the heights from which objects are dropped and watching what happens as well as how the different effects vary. Young children also acquire the ability to form mental representations, progressing from “out of sight, out of mind” to remembering another person’s behavior and imitating it the day after it occurred. It is only toward the end of the period that children develop this ability to mentally represent the world as well as to manipulate their thoughts and construct their own knowledge in response to their experiences.

Cross-References

- [Newborn Behavior](#)
- [Object Play](#)
- [Play and Tool Use](#)
- [Social Play](#)

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Sensorimotor Stage

- ▶ [Newborn Behavior](#)
- ▶ [Sensorimotor Play](#)

Sensory Aphasia

- ▶ [Broca's and Wernicke's Aphasia](#)

Sensory Bias

- ▶ [Sensory Exploitation Hypothesis](#)

Sensory Drive

- ▶ [Sensory Exploitation Hypothesis](#)

Sensory Exploitation Hypothesis

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Synonyms

[Sensory bias](#); [Sensory drive](#); [Sensory trap](#)

Definition

Mating preference for a courtship signal trait evolves as a preexisting sensory bias from a non-mating context and is then exploited by the opposite sex, increasing mating opportunities.

Introduction

An important evolutionary driver of animal signal diversity is female mate choice. Throughout the animal kingdom, mating success between the sexes is asymmetric; most females in a population procure mates while some males mate multiply and many males fail to mate at all. This asymmetry results in differential selection on male traits and influences the evolution of male courtship signals (Andersson 1994). Virtually all mating systems include some component of communication whereby receivers must be able to detect and discriminate the sender's courtship signal. This communication is critical for female mate choice, and in particular, females must be able to recognize members of their own species. Failure to perform this recognition often imposes severe fitness costs on the female, as a hybrid mating typically yields offspring with reduced vigor. Species recognition occurs through the assessment of specific characteristics of courtship signals. These signals can take on a myriad of different forms and may be communicated through virtually any sensory system (Ryan 1985; Basolo 1990; Partan and Marler 1999; ter Hofstede et al. 2015).

A large body of research has examined how the tuning of animal sensory systems generates signal recognition and influence mate choice (Capranica and Moffat 1983; Ryan 1990; Guilford and Dawkins 1991; Shaw 1995; Endler and Basolo 1998; Ryan and Cummings 2013). This work has connected signal evolution to receiver bias or more broadly, receiver psychology. Classically, sensory bias has been considered in three non-mutually exclusive contexts: sensory trap, sensory drive, and sensory exploitation (Endler and Basolo 1998). A sensory trap occurs when males produce a signal that elicits a positive mating response from a female because the signal mimics

a stimulus from another context (Christy 1995). For example, in fiddler crabs (*Uca* spp.), females preferentially choose males that build pillars since the pillars mimic natural structures that allow females to escape predation. Sensory drive integrates evolutionary processes, environmental factors, and sensory systems that can lead to changes in signals and then behavior. For example, in two species of African cichlid, *Pundamilia* spp., female preference for red and blue nuptial coloring coincide with the spectral depth gradient in the natural habitat of the fish (Seehausen et al. 2008). This in turn may result in sexual selection on male coloration through female mate choice via sensory drive. Finally, Ryan (1990) proposed sensory exploitation to explain how male courtship signals evolve to exploit preexisting biases of the female's sensory system. Mate choice via sensory exploitation predicts that male signals should evolve to increase stimulation of the female's sensory systems and specifically should evolve to align with female sensory systems in regions that are most sensitive. Thus, females should be predisposed to prefer a particular courtship trait or character if it better stimulates her nervous system. Additionally, this preexisting bias must be present before the signal arises, otherwise the trait will fail to spread in the population. This review of the sensory exploitation hypothesis will focus on the sensory physiology, organismal behavior, and perception in three animal groups that have been extensively studied.

Animal Mating Systems via Sensory Exploitation

Anuran amphibians: Frogs have proved to be an outstanding system to investigate the sensory basis of mate choice (Ryan 1985; Bee 2015). Many frogs breed in a lek system where multiple males congregate at a pond and produce courtship vocalizations. The conspicuous inflated vocal sac, characteristic of most calling frogs, is easily seen located between the frog's mouth and forelimbs (Fig. 1).

Often multiple species occupy a breeding pond, where males vigorously call and defend small territories against rival conspecifics. This vocal competition generates an acoustically complex environment. Females arrive at the pond and choose a mate by listening for males, distinguishing among different species, as well as individual calls of conspecific males.

Frogs possess two inner ear organs, the amphibian papilla (AP) and the basilar papilla (BP). These organs are tuned to relatively low sound frequencies (AP) or relatively higher frequencies (BP). Within a species, there is a strong correlation between the tuning of the inner ear organs and the frequency of the male courtship call; quite simply, if a male's call falls within the region of best sensitivity of the female ear, he is most likely to be detected and hence attract a mate. This correlation between signal properties and neural sensitivity has been described as matched filter detection (Capranica and Moffat 1983).

Sensory Exploitation Hypothesis, Fig. 1 A calling male túngara frog with waveform and spectrogram of call (*inset*)



As a system of study, the túngara frog, *Physalemus pustulosus*, has played an important role in elucidating the sensory basis of mate choice (Ryan 1985). In this species, males produce a two-note courtship call (Fig. 2).

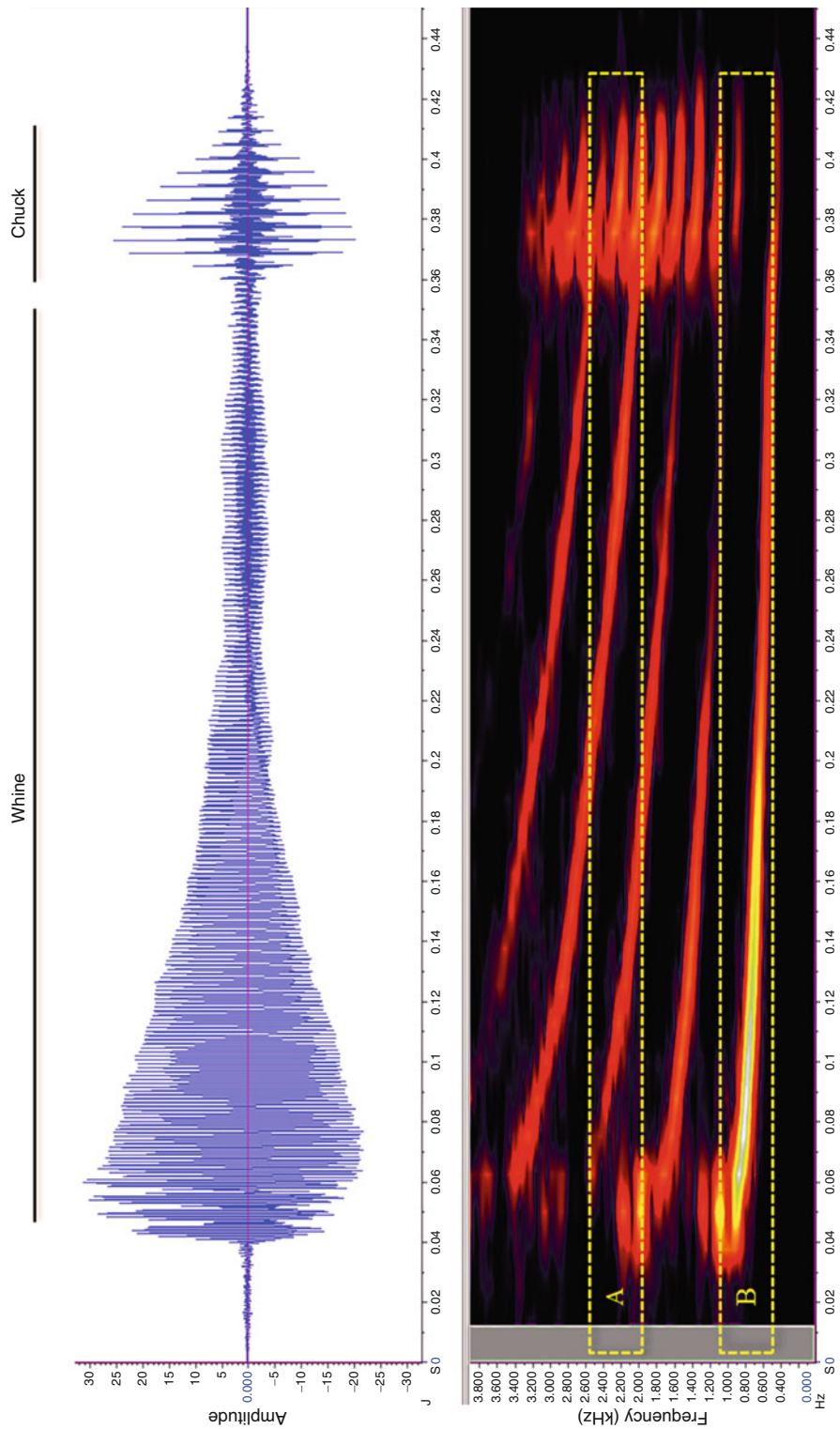
The first note is called a “whine,” and males always produce this while calling. The second note, the “chuck,” can be voluntarily appended to the whine. Males almost never make a chuck in isolation and females do not respond to a chuck produced artificially in the absence of a whine. The whine is both necessary and sufficient for mate attraction. When males append one or more chucks to a whine, however, this makes the call five times more attractive than the whine alone. The dominant frequency of the whine matches the best sensitivity of the túngara AP, and the dominant frequency of the chuck closely matches the greatest sensitivity of the BP (Fig 2). Interestingly, a related species, *Physalaemus coloradorem*, also makes a “whine-type” advertisement call, but males do not make chucks. If a chuck is artificially appended to the *P. coloradorem* call, females prefer it, even though they have never been exposed to a chuck under natural conditions. Further, the BP in *P. coloradorem* exhibits similar tuning frequencies to the túngara frog, indicating that the artificial chuck is stimulating this additional inner ear organ. This illustrates that for túngara frogs, the chuck spread in the population when a mutation generated an early chuck-type note in the call, matching the spectral sensitivity (e.g., preexisting bias) of the BP.

In addition to frequency cues, female frogs have also been shown to use temporal aspects of call pulses for species recognition. This has been especially well studied in gray treefrogs. These consist of two species, Cope’s gray treefrog *Hyla chrysoscelis* and the gray treefrog, *Hyla versicolor*. *H. versicolor* is a tetraploid of the diploid *H. chrysoscelis*. The species are morphologically identical but produce distinct pulsed courtship calls. Males of *H. chrysoscelis* produce a courtship call typically consisting of around 50 pulses/s. Males of *H. versicolor* typically produce calls of about 20 pulses/s, although this can vary with temperature in both species (Gerhardt

and Huber 2002). Both species use pulse rate as a mechanism for identifying conspecifics, with females showing strong mating preferences for conspecific pulse rates.

In more detailed neurobiology experiments, researchers have been able to examine the neural underpinnings of hearing perception in frogs (Wilczynski and Capranica 1984). For example, counting neurons have been identified in the auditory midbrain that responds to species-specific pulse rates in two species of frogs (Edwards et al. 2002). Recently, Schrodde et al. (2014) used the minimally invasive auditory brainstem response (ABR) to develop a frequency tuning curve for Cope’s gray treefrog. They found two peak sensitivities, corresponding to the expected tuning of the two inner ear organs and also closely matching the frequencies of male’s advertisement calls (Schrodde et al. 2014). In addition, this matched previously documented frequency preferences by females.

Orthopteran insects: Like frogs, Orthopteran insects (crickets and katydids) have provided a unique system to study behavior and signal evolution (Gerhardt and Huber 2002). In most species, males produce acoustic signals to attract mates by rubbing their fore wings together. The sound is produced by scraping one wing, which possess a series of teeth, against the anal margin of the other wing, which acts like a scraper. Generally, crickets communicate at frequencies around 5 kHz, and katydid calls are broadband signals with a frequency spectrum that may extend from the sonic to ultrasonic range (10–60 kHz). Both crickets and katydids possess tympanal ears for hearing on their legs. This sensory system, particularly in crickets, is tuned for the frequency of the male call. For example, in the cricket *Gryllus bimaculatus*, it has been shown that the tympanal sensitivity was best tuned to the carrier frequency of the male song, about 5.3 kHz, thus songs produced at higher or lower frequencies were not detected as easily. In addition to frequency, crickets and katydids produce chirps in specific temporal patterns, and detecting these species-specific pulse patterns is also an important part of recognition. In an elegant review, Hedwig



Sensory Exploitation Hypothesis, Fig. 2 Waveform (*upper*) and spectrogram (*lower*) of a male tungara frog call. In the spectrogram, the two boxes correspond to the peak hearing sensitivities of the tungara frog's two inner ear organs, *A* basilar papilla, *B* amphibian papilla. Although harmonic energy from the whine extends into the BP sensitivity range (*box A*), there is relatively little energy there to stimulate the BP. Instead, the majority of the call energy in the BP sensitivity range is contained within the chuck. Conversely, most of the energy from the whine falls within the range of the AP sensitivity (*box B*), thus the whine primarily stimulates the AP

(2016) showed that the species recognition system in crickets works as a set of serial filters, with each filter responding to specific features of the song such as frequency, chirp duration, and repetition rate.

Katydidids are categorized by a high diversity of acoustic communication signals. In a comparison between partially sympatric sibling species, *Neoconocephalus robustus* and *N. bivocatus*, Deily and Schul (2006) found that they exhibit different call recognition mechanisms. *N. robustus* males produce calls with a single pulse rate and females of the same species are attracted to calls without amplitude modulation. In *N. bivocatus* females require amplitude modulation for call recognition. More broadly, in a phylogenetic comparative analysis of katydid call diversity, three important call properties were identified: call structure, pulse pattern, and pulse rate (Frederick and Schul 2016). This analysis compared 17 katydid species in the genus *Neoconocephalus* and revealed convergent evolution in call traits. Call diversity and the ability of a species to recognize conspecifics appeared to limit species diversity in particular locations. Two species with the same call trait do not co-occur. This coupled with changes in call structure and pulse rate produce clear acoustical niches, generating distinct species recognition.

Thus far, sensory exploitation has been described via neural tuning and female mate choice, the context in which it is normally considered. In the Hawaiian cricket, *Teleogryllus oceanicus*, a preexisting bias in males, however, has rendered a mutation adaptive. Like most crickets, males of this species produce songs to attract a mate. This song also attracts parasitoid flies (Zuk et al. 1993). A wing mutation, rendering some males silent, occurred in the population. Normally this mutation would have been eliminated from the population as silent males would fail to procure mates and pass on the trait. A preexisting behavior, the propensity for males act as satellites, rendered this trait adaptive, however, and allowed it to spread rapidly in the population. With satellite behavior, males sometimes approach another calling male, remain silent, and intercept females attracted to the caller. By exploiting the calling behavior of other males,

the mutated silent males maintain their ability to procure a mate and also reduce their chance of attracting parasitoid flies (Tinghitella and Zuk 2009).

Another example of sensory exploitation in crickets is the conversion of a vibration startle response to a mate-pairing signal (ter Hofstede et al. 2015). Generally, female field crickets approach males with a low-frequency call and avoid high-frequency calls. In lebinthine crickets, the males produce an extremely high-frequency call and in response, the females produce a vibration instead of moving towards the male. The male then follows the vibrational signal to the female ter Hofstede et al. (2015) documented that field crickets closely related to the lebinthine crickets show an acoustic startle response to high-frequency sound and generate vibrations similar to those produced by female lebinthine crickets. The lebinthine vibrational signal thus likely arose from the preexisting startle response.

Fish: In contrast to crickets and frogs, courtship communication in fish primarily occurs via visual signals. Male Trinidadian guppies (*Poecilia reticulata*) display complex color patterns to females, and females prefer males with intense orange colors. Both male and female adult guppies are more responsive to orange-colored objects, even outside mating contexts (Rodd et al. 2002). The orange color is generated from carotenoid pigments in the diet and guppies are attracted to orange-colored food items. The cabrehash tree and several other trees produce bright orange fruit, but it is a rare, high quality food source for guppies. Thus, this preference for orange objects may have arisen in the context of food detection.

Another fish system, the genus *Xipophorus*, contains species where males bear a decorative extension of the caudal fin (swordtails) as well as unsworded species (platyfish). Female swordtails typically prefer to mate with males possessing longer swords. Interestingly, female platyfish, whose males lack swords, also prefer to mate with males who have had a sword artificially affixed to their tail. The sword is a derived character in this group, demonstrating that the female bias for the ornament predated the

evolution of the sword (Basolo 1990). Recent data also support the hypothesis of sensory exploitation for the sword ornament in a group distantly related to *Xipophorus*. Mollies are composed of two clades, the long-fin clade and the short-fin clade, which differ in the presence of the sword phenotype. The tamesi molly, *Poecilia latipunctata*, was historically classified as a short-fin molly based on morphology and ecology but is grouped with long-fin mollies based on molecular and behavioral data. Tamesi molly females prefer the sword ornament, even though the males of this species do not express the trait (Makowicz et al. 2015).

African rift lake cichlids have undergone rapid evolutionary radiation, evolving hundreds of species within a relatively short time frame. This group exhibits a wide array of ecological and morphological variation, as well as variation in sexually selected courtship signals. These courtship signals are especially prominent as variable color patterns and have evolved through mate choice. For example, Egger et al. (2011) tested female preference for “egg spots,” the prominent light-colored spots that males of many species exhibit on their anal fins. They presented female haplochromine cichlids, *Pseudocrenilabrus multicolor*, with images of males where egg spots were artificially added; males of this basal species lack egg spots. Even though males of their own species lack them, females expressed a pre-existing preference for these egg spots. The authors suggest that this preference may have arisen because the yellow-orange color of these spots was previously adaptive for locating carotenoid rich foods. Other work examining spectral tuning of retinal photoreceptors have provided clear evidence that different species have diverged in their sensitivities to particular wavelengths of light and these sensitivities have driven subsequent mate preference behaviors and color evolution (Seehausen et al. 2008).

Perception and Behavior

Information on sensory tuning, mate preference, and phylogenetic relationships have been

important in elucidating the process of mate choice via sensory exploitation (reviewed in Ryan and Cummings 2013). More recently, some of this work has incorporated techniques from the human psychophysics literature, providing glimpses into the role of sensory perception in mate choice and signal evolution. Historically, understanding sensations and perception were considered to be outside the realm of science because these phenomena are “private” to each individual. Researchers working in human psychophysics developed experimental techniques to test perception; specifically they measured stimuli and asked individuals if they could detect or discriminate, and hence perceive them (e.g., Fay 1988). The biology of some nonhuman organisms also lends itself well to these psychophysical methods and has allowed researchers to make important cross-taxonomic comparisons in auditory processing, perception, and mate choice. Here again, Orthopteran insects and Anuran amphibians have proved successful models (Wytenbach and Farris 2004; Bee 2015).

Phelps et al. (2006), for example, presented female túngara frogs with a series of digitally manipulated calls. This series consisted of calls that were digitally “morphed,” from a normal túngara frog call into the call of another species that the female túngara frogs do not recognize. By presenting female túngara frogs with this series of calls, they were able to test the limits of acoustic recognition and discrimination. This allowed the researchers to then build a cognitive framework defining the acoustic recognition space in this species.

In another series of studies with the túngara frog, Farris and colleagues demonstrated a surprising auditory grouping behavior (Farris et al. 2002; Farris and Ryan 2011). Many animals use spatial cues to group segments of sound together and generate a coherent “auditory object,” that is, assigning a particular complex sound to its source location (Bregman 1990). In a series of clever experiments, Farris et al. (2002) explored the basis of auditory grouping in the túngara frog. As discussed previously in the chapter, females respond to the male’s whine call, but

not an isolated chuck. In their experiments, Farris et al. (2002) presented females with a whine and chuck that were physically separated and females responded to the spatially separated chuck as if it were produced in the same location as the whine. Based on these data from a single whine and chuck, it appeared that female túngara frogs do not use spatial cues in auditory grouping. In a subsequent study, they presented females with a whine and two spatially separated chucks. In this case, females appeared to take advantage of relative comparisons, favoring chucks that were placed closer to whines in either space or time (Farris and Ryan 2011). This indicates that auditory grouping was not absent in túngara frogs. Instead, like humans communicating in noise, strategies for assigning sounds to their source by túngara frogs seem to be flexible.

In humans, a well-known phenomenon, the continuity illusion or auditory induction, occurs when brief silent gaps in sound are filled with white noise. The auditory system then fills in the masked gaps and generates the perception of an unfragmented “auditory object.” This process in humans likely improves speech comprehension in noisy environments where segments of speech become masked by noise (Bregman 1990). Baugh et al. (2016) tested auditory induction in the túngara frog and surprisingly found that they seem to lack this ability. Because túngara frogs communicate in noisy environments, analogous to noisy human speech conditions, it might be predicted that frogs would incorporate a similar mechanism for improving acoustic discrimination. Interestingly, Taylor and Ryan (2013) performed a similar type of test, but combined both acoustic and visual signals. In this study, they “sandwiched” a visual stimulus of a calling male frog between two temporally separate male call components, the whine and chuck. Normally, the temporally separated call components fail to elicit full recognition of the call. When the visual stimulus was placed in between the separated whine and chuck, however, this perceptually rescued the acoustic components and restored recognition, indicating the presence of a multisensory continuity illusion.

Conclusion

Since the early 1990s, tests of sensory exploitation as a mechanism for signal evolution via mate choice have required a multidisciplinary approach, employing methods from neurobiology, behavior, and phylogenetics (Ryan 1990; Shaw 1995). Further investigation of sensory exploitation still requires this integrative approach, since the evolution of the signal and receiver preference may not be closely coupled, the disconnect occurring as the preference predates the signal origin. Ryan and Cummings (2013) support a conceptual shift from the broad term sensory bias to perceptual bias to further expand our understanding of signal evolution via mate choice. The inclusion of theory from human psychophysics is an example of this shift, but there are also new approaches that will further the field. One is to gain fine-scale information about the focal communication system by utilizing genomic or transcriptomic tools. This is already being done by some behavioral researchers (Hofmann et al. 2014) and more are coming.

Another area under investigation is a focus on the female brain at the neuromolecular level, linking neural processes responsible for sensory processing to motor output leading to female mate preference behavior (Cummings 2015). Finally, an exciting area of research is beginning to focus on individual differences in sensory perception and mate choice. This area of research could focus on repeated measures of female preference, individual differences in central and peripheral signal processing, and/or individual genomic links to behavioral preference (Ronald et al. 2012; Patricelli et al. 2016). The previous several decades have provided profound insights into the role of sensory exploitation in mate choice and signal evolution. Current and developing technologies and concepts that allow researchers to link individual differences in genes, physiology, and behavior promise to offer an unprecedented understanding of this evolutionary process.

Cross-References

- [Female Choice](#)
- [Female Mate Choice](#)
- [Intersexual Competition](#)
- [Supernormal Stimuli](#)

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Sensory Trap

- [Sensory Exploitation Hypothesis](#)

Sentence Structure

- [Grammar](#)

Sequential Hermaphroditism

- [Sex Switching](#)

Sequential Tool Use

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Synonyms

[Associative tool behavior](#)

Definition

The use of two or more tools to obtain a goal.

Introduction

Tool use is a widespread behavior among many nonhuman animal species (e.g., Shumaker et al. 2011). However, nonhuman primates and corvids have produced the most extraordinary examples of tool-use behaviors. In the wild, for example, chimpanzees at Gombe (Tanzania) have been reported to plunge little sticks into termite mounds in order to access the termites. Similar behaviors have been described in New Caledonian crows – they use small twigs to extract insects from holes in logs. These two examples represent instances of using a single tool to obtain food (Shumaker et al. 2011).

Although more uncommon, instances in which the use of two or more tools is required to obtain a particular goal – so-called *associative tool behavior* (Shumaker et al. 2011) – have also been demonstrated in animals. Associative tool behaviors encompass cases in which animals use a tool to support another tool, so-called *metatool use*, to modify or manufacture another tool, *secondary tool use*, as well as instances in which two or more tools are used in sequence and each tool is used in a different mode, so-called *serial tool use* or *tool set*. An example that falls in the last category has been described in the chimpanzees of the Goulougo Triangle (Republic of Congo). When trying to access the termites from subterranean nests, the chimpanzees first use a puncturing stick on the ground and second a fishing probe that allows them to obtain the termites (Sanz et al. 2004).

Importantly, a tool can also be used to obtain a second out-of-reach tool, which subsequently will serve to obtain an out-of-reach goal – so-called *sequential tool use*. According to Shumaker et al. (2011), in the animal tool-use research, the categories *metatool use* and *sequential tool use* have been mistaken and considered to be equivalent categories. However, as pointed out by Shumaker et al. (2011), “a metatool is not used

to acquire another tool but rather to increase the efficiency or effectiveness of the second tool” (p. 20). Thus, an orangutan using a stick to push a paper towel into a puddle of edible liquid is not an example of sequential tool use but an example of metatool use (Shumaker et al. 2011). In addition, whereas sequential tool use has been reported in primates and corvids, metatool use has only been observed in primates.

Empirical Evidence

Sequential tool use has been commonly tested in lab settings by presenting subjects with an out-of-reach reward, an immediately available tool, and an out-of-reach second tool. The first tool is not useful to obtain the reward but useful to reach the second tool, which can then be used to obtain the reward. For example, Bird and Emery (2009) showed that rooks could spontaneously drop a large stone into a container to release a small stone, which was then used to acquire food. New Caledonian crows could use a directly available short stick to reach for an out-of-reach long stick, and then use the long tool to reach for a reward placed in a vertical tube (e.g., Taylor et al. 2007). Likewise, Bluff et al. (2007) showed that New Caledonian crows could first obtain a tool by pulling up a string; next, use the tool to extract a longer second tool from a toolbox; and finally, use the long tool to obtain food from a hole. Using a very different setup, Wimpenny et al. (2009) presented New Caledonian crows with the following situation: an out-of-reach reward, two tools that were available but too short to reach the food, and four out-of-reach tools differing in functionality. The distance of the food and/or which tools (and how many) were needed to obtain the food defined the sequence of actions required for successful performance. Wimpenny et al. (2009) found that crows could use up to three tools in sequence in order to obtain the reward.

As mentioned above, nonhuman primates have also been reported to use tools to access other tools. For example, Martin-Ordas et al. (2012) showed that apes could *spontaneously* use up to

five tools in sequence. Macaques (Hihara et al. 2003) and cotton-top tamarins (Santos et al. 2005) can also do so – although only after receiving some training.

Cognitive Mechanisms Involved in Sequential Tool Use

Wimpenny et al. 2009 (see also Shumaker et al. 2011) argued that the use of two or more tools is more cognitively demanding than the use of a single tool – the number of objects required to succeed will certainly increase the level of difficulty of the task (see also Fragaszy and Cummins-Sebree 2005). Taylor et al. (2007; see also Bird and Emery 2009) have also suggested that using tools in sequence is a demanding task because the individual has to (1) understand that the tool can be used to access food but also to access nonfood items, (2) inhibit the drive to use the tool to access the food, and (3) plan the sequence of actions, that is, anticipate the series of sub-actions needed to achieve a final goal. Importantly, Wimpenny et al. (2009) stressed that most of the research done on sequential tool use did not help to unravel the cognitive underpinnings of animal performance. In particular, they argued that learning history or trial error – as opposed to planning or causal understanding – could explain animals’ performance in those particular tasks. Wimpenny et al.’s (2009) task controlled for some of these issues (see also Martin-Ordas et al. 2012). Consequently, the authors concluded that, at least, the performance of one subject “in particular leaves open the possibility that crows may solve sequential tool problems by planning their actions, rather than having to build up associations by repeated experience.” (p. e6471).

Conclusions

Sequential tool use is defined as the ability to use a tool in order to obtain a second out-of-reach tool, which subsequently will serve to obtain an out-of-reach goal. Whether planning, reasoning, or associative learning are cognitive mechanisms

involved in sequential tool use is still an open question. As such, future research should develop experimental paradigms to further investigate the cognitive mechanisms underlying this particular tool-use behavior.

Cross-References

- [Nonhuman Tool Use](#)
- [Primate Tool Use](#)
- [Problem Solving](#)
- [Tool Use](#)

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Sequestered Ovulation

- [Concealed Ovulation](#)

Sequestration

- [Types of Sexual Coercion](#)

Serotonin and Dominance

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Synonyms

[Dominant](#); [Serotonergic system](#); [Serotonin transporter](#); [Social dominance structure](#); [Social hierarchy](#)

Definition

Dominance describes high status of an individual in social hierarchy that allows for priority access to limited resources such as food, mates, and space. Serotonin, a monoamine neurotransmitter, contributes to the formation of social hierarchy and positively affects dominance in humans and other primates.

Introduction

Social hierarchy is a key element in the organization of many human and nonhuman groups that undertake collective and cooperative activities. Dominant group members standing at the top of the hierarchy are privileged with various benefits including priority access to limited resources (food, mates, space) over the subordinate

members. In order to maintain their position, dominant individuals exercise behavioral tactics that rely on subtle interplay between cooperation, affiliation, and aggression directed toward subordinates. In contrast, submission, although limits the access to resources, allows weaker and less skillful individuals to minimize consequences of aggressive encounters with conspecifics.

Misinterpretation or ignorance of the social dominance structure has profound consequences for individual's life including aggression from conspecifics, exclusion from the social group, or death (Watanabe and Yamamoto 2015). Because of this, one can expect that during evolution, there had to be a selection pressure on efficient neurophysiological mechanisms for recognizing and interpreting cues for social status in conspecifics and expressing social status of oneself. Neuroscientific studies conducted during the last decade helped to elucidate these mechanism and pointed to the important role of serotonergic system in establishing of the social hierarchy both in primates and in humans (Kiser et al. 2012).

Serotonin and Social Hierarchy

Serotonin (5-HT) is a conservative monoamine neurotransmitter derived from the amino acid L-tryptophan, found in all bilateral animals. In the central nervous system (CNS), primary sources of 5-HT production are raphe nuclei located in the brainstem; however, 90 % of serotonin is synthesized outside CNS, in gastrointestinal tracts. The synthesis of serotonin in the brain is dependent on the availability of its precursor amino acid, tryptophan. Serotonin is reabsorbed from synapses through serotonin transporter located on the pre-synaptic neuron, and levels of synaptic serotonin might be regulated via selective serotonin reuptake inhibitors (SSRI). Degradation of 5-HT in the brain is mediated by monoamine oxidase A (MAOA), which results in producing 5-hydroxyindoleacetic acid (5-HIAA).

Serotonin was found to directly support dominance structure in primate groups. Studies conducted in vervet monkeys (*Cercopithecus aethiops*) demonstrated that alpha-male

individuals had higher levels of blood and brain serotonin that decreased when dominant position was lost (Raleigh 1984). Furthermore, experimentally induced rise in 5-HT level promoted dominance acquisition in these animals (Raleigh et al. 1991). Similar effects were observed in humans. Experimental treatments with tryptophan and selective serotonin reuptake inhibitor (both act to rise 5-HT level) were associated with increased self-assessed dominance (Moskowitz et al. 2003), increased dominance judgments by peers, and dominant pattern in a stranger-dyadic social interaction (Tse and Bond 2002) in healthy men and women.

Studies in several different areas such as serotonin involvement in processing of facial cues, voice cues and mechanisms of aggression and cooperation elucidates how serotonergic system affects recognition and the establishment of social dominance structure.

Serotonin Affects Facial Cues Recognition

Social status is most frequently signaled in close proximity. In such conditions, individual's face represents an ideal source of transmission of the dominance signals and facial expression constitutes one of the best recognizable cues to communicate social status. Numerous studies confirmed that people, similarly to primates, read and identify cues of dominance from various characteristics of the face such as shape, facial expression, or gestures (Keating 1985; Little et al. 2007; Re et al. 2013). It is hypothesized that these facial clues evolved from the preparatory or support responses associated with attack or defense. Facial characteristics such as chin prominence, heaviness of brow ridges, and facial muscularity were also found to be predictive on current and future social status and reproductive success of their holders (Mueller and Mazur 1997; Rule and Ambady 2010).

Facial expression perception depends on serotonergic system, and 5-HT level influences recognition of emotion from the face (Harmer 2008). Higher synaptic 5-HT level induced by repeated administration of selective serotonin reuptake inhibitors (SSRI) is associated with decreased accuracy of recognizing angry, fearful, and

disgusted faces (Harmer et al. 2003) and increased tendency to interpret ambiguous faces as happy (Harmer et al. 2004). In addition, the same experimental procedure is associated with reduced neurophysiological response to fearful faces from the amygdala, hippocampus, and medial prefrontal cortex observed in functional magnetic resonance imaging (fMRI) (Harmer et al. 2006). These observations suggest that dominant individuals characterized by higher 5-HT levels (Raleigh 1984) might be less responsive to angry and fearful faces and react with lower anxiety to threats from conspecifics. In contrast, submissive individuals with lower 5-HT levels might be more sensitive to angry expressions, which allow them to avoid aggressive attacks from dominants.

Serotonin Affects Voice Processing

Voice is another important cue to social status. Voice pitch in male primates, including humans, is associated with testosterone level (Dabbs and Mallinger 1999) and perceived attractiveness and dominance (Puts et al. 2006), thus might be indicative of reproductive success. Moreover, studies on CEO's of companies registered on the American Stock Exchange showed that voice may also predict professional status and income – CEO's with lower voices make more money and enjoy longer tenures at the companies (Mayew et al. 2013). Interestingly, polymorphism in serotonin transporter gene (5-HTTLPR), which regulates synaptic serotonin concentrations and possibly modulates dominance hierarchy (Miller-Butterworth et al. 2007), is also associated with voice perception and processing. In particular, study finds that carriers of the short allele of 5-HTTLPR, associated with increased synaptic serotonin level, showed a decreased differentiation in the event-related potential (ERP) responses elicited by happy and angry tone of voice. The number of short alleles was associated with linear decrease in the amplitude of the ERP in response to a happy voice. This suggests that the facilitatory effects of processing positive (happy) voices were reduced in individuals carrying the short allele. In contrast, facilitation through positive voices was strongest for individuals homozygous for the long allele (Grossmann et al. 2013).

Serotonin Affects Aggression, Cooperation, and Affiliation

To reach and maintain dominant rank in social hierarchy, individuals use specific tactics that include mixture of affiliative, cooperative, and aggressive behavior. The intensity of each of these behaviors depends on species, its social organization, and ecological niche. While general aggressiveness and physical strength defines position of the individual in the social hierarchy of simply organized groups, these characteristics are insufficient in communities where cooperative skills are required (Kiser et al. 2012).

Serotonergic system was demonstrated to support all of these behaviors, i.e., aggression, cooperation, and affiliation, however not in a simple manner. In vervet monkeys, subordinate group members treated with serotonin enhancers achieved dominance by first increasing affiliative behavior toward group members and creating support group. During this period, aggressive behavior significantly decreased, while affiliative behavior (approaching and grooming) was significantly increased. Only after coalitions with other individuals were established dominant individuals engaged in aggressive encounters with conspecifics (Raleigh et al. 1991). Similar effect was observed in humans – application of selective serotonin reuptake inhibitor to the subjects was associated with increase in peer-rated dominance and increased eye contact when subjects were speaking. At the same time, subjects were more prone to reduce their award in favor of their opponents and increase number of cooperative messages sent to opponents during the mixed-motive games (Tse and Bond 2002). These observations concur with general effects of serotonin on aggression and cooperation. Experimental studies conducted in humans and nonhuman primates confirm that serotonin depletion increases aggression (Siever 2008), learning of cooperation, and perception of trustworthiness (Wood et al. 2006).

Conclusion

Neurophysiological studies conducted in non-human primates and in humans suggest an

important role of serotonergic system in shaping dominance hierarchy. Results of these studies demonstrate serotonin involvement in mechanism of achieving and maintaining dominant rank in social hierarchy. They also highlight possible alterations in dominant and submissive processing of emotions from nonverbal characteristics, such as face expression and voice pitch that signal social status. These alterations might result from differences in serotonergic system activity between dominant and submissive individuals.

Cross-References

- Aggression
- Cooperation
- Dominance Hierarchies
- Facial Expressions
- Function of Dominance
- Nonverbal Indicators of Dominance

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Serotonin Transporter

- [Serotonin and Dominance](#)

Serotonergic System

- [Serotonin and Dominance](#)

Servant Leadership

- [Employer Versus Employee](#)

Service-for-Prestige Theory of Leader-Follower Relations

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Definition

An evolutionary theory of leader-follower relations that aims to explain why these relations can range from being “bad” (i.e., based on coercion) to “good” (i.e., based on mutually beneficial exchange).

Introduction

The service-for-prestige theory (Price and Van Vugt 2014, 2015) takes an evolutionary perspective on leader-follower relations in order to accomplish two main aims. The first aim is to explain why these relations can range from being “bad” and coercive (i.e., based on a leader’s ability to harm followers) to “good” and voluntary (i.e., based on a leader’s ability to benefit followers). The second aim is to propose that “good” leadership is governed by the logic of reciprocity, whereby leaders deliver public goods to followers in exchange for elevated social prestige. Both of these aspects of leader-follower relations are examined in more detail below.

What Are the Characteristics of “Bad” Versus “Good” Leadership, and Why Does Leadership Quality Vary So Widely?

People from a diverse variety of cultures tend to agree about what constitutes good leadership. The GLOBE survey (Den Hartog et al. 1999) measured preferences for leader traits across 61 cultures. The most consistently valued leader attributes were those which allow a leader to benefit followers via prosociality (e.g., trustworthiness, fairness) and ability (e.g., intelligence, competence). Similar findings are reported in a review of characteristics of successful leaders (Hogan and Kaiser 2005). These sources both suggest that followers prefer leaders who would make good exchange partners: people who have the skills that would enable them to benefit followers and who can be trusted to not be deceptive or exploitative. By the same token, these sources also suggest universal aversion to traits indicating that a leader would be a poor exchange partner (e.g., dominance, selfishness); leaders are generally reviled if they exploit their positions for their own benefit and at the expense of their followers (Tooby et al. 2006).

This spectrum of leadership styles, from bad (self-serving and exploitative) to good (trustworthy and productive of group benefits),

can be observed in modern environments. These leadership styles map on fairly well to the two kinds of social status that are commonly distinguished in behavioral science: dominance and prestige (Henrich and Gil-White 2001). The high status of bad leaders constitutes dominance, and leaders extract this status coercively, via their ability to harm followers. In contrast, the high status of good leaders constitutes prestige and is conferred voluntarily on leaders by followers, in exchange for the benefits that the leader provides. Humans obviously possess the psychological machinery necessary for engaging in both dominance-based and prestige-based leader-follower relations in modern environments, and service-for-prestige (Price and Van Vugt 2014, 2015) describes the kinds of hunter-gatherer environments of the evolutionary past that could have selected for this machinery.

Prestige-based leadership is common in the kinds of societies that were probably most typical of our evolutionary past: small (25–50 members) bands of nomadic hunter-gatherers. In contemporary examples of such societies, good leaders are described as skilled individuals who are voluntarily appreciated, respected, and followed by others, whereas bad leaders are group members who attempt to become too pushy, dominant, and coercive (Price and Van Vugt 2014, 2015). It's difficult to be a bad leader for very long among nomadic foragers because people will be both eager to get away from you and also relatively able to do so; in the fission-fusion societies of nomadic hunter-gatherers, it's relatively easy to leave one band and join another, and bands commonly break apart due to social conflict (Kelly 1995). Moreover, because these groups tend to be so small, organizing group members for collective action tends to be a relatively simple undertaking, and there is no great need for strong leadership in order to solve problems related to group coordination and free rider punishment. These two aspects of typical nomadic hunter-gatherer societies – the relative ease with which members can escape bad leaders and the reduced need for leaders to solve collective action problems –

combine to create an environment in which follower dependence on leaders is relatively low.

In other kinds of hunter-gatherer environments, however, the dependence of followers on leaders – and thus the power of leaders – can become much stronger. Indigenous peoples of the North American northwest coast lacked agriculture, but were nevertheless able to live in sedentary villages, because they settled close to rivers which allowed their main protein source – salmon – to deliver itself directly to them. These villages could grow to include hundreds of residents, much larger than nomadic hunter-gatherer bands, and so their collective action problems were more challenging to solve without strong leadership. Moreover, the sedentary nature of these settlements made fission-fusion social organization less feasible, and it therefore became harder to simply pack up and leave a leader who became too dominant. Increased dependence on leaders along the northwest coast created a niche for the emergence of leadership that was significantly more dominant than that seen among nomadic foragers; for example, although slavery is unknown among nomadic hunter-gatherers, it was common along the northwest coast (Kelly 1995).

According to service-for-prestige, the kinds of hunter-gatherer environments that selected for dominance-based and prestige-based leader-follower relations in the ancestral past are both represented in the modern world. The theory expects that in modern environments, dominance-based leadership will emerge most often in social environments more similar to northwest coast, that is, environments in which followers have low ability to reject or escape leaders (due to, e.g., poor exit options) and/or in larger social organizations in which strong leadership is required to solve collective action problems. In contrast, prestige-based leadership should more likely emerge in environments more similar to those of nomadic foragers, that is, environments in which followers have greater freedom to desert or depose leaders, and/or in smaller organizations in which coordination problems are relatively easily solved at a local level.

Leader-Follower Relations Are Perceived as Good When They Involve Voluntary, Mutually Beneficial, Service-for-Prestige Exchange

It was noted above that according to surveys of leadership preferences such as the cross-cultural GLOBE study, followers prefer leaders who would make good exchange partners: leaders who are willing and able to produce benefits for followers and who can be trusted to not abuse their power for their own narrow self-interest. Service-for-prestige (Price and Van Vugt 2014, 2015) suggests that people prefer leaders to be good exchange partners because in the evolutionary past, this preference would have enabled followers to engage benefit-generating leaders in mutually advantageous and therefore sustainable relationships.

How would this mutually beneficial exchange have played out in the evolutionary past? In hunter-gatherer environments, competent leadership benefits follower fitness by facilitating cooperation in activities such as warfare, big game hunting, forging political alliances, maintaining within-group order, and camp migrations. However, leadership roles often involve substantial costs for leaders, such as time and energy investments, stressful decision-making, and physical risk-taking. For these costs to pay off, and for leaders to be motivated to continue to lead, they must be compensated by some kinds of return benefits.

Accordingly, leaders do appear to be rewarded for the contributions they make. As high-prestige individuals, leaders are highly valued as friends, allies, and mates; and therefore social, material, and sexual resources tend to flow their way. Evidence that hunter-gatherer leaders receive relatively large shares of material and social resources can be challenging to collect, since this increased access may be observable only over the long term or under conditions of unusually great need such as sickness or sustained hunger. Nevertheless, respected leaders in small-scale societies have been observed to be rewarded over the

long term with social, political, and material support (Bird and Bliege Bird 2010; Gurven et al. 2000; Von Rueden et al. 2014). And when the focus is on reproductive rather than social and material resources, the rewards of leadership become relatively easy to observe. The high status of male leaders is attractive to women (Ellis 1992) as well as to parents who wish to form alliances with a leader by betrothing their daughter to him (Kelly 1995). In small-scale societies, higher status men are reported to have more wives and sexual partners, higher-fertility wives, and more surviving offspring (Chagnon 1979, 1988; Von Rueden et al. 2008, 2011).

Service-for-prestige suggests that just as leadership services were costly for leaders to provide, prestige allocations to leaders were costly for followers to make. Prestigious leaders have high power to benefit followers, so followers will invest time and resources to remain in good standing with them. Such investments may take the form of, for example, deferring to leader interests, sharing resources with the leader, taking pains to avoid harming the leader, and cooperating with a leader's directions instead of pursuing one's narrow self-interest (Price and Van Vugt 2014, 2015).

Prestige-based leader-follower relations constitute reciprocal exchange (Price 2003), then, because just as leaders voluntarily pay costs to deliver leadership services in exchange for prestige, followers voluntarily pay costs to deliver prestige in exchange for leadership services. However, because this prestige must often be allocated to the leader by a whole group of followers, it's a more complicated form of reciprocity than the dyadic reciprocal altruism first described by Trivers (1971). Although leader-follower reciprocity has aspects in common with dyadic reciprocal altruism, it also shares characteristics with *n*-person reciprocity (Tooby et al. 2006) and can be considered a form of collective action. And as in any collective action, a free rider's advantage (Olson 1965) will accrue to group members who accept the benefits of cooperation (in this case, a share of the services that the leader is motivated to provide, by virtue of

being compensated with prestige) but who do not pay contribution costs (in this case, the cost of allocating prestige to the leader). Service-for-prestige predicts that in order to neutralize this free rider's advantage, high contributors – that is, high allocators of prestige – will experience punitive sentiment towards those who fail to “pay respect” to leaders (Price et al. 2002). This phenomenon could be observed repeatedly in the notoriously violent rallies that occurred during Donald Trump's campaign to become the US Presidential nominee for the Republican Party, beginning in the latter months of 2015. A pattern developed at these rallies in which attendees who were perceived as not being sufficiently supportive of Trump would be humiliated and forced to leave, or even physically attacked, by other attendees who apparently considered themselves vociferous Trump supporters (Jacobs 2016).

Finally, it should be noted that the free rider problem described above applies only to prestige-based leadership scenarios, in which leaders are perceived by the group as being valued providers of public goods. In dominance-based leadership scenarios, in which the power of leaders is based on their ability to harm and intimidate followers, the logic of this collective action should essentially flip. If a leader is perceived as exploitative and parasitic rather than benefit-producing, then the collective action should focus not on maintaining leader motivation to lead but on removing the leader from power. In this flipped context, the role of selfless contributor would now be played by the member who undermines the leader's authority by rebelling against it and who thus risks attracting the leader's wrath. The free rider, meanwhile, would now be the member who continues to allocate status and thus lend support to the harmful leader. A real-world example of this sort of collective action would be Boston's famous 1773 “tea party,” initiated by rebellious colonists to outrageously undermine the authority of what they perceived to be an exploitative royal regime. From the perspective of tea party supporters, the rebels were heroic risk-takers, whereas the King's supporters were traitors who deserved to be publically humiliated (tared and feathered).

Conclusion

Leadership is not unique to humans and indeed is a feature of a vast variety of species, from bees to ravens to nonhuman primates (King et al. 2009). But whereas leader-follower interactions enable many species to solve coordination problems and share information, it is apparently only in humans that these interactions occur as reciprocal interactions, in which followers reward high-contributing leaders with allocations of social status. This context of reciprocity would have enabled human followers to allocate relatively large incentives (in the form of prestige) to their leaders and to thus embolden their leaders to make relatively costly and substantial leadership contributions. Thus, because they occurred as reciprocal exchanges, human leader-follower relations may have enabled the emergence of a kind of leadership that was more risk-seeking and self-sacrificial, more creative and committed, and generally higher quality than leadership in other species. Even if reciprocity-based leadership is indeed higher quality, however, this was apparently not enough to permit its evolution in nonhuman species. It seems that leader-follower reciprocity, like other forms of complex cooperation that can occur among nonkin (Tooby et al. 2006), is a behavior that the human brain is especially well adapted to achieve.

Cross-References

- ▶ [Adaptations for Reciprocal Altruism](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Coalition Leaders](#)
- ▶ [Contingent Reciprocity](#)
- ▶ [Emotional Solutions to Free Riding](#)
- ▶ [Evolution of Punishment](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Nonhuman Reciprocal Altruism](#)
- ▶ [Non-Human Leadership](#)
- ▶ [Psychology of Reciprocal Altruism](#)
- ▶ [Punitive Sentiment](#)
- ▶ [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- ▶ [Theory of Reciprocal Altruism](#)

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Setting

- [Environmental Influences](#)

Settlement

- [Reconciliation](#)

Sex

- [Human Copulation](#)
- [Relationship Between Sexuality and Gender](#)
- [Reproduction](#)
- [Sexual Reproduction](#)

Sex as a Mate Guarding Strategy

- [Direct Guarding](#)

Sex as Bonding Mechanisms

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Synonyms

[Affiliation and sexual behavior](#); [Affiliation and sexuality](#)

Definition

The way in which sexual behavior promotes the formation and maintenance of social relationships

Introduction

Sexual behavior is the means to reproductive success, the currency of evolution. Sexual behavior is promoted by sexual pleasure and orgasm; both of these, in behaviorist terms, are unconditioned stimuli that reinforce behavior (Fleischman 2016). Sexual pleasure and orgasm increase the positive associations of an individual towards a specific conspecific. In species that care for offspring, sexual pleasure facilitates close bonds and cooperation to care for offspring. In species where only one parent cares for offspring and in species that do not pair bond, sexual pleasure facilitates repeat copulations with a partner who is more likely to choose them compared with unfamiliar others. Pair-bonded species may develop longer-term preferences than more promiscuous species (Coria-Avila et al. 2016).

Biological Mechanisms of Bonding

Sexual behavior facilitates pair bonds through a few different mechanisms; these have mostly been extrapolated from work on nonhuman animals. Some of the major facilitators of sexual bonding are dopamine, oxytocin, and vasopressin. In species of rodents like rats and mice as well as the

monogamous prairie vole, it has been found that oxytocin and vasopressin are necessary for developing partner preferences (Young and Wang 2004). In humans, oxytocin and vasopressin are shown to be elevated during sex and orgasm in the blood of women and men, respectively (Young and Wang 2004). In women, oxytocin levels during sex have been shown to be associated with positive affect and thus also implicated in improved sexual bonding (Meston and Frohlich 2000). Dopamine is also implicated in the reward circuitry around sexual behavior and pair bonds and may be maintained by partner proximity showing reinforcing properties through previous sexual behavior.

Human Social Bonding Facilitated Through Sexual Behavior

Sexual behavior is inherently reinforcing because of its link to reproductive success, but this pleasure is also expected to reinforce other kinds of social bonds. In nonhuman primates, same-sex sexual behavior is not uncommon and much is thought to be affiliative (Vasey 1995). For example, female bonobos often have sex with one another and the bonds forged in this way allow them to form alliances to challenge larger stronger males (Vasey 1995). In humans, same-sex sexual behavior or homoerotic behavior may be used to promote affiliation. Progesterone, a hormone associated with affiliation, is associated with greater self-reported desire to engage with others of the same sex, and men who are primed with affiliation related words are more likely to report wanting to engage in homoerotic behavior, but especially when male subjects had higher salivary progesterone (Fleischman et al. 2015). Women are more likely to be bisexual than men and this may have evolved to promote alloparenting, sharing attention, and resources in caring for offspring (Kuhle and Radtke 2013). Similarly, men may have evolved the propensity for same sex behavior for the purposes of affiliation (Kirkpatrick 2000). The human propensity to engage sexually with those of the opposite sex, even when there is no possibility of reproduction, may also have the

function of promoting and maintaining adaptive social bonds (Fleischman 2016).

Conclusion

Sexual behavior has a number of neurobiological correlates that show evidence for design in the service of forming and maintaining social bonds such as oxytocin, vasopressin, and dopamine. Sexual behavior has rewarding properties that reinforce bonds between people of the opposite sex, often in the service of caring for offspring, but also can reinforce other kinds of social relationships.

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Sex Categorization

- [Categorization by Sex](#)

Sex Cell Size

- [Gamete Size](#)

Sex Changing

- [Sex Switching](#)

Sex Difference in Reproductive Success Variance

- [Bateman's Principle: Sex Differences in Reproductive Success Variance](#)

Sex Differences

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Synonyms

[Attractiveness](#), [Parental behavior](#), [Reproduction](#), [Sexual behavior](#), [Sexual selection](#)

Definition

Evolutionary theory predicts sex differences among humans, which may extend (or be amplified) after having children.

Introduction

This entry provides an evolutionary theoretical framework to help explain sex differences in mate preferences among human parents. Few data enable directly testing sex differences in mate preferences. However, various lines of inferential evidence, including patterns of sexual behavior, causes for divorce, and dating information on single parents, are presented.

Sex Differences After Having Children

The evolutionary foundation of sex differences in mate preferences draws upon theoretical insight into the evolution of sex differences in reproductive effort more broadly (see ► [Sex Differences in Human Mate Preferences](#) (Buss, 1989); ► [Sex Differences in Parenting and Parental Investment](#)). Sex differences have been variably linked to gamete size (see ► [Sex Differences in Same-Sex Aggression](#); ► [Gamete Size](#)), relative parental investment, potential reproductive rate, and actual reproductive rate. If females typically have a lower actual reproductive rate than males, this observation helps account for sex differences in mate preferences; for example, males may have lower minimal standards in a mate given relative reproductive constraints.

Sex differences in mate preferences that preexist having children may persist after having children. However, there is reason to theorize that having children may also alter the nature of sex differences in mate preferences. Reproductive effort can be portioned into mating and parenting effort. Multiple lines of evidence from various societies indicate that women allocate a relatively higher proportion of their reproductive effort to parenting effort compared to men. After having young children, women may expend considerable time and energy nursing their offspring and tend to engage in higher rates of direct child care than fathers. For such reasons, sex differences in actual reproductive rates may be magnified, contributing in turn to life history stage-specific sex differences in mate preferences. For example, mothers may place a greater premium on a partner's ability to

provide the resources she and her child need than she did before having children, compared with fathers' preferences (see Weeks-Shackelford et al. 2007).

There are few data directly addressing sex differences in human mate preferences after having children. In a recent study of 747 single parents drawn from a demographically representative US sample of adult singles, several sex differences in mate preferences emerged among parents (Gray et al. 2016). Mothers were more apt than fathers to take seriously their children's opinion of their dating partner, while fathers were more likely than mothers to allow their children to set them up on dates. In a related national US sample, single fathers reported more often thinking about sex, having sex, having more sexual partners the past 12 months actively seeking a new partner, and going on more dates compared with single mothers (Gray et al. 2015a). The remainder of this entry draws largely upon inferential studies to help shed light on sex differences in mate preferences among parents.

Classic research on sex differences in mate preferences showed that women tended to value cues of male status and resources more than did men, whereas men tended to value cues of a partner's attractiveness more than did women. There is good reason to believe these sex differences persist, if not increase in magnitude, after having children. Sources of marital conflict and divorce highlight sex differences in the causes of relationship challenges. These show in Western and cross-cultural records that men are more likely than women to specify infertility and infidelity as causes of divorce; these observations fit with a view that men's mate preferences are attuned to cues of fertility and fidelity. Conversely, women's grounds for divorce more often cite physical abuse and inadequate resource provisioning, consistent with mate preferences that value relative safety and support in helping raise her offspring.

Research suggests sex differences in sexual desire and partner variety after having children (Gray and Garcia 2013). These observations are related to mate preferences – in whether desiring to mate at all and with how many partners.

Importantly, these aspects of sexuality are likely magnified in later pregnancy and in early stages after having children relative to pre-parental or later-parental stages. A way to conceptualize these enhanced sex differences begins with the recognition that women's reproductive effort privileges current over future reproduction during pregnancy and intensive postpartum parental care (Escasa-Dorne et al. 2013). Time and energy devoted to caring for a newborn draws away from maintaining psychological and physiological support for conceiving the next child. These life history shifts are orchestrated in part by changes in maternal hormone levels. Mothers' testosterone and estradiol levels decrease after birth, two hormones important in sexual activity. Conversely, elevated oxytocin and prolactin levels, which increase in women after birth to aid in lactation and direct maternal care, may have consequences for partnership behaviors (i.e., enhancing an infant bond at expense to that with a mate).

While becoming a father can impact men's psychology, physiology, and overall reproductive effort, those relative impacts are less than among mothers. Consistent with such views, mothers of young children tend to exhibit lower sexual desire and more pain during sex compared to fathers of young children. In several societies such as St. Louis in the mid-twentieth century and among the Ngandu farmers of Central Africa, the increased sexual conflict over desire for sex has been reported to lead to elevated risk of fathers seeking extra-pair partners. In a study of some 3410 Jamaican fathers of newborns, about half of men reported no sex the previous week. Yet approximately 30 % of fathers reported multiple sexual partners the previous 12 months, with younger men, men in visiting relationships, and men in lower quality relationships those more likely to report more sexual partners (Gray et al. 2015b). Relatedly, some mothers of infants in Manila, the Philippines, reported engaging in sex with their husband in what amounts to a relationship maintenance strategy – having sex to appease a valued partner rather than driven by one's own inner desire (Escasa-Dorne 2015).

Most of human reproduction ancestrally and today occurs within long-term partnerships that

are often codified by marriage (Gray and Garcia 2013). The same classic studies of cross-cultural mate preferences that showed some evidence of sex differences also showed considerable sex similarity: the most preferred traits indicated the importance of character and compatibility, consistent with a preference for cues suggesting success in maintaining a long-term partnership. Continued maintenance of a long-term partnership may be beneficial after having children, given the considerable time and resources humans expend on their offspring. Nonetheless, the death of a partner or dissolution of a relationship regularly leaves many parents single. Hunter-gatherer demographic studies suggest that divorces and re-partnering after having had children are regular occurrences. Yet apart from the US study cited above, what sex differences might be expected in the mate preferences of single parents?

Inferential insight suggests single mothers may be more attuned to partner cues indicative of safety for herself and her offspring. Research by Martin Daly and Margo Wilson, among others, showed that young children face elevated risk of physical abuse and death among step-figures, particularly stepfathers. A public health campaign deployed in parts of the USA entitled, "Choose Your Partner Carefully" focuses on single mothers rather than single fathers for this reason. Mothers may prefer cues of a potential partner's kindness (e.g., in faces, voices, and personality), perhaps to invest in her and her offspring but also to do her and her offspring less harm (Escasa-Dorne et al. 2013; Weeks-Shackelford et al. 2007). Relatedly, among Hadza hunter-gatherers of Tanzania, breastfeeding women preferred high-pitched male voices while women who were not breastfeeding preferred low-pitched voices (Apicella and Feinberg 2009). Several studies from the UK, the USA, and the Philippines focused on mothers' evaluations of male faces have shown that mothers of young children exhibited preferences for feminine male faces (Cobey et al. 2014; Escasa-Dorne et al. 2016). Moreover, parenting effort may influence women's preferences for a healthy partner, particularly in high pathogen load areas. For example, pregnant and breastfeeding Hadza women had an increased preference for

symmetrical male faces compared to non-pregnant and non-nursing women (Little et al. 2007).

All else being equal, single parents may hold lower mate value on the mating market. A parent's child can take away time spent between partners, and children may require resources and time that a prospective partner may not wish to share. In the same US singles study previously noted, there was no sex difference in the interest of single parents in dating other single parents (Gray et al. 2016). Yet single parents may collectively express less discerning mate preferences, consistent with a lower mate value attendant to having children. Relatedly, it may benefit a single parent to prefer a partnership with someone who has a lower self-perceived mate value or lower mate quality, as it may free them from having to continuously maintain the relationship (i.e., mate guarding) allowing a parent to direct her attention to parenting. It also bears underscoring that many single parents weigh their children's presence and views in parental dating and mating behavior.

Individual mate preferences are contingent on individual (e.g., mate value), relationship (e.g., relative mate values between partners), and wider social contextual (e.g., availability of alternative partners) factors. This means that the nature of sex differences in parents' mate preferences is also contingent on these same considerations. Just as variation in the social ecology of physical threats may impact how desirable a man's formidability or other cues indicative of protective capacity, so the magnitude of parents' sex differences in mate preferences for cues of protective abilities may also vary. Future work might seek to quantify the relevance of variable male provisioning, other features of a sexual division of labor, parental manipulation, and single parent child custodial time, among other factors, in impacting sex differences in parents' mate preferences.

Conclusion

Few studies directly address sex differences in mate preferences after having children. However, multiple inferential lines of evidence such as

patterns in sexual behavior, causes of divorce, and cross-cultural data on mothers' mate preferences point to the continuation if not amplification of sex differences in mate preferences after having children.

Cross-References

- [Benefits of Short-Term Mating](#)
- [Biology of Human Gender, The](#)
- [Differential Parental Investment](#)
- [Dominant Acts Expressed \(Buss 1981\)](#)
- [Gamete Size](#)
- [Information About Likely Combat Success](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Sex Differences in Emotional Communication](#)
- [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Sex Differences Versus Gender Symmetry](#)
- [Sex Differences, Initiating Gossip](#)
- [Sexual Dimorphism](#)
- [Social Dominance Orientation \(SDO\)](#)
- [Sociosexuality and Sexual Conflict in Mating Strategies](#)
- [Unknown Territory](#)

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Sex Differences for Pursuing

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Synonyms

Affair; Cheating; Extra-dyadic interaction; Extra-dyadic sex; Extra-pair sex; Infidelity; Unfaithful behavior

Definition

Extra-pair mating is a promiscuous mating strategy adopted by individuals in a monogamous relationship. It involves one individual engaging in sexual relations outside of the exclusive pair.

Introduction

The visibility of extra-dyadic interactions among high-profile celebrities in the media suggests a preoccupation with infidelity among the general public. Monogamy in intimate relationships is a traditional norm, and many individuals consider unfaithful behavior as intrinsically wrong. Despite these common beliefs, a meta-analysis conducted by Tafoya and Spitzberg (2007) suggests 34 % of males and 24 % of females have engaged in sexual relations outside of their marriage. Although infidelity is deemed an atypical behavior, it appears many people have, and will continue to, engage in extra-pair sex. This is concerning as the consequences of infidelity are often tragic. Daly and Wilson (1988) found an awareness of a partner's infidelity can elicit dangerous behaviors such as physical violence and even murder. This entry will explore sex differences in the pursuit of extra-pair mates by reviewing empirical and theoretical research.

Why Do We Engage in Infidelity?

A consistent finding in previous research is that of a sex difference, males appear to engage in infidelity more often than women cross-culturally. A considerable amount of research demonstrates men have stronger urges to engage in infidelity than women and are more likely to engage in sexual infidelity (Martins et al. 2016). In addition, men are likely to engage in more cases of infidelity than women (Brand et al. 2007). Research proposes the consistent sex difference can be explained via the application of evolutionary theory (Buss and Schmitt 1993), specifically, parental investment theory (PIT; Trivers 1972). PIT is grounded on the notion that women and men have different levels of obligatory minimal investment to their children. Women are obliged to invest at least 12 months of time and energy into pregnancy and lactation; in contrast, males only need to invest in sex if they wish. This difference in parental investment means men and women will benefit from different mating strategies. PIT proposes the sex which invests the least (males), can

benefit reproductively by adopting a quantity-over-quality strategy. PIT suggests males are likely to engage in short-term mating with multiple partners. This idea is consistent with the aforementioned research (e.g. Martins et al. 2016). For females, however, every child requires at least a 9-month internal gestation period. Therefore, females are more likely to adopt a quality-over-quantity strategy. Reproductive fitness among males is highly variable and, due to a minimal level of parental investment, the number of children a male can have is effectively unlimited. Reproductive fitness among females is considerably less variable due to the restraint of parental investment. A married woman could not increase her direct reproductive fitness by engaging in infidelity unless her partner was infertile or uninterested in sex (Greiling and Buss 2000).

However, women do engage in infidelity. Obvious clues to an evolutionary history of female infidelity derive from research concerning male sexual jealousy. Male sexual jealousy is a vicious reaction induced when males suspect sexual infidelity and often leads to physical abuse and occasionally homicide (Daly and Wilson 1988). Due to internal fertilization, women are 100 % certain their offspring are their own. However, men can never be completely sure. Research suggests male sexual jealousy is initiated by cues of infidelity (Greiling and Buss 2000) as extra-dyadic sex compromises paternal certainty. If females always remained in monogamous partnerships, why would males have evolved a psychology of sexual jealousy (Greiling and Buss 2000)? Behavioral evidence of female infidelity also suggests women do not always pursue a monogamous long-term mating strategy. Extra-marital sexual liaisons have been documented in both Western societies and in more primitive communities, such as the Yanomamo of Venezuela (Greiling and Buss 2000).

The reason for ancestral male infidelity is obvious; there is a direct reproductive benefit. Men who have sex with multiple partners will have greater reproductive success compared to males who only have sex with one female. Buss (2003) reported extra-dyadic sex comprises 20 % of males' sexual activity between ages 16 to 35 and

steadily increases to 35 % between ages 46 to 50. It is likely that this increase in extra-dyadic sex corresponds to a decrease in their partner's attractiveness and fertility (Buss 2003). For males who engage in sexual infidelity, casual sex becomes increasingly significant with age at the cost of sex with their wives. The benefits of female infidelity are less apparent and may have been masked by the noticeable costs of extra-pair mating. Females who engage in infidelity are confronted with risks of catching a sexually transmitted disease, a damaged reputation as a long-term partner, a loss of resources from their current partner (Buss and Schmitt 1993), and are at risk of suffering the effects of male sexual jealousy (Daly and Wilson 1988). What benefits could possibly outweigh all these costs?

Symons (1979) proposed a resource acquisition hypothesis for female infidelity. Symons suggested ancestral females may have benefited from infidelity by exchanging sex for goods, such as meat or jewelry. Research has shown women do obtain resources for sex. In many communities males are required to bring gifts to their mistresses and women may decline sex if these gifts are absent (Greiling and Buss 2000). Buss and Schmitt (1993) found further evidence supporting the resource acquisition hypothesis by assessing desires in the context of long- and short-term mates. They demonstrated females valued resource acquisition significantly more in a short-term context. Men who upheld an expensive lifestyle and showered women with gifts were seen as more desirable in a short-term context than a long-term context.

A further potential benefit of female infidelity is the acquisition of "good genes" (Symons 1979). Women may engage in extra-dyadic sex to secure genes that are superior to those of her current partner. A highly attractive man is often willing to have sex with a less desirable woman if she places no burden of commitment (Buss 2003). A less desirable female may be able to obtain reliable resources from her current partner and superior genes from an affair partner. Women who obtain "better genes" could increase the reproductive success of her children, thus increasing her own inclusive fitness. For example, if a

woman has sex with a highly attractive man, it is likely that her sons will be highly attractive too. Highly attractive sons may spark more interest from choosy females, resulting in more grandchildren. Gangestad and Thornhill (1997) investigated the good gene hypothesis by asking women about qualities they seek in extra-pair mates. They examined numerous variables including age, income, and sexual experience. The researchers also measured two characteristics of “superior genes” – physical symmetry and attractiveness. The results showed women are more likely to choose symmetrical men as affair partners than long-term mates. Symmetrical men are usually muscular, healthy, and intelligent in comparison to their nonsymmetrical counterparts (Gangestad and Thornhill 1997). However, physically symmetrical men have been shown to be more adulterous and dishonest to partners (Gangestad and Thornhill 1997) and so would not be suitable as long-term mates.

In addition to acquiring “good genes,” obtaining a different mate is another significant benefit of female infidelity. The mate switching hypothesis (Buss 2003) suggests women may engage in affairs to leave unhappy relationships, often by encouraging her long-term partner to break up with them. Females may also engage in infidelity as a practice run with another mate to assess if they are compatible. There is an abundance of empirical evidence supporting the mate switching hypothesis. Many studies have found women who engage in infidelity are significantly less happy with their marriages both emotionally and sexually, compared to their non-adulterous counterparts (Brand et al. 2007). In addition, strength and frequency of affairs are significantly related to the level of dissatisfaction women experience in their long-term relationship (Tsapelas et al. 2011).

Greiling and Buss (2000) conducted four studies investigating women’s sexual strategies. The studies assessed different hypotheses concerning the benefits women may gain from engaging in extra-pair mating and the situations in which they do so. Strong support across all four studies was found for the mate switching hypothesis and the resource acquisition hypothesis. The results

indicated that women believed they would find a more desirable mate by engaging in infidelity. In addition, study three found the situations most likely to promote infidelity among females were feeling that she can find a more compatible partner and meeting someone who seems more interested in her. These findings provide strong support for the mate switching hypothesis. Resource acquisition also emerged from the research as a conceivable adaptive function of infidelity. Study one showed women often acquire money, free dinners, and jewelry after engaging in extra-pair sex. Study four also found females who engage in infidelity perceived resource acquisition as highly beneficial. Recent research conducted by Brand et al. (2007) further supports the mate switching hypothesis. They found women were significantly more likely than men to cheat on their partner because they were unhappy with their current relationship.

The research discussed in this entry so far suggests that women not only benefit from long-term mating but also reap rewards from engaging in extra-pair liaisons. The studies provide a glimpse into why women may risk the dangerous consequences of infidelity and the situations in which infidelity may be profitable.

Is the Gap Closing?

The majority of infidelity research has focused on sexual intercourse (Brand et al. 2007); however, studies are now exploring nonsexual infidelity. When definitions of infidelity include kissing or dating, sex differences appear to diminish. Using both student and community samples, Brand et al. (2007) found men were not more likely to engage in infidelity than women; in actuality, women reported a higher incidence of infidelity than men. The authors suggest sex differences apparent in past research may be outdated and inaccurate. Tsapelas et al. (2011) propose the decreasing sex difference may be attributed to socioeconomic changes – females are becoming increasingly independent both in the workplace and within the home. Although recent research suggests the amount of women and men who

commit infidelity is similar, studies have reported that men engage in more episodes of infidelity than women (Brand et al. 2007). Martins et al. (2016) investigated rates of online infidelity such as cybersex and “sexting” and found that although rates of infidelity are converging, men still report higher episodes of infidelity. These results are consistent with PIT (Trivers 1972); males may be adopting a quantity-over-quality strategy (Brand et al. 2007).

Limitations

Considering the sensitive nature of infidelity, research findings should be interpreted with some caution. Many of the empirical studies cited previously rely on self-report measures. Due to the negative connotations associated with extra-dyadic involvement, participants may not be entirely truthful and present answers which are more socially desirable (Tsapelas et al. 2011). It is also important to be aware that some of the studies are correlational meaning causation cannot be assumed. There are also methodological problems within infidelity research. Authors often define infidelity differently; some studies include flirting, kissing, and cybersex in their definition of infidelity, while others only define infidelity as extra-pair sex (Brand et al. 2007). This may have skewed results. Tsapelas et al. (2011) suggest future research could consider gathering data from the individual and their affair partner; this may increase the understanding of infidelity. In addition, longitudinal studies may provide accurate information about relationships and the reasons why infidelity occurs.

Conclusion

Films, books, and television shows often portray women as faithful partners, while men are depicted as having animalistic urges, leading them to cheat on their wives. Past research proposed men were considerably more unfaithful; however, recent research has suggested this is not the case. Although it seems the incidences of

men and women engaging in extra-pair sex are becoming increasingly similar, the reasons for pursuing an extra-pair mate remain very different. Men engaging in infidelity are likely to be “spreading the seed” and may be seeking opportunities to have sex with a variety of women. However, it seems women engage in affairs when they are truly unhappy in their current relationship. Infidelity may give females an opportunity to find someone who is more compatible. Although this entry has explored why the pursuit of extra-pair sex may be beneficial, it is important to remember it is not inevitable.

Cross-References

- ▶ [Parental Effort Versus Mating Effort](#)
- ▶ [Sex Differences in Long-Term Mating Preferences](#)
- ▶ [Sex Differences in Short-Term Mating Preferences](#)

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Sex Differences in Ability to Assess Fighting Ability

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Synonyms

[Formidability assessment](#)

Definition

Empirical evidence supports the conclusion that men and women are equally skilled at assessing fighting ability in men.

Introduction

Humans show a large degree of sexual dimorphism in upper body strength. Because of the tight relationship between upper body strength and fighting ability, men are much better equipped to engage in physical aggression than women. Historical records of human activity support the idea that widespread intrasexual (same-sex) competition was a common occurrence between human males. This historical pattern suggests that any cognitive program that developed through natural selection might be especially tuned to assess cues to fighting ability in men.

Empirical Evidence

Evidence in support of this idea comes from work by Sell and colleagues (2009, 2010). Strength ratings of men judged from facial photos correlate more strongly with upper body strength ($r = .39$) than strength ratings for women ($r = .21$). Similarly, strength ratings of men judged from voice recordings correlate more strongly with actual upper body strength ($r = .51$) than strength ratings for women ($r = .26$). However, ratings of the body (excluding the face) are less supportive; ratings of men ($r = .57$) only correlate slightly more strongly with upper body strength than women ($r = .51$). This small difference is surprising given that men in those studies were photographed shirtless, whereas women were photographed wearing shirts. If anything this should exaggerate assessment differences, as it is more difficult to see women's musculature.

Another problem with the conclusion that humans are better equipped to assess male strength is due to the methodology of strength assessment in men and women. Typically, these studies take strength measurements as well as pictures or voice recordings of various men and women. Participants are then asked to rate the individuals in the pictures or recordings on their strength and/or fighting ability as compared to the population of men or women. However, this method confounds the issue of mean level sex differences in strength with differences in the within-sex variability of strength. Not only are men stronger than women, but there is more variability in strength within men than there is with women (Lassek and Gaulin 2009). This creates a situation where the cognitive program that assesses upper body strength must make finer grained distinctions between women than men. Thus, it is possible that the attenuated relationship between rated and measured strength for women may simply be due to the restricted range of female strength relative to male strength.

Finally, there is little evidence of sex differences in rater accuracy of upper body strength and fighting ability. Untrained men and women are equally skilled at assessing the winners of mixed martial arts competitions (Little et al. 2015) and

assessing upper body strength from the voice. There is some evidence that men might be better able to assess women's strength from photographs (relative to women), but these differences are generally small and inconsistent. This reflects the fact that being able to predict the victor of physical conflict was important for both men and women throughout evolutionary history, even though women were historically less likely to engage in and be victims of aggression.

Conclusion

Future research could address the issue of restricted range by using a forced choice paradigm where raters see pictures of two same-sex individuals and must assess which person is stronger. Individuals could be paired so that they were relatively similar in strength, eliminating the issue of within-sex variability differences. If humans are better equipped to assess male strength than female strength, then they should be better able to accurately assess what person is stronger in male pairs than in female pairs. Thus, it remains unclear whether sex differences in strength assessment result from the cognitive program being better "tuned" for men or just a methodological artifact.

Cross-References

- ▶ [Aggression](#)
- ▶ [Assessment of Fighting Ability](#)
- ▶ [Evolution of Fighting Assessment Abilities](#)
- ▶ [Fighting Assessment](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Male Adaptations to Assess Fighting Ability](#)
- ▶ [Male-Male Competition](#)
- ▶ [Mate Preferences](#)
- ▶ [Physical Aggression](#)
- ▶ [Psychological Mechanisms](#)
- ▶ [Resource Competition](#)
- ▶ [Self-Assessment of Fighting Ability](#)
- ▶ [Signals of Body Size](#)
- ▶ [Size and Dominance](#)
- ▶ [Tactics to Solve Adaptive Problems of Sperm Competition](#)

- ▶ [Upper Body Strength](#)
- ▶ [Upper Body Strength and Fighting Ability](#)
- ▶ [Upper Body Strength from Photo](#)
- ▶ [Vocal Indicators of Dominance](#)

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Sex Differences in Aggression

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Synonyms

Assault; Hostility; Physical aggression; Rape; Social aggression; Violence

Definition

A forceful, hostile, or violent behavior or attitude towards another, especially when intended to dominate or master.

Introduction

The relationship between sex and aggression is now undeniable, with countless studies revealing

males are more aggressive than females. Empirical research consistently finds that males are more aggressive than females in virtually every society across time and place (e.g., see Junger-Tas et al. 2004). Furthermore, gender disparities in offending are greatest for violent and serious property crimes such as murder, robbery, and burglary. While the correlation between gender and crime is robust, the theoretical explanation for why this gender gap in offending exists continues to be hotly debated in the field of criminology. Criminological research attempting to explain the nexus between sex and aggression has mainly focused on sociological explanations, but a growing line of research has revealed that biological and genetic roles may also play a vital part in explaining gender disparities in antisocial behavior.

Gender-Gap in Offending

Sex is generally recognized as one of the most robust correlates of crime within the field of criminology, wherein males are significantly more likely to exhibit antisocial behaviors than are females. These gender disparities comprise what is known as the gender gap in offending (Moffitt et al. 2001) and have been consistently found in research examining male-female differences in aggression. Empirical research demonstrates that the gender gap exists in virtually every culture, as well as across various time periods and places (e.g., see Junger-Tas et al. 2004). Moreover, sex differences in offending are more pronounced when looking at more serious and violent crimes. Official records within the U.S. reveal that adult males were responsible for approximately 81% of all violent crime arrests made within 2009, with males accounting for nearly 88% of arrests for robbery and 90% of the arrests for murder (e.g., see U.S. Department of Justice, Federal Bureau of Investigation 2009). These numbers are also reflected in juvenile statistics, with several self-report studies reporting that 80% of the youth who report carrying a weapon are male (Archer 2004). Consistent with these findings, results from observational studies and parental reports have

demonstrated that sex differences in physical aggression emerge early in the life course, even prior to the preschool years (Archer 2004; Tremblay 2006).

Although female violence is a rare phenomenon, some females are indeed found guilty of committing violent offenses. Compared to males, however, females tend to begin and end their violent careers earlier in the life course and are also far less likely to repeat their violent offenses (Moffitt et al. 2001). According to a longitudinal study conducted by Moffitt et al. (2001), less than 1 in 100 females in a cohort are on the path to becoming a life-course persistent offender when held to the same standards as their male counterparts (Moffitt et al. 2001).

Even though empirical evidence demonstrates a close relationship between sex and aggression, some scholars have argued that the gender gap in offending is not as clear-cut as it may seem. For instance, some researchers have found that gender ratios appear to be greater in studies utilizing official statistics such as arrest records versus studies employing data garnered from self-report surveys (Moffitt et al. 2001). This may be due to a number of possibilities, some which may not be related to actual offending behavior. That is, variation in the gender gap may be due to police bias in determining who is arrested, with females often being arrested less than men, or it may be because the majority of crimes committed by females tend to be minor, and therefore go unnoticed by the police. Despite females reporting higher levels of antisocial and criminal behavior in self-report surveys than is reflected in official reports, males remain the dominant sex in nearly every crime category, especially those reflecting serious and violent crimes (Moffitt et al. 2001).

Researchers have also suggested that the gender gap varies based upon the type of crime or aggression measured. For example, sex disparities tend to shrink when examining minor crimes such as drug and alcohol offenses and females even exceed the number of male arrests in two categories: prostitution (70% of all arrests) and truancy (55% of all arrests) (U.S. Department of Justice 2009). Perhaps even more shocking, data has revealed that in regards to partner abuse, females

match or even exceed the physically violent behavior of males (Moffitt et al. 2001). Furthermore, some scholars claim that females are not necessarily less aggressive than men but instead exert a different form of aggression. That is, while males are typically physically aggressive, females tend to exhibit greater levels of indirect, or relational, aggression. These scholars argue that the choice of aggression diverges between sexes due to their biological differences that are continually reinforced by social norms. Females choose to utilize indirect forms of aggression because they are physically weaker than males and therefore are forced to find an alternative way to achieve their desired results other than using physical aggression. Therefore, females should not be considered less hostile than males due to the fact that hostility is subjective based upon which sex is being studied. In other words, these scholars suggest that the differences most studies find in regards to male-female aggression are due to the focus on physical aggression, which is primarily used by males and typically avoided by females. Empirical evidence seems to contradict these claims, however. For example, a meta-analysis conducted by Archer (2004) found that although females were more likely to exhibit indirect aggression, the difference between sexes was extremely small. Results for physical aggression were in line with previous research, wherein males were significantly more likely to be implicated than females. A more recent meta-analysis conducted by Card et al. (2008) mirrored these results, finding that gender differences were greatest for direct aggression – with results favoring males – while gender differences in indirect aggression were nonsignificant.

Taking this evidence into account, gender disparities in antisocial behavior appear to be robust, with results consistently finding males to be more aggressive than females regardless of how the construct is measured. Although the correlation between sex and aggression is robust within the empirical literature, biological sex cannot in itself be considered a “cause” of crime. That is, simply being male does not cause an individual to become aggressive or lead them to commit an offense. Therefore, the reason why the gender gap in offending exists remains a matter of

significant debate. Criminologists researching the gender gap have traditionally explored which sociological variables may be responsible for the observed sex differences in aggression. A separate line of research, however, has begun to demonstrate the role of biological and genetic variables in the etiology of antisocial behavior and suggests that they may play a critical role in the developmental differences of male-female antisocial behavior.

Social Influences on Offending

Historically, criminological theory and research has focused on the environmental and social factors that influence aggression. This body of research emphasizes the role of cultural and community influences, peer influences, and parental management technique.

Cultural and Community Influences

One line of this research examines whether cultural influences and community influences, such as social-structural processes, traditional male and female social roles, school, and neighborhood contexts, are responsible for the observed sex disparities in aggression. Social-structural processes are often explored in the quest to find the variables responsible for the observed gender disparities in aggression. Theories taking this stand (i.e., social role theory, power control theory) argue that in patriarchal societies, males and females are socialized based upon the roles found in traditional division of labor in which males are employed outside the house while females’ duties take place within the home. Therefore, societal norms lead parents to exert more control over their daughters than their sons in an effort to reproduce the gender division between family and work. As a result, females are socialized to avoid responding to situations with aggression and are taught to empathize and care for others, while males are taught that risk-taking and aggression are masculine qualities and are socialized to use aggression as an appropriate response to some social situations (Archer 2004). Data tends to support this view; that is,

males are more likely to commit assault against an acquaintance or stranger than are females and, when females are arrested for a violent offense, the victim is typically a family member (Moffitt et al. 2001).

Empirical evidence investigating the influence of social-structural processes that occur within the family on aggression has been mixed. While some studies have found that gender and delinquency were related to parents' relative authority in the workplace, other studies have found that gender differences in several forms of delinquency occur regardless of the social-structure of the youth's family (Archer 2004).

In addition to cultural influences, criminologists have found that community factors such as school may play an important role in the etiology of aggressive behavior. Attachment to school and teachers, enthusiasm for learning, and high academic performance have been implicated as protective factors against the etiology of delinquent behavior for both sexes (Fagan 2015). Empirical studies have consistently revealed that males, however, not only have a higher risk of experiencing academic difficulties, they are also more affected by school problems than are females. For example, a meta-analysis conducted by Maguin and Loeber (1996) found that poor academic performance not only predicted delinquency, but that this association was stronger for males than for females. Furthermore, a growing body of research has demonstrated that poor verbal skills are significantly predictive of antisocial behavior both in the early school years and later in life, and that males exhibit language deficits at a higher rate than females.

While some empirical studies find evidence to support the theory that difficulties in academia may have a greater effect on delinquency for males than females, school variables fail to account for a large portion of the variance between sex and aggression. Even when utilizing multivariate statistical models able to control for various academic factors, the effect of sex on aggression typically remains statistically significant (Junger-Tas et al. 2004; Yun et al. 2014). For example, a recent multivariate analysis found that while lower levels of academic performance were

predictive of a greater number of arrests, sex remained a statistically significant predictor of arrests as well (Yun et al. 2014). Males reported more arrests than females regardless of academic performance, suggesting that other factors may be important in explaining sex differences in criminal activity. This study also incorporated models which included two well-documented criminogenic risk factors: low levels of self-control and prior delinquency. In these multivariate models, the effects of gender were somewhat attenuated, yet remained statistically significant in the prediction of number of arrests (Yun et al. 2014).

Researchers have also explored whether or not neighborhood characteristics, such as economic status and availability of social control sources, influence the etiology of sex differences in offending. It is theorized that because boys receive less monitoring by parents than females, they are likely to spend a greater amount of time in the neighborhood participating in both structured and unstructured activity. Therefore, males are exposed to a greater number of neighborhood risk and protective factors, suggesting that neighborhood characteristics may be more influential for males than females.

Empirical studies investigating the influence of neighborhood factors on the variation between male and female offending behavior are limited. Evidence from these studies provides mixed support for the theory that neighborhood characteristics cause sex differences in antisocial behavior. For example, a handful of studies have found neighborhood characteristics such as economic disadvantage, informal social control, and collective efficacy have equal effects on both sexes. In contrast, a study conducted by Zimmerman and Messner (2010) found that gender differences in violence and offending reduced as neighborhood disadvantage increased, with sex differences becoming nonsignificant in the most disadvantaged neighborhoods. These results indicate that economic disadvantage can account for the entire gender gap in offending. Furthermore, Fagan and Wright (2012) found neighborhood characteristics may actually be more influential for females than for males. Specifically, an increase in

collective efficacy was significantly associated with an increase in the number of delinquent acts reported for females but not males, and concentrated disadvantage was related to significantly lower violent acts for females but not males. Collective efficacy and concentrated disadvantage were not able to significantly predict the likelihood that either sex would participate in general or violent crime, however (Fagan and Wright 2012). Findings from this body of research highlight the need for future research assessing the relationship between neighborhood factors and the gender gap.

Peer Influences

One of the more prominent theories in criminology, social learning theory, claims that cultural values are transmitted through formal and informal systems of social control (i.e., school, parents, peers) and, therefore, aggressive behavior is learned and maintained throughout an individual's development by these sources. In terms of peers, social learning theory claims that an increase in exposure to delinquent peers increases an individual's chance to learn delinquent definitions and in turn increases that individual's acceptance of aggressive values and subsequent participation in delinquency. Researchers have sought to determine whether differences in delinquent peer associations may in fact explain the gender-crime association.

Specifically, these studies investigate whether gender has an effect on an individual's exposure to delinquent peers and definitions as well as what the effect this delinquent exposure has on each sex. Studies typically find that males do have more delinquent associations than females (Moffitt et al. 2001; Piquero et al. 2005; Zimmerman and Messner 2010). For example, Piquero et al. (2005) found that delinquent peer associations are a better predictor of male delinquency than female delinquency, while other studies have demonstrated that both sexes are equally affected by delinquent associations and definitions (Moffitt et al. 2001; Yun et al. 2014). Furthermore, a study conducted by Haynie et al. (2007) revealed that females' contact with delinquent males increased female violence, but male

contact with female delinquents had no effect, suggesting that the relationship between delinquent peer contact and aggression is more complicated than it may appear. These mixed results indicate that while delinquent peer variables might partially explain the correlation between sex and aggression, further research is required in order to fully understand the relationship.

One methodological problem that plagues the majority of delinquent peer research is that these studies rarely account for the possibility of self-selection effects (Fagan 2015). That is, it may not be that the bonds with delinquent friends cause an individual to commit crime, but that participating in criminal acts leads one to seek out delinquent friends. Because males are more likely to be involved in delinquency than females, they are also more likely to come across other delinquents and bond with them based upon their shared interest in offending (Fagan 2015). This line of reasoning suggests that although there appears to be a relationship between delinquent peers and aggression, other variables (such as genetics) likely play a critical role in this relationship. Therefore, the likelihood that peer variables are responsible for the variation in male and female offending is small.

Family Influences

Parental socialization factors are perhaps the most studied variables in the quest to determine why some individuals commit crime. Parents can influence their child's antisocial behavior in a multitude of ways. Theoretical explanations posit that parents supervise and socialize males and females differently, thereby leading each sex to develop a different propensity toward antisocial behavior. For instance, criminologists state that parents can thwart the etiology of delinquency for both males and females by closely supervising their children, recognizing deviant behavior when it occurs, and punishing that behavior in an appropriate manner. Parents tend to monitor daughters more closely than sons, however, therefore consistently discouraging antisocial behavior among females while simultaneously allowing males greater opportunity to misbehave and escape detection.

Empirical studies investigating the relationship between gender disparities in parental management techniques and their subsequent effect on delinquency provide mixed evidence. While some evidence demonstrates that daughters experience a greater amount of parental monitoring (Junger-Tas et al. 2004), other studies have contradicted these results, finding similar levels of parental monitoring and discipline between the sexes (Lytton and Romney 1991). Moreover, parental socialization factors tend to have comparable effects on delinquency for males and females.

Another consequence of the differential ways parents socialize their sons and daughters is that females seem to develop stronger social bonds with their family members than males. As a result, the influence of parental management techniques such as supervision and discipline may be greater for females than males, thereby reducing future female delinquency. Empirical evidence investigating this claim is also mixed, however. A number of studies have found that girls have a greater attachment to their parents than males (Junger-Tas et al. 2004), and that this attachment reduced violence for females but not males. However, studies have also found that parent-child attachment also reduced aggression for males as well. The claim that increased parenting practices are the result of greater social bonds between females and their parents has also received mixed empirical support. For example, while some studies have found that the effect of parental socialization has a stronger influence on antisocial behavior for females than males, others have demonstrated that parental socialization factors have a greater effect for males (Fagan 2015). Still other studies have revealed that the influence on the majority of parental socialization factors on aggression have an equal influence for males and females (Moffitt et al. 2001).

In addition to the variation in parental management techniques, parents frequently socialize girls to be aware of others' feelings and teach them how to empathize with others. As a result, scholars have theorized that females typically have a greater capacity for empathy, which has been demonstrated to have a strong inhibitory effect

on criminal involvement. While empirical evidence has found that females exhibit higher levels of empathy at a greater rate than males, the evidence also demonstrates that empathy's protective factors appear to reduce offending for both sexes (Broidy et al. 2003). The link between parental socialization factors and the development of empathy is unclear; however, empirical evidence from biological studies have found that other factors, such as neurological differences, account for the majority of variance displayed in male and female emotions, including empathy (Tibbetts 2013).

Although the majority of criminologists favor parental socialization as the main factor behind the differences in male and female aggression, empirical evidence suggests that this relationship may not be as strong as was once thought. To start, although parental socialization factors are often found to be statistically significant in the relationship with criminality, these coefficients tend to be relatively small and are often rendered nonsignificant when genetic factors are also included in the statistical models (Beaver and Nedelec 2015). Therefore, the ability of parental management techniques to predict antisocial behavior in general is questionable at best. Furthermore, while studies utilizing separate statistical models for males and females often find marked gender differences, the majority of these studies fail to statistically test whether these gender disparities are statistically significant (Fagan 2015) making it difficult to assess whether these observed gender differences are actually meaningful. On a separate note, if parenting factors are to explain male-female differences in offending, females must be exposed to protective parenting practices more frequently than are males, while males must be subjected to a greater amount of parenting practices that are linked to delinquency than females (Beaver and Nedelec 2015). Although many scholars have theorized that parents socialize their sons and daughters differently, a meta-analysis investigating this claim found that only 1 out of 19 areas of parenting styles was significantly different between boys and girls (Lytton and Romney 1991). Taken together, the empirical evidence suggests that parental socialization

factors can, at best, account for only a small portion of the observed variance in male-female aggression.

Much of the research just reviewed indicates that social factors do in fact influence sex differences in aggression to some degree. None of the social variables mentioned, however, can fully account for the relationship between sex and aggression, leading criminologists to investigate the association using multivariate models. Multivariate models are beneficial because they are able to examine the effects of multiple risk- and protective-factors simultaneously. Findings from multivariate studies including cultural, peer, and parental variables reveal that even though the effect of gender may be substantially reduced in such models, sex differences do in fact persist (Junger-Tas et al. 2004; Moffitt et al. 2001). For example, a multinational study conducted by Junger-Tas et al. (2004) controlled for a wide range of social variables that have demonstrated an association with antisocial behavior in prior research. Although they found that males were significantly more delinquent than females in each country they surveyed, their multivariate analysis found no significant sex differences for the majority of the social variables studied, including familial social controls, school ties, and peer influence. Empirical evidence such as this has led some researchers to investigate the possibility that nonsocial influences account for the sex differences in aggression.

Biological Influences on Offending

Although the variables responsible for the sex disparities in antisocial behavior remain under investigation, this body of research has confirmed two things. First, sex differences in behavior emerge shortly after birth, with one study revealing that gender differences in assertiveness can be observed even at the early ages of 13 to 24 months, with males being much more assertive than females (Tremblay 2006). Second, the gender differences in aggression that emerge early in life continue throughout virtually every stage of the life course (Moffitt et al. 2001). These two pieces

of information suggest that variables capable of explaining the sex differences in offending must also occur early in life and continue over time. Thus, while criminological research has historically focused on social variables to explain the fundamental differences in male and female antisocial behavior, an emerging body of research has begun to investigate the influence of biological and genetic factors. This growing body of research indicates that several biological factors play an important role in the gender gap in offending. These factors include neurological features, social cognitive skills, differential exposure to hormones, as well as genetic risk and susceptibility.

Neurological Influences

The early emergence of sex differences in behavior have led scholars to question whether neurological factors may be responsible for the male-female differences in antisocial behavior. One area of this research investigates developmental differences in the brain that occur between the sexes. Developmental differences begin to occur in utero and are responsible for differences in both the structure and function of male and female brains. These differences are proposed to play a significant role in the variance between male and female behavior (Wright et al. 2015). For example, empirical research has demonstrated that one outcome of these structural and functional disparities is that females tend to experience greater feelings of empathy than males (Tibbetts 2013). As mentioned previously, empathy is a strong protective factor, decreasing one's odds of participating in antisocial behavior and therefore explaining some of the variance in male-female offending rates. Furthermore, females generally score higher compared to males on other measures of self-conscious emotions such as shame and guilt (Tibbetts 2013). Women therefore possess a greater amount of inhibitory social emotions than males (Tibbetts 2013) and these emotional differences are likely behind some of the variance in the association between sex and aggression (Tibbetts 2013). It is likely that the differences men and women experience with regards to self-conscious emotions and social cognitive skills are linked to

structural and functional differences located within the brain.

On average, male brains are approximately 100 grams heavier than female brains are. While at one point in time, this led researchers to believe that male brains were superior to female brains, a closer investigation has resulted in this theory becoming mainly obsolete in the academic world. Specifically, although female brains have less mass than male brains, female brains have a greater efficiency in communication between brain cells which is likely due to the greater number of dendritic connections present (Wright et al. 2015). Moreover, females tend to have a higher level of neurotransmitters, including those which have been directly implicated in the brain's ability to regulate emotions and behavior (Wright et al. 2015). Research suggests that neurotransmitter interactions differ between males and females, and these differences are likely to contribute to the observed sex differences in self-conscious emotions and social cognitive skills (Wright et al. 2015). In addition to having more efficient communication between brain cells, the left and right hemispheres of the female brain appear to be better connected than in the male brain, allowing females to transfer information between hemispheres more quickly and efficiently than males. This superior connectivity may be a consequence of a larger corpus callosum in the female brain. The corpus callosum is one region responsible for the connectivity between brain hemispheres, and empirical research has demonstrated a link between the corpus callosum and the acquisition of self-awareness and intelligence (Halpern 2000).

Structural differences between the sexes are not only revealed when studying the brain as a whole but can also be seen when studying various regions within the brain. Studies assessing the neurological effects on aggression, violence, and impulse control have implicated several of these brain regions in the development of these behaviors (Raine 2008), therefore suggesting they may play a critical role in the gender disparities in antisocial behavior. In particular, research has revealed two brain regions that likely play an important role in explaining the sex disparities in

aggression: the limbic system and the prefrontal cortex.

The limbic system, considered a more primitive part of the brain, controls for basic emotions (i.e., anger, fear, pleasure) and human drives (i.e., sex, hunger) and includes structures such as the hippocampus, hypothalamus, cingulate gyrus, and the amygdala, among others. This area of the brain has been consistently linked to aggression, with an emphasis on the more serious forms of violence, including murder (Beaver 2009; Wright et al. 2015). Neuroimaging studies have consistently shown significant differences between the sexes in regard to the size of the neurological structures within the limbic system. For instance, females tend to have a larger cingulate gyrus than males, and this structure plays an important role in regulating emotions and behavior (Wright et al. 2015). Research is currently investigating whether having a larger cingulate gyrus may be responsible for the greater emotional responses reported by females. On the other hand, neuroimaging studies have revealed that the hippocampus, hypothalamus, and amygdala are larger in male brains versus female brains (Wright et al. 2015). Numerous studies have consistently demonstrated that these structures, especially the amygdala, are associated with the most serious forms of antisocial behavior such as murder and psychopathic personality traits (Raine 2008; Wright et al. 2015). Because these structures are larger and more active in males than females, the limbic system may be a key variable in understanding male-female differences in aggression.

Significant differences in size and performance between male and female brains have also been noted in the prefrontal cortex. The prefrontal cortex is perhaps the most studied area of the brain in regard to its association with antisocial behavior, with results consistently demonstrating a significant and fairly strong relationship between disruption in – or damage to – the prefrontal cortex and aggression (Beaver 2009; Raine and Yang 2006; Wright et al. 2015). The prefrontal cortex is responsible for higher-order cognitive processes, collectively known as executive functions. The most important higher-order cognitive processes

in reference to antisocial behavior include interpreting incoming stimuli, processing emotions, and deciding on an appropriate response to the incoming stimuli. Neuropsychological studies have repeatedly found that damage to the prefrontal cortex results in executive functioning deficits, and, in turn, an increase in antisocial behavior (Raine 2008).

Results from brain imaging studies have confirmed that women typically have larger and more active prefrontal cortices than men (Wright et al. 2015). This is an important fact when considering the role of the prefrontal cortex in regards to male-female differences in offending and aggression. The executive functions that occur within the prefrontal cortex serve as an “emergency brake” on the strong emotions generated by the limbic system (Beaver 2009; Raine 2008; Wright et al. 2015). Because males have larger and more active limbic structures than females combined with a comparatively smaller, less active prefrontal cortex than females, they are expected to participate in antisocial behavior at a greater rate than females. Empirical studies confirm that this is a strong possibility by consistently demonstrating that males not only commit more crime than females but also that males report higher levels of impulsivity and lower levels of self-control than females.

In a more general sense, Raine and Yang (2006) proposed a neural moral theory of antisocial behavior in which abnormalities occurring to the neural circuit activated during the normal moral decision-making process can lead to an increase in antisocial behavior. That is, if one of the brain regions critical to moral feelings and decision-making does not function properly or is structurally altered or damaged, that individual is at an increased risk for a breakdown in moral feeling which can ultimately lead to a rise in criminal behavior. Male’s neural morality may naturally be lower than female’s neural morality due to the fact that regions of the brain imperative for morality and decision-making are comparatively smaller and less active in male brains than they are in female brains. Although more research is needed, the available empirical evidence suggests that neurological differences may play a

vital role in the explanation of male-female differences in aggression.

Hormones

Androgens, the group of hormones that primarily influence the growth and development of an individual (i.e., testosterone, estrogen), may play a critical role in the gender disparities in aggression. All human brains begin to develop according to a female trajectory. Around the 8th week of gestation, a gene located on the Y chromosome – a chromosome specific to males – signals the brain to create testosterone which initializes a separate growth trajectory for males. Researchers believe that the formation of sex differences in the structure of the brain primarily takes place at approximately 34–41 weeks of pregnancy (Halpern 2000). Studies have discovered that during this time period, androgens are typically ten times greater in male fetal brains than in female fetal brains (Halpern 2000). Therefore, hormones – specifically testosterone – are thought to be primarily responsible for the significant structural and functional differences in male and female brains (Baron-Cohen 2004).

Empirical research investigating the effects of hormones on sex differences in antisocial behavior are limited, however, most likely due to the difficulty in measuring hormone levels. Prenatal exposure to testosterone is considered one of the key causal factors behind the variation in male and female brain structure (Baron-Cohen et al. 2004) but gaining access to measures of testosterone levels in utero is quite difficult. According to a review by Beaver and Nedelec (2015), the only means of gaining direct measures of prenatal testosterone are rather invasive and include testing blood from the umbilical cord after birth, testing maternal serum derived from venipuncture, or by testing amniotic fluid which is acquired through amniocentesis. These obstacles in gaining access to prenatal testosterone levels have limited the amount of empirical evidence garnered from studies utilizing direct measures. Moreover, studies that do include such measures typically do not include measures of antisocial behavior (Beaver and Nedelec 2015). Findings from this small body of research reveal that higher testosterone levels

occurring in utero are associated with a higher degree of masculine behavior (Baron-Cohen et al. 2004).

A small but growing body of research has utilized indirect measures of prenatal testosterone levels to examine the association between testosterone and behavior. The 2D:4D ratio is perhaps the most popular of the indirect methods and is calculated by dividing the length of the index finger by the length of the ring finger. This ratio is sexually dimorphic, becomes relatively stable around the 14th week of gestation, and changes little, if at all, over the life course. The 2D:4D ratio thereby serves as a rudimentary measure of exposure to testosterone in utero, where a lower ratio indicates higher levels of prenatal testosterone (Lutchmaya et al. 2004). Males typically have a lower 2D:4D ratio than their female counterparts (Lutchmaya et al. 2004), which is not surprising considering the evidence that has demonstrated greater testosterone levels in male fetus brains versus female fetus brains (Halpern 2000). Less obvious, however, is the relationship between the 2D:4D ratio and antisocial behavior. A number of studies investigating this association have found that a lower 2D:4D ratio is positively correlated with an increase in aggressive behaviors (McIntyre et al. 2007). Moreover, these studies typically show that the 2D:4D ratio is associated with an increase in aggression for males but not females (McIntyre et al. 2007), although at least one study found that this ratio did predict an increase in reactive aggression for females. Taken together, these studies seem to indicate that greater exposure to testosterone in utero can lead to an increased risk in antisocial and aggressive behavior.

Although findings from these initial studies are positive, the results from a recent meta-analysis are varied. Hönekopp and Watson (2011) found a moderate difference in the 2D:4D ratio between the sexes with a lower ratio for males. Their study also found that research investigating the correlation between the 2D:4D ratio and various outcomes suffered from measurement bias, with results varying based upon whether the studies used self-reported ratios or ratios measured by experts as well as the parts of the finger included

in the measurement (Hönekopp and Watson 2011) making it difficult to assess the validity of previous studies. These mixed results indicate more work is needed in this area before any conclusions can be drawn.

Another indirect measure of prenatal testosterone levels examines individuals who suffer from disorders that disturb the normal exposure of testosterone in utero. Females suffering from congenital adrenal hyperplasia (CAH), a disorder that causes an increase in testosterone levels in both prenatal and postnatal life stages, are often analyzed in clinical studies investigating the association between increased testosterone and an array of behaviors (Beaver and Nedelec 2015). These females are exposed to much higher levels of testosterone in utero than are females who are not afflicted by this disorder, and scholars therefore theorize females with CAH will differ significantly in behavior and cognition. In regards to aggression, overall results suggest a positive correlation between CAH and an increase in antisocial behaviors (Pasterski et al. 2007). The most recent study conducted by Pasterski et al. (2007) found that although females stricken with CAH were significantly more aggressive than their sisters not suffering from CAH, males – both with and without CAH – continue to display more aggression than both female groups.

Taken together, results from these three lines of research indicate a positive relationship between greater levels of testosterone in utero and an increase in antisocial personality traits and aggressive behavior. In addition, adolescent testosterone levels have also been linked to antisocial behavior. When male and female offending is at its peak, they are simultaneously experiencing a surge in the production of androgens (Beaver 2009). Therefore, the majority of female offending occurs during the age span that testosterone production is at its highest rate since before birth.

Aside from producing aggressive behavior, androgens also have the ability to protect an individual against engaging in antisocial behaviors. For example, at least one study has found that estradiol, or estrogen, appears to aid an individual in their ability to cope with stress. Estradiol/estrogen is primarily produced in the ovaries, and

therefore women tend to have higher levels of estrogen when compared to males. This finding is important since stress is a known risk factor for criminal involvement and aggression. Collectively, initial evidence from empirical studies seems to suggest that while androgens act as a risk factor for delinquency in males, they also serve as a protective factor for females. There is a need for replication of these findings, and therefore, the ability of the relationship between androgens and aggression to explain the difference between male and female aggression remains an open empirical question and should be addressed in future research.

Genetics

Differential genetic makeup between males and females may also play a role in explaining the gender gap in offending and aggression. For example, a study conducted by Vaske et al. (2011) proposed that the genetic risk threshold is higher for females than it is for males. That is, males require less genetic risk factors to influence their criminal behavior than do their female counterparts. Findings from this study yielded mixed support for the theory, however. While the study found that the genetic risk threshold was indeed higher for males than females, females that did commit an offense had significantly less genetic risks than the male offenders (Vaske et al. 2011). Although these findings provide some evidence for the role of genes in the differential development of antisocial behavior between the sexes, it is clear that more research is needed before any solid conclusions can be drawn.

One possible explanation for the gender differences in antisocial behavior may be the location of the genes associated with aggression. While males possess both an X and Y chromosome, females possess two X chromosomes. Therefore, if a risk allele is located on the X chromosome females have two copies of this gene, while males only have one. This makes risk alleles located on the X chromosome particularly risky for males because a female's second X chromosome can help counteract the genetic risk by providing a second, potentially unaffected, version of this gene (Beaver 2009). This line of thinking has

been substantiated in the case of the low activity allele for monoamine oxidase A (MAO-A), which has been consistently found in empirical studies to have criminogenic effects on males (Beaver 2009; Caspi et al. 2002).

In a landmark study, Caspi et al. (2002) demonstrated that a polymorphism of the MAO-A gene, specifically the low activity allele, interacted with childhood abuse to predict an increase in feelings of violence, conduct disorder, antisocial personality disorder, and violent offenses for males. Although this study did not include females, empirical research conducted since this study has begun to examine the effect genetic polymorphisms of MAO-A have on females as well. Results from these studies reveal that the low activity allele of MAO-A does not predict female antisocial behavior as it does with males (Prom-Wormley et al. 2009). These results do not indicate, however, that females are not affected by MAO-A at all. In fact, multiple studies have found that an interaction between the long variant of the MAO-A polymorphism and childhood abuse significantly predicted an increase in delinquency for females but not males (Prom-Wormley et al. 2009). While findings from this body of research demonstrate a robust correlation between MAO-A and aggression, the ability of MAO-A polymorphisms to partially explain the gender gap in offending requires further investigation.

In addition to the MAO-A gene, genetic polymorphisms from the dopaminergic and serotonergic system have also been implicated in the etiology of various antisocial and violent behaviors (Beaver 2009). These studies do not typically include females, however, so whether genetic polymorphisms from these systems can explain the differences in male-female aggression remains undetermined and should be investigated in future research. Although research assessing the relationship between genes and gender disparities in aggression are rather limited, evidence from the few studies available seem to point to a positive relationship between genetic risk and aggression. Genetic research therefore has great potential for explaining sex differences in aggression and offending.

Conclusion

Across time and space, males have been found to be more criminally prone than females, so much, so that criminological inquiry is virtually required to statistically control for the effects of gender. Empirical research has consistently found that sex differences in aggression begin shortly after birth and remain relatively stable over various stages of the life course. Males are far more likely than females to become life-course persistent offenders (Moffitt et al. 2001), and gender disparities are greatest for more serious and violent crimes such as robbery, rape, and murder (U.S. Department of Justice 2009). Although the relationship between gender and crime is robust, the causes of male-female differences in criminal behavior remain largely undetermined. Researchers have investigated both social and biological variables in the quest to discover what factors produce sex differences in aggression and crime.

While studies have consistently found a relationship between sociological factors such as cultural values, community influences, peer associations, and familial factors and the gender disparities in aggression, the possibility that these variables are the sole factors behind the gender gap is unlikely. For example, studies consistently find that gender remains a significant predictor of a range of antisocial behaviors, even when utilizing multivariate models that account for multiple sociological risk factors. Furthermore, the early emergence of male-female differences in aggression coupled with the relative stability of the relationship over the life course sheds doubt upon the claim that environmental factors can explicate the relationship between sex and antisocial behavior. In order for socialization factors to be able to explain male-female differences in aggression, they would need to occur shortly after birth and have a major and salient effect on the individual over the life course. Empirical studies have yet to discover an environmental factor that fulfills these criteria and therefore cannot currently support this claim (Beaver and Nedelec 2015).

Given that sociological variables leave a large portion of the variance between male and female offending unexplained, scholars have turned to

biologic and genetic factors to potentially explain such sex differences. Differential neurologic development results in structural brain differences between males and females in utero. These enduring structural differences are responsible for functional disparities in male and female brains that transpire over the life course. These structural and functional discrepancies in male and female brains have been linked to sex differences in an array of phenotypes, including antisocial behavior (Raine 2008; Wright et al. 2015). Variation in androgen production between the sexes may also be partially responsible for sex differences in aggression throughout the life course. Androgens are partially responsible for the differences in neurological development that occur in utero, and increased androgen production in adolescence has been correlated with the increase in antisocial behavior seen during this life stage (Beaver 2009). Empirical research has also begun to discover that differences in genetic makeup between the sexes may also partially explain male-female differences in aggression (Beaver 2009). Biological and genetic differences therefore have the capability of explaining male-female differences in aggression that are evident shortly after birth and continue over time.

Although neurological, hormonal, and genetic factors appear to explain a greater portion of the variance in male-female antisocial behavior than purely environmental factors, a percentage of the variation remains unexplained. Taking into consideration the evidence reviewed here, it seems plausible that the effects of sociological factors enhance the naturally occurring biologic and genetic differences in males and females to create sexual differences in antisocial behavior. That is, biological or genetic risk factors may exist within an individual but remain dormant or underactive until exposed to certain environmental factors (i.e., child abuse). Although research in this area is just beginning to emerge, the limited amount of empirical evidence available demonstrates that genetic factors interact with environmental variables to produce antisocial behavior (Caspi et al. 2002; Raine 2008). Furthermore, research has demonstrated that males possess a greater number of genetic risk factors than females (Vaske et al.

2011) and also report higher rates of environmental criminogenic risk factors (Moffitt et al. 2001).

Future research would benefit from integrating the vast knowledge concerning biological differences between males and females into sociological theories of crime causation. Biosocial factors appear to have the greatest potential for explaining the variance in male-female aggression. Understanding how biological and genetic factors may interact with environmental factors to create disparities in offending behavior between the sexes can lead to public policies of crime control that are more fully informed. For example, programs aimed at changing criminogenic environments and lowering biological risk factors may effectively lower criminal propensity for both males and females. Identifying the causes behind sex differences in crime and aggression can also lead to the creation of effective treatment programs. Much of the available evidence suggests that the influence of criminogenic risk factors vary between males and females, therefore treatment programs would benefit from identifying and focusing on the factors that are most salient for each sex.

Cross-References

- [Female-Perpetrated Violence](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Meta-analysis of Sex Differences in Aggression](#)
- [Male-Male Competition or Male Provisioning?](#)
- [Physical Aggression](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Self-Defense and Female-Perpetrated Violence](#)

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Definition

Some elements of anger proneness demonstrate sex differences.

Introduction

Psychological sex differences have been documented for numerous traits in many cultures. The current debate in the field addresses the magnitude, uniformity, and basis of these differences. Traditionally, psychological sex differences have been attributed to social roles. Evolutionary psychology, however, views sex differences as rooted in genetic variations that have developed through natural selection. According to evolutionary theory, males and females exhibit different behaviors since each had to deal with different challenges in the prehistoric past. For example, physical aggression is more prevalent in males than in females. Archer (2009) suggested that this is a result of an evolutionary cost-benefit analysis. For males, aggression can confer benefits of increased reproduction, which may outweigh the costs of danger and injury. For females, however, aggression bears more severe risks and delivers smaller gains. Unlike physical aggression, Archer (2009) claimed that indirect aggression and anger would not offer a clear benefit for one of the sexes, and therefore, sex differences would not be anticipated (Archer 2009). Archer theorized that while both sexes have reasons for becoming angry, males have stronger reasons for expressing that anger aggressively. As a result, this has led to a sexual selection for aggression, but not for anger (Archer 2009).

S

Sex Differences in Anger Proneness

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Synonyms

Aggression; Hostility; Trait anger

Sex Differences in Anger

Meta-analyses on sex differences in anger have revealed mixed findings. Archer (2004) conducted a meta-analysis of 46 samples that assessed sex differences in the anger subscales of aggression scales. Consistent with his theory, he found a sex difference for physical aggression, but not for anger ($d = -0.003$). A more recent

meta-analysis conducted by Chaplin and Aldao (2013) comprised 77 studies on anger expression in children. This analysis used a wider measurement of anger, including not only scales measuring aggression but also any scale the original authors identified as an anger scale. Contrary to Archer's suppositions (2004), Chaplin and Aldao (2013) found that boys expressed more anger than did girls ($g = 0.10$).

Large-scale studies of anger have also provided mixed results. Kajonius and Johnson (2018) studied the responses of 320,128 Americans to the IPIP-NEO-120 (the open access version of the five-factor model of personality). The anger subscale of neuroticism revealed no statistically significant sex difference for anger ($d = -0.16$, with females scoring slightly higher in anger than did males).

On the other hand, Asgeirsdottir and Sigfusdottir (2015) found different outcomes in their assessment of 8038 Nordic adolescents' anger. They used five anger items based on the Symptom Checklist-90 (SCL-90), a measure of psychopathological symptoms. In their study, girls reported higher levels of anger in four of the five countries studied.

Components of Anger

The reason for these discrepancies may lie in the operationalization of the anger construct. Spielberger was one of the first to assess and define anger (see the historic review of Spielberger and Reheiser 2009). Spielberger distinguished between state and trait anger. State anger was defined as "a psychobiological state or condition, consisting of angry feelings that may vary in intensity...with associated activation of the autonomic nervous system" (Spielberger and Reheiser 2009, p. 281). Trait anger is determined by the frequency that state anger is experienced (Spielberger and Reheiser 2009, p. 281).

In addition to differentiating between state and trait anger, Spielberger theoretically recognized the overlap of three concepts, anger, hostility, and aggression, which he named collectively as AHA! A later psychometric study confirmed that anger comprises a three-factor construct (Martin et al. 2000). The

researchers explored eight self-report anger scales, with 24 subscales, using a sample of 457 American undergraduates, confirming that indeed anger scales measure three factors: anger, hostility, and aggression. Each of these factors has different associations with the Big Five personality traits. Anger is the affective component, linked to neuroticism. Aggression is the behavioral component, related to low agreeableness. Hostility (or cynicism) is the cognitive component, linked to both neuroticism and low agreeableness (Martin et al. 2000).

Sex Differences in the Elements of Anger

This three-factor structure of trait anger did not differ between men and women. When considered separately, the male and female data yielded almost identical three-factor solutions (Martin et al. 2000). These similarities notwithstanding, there were, nonetheless, significant sex differences in the factor scores. Women scored higher than did men on the affective component of anger ($d = 0.40$). This pattern was reversed for behavioral aggression, with men scoring higher than did women ($d = -0.98$). Hostile or cynical cognitions showed no significant sex difference ($d = -0.02$; Martin et al. 2000).

Conclusion

Meta-analyses and large-scale studies have produced mixed results regarding the sex differences in anger. These discrepancies may result from the lack of uniformity in their measurement. It appears that while women score higher on the affective element of anger, men score higher on its behavioral element.

Cross-References

- Anger Proneness
- Recalibration Theory of Anger
- Sex Differences in Aggression
- Sex Differences in Same-Sex Aggression
- Strength and Anger-Proneness

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differences in adult attachment and that these differences may be first evident during middle childhood. Despite the controversy, I would propose that the suggestion that there may be sex differences in attachment should not be surprising. It is well accepted that women and men tend to be socialized differently from birth (Bem 1993) and, as a result, men are typically less emotional and less nurturing than women. Furthermore, there is support that women and men may perceive social interactions differently and consequently behave differently in their relationships. Despite the proposal that attachment representations and gender roles have a joint influence on behavior of adults, sex differences in attachment do not seem to be evident during infancy and preschool years, and there are inconsistent reports of sex differences during the school age years (see Del Giudice 2008 for summary of this research). Furthermore, sex differences in adulthood are not consistently reported but tend to be evident with self-report questionnaire measures, in particular measures of Bartholomew's four-category model. It does seem clear that the ability to detect (or not) sex differences in attachment may be associated with the type of assessment, the power to test for differences, and characteristics of the sample.

Sex Differences in Attachment

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Definition

There is some evidence that men and women have moderately different distributions of insecure adult attachment styles. Generally, men may tend to report higher avoidance and women may tend to report higher ambivalence, but these findings are somewhat inconsistent and controversial.

Introduction

Although controversial, there is some empirical evidence that there may be small to moderate sex

Sex Differences in Attachment

Over the past 40 years, attachment researchers have consistently reported that most individuals in low risk or nonclinical samples, regardless of the age of the participants or method of assessment, are secure. Although there are no sex differences in the proportion of secure and insecure individuals, some researchers have reported sex differences in proportions of the type of insecure attachment. Furthermore, some researchers have proposed that these differences may be adaptive and predictable. For example, Del Giudice (2009) proposed an evolutionary model that, among other things, proposed that women develop insecure-ambivalent attachment in conditions of moderate stress in childhood and avoidant attachment under conditions of high stress whereas men

develop insecure-avoidant attachment when they experience stress in childhood. Interestingly, very little attention has been paid to the effects of the gender of the caregiver on the developing attachment relationship. Mothers typically invest more in the parent-child relationship and are usually a child's primary caregiver. However, it is unknown if this primary attachment is more influential, in particular, in situations where, for example, the attachment relationship with the mother is different than the attachment relationship with the father.

Del Giudice and colleagues have proposed that sex differences in attachment may develop in middle childhood (see Del Giudice and Belsky 2010) although the proposal is somewhat controversial (see Thompson 2010; van IJzendoorn and Bakermans-Kranenburg 2010). Early work measuring infant attachment using the Strange Situation tends not to mention sex differences in attachment; however, early behavioral work consistently reports that, in preschool aged children, insecure males tend to be more aggressive whereas insecure females tend to be more dependent and compliant. These findings are consistent with the observed sex difference that when stressed males tend to engage in "fight or flight" behaviors, females tend to engage in "tend and befriend" behaviors.

There are a few studies reporting sex differences in middle and late childhood and nearly all report a sex difference in the categorization of the insecure children: more ambivalence in females and more avoidance in males. These gender differences have been reported in studies using several different methods of assessment including versions of the Doll Story Completion Task, The Manchester Child Attachment Story Task, and the Coping Strategies Questionnaire. Although some researchers continue to insist that these sex differences are not meaningful, Del Giudice and Belsky (2010) proposed that the life history perspective and neurobiological developmental changes may help to understand why middle childhood may be an important transition with respect to the development of sex differences in attachment.

Del Giudice (2009) proposed an integrated evolutionary model of the development of attachment,

which among other things, may explain how and why middle childhood acts as a transitional stage in both the development of attachment and reproductive strategies. He proposed that this phase of reorganization of attachment may be due to "intrasexual competition in the peer group" and physiological and hormonal changes associated with adrenarche – both contributing to the development of sex differences to improve the adaptation of the insecure child. Although further work is needed to test his model, it builds upon Bowlby's original theory, which was firmly rooted in evolutionary thinking at the time, and provides insights from modern evolutionary theory to explain why attachment researchers may observe sex differences in adult attachment.

Sex Difference in Adult Attachment

Early work using the AAI does not suggest sex differences in attachment, however, as with many studies using interview assessments; the samples were typically small and may not have had sufficient statistical power to test for differences. Bakermans-Kranenburg and van IJzendoorn (2009) summarized the data from over 10,000 AAI interviews addressing issues of base-line proportions in clinical and nonclinical samples, gender distributions, as well as differences in distributions for adolescents and individuals from low SES samples, ethnic minorities, and non-Western countries. Using the AAI four-category classification of a sample of nonclinical mothers ($n=700$) as their baseline, their findings indicated that nonclinical fathers were more likely to be classified as dismissing. Although there were no significant differences with the preoccupied category, despite the large number of interviews in both groups, the authors only had sufficient power to test for large differences between the proportions of individuals categorized as preoccupied. Using the AAI dimensions, which increases the power to test for differences, Simpson et al. (2002) reported that men scored significantly closer to the dismissing end of the activation continuum whereas women scored significantly closer to the preoccupied end.

Although Hazan and Shaver (1987) did not report sex differences in their original article using the three-category measure, researchers consistently report sex differences with Bartholomew's four-category model (see Bartholomew and Horowitz 1991). Bartholomew and colleagues have reported that females and males do not tend to differ on their secure or fearful ratings; however, females tend to score higher than males on the preoccupied scale and lower than males on the dismissing scale. These sex differences are evident when using both Bartholomew's family and peer interviews as well as both the categorical and continuous self-report surveys. Partner- and friend-reports reveal similar sex differences (see also Scharfe and Bartholomew 1994). Interestingly, Schmitt et al. (2003) analyzed the RQ data across 62 countries and reported small to moderate sex differences in dismissing attachment across most cultures – in particular, cultures characterized by low stress and low fertility environments – and concluded that greater levels of dismissingness in males is “near universal.”

The introduction of the ECR and the ECR-R did not include a discussion of sex differences so it is not known whether or not sex differences were tested in the original data (see Brennan et al. 1998; Fraley et al. 2000). Furthermore, there are few researchers who test (or report) sex differences in published work using the ECR or the ECR-R, although it is not clear whether or not there are no sex differences on the two dimensions or that the researchers simply did not test for sex differences; however, there are a few exceptions. For example, in a recent meta-analysis, Del Giudice (2011) reported a significant but small sex difference in that men scored higher on the avoidance dimension and lower on the anxiety dimension. Interestingly, he found that these sex differences were stronger in community samples. Del Giudice suggested that there are consistent sex differences in attachment; however, there are variables such as the distribution and type of the sample, geographic region, the non-normal distribution of the data, unreliability of the measures, and effect of age that may confound the results.

As pointed out by some scholars (see Del Giudice and Belsky 2010), the fact that researchers find sex differences with some measures, and in some samples, and not with other measures or samples is likely meaningful and should not be ignored. As suggested above, it is well accepted that women and men are socialized differently and perceive and behave differently in their relationships and perhaps it would be productive to examine the joint influence of attachment representations and sex role on behavior in relationships. For example, it is well accepted that attachment avoidance is related to a greater number of less-committed relationships for both men and women whereas attachment anxiety is associated with dependency and possessiveness for both men and women. Perhaps a fruitful direction for research – to help to understand the importance of sex differences – would be the examination of those findings in which gender boundaries are crossed. In particular, it may be helpful to examine the research describing relationship characteristics of anxious-ambivalent men or avoidant women. The few studies that have highlighted these unexpected sex differences highlight the importance of these differences in understanding the effects of attachment representations on adult relationships.

There is some evidence that preoccupied or ambivalent attachment for men and dismissing or avoidant women may have a more negative effect on their relationships and well-being. For example, Simpson et al. (1999) reported that highly ambivalent men's relationships (as compared to relationships of other men and all women) were more likely to have ended over a 4-month period suggesting that highly ambivalent men may have less successful relationships. Furthermore, Kanninen et al. (2003) reported that preoccupied men had a heightened affected response to traumatic events and were proposed to be vulnerable to the emotions and distress associated with past traumatic events suggesting that highly ambivalent men may have more difficulty coping with difficult life events. Similarly, Bodner et al. (2014) reported some evidence that, in early adulthood, preoccupied men may experience a significant decline in their reports of the meaning

of life. Consistent with the suggestion that women may develop avoidant attachment under extreme stress, there is also some support that avoidant women may have more difficulty in their interpersonal relationships. For example, Mikulincer and Florian (1999) reported some evidence that avoidant women showed weaker attachment to their fetus and more negative prenatal mental health. Rholes et al. (1999) reported that more avoidant women displayed more anger while waiting for an “anxiety provoking” situation with their partners, and Simpson et al. (2002) reported that more avoidant women provided less support to their partners regardless of his attachment. Although these studies provide some evidence that anxious-ambivalent men and avoidant women have more difficulty in relationships and coping with life events, very few studies systematically examine the differential effects of attachment across gender, and a more comprehensive examination of this issue is needed.

Conclusions

In summary, although the findings are inconsistent and controversial, there is some support that, at least in adulthood, men may tend to report higher avoidance and women may tend to report higher ambivalence. There are, however, incidences where women report higher avoidance and men report higher ambivalence and these findings might be more interesting and productive to understand the importance of sex differences in attachment. As researchers continue to explore this controversial issue, it will be interesting to pay particular attention to the effect when individuals go against the “norm” – what is the effect when the insecure female or male is “different” than what would be expected. I would suggest that both the typical and the atypical sex differences will be informative.

Cross-References

- [Attachment in Adulthood](#)
- [Attachment Theory](#)

- [Individual Variations in Attachment](#)
- [John Bowlby](#)
- [Measurement: Categorical Versus Continuous](#)

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Sex Differences in Attractiveness of Humor

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Synonyms

Attractiveness; Courtship; Humor; Mating preferences

Definition and Introduction

A good (sense of) humor is among the most frequently desired qualities in potential short- and long-term partners, and numerous studies found humor to be an important characteristic that people seek in close others. This entry gives a short overview on why humor is considered to be

among the most attractive traits and also on the role of sex differences, from a theoretical and an empirical view.

Theoretical Suggestions on Why Humor Is Perceived as an Attractive Trait

While humor can be described across several quantitative and qualitative characteristics, we will use the term in a broad sense in this entry and primarily differentiate between humor *production* and *appreciation* (in the sense of responding to a humorous stimulus); for an overview, see Martin and Ford (2018) and Ruch (2007, 2008). Numerous studies have shown that humor plays a role in social life across different social domains (e.g., work vs. romantic life) because people use humor for bonding, cooperation, and maintaining relationships (e.g., by decreasing tension in conflicts). Hence, humor contributes to social interplay and appears to be one of the most desired traits in close partners.

The question *why* humor is valued as an attractive trait in partners has been discussed across two theories. Firstly, *sexual selection theory* (SST) assumes that individual differences in humor appreciation, comprehension, and production signal underlying qualities that are important for sexual selection and mating choices, as they signal the genetic quality that contributes to survival and reproduction. Among others, Miller (2000) argued that producing and understanding humorous content is based on cognitive efforts, which reflect abilities such as intelligence and creativity. This notion found substantial support across studies, as measures of humor production and preferences were positively related to a wide range of psychometric tests of cognitive functions such as verbal, figural, and general intelligence, as well as indicators of creativity (for an overview, see Greengross 2014; Kaufman et al. 2008). In line with the notion of humor being relevant for sexual selection and indicating underlying qualities, one might expect that humor-related traits would be passed on genetically. Initial evidence from twin studies lends support to this view, as shared

genetic variance explains humor appreciation to an extent that cannot be traced to environmental influences (e.g., Weber et al. 2014; see also Kaufman et al. 2008). Finally, positive relationships among intelligence, creativity, and humor abilities (i.e., producing humorous content) and their unique relationships with mating success support SST (e.g., Greengross and Miller 2011). Overall, the literature supports the notion that humor is related to important qualities that have reproductive value (i.e., intelligence, creativity; also referred to as *genetic quality*).

In SST, sex differences are emphasized. Men are expected to engage in producing humor to signal their humorous qualities, whereas females evaluate men's humor. Women participate in courtship by means of their responses to men's humor: namely, they signal romantic interest by appreciating men's humor attempts (e.g., by openly displaying appreciation through laughter). Moreover, it has been suggested that men use humor for intrasexual competition, when it is used to gain status in comparison to other men in order to attract the attention of a potential female partner.

Alternatively, Li and colleagues (2009) proposed the *interest indicator model* (IIM), which assumes that humor is a means of communicating mating interest *after* attraction to a potential partner is established. It has been observed in animals that a playful and humorous interaction (i.e., *play face*) creates an interpersonal environment in which actions and communication are of low seriousness. Based on this notion, Li et al. argue that using humor can convey romantic interest within such a safe environment and can save face in case of rejection by the partner. Therefore, the IIM would predict that humor does not signal underlying qualities of cognitive ability but that indicators of intelligence (e.g., engaging in a meaningful conversation) would predict mating success independently from humor. Moreover, the IIM assumes no sex differences in the usage of humor and as an indicator of interest it is not limited to the romantic domain (e.g., it also occurs with colleagues at work). While initial evidence supports the notions of the IIM, further research is warranted.

Major Findings on Sex Differences

The role of humor in courtship has been studied empirically using numerous methods since the 1950s. For example, analyses comprised people's rankings of desired characteristics and behavioral acts (e.g., "display a good sense of humor"; "appreciating his/her humor") for different types of relationships (e.g., short-term vs. long-term partners), interactions in the laboratory (e.g., speed-dating), reactions to scenarios and vignettes displaying fictitious partners, or the analysis of adverts and profiles on dating platforms in online and print media. An overview of key studies on the topic, which aims to give a short overview of important studies in the field, sample sizes, the employed methods, and key findings, can be found under osf.io/jxkg8/.

Studies examining mate preferences by asking people what attributes they desire in romantic partners have shown that "(good sense of) humor" is ranked among the most important qualities independently from sex. This finding has also been replicated numerous times since the 1950s and across methods: for example, when using economic games in which participants can distribute money to attributes in a potential partner according to what they view as important. Moreover, this finding is robust across different types of relationship-partners (e.g., dating-, short-term, and long-term partners) and sexual preferences (homo- and heterosexuality). People also report that displaying a good sense of humor is perceived as a successful tactic to attract a potential partner.

While no robust sex differences exist for desirability rankings when humor is treated as a broad trait, the distinction between *appreciating* and *producing* humor reveals differences in what men and women prefer. In line with expectations derived from SST, females strongly prefer men who produce humor, with robust effect sizes across relationship types varying from loose (e.g., one-night stands) to strong bonding (e.g., marriage partner). Furthermore, there is evidence that men prefer females who appreciate their humor attempts, but findings are mixed for this association because the magnitudes of effects vary across studies. Interestingly, women also prefer

men who appreciate their humor attempts but only when men are also high in humor production. Thus, it has been suggested that humor appreciation by men is seen as a “luxury” addition, whereas humor production is a necessity for females’ attraction toward men. When extending research toward individual differences in dealing with ridicule and laughter, initial evidence shows that females who enjoy laughing at others are with male partners who engage in making others laugh, whereas the association is negligible for females’ dispositions to engage in making others laugh and men’s joy of laughing at others.

When testing SST assumptions in laboratory experiments, findings were in the expected direction but tended to yield small effect sizes. Generally, men were more inclined to produce greater quantities of humor than women, and women signaled greater appreciation in order to display romantic interest compared with their male counterparts. Overall, interaction studies support the sex effects of humor production, but findings for sex differences in humor appreciation and its relation to signaling dating interest are mixed, as some studies showed no association with romantic interest outcomes and/or differences in females’ and males’ usage. Moreover, studies using naturalistic interaction settings show that *shared* laughter may be an even better predictor of dating interest than one-sided appreciation, as it might suggest that both partners prefer and enjoy similar humor (i.e., quality and quantity).

Another line of research has studied the occurrence of desire toward producers and appreciators by analyzing dating ads. Findings from this line of research also support the notion that men are inclined to offer humor whereas women are more frequently described as seeking humor in men, although it has to be noted that findings for appreciation were less robust.

Conclusion

The literature in this field has generated two main findings. Firstly, humor is viewed as an attractive trait in others and is strongly desired,

independently of gender. This finding is stable and has been replicated well over the last 60 years. Secondly, distinguishing between humor appreciation and humor production is related to sex differences in perceptions of attractiveness. The majority of findings support the notion of SST, as females are attracted to males who produce humor whereas men prefer women who engage in appreciating their humorous attempts. However, it must be noted that findings on humor appreciation and effects of sex differences are less robust than those on humor production. Overall, SST gives a theoretical framework for the study of sex differences in attractiveness of humor.

Further research is needed to understand the role of humor in courtship. For example, one might assume that more fine-grained analyses of sex differences in the quality and quantity of humor attempts (cf. Ruch 2007, 2008; Ruch et al. 2018; see also Martin and Ford 2018) are differentially related to perceptions of attractiveness. Moreover, preferences of humor producers and appreciators may have interactive effects on mating outcomes (e.g., romantic interest).

Cross-References

- Charles Darwin: Theory of Sexual Selection
- Humor
- Humor as a Signal of Sexual Interest

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Sex Differences in Cognitive Development

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Synonyms

Intellectual differences between boys and girls, gender characteristics of cognition during childhood

Definition

The differences between boy and girls in cognitive development

Introduction

A diversity of studies in psychology and neuropsychology has approached the question of gender differences in cognitive abilities (e.g., Bjorklund and Causey 2017). Three major gender differences in cognitive abilities have been reported: (1) higher verbal abilities in women, (2) higher spatial abilities in men, and (3) higher arithmetical abilities in men. However, these three differences may be collapsed in only two as differences in calculation abilities may be the result of men's superior spatial abilities (Geary 1996).

Women usually score higher in a variety of verbal tests (e.g., Burton et al. 2005). They also present a faster language development (Berglund et al. 2005) and have a larger vocabulary, more accurate speech production, and greater fluency (Mildner 2008).

Gender Differences in Language Abilities

Despite the aforementioned reports and numerous publications in the same direction, gender differences in language abilities remain a controversial topic, as there are also judicious studies questioning the presumed higher verbal abilities in women. A meta-analysis of 165 language studies involving both children and adults and including a broad range of language tests (vocabulary, analogies, anagrams, reading comprehension, speaking or other verbal communication, essay writing, the Scholastic Aptitude Test (SAT) - Verbal, and general verbal ability tests) was conducted. Results were mixed: 44 (27%) of the studies reported that females outperformed males, 109 (66%) found no significant gender differences, and 12 (7%) found males outperforming females. The authors concluded that “the magnitude of the sex difference in verbal ability is currently so small that it can effectively be considered to be zero” (Hyde and Linn 1988, p. 64). An extensive review of gender differences in language among children concluded that “A small but consistent female advantage is found in early language development, but this gender difference

seems to disappear during childhood” (Wallentin 2009, p. 181). Reynolds et al. (2015) found in a sample of children and adolescents ranging from ages 7–19 years that girls scored higher on spelling and written expression.

In adults, sex differences in verbal abilities and in language-related brain structure are not readily identified. If they exist, they are not easily picked up with the current research methods used today (Wallentin 2009). Gender differences in language have also been reported during aging. It has been also observed that spontaneous language in general decreased with age; however, a significant interaction-effect between age and gender was observed. A steady and pronounced spontaneous language decrease across age-groups was observed in males. However, only mild differences across age-groups were found in females. Interestingly, the ratio among different phrase elements (nouns, verbs, adjectives, and grammatical connectors) was found to be very uniform across age, educational level, and gender groups (Ardila and Rosselli 1996).

There are also publications reporting boys outperforming girls in language skills. For example, (Ardila et al. 2011) analyzed gender differences in cognitive test performance among a large sample of Latin-American children from continuous age groups (5–16 years). Boys outperformed girls in oral language (language expression and language comprehension). However, gender accounted for only a very small percentage of the variance (1%–3%).

Why Gender Differences in Cognitive Development?

Some authors have emphasized that gender differences may arise from the dispersion in cognitive abilities between men and women rather than just the mean gender differences, for example, based on analyses of mental test scores from different studies. Although average sex differences have generally been small and stable over time, the test scores of males have consistently shown greater variance. Moreover, except for tests of reading comprehension, perceptual speed, and

associative memory, males typically outnumber females substantially among high-scoring individuals (Hedges and Nowell 1995).

The origin of gender differences in cognitive abilities is not clear yet, though it has been assumed that both biological and environmental factors contribute to the variation that has been demonstrated between males and females. Among the biological factors identified, differences in neurological structure and function have been pointed out (e.g., Blanch et al. 2004). Some authors have also found that hormones are associated with certain aspects of brain differentiation (e.g., Burton et al. 2005). Others have suggested that boys’ brain activity measure using functional magnetic resonance imaging (fMRI) differed from that of girls’ depending on individual cognitive process (Asano et al. 2014).

Gender differences have been attributed to environmental factors associated with changes in living conditions and cognitive stimulation taking place over time. Some studies investigating math performance in adolescents have found that gender differences favoring boys are smaller in more gender-equal societies (Guiso et al. 2008; Else-Quest et al. 2010), suggesting that gender equity positively affects girls’ math performance (Weber et al. 2014). In the United States, gender differences in mathematics performance are declining. More recent data indicate that the gender difference in math achievement has narrowed (Else-Quest et al. 2010). A study of statewide mathematics tests administered between 2005 and 2007 for Grades 2–11 did not find the increased gender gap in adolescence found with earlier data (Hyde et al. 2008). Moreover, reviewing evidence from research with infants and preschoolers, Spelke (2005) concluded that gender similarities are the rule in the development of early number concepts. However, gender differences could emerge in the high school years particularly for complex problem-solving students favoring males (Lindberg et al. 2010).

Some gender differences in the brain organization of language, including differences in connectivity, have been suggested. Evidence of cross-frequency dependence between functional networks in resting state fMRI (rs-fMRI), which

was associated to the subject gender have been found (Yaesoubi et al. 2017). Others authors utilized resting state fMRI (rs-fMRI) and graph theoretical approaches to investigate the hemisphere- and gender-related differences in the functional networks of the adult brain functional networks (Tian et al. 2011). These authors found was that males lean towards being more locally efficient in their right hemispheric networks, whereas females tended to be more locally efficient in their left hemispheric networks. It has been also suggested that male brains are optimized for intrahemispheric communication and female brains for interhemispheric communication. The developmental trajectories of males and females diverse at a young age, demonstrating wide differences during adolescence and adulthood (Ingallhalikar et al. 2014).

Conclusion

It has been frequently reported that girls present a faster language development, but boys outperform girls in the development of spatial abilities. Some authors have found that these differences are also observed during adulthood, and even during normal aging. However, the magnitude of these differences is small and several studies have been unable to support them. Recent reports have found that the gap in numerical abilities between boys and girls reported decades ago has narrowed in recent years.

Cross-References

- [Age of Child](#)
- [Cognitive Changes in Adolescence](#)
- [Development of Sex Differences](#)

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Sex Differences in Commitment Skepticism

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Definition

Women are more prone than men to show commitment skepticism bias, which is a tendency to believe people are unwilling to commit to a long-term intimate relationship.

Women are more likely than men to show a *commitment skepticism bias*, which is a tendency to believe that potential mates are unwilling to commit to a long-term intimate relationship (e.g., Haselton and Buss 2000). Error Management Theory has been used to explain these sex differences. Generally, Error Management Theory suggests cognitive biases towards either making a Type I error (believe X when X is not true) or Type II error (believe “not X” when X is true) could have evolved if one type of error, relative to the other, conferred a benefit or minimized a cost (Johnson et al.

2013). Assumptions about the intentions of mating partners could lead to one of two types of errors: believing a person would be committed to a long-term relationship when the person is not (Type I error) or believing a partner would not be committed to a long-term relationship when they are (Type II error). Because the sexes are different on the cost-benefit ratio of these errors, we would expect the sexes to be different on how likely they are to commit either error.

Because women’s minimum obligatory parental investment is higher than men’s, women can increase their reproductive success by securing a mate with ample resources and a willingness to share in parental investment over the long-term. Thus, women may be more prone to making a Type II error (i.e., show commitment skepticism) because incorrectly thinking a potential partner will commit to a long-term relationship is more costly than incorrectly thinking a potential partner will not commit to a long-term relationship. Men may not show this tendency because their reproductive strategy can maximize fitness through mate number, so incorrectly predicting a partner’s level of commitment is not as costly.

Empirically, one study found a sex difference in commitment skepticism bias (Haselton and Buss 2000), and another study found that such skepticism was only true among premenopausal women (Cyrus et al. 2011). This latter finding is consistent with Error Management Theory because mistaking a potential partner’s long-term commitment would be most costly at an age when raising offspring was likely. A third study also found results consistent with this commitment skepticism bias, where women’s ratings of men’s commitment were lower than men’s self-report commitment rating (Henningsen and Henningsen 2010).

Cross-References

► [Error Management Theory](#)

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Sex Differences in Costs and Benefits of Mate Poaching

► Costs and Benefits of Mate Poaching

Sex Differences in Crying

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Synonyms

[Sex differences in Lacrimation](#); [Sex differences in Lachrymation](#); [Sex differences in Sobbing](#); [Sex differences in Weeping](#); [Gender differences in Lacrimation](#); [Gender differences in Lachrymation](#); [Gender differences in Sobbing](#); [Gender differences in Weeping](#)

Definition

Differences between males and females in the frequency and duration of increased tearing of

the eyes and other associated behaviors in response to internal emotional states.

Introduction

It is well established that, apart from reacting to chemical or physical irritants, adult females shed tears more often than adult males. This crying occurs in response to emotional states, sometimes induced by external events. Here, we will examine the extent of this sex difference and its possible explanations.

Sex Differences in Frequency and Duration Across the Life Span

Infants produce cries from birth but seem to weep only after 3 months of age. Because the function of signaling distress is reasonably the same throughout infant- and toddlerhood, the early absence of tears probably reflects an arbitrary anatomical or developmental age effect. Inflicting pain through the PKU test yields no sex difference in crying, but girls exhibit stronger facial expressions of pain (Guinsburg et al. 2000). Boys are somewhat overrepresented among the approximately one fifth of all children that are perceived by their parents to cry excessively. In a representative population sample, 22.7% of boys and 19.3% of girls cried excessively during the first 3 months, while 10% of boys and 6.6% of girls did so after 3 months (Wurmser et al. 2001).

Males begin to cry less during childhood. Females' values did not change across 11 to 16 years of age but were essentially constant at having cried 4 times in the previous 4 weeks, while across the same age interval, males dropped from about 2.5 to 1 times per 4 weeks (Van Tilburg et al. 2002). Among 9–13-year-old children ($M \sim 10.6$), females self-rated having cried 3.8 times and males 2.9 times in the previous 4 weeks (Jellesma and Vingerhoets 2012).

Adulthood exhibits the largest sex difference in crying. A review of 14 studies concluded that

females exhibit higher levels of all crying-related behaviors (Vingerhoets and Scheirs 2000). Studies report that females cry between 2.5 and 7.4 times more often than males, with effect sizes from around 1.0 and up. It has been suggested that changing sex roles and increased sex equality across the last 50 years would have diminished the sex differences in crying, but both frequency, intensity, and reasons for crying were similar across a 15-year period (Lombardo et al. 2001). More recent studies also report similar sex differences which replicate across 37 countries with effects sizes of 1.11 for crying proneness and 0.94 for crying frequency (van Hemert et al. 2011). Among people in their late 60s, females reported having cried on average 31.1 times in the last 12 months, as compared to 16.3 times for males (Hastrup et al. 1986). This ratio of 1.9 is less than half the typical sex ratio for young and middle-aged adults.

Sex Differences in Types of Crying and Self-Reported Reasons for Crying

Compared to males, females more often exhibit flowing tears, sobbing, and convulsive breathing, while males more often exhibit watery eyes (► “Types of Crying”). More than three times as many females than males report crying because they are angry and more than twice as many because they feel helpless. Crying and anger are in fact negatively correlated in males, but positively in females (Choti et al. 1987). In contrast, males’ crying was more than twice as often provoked by positive events, such as intense joy (Bylsma et al. 2008). Although sex differences in crying are large and consistent, the results are more mixed regarding crying-evoking situations. For example, no sex differences were found in response to highly evocative events like the death of someone close (Williams and Morris 1996).

Crying is correlated with state traits such as neuroticism and extraversion and with more transient states such as depression (► “Crying”) (Vingerhoets et al. 2009), all of which are more prevalent in females. The essence of neuroticism

is “feeling negative feelings strongly,” and it has been suggested that there is a negative aspect even to joyful crying, because it involves being overwhelmed and feeling a loss of control or because intense happiness reminds a person that they have been unhappy in the past (Vingerhoets et al. 2009).

Causes of Sex Differences in Crying

Although adult females cry more than adult males, there remains debate over why this should be the case. Social conditioning is a common explanation in the literature: crying and other emotional expression are encouraged in females and discouraged in males. Several arguments are advanced in support of these hypotheses: attitudes are less favorable toward crying males than crying females, males report more shame and discomfort when crying, sex-typical crying behaviors are associated with individual differences in masculinity and femininity (Ross and Mirowsky 1984; Lombardo et al. 2001), and the sex differences emerge when socialization and the desire to impress and attract the other sex are elevated in adolescence. However, females’ attitudes are quite similar toward male and female criers (Cretser et al. 1982), both sexes have similar attitudes when the context is taken into consideration (Labott et al. 1991), and that the effect size of the sex difference in experienced shame is only about one fifth that of crying itself (Becht and Vingerhoets 2002).

A simpler explanation is that crying-related behaviors constitute a sex-dimorphic adaptation, partly mediated by hormones. The emergence of sex differences in crying in puberty and their decrease in late adulthood is thus consistent with changes in male testosterone levels across the life span (Harman et al. 2001) and with females crying four times as much during the hormonal surge before and during menses compared to the intermenstrual period (Horsten et al. 1997; Moos 1968). A social explanation would predict that there be considerable variation across cultures and countries by chance, as social norms regarding crying are intrinsically arbitrary. It would also

predict that countries with less sex equality have larger sex differences. However, every 1 of 37 countries surveyed exhibited higher crying proneness and frequency for females, and sex differences tended to be larger in more developed and sex-egalitarian countries (van Hemert et al. 2011). The evolutionary perspective would predict that females, by making huge and self-debilitating investments in their offspring, at the same time as being physically weaker, would be considerably more prone to cry inasmuch as it attracts help and staves off aggression (Hendriks et al. 2008). Such a strategy would be further motivated by the fact that female exogamy entails dependence upon non- or distant kin (e.g., Madison 2009) and may rationally be complemented with the ability to convincingly “fake cry” in order to induce sympathy and assistance (Vingerhoets et al. 2016).

Conclusions

Females tend to be more concerned about the happiness of everyone in the group and about the feelings of others. In prehistory, this would have permitted them to bond more strongly with their children, be more loving mothers, and be better able to persuade others to assist them. It would thus be more beneficial for females to be able to more clearly express their emotions, in order to signal the need for help or support and reduce the possibility of conflict. Inasmuch as there is a degree to which crying signals a loss of control, we might speculate that it would not be an attractive quality in males in terms of sexual selection, with females being attracted to males with higher social capital (Buss 2016). Thus, the sex differences would have evolved to be what they are today under the Darwinian conditions prevalent until the Industrial Revolution, where social status heavily predicted completed fertility (Dutton and Woodley of Menie 2018, Chapters 3–4). At least, this would seem to be the most parsimonious explanation for the multifaceted sex differences in crying behaviors and attitudes toward them.

Cross-References

- [Communication, Cues, and Signals](#)
- [Crying](#)
- [Manipulation and Dishonest Signals](#)
- [Sex Differences in Aggression](#)
- [Sex Differences in Emotional Communication](#)
- [Sex Differences](#)
- [Types of Crying](#)

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Sex Differences in Cyber Bullying

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Synonyms

Cyber harassment; Cyberaggression; E-bullying; Electronic bullying

Definition

Cyberbullying has been defined as “an aggressive, intentional act carried out by a group or individual, using electronic forms of contact, repeatedly and over time against a victim who cannot easily defend him or herself” (Smith et al. 2008, p. 376). In all respects, save the use of electronic media, it is similar to traditional, in-person forms of bullying. All forms of bullying, including cyberbullying, are not reactive, impulsive actions, but rather are intentional, planned, and functional behaviors (Volk et al. 2014). Like traditional bullying, cyberbullying consists of direct and indirect forms including verbal, such as emailing, texting, or calling the victim to derogate or threaten them, and relational forms, such as exclusion from groups of friends, ignoring victims, or spreading rumors (Kowalski et al. 2014). However, cyberbullying can also include specific acts, such as posting embarrassing pictures or videos of others, or using deception to impersonate or pose as someone else, which fall outside of the domain of traditional bullying.

However, some investigators question whether repetition is a necessary component of cyberbullying, in light of evidence that single incidents may be harmful, especially cases that involve embarrassing or hurtful information being posted on the internet, which may be accessed by a large audience over a long, indefinite period of time (Volk et al. 2014). Furthermore, investigators have queried how the concept of a power imbalance between the aggressor and the victim – a key element in the definition of all forms of bullying – applies to cyberbullying, given that domains of power such as physical strength and popularity have clearer applications in traditional forms of bullying, including physical or relational varieties (Volk et al. 2014). Conceptual complications include whether aggressive acts using technology could be considered bullying in the absence of a clear power imbalance when anonymity afforded by pseudonyms makes these attacks difficult to defend against, and conversely, whether physical strength or popularity may affect the power balance when in-person retaliation is possible. As with other forms of aggression, Volk

et al. (2014) have concluded that aggressive acts using electronic devices should be considered cyberaggression rather than cyberbullying if an imbalance of power favoring the aggressor cannot be established.

Introduction

In line with evolutionary psychological research on traditional bullying (e.g., Vaillancourt 2013), sex differences in cyberbullying may be conceptualized with regard to theories of sexual selection and differential parental investment. In general, adolescent males are more likely to participate in bullying overall and to utilize direct forms of traditional bullying, such as physical and verbal acts, whereas females prefer using indirect, relational forms of bullying (Wang et al. 2009). According to parental investment theory, females' greater obligatory parental investment in their offspring results in their being less willing to compete for mates using risky physically aggressive strategies, in order to avoid physical harm (Vaillancourt 2013).

Sex differences in traditional bullying have also been explained with the theory of sexual selection, which is based on adaptations that have increased successful mating (Vaillancourt 2013). According to the theory of intersexual selection, the selection of mates is based on preferences for qualities that are thought to be indicative of their ability to produce, protect, and support offspring. From this perspective, females typically prefer potential mates who display strength, masculinity, and social status, as these qualities are thought to be representative of their ability to provide for and protect their partner and potential offspring. In contrast, males prefer physical ideals including youthfulness and a favorable hip-to-waist ratio, as well as sexual fidelity in potential partners, as these qualities are believed to be representative of the female's fertility and desire to mate exclusively. Thus, direct forms, such as physical bullying, would not appear adaptive for females, as it would not display preferred mating qualities and may incur large costs through exposure to retaliation. However, physical

bullying would enable males to display attractive qualities at minimal cost, as the weaker victim is unlikely to retaliate.

Relatedly, the theory of intrasexual competition indicates that same-sex individuals compete for access to resources and for desirable mates (Vaillancourt 2013). Bullying may facilitate intrasexual competition, in that physical forms may be used to make oneself look attractive in comparison to rivals, while relational and verbal forms can be a vehicle for derogating sexual competitors to reduce their appeal to potential mates. For example, females typically derogate their rival's attractiveness and sexual fidelity, whereas males tend to target their rival's physical abilities and resources (Vaillancourt 2013).

Consistent with theories of sexual selection and differential parental investment, research on traditional bullying has shown that females prefer nonphysical forms of bullying, particularly relational aggression, are slightly but significantly more likely than males to engage in relational aggression, and tend to direct relational aggression toward female peers (Vaillancourt 2013). In addition, relational aggression is associated with reproductively relevant outcomes, such as perceived popularity, dating, and sex, more strongly and consistently for females. In contrast, relational victimization reduces perceived attractiveness and dating onset only for females and places females at greater risk than males for negative outcomes, including internalizing problems and suicidal ideation and attempts, which are markers of low fitness and which reduce willingness and ability to engage in intrasexual competition (Vaillancourt 2013). Finally, females but not males who pose threats as rivals in intrasexual competition, due to being physically attractive, dressing provocatively, or having had more sexual partners, are more likely to be relationally victimized (Vaillancourt 2013).

Although research on cyberbullying from an evolutionary perspective is sparse, some findings are consistent with those for traditional bullying in suggesting that it may be used as a tool for intrasexual competition. For example, many incidents of cyberbullying occur within a dating relationship context, predominately as a result of

breakups or envy/jealousy (Hoff and Mitchell 2009). Furthermore, as with traditional bullying, youth who engage in cyberbullying in early adolescence are perceived by their peers as popular (Wegge et al. 2016).

Thus, several sex differences in cyberbullying may be predicted in light of sexual selection and differential parental investment theories, and previous evolutionary psychological research identifying sex differences in traditional bullying. Specifically, the following would be predicted: (1) females but not males would perpetrate and be victimized by cyberbullying more than physical bullying; (2) females would perpetrate and be victimized by cyberbullying more than males; (3) females would derogate rivals' physical attractiveness and promiscuity whereas males would impugn rivals' physical strength and masculinity; (4) females should experience reproductively relevant outcomes more than males as a function of cyberbullying; and (5) females victimized by cyberbullying should experience more negative outcomes than males.

Sex Differences in Cyberbullying

The evidence is inconsistent with hypothesis 1. Contrary to this prediction, research suggests that both sexes use physical bullying more than cyberbullying (Wang et al. 2009). Furthermore, similar percentages of females experience physical and cyber victimization (Wang et al. 2009). Unlike relational bullying, which is usually indirect and covert, cyberbullying may place perpetrators at greater risk of experiencing retaliation because messages sent through email, texts, and various social media are not typically anonymous. In this sense, it may not be a safer alternative to physical bullying.

Research provides mixed evidence regarding hypothesis 2. Although research in this area has been inconsistent, a recent meta-analysis found that males were significantly more likely than females to cyberbully, albeit with a small effect size ($r = 0.04$; Barlett and Coyne 2014). This finding is concordant with research showing that males and females do not differ greatly in their use

of nonphysical traditional bullying (Wang et al. 2009). Female preferences for less risky, nonphysical forms of bullying do not preclude males from taking advantage of nonphysical bullying options such as cyberbullying, especially given evidence that it yields adaptive outcomes, such as perceived popularity, for them as well (Wegge et al. 2016). Furthermore, it appears that age moderates the relation between sex and cyberbully status. Females were found participate in cyberbullying more often than males in early adolescence, with perpetration rates becoming comparable around age 11. Males become more likely to engage in cyberbullying in later adolescence (Barlett and Coyne 2014). However, a recent meta-analysis has suggested that females are more likely to be victimized by cyberbullying than are males (Hamm et al. 2015), consistent with expectations. Moreover, consistent with parental investment theory, males are more likely than females to physically retaliate in person when victimized by cyberbullying, whereas females are more likely to ignore it, avoid using technology, retaliate with negative cyber messages, or report the incident to adults (Hoff and Mitchell 2009).

In support of hypothesis 3, males using cyberbullying against same-sex rivals typically derogate their sexual orientation or physical capabilities, whereas females are likely to insult the physical appearance and reputation of same-sex rivals (Hoff and Mitchell 2009). Thus, as with relational bullying, male and female perpetrators of cyberbullying appear to target cross-sex mate preferences, possibly to reduce the appeal of rivals in intrasexual competition for mates.

Findings are not consistent with hypothesis 4, as cyberbullying predicts higher perceived popularity for both sexes (Wegge et al. 2016), providing preliminary but sparse evidence that the adaptiveness of cyberbullying is not sex specific. However, the findings of Kowalski et al. (2014) support hypothesis 5, as depression was predicted by cyber victimization in female adolescents but not males. Consistent with parallel evolutionary research on relational victimization (Vaillancourt 2013), females but not males experience internalizing problems as a result of

cyber victimization, which may reduce their willingness or ability to engage in intrasexual competition.

Conclusion

In conclusion, research indicates that there are important sex differences in cyberbullying. Consistent with evolutionary psychological theories of sexual selection, parental investment theory, and previous evolutionary studies on traditional bullying, cyber victimization was more common amongst females; the derogatory content of cyberbullying corresponds to cross-sex mate preferences, and the link between cyber victimization and internalizing problems, a marker of low fitness, is stronger for females. Conversely, cyberbullying is used by females less than physical bullying, and positively associated with perceived popularity for both sexes, inconsistent with evolutionary theory and previous research. Further research is needed, however, as there are few studies specifically examining cyberbullying from an evolutionary perspective.

Cross-References

- ▶ Ability and Willingness of Victim to Retaliate
- ▶ Access to Resources
- ▶ Adaptation
- ▶ Adaptation and Natural Selection
- ▶ Aggression
- ▶ Aggression for Sexual Access
- ▶ Antisocial Behavior
- ▶ Appearance/Beauty in Girls
- ▶ Benefit Provisioning
- ▶ Bullying
- ▶ Charles Darwin: Theory of Natural Selection
- ▶ Charles Darwin: Theory of Sexual Selection
- ▶ Competition for Resources Desired by Females
- ▶ Cost-Benefit Analysis
- ▶ Costs of Aggression
- ▶ Cyberbullying
- ▶ Dating
- ▶ Defending Against Attack
- ▶ Depression
- ▶ Derogation of Attractiveness
- ▶ Derogation of Attractiveness Among Women (Intrasexual Rivalry)
- ▶ Derogation of Promiscuity
- ▶ Derogation of Promiscuity Among Women
- ▶ Derogation of Rivals
- ▶ Development of Aggression
- ▶ Development of Sex Differences
- ▶ Differential Parental Investment
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Female Mate Choice
- ▶ Female Mate Choice (Intersexual Selection)
- ▶ Female-Female Competition
- ▶ Indirect Aggression
- ▶ Intersexual Selection
- ▶ Intrasexual Competition Between Females
- ▶ Intrasexual Male Competition
- ▶ Intrasexual Rivalry Among Men
- ▶ Intrasexual Selection
- ▶ Mate Value
- ▶ Maternal Investment
- ▶ Men Riskier, More Aggressive
- ▶ Men's Mate Preferences
- ▶ Observed Mating Behavior and Women's Long-Term Mating
- ▶ Parental Investment
- ▶ Parental Investment and Sexual Selection
- ▶ Parental Investment Theory
- ▶ Paternal Investment Relative to Maternal Investment
- ▶ Physical Aggression
- ▶ Relational Aggression
- ▶ Reproductive Benefits Must Outweigh Costs
- ▶ Reputation as a Context for Men's Aggression Against Men
- ▶ Resource Competition
- ▶ Risky Behavior
- ▶ School Bullying
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ Sex Differences in Aggression
- ▶ Sex Differences in Human Mate Preferences (Buss, 1989)
- ▶ Sex Differences in Same-sex Aggression
- ▶ Sexual Conflict and Sex Differences in Parental Investment
- ▶ Sexual Selection
- ▶ Sexual Selection in Evolutionary Psychology

- Social Aggression
- Social Consequences of Initiating Gossip
- Social Dominance and Sexual Access
- Status Competition and Peer Relationships in Childhood
- Women's Mate Preferences
- Women's Use of Direct versus Disguised Social Aggression
- Youth and Fertility

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Sex Differences in Death by Filicide

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Synonyms

Child abuse; Child murder; Filicide; Gender differences; Homicide; Parent(s); Victim

Definition

Filicide is defined as the deliberate act of a parent, stepparent, or parental figure killing their own child. Subcategories of filicide include neonaticide, when the child is killed within the first 24 h of its life by his or her parents, and infant homicide (sometimes infanticide), although in some countries the term “infanticide” only applies to the mother and has medicolegal implications.

Introduction

Filicide is a multifaceted phenomenon with various causes and characteristics (Bourget et al. 2007). It was first studied from an evolutionary perspective by Daly and Wilson in the 1980s and 1990s. As early as 1985, links were found between child abuse and the child not living with both parents. This led to an investigation of filicide, which looked at the differences between genetic parents and stepparents. Studies have shown that children are more likely to be killed by their stepparents than by their genetic parents. The literature on filicide also looks at the sex differences of those who commit filicide. Research focuses mainly on mothers, as fathers are less often considered as the perpetrators in filicide cases, and this is reflected in the amount of literature on the topic (West 2007). Sex differences in becoming victims of filicide have also been studied, although the current body of research available is very small.

Sex Differences in Perpetrators of Filicide

The main literature within the topic of filicide studies sex differences in biological parents. Most of the research has focused on the mothers and fathers individually; however, there is far more existing literature on maternal filicide than paternal filicide (West 2007).

Many studies have found that mothers commit filicide more often than fathers (e.g., Resnick 1969). This seemingly high number of maternal filicides may however be due to media bias or because neonaticides are included in some studies which considerably raises the number of maternal filicides (Bourget et al. 2007). Other research has suggested that paternal filicide is as frequent (e.g., Bourget et al. 2007) or possibly even more frequent than maternal filicide (e.g., Bourget and Gagne 2005). This is supported by Lucas et al. (2002), who found that out of 32 filicide cases within the United States Air Force, the perpetrator was male at least 75 % of the time. Bourget and Gagne (2005) found similar results after studying 77 cases of paternal filicide between 1991 and 2001 in Quebec.

In a study conducted in England and Wales, 2660 cases of infant filicide between 1974 and 2003 were analyzed, and it was found that fathers were responsible for 50 % of the cases, whereas mothers were only responsible for 31 %, with stepparents accountable for 8 % (Flynn et al. 2007). In 2013, Flynn, Shaw, and Abel conducted a very similar review looking at filicide and child homicide cases between 1997 and 2006. They suggested that fathers were responsible for a significantly higher number of filicides than mothers, with a male to female ratio of 2:1.

Mothers were found to be almost always responsible for the deaths of neonates (Resnick 1970). Mothers were also more likely than fathers to kill within the first month of their infants' lives (Flynn et al. 2007). Fathers were overrepresented in cases where the child was older than 4 weeks, with fathers being the most frequent perpetrators of filicide in later childhood (Bourget et al. 2007).

On average, victims in paternal filicide cases were generally older than those in maternal filicide cases as fathers are rarely responsible for neonaticides (West 2007).

Most research on paternal filicide have had limited samples, which doesn't allow for much generalizability (Bourget et al. 2007). One study with a larger sample showed several characteristics that seemed to occur frequently in cases of paternal filicide (Bourget and Gagne 2005). First, violence and a history of family abuse were recurrent, where more than a quarter (27 %) of the fathers had a history of repeated violent behavior. This violence is reflected in the method of killing which was consistently violent across the literature, with the most common method being a firearm (34 % of the time) and the second most frequent method being battery (22 %) (Bourget and Gagne 2005). Resnick (1969) found head trauma to be the most common method of filicide, which occurred in 38 % of the paternal filicide cases. Flynn et al. (2013) found the most frequent method of filicide to include multiple injuries, skull fractures, and shaking (43 %), with 25 % of the perpetrators having previous convictions of violence, fathers significantly more than mothers. Several life stressor factors were present preceding the offense (Marleau et al. 1999), with a large number of paternal filicides occurring after ruptures in the marital relationship (40 %) (Bourget and Gagne 2005). Being separated at the time of the crime has also been shown to be a predisposing characteristic (e.g., Lucas et al. 2002). Psychosis was found to be a common factor in men who commit filicide (West 2007) with studies showing it to be present between 30 % and 40 % of the time in several studies (30 %, e.g., in Bourget and Gagne, 2005, and 40 % in Marleau et al. 1999). Cases of filicide-suicide also had quite high rates of around 60 % (e.g., Marleau et al. 1999).

The existing research on maternal filicide is wider and looks at the crime from a variety of different perspectives (West 2007). Friedman, Horwitz, and Resnick's critical analysis (2005) indicated that although the proportion of filicide

is slightly higher among fathers (31 % compared to 30 %), the research on mothers seems to be wider, possibly because mothers are overrepresented in infant filicide cases (Bourget et al. 2007). Many overviews of filicide have focused on mothers as the perpetrators of filicide as mothers often have sole or predominant responsibility for their children. However, although there seems to be more literature regarding maternal filicide, it is a lot harder to find general characteristics that define a mother who commits filicide, as there are many different circumstances in which maternal filicide occur. Neonaticide is most often committed by mothers who are typically younger and unmarried, who have no prenatal care and who often deny and/or conceal their pregnancies (e.g., Bourget et al. 2007). The main motivator for neonaticide is most possibly the undesirability of the child (e.g., Resnick 1970). Mental illness plays a huge factor in maternal filicide; however, it is mostly present in mothers who have killed older children, as mothers who commit neonaticide present less signs of depression, psychotic illness, or suicidal attempts. Mothers who have committed filicide generally were socially isolated, full-time care providers, who may have been victims of domestic violence themselves.

Differences were found between mothers from psychiatric and correctional populations, as mothers from the psychiatric population were generally unemployed, married, used alcohol, and had an abusive history. Those from the correctional population were often unmarried and unemployed with little or no social support, had a limited education, and a history of substance abuse (West 2007). This reflects another risk factor, as mothers whose own mothers were unavailable because of alcoholism, abuse, or mental health problems were more likely to commit filicide.

Sex Differences in the Victims of Filicide

The current literature on gender differences in neonaticides has suggested no significant difference in the quantity of male and female victims

(e.g., Lucas et al. 2002). In a review of filicide cases, including neonaticides, there was an equal amount of male and female victims (Flynn et al. 2013). Analysis of the sex of victims in maternal filicide also showed no significant differences between the number of sons and daughters killed (Friedman et al. 2005). Between the ages of 4 and 15 years old, some studies have found that the victims are mostly male, whereas others have noted the number of male and female victims to be equal. Victims of maternal filicide seem to be predominantly female, and conversely, fathers seem more likely to kill their sons, especially boys over the age of 15 (Bourget et al. 2007).

Conclusion

In summary, there is still a debate as to which gender is more responsible for filicide, as there is research to support both sides. However, it does seem that the research on maternal filicide is more extensive. Research consistently suggests that mothers are almost always responsible for the deaths of neonates and are also more likely than fathers to be responsible for the deaths of younger children, whereas fathers tend to commit more filicides involving older children. Studies focusing on paternal filicide have had limited sample sizes; however, some characteristic traits have been identified. Many paternal filicides include violence and a history of family abuse, which is reflected in what is usually a violent method of killing. Relationship issues have often been a predisposing factor, such as being separated from their partner or ruptures within the marital relationship. Psychosis was also often present between 30 % and 40 % of the time. There seems to be a wider literature present regarding maternal filicide; however, this may be because of the inclusion of neonaticides in samples. Neonaticides tend to be a result of an unwanted pregnancy, and the perpetrators are usually mothers who are younger and unmarried and often deny and/or conceal their pregnancies. However,

mothers responsible for neonaticides generally present less signs of depression, psychotic illness, or suicidal attempts compared to mothers who are responsible of filicides of older children. The latter are generally socially isolated full-time care providers who were often victims of domestic violence abuse themselves.

Cross-References

- [Child Abuse](#)
- [Child Homicide](#)
- [Child Mortality](#)
- [Ficide](#)
- [Methods of Ficide](#)
- [Sex Differences in Death by Homicide](#)

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Sex Differences in Death by Homicide

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Synonyms

[Homicide](#); [Homicide and life history theory](#); [Individual differences and homicide](#); [Lethal intrasexual competition](#); [Uxoricide](#); [Honor killing](#)

Definition

Sex differences in the frequency and risk factors associated with homicide (as measured by standardized rates and percentages).

Sexual Selection and Male Homicide

Cross-national epidemiological analyses suggest that, in general, males are more likely to be both the perpetrators and the victims of homicide (UNODC 2013, 2018). The UNODC's 2013 *Global Study on Homicide* concluded that males comprised close to 79% of all victims and 95% of the perpetrators of homicides worldwide (UNODC 2013). Standardized homicide rates support this difference. Current data places the global male homicide rate at 9.7 per 100,000 individuals, relative to 2.7 per 100,000 for women (UNODC 2013). The gap remains even after the information is broken down by UN

regions, with some regions having higher male homicide rates than others. For instance, whereas in the Americas the rate is of 29.3 per 100,000, in Asia the rate is of 4.0 per 100,000 (UNODC 2013). The data also indicates, globally, young males are frequently the victims of homicide. The value increases from 2.0 per 100,000, between ages 0 and 14, to 16.7 per 100,000, between ages 15 and 29 (UNODC 2013). At age 30, the value drops to 14.4 per 100,000, continuing its decline throughout the rest of adulthood. These values reflect the fact that younger males are especially at risk of dying due to homicide.

Even though some perspectives (e.g., social role theory), emphasize the influence of socialization and cultural practices have on the observed sex differences in homicide rates, these perspectives do not account for how widespread this variation is across societies. Over the last 30 years, ethnographic data indicates lethal, inter- and intra-group violence is pervasive in small-scale societies, with the percentages of males dying due to conflict not only exceeding the estimates of nation-states but also occurring more frequently than female homicide (Buss 2005). Alternatively, evolutionary hypotheses not only address the persistent sexual differences in homicide across societies, but it also predicts a significant increase in male homicide in young adulthood and its subsequent decrease in later life stages. According to the sexual selection hypothesis, male intragroup lethal aggression is as an extreme manifestation of male intrasexual competition (Daly and Wilson 1990; Daly 2017). According to this view, anisogamy (the cytological variation of gametic features), the higher level of female parental investment and a wider male fitness variance (Daly and Wilson 1990), selects in favor of male risk-taking behaviors, increasing the likelihood of both perpetrating and being a victim of a homicide.

Furthermore, the positive correlation between homicide rates and indicators of wealth and income inequality, above and beyond the effects of other economic metrics (e.g., absolute poverty or economic growth; Daly 2017; Peñaherrera-Aguirre et al. 2019), supports the hypothesis that some males will

adopt violent and riskier strategies, when they have fewer resources relative to other males (Pound et al. 2009). Cross-species comparisons indicate that, in various taxa, males' ornaments used to attract females are also employed as armaments against rivals. In humans, males' access to resources serves as armament for indirect non-lethal competition and as an ornament for intersexual selection. Consequently, relatively disadvantaged males with limited access to resources are predicted to compete with other males through direct physical aggression, leading, in some instances, to homicide (Daly 2017; Peñaherrera-Aguirre et al. 2019). It is worth noting that the sexual selection hypothesis does not reject any potential cultural effects; however, from this perspective, culture operates on pre-existing, morphological, physiological, cognitive, and behavioral differences, amplifying them under varying conditions.

Homicide Rates and Individual Difference Variables

Male homicide rates additionally exceed female homicide rates because males systematically show elevations among individual difference variables predictive of risk-taking and future discounting. The study of such individual differences, which vary within and between groups, simultaneously explain how males as a group evince higher homicide rates, and why, within any particular population of males, there is a range of risk-taking, violence, and murder. Life histories are one such individual difference variable, as life histories are related to time relevant investment, and represent constellations of correlated variables evolved and developed along a continuum of *fast* and *slow*. For instance, males, on average, tend to fall on the faster end of a life history continuum, which is positively correlated with risk-taking, future discounting, and lower impulse control (Figueredo et al. 2006). Faster life histories, with their relative presentism and impulsivity, develop and evolve in response to high morbidity and mortality, both of which are acutely elevated among males in most human

populations, in large part due to contest competition. The foregoing variation among homicide rates across cultures and continents are explicable in terms of life history evolution, which tends to be faster in tropical climates (Peñaherrera-Aguirre et al. 2019).

Additionally, life histories correlate with certain personality traits, which, in and of themselves, represent individual difference variables correlative to homicide. For instance, those with faster life histories score higher in dark triad traits such as psychopathy (Figueredo et al. 2006) and, in turn, more often commit calculated murders (Woodworth and Porter 2002). Moreover, low levels of agreeableness, or high level of antagonism, were related to violence via moderating effects of trait aggression (Miller et al. 2009).

Intimate Partner Violence, Uxoricide, and Honor Killings

Although the overall frequency of homicides is higher in males than females, when the data are classified based on whether the killing was a product of intimate partner or family violence (where the perpetrator is a parent, sibling, offspring or other relatives), these sex differences are attenuated. According to 2018 UNODC report (2018), worldwide, 82% of victims of lethal intimate partner violence are women (i.e., uxoricide), relative to 18% of men dying of the same cause (i.e., mariticide). Even though this gap slightly decreased when the data are aggregated for both family and intimate partner violence (i.e., domestic violence), women worldwide are victimized at higher percentages relative to males (women = 64%; males = 36%). The report indicates that the global homicide rate of women due to intimate partner violence was of 1.3 per 100,000, with African countries displaying the highest value with 3.1 per 100,000, whereas European states lowest with .7 per 100,000 (United Nations Office on Drugs and Crime 2018). In several instances of mariticide, however, women opt for killing their partners in response to

the recurrent violence suffered in the relationship. Homicide then is the outcome of women's defensive rather than offensive aggression, further evidencing the underlying sex differences.

Concerning some of the risk factors correlated to the likelihood of lethal intimate partner violence, the partner's unemployment has been found to be one of the main predictors of uxoricide (Khaigodabi et al. 2012). Similarly, the risk increases fivefold in circumstances where the victim left the attacker for another male (Khaigodabi et al. 2012). For example, cross-national studies based on data collected in Australia, Canada, and the USA concluded that women living with their male partner experienced lower homicide rates compared with those who were separated (Wilson et al. 1997). In addition to the quality of the relationship, the presence of the victim's offspring in the household, unrelated to the attacker, is also associated with a twofold increase in the risk of lethal intimate partner violence (Khaigodabi et al. 2012). Other factors include (1) the age of the male partner (older males fearing their younger mates will abandon the relationship); (2) females displaying higher mate values relative to their mates (e.g., better education, income, status, physical attractiveness); (3) the occurrence of female infidelity; and (4) how much time has passed since the separation (women leaving abusive partners are especially at risk during the first year after the relationship ended; Buss 2005).

Two evolutionary hypotheses were developed to address the apparent evolutionary contradiction of male perpetrators eliminating a romantic partner (e.g., a risk of retaliation of the victim's kin and allies, reputation loss, increased risk of offspring death due to lost maternal investment, decreasing the likelihood of future reproductive opportunities; Khaigodabi et al. 2012). According to Daly and Wilson, uxoricide is a by-product of sexually selected traits in males. From this perspective, a malfunction of males' sexual proprietariness, meaning the desire for control over their partner's sexual behavior, is the leading cause of this maladaptive overreaction (Khaigodabi et al. 2012). Alternatively, Buss (2005) suggested that the

by-product hypothesis does not account for the occurrence of premeditated uxoricides, such as planning the murder or hiring someone to kill the victim (Buss 2005; Khaigodabi et al. 2012). For Buss, murdering a sexual partner was selected in small-scale societies as a signal directed toward future mates, indicating the costs of defection, such as leaving the relationship or copulating with other males, and as a deterrent to rival males who may intend to poach the female.

Although some states consider the honor killings of females to be equivalent to uxoricide (when the partner is the perpetrator), male consanguineal relatives or in-laws in general often commit those murders. According to the UNODC 2018 report, honor killings occur in response to the alleged reputation loss suffered by a family due to a female's behavior or condition, such as having pre-marital sexual intercourse, being the victim of sexual coercion, or eloping against their family's wishes (UNODC 2018). Risk factors associated with honor killings include the young age of the victim, as well as being single (UNODC 2018).

Conclusion

Significant sex differences exist in the frequency of homicide; most perpetrators and most victims are men. The attackers, as well as the victims, are often young males between 15 and 30 years old. Although homicide rates are higher for men, these rates vary across regions. Whereas Europe displays the lowest value, the Americas exhibit the highest. Even though several social theories provide an approximation to these differences, the sexual selection hypothesis also accounts for curvilinear pattern observed between homicide rate and age, as well the pervasive nature of this phenomenon across state and pre-state societies. This pattern reverses for lethal intimate partner violence, in which females are often the principal victims, whereas males are often the perpetrators. Sexual jealousy, infidelity, separation, and the partner's low mate value are significant predictors of uxoricide.

Cross-References

- [Most Perpetrators Are Men](#)
- [Most Victims Are Men](#)
- [Partner Abuse and Homicide](#)
- [Same-Sex Homicide](#)
- [Violence from Women's Kin](#)

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Sex Differences in Emotional Communication

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Synonyms

Emotion; Emotional communication; Evolution;
Sex differences; Social signals

Several studies seem to indicate that women have better interpersonal skills than men (McClure 2000), that women are more emotionally expressive than men in response to stimuli and during mental imagery (Schwartz et al. 1980), and that women report expressing their emotions more frequently and more intensely than men (Kring and Gordon 1998). Men and women also differ in the control they have over their emotional expressions, as when preschool girls appear to mask negative expressions better than boys when receiving an unattractive gift (Davis 1995). The goal of this section is to provide a brief overview of the main findings about sex differences in emotional communication, using the framework of evolutionary theory. In doing so, I will first clarify (1) the nature and function of emotional communication and (2) the evolutionary roots of sex differences in social behavior. Rather than an exhaustive review of the literature on sex differences in emotional communication, this section emphasizes the relevance of evolutionary theory in understanding why women and men differ in the way they produce and process emotional signals.

Evolution of Emotional Communication

A number of scholars agree that emotions are integrated psychobiological processes that have evolved to foster adaptation of organisms to their environment (Cosmides and Tooby 2000; Nesse

1990; Scherer 2005). Emotion involves the coordination of several organismic subsystems (e.g., the central and peripheral nervous systems and the muscular system) to optimize adaptation to a variety of circumstances, both social and nonsocial (Scherer 2005). In this framework, emotional communication is a set of responses that specifically address the social environment. These responses belong to the larger category of social signals, which function to influence perceiver's behavior to the advantage of the signaler (Mehu 2015) and which conspecifics use in relation to environmental cues in order to infer a variety of information about the signaler's internal states and likely intentions (Russell et al. 2003). Emotional signals are therefore essential to assess and manage the social environment, to navigate and adapt to ever complex social structures, and, ultimately, to enhance survival and reproduction.

Paradigmatic to evolutionary approaches to behavior is the idea that sex differences in reproductive strategies lead to sex differences in important aspects of social behavior such as parental investment and mate preferences (Kenrick and Keefe 1992). Sex-specific reproductive strategies likely interacted with environmental factors to shape the social environment that provided the selective pressures responsible for the evolution of social signals and emotional communication. The sex differences currently observed in emotional communication may therefore result from adaptive sex-specific signaling strategies developed by men and women to manage their social environment (Mehu et al. 2008; Vigil 2009).

For most of their evolutionary history, humans have lived in multi-male/multi-female groups in which they frequently interact with genetically related and unrelated individuals. The distribution of kin and non-kin in relation to a given sex depends on the residence pattern adopted by the species. Humans show flexible residence patterns in comparison to other primates; hence, it is hard to determine whether any of these patterns (patrilocal, matrilineal, and bilocal) is specific to our species. However, it was suggested that patrilocal has been the dominant pattern over the course of human evolution (Ghiglieri

1987), whereby males tend to stay in their native group and females tend to migrate to other groups. According to the male philopatry hypothesis, men are expected to form kin-based coalitions which aim at acquiring and defending resources but also at dealing with the selective pressures of intraspecific aggression and intergroup competition. On the other hand, female dispersion in society implies that women will mostly interact with genetically unrelated individuals and base their relationships on reciprocal altruism. These long-term and committed relationships would ensure access to the resources needed for the development of their offspring (Vigil 2009).

In order to succeed in male coalitions, men must acquire social status, dominance, and competence and, hence, display emotional expressions that are conducive to these goals, for example, anger and disgust (Stewart et al. 2015). Men are expected to be more sensitive to, and to display, emotional signals which function is to regulate social hierarchies but also to foster intra-sexual cooperative bonds. Women, on the other hand, are expected to be more sensitive to, and to display more cues of, affiliation, nurturance, and caring. Women are also expected to display emotions that promote group inclusiveness and stability (Vigil 2009). Expressions of fear, sadness, and joy are expected to be particularly important in women, as these expressions allow them to avoid conflict and increase safety (fear), to enter coalitions after a drawback (sadness), and to elicit prosocial behavior from others (joy). Does the pattern of sex differences in emotional communication observed in the literature reflect the evolutionary arguments discussed above? In the next paragraphs, I will discuss the results of both perceptual and production studies in the light of evolutionary theory.

Sex Differences in the Perception of Emotional Signals

Social psychologists have long recognized the relationship between emotions and interpersonal dimensions of personality like dominance and

affiliative tendencies (Knutson 1996). Empirical research indeed shows that perceivers' expectations about a signaler's disposition to show particular emotions are strongly affected by the sex of the signaler (Hess et al. 2005). More specifically, the perceived disposition to show anger, contempt, and disgust is associated with the male sex, whereas the perceived disposition to show fear, sadness, happiness, and surprised is associated with the female sex (Hess et al. 2005). In addition, men's perceived disposition to show anger, contempt, and disgust was partially mediated by their higher perceived social dominance and their lower perceived affiliation. On the other hand, the tendency for women to show more fear and sadness was partially mediated by their lower perceived dominance.

In a related study, the sex of the signaler had an effect on the accuracy of emotion identification by perceivers: While anger and fear (two emotions related to the regulation of hierarchical relationships) were more easily identified in male faces; sadness (an emotion related to affiliative relationships) was more easily identified in female faces (Stewart et al. 2015). Similarly, when people have to report the emotional expression of faces they have perceived for a very brief amount of time while having to perform an unrelated task, they are more likely to mistakenly attribute anger to male faces than to female faces and to mistakenly attribute happiness to female faces more than to male faces (Neel et al. 2012). These results can be taken as evidence of a bias whereby cues to threat present in the environment are attributed to individuals most likely to inflict harm (men) and cues to friendliness are attributed to individuals most likely to represent social bonding opportunities (women). Using a different paradigm, Smith et al. (2015) showed that perceivers were quicker at attributing gender to faces when these faces showed expressions that were "congruent" with cultural expectations (men show angry faces and women show happy faces). All in all, these findings support the idea that people's expectations about men and women's emotional communication styles are connected to evolved interpersonal strategies such as dominance and affiliation.

Women are considered better than men at processing emotional expressions (McClure 2000). In a perceptual study, Hampson et al. (2006) evaluate two evolutionary-based hypotheses to explain female advantage in emotion recognition: the attachment promotion hypothesis and the fitness threat hypothesis. Both hypotheses are based on the assumption that women, as primary care givers, have evolved particular abilities to recognize emotions displayed by their infants to promote their attachment and to better react to potential threats to their infant's survival. Hampson et al. (2006) found that women were indeed faster than men at labeling all kinds of facial expressions of emotions, supporting the primary caretaker hypothesis (Babchuk et al. 1985), and that the sex difference was particularly large for negative emotions, supporting the fitness threat hypothesis. This effect may be based on hardwired automatic processes, as women were also found to give significantly higher (correct) emotional ratings than men when negative facial emotional expressions were presented for less than a second (Hall and Matsumoto 2004).

Sex Differences in the Production of Emotional Signals and Their Consequences

Beyond women's perceptual advantage in the processing of emotional cues, this sex difference also seems to hold for the production of emotional signals. For example, an observational study looking at parents and child interactions revealed that girls expressed more submissive emotions, like sadness and anxiety, than boys (Chaplin et al. 2005). A meta-analysis of sex differences in smiling showed that women and adolescent girls tend to smile more than men and adolescent boys (LaFrance et al. 2003) and that this sex differences is modulated by a variety of contextual factors such as gender-based norms, situational constraints, and emotion salience. Observational studies performed in public places

revealed that sex differences in smiling depend on the person's age, on the immediate social context (who the person is interacting with), and on the type of expression displayed (Mehu 2011; Mehu and Dunbar 2008). For example, men in dyadic interactions displayed significantly higher frequencies of closed smiles than women but only when interacting with other men (Mehu 2011). In group interactions, men show disproportionately more deliberate smiles than laughs when interacting with older men, whereas this effect is not observed in women (Mehu and Dunbar 2008). Among people who engaged in friendly body contacts during dyadic interactions, women displayed more open smiles than men (Mehu 2011). Different forms of smiles may therefore be connected to different social contexts and goals, which in turn modifies the extent to which men and women differ in their emotional displays.

Not all studies find sex differences in emotional communication. In a meta-analysis of empathic and socio-emotional abilities, Eisenberg and Lennon (1983) reported that the female advantage in emotional skills is present in studies using self-reports and in studies performed in laboratory settings but tends to disappear in studies using physiological measures and unobtrusive observations of nonverbal behavior. In an observational study, Mehu and Dunbar (2008) did not find sex differences in overall rates of smiling and laughter, though the frequency of these expressions in men and women were affected by different factors, like the age and sex-composition of the groups in which they were observed interacting. As a general rule, smiling and laughter were significantly more likely to be targeted at same-sex individuals, suggesting that these expressions are used in the regulation of intra-sexual coalitions. In addition, women tended to laugh more frequently when interacting in mixed-sex groups, whereas men laughed more when interacting with other men. In mixed-sex dyads, women tended to laugh in response to men's laughter more readily than men laughed

in response to women's laughter (Smoski and Bachorowski 2003). Cashdan (1998) found no sex difference in smiling but she observed a significant negative correlation between the frequency of women smiling in the presence of strangers of the opposite sex and self-reported masculine characteristics. Cashdan (1998) also found that the more women were smiling in interactions with opposite-sex strangers were also rated as being more popular and caring, whereas these correlations were not observed in men. Therefore, although men and women may not always differ in the amount of positive emotional expressions they display, these expressions are affected by different social factors, suggesting that they have evolved under different selective pressures, as postulated by evolutionary theory.

Regarding the effect emotional expressions have on perceivers, research suggests that men and women may yield different consequences from the emotional signals they display. For example, ambiguous expressions (representing a blend between sadness and anger) are rated as sadder when posed by a woman than by a man but are rated as angrier when posed by a man than by a woman (Plant et al. 2004). The same study reported that female faces showing ambiguous expressions were rated more positively than male faces showing the same expressions. The level of affiliative intentions attributed to a smile is also higher when the person smiling is a woman than if it is a man (Hess et al. 2000). Similarly, female smiling faces appeared to have a more positive impact on perceivers' evaluations of personality characteristics than male smiling faces (Mehu et al. 2008). In an observational study, boys and girls were found to be rewarded differently by their parents for expressing evolved sex-specific emotions, and differential responses to some of these expressions influenced their subsequent use in social interactions (Chaplin et al. 2005). Therefore, the consequences for expressing a particular emotion are different for men and women, and these consequences may feedback

on the future use of these expressions in social relationships. Such feedback loops between sex-specific emotional expressions and the social environment may reflect flexible patterns of adaptation whereby people learn whether a given strategy is likely to work in a specific social context.

Conclusion

All in all, the findings reported above are compatible with the evolutionary hypothesis that women and men use emotional communication for different reasons and that women who are prosocial and caring display positive emotional expressions which promote group inclusiveness (Vigil 2009). Regarding socio-emotional skills, men may be better equipped to deal with hierarchical and competitive interactions, whereas women may be better equipped to deal with prosocial interactions. A few reservations can nevertheless be added to these conclusions. First, the vast majority of studies in the field have not directly addressed evolutionary hypotheses, which decreases the validity of the interpretations made above. Second, most studies are performed using a perceptual paradigm in which social context variables are not always taken into account. Third, past research usually focused on six to eight basic emotions with an overrepresentation of negative emotions, as joy is typically the only positive emotion in the set. In addition, using patrilocality as an evolutionary model to represent the social structure in which emotional communication has evolved (e.g., Vigil 2009) may not accurately depict human evolutionary history. Alternative predictions could be derived by using other models of human social organization (e.g., matrilocality or mixed residence patterns), in which a larger variety of socio-ecological variables are investigated. Finally, future investigations of the social contexts in which emotional communication strategies are adaptive should also consider the interaction between biological sex and sociocultural roles attributed to men and women in a given culture.

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Sex Differences in Guarding Behavior

► Daughter Guarding

Sex Differences in Human Mate Preferences (Buss, 1989)

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Introduction

Evolutionary psychology owes its origins to a number of eminent scientists. Among them are Charles Darwin (1871), Ronald Fisher (1930), Robert Trivers (1972), George Williams (1975), and Donald Symons (1979). Many more eminent researchers have emerged since, influenced by their work, following in their pioneering footsteps. David Buss is one such example. His seminal 1989 paper “Sex Differences in Human Mate Preferences” evolved from this rich and varied backdrop of scientific endeavor and has informed, enlightened, inspired and occasionally provoked readers ever since. This paper is the focus of the present chapter.

Overview

This chapter will begin by providing an overview of the main aspects of the original 1989 paper and then consider some of its limitations. It will subsequently focus on more recent research, in how it relates to the paper, and finally conclude, reflecting on its overall impact and importance.

Buss’ dedicated work on evolutionary theory began in 1981, at Harvard University; a year later, he commenced the study that would become the one discussed in this chapter (Buss 2008, p. xvii). It is indisputable that “Sex Differences in Human Mate Preferences” (Buss 1989) has had a profound impact on psychological research and researchers: at the time of writing, it has been cited approximately 4,000 times (Google Scholar). It features “37 samples, drawn from 33 countries, located on six continents and five islands (total $N = 10,047$)” (Buss 1989, p. 1). Though not without issue, its

scale – and its content – is impressive. Its premise and the questions it poses, however, are comparatively straightforward.

The primary purpose of Buss (1989) is to explore the characteristics that humans find attractive in potential mates. Five candidate values were considered: earning capacity, ambition/industriousness, youth and physical attractiveness, and chastity (as measured here, equating to virginity). Buss made predictions as to how each sex might differentially value each characteristic – namely, that women, more than men, would value earning potential and ambition. Conversely, men, more than women, were predicted to place greater value on (relative) youth, physical attractiveness, and chastity.

Preferences for these attributes were hypothesized to have evolved over generations, impacting both current and ancestral mate choice. As a result, they affect inter- and intrasexual selection (i.e., opposite-sex preferences and same-sex competition, for access to desirable mates). Mate choice is not random; it is underpinned by nonconscious influences relating to the likelihood of successful reproduction, for the individual organism and, should they succeed, their offspring in turn (see, e.g., Miller 1998). At the time Buss’ (1989) research was published, little was known as to which specific characteristics were preferable, to which, if not both sexes, and whether preferences might be consistent across cultures.

Trivers (1972) previously argued that sexual selection is driven by the investment that males and females differentially make into producing and raising offspring. In humans, females typically make the greater investment, from the gamete (i.e., ova) level, through to costly gestation and nurturing periods. Thus, Buss (1989) posited the potential for a male to provide resources – via their earning potential and ambition/drive – would be a germane factor in females’ preference for a specific partner. High levels of these characteristics would enhance a female’s, and any offspring’s, chances of survival and ongoing reproduction.

For males, Buss (1989) argued potentially costly investment in a mate maybe affected by

their likelihood of fertility and/or future reproductive value, influencing the potential for conception(s) (see also Williams 1975). In human females, fertility peaks in the mid-teens and declines thereafter, typically to menopause. Age is therefore a germane factor, affecting male mate preferences: simply put, men who did not prefer fertile females would limit their reproductive success. Physical attractiveness is inexorably linked to this issue. Features associated with youth (e.g., good hair and skin, full lips) suggest reproductive capacity and are thus typically found attractive by males. Buss argues that, while there may be cultural variation in specific preferences (e.g., body shape), an attraction on the part of males to these features should be species typical. Finally, in respect of chastity, males who value chaste females are likely to have greater paternal certainty than those who are more indifferent toward a partner's sexual contact. Such males may also more likely engage in tactics that maintain a partner's chastity, such as mate guarding (Platek and Shackelford 2006). The absence of this preference would increase paternal uncertainty and the potential for unknowingly investing in another's offspring/genes. Maternal certainty, by contrast, is never in doubt, explaining the hypothesis that a preference for this characteristic will be stronger in males than females.

The methodology (Buss 1989, p. 5) consisted of two instruments, translated as necessary. The first gathered demographic data from participants asked participants to state their preferred age for marriage, desired age difference between themselves and their spouse, whom they desired to be older, and number of desired children. Participants were also asked to rate 18 characteristics on a four-point scale; among them were the target variables of "good financial prospect," "good looks," "chastity" (virginity), and "ambition and industriousness." The second instrument featured 13 characteristics that participants were asked to rank from 1 to 13 in terms of desirability; these included "good earning capacity" and "physically attractive."

In testing hypotheses regarding males' (youth; attractiveness; chastity) and females' preferences (ambition/drive; earning potential), results reading women's preferences indicated that in 36 of the 37 samples, predicted sex differences emerged for earning potential. Buss later queries whether this reflects an ability to provide for offspring, or an increase in status, protection, and, in general, "good genes" (per Trivers 1972). For ambition/industriousness, 29 of 37 significant sex differences emerged in the same, predicted direction; in one sample (Zulu participants), results were significant in the opposite direction (higher male preference). Buss (1989) notes that his collaborator (unnamed) suggests this is a cultural issue, whereby Zulu women are expected to build houses, fetch water, and complete other laborious undertakings.

For hypotheses regarding males' preferences, beginning with age, in all 37 samples, males reported a significant preference for younger partners; these were the largest or strongest findings across the study, showing significance <0.0001 in all cases. Additional demographic analyses suggested the mean age for marriage, across all participants, was 24.83 years old, close to peak female fertility, though not reproductive value (Females also reported a preference for older male partners, in all cases.) Buss (1989, p. 9) additionally reports analyses of actual age at marriage compared with self-reported preference, where applicable, briefly put actual age of marriage seem to validate self-reported preferences, and support the evolutionary proposal that males prefer and choose females displaying cues regarding high reproductive potential. For males' greater preference for physical attractiveness (per "good looks"), 34 of 37 samples showed significant results in the predicted direction; the other three (India; Poland; Sweden) showed significant male preferences for the ranked variable "physically attractive."

Finally, regarding males' greater preference for "chastity" (virginity), samples showed great variety. Ultimately, 23 of the samples returned significant results in the expected direction. All Eastern

European and most Asian samples reported a significant preference; most Western European, Canadian (English and French), New Zealand, Chinese, Indonesian, and white South African samples did not report a significant preference. Buss (1989) subsequently notes that, unlike the other variables, chastity cannot be directly observed *per se*, but concludes that whether this may bear relevance to the present results is speculative and reflects gaps in contemporary knowledge.

Across results outside of the chastity characteristic, even where results did not achieve significance, in the majority of cases, the direction of the results was aligned to the hypotheses. Ultimately, therefore, each of the predictions made by Buss (1989) was supported, though with only moderate support regarding a female preference for ambition/industriousness.

Limitations and Reflections

Despite the generally strong support for the hypotheses, the study is not without its flaws. Buss (1989) himself acknowledges several. The first is that the samples are not representative of the populations of each country, citing underrepresentation of rural populations. This may well be an issue; a Bolivian study (Schvaneveldt and Huler 2012; $N = 500$, 50% rural) found a number of significant “deal breakers” for potential long-term partnerships, several of which would fall under ambition/industriousness, chastity, or physical attractiveness categories (the latter two include direct questions about these issues); all were less important to rural participants.

In addition, Buss (1989) raises the issue of arranged marriages within some cultures as a potential confound for the evolution of mate preferences. Available evidence suggests this bears consideration. Buunk et al. (2008) explored parent-offspring conflict and found this was greatest where disagreements emerged over issues regarding a mate’s heritable fitness or parental investment indicators. Buunk et al. also echoed a call (citing Buss and Schmitt 1993) for

researchers to explore the implications of constrained mate choice – i.e., in opposition to preferences. Regarding the somewhat unexpected findings as to variation across cultures in males’ preferences for female chastity/virginity, Buss (1989) notes that assorted cultural reasons for this unanticipated finding, but not specifically, or at length.

Another candidate limitation was that sex distributions overlapped, despite significant mean differences. This may reflect an absence of sex differences across multiple items; the issue of similarity in preferences across males and females is explored more below (cf. Li and Kenrick 2006).

A suite of issues acknowledged by Buss (1989) surrounds the methodology of the study. There are problems associated with using a stand-alone self-report format, which presents numerous issues (such as socially desirable responding), as well as the use of some single items, compared with item clusters (per Nunnally 1978).

Beyond Buss’ (1989) own reflections, one could argue that the paper focuses on a limited range of factors (i.e., five). Indeed, there is a vast range of human characteristics that have been argued or found to be desirable, beyond the five featured in the original paper. Among these are intelligence (i.e., “*g*”; Miller 2000), and female body odor, such that it may indicate menstruation/high fertility (Kuukasjärvi et al. 2004). Other studies have reported specificity in some characteristics that Buss measured: Jonason et al. (2012), for example, found that female preference for males possessing resources was higher when the target had “earned” rather than inherited or embezzled them. Undoubtedly, a broader range of characteristics could have been studied; however, Buss could – understandably – have only ever assessed a fraction of “human mate preferences.” It bears noting, however, in respect of influence, that each of the citations above directly refers to Buss.

While the geographical scope of Buss (1989) is vast, sample sizes are considerably uneven. The

samples from the USA and Germany, for example, are by far the largest (USA, $n = 1,670$; Germany, $n = 1,083$) and dwarf samples from the African continent (South Africa (white and Zulu), $n = 228$; Nigeria, $n = 172$; Zambia, $n = 119$). Samples from Arabic cultures are also represented only by Palestinian ($n = 109$) and Iranian ($n = 55$) participants. While this is an underrepresentation of some specific communities, a considerable proportion ($>50\%$) of Buss' sample is not from "WEIRD" demographics (i.e., Western, Educated, Industrialized, Rich, and Developed; Henrich et al. 2010). Importantly, particularly in relation to the results discussed above in relation to males' value regarding chastity, this highlights "Western" versus other demographic preferences. The recruitment of samples of this nature remains an ongoing issue in psychological and some evolutionary psychological research; Buss is, in this respect, an early adopter.

In addition to the above, there are some issues surrounding this paper's interpretation. This is not Buss' (1989) fault, as the current paper does not reduce its conclusions thusly, but it can be (and often is) misinterpreted as "men want attractive women; women want wealthy men," which is misogynistic. Regrettably, this is frequently the way it is interpreted, or broadcast, by media outlets, even when researchers cite apposite theory (e.g., Ting 2015, citing Buss (1989) and Fales et al. (2016)). In fact, Buss directly states that "male and female preference distributions overlap considerably, in spite of mean differences" (Buss 1989, p. 13).

From Li and Kenrick (2006), it is clear that there is variation in human mating preferences based on short- or long-term scenarios, which Buss (1989) does not distinguish between, methodologically. Rather than sex differences, Li and Kenrick found a similar preference for physical attractiveness in men and women in the case of a short-term scenario and for kindness, intelligence, and general well-roundedness in a long-term one. Some sex differences remained – resources and attractiveness were more important to women and men respectively in the long-term scenario, but

this paper highlights the relevance of context to mate preferences.

Looking at socioeconomic status (SES) preferences, Greitemeyer (2007) found that males actually reported a preference for women with lower resource provision (by extension). The female preference for men with higher SES (per Buss 1989) remained, but Greitemeyer notes that the strength of the preference varied according to short- (weaker) or long-term contexts. Greitemeyer also reported that mediation analyses showed that males' preference in this respect was mediated by candidate partners' educational levels (and by extension potentially greater SES/independent resources), with males perceiving highly educated women as less likeable and faithful. This may reflect a response to recognizing where males' own mate value is lessened.

Eastwick and Finkel (2008) also found no evidence for sex differences in preferences for attractiveness or earning potential in reports based on real-life encounters, compared with Buss' (1989) use of pen-and-paper self-reports. Context and methodology therefore both appear pertinent to fully understanding sex differences/similarities.

A final suite of proximate mechanisms (social, psychological, physiological, and ontogenetic) that may contribute to the results in this study is proposed by Buss himself (1989). Buss flags genetic differences, sensory preferences, socialization differences during development, and structural differences at a societal level, such as patriarchal issues that may limit female access to resources – see, e.g., Carli and Eagly (2001) – as candidates.

Ultimately, several of these issues can be at least partially attributed to Buss (1989) being a "starting point," or catalyst, in many respects, with subsequent acknowledgement that preferences are highly complex (see, e.g., Buss 2003; Li and Kenrick 2006). Buss (1989), instead, represents a milestone – and not simply in evolutionary psychology but in the field of psychology as a whole.

Conclusion

While not without issue, particularly in regard to culture, the considerations of the relationship between cultural variations in sex differences Buss (1989) reports are novel, and generally presented well, conceptually. Buss also acknowledges that “currently unknown are the cultural and ecological causes of variation from country to country” (p. 13). Equally, while methodological issues are present, which Buss acknowledges, the paper breaks new ground and raises important issues. The results fundamentally support the proposal that males and females have developed, over evolutionary time, in response to different issues regarding reproduction (such as lengthy gestation, for females, and wasted effort, on the part of males) and reproductive success.

Moreover, the results have implications for human intersexual competition, and abandoning – at the time Buss (1989) was writing – notions of “choosiness” being exclusive to females (per Buss 1988; Darwin 1871). The proposal Buss (1989) makes in the conclusion regarding the need to test hypotheses regarding human and particularly female intrasexual competition has been taken forth by researchers such as Campbell (2004, 2013) and Fisher and Cox (2011).

In addition, Buss (1989) has undoubtedly (per the volume of citations) had a substantial influence. More researchers have adopted an evolutionary perspective as a result; more undergraduates and postgraduates will have been exposed to evolutionary theory as a consequence. The effect of this cannot be underestimated – indeed, Buss dedicates his “New Science of the Mind” textbook, in part, to all students of evolutionary psychology, past, present, and future (Buss 2014). Individual researchers (Jonason, personal communication) who have themselves had considerable influence have even been drawn to psychology, specifically evolutionary psychology, as a discipline,

due to Buss (1989), and its successor, the book “Evolution of Desire” (Buss 1994, 2003).

Perhaps most importantly, the paper has been a major catalyst in prompting researchers to undertake large-scale, cross-cultural projects that attend issues germane to humanity’s evolved psychological mechanisms (e.g., Schmitt 2005 Sorokowski et al. 2011). Simultaneously, it has had a trickle-through influence on smaller-scale evolutionary studies that consider how ecological and environmental variation(s) may explain specific competencies and traits in humans, within (Sorokowski and Sorokowska 2012) and beyond sexual preferences.

Where ideas that emerged from Darwin’s (1871, 1968) works lay dormant for decades, due to the controversy that surrounded them, Buss (1989) was among the first to empirically test their hypotheses in relation to human mating, certainly on such a scale. Moreover, Buss’ paper is one of the first to attempt to assess, on such a scale, what would now be called non-“WEIRD” individuals. These are perhaps the greatest strengths of Buss (1989); in both cases, it has proven a highly potent catalyst for myriad researchers since its publication.

A decade ago, Penke et al. (2007) observed that “with the growing acceptance of evolution as a meta-theory for psychology, more and more personality psychologists are trying to conceptualize personality within an evolutionary framework” (p. 553). Evolutionary psychology has continued to progress since then; Buss (1989) was a substantial part in the discipline arriving at this point and will no doubt continue to play a role in propelling it forward.

Cross-References

- [Cross-Cultural Expression](#)
- [Cross-Cultural Studies](#)
- [Cultural Differences in Mate Preferences](#)
- [Female Mate Choice](#)
- [Mate Preferences](#)
- [Men’s Mate Preferences](#)

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Sex Differences in Inferring Sexual Interest

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Definition

Men, likely due to asymmetrical costs, are more likely to incorrectly infer sexual interest from women than incorrectly infer sexual disinterest. This tendency is known as the sexual overperception bias.

Cross-List: Error Management Theory

Men appear to have a greater tendency than women to infer sexual interest from members of the opposite sex. For example, men are more prone to perceive women's friendliness as sexual interest (e.g., Levesque et al. 2006). Men's tendency to erroneously perceive sexual interest from women is known as the sexual overperception bias (Kohl and Robertson 2014). This general pattern has been replicated across many studies using different methodologies, suggesting it is a robust effect (e.g., Haselton and Buss 2000; Henningsen and Henningsen 2010), and some research has also looked at the moderating effects of interest in short-term mating and attractiveness on overperception bias (Perilloux et al. 2012).

Haselton (2003) applied Trivers' theory of parental investment to explain sex differences in inferring sexual interest. According to parental investment, the sex with lower minimal obligatory parental investment is less choosy in their mating partners because they can increase reproductive success through mate number, resulting in increased intrasexual competition for mateships. The sex with the higher minimal obligatory parental investment is more choosy in their mating partners and are unable to increase reproductive success through increasing mate number. Since

men have lower minimal obligatory parental investment, missed opportunities for copulation would be more costly than time and energy expended on unsuccessful mateships, so theoretically it would benefit men to err on assuming members of the opposite sex are sexually interested in them.

Error management theory has been used to explain why men are more likely to incorrectly overperceive than underperceive sexual interest (Haselton and Buss 2000). Generally, error management theory suggests that people may have evolved a cognitive bias toward making a false positive (thinking X is true when it is not) or a false negative (thinking X is not true when it is) when one error either confers a stronger net benefit or minimizes costs. This model can be applied to perceptions of sexual interest, because people can be wrong in one of two ways: false positive is thinking a person is sexually interested when they are not; and false negative is thinking that a person is not sexually interested when they are. Since men can increase reproductive success through mate number, such a false negative would impose a greater cost than a false positive. Thus, men may have evolved a tendency to err on the side of perceiving sexual interest, even if incorrect. Since women cannot increase reproductive success through mate number, a false negative is not as costly, and so a sexual overperception bias does not appear to serve a function among women. Data support these hypotheses (e.g., Haselton and Buss 2000; Henningsen and Henningsen 2010).

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Sex Differences in Intimate Partner Violence

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Synonyms

Domestic violence; Gender differences; Partner violence

Definition

Intimate partner violence is physical, sexual, or psychological aggression between intimate partners. Traditionally, men have been portrayed as the perpetrators of IPV with women only engaging in partner-directed violence in self-defense. More recent research has demonstrated that patterns in IPV may be more gender symmetric in some cultures. A context-sensitive model of violence serves to explain how evolved sex differences can be moderated by contextual cues.

Introduction

There has been some debate about the gender patterns in intimate partner violence (IPV). Early research suggested that men were the primary perpetrators of IPV, and when women were aggressive, it was done in self-defense (e.g.,

Dobash and Dobash 2004). However, much of the research on IPV has reported a more symmetrical pattern of IPV perpetration between the sexes (e.g., Bookwala et al. 2005). Other researchers have reported asymmetry in IPV rates between the sexes with the rates of female-to-male acts being higher relative to male-to-female rates (Archer 2000, 2006). Both of the latter findings are in conflict with the traditional view of gender asymmetry for IPV perpetration being in the male direction. To fully understand the diverse findings on gender patterns in the IPV literature base, differences in operationalization and methodology across studies need to be reviewed. This entry will include a brief overview of IPV and the range of methods used to assess it. Finally, an overview of the use of aggression in the context of intimate relationships within an evolutionary psychological framework will be examined.

Intimate Partner Violence Definition and Typology

Intimate partners include both current and former romantic or sexual partners such as spouses, domestic partners, girlfriends, or boyfriends. IPV has been documented in both same-sex and opposite-sex relationships, but this entry is focused on relationships involving opposite-sex relationships. IPV generally refers to physical, sexual, or psychological aggression between intimate partners and also may include stalking (Breiding et al. 2015). Physical forms of IPV include acts of hitting, scratching, kicking, biting, choking, shoving, or throwing victims as well as other forms of physical violence. Sexual violence includes rape and other unwanted sexual contact. Examples of stalking include watching, following, or contacting a victim. Psychological IPV involves name calling, mind games, and other intentions to harm another person mentally or emotionally.

Intimate Partner Violence Assessment

Much of the data on IPV has been collected through reports to law enforcement or domestic violence assistance agencies, examining homicide data, and through self-report surveys. Sex differences in rates of IPV vary as a function of which

methodology is used to collect the data. Data from law enforcement or domestic violence assistance agencies suggest that men are more likely to be perpetrators of IPV. However, it must be noted that there may be some reporting bias to these agencies. Given our societal gender roles, male-directed aggression from women is not deemed as troublesome as is victimization of women. Further, women are more likely to have increased severity of injury as a result of IPV incidents (Archer 2000) and consequently are more likely to seek treatment or be referred to domestic violence agencies. It follows that only a portion of IPV incidents are included in the data provided by law enforcement or domestic violence assistance agencies. However, homicide data, which is less prone to reporting bias, also suggests that men are more likely to be the perpetrators of IPV. For example, reports from the FBI suggest that men are the perpetrators in nearly 75% of all intimate partner homicides. This supports the view that there is gender asymmetry in IPV perpetration. Nonetheless, the analysis of self-report measures of IPV has resulted in contradictory findings about the gender patterns in IPV. Hamby (2016) speculates that this may be due to the characteristics of the scales used and the populations studied, but the suggestion of female-perpetrated IPV does need consideration.

Causal Factors of Intimate Partner Violence

Psychologists suggest that behaviors are a result of both proximate and ultimate causes. Causal variables that are thought to be immediately related to the occurrence of some behavior are proximal. Underlying the various proximate causes for behaviors are the more distal or ultimate causes. Both levels of analysis are important to understanding IPV.

Proximate variable: Abuse history.

Researchers have proposed that a number of proximate variables are involved in IPV. For example, one of the strongest predictors of becoming involved in violent intimate partner relationships is being exposed to violence during childhood (Widom 1989). Large reviews have revealed consistent support for this intergenerational transmission of violence theory (e.g., Hotelling and

Sugarman 1986), but more in-depth research has revealed gender differences in the effects of past abuse (Langhinrichsen–Rohling et al. 1995). Having a history of abuse in the family of origin is related to male perpetrators not only having less likelihood of injury but also using more severe violence in marital conflicts relative to women with abuse histories. Further, who the perpetrator was in the childhood abuse made a difference in the role men and women took in abusive relationships. Violence from mothers was predictive of being an IPV perpetrator as an adult, whereas being victimized by a father was related to being a future victim. In other research, Ansara and Hindin (2009) found that having witnessed violence between their parents as a child was predictive of wives being the sole perpetrator of IPV as well as their being involved in relationships characterized by reciprocal perpetration patterns.

Kaukinen et al. (2015) also found evidence that abuse in the household during childhood was associated with experiencing IPV in adulthood. However, they found that race and gender moderated this effect. Caucasian women who did not have a childhood history of family violence were at a significantly lower risk for dating violence than non-abused African American women, but this racial difference disappeared in women from abusive homes. Further, Caucasian men who did not have a childhood history of violence exposure were found to be more likely to be involved in mutually violent relationships relative to African American men. For those men who were abused in childhood, this pattern was reversed. The above findings highlight the need to consider how proximate variables may interact with one another as causal factors of violent behavior in relationships.

In addition to having a history of childhood abuse, past abuse in the current intimate relationship has been implemented as being a contributing factor to partner violence. In fact, it has been long believed that women's use of IPV is used as a self-defense mechanism within the context of ongoing abuse by male partners (e.g., Dobash and Dobash 2004). Swan and Snow (2002) studied 108 women who had been identified as using violence against their male partners. In support of the self-defense hypothesis, they found that

only 12% of the sample could be classified as being the aggressor in the abusive relationship. The remainder of the sample reported violence toward their abusive male partners (34%) or were involved in mutually combative relationships. Of the latter group, the male partners were found to be more in control of the relationship violence. Overall, about 75% of the sample of women reported that their use of violence was in the context of self-defense against ongoing violence from their male partners. Women also report that they use violence against male intimate partners out of fear for their children (e.g., Johnson and Hotton 2003). Although it is not an excuse for engaging in violence, being at risk for being victimized by their male partners is an important contextual factor to be considered in women's IPV experiences. Further, the view that woman's use of violence against men is often self-defensive in nature has colored how women's use of violence against men is viewed relative to male-/female-directed violence.

Proximate factor: Culture. Much of the research on IPV has taken place in the United States. A review of the literature on this topic reveals that patterns of IPV in the United States may be unique in that men are more violent in some other countries. Men's and women's levels of violence are likely to covary as a function of social attitudes and environmental pressures. For example, Adinkrah (2009) reports low rates of women killing their husbands in Fiji where male-perpetrated violence against women is condoned and women are expected to comply with patriarchal control. Similarly, in the Philippines, when husbands were dominating and controlling, they were more likely to be the sole perpetrator of IPV (Ansara and Hindin 2009). Hitting women is less acceptable in the United States where patriarchy is less prevalent and American women are also more likely to fight back.

In an international review, Krahé et al. (2005) found that sex differences in victimization varied across cultures. However, similar to the contradicting reports of gender patterns found in literature from western samples, they found conflicting reports of gender patterns in IPV. Across cultures, the prevalence of physical

violence perpetration was about even for men and women with incidence rates showing asymmetry between the sexes but with no clear direction. Another meta-analysis of 16 countries revealed that gender patterns of victimization were correlated with gender empowerment and the individualistic-collectivist dimension of the cultures (Archer 2006). In countries with higher levels of gender equity and individualism, women were found to use more physical aggression toward their intimate partners. In a second analysis, Archer found that sexist attitudes and social acceptance of abuse of women were related to women's victimization rates and inversely related to gender empowerment. Together, these findings suggest that IPV typology varies cross-culturally as a function of social attitudes.

Ultimate factor: Evolutionary history. Studying the proximate factors involved in IPV, such as socioeconomic variables, gender roles, and cultural norms of aggression, has provided researchers with a plethora of information about risk factors for and sex differences in partner violence. To gain a comprehensive understanding of the gender patterns in IPV through, researchers need to consider the ultimate causes of behavior as well. Evolutionary theories provide a framework for examining the sex differences and similarities found in the IPV literature.

Both sexes face the evolutionary problem of finding and maintaining intimate partners. Parental investment (PI) is a constituent of sexual selection theory (SST). Trivers (1972) identifies PI as the expenditure of attention and resources that serve to increase the likelihood of an offspring's survival and reproduction at the cost of other components of fitness for the parent. Together, PI and SST dictate that men and women benefit from sex-specific mating strategies as a function of their obligatory parental investment. Men and women differ in their reproductive investment, with women investing more in offspring than do men. From an evolutionary perspective, being reproductively successful takes more time and energy for women relative to men. Given the heavy cost for women, it benefits them to limit men's reproductive access and to be selective in their mate choices. Conversely, the cost of reproduction is lower for men

relative to women, and therefore they increase their reproductive rewards by mating with multiple partners. This evolutionary arms race between the sexes results in high competition between men for access to quality mates. Aggression serves as one of many adaptive strategies that men use as they engage in this intrasexual competition. Although women may benefit from the use of aggression as well, there is reason to believe that women are less likely to resort to risky competition strategies than are men.

Aggressive encounters put people at risk for serious injury and can be lethal. Since women invest more in their offspring, we should expect that it may be more detrimental to children to lose their mother's relative to their fathers. Research has supported this proposition. Sear and Mace (2008) found that across 22 cultures, the death of a father had almost no effect on the survival of offspring, but the loss of a mother significantly reduced the likelihood of children's survival. Evolutionarily speaking, engaging in aggression is more costly to women and their children than it is for men. Campbell (1992) suggests that the evolutionary imperative for mothers to survive results in females favoring low-risk, indirect, or verbal aggression rather than physical aggression. However, adaptive strategies are flexible and therefore are sensitive to context. Physical aggression may serve as a mechanism for survival and reproductive success in some situations.

In general, it has been found that men engage in aggression more often than women, and evolutionary psychologists have suggested this is related to the different reproductive strategies of the sexes. However, there is some debate about sex differences in aggression between partners in the context of domestic relationships. Traditionally, men have been portrayed as the perpetrators of IPV, but there is evidence that men and women use aggression at similar rates in the context of domestic relationships (Bookwala et al. 2005). In fact, in a meta-analytic review, Archer (2006) found that women were more likely than men to engage in aggressive acts against their partners. Reports of domestically violent women have been problematic for social and evolutionary scientist alike.

Early explanations for the phenomena centered on portraying female-initiated IPV as a self-defense strategy against male-initiated abuse (e.g., Dobash and Dobash 2004). Counter to this suggestion, Stets and Straus (1992) reported that even when violence against nonviolent men was considered, rates of women's use of aggression in IPV cases remained higher than male rates. Controversy surrounding which sex is more aggressive in IPV situations or if the violence is mutual may be due to how aggression is conceptualized in research on the matter. Early reviews of the IPV literature focused exclusively on physical aggression, a male-dominated form of aggression. Sex differences are found when the behavioral expressions of aggression examined are physical acts, but when indirect aggression is considered, the sex difference disappears (Archer 2004). It should be noted that men are more likely to kill their partners (e.g., Langan and Dawson 1995) or seriously injure them in sublethal intimate partner conflicts though (Bookwala et al. 2005). Therefore, conflicts that escalate to a physical level appear to have more severe consequences for women, and therefore an explanation for why they may resort to physical aggression in some circumstances is needed.

Interaction of Proximal and Ultimate Causation

Proximate and ultimate causes of behaviors do not operate in isolation. Goetz (2010) has suggested that the use of violence is a context-sensitive strategy for solving some evolutionary problems. Both sexes likely benefitted from this solution in some context in our evolutionary history, and therefore Cross and Campbell (2011) suggest that the mechanism underlying aggression is the same for men and women. However, since the costs of aggression are higher for women, they may be less likely to use riskier forms of aggression. Consistent with this proposition, the research demonstrates that women use more indirect forms of aggression than they do physical aggression. Women do resort to physical violence sometimes though.

An examination of the role of emotion in aggression may offer an answer as to when women may use physical violence. Both anger and fear have been associated with aggression. Further, Winstok (2007) postulated that anger motivates aggression while fear serves to inhibit it from occurring. In a meta-analysis, Archer (2004) found no sex differences in anger, but there is evidence of differences in frequency and intensity of fear across the sexes. Cross and Campbell (2011) suggested that the sex differences seen in aggression levels are explained by women's higher responsivity to fear. The authors go on to argue that the inherent release of oxytocin that accompanies intimate partner interactions also serves to reduce fear. In situations where fear reactivity has been reduced, the chance of violence being used by men and women may equalize. This proposition serves to offer an explanation for why IPV is the one context for violence in which similarities may be expected between the sexes. In cultures where gender empowerment is higher and women's use of violence against men is condoned, we would expect to see even more evidence of this, a proposition that is supported by the findings in the literature (e.g., Archer 2006).

Conclusion

Conflicting findings in the IPV literature may be a result of differences in operationalization and a lack of validity of some of the measures used in IPV research. Viewing violence as being a result of a context-sensitive problem-solving mechanism explains why so many proximate variables are associated with IPV. In addition to acquiring aggressive schemas through observation, individuals who have been exposed to violence in childhood may have altered sensitivity levels to violence than those who did not experience abuse in their family of origin. Different ecological factors also can serve as cues for using violence more frequently or aggressively in some cultures. Finally, a context-sensitive model of violence serves to explain how evolved sex

differences can be moderated by contextual cues such as gender empowerment.

Cross-References

- [Contexts for Men's Aggression Against Women](#)
- [Contexts for Women's Aggression Against Men](#)
- [Male Sexual Jealousy](#)
- [Men's Suspicions of Partner Infidelity and Women's Defection](#)
- [Violence to Control Women's Sexuality](#)

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Sex Differences in Jealousy

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Synonyms

Sex differences in sexual versus emotional jealousy; Sexual versus emotional infidelity; Sexual versus emotional jealousy

Definition

Sex difference in jealousy is any quantitatively or qualitatively significant difference between males and females in any jealousy-related measure of any effect size, despite of an overlap on the population curve.

Introduction

Jealousy is an affective state that occurs in response to a perceived, potential or real, threat to a social relationship caused by a third party. Romantic jealousy is specifically aimed at securing and maintaining the current partner and relationship and/or competing with actual or potential rivals. An extra-pair involvement poses risks to the current relationship, and thus both parties are facing a potential loss of the current partner, relationship, resources, status, and extra-pair allies linked to the relationship, such as friends and family of the partner. From the distal perspective, jealousy helps to secure a valued reproductive partner and maintain the pair bond, which, in turn, increases the chances for survival of potential offspring because of its necessity of biparental care (Buss 2013).

Interestingly, in some polygynous societies, women report high jealousy when a new wife arrives, while in others, where the social status

of the women is guaranteed, the older wives report lower jealousy and actively leave sexual activities between the husband and the new wife (Madhavan 2002). Thus, jealousy can be evoked in particularly when connected with loss of status. Accordingly, instead of preserving the relationship, in particularly, women tried to preserve their self-esteem when dealing with jealousy (Bryson 1991). Losing one's status and reputation in an intrasexual competition or mate poaching context might have had serious consequences in the ancestral lifestyle. In general, intrasexual conflict and jealousy seem to be much higher than cooperation among co-wives and co-husbands in polygamous marriages (Jankowiak et al. 2005; Starkweather and Hames 2012), and thus romantic jealousy constitutes an integral strategy of intrasexual competition.

Although the loss of a romantic partner to a rival seems to be similarly significant for both partners, there are some systematic differences between men and women in jealousy. Women, on average, report more intense overall jealousy response than men (Buunk 1997), women more than men are prone to emotional and cognitive reactions when expressing jealousy (Güçlü et al. 2017), and women more than men are upset by an emotional involvement compared to sexual involvement of the partner with a third person (for meta-analyses, see Sagarin et al. 2012; Tagler and Jeffers 2013). These results can be a part of a more general pattern, such as, higher emotional processing among women than in men (Barrett et al. 1998).

Sex Difference in Emotional Versus Sexual Jealousy

The relative sexual versus emotional jealousy is systematically higher among heterosexual men than among heterosexual women, with no significant effect of socioeconomic status, length of relationship, age, history of infidelity gender-role beliefs, interpersonal trust, attachment style, sociosexuality, and culture of honor beliefs on this sex difference (Brase 2014; Frederick and Fales 2016). Importantly, the sex difference in sexual versus emotional jealousy is specific to

heterosexual individuals. More specifically, heterosexual men are more frequently upset about sexual infidelity scenario versus the emotional infidelity scenario than heterosexual women and both homosexual men and women (Frederick and Fales 2016).

Sex differences in jealousy were supported by fMRI studies showing sex difference in jealousy-related brain activation (Takahashi et al. 2006). Furthermore, men recall more cues to sexual infidelity, while women recall rather cues to emotional infidelity (Schützwohl and Koch 2004). Finally, although there are no sex differences in physiological arousal to sexual versus emotional infidelity cues, men show greater startle response to sexual scenarios than women (Baschnagel and Edlund 2016). Thus, sex differences in emotional versus sexual jealousy are not a by-product of self-reports.

Although cross-cultural studies are still rather scarce, the evidence suggests that these sex differences are culturally universal, appearing in populations as different as Canada, the United States, Norway, the Netherlands, Romania, Brazil, Chile, Australia, China, Japan, or Korea (see Buss 2013; Buss and Haselton 2005). However, the magnitude of the sex differences can vary. For example, among the Himba of Namibia, a small-scale natural fertility population, sexual jealousy is much higher than emotional jealousy in both sexes, although the relative sex difference remains (Scelza 2014). Further, a study employing a cross-cultural sample of Hawaiian students reported higher sex differences specifically in emotional jealousy, while sexual jealousy was more influenced by the individualist or collectivist culture of the participants than by sex (Zandbergen and Brown 2015). Moreover, in a majority of studied traditional non-WEIRD populations, higher sexual than emotional jealousy was more frequent than in Western populations (Scelza et al. 2019).

Jealousy as an Evolved Sex-Specific Mechanism

Supposedly, selective pressures acting upon male and female reproductive strategies during the

human evolution are part of the broader picture of the observed sex differences in jealousy. In particular, internal fertilization among mammals leads to paternity uncertainty, which makes the males concerned relatively more with sexual than emotional infidelity of their female partner. For male, female sexual infidelity poses the risk of loose valuable resources by investing into non-biological offspring, which is not the case for females. However, female emotional infidelity poses the risk of losing direct female investments into offspring if leaving with a new male without the offspring or maltreatment or infanticide by another male if leaving with a new male with the offspring. Females are supposed to be concerned with survival of their offspring even more than males, because female minimal necessary biological investment into reproduction is relatively higher and riskier. In species with prematurely born infants, like humans, biparental care is essential for their survival, in particularly during the first years of life. Losing paternal long-term protection and investments because of emotional involvement with another female would thus be more costly for the female and the child/children. Women thus feel more threatened by emotional involvement of their partner, because they are at risk of losing direct investments, such as resources, protection, and/or paternal care (Buss et al. 1992; Daly and Wilson 1988). In general, this logic would predict higher emotional than sexual jealousy in both men and women (e.g., Buunk et al. 1996) but also a relatively higher sexual versus emotional jealousy in men than in women. As outlined above, this has been supported by some research (Sagarin et al. 2012; Tagler and Jeffers 2013).

Moreover, men more than women are sensitive to loss of paternity opportunities than to paternity uncertainty (Edlund et al. 2019). Thus, when losing an opportunity to reproduction with a valued potential or real partner, men become more distressed than women. Accordingly, jealousy is being evoked particularly when the partner is perceived as of a high mate value (Güçlü et al. 2017), and also rivals of high mate value evoke relatively more jealousy (Dijkstra and Buunk 2002). Thus, involvement with a third party

implies not only the risk of paternity uncertainty, loss of the resources, allies, relationship, status, and self-esteem, but also, in particularly for men, loss of the reproductive opportunities.

Further, if the evolutionary rationale is true, then we might expect similar sex differences in jealousy among other nonhuman primates with monogamous bonds and dependent prematurely born offspring. There is some evidence that behaviors similar to jealousy and mate guarding exist in monogamous primates, such as *callicebus* (Cubiciotti and Mason 1978). Among these primates, situations evoking jealousy when placing a female near another male increases testosterone and cortisol in males which is connected to stress and aggressiveness, respectively, and activates the cingulate cortex which is associated to social exclusion (Maninger et al. 2017). Differences specifically in sexual versus emotional jealousy are yet to be tested. We would expect higher jealousy in less promiscuous species and higher sexual jealousy in males in species with relatively smaller testicles which does not favor sperm competition, such as in gorillas.

Conclusion

In general, sex differences in jealousy are one of the frequent critiques of the evolutionarily based research on human psychology and behavior. Sex differences in emotional versus sexual jealousy can be influenced by methodological specificities of the studies. For example, student sampling leads to larger sex differences in jealousy than nonstudent or random sampling (Sagarin et al. 2012). Further, forced-choice measures of emotional versus sexual jealousy may lead to different results although it rather seems that both report result in the same direction (Bendixen et al. 2015). Although there are some methodological discrepancies between specific studies, leading to divergent results, the sex difference in emotional versus sexual jealousy seems to be robust and universal (Sagarin et al. 2012). Importantly, the sex differences in jealousy do not represent categorical differences but rather dimensional differences which reflect differences in magnitude between

the two groups with a significant overlap between them.

The focus on differences between men and women should not overshadow other individual differences in jealousy that might be important for the evolutionary and other interdisciplinary theories. Other factors might predict jealousy more strongly than sex, such as population, sexual orientation, type of relationship, life history strategy, self-esteem, attachment, and others (Martínez et al. 2017). Mapping the proximate and ultimate mechanisms underpinning jealousy should be the focus of future studies.

Cross-References

- Emotional Jealousy
- Infidelity
- Jealousy
- Mate Guarding
- Mate Retention
- Sexual Jealousy
- Sexual Strategies Theory

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Sex Differences in Lachrymation

► Sex Differences in Crying

Sex Differences in Lacrimation

► Sex Differences in Crying

Sex Differences in Long-Term Mating Preferences

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According to Sexual Strategies Theory (Buss and Schmitt 1993), our species comes equipped with specialized mate preference adaptations. Some

mate preference adaptations are designed for *long-term mating*, and many of those are designed to motivate men and women to pursue long-term mateships differ in different ways.

Women's Specialized Long-Term Mating Psychology

Evolutionary psychologists have hypothesized women possess long-term mate preferences for cues to a man's *ability* and *willingness* to devote resources to her and their offspring (Buss 1989; Ellis 1992). Such cues include a man's status and prestige which, depending on culture, may involve hunting ability, physical strength, or other locally relevant attributes, as well as his ambition, work ethic, intelligence, social dominance, and age. Several lines of evidence support the hypotheses about women's long-term mate preference adaptations, including self-reported mate preference surveys, reactions to experimental manipulations, ethnographic evidence from pre-industrial cultures, examinations of marital mate choice, and evidence from men's courtship effectiveness and associated fertility outcomes.

Using self-report surveys, Buss and Barnes (1986) were among the first to test whether women (more than men) prefer cues related to a man's ability and willingness to devote resources. They documented women more strongly prefer long-term mates who have a good earning capacity ($d = -0.82$), are a college graduate ($d = -0.60$), and possess intelligence ($d = -0.19$). In 1992, Feingold (1992) meta-analytically reviewed the extant literature (including 32 independent samples) on self-reported mate preferences and found sex differences were prevalent across college students and community samples with women more greatly desiring socioeconomic status ($d = -0.69$), ambition ($d = -0.67$), and intelligence ($d = -0.30$) in potential long-term mates. Numerous additional investigations have since replicated these basic sex differences in long-term mate preferences among college students (Buss and Schmitt 1993; Buunk et al. 2002; Kenrick et al. 1993; Regan 1998; Regan and Berscheid 1997).

In 1994, Sprecher examined mate preferences across a nationally representative sample of the United States and found women, more than men, valued a long-term mate who had a steady job ($d = -0.73$), earned more than they did ($d = -0.49$), was highly educated ($d = -0.43$), and was older by 5 years ($d = -0.67$). In a 2001 cross-generational analysis of identical mate preference questionnaires administered to Americans from 1939 to 1996, both men and women increased valuing the attribute good financial prospects and decreased valuing ambition/industriousness, though the degree of sex differences in these items largely persisted in strength across more than 50 years (Buss et al. 2001).

Cross-culturally, Buss (1989) found across 37 cultures that women, more than men, universally desired a slightly older long-term mate. Buss also documented sex differences in preferences for good financial prospects were nearly universal (97%), and sex differences in preferences ambition/industriousness were prevalent (78%). Others have replicated these cross-cultural findings, documenting sex differences in resource-related mate preferences for good financial prospects, social status, ambition, and slightly or somewhat older age as *pancultural* universals across 100% of more than 50 studied nations (Lippa 2007; Zentner and Mitura 2012).

An additional source of evidence regarding women's hypothesized preferential emphasis on men's ability and willingness to devote resources comes from studies involving reactions to randomly assigned scenarios or actual real-life interactions with randomly assigned experimental confederates. Townsend and Levy (1990) exposed samples of women (undergraduates and law students) to photographic slides of men and had the women rate how likely they would be to date, engage in short-term mating, or engage in long-term relationships with the men. Men's physical ornamentation in the slides was experimentally manipulated to provide cues to high status (i.e., men wore a blazer and Rolex watch), moderate status (i.e., white t-shirt), or low status (i.e., Burger King outfit). The photographs further contained either a physically attractive man or a homely man. Across samples, Townsend and

Levy repeatedly found women preferred to mate with homely/high-status men much more than handsome/medium-or-low-status men, and these effects were most pronounced when women considered the men as *long-term* mates.

Sadalla et al. (1987) had participants view videos of experimental confederates (either men or women) engaging in same-sex encounters within which they were randomly assigned to act as either high in dominance (i.e., upright posture, shoulders straight, move with ease and confidence) or low in dominance (i.e., smiled a lot to appease others, averted their eyes a lot, avoid invading personal space). Women who viewed the videos found high dominance men much more attractive than low dominance men, whereas men did not find high dominance women attractive (see also Ahmetoglu and Swami 2012).

In a real-world test of women's mate preferences for status, Guéguen and Lamy (2012) conducted a naturalistic experiment to evaluate whether women's reactions to a request for their phone number were affected by men's apparent status (in this case, driving different types of cars). Women approached by a man driving an expensive Audi A5 Ambition Luxury gave their number to the man 23% of the time. Women approached by a man driving a mid-priced Renault Mégane gave their number 13% of the time. Women approached by a man driving a 15-year-old Renault 5 Super Campus (worth only a few hundred dollars) gave their number 8% of the time. Women's preferences for resource-related cues appear to affect their real-world mating behavior.

Another test of women's long-term mate preferences for men's ability and willingness to provide resources comes from examining whether the preferences disappear or become sharply attenuated when women have ample resources of their own, as predicted by the structural powerless hypothesis (Buss and Barnes 1986) and traditional social role theory (Eagly and Wood 1999). It could be women prefer cues to men's ability and willingness to provide resources, but only because women are structurally denied access to resources in a particular culture (Buss 1989). Addressing this alternative explanation, Townsend (1989) found women in medical school are *more*

selective of a future mate's financial status, not less. Regan (1998) found as women's mate value goes up, so does their insistence on men's high status and resources (i.e., they "want it all"; see also Buss and Shackelford 2008). Having higher status and resource-related traits appears not to attenuate women's mate preferences for men's ability and willingness to provide resources.

Most studies of real-world *marital* choice find women, but not men, tend to marry partners higher than average in terms of status and resource-related traits (men with well-below average status and resources are more often shut out of the mating market altogether); and women, but not men, tend to marry partners who are older – a potential cue to his accrued status and resource levels (Kenrick and Keefe 1992; Perusse 1994; Trivers 1985). Lichter et al. (1995) found this effect was particularly conspicuous when men are especially plentiful (due to male-biased sex ratios). Thus, women's long-term mate preferences do appear to drive their actual choices in the context of marriage.

In pre-industrial cultures, men's status and hunting ability, and where applicable wealth, are often linked to increased fertility (Betzig 1986; Hurtado and Hill 1992; Smith 2004). Wealth is also linked to increased fertility among men, but not women, in modern cultures (Cashdan 1996; Mealey 1985; Nettle and Pollet 2008). Height, a cue to physical health and interpersonal dominance, is a key factor in both women's long-term mate choice and men's long-term courtship and fertility success (Fink et al. 2007; Nettle 2002; Stulp et al. 2013). Pawlowski et al. (2000) found childless men were 1.25 inches shorter than men with children, and women rate 5'11" as ideal height for partner, but 80% of men's personal ads list their height as 6' or more (Kenrick et al. 1990). Other masculine traits preferred by women have also been linked to increased fertility in men (e.g., deeper voice; Apicella et al. 2007). Some evolutionary psychologists view men's status and dominance contests as more about intimidating other men than about fulfilling women's desires (Puts 2010). Men's long-term mating psychology matters, as well, when it comes to courtship and fertility.

Men's Specialized Long-Term Mating Psychology

According to Sexual Strategies Theory (Buss and Schmitt 1993), men have evolved preferences for cues to youth, health, and genetic quality as these provide signals of a woman's fertility status (i.e., odds of conceiving *currently*) and potential reproductive value (i.e., number of children a woman could have *into the future*). Consequently, men are expected to desire physical features indicative of a woman's relatively youthful age (e.g., neonous face, full lips, clear and glowing skin, clear and wide eyes, small chin, lustrous and long hair, good muscle tone; Sugiyama 2005), to desire physical features indicative of high-fertility estrogen levels (e.g., high femininity in face, voice, finger lengths, and a 0.7 waist-to-hip ratio of body fat distribution), and to desire physical features indicative low genetic mutation load (e.g., facial and bodily symmetry). Additionally, men should preferentially desire attributes that indicate a woman would not be unfaithful in a long-term partnership (deleteriously affecting paternity certainty), has good parenting skills, and would have a compatible personality (Buss and Schmitt 1993).

One source of evidence for evaluating these hypothesized preferences comes from self-report surveys that ask men and women to rate, rank, or nominate what they prefer in long-term mates. In 1986, Buss and Barnes found men ranked physical attractiveness as more important in long-term mating than women do ($d = 0.92$). Feingold (1990) conducted a meta-analysis of self-reported mate preferences surveys and confirmed men prefer physical attractiveness in potential long-term mates more than women do (overall $d = 0.54$). Numerous studies since have replicated these basic sex differences in long-term mate preference for physical attractiveness (Buss and Schmitt 1993; Buunk et al. 2002; Kenrick et al. 1993; Regan and Berscheid 1997). Buss (1989) surveyed long-term mate preferences *across 37 cultures* and found men prefer younger women as long-term mates in 100% of cultures, and men preferred "good looks" in potential long-term mates more than women did across 34 of 37 cultures (92%). In no cultures did women prefer

physical attractiveness significantly more than men did in long-term mates.

In explaining cross-cultural variation in the size of sex differences in preferences for physical attractiveness, Gangestad et al. (2006) showed women's and men's mate preferences for good looks are closely linked to local pathogen levels, with good looks being more important in high pathogen cultures, even after controlling for income, geographical region, and latitude (see also, Little et al. 2007). Lippa (2007) found sex differences in long-term mate preferences for good looks were a *pancultural universal*, evidenced in 100% of 53 nations, with an average effect size of $d = 0.55$. Zentner and Mitura (2012) found sex differences in long-term mate preferences for good looks were a *pancultural universal* across 100% of 10 nations, and counter-intuitively sex differences were *larger* as sociopolitical gender equality increased across nations, with low sociopolitical gender equality nations displaying smaller sex differences ($d = 0.24$) compared to medium ($d = 0.43$) or high sociopolitical gender equality nations ($d = 0.51$). This last finding suggests increased sociopolitical gender equality in a nation does not reduce the size of sex differences in mate preferences. If anything, sociopolitical gender equality increases psychological sex differences (Schmitt 2015).

Sprecher et al. (1994) examined long-term mate preferences in representative sample of the USA and found men, more than women, especially value good looks ($d = 0.65$) and younger age ($d = 0.99$). In a review of mate preferences changes in the USA across 57 years, Buss et al. (2001) found both men and women have increased the relative importance they place in physical attractiveness in long-term mates. However, men's increased ranking of good looks (from 14th place in 1939 to 8th place in 1996) was greater than women's increased ranking (from 17th place in 1939 to 13th place in 1996). It seems the relative emphasis that men, relative to women, place on physical attractiveness has at least persisted, if not grown, across American generations.

Many hypothesized sex differences in mate preferences persist across developmental age, as

well. As men and women get older, sex differences in age preferences become *more* intense. Kenrick and Keefe (1992) found men at age 25 prefer to marry a woman who is about four years younger, with minimum acceptable age of 20 and a maximum age of 30. Women at age 25 would marry a man who is between 25 and 35, ideally about 4 years older. At age 65, however, men would marry a woman between the ages of 50 and 60 (ideally about 10 years younger), whereas at 65 women still want an older man, between 65 and 75 years old. Similarly, Schwarz and Hassebrauck (2012) surveyed 21,245 single people between 18 and 65 (average age = 31) and found men valued physical attractiveness and relative youth more than women, regardless of age or education level. There is one revealing caveat to the youthful desires of men, however. Kenrick et al. (1996) documented that teenage men prefer a mate who is a little older, which was explained as men's preferences being sculpted to desire the highest fertility women (women in their 20s). It is not the case that men simply want someone similar, or perhaps a little younger. Men's long-term preferences for age are anchored by the actual peak fertility levels of women. Finally, studies that have examined long-term versus short-term mate preferences have documented that men's heightened preferences for physical attractiveness and youth are specific to long-term mating.

An additional source of evidence regarding men's hypothesized emphasis on fertility-related cues such as youth and physical attractiveness in long-term mates comes from studies involving personal responses to randomly assigned scenarios or actual real-life interactions with randomly assigned experimental confederates. Meta-analyses of experimental interactions show men react more positively than women do when they personally interact with a highly attractive opposite-sex partner (effect size in men $d = 1.23$; effect size in women half as large, $d = 0.61$; Feingold 1990). Cues related to relative youth and high fertility also show evidence of special design in men's mate preferences. Schaefer et al. (2006) showed men exposed to targets with feminine faces or voices react to those women with greater feelings of attraction.

Johnston and Franklin (1993) had male participants morph female faces until they achieved an “ideal” face. The final female face had geometric proportions indicative of a 14-year-old girl. Many of these cues to youth and fertility are universally valued by men across cultures and time periods (Cunningham et al. 1995; Jones 1995; Langlois et al. 2000). Men across most cultures, for example, prefer feminized faces and body shapes indicative of high estrogen (Perrett et al. 1998; Singh and Young 1995). Men across most cultures prefer waist-to-hip ratios in women that are linked with adaptive estrogen levels and higher fertility (Singh 1993), a preference finding documented even among blind men feeling mannequins (Karremans et al. 2010). It appears many of these specific cues to youth and fertility activate domain-specific areas of men’s brains (Thornhill and Gangestad 1999), especially in the nucleus accumbens (Platek and Singh 2012). One caveat to this is that in cultures with frequent warfare the need for more masculine sons may attenuate the preference for a feminine waist-to-hip ratio (Cashdan 2008). Moreover, cultural variations in disease prevalence, paternal investment, and visual experiences can predictably moderate mate preferences for adaptive physical attributes (see Pisanski and Feinberg 2013).

Behaviorally, when men are experimentally exposed to physically attractive women they react by being more likely to value money, experience greater ambition, are more creative, and are willing to take more risks (Ronay and von Hippel 2010). Conversely, just holding \$2000 in one’s hands elicits in men, but not women, stronger desires to mate with a physically attractive partner (Yong and Li 2012). Men told they were making phone call to a woman lowered their voice (a feature women typically find attractive; Puts 2005), but only if the woman was portrayed in a picture as highly physically attractive (Hughes et al. 2010). Men also give bigger tips to women if they are physically attractive, younger, have larger breasts, and smaller body size (Lynn 2009), buy bigger engagement rings for younger women than older women (Cronk and Dunham 2007), and are more likely pay for dinner

if their date is physically attractive (with no such effects seen in women; Stirrat et al. 2011).

If men’s preference for physical attractiveness in long-term mates is a psychological adaptation, physically attractive women should tend to have more children (assuming no modern confounds such as contraception use). In a study of 88 postmenopausal Austrian women from a rural community, among those who did not use contraception in their lifetime, higher objective symmetry, facial femininity, and overall physical attractiveness were linked to having more children (Pflüger et al. 2012). Women who have lower testosterone (Barrett et al. 2012) and higher estrogen (Law Smith et al. 2012) tend to be more feminine and have fertility-linked traits such as wanting more children. Women who, in their grade school photos, are judged more physically attractive have higher lifetime fertility (attractive women had 11% more children than those who were unattractive; Jokela et al. 2010) and are more likely to be married (Harper 2000). Hill and Hurtado (1996) found physically attractive women among the foraging Ache foragers also have higher lifetime fertility. In a study of women who do not use contraception, physically attractive women were found to have more children (Pflüger et al. 2012). These results provide supportive evidentiary breadth for viewing men’s preferences for long-term mates who are physically attractive as evolved psychological adaptations.

Perhaps the strongest test of the existence of long-term mate preference adaptations comes from analyzing actual marriages, especially who marries whom and how reproductively valuable those choices are over the long run. Most studies have found that men, more than women, tend to marry younger partners who are closer to peak fertility (Kenrick and Keefe 1992; Perusse 1994). As men age, this mate preference mechanism results in newly married men marrying younger and younger women (Kenrick et al. 1990). In the United States, the average man’s first marriage is to a woman who is 3 years younger, the average man’s second marriage is to a woman who is 5 years younger, and the average man’s third marriage is to a woman who is 8 years

younger (Guttentag and Secord 1983). In a study of the wealthiest 400 people in the United States, wealthy men tend to be married to someone 7 years younger, and among second marriages wealthy men are married to someone 22 years younger, on average (Pollet et al. 2013). Wealthy women's spouses, in contrast, did not differ in age from the general population of the United States. In Sweden, a retrospective look at marriages in the 1800s found the average man's second marriage was to a woman 11 years younger (Guttentag and Secord 1983). Also in Sweden, men who marry first wives who are 6 years younger have the highest levels of lifetime fertility (Fieder and Huber 2007). Long-term mate preferences for youth appear to pay men actual dividends in the currency of reproductive success.

As noted earlier, men who have higher social status tend to emphasize physical attractiveness more in potential long-term mates. Researchers have found men with more masculine or male-typical psychologies tend to prefer feminized female faces (Smith et al. 2010), as do men who consider themselves more attractive to the opposite sex (Burris et al. 2011; Kandrik and DeBruine 2013), and those who have high testosterone (Welling et al. 2008). When men can afford to, they insist on physically attractive mates. Gay men and heterosexual men show very similar long-term mate preferences with physical attractiveness being critical to both (Bailey et al. 1994), suggesting that mate preference adaptations for physical attractiveness are specific to the psychology of the desirer (men), not the biological sex of the target of desire (whether men or women).

Conclusion

Several lines of evidence confirm the existence of women's and men's long-term mate preference adaptations, including self-reported mate preference surveys, reactions to experimental manipulations, historical records, ethnographic evidence from pre-industrial cultures, examinations of actual mate choice, and evidence from courtship effectiveness and associated fertility outcomes.

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Sex Differences in Mental Rotation

► Sex Differences in Spatial Abilities

Sex Differences in Morbid Jealousy

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Synonyms

Conjugal paranoia; Delusional jealousy; Othello jealousy; Pathological jealousy

Jealousy is an affective response to a real or perceived threat to a valued relationship by a rival, as is seen in sexual, romantic, familial, and platonic relationships. Jealousy may be functional because it elicits a response that aims to restore that relationship. For example, sexual jealousy motivates the individual to secure exclusive sexual access to one's partner (see "Jealousy" entry).

Though levels of romantic jealousy are approximately equal between men and women, men tend to react more negatively to sexual infidelity, whereas women tend to react more negatively to emotional infidelity (Bendixen et al. 2015; Easton et al. 2007; Sagarin 2005; Schützwohl 2004). Theoretically, sexual infidelity is more costly for men because it increases the risk of cuckoldry, loss of partner, and enhances the reproductive success of rivals, whereas emotional infidelity is more costly for women because it may indicate that a partner is redirecting time and resources to a rival.

There are times when romantic jealousy is hypersensitive and no longer functional. One such example is *morbid jealousy* (also referred to as *pathological jealousy*, *delusional jealousy*, *Othello syndrome*, and *conjugal paranoia*; Easton et al. 2007). A morbidly jealous individual experiences persistent, extreme, and irrational beliefs

surrounding their partner's sexual and/or emotional infidelity without any logical evidence (Kingham and Gordon 2004). Symptoms may include delusions, accusations, stalking, threatening, or spying, which may result in domestic violence, suicide, or homicide (Soyka and Schmidt 2011; Mullins 2010; Seeman 2016). These behaviors are costly because they use time and resources to combat a nonexistent or exaggerated threat (Kingham and Gordon 2004) and can be quite costly as it sometimes results in suicide or homicide.

Morbid jealousy may be a disorder of sexual and emotional jealousy mechanisms. Easton, Shipper, and Shackelford (Easton et al. 2007) tested this hypothesis by reviewing case histories from individuals diagnosed with morbid jealousy. Specifically, they found that among those with morbid jealousy, more men than women showed signs of sexual jealousy, whereas more women than men showed signs of emotional jealousy. Also similar to non-clinical samples, men's description of rivals, more so than women's, focused on their status and resources, whereas women's description of rivals, more so than men's, focused on youth or physical attractiveness. These data are consistent with the notion that morbid jealousy is a disordered manifestation of evolved jealousy mechanisms.

Conclusion

Men and women show differences in the symptoms of morbid jealousy.

Cross-References

- Jealousy
- Jealousy: Psychiatric Diagnosis

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Sex Differences in Navigation

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Synonyms

Division of labor; Navigational strategies; Reproductive roles; Sexual dimorphism; Spatial abilities

Definition

Some of the few reliable differences between women's and men's cognitive abilities are in the domain of spatial cognition. While reflecting a number of social, cultural, and experiential

factors, these cognitive sex differences have also been attributed in evolutionary accounts to a number of ultimate causes. In these accounts, men and women were inhered with some differentiated spatial abilities and predispositions over evolutionary time – distinctions which reflected the specific adaptive problems that confronted women and men in their respective reproductive roles and primary foraging labors.

Introduction

The necessity of navigating the environment has undoubtedly constituted a powerful selective force on the cognitive abilities of humans for encoding, representing, remembering, and using spatial information (Silverman and Eals 1992). Any individual who leaves their home is at risk of becoming lost and separated from their group – which in ancestral environments and hunter-gatherer societies would present many potential dangers including exposure to the elements, predators, hostile people, and other physical hazards. Males and females develop and survive in the same physical world – and should correspondingly have largely similar cognitive mechanisms for navigating (Shepard 1994). However, natural and sexual selection may, in some cases, have impacted men and women differently and brought about distinctions in their spatial abilities through modification, elaboration, or enhancement (Geary 1995).

There is long-standing evidence and general acknowledgment that some of the most reliable sex differences are in the domain of spatial perception and representation. These sex differences for mental rotation (Silverman et al. 2007), object location memory (Silverman and Eals 1992), and wayfinding (Malinowski and Gillespie 2001) have been central to many theories – and debates about – the origins of such sex differences. Although these differences have been variously ascribed to proximate causes of a biological (e.g., neurological structures and hormones) and socio-cultural nature (e.g., experience and stereotypes), a number of evolutionary accounts have been advanced which vary

considerably in their explanatory scope, weight of empirical support, and emphasis on either reproductive roles and strategies or on foraging activities as their ultimate causes.

Spatial Cognition in Women and Men

Many decades of research have led to the consensus that spatial abilities are among the few domains of cognition that reliably differ between men and women – seminally documented as only one of four domains to be considered well-established by Maccoby and Jacklin (1974) and later confirmed in a number of meta-analyses (e.g., Voyer et al. 1995). The effect sizes of these differences do depend greatly, however, on the particular type of spatial ability being considered. Although many tasks reveal no, or only small sex differences, there are large and reliable sex differences in which men outperform females in tests of spatial perception – identifying spatial relations among distracting information, and spatial visualization – the mental transformation of spatial information in multiple stages. However, it is the third ability identified in these influential meta-analyses, mental rotation, that exhibits the largest and most reliable male advantage. Men’s greater abilities for imagining and transforming mental representations of two- and three-dimensional objects have been extensively and cross-culturally replicated (Silverman et al. 2007). These well-founded male advantages for mental rotation and other spatial abilities, along with the later discovery of women’s superiority at remembering object locations (Silverman and Eals 1992), have been focal points in the debate about whether men and women do have any inherent cognitive differences – unlike their similarities in so many other cognitive abilities (Hyde 2005).

Such sex differences in spatial abilities were, early on, largely considered from influential perspectives as the consequences of socialization and learning, as well as gender identity, roles, and stereotypes (see Eagly and Wood 2013 for review). Empirical evidence has steadily accrued that these socio-cultural factors

can moderate – if not necessarily cause – such sex differences. Despite the general acknowledgment that spatial abilities are the results of socio-cultural factors interacting with innate abilities and predispositions (cf. Eagly and Wood 2013), these proximal factors have been investigated largely in parallel with the more distal accounts advanced from an evolutionary perspective. A number of evolutionary hypotheses have been proposed, starting with those arising out of comparative studies of spatial cognition (i.e., mating systems), and later from those domains increasingly unique to human beings (e.g., the sexual division of foraging labor). These adaptationist theories, though distinct, are largely divisible into two groups according to their emphasis on the underlying selective pressures – whether focusing on the differences in women and men’s reproductive roles and strategies or their primary activities for obtaining nutritional resources.

Home Ranges

Sexual selection is more likely than natural selection to bring about phenotypic differences between the males and females of a species (Trivers 1972). Unsurprisingly, the first – and most of the adaptationist accounts to follow – concerned how differences between females’ and males’ reproductive roles and strategies could have brought about such differences in their spatial abilities. A first theory of this kind, though now largely set aside, was based on natal dispersal – wherein the sex which travels further from its birthplace to its breeding site should be proportionally more proficient at navigating (Silverman and Eals 1992). However, in humans, juvenile dispersals are larger by females (Koenig 1989), whereas males perform better at the relevant spatial tasks (e.g., wayfinding; Moffat et al. 1998; Silverman et al. 2000). Likely, the more relevant metric of overall mobility to sex differences in humans is that of home range size – the area in which an individual lives and customarily navigates throughout while pursuing resources, seeking mating opportunities, and caring for

offspring. Differences in home range sizes between the males and females of a species commonly reflect their mating system (Gaulin and FitzGerald 1986) – notably in polygamous species in which the males travel more extensively in their competitive efforts to mate with multiple females. Gaulin and FitzGerald reasoned that the larger home range of males in such species – and the greater information-processing requirements in reaching potential mates – would bring about a corresponding enhancement in their spatial abilities (1986). This relationship between spatial abilities and range size as a function of mating system was supported in their oft-cited series of studies comparing monogamous and polygamous species of voles. Males of the polygamous species had larger home ranges, spatial abilities superior to females of the species, and larger neural structures implicated in spatial navigation. By comparison, males of the monogamous vole species did not differ significantly from the species' females with respect to home range size, spatial abilities, or their associated neural structures (Jacobs et al. 1990).

Human males do exhibit an early-appearing and persistently larger home range than females (Ecuyer-Dab and Robert 2004). Several avenues of anthropological and comparative research suggest that humans are a mildly polygynous primate species (Alexander et al. 1979; Low 1988) and have been for most of their history – a characterization that population genetic research is increasingly supportive of (e.g., Dupanloup et al. 2003). Studies of the Tse and Tjimba of Namibia, for instance, illustrate this scenario – males travel more extensively than women, and those men travelling further father children with more women (Vashro and Cashdan 2015). This first systematic account of sex differences in spatial abilities does, therefore, readily anticipate a male advantage in human spatial abilities, as it does for analogous effects in other animal species. However, the core relationship of this mating-competition hypothesis between range size and spatial abilities is equally central to other accounts but which attribute the differences in range size to other domains of selective pressures such as foraging activities and warfare.

Reproductive Roles

Another account concerning the reproductive domain, the fertility and parental care hypothesis, proposes that such range size differences result, at least in part, from selection pressures on females to reduce their spatial abilities during particular reproductive periods (Sherry and Hampson 1997). The greater dependence of offspring on the continued survival and parental efforts of the mother (Campbell 1999) may have acted selectively on females to more closely circumscribe their travel and exposure to dangers (Sherry and Hampson 1997). Females far less frequently involve themselves in aggressive situations (Wilson and Daly 1985), primarily pursue gathering (Marlowe 2007) and – if any – lower-risk hunting strategies (e.g., trapping and netting; see Ecuyer-Dab and Robert 2004 for discussion), and are less inclined towards long-range navigating – an energetically costly and hazardous activity in natural environments (Ecuyer-Dab and Robert 2004). This hypothesis also accounts uniquely well for a number of related characteristics such as females' greater anxiety (Lawton 1994) and lower confidence in navigation (Picucci et al. 2011) and a systemic relationship between spatial cognition and the fluctuation of female sexual hormones (Hampson 1990).

Considerable evidence supports the organizational and activational effects of sex hormones on spatial abilities (see Liben et al. 2002 for review). The fertility and parental care hypothesis provides a structured adaptationist rationale for their effects in sexually mature adults, beyond that of conventional perspectives in which sex hormones are seen as proximal, yet sufficient causes in themselves of such differences (cf. Miller and Halpern 2014). The fertility and parental care hypothesis finds these proximal mechanisms on more distal causes – that women's spatial abilities and mobility are decreased in rough correspondence with periods of potentially elevated reproductive and childrearing demands (Sherry and Hampson 1997). In line with such reasoning, women's lowest performance in spatial tasks is observed during the periods of highest estrogen levels in their cycle (e.g., Hampson 1990) and during pregnancy

(Woodfield 1984). Conversely, women's best performance in some spatial tasks is observed during the low-estrogen phase of the monthly cycle when they perform comparably to males (e.g., Chabanne et al. 2004). It has also been strongly advanced that humans' sexual dimorphic spatial abilities might reflect compounded selection pressures acting to both increase men's spatial abilities while conversely curbing women's spatial abilities and mobility during particularly important reproductive periods (Ecuyer-Dab and Robert 2004).

One other account of sex differences in spatial abilities – more complexly related to reproductive strategies – concerns the far greater involvement of males in hunter-gatherer societies in small-scale warfare (Daly and Wilson 1988). In one of the earliest proposals relating intrasexual competition to spatial abilities in humans, Geary (1995) advanced that long-range expeditions to ambush and raid other groups of people carried out mostly, if not entirely, by men would have selected for their greater large-scale navigational abilities. In hunter-gatherer societies, such high-risk forays figure prominently in male mortality and individual differences in male reproductive success. By this account, mental rotation and a number of other dynamic spatial abilities that show a male advantage – such as estimating velocities, and intercepting and throwing objects – may have arisen for other purposes, notably physical competition and warfare (see Ecuyer-Dab and Robert 2004 for review).

Sexual Division of Labor

An entirely different domain of selection pressures has been emphasized in a prominent evolutionary account – one concerning how women and men have primarily obtained nutritional resources and the division of foraging labors between hunting by men and gathering by women. In the overarching sexual division of labor hypothesis, women are purported to have been largely engaged in gathering sessile plant resources and catching small game within smaller ranges whereas men predominantly hunted for larger

game animals over greater ranges (Silverman and Eals 1992). Although the hypotheses concerning reproductive goals and strategies have principally addressed men's greater performance in tests of spatial abilities, the closer consideration of spatial skills necessary for successfully gathering and for hunting have provided finer-grained expectations about men's and women's relative strengths and weaknesses in spatial cognition. Rather than presuming that one sex possesses roundly superior spatial abilities, the predominant engagement of women in gathering and of men at hunting may have separately enhanced, modified, or elaborated each spatial ability in proportion to their usefulness for foraging activities – enhancing those spatial abilities that would have proven especially useful to women in their gathering activities and to men in their hunting activities (Silverman and Eals 1992).

In their sexual division of labor hypothesis – also termed the hunter-gatherer hypothesis for its emphasis on foraging labors – Silverman and Eals advanced that humans' sexual dimorphism in spatial abilities reflected the primary engagement of women in gathering and of men in hunting over evolutionary time (1992). The sexual division of labor hypothesis is one of the most extensively articulated – and empirically tested – evolutionary accounts of spatial sex differences. It is a long-held and extensively supported feature of hunter-gatherer societies that men have predominantly hunted and women primarily gathered (e.g., Marlowe 2007) – although this sexual division of labor may have emerged more recently in human evolutionary history than commonly presumed (e.g., Kuhn and Stiner 2006). Whenever this division emerged, many of the greater abilities that males exhibit in spatial tasks would have undoubtedly proven advantageous to males in their hunting of large, mobile game over large distances and over unpredictable routes. As Silverman and Eals originally cite – and which have been more thoroughly evidenced since – males are especially capable at mentally rotating objects (e.g., Voyer et al. 1995), reading maps (e.g., Malinowski 2001), and learning mazes (e.g., Moffat et al. 1998). Of these spatial abilities, the male advantage is largest and most reliable for

mental rotation – an ability for representing and transforming spatial information which has been related to navigation skills (Hegarty et al. 2006; Malinowski 2001; Moffat et al. 1998) and is likely subserved by some of the same neurological mechanisms (see Saucier et al. 2002 for discussion). In tests of wayfinding, individuals identify their position and then navigate to an unseen target location – a critical spatial competence for successfully hunting and efficiently transporting game directly home. Men have been found in the majority of studies to perform better in general wayfinding tasks (Coluccia and Louse 2004), whether in virtual (e.g., Moffat et al. 1998; Sandstrom et al. 1998) or real-world environments (Malinowski and Gillespie 2001; Silverman et al. 2000).

The general advantages for males at large-scale wayfinding may also reflect sex-specific tendencies to use navigation strategies that are best suited for larger ranges – in addition to the underlying spatial abilities that differ between men and women. Men typically favor the use of top-down, survey representations of their environment, and navigate with respect to cardinal directions, physical distances, and relatively few landmarks (Lawton 2010). These orientation strategies are positively correlated with successful navigating (Hegarty et al. 2006) and may have proven an optimal approach for traversing larger and less-familiar spaces over new and erratic courses (Ecuyer-Dab and Robert 2004). Men's advantages for wayfinding at the environmental scale may result, in part, from their greater reliance than women on Euclidean strategies and more distal information to navigate. Accordingly, this difference between men and women's abilities for navigation can be sizably reduced, or even eliminated, by testing participants in a smaller, indoor environment where distal, absolute information (i.e., cardinal directions) is unavailable (Sandstrom et al. 1998).

The sexual division of labor hypothesis readily accounts not only for the male advantages in spatial abilities but also for the spatial task in which women are uniquely found to consistently outperform men. First reported by Silverman and

Eals (1992) in support of their hunter-gatherer theory, women were found to have superior memory for the locations of objects in an array. Although the effect size of females' advantage for object location memory is smaller than that of men's advantages for mental rotation, it has been oft-replicated (Choi and Silverman 1996; Dabbs et al. 1998), and demonstrated in adolescents and adults (Voyer et al. 2007), in paper-and-pencil tasks and real-world environments (Silverman and Eals 1992), and in most of the ethnic groups and countries tested thus far (Silverman et al. 2007).

This female advantage for object location memory (OLM) has been largely demonstrated in small-scale spatial tests (e.g., desktop) – a scale at which gatherers were theorized to commonly search for, and periodically revisit, food plants in complex banks of vegetation (Silverman and Eals 1992). However, gathering also requires navigating to, and often between, the locations of potential nutritional resources over far greater distances than OLM appears to function. There is some evidence that females may be advantaged in their survey (geometrical) representations of gathering-relevant locations over greater spatial ranges (New et al. 2007). These demonstrated abilities for precisely encoding and recalling the locations of particular items may have been selectively enhanced in women in support of their primary foraging efforts – notably the periodic return to locations of potential nutritional resources such as fruiting trees and traps set for smaller prey.

Whereas men favor Euclidean approaches that rely less on landmarks, women generally favor non-Euclidean spatial strategies – navigating according to environmental information (i.e., landmarks) along specified routes when available (Dabbs et al. 1998; Lawton 2010). This makes the ability to implicitly encode navigational landmarks particularly useful for women. Accordingly, women possess better knowledge of landmarks than of Euclidean knowledge (Sandstrom et al. 1998), navigate better when using landmark information (Saucier et al. 2002), and provide more landmarks and landmark relationships when giving directions (Choi and

Silverman 1996; Dabbs et al. 1998). Whereas Euclidean strategies may have been optimal for hunting over larger and less familiar ranges, landmark strategies could have proven more useful to gathering activities in smaller and more familiar areas. Destinations with routes specified by orienting and confirming landmarks can not only be followed accurately, efficiently, and reliably – they can themselves be easily and accurately communicated to others.

Conclusion

Navigating the physical environment has constituted a powerful and constant selective force on humans – bringing about considerable cognitive abilities in women and men for learning and using spatial information. These spatial abilities, however, constitute one of the relatively few domains in which males and females demonstrate substantive and reliably different cognitive capacities. Such abilities – and noted sex differences – are undoubtedly attributable in some part to social, cultural, and experiential factors (Coluccia and Louse 2004). However, a number of evolutionary frameworks have advanced that there are also inherent differences between females' and males' capacities and predispositions for spatial knowledge and reasoning. These theories about the sexual dimorphism of human spatial cognition have been largely motivated by either an emphasis on males' and females' different reproductive roles and strategies or by their primary foraging activities in ancestral environments. These evolutionary frameworks account for many recognized sex differences in spatial cognition – such as the male advantage for wayfinding and mental rotation – and have been uniquely predictive of specific spatial tasks and contexts in which females outperform males (e.g., OLM). However, further research is necessary to determine the unmoderated extent of such sex differences, which adaptive pressure(s) caused their engrainment in human spatial cognition, and the processes in which these inherent differences interact with social, cultural, and experiential factors.

Cross-References

- [Coalitional Hunting](#)
- [Unknown territory](#)

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Sex Differences in Parenting

► Paternal Investment Relative to Maternal Investment

Sex Differences in Parenting and Parental Investment

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Synonyms

Biparental care; Maternal investment; Paternal investment; Sexual asymmetry; Sexual dimorphism; Sexual selection

Definition

In many animal species, including humans, females tend to invest more heavily in their offspring than males.

Introduction

In general, parenting costs parents. As parenting usurps parents' resources, they may lose additional chances of mating and having children in the future. Many species, in fact, show no engagement in parental care (Alcock 2009). However, parenting might enable the offspring to succeed, survive, and reproduce, which offers larger benefits that outweigh the costs (Bjorklund et al. 2002). Many animal species, including humans, engage in parental care, although it is relatively rare among animals as a whole (Alcock 2009). Particularly in mammals, parenting is crucial for rearing an offspring, because mammalian babies are weaker at birth. Despite the necessity of parenting, males and females do not equally invest their resources in their offspring. There is variation among animal species in terms of the sex that primarily engages in parental care (Reynolds et al. 2002). Both males and females are apt to specialize in their parental care, often with a clear division of labor by sex (Clutton-Brock 1991; Emlen and Wrege 2004; Itzkowitz et al. 2001). In many cases, females specialize in caring for their

offspring and providing parental care much more than males do (Bjorklund and Pellegrini 2002; Geary 2000, 2010). These sex differences in parental investment can be explained by (1) anisogamy, (2) mating opportunity cost, and (3) paternity uncertainty.

Background

Although there are some species that do not provide parental care to their offspring, many animal species exhibit parenting behaviors. The level of parental investment provided by females and males varies according to species. In many species, females invest much more resources in their offspring than males do. Although parental care from males is relatively rare; paternal care, which generally includes provisioning and/or protecting an offspring, is observed in some species of birds, fishes, and insects (Perrone and Zaret 1979; Thornhill 1976; Wolf et al. 1988). For example, male birds often build nests and feed their offspring. Among some primates, carnivores, and rodents, males provide a great deal of parental care; however, they provide paternal investment in their offspring in less than 5% of mammals (Clutton-Brock 1991). In addition, many mammalian males often give care indirectly, such as by guarding crops. Moreover, parental care by males has been reported in many primates. According to these findings, males do provide parental care to their offspring, although male parenting is relatively rare (Hrdy 2000). However, sex differences in parental investment, namely, that females invest more heavily in their offspring than males do, are consistent for many species. Various factors have been alleged as reasons behind these sex differences: (1) anisogamy, (2) mating opportunity cost, and (3) paternity uncertainty. Each of these points is discussed below.

Anisogamy

Anisogamy refers to differences in reproductive strategies at the gamete level. The gametes of the sexes differ in size; they are larger in females than in males (Trivers 1972). Parental investment

theory holds that parental investment is a burden on parents. Various factors of life history relevant to the costs and benefits of caring and competing become specific to each sex. Therefore, Trivers' work implies that there are differences in parental investment between males and females.

Reproductive strategies might require resource allocation trade-offs between investments in mating effort and parental effort. For males, investing in mating efforts means mating with as many females as possible, which maximizes the number of offspring. Parenting effort involves investing resources, such as energy, time, and money, into a smaller group of the long-term mating partner and offspring, resulting in influencing the survival of the offspring. At the gamete level, as females produce eggs, which are much larger than male sperms, they have made a larger premating parental investment than males. In contrast, as males produce small, cheaper sperms rather than large, costly eggs, males are able to refill their gametes and more quickly go back to the mating market than females can. In other words, male ejaculations are considered smaller total amounts of gametic investment per mating than the gametic investment in the eggs released by females. Thus, the female bias in investment can be explained by the sex differences in gamete sizes that are a form of premating parental investment (Trivers 1972, 1983).

This phenomenon, that asymmetries in gametic investment are amplified to distinct sex roles in a self-reinforcing manner, is called sex-role divergence (Kokko and Jennions 2008). Trivers (1972) argues that two distinct interpretations might explain the divergence in sex roles. First, compared to males, females are more inclined to provide parental care, because females do not wish to lose their past premating investment. Second, compared to females, males are more inclined to compete for mates due to the male bias in operational sex ratio. Both explanations seem to partly account for sex-role divergence. However, neither is convincing in its association between sex differences in gamete sizes and those in parental investment (Kokko and Jennions 2008). Therefore, sex-role divergence in parenting remains an evolutionary difficult issue.

Mating Opportunity Cost

Parents put their reproductive energy into mating or parenting. As noted above, resource allocation between these two is a trade-off between current parental investment and future reproduction. The mating opportunity cost refers to the extra mating missed due to investment in the offspring. When both male and female are taking care of their offspring, it is quite difficult for them to mate with additional partners. The mating opportunity cost is considered a burden on both males and females. However, males bear a much greater mating opportunity cost than females, because the reproductive strategies by males depend on the availability of fertile females. If the number of fertile females is relatively high (female-biased operational sex ratio), males shift to investing their resources more into mating than parenting. If the number of fertile females is relatively low (male-biased operational sex ratio), males shift to investing their resources more into parental care. There are differences in trade-offs between mating and parenting among the Ache, a hunter-gatherer society in Paraguay, and the Hiwi, a hunter-gatherer society in southwestern Venezuela. Males among the Ache, who have a highly female-biased sex ratio, tend to invest their resources into mating efforts. In contrast, males among the Hiwi, who have a male-biased sex ratio, are likely to invest their resources into parenting efforts (Hurtado and Hill 1992). These findings are consistent with the notion that the mating opportunity cost of parental investment is much higher for males.

As just described, as males bear a greater mating opportunity cost in parenting than females do, males are less inclined to invest their resources into parental care than females. This notion leads to the expectation that male parental care is relatively rare when the mating opportunity cost of males is high (Alcock 2009). Conversely, when the mating opportunity cost of males is low, male parental care is favored. Thus, on an average, parenting and parental investment by males are less than those by females in many taxa. This theory of mating opportunity cost might also explain individual differences in parental care within a particular species. Differences in parenting among the Ache and the Hiwi are a good

example (Hurtado and Hill 1992). Pedersen (1991) investigated secular trends in human sex ratio and showed that male-biased sex ratios are associated with lower divorce rates (long-term mating strategies) and male willingness to commit care for their offspring. This finding is consistent with the mating opportunity cost theory.

Paternity Uncertainty

In nature, maternity is always certain; in other words, mothers are absolutely sure about their genetic contribution to their offspring. In contrast, paternity is never absolutely certain, that is, fathers can never be sure about their genetic relatedness to the offspring. This doubt regarding biological fatherhood is termed paternity uncertainty. In species that have concealed ovulation and/or internal fertilization, paternity uncertainty is a major problem for males. Due to internal fertilization, a new offspring might not be genetically related to a given male. Thus, possibly, males insidiously invest their resources into another male's offspring. The cost derived from misdirected parental investment makes paternal care less beneficial for males. Therefore, this asymmetry in parental certainty is conducive to sex differences in parental investment (Bjorklund and Shackelford 1999; Dawkins and Carlisle 1976; Geary 2000).

Paternity uncertainty has a relatively large influence particularly on human parental care. Since physical anthropometric traits are highly heritable (Canela-Xandri et al. 2016), greater similarity between a father and his offspring implies more paternity certainty. Therefore, fathers who perceive resemblance between themselves and their children are expected to provide more investment into parental care. In fact, perceived similarity between fathers and their children is correlated with emotional closeness (Alvergne et al. 2010) and with paternal investment (Apicella and Marlowe 2004) reported by fathers. These empirical findings support the notion that greater paternity uncertainty is associated with less paternal investment, which might cause sex-based differences in parenting and parental investment.

The foregoing mainly focus on the reduced amount of parental investment by males. On the

contrary, females are absolutely certain of their parenthood and have less mating opportunity cost than males. Due to these advantages of females, they should favor parental care. The primary caretaker hypothesis argues that the sex that cares more for an offspring will differentially obtain the skills necessary for parenting (Babchuk et al. 1985). For example, females, generally the primary caretakers, show a stronger preference for infants and a greater motivation to look after infants than males do (Charles et al. 2013). These female skills are evolved adaptations that enhance the odds of the survival of one's offspring (Babchuk et al. 1985). This primary caretaker hypothesis can clearly explain the intense, highly obligating maternal investment.

Conclusion

Parental investment by males is relatively rare, and even if males invest in parenting, the level of their investment is usually less than that of females. This sex difference in parenting and parental investment is found in many animal taxa. There are various reasons why males provide less parental investment in their offspring than females do. Anisogamy, the initial bioenergetic allocation of parental effort, might explain the sex differences in parental investment. In addition, sex differences in mating opportunity cost and in parental certainty might also give some account for the asymmetry in parental investment. Sex differences in parental investment embrace both the relatively low paternal investment and the generally abundant maternal investment. The arguments here generally focus on the relative amount of parental investment by males; however, the primary caretaker hypothesis might provide an account of female maternal investment.

Cross-References

- [Parental Investment and Parenting](#)
- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Paternal Investment](#)

- [Paternal Investment Relative to Maternal Investment](#)
- [Paternity Uncertainty Hypothesis](#)

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Sex Differences in Participation

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Synonyms

[Gender differences](#); [Gender schema](#); [Sex typing](#)

Definition

Because of societal expectations around gender roles, individuals generally engage in behaviors consistent with their gender role and avoid acts

that are not, leading to significant sex differences in participation within certain activities like politics, sports, and mathematics.

Introduction

Sex differences in participation have been found within many different domains of life, such as participation in politics, sports, and mathematics. While some contend that these discrepancies are due to biological influences and differences, they are often found to instead be the result of societal and cultural influences that enforce a strict gender dichotomy on individuals, pressuring people to only participate in those domains deemed “appropriate” for their sex while discouraging participation in domains regarded as “inappropriate” for their sex.

Gender Schema Theory

Introduced by Sandra Bem in 1981, the *gender schema theory* argues that societal forces construct strict gender roles that individuals learn from and adhere to, which become assimilated and passed down to other individuals within a culture. A schema is a “cognitive shortcut” or a tool that is used to process incoming information in a quick and efficient way. According to the gender schema theory, individuals are more likely to relate with information consistent with their gender schema and are quicker to identify gender-appropriate information. Consistent with this, individuals who complete the Bem Sex-Role Inventory (BSRI) rate characteristics that are consistent with their gender role as being more relatable to themselves than those that are inconsistent (Bem 1981).

The gender schema theory underlines society’s insistence on a gender dichotomy, labeling certain actions and behaviors as “feminine” and meant for females, while others are thought of as “masculine” and strictly for males to participate in. The gender schema theory has important

implications for human beings. As they begin to learn about societal constructs and gender roles, people internalize the characteristics and attributes that are believed to be “appropriate” for their gender and attempt to act in accordance with these. Individuals learn to assess their self-esteem and self-worth according to their conformity to the gender roles placed on them by society. People will often adjust their behavior and characteristics to ensure they are engaging in things deemed “appropriate” for their sex and refraining from things that are not, so as to avoid being condemned by society. Thus, gender schemas can lead to significant disparities in the participation of males and females in certain activities that may not be stereotypically “appropriate” for their sex (Bem 1981).

Sex Differences in Political Participation

Research has shown significant sex differences exist within participation in politics, with women thought of as being less involved in politics than their male counterparts. This discrepancy in political participation has led many to speculate on the potential reasons why: some say that socio-economic resources are less available to women, while others attribute it to societal constraints and gender norms that discourage women’s participation in politics, an often male-dominated field (Coffé and Bolzendahl 2010). However, this disparity brings into question whether these sex differences exist throughout all forms of political participation – maybe women do not necessarily participate less in politics, but rather they engage in politics differently.

Researchers Coffé and Bolzendahl (2010) investigated this question using data from the 2004 International Social Survey Program (ISSP) and examined men and women’s participation in four domains within politics: private political action, political party membership, collective activism, and political contact. The researchers found that women do not in fact participate less than men in politics, but rather they invest their efforts differently. Women participants were found to be significantly more

involved in private political action than men, which entails actions such as signing petitions, donating or raising money for political reasons, and boycotting and/or marching for political action.

Sex Differences in Sports Participation

It is undeniable that sports are often considered by many to be a masculine realm. However, too often this is considered to be the result of biological influences rather than societal and cultural influences – many individuals postulate that discrepancies between men and women’s participation in sports is attributable to physical differences that naturally put men at an advantage for participating in sports. While physical and biological differences between the sexes do exist, these differences do not adequately account for the significant sex differences within participation in sports (Chalabaev et al. 2013). Instead, it is necessary to consider the cultural and societal forces that contribute to such differences.

Gender norms and stereotypes have a significant influence on the sex differences seen in sports participation. Sports are often categorized as being masculine, feminine, or neutral, based on the percentages of each sex that participate in them; for example, soccer and football are considered to be “masculine” sports, while gymnastics and dancing are thought of as “feminine” sports. These “masculine” sports are often considered to be representative of what sports as a whole are – when asked to portray what sports and a sportsperson look like, both male and female adolescents drew pictures of a male playing soccer, indicating that this is the stereotypical representation of what sports *should* be. Such representations create a stigma around females who choose to participate in sports, especially “masculine” sports. Women who do choose to participate in “masculine” sports are often regarded as less “feminine” and aesthetically pleasing; these conceptions of women in sports frequently discourage their participation in such sports (Chalabaev et al. 2013).

Sex Differences in Mathematics Participation

Large sex differences exist within the field of STEM. Female adolescents, especially racial minorities, are significantly less likely to enroll in all mathematics-based AP courses, including computer science, calculus, statistics, etc. (College Board 2016). According to data collected by the National Science Foundation in 2010, women comprised only 27.5% of all STEM-related jobs (National Science Foundation 2010). Some have proposed that men are more represented and exhibit higher achievement within STEM because of intrinsic differences between males and females that favor men’s performance in mathematics. However, cognitive research has shown that there is no empirical evidence to support that either sex is inherently better than the other in terms of mathematics ability (Buckley 2016). Instead, empirical evidence has demonstrated that males and females have similar abilities within mathematics and learn mathematical concepts in the same ways (Spelke 2005). It is evident that women are significantly underrepresented within the STEM field and that these differences are not due to intrinsic capabilities, which begs the question: What contributes to these immense sex differences in participation in STEM?

A study conducted by Fryer and Levitt (2010) found that there were no differences between males and females’ achievement in mathematics when children first entered school; however, after 6 years of enrollment within school, significant sex differences emerged, with females displaying lower levels of achievement and participation compared to their male peers. Initially, some put forth the idea that men and women are neurologically different, enabling men to be “superior” at mathematics – however, this idea was proven to be ultimately unfounded, as there is not sufficient research supporting the idea there are profound differences between the male and female brain. Instead, these sex differences in mathematics participation seem to be the result of socialization rather than differences in

apptitude, such as differential treatment from teachers or parental expectations, with males' participation in mathematics being favored and encouraged while dissuading females from participating. Women appear to have as much aptitude as men for participating and succeeding in mathematics; however, socialization and gender stereotypes ultimately discourage women from entering and succeeding in mathematics (Fryer and Levitt 2010).

Conclusion

While it is unequivocal that sex differences exist within many domains of life, these discrepancies do not seem to exist because of inherent distinctions between men and women's biology. Instead, these differences are often attributable to societal influences and the process of socialization. Beliefs about the role of gender in society significantly contribute to what members of each sex decide to engage in, encouraging individuals to pursue things that seem "appropriate" for their sex and avoid those that are "inappropriate." In order to reduce sex differences in participation, it is important to treat men and women equally and try to avoid unconscious bias that discourages individuals from participating in behaviors solely because of their sex.

Cross-References

- [Emergence of Social Reasoning About Hierarchies](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Gender Schema](#)

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Sex Differences in Pursuit

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Synonyms

[Hierarchy](#); [Social standing](#); [Within-group competition](#)

Definition

Competition for achieving and maintaining positions of high social standing.

Introduction

Humans are group-living mammals, and our societies consist of stable dominance hierarchies,

defined as a set of relationships based on a structured ranking (Clutton-Brock and Huchard 2013). These social hierarchies can be either informal such as family units or formal such as governments or corporations. Obtaining a position of high status, i.e., an individual's prominence, respect, and influence in the eyes of others, should offer benefits to the survival and fitness of both sexes (Anderson and Kilduff 2009), for example, by leading to increased access to resources and mates – boosting survival and resulting in greater reproductive success. The route by which high social status is achieved, however, can be different for males and females.

Classic parental investment theory suggests that females should not be engaging in aggressive behavior for mate access due to the differential level of investment in offspring (Trivers 1972). Investment is defined as parental contribution which increases the offspring's survival at the expense of parent's future reproductive potential. As Trivers (1972) stated, "The sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex. Individuals of the sex investing less will compete among themselves to breed with members of the sex investing more." (p. 140)

The typical mammalian pattern of parental investment places human females in the first category, concerned with resources and offspring survival, and human males in second, concerned with access to mates. Therefore, achieving status through aggression and displays of aggression should be a viable strategy for males, but not females. This plays out when one examines differences between male-male and female-female competitive strategies.

Male/Male Competition

While engaging in direct aggression may involve obvious costs such as physical injury or even death, an evolutionary cost-benefit analysis suggests that if the payoff is worth the cost, it's worth engaging in such behavior. For males, aggression displays have two reward outcomes – obtaining

status by winning the conflict and also as a demonstration of formidability level which should reduce the potential of other males risking an aggressive encounter.

Researchers have consistently found that human males are far more likely to engage in direct aggression in the pursuit of status, i.e., behavior intended to cause physical harm or pain, than females. This sex difference in aggressive competitive behavior begins at an early age and continues throughout puberty and beyond. Males are more likely than females to engage in physically aggressive acts during dyadic competition, i.e., one on one, and within groups, i.e., a gang (Campbell 2007).

Indeed, sex differences in aggressive status pursuit behaviors appear to be robust and consistent across the majority of human cultures (Campbell 2007) and may extend back at least 200,000 years (Keeley 1996). Evidence from the fossil record suggests that violent conflict may have been an important selection pressure for our evolutionary ancestors (Keeley 1996).

While it could be said that males are only engaging in physical aggression to protect themselves or family when under attack, apparently trivial motives for violent conflict such as mere verbal insults account for higher rates of aggression and homicide than any other reason (Daly and Wilson 1988). This suggests that the high costs of violence for males are offset by the potential long-term damage to a male's position within the hierarchy by ignoring a challenge, either verbal or physical. In a recent study of university students, 48 % of males stated status concerns as behind their last act of direct aggression (Griskevicius et al. 2009), suggesting that pursuing status through direct aggression is still a common strategy in current-day societies.

Female/Female Competition

According to Trivers (1972) as females need to remain healthy in order care for offspring, they are only expected to engage in direct aggression if the benefits, such as access to needed resources, far

outweighed the costs of risking their life and consequently their offspring.

It is wrong to say that direct female aggression does not occur. For example, in the previously mentioned study by Griskevicius et al. (2009), 45 % of females who had engaged in direct aggression also stated that the purpose was to defend their status. In general however, females avoid direct aggression where possible due to the high risk to themselves and the survival of their offspring (Campbell 2007) and instead rely on other tactics to pursue status, for example, indirect aggression.

Indirect aggression includes behaviors such as verbal critiques of another female's appearance, engaging in malicious gossip such as spreading rumors, and practicing social exclusion. These behaviors have been found to be most commonly directed against attractive and sexually available females and used as a weapon within competitions for status and mates (Vaillancourt 2013).

The strategy is to reduce the relative social standing and mate value of other rival females and thus boost their own. Research on mate preference has shown that males preferentially prefer young attractive females who are not promiscuous and a common indirect aggression strategy involves negative comments against a rival's appearance and spreading rumors about their sexual activity (Vaillancourt 2013). This derogation strategy is consistent with parental investment theory as it holds no physical dangers that could hamper their survival but is still an effective way of beating rivals and gaining status.

Dominance Versus Prestige

So far, the focus has been on the use of aggressive or dominance strategies to gain positions of status, but this is not the only way to ascend to the top of the human social hierarchy. Henrich and Gil-White (2001) have suggested that high social rank in human society can actually be reached by two distinct strategies: either by force, through threat or intimidation (dominance), or achieved freely

through demonstrating unique skills and knowledge (prestige).

In their paper on pursuing status in human social groups, Anderson and Kilduff (2009) presented a review of the evidence of status pursuit strategies that appeared to complement Henrich and Gil-White (2001)'s theory. They suggested that individuals in human societies don't necessarily attain status by bullying and aggressively intimidating others, but rather do it either by acting in a confident manner – and therefore suggesting superior competency – or by behaving in a generous manner, suggesting a commitment to the group as a whole, in other words, using prestige strategies to obtain status. However, Anderson and Kilduff (2009) failed to make any assumptions about whether there would be any difference in the use of this strategy between males and females.

One study by Cheng et al. (2013) helps to throw some light on this topic. Firstly, they found that both dominance and prestige strategies were equally successful in obtaining leadership positions and appeared to be used interchangeable by individuals, contrary to Anderson and Kilduff (2009)'s suggestions. Secondly, when the behaviors of men and women were analyzed separately, the effect sizes of the association between dominance and prestige and the measures of social influence were almost identical, i.e., there were no significant gender differences in the use of either strategies. This suggests that females and males are both adept at using forms of dominance and prestige strategies in the pursuit of status.

Conclusion

While both males and females actively pursue status, there is some difference in the methods they use to do so. Males are more likely to engage in acts of direct aggression to achieve and maintain status, while females use indirect aggression to belittle rivals and raise their own positions. However, when breaking status into prestige versus dominance, similarity appears between the sexes, suggesting that both sexes can flexibly use

a range of strategies in order to climb the ladder of our hierarchical societies.

Cross-References

- [Aggression](#)
- [Dominance](#)
- [Hierarchies](#)
- [Mate Competition](#)
- [Sex Differences](#)
- [Status](#)

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Sex Differences in Same-Sex Aggression

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Definition

With few exceptions, males tend to exhibit higher levels of aggressive behaviors than females. This sex difference reflects differences in evolutionarily adaptive reproductive strategies based on mating versus parenting trade-offs, with males competing to maximize sexual access to females.

Introduction

Aggression and its intricacies are widely studied in the social sciences, and its potentially criminal nature propels it to the forefront of social policy development in modern society. Aggression is far from simplistic however, covering many different definitions, multiple subtypes, being criminal or noncriminal and is assessed by multiple measures. Indeed, Campbell (2005, p.68) goes as far as to say that aggression has historically been “taken to be innate and learned, universal and culturally prescribed, a pervasive trait and a contextualized response, functional and dysfunctional, behavioral and cognitive and a phenomenon not to be measured and modelled or experienced and described.” Internationally and historically, academics across disciplines have explored aggression from many perspectives, covering almost every aspect from its etiology to classifications of subtypes. Within all of this, perhaps the one most consistent element of this complicated behavior is the manifestation of universally stable sex differences. It is to this central theme that this chapter will be dedicated.

Evolution and Aggression

Few disciplines parsimoniously detail all of the intricacies of this phenomena as well as the

evolutionary sciences. Evolutionary psychology offers a theoretical framework from which testable hypotheses regarding a behavior can be generated. Thus, evolutionary psychology readily predicts sex differences across many domains of human behavior, aggression being one of them. It also provides a more parsimonious explanation as to the origins of the behavior than traditional social role-based theories. Note from the onset however that an evolutionarily driven theory does not imply determinism, and evolved, genetic mechanisms do not imply that certain cognitions or behaviors will be expressed. As shall be noted later, the environment plays a crucial role, providing important input to evolved mechanisms and consequently influencing their later output(s).

So why should sex differences in aggressive behavior be expected? Answering that requires an understanding of the purpose of aggression and the problem(s) that it emerged to solve. As our ancestors became the most dominant species on the planet and began to master many of the complexities of the earth's ecology, one of the most pressing threats to individual survival became each other. Conspecific competition became an issue that all men and women would have to cope with in order to maintain reproductive fitness. Competition is necessary to secure the resources required to survive. These resources can be material (food, shelter) but are not limited to this domain and include status and mate access. However, competition often entails the use of aggression and violence. It is an adaptive strategy that can be employed when necessary. Aggression can achieve many things: the acquisition of food, water, or territory, securing reproductive access to the opposite sex, defending against attackers, and eliminating threats to survival and reproduction. But this is not without limitations. Costs of aggression can be high, potentially catastrophic, including: the loss of resources, social ostracism, injury, or even death (eliminating the ability to reproduce permanently). Thus aggression is not necessarily the first response to a problem, and individuals carefully consider the costs and benefits of its use. While in some cases it may appear to be so, this decision-making process is not necessarily conscious, and our sophisticated evolved

neural architecture can manage this without explicit, conscious processes.

As competition is a fundamental part of life, necessary for both males and females, it is helpful to understand where the sexes are in fact similar where aggression is concerned. There are strong correlations between male and female aggression (including violent and/or criminal – Campbell et al. 2001). Male and female aggression levels are moderated by many shared environmental factors including: impoverishment, sex ratios, and population densities, to name but a few of the most common factors. Many underlying psychological mechanisms associated with aggression (traits such as anger, hostility, self-esteem) do not demonstrate the sex differences many would expect where aggression is concerned. Moreover, increasing levels of provocation decrease the magnitude of the sex difference in aggression (Archer 2004). The conclusion is thus obvious: male and female aggression is inextricably linked. The question therefore becomes, why should levels of aggression differ between men and women?

The Evolution of Sex Differences

Before examining why men and women should differ in terms of aggression, one must understand the differences in selection pressures they each face. The prevailing view in the evolutionary sciences for the basis of sex differences (not just in aggression) is one of differences in fitness variances. Two principles within the evolutionary discipline form the core explanation of many sex differences (across all species): sexual selection (Archer 2009) and parental investment theory (Trivers 1972). It should be noted that these two theories predominantly detail the benefits of male aggression. The costs and benefits of female aggression will be explored in section “[Explaining the Sex Difference: Male and Female Competition](#).”

The sex that makes the larger investment (predominantly the female) acts as a limiting factor for the sex with the smaller investment (predominantly the male). Investment in this

context means the allocation of bioenergetic resources critical for successful reproduction. Investment levels differ between males and females. For males, reproductive investment can potentially end at conception, meaning a strategy focused on accessing as many mates as possible can potentially grant greater fitness returns. For females, investment is protracted, entailing gestation, lactation, and resource acquisition to sustain any resulting offspring (potentially for many years post-pregnancy). While males can quickly reenter the mating arena and repeat this process with as many other females as they can access, females cannot usually do so for some time after birthing, creating a skewed operational sex ratio with an excess of reproductively active males.

Directing resources to parenting is generally more advantageous for females to ensure reproductive fitness, despite the resource burden of reproduction reducing their overall reproductive rate. The sex with the lower rate of reproduction thus benefits more from parenting than mating. Male reproductive rates can be much higher given low obligatory costs that females must bear. Despite low reproductive rates, however, a female is rarely unable to mate, thus reducing their reproductive variance. Females (who bear the real costs of reproduction) aim to maximize their investments and usually seek high genetic quality or the offer of high levels of male offspring investment from potential partners. For males, there is no ceiling on reproductive rate. This, however, is contingent on males competing for sexual access to mates, either through female choice or aggressive intrasexual competition. As such, while females are nearly assured to have mating opportunities, the risk of reproductive oblivion for males is much higher. Consequently, reproductive variance is much higher for males than for females. According to Trivers (1972), "The sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex. Individuals of the sex investing less will compete among themselves to breed with members of the sex investing more" (Trivers 1972, p.140).

Consequently, fitness variances between males and females shape sexual strategies. Males

compete for females, and females strive to access high-quality males. Male competition in particular fostered sexual dimorphisms that enhanced their reproductive success. Indeed, it appears that across species (including our own), greater variability exists for sexually selected traits rather than nonsexually selected traits in males and females (Archer and Mehdikhani 2003). To take an example from the animal kingdom, the northern elephant seal's (*Mirounga angustirostris*) physical size is a sexually selected characteristic through which it establishes social dominance. Large males more ably monopolize access to females and defend against (or remove entirely) subordinate male rivals. Mate competition is intense, with over 75% of all seal pups being the resulting offspring of approximately 5% of adult males. Furthermore, merely 10% of males actually survive to reproduce at all. As if the competition was not enough for males, female elephant seals deliberately attempt to mate with the most socially dominant and "protest" against the advances of subordinate males. This further increases male-male conflict and allows females to effectively choose the best mates. Physical size in the elephant seal thus allows males to compete while simultaneously acting as a signal of quality to females, increasing the likelihood that the largest males reproduce and increase their overall fitness. Sexually dimorphic traits have evolved in hominid species also, such as facial hair, voice pitch, and physical size, and likely evolved as a result of inter- and intrasexual selection (Archer 2009). Furthermore, archaeological evidence suggests that aggression can increase male fitness benefits (Grauer and Stuart-Macadam 1998).

From the principles of sexual selection and parental investment theory, testable hypotheses regarding the expression of behaviors or traits can be generated. In the case of aggression, the following predictions can be made:

1. As reproductive variances are higher for males than for females, so to should variances in sexually selected behaviors such as aggression.
2. As males compete for female access, aggression should be more often invoked by males than females.

3. Ecological factors such as density, resource scarcity, and sex ratio should increase levels of aggression.
4. Aggression (and any subsequent sex differences) should be universal across all cultures and time periods.
5. Levels of aggression should increase through development, reach its zenith during the most reproductive phase of the lifespan, and decline with increasing age.
6. In our evolutionary past, males who use aggression successfully should achieve fitness gains.
7. The magnitude of the sex difference should increase as the behavior becomes increasingly violent and dangerous.

The discussion above has touched on data pertaining to hypotheses 1, 3, 4, and 6, and there is relative consensus that aggression is likely a sexually selected trait (Archer 2009). The remainder of the chapter is dedicated to detailing where human men and women differ in terms of aggressive behavior.

How Do the Sexes Differ in Terms of Aggression?

As the mating arena poses different challenges for men and women, it is reasonable to predict that they will express aggression differently. Research confirms this, with males being ubiquitously more aggressive. Gender differences appear in almost all forms of aggression, and this effect appears universally across age, time, culture, and geography. Numerous meta-analyses have confirmed these effects (e.g., Archer 2004). This provides further evidence to support hypotheses 2 and 4: that males should resort to aggression more than females and that this effect should be consistent across cultures. As noted earlier, aggression has multiple forms, subtypes, and categorizations, and it is impossible to cover all of them here. The most obvious place to start, however, is with an analysis of sex differences in direct aggression.

Sex Differences in Direct Aggression

Direct aggression represents the propensity to intentionally inflict either physical and/or psychological harm or injury or reputational damage upon another person and can be physical, verbal, violent, nonviolent, criminal, or noncriminal. In all cases, the target can identify the aggressor and is able to retaliate immediately. As such, direct aggression is a strategy of high risk, and the costs of such an action can be high. It is also the type of aggression in which the differences between men and women are most pronounced, supporting prediction 7 which suggests that the sex difference should increase in line with increasingly violent or dangerous aggressive behaviors.

Across almost all measures of direct aggression, men universally express higher levels of it (Archer 2004, 2009) and show greater variation within it (Archer and Mehdiakhani 2003). While men and women are more likely to aggress against members of the same sex, men are most likely to be the victims of aggression, not just from other men but also from women (Archer 2004). Physically aggressive activity (such as hitting, kicking, etc.) show male-biased effect sizes between $d = 0.91$ and $d = 0.59$, with smaller effect sizes for nonphysical aggression such as abuse and threats, $d = 0.46$ and $d = 0.28$ (Archer 2004). Men are more likely to aggress toward known, rather than unknown, targets, but lowering aggression in line with greater levels of intimacy, while females report more aggression toward unknown than known targets. Females are more likely however to aggress toward an opposite sex intimate partner than males (to be discussed later).

Homicide is overwhelmingly male biased, with 97% of killings involving men and 99% of same sex homicides being male-male (Daly and Wilson 1988). The likelihood of hospitalization through violence induced harm is significantly higher for men than women (Shepherd 1990). Approximately three quarters of violent offences committed by women, however, are classed as simple assaults (Greenfeld and Snell 1999). Men are much more likely to carry and aggress with weapons (Archer 2004), while women fight mainly with their fists and/or feet (Ness 2004). Pathologies characterized by high levels of

aggression, violence, and criminality tend to be heavily male biased (American Psychiatric Association 2000). Consistent with the theory of sexual selection and parental investment, introducing the motivation to mate appears to increase direct aggression in men but not women, with this increase directed predominantly at the most viable same-sex targets such as single, unmarried men (Ainsworth and Maner 2014). Sex differences appear very early in childhood, often observable from 12 months of age (Baillargeon et al. 2007), and while the actual magnitude of these differences remain relatively stable until the early teens, male aggression then begins to peak (Archer 2004). Throughout adulthood, this difference remains but declines in magnitude with age. These data provide support for prediction 5 with aggression being at its highest levels during our core reproductive years.

Sex Differences in Indirect Aggression

Indirect aggression is conceptually ambiguous, often used synonymously with terms such as relational and social aggression. Here, indirect aggression is used to cover all of these subsets, following Archer and Coyne (2005) who claimed these terms are best integrated due to their conceptual overlap. Indirect aggression is more veiled than direct aggression and is used as an alternative way to harm the target, for instance, via manipulating other people to conceal one's own identity. It includes actions such as gossiping, rumor spreading, ostracism, and defamation and acts where the perpetrator often remains anonymous to victims. Indirect aggression is a low-cost attack on a target. It is also a type of aggression relatively unique to our own species, with analogous behavior in animals being almost nonexistent (Archer and Coyne 2005).

Meta-analytic studies to date suggest that in this domain, sex differences do not exist, with either trivial effect sizes in the female direction or parity between the sexes (see Archer 2004). However, variation between these studies is considerable (potentially due to measurement issues), and, while the precise nature of the sex difference within indirect aggression remains inconclusive, there are specific sex differences noteworthy of

discussion. This provides us some support for prediction 7, as in the case of indirect aggression, sex differences are difficult to detect due to the inherently nonviolent nature of the behavior.

Research shows that girls preferentially used indirect aggression compared to boys (52% versus 20%, respectively, in 15-year-olds) when comparing engagement rates. Women also show stronger preferences for this strategy (even after controlling for perceptions of social norms and approval). Girls rate these forms of aggression as more harmful than boys (Coyne et al. 2006). In the media, indirect aggression is likely to be enacted by an attractive female aggressor, the characters often portrayed as justified for and rewarded by its use. Girls who exhibit higher levels of indirect aggression watch such programs more than less-aggressive peers, and viewing this form of aggression appears to increase its use by girls in real-world settings (Archer and Coyne 2005). Gossip patterns also vary between males and females. While both sexes attend more to same-sex gossip, this effect is stronger in women, who engage in more of it and also remember more details regarding other women who were subject to it, particularly if the victim is physically attractive. The use of exclusion tactics is more prevalent in girls than boys, appearing in some form from as young as age three and persisting into adolescence and adulthood (Benenson 2013). While aggregations on a meta-analytic level do not display consistent sex differences, particular subtypes, when examined individually, demonstrate differences favoring women.

Sex Differences in Other Aggression Related Areas

Unsurprisingly, there are sex differences in a number of psychological areas pertinent to aggression. Men and women mentally represent their beliefs about aggressive behavior differently. Beliefs and justifications, or social representations, separate into two distinct dimensions: instrumental (believing aggression is a means to an end) and expressive (believing aggression results from loss of control). Men are more likely to view aggression instrumentally while women are more expressive (Tapper and Boulton 2004).

Differences in social representations of aggression emerge in childhood from an early age (Tapper and Boulton 2004). Instrumental beliefs tend to show a positive correlation with verbal and physical aggression. Expressive beliefs however show more inconsistent patterns of results with actual levels of aggression (Tapper and Boulton 2004). Representations also demonstrate relationships with forms of noninjurious outbursts of angry behavior.

Males and females also differ on unconscious levels when it comes to aggression. Noted earlier was the male propensity to aggress with weaponry (Archer 2004). Related to this, men are also more sensitive to the presence of weapons (Sulikowski and Burke 2014). From early childhood, men even report higher frequencies of aggression and violence in dreams than women, and within dream manifestations of these aggressors are far more likely to be male (Schredl 2009). Finally men and women are more likely to form false memories regarding aggression in a way consistent with sex differences in actual aggression. Laney and Takarangi (2013) demonstrated using false feedback procedures that men were more likely to form false memories about causing a black eye while women were more likely to form false memories about spreading malicious gossip. These reflect the differences observed in direct and indirect aggression. While these more unconscious elements of aggression receive less empirical attention in the literature, it is the nonetheless interesting that they exist and that the evolved minds of men and women process information on the periphery of aggressive behavior differently, but not irreconcilably so from the actual expression of aggression itself.

Explaining the Sex Difference: Male and Female Competition

So why should men be so much more likely to attack, wound, and kill each other compared to women? Why should women prefer a more circuitous form of aggression? These two important questions require answering in order to truly understand why the sexes differ. Referring back

to the earlier discussion on differences in reproductive variances, the answer becomes apparent. For men, the reproductive stakes are high and the drive to compete is more imperative. Men compete for mating opportunities with women, and aggression allows men to establish dominance hierarchies, suppress challengers, and remove threats to reproductive success. For men struggling to access mates, the impetus to aggress increases, as failure to mate means lineage extinction. Although potential costs are high, men will risk injury, and potentially death, in order to achieve fitness gains. As the alternative is to not reproduce, however, the potential reward of reproductive success becomes all the more salient. Combine this impetus with ecological disadvantages, such as an operational sex ratio with more men than women (making access harder), lack of status or resources to attract women (making them less desirable than the competition) or high concentrations of young men (who particularly lack the status and resources of older, more experienced conspecifics) and the overall likelihood of male-male competition increase further. Reproductively active men become more accepting of the risks involved in aggression, and this increases the frequency and magnitude of male aggression. This phenomena was termed by Wilson and Daly (1985) as the “young male syndrome.” Note that this competition for female access is not necessarily conscious and indeed is not usually directly about aggressing over women. Men fight over status and their overall position in the dominance hierarchy. The hierarchy symbolizes their worth to women and thus their desirability as a mating prospect (recall the example of the elephant seal). Thus it is status that, in the environment of evolutionary adaptiveness, would have translated into reproductive success and it this that they are willing to use aggression to achieve and maintain.

Status acquisition in males begins early in development. Hierarchical structures appear in groups of boys as early as age six. The position a boy occupies is even predictive of their dominance 9 years later. Rough and tumble play is more important to and engaged in more by boys, allowing them to establish who is tougher. Boys more than girls are also better at identifying who

among a group is the strongest (Archer 2009). This early development of competitive behavior suggests boys are effectively preparing themselves for status competitions that will emerge in young adulthood. While high-status men will not necessarily be more aggressive, the pursuit of status from those who seek it may necessitate aggressive strategies to retain it. Group living has fostered norms that punish aggression in most cases, and status can be awarded in a variety of other ways such as demonstrating wealth or excelling in competitive sports. However, men can use aggression in certain circumstances to gain status if they can maintain an image of strength and of credible threat to challengers. Men are particularly sensitive to attacks on status and position (Daly and Wilson 1988), and the need to defend it results in violent escalations and retaliations to “save face.” This is one reason why many male-male altercations begin with startlingly banal causes (jests, jostling, insults, etc.) and can ultimately lead to homicide. Despite the risks entailed in escalation, the potential loss of status is too great a cost, and aggression often ensues to prevent it.

Many authors (see Campbell 2013) note that this explanation of sex differences in aggression focuses almost exclusively on why men should aggress and not on why women should. According to Triver’s principles, females aggress less simply because their likelihood of not reproducing is comparatively lower. But women are also locked in their own competitive struggles which may manifest in aggression, if not necessarily as often or as directly as men (Benenson 2013; Campbell 2013). It is important to explain when and why women will resort to physical force if necessary. As with men, status loss and the avoidance of victimization are prime motivations. Women who successfully fight can force other women to withdraw and establish a reputation to disincentivise challengers (Campbell 2013; Ness 2004). As with men, these reputations often require defending. Retaliation over insults, particularly those deriding either their sexual reputation or attractiveness, are also key determinants of aggressive escalation in women (Campbell 2013; Ness 2004). A second motivation in women stems

from jealousy and the need to protect an existing relationship, or the status that such a relationship may bring (Campbell 2013; Ness 2004). These escalations likely increase in situations where there is variation in men’s resources or a general paucity of males exists, making competition for well-resourced mates (even in the short term) worth fighting for. While these are pertinent explanations of why women physically aggress, they do not explain why women’s aggression is lower in magnitude when compared to men. As noted earlier however, there are distinct sex differences in indirect aggression that clearly favor women, and in understanding these, an explanation as to why women are less likely to resort to physical aggression becomes clear.

The so-called young male syndrome claims that men take risks to achieve status that translates into fitness gains. But, women rarely fail to find a partner: their fitness is thus not at stake in the same way. However, the tactics employed by males affect females in other ways. Male investment in offspring is low as men often aim to invest more time in mating effort rather than parenting (Trivers 1972). Consequently, males do little to no child rearing, largely due to the fact that a male can never be 100% sure that an infant is his; cuckoldry is after all a potential risk. To reinforce this point, note that the loss of a father (and thus his provisioning power) has little impact on offspring fitness (Sear and Mace 2008). Thus, the survival of children depends almost exclusively on continued investment from mothers. Research shows that this is the case across human societies (Sear and Mace 2008). The optimal use of a women’s resources is therefore to ensure continued investment in her children. If the mother was harmed in such a way that she could not adequately provision her family, her children’s survival (her inclusive fitness) would be endangered. Were she to die, the consequences would have been likely fatal to the offspring, and lineage extinction would be increasing likely (Campbell 2013). Thus, women benefit from staying alive, because this, ultimately, will keep her children alive as well. Given the importance of survival of the mother to survival of the offspring, selection pressures should favor less costly means of competition in women.

Women however still need to compete (not just indirectly) despite potential costs. They still require resources to survive and provision. They still aim to access higher-quality males for reproductive purposes (and aim maintain access for as much investment as possible). Their propensity to aggress also increases as males aggress, driven by the same environmental factors that heighten competition and make survival harder. The necessity for women to use aggression does not disappear in the face of rising costs. Female aggression, however, still entails higher costs than the equivalent action in males, and this should translate into a less confrontational style of competition. If an opponent cannot retaliate, a woman may be able to increase the survival odds in favor of her own progeny. Indirect aggression provides a means of achieving this end.

This explains why most indirect aggression (1) shows a female bias, (2) from females, is predominantly aimed at other females, (3) is used primarily during adolescence and young adulthood (the peak reproductive window for females and when competition for mates is most salient, Vaillancourt 2013), and (4) increases in females when mating motivation is experimentally primed. These elements of indirect aggression parallel the major trends demonstrated earlier in same-sex male direct aggression. There is therefore a growing consensus that indirect aggression is an intrasexual competition strategy among women (Benenson 2013; Campbell 2013).

From an early age, women, like men, form dominance hierarchies between themselves. Dominance hierarchies in females confer fitness benefits such as higher offspring survival rates (Campbell 2013). A woman's status can be based on a number of factors such as her mate value, her alliances with other females, and the status of her mate(s) and/or kin (Benenson 2013). Other women act as a barrier to achieving reproductive goals, and so female-female competition tends to be disguised, aims to punish other females who strive for similar goals, and potentially leads to the elimination of unrelated females via exclusion tactics (Benenson 2013). High-status women also have a competitive edge and can compete more overtly, either through their

mate value or alliances, as the threat of retaliation from lower status targets is less likely (Benenson 2013). Women do not necessarily need to cause direct physical harm to other females in order to inhibit their reproductive success. Character defamation and rumor spreading, particularly regarding a woman's sexual reputation, are seen as successful aggressive tactics designed to reduce the status of females in the community, as female mate value is often contingent on sexual fidelity (Vaillancourt 2013). Similarly, attacking another woman's appearance can reduce the target's attractiveness as a mate to men and as an ally to other women. This explains why name calling (such as "slag" and "slut" or "ugly" and "fat") is perceived as more damaging to women and why this may result in escalation to physical retaliation (Campbell 2013; Ness 2004) as they are challenges to a woman's mate value. These escalations are still much lower in magnitude (and in their consequences) than typical male-male aggression as, in the vast majority of circumstances, fitness costs remain much higher than reproductive benefits. Avoiding direct conflict (and thus harm) for the sake of offspring survival is still a safer strategy for women (Campbell 2013).

Risk and Fear

Two key elements have been identified in this analysis of sex differences – the salience of risk in pursuit of reproductive reward to males and the avoidance of high costs in safeguarding reproductive fitness for females. Sexual selection theories focusing on male risk-taking as a driver of aggression (Wilson and Daly 1985) are complementary to theories regarding female avoidance of direct aggression (Campbell 2013). As the propensity of the sexes to accept risks differs, with women being more avoidant than men, risk-taking could be a proximal mechanism that mediates the sex difference in aggression.

It is thus not surprising that sex differences in risk-taking are evident and in directions that parallel sex differences in aggression. Men have significantly higher scores on measures of risk-taking and sensation seeking than women across

almost all measurement types (Byrnes et al. 1999; Cross et al. 2011). The magnitude of this sex difference increases with the potential costs (Byrnes et al. 1999). In tasks involving rating situations on the level of risk entailed, women's estimates are significantly higher than men's (Eagly and Steffen 1986). Furthermore men and women classified as greater risk-takers and sensation seekers exhibit aggressive behaviors more frequently (Wilson and Scarpa 2010). Measures of risky impulsivity completely mediate the sex differences in physical and verbal aggression. The parallels between aggression and risk-taking are suggestive of a potential link.

If sensitivity to risk drives human aggression, what motivational factors, for women in particular, curtails this trait? Campbell (1999, 2013) suggested that the underlying driver of sex differences in risk and aggression can be reduced to an evolved sex difference in fear-based inhibition. Risk-taking (and synonymous measures such as sensations seeking) can broadly be classified as the reverse of fear. Strong emotional responses to fearful stimuli are likely to inhibit the urge to take risks. If this is so, sex differences should be evident in this domain, with women experiencing it more strongly than men. Campbell's review of the evidence suggests that this appears to be the case, with levels of fear being significantly higher for women being observed cross-culturally while reporting to experience it more intensely. Girls also express fear developmentally earlier than boys. Psychometric analyses of measures containing items with fear and anxiety connotations show gender differences in the female direction, while indices of sensation seeking lacking elements of danger show no sex differences. This fear-based mechanism may be specific to real physical danger, as there are few sex differences in measures that examine social fears only. Research also indicates that fear appears to more strongly suppress aggression in women than in men, while harm avoidance is a significant mediator in the relationship between gender and expressive representations of aggression. A wealth of neuropsychological evidence supports the proposition that differences in sensitivity to fear is perhaps the underlying mediator of

gender differences in aggression. Neuroimaging studies show that subcortical structures such as the amygdala (located in the temporal lobe) and the orbitofrontal cortex may be pivotal in managing responses to fearful stimuli. Wider and longer activation patterns of the limbic system (which includes the amygdala) are evident in women who are presented with threatening stimuli. Similarly, sex differences are evident in response to angry, threatening faces. Orbitofrontal activation is also greater for women than for men in response to facial stimuli that express negative emotion. Similar relationships between the orbitofrontal cortex and the amygdala have been reported previously in aggressive individuals, which may suggest that women show higher levels of restraint and more effectively regulate negative emotions.

These sex differences in fear may explain one of the intricacies of aggressive behavior, the somewhat unexpected sex differences found in intimate partner violence or IPV (Cross and Campbell 2011). While most homicides resulting from IPV are committed by males (Daly and Wilson 1988), this is largely a function of the fact that men are much stronger and kill more generally. Jealousy accounts for a much larger proportion of female-perpetrated homicides than male-perpetrated homicides, suggesting that, as males are physically larger and stronger, the higher number of male perpetrated partner deaths may just be a factor of their greater physical ability to kill rather than jealousy led motivation. Thirty-five percent of IPV-related injuries are sustained by men, while a meta-analysis of IPV measures (based upon different acts) found a small but significant effect in the female direction, suggesting that females are more likely to aggress toward partners than vice versa. Female aggression toward partners is also not only limited to minor acts. Cross-culturally, even allowing for national levels of female empowerment, men are more likely to be victims of IPV (Archer 2006). However, women do not just aggress toward men generally, it appears only disinhibited toward men they are intimate with. This suggests that there is something specific to intimate partner dyads that may invoke a muted fear response.

So why are women more likely to attack intimate partners than other men (or women) generally? Campbell (2010) suggests this could be due to fear reduction in women who are emotionally invested in their partners. In this model, the non-peptide hormone oxytocin (which is secreted during and has a functional role in several bonding, nurturing, and sexual behaviors) serves to reduce the level of fear and stress in females. Forming a sexual relationship requires a female to decrease inhibitions. As selection pressures on female mate choice make choosing the wrong partner a costly business, it is advantageous for females to be more generally inhibited sexually to allow time to choose appropriate partners carefully and to reduce the risk of injury from sexually aggressive partners. The release of oxytocin thus serves as an anxiolytic to the fear that normally inhibits sexual behavior and allows copulation to occur. The effect of oxytocin is likely to be one of general disinhibition to facilitate mating but potentially disinhibiting aggression as a by-product. Campbell cites evidence suggesting that oxytocin release increases during interactions with a partner simply increase the odds that a female may be more likely to aggress toward them as opposed to strangers and explains this reversal of the sex difference in IPV. This functional account of oxytocin moderated changes to fear-based inhibition allows us to reconcile why women may be more aggressive than men in intimate situations in a way that is still entirely consistent with complementary evolutionary explanations. It should be noted, however, that recent work challenges this hypothesis in finding that the administration of oxytocin can cause fear reductions in men and the opposite effect in women. Further work is required to comprehensively understand the wider implications of oxytocin as well as how it may act differently within the male and female brain (Campbell 2013).

Conclusion

Understanding aggression as an adaptive response provides a functional purpose for both the behavior and the gender differences within it. Contrary

to popular belief, aggression is not a pathology and is a strategy that all are capable of under specific conditions to facilitate survival. It is essential that we understand how the sexes differ if we are to have a full understanding of this broad phenomenon, and this review represents only a small fraction of the research conducted in the field to date. While the underlying psychology of the sex differences in aggression is not wholly clear, the recent advances in theory regarding fear-based inhibition (Campbell 2010, 2013) go a long way in reconciling why men and women appear more or less aggressive across different situations. Although these theoretical developments contingent on models of oxytocin and evidence from small scale neuropsychological studies are in their relative infancy, research stimulated by these newer ideas and continued advances in neuroscience will no doubt enhance our understanding of the neuromechanisms responsible for the universal behavioral differences observed between men and women.

Gender is equally pivotal for the purposes of policy and intervention in aggression, violence, and crime. We must understand how and why men and women act and react differently if any degree of success is to be expected from strategies society implements to reduce these potentially dangerous characteristics. Much of this work also needs to focus on what we know to be the shared antecedents of aggression, namely, environmental factors that increase the likelihood of competition: poverty, lack of educational opportunities, population densities, and social and gender inequalities. This is by no means a small task, but greater work is required to examine how these various factors impact strategies that include aggression (Copping and Campbell 2015). Finally, it is worth reiterating that much of the historic literature has focused on predominantly male aggression. While this has been vital to our understanding of behavior, it is encouraging to note that there is an increase in work focusing on female aggression (Benenson 2013; Campbell 1999, 2013; Cross and Campbell 2011). As noted earlier, women are not passive compared to men in their use of aggression and have their own reproductive agenda to which aggression can

be used to pursue. Future work should continue to integrate accounts of male and female aggression into their theoretical underpinnings in order to help advance the field constructively.

Cross-References

- ▶ Ability and Willingness of Victim to Retaliate
- ▶ Aggression
- ▶ Aggression for Sexual Access
- ▶ Anne Campbell
- ▶ Antisocial
- ▶ Antisocial Behavior
- ▶ Anxiety
- ▶ Anxiety (Randolph Nesse)
- ▶ Charles Darwin: Theory of Sexual Selection
- ▶ Competition Between Groups
- ▶ Competition for Parental Investment
- ▶ Competition for Resources Desired By Females
- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Men's Aggression Against Women
- ▶ Contexts for Women's Aggression Against Men
- ▶ Contexts for Women's Aggression Against Women
- ▶ Correlates of Fear
- ▶ Costs of Aggression
- ▶ Culture of Honor and Retaliation
- ▶ Defense Against Attack
- ▶ Development of Aggression
- ▶ Development of Sex Differences
- ▶ Evolution of Crime, The
- ▶ Female Age as a Predictor of Men's Aggression Against Women
- ▶ Female Choice
- ▶ Female Choice and Sexual Conflict Theory
- ▶ Female Mate Choice (Intersexual Selection)
- ▶ Female-Female Competition
- ▶ Female-Female Strategies
- ▶ Female-Perpetrated Violence
- ▶ Function of Dominance
- ▶ Gossip, Rumors, and Social Exclusion
- ▶ Homicide
- ▶ Indirect Aggression
- ▶ Intrasexual Competition
- ▶ Intrasexual Competition Between Females
- ▶ Intrasexual Male Competition
- ▶ Intrasexual Rivalry Among Men
- ▶ Intrasexual Rivalry Among Women
- ▶ Intrasexual Selection
- ▶ Lethal Violence
- ▶ Male-Male Competition
- ▶ Mate Preferences
- ▶ Men Riskier, More Aggressive
- ▶ Meta-Analysis of Sex Differences In Aggression
- ▶ Partner Homicide
- ▶ Physical Aggression
- ▶ Psychological Mechanisms
- ▶ Resource Competition
- ▶ Same-Sex Homicide
- ▶ Sex Differences in Aggression
- ▶ Sex Differences in Death by Homicide
- ▶ Sex Differences in Intimate Partner Violence
- ▶ Sexual Selection
- ▶ Sexual Size Dimorphism
- ▶ Signals of Body Size
- ▶ Size and Dominance
- ▶ Social Aggression
- ▶ Social Consequences of Initiating Gossip
- ▶ Tactics to Solve Adaptive Problems of Sperm Competition
- ▶ Victims of Violence
- ▶ Violence
- ▶ Vocal Indicators of Dominance

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Sex Differences in SDO

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Synonyms

Gender differences in SDO

Definition

Gender predicts social dominance orientation (SDO) such that men typically express higher levels of SDO than women.

Introduction

Research across a wide variety of cultures has provided a great deal of evidence showing that

men, compared to women, have generally higher levels of social dominance orientation (SDO), an individual difference variable reflective of support for unequal, hierarchical relationships between groups. Although the sex difference in SDO is relatively well established in the literature, the questions of (i) how contextually invariant the relationship between sex and SDO is and (ii) what underlies this sex difference in SDO contribute to an ongoing debate among scholars.

Sex and SDO

Social dominance theory (SDT; Sidanius and Pratto 1999) states that the purpose of group-oriented social hierarchies is to reduce conflict between groups and maintain human survival over time. According to SDT, individuals differ in their preference for hierarchical group-based systems of inequality, with this preference being termed “social dominance orientation” (SDO). Individuals high on SDO endorse group hierarchy and believe that groups do and should differ in status and power, whereas individuals low on SDO endorse group equality and oppose differentiation of groups based on status and power (Pratto et al. 2000). This individual-difference variable is assumed to have its origin in both cultural (socialization) and biologically influenced factors (Sidanius et al. 1994).

The gender hierarchy is one of the most prominent group-based hierarchies in societies around the world. Gender has been found to consistently predict SDO with men as members of the higher-status group expressing higher SDO than women as members of the lower-status group. Men’s greater expression of SDO compared to women’s helps in explaining the existing gender difference in women and men’s attitudes in a wide range of sociopolitical domains (see Pratto et al. 1997). For example, women are more politically liberal than men (e.g., Feather 1977) such that they express less prejudice (Ekehammar et al. 1987) and authoritarianism (Altemeyer 1981) and show more support of social equality (Ekehammar and Sidanius 1982). In addition, women have less punitive attitudes than men (e.g., Ekehammar

1985), and they are more likely to favor policies that support the disadvantaged (e.g., Shapiro and Mahajan 1986).

SDO and the Gender Invariance Hypothesis

Men’s greater scores in SDO compared to women’s is one of the most consistent findings in research examining SDO and has led to the formulation of the *gender invariance hypothesis* (Sidanius et al. 1994). The gender invariance hypothesis asserts that, *all else being equal*, gender differences in SDO will be found such that men will exceed women in SDO scores and that this difference will be relatively universal and invariant across cultural, social, and situational factors. Sidanius et al. (1994) however differentiate between a strong and a weak version of the invariance hypothesis. According to the strong version, the gender difference in SDO should remain invariant across cultural factors, situational factors, or both – i.e., no significant interaction between sex and cultural-situational factors should be found. In contrast, according to the weak version, the gender difference in SDO might vary somewhat across certain cultural-situational factors, but women should not exceed men on SDO scores – i.e., sex might interact with cultural-situational factors, but this interaction will always be of ordinal and not disordinal nature.

The gender invariance hypothesis has been supported by numerous studies including student and general-population samples that produced one of the most robust findings in SDO research even when considering a range of covariates and moderators (e.g., Pratto et al. 2000; Sidanius and Pratto 1999; Sidanius et al. 1994). Some scholars have however challenged the gender invariance hypothesis (e.g., Huang and Liu 2005; Schmitt et al. 2003; Wilson and Liu 2003; Zakrisson 2008). For example, Wilson and Liu (2003) found an apparent cross-over interaction between sex and gender identification such that women with low levels of gender identification have higher SDO scores than men with low levels of

gender identification, whereas men with high levels of gender identification have higher SDO scores than women with high levels of gender identification. These findings however were criticized by Sidanius and Pratto (2003) who argued that the “*ceteris paribus*” principle of all else being equal was violated and stated that the “analysis is about as meaningful as comparing female members of police death squads (hierarchy-enhancers) with male social workers (hierarchy-attenuators), a comparison also likely to find women with higher SDO scores than men” (p. 210). Wilson and Liu (2003), in both studies, however also included gender identification as a covariate instead of a moderator in additional analyses and found that the previously significant sex difference in SDO disappeared. Other scholars also obtained evidence inconsistent with the gender invariance hypothesis. For example, when women and men were exposed to a majority of female members in voluntary associations (Zakrisson 2008), or when ethnic rather than gender identity was made salient (Huang and Liu 2005), men and women did not differ in SDO scores. Cross-cultural research also sometimes failed to show the expected sex difference (e.g., in two out of six samples, see Pratto et al. 2000). Taken together, the inconsistent findings regarding the relationship of sex with SDO shows that the dispute about the gender invariance hypothesis is far from being settled.

Causes for Sex Differences in SDO

According to the biocultural interactionist perspective, biologically influenced factors (e.g., temperament, personality) as well as cultural factors (e.g., socialization) contribute to individuals’ SDO (see Sidanius et al. 1991, 1994). Greater SDO in men than women is seen as important for the male reproductive strategy, where dominant groups of males aim to monopolize female reproductive resources (Sidanius and Pratto 1999). Gender-role socialization into typically female roles, such as teacher, nurse, or children’s caretaker, requires concern for other people, which is negatively correlated with SDO. In

contrast, gender-role socialization into typically male roles, such as police officer, soldier, or manager, requires a willingness to dominate other groups with legal means or violence (Pratto et al. 1994). The “gendered” roles of caretaker and war maker are consistent across cultures and might also contribute to explaining the consistent sex difference in SDO and the invariance hypothesis (Pratto et al. 1997).

Some scholars however feel that this biocultural interactionist perspective is too backward looking and that it leads to “SDO being an outcome of the past rather than the present” (p. 805; Batalha et al. 2011). These scholars therefore favor a cultural-deterministic perspective and more immediate situational explanations for the presence or absence of sex differences in SDO (e.g., Batalha et al. 2011; Huang and Liu 2005; Schmitt and Wirth 2009; Wilson and Liu 2003). From a cultural-deterministic perspective, the invariance hypothesis should not hold as any sex differences in SDO are the result of a specific gendered socialization pattern, culturally transmitted gender roles and self-stereotyping, and contextual or environmental factors. For example, demonstrating the importance of context rather than gender, Batalha and colleagues found women and men to differ in SDO when the ideologies that they were exposed to sanctioned values that promoted group hierarchy. In contrast, the authors found that men and women converged in their SDO beliefs, when these ideologies were minimized.

Conclusion

Gender is one of the most consistent predictors of SDO with men typically exceeding women in their preference for group hierarchy and for differentiation of groups along the lines of status and power. The question to what extent this sex difference is invariant is part of a lively scholarly debate and awaits further careful and systematic investigation of the “all else being equal” principle of the gender invariance hypothesis. In addition, scholars also cannot definitively conclude the origin of the sex difference in SDO,

but they found considerably evidence that SDO is related to a large number of gender differences such as mating strategies, occupational role, and political attitudes. Future research might shed further light on the questions of *why* and *when* examined “gendered” preferences for group hierarchy are stable or malleable as a function of the context that we are socialized and embedded in.

Cross-References

- ▶ [Dominance Hierarchy](#)
- ▶ [Self-Stereotyping](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Social Dominance Orientation \(SDO\)](#)

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Sex Differences in Sexual Socialization

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Synonyms

[Treatment of Males in Sexual Socialization](#);
[Treatment of Females in Sexual Socialization](#)

Definition

How the social environment influences males' and females' expression of sexuality and gender identity.

Introduction

Sexual socialization is a process by which an individual develops his or her own identity by acquiring the skills, knowledge, and values of the gender they prefer (Schneewind 2001). In most societies, women are viewed as communal, warm, gentle, kind, and passive, whereas men are viewed as tough, aggressive, and assertive (Huddy and Terkildsen 1993). This entry will explain in further detail the differences between the socialization of gender roles and how they affect males and females differently throughout the lifespan.

Parental Influence

Parenting is one source of sexual socialization. There are a number of studies that have highlighted sex differences in communication between parents and their children. For example, conversations between fathers and adolescent sons typically contain more topics on sexual activity than mothers and adolescent daughters (Nolin and Peterson 1992). However, adolescent males and females report that their fathers tend to be less available for personal conversation than their mothers, and fathers have reported experiencing significantly more discomfort than mothers when discussing topics of a sexual nature with their children (Nolin and Peterson 1992).

When it comes to sexual behavior, parents often treat their daughters differently than their sons. It has been noted that parents' communication with their adolescent daughters is often conducted in an effort to control their daughter's sexual behavior (Nolin and Peterson 1992). In fact, "mothers give their daughters important cues about desirable appearance and body image, which may have implications for self-sexualization" (Starr and Ferguson 2012, p. 465). This is not the case with male children. It has also been theorized that mothers who possess high levels of self-objectification as well as low levels of religiosity can cause early sexualization in their daughters (Starr and Ferguson 2012). Belsky, Steinberg, and Draper

theorized that without the presence of a father in the child's early life, parenting expectations are not reliable whereas those with the presence of fathers in their early years develop a different kind of expectations about the nature of others (Belsky et al. 1991).

There are other cultural variables to be considered when socially constructing gender in society. These factors include the relative status of men and women, the division of labor by gender, fathers' involvement in caregiving, economic opportunities, and religious beliefs and values (Best and Williams 1997).

Cultural Influences

Gender roles and stereotypes are culturally constructed. As early as 2 years old, males and females have a gender preference (Leaper and Friedman 2007). Girls are likely to favor feminine, domestic toys such as dolls, cooking sets, and dress-up materials, while boys prefer masculine toys such as cars, trucks, tools, and sports equipment (Leaper and Friedman 2007). Toys create this expression of what is socially acceptable to boys and girls. Young girls will imitate their dolls by wearing makeup or similar clothing, not understanding that these items influence the socialization between males and females (Starr and Ferguson 2012). In addition, some research has also shown that young females will favor sexualized dolls over non-sexualized dolls (Starr and Ferguson 2012). Similarly, video games intended for young males hypersexualize women by accentuating the female physical characteristics and dressing them in promiscuous clothing (Starr and Ferguson 2012). Young males are also exposed earlier to the idea of self-efficacy with toys reinforcing constructive goals (e.g., LEGOs and Lincoln Logs) (Block 1983).

Gender stereotypes are commonly used in children's television shows. Many of these shows perpetuate the idea that men hold a higher status than women due to overrepresentation of males (Leaper and Friedman 2007). Sexualized models on television, magazines, and music videos are appealing to young females, which can lead

young females to pursue behaviors and styles that resemble what they see in popular culture (Starr and Ferguson 2012).

Scharrer's (2013) content analysis research suggested that television disproportionately values thinness in females and males. She also noticed there was consistency with media characters thinner than the rest of the population, where just 24% of women in the population met the clinical definition of "thin" according to the US Center of Disease Control (Scharrer 2013). In an evolutionary perspective, extreme thinness does not show fertility, rather a lack of. These are two diametrically opposed ideas, where society suggests thinness is standard, and in evolution, women were selected by their bodies based on fertility. Television is an influential source of information from which modern day children often develop ideas regarding how men and women differ in physical appearance, domestic roles, gender roles, and occupation (Scharrer 2013).

Bandura's social learning theory is where individuals learn either by observation or direct experience (Bandura 1971). He emphasizes that actions are governed by reward and punishments, where it is an individual's free will to carry out these actions (Bandura 1971). Children learn reward and punishment at home by their parents. Peers influence each other as young as 2 years old when it is the appropriate time that mothers take their child to daycare. Evolutionary theories look to explain why girls would naturally behave passively in the presence of boys. Females paired with males displayed more passive behavior and a significant decrease in social interaction with the opposite sex (Jacklin and Maccoby 1978).

Abusive Influence

Some psychologists have argued that children who experience sexual abuse may exhibit advanced sexual behavior in their adolescent years (Finkelhor and Browne 1985). When children are rewarded for sexual behavior, they learn to use this behavior as customary to manipulate others to satisfy their needs (Finkelhor and

Browne 1985). Adolescent boys who have been victims of abuse can be sexually aggressive towards their peers (Finkelhor and Browne 1985), which may be a symptom of a distorted idea regarding what is considered appropriate social behavior.

Verbal, mental, physical, and emotional abuse can have lasting effects into adulthood that may cause problems in one's daily life. Victims of abuse may experience traumatic memories, dislike for sex, or sexual dysfunction (Finkelhor and Browne 1985). As the abused child matures, he or she may experience problems in their adult relationships. Some have argued that those who have been abused are more likely to become the abusive adult (Finkelhor and Browne 1985).

Some researchers have suggested that female victims of domestic violence are more likely to bare male children (Kanazawa 2006). Although this stance is controversial, Kanazawa's (2006) data supports this theory. Violent men seem to produce more male offspring than female offspring, and violent men produce more male offspring than nonviolent men. However, the cause of this correlation is unknown. It is uncertain whether this increase in male offspring production is caused by the violent men (i.e., violent men produce more male offspring) or by the victimized women (i.e., battered women produce more male offspring). Regardless of the cause, if this phenomenon is true, then these children may be socialized by their violent parent to display aggressive behaviors.

Conclusion

Children can acquire skills and knowledge regarding gender identity via social learning (Bandura 1971). This social learning can be the product of parents, peers, and/or media influence. Regardless of the source, "... the child becomes motivated to seek similar positive outcomes by imitating the rewarded behavior" (Starr and Ferguson 2012, p. 464). Children learn through their environment and often adopt these gender roles based on what they believe is considered socially acceptable. In the first years of life, parents hold a strong

influence over this socialization process because children spend most of their time with their parents. As children grow into adolescents, peers and other environmental influences begin to play an increasingly larger role in sexual socialization. However, research also shows that not all aspects of gender identity and sexual socialization are caused by social influence (Kahlenberg and Wrangham 2010) so research in this area is still needed to fully understand this phenomenon.

Cross-References

- [Cultural Differences in Sexual Socialization](#)
- [Positive Sexual Development](#)
- [Sexual Contact and Sexual Disgust](#)
- [Sexual Socialization](#)
- [Sexuality](#)

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Sex Differences in Sexual Versus Emotional Jealousy

- [Sex Differences in Jealousy](#)

Sex Differences in Short-Term Mating Preferences

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According to Sexual Strategies Theory (Buss and Schmitt 1993), our species comes equipped with numerous mate preference adaptations. Some are specially designed for *short-term mating*, including mechanisms guiding how often and with whom we prefer to engage in casual sexual encounters and extra-marital affairs. Some short-term mate preferences differ between men and women. Men tend to desire easy sexual access when short-term mating and functionally relax

their desires to create more opportunities for consummation. Women, in contrast, are relatively selective when short-term mating. Two leading hypotheses for the function of female short-term mating are the “good genes hypothesis” (e.g., preference for hypothesized good genes markers such as symmetry, masculinity, and physical attractiveness) and the “mate switching hypothesis,” using affairs as a strategy to exits one mating relationship, evaluate potential alternative mates, or re-mate with a more beneficial or less cost-inflicting partner (Buss et al. 2017; Buss and Schmitt 1993).

Evidence of Women’s Specialized Short-Term Mating Psychology

Survey studies document women tend to particularly prefer physical attractiveness in short-term mates compared to long-term mates (Buss and Schmitt 1993; Buunk et al. 2001; Gangestad and Simpson 2000; Kenrick et al. 1990). Regan et al. (2001) found women rated physical attractiveness 7.80 on importance in short-term mate choice, but only 6.32 in long-term mating (on a 9-point scale). Castro and Lopes (2011) found women prefer a “pretty face” 3.42 in short-term mates, but only 2.17 in long-term mates (on a 5-point scale), and women prefer a “beautiful body” 3.08 in short-term mates, but only 1.83 in long-term mates.

Supporting the “good genes” view of women’s short-term mating psychology, women emphasize specific physical attributes much more in short-term mating than long-term mating, such as facial symmetry, facial masculinity, large muscles, and other testosterone-related cues (Johnston 2006; Waynforth et al. 2005). Women also report physical attractiveness-related *motives* for short-term mating 24% of the time (in men it is only 10%; Regan and Dreyer 1999).

Women more often choose and more strongly react to physical attractiveness in their *actual* behavior within short-term mating contexts. For instance, women tend to have affairs with especially symmetrical men (Gangestad et al. 2005), and women have more frequent and consistent copulatory orgasms with physically attractive

men (Puts et al. 2011). Women are judged more likely to consent to short-term mating with a male stranger if he is high in physical attractiveness (7%), compared to only moderate physical attractiveness (3%) or low physical attractiveness (2%) (Schützwohl et al. 2009). When approached by *actual* strangers in real life situations, women tend to say “yes” to a real stranger’s query “will you go to bed with me?” if the man is high in physical attractiveness (3%) versus only average in physical attractiveness (0%; Guéguen 2011). In a Danish study, whether women said yes to an actual stranger’s asking for sex was influenced by the physical attractiveness of experimental confederates (Danish men were not so influenced; Hald and Høgh-Olesen 2010). Evidence suggests men’s physical attractiveness matters to women in their real-life casual sex experiences involving short-term mating.

If women are to maximally gain the “good genes” benefits of selective short-term mating, they would be most effective at choosing attractive men for casual sex when the women are nearing ovulation (the time of maximum conception probability). Several studies have found women’s preference for physical attractiveness in potential mates peaks around ovulation (Thornhill and Gangestad 2008). Women’s preferences for men who have facial symmetry, body masculinity, vocal masculinity, and social dominance all peak around ovulation (Gildersleeve et al. 2014). These findings are especially true if women are of low mate value and if a woman’s husband is physically unattractive (hence, her adaptive need for “good genes” is intensified; Pillsworth and Haselton 2006).

Another useful tool for evaluating women’s short-term mate preferences is to compare women who engage in a lot of short-term mating to women who are exclusively long-term maters. Women who engage in more short-term mating during their lifespan tend to emphasize physical attractiveness, masculinity, and interpersonal dominance more in mate choice (Gangestad et al. 2005). Women high in unrestricted sociosexuality (i.e., short-term oriented women) tend to perceive smiles as flirting (much like most men do, Howell et al. 2012). If single, women high in

sociosexuality prefer especially masculine men (whereas already-mated women do not; Sacco et al. 2012). Women who are more likely to engage in short-term mating tend to prefer men who possess masculine attributes (Frederick and Haselton 2007) even including the way masculine men walk (Provost et al. 2008). In summary, women who actively engage in short-term mating are more likely to exhibit the short-term mate preferences hypothesized by Sexual Strategies Theory

Women may engage in short-term mating for a variety of adaptive reasons (Greiling and Buss 2000), not just to obtain good genes from physically attractive men. Women can benefit from confusing their partners about paternity, from directly obtaining resources, from obtaining physical protection of multiple males, from evaluating their own mate value, and from the potential of a short-term mating experience to lead to a long-term mateship. For instance, women engaged in short-term mating tend to prefer men who provide immediate resources (especially as opposed to men who just have future resource *potential*; Buss and Schmitt 1993), and men are typically judged more effective in short-term contexts when they provide immediate resources (Schmitt 2002). Resource levels are closely related to age, and in a study of 25 year olds (Buunk et al. 2001), researchers found women tend to prefer short-term mates who are older than themselves by about 4 years (age 29, with an average maximum acceptable age of 38), whereas men prefer women of about 1 year younger as short-term mates (age 24, with an average maximum acceptable age of 31). The typical findings in studies of prostitution (e.g., Bonnerup et al. 2000) and pornography consumption (Hald 2006) also support the view that women more often than men engage in short-term mating in exchange for resources. In short, there is some empirical support for the resource acquisition function of women's short-term mating.

Evidence has been accumulating for the mate switching function to explain why mated women have affairs (Buss et al. 2017). The findings include: (1) women who are emotionally and sexually dissatisfied with their regular partner tend to

have affairs; (2) women tend to fall in love with their affair partners, (3) women perceive mate insurance and trading up to a better mate as a key benefit of affairs, and (4) women's mate preferences for affair partners mimic closely those they desire in long-term committed mates (see Buss et al. 2017 for summaries and citations). None of these findings are well explained by the good genes hypothesis but are well explained by the mate switching hypothesis. Falling in love with an affair partner, for example, would interfere with the dual mating strategy of securing genes from one man while securing investment from another. The two hypotheses, of course, are not mutually incompatible. It is possible that some women pursue a dual mating strategy while others use affairs for a mate switching function.

Men's Specialized Short-Term Mating Psychology

Evolutionary psychologists have hypothesized men can reap strong reproductive benefits from engaging in short-term mating. Indeed, as the lesser-investing sex in terms of gametes (Bateman 1948) and obligatory parental investment (Trivers 1972), men should be more eager than women are for opportunistic short-term mateships and should be less discriminating than women in their selections of casual sex partners. Several sources of evidence have confirmed these fundamental features of men's short-term mating psychology (see Schmitt 2014).

One source comes from surveys that ask men and women the degree to which they eagerly desire short-term mating. In 1993, Buss and Schmitt asked a college student sample the extent to which they were *currently seeking* short-term mates, the *number of sex partners* they ideally desired at limited time intervals into the future, and whether they would *consent to sex* with someone they viewed as desirable if they had known the person for limited amounts of time. In nearly every instance, men more eagerly desired and more quickly consented to short-term sex than women did. Schmitt et al. (2003) replicated these findings across more than 10,000 college students

representing 10 major regions of the world. Sex differences in self-reported desires for short-term mating are likely a pancultural universal (see also, Lippa 2009).

An important caveat to these findings, however, is that many men report they are relatively uninterested in short-term mating. Evolutionary psychologists do not expect all men to be eager for short-term mating at all times. Instead, only some men eagerly pursue short-term mating strategies, especially those who can successfully pursue the strategy given their own physical attractiveness, status, and overall mate value (Gangestad and Simpson 2000). Early attachment experiences, local pathogen levels and sex ratios, and heritable differences also influence the degree to which men pursue short-term mating as a sexual strategy (Schmitt 2016). For example, considerable evidence suggests when there is a surplus of women in the mating pool, men are inclined to shift to a short-term mating strategy and become more reluctant to commit to a single partner (Buss 2016). The logic of Sexual Strategies Theory suggests that *when* men pursue short-term mating, they do so guided by evolved desires that are different from the desires of women who pursue short-term mating. Men who short-term mate tend to desire more numerous mating partners, be quicker to consent to sex, and more eagerly engage in brief sexual encounters compared to women who short-term mate. A wide variety of data sources supports this view (Buss and Schmitt 2011).

Beyond simply asking men and women the extent to which they eagerly desire short-term mating, *per se*, sex differences exist in numerous sex-related attitudes and behaviors closely associated with short-term mating. For instance, men have significantly more positive attitudes than women toward casual sex, permissive sexuality, and emotion-free sexual experiences (Petersen and Hyde 2010). Carroll et al. (1985) asked men and women if they always needed to be emotionally close in order to have sex with someone, with 45% of women and only 8% of men responding they required emotion for sex. Also asked was the somewhat awkward question of whether they would *never refuse a sexual offer*, with 46% of

men saying they would never refuse a sexual offer, but not a single woman (0%) reporting she would never refuse a sexual offer. In the context of short-term mating, evidence suggests that *all* women are at least somewhat selective, whereas about half of men apparently have quite low minimum standards.

In a meta-analysis of 30 sexuality-related attitudes and behaviors, Petersen and Hyde (2010) found men had more positive attitudes toward casual sex ($d = 0.45$) and toward sexual permissiveness ($d = 0.21$). Men were also more likely to engage in extra-marital sex ($d = 0.33$) and casual sex ($d = 0.28$). Petersen and Hyde (2010) erroneously reported that “most gender differences in sexual attitudes and behaviors were small” (p. 21), but this was not true for sex differences in eagerness for short-term mating, nor is it true for evolutionary psychology’s many predictions concerning mate preferences (which were empirically ignored by Petersen and Hyde). Indeed, many sex differences in mate preferences hypothesized by Sexual Strategies Theory are rather large in size, far exceeding the effect sizes typical in psychology.

In 1991, Simpson and Gangestad developed a measure of a trait called sociosexuality. This measure was specifically designed to assess whether someone is willing to have sex without commitment (i.e., is sociosexually unrestricted). Across every sample that has ever been studied, men report more unrestricted sociosexual attitudes and behaviors than women (Schmitt 2005). Schmitt (2005) assessed the sociosexuality of men and women across 48 nations and found men were more unrestricted than women in every culture (average $d = 0.74$). In 2009, Lippa replicated Schmitt’s results across a larger sample of 53 nations, including exactly replicating the overall sex difference of $d = 0.74$.

Emotionally, men tend to experience less regret than women do after engaging in short-term sex or “hook-ups” (instead men particularly regret *missed opportunities* for short-term mating; Bradshaw et al. 2010; Galperin et al. 2013). Men also tend to over-perceive sexual interest from opposite-sex strangers more than women do (Haselton and Buss 2000; Perilloux et al. 2012);

men tend to want, initiate, and enjoy a wider variety of sex practices than women do (Baumeister et al. 2001); and men tend to have higher general sex drives in all cultures that have been studied (Lippa 2009).

Men generally relax their mate preferences in short-term mating, whereas women *increase* their selectivity in short-term mating, especially for physical attractiveness (Gangestad and Simpson 2000; Kenrick et al. 1990). Men, but not women, also prefer short-term mates who are easily sexually accessible. In an experimental study, men found women who give cues to “easy sexual access” as more attractive for short-term mating but not for long-term mating, and women showed no increased attraction toward easily sexually accessible men in any mating context (Schmitt et al. 2001).

Although men *self-report* that they value and desire large numbers of short-term sex partners more than women do, it is possible such findings do not reflect what men actually do when offered short-term sex. In studies of actual mating behavior, however, men are more likely than women are to consent to sex with a stranger (Clark and Hatfield 1989; Hald and Høgh-Olesen 2010; Schützwohl et al. 2009). In 1989, Clark and Hatfield had experimental confederates approach college students across various campuses and ask if they would like to have sex. Around 75% of men agreed to have sex with a complete stranger, whereas no women (0%) agreed to sex with a complete stranger. Twenty years later, Hald and Høgh-Olesen (2010) largely replicated these findings in Denmark, with 59% of single men and 0% of single women agreeing to the proposition, “Would you go to bed with me?” Interestingly, they also asked participants who were already in relationships, finding 18% of men and 4% of women currently in a relationship responded positively to the request.

Schützwohl et al. (2009) asked participants to judge what men and women would do in a similar situation, but they also manipulated the physical attractiveness of the confederate. For men, they were thought to agree to sex with a stranger if she was highly attractive 54% of the time, whereas women were thought to agree to sex with a

stranger if he was highly attractive 8% of the time. Guéguen (2011) had confederates of various levels of physical attractiveness *actually* approach real-life strangers and ask if they would have sex, finding 83% of men agreed to have sex with a highly attractive woman and 60% of men agreed to sex with a woman of average attractiveness. For women, 3% agreed to have sex with a highly attractive man, but no woman (0%) agreed to sex with a man of average attractiveness. As noted earlier, men of high physical attractiveness are most able to successfully pursue a short-term sexual strategy. For the average-looking man, short-term mating may not represent a viable reproductive option.

Numerous studies have confirmed that men are more likely than women to engage in extra-marital sex (Petersen and Hyde 2010) and short-term mate poaching (i.e., seeking short-term sex partners who are already mated; Schmitt et al. 2004). Behaviorally, men are more likely than women to pay for short-term sex with (male or female) prostitutes (Bonnerup et al. 2000). In a Danish study, 16% of men and no women (0%) reported that they had “ever had sex with a prostitute?” (Bonnerup et al. 2000). Men are also more likely than women to enjoy sexual magazines and videos containing themes of short-term sex and sex with multiple partners (Salmon and Symons 2001).

Conclusion

According to Sexual Strategies Theory (Buss and Schmitt 1993), our species comes equipped with specialized adaptations (including mate preferences) that profoundly influence on our appraisal, desire, pursuit, and selection of mates. The evolved mate preferences that drive men and women when pursuing short-term mating strategies differ in fundamental ways. When short-term mating, men preferentially desire easy sexual access and relax their desires so as to obtain large numbers of sex partners. Women’s short-term mating is likely more complex. Leading functional hypotheses include selection for “good genes” as part of a dual mating strategy,

mate switching, and resource acquisition, all of which could be correct for some women in some contexts. Much remains to be explored in the evolutionary psychology of human mating, but at present the evidentiary status of most sex differences in short-term mate preference adaptations postulated by Sexual Strategies Theory, evaluated using multiple lines of evidence as advocated by Schmitt and Pilcher (2004), is both broad and deep.

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Sex Differences in Sobbing

► Sex Differences in Crying

Sex Differences in Social Development

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Synonyms

Boy and girl social learning; Early male and female socialization; Early relationship processes

Definition

The alternative socialization processes in childhood that enhance and solidify male and female stereotypic behavior.

Introduction

From the very beginning of childhood, social structures facilitate and influence evolutionarily constructed sex differences to emerge and become strengthened as children become older. This social development is tailored to enhance sex differences and prepare each sex for competition in mating strategies once they reach sexual maturity and into adulthood. It begins at home with parental socialization, and then moves into peer groups, with most socialization coming from same sex peer groups. These same sex peer groups often mirror the same sex parental socialization found in the home. Ultimately, this lays the foundation for the types of relationships each sex will end up having, with boys having greater and more inclusive social networks based on competition and social dominance hierarchies and girls having smaller and more intimate relationships based on self-disclosure. This then plays itself out in terms of the different mating strategies and forms of competition each sex finds itself in when they reach sexual maturity and adulthood. This entry will discuss the major social factors that differentially influence the socialization of sex differences during childhood.

Parental Socialization

Cross-cultural research has demonstrated that a very large and important sex difference arises early in childhood, especially when children are raised in cultures that are not socially restrictive – namely, that boys tend to be more assertive and dominant, whereas girls tend to be more nurturing and empathic (Schmitt et al. 2008). Part of the reason that these sex-typed characteristics emerge so early is in response to differential parental reinforcement or punishment of sex-typical behavior. For instance, shyness is a personality characteristic that would undermine the valued assertiveness characteristic in boys, but not the valued nurturing and empathic characteristics of girls. Indeed, Simpson and Stevenson-Hinde (1985) found that for 3.5–4-year olds, parents reacted to girls' shyness with positive behaviors

like acceptance, whereas for boys parents expressed concern and fear for their future.

In addition, parents of boys and girls tend to vary in their use of discipline in regard to their child's early interaction with others. As early as age two, parents of girls react to their child's struggle over an object with another child by stressing the importance of perspective taking and prosocial behavior while relinquishing the object to the other child, whereas parents of boys tend to favor their son's claim to the object much more often (Ross et al. 1990). Thus, parental encouragement and intervention early on in childhood works to enhance sex stereotypic traits, emphasizing communal relationships in girls and independent and dominant relationships in boys. Much of this parental involvement is in preparation for the same-sex peer socialization that is to become a major influence in the further delineation of sex differences.

Same-Sex Peer Groups

Young children tend to naturally segregate themselves into same sex peer groups, and the time spent socializing with same sex peers tends to increase as the child grows older (Maccoby and Jacklin 1987). As noted by Maccoby (1988), much of the reason for this increasing peer segregation is based on the interaction styles that are prevalent for each sex and the lack of responsiveness each sex has toward the social style of the other. Young boys tend to utilize the assertive and dominant tactics that are inherently stereotypic and were reinforced by parents, whereas young girls tend to focus their social style on promoting intimacy and equality. These social styles produce very different peer group structures that further exacerbate these sex differences.

The social structures of boys tend to be large and complex, with emphasis on dominance hierarchies and ingroup cohesiveness, whereas the social structures of girls tend to be more dyadic in nature, with emphasis on self-disclosure and personal connections (see Geary 2010). These group dynamics and associated group behavior plays a significant part in preparing each sex for

engaging in competition for mates when older. The social styles of each sex contributes to the size and complexity of group dynamics namely in regards to the cost and rewards of utilizing each style in reference to the size of groups. The assertiveness of boys lends itself well to intergroup competition and the formation of social hierarchies, whereas the tender-mindedness of girls lends itself to intimate dyads. Geary et al. (2003) notes that the fundamental difference is the ease by which boys' ingroup competition allows for larger groups, which allows for better intergroup dominance. The low level of interpersonal investment allows for group growth and maintenance. On the other hand, the emotional investment required in girls' dyadic relationships preclude the formation of larger and more interconnected ingroups – the costs are merely too high. This difference is highlighted in research examining the formation of male and female peer groups during camps that lasted for several weeks (Savin-Williams 1987). At the end of these camps, boy peer groups tended to be very strong, large, and inclusive with increased stability over time. Conversely, girl peer groups tended to be decreasingly stable with time, as they became segmented and fractured into smaller dyads.

Ultimately, as Geary (2010) explains, the larger and more dense social networks of boys create opportunities to engage in competition and learn the dynamics of social hierarchies, which will provide them with a framework for competitive interactions in the future with other males over resources and access to females, while also providing a necessary foundation for ingroup formation that is essential for intergroup competition. In this way, boys can individually find their place within the ingroup social hierarchy and remain committed to the group's goals given the stability of male ingroups. The smaller and more intimate dyadic relationships of girls play an entirely different function in the preparation for adult interactions. Girl relationships require much more emotional investment but also are much less stable and more prone to deterioration. In the end, though, the benefits of girls relationships in terms of self-disclosure and social support help prepare

girls for deep relationships with other women in adulthood.

More importantly for girls, however, is the knowledge gained regarding social relationships and their mechanisms, which confers benefits to them and their eventual offspring. These benefits include assimilation into the mate's social structure and gaining strong social support with that social structure from other women, as Geary (2010) proposes that boy and girl social strategies partially arise in response to the tendency of ancestral females to emigrate into the ancestral males group, leaving behind their previous modes of social support. Furthermore, in the competition for mates the social skills gained through intimate relationships allows females to use social manipulation and relational aggression to put themselves in a more advantageous position to acquire a mate (Crick and Bigbee 1998). The depth and intimacy of female relationships also mirrors the level of investment required for reproductive purposes and subsequent care for the offspring, something that is not required of males according to the parental investment theory (Trivers 1972).

Conclusion

Overall the natural sex differences that exist are met with a confluence of socialization influences that help strengthen those sex differences and prepare boys and girls for their separate paths toward relationships and mating strategies. Parental differences in socializing sex stereotypic behaviors are evident from infancy, and once children become old enough to interact with peers they often segregate themselves into same sex peer groups, which exacerbates sex differences by the formation of different types of groups built on different styles of interaction. Boys tend to be more directly assertive in their interaction style, which helps create large and interconnected social networks built on competition and social dominance hierarchies. Girls, on the other hand, tend to be more inclined toward cooperative and intimate interaction styles, which require large amounts of resources and investments into

relationships, thereby producing smaller interaction groups more characterized by dyads. This combined parental and peer socialization facilitates the type of relationships typically exhibited by each sex in adulthood and contributes to differences in mating strategies as well.

Ultimately, the large social networks of boys help establish competition within the group for dominance and subsequent access to the more valued female counterparts, but also cooperation in response to outgroup competition which helps the group as a whole to overcome outside threats and secure resources. The smaller social networks characteristic of girls then helps not only to increase knowledge of intimate relationships, but this knowledge increases the ability to form close relationships with other females when emigrating into a new social structure, as females may have historically been more likely to move into their mate's social group. Finally, this level of intimacy and nurturing that has been cultivated through early female social interaction greatly assists with the extensive investment requirements of reproducing offspring and caring for that young. Together, sex socialization in early childhood is a dynamic force that enhances innate sex differences in order to best formulate relationships and contribute to the next generation.

Cross-References

- [Dyadic Relationships Versus Group Processes](#)
- [Social Learning](#)
- [Status Competition and Peer Relationships in Childhood](#)

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Sex Differences in Spatial Abilities

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Synonyms

[Sex differences in mental rotation](#); [Sex differences in spatial information processing](#); [Sex differences in spatial rotation](#); [Sex differences in spatial visualization](#); [Sex differences in Three-dimensional processing](#); [Sex differences in Visuospatial ability](#)

Definition

Differences between males and females in the faculty that processes neural representations of physical space, such as the orientation and movement of objects.

Introduction

Spatial ability (SA) is an overarching concept for a wide range of abilities that involve neural representation and manipulation of physical space. Examples include wayfinding, running, jumping, and ballistic feats, such as hitting game in hunt or enemies in warfare, as well as the invention and construction of machinery, writ large. While human (gonadal) sex differences in cognitive abilities are generally small, males systematically and substantially outperform females on tests of SA, with meta-analytic effect sizes in the range 0.48–0.94 (Linn and Petersen 1985; Voyer et al. 1995; for reviews, see Hirnstein et al. 2019; Zell et al. 2015). Such tests include judgments of how gravity affects liquid in a vessel, judgments about how objects are rotated in two- or three-dimensional space, and understanding of the operation of cogwheels, pulleys, and gears.

Real-World Significance

Domains that involve spatial processing tend to exhibit the largest sex differences in terms of average performance, interest, and the proportion of males to females involved in professions to which such abilities are central (Lippa 2010b; Valla and Ceci 2014; Wai et al. 2018; Su and Rounds 2015). Examples of such professions include controlling tools and vehicles (e.g., aircrafts, cranes, excavators, trucks, and submarines) mechanical construction and repair (e.g., buildings, roads, bridges, and infrastructure in general), engineering and the STEM fields in academia (Peers 2016), and ball games and other sports that involve spatial ability, such as shooting and racing (partly reviewed in Li 2014). Specific performance differences include furniture assembly (Wiking et al. 2016), wayfinding in real terrain (Silverman et al. 2000), and chess (Blanch et al. 2015).

SA and mathematical ability are correlated even when intelligence has been controlled for, particularly for higher levels of mathematical problem-solving ability (Casey et al. 1995). This suggests that SA is important for even more

abstract cognitive performance that involves mental manipulation of quantities and relations, such as in chemistry, physics, and computer programming (for reviews, see Heilbronner 2013; Valla and Ceci 2011; Berenbaum and Beltz 2016; Lippa 2010a).

Etiology of Sex Differences in Spatial Ability

Sex differences are present before puberty, extant studies beginning at 8–9 (Gur et al. 2012, Fig. 4) to 10 years of age (Linn and Petersen 1985), and increase across puberty and into adulthood (Barel and Tzischinsky 2018; Gur et al. 2012). It has been suggested that androgens mediate genetically influenced, adaptive sex differences that originate from natural or sexual selection pressures (Lynn 1994). Consistent with this theory, SA is not related to prepubertal androgen exposure, in terms of the androgen marker of 2D:4D digit ratio (Hampson et al. 2008), but to adult androgen levels in both sexes, such as testosterone (Barel and Tzischinsky 2017; Christiansen and Knussmann 1987). Specifically, females' SA increases with testosterone over the natural variation in the menstrual cycle (Celec et al. 2002; Harrison 2000), is increased by administration of exogenous testosterone (Aleman et al. 2004; Pintzka et al. 2016), and is elevated in females with congenital adrenal hyperplasia, a condition in which females become masculinized due to incorrect steroid metabolism (for reviews, see Hampson and Rovet 2015; Puts et al. 2008). Associations between masculinity/femininity and SA suggest that sex roles mediate the effects of sex (Signorella and Jamison 1986; Reilly et al. 2015; a recent meta-analysis is found in Reilly and Neumann 2013). On the other hand, this may be a trivial effect of natural variation in physiological masculinization in both sexes (Berenbaum and Beltz 2016; Puts et al. 2008; Halari et al. 2005).

Conclusions

It has been suggested that sex differences in spatial abilities constitute evolved adaptations

that reflect division of labor in ancestral, hunter-gatherer ecologies (these arguments are summarized in Silverman et al. 2007). SA may therefore be a particularly useful trait for investigating heritable and adaptive mechanisms by examining relations between sex, masculinity/femininity, and other variables (for overviews of this field, see Gur and Gur 2017; Berenbaum and Beltz 2016; Valla and Ceci 2011).

Cross-References

- [Intelligence](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Specialized Cognitive Skills](#)

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Sex Differences in Spatial Information Processing

- [Sex Differences in Spatial Abilities](#)

Sex Differences in Spatial Rotation

- [Sex Differences in Spatial Abilities](#)

Sex Differences in Spatial Visualization

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Sex Differences in Standard Deviation

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Sex Differences in Variability

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Sex Differences in Variance

- [Sex Differences in Variance Traits](#)

Sex Differences in Variance Traits

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Synonyms

Sex differences in standard deviation; Sex differences in variability; Sex differences in variance

Definition

Members of one sex (male or female) have significantly greater dispersion or variability on a trait than members of the other sex. They contrast with sex differences in the mean of a trait.

Introduction

In statistics, the *mean* (or median or mode) is a measure of central tendency, whereas the *variance* (or standard deviation) is a measure of dispersion. Scientists commonly study mean differences between groups, when one group has a higher (or lower) mean level of a trait than (an) other group(s). As a result, most statistical techniques and tests of statistical significance involve the mean. It is less common for scientists to study group differences in variances, and there are fewer statistical techniques and tests of statistical significance that involve the variance. Nevertheless, scientists sometimes focus on group differences in variances because they are of theoretical or empirical importance, and sex differences in variance are no exception. Sometimes men exhibit greater variance in a trait; other times (though less frequently), women exhibit greater variance in a trait.

Potential Causes of Sex Differences in Variance

There are at least two potential causes of sex differences in variance: genetics and polygyny. For the most part, both of these factors function to produce significantly greater variance among men than among women.

Genetics: X Chromosome

Males of mammalian species (including humans) have an X chromosome and a Y chromosome in their genome, whereas females of such species have two X chromosomes. This means that any phenotype (observable trait) that is coded in the X chromosome is an expression of one X chromosome among males and an expression of two X chromosomes among females. When the phenotype is an expression of one gene (housed in one X chromosome for males), it has greater variance than when the same phenotype is an expression of two genes (housed in two X chromosomes for females). This is because the expression for the female is the average of the two genes, whereas the expression for the male is a singular value. Statistically, the average of two values is always more likely to be closer to the overall mean of the distribution (and thus is less variable) than a singular value.

Suppose you have a bag containing 101 marbles, each inscribed with a number from 0 to 100. If you are a man, you draw one marble from the bag and the number written on the marble you draw will be your “score” (phenotype). If you are a woman, you draw two marbles, and your “score” (phenotype) will be the average of the two numbers written on the two marbles you draw. If you are a man, you are just as likely to draw a large number as to draw a small number; you have an equal probability of drawing any of the 101 numbers, so your “score” can be anywhere on the scale from 0 to 100. In sharp contrast, if you are a woman, your “score” is more likely to be closer to the mean of the scale (50) than to be an extreme value far away from the mean. If you get a very high number – say,

75 – on your first draw, your second draw is statistically likely to be a less extreme value – say, 60 or 40 – than to be an even more extreme value – say, 85 – because, if your first number is very high, then, for your second draw, there are fewer numbers left in the bag that are even higher than your first draw; most numbers still left in the bag are lower than your first draw. The same is true if your first draw is a very low number; you have many more chances to get a higher number on your second draw than to get an even lower number. So, if you are a woman, the average of the two numbers you draw is statistically more likely to be closer to the mean of the scale than the singular number that a man is likely to draw. And this is true of all women and all men; as long as a man's score is a singular value and a woman's score is the average of two values, then women's scores are more likely to be closer to the mean of the scale than men's scores. In other words, the distribution of women's scores will have a *smaller variance* around the mean than the distribution of men's scores. This is why any phenotype that is primarily derived from the X chromosome has a smaller variance among women (who have two X chromosomes, and thus “draw” two values to determine their “score”) than among men (who have one X chromosome, and thus “draw” only one value to determine their “score”). For readers familiar with elementary statistics, this is the manifestation of the Law of Large Numbers at the extreme small end, with $n = 1$ and $n = 2$. Alternatively, one can think of this as a manifestation of the regression to the mean.

General intelligence is a case in point. There is some evidence that genes that affect general intelligence may be located in the X chromosome (Lehrke 1972, 1997; Turner 1996a, b) although more recent studies suggest that other chromosomes might be involved (D'Angelo et al. 2016; Deary et al. 2006; Johnson et al. 2016). Accordingly, studies, reviews, and meta-analyses published during the second half of the twentieth century nearly universally concluded that men and women have identical mean intelligence, but

men have greater variance than women (Ellis 1904; Deary et al. 2003; Eysenck and Kamin 1981; Geary 1998; Herrnstein and Murray 1994; Jensen 1998; Lehrke 1997; Lubinski 2000; Penrose 1963). They used to say “Most geniuses are men; most imbeciles are men,” while most women are near the center of the IQ distribution. The greater variance in intelligence among men than among women is precisely what we would expect if the genes for intelligence are located in the X chromosome.

This universal conclusion from the latter half of the twentieth century, however, has come under increasing attack during the first decades of the twenty-first century. The equality of the mean intelligence between the sexes was partly politically manufactured and achieved partially by the practice by psychometricians of discarding any item on a cognitive test that showed large sex differences (Jackson and Rushton 2006, p. 480). After discarding all test items that showed sex differences, psychometricians naturally achieved the equality of the sexes. There have now been several studies with samples from many nations that show that men may have very slightly (but, in large samples, statistically significantly) higher mean intelligence than women, by about 3–5 IQ points (Irwing and Lynn 2005; Jackson and Rushton 2006; Lynn and Irwing 2004; Nyborg 2005). Some of the confusion and conflict from earlier studies stems from the fact that past researchers have often failed to distinguish between children (boys vs. girls) and adults (men vs. women). Because girls mature earlier than boys, prepubescent girls typically have higher average intelligence than boys of the same age, but the female advantage often reverses after puberty (Lynn 1994, 1999; Lynn and Kanazawa 2011). Some suggest that men have a higher mean intelligence than women, not because they are men but because they are taller – taller individuals regardless of sex tend to have higher intelligence (Jensen and Sinha 1993) – and that, net of height, women are actually very slightly (but, in large samples, statistically significantly) more intelligent than men, by about 1–2 IQ points

(Kanazawa and Reyniers 2009). More importantly for our current purposes, some of these recent studies also show that women have greater variance in intelligence than men do (Irwing and Lynn 2005; Lynn and Irwing 2004). Thus the debate on the sex differences in the mean and variance in intelligence continues.

Polygyny: Sex Difference in Fitness Variance

Another trait that exhibits a large sex difference in variance is reproductive success. Men have much greater *fitness variance* – the difference between the *fitness ceiling* (the best one can potentially do) and the *fitness floor* (the worst one can potentially do) – than women do. The primary cause of the sex difference in fitness variance is the human evolutionary history of mild polygyny.

Clear evidence of our ancestors' polygyny is embodied in each of us: Men are on average taller and heavier than women. Both among primate and nonprimate species, the species-typical degree of polygyny – how polygynous members of a given species are on average – highly correlates with the degree of sexual dimorphism in size (the extent to which males of the species are taller and heavier than females) (Alexander et al. 1979; Leutenegger and Kelly 1977). The more polygynous the species, the greater the size disparity between the sexes. For example, among the completely monogamous gibbons, there is no sexual dimorphism in size; both by height and weight males are about the same size as females. In contrast, among the extremely polygynous gorillas, males are 1.3 times as large by height and twice as large by weight as females (Alexander et al. 1979, pp. 428–430, Table 15–3). On this scale, humans are somewhere in the middle, but closer to the gibbons' end than the gorillas'. Typically, human males are 1.1 times as large by height and 1.2 times as large by weight as human females (Eveleth and Tanner 1976, 1990). This suggests that, throughout evolutionary history, humans have been *mildly* polygynous, not as polygynous as gorillas but not completely monogamous like gibbons either. (For a discussion of *why* the species-typical degree of polygyny correlates with the sexual dimorphism in size, see Miller and Kanazawa 2007, pp. 87–89.)

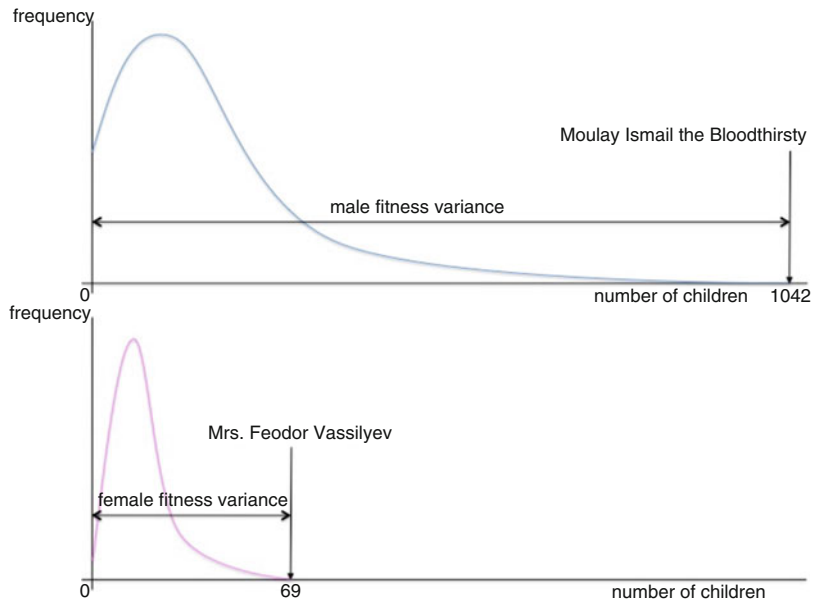
In a polygynous breeding system, virtually all women reproduce but a large number of men are excluded from reproductive opportunities. Given the roughly 50–50 sex ratio, every man who takes a second wife leaves another man mateless; every man who takes four wives leaves three other men mateless; a king or sultan who maintains a harem of 1,000 concubines leaves 999 men mateless. The more highly polygynous the society, the larger number of men are left out of reproductive opportunities. Under polygyny, reproductive opportunities are roughly equally distributed among women and most women have more or less the same number of children, whereas they are unequally distributed among men and some men have a large number of children while many other men die childless.

The largest number of children that a woman has ever had is 69. The wife of an eighteenth-century Russian peasant, Feodor Vassilyev, had 27 pregnancies in her life, including 16 pairs of twins, seven sets of triplets, and four sets of quadruplets. Amazingly, Mrs. Vassilyeva (her first name is lost to history) never gave birth to a singleton in her entire life! Even more remarkably, all but two of her 69 children survived to adulthood. In contrast, the largest number of children that a man has ever had is *at least* 1,042 (Young 1994, p. 10). The last Sharifian emperor of Morocco, Moulay Ismail the Bloodthirsty, maintained a large harem and had at least 700 sons and 342 daughters. The exact number of children that Moulay Ismail had in his lifetime is not known; the court officials stopped counting daughters after 342, and eventually stopped counting sons after 700, hence the large disparity in the number of sons and daughters. It is true that men of high status are slightly more likely to have sons than other men are (Trivers and Willard 1973) but *not* twice as many. If we assume that Moulay Ismail must have had *roughly* the same number of daughters as sons, then he must have had at least about 1,400 children altogether.

The exact number of children that Moulay Ismail and Mrs. Vassilyeva had is not important. What is important is that the largest number of children that a man can potentially have is *two orders of magnitude greater* than the largest

Sex Differences in Variance Traits,

Fig. 1 Sex differences in fitness variance



number of children that a woman can potentially have (thousands vs. tens), while at the same time many men, but few women, face a great chance of ending their lives as total reproductive losers (leaving no genetic offspring).

Figure 1 presents the theoretical distribution of children that men and women typically have. There are two notable sex differences: The fitness ceiling is much higher for men than for women (men can potentially have a much larger number of offspring), and the fitness floor is much lower for men than for women (the prospect of ending their lives as total reproductive losers is much greater for men than for women). As a result, the fitness variance (the distance between the fitness ceiling and fitness floor) is much greater for men than for women. Men have much greater variability in the number of children they have than women do.

However, while the institution of polygyny creates greater male fitness variance than female fitness variance, other consequences of polygyny can potentially create greater variance among women than among men. Because only some men can reproduce under polygyny while most women do, any sex-linked heritable trait (phenotypes that sons genetically inherit from their fathers and daughters genetically inherit

from their mothers) should exhibit greater variance among women than among men. However, most heritable traits are *not* sex-linked; sons inherit most of their traits equally from their fathers and mothers, and daughters inherit most of their trait equally from their fathers and mothers (Kanazawa and Novak 2005).

Conclusion

While scientists most frequently focus on sex differences in the mean of some trait, sex differences in variance are sometimes of great theoretical and empirical importance. Two primary factors that produce sex differences in variance are genetics and polygyny, both of which typically create greater variance among men than among women. Any phenotype that primarily derives from the X chromosome has greater variance among men than among women because men have only one X chromosome where as women have two X chromosomes, and men have greater fitness variance than women due to polygyny. Sex differences in variability are an often neglected research topic, which can benefit from greater attention in future research.

Cross-References

- [Female Reproductive Variance](#)
- [Male Reproductive Variance](#)
- [Polygyny and Effective Population Sex Ratio](#)
- [Reproductive Variance](#)
- [Variance in Female Reproductive Success](#)

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Sex Differences in Visuospatial Ability

- [Sex Differences in Spatial Abilities](#)

Sex Differences in Weeping

► Sex Differences in Crying

Sex Differences Versus Gender Symmetry

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Synonyms

Assortative mating; Mate preferences; Mate selection; Sex differences; Sex similarities

Definition

Men and women have similar and different mate preferences, which include preferences for type of relationship duration as well as the types of traits that are sought out within each mating duration.

Introduction

Mate preferences include preferences for relationship duration (long-term versus short-term) as well as the types of traits that are sought out in a potential mate within each relationship duration. Men and women are similar on some aspects and different on others. This entry covers some of the key similarities and differences in preferences for both mating context and partner traits within context.

Sex Differences in Relationship Duration Preference

Around the world, both men and women engage in both long-term committed relationships,

including marriage, and short-term sexual relationships, which include casual sexual encounters. There are, however, important sex differences in relationship duration preference such that men, more than women, are likely to prefer casual, short-term sexual relationships; conversely, women, more than men, prefer relationships to be committed and longer term (Buss and Schmitt 1993; Li and Kenrick 2006).

Much of the difference in relationship preference stems from sex differences in minimum obligatory parental investment (Trivers 1972). That is, whereas women are required to invest heavily in offspring because fertilization, gestation, and placentation occur internally and women also carry the additional parental investment associated with lactation after offspring are born, men are physiologically required to contribute only a few sex cells during sexual intercourse to produce offspring. Women's various forms of required physiological investment limit the number of children women can successfully produce; typically the upper bound is about a dozen under optimal conditions, and that upper bound is seldom reached. In contrast, men's minimal constraints enable men to have a much higher reproductive ceiling as the number of offspring a man can have can be increased by pursuing multiple mating opportunities.

Thus, in reproductive terms, the costs of a short-term sexual relationship typically outweigh the benefits for women more so than for men (Li and Kenrick 2006; Symons 1979). Although each individual offspring provides equal reproductive benefits to both parents, they present much higher costs to women if they result from uncommitted sex. Women have therefore evolved to be more selective about potential mates relative to men, as failure to procure the long-term commitment of a mate who provides protection and resources would have been particularly detrimental to survival for impregnated ancestral females, who lived without the benefits of modern food production, public health, medicine (Daly and Wilson 1983), and social welfare. On the other hand, reflecting their rather minimal physiological constraints, men evolved to have greater eagerness for short-term casual relationships and desire

for sexual variety than women (Buss and Schmitt 1993; Kenrick et al. 1990; Symons 1979).

Basic sex differences in sociosexuality (Simpson and Gangestad 1991; Schmitt 2005) reflect these varied preferences between men and women for short- versus long-term relationships. Sociosexuality is a strategic dimension of human mating with a sociosexually restricted orientation associated with lengthier courtships and heavier emotional investments in longer term relationships on one end, and sociosexually unrestricted orientation associated with greater promiscuity, shorter courtship durations, and lesser romantic relationship closeness, on the other end. Individuals who require love and commitment in order to have sexual relations are restricted, whereas those who feel comfortable having sex without love and commitment are unrestricted. Various studies have found that men tend to be more sociosexually unrestricted than women (e.g., Simpson and Gangestad 1991). Schmitt et al. (2001) comprehensive review identifies three areas where sex differences in sociosexuality arise, namely that men possess a greater desire for short-term, casual sexual relationships than women, men prefer larger numbers of sexual partners over time than women, and men require less time before consenting to sex than women. Schmitt's (2005) large study across 48 nations confirmed that sex differences in sociosexuality were generally large, men had higher sociosexuality scores and were thus more sexually unrestricted than women, and these sex differences were cross-culturally universal (although the sex difference appears to be reduced, but not eliminated, by factors such as greater economic gender equality).

Long-Term Mate Preferences

While it has been robustly documented across multiple studies that men are more likely than women to prefer short-term mating (e.g., Buss and Schmitt 1993; Gangestad and Simpson 2000; Kenrick et al. 1990, 1993; Li and Kenrick 2006), humans are also among the few mammals where males develop long-term bonds with their mates and invest in care and nurturance of

offspring (Geary 2005). As humans spend more time in a juvenile state than other mammals, requiring more years of brain and social development before being capable of functioning independently (Björklund and Shackelford 1999), fatherhood as an adaptation carries with it improved fitness of offspring, such as lower child mortality and greater social competitiveness of offspring later in life (e.g., Kaplan et al. 1998). Additionally, human males have relatively higher levels of paternity certainty and lower levels of reproductive success from multiple short-term matings compared to other mammals (Geary 2005), the latter resulting from adaptations in our female ancestors that are both physical (e.g., concealed ovulation; Shackelford et al. 2004) and psychological (e.g., aversion to casual sex and preference for commitment; Schmitt et al. 2001). Therefore, although men can benefit greatly from enacting a short-term mating strategy, various constraints also increase the evolutionary incentive for men to commit to long-term relationships.

When seeking a long-term relationship, the sexes exhibit various similarities – for instance, both men and women are choosy overall when selecting a long-term mate (Kenrick et al. 1990). Humans are like other mammals in that a male's *minimum possible* parental investment is relatively small compared to conspecific females, but different from other mammals in that a male's *typical* parental investment is relatively large compared to males of other mammals. In long-term relationships wherein a male's parental investment and relationship commitment reaches a level comparable to that of females', men become as selective and stringent as women on important partner traits (Kenrick et al. 1990). Buss's (1989) large study on mate preferences across 37 cultures found that the sexes place similarly high importance on traits that include kindness, love, pleasing disposition, and emotional stability in a marriage partner (for a review of universal dimensions of people's mate preferences, see Shackelford et al. 2005).

However, important differences between the sexes also exist. When seeking long-term mates, men value physical attractiveness more than

women do, whereas women value social status and resources more than men do (e.g., Buss 1989). Because women's fertility declines relatively quickly as a function of age, men's reproduction is constrained by access to reproductively valuable or fertile mates (Symons 1979; Trivers 1972). Identifying fertile and healthy mates is thus a primary adaptive problem in both long-term and short-term mating for men. As such, men have evolved a preference for physical features found in young, sexually mature women. Such features, which include firm skin, long and luscious hair, firm breasts and buttocks, and a low waist-to-hip ratio, are predictive of age, health, and fertility (e.g., Buss and Schmitt 1993; Li et al. 2002; Singh 1993), and tend to be preferred by men in both long- and short-term mating contexts.

In contrast to women, men face a much slower decline in fertility across the lifespan, so identifying fertile partners is not as important for women. However, ancestral men varied considerably in their ability to provide resources necessary to the survival of women and their offspring. Thus, women, more than men, evolved to value the ability of a partner in a long-term mating context to provide resources and protection (Buss and Schmitt 1993), which would have been especially important in ancestral times when women were less capable of acquiring resources for or defending themselves and their offspring when burdened with pregnancy and child-rearing. In humans as well as other mammals, social status is an effective proxy for abilities including those to acquire and retain resources. Accordingly, women may have evolved to place a premium on men's social status (Symons 1979) when choosing long-term mates.

There is much empirical support for this evolutionary perspective on long-term mate preferences. Alongside similarities between the sexes on traits such as love and dependability (Shackelford et al. 2005), numerous studies have found that men value physical attractiveness more than women do, and women value social status more than men do. Such studies include experiments that manipulate physical attractiveness and social status in opposite sex target photographs and descriptions and speed-dating contexts (e.g.,

Li et al. 2013), as well as in studies of personal advertisements, consumer behaviors, folk tales, self-concept, self-ideals, and self-esteem, among other contexts.

Short-Term Mate Preferences

Due to the higher reproductive payoffs for men than women when enacting a short-term mating strategy, men have evolved psychological adaptations that facilitate the pursuit of short-term mates. For instance, men are more eager than women to enter short-term relationships (Buss and Schmitt 1993) and report being much more willing than women to engage in sexual relations after any length of acquaintance from one hour up to 5 years. A now-classic study at Florida State University found that when approached by an opposite-sex stranger who immediately made an invitation for casual sex, 75 % of men said "yes," whereas 100 % of women said "no" (Clark and Hatfield 1989). Men are less selective than women when presented with the chance of entering a short-term relationship (Li and Kenrick 2006), which makes it easier and more likely for short-term, casual, and noncommittal sexual relations to occur. Studies have also shown that although both sexes have relatively high minimum requirements for various traits in long-term mates, men but not women significantly lower their standards for casual sexual partners and one-night stands (Kenrick et al. 1990, 1993). Moreover, men may have psychological adaptations designed to minimize commitment after sex (Haselton and Buss 2001). Men who have had more sexual partners (i.e., men who are capable of successfully enacting a short-term mating strategy) are more likely to experience a decrease in how sexually attractive they find their partner immediately following intercourse, whereas neither men with less sexual experience nor women show this decline.

Another source of evidence for men's greater penchant for casual sexual relations or sexual variety comes from studies of homosexual individuals. Gay men, who deal with other men's similar preferences for casual sex (e.g., Symons

1979), tend to have significantly higher numbers of sexual partners than heterosexual men and lesbian women, who have to contend with the commitment-seeking preferences of women. Blumstein and Schwartz's (1983) large study on American couples found that only 36 % of gay men stated that it was important to them to have a sexually monogamous relationship, compared to 71 % of lesbians, 75 % of heterosexual men, and 84 % of heterosexual women. When actual sexual behavior was examined, only a minority of lesbians (28 %), heterosexual men (26 %), and heterosexual women (21 %) had engaged in sex outside their primary relationship, while majority of gay men (82 %) engaged in sexual intercourse outside their primary relationship. The authors also reported a positive correlation between sexual fidelity and relationship satisfaction that applied to lesbian and heterosexual couples but not for gay male couples. Gay men in relationships are therefore more likely to have shared sexual preferences that allow for agreements permitting casual sex outside their primary relationship.

Despite this well-documented sex difference in relationship duration preference, many women also engage in short-term mating. Given that each act of heterosexual sex involves a man and a woman, the average number of sexual partners for men and women who engage in short-term mating should be identical (Greiling and Buss 2000). Additionally, if women in ancestral times had never engaged in short-term mating, men could not have evolved the desire for sexual variety. Therefore, regardless of preferences for a longer versus shorter relationship duration, women often engage in short-term mating and have likely evolved to value specific traits in a short-term mate that differ from those they seek in a long-term mate.

A relationship that is primarily sexual and uncommitted makes obtaining a continuous flow of resources much less important, if not irrelevant (Li and Kenrick 2006). Thus, women likely did not evolve a strong preference for resources in a short-term mating context. Instead, women may have evolved to value the quality of a short-term partner's genes, which can be conferred to

offspring (Buss and Schmitt 1993; Gangestad and Simpson 2000). Specifically, women may have evolved to be physically attracted to short-term mates displaying visible markers of good quality genes. Such markers may include the presence of both masculinity and symmetry, which indicates that despite having abundant testosterone (which increases masculine features but also suppresses the immune system), a male has effectively resisted pathogens that can cause asymmetrical development. Consistent with this reasoning, studies have shown that women find symmetry and masculinity to be desirable when considering a short-term mate and when ovulating (Gangestad and Simpson 2000; Gangestad and Thornhill 1997). Women also value size, muscularity, and physical strength in their short-term mates (Frederick and Haselton 2007; Li and Kenrick 2006), which may help them obtain physical protection (Smith 1984).

Women's fertility is especially important for a short-term context, where other considerations, such as the coordination of parenting, are less or not relevant. As such, men likely evolved to value physical attractiveness across both long- and short-term mating contexts (Buss and Schmitt 1993). Indeed, both sexes have been found to value and prioritize physical attractiveness above other traits in short-term mates (Kenrick et al. 1990; Li and Kenrick 2006), with men valuing and prioritizing physical attractiveness even more in a short-term mate than in a long-term mate (Kenrick et al. 1990; Li and Kenrick 2006). So, both sexes highly value physical attractiveness when considering short-term mates, though for different underlying adaptive reasons.

Criticisms and Responses to Criticisms of Evolutionary Perspectives on Mate Preferences

Recently, various criticisms have been levelled at evolutionary theories of sex differences in mate preferences. First, as raised by Li et al. (2002), preferences for physical attractiveness and social status do not seem to be rated or ranked highly enough in empirical studies to warrant the critical

importance espoused by evolutionary theory. For example, physical attractiveness was ranked sixth out of 13 in importance by men and good earning capacity was ranked tenth in importance by women (fairly low rankings for supposedly important traits; Buss and Barnes 1986). Second, as raised by Eastwick and Finkel (2008), various studies conducted in live interaction settings failed to find these sex differences (e.g., both sexes appeared to equally value physical attractiveness) as well as links between people's stated mate preferences and the criteria they use in selecting actual mates. However, these concerns were addressed by theories and findings guided by the *mate preference priority* model (Li et al. 2002, 2013; Li and Kenrick 2006; Li and Meltzer 2015).

According to this model, although numerous traits are valued in a mate, such as kindness and creativity, many of these traits are "luxuries" compared to traits that are more critically vital to reproductive value, such as physical attractiveness for men and social status for women. These traits are evolutionary "necessities" in mating – traits that must be present at some minimum level of requirement in a potential mate in order for reproduction to be successful. Accordingly, it is adaptive for individuals to reject potential mates with low levels of necessity traits – those who, in ancestral times, would not have been able to reproduce or contribute to the survival of offspring – at initial stages of mate selection to minimize the costs of poor mate choice later on. Thus, despite having similar preferences for an ideal well-rounded mate, men and women likely have evolved mechanisms that first prioritize different necessity traits in long-term partners before other luxury traits (Li et al. 2002).

Specifically, men may have evolved to first seek mates who pass a minimum threshold on physical attractiveness, whereas women may first seek mates who pass a minimum threshold on social status. After acceptable levels of these necessity traits have been acquired or verified, other luxury traits – which also contribute to reproductive fitness – are then considered and become more highly valued. Direct support for the mate preference priority model comes from studies using a budget allocation methodology as

well as a mate screening paradigm, which have shown that sex differentiation in mate preferences occurs in the predicted directions when choices are made between low levels of necessity traits during the initial stages of selection for long-term mates (Li 2007; Li et al. 2002, 2011; Li and Kenrick 2006). Moreover, Li and colleagues (2013) experimentally tested this paradigm by manipulating the physical attractiveness and social status of chat partners in a live, speed-dating context. This work addressed a key limitation of previous live interaction studies in which participants representing the low end of necessity traits such as social status may have been absent, hence undermining the relevance of those traits to mate selection. Indeed, when physical attractiveness and social status were manipulated such that individuals at the low end of these traits were present, the predicted sex differences then emerged as men declined potential mates low in physical attractiveness while women shunned those who were low on social status. When mating duration was clearly specified, these sex differences were pronounced for long-term but not for short-term relationships. For short-term relationships, both sexes avoided partners with low physical attractiveness.

Compromises in Mate Preferences

Given that the sexes ideally desire different types of relationships, compromises need to occur in order for mating to actually occur, thereby leading mating strategies to converge and reflect a greater degree of similarity than what each sex ideally prefers. For instance, many men likely have to compromise on their preference for short-term casual relationships in order to attract women, who tend to have a strong preference for long-term committed relationships. Similarly, women may have to yield on some of their desired commitment due to men's ideal preference to not provide it. Compromise and convergence of mating strategies and preferences are by-products of each sex pursuing different strategies and imposing mutual constraints, though the ability for mating strategies and preferences to adjust to such

constraints needs to have evolved in order for the flexibility to occur. Below, several lines of research that illustrate such compromises are described.

Firstly, mating strategies have been shown to be facultatively responsive to the adult sex ratio of the local ecology (i.e., ratio of men to women in a population; Schmitt 2005). In environments where high-quality men are a scarce and valuable commodity (e.g., places plagued by war), these desirable men can demand short-term mating and obtain it, as it may be in a woman's best reproductive interests in these circumstances to agree to short-term mating than risk not reproducing at all. Conversely, in female-scarce environments (e.g., China, where a combination of favoring male offspring and the one-child policy has created a large male-to-female sex ratio), relationships tend to be longer term and monogamous. As women are highly sought after and have high value in female-scarce mating markets, it makes greater reproductive sense for a man who is fortunate enough to attract a mate to focus on keeping her (by fulfilling her ideal desires) rather than losing her to the next guy who does, or by futilely seeking additional mates.

Secondly, as mentioned above, homosexual relationships can be meaningfully compared to heterosexual relationships to gain insights into mating psychology. In homosexual relationships, individuals are unencumbered by the different preferences of the opposite sex; thus, there is less need to compromise on dimensions where the sexes differ. So, whereas heterosexual men have to contend with and compromise due to women's preference for committed, long-relationships, homosexual men, whose partners are other men, do not face this constraint. Similarly, lesbian women deal with the mostly long-term preferences of other women rather than the largely short-term, sexual preferences of men. Indeed, reflecting these differences, studies have found that lesbian relationships tend to be committed and longer term, while gay men engage in casual short-term relationships more frequently than heterosexual men (Symons 1979).

Third, while much research on human mating relationships has focused on long-term relationships (e.g., cohabitation, marriage) and short-term relationships (e.g., one-night stands, hook-ups) as two polar-opposite and competing relationship

types, other evidence suggests that the range of potential relationships extends beyond this relationship dichotomy and can include other arrangements such as "friends with benefits" and "booty-calls" (e.g., Jonason et al. 2009). These alternative arrangements emerge as compromise relationships resulting from men and women pursuing their different, preferred mating strategies. Booty calls tend to utilize various communication mediums to facilitate sexual contact among friends who, for men, may represent low-investment, attractive sexual partners and, for women, may represent attractive test-mates and long-term possibilities (Jonason et al. 2009). Such relationships serve as a compromise between men's and women's ideal mating strategies that allows men greater sexual access and women an ongoing opportunity to evaluate and obtain potential long-term mates.

Finally, assortative mating, where individuals of similar "mate value" tend to partner up, also occurs as a result of people's ability to compromise in competitive mating markets. An individual's overall mate or reproductive value can be defined as the sum of his or her traits (e.g., Kirsner et al. 2003). In a competitive mating market, a person's reproductive value should be reflected by their overall desirability to the opposite sex. While self-reported preferences predict that people find high mate value individuals attractive and would prefer to mate with them, the constraints of the mating market typically create gaps between ideal mate preferences and actual choices, especially for exclusive long-term relationships. For example, most women might prefer a generous husband with a high income and lavish lifestyle (Buss and Barnes 1986), but not all women can actually obtain such a husband. People are therefore expected to mate based on what positive qualities (i.e., mate value) they possess relative to a prospective partner's mate value in an assortative manner (Kenrick et al. 1993). Pursuing partners with a significantly different mate value is likely to be costly; for instance, it is difficult to attract as well as retain a mate whose mate value is higher than oneself, while acquiring a partner whose mate value is too low may lead to relationship dissatisfaction and wasted mate value. Therefore, the constraints of the mating market drive

individuals to adjust their standards in a partner such that they are eventually assortatively mated based on their perceived mate value. Studies have indeed demonstrated that individuals' mate preferences are indexed to their self-perceived value on the same traits (Kenrick et al. 1993) and couples tend to comprise of individuals of similar mate value (e.g., Figueredo et al. 2006).

Conclusion

This entry has described how men's and women's mate preferences, which include preferences for both mating context and traits within a context, are both different as well as similar. The sex differences are robust across time and culture and have likely evolved due to key differences in minimum obligatory parental investment as well as differences in fertility across the lifespan. Likewise, the considerable overlap that men and women share in their preferences also likely reflect evolved preferences, such as both sexes' preference for physical attractiveness in a short-term mating context (though for different underlying reasons), as well as processes of convergence due to both sides needing to compromise, such as when men and women adapt their relationship strategy to the other side's demands or when individuals mate assortatively. Together, these similarities and differences reflect a wide range of human mating behaviors.

Cross-References

- ▶ "Good Genes"
- ▶ "Good Parenting" Qualities
- ▶ Evolutionary Standards of Female Attractiveness
- ▶ Female Choice
- ▶ Female Mate Choice
- ▶ Female Reproductive Variance
- ▶ Friends with Benefits
- ▶ Local Sex Ratio
- ▶ Lowering Partner Standards in a Short-Term Mating Context
- ▶ Male Mate Choice
- ▶ Male Protection

- ▶ Male Reproductive Variance
- ▶ Men in Positions of Power
- ▶ Obligatory Parental Investment
- ▶ Parental Investment and Sexual Selection
- ▶ Preferences in Long- Versus Short-Term Mating
- ▶ Quantity Versus Quality of Offspring
- ▶ Sex Differences for Pursuing
- ▶ Sex Ratio
- ▶ Sexual Conflict in Mating Strategies
- ▶ Sexual Receptivity
- ▶ Social Status and Economic Resources
- ▶ Sociosexuality
- ▶ Women's Mate Value

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Sex Differences, Initiating Gossip

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Synonyms

Adaptive problems; Gossip; Indirect aggression; Intrasexual competition; Sex differences

Definition

Adolescent girls' and women's penchant for indirect aggression has led to the prediction that gossip may be their preferred tactic of choice when competing against intrasexual rivals. Consequently, girls and women are predicted to initiate and engage in gossip more frequently than boys and men.

Introduction

Gossip has been defined as a form of evaluative communication that permits individuals to exchange positive and negative information about absent third party others (Leaper and Holliday 1995; Levin and Arluke 1985). It is a construct that overlaps conceptually with rumor, but is distinct in that it tends to be truthful and about people as opposed to events (Foster 2004). The historic and cross-cultural ubiquity of gossip, as well as the consensus among researchers that it plays a vital role in human social relationships, has led to the proposal that it may be an evolved psychological adaptation that enabled our ancestors to survive and reproduce (Barkow 1992; Dunbar 2004; McAndrew and Milenkovic 2002; McAndrew et al. 2007). This evolutionary perspective challenges the notion that gossip constitutes idle "chitchat" and the mere passing along of trivial everyday details for the purpose of enjoyment. It also helps to contradict the pejorative gender stereotype sometimes associated with women's gossip by demonstrating that men also gossip to a significant extent. From this view, gossiping plays an essential role in how both sexes relate to and choose to coexist with other human beings (Foster 2004; McAndrew 2014); perhaps even to the point of defining the social group itself.

Gossip as an Adaptation to Overcome Adaptive Problems

As an adaptation, gossip is posited to be a heritable trait that was selected for because it helped to

solve problems linked to survival (e.g., locating food) and/or reproduction (e.g., gaining access to potential mates; see Davis et al. 2018 and McAndrew 2014 for discussion). Gossip has likely been preserved and has proliferated throughout human populations over time because it ultimately enhanced the reproductive success of our ancestors in the environment within which it was selected. What adaptive problem(s) might gossip have solved? For Dunbar (2004), the key adaptive challenges that gossip helped to overcome were those linked to group living.

In comparison to other primates, humans are unparalleled in their capacity for, and reliance upon, cooperation, cultural transmission, conformity, coalitional alliances, and "group-mindedness" (Barkow 1992; Dunbar 2004). To function in highly expansive communities requires an efficient means of gathering, sharing, and vetting information about others, as well as ways of encouraging cooperation and minimizing rule breaking (Foster 2004). Dunbar (2004) proposed that gossip helped to meet these challenges by (1) keeping track of others embedded in complex social networks, (2) emphasizing one's potential as an ally, friend, or mate, (3) soliciting help from others regarding personal dilemmas, and (4) policing the duplicitous and exploitative actions of others. Similarly, Barkow (1992) argued that social living necessitates tracking the actions of peers and developing the capacity to predict and influence the behavior of others in order to vie for finite resources linked to fitness. To this end, gossip may be instrumental for our success in social competition as a tactic for reputation management and to facilitate the creation of internal representations of others who are likely to impact our fitness such as kin, allies, mates, and rivals (Barkow 1992; McAndrew et al. 2007).

Over evolutionary time, women and men have faced many of the same adaptive hurdles, such as detecting the presence of dangerous predators and competing for potential mates. However, it is evident that the favored competitive strategies, reputational concerns, mating interests, as well as the character of kin networks and alliances differ substantially by sex (Barkow 1992; Campbell 1999, 2004; Vaillancourt 2013). This is the case because

women and men have recurrently faced many different adaptive problems over their evolutionary histories, which has led to the selection of divergent adaptations with sex-specific design features (Arnocky 2016; Arnocky and Vaillancourt 2017; Buss 1989). The domains within which women and men have faced different adaptive problems are defined by the process of sexual selection, whereby traits like gossip are selected because they provide a reproductive advantage (Arnocky 2016; Buss and Dedden 1990). Sex can be defined as consistent, but flexible, variation in reproductive anatomy and function, hormone levels, and chromosomal makeup (Davis et al. 2018). Sex is distinct from, but inseparably interrelated with gender, which tends to be defined as the attitudes and behavior that a particular culture associates with sex.

Adaptations that emerge through the process of sexual selection manifest as a consequence of choosing preferred mates (i.e., intersexual selection) and through competition with members of the same-sex for access to opposite-sex mates (i.e., intrasexual competition; see Davis et al. 2018 for discussion). In the realms of social and mating competition, our primary rivals tend to be same-sex others because they have faced the same adaptive problems and thus seek the same resources to meet these evolutionary challenges (Barkow 1992; Buss 1989). Importantly, sexual selection embodies competition for mates and resources that influence the probability of mating, such as popularity and status (Arnocky 2016). Intrasexual competition among humans involves diverse tactics including, but not limited to, emphasizing one's desirable qualities as a mate (i.e., self-promotion) and manipulating the reputations of competitors to lower their desirability as a mate relative to ourselves and diminish their capacity to compete (i.e., competitor derogation; Buss and Dedden 1990; Campbell 2004).

Gossip as an Intrasexual Competition Strategy

Evidence supports the argument that gossip is a key tactic for intrasexual rivalry. Davis et al.

(2018) found positive relations between self-reported intrasexual competitiveness, a tendency to gossip, and positive attitudes toward gossiping for both women and men. Furthermore, researchers have confirmed that we are most interested in, and share more negative gossip about, same-sex others of a similar age who are our primary intrasexual competitors in the context of heterosexual mating (McAndrew et al. 2007; McAndrew and Milenkovic 2002; McDonald et al. 2007; Owens et al. 2000). In the domain of mate competition, malicious gossip and rumor may be used to derogate rivals in an effort to lower their mate value and to access and retain reproductive resources (Arnocky and Vaillancourt 2012; Buss and Dedden 1990; Campbell 2004). This negative gossip is described as a type of indirect aggression which refers to a range of covert acts intended to influence and exploit interpersonal relationships, including social exclusion, spreading harmful gossip and rumors, and breaking confidences (Vaillancourt 2005, 2013).

Spiteful gossip, like other types of indirect aggression, is an effective mate competition tactic because it can be damaging to its targets (e.g., lowering self-esteem and increasing risk of depression for victims; see Vaillancourt 2013 for review) and it can be used to elevate our social standing (Vaillancourt and Hymel 2006), providing greater access to reproductive opportunities (Arnocky 2016; Arnocky and Vaillancourt 2012). Furthermore, gossip can be employed to manipulate social information in our favor and to impugn the reputation of rivals while disguising the identity of the gossiper, which reduces the probability of physical, verbal, or social retaliation (Arnocky 2016; Arnocky and Vaillancourt 2017; Vaillancourt 2013). Nonetheless, many social norms govern gossiping, which if violated can result in reputational damage and social exclusion (Foster 2004). Therefore, spreading and listening to malicious gossip carries a certain level of risk, despite its stealthy nature. Cross-culturally, adolescent girls and women have been shown to prefer more covert and circuitous modes of aggression such as negative gossip and social exclusion, whereas boys and men are more likely to engage in risky and direct forms of aggression

(e.g., verbal taunting and physically hitting another; Benenson et al. 2013; Björkqvist 1994; Campbell 1999, 2004; Owens et al. 2000; Vaillancourt 2005, 2013; Vaillancourt et al. 2010). This sex difference in the proportional use of different types of aggression corresponds to the unique adaptive challenges faced by ancestral women and men.

Despite being a species that engages in biparental care, women's higher degree of obligatory parental investment, through gestation, child bearing, and post-partum care, and their smaller number of gametes translates into a lower lifetime reproductive potential in comparison to men (Arnocky and Vaillancourt 2017; Campbell 1999, 2004). In contrast, men's reproductive output is largely constrained by their capacity to outcompete same-sex rivals to obtain reproductive opportunities. A mother's death has also been found to increase the risk of child mortality more than a father's death, underscoring the importance of maternal investment. Ancestral women, therefore, could less afford to engage in risky and violent forms of intrasexual competition and benefited by carefully selecting successfully competitive mates who were able and willing to invest (Arnocky 2016; Campbell 1999, 2004; Vaillancourt 2013). The larger cost associated with women's use of risky and directly aggressive mate competition tactics can be seen in their preference for indirect aggression and their relative absence of armament designed for direct intrasexual combat (e.g., smaller stature, less muscle mass) in comparison to men. Girls and women, relative to boys and men, are therefore predicted to use gossip as a mode of indirect aggression to compete against intrasexual rivals for mates and to establish and maintain status within their peer groups (Eckert 1990; Leaper and Holliday 1995; McDonald et al. 2007; McAndrew 2014; Vaillancourt 2005, 2013). This proclivity may correspond to a greater tendency to gossip, greater enjoyment of the activity, and a stronger inclination to gossip for intrasexually competitive purposes. For the same reasons, girls and women may be more likely to initiate the spreading of gossip than boys and men.

Several studies have supported the hypothesis that girls and women tend to gossip more than boys and men (Björkqvist et al. 1992; Davis et al. 2017; Leaper and Holliday 1995; Levin and Arluke 1985). There are also sex differences with whom men and women gossip. McAndrew et al. (2007) found that women were just as likely to share gossip with a same-sex friend as with their romantic partner, whereas men were significantly more likely to share gossip with their mates than with anyone else. Furthermore, women have been shown to express a stronger desire to hear gossip about members of their own sex and are more likely to gossip about same-sex friends and relatives in comparison to men (Leaper and Holliday 1995; Levin and Arluke 1985; McAndrew and Milenkovic 2002). Björkqvist et al. (1992) demonstrated that adolescent girls were nominated by their peers to be significantly more likely to spread malicious gossip in comparison to boys. Low et al. (2010) found that preadolescent and adolescent girls transmitted more malevolent gossip than boys and were more likely to be the targets of negative gossip. Women and men appear to spread a similar proportion of negative and positive gossip about other people in general (Levin and Arluke 1985); however, higher rates of spiteful gossip have been found to occur in female friend groups in comparison to male friend and female-male friend groups (Leaper and Holliday 1995). These findings support the idea that girls and women initiate gossip more than boys and men, particularly when spreading derogatory gossip about familiar others to same-sex peers.

Sex Differences in Initiating Gossip Episodes

To our knowledge, only one study has directly examined differences between women and men in who is more likely to be the first person to spread real or fake information about someone among mixed-sex groups. Levin and Arluke (1985) found that female friends initiated more negative gossip than male friends and cross-sex friends. Male friends were less likely to initiate the

spread of positive gossip; however, cross-sex friends were just as likely as women to initiate favorable gossip. Further investigation of sex differences in the initiation of gossip is needed to examine if women are more likely to start an episode of gossip in comparison to men within cross-sex groups. Women may be more likely than men to initiate gossip, particularly of a negative valence, with opposite-sex others because of their greater tendency to gossip among same-sex friends and their preference for using gossip as an indirect mode of aggression to compete against intrasexual rivals (Campbell 1999, 2004; Davis et al. 2018; McAndrew 2014). Nonetheless, a range of developmental, individual difference, interpersonal, and contextual factors are expected to influence this predicted sex difference.

Adolescent girls and young women are predicted to compete more intensely for mates and things linked to fitness (e.g., status, popularity) than younger girls and older women because of their relatively greater reproductive capacity and mate value (Campbell 1999, 2004; Massar et al. 2012; Vaillancourt 2013). Low et al. (2010) found that girls in grade six (aged 11–12) were more likely to gossip and to be the targets of gossip than girls in grade three (aged 8–9). Similarly, Björkqvist et al. (1992) found that 15-year-old girls were peer-nominated to be significantly more likely to spread negative gossip than their 8-year-old counterparts. Massar et al. (2012) demonstrated that young adult women reported gossiping more than their older same-sex peers. The authors found that this relation was mediated by mate value, such that more physically attractive women gossiped more often than their less attractive counterparts (Massar et al. 2012). Therefore, physically attractive adolescent girls and young women are more likely to initiate gossip about same-sex others because of their greater tendency to engage in the activity and their greater susceptibility to being the targets of gossip.

In comparison to boys and men, girls and women should be particularly likely to initiate gossip when it is being used to attack the relationships of same-sex peers. This is because girls and women regard close intimate friendships as more important than do boys and men and have tighter

social structures (Eckert 1990; McDonald et al. 2007). Researchers have supported that girls and women are more likely to be the targets of indirect peer victimization, such as malicious gossip, and are more susceptible to the psychological harm caused by this behavior (e.g., increased risk of depression, suicidal ideation; Benenson et al. 2013; Owens et al. 2000; see also Vaillancourt 2013 for discussion). At the same time, gossip can be a powerful social bonding mechanism that enhances intimacy and solidarity (Eckert 1990). This is likely of greater importance to girls and women who prefer close dyadic relationships characterized by intimacy, security, closeness, and trustworthiness (McDonald et al. 2007). Among older adolescent girls, qualitative reports have confirmed that aggressive gossip can play an important role in developing close personal relationships and peer acceptance (Owens et al. 2000). Perhaps girls and women initiate gossip more than boys and men when seeking to damage the relationships of same-sex others via indirect aggression and initiate the spread of negative gossip about others more often to enhance intimacy and acceptance among the peer group.

Because girls and women appear to place more value on their intimate same-sex friendships, are more relationally aggressive, and are more susceptible to the damage wrought by relational victimization relative to boys and men (see Eckert 1990 and Vaillancourt 2005, 2013 for discussion), it is sensible to predict that they may gossip more about social information (Davis et al. 2018). This would presumably allow girls and women to acquire vital knowledge about people in their social circles, to derogate intrasexual rivals, and to protect their relationships and themselves. In previous work, girls and women have been shown to gossip more about peers, friends, family members, the dating and romantic relationships of others, and to read gossip more often in the media (Davis et al. 2018; Eckert 1990; McDonald et al. 2007). Women have also been found to perceive more value in gossiping and to find the activity more enjoyable than men (Davis et al. 2018). Girls and women may then be more likely to initiate gossip when it concerns social information because these details are argued to be more

pertinent to their intrasexual competition than amongst boys and men.

Along with social information, several sex differences in the initiation of gossip likely vary across different content domains where women and men have encountered divergent adaptive problems (Buss and Dedden 1990). The mate preferences of one sex become the traits over which the opposite sex competes (Arnocky 2016; Arnocky and Vaillancourt 2017). Women's greater obligatory parental investment, the importance of maternal investment for the survival of offspring, and the fact that humans have more altricial young translates into women facing the adaptive challenge of securing mates who are both able and willing to invest significant resources in them and their offspring and to offer protection. Therefore, men are predicted to compete with one another to display and to derogate each other on traits linked to resource acquisition and holding potential such as status, achievement, ambition, and industry, as well as their physical strength and stature (Buss and Dedden 1990).

Davis et al. (2018) found that men gossiped more about achievement-related content in comparison to women, such as the salaries and work successes of others. Similarly, people also spontaneously recall gossip about the status and wealth linked to a hypothetical man more often than a similar fictional woman (De Backer et al. 2007). However, Levin and Arluke (1985) found that women were more inclined than men to gossip about schoolwork, such as teacher evaluations, exams and papers, and other students' grades. Men's frequent gossip about televised sports has been noted by previous researchers (e.g., Johnson and Finlay 1997). Unsurprisingly, adolescent boys and men have been found to gossip more about athletic performance and sports figures (Levin and Arluke 1985). These results suggest that the content of boys' and men's gossip generally corresponds to the evolved mate preferences of girls and women. Therefore, boys and men are predicted to initiate gossip about achievement and athletics more often than girls and women.

Due to men's paternity uncertainty, higher reproductive potential, cheap and replenishing gametes, as well as the inconspicuous nature of

women's ovulation, ancestral men faced the adaptive challenge of finding, courting, and securing fertile and sexually faithful mates (see Arnocky 2016 and Arnocky and Vaillancourt 2017 for discussion). Consequently, men have evolved to prefer women displaying cues linked to health, reproductive value, and fertility (e.g., youth, facial femininity, unblemished skin, full lips, large breasts, and a low waist-to-hip ratio), as well as sexual fidelity (Buss 1989). Therefore, women are predicted to compete primarily with same-sex rivals over traits like youthfulness, physical appearance, and sexual reputation.

Girls and women, more than boys and men, have been shown to derogate each other on their appearance using terms such as "ugly" and "fat" (Buss and Dedden 1990; Campbell 2004; Vaillancourt 2013). Key drivers for adolescent girls' malicious gossip and social exclusion are envy over the appearance of same-sex others and jealousy over preferred male mates (Owens et al. 2000). Women have also been found to report greater feelings of jealousy and competitiveness when exposed to images of attractive women or when they perceive other women as being more physically attractive than they are (Arnocky et al. 2012). Similarly, women have been found to gossip more about the physical appearance of others (Davis et al. 2018). In addition, women and men have better spontaneous recall for gossip about the attractiveness of a fictional woman relative to a fictional man (De Backer et al. 2007). These results support the hypothesis that girls and women are more likely to initiate gossip about the physical appearance of others, particularly when the gossip is targeting a same-sex rival.

The most common insults that women direct toward same-sex rivals concern their sexual faithfulness and drawing attention to, or exaggerating, their promiscuity (Buss and Dedden 1990). Pejorative terms like "slut," "whore," and "ho" are common in the gossip and rumors of women's competitor derogation (Vaillancourt and Sharma 2011; see Campbell 2004; Vaillancourt 2013). Although rare among women, the most commonly reported reason for women's physical violence is retaliation in response to allegations of being licentious (see Campbell 1999).

Vaillancourt and Sharma (2011) demonstrated experimentally that women voluntarily derogated a promiscuously dressed female research confederate more than the same woman dressed in more conservative clothes. These results indicate that women compete against same-sex others and often maliciously manipulate the sexual reputation of their victims using gossip. Therefore, adolescent girls and women may initiate more derogatory gossip about a same-sex rival's sexual reputation in comparison to boys and men.

Conclusion

Gossip plays an important role in the social dynamics and interpersonal relations of human beings (Dunbar 2004; Foster 2004). It is likely an adaptation that was sexually selected because it provided a reproductive advantage to ancestral human beings. Gossip may have evolved to solve adaptive problems in several domains that differentially impinged on the survival and reproduction of ancestral women and men. Thus, several authors have predicted that gossip has sex-specific design features (Campbell 1999, 2004; Davis et al. 2018; McAndrew 2014; Vaillancourt 2013). Evidence to date supports the hypothesis that girls and women initiate gossip more than boys and men, particularly when gossip is negative and shared among same-sex friends. It is somewhat unclear, however, whether women initiate more gossip episodes than men within mixed-sex groups. Due to their greater tendency to gossip and to use gossip to gather valuable social information as well as to derogate rivals, girls and women likely initiate gossip more often than boys and men in cross-sex groups. This propensity may be stronger for attractive adolescent girls and women, particularly during their earlier reproductive years when mate competition intensifies (Massar et al. 2012; Vaillancourt 2013) and when the content relates to a rivals physical appearance and sexual reputation. In contrast, boys and men may initiate gossip more often when it concerns content related to women's evolved mate preferences, including cues to resource holding potential and physical formidability.

Cross-References

- ▶ Contexts for Men's Aggression Against Men
- ▶ Contexts for Women's Aggression Against Women
- ▶ Derogation of Attractiveness
- ▶ Derogation of Promiscuity
- ▶ Development of Sex Differences
- ▶ Gossip and Grooming Hypothesis
- ▶ Gossip, Rumors, and Social Exclusion
- ▶ Intrasexual Rivalry Among Women
- ▶ Meta-analysis of Sex Differences in Aggression
- ▶ Relational Aggression
- ▶ Sex Differences in Aggression
- ▶ Sex Differences in Human Mate Preferences (Buss, 1989)
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Verbal Derogation
- ▶ Women's Use of Direct Versus Disguised Social Aggression

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Sex Ed

► Sex Education in Schools

Sex Education

- [Cultural Differences in Sexual Socialization](#)
- [Goals](#)

Sex Education in Schools

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Synonyms

[Comprehensive sexuality education](#); [Holistic sexuality education](#); [Sex Ed](#); [Sexuality education](#)

Definition

The process of gathering accurate information, developing attitudes and beliefs, and gaining skills on the biological, sociological, and psychological facets of sexuality in a formal academic setting.

Introduction

Sexuality education provides individuals with information about their bodies, identities, relationships, and health-promoting skills as they relate to sexuality. International health and human rights organizations assert that access to developmentally and culturally appropriate sexuality education is a basic human right (UNESCO 2018). Adolescents receive sex education from formal sources, like schools or clinics, and informal sources, like family members, friends, or digital resources. While these can all be important, affirming sources of information, formal sources are more likely to provide students with accurate and age-appropriate information (UNESCO 2018). Formal sex education is most commonly implemented within a school setting, which has

the potential to provide additional benefits to the students. Schools are already equipped to provide education and, ideally, foster a supportive learning environment. Additionally, schools are often already connected with other community resources and can reach out for support, information, or special needs as needed (UNESCO 2018). Developmentally appropriate sex education can be offered to students of any age within schools; however, research has overwhelmingly focused on youth between the ages of approximately 9 and 18. Similarly, this entry will focus on the impacts of sex education in schools that is delivered to students ages 9–18.

While the goals of sex education in schools have historically focused on improving health outcomes, these goals have been expanded as sex education programs increasingly adopts a human rights framework (Haberland and Rogow 2015; UNESCO 2018). The quality of sex education programs can be assessed with a wide variety of metrics. At the individual level, the ideal sex education program would increase knowledge on delivered topics, help students understand their identity and culture, and promote the development of health-promoting skills (Haberland and Rogow 2015; Kirby 2008; Kohler et al. 2008; UNESCO 2018). As a result of targeting student knowledge, attitudes, and beliefs, an ideal program would also improve students' biological, psychological, and social health outcomes. These outcomes may include STI (sexually transmitted infection) status, unintended pregnancy, or experiences with intimate partner violence. A program's effectiveness may also be evaluated at the social level, measuring a programs effect on issues like community-wide health outcomes, gender equity, discrimination, etc. (Haberland and Rogow 2015; UNESCO 2018).

Sexuality education programs vary in their ability to impact health. The most successful programs employ a holistic view of sexuality, empower their students, are inclusive of students with different identities and experiences, and explicitly discuss structural and cultural issues (UNESCO 2018). Moving forward, educators, policy makers, and researchers across the globe are advocating for more programs that feature

these qualities. Additionally, sex educators are exploring ways to build new, interdisciplinary organizational partnerships and to integrate new technology into their programs to create programs that have a greater impact and reach.

This entry will focus on comprehensive sexuality education programs and exclude abstinence-only and abstinence-plus programming. Comprehensive sexuality education programs provide students with age-appropriate, accurate, and inclusive information on biological, psychological, and sociological aspects of sexuality (UNESCO 2018; WHO Regional Offices for Europe and BZgA 2010). In contrast, abstinence-focused programs are designed to encourage adolescents to delay sexual activity, often until marriage, and highlight the risks related to sexual activity (Santelli et al. 2017; Underhill et al. 2008). While these programs are often labeled as sex education, they often feature misinformation, exclude LGBTQ+ students, and limit the information available to students about their bodies and identities (Santelli et al. 2017). As abstinence-focused programs are not designed to provide accurate, inclusive, and developmentally appropriate information on the biological, psychological, and sociological facets of sex, they do not fit within the definition of sex education.

The Need for Sex Education in Schools

Developmentally appropriate sex education can provide valuable information to individuals of all ages, but is of particular value to adolescents. Adolescence marks the time when an individual is transitioning, physically and socially, from a child to an adult. This transition is often marked by changes to an individual's body, identity, relationships, and social role. Providing sex education in schools can help foster a more supportive and safer environment for adolescents as they process not only their own transition, but the transition of their peers. Additionally, it provides students with valuable experience discussing topics related to sexuality with their peers. The communication skills developed during these discussions can

then later be applied to conversations they have with partners, friends, family members, and healthcare providers.

Goals of Sex Education

As the contents of sex education programs have expanded beyond the individual to provide students with information on interpersonal and social factors that may influence a broad understanding of sexuality, so have the goals of the program expanded. These goals are then translated into metrics by researchers to evaluate the effectiveness of sex education programs. The following are common goals of sex education programs (Haberland and Rogow 2015; Hirst 2012; UNESCO 2018):

Improved safer sex behaviors. This includes behaviors such as condom use, contraceptive use, or seeking medical care as needed. Sex education programs often promote safer sex behaviors by providing information on the benefits of these behaviors and practicing skill building, like putting a condom on a model. Some programs even go one step further and teach students how to communicate with partners about safer sex behaviors and how social ideas about gender and power may influence and impact safer sex behaviors.

Reduce STI rates. Programs often work to reduce STI rates by promoting safer sex behaviors that can prevent STI transmission, along with providing information on testing and treatment. The information provided to students on STI transmission has evolved in response to changes in available medical care and the infections themselves. Reduction in HIV transmission, specifically, has been a primary goal of sex education programs globally since the 1980s.

Improve adolescent reproductive health. This goal may include a reduction in unintended adolescent pregnancies and births, improved access to contraceptives, and improved access to safe medical services, such as abortions. Similar to the method for reducing STI transmission, programs often target adolescent reproductive health by improving safer sex behaviors and providing

information on how to access appropriate resources.

Age of first penile-vaginal intercourse and number of partners. Many sex education programs seek to increase the age of first penile-vaginal intercourse and reduce the number of partners. Though these measures are correlated with health behaviors and outcomes, this relationship appears to be heavily affected by mediating variables (Sandfort et al. 2008). For example, research suggests that individuals who are younger at the age of first penile-vaginal intercourse, as compared to their peers, are more likely to report engaging in risky sexual behaviors and have an STI (Cavazos-Rehg et al. 2010; Ma et al. 2009; Magnusson et al. 2012; Sandfort et al. 2008). However, age of sexual intercourse, STI rates, and safer sex behaviors also correlate with gender, ethnicity, culture, family systems, mental health, and drug and alcohol use, among others (Cavazos-Rehg et al. 2010; Sandfort et al. 2008; Udell et al. 2010). Additionally, the way researchers address the variables of age at first intercourse, and number of partners varies greatly with differences in researchers' cultures and societal attitudes toward adolescent sexuality (Sandfort et al. 2008; Udell et al. 2010). Programs achieving their goal of increasing age at first intercourse and reducing the number of sexual partners an individual have may improve health, but the mechanics of this pathway are still unclear.

Reduce intimate partner violence, gender-based violence, violence against LGBTQ+ individuals, and discrimination. Violence and discrimination related to sexuality exists internationally at interpersonal and cultural levels (Gay et al. 2010; Haberland and Rogow 2015; UN Human Rights Council 2015; UNESCO 2018). In the twenty-first century, innovative programs have worked to reduce violence and discrimination by teaching about both the behaviors and the cultural context in which they exist. This information can empower students to reflect on social norms, their own behavior, and the behavior of others. Research suggests that programs designed to target these issues not only reduce violence and discrimination, but they also appear to have a greater positive impact on engagement in safer

sex behaviors, STI rates, and reproductive health outcomes than programs that do not address relational violence and discrimination (Haberland and Rogow 2015; UNESCO 2018).

Reduce health inequities. Members of vulnerable populations, including LGBTQ+ individuals, individuals with disabilities, those who have experienced intimate partner violence, those who have experienced homelessness, and refugees, often experience the worst sexual health outcomes (Haberland and Rogow 2015; UNESCO 2018). This disparity is driven by issues such as a lack of resources and discrimination. Unfortunately, these individuals and their specific needs and experiences are also the most likely to be overlooked within sex education curriculum. Sex educators are beginning to place a stronger emphasis on creating more inclusive programs that not only provide their students with information that is applicable to members of these populations, but that also empower these students and emphasize their right to sexual health.

Increase pleasure. Pleasure is one of the primary reasons individuals engage in sexual activity, but it is largely ignored within school sex education programs (Hirst 2012). Programs that incorporate discussions on pleasure often resonate more with participants and provide them with more skills to navigate conversations about sex and pleasure than programs that do not discuss pleasure (Hirst 2012). For example, worries about pleasure are a commonly reported barrier to using condoms. Programs that address ways to increase pleasure while using an external condom have overwhelmingly demonstrated a greater impact on condom use than programs that focus solely on the health benefits of using a condom (Hirst 2012). Providing students with information and vocabulary surrounding pleasure can help them evaluate what they want, what feels good to them, and how to communicate about that with others.

Content and Characteristics of an Effective Sex Education Program

Content. In 2018, the United Nations Educational, Scientific, and Cultural Organization (UNESCO),

in partnership with other UN organizations and the World Health Organization (WHO), published their international recommendations for sexuality education (2018). The programming they recommend, informed by current research, is comprehensive and should address:

- Relationships
- Values, rights, culture, and sexuality
- Gender
- Violence and staying safe
- Skills for health and well-being
- Human body and development
- Sexuality and sexual behavior
- Sexual and reproductive health

Implementation. For these programs to be as effective as possible, research says they should be delivered by educators who are comfortable talking with students about sexuality and who have adequate training and support from school administrators (Browes 2015; Mkumbo 2012; UNESCO 2018). These classes should be delivered in a mixed-gender group of peers that are of similar age or developmental stage. Facilitation of lessons should be spread out, providing students with sex education each year. The time a school spends on sex education may vary widely, and research indicates that it is important for program planners to address both the quality and quantity that they can deliver to their students. Generally, better impacts correlate with more time spent facilitating, provided that the quality of facilitation is maintained (UNESCO 2018).

The program should also acknowledge the environment in which the curriculum is being delivered. This is particularly important when there are contradictions between what is promoted in a program and what students experience in their daily lives at school, home, and in the community. For example, some students receive information on the harm of sexual harassment or gender violence from school-based programming, while sexual harassment and gender violence continue to thrive as social norms within their school-based peer groups (Browes 2015; Rasmussen et al. 2017). If left unaddressed, contradictions like

this may undermine the program and reduce or even reverse its impact.

Intersectionality. All students are affected by issues like racism, sexism, ableism, heterosexism, and transphobia. This is true even if systemic issues are not readily apparent within a school or in the immediate community surrounding a school. These problems have been shown to directly impact a host of sexual health outcomes, and students should be provided with the tools and information to identify and address them. This information not only helps students face these problems as individuals, but it can also empower them to create more equitable communities.

Information provided in a sex education program should also be actively inclusive of students of different identities and experiences. This can be done by including new information or employing different, culturally appropriate language. For example, to be more inclusive of intersex, transgender, or nonbinary students, educators could replace the phrase “during puberty, girls begin menstruating” with “during puberty, people with ovaries and a uterus usually begin menstruating.” This shift in language is not only more inclusive, but more accurate.

Future Directions

To better achieve the goals of sex education, future programs should continue to improve content and program implementation, connect with other services and organizations, and adopt new and developing technology. Improvements in content and program implementation should continue to focus on providing information on a wide range of topics related to sexuality, empowering students, creating more inclusive content, addressing systemic issues, and supporting individuals delivering the information (Haberland and Rogow 2015; UNESCO 2018). These program goals have primarily been driven by research, which is a crucial tool for improving programs and health outcomes. More research is needed to understand how changes in the above areas may impact students, especially those that are members of more vulnerable populations. More

longitudinal research is specifically needed to understand how these programs may impact students and the communities they live in years and decades after implementation.

Health professionals are increasingly advocating for an integrated system of services to address needs, as programs that are connected with complementary services often see better sexual health outcomes when compared to programs that are not integrated (UNESCO 2018). School-based programs addressing sexual health are no exception. Sex education programs should seek out connections and partnerships with other related services and organizations within a community, such as condom distribution programs, clinics, and LGBTQ+ resource centers. Connected organizations can communicate, ensure they're providing complementary services, and provide more services to a greater number of people.

Sex educators also have the opportunity to integrate new and developing techniques and technology into their classrooms (UNESCO 2018). Technology can improve the reach of formal, trained educators and facilitators through online courses or live streams, providing sex education in a curricular format which students would not otherwise have had access to. This may be especially effective in rural or other areas that are difficult to access.

Conclusion

Sex education is a human right. Sexuality education offered in schools is an increasingly powerful tool that can be used to improve health, reduce inequities, and combat systematic discrimination. The most effective programs deliver accurate, inclusive, positive, and empowering information on a wide range of sexuality topics to students. All adolescents deserve access to sex education programs that educate and support them.

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Sex Effect

- [Grandfather Investment Versus Grandmother Investment](#)

Sex Hormone

- [Testosterone](#)

Sex of Offspring

- [Offspring Sex](#)

Sex Ratio

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Synonyms

[Operational sex ratio](#)

Definition

Sex ratio is the relative number of men to women in a given population

Introduction

The ratio of men to women within a mating population varies significantly across time and culture. Evolutionary psychologists expect, and find, that variations in human sex ratios are predictably associated with differences in human mating strategies, such as changes in sociosexual attitudes, intensity of mate competition (e.g., intrasexual violence), and patterns of courtship and mate choice.

Mating Strategies

Every primate species seems to have a “natural” mating strategy. Some primates are monogamous (e.g., gibbons), some polygynous (e.g., gorillas), and some engage in multimale-multifemale mating as their primary means of reproduction (e.g., chimpanzees; Dixson 1998). The human primate, however, appears to have a diverse and varied menu of reproductive strategies, with different people deploying different strategies as individuals, and within their own lives over time. For instance, although over 80% of foraging cultures have polygynous mating systems (i.e., men may have more than one wife; Marlowe 2003), most men and women within foraging cultures are

officially married to only one other person (Stewart-Williams and Thomas 2013). Moreover, premarital and extramarital sex is common among foraging cultures (Barash and Lipton 2002), as is frequent divorce and re-marriage (functioning as serially monogamous mating systems; Fisher 1998). It appears, humans, unlike most primates, are designed to be flexible and to pursue, across varying times and situations, both long-term and short-term mateships as strategic means of reproduction (Buss and Schmitt 1993; Symons 1979).

The apparent flexibility of humanity's fundamental mating repertoire may stem, in part, from its having a highly *facultative* design. That is, much of our mating psychology may be calibrated to adaptively respond to key developmental, socioecological, and personal contexts (Gangestad et al. 2006). For instance, human mating psychology appears specially designed to shift to a more short-term oriented strategy as in response to stressful attachment experiences during development (Belsky et al. 1991; Ellis et al. 2009) to low levels of pathogens in the local ecology (Schaller and Murray 2008), and, among men, short-term mating is adaptively evoked in response to high levels of personal strength and physical attractiveness (Lukaszewski et al. 2014). In terms of affecting both men's and women's human mating strategies, however, perhaps no contextual factor has turned out to be more influential than the numerical ratio of men and women in the local mating pool (Ember 1974; Guttentag and Secord 1983; Marlowe and Berbesque 2012).

Operational sex ratio (OSR) is defined as the numerical ratio of reproductive-age males to reproductive-age females in a given mating population (Emlen and Oring 1977). In humans, "high" OSRs refer to populations with more reproductive-age men than women, whereas "low" OSRs refer to populations with more reproductive-age women than men (Pedersen 1991). Because OSRs can influence the availability of potential mates, unbalanced OSRs can affect sexual selection pressures by heightening the intensity of intrasexual competition within the sex that is more numerous and heightening the intensity intersexual selection among the rarer

sex (Trivers 1972). Put simply, because there are fewer of the rarer sex to go around within unbalanced OSR populations, the plentiful sex has to compete more intensely to fulfill the stronger desires of the rarer sex (Guttentag and Secord 1983). When there are many more men than women, for example, the plentiful men must intrasexually compete more forcefully against one another to effectively provide the highly selective women with what they desire (Barber 2001a; Stone et al. 2007).

In humans, women generally desire higher levels of commitment before consenting to sex than men do (Simpson and Gangestad 1991). As a result, evolutionary psychologists expect, and have found, that higher OSR contexts (within which women are rarer than men and can command the mating marketplace; Guttentag and Secord 1983) are associated with increases in indexes of long-term mating and "sociosexually restricted" attitudes and behaviors (Pedersen 1991; Schmitt 2005). For instance, historical analyses have found higher marriage rates, lower divorce rates, fewer illegitimate births, fewer teen births, and higher paternal investment when OSRs are higher (Barber 2001a; Guttentag and Secord 1983; Kruger and Schlemmer 2009; Pedersen 1991; Pollet and Nettle 2008). Higher OSRs also are historically associated with men enhancing their appeal to more highly selective women through heightening their masculinity, such as sporting more mustaches and beards (Barber 2001b).

Cross-culturally, higher OSRs are empirically associated with increases in indexes of long-term mating and "sociosexually restricted" attitudes and behaviors in men and women (e.g., lower levels of sociosexuality, Kandrik et al. 2015; Schmitt 2005). Again, this is presumably because when women are rare they are better able to command the mating marketplace and impose their greater interest in high-commitment mating (Pedersen 1991). High OSRs across cultures also are associated with more relaxed long-term mate preferences by men, possibly in order to facilitate the acquisition of the less numerous and highly selective women partners (Stone et al. 2007).

Experimentally, manipulating impressions of OSRs by making men appear more common

than women is associated, as expected, with more long-term mating and restricted levels of sociosexuality (Moss and Maner 2016). Also as expected, when men are rarer than women and men are therefore better able to command the mating marketplace, such low OSRs are historically, cross-culturally, and experimentally associated with the opposite – increases in indexes of short-term mating and more “sociosexually unrestricted” attitudes and behaviors (Baumeister and Vohs 2004; Guttentag and Secord 1983; Pedersen 1991; Schmitt 2005).

Further support for the view that human mating psychology is designed to strategically shift in response to OSR variation comes from studies of intrasexual competitiveness and direct mating effort (Arnocky et al. 2014; cf. Schacht et al. 2014). For instance, higher OSRs are historically and cross-culturally associated with higher levels of men’s intrasexual aggression and violence (Barber 2000, 2003; Hudson and Den Boer 2004). Across 120 cities in the United States, higher OSRs were associated with indexes of men’s impulsiveness, such as owning more credit cards and having a higher amount of debt on the credit cards they do have (Griskevicius et al. 2012). Experimentally, higher OSRs are linked to men focusing on immediate rewards, rather than saving for the future and appear to lead men to spend more money during courtship (e.g., paying more for engagement rings, Griskevicius et al. 2012). Higher OSRs seem to evoke tendencies in men to diversify financial resources less and instead concentrate investment in high-risk/high-return options when making lottery, stock-pool, retirement-account, and research-funding decisions (Ackerman et al. 2016).

There is growing evidence that women also adjust their mating efforts in response to shifts in OSRs (Dillon et al. 2017). For instance, Arnocky et al. (2014) experimentally manipulated perceived OSRs and found women who were exposed to a low OSR mating market with a scarcity of men reported more intrasexual competition, jealousy, and willingness to aggress indirectly against a mate poacher compared to those exposed to an abundance of males. Dillon (2012) found already-mated women exposed to a low

OSR mating market tended to feel more positively toward their current partners, including finding them more attractive than women randomly assigned to high OSR mating markets with a surplus of men. Durante et al. (2012) demonstrated across historical data and experimental manipulations that lower OSRs are associated with women (especially low mate value women) seeking high-paying careers and delaying the start of their families. In contrast, women in higher OSR nations tend to marry early as a reflection of a more restricted sociosexuality (Trent and South 2011).

There is much work to be done in elucidating the precise mechanisms by which OSRs influence human mating psychology. At present, it appears likely that OSRs play key roles in evoking adaptive changes in men’s and women’s sociosexuality, intensity of intrasexual mate competition, and patterns of intersexual mate choice. When OSRs are high, both men’s and women’s sociosexuality is restricted, men engage in more intense intrasexual competition, and women’s intersexual mate choice is more selective. When OSRs are low, sociosexuality and indexes of short-term mating tend to increase as men become the rarer sex and are able to command more value in the mating marketplace, and women engage in greater intrasexual competition to fulfill the desires of the opposite sex.

Conclusion

Given the extant evidence from cross-cultural, historical, and experimental studies, variations in operational sex ratios appear to be associated with changes in human mating behavior, including predictable features of sociosexuality, intrasexual mate competition, and intersexual mate choice.

Cross-References

- ▶ [Contexts for Men’s Aggression Against Men](#)
- ▶ [Sex Differences in Short-Term Mating Preferences](#)
- ▶ [Sexual Conflict After Conception](#)

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Sex Ratio and Men's Long-Term Mating

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Synonyms

Adult sex ratio; Committed relationship; Operational sex ratio

Definition

- Sex ratios are defined as the number of men per 100 women (in pre-defined age groups).
- We define long-term mating as a mating strategy in which men are seeking a partner for a long-term relationship.

Introduction

Human mating strategies are not fixed but constitute facultative responses to developmental,

individual- and population-level, social, and ecological circumstances. As a consequence, men's preferences for and likelihood of engagement in long-term mating have been shown to be subject to variation across contexts (Schacht and Kramer 2016; Uggla and Mace 2017) ► “Sex Ratio” by D. Schmitt.

A growing body of literature identifies the sex ratio as such a contextual factor for mating behavior. The sex ratio is commonly defined as the number of men per 100 women, yet operational definitions vary across the literature. Variants include the adult sex ratio (ASR) which is calculated on the basis of age cohorts between puberty and menopause and the operational sex ratio (OSR) which is defined as the ratio of unmarried adult men to unmarried adult women in a population. In monogamous societies, OSR and ASR should be highly correlated. In either case, low sex ratios indicate a relative oversupply of women, whereas high sex ratios indicate a relative oversupply of men.

Mating Behavior and Sex Ratios

Evolutionary and social scientists conceptualize the local number of males and females as a mating market which is driven by supply-and-demand dynamics. Following this conceptualization, an oversupply of one sex on the mating market increases mating opportunities for the other, scarcer sex. A common hypothesis posits that both women and men's likelihood of engaging in a sexual or romantic encounter or relationship increases with the relative number of opposite sex partners. This perspective is often referred to as the “demographic opportunity thesis” (Adkins et al. 2015). A number of scholars argue that an imbalance of mating opportunities further translates into asymmetries in bargaining power on the partner market (Arnocky et al. 2016; Schacht and Kramer 2016; Uggla and Mace 2017). When either sex outnumbers the other, the scarcer sex has a larger pool of potential partners to choose from and thus a higher likelihood to find a partner that best fits his or her own preferences. On the other hand, individuals of the more common sex

face tougher competition to find a partner. In view of such intensified competition on the partner market, an optimal strategy may be to cater to the preferences of scarce partners.

Parental investment (PI) theory predicts that due to women's higher physiological parental investment (gestation and breastfeeding), men and women have evolved different mating psychologies. Although both men and women exhibit short- and long-term mating strategies across life course stages and socio-ecological contexts (David P. Schmitt – ► [Sex Ratio](#)), PI theory suggests that, on average, men exhibit a higher tendency toward short-term and uncommitted mating than women (Robert Trivers: ► [Parental Investment and Sexual Selection](#)). Against this background, sex ratio theory suggests that the ability to realize these sex-specific mating preferences is co-determined by partner availability. When males are in short supply, they are more likely to have their preferences met because women compete for a partner by appealing to male mating preferences. Given the assumed higher average preference for short-term mating in males, this implies that, in a low sex-ratio context, males can behave more promiscuously, offer little parental investment, and still be able to find a partner. However, when women are less plentiful, men will appeal more to female preferences and be more willing to commit to a single partner. In sum, local sex ratios are theorized to shift incentives to pursue different partner market strategies and to display different mating behaviors (Arnocky et al. 2016; Schacht and Kramer 2016; Uggla and Mace 2017).

Empirical Evidence

Empirical evidence only partially supports the prediction that men are less likely to commit themselves to a single relationship when partner markets are favorable, i.e., sex ratios are female-biased. Until recently, the bulk of empirical studies analyzed indicators of female mating behavior to infer on male mating behavior. Specifically, studies analyzed associations of sex ratios with rates and timing of women's marriage or rates of single-mother households and interpreted low rates of marriage or two-parent families as

indicative of low male relationship commitment. However, recent studies undertook steps toward a more direct measurement of male mating behavior. For instance, Schacht and Kramer (2016) analyzed male marriage rates from US census data and found that male abundance correlates with higher shares of men being married. In addition, the authors report that high sex ratios are associated with lower rates of extramarital fertility and female-headed households. Overall, the authors interpret these results as indicative of higher rates of male long-term mating strategies when women are scarce. However, inferences on individual-level correlations from aggregated data bear the risk of ecological fallacies. Testing hypotheses on individual behavior patterns should ideally involve individuals as units of analysis.

Studies in the field increasingly address this concern by analyzing individual-level data but yield contradictory results. One study shows that men in female-biased US census tracts were less likely to cohabit with a romantic partner and had a greater number of dating partners (Warner et al. 2011). Similarly, a relative abundance of women in their community increases the likelihood for Chinese men to engage in premarital intercourse (South and Trent 2010). However, there is also evidence suggesting that ASRs are inversely associated with the male propensity to form a committed relationship. For instance, Eckhard and Stauder (2018) report that education and age-specific sex ratios correlated positively with union formation among men in Germany. Moreover, Uggla and Mace (2017) report that while *female* cohabitation is associated with male-biased sex ratio wards in Northern Ireland, *male* cohabitation did not correlate significantly with ward-level ASRs in Northern Ireland. A study of union formation in Mexico finds neither significant associations between female nor between male union formation and municipality sex ratios (Parrado and Zenteno 2002).

Discussion

One explanation for these contradictory findings could be that union and marital formation are only

weak indicators for long-term mating strategies when social costs and stigma associated with separation are low. Consequently, associations of sex ratios with indicators such as marriage or premarital intercourse might vary across time and space. Also, associations should be sensitive to different operationalizations of similar indicators. For instance, marriage and cohabitation might reflect different levels of commitment across societies.

Another point to be made is that studies of long-term mating strategies should seek to include larger portions of individuals' relationship trajectories beyond just the transition to *first* marriages, cohabitation, or parenthood. Besides these early transitions, for instance, the stability of pair bonds, or the likelihood for infidelity to one's partner, might be relevant correlates of sex ratios as well. Men might at first commit to a partner but only later choose to opt out of the relationship to that partner. This follows from the higher opportunity costs men in a numerically favorable partner market have for staying in a relationship as compared to men in a less favorable partner market. Empirically, Arnocky et al. (2016) could show, for instance, that partnered men exhibited stronger infidelity intentions in an experiment when led to believe that mates are abundant instead of scarce. Similarly, female-biased sex ratios correlated with greater risks of separation for both men and women in an analysis of register data from Northern Ireland (Uggla and Mace 2017).

A further explanation for contradictory findings could be that regional or local sex ratios do not correspond closely with individual experiences of partner availability. Experimentally, participants have been shown to adapt in response to clues of local sex ratios. For instance, men were less favorable to engaging in casual, uncommitted sex when treatments suggested that potential female partners are scarce versus plentiful in an experiment (Arnocky et al. 2016). However, explicitly providing participants with information on local sex ratios in a lab experiment might not have high external validity for how individuals normally perceive partner availability on the partner market. Social everyday interactions in modern societies

are structured into social foci, such as workplaces, schools, colleges, hangouts, or friendship networks. Sex ratios in these local contexts might not necessarily be representative of the local proportion of men and women: even in a high-sex-ratio society, for instance, male and female networks may be highly segmented by sex and gender. Consequently, individuals likely perceive partner pools selectively based on their respective social foci. This is supported by a recent study of nationwide survey data which finds no correlation between a variety of local sex ratio measures and subjective partner availability in Germany (Filser and Preetz 2019). If indeed local sex ratios are only loosely, if at all, correlated with individual perceptions of sex ratios, this may be one explanation for the contradictory results on the purported association between sex ratios and male mating behavior. In general, operationalizing sex ratios more closely based on what individuals actually perceive as their partner market might yield more consistent results when studying social outcomes of sex ratios.

Observational studies of sex ratios in social foci such as campuses seem to be a promising approach to circumvent such problems. For instance, sex ratios of colleges might be a closer approximation of students' peer group sex ratios and therefore capture subjective experiences of partner availability more accurately. Yet, empirical evidence on campus sex ratios remains contradictory as well. For instance, female-biased college campus sex ratios have been reported to correlate with more frequent hookups and a higher number of sexual partners. Moreover, when female students outnumbered men on campus, both men and women were less likely to consider love a necessary prerequisite for sex, an indication for a less restrictive socio-sexual orientation (Adkins et al. 2015). However, this is at odds with a recent study which finds that in high schools in which girls outnumber boys, students report a less sexually permissive normative climate and girls report less casual sex when compared with their counterparts at schools in which boys outnumber girls (Harknett and Cranney 2017). Of course, both studies differ in the age structure of their study

populations. However, the opposite associations suggest that more research on school and campus sex ratios is warranted.

Conclusion

Sex ratios have been theorized to affect men's propensity for long-term versus short-term mating behavior. Specifically, men are predicted to be more committed to a single partner when alternative options are scarce, i.e., sex ratios are male-biased. While there is some experimental and observational evidence to support these predictions, the literature remains contradictory and fragmented across the social and biological sciences.

More research is needed to establish a better understanding of how sex ratios affect mating. Specifically, future research should focus on individual-level data instead of studying population-level indicators to avoid ecological fallacies. Analyses of individual-level data further enable researchers to study potential variation of behavioral responses to imbalanced sex ratios across social status groups or other individual characteristics (Uggla and Mace 2017). In addition, more longitudinal analyses are necessary to substantiate how sex ratios affect mating strategies across the life course. Finally, paying closer attention on how responses to comparable sex ratios vary across cultural contexts seems indispensable. Social norms concerning sexual activities and union formation, particularly social sanctions against pre- or extramarital intercourse, may limit the viability of mating options.

While both theoretical and empirical clues that sex ratios are associated with men's long-term mating exist in the literature, an integrated and empirically well-substantiated model has yet to be established.

Cross-References

- [Operational Sex Ratio](#)
- [Preferences in Long- Versus Short-Term Mating](#)
- [Sex Differences in Long-Term Mating Preferences](#)

- [Sex Ratio](#)
- [Social Outcomes and Sex Ratio](#)

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Sex Reversal

- [Sex Switching](#)

Sex Segregation

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Synonyms

[Gender segregation](#)

Definition

Unequal distributions, or separation of people according to their biological sex.

Introduction

Sex segregation, or gender segregation, is an enduring phenomenon that is typically defined as an imbalanced distribution of men and women within a given locational dimension such as occupation, professional specialization, industry membership, or education (Charles 2015). While absolute separation between the sexes is much less common in the Western world today than it was in the past, relative sex segregation is still a prevalent phenomenon in the workplace. The present entry focuses on *occupational sex segregation*, which is the separation of men and women into different jobs or different roles within organizations (Harcey and Prokos 2017).

Types of Segregation

There are two fundamental types of sex segregation – *horizontal sex segregation* and *vertical sex segregation*. Horizontal sex segregation refers to men and women's unequal dispersion across different occupations, for example, teachers, doctors, lawyers, cashiers, nurses, and construction workers, or across different occupational specifications, such as pediatric surgeon versus heart surgeon or science teacher versus arts teacher. Horizontal segregation shows at least three distinctive

features, which are (1) the magnitude of gender distributions across disciplines, (2) the crowding of women into a narrower range of professions than men, and (3) the likelihood of men and women sharing an occupation. In contrast, vertical sex segregation refers to men and women's unequal dispersion within an organizational hierarchy such as first-level manager versus executive manager, school teacher versus headmaster, or assistant professor versus full professor (see Charles 2015).

In general, sex segregation has substantially dropped since the early 1970s but reached a relative plateau in the 1990s. Vertical sex segregation is a nearly universal phenomenon that occurs within almost every profession and culture (Gutek 2001). Even today, women's presence within different hierarchical levels in the workplace still takes a pyramid-like shape representing an increasing gender imbalance at higher stages of the career ladder. However, through a variety of governmental, organizational, and societal initiatives focused on improving gender equality in the workplace, vertical segregation has decreased moderately in industrialized countries, and invisible leadership barriers for women (i.e., glass ceiling) have become more permeable (Bosak and Kinahan 2014; Charles 2015). In contrast, horizontal segregation has not changed considerably over the past decades. Instead, occupations continue to be prone to gender labeling or gender typing. More specifically, gender typing implies that roles and responsibilities are assigned based on a traditional division of labor, wherefore men and women occupy positions with traditionally gendered job descriptions (Costen 2012). Thus, certain occupations like truck drivers or construction workers are still categorized as “men jobs,” whereas other professions such as nurses or primary school teachers are perceived to be “women jobs” (see Charles 2015).

Causes and Consequences of Sex Segregation

Research presents several explanations for occupational sex segregation (e.g., Harcey and Prokos 2017), among which the three most common

explanations for occupational sex segregation are (1) evolutionary, (2) economic, and (3) sociological. The *evolutionary perspective* explains sex segregation with innate biological differences between men and women that arose from human evolutionary history (Browne 2006). According to Buss (1995), these biological differences emerged because in human evolution men and women have faced “recurrently different adaptive problems” (p. 19). More specifically, for large parts of human history, men faced the adaptive problem of hunting, whereas women faced adaptive problems of gathering and caring for offspring. The evolutionary perspective thus argues that men and women are fundamentally different and therefore equipped to fit occupations, which are congruent with their biological characteristics.

In contrast, the *economic or human capital view* of sex segregation argues that differences in men and women’s hierarchy and role in an organization are attributable to differences in their human capital, that is, their specific KSAOs (knowledge, skills, abilities, and other characteristics; Costen 2012). Because women are often more invested in domestic work, childcare, and eldercare than men, it is claimed that they develop less human capital. According to the rational choice concept, households are likely to focus on the career development of the party with more human capital as primary breadwinner (Blackburn et al. 2002).

Stemming from sociology and social psychology, *social role theory* emphasizes men and women’s adaptation to a traditional division of labor in which men typically served as the provider and women as the caretaker (Eagly 1997) rather than biological or evolutionary positions. Specifically, social role theory views traditional gender roles as “socially constructed sets of ideas that are firmly grounded in the requirements of a society’s productive activity” (Eagly 1997, p. 1381). As an explanation for occupational sex segregation, social role theory suggests that the traditional distribution into different social roles resulted in the generation of gender stereotypes. For example, women are perceived to be more communal (e.g., caring, helpful), while men are believed to be more agentic (e.g., assertive, dominant); thus, gender

role stereotypes reinforce traditional sex segregation, in which women typically occupy roles that are characterized by nurturing acts, care, and helping, whereas men usually occupy positions that are characterized by assertiveness and dominance (Eagly and Wood 2016).

Other explanations for sex segregation focus on factors pertaining to employer behavior and the broader societal context. For example, the increased availability of part-time work is viewed as facilitating increased segregation, with child-rearing women leaving their occupational path for part-time hours and lower-skilled, feminized work (Blackwell 2001). Other work emphasizes the influence of governmental policies such as maternity leave, anti-discrimination, and protective legislation on occupational segregation (Chang 2004).

While sex segregation always entails an unequal distribution of men and women, it does not automatically imply discrimination (Browne 2016). It is however strongly linked to gender inequality (Hesmondhalgh and Baker 2015), with typical jobs and occupations performed by women rather than men being valued and paid less. For example, research using US census data from 1950 to 2000 found substantial support for the view that increased feminization of occupations diminishes their relative pay, which is indicative of the devaluation of jobs with large shares of females (Levanon et al. 2009). The mere existence of sex segregation and thus people’s observation of women and men in different roles further limit (a) women’s and men’s autonomy and individual choices and (b) collective flourishing. For example, Bosak and Sczesny (2008) found that, despite comparable qualifications and skills, female business students felt less suitable for an entry-level leadership position than their male counterparts because they believed to possess less of the masculine attributes typically ascribed to leaders. These internalized gender beliefs limit women’s choices and career behaviors and contribute to the underrepresentation of women in traditionally male-dominated roles such as leadership. The same applies to men with ambitions to pursue female sex-typed roles albeit the proportion of women wishing to pursue nontraditional occupations is more pronounced than that of men, with

occupational segregation thus disadvantaging women more than men. Sex segregation in the workplace might also constrain organizational performance and collective flourishing. Research has found that a positive association between gender diversity and firm performance is only achieved in the presence of a critical mass of women rather than “token women” on corporate boards (Joecks et al. 2013). Further, Bettio and Verashchagina (2009) state that, at a macroeconomic level, “segregation may be exacerbating skill shortages insofar as it impedes the efficient reallocation of male and female workers and distorts the allocation of future flows of workers” (p. 46). Finally, occupational sex segregation both builds on and, in turn, fosters cultural beliefs about women and men, with these stereotypes shaping gender-differentiated aspirations and choices – reinforcing the prevailing pattern of occupational segregation by sex (Hesmondhalgh and Baker 2015).

Sex Segregation and Social Change

Some scholars adopting functionalist and neo-institutionalist views of gender inequality believe that sex segregation will gradually erode due to economic (e.g., gender inequality is argued to be inefficient and not compatible with liberal capitalism) and cultural (e.g., nation-states show increased commitment to gender equality and non-discrimination) factors (see Charles 2015). Other scholars emphasize the persistence of cultural beliefs or stereotypes about men and women, which justify, rather than undermine, the existing sex segregation in employment and hierarchy in organizations (Bosak and Eagly 2014). According to social role theory, people’s beliefs about women and men follow from their observed role behaviors. The slow but gradual change in women’s social position and roles in society thus might foster a change of gender stereotypes over time. For example, Bosak and Sczesny (2011) found that those participants, who believed that more women would move into leadership roles over time, also expected the perceived incongruity between women and leaders to erode in the future. In general, vertical and horizontal forms of sex

segregation are strengthened by descriptive and prescriptive gender norms about what women and men are like and should be like, which contribute to gender bias and discrimination in the workplace, and men’s and women’s own gender identity, which has implications for their job search behavior and career decisions (Bosak and Eagly 2014; Bosak and Kinahan 2014). Another factor limiting change pertaining to sex segregation is women’s compared to men’s continued greater involvement in domestic work and child-rearing, which – paired with a lack of family-friendly practices in organizations and/or high childcare costs – makes women often leave their careers or perform non-elite, less skilled work (Blackwell 2001).

Interventions directed to reducing sex segregation have therefore focused on educating individuals about stereotypes and biases through diversity training and unconscious bias training with somewhat positive effects. Other interventions aim to change the gender composition of study programs, occupations, and leadership positions through organizational policies, government mandates, and initiatives including affirmative action, gender pay reporting, the introduction of gender quotas, and the formal institution of family-friendly work-life policies (see Eagly and Heilman 2016). While these direct interventions at organizational level can yield positive effects, research (e.g., Heilman and Haynes 2006) has also shown that they can foster (i) resistance in organizations who might seek to opt out of the mandate; (ii) negative reactions among non-beneficiaries who feel unfairly treated, and (iii) stigmatizing effects toward beneficiaries (e.g., the professional success of some women may be unfairly perceived by some to be the result of affirmative action rather than performance). Finally, interventions might also entail increasing women’s human capital via education and training in nontraditional occupations and leadership capital via opportunities to gain leadership experience.

Conclusion

Sex segregation refers to an imbalanced distribution of men and women within a given locational dimension such as occupation, professional

specialization, industry membership, or education. Vertical occupational segregation, i.e., over (under) representation of women and men into elite versus non-elite roles, can be distinguished from horizontal segregation, i.e., over (under) representation of women and men across professions. Both horizontal and vertical sex segregation are strongly associated with gender inequality and contribute to the prevailing gender pay gap through (a) a general devaluation of work that is performed by women and (b) women's higher prevalence in non-elite jobs. The prevailing sex segregation can be explained by evolutionary, economic, and sociological theories. It has implications and potential costs at individual and macroeconomic levels. Many organizations and policymakers, therefore, aim to reduce occupational sex segregation via various, sometimes controversial, interventions.

Cross-References

- [Adaptation](#)
- [Biases](#)
- [Individual Discrimination](#)
- [Social Roles](#)

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Sex Similarities

- [Sex Differences Versus Gender Symmetry](#)

Sex Steroid Hormones

- [Dominance, Testosterone, and Cortisol](#)

Sex Switching

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Synonyms

[Dichogamy](#); [Sequential hermaphroditism](#); [Sex changing](#); [Sex reversal](#)

Definition

Sex switching is the process by which an organism changes sexual characteristics, including gonads and gamete production, from one sex to another.

Introduction

Sex switching occurs when an organism changes from one sex to another. This switch is

accompanied by a shift in gamete production and reproductive strategy corresponding to the new sex. Sex switching often occurs due to environmental pressures that inhibit the reproductive prospects of one sex over another, such as when one sex is overabundant within a group or when mates of the opposite sex are otherwise difficult to find. Although sex switching is relatively common in plants, it is almost exclusively restricted to fish and invertebrates in the animal kingdom. There are three types of sex switching: protandry, protogyny, and bidirectional.

Evolution of Sex Switching

The evolution of sex switching is often understood via sex allocation theory, which predicts the patterns by which organisms in a population are likely to divide sex distribution of progeny (Charnov 1982). According to sex allocation, the abundance of one sex makes the production of the other sex beneficial as the scarcer sex will have a larger pool from which to draw mates. As selection favors one sex over the other with more ample mating opportunities and reproduction, the sex ratio within the population will shift back toward equilibrium. This phenomenon is frequency-dependent natural selection working on the ratio of sexes within a population (Charnov 1982). Protandrous species often display male-biased sex ratio, and protogynous species often display a female-based sex ratio (Allsop and West 2004). Thus, sex switching is favored when it increases the fitness of an organism by altering its sex later in its lifetime or development. Complementary to this theory is the size-advantage model which states that sequential hermaphroditism will be favored where size and sex combine to predict reproductive success (Ghiselin 1969; Warner 1975). Across species that demonstrate sex switching, it is most likely to occur later in development, usually when the individual is around 72% of maximum body weight (Allsop and West 2003).

True sequential hermaphroditism is limited to fish and invertebrates in the animal kingdom (Charnov 1982). It should be noted that sex

switching is differentiated from transgenderism in humans. Sex switching is part of a reproductive strategy in which individuals achieve fecundity as the assumed sex after changing. This is contrasted to transgenderism in humans, which is categorized by dysphoria in an individuals' perceived gender not matching their biological sex. Gender reassignment surgeries do not alter reproductive abilities as these individuals remain only able to produce gametes of their birth sex. Similarly, sequential hermaphroditism must be distinguished from simultaneous hermaphroditism. As the name suggests, simultaneous hermaphroditism consists of concurrent possession of male and female reproductive systems. Both systems may be functional, and simultaneous hermaphrodites may be able to reproduce using male or female gametes. Sometimes, simultaneous hermaphrodites can self-fertilize, a behavior found even in the animal kingdom (Jarne and Auld 2006). This is contrasted to sequential hermaphroditism, which is characterized by a sex switch by the organism whereby it gives up reproductive abilities as one sex to become another.

Protandry

Protandry occurs when an organism begins life as a male, but changes into a female later in life. Often, this sex change is a response to environmental cues in species in which female fecundity increases with age (Warner 1975). Anemonefish of the *Pomacentridae* family, especially the *Amphiprion* subfamily, are among the best studied groups of protandrists (Avisé and Mank 2008). While some protandrous species mate at random (Warner 1975), others live and reproduce according to a predictable hierarchical social structure. In one of the best understood species, *Amphiprion percula*, this structure consists of one dominant breeding male, one breeding female, and several submissive juvenile males. Dominance is determined by size with the dominant female being the largest in the group (Fricke and Fricke 1977). Sex change is triggered by the removal of the dominant female (e.g., by death), after which the breeding male changes into the

breeding female and the dominant juvenile male undergoes a period of rapid development to become the breeding male. Although non-dominant males do not breed, it is theorized that they persist within this mating strategy because of the potential for reproductive benefits from future mobility within the social structure (Buston 2004).

Protogyny

Protogyny occurs when an organism begins life as a female, but changes into a male later in life. Protogyny is much more common than protandry and bidirectional hermaphroditism (Allsop and West 2004). Because the relationship of size and sexual output typically favors large males more than large females, selection pressures in protogynous species are on males (Avisé and Mank 2008). Protogynous species often feature harem social structures in which a dominant male secures reproductive access to a number of females, which constitutes the bulk of reproductive behavior (Black and Grober 2003). In many species, such as the rock wrasse (*Halichoeres semicinctus*; Adreani & Allen 2008) initial phase (i.e., immature, small) males demonstrate differing mating strategies from terminal phase (i.e., mature, large) males, with terminal phase males most often attempting to defend territory in pursuit of pair mating or spawning. Terminal phase males in protogynous species maintain advantageous mating benefits over initial phase males and non-changing females, which favors the inclusion of sex changing in the gene pool (Warner 1975).

Bidirectional

Bidirectional hermaphroditism is the least common form of sex switching in the animal kingdom and is characterized by changing from one sex to another, followed by reverting to the initial phase sex. Bidirectional changes can be either protandrous or protogynous and often occur in response to a change in status within the social hierarchy of a group (e.g., *Lythrypnus dalli*; Rogers et al. 2007). This plasticity of sex is

often manifest by changes in the group, whereby an alteration in the social status of an individual can result in a change in sex. In some species, individuals can change their sex to accord with their social position many times. In these cases, where changes in the social structure are frequent, individuals may retain the gonads of the non-functional sex (e.g., *Trimma okinawae*; Yamaguchi and Iwasa 2017), effectively making them simultaneous hermaphrodites. Despite the potential benefits, retaining the gonads of the non-functional sex is costly and far from ubiquitous among bidirectional hermaphrodites (e.g., *Paragobiodon echinocephalus*; Yamaguchi and Iwasa 2017).

Conclusion

Sex switching, or sequential hermaphroditism, is used as part of the mating strategy of some organisms, but is limited to some fish and invertebrates in the animal kingdom. Species may be born male and switch to female (protandry), female and switch to male (protogyny), or more rarely both (bidirectional). Typically, sex changing occurs later in an organism's development and is a result of environmental cues. Population sex ratios are usually biased toward the initial phase sex in sex-switching species. The ability to change sex increases the fitness of an organism by increasing reproductive opportunities that might otherwise be limited by remaining its birth sex, thus increasing the likelihood of sex switching being included in subsequent generations.

Cross-References

- [Frequency-Dependent Selection](#)
- [Local Sex Ratio](#)
- [Operational Sex Ratio](#)
- [Sex Ratio](#)
- [Sexual Conflict Theory](#)
- [Sexual Contact and Sexual Disgust](#)
- [Sexual Dimorphism](#)
- [Social Outcomes and Sex Ratio](#)
- [Social Dominance and Sexual Access](#)

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Sex Trade

- [Prostitution and Legal Regulation of Sex](#)

Sex Typing

- [Sex Differences in Participation](#)

Sex Work

► Prostitution and Legal Regulation of Sex

Sex, Power, and Conflict

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Introduction

Our knowledge of the world comes from the history of mankind. Through the ages, civilizations have risen and fallen, and cities have developed and vanquished; the earliest accounts of mankind tell tales of conflicts and conquests. When we look back into history we see a reflection of the lives of people. One distinct pattern is visible: an evolutionary desire to leave one's genes in the population and secure one's lineage, to create a stable environment for offspring to live their lives in the attained glory of their ancestors, and to establish an identity by conquest. In short, this shows us that sex, power and conflict have been present in society throughout our evolution. Over the millennia, the argument about differences in sex has evolved significantly. Challenges to the patriarchy are being observed and people are breaking down stereotypes, challenging their own potential and diluting gender roles from one side to the other side of the continuum. Yet, there is increasing gender-directed violence, intolerance and hate (Buss and Malamuth 1996). The great epics such as *Mahabharata*, *Ramayana*, *The Iliad* and *The Odyssey* all contain central themes of sex, power and conflict. Moving forward from classical to modern literature, sex, power and conflict have been central themes of stories and poetry. The recent worldwide megahit fantasy epic *The Song of Ice and Fire* (written by George R. R. Martin)

and its television adaptation, *Game of Thrones*, also majorly revolve around this topic. From classical to contemporary times, sex, power and conflict have surrounded the world in various versions with and without alterations and remain captivating topics for academicians, writers and the general public. This article briefly discusses the concepts of sex, power and conflict.

Definitions

Sex: According to the *Merriam Webster English Dictionary*, sex can be defined as “the sum of the structural, functional, and sometimes behavioural characteristics of organisms that distinguish males and females” (Merriam Webster 1996). Alternatively, it can be defined as an act of intercourse between two or more people; its synonyms include coitus, intercourse, fornication, congress, copulation, and mating.

Power: This means an ability to act or produce an effect; to give impetus to; to be able to utilize strength. Power is synonymous with authority, clout, command, grip, dominion and mastery (Merriam Webster 1996).

Conflict: This can be defined as a fight, battle or war; a difference, opposition, contradiction or failure to be in agreement or accord; or a struggle as a result of incompatibility between one's needs, drives, desires, or external or internal demands (Merriam Webster 1996).

Sex, power and conflict in the great epics: The story of *Ramayana*, when we look at it, revolves around the main themes of sex, power and conflict. Rama was the son of Dasharatha, the king of Ayodhya. Dasharatha had three wives and four children. The son of the first queen, Kaushalya, was Rama; the son of the second queen, Kaikei, was Bharat; and the third queen, Sumitra, had two sons: Laxman and Shatrughna. During the illness of King Dasharatha, Kaikei cared for him and he bestowed three promises upon her. Kaikei requested him to fulfil these promises when the time came. When the children grew up and it was time for the coronation of Prince Rama, Kaikei asked Dasharatha to fulfil his promises to her, and she, with the guidance of her maid Manthara, asked

him to send Prince Rama into exile for 14 years so that her son would become the king (Pattanaik 2013). This led to the death of King Dasharatha, but, to honour his father's promise, Rama, with his wife and brother Laxman, left and went into exile. A bias towards Queen Kaikei from her husband led to a shift in power in the family and created an internal conflict within the royal family of Ayodhya. Thereafter, we observe the main theme of *Ramayana*: the abduction of Sita by Ravana, which resulted from the proposal of marriage by Surpanakha (Ravana's sister) to Laxman. The story after that revolves around the power and conflict of Ravana, who was an immensely great and powerful king, and Prince Rama in exile. The final result of the destruction of Swarana Lanka (Golden Lanka, currently known as Sri Lanka) and the death of Ravana marks the victory of good over evil. This theme is still related to sex, power and conflict at a basic level. Even at the end of *Ramayana* we see the plight of Queen Sita as she is forced to undergo the Agni Pariksha (a trial by fire) for being in Ravana's place for so long to prove her dedication to her husband. She is driven out of the kingdom in a pregnant state and later gives birth to twins, Luv and Kush, who stop the Ashwamedha Yagya horse to finally reunite with their father. However, when Queen Sita is forced to go through another Agni Pariksha to prove her dedication to her husband, in her plight, she goes into the earth, never to return. All of this is done to please the people of the kingdom. We find that sex, power and conflict are central themes of this story, and we observe that they have led to devastation, loss of life and other calamities happening to the protagonists (Buck and Triest 2000). The same themes can be observed in the great epics of *The Iliad*, *The Odyssey* and *The Epic of Gilgamesh*; there we can observe that the lust of Prince Paris led to the war between Greece and Troy. Even the gods were involved in showcasing their power; they created various situations and interfered in human feelings, and the ultimate result led to the devastation of Troy (Kullmann 1985). Carefully observed, this shows how men can be manipulated by lust, sex and greed; how glory can be a goal of one's life; and how conflict can bring about devastation and turn cities into dust.

Evolution Relating Sex, Power and Conflict

Before the theory of evolution was published by Charles Darwin, there was a hypothesis that humans were created by a being of superior intellect and power (creationist theory), although this had no substantial evidence. Darwin's theory stated that there were spontaneous variations in reproduction, leading to diversification, and that individuals with favourable mutations would survive, while those with unfavourable ones would perish. This gave an opportunity to explain a lot of the current scenarios and development of various taxa in the animal kingdom (Dawkins 1986).

The Biological Battle of the Sexes

Human beings are considered to be special animals, as we are users and makers of tools and use vocal and pictorial signs to communicate universally, including use of grammar and other advancements. Recent discoveries have changed the perception of humans as being so unique, as we now understand more secrets of the behaviour of other animals. Unlike many organisms, humans reproduce sexually, which leads to adaptation to the environment and variation of traits in the gene pool. Changes in genetic material mean that a mother may be adapted to her surroundings but her offspring may not have the capacity to adapt. This can be explained by the example that if men who are physically powerful kill other men who are not as powerful, the average life expectancy of men will come down and more aggressive traits will be present in the next few generations, but as less strong people live longer, their traits will persist for a longer time in the generations to come (Buss and Malamuth 1996). The scientific literature describes human beings as "dioecious," meaning that they come in two varieties – male and female – primarily, and in terms of reproduction, their combined genetic material can only give rise to another human being. To maintain traceable and desirable genetics, humans have developed the concept of marriage; although the offspring have their own unique genetics, their history can usually be traced back through their morphologies. If we look into the investment

made by women biologically, their eggs are bigger than the male's sperm and, because of the mammalian form of reproduction and lactation, mothers invest a lot of time and energy in their offspring. Observing the dioecious nature of humans, there is an innate battle of the sexes. This is also a reason why humans focus on parental investment. The differences in the roles of both sexes vary biologically, and nature gives both perspectives, with agonistic as well as antagonistic factors between both sexes (Buss and Malamuth 1996).

Marriage and humans: Marriage is a phenomenon observed in all human societies. It legitimizes the relationship in an economic manner as well as a reproductive manner, it gives the couple socially accepted access to sexual reproduction, and it also keeps society intact by providing legitimacy for the rearing of children. Marital obligation goes far beyond just conception: it also gives rise to a lot of expectations of a varied nature; moreover, marriage is a process of cross-generational relay of heritable material. Although marriage is a method of producing and rearing children, marriages are often observed to fail with or without attainment of the reproductive goal. There are similar such unions in the animal kingdom, but the investment of both parties is seldom so apparent, thus making marriage a uniquely human phenomenon (Buss and Malamuth 1996).

Marital Conflict

The union of marriage has been thought to be both economic and reproductive in nature, but the companionship designed through marriage often does not work out. The reasons can be arbitrarily divided into three categories: when the female invests in relationships other than the marriage, when the male invests more in out-of-marriage relationships, and power clashes between the partners. Female partners may not be satisfied with the investments that their partner makes in the relationship; they may be attracted to more comforting partners, and this may give rise to conflict with the current marital partner. Here, the male often resorts to physical strength to gain control and power over the female. In the

other case, it has been observed that when the male wishes to resort to sexual relationships outside the marriage and starts investing more in another relationship, with or without the desire to mate and procreate, the female feels the dearth of emotional investment, which leads to dissatisfaction between them. The third reason is often related not to sexual or mating desires but to social power-related struggles; this kind of conflict often occurs because of excessive intervention on the part of in-laws from either side, and this probably relates to most of the married couples in the world. There can be issues of conflict between the partners regarding children; it has often been observed that a mother wants her partner to invest more in her biological children that he is willing to give, leading to conflict and violence against children and women alike. This leads to a conflict of rearing in which males who do not father the children are not interested in investing their resources in the children of that mother, leading to marital conflict and suffering of the offspring (Buss and Malamuth 1996).

Violence against women: Recent worldwide statistics have shown that one in three women experiences violence in their lifetime and 30% of women are victimised by their intimate partners. Globally, 38% of murders of women are committed by their male intimate partners (WHO 2017). This shows us the grave nature of the conflict that occurs, and fatal outcomes affect not only the women but also their children and the whole family. Violence against women is also caused by the struggles of sex, power and conflict. Patriarchal societies often give rise to a feeling of dominance among men, with women being considered property; thus, to maintain the stance of power to discipline them, men often resort to use of power and coercion. When this is met with resistance, they resort to conflict and inflict injury and pain on their victims (women).

Sexual Harassment

Sexual harassment has been one of the most talked-about topics in recent times. Most workplaces have developed policies regarding sexual harassment as a policy protocol (Government of India 2015), and regulatory acts have been

introduced to prohibit and prevent sexual harassment in the workplace. Sexual harassment has been a phenomenon causing women to abstain from public life and has created fear among women since ancient times. The Renaissance brought about a change in the conditions and the behaviour of women. Then came the Industrial Revolution, and the West transformed completely after that. As the number of women increased in the workplace, workplace exploitation started for them as well. The patriarchal societies of the world have discriminated against women in terms of their working hours, equality of pay and benefits. These trends are also seen today. Many women desperate to climb the ladder of success submit to harassment for an increase in salary or because of pressure to avoid losing their job (Government of India 2015). This phenomenon is worldwide in nature. It is representative of the biological feud between men and women. Although women have increased their socio-economic status, they are still dominated by the males of the world, who do not want to share their power with females, thus creating the essence of conflict. People in the workplace are often in an advantageous situation and exploit their superiority and power to obtain sexual advantages, to breach the morals of female employees or to maintain their level of power, creating a situation of hostility in the workplace and making it difficult for women to work.

Offenders and Victims of Sexual Coercion

Sexual coercion means forcing someone to commit a sexual act with the perpetrator. This in itself brings out a very violent nature or force applied to sexual activities for the victims. Often it has been observed that the victims are well known or stalked by the perpetrator with a intention to violate their self-esteem and to hurt, exploit or kill them; just as a measure to control their behaviour so that the victim loses their social status or brings shame upon their kin and other members of their social group; or to express their power over the victim. Most of the time, the perpetrators are actually successful in achieving their intentions: the victims suffer injuries, broken or shattered self-esteem, and loss of social status and

desirability as mates for others, which has a huge impact on the victims' lives. Often it has been observed that they suffer from anxiety disorders and post-traumatic stress disorder (Thornhill 1996). Commonly, females are the victims of sexual coercion, leading to a disturbed state of mind and a broken spirit. This can be evolutionarily observed in other mammals; for example, when the alpha male of a pride of lions is defeated in a fight, the winning lion automatically gains access to copulate with the females of the pride. Similar behaviours have also been observed in humans and other animals. We can observe that sexual coercion has been used by humans to create an exhibition of power over those who are defeated.

The Feminist Perspective

A discussion about the feminist perspective cannot take place without an elaboration of feminism. Feminism essentially is a collective, social, political and technological ideology to establish equality for both sexes. Feminism deals not with the phenomenon of the things that currently exist but with the phenomenon of what should be. The feministic ideology fights fiercely with the concept of the superiority of one sex to another; it advocates for equality for both sexes and supports all efforts to achieve this in all aspects: social, political, legal, educational, work and benefits. It aims to show the unseen and neglected part of society, which needs attention to bring about stability in the world.

Is Rape About Sex or Violence?

There has been a long-standing and ongoing discussion about rape. The word "rape" is something we understand as a man using force to commit copulation with a female. A 1993 description by Campbell states that rape is actually a calculated act of violence, which is mainly committed in cold blood not to let off steam or to express anger but as an act in which the aggressor actually feels no anger towards the victim (Greathouse et al. 2015). This discussion has fuelled a discussion about the goal of rape. The majority of theorists

have said that the goal is to have sex, but feminist theories suggest that it is more of a method of aggression used by males to achieve the goal of dominance and exert the power of control over their female counterparts (Buss and Malamuth 1996). Examples of marital rape show that many times, males have sex with their wives whenever and wherever they wish in order to exert complete control over their lives and to showcase their dominance of the females. Thus, rape is a violent act with the aim of destroying the integrity of the victim, and nothing less.

Substance Use and Its Impact on Perception and Behaviour

The discussion on substance use is a very important one. Psychoactive substances have been known to man from time immemorial. People use them for recreation and many other purposes. Substances such as alcohol were considered in ancient Greece to be aphrodisiac (Kullmann 1985). Since then, humans have experimented with them. Biomedically, alcohol is known to cause lack of inhibition and distort the judgement of people consuming it; initially, this has an effect on the sexual desire of people. When we observe the patterns of sexual violence, the characteristics commonly observed are that both men and women usually drink in heavy amounts, there is a history of sexual abuse in childhood, and most men who rape have a notion that women who drink are easily available targets for sexual exploitation. Both men and women party a lot and go to bars. Men use alcohol as an excuse for inappropriate behaviour. Alcohol can lead to cognitive and motor disturbances, misleading both men and women to perceive that they are being led on (Abbey et al. 2001). Thus, alcohol and other substances can be a reason for an increase in the incidence of violence directed towards women.

Sexual Politics

Politics is the science of governance; we can observe the play of sex, power and conflict in a very integrated manner. The evolutionary sciences tell us that aggressive and dominant traits are observed among the males of many hominids. There is a strong chance that such men father more

children; thus, the dominating trait is more commonly observed among men around the world, giving rise to a patriarchal system in society. Polygamous societies tell us tales of men having many wives. There are societies where women have accepted the dominance of men and it is observed that less coercion is needed from the men to achieve the goals of sex, dominance and labour (Thornhill 1996). The oppressive nature of the men has led them to acquire land and fight among themselves to acquire more women and children who will help them in providing for the males of the house. When we look at classical texts and poetry, we observe this pattern of acquiring new lands among the leading societies. Acquiring more women has also become a status symbol among men to showcase their power. This has led to the politicising of sexual preference, making males the source of the strength of the family and thus bringing in a linear hierarchy of sons and making women merely a source to get more power. When we look into politics, we observe that certain monarchs marry the daughters of other monarchs to establish political gain for both houses, thus making women a commodity to be traded for power or acquired to showcase power (Buss and Malamuth 1996). This has been a trend to establish and forge political ties. There are also accounts that after a king or ruler was defeated, his wives were taken away by the aggressors and raped; here, sex was made a weapon to punish the losers and harm their integrity.

Conclusion

There are three gates to the self-destructive hell:
lust, anger and greed. – Lord Shree Krishna

The words of Lord Krishna in *Mahabharata* resonate with this topic immensely (Roy 2010). The words are *lust*, which leads to *sex*, and this can be attributed to suppression of the other sex (suppression of the female by the male) to achieve reproductive or other goals. This leads to a feeling of superiority and a sense of strength (*power*), which leads to a feeling of *anger*. Anger can be triggered by a threat from the other sex or from the

same sex, in order to acquire something that is a desire or a possession. This leads to a feeling of *greed*, which can manipulate a man to attack or create a situation of *conflict*. Conflicts occur between and within nations or states, between people and within the individual. They can lead to a self-destructive hell. We may argue that sex, power and conflict have been present in human society throughout our evolution, but the ultimate effect of these phenomena cannot shape the future of mankind for the better. When people are not given equal opportunities and greed dominates power, then only conflict and destruction can occur. Unless mankind is able to control our innate animalistic desires, sex, power and conflict will remain. To become the superior human that is desired can be achieved only with *equality of both sexes*. *Power struggles* should not be the main issue; rather, *peaceful coexistence* should be. Ultimately, *conflict* should be of the intellect and spirit for growth; conflict among people has brought only destruction and devastation to the world. Since the start of the twentieth century, humans bore the brunt of World Wars I and II, which affected the whole world and led it to the verge of destruction by nuclear weapons. It is to be hoed that understanding of this topic will help people understand themselves and choose a path of self-betterment.

Cross-References

- [Mate Poaching](#)
- [Patriarchy and Feminist Perspectives](#)
- [Premarital Sexual Permissiveness](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Conflict Theory](#)
- [Sexual Debut](#)

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Sex-Biased Parental Investment

- [Daughter Guarding](#)

Sex-Biased Transcription

- [Sexual Dimorphism and Sex-Biased Gene Expression](#)

Sex-Differences in Disease Avoidance

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Synonyms

[Gender differences in disgust](#)

Definition

The degree to which men and women avoid cues that indicate contagious illness or that elicit the emotion of disgust.

Introduction

Pathogens, the organisms and viruses that cause disease, are a central adaptive problem for almost all organisms. Pathogens, like bacteria, helminths (worms), viruses, and protozoa, take nutrients from their hosts, the larger multicellular organism. They also shelter in their host and often use the host's own cellular processes to make copies of themselves. While there are many bacteria, microorganisms, and even viruses that do not cause harm to their hosts, pathogens are defined as agents that cause disease and by definition undermine the normal functioning of the host organism.

Because of the constant threat of pathogens, immune systems have evolved in many organisms. Humans and other mammals are equipped to fend off pathogens with a variety of different cellular functions from creating molecules that coat the pathogens (antibodies) to having specialized cells that absorb the pathogens (e.g., macrophages). However, launching immune attacks is energetically costly. Thus, it is in the organism's best interests to avoid being exploited by these organisms in the first place. The way that organisms prevent pathogens from triggering these other physiological defense mechanisms is called disease avoidance.

Disease Avoidance

Disease avoidance is widespread. Even organisms as simple as worms can avoid toxins in their environment. Rodents avoid diseased conspecifics and even rats who are known to eat a wide variety of foods display a “cannibalism taboo,” avoiding eating other rats for the purposes of disease avoidance (Hart 1990). Humans also engage in various disease avoidance strategies common in other species; however, humans are the only species who demonstrate disgust.

Disgust

The central adaptive function of disgust is thought to be to reduce the risk of infection by motivating distance from cues of pathogens. While so-called pathogen or disease avoidance disgust is likely central to its function, disgust also deters mating with humans who do not show signs of good genetic endowment (Tybur et al. 2013). Disgust is measured in humans in a variety of different ways, through word-based questionnaires, through image-based ratings, through measuring disgust facial expressions, and through behavioral tests (for a review see Fleischman 2014).

Differences in Disgust and Disease Avoidance

Decades of research have shown that there are robust sex differences in disgust sensitivity, defined here as the tendency to experience disgust. Women have been shown to be more disgust sensitive than men using verbal measures and across all domains (Fleischman 2014). Specifically in the pathogen domain, women are more disgust sensitive when rating disgusting images (Curtis et al. 2004) and when engaging in disgusting tasks (e.g., eating a piece of feces-shaped fudge) (Rozin et al. 1999). As adults, women are more likely to develop obsessive-compulsive disorder, more likely to present with cleaning compulsions and contamination obsessions (Altemus et al. 2014). In nonclinical samples, women score

higher than men on measures of OCD-related contamination fear (Mancini et al. 2001).

Sexual disgust has been shown to be very different between men and women. In studies using the established three domains of disgust scale, the largest sex difference is in the sexual domain $d(475) = 1.44$ as compared to the pathogen domain $d(475) = 0.32$ (Tybur et al. 2011). Women are less inclined toward casual sex and more disgusted by pornography than men (Koukounas and McCabe 1997). Finally, while sexually aroused men have been shown to have reduced disgust sensitivity, sexually aroused women do not always show this effect and may even show increased pathogen disgust sensitivity (for a review, see Fleischman 2014).

Functional Reasons for Sex Differences in Disgust Sensitivity

Compared to men, women have faced unique circumstances over evolutionary history that may have led to heightened pathogen disgust sensitivity. Women show changes in immunity across the menstrual cycle and as a function of pregnancy that make them vulnerable to disease. Women also must protect children and infants who are vulnerable from disease, perhaps making pathogen disgust sensitivity more important (Curtis et al. 2004). Finally, women are uniquely able to pass on sexually transmitted and other infections to their offspring during pregnancy, birth, and lactation (Fleischman 2014; Madkan et al. 2006). Men's greater propensity for risk taking more generally might also be contributing factor to their relatively lower disgust sensitivity.

There are several adaptive reasons why women might have heightened sexual disgust. Women can have fewer offspring than men and have a greater burden of parental investment. Thus, they have less to gain from engaging in promiscuous sex. If sexual disgust serves to prevent one from engaging in sexual activity with someone who is not genetically fit, men have less to lose and thus lower disgust sensitivity in this domain. Anatomical differences between men and women lead to large differences in rate of infection and disease

burden for sexually transmitted disease. Women have a greater area of mucous membranes and experience more damage during intercourse. In women, the fallopian tubes open into a central pelvic cavity making them much more likely to get systemic infection from bacteria that are sexually transmitted. Women with a sexually transmitted infection are much more likely to die or become sterile (Madkan et al. 2006).

Conclusion

Selection pressure has acted differently on men and women with regard to disease avoidance. Disgust, the uniquely human emotion thought to have evolved specifically for disease avoidance, tends to be greater in women than in men. In particular, sexual disgust sensitivity is greater in women. This is likely due to disease risk and burden from sexually transmitted infection as well as greater obligate parental investment.

Cross-References

- Disease Avoidance
- Disease Avoidance Hypothesis
- Disgust
- Pathogen Disgust and Perceptions of Attractiveness
- Sexual Contact and Sexual Disgust

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Sex-Differentiated Behavior

► Self-Stereotyping

Sexism

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Synonyms

Gender inequality; Patriarchy; Sexual control; Sexual discrimination

Definition

Sexism is discrimination or prejudice directed toward an individual based on his or her gender or sex.

Introduction

Women and girls tend to be recognized as the primary victims of sexism across cultures. For example, worldwide, women earn less, have less representation in politics, lower participation in the labor force, and receive less education than their male counterparts (United Nations Development Programme 2015). However, men and boys are also affected by sexism. For instance, men are more likely to be the victims of corporal punishment, capital punishment, aggression, violence, have higher mortality rates, and are less likely to gain child custody (see Benatar 2012).

Contemporary social movements such as *feminism* seek to eliminate inequality between the sexes in employment, education, politics, social roles, and reduce the occurrence of sexual coercion and violence that disproportionately affects women. Evolutionary accounts of patriarchy, or widespread male domination, have been offered by some theorists (e.g., Buss and Malamuth 1996; Smuts 1995) in an effort to better explain the suppression of women's autonomy by males and identify the contexts in which it is most likely to occur. Evolutionary biologists and psychologists propose that patriarchy can be contextualized as arising from the interaction between evolved psychological mechanisms and social/cultural contexts. Two foundational components that evolutionary theorists have argued underlie patriarchal practices include: the control of women and girls' sexuality and the coevolution of men's intrasexual competition and women's partner preferences. These features of patriarchy are discussed below, in regards to lower resource control (e.g., economic resources, property) and higher rates of sexual victimization experienced by women (Clinton Foundation 2015), respectively.

Control of Female Sexuality

An evolutionary perspective predicts that human males will monitor and attempt to control the sexual behavior of females in effort to assure their paternity, as observed in other pair-bonded, sexually reproducing species (Trivers 1972). Over

human history, men have faced the adaptive problem of determining whether their children are indeed their own genetic offspring, or the offspring of another man that resulted from an infidelity committed by their female partner. Thus, it is hypothesized that attempts to control female sexual behavior represent strategies by men to ensure their paternal certainty, and these behaviors evolved because they contributed to men's reproductive success (i.e., men who were better able to avoid being cuckolded were more likely to pass on their genes).

Evidential support for this theory comes from observable patterns in physical and sexual violence perpetrated against women and girls. For example, millions of women and girls are subjected to severe genital mutilation procedures that are psychologically and physically harmful to ensure their chastity (World Health Organization 2016). These procedures are frequently practiced because they are believed to guarantee a woman's virginity and reduce her libido, thereby ensuring that she will remain faithful to her husband (World Health Organization 2016). Often, in cultures practicing female genital mutilation women who do not undergo these surgeries face social rejection and are no longer considered viable for marriage.

An evolutionary perspective also predicts that increasing the likelihood of paternity certainty underlies violence, sexual coercion, and rape directed at women. Research stemming from evolutionary theory suggests that men's fear of cuckoldry is strongly related to these violent acts. Specifically, both physical and sexual violence (i.e., rape) directed at men's intimate partners are predicted by accusations or suspicions of their partners' infidelity (reviewed in Kaighobadi et al. 2009). It is hypothesized that physical aggression towards men's romantic partners may function as a threat against or punishment for committing infidelity. Additionally, partner rape could be an unconscious attempt to minimize the chance of insemination by another male by means of displacing rival sperm (see ► [“Sperm Competition,”](#) this volume). In fact, rape is frequently perpetrated by intimate partners and husbands (see Clinton Foundation 2015; Kaighobadi

et al. 2009). Importantly, these findings do not justify men's aggressive acts towards their partners whatsoever; instead, evolutionary theorists seek to better understand the motivations behind such violent behaviors in order to more effectively predict and prevent them.

Coevolution of Men's Intrasexual Competition and Women's Partner Preferences

Another key component of patriarchy hypothesized to contribute to the control of human females is the coevolution of intrasexual competition by men (i.e., competition between men for access to mates), and women's mate preferences for partners with resources. Buss and Malamuth (1996) suggested that men's greater access to and control of resources is attributable to the discrepancy in selection pressures on men and women to acquire them. Specifically, because women more than men prefer romantic partners who have access to economic resources such as income, men have evolved to compete for access to resources as a means of attracting female mates, whereas comparatively, women have not (see Buss and Malamuth 1996). Consequently, the inequality between men and women with respect to control over economic resources, manifesting in a higher worldwide poverty rate and unequal participation and compensation in the workforce (United Nations Development Programme 2015), is a likely by-product of this sex difference. To counteract this inequality, Smuts (1995) recommends establishing institutional policies (e.g., laws) to guarantee women's access to resources, such as property, in societies where economic disparity between the sexes is more pronounced.

Conclusion

Evolutionary theorists have proposed evolved functions of behaviors underlying the most pervasive manifestations of sexism, including the unequal distribution of economic resources and sexual victimization experienced by women and

girls across cultures. With its unique insights into human psychology and behavior, an evolutionary framework can be used to gain a more thorough understanding of sexism and reduce sexist attitudes and practices (e.g., Smuts 1995). Although historically there has been less attention given to sexism perpetuated against boys and men (see Benatar 2012), an evolutionary perspective may shed light on some of the specific disadvantages they face. For example, Archer (2009) hypothesizes that intrasexual competition may account for why they are disproportionately the victims of violence.

It is critical to note that addressing sex-based inequality will be most effectively accomplished by studying the interaction between the biological and environmental contexts (e.g., personality traits, situational factors). Moreover, an evolutionary perspective does not discount the importance of human learning and social change in rectifying these injustices. There is evidence to suggest that sociopolitical movements can be effective. For example, feminist movements are associated with declines in the rates of crime and rape since the 1990s (Pinker 2011). Indeed, Smuts (1995) asserts that instituting policies that offer women legal protection against sexual violence/coercion and against men's control over their economic assets will likely facilitate gender equality. Accordingly, cultural and social revolutions, including those focusing on women's interests, have been responsible for a worldwide decline in violence in the past 10,000 years. This indicates that men also stand to gain from more equitable sociopolitical circumstances. Nevertheless, Benatar (2012) believes it is unlikely that sexism will be completely eradicated when one sex no longer dominates the other and suggests that legal protections also be made in favor of men and boys where they are specifically disadvantaged.

Cross-References

- [Origins of Patriarchy](#)
- [Patriarchy and Feminist Perspectives](#)
- [Prejudice](#)
- [Second Sexism](#)
- [Sexual Stigmatization](#)

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Sexism Against Male

- [Second Sexism](#)

Sex-Role Inventory, The

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Synonyms

[Gender role inventory](#)

Definition

Sex role (or gender role) refers to the characteristics, expectations, and values associated with being male or female in a particular culture. Sex-role inventories have been designed to assess people's endorsement of masculine and feminine characteristics.

Introduction

The first self-report to measure masculinity-femininity (M-F) was published in 1936 by Terman and Miles. It was tacitly assumed that masculinity was normal and natural in males, yet not in the case of females, and the parallel was held true for femininity (Ashmore 1990). This construct became popular and widespread in the field of psychology, and M-F scales were included in new omnibus personality inventories published in the following three decades. So far, a variety of instruments to evaluate sex roles and other gender-related constructs have been published in different countries across the world. This entry focuses on the one of the pioneering and most extensively used ones ever since its publication in 1974: the Bem Sex-Role Inventory, developed by Sandra L. Bem.

The Bem Sex-Role Inventory (BSRI)

The BSRI (Bem 1974) is a paper-and-pencil self-report instrument that asks a person to indicate, by using a 7-point scale, how well each of 60 different attributes describes him or her. The masculinity scale is made up of 20 of those characteristics, namely, "acts as leader," "aggressive," "ambitious," "analytical," "assertive," "athletic," "competitive," "defends own beliefs," "dominant," "forceful," "has leadership abilities," "independent," "individualistic," "makes decision easily," "masculine," "self-reliant," "self-sufficient," "strong personality," "willing to take a stand," and "willing to take risks." The femininity scale consists of 20 characteristics ("affectionate," "cheerful," "childlike," "compassionate," "does

not use harsh language," "eager to soothe hurt feelings," "feminine," "flatterable," "gentle," "gullible," "loves children," "loyal," "sensitive to need of others," "shy," "soft spoken," "sympathetic," "tender," "understanding," "warm," "yielding"). The remaining 20 items are fillers (e.g., "adaptable," "conventional," "jealous," "sincere," "solemn," "inefficient"). The respondent is unaware of these categories and response scale ranges from 1, for "never or almost never true," to 7 being "always or almost always true."

On the basis of his or her responses, each person receives three major scores: a femininity score, equal to the total number of femininity scale points; a masculinity score, equal to the total number of masculinity scale points; and an androgyny score. Subjects whose score is significantly higher on the masculinity scale than on the femininity scale are labeled masculine; those who score high on the femininity but not on the masculinity scale are labeled feminine; those who score high on both the masculinity and the femininity scales are identified as androgynous; and those who score low on both scales are labeled as undifferentiated. Masculinity and femininity scores are independent to one another and "indicate the extent to which a person endorses masculine and feminine characteristics as self-descriptive" (Bem 1974, p. 158).

The BSRI contains a number of features that make it stand out from other scales so far used to evaluate M-F (Bem 1974). (1) It includes both a masculinity scale and a femininity scale, each one containing 20 attributes. Positing that, either from a psychological or a social perspective, masculinity and femininity act against consideration as bipolar ends of a single dimension (whereby a person is necessarily to be either masculine or feminine, yet not both as sexes stand in an oppositional relation), the BSRI represented a new type of sex-role inventory where masculinity and femininity could be evaluated independently. (2) These characteristics were selected as feminine or masculine on the basis of what was culturally defined as gender appropriate in the United States at that time. The BSRI was based on the conception of a conventionally gendered, sex-typed individual "as someone whose self-

definition and behavior are thoroughly intertwined with the stereotyped definition of gender appropriateness in his or her culture” (Bem 1993, p. 119). Judges rated a list of approximately 200 personality characteristics in terms of how desirable they were considered to be for either a man or a woman in American society. (3) It allows the characterization of a person as masculine, feminine, or androgynous. A person is sex typed as either masculine or feminine, whereas the androgynous person was one who displayed both masculine and feminine traits. Psychological androgyny implies the possibility for an individual to be both compassionate and assertive, expressive and instrumental, and feminine and masculine, according to the situational appropriateness of the behaviors; and the individual may even blend these complementary modalities in a single act (Bem 1977). Androgynous people were supposed to have the greatest behavioral flexibility and the best psychological adjustment.

In 1981 Bem developed a short 30-item version of the BSRI that observes a strong correlation with the original BSRI. The short form rules out some items such as “feminine,” “masculine,” “athletic,” “gullible,” or “childlike.” Both the masculinity and the femininity scales consist of ten items, whereas the rest are filler items. Original and shorter versions of the BSRI have been used and validated in various countries and continue to be used, which has proved its usability and value as it allows to claim the relevance of the self-attribution of the stereotypically male and female personality characteristics in different areas, such as the personal well-being, distress, stress and coping, marital satisfaction, leadership, or violence, among others.

Debate Over Bem’s Sex-Role Inventory

The BSRI has triggered discussion of the matter to the point of being criticized on theoretical and methodological grounds. Some controversies have revolved around Bem’s conceptualization of psychological androgyny, which was seen as a form of flexibility that promoted better psychological adjustment. But evidence linking

androgyny and adjustment was mixed (Whitley 1983), although some interest in the topic has continued to be (Martin et al. 2017).

Some authors consider that the BSRI measure of femininity and masculinity is partial as it only assesses the socially desirable gender-related personality traits. They have argued that the femininity scale reflects an expressive or communal orientation, whereas the masculinity scale reflects an instrumental or agentic orientation (Helgeson 2015). Researchers have acknowledged that masculinity and femininity are broad constructs that consist not only of the personality traits but also of behaviors, interests, physical appearance, and occupational preference. But, although BSRI findings cannot be generalized to sex-role behaviors in general, research suggests that instrumentality and expressiveness per se entail important implications. Differences in instrumentality and expressiveness are considered to be core distinctions between women and men, an idea that has been used to account for traditional sex-role ideology (Spence and Helmreich 1980).

The factor structure of the BSRI also was subject to criticism. Findings from factor analysis studies have raised concerns for the replicability of a two-factor structure as it has been found that the masculine construct tends to be more complex in its structure than the feminine (Choi and Fuqua 2003). It has also pointed out that the BSRI may not be suitable for all cultures and time periods, since stereotypes and gender roles vary between cultures and change over time, so it is possible that the BSRI scale items do not match modern gender stereotypes (Donnelly and Twenge 2017).

However, despite men and women roles have changed in recent decades in most societies, these changes highlighting the increased participation of women in the workforce, there is still no evidence of gender equality. Thus, gender division of labor persists, women are underrepresented in top leadership roles in corporations and government, and they still perform most of the domestic work. Moreover, the media continue to depict women and men in very traditional roles, while society keeps making evident the endurance of traditional role expectations and dichotomized gender stereotypes informing the traits, role behaviors,

occupations, and physical characteristics attributed to women and men (Haines et al. 2016).

Conclusion

The Bem's Sex-Role Inventory is a self-report instrument that assesses people's endorsement of socially desirable personality traits that are stereotypically associated with women and men. The femininity scale reflects an expressive or communal orientation, whereas the masculinity scale presents an instrumental or agentic orientation. The original 60-item and shorter versions of the BSRI are still widely used in several countries as a measure of gender-linked expressive and instrumental personality attributes, so the BSRI has proved to be useful so as to claim the importance of the self-attribution of the stereotypically male and female personality characteristics in different areas, such as personal well-being, distress, stress and coping, marital satisfaction, leadership, or violence, among others.

Cross-References

- [Biology of Human Gender, The](#)
- [Gender Schema](#)
- [Masculinity and Femininity](#)
- [Self-Stereotyping](#)
- [Sex Differences in Sexual Socialization](#)
- [Social Roles](#)
- [Socialization Processes](#)

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Sex-Specific Link Between Self-Esteem and Mate Value

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Synonyms

[Romantic desirability](#); [Self-worth](#)

Definition

Self-esteem is an individual's overall evaluation of their worth. It includes both attitudinal and affective components.

Mate value refers to the desirability of an individual as a long- or short-term sexual partner, relative to intrasexual competitors.

Introduction

In their extension of sociometer theory, Kirkpatrick and Ellis (2004) posit the existence of a specific system, the mating sociometer, which functions to monitor and regulate short- and long-term sexual relationships. They suggest that relational status, experiences of romantic acceptance or rejection, and self-evaluations of mate value and its components all influence self-esteem, which then motivates adaptive behavioral responses. There are well-established differences in the determinants of mate value between sexes (Buss 1989), and thus the mating sociometer perspective would predict that there should be sex differences in relationships between specific self-evaluations in domains which contribute to mate value and self-esteem.

Physical Attractiveness and Self-Esteem

One well-established sex difference in the determinants of mate value is the finding that across a variety of cultures, physical attractiveness contributes more to mate value in women than in men (Buss 1989). Consequently, a mating sociometer perspective would predict that physical attractiveness should more strongly predict self-esteem in women than in men. There is a wealth of empirical evidence to support this, and in his comprehensive meta-analysis of the literature, Feingold (1992) found a significantly stronger average correlation between self-perceived physical attractiveness in women than in men.

Moreover, there is evidence from studies of contingencies of self-worth that individuals are consciously aware of this sex difference in the importance of physical attractiveness. Contingencies of self-worth reflect the specific traits which individuals consider most important in determining their self-esteem. Crocker et al. (2003) found that women placed a greater emphasis on physical attractiveness as a determinant of their self-esteem than did men, supporting the prediction that the sociometer system is differentially sensitive to the relative importance of determinants of mate value in each sex.

Social Status and Self-Esteem

While female mate value has been shown to be especially dependent on physical attractiveness, in a number of cultures it has been shown that male mate value is more strongly related to traits which relate to parental investment, such as social status and access to resources (Buss 1989). Thus, a mating sociometer perspective would predict that self-esteem in men should be more strongly related to their wealth and social status than is the case in women. Accordingly, in a meta-analysis of the relationship between self-esteem and socioeconomic status, Twenge and Campbell (2002) found that this relationship was strongest in middle-aged men.

Brase and Guy (2004) also inferred sex-specific links between socioeconomic status, physical attractiveness, and self-esteem in their analysis of demographic differences in relationships between mate value and self-esteem. They found that while both self-perceived mate value and self-esteem increased with age in men (at least until middle age), the opposite pattern was true for women. They suggested that this may reflect the fact that while socioeconomic status tends to increase with age, physical attractiveness decreases, and so these findings would support the existence of a mating sociometer which is attuned to sex differences in the traits most relevant to mate value.

Experimental Research

In addition to the correlational evidence reviewed above, experimental research has demonstrated sex differences in how self-esteem in males and females responds to manipulations of self-perceptions of specific components of mate value.

Pass et al. (2010) took photographs and physical measurements of participants and asked them to complete fake personality assessments. They then provided participants in manipulation conditions with false feedback that they were likely to be repeatedly rejected by potential romantic partners. Half of these participants were informed that this was due to their physical attractiveness

(attractiveness manipulation condition) while the remainder were told that it was a result of their lack of competence and status (status manipulation condition). Female participants in the attractiveness manipulation condition subsequently reported lower levels of self-esteem than women in both the status manipulation and control (no feedback) conditions. Conversely, male participants in the status manipulation condition reported lower levels of self-esteem than men in both the attractiveness manipulation and control conditions. These results support a mating sociometer perspective that self-esteem responds to individuals' perceptions of their mate value and further demonstrate sex-specific links between different components of mate value and self-esteem in men and women.

Conclusion

Correlational and experimental studies support the mating sociometer perspective by demonstrating sex differences in the determinants of self-esteem, which mirror sex differences in the importance of different components of mate value. In particular, as this perspective would predict, self-esteem in women is more sensitive to physical attractiveness, while men's self-esteem is more strongly related to their wealth and social status.

However, at present, there is little research examining how these effects interact with other variables relevant to mating relationships. For example, traits differ in their importance to mate value when considered in the context of short-versus long-term relationships, with physical attractiveness generally being emphasized in short-term relationships (e.g., Regan et al. 2000). There are also sex differences in preferences for short- versus long-term mating, with men showing a relative greater preference for short-term pairings (Schmitt et al. 2001). Accordingly, Penke and Dennisen (2009) demonstrated interactions between measures of men's short- versus long-term mating orientation and their mate value, in predicting their self-esteem. Future studies could profitably further explore similar interactive effects between mate value, mating contexts, and

self-esteem to further investigate the complexities of the mating sociometer.

Cross-References

- [Mate Value](#)
- [Self-Concept](#)
- [Self-Esteem Reflects Assessments of Valuation](#)
- [Self-Esteem Tracks Mate Value](#)
- [Self-Evaluations Track Perceived Mate Value](#)
- [Sociometer Theory](#)
- [Women's Mate Value](#)

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Sexting

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Definition

The sending of self-made sexually explicit text message, photographs, or videos through electronic media.

Introduction

Scholars have defined sexting in a variety of ways, from broad definitions that include the sending of all types of self-made sexually explicit media (Barrense-Dias et al. 2017) to more specific definitions that are limited to sending photos and videos of particular body parts. Studies also differ in the timeframe; respondents were asked to recall (e.g., 6 months vs. a year), and whether the studies were conducted among adolescents or adults. This discrepancy in methodology has resulted in muddling the accuracy of research findings (Barrense-Dias et al. 2017). For example, the prevalence of sexting defined as the sending of both sexually explicit text messages and photographs has ranged from about 1% to 30% for adolescents and as high as 57% for young adults (Klettke et al. (2014).

While sexting can take place through all types of electronic media, qualitative research finds that it most often occurs through smartphone applications, such as standard texting, Snapchat, or WhatsApp, as some people might feel that it increases their feeling of privacy and security (Van Ouytsel et al. 2017). Although sexting was originally treated by the literature as a deviant behavior, it is now increasingly viewed as a

normative part of sexual communication and expression (Barrense-Dias et al. 2017; Kosenko et al. 2017; Temple 2015).

Motives

For adolescents, sexting can be part of their sexual development and romantic relationship experimentation. Furthermore, it might provide some adolescents with an alternative means to experiment with and to develop their sexual identity (Van Ouytsel et al. 2017). For both adolescents and adults, sexting mainly takes place within the context of establishing a romantic relationship or within an already established romantic relationship, as a sign of love, in order to flirt, or as a gift or surprise to the romantic partner (Barrense-Dias et al. 2017; Englander 2015; Van Ouytsel et al. 2017). Outside of a relationship context, sexting has also been found to occur as a joke, a dare, or as a bonding ritual between friends (Lippman and Campbell 2014; Van Ouytsel et al. 2017). Because of the more distant and asynchronic nature of digital communication, it might make some users more comfortable to express their emotions and sexual desires through digital sexually explicit messages, as opposed to in-person contact (Van Ouytsel et al. 2017). Research has also found that sexting among adolescents could function as a first step towards sexual activity, as it has been found to precede and co-occur with offline forms of sexual contact (Kosenko et al. 2017; Temple and Choi 2014). Longitudinal research has shown that sexting is significantly more likely to precede offline sexual activity, but not sexual risk behavior, among adolescents. Some adolescents could use sexting to indicate their willingness to engage in offline sexual behavior or they could use it to indicate their readiness to take the relationship further (Temple and Choi 2014). Among adults, sexting has also been found as way to engage in sexual hook-ups (Dir et al. 2013).

Risks Associated with Sexting

In some cases, sexting can occur under pressure. Coerced sexting appears to occur most frequently

among (young) women, who report that they felt pressured to engage in sexting by peers, friend groups, or romantic partners (Barrense-Dias et al. 2017; Drouin et al. 2015; Lippman and Campbell 2014; Walrave et al. 2015). A study by Englander (2015) found that 70% of undergraduate college students had experienced a form of pressured or coerced sexting in the 4 years prior to the survey. This study also revealed interesting gender differences with respect to coerced sexting. Males were significantly more likely to report that they never experienced a form of pressure, whereas female students were more likely to report that they always or sometimes felt pressured when engaging in sexting (Englander 2015). Next to forms of explicit pressure and coercion, women are sometimes confronted with more implicit forms of pressure, with men insisting and repeatedly asking them to engage in sexting, making women feel obligated to engage in sexting, or arguing that they have to engage in sexting to prove their love (Drouin et al. 2015; Van Ouytsel et al. 2017).

Next to the potential for sexting messages to occur under pressure, the behavior has gained research attention related to potential reputational risks of engaging in this behavior. Leaked sexting messages could lead to reputational damage for the person who created them (Lippman and Campbell 2014; Van Ouytsel et al. 2017). Qualitative studies identified three major ways in which sexting images could be abused (Van Ouytsel et al. 2017). First, sexting images could be distributed out of revenge, after a romantic break-up. Second, victims could be blackmailed in exchange for additional sexting pictures or offline sexual acts. A third way in which sexting content could be distributed is when boys show the content in order to boast about getting these types of messages. Especially among males, sexting has been found to enhance their social status within the peer group, while a leaked sexting message could harm a girl's reputation (Van Ouytsel et al. 2017).

Conclusion

Sexting takes place through digital media in general and mobile applications in particular. While

sexting may be a normative behavior and can be used to express romantic interest and sexual intimacy, it can also be problematic when it occurs under pressure or when the sexting content is abused by others. Early scholarly research treated the act of merely sending sexting messages as a deviant act, but it is now mostly understood within the need for sexual expression and sexual development from both adolescents and adults alike.

Cross-References

- Adolescent Issues
- Anonymity of Cyberbullying
- Cyberbullying
- School Bullying
- Sexual Behavior
- Sexual Identity
- Sexual Socialization

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Sexual Abuse

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Synonyms

Childhood sexual abuse; Childhood sexual victimization; Sexual trauma

Definition

Sexual abuse (SA) is defined by the involvement of a child in sexual activity the child cannot fully comprehend, for which the child is unable to give informed consent or is not developmentally prepared, or that violates the laws or social taboos of society. Sexual aggression endured in adulthood is termed sexual assault. Perpetrators of SA may be an adult or another child who by age or developmental stage is in a relationship of

responsibility, trust, or power with the child. SA also includes the inducement or coercion of a child to engage in sexual activity or the sexual exploitation of a child (WHO 1999). In the USA, statutory rape laws assert that sexual activities with a minor under the age of consent (varies from 16 to 18) are illegal and therefore considered SA.

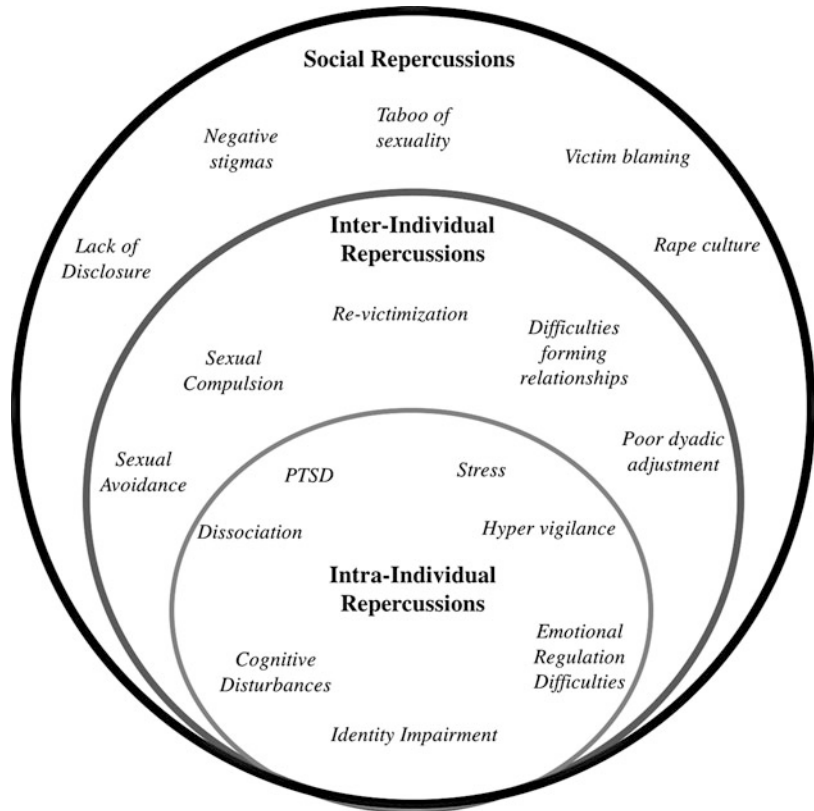
Introduction

Research and clinical work indicate that exposure to SA can result in a wide variety of immediate and long-lasting outcomes which can impair an individual's development. This entry summarizes the prevalence of SA, intraindividual and interindividual effects of SA, and the social contexts impacting effects of SA (see Fig. 1).

Prevalence

SA is an international epidemiology with average estimates of 18–20% in women and 8% in men (Barth et al. 2013). Yet, rates vary according to definitional issues the criteria used to define sexual abuse. For example, self-defined SA (i.e., subjective identification as victims) yield lower rates of SA by a ratio of at least 1:2 as compared to rates obtained using an objective definition (i.e., based on legal definition, Vaillancourt-Morel et al. 2016). Based on SA divulged to the US Child Protective Services (2016), about 63,000 children were victims of SA yearly. Yet, this incidence number reflects the tip of the iceberg as only 30% of cases of SA are reported to authorities. Different barriers may refrain disclosure including intraindividual (e.g., internalized blame), interindividual (e.g., dysfunctional family, lack social networks), and social (e.g., stigma) barriers (Collin-Vézina et al. 2015).

In the majority of cases, SA victims knew their perpetrators; 25–35% are abused by family members (including 8–20% by a parental figure), 31–60% by other known abusers, and 5–15% by strangers. The majority of SA is perpetrated by men, and SA often happens in toxic

Sexual Abuse,**Fig. 1** Three levels of repercussion

environments. Indeed, victims of SA are, on average, victims of five other forms of child maltreatment such as violence or neglect. The occurrence of multiple types of child maltreatment is associated with more severe and complex repercussions.

Intraindividual Effects

Psychological Distress: Adapting to Trauma

Victims of SA tend to report dissociation and psychological distress are about three times more likely to experience a major depressive episode and are four times more likely to experience *post-traumatic stress disorder (PTSD)* as adults than nonvictims (Dugal et al. 2016). PTSD includes four cluster of symptoms: re-experiencing (i.e., intrusive re-experiences of the SA, flashbacks or nightmares), avoidance (behavioral, cognitive, or emotional responses to avoid trauma-related distress), negative alterations in cognition and mood (e.g., inability to remember the SA, distorted

cognitions, feelings of estrangement from others), and hyperarousal (i.e., hyperactivation of the sympathetic nervous system with insomnia, irritability, hypervigilance, and a heightened startle response). Psychological distress related to SA may be persistent and cause significant impairment in social, occupational, or other important areas of functioning. Yet, those psychological responses are thought to be, not mere dysfunctional symptoms, but intrinsic mechanisms that serve important functions, such as the avoidance of suffering and the processing of SA-related thought/memories through repetitive activations, until the trauma loses its distress producing characteristics and is processed.

Neurobiological Effects: The Impact of Stress

Neurobiological models suggest that chronic stress caused by traumatic experiences such as SA affects the secretion of cortisol through the hyperactivation of the hypothalamic-pituitary-adrenal axis, which hinders the maturation and

organization of neurons during brain development (see Lupien et al. 2009). Traumas experienced in childhood are associated with hypotrophy (loss of cells) of the hippocampus, which can affect the mnemonic structures. Traumas experienced during adolescence are associated with hypotrophy of the frontal cortex, involved in higher cognitive functions such as reasoning. In addition, hypertrophy (enlargement) of the amygdala is observed in survivors. These three structures play an important role in stress sensitivity and emotional regulation. Through these neurobiological modifications, SA can lead to *stress hypersensitivity*. Therefore, new stimuli (e.g., events) may directly activate the amygdala, leading to impulsive emotional responses (e.g., fight, flight or freeze) without evaluation by the more rational brain structures (e.g., hippocampus, frontal lobe). While those responses (e.g., hypersensitivity) can be adaptive at the time of the SA by promoting survival, they become dysfunctional in the long term. In addition, trauma-related information (e.g., intense fear) tends to become deeply etched into the brain, which in turn promotes the development of PTSD symptoms such as flashbacks. Whenever the individual is confronted with events that activate memories of the SA (e.g., intimate relationships), hyperconsolidated mnemonic residues are brought back to consciousness altering the optimal functioning of the survivors and making them re-experiment the trauma or leading to impaired functioning.

Identity Impairment and Emotion Regulation

SA trauma can impact the survivor's sense of self or identity, including a loss of life goals, confusion about who one "really" is or a view of self as weak and incompetent. Childhood trauma such as SA also tend to inhibit self-awareness, since awareness in this context leads to greater contact with painful trauma-related internal states, and hypervigilance or externally focused attention, associated with survival in dangerous environments leads to sustained absence of internally directed attention. As such, SA survivors may suffer from a relative inability to access a stable sense of identity from which to interact with the external world and experience chronic feelings

of emptiness. These deficits may lead to a generalized lack of knowledge about internal states, insecure and unstable models of self, and poor self-other boundaries. In turn, reduced self-awareness may lead to difficulties in emotion regulation and reduced insight into the effects of SA. This general tendency toward lessened internal awareness and heightened external attention has been referred to as *impaired self-reference* or *other-directness* and is linked to a tendency to rely on others for information about self, including one's worth and entitlements.

Cognitive Disturbances

SA often leads to the development of dysfunctional self-schemas, which are characterized by confusion, shame, deep mistrust, aggressiveness. Besides impacts on internal models of self, survivors often develop cognitive distortions such as guilt or shame and may blame themselves for having somehow provoked or deserved their victimization in attempts to understand why the abuse happened. Such conclusions may lead to self-blame, perceptions of self as bad or unworthy, and distorted views of the perpetrator as benign or blameless, which feeds into the dysfunctional self-schemas and further reinforces them. This cycle often leads to low self-esteem, feelings of helplessness, or hopelessness, as survivors develop and strengthen trauma-based perceptions of themselves and others.

Interindividual Effects

Social and Relational Difficulties

The peculiarity of SA lies in its relational context, and difficulties in social and relational functioning are common ranging from social isolation, trust issues, and detachment from others, to highly anxious attachment, concerns over burdening others, sensitivity to signs of abandonment or betrayal, interpersonal conflicts, and arguments. SA is particularly associated with issues in forming and maintaining intimate connections in adult life, including long-term, stable, sexual-romantic relationships. Indeed, adult SA survivors tend to have difficulties forming close

relationships, have poorer dyadic adjustments, and experience more severe partner violence (Dugal et al. 2016; Godbout et al. 2017). This may occur for several reasons. Survivors who develop posttraumatic numbing may have difficulty experiencing positive attachment affects, leading to decreased experiences of love in interpersonal relationships. In some cases, survivors of SA in their family may not have had the opportunity to develop the relational skills they need to establish and maintain satisfactory intimate relationships. Commitment and intimacy may increase feelings of vulnerability and trigger unresolved issues, emotions, and cognitions associated with SA. Additionally, SA can induce fears of intimacy or vulnerability that, along with a coexisting hunger for connectedness, may lead to ambivalent, chaotic, or short-lived relationships.

Attachment and Negative Relational Schemas

SA, especially if committed by a parental figure or in the absence of support, tends to impact the attachment systems, resulting in chronic, negative expectations and perceptions of the self and others (negative relational schemas), leading to safety, trust, esteem, intimacy, and control issues. SA may also lead to a perception of one-self as unlovable, stigmatized, different, or contaminated, and a view of others as unavailable, untrustworthy, or unavailable in time of needs. These negative models of self and others, thought to reflect the effects of insecure attachment, often persist onto the long-term, producing lasting relational problems.

Revictimization

SA increases the vulnerability to experience further victimization, such as greater risk of psychological, physical, and sexual dating violence and partner violence (Hébert et al. 2017). This could be explained through the *traumagenic dynamics model* (Finkelhor and Browne 1985), where the inappropriate and traumatic development of sexuality and interpersonal relationships accompanied by a sense of shame related to SA make survivors more anxious about their sexuality and lower their self-esteem as valuable intimate partners deserving respect. This could increase their

vulnerability through expectation or tolerance of further violence in relationships or lack of ability to identify potentially dangerous situations, thus increasing their risk of revictimization. Feelings of learned helplessness could also play a part in revictimization. Indeed, survivors may believe they will always be victimized, not feel capable of escaping violent relationship, show inhibited self-protection behaviors when they face situations at risk of victimization. Similarly, the lack of emotional regulation abilities, lack of contact with inner world, and high hypervigilance associated with SA make victims less inclined to detect threats, end a violent relationship, and discriminate between false alarms and real danger, exposing them to greater risks of revictimization.

Sexuality

Sexual impacts of SA fall into two main trajectories: sexual avoidance and sexual compulsion. Sexual avoidance is characterized by sexual aversion and negative sexual attitudes and tends to lead to a wide range of sexual dysfunctions, such as orgasmic disorders. Inversely, sexual compulsion is characterized by an excessive preoccupation with sex, and a conception of sex as necessary to obtain affection. Compulsion tends to lead to sexual relations at an early age, a high number of sexual partners, risky sexual behaviors, and extra-marital relationships.

Social Context: How Culture and Society Shape SA and Its Effects

Social contexts also shape the understanding and repercussions of SA. For example, negative stigmas associated to being a victim of SA are partly promoted by what is known as *rape culture*, defined as a cultural setting in which rape is pervasive and normalized due to societal attitudes about gender and sexuality. Rape culture leads to behaviors such as victim blaming, where victims of sexual crimes are perceived as responsible for their victimization (e.g., by the way a woman dresses). Inefficient judicial responses also impact the perception of survivors that their society is failing in providing a safe and fair environment.

The taboo on sexuality may prevent survivors from disclosing and processing the sexual crime they endured. Well-tailored services available to SA survivors may make a crucial difference in their recovery, while a lack of services may maintain or worsen SA-related negative outcomes. Finally, trauma-informed practices and approaches have determinant effects for survivors. Trauma-informed approaches, grounded in the recognition of the widespread impacts of SA and potential paths for recovery, as well as the signs and symptoms of trauma in survivors, can provide appropriate, *non-retraumatizing*, responses based on scientific knowledge of SA through their policies, procedures, and practices.

Conclusion

SA is not only highly prevalent but also related to a host of durable negative repercussions which often feed into each other, creating a complex negative and dynamic web. Protective intra- and interpersonal factors (e.g., emotion regulation skills, relational support and care), and positive trauma-informed social contexts may however buffer the effects of SA and foster recovery in survivors. Furthermore, these factors may contribute to reducing revictimization and break the cycle of violence in our societies.

Cross-References

- [Ecological Factors and Rape](#)
- [Increased Cortisol](#)
- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
- [Orgasmic Disorders](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Stress Reactivity](#)

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Sexual Abuse in the Workplace

- [Sexual Harassment in the Workplace](#)

Sexual Access

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Synonyms

Mating prospects of gang members; Sexual motivations of gang members

Definition

A key motivation for men who join gangs is the prospect of increased mating opportunities; men who are members of gangs experience greater mating success, particularly gang leaders.

Introduction

As the lower-investing sex, men are capable of having many more offspring over the course of their lifetime than are women. Indeed, access to mating opportunities is a key limiting factor in men's reproductive fitness. As a result, men are willing to engage in intrasexual competition, sometimes extremely risky and violent competition, in order to increase their mating prospects. One such means of fostering access to women is joining a gang. Qualitative data suggests that this is a key motivation for men who join gangs (Wong 1982), and survey data shows that gang members, especially their leaders, do indeed experience greater mating success than non-gang members (Palmer and Tilley 1995). A more detailed evolutionary account of this phenomenon is described below.

Parental Investment and Sexual Selection

Men and women display clear evidence of distinct reproductive strategies, owing to differences in

their obligatory parental investment (Trivers 1972). Given their relatively small investment, men's reproductive fitness can be maximized by increasing their number of sexual partners. However, women have a large obligatory investment in offspring that places greater constraints on their reproductive capacity. Thus, men's ability to maximize their reproductive fitness is dependent on their sexual access to females. This engenders a high degree of intrasexual competition among men in order to gain access to women, with women expressing greater interest in long-term mates, and a high degree of discretion in selecting short-term mates.

Men may increase their appeal to women by increasing their status, prestige, and reputation. Women may be attracted to men with high status, as it indicates their ability to acquire resources that can be used to help provision shared offspring. High status may also indicate the ability to protect a woman and her offspring from predators and conspecific threats, particularly in uncertain and harsh environments (Snyder et al. 2011). Thus, even if it entails great risk, men may be predisposed to engage in behaviors that have the potential to increase their status. This provides an explanation for the tendency for men to seemingly *over-react* to challenges to their status; a violent response serves to protect their reputation (Daly and Wilson 1988).

Gang Membership and Sexual Access

Membership in gangs may serve a similar function to that of the male coalitions of humans' hunter-gatherer ancestors. Members of gangs and coalitions are often connected by kinship; they work together to protect a territory and defend their group's resources. Moreover, they may engage in offensive aggressive behavior against other groups to increase their access to resources. The tendency for gangs to be very violent and to engage in illegal activity is likely a result of the low socioeconomic status of the members and the lack of opportunities to ascend a status hierarchy using legal means. Thus, for men with few other opportunities, gang membership

may provide a means to acquire status and increase mating access.

Qualitative reports from gang members suggest that at least some of their motivation for joining gangs is the prospect of increasing one's sexual access to women (Padilla 1992). Indeed, the men who join gangs are typically between the ages of 14 and 24, when sexual drives and mating goals loom largest (Palmer and Tilley 1995). Increased sexual access to women may be used as an explicit recruitment tool by existing gangs or may be readily observed by outsiders in the community (Palmer and Tilley 1995). Sexual access may result from the increased prestige and access to resources afforded to gang members and recognized as desirable by women outside of the gang. Additionally, qualitative reports from gang members discuss having ready sexual access to female gang members (Covey et al. 1992), though female gang members are relatively rare compared to that of men.

The expectations of increased sexual access are borne out by data examining reports of gang members as compared to non-gang members (Palmer and Tilley 1995). Individuals reported on the numbers of sexual partners in the last 30 days for a study originally conducted to examine an outbreak of STDs in Colorado. On average, members of gangs reported a significantly greater number of sex partners during this time period than did non-gang members. However, this effect was driven in large part by the number of partners of the highest status members of the gang. Indeed, two gang leaders reported 10–11 sex partners in the past 30 days, a number that exceeds the number of sexual partners for most men over the course of a year.

High status within a gang may be afforded to those men willing to act in the most risky and violent means (Campbell 1993), behavior that is then rewarded by a greater number of sexual partners (Buss 2011; Palmer and Tilley 1995). These findings are reflective of a broader pattern in which high-status males are viewed as more attractive by females. For example, females find men displaying greater dominance and social presence as more attractive (Gangestad et al. 2004). A similar pattern is observed among

younger males, in which bullies that demean and hurt weaker individuals are often the recipients of greater resources (Buss 2011) and mating opportunities (Connolly et al. 2000; Volk et al. 2015).

Conclusion

The theories of parental investment and sexual selection suggest that the mating strategies of males and females differ due to men's lower parental investment which necessitates increased access to mating opportunities as an avenue to maximize their reproductive success. Therefore, men, more than women, will engage in intrasexual competition to improve their likelihood of obtaining mating opportunities. With female preferences for males of high status and access to resources, males may participate in risky behaviors such as gang involvement to compete for mates when other opportunities are limited. Research on gangs indicates male gang members have increased sexual access to women, particularly among higher-ranking leaders. Thus, men participate in dangerous activities that improve their status and, therefore, their mating prospects.

Cross-References

- [Access to Resources](#)
- [Male Coalitions for Hunting](#)
- [Reproductive Strategies](#)
- [Social Dominance and Sexual Access](#)
- [Special Case of Bonobos and Female Counter-Adaptations to Rape](#)

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Sexual Access and Friendship

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Synonyms

[Back-burner relationships](#); [Friends with benefits](#)

Definition

Sexual interaction with a person considered a friend, but not a romantic partner.

Introduction

Sexual access can come from a variety of sources as sexual interaction can involve short-term (i.e.,

no desire for an ongoing relationship) or long-term mating (i.e., sex representative of closeness and loving) goals or all points in between (Buss 1995). Although they can range from strangers to spouses, sexual partners are typically known and liked others (Perlman and Sprecher 2012). As a consequence, cross-sex friends (CSFs) seem like a natural choice to fulfill this role (among heterosexuals at least). Friends typically know each other well, have developed a close relationship, and, put simply, like one another. Friendships are characterized by warmth, closeness, and intimacy (both psychological and communicative). If friends are intimate communicatively (e.g., self-disclosing personal information on a variety of topics), then it would seem that sexual interaction should follow.

The reality of how platonic and sexual interaction mix is considerably more complicated than our simplistic view would suggest. In particular, the interplay of sexual access and friendship has changed dramatically over the past half century. The traditional view, dominant in the mid- to late-twentieth century, drew a strict boundary between friendship and sexual engagement. The dominant narrative suggested that crossing that boundary was, effectively, asking for trouble. In fact, sexual interaction was typically described as being inconsistent with the very notion of friendship. In the past few decades, that stigma has eroded (or at the very least, shifted). Friends are engaging in sexual interaction in a variety of contexts and under multiple labels. As a consequence, the primary goal of this entry is to review contrasting literatures from the past 50 years as it relates to sexual interaction between friends.

Twentieth-Century Views on Sexual Access and Friendship

For much of the twentieth century, dominant social narratives depicted sex as almost exclusively linked to love and romantic relationships. The dominant script on college campuses throughout 1950s and early 1960s was “abstinence” as sex was considered inappropriate outside of marriage (Reiss 1967), particularly for women. Traditional views of sex created a double standard where women were

(and still are) encouraged not to be too sexually active, as it may lead to negative labels of promiscuity, ultimately hindering their chances of securing a long-term mate (Bogle 2008). Given the sexual revolution of the late 1960s and beyond, the dominant sexual norm on college campuses shifted such that sexual interaction was considered appropriate in both marriage and intimate premarital relationships (i.e., representing a relational orientation; Sprecher 1989). Although a recreational orientation (i.e., sex outside a close intimate romantic relationship) also became more popular during these years, it was derailed somewhat by the AIDS crisis of the 1980s such that it remained less prominent than the relational orientation (Sprecher 1989).

Social norms in the mid-to-late twentieth century suggested, “love and sex are fused together in the ideology of romance” (Werking 1997, p. 29). For both men and women, marriage was the desired relational goal and represented the standard against which all other relationship forms were compared. As relationships developed (from dating to courtship to engagement or cohabitation), partners’ behavior more closely approximated that which occurs in marriage. For example, the sexual script suggested that development of psychological and communicative intimacy between partners would match sexual intimacy. In short, as partners’ relationship became closer (i.e., more closely resembled marriage), the intimacy of their sexual interaction would increase to match (Bailey 1989; Werking 1997).

Given the link between relational development and sexual intimacy, partners’ sexual interaction was thought to generate several important relational changes. For example, sex involved passion, attraction, and consummation such that it represents and motivates a joining of selves (both physically and psychologically). Thus, sexual interaction erodes, and eventually eliminates, boundaries between partners. Moreover, as romantic and sexual relationships become more intimate, partners become progressively more interdependent, relying increasingly upon each other for sexual and personal interactions. Thus, sex in romantic relationships can create feelings of possessiveness and jealousy toward others considered potential romantic threats.

For much of the twentieth century, the egalitarian and open bonds that characterize friendships were considered different (even antithetical) to those that join romantic partners. For example, friendships are relationships among equals, whereas romantic relationships were seen as reflecting society’s patriarchal bias (reflected, e.g., in the sexual double standard). What is more, friendships were generally considered “attraction of the spirit” (Werking 1997, p. 30). Finally, friendship is not typically considered exclusive, as participants are free to form outside friendships, romantic relationships, and work relationships.

Sexual interaction between friends was considered problematic at best (and abhorrent at worst) because it complicated their open bonds. Sexual interaction was thought to create changes that were diametrically opposed to the very nature of friendship. Sex effectively obliterates boundaries between partners and creates a desire for union and merging that generate possessiveness and jealousy. Friendships, on the other hand, are built upon a respect for partners’ separateness and an ability of either friend to engage in other relationships.

Although sex in friendships was seen in very negative terms, some positives were thought to come from this sexual attraction. In fact, physical and sexual attractions are both relatively common motivations for forming CSFs. For instance, participants found romantic attention from a friend to be validating of their attractiveness and added a certain “zing” to the relationship (Werking 1997). Sexual interaction, however, was considered best left implicit. Indeed relatively few friends explicitly discussed the issues related to attraction, sexual desire, or the state of their relationship (Baxter and Wilmot 1985). Although there are positive aspects to (implicit) physical and sexual attraction in CSF, actually acting upon those feelings was strongly and consistently frowned upon.

For the better part of the twentieth century, scholars assumed that sexual interaction between friends was both rare and taboo. At the turn of the millennium, however, several studies challenged that claim. For example, reports indicated that a fairly large proportion of college students (e.g., between 49% and 62%) have engaged in sexual

behavior with an otherwise platonic friend (Afifi and Faulkner 2000; Reeder 2000). Afifi and Faulkner (2000) probed this percentage of college students and uncovered that over half of them engaged in sexual activity with their friend more than once. Moreover, these authors found that nearly 60% of CSFs who engaged in sexual experimentation eventually transitioned into a romantic relationship. Attraction in CSFs comes in many different forms, such as romantic, objective sexual (attractive in general, but not to me), subjective sexual (attractive to me), and platonic (Reeder 2000). This is important because, as noted in the same study, subjective attraction in friendships leads to quicker relational deterioration of friendship.

Perhaps because of the perils that CSFs encounter in the face of sexual attraction (Bailey 1989), the recent flurry of scholarship indicates that removing love and romantic overtones from sexual interactions creates a new way of *doing* CSFs. The emergence of *hookup culture* (Bogle 2008) and *friends-with-benefits relationships* (e.g., Mongeau et al. 2013) allows friendships to exist on a fluid spectrum, rather than being categorized as sexual or nonsexual. Thus we now turn to the literature that accounts for the twenty-first-century perspective on sex within friendships.

Modern Views on Sexual Access and Friendship

In the past two decades, scholarship suggests that (even though dating, courtship, and marriage still occur) multiple forms of nonexclusive, but sexual, relationships are becoming increasingly normative (Afifi and Faulkner 2000; Bogle 2008; Mongeau et al. 2013). Indeed, whereas it was once common to wait between 9 and 22 weeks to engage in a first act of sexual intercourse (Perlman and Sprecher 2012), couples (including CSFs) are now having sex with minimal (or perhaps no) prior interaction (Bogle 2008). The prevalence of sex in early interactions has rewritten the social script of friendships, as well as for romantic partners. This section, then, discusses two unique

ways that modern friendships intertwine with sexual interaction: *friends-with-benefits relationships* and *back-burner relationships*. Both of these relationships come with a unique form of sexual access. Moreover, we offer an evolutionary explanation for the persistence of each of these relationships.

Friends-With-Benefits Relationships

The interplay of sexual access and friendship is seen most clearly in the notion of a friends-with-benefits relationship (FWBR). Working from the lay definition of a relationship that comes with *no strings attached*, friends with benefits were initially defined as friends who engage in repeated episodes of sexual interaction without the expectation of romantic motivation and/or escalation (Hughes et al. 2005). The no-strings-attached notion suggested that the sexual aspect of an FWBR does not restrict partners' ability to interact (communicatively or sexually) with other individuals. In short, FWBR partners are not supposed to hinder one another's extradyadic interaction in any way.

Given initial definitions as friends who have sex on multiple occasions with no strings attached, early research assumed that all instances of FWBRs were all pretty much the same. After closely reviewing a decade of research, Mongeau et al. (2013) painted a more complex picture. Some FWBR partners tend to shun romantic motivations, while other partners embrace romantic involvement. Some FWBR partners were indeed friends or even prior romantic partners, whereas others were strangers or nodding acquaintances. Based on their alternative reading of the literature, Mongeau et al. (2013) claimed that friends with benefits come in multiple forms that vary in relational and sexual characteristics. Specifically, they described seven types of friends-with-benefits relationships that range from close friends who engage in intercourse (i.e., *true friends*), to couples who meet exclusively to having sex (i.e., *just sex*), and to mutual *sexual fail-safe* with overlapping social networks (i.e., *network opportunism*). What is more, Mongeau and colleagues

reported that FWBRs can lead to romantic relationships (three types of *transition in*: successful, accidental, and failed) or stem from one (*transition out*).

Perhaps the growing popularity of friends with benefits among emerging adults (i.e., individuals aged 18–25) is related to simultaneously enjoying increased independence and desiring sexual experimentation (Teachman 2003). In some ways, the norms and expectations from earlier generations remain in the friends-with-benefits realm. For example, in friends with benefits, the sexual double standard (where recreational sex was seen as positive for men but negative for women) emerges, though in a different form. Repeated casual sex is considered as a performance of status for men and as a desire for relational commitment for women (Impett and Peplau 2003). Despite potential conflicting motivations, it does appear that both men and women prefer to have repeated sex with a trusted friend (Epstein et al. 2009) as opposed to a stranger (i.e., a hookup; Bogle 2008).

The FWBR phenomenon presents a unique set of communicative, relational, and sexual challenges. For example, relationship talk (e.g., *labeling* or rule setting) is typically seen as threatening and something to be avoided in FWBR (Knight 2014). In some ways, this finding parallels the twentieth-century notion that explicit talk about, or performance of, sex in friendships as taboo and damaging. Unlike romantic relationships, however, FWBRs are thought to be so simple that they do not require explicit relationship talk and should, instead, emerge organically. This lack of communication manifests in a number of unique ways in FWBRs. For example, it appears as though the inherent friendship at the center of FWBRs stifles safe-sex practices (Vanderdrift et al. 2012). Still, the growing frequency of FWBRs among young adults implies that these are not major hurdles en route to engaging in this form of relationship. Indeed, FWB partners appear to value their friendships more than they do the sexual benefits that they entail (Lehmiller et al. 2011).

There is also considerable variability between the ways that men and women experience FWBRs.

Consistent with work on dating (e.g., Mongeau et al. 2004), men and women espouse different goals in FWBRs. Not surprisingly, men are more motivated by sexual factors (i.e., desire and report more sex) than are women (Green and Morman 2011), whereas women are more motivated by emotional connection than men (Lehmiller et al. 2011). Moreover, increased sexual contact appears to mitigate depressive symptoms in males, while increasing such symptoms in women (Grello et al. 2006). This suggests that FWBRs are healthier for men than women. Such a conclusion is in line with evolutionary theories that posit men prefer short-term sexual relationships to women's long-term commitment goals (Buss and Schmitt 1993).

Friends-with-benefits relationships can be used as a bridge between platonic friendships and romantic relationships (Owen and Fincham 2012). Such a path, however, needs to be agreed upon by both FWB partners, as feelings of constraint tend to lead to negative relationship appraisals, as well as psychological distress (Owen and Fincham 2011). What is more, mutual relationship agreement may be tricky given the proscription against explicit relational talk. For example, FWBRs vary in their degrees of expressed sexual and romantic desire (Mongeau et al. 2013). As a result, partners often differ in whether and how they enact relational maintenance behaviors (Guerrero and Chavez 2005), including the escalation (or de-escalation) of a relationship. Of course, the nature and meaning associated with such behaviors are contingent upon the goals that each partner has for their relationship.

Finally, FWBRs (in one form or another) are generally considered to be an example of *casual sex*. Although the overriding assumption considering FWBRs is a lack of exclusivity, FWBR types experience varying sexual motivations. As a consequence, it may be that one or both partners engage in an FWBR so they can engage in sexual interactions with multiple partners (Hughes et al. 2005) while at the same time maintaining a close emotional connection with a trusted friend (Epstein et al. 2009). Another way that people in FWBRs may balance these competing desires is through the use of *back-burner* relationships, to be discussed below.

Back-Burner Relationships

A *back burner* can be defined as a person “with whom one is not presently committed, that he or she maintains some degree of communication with, in order to keep or establish the possibility of future romantic and/or sexual involvement” (Dibble et al. 2015, p. 330). In other words, back-burner relationships are backup plans for individuals who are in some way removed from the person in question or already in an alternative relationship. Back-burner relationship appears to be more common than FWBRs, as Dibble et al. report that between 66% and 92% of college students have experienced at least one. One important difference between back burners and FWBRs is the importance that is placed on communication. Although FWBRs are marked by their lack of direct relationship talk (Knight 2014), back-burner relationships revolve entirely around communication, especially mediated communication. For example, computer-based technologies (such as texting, Facebook, and Skype) are commonly used to maintain contact with back burners (Dibble and Drouin 2014).

Another interesting aspect of back-burner relationships is that some partners are unaware that they have been placed on the back burner – primarily due to the abundance of online communication in maintaining such relationships (Dibble and Drouin 2014). As online communication is integral to developing and maintaining friendships (Subrahmanyam and Greenfield 2008) and a breeding ground for various forms of deception (Caspi and Gorsky 2006; Hancock 2007), sexual desire in a back-burner relationship can be disguised as platonic interest and friendship. Similarly, back burners can be hidden from one’s current romantic/sexual partner(s) and vice versa. Thus, back burners allow for the potential for sexual interaction *through* the maintenance of friendship.

Individuals may enter FWBRs and/or back-burner relationships for similar reasons. It may be that people engage in FWBRs to facilitate intimate contact with their back burners. Buss (1995) explains the importance of maintaining multiple potential sexual partners, especially for men. So, too, people may choose to engage in multiple FWBRs and back-burner relationships

in order to establish a larger pool of potential romantic and/or sexual partners. What is more, relationships with low levels of involvement (such as back burners and some FWBR types) carry lower levels of physical, emotional, and psychological expectations (Buunk et al. 2002). This lack of expectations may be why people tend to cast such wide back-burner *nets* – an average of 32 partners per person (Dibble et al. 2015). This strategy tends to oppose other online methods of sexual communication, which are often individually centered (Drouin 2015).

Conclusion

The interplay of friendships and sexual access (and the research literature investigating them) has changed significantly over the past 50 years or so. Whereas sex between friends was once considered fulsome, the notion of friendship has evolved to include the potential for sexual interaction. In addition, sex is now initiated much earlier in relationships than in decades past. Thus, the window for sexual access vis-à-vis friendships has expanded considerably. The role of sex has shifted from an act that consummates a close relationship to one that serves to investigate romantic potential. Future work may document further evolutions of sex in friendships as sexual intimacy becomes more normative in a wider variety of contexts and between a wider variety of partners.

Cross-References

- [Casual sex](#)
- [Drugs and Rape on College Campuses](#)
- [Friends With Benefits](#)
- [Friendship](#)
- [Hookup Culture](#)

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Sexual Access as Benefit of Victory in War

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Synonyms

Females as the spoils of war; Sexual access as the reason for going to war; Sexual access during warfare

Definition

Warfare, defined as lethal coalitional violence, is a human universal and may be partially explained as a result of evolved psychological mechanisms in males for increased sexual access to females.

Introduction

J. M. G. van der Dennen described how, at the Fifth Annual Meeting of the Human Behavior and Evolution Society (1993), Leda Cosmides posed the question “Why would anyone be so stupid as to initiate a war?” and then provided the answer: “To get women” (quoted in van der Dennen 1995, p. 327). Although this answer is often rejected out of hand by most social scientists, and modern scholars of war rarely consider sexual access as a motive for warfare, the notion that coalitional violence is waged by men to gain sexual access to women is far from new. Descriptions of success in war leading to increased sexual access to women are found in both ancient texts and ethnographic accounts of people living throughout the world. Such descriptions are so common that Vallacher and Brooks (2014) list “battles for dominance and mating opportunities” among those causes of war that are “self-evident and do not

warrant detailed consideration” (p. 191). Given that increased sexual access to females can potentially increase the reproductive success of males, the hypothesis that sexual access to females is an *evolutionary* reason for the existence of coalitional violence is also not new. van der Dennen (1995) points out that “similar and comparable theories about the influence of sexual competition on the evolution of male behavior have been put forth by Alexander, Borgia, Manson & Wrangham, van den Berghe, Symons, Tiger, E. O. Wilson, Chagnon, and Low” (p. 327; see also Van Vugt 2012; Daly and Wilson 1988; Keeley 1996; Wrangham and Peterson 1996; Tooby and Cosmides 1988). This paper explores some of the evidence relevant to establishing the exact role increased sexual access to women may have played in the evolution of male coalitional violence.

Adaptation vs By-Product Hypotheses on Male Coalitional Violence and Sexual Access

The role increased sexual access to women played in the evolution of male coalitional violence is not settled by the mere fact that males who were successful in male coalitional violence sometimes gained increased sexual access to females. The evolutionary question is whether or not the increased reproductive success sometimes resulting from participating in coalitional violence caused natural selection to favor males who engaged in coalitional violence over those who did not. If this was the case, coalitional violence (and/or one or more of the various evolved mechanisms contributing to coalitional violence) could be considered *adaptations*, whose *function* was an increase in reproductive success through increased sexual access to females (see ► “*Adaptation*” and ► “*By-Product*”). The mere existence of coalitional violence leading to increased sexual access to females would not constitute such evidence because coalitional violence could exist even if it itself was not favored by natural

selection. If this was the case, coalitional violence would be a by-product, or side effect, of mechanisms selected for other purposes. For example, evolved mechanisms for *individual* violence could sometimes be combined with mechanisms for creating cooperative social relationships and lead to coalitional violence. Then, mechanisms designed by natural selection for sexual behavior in low-cost contexts other than coalitional violence could produce the sexual behavior that sometimes occurs in the low-cost contexts following success in coalitional violence.

There are also several reasons why attempts to calculate if the reproductive benefits of male coalitional violence exceed the costs of male coalitional violence are not necessarily definitive in determining if male coalitional violence is an adaptation or by-product. First, as van der Dennen (1995, p. 331) points out, calculating the costs and benefits in modern wars is of little use because “it is almost certainly true that past correlations between a warrior’s behavior and reproductive success no longer hold.” Further, even demonstrating that the potentially high costs of male coalitional violence, ranging from the obvious complete termination of reproductive opportunities as a result of death to disfigurement and to health costs associated with exposure to pathogens, would *usually* outweigh the benefits of such acts in ancestral environments (i.e., the environment of evolutionary adaptedness or EEA) is not conclusive. This is because such evidence does not rule out the possibility that selection favored engaging in male coalitional violence precisely under those limited circumstances when the benefits of the act outweigh the costs. As Van Hoof (1990, p. 50) points out, “if gaining an additional wife, or even additional copulations, is possible, and the risk of dying in any given encounter/skirmish is low, then it could make [evolutionary] sense to go to war” (see Tooby and Cosmides 1988; see also Navarrete and McDonald 2014; Camilleri 2012). Indeed, the best reason for favoring the adaptation hypothesis over the by-product hypothesis would be evidence of design in the form of coalitional violence accomplishing the proposed function with more efficiency, precision, and complexity than could be expected by chance alone.

To help determine if increased sexual access can be considered the function of coalitional violence, examination of evidence related to the following predictions will be integral. The better the evidence fits each of these predictions, the stronger the case is made that increased sexual access to women is the function of male coalitional violence.

Prediction One: Coalitional Violence Has Been Ancient and Widespread

Fry (2009, p. 4) insists “*warfare is not ancient*” (italics in original). If this proclamation is accepted at face value, the hypothesis that increased sexual access to females was the evolutionary function of war (and/or the mechanisms producing war) is falsified. This is because natural selection is a relatively slow process that could not have designed humans to engage in coalitional violence if such violence was restricted to merely the last few centuries or even millennia. There are, however, numerous reasons for not accepting Fry’s proclamation on face value.

The first indication that war is ancient is that although many aspects of modern warfare are neither ancient nor universal, lethal coalitional violence is present in every corner of the globe and has been throughout human history. Thus, if war is defined as lethal coalitional violence, “war, then, is universal” (Gat 2006, p. 9). Further, cultural anthropologists have found coalitional violence to occur among foragers and other societies living in ways that most closely resemble the social environments of our ancestors. Although there is considerable controversy over this evidence, much of which is fueled by mistaken notions that evolutionary explanations imply a form of genetic determinism (see “[Conclusion](#)”), there is evidence of at least sporadic male coalitional violence in foragers in general, and “the anthropological literature on war offers many examples of chronically hostile intergroup relations among hunter-gatherers” (Schaller and Neuberg 2008, p. 404; see also Wrangham and Peterson 1996).

There is also evidence indicating that the universality of coalitional violence has existed for

many generations. For example, “Mythologies abound in recitals of wars and the superhuman deeds of warriors, and in them war holds the chief interest in life” (Gat 2006, p. 1; Scalise Sugiyama 2014). There is also archaeological evidence of coalitional violence (Keeley 1996, 2014; Schaller and Neuberg 2008; LeBlanc 2014), including evidence of Neanderthal violence (Liddle et al. 2012).

Although lethal coalitional violence could have evolved in only one species, the adaptation hypothesis is strengthened by evidence that such violence has also evolved in other species (Wrangham 1999). Evidence of coalitional violence in our nearest living relatives is also consistent with the hypothesis that it existed long enough in our own lineage to have been subject to natural selection. Liddle et al. (2012) also point out that “Some degree of violence has been observed in virtually every known animal population, and the majority of this violence exists in the context of resource competition with one sought-after resource being access to mates” (p. 7). Liddle et al. (2012) also write, “The coalitional violence observed among male chimpanzees is especially noteworthy in that it most closely resembles human warlike behaviors” (p. 8; see also Schaller and Neuberg 2008). Thus, the evidence indicates that coalitional violence was frequent enough over a sufficient span of time that it may have been subject to natural selection, but further evidence of design is required before concluding that the function of such violence was increased sexual access to women.

Prediction Two: Coalitional Violence Will Be Perpetrated by Males

The hypothesis that the function of male coalitional violence is increased sexual access to females obviously generates the prediction that the frequent and ancient forms of coalitional violence have been perpetrated, almost exclusively, by males. In regard to ethnographic evidence, despite the existence of relatively rare participation by females (Keeley 1996), this prediction is met because “Engaging in war, ... is

almost exclusively a male enterprise ...” (Liddle et al. 2012, p. 15; see also Daly and Wilson 1988; Wrangham and Peterson 1996; Navarrete and McDonald 2014, p. 99). The archaeological evidence also supports the conclusion that “... men are both the primary participants and victims of lethal aggression (Keeley 1996)” (Lambert 2012, p. 325). The same pattern is observed in our closest living relatives: “Among the primate species most closely related to human beings, intergroup hostilities involve males more than females” (Schaller and Neuberg 2008, pp. 403–404). A review of aggressive behavior in primate species also suggests that male aggression is strongly linked to intrasexual mating competition (Wrangham and Peterson 1996; Lambert 2012, p. 325).

Further evidence of design might be found in the form of evidence supporting predictions about which men would be most likely to engage in coalitional violence. The adaptation hypothesis predicts that young males around the age of peak competition for mates will be the most likely to engage in coalitional violence. This tendency has been given the name “the young male syndrome” (Wilson and Daly 1985; Daly and Wilson 1988). It is possible to generate even more precise predictions because “While the need for reproductive opportunities would be present among most young males, some males would be more successful in gaining these through warfare” (Petersen 2012, p. 123). This might be true especially for physically strong and aggressive males. This is because, as Petersen (2012) explains, “Ancestral hunter/gatherer bands would most likely not contain more than a dozen adult males and, hence, the fighting ability of each and every individual male would have influenced the probability that the group as a whole prevailed” (p. 124). Consistent with this prediction, but far from conclusive, Petersen (2012) reports that “physical strength shapes modern attitudes about war: stronger males are more supportive of using war as a means of solving international disputes” (p. 124). Petersen points out that this is consistent with previous studies that found “... countries with many young males are particularly likely to engage in deadly warfare” (Petersen 2012, p. 123).

Prediction Three: Male Coalitional Violence Increases Sexual Access to Women

There is no question that success at male coalitional violence sometimes increases sexual access to women, but the question is whether or not male coalitional violence leads to sexual access with a frequency, efficiency, and precision that indicates design by natural selection. Answering this question is complicated by the fact that male coalitional violence may have led to increased sexual access to females in two fundamentally different ways, and one, both, or neither of these may show evidence of design by natural selection. These two forms of access are sometimes divided into those involving “out-group” females, where males gain sexual access to the females associated with the defeated enemy, and those involving “in-group” females, where the wealth and/or status gained by victorious males leads to them being chosen as sexual partners by their own “in-group” females. Such simplistic group concepts are problematic in many ways, and thus it would be more accurate to classify the forms of sexual access resulting from male coalitional violence into the categories of “direct” and “indirect.” Direct forms of sexual access involve a male gaining sexual access without female choice being involved. These forms would include such things as rape, wife capture, forced prostitution, and sexual slavery. Indirect forms of sexual access are those in which female choice is involved and include females choosing males who are successful at coalitional violence as long- or short-term mates. van der Dennen (1995, p. 330) makes this distinction between direct and indirect sexual access when writing “The benefits of warfare to males in preindustrial societies include increased direct access to reproductive females, and increased material resources . . .” (p. 330) which could then be used to indirectly gain sexual access by making the male more likely to be chosen by females. Konner (2015) also distinguishes between the direct and indirect forms of sexual access when describing both the seizing and rape of “women left behind by . . . fallen enemies” and how “war can bring the

reputation and spoils that enable a man to marry back home” (p. 169). Similarly, Navarrete and McDonald (2014) describe how “... the winners of such conflicts may be rewarded with additional territorial and food resources, increased status, and direct acquisition of females from the defeated group” (p. 103; see also Gat 2006; Wrangham and Peterson 1996; Tooby and Cosmides 1988; Konner 2015). Liddle et al. (2012) ask the question: “how does violence translate into mating opportunities?” (p. 11). Their answer reveals that the distinction between direct and indirect sexual access corresponds to the two forms of sexual selection: “It seems that both intrasexual competition and intersexual selection play important roles, in that intrasexual competition between men is often directly related to status or reputation, and women preferentially choose partners of high status, . . .” (p. 11).

There are also various other forms of evidence that human males may be designed to efficiently exploit sexual opportunities following success in male coalitional competition, but it is not clear whether these are designed for direct or indirect access. Testosterone levels are known to increase in athletes after a win and even in a political candidates’ supporters after their candidate has won (see ► “[Dominance, Testosterone, and Cortisol](#)”). Navarrete and McDonald (2014) point out that in a previous study, men were also found to be “more likely to endorse statements supporting war after they had been primed with attractive members of the opposite sex” (p. 104).

It is important to note that both the direct and indirect hypotheses generate predictions about potential female adaptations. The direct access hypothesis generates the prediction that females have evolved various mechanisms to deal with being captured by enemy men. The indirect hypothesis generates the prediction that females have evolved to be sexually attracted to males who are successful in coalitional violence. A focus on female adaptations, combined with the often blurry distinction between the direct and indirect forms of sexual access, draws attention to an important point. While useful, the application of the direct and indirect categories of sexual violence to specific instances of male

coalitional violence must carefully consider the context of a mating to make sure that an act that might appear to be the result of female choice might actually be an example of "... women's need to behave adaptively in the presence of aggressive males, not women's attraction to dominant men" (Graziano et al. 1997, p. 148). With this in mind, examining the evidence that either or both of these forms of access show evidence of design will provide potential support for the premise that sexual access is a primary function of warfare.

Direct Access

There is no doubt that rape has been an all too common aspect of both modern wars and acts of male coalitional violence in band and tribal societies (for overviews see Chagnon 1997; Thornhill and Palmer 2000). Further, Gottschall (2004) points out that "The promise of sexual access to outgroup women has often been identified by anthropologists, ethnographers, and native informants... as a primary instigator of conflict in prestate societies" (Gottschall 2004, p. 130, and sources therein). Similarly, Konner (2015) writes, "Slaughtering men to get their wives and daughters was routine in ancient war, and women were one main reason for war" (p. 163). Also consistent with this hypothesis is the fact that male coalitional violence is often undertaken to prevent other males from gaining sexual access to females (Van Hoof 1990). There is also evidence that this access could have resulted in reproductive success. Camilleri (2012, p. 175) points out that "Recent evidence suggests that pregnancy is just as likely, if not more likely, to result from rape than from consensual sex..."

The frequency of occurrence of direct sexual access and the evidence that it could lead to reproduction are both consistent with the adaptation hypothesis, but they do not in themselves provide definitive evidence of design. Another possible source of such evidence is the specific and precise instructions sometimes given to male soldiers and warriors that appear to maximize the reproductive efficiency of male coalitional violence. For example, Konner (2015) quotes the following from Numbers 31: "Now therefore kill every male

among the little ones, and kill every woman that hath known man by lying with him. But all the women children, that have not known a man by lying with him, keep alive for yourselves" (p. 164). Lerner (1986) also writes, "There is overwhelming historical evidence for the preponderance of the practice of killing or mutilating male prisoners and for the large-scale enslavement and rape of female prisoners" (p. 81).

While such evidence is supportive of the adaptation hypothesis, there are still reasons for considering it not to be definitive. First, there are examples where such precision and efficiency are not found. Keeley (2014) points out that "Indeed, the capture of women, especially young women, is a common but non universal feature of warfare among the non-state societies known to ethnography and has been documented among several prehistoric people" (p.29; see also Keeley 1996). However, Keeley (2014) also points out that "ethnology, history and archaeology document many instances in which nubile women were not kidnapped, either because they were killed along with everyone else or because they were left alive with all survivors" (p. 29). It could also be argued that instructions to keep young female captives alive while killing the other captives imply that the acts of direct sexual access might not occur as efficiently without the instructions, although it is perhaps more plausible to see the instructions as fine-tuning a tendency that would already be present. There are also examples of efforts trying to prevent rape during war, including establishing rules against raping, including the Geneva Convention IV. However, it could be argued that such rules imply the tendency to engage in such acts if they are not prohibited and punished. Also inconsistent with the adaptation hypothesis are the sexual acts during war that cannot lead to reproduction. While it is common knowledge that the majority of sexual assaults are committed by males against females, the reverse does occur and must be accounted for. Complicating the evaluation of the direct access hypothesis even further is the problem of accurately accessing the frequency of rape during war as it is often unreported and even denied.

The frequent reluctance of women and girls to report rape in some circumstances brings up the argument made by Navarrete and McDonald (2014) that, whether or not male coalitional violence is an adaptation, there is evidence that both the male coalitional violence and the accompanying direct sexual access (e.g., rape) “have occurred often enough throughout history to have been an important selection pressure on the psychology of human *females*” (p. 107; emphasis in original; see also Thornhill and Palmer 2000). Scalise Sugiyama (2014) explains this is because “Results suggest that lethal raiding has recurrently imposed fitness costs on women, and that female cognitive design bears reexamination in terms of the motivational and decision-making mechanisms that may have evolved in response to them” (p. 476). Liddle et al. (2012) point out that these adaptations may include not only means of rape avoidance but also decision-making mechanisms to facilitate the “assimilation of females from the defeated group” (pp.8–9).

Indirect Access

It is also possible that indirect sexual access to women is the function, or one of the functions, of male coalitional violence. For example, Campbell (2005) points out that usually “Contemporary men are not directly fighting *about* women . . . Rather, they are fighting for status in relation to other men because in ancestral times this would have translated to increased reproductive success” (p. 634). LeBlanc (2014) points out that, far from this indirect access being limited to only modern societies, in many societies “Warriorhood is a prime avenue to prestige among young men” (p. 88). Similarly, Konner (2015) points out that not only do wars often lead to the capture of women, they also often lead to the attainment of “the means to acquire women-bridewealth to present to a woman’s family” (p. 160). Further, Konner (2015) emphasizes that “every successful warrior who didn’t get killed or maimed was also acquiring something else: reputation” (p. 160). Sometimes the reputation attained through warfare is formalized as a rite of passage: “In many primitive societies, for example, a male was not entitled to full status as a man until he

distinguished himself in warfare, usually by killing an enemy” (Turney-High 1971, p. 161). Further, Camilleri (2012) points out that “Male warriors in traditional societies have higher status, more sexual partners, and more children. . . , suggesting a direct reproductive benefit” (p. 294; Wrangham and Peterson 1996). Despite the overwhelming and varied types of evidence that men often gain status through success in male coalitional violence, there has been great controversy over this topic, largely because of the mistaken notion that it leads to the conclusion that war is the result of some form of genetic determinism that makes such violence inevitable (see “Conclusion”).

Other possible sources of evidence for design related to the indirect sexual access hypothesis are potential female adaptations concerning mate choice. Van Vugt (2012) discusses evidence that “military men have greater sex appeal, especially if they have shown bravery in combat” (p. 224). At the very least, it appears safe to conclude that Westermarck was correct in observing that women “instructively prefer strong and brave men to feeble and cowardly ones. History of Human Marriage cf.” (quoted in Gat 2006, p. 101; see also Scalise Sugiyama 2014).

Conclusion

The available evidence indicates that human male coalitional violence has been relatively frequent, widespread, and ancient. It also appears that such violence frequently led to forms of increased sexual access to females that probably increased the inclusive fitness of the males who were successful in male coalitional violence. Thus, there is no currently available evidence that falsifies the hypothesis that male coalitional violence in humans is an adaptation and that at least one of the functions of such violence was increased sexual access to females. More specifically, the available evidence is consistent with both the hypotheses that natural selection favored males who gained direct sexual access to women through male coalitional violence and males who gained indirect sexual access to women resulting

from the enhanced status and reputation gained through success at male coalitional violence. However, further investigation of both of these hypotheses is still required to provide definitive evidence of adaptations designed by natural selection and the exact characteristics of these adaptations.

Several forms of future research may shed further light on if, and how, humans are designed to engage in, and respond to, male coalitional violence. Further evidence of design for the direct access hypothesis may be found in ethnographic, historical, archaeological, and cross-species studies of the prevalence of female captives being treated differently than male captives. Currently, there are examples where the treatment of female captives meets the predictions of the direct access adaptation hypothesis, but also examples that do not. Further studies of the relationship between male sexual arousal and outcomes of coalitional violence, especially in contrast to male individual violence, could help to evaluate the direct access hypothesis. These studies should be informed by further studies on potential human female adaptations to deal with such situations. The indirect access hypothesis can be further evaluated by future research on how human males respond to success and failure in male coalitional violence, as well as how they respond to cowardice and non-participation by both themselves and others. Even greater insights may be gained by more research on how male participation, or nonparticipation, in coalitional violence influences female choice of long-term and short-term sexual partners.

The successful undertaking of such studies, and the accurate interpretation of their results, will require the avoidance of several of the misunderstandings that still plague research on areas of human behavior, such as violence and sex, strongly tied to moral judgments and political ideologies. The first misunderstanding that must be avoided is the mistake of equating evolutionary explanations with genetic determinism. Not only do evolutionary explanations address the ultimate level of causation of living things, while the influence of genes is part of the proximate level of causation, but all traits (behavioral and otherwise) of phenotypes are the result of a complex

interaction between genes and numerous environmental factors ($G + E = P$). Although the complexity of these interactions continues to be discovered, it has been known for over half a century that when it comes to identifying the interaction of the genetic and environmental factors in the proximate causation of any trait of any living thing, even trying to argue that one is more important than the other is fallacious to the point of being ridiculous (Thornhill and Palmer 2000). Understanding that no trait is determined solely by genes is crucial because when genes are thought to determine behavior, attempts to change behavior through modifications in the environment are seen as doomed to failure. Thus, an evolutionary approach becomes wrongly equated with acceptance of current levels of such acts as coalitional violence and rape.

The second misunderstanding that must be avoided is the naturalistic fallacy. This is the fallacy of drawing the conclusion that an explanation of a behavior *implies* a moral or ethical judgment of a behavior as good or bad or that an explanation *has* to influence a moral judgment. Of course, an individual is free to make the naturalistic fallacy even after they have been told it is a fallacy. That is, an individual is free to include an explanation when formulating a judgment or even use an explanation as the sole reason for their moral judgment. The naturalistic fallacy just means it is a fallacy to hold that an explanation *must* be part of a moral judgment. Wilson et al. (2003) object to this conception of the naturalistic fallacy by arguing that a person can derive a moral judgment from an explanation *if* an ethical premise is added to the explanation. This is a false objection because there is no logical necessity to include the “if” statement (e.g., evolutionary explanation) among the factors contributing to an ethical judgment. Thus, the Wilson et al. (2003) argument is merely that someone *can* include an explanation of a behavior in their ethical judgment of that behavior *if* they choose to do so. This obvious point is irrelevant to the naturalistic fallacy, because the naturalistic fallacy only refers to the fact that no one is logically *obligated* to include an explanation of a behavior in their moral judgment of a behavior. This point is crucial because the

Wilson et al. argument may encourage people to think there is a logical reason that they have to base their moral judgments of a behavior *at least partially* on the evolutionary explanation of that behavior. Such views may retard efforts to increase knowledge about the evolutionary causes of behaviors like rape and male coalitional violence. This may in turn hinder attempts to decrease the occurrence of such behaviors.

Cross-References

- [Adaptation](#)
- [Aggression for Sexual Access](#)
- [By-Product](#)
- [Condition-Dependent Mating Tactic](#)
- [Conditions Required for Evolution of Warfare Adaptations](#)
- [Costly Signaling](#)
- [Dominance, Testosterone, and Cortisol](#)
- [Evolved Psychology of Warfare](#)
- [Female-Perpetrated Violence](#)
- [Naturalistic Fallacy, The](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)

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Sexual Access as the Reason For going to War

- [Sexual Access as Benefit of Victory in War](#)

Sexual Access During Warfare

- [Sexual Access as Benefit of Victory in War](#)

Sexual Access Manipulation

- [Manipulation by Others](#)
- [Men with Poor Mating Prospects](#)

Sexual Access Manipulations

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Synonyms

[Mating psychology manipulation](#)

Definition

Sexual access manipulations in the context of suicide terrorism occur when terror organizations promise metaphysical sexual rewards as a deceptive form of reciprocal altruism or when the sociocultural environment triggers intrasexual competitive behaviors.

Introduction

Some theorists contend that sexual access manipulations provide an evolutionary explanation for suicide terrorism (Kanazawa 2007). Though sexual access manipulations are evidenced in the rhetoric of some political organizations that recruit potential combatants for suicide terror missions (e.g., Al Qaeda, Hamas, Hezbollah), the empirical evidence that sexual access manipulations are the sole motivation to undertake these missions is specious.

Sexual Reward in the Afterlife

When evolutionary theorists discuss sexual access manipulations in relation to suicide terrorism, they are typically referencing promises of sexual rewards in the afterlife (i.e., “72 virgins”). This promise of sexual reward, though deceptive, relies on mechanisms for reciprocal altruism wherein one agent assists in increasing the fitness of

another agent at an initial cost to himself or herself on the assumption that he or she will be repaid in kind at a future time (Trivers 1971). However, Qirko (2009) noted that the religious teaching that martyrs will be rewarded 72 virgins in the afterlife has been played up and exoticized by Western media outlets. Nevertheless, supporters of certain Islamic terror organizations by all accounts appear to sincerely believe in and promote the teaching that martyrs will be awarded sexual access in death.

Intrasexual Competition

A second potential form of sexual access manipulation is the veneration of suicide terrorists as martyrs by local communities. In humans, male reproductive success is tied to social status (Smith 2004), and the promise of glorification through martyrdom could theoretically act on mechanisms that evolved to motivate males to achieve status through intrasexual competition. In species with intrasexual selection, risk-taking through combat improves reproductive success (Wilson and Daly 1985). A review of the literature indicates that one of the major motivations for suicide terrorism is the attainment of a higher status through the vehicles of religious zeal and the belief that such a sacrifice furthers the cause of the wider society. Kruglanski et al. (2009) stated that the sociocultural climate of suicide terrorism often includes: "...[an] ideology whereby a suicide attack is portrayed as an act of heroic sacrifice... lending one's existence and demise an aura of supreme glory (p. 337)."

Limitations of Sexual Access Manipulation Models

There is mixed empirical evidence to support the sexual access manipulation model as an evolutionary explanation for suicide terrorism. In support of the model, belief in the attainment of rewards in the afterlife is amongst the top three motivations for suicide attack among Palestinian

combatants (Hafez 2006). Secondly, the vast majority of suicide terrorists are males in their early to mid-twenties according to. This age and sex bracket is associated with peak risk-taking behavior – a trait associated with status attainment and high reproductive success (Wilson and Daly 1985). Furthermore, the families and communities of suicide attackers often celebrate them as martyrs in death (Hafez 2006). On the other hand, there is no evidence that suicide terrorists have significantly lower status than the populations from which they come in terms of income and education (Berrebi 2003). Though most suicide attackers are young, unmarried men, there is no evidence to suggest that these males are more likely to remain unmarried in later life (Lawson, Jordan, and Magid 2008). Finally, sexual access manipulations in the context of suicide terrorism must entail a self-deception concerning death such that it does not activate cheating detection (Qirko 2009). Though belief in an afterlife is common among humans, the influence of afterlife beliefs in reciprocal exchange is a feature of the model that remains to be tested.

Conclusion

In conclusion, sexual access manipulations appear to factor into the motivation for suicide terrorism. However, the evidence that sexual access manipulations alone can explain willful self-sacrifice in this context is insufficient. Particularly problematic is data suggesting that suicide attackers otherwise, in fact, have access to mates.

Cross-References

- ▶ [Benefits to Kin](#)
- ▶ [Kinship Psychology Manipulations](#)
- ▶ [Men with Poor Mating Prospects](#)
- ▶ [Monetary](#)
- ▶ [Reputation](#)
- ▶ [Suicide as Kin-Directed Altruism](#)
- ▶ [Suicide Terrorism](#)
- ▶ [Unemployed](#)

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- [Sexual Conflict in Mating Strategies](#)
- [Violence as Coercive Control](#)

Sexual and Reproductive Development

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Synonyms

[Fitness](#); [Parenting](#); [Puberty](#); [Reproductive strategy](#)

Definition

An evolutionary biological perspective on the effects of the environment on multiple psychological, behavioral, and even somatic features of children's development challenges much thinking about human sexual, behavioral, and reproductive development. Rather than treating some environmental conditions and their effects on sex and reproduction as “good” and others as “bad,” it cast such phenomenon in terms of the contextual regulation of reproductive strategies in the service of fitness enhancement.

Sexual Activities

- [Sexual Outcomes](#)

Sexual Aggression

- [Aggression for Sexual Access](#)
- [Ecological Factors and Rape](#)
- [Female Age as a Predictor of Men's Aggression Against Women](#)
- [Sexual Coercion and Rape](#)
- [Sexual Coercion and Violence](#)
- [Sexual Coercion as a Mechanism of Sexual Selection](#)

Introduction

Most research designed to advance understanding of how developmental experiences influence human development is based on a mental-health perspective which presumes that certain environmental influences and developmental outcomes are good (e.g., sensitive parenting/secure attachment) and others bad (e.g., harsh parenting/aggression). A reproductive-strategy perspective, based as it is on life-history theory – an evolutionary-biological approach to development – conceptualizes developmental processes and products rather differently. What are typically

regarded as manifestations of “nonoptimal” development (e.g., insecure attachment, aggression, risk-taking, early sexual debut), evolutionary-minded thinkers cast as alternative tactics for enhancing reproductive fitness under the ecological conditions that give rise to them. An evolutionary perspective is thus appreciative of the benefits of putatively problematic functioning, not just the costs. Life-history-informed research on modern human development, initiated some quarter century ago, has made significant contributions to the field, though many issues merit additional attention.

In the Beginning

More than three decades ago, anthropologists Pat Draper and Henry Harpending reconceptualized how father absence affects psychological and behavioral development. Rejecting traditional psychoanalytic theory and even more contemporary psychological thinking as to why father absence “adversely” affects children’s development, Draper and Harpending (1982) recast such effects in reproductive-fitness terms.

According to Draper and Harpending (1982) father-absent girls develop psychologies and behavior – that is, a “reproductive strategy” – consistent with the expectation that paternal investment in childrearing will not be forthcoming and that pair bonds will not be enduring; this leads them to behave in sexually promiscuous ways. In contrast, girls who grow up in homes in which fathers are present develop to anticipate the opposite – that men can be counted on as partners and parents. In consequence, they defer sexual activity once they reach biological maturity while seeking to establish and maintain enduring, close, heterosexual relationships.

Beyond Father Absence

What was unique to Draper and Harpending’s (1982) argument was the casting of early experience influences within the family in evolutionary terms emphasizing reproductive fitness, parental investment, pair bonds, and, thereby, reproductive strategy (i.e., not mental health). Indeed, their ground-breaking paper stimulated a somewhat-delayed cascade of theoretical developments and

empirical studies on the role of childhood experience in shaping reproductive strategy. Belsky et al. (1991) were the first to build on Draper and Harpending’s (1982) seminal contribution, appreciating that two things were missing from the latter’s analysis: an explanation as to *how* father absence shapes adolescent and adult functioning and an original prediction that would distinguish an evolutionary-developmental – or evo-devo – perspective from more widely embraced ones. In other words, there was reason to wonder whether the introduction of reproductive-strategy thinking into the study of human development represented anything more than old wine in a new bottle.

Considered reflection on this matter led Belsky and associates (1991) to advance an evolutionary theory of socialization linking childhood experience, interpersonal orientation, and reproductive strategy, one that expanded the scope of thinking about environmental influences well beyond father absence. It has come to be known as “psychosocial acceleration theory,” although it is expressly about the regulation – not just acceleration – of psychological, behavioral, sexual, and reproductive development by a variety of contextual conditions and developmental processes.

Central to the theory, based as it was on more general life-history thinking, was the claim that multiple stressful and supportive extrafamilial environmental factors (e.g., poverty) influence family dynamics, most especially parent-child and marital/pair-bond relations. These in turn shape children’s emotional and behavioral development in the first 5–7 years of life, including attachment security, and, thereby, subsequent social development, including sexual/mating behavior, pair bonding, and parenting. In line with Draper and Harpending (1982), Belsky et al. (1991) argued that this complex and environmentally sensitive developmental system – and thus a suite of interrelated phenotypes – evolved as a means of fitting the organism to its anticipated future environment in order to enhance reproductive fitness (i.e., not mental health) – or at least did so in the ancestral environments in which human development evolved.

Central to psychosocial acceleration theory was the view that parent-child processes and, in

particular, attachment security/insecurity mediated the influence of stressors and supports external to the parent-child relationship, such as family economic situation and marital processes, on (a) the child's general trustful-mistrustful outlook on the world, (b) his/her opportunistic-exploitative versus mutually beneficial orientation toward others, and (c) his/her behavior. But what critically distinguished this theory from all others addressing family and other influences on human development, including the thinking of Draper and Harpending (1982), was its prediction regarding environmental influence on rate-of-development. Specifically, developmental experiences and psychological orientations regulate reproductive development by affecting *the timing of puberty* and, thereby, a cascade of processes involving sexual behavior, pair bonding, and parenting.

Thus, accelerated development eventuating in a fast, quantity-oriented reproductive strategy was most likely to emerge in the context of a variety of stressors, including inadequate financial resources and marital discord, which would undermine parental well-being, thereby giving rise to harsh, rejecting, insensitive, and/or inconsistent parenting; such developmental experiences and environmental exposures would then foster in the child an insecure attachment, a mistrustful internal working model, and an opportunistic, advantage-taking interpersonal orientation. And these developments would stimulate earlier pubertal maturation, a younger sexual debut and, eventually, short-term and unstable pair bonds and limited parental investment as individuals sought to bear more children but not care for them intensively. The alternative, slower, quality-oriented developmental trajectory would emerge in response to a supportive rearing environment, characterized by spousal harmony and adequate financial resources. Such intrafamilial conditions, shaped as they would be by extrafamilial ones, would provide the basis for sensitive, supportive, responsive, and positively affectionate styles of mothering and fathering and, thereby, secure attachments, a trusting internal working model and a reciprocally rewarding interpersonal orientation. Collectively, these developments would

delay pubertal maturation and defer the onset of sexual activity, eventually fostering enduring pair bonds and greater parental investment in fewer offspring.

The underlying bio-logic on which psychosocial-acceleration theory was based was consistent with more general life-history thinking. Under conditions of adversity which convey that the world is – and is likely to remain – a risky place and the future is precarious, organisms should accelerate development to insure that they reproduce before succumbing to the undermining effects of their developmental circumstances, including compromised well-being and/or an early death. Whereas the latter would make reproduction impossible, the former could compromise mate value and thus one's ability to bear and raise robust progeny capable of doing the same. In contrast, under supportive conditions, the organism should grow slowly and become reproductively mature later in life so as to incorporate and thus embody the multiple resources to which it would be exposed, be those nutritional, psychological, or behavioral. As a result, the individual would be a more healthy and attractive mate, as well as someone with the skills to take good care of its offspring. Thus, whereas the fast developer might require, or at least once would have, four children to generate, eventually, two grandchildren, this could be accomplished by the slow developer with fewer offspring and ones cared for in a more nurturing manner.

Testing the Puberty Prediction

In a thoughtful critique published alongside the original presentation of psychosocial acceleration theory, Maccoby (1991) argued that it fit males more than females. Empirical evidence reveals just the opposite, however (Belsky 2012). Not only does research indicate that the general lack of prediction of pubertal timing in males is not just a function of measurement challenges (Belsky et al. 2007), but new thinking suggests that female reproductive strategies are more sensitive to familial and ecological conditions, whereas male strategies are more sensitive to peer experiences (Del Giudice et al. 2011; James et al. 2012). Thus, the remaining focus of this contribution is

principally on female reproductive strategies given Belsky et al.'s (1991) original theory-distinguishing puberty prediction. Recent, nonpuberty-oriented, male-specific extensions of the theory, grounded in sexual selection theory and emphasizing the influence of peers, have been advanced and subject to empirical scrutiny (Del Giudice 2009; James et al. 2012).

A comprehensive review of the evidence related to the puberty prediction led Ellis (2004, pp. 935–936) to conclude that “empirical research has provided reasonable, though incomplete” support for Belsky et al.'s (1991) original theorizing. Upon observing the existence of “converging evidence... that greater parent-child warmth and cohesion is (sic) associated with later pubertal development” in females, he insightfully noted that “the proposed accelerating effect of parent-child conflict and coercion on pubertal development is yet to be clearly established.” Subsequent research, including by Ellis himself, has altered the evidentiary landscape. Ellis and Essex (2007) reported that a composite index of family non-supportiveness during the preschool years – which included measures of authoritarian parenting and negative family relationships – was associated with females' advanced adrenarcheal status at age seven and more mature secondary sex characteristics in 5th grade. Additional Ellis research revealed that family disruption and, especially, father's social deviance – considered to be an index of problematic father-daughter relationships – forecast earlier age of menarche (Tither and Ellis 2008). Relatedly, Costello and associates (2007) discovered that maltreated girls reached pubertal maturity 8 months earlier than non-maltreated girls. Belsky and associates (2007, 2010) extended such longitudinal work. Not only did they observe that early maternal harshness predict earlier menarche but, that via this effect, it indirectly fostered greater sexual risk taking in adolescence. Finally, Pesonen and associates (2008) observed, upon taking advantage of a natural experiment, that young Helsinki girls evacuated from their homeland during World War II and sent to live elsewhere reached menarche at a younger age; notably, they also bore more children by late adulthood than members of the

same birth cohort who remained at home, thereby avoiding the trauma of separation from their families.

However noteworthy these (and other) findings, it is imperative to highlight the fact that the accelerating effect of rearing on pubertal timing proves to be modest, in the range of 2–8 months (Ellis 2004). But, critically, this does not preclude the functional importance of such seemingly modest change in sexual maturation given Ellis's (2004, p. 936) insightful observation that “the time from menarche until 50% of (menstrual) cycles are ovulatory is approximately 1 year if menarche occurs before age 12 and 4.5 years if menarcheal age is 13 or older.” To be appreciated as well is that it is certainly possible that female pubertal timing was far more plastic before its dramatic decline over the past 150 years in the Western world and, consequently, far more susceptible to rearing effects (Belsky et al. 1991).

Genetics, Gene-Environment Interaction, and Differential Susceptibility

It is well established that pubertal timing is substantially heritable. This raises the possibility that the rearing effects under consideration are an artifact of genes shared by parents and daughters. Yet when Rowe (2000, p. 165) directly tested this proposition using a genetically informative design, he acknowledged that “the behavioral genetic view gave no knock out punches.” Moreover, even if Mendle and associates (2006) observed – using a children-of-twins' design that controlled for genetic inheritance through the maternal line – that step-father effects on pubertal timing were most likely, even if not certainly, genetically mediated, Tither and Ellis's (2008) work – which relied on a sibling design that controlled for maternal- and paternal-genetic and family influences in their research on biological father – provided support for just the opposite conclusions.

Instead of pitting genetic and environmental effects against one another, as so many are still inclined to do, it appears more productive to adopt the life-history view that there can be *alternative* and *conditional* reproductive strategies (Belsky 2000), with the former more and the latter less

susceptible to contextual regulation. Notably consistent with this differential-susceptibility-to-environmental-influence perspective (Ellis et al. 2011a) are results from three recent studies showing that both an estrogen-receptor gene (Hartman et al. 2015; Manuck et al. 2011) and physiological reactivity (Ellis et al. 2011) can be used to distinguish females whose pubertal development – and perhaps reproductive strategy more generally – is more and less regulated by rearing experiences.

The Distinctive Influence of the Father

Whereas Belsky et al. (1991) purposefully cast the net wider than father absence when it came to delineating developmental experiences and environmental exposures that regulate the development of reproductive strategies – by highlighting the *quality* of parent-child and marital relations and extrafamilial determinants of these – others embrace Draper and Harpending's (1982) original formulation emphasizing fathers' influence: "girls detect and internally encode information *specifically* about the quality of *paternal* investment. . . as a basis of calibrating. . . the timing of pubertal maturation and certain types of sexual behavior" (Ellis 2004, p. 938, emphasis added).

Even if it is the case that some research implicates the influence of fathers on female pubertal development (e.g., Ellis and Essex 2007) and risky sexual behavior (Ellis et al. 2012), it seems notable that Belsky et al. (2007) failed to chronicle any paternal influence on pubertal development – while documenting maternal influence. What is needed ultimately are more studies like Ellis et al. (1999) examining the (unique) effects of one parent while discounting the effects of the other. Needless to say, such research is challenging to undertake given the difficulty in obtaining the involvement of or information on absent fathers and men whose parental investment is especially limited.

Conceptualizing the Environment

Recall that psychosocial acceleration theory highlighted stressful and supportive rearing environments, broadly conceived, arguing that under contextual conditions of risk and uncertainty there

was an inherent bio-logic to accelerating reproductive development. Although Belsky et al. (1991) appreciated that costs associated with accelerated development represented trade-offs geared toward reducing the risk of dying before reaching reproductive age, it was Chisholm (1999) who called especial attention to local mortality rates. These, he argued, were especially informative cues that natural selection had shaped humans to monitor in order to more accurately forecast the future and regulate reproductive development. Certainly consistent with this claim is evidence linking more dangerous rearing environments and shorter life expectancy with younger age of first birth (e.g., Giskevicius et al. 2011; Nettle et al. 2011). What remains unknown, however, is whether these factors relate to pubertal timing or whether pubertal timing mediates effects of these on reproductive functioning.

In an effort to advance thinking about important features of the environment that regulate the development of life histories, Ellis and associates (2009) undertook a cross-species analysis of existing evidence. In so doing, they extended prevailing psychological models of how stress and support shape human development. These evolutionary-minded developmentalists specifically called attention to extrinsic (or uncontrollable) morbidity-mortality (i.e., environmental harshness) and environmental unpredictability (i.e., extent to which conditions fluctuate across individual lifespan). Under harsh environmental conditions, the risk is of dying before reaching reproductive age, thereby making it bio-logical to develop faster, mature earlier, and initiate sexual activity sooner rather than later. Because of challenges to predicting the future under unpredictable environmental conditions, efforts to mitigate risk are less likely to pay off in terms of enhancing reproductive fitness than might otherwise be the case. Parental investment should thus be less than it otherwise would be, thereby stimulating faster offspring development. Although this new framework has yet to inform pubertal-timing research, recent inquiry underscores its utility in forecasting faster life-history strategies in adolescence (Belsky et al. 2012) and young adulthood (Simpson et al. 2012; see also

Nettle et al. 2011). Future work should not only focus on pubertal timing but test this formulation of critical environmental parameters that regulate reproductive strategies against alternative ones.

Further thinking about the influence of environmental unpredictability on human life history led Frankenhuis and Panchanathan (2011) to offer a novel prediction regarding developmental plasticity and, thereby, the development of reproductive strategies: The time before an individual “commits” to a particular developmental pathway should vary depending on the stability of cues that are reproductively informative. When such cues are stable, they provide a seemingly reliable basis for predicting the future; thus, developmental commitment to a conditional adaptive strategy should be made earlier rather than later in life. When such cues prove less reliable, however, the organism should maintain a more “open mind,” deferring developmental commitment to one or another (conditional) reproductive strategy.

Mechanisms of Influence

Upon first advancing psychosocial acceleration theory, Belsky et al. (1991) highlighted the role that the child’s attachment security played in conveying information about risk and uncertainty from the extrafamilial world through the parent-child relationship to the child. Given a great deal of research showing that diverse contextual sources of stress and support influence parenting, longitudinal evidence linking insecure infant-mother attachment at age 15 months with earlier age of menarche (Belsky et al. 2010) becomes especially noteworthy. After all, it is supportive of the view that attachment is one mechanism by which what occurs both in and outside the family becomes “biologically embedded” and regulates reproductive development.

While psychosocial acceleration theory emphasized the first 5–7 years of life as a sensitive period for the contextual regulation of reproductive strategy, Del Giudice (2009) drew on sexual selection theory to highlight the middle-childhood years, contending that this is a period during which the nascent reproductive strategies established in early childhood can be maintained or revised. Of critical importance were peer relations and intrasexual competition, processes, in

fact, that appear to mediate effects of environmental context on reproductive strategies (James et al. 2012). Indeed, the period when the adrenal glands mature and sexual feelings first become evident – adrenarche – is regarded as a “juvenile transition” and “developmental switch point.” One consequence, Del Giudice (2009) theorizes, is the emergence of sex differences in insecure attachments.

Beyond attachment, Chisholm (1999) called attention to time preference as another important psychological mechanism influenced by developmental experiences that regulates and perhaps even characterizes reproductive strategy. From a theoretical standpoint, individuals who grow up in highly risky and uncertain environments should discount the future, preferring smaller payoffs in the present over larger ones later on. Here, of course, payoff refers to the likelihood of reproducing. The fact that children growing up in more economically, socially, and psychologically disadvantaged families have a more difficult time than others waiting to secure a more attractive reward and are more inclined to settle for a lesser one sooner (e.g., Evans and English 2002) would seem consistent with Chisholm’s claim. It remains to be determined, however, whether time preference itself relates to pubertal development or links rearing experience with reproductive functioning.

When it comes to physiological rather than psychological mechanisms of influence, elegant animal work reveals an entire epigenetic and developmental cascade that is strikingly consistent with Belsky et al.’s (1991) original theorizing. Indeed, Cameron and associates (2005) acknowledged just this in reviewing their experimental research showing that that maternal licking and grooming of newborn rat pups, itself influenced by stressful versus supportive contextual conditions, regulates gene expression and, thereby, stress reactivity, rate of sexual maturation, sexual behavior, and eventual parenting.

Conclusion

Although many social and behavioral scientists continue to regard certain psychological,

behavioral, physiological, and somatic developments as “optimal” – including deferring sexual debut, being faithful to a partner, and caring intensively for one’s children – an evolutionary-biological perspective casts many of these and their opposites as alternative means to the same reproductive-fitness-enhancing end. Different developmental processes reflect, ultimately, different strategies that fit different ecological circumstances. This view, of course, stimulated an original theory-distinguishing prediction regarding pubertal timing, one that has garnered a good deal of empirical support. Moreover, it has encouraged further theory development highlighting (a) the critical importance of harshness and unpredictability as core regulatory dimensions of the environment, (b) adrenarche as an important juvenile switch point, and (c) the fact that individuals likely vary in their developmental susceptibility to contextual regulation. Entertaining these new issues simultaneously raises a host of new questions and avenues for inquiry. Consider just the following: Are some individuals susceptible to harshness and/or unpredictability only early in life? Are others susceptible to one or both only later in life? And are some susceptible to both early and later, with still others susceptible to neither across the lifespan? To the extent that these questions get answered in the affirmative, it would go a long way toward explaining why field studies document environmental effects less powerful than traditional socialization theory has long presumed.

Cross-References

- Adaptation
- Adaptation and Natural Selection
- Adaptive Plasticity
- Adolescent Issues
- All Psychology Is Evolutionary Psychology
- Attachment Theory
- Bruce J. Ellis
- Children Without Paternal Investment
- Competition for Parental Investment
- Conditional Strategies
- Cultural Variation
- Daniel Nettle
- Development of Adaptations
- Early Childhood and Adolescence
- Ecology of Paternal Investment
- Effects of Attachment Quality and Organization
- Environmental Harshness
- Environmental Harshness/Mortality
- Environmental Influences
- Environmental Risk
- Familial Violence
- Father Absence and Stress Reactivity
- Function of Reproductive Strategy (Kurzban)
- Harsh Environments
- History of Attachment Theory
- Human Behavioral Ecology
- Jay Belsky
- John Bowlby and Attachment Theory
- Life History Strategies
- Life History Theory
- Menarche
- Offspring–Parent Attachment
- Organized-Insecure Attachment
- Pair-Bonding
- Parent Influences
- Parental Investment
- Paternal Investment
- Peer Relationships in Childhood
- Psychology
- Puberty
- Puberty in Boys
- Puberty in Girls
- Reproduction
- Reproductive Strategies
- Reproductive Strategy
- Reproductive Timing
- Risky Behavior

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Sexual Antagonism

- [Intralocus Sexual Conflict](#)
- [Intralocus Sexual Conflict Across the Genome](#)

Sexual Antagonistic Co-evolution

- [Sexually Antagonistic Hypothesis](#)

Sexual Antagonistic Selection

- [Sexually Antagonistic Hypothesis](#)

Sexual Arousal

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Synonyms

[Genital arousal](#); [Sexual response](#); [Subjective arousal](#)

Definition

An emotional state triggered by internal (e.g., fantasy) and/or external (e.g., visual) sexual cues, consisting of interacting components including physiological (particularly genital) changes and subjective experience (Chivers 2005).

Introduction

Sexual arousal is one of several components of the human sexual response cycle. It is characterized by changes in physiology and/or subjective experience, though these facets may not always coincide with each other (Chivers et al. 2010; Janssen 2011; see below). Physiological changes resulting from activation of the sympathetic nervous system include pupil dilation, increased heart rate, and increased respiration rate; these changes, however, are not unique to sexual arousal, therefore researchers focus physiological measurements of sexual arousal on genital changes associated with vasocongestion (Chivers et al. 2013). *Subjective sexual arousal* refers to one's emotional experience of sexual arousal and involves the integration of physiological and psychological responses (Chivers 2005). There is often considerable overlap between subjective sexual arousal and *sexual desire*, a motivational state that directs behavior (reviewed in Janssen 2011); however, most research has, to date, focused on sexual arousal. Common sexual arousal methodologies are outlined below, along with men's and women's sexual arousal patterns.

Measuring Sexual Arousal: Genital Responses

Physiological sexual arousal in both men and women involves changes in *genital vasocongestion*, in which the genital tissues swell because of increased blood flow to the genital region. Genital vasocongestion leads to penile erection in men and engorgement of vulvar, vaginal, and clitoral epithelium and subsequently vaginal lubrication in women. Genital temperature also increases as a result of genital vasocongestion. Thus, the majority of research on physiological sexual arousal involves assessing genital vasocongestion or outcomes related to genital vasocongestion, such as increased genital temperature or vaginal lubrication (reviewed in Chivers et al. 2013). Because genital responses tend to be relatively difficult for participants to alter (whether consciously or not), genital responses are often viewed as a more

objective measure of sexual arousal compared with self-report.

The most commonly used measure of men's genital vasocongestion is the *penile plethysmograph*, which assesses erectile responses. *Circumferential plethysmography* assesses changes in penile circumference. In circumferential plethysmography, a man places either a thin rubber band or metal cuff on the midshaft of his penis; these devices measure mm of change in penile circumference. *Volumetric plethysmography* involves a glass cylinder placed over a man's penis (by a researcher); the cylinder is attached to a pressure transducer, which detects changes in air displacement as a measure of penile volume (reviewed in Chivers et al. 2013).

Women's genital vasocongestion is most commonly assessed using a *vaginal photoplethysmograph*. The vaginal photoplethysmograph is a clear, tampon-shaped probe that contains a light source and light detector. A woman inserts the probe into her vagina; the light within the probe illuminates the vaginal wall and the blood circulating within it, and the amount of back-scattered light detected is an indirect measure of vasocongestion, because the degree to which light reflects varies relative to the amount of blood in the vaginal tissue. The vaginal photoplethysmograph assesses two aspects of vaginal vasocongestion, however, only one of these is specific to sexual stimuli: *Vaginal pulse amplitude* (VPA) is an indicator of dynamic changes in vasocongestion with each heartbeat, with higher amplitudes (measured in mV) indicating greater arousal. Other less commonly used measures for assessing women's genital vasocongestion include the *clitoral photoplethysmograph* (for assessing changes in clitoral bulb blood volume), the *labial photoplethysmograph* (for assessing changes in vasocongestion in the labia minora), and laser Doppler imaging (to assess changes in cutaneous vulvar blood flow; reviewed in Chivers et al. 2013).

Thermographic measures assess changes in genital temperature that result from increased genital blood flow. They include *thermal imaging cameras* used to detect/record changes in the skin's electrochemical energy and *thermistors* or

small temperature gauges that attach to the penis or labia. Participants attach thermistors to their genitals and researchers position thermal imaging cameras for participants. Thermographic measures may be used with both women and men.

Measuring Sexual Arousal: Subjective Sexual Arousal

Subjective sexual arousal typically refers to one's overall feelings of sexual arousal (e.g., "How sexually aroused/turned on do you feel?"), though participants may be asked to report on their perception of their genital sensations (e.g., "Do you feel warmth in your genitals?"; reviewed in Chivers et al. 2010). These aspects of subjective sexual arousal are positively correlated, suggesting that overall feelings of sexual arousal and perception of genital sensations are strongly linked; the extent to which one is influenced by the other is currently unknown (Chivers et al. 2010). Participants may be asked to report their subjective sexual arousal using *discrete* and/or *continuous* responses. *Discrete* responses are given once or repeatedly at different intervals; they are usually given after a stimulus presentation, however, providing pre- and post-stimulus responses allows for assessing change in sexual arousal associated with a sexual stimulus. *Continuous* responses require participants to rate their subjective sexual arousal throughout a stimulus presentation. Participants may respond to questions about their sexual arousal using a variety of methods; the most common methods used today include using a computer keypad to enter discrete responses or move a bar that represents one's arousal, moving a lever or computer mouse with visual or haptic feedback, and verbal reports.

Sexual Arousal Patterns

It may seem intuitive that the physiological and psychological aspects of sexual arousal should occur in a relatively coordinated fashion, with genital responses coinciding with feelings of sexual arousal and perceptions of genital sensations.

Likewise, one might expect both aspects of sexual arousal to occur when one encounters stimuli that match one's sexual interests. Using several of the measures described above, researchers have found that these expected patterns are not always present and highlight the importance of assessing both physiological and subjective aspects of sexual arousal.

Sexual concordance refers to the relationship between genital and subjective sexual arousal (Chivers et al. 2010). On average, there is a consistent gender difference in sexual concordance, with men exhibiting a strong and positive relationship between their genital and subjective sexual arousal (Pearson's $r = 0.66$; Chivers et al. 2010); men may, however, exhibit genital responses in the absence of feelings of sexual arousal and vice versa (reviewed in Janssen 2011). Women's sexual concordance tends to be positive (on average, Pearson's $r = 0.26$; Chivers et al. 2010) and lower than that of men's. Women's sexual concordance tends to be stronger when thermographic measures are used, relative to when vaginal photoplethysmography is used. The relationship between genital and subjective sexual arousal is also more variable in women, regardless of the genital response measured – some women show a strong positive correlation, others show little to no correlation, and some even show a negative relationship (reviewed in Suschinsky et al. 2016).

A related gender difference involves the degree to which genital and subjective sexual responses correspond with self-reported sexual attractions and interests. Men's genital and subjective sexual responses are *category-specific*, meaning that men's sexual responses coincide with their preferred sexual stimulus categories for gender, activities, and age (reviewed in Chivers 2005). Women's subjective responses tend to be category-specific, such that they match with their self-reported sexual interests. Women's genital responses are not always limited to sexual stimuli that match their preferred sexual partners' gender or preferred sexual activities (reviewed in Chivers et al. 2013); women, unlike men, even exhibit significant genital responses to nonpreferred sexual activities and nonhuman sexual stimuli

(reviewed in Chivers et al. 2013). Recent research suggests that *gynephilic women* (i.e., sexually attracted to women) exhibit genital and subjective responses that correspond with their preferred gender, but that exclusively *androphilic women* (i.e., sexually attracted to men only) do not (reviewed in Chivers 2016).

It is unclear why the differences in sexual concordance and category-specificity exist. The differences are unlikely the result of poor measurement – variation in women's sexual concordance is seen across measures of both internal and external genital responses (reviewed in Suschinsky et al. 2016), and the gender difference is not affected by methodological factors such as stimulus characteristics (e.g., male- vs. female-orientated erotica), sample characteristics (e.g., age of the sample), and statistical factors (e.g., type of correlation calculated; Chivers et al. 2010). Likewise, recent research using thermographic measures of genital responses (which allow better cross-sex comparisons than penile plethysmography and vaginal photoplethysmography; Chivers et al. 2013) and other non-genital measures of sexual interest (e.g., viewing time; Chivers et al. 2013; Chivers 2016) reveal a gender difference in specificity of sexual response.

Gender differences in sexual arousal patterns may reflect evolved traits. For example, given the substantial threat of unwanted sex over the course of human evolutionary history, there would have been strong selection pressure on women to either avoid unwanted sex or minimize its costs. The *preparation hypothesis* suggests that any sexual stimulus elicits an automatic genital response (increased vaginal vasocongestion), which then leads to vaginal lubrication to protect women via pain reduction and/or minimizing injury. Currently, there is mixed evidence to support this hypothesis (reviewed in Chivers 2016).

Women's lower sexual concordance may stem from selection pressures, as well. Sexual arousal influences decision-making (e.g., Skakoon-Sparling et al. 2016), potentially leading women to make poor decisions related to potential mates and sexual activities (Suschinsky et al. 2016; Suschinsky et al. 2009). Gender differences in

potential reproductive rates (i.e., the number of offspring an individual can produce, based on the minimum investment required to procreate) have resulted in different sexual strategies for women and men. Women should be more selective regarding their sexual partners to yield a few high quality offspring; men should be less selective and increase the quantity of sexual partners to ensure multiple offspring. Thus, selection may have favored women with lower sexual concordance to facilitate better mate-related decisions in women. High sexual concordance may have been favored in men, to the extent that both feelings of sexual arousal and a physiological response are required for sexual intercourse in men; the subjective feelings of sexual arousal may motivate interest in sexual activity, and a corresponding penile erection is required for penetration (reviewed in Chivers et al. 2010). Further research is required to test this hypothesis.

Conclusion

Sexual arousal is a complex, multifaceted response, and researchers assess multiple aspects of sexual arousal in laboratory settings. Although genital responses are considered to be more objective than self-reports of sexual arousal, physiological responses do not always correspond with subjective feelings of sexual arousal in both women and men. Thus, it is important to consider both physiological and subjective responses for a comprehensive understanding of sexual arousal.

Cross-References

- [Adaptation](#)
- [Evolution of Genitalia, The](#)
- [Female Counter-Adaptations to Rape](#)
- [Forced Copulation](#)
- [Individual Differences](#)
- [Partner Rape](#)
- [Reproductive Strategy](#)
- [Sex Differences](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Sexual Coercion](#)

- [Sexual Fantasy](#)
- [Sexual Orientation and Human Sexuality](#)
- [Sexuality](#)
- [Victims of Violence](#)

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Sexual Assault

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Sexual Assault and Intimate Partner Violence

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Synonyms

Domestic violence; Interpersonal aggression;
Mate retention; Rape; Sexual abuse; Sexual
coercion

Definitions

Rape can be defined as “copulation resisted” by a victim “unless such resistance would probably result in death or serious injury to the victim or in death or injury to individuals the victim commonly protects.” *Sexual assault* can also include “oral or anal penetration of a man or woman” (Thornhill and Palmer 2000). We use the term *sexual coercion* (SC) broadly to mean the use of force, intimidation, lying, or psychoactive substances to receive or perform sexual acts involving another individual without that individual’s consent and sometimes without their knowledge or explicit awareness of that act (Gladden et al. 2008). *Intimate partner violence* (IPV) is a broad term including acts of stalking as well as physical abuse and violence, psychological abuse, and sexual abuse and/or violence directed toward a romantic or sexual partner (Centers for Disease Control 2008).

Introduction

Sociocultural theorists of both sexual assault and intimate partner violence often ignore and reject (or sometimes vilify) discussion of evolutionary analyses and genetic influences on these behaviors as irrelevant at best (or pernicious and dangerous at worst). However, evolutionary

perspectives often emphasize environmentally contingent adaptations which point to situational and socio-ecological influences interacting with evolved psychological mechanisms. Because all behavior depends on evolved behavioral mechanisms and because evolved mechanisms are adaptively responsive to socio-ecological conditions (e.g., Buss 1991), understanding sexual coercion and intimate partner violence with evolutionary perspectives shouldn’t, in principle, present a threat to the shared goals of (1) an accurate scientific understanding of the phenomena or (2) the moral obligation of trying to gain control over those influences to stamp them out to the degree possible. A complete and accurate scientific understanding of the causes (rather than ideological beliefs about the causes) should be the best potential way to try to control these behaviors. Here we review some of the theory and evidence that account for sexual coercion (SC) and intimate partner violence (IPV) as related phenomena understood from evolutionary perspectives.

Theoretical and Empirical Review

Behavioral Genetics of IPV and Sexual Assault: (Epi)Genetic Differences Matter

There are individual differences in most behavioral traits including sexual coercion and intimate partner violence (IPV). Turkheimer (2000) suggested that the first law of behavioral genetics is that nearly every trait that varies is partially heritable and discussed how best to interpret such empirical findings (see also Polderman et al. 2015). Although evolutionary psychologists have tended to focus on explaining human universals and sex differences, a comprehensive evolutionary understanding of human psychology needs to include explanations for the maintenance of heritable genetic differences correlated with phenotypic psychological differences. Selection acts on reproductive outcomes, influenced by traits that develop *within one individual*, often through complex, epigenetic gene-by-gene and geneXenvironment interactions (Turkheimer 2000). In other words, selection acts on the reproductive results of differences in *intraindividual*

gene-experience interactions, not on the effects of genes alone in a vacuum, somehow miraculously separated from the effects of the environment (Tooby and Cosmides 1992). (Note: *Within each individual* and *intraindividual* are in italics above to distinguish the mechanisms of *individual* development from the sources of variation causing individual differences.) Thus, a scientifically coherent explanation of any complex human behaviors, including IPV and sexual coercion, must consider (1) how genes adaptively respond (e.g., epigenetically) to particular situations and experiences, (2) that “selection regulates how environments shape organisms” (Tooby and Cosmides 1992), and (3) heritable individual differences in behavioral traits rather than just sex-differentiated human universals.

Shared genetic variation within families might at least partially account for the “intergenerational transmission” of IPV. Using a nationally representative sample of American adolescents, Barnes et al. (2013) found that heritable variation accounted for “24% of the variance in hitting one’s partner, 54% of the variance in injuring one’s partner, and 51% of the variance in forcing sexual activity on one’s partner.” The unshared environment accounted for the rest of the variance. As is common in behavioral genetics results, the shared environment explained *none* of the variance in IPV. These findings seem to contradict a within-family social learning account of why IPV consistently runs in families. However, it’s possible that genetic differences between individuals lead some individuals to be more (and others less) likely to develop violent behaviors via social learning. If this were the case, heritable variation would be the correctly identified source of variance in IPV, despite exposure to violence (within and/or outside of families) mechanistically interacting with genes in the development of mechanisms underlying IPV. As Barnes et al. (2013) point out, epigenetic research indicates that “environmental” stimuli affect genetic “switches,” which turn genes “on” and “off.” “To the extent that exposure to IPV in the home environment flips these relevant switches,” trying to identify “genetic” versus “environmental” causes of behavioral variation in IPV is futile

because genes would be causally involved in the “effects of social learning.” From an evolutionary perspective, genes and gene switches are designed to respond to the environment in ways that have been regularly adaptive. This view points to a need for sociocultural influences to be integrated with evolutionary thinking and genetic/epigenetic research in order to identify new predictions about how such socialization interacts with evolved psychological mechanisms.

Some heritable variation is also implicated in whether someone rapes an adult victim (Långström et al. 2015). It is beyond the scope of this entry to do a thorough review of heritability research and its limitations, but the evidence reviewed here implies that genetics contributes something important to the etiology of IPV and SC (however tortuous, indirect, and synergistic those causal routes may be). The relevant point for us concerning the evolutionary hypotheses regarding IPV and SC discussed below is that genetic variation in something or other matters for understanding the etiology of IPV and SC.

Intimate Partner Violence as a Form of Sexually Coercive Mating Effort

As implied in the definition of IPV above, IPV often involves sexual coercion of a partner. Evolutionary psychologists have interpreted IPV, more generally, as a form of sexual coercion wherein perpetrators use violence to guard and retain a mate, restrict their potential choice of another mate, and prevent rivals from trying to poach a mate. For example, Figueredo and McCloskey (1993) interpreted IPV as a sexually coercive mate retention strategy used by competitively disadvantaged males (i.e., relatively low mate value) to secure mates. Rowe et al. (1997) define *mating effort* as the psychological effort used to “obtain and guard short-term mates.” If IPV is a set of mate retention behaviors, it is, thus, a form of mating effort. Consistent with this idea, mating effort is associated with being male, intrasexual competition, sexual coercion (Lalumiere and Quinsey 1996), and delinquency in general (Rowe et al. 1997). If male-perpetrated IPV functions to sexually coerce a female partner, we should expect IPV to effectively prevent rivals

from mate poaching, prevent sexual infidelity or cuckoldry, and prevent partners from defecting from the relationship. We should also expect sexual jealousy to be linked with IPV because men's jealousy is thought to function to prevent infidelity and increase paternity certainty. Jones et al. (2007) found that higher self-reported mating effort (on which men score higher) predicted (1) higher levels of upset in response to imagined sexual infidelity and (2) self-reported "punitive intentions" in response to imagined sexual and emotional infidelity. Figueredo and McCloskey (1993) found a large negative relationship between *quality* of a couple's sexual relationship and male-perpetrated IPV. Both female infidelity and male jealousy were part of the sexual relationship quality variable that strongly predicted IPV.

Some evolutionary hypotheses suggest mate guarding and intimate partner violence will be directed more often toward jealously guarding someone *more* desirable (Buss and Shackelford 1997) because they have more options to leave the relationship partner in favor of a rival. Surprisingly, Figueredo et al. (2001, 2009) found that perceptions of a partner's high mate value predicted *less* spousal abuse perpetrated by both sexes. In other words, when a partner perceived the other partner as having more desirable and attractive traits, they were less likely to abuse them. Figueredo et al. (2001) argued the reason is that there is a correlation between one's own mate value and their partner's mate value (0.50 in their own sample). Therefore, "competitively disadvantaged females" (CDFs) tend to partner with competitively disadvantaged males (CDMs) in long-term relationships. They suggested CDMs perpetrate escalated mate guarding (including IPV) toward a low-quality partner because females, more so than males, can obtain a better quality mate as a *short-term* sexual partner (possibly to capture a rival's genes for her offspring), even if unable to attract the affair partner as a long-term mate. This increases her CDM partner's paternity uncertainty. Partly consistent with this interpretation, the mate retention efforts of relatively "unsexy" men (at risk of infidelity) evidently increase when their partners are most

fertile (Gangestad et al. 2005). Whereas male partners of highly attractive women guard them more *throughout* their ovulatory cycle, partners of less attractive women intensify their mate guarding *only when it matters for preventing impregnation* by another male.

Extra-Pair Copulation and Sperm Competition: Sexually Coercive IPV as an Anti-Cuckoldry Tactic in Men

Goetz and Shackelford (2009) tested the hypothesis that partner rape is an adaptation for sperm competition. According to this view, partner rape by men becomes more likely when a female partner is sexually unfaithful or suspected of being unfaithful – and functions to prevent a male rival from successfully fertilizing one's partner. They found, across two studies, that men's partner-directed sexual coercion was somewhat positively correlated with women's infidelity and suspected infidelity. Men's (nonphysical) controlling behaviors also predicted their partner-directed sexual coercion.

Time spent apart from one's partner increases risk/opportunities for extra-pair copulations. If sexual coercion toward a partner is an anti-cuckoldry tactic toward increasing paternity certainty, we should expect increased interest in copulation with a partner and sexual coercion directed toward a partner when the couple has spent an increased proportion of time apart (a cue to the risk of female infidelity). Shackelford et al. (2007) found that risk of infidelity, as measured by increased proportion of time away from a partner since the couple's last copulation, predicted men's greater "sexual interest in his partner," "distress in response to his partner's sexual rejection," and "sexual persistence in response to his partner's sexual rejection...independent of total time since the couple's last copulation and the man's relationship satisfaction." McKibbin et al. (2011) found that proportion of time spent apart since last in-pair copulation also correlates with male use of sexual coercion toward a partner *but only among men who perceive higher risk of partner infidelity*. McKibbin et al. (2011) note that partner-directed sexual coercion is related to the total proportion of time spent *apart* since last in-pair copulation, not total time since last in-pair

copulation, supporting the sperm competition hypothesis while contradicting an alternative view that partner-directed sexual coercion is the result of general sexual frustration or mating deprivation. Similarly, risk of infidelity correlates with mate retention behaviors, including intrasexual competition tactics such as threatening rivals (Starratt et al. 2007).

If IPV is ultimately about mating competition, as evolutionary theorists hypothesize, we should expect mate retention and intrasexual competition tactics to be used by the same individuals when faced with threats or perceived threats of infidelity. Figueredo et al. (2018) reported that in samples of both sexes, across five countries, interpersonal aggression toward both opposite-sex partners and toward same-sex rivals was positively correlated with each other and with other measures of mating aggression. In other words, measures of IPV, measures of aggression toward one's same sex, and measures specifically created by evolutionary psychologists to measure "mating aggression" (i.e., intrasexual competition, competitor derogation tactics, mate retention, and mate guarding) were loaded upon by a single *interpersonal aggression* factor. Interpersonal aggression toward both sexes was accounted for by the same influences in a model including self-reported "psychopathic and aggressive attitudes" (including high mating effort), short-term mating orientation (sociosexuality), antagonistic social schemata, poor executive functioning, and fast life history strategies. In other words, the same basic model of influences that accounted for IPV accounted for interpersonal aggression directed toward one's own sex as well as toward the opposite sex, suggesting that many individuals committing IPV are *generally* antisocial and aggressive (rather than "specialists" in IPV). Also, since fast life history strategies (described below) are characterized by short-term mating and promiscuity, such individuals are particularly at risk of infidelity (both their partner's and their own) and, thus, might be more likely to exhibit violent jealousy. Taken together, these results support the evolutionary interpretation that much interpersonal violence (directed toward both sexes) is ultimately about mating competition.

Men's Pornography Preferences, Sperm Competition, and Sexual Coercion of a Partner

Since a partner's infidelity is bad for men's paternity certainty and many men desire sexual variety, it is, perhaps, surprising that some studies (Pound 2002; McKibbin et al. 2013) find evidence that pornographic depictions of sexual situations involving one female with multiple males (i.e., high sperm competition situations) are more common than depictions involving one male with multiple females (i.e., low sperm competition situations) (Pound 2002) and that many men may prefer to view those high sperm competition situations (McKibbin et al. 2013; but see Prokop 2015). Kilgallon and Simmons (2005) reported that when men masturbated while viewing images depicting high sperm competition situations, they produced a higher percentage of more motile sperm compared to when masturbating to images depicting low sperm competition situations. These results seem to suggest that some men may become more aroused while viewing high sperm competition situations, including cuckoldry risk depictions. Wright (1994) suggested that mechanisms such as these might make adaptive sense to outcompete rival males' sperm in situations where a partner has copulated with another man. In other words, these findings fit well with findings that men's sexual interest in and sexual coercion of a partner increase when there has been a risk or perceived risk of infidelity (McKibbin et al. 2011; Shackelford et al. 2007; Starratt et al. 2007).

Rape: Adaptation or By-Product?

Thornhill and Palmer (2000) considered whether, over evolutionary time, human rape was reproductively advantageous to some men under some socio-ecological conditions, favoring specific mechanisms for forced copulation, or if human rape is better explained as a maladaptive by-product of other psychological adaptations that evolved for other functions. In other words, they debated whether or not rape is a specifically evolved reproductive tactic. If rape were an evolved reproductive tactic, it must have increased reproductive success regularly for some men under certain socio-ecological

conditions. Consistent with this possibility, it appears that forced copulation is more likely to lead to pregnancy than consensual copulation after controlling for use of oral contraception (Gottschall and Gottschall 2003). Thornhill and Palmer (2000) considered several possibilities for rape-specific adaptations including potential psychological mechanisms for (1) evaluating the vulnerability of victims (e.g., during wartime when unprotected), (2) motivating some men to rape when under conditions where they are deprived of mating opportunities or when lacking sufficient resources to attract desirable mates, (3) evaluating the attractiveness of potential victims differently than consensual partners (e.g., different age preferences for victims at peak fertility), (4) resulting in differences in male sexual arousal in response to depictions of forced sex compared to consensual mating, (5) resulting in differences in sperm counts in rape contexts compared to consensual contexts, and (6) motivating males to rape as a sperm competition/anti-cuckoldry tactic.

In contrast, the maladaptive *by-product hypothesis* of rape proposes that sexual coercion is a maladaptive side effect of selection for (sexually dimorphic) traits important for men's consensual reproductive opportunities: (1) desire for sexual variety without commitment and (2) inclinations toward instrumental aggression (Palmer 1991). The by-product view predicts that sexual coercers will have particularly high levels of consensual sexual activity (as well as unconsensual sexual activity), so the *by-product hypothesis* is supported by findings that sexual coercers report higher levels of mating effort (Lalumière and Quinsey 1996) and sexual experience (Lalumière et al. 1996). The by-product theory shares similar features with the confluence model (Malamuth et al. 1995), which suggests that sexual aggression results from two "paths" that may converge: *hostile masculinity* and *promiscuous and impersonal sex*.

Are Sexually Coercive Men Competitively Disadvantaged, Mate Deprived, Both, or Neither?

Thornhill and Thornhill (1983) hypothesized that sexual assault may be a conditional

(environmentally contingent) adaptation expressed among some men when they are outcompeted for resources and status, which are important for attracting desirable romantic and sexual partners. Consistent with this *competitively disadvantaged male hypothesis*, Figueredo et al. (2000) found that male adolescent sexual offenders were "competitively disadvantaged" (i.e., low mate value), particularly by having psychosocial deficiencies: poor mental abilities, poor social skills, and more psychopathology. According to their interpretation of their evolutionary-developmental model, these psychosocial deficits indirectly led to sexual offending over time as a result of "repeated frustration and failure" in sexual relationships, "leading to an escalation of more and more extreme means of obtaining sexual gratification" (p. 322).

Alternatively, the *mate deprivation hypothesis* suggested deprivation of sexual access *itself* increases likelihood of sexual coercion in some men. The *competitively disadvantaged male (CDM) hypothesis* has been conflated with the *mate deprivation hypothesis*. For example, Lalumière et al. (1996) suggested "if sexually coercive males are disadvantaged in mate competition, they should report a less extensive history of sexual experience (e.g., smaller number of different sexual partners)" (p. 301).

Lalumière et al. (1996) found sexually coercive males report a higher number of sexual partners and a more, not less, extensive sexual history. Similarly, psychopathy, which correlates with sexual coercion of both partners and non-partners (Camilleri and Quinsey 2009b), is associated with higher sociosexuality and mating effort (Figueredo et al. 2018). These findings falsify the mate deprivation hypothesis. Both the *mate deprivation* and *CDM* hypotheses suggest sexually coercive behaviors are conditional adaptations, and it seems like "competitively disadvantaged" in mating competition would imply a likelihood of being deprived of mates and fewer sexual partners, but Figueredo (personal communication) argues that they are divergent theories and that a *CDM* view is consistent with the findings of a more extensive sexual history among sexual coercers. For example, Figueredo et al. (2000) reported that psychosocial deficits directly

predicted higher “noncriminal sexual deviance” on the path to predicting nonsexual general criminality and finally sexual criminality. Their interpretation was that competitive disadvantages “might lead to frustration in the mainstream sexual marketplace and therefore to the selection of deviant avenues of sexual expression.” According to this view, these “deviant expressions,” driven by an “escalation of means of obtaining sexual gratification,” are consistent with a developmentally contingent increase in mating effort (and, perhaps, relaxation of mate standards) and short-term mating tactics *generally*, which predict more sexual activity (including, evidently, non-consensual sexual activity). In other words, a *CDM* mating strategy may be to mate with as many females as possible, regardless of her desirability (favoring quantity over quality). So, the *CDM* hypothesis should not necessarily be conflated with the refuted mate deprivation hypothesis. But, the available evidence doesn’t currently support the *CDM* hypothesis over the maladaptive *by-product hypothesis*, which predicts *generally* higher levels of sexual activity among sexual coercers.

In our view, the currently available evidence that male-perpetrated sexual coercion of partners may function as a sperm competition tactic is stronger than evidence suggestive of specific adaptations for sexual coercion of nonpartners. This raises the possibility that men coercive of partners are *CDMs* since coercion of partners is a form of IPV. Starratt et al. (2008) found that if men perceived their partner as more desirable than themselves *as a long-term partner*, perception of his partner’s infidelity predicted increased use of sexually coercive “commitment manipulation.” If men perceived their partners as roughly equally desirable *as long-term partner*, his partner’s infidelity also predicted higher levels of other sexually coercive tactics. But there was no relationship between perceptions of women’s infidelity and sexually coercive tactics among men who perceived their partner as relatively more desirable than themselves *as a long-term partner*. This seems to contradict the *CDM* hypothesis with respect to partner-directed coercion because we

might expect relatively less desirable males to coerce more desirable female partners. However, in light of Figueredo et al.’s (2001) interpretation of their findings on IPV generally (see above), because *CDFs* tend to pair with *CDMs* as *long-term partners*, a less desirable female partner is often mated with a low desirability male (*relative to rivals*), and she may have many *short-term* opportunities for infidelity, regardless of her *long-term* desirability *relative to her partner*. So, her relative desirability *as a long-term partner* compared to her partner may not be terribly important for testing the *CDM* hypothesis.

Use of Sexual Coercion in Both Sexes

Up to this point, we have mostly considered male-perpetrated sexual coercion and IPV as forms of mating aggression and mate retention. But females report using some forms of sexual coercion too, though not as frequently as males. Camilleri and Quinsey (2009a) reported finding that, unlike in males, interest in partner-directed sexual coercion in females is unrelated to changes in the risk of infidelity. Considering females have maternity certainty, these findings support the anti-cuckoldry risk hypothesis of men’s sexual coercion of a partner. And while female sexual coercion of men may function to capture a particular man’s genes or to force a particular man into long-term paternal investment, a relationship, or as an attempt to extract immediate resources, it cannot function to ensure maternity certainty.

Life History Strategy, Antagonistic Social Strategies, and Sexual Coercion

Life history (LH) theory suggests that individuals developing in unpredictable and uncontrollable conditions (e.g., high extrinsic morbidity and mortality risk, low parental support) will exhibit clusters of “fast” LH strategy traits including low somatic effort, low parental effort, high mating effort, short-term mating orientation (e.g., high quantity of genetically diverse offspring), high risk-taking, and decreased rule governance (Rushton 1985). In contrast, individuals living in safe, stable, and controllable socio-ecological

conditions will exhibit clusters of the opposite pattern of traits (“slow” LH strategy traits).

Figueredo and Jacobs (2010) argued that fast LH strategists develop antagonistic social schemata and interpret the world as a zero-sum game in that they perceive others’ interests as in conflict with theirs and focus on immediate gratification of their own interests (e.g., obtaining and securing a mate). In contrast, slow LH strategists perceive others’ interests as mutually consistent with their own and tend to delay gratification to serve long-term goals, including mutually beneficial altruism and supportive interpersonal and romantic relationships. Thus, a fast LH strategy is more strategically consistent with low self-control (Dunkel et al. 2013), risk-taking, breaking rules, and interpersonal aggression and conflict than a slow LH strategy. These fast LH traits seem consistent with the use of both IPV and sexual coercion.

Using a college student sample including both sexes, Gladden et al. (2008) found that various apparent intercorrelated indicators of slow LH strategy predicted reduced frequencies of sexually coercive behaviors. Slow LH indicators included long-term mating orientation, low psychopathy, and high self-perceived mate value. According to comparisons of path-analytic models, this “protective” slow LH factor fully mediated the relationship between biological sex of participants and frequencies of sexually coercive behaviors. As in the cross-cultural studies on interpersonal aggression discussed earlier (Figueredo et al. 2018), these results were interpreted as suggesting that slow LH strategy inhibits sexual aggression. Consistent with a LH strategy explanation of sexual coercion, Dunkel and Mathes (2011) found that individuals’ (both men’s and women’s) self-reported willingness to use sexually coercive tactics changed when they were asked to imagine different life expectancies (5 months left to live, 5 years left to live, or at least 50 years left to live). Furthermore, fast LH strategy correlated with willingness to use sexual coercion at the shortest and longest imagined life expectancy conditions, and short imagined life expectancy increased willingness to use sexual coercion in individuals that reported a short-term mating orientation. Since

LH theory suggests that developing under short life expectancy conditions will lead to a faster LH strategy and a more short-term mating orientation, these results support a LH perspective on sexual coercion. Using the same approach, Dunkel et al. (2013) found that both reported self-control and general criminal intent also increased when asked to imagine different life expectancies as described above. Furthermore, self-reported LH strategy moderated these imagined behavioral effects such that trait LH strategy was most associated with self-control and criminal intent when imagined life expectancy was short. This suggests that slow LH may be protective factor against general criminality (including sexual coercion and interpersonal aggression).

LH Strategy, Negative Androcentrism, and Mating Aggression

Since fast LH strategies are associated with interest in short-term mating, mating effort, aggression, and psychopathy (Gladden et al. 2008), fast LH strategies appear to be linked with both aspects of the maladaptive *by-product hypothesis* of sexual coercion and, perhaps, both “paths” of the *confluence model* of sexual coercion (Malamuth et al. 1995). The confluence model implicates hostile masculinity and other forms of negative androcentrism (bias against women), along with interest in impersonal sex, in causing sexual coercion. Gladden et al. (2013) found that fast LH directly predicted forms of negative androcentrism *among both sexes* and that fast LH strategies fully mediated between being male and negative androcentrism. So, according to the model, men only expressed higher average levels of hostile attitudes toward women because of average sex differences in various fast LH characteristics. This parallels the findings of Gladden et al. (2008) that fast LH traits fully mediated between being male and sexually coercive behaviors. So a LH explanation of sexual coercion is consistent with the possible influence of negative androcentric attitudes on men’s sexual coercion. But the results also show more hostile attitudes toward women among fast LH women. This was expected because fast LH

strategy individuals should exhibit increased intrasexual competition and antagonistic social attitudes and interactions toward both sexes *generally* (Figueredo and Jacobs 2010). Since women exhibited significant hostile attitudes toward other women, these results seem inconsistent with perspectives suggesting a sociocultural problem found particularly among men. In sum, fast LH strategies are linked with traits theorized to influence sexual coercion (and IPV) including psychopathy, aggression, negative androcentrism, short-mating preferences, low perceived mate value, and low self-control. A LH strategy account of sexual coercion is consistent with sexual coercion as either a specific design feature of an overall LH strategy or as a by-product of a combination of various LH traits that are designed for consensual mating (Gladden et al. 2008).

Conclusion

There are a variety of evolutionary perspectives on IPV and sexual coercion. Some are adaptationist hypotheses, and others suggest these behaviors result as side effects of selection for other traits. But each suggests that IPV and sexual coercion are ultimately linked in some way to mating competition.

Many personality characteristics have been repeatedly identified as correlates of IPV and sexual coercion overlap (e.g., psychopathy, hostile masculinity, mating effort). LH theory is a broad theoretical framework that tries to explain many somewhat interrelated psychological traits. Figueredo et al. (2018) suggest LH theory is an inclusive framework for integrating many seemingly disparate findings about interpersonal aggression and sexual coercion. For example, LH strategies are theoretically and empirically associated in some way with various proposed influences on sexual coercion and IPV. Although LH theory may help as an integrative evolutionary framework to better understand relations among various findings that were not all originally considered from an evolutionary LH theoretical perspective, much more work needs to be done to identify and understand how specific characteristics associated with

an overall LH strategy uniquely lead to the behavioral expression of interpersonal aggression and sexual coercion. Evolutionary perspectives on IPV and sexual coercion have much to gain by considering influences identified by standard social science perspectives and vice versa.

Cross-References

- Cuckoldry
- Life History Strategies
- Mating Effort
- Psychopathy
- Sociosexuality
- Sperm Competition

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Sexual Asymmetry

- [Sex Differences in Parenting and Parental Investment](#)

Sexual Attitudes

- [Sexual Outcomes](#)

Sexual Attraction

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Sexual Aversions

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Sexual Behavior

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Synonyms

[Competition for mates or resources required to mate](#); [Copulation](#); [Intercourse](#); [Masturbation](#); [Mate attraction](#); [Mating behavior](#); [Oral sex](#); [Same-sex sexual behavior](#); [Stimulation of partner's genitalia and having partner stimulate genitalia](#); [Vaginal-penile sex](#)

Definition

Sexual behavior may be broadly defined as all behavior motivated by sexual feelings, desires, or gratification, whether reproductive or not. While a lot of this behavior may be understood and predicted from a reproductive, evolutionary framework, the modern context including different forms of contraceptives might render the current behavior nonreproductive. It is important to note that nonreproductive genital stimulation and same-sex sexual behavior are also covered by the definition. An interesting point in the human context is that sexual behavior is necessary to cover nonreproductive intercourse and intercourse outside of estrus, which is rare in other species.

Introduction

The following entry will provide a short introduction to the many facets of human sexual behavior

from an evolutionary perspective. It will start off considering evolutionary theories relevant to the study of sexual behavior, consider reasons and motivation for sexual behavior, and consider different forms of specific sexual behaviors before considering possible effects of culture and ecological context.

Evolutionary Theories of Sexual Behavior

Sexual behavior is one of the areas of psychological research that shows the largest sex differences. This needs explaining and understanding. Given the context of the current entry, the following text will describe how sex differences arise through evolution. Toward the end of the entry, cultural influence on sexual behavior from an evolutionary perspective will also be considered.

Sexual Selection

The major theory for explaining and understanding sex differences is Darwin's (1871) theory of sexual selection, presented in great detail in "The Decent of Man and Selection in Relation to Sex." Sexual selection is selection for traits that promote mating success (Andersson 1994). Such traits include ones that promote attractiveness, like the extravagant visual ornaments of the peacock's tail, the complex song of the nightingale, chemical signals as used by mammals and insects, or other elaborate mating displays. Sexual selection also selects for traits that promote success in intra-sexual competition, either physically, through weaponry or large body size, or behaviorally, through threatening displays or aggressive behavior (Andersson 1994; Darwin 1871).

Behaviorally, intra-sexual conflicts to gain access to mates or resources required to mate can be resolved by low-cost signaling (non-exaggerated conflict behavior) or physical contest (exaggerated conflict). Generally, conflicts are more often resolved by nonphysical means than by physical fighting. Physical conflicts mostly occur when the contestants are similar in size and are typically preceded by a phase of visual and/or vocal aggressive displays. Two main factors settle the outcome of intra-sexual conflict:

resource holding potential and resource value. Resource holding potential is fundamentally physical "power," which is strongly affected by relative body size but which can also be affected by the condition of the contestants (health, nutritional status). Resource value, on the other hand, relates to the potential differential value of the resource for the two contestants. With asymmetries in both resource holding potential (e.g., body size) and resource value (e.g., territory ownership), the outcome of conflicts is less predictable, but resource value sometimes trumps resource holding potential.

Darwin considered sexual selection to act on both sexes in humans; something that he considered not to be the case in any other species. When it comes to other species, Darwin has later been proven wrong: sexual selection can indeed work on both sexes, at the same time or at different times, and with similar or different strength ("mutual sexual selection"; e.g., Amundsen 2000; Clutton-Brock 2009). Today, it is becoming increasingly clear that sexual selection acts on both sexes in a multitude of animal species, including humans.

Social Mating Systems

Animal mating systems are defined by the number of individuals of each sex that constitutes a mating unit (Emlen and Oring 1977). By far the most common mating system is polygyny, in which a single male mates with two or more females. Polygyny is the predominant mating system in a range of animal taxa including mammals and is common in several others, for instance, birds. There are two major forms of polygyny: resource defense polygyny in which the male defends a territory within which several females reside and female defense (harem) polygyny in which the male defends a group of females as such but no particular area (Emlen and Oring 1977). Polygyny can involve long-term relationships with multiple females, including paternal care to multiple clutches, as in several biparental passerine bird species. However, relationships can also be brief, as in lekking birds where copulation is preceded by time-consuming assessment and choice by the female, but with no male involvement post copulation. It is worth noting that, in "polygynous

species,” only a fraction of the males mate with more than one female, whereas many, often most, males are bachelors. An example of such a system is the harem-forming red deer. In some polygynous species the mating skew can be extreme, like in elephant seals where a dominant male can mate with up to 50 females. In such systems, male-male competition can be fierce.

Compared to polygyny, monogamy is relatively rare among animals. It is, however, the predominant social mating system in the majority of birds and occurs in some species belonging to other taxa (e.g., butterflyfishes and certain beetles). Monogamy is relatively rare among mammals but occurs, for instance, in several canids. Humans are unique among primates in (sometimes) practicing monogamy. The common occurrence of social monogamy in birds is related to most birds having altricial young: the offspring have a long period of dependence after hatching during which they are usually tended for by both parents. Hence, monogamy in the only taxon in which it predominates is tightly linked to extensive care by both parents. Social monogamy does not, however, necessarily imply sexual monogamy. On the contrary, the majority of socially monogamous bird species show greater or lesser degrees of sexual infidelity (see below). Moreover, many bird species where the vast majority of breeding units are monogamous also have a low frequency of polygynous trios (e.g., blue tits and bluethroats). In such species, a considerable fraction of the males may try to attract a second mate but only a few succeed. The distinction between monogamous and polygynous species is therefore not strict and the terminology settled by convention on a cutoff maximal fraction of males mated polygynously in “monogamous” species.

There is a debate as to whether humans are inherently monogamous or polygamous. In the world today, there are numerically more monogamous than polygynous relationships. However, what is inherently human cannot be judged on the numerical prevalence today, but must be analyzed through history and across cultures. Through history and measured by the number of (relatively) independent cultures, polygyny is and has been the predominant human mating system.

Further, in many Western countries, there is typically a practice of serial monogamy. Further, as considered below, there is ample evidence of extra-pair copulations in seemingly monogamous mating system cultures. Due to extra-pair copulations, it might be relevant to consider a distinction between social mating systems and genetic mating systems, to some degree, as one does with other species. On the other hand, in some recent studies, the number of offspring due to extra-pair copulations is quite small, but they may vary according to ecological features across evolutionary time.

Apart from polygyny and monogamy, two other mating systems occur in animals: polyandry, in which a female mates with several males, and polygynandry, involving multiple individuals of each sex. Neither of these mating systems are common. They are best documented in birds and in some mammals. Examples of polyandry in birds include several species of phalaropes and jacanas. In these species, males care for the offspring alone, which creates a greater mating skew among females than males, with consequently stronger sexual selection on females. A similar situation occurs in several species of pipefishes in which females deposit their eggs in a “brood pouch” on the belly of the male.

Polygynandry, with several mates of each sex, is best studied in two bird species: the dunnock and Smith’s longspur. Polygynandrous units in dunnocks consist of mostly two to three females that each tend its own clutch but which all have copulated with a similar number of males in the unit. These males contribute to feeding of offspring in the nests of any female with whom they have copulated. Notably, studied dunnock populations include all four types of mating systems: polyandrous trios, monogamous pairs, polygynous units, and polygynandrous units. The dynamics of such systems are fluid, as the interests of the two sexes are in conflict. For instance, monogamously mated females would benefit from a second male mate to help care for her offspring; the male, on the other hand, would benefit from breeding with two females rather than one. This fundamental sexual conflict is crucial for understanding mating systems and their

dynamics: what is beneficial for one sex is normally detrimental for the other.

Polyandry in humans is rare and only found in a few cultures. In general males in this circumstance will be brothers, as predicted by inclusive fitness theory. Other relevant factors to consider, though, are ecological constraints. Some have pointed out that the elder brother might have more access; such competition among siblings would be predicted by evolutionary theory, too.

Mating Competition in Males and Females

In animals including humans, mating success is generally more variable among males than among females. The simple reason is that males have the potential to fertilize a large number of female mates (and consequently produce more offspring). Females can mostly gain genetic benefits by acquiring better mates through extra-pair mating. She may also elicit protection or resources from multiple males due to reduced paternal certainty. In consequence, male reproductive success is largely limited by access to females, whereas females are typically limited by resources (to produce and care for offspring) (Trivers 1972). However, the difference in potential reproductive rate between the two sexes varies greatly among species. In birds, lekking species like the black grouse exemplifies species with a strong mating skew where males have a much higher potential reproductive rate than females (i.e., they can mate many more times per time unit). Emperor penguins, for which extensive care by both the male and the female is essential for reproductive success, represent the other end of the scale, with little difference in reproductive rate between the sexes.

With large differences in potential reproductive rate, as in polygynous species, sexual selection will act predominantly on males (Andersson 1994). This is the more common situation in the animal kingdom and leads to stronger mating competition among males than among females (Emlen and Oring 1977). This situation is termed “conventional sex roles” in evolutionary biology and typically selects for extravagant traits and large body size in males. Conventional sex roles and predominant male mating competition are

often associated with strong sexual size dimorphism (like in elephant seals) or sexual dichromatism (like in pheasants or mallards). In species that are socially monogamous, sexual selection may act with similar strength on the two sexes, resulting in similar ornamentation and mating competition (e.g., many seabirds; reviewed in Amundsen 2000). Finally, in polyandrous species, where the female potential reproductive rate is higher, sexual selection acts more strongly on females and can lead to the evolution of more extravagant ornamentation (Amundsen 2000; Darwin 1871) and mating competition behavior in females than in males (Clutton-Brock 2009). Cases where mating competition is stronger in males than in females are termed “reversed sex roles.” The term can be seen as a reflection of the more common nature of predominant male competition and of a historically stronger focus on sexual selection in males.

Variance in mating success and consequent sexual selection is not only affected by the social mating system but also by the sexual mating system. The sexual mating system may deviate significantly from the social mating system when males and females copulate with nonsocial partners, as what frequently occurs in many animal taxa including birds. Extra-pair sexual behavior has been documented in about 90% of bird species, with on average about 10% of offspring being extra-pair. The extent of extra-pair paternity varies greatly among (and within) species in other taxa as well.

Interspecific Variation in Sexual Selection

The strength of sexual selection can vary between and within species. One major determinant of such variation is the operational sex ratio (OSR), the ratio of males relative to females that are ready to mate at a given point in time and space (Emlen and Oring 1977). The operational sex ratio is determined by the potential reproductive rate of the two sexes and by variation in the adult sex ratio, which can deviate quite significantly from 1:1 in many species. When the operational sex ratio, and hence mating competition among males and females, varies significantly on a temporal (or spatial) scale, sex roles become dynamic

(Forsgren et al. 2004). In such cases, sexual selection may act on both sexes, but not at the same time, as in two-spotted gobies, a small marine fish (Forsgren et al. 2004).

Parental Investment

Most animal species display no parental care at all, but when it exists, it is more commonly performed by females than by males, as in mammals and other species with internal fertilization. Internal fertilization is, however, not always associated with uniparental female care. In birds, which also have internal fertilization (yet not internal care of embryos), both sexes typically provide parental care and often with similar parental investment (Trivers 1972). However, levels of investment by the two sexes are fluid, at any given point of time reflecting a sexual conflict over which sex should pay the highest cost of care. Similarly, the maintenance of biparental care in many bird species may reflect an evolutionary game in which the payoff (the net benefit) of staying for the male is assumed to be greater than the potential payoff from deserting (Maynard Smith 1977).

In fishes, the most common care system is by males only. Female only and biparental care also exist but are less prevalent. Uniparental male care occurs, for instance, in species with external fertilization where females deposit large clutches of eggs on a substrate, with the eggs thereafter tended by the male until hatching (Amundsen 2003). Several hypotheses have been suggested to explain uniparental male care in substrate-brooding fishes. While not completely resolved, male care is likely to reflect different payoff functions for the two sexes.

Costs of Reproduction and Life History Strategies

Parental care is costly (Williams 1966) and may negatively impact survival, future fecundity, future attractiveness, and quality of future offspring. For this reason, the optimal investment of an individual at a given time, age, or state will vary, shaping the life history of animals (Stearns 1992). An animal's life history includes age at first reproduction, whether to reproduce once or

multiple times (semelparity vs. iteroparity), number and size of eggs or offspring at a given breeding event, interval between breeding events, and longevity (Stearns 1992). Life history tactics, including age at first reproduction and investment in current vs. future offspring, may vary within species, including humans. With the exception of alternative reproductive tactics such as "sneaker" or "female mimetic" tactics, interspecific variation in life history traits is typically continuous rather than discrete.

The proximate nature of the cost of reproduction varies between, and to some extent within, species. Proximate costs include negative impacts on condition, health, or the cost of a "time-out" from mating (Parker and Simmons 1996). The opportunity cost of being prevented from mating during periods of care feeds back on sexual selection, via potential reproductive rates and consequent effects on the operational sex ratio (Parker and Simmons 1996).

In Trivers' pioneering work (Trivers 1972), sex differences in parental investment were suggested to mainly reflect the relative investment in each gamete by males and females. However, later work has refined the theory to take into consideration total gamete investment and focus on the relative benefits and gains for the two sexes from parental care (the payoff functions for males and females). These payoff functions may vary widely among and within species, depending on demographic (e.g., the operational sex ratio) and ecological (e.g., when a rich source of food for the young reduces the cost of partial or complete desertion) factors.

Most primates display some form of polygyny, with limited male care apart from group defense, as in gorillas. In this respect, *Homo sapiens* deviate from the other primates. Modern, and in particular Western, human populations typically display biparental care including extensive male care. Biparental care also is widespread in other cultures, but is highly variable in form and extent of care. While male and female care may be of similar form in Western industrialized societies, male and female parental roles are more differentiated in most other extant cultures and also in historical societies (Low 2000). Polygynandry is

maybe overlooked as a typical mating pattern of humans over the life course. Members of both sexes have variable numbers of partners during life, while extra-pair copulations are possible and possibly frequent (Fincham and May 2017), although in Western samples this behavior rarely results in offspring.

Buss and Schmitt (1993) have formulated a specific version of how sexual selection and parental investment may affect human sexual behavior called sexual strategies theory (SST). SST is therefore a species typical constriction of the general theories above, including inherently sex-differentiated features such as lower minimal, but present, paternal investment (only typical in 5% of mammalian species), at least partially hidden estrus, paternal uncertainty, and especially the different mating contexts provided by long-term committed romantic relationships and short-term sexual relations (Buss and Schmitt 1993). SST thus suggests that there will both be effects of mating context and sex for different aspects of sexual behavior and motivation. From the theory it is predicted that both sex and mating context will influence sexual behavior. Relative to women, men will, for example, have more to gain from short-term relations resulting in short-term mating representing a larger component of men's sexual strategies. Certain features like physical attractiveness is expected to be preferred by women to a stronger degree in short-term relationships than in long-term relationships potentially due to reproductive benefits by passing genes related to features of attractiveness to the offspring.

Individual differences from an evolutionary psychology perspective have been given more attention the last few years. Some of these approaches consider the evolution of the Big Five personality traits, whereas others consider fast and slow life history and psychopathology. From a sexual behavior perspective, the most relevant individual difference measure is restricted or unrestricted sociosexual orientation as measured by SOI-R (Penke and Asendorpf 2008). This measures to what degree a person is willing to partake in short-term sexual relations with low intimacy and commitment, including

actual number of short-term partners, positive attitudes to short-term sex, and spontaneous desire and fantasizing about people one meets.

There are individual differences in traits that predict life history-relevant sexual behaviors. Sociosexual orientation differs between those who are restricted and those who are unrestricted in seeking short-term sexual relations. There are stable sex differences in sociosexuality, with men being in general more unrestricted, especially for the desire component. But there are also large individual differences. One controversial suggestion is that there are two mating orientation morphs in the population (short-term vs. long-term), although most SOI data suggest a normal distribution.

Age is another relevant measure of individual difference. Human sexual behavior appears relatively late, due to slow maturation. Moreover, humans have menopause that is rarely observed in other species. Women's fertility and reproductive value are strongly linked to age, with fertility peaking in the early 20s and declining until menopause. Since men seem to have strong preferences for cues of fertility, evolutionary psychologists have investigated how sexual attraction and partner preferences change with age (e.g., Buss 1989) – especially for women's age. As shown below, patterns of sexual behavior in humans wax and wane across the lifespan.

Reasons for Sex?

As the ultimate explanation of sexual activity is to produce offspring, the answer to the question of motivation or reasons for sex might seem given. Many mammalian females are only sexually active during the conceptive phase of the menstrual cycle when offspring can be produced. However, most anthropoid primates are sexually active during nonconceptive phases as well, which suggests that there are other reasons for engaging in sexual intercourse than producing offspring. Motives for such sexual behavior in our close relatives might be to create paternity uncertainty, tension reduction, reconciliation, or exchanging sex for food. Humans also engage in sexual activity in nonconceptual

phases, to a very large degree. Brewis and Meyer (2005) found, for instance, no difference in frequency of sex between different menstrual cycle phases in a sample of about 20,000 women across 13 countries.

However, the proximate reasons or motivations for this kind of nonconceptive sexual behavior have not been investigated until recently. As predicting and understanding sexual behavior need to consider sexual motivation, this lack of studies is surprising, and most previous studies have considered motives for sex in humans to be few and simple, including reproduction, to relieve sexual tension and to experience sexual pleasure. More recent studies suggest that reasons for sex and sexual motivations are much more numerous. Meston and Buss (2007) discovered that there are four major groups of motivations for engaging in sexual intercourse and that these may be subdivided into 13 sub-factors. The four main factors consisted of physical reasons, reasons related to goal attainment, emotional reasons, and insecurity reasons for engaging in intercourse and contained 142 distinct reasons in total (i.e., across the four factors). The reasons are far from few and not as simple as prior research had indicated, ranging from physical pleasure (e.g., "It feels good"), emotional attachment (e.g., "I desired emotional closeness"), gaining something (e.g., "I wanted to be popular"), physical attraction (e.g., "I saw the person naked and could not resist"), and pressure (e.g., "I felt obliged") to relationship attainment (e.g., "I wanted to increase the emotional bond by having sex"). Both personality and individual differences in sexual strategies were linked to different factors of sexual motivation. For instance, among women, agreeableness (Big Five personality traits) was significantly negatively associated with each of the physical, goal attainment, and insecurity factors. This is consistent with previous research suggesting that more disagreeable women were more sexually experienced and more likely to engage in unrestrained sexual behavior than were agreeable women (Meston and Buss 2007). High scorers on SOI also tended to endorse more reasons for having sex than low scorers with the exception of reasons related to love and commitment, which is not surprising as

high scores express favorable attitudes toward casual sex. The factor structure was recently replicated in a Norwegian sample, and the replication utilized sexual strategies theory to predict both sex differences and difference between mating strategies, with findings mostly consistent with the theoretical hypothesis.

Previous studies have found that, relative to women, men tend to initiate sexual activity more often and to be less satisfied with the frequency of sexual activity (Okami and Shackelford 2001; Grøntvedt et al. 2015). However, few studies have investigated which factors influence men and women's initiative for sexual activity in different mating contexts. Considering the impact of multiple predictors for initiative of sexual intercourse, Grøntvedt et al. (2015) found different factors predicting sexual initiative for men and women within both relationship contexts. In long-term relationships women increased initiative taking as a function of the length of the relationship and the compatibility with their partner, as in shared interests and values with partner, whereas, for men, independence in women increased initiative taking. Both sexes increased initiative as a function of the desire component of sociosexuality in a short-term context. Moreover, initiative increased as a function of Meston and Buss' pleasure reasons (i.e., "I was horny"; "I wanted an orgasm") for sex, but only for men.

Specific Types of Sexual Behaviors

The following list of human sexual behaviors is not exhaustive or meant to provide a complete catalogue of all possible types of sexual behaviors. It is meant to illustrate some relevant sexual behaviors and consider them from an evolutionary psychology perspective.

Reproductive Sexual Behavior

A lot of heterosexual sexual behavior, both in short-term and long-term relationships, may be considered from a reproductive perspective. According to Herbenick et al. (2010), findings from a national sample show that incidence of vaginal intercourse last month increases from the

lowest rates in the youngest studied group (14–15 years), 8% reported by adolescent men and 6% reported by adolescent women, with a peak for the age group 25–29 years, 74% for both men and women. Thereafter there is a steady drop to the eldest studied group (+70), 28% and 12%, for men and women, respectively. Interestingly these numbers mirror similar findings (see below) for last month incidence of masturbation, suggesting that this reflects general sexual desire. While intercourse is potentially reproductive, birth control interventions will routinely be used to regulate unwanted pregnancy.

A recent study found that the hormones that make these hormonal contraceptives effective also may influence sexual behavior (Grøntvedt et al. 2016). Thus from a conceptual perspective, it is not always clear whether the behavior has a pair-bonding, extended sexuality foundation, rather than reproductive motivation. Also relevant for is the findings that reproduction is not often the explicit aim for most sexual encounters and behavior (Meston and Buss 2007). Typically, reproduction does not depend on conscious reproductive aims in any species. Reproduction is a consequence of sexual desires, pleasure, and behavior. As such one will see age preferences for slightly older women in men younger than women's peak reproductive age. Further, evolutionary predictions suggest that increasing age will cause reproductive expediting as women get closer to menopause.

Nonreproductive Sexual Behavior

It is typical for humans to engage in non-reproductive sexual behavior. Most non-reproductive sexual behavior is probably heterosexual foreplay followed by intercourse during low risk of conception periods of the cycle and while participants are using contraceptives. In addition, self-stimulation behavior or masturbation would be a human nonreproductive sexual behavior.

Extended Sexuality

Typically, most mammalian species concentrate most sexual behavior to periods of high conception. Intercourse outside of estrus might still have

a small chance of resulting in conception, but while this may be the case there may be a specific function of extended sexuality in humans (Grebe et al. 2013). Extended sexuality may not therefore be an elongation of estrous sexuality; rather it may be shaped within the context of pair-bonding with nondominant males gaining sexual access and paternity assurance through the evolution of extended sexuality. Grebe et al. (2013) found support for this view as coupled women's initiation of sex during the nonconceptive luteal phase was found to be particularly sensitive to their own investment in the current relationship. When controlling for women's own investment, male partner's investment in the relationship negatively covaried with women's initiation of sex during the luteal phase, suggesting that women are particularly sensitive to threats of low investment from partners in ongoing relationships during this phase.

From an evolutionary functional perspective, likelihood of conception is hypothesized to account for differences between estrus and extended sexuality. Physiologically, selection has likely shaped these phases to differ through the effects of reproductive hormones with estradiol peaking mid-cycle. Hence, this might promote fertile-phase sexuality, and progesterone rising during the luteal phase might suppress fertile-phase sexuality. Using data from women in relationships, using hormonal contraceptives, Grøntvedt et al. (2016) found interactions between different amounts of different synthetic hormones and differences in specific relationship qualities on rates of sexual intercourse. More specifically the study found that when women lack loyalty and faithfulness in their relationships, high estradiol and low progesterone activity from contraceptive hormones (similar to the estrus phase of the ovulatory cycle where chances of conception is relatively high) were associated with higher rates of sexual intercourse than were high progesterone and low estradiol levels (similar to the luteal phase where chances of conception is relatively low). But this difference was reversed when women perceived themselves as highly loyal and faithful to their relationships. This suggests that hormonal contraceptives not only mimic physical

effects of natural hormones, but they may affect patterns of women's sexual interests as well.

Masturbation

Masturbation or self-stimulation is a frequent type of human sexual behavior and also found across a large range of species. As would follow from greater male sexual desire, men masturbate more than women. A meta-analysis of 177 sources on sex differences on 21 different measures of sexual attitudes and behaviors found the largest sex difference for masturbation incidence, $d = 0.96$ (Oliver and Hyde 1993). The authors note that there was a small sex difference in attitudes toward masturbation. Herbenick et al. (2010) present data from an American probability sample: they find that men masturbate more than females for all age groups. There is an increased difference from the youngest age group (14–15 years) with 43% last month for adolescent men and 24% last month for adolescent women to the highest monthly incidence of 69% men and 52% women, respectively, for the age group 25–29 years. This is followed by a steady decline until the highest age group (70+) with 28% and 12% for men and women, respectively.

Extra-Pair Sex

The estimate of nonpaternity (children sired by another man than the woman's partner and presumed father) has fallen during the past decades and is currently closer to 1–3% (Larmuseau et al. 2016) but varies between subpopulations. This number may have been higher in our species' relevant evolutionary past, but they are still high enough to act as selection pressures for jealousy and mate guarding.

Infidelity is the most typical form of extra-pair sex. There are inherent problems involved in studying behavior based on deceit and with a motivation for secrecy, and the results must therefore be considered conservative. In a current review Fincham and May (2017) summarize the consensus estimates as follows: 2–4% of spouses engage in sexual infidelity in a year. They further estimate the lifetime prevalence of sexual infidelity to be in the range of 20–25% of all marriages.

There has been an increase in rates of infidelity since the early 1990s. With lower degree of commitment and formalization of the relationship, there seems to be an increase in rates of infidelity. Also there is a positive relationship between infidelity and male sex, previous infidelity behavior, unrestricted sociosexuality, and number of partners prior to the current relationship (Fincham and May 2017).

All forms of extra-pair sex are not infidelity. Obviously polygamous mating systems involve sex with more than one partner, but this will not be addressed further in this entry. Consensual non-monogamy involves both sexual and non-sexual extra-pair relations, including swinging and polyamory. Swinging involves couples meeting up with other couples and swapping partners for sexual relations, where emotional ties are not encouraged. Estimates suggest the incidence of swinging in married couples to be approximately 2%, although most partake in swinging only once. While these numbers may be dated, it is hard to find more recent estimates. Swinger parties including several couples follow specific rules, including rules generally for not allowing non-coupled males and sometimes encouraging single females. Most often couples enter swinging through the initiative of the husband, and the major reason for swinging is sexual variety, consistent with sexual strategies theory. The second most popular motive is excitement and physical pleasure.

Open sexual relationships are a third form of consensual non-monogamy, where one or both partners stay in a committed but sexually non-exclusive relationship and have sex with others. Prevalence is hard to measure and there are a very limited number of investigations. National representative samples of single Americans suggest that one-fifth report, at some time, having been in a consensual non-monogamous relationship.

Sexual Harassment and Coercion

Sexual harassment encompasses unwanted or offensive sexual attention or hostile behaviors that focus on gender. Operationalizations of sexual harassment regularly include sexist jokes,

degrading and obscene sexual comments, and homophobic insults, the spreading of sexual rumors, being shown pictures of nudity, and being asked for sexual favors. Often the use of physical force (coercion) is included in measurements of sexual harassment, but researchers are advised to treat harassment and coercion as separate concepts (Bendixen and Kennair 2017). Being subject to and performing sexual harassment (but not coercion) is commonly reported among high school girls as well as among boys.

Mainstream social science theories strongly alluding to feminist perspectives have explained harassment as male power, paternalism and dominance of women typically reflected in measures of acceptance for sexual violence, gender inequality, and hostility toward women. In contrast, the evolutionary perspective has suggested that the desire for sex, and not paternalism or male power, is the driving force for sexually harassing others (Buss 1996). Several studies of adolescent populations find that casual sex experiences and preferences for uncommitted or unrestricted sex (sociosexuality) predicts being subject to and performing sexual harassment (e.g., Bendixen and Kennair 2017) supporting evolutionary perspectives while competing variables from feminist perspectives have performed less well. In addition, a significant proportion of sexual harassment is same-sex behavior, better explained by the evolutionary perspective through sexual derogation tactics, while opposite-sex harassment appears to be a form of sexual solicitation behavior partly rooted in sociosexuality (Bendixen and Kennair 2017).

Inbreeding Avoidance

As for other species inbreeding will have fitness costs. Human kin detection is necessary for both kin selection-based altruistic behavior and also incest avoidance (Lieberman et al. 2007). Such circuitry may be based on both Westermarck effects (duration of sibling co-residence during childhood) and perinatal association with the individual's biological mother. Lieberman and coworkers have found that moral disgust of incest is tied to specific brain networks.

The Use of and Response to Erotica, Pornography, and Sexual Stimuli

Pornographic material is typically characterized by women and men engaging in casual noncommittal sexual acts devoid of feelings of attachment and love. Compared to hardcore pornography, softcore is less sexually graphic and intrusive, while erotica denotes works of art or literature that deal with sex meant to cause sexual feelings. Following sexual strategies theory, men are expected to be more oriented toward this kind of stimuli and be easier aroused by it. In meta-analytic reviews of research on gender differences in sexuality, the use of pornographic material is more common among men than among women, and men also report more sexual arousal in response to sexual stimuli compared to women. Sex differences were slightly larger for studies using pornographic vs. erotic stimuli. Still, these general patterns of findings are affected by several factors. The sex difference in frequency of porn use among adolescents is particularly large and also varies by type of material (Bendixen and Kennair 2017). Moreover, relative to women, men have preferences for a wider range of pornography and prefer hardcore over softcore pornography. On the other hand, women use pornography more often with a regular sexual partner than men do. Finally, there is a sex difference in the specificity of sexual arousal, with men reporting particularly less arousal by watching other men having sex.

Same-Sex Sexual Behavior

Same-sex sexual behavior is observed in a multitude of species. What is very rare is exclusive same-sex sexual behavior. It is quite likely that this has, especially for women, been quite unusual through evolutionary history, too, as freedom to choose may have been low. From an evolutionary perspective, same-sex sexual behavior is neither a mystery nor a problem; exclusive same-sex behavior would be more difficult to explain. With greater sexual liberalism and an increased focus on sexual orientation as an identity, it is possible that individual preferences are more expressed. There are a great number of possible

combinations of sexual orientation, identity, roles, and behavior. Focusing primarily of same-sex sexual behavior, findings consistently find that more people of both sexes engage in same-sex sexual behavior than identify as bisexual or homosexual (Herbenick et al. 2010). Further, twice as many women as men (12% and 5.8%, respectively, aged 25–44) report any lifetime same-sex contact (Chandra et al. 2011).

Prostitution

Prostitution is defined as the act of engaging in sex for material benefits. It is characterized by being low skilled, labor intensive, well paid, and female – although the numbers of male prostitution especially among young men are higher than many acknowledge. Although it is unclear how many women and men are forced or coerced into prostitution, some people, because of restricted alternatives, choose prostitution over regular jobs (and a partner) because it provides a quick and lucrative source of income. From an evolutionary perspective, prostitution exists because of men's powerful desire for sexual variety, combined with the inability of some men to attract women as mates. Some women and men are able to “pursue a strategy of exploiting men's sexual desires to extract money and other recourses in exchange for sex” (Buss 1996, p. 312). Similar strategies are observed in other species, e.g., in macaques and penguins.

Effects of Culture

Typically, human sexuality and sexual behavior are considered to be influenced by culture and ecological factors. Only a simplistic understanding would consider biology and evolved sex differences and adaptations deterministic. On the other hand, cultural differences will often be a result of evolved mental mechanisms. Culture, including factors such as sexual liberalism, egalitarianism, secularism, etc., is often invoked to explain or predict differences in sexual behaviors, including sex differences in sexual behaviors and preferences. In social role theories, the relevance of biological sex differences is downplayed, and

the observed sex differences are attributed to the effects of the relevant society's gender roles. As such the theory presupposes a largely monomorphic sexual psychology. The effects of context or culture might not always work in making the sexes more similar. Also, other factors might be more influential than gender roles, including parasite load, functional sex ratios, or a specific culture's mating system. One example may be increased paternal investment, which might explain greater sex differences in jealousy responses rather than smaller (Bendixen et al. 2015). On the other hand, for some features of sexual psychology, such as male interest in partner virginity (Buss 1989), sexual liberalism may be associated with less and smaller sex differences.

Beyond culture one might consider different effects of ecological differences. Environmental features such as pathogen prevalence and resource scarcity may influence women's partner choice. According to Thornhill and Fincher (2014), there is support for parasite stress affecting human sexual selection and mating systems; parasite stress is positively associated with women's sexual restrictiveness across nations. Female scarcity has also been suggested to be more important than wealth and parasite load in shifting people between short-term sexual behavior and long-term committed relationship. Scarcity of females in geographic regions predicts a reduced willingness of the population to engage in uncommitted sexual relationships. These effects of the operational sex ratio have recently been confirmed experimentally; with more men than women present, men and women shift toward a more restrictive sociosexuality, while both sexes shift toward a less restrictive sociosexuality in ecologies with more women than men.

Conclusions

Sexual behavior encompasses a wide range of different behaviors. Human sexual behavior varies between cultures given different degrees of sexual liberalism, egalitarianism, and mating systems. But there is also variation within nations

based on age, orientation, and ethnicity, and there might also be geographical and temporal effects of different local operational sex ratios. Further human sexual behavior is influenced by sex and mating context (Buss and Schmitt 1993). The same processes and theories that explain animal sexual behavior are to a large degree the best current predictors cross-culturally of human sexual behavior.

Cross-References

- ▶ Female Sneak Copulation
- ▶ Human Copulation
- ▶ Mate Preferences
- ▶ Mating Systems
- ▶ Oral Sex and Human Sexual Behavior
- ▶ Orgasm
- ▶ Ovulation
- ▶ Parental Investment Theory
- ▶ Penile-Vaginal Sex
- ▶ Polygamy in Humans
- ▶ Relationship Between Sexuality and Gender
- ▶ Reproductive Strategies
- ▶ Same-Sex Sexual Behavior
- ▶ Sex Differences
- ▶ Sexual Coercion
- ▶ Sexual Selection
- ▶ Sex Differences in Long-Term Mating Preferences
- ▶ Sex Differences in Short-Term Mating Preferences
- ▶ Sexual Arousal
- ▶ Sexual Intercourse
- ▶ Sexual Orientation and Human Sexuality
- ▶ Sexual Strategies Theory

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Sexual Behaviors

► Sexual Outcomes

Sexual Coercion

- Aggression for Sexual Access
- Contexts for Men's Aggression Against Women
- Ecological Factors and Rape
- Life History Theory and Rape
- Origins of Patriarchy
- Rape
- Rape and Dating
- Rape in Warfare
- Sexual Assault and Intimate Partner Violence
- Special Case of Bonobos and Female Counter-Adaptations to Rape
- Violence to Control Women's Sexuality

Sexual Coercion and Dating

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Synonyms

Interpersonal violence; Partner or acquaintance rape; Rape; Reproductive coercion; Sexual harassment; Sexual manipulation

Definition

The manipulation of one's romantic partner into engaging in unwanted sexual acts.

Introduction

Sexual coercion in humans occurs when one partner – often the female – are manipulated, tricked, or influenced in to sexual activity. Methods of sexual or reproductive coercion can take many subtle forms, such as financial withholdings, pay-offs, as well as physical or psychological abuse. In more extreme coercion, alcohol and drugs may be used to decrease the resistance of the targeted individual. Rohypnol and ketamine are among several substances used to sexually coerce women and ultimately lower the social consequence for males who engage in sexual coercion (Crooks and Baur 2014). When a woman refuses to consent via coercion, a mate's efforts may be elevated to include coercion through aggression, threats, physical violence, and rape. Like other sexual assaults, coercion is uninvited, unwelcome and without consent. Interpersonal violence and forced in-pair copulation are other existing variables when sexual coercion takes place, both variables affecting the reproductive health and well-being of women.

Forced In-Pair Copulation

The term *forced in-pair copulation* is used to describe when mates rape romantic partners. Observations of aviates have shown that forced in-pair copulation will occur after an extra pair copulation has occurred (i.e., when the female has mated with a new male), so that the in-pair male's sperm must compete for fertilization (Bailey et al. 1978). Evolutionary research posits that this type of sexual coercion is a response to partner infidelity and sperm competition, as an anti-cuckoldry tactic that reduces the males cost of investment on offspring belonging to another (Goetz 2005; Goetz and Shackelford 2009). While the sperm competition hypothesis has an expanding body of evidence to support existence in humans, critics debate the intensity of the adaptation in humans (Goetz 2005).

Rape is the outcome of unsuccessful coercive tactics of mating. Sexual coercion is often an antecedent to forced in-pair copulation when a male partner rapes an already acquired mate in response to suspicion of infidelity. This behavioral

pattern serves the purpose of sperm competition and control over reproduction (Goetz 2005). It has been estimated that 10–17% of wives have experienced spousal rape (Finkelhor and Yllo 1987). Rape includes different varieties of coercion, and not all coercive behaviors result in rape. The term acquaintance rape distinguishes unwanted sexual activity when individuals know, or are acquainted, with each other. Approximately 90% of rapes qualify as date/acquaintance rape (Crooks and Baur 2014).

Evolutionary Evidence from Animal Research

Observational evidence supports the idea that sexual coercion has roots as an evolved mating strategy (Mc Kibbin 2008), and researchers agree that sexual coercion is a conditional precursory tactic to rape. Scorpionflies (*Panorpa vulgaris*) will engage in rape when coercive tactics have been rejected. Specialized anatomical structures (viz., *notal* organ) provide evidence that coercion and rape exist as conditional mating tactics evolved as adaptations (Thornhill and Palmer 2000).

In Non-human primates, a significant level of aggression and forced copulatory behavior exists as males compete for attention of females in estrus. When female chimpanzees reach sexual maturity, males will compete for opportunities to mate. Lower ranking males will attempt to coerce females away from the group if the alpha male has not yet gained access. Dr. Jane Goodall recorded that when the female is unwilling, “a fair amount of brutality” was demonstrated to coerce the female for mating opportunity (as cited in Buss and Malamuth 1996, p. 234). In this capacity, intrasexual competition serves as sexual coercion of females into submission before rape occurs.

Violence between mates has been documented in animal studies, specifically non-human primates, and male sexual coercion also plays a key role in human mating habits to include interpersonal violence. Female orangutans keep solitary lives away from other females or familial groups who may protect them from forced copulation with uninvited males (Wrangham and Peterson 1996). “Morphs” differentiate the male patterns of behavior associated with their category of physical size. Females prefer to mate with the

larger, slower morphs while smaller morphs have more difficulty acquiring willing mates, and are more likely to engage in rape as a mating strategy. Smaller and faster morphs are more likely than larger orangutans, to employ aggressive, violent, and forceful tactics for gaining mates (Mc Kibbin 2008).

Observers have noted that – in silverback mountain gorillas – infanticide is a selective force that causes them to live in group settings (Buss and Malamuth 1996; Wrangham 1979). Male silverback mountain gorillas are known to protect ‘in-group’ females and infants, which increases the females’ and infants’ probability of survival. Infant offspring from out-group males are usually killed. Infanticide coerces females to mate with in-group males because of the increased survival rates of the offspring.

In some ape species, female coalitions are bonded to protect each other from male aggression. Similar familial and social bonds occur between humans when parents and friends protect female children from would-be (undesirable) suitors. ‘In-group’ members of both humans and primates help to conserve reproductive resources, which ultimately affects the social systems in place. Sexual coercion is expressed through life ending violence in the primate world, either through infanticide or matricide (Buss and Malamuth 1996).

Psychological adaptations occur when coercive behaviors have reproductive success over time. Evolutionary researchers hypothesize that these adaptations are mechanisms that allow men to evaluate potential unwilling mates differently than cooperative mates based on the probability of fertility (Mc Kibbin 2008). Young women of reproductive age are more likely than older women to be victimized and experience sexual coercion and rape, supporting the evolutionary theories of mate fitness (Buss and Malamuth 1996). The same is true within the animal world, as reproductive fitness is essential for a species to survive.

The Feminist Perspective

The feminist standpoint provides interference to research through naturalistic fallacy and faulty

belief in males’ genetic determination (Mc Kibbin 2008). However, it is from supporting evidence within the feminist perspective that evolutionary psychologists come to further examine the power hypothesis of sexual aggression. The power hypothesis, as it relates to sexual aggression, can be understood as the male attempt to control or dominate females with the use of physical force, emotional manipulation, resource provision, or denial which keeps women in a state for fear (Buss and Malamuth 1996). This concept stems from the feminist political position, and has validity within the evolutionary study of coercion to gain sexual access consensually. To fully understand sexual coercion, its origin must be explored to help reduce the behavior and the negative consequences that stem from it. Evolutionary psychologists study ‘what is’ and not necessarily ‘what should be’ and from this perspective, coercion and rape are conditional tactics in the mating process. Not all males are prone to become rapists and evolutionary psychology does not attempt to explain rape as a genetically inherited trait, rather an adaptation in response to environmental demands to gain partners at low investment. No ethical research justifies the existence of sexual violence, and study of coercion, rape, harassment and forced in-pair copulation is meant to better understand the origins of significant social problems in tandem with feminist and sociological perspectives (Mc Kibbin 2008).

Types of Men Who Sexually Coerce and Rape

Shields and Shields (1983) reported that one-third of men said they would conditionally use rape as a mating strategy, and that many men also admitted to having coercive fantasies (Mc Kibbin 2008). Eighty-two percent of male college students report having used coercion as a method to gain sexual access, and 21% of males report using physical coercion. One-third of men admitted that, under certain conditions, they would rape (Mc Kibbin 2008). While most men are able to commit rape, there are some unique types of men who may be more likely to rape, and of those men some of these psychological adaptations make them more likely to seek out victims using coercion.

Researchers have identified five potential psychopathological personalities that are more likely to exercise manipulation and violence in gaining sexual access to females. Of these five personality types, there are three which are more likely to engage in coercion. *Opportunistic rapists* will seek out women who seem receptive, but will have a lower possibility of retaliation from the victim or her 'in-group.' He may use coercive methods, such as drugs or alcohol, to seek out low-investment partners to lower the cost or likelihood of being caught in the act of rape. *High mating effort males* will also seek low-investment partners and use coercion to gain sexual access, but these men are noted as having lower fluctuating facial asymmetry (i.e., higher in physical attractiveness), hold themselves in high esteem, and are sexually experienced. *Partner rapists* are perhaps the most frequent to engage in sexual coercion, with interpersonal violence and forced in-pair copulation as contributing variables (Mc Kibbin 2008).

Partnered males will use coercive language in the form of threats, reminders, and persuasion to encourage their mates to have sex. Recent research has discovered evidence of a link between interpersonal violence (IPV) and more subtle methods of coercion that negatively impact the overall health and reproductive consequences of women. The connections between IPV and sexual coercion explain the increased risks associated with unintended pregnancies and women's reproductive health. Reproductively coercive behavior is defined as the use of pressure or influence that compels a woman to abandon her reproductive rights, through manipulation, intimidation, threats, and/or actual acts of violence (Miller and Silverman 2010). Twenty to 45% of teenage and adult women report having been coerced into sexual activity (Crooks and Baur 2014).

Conclusion

Evolutionary psychologists look to explain sexual coercion as a method of mate retention when the female is suspected of infidelity. Furthermore, coercion provides an anti-cuckoldry tactic for males to

protect their investment of resources (Goetz and Shackelford 2009). It is most important to understand that coercion under certain circumstance is not only non-consensual, but against the will or choice of another. In this light, sexual coercion is a side effect or response to sperm competition and women's infidelity. Reports from those who have been raped or abused by their partner usually connect sexual coercion with violence. In fact, abused women are more likely to be raped, physical assaulted, and even murdered by their abusive partner if they attempt to defect from the relationship (Mc Kibbin 2008; Thornhill and Palmer 2000). While this is one hypothesis that explains the cause of sexual coercion, evolutionary perspectives also acknowledge the possibility of an inverse relationship that female infidelity may be a response to sexual coercion (Goetz 2005).

Sexual activity in the animal world is widely studied and has applications within human sexual experiences including those associated with sexual coercion. Evidence in the mating habits of several different animal species, including non-primates (e.g., birds) and non-human primates (e.g., orangutans, chimpanzees, and gorillas), supports evolutionary theories of human sexual behaviors, including mate seeking and mate retention via aggression, sperm competition, and anti-cuckoldry tactics. Parental investment and social coalitions assist young females' resistance to, and protection from, coercion. The role of infidelity is a predictor of male sexual coercion to reduce male cuckoldry, and coercion serves to express dominance and power within a relationship while also increasing the male's chances of reproducing. Although scientific evidence points to sexual coercion being an adaptive reproductive strategy, it must be noted that this behavior is not condoned by evolutionary scientists. Understanding the cause and reasons for sexually coercive behavior may also help decrease, and eventually eliminate, these behaviors in the future.

Cross-References

- Rape and Dating
- Sexual Abuse

- Sexual Harassment
- Sexual Intercourse
- Sperm Competition

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Definition

The summary term *sexual aggression* (also sexual violence) encompasses sexual activities, for example, sexual intercourse, oral sex, and sexual touching, which are imposed on another person against her or his will. It comprises different coercive strategies, such as the use or threat of physical force, the exploitation of the victim's incapacitated state (e.g., due to alcohol or drugs), or verbal pressure. More specifically, *sexual coercion* refers to penetrative sexual contacts through verbal pressure, whereas *rape* involves sexual intercourse or other forms of sexual penetration through physical force or the exploitation of the victim's incapacitated state, for instance, through alcohol or drugs (cf., Koss et al. 2007). Definitions in the legal context can, however, differ from these research definitions, particularly regarding what specific sexual acts and coercive strategies constitute rape or other sexual offences.

Introduction

Sexual aggression is a severe social and health problem in all countries around the world, entailing numerous adverse effects on victims' health and well-being. The present article reviews the current state of the art of measuring sexual aggression, including its challenges, prevalence rates of women and men, and factors that have been linked to a higher probability of becoming a victim or a perpetrator. Finally, consequences for physical and psychological health are described.

Measurement

Sexual aggression can be assessed from two different perspectives – from the side of the victim, referring to *sexual victimization*, and from the side of the perpetrator, referring to *sexual aggression perpetration*. The precise measurement of sexual aggression victimization and perpetration constitutes a major challenge given the topic's sensitive nature. As it is considered a taboo topic in many countries worldwide, this may preclude the disclosure of such incidents. However, not only

Sexual Coercion and Rape

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Synonyms

Sexual aggression; Sexual assault; Sexual violence

social challenges are linked to the measurement but also conceptual and methodological issues arise. Particularly, the phrasing of items is crucial for the detection of sexual aggression. Broad questions – such as “Have you been raped?” – may contribute that responses are affected by stereotypical notions of sexual aggression (e.g., rape is primarily committed by a stranger in a dark lonesome place), which in turn may result in an underdetection (see Cook et al. 2011, for an overview). To overcome this bias, the current “gold standard” for the assessment of sexual aggression is using behaviorally specific items, describing an incident in graphic language without mentioning the word rape. A validated and commonly used instrument is the Sexual Experiences Survey (SES; Koss et al. 2007) which crosses sexual acts (e.g., fondling, oral sex) with coercive strategies (e.g., use of physical force, verbal pressure). Different categories, ranging in their severity from no victimization/perpetration to rape, can be derived based upon the reported incidents. Another validated instrument is the Sexual Aggression and Victimization Scale (SAV-S; Krahé and Berger 2013). Similar to the SES, it assesses the coercive strategy and type of sexual activity but allows, unlike the SES, a cross-classification with the relationship between the victim and the perpetrator.

The Scale of Sexual Aggression

The two major sources to estimate the scale of sexual aggression are crime statistics and representative surveys. Crime statistics typically reveal the annual number of reported incidents to law enforcement agencies. Although these numbers provide a first insight into the scale of sexual aggression in a country, there is broad consensus that these statistics only reveal a minority of the cases. In addition, there is a great variation of legal definitions across countries, impeding comparison of prevalence rates. To get a better estimate of the scale, surveys with representative samples are used. In the United States, the National Intimate Partner and Sexual Violence Survey (NISVS) is an ongoing, representative victimization survey. According to data from 2015, 21.3% of women and 2.6% of men reported attempted or

completed rape at some time in their life, defined as vaginal, oral, or anal penetration against the person’s will through the use or threat of physical force or the exploitation of the victim’s incapacitated state (e.g., through alcohol or drugs). Sexual coercion, referring in this survey to unwanted vaginal, oral, or anal penetration through non-physical pressure, was reported by 16.0% of women and 9.6% of men (Smith et al. 2018).

A large body of research has also examined sexual aggression among college students. The so far largest study on sexual victimization was the AAU Campus Climate Survey on Sexual Assault and Sexual Misconduct which included 27 US higher education institutions, with 150,072 students participating (Cantor et al. 2017). In this survey, 18.1% of women and 4.2% of men reported experiences of completed penetration or sexual touch through incapacitation or the use of physical force since entering college. Generally, prevalence rates of sexual victimization have been found to be higher for women compared to men, whereas perpetration rates were higher for men than for women. However, in recent years, substantial rates of male victimization and female perpetration have been revealed in some countries (e.g., Krahé et al. 2015). Although the stereotypic rape script involves a perpetrator who is a stranger, there is broad evidence that most victims have been assaulted by someone they knew, often by their current or former partner (Krahé et al. 2015).

Risk and Vulnerability Factors

For explaining sexual aggression, studies focus under what circumstances experiencing or engaging in sexual aggression is more likely. In this line of research, risk factors, which are factors that predict an increased probability of engaging in sexual aggression, and vulnerability factors, which are factors that predict an increased probability of experiencing sexual victimization, are examined. It is important to point out that studying vulnerability factors does not imply any responsibility of the victim or that she/he is to blame for the incident. Instead, the goal of this line of research is to identify conditions or

situations which may make a person more vulnerable to sexual victimization. This knowledge may in turn be used for intervention programs to prevent sexual victimization. Comprehensive reviews synthesizing past research were conducted by Tharp et al. (2013) on risk factors of sexual aggression perpetration and by Ullman and Najdowski (2011) on vulnerability factors of sexual victimization. Tables 1 and 2 present a summary of the respective factors. Particularly, childhood maltreatment, prior sexual victimization, and having many sexual partners have been shown to be both risk and vulnerability factors of sexual aggression.

Consequences

Sexual victimization often results in both immediate and long-term negative consequences for physical, psychological, and behavioral health. As comprehensively summarized by Martin et al. (2011), sexual victimization of women is associated with a higher likelihood of different psychological problems, including anxiety, depression, posttraumatic stress disorder (PTSD), and suicide ideation and attempts. In addition, physical health may be affected, including injuries, gynecologic/reproductive health problems, functional limitations, sleep problems, headaches, gastrointestinal problems, and even death. Beyond adverse effects on psychological and physical health, sexual victimization may also result in high-risk health behaviors, such as unsafe sex behaviors and the use of alcohol, drugs, and/or tobacco. Because most research has been conducted with female victims, to date, little is known about adverse effects on male victims. However, the limited evidence for men also suggests that sexual victimization can have notable negative consequences for them (see Peterson et al. 2011, for a review).

Conclusions

Sexual coercion and rape are severe public health issues worldwide. In particular, high victimization rates were revealed for women. Against

Sexual Coercion and Rape, Table 1 Risk factors of sexual aggression perpetration. (Based on Tharp et al. 2013)

Prior victimization history	Sexual, physical, or emotional abuse in childhood Childhood maltreatment Sexual victimization in adolescence or adulthood
Prior perpetration history	Prior sexual aggression perpetration
Family dynamics	Family conflicts Exposure to parental violence Quality of the relationship between child and parents
Partner dynamics	Relationship conflict Avoidance and controlling behaviors Casual relationship status
Sexuality-related cognitions	Sex fantasies
Attitudes	Willingness to engage in sexual aggression Victim blaming Rape myth acceptance Hostility toward women Adherence to traditional gender roles Hypermasculinity Acceptance of violence
Behavior	Fraternity membership Sports participation Gang membership
Sexual risk-taking behaviors	Having many sexual partners Impersonal sex Early sexual initiation Pornography use Sex drive Sexual risk taking
Peer attitudes/behavior	Peer pressure for sex Approval for forced sex by peers Peer sexual aggression perpetration
Risk perception	Failures to interpret cues
Mental health	Delinquency/conduct disorder Suicide attempts Empathic deficits

stereotypical expectations, research has shown that men may also experience sexual aggression and women may be perpetrators as well. Due to the adverse effects of sexual aggression on victims' health and well-being, a broad implementation of prevention programs is needed in the future.

Sexual Coercion and Rape, Table 2 Vulnerability factors of sexual victimization. (Based on Ullman and Najdowski 2011)

Prior victimization history	Sexual, physical, or emotional abuse in childhood or adolescence Sexual victimization in adulthood History of relationship conflict
Trauma history	History of stressors or traumas
Family dynamics	Running away from home Having a mother who had been arrested or who was unavailable because of emotional problems, medical conditions, or alcohol/drug use problems Low paternal care/warmth
Attitudes	Liberal sexual attitudes Rape-supportive attitudes
Sexual risk-taking behaviors	Having many sexual partners
Risk perception	Failures to perceive risk or detect danger cues
Mental health	Intellectual disabilities Psychological disorders (e.g., schizophrenia, depression) Chronic mental health problems Psychological distress as a consequence of prior sexual assault
Alcohol and drug use/abuse	Heavy alcohol use Drug use
Demographics	Being female Being young Being an ethnic minority Being unmarried or separated Low education Low income Living away from home Living in a shelter or being homeless

Cross-References

- Sexual Assault and Intimate Partner Violence
- Sexual Coercion and Dating
- Sexual Coercion and Violence
- Sexual Coercion as a Mechanism of Sexual Selection

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Sexual Coercion and Violence

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Synonyms

Aggression; Sexual aggression; Sexual assault; Sexual violence

Definition

According to the World Health Organization (WHO; Krug et al. 2002), violence, considered as a leading public health problem, is a broad term divided into self-directed, interpersonal, and collective violence of which, except for the self-directed type, all of them can be physical, sexual, psychological, or involving deprivation or neglect. Therefore, the term *violence* includes the term *sexual coercion*. Apart from the broad definition provided by the WHO, other disciplines are trying to narrow down this phenomenon to better understand it. For example, social psychology conceptualizes *violence* as “behaviors carried out with the intention of causing serious harm that involve the use or threat of physical force, such as hitting someone over the head, or – in the ultimate form – taking another person’s life” (Krahé 2013, p. 12). *Coercion* is defined as a form of an instrumental aggression “[...] with the intention of imposing harm on another person or forcing compliance” (Tedeschi and Felson 1994, as cited in Krahé 2013, p. 12). The term *sexual* refers to the nature of the behavior, for example, someone is coerced (through physical force or threat, verbal or other type of influence) to a specific sexual activity (see ► “Sexual Coercion and Rape”). Finally, according to social psychology, both sexual coercion and violence are part of a broader term of *aggression*, which is defined as “any form of behavior directed toward the goal of harming or injuring another living being who is motivated to avoid such treatment” (Baron and Richardson 1994, p. 7). In the further course of this chapter,

we refer to the narrower definition of sexual coercion and violence provided by social psychology and concentrate on adulthood rather than on childhood.

Introduction

Although sexual coercion and violence are different forms of harm, *sexual* and *physical*, and can be considered separately, this contribution focuses on the association between the two. In this article, we will look at the measurement of sexual and physical forms of violence, related problems, their prevalence, and factors contributing to their co-occurrence.

Measuring Sexual and Physical Violence

Because of the sensitive nature of this topic, for those who experience sexual and/or physical harm, and the socially undesirable or even the penal nature for those who commit it, the accurate recording of sexual and physical violence is very challenging. Criminal statistics, representative victimization studies, and research studies are the main data sources for different forms of sexual and physical violence. For example, legal agencies record *crime statistics* based on countries’ legal definition, such as the Federal Bureau of Investigation (FBI) in the United States, the National Crime Agency (NCA) in the United Kingdom, or Bundeskriminalamt (BKA) in Germany. *Representative victimization studies*, for example, the National Crime Victimization Survey (NCVS) in the United States or the Crime Survey for England and Wales (CSEW) provide annual crime statistics based on the national legal definition of the respective crimes. *Research studies* mostly adopt a definition that goes beyond the legal one, which is why the scope in legal terms cannot be assessed. In research, a widely used instrument for collecting data on sexual and physical violence toward an intimate partner is the Revised Conflict Tactics Scales (CTS2) from Straus et al. (1996). This scale measures physical violence, presenting participants with a list of

several actions, both minor (e.g., “slapped partner,” “threw something at partner that could hurt”) and severe (e.g., “slammed partner against a wall,” “kicked partner”). A parallel version addresses acts of sexual harm, again both minor (“insisted on sex,” “insisted on sex without condom”) and severe (“used force to make partner have sex,” “used force to make partner have anal sex”). Participants are asked to respond to the respective items from both victim and perpetrator perspectives. Regarding sexual coercion (also sexual violence or aggression), several other instruments have been developed in the last years. These are described in the section ► [“Sexual Coercion and Rape”](#). In addition, an extensive compendium of assessment tools for measuring sexual and physical violence from the victim and perpetrator perspectives is provided by the Centers for Disease Control and Prevention (CDC; Thompson et al. 2006).

Given the great heterogeneity of definitions, direct comparisons of information from different sources are often difficult. However, having broader definitions, as in research studies, may help to detect milder but still potentially harmful forms of violence.

The Scale of Sexual and Physical Violence

Official Statistics and Victimization Studies

According to the official crime statistics of the FBI in the United States, in 2017, there were 5.3 murders per 100,000 inhabitants. The estimated rate of aggravated assaults in the same year was 249 per 100,000 inhabitants. Around 135,755 rapes, defined as attempted or completed vaginal or anal penetration with any body part or object, or oral penetration by a sex organ without consent, were reported to law enforcement (FBI 2017, see respective sections for murder, aggravated assaults, and rape). Looking at the representative victimization studies, in the NCVS study, the rate for simple and aggravated assault in 2017 was 13.6 per 1,000 persons age 12 or older (Morgan and Truman 2018). In the same study, rape (defined as coerced or forced, attempted or

completed vaginal, anal, or oral penetration) and sexual assault (defined as attacks or attempted attacks of unwanted sexual contacts other than rape) were reported in 393,980 cases (1.4 per 1,000), of which only about 40% were reported to the police. According to one of the few annual representative victimization studies in Europe, the CSEW, there were 533,248 incidents of violence with injury and 638,894 without injury between October 2017 and September 2018 (CSEW 2018a). In terms of sexual offences, 0.5% of persons aged between 16 and 59 reported being a victim of completed sexual assault by rape or penetration (CSEW 2018b, see Table S36).

Research Studies

Another data source, for both sexual and physical violence, is research studies, such as the recent EU-wide study on violence against women conducted by the European Union Agency for Fundamental Rights (FRA 2014). The FRA study asked women about different acts constituting physical violence (e.g., being pushed or shoved, spalled, grabbed, pulled on hair by someone) from the victim perspective since the age of 15 and in the past 12 months. With respect to sexual violence, the time reference was the same and the scope of considered behaviors ranged from forced oral, vaginal, and anal attempted or completed penetration to any other form of unwanted sexual activity, including being unable or afraid to refuse. Based on interviews with 42,000 women from the 28 EU member states, 33% of them reported physical and/or sexual violence ever, whereby 22% experienced it by a current and/or previous partner. The highest rates were found in Sweden and Denmark (30–39%), the lowest in Poland and Portugal (10–19%). In terms of the last 12 months, 8% of the sample reported physical and/or sexual violence. Extrapolating the figures from the FRA study to the entire EU female population, about 13 million women have experienced physical violence and 3.7 million have experienced sexual violence in the past year.

Important data for both females and males comes also from research studies using the CTS2 (see description in the section [“Measuring Sexual and Physical Violence”](#)). As stated in the recent

article from Straus and Douglas (2017), the CTS2 provides valuable data on the dyadic concordance of experienced acts of violence within a couple. According to the authors, there is a high percentage of violent acts that are experienced by both female and male partners (from their heterosexual partners). As found by other researchers, rates of physical violence toward the partner based on the CTS2 measure were higher in females than in males, i.e., women reported more perpetration toward men and men reported more victimization by women (see Krahé 2013). As Krahé (2013) pointed out, the unexpected difference compared with the well-known gender imbalance in the official crime statistics may be due to different recordings. Official statistics record more severe acts of physical violence compared to research studies based on the CTS2 and generally, more women than men report such acts to the police.

Co-occurrence of Physical and Sexual Violence

While many sources provide data on both physical and sexual violence separately, only some research studies considered both. Based on studies that focused on women who sought help for severe physical partner violence (i.e., battered women), it was found that approximately 30–70% of those women also experienced sexual violence. For example, McFarlane et al. (2005) have shown that 68% of battered women also experienced sexual assault by their partner at least once. Compared to women who were physically abused only, women who experienced both forms of violence started to consume or increased their consumption of alcohol, nicotine, or illicit drugs after the sexual assault. Additionally, those women were 5.3 times more likely to threaten to commit or attempt to commit suicide. Furthermore, a review on marital rape from Bennice and Resick (2003) indicates that victims of marital rape often experienced others forms of trauma, such as physical partner violence, adult stranger rape as well as child sexual abuse, and therefore are at greater risk for posttraumatic stress disorder (PTSD). Similarly, the limited research on male

victims who sought help due to severe physical partner violence (e.g., punching, beating up) has shown that almost 50% of the men reported the experience of minor sexual aggression and 28% reported severe sexual aggression (see paragraph on minor and severe forms of sexual aggression of the CTS2). Among these males, all victimization reports were higher than their perpetration reports. Furthermore, almost all males, who reported severe sexual victimization from their partner, also reported severe physical aggression victimization. As in the battered women samples, male victims of physical violence who also experienced sexual victimization reported more PTSD and depressive symptoms and generally suffered from poor health (Hines and Douglas 2016).

Conclusion

Sexual and physical violence are serious forms of interpersonal violence and social psychology considers them within a broader term of aggression. Data from many sources indicates that a significant percentage of women and men suffer from sexual and physical harm, mostly from people they know. Experiencing both forms of violence increases the risk of suffering more and longer from the consequences of violence.

Cross-References

- Sexual Assault and Intimate Partner Violence
- Sexual Coercion and Dating
- Sexual Coercion and Rape
- Sexual Coercion as a Mechanism of Sexual Selection

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Sexual Coercion as a Mechanism of Sexual Selection

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Synonyms

Sexual aggression; Sexual violence

Definition

Use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile and to decrease the chances that she will mate with other males, at some cost to the female (Smuts and Smuts 1993, pp. 2–3).

Introduction

Sexual selection theory traces its origin to *The Descent of Man, and Selection in Relation to Sex*, in which Charles Darwin theorized about the evolution of traits involved in reproduction (Darwin 1871). Darwin described two processes: the competition among one sex for sexual access to the other and the expression of choice by one sex for traits expressed in the other. Barbara and Robert Smuts proposed that intersexual coercion be considered as a third mechanism of sexual selection, arguing that there is abundant evidence that males use aggression against females to influence their reproductive success (Smuts and Smuts 1993). Sexual coercion is rooted in interlocus sexual conflict (Watson-Capps 2009), the antagonism that occurs when the optimal reproductive strategy of one sex imposes a fitness cost on the other (Chapman et al. 2003).

Forms of Coercion

Sexual coercion can be divided into two component categories of behaviors (Muller et al. 2009). The first and more widely recognized is *direct coercion*, comprising behaviors that increase the mating access of the coercive male. Direct coercion functions to overcome resistance of a female, either because the male is not preferred or because mating is not desirable at that time. Three major types of direct coercion have been described (Clutton-Brock and Parker 1995). *Forced copulation*, sometimes referred to as rape, involves the use of aggression, restraint, or threat to directly facilitate copulation. *Intimidation* entails retaliation against female mating resistance, decreasing the likelihood of resistance to future attempts. Sexual *harassment* involves repeated attempts to mate which can counteract female resistance when the costs of rebuffing the male become too great. Forced copulations are relatively rare in animal societies but are reported at high rates in humans, orangutans, and some species of waterfowl, cetaceans, and insects. Intimidation and harassment are likely to be commonplace whenever females encounter multiple males, though these tactics have rarely been systematically studied.

Indirect coercion, or coercive mate guarding, includes behaviors used to decrease the likelihood that a female will mate with other males (Muller et al. 2009). *Herd*ing is the use of force to maintain a close proximity between the male and female. *Sequestration* involves physical isolation of females from exposure to other males. *Punishment* entails the use of aggression against females who attempt to associate with or mate with other males. Males using indirect coercion may not encounter resistance to their own mating attempts, and may even be highly desirable mates, but instead use coercive tactics to constrain female promiscuous behavior. There is high potential for indirect coercion in multi-male mating systems, such as those of chimpanzees and baboons, where male competition for fertilization opportunities is intense. However, indirect coercion also arises in pair-bonded species due to the high costs of cuckoldry. In humans, for example, the

prevalence and diversity of female claustration practices across cultures have been attributed to selection for men to protect their significant paternal investment in offspring (Wilson and Daly 1995).

Sexual selection has also shaped the occurrence of infanticide by males of many species (van Schaik and Janson 2000), and this behavior is also broadly consistent with the definition of sexual coercion. Infanticide increases the opportunity for a male to mate with a female, at a clear cost to her fitness, by eliminating the offspring of a rival and decreasing the latency to the next fertile cycle.

Sexual coercion is not synonymous with male aggression against females. Aggression need not be sexual in nature, as males and females encounter other kinds of conflicts (e.g., feeding competition). Conversely, sexual coercion need not include direct aggression, as it may be accomplished by threat of aggression or, in the case of humans, through verbal manipulation or by invoking collateral costs. It can be predicted that males will be most likely to be coercive to females that have a high probability of conception. However, aggressive interactions outside of fertile periods can alter female mating behavior in the future. For species with long-lasting male-female social relationships, males may use aggression as a form of conditioning to alter the future mating behavior of females.

Female Counterstrategies to Coercion

Given the costs of coercion, females should experience selection for counterstrategies (Smuts and Smuts 1993). Females of most mammal species are smaller than males, often significantly so, making it difficult to resist or fight back against a coercive male. Females of some species form coalitions among themselves (e.g., bonobos) or with male “friends” (e.g., savannah baboons) to protect against coercive males. Many female primates exhibit extended receptivity, a feature that can reduce coercion by allowing them to mate with non-preferred males at times when conception is unlikely. Among human societies, sexual

aggression is reduced in human societies where women have access to support from other women and from kin (Smuts 1992). Additionally, while itself the subject of coercive control, women's economic and political power appears to be an important limiter for coercion.

Conclusion

Viewing sexual coercion within the lens of sexual selection theory provides the opportunity to generate and test hypotheses about the evolutionary origins and socioeconomic predictors of intersexual violence, a common occurrence in many animal and human societies. Coercion has been a prominent source of recent research in human evolution psychology, particularly since the publication of the *Natural History of Rape* (Thornhill and Palmer 2000). While that text proposed that human rape may have evolved to overcome female resistance to non-preferred partners, others have argued that many incidences of rape and other forms of sexual violence are attempts to control partner infidelity (Camilleri and Quinsey 2012).

Cross-References

- ▶ [Barbara Smuts and Robert Smuts](#)
- ▶ [Evolution of Female Resistance](#)
- ▶ [Female Choice](#)
- ▶ [Female Choice and Sexual Conflict Theory](#)
- ▶ [Female Counter-Adaptations to Rape](#)
- ▶ [Forced Copulation](#)
- ▶ [Male Sexual Jealousy to Deter Partner Infidelity](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Conflict in Nonhumans](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Sexual Jealousy](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)

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Sexual Conflict

- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)
- ▶ [Violence as Coercive Control](#)

Sexual Conflict After Conception

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The Adaptive Function of Marital Dissatisfaction During Child-Rearing

It can be argued that the dissatisfaction that occurs in a marriage serves an adaptive function (Shackelford and Buss 1997). Pair-bonding among humans, in particular a union of marriage, likely evolved to increase the reproductive benefits for both sexes (Betzig 1989; Buss and Schmitt 1993). If a marriage is not maximizing the potential benefits and the costs that incur from the relationship outweigh the benefits, then the dissatisfaction that arises would serve to bring awareness of the issues that occur in the marriage. If a couple decides that a relationship is no longer beneficial, then the negative emotions associated with this dissatisfaction would cause one or both of the individuals involved to either address the problems or to end the current relationship to find a more beneficial partnership.

The adaptive challenges for both sexes during a union following conception would have been mate retention and the care of offspring. Since men and women have different reproductive strategies (Buss 1989a), those differences in selective pressure would also lead to men and women facing different adaptive problems during a marriage. A major sex-specific conflict that can arise centers around the issue of paternity certainty. Evolutionary psychologists point out that worldwide cuckoldry rates range from 1.7% to 29.8% (Anderson 2006; Shackelford and Goetz 2007). Additional related conflicts such as violence, decrease in intercourse frequency, kin resemblance, the 4-year itch, and infidelity may also arise after conception.

Research by Lucas et al. (2008) suggests some cultural and evolutionary components to marital satisfaction in general. This research reveals that there may be some universal component to effective communication skills when it comes to raising an offspring, which would have been adaptive in order to successfully raise a child. This theory is further extended by Cox et al. (1999), who found that those couples who had at least one partner with positive problem-solving skills prenatally had higher marital satisfaction than those couples in which neither partner showed this set of skills. Those couples with better problem-solving skills also reported less of a drop in how satisfied they were after the child was born.

Violence During Pregnancy

Violence during pregnancy has been seen throughout history, often being viewed as a product of a patriarchal society. However, evolutionary psychologists view violence during pregnancy as a product of male sexual jealousy stemming from anxiety that the child their partner is carrying is not theirs (Deacy and McHardy 2013). Since men do not have paternity certainty, they may resort to violence against their partner. For women, there is certainty of paternity because fertilization is internal, and women carry the child. Men, however, can be cuckolded and wind up contributing resources to a child who is his genetic offspring.

Cuckoldry ultimately decreases a man's fitness and increases another man's fitness. This potential of being cuckolded is why men are often more upset if their partner commits sexual infidelity rather than emotional infidelity (Kuhle 2011). Upon discovering that a man's partner has become pregnant by someone else, the said man may direct violence against his partner to kill the developing offspring (Friedman and Shackelford 1999 as cited in Buss and Duntley 2011).

Given this risk intimate partner violence is twice as likely in response (Burch and Gallup 2004), and the prevalence of intimate partner

violence during pregnancy ranges from 1% to 20% (Gazmararian et al. 1996). Cross-culturally, this statistics holds true also. A South African study indicates that at least 20% of women experience at least one act of physical violence during their pregnancy (Groves et al. 2015). Additionally, women who are abused are more likely to be pregnant with another man's child (Martin et al. 2004). Similarly, longitudinal research indicates that partner jealousy and partner suspicion of infidelity are strongly correlated with intimate partner violence (IPV) (Hellmuth et al. 2013). These findings clearly show that abuse during pregnancy can be attributed in part to a man's suspicion of infidelity on the part of his partner.

From this previous research, one may reason that IPV could be seen as a form of infanticide also. While abuse may seem to be directed toward the woman herself, a Nicaraguan study indicates half of the women who were pregnant and subjected to violence were injured from attacks directed to their abdomen (Valladares et al. 2005). The abdomen may be targeted in an attempt to kill the offspring, thus terminating the pregnancy.

Prior research indicates that when a man has sex with a spouse, he establishes sexual precedence over her giving him access to her future sexuality (Shotland and Goodstein 1992). This also happens when a man impregnates a spouse (Sales and Murphy 2000). This sexual precedence can be interpreted from an evolutionary perspective where it occurs to try to ensure paternity certainty and monopolize a spouse's reproductive potential.

Male feelings of sexual precedence can also lead to abuse in the form of threats (McFarlane et al. 2002). Communicating threats to a pregnant spouse may serve as a method of mate retention designed to lower her mate value in her eyes which makes it harder for her to feel she can attract another quality mate, keeping her with the father of her offspring. McKibbin et al. (2007) indicate that men can insult their intimate partners as a form of mate retention. But, this has not been tested with men and their pregnant spouses/partners.

After Delivery: Resemblance to Kin as a Decision-Maker to Investment

Due to paternity uncertainty, men may never know if the child they are providing resources for is his genetically related offspring. But, one way a man may seek to resolve this issue is via facial resemblance between him and his offspring. Research indicates that when families observe newborn babies, both the mother and her family claim the newborn looks like the father (Daly and Wilson 1982). This represents an underlying mechanism attuned to familial resemblance of the father in order to facilitate parental investment by the father. Research supports this. Burch and Gallup (2000) report that violence directed to the child and the mother is negatively correlated with a greater sense of paternal resemblance. Also, men react in a more positive manner and invest more, hypothetically, when an offspring resembles them (Platek et al. 2002, 2003). As paternal resemblance and mate fidelity increase, so does the increase in investment to the offspring (Apicella and Marlowe 2004). Furthermore, the area of men's brains that play a role in decision-making respond differently to resemblance, compared to women's brains (Platek et al. 2004). These findings suggest that facial resemblance is an important factor for paternal investment in offspring and as such suggest that kin resemblance may play a role in conflict after conception occurs.

Problems After the First Child

Four-Year Itch

Couples often have a decline in marital happiness after approximately 4 years (Fisher 1989; Kurdek 1999), and researchers have speculated that it could be the outcome of boredom in a marriage (Kurdek 1999). From an evolutionary perspective, there may be a biological drive for a new partner after 4 years because 4 years are the typical amount of time needed to ensure the survival of the hominid infant through weaning (Fisher 1989). Infants are altricial when they are born and require an extensive amount of care.

Therefore, infants are mother nurses, and nursing stimulates a release of oxytocin which facilitates attachment between mother and infant (Feldman et al. 2007; Galbally et al. 2011).

Transition to Parenthood (TTP)

Prior to having their first child, the couple begins to make plans and anticipate the future with one another, and after the birth of the first child, they experience joy but also experience negative effects like an extreme focus on their health and the offspring's health. Additionally, they experience a decline in income and an increase in labor (Myrskylä and Margolis 2014). Given this conflict, not surprisingly, when a child is born, it has negative impacts on the couple's marital relationship (Belsky et al. 1983). In fact, Kurdek (1999) reports that couples with children experience the steepest decline in marital quality. Similarly, Twenge et al. (2003) in a meta-analysis from 148 samples report that across 90 studies parents had less marital satisfaction than non-parents, with a 10% difference among these groups in the reports of above average marital satisfaction. Research shows that married couples experience a decrease in satisfaction and confidence in their relationship and an increase in negative communication and poor conflict management (Doss et al. 2009).

From an evolutionary perspective, the decline in satisfaction due to conflict can be accounted for by selective pressures. For example, men take the role of fatherhood more negatively than women (Gray and Crittenden 2014), since men typically are more interested in short-term mating (Buss and Schmitt 1993), consistent with parental investment theory. A woman may not be as stressed with the arrival of a child because she is more interested in long-term mating (Buss and Schmitt 1993) and because she is certain that the offspring is hers, whereas men may not have paternity certainty (Trivers 1972).

In our current world, children are also weaned earlier than they were in ancestral societies which lead to more involvement in child-rearing from the father. This adds an additional stressor of an increased need for cooperation between parents to raise their young. This stressor likely contributes

to fathers experiencing less marital satisfaction (Doss and Rhoades 2017).

Other moderating factors that may also contribute to increased conflict and decreased marital satisfaction are the gender of the parent, the age of offspring, and the number of offspring (Twenge et al. 2003). Correlational data indicate that women typically have less marital satisfaction than men. Furthermore, women who had infants also reported less satisfaction than women who did not have infants, while those women with infants had only a slight difference in reports of satisfaction compared to those women with older children. The age of children did not affect men's marital satisfaction. Furthermore, those parents who had a greater number of children also revealed less marital satisfaction (Twenge et al. 2003). Overall, this research suggests that parents with multiple children and women with children have less marital satisfaction than parents with one child and childless women.

As Trivers (1972) details, there is a sex difference when it comes to parental investment. Fertilization and gestation occur internally for females, with male's minimal contribution to having offspring being ejaculation. After birth, women are the providers of nutrients to the child through breastfeeding, which in previous times occurred for the first 3–4 years of a child's life. From a parental investment theory perspective, it is not surprising that women with younger children have less marital satisfaction since they have to devote greater time and effort to care for a younger child. The mothers also tend to do significantly more housework, 9 h more than their childless counterparts, while fathers only completed an hour more than those childless men (Nomaguchi and Milkie 2003). This dissatisfaction can be offset by a husband who invests more in the child by dedicating more time to the rearing of the child (Gjerdingen and Chaloner 1994). A greater investment by a male into his offspring is something women typically look for when choosing a mate (Buss 1989a). Therefore the greater investment by a man would fulfill this preference and cause less strategic interference among the couple (Buss 1989b, 2001). Overall, there would be less conflict because the burden of child-rearing and care would be lessened.

Socioeconomic status (SES) is another moderator variable that affects marital conflict and satisfaction. Twenge et al. (2003) report that parents of higher SES, as well as the cohort of parents from the newer generation, reported greater marital dissatisfaction. The authors suggest that these findings may be explained using two models: role conflict model and restriction of freedom models. It may be that greater emphasis that is put on autonomy (Frum 2000), as well as an increase in the choice of activities that can be restricted when one becomes a parent, that contribute to greater dissatisfaction in marriage. The role that each sex typically takes on when it comes to parental investment applies also. With a greater shift in women entering the workforce now, married/partnered women of higher SES may be experiencing greater dissatisfaction than those married/partnered women of lower SES or married women of previous generations because the transition to parenthood may be more pronounced. Also, with more women working now, additional conflicts may arise because women have less time to devote to child-rearing and may need additional support from the child's father.

Sex After the First Child

A common feature throughout the human population is a decline in sexual intercourse (Brewis and Meyer 2005). Before the birth of the child, women's sexual interest and activity declines during the first trimester and continues to decrease into the third trimester (von Sydow 1999). Additionally, after the child is born, sexual interest is usually lower than normal for several months. Furthermore, research on women's sexual interest indicates that they have less of a desire to have sex after having children (Brewis and Meyer 2005; Abdool et al. 2009; Escasa-Dorne et al. 2013). Men's sexuality also shifts during the TTP. Although they do have a satisfying sex life, men's sex drive is more inconsistent after the first child is born (Gray et al. 2015). This decreased libido on the part of men can be due to a decrease in testosterone since men's testosterone goes down after they have a child (Gray et al. 2002). Since men and women, respectively, are

less interested in sex after a child is born and sexuality in personal relationships is the result of an underlying motivation to maximize the transmission of genes to succeeding generations (Sprecher and Cate 2004), conflicts can arise regarding the amount of sex desired. Long et al. (1996) report that sexual conflict is negatively related to relationship satisfaction.

Infidelity and Jealousy

Two common types of infidelity that occur in relationships are sexual and emotional infidelity. Sexual infidelity involves having sex with someone other than your primary partner, while emotional infidelity involves falling in love or diverting resources such as time investment, attention, and emotional support to someone other than the primary partner (Shackelford et al. 2004; Shackelford and Buss 1997). While both types of infidelity can be distressing, a sex difference emerges for reactions to infidelity dependent upon the type of infidelity committed. For men, if a woman is adulterous, it threatens his paternity certainty and opens the possibility of him being cuckolded into raising offspring that would not contribute to furthering his genetic line. This potential risk causes men to be more upset by sexual infidelity compared to emotional infidelity (Buss et al. 1992).

For women, a male partner who commits emotional infidelity signals a loss of investment in the couple's offspring since some of the man's time and resources are diverted to another woman and possibly to this other woman's offspring. Thus, women are more upset by a partner's commission of emotional infidelity. So, the jealousy each sex experiences most is dependent on the type of infidelity their partner commits (Wiederman and Kendall 1999). This differential jealousy adaptation helps to ensure one's own fitness (Bendixen et al. 2015).

Researchers have discovered that during pregnancy, men are more likely to commit infidelity (Whisman et al. 2007). This may occur because there are reproductive advantages gained by having extra-pair copulations. If a man has multiple

partners that he reproduces with, then his fitness is increased, and his genetic legacy is likely to continue. But, getting caught cheating on a partner can cause a high level of conflict, leading to mate expulsion, depending on the type of infidelity committed (Shackelford et al. 2002).

Since men are likely to commit infidelity when a woman is pregnant, conflict may arise in the couple such that women engage in more mate guarding. This would be adaptive since sexual infidelity on the part of her male partner could lead to a loss of investment in her offspring. Not surprisingly, Graham-Kevan and Archer (2009) report that pregnant women do engage in more mate guarding than nonpregnant women.

Conception may lead to conflict based in error management theory (EMT) because Buss (2001) reports that inferential biases are made about potential infidelity. From an EMT perspective, there are costs and benefits associated with overestimating the potential for sexual infidelity. So, in certain contexts, as in the case of a pregnant partner, it would be especially advantageous for a man to use heightened mate retention and mate-guarding tactics due to an overestimation that the partner would commit sexual infidelity. A man with a pregnant partner could experience reproductive losses if he underestimates his pregnant partner's potential for sexual infidelity. Each of these situations could cause conflict among the couple because the mate-guarding tactics utilized by the man could become too controlling, or they could become not controlling enough to guard against a loss.

Child Custody and Child Support Conflict

Shackelford and Buss (1997) explain that marital satisfaction is an adaptive function because it allows the couple to realize it is time for them to find a different partner. If the couple decides to dissolve their relationship, and they have children, conflict can arise.

Since, the individuals are no longer living together, one of the individuals must help provide for the child. Consistent with parental investment

theory (Trivers 1972), usually women are the ones in heterosexual relationships to gain custody of the child (Anderson 2011; Grall 2007). Men's largest investment is financial which can lead to conflict after relationship dissolution.

In 2011 the US Census Bureau estimated that \$37.9 billion dollars in child support was owed during the year of 2011, and 53.4% were single mothers (U.S. Census Bureau 2013). This statistics suggests that men are being forced to pay their ex-wives money to help provide for their child. Research speculates that although it may be advantageous for men to invest in their child, even if they are not living with them, it may also benefit them in not supporting the child (Shackelford et al. 2005). Men may refuse or want to reduce their payments of child support, because if they are giving money to an ex-partner they do not have 100% certainty that the money is going to their offspring and not to their ex-partner or their ex-partner's new partner. If this occurs, then the man is ultimately decreasing his fitness by giving up resources to an individual that is not his mate. A man may also want to reduce or not pay his child support if he has a new partner, since women tend to prefer men who are good financial providers (Buss 1989). Men may want to divert funds away from their child support and use those funds to attract a new mate, which will ultimately increase his fitness. This can create conflict among the man and the mother of his child requesting the child support. The aforementioned research shows that evolutionary theory can explain sexual conflict after conception occurs.

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Sexual Conflict and Sex Differences in Parental Investment

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Sexual conflict occurs when the evolutionary interests of males and female diverge, leading to antagonistic coevolution (Härdling and Smith 2005; see Parker 1979, 2006; Trivers 1972). There are two types of sexual conflict: *Intralocus sexual conflict* occurs when a trait is expressed in males and females but has opposing fitness outcomes, whereas *interlocus sexual conflict* is when a trait in one sex conflicts with a different trait in the other sex.

There is sexual conflict over parental care because one sex would benefit if the other sex invested more in their offspring. More specifically, mating strategies differ between the sexes due to differences in minimal obligatory parental investment (i.e., minimal investment required to produce offspring). Parental investment theory (Trivers 1972) suggests that the sex with greater obligatory parental investment, typically females, can increase fitness by being more discriminative in mating partners (e.g., screen for those with better genes, resources, or willingness to invest in offspring), whereas the sex with lesser obligatory parental investment, typically males, can increase fitness through increasing the number of mateships with the more investing sex. In humans, women's minimal obligatory investment is greater than men's because it includes 9 months of gestation and early child care until weaning, whereas men's minimal obligatory investment amounts to a single mating. Thus, there is conflict over mating effort and parental investment when each sex pursues their optimal strategy (Bjorklund and Shackelford 1999; Goetz and Shackelford 2009).

In humans, parental investment can be understood as a form of interlocus conflict if men's high

mating effort with low parental investment conflicts with women's preference for a committed and investing mate. Parental investment can also be understood as a form of intralocus conflict if there are opposing fitness outcomes to parental investment. These examples meet the criteria for sexual conflict if the beneficial trait in one sex is associated with a cost to the other sex. To date, no direct empirical tests of sexual conflict in parental investment have been conducted with humans, though some research is consistent with these ideas. Women generally invest more time in child care than do men; women are also more likely to gain child custody; and there is conflict over men failing to provide child support (see ► [“Child Custody”](#) and ► [“Child Support”](#) entries).

Sexual conflict over parental investment has been more directly applied and empirically tested with nonhuman species (Westneat and Craig Sargent 1996), particularly birds (Royle et al. 2002; Slagsvold and Lifjeld 1989), with at least one study using meta-analytic methods (Harrison et al. 2009). Mathematical models also show promise in understanding sexual conflict and sex differences in parental investment (Lessells and McNamara 2012). Applying such methods to humans would address some of the difficulty in studying fitness outcomes from parental investment.

Cross-References

- [Child Custody](#)
- [Child Support](#)
- [Parental Investment and Sexual Selection](#)

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Sexual Conflict in Mating Strategies

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Synonyms

Error management theory; Rape; Sexual aggression; Sexual conflict; Sexual harassment; Strategic interference

Definition

Sexual conflict in mating strategies occur when men and women come into conflict as a result of pursuing different mating strategies with non-overlapping or opposing objectives.

Introduction

Why do men and women come into conflict over mating and sex? This chapter examines the adaptive reasons, which trace back to key differences in minimum obligatory parental investment (Trivers 1972). Reflecting these differences, men tend to be relatively eager for casual sex, whereas women are relatively more cautious, requiring their sexual partners to be of higher quality or committed for a longer duration. As each side strives for its own reproductive interests, the other side's strategy is often interfered with, resulting in conflict.

Evolutionary Roots of Sexual Conflict in Mating Strategies

In most sexually reproducing species, females are physiologically obligated to make a larger minimum investment than males of time, energy, and resources to produce and develop offspring. In mammalian species, offspring develop inside the female and rely on the mother for nourishment and nurturance for the first few years of life. Although males often make significant parental investments, their *minimum obligatory* investment consists mainly of their sperm. Due to the large discrepancy in minimum required investment, females are more reproductively valuable and have evolved to be choosier about potential mates because mating mistakes are costlier to them. That is, females increase their overall reproductive success by ensuring that their sexual partners have sufficient genetic and material resources that they are willing to share (Buss and Schmitt 1993; Symons 1979). Human males, on the other hand, are much less biologically constrained and have evolved to compete for sexual access to

females (Bjorklund and Shackelford 1999; Trivers 1972). Indeed, males are able to increase their overall reproductive success by increasing the number of partners that they inseminate – a generally undesirable strategy for human females, who are potentially bound to several years of maternal investment for any given sexual encounter. Therefore, whereas human males tend to benefit relatively more than females from pursuing a mating strategy of quickly amassing reproductive *quantity*, human females tend to benefit more relative to males from pursuing a strategy of slowly and carefully ensuring *quality*.

This asymmetry in reproductive costs and benefits shapes the variation in strategies preferred by men and women in their pursuit of sexual relationships with each other. As shown below, the resulting divergence in mating strategies is a source for much potential sexual conflict (Goetz and Shackelford 2009).

Sex Differences in Standards and Eagerness for Casual Sex

Stemming from differences in minimum required parental investment and the associated asymmetry in costs and benefits, men have evolved lower standards and greater eagerness for casual sex, whereas women have evolved to have higher standards and greater caution toward casual sex (Symons 1979). Men's lower standards have been demonstrated across numerous surveys (e.g., Buss and Schmitt 1993; Li et al. 2002). For instance, one study asked people to indicate the minimum acceptable percentile level for 24 different characteristics pertaining to a potential partner for a single date, sexual relations, steady dating, and marriage (Kenrick et al. 1990). Whereas women's minimum requirements started out relatively low for a date and rose steadily as the relationship became more sexual and significant, men's minimum requirements were significantly lower than women's for both dates and for sexual relations.

Take intelligence for instance. Both sexes required potential dates to be at the median level of intelligence, and both sexes required their

steady dating and marriage partners to be clearly above the median. However, whereas women required their sexual partners to be above the median on intelligence, men were willing to accept a one-night stand whose intelligence was low (31st percentile; Kenrick et al. 1990). Other surveys have similarly indicated that compared to women, men desire and anticipate having more sexual partners (e.g., Simpson and Gangestad 1991), desire greater sexual variety, and have more sexual fantasies.

Behaviorally, men are the primary consumers of pornography and prostitution, and are also more likely to engage in extramarital affairs. In a set of classic field studies (Clark and Hatfield 1989), opposite-sex students were randomly approached on campus by experimenters and told, "I have been noticing you around campus. I find you to be very attractive." They were then either asked to "go out with me," "come over to my apartment," or "go to bed with me" that evening. For a simple date, men and women were similarly likely to accept the invitation – roughly half of each sex said yes. However, as the likelihood of immediate sexual intimacy increased, the sexes sharply diverged in their responses. While a meager 3% of the women agreed to go back to the man's apartment, nearly 70% of men consented to heading to the woman's apartment. For the more direct sexual request, not one woman agreed, and many were clearly upset at having been sexually solicited (e.g., "What is wrong with you? Leave me alone."). In stark contrast, more than 70% of men agreed to the sexual invitation, with some expressing greater urgency (e.g., "Why do we have to wait until tonight?"). Men who declined made sure to indicate mitigating circumstances ("I'm going with someone") or affirm their underlying interest (e.g., "I can't tonight but tomorrow would be fine.").

Conflict Concerning if and when Sex Occurs

Given that men and women diverge significantly in their focus on short-term quantity versus long-term quality and their attitudes toward casual

sexual relations, it is not hard to imagine men's and women's mating strategies coming into conflict. Whereas women are more interested in having sexual relations with partners of sufficient quality who can invest, men prefer having many low-cost sexual relationships and to have them sooner versus later. The subsections below describe how these strategies come into conflict in the way that men and women infer sexual intent and how men, being more eager, may push for their interests while women, being more cautious, resist.

Error Management Theory

People often make judgments under conditions of uncertainty, whereby they do not know the exact states of factors relevant to their decisions. According to error management theory (Haselton and Buss 2000), such decisions effectively pit a Type I error (falsely inferring the existence of a particular state) against a Type II error (falsely denying the existence of that state). For recurrent situations of reproductive significance, humans likely evolved a systematic bias to make related decisions that favor committing the less costly error.

One such situation involves inferring sexual intent in opposite-sex others. For men, additional sexual partners can contribute directly to reproductive success. However, because women tend to be cautious about casual sex, most men do not have access to many casual sexual partners (Symons 1979). Thus, a Type II error – incorrectly inferring a lack of sexual interest when it is actually present – means losing valuable reproductive resources. In comparison, a Type I error – incorrectly inferring sexual interest when it is absent – results in a comparatively smaller cost of wasted time and effort (Haselton and Buss 2000). Given this cost asymmetry, men may have evolved to overinfer sexual interest in women.

For women, casual sex does not offer the same gains in reproductive success, and potential casual sexual partners are not scarce. Thus, missing a sexual opportunity from falsely inferring a lack of sexual interest is not particularly costly for women. However, women would incur a potentially expensive error if they were to have sexual

relations after falsely inferring commitment from their potential mates (Haselton and Buss 2000). Such a mistake could lead to tying up years of reproductive resources without the support of paternal resources. In comparison, incorrectly inferring that male commitment is insufficient is not as costly, as such an interpretation may also encourage additional or greater displays of quality, investment, and commitment from potential partners. Thus, due to asymmetries in the costliness of errors associated with assessing male relationship commitment, women have likely evolved a commitment skepticism bias (Haselton and Buss 2000).

Directly investigating sexual intent, a classic study randomly placed people into male–female pairs and assigned them to be actors chatting for 5 minutes, or observers instructed to watch the conversation through a one-way mirror (Abbey 1982). Both male observers and actors perceived females having conversations to be more promiscuous and more platonically, romantically, and sexually interested than female observers and actors did. Male actors and observers also reported greater sexual attraction toward the female actor than female actors and observers reported toward the male actor.

Although various explanations have been proposed for these findings, Haselton and Buss (2000) empirically demonstrated that sex differences in the perception of sexual intent reflect error management theory. Specifically, they showed that people are not simply projecting their own views onto their perceptions of sexual intent in opposite-sex others, and that men's perceptions of women's sexual intent differ for a potential mate versus their sister. The latter finding indicates that men are not simply ascribing greater sexual intent to all women but, rather, just to those who constitute potential mates.

Sexual Aggressiveness

Behavioral conflicts may also be induced by sex differences in perceptions of sexual intent as well as the underlying sex differences in desired sexual urgency. This section covers two broad categories of sexually aggressive behavior: sexual

harassment and rape. Whereas sexual harassment involves unwanted or unsolicited sexual attention in general, rape more specifically focuses on the use of coercive physical force to achieve sexual intercourse.

Sexual harassment: Mating conflict in the workplace. In the modern workplace, men and women spend a significant amount of time coming into close contact and getting acquainted with each other. Such an evolutionarily novel environment may be especially conducive to the development of conflicts in mating strategies, as opposite-sex co-workers who can potentially be attracted to each other are expected to interact nonsexually. Indeed, in some work environments, up to 90% of women have reported being sexually harassed in some form.

In the United States, sexual harassment laws grant legal recourse to individuals who receive “unwelcome sexual advances, requests for sexual favors, and other verbal or physical conduct of a sexual nature.” Such conducts cover an extensive range of behaviors, including staring in a sexually suggestive manner; making remarks considered offensive about looks, clothing, or body parts; touching (e.g., patting, pinching, or intentional brushing against another’s body); telling sexual jokes or displaying sexually suggestive posters; making sexual gestures; and sending, forwarding, or soliciting sexually suggestive letters, notes, e-mails, or images. Since the mid-1990s, over 10,000 sexual harassment charges have been filed each year. Consistent with sex differences in reproductive strategies, the large majority of filers are female.

A well-publicized sexual harassment case occurred when Paula Jones filed charges against President Bill Clinton in 1994. According to Jones’ testimony, while Clinton was governor of Arkansas, he exposed his penis to Jones, who was then an employee of the state of Arkansas, and asked her for oral sex in a hotel room. Over the next few years, the president’s sexual history was investigated and made public, but the eventual ruling was that there was insufficient evidence that Jones had suffered any emotional damage. Nevertheless, Clinton settled out of court for \$850,000 (with no apologies).

Another interesting case involves the supermarket chain Safeway, which, in the late 1990s, reinstated a “superior customer service” policy requiring employees to smile, make eye contact with, and warmly greet customers by their name. In the duration of the Safeway program, various female employees were asked about their marital status, propositioned for dates, touched, grabbed, and followed after work to their cars by male customers. Five female employees filed formal charges with the Equal Employment Opportunity Commission, alleging that the Safeway program encourages sexual harassment by creating a hostile work environment.

Both the Clinton and Safeway cases reflect mating-related *strategic interference* (Buss 1989) – violations of one’s preferred mating strategy – in the workplace. That is, much of the sexual harassment that occurs ultimately stems from fundamental sex differences in preferred mating strategies, whereby men are more eager for sexual relations and women are more cautious. In this view, laws governing sexual harassment specifically target the violation of a slow mating strategy by discouraging men (and some women) from pursuing or showing signs of a relatively eager sexual strategy and acting upon potential over-perceptions of sexual interest (as well as strategically feigned displays of interest).

Studies focusing on the characteristics of alleged targets of sexual harassment lend further support to a strategic interference perspective. For example, younger women tend to be more frequently harassed than older women, reflecting men’s preference for younger, and implicitly more fertile, mates (Buss and Schmitt 1993). In fact, people are less likely to believe that a woman who claims sexual harassment was actually harassed if she is physically unattractive – and thus, less sexually desirable – than if she is attractive (Seiter and Dunn 2001). Similarly, women are more likely to be upset by persistent unwanted advances from low-status men such as garbage collectors and janitors than by high-status men such as graduate students and rock stars (Buss 2003). Such findings indicate that sexual harassment is not random conflict, but rather, it stems from one sex pursuing their evolved mating

preferences without the full consent of the other sex, who has their own preferences and standards.

Although men are typically blamed for their unwanted sexual advances, some findings suggest that women's behaviors may play a role in triggering men's overperception of sexual interest. For instance, women, significantly more than men, report smiling and flirting to elicit special treatment from the opposite sex, despite having no sexual interest toward such individuals (Buss 2003). In such cases, men's evolved sexual eagerness is being exploited which may, at times, contribute to sexual harassment.

In summary, the modern-day workplace presents an evolutionarily novel context in which men and women work, interact, and come into close contact with each other. As such, it constitutes a potential mating market as well as a stage for sexual conflict. Various studies are consistent with the possibility that sexual harassment typically occurs as a result of sexual conflict over mating strategies. Although co-workers or customers and service staff are not expected to get sexually involved, they might get attracted to desirable members of the opposite sex in these contexts. Regardless of their social or work roles, men who are relatively more eager for sex may be suggestively indicating their interests toward women, who are strategically more hesitant and who may falsely suggest sexual interest in order to coax other forms of investment from the men. Importantly, and consistent with an evolutionary perspective, sexual advances are more likely to be unwanted, and thus, viewed as harassment, if they involve less socially desirable male perpetrators and younger and more physically attractive female targets.

Rape. A more direct and serious conflict involves forced sexual intercourse or rape – an act that is not limited to humans. Take scorpionflies for instance. When male scorpionflies have access to viable food sources (e.g., arthropods), they typically present food gifts to females, who accept such gifts while offering sexual access in return. However, when food gifts are unobtainable, males will sometimes use their anatomical clamps, or “genital claspers,” to hold the wings of female scorpionflies in place in order to force copulation. Males that are

smaller and less capable of securing food are typically the ones who use their clamps to secure matings (Thornhill and Palmer 2000).

An example closer to humans involves orangutans (Wrangham and Peterson 1996), for which there are two male forms: adult and subadult types. Whereas adults are physically larger, more dominant, and more adept at obtaining consensual matings with females, subadults are generally smaller and less dominant and have difficulty finding interested and willing sexual partners. Consistent with this distinction, subadult males have been observed to be more likely to force copulation onto females than adult males. As with the scorpionfly, the forced matings pursued by subadult orangutans are more the exception than the norm and seem to reflect conditional mating strategies. That is, when such males fail in intrasexual competition or are otherwise unable to provide females with the necessary resources to facilitate consensual sexual relations, the males adopt sexual coercion as a last resort to gain sexual access.

Rape in humans is a widely studied topic. As with sexual harassment, the victim is usually female. In one survey, 54% of American women reported some form of sexual victimization, while 27% reported experiencing rape or attempted rape (Koss et al. 1987). Perpetrators might be strangers, but more than 80% of sexual victimization cases deal with acquaintances, boyfriends, or husbands.

Drawing from an evolutionary perspective, some theorists have proposed that male rape might be an adaptive, conditional mating strategy, such as the ones employed by male scorpionflies and orangutans. Specifically, Thornhill and Thornhill (1983) argued that men may have evolved to rape (or be more likely to rape) when they are unable to obtain a mate through intrasexual competition. This view has been termed as the “mate-deprivation hypothesis” (Lalumiere et al. 1996). Shields and Shields (1983) proposed a similar hypothesis with an additional integration of sociocultural theories of male hostility and power. Both sets of researchers argued for greater attention to be paid to an evolutionary perspective and advocated

the use of a reproductive cost–benefit approach to understanding rape.

More recently, Thornhill and Palmer (2000) presented and evaluated two evolutionary conceptions of rape. On the one hand, rape may be a by-product of other evolved mating mechanisms, such as the male desire for low-cost (minimal courtship) mating and sexual variety. On the other hand, rape could represent a specialized adaptation that activates under certain circumstances. As part of the adaptation, men are hypothesized to have various psychological mechanisms that promote this strategy, including the ability to assess the vulnerability of potential rape targets, a rape mindset that activates when sexual access to consenting partners is blocked, preferences for young and fertile females, and sexual arousal in response to female resistance to men's sexual advances (Thornhill and Palmer 2000).

There is a fair amount of evidence for rape as an evolved mating strategy (see Camilleri and Stiver 2014). For instance, an important prediction made by the rape-as-adaptation hypothesis is that male rapists should have a preference, if not requirement, for fertile females. The potential costs of rape in ancestral times were relatively large and included retaliation from the female, her kin, and her long-term romantic partners. Given such costs, an evolved strategy for male rape should be designed by selection to be particularly attuned to targeting females most likely to bear children. Indeed, similar to those claiming sexual harassment, rape victims appear to be disproportionately in their early 20s (Shackelford 2002) when fertility is highest, with almost 80% of rape victims in the age range of 16–34. It might be argued that this finding is a by-product of women in this age group being more likely to associate with young men, who are themselves the age group most likely to engage in criminal activities in general. However, a comparison between the age distributions of rape and murder victims contradicts this explanation (Thornhill and Thornhill 1983) – murder victims tend to be older than rape victims and are not concentrated among individuals in their 20s.

The most direct evidence of rape's potential reproductive gains for men comes from

pregnancy rates of rape victims. Whereas consensual-pregnancy rates are around 3%, rape-pregnancy rates are significantly higher, near 8% (Gottschall and Gottschall 2003). The majority of rape pregnancies were also concentrated in the 15–24 victim age range. However, rapists' targeting of reproductively aged women may be interpretable from other mating mechanisms. When choosing partners, men are found to have a preference for young women, especially those in the most fertile age range (Buss and Schmitt 1993; Symons 1979). Thus, rapists' choice of fertile targets might reflect an expression of typical male mate preferences. Greater pregnancy rates in rape victims might be due to male sensitivity to female ovulatory cues, coupled with the fact that the rapist is, unlike nonrapists, unconstrained by female choice.

On the other hand, the mate deprivation hypothesis has not received much support for its prediction that men who are unable to obtain mates will tend toward rape (e.g., Lalumiere et al. 1996). In fact, men who reported being physically and non-physically sexually coercive also reported having *higher* mating success and *more* sexual experience. Although this appears to contradict the adaptation hypothesis, it is possible that this survey tapped into a more modern form of “date rape” committed by males who are capable of getting dates but use aggression to speed up or increase the likelihood of copulation, rather than deprivation-motivated (or “loser male”) rape, which could involve strangers and is likely rare among college students. Indeed, a more nuanced evolutionary conception of rape has been proposed by others (McKibbin, Shackelford, Goetz, and Starratt 2008; but c.f. Camilleri 2012). Taking a domain-specific approach, they proposed that five distinctly different types of rapists may have evolved for specific functions: disadvantaged men, specialized rapists, opportunistic rapists, high-mating-effort men, and partner rapists. Perhaps it is useful to conceive of mate-deprivation motivated rape not as a single adaptation but as an initial filter through which other rape adaptations have evolved (Camilleri 2012, p. 180).

While further support for general or specific male rape adaptations is still needed, rape

nevertheless constitutes a violation of females' mate choice and preferred mating strategy. Regardless of its ultimate cause, rape, to the extent that it recurrently occurred in the ancestral past, would have exerted selection pressures for female adaptations to prevent rape.

Evidence for Female Antirape Adaptations

One candidate for a female antirape adaptation is psychological pain from rape. Physical pain draws attention to a part of one's physiology that needs tending to, whereas mental pain draws attention to the social circumstances leading to the pain and motivates avoidance of future similar situations. For example, people become upset in response to having been sexually deceived, which prevents similar mistakes in the future (Haselton et al. 2005). A series of studies reported by Thornhill and Palmer (2000) found that rape victims who were reproductively aged experienced more psychological trauma from rape, as compared with pre- and post-reproductively aged women. Furthermore, vaginal intercourse during rape led to greater psychological trauma – but only in reproductively aged victims. This highlights the sensitivity of psychological pain to the magnitude of the reproductive costs involved, whereby reproductively aged women are the most likely to be impregnated by an undesirable mate as a result of rape.

Trauma experienced by rape potentially serves a corrective purpose, driving the victim to be acutely aware of relevant dangers and to avoid them at all costs. But without previous experience, women also seem instinctively avoidant of risky behaviors, especially when the cost of rape is highest. One such situation is when women are in their ovulatory phase – the one-or-two-day window each month when the chance of conception is highest. For instance, one study asked female participants to evaluate a set of activities on how likely these activities would place someone in a position that is “vulnerable to sexual assault” (Chavanne and Gallup 1998, p. 29). A separate group of females indicated which activities, among the set, they had carried out in the past 24 hours. As predicted, using a composite

score across all activities, participants indicated taking the least amount of risks during their ovulatory phase. Criticizing their use of a composite risk-taking score, others performed a follow-up variant of the study and found that ovulating women specifically increased their nonrisky activities, such as reading at home, while avoiding risky activities, such as getting drunk or walking alone in a park. Another intriguing study found that female handgrip strength significantly increased after women read a hypothetical sexual assault scenario and that this effect was specific to women in their ovulatory phase (Petrallia and Gallup 2002). The researchers interpreted the findings as tentative evidence for a female adaptation to resist rape when pregnancy risk is highest.

Female rape avoidance behaviors have also been found to increase with other individual factors, such as greater physical attractiveness, already having a mate, and not being socio-sexually oriented towards short-term, casual sex (McKibbin et al. 2010). In general, women's rape avoidance behaviors may serve the functions of avoiding: strange men, being viewed as sexually receptive or being alone, and having a heightened awareness of one's surroundings in the interest of defensive preparedness.

To the extent that rape is a sexual conflict, its enactment (versus prevention) confers reproductive benefits onto one sex while exacting costs on the other. Rape is not only costly to females by circumventing their mate and reproductive timing choices, but can also cause physical injury and might lead to abandonment by the female's current mate (Thornhill and Thornhill 1983).

Conflicts of Deception

Conflict can also occur when individuals misrepresent themselves or their intentions to further their own mating strategy but are later found out. Although some deception is not specific to a particular sex, an evolutionary perspective would also predict that much deception would be patterned around the different mating strategies and

mate-selection criteria used by men and women (Buss 1989; Haselton et al. 2005). The prevalence of mating-related deception has been documented in many studies. For instance, people lie to others in more than 25% of their daily social interactions. In mating contexts, both sexes use a diverse set of deceptive acts, both intra- and intersexually (Haselton et al. 2005).

One major type of sexual deception involves misrepresenting one's sexual intentions. As described earlier, men around the world consistently desire a greater number of sexual partners than women do (Buss and Schmitt 1993). Given that men are more eager for sexual relations than women are, it comes as no surprise that men, more than women, are deceptive in service of obtaining sex. In one study 71% of college men admitted to having exaggerated their love and commitment to their potential mates in order to have sex (Buss 2003).

Women, more than men, report having used sexual teasing – intentionally offering some form of sexual contact and withdrawing that offer (Meston and O'Sullivan 2007). As described above, many women admit to flirting with men with whom they have no intention of having sex in order to extract favors from these men (Buss 2003). Correspondingly, more men than women report having been sexually “led on” and being emotionally upset in response to being deceived about sexual access (Haselton et al. 2005). Newlywed women are more likely than newlywed men to report having acted coy and having played hard to get as tactics in attracting their spouse. Thus, while sexual teasing might be an effective female strategy to extract favors and resources from men who are trying to employ a short-term mating strategy, it may also have the effect of allowing women to more effectively fulfill a long-term mating strategy.

On the other hand, men, more often than women, misrepresent their commitment and interest in long-term relations in order to obtain sexual access. This strategy is especially favored by men who are narcissistic, Machiavellian, and psychopathic – “Dark Triad” traits associated with being more sociosexually unrestricted, having

more lifetime sexual partners, and more actively seeking out short-term sexual partners (Jonason et al. 2009). Taken together, these patterns suggest that, regarding sexual access, each sex may be misrepresenting compliance with the other sex's preferred mating strategy in order to promote their personal interests and mating goals.

Conclusion

Sexual conflicts in mating often involve differences in how sexual intent and sexual deception are perceived by men and women. These differences originate from asymmetries in parental investment and can result in sexual harassment and rape. Although men often invest heavily in their children, only women are physiologically obligated to make a substantial initial parental investment (Trivers 1972). This key difference selects for different optimal mating strategies for men and women. Whereas men have evolved to seek greater numbers of fertile mates, women have evolved to be more careful about ensuring that potential sexual partners are of high quality and are willing and able to invest in them and their offspring (Buss and Schmitt 1993; Symons 1979). Therefore, as many studies show, the sexes' preferred mating strategies will often come into conflict. Compared with women, men's eagerness for sex tends to induce overperceptions of sexual intent and greater sexual aggressiveness, which may result in sexual harassment and even coerced sex. Furthermore, members of each sex often deceive the opposite sex (potential mating partners) to induce them to comply with their own preferred sexual strategies. This is done by creating the false impression in the opposite sex that they (the opposite sex individuals) are successfully enacting their own preferred sexual strategies.

Although research has covered a lot of conceptual and empirical ground, there are still various important dimensions related to this topic that have yet to be investigated or considered. For instance, female harassers have been found to be disproportionately younger, single, and more

attractive than the average working woman (e.g., Studd and Gattiker 1991). From an evolutionary perspective on mating conflict, such female harassment might be interpreted as attempts by unmated women to solicit potential partners. However, why especially desirable women would need to harass their potential mates is baffling and requires further explanation. Readers are advised to keep posted for future developments on this topic.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Commitment Skepticism](#)
- ▶ [Error Management Theory](#)
- ▶ [Female Manipulation of Men](#)
- ▶ [Female Mate Choice](#)
- ▶ [Intersexual Selection](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Long-Term Mating](#)
- ▶ [Male Mate Choice](#)
- ▶ [Male Protection](#)
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- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Paternal Investment](#)
- ▶ [Preferences in Long- Versus Short-Term Mating](#)
- ▶ [Sex Differences Versus Gender Symmetry](#)
- ▶ [Sexual Conflict Theory](#)
- ▶ [Sexual Receptivity](#)
- ▶ [Sexual Selection](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Short-Term Mating](#)
- ▶ [Sociosexual Orientation](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)
- ▶ [Violation of Long-Term Mate Preferences](#)
- ▶ [Violation of Short-Term Mating Preferences](#)

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Sexual Conflict in Nonhumans

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Synonyms

[Conflict between the sexes](#); [Precopulatory sexual selection](#); [Postcopulatory sexual selection](#); [Sexual selection](#)

Definition

Sexual conflict is the disagreement over investment that ensues because males and females adopt or develop strategies that are only aimed at increasing their own fitness, but that impose a cost on the mating partner.

Introduction

Males and females differ in their reproductive investment, resulting in what is called “sexual conflict”. In this review we start by offering a brief description of what sexual conflict is and what the important variables are that shape the way in which it is expressed (and can be measured). We subsequently analyze the causes of sexual conflict following Tinbergen's four questions, with a special emphasis on the ontogenetic level, the latter with the specific aim to provide a more integrative view of sexual conflict and its evolution.

What Is Sexual Conflict?

Tregenza et al. (2006) noted that there is no clear or widely accepted definition of sexual conflict, pointing out that “biologists are often reluctant to

commit themselves to narrow definitions of concepts” in order to avoid limits in their thinking (p. 229), something that can be easily verified when looking at different publications on sexual conflict in which no definition whatsoever is provided. However, we consider that providing a definition, even if it is tentative and subject to future modifications as research progresses, is the very first step for constructing a solid theoretical framework in any research field. In the few papers on sexual conflict where a definition is adopted, authors most commonly cite what was put forward by Parker (1979, p.124): sexual conflict is “a conflict between the evolutionary interests of individuals of the two sexes.” Although this definition serves as a good starting point for evolutionary questions, we feel it is not completely accurate since males and females do not have themselves evolutionary interests as such but rather individual interests with evolutionary consequences. Moreover, the interest of males and females when they mate is actually the same: obtaining the highest benefits with the lowest costs (i.e., maximum fitness). One way to increase one’s reproductive fitness is by developing different strategies that increase the likelihood of being chosen by a given partner or by adopting high-quality mate-choice criteria, which result in what is called intrasexual competition for mates (e.g., males competing for access to a female) and mate choice mechanisms. Yet another possibility to increase one’s benefits while keeping costs low is to induce the other partner to increase his/her investment. Such a strategy will then imply a cost for the partner, who is expected to counter-adapt to avoid being manipulated. These two possibilities lead to two different types of conflict: one among subjects of the same sex, which is generally referred to as intrasexual competition, and the other one between the two mating partners, which represents actual sexual conflict. It is crucial to note here that the two can be intricately intertwined, making it difficult to disentangle them fully (see Brennan and Prum 2012).

Thus, sexual conflict is the disagreement over investment that ensues because males and females adopt or develop strategies that are only aimed to increase their own fitness but that imposes a cost

on the mating partner. In other words, what is beneficial for one is detrimental for the other. Such conflict stems from the unequal or differential investment in reproduction of a particular male and female when they mate. This differential investment is already seen at the very early stages of the reproductive cycle due to the fact that the cost of producing gametes is assumed to be different between males and females, which finds its origin in anisogamy (see Table 1; Schärer et al. 2012). Due to differences in gamete size, the production of eggs is generally considered to be more costly than the production of sperm, and consequently, for females, reproductive success is limited by their capacity to produce eggs, whereas for males, reproductive success is more dependent on their access to females (e.g., see Arnold (1994) for a review but see also Janicke et al. (2016) for a meta-analysis on the selection pressures suffered by males, which are stronger than those suffered by females, potentially equating the costs experienced by both sexes). This difference in the costs of gamete production entails a difference in the benefits obtained per unit of energy invested that does not allow males and females to reach their optimal reproductive fitness simultaneously (Parker 2006). As a result, any trait that increases males’ fertilization success will be selected even if such a trait implies a cost for their female partners. The conflict then arises because the strategies that males employ to increase the investment of females are actually decreasing the reproductive fitness of females. Of course, the development of manipulative mating strategies is not exclusive to males, as females also contribute to this conflict by evolving their own mechanisms that lead to increases in male investment and a reduction of their own costs (e.g., Chapman et al. 2003). To give one classic example, a male’s paternity success will be significantly increased if he manages to prevent the female he has mated with from remating with other males (e.g., via mate guarding). This will secure his paternity, but at the same time, it implies an important cost for the female in that she will lose future opportunities to mate with other males. Under that particular scenario, females are expected to develop other strategies

that will allow them to somehow avoid the costs of such mate guarding. This adaptation of the females would not benefit the males and would again lead males to counter-adapt and so forth. Hence, the conflict between the individual interests initiates a process of adaptation and counter-adaptation to the strategies employed by one sex and the other that, over time, results in a continuous evolutionary arms race between the sexes (e.g., see Koene 2012). It is important to note that there are some authors who have criticized this view and instead suggest that mating should be seen as cooperative rather than as a conflict (e.g., Cordero and Eberhard 2003). These authors claim that, for example, females actually increase their fitness from mating with males that are able to manipulate them because they will sire sons that will also be able to manipulate next-generation females (and the same would be true for males who mate with manipulative females). From this perspective, sexual reproduction can be viewed as a cooperative task where males and females have a common goal that is to obtain better-quality offspring. However, we will here stick to the term “sexual conflict” as it allows us

to refer to manipulative traits that are initially harmful for the other sex although they may become beneficial in the long run (see also Brennan and Prum 2012).

Who Is Involved in the Conflict?

Although sexual conflict arises from the different interests of males and females, it can involve more participants than just a male and a female. Generally speaking, it could be argued that as long as there is polygamy, more individuals than just the mating couple will be affected by sexual conflict. In the case of polygamous males, multiple mating can have different costs for the female. For example, males may be sperm-depleted, which could lead to a lower fertilization rate or they may reduce parental care (because they are busy somewhere else) compromising the survival of the offspring. Similarly, polyandry (i.e., a female mating with multiple males) is costly for males: the costs of producing sperm and other accessory gland substances will be high when considering that paternity will be shared with other males (see

Sexual Conflict in Nonhumans, Table 1 Definitions of important psychological and biological concept that we use in the text but that may not be familiar to readers of either field of research

Definitions	
Circular reaction	Repeated display of a basic sensory-motor schema (that animals are born with). It allows animals to interact with the environment and to satisfy their needs, but, as a result of repetition, the schema is modified, resulting into a new one. The new schema will again affect the way an animal interacts with and alters its environment, as well as the schema itself
Anisogamy	Size difference between the types of gametes; generally, females produce large gametes that are usually non-motile (eggs or ovules), and males produce smaller gametes that are often motile (sperm or pollen)
Accessory gland substances/ products/proteins	Products of (male) accessory reproductive glands, usually peptides or proteins. They can be transferred to the mating partner during sperm transfer (along with the sperm) or disassociated from sperm transfer (e.g., via injection using a specialized organ). These substances are also referred to as seminal fluid products/proteins (SFPs) when they are added to the sperm before transfer of the semen (i.e., sperm plus SFPs)
Allohormones	Substances, such as proteins and peptides, that are transferred between individuals of the same species and that induce a direct physiological response, bypassing sensory organs
Organic selection	Organic selection refers to the fact that each individual has the ability to accommodate to the new circumstances of the environment, contributing to its own selection. This is also referred to as the <i>Baldwin effect</i> (i.e., changes in behavior affect reproductive success and adaptation but it does not necessarily imply a change in the genome)

Parker and Birkhead 2013 for a review on polyandry). In this case sexual conflict is tightly related to intrasexual competition and mate choice, which does not only occur before mating but can also happen after mating (i.e., post-copulatory). For example, when a female mates with more than one male, sperm of different males will compete for the fertilization of the ova, and the female can exert a choosy role over the sperm received, reducing the benefits of some of the males she had mated with. This **cryptic female choice** can be inferred, for instance, by looking at paternity biases in her offspring or by looking at the differential reproductive investment that the female performs (see Chapman 2006 for a brief comment on this). One example of such cryptic female choice that leads to sexual conflict can be observed in the female decorated cricket (*Gryllodes sigillatus*). In this species the male transfers a spermatophore (an ampulla that contains the sperm) that is covered by a gelatinous substance called spermatophylax. The female detaches the spermatophylax from the spermatophore and eats it right after copulation has taken place. Once she has eaten it, she removes the spermatophore and thus sperm transfer is terminated. This allows females to bias paternity: the longer she takes to remove the spermatophore, the more sperm she accepts from the male, which is directly related to the male's paternity success. In a study conducted by Ivy and Sakaluk (2007), females of this species were allowed to mate two times with two different males that were either attractive or unattractive. When the second male they mated with was attractive, females retained the spermatophore for longer (i.e., they accepted more sperm) regardless of whether the first male they had mated with was attractive or unattractive. Females thus reduced the first male fitness just by accepting the spermatophore of the second male. This could also be seen as a female mate choice strategy that results in costs for the first male. The female would accept more sperm from the high-quality male because it is beneficial for her, and as a side effect, the first male will lose fitness. This example illustrates why sometimes it is difficult to establish clear boundaries between mate choice and sexual conflict.

Another situation in which more individuals are involved is that of **infanticide**. Infanticide usually takes place when a female is taking care of her offspring. In this situation the target of this harmful strategy is the offspring, sired by a different male, that the female is taking care of. By killing her offspring, the male increases its own reproductive success as it can shorten the interval to the next ovulation, and therefore he can induce mating responsiveness in the female (see Hrdy 1979 for a review on infanticide). An example of infanticide can be observed in a spider species, *Stegodyphus lineatus*. The female of *S. lineatus* guards her fertilized eggs in a sac for about 30 days, after which she opens the sac and the young hatch. Once the eggs hatch, she feeds her offspring by regurgitation and then she gets eaten by the spiderlings. Given the suicidal maternal care and the fact that encounters between a male and a female are very rare (one or two in their lifetime), when a male encounters a female that is guarding an egg sac, he will attempt to mate with her. To do so, males need to remove the egg sac from the female so that she is induced to re-lay eggs and remate. This is very costly for the female because even if she remates, the egg cluster size will be significantly smaller, and hence, her reproductive fitness will be significantly reduced. For this reason, females defend their eggs when they encounter a male (Schneider 1999, and references therein).

Finally, although until now we have discussed sexual conflict between males and females, sexual conflict also occurs in hermaphrodites (reviewed by Schärer et al. 2014; Koene 2016). Since hermaphrodites are both male and female, in order to distinguish between the two sexual functions, we will use the term "sperm donor" to refer to the male function, whereas "sperm recipient" will refer to the female function. In the case of hermaphrodites that take turns when mating (i.e., they are functionally both male and female but at each mating encounter then can only perform one of the two roles), a conflict will ensue whenever the two mating hermaphrodites want to adopt the same, and thus incompatible, role. This can lead to a situation in which only one of them performs the desired role, reducing the fitness of its partner.

Even if there is no conflict over the sexual role to be performed, sperm donors, as in separated-sex animals, will attempt to affect the female function of the sperm recipient. This can be done by means of accessory gland proteins that increase the sperm recipient's allocation to the female function (e.g., by inducing the sperm recipient to lay larger eggs). A clear example has been described in the great pond snail *Lymnaea stagnalis*, a simultaneous hermaphrodite that chooses roles when it mates. The snail that performs the male role transfers accessory gland proteins, among which LyAcp10 (called ovipostatin) that causes a delay in egg laying in the snail that performs the female role (Koene et al. 2010). This delay is followed by a higher investment per egg in snails that repeatedly received inseminations (Hoffer et al. 2012), which increases hatchling success (Hoffer et al. 2017) and thus overall fitness of the sperm donor. A more traumatic manipulation can also be found in banana slugs (*Ariolimax dolichophallus*), which have been reported to bite off the penis of the partner after copulation. Such a strategy seems to force the partner to allocate all its resources to its female function, preventing it from mating in the male role (Reise and Hutchinson 2002).

In short, sexual conflict results in costs or harmful consequences for the partner, but sometimes those costs are suffered by someone else, as it happens in the case of infanticide. Cryptic female choice can also reduce the reproductive benefits a male would obtain when the female mates with more than one male. Finally, although for a long time it was widely accepted that hermaphrodites would not experience sexual conflict, recent empirical research has now revealed that it does occur.

When Is There a Conflict?

The conflict between males and females over reproductive investment can occur at different levels. Here, we will focus on only four of these, namely mate access, paternity, egg investment and parental care, but see Kokko and Jennions (2014) for more. In some species **mate access** is already an important source of conflict even in the

absence of competitors. For example, the female alfalfa leaf-cutting bee (*Megachile rotundata*) actively resists mating with a male by kicking him with her legs and using abdominal thrusts to dislodge him. A female's success at avoiding mating represents a high reproductive cost for the male but is beneficial for the female as she avoids the costs of (superfluous) mating. On the contrary, a male's success at mating reduces a female's fecundity, longevity, and ability to forage (Rossi et al. 2010).

In species that mate more than once, another or a more attractive partner may be encountered. In such a situation, it would be interesting for both males and females to be able to mate again, but this would reduce paternity success of both the former and current mating partners, prompting a conflict over **paternity**. One way of preventing such a paternity cost is by mate guarding, which can be done either pre- or postcopulatory. For example, after mating, males of the moth *Achroia grisella* start signaling to attract other females, increasing the likelihood of engaging in a second copulation. However, because males have just mated, they need to produce new sperm and this takes several hours. In order to increase their paternity success, males copulate for several hours, while the new second ejaculate is being produced. These long second copulations represent a precopulatory mate guarding strategy because it prevents the female from mating with a virgin male and increases the paternity success of the male that performs such guarding. Indeed, when males perceive a male competition situation (i.e., another male competitor's song), the latency to start a second copulation is significantly reduced: they engage quicker in precopulatory mate guarding (Jarrige et al. 2016). Mate guarding can also take place after mating and a typical example of such postmating guarding strategies are mating plugs, which can, for example, be found in male bumblebees (*Bombus terrestris*). They transfer a sticky substance into the female sperm-receiving organ that reduces her willingness to remate (Baer 2003 and references therein). Bumblebees also make use of a more simple strategy to increase their paternity success. They engage in long-lasting copulations so that half of

the female's spermatheca (i.e., where the sperm are stored before fertilization takes place) is filled with their sperm (Baer 2003). Some other animals, like dragonflies, use sperm removal strategies to overcome conflicts over paternity. Their copulatory organs possess small spines that trap the sperm from previous mating encounters and that allow them to remove the other males' sperm from the females' sperm storage organ before transferring their own sperm (Córdoba-Aguilar et al. 2003). All the mentioned displays provide males with advantages since they reduce male-male competition and increase their paternity success; however, for females this is not necessarily optimal (see Brennan and Prum 2012 for a discussion on this). This again illustrates that intrasexual mate competition is highly linked to sexual conflict, blurring the boundaries between the two concepts.

Females can also reduce a male's paternity success by preventing males' sperm from reaching the eggs. For example, red jungle fowl (*Gallus gallus*) females expel males' sperm. Such a strategy can be of great advantage for reducing the costs of mating with a lower-quality male, as it would happen in the case of inbreeding. As shown by Pizzari et al. (2004), when females of this species were inseminated by a brother, the number of sperm that reached the eggs or that was stored in the female's sperm storage organs was significantly lower (no differences were observed in the amount of sperm that males transferred to their sisters or to the unrelated females). An even simpler method of discarding sperm is that of sperm digestion. For example, in many hermaphrodites the sperm that is received can either be digested in a specialized organ or stored for fertilization. In the land snail *Cornu aspersum* (formerly *Helix aspersa*), most – about 99% – is digested (Rogers and Chase 2001).

Another source of conflict between males and females is the offspring, and the first stage at which this conflict can be observed is that of **egg investment**. As previously described, in *Lymnaea stagnalis* the individual that performs the female role receives an accessory gland protein (LyAcp10) that induces a delay in egg laying. Such a delay seems costly for the sperm recipient

because its egg investment is increased and the number of offspring decreased (Hoffer et al. 2012), and, as a result, this may move the sperm recipient away from the optimal division of investment in current and future female reproduction (Hoffer et al. 2017).

In some species, both parents need to take care of their young as otherwise it would be difficult for the latter to survive. This particular situation leads to two different conflicts. One is over the amount of resources that each of the parents is going to invest in the current offspring, and the other is over the optimal moment they should stop investing in the current partner's offspring and divert their resources to new offspring (that could be sired by a different partner or not). There are a number of experimental studies in which the sexual conflict over **parental care** is assessed, especially in birds. To study this, researchers have experimentally manipulated the amount of parental investment performed by either the male or the female. In some cases, one of the parents was removed (which allowed to see if a single parent could provide the same amount of care that is usually provided by two parents), and, in some others studies, the care provided by one of the parents was reduced (e.g., by handicapping one of them). In a recently published meta-analysis on how sexual conflict is resolved in different species of birds (Harrison et al. 2009), it was shown that when one of the parents reduced its caring behavior in terms of food provisioning, the other one compensated by increasing its parental effort although it did not compensate fully. Concerning the moment a parent should stop investing in the current offspring and try to reproduce again, one of the cues an animal can use is partner attractiveness. The attractiveness of the current partner is an indicator of the quality value of the current offspring: the more attractive the partner is, the higher the perceived value of the offspring when compared to future offspring (that may not be sired by an attractive mate), and thus investment in the current offspring is expected to increase (see, e.g., Limbourg et al. 2004). An example of how longer or shorter investment in the current offspring is dependent on the partner's attractiveness can be seen in blue tits (*Parus*

caeruleus). The crown of blue tits presents a UV coloration that is different for males and females and that indicates sexual attractiveness in both sexes. In an experiment conducted by Limbourg et al. (2004), the coloration of the UV component was reduced by using UV-blocking chemicals during the nestling period (i.e., after mate choice had taken place). The results showed that females that had been paired with males of reduced UV coloration invested less in their offspring (they fed them at lower rates) than females that had been paired with non-manipulated males. Taken together, these studies on parental care show that when one of the parents reduces feeding or care-providing rates, this immediately exerts a reduction in the gains that the other parent obtains from having mated with him or her.

In summary, we have reviewed four of the possible reasons why males and females are in conflict. The first one is the act of mating in itself, where animals may not be willing to mate or they may prefer others as partners. The second source of conflict is paternity. Mating with more than one partner will increase genetic variation among the offspring, which can provide great advantages. Because sperm are relatively cheap to produce, males will benefit from fertilizing all the eggs produced by different females, whereas for females it would be more profitable to have their eggs fertilized by different males. The allocation of resources to the eggs once they are fertilized is another source of conflict between males and females, as well as the resources that each of the parents invests in raising the offspring when they need parental care. All these situations suppose a conflict for both parents that will be dealt with differently, as described below, depending on the particular way each species mates.

How Does Sexual Conflict Vary Depending on the Species' Specific Mating Strategy?

There is only one mating system in which sexual conflict would be expected to be more limited: **monogamy**. In situations in which there is strict monogamy, meaning that mating takes solely

place with a single partner, the traits that decrease the reproductive fitness of one sex will also cause a decrease in the reproductive fitness of the other sex (Hosken et al. 2001). Hence, males would be expected to be less harmful for females, and females would be expected to suffer more if they were to adopt a promiscuous strategy versus monogamy (Crudgington et al. 2005). However, the absence of sexual conflict in monogamous mating species can usually only be inferred, since absolute strict monogamy seems to be extremely rare, and even under strict monogamy, conflict can still arise over other mating aspects such as when to reproduce, how often or how many offspring to produce.

In some species, mating occurs in a very traumatic fashion: males cause injuries to the female's genital or non-genital structures. These injuries increase males' fitness for several reasons. For example, **traumatic mating** can allow males to better anchor to the female, but it also represents a more effective way of transferring accessory gland proteins that boost females' investment in reproduction (reviewed by Lange et al. 2013). This reproductive strategy is, for example, observed in the land snail *Cornu aspersum*. During courtship, snails of this species force a calcareous dart through the partner's body wall. Once they have "shot" each other, they mate simultaneously as male and female, transferring a spermatophore to each other. The mucus that accompanies the dart contains substances (called all hormones; see Table 1) that shorten the distance to the spermatophore-receiving organ (so the distance the sperm need to travel is shorter; Lodi and Koene 2016a) and close off the tract that leads to the sperm digesting organ (so less sperm gets digested), thereby increasing paternity success (reviewed by Lodi and Koene 2016b). Between species, the female function of land snails with love darts has counter-adapted to the manipulation of the dart by increasing the length of the duct through which the sperm travel (Koene and Lodi 2016b).

Another mating strategy is called **sexual parasitism**. An example of sexual parasitism is that of deep-sea anglerfishes, in which the males attach to the females either temporarily or permanently. In

Krøyer's deep-sea angler fish, *Ceratias holboelli*, the tissues of the male fuse with those of the female, and even their circulatory systems become shared. The male is then dependent on the female, and he fertilizes her via the circulatory system (Pietsch 2005). Sexual maturity of both sexes is only reached when the male attaches himself to the female. Interestingly, more than one male can be attached to a single female, a situation that would cause high male-male competition over the siring of the offspring. However, to date no studies have addressed how this sexual conflict is dealt with (which is not surprising given that the natural habitats of these animals makes such studies very difficult).

In some species, females display **sexual cannibalism**. Clearly, the male will not achieve any reproductive fitness when the female cannibalizes the male before sperm transfer. On the contrary, sexual cannibalism after copulation presents a (somewhat) more beneficial situation for the male in terms of reproductive success. But in either case, the female's reproductive strategy leads to a very high cost for the male since he loses any future reproductive opportunities. As a result, males can develop different strategies to avoid being eaten by the female. For example, in the web spider *Pisaurina mira*, males have evolved to wrap the female's legs with silk before mating with her, thus increasing his own mating success and survival (Anderson and Hebets 2016).

In many insects and spiders, males provide females with **nuptial gifts** in order to entice females to mate. A particular effect of edible nuptial gifts is that they also serve to prolong ejaculate transfer (e.g., Vahed 2007). For example, in the cricket *Gryllodes sigillatus*, successful copulation occurs after the spermatophore has been transferred to the female. As already reported, this spermatophore is attached to a gelatinous substance called spermatophylax that the female detaches from the spermatophore and eats right after copulation has taken place. Females will take a considerable time to eat the spermatophylax (about 40 min) after which they will remove and eat the spermatophore. When the spermatophylax quantity is small, females will

take less time to eat it and will remove the spermatophore sooner, diminishing the amount of sperm transferred and thus resulting in a lower rate of male fertilization success (Sakaluk et al. 2006). Contrarily, larger spermatophylax result in increased quantities of sperm transferred, leading to a higher proportion of eggs fertilized by that male (i.e., reduced sperm competition). Moreover, prolonged ejaculate transfer will also result in a higher transfer of (allo)hormonal substances (i.e., accessory gland secretions) that are known to reduce female mating receptivity (again reducing sperm competition) or to increase the rate of oviposition (increasing paternity success). Thus, accepting such nuptial gifts from the males implies several costs for the females, such as longer sexual refractory periods that prevent females from mating with other males, thus reducing the benefits that the female can obtain from polyandry (reviewed in Vahed 2007).

All the examples given in this section illustrate that sexual conflict is a constant but that the particular mechanisms that animals use to influence the mating partner vary from species to species. Together with the examples of the previous sections, this overview shows that males of different species try to increase their reproductive success via different strategies that are all aimed at increasing the likelihood of siring the female's offspring. These strategies range from preventing the female from mating with another mate, reducing her willingness to mate again, to increasing her investment in egg production. Sometimes they can even evolve to such extremes that result in physically injure to the partner, as illustrated by the case of traumatic mating. Likewise, in an attempt to maximize their own fitness and at the same time reduce the costs of mating, females have also evolved different behavioral (e.g., cannibalism) and physiological (e.g., sperm digestion) strategies to avoid mating or to bias paternity.

Causes of the Conflicts

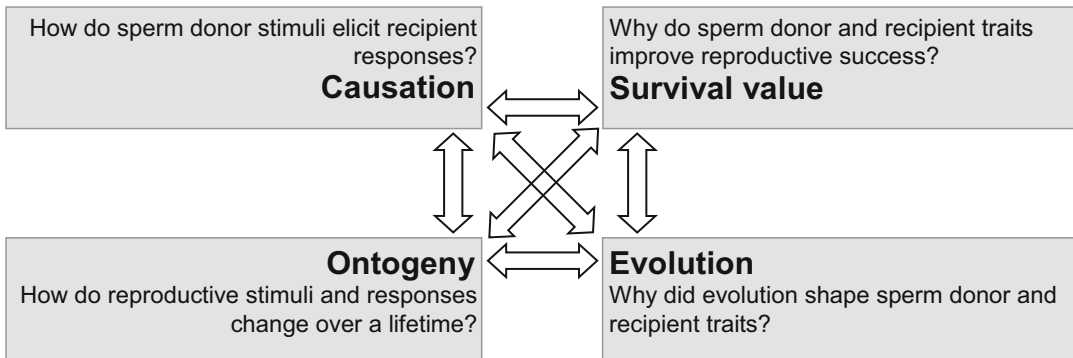
In this section, we will look at the causes of sexual conflict following the scheme suggested by Nico

Tinbergen (1963) for the study of animal behavior. According to him, a particular behavior can be explained in terms of its causation (physiology), survival value (function), ontogeny (development), and evolution (phylogeny). We will provide examples of how sexual conflict can be addressed at each of the four levels, but since one of the main aims of this review is to emphasize how sexual conflict can be affected by experience, we will specifically focus on the ontogenetic aspects that underlie mating behavior and sexual conflict.

The main reason why we will focus at the ontogenetic level is that when considering the different aspects that affect evolution, behavior has long been recognized as one of the main driving forces (e.g., Baldwin 1896). Indeed, behavior and cognition are present in all daily aspects of an animal's life, from foraging to predator-avoidance and sexual decisions, and they can be a source of new and fast adaptations. Surprisingly, the role that they play in some of these domains has been widely overlooked, or even denied, and only very recently have researches started to pay attention to them (West-Eberhard 2003). Concerning sexual selection, some authors have begun to acknowledge that learning has significant implications for mate choice (Witte and Nöbel 2006) or for speciation through sexual selection (Verzijden et al. 2012). Sexual conflict is tightly linked to sexual selection and forms a very important factor that affects the evolution of male and female traits (e.g., Panhuis et al. 2001), but is exclusively explained in terms of genetic mechanisms (i.e., intra-locus and inter-locus sexual conflict; see Koene 2012 for these concepts). Neither in a comprehensive book (Arnqvist and Rowe 2005) nor in a recent edited volume (Rice and Gavrillets 2014) on sexual conflict was any special attention paid to the role played by the psychological aspects of behavior and cognition, while a recent chapter (Chapman 2015) barely skimmed the surface of this important topic within evolutionary psychology. For this reason, we would like to highlight the fact that psychological processes (attention, perception, motivation, learning, memory, and decision-making) are also at play in the context

of sexual conflict and that their study is of great relevance for shedding light on this field of research. Tinbergen used the term “ontogeny of behavior” to refer to the way in which an animal acquires knowledge or a skill (Tinbergen 1963, p. 423). Animals are born with simple and innate sensory-motor coordinations that guide their first experiences, but the outcomes of those experiences will affect the way in which the animal behaves in a circular reaction (see Table 1) that is in constant development (Piaget 1976; see Sánchez and Loredó (2007) for a more detailed definition of this Baldwinian effect). As a result, any behavior performed by an organism is affected by experience, and not solely determined by instincts. The responses that every individual constructs based on its sensory-motor coordinations and experience constitute new learned adaptations, skills, or behavioral responses that have a positive effect on the survival of organisms, as they allow animals to better adapt to the changing demands of the environment or even to certain genetic variations that constrain their survival. This has clear implications in evolutionary terms, and for this reason, the analysis of psychological processes that are involved in the construction of new adaptive habits is of great importance despite the fact that they are not themselves directly determined by the genes (reviewed by Sánchez and Loredó 2007). Although Tinbergen explicitly referred to learning when talking about ontogeny, it must be taken into consideration that learning is intrinsically linked to other cognitive processes (such as attention, perception, or decision making) in such a way that experience affects them and they affect experience. Because of this, when examining the ontogeny of behavior, we will not only address the importance of learning but also of other cognitive aspects that are relevant for sexual conflict.

Importantly, as will become apparent, these four categories are not mutually exclusive, and none of them, when analyzed in isolation, provide a definite answer to sexual conflict (or any other question), but, when taken together in an integrative perspective (see Fig. 1), they can serve to reach a comprehensive understanding of sexual conflict.



Sexual Conflict in Nonhumans, Fig. 1 Schematic illustration of the four questions of Tinbergen applied to the field of sexual conflict. Sperm donors (males) are endowed with physiological mechanisms (causation) that affect sperm recipients' (females') reproductive resource allocation and vice versa. However, physiological responses to reproductive stimuli can be affected by animal's experiences over their lifetime (ontogeny). The way in which sperm donors and recipients deal with sexual conflict situations has an important effect on their reproductive success (survival value) that affects the way in which reproductive

traits evolve (evolution). Importantly, as depicted in the figure, all four questions are interlinked, and thus, an integrative study of the four of them is important in order to comprehensively understand sexual conflict. It is also useful to note that causation and ontogeny topics are generally addressed with "how?" questions, while survival value and evolution with "why?" questions. Moreover, it is useful to realize that causation and survival value focus on the here and now, while ontogeny and evolution look at changes over time

Causation

Causation essentially refers to the physiological mechanisms that underlie a given response, and one example of how physiological responses affect sexual conflict can be seen in the already mentioned case of the land snail (*Cornu aspersum*). In this species, dart shooting enhances sperm storage as it prevents sperm from being digested. However, the female function of the snail that receives the dart and the mucus that covers the dart can counteract this attempt of manipulation by means of sperm digestion, which drastically reduces paternity success of the sperm donor (Rogers and Chase 2001, reviewed in Lodi and Koene 2016a). As a result, these two physiological responses create a constant arms race, which is also commonly seen in separate sexed species.

Survival Value

When studying the function of specific traits of males and females that affect reproductive fitness, one essentially addresses the question of why this has evolved (what is the survival value?). From the neo-Darwinian or modern synthesis perspective, survival value or fitness is often inferred by

looking at genetics: if a trait contributes to an animal's survival and reproduction, it will be selected and passed on to the next generation. Although this parallelism between survival value and genetics is oversimplified, for our purpose it suffices here as it allows us to illustrate how survival value can be measured.

Drosophila melanogaster provides a great model for the genetic measurement of survival value. In this species, different accessory gland proteins affect sperm competition among males. One of them is Acp36DE, a protein that binds to sperm and that enters into the spermathecae of the females, facilitating sperm storage. Genetically modified males that cannot produce Acp36DE transfer normal amounts of sperm to the female when copulating, but their sperm are not accumulated in the sperm storage organs of the female. Because of this, no displacement of previous males' sperm takes place and a lower fertility rate is achieved (Chapman et al. 2000), thus revealing the adaptive (survival) value. Likewise, mutations in a different protein (Acp26Aa, called ovulin) impair the capability of inducing females to lay eggs. This protein has been shown to be responsible for the stimulation of the ovary to

release oocytes. Females that were mated to mutated males that were not able to produce this protein laid significantly fewer eggs than females that were mated to wildtype males (Heifetz et al. 2000). These two studies show how sexual conflict strategies can be addressed at a genetic level and how sexual conflict is of great importance for animals' survival or fitness.

Ontogeny

Throughout this review we have been talking about mating as if it was a simple behavioral response or action that all animals can display automatically or innately (i.e., determined by physiological or genetic aspects). Nevertheless, cognitive processes are also involved. For copulation to happen, "animals must be able to respond to hormonal and neurochemical changes that signal their own sexual desire and arousal, to identify external stimuli that predict where potential sex partners can be found, to actively seek out or work to obtain sex partners, to distinguish external chemosensory cues or behavioral patterns of potential sex partners from those that are not sexually receptive, and to pursue desired sex partners once sexual contact has been solicited. At each step, animals depend not only on the perception of their own internal state, but on the accurate prediction of external events. Such predictions are based on experience, both with the relation between external and internal stimuli and the relation of these stimuli to their sexual consequences" (Pfaus et al. 2001, p. 291). In this description of mating, many psychological processes are involved (e.g., motivation, perception, identification or even prediction). Such processes and the responses that animals display, as claimed by these authors, are mediated by their previous experience, in which learning and memory play a crucial role.

One way of experimentally measuring the effect of learning in a sexual conflict situation is by means of *associative learning*, which is one of the most thoroughly studied forms of learning. As described by Pavlov (1927/2003), this type of learning takes place when an initially neutral stimulus (e.g., an acoustic stimulus) is presented together with a biologically relevant stimulus

(e.g., food). When the neutral or conditioned stimulus (CS) is repeatedly paired with the meaningful or unconditioned stimulus (US), animals start displaying a conditioned response (CR) in the presence of the CS alone. In Pavlov's classical experiment, the sound produced by a metronome (CS) was paired with food powder (US) that was fed to the dogs. After several learning trials, dogs started to salivate (CR) when exposed to the metronome alone, without needing the food to be present.

This type of learning has been shown to be adaptive for animal reproduction as well as it can increase their reproductive fitness at different levels, and one of the first experiments to show this adaptive value was that of Karen Hollis. In her most influential work, she exposed male blue gouramis (*Trichogaster trichopterus*) to a light (CS) followed by either the presence of a male or a female (US). After training, animals were allowed to interact in a test that was signaled by the CS. Animals of the Pavlovian group were able to predict their encounter with a female and responded less aggressively to the females. They delivered significantly less bites compared to the males that were not able to rely on the CS to predict the presence of the female, and they also spent more time in the courtship appeasement posture than the control males (Hollis 1999). This training did not only result in less aggressive behavior toward the female, but it also increased male blue gouramis paternity success: Pavlovian males took less time to induce spawning in the female, and they also produced significantly more offspring than control males. On the contrary, when the lightning of the red light was used to signal the presence of another male, the experimental males increased the number of aggressive responses (frontal displays, bites, and tail beatings) toward the intruder (Hollis 1999). This work demonstrates how Pavlovian conditioning in the blue gourami can help in the identification of a conspecific (male or female) as well as in the selection of the right behavioral repertoire to be displayed at a given encounter (courtship or aggressive behavior). Furthermore, these results show that associative learning had a great impact in terms of sexual conflict: it reduced the level

of male-female sexual conflict (i.e., it induced a faster and higher spawning response in the female). This in turn increased the reproductive and paternity success of the learning males as exhibited by the large amount of offspring sired by the males who were able to use the red light as a predictor of the female.

Comparable results have been observed in the Japanese quail *Coturnix japonica*. In a study conducted by Domjan et al. (1998), a context was used as the CS to signal a mating encounter (US) for the males in the learning group, whereas males of the control group were exposed to the same stimulation but in such a way that they were not able to associate both events. Males in the learning group produced larger ejaculates and a larger number of spermatozoa compared to the control group. These results show how being able to predict a mating encounter can increase sperm competition-related physiological responses in the male Japanese quail while increasing the male's chances of siring a higher proportion of the female's eggs. More notably, the effect of Pavlovian conditioning over paternity success can go even beyond the production of sperm. As Adkins-Regan and MacKillop (2003) reported, the number of fertilized eggs significantly increased when either the male or the female had been subjected to Pavlovian conditioning, which also shows that physiological resistance responses of females can be modified depending upon the females' ability to predict a mating encounter. This type of training can also provide advantages in those situations in which there is male-male competition. This was experimentally tested in a study in which two different males had the opportunity to copulate with the same female, but only one of them received classical conditioning training. In the test, both males copulated with the female and whether the learning or the control male copulated first or second with the female was counterbalanced. The male who had been subjected to classical conditioning training was not only quicker at mating but also sired significantly more offspring (78% vs. 28% instead of the usual 50–50% rate that is found in this species) regardless of who mated first with the female (Matthews et al. 2007). Notwithstanding, how

such male-driven paternity bias can affect female fitness remains unexplored (i.e., the learning male is not necessarily the best one in terms of genetic quality).

Taken together, these studies demonstrate that Pavlovian conditioning can facilitate several stages of the mating sequence by somehow reducing the different sexual conflicts that may be present. The reduction of sexual conflict can be achieved by a change in the behavioral response, as in the case of the blue gourami: increased or decreased aggressive or courtship responses. Importantly, such behavioral changes had an effect of significance on the spawning response of the female. Likewise, learning mediates the physiological responses of the Japanese quail as manifested by the increase of sperm production, fertilization rate, or even paternity rate.

However, not all the experience that affects sexual conflict is acquired through associative learning and experience does not necessarily lead to a reduction of the sexual conflict. Experiments with guppies (*Poecilia reticulata*) have shown that when females are allowed to choose between two different males, they consistently prefer the same given male but that this preference can be reversed if they are allowed to observe a second female near the non-preferred male (Dugatkin and Godin 1992). In this scenario, females are conducting two different perceptual assessments: they are evaluating the quality of the two males but also the quality of the model female. Indeed, it has been observed that guppy females will choose the same male an older female has chosen, but not the one chosen by a younger female (Godin et al. 2005). In this case, age-dependent *imitation* would actually increase sexual conflict in terms of female-female competition. In a situation in which there are several females that select the same male, the male might experience sperm depletion, thus reducing the benefits the female would obtain.

In some of the examples already mentioned in the previous sections (e.g., the males of the moth *Achroia grisella* who reduced the latency to their second mating when they heard another male's song; the female of the red jungle fowl that was able to get rid of sperm coming from a brother, or

the birds who reduced their investment in their offspring as a consequence of a reduction of their partners' attractiveness), it is clear that animals assess the quality of their partners and invest accordingly. In all these examples, animals perceive a situation, assess the information they have processed, and make a decision on the quality of the mate. However, in none of these examples was the role of experience examined, and one could feel tempted to attribute the responses observed in each case to instincts or physiological mechanisms. In turn, studies in which learning has been shown to be relevant (see below) invite us to be cautious about such attributions.

Within the mating sequence, psychological processes have been shown to especially affect mate access, which is the first level at which sexual conflict is observed. As just illustrated, mate choice can be affected by learning from other conspecifics, but it can also be modified upon individual experience. For example, mate choice preference can be determined by simple exposure to a given phenotype (i.e., *familiarity*). Female wolf spiders (*Schizocosa uetzi*) do not display any innate preference for two extreme male phenotypes (brown or black pigmentation of a portion of the tibia of the forelegs) when they had not been exposed to either phenotype as subadults. However, they did show learned preferences after having been exposed to one or the other phenotype before reaching maturity: they were more likely to mate with the male of the familiar phenotype and also more likely to cannibalize the male that had the unfamiliar phenotype (Hebets 2003). This demonstrates the impact that learning can have on a sexual conflict situation, with extreme consequences for the males. In naturalistic situations, this conflict is reduced because males mature earlier than females and court them while they are still in their last stage before reaching maturity. This allows females to learn about the different male phenotypes so that the likelihood of mating with a particular phenotype increases and the chances of cannibalizing the male of that familiar phenotype are reduced.

For other species, familiarity is not enough and successful mating provides animals with

cumulative experience that shapes the way sexual conflict is dealt with, as it occurs in the Pacific field cricket (*Teleogryllus oceanicus*). In this species males produce two songs, a short-range one and a long-range one, the long-range ones being the most preferred by females. Nonetheless, it was experimentally shown that if females mated with an unattractive male (short-range song producer) and on the following day they encountered another unattractive male, in this second mating, females took less time to mount males (which signals female's willingness to mate), and they also retained this second male's spermatophore for longer (Rebar et al. 2011). The longer retention of the spermatophore correlates with the amount of sperm that is transferred and therefore paternity (see above), so, in this situation, females' previous experience would reduce sexual conflict with the second mating male.

All the examples mentioned above show that mate choice is not innate but a cognitive process that starts with the detection and perception of the mate (or of a model) and that it also implies an evaluation of the processed information as well as a decision-making process that is influenced by different sorts of past experience (Ryan et al. 2009). The outcome of this complex series of processes is going to affect one of the most important decisions that animals make in terms of reproduction, and it will also have important consequences in terms of sexual conflict. Based on the experiments reported, learning and cognition affect sexual conflict at the level of mate choice and paternity success (as shown in the case of the female crickets that retained the spermatophore for longer), but it can also have major implications for the offspring. In several studies it has been observed that parents' investment in their offspring varies according to their mate preferences. For example, in a study conducted with house mice, male preferences between two females were assessed before pairing half of the males with their preferred females and the other half with their non-preferred females. The litter size and the number of offspring that survived to the reproductive age (among other variables) were greater when males were allowed to mate with their preferred female than when they had to

mate with their non-preferred female (Gowaty et al. 2003). Similarly, female canaries of the species *Serinus canaria* allocate different amounts of testosterone to the eggs they laid depending on the attractiveness of the males' song to which they had been exposed. They allotted more testosterone to the eggs they laid when they were exposed to attractive male songs than when they were exposed to unattractive songs. This difference in the allocation of testosterone leads to hatching asynchrony that in turn affects the survival of the offspring, so the male whose offspring has received less testosterone will see his parental success significantly reduced (Gil et al. 2004). These results certainly show that there is an ongoing assessment of the quality of the partner and that such evaluation has important consequences on the total fitness of both males and females. In both examples given, males and females were investing less in the offspring they had sired, thus increasing the partners' costs. Interestingly, so far there are no studies that test the possible changes in offspring number or viability after preference for a given mate has been altered as a result of learning.

In short, learning and other cognitive processes are involved in sexual conflict situations. They can affect sexual conflict at, at least, two of the four levels: mate access and paternity. Concerning egg investment and parental care, it is certain that animals do assess their partner's quality to invest accordingly; however, the role of learning still needs to be more convincingly explored and integrated into our thinking. Thus, although ontogeny exerts an important effect, it must be acknowledged that a systematic evaluation of how animal psychology affects sexual conflict is still needed in order to fully appreciate the role that ontogeny plays in this domain.

Evolution

Phylogenetic analyses can shed light on the evolution of genetic, physiological, or behavioral responses that we observe in the field of sexual conflict. This type of analyses would allow us to identify the preceding events that have

contributed to the occurrence of such adaptations. For example, regarding physiological traits that are involved in sexual conflict, phylogenetic comparisons have revealed how males and females have developed adaptations and counter-adaptations to overcome sexual conflict. An example of this can be observed in male seed beetles (Coleoptera: Bruchidae), who possess spiny genitalia that injure the wall of the female copulatory duct. This trait is thought to provide benefits to the males as it allows them to better anchor themselves to the female during copulation and seems to also transfer accessory gland proteins (Hotzy et al. 2012). However, the presence of spines on males' genitalia imposes a cost for the females, and a comparative study of the male and the female genitalia of three different species of seed beetles has shown that, as males developed more harmful genitalia, females counter-adapted by evolving a more resistant copulatory tract, protected with thicker connective tissue (Rönn et al. 2007).

Regarding the phylogenetic analyses of behavioral responses, studies are not very abundant, but one example can be found in the diving beetles (Coleoptera: Dytiscidae). In this family, females of two different species (*Rhantus binotatus* and *Dytiscus alaskanus*) have been observed to exhibit behavioral mating resistance (rapid and erratic swimming and attempts to dislodge the male by driving him into the substrate or against objects). In contrast, females of two other species (*Ilybius gagates* and *Neoporus undulatus*) do not show any resistance behavior when males attempt to mate with them. The behavioral resistance response seems to have coevolved as a counter-adaptation to long-lasting matings: the two species that do not resist male mating attempts take shorter to mate than the other two (Miller 2003 and references therein). However, no intermediate stages have been described so far, so this analysis remains inconclusive.

Finally, species' general mate preferences have been reported to also have an evolutionary origin as it has been observed in the platyfish preference for long-sword males. Swordless platyfish are thought to be more ancestral than swordtails, and female preference for the morphological trait

has been suggested as a pre-existing bias that shaped the evolution of the genus *Xiphophorus*. Swordtail females of two species that do not possess swords (*X. maculatus* and *X. variatus*) display clear preference for males that have artificially longer swords than normal males. Moreover, the exact same pattern of results was observed in females of a sister genus (*Priapella*) that do not possess swords at all. These results indicate that female preference for a sword-bearing male had to arise in an ancestor of the two genera (Basolo 1995).

In summary, phylogenetic analysis can help us to better comprehend the evolution of morphological, physiological, or behavioral traits that are involved in sexual conflict. However, as at the level of ontogeny, more studies that analyze the evolution of the aforesaid traits are needed for a complete understanding of sexual conflict.

Summary and Concluding Remarks

While the boundaries and definition of sexual conflict are still a matter of debate, in this review we have defined it as a consequence of the differential investment in reproduction of males and females (or the sperm donor and recipient in the case of hermaphrodites). This differential investment leads to more or less harmful mating strategies that can be displayed (at least) at four basic different levels: mate access, paternity, egg investment, and parental care. The participants involved in a sexual conflict scenario and the general strategy that allows overcoming the sexual conflict will vary depending on the level at which sexual conflict takes place and the species under study. When the sexual conflict is over mate access, animals can harass their mates or even cannibalize them. This immediately implies mate-avoidance responses or the development of different choice criteria by the individual that is competed for (usually the female). When the conflict is over paternity, strategies such as mate guarding, cryptic female choice, sperm digestion, sperm removal, or accessory gland proteins will be used to influence the partner's investment or to avoid

being manipulated. Seminal fluid proteins are also important when there is a conflict over egg investment, just as some other resource allocation mechanisms that can be displayed by the females (e.g., time of spermatophore acceptance). Finally, when the conflict is over parental care, a reduced investment in terms of feeding or protection can be observed among some animals, especially birds.

The particular way in which sexual conflict takes place and is dealt with at each level will strongly depend on the mating strategy of the species of focus (e.g., male spiders that wrap females to avoid being cannibalized and to increase paternity success). All the mentioned adaptations that animals have developed to increase the partner's investment lead to counter-adaptations on the other sex. It is for this reason that sexual conflict plays a fundamental role in evolution. Importantly, behavior is a ubiquitous component of animals' lives; however, the way in which psychological processes shape how sexual conflict is dealt with has been widely overlooked in the literature on sexual conflict. The studies reviewed in the preceding show how different psychological mechanisms, especially learning, affect the investment of males and females in reproduction, reducing or increasing it.

Analyzing sexual conflict in terms of Tinbergen's four questions, especially in terms of ontogeny, has allowed us to understand sexual conflict and its role in evolution in a more comprehensive way. Notwithstanding, caution should also be taken when doing this, for two main reasons. The first one is that although it might seem that the four questions about behavior are independent from one another, they are fully interlinked (sometimes overlap), and all contribute to a full explanation of a behavior (Tinbergen 1963; see also Fig. 1). The second one is that, due to the current focus of genetics as the causal factor of any aspect of an animal's life, it has been somehow implicitly accepted that Tinbergen's four questions are hierarchical; being changes in the genes that causes changes in the physiological response, what in turn allows animals to develop behavioral changes to finally cause phylogenetic changes that lead to evolution. As a consequence

of this, ontogeny has not received the deserved attention from an evolutionary perspective, or, if it has, it has been reduced to genetics. Indeed, conventional thinking considers that evolution is solely gene-mediated and behavior is very often also explained in terms of a genetic trait that can be selected upon (see, e.g., Gottlieb 2002). According to this perspective, all the possible behaviors an animal can display are encoded in that animal's genome, and if a given behavior leads to successful adaptation, it will be passed onto the offspring of that animal until it becomes a common trait (i.e., instinct) among a given population. Conversely, from the perspective of organic selection (see Table 1; Baldwin 1896) and EvoDevo, the *ability* to produce a behavior or a response in itself can become common due to a genetic change but not the adaptive evolutionary response per se (e.g., a behavioral innovation, such as the use of a tool, can become general within a group or population and be maintained along generations through social influence resulting in adaptation but not in evolution; West-Eberhard, 2003). Behavior and physiology are the two most flexible, faster, and reversible responses animals can display in a changing environment situation. They allow animals to express a novel phenotype, increasing the adaptation and the accommodation of the phenotypic change, but such adaptation and accommodation of the phenotype does not necessarily imply a genetic change. Like any other advantageous phenotypic variation (e.g., morphological variations), behavioral changes that increase adaptiveness will also be selected, but they will not be necessarily inherited (Sánchez and Loredó 2007; West-Eberhard 2003). Because of its high level of flexibility and its fundamental role on adaptation, behavior has long been recognized as a leading factor in evolution by some authors (Baldwin 1896), but its importance as such has only started to receive attention very recently. Experimental work like that of Karen Hollis in the blue gourami or that of Michael Domjan in the Japanese quail showed how associative learning (a change at the ontogenetic level) does actually have a major effect in the physiological responses involved in

reproduction. There is also experimental evidence from the field of epigenetics that shows that changes at the ontogenetic level can have important effects not only at the physiological but also at the genetic level (it can affect gene expression). This evidence questions the general assumption of a one-way genetic causation mechanism, and it contributes to the growing body of evidence on the connections between the different levels of causation (as depicted in Fig. 1) as well as to the acknowledgment of behavior as a crucial factor in evolution. Again, it must be emphasized that behavioral responses are not a genetically driven display. Behind any behavior that we observe, psychological processes such as perception, learning, memory, or decision-making are constantly present. They are the mechanisms that allow animals to interact with and to adapt to a changing environment. For this reason, whether our aim is to understand foraging, predator-avoidance, or sexual conflict, an integrative approach in which psychological processes and ontogeny are considered must be adopted. This does not deny the importance of genetics, but a complete picture of animal evolution will only be achieved if the different levels of analysis are fully integrated. In this work we have tried to provide a more integrative overview of sexual conflict by gathering examples of the four levels as a first step to a full and comprehensive understanding of sexual conflict and its evolution, although as noted in different parts of the manuscript, more work needs to be done to achieve this goal.

Cross References

- [Classical Conditioning](#)
- [Copulatory Plugs](#)
- [Copulatory Intrasexual Competition](#)
- [Counteradaptations/Female Counterstrategies](#)
- [Cryptic Female Choice](#)
- [Evolutionary Arms Race](#)
- [Intralocus Sexual Conflict](#)
- [Nonhuman Sexual Conflict](#)
- [Ontogenetic Versus Deferred Adaptations](#)
- [Sperm Competition: Evidence in Nonhumans](#)

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Sexual Conflict Theory

► Evolutionary Psychology and Intimate Partner Violence

Sexual Conflict Theory (Middle-Level Theory in Evolutionary Psychology)

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Definition

Intraspecific selection that occurs when an adaptive trait in one sex comes at a fitness cost to the other sex, which creates a condition for antagonistic counter-adaptations to evolve.

Introduction

Sexual conflict refers to intraspecific selection that occurs when an adaptive trait in one sex comes at a fitness cost to the other sex, which creates a condition for antagonistic counter-adaptations to evolve, sometimes appearing like an arms race.

Sexual conflict occurs in one of two ways: intralocus and interlocus sexual conflict. *Intralocus sexual conflict* is when a trait is expressed in both sexes (i.e., allele variation occurs at the same locus), but fitness outcomes of the trait for each sex are different. An example of intralocus sexual conflict among humans is height – the relationship between height and number of offspring is curvilinearly related among men, but negatively related among women. Specifically, shorter height is associated with more offspring among women and fewer offspring among men, and average height is associated with more offspring among men and fewer offspring among women (Stulp et al. 2012). *Interlocus sexual conflict* is when different traits from each sex have conflicting interactions (i.e., alleles from different loci are in conflict), creating the possibility of agonistic coevolution. A common example comes from water striders where female copulatory resistance and male forced copulation represents a conflicting interaction. Sexual conflict may also result in palliative adaptations when sexual conflict produces collateral harm (harmful side effect of the trait that may impact both sexes). Though much of the literature has focused on nonhuman sexual conflict, this review will outline how sexual conflict has been applied to human psychology.

History

Sexual dimorphism was initially understood as a function of female mating preferences resulting in either indirect reproductive benefits (see ► [Fisher Process](#) or ► [Good Genes](#)) or direct reproductive benefits, such as receiving more resources or acquiring a mate who invests in their offspring (reviewed in Chapman et al. 2003). Sexual conflict is an alternative model that views sexual dimorphism as a cause or consequence of conflicting traits. Prior to Parker's formal articulation of sexual conflict theory, a few scholars had similar insights. Williams (1966) elaborated on R. A. Fisher's early suggestion of this idea by describing how a conflict between female choosiness and male dishonest signaling creates

an “evolutionary battle of the sexes” (p. 184). Trivers (1972) later described how sex differences in parental investment influences mating behavior: high parental investment is associated with being more selective in a mate whereas low parental investment is associated with greater competition for acquiring mateships. Such a scenario suggests there are conflicting interests between the sexes. Dawkins (1976) also suggested that if parent-offspring conflict occurs when they share 50% of genes, then conflict between mates should be much higher.

Sexual conflict was formalized by Parker (1979), who provided the most thorough investigation of the topic by using mathematical modeling to explore conditions and the extent to which sexual conflict could occur and by reviewing species that likely exhibit forms of conflict. Since Parker's seminal work, the concept of sexual conflict has received considerable attention, challenged traditional explanations of cooperative breeding, been widely applied across taxa to understand sex differences in physical and behavioral traits, and used to understand speciation (Parker and Partridge 1998), sperm competition (Stockley 1997), mate choice (Gavrilets et al. 2001), sexual coercion (Muller et al. 2009; Watson-Capps 2009), aging (Bonduriansky et al. 2008), among others. For reviews of sexual conflict in the nonhuman animal literature, see Arnqvist and Rowe 2013; Chapman et al. 2003; Parker 2006; Stockley 1997; Tregenza et al. 2006.

Middle-Level Theory in Evolutionary Psychology

More recently, sexual conflict has been applied to human psychology. Sexual conflict can be understood as a middle-level theory because it explains how sexual selection applies to a particular domain; it explains both the causes and consequences of traits that confer unequal fitness between the sexes. Though intralocus sexual conflict (see [Intralocus Sexual Conflict](#) section) has been applied to humans, such as conflict over height (Stulp et al. 2012), most psychological traits are addressed by interlocus sexual conflict

(see [Interlocus Sexual Conflict](#) section). Although much of the reviews have focused on applying sexual conflict to preexisting data and research, studies directly testing the application of sexual conflict theory to humans has been scarce. To date, only a few studies have been published that tested for the presence of intralocus sexual conflict in humans.

Intralocus Sexual Conflict

Intralocus sexual conflict occurs when a trait is expressed in both sexes but is beneficial to one sex and costly to the other. For example, a preference for indiscriminate sex would benefit men, but the same trait among women would be costly because of high investment in offspring with nonpreferred traits. Likewise, choosiness among women would benefit them by ensuring reproductive success through mate quality, but this same trait among men would be costly because it would reduce mate number. Only a few empirical studies have directly tested hypotheses informed by intrasexual sexual conflict among humans.

Garver-Apgar et al. (2011) demonstrated how men with more physically masculine traits had a higher mate value than their sisters, that estrogen was associated with greater mate value for women relative to their brothers, and that testosterone was associated with greater mate value for men relative to their sisters. These findings suggest that genes that code for either more masculine or more feminine traits benefits one sex while coming at a cost to the other. A similar study looked at facial masculinity and attractiveness: not only was masculinity correlated between male-female twin and sibling pairs, but there was a negative correlation between brother masculinity and sister attractiveness, though masculinity was not associated with attractiveness among men (Lee et al. 2014).

There is also evidence for intrasexual conflict over height in humans: amongst shorter male-female sibling pairs, females had more reproductive success, whereas the opposite was true for average height pairs (Stulp et al. 2012). This study more accurately used direct measures of reproductive success, rather than perceived

attractiveness (which should correlate with reproductive success or one's mate value).

Sexual conflict theory provides interesting insight into the evolution of female mating resistance by questioning whether it functions to screen potential partners or functions by reducing the costs of multiple matings (costs include time, energy, exposure to risk for injury, infection, toxins, reduced parental investment, etc., see Gavrilets et al. 2001). Though no clear answer has emerged, this example shows how sexual conflict can be used to generate new or competing hypotheses about the evolution of certain traits (Chapman et al. 2003). Similarly in humans, women's "choosiness" has been suggested to evolve through sexual selection to screen for potential mates, though such a trait could be a response to the costs of multiple mateships pursued by men or could even be a source of conflict towards men (choosiness is costly to men's optimal strategy of mate number/frequency). Still, a large amount of empirical and theoretical work is needed to understand how female mate choice and mating resistance can be explained through intralocus sexual conflict (Arnqvist and Rowe, book; Chapman et al. 2003), and although applications to humans are being proposed (e.g. Buss 2017), direct empirical tests are needed. Still, since humans meet many of the conditions that give rise to sexual conflict, such as variance in mate quality along with sex differences in reproductive rate (Arnqvist and Rowe 2013), intralocus sexual conflict may provide insight into the evolution of human mate choice.

Interlocus Sexual Conflict

Interlocus sexual conflict is when different traits in each sex are in conflict. Much of the psychological literature on interlocus sexual conflict focused on theoretical possibilities – how sexual conflict *could* apply to humans (Buss 2017; Mulder and Rauch 2009; Shackelford and Goetz 2012), and draw from supporting empirical work, but do not directly test for interlocus sexual conflict. Though terms sometimes vary, they generally categorize interlocus conflicts based on when

they occur: before mating (i.e., precopulatory or before sperm transfer), during mating (i.e., in copula or during and after sperm transfer but before conception), and after conception (post-conception, after birth; see Koene 2012; Shackelford and Goetz 2012).

Sexual Conflict Before Mating

Before mating, these are actions towards an opposite sex target that increases the probability of mating, but such actions are costly to that target. In other species, infanticide has been used as an example of this (Koene 2012). There is evidence to suggest how infanticide by males in some species functions by ceasing lactational amenorrhea and speeding up the time a female can mate with him. As Palombit (2015) reviewed, more recent research considered female counter-strategies to such conflict, including multi-male mating for paternity confusion (with a male counter-strategy of recognizing kin among multiple pups), female aggression as a deterrent, social isolation, building social coalitions, and social monogamy. Sexual conflict is an unlikely explanation for infanticide among humans because women are more likely than men to commit infanticide, and its prevalence is quite rare.

Sexual conflict could arise outside pair-bonded individuals when there are sex differences in optimal mating strategies (i.e., there is a conflict between men's interest in mating frequency and women's choosiness in mating partner). Conflict could still arise within pair-bonds when optimal reproductive rates differ (women may want a longer interval between children, whereas men may prefer a shorter interval), or when one partner pursues extra-pair mating.

Sexual deception and anti-deception have been cited as a source, and response to, conflict prior to mating (Buss 2017). Men may use sexual deception by displaying false signals of relationship commitment and love, whereas women could use sexual deception through false signals of sexual interest to secure resources, while both sexes could use sexual deception by falsely advertising their mate value. These sources of sexual conflict

are predicted to have led to antagonistic counter-strategies, such as anger and the ability to detect cause of deception.

Sexual coercion, which are actions that diminish female choice in mating (see Muller and Wrangham 2009), seem to meet the criteria for sexual conflict before mating among humans. These acts include herding (aggressive separation of women from other men), sequestration (aggressive removal of women from their social group), and harassment (persistent sexual pursuit until female capitulates or flee) that function to prevent extra-pair copulations. They benefit the male coercer by increasing his probability of mating while being costly to females due to restricting their mating options, such as offspring interval or extra-pair copulation.

Sexual Conflict During Mating

Sexual conflict during mating occurs during or after sperm transfer but before conception. There is a growing number of topics that may be relevant to sexual conflict during mating, such as orgasm, cryptic female choice, nuptial feeding, semen and vaginal chemistry, forced copulation and rape, intimate partner rape, and sexual cannibalism (see Shackelford and Goetz 2012).

The specific costs and benefits of traits during mating have been directly tested in nonhuman species. Fruit flies, for example, have been studied extensively. There are numerous costly effects of male accessory gland products that increase male reproductive success through improving the chances of successful sperm competition (Arnqvist and Rowe 2013), but are costly to females. These costs include decreasing female attractiveness to other males, reduced sexual receptivity, and increasing egg production.

In humans and other species that form pair bonds, a likely source of conflict during mating is cuckoldry risk, defined as the increased probability a female partner has an extra-pair copulation. Under such a scenario, females may benefit from offspring with better genes, but such actions come at a reproductive cost to their male partner, whose resources unknowingly go to unrelated

offspring. Considering cuckoldry incurs a steep cost to males, several counteradaptations to minimize cuckoldry risk may have evolved. These counteradaptations include various sexually coercive tactics, such as sexual harassment and intimate partner rape (see Camilleri 2012; Camilleri and Quinsey 2012). These actions are hypothesized to function by minimizing the risk of cuckoldry by engaging in sperm competition (i.e., sperm from multiple males within one reproductive cycle compete for insemination). Intimate partner rape creates a new source of conflict to females, whereby insemination may occur from a non-preferred male, or incurring physical injury. Several studies have linked cuckoldry risk with intimate partner violence and sexual coercion. Indirect preventative actions could also have evolved, such as aggressively herding to separate females from other males, or sequestering females from her social group, both functioning to prevent extra-pair copulations. Although findings are consistent with sexual conflict, specific tests of its relevance to sexual conflict are needed. For example, indirect benefits of having sexually coercive sons still need to be ruled out to qualify as a form of sexual conflict.

Sexual Conflict After Conception

Sexual conflict after mating occurs when there are conflicts in parental care of offspring because greater parental care can be costly by decreasing opportunities for additional mateships. Generally, one sex would benefit if the other sex invested more in their offspring. In nonhumans, this has been studied in the context of mate desertion and amount of offspring care. These ideas are now being applied to humans. For example, kin detection may impact parental investment (Platek and Ryan Porter 2012), and some evidence found that mothers and their family members typically suggest babies resemble fathers, possible to increase paternal care (Daly and Wilson 1982). Sexual conflict after conception also has implications on mate expulsion. Relationship dissolution may occur in response to costly actions from one's partner, such as infidelity, lack of investment, or

reduced sexual interest (Wade 2012). The operational sex ratio may impact sexual conflict where, for example, in female-biased sex ratios, men may be less inclined to invest in their partner and offspring. Buss also proposed how sexual regret could be a form of sexual conflict, presumably because its effect on increasing choosiness becomes costly to her pursuer.

Limitations to Sexual Conflict Research

There are several issues that limit research in sexual conflict (see Arnqvist and Rowe 2013), which includes isolating the effect of traits on fitness, and correlating the evolution of conflicting traits in males and females. Even if such correlations are found, there may be other explanations for such a relationship. Also problematic is that some traits are difficult to measure, analyses are based on the current function of a trait, and their effects are also difficult to measure because counterstrategies may mask preceding sources of conflict. There is also difficulty in ruling out indirect benefits, as was the case of females who are sexually coerced having sexually coercive sons, and in determining whether harm is a byproduct of a trait (i.e., *collateral harm*, neither sex benefits). Limitations to studying sexual conflict are even greater among humans since fitness costs and benefits are difficult to measure and experimentation is not possible. Attention to mathematical models, and triangulating results from multiple empirical methodologies, can help overcome such issues.

Conclusions

Sexual conflict may prove to be powerful theoretical model to explain the etiology of various human sex differences. Though much of the theoretical and empirical work has been conducted with non-humans, scholars are now pursuing its application to human psychology. Examples of human sexual conflict includes sexual deception and sexual exploitation (conflict before mating), cuckoldry risk (conflict during mating), and child

support (conflict after mating). However, only a few studies have directly tested hypotheses derived from intralocus sexual conflict in humans, and to the author's knowledge, no direct tests of human interlocus sexual conflict have been conducted. The application of sexual conflict to human psychology would benefit from careful empirical tests of specific hypotheses derived from this middle level theory.

Cross-References

- Fisher Process
- Good Genes
- Sexual Coercion
- Sexual Selection

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Sexual Congress

- ▶ [Penile-Vaginal Sex](#)
 - ▶ [Sexual Intercourse](#)
-

Sexual Contact and Sexual Disgust

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Synonyms

[Sexual aversions](#); [Sexual avoidance](#); [Sexual preferences](#)

Definition

Sexual disgust is an emotion that functions to motivate individuals to avoid the pursuit or acceptance of fitness-compromising sexual behaviors.

Introduction

Sexual reproduction likely evolved because, relative to asexual reproduction, it produces offspring that are better equipped for battle in arms races

against pathogens (Ridley 1993). In light of its evolutionary history, the fact that sexual intercourse can result in genital warts, herpes, chlamydia, and HIV (among other infectious diseases) can seem like a humorous counterattack from pathogens. Of course, the pathogens transmitted sexually are not necessarily the same ones that would benefit from a pool of genetically homogeneous hosts; specific viruses and bacteria (along with other critters) have evolved to occupy a niche in the ecological space created by reliable genital-to-genital contact between conspecifics. These sexually transmitted pathogens – along with other consequences of sexual contact – have favored host counter-adaptations that function to reduce the fitness-impairing consequences of sex. Some of these adaptations are psychological, and some of these psychological adaptations shape sociosexual orientation, preferences for sexual variety, preferences for specific traits in partners, and emotional sensations, including sexual disgust.

Sex and Pathogens

Whereas mammalian predators have evolved to use stealth attacks and brute strength to make contact with (and, then, consume) their prey, pathogens have evolved to invisibly hitchhike into their hosts (including us) via our food, our water, our air, and our social partners (Tybur et al. 2013). Given that all humans must eat, breath, drink, and share contact with conspecifics, the psychological adaptations regulating these behaviors are likely designed to trade off benefits of contact against (pathogen) costs of contact (Tybur and Lieberman 2016). The psychological adaptations regulating mate choice should similarly weigh the benefits of contact (typically, a chance at conception) against the pathogen costs of sex.

The genitals are warm and moist, and one of their functions (transmitting or receiving gametes) requires sustained contact with another individual's genitals. They are, then, an ideal location for pathogens to reside, comfortably housed within one host and ready to be transmitted to another. Further, sexual behavior also involves extensive

nongenital contact, with skin touching skin and, in many cases, mouths touching skin, mouths, and genitals. Although pathogens transmitted via air droplets (e.g., tuberculosis) and skin contact (e.g., ringworm) are not typically referred to as “sexually transmitted” infections, they are more readily transmitted during sexual interactions than during other social interactions that require less contact.

The pathogen consequences of physical contact have likely shaped the evolution of human sexuality; indeed, researchers have proposed that the pathogen costs of multiple sexual partners can favor the evolution of monogamy (Loehle 1995) and may have done so especially in humans (Mackey and Imerman 2000). Mathematical simulations suggest that the pathogen costs of sex can affect sexual strategies, though they do not necessarily uniformly favor monogamy; instead, they can increase variability in monogamy versus promiscuity (Boots and Knell 2002; Kokko et al. 2002b), or they can favor monogamy versus promiscuity depending on pathogen virulence (McLeod and Day 2014). In sum, simulation studies suggest that pathogen costs of sex can influence sexual strategies and they detail the nature of these consequences under different transmission conditions.

Of course, while we can be confident that sexually transmitted pathogens were present in the human ancestral past, their virulence, frequency, and fitness consequences (and, hence, their ultimate impact on human sexual psychology) are difficult to estimate. Research programs dedicated to understanding how pathogens have shaped human sexual psychology have thus more frequently generated and tested hypotheses of how mate preferences vary across individuals and contexts.

Pathogen Avoidance and Sexual Strategies

Having a large number of sexual partners can provide several benefits, including protection, increased offspring number, and increased offspring diversity (Buss and Schmitt 1993). Of course, people do not seek to maximize their number of sexual partners, since the costs of having more partners often exceed these benefits (Gangestad and Simpson 2000). One of these

costs is pathogenic – each successive sexual partner risks exposing an individual to a new collection of pathogens. Individuals might weigh these benefits and the pathogen costs of sex differently, with those who are more invested in avoiding pathogens favoring a less pathogen-risky sexual strategy (i.e., fewer partners). Some research is consistent with this idea. Sociosexual orientation – the degree to which an individual is open to sex outside of a long-term relationship – is negatively related to the degree to which an individual is motivated to avoid pathogens, as assessed by measures of (pathogen) disgust sensitivity and contamination sensitivity (Duncan et al. 2009; Murray et al. 2013; Tybur et al. 2015). Such patterns are mirrored at the national level, with individuals in higher parasite stress countries having more restricted (monogamous) sociosexual orientations (Schaller and Murray 2008).

Reducing sexual partner number is not the only way to mitigate the pathogen costs of reproduction; one can also limit sexual contact to the minimum required for conception (i.e., penile-vaginal intercourse). Individuals more invested in avoiding pathogens appear to do so. Sensitivity to pathogen disgust and contamination sensitivity both relate to the degree to which individuals report being disgusted by a range of sexual acts, including anal sex, oral sex, multiple partners, and even watching erotic videos (Tybur et al. 2009, 2015). Again, cultural level findings mirror individual differences findings, with individuals in higher parasite stress cultures engaging in less romantic kissing (Murray et al. 2017).

Pathogen Avoidance and Mate Preferences

In addition to influencing sexual openness, pathogen-neutralizing aspects of our mating psychology might also influence the types of sexual partners an individual prefers. Potential partners vary in both their current infectiousness (sexually transmitted or otherwise) and their likelihood of being infectious in the future (see Tybur and Gangestad 2011, for an overview). To an individual selecting a mate, the former has immediate infection consequences, and the latter can have future infection or investment (parental or otherwise) consequences, should a long-term,

interdependent relationship be established and maintained. If infection consequences of partner choice have shaped mate selection psychology, we might observe that individuals who invest effort in avoiding infections prefer individuals with a lower likelihood of infection. A body of evidence suggests that this is indeed the case. Multiple studies have found that women who are more disgusted by cues to pathogens have stronger preferences for masculine faces, voices, and body shapes in men (DeBruine et al. 2010b; Jones et al. 2013), which putatively signals health (Folstad and Karter 1992). Individual differences studies on pathogen disgust and masculinity preferences are complemented by evidence suggesting that, in nations with greater health problems, women prefer greater masculinity in male faces (DeBruine et al. 2010a). Another study finds that individuals exposed to cues to pathogens report greater preferences for dimorphism and symmetry in opposite-sex faces (Little et al. 2011), and another finds that childhood illness predicts preferences for dimorphism in opposite-sex, but not same-sex, faces (de Barra et al. 2013). Still another finds that men higher in pathogen disgust prefer women with lower waist-to-hip ratios (Lee et al. 2015), which are associated with long-term health and fertility (Jasienska et al. 2004; Singh 1993). Finally, evidence suggests that individuals higher in pathogen disgust sensitivity are especially unattracted to individuals low in physical attractiveness (Park et al. 2012), which can be viewed an aggregate perception of a bundle of reproductively relevant qualities (Miller and Todd 1998), one of which might connote current infectiousness or parasite resistance (Henderson and Anglin 2003; Thornhill and Gangestad 1993).

Although this literature indicates that there is a relationship between mate preferences are influenced and pathogen-avoidance motives, the exact nature of that relationship – and its implications for understanding how mating preferences function to neutralize the infection consequences of sex – remains opaque. The relationship between human sexual dimorphism and current or future infectiousness is unclear (Kokko et al. 2002a; see also Scott et al. 2012), as is the

relationship between attractiveness and global health (Weeden and Sabini 2005). Further, findings from one study suggest that pathogen disgust sensitivity relates to masculinity preferences only among young adults (Lee and Zietsch 2015). And other findings suggest that masculinity preferences in health-challenged societies reflect preferences for intrasexual competitive ability (and, perhaps, protection) rather than immunocompetence (Brooks et al. 2011). In sum, then, some evidence casts doubt on the hypothesis that preferences for sexual dimorphism or attractiveness function to select mates who are able to resist infection. Nevertheless, pathogen-avoidance motives could relate to preferences for certain traits (including sexual dimorphism) even if those traits connote benefits apart from immunocompetence. Any physical contact with a conspecific – and, especially, sexual contact – presents an infection risk. Individuals more avoidant of pathogens might show stronger preferences for dimorphism, attractiveness, or symmetry if they require higher-quality mates (e.g., in terms of fertility or intrasexual competitive ability) to risk the infection chance of any contact. Further research is needed to test this possibility and to clarify apparent inconsistencies in the literature.

Sexual Disgust: More Than Just Pathogens

When asked to describe things that are “disgusting,” many individuals nominate sexual behaviors (Tybur et al. 2009). Given the fact that disgust motivates the avoidance of pathogens (Tybur and Lieberman 2016), disgust toward sex can, at first blush, appear to solely function to motivate the avoidance of the pathogen consequences of sex. A closer look at sexual disgust suggests something different. Consider incest, the most universal of sexual disgust elicitors. Although sex with a sibling exposes an individual to comparable infection risk as sex with an unrelated individual of a similar age and attractiveness, the former elicits disgust, and the latter can elicit arousal (or, perhaps, less disgust). The consequences of incest that lead to disgust are thus unlikely to be pathogenic; instead, they likely reflect the poor genetic compatibility of close relatives and, ultimately, the opportunity costs that come along with

investing finite time and energy into a poor reproductive partner (Tybur et al. 2013). Other instances of sexual disgust might similarly function to attenuate broader costs than those imposed by pathogens. A physically unattractive individual might elicit disgust when considered as a sexual partner, but might be a perfectly acceptable partner for another task that requires close physical contact and, hence, risks pathogen transmission. Again, disgust toward sex with this partner would primarily be reflecting motivations to avoid the opportunity costs of reproducing with an individual of limited sexual value rather than avoiding contact with an infectious individual.

Sex differences in sexual disgust are consistent with this perspective. In the development of the Three Domain Disgust Scale, Tybur et al. (2009) report that women score 1.51 standard deviations higher on a sexual disgust instrument, but they score only 0.15 standard deviations higher on a pathogen disgust instrument. Whereas the sexes pay similar infection costs in the event of contact with pathogens (cf. Fleischman 2014), they suffer vastly different opportunity costs from sex. Whereas men can be saddled with reputation costs and social pressure to invest in a sexual partner or offspring, women can lose the opportunity to reproduce for the period of gestation and beyond and pay high energetic costs in the event of pregnancy (Buss and Schmitt 1993).

The Function of the Qualia

In comparison to the sensation of pathogen disgust, which seems tailored to motivating the avoidance of physical contact with pathogens (Oaten et al. 2009; Tybur et al. 2013), the function of the sensation of sexual disgust is less clear. On the one hand, it could function to motivate physical avoidance of individuals perceived as having low sexual value (e.g., relatives, individuals of poor genetic quality). On the other hand, other emotions more efficiently motivate avoidance (i.e., fear) or dissuade others from pursuing sexual contact (i.e., anger). Of course, flight and/or aggression in response to sexual advances is also costly, and sexual disgust might motivate sufficient avoidance to communicate a lack of sexual receptivity to a courting individual. That said, if

sexual disgust functions primarily to communicate a lack of interest, then the sensation of disgust might motivate verbal and nonverbal behaviors, including facial and vocal expressions of disgust, that signal a lack of interest to a courting individual. More empirical work is necessary to elucidate the manner in which sexual disgust might mitigate the costs of sex.

Conclusion

Mathematical simulations and behavioral science data support the theory-based arguments that some aspects of human sexual psychology function to neutralize pathogens. The precise nature of these psychological mechanisms remains unclear, though, as is their contribution to acquiring mates who are currently noninfectious or who are likely to be noninfectious in the future. Similarly, although humans clearly experience sexual disgust, the function of the qualia remains unclear, and further research is needed to adjudicate between competing hypotheses.

Cross-References

- [Disease Avoidance](#)
- [Disease Avoidance Hypothesis](#)
- [Disgust](#)
- [Human Sexuality](#)
- [Oral Sex](#)
- [Pathogen Disgust and Perceptions of Attractiveness](#)
- [Sex-Differences in Disease Avoidance](#)
- [Sexual Orientation and Human Sexuality](#)

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Sexual Control

- [Origins of Patriarchy](#)
- [Sexism](#)

Sexual Daydreaming

- [Sexual Fantasy](#)

Sexual Debut

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Synonyms

[First coitus](#); [First intercourse experience](#); [First sexual behavior](#); [Sexual initiation](#)

Definition

Generally, the time one experiences heterosexual sexual intercourse (e.g., vaginal-penile) for the

first time; increasingly, sexual debut also includes sexual experiences not involving penile/vaginal intercourse such as anal intercourse.

Introduction

Evolutionary theory posits that an integral developmental process in adolescence is the attainment of reproductive status. This occurs when an adolescent develops “physical and social competencies needed to gain access to a new and highly contested biological resource: sex and, ultimately, reproduction” (Ellis et al. 2012, p. 615). Through developing these competencies, adolescents and young adults may become sexually promiscuous and competitive (Weisfeld and Coleman 2005) leading them to engage in sexual behavior or experiencing their sexual debut. Considering the importance of this evolutionary milestone, it is essential that a holistic understanding of the precursors and implications of sexual debut is constructed. Research on sexual debut, and therefore the organization of this entry, has mainly focused on: (1) rates and timing of sexual behavior; (2) risks associated with early sexual debut; (3) protective factors against early sexual debut; (4) outcomes of early sexual debut; and (5) additional considerations in understanding sexual debut.

Rates and Timing

The average age of sexual debut for girls and boys in the United States is 17 (Carlson et al. 2014). When considering timing of sexual debut beyond the age of the adolescent in years, developmentally appropriate age cutoffs are often selected. Based on current norms in the United States, three categorizations are utilized to show early (before age 15), middle (or normative, between ages 15 and 19), and late sexual debut (after age 19; Harden 2014). Other studies contextualize the timings a bit differently considering sexual debut that occurs before the age of 16 early, and normative between the ages 16 and 19 (Spriggs and Halpern 2008). These differences can be explained through understanding the different

definitions of sexual debut. For example, in one study, earlier ages of sexual debut often include both sexual intercourse and other sexual behavior. On the other hand, when the later ages are used, the authors of the studies are usually considering only intercourse, or coitus. Taking into account the differing psychological and social outcomes of having sexual experiences at different development stages can help determine the long-term implications that timing of sexual debut has on personal well-being and romantic relationships in later adolescence. Effects of early sexual debut, such as drug and alcohol use, mental health problems, or divorce, extend into adulthood as well. We discuss the findings in these areas in section four.

There are a host of demographic characteristics that affect the age at sexual debut. For instance, boys (as compared to girls; Jordahl and Lohman 2009) and sexual minorities are at higher risk of having earlier ages of sexual debut (Brown et al. 2015). Further, African-American adolescents are more likely than their Hispanic counterparts to have their sexual debut before the age of 14. Hispanic adolescents, in turn, are more likely than White adolescents to have their first sexual experience prior to age 14. In addition, Asian males experience later sexual debut than their Hispanic, White, or African-American counterparts (Cavazos-Rehg et al. 2009). Pubertal timing has also been shown to influence the age of sexual debut in that individuals who reach puberty earlier than their peers are more likely to have early sexual debut (De Genna et al. 2011).

Given the increase in attention paid to sexual relationships that occur outside of a romantic relationship (e.g., hooking up), it is important to consider not only when adolescents are choosing to have sex but also with whom (Boislard et al. 2016). For example, although the majority of teenagers were “going steady” with the partner with whom they had their first sexual experience, 13% of girls and 27.3% of boys had their first sexual encounters with a friend, not a romantic partner. These rates vary greatly by race/ethnicity. While 20.7% of White teen males had their first sexual encounter with someone with whom they were “just friends,” 40.5% of non-Hispanic Black teen males experienced their first sexual encounter

with a friend (Abma and Martinez 2017). Thus, an evolving research area calls for investigation into the context of adolescents’ first sexual experience rather than simply the age alone. That is, the relationship of the adolescent to their partner may be important given almost a quarter of adolescents have their sexual debut with a friend rather than someone with whom they are in a romantic relationship (Abma and Martinez 2017). While most people experience their sexual debut in adolescence, the aforementioned contextual factors vary greatly among individuals. It is therefore important to note these as well as the following risk and protective factors in developing programs, policies, and research to encourage optimal development.

Risks Factors

Numerous characteristics are shown to influence or promote early sexual debut. Many are typically defined as characteristics of adverse environments that lead the adolescent to adopt an accelerated reproductive strategy including initiating sexual behavior at an earlier age. For example, adolescents raised in low family income households and those whose fathers are absent (specifically in boys) tend to have earlier ages of sexual debut (Xu et al. 2018). Moreover, research has shown specific family structures such as parental cohabitation, single-mother headed households, and stepfamilies are associated with adolescent engagement in early sexual debut (McCutcheon et al. 2018). These associations clearly demonstrate the importance of the family context on sexual debut.

Further, delinquent adolescents have a higher likelihood of experiencing early sexual debut than their nondelinquent peers (Jordahl and Lohman 2009). This may be due to the strong influence peers have on adolescent sexual behavior (Savolainen et al. 2015) and the link between early sexual debut and delinquency. Further, drug use and depression are both linked to early sexual debut (Koleva and Stuart 2014). Taken together, it is important to consider many of these risk factors concurrently when working

with adolescents in a clinical, research, or educational setting.

Protective Factors

A positive framework surrounding sexuality in adolescence is only recently gaining traction in this field of research. Thus, information on protective factors is dwarfed by the details discussed pertaining to the risk factors. Despite this, there *are* protective factors that help to delay early engagement in sexual experiences. For instance, rather than family composition, recent research has shown that the family context has a protective influence on sexuality (Brown and Shillington 2017). That is, while adolescents whose parents are divorced are more likely to experience early sexual debut, a positive mother-child relationship can help overcome this risk factor (Sieving et al. 2000). Further, there is evidence showing that high maternal education (Jordahl and Lohman 2009), parental support (Moore and Chase-Lansdale 2001), and, in boys, early parental monitoring (Lohman and Billings 2008) can all serve as protective factors against early sexual debut.

Beyond the immediate family context, school environment and peers can also serve as protective factors. As stated above, peers have a strong influence on adolescent sexual behavior (Sieving et al. 2006). Specifically, when peers delay sex, adolescents are also more likely to engage in this behavior at later ages (Ajilore 2015). Moreover, performance in school is also associated with sexual behavior in adolescence such that higher grades are indicative of fewer sexual partners (Paat and Markham 2016). Given the outcomes of early sexual behavior, discussed below, it is imperative that both risk and protective factors are incorporated in efforts to create policies and interventions that delay sexual behavior.

Outcomes of Early Sexual Debut

Rates of early sexual initiation are associated with a host of psychological and behavioral outcomes during adolescence as well as over the lifespan.

For example, individuals who have sex at earlier ages are more likely to be diagnosed with lifetime sexually transmitted infections (STIs) in adulthood. Those who have sexual debut early are also more likely to experience teenage pregnancy (Finer and Philbin 2013). However, this is typically also associated with a lack of use on contraception in younger ages. In addition, teens who experience their first sexual encounter at earlier ages will delay the use of contraception (Finer and Philbin 2013), not use condoms, and have more sexual partners (Lowry et al. 2017) leaving them at risk for STIs and unintended pregnancies. These teens are also less likely to complete high school (Bengesai et al. 2018; Spriggs and Halpern 2008).

Also considered a risk factor (discussed above), delinquency has been shown to be an effect of early sexual debut in that adolescents who have earlier sexual debut are more likely to engage in delinquent behavior than their peers who have late or on time sexual debut (Armour and Haynie 2007). Research needs to address the co-occurrence of these behaviors prospectively over time.

Early sexual debut has also been associated with mental health symptoms in adolescence and adulthood. Specifically, Vasilenko et al. have found that having an early sexual debut predicts depression in adulthood (Vasilenko et al. 2016). However, others have shown that early sexual debut was associated with depression in adolescence, but not in adulthood and only in adolescent girls under the age of 16 (Spriggs and Halpern 2008). This association does not appear in boys or girls who have on time initiation or had not yet had their sexual debut. Finally, this association dissipated over time indicating that the long-term effects are less or nonexistent.

Further Considerations

The literature on sexual debut mainly focuses on sexual behavior in adolescence in opposite sex encounters with few studies asking for specific information on same sex sexual experiences. Recent estimates show that 20% of individuals

age 18–34 identify as LGBTQ (lesbian, gay, bisexual, transgender, or queer) compared to 12% of adults age 35–51 and 7% of adults age 52–71 (glaad 2017). Therefore, there is room for growth in this area of research and practice. One way to change the heteronormative research surrounding sexual debut may be to ask about specific sexual behavior at different ages. Indeed, while the majority of individuals report vaginal intercourse at their sexual debut, other behaviors such as oral or anal sex should also be considered.

Further, there is a large body of literature looking at sexual debut among adolescence; however, there is a dearth of research focusing on same-sex sexual debut. While most people can agree on the definition of “coitus,” an agreed upon definition of sex that transcends orientations is nonexistent (Carpenter 2001). This lack of an overarching definition of sexual debut that encompasses all sexual orientations complicates our understanding of the influences and outcomes of sexual debut among sexually minoritized individuals. Indeed, the experiences of individuals whose first sexual experience is with a person of the same gender have been heretofore often excluded (Kreager et al. 2016). It is important that the term “sexual debut” is operationally defined clearly in studies so practitioners, researchers, and policy analysts can successfully contextualize the study findings so as to accurately apply them to specific populations.

Conclusion

Further clarification is warranted in our understanding of what exactly sexual debut means (e.g., how is it defined) and how it fits into the evolutionary understanding of human development. While there is a wide body of literature regarding the influences and outcomes of normative and nonnormative sexual debut, simply referring to sexual debut as “coitus” or initiating sexual behavior leaves inordinate ambiguity in our understanding of how this behavior affects adolescents. Acknowledging the variables associated with early sexual debut, clinicians should assess patients with early sexual debut for substance

use, sexual risk taking, depression, and STIs. Moreover, due to the simultaneous existence of many of these constructs, adolescents exhibiting any of these should be screened for these poor mental health symptoms, STIs, substance use, and other risk behaviors.

Given that many of the aforementioned outcomes are also risk factors of early sexual debut (i.e., delinquency), comprehensive sexual education should be developed to include information about sexual abuse – coercion – and delinquency – such as drug use – prevention (Lowry et al. 2017). Additionally, this education should be implemented early, giving adolescents accurate information regarding aspects of sexual behavior using age appropriate techniques. It is important to remember that sexual debut at younger ages is more likely to be coerced than when it occurs at later ages (Finer and Philbin 2013). Considering this association between coercion and early sexual debut, adolescents would benefit from learning about consent from their teachers and parents as early as kindergarten. Engaging adolescents in these discussions at younger ages, before sexual risk behaviors occur, may help to deter adolescents from experiencing early sexual debut and therefore mitigate the negative, long-term effects (United Nations 2009).

In sum, existing research on sexual debut focuses heavily on risks and outcomes of first coital experience. Future research should thus consider, not only additional behaviors beyond penile/vaginal intercourse, but also other sexual behaviors which, when excluded, further marginalize LGBT populations. Additionally, policy makers should focus efforts beyond simply delaying age of sexual debut. Rather, focus should be redirected educating adolescents and children about sexuality to allow them the autonomy to make healthy, smart decisions about sex (Carter 2012).

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Sexual Deviation

► Sexual Pathology

Sexual Differentiation

► Development of Sex Differences

Sexual Dimorphism

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Synonyms

Gender differences (i.e., culture and sense of being male or female); **Sex Differences**

Definition

Structural and behavioral differences between the sexes that have biological origins.

Introduction

Dimorphism in human secondary sexual characteristics is similar to those of other primate species in which competition between males (intraspecific) is coalitional in nature. However, humans are unique in the complexity of social competition, necessitating sexually differentiated and sophisticated socio-competitive competencies that require elaboration within the particular social and cultural ecology. Preferences begin with prenatal organization by androgens, resulting in sexually segregated social groups in childhood, which promote the sex specific elaboration of socio-competitive competencies necessary for adult reproductive competition and parenting.

Evolution of Sexual Dimorphism

Darwin (1871) noted that selection can occur in response to ecological conditions (natural selection), as well as interactions within a species (social selection), of which mate competition is a component (sexual selection). Sexual selection describes competition between males (intrasexual) for access to costly female gametes and parental investment, as well as discriminatory female choice (intersexual). Male competition and female choice are the general pattern, but there are role reversals and other nuanced discussions beyond the scope here (e.g., Clutton-Brock 2007). Sexual selection has been utilized to describe sexual dimorphism in hundreds of species as well as humans (Geary 2010). Sexual selection is especially powerful in species with internal gestation resulting in larger, aggressive males, with weapons, armor, or costly honest displays of fitness.

In primates, the intensity of competition between males is associated with sexual body size and canine size dimorphism (Plavcan 2001). When one male can monopolize many females

and competition is decided through contests, such as Gorilla, males are nearly twice the size of females. Monogamy and coalitional competition are associated with reduced dimorphism (Plavcan et al. 1995), which appears to be the case for chimpanzees and humans. The hominin fossil record describes extreme dimorphism early, which is diminished in humans, though men have on average 61% more muscle mass and 75% more upper body strength (Lassek and Gaulin 2009), suggesting that humans exhibit characteristics of combat competition (Hill et al. 2017).

Human Reproductive Ecology and Adaptations

To understand how selective pressures differ between the sexes, it is important to understand a species' reproductive ecology. Humans are generalists regarding ecological adaptations having achieved some amount of ecological dominance (Alexander 1990). The most uniquely human adaptation is the neocortex resulting in sophisticated cognitive capacities that support competition with conspecifics (for review Flinn et al. 2005). Working memory and executive functioning create the ability to mentally simulate social scenarios allowing planning, foresight, and mental time travel. Theory of mind allows humans to understand others and enables empathy. Moral emotions connect individuals and promote group beneficence in decision-making (i.e., guilt, pride, and embarrassment). Consciousness and multiple order reasoning allow complex deception and deception detection mechanisms. The end result is a brain that is three times larger than earliest fossil hominin and consumes 20% of our resting metabolism and 40% in infants. As a result, human infants are born uniquely altricial requiring the longest development and the most intensive parental investment, including paternal investment, which is unique for primates in the context of multi-male groups and extremely rare in mammals generally. Humans exhibit adaptations that promote male-female pair-bonding in adulthood, such as concealed ovulation, nonreproductive sexual intercourse, female orgasm, and romantic

love (Flinn et al. 2005). The nested human family with its extensive network of kin and affines serves to provision and nurture the most socially competent and competitive primate in accruing and elaborating extreme socio-competitive competencies necessary for successful mating in groups comprised of other such individuals (Geary and Flinn 2001).

Developmental activities are thought to result in refinement of physical, cognitive, behavioral, and social competencies that enhance reproductive prospects in adulthood (Geary 2010). Sex differences in developmental activities are predicted to the degree that the sexes differ in patterns of intrasexual sexual competition, intersexual choice, and parental investment (Geary et al. 2003). In humans the specifics of adult social competition occur across cultures, but the subtleties are specific to the social and cultural ecology, to which the human child is adapted during its developmental period (Geary 2006). For humans, coalitional competition between groups is lethal in nature, placing a premium on group size and cohesion, facilitated by within-group cooperation. Competition between women tends to be about the resources needed to reproduce, and as direct physical aggression reduces a woman's reproductive potential, it tends to be of an interpersonal nature placing a premium on sophisticated social skills that are both prosocial and indirectly self-serving.

Development of Human Sex Differences

Sexual differentiation begins with sex chromosomes, with males getting a Y chromosome which contains the SRY gene and begins the production of androgens, the most important of which is testosterone. Testosterone has masculinizing effects during critical periods. Once organized prenatally, testosterone remains low until puberty at which time it again organizes the brain and body, promoting male-typical secondary sexual characteristics. After puberty testosterone increases acutely in response to particular reproduction-related stimuli, such as status challenges and sexual stimuli. The organizational-activational framework describes the majority of

phenotypic differences between the sexes, though some have been shown to be related directly to the sex chromosomes, through genetic or epigenetic effects (for review Arnold 2017).

The prenatal organizational effects of testosterone result in early differences between the sexes in preferred stimuli and activities. For example, before social and cultural influences, looking time preferences in newborns indicate that females prefer looking at a human face as opposed to males looking longer at a mechanical object (Connellan et al. 2000). By 3–4 months, using looking times, males appear to recognize spatially rotated objects (Quinn and Liben 2008). By 6–8 months, viewing images of actual children, boys preferred looking at a group, while girls preferred looking at an individual (Benenson et al. 2007). Preferential looking time at 12, 18, and 24 months show girls preferring to look at dolls and boys prefer to look at cars (Jadva et al. 2010). That the sex differences occur so early suggests they are not the product of socialization, but rather the origin of social preferences and the resultant sexually differentiated behaviors, even in cultures where gender behaviors are not encouraged (Nelson 2005).

Beyond stimuli, preferences for activities are affected by prenatal testosterone measured in amniotic fluid which is associated with the development of male-typical play in boys (Auyeung et al. 2009). Even females exposed to high levels of testosterone prenatally (i.e., congenital adrenal hyperplasia) show a preference for male-typical toys, rough-and-tumble play, and male playmates (for review Hines 2014). However, genetic males (XY) unable to utilize testosterone (i.e., complete androgen insensitivity syndrome) develop as normal well-adjusted women (Wisniewsky et al. 2000). Early exposure to androgens appears to set in motion the development of preferences for male-typical social activities.

Developmental Elaboration of Sexually Differentiated Socio-Competitive Competencies

While many of the competencies elaborated during human development are similar between

the sexes, social and competitive styles are the exception. Beginning in infancy, females are more attuned to subtle social cues, such as looking at faces and identifying adult emotions, showing greater self-regulation, and exhibiting fewer negative emotions (Benenson 2013), whereas boys are more object oriented. Not surprisingly, as soon as the sexes begin to socialize, interpersonal style and differences in preferred activity push them apart into self-segregated peer cultures (Maccoby 1990), which provide separate venues for skill rehearsal and elaboration.

For boys, in an extensive review of the literature, Rose and Rudolph (2006) found that boys tend to have larger playgroups with well-defined dominance hierarchies and engage in rough-and-tumble and competitive play. Without direction, boys appear to be inherently biased to form groups and compete at the group-level (i.e., between groups) (Geary et al. 2003). Indeed, humans are the only species that engages in group-level social play (Alexander 1989). In contrast to girls groups, in which conflict tends to increase over time, boys' groups show conflict early on, but once the hierarchy is formed, within-group conflict ceases and between-group conflict increases (Savin-williams 1979). Girls' relationships are generally characterized as more prosocial interactions, however boys tend to be more socially gregarious given the opportunity, seeking out unfamiliar same-sex peers (Benenson et al. 2012) and forming relationships more readily. Boys tend to have more integrated social networks as their friends tend to also be friends with one another. Once formed, relationships are more durable (Benenson and Alavi 2004), and males are more likely to resolve conflicts with peers when they arise (Benenson et al. 2014) and more likely to express affiliative or reconciliatory behaviors after competitive encounters (Benenson and Wrangham 2016). As males progress through adolescence, the coalitions show greater role differentiation, with explicit goals, and less conflict within group.

In contrast to boys, girls' pretend play often involves parenting, dolls, and activities involving less explicit winners and losers. Girls tend to interact with one or two other girls; their

interaction tends to be characterized by greater expression of emotion and connection-oriented goals, self-disclosure, sensitivity to distress in peers, and seeking and providing of support (Rose and Rudolph 2006). In middle childhood, girl's dyads become more intimate and exclusive, characterized by unconditional acceptance, bonding through reciprocal discussions, and sharing vulnerabilities. Girls tend to compete through indirect means, disguising true intent, and use of gossip and backbiting aimed at damaging reputation and social networks of other girls. As girl's progress through adolescence and skills in interpersonal intimacy and indirect competition are honed, relationships become more stable and mutually beneficial, facilitative alliances which enforce egalitarianism in resource distribution (Benenson 2013). As a woman's concurrent and future offspring are in jeopardy if she is injured, women avoid direct aggressive confrontation (Campbell 1999).

By puberty, sex differences in social styles are divergent enough that the process of *coming together* is somewhat problematic (Maccoby 1998) and requires another period of skill development, one unique to humans termed adolescence. The hallmark of which is the assimilation of adult-like sociosexual and economic behavior (Bogin 1992). Sex hormones shift focus to cross-sex relationships and provide the impetus for the development of new skills that promote collaboration and ultimately reproduction.

Conclusions

As with other species, humans are relatively monomorphic until puberty. At puberty men exhibit traits associated with combat competition occurring between coalitions of males, and females display traits of fertility. As human social and cultural ecology is increasingly complex, sex differences in the socio-competitive competencies necessary for adult reproduction, require calibration and elaboration throughout the long developmental period. Sex differences in children's self-

initiated play activities are proposed to result in recreation of the social dynamics associated with sex differences in mate competition and parenting, and in so doing allow the practice and refinement of successful strategies (Geary 2010). Boys play in larger groups, prefer rough-and-tumble play, form dominance hierarchies, and practice competition between coalitions. Girls engage in play parenting and intensive dyadic social relationships, developing sophisticated linguistic and interactional skills that in adulthood allow indirect competition and reciprocal relationships with nonkin.

Cross-References

- ▶ [Adaptation And Natural Selection](#)
- ▶ [Boys' Rough-and-Tumble Play](#)
- ▶ [Charles Darwin: Theory Of Natural Selection](#)
- ▶ [Charles Darwin: Theory Of Sexual Selection](#)
- ▶ [Eye Contact with Adults Versus Babies](#)
- ▶ [Hormone Effects on Human Fetal Development](#)
- ▶ [Life History Theory](#)
- ▶ [Male Coalitions for Hunting](#)
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- ▶ [Prenatal Environment, The](#)
- ▶ [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
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- ▶ [Social Play](#)

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Sexual Dimorphism and Sex-Biased Gene Expression

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Synonyms

Sex-biased transcription; Sexually dimorphic gene expression

Definition

How evolution of sex differences in secondary sexual characteristics is mediated by evolution of sex differences in the relative expression of genes present in both sexes.

Introduction

In many species of animals and plants females and males differ dramatically in appearance, behavior, and physiology, referred to as sexual dimorphism. Such differences have evolved due to natural and/or sexual selection acting differently on the sexes. Sex-specific natural selection acts on traits that improve general reproductive success or survival in the given sex, while sexual selection

favors traits that improve mating or fertilization success, operating through competition among the individuals of the same sex or through mate choice. Such traits include, for example, sexual ornaments, weapons, and territorial behaviors that secure access to mates.

In most species with separate sexes females and males are genetically identical apart from the genes in the sex chromosome unique to only one of the sexes (such as Y of human males). In many others the sexes share all of the genes. How, then, do the vast phenotypic differences arise? The answer lies in how the shared genes are expressed in each sex. Studies from fruit flies (Zhang et al. 2007), mammals, birds (Ellegren and Parsch 2007), and plants (Zemp et al. 2016) to brown alga (Lipinska et al. 2015) show that a high proportion of the genome is differentially expressed in females and males. Genes that show higher expression in one sex relative to the other are referred to as sex-biased genes, detected using microarray and RNA sequencing technologies.

Transcriptional and Phenotypic Sexual Dimorphism Are Correlated

Sex-biased expression is a dynamic phenomenon, and the number of sex-biased genes as well as the degree of expression differences between the sexes depends on the tissue in question, the life stage (Perry et al. 2014), and the reproductive state of individuals (Immonen et al. 2017). Although the patterns can be variable, there is generally a strong correlation between gene expression dimorphism and sex differentiation of tissues, indicative of the importance of sex-biased expression in the development of sex-specific phenotypes (e.g., Mank et al. 2008; Perry et al. 2014; Immonen et al. 2017). A study on the male-polymorphic wild turkey also shows that the magnitude of sex-biased expression correlates with the degree of masculinization in plumage and behaviors of males (Pointer et al. 2013). Although not causative, this work provides important evidence of the relationship between phenotypic and transcriptomic sexual dimorphism.

Sex-Biased Expression Evolves to Resolve Sexual Conflict

Many researchers are interested in sex-biased genes because they are expected to evolve under sex-specific selection to allow females and males to optimize their reproduction differently, and thus to evolve sexual dimorphism. By doing so, sex-biased expression should resolve the so-called intralocus sexual conflict that arises when the sexes face contradictory selection pressures for the expression of shared genes (Ellegren and Parsch 2007). Intralocus sexual conflict can be measured as the genetic correlation between the sexes under sexually antagonistic selection. Compatible with the prediction, sex-biased loci tend to have a lower intersexual genetic correlation than loci with similar expression between the sexes (Mank 2017). It is unclear, however, whether the breakdown of intersexual correlation is the *result* of evolution of sex-bias, or if sex-biased genes have initially a lower intersexual correlation (Mank 2017). Other evidence comes from studies of genomic locations of sex-biased genes. Due to their unique inheritance pattern, sex chromosomes are predicted to be hot spots for loci with sexually antagonistic effects, resolved through evolution of sex-specific transcriptional regulation. If the process is cumulative, one can also expect the older sex chromosomes, or regions, to show a greater degree of sex-biased expression. Consistent with these, there is excess of sex-biased genes in the sex chromosomes of birds, *Drosophila*, mammals, aphids, and flour beetles (Wright et al. 2015), and in birds older regions of sex chromosomes show a greater magnitude of sex-bias compared to younger regions (Wright et al. 2015).

Sex-biased genes evolve rapidly both at the sequence and expression levels (Ellegren and Parsch 2007). Males often experience a higher intensity of sexual selection with a rapid evolution of male traits, and in many taxa (including *Drosophila*, mammals, *Caenorhabditis elegans*, and birds) genes with a higher expression in males (i.e., male-biased genes) follow the same pattern of fast divergence (Mank 2017). However, this is not the case in all taxa (e.g., Lipinska et al. 2015),

and it is also possible that in many cases faster evolution of male-biased genes may result from relaxed selection and drift rather than adaptive evolution (Mank 2017). Also, at any given life stage the direction of sex-bias may not necessarily indicate in which sex their function is most important, and thus when in the reproductive cycle and in which sex the selection is strongest (Immonen et al. 2017; Mank 2017). Nevertheless, sex-biased expression is a good molecular predictor of past or ongoing selection that operates differently on the sexes.

Sex Steroids Regulate Sex-Biased Expression

How sexual dimorphism develops over ontogeny is under endocrine control. Although studies of this are still scarce, sex steroids, such as testosterone and estrogen of vertebrates, should be especially important in modulating sex-biased expression and thus in alleviating intralocus sexual conflict. A work on the sexually size dimorphic brown anole lizard shows how intersexual genetic correlation for body size decreases during development, mirrored by increased sex-biased expression for genes involved in growth and metabolism. Testosterone is likely involved in this: treatment of juvenile females with testosterone causes a male-like pattern of gene expression, growth, energetics, and ornamentation (Cox et al. 2017). At the molecular level, conjectures about the mechanisms that allow expression to be decoupled in the sexes largely remain to be discovered.

Conclusion

Studying how genes are regulated in each sex is not only important for our fundamental understanding of biological differences between the sexes and how many dazzling ornaments and extravagant behaviors have evolved, but also vital for medicine where genetic differences between men and women can have clinical consequences. Overall there is good circumstantial support for the prediction that sex-biased expression is required for the evolution of sexual

dimorphism and alleviation of genetic conflict between the sexes, but several outstanding questions remain regarding the mechanisms and how selection operates on sex-biased genes. No doubt this vibrant field will continue to offer many important insights that increase our knowledge and awareness of exactly how different females and males are at the molecular level.

Cross-References

- [Conflict Between the Sexes](#)
- [Evolutionary Arms Race](#)
- [Intralocus Sexual Conflict](#)
- [Sex Differences in Variance Traits](#)

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Sexual Dimorphism in Body Size

- [Sexual Size Dimorphism](#)

Sexual Discrimination

- [Sexism](#)

Sexual Exploitation at Work

- [Sexual Harassment in the Workplace](#)

Sexual Expression

- [Ancient Homosexuality](#)
- [Non-Western Homosexuality](#)

Sexual Fantasies

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Definition

Mental images, thoughts, or imagined sexual experiences that can entertain, preoccupy, and promote sexual arousal

Introduction

Sexual fantasies are perhaps the most common human sexual experience. Unlike many sexual activities, they are private and thus unconstrained by reality in terms of partner choice or the behaviors engaged in. As such, they are interesting because they can provide insight into the psychological mechanisms underpinning human sexual desires as well as resulting behaviors. The majority of people engage in sexual fantasy and, on average, men do so more frequently than women.

How Are They Studied?

Typically, the frequency and content of sexual fantasies are studied cross-culturally via questionnaires. Such measures may assess fantasies in terms of endorsing items on a sexual fantasy scale, asking participants to complete sentences in sexual scenarios, as well as describing their own fantasies with open-ended questions. They can also be studied by examining commercial erotic fantasy in the form of pornography or romance/erotic literature. These commercial products are unobtrusive measures of sexual fantasy. The results of surveys and unobtrusive measures are more often in agreement than not.

Common Fantasies

Some of the most common fantasies, as assessed by survey, reflect actual behavior, including touching/kissing and doing so while naked, watching a partner undress, oral sex, masturbating your partner, and intercourse in unusual positions.

When we examine fantasies as depicted in online pornography, for example, Pornhub reports that the top search terms in 2016 included lesbian, stepmom, MILF, teen, and stepsister, reflecting the “partner” being fantasized about (most frequently by men, the majority consumers on Pornhub). The most frequently searched for activities included massage, anal, threesome, lesbians scissoring, and creampie. Interestingly, some

categories viewed more often by women include gang bang, rough sex, and bondage.

Perhaps unsurprisingly, the sexual fantasies of lesbians and gay men tend to be similar to those of heterosexual members of their gender, aside from the sex of their imagined partner.

Rape Fantasies

Many women and some men report that the content of their sexual fantasies includes imagined scenes of rape or sexual coercion. In Bivona and Critelli’s (2009) study, 62% of female undergraduates had experienced rape fantasies, some as often as once a week. While a small percentage found them completely aversive, the rest of the sample was split between those who found such fantasies erotically exciting and those that experienced them with a mix of aversion and arousal. The researchers interpreted this as attempts to deal with fears of rape but they also reported that most participants rated these fantasies as positive. The fact that these fantasies reportedly involved perpetrators who were known to the women experiencing them, good-looking, desirable men who in the fantasies exhibited an irresistible attraction to the woman echoes the theme of rape in romance, that is, can be about the appeal of the heroine as well as the sexual appeal of dominant men (Hazen 1983).

Do such fantasies indicate anything about the women who experience them? Not in the way that many people might assume. Strassberg and Lockerd reported in a (1998) study that women who engaged in forceful sexual fantasies, rather than experiencing some sexual pathologies, were in fact better adjusted sexually in that they experienced less sexual guilt and experienced more sexual fantasies in general.

Theoretical Approaches and Sex Differences

While social scientists usually attribute sex differences in sexual fantasies to sex differences in life

experiences, and it may be the case that much intrasex variation in sexual fantasy is due to such environmental effects, from an adaptationist perspective, one would expect selection to have shaped sexually dimorphic mechanisms underlying human sexual desires and dispositions. This would be expected because throughout human evolutionary history, men and women encountered substantially different reproductive opportunities and constraints. The male problem of paternity uncertainty and differences in the minimum possible parental investment between mammalian males and females are just two features of human sexual reproduction that would produce sex differences in human sexual psychology. Behavioral differences between men and women in sexual behavior and mate preferences are well documented.

In addition, there are many empirical studies of the frequency and content of male and female sexual fantasies that have documented substantial sex differences (Ellis and Symons 1990; Leitenberg and Henning 1995). Men engage in fantasy more frequently than women during the day as well as during masturbation or sex with a partner. Studies over the past 20–30 years have reported not only sex differences in frequency but also in the content of these fantasies. Women's fantasies are less dominated by physical images and more commonly emphasize touching, feelings, their partner's response (being the focus of their partner's desire), their emotional states, the special nature of their partner, and are more personal, often being focused on someone they were or had been romantically involved with. Men's fantasies are more visual, especially with relation to the genitals, involve more partners and more variety, and are more impersonal. In other words, they are more about just sex than about sex with a specific individual, which should not be surprising considering the importance of variety and partner number to maximizing mammalian male reproductive success and the importance of female choice to mammalian female reproductive success (Salmon and Symons 2003).

Conclusions

Sexual fantasies, like sexual behavior, reflect sexual psychologies shaped by the problems ancestral men and women faced in the mating domain. In some ways, sexual fantasies reveal more about the design of our sexual psychological mechanisms than behavior itself does, as fantasies or desires are unconstrained by reality in terms of ideal partners and behaviors. In particular, if real-life heterosexual encounters are constrained by inevitable compromises between men and women and thus blur their differences, the study of sexual fantasies can facilitate a more clear understanding of some of these sex differences in sexual psychology.

Cross-References

- ▶ [Mate Preferences](#)
- ▶ [Men's Mate Preferences](#)
- ▶ [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- ▶ [Sexual Fantasy](#)
- ▶ [Women's Mate Preferences](#)

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Sexual Fantasy

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Synonyms

Mental imaging; Sexual arousal; Sexual daydreaming; Sexual reverie

Definition

Sexual fantasy refers to any mental imagery that is sexually arousing or erotic to the individual (Leitenberg and Henning 1995).

Introduction

Contrarily to traditional psychanalytic points of view, sexual fantasies are associated with a more active and satisfying sexuality. In this entry, it will be suggested that sexual fantasies are generally adaptive from an evolutionary perspective because they serve to enhance sexual arousal which, in turn, increases the likelihood of intercourse, orgasm, and, eventually, reproduction. However, the number of studies devoted to sexual fantasies of adults from the general population is still surprisingly low.

Sexual Fantasies Among the General Population

Approximately 90% of the general adult population acknowledge having sexual fantasies. This type of mental imaging is important for sexuality as it is closely associated with sexual arousal, better sexual satisfaction, and higher odds of interpersonal sexual relation (Leitenberg and Henning 1995). In opposition, paucity or the absence of

sexual fantasy is associated with elevated age, low steroid hormone production, and asexuality. Therefore, and contrarily to classic Freudian assumptions, sexual fantasies do not reflect an absence of sexual activity or a compensatory mechanism for sexual dissatisfaction and deprivation, on the contrary. Higher diversity of sexual fantasies is also reported by persons with higher rates of sexual arousal (Joyal et al. 2015). Thus, sexual fantasies could be considered as adaptive from an evolutionary point of view, elevating the odds and frequency of interpersonal sexual relations.

Traditionally, emphasis is put on gender differences in studies of sexual fantasies. Although both men and women have intimate fantasies (e.g., involving their current partners) in similar proportions, men, on average, fantasize more about impersonal relationships, visual descriptions, and dominating behaviors, whereas women fantasize more about romance (feeling, ambiance, and location) and submission, in more emotive and cognitive descriptions (Ellis and Symons 1990; Leitenberg and Henning 1995). It should be noted, however, that these differences are based on group average comparisons. A more nuanced picture emerges when different subgroups of men and women are defined according to their sexual fantasy patterns, i.e., as a function of the type, diversity, and intensity of their sexual fantasies. For instance, there are at least four subgroups of women with different sexual fantasy profiles among the general population, including two with sexual fantasies as intense and diverse (if not more) than those of men (Joyal 2015). Interestingly, women with both typical fantasies and fantasies of domination–submission report higher diversity and intensity of fantasies in general and sexual satisfaction in general (Joyal et al. 2015; Joyal and Carpentier 2017). These women have intimate and romantic fantasies, and they include their current partner in their fantasies, but they also report a diversity of domination–submission themes that are still considered as “anomalous” in current psychiatric diagnosis manuals (APA 2013; see ► “Paraphilia” entry).

Therefore, it seems that diversity, more than content of sexual fantasies, is a sign of a healthy sex life. Diversity of sexual fantasies is associated with higher libido and, maybe, better reproduction fitness by virtue of a higher frequency of coital relations. This hypothetical link between diversity of sexual fantasy and higher rates of intercourse deserves to be tested.

The difference between a sexual fantasy and a sexual wish should also be underscored. Although the majority of male sexual fantasies are wishes, this is not necessarily the case for female sexual fantasies, especially those with submission themes. Women with coercive submissive or forced sexual fantasies commonly specified they would never want to act them out (Joyal et al. 2015; Leitenberg and Henning 1995). These sexual fantasies are simply mental scenarios helping to increase sexual arousal, not the sign of a genuine interest in the behavior. Therefore, sexual fantasies should not be confounded with sexual interests, especially in women.

Sexual Fantasies Among Sexual Offenders

Sexual fantasies may be useful in risk assessment of sexual offenders because they commonly precede (and succeed) aggressions in line with the fantasy (e.g., Grundmann et al. 2016). However, content is less important than usually expected in the prediction of an acting out. First, many men from the general population have similar sexual fantasies with illegal content (e.g., coercion, rape, voyeurism; Joyal and Carpentier 2017). Second, contrarily to popular belief, sexual offenders generally have less numerous and less diverse sexual fantasies than men from the general population, on average. Mental imaging, daydreaming, and fantasies are associated with mentalization capacities (i.e., taking the perspective of others, evaluating future consequences of a behavior, reflecting before acting) and executive functions (i.e., behavioral inhibition, problem solving). Given that these cognitive aptitudes are severely impaired, on average, in sexual offenders, it is not surprising that most of them possess a poor

inner world with few sexual fantasies. These sexual fantasies, however, are much more intense and frequent, if not obsessional, than those of men from the general population. Thus, it is not solely the content of a sexual fantasy but also (and mostly) its recurrence, intensity, necessity, and the lack of overall diversity that seem crucial to evaluate risk of acting out.

Conclusion

It is clear today that sexual fantasies are usually healthy unless they are rigid, rather exclusive, recurrent, and intense. In these cases, poor mentalization and executive functioning might lead the person to act out his/her sexual fantasy even if it is illegal. For the vast majority of people, sexual fantasies are diverse, and they serve to enhance sexual arousal, odds of interpersonal sexual relation, and higher sexual satisfaction.

Cross-References

- ▶ [Human Sexuality](#)
- ▶ [Paraphilia](#)
- ▶ [Positive Sexual Development](#)
- ▶ [Sexual Abuse](#)
- ▶ [Sexual Arousal](#)
- ▶ [Sexual Coercion](#)

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Sexual Fluidity

► Female Homosexuality and Bisexuality

Sexual Harassment

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Synonyms

Impropriety; Offensive sexual advance; Sexual intimidation; Unwanted sexual advance

Definition

Any unwelcome sexual conduct.

Introduction

The definition of harassment may vary depending on its social or legal context, however the *Equal Employment Opportunity Commission* provides the widely accepted definition as “unwelcome sexual advances, requests for sexual favors, and other verbal or physical conduct of a sexual nature...” (Equal Employment Opportunity Commission 1980). The women’s advocacy group *Arming Women against Rape and Endangerment* (AWARE.org) differentiates the methods of harassment into three categories: verbal, visual, and physical.

Types of Sexual Harassment

Verbal sexual harassment constitutes any comment or remark that is of a sexual nature, or any sexually obscene or insulting sounds. This also includes any unwelcome and offensive names or terms of endearment. Examples of verbal sexual harassment include, but are not limited to, cat calls, kissing sounds, howling, whistling, and smacking lips, unwanted sexual teasing, jokes, remarks, or questions and comments of a sexual nature (A.W.A.R.E.org).

Visual Sexual Harassment is an assault to the sense of vision in which someone exposes his or her genitals or repeatedly stares at another person’s body in a way that is offensive or uncomfortable for the person at whom is being stared. Being made to look at sexually explicit images or being shown obscene sexual gestures may constitute visual sexual harassment as well. Other examples of visual sexual harassment can include obscene or unwanted sexual looks or gestures, unwanted letters, emails, text messages, and lewd images (A.W.A.R.E.org).

Physical Sexual harassment is the act of being coerced into unwanted physical contact, such as being brushed against, hugged, kissed or touched in any way that is unwelcome and discomforting. It may also include being forced to touch someone. Some examples of physical sexual harassment include unwanted pressure for sexual favors, touching an employee’s clothing, hair, or body in an inappropriate and non-consensual manner, making sexual gestures with hands or through body movements, and any attempt toward sexual assault and/or rape (A.W.A.R.E.org).

Sexual Harassment in the Workplace

In the workplace, the term *quid pro quo* describes harassment as sexual bribery if a person is coerced to submit to, or engage in sexual activity for professional advancement and receives favorable outcomes from the interaction, as in a favorable review (e.g., positive evaluation, better grade, etc.), promotion, or bonus. Sexual negotiations offer the can provide evolutionary explanations

for quid pro quo harassment depending on the status of the harasser, for example age, marital status and perceived attractiveness. *Hostile work environment* is a form of sexual harassment that is created when the individual in power presents a threat as a method to coerce the victim, requiring them to participate in an unwanted sexual behavior or suffer academic, professional, financial, or other loss. Although there is a distinction between the two, each is considered nonconsensual and abuse of power. Ultimately both subtle and unsubtle types of sexual harassment create problems in the workplace, for the person being harassed (Crooks and Baur 2014).

Sexual harassment is a modern socially constructed concept, specifically related to unwanted or coerced sexual attention or interaction. Evolutionary and feminist psychologies debate the causes of sexual harassment due to social contact, sexual motivation, and power expression to explain the complexity of this evolved characteristic of sexual behavior (Studd 1996).

Evolutionary Psychological Perspective

From the evolutionary psychological perspective, sexual harassment is the result of “evolved mechanisms guiding male motivation to strive for sexual access to females, which in ancestral environments had direct positive payoffs for male reproductive success in competition with other males” (Studd 1996, p. 61). In other words, males sexually harass as a means of attempting to increase their reproductive opportunities. Evolutionary psychological research has found support for this theory – noting that females who possess traits that are indicative of fecundity and reproductive availability (e.g., single, young, physically attractive) are more likely to be sexually harassed (Buss 2016). Reports have also concluded that unmarried males – those who have not secured a long-term mate – are more likely to engage in sexual harassment (A.W.A.R.E.), and women react more negatively to sexual advances by an offender who is married (Buss 2008; Studd 1996). Women also perceive sexual harassment as significantly more disturbing when the harasser is of

lower occupational status (Buss 2016), indicating that advances from males with low mate value (e.g., low status career with fewer resources) are more unwelcome than advances from males with higher mate value.

Sexual motivation hypothesis is an evolutionary perspective suggesting that sexual energy and activity are motivating factors behind harassment, and that these mechanisms have different reproductive investments for each gender (Buss and Malamuth 1996). Men that harass women through staring and implied or actual physical contact may be expressing an evolved behavior to measure waist-to-hip ratio and other signs of youth and symmetry of possible mates (Geher 2014; Platek and Singh 2010). This is consistent with evolutionary theory that males seek fecund females as potential mates.

Each sex’s perception and interpretation of mating-related behaviors may also be different. Error management theory posits that cognitive differences between the sexes can play a role in dating and mating strategies where persistent men mistake harassing behavior as flirtation (Haselton and Buss 2000). Men and women share a misperception that there is no difference in the perception of feelings toward aggressive behavior between the sexes; however, in reality, research shows that men often overperceive sexual interest from females – which may cause the male to pursue the female even though she is not interested, which may lead to sexual harassment – while women tend to underperceive sexual interest from males – which may cause the female to interact with a male who is sexually interested in her, but she is unaware of it (Haselton and Buss 2000).

Cognitive processes of human ancestry are slow to change, but consequences of the behavior have been adapted to create the modern cultural views against sexual harassment. When individuals do not welcome the advances or attention, the act is then defined as harassment. While these actions may seem harmless, research has shown that women find sexual aggression to be more disturbing than men do (Crooks and Baur 2014; Studd 1996). Investigations of legal documents from sexual harassment cases support

this evolved mechanism of defense – the more blatant harassment led to more negative responses from the women who were harassed (Studd 1996, p. 63).

The social contact hypothesis predicts that men who have prolonged contact with women young enough and available to reproduce, motivates men to initiate sexual intentions, whether the behavior is welcome or not (Studd 1996). Women's presence in the once male-dominated work and educational environments has given rise for social contact to work. Opportunities are made available through social contact, which helps to explain the motivations of inappropriate sexual behavior in the workplace and in educational settings. When men and women share personal interests and functions such as school, work, or military service, they have accessibility to potential partners with common interests. Understandably, men and women who work together can and do develop genuine affection and attraction towards each other when they work, study, or serve together (Buss 2008). When one of the two do not consent, the dynamic of the interaction fits the legal definition of sexual harassment.

Feminist Psychological Perspective

The feminist perspective holds that power and male dominance are motivating factors behind sexual harassment, and are logical cornerstone concepts to the explanation in social psychology. In other words, the feminist view regards actions of harassment as expressions of power over women, rather than sexual in nature. This is often referred to as the power hypothesis (Studd 1996). "In general the feminist perspective on sexual harassment proposes that the exercise of power is the causal factor for the occurrence of unwanted sexual attention in the workplace" (Studd 1996, p. 56). As women strive to gain equality through professional success, 40–70% of American women have experienced sexual harassment in the workplace according to data analysis from the Equal Employment Opportunity Commission in 2009 (Crooks and Baur 2014).

Between 75% and 90% also report adverse psychological effect from this behavior and findings estimate that of those who have been sexually harassed only 5–15% will file an official complaint (Crooks and Baur 2014). Sexual harassment is not reported due to fear of losing one's career and therefore financial/economic security, as well as fear of personal embarrassment and professional alienation. (Crooks and Baur 2014).

Although the expression of power may not be the ultimate goal of sexual harassment, it is clearly a tool some men use as a means to gain sexual access to the women with whom they work and study (Studd 1996). However, the power hypothesis does not make any claims regarding markers of female reproductive potential (e.g., age, marital status, etc.). In addition, if power were the key motivator of sexual harassment, then women in powerful positions would also be more inclined to sexually harass, which data does not support (Studd 1996).

Conclusion

Sexual harassment is historically a concern for feminist psychologists and sociologists as a method for men to oppress, objectify, and control women's opportunities and successes. The Women's Movement of the 1960s brought sexual harassment into light as a matter of legal and social debate in efforts to achieve women's liberation and as a call for change within social structures to strive for gender equality (Rowe 1977). Women rallied for equality in the contemporary workforce, rights to participate in sports, rights for educational and professional access, and reproductive behavior. In the early 1970s, a small group of academic women agreed that sexual intimidation on the job was problematic enough to warrant a name for the behavior which encompasses unwanted male attention, flirtation, and sexual coercion of women (Brownmiller 1999). As women began to compete with men, and take on the roles once exclusively held by men, they also posed a threat to men's power in the home and in the workplace. Female competition in the workplace is an added confound

to the evolutionary perspective on sexual harassment. Harassment can occur in all workplaces, academic settings, within the military, and other social settings. It is also important to note that, although women are the predominant victims of sexual harassment, men do experience sexual harassment – usually from other men (A.W.A.R.E.; Crooks and Baur 2014).

Cross-References

- ▶ Rape and Dating
- ▶ Sexual Abuse
- ▶ Sexual Coercion and Dating
- ▶ Sexual Conflict in Mating Strategies
- ▶ Types of Sexual Coercion

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Sexual Harassment in the Workplace

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Synonyms

[Sexual abuse in the workplace](#); [Sexual exploitation at work](#); [Workplace harassment](#)

Definition

Unwelcome sexual advances, requests for sexual favors, and other verbal or physical conduct of a sexual nature that negatively affects an individual's employment, work performance, or work environment.

Introduction

Workplace sexual harassment in the United States is legally defined as a form of sex discrimination that violates Title VII of the Civil Rights Act of 1964, and includes unwelcome sexual advances, requests for sexual favors, and other verbal or physical conduct of a sexual nature that negatively affects an individual's employment, work performance, or work environment (Equal Employment Opportunity Commission 2010). Although academics have often disagreed on the specific behaviors that constitute sexual harassment, research has shown that less severe forms of sexually harassing behaviors – such as remarks, jokes, looks, and gestures – are the most prevalent, whereas the most severe ones such as assault and attempted rape still remain low (Pina et al. 2009). Even though evidence is mixed about the incidence of sexual harassment, the majority of women will experience some type of sexual harassment during their working lives (European Commission 1999).

Evolutionary Perspective and Sexual Harassment in the Workplace

Many theories have been proposed in order to explain the ongoing occurrence of sexual harassment in the workplace. For example, classic explanations such as sexism, gendered environments, power misuse/abuse, and hierarchical issues (Pina et al. 2009). However, many of these explanations are just proximate pieces and cannot explain the underlying psychological mechanisms that produce sexual harassment. Applying the lens of the evolutionary perspective, we consider that although some actions at work are motivated by gaining social status, others could be about prioritizing kin, and yet others could be motivated by a need to find mates (Jonason et al. 2014). For a critical clarification, we suggest that it may be important to consider sexual strategies – along with perspectives emphasizing sexism – when trying to understand sexual harassment. Conflicts about sociosexual interactions – which are likely to be an expression of a desire to become sexually involved – are the main elements for understanding sexual harassment in the workplace (Studd and Gattiker 1991).

The differences in reproductive biology and consequently the conflict of sexual strategies would be the ultimate cause of sexual misunderstanding and harassment in any social environment (Buss 1989), including modern environments, despite deep social and technological changes. As an evolved psychological mechanism for seeking out available sexual opportunities, there is a higher tendency for males to use a continuum of aggressive tactics in order to obtain mates. So, because humans bring the same psychological mechanisms to the workplace, the observed patterns of sexual harassment are a consequence of the evolution of sex-specific opportunistic mating strategy. Thus, this may be one possible explanation regarding why sexual harassment is a chronic problem in organizations (Studd and Gattiker 1991).

Although it may be misleading to generate a typical profile of the sexual harasser and the victim based on sociodemographic characteristics,

the research literature points predominantly to men's harassment against women, with scarcely few exceptions (e.g., American Association of University Women 2001). It also tends to have a much greater impact on women, who suffer besides occupational consequences, intense negative emotional responses (sometimes similar to that experienced by victims of rape; Koss 1990). Sexual harassers appear to permeate all social strata, occupational levels (it more often involves advances made by coworkers or subordinates than by superiors; Studd and Gattiker 1991), and age categories (Pina et al. 2009).

It is important to note that there may be individual differences in personality that may further our understanding of who is more likely to engage in sexual harassment.

For example, past research has found connections between sexual harassment and callous exploitation of others and lack of empathy (Gannon et al. 2008), as well as the dark triad traits and sexual harassment tendencies (Zeigler-Hill et al. 2016). Therefore, dark personality traits are seen not just in terms of their problematic associations but also as adaptive mechanisms (Jonason et al. 2014).

Conclusion

Finally, a hypothesis based on sexually dimorphic psychological mechanisms is not the same as saying that sexual harassment is morally legitimate in any sense. We do not want our assumptions to have the effect of trivializing sexual harassment or assuming change efforts must be futile. Rather, the attempt to expand our understanding of sexual harassment is in order to examine the potential causes and develop effective solutions for such deplorable side effects of human nature (Studd and Gattiker 1991).

Cross-References

- [Sexual Abuse](#)
- [Sexual Harassment](#)

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Sexual Identity

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Synonyms

Gender and sexual minorities (GSM); LGBTQ+ identity; Romantic identity; Sexual life; Sexual nature; Sexual orientation identity; Sexual personality; Sexual self;

Definition

An individual's identification and self-definition based on the magnitude and type of intrapersonal and interpersonal attractions, desires, fantasies, and behaviors pertaining to sex, sexuality, and intimacy.

Introduction

Identity is the chosen term or terms used by an individual as a label denoting the representation of their values, beliefs, characteristics, behaviors, attractions, and roles. The construction of a personal, or ego, identity begins with two main components, distinguished by psychologist Roy Baumeister as continuity and differentiation (Baumeister 2011). Continuity refers to the ability to see oneself as fundamentally the same over time, while differentiation refers to the ability to distinguish oneself from other individuals or groups; thus, what is required for a personal identity is to see oneself as different and for that difference to be maintained over time and contexts. Prominent identity researcher, Erik Erikson, recognized adolescence as the point during which identities of all kinds begin to form. In fact, Erikson named identity formation as the critical developmental task of the teen years, as these individuals have the flexibility to explore different options for their identity before making long-term commitments, known as psychosocial moratorium (Erikson 1968). James Marcia built on this theory of identity conflict during adolescence by understanding it as a time when individuals are able to explore and commit to their identities, though some do both while others do neither, to establish an internal locus of self-definition (Marcia 1966).

Theories of Sexual Identity

There are many different types of identities that a person may have including gender, race, ethnicity, religion, culture, socioeconomic status, and sexuality. Due to the coinciding of biological,

emotional, behavioral, social, and psychological changes accompanying puberty with the identity exploration of adolescence, *sexual* identity becomes particularly salient for many individuals at this time. Sexual identity is the term chosen by an individual that they find most representative of their sexual life. While sexual identity is often conceptualized as the amount of same- and other-sex attractions, there are many facets. In fact, recent research has proposed a framework for sexual identity that encompasses the multi-dimensional nature of sexual identity for all individuals, including those who identify as a sexual majority like heterosexuals (Dillon et al. 2011). This structure for sexual identity is formed from one or more of the six bases of sexual identity: basic sexual needs, preferred characteristics of partners, specific activities or behaviors, preferred interpersonal contexts for expression, values, and preferred modes of expression (Worthington et al. 2002).

Basic sexual needs describe an individual's internal experience of sexual desire, drive, impulse, interest, and/or libido (Worthington et al. 2002). Examples of a sexual identity that centers on basic sexual needs would be asexuality or hypersexuality. This facet of sexual identity would also refer to an individual's sociosexuality, or desire for uncommitted sexual encounters, such as one-night stands (Penke and Asendorpf 2008). Preferred characteristics of partners refer to the physical, emotional, intellectual, economic, spiritual, and other characteristics that an individual is specifically sexually interested in. Examples of sexual identities centered on preferred partner characteristics would be sapiosexuality (attracted to intelligence), a "gold digger" (attracted to wealth), or a hebephile (attracted to early pubescent characteristics). Preferred characteristics of partners also refer to the preferred sex and gender of a sexually attractive partner; this is the most common basis for a sexual identity, such as lesbian, gay, bisexual, or pansexual (Worthington et al. 2002). Specific sexual activities or behaviors refer to what an individual prefers to take place during a sexual encounter. Examples of sexual identities centered on sexual behaviors would be an exhibitionist or someone classifying as

celibate. Interpersonal contexts for expression refer to how an individual prefers the dynamics of a sexual encounter with their partner or partners. Examples of sexual identities centered on interpersonal dynamics would be swingers, polyamorists, dominants, or submissives. Values refer to an individual's moral standards about what is sexually appropriate, acceptable, and desirable. Examples of sexual identities centered on values are virginity pledger or born-again virgin. Finally, modes of expression refer to the preferred way an individual articulates sexual affection and interest such as through tone of voice, eye contact, body movements, and physical touch. Examples of identities centered on modes of expression would be individuals who identify as "huggers" or "flirts" (Worthington et al. 2002).

Just as there are multiple bases for a sexual identity, an individual may have multiple sexual identities at one time, such as a BDSM practitioner and pansexual, which can overlap or be distinct. Additionally, an individual may have multiple sexual identities over the course of their lifetime, such as a woman who may have once identified as bisexual, but now identifies as lesbian. There are many factors that contribute to which sexual identities an individual adheres to at any point in their life, most importantly the individual's sense of self, micro-social contexts, and macro-social contexts (Dillon et al. 2011). The individual's internal relationship to their sexual identity is the sense of self as a sexual being formed through recognition and acceptance of one's sexuality. This sense of self can be affected by biology, early and later sexual experiences, and sexual desires and attitudes. The social context of sexual identity focuses on how the individual's sexuality is related to other people. A micro-social context of family, friends, and community influences contributions to sexual identity such as sexual values, morality, access to sexual knowledge, and sexual and gender norms. A macro-social context influences these same sexual outlooks and access on a national, cultural, or global level. Together, the micro- and macro-social contexts create an implicit or explicit sense of belonging to a sexual group based on an individual's sexual identity, be it a majority or minority

group, and allow the adopting of attitudes, beliefs, and values about the individuals and other possible sexual groups. The integration of the many facets of sexual identity existing within these contexts thus allows the development of a multi-dimensional sexual identity construct (Dillon et al. 2011).

A new, promising perspective of sexual identity, Sexual Configurations Theory (SCT), addresses this multifaceted nature of sexual identity (van Anders 2015). In SCT, individual and partnered sexualities are considered separate domains and include aspects such as individual gender/sex, gender/sex sexuality, partner number sexuality, sexual parameters (which are similar to modes of expression), and eroticism/nurturance. For each domain, an individual can place themselves on a three-dimensional spectrum, which also allows for an indication of the level of importance each facet has for them. An individual's sexual identity is thus a particular configuration of these sexual features and is not discrete or fixed, theoretically mirroring lived experiences of sexual multimodality and allowing for identities that occur at intersections with other identities, such as gender/sex, race, or age (van Anders 2015).

Commonly, though, the most salient facet of sexual identity for an individual is sexual orientation identity, particularly for people who have same-sex attractions (Savin-Williams 2009). This is also the facet that has been socially constructed as the most important aspect of our sexual identity. Sexual orientation identity is the representation label chosen by an individual to best describe their sexual relationship, or lack of sexual relationship, with others based on gender or sex, and may be anchored in the individual's sexual behaviors, attractions, fantasies, social preferences, and emotional preferences. By its nature, sexual orientation identity is formed by the socially distinguishing features of sexual preference that are unchangeable but socially consequential. The Klein Sexual Orientation Grid (KSOG), a detailed system for describing sexual orientation preferences used in academia, measures all of these components of sexual orientation in the present, as well as in the past and in an ideal

future (Klein et al. 1985). KSOG is therefore able to account for the possibility of an evolving sexual orientation identity over time, as well as acknowledging that there are many factors, including an individual's social, political, and cultural climate, which may not allow for them to fully realize their ideal sexual life. An alternative measure of sexual orientation in academia is the Kinsey Scale of Sexual Responses, which focuses entirely on attractions, as opposed to behavior or fantasies, but also allows individuals to declare varying levels of attraction to males, females, or both (Kinsey et al. 1948).

Common sexual orientation identities include, but are in no way limited to, many represented by the LGBTQ+ umbrella: lesbian, gay, bisexual, queer, questioning, asexual, pansexual, polysexual, pomosexual, and omnisexual. Additionally, there are prevalent sexual orientation identities not always included in the LGBTQ+ umbrella, such as heterosexuality or those who identify as mostly gay or mostly straight. Research on individuals identifying as mostly straight and mostly gay, in particular, has blossomed only in the last 5 years; however, their inclusion in discussion of sexual orientation identity is important due to the increasing prevalence of the label. When the option to identify as "mostly" straight or gay is presented, as opposed to simply gay, straight, or bisexual, a significant number of men and women choose those labels (Vrangalova and Savin-Williams 2012). This marked difference between the two sexuality spectrums signifies the importance of the unique and multifaceted nature apparent in sexual orientation identity – itself just one facet of sexual identity.

People with marginalized sexual identities, such as those who will eventually form sexual identities of minority or socially unacceptable groups, are more likely to explore their sexual identity than those with mainstream sexual identities, such as heterosexuals. While sexual minority adolescents begin their identity development with greater uncertainty than their sexually mainstream peers, this diminishes significantly with chronological age as more and more individuals construct a consistent and distinct sexual orientation identity (Savin-Williams 2009).

There are several academic models for the construction of sexual orientation identity, all of which begin, as most identity constructions, in adolescence. First was the Cass Model of Gay & Lesbian Identity Formation developed by Vivian Cass in 1979 (Cass 1979). This was the first normative development model proposed in a society dominated by heterosexual ideals. The Cass model is a linear stage model of sexual orientation development that takes place in six consecutive stages: identity confusion, identity comparison, identity tolerance, identity acceptance, identity pride, and identity synthesis. The first stage, identity confusion, begins the process of sexual orientation identity development by questioning the presence of sexual feelings, thoughts, and behaviors, essentially leading to the question: "Could I be gay?" Some individuals in this phase will actively choose to deny and avoid contact with or information about gays and lesbians (Cass 1979).

The second phase of the stage model is identity comparison during which the individual accepts the possibility of being gay or lesbian and starts coming to terms with the subsequent social ramifications (Cass 1979). An individual during this phase may compartmentalize their sexuality, such as by believing their thoughts, feelings, and behaviors which apply only in specific contexts and are not indicative of a consistent and persistent sexual identity. As a result of this, each individual may create or adapt a label or definition that feels most right to them at that time, but this will most likely evolve over time. During this stage, happiness, life satisfaction, and self-esteem begin to decrease, while loneliness increases, from unawareness and identity confusion (Halpin and Allen 2004).

The third stage, identity tolerance, is when the person finally recognizes that they are likely a sexual orientation minority and look for membership within the gay community, both to battle feelings of alienation and to gain greater information about and comfort with being a sexual minority (Cass 1979). It is during this stage that most individuals feel the disconnection from the heterosexual majority, which makes contacts within the gay and lesbian communities so crucial. It is

during identity tolerance that happiness, life satisfaction, and self-esteem are at their lowest, while loneliness is at its highest, among all the stages (Halpin and Allen 2004).

The goal of the fourth stage, identity acceptance, is to reach the point where there is an affirmative acknowledgment of the sexual minority orientation that is confident and optimistic, as opposed to merely tolerant (Cass 1979). Although acceptance of the sexual minority identity occurs, an individual may still compartmentalize their gay or lesbian life from other facets of their world. However, many choose, at this time, to come out to those close to them. During this stage, self-esteem begins to increase significantly (Halpin and Allen 2004).

Identity pride, the fifth stage, is, as the name implies, all about taking pride in the individual's accepted sexual minority identity. Individuals during this stage are fully out about their identity and are often actively involved in gay and lesbian communities (Cass 1979). However, Cass's theory states that as the positive assessment of a gay or lesbian identity increases, the ensuing negative opinion of heterosexual and the sexual majority increases as well (Cass 1979). The individual develops an us-versus-them mentality, seeing anything nonsexual minority with negative affect, immersing themselves in gay culture to the point of aggressively limiting contact with heterosexuals, and viewing support as only coming from the gay community. During identity pride, individual's happiness, life satisfaction, and self-esteem begin to significantly increase, while loneliness significantly decreases (Halpin and Allen 2004).

The sixth and final stage is identity synthesis. In identity synthesis the individual realizes that their sexual orientation minority identity is just one part, albeit an important part, of their multifaceted sexual and self-identity (Cass 1979). This is due to the individual being able to integrate their sexual orientation with their sexual identity and their sexual identity with all other aspects of self; therefore, sexual orientation no longer makes up the entire identity. At this point, the individual continues to be part of the gay community, but also is able to move in other spaces, and does not feel the need to categorize simply on the basis of

sexual orientation. It is during this phase of identity development that life satisfaction and self-esteem are at their highest, while loneliness is at its lowest (Halpin and Allen 2004).

Fassinger's Model of Gay and Lesbian Identity Development is an alternative model published in 1997 (Fassinger and Miller 1997). Fassinger's model, unlike Cass's, highly emphasizes the importance of cultural and contextual influences and as such delineates two processes of sexual orientation identity development: individual sexuality and social sexuality. Individual sexuality is determined by the internal exploration, awareness, and acceptance of the self's sexuality, while social sexuality is determined by perceived sexual orientation group membership – either within a small group, community, or a macro-social context. Fassinger's model is also a stage model with four distinct, linear, consecutive stages: awareness, exploration, deepening/commitment, and internalization/synthesis. Identity development begins with an awareness that individuals exist with different sexual orientations, which leads to the exploration of one's feelings to determine group membership. This exploration includes internal curiosity and questioning, as well as one's social context in relation to the gay and lesbian community. Once explored, an individual commits to their sexual orientation group, social community, and both positive aspects of identity and belonging and the negative consequences of prejudice. It is at this point that the individual's sexual orientation identity becomes the most salient facet of their identity, but eventually the individual is able to internalize their identity as important and consistent regardless of context (Fassinger and Miller 1997).

There have been several valid critiques of the models of sexual orientation development proposed thus far. Though the models' development fit those they were developed on, those people were primarily white, gay men coming out in the 1970s and 1980s in the USA. While some lesbians were also included in the creation of these models, the majority of participants in sexual identity research were male, and almost exclusively white, American, and middle-to-upper class socioeconomic status (Savin-Williams 2001).

These models were also not fit for people who identify as anything other than exclusively gay or lesbian, such as bisexual, pansexual, or asexual, though many of the experiences, such as coming out or understanding the social ramifications of having a sexual minority orientation, may still apply. Additionally, sexual minority individuals are not a homogeneous group and experience many differences in identity development over time, especially among those who may have same-sex desires, but may not adopt a culturally defined sexual identity label (Savin-Williams 2001). Even the relationship among sexuality labels has changed, for example, social stigma has, and is continuing to, shift significantly. Some other sociocultural factors that influence development yet are not accounted for by sexual orientation identity development theory, including race, socioeconomic status, education, religion, culture, gender, and ability (Kaufman and Johnson 2004).

Another critique is in the stage model aspects of the proposed identity models. There is an assumption that they are inevitable, invariable, linear, and normative. Inevitable in that all people identified as gay or lesbian must go through all the stages in the model in an invariable and linear order – that is, all the stages must happen one at a time, in the same order for every individual, unidirectionally with no back and forth or regression (Langdrige and Moon 2008). Normative in that every individual who identifies as gay or lesbian concludes in the final stage of integration, as opposed to staying in an earlier stage such as Cass model's identity pride and never moving into identity synthesis. Many people have found that these factors make it difficult for sexual identity theories to describe a variety of experiences. Because people, and their experiences, are unique, no one theory will describe all people.

Some alternatives to the sexual orientation minority theories previously discussed have been proposed. One such alternative theory is by D'Augelli (1994). This theory focuses more on the sociopolitical context of identity formation and, as such, takes a more historical viewpoint to creating a model for identity development in same-sex attracted individuals. D'Augelli's

process, unlike the linear models of Cass and Fassinger, proposes a series of six unsystematic and independent identity processes. Though this model is theoretically variable, the first process often begins with relinquishing a heterosexual sexual orientation identity label. The following five processes may happen in any order but are important to the sociopolitical context of becoming a sexual minority-identifying person: understanding and developing an individual sexual minority identity; announcing a sexual minority identity socially; coming out to important family members, especially parents; developing a relationship with a person who either affirms and/or understands sexual minority identification; and entering and feeling part of a sexual minority community. Many people experience these processes at different times and in different ways, especially given that this model focuses primarily on the relationship of one's sexual minority identity to others in the sociopolitical climate (D'Augelli 1994).

Another sexual identity development alternative is to look specifically at sexual orientation development milestones, not as a stage model, but as general guidelines for understanding normative sexual orientation identity development (Katz-Wise et al. 2016). There are five identified major sexual orientation development milestones: same-gender attractions, other-gender attractions, same-gender sexual experience, other-gender sexual experience, and sexual minority identification. While these milestones may not happen in any particular order, nor are all milestones inevitable, many individuals who go through the sexual orientation identity development process indicate the importance of their first experience of attractions toward another person (same or other sex), their first sexual experience with another person, the first questioning of their sexual orientation, the first disclosing of a sexual minority identity to others (coming out), their first romantic feelings for another person, or the first relationship (Katz-Wise et al. 2016). Statistically, there are two main groups that have evolved from research investigating sexual orientation development milestones: those that experience the first same-sex attraction during childhood and those who

experience it in adolescence (Katz-Wise et al. 2016). Predominantly, people who eventually identify as exclusively same-sex orientated tend to experience their first same-sex attractions in childhood, as well as being more likely to present as less traditionally gender conforming. Those that experience their first same-sex attraction in adolescence are more likely to identify as a non-exclusive sexual minority, such as bisexual, mostly heterosexual, pansexual, or unlabeled. Women are also more likely to experience their first same-sex attraction in adolescence and are also more likely to experience all five milestones of sexual orientation identity development – including same- and other-sex sexual experiences (Katz-Wise et al. 2016).

Due to women's unique experience, another proposed theory for development is female sexual fluidity, a theory of female sexual identity development proposed by Lisa Diamond and popularize in her book by the same name in 2008 (Diamond 2008). Female sexual fluidity is defined as "a situation-dependent flexibility in women's sexual responsiveness." This posits that it is possible for some women to experience sexual desire for men or women in specific circumstances, despite her sexual orientation identity, building off of the theory of erotic plasticity that postulates that women's sexual arousal is more affected by environment than men's sexual arousal (Baumeister 2000). This is not to say that sexual orientation does not have a biological component, as it certainly does; however, for women especially, the biobehavioral links between affectional love and sexual desire, though independent, are bidirectional. Sexual attractions are affected by both biological and sociocultural factors. Therefore, in a situation where there are strong emotional, romantic feelings, this can lead to feelings of sexual desire, even for someone who would not typically be the target for a specific sexual orientation identity. These strong feelings, both love and sexual, can lead to a change in sexual orientation identity over time, as has been found in the research (Diamond 1998). In fact, as opposed to being a transitional stage between heterosexuality and homosexuality, many women actively adopt sexual orientation identities such as unlabeled,

queer, or bisexual throughout adolescence and adulthood. While there is some new, and as yet unpublished, evidence suggesting this same relationship exists in men, but to a lesser extent, this phenomenon has been shown to exist in women over decades of research.

Female sexual fluidity as an alternative theory of sexual orientation identity development highlights that there are significant sex differences in sexual identity development – both biological and sociocultural (Diamond 2008). For example, men reach the sexual orientation development milestones earlier than women, which is certainly affected by women being sexually active and aware later in life in general, at least partially due to the sociocultural climate toward female sexuality (Katz-Wise et al. 2016). This sociocultural climate may also contribute to twice as many women reporting any same-sex sexual contact as men. Gay males also tend to feel different as children and usually identify as gay around age seventeen, after their genital experience with another person. However, lesbians, who tend to identify as gay around age eighteen, on average, don't have their first genital experience with another person until around age twenty (McClelland et al. 2015). Additionally, the timing of a man's first same-sex attraction is associated to his sexual orientation identity development; however, the quality and context of a woman's early attraction and behavior are more important. This returns to what may be a fundamental difference between male and female sexual identity – the importance of the individual and the environment.

The distinction between sexual attraction and sexual behavior is important to emphasize when discussing sexual identity. While sexual attraction and sexual identity are correlated closely with each other, they are not completely correlated with reports of sexual behavior (Chandra et al. 2013). This is perhaps because attraction often lacks coherent definition. From an academic standpoint, attraction consists of three major categories: onset of attractions, frequency of attractions, and the intensity of attractions (Savin-Williams and Joyner 2014). While sexual attraction is often synonymous with sexual orientation, sexual attraction is simply one facet of sexual orientation identity. However, sexual attraction is

better correlated with sexual identity than sexual behavior and is the preferred measurement used by academics to determine sexual interests overall for this reason. Several studies have found a substantial incongruence between the behavioral and identity dimensions of sexual orientation identity. For example, there are many individuals who identify as exclusively heterosexual who have had same-sex experiences, who identify as exclusively homosexual who have had other-sex experiences, or who identify as bisexual and have only other-sex experiences, but intense same-sex sexual fantasies (Morrison et al. 2005). In addition to being a preferred measurement tool, the three facets of attraction are more influential than sexual behavior in determining how an individual will construct their sexual identity. While sexual behavior is observed as external and context-dependent, the importance of sexual attraction in developing and defining an individual's sexual identity is a consequence of the individual's perception of attraction as a differentiating and consistent aspect of the self, the two components necessary to create a personal identity relevant to the sexual life.

Conclusion

Sexual identity is multifaceted, multimodal, variable, mutable, and highly personal. Though its unsystematic nature increased the difficulty in studying sexual identity, many researchers have dedicated themselves to understanding its foundation and development, especially during adolescence, a sensitive period for both sexual and identity development. Researchers have argued about the nature of this development, and how best to measure it, for decades, and will continue to do so for decades more. At this moment, however, we know that sexual identity, though in common parlance is focused on same- and other-sex attractions, includes facets of fantasy, desire, past behavior, current behavior, ideal behavior, sociopolitical context, romantic feelings, sexual attractions, preferred characteristics of partners, preferred number of partners, preferred levels of commitment, values and morals, and interpersonal desires. Though not every facet will be

important to every individual at every point in time and both the content and importance can change over time, each one aspect of sexual identity contributes to an understanding of a complete sexual identity.

Cross-References

- [Derogation of Promiscuity](#)
- [Ecology of Pair-Bond Stability](#)
- [Exotic-Becomes-Erotic Hypothesis](#)
- [Genetic Hypotheses of Homophobia](#)
- [Lesser-Known Theories of Homosexuality](#)
- [Mate Preferences](#)
- [Sex Differences](#)
- [Sexual Arousal](#)
- [Social Hypotheses of Homophobia](#)
- [Women's Mate Preferences](#)

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Sexual Imprinting

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Synonyms

Positive sexual imprinting

Definition

The process through which sexual preferences are acquired from the characteristics of the parents.

Introduction

Sexual imprinting is a special type of imprinting which is thought to be related to sexual or mate preferences of animals. As evolutionary psychology mainly focuses on behavioral traits involved with survival and reproduction, sexual imprinting has been intensively studied, especially the sexual imprinting in human beings.

In fact, sexual imprinting can be either positive or negative. Positive sexual imprinting refers to acquiring sexual preferences according to the characteristics of one or both of the foster parents. The frequently mentioned “sexual imprinting” usually refers to positive sexual imprinting. On the contrary, negative sexual imprinting refers to acquired avoidance of mating with individuals who resemble kin, which is also known as Westermarck effect. The phenomenon of sexual imprinting has been found in both nonhuman animals and humans and has brought new inspiration to the field of mate choice of animals and human beings.

The Evolutionary Function of Sexual Imprinting

Individuals may acquire preferences for specific physical traits during a sensitive period from their parents and then form the sexual preferences for the potential mate. This process has been described as sexual imprinting or positive sexual imprinting (e.g., Rantala and Marcinkowska 2011). In Immelmann’s studies (Immelmann 1972), birds such as male zebra finches tended to prefer mates that possessed the characteristics of the female bird who reared them. Similar studies have obtained the same results which verified the existence of sexual imprinting and suggest that individuals acquire sexual preferences from the one who gives them parental care rather than the birth parent when they are different (ten Cate and Vos 1999). The phenomenon of sexual imprinting occurs not only in birds but also in mammals. For example, male sheep fostered by goats appeared to be more attracted to females of the same species of their foster mother, and the effect turned out to be irreversible (Kendrick et al. 1998).

Previous studies suggested that sexual imprinting served as an important factor of species recognition (ten Cate and Vos 1999), which was also a function of imprinting. Through sexual imprinting, individuals learn the phenotype of those who rear them, and this may affect their mating process during adult period. By forming the preferences for mates according to early experience with parents, sexual imprinting may help reduce the probability of hybridization, because it enables the individual to find a conspecific mate when they become an adult.

Evidence for Sexual Imprinting in Humans

Recently, more and more studies have suggested that sexual imprinting also influences the process of human mate selection. The major topic of discussion would be the similarity of facial traits between one’s spouse and the opposite-sex parent. For instance, Bereczkei et al. (2002) asked participants to rate the similarity of a set of photos, among which the photos of wives and their mothers-in-law are included. The results showed that wives and their mothers-in-law are more easily to be matched correctly than by chance, indicating that men were more likely to choose

women who possessed the facial characteristics of their mother as wives. Similar preferences were also found in women, even if the woman was adopted as a child (e.g., Wiszewska et al. 2007). Furthermore, recent study showed that the preference for parents' facial traits can be found in 9-year-old children, particularly when parent-child relationship quality is positive (Vukovic et al. 2015).

Other evidences supporting the sexual imprinting in humans include the hair and eye color of one's partner and opposite-sex parent (e.g., Little et al. 2003). Besides, imprinting-like effect has been found in preferences for female physical characteristics such as breast size and shape in both heterosexual men and homosexual women (Valentova et al. 2017).

In addition, it is inferred that information related to age of parents can also be learned through sexual imprinting during early experience. Ages of women's actual partners and their parents turned out to be correlated (Wilson and Barrett 1987). In later experiments, participants born to older parents were more attracted to older faces (Heffernan and Fraley 2013), suggesting that early interaction with parents may play a role in shaping later mate preferences.

Conclusion

Sexual imprinting was first found in animals such as birds and mammals, describing the phenomenon that individuals would show sexual preferences for those who possess the characteristics of their parents. Then similar behavioral patterns were found in humans in several aspects, including the most discussed preference for facial traits. Although some of the research findings may have alternative explanations, sexual imprinting is still of great significance in predicting human mate selection, and more studies are needed to establish the theory of human sexual imprinting.

Cross-References

- [Facial Attractiveness](#)
- [Imprinting](#)

- [Intersexual Selection](#)
- [Mate Choice Copying](#)
- [Mate Preferences](#)
- [Phenotypic Resemblance and Kinship Detection](#)
- [Westermarck Effect](#)

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Sexual Infidelity Versus Emotional Infidelity

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Synonyms

Cuckoldry; Emotional unfaithfulness; Sexual unfaithfulness

Definition

Sexual infidelity is unfaithfulness that involves a sexual component (e.g., engaging in sexual intercourse), and emotional infidelity is unfaithfulness that involves an emotional component (e.g., forming an emotional attachment).

Introduction

Both men and women exhibit negative emotions over both sexual and emotional infidelity (Sabini and Green 2004). However, research has found that men and women exhibit different levels of distress depending on whether the infidelity is sexual or emotional (Buss et al. 1992; Edlund et al. 2006; Fernandez et al. 2006; Kuhle 2011; Shackelford et al. 2002).

Evolutionary View on Sexual Versus Emotional Infidelity

From an evolutionary perspective, men and women face different adaptive problems, and therefore level of distress over infidelity should correspond to which risk is greatest for each sex (Buss 2005). Due to paternity uncertainty, males risk channeling their efforts into offspring that may not be their own. Thus, being more distressed over sexual infidelity would help guard against being cuckold. On the other hand, women risk

losing the aid and resources of a partner to someone else. Thus, being more distressed over emotional infidelity would help guard against losing partner investment.

There is research that provides evidence for differing levels of distress in men and women over sexual versus emotional infidelity (Buss et al. 1992; Edlund et al. 2006; Fernandez et al. 2006; Kuhle 2011; Shackelford et al. 2002). For example, Buss et al. (1992) asked participants to think about a serious committed relationship and then asked them which of the following two scenarios would upset them more: “Imagining your partner forming a deep emotional attachment to that person” or “Imagining your partner enjoying passionate sexual intercourse with that other person.” Men were more likely to report greater distress over sexual infidelity, whereas women were more likely to report greater distress over emotional infidelity. Physiological responses were also found to follow the same pattern (Buss et al. 1992). Men showed greater electrodermal activity when imagining sexual infidelity, whereas women showed greater electrodermal activity when imagining emotional infidelity.

Likelihood of forgiveness and recall of cues have also been found to be influenced by the type of infidelity (Schützwohl and Koch 2004; Shackelford et al. 2002). With regard to likelihood of forgiveness, Shackelford et al. (2002) found that men were more likely to indicate that they would find it more difficult to forgive sexual infidelity than emotional infidelity, whereas women were more likely to indicate that they would find it more difficult to forgive emotional infidelity than sexual infidelity. With regard to recall of cues, Schützwohl and Koch (2004) found that men preferentially recalled cues to sexual infidelity, whereas women preferentially recalled cues to emotional infidelity.

Conclusions

There is much evidence supporting the evolutionary view that distress to infidelity is a sexually dimorphic adaptation (Buss et al. 1992; Edlund

et al. 2006; Fernandez et al. 2006; Kuhle 2011; Shackelford et al. 2002). However, it should be noted that the sex difference has failed to replicate with certain samples (e.g., Carpenter 2012; Sabini and Green 2004). Additionally, alternative accounts for such effects have been proposed (Harris 2000). For example, Harris (2000) proposes that men are simply more reactive to sexual stimuli than emotional stimuli and that women have greater ease at imagining emotional stimuli than sexual stimuli. Therefore, future research is still needed but the existing literature has given us great insight into these differing forms of infidelity.

Cross-References

- [Emotional Jealousy](#)
- [Sexual Jealousy](#)

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Sexual Initiation

- [Oral Sex and Sexual Debut](#)
- [Predictors of Sexual Debut](#)
- [Sexual Debut](#)

Sexual Injustice

- [Sexual Stigmatization](#)

Sexual Intercourse

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Synonyms

[Coitus](#); [Copulation](#); [Making love](#); [Sexual congress](#); [Sexual relations](#)

Definition

Sexual Intercourse: Genital contact, especially the insertion of the penis into the vagina, perhaps followed by orgasm.

Introduction

Poets and novelists have always been fascinated by sexual passion but until recently scholars had conducted very little scientific research on the topic. Such research was considered taboo, trivial, vulgar, and unscientific. One exception to this prohibition was evolutionary theory. Since Darwin's (1859/1988) classic *The Origins of Species*, anthropologists have been interested in how men and women go about selecting sexual partners and mates, what people prefer in potential sex partners, whether or not men and women differ in their desire for sexual intercourse, and how often people of various ages, genders, and ethnicities engage in sexual intercourse. Evolutionary psychologists provided a scientific rationale for such investigations and made it clear that such investigations were vitally important, since such preferences shaped the future of humankind. Let us now consider their findings.

Who Do Men and Women Prefer for Sexual Partners?

Evolutionary psychologists contend that there are cultural universals in what men and women desire in a mate and sexual partner. This contention is supported by a landmark cross-cultural study conducted by Buss (1994), who asked more than 10,000 men and women from 37 countries to indicate what characteristics they sought in potential mates. These people came from a variety of geographic, cultural, political, ethnic, religious, racial, economic, and linguistic groups. Buss found that, overall, the single trait that men and women in all societies valued most was "mutual attraction-love." After that, people cared next about finding someone who possessed a dependable character, emotional stability and maturity, and a pleasing disposition.

People also tend to end up with mates and sexual partners who are very similar to themselves. This is called assortative mating. Buss and Barnes (1986) observed that the number of traits on which couples were matched was "staggering." Couples show such matching for age,

race, religion, personality dispositions, attractiveness, drinking, height, weight, smoking, interests, attitudes, and a host of other variables (see also Hatfield and Rapson 1993; Hatfield et al. 2012 for a list of universally desired characteristics).

Although evolutionary psychological research has provided fairly robust explanations for mate preferences, research so far has failed to sufficiently infer mating behavior for mate trait preferences. Conroy-Beam and Buss (2016) found that mate preferences predict actual mating decisions using evidence from computer simulations and real-world couples. Conroy-Beam and Buss showed that mating preferences strongly predict mate selection in preference-driven simulations but not in simulations in which mate selections were random. Moreover, mate preferences significantly predicted mate decisions in real-world couples. These conclusions offer support for the notion that mate selection is a cause of stated mate preferences rather than a consequence of the individual updating his/her mate preferences to fit the chosen mate.

As evolutionary theory would suggest, Buss (1994) found some marked differences in what men and women want in mates and sexual partners. As discussed in earlier entries, men and women must employ somewhat different strategies in order to maximize their genetic contributions to the next generation. As predicted, men tended to care more about the physical appearance and youth of their partners than did women; women tended to be more insistent that their mates possess high status and the resources necessary to protect themselves and their children.

Petersen and Hyde (2010) conducted a meta-analysis of research into gender differences in sexuality, conducted from 1993–2007. They analyzed the impact of gender on 30 sexual attitudes and sexual behaviors for men and women from 87 countries and 6 continents. They included 834 individual samples and 7 large national data sets in their analyses. Consistent with evolutionary psychology, they found that men did indeed report more permissive attitudes toward casual sex and slightly more sexual experience than did women. However, they also found that (1) in nations and ethnic groups with greater gender

equality, people display smaller gender differences in attitudes and behaviors than do people from more traditional nations and ethnic groups, (2) over time, many traditional gender differences seem to be disappearing, and (3) in all nations, those gender differences in sexual attitudes and behaviors which did still exist were surprisingly small. Exceptions were in the incidence of masturbation, pornography use, attitudes toward casual sex, and the incidence of participating in casual sex – all of which yielded medium effect sizes. As predicted, men possessed more permissive attitudes toward casual sex and engaged in slightly more casual sexual behavior than did female participants.

Appearance

In choosing sexual partners, people tend to focus on the potential partner's physical appearance. Men desire young and beautiful women with symmetrical faces, smooth skin, medium to large plump breasts, a 7:1 waist to hip ratio, rounded buttocks, and long shapely legs. Women desire men with strong masculine features, a V shape (muscular shoulders with small hips) and a large penis (see Singh 1995). These traits, for both sexes, are overt indications of the potential mate's physical health and reproductive ability.

Evolutionary psychologists have focused on primary and secondary sexual characteristics. They ask: Why do penises, vaginas, and breasts have the size and shape that they do? When compared to other primates, why do humans have larger penises and vaginas than other hominoids (apes)? (Dixon 2009).

Evolutionary theorists have argued that breasts evolved as a way to signal to men that a woman was youthful and nutritionally advantaged, and thus would be a promising mate. A paper in the *Proceedings of the Royal Society* by Jasienska et al. (June 22, 2004) reported that women with large breasts and narrow waists possess higher fecundity (as measured by daily levels of 17- β -oestradiol and progesterone).

Do men in various societies consciously recognize these cues? Maybe not. In a study of

191 cultures, Ford and Beach (1951) found that in only 13 of these cultures was breast size considered important: nine preferred large breasts, two preferred long pendulous breasts.

Why is the human vagina so large, compared to other primates? Humans are unique in that they come into life prepared to fit into their environment. Infants take longer in gestation, have larger brain size, and larger newborn body size than their peers. That means that women's vaginas and birth canals must be unusually large to accommodate the infant (Mautz 2012).

Given the size of women's vaginas, men must compensate by having larger penises (in girth). When erect, it measures between 5 in. and 6 in., on average, and about 5 in. in circumference. That is twice as big as that of chimps, for example (Bering 2012). Women prefer a large phallus in men. When women are shown life-sized projections of naked men, they say the ones with bigger organs are more attractive (Mautz 2012).

Why is the penis shaped as it is? Gordon Gallup concluded that the oddly shaped member, with the bulbous head, coronal ridge, and long, rigid shaft is designed to "shovel out" the sperm of previous sexual partners and deposit their own. In research with various types of penises, with different shapes, he finds that the male penis is especially efficient at this task.

How Often Do Men and Women Have Sexual Intercourse?

The physiological responses during sexual stimulation are fairly similar for both men and women. There are four phases in the human sexual response cycle (Masters and Johnson 1966.)

- During the excitement phase, the body prepares for sexual intercourse. Heart rate and breathing rate increase and blood pressure rises. Men and women experience a "sex flush" on the face and upper body. Typically, a woman's vagina becomes lubricated and her clitoris becomes swollen. A man's penis becomes erect.

- During the plateau phase, heart rate and muscle tension increase further. A man's urinary bladder closes to prevent urine from mixing with semen. A woman's clitoris may withdraw slightly and there is more lubrication, outer swelling, and muscles tighten and reduction of diameter.
- During the orgasm phase, breathing becomes extremely rapid and the pelvic muscles begin a series of rhythmic contractions. Both men and women experience quick cycles of muscle contraction of lower pelvic muscles and women often experience uterine and vaginal contractions; this experience can be described as intensely pleasurable, but roughly 15% of women never experience orgasm and half report having faked it.
- During the resolution phase, muscles relax, blood pressure drops, and the body returns to its resting state. After this period, men (and some women) are no longer able to experience an additional orgasm, or multiple orgasms soon after the first.

According to Masters and Johnson (1966), men are physically incapable of bypassing the resolution phase. Women, however, are able to enter the orgasm phase, return to the plateau phase, then continue to the orgasm phase again. The ability to circumvent the resolution phase allows women to experience multiple orgasms in one sexual episode.

In 1994, Laumann and his colleagues released data from a survey of Americans asking about their sexual practices. Most previous studies were limited to small samples of Americans, based on convenience samples rather than random samples. Laumann et al.'s study was the gold standard in that it used a large random national sample. Similar scientific studies exist for other cultures.

When people speak of "sexual behavior" they might mean marital partners, a dating couple, or casual sex. It may mean vaginal sex, oral sex, anal sex, or masturbation (which evolutionary psychologists say should be less attractive than sexual intercourse, since it does not give people a chance to contribute to the gene pool). It could be

heterosexual, homosexual, one-on-one sex, or group sex. Because of space limitations, we will present only a few of Laumann et al.'s (1994) findings. People interested in more complete data may consult the surveys we have referenced.

- Most married couples have intercourse seven times a month (Laumann et al. 1994; Call et al. 1995; Donnelly 1993).
- There is tremendous variability in how often couples have sexual intercourse in marital relationships. Some couples are celibate or have intercourse very infrequently while others have sex daily. Cathy Greenblat (1983) interviewed 80 people who had been married 5 years or less. She found that couples reported having intercourse ranged from once a month (12 times a year) to 540 times a year.
- Sexual activity declines with age (specifically from 44 to 72). Factors responsible for the decline are changes in marital health, happiness, and poor physical health (Karraker et al. 2011).

Conclusion

Evolutionary psychology has sparked a great interest in human sexuality. In recent years, sexologists have accumulated a great deal of information on the ability of social psychologists and evolutionary theorists to predict who, what, why, and when people engage in sexual intercourse.

Cross-References

- [Cunnilingus](#)
- [Human Copulation](#)
- [Penile-Vaginal Sex](#)

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Sexual Intimidation

- Sexual Harassment
- Types of Sexual Coercion

Sexual Jealousy

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Synonyms

Aggression; Emotional jealousy; Infidelity; Mate guarding; Mate poaching

Definition

Men's sexual jealousy is an evolved emotional response to a real or perceived threat of a partner's sexual infidelity. It is a functionally flexible response that serves to motivate men to engage in mate-guarding behavior designed to deter intrasexual rivals and to maintain valued relationships.

Introduction

Over evolutionary history, human men have recurrently faced the challenge of finding and securing viable mating partners. Although humans evolved to form successive long-term relationships with one mate, infidelity has also been a recurrent theme in our evolutionary history.

In order to maintain their mateships, men would have had to fend off same-sex rivals, as well as signal to their partner their level of commitment to her. Likewise, it would have been crucial for men to ensure that their partners remained faithful to them. The fact that fertilization of the sperm and ovum takes place internally within the women's reproductive tract means that men, unlike women, can never be certain that the children they invest in are genetically theirs. The potential for a female partner to commit infidelity results in *paternity uncertainty* for men, which translates into a threat to men's reproductive success (Daly et al. 1982; Symons 1979). Thus, it would have been advantageous for men to have a means of identifying potential rivals, showing commitment to their mates, and remaining vigilant to suspected infidelity. Jealousy involves a constellation of emotions and behavior which have been argued to help in coordinating these interrelated efforts.

Jealousy has been defined as a distinct, yet complex, aversive emotional response to a real or imagined threat to a valued relationship (Buunk et al. 2008; Daly et al. 1982). Two basic types of jealousy have been identified which correspond with two kinds of betrayal one might experience in the context of a romantic relationship. *Sexual jealousy* is evoked in response to an actual or perceived threat of sexual infidelity, where a person may be having sexual relations with someone other than their primary partner (Buss 2013). In contrast, one may believe that their primary partner is forming a deep emotional romantic bond with someone outside of the relationship and committing emotional infidelity, which in return can elicit *emotional jealousy*. Over evolutionary time, both ancestral men and women have had to maintain mating relationships; thus, in contemporary society, men and women do not differ in the overall frequency or intensity of their jealousy (Goetz et al. 2008). However, a sex difference does emerge in regard to the two types of jealousy (sexual and emotional) owing to the differential *adaptive problems* – challenges that impact an organism's ability to reproduce (e.g., gaining access to mates) – faced by ancestral men and women (Symons 1979).

Ancestral women, given their higher obligatory parental investment (e.g., gestation, child-bearing, lactation), have primarily faced the adaptive problem of securing paternal investment for their offspring (Buss 2012). As a consequence, women demonstrate a heightened sensitivity to cues of emotional infidelity, which may signal the loss of parental resources. In contrast, ancestral men have principally faced the problem of paternity uncertainty, resulting in a lower threshold for cues to sexual infidelity. The totality of evidence to date supports the hypothesis that men express a heightened response to sexual infidelity in comparison to women, whereas women are more distressed by emotional infidelity in comparison to men (Frederick and Fales 2016). Because men, unlike the males of most other mammalian species, invest relatively heavily in their offspring, we expect that they should be particularly sensitive to signals associated with the misdirection of resources toward genetically unrelated offspring (Buss 2012).

A meta-analysis of 50 studies indicated that 24 % of women reported engaging in extramarital sexual activities (Tafoya and Spitzberg 2007). Globally, between 1.7 and 29.8 % of men are unwittingly raising children that they are not the genetic fathers of as a result such infidelity (Anderson 2006). *Cuckoldry*, unknowingly raising a genetically unrelated offspring, remains an issue pertinent to men's reproductive success. For men, a partner's sexual infidelity would have posed a major threat to their reproductive potential. For instance, unknowingly fathering a rival's child could have resulted in squandering parental investment resources, failing to benefit from a female partner's maternal effort, an opportunity cost of not being able to pursue other mateships, and becoming vulnerable to reputation damage, which could influence one's status and attractiveness as a mate (Goetz et al. 2008).

Jealousy as an Adaptation

Evolutionary psychologists have hypothesized that jealousy is a functional emotional adaptation that evolved to solve recurrent problems related to

reproduction (Buss 2013). From this perspective, it has been argued that jealousy can (1) alert an individual to threats to a valued relationship, (2) be evoked in the presence of same-sex competitors who may be interested in mating with one's romantic partner, and (3) motivate behavior meant to deter partner infidelity and relationship abandonment. As an adaptation, this means that jealousy has specific inputs, if/then decision rules, and behavioral outputs that collectively may benefit reproductive success.

Threats to a valued sexual or romantic relationship can derive from sources external to the dyad, such as a *mate poacher* who intrudes on an existing romantic relationship in an attempt to steal one's partner for either short-term copulation or to form a long-term romantic relationship. The presence of mate poachers is a common adaptive problem faced by men, because it may signal the potential loss of valued reproductive sources. In one study, it was found that approximately 60 % of men have admitted to having tried to entice another's mate into a committed relationship (Schmitt and Buss 2001), with 35 % of these men reporting that they had been successful in poaching the desired mate. Furthermore, despite expected cross-cultural variability, evidence of mate poaching has been discovered in 53 nations around the world (Schmitt 2004).

Cues to threatened stability of the romantic relationship can also derive from the dyad itself, such as when one's mate displays signs of disinterest or cues to their potential infidelity (Buss 2012). Sexual jealousy resulting from any of the aforementioned inputs may promote specific behavioral outputs that serve to maintain access to a mate, deter intrusions of same-sex rivals, and prevent a female partner from defecting from the mateship. Collectively, these actions have been termed *mate-guarding* behavior, which can range from pointing out a competitor's flaws to physically attacking another man for flirting with one's partner (Buss 2012). Notably, men's sexual jealousy has been argued to constitute the focal psychological mechanism that coordinates various mate-guarding behavior following a perceived threat to the valued relationship (Buss,

Larsen, Westen, and Semmelroth, 1992. Daly et al. 1982; Symons 1979).

Amid a chaos of conflicting social signals and cues, however, deciphering when sexual infidelity may be afoot and which intrasexual rivals pose a threat to a valued relationship is a challenging endeavor, especially when considering that the perpetrators of sexual infidelity are frequently trying to conceal their deception. These signals are often intentionally muted, such as an unfamiliar scent or an unexplained absence, which may or may not be indicative of infidelity, thus resulting in a *signal detection problem* (Buss 2012). A critical function of men's sexual jealousy is to render him more sensitive to these signals. Consider also that jealousy can be quite costly for a mateship if misdirected or unrestrained. A woman may leave her partner who falsely accuses her of cheating for a more trusting companion. Likewise, if consistently the target of *delusional jealousy* – denoting irrational and unfounded accusations about a partner's fidelity – she may defect from a relationship in search of a more emotionally stable mate, a highly valued trait for women within the context of long-term romantic relationships (Buss 2012). Furthermore, jealousy and mate-guarding efforts necessarily involve the expenditure of resources that could be allocated elsewhere, such as acquiring food and parental investment (Graham-Kevan and Archer 2009). Thus, we would expect jealousy to be functionally flexible, to produce a behavioral response based on the perceived seriousness and likelihood of losing a mate (Buunk et al. 2008).

Men's Sexual Jealousy and Aggression

Sexual infidelity can be a particularly potent stimulus for the expression of rage and anger, which tend to be directed toward same-sex rivals and/or to the romantic partner. Studies show that men's sexual jealousy is a leading cause of intimate partner violence, such as battery and spousal homicide, which is argued to constitute a strategy used by men to limit a female partner's sexual behavior (see Goetz et al. 2008). As deplorable and damaging as this behavior is, violence and

aggression might constitute evolved responses to several different but interrelated survival and reproductive problems that ancestral humans likely encountered with some consistency. For instance, aggression could have functioned to defend against an attack, to co-opt the resources of another, or to increase one's status within a social hierarchy (Buss 2012). Within the context of romantic relationships, aggression has been argued to serve three important functions: (1) to deter intrasexual rivals from pursuing one's partner, (2) to prevent long-term relationship partners from committing sexual infidelity, and (3) to reduce the probability that a partner may defect from a valued relationship (Buss 2012). In this way, aggression constitutes the context-specific behavioral output of jealousy that manifests as a range of different mate-guarding tactics designed to retain access to a desired mate, while deposing intrasexual rivals and deterring one's mate from defecting from the relationship.

Detering intrasexual rivals. The costs inflicted on an intrasexual rival could range from derogating a competitor by pointing out their flaws to using physical force to hurt or damage them and perhaps even to kill the rival. Spreading gossip about a potential competitor's imperfections constitutes a form of *indirect aggression*, where the perpetrator seeks to harm the target while simultaneously trying to conceal their intent (Vaillancourt 2013). Indirect aggression can be a useful tactic because it tends to be obscure and carries a lower probability of verbal or physical retaliation (Buss 2012). In contrast, *direct aggression*, such as punching another man who flirts with one's romantic partner or verbally threatening a rival, is conspicuous in its intent. Because men have evolved to compete with same-sex rivals for access to women, they are more often the perpetrators and the recipients of direct aggression (Archer 2004). Homicide data demonstrates that cross-culturally men kill other men at a much higher rate than women kill other women (see Goetz et al. 2008). Moreover, young boys tend to be the instigators and the victims of physical bullying (e.g., being hit) more often than girls (Swearer et al. 2010). In adult men, being unmarried and unemployed and thus lacking resources

which would benefit procuring and maintaining a mate are characteristic of both the victims and the killers involved in intrasexual homicide (see Goetz et al. 2008).

Preventing and anticipating a partner's sexual infidelity. One troubling reaction to suspected or actual sexually infidelity is men's use of intimate partner violence, which can take several forms (Arnocky et al. 2015). For instance, men may use *psychological aggression* such as attempting to reduce their female partner's self-esteem, perhaps in order to decrease how attractive and desirable she feels to members of the opposite sex (Arnocky et al. 2015). Men may also forcibly initiate sex or emotionally manipulate a partner into having sex (i.e., *sexual coercion*) if they are suspicious or know of their partner's sexual infidelity. Forced in-pair copulation in nonhuman animals follows a similar pattern, occurring more frequently after female sexual infidelity in some species (see Goetz et al. 2008). It has been argued that because sperm can survive in a women's reproductive tract for up to 5 days, inseminating a female partner can allow for one's sperm to either compete with or through the act of sexual intercourse to displace, a rival's semen. Importantly, the behavioral manifestation of jealousy does not require or imply conscious deliberation (Symons 1979). Rather, jealousy seems to motivate behavior on an implicit, nonconscious level (Buss 2012).

Men may also engage in acts of violence to prevent their partner from defecting from the dyad. This may at first seem counterintuitive; however, research has shown that women who leave their husbands are at a higher risk of being pursued, threatened, and assaulted compared to those who remain in the mateship (see Goetz et al. 2008). Shields and Hanneke (1983) reported that women who had been sexually unfaithful to their husbands were at an increased risk of battery and physical and/or sexual abuse.

In conjunction with sexual jealousy, men's feelings of anxiety also share an important link with anticipated infidelity and intimate partner violence. In many mammalian species, including humans, anxiety has been associated with aggressive behavior, and men who exhibit higher levels

of anxiety have been shown to engage in more relational aggression directed toward their intimate partners (see Arnocky et al. 2015). Interestingly, Arnocky and colleagues (2015) found that self-reported feelings of anxiety mediated a range of behavior constituting intimate partner violence such as physical, psychological, and sexual aggression in male undergraduate students. A mediating variable is one that explains the relation between two other associated variables. Men's sense of anxiety can be precipitated by feelings of uncertainty about their partner's faithfulness, and research has shown that men tend to overestimate the probability that their partner is going to or has committed sexual infidelity (Paul and Galloway 1994). This bias may however be functional, as it could serve to arouse men's suspicions, incite sexual jealousy, and motivate mate guarding and intrasexual competition, potentially allowing men to retain valued reproductive resources.

Factors that Influence the Intensity of Jealousy and Aggression

The context specificity of sexual jealousy, owing in part to its costly expression, means that individual differences likely modulate the intensity of men's jealousy and mate-guarding efforts. One such individual difference lays in the mate-value characteristics of an intrasexual rival, such that high-mate-value men represent a stronger threat to a valued relationship and should serve as a potent trigger for men's jealousy. Logically, these characteristics should also correlate with the traits that women find most desirable and attractive in a male partner. When asked to rank the qualities in a potential rival that would be most distressing, men from the Netherlands, Korea, and America consistently responded that it would be upsetting if a rival surpassed them in regard to financial prospects, occupation, and physical strength (Buss et al. 2000). Similarly, Dijkstra and Buunk (2002) found that when asked about a rival to whom one's partner might feel attracted, men, more than women, reported increased jealousy when the rival was high in social dominance,

physical dominance, and social status. In a study of participants in Argentina and Spain, Buunk and colleagues (2011) found that men, relative to women, experienced more jealousy when their rival was more physically dominant.

This research suggests that strong, dominant, physically attractive, financially secure, and high-status rivals are of particular concern to men in committed relationships. Unsurprisingly, these are among the very same qualities that women tend to seek out in sexual partners (Buss 2012). Research on individual differences among successful versus unsuccessful mate poachers also corroborate these findings. Effective male poachers tend to be attractive, tall, and have higher levels of self-esteem (Schmitt and Buss 2001; Sunderani et al. 2013), characteristics that denote high mate value which concerns one's desirability to members of the opposite sex (Buss 2012). Thus, high-mate-value rivals pose a particularly salient threat to men's mating success, and jealousy is more often experienced in their presence, relative to lower-mate-value rivals.

Similarly, men are expected to guard more intensely women of higher reproductive value because they are more desirable to members of the opposite sex as a mate and will more frequently be the target of mate poaching efforts (Sunderani et al. 2013). For instance, a woman's reproductive value declines as she ages from young adulthood onward, and it has been shown that men tend to engage in more mate-guarding behavior and more spousal violence (see Graham-Kevan and Archer 2009) toward younger partners than older partners. Flinn (1988) reported that men living in a Caribbean village, who were partnered with pregnant women (and thus unable to conceive at the time of study), spent less time with, and were less aggressive toward, their partners in comparison to men partnered with *fecund* (i.e., having higher reproductive potential) women. Men have also been shown to experience more jealousy and to guard partner's more fiercely around ovulation, the point of peak fertility across the female menstrual cycle (e.g., Gangestad et al. 2002). This demonstrates that, although ovulation is cryptic, men are able detect the subtle cues that emerge around ovulation to gauge a

women's fertility status. These signals may range from changes in body odor to differences in vocal pitch (Buss 2012).

Not all men, however, are equally concerned with or capable of establishing and maintaining long-term committed relationships, which results in differences in the expression of sexual jealousy and mate-guarding behavior. Some men effectively exploit short-term sexual relationships because they possess characteristics that connote genetic quality such as height, dominance, muscularity, and facial symmetry that are valued by women for their potential offspring (Buss 2012). These traits also reflect men's mate value (Symons 1995). High-mate-value men, in comparison to their lower-mate-value counterparts, are more sexually precocious, go on more dates, and have more sexual partners throughout their lifetime; however, they are also more likely to commit sexual infidelity (Buss 2012). Unsurprisingly, these men have been found to have a high *socio-sexual orientation*, which denotes more liberal sexual attitudes and behavior, requiring less love and commitment prior to entering into a sexual relationship (Clark 2006). Furthermore, taller men are, on average, less jealous than their shorter counterparts and experience less jealousy when confronted with socially influential, physically dominant, or physically attractive same-sex rivals (Brewer and Riley 2009; Buunk et al. 2008). Taller men have also been found to engage in less mate retention behavior overall (Brewer and Riley 2009). These findings demonstrate that high-mate-value men express less jealousy and engage in less mate-guarding behavior because there is a lower probability that they will lose their mate to a rival. These men are also more successful at procuring and establishing relationships resulting in a lower cost of mate desertion.

Lower-mate-value men are "competitively disadvantaged" having lower attractiveness, social competence, and financial prospects, leaving them at a greater risk of cuckoldry and mate defection (Figueredo and McCloskey 1993). Because these men face a larger cost associated with a partner leaving the mateship, they are likely to employ more direct, violent, and damaging forms of mate-guarding behavior in their

relationships. Indeed, men lower in mate value have been found to use more cost-inflicting mate retention tactics (Miner et al. 2009), as well as more controlling behavior and physical aggression directed toward their romantic partners (Graham-Kevan and Archer 2009). Men lower in mate value have been shown to experience more sexual jealousy at the prospect of sexual infidelity, and this jealousy has been shown to predict violence against intimate relationship partners (Cousins and Gangestad 2007). Also, men who are more invested in their relationships, as indicated by a higher degree of relationship satisfaction, have been found to exhibit more jealousy when subliminally primed with words relating to rival mate-value characteristics (especially with respect to social dominance; Massar et al. 2009).

Conclusion

Mixed findings have been reported for the association between jealousy and relationship longevity (e.g., Sheets et al. 1997), which seems to weaken the evolutionary logic of jealousy's adaptive benefits. However, it may not be the general tendency to become jealous that is important, but rather how this signal is interpreted by the recipient (i.e., the romantic partner), that determines its efficacy in solving adaptive problems. It has been shown that a partner's jealousy increases our confidence in their romantic commitment and provides reassurance of their in-pair attraction, which is positively associated with relationship stability (Sheets et al. 1997). Despite the fact that jealousy tends to produce an immediate negative response, its accompanying verbal and behavioral reassurances can help maintain long-term relational commitments. Men are particularly sensitive to cues of sexual infidelity in their romantic partners because, relative to other mammalian species, they invest heavily in their offspring and have recurrently faced the problem of paternity uncertainty over evolutionary time. Sexual jealousy is a specific emotional response to the threat of sexual infidelity, which serves to motivate mate-guarding behavior such as aggression directed toward one's partner and/or an interested

mate poacher. Despite the dangerous and damaging manifestations of excessive jealousy, contextually appropriate experiences and expressions of this emotion may have helped to solve a crucial reproductive dilemma for ancestral men: ensuring paternity by maintaining and defending valued relationships (Buss 2013). An evolutionary approach in no way justifies the deplorable manifestation of jealousy in society, such as men's use of intimate partner violence. It does however address the ultimate, root causes of this emotion and provide insight into when and in whom the more damaging behavioral output of jealousy is more likely to emerge.

Cross-References

- Contexts for Men's Aggression Against Women
- Evolutionary Psychology and Intimate Partner Violence
- Jealousy
- Jealousy and Infidelity
- Male Sexual Jealousy to Deter Partner Infidelity
- Morbid Jealousy
- Sex Differences in Jealousy
- Sex Differences in Morbid Jealousy
- Sexual Jealousy in Long-Term Relationships
- Violence as Coercive Control

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Sexual Jealousy Among Women

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Synonyms

Female jealousy; Women romantic jealousy

Definition

Sexual jealousy is a strong emotional reaction evoked by a perceived threat or the actual loss of a valued romantic partner (Buss 2013a). Sexual jealousy activates mate retention/guarding, as well as intrasexual competition behaviors (Buss 2013b; Buunk and Fisher 2009), which are deeply rooted in the adaptive problems that parental investment imposed on women and men throughout evolution.

Introduction

The study of sexual jealousy as an evolved psychological feature of the human mind began with the seminal work of Trivers (1972), whereas specific predictions regarding sex differences in the function of jealousy were advanced by Symons (1979) and Daly et al. (1982), to become later

embedded in a bigger theory of human mating by Buss (1989). The observation of mate retention behaviors, as well as competitor derogation, was also integrated into the bigger picture of sexual strategies theory (Buss 2013b), while the inquiry into the characteristics of rivals that strongly evoke jealousy were incorporated by Dijkstra and Buunk (2002). Accordingly, evolutionary psychology proposes that jealousy was retained in our species given its adaptive value throughout the Pleistocene, otherwise it would not have been selected and passed on to the present day (Cosmides and Tooby 2013). Finally, the specific tactics that underpin women's sexual jealousy as well as the investigation of female intrasexual competition were incorporated to the field by the research of Campbell (2004) and Fisher (2004).

The origin of women's sexual jealousy has its roots in biological sexual asymmetries in parental investment (Trivers 1972). Women's large investment in offspring causes them to be highly demanding in terms of courtship and signals of commitment in mating and pressuring men into ensuring a high rate of investment in child rearing. In contrast, men center their reproductive efforts in preventing cuckoldry and attaining highly fertile partners (Buss 2013a). Some have proposed that conflicting interests among the sexes have led men and women, through sexual selection, to the coevolution of psychological features that are preferred by the opposite sex. Men's and women's expectations pressure the opposite sex into reciprocal equilibrium in order to fulfill their common reproductive goals or lead to negotiation and recalibration of their needs in the opposite sex according to the benefits attainable on their mutual mate choice (Conroy-Beam et al. 2015). However, relationships are a dynamic process in which social contracts can be violated by a cheating partner. Within this scenario, an effective mechanism to prevent cheating by a partner is sexual jealousy.

The function of the sexual jealousy adaptation is protecting a mating relationship from interlopers, motivating guarding strategies directed at the partner, and aggressive/distancing behaviors directed at the rival (Al-Shawaf et al. 2015; Buunk and Fisher 2009). There are asymmetries between

the sexes in the specific situations that evoke this emotion (Buss et al. 1992), as well as the features of rivals that trigger sexual jealousy more strongly (Dijkstra and Buunk 2002).

One of the most important findings regarding the evolutionary approach to human jealousy are sex differences in the adaptive problems surrounding reproduction, which underlie the specific challenges to the pair-bond that activate jealousy in women and men (Buss et al. 1992). As parental investment theory states: women have the biggest share of biological costs in reproduction and therefore exert pressure on men to contribute extended commitment and resources in parenting. This dynamic in which men and women receive equal benefits from reproduction in a pair-bond with unequal investment is a central adaptive problem for women. As a result, women's sexual jealousy is triggered more strongly than men's when faced with the threat of their partner diverting resources, love, and/or commitment toward another woman. This has been termed *emotional jealousy*. Men face a different adaptive problem, namely, cuckoldry. A woman's sexual infidelity may result in her partner's extended investment benefitting another man's child and not his own offspring, reducing his fitness. This has been labelled *sexual jealousy*, which underlies the increased experience of male jealousy compared to women's, when faced with the possibility of their partner being sexually unfaithful (Sagarin et al. 2012).

Much of the literature in evolutionary psychology has explained male sexual jealousy as being directed at preventing cuckoldry. In its most extreme form, this motivation can lead to men's aggression toward a rival or a potentially cheating partner and even the homicide of a young unfaithful woman and/or her lover (Busche et al. 2013; Daly et al. 1982).

Female sexual jealousy can also lead to emotional distress, as well as the use of mate retention tactics and aggressive behavior directed against the rival or the cheating partner. However, sexual jealousy among women does not typically lead to the same level of physical violence as it does among men. Moreover, women's sexual jealousy rarely leads to killing of a cheating partner or his lover (Campbell 2004; Fisher and Cox 2010).

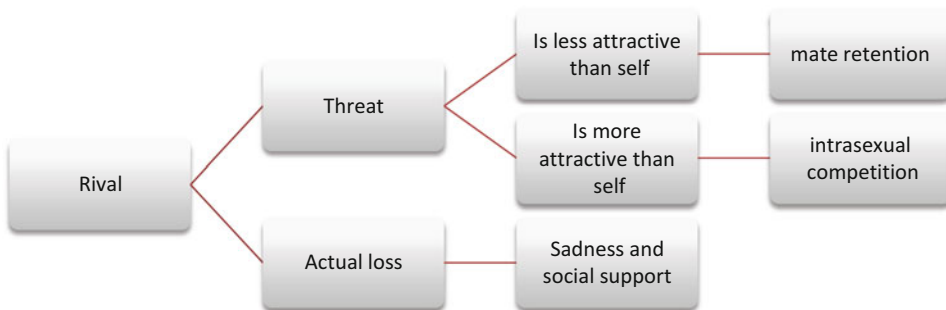
Affectively speaking, jealousy has been proposed to be similar to the fight or flight stress response, evoking negative emotions such as anger, fear, distress, and sadness (Buss 2013a; Fernandez and Palestini 2010). Pines and Friedman (1998) reported that sadness by the loss of a romantic bond is more representative of the experience of jealousy in women, which may function to accrue social support from close kin and allies, in times of intense distress, when commitment and support from a partner is lost to a rival (Hrdy 2009). It has been suggested that women's sexual jealousy is more reminiscent of freezing and immobilizing feelings, probably associated with intense fear and sadness, facilitating the recruitment of cognitive resources to cope with the loss (Fernandez and Palestini 2010).

Therefore, it can be expected that women's sexual jealousy in reaction to threats to the pair-bond will differ from the experienced affective states that follow from actually losing a pair-bond to a rival (see Fig. 1). Indeed, recent advances in research on intimate partner violence have hypothesized that aggressive reactions toward the partner are more frequent than commonly thought, with sexual jealousy being one of the main sources of fear that causes women to engage in fierce aggression directed at the partner or a rival, possibly mediated by an oxytocin surge when a highly intense pair bond is threatened (Cross and Campbell 2011).

The Adaptive Function of Women Sexual Jealousy

Sexual jealousy appears to be an emotion that is not independent of deep feelings of attachment toward a romantic partner – on the contrary, the more committed a person is to their partner, the more sexual jealousy she will experience toward rivals (Rydell et al. 2004).

Adaptively speaking, a characteristic of women's reproduction is that diversity of sexual encounters does not increase their reproductive rate, e.g., mating with one or several partners does not raise the number of offspring a woman will bear (Buss 2013b). Therefore, the focus of female jealousy seems oriented toward safeguarding and maintaining the investment from a valuable reproductive partner, which will secure her fitness by maintaining the commitment and resources of the man toward her and their common progeny (Buss 2013a; Symons 1979). Similarly, comparative work on other primates suggests that the presence of social support and alloparenting in the human species (Hrdy 2009) could function to ensure care of one's offspring in the event a partner betrays her and leaves her without resources as well as when a jealous woman attacks the reputation and social support of other women who are perceived as rivals (Campbell 2004; Fisher and Cox 2010).



Sexual Jealousy Among Women, Fig. 1 Activation of women sexual jealousy by a rival and its strategic consequences. When women are faced with a rival, they must initially determine if the rival poses a threat or if the partner has been lost to the rival. If there is a perceived threat, sexual jealousy will motivate women to assess the attractiveness of the rival compared to oneself. If this evaluation

determines that the rival is less attractive, mate retention will probably be the reaction. If the rival is more attractive than oneself, this will activate strong intrasexual competition. If the partner is lost to the rival, women's sexual jealousy will induce sadness and withdrawal, drawing close allies and social support to cope with the loss

Women's sexual jealousy leads to cognitive and behavioral responses that are highly intense in nature and are aimed at preventing the loss of a significant pair-bond (Campbell 2004). Love and care are universally the most effective strategies to retain a partner (Buss 2013b; Salkicevic et al. 2014), probably by signaling the willingness to invest and commit in a long-term relationship with the other person, and the exchange of benefits and caring for the welfare of the partner and offspring (Buss 2013b; Conroy-Beam et al. 2015).

Research based on interviews with the Himba of Namibia, a natural fertility population in which extra pair sexual activity is allowed, suggests that female jealousy in non-Western contexts also functions to prevent the diversion of resources toward other women with whom the partner may father a child (Scelza 2014). In our current context, the function of sexual jealousy is likewise aimed at maintaining men's investment in potential common reproduction. Therefore, sexual and erotic interactions with other women who are perceived as attractive rivals (Buunk and Fisher 2009), as well as more subtle intimate affectionate behaviors, such as sharing hugs, kisses, and cuddling, are prototypical actions that induce women's sexual jealousy in Western societies. And giving large amounts of money to an opposite sex individual, as well as many other forms of investments in rivals, triggers sexual jealousy in female college students (Kruger et al. 2013). Once jealousy is activated, psychological mechanisms assess the context and the characteristics of the opponent to decide whether the response will be directed at the partner, the rival, or both (Buss 2013a).

There are diverse manners in which jealousy motivates mate-guarding behavior, and there are particular strategies and tactics that are differentiated by sex in the realm of mate retention and intrasexual competition (Buss 2013b; Fisher and Cox 2010). One purpose of women's sexual jealousy is to alert the individual to engage in mate retention strategies which are specialized ways to protect the mating bond from rivals (see Fig. 1), such as enhancing the individual's own attractiveness and the benefits they bring to their relationship (with the costs that they will cause if they were to end the relationship). Moreover, women's jealousy

may also motivate distancing and derogating and sometimes physically aggressive behaviors toward the rival (Cross and Campbell 2011).

For example, a very attractive female rival is a stimulus that readily activates jealousy in women across different cultures and contexts (Buunk and Fisher 2009; Dijkstra and Buunk 2002). Attractive rivals lead to a diversity of "strategies" which are deeply rooted in our inherited ancestral wisdom, which ultimately allow one to move the rival away from one's mate and eliminate the threat of partner desertion. A jealous woman may react by enhancing their attractive attributes, bringing costs to the partner (like threatening to break up with him), or removing the partner from the context in which the threat occurs (e.g., by offering to spend quality time together, performing sexual favors, or engaging in love acts or declarations). There are also particular ways in which women may reduce the threat posed by the rival with indirect aggression toward the other woman: derogating her appearance and reputation, isolating the rival from social networks, or as a more radical resource (particularly when males are scarce), women may physically aggress against the rival in order to eradicate the threat (Buss 2013b; Campbell 2004).

The evolved function of women's sexual jealousy is alerting the individual to display mate retention behaviors and/or intrasexual competition, in order to preserve the pair-bond. Directing efforts at minimizing the relevance of the rival with the partner (Fisher 2004), or enhancing self-attractiveness compared to the rival, are some common behaviors to deal with sexual jealousy (Massar and Buunk 2016; Fisher and Cox 2010). Similarly, female intrasexual competitive behaviors are aimed at derogating the rival or directly attacking and distancing the competitor from the partner and are quite frequently motivated by women's jealousy (Cross and Campbell 2011; Grabe et al. 2012).

Female Jealousy Specializations for Detecting Potential Rivals

Sexual jealousy is exacerbated in women of low mate value relative to their high mate value counterparts, and low mate value women tend to

engage more frequently in indirect aggression, which may be caused in the less attractive women by an intensified perception of other women as potential rivals (Campbell 2004; Fisher and Cox 2010; Massar and Buunk 2016). This can be explained, as Fig. 1 shows, because when women encounter other women who are attractive competitors, jealousy gets activated, leading to feelings of the relationship being threatened. Conversely, given that mate-guarding may be less effective in the face of a more attractive rival the best option may be reacting aggressively toward the rival, as well as activating manipulative mate retention tactics, which are enhanced by the sexual jealousy mechanism.

For example, it has been documented elsewhere that sexual jealousy operates by capturing attentional resources such as visual perception, making females who are exposed to attractive women *blind* to other relevant information, possibly favoring the direction of cognitive and affective attention toward the retention of the romantic partner (Most et al. 2010). Likewise, it has been experimentally established that in the context of professional news reporting dynamics, women excel over men in attending to the content of information reported by highly attractive *sexualized* women journalists, which suggests a female specialization for attending to the professionalism and the message of other attractive women, which could be later used with very refined tactics to diminish the threat posed by the rival (e.g., by derogating the content or the intellectual/professionalism of the rival, Grabe et al. 2012).

Massar and Buunk (2009) found that women's sexual jealousy is also dependent on individual differences in jealousy, showing that jealousy leads to intrasexual competition more strongly in women possessing higher levels of basal preventive jealousy, which is characterized by a general tendency to prevent contact of the partner with any other woman. Correspondingly, when priming women with a highly attractive rival, they experience negative feelings (without being conscious of the stimulus). Women of relatively low mate value respond with increased jealousy to subliminally presented rivals flirting with the

partner in any condition, and high mate value females increase their jealousy only when the rivals are portrayed as attractive. In a Chilean study (Fernandez et al. 2014), age has been shown to mediate female jealousy having an inverse association to intrasexual competition, with young women averaging more jealousy and intrasexual competition than women passed their reproductive peak (over 27 years of age).

Similarly, recent findings documented women as significantly more efficient than men at detecting potential cues to infidelity, such as a very attractive woman flirting with a committed man, while there are no sex differences in detecting other kinds of socially threatening stimuli (Ein-Dor et al. 2015).

Women's Mate-Guarding Behavior

One way of dealing with sexual jealousy in both sexes is watching over or guarding a mate, which involves monitoring their social network, removing the mate from potential rivals (see preventive jealousy in Massar and Buunk 2016), trying to monopolize the partner's attention, securing social engagement with the partner, and the like, which are all forms of what has been labelled *mate guarding* (Buss 2013b).

Explorations of women's sexual jealousy relative to the availability of attractive rivals in the mating market has led researchers to posit that female jealousy in high-risk social contexts motivates monitoring and focusing on the partner's behavior in order to detect deception cues more so than focusing on the rival's behavior. On the other hand, when women perceive there is a low-risk social context of same sex rivalry, they tend to center their attention on the rival's characteristics more so than on the partner's deceptive behavior (Hanson et al. 2014).

Women's self-promotion (i.e., augmenting attributes of oneself which are highly valued by men) is a commonly used strategy to retain a partner and outcompete rivals (Buunk and Fisher 2009; Fisher 2004). According to findings of intrasexual competition, when faced with sexual jealousy, women's self-promotion allows them to enhance, imitate, or fake traits that are attractive to men, which increases the probability of driving away partner's

attention from a rival and redirecting it to oneself (Fisher and Cox 2010).

Benenson et al. (2013) found that an effective way that women use for discouraging rivals and distancing them from a valued partner is socially isolating them, which has the advantage of reducing the number of competitors in a given mating context.

Research in the field of evolutionary psychology, as well as the literature on relationship satisfaction and commitment, and mate retention and romantic attachment, has suggested that the delivery of benefits is an optimal mate retention strategy, being more effective than cost-inflicting mate retention tactics. This is to say that giving love and care, enhancing attractiveness, and increasing sexual activity are highly effective female strategies to guard and retain a partner. Threats of ending the relationship and derogating the partner or the partner's close social network may be weaker strategies to retain a mate in face of sexual jealousy (Salkicevic et al. 2014).

Women's Intrasexual Competition and the Green-Eyed Monster

Derogation of Competitors

Women's sexual jealousy motivates in the jealous female intrasexual competitive behaviors directed at enhancing the attractiveness of oneself and derogating the rival (Fisher and Cox 2010). The prevalence of strong intrasexual competition as the result of perceived mating rivalry from other women has been extensively documented in the last couple of decades (as it can be read in more detail in the respective entry of this volume).

Similarly, in the context of being surrounded by women who are perceived as more attractive than oneself, females systematically derogate other women, diminishing their ratings of facial attractiveness of other females (Fisher 2004). Competitor derogation when experiencing sexual jealousy includes making other women less attractive to the eyes of the partner, or enhancing other female's negative attributes, which rises the likelihood that the rival will be perceived as less attractive than oneself, and positing negative attributes of the rival, such as saying that she is unfaithful or that

she has an unattractive body (Campbell 2004; Fisher 2004). As Fisher and Cox (2010) showed, in the face of female sexual jealousy, an attractive woman can benefit more from derogation of rivals, since men give credibility to attractive woman's judgements about other women. But in the context of a jealous, less attractive woman, derogation can be interpreted as envy and even lower the mate value of the woman in relation to the more attractive rival (see the chapter on ► [“Women's Use of Direct Versus Disguised Social Aggression”](#) in this volume).

Women's Aggression in Response to Sexual Jealousy

Jealousy among females activates mate retention behaviors which have been shown to be very specific to the context and circumstances that surround women in particular: in contexts where reproductively valuable men are scarce, women engage in intense indirect as well as direct aggression toward other women, and they can also engage in direct aggressions toward the partner (Cross and Campbell 2011).

Female jealousy motivates aggression toward other women who are perceived as rivals, particularly when self-assessment indicates that there is a high chance that the partner may defect from the relationship for the other woman (Fisher and Cox 2010), or when the rival is significantly more attractive than oneself.

Conclusion

According to current advances in evolutionary psychological science, women's sexual jealousy is an adaptive response to a salient ancestral problem posed by the loss of a valued reproductive partner to another woman. This entry has reviewed the strategic fashion in which women's sexual jealousy orchestrates the feelings, responses, and the behaviors that follow, directed at retaining the pair-bond with the partner and distancing the rival.

One of the main characteristics of women's sexual jealousy is the fine calibration of this psychological feature for attending to the conditions

and the context in which jealousy occurs, which activates different cognitive and behavioral responses for retaining the partner, distancing the rival, or enhancing oneself in the eyes of the partner. These features of women's sexual jealousy suggest its selective attunement to adaptive problems.

Cross-References

- ▶ [Derogation of Rivals](#)
- ▶ [Female-Female Competition](#)
- ▶ [Female-Female Strategies](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Intrasexual Rivalry Among Women](#)
- ▶ [Mate Retention](#)
- ▶ [Sexual Jealousy](#)
- ▶ [Women's Use of Direct Versus Disguised Social Aggression](#)

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Sexual Jealousy in Long-Term Relationships

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Definition

An emotional state that occurs in response to a perceived or real threat to one's intimate relationship from sexual infidelity.

Sexual Jealousy in Long-Term Relationships

Jealousy can be defined as an emotional response to a threat to one's valued relationship, which motivates actions that reduce the threat. Sexual jealousy is a specific form of jealousy in intimate relationships when there is a perceived threat of sexual infidelity and is different from *emotional jealousy*, which is when there is a perceived or real threat that a partner is emotionally involved with someone else (see *emotional jealousy* entry).

Generally, men are more prone to responding to sexual infidelity, whereas women are more prone to responding to emotional infidelity (Sagarin et al. 2012). For men in long-term relationships, sexual jealousy may be adaptive because it functions by alerting them to cuckoldry risk (i.e., probability of unknowingly raising unrelated offspring), motivating them to reduce this risk (Daly et al. 1982). Women's concealed ovulation meant that men can never be entirely certain about their paternity and may therefore unknowingly invest significant time and resources on a rival's child. Cuckoldry, therefore, likely posed a significant cost to men's reproductive success. Such a strong selection pressure suggests traits evolved to identify and reduce such a risk. Cuckoldry risk does not apply to women because mothers are always 100% certain their child is genetically related to them.

Evidence supporting sexual jealousy as an evolved response includes associations between

infidelity risk and various mate retention tactics and violence (Goetz et al. 2005; Daly et al. 1982) to prevent or punish infidelity (Wilson et al. 1995). Risk of infidelity is also associated with semen displacement and sexual coercion, suggesting these tactics reduce cuckoldry risk by engaging in sperm competition if infidelity already occurred (Goetz and Shackelford 2006; Camilleri and Quinsey 2009). Jealous actions, including those that limit the autonomy of one's partner (e.g., trying to limit her contact with family, friends, or other men), seem to target younger (i.e., more reproductively valuable) women, probably because these women are at an age that elicits stronger competition from potential suitors (Buss and Shackelford 1997).

Jealousy may not always accurately indicate infidelity. Judgments about partner infidelity may be incorrect in one of two ways: Believing a partner is having sexual relations with another person when they are not is known as a type I error, or a false positive, whereas believing a partner is not having sexual relations with another when they are is known as a type II error, or a false negative. Haselton and Buss (2000) suggested we can understand these errors as *adaptive errors*, where it is possible that a bias toward making one type of error may have evolved because it is less costly or more beneficial than making the other error. In the case of jealousy, it may be more costly for men to assume their partner is faithful when they are not and less costly to assume a partner may not be faithful when they are. Some data support this hypothesis. Goetz and Causey (2009) found that men are more prone to making mistakes in overestimating the likelihood their partner is unfaithful.

Although jealousy may be adaptive because it motivates mate retention and sexual coercion, there may be unintended by-products of these actions. For example, Daly and Wilson (1998) suggested that coercive responses to perceived infidelity may sometimes be so severe that it results in uxoricide. Even though coercion may be adaptive to prevent infidelity, killing a spouse under such a scenario would not have been adaptive because losing a mating partner and familial retribution is costly. Thus, even though uxoricide

is linked to sexual jealousy, it does not mean uxoricide is an adaptive response to jealousy. Jealousy may also be disordered among some individuals, leading to delusional beliefs about partner infidelity (see *Jealousy: Psychiatric Diagnoses* entry).

Though women are not immune to sexual jealousy, there is evidence to suggest they tend to show greater distress to emotional infidelity because of the potential loss of their partner's commitment and resources (Buss and Haselton 2005; Buss et al. 1992; see *Emotional Jealousy* entry). A barrier to women's fitness is mate quality, which includes having a mate who shares resources to assist with raising and protecting offspring. Women whose partners pursue emotional relationships with other women face reproductive costs due to reductions in parental investment (Sagarin et al. 2012). Thus, women are more susceptible to emotional jealousy because it alerts them to a costly scenario.

The costs of infidelity are particularly salient for individuals in long-term relationships: men risk larger losses from long-term investment in a rival's offspring, whereas women risk larger losses of resources that are redirected to rivals over time. Unfortunately, empirical research on infidelity and sexual jealousy across the life span are not well-established – much of the developmental research on sexual jealousy is cross-sectional rather than longitudinal (see *Jealousy: Developmental Trajectory* entry). From the limited research, it appears as though as people age, sex differences in jealousy still exist, but the magnitude of the effect decreases (Shackelford et al. 2004). This reduced effect is consistent with the notion that risks associated with infidelity decrease with age.

Various studies have confirmed sex differences in jealousy. For example, men find it more difficult to forgive their partner for sexual infidelities, and women find it more difficult to forgive emotional unfaithfulness (Shackelford et al. 2002). Although not all studies find these patterns, a meta-analysis found an overall pattern where men are more prone to sexual jealousy, whereas women are more prone to emotional jealousy (Sagarin et al. 2012).

To summarize, sexual jealousy in long-term relationships appears to be a functional response because it orients people toward reproductive threats and motivates them to reduce such threats through mate retention, violence, and sexually coercive tactics. Jealousy may not always result in adaptive responses. Uxoricide may be a by-product and pathological jealousy is a disorder. Though sex differences in jealousy are empirically well-established, little longitudinal research has evaluated sexual jealousy in late adulthood.

Cross-References

- [Emotional Jealousy](#)
- [Jealousy](#)
- [Jealousy: Developmental Trajectory](#)

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Sexual Life

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Sexual Manipulation

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- [Genetic Influences of Puberty](#)

Sexual Minorities

► Sexual Orientation and Human Sexuality

Sexual Motivations of Gang Members

► Sexual Access

Sexual Nature

► Sexual Identity

Sexual Onset

► Predictors of Sexual Debut

Sexual Orientation

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Synonyms

[Orientation](#); [Sexual preference](#)

Definition

Sexual orientations are enduring patterns of sexual attraction.

Introduction

Sexual motivation is central to some of our strongest emotions and deepest commitments. Its

influence is so pervasive that many of our actions would be incomprehensible without taking it into account. Although the complexity of human sexuality should not be underestimated, it can be reasonably hypothesized that one of the main reasons people are so motivated by sex is because they experience sexual activities as highly rewarding. From an evolutionary perspective, the motivating nature of sexual experience is best explained as an adaptation for ensuring successful reproduction.

Evolutionarily speaking, one would predict that most women would prefer to have sex with men, and most men would prefer to have sex with women. This is precisely what is observed: although a significant number of individuals also report bisexual and homosexual attractions and orientations, most individuals report primarily heterosexual orientations (Bailey et al. 2016). Indeed, the sex of the person that one tends to desire is one of the largest factors differentiating men and women (Lippa 2009).

The term orientation is sometimes used to indicate individuals' self-defined sexual identities. Here, *sexual orientation* will be defined as an *enduring pattern of sexual attraction*. *Sexual preferences*, in contrast, can be thought of as *motivations for particular types of sexual experiences*, regardless of whether or not these motivations are driven by sexual attraction and irrespective of duration or stability. Although sexual preferences are frequently motivated by orientations and identities, preferred sexual expression can also result from a combination of factors that may have little to do with sexual desire.

Nature and/or Nurture

Among attempts to explain the origins of sexual orientations, a major difference between models is the degree to which they emphasize innate and learned factors. An extreme innateness perspective would argue that humans and other animals are genetically programmed to be attracted to features of the opposite sex. In contrast, an extreme learning perspective would argue that all humans are born with a general capacity for

sexual experience, but they are then shaped to have different patterns of attraction and aversion on the basis of their different social roles and personal histories. Debate continues regarding the ways and extent to which nature and nurture shape human sexuality.

To the extent that sexuality is influenced by evolution, adaptations are thought to depend on the relative “feminizing” and “masculinizing” effects of sex hormones on the developing brain (LeVay 2010; Savic et al. 2010). Hormones are believed to be necessary mediators for shaping nervous systems to respond in particular ways toward physical and behavioral characteristics typical of male and female organisms. According to this model, non-heterosexual attraction results from these processes of developmental masculinization and feminization proceeding in ways that are sex-atypical.

Although genetic effects on sexual orientation have been observed, among identical twins where at least one sibling reports homosexual preferences, the probability of the other sibling reporting homosexuality has been estimated to be as low as 24% (Bailey et al. 2016). This limited heritability demonstrates that orientation cannot be completely determined by genetic factors. Aspects of developmental programs contributing to sexual orientation may be genetically specified, but the underlying processes could be disrupted by a variety of environmental factors, especially prenatally. One notable example is the “older brother effect,” wherein each successive older brother increases the odds of the development of homosexuality in men (but not in women), which has been suggested to result from the maternal immune system developing increasingly strong reactions to Y-chromosome proteins found in male fetuses (Bogaert et al. 2017). This kind of model demonstrates how there can be influences on sexuality that are innately determined without being genetically specified.

Alternatively, the intensely pleasurable nature of sexual activity implies that reward learning can have profound impacts on sexuality. Indeed, some have argued that classical and operant conditioning may be a primary means by which adult sexual preferences are established in humans as well as

other species (Hoffmann 2017; Pfaus et al. 2012). The centrality of reward learning has also been suggested by Toates’ Incentive Motivation Model of sexual behavior (Toates 2009).

These proposals are generally dismissed on the grounds that reproduction is central to evolutionary fitness, and so natural selection must have produced specific and robust mechanisms for ensuring adaptive behavior. However, even for behaviors as fundamental to survival as drinking or eating, experience is required for newborn rats to learn the association between approaching water and obtaining hydration when thirsty, or between approaching food and obtaining nutrition when hungry (Changizi et al. 2002). Further, experience-focused models may become increasingly plausible as domain-general learning processes are discovered to be more powerful than previously recognized (Hassabis et al. 2017). Theoretically, evolutionary fitness may have been maximized most effectively by allowing organisms to utilize complex world models learned through experience.

Correlations between differences in sexual orientation and sexually dimorphic brain structures (and their functioning) have been influential in suggesting the importance of innate factors (LeVay 2010). Yet, these neurological differences remain poorly understood, particularly the means by which they impact behavior. Genetically and hormonally differentiated neural systems may indirectly influence what developing organisms learn as they interact with their environments. However, these differences could also result from the brain’s ability to plastically change itself through experience, rather than being caused by organizational effects of sex hormones.

The fact that male sexual orientation is extremely difficult to change is perhaps the strongest objection to the idea that experience may play an appreciable role in shaping outcomes (Bailey et al. 2016). However, this challenge could be addressed by considering sensitive periods of development, as well as the greater plasticity of young brains, which are still in a period of dynamic alteration due to factors such as changing hormones, progressive myelination, and ongoing neuronal and synaptic pruning (Kuhn et al. 2010).

Indeed, sexual orientation could be entirely learned and still be immutable in adulthood. Of course, it is clearly not the case that sexual orientation lacks innate contributions. However, the precise contributions from nature and nurture (as well as their interactions) remain unclear.

Homosexuality: An Evolutionary Enigma

While exclusive homosexuality is rare in the animal kingdom (Sommer and Vasey 2006), prevalence in humans has been estimated to range between approximately 1–5%, with similar rates observed cross-culturally (Bailey et al. 2016). Homosexuality has been shown to have appreciable heritability, with genetic bases suggested by correlates such as gender-nonconformity emerging early in development. Why would such genes persist in the population if they sometimes result in attraction to partners with which reproduction is impossible?

Several solutions to this enigma have been proposed whereby genes contributing to non-heterosexuality may have enhanced evolutionary (inclusive) fitness (Bailey et al. 2016; Sommer and Vasey 2006). One proposal involves increased altruism toward reproducing family members sharing those genes. Or, within a sexually antagonistic selection model, genes for gender atypicality (including in attraction) could enhance the gender typicality and fitness of opposite sex family members. Both of these hypotheses receive some support from studies of cultures where gender atypicality is constructed in terms of a “third sex,” which might have been the most common manifestation of male androphilia over the course of evolutionary history. Alternatively, it may have been the case that genes contributing to homosexual attraction may have increased fitness in other ways when present in some combinations, akin to heterozygote vigor. It has also been suggested that same-sex attraction could have enhanced fitness by furthering alliances, akin to a kind of social grooming. All of these dynamics could have contributed to selection to varying degrees over the course of evolutionary history, and at the present time there is currently

insufficient evidence to know which were most important.

Male proto-homosexuality genes may have been more likely to persist if it were the case that most men had limited reproductive success, potentially reducing the power of stabilizing selection for highly specific sexual preferences. That is, if expected fitness is low by default, there would have been reduced opportunity costs associated with attempting the alternative strategies described above. However, this account would be less applicable to female proto-homosexuality genes, since ancestral women might have been more likely to achieve at least moderate reproductive success, as would be predicted if female choice is the primary bottleneck for mating (Buss and Schmitt 1993).

Bisexuality and Evolutionary Strategies in Women and Men

Genes for same-sex attraction may have been far less deleterious if they were more likely to contribute to bisexual (as opposed to exclusively homosexual) attraction. Indeed, it should be remembered that degree of homosexual or heterosexual attraction is not all-or-nothing, that same-sex sexual behavior is quite common among heterosexually identified people, and that non-exclusive same-sex attraction is much more common than exclusive same-sex attraction (Bailey et al. 2016).

While men appear to have slightly higher rates of exclusive heterosexuality and homosexuality, women appear to be more likely to identify as bisexual, and are much more likely to identify as “mostly heterosexual” (Savin-Williams and Vrangalova 2013). In contrast to men, women often show nonspecific responses to male and female erotic stimuli in terms of genital arousal, attention, and even neural reward system responses (Safron et al. 2017b). Further, women’s sexuality appears to be characterized by sensitivity to social context, or “erotic plasticity” (Baumeister 2000), as well as capacity for change over time, or “sexual fluidity” (Diamond 2016). Indeed, it has even been (controversially) argued

that sexual orientation is best conceptualized as an evolutionary adaptation in which stable sexual arousal patterns are capable of consistently driving behavior over time, and that this mechanism may be present in most men, but not most women (Bailey 2009). Some limited support for this suggestion can be obtained in the finding that paraphilias (i.e., atypical sexual orientations) are more common in men than women.

This potential difference in male and female orienting is also supported by comparative studies of nonhuman mammals (Goy and Goldfoot 1975), wherein bisexual behavior is usually observed in either males or females of a species, but not both. Theoretically, if males could be reliably expected to approach females for mating, then it would have been less important for females to have exclusive orientations, and possibly even beneficial (e.g., in promoting alliances).

Speculatively, less directed sexual orientations in women could have been adaptive in affording greater inclusion of more complexly determined factors in mate choice, such as social status or tendencies toward parental investment. In some cases, a strongly directed arousal pattern could even represent an evolutionary liability for women, considering the potential difficulty of raising a child without male parental investment (Buss and Schmitt 1993). However, there were likely multiple evolutionarily stable strategies among ancestral women and men. It should also be noted that male sexuality might exhibit more plasticity and fluidity than previously assumed (Diamond 2016).

Proximate Mechanisms of Orienting: An Evolutionary-Developmental Enigma

What are the mechanistic bases for sexual orientation? In a seminal investigation of postmortem brains (LeVay 2010), the third interstitial nucleus of the anterior hypothalamus (INAH 3) was approximately twice as large in heterosexual men than in heterosexual women and homosexual men. This particular structure was examined because of its homology with the sexually dimorphic preoptic area, which has been established to

underlie the control of mating behaviors in numerous species (Roselli and Stormshak 2009).

Subsequent investigations partially replicated the gender differences in INAH 3, but only found a nonsignificant trend for smaller volumes in homosexual men, with no differences in neuron number. Perhaps most compellingly, female-typical characteristics of preoptic hypothalamic nuclei have been found to correlate with male rams preferring to exclusively mount other male rams. While these studies appear to constitute converging lines of evidence, it is important to keep in mind both the heterogeneity of these phenomena (e.g., a male rodent exhibiting lordosis is quite different from a male ram that mounts other males), as well as the need for replication with larger samples. Disclaimers notwithstanding, this kind of evidence suggests that a substantial part of sexual orientation might be related to hypothalamic nuclei.

But what is it that the hypothalamus is supposed to be doing with respect to orientation? The most straightforward assumption is that hypothalamic nuclei first detect sexually dimorphic stimulus features and then generate sexual behaviors and motivation. However, determinations of sexual significance are probably made upstream to the hypothalamus in structures such as cortex and the amygdala (Maras and Petrulis 2010; Terzoian and Ore 1955), in which case hypothalamic nuclei would not constitute a direct basis for sexual orienting. While the generation of sex-specific mating behaviors such as mounting or back arching would influence the likelihood of sexual interaction with other males or females, on their own this would not constitute a “hard-wired” sexual orientation, perhaps especially in species with greater degrees of freedom and complexity in available responses.

It is intuitive to assume that most of sexual orientation has its origins in innate responses to visual stimuli. Some of this intuition may be warranted. If nervous systems inherently try to minimize prediction error (Friston 2010), then the enhanced predictability of symmetrical structures and smooth textures could potentially act as primary “rewards” in terms of producing less sensory uncertainty. Yet, definitive evidence has not

been found that mammals are capable of having inborn responses to complex geometric features. However, ambiguous evidence is plentiful, as well as commonly (albeit mistakenly) cited as constituting strong evidence.

There has been a clear primary basis for sexual orientation in vertebrates for hundreds of millions of years: detection of the pheromonal signatures of conspecifics by the accessory olfactory system (Zhang and Webb 2003). However, the claim that humans are responsive to pheromones is challenged by the deterioration of the accessory olfactory system into vestigiality that began with the evolution Old World primates. This system is usually responsible for sensing phylogenetically relevant classes of olfactory compounds from other organisms, and then triggering species-specific fixed action patterns through connections to structures such as the medial amygdala and then the hypothalamus and brainstem. Although primates have shown phylogenetically relevant affective reactions to such odorants (Snowdon et al. 2011), these responses could have been learned, and the vestigiality of the accessory olfactory system further suggests that it may be misleading to refer to these compounds as “pheromones,” *per se*.

Some indirect support for the importance of the accessory olfactory system for innate heterosexual orienting is suggested by reports of frequent bisexual and nonreproductive sexual behaviors in apes and dolphins. These large-brained species lack functioning vomeronasal systems, and their dynamically constructed social niches may have benefited from action selection being driven by more complex (and learned) cortical representations. Indeed, the greater sophistication of cortical controllers may be a primary reason that the vomeronasal organ became vestigial.

However, even in species without functioning vomeronasal systems, smell is a unique sense in several respects. First, compared with other stimulus modalities, smell is more likely to be capable of influencing phylogenetically significant behaviors due to closer proximity of olfactory inputs to core structures for emotion selection, neurophysiological regulation, and memory encoding. Although these areas receive extensive projections from

other sensory modalities, these connections are achieved through pathways with a far greater number of intervening synapses through a dynamically self-organizing cortex. Second, a large number of genes specifically code for odor receptors, which are sensitive to specific compounds. Although only ~400 of our 1000 odor-receptor specific genes remain functional – compared with ~1100 functional olfactory genes in mice – the number of permutations of gene-expression profiles is still enormous. Thus, it is not unreasonable to suggest that evolution was able to use the primary olfactory system to adaptively shape behavior in human and nonhuman animals. Theoretically, if the relationship between the degree of smell-induced arousal and reward is characterized by an “inverted U” function – that is, too weak being unnoticeable, and too strong being aversive – then increasing or decreasing the sensitivities of the innate olfactory system could have provided an elegant means for evolution to cause different smells to have different affective associations. Yet the extent to which this is the case remains unclear.

Potential bidirectional conditioning between olfactory and nonolfactory stimuli suggests that caution is appropriate in interpreting studies of responses to sexually dimorphic smells. For instance, studies using androgen and estrogen related olfactory compounds have demonstrated both differential activations in heterosexual women and men, as well as sex-atypical activations in homosexual women and men (Savic et al. 2010). These studies were invariably reported as suggesting innate bases for preferences. But this sort of inference cannot be made from non-longitudinal observations of adults shaped by a lifetime of experiences with sexual partners.

For example, male marmoset monkeys exhibit increases in serum testosterone in response to sexual odors (Snowdon et al. 2011), potentially suggesting pheromone-like properties. However, after sexual cues were paired with an arbitrarily chosen lemon odor, these novel olfactory associations were capable of stimulating erections, as well as increased exploration of locations where males previously experienced a receptive female. This study demonstrates that learned olfactory associations could potentially produce pheromone-like

effects without relying on specific receptor mechanisms.

To the extent that there are innate biases toward sexual stimuli, the amygdala complex is probably the most likely supporting mechanism in most vertebrates. This system receives extensive olfactory inputs, has been implicated in emotional learning and responses for appetitive and aversive stimuli, and has been shown to regulate sexual behaviors in a variety of animals. Although the amygdala receives multi-modal inputs, complex visual stimuli are unlikely to produce specific innate responses via cortex, given the dependencies of cortical development on idiosyncratic experiences of individual organisms. Theoretically, the superior colliculus could provide this input using connections that are simpler and more predictable than a cortical pathway. However, although this structure receives substantial projections from the retina, receptive field properties of collicular neurons are not sensitive to shape or color (Redgrave et al. 2008), and thus it is unlikely that specific connections from this structure could form the basis for an innate visual stimulus detector.

There are likely many means by which organisms could be innately biased towards sex-specific stimulus features across multiple modalities. For all of these biases, it is important to distinguish between increased salience and specific valence. Attentional biases are likely relatively more simply implemented and evolvable, relative to adaptations for specifically valenced responses. However, if valence can be discovered from experience, then salience biases may be sufficient for ensuring adaptive behavior. Along these lines, if organisms with particular appearances have greater fitness in the evolutionary sense, they may also have greater fitness in the everyday functional sense, and as such it may be unnecessary (and possibly not evolvable) to instill a specific valenced bias for those visual features. For example, if individuals with pronounced sexually dimorphic stimulus features have stronger immune systems, then aversion to sickness could be sufficient for reliably learning the attractiveness of these features (as honest indicators of fitness). Or, if individuals with pronounced sexual

dimorphism are more robust in other ways, then their inherent salience could be sufficient for increasing their ability to generate arousal and possibly desire. In these ways, features such as anatomical symmetry or sexually dimorphic physiology can be nearly universal without necessarily involving innate biases.

Experiments of Nature: Against Nurture?

Ethical considerations preclude an experimental approach in attempting to assess causation in the development of sexual orientations. However, it may be possible to approximate such data by studying “experiments of nature” in which relevant variables have been altered due to chance (Bailey et al. 2016).

In distinguishing between the roles of genes and hormones, androgen insensitivity syndrome (AIS) provides a scenario in which a genetic male has feminized hormonal conditions. AIS demonstrates that the direct effects of male genes on development are insufficient for determining orientation, suggesting the importance of either hormones or experience.

Another class of quasi-experiments involves infantile gender reassignment. The male→female experiment is approximated by male cloacal exstrophy or penile ablation during circumcision, followed by attempted female socialization. The female→male experiment is approximated by congenital adrenal hyperplasia (CAH) in females. Both of these classes of experiments are associated with increased homosexual preference and transsexual identity, showing that (a) sex atypical hormonal conditions at the very least contribute to sex atypical preferences and identities, and (b) genital morphology and attempted gendering are not sufficient conditions for determining orientation.

Outcomes associated with penile removal and CAH provide a strong challenge to learning perspectives on orientation development. Yet for these various scenarios, it is questionable whether someone with constructed genitalia and frequent medical procedures during childhood would relate to their gender and sexuality in exactly the

same way as a natal male or female. Also, these cases all suffer from the confound of overall masculinity or femininity also being sex atypical, which could go on to influence social interactions, which could potentially mediate atypical development of sexual identities and orientations. That is, theoretically, being highly gender-atypical could potentially impact the development of one's sexual orientation.

More broadly, present evidence is insufficient to disambiguate which causal pathways contribute to associations between sex-atypical sexual attraction and other sex-atypical characteristics (Fig. 1). These associations could arise from common origins in shared processes of hormonally mediated neurodevelopment, where sexual differentiation may be disrupted across multiple mechanisms. Alternatively, neurohormonal factors could increase the probability of developing gender-atypical characteristics more generally, through which the probability of sex atypical orientations could also increase. Both of these scenarios may apply to different degrees, depending on the particular contexts that shape particular individuals.

Another class of quasi-experiments involves childhood sexual experiences. The case of self-directed sexual encounters is of limited use due to confounds between preexisting and experience-dependent interest. A better test is provided by non-self-directed sexual activity. The most compelling evidence along these lines may be found in the New Guinea highlands (Baldwin and Baldwin 1989), where all young adolescent males were traditionally encouraged to engage in homosexual activity as a kind of masculinizing initiation ritual. Yet, the vast majority of these men went on to develop heterosexual orientations. While this suggests that childhood homosexual experience is not sufficient for instilling homosexual orientations, it should be kept in mind that these rituals took place in the context of otherwise strong pressures for heteronormative conformity. An additional potentially relevant detail is that this homosexual activity initially happened in a context where the boys mostly performed oral sex, without self-stimulation or explicit eroticization. Theoretically, this sort of noneroticized sexual experience could even lead to habituation or de-valuation. Although these boys also later took on different

Two models of the development of sex-atypical characteristics and sexual orientation

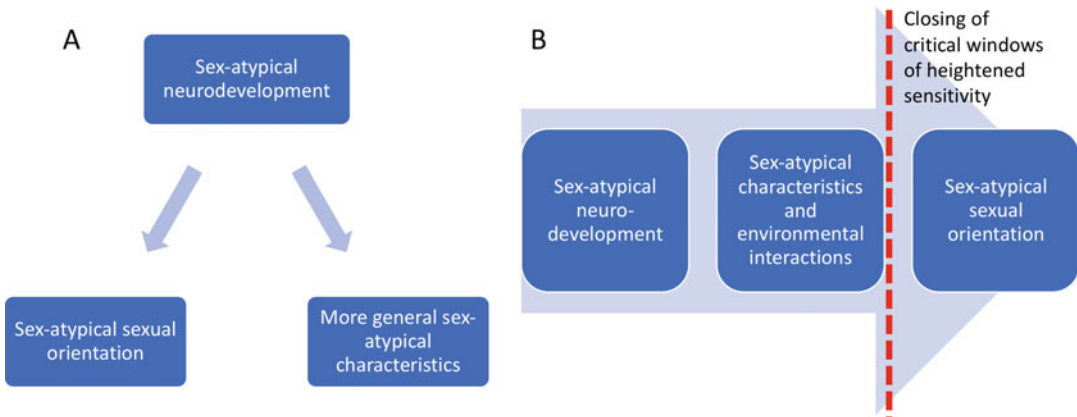


Fig. 1 (A) Standard models assume that sex-atypicality in orientations (i.e., homosexuality) and more general sex-atypical characteristics (e.g. gender non-conformity) both result from a common process of sex-atypical neurodevelopment. (B) However, the same evidence is also consistent with a model in which the relationship

between sex-atypical neurodevelopment and sexual orientations is mediated by sex-atypical characteristics and environmental interactions. Note: An experience-dependent causal pathway should not be taken to imply that sexual orientations are arbitrarily malleable, perhaps especially as plasticity decreases as development proceeds in time

roles where they received sexual pleasure, this only happened in late adolescence. Finally, strong gender-segregation could potentially contribute toward heterosexual preferences based on the (highly contested) proposal that finding male or female conspecifics be erotic may be preceded by finding something to be exotic, and then reattributing that arousal (LeVay 2010).

Further quasi-experimental evidence regarding contributions to orientation development may be provided in coming decades by increased acceptance of nonheterosexuality, as well as increased exposure to different forms of erotica during childhood and adolescence. If experience matters, then prevalence of nonheterosexuality may increase over time and may have already started to change. However, this test is also confounded since it may merely be the case that people are more likely to self-report nonheterosexual preferences and identities if they are less concerned about social rejection.

The Development of Sexual Preferences in Nonhuman Animals

The most powerful experiments for assessing the roles of nature and nurture involve studies of nonhuman animals. This literature suggests that numerous aspects of mating behavior can be shaped by experience, with initially nonsexual stimuli acquiring sexual incentive value (Pfaus et al. 2012). Examples of sexual conditioning range from rats with “fetishes” for the velcro-jackets they wore during early sexual experiences, to rats that desire the smell of the initially unconditionally aversive odor of cadaverine. Sexual imprinting has been observed in numerous species, as in the examples of adult male mice and geese both mating preferentially with females that have attributes similar to those of the females that nursed them early in life. An even more extreme example can be found in inter-species partner preferences resulting from the cross fostering of goats and sheep.

Some potential counter-evidence for the impact of experience can be found in the

observation that while homosexual preferences can be conditioned in male rats, this requires the administration of dopamine agonists (Pfaus et al. 2012). However, the fact that dopaminergic agents facilitate the development of homosexual preferences is not actually an argument against the importance of reward-learning, but rather, may instead suggest that sexuality should be understood similarly to other kinds of motivations, all of which depend upon dopaminergic functioning across countless species.

Brains appear to utilize common general-purpose systems for action selection and reinforcement learning, regardless of the types of value being pursued. This is evolutionarily sensible, since in order to prioritize and decide among heterogeneous alternatives to produce adaptive behavior, organisms must be able to weight and trade off among various kinds of incentives, integrating them into a “common neural currency” of value. The dopamine-sensitive ventral striatum is a particularly important structure for these reward functions in the vertebrate brain, including with respect to sexual rewards (Safron et al. 2017a). Perhaps unsurprisingly, neuroimaging studies have found ventral striatum activation patterns in response to male and female sexual stimuli to be a strong predictor of orientation in men.

Some of the most compelling developmental data of sexual behavior involves male rhesus macaque monkeys, which initially mount other males and females in equal proportions as juveniles, but switch to exclusively heterosexual mounting after puberty (Wallen 2001). Intromissions with other males do occur, but they are more likely to ejaculate with females. Notably, these heterosexual ejaculations are the strongest predictor of the timing of the transition to predominantly heterosexually biased mountings. Although not definitive, these data suggest that copulatory experience is a potentially sufficient mediator for heterosexually directed mating behavior to develop. At least in rhesus macaques, it appears that evolutionary pressures for successful reproduction could potentially be subserved by general-purpose reward-learning mechanisms. Theoretically, the innate basis of orientation may

be found in the body-plan itself – and resulting interactions that it affords – rather than being “hard-wired” in the brain.

However, to the extent that animals engage in social learning, they need not rely on direct experience to discover what behaviors are likely to be rewarding. Rather, animals can partially depend on the fact that evolution may also occur on the level of group behavioral dynamics, with pervasive and enduring selective pressures potentially resulting in aspects of homeostasis extending into culture. With respect to sexual reproduction, cultural evolution might favor groups with norms supporting heterosexual interaction. In this way, evolutionarily adaptive behavior need not depend on complex innate factors, many of which may be expected to become vestigial if selective pressures are reliably satisfied by other means (e.g., whether through rewarding experiences or social learning).

Conclusion

Orientation and Universal Darwinism

Sexual orientation remains an evolutionary and developmental mystery. We do not know the specific ways that innate and learned factors combine to shape orienting. In order to make scientific progress, it will be necessary to obtain a deeper sense of the underlying causal processes in terms of mechanism, development, and phylogeny. Toward this end, a model is proposed for describing orienting on all three of these levels, with the intention of illustrating their fundamental similarity (Figs. 2, 3, and 4).

In generalized evolution, outcomes result from processes wherein the characteristics of systems and their environmental niches cause some interactions to be more likely than others, which then cause differential selective pressures to shape dynamics. When these selected dynamics

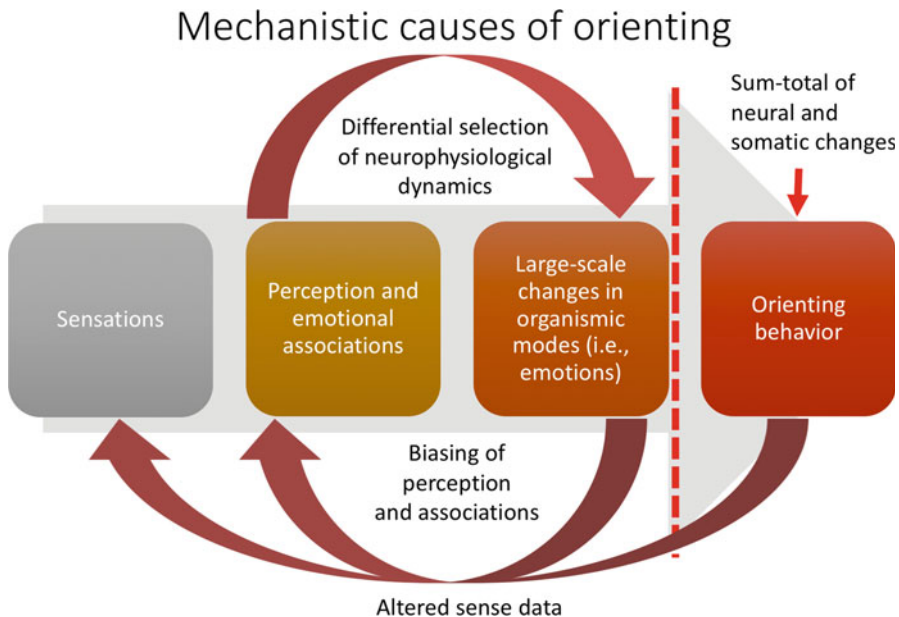


Fig. 2 Mechanistically, orienting emerges from a process of sensation being assessed for affective value, so resulting in differential selection of neurophysiological dynamics (e.g., patterns of neural activity, autonomic and neuroendocrine changes). These affective assessments contribute to the selection of global organismic modes, which in turn bias perception in a circular process of

affective construction (i.e., emotions/feelings). The sum total of this dynamic processing shapes overall neuronal activity selection, which may contribute to orienting sexual behavior, so influencing likely future experiences. However, incentive motivation of sufficient strength to influence actions will only be likely to occur if sufficiently robust orienting is present

Developmental causes of orienting

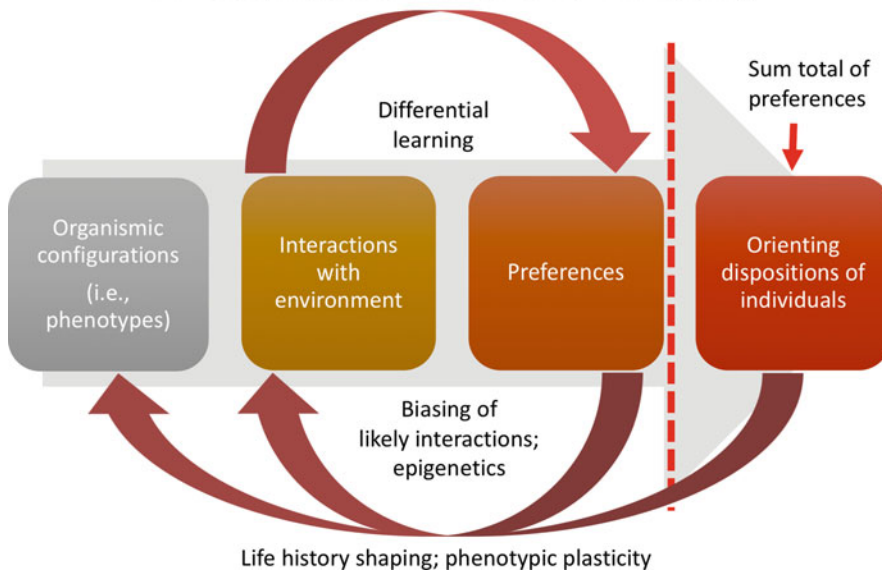


Fig. 3 Developmentally, orientations emerge from a process of ontogenic programs shaping plastic phenotypes and likely affective experiences, so resulting in differential learning (i.e., selection of neural connections). These affective experiences contribute to the shaping of different preferences, which in turn bias future likely experiences in a circular process of niche construction for individuals (i.e., the ways in which organisms both adapt themselves to

their environments and adapt their environments to themselves). The sum total of this experience-dependent affective learning shapes overall preferences, which may result in enduring orientations, so influencing the overall unfolding of a life history. However, preferences of sufficient strength and robustness to be considered to be orientations may only develop if sufficiently robust reward learning occurs during sensitive periods of development

influence the processes that give rise to them, this circular causality constitutes niche construction. Sometimes these feedback cycles cause qualitative differences in system-environment characteristics and resultant selective pressures, surpassing thresholds of organization for the creation of new attractor networks, such that emergent patterns become self-sustaining, potentially increasing their temporal stability. When these emergent processes are allowed to operate over extended periods of time, they influence the overall trajectory of systems and their environmental contexts. This process of selection and feedback is called evolution, and it can be used as a general framework for characterizing all dynamical systems at all levels of analysis. It appears to be the only process in the universe that allows order to be created and entropy to be (locally) resisted.

The similarity of various orienting dynamics is to be expected on account of each level of analysis being constituted by sui generis evolutionary systems (Edelman 1987), operating and interacting on various spatiotemporal scales. That is, to the degree that differential selection among varying patterns can be observed, that is the degree to which a system can be characterized as evolutionary. This includes the differential persistence of neuronal ensembles, emergent behaviors, or types of organisms. Further, each of these evolutionary processes are mutually nested on different timescales, with present moment proximate orienting resulting from historical developmental and phylogenetic causes, which in turn determines future developmental and phylogenetic trajectories. In this way, the principles governing orientations (sexual or otherwise) are shown to reflect, emerge from, and shape the overall evolution of the tree of life.

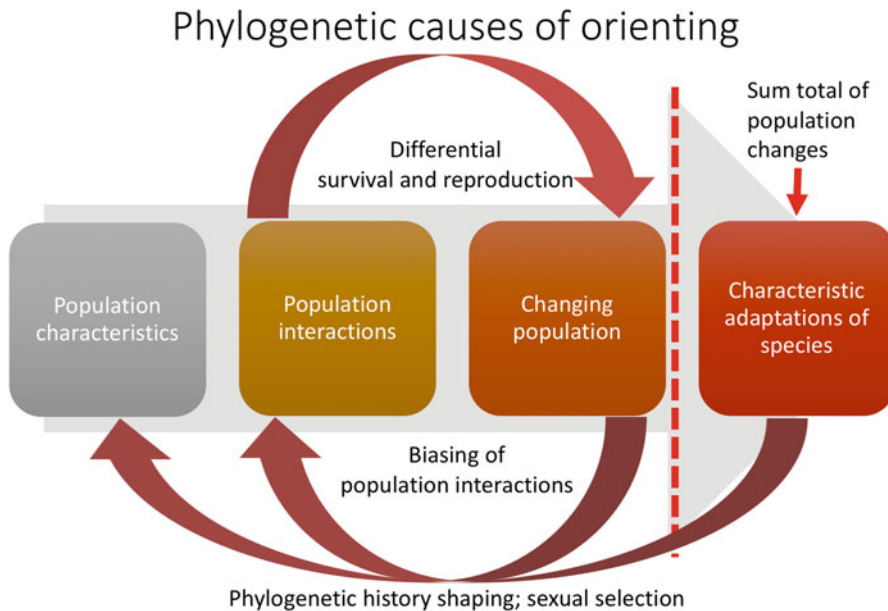


Fig. 4 Phylogenetically, changes in population characteristics emerge from a process of members of a population interacting with each other and the broader environment, so resulting in differential survival and reproduction (i.e., natural and sexual selection). The consequences of these interactions define operative selective pressures, which in turn bias the conditions of selection in a circular process of population-level niche construction. The sum total of these

pressures shapes the overall direction of selection, which may result in appreciable fitness consequences for different phenotypes, so influencing future population characteristics over phylogenetic history. However, selection of sufficient strength and robustness to produce appreciable fitness consequences (sometimes yielding novel adaptations) may only develop if sufficiently robust selective pressures are present for multiple generations

Cross-References

- [Ancient Homosexuality](#)
- [Exotic-Becomes-Erotic Hypothesis](#)
- [Fa'afafine](#)
- [Female Homosexuality and Bisexuality](#)
- [Fraternal Birth Order, The](#)
- [Kin Selection Hypothesis](#)
- [Non-Western Homosexuality](#)
- [Sex as Bonding Mechanisms](#)
- [Sexual Arousal](#)
- [Sexual Orientation and Human Sexuality](#)

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Sexual Orientation and Human Sexuality

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Synonyms

Bisexuality; Heterosexuality; Homosexuality; Same-sex sexuality; Sexual attraction; Sexual minorities; Sexual preference

Definition

Sexual orientation refers to a psychological mechanism directing one's sexuality towards

individuals based on their apparent sex. Individuals form a continuum between extreme point of exclusive heterosexuals, i.e., oriented exclusively towards individuals of the opposite sex, and exclusive homosexuals, i.e., oriented exclusively towards individuals of the same sex, with bisexuals being similarly attracted to both sexes and other individuals being attracted to both sexes in various degrees (e.g., predominantly heterosexual with some potential to same-sex attraction). Sexual orientation refers more to attraction or desire than behavior or identity, because orientation is not necessarily manifested by overt sexual behavior, associated with self-identification of sexual orientation label, or aligned with affectional bonding (love).

Introduction

The majority of males and females predominantly prefer opposite-sex sexual and/or romantic partners. Such sexuality has been accepted as a standard default, possibly because it is easier to see its biological/evolutionary relevance. Indeed, in sexually reproducing species, preference for and sexual activities with opposite-sex partners evolved as a mechanism for combining genomes through complementary gametes gaining genetic variability and direct fitness. Thus, scholars have argued that homosexuality is an evolutionary puzzle because it impedes the reproductive success of their owners. However, on the phylogenetic level, evolutionary fitness is more than direct fitness, and on the ontogenetic level, sexuality is more than fertile heterosexual penile-vaginal intercourse. Although direct reproduction is the ultimate evolutionary force behind most sexual activities, sexuality in general gained many other proximate functions during its evolution, e.g., as a social and pair bonding mechanism or means of resource acquisition. Such functions are intermediate goals to achieve direct reproduction, e.g., by means of survival and alliance formation and/or indirect reproduction by helping kin, also known as inclusive fitness. Therefore, many forms of sexuality, such as oral or anal sex, masturbation, sexual preferences for different species,

preferences of same-sex individuals, or individuals outside of reproductive age, cannot *per se* offer direct reproductive success of the individual, but still these nonfertile forms of sexuality can offer other adaptive sociosexual functions (e.g., pair bonding, alliance formation, resource acquisition, well-being, etc.) that might indirectly foster future reproduction, regardless of sexual orientation. It is important to note that personal motivations for sexual activities, homosexual or heterosexual ones, are quite different from their possible sociosexual functions or possible evolutionary adaptive values. Sexual relations are mostly motivated by pleasure, love, self-esteem/revenge, and/or obtaining resources. Such personal motivations triggering homo/heterosexual behavior should not be confused with the socioecological or evolutionary reasons that maintain sexual activity in the population.

Further, sexual orientation is a psychological mechanism that generates a continuous array of individual variation and not a dichotomous psychological trait (e.g., Kinsey et al. 1948; Petterson et al. 2015). In this sense, exclusive homosexuality and exclusive heterosexuality present the extreme opposite poles of the continuum, while the majority of individuals fall in between, although closer to the heterosexual extreme. Following this line, homosexuality or non-heterosexuality (including bisexuals) is more than exclusive homosexuality, and sexual orientation does not equal homosexuality. One possibility would be to focus on the adaptive value of the mechanism itself (i.e., sexual orientation); the other would be to explore the possible adaptive value of one of its manifestations (e.g., exclusive homosexuality). The adaptiveness of the mechanism itself is usually not the focus of the debate. The debate is mostly centered on whether and how the individual differences generated by this mechanism are adaptive. A mistake would be to extrapolate a possible nonadaptiveness of an extreme point within the continuum (exclusive homosexuality) to the other variations along the whole continuum of sexual orientation (e.g., predominantly heterosexual, bisexual, predominantly homosexual, etc.). Similarly, a severe clinical depression or severe forms of autism are

most probably not adaptive; they are not only neutral but rather maladaptive. However, they both are extremes on a continuum of adaptive variation, such as the capacity of sadness and systemizing abilities, respectively (for an overview about adaptive individual differences see, Buss and Greiling 1999). In the same line, bisexuality or some degree of homosexual tendencies among predominantly heterosexual individuals as well as some heterosexual tendencies among predominantly homosexual individuals could be viewed as adaptive variation of sexual orientation. From this perspective, even if exclusive homosexuality does not have any possible adaptive value, it would be a mistake to assume that the same is true for the whole continuum of sexual orientation.

Evolutionary Theories of Sexual Orientation

Sexual orientation has been described as a mechanism navigating or directing sexuality towards individuals of the opposite sex, same sex, or in varying degrees to both sexes (Bailey 2009; Bailey et al. 2016; Savin-Williams 2016; Vrangalova and Savin-Williams 2012). Similar to some heterosexual practices (e.g., extra-pair affairs), attitudes toward same-sex sexuality can vary greatly between cultures. In some cultures, same-sex sexuality constitutes an integral part of the sociocultural system; in others such sexuality is criminalized and persecuted (for review see, Bailey et al. 2016). For these reasons, individuals can vary in their overt manifestation of sexual preference, from a tendency hidden from public or even self to open preferences and behaviors. There are also other motives why sexual preferences, behaviors, and identities do not need to be aligned. Nonpreferred sexual behavior can be manifested, for example, under conditions without access to preferred sexual partners; it can be done for financial motives or simply to satisfy one's partner. Similarly, romantic affection can be largely disconnected from sexual desires (Diamond 2003). For example, a person can repeatedly fall in love only with individuals of the same sex, but prefer

and actively seek sexual partners of both sexes. Thus, sexual orientation refers to sexual desires, attraction, and preferences rather than to overt sexual behavior, identity, or affective feelings.

Sexual orientation has a genetic component that explains approximately one third of the variation between individuals (e.g., Zietsch et al. 2012; for review, see Bailey et al. 2016). This suggests that sexual orientation is a complex trait that is influenced by genetic and environmental factors. Sex hormones are one of the environmental factors that influence the development of sexual orientation. According to the organizational hypothesis, the neural system of homosexual individuals is influenced by sex-atypical hormone levels during early developmental phases. Systematic differences in neuroanatomy between homosexual and heterosexual individuals suggest that compared to their heterosexual counterparts homosexual men were, on average, less androgenized and homosexual women more androgenized during early, probably prenatal, development (for review, see Bailey et al. 2016; LeVay 2010; Wilson and Rahman 2005). Neither genetic nor hormonal influences suggest that sexual orientation is necessarily fixed and rigid over the lifespan. Sexual orientation develops during ontogeny whereas sexual identity can change over time, particularly among women (Diamond 2008). Such a fluidity of sexual orientation does not equal to a conscious choice of different sexual desires and attractions (Diamond 2008). Thus, sexual orientation is not a choice nor a cultural invention; it has genetic and neurohormonal underpinnings and is not necessarily immutable. Furthermore, occasional same-sex behavior and stable same-sex preferences have been documented along a number of nonhuman animal species (Sommer and Vasey 2006). Thus, a variation on the sexual orientation continuum is not a human specific and has its phylogenetic roots.

Moreover, it is commonly accepted that homosexuals do not have any reproductive success. Although it has been shown that reproductive success of transgendered male homosexuals (males who adopt female look and behavior) is close to zero (Vasey et al. 2014), this does not need to apply to other forms of nonheterosexual

individuals. In one study, 32.8 % of men and 65.4 % of women reported a potential for homosexual response, suggesting that a huge percentage of predominantly heterosexual people do have a propensity to experience same-sex sexual attraction and/or interaction (Santtila et al. 2008). In this study, the potential for homosexual response was based on responses (quite impossible, very unlikely, quite unlikely, not likely, not unlikely, relatively likely, very likely) on the following question: "If a, in your opinion, handsome man [to male participants]/beautiful woman [to female participants], whom you like, suggested sexual interaction with you, how likely would you be able to do it (if you could define the nature of the interaction and nobody else would know about it)?" In line with this finding, a large-scale study demonstrated that almost 10 % of heterosexually identified men reported that they have engaged in same-sex sexual activities (Pathela et al. 2006). This applies even more to non-Western populations, such as Samoa, where the majority of predominantly heterosexual men engage in sex with both women and transgender males called Fa'afafine (Pettersen et al. 2015). Further, 20 % of homosexually identified white American men reported having been married to a woman at some point in their life, and 50 % of homosexual men reported having produced at least one child (Bell and Weinberg 1978). According to the more recent demographic data (2013) of the USA, 37 % of LGBT-identified individuals report having at least one child. Keeping in mind these assumptions, we can outline some of the empirically supported evolutionary theories explaining the adaptiveness of human homosexuality and nonheterosexuality.

1. Homosexuality as an adaptation: Kin selection theory

One of the oldest and partly supported theories of homosexuality as an adaptation was postulated by E. O. Wilson (1978), inspired by Hamilton's kin selection theory. Homosexual individuals, who do not invest into their own exclusive reproduction, may propagate their genes indirectly by supporting reproduction of close relatives, with

whom he/she shares own genes. Studies conducted in the USA, Great Britain, or Japan did not support the theory (for review, see Bailey et al. 2016), which can be explained by persisting relatively negative attitudes toward homosexual individuals in these countries. On the other hand, systematic investigations of Fa'afafine, who are officially recognized as "third gender" or a transgender type of male homosexuals (individuals who are biologically males but have feminine characteristics and adopt feminine gender roles) among the population of Samoa, supported the theory of kin selection. In particular, Fa'afafine show higher avuncular tendencies (support of nieces and nephews) compared to men who prefer women as sexual partners, which supposedly increases their fitness (e.g., Vasey and VanderLaan 2010). Samoan Fa'afafine fit a specific subgroup of homosexual men, the transgender type of male homosexuals that is a specific although still heterogeneous group. This subgroup of transgender individuals whose sexuality is aimed at individuals of the same biological sex is frequent in many other societies, such as India (Hijra), Thailand (Kathoei), or native North American tribes (Berdache). The transgendered homosexuals mostly prefer same-sex relationships, although usually with cisgender (i.e., biological sex aligned with gender role) men. Sexual and/or romantic relations between partners of different gender roles are documented in numerous populations around the world (Crapo 1995). Furthermore, age stratified type of same-sex relationships (i.e., one of the partners is much younger than the other) has been documented across populations, such as ancient Greece, Middle Ages Japan, or contemporary New Guinea (Crapo 1995). Such relationships, as opposed to gender-stratified ones, do not need to imply one transgendered and one cisgender partner, rather both of them are cisgender but of different age categories, although such interactions can be temporary and do not need to imply predominant same-sex preferences of none of the partners. Both age-stratified and gender-stratified styles of same-sex relationships exist in the modern Western culture, although the most frequent style of relationships is egalitarian between two individuals who identify as homosexuals and are of similar gender role, status,

education, and age. This latter style of same-sex relationships seems to be specific for contemporary Western populations. On the other hand, the other two styles of same-sex relationships appear in populations that share more common sociocultural characteristics with human ancestral populations (e.g., geographical connectedness of the kin and strong familiar bonds), and the evolutionary strategy can thus still be adaptive in the present as it could have been advantageous in the ancestral environment (VanderLaan et al. 2014). Importantly, evolutionary strategy of transgender homosexuals can differ from the one adopted by cisgender homosexuals or nonheterosexuals. In other words, some evolutionary hypotheses (e.g., kin selection) can be supported in one specific subgroup of homosexual individuals (e.g., in transgender homosexual men) in specific society contexts (e.g., large families, close kin bonds, geographical proximity) but not in others (e.g., in cisgender homosexual men in big anonymous cities with prevalent homophobia).

2. Homosexuality as a by-product of sex-atypicality

Miller (2000) suggested that male homosexuality per se is not adaptive, but rather it is a by-product of another adaptation. He proposed that some characteristics that are, on average, more typical for women than men, such as lower aggressiveness, higher cooperation, and social skills in general, became adaptive also in men during the changes in social structure of relatively recent human evolution. Further, more feminine characteristics in men can be typical for slow life history of men who invest more in relationship commitment and parental care than in mating success (Jeffery 2015). Thus, men who have more feminine and fewer masculine characteristics can thrive better in a more complex and predominantly monogamous society, including having relatively higher reproductive success. In this scheme, male homosexuality would thus be an extreme nonadaptive by-product of a general adaptive male shift to feminization. Gender non-conformity (lower masculinity in men) has a strong genetic component (for review, see Bailey

et al. 2016), and women find femininity in men attractive (Perrett et al. 1998). Furthermore, numerous studies indicate that nonheterosexual men are, in comparison to heterosexuals, more feminine (for review, see Bailey et al. 2016). Homosexual men would thus form an extreme point on a continuum between male masculinity and male femininity, while relatively feminine heterosexual men would have some adaptive advantages, at least in urban, middle class Western groups. In line with the kin selection theory outlined above, this theory also aims to explain the existence and maintenance of feminine male homosexuals in the population. This theory, nonetheless, does not apply to masculine male homosexuals and other nonheterosexuals nor to female homosexuals. Rice et al. (2013) suggested that homosexual orientation is a by-product of sex-atypical epigenetic marks that feminize males and masculinize females during embryonic development. Thus, the opposite logic of the theory could also be applied to explain masculine female homosexuals who would represent an extreme pole of a general female masculinization. This might have been adaptive for some women during the evolutionary past, for example, by concentrating more social and physical power, leading to higher independence, better self-defense and defense of their kin, and higher resource acquisition. Such characteristics might have been advantageous in the ancestral and also recent society, where mortality in men has been relatively higher than in women.

3. Predominant homosexuality as an adaptation: Sneaking and conditional sexual strategy

Following the previous line of reasoning, predominant homosexuality in feminine males can be also understood as a sneaking sexual strategy (Jeffery 2015). In humans, it has been suggested that the most frequent strategy would be exclusive or at least predominant heterosexuality with males of rather masculine characteristics, while bisexuality and predominant homosexuality linked to increased femininity in men would represent a sneaking sexual strategy. From this point of view, feminine men who have some potential for

opposite-sex activities can be successful in opportunistic heterosexual activities and secure direct reproductive success. This can happen in particular because feminine characteristics were shown to be attractive to women (e.g., Perrett et al. 1998), at least under certain conditions. At the same time, more feminine bisexual or predominantly homosexual men can be perceived as weak rivals to more masculine exclusively or predominantly heterosexual men and can thus reduce intrasexual male-male competition. Consequently, feminine predominantly homosexual men can be accepted more as friends of heterosexual men's female partners, thus offering opportunities to sneak copulations. High numbers of predominantly homosexual individuals reporting some opposite-sex attraction, behavior, and also biological offspring (see above) would tend to support this theory. The theory thus does not attempt to explain exclusive homosexuality or transgender homosexual men who do not have any interest in sexual encounters with opposite-sex partners. It rather shows that various degrees of bisexuality and predominant homosexuality can serve as an alternative and successful reproductive strategy. This theory need not apply only to men because bisexual and predominantly homosexual women can also show some opposite-sex attraction and behavior, as well as some reproductive success. On average, lesbian women are more masculine than heterosexual women (Bailey and Zucker 1995), and masculine heterosexual women report higher sociosexuality (tendency for uncommitted sexual variety) than feminine women (Mikach and Bailey 1999). We can thus speculate that masculine predominantly homosexual women can secure direct reproductive success without the necessity of creating and maintaining long-term bonds with men but rather with other women. Compared to predominant female homosexuality or bisexuality, a fluid sexual orientation might have helped ancestral women secure resources and care for their offspring under conditions without a primary male partner by receiving parental investment from other women (Kuhle and Radtke 2013). According to this theory, fluidity of female sexual orientation can be understood as a conditional sexual strategy, meaning that variations between opposite-sex and same-sex sexuality can be

adaptive in different conditions, such as different age or life phases.

4. Nonheterosexuality as an adaptation: Same-sex alliance formation

This theory holds that various degrees of sexual feelings and behaviors aimed toward both males and females offer an individual advantage over an exclusive orientation toward only one sex (Kirkpatrick 2000). The main reason towards non-heterosexual interactions would be formation and maintenance of same-sex alliances that are crucial in many other primates and in particular in the human evolutionary past. The author shows anthropological and primatological evidence supporting the view that strong and emotional same-sex alliances can offer a reproductive advantage to the individual. More specifically, same-sex alliances reduce competition and increase cooperation between members of the same sex, while maintained access to partners of the opposite sex ensures potential reproductive success. In this perspective, heterosexual sex among stable partners outside the fertile period (i.e., outside the fertile window within the female menstrual cycle and after menopause) or any sexual activities that do not lead to fertilization (e.g., oral or anal sex) serve the same function, i.e., reducing disputes, increasing cooperation, and thus maintaining the stable dyad (Bártová and Valentová 2012). The question is whether non-heterosexual behavior was originally selected for alliance formation or whether alliance formation is rather a newly acquired sociosexual function of same-sex sexual behavior. In this sense, non-heterosexuality would serve proximate sociosexual functions for which nonprocreative sexuality in general was co-opted, such as alliance formation, dyad maintenance, lowering stress, peacemaking and reconciliation, or resource gains.

5. Homosexuality as a by-product: Overdominance and sexually antagonistic gene hypothesis

Both behavioral and molecular genetic studies have shown that the male homosexuality is linked, among others, to the X chromosome and is thus inherited from the maternal lineage

(Sanders et al. 2014). Further, female relatives of male homosexuals have more children and grandchildren than control group of women with no homosexual individuals among relatives (e.g., Ciani and Pellizzari 2012; for review, see Bailey et al. 2016). It is thus suggested that greater fecundity and fertility of female relatives of homosexual men can explain the persistence of a nonadaptive form of male sexuality through sexually antagonistic selection (e.g., Ciani and Pellizzari 2012; Zietsch et al. 2008). In other words, sexually antagonistic genes can bring advantages for one sex (e.g., higher fecundity in women) but can be principally disadvantageous for the other sex (e.g., can cause exclusive homosexuality in men). However, as shown by recent models, the frequency of only female carriers cannot explain a stable proportion of exclusive male homosexuals in the population but a large proportion of both nonhomosexual female and male carriers can (Chaladze 2016). Based on behavioral genetic studies, a considerable proportion of men carrying the homosexual genes are not exclusively or predominantly homosexual. It was suggested that homosexual phenotype can only be expressed in a homozygous form of the underlying alleles, while individuals with a heterozygous form (only one allele of the gene) carry the phenotype but the phenotype is not expressed (for review, see McKnight 1997). Such heterozygous carriers are supposed to possess some advantageous characteristics that can increase reproductive success of their owners. So far, this theory was supported by a study showing that heterosexual twins of homosexual men, who most probably share the genetic component of homosexuality although not homosexual orientation, report higher number of female sexual partners than heterosexual men with a heterosexual twin (Zietsch et al. 2008). Thus, heterosexual men who carry the homosexuality-linked genetic component, potentially in a heterozygous form, do have higher mating success (considered a proxy of a reproductive success) than the control group of heterosexual men, which can explain its relatively stable prevalence in the population.

The theories of by-product thus focus more on explanation of the extreme exclusive form of male homosexuality, rather than the rest of the

nonheterosexual continuum. The theories can apply to other forms of nonheterosexuals, though, because they can also be carriers of the homosexual genotype. It has been shown that a potential for homosexual response has a stronger genetic component than homosexual behavior or self-labeled identification (Santtila et al. 2008). Thus, any degree of nonheterosexual tendencies might be more suitable for genetic analyses than exclusive homosexuality with no heterosexual potential.

Furthermore, the theories of homosexuality as a by-product originally did not apply to women, although in principle they can work similarly, since genetic component has been documented also in female sexual orientation (for review, see Bailey et al. 2016), and the potential to homosexual response is even more frequent in women than men (Santtila et al. 2008). Thus, exclusive male and female homosexuality indeed can be a by-product of otherwise adaptive variation of sexual orientation.

Conclusion

During the last century, human and other animal (vertebrates and invertebrates) sexual orientation has been extensively studied within many scientific areas. Despite important findings in the areas of psychology, anthropology, medicine, neuroscience, genetics, endocrinology, and development, evolutionary reasoning has suffered numerous conceptual and terminology issues. These misconceptions have led to the view that homosexuality can only be exclusive and thus an evolutionary paradox. However, when essentialist categorical thinking is discarded, it might become clearer that the majority of variation on the continuum of sexual orientation can offer adaptive advantages for their carriers. This view can be supported by changing the perspective of sexuality equaling only with reproduction, and by acknowledging the fact that at least some homosexual and nonheterosexual individuals within the whole spectrum of sexual orientation do reproduce and raise their offspring.

Most outlined theories present adaptive reasons for the evolution of nonheterosexual orientations, either by stressing indirect reproduction via kin selection or direct reproduction via sneak

populations or same-sex alliance formation that can increase survival and future direct reproductive capacity. Even by-product theories offer plausible evolutionary reasoning for the origins and maintenance of nonheterosexual orientations. In this sense, nonheterosexual orientations would have been passed on throughout generations together with the adaptive trait of sex-atypicality, advantages of an increased fertility in the other-sex kin, or in carriers who do not express the homosexual phenotype. These theories are not mutually exclusive, and together they can explain a bigger proportion of the sexual orientation continuum. Moreover, these theories offer a stronger case against the argument that it is impossible for any form of homosexuality to have evolved.

Finally, it is important to realize that the outlined theories are not *just-so-stories* nor naïve panadaptationism as critics often portray it. The theories offer specific hypotheses with predictions that can be empirically tested. We attempted to provide the existing empirical support for each theory, although we realize that more research using a variety of sources of evidence and methods is still needed. Only convergent evidence of numerous empirical tests can give decisive support and scientific credibility to a particular adaptive hypothesis.

Sexual orientation is a complex psychological mechanism that can profit from analysis within an evolutionary framework, where otherwise heterosexuality might be taken for granted. Future studies should pay more attention to female nonheterosexuality, to sex-typical nonheterosexuals, bisexuals, integration and empirical confrontation of the existing theories, and to empirical testing of the theories in Western as well as non-Western populations with varying concepts of same-sex sexuality.

Cross-References

- [Homosexuality](#)
- [Kin Selection](#)
- [Mate Preferences](#)
- [Sexual Strategies Theory](#)

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Sexual Orientation Identity

► Sexual Identity

Sexual Outcomes

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Synonyms

[Sexual activities](#); [Sexual attitudes](#); [Sexual behaviors](#); [Sexual maturation](#)

Definition

Sexual outcomes caused by different life history strategies refer to biological outcomes such as timing of puberty or sexual maturation and behavioral outcomes such as effort in mating, frequency of sex, number of sex partners, and risky sexual behaviors.

Introduction

Sexual outcomes are among the major manifestations of life history (LH) strategies that lie along the fast–slow continuum. Organisms with fast LH

strategies sexually mature and reproduce early, have high numbers of offspring with small body size, and invest more energy and effort in mating than in parenting, whereas organisms with slow LH strategies exhibit the opposite pattern of sexual outcomes. In evolution, human beings have generally adopted slow LH strategies, as compared to other animals. However, individual differences in LH among human beings are observable because people grow up under different ecological conditions and ambient environments, which triggers different LH strategies (Belsky et al. 2012). Specific sexual outcomes caused by LH include biological outcomes, such as the timing of puberty and sexual maturation, and behavioral outcomes such as sex debut, frequency of sex, number of sexual partners, mating effort, conservative versus unrestricted sociosexual orientation, and risky sexual behaviors.

Known as LH tradeoff strategies, the essence of LH theory is the allocation of finite energy resources among an organism's growth, reproduction, and body maintenance functions (Belsky et al. 2012). Less allocation to body maintenance and growth but more allocation to reproductive functions is characteristic of fast LH strategies, whereas more energy allocation to growth and maintenance over reproduction is characteristic of slow LH strategies. Furthermore, efforts in reproduction include mating associated with offspring quantity and parenting associated with offspring quality. Mating and parenting represent energy tradeoffs in that more energy investment in mating trades quality for quantity of offspring in fast LH strategists, whereas slow LH strategists trade quantity for quality by investing more in parenting than mating. Timing of puberty is a transition of energy allocation from physical growth to reproduction, and subsequent mating behaviors reveal energy allocation among mating, maintenance, and parenting.

Biological Outcomes

In harsh but stable environments where resources are scarce, individuals adopt slow LH strategies whereby they allocate a large proportion of limited bioenergy to physical development and body maintenance rather than reproduction and thus

exhibit late puberty. For example, insufficient nutrition delays the age of menarche (Soliman et al. 2014). Improvements in nutrition provision from the 1920s to 1980s have lowered the mean menarcheal age from 13.3 to 12.4 years among American girls (McDowell et al. 2007). In Western European and Scandinavian countries, menarcheal age declined from approximately 17–18 years in the mid-nineteenth century to the present population means of 12 or 13 years. In recent decades, the age of menarche in China and Japan has declined by 3.5 months for every 10 years, which is also consistent with data from Copenhagen showing a 3-month decline in menarcheal age from 1991 to 2008 (Soliman et al. 2014). Furthermore, insufficient nutrition results in smaller sexual organs. After puberty, adolescents who were born with a low birth weight because of insufficient fetal nutrition showed small testicular volumes for boys and small internal genitalia for girls (Soliman et al. 2014). In addition to resource scarcity, high intraspecies competition for limited resources also triggers slow LH strategies, which are characterized by high parenting and skill training of the young so that they become able competitors to monopolize the limited resources (Ellis et al. 2009). The bioenergy of children is thus allocated to building the body and skills more than to reproductive readiness.

In unpredictable and harsh environments resulting from warfare or pandemics on the macroenvironmental level or familial dysfunction or unstable parent–child relationships on the microenvironmental level, individuals adopt fast LH strategies to reproduce as fast and as early as possible before extrinsic mortality and morbidity strike (Ellis et al. 2009). An obvious example is menarche in girls, whose reproductive life lies in the interval between menarche and menopause. Although early menarche results in a longer reproductive tenure than menarche at the normative age does, early menarche does not necessarily lead to high fecundity throughout the lifespan because of the elevated risk of miscarriage and long protogenetic intervals. The major benefit of early menarche is the increased chance of early reproduction prior to potential unexpected mortality.

For example, paternal absence and consequential harsh maternal parenting (Belsky et al. 2012) are significant cues of early puberty. In evolutionary history, paternal absence indicated insufficient resource provision and a lack of paternal protection from unsafe environments or predators. Thus, paternal absence signaling a harsh and unpredictable environment ahead causes early maturation and reproduction before unpredictable mortality and morbidity strike.

To a lesser extent, biological outcomes that have been observed in men can help distinguish between fast and slow LH strategists. For example, earlier onset of puberty predicted more masculine facial morphology, larger biceps circumference, and higher BMI among young male adults (Doll et al. 2016). These characteristics contribute to reproductive success by improving intra- and intersexual competitiveness as opposed to parental investment. In men but not women, earlier onset of puberty representing fast LH strategies has also been found to predict greater sex drive, interest in casual sex, and reported number of lifetime sex partners (Ostovich and Sabini 2005). Other studies show that men growing up without fathers or with low paternal involvement matured earlier, had sex earlier, and became fathers at younger ages (e.g., Sheppard and Sear 2012).

Behavioral Outcomes

Numerous studies have focused on the behavioral and attitudinal outcomes of fast versus slow LH strategies in allocating energy resources to mating versus development. For example, young adults growing up in an unpredictable environment characterized by parental employment transitions, household relocations, and paternal transitions (e.g., paternal absence) were found to have more sexual partners and be more active with oral sex and sexual intercourse (Belsky et al. 2012). Adults who grew up in a stable environment were found to be more committed to long-term relationships, were more likely to use contraceptive measures to control birth, and showed more restricted attitudes toward sex (Brumbach et al. 2009). In addition, slow LH strategies have been shown to correlate negatively with high effort in mating and short-

term mating orientation, suggesting that individuals with slow LH strategies do not concentrate time and energy on mating or switching sexual partners. Moreover, environments triggering different LH strategies also affect mate selection. In resource-scarce environments where slow LH strategies are likely to be adopted, people prefer long-term partners with characteristics of good parents and resources provisioning capacity. When primed with environmental stability, women prefer good fathers over good genes in selecting long-term partners (Lu et al. 2015). Similarly, women with insecure attachment styles or with unrestricted sociosexuality, both of which represent a fast LH strategy, preferred short-term relationships more than other women and preferred men who pursue a short-term mating strategy (Kruger and Fisher 2008).

Individuals with fast LH strategies show unrestricted patterns of sexual behaviors. In general, they invest more effort in reproduction than in personal development and more effort in mating than in parenting. In unpredictable environments that trigger fast LH strategies, because future survival is uncertain, investment in developing personal skills and competence does not guarantee a return on the investment. In such cases, investment in reproduction rather than future development is more likely to facilitate fitness enhancement or gene continuity. Similarly, survival of offspring is also uncertain in unpredictable, harsh environments such as those affected by warfare or disease. An unexpected bomb explosion may nullify intensive parental efforts invested in few offspring. Adapted strategies are to mate and reproduce as much as possible to hedge against unpredictable mortality, rather than to bet on few high-quality offspring vulnerable to stochastic unpredictability. In neighborhoods with high homicide rates (indicative of environmental unpredictability), women have their first birth earlier than those in more peaceful neighborhoods (Wilson and Daly 1997). Similarly, chronic childhood illness, conflictual family interactions, and paternal absence or underinvolvement have been associated with early reproduction and sexually promiscuous mating strategies, whereas people who grow up in

stable environment and intact families are more likely to delay sexual experience, have positive attitudes toward, and develop stable pair-bonds (Belsky et al. 2012). Longitudinal data also show that slow LH measures taken at 14 years of age were a significant predictor of timing of first sexual act, frequency of sexual activities, number of sexual partners, number of abortions, and likelihood for having contracted venereal disease measured at subsequent ages up to 32 years of age (Dunkel et al. 2015).

Conclusion

LH strategies are manifestations of tradeoffs in bioenergy allocation between development and reproduction. Timing of puberty reveals the tradeoff between physical development and reproduction, and late puberty and small sexual organs are biological sexual outcomes of slow LH individuals who primarily allocate energy to the development of the brain and body. Efforts invested in sexual behaviors reveal the tradeoff between personal or future development and reproduction, and slow LH individuals allocate energy and time in skill development to enhance their personal competitiveness and in parenting in order to improve the adaptiveness of their offspring. Individuals with fast LH, by contrast, exhibit early puberty and emphasize offspring quantity over quality. They invest energy and time in mating with more partners and reproducing more offspring and thus show unrestricted sociosexual orientations and favor good-gene over good-parent characteristics in their sexual partners. The literature and the present review have focused on sexual activities and physiological characteristics related to sexual maturation, both of which are under natural selection. Future research can also examine sexually selected traits (e.g., fluctuating asymmetry, voice pitch, waist-to-hip ratio, as well as culturally acquired traits such as creativity and sense of humor) in relation to the fast-slow LH strategic continuum. Such an approach is particularly relevant to men who are under much stronger sexual selection pressure than women. Because sexually

selected traits that are costly to build and maintain represent investment in reproductive effort, they are subject to the same LH tradeoff in relation to somatic and body maintenance effort. For example, it will be interesting and informative to explore how fast vs. slow LH strategists allocate energetic budget between sexually selected traits and behaviors and those related to growth and development.

Cross-References

- [Bruce J. Ellis](#)
- [Father Absence](#)
- [Jay Belsky](#)
- [Life History Strategies](#)
- [Puberty](#)
- [Sociosexual Orientation](#)

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Sexual Pathology

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Synonyms

Disorders of sexual preference; Paraphilias; Sexual deviation; Sexual variants

Definition

Sexual pathology or disorders of sexual preference refer to persistent and intense sexual interests lasting at least 6 months, where sexual arousal is in response to atypical fantasies, behaviors, objects, situations, or partners. These behaviors, fantasies, or urges can cause distress, interpersonal difficulties, or functional disorders and usually involve non-consenting persons, nonhuman objects, juveniles, or the infliction of humiliation and suffering.

Introduction

At present, the evolutionary approach is a relatively common theoretical framework for describing and interpreting various aspects of human sexuality, such as differences in sexual behavior between sexes or common sexual responses in the general population. This is coherent considering the fact that the main success criteria are from an evolutionary perspective reproductive success – all psychological, physical, and behavioral traits directly linked to reproduction are of primary interest, and the search for adaptations in this area is intuitive. However, the search for the adaptive meaning of sexual deviations (paraphilias, disorders of sexual preference) is more complicated. This text will introduce the evolutionary approach to the study of paraphilias (or, using evolutionary terminology, “sexual variations”). Firstly, a definition of evolutionary sexology as a scientific framework will be given, along with an explanation of the specifics of the evolutionary frame applied to the disorders and variations linked to sexuality, and finally, with the aid of specific examples of paraphilias, an explanation of the ways in which an evolutionary analysis of particular symptoms in currently diagnosed disorders of sexual preference can be achieved will be given.

What Is Evolutionary Sexology?

Evolutionary sexology is a specific area of evolutionary psychiatry, which, to quote R. Nesse (2002), helps one understand why psychiatric syndromes exist at all and why some of them are so common today. It focuses mainly on evolutionarily ultimate sources, (i.e., what given trait was/is adaptive in the history of evolution for and how it brought reproductive success to our ancestors and also to us). According to Bailey (1991), from the evolutionary perspective, sexual paraphilias are phylogenetic regressions, updated repressed mechanisms, which were adaptive in the past. Evolutionary sexology utilizes a few existing indirect evidences of adaptiveness (behavior strategies or cognitive mechanisms):

1. *High population prevalence.* The prevalence of homosexuality, which was until recently seen as a deviation, ranges today between 5% and 6% across the populations (Diamond 1993). Some sexual paraphilias and dysfunctions, which are still psychiatric diagnoses, have a similar degree of prevalence, for example, various fetishes or sadomasochism.
2. *Similar prevalence across different sociocultural environments.* For example, the sexuality incorporating the submissive or afflicted position of one of the partners and the dominating or pain-inflicting position of the other is found in many human cultures and societies across historical periods studied to date.
3. *Existence of complementary (i.e., opposite) paraphilia in potential or realistic partners.* For example, mutually consenting sadistic/masochistic practices.
4. *Occurrence among different species closely connected on the phylogenetic tree.* For example, male and even female sexual behavior focused on sexually immature individuals is commonly found in various animal species, including primates, chimpanzees, and bonobos (Dixson 1998).
5. *Connection between the high prevalence of a specific sexual strategy and a specific environment type that can provide reproductive success.* For example, the accelerated arrival of first menstruation has been found to occur in dangerous, scarcely resourced, low-income environments, coupled with a high birth rate and low parental care. First sexual encounters occur sooner and demonstrably more offspring are produced. In these types of environments, greater mating activity is a valuable countermeasure against a relatively truncated life expectancy. It is interesting to note that it is not only a case of adaptation in behavior but also physiology – a significantly lower age of first menstruation means that the timing of biological reproduction forms part of this complex adaptive sexual strategy (Gangestad and Simpson 2000).

The specifics of evolutionary scope applicable to disorders of sexual preference and variations

can, therefore, be summarized into the following points: (1) independence of determining what is normal from contemporary environment, society, and culture; (2) emphasis on specific symptoms and relative independence from presently valid medical diagnoses; (3) utilizing findings from classical and human ethology and evolutionary psychology; (4) acknowledging the fact that nature and nurture, the innate and taught, put the finishing touches to the final result of human sexuality; and (5) taking into account the phylogenetic history of sexual behavior, variation, or deviations (Klapilová et al. 2016; Stevens and Price 2016).

Determining Sexual Normality and Abnormality Is Independent from Contemporary Environmental, Societal, and Cultural Norms

While a physician may view rarely occurring phenomena as proof of defects and deviations that are to be normalized or treated, the evolutionary approach considers the same phenomena as a part of natural diversity and variation or as a specific sexual strategy that can, under certain conditions, be adaptive and bring some evolutionary advantages (Nesse 2002). According to the classical Euro-American medical sexology, sexual behavior is “normal,” when between consenting, mature, non-related individuals and when it does not incur psychological or physical damage to either partner. When diagnosing sexual preference disorder, specifying what appears in the sexual fantasies of a person is crucial, specifically the object the person presents sexual attraction toward and who he/she desires to form a partnership with. A psychiatric diagnosis is only necessary when the personal orientation causes the individual (or his/her surroundings) excessive psychological difficulties or adverse effects to their quality of life (excessive stress, suicidal tendencies, feelings of shame and/or guilt) or has led to socially unacceptable or illegal behavior (e.g., the search for underage sexual partners). In other words, paraphilias become a psychiatric problem only when society (or the individual) deems them to be so.

It is important to realize that sexuality is not demonstrated only through behavior, meaning how and with whom one has sex. It does not have to reflect internal preference (Laws and O'Donohue 2008). Apparently, only a minority of people with paraphilias realize their preferred sexuality. Likewise, some sexually *normal* individuals can engage in deviant behavior, even though their preference and sexual fantasies fulfill (in their particular society) traditional concepts of sexual objectification and activity. Therefore, the number of individuals in the population with paraphilic tendencies remains unknown. To determine the prevalence of paraphilic preferences across a population, it is necessary to research not only behavioral experience but also thoughts, fantasies, and arousal toward paraphilic material as well as love emotions toward paraphilic objects.

The Swedish representative research focusing directly on paraphilic behavior noted that 3.1% of men confessed at least one exhibitionist and 7.7% at least one voyeuristic incident (Långström and Seto 2006). Studies targeting pedophile preferences state a prevalence from 0.3 to 3.8% (Mohnke et al. 2014). And lastly, the studies aimed at sadomasochistic experience show, in the USA and Australia, a prevalence from 2.2 to 11% (Hite-Corrie 2012). The fairly high percentage of occurrence detected in previously published studies and their comparisons across different nations and cultures indicate that thinking about the adaptiveness of these sexual strategies is worthy of research.

Emphasis of Individual Symptoms and their Relative Independence from Presently Valid Medical Diagnoses

Another advantage of the evolutionary approach is the perception of individual symptoms (which are part of contemporary medical diagnoses) as independent elements that can have, in different contexts, differing developments and adaptive significance. Individual symptoms may have more adaptive functions, and therefore, it is necessary to look at them from different angles as to avoid their misinterpretation. A fitting example would

be that when watching women's physiological reactions under laboratory conditions, women with "normal" sexual preferences (as opposed to paraphilic patients) have been known to react with a significantly more arousal and vaginal lubrication to stimuli showing aggressive sexual activities (Suschinsky and Lalumière 2011). This, however, cannot simply be explained by presuming that most women are sadomasochistic. The evolutionary explanation presents a hypothesis of preparedness, which is an advantage whenever there is an increased chance of forced penetration, lowering the risk of significant genital harm. Lubrication, therefore, functions as an independent body expression, a symptom present in more contexts than simply being reflective of sexual arousal during intercourse with a preferred partner. It also occurs as part of a defense reaction to an expected incident of sexual attack.

The Application of Knowledge from Classical Ethology, Human Ethology, and Evolutionary Psychology

In evolutionary sexology, the application of knowledge from classical ethology, human ethology, and evolutionary psychology is a key. Sexual behavior in humans is derived from a reproductive function. However, throughout human evolution, social groups have gradually grown and gained complexity, and child-rearing has high demands, especially in the acquisition of complicated social abilities. The combination of these factors meant that, during human evolutionary history, sex took on a number of social functions and began to show in different interactive contexts (Thornhill and Gangestad 1996). It is therefore necessary for humans to understand sexuality as more than just a reproductive tool and rather as a collection of adaptations including mate preferences, mate choice, courtship, and finally partnership formation. The ultimate evolutionary function of sex (i.e., reproduction) is not independent of many other adaptive and social functions of sexuality.

Sexuality is not only about sex, but a genital phase, but is also another step forward in establishing a potential partnership or sexual

relationship. From the viewpoint of basic sexology research into disorders of sexual preference and sexual dysfunctions, this forms an important perspective. From the evolutionary view, we can consider them, mainly, as disruptions in partner selection and partnership formation (i.e., courtship disorders) leading to the inability to sexually function within partnerships (Freund 1990). Sexuality can also be looked at as a hierarchal system of ordered motivational states (SMS, sexual motivation system), a superior brain mechanism running the functional structuring of fragmentary phases of sexual interaction, defined by authors as the potential partner location, non-tactile/affiliative interaction, tactile interaction, and genital interaction (Madlafousek et al. 1981). This theory was strongly inspired by ethological knowledge of mammals gained in the 1970s, in which courting was distinguished by three phases: (1) attractiveness (paying attention to an object's sexual stimuli with specific physical signs), (2) proceptivity (viewing signals of male/female interest and the attempts at courtship), and (3) receptivity (viewing signs of a female's preparedness for coitus and exercising sexual intercourse; Beach 1976). Before making the next step in the motivation system, the lower motivation level must be satisfactorily completed (e.g., before proceptivity, attractiveness must be established). A male's sexual reaction must therefore proceed in this order: recognizing the female's attractiveness and her sexual interest and then interacting with her until after genital contact. If any of these parts takes place outside its order or is skipped, sexual excitement will be reduced (Madlafousek et al. 1981). Apart from the prioritization of positive patterns that lead to sexual arousal, every motivational level has a matching adverse pattern that lowers sexual excitement and interrupts the transition to the next phase. The key is therefore emphasizing the processes around the perception and production of nonverbal expressions (both positive/stimulant and negative/inhibit) in different phases of courtship. People with paraphilia are therefore, in some older ethological theories, seen as individuals who differ from the typical population exactly in their interpretation of perceived

interest/disinterest signals and in their inability to conduct adequate courtship expressions at the correct moment (Freund 1990; Money 1986). This is especially the case with paraphilic individuals who reach sexual arousal and satisfaction atypically (voyeurism, exhibitionism, frotteurism, toucherism, and sexual aggression). The sexual aggressor is able, for example, to perform sexual intercourse with a woman (genital phase), only if not subjected to any signs of seduction from her side. Of course, he himself does not conduct courting behavior. He skips the pre-tactile phase straight to the tactile and genital phases and avoids any interactive synchronization with the woman.

Theoretically, unusual sexual preferences can also arise from an effect similar to imprinting (i.e., an instinctive learning mechanism that takes place during critical development periods). According to Aronsson (2011), the internalization of non-adaptive preference mechanisms (e.g., shoes or other fetishes) is analogical to adaptive preference internalization mechanisms (e.g., our parents' characteristics). Likewise, according to the *erotic target location errors* theory, it is possible to define some paraphilic groups (especially fetishism and transvestism) as development errors when determining the sexual (erotic) object. These errors then lead to a sexual preference for an object's sexually unimportant attributes, for example, a focus on a woman's shoes instead of the woman herself (Freund and Blachard 1993). It is not clear, though, why some sexual preferences, such as fetishism or transvestism, occur only in a small part of the population. The objects preferred by these people are also, during particular sensitive periods, subjected to individuals who do not embody this specific sexual preference. It is therefore probable that other factors also play an important role in the development of these preferences.

Nature/Nurture and the Innate/Acquired Together Complete the Final Result of Human Sexuality

To a great extent, innate and universal human-specific traits are particular signs of attractiveness

(in both genders) that signify genetic quality and fertility. There are such signs of attractiveness in which people from all cultures across history, even across age categories, agree on (e.g., face symmetry). Perceiving these universal signs is mainly genetically conditioned (even newborns automatically give them their increased attention), though it calibrates during their lifetime. Some parts of sexual behavior seem to have a strong innate part, e.g., copulatory pelvic thrusts are already present at a young age (Yang et al. 2005). In human behavioral displays, however, it is rarely the case that it would emerge automatically without being activated by an important stimuli, which must come from an environment (or fantasy). Contact with the demanded stimuli is mostly necessary in order to activate the adaptive strategy in a given sensitive period of ontogenetic development. These are seen as relatively long developmental periods in the individual's development when the nervous system is ready to increasingly react to specific stimuli from an environment that activates the occurrence of a given behavior. According to the neurodevelopmental sexual trajectories of Pfaus et al. (2012), there exist a few basic sensitive developmental periods in which the basic form of sexual (and partnership) life is constructed and in which we learn *who* will sexually attract us, *with whom* we will want to form a partnership, and *what activities* will bring us the biggest sexual pleasure.

Our sexuality is gradually shaped in these sensitive periods, starting with the consolidation of strongly innate sexual orientation and gender differentiation by creating preferences to/aversions toward sexual partners similar to the preferences/aversions of the people surrounding us (primary family), all the way to forming strong individual preferences for characteristics of a sexual partner, objects, or favorite sexual activities. This formation mainly takes place through experiences with sexual arousal and reward, meaning pleasurable feelings derived from arousal and orgasmic experience. The chosen behavioral displays continue to be reinforced by positive or negative experience during the following development stages (Pfaus et al. 2012), and according to recent theories and knowledge on brain neuroplasticity, these

displays are fine-tuned throughout their life (Doidge 2007).

This long journey toward an individual's sexual "maturity" suggests huge variability and flexibility in the forming effects of experience and environment. Within the scope of innate variability, individuals differ precisely in this flexibility. Genetic predispositions to various paraphilias evidently determine how much an individual is genetically predisposed to internalize unusual objects into their SMS (e.g., in fetishism). Similarly, genetic components can determine the length of the sensitive period and the degree of SMS rigidity toward transcripts based on later sexual experiences. For one person, a fetish can be the only and necessarily demanded object for inducing sexual excitement, whereas for another, its usage by a partner only increases attractiveness and sexual arousal.

The Importance of the Phylogenetic History of Sexual Behavior, Variation, or Disorder

It is important to take into account the phylogenetic history of behavior, variations, or deviations, which, in practice, means to assess whether the given element appears in other (close and also far related) species and in what frequency. The systems clearly linked to reproduction are very basal and are driven by ancient (in terms of phylogenesis) parts of the brain. The systems related to hierarchies appear in species with growing social groups. The systems and adaptations, which concern the creation of deeper dyadic links, whether between partners or between caregiver (parent) and offspring, are then rather young and inclined to changes in environment and mutations (Stevens and Price 2016). All of these systems use an identical arsenal of neural mechanisms linked to motivation and perception of reward. For example, according to evolutionary psychiatry, sadomasochism has its origins in the linkage of two phylogenetically ancient adaptive systems – reproduction and social hierarchy. They joint to be a part of a specific sexual strategy losing its original function and together provide a

reward in the form of sexual satisfaction. The key events in sensitive childhood periods (e.g., physical punishments or abuse during adolescence) may activate both these systems simultaneously. This association via conditioning consequently strengthens the preferred sexual strategy and begins to produce sadomasochistic fantasies and motivate similarly tuned behavior. It is probable, however, that some people are more genetically predisposed than others for this bonding (Stevens and Price 2016). The results of intercultural studies focused on sadomasochistic practices indirectly support this theory. These practices often have a strongly ritualized form that obviously copies phylogenetically ancient forms of ritualized pain-inflicting behavior already present in lower vertebrates (Stevens and Price 2016). This genetically affected behavior helps establish social hierarchy and sustain differences between dominant and submissive individuals, consisting in signal use designed to increase one individual's status and reduce that of a submissive. The repertoire of signals differs between species, but it is possible to isolate universal patterns in them. Dominance across species is indicated by erecting one's posture and looking at the rival directly, while in contrast, the submissive will crouch and avoid eye contact (Darwin et al. 1998). Escalating signals during hierarchal battles include using physical strength and causing the opponent pain. In terms of human sadomasochistic activities, this sequence is also kept – the dominant figure emphasizes his supremacy through signs of social status, power, or physical size (uniforms, heels), begins a ritual of verbal aggression (degrading comments), threatens and intimidates, and even commits physical punishments and inflicts pain, with gradual intensification (Kamel 1980).

Zillmann and Bryant (1984) describe how the connection between hierarchal and sexual systems can mechanically occur within the framework of the *excitement shift* theory. According to which, the connection is possible because, on the sympathetic nervous system activation level, the activity is not linked to aggression or distinguished by fear and sex, and within the scope of sex play the two systems can *help each other* in escalating physical arousal. It seems that it is not only a case of

hierarchal systems but any emotion from so-called *agonistic systems* to which classical ethology classifies aggression, dominance, and power, as well as submissiveness, fear, and flight. Dominance and submissiveness and aggression and fear are then two sides of the same coin, which, hand in hand, can be used even in the sexual context. The connection between these systems is strengthened, thanks to the secretion of endogenic opiate endorphins, which are released as a reaction to a threatening stimulation (pain, fear), reducing the intensity of physical and mental pain and increasing the feeling of satisfaction. In combination with sexual arousal, it can multiply the submissive's postcoital satisfaction. This theory, though, does not explain why most sadomasochists describe the occurrence of sadomasochistic fantasies unambiguously preceding realistic experiences with these activities. It therefore seems that the described linking can occur beyond being mediated, through imagining psychic pain or causing pain.

Another example can be pedophilia (Seto 2008). For diagnosing pedophilia, constant sexual interest in prepubescent children is pivotal, being expressed for at least 6 months through fantasies, desires, sexual arousal, or behavior and causing the investigated persona distress. The most cogent symptom is falling in love with a child object. As in the case of sadomasochism, the evolutionary explanation behind the origin of pedophilia refers to the fusion of two evolutionarily ancient adaptive systems – reproduction and nurturing. Money (1990) states that a pedophile's relationship to a child qualitatively, and also neurologically, resembles a blend between parental and erotic love. Likewise, it can be linked to the close cohesion between these two systems that can be observed also between phylogenetically close species. For example, baboons create coalitions between young males and sexually immature females, even though the males behave sexually toward them only after they have reached sexual maturity. The founder of the human ethnology field, Irenäus Eibl-Eibesfeldt (1973), directly warns about the type of affiliative-erotic relationship that connects to the composition of long-term partnership, which was developed both in mammals and birds together with nurturing behavior,

and therefore it is not surprising that they are occasionally mixed in humans. This explanation corresponds with the ethological viewpoint; therefore, it is a case of dysfunctional interaction and preference of nonverbal behavior that is typical for children, not of the pedophile's primary preference of a child's bodily figure. It is however unquestionable that treated pedophiles react with penile arousal also when seeing static pictures of child objects.

Conversely, Quinsey and Lalumiere (1995) presume that the emergence of pedophilia is related to the displaced mechanism of sexual preference. According to them, the male sexual preference system is one of complex modules that is often tuned to such characteristics that are important mainly when selecting a partner. These modules are relatively independent from each other and serve to detect the object's gender and his age (youth), body shape (mainly waist-hips ratio), and health. Furthermore, the authors claim that there is a failure of the module detecting and evaluating body shape, which causes the module for distinguishing age to malfunction. This claim is supported also by the fact that in opposition to non-pedophilic men, there is a higher percentage representation of homosexual and bisexual individuals among pedophiles, i.e., individuals who prefer the male figure, whose shape (waist-hips ratio) resembles prepubescent individuals (Quinsey and Lalumiere 1995).

The child's adaptive behavioral function to demand nurture from adults and his prospective urge to perform sexual activities is not mentioned too often. Still, it is a rather widespread behavior across cultures and historical periods that can help the child receive extra resources not available from their own parents. It would therefore be a complementary strategy – from the pedophile's side, there is the eroticization of nurturing behavior and attraction to signalization that encourages caretaking, whereas from the child's side, it is a functional, environmentally conditioned strategy that brings benefits in the form of resources and possibly even acquisition of sexual experience and calibration of child sexuality (Stevens and Price 2016). It is then interesting that such a large percentage of the common population associates behavior of

providing care and signaling need with erotic charge, attaching sexual practices and fantasy scenarios to them (e.g., schoolgirl and teacher).

From an evolutionary perceptive, of course, there are differences between pedophilia and the so-called hebephilia (sexual attraction to pubescent children between 11 and 14) and ephebophilia (sexual attraction to adolescents between 15 and 19, Blanchard et al. 2009). Despite the unacceptable nature of pedophilia, it is necessary to note that pictures of partially developed pubertal naked girls can create arousal in non-pedophilic heterosexual males (Blanchard et al. 2009). From an evolutionary perspective of men's reproductive success, it would be illogical to avoid female objects already able to reproduce, even though the strongest arousal is present with women around 25 years old. The occasional pairing with pubescent girls can therefore fall into the spectrum of normal variability in heterosexual preferences.

Conclusion

The evolutionary approach allows one to look at disorders of sexual preference as adaptive behavioral strategies, which have an innate element. It also suggests that the most important specifically human adaptation is the ability to modify one's sexual preference in relation to their environment, society, and culture. This carries, to an extent, the ability to change the adapted or, in critical periods, taught aspects of sexual scenarios even in later life, even if these changes are within inherited predispositions. The approach facilitates the distinguishing between parts of a sexually motivated system that are rigid to modification (and have a strong inherited component and ancient phylogenetic origin) and parts of a sexually motivated system dependent on environment and experiential influences. An emphasis on ontogenetic development and the concept of genetically programmed sensitive periods allow key factors for the forming of sexuality described in earlier psychology literature of different paradigmatic settings to be taken into account (e.g., repeated formulas of sexual abuse, physical punishments during childhood).

Cross-References

- [Aggression for Sexual Access](#)
- [Paraphilia](#)
- [Sexual Abuse](#)
- [Sexual Coercion and Rape](#)

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Sexual Personality

- ▶ [Sexual Identity](#)

Sexual Preference

- ▶ [Hormonal Component of Homosexuality](#)
- ▶ [Sexual Orientation](#)
- ▶ [Sexual Orientation and Human Sexuality](#)

Sexual Preferences

- ▶ [Sexual Contact and Sexual Disgust](#)

Sexual Prejudice

- ▶ [Genetic Hypotheses of Homophobia](#)
- ▶ [Homophobia](#)
- ▶ [Social Hypotheses of Homophobia](#)

Sexual Prejudice (Personality Correlates of)

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Synonyms

[Homophobia](#); [Heterosexism](#); [Homonegativity](#)

Definition

A negative attitude toward individuals or groups on the basis of their sexual orientation.

Introduction

Sexual prejudice involves negative thoughts about, feelings toward, and action orientations toward non-heterosexual people (Herek 2009). Although the word homophobia is sometimes used to refer to sexual prejudice against gay men and lesbian women, it emphasizes a particular affective response – fear – and has fallen out of favor among many researchers due to its presupposition that sexual prejudice stems primarily from fear. Most research on sexual prejudice has focused on negative attitudes toward gay and lesbian people, with some recent attention to bisexual people, but the phrase can also refer to prejudice against other sexual orientation groups (e.g., asexual people). Herek's (1994) Attitudes toward Gay Men and Attitudes toward Lesbians Scales are commonly used measures of individual differences in sexual prejudice.

Bases of Sexual Prejudice

Sexual prejudice is rooted in both intergroup and intragroup psychological processes. With respect to intergroup processes, some heterosexual people view gay, lesbian, and bisexual people as members of one or more different social groups whose existence and actions threaten heterosexual people's values and well-being. In terms of intragroup processes, some heterosexual people may perceive non-heterosexual people as individuals who deviate from norms of sexual behavior in their larger social context and thus are believed to merit negative attitudes and treatment.

Personality and Individual Differences in Sexual Prejudice

Social dominance orientation (Sidanius and Pratto 2011) is one of the most robust individual-difference measures for predicting a range of biases against groups perceived to have low social status. People who are higher in social dominance orientation believe more strongly that group

hierarchies are inevitable and desirable and see the world as involving greater zero-sum competition between groups for resources. Individuals who score higher in social dominance orientation exhibit greater sexual prejudice.

Because some people view non-heterosexual people, either individually or as a group, as deviating from the sexual standards of a society, sexual prejudice often also reflects rejection of perceived norm violators. Many cultures (including the US) have historically valued heterosexual relationships through laws, religious doctrines, and social traditions. Sexual prejudice relates to a range of personality and individual-difference factors associated with negative responses to violations of traditional norms.

Authoritarianism, which is a personality variable that involves a strong motivation to maintain social order and stability, predicts biases against a variety of groups that are perceived as violating social norms, including sexual minorities. The most widely used measure of this construct is the Right-Wing Authoritarianism Scale (Altemeyer 1998). This measure represents a core “attitudinal cluster” that includes authoritarian submission (an inclination to submit to those of greater authority), authoritarian aggression (general hostility toward deviants and outsiders), and conventionalism (a strong commitment to the traditional norms and values of one’s group).

Several demographic variables related to adherence to normative standards also predict sexual prejudice in North America. Because many religious doctrines present same-gender relationships as inconsistent with their values, people who are more religious tend to display greater prejudice against sexual minorities (Whitley 2009). In addition, political conservatism consistently predicts such prejudice. Older age predicts greater sexual prejudice in contemporary studies, perhaps reflecting changing social norms, and higher levels of formal education are related to less sexual prejudice (Herek 2009).

Sexual orientation is intrinsically linked to gender, because it is defined by the experience of sexual or romantic attraction to people of particular gender groups. The norm against same-gender relationships can be viewed, therefore, as a gender norm. Thus, individuals who endorse traditional gender roles

more strongly or are more sexist (e.g., as assessed by the Ambivalent Sexism Inventory; Glick and Fiske 1996) exhibit greater sexual prejudice.

Several demographic factors related to the endorsement of conventional gender norms systematically relate to sexual prejudice. For example, displaying one’s heterosexuality appears to be a vital piece of modern gender norms, especially for men. In part because masculine gender norms are often perceived as less flexible than feminine norms, men’s prejudice against sexual minorities tends to be stronger than women’s. Although men and women differ in their levels of prejudice against other groups as well, strength of gender identification appears to be an especially important predictor of heterosexual men’s sexual prejudice.

Conclusion

Sexual prejudice is rooted in both perceived group status differences and perceived violation of social norms – both intergroup and intragroup processes. As a result, personality and individual differences in factors related both to relations between groups and to social stigmatization within a group predict sexual prejudice. One implication of this observation is that the relative influence of personality factors on sexual prejudice may vary as a function of whether sexual orientation is framed as a set of discrete groups. A second implication is that the dynamics of sexual prejudice may vary for responses to different sexual minority groups. For example, gay men and lesbian women may be more likely to be seen as a discrete group than bisexual people, thus engaging different bases of sexual prejudice. Understanding the personality and individual differences that contribute to these processes is an active area of research.

Cross-References

- ▶ [Homophobic Bullying](#)
- ▶ [Religious Beliefs](#)
- ▶ [Same-Sex Relationships](#)
- ▶ [Sexism](#)
- ▶ [Sexual Stigmatization](#)

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Sexual Promiscuity

► Sperm Competition: Evidence in Nonhumans

Sexual Receptivity

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Synonyms

Sexually accepting, Open to sex

Definition

Acceptance of attempts at, or offers of, sexual intercourse

Introduction

Sexual receptivity refers to an acceptance of sexual intercourse and is contrasted with (although not necessarily distinct from) proceptivity (initiating and/or maintaining sexual intercourse) and attractivity (attracting others to engage in sexual intercourse). Since the male of the species is typically always receptive to female sexual advances, female sexual receptivity imposes a reproductive limitation.

Continuous Sexual Receptivity

Human females possess an extended sexuality, whereby they are receptive to sexual intercourse across both the fertile and non-fertile phases of the menstrual cycle, suggesting human sexuality is solely defined by conception (which can only occur within a brief window of the menstrual cycle, MC). This extended sexuality differs from the majority of the great apes, with the notable exception of the female bonobos, *Pan paniscus*. Although other nonhuman primates show signs of extended sexuality (e.g., wild Assamese macaques, *Macaca assamensis*). This extended sexuality is closely linked with concealed ovulation, that is, lack of external signals of estrus (but see Haselton and Gildersleeve 2011, for a discussion of potential cues to cyclical fertility in humans). Scholarly debate has centered on the evolutionary advantage of this continuous receptivity and whether the adaptation was driven to the benefit of the male or female or instead evolved as a by-product of changes in morphology and physiology. For example, Alexander and Noonan (1979) proposed that extended sexuality increases paternity uncertainty, an advantage for the female who then reaps resource benefits from the male at all times. Alternatively, Thornhill and Gangestad (2015) argue that continuous receptivity evolved as a means enabling cuckoldry of the primary partner, allowing the female to seek good genes elsewhere, in line with strategic pluralism (Gangestad and Simpson 2000). Still other researchers have argued continuous receptivity serves a social-bonding mechanism or facilitates a system of trading sex for reward.

Sex Differences in Sexual Receptivity

Despite women's continuous sexual receptivity, they are not indiscriminate in their acceptance of sexual offers, with sex differences in receptivity readily observable. Clark and Hatfield's (1989) classic experiment demonstrated that women and men who were approached on a college campus by an opposite-sex stranger were equally willing to accept a date from the stranger, but only men were willing to accept an offer to "go to bed." These differences in sexual receptivity reflect evolved sex differences in sexual strategies theory (SST). Specifically, SST argues that both sexes have evolved short-term and long-term sexual strategies, although context will differentially affect the extent to which men and women pursue these strategies (Buss and Schmitt 1993). Because women are the more discerning sex (they are choosier), they are less likely to pursue a short-term sexual strategy than men are.

Hormonal Variation in Sexual Receptivity

Women may show a pattern of sexual receptivity which varies across the MC. Guéguen (2009) demonstrated that women were more likely to accept an offer of sex from a stranger when in the fertile phase of the MC than the non-fertile phases. Other researchers have demonstrated that women engage in more sexual activity when fertile. For example, Harvey (1987) demonstrated fertile phase peaks in both male-initiated and female-initiated sexual intercourse episodes, implying MC effects on both receptivity and proceptivity. Recent advancements in hormonal and MC research and recommendations for how to calculate MC phase (Gangestad et al. 2016), however, limit the reliability of these findings. Specifically, while a large body of research has previously found evidence for the effect of the MC on women's sexuality and sexual strategies, more recent, methodologically rigorous, research contradicts some of these findings. Relatively little recent research has investigated the effects of reproductive hormones or the MC on sexual receptivity in human females. For example, Jones et al. (2018) found only an effect

for general sexual desire, however, did not measure receptivity, specifically.

Cues to Sexual Receptivity

Women may actively signal their sexual receptivity to men. In nonhuman primates, wild female chimpanzees, *Pan troglodytes schweinfurthii*, use copulation calling as a signal of receptivity to high-ranked males. In humans, perceived cues to sexual receptivity may include clothing choice, walking style, and other nonverbal behaviors. One body of research proposes red clothing serves a sexual signal in human females. For example, women wearing red (compared to white) are perceived to be sexually receptive by both men and women. However, recent research has called the association between red clothing and perceived sexual receptivity into question.

Conclusion

Sexual receptivity in human females is a limiting resource in reproduction. Women show continuous sexual receptivity, the evolutionary advantage of which is debatable, and may reflect attempts at facilitating cuckoldry, or serve to increase paternity confusion. Despite continuous receptivity, women show variation in receptivity which is possibly linked with MC. The extent to which women signal sexual receptivity is unclear.

Cross-References

- ▶ [Bonobo Sexuality](#)
- ▶ [Concealed Ovulation](#)
- ▶ [Menstrual Cycle](#)
- ▶ [Problems of Assessing Fertility](#)
- ▶ [Sexual Strategies Theory](#)

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Sexual Regret

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Synonyms

Action regret; Inaction regret; Negative postcoital emotions; Rumination

Definition

Regret is a counterfactual cognitive-emotional response to past events, where one in hindsight wishes the past had been different. Regret comes

in two forms: inaction regret, which is the regret of not having acted when one had the chance and missed out on what proved in hindsight to be an attractive opportunity, and action regret, which is the regret of having done something that in hindsight proved to be less positive than one assumed at the time of acting. Casual sex regret is therefore the specific regret of either having had casual sex or passing up an opportunity for having casual sex.

Introduction

Research on regret finds that sex differences are domain specific. The major sex difference in regret is for romantic relationships and is not present for other domains such as parental relationships, friendships, or academic achievement (Roese et al. 2006). In two studies involving romantic relationship regret, Roese and colleagues found that men reported markedly more inaction than action regret, whereas women reported less different amount of inaction and action regret for romantic relationships. Evidently, relative to women, men report far more frequent regret having passed up sexual or dating opportunities. This sex difference has proved empirically robust across studies focusing more specifically on brief or casual sex encounters (Eshbaugh and Gute 2008; Fisher et al. 2011; Galperin et al. 2013) and reproduced in a more sexually liberal, less religious, and gender-equal nation (Bendixen et al. 2017; Kennair et al. 2016, 2018). To illustrate, Galperin et al. (2013) found in a national US sample covering 22,815 heterosexual participants (Of these, 6264 men and 6470 women reported their level of regret for their most recent casual sex encounter, and 7351 men and 6784 women reported on their level of regret passing up casual sex.) that men (43%) more than women (26%) reported that they regretted having passed up their most recent casual sex opportunity ($d = 0.60$). Moreover, relative to men (22%), more women (47%) regretted their most recent casual sex encounter ($d = 0.73$). Applying identical materials, the magnitude of these sex differences was reproduced in three separate student samples, one American and two

Norwegian (Bendixen et al. 2017; Kennair et al. 2016). However, in these samples of younger participants, there were generally less regrets related to passing up the most recent casual sex encounter. It is important to note that people do not in general regret casual sex, but the research attempts to answer the question: why do people regret casual sex, when they indeed do regret?

These findings are expected from a sexual strategies theory approach to sex differences in sexual behavior (Buss and Schmitt 1993), as there are stable differential adaptive consequences of casual sex for each of the sexes across our species' evolutionary history. This same approach predicted sex differences in negative postcoital emotions (Fernandes et al. 2016) sometimes referring specifically to affective shifts or changed attraction following sexual intercourse (Campbell 2008; Haselton and Buss 2001).

Sexual strategies theory predicts that men would report more casual sex inaction regret than women do, since they should not wish to forego short-term reproductive chances, as men may have greater reproductive success due to multiple matings. There are no comparable reproductive benefits for women who pursue multiple sexual partners. On the contrary, it is expected that women might, due to the greater costs involved in becoming pregnant, both show greater choosiness but also have greater reason for regret due to any cues or indications of incurred costs (including partner's lack of interest in committing after sex).

Evolutionary Psychological Theory of Casual Sex Regret

Galperin et al. (2013) suggested that casual sex regret is a sex-linked adaptive emotional response with the specific function of flagging maladaptive choices related to sexual encounters. The functional output would therefore be more adaptive future choices, resulting in less future regret. There is currently no evidence of actual behavioral change due to casual sex regret, although there is some research on the intention to change behavior due to regret in lab settings on consumer behavior (see Roese et al. 2007, for comments on

the necessity to alter behavior due to regret). Galperin and colleagues are explicit about the necessity that regret needs to have behavioral consequences to be able to have evolved or to be adaptive.

Predictors of Casual Sex Regret

Beyond sex, there may be a number of factors associated with regret having had and having passed up casual sex. Galperin and colleagues (2013) found that sex differences in regret having had casual sex held up across groups of differing sexual orientations but that both lesbian and bisexual women reported less casual sex regret. For men the level of casual sex regret did not differ between hetero-, bi-, and homosexuals. Relative to heterosexual women, lesbian and bisexual women also reported regretting passing up casual sex more. In their multiple regression analyses of heterosexuals, Galperin et al. (2013) found no age effects for neither action nor inaction regrets, but coupled respondents tended to report more action regret and less inaction regret compared to singles. In addition, higher levels of education tended to be associated with less inaction regret, but the effects were small and did not affect the overall sex differences. Sex differences in action and inaction regret were also smaller in gay/lesbian and bisexual samples compared to heterosexual samples.

Galperin and colleagues (2013) hypothesized that some social or proximate factors might moderate or exacerbate the above sex differences in casual sex regret. These included worry about becoming pregnant, which would be expectably higher in women, and level of physical gratification, which was expected to be lower in women. Here one needs to consider a caveat; accounting for any proximate factor that is related to sex in a statistical analysis may effectively reduce any sex differences in the level of casual sexual regret. Still, when considering sex differences, one needs to show constraint when *explaining* differences in one biologically sex-linked psychological trait or disposition with predictors that also are sex-linked psychological traits or dispositions. This might in

many cases result in the variance due to sex that is accounted for by proximal sex-linked factors (as in a mediator model); but it is conceptually equivalent to the proverbial “throwing the baby out with the bathwater.” A better analytical strategy would be either to perform separate analyses of predictors of sexual regret for women and men or to add an interaction term to examine if the effect of a main predictor of regret is moderated by participant sex.

Two studies covering three separate samples examined what proximate factors may be associated with casual sexual regret (Bendixen et al. 2017; Kennair et al. 2016, 2018). These studies inform us about the question why women regret casual sex more than men do and why men regret passing up sexual opportunities more than women do. In their first paper, Kennair et al. (2016) included three measures of worry (pregnancy, STI, and reputation), three measures of physical gratification (pleasure, orgasm achieve, and orgasm importance), and three measures of sociosexual orientation (behavior, attitudes, and desire). In the multivariate regression model, higher acceptance for short-term sex (SOI-attitudes), increased sexual pleasure, and less worry about reputation all predicted lower levels of regretting having had casual sex in women. For men, more sexual pleasure and stronger desire for casual sex partners predicted lower levels of casual sex regret. Women and men who worried about their reputation following casual sex reported less regret passing up casual sex opportunities. In addition, women who had higher acceptance for casual sex reported higher levels of regret passing up.

In their second study, Bendixen et al. (2017) analyzed comparable samples of Norwegian and American students. Predictors were level of religiosity (religious beliefs and adherence to religious doctrines) and the three sociosexual orientation dimensions (behavior, attitudes, and desire) of SOI-R (Penke and Asendorpf 2008). The two national samples differed predictably in levels of religiosity and sociosexuality, given expected cultural differences in religiosity and sexual liberalism. American students were far more religious than Norwegian students were

($d = 1.19$) and reported moderately lower levels of SOI-behavior and SOI-attitudes. Despite this, the level of regret having had casual sex or passing up casual sex was similar across nations. In addition, the sex differences in action and inaction casual sex regret found in Kennair et al. (2016) were reproduced in both the Norwegian and the American sample. Higher levels of religiosity predicted somewhat higher levels of regret having had casual sex and somewhat lower levels of regret passing up casual sex opportunities. As for the above study, higher acceptance for casual sex and more desire for casual sex (SOI-attitudes and SOI-desire) predicted lower levels of regret having had casual sex and higher levels of regret passing up. These effects were general and not moderated by neither participant sex nor nation.

The third and most recent study (Kennair et al. 2018) examined the effect of a number of additional proximate factors for regret having had casual sex. The study covered the same measures of worry and physical gratification as in the first paper. New, additional predictors included three domains of disgust (sexual, pathogen, moral), two items on feeling pressured to have sex, two items on the sexual competence of the partner, and a single item on the level of initiative to casual sex. When controlling for sex and nation, regression analyses of separate predictors suggested that worry, feeling pressures, and disgust predicted higher levels of casual sex regret and that the associations were higher in women than in men. Further, gratification, competence, and initiative predicted lower levels of casual sex regret. Again, the associations were stronger for women than for men. When regressing casual sex regret on all six predictors in a multivariate model, disgust turned out to be a particularly strong predictor. A variable that combined the level of gratification and competence was also significantly associated with regret, along with worry and initiative. In the multivariate model, the only sex-differentiated predictor was initiative; there was no effect of this for men. None of the other predictors was moderated by either sex or nation. Additional analyses of three domains of disgust showed that moral disgust turned out to be most important. Despite national differences in level of worry,

disgust, sexual competence, and the other predictors, the proximate factors associated with regret having had casual sex were similar across the Norwegian and the American samples.

Future Research and Unanswered Questions

Despite having reproduced the predicted sex differences in action and inaction casual sex, along with repeated attempts to examine personality and proximate factors related to sexual regret, it is worth noting that one has not tested the adaptive hypothesis suggested by Galperin et al. (2013). Such testing would require data that show evidence of regret predicting later increase in adaptive choice or behavior. For example, one might find that while controlling for different factors such as age or changing from single status to long-term committed partner status, those who have regretted most in earlier measures show the greatest changes in satisfaction with later mate choice. Alternatively, maybe they will show greatest decrease in new short-term partner or greatest likelihood of choosing to enter committed long-term relationships. In some way, higher levels of regret at any point need to predict subsequent more adaptive choice followed by lower levels of regret. The adaptive hypothesis thus needs testing in studies using longitudinal designs. The alternative prediction might be that different levels of regret represent individual differences in likelihood of regretting, including metacognitive beliefs about the benefits of regret (as the adaptive hypothesis actually is an example of), or individual differences in the likelihood of engaging in casual sex and thus having regrets, but without any feedback that results in behavioral change.

Further, there is a need to consider in greater depth what factors may predict different levels of inaction regret. Kennair et al. (2016, 2018) focused mostly on predictors of action regret, considering what likely predictors – theoretically and empirically – that would reduce or increase regret in men and women. Factors associated with regret passing up casual sex are clearly under-

researched. Given men's higher levels of inaction regret, future research need to include a variety of possible factors and examine the extent these affect inaction regret differently for men and women. Finally, possible effects of being intoxicated (alcohol or other substances) during casual sex on casual sex regret need to be considered fully in future research.

Conclusions

The sex differences in casual sex regret are robust. Men regret casual sex inaction more than women do, and women regret having had casual sex more than men do. This finding is not surprising from an evolutionary psychology perspective, as there have been stable differences in adaptive costs and benefits to the two sexes in engaging in casual sex.

Recent research on multiple factors have provided us with insights into what predicts both casual sex action and inaction regret. What predicts casual sex regret appears to be largely invariant across cultures that differ in three relevant dimensions: religiosity, sexual liberalism, and gender equality. The major predictors of casual sex inaction regret are unrestricted attitudes toward – and stronger desires for – casual sex. The major predictor of casual sex action regret is disgust; the largest single sex-differentiating factor is the degree to which one took the initiative to having casual sex, which only affects women's regret (less regret with greater initiative). Rather than less sexual gratification and pregnancy concerns, the results so far suggest that the proximate mechanisms involved in regret having had casual sex may be social in nature. The moral domain of disgust and the reputational aspect of worry appeared to be particularly good predictors of action regret. Throughout human evolutionary history, the transparency of men and women having short-term sexual relations might have been higher, and possibly sanctioned. Possibly, the social nature of factors affecting casual sex regret is a reflection of humans' hypersensitivity to signals of social exclusion or sanction.

Future research needs to specify better how the evolved mechanisms underlying sexual regret would have worked in the EEA. Thus far, there is no test of the evolutionary hypothesis. Such tests demand longitudinal studies. Current research sheds light on why people regret having or having passed up casual sex but cannot address the adaptive hypothesis, which might better explain negative postcoital emotions (Fernandes et al. 2016), rather than explain the function of regret. Future research needs to consider whether regret actually changes future choices in an adaptive direction.

Cross-References

- [Casual Sex](#)
- [Cross-Cultural Research on Grandparental Investment](#)
- [Disgust](#)
- [Pathogen Disgust and Perceptions of Attractiveness](#)
- [Pregnancy](#)
- [Religiosity](#)
- [Sexual Behavior](#)
- [Sexual Contact and Sexual Disgust](#)
- [Worry](#)

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Sexual Rejection

- [Circumventing Mate Choice](#)

Sexual Relations

- [Sexual Intercourse](#)

Sexual Reproduction

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Synonyms

Amphimixis; Procreation; Sex

Definition

Sexual reproduction refers to the mating system by which offspring with a double set of chromosomes (diploid) are created by the union of a set of chromosomes from the haploid gametes of one sex (male) with another set of chromosomes from the haploid gametes of another sex (female).

Introduction

We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements. . . The whole subject is as yet hidden in darkness. (Charles Darwin 1862)

Why did sexual reproduction evolve? When posed with this question one might think that sexual reproduction evolved because it is pleasurable. But this is no better an explanation for sexual reproduction than it is for hunger. Pleasure is something that natural selection attached to the activities that when engaged in led to the greater survival and reproduction of those individuals through evolutionary time.

Another potential answer to the question of why sex evolved is that it allows organisms to produce offspring. However, organisms with non-sexual forms of reproduction, such asexual reproduction, also produce offspring. In fact, asexual

organisms produce more offspring and at a faster rate than organisms that reproduce sexually. Additionally, asexual reproduction is not as costly as sexual reproduction (Roze 2012). The costs of reproducing sexually include finding a mate, engaging in courtship practices, and combining gametes from distinct individuals, among others (Roze 2012). Therefore, it appears that the cost-benefit ratio of sexual versus asexual reproduction in terms of the ultimate currency of natural selection – that is, reproductive fitness – is in favor of asexual reproduction. However, sexual reproduction has been widely favored by evolution and is the major reproductive system found throughout multicellular organisms in nature (Otto 2008).

From an evolutionary perspective, that sexual reproduction is pleasurable and that it leads to offspring are both answers to proximate- rather than ultimate-level questions about the purpose of sexual reproduction. The ultimate question regarding the origins of sexual reproduction is why did it evolve in the first place? Why was sexual reproduction favored throughout evolutionary history over the alternatives? Far from quick answers, this problem has eluded researchers for decades and has inspired some of the greatest evolutionary researchers in history, such as Ronald Fisher, William Hamilton, John Maynard Smith, and George Williams, to rise to the challenge.

The Origins of Sex

A complete understanding of how sexual reproduction evolved requires tracing evolutionary history back billions of years to the origins of life itself. Data from molecular sequencing studies have made it possible to date the origin of life to somewhere between 3.5 and 4 billion years ago (Weiss et al. 2016). The first life form, the most recent common ancestor of all of life, was likely a bacteria-like, intermediate organism being the common ancestor of the two major domains of life: bacteria and archaea (Weiss et al. 2016). Newer analyses have found support for the hypothesis that eukaryotes – organisms that eventually gave rise to all multicellular organisms such

as animals and plants – arose from prokaryotes, more specifically, from the domain archaea (Raymann et al. 2015; Williams et al. 2013).

In contrast to prokaryotes, eukaryotes do not strictly reproduce asexually, but also sexually. In other words, prokaryotes are obligately asexual, whereas most eukaryotes are facultatively sexual. Therefore, the origin of eukaryotic life is closely associated with the origin of facultative sexual reproduction, which is asexual reproduction with occasional sexual cycles (Dacks and Roger 1999). Eukaryotes sexually reproduce by complementing the system of mitosis or cell division – resulting in two genetically identical cells arising from one – with meiosis. Contrary to mitosis, meiosis consists of two rounds of cell division resulting in four daughter cells each of which possess only one set of chromosomes from the parent. In other words, meiosis results in four haploid cells, known as gametes. Gametes from two sexes combine to create a zygote.

Dacks and Roger (1999) show that the most parsimonious interpretation of their phylogenetic tree of eukaryotic taxa is that facultative sexual reproduction is the ancestral sexual cycle of eukaryotes. They speculate that because facultative sexual reproduction is characteristic of all protist eukaryotes, then obligate sexual reproduction in eukaryotes may be intertwined with multicellularity. Additionally, Goodenough and Heitman (2014) argue that the last eukaryotic common ancestor was sexually reproductive based on several studies that found evidence of genes exclusively involved in meiosis in all the main eukaryotic radiations. Goodenough and Heitman (2014) also describe several gradual changes that were likely taking place in between the transition from protoeukaryote to the last eukaryotic common ancestor that was sexual. One such change was cell-cell fusions, which result in greater chromosome number, likely a key prerequisite for meiosis to take place (Goodenough and Heitman 2014).

Additionally, there is evidence that many current day asexual eukaryotic organisms evolved from sexual ancestors. For example, the asexually reproducing protozoan *Trichomonas vaginalis*, a cause of vaginal infections, likely evolved from a

sexual ancestor (Malik et al. 2008). Research has shown that *Trichomonas vaginalis* contains genes that are exclusively used for meiosis, a necessary part of sexual reproduction, and that these genes were already present early in eukaryotic evolution (Malik et al. 2008). Another example is the unicellular eukaryotic pathogens microsporidia that are a common cause of human infections. They include many asexual species. Evidence suggests, however, that they evolved from a zygomycete fungus ancestor and possess genes related to sexual reproduction that are similar to the sex genes that zygomycetes possess (Lee et al. 2008).

Far from being an evolutionary novelty, sexual reproduction appears to be as old as the appearance of eukaryotes. Studies that analyze molecular and genetic data of these early eukaryotes show that evolutionary processes must have favored sexual reproduction, so much so that it has become the dominant mode of reproduction among eukaryotic organisms. However, a deep problem remains.

The Problem of Sexual Reproduction

The central problem of the evolution of sexual reproduction arises from its ubiquity throughout nature on one hand, and its enormous and obvious costs on the other. Over 99% of multicellular eukaryotes reproduce sexually making it the most commonplace mating system in multicellular eukaryotes (Otto 2008). However, from the level of the gene's eye view, sexual reproduction is extremely problematic.

Imagine a population of 100 sexually reproducing organisms with an equal ratio of males to females (50:50). Assuming the first generation reproduces once, a maximum of 50 offspring can be produced. Compare this to an asexual population of 100 organisms in which each individual organism can produce offspring. If the first generation reproduced once, a maximum of 100 offspring would be produced. This results in the per capita birth rate of an asexual species being twice that of a sexual species. And so, an asexual mutant that arises in a sexual population should double in frequency each

generation and quickly replace the sexual population. This problem is known as the twofold cost of sex. It is also referred to as the “cost of males”, since in sexually reproducing species, males do not directly produce offspring (Maynard Smith 1978).

This problem was first formulated and described in depth by John Maynard Smith (1978). From the point of view of natural selection at the level of the gene, sexual reproduction should never evolve, and yet, it has, hence the longstanding problem in evolutionary biology. How could sexual reproduction evolve and, in fact, become vastly ubiquitous throughout nature given the enormous costs of sexually reproducing?

Genetic Diversity as an Outcome of Sexual Reproduction

One of the first evolutionary theories for sexual reproduction was the variability of offspring hypothesis first proposed by the German biologist August Weismann in the 1800s (Weismann 1889). This hypothesis states that sexual reproduction results in the combination and rearrangement of genes that provides necessary variability for selection to act. Due to the continuous mixing of genes under sexual reproduction, offspring will have more variable phenotypes, which allows for selection to act and for populations to evolve more rapidly.

This hypothesis arises from the fact that compared to asexual reproduction which produces genetically identical offspring, sexual reproduction results in genetically unique offspring. A large part of this genetic variation comes from genetic recombination during the first cell division stage of meiosis. During genetic recombination, homologous chromosomes within the two haploid cells pair and exchange genetic information creating new allelic combinations and hence genetic variability. This results in all gametes within just one individual being genetically unique from each other. Moreover, sexual reproduction leads to fertilization, whereby gametes from one parent are combined with the gametes from the other, resulting in genetically unique offspring.

Therefore, according to this theory, populations of sexually reproducing organisms will produce offspring with more variable phenotypes allowing for the faster and more effective attainment of favorable mutations and response to environmental changes. This process should benefit the population, but not necessarily the individuals within it, and is thus a group-selectionist evolutionary theory. Other researchers have revised and reformulated the theory considering new scientific tools and evidence, such as population genetics, and mathematical formalisms to model the evolutionary dynamics under specific conditions (Fisher 1930; Muller 1932; Crow and Kimura 1965).

Maynard Smith (1971) refers to the variability hypothesis of sex explanation as the “long-term explanation” for sex. Fisher (1930) and Muller (1932) contribute to this long-term explanation of sex by describing how if two favorable mutations arise separately in a population, sexual reproduction allows for them to be incorporated into individuals. In contrast, the absence of sexual reproduction in asexual populations ensures that favorable mutations are stuck within their common descent lineages since there is no gene mixing between unrelated individuals.

Researchers putting the variability hypothesis of sex, also known as the “Weismann effect,” to the test have found support for it as an explanation for why sex may have been favored by evolution. Goddard et al. (2005) found support for the Weismann effect by genetically engineering some yeast to be sexually reproducing and others to be asexually reproducing and raised them both in a stressed, low nutrient diet. The sexually reproducing yeast were able to adapt faster to the new environment with greater rate of growth than the asexual yeast. Indeed, many other studies support Weismann’s variability of sex hypothesis (Becks and Agrawal 2010, 2012; Colegrave 2002; Cooper 2007).

Crow and Kimura (1965) add quantitative models and mathematical formalisms to the variability of sex hypothesis. They model the incorporation of favorable mutations in populations with and without recombination (corresponding roughly with the modes of sexual and asexual

reproduction, respectively) and represent parameters such as population size, generation number, selective advantage of the mutation, and the rate of favorable mutations. They show that the advantage of sex is greatest when the population size is large, when the rate of mutations is high, and when the selective advantage of the mutations is small. In other words, sex has less of an advantage over asexual reproduction if favorable mutations spread too quickly through a population (i.e., if the selective advantage is high and if the population size is small) and thus are wasted, because there is not enough time for them to be incorporated.

Crow and Kimura (1965) also add important limitations and nuance to the notion that sexual reproduction leads to greater genetic variability compared to asexual reproduction. These nuances include the fact that the number of genetic combinations produced in any generation is limited by the population size. Additionally, while recombination leads to several unique genetic combinations, recombination also breaks up the number of combinations, reducing the amount of variability.

Maynard Smith (1971) addresses potential shortcomings in the model of Crow and Kimura (1965) and also raises a counterargument to the “long-term explanation of sex” originally voiced by Williams (1966), which is that it requires selection to act at the level of the group or species rather than at the level of the individual or the gene. Maynard Smith (1971) calls Williams (1966) explanation the “immediate advantage” explanation for sex, in that it posits that sexual reproduction confers an immediate advantage in terms of creating variable offspring, some of which will be high in fitness. Maynard Smith (1971) models this explanation and finds it lacking, because if true it would suggest that environments must vary tremendously for sexual reproduction to be immediately advantageous. He states it thus “sexual reproduction is an immediate advantage only if the correlations between selectively relevant features of the environment commonly change sign between one generation and the next” (Maynard Smith 1971, p. 332). Indeed, many studies have found evidence that changing environments have

something to do with the evolution of sexual reproduction (Colegrave 2002; Goddard et al. 2005; Cooper 2007).

Purging Bad Genes

Another major theory for the evolution of sexual reproduction is that sex allows for a way to effectively remove “bad” genes – that is, mutations that have a negative impact on an organism’s fitness – from a population. Muller first described this process in what has come to be called “Muller’s Ratchet” (Muller 1964). Muller’s Ratchet refers to the problem of asexual species accumulating deleterious mutations in an irreversible manner. Deleterious mutations accumulate because in an asexual species, the offspring end up carrying at least just as many mutations as their parents because of the absence of recombination. Muller (1964) proposed this as one of the reasons why sexual reproduction may have been favored over asexual reproduction, as it allows for the purging of deleterious mutations through recombination, resulting in offspring with unique combinations of genes and traits.

Experimental evidence for this theory is mixed at best. Ridley (1993) describes how this theory requires unrealistic expectations about nature such as mutation rates to be higher than they really are and works too slowly when pitted against the rate of asexual reproduction. Even if there were ample evidence of the purging effect of sexual recombination on deleterious mutations, this alone only explains one effect of sexual reproduction and not the reason for why it evolved in the first place (Ridley 1993).

Pathogen Resistance

Perhaps the best theory for the evolution of sexual reproduction comes not from the preservation of good genes, the removal of bad genes, or the creation of variable offspring, but from parasites. Many researchers seemed to have confused a consequence of sex, variability, with its purpose. But as shown above, variability can mean many

things. The key question regarding the variability that sexual reproduction leads to is the following: what is the variability for?

Previous models of the evolution of sexuality posited a correlation between environmental uncertainty and sexuality (Maynard Smith 1971). However, when biologist Graham Bell assessed various species in nature and the relation between their sexuality and environmental harshness and uncertainty, he found the opposite of the expected pattern (Ridley 1993). Asexual species tended to live in the highly variable environments of freshwater compared to saltwater. They tended to live at high latitudes and high altitudes, where weather is more variable and harsher, and on disturbed ground.

It turns out that the kind of variability that sex leads to might be for the purpose of thwarting a variable and ever-changing foe, parasites. Maynard Smith (1971) showed that for an obligate sexual population to be favored over an asexual population, the environments would have to change radically every generation. Host-parasite coevolution might provide the radically changing environmental conditions that Maynard Smith (1971) speculates must be in place in order to sex to evolve.

Many are familiar with the idea of coevolutionary arms races between predators and prey and between hosts and parasites. Coevolution is a process in which two or more species affect each other's evolution through reciprocal evolutionary changes. The change in one species confers selective pressure on another species, causing the other species to evolve countermeasures that, in turn, confer selective pressures back on the other species, and so on. For example, in predator-prey interactions, a predator is selected to possess adaptations that help enable the catching, killing, and eating of its prey. However, the prey also possesses anti-predator adaptations, such as keen senses to detect a predator and running speed to escape from it. Better antipredator adaptations in the prey place selective pressures on the predator for better antiprey adaptations, and vice versa, resulting in a coevolutionary arms race.

This dynamic is also in place for host-parasite coevolution. Better immune systems protect a

host from infectious parasites, which places selective pressure on parasites to fool the host's immune system and be more effective and infectious. More parasitic parasites then, in turn, place selective pressure on the host's immune system, and so on, in a coevolutionary arms race.

This idea of coevolutionary arms races came to be known as the Red Queen hypothesis after Lewis Carroll's book *Through the Looking Glass*, where the Red Queen takes Alice on a run that never seems to go anywhere. It was first proposed in an evolutionary biological context in Van Valen (1973) as a hypothesis for why many species' probability of extinction does not depend on the lifetime of the population. Rather, many populations of organisms remain extant or go extinct by constantly adapting to changing environments including coevolving with other antagonistic species. In other words, the Red Queen hypothesis gets its name from the fact that organisms continually evolve to changing environments, which include other antagonistic species, but there is no progression. There is constant adaptation just to stay in place.

In the case of the evolution of sexual reproduction, the Red Queen hypothesis has been mathematically modeled to understand both how sex evolved and how it has been maintained considering its twofold cost (Hamilton 1980; Hamilton et al. 1990). Evidence from these models show that even with conditions similar to that of human evolution – namely, relatively low fecundity and long generational time spans – sexual reproduction is favored over asexual reproduction in the presence of parasites and hosts with resistance genes to the parasites. Asexual hosts with unfavorable genes were more often driven to extinction. However, sexual hosts with unfavorable genes at one time can store, reshuffle, and reuse these genes at another time when they are needed to thwart parasites (Hamilton et al. 1990). And so, evidence suggests that sexual reproduction via recombination leads to unique genetic arrangements in offspring each generation. This genetic reshuffling process of sexual production provides sufficient change to effectively thwart parasites that rapidly adapt to host genotypes each generation via their extreme fecundity and short

generational time spans (Hamilton 1980; Hamilton et al. 1990; Ridley 1993).

Conclusion

While sexual reproduction is extremely common in nature, its evolutionary explanation has eluded researchers for decades, going all the way back to Charles Darwin. Most explanations of sexual reproduction have drawn on one of the most striking differences between sexual reproduction and asexual reproduction, namely, that sexual reproduction creates genetic variability.

One variant of this hypothesis is that sexual recombination results in a unique rearrangement of genes in offspring, which provides the fuel for natural selection to act, allowing more variable populations to evolve more quickly. Other researchers refined this idea using mathematical models and formalisms (Fisher 1930; Muller 1932; Crow and Kimura 1965). Fisher (1930) argued that sexual reproduction allows for the incorporation of beneficial mutations, whereas mutations in asexual organisms would remain in a single line of common descent. Others reformulated this hypothesis in terms of benefits for individuals rather than populations, since greater variation can result in offspring with greater fitness (Williams 1966). Others explained that the benefits of sex come from the need for rapid adaptation to varying environments (Maynard Smith 1971). Another potential explanation for sexual reproduction is that it allows for the effective purging of bad mutations from the population (Muller 1964).

The parasite-resistance theory of sexual reproduction takes many elements from these previous theories but in the service of a different problem, namely, thwarting parasites. Indeed, evidence does support this theory, such as research in snails (Lively and Dybdahl 2000). However, even this theory may not tell the full story of how sexual reproduction evolved. It is conceivable and very likely that there is no single explanation for the evolution of sex, given that it has evolved numerous times throughout nature and is found in organisms as different from each other as single-celled protists and human beings.

Future research should continue to complement mathematical models of evolutionary dynamics with natural experiments to put the different theories and hypotheses of sexual reproduction against the evidence of nature.

Cross-References

- Gamete Size
- Intralocus Sexual Conflict
- Production of Eggs and Sperm
- Red Queen Hypothesis, The
- Reproduction
- Sexual Intercourse

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Sexual Response

- ▶ Orgasm
 - ▶ Sexual Arousal
-

Sexual Response Pattern

- ▶ Four-Stage Model of the Sexual Response
-

Sexual Reverie

- ▶ Sexual Fantasy
-

Sexual Selection

- ▶ Alfred Russel Wallace (1858)
 - ▶ Female Reproductive Variance
 - ▶ Genital Evolution
 - ▶ Good Genes
 - ▶ Intrasexual Selection
 - ▶ Observations of Sexual Dimorphism
 - ▶ Parental Investment as Mating Effort
 - ▶ Physical Attractiveness
 - ▶ Reproductive Variance
 - ▶ Reputation as a Context for Men's Aggression Against Men
 - ▶ Self-Assessment of Fighting Ability
 - ▶ Sex Differences
 - ▶ Sex Differences in Parenting and Parental Investment
 - ▶ Sexual Conflict in Nonhumans
-

Sexual Selection and Humor

- ▶ Humor as a Signal of Sexual Interest

Sexual Selection Hypothesis

► [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)

Sexual Selection Hypothesis of Infanticide

► [Infanticide in Nonhumans](#)

Sexual Selection in Evolutionary Psychology

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Synonyms

[Intersexual selection](#); [Mate preferences](#)

Definition

When the selective force in evolution is specifically the behaviors of potential mates and rivals, it is often distinguished as *sexual selection*, as contrasted with other selective forces. A key reason for doing this is because sexual selection can lead to many distinct results that reflect the contrast between sexual success (reproduction) and survival success. Survival is necessary for reproduction, but not sufficient by itself. Sexual selection helps to account for non-survival aspects of between-sex attractiveness between potential mates (e.g., ornaments, displays, and other courting features) and features related to within-sex competition (e.g.,

weapons, sexual dimorphism). The tension between survival and reproduction sometimes emerges in the form of “handicaps,” costly, survival-harming traits that an organism possesses in order to honestly signal to potential mates the ability to nevertheless thrive.

Introduction

Evolution by natural selection focuses on adaptations and the ways in which useful mutations have led, over the course of evolutionary history, to the survival of the fittest. Of course, in this case, “the fittest” does not necessarily mean an individual that is our cultural idea of “physically fit” but more an individual that knows how to survive and adapt best to their environment. When discussing evolution, the idea of fitness is more specifically based on the process in which mutations useful to individuals within their environment are passed down via their genetics until those without these mutations were no longer part of the population. For example, Darwin noted on the *Voyage of the Beagle*, in regard to the finch beaks on the Galapagos Islands, natural selection is the mechanism for evolutionary change and progress. Each island had a finch beak variant that was beneficial to that specific island’s ecosystem (i.e., food source). On the islands where seeds were a primary food source, the finches had large crushing bills – yet on the islands where insects were a primary food source, the finches had narrow probing bills to aid in the extraction of insects from trees. Another popular example of natural selection is that of peppered moths in Manchester England and the influence of the industrial revolution: Prior to the industrial revolution, the typical phenotype of these moths was white (with only about 1% of the population being black) because it helped them blend into the white lichen on the trees, increasing their camouflage and reducing likelihood of predation. During and after the industrial revolution, the trees became covered in black soot, and the black peppered moths (which previously had only made up 1% of the population) suddenly had the survival advantage. The fitness of the

phenotypic variations in the peppered moths changed due to a change in the environment, ultimately resulting in a change in allelic frequency due to natural selection. Importantly (included in both examples mentioned above), variation within a species must be present in order for natural selection to operate. Random mutations came about that gave individuals within a species a survival advantage, and over many generations this trait was continuously selected for due to its fitness.

Natural Selection Versus Sexual Selection

Natural selection is not the only selection that takes place in the process of evolution. In fact, it is sometimes the case that the presence of specific traits seems counterintuitive to an individual's fitness. Take peacocks, for example – the presence of their ornate elaborate trains was said to have kept Darwin up at night. From a strictly natural selection perspective, these traits made absolutely no sense: standing out to predators has the potential to be incredibly risky – yet, generation after generation we see individuals within various populations with traits that seem counterintuitive to their survival/fitness (Gray and Garcia 2013). Whereas natural selection is the evolution of characteristics that provide a survival advantage, sexual selection is the evolution of characteristics that provide a reproductive advantage (even if it sometimes means encroaching on a survival advantage). Simply put, both natural and sexual selection play important, but distinct roles as mechanisms of evolution. Some may argue that sexual selection is the more important mechanism of recent selection (within our species), simply due to the fact that it is (or was until evolutionarily recently) necessary for the flow of our genetics through the generations (e.g., Miller 2000). In an ultimate sense, survival is only important in light of reproduction. It is easy to comprehend the ways in which certain characteristics may provide a survival advantage – better vision leads to better resource acquisition, better grip strength leads to safety, while in a tree, camouflage leads to being

able to blend into the surrounding environment. Yet, when it comes to characteristics that provide a reproductive advantage, it becomes less clear.

Sexual selection is based on attraction to an individual in some way, shape, or form. Certain traits (like clear skin and facial symmetry) are cross culturally considered attractive due to their links to underlying health, fertility, and overall fitness (Gray and Garcia 2013). Sexual selection operates based on traits that members of the opposite sex find attractive, whereas natural selection is based on traits that help overcome some sort of adaptive problem. Attractiveness can take many forms – typically ascertained when looking at any battery of terms used to describe mate value. Sexual selection tends to focus most on physical, facial, body, vocal, and even behavioral attractiveness (Bressler et al. 2006; Frederick and Haselton 2007; Gallup and Frederick 2010; Greengross and Miller 2008, 2011; Miller 2000; Singh 1993; Hughes et al. 2004). Although there are nonphysical factors that are related to assessments of attractiveness (e.g., financial status), physical and behavioral traits are most directly related to the inner workings of an individual and can possibly be a cue to the health and well-being of that person. This is especially important for reproductive purposes.

The Science of Sex Appeal and Human Sexual Selection

Dawkins (1976) presented an evolutionary argument that each and every member of all living species on the planet exists to pass on its genetic material to subsequent generations (the gene-centered view of evolution). Furthering this theory, we must assume that we do not want to pass on our genetics to offspring who will not survive, and thus we get to the *why* of sexual selection. Species do not have meetings wherein all the members of one sex get together and decide only to mate with those who possess a certain trait – these traits are adaptive in nature and not consciously decided upon. The science of sex appeal, across all species, comes down to a single fact about attractiveness: what one sex finds attractive in the opposite sex is linked in some way to

underlying health and fertility. Sexual selection is therefore based on selecting mates of high fitness – healthy and fertile individuals who will be good partners for making offspring who will ultimately serve as a way to pass along our own genes. These offspring will be healthier and more likely to live to the age of reproduction themselves, which increases an individual's overall reproductive success. Examples of attractive features being linked to underlying health and fertility can be found in various forms (Gallup and Frederick 2010). In humans, some traits found attractive in women (by heterosexual males) include a relatively low waist-to-hip ratio (WHR) which, when closest to 0.7, is universally found to be the most attractive body shape across a wide range of body sizes and weights (Singh 1993; Gallup and Frederick 2010; Gray and Garcia 2013). This 0.7 ratio has also been linked to higher fertility; thus, the feature is physically attractive due to a fundamental relationship to fertility.

Another example (Gallup and Frederick 2010) is gluteofemoral fat – a type of fat located around the thighs and buttocks of a woman, which is thought to provide brain-building resources, for both a mother and potential offspring. Sir Mix-a-Lot, an early 1990s hip-hop artist, described his love of big butts in a surprisingly catchy, enduring pop song entitled *Baby Got Back*. Sir Mix-a-Lot, a rapper who wrote his one-hit wonder and released it in 1992, was almost certainly not thinking about the fertility or fecundity related to the “back” that he sang about, yet his lyrics demonstrate a desire for features known for fertility and fitness. “Oh’rumpo smooth skin” may sound like Rumpelstiltskin or a way to describe the derrière of a woman using a word other than “butt” or “back,” but it gets at another physical aspect related to health – smoother skin often suggests less mutations and healthier genetics. Though a bit tangential, fascinatingly, *Baby Got Back* also depicts other aspects of mating – including mate poaching, wherein a committed individual is “stolen” by a new mate. “Some brothers want to play that hard role/And tell you that the butt ain’t go! / So they toss it and leave it/And I pull up quick to retrieve it” – Sir Mix-a-Lot essentially described a mate poaching scenario.

Female bodies are clearly also not the only traits which matter in terms of sexual selection. For male bodies, shoulder-to-hip ratio (SHR) is an aspect of body configuration related to mating. Broad shoulders and narrow hips (high SHRs) are – in some ways – the male correspondent to female large hips and small waists. A student once described the physique as “the Dorito body,” though “Superman Torso” seems more easily accessible as slang for the body configuration. Shoulder-to-hip ratios also are thought to be an indicator of fitness, with broad shoulders and narrow hips in males being linked to higher levels of testosterone (Gangestad and Scheyd 2005; Gray and Garcia 2013; Hughes and Gallup 2003). In fact, Hughes et al. (2004) found that ratings of vocal attractiveness were highly correlated with optimal indices of WHR and SHR and proposed that this link is due to sex hormones shaping these sexually dimorphic configurations (like estrogen and testosterone). From a costly signaling perspective, high levels of testosterone can be harmful to an individual's body because it weakens the immune system, so if an individual is displaying signs of relatively high testosterone, this may be deemed as “attractive” simply because of the cost vs. benefit ratio. Males with higher SHRs tend to be stronger and more aggressive, thus more likely to win in intrasexual competition for mates. Additionally, high SHR males have been found to have sex earlier and have a higher number of overall sex partners throughout their lifetime than males with lower SHRs. Frederick and Haselton (2007) proposed that females have an evolved attraction to muscles and overall physical prowess in men – muscularity requires extensive calories and testosterone to maintain. This links back to a “handicapping” theory that a sexually selected trait can actually be detrimental to survival (testosterone compromises immune function, and increased muscle mass demands a lot of energy). However, overcoming these costs may also serve as a signal of better health and overall fitness quality, demonstrating that an individual is nevertheless able to successfully maintain their fitness as well as their overall health.

Aside from body shape, research has found that we have an (evolved) preference for attractive

faces. How individuals rate attractiveness in faces is largely independent of many variables that tend to mediate preference (e.g., gender, culture, sexual orientation, age). In fact, there is a considerable degree of cross-cultural consensus regarding facial attributes that are considered attractive (Gallup and Frederick 2010; Thornhill and Gangestad 1999). Importantly, research has found that there are links between facial attractiveness and health, intelligence, and fertility. In other words, facial attractiveness seems to be an honest phenotypic indicator of genetic quality. Henderson and Anglin (2003) sampled old high school yearbook photos, matched them with obituary records, and had college students rate the photos for attractiveness. Both men and women that were rated as attractive lived longer on average. Longevity is an indicator of health, and importantly, the transmission of the genes that code for longevity is highly heritable.

In addition to longevity, there have been positive correlations between intelligence and fertility as well. Using an archived sample of 425 Army veterans, Arden et al. (2009) found a significant positive correlation between semen quality and general intelligence. Again, due to the idea that various forms of intelligence can be highly heritable, it is adaptive to select a mate who will pass on these genes to future generations. Furthermore, there have been many findings indicating that there is a link between ratings of facial attractiveness and fertility in both males and females. Soler et al. (2003) took photos of participants' faces and collected semen samples from college students. The males that were rated as more attractive had a higher sperm count, motility, and morphology (the composite index of sperm quality) when compared to males that were rated as less attractive. Just as optimal shoulder-to-hip and waist-to-hip ratios were linked to fertility (as well as testosterone levels in males), attractiveness ratings of female faces were positively related to estrogen levels and reproductive health (Law-Smith et al. 2006).

Females are particularly interesting when it comes to the link between ratings of attraction and genetic quality because *concealed ovulation* is a factor as well. Though our closest primate

ancestors all have varying degrees of sexual swellings to notify potential mates that they are sexually receptive, human's cues to ovulation are much more subtle. It was historically thought that human females show no outward signs that they are in their fertile phase of their ovulatory cycle, but in actuality there are many physiological and behavioral cues that fluctuate slightly depending on where a female is in her cycle. Behaviorally, during peak fertility days, women were more likely to agree to dance with an attractive male confederate, show greater interest in going out to dance clubs and/or parties, and dress more provocatively (for a review on this research, see Haselton and Gildersleeve 2011). Physiologically, there are changes in body odor around ovulation, and males have rated these odors as smelling more pleasant than odors taken from other phases in the ovulatory cycle (known as the "stinky t-shirt studies" Thornhill et al. 2003). In a study on the effects of subtle ovulatory cues on males, Miller et al. (2007) found that lap dancers received substantially more in tips on high fertility days as compared to low fertility days. So, in a general sense, even though there is no *obvious* physiological display of fertility in humans, there are unseen, subtle cues that could influence mate selection.

Surprisingly, the use of specific types of humor can be an underlying indicator of genetic fitness and can also influence mate selection. Miller (2000) posits that the use of (appropriately timed) humor evolved as mental fitness indicator due to sexual selection via mate choice. Bressler et al. (2006) found that, although both sexes prefer someone with a "good sense of humor" as a potential mate, it means something slightly different to men and women. Women prefer mates who use humor, while men prefer mates who are receptive to their own humor – especially when it comes to intimate relationships. This suggests that sexual selection could have operated on men and women in different ways, resulting in a noticeable discrepancy in desire for various forms of humor in mates. Taking this a step further, Greengross and Miller (2008) attempted to get at the type of humor individuals use when interacting with potential mates. Evolved

mate preferences came to light when assessing a potential long-term mate with high status: in both males and females, individuals that used self-deprecating humor (i.e., “dissing oneself”) as opposed to other-deprecating humor (i.e., “dissing rivals”) were rated as more attractive. In summary, mate choice is influenced by a multitude of factors behind the scenes, but all of these factors have been subtly shaped by sexual selection.

Intrasexual Competition

What happens when two individuals are interested in the same potential mate? What if that potential mate is not interested in either of those individuals? Sexual selection occurs through two forms of competition: intra- and intersexual competition. *Intrasexual competition* is used to discuss competition within members of the same sex for access to the other sex. This can be either female competition with other females or male competition with other males. Whatever traits aid in successful competition among members of the same sex (such as size, strength, social charisma, etc.) will be selected for, and thus those who possess those traits gain a reproductive advantage due to an increase in access to the more desirable and/or a larger pool of receptive mates. Classic examples of intrasexual competition include the selection for large deer antlers (for males) used for fighting and to display dominance within herds of deer. Similarly, within humans, intrasexual competition typically plays out in terms of competition within males. We see this regularly in organized sports and the large industry that exists for boxing and MMA (mixed martial arts) fighting. In females, we also see indices of competition, but it is typically broken down into four distinct forms: self-promotion (displays of physical attractiveness), competitor derogation (making rival seems less attractive with rumors, etc.), competitor manipulation (downplay potential mate’s worth to rivals), and mate manipulation (remove potential mate’s attention from rivals) (Fisher and Cox 2010). Classically, it was thought that intrasexual competition existed solely in males due to the

differential investment in gamete production and parental investment. Consider the difference: females typically release one egg per month; males produce millions of sperm each day. Once sexual intercourse is over and a female conceives, the next 10 months of her life (but not necessarily the father’s life) is increasingly consumed by the growing demands of the fetus. This drastic difference in energy expenditure and parental investment is thought to drive males to be more intrasexually competitive due to the fact that females are the “choosier sex” (Trivers 1972).

Intersexual competition, on the other hand, is competition among members of the same species but *between* the sexes – in other words, one sex may exhibit preference for a particular trait, which gives members of the other sex who possess those traits a reproductive advantage (Buss 1995). Often, when a trait is selected for by one sex, we refer to the selection as *epigamic*.

Maladaptive-Seeming Traits that Are Adaptive for Sexual Selection

Sexual selection has seemed to be the answer for many adaptations that do not necessarily make sense for survival purposes. For example, why would male deer have tall antlers that could become stuck in trees and bushes? How is that possibly adaptive? At first glance, large antlers seem like a mistake; they may hinder survival by making these deer easier prey for predators. We understand now, though, that deer use their antlers for intrasexual competition for mates. Darwin noticed these traits that seemed to be counterintuitive to natural selection’s influence in evolution – upon pondering this anomaly in natural selection, he noted that there must be a reason for these hindering traits that species seemed to display. An overly simple analogy for this could be if a person had never before encountered a door. Now, this person would probably easily figure out that the door was an entry way into a domicile. They could understand it remaining closed, to keep out others. Imagine this person then attempts to open the door, only to find it locked. Assuming this

person does not assume that the locked door is simply another wall of the domicile and they realize that it can be locked and unlocked (perhaps after observing people going in and out), common sense would likely lead to the notion that the door may be closed off entirely (locked) in order to keep out those who are unwanted. This analogy is similar to the problems faced by scientists and naturalists when attempting to understand a trait that appears maladaptive. There is a thing, the door, but it locks and is often closed, therefore defeating its purpose of allowing people in and out of a structure. However, realizing it can be unlocked for friends and locked for foe suddenly makes the locking a reasonable and understandable aspect to the door. From this, we can begin to understand sexual selection – it is the caveat for natural selection’s adaptive traits. A trait may seem maladaptive at first glance, but is often adaptive according to the rules set forth by sexual selection, i.e., does this trait help with intrasexual or epigamic selection? If so, the trait can no longer be seen as maladaptive, as long as we uphold the notion that reproduction is the ultimate goal.

Sexual Selection in the Animal Kingdom

Sexual selection is more easily understood across the rest of the animal kingdom, rather than in humans, partly due to the fact that sexual dimorphism is often more easily observed in other species. *Sexual dimorphism* is a phenotypic trait difference between the male and the female of a species (driven by mating systems). Often when discussing sexual selection (or sexual dimorphism for that matter), the most salient example is the peafowl. Peafowl have a great degree of sexual dimorphism; the peahen is rather plain, while the peacock has a plumage of tail feathers that he spreads to show off when seeking a mate. This example gives insight to several aspects of sexual selection; first, we see the peacock tail as an example of a phenotypic trait which has been selected for due to the preference for said trait in peahens, which demonstrates intersexual selection. Second, the selected phenotypic trait may

be advantageous for accessing mates while also serving as somewhat of a hindrance to natural selection (how much easier must it be for a peacock to be caught by a predator, dragging his tail behind him, compared against the catchability of a peahen). Continuing with the peafowl example, we can examine epigamic selection’s outcomes – in other words, how does mate choice take place when sexual selection has occurred through intersexual competition? Peafowl (as with numerous species) begin their mating with a display in a lek. A lek is a place where animals that use mating displays come to show off their “goods” and to choose mates. Peacocks display their extraordinary tails, opening the feathers up like a paper fan, while peahens observe the peacocks and choose mates based on the quality of the peacock tail. Showing off a phenotypic trait is not the only way mating displays can be done – bowerbirds (small dark birds indigenous to New Guinea and Australia) show their mate value in a different way. Rather than parade a specific physical feature, they build nests at the lek, lining the little hut-like shelters with shiny, colorful objects. Female bowerbirds descend upon the lek and try out the nests, often visiting the same male’s creation numerous times before making a mating decision. The males exhibit their shiny and colorful objects for the females to view. This form of sexual selection brings us to *why* certain traits are selected.

One of the most interesting aspects of sexual selection in terms of traits that seem maladaptive is the *handicap hypothesis* (Zahavi 1975). The handicap hypothesis has many definitions, depending on the usage. First, the handicap hypothesis was said to stem from costly signaling – it has been discussed that signaling is a way for many species to begin the mate selection process. The more costly a trait is (e.g., a peacock’s large and luminous tail must make it terribly hard to escape from predators), the more “honest” and reliable it is, therefore making it more attractive. The cost-benefit analysis here shows the costliness of the trait and the likelihood of being noticed as a beneficial aspect. In the case of the peacock, the ornate nature of its tail is thought to correlate with the amount of point mutations that the peacock has – signaling genetic quality to potential mates. In

sum, the handicap hypothesis essentially demonstrates exactly the problem that sexual selection answers for natural selection – why do ostensibly maladaptive traits continue to be passed down to subsequent generations?

Costly Signaling in Humans

When it comes to costly displays in humans, it gets more complicated. Though plastic surgery and cosmetics could arguably be considered costly signaling, they are also both used as dishonest signals that are supposed to conceal the link between our genotype, phenotype, and environment. Instead, we turn to the idea that forms of body modification (including scarification) are used as a way to physically display our genetic fitness. Historically, scarring, tattooing, and piercing the body had ritualistic tribal origins and signified the passage into adulthood or other important life events. From a costly signaling perspective, if individuals (especially in pre-industrialized societies) open up their body to infection and various blood-borne diseases, it is extremely risky. Specifically, if bacterial infections are not addressed properly, it can lead to soft tissue infections, sepsis, and toxic shock syndrome – all of which are potentially life-threatening (Koenig and Carnes 1999). If an individual is able to heal properly, it means that their immune systems are healthy and viable enough to fight off foreign pathogens. It is hypothesized that in industrialized societies, due to access to modern medicine/healthcare, the costly displays in which body ornamentation takes place have increased noticeably in order to stand out to potential mates (known as the “upping the ante hypothesis,” Carmen et al. 2012). Additionally, body ornamentation could be potentially viewed as an extended phenotype due to the extension of our genes via behavior to stand out to potential mates as an indicator of fitness (known as the “human canvas hypothesis,” Carmen et al. 2012). From an ultimate, evolutionary perspective, sexual selection selects for behaviors that will increase the likelihood of finding a mate and producing offspring, resulting in the flow of genetic material

through the generations. Sexual selection has encouraged costly signaling.

How Humans Have Shaped Selection: Selective Breeding of Dogs and Cats

As humans, we have taken our understanding of evolution to another level and begun selectively breeding different species to get results which we consider favorable outcomes. A popular example would be the domestication of dogs and cats, ultimately resulting in an impressive array of phenotypic variations. A pug, a German shepherd, and a Great Pyrenees all share the common ancestor of the wolf, yet they are physically and behaviorally all very different. Interestingly enough, an experiment that began in the 1950s (and is still going today) in the Soviet Union/Russia led way to some interesting and informative findings regarding the relationships between genotypic, phenotypic, and behavioral traits. In 1959, Dmitri Belyaev and a team of researchers began selectively breeding red foxes for the retention of juvenile traits (tamelessness) throughout adulthood. By selecting for a behavioral trait, the researchers were essentially manipulating the natural and sexual selection of these foxes. Along with the selection of the behavioral trait came interesting phenotypic changes like spots in their coat color due to decreased adrenaline and floppy ears (Trut 1999). By attempting to isolate a specific feature of a species (in this case the behavioral trait of “tamelessness”), other traits essentially came along for the ride and began to typify that population.

Before humans began manipulating what was once a purely evolutionary outcome, sexual selection was perhaps the sole reason that specific traits which appeared to be detrimental to survival emerged in any given species. Since the human psyche is considerably complex, it should be no surprise that the ways in which we are attracted to one another is mediated by a multitude of variables, including sexual selection. Though humans have tried desperately to draw a thick line between us and the rest of the animal world, we actually share far more in common with the rest of the animal kingdom than we like to admit.

Conclusion

Sexual selection provides us with a way to understand what was once a seemingly puzzling phenomenon: the presence of traits that could apparently impede survival in one way or another. Natural selection was easily understood in terms of the effect of the environment on an individual's traits and attributes, but this limited our understanding of the power that *sexual* selection can have on the very same traits and attributes. Our preferences for specific traits in potential mates have been shaped in countless ways by sexual selection and will continue to evolve along with us.

Cross-References

- [Body Attractiveness](#)
- [Body Modification](#)
- [Cosmetics](#)
- [Facial Attractiveness](#)
- [Human Copulation](#)
- [Human Courting](#)
- [Human Ornamentation](#)
- [Humor Production](#)
- [Ovulatory Hormones](#)
- [Ovulatory Shifts in Psychology](#)
- [Physical Attractiveness](#)
- [Risk of Conception](#)
- [Scarification](#)
- [Vocal Attractiveness](#)

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Sexual Selection via Direct Male-Male Interactions

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Synonyms

Contests of aggressiveness; Male battles; Sperm competition

Definition

Direct competition between members of one sex (usually males), through contests of threats, battles, or sperm, to obtain reproduction with the other sex.

Introduction

There are traits in animals that are not related to ecological adaptation. These other adaptations are the outcome of sexual selection: intraspecific competition, usually between males for access to females and their gametes. Such competition takes

the form of displays to attract females, ritualized threats to dissuade competitors, or actual physical fights. Darwin (1859) recognized these processes as being different from natural selection; in his own words: “Sexual Selection...depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring.” The evolutionary consequences of failing to obtain a mate are severe; they are equivalent to those of not having survived to adulthood: such individuals do not pass any of their genes to the next generation.

Darwin (1871) noted that competition for females takes two general forms: direct, male-male battles that involve either threats or actual fights and female choice, in which males attempt to induce females to accept them as mates. One common but unfortunate terminology distinguishes these as *intrasexual* and *intersexual* selection. Sexual selection, however, is *always* intrasexual; that is, individuals of one sex (usually males) compete with each other for access to individuals of the other sex (see West-Eberhard 1979, 1983). Regardless of the specific type of interaction, it is always true that individuals of one sex compete with each other; this intrasexual aspect gives sexual selection its particular characteristics in relation to natural selection, (see section “[Special Characteristics of Sexual Selection Versus Natural Selection](#)”).

Further, such terminology gives the idea that sexual selection processes are discrete and non-interacting. Separating the different types of sexual selection is not always feasible. Take, for example, the common cases in which males have battled not over females but over mating sites; when losing males are able to mate at least occasionally at other uncontested sites, then a female which mates at a contested site is exercising indirect choice in favor of fighting ability (Wiley and Poston 1996). Still another difficulty in classifying a situation occurs when alternative mating tactics are in play, so that some males gain access to females through combat or forceful copulations and others through courtship (Oliveira et al. 2008), or when a male succeeds in being accepted by a female, but his copulation is

prevented by another, dominant or “astute” male (see Thompson and Wrangham 2008; Painting and Holwell 2014). Another type of behavior that does not fit this terminology occurs when some males take advantage of the courtship of other males and gain acceptance by the courted females; an example would be the small male fish (“streakers”) that dump their sperm onto eggs that a larger male has induced the female to release into the water column to be fertilized (Oliveira et al. 2008).

As detailed below, the different types of sexual selection (i.e., contests of attractiveness, of threats, and of physical battles) can interact in complex ways. Analyzing the interaction between types of sexual selection on the evolution of sexually selected traits may provide important evolutionary insights for understanding details of this process (see the section on “[An Example of Conflict Between Types of Sexual Selection: The “Beautiful Weapons” of Fiddler Crabs](#)”).

This brief review begins by advocating that sexual selection be included in the broader evolutionary framework of social competition to highlight its peculiarities in relation to natural selection. The interactions between natural and sexual selection and their consequences for the evolution of traits under different types of sexual selection are discussed, with a focus on the exaggeration of sexual traits used in direct male-male battles and threats. Also, the ubiquitous existence of alternative tactics and rituals in male-male battles and threats is mentioned. Later, the different stages at which these male-male interactions occur (precopulatory, copulatory, and post-copulatory) are examined. Finally, the interaction between several types of sexual selection for shaping individual traits is analyzed using a specific case.

Before beginning, it is important to clear up possible problems for understanding direct male-male competition and confusions in terminology. Natural selection (differential survivorship that leads to differential reproduction) and sexual selection (differential reproduction) act most powerfully at the level of the individual, rather than at the level of the species. Therefore, it is not appropriate to consider traits observed in a species as

having evolved to “adapt the species” or “for the good of the species.” For example, it is inappropriate to perceive a mating strategy as being a strategy to favor the species; instead it is the outcome of evolutionary processes that favored in the past particular individual strategies under particular ecological scenarios. Polygamy, for instance, is not a strategy for achieving reproductive success for the species, but is instead the outcome of selective pressures acting on individuals.

Secondly, there are several possible payoffs to females for accepting some males but not others as mates. In some cases, the female gains access to resources controlled by the male (e.g., good oviposition sites); these are called “direct” benefits. In other cases, the female gains superior genes from the male for her offspring (“indirect” benefits, because the payoff is in the following rather than the current generation). There are two types of superiority. Some genes are associated with superior male survivorship traits (foraging ability, disease resistance, etc.), and in these cases there is selection on males to send courtship signals that correlate with these superior male qualities (the signals involve “indicator” traits) and on females to respond to such indicator stimuli. Another type of superiority in male genes concerns the male’s ability to elicit greater acceptance by females; the female gains by having sons that are better able to gain access to females in the next generation (“sexy sons”). In this case, there is no necessary correlation between the courtship signal and the male’s survivorship capabilities, so the signals are sometimes called “arbitrary” signals that pay off in producing sexy sons. Unfortunately, the terms “male quality” and “good genes” have often been used imprecisely, without clearly specifying which of these two contexts is in play. One final type of payoff for rejecting males is when the female avoids possible harm from the male that can compromise her own future survival or reproduction (e.g., avoiding a male who would induce her to produce his offspring at a suboptimal time for her); this has been called “chase away” selection (Holland and Rice 1998) and can lead to sexually antagonistic coevolution between the sexes (“SAC”).

Special Characteristics of Sexual Selection Versus Natural Selection

Darwin (1871) was the first to note the differences between sexual selection and natural selection. The contrasts between these justify including sexual selection under the wider evolutionary framework of *social competition*, which includes intraspecific competition for other resources besides mates (such as competition for social status, food, or parental care) (West-Eberhard 1979). Visualizing sexual selection as a specific case of social competition, in which members of one sex compete for members of the other sex as a critical resource in reproduction, provides an evolutionary framework for understanding several aspects of evolutionary importance (West-Eberhard 1983).

Sexual selection is relentless. Natural selection on some traits is intermittent according to variations in ecological conditions (e.g., resistance to cold, coping with food scarcity, or dealing with parasites) (West-Eberhard 1983); in contrast, the competition for mates nearly always occurs in every generation without fail. In addition, the payoffs for winning this competition can be huge in some contexts, such as social groups in which only one or a few individuals get most or all of the matings, while many individuals get few or none (West-Eberhard 1979). Another crucial aspect of sexual selection (and of social selection in general) is that success is always determined by comparisons. The ability of an individual to obtain fertilizations does not depend solely on his *absolute* capabilities, but most importantly on their *relation to* those of his competitors. Because the traits of a male's rivals change over evolutionary time, this relative nature of sexual selection tends to result in sustained evolution. A trait that is advantageous at one point in time (e.g., a novel design of a weapon or a signal) may currently yield a huge reproductive advantage because few other individuals have this trait. But in the future, when other males also have this trait, it may confer no advantage at all, and further innovations will be necessary to win out in the competition for females.

Because of this relative aspect of the process, the problems that sexual selection presents an

animal have no solution. Since the competitive environment changes with each improvement or modification made on a sexually selected trait, the race among rivals can be unending (West-Eberhard 1983). One form of this endless race is the “runaway process” in female choice, first identified by Ronald Fisher in his “Genetical Theory of Natural Selection,” in which male courtship traits and female preferences for these continually change (see Andersson 1994). This dynamic interaction contrasts strikingly with many ecological problems under natural selection, for which an adaptation can theoretically reach an optimum form and then undergo relatively little additional change.

In consequence, it is common for sexually selected traits to diverge more rapidly than naturally selected traits (West-Eberhard 1979, 1983). Furthermore, the sustained race between competitors can be at least partially decoupled from ecology, because the focus for sexual selection is the ability to obtain fertilizations over rivals, even if these come at certain expense for survivorship (see section “[Conflict Between Natural Selection and Different Types of Sexual Selection](#)” below).

Alternative Tactics

Even when certain sexually selected traits are superior to others (i.e., they tend to produce more offspring), it is common for some males of a species to have alternative traits that function to gain access to females using different tactics (e.g., by “sneaking” rather than battling for females). Alternative traits are especially frequent in male-male threats and battles (Blum and Blum 1979; Andersson 1994; Oliveira et al. 2008). The prevalence of such lower payoff tactics might seem difficult to explain, considering the frequently high intensity of sexual selection. Nevertheless, there are several reasons for actually expecting alternative tactics to be common.

The advantage of an alternative tactic can be appreciated by thinking about direct male-male competition from the point of view of a disadvantaged male (e.g., a small male who is unable to win physical fights with most of the other males in

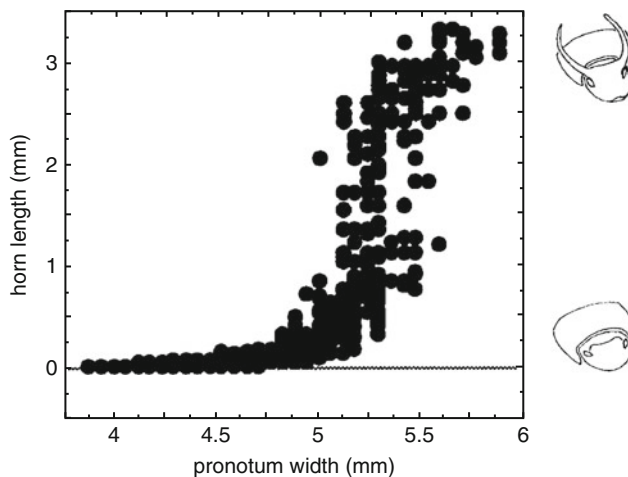
the population). If such an individual is unable to obtain mates through the “main strategy” (such as defending a territory from other males), any other alternative, even one with relatively small pay-offs, is better than nothing. For example, in species in which the main strategy for males is to defend territories where females arrive to reproduce, individuals unable to win physical fights often sneak into the territories of dominant males to gain access to females there (sometimes disguising themselves morphologically or behaviorally as females or juveniles), or linger surreptitiously (like a “satellite”) at the edge to intercept the females as they arrive (Eberhard 1983; Oliveira et al. 2008). Occasionally, such alternative strategies yield matings.

In some species the alternative tactics by males simply represent different extremes along a continuous range of variation. Perhaps the easiest examples to document and understand occur in vertebrates in which the males, as they grow, gradually shift from one tactic to another (e.g., readiness to engage in physical fights) (Andersson 1994; Emlen 2014). Other alternatives are more discrete: some males utilize the main strategy, while others utilize an alternative

tactic throughout their lives. These “alternative reproductive tactics” or “ARTs” were reviewed recently by Oliveira et al. (2008) who distinguished “bourgeois” from alternative, “satellite” or “sneaker” male tactics. In species with morphological weapons, such a dichotomy is sometimes clearly marked between bourgeois males with large horns and satellite males without horns, with few if any males having intermediate-sized horns (Simmons et al. 1999; Emlen 2014) (Fig. 1).

Flexibility Versus Rigidity: Conditional Strategies Versus Evolutionarily Stable Strategies

The mechanisms by which two discrete male tactics are maintained in the same species have been the subject of much theoretical and empirical work (Oliveira et al. 2008). Two mechanisms that could explain how discrete alternative male tactics are maintained in the same population are the following. The two different male phenotypes could be the products of two different genotypes, and the selective advantages of the two alternative tactics could be balanced in such a way (i.e., frequency-dependent selection in which the rarest form is in advantage over the more common form)



Sexual Selection via Direct Male-Male Interactions,

Fig. 1 Distribution of horn length in relation to pronotum width in *Onthophagus taurus*, indicating a nonlinear relationship between these variables. Even though there is a continuous distribution on body size (pronotum width), there is a discontinuous distribution of horn length,

indicating a clear morphological dimorphism for this species. Horned morphs employ the main strategy (defending resources that attract females) and hornless morphs the alternative one (sneak copulations). Note that there are no small males with long horns and no large males with small horns (After Simmons et al. (1999), with permission)

that both sets of genes are maintained in the population. This possibility has been discussed in the large theoretical literature on evolutionarily stable strategies (“ESS theory”). A second possibility is that all males carry the genes for both phenotypes, but that any given male facultatively expresses one set or the other, depending on his particular circumstances (e.g., if he is large due to good larval nutrition as an immature, he expresses the fighting morph genes and represses the satellite morph genes). While the discussion continues to rage, the general consensus is that most alternative male mating strategies arise from facultative expression.

Perhaps the most obvious reason that phenotypic flexibility will generally be favored over ESS is that the ecological conditions that an individual experiences are often relatively unpredictable (for instance, being born in a lean vs. rich year or a rich or poor habitat). The social condition in which an individual is born can also be extremely variable (e.g., being the single male in a group vs. living in a group with several males). Any individual that is flexible and is able to adapt his phenotype to better suit the conditions he is called upon to deal with (e.g., having the ability to express the horned morph genes rather than the hornless morph genes when he is large) is likely to have an advantage over less flexible individuals who are condemned by their genes to utilize only one of the two options (see West-Eberhard 1979).

Consider, for example, a case where males fight for territories containing resources attractive to females. A fixed strategy of always fighting against challenging males would not be convenient for males that are small due to poor nutrition when they were young or for males that are challenged by more powerful opponents. Similarly, a fixed alternative strategy in which the male avoids interactions with other males and attempts to copulate only with females at the peripheries of territories would be disadvantageous if such a male is a good fighter because he is large and well nourished or when he encounters a territory with a relatively weak owner.

A second general line of evidence concerns the ESS supposition of equal reproductive success for

both types of male in the long run. The fact that large males choose to grow large weapons and adopt the main strategy rather than the alternative, weaponless strategy is evidence that the armed morph has greater reproductive success than the hornless morph. In essence, large males can choose either strategy, but consistently choose the main one, indicating that such strategy is likely to produce more offspring. Small males have no choice (they cannot be successful fighting males) and must make the best of a bad lot (e.g., Eberhard 1983).

One further general line of evidence suggesting that phenotypic flexibility is most common concerns the clear association in many (most) groups between larger male size and bourgeois male morphology and behavior (for instance, the tendency for large males to bear horns) (Oliveira et al. 2008). Because there is a strong correlation between an individual’s nutrition as it grows (strongly influenced by environmental factors such as season, year, habitat, etc.) and its final, adult size in many (most) species, one would expect that some individuals in a population would be large because of such nongenetic, environmentally determined factors. If there are separate genotypes for the bourgeois and alternate morphs, then some individuals with the satellite genotype will have, by chance, fed well as juveniles, and some with the bourgeois genotype will have fed poorly. The expectation is thus that there would be some large individuals in the population with no horns and some small individuals with horns. This expectation is not met (see Fig. 1) (also Eberhard and Gutiérrez 1991). Size and morph identity are tightly linked, something not expected under the ESS model.

Female Acceptance

There are several reasons to expect that females will not necessarily reject satellite males as mates (see Qvarnström and Forsgren 1998). First, even for females that are selecting males based on “good survivorship” genes, a male’s fighting ability is not necessarily reflective of his gene quality in this sense, as it will often be due to the particular environmental conditions he has experienced earlier in life (Simmons et al. 1999; Oliveira

et al. 2008; Emlen 2014). Second, for the reasons just given, a female can gain by having offspring that are flexible, and a male's flexibility can be signaled by his having of an alternative phenotype. Lastly, even when male phenotypes stem from genetic differences, it would be unlikely for alternate males to have inferior genes in relation to both survivorship (ecological adaptation) and reproduction (sexual selection), which is necessary to imply overall genetic inferiority that is not convenient for the female. Alternative strategies do not necessarily imply poor "survivorship genes," and main strategies are not always synonymous with good "survivorship genes."

Ubiquity of Alternative Strategies

The existence of trade-offs as a general rule in nature seems to always leave the door open for alternative strategies. For example, it is impossible for alpha male mandrills (*Mandrillus sphinx*) to have ever increasing numbers of females in their groups (thereby augmenting their matings), without paying the price of not being able to consort all fertile females at the same time. This leaves opportunities for other males to reproduce with at least some of them through alternate tactics such as behaving subordinately and mating in places that are not visible to alpha males (Setchell et al. 2005; Oliveira et al. 2008). Another trade-off concerns traits that provide advantages in postcopulatory interactions (e.g., large testes to transfer large ejaculates – see below) as opposed to traits that confer advantages in precopulatory interactions (e.g., Simmons et al. 1999; Simmons 2001).

As an example of trade-offs, consider male horned beetles of the genus *Onthophagus*; some males have large horns that they use to battle rivals by prying and blocking them. Fights take place at tunnel entrances that females dig under food resources (dung) with which they provision their offspring. Hornless males are nevertheless sometimes able to reproduce by digging tunnels that allow them to gain access to females deeper underground, in essence, by going around the horned males (Simmons et al. 1999). Large-horned males are less agile in maneuvering inside the tunnel and are inferior diggers because their

large horns get in the way. Small males that employ sneaking tactics invest more in traits associated with postcopulatory competition: they have larger testes and ejaculate more sperm than horned males (Simmons et al. 1999; Simmons 2001). The flexible nature of these alternatives has been documented by altering the amount of food provided to male larvae; well-fed larvae become large-horned adults, while poorly fed larvae become small, hornless adults (see Fig. 1). Other illustrations of alternative morph behavior occur in male giraffe and bottlebrush weevils. Larger males have longer rostrums which they use to defeat smaller males in fights that take place out in the open, where they then copulate with and guard females. However, very small males with shorter rostra are able to occasionally obtain copulations by sneaking close (often while the large male is distracted in a fight with a large rival) and hiding alongside or beneath the female (Eberhard 1983; Painting and Holwell 2014).

Because of the existence of trade-offs, the intense male-male competition that often leads to the exclusion of inferior males from females, and the variable, often unpredictable nature of ecological and social scenarios, alternative strategies are expected to be the norm in nature. This expectation is met, as alternative strategies in male contexts are common and taxonomically widespread (Andersson 1994; Oliveira et al. 2008). In ritualized threats and battles, the evolution of alternative strategies allows inferior fighters to salvage some reproduction in contexts where following the main strategy would have led to zero reproduction.

Why Male-Male Battles Are So Often Decided by Threats and "Honest" and "Dishonest" Signals

The use of threat displays to resolve battles can be advantageous to both the winner and the loser of an interaction. For the winner, avoiding a fight is probably generally cheaper in terms of energy expended and surely cheaper in terms of possible damage he might suffer. Giving up without a fight can also be selectively advantageous for the loser.

If an individual can correctly judge, on the basis of his rival's threat displays, that he could not win an actual fight, then ceding without fighting can save him time, energy, and possible physical injuries. It is striking that only very seldom does a winning male pursue his advantage and punish or attempt to kill a retreating rival. Presumably this is also because of likely costs and benefits: the low additional payoff if the loser is indeed leaving the vicinity, combined with the danger of being injured by a desperate rival trying to defend his life. Also, as will be detailed below, males can make mistakes when judging fighting abilities of their opponents, so sometimes it is not convenient for a winning male to risk a revaluation of his status if it was judged inaccurately by the losing male.

In contrast to courtship displays, evolution of threats to rival males are not expected to result in "arbitrary" signals like those in some female choice processes. This is because threat signals are thought to be periodically tested (possibly within an individual's lifetime and certainly on the evolutionary time scale) by actual combat as indicators of fighting ability (West-Eberhard 1979). A male will be favored if his threat displays are so convincing that he sometimes intimidates rivals who are superior fighters. But it is disadvantageous for a superior fighter to give up after being threatened by an inferior fighter: males are thus under selection to detect "dishonest" signals or bluffs by their rivals. In other words, a male's threat displays must be backed up by his ability to fight; a male cannot permanently afford to bluff concerning his physical ability to win fights, and overly ambitious bluffing males can be punished by losing costly fights. Aggressive displays are thus expected to give relatively, though not perfectly accurate ("honest") indications of each male's fighting abilities (or "resource holding potential" in the jargon). As will be described in the fiddler crab example (section "[An Example of Conflict Between Types of Sexual Selection: The 'Beautiful Weapons' of Fiddler Crabs](#)"), there is a certain amount of room for dishonesty, opening the door for intense selection on sensory and analytical capabilities.

These exchanges of information (truth and lies) are often accomplished during ritualized, gradually escalating threats that allow each individual to assess his opponent's fighting abilities. Usually the longest interchanges of threats, and the ones that escalate furthest, are those that occur between evenly matched, similarly sized individuals (Blum and Blum 1979; Andersson 1994; Emlen 2014). Contests between males that differ greatly in size, weapons, or endurance are usually settled rather quickly. The escalated nature of threats is likely a consequence of the males attempting to accurately judge their opponent's fighting abilities. For either male, an accurate judgment of an opponent's true fighting abilities (without incurring the costs of a full fight with a superior opponent) seems more likely when more information is available.

Accurate judgment of an opponent's fighting ability seems to be a major selective force in the evolution of weapon design. In several different evolutionary trajectories, weapons have evolved toward more complex or larger structures that reduced harm while allowing assessment of subtle differences in the fighting ability between opponents. In contrast, it appears that crude unimpressive weapons have a tendency to inflict more damage (Emlen 2008).

Exceptions to the advantages of ceding without a fight occur in situations in which a male has no alternative opportunity to reproduce. For instance, the wingless, heavily armed males of *Idarnes* fig gall wasps live in the internal cavity of a closed fig and fight with each other over the chance to mate with the females that emerge within the enclosed cavity. Females mate only once before they gnaw a tiny hole and leave the fig to search for another host to lay their eggs. In these wasps, males frequently fight to the death, using their giant mandibles and the powerful muscles in their oversized heads (Blum and Blum 1979). A given male lives and dies inside a single fig and cannot leave to find females elsewhere. Thus, for these males, there is no payoff from avoiding possible injuries or death by ceding to an opponent's threats; they have no other mating options. The numbers of deaths can be astronomical. William D. Hamilton (in Blum and Blum 1979) estimated that the number of

male wasps killed in battles in 1 year's crop of figs on a single large tree may be greater than all of the casualties of World War II. This mayhem contrasts with other species of fig wasps in the same trees in which the males have wings; they seldom engage in mortal combat and have the option of finding females elsewhere.

Conflict Between Natural Selection and Different Types of Sexual Selection

Although natural and sexual selection were recognized by Darwin as different processes, there exists the common misconception (in part due to the term "survival of the fittest") that those individuals that are better adapted to ecological conditions are also the ones that are better adapted for reproduction. Even though both natural and sexual selection refer to differential reproduction of individuals, it is important to bear in mind that the selective advantages that produce differences in reproduction can be different. Natural selection refers to higher reproduction due to higher ecological success (i.e., greater survival translates into more mating opportunities and greater ability to amass resources translates into production of more abundant or better endowed offspring). Sexual selection, on the other hand, argues that differential reproduction is due to differential success in fertilizing eggs (through contests of attractiveness, of threats, or of physical battles), even if this success comes at the expense of reduced survival. In sum, individuals that win in contests of attraction or direct combat are not necessarily the most adept at surviving. Also, individuals that are superior in many ecological aspects may achieve little or no reproduction if they are not superior in sexual contests.

The selective pressures that operate in natural versus sexual selection are different, so it is not unexpected that the two processes sometimes interfere with each other. Sexual selection theory posits that further exaggeration of sexually selected traits is often prevented by opposing natural selection (i.e., pressures for ecological adaptation) (Darwin 1871). Empirical, experimental tests for this aspect of the theory are surprisingly

scarce (see Andersson 1994; Kotiaho 2001). However, conflict between the processes is quite obvious in many cases. For example, predators and parasites are often strongly attracted to the sounds, pheromones, or visual signals produced by courting individuals (Andersson 1994). The large size of male lions, which makes them better fighters in competition for exclusive access to a band of females, makes them inferior hunters, and they depend on females to capture prey (which they then appropriate until they are satisfied). The same effect occurs in male courtship traits. Male swallows with longer tails attract more females, but longer tails have aerodynamic costs and make individuals less adept at catching profitable insect prey (see Andersson 1994; Kotiaho 2001). Similarly, the ornaments in the wings of predatory male damselflies (*Hetaerina americana*), which are used to threaten other males that invade their territories, render them more conspicuous to their prey and thus less adept at catching them (see Kotiaho 2001). In some groups, these costs are presumably large enough that males get rid of their sexually selected traits during the non-reproductive periods of the year. Cervids such as deer produce large, expensive heavy antlers that are shed after the reproductive season and regrown each year, presumably because of the higher costs associated with carrying them during the rest of the year (Emlen 2014).

The costly nature of some sexually selected traits makes it possible that they can be used as "indicator signals" to females, providing evidence that the male possesses superior survivorship genes because he is better able to pay these costs. It is also possible that rival males might use the costliness of the aggressive displays of a rival to judge his overall vigor. Many studies have shown that both courtship and threat displays are "costly" or energy demanding (e.g., see Andersson 1994; Kotiaho 2001). The consequence of this correlational link has been disputed, and Kotiaho (2001) argued that this does not imply that such activities have fitness costs (lowered survival and/or reproduction of the individual) because individuals may compensate somehow for this energy expenditure (e.g., by feeding more often). This may be true, but leaves

open the possibility for other ecological costs, such as the possibility that feeding per se involves risks from predators or from infections by disease-causing organisms. In any case, courtship and aggressive displays directed toward other males clearly require energy, and it is common for individuals in better body condition to engage in longer and more intense periods of display (see Andersson 1994).

Two additional types of cost are internal. One, which has received little attention until recently, results from possible competition over cell resources within the developing individual. For example, the production of elongated beetle horns during larval development is correlated with a reduced growth of nearby organs like the eyes and antennae (Emlen et al. 2005); stag beetles with larger mandibles have relatively smaller wings (Emlen 2014). This competition could be played out on two scales. At the level of an individual's development, depletion of resources in the vicinity of a growing organ may result in reduced growth of nearby organs. On the evolutionary time scale, the developmental program of a species needs to make adjustments of the distribution of the available resources in the most advantageous manner among different possible growth functions. This second evolutionary factor seems especially likely to be important, and indeed, some observations that have been cited to support the first (e.g., smaller wings in beetles with larger mandibles) have an alternative interpretation in this second context (larger males with larger mandibles may need to fly less between mating sites because they will less often be obliged to decamp after having failed to win a battle with another male).

A second "internal" cost is the general redirection of resources in the male from maintenance and survivorship functions to his sexually selected traits. Thus, for instance, it is common that relative investment in immune defenses against pathogens is reduced in males compared with females, especially during reproduction. For example, male baboons that maintain an alpha status within their group (and are thus able to constantly guard fertile females from rival males) have elevated concentrations of testosterone and stress

hormones that can suppress their immune system, in relation to beta males (Gesquiere et al. 2011). Similarly, in socially competitive environments, the more dominant and aggressive red morph of the Gouldian finch (*Erythrura gouldiae*) suffers from greater immunosuppression when compared to the more passive and submissive black morph (Pryke et al. 2007). A particularly dramatic case are the species of salmon fish which migrate from the ocean up to rivers and streams to spawn. The males undergo changes in the forms of their mouths which make them into weapons that are used in male-male battles, but make it impossible for the males to feed. In addition, the males' abilities to resist infections and repair incidental damage become reduced during the migration, and they often have numerous infections by the time they have reached the headwaters and are defending their spawning sites.

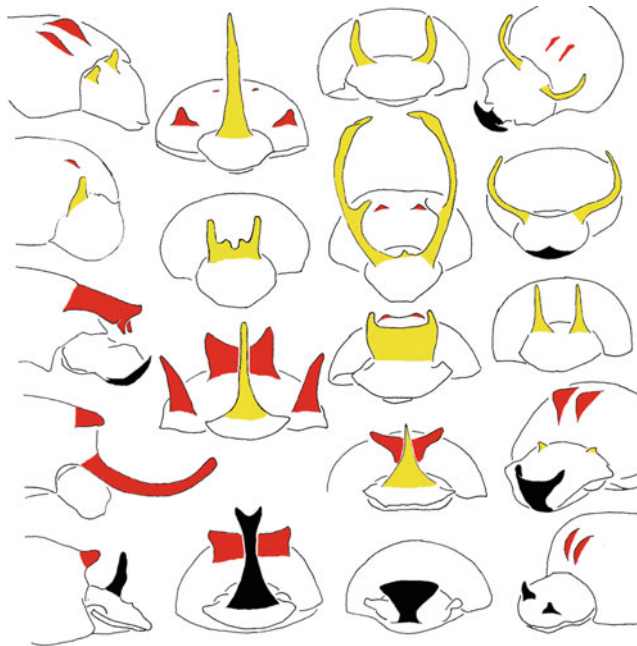
Finally, it is usually males who are exposed to greater ecological risks, simply because of their greater degree of movement while actively searching for females, who usually invest little in mate searching (Andersson 1994). A greater degree of movement results in higher mortality due to predation, as has been corroborated in studies that evaluate differential mortality between the sexes in a variety of organisms (see Andersson 1994). Another interesting possibility that has received little attention is that both searching and courting individuals may be more vulnerable to predation not only because they are more exposed to predators but because they are paying less attention to possible danger (see Dukas 2009). Reduced attentiveness may represent a danger for both sexes during courtship and copulation.

Exaggerated Traits and How to Measure Them

Male traits under sexual selection are often seemingly exorbitant or exaggerated (e.g., extravagant colors, elaborate songs, disproportionate morphologies, displays, etc.). Examples include both traits utilized to attract mates and to threaten and fight with rival males. For example, while female

beetles commonly lack traits that function for winning fights against conspecifics, male weaponry evolved several times in different beetle lineages, in the form of exaggerated mandibles, enlarged legs, or rigid horns (Fig. 2). Some weapons, such as beetle horns and earwig cerci, appear to be used only as weapons per se, without being previously displayed from a distance during threat behavior, but many other male armaments are also used in visual threat displays, as in deer and fiddler crabs, before being employed in physical battles (see Emlen 2014). However, some portions of weapons such as deer or insect horns allow “safe” interlocking that permits assessment of physical strength while reducing possible harm, and in these cases the distinction between threat displays and actual battle is blurred (Emlen 2008).

In morphology, the degree of exorbitance of structures that are involved in male agonistic interactions (say the length of a fiddler crab’s enlarged claw or of a beetle’s horn) can be expressed quantitatively, in terms of the relative size of such a structure when compared with the sizes of other body structures that are not under sexual selection and are indicators of overall body size (e.g., leg length, wing length, eye diameter, etc.). There is a very general trend for larger body size to be associated with disproportionately large weapons or threat devices, both in comparisons among individuals of the same species and in comparisons among different related species (Eberhard and Gutiérrez 1991). Stated in another way, the proportion of a male’s body that is dedicated to such sexually selected structures is



Sexual Selection via Direct Male-Male Interactions, Fig. 2 Horned beetles of the genus *Onthophagus* (Scarabaeidae), illustrating the diversity of form and location of horns (head and prothorax). Individuals shown are males unless otherwise specified (females with horns are presumed to use them to defend resources from other females). Top row: *O. xanthomerus* (female), *O. tersidorsis*, *O. gazella*, *O. xanthomerus*. Second row: *O. nuchicornis*, *O. sugillatus*, *O. rangifer*, *O. taurus*. Third row: *O. hecate*, *O. pentacanthus*, *O. capella*, *O. asperulus*.

Fourth row: *O. nigriventris*, *O. ferox*, *O. praecellens*. Bottom row: *O. sagittarius* (female), *O. haagi*, *O. sharpi*, *O. sagittarius*. The horns of *O. tersidorsis* and *O. rangifer* curve back over the dorsum, but are shown in an artificial vertical position to illustrate their form. The colors indicate different portions of the male where horns arise: black anterior portion of the head, yellow posterior portion of the head, red prothorax (Modified with permission from Emlen et al. (2005))

usually greater in larger individuals. A common way to quantify this exorbitance is to measure the slope of a log-log graph of weapon on body size; a slope of 1.0 would describe perfect proportionality between the two; many weapons have a slope >1.0 (often termed “positive allometry”). The trend for weapons to show positive allometry is so strong that some have mistakenly claimed that it is universal (see critiques by Bonduriansky 2007).

The selective explanation for positive allometry in weapons is probably related to the very general trend noted above for larger males to win when they fight smaller males (see Andersson 1994). A relatively large weapon can be a more effective threat device and also a more powerful weapon. In addition, while larger males can benefit from larger weapons with which they can outcompete more rivals (through effective intimidation or combat), smaller males may be unable to produce, carry, or effectively wield larger weapons. Also, as noted previously, smaller males are less likely to benefit long term from bluffing or exaggerating their combat abilities. Therefore, in relation to small males, large males might experience stronger selective pressures for increased weapon size; such a disparity could lead to positive allometry of male weapons in particular circumstances (Petrie 1988). Nevertheless, there are sometimes limits to the correlation of larger structures being more powerful weapons or functioning as more effective threat devices (see the section “An Example of Conflict Between Types of Sexual Selection: The “Beautiful Weapons” of Fiddler Crabs”).

Sexual Selection at Different Stages: Precopulatory, Copulatory, and Postcopulatory

Male-male competition does not end after mating; fertilization (or more accurately, offspring production), which is the ultimate goal of such competition, generally does not automatically occur once mating has begun. In the first place, ejaculation is often not immediate, and other males often attempt to disrupt copulations before sperm

transfer is complete. Physical displacement of copulating males has been documented in several vertebrate and invertebrate species (see Birkhead and Møller 1998). For instance, male *Pan troglodytes* interrupt the copulations of lower-ranking males by threatening them, but do not interrupt those of higher-ranking males (Tutin and McGinnis 1981); and they do so more often when females are more likely to be ovulating (Thompson and Wrangham 2008).

Even after sperm transfer occurs, fertilization is not guaranteed; males almost never transfer sperm directly onto the female's eggs in species with internal insemination, and females often mate with more than a single male during their lifetime (Eberhard 2009). A male's sperm may thus have to compete with sperm from previous or subsequent mates of the female. As a result of sexual selection, the male may utilize several different mechanisms to improve the chances that his own sperm is used for fertilization (Simmons 2001; Eberhard 2009). One simple technique is to dilute the sperm from previous (or subsequent) males with his own voluminous ejaculate, or by mating with the female repeatedly (he can thus win what has been called the “raffle” competition). Some birds perform “retaliatory copulations”, in which the male immediately copulates again with the female after he has seen her copulate with another male (Birkhead and Møller 1998). There is a positive correlation between the intensity of raffle competition and the relative size of testes in different species in several groups of vertebrates (see Birkhead and Møller 1998; Eberhard 2009).

A second male technique is to flush out or directly remove the sperm from previous males; this occurs, for instance, in several insect species such as dragonflies and beetles (Simmons 2001). Still another widespread tactic is to reduce the chances that the female will mate with additional males. Males accomplish this by defending her from other males (“mate guarding”) or by modifying her reproductive tract to make future copulations more difficult. Most often, this is accomplished by physically plugging her tract with a “sperm plug” or “copulatory plug.” This set of tactics is typically called “sperm

competition” and corresponds to the classic, direct male-male battles preceding copulation. Still other tactics used to win postcopulatory competition involve inducing the female to modify her postcopulatory physiology or behavior and correspond to classic, precopulatory female choice. There are more than 20 different known female responses that can bias the reproductive success of her different mates; among others, they include inducing the female to discard sperm from previous males, inducing the female not to discard or kill the sperm from the current male, inducing her not to mate with additional males, and inducing her to oviposit quickly before other males have a chance to find her (Eberhard 2009). Because the necessary female cooperation generally occurs hidden from view within the female’s body, this is commonly called “cryptic female choice” (see Eberhard 1996).

Copulatory plugs have been found in a variety of animal taxa, including vertebrates and invertebrates (Birkhead and Møller 1998; Simmons 2001; Uhl et al. 2010); they work in several ways. In some species they may serve as signals to discourage other males from attempting to mate with the female (Birkhead and Møller 1998; Simmons 2001). Some plugs in mammals and arthropods represent physical obstacles to the genitalia of subsequent males, as they are located at the entrance to the female or are deeper inside, blocking access to preferred sites for sperm deposition (Birkhead and Møller 1998; Uhl et al. 2010). Plugs sometimes involve subtle interactions between males and females. For instance, in some spiders, both male and female products are used to form the plug (e.g., Aisenberg et al. 2015); in squirrels, females sometimes immediately remove the plug when copulation ends and sometimes leave it in place. The use of plugs in these species may be the result of a combination of both direct male-male competition and indirect male competition via female choice. These interactions can be quite subtle. In the spider *Agelena limbata*, the openings of each of the female’s two insemination ducts are surrounded by a smooth cavity; smaller males are less able to fill this cavity sufficiently with plug material to prevent future males from achieving intromission,

while larger males more often fill it (see Eberhard 1996). By having this cavity, the female biases male-male competition via plugs in favor of larger males. There are some plugs, as in some primates, carnivores, spiders, and flies, that are not appropriately designed to exclude other males and may instead serve to reduce sperm loss or to stimulate the female (Birkhead and Møller 1998).

Another tactic which males use to avoid possible sperm competition from other males is to mate guard after insemination. In a variety of taxa, mate guarding has been shown to increase the male’s fertilization success by reducing the number of copulations by the female with other males or her future acceptance of sperm from other males (see Eberhard 1996; Simmons 2001; Setchell et al. 2005). Males can guard mated females by remaining coupled through genitalic contact (Blum and Blum 1979) or through non-genitalic contact (e.g., Painting and Holwell 2014), or by staying nearby (e.g., Setchell et al. 2005). Some males apparently guard mated females by mimicking them, thus diverting copulatory attempts from other males (see Simmons 2001). Males also guard females prior to copulation (e.g., before the female becomes sexually receptive); in some of these species, females mate only once or have short periods of receptivity or are difficult to find, and in this way, males increase their chances of future fertilizations (see Birkhead and Møller 1998).

There is often substantial intraspecific variation in several aspects of male sperm, including their general morphology, length, motility, and longevity (Eberhard 1996; Snook 2005). These sperm traits are probably the outcome of evolution under sperm competition and cryptic female choice (see Eberhard 1996, 2009). For example, in several vertebrates and invertebrates, males may produce sperm that can hook to each other and thus swim faster (i.e., sperm linking). Also, the evolution of parasperm (infertile sperm) in some groups, and their high abundance in ejaculates of some species, leads to suspicion of several possible functions of these under postcopulatory sexual selection. Similarly, the immense variety of seminal products, and their importance in achieving fertilization success, makes these targets of

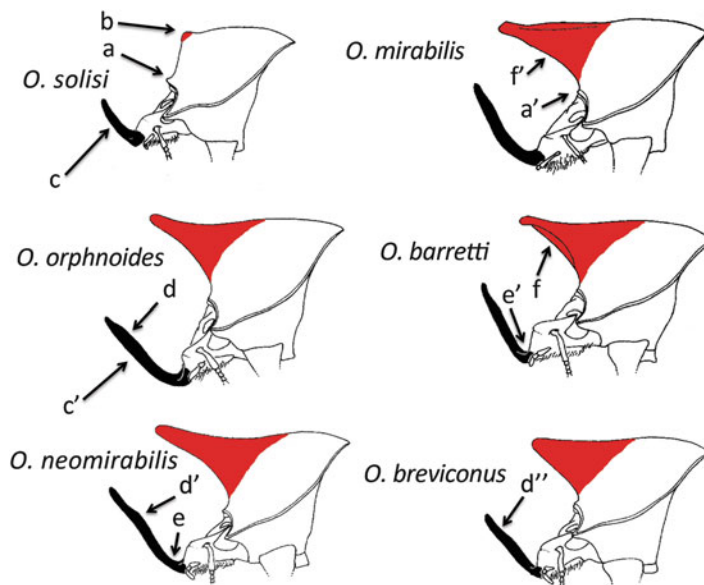
postcopulatory sexual selection through sperm competition and cryptic female choice. After a long period in which sperm and seminal products were studied without reference to their likely functions under sexual selection, the functions of these structures are just beginning to be understood (Snook 2005; Eberhard 2009).

An Example of Conflict Between Types of Sexual Selection: The “Beautiful Weapons” of Fiddler Crabs

Fiddler crabs illustrate especially clearly some subtleties in the topics just discussed and offer a window on one particularly poorly understood aspect of the evolution of male weapons and threat devices. While it is well known that male weapons and threat devices tend to diverge especially rapidly over evolutionary time (see Fig. 3) (as is typical of sexually selected traits in general – e.g., Andersson 1994; Eberhard 2009), the immediate advantages of variant traits when they first

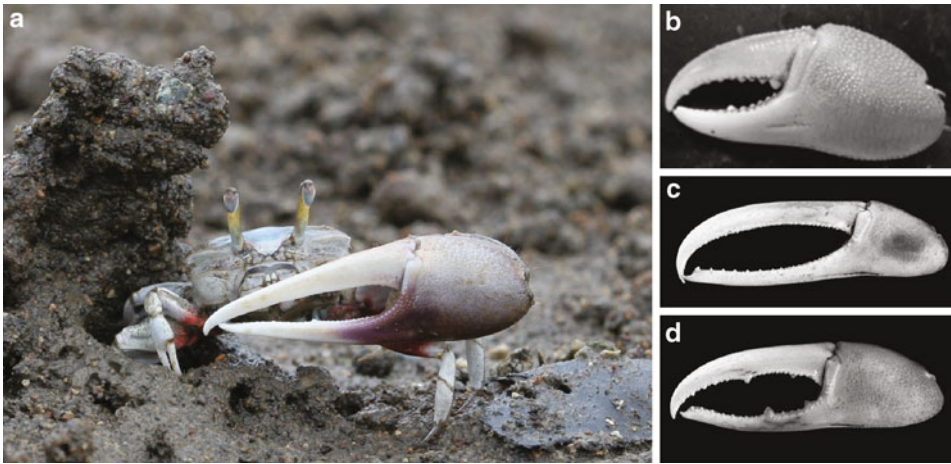
appear in a given lineage are much less well understood (Emlen et al. 2005; Dennenmoser and Christy 2013). It seems likely that the complex and probably unstable balances between the effects of different types of sexual selection (i.e., contests of attractiveness, threats, and physical fights) on such traits, which have been documented in special detail in fiddler crabs, have played important roles in the evolution of diversity.

While sexual selection favoring male weapons is often said to be balanced by one or more of the costs under natural selection that were discussed above, the situation in fiddler crabs is considerably more complicated (probably this complexity is typical, though less well documented, in many other species). There are complex webs of trade-offs because, as is also very often the case in other species, the fiddler crab’s weapon, his spectacular, sexually dimorphic fighting claw (Fig. 4) (in some species this claw constitutes up to one half or two thirds of the male’s body weight), is under several types of both natural and sexual selections. Sexual



Sexual Selection via Direct Male-Male Interactions, Fig. 3 Head and thoracic horns of males in the six known species of the *mirabilis* subgenus of *Onthophagus*, illustrating the small variations in horn shape and length in closely related species. Details with the same letter indicate comparable traits that vary among these species: *a* small

horn on anterior edge of prothorax, *b* long or short horn on anterior half of the prothorax, *c* long or short horn on anterior edge of head, *d* bump on head horn, *e* angle of head horn with rest of head, *f* indentation in lower surface of thoracic horn (Drawing after Génier and Howden 1999, with permission)



Sexual Selection via Direct Male-Male Interactions, Fig. 4 Fiddler crabs' beautiful weapons. (a) Male *Uca beebei* showing the oversized "major" claw used in displays and battles as well as the normal "minor" claw (on the left). Female claws resemble minor claws. Note also conspicuous coloration of the large claw (Photo

courtesy of John H. Christy). (b–d) Variation in major claw form (the claws are not shown all to the same scale). (b) The major claw of *U. argolicola* is short and robust (Modified with permission from Swanson et al. (2013)). (c) Regenerated and (d) original major claws of *U. annulipes* (Modified with permission from Backwell et al. (2000))

selection acts on the male's claw to attract females, to intimidate rival males in prefight interactions, and to accomplish both offensive and defensive functions that enable him to win physical fights. In addition, it has naturally selected consequences, attracting the attention of some predators, but defending against others, and it may also aid in thermoregulation. Several types of interactions between these kinds of selection, and their possible roles in the generation of evolutionary diversity, are illustrated particularly clearly in the fiddler crab genus *Uca*.

First, the stage must be set. Males of two especially well-studied species, *U. beebei* and *U. terpsichores*, fight over burrows that they dig in sandy beaches and mud flats. The burrows are costly to build, but they are valuable in attracting females as mates, and most agonistic interactions between males are tightly linked to both their burrows and their enlarged claws. Males display these claws prominently when courting females and threatening other males. Larger males tend to have larger claws, and those with larger claws tend to win both threat displays and physical fights. When one male *U. terpsichores* approaches another who is defending a burrow, each male waves his enlarged claw back and forth and up

and down rapidly. When males differ substantially in size, these claw-waving threat displays (sometimes accompanied by pushing) usually result in one male (usually the smaller) surrendering and leaving the burrow without a fight. Some displays, however, fail to resolve the conflict, and the males then fight each other physically by interlacing their enlarged claws jerkily; then each pinches the enlarged claw of the other. The claws are packed with muscle, and the pinches are so powerful that they sometimes puncture or crush the cuticle of the opponent (the scars from this damage signal the exact sites where a male's claw has been squeezed by rivals and thus where his cuticle has had to resist such squeezes).

A longer claw is a more effective display device, both for intimidating other males and for courting females; but it also tends to be an inferior weapon because of its reduced mechanical advantage (longer claws deliver weaker pinches with their tips). This conflict between the signaling and the physical properties of claws (between "beauty" and "brawn") has been elegantly confronted in *U. beebei* and *U. terpsichores* by subtle changes in claw morphology: subapical teeth on the claw deliver the squeezes in fights, rather than the claw tips. In larger individuals (and

in the same individual as he grows), these teeth are relatively more distant from the tip, thus reducing or eliminating the loss of pinching force (brawn) produced by longer claws without sacrificing the intimidating effects of their length (“beauty”).

There are still other axes of variation in sexual selection on claw morphology. Animal weapons often have defensive as well as offensive properties; in these crabs the cuticle of the claw must be thick not only in the regions where squeezing muscles are anchored but also in the areas that receive pinches from rivals to avoid being damaged. There is also another axis of trade-offs regarding the thickness of the claw’s cuticle. Lighter claws are better for signaling females (and males), because males can wave them more vigorously and for longer compared with heavier claws. In contrast, heavier claws make better weapons. Comparing pinching forces across 21 *Uca* species, most had claws that were just heavy enough to resist being crushed in a fight (Swanson et al. 2013). A comparable type of defensive structure are the basal tines on the antlers of stags which intercept stabbing movements by the antlers of rival males (Emlen 2014).

What would happen if males attempted to falsify signals about their fighting abilities and pretended to be better than they really were? Just such prevarications occur sometimes in fiddler crabs. When a predator seizes a male’s enlarged claw, he causes it to break off while the crab attempts to scramble to safety. Such an “autotomized” male, when he reaches the following molt, does not have enough resources to regenerate an entire claw of the size appropriate for his body size. One “truthful” option would be to make a smallish claw that is only as large as he is capable of filling with muscle and providing it with an appropriately thick cuticle; such a small claw would be relatively unattractive for females and also relatively ineffective in intimidating rival males (even those of comparable body size). The opposite “liar” extreme would be to regenerate a partially empty claw that showed a length typical for a male of his body size, but that had less muscle mass and hence could not pinch as forcefully or had a thinner cuticle that was less able to resist the pinches of rival males.

Several species of *Uca* regenerate such “dishonest” claws (see Fig. 4). In *U. annulipes* and *U. mjoebergi*, neither other males nor females were able to visually distinguish such a regenerated “dishonest” claw in threats or courtship (Backwell et al. 2000; Lailvaux et al. 2009). Regenerated males compensated for their inferior weapons by avoiding the possibility that interactions with rival males would escalate from threats to physical fights (Backwell et al. 2000). In effect, regenerated males “parasitize” the responses of other individuals to their dishonest claws, which evolved in response to the general honesty of the morphology of unregenerated males. Males in nature can thus be confronted with a mixture of more and less honest signals from rivals; and the frequencies of liars are sometimes alarming (up to 44 % of natural populations of male *U. annulipes* have regenerated claws – Backwell et al. 2000). Selection on male criteria for ceding without fighting is likely to vary as percentages like these change.

General Lessons

When selective forces act in opposition to each other, variation in the timing, intensity, and direction of selection can produce a range of possible outcomes. These well-studied fiddler crabs confirm this prediction. They enable one to appreciate the possible importance of several different factors at once and thus to begin to sense the likely importance of the balances between multiple selective pressures in the evolution of male traits under sexual selection. Trade-offs and adjustments occur in several dimensions: (A) a design adjustment to allow both improved signaling and fighting by larger males, (B) a trade-off between advantages resulting from the offensive versus defensive capabilities of a weapon, (C) a possible trade-off in signaling males as opposed to females (signal traits which increase the signal’s effectiveness as a threat when directed to other males may not be maximally effective in courting females), and (D) the uncertainty that males may experience in relation to the signals of rivals regarding their fighting abilities. This last problem could result in

relentless coevolutionary races between male cognitive abilities to perceive and distinguish honest from dishonest signals and to produce ever more effective dishonest signals.

A complex web such as this, composed of interacting factors whose importance relative to each other is likely to vary over both ecological and evolutionary time, is also likely to be affected by still other factors such as the population density (greater advantage in giving up without a fight in populations where alternative opportunities are more likely), the male's age (e.g., self-defense becomes less important as the male becomes older and has less future reproduction to lose), the male's size (brawn adaptations will be more important if he is larger), and his previous experience (e.g., opportunity to learn to distinguish honesty from dishonesty). Such a gumbo of interacting variables seems a recipe for variation in selective pressures and could thus offer an explanation for the rapid diversification of male weapons and threatening devices in different closely related lineages (see Fig. 3).

General Significance for Psychobiology

There are several general lessons to be learned from the fiddler crabs. In the first place, the same traits can function both as weapons and as display devices, and these displays can be directed at males as well as females. Probably the majority of male weapons are also used as display devices in agonistic interactions. Secondly, the aspects of a structure that make it a more effective weapon are not necessarily those that make it a more effective signal to intimidate a rival male. This disconnect means that there may be a dynamic balance between selection on a signaling male to overemphasize (or lie about) the fighting prowess correlated with his weapon and selection on the receiving male to evaluate this correlation correctly and not be fooled by bluffs. Conflicting pressures of this sort will also be in operation in the evolution of other, "pure" signaling traits such as territorial songs, even though in this case the correlation between the male's signal and his fighting ability is more indirect. Periodically,

males will be called upon to back up their threats with physical prowess. As illustrated in the fiddler crabs, this balance of selective pressures on a single trait is likely to be subtle and dynamic, with occasional "errors" made in both directions. Such errors could lead to the development of new traits and evolutionary divergence in the weapons.

While the authors do not know of examples of similarly elaborate trade-offs in sexual traits involved in direct male-male conflicts, in which strategy and counterstrategy have been worked out in elegance similar to that of these morphological studies, it is reasonable to assume that this lack is because of the greater intrinsic difficulties of quantifying behavioral details and contexts with comparable precision, rather than because behavior does not lend itself to subtle conditional strategies. In fact, of course an animal's behavior is much more plastic than its morphology and can be adjusted almost instantaneously to that of a rival (perhaps because of selection on these strategies and counterstrategies). This expectation of rich complexity, plus the basic, well-established theoretical background of sexual selection theory and the clear trend for sexual selection to produce rapid, divergent evolution, makes exploration of the psychobiology of direct male-male interactions under sexual selection an attractive subject for further study.

Conclusion

The evolutionary consequences of the competition between members of one sex (usually males) to gain access to the opposite sex can be better understood as a form of social selection. This intrasexual competition starts before copulation and often continues during and even after copulation. The mechanisms and processes of sperm competition, cryptic female choice, and sexually antagonistic coevolution are just beginning to be understood. Intrasexual competition can take many forms (threats, battles, courtship), so that different sexual selection pressures may interact in complex ways to shape the design of sexually-selected traits; these complex interactions may lead to the evolution of diversity in weapons.

Most weapons probably also function as threat devices besides their obvious use in combat. There are theoretical reasons why to expect approximate (though not perfect) honesty in these signals. Similarly, there are evolutionary reasons to expect that alternative reproductive tactics are a general norm in nature. The intense nature of social competition, along with the need to accurately detect honest and dishonest signals between rivals, may pose never-ending cognitive challenges to the members of the competing sex.

Cross-References

- [Aggression](#)
- [Charles Darwin: Theory of Sexual Selection](#)
- [Communication, Cues, and Signals](#)
- [Conflict Between The Sexes](#)
- [Mating Systems](#)
- [Mating Strategies](#)
- [Parental Investment Theory](#)
- [Pregnancy](#)
- [Relationship Between Sexuality and Gender](#)
- [Sex Differences](#)
- [Sexual Conflict Theory](#)
- [Sexual Selection in Evolutionary Psychology](#)
- [Sexuality](#)
- [Social Status](#)
- [Sperm Competition Theory](#)

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Sexual Self

► Sexual Identity

Sexual Signal

► Color Red

Sexual Signaling During Ovulation

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Synonyms

Attractiveness; Concealed ovulation; Fertility

Definition

Women may signal or inadvertently communicate to others their fertility status, which varies over their menstrual cycle.

Introduction

The likelihood that a single act of sexual intercourse will lead to conception varies over a woman's menstrual cycle, peaking in the days preceding ovulation (during estrus, sensu Thornhill and Gangestad 2008). Some species of primate advertise fertility status with conspicuous signals, such as bright pink sexual swellings. Women do not conspicuously advertise their fertility, but neither is estrus completely concealed. In an oft-cited study, Miller et al. (2007) asked professional exotic dancers to keep a record of their nightly tip earnings for 2 months. The dancers received about US\$67 per hour when they were near ovulation,

but only US\$52 at less fertile times of the month. Why did patrons give larger tips to ovulating dancers? Research has shown that women's appearance, body odor, voice, and behavior vary over the cycle and that men and women are able to detect these changes in others (reviewed in Haselton and Gildersleeve 2015).

Attractiveness and Cycle

There is converging evidence that women are more attractive during estrus. When women's voices are recorded at multiple times over the cycle, recordings made when women are most fertile are rated as more attractive by men and women, possibly because of the effects of estrogen on the larynx. Both men and women prefer the natural body odors of women who are in the high rather than the low fertility phase of their cycle. Women rate t-shirts worn by women near ovulation as smelling more pleasant; men rate them as more pleasant and more sexy. The effects of the cycle on voice pitch are relatively weak; effects on body odor are stronger (Haselton and Gildersleeve 2011).

Photographs of women's faces taken near ovulation are rated significantly more attractive than photographs of the same woman taken later in the cycle, when fertility is lower (Roberts et al. 2004). Recent research suggests that this effect can partially be explained by changes in face shape, possibly attributable to head posture. Women's faces, like those of some nonhuman primates, may also vary cyclically in color, although this change may not be perceivable.

Women move differently over the cycle. In one study, women were videotaped dancing to pop music and men rated those dances for attractiveness. Dances were more attractive when performed at high fertility (Fink et al. 2012). Evidence that women's gait varies cyclically is mixed.

Voluntary Signals?

Indiscriminate signaling of fertility status is unlikely to be adaptive, as such signals would

attract the attention of undesirable as well as desirable men (and possibly rival women). But there may be instances when it is advantageous for women to behave in a manner that effectively signals fertility. The biologist Bernard Campbell (1974) has suggested that researchers might find "voluntary signaling by the female replacing the involuntary physiological signals of estrus." His prediction has been borne out by research on women's clothing preferences. Durante et al. (2008) had women draw pictures of outfits they would choose to wear to an evening social event. Women in their fertile phase drew outfits that others rated as more revealing and sexy. Further research shows that women also wear more red and pink clothing – which men find attractive – when fertile, especially when the weather is inclement and revealing clothing is not an option (Tracy and Beall 2014). Women also spend more time on personal grooming near ovulation.

This is not to say that women consciously signal their fertility status through clothing and other forms of ornamentation, but psychological changes associated with the cycle (including a greater desire for men other than the primary partner during estrus) may motivate behaviors that are perceivable by others and therefore convey information about a woman's fertility.

Clothing and other behavioral cues to ovulation can also be deployed facultatively, when it is advantageous for a woman to signal her sexual interest toward desired mates. When women are fertile they are more interested in short-term relationships, and one way of expressing this interest is to flirt. But fertile women do not flirt with every man they encounter, instead directing their proceptive behavior toward men who are attractive (Cantú et al. 2014).

Conclusion

Women's fertility status is not as easily discernible as it is among females of some other primate species. It may be beneficial to conceal estrus, both to limit unwanted advances from males who seek to monopolize female sexuality and to

reduce harassment from rival females. If this is true, why do women signal their fertility at all? The *leaky cues hypothesis* proposes that women do not benefit from advertising their fertility status to others, but that it is maladaptive to suppress all cues to estrus as this would have an adverse impact on fertility. At the same time, the selection pressure on men to detect any physical or behavioral cues to ovulation is likely strong, because men who are able to direct their mating efforts toward women who are at peak fertility will be more reproductively successful. What appear to be signals of estrus are cues that are too costly to conceal entirely and which third parties are adapted to detect.

Cross-References

- ▶ [Concealed Ovulation](#)
- ▶ [Dual-Mating Hypothesis](#)
- ▶ [Evolution of Long-Term Pair-Bonding in Humans](#)
- ▶ [Male Counter Strategies to Cyclic Shifts](#)
- ▶ [Menstrual Cycle](#)
- ▶ [Ovulation](#)

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Sexual Signalling

- ▶ [Pathogen Load and Attractiveness](#)

Sexual Size Dimorphism

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Synonyms

[Sexual dimorphism in body size](#)

Definition

A characteristic difference in body size (height, length, mass) between males and females of a population or species.

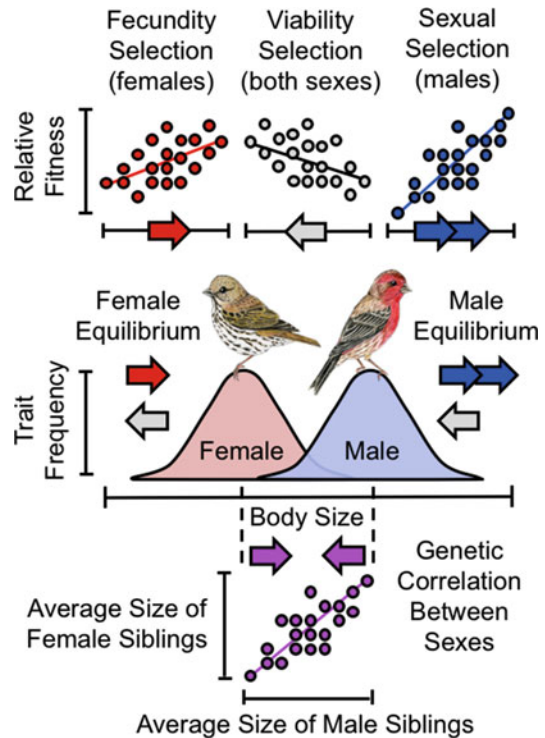
Introduction

Sex differences in adult body size are common throughout the animal kingdom and are generally thought to arise from the joint influences of sexual selection, which often (but not always) favors

large body size in males, and fecundity selection, which often (but not always) favors large size in females. In humans, as in other organisms, these inferences are based in large part on comparative studies of correlated evolutionary patterns between sexual dimorphism and proxies for the intensity of sexual or fecundity selection across entire evolutionary lineages, such as primates or mammals. The evolution of sexual size dimorphism is also constrained by the shared genome of a species, which can give rise to intralocus sexual conflict over body size and other traits. Adaptive hypotheses for sexual size dimorphism and the dynamics of intralocus sexual conflict are discussed in a general evolutionary framework that applies to diverse animal taxa, with specific reference to humans and related primates and mammals.

Sexual Size Dimorphism

Sexual size dimorphism is ubiquitous throughout the animal kingdom and often varies considerably in its direction (i.e., which sex is larger) and magnitude (i.e., by how much), even at the level of family, genus, or species (Fairbairn et al. 2007). Body size is determined by a combination of genetic and environmental factors that interactively influence growth and development throughout an organism's lifetime. In turn, body size influences most aspects of an organism's anatomy, physiology, ecology, and life history. This complexity of both cause and consequence is one reason why it has proven challenging to develop a general theory capable of predicting the direction and magnitude of sexual size dimorphism for a given species, even within particular lineages such as mammals or primates (Fairbairn et al. 2007; Fairbairn 2013). An additional layer of complexity stems from the fact that males and females share the vast majority of their genomes, including many of the genes that influence growth, development, and body size (Badyaev 2002). Consequently, the magnitude of sexual size dimorphism should reflect not only the balance of selective pressures acting on the body sizes of males and females but also the extent to which a shared genome constrains the sexes from



Sexual Size Dimorphism, Fig. 1 Differential equilibrium model for sexual size dimorphism (modified from Blanckenhorn 2007). Covariance between body size and components of relative fitness gives rise to fecundity selection (component of relative fitness = fecundity), viability selection (probability of survival), and sexual selection (mating and fertilization success). The balance of these selective forces sets the equilibrium body size for each sex. The observed level of sexual size dimorphism is determined by the offset in these equilibria and the counteracting effects of genetic constraints, as illustrated by a positive correlation between mean body sizes of brothers and sisters, as commonly observed in contemporary human populations. The direction and strength of each type of selection are purely hypothetical in this figure

evolving independently in response to these selective pressures (Fig. 1) (Gordon 2006; Cox and Calsbeek 2009).

Evolutionary Hypotheses for Sexual Size Dimorphism

Most evolutionary hypotheses for sexual size dimorphism focus on the ultimate, selective advantages of larger or smaller size in one or both sexes. In general, larger body size tends to facilitate the production of more and/or larger

eggs or embryos, the avoidance of predators, and success in competition for mates and other resources, but it can also reduce agility, require greater skeletal support, and demand a larger overall energy budget and increased offspring provisioning. Despite this potential for body size to influence fitness in a variety of ways, it is broadly accepted that sexual selection (on male size) and fecundity selection (on female size) are the two primary factors responsible for the evolution of sexual size dimorphism across diverse animal lineages (Cox et al. 2003; Fairbairn et al. 2007). Sexual selection arises from variance in mating success (which is often, but not always, greater in males than in females) and tends to favor large size when males compete aggressively for mates and small size when males engage in agile displays or scramble competition for widely dispersed females (Fairbairn 2013). The latter scenario may explain some of the most extreme cases of sexual size dimorphism in the animal kingdom, in which tiny “dwarf males” persist as little more than accessory sperm donors for females that exceed them by orders of magnitude in body size, a situation that has evolved independently in deep-sea anglerfish, pelagic octopuses, bone-eating marine worms, and shell-dwelling barnacles (Fairbairn 2013). Fecundity selection arises from variance in the number of offspring produced and will favor large females under conditions where larger size provides more space for developing eggs and embryos or larger nutrient and energy reserves with which to provide a greater number of offspring. The near ubiquity of this condition is believed to be the primary reason why females are larger than males in the vast majority of animal taxa, which runs counter to the more familiar pattern of male-biased sexual size dimorphism in humans and many other mammals (Fairbairn 2013).

Sexual and fecundity selection act in concert on males and females, so the level of sexual size dimorphism for a given species is predicted to reflect a “differential equilibrium” between the strength and direction of sexual selection on male size versus that of fecundity selection on female size (Fig. 1) (Blanckenhorn 2007). Natural selection acting through differential survival also

influences the equilibrium body size in each sex and is often conceptualized as a force that counteracts sexual and/or fecundity selection for ever-increasing body size (Blanckenhorn 2000). However, natural selection for viability also favors large body size in many situations and may sometimes generate or reinforce sexual size dimorphism by acting in opposite directions on each sex (Cox and Calsbeek 2010). Natural selection is also the primary force invoked by “ecological hypotheses” proposing that sexual dimorphism reflects the independent adaptation of males and females to different aspects of their shared environment, often as a means of adaptively reducing intraspecific competition by allowing the sexes to exploit different resources (Shine 1989). Ecological hypotheses are difficult to test because divergence in resource use is likely often a consequence of sexual size dimorphism arising for other reasons. Moreover, many species exhibit pronounced sex differences in body size without apparent differences in resource use or differences in size opposite those predicted by resource partitioning (Shine 1989).

Sexual Size Dimorphism in Humans and Other Primates

Contemporary humans are sexually dimorphic in a number of morphological traits related to shape and size. Relative to females, males generally have broader shoulders and wider rib cages, narrower pelvis, and longer and heavier bones with larger areas for muscle attachment (Plavcan 2012). As adults, human males average 7% taller and 15% heavier than females (Gustafsson and Lindenfors 2004). Although much of this dimorphism emerges gradually during development, minor sex differences in body size are present at birth and can be traced back as early as the first trimester of pregnancy (Bukowski et al. 2007). This modest degree of sexual size dimorphism falls toward the low end of dimorphism across nonhuman primates, which ranges from a few species in which females are equivalent to or slightly larger than males (e.g., gibbons) to extremes in which males average more than

twice the mass of females (e.g., gorillas) (Plavcan 2012). Across mammalian orders, male-biased sexual size dimorphism is the rule, particularly in diprotodonts (kangaroos), rodents, carnivores, ungulates, and primates, while sexual monomorphism or modest female-biased size dimorphism typifies chiropterans (bats) and lagomorphs (rabbits) (Lindenfors et al. 2007). Viewing *Homo sapiens* against the backdrop of diversity throughout the animal kingdom, Fairbairn (2013) concluded that humans “show a fairly typical pattern of sexual dimorphism for a large, terrestrial mammal, with males maturing later and at a slightly larger size than females, and female shape being adapted for gestation, birth, and parental care (p. 191).”

Hypotheses invoking sexual selection and fecundity selection as the causes of sexual size dimorphism can be tested by taking the phylogenetic relationships among a group of species into account and then asking whether evolutionary changes in dimorphism are associated with changes in variables that reflect the level of sexual or fecundity selection (Cox et al. 2003; Fairbairn et al. 2007). Across mammals and specifically within primates, evolutionary changes in categorical proxies for the strength of sexual selection, such as mating system (e.g., polyandry/monogamy < polygynandry < polygyny), explain a large and significant amount of the evolutionary change in sexual size dimorphism (Lindenfors et al. 2007; Plavcan 2012). Among nonhuman anthropoid primates, the occurrence of agonistic contest competition among males is the best predictor of sexual dimorphism in body size and in the size of the canine teeth, which are often displayed and used as weapons in these contests (Plavcan 2012). Nonetheless, simple categorical predictors such as mating system and the presence or absence of agonistic male-male contests leave much of the statistical variation in sexual size dimorphism across primates unexplained, raising the question of whether this indicates a need for more precise and quantitative estimates of sexual selection or consideration of additional selective pressures.

The influence of fecundity selection on sexual size dimorphism in primates and other mammals

has been frequently debated, with some evidence supporting the counterintuitive hypothesis that fecundity selection actually favors smaller body size as a means of increasing lifetime fecundity through earlier and more frequent reproduction involving less energy expenditure per reproductive episode (Lindenfors et al. 2002; Lindenfors et al. 2007; Plavcan 2012). Though reproductive rate and lifetime fecundity tend to correlate negatively with mean body size across species (Lindenfors 2002; Lindenfors et al. 2007), intra-specific correlations between individual size and reproductive rate tend to be weak or absent in most primates, suggesting that current fecundity selection does not act strongly on female body size (Gordon 2006). Though sexual selection via both male and female mate choice has received considerable attention in the evolutionary psychology literature, and may often act on dimensions of body size and shape in both sexes (Pawlowski et al. 2000; Courtiol et al. 2010; Mautz et al. 2013), there is little direct evidence to confirm a role of mate choice in shaping sexual size dimorphism (Puts 2010). Consequently, the modest male-biased sexual size dimorphism exhibited by humans is generally interpreted as a consequence of historical patterns of sexual selection favoring large male size in relation to agonistic competition for mates, though factors such as fecundity selection, viability selection, and mate choice acting on one or both sexes may have also played a role in establishing the precise magnitude of this dimorphism.

Intralocus Sexual Conflict over Body Size

When selection on a given trait acts in opposite directions in males and females, it is said to be sexually antagonistic. When a trait subject to sexually antagonistic selection is influenced by many of the same underlying genes in each sex, then the trait and its underlying genes are said to be subject to intralocus sexual conflict (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009). Because any gene located on an autosome will spend roughly half of its time in males and half of its time in females, genes that are detrimental

when expressed in males can be maintained in a population because they are beneficial to females and vice versa (Stearns et al. 2012). When manifest across numerous traits and underlying genes, this genome-wide conflict can reduce the overall fitness of a population by constraining males and females from evolving toward their respective fitness optima for the phenotypes under selection. Intralocus sexual conflict can therefore be viewed as a specific (and nearly ubiquitous) case of the more general evolutionary problem of producing two different phenotypes from what is predominantly the same underlying genome (Pennell and Morrow 2013). Over long evolutionary time-scales, this genomic conflict can be resolved (at least partially) through a variety of mechanisms that facilitate the sex-specific inheritance (e.g., sex chromosomes) and expression (e.g., hormonal regulation of transcription) of shared genes, thereby permitting the evolution of sexually dimorphic phenotypes (Stewart et al. 2010). Indeed, the fact that so many traits are sexually dimorphic indicates that, given sufficient time, these genetic constraints can be overcome. Nonetheless, a variety of theoretical considerations and empirical results suggest that a complete and lasting resolution to intralocus sexual conflict is unlikely (Bedhomme and Chippindale 2007; Mank et al. 2008; Pennell and Morrow 2013). This conclusion is consistent with the observation that many highly dimorphic phenotypes are still subject to ongoing sexually antagonistic selection favoring even greater sexual dimorphism (Cox and Calsbeek 2009).

In haplorhine primates, evolutionary patterns in body size suggest that sexual selection for larger body size in males has, via a correlated evolutionary response, displaced females of polygynous species from their optimal size for lifetime fecundity by necessitating greater postpartum investment in larger offspring (Lindenfors 2002). In human populations, body size or stature is heritable (Silventoinen 2003), and its genetic covariance between males and females is estimated to be quite high, meaning that selection on body size in one sex should produce a highly correlated evolutionary response in the opposite sex (Rogers and Mukherjee 1992). Based on these

genetic estimates, the rate of evolution in the mean body size of a human population in response to selection should be more than 60 times greater than the rate of evolution for sexual dimorphism in mean body size (Rogers and Mukherjee 1992). These estimates suggest that the prolonged displacement of one or both sexes from their respective fitness optima is a likely consequence of sexually antagonistic selection on body size.

Longitudinal studies of lifetime fitness (number of children) in sibling pairs from contemporary human populations provide direct evidence for intralocus sexual conflict over body size (Stulp et al. 2012). Whereas sisters have relatively greater lifetime reproductive success than their brothers in sibling pairs of shorter height (the optimal height for female reproductive success), brothers have relatively greater reproductive success than their sisters in sibling pairs of average or slightly above average height (the optimal height for male reproductive success). Similar conclusions have been reached from studies simultaneously quantifying sexually antagonistic selection and predicting evolutionary responses based on the quantitative genetic architecture of body size and a variety of correlated physiological traits in a contemporary human population (Stearns et al. 2012). These studies collectively suggest that sex differences in human body size are subject to ongoing sexual conflict that maintains genes with deleterious effects in one sex due to their beneficial effects in the opposite sex.

Conclusion

Human males average 7% taller and 15% more massive than females as adults. These size differences are toward the low end, but not atypical, relative to other primates and large terrestrial mammals. As in other species, this sexual size dimorphism is generally thought to reflect a history of sexual selection for a larger and more robust physique in males due to agonistic contests over mating opportunities. However, fecundity selection, viability selection, and sexual selection via mate choice have likely also shaped the evolution of body size in both sexes. Body size is

moderately heritable in many contemporary human populations and also strongly genetically correlated between males and females, which inhibits the evolution of sexual size dimorphism and leads to intralocus sexual conflict over body size and related traits.

Cross-References

- [Adaptation](#)
- [Intralocus Sexual Conflict](#)
- [Intralocus Sexual Conflict Across the Genome](#)
- [Observed Mating Behavior and Women's Long-Term Mating](#)
- [Polygyny](#)
- [Primates](#)
- [Reproduction](#)
- [Sex Differences](#)
- [Sexual Dimorphism and Sex-Biased Gene Expression](#)
- [Sexual Selection](#)

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Sexual Socialization

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Definition

Adolescents' development of attitudes, norms, beliefs and behaviors regarding sexuality in response to socialization agents.

Introduction

During adolescence, sexual processes take up a central position. The acquisition of a positive sexual identity is considered to be a key developmental task for adolescents (Tolman and McClelland 2011) and can be described as the

process of “understanding [one’s] own sexual orientation as well as sexual needs and values, preferences for sexual activities, partner characteristics, and modes of sexual expression (Worthington et al. 2002, p. 512).” Modern evolutionary theory explains that this process is driven by biological stimuli, such as pubertal maturation and sexual hormones (Steinberg 2005), and is influenced by environmental factors as environmental flexibility helps to meet biological goals (Belsky et al. 1991).

The most significant environmental factors are so-called sexual socialization agents (i.e., parents, peers, and media) that guide adolescents' development of attitudes, norms, beliefs, and behaviors regarding sexuality (Tolman and McClelland 2011; Ward 2003). Social cognitive theory explains that these agents (e.g., peers or media characters) may model sexual and relational behavior that can be observed and adopted by adolescents, especially if the behavior is rewarded (Bandura 1999). In addition, these agents inform adolescents on attitudes, norms, and beliefs towards sexuality that are considered as favorable (Bandura 1999).

Importantly, sexual socialization agents differ in the *type* of messages they promote as being favorable. More precisely, the literature distinguishes positive and negative messages. Positive messages are messages that socialize adolescents towards a positive sexuality defined as “sexuality that is consensual, honest, mutually pleasurable, non-exploitative, and protected against unintended pregnancy and sexually transmitted diseases (STDs)” (Ward et al. 2006, p. 59). When messages deviate from this description of a positive sexuality, they are regarded as negative or risky in the literature.

Because of the substantial impact that the development of a sexual identity has on adolescents' current, but also their future well-being, research has studied extensively the relationships between sexual socialization agents and adolescent sexual maturation (Tolman and McClelland 2011). Over the years, three (related) areas of research have been developed that each focus on a key socialization agent: (1) parents, (2) peers, and (3) media.

Parents

Parents are considered to be the prime socialization influences in children's life (Belsky et al. 1991). During childhood, parents model and structure children's early understandings of sexual relations and the roles of women and men in sexual interactions (Belsky et al. 1991; Inazu and Fox 1980). The influence of parents in sexual maturation persists in adolescence (Tolman and McClelland 2011), but takes on different shapes. Adolescents increasingly start to explore their own sexuality and talk with their parents about sexuality (Tolman and McClelland 2011), though, at the same time, they start to rely less on their parents in general (Fulgini and Eccles 1993). Adolescents identify their parents as sources of information on physical health risks and responsibilities that come with sexual behavior (Epstein and Ward 2007). The importance of developing a sexual agentic self-concept, sexual desires, and respect for sexual minorities is in general less likely to be covered in the sexual socialization messages of parents (Epstein and Ward 2007).

The inherent, hyper personal nature of sexuality is a burden on parent-child interactions regarding sex and may explain why topics, such as masturbation, are rarely covered in parental conversations about sex (Diiorio et al. 2003). Such conversations are characterized by feelings of discomfort, shame, and guilt, especially on the side of the adolescent (Epstein and Ward 2007; Ogle et al. 2008). Mothers seem to handle these (somewhat) uncomfortable situations better than fathers as they talk more often to their sons and daughters about sexuality (Bleakley et al. 2009; Diiorio et al. 2003).

In general, research suggests that parental sexual messages socialize adolescents towards attitudes and behaviors that are characterized by a focus on (health) responsibilities and a less supportive view of an early initiation of sexual behaviors (Bleakley et al. 2009; Inazu and Fox 1980; L'Engle and Jackson 2008), though inconsistent findings have also emerged (Diiorio et al. 2003). In this view, the relationship between parental socialization and sexually protective behaviors has been found to vary according to factors,

such as the timing of the parental message (before or after an adolescent's sexual debut) and the communication style of the parent (open vs. restrictive) (Miller et al. 1998; Whitaker et al. 1999).

Also the literature warns that stereotypical beliefs about sexual gender roles seem to affect parental sexual socialization (Lottes and Kuriloff 1994). Such stereotypical beliefs are believed to be rooted in different inherited strategies for reproductive success by men and women (Eagly and Wood 1999). These strategies encourage promiscuous sexual behavior among men (for instance, because men face the risk of raising children whom they are not biologically bounded to) and long-term committed relationships among women (for instance, because male partners can help to protect the family) (Eagly and Wood 1999). In line with these strategies, socialization research has noticed that especially girls are socialized towards restrictive sexual attitudes and behavior, while boys are sometimes even supported to gain (early) sexual experience by parent-sex communication (Diiorio et al. 2003; Lottes and Kuriloff 1994).

Overall, the literature indicates that parents can play an important role in postponing early sexual behavior and preventing a sexual risk trajectory (L'Engle and Jackson 2008). At the same time, the literature also suggests that the diversity of topics covered in parent-child conversations is sometimes limited (Epstein and Ward 2007; Ogle et al. 2008) and that factors, such as gender stereotypes and communication style, partly determine the strength and direction that the influence of parental sexual socialization messages takes on.

Peers

While the importance of parents decreases during adolescence, peers gradually take on a more central role in adolescents' life (Fulgini and Eccles 1993). In general, adolescents heavily rely on peers in their everyday life and in particular for providing them with sexual information (Bleakley et al. 2009). Peer conversations about sex are

common and focus on a variety of themes, such as exchanging their (emerging) experiences with sex and beliefs about (successful) sexual relationships (Epstein and Ward 2007). Such conversations are likely to signal which sexual attitudes and behaviors are considered as normative in the peer group and seem to evoke pressure to comply to these peer standards.

While parents are known to rather support sexual abstinence in the literature, peers tend to socialize adolescents towards more positive liberal attitudes regarding sex and to support the initiation of (risky) sexual behavior (Bleakley et al. 2009; Epstein and Ward 2007). This is demonstrated by research showing that adolescents become more popular when they gain sexual experience (Prinstein et al. 2003; Sieving et al. 2006). Moreover, research has reported that peer factors, such as perceived peer approval of teen sex, perceived peer sexual behavior, and general sexual communication with friends, increase adolescents' chances to initiate sexual intercourse and oral sex (L'Engle and Jackson 2008; Prinstein et al. 2003).

(Perceived) social rewards from peers thus seem to accelerate adolescents' sexual trajectory. However, null findings have also been found (Frison et al. 2015; Prinstein et al. 2003). In line with the literature explaining inconsistent results on parental sexual socialization, peer socialization processes may also differ for boys and girls. Stereotypical norms suggest girls should have some sexual experience, but cannot be seen as sexually promiscuous (Lottes and Kuriloff 1994), while boys consistently gain social status when having more sexual experience (Lottes and Kuriloff 1994). These stereotypes seem to shape peer sexual socialization as adolescent boys indicate to experience more peer pressure to initiate sexual activities at an early age than girls (Potard et al. 2008). Accordingly, adolescents also believe that male peers are more sexually experienced than female peers (Frison et al. 2015).

Apart from these gender differences, other characteristics of peer networks, such as the religious background of one's close peers or their socio-economic status, may further determine the sexual norms that are promoted (Tolman and

McClelland 2011). Moreover, the sexual norms promoted by one peer group may include some messages that are considered as risky for sexual maturation but, at the same time, also other messages that are protective for adolescent health. For instance, one study reported that the peer network of French adolescents socialized them towards positive attitudes towards contraception. The same peer group also promoted an early sexual debut, though (Potard et al. 2008).

Together, the literature suggests that the peer group socializes adolescents into a wide variety of themes regarding sexuality and (in general) tends to support adolescents to engage in (early) sexual behavior. Such pressure is intertwined with traditional gender roles. Some literature also points to the importance of peer characteristics, such as the type of friends, to determine whether the peer network functions as a positive versus negative sexual socialization agent. Moreover, the influence of a particular peer group on adolescent sexuality may be positive or negative depending on the area of sexuality that is being considered. More knowledge is needed to further explain under which conditions peers may positively affect adolescent sexuality. This knowledge is particularly relevant as peers may perhaps have the most significant influence on adolescent sexuality.

Media

Adolescents indicate to spend a considerable amount of their daily time with using media (Vandenbosch 2013). In the media popular among adolescents, sexual messages are prevalent (Ward 2003). To illustrate, an average adolescent will be exposed to approximately 35,328 sexual television messages when he/she reaches adulthood (Vandenbosch 2013). Media scholars argue that entertainment media (e.g., television and magazines), but also pornographic media are particularly appealing as sexual information sources because of their anonymous nature, prevalent and (in case of pornography "highly") explicit references to sex, and power to engage users in stories (Brown et al. 2005; Peter and Valkenburg 2016;

Ward 2003). As for social media, their features can provide an online playground to experiment with one's sexual identity, but also to observe how other peers express their sexuality (e.g., through sexy selfies and sexting) (Ringrose 2009).

In line with this reasoning, entertainment, social, and pornographic media have been identified as valuable sexual information sources by adolescents (Bleakley et al. 2009; Ringrose 2009; Vandenbosch et al. 2018). These media can contain positive or negative information about sexuality. More precisely, some television shows and (online) magazines discuss potential risks and responsibilities that come with engaging in sexual activities (Aubrey 2004; Hust et al. 2008). Most literature has, however, warned for media's role as a risky sexual socialization agent (Brown et al. 2005) and in particular their promotion of the so-called *Reductionist Script of Instant Gratification* (Vandenbosch 2013). In this script, sexuality is predominantly focused on receiving sexual satisfaction which is inherently linked to sexual attractiveness and stereotypical gender roles. Romance is reduced to a sexual, hedonistic game with differential play styles for boys and girls (i.e., sexual double standard), though both are expected to comply with narrowly defined appearance ideals (i.e., being thin or muscular) (Vandenbosch 2013).

Numerous studies have examined whether the components of this Reductionist Script of Instant Gratification in popular media lead to adversarial consequences for adolescent sexual maturation. For the associations between mainstream entertainment (i.e., television and magazines) and social media, and adolescent sexuality, inconsistent results have led to question the media's role as a socialization agent (van Oosten et al. 2018). As for pornographic media, consistent support has emerged for the links between sexually explicit media use and adolescents' recreational attitudes towards sex, views of women as sex objects, and increased (risky) sexual behavior (Peter and Valkenburg 2016; Vandenbosch 2013).

Importantly, research across media genres agrees that inconsistent findings have resulted from poor attention to the conditions that explain when and how adolescents may be affected by

sexual media content (Vandenbosch 2013). As such, the role of differential susceptibility factors and response states in sexual media effects (Peter and Valkenburg 2016; Vandenbosch 2013; Ward 2003) has been more systematically studied during the last decade. This research identified groups of adolescents who not only have an increased likelihood of being affected by exposure to the Reductionist Script of Instant Gratification in popular media, but also those who may benefit from media exposure (Vandenbosch 2013). Important differential susceptibility factors refer to developmental traits (e.g., age, puberty), social factors (e.g., family environment), and dispositional characteristics (e.g., sensation seeking, hyper gender identity) (Peter and Valkenburg 2016; Ward et al., 2013). Studies on response states have shown that sexual media effects often occur "indirectly" through processes, such as excitative (e.g., arousal) or cognitive (perceived utility of media content) responses (Peter and Valkenburg 2016; Vandenbosch et al. 2018).

Together, the literature has described the affordances that media may offer as a sexual socialization agent for adolescents and the risks associated with the adoption of the information on sexuality that is (frequently) promoted in (popular) media. Current research seems to agree that media exposure may affect adolescent sexuality, but that these sexual media effects depend on differential susceptibility factor and (partly) develop through indirect processes (i.e., response states).

Reflections to Consider in Future Research

This review indicated that there is a substantial body of research on sexual socialization agents. Past research especially aimed to understand under which conditions parents function as protective sexual socialization agents, and peers and media as negative sexual socialization agents. The current overview of the literature has led to several critical gaps in the literature. These gaps suggest, at least, four major directions for future research.

First, research has mainly investigated sexuality from a reproductive health perspective

focusing on sexual (risk) behavior and liberal sexual attitudes. The definition of a positive sexuality however points at different areas of sexuality including sexual desire, sexual intimacy, and respect towards sexual minorities (Ward et al. 2006). Little is known about which roles peers, parents, and media may play in these areas with some notable exceptions, e.g., pornography effects on sexual satisfaction (Peter and Valkenburg 2016) and peer effects on homophobic behavior (Birkett and Espelage 2015).

Second, the general assumption that parents versus peers and media are, respectively, protective and risky sexual socialization agents seems to prevent research from exploring whether these roles are not univocal and potentially may differ in regard of the considered area of sexuality and the type of adolescent. For instance, the representation of homosexual individuals in popular media is considered favorable for their visibility in the society, but the stereotypes surrounding their representation in media content is evaluated as problematic (Calzo and Ward 2009). Given the pros and cons attached to the televised messages on homosexuality, it is not surprising that research suggests some groups develop more positive attitudes towards homosexuality, while other groups seem to become less tolerant towards homosexuality when watching more television (Calzo and Ward 2009). More precisely, women and less religious individuals have more favorable attitudes towards homosexuality in general. As a result, television exposure may cause them to develop less positive attitudes towards homosexuality. The reverse is true for men and more religious individuals, though. These groups appear to be less tolerant towards homosexuality in general, but seem to be more tolerant when watching more television (Calzo and Ward 2009). Overall, more knowledge to explain under which conditions different socialization agents have a protective versus risky influence in various areas of sexuality is needed. Such insights will help to reveal the complex role that agents have in different groups of adolescents.

Third, the dynamic, reciprocal nature of the sexual socialization process is rarely examined in research. Theoretical models explaining how

(sexual) socialization processes manifest themselves underline a dynamic interaction between an individual and his/her environment (Bandura 1999). Individual or environmental traits will affect how the individual responds to sexual socialization messages. In turn, these responses will shape the future messages an individual receives from a socialization agent (Bandura 1999). For instance, a mother may first socialize her daughter towards the adoption of rather liberal sexual attitudes. Because of the sensation seeking personality of the daughter, she may respond to this socialization by engaging in risky sexual activities. When the mother observes this behavior, she may (temporarily) change her approach and socialize her daughter towards more restrictive sexual attitudes and behavior. In this example, the socialization agent thus adapted her approach in response to the child's behavior. Although theory predicts such dynamic processes in socialization approaches, empirical research is largely lacking. Such research may provide useful insights in the conditions that shape different socialization influences, though. Longitudinal or dyadic daily experience studies may be especially warranted to examine such dynamic processes. Such studies are overall rather rare in the field of sexual socialization research.

Fourth, research has mainly studied the influence of socialization agents as separate entities, while (1) multiple socialization agents may simultaneously affect adolescent sexual maturation and (2) socialization agents may affect each other, which, in turn, may influence adolescents sexuality. First, a scarce set of studies has untangled how the influence of a sexual socialization agent can be strengthened, weakened, or changed by the influence of another socialization agent on adolescent sexuality. These studies have shown that the (protective) influence of parents may interact with the (risky) influence of media and peers (Vandenbosch and Eggermont 2011a; Whitaker and Miller 2000). For instance, when adolescents discuss sexual subjects with their parents more frequently, peer pressure to have sex tends to relate less strongly to adolescents' sexual behavior (van de Bongardt et al. 2014; Whitaker and Miller 2000).

Second, limited research has examined models that propose interactions with other socialization agents as fundamental processes to explain the links between a socialization agent and adolescent sexuality. In this research, media use (e.g., increased exposure to reality TV) and parental interactions (e.g., lower parental support) were found to affect peer processes (e.g., increased sexual communication with peers, having more sexually active peer friends). In turn, these peer factors have been related to adolescents' (advanced) sexual experiences (Vandenbosch and Eggermont 2011b; Ward 2002; Whitbeck et al. 1993).

Such research supports that the influence of sexual socialization agents cannot be considered as working independently from each other, but necessitates an interactive approach to truly unravel how sexual socialization processes influence adolescents' emerging sexualities.

Conclusion

Together, it has become clear that the role of sexual socialization agents needs to be considered by taking into account the complexity that surrounds the process of developing a sexual identity and in which multiple factors play a role. This review will hopefully help future research in revealing the interplay between different sexual socialization agents, different types of adolescents, and their sexual maturation processes.

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Sexual Stigmatization

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Synonyms

Sexism; Sexual injustice; The sexual double standard

Definition

A form of sexism where men and women are judged differently for engaging in the same sexual behavior (with women carrying the stigma).

Introduction

Sexual stigmatization refers to a sexual double standard within sexuality, where men and women engaging in the same sexual conduct are judged differently – with women carrying the stigma. The idea comes from traditional concepts of heterosexuality, where male and female sexuality are understood differently. Here, open and expressive female sexuality is disparaged, whereas desirous male sexuality is sanctioned and celebrated. Although the norms of Western heterosexuality are shifting – the sexual double standard remains powerful in shaping heterosexuality in various domains. In this entry, the history, norms, and current context of the sexual double standard in the West are covered.

The Sexual Double Standard

The sexual double standard is a form of sexism within heterosexuality where the same sexual behavior enacted by men and women are judged differently. For example, men who have many sexual partners are positively deemed as “studs” and women negatively judged as “sluts,” “skanks,” or “whores” (Farvid et al. 2017, p. 544–545, see also: Crawford and Popp 2003; Jackson and Cram 2003; Lai and Hynie 2010; Lees 1993; Ringrose et al. 2013; Ronen 2010; Hess et al. 2015). One of the explanations typically given for this phenomenon is that men are raised to value sexual experience, where women are taught to focus on emotional aspects of sex and committed relationships. Furthermore, the reason the sexual double standard is seen as a sexual injustice is because men are given more sexual freedom while women are socially stigmatized for engaging in the same behavior and hence have their sexual expression curtailed (Lyons et al. 2011).

The sexual double standard creates a narrow ideal of male sexuality as well – requiring men to demonstrate overt sexual interest and prowess (Kettrey 2016). Such ideals stem from traditional

concepts of male and female sexuality as identified by the seminal work of Wendy Hollway and Michelle Fine. Hollway’s (1984, 1989) work was able to showcase a widespread cultural acceptance that male sexuality is biologically needy and uncontrollable, whereas Fine’s (1988) work elucidated how sexual desire and pleasure is absent when it comes to female sexuality. These dominant cultural tropes, or sex-role stereotyping, position men as active sexual agents and women as passive and responsive, creating a social and cultural climate where something like the sexual double standard can exist (Milnes 2010).

Historical Context

The expression of the sexual double standard has varied across time. For example, in the Victorian Era women were desexualized and the enjoyment of sex was seen as exclusively a male domain (Gordon 1994). There were different gendered ideas of sexual purity – where men engaging in adultery or prostitution were dealt with more leniently socially and legally than women. Women were required to be chaste and moral and only engage in sex to bear offsprings, otherwise they were “fallen” women who had sex outside of marriage, for pleasure, or for money. Even being out in public without a chaperon might relegate a woman to the status of “prostitute.”

The work of early sexologists such as Sigmund Freud and Richard von Krafft-Ebing in the late 1800s and early 1900s created a different model of sexuality, focused on science (description and categorization) rather than religion (morality and regulation) (Farvid 2012). This, along with increasing discussion and display of sexuality allowed for more liberalizing attitudes about sex to gather traction. The “roaring twenties,” for example, is referred to by some historians as revolutionary in relation to sex (Dean 1996). By the 1960s and 1970s, this had culminated in fully fledged sexual permissiveness in various sectors of Western society (Allyn 2000).

Permissive sexuality situates both men and women as desiring agents who can have consenting sex in any context: “anything goes, as long as no one gets hurt” (Braun et al. 2003, p. 238). Based on this model, sex is positioned as inherently good and the right of men *and* women to enjoy. While permissive attitudes toward sex spread and pre-marital sex were on the rise (Reiss 1960, 1967), the experience and outcomes of permissiveness were often very different for men and women in this period. For example, women still carried the stigma of being considered “loose” or “easy” as well as having to deal with contraception and unwanted pregnancies (Campbell 1980).

At the turn of the twenty-first century, norms about sexuality and men’s and women’s sexual behavior are arguably at their most liberal, particularly when it comes to female sexuality. As Farvid and Braun (2006) noted, we are very much in the midst of a “pro-sex” cultural climate, characterized by a sexualization (Evans et al. 2010) and pornification of culture (Mulholland 2015) and a mediatization of sexuality (Couldry and Hepp 2016). For example, an active, desiring, and pleasure-focused female sexuality is depicted in women’s magazines, online and in popular television shows (e.g., *Sex and the City*, *Girls*, *Broad City*) and movies (i.e., *How to be Single*, *Trainwreck*). Yet, sexuality continues to be a tenuous terrain for heterosexual women – who must now walk a tightrope between being an over-sexed slut or an uptight prude. Women need to embody a sexually “liberated,” desiring and active sexuality, while at the same time avoiding activities or behaviors that may tarnish their sexual reputation.

Early Sexual Double Standard Research

Seminal work on the sexual double standard was carried out by sociologist Ira Reiss in the 1950s and 1960s. He examined attitudes related to “pre-marital sexual intercourse” – where it was typically seen as wrong for women but acceptable or even desired for men (Reiss 1956, 1960, 1967). Towards the end of the 1960s, he identified a loosening of the premarital sexual standard,

where pre-marital sexual activity was accepted among both men and women, as long as it was in the context of an affectionate or loving relationship (Reiss 1967). Indeed research in the 1970s indicated that premarital sex was no longer subjected to a sexual double standard (King et al. 1977) – but the sexual double standard did not disappear.

Research in the 1980s and 1990s produced mixed results – but clearly indicated a shift in how the sexual double standard manifested and in relation to what sorts of behaviors. In their review of this material (between 1981–2001), Crawford and Popp (2003) noted that although sexual attitudes and norms had become more egalitarian – men and women were still judged differently with regards to specific sexual *behaviors*. For example, women were judged more harshly for having sex at a younger age, for having sex outside of committed relationships (casual sex, infidelity), and for having sex with many partners (Crawford and Popp 2003). Furthermore, carrying condoms, wearing certain types of clothing, or acting flirtatious or in a sexual manner could also garner negative reactions and labeling (Hillier et al. 1998; Lees 1993). In addition, women were judged more harshly for being the initiators of sex or dates, and if there were negative outcomes in a dating or sexual situation, women were seen as more culpable if they were initiators.

Hence, there was a more subtle “fine line” that girls/women may cross when it came to the sexual double standard in this period but concerns about negative sexual reputation were evident (Kitzinger 1995). Furthermore, the sexual double standard, concerns regarding negative social judgments or a sexual reputation, had negative health outcomes. There were more negative individual, emotional, and social consequences for women (for example, women were less likely to carry condoms or initiating condom use due to the concern of being deemed a “slut”).

More Recent Work

From the early 2000s until now, a plethora of diverse work on the sexual double standard has continued to be published (Bordini and Sperb

2013). Such work has been able to map the changing nature of the sexual double standard, examining the complex and contradictory ways it manifests in the contemporary context. Before discussing this work – it is useful to outline the different theoretical approaches typically utilized in such research.

Theoretical Frameworks

There are three major theoretical clusters used to make sense of the sexual double standard. These are the biological/evolutionary approach (Buss 1994), sociocultural/social role theories (Gagnon and Simon 1973), and cognitive social learning (Bandura 1986). Biological theories tend to stem from evolutionary perspectives and posit that the sexual double standard stems from adaptive survival tendencies related to reproductive success. Men need only to invest a small amount in the biological aspect of reproduction, and it is women who carry and give birth to a child. Here women become more selective about how much sex they have and with which partners, as they prefer long-term mates who will help raise any off-spring that may be born as a result of sexual activity. Whereas men can be less discriminate and may seek to spread their seeds far and wide to garner as many offsprings as possible. Although this theory seems plausible, direct scientific evidence that captures prehistoric drives is impossible to gather. Attitudes and behaviors explained by this approach are also explainable by the following theories.

Sociocultural/social role theories tend to better contextualize why the sexual double standard might occur by highlighting dominant constructions of male and female sexuality and the way in which society expects different behaviors from men and women. For example, the sexual double standard is perpetuated by socially produced gender ideals or *scripts* that determine the norms regarding how men and women ought to behave, sexually (Greene and Faulkner 2005; Lai and Hynie 2010). Gender roles and gender role expectations play a huge role in how both actors and observers interpret and respond to the sexual behavior of men and women (Zaikman and Marks 2017). We respond more positively to behaviors that reinforce our gender specific

expectations, and vice versa. In this context, female sexuality is monitored and scrutinized in a way that male sexuality is not, because of the restrictive ways female sexuality has been constructed. Feminist and gender theorists have used this approach to highlight the sexist ways dominant heterosexuality operates, with a view to challenging and disrupting the sexual double standard (see Farvid et al. 2017).

Cognitive social learning theory posits that the sexual double standard exists because behaviors that are gender-role specific are reinforced within our society, and those that are inconsistent are punished (Zaikman and Marks 2017). Although similar to behavioral theories, there is an element of modeling in this theory. It posits that individuals imitate the behaviors of others that result in social rewards, avoiding those that result in social punishments – however subtle or overt (Zaikman and Marks 2017). For example, boys and men are usually evaluated positively for having many sexual encounters and are judged harshly if they fail to express overt sexual success yet, the situation is reversed for girls and women (Bordini and Sperb 2013). Among teenagers, the popularity of girls decreases with the number of sexual partners she has (regardless whether this occurs within the context of a relationship or not), while the popularity of boys increases with the more sexual partners they have (Kreager and Staff 2009).

Although various researchers utilize these theories separately, Zaikman and Marks (2017) argue that each theory mostly likely has some predictive power when explaining the sexual double standard:

First, evolutionary theory is a likely explanation for the origins of the traditional double standard. Second, social role theory can explain more proximate manifestations of the sexual double standard through considering the influence of context, culture, and historical era. Finally, cognitive social learning theory can explain the manner in which the SDS is perpetuated (p. 418).

Current Research

The prevalence of a sexual double standard continues to be documented, both in quantitative

(Greene and Faulkner 2005; Lyons et al. 2011; Marks and Fraley 2006; Zaikman et al. 2016) and qualitative investigations (Farvid et al. 2017; Jackson and Cram 2003; Marks and Farley 2007; Reid et al. 2011). Although the nature and expression of the sexual double standard has shifted, at its core, the sexual double standard invokes traditional discourses of heterosexuality, such as the Madonna/whore binary (virtuous versus promiscuous), to negatively construct women's desire for, and participation in what is socially, culturally, or morally defined as "too much" sex (Ussher 1989). Research in the last decade has garnered some interesting insights into the morphing, yet persistent, nature of the sexual double standard, which affects women's and men's expression of sexuality differently.

For example, women, but not men, still report more shame and guilt after having casual sex due to the way this behavior can still garner negative judgment from others towards them (Campbell 2008; Littleton et al. 2009). Female university students also report engaging in less hookups or coital casual sex to avoid garnering a negative sexual reputation or pejorative labeling (Hamilton and Armstrong 2009).

Although there have been shifts in sexual norms, and pre-marital sex and sex in relationships is now acceptable for women, showing explicit sexual desire and engaging in "unconventional" sexual behaviors that are considered out of the norm for feminine sexuality can still be risky for women (Bordini and Sperb 2013). For example, women are judged more harshly than men for engaging in threesomes, having multiple sexual partners, and having sex with a much younger partner (Kreager and Staff 2009). Sexting is another arena where the sexual double standard is identified. Research indicates that teenage girls who are asked to produce specific forms of sexual display by teenage boys face moral condemnation and "slut shaming" (by peers, parents and adults) (Ringrose et al. 2013).

"Slut shaming" is new phrase that names (and critiques) the act of openly criticizing people, usually girls and women, for transgressing the boundaries of what is perceived appropriate conduct in relation to sexuality. Recently, a "reverse"

sexual double standard has also been identified – where men are judged more harshly for engaging in overtly sexual conduct (Thompson et al. 2017), as well as a backlash to individuals who openly "slut shame" (Papp et al. 2015). Such shift indicates that stereotypical and open expressions of the sexual double standard are becoming less socially acceptable. Yet, the sexual double standard has definitely not disappeared.

For example, in the liberated context of Norwegian high school graduation celebration, researchers have found that while overt slut shaming was rare among young adults, women who were perceived as engaging in sex and casual sex in specific ways were subjected to subtle moral judgments (Fjær et al. 2015). In this context, a slut was always positioned as "other" and seen as someone who did not value physical and sexual safety or lacked self-control when it came to sex. Hence the sexual double standard was still identified, but the boundaries of what constituted problematic sexual conduct, for women, had shifted.

Similarly, research by Farvid et al. (2017) with women who explicitly identified as engaging in and enjoying casual sex identified that:

At the outset, casual sex was framed as being pleasurable and acceptable for women to engage in and a sexual double standard in relation to casual sex was directly challenged by all the women. . . The threat of garnering a negative sexual reputation however, was linked to the women's silence around their casual sex experiences and overt displays of sexuality. . . [yet] certain types of casual sex display were talked about as not acceptable and rightly procuring someone (although, never them) a negative sexual reputation (p. 556).

Women who engage in what was considered "too much" casual sex (e.g., every night or every weekend) and for the "wrong" reasons (e.g., feel better about themselves or to get attention, or address emotional or psychological issues) were stigmatized in this context. We know that not only men but women evaluate other women based on the sexual double standard (Zaikman and Marks 2014). A phenomena called "defensive othering" has been used to explain how women who endorse the sexual double standard do so to distance themselves from what is perceived as a lower status women; conversely, men who endorse a reverse

sexual double standard distance themselves from the dominant group (Kettrey 2016).

The sexual double standard has been identified as operating on multiple layers. For example, there is a difference between identifying a societal level sexual double standard, a larger peer group double standard, and the standards by which women themselves buy into or adhere to (Farvid et al. 2017). In one study, teenage girls identified a societal and school-level prevalence of the sexual double standard, but support from close friends and peers was a buffer to such ideals being fully accepted or affecting the girls negatively (Lyons et al. 2011).

Other studies of adult women and men have indicated that an active and desiring sexuality for women is, overall, supported or validated (Farvid 2014; Reid et al. 2011), yet explanations of men's and women's behavior in specific contexts can produce double standards (Beres and Farvid 2010). For example, in a study looking at a hookup scenario followed by a "sexless" date indicated that while men and women were not judged differently for engaging in a hookup or desiring a date, the explanations given for the sexless date were imbued with a double standard (Reid et al. 2011). Women were described as seeking to remain chaste (on the date) in order to regain any loss of their sexual reputation (during the one-night stand), and the men were seen as going on a date in order to make the woman feel better about the hookup (i.e., a "pity date") (Reid et al. 2011).

While some research indicates that the sexual double standard is being openly challenged (Allen 2003; Farvid et al. 2017; Jackson and Cram 2003; Milnes 2010), deep analyses indicate that it has not fully lost its grip on how we understand, interpret, and judge sexual behavior. Beyond general sexism, the sexual double still results in more negative outcomes for women. Girls and women spend a considerable amount of energy negotiating the risks of expressing an unfettered sexuality, with reports of worry, anxiety, and shame in this context (Ringrose et al. 2013). Furthermore, women who endorse the sexual double standard are more likely to refrain from sex altogether and leave sexual safety measures in the hands of men

(Danube et al. 2016). Lastly, the sexual double standard still affects how women judge other women (Farvid et al. 2017; Lyons et al. 2011). The sexual double standard is hard to escape, even for individuals who are aware and critical of it (Farvid et al. 2017).

Conclusion

The sexual double standard represents a gender-specific dilemma when it comes to sexual conduct, which affects girls and women much more negatively. The expression and contours of the sexual double standard have varied historically, with liberalizing attitudes towards sex and female sexuality softening its expression. Yet, as this entry has demonstrated, while the boundaries of the sexual double standard have shifted, it remains a powerful force in contemporary culture, in shaping male and female sexuality, as well as how sexual behavior by men and women is understood and interpreted. It seems that a radical reworking of heterosexuality is still needed if the sexual double standard is to ever lose traction.

Cross-References

- Human Sexuality
- Sexism

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Sexual Strategies Theory

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Synonyms

Intersexual relations; Mating strategies

Definition

Sexual strategies theory (SST) is a middle-level evolutionary theory of mating strategies that both males and females adopt under different circumstances. It differs from previous theories in that it includes multiple motives each individual can have, such as short-term versus long-term mating, as well as when and why different motives would be predominant.

Introduction

Sexual strategies theory (SST) posits that humans have evolved a complex menu of mating strategies, that some of these mating adaptations are tethered to the temporal dimension of mating, and that although some mating adaptations are similar in women and men, some differ profoundly between the sexes (Buss and Schmitt 1993). Before describing the major premises, predictions, and empirical tests of SST, it is useful to briefly describe theories of mating prior to its articulation.

Previous theories typically posited singular mating motives, such as a quest for similarity, a search for complementarity, or the desire for equity. These theories had five major limitations that SST sought to rectify: (1) each posited a single mating motive, rendering them extremely simplistic; (2) all failed to explain why humans would be motivated by the singular drives; (3) all failed to specify the domains or contexts in which people sought similarity, complementarity, or equity, a degree of generality that precluded any domain-specific predictions; (4) all assumed that mating psychology was identical for men and women, precluding any sex-differentiated predictions; and (5) none specified functions, the adaptive problems solved by its central mating motive, thus divorcing mating psychology from any evolutionary anchoring. SST sought to rectify these limitations.

Nothing is closer to the central engine of the evolutionary process – differential reproductive success – than mating. Those who fail to select and attract a mate fail to become ancestors. To an evolutionary psychologist, it would defy scientific logic if evolution by selection had failed to forge a powerful set of adaptations surrounding mate selection, as it has in all known sexually reproducing species. SST posits, therefore, that whatever mating motives humans have exist because they solved adaptive problems that contributed directly or indirectly to successful reproduction over the long course of human evolutionary history.

The Two Major Axes of Sexual Strategies Theory

The two major axes of SST are temporal duration of mating (ranging from short-term casual sexual encounters to long-term committed mating relations) and biological sex (male, female). Biological sex is critical because humans differ in their fundamental reproductive biology. One difference is that fertilization occurs internally within women, not within men. A second difference is that women require a heavy 9-month investment of pregnancy

to produce a single child; men can produce that same child with as little as one act of sexual intercourse. And there are other key differences – women's fertility is cyclical, whereas men's fertility is not; women's fertility is sharply age-graded, whereas men's fertility is only gradually age-graded; post-partum, women incur the costs of breast-feeding, whereas men do not. SST posits that humans have evolved psychological and strategic mating adaptations to these sex-linked differences in reproductive biology.

Regarding the temporal dimension, humans have evolved a long-term mating strategy marked by heavy commitment, long-term pair-bonding, and biparental investment. This may seem obvious, but this sort of long-term committed mating is extremely rare among mammals, characterizing only 3–5%. Humans also have short-term uncommitted matings – one-night stands, casual hookups, brief affairs (e.g., Scelza 2011; Symons 1979). SST posits that the adaptive problems men and women recurrently had to solve differed as a function of this important temporal dimension.

Biological sex and temporal context generate a two-by-two matrix of adaptive problems, as shown in Table 1.

The Psychology of Short-Term Mating for Men and Women

Based in part on Trivers's (1972) theory of parental investment and sexual selection, SST posits that men had to solve adaptive problems of short-term mating such as increasing the number of sex partners accessible, identifying which women are sexually available or accessible, and minimizing the cost, risk, and amount of investment in each mating opportunity. A large volume of empirical data supports these predictions. Men, compared to women, are more motivated by short-term sex, desire a larger number of sex partners, let less time elapse before seeking sexual intercourse, find attractive women who display cues to easy sexual accessibility, and show a

Sexual Strategies Theory, Table 1 Mate selection problems men and women confront in short-term and long-term mating contexts

Mating type	Men	Women
Short-term	Increasing partner number	Immediate resources
	Identifying sexually accessible women	Evaluating ST as LT mates
	Minimizing cost and risk	Identifying good genes
	Minimizing commitment	Mate insurance, backup mates
	Identifying fertile women	Mate switching
Long-term	Paternity probability	Men able to invest
	Female reproductive value	Men willing to invest
	Commitment	Commitment
	Good parenting abilities	Good parenting abilities
	Gene quality	Gene quality
	Relationship load	Relationship load
	Longevity probability	Physical protection

Table is adapted from Table 1 of Buss and Schmitt (1993), p. 207

psychology and attendant behavior to minimize investment and entangling commitments in short-term mating contexts (Buss and Schmitt 1993; Haselton and Buss 2001; Schmitt 2003).

Women pursuing a short-term mating strategy face a different set of adaptive challenges. These include securing immediate access to economic resources, choosing sex partners with high-quality genes, evaluating short-term mates as potential long-term prospects, and cultivating potential backup mates for the goal of mate switching. Numerous studies support these predictions. Women prioritize extravagant resource displays in short-term mating (Buss and Schmitt 1993). They shift to preferring men high in masculine appearance and symmetrical features, two of which are hypothesized cues to good genes

(Gildersleeve et al. 2014). They cultivate backup mates, become distressed when their backup mates fall in love with others, and sometimes use short-term mating to exit an unhappy mating relationship to trade up to a better partner (e.g., Buss et al. 2017). SST, in brief, posits that both women and men have short-term mating within their strategic repertoire and that their psychology of short-term mating is differentiated in precisely the domains in which the sexes have had to solve different adaptive challenges of short-term mating recurrently over evolutionary history.

The Psychology of Long-Term Mating for Men and Women

In long-term mating, women and men face many similar adaptive problems, such as identifying a mate who will commit to them over the long haul, someone who will be a reliable partner, and someone who will be a good parent. Both sexes appear to have adaptations to solve these problems, such as looking for signs of love (a cue to commitment), prioritizing dependability and emotional stability in long-term mate preferences, and valuing good parent and good partner qualities such as kindness and agreeableness (Buss 1989, 2016; Buss and Shackelford 2008).

Men seeking a long-term mate have had to solve a critical adaptive problem – choosing a fertile mate or one who has high future reproductive potential. Since ovulation is relatively concealed in humans and fertility cannot be detected directly, SST posited that men would prioritize cues statistically correlated with fertility. Since women’s fertility is sharply age-graded, this yielded the predictions that men would prioritize physical attractiveness, since appearance provides a bounty of observable cue to youth and health and hence to fertility. Abundant empirical evidence supports this set of predictions. Men worldwide, compared with women, place a greater priority on physical attractiveness and relative youth in long-term mating (Buss 1989; Buss and Schmitt 1993; Kenrick and Keefe 1992). Due to

the adaptive problem of internal female fertilization and gestation, men seeking long-term mates also had to prioritize cues to mates that would increase probability of their paternity in offspring. And indeed, men place tremendous value on sexual fidelity in a long-term mate and dislike any indications of a history of promiscuous mating (Buss and Schmitt 1993). Men also have post-mate selection adaptations, such as sexual jealousy and mate-guarding effort, that function to increase the odds that their long-term commitment in one woman will result in offspring that are their own rather than those of rivals (Buss 2000; Daly et al. 1982).

SST posits that women pursuing a long-term mating strategy will prioritize, among other things, men who are both able to acquire resources and willing to invest those resources in them rather than in rival women. A large body of cross-cultural evidence supports this hypothesis. Women worldwide, compared to men, value resources and the qualities that lead to resources in long-term mates such as social status, ambition, and industriousness (Buss 1989). SST also posits that women had to solve the problem of protection and so will value men capable of protecting them from other men. Women indeed prioritize physical formidability, tallness, and athletic prowess, suggesting adaptations to solve this adaptive problem (Buss 2016).

Mating Psychology Is Context Dependent

Sexual strategies theory was designed as a complex theory of mating, positing a psychology contingent on biological sex and temporal context as central. Although abundant evidence has cumulated since it was first proposed in 1993, SST was designed to be open ended rather than the “last word” on evolved human mating strategies. Indeed, its authors articulated an agenda for future theorists and researchers that identified other likely contexts to which our psychology of mating would be contingent. One is *mate value* or a person’s level of desirability on the mating market. A second is *sex ratio* or the relative proportion

of men to women in any given mating pool. A third is an ecology of *parasite prevalence*. Research has confirmed that these and other contexts do importantly influence mating strategies (e.g., Buss and Shackelford 2008; Gangestad and Buss 1993; Schmitt 2016).

The authors of SST also speculated that individual differences were important and had to be explained by any complete theory of human mating strategies. Research since 1993 has increasingly focused on individual differences. As one example, research on the “dark triad” of personality traits (narcissism, Machiavellianism, and psychopathy) has shown that high scorers are more likely to pursue short-term mating, more likely to use deception as a mating tactic, and may even be more likely to use coercion or force by bypassing a cardinal feature of women’s mating strategy – female choice (Jonason et al. 2009). A second example, only dimly recognized by SST in 1993, is the importance of “good genes” in mate selection (e.g., Miller 2000).

Conclusions

Our evolved psychology of mating is extremely complex. We now know that theories of mating prior to SST were extraordinarily simplistic. Humans do not have a single mating motive that remains invariant across domains, temporal contexts, and biological sexes. Instead, humans have mating adaptations sensitive to temporal context, to the challenges each sex has recurrently faced, and to personal, social, and ecological factors such as mate value, sex ratio, and parasite prevalence. Every month, new “design features” of mating adaptations are being discovered, such as the importance of cues to sexual exploitability to short-term sexual attraction (Goetz et al. 2012), the relevance of personality to mating strategy pursued (Jonason et al. 2009; Schmitt 2016), and shifts from one sexual strategy to another depending on circumstances such as age, relationship history, ecology, and culture. Although we believe that SST, as originally formulated, provides many of the fundamentals of human mating that have been robustly supported by subsequent decades of

empirical research, much new knowledge has been discovered about mating that requires additions and expansions of its original formulation.

Cross-References

- [David Buss](#)
- [Differential Parental Investment](#)
- [Evolution of Desire, The](#)
- [Long-Term Mating](#)
- [Mating Strategies](#)
- [Sex Differences in Parenting and Parental Investment](#)
- [Sex Differences in Short-Term Mating Preferences](#)
- [Sex Differences in Long-Term Mating Preferences](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Short-Term Mating](#)
- [Women's Long-Term Strategies](#)

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Sexual Timing

- [Reproductive Timing](#)

Sexual Trauma

- [Sexual Abuse](#)

Sexual Unfaithfulness

- [Jealousy and Infidelity](#)
- [Sexual Infidelity Versus Emotional Infidelity](#)

Sexual Variants

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Sexual Versus Emotional Infidelity

- ▶ [Sex Differences in Jealousy](#)

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Sexually Accepting

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Sexually Antagonistic Genetic Variation

- ▶ [Intralocus Sexual Conflict](#)
- ▶ [Intralocus Sexual Conflict Across the Genome](#)

Sexually Antagonistic Hypothesis

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Synonyms

[Intralocus sexual conflict](#); [SAS](#); [Sexual antagonistic co-evolution](#); [Sexual antagonistic selection](#)

Definition

Sexual antagonism happens when selective pressures influencing males and females differ and the genes experiencing these conflicting evolutionary forces are said to be sexually antagonistic (Innocenti and Morrow 2010).

Hence sexually antagonistic genes produce a “sexually antagonistic” phenotype, which is selectively favored in one sex but disfavored in the other sex (Rice 1984).

The Sexually Antagonistic Hypothesis tests possible models of genetic transmission of a trait (phenotype) and compares with other selective hypotheses and models such as direct selection, mutation-selection, stabilizing selection, frequency-dependent selection, genomic imprinting, maternal effects, and overdominance in order to understand how genetic variability is produced and maintained.

Introduction

Sexually antagonistic selection has been hypothesized and then empirically tested to understand why genetic variation is maintained at a much higher level than mutation-selection models would predict (Foerster et al. 2007) and has been studied as a counteracting force against extreme sexual selection (Rice 1984; Pischedda and Chippindale 2006; Chippindale et al. 2001).

Evolutionary theory predicts, in the absence of other counteracting forces, the progressive depletion of genetic variation in natural populations as a result of the effects of selection. However, empirical observations suggest that genetic variation is preserved for many traits, even if they are supposed to be under directional or stabilizing selection. Researchers commonly explain this paradox with mechanisms that may lead to a balance between mutation and selection. On the contrary, theoretical models testing the genetic variance equilibrium under mutation-selection balance predict a substantially lower genetic variance than the empirically observed one. This suggests a role for sexual antagonistic

selection (Foerster et al. 2007). If the optimal fitness diverges between sexes, as in the Sexual Antagonistic Hypothesis, then a high-fitness male transmitting its genes to daughters could produce low-fitness individuals, and conversely high-fitness females could do the same with sons. In a detailed analysis with *Drosophila* strains, Pischedda and Chippindale (2006) indeed found that in the case of sexually antagonistic traits, any potential genetic benefits of sexual selection are significantly reduced, and in some cases even reversed over one generation, again because high-fitness males produce low-fitness daughters and high-fitness mothers produce low-fitness sons.

Sexual Antagonistic Selection in Animals

Evolution based on the benefits of acquiring “good genes” in sexual selection is only plausible with the reliable transmission of genetic quality from one generation to the next. Accumulating evidence suggests that sexually antagonistic genes with opposite effects on fitness when expressed in the two different sexes may be common in animals and even plants. These sexually antagonistic genes should then weaken the potential indirect genetic benefits of sexual selection by reducing the fitness of opposite-sex progeny from high-fitness parents. The fitness reduction of opposite-sex offspring of high-fitness individuals has been shown in not only in *Drosophila* but also in birds and mammals.

This is particularly apparent in the Lek paradox. In birds such as the sage grouse which seasonally reproduce in leks, males gather to engage in competitive displays, and females chose the best males after carefully inspecting the display. In the lek there is strong female mate choice, and apparently nothing else than sperm is contributed by the male. Under these conditions, a persistent female choice for particular male trait should erode genetic diversity in male traits and thereby remove the benefits of choice. Logically female choice should lead to directional runaway selection, resulting in a

greater prevalence for the selected traits. This, however, does not happen in lek-breeding animals. One possible solution is the handicap principle. The handicap principle describes how costly male ornaments provide females with information about the male's inheritable fitness (Zahavi 1975). Another possible explanation is the presence of sexually antagonistic selection that continues to maintain genetic variation among males from one generation to the other, despite strong female choice.

Intralocus sexual conflict is in this case the sexual antagonism between alleles at the same locus, one at the advantage of one sex and the second at the advantage of the other sex. This kind of conflict represents a tug of war between natural selection on both sexes and sexual selection on one sex. For example, the bill color in zebra finches. This ornamentation could be costly to produce; it is important only for males in mate choice but also makes an individual vulnerable to predators. The alleles for such phenotypic traits are under antagonistic selection, and this conflict is resolved via elaborate sexual dimorphism thus maintaining sexually antagonistic alleles in the population. Evidence indicates that sexual antagonistic selection may be an important constraint in the evolution of many traits (Arnqvist, and Rowe 2005).

In mammals an emblematic example of sexually antagonistic selection in a natural population has been studied in the red deer (*Cervus elaphus*). The researchers, based on a very long-term individual observation across generations, suggested that male red deer with relatively high fitness fathered, on average, daughters with relatively low fitness. This was due to a negative genetic correlation between estimates of fitness in males and females and selection favors males that carry low breeding values for female fitness (Foerster et al. 2007).

Mountain sheep (*Ovis canadensis*) might present similar sexually antagonistic traits; the horns serve for defense from predators but also for head to head contest in male intrasexual competition, while horns in females serve only for predator

defense; hence the optimal fitness trait (shape of the horns) differs sharply from the optimal fitness trait in females (Rice 1984).

X chromosomes have been considered as hot spots for accumulating sexually antagonistic alleles, as W chromosomes in birds and butterfly; other autosomal locations have also been reported to harbor sexually antagonistic alleles (Pischedda and Chippindale 2006). Recently it has been estimated that around 8 % of the *Drosophila* genome could be sexually antagonistic and not only in the X chromosome but also chromosome n 2,3 and elsewhere in the genome (Innocenti and Morrow 2010). All these sexually antagonistic genes might result in strong, and previously unsuspected, counterbalancing effects on sexual selection and maintain trait variability despite selective forces.

The Sexually Antagonistic Hypothesis in Humans

In humans the Sexually Antagonistic Hypothesis has contributed to explorations of the Darwinian homosexual paradox. Recently, some researchers found that the evolutionary origin and maintenance of male homosexuality in human populations could be explained by the sexually antagonistic model, in which genetic factors spread in the population by giving a reproductive advantage to one sex while disadvantaging the other. In this case, contrary to what has been commonly found in animals, the advantage is to the female and the disadvantage to the male.

Homosexuality has for long time been considered a Darwinian paradox. Genetic evidence suggests that in part homosexuality is influenced by genetic factors. This does not, however, explain the persistence in the population of a (direct) fitness-reducing trait (homosexuality). As it was previously discussed in animals, fitness-reducing genetic factors should progressively disappear from the population, supplanted by the most fit trait, but this has not happened in the case of human homosexuality.

Empirical Data

Previous empirical work showed a genetic influence (Getz 1993; MacIntyre and Estep 1993). Further studies suggested that at least in male homosexuals there are more male relatives which are homosexuals in the maternal line. In parallel the female relatives on the maternal side of homosexual men show a significantly higher fecundity as compared to relatives of heterosexual men (Camperio Ciani et al. 2004; Jannini et al. 2010; Iemmola and Camperio Ciani 2009; Camperio Ciani et al. 2009).

Up to recently, most genetic models have failed to explain the maintenance of homosexuality in all population and at all times at a low frequency (2–10 %) but much higher than expected by a mutation selection model; hence the paradox was used to suggest homosexuality as a learned behavior (Nicolosi 1997).

Models Tested

Researchers have considered a range of different hypotheses for the genetic diffusion of male homosexuality. These included: direct selection modes in which the fitness is solely influenced by an individual's genotype; models based on overdominance (the genetic maternal effects on sons; models for the heterozygote advantage (as is found in malaria resistance) (King et al. 2005); and other selection models for male homosexuality which included maternal effects and genomic imprinting; possibly involving epigenetic activity; and finally a Sexually Antagonistic Hypothesis based model.

Gavrilets and Rice (2006) first showed that single locus genetic models could produce a stable low-frequency homosexuality distribution. Challenged by these competing hypotheses, Camperio Ciani et al. (2008) have studied a number of models for a single di-allelic locus at either an autosomal or X-linked location, and various selection modes in each case, under the assumption of random mating. Their analysis first identified the

range of selection parameters guaranteeing a stable polymorphism and the persistence of the trait in the population. These results confirmed Gavrilets and Rice's (2006) findings that single-locus models are largely unstable as their parameter ranges are too narrow to allow for stable polymorphism under the normal variability of population conditions. This leads to either fixation or extinction of the genetic factors, contrary to all empirical findings.

However, once all single locus models were excluded, Camperio Ciani et al. (2008) screened a large set of di-allelic models and excluded them one by one. It was concluded that only a sexually antagonistic model could explain all the empirical findings including stable low frequency homosexuality, higher fecundity only in females of the maternal side, and higher frequency of homosexuality in the maternal line. The winning model of sexually antagonistic selection involving at least two genetic factors – at least one of which must be on the X chromosome (inherited in males only through their mother) and the other on the autosomes – accounted for all the known empirical data such as stable persistence of homosexuality at relatively low frequency, higher frequency of homosexuals on the maternal side, and higher fecundity on all maternal side female relative to the homosexual probands.

All other models did not fit the empirical data, either implying that the alleles would become extinct too easily, or otherwise invade the population, or failing to describe the distribution patterns of male homosexuality and female fecundity observed in the families of homosexuals.

The sexually antagonistic model further suggested a higher fecundity of paternal aunts of heterosexual samples as compared to homosexuals which was overlooked in the empirical observation and subsequently confirmed (Camperio Ciani and Pellizzari 2012).

The strongest confirmation of the sexually antagonistic model, however, came recently by Sanders et al. (2015). These authors conducted a genome-wide linkage scan on 409 independent pairs of homosexual brothers (908 analyzed

individuals in 384 families) searching for genes influencing the development of male homosexual orientation. These researchers found the presence of gene(s) on the X chromosome in the q28 region (as suggested long ago by Hamer et al. (1993)) and presence of gene(s) in the pericentromeric region on the autosome n°8. These findings are strong empirical confirmation of the previous sexually antagonistic theoretical model and mathematical findings (Camperio Ciani et al. 2008).

The sexually antagonistic model best fit the interaction of male homosexuality with increased female fecundity within human populations, in a rather complex dynamic, resulting in the maintenance of male homosexuality at stable and relatively low frequencies, and highlighting the effects of heredity of homosexuality in males and fecundity in females, through the maternal line.

The sexually antagonistic model suggests new insights into male homosexuality in humans. In particular, these findings point, with a particularly relevant example, to the occurrence of firstly well-identified sexually antagonistic characters in humans. This perspective may help shift the focus away from male homosexuality per se: Rather than concentrating on the sole aspect of the reduced male fitness that it entails, this places male homosexuality within the more general sexual-conflict framework of a genetic trait with gender-specific benefits, which may have evolved by increasing the fecundity of females and which neither disappears nor completely invades the gene pool. Increasing fecundity in females might be the evolutionary origin of this genetic trait in human beings (Camperio Ciani, et al. 2012).

An unexpected implication of the new models concerns the impact that the sexually antagonistic genetic factors for male homosexuality have on the overall fecundity of a population. The findings suggest that the proportion of male homosexuals may signal a corresponding proportion of females with higher fecundity.

In other words, the Sexually Antagonistic Hypothesis for male homosexuality as a corollary

to the empirical findings suggest, contrary to common prejudice, that due to male homosexual influencing genetic factors when a population reduces fecundity (due to cultural or gene culture coevolution) the relative frequency of male homosexuals increase while the female fecundity in the maternal line of male homosexual relatively increases, thus buffering fecundity decline.

The possible widespread occurrence of sexually antagonistic characteristics in selective processes, which play their evolutionary game by giving a fecundity benefit to one sex while disadvantaging the other, has only recently begun to be appreciated both in animals and in humans (Camperio Ciani et al. 2015). Sexually antagonistic selection might be soon confirmed as a key mechanism through which high levels of genetic variation are maintained in biological populations.

Other candidate traits subject to sexual antagonistic selection in humans could be male nipples. Nipples in males may serve no selective function (Kunz and Hosken 2009) but carry the cost of a differentiated tissue subject to tumors and possibly degeneration (Korde et al. 2010). This trait is, however, maintained in males at a relative cost due to the large fitness benefit that nipples have in females for nurturing and infant survival. This might be the trait among others explained by the Sexually Antagonistic Hypothesis which benefits the female fitness at a relative cost of the male one.

Conclusion

In conclusion, sexually antagonistic traits and sexually antagonistic selection could be much more common than previously expected both in animals and humans. Male homosexuality is just the first example of an unknown number of sexually antagonistic traits, which contribute to the maintenance of the natural genetic variability of humans. The new perspectives opened by the models developed for sexually antagonistic selection may also contribute to a better

understanding of most genetically based sexual conflicts, which are, at present, poorly understood in humans.

Cross-References

- [Adaptation](#)
- [Conflict Between the Sexes](#)
- [Controversies in Evolutionary Psychology](#)
- [Cost Inflicting](#)
- [Disruptive Selection](#)
- [Evolution of Female Resistance](#)
- [Evolution of Genitalia, The](#)
- [Evolutionary Arms Race](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Forced Copulation](#)
- [Frequency-Dependent Selection](#)
- [Genetic and Prenatal Components of Homosexuality](#)
- [Homosexuality](#)
- [Homosexuality Paradox, The](#)
- [Nonhuman Sexual Conflict](#)
- [Reproductive Strategies](#)
- [Semen Toxicity](#)
- [Sex Differences](#)
- [Sexual Behavior](#)
- [Sexual Coercion as a Mechanism of Sexual Selection](#)

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Sexually Antagonistic Polymorphism

- [Intralocus Sexual Conflict](#)
- [Intralocus Sexual Conflict Across the Genome](#)

Sexually Communicable Disease/Infection

- [Prevalence of STDs](#)

Sexually Dimorphic Gene Expression

- [Sexual Dimorphism and Sex-Biased Gene Expression](#)

Sexually Explicit Material

- [Pornography as a Human Product and Source of Data](#)

Sexually Transmitted Infection

- [Prevalence of STDs](#)

Sex-Work

- [Prostitution and Women's Short-Term Mating](#)

Sexy Son Hypothesis

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Synonyms

[Sexy Sons Hypothesis](#); [Fisher process](#); [Fisherian process](#); [Fisherian runaway process](#)

Definition

The *sexy son hypothesis* provides a theoretical framework to explain the evolution of social polygyny by female choice (Weatherhead and Robertson 1979). In some circumstances, a female would benefit in long-term fitness (number of grand-offspring) by forming a pair with an already-mated male instead that with an unmated competitor. The advantage, the SSH claims, arises because their sons inherit the father's propensity to be polygynous and, therefore, prolific. The hypothesis was conceived for bird species where some females, as a consequence of mate sharing, achieve less reproductive success if they form a pair with a

polygynous male instead that with a monogamous one. Over time, the hypothesis has been applied to other species, such as humans, and its conceptual framework extended to different aspects of mating system theory.

Introduction

According to Fisher (Fisher 1915), male ornaments result from the intersexual selection, that is, the female choice of males with exaggerated sexual secondary characteristics (ornaments). This hypothesis, known among others as the *Fisher process* or *runaway Fisherian process* (or selection), fell into oblivion for many decades and was rediscovered only in the 1980s (reviewed by Andersson 1994). The *sexy son hypothesis* (SSH) dates back a few years, which is probably the reason why the authors (Weatherhead and Robertson 1979) did not mention Fisher's work. Though, notable similarities exist between the two theoretical frameworks to the point that the two hypotheses are often confused with each other and, in the evolutionary literature, the term *sexy son* (or *sexy sons*) is usually a synonym of the *Fisher process*. The SSH was framed within a different context, that of the Polygyny Threshold Model (PTM, Orians 1969), which attempts to explain the evolution of social polygyny through female choice. According to the PTM. The breeding situation provided by a polygynous male to the female, according to the PTM, might be so much better than that of a monogamous male, that this difference would compensate for the loss of male assistance. The PTM yielded little empirical support as, on average, the females paired with monogamous males tend to raise more offspring than those mated to polygynous males (but see Santoro 2019 for a critical review of the hypothesis-testing framework of both PTM and SSH). Thus, the SSH expanded the PTM framework from the direct (offspring) to the indirect (grand-offspring) benefits the females mated to polygynous males would obtain through *sexy sons*. Overall, the foundation of both the PTM and SSH lays on the concept of *polygyny threshold*, that is, the point at which the difference

between the breeding situation (PTM) or genetic (SSH) quality of a monogamous and a polygynous male is great enough that a female would have similar fitness by forming a pair with one or another.

Controversies and Obstacles for the Hypothesis Testing

The SSH has been thought-provoking and controversial, raising many doubts in the theoretical and empirical field, especially regarding the hypothesis-testing framework (Huk and Winkel 2008; Santoro 2019). The first controversy raised by the SSH was about the possibility that males mislead females about their mating status. If the female cannot discern the mating status of the available-to-mate males, then the SSH's starting argument no longer holds. The chance this happens should depend on the reproductive biology of a species or even of a given population. Experimental evidence shows that females can discriminate the mating status of males, even in small passerine birds. Another controversy was on whether females might recoup initial (i.e., offspring) reproductive losses through *sexy sons*. This issue, raised by Kirkpatrick (1985), reveals the underlying similarity and difference between the SSH and the *Fisher process*. Both of them entail costs, but for different sexes. In the *Fisher process* the cost is for the chosen sex whose trait (e.g., ornament) evolves by the trade-off between sexual and natural selection, which respectively favors and limits it (the latter when the trait becomes detrimental to its survival). In the SSH, however, the cost is for the choosy sex. Kirkpatrick's models suggested that such an evolutionary process was impossible, something that, however, posterior analyses confuted (Pomiankowski et al. 1991). Other two controversies were on the unclear predictions of the SSH about the difference in fitness of the first (or primary) and the second (or secondary) female, and on the focus being on the population-level average outcomes instead that on the individuals' fates (Santoro et al. 2019).

The Sexy Son Hypothesis in Humans

Albeit the SSH was ideated for socially polygamous mating systems, where a female forms a breeding association with a male; it has been expanded especially in humans to the case of genetic polygamy by promiscuity. Thus, in *Evolutionary Psychology* (Wright 1994), the *sexy son* strategy consists of some females “mating promiscuously with sexually attractive males (handsome, brainy, brawny, and so on), risking the high male parental investment they might extract [by a monogamous relationship] but gaining the likelihood that any sons will be, like their fathers, attractive and therefore prolific.” The *sexy son hypothesis* in humans, therefore, seems to be used more frequently in a sense more akin to the *Fisher process* than to the original idea of SSH to explain the evolution of social polygyny.

Conclusion

The scope of the SSH is to provide a theoretical framework capable of explaining the evolution of social polygyny by female choice. Although often equated in literature, the *sexy son hypothesis* and the *Fisher process* are not equivalent so that it would be appropriate to differentiate the intellectual authorship of the two conceptual brands. Finally, it is worth mentioning that the female choice alone may not be sufficient to justify the mating systems evolution. As some think (e.g., Davies 1989), at least to some extent, sexual conflicts are likely to exist with one sex gaining benefits to the expense of the other.

Cross-References

- ▶ [Bright Male Hypothesis](#)
- ▶ [Female Choice and Sexual Conflict Theory](#)
- ▶ [Female Mate Choice](#)
- ▶ [Fisherian Runaway Selection](#)
- ▶ [Good Genes](#)

- ▶ [Male Ornamentation](#)
- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)
- ▶ [Mate Value](#)
- ▶ [Mate Selection Strategy \(Version of Sexy Sons Hypothesis\)](#)
- ▶ [Natural Selection](#)
- ▶ [Polygyny Threshold \(Behavioral Ecology\)](#)
- ▶ [Polygyny Threshold, The](#)
- ▶ [Secondary Sexual Characteristics](#)
- ▶ [The Handicap Principle](#)

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Sexy Sons Hypothesis

- ▶ [Sexy Son Hypothesis](#)

Shamanism

► Ancestor Worship

Shaping

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Synonyms

Method of successive approximations

Definition

The development of a new operant behavior using reinforcement of successive approximations of that behavior.

Introduction

Shaping is a procedure developed by Skinner, involving the presentation of reinforcement for exhibiting successive approximations of a target behavior. Successively closer approximations of a behavior are reinforced until the individual exhibits the desired response (terminal behavior).

Skinner's First Experiments and the Invention of the Term "Shaping"

Skinner first described the method of response differentiation by mechanically reinforcing successive approximations in 1938 (Skinner 1938) but had not used the term shaping until several years later in 1951. He conducted the first experiment using free-form shaping by hand (as opposed to via a mechanical device) a few years later in 1943, while working on Project Pigeon in Minnesota (Peterson 2004). Skinner

later said, referring to this occasion that "possibly our most impressive experiment concerned the shaping of behavior" and also noted "how much easier it was to shape behavior by hand than by changing a mechanical device" (Skinner 1979, p. 268). This event helped Skinner appreciate the significance of the reinforcement being mediated by biological connections with the animate social environment, as opposed to solely mechanical (Peterson 2004). The term *shaping* was first formally introduced in 1951: "The reinforcement gives you a means of control over the behavior of the animal. It rests on the simple principle that whenever something reinforces a particular activity of an organism, it increases the chances that the organism will repeat that behavior. This makes it possible to shape an animal's behavior almost as a sculptor shapes a lump of clay" (Skinner 1951, pp. 26–27).

The Shaping Procedure

Shaping (Skinner 1951) is a process where successive approximations of a behavior are reinforced, resulting in a gradual generation of the desired response (Powell et al. 2017).

According to Martin and Pear (2015), the following dimensions of behavior can be modified via a shaping procedure:

- Topography (form): Physical movements involved in the behavior
- Frequency: Number of instances of the behavior in a time period
- Duration: Continuous amount of time that the behavior lasts
- Latency: Time between the controlling stimulus and the behavior
- Intensity (force): Amount of energy expended on the behavior

An effective use of shaping involves (1) defining a well-specified terminal behavior, (2) choosing a starting behavior that is within the individual's repertoire, (3) preselecting the steps that qualify as successive approximations, and (4) moving through the shaping steps at an

appropriate pace – neither too fast nor too slow but be remaining flexible as progress is monitored (Martin and Pear 2015).

Behavior Modification Using Shaping

Shaping can be used to facilitate the demonstration of a particular response when an organism either lacks the skill or is not inclined to perform a desired behavior. Shaping can successfully be used in the process of learning a complex behavior or skill and has therefore useful applications in education (Snowman and McCown 2012). By reinforcing gradually increasing in complexity behaviors that resemble the desired outcome and ignoring those that do not, a person gradually develops the necessary skills and moves closer to completing a complex task.

Miltenberger (2016) advises to use the steps below to ensure that shaping is used appropriately:

- (i) Define the target behavior
- (ii) Determine whether shaping is the most appropriate procedure (shaping is appropriate for acquiring new behaviors)
- (iii) Identify the starting behavior (the first approximation, which must have some relevance to target behavior)
- (iv) Choose the shaping steps (each step must come closer to target behavior, but must require neither a too close or a too far change in behavior)
- (v) Select the reinforcers to be used in the procedure (ensure that the consequence is reinforcing for the individual, and reinforce immediately)
- (vi) Differentially reinforce each successive approximation of the target behavior when it occurs (when the behavior occurs reliably, start reinforcing next approximation while ceasing to reinforce the previous one)
- (vii) Move through the steps at a proper pace (move to the next approximation after a few successful exhibitions of behavior, and facilitate behavior by communicating

expectations and prompting appropriate behaviors)

Miltenberger (2016) describes a number of studies showing that shaping has various successful applications. Target behaviors such as verbal communication, toilet training, athletic performance, compliance with medical interventions, etc., can be facilitated through shaping in a variety of settings (classroom, home, therapeutic centers). It can also be used across various populations including children (Smeets et al. 1985), adults (Howie and Woods 1982), individuals with intellectual disabilities (Hagopian and Thompson 1999), and children with autism (Newman et al. 2009).

Conclusion

Shaping, the reinforcement of successive approximations of a behavior, can be used to facilitate the demonstration of a behavior when an individual may lack the skill or may lack motivation to perform it. Through shaping, several dimensions of a behavior can be modified, such as form, frequency, duration, latency, and intensity. The shaping procedure has several successful applications with a variety of populations and settings.

Cross-References

- [Operant Conditioning](#)
- [Positive and Negative Reinforcement and Punishment](#)

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Shared Genetic Material

- [Alarm Calling upon Predator Detection](#)

Sharing

- [Prosocial Behavior](#)

Shelter and Protection

- [Resources](#)

She-Male

- [Female Mimics](#)

Shifting Dominance

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Definition

Dominance alludes to a superior social status over other conspecifics that allows an individual exclusive or preferential access to resources. Shifting dominance denotes the alteration of social status such that a dominant individual becomes subordinate or vice versa. Transitional Power, Temporary Hierarchies, RHP.

Introduction

The establishment of dominance relationships dictates an organism's ability to access resources necessary for survival and reproduction. These dominance relationships are established based on intrinsic (i.e., body size, weaponry, aggressiveness) or extrinsic (i.e., prior experience, resource ownership) variables and result in a dominant and subordinate individual. Often, the status of "dominant" and "subordinate" is reference against individuals and are not necessarily global attributes of an animal. In animal populations, dyadic dominance relationships have the potential to manifest as multiindividual dominance hierarchies in which some individuals are consistently dominant to others. The establishment and maintenance of these hierarchies are beneficial in that they can allow organisms to reduce the time and energy allocated to contests (recognizing and submitting to a dominant individual reduces the chance of injury). However, hierarchical status can also be costly if organisms are unable to break away from a subordinate rank (subject to lower amounts or reduced quality of resources) or if a dominant

animal must constantly patrol and engage in intimidation tactics to maintain a dominant rank (Sapolsky 2005).

Hierarchy Formation

Crayfish (decapod crustaceans) are well known for their agonistic behaviors and the subsequent hierarchies that result from these contests. Due to high population densities, crayfish are in constant competition over access to resources and ideal microhabitat conditions. One of the most highly embattled resources is access to shelters as crayfish are preyed upon by several terrestrial and aquatic species, including conspecifics (Moore 2007). Establishment of dominance relationships and subsequent hierarchies can reduce the time and energy used to engage in contests and can guarantee resource access. Consequently, crayfish are known to rapidly establish stable, linear hierarchies (within 6 to 12 hours) that are considered relatively long lasting (up to 1 week) (Goessmann et al. 2000). However, the establishment of these hierarchies is chaotic, with several agonistic interactions and dominance shifts occurring. Furthermore, the duration of the stability of these relationships has been called into question. Firstly, the bulk of hierarchical stability studies that have been carried out are commonly performed in populations of no more than ten individuals confined to a finite space. This sets up a limited contestant pool with inhibited chances for escape which is not ecologically realistic. Moreover, there are several factors that play a role in agonistic interactions and subsequent establishment of dominance relationships which, when altered, can introduce very different hierarchical dynamics (Breithaupt 2011; Moore 2007).

Studies of agonistic interactions in crayfish have revealed that dominance relationships can shift due to alterations in contest experience (i.e., winner/loser effects), hormonal concentrations (e.g., serotonin), or information availability (Huber et al. 2001; Moore 2007). While each of these factors has been studied, and will be

presented here, as separate variables, it is important to note that each of these variables is intricately linked to affect dominance relationships and hierarchy establishment.

Several studies have shown that olfactory or chemical information plays a significant role in the dynamics and outcome of dyadic contests and hierarchy establishment. Specifically, crayfish urine has been implicated as a major source of chemical information during agonistic interactions. Although the primary function of this urine release is osmoregulatory, (Vogt 2002) individuals release urine significantly more often during agonistic contests than in nonagonistic behaviors. Furthermore, the timing, frequency, and amount of urine released are linked to the status of an individual and the eventual outcome of the contest (Breithaupt 2011). It is currently unclear whether urine release is meant as a signal of dominance or subordination. However, recent work has suggested that the chemical message might be context dependent. Regardless, absence or alteration of this chemical information can delay or inhibit the establishment of dominance relationships. Alternatively, exposure to chemical signals, even without social contact, has the ability to influence one's subsequent hierarchy rank (Breithaupt 2011).

Changes to an organism's social experience (i.e., winning or losing a contest) can also significantly affect subsequent interactions and establishment of dominance relationships. Crayfish have shown evidence of both winner and loser effects, as both winning and losing experiences have influenced the outcome of successive interactions (Moore 2007). For example, individuals that were given winning experiences, by being paired with smaller animals, were more likely to win future contests even when paired against hypothetically superior opponents (i.e., larger or resource-holding opponents) (Daws et al. 2002). However, winner and loser effects are finite. Winner effects have been shown to last anywhere from 40 minutes to 24 hours in crayfish (Moore 2007; Seebacher and Wilson 2007). Loser effects have been demonstrated, but duration of the effect is currently unknown. Furthermore, the frequency

with which individuals interact with each other can influence the stability of these dominance relationships. Larger populations (>30 individuals) of crayfish have been shown to exhibit varying fight dynamics (i.e., fewer, shorter contests) and reduced longevity of social recognition, causing the dominance relationships to be much more loosely associated (Patullo et al. 2009).

Changes in status through altered social experiences are accompanied by modification of hormonal composition and concentration which, in turn, influences behavior. For instance, social status (i.e., dominant or subordinate) affects the responsiveness of some neurons to circulating serotonin, in turn, altering the likelihood of an escape response (Yeh et al. 1996). Likewise, manipulative changes to circulating hormone concentrations can alter behavior. Exposure to certain neuromodulators (e.g., monoamines such as octopamine or serotonin) can influence performance in subsequent contests in crayfish. Serotonin has been shown to modulate aggression, agonistic displays (e.g., meral spread), and contest escape response (i.e., tail-flips) in such a way that serotonin injections prior to or during a contest can influence dominance rank outcome (Huber et al. 2001).

Conclusion

Establishment of dominance relationships is beneficial due to the reduction in time and the energy utilized to obtain vital resources when in competition with conspecifics. However, the stability and longevity of these relationships are dependent on several, interconnected factors. As social contexts and information availability change, so do contest dynamics and dominance relationships.

Cross-References

- [Baringa's \(1996\) Crayfish](#)
- [Dominance and Territory](#)
- [Dominance Hierarchies](#)
- [Function of Dominance](#)

- [Social Dominance Reduces Fighting](#)
- [Status and Dominance Hierarchies](#)

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Short and Long Term Preferences

- [Preferences in Long- Versus Short-Term Mating](#)

Shortcomings in the *Origin of Species* Related to Darwin's/Wallace's Theory of Natural Selection

► Gaps in Darwin's Initial Theory

Shortcomings of the SSSM

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Definition

The term "Standard Social Science Model" (SSSM) was first proposed by John Tooby and Leda Cosmides in their contribution to *The Adapted Mind* (Tooby and Cosmides 1992). The SSSM is based on the assumption that "the human psychological architecture consists predominantly of learning and reasoning mechanisms that are general-purpose, content-dependent, and equipotential . . . That is, the mind is blank-slate like, and lacks specialized circuits that were designed by natural selection to respond differentially to inputs" (Tooby and Cosmides 2005, p. 6). In the SSSM, the pre-existing or innate architecture of the mind is posited to have little or no role in determining behavior, which is instead conceived as being determined by social learning processes plus cultural traditions and environmental contexts.

Introduction

This entry will expand on the nature of the criticisms of the SSSM provided by evolutionary psychologists such as Tooby and Cosmides in part by contextualizing these criticisms alongside the various different extant methodologies of the SSSM. It will also discuss the relevance of evolutionary psychology more specifically to the methodology

of economics, outline the history of the development of the SSSM, consider some reasons why the SSSM has been so persistent, and also discuss some criticisms of Tooby and Cosmides' presentation of the SSSM that have been made in the literature.

In contrast to the SSSM, evolutionary psychologists assert that the mind is (in substantial part at least) composed of many evolved psychological mechanisms that are very specific in content and problem-focused in nature, and which play a very significant role in determining behavior. Two of the founders of evolutionary psychology have, in consequence, argued that "the social science project of the past century is not only wrong but radically misconceived" (Tooby and Cosmides 2005, p. 6). As they have explained:

The blank-slate assumption [of the SSSM] removes the central causal organizers of social phenomena - evolved psychological mechanisms - from the analysis of social events, rendering the social sciences powerless to understand the animating logic of the social world . . . For example, the nature of the social interactions between the sexes are partly rooted in the design features of evolved mechanisms for mate preference and acquisition. (Tooby and Cosmides 2005, pp. 6–7)

The SSSM is, therefore, methodologically stunted in this instance because it assumes that men and women make decisions about partner choice and reproduction using the same behavioral criteria, when, in fact, the cognitive architectures relating to these issues that have evolved in the two sexes are different in some very significant ways.

The Methodologies of the Social Sciences

Before claiming that something is "wrong and radically misconceived," as has been suggested by Tooby and Cosmides vis-à-vis the SSSM, the precise nature of the "something" needs to be carefully outlined. By inventing and promoting the phrase "Standard Social Science Model" (SSSM), Tooby and Cosmides might be taken to imply that all the social sciences utilize the same method or, at the very least, all the different social science methodologies share some common

methodological features. It will be suggested here that this latter proposition is much more accurate, as the social sciences evidently employ various different methodologies, but they do have some significant features in common. Therefore, it is necessary to explicitly outline the various different social science methodologies, in order to then identify their essential common features.

The three basic methods that have been identified as being employed in the mainstream social sciences are positivist, interpretive, and critical methodologies. Positivist methodology employs objective empirical observations combined with deductive logic in order to attempt to detect causal laws relating to human behavior; it is, therefore, quantitative and objective in nature. Interpretive methodology attempts to detect the meaning behind social actions and behaviors and how people create and maintain their social worlds; it is, therefore, constructivist and analytical in nature. Critical methodology attempts to uncover the real structures and processes that underlie the social world and also how they can be improved; it is, therefore, activist and quasi-political in nature (Garcia and Poston 2008, pp. 108–109). It can readily be seen that these three methodologies are in some senses quite different, but even so, they do share some important common elements.

From the perspective of evolutionary psychology, the three common most central (and erroneous) features of all three social science methodologies are as follows:

1. Social constructivism: that all human behavior is primarily determined by external social structures or exogenous cultural phenomena, such as class or gender
2. Individual homogeneity: that human beings are all behaviorally homogeneous, that is, they all calculate mentally in the same way when making behavioral computations
3. Cognitive void: that every human mind is born as a “blank slate,” with only a few inbuilt general processing mechanisms, on which cultural impressions, socialization, and “learning” are then applied (Barnett 2015, pp. 652–653)

In contrast to these three erroneous assumptions of the SSSM, evolutionary psychologists posit instead that a significant portion of (but certainly not all) human behavior is primarily or at least partly determined by inbuilt programming; that human beings are behaviorally heterogeneous, for example, that men behave (on average and in some ways) very differently from women; and that the human mind is born containing a significant amount of inbuilt cognitive architecture that has been evolved by processes of natural and sexual selection.

In addition, there are some other aspects of the SSSM that are questioned by evolutionary psychologists. For example, “the concept of ‘learning’ within the Standard Social Science Model itself tacitly invokes unbounded rationality, in that learning is the tendency of the general-purpose, equipotential mind to grow” (Tooby and Cosmides 2005, p. 13). Therefore, according to the SSSM:

... humans are endowed with a powerful, general cognitive capacity (intelligence, rationality, learning, instrumental reasoning), which explains human thought and the great majority of human behavior. In this case, humans putatively engage in successful social exchange through exactly the same cognitive faculties that allow them to do everything else. (Cosmides and Tooby 2005, p. 585)

This notion of learning equipotentiality is challenged by evolutionary psychologists, who maintain instead that natural and sexual selection processes would have favored the evolution of very specific cognitive architecture devoted to solving very particular problems. For example, specialized cognitive architecture devoted to social exchange calculations would have evolved, and this architecture would be computationally separate from other psychological mechanisms devoted to other specific tasks.

The Ten Steps of the SSSM

In addition to the basic case against the SSSM presented thus far, Tooby and Cosmides have also outlined a more detailed account of the intellectual

assumptions of the SSSM in 10 separate steps as follows:

- Step 1: Genetic variation does not explain why human groups differ dramatically from each other in thought and behavior. According to Tooby and Cosmides, this is the only step of the SSSM that is correct.
- Step 2: Although infants everywhere are the same, adults everywhere differ profoundly in their behavior and thought; therefore a fixed human nature cannot be the cause of these profound differences.
- Step 3: Because adult mental organization is absent from infants, they must acquire it from outside sources during their childhood development.
- Step 4: These outside sources are existing behavior in the social world and also culture.
- Step 5: The social and cultural elements that mold the individual both precede them and are external to them.
- Step 6: What determines the substance of human life – behavior, traditions, knowledge, social structures, and so on – is extragenetic culture.
- Step 7: The directional flow of influence is from the outer social world inward into the individual person.
- Step 8: Phenomena at the sociocultural level are mostly or entirely caused by other phenomena at the sociocultural level.
- Step 9: Therefore, something called human nature cannot play any notable role in generating social organization.
- Step 10: Psychology is, in consequence, merely the discipline that studies the processes of socialization through learning and through which individual psychological character is acquired (Tooby and Cosmides 1992, pp. 25–30).

Tooby and Cosmides argue that steps 2–10 are all based on faulty or naïve reasoning. For example, the fact that some aspects of adult mental content appears to be absent at birth is not relevant to deciding whether they are part of the inbuilt architecture of the mind or not, as female breasts are absent at birth, yet they still develop during

maturation. As they have explained: “In the worldview of the SSSM, biological construction goes on in the uterus, but at birth the child is ‘biologically complete’ except for growth; at this point, it is surrendered into the sole custody of social forces” (Tooby and Cosmides 1992, p. 81). This view is mistaken because it conflates the question of whether something is fully expressed at birth with whether a developmental mechanism for it is present at birth, which will be expressed at some point during maturation.

As another example, the idea present in the SSSM that “biological factors” are entirely separate from environmental factors is a naïve formulation of the relationship, as environmental influences require evolved cognitive architecture to act upon. As Steven Pinker has outlined:

The SSSM proposes a fundamental division between biology and culture. Biology endows humans with the five senses, a few drives like hunger and fear, and a general capacity to learn. But biological evolution, according to the SSSM, has been superseded by cultural evolution. Culture is an autonomous entity that carries out a desire to perpetuate itself by setting up expectations and assigning roles, which can vary arbitrarily from society to society. (Pinker 1999, pp. 44–45)

Instead of biology being “completely abdicated as an explanatory force in shaping human behavior” in the SSSM, evolutionary psychologists posit the accuracy of an interactive model in which both cultural and biological factors play important roles in determining this behavior (Saad 2011, p. 27). As Tooby and Cosmides have explained, “any learned behavior is the joint product of ‘innate’ equipment interacting with environmental inputs” (Tooby and Cosmides 2005, p. 31). They call this more realistic interactive model the integrated causal model (ICM), which posits the existence of a large number of content-specific psychological mechanisms that are adaptations to various problems that were faced in the evolutionary past (Tooby and Cosmides 1992, p. 49).

Another example of the difference between the SSSM and the ICM is that instead of the general and rather vague notion of “culture,” which forms a key part of the SSSM, Tooby and Cosmides posit that, in fact, culture is divided into two basic but separate components, evoked culture

and transmitted culture. Transmitted culture is what adherents of the SSSM usually mean by the term culture, i.e., ideas and behaviors that have been created in one mind and then transmitted to others. The concept of evoked culture is something unique to evolutionary psychology and the ICM, as it is pre-existing but dormant programming that is triggered in some groups more than others in relation to contingent encounters with specific environments. This distinction in the ICM is important in that it allows a more sophisticated account of cultural evolution than is possible in the SSSM, as evoked culture encompasses the differential activation of psychological mechanisms across space and time.

Finally, Tooby and Cosmides have explained that, when it appears that something could be an innate property of the mind, “the SSSM-oriented anthropologist or sociologist riffles through the ethnographical literature to find a report of a culture where the behavior (or whatever) varies . . . Upon finding an instance of reported variation,” the behavior is deemed to be socially constructed rather than innate (Tooby and Cosmides 1992, p. 43). The founding text of this “find behavioral variation” method of social attribution is declared to be Emile Durkheim’s late nineteenth-century book *The Rules of Sociological Method* (Durkheim 1962 [1895]). This method was subsequently adopted within anthropology by Franz Boas, whose student Margaret Mead was the author of the infamously misleading statement: “human nature is almost unbelievably malleable” (Salmon and Crawford 2008, p. 8).

However, the fact that, for example, many diverse languages are found across the globe is not in itself conclusive proof of the hypothesis that there is no species-general language acquisition instincts present in humans being at birth. It is quite possible that everyone is born with innate language-use programming, but how this programming is deployed in each individual is framed by the cultural traditions of the particular regions in which they are born and live, this combination of innate instincts plus cultural variations producing the many diverse languages across the globe.

A Short History of the SSSM

In order to understand how the SSSM has become so prevalent, its historical development requires some consideration. It can reasonably be suggested that the contemporary SSSM was created out of intellectual foundations developed across the nineteenth century and into the early twentieth century. However the idea of the human mind as a “blank slate” goes back to the philosopher John Locke, who used the phrase *tabula rasa* to describe the mind at birth in his *Essay Concerning Human Understanding* (1690).

By the mid-nineteenth century, social theorists such as Auguste Comte and Karl Marx had developed various social science concepts such as class, intuitively building on Locke’s assumption that experience rather than innate knowledge was the driving force of all social understanding. In the second half of the nineteenth century, a proto-Darwinian approach to psychology was developed in the works of Herbert Spencer and William James. Spencer and James both wrote the book entitled *The Principles of Psychology* in which evolutionary approaches to understanding the nature and function of instincts were promoted (Spencer 1855, p. 542; James 1891). Darwin explicitly acknowledged Spencer’s claim to priority in this innovation at the end of *The Origin of Species* (Darwin 1872 [1859], p. 428).

However, in the early twentieth century, the influence of behaviorism in psychology (and in the social sciences more generally) grew significantly, mainly through the work of J.B. Watson and B.F. Skinner. The behaviorist program “adopted the mechanist conditioning paradigm, focusing on the search for universal laws of learning,” for example, through experiments on the conditioning of small animals such as rats (Parker 1990, p. 23). As Watson explained, in a completed system of behaviorist psychology “given the response the stimuli can be predicted; given the stimuli the response can be predicted,” a simple mechanical view of animal behavior (Watson 1996 [1913], p. 262). Equipotentiality was also asserted: the same learning mechanisms were seen to apply to all stimulus/response reactions. Investigations into “mental states,”

consciousness, or constituent elements of the mind – i.e., consideration of instincts – were subsequently banished from psychology as being overly speculative and too imprecise for accurate measurement. By this means, investigations into the cognitive aspects of behavior were dropped from the psychologist's research program.

In parallel with this de-cognitization process in psychology, some of the other social sciences such as economics underwent similar de-psychologization trends. This is illustrated by the fact that some early twentieth-century economists had explicitly operated within a James-type instinct psychology framework (Barnett 2017a, b; Cosmides and Tooby 1994) and that at the end of the nineteenth century, it was declared by one well-known economist that “psychology must be to political economy - like the deity of Boethius – ‘path, motive, guide, origin, and end’” (Wicksteed 1899, p. 140). However, even though psychology had been an important component of many early economic theories, the formal separation of economics from psychology based on mathematical maximization concepts was eventually completed by economists in the 1930s/1940s (Bruni and Sugden 2007, p. F1). This meant that any pre-existing or residual focus on instincts in economics was dropped completely after World War II.

In turn, most of the social sciences subsequently adopted the social constructivist approach: focus was placed only on external structures and processes, e.g., class and gender in the case of sociology or kinship systems and linguistic structures in the case of anthropology (Evans 2005, p. 50). The concept of instinct still remained alive within the mid-twentieth-century ethology program, but this type of ethological approach had no influence at all on any of the social sciences after World War II.

Shortcomings in the Methodology of Economics

In parallel with the SSSM/ICM contrast, it can be argued that much contemporary mainstream

economics is also founded on “wrong and radically misconceived” principles, as it is based on the doctrines of methodological individualism and rational choice theory. These state that individual human beings are atom-like, separate units, the behavior of which is invariably grounded in individualistic motivations and which are focused exclusively on the maximization of certain specified units such as utility, consumer satisfaction, or pleasure, subject to various constraints (Basu 2008, p. 586; Rubin and Capra 2012, p. 7).

For example, one well-known and influential definition from the 1930s stated that economics studied human behavior as the relationship between ends and scarce means with alternative uses, clearly implying a type of resource-use optimization process. In direct contrast with this, the concept of inclusive fitness (or close family interest) proposed by evolutionary biologists as a foundation for their subject directly contradicts the individual maximization approach of mainstream economics. For evolutionary biologists, individuals attempt to maximize their inclusive fitness rather than their individual self-interest, which means that they aim to maximize their reproductive success rather than their individual utility, and any optimizing use of external resources is focused on fulfilling family interests, not individual self-interest.

In contrast to both economics and evolutionary biologists, evolutionary psychologists maintain that “observed human behavior dramatically and systematically departs from sociobiological predictions of generalized fitness striving (as well as the predictions of economic rationality ...)” (Tooby and Cosmides 2005, p. 13). Instead of single-factor maximization models, which posit, for example, that either individual fitness or inclusive fitness is maximized, evolutionary psychologists maintain that organisms act by following the evolved logic of the many psychological mechanisms that have been built into their neural architecture by natural and sexual selection processes that have operated over the evolutionary past. This means that animal behavior is much more complex than any single-factor maximization

model; instead, a range of different aims and goals are pursued at different times and in relation to different ecological contexts by the activation of various different psychological mechanisms, these goals sometimes being in conflict with each other.

This means in turn that the approaches of both methodological individualism and rational choice theory as currently deployed within mainstream economics are far too simplistic to be accurate. In addition, heterodox approaches to economics such as institutionalism and Marxism are also inaccurate in that even though they posit different foundations for the subject than the mainstream approach, these foundations are also too simplistic in their presentations of the many factors that go toward determining human behavior.

Why Has the SSSM Remained So Persistent?

It is worth considering some reasons for why the SSSM has persisted for so long in the social sciences across much of the twentieth century, despite recent research suggesting that it is flawed. One reason or part of the explanation is that Locke's tabula rasa conception of the mind as a "blank slate" goes back so far in the Western philosophical tradition that it has become ingrained in the social science collective consciousness and is accepted by some without question.

Another hypothesis for part of the explanation could be termed the political agenda hypothesis, and relates to the prevalence of what was previously characterized as critical methodology in some of the social sciences. The use of the critical method entails that some social scientists do not see themselves as neutral scientific observers, i.e., as devoted to presenting an objective view of how societies function, just as natural scientists do for the natural world. Instead, many "critical method" social scientists see themselves more as political activists devoted to changing the world for the

better, in terms that they define individually for themselves. In this case, they do not want to employ a methodology that is scientifically objective, but instead choose to adopt an instrumentalist methodology which supports their particular vision of social change.

However, when critical methodology is presented in this way it becomes apparent that it is not social science; it is political activism acting under the guise of science. This activist methodology is very reluctant to accept that there are any biological influences on behavior, as this is seen to potentially constrain or hinder the process of transforming the existing "wrong" world into the future "correct" world. Thus, the SSSM is still thriving, in part, because it is seen as providing a natural intellectual platform for critical method political activism.

Criticisms of Tooby and Cosmides' Account of the SSSM

Various criticisms of Tooby and Cosmides' articulation of the SSSM model have been presented, as in the book *Alas, Poor Darwin: Arguments Against Evolutionary Psychology* (2001), which (as the title suggests) is generally skeptical of the evolutionary psychology framework. In this book it is suggested that Tooby and Cosmides' argument against the SSSM illicitly switches between stating that in the SSSM the social is posited as not reducible and then suggesting that the cultural is posited as not reducible. As has been explained:

Where in the case of Durkheimian sociology the model is flawed because it postulates the social is not reducible to another level, Geertzian anthropology is flawed because it argues that the cultural is not reducible. Thus the central concept of the SSSM slips opportunistically between the "social" and the "cultural" according to the discipline under criticism. (Rose 2001)

However this criticism is easily dealt with in that Tooby and Cosmides actually suggest that, in their ICM, both the social and cultural realms are seen as being inextricably linked to the psychological

mechanisms that have evolved within the environment of evolutionary adaptedness (EEA). The fact that Tooby and Cosmides' criticism applies to both social and cultural realms is not therefore fatally problematic.

Other more substantive criticisms have been made of Tooby and Cosmides' use of the EEA concept. It has been argued that their view of the EEA is too simplistic and uniform, in that the EEA(s) might have been more diverse and heterogeneous than Tooby and Cosmides suggest. It could also be more difficult to accurately specify what adaptive problems were faced by our Pleistocene ancestors than Tooby and Cosmides allow; hence it might be more difficult to specify what psychological mechanisms have evolved (Mameli 2007, pp. 26–28). Elsewhere, it has been argued that the Tooby and Cosmides theory of mind – the brain conceived simply as an information-processing computer – is deficient in that it neglects environmental and bodily interactions (Barrett 2012, p. 24).

In response to such a range of criticisms, it is important to distinguish between those criticisms that reject the Tooby and Cosmides framework entirely, and those that accept many of the basic premises, but suggest that some of the specific ways in which Tooby and Cosmides apply evolutionary theorizing to understanding neural architecture might be flawed in some ways. The latter types of criticisms are generally more plausible than the former. As another example, it has been argued that, in order to become more realistic, evolutionary psychology needs to re-employ the nongenetic evolutionary processes that help individuals to adapt to their current environments that have been mistakenly rejected as part of the wider rejection of the SSSM by evolutionary psychologists such as Tooby and Cosmides (Wilson 2010, p. 122). Tooby and Cosmides might respond by pointing out that their concept of transmitted culture should be taken to include such nongenetic evolutionary processes within it.

Conclusion

Tooby and Cosmides' critique of the SSSM is a powerful and original – if highly controversial

outside of the bounds of evolutionary psychology – means of conceptualizing the development of the mainstream social sciences as they have developed over the past two centuries or so. If their criticisms of the SSSM are correct, as they have outlined, it would then mean that “the existing superstructure of the social and behavioral sciences . . . will have to be dismantled” (Tooby and Cosmides 2005, p. 6). Put more bluntly, the social sciences are all currently constructed on faulty foundations. In fact it could be suggested that, in addition to the social sciences being falsely constructed, the humanities are similarly erroneously grounded, as they currently utilize similar methodologies to the social sciences (Wilson 2010).

However in terms of outcome, it might (politely) be suggested to Tooby and Cosmides that they are being somewhat naïve in assuming that the social sciences (and the humanities), as they are currently constituted, will simply accept Tooby and Cosmides' profound criticisms on purely intellectual grounds and then transform themselves in the image of evolutionary psychology by their own volition. More likely to be the case is that the mainstream social sciences (and the humanities) will either ignore these criticisms for as long as possible or they will advance counterarguments against evolutionary psychology, or (most likely) a combination of both of these strategies. As the title of the book *Alas, Poor Darwin: Arguments Against Evolutionary Psychology* suggests, the latter strategy has been deployed for some time now.

Moreover, as this entry has suggested, there are strong reasons why the erroneous SSSM has prevailed for so long in academia, such as the political agenda of much of the contemporary social sciences (and the humanities), which dovetails closely with the “blank slate”/infinite malleability assumptions of human nature and the *Homo sapiens* brain that are promoted within the SSSM.

As has been outlined by other scholars, scientific revolutions do not often proceed purely through victories in rational debate. Holders of older, outdated views often cling to their pre-existing ideas until they die, regardless of the validity of their arguments, a good example of

this being Albert Einstein's opposition to quantum mechanics. In such cases, the new intellectual order only triumphs completely when the last of the old guard have passed away. Since there are very large numbers of individuals currently working in the mainstream social sciences, it might, therefore, take some considerable time for the Darwinian revolution to take full hold in this realm.

Cross-References

- [Behavioral Economics](#)
- [Blank Slate, The](#)
- [Economists and Evolutionary Psychology](#)
- [Evoked Culture](#)
- [Modularity of Mind](#)
- [Standard Social Science Model](#)

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Short-Term Mating

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Synonyms

Short-term mating strategies

Definition

Defining and outlining short-term mating.

Introduction

When researching mating behaviour, it is important to take mating strategies into consideration. It is evident that men and women seek a variety of characteristics when seeking a short-term or long-term mate, which are often guided by parental investment (Trivers 1972) and sexual selection. Wiederman and Dubois (1998) suggest that short-term mating refers to choosing and engaging in sexual activity with someone on a short-term basis, where the probability of cementing a long-term relationship is relatively low. In contrast, “long-term mating implies increased probability that the relationship will be long-lasting” (p. 154).

According to sexual strategy theory (Buss and Schmitt 1993), men and women seek traits, depending on whether they are engaging in short-term or long-term mating. For example, when seeking short-term mates, women typically seek status indicating traits which signal genetic quality, such as physical attractiveness and strength (Takahashi et al. 2006). One potential reason for choosing mates of genetic quality is that women have a stronger chance of producing

offspring who possess traits of genetic quality, thus increasing their offspring’s future reproductive success.

Both sexes value attractiveness, especially when seeking short-term mating opportunities, placing a great emphasis on body shape and size because they signal good health and genetic quality. Women may also view short-term mating as an opportunity to gain a long-term mate, choosing their mating partner by comparing his ability to provide resources and compare it to the quality of others. When seeking short-term and long-term mates, men typically seek youthful, attractive women, as youth is correlated with fertility (Karthikeyan and Locke 2015). These are/may be important indicators of reproductive fitness/success.

It is argued that men are more prone to engaging in short-term mating compared to women (Clark and Hatfield 1989), as men increase their reproductive successes through increased short-term sexual encounters. Furthermore, men engage in short-term mating as they have less to invest and lose compared to women (biologically speaking), thus linking to parental investment theory. Women have more to lose with short-term mating encounters due to risk of unwanted pregnancy, rearing offspring and an arguably damaged sexual reputation, deterring potential mates and increasing paternal uncertainty. As a result, our mate preferences can be guided by whether we seek short- or long-term mates.

Short-term mate seeking may provide women with an opportunity to assess a male’s ambition to succeed which may be a cue to earning potential in the future (Wilbur and Campbell 2010). In support, previous research has found that women value ambition when seeking short-term partners, which may be indicative of status and wealth (Wilbur and Campbell 2010) all of which can be explained by sexual selection theory and parental investment.

According to parental investment theory, women should exert more choice when selecting a mate. In support, men, especially when seeking short-term mates, are less choosy than women (Bhogal et al. *in press*). This may be because when engaging in short-term mating, men may be seeking sexual access and evaluating

physical cues related to sexual value, instead of long-term commitment. There are benefits in engaging in short- and long-term mating. For example, Margana et al. (2019) found that women were attracted to heroic and altruistic men for long-term relationships compared to short-term relationships.

A woman nurtures a child through breastfeeding, rearing, and nurturing. As a result, the secondary sexual characteristics evolved for men and women will naturally vary, with a male's resources and commitment valued by a woman and a woman's fertility and attractiveness valued by men. This may be a reason as to why physical attractiveness may be a marker of genetic quality, relating to the "sexy son hypothesis" which suggests that females choose attractive males in order to produce attractive offspring, which in turn leads to the child having increased reproductive successes and passing on their genes successfully. This could relate to several behavioral and physical traits. Physical attractiveness offers heritable benefits, assists in increasing the survival of good genes, and offers an array of advantages throughout one's life. By choosing a mate with heritable, quality traits, a female provides her child with a survival and reproductive advantage over others who do not possess these traits. In support, recent evidence suggests that women find physically attractive men more desirable than men of low attractiveness (Margana et al. 2019).

The benefits for women who engage in short-term mating may be gaining resources or producing offspring of a high genetic quality (Cashdan 1993). This argument suggests that women value attributes which relate to genetic quality, such as height, health, and masculinity, linking to the finding mentioned previously that women do also value physical attractiveness. This creates a market style environment which gives rise to competition for mates and gaining access to the highest quality mates available, creating a perfect environment for sexual selection to take its course.

Men of high mate value (those who are more physically attractive, are strong and have status/resources) invest more in gaining as many short-term mates as possible, whereas males with lower mate value invest more in long-term relationships.

Conclusion

In summary, short-term mating refers to mating behaviour which typically occurs without the intention of cementing a long-term relationship. As discussed, short-term mating involves using mating strategies that differ compared to when engaging in long-term mating, evident by sexual strategies theory.

Cross-References

- [Mating](#)
- [Mating Behavior](#)
- [Mating Strategies](#)
- [Violation of Short-Term Mating Preferences](#)

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Short-Term Mating Strategies

► [Short-Term Mating](#)

Short-Term Mating Strategy

► [Relationship Choices and Sexuality](#)

Showing-Off

► [Male-Male Competition or Male Provisioning?](#)

Shunning

► [Adaptations to Avoid Ostracism](#)

Siblicide

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Synonyms

[Fratricide](#); [Sororicide](#)

Definition

The killing of one sibling by another.

Introduction

Siblicide is the most extreme form of sibling conflict. Although somewhat rare in humans, siblicide is much more common in other animal species (e.g., various avian species). Sibling conflict (even though it may be intense at times) is considered to be a normal part of development, and the developmental literature indicates that most siblings outgrow these patterns of intense jealousy and conflict when they reach adulthood and move away from their parents' home (Buhrmester and Furman 1990). Siblicide, however, is most likely to occur in early and middle adulthood (Underwood and Patch 1999) when this is not the case – that is, when adult siblings continue to live together (Ewing 1997).

Relative to other types of familial homicides (e.g., spousal homicides, filicides – parents killing their offspring, and parricides – children killing their parents), siblicide is the rarest form of family homicide (Diem and Pizarro 2010). Investigations of siblicide in both US and Canadian samples indicate that siblicides account for approximately 1.4–2 % of all homicides (e.g., Daly and Wilson 1988). The most common form of siblicide is brother-killing-brother with over 70 % of siblicides fitting this pattern (Underwood and Patch 1999). Consistent with an evolutionary perspective, when siblicides do occur, the cause has typically been found to be competition over limited resources (Daly and Wilson 1988; Pollet and Hoben 2011). In addition, the fact that siblicide is rare among humans is consistent with predictions from Hamilton's kin selection theory (1964) that it would be more likely for siblings to join forces and cooperate with each other against nonkin versus kill each other. Siblicides do still occur, though, so the question becomes why? What factors influence the likelihood that one sibling will kill another versus form an alliance with their sibling?

Factors that Influence the Likelihood of Siblicide

Several proximate as well as ultimate factors have been identified as influencing the likelihood

that one sibling would kill another. Some of the proximate factors include poverty, mental illness, unresolved conflicts, stress, and substance abuse (Diem and Pizarro 2010; Ewing 1997). From an evolutionary perspective, ultimate factors include age (or birth order), sex, and degree of relatedness.

Age and Birth Order. As mentioned above, siblicide is most likely to occur in early and middle adulthood, not in adolescence as one might expect (Underwood and Patch 1999). Analysis of siblicide data in the USA from 1993 to 1995 found the mean age of siblicide perpetrators is 34.4 years of age, the mean age of siblicide victims is 33.3 years of age, and overall that 86 % of siblicide victims are between the ages of 20 and 59 (Underwood and Patch 1999). Crossculturally it also appears to be more likely for a younger sibling to kill an older sibling than the other way around (Daly et al. 2001; Underwood and Patch 1999). Furthermore, siblicides are most likely to occur between siblings who are within 5 years of age of each other. Interesting, the pattern of juvenile siblicides (in which both victim and perpetrator are under the age of 18) is reversed with older siblings being more likely to kill their younger sibling. One study found this opposite pattern of juvenile siblicide in 65 % of juvenile siblicide cases (Daly et al. 2001).

Circumstances that lead a younger sibling to kill an older sibling seem to involve a power struggle in which the older sibling attempts to assert his own dominance in the relationship (e.g., with regard to familial property, money, and entitlement) and the younger sibling defies the older sibling's presumed authority (Daly et al. 2001). This pattern was found crossculturally across societies in which older siblings are given privileged status over younger siblings (e.g., Japanese, American, British, Canadian, and tribal societies; Daly et al. 2001).

Sex. Analysis of siblicide data indicates that 76.1 % of siblicides have been brother-killing-brother, 11.9 % have been brother-killing-sister, 8.2 % have been sister-killing-brother, and 3.9 % have been sister-killing-sister (Underwood and Patch 1999). This pattern has been consistent across several studies (e.g., Daly et al. 2001).

This is consistent with the expectation that same-sex siblings would have more intense conflict given they would be more likely to be competing over the same parental resources and attention, which would be expected to increase as siblings are closer in age.

Degree of Relatedness. Perhaps due to its infrequency as well as the lack of clear relatedness information in many of the available homicide data sets, the effect of relatedness on siblicide has been greatly understudied and therefore is not well understood. From an evolutionary perspective, one would expect the likelihood of one sibling killing another would be moderated by their degree of relatedness, such that less relatedness would lead to more conflict and more incidence of siblicide. That is, fewer incidents of siblicide among full siblings (relative to half-siblings and step-siblings) would be expected. One study that investigated the relationship between relatedness and siblicide, however, found evidence inconsistent with that prediction. Specifically, findings indicated that approximately 93 % of siblicides involved full siblings, 4 % involved half-siblings, and 3 % involved step-siblings (Russell et al. 2007). However, consistent with evidence that step-parents use more brutal methods to murder their children than do biological parents (Daly and Wilson 1994), the siblicide data suggested that siblicides involving half-siblings and step-siblings were more brutal than those involving full siblings. Overall, the question of the relationship between relatedness and siblicide is still largely unanswered and more studies in this area are needed.

Conclusion

Although siblicide in humans is quite rare relative to nonhuman species, the underlying cause seems to be availability of (and conflict over) resources. Specifically, among humans, siblicides tend to be committed by adult siblings (with the younger sibling killing an older sibling) who are still living together in intense competition over parental resources, status, and power. Males are more

likely to be both victims and perpetrators of siblicide, whereas females are more likely to be victims. One key factor that requires more investigation is the effect of relatedness on human siblicide.

Cross-References

- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Kin Selection](#)
- ▶ [Sibling Conflict](#)
- ▶ [Sibling Studies](#)
- ▶ [Siblings](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)
- ▶ [Sibships](#)

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Sibling

- ▶ [Competition for Parental Investment](#)
- ▶ [Kin Elders Encourage Youth to Cooperate](#)
- ▶ [Sibships](#)

Sibling Comparison

- ▶ [Sibling Studies](#)

Sibling Configuration

- ▶ [Birth Order and Sibling Relationships](#)

Sibling Conflict

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Synonyms

[Sibling rivalry](#)

Definition

Competition and animosity among siblings.

Introduction

Sibling relationships in humans are often marked by feelings of love as well as hate for each other, providing a quintessential example of ambivalent relationships. In fact, relative to other types of familial violence (e.g., spousal and parent–child violence), sibling violence is the most common form of nonlethal familial violence (Wiehe 1997).

Although this conflict and animosity between siblings can be quite intense at times, it is typically considered to be a normal part of development (Cicirelli 1995). As such, sibling conflict has been linked to both potential benefits and costs in terms of psychosocial and cognitive development. For example, potential benefits identified include the development of greater empathy and perspective taking (Dunn and Brown 1994) as well as practice with social negotiation leading to greater conflict resolution and problem-solving abilities (Campione-Barr and Smetana 2010). Potential costs have been found to stem from especially intense and unresolved sibling conflict which may lead to a host of behavioral, psychological, and academic problems by early-mid adolescence (e.g., delinquent behavior and peer rejection; Cohen 2004). Although sibicide is rare in human siblings, extreme cases of sibling conflict can lead to the death of one sibling at the hands of another.

Sibling Conflict Theory: Predicting Likelihood of Competition Versus Cooperation

From an evolutionary perspective, sibling conflict would arise from competition over limited resources. For human siblings, this would mean rivalry over limited parental resources. Whereas across our evolutionary past, those resources may have been limited food and basic resources such as shelter; in modern societies, parental resources would involve time, attention, and money given to one's self versus their sibling(s). So, while factors such as availability of resources and number of siblings (i.e., number of potential competitors for those limited resources) would predict competition, what factors would predict the likelihood of cooperation among siblings (or other kin)? This question was difficult to answer from an evolutionary perspective until Hamilton (1964) proposed *kin selection theory* as well as the concept of *inclusive fitness*. According to Hamilton (1964), fitness not only involves one's own successful survival and reproduction (i.e., transmitting one's genes to subsequent generations) but

also the survival and successful reproduction of genetically related individuals. According to this theory, individuals may indirectly increase their own inclusive fitness by directing altruistic behavior towards their kin. According to *Hamilton's rule* (1964), the amount of altruism directed at one's kin is a function of whether the degree of relatedness and the potential fitness benefit the other person would receive outweighs the potential fitness cost to oneself (i.e., $r * b > c$). Therefore, we would expect to see greater cooperation (and less conflict) among individuals with greater genetic relatedness (e.g., full siblings vs. half siblings vs. nonbiologically related siblings). This prediction has been supported by evidence demonstrating adults report greater feelings of subjective closeness to closer related kin (e.g., sibling vs. cousin) as well as to kin relative to nonkin (Neyer and Lang 2003).

Observations of sibling conflict, including suggestions that it is a normal part of development such that animosity towards one's siblings should be expected, however would suggest that the relationship between genetic relatedness and cooperation (or altruism) is not that straightforward. *Parent-offspring conflict theory* (Trivers 1974) provides another example of how genetic relatedness does not always predict common interests nor altruistic behavior directed toward one another. Specifically, the genetic interests of parents and their offspring are often not identical and each will be selected to manipulate the other in order to suit their own genetic interests. While the offspring will want more parental investment (e.g., time, food, etc.), the more a parent invests in any one offspring, the less s/he may invest in other offspring. According to *parental investment theory* (Trivers 1972), how much a parent invests in any one offspring depends on the amount of resources available to the parent, the quality of the offspring, as well as their other offspring (current as well as potential future offspring). Assuming availability of resources and equal quality offspring, a prediction of this theory is that parents would invest equally in their offspring. Sibling conflict could still arise, however, because offspring are more closely genetically related to themselves than to their siblings and so would be

motivated to compete with their siblings for a greater share of the resources.

Evidence suggests that family size does predict levels of sibling conflict. Specifically, it has been found that although more siblings are associated with more overall incidents of sibling conflict, fewer siblings are associated with more severe acts of violence (Straus et al. 2006). Studies which have investigated proximate explanations of sibling conflict found the most commonly cited sources of conflict (cited by both older and younger siblings) involved issues of relative power, self-interest (e.g., sharing of personal items), violation of rules (e.g., perceived immaturity and inappropriate behavior), as well as interests outside the family (McGuire et al. 2000). Across different ages from toddlerhood through adolescence, the most commonly cited source of conflict (in terms of both frequency as well as intensity) has been the sharing of personal space and possessions, while the least cited source of conflict has been competition over parental attention (Campione-Barr and Smetana 2010; Dunn and Munn 1987; McGuire et al. 2000; Steinmetz 1977).

Factors That Affect the Prevalence and Intensity of Sibling Conflict

Some proximate and ultimate factors have been found to influence both the prevalence as well as the intensity of sibling conflict. Proximate factors include temperament and differential parental treatment and ultimate factors include sex, relatedness, birth order, and birth spacing (including length of coresidence).

Temperament. Brody and colleagues (1987) found that differences in temperament of younger children – or personality differences in older children – are associated with sibling conflict. Specifically, it was found that higher levels of activity and emotional intensity lead to greater levels of aggression (and less prosocial behavior) directed toward their sibling. For female sibling pairs, this was true when both the older and younger sisters had higher levels of activity and emotional intensity. For male sibling pairs, greater levels of

conflict were found when the younger brother had higher levels of activity and the older brother had higher levels of emotional intensity. Furthermore, in the male sibling pairs, it was found that any aggressive behavior from the younger brother led to reciprocated aggression from the older brother. Although temperamental differences predicted frequency and intensity of sibling conflict, overall the greatest conflict was observed among siblings in which both possessed traits of higher activity and/or emotional intensity.

Differential parental treatment. Evidence suggests that children as young as 3 years of age actively monitor their siblings' relationships with their parents relative to their own and are sensitive to differences in parental treatment between themselves and their siblings (Dunn and Munn 1985). Perception of differential parental treatment between siblings has been associated with greater levels of sibling conflict (Brody et al. 1992a, b). Shanahan and colleagues (2008) found that the effect of perceived differential treatment on the sibling relationship is moderated by birth order. Specifically, firstborn children who perceive more favorable maternal treatment directed at their younger sibling tend to withdraw from the relationship; whereas secondborn children tend to respond by directing more aggression to the favored older sibling.

Sex. Evidence suggests that not only do boys have more conflict with their siblings than do girls (Brody et al. 1985) but boys also are more violent toward their siblings than are girls with the highest level of sibling violence occurring among brothers (Straus et al. 2006). Boys tend to be less violent with sisters than with brothers. Although across all ages girls are less likely to use physical violence relative to boys, girls with brothers tend to be more violent than girls with sisters. While not physically violent, opposite-sex siblings have more conflict than same-sex siblings (Campione-Barr and Smetana 2010).

Relatedness. Surprisingly, despite the already mentioned theoretical relevance of genetic relatedness to the question of sibling conflict, the effect of relatedness on the frequency and intensity of sibling conflict has been understudied in human research. Instead, studies investigating the effect

of relatedness on sibling relationships have mainly focused on the solidarity of sibships finding a preference for full siblings over half-siblings (Jankowiak and Diderich 2000), greater interaction and contact as a function of closer relatedness (Pollet 2007; White and Riedmann 1992), as well as higher levels of cooperation and closer relationships between monozygotic twins than dizygotic twins (Segal 2005). One recent study investigated the effect of relatedness between siblings on the level of sibling conflict and found greatest levels of conflict between nonbiological siblings, followed by full siblings, with the lowest level of conflict between half-siblings (Salmon and Hehman 2015). These findings were not consistent with predictions that full siblings would have the least amount of conflict nor were they consistent with findings from the sibling solidarity research. The discrepancy in findings regarding the effect of relatedness on solidarity versus conflict may suggest that different mechanisms underlie those two relationship outcomes such that relatedness does not decrease conflict as it increases solidarity (at least when it comes to conflict between full vs. half-siblings). Future research is needed to explore possible explanations for the differences found with regard to the effect of relatedness on sibling relationships.

Birth order. Firstborns are more likely to invest in their siblings as well as maintain closer contact relative to laterborns (Pollet and Nettle 2009). Middleborns tend to have less positive perceptions of their parents relative to first- and lastborns and prefer to have close relationships with a nonrelated friend versus kin (Salmon 2003). There also appear to be birth order effects on the sources of sibling conflict with older siblings citing the younger sibling's immaturity as a source of the conflict and younger siblings citing rejection and aggression from the older sibling as a source of the conflict (Buhrmester and Furman 1990).

Birth spacing and length of coresidence. Greater levels of conflict have been observed in siblings who are closer in age, with the greatest level of conflict occurring between siblings who are within 2 years of age of each other and presumably would be competing over similar

parental resources as they would be in similar stages of development with similar needs (Cicirelli 1995; Pollet 2007). Evidence suggests that birth interval does influence the level of conflict with longer birth intervals (i.e., greater spacing) associated with less conflict (Salmon and Hehman 2015). Length of coresidence could also affect levels of sibling conflict with longer duration of coresidence perhaps contributing to a greater sense of solidarity and sibship, hence less conflict. To date, only one study has investigated the role of coresidence on levels of sibling conflict, but contrary to what was expected it found that less coresidency was associated with less conflict (Salmon and Hehman 2015). This could be simply due to less opportunity for conflict (as well as solidarity) to arise with less coresidency, but further research is needed in this area.

Conclusion

Given that sibling relationships are some of the most enduring relationships across the life span (Cicirelli 1995), there is great potential for competition as well as cooperation among siblings. Proximate factors that lead to increased sibling conflict include temperament (with greater conflict among sibling pairs in which at least one has higher levels of activity and/or emotional intensity) as well as differential parental treatment (with greater recognition of differential parental treatment leading to greater conflict). Ultimate factors that lead to increased sibling conflict include sex (with boys being more aggressive towards their siblings than girls and brother-brother pairs experiencing the greatest levels of conflict), relatedness (with greater conflict between nonbiological siblings vs. related siblings), birth order (with birth order affecting perception of the source of the conflict), and birth spacing (with greater conflict between siblings who are closer in age). The effects of relatedness and length of coresidence on the frequency and intensity of sibling conflict is still understudied and needs further investigation to fully understand how those factors influence sibling relationships.

Cross-References

- [Hamilton's Rule and Genetic Relatedness](#)
- [Kin Selection](#)
- [Siblicide](#)
- [Sibling Studies](#)
- [Siblings](#)
- [Siblings Pose Unique Adaptive Problems](#)
- [Sibships](#)

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Sibling Constellation

- [Birth Order and Sibling Relationships](#)

Sibling Design

- [Sibling Studies](#)

Sibling Method

- [Sibling Studies](#)

Sibling Order

- [Birth Order](#)

Sibling Position

- [Frank Sulloway \(1996\) On Birth Order](#)

Sibling Position Effects

- [Birth Order and Parental Investment](#)

Sibling Relationships

- [Full Siblings Versus Half Siblings](#)

Sibling Rivalry

- [Sibling Conflict](#)

Sibling Spacing

- [Competition for Parental Investment](#)

Sibling Studies

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Synonyms

[Sibling comparison](#); [Sibling design](#); [Sibling method](#)

Definition

Research designs that use sibling comparisons to infer genetic and environmental contributions to phenotypes.

Introduction

Sibling studies are a class of research methodologies that compare siblings within and/or between families. A genetically informed subtype of sibling study utilizes information about genetic relatedness between siblings and principals of genetic inheritance to infer both environmental and genetic influences on phenotypes. Genetically informed sibling studies include monozygotic (MZ) and dizygotic twins (DZ), nontwin full siblings, half-siblings, and adopted siblings.

Twin Designs

Basic twin studies compare concordance or correlations between pairs of MZ and DZ twins to evaluate trait heritability. Monozygotic twins are genetically identical (i.e., identical twins) whereas dizygotic twins share only 50 % of their genes, on average, and are genetically the same as full siblings (i.e., fraternal twins). Within-pair correlations between MZ and DZ twins provide information about the relative contributions of additive genetic, shared environment, and

nonshared environmental influences through statistical modeling. Twin studies operate under a number of statistical and conceptual assumptions that are generally robust against violations (Barnes et al. 2014). Classic twin studies can also include other sibling types, such as full, half-, and stepsiblings (e.g., McGuire et al. 1994; O'Connor et al. 1995). Additionally, more complex research designs have been developed based on twin methodology such as twins reared apart (Bouchard et al. 1990), the Children of Twins (CoT; D'Onofrio et al. 2003; Silberg and Eaves 2004), and Extended Children of Twins designs (ECOT; Narusyte et al. 2008; see ► “Twin Studies”)

Differential Sibling Exposure Design

Unlike twin designs that compare within-twin correlations between MZ and DZ twins (and other siblings), the differential sibling exposure design relies exclusively on full siblings reared in the same family. This method is a form of matched-pair design where siblings are effectively matched on potentially important and unmeasured factors such as culture, socioeconomic status, and religion by virtue of developing within the same household. Consequent within-family sibling analyses are therefore adjusted for these kind of family-wide confounds. Importantly, this within-family sibling design also controls for genetic liability (through randomization), since genetic effects are assumed to vary randomly as a function of birth order (i.e., the alleles of parents' genes are randomly distributed across siblings through meiosis). In other words, because there is no reason to suspect that genetic liability for anything will vary systematically with birth order, in sufficiently large samples of sibling pairs, random deviations in genetic liability are averaged out.

Measuring sibling differences in environmental exposures is key to the differential sibling exposure design. For example, this design has been used to examine the effects of father absence and paternal characteristics on adolescent girls' age at menarche and risky sexual behavior.

Consider an older and younger sister whose parents divorced when the older daughter was 9 and the younger daughter was 3 years old. In this scenario, the older daughter will have been exposed to a father present household for 6 additional years compared to her younger sister. The older and younger sister, therefore, differ in their exposure dosage to a father absent household and associated paternal characteristics (Tither and Ellis 2008; Ellis et al. 2012). Because the research design controls for both genetic liability and family-wide environmental confounds, this design is a causally informative method for evaluating the impact of differential exposure to fathers on sisters' developmental outcomes (in this case reproductive functioning). This design could potentially be used to examine differences between siblings in any trait as a result of differential environmental exposures that were not caused or influenced by the siblings themselves (e.g., differential prenatal exposure to smoking; D'Onofrio et al. 2012).

The differential sibling exposure design rests on a number of assumptions. These include that the siblings are full biological sibling pairs (same mother, same father), that the candidate environmental factor differs across siblings, that differential exposure to the candidate environmental factor was not influenced by either of the siblings' characteristics or behavior (as occurs with self-selection into environments), that one sibling does not influence the other sibling's exposure to the candidate environmental factor, that the differential environmental exposure was large enough to influence the target phenotypic outcome, and that there was a large enough number of sibling pairs to randomize genetic effects across birth order.

An additional assumption common to this and other sibling designs is generalizability. Generalizability in sibling studies stipulate that the findings derived from sibling comparisons apply to individuals. The generalizability assumption may be particularly important for twin studies given the uniqueness of twin rearing experiences relative to singletons. However, there demonstrated similarities on a number behavioral and developmental outcomes between twins and singletons (Barnes and Boutwell 2013).

Conclusion

Sibling studies are a collection of research designs useful for teasing apart genetic and environmental influences on behavior and other outcomes. Sibling designs utilize similarities and differences in genetic relatedness within and/or between families to draw conclusion about the relative contributions of genes and environments. These family-based methodologies may include monozygotic twins, dizygotic twins, full siblings, half-siblings, stepsiblings, and/or adopted siblings. Twin studies are a common genetically informed sibling design although there are many other sibling designs that permit inferences about genetic and environmental contributions, such as the differential sibling exposure design.

Cross-References

- [Genetic Influences of Puberty](#)
- [Siblings](#)
- [Problem of Genetic Inheritance, The](#)
- [Twin Studies](#)

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Sibling Violence

- [Familial Violence](#)

Siblings

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Synonyms

[Brothers](#); [Close kin](#); [Full sibling](#); [Sisters](#)

Definition

Individuals born of the same mother and father.

Introduction

The term *sibling* refers to the biological relationship between two individuals who share the same biological mother and biological father. This term is often qualified with the adjective *full* (i.e., *full sibling*) to differentiate between other types of sibling relationships such as *half sibling* – which indicates that two individuals have only one biological parent in common – and *step sibling* – which indicates that two individuals do not share the same biological mother nor the same biological father. Step siblings are labeled as such because one of the individuals' parents (i.e., the mother or the father) has courted and married either the mother or the father of the second individual.

Sibling relationships have often been the subject of study in evolutionary psychology. In fact, many evolutionary psychological theories have accounted for the variance in behavior between siblings, as well as the differences in behavior between full siblings, half siblings, and step siblings. Evolutionary psychologists have been able to adequately explain the variance in altruism between siblings (Burnstein et al. 1994; Fitzgerald and Colarelli 2009), the reasons for sibling rivalry (Michalski and Euler 2008), and personality differences in siblings based on the order of their birth (Sulloway 1995, 1996). Each of these theories will be briefly addressed in this entry.

Kin Selection Theory

Kin selection theory accounts for altruistic actions between kin members as a means of maintaining and/or improving the reproductive success of one's genes (Burnstein et al. 1994; Fitzgerald and Colarelli 2009; Hamilton 1964). Theoretically, if one possesses a gene that is responsible for motivating life-threatening altruistic behavior

(e.g., running into a burning house to save someone, willingness to donate an organ, etc.), that particular gene stands a greater chance of survival and reproduction if it motivates altruistic behavior toward one's kin (i.e., individuals who have a greater chance of also possessing a copy of this altruism allele). Therefore, one may be more inclined to risk his/her life to save an individual if the recipient of this altruistic act is closely related to the altruist (Burnstein et al. 1994; Hamilton 1964).

Because individuals receive half of their genes from each parent, and full siblings share both biological parents, there is an approximate 50% probability of both siblings possessing the same gene – in this case, the gene that is responsible for altruistic behavior. This is often referred to as $r = 0.50$, in which r refers to the genetic relatedness between the two individuals (Hamilton 1964). Half siblings, only sharing one biological parent, possess $r = 0.25$ (an approximate 25% probability of both siblings possessing the same gene), and step siblings do not share any biological parents, so they possess $r = 0$ (Burnstein et al. 1994; Fitzgerald and Colarelli 2009; Hamilton 1964).

If kin selection theory is true, then studies should show an increased likelihood of life-threatening altruistic behavior between individuals of greater genetic relation. In fact, data from several studies have found support for this claim. Individuals are significantly more likely to risk their lives to save full siblings over half siblings (Fitzgerald and Colarelli 2009) and step siblings (Burnstein et al. 1994).

Sibling Rivalry

While full siblings share $r = 0.50$ and are therefore more likely to risk their lives to save each other, research into sibling rivalry has indicated that individuals may also place greater emphasis on one's own survival – at least in regard to parental resource acquisition – than a sibling's survival (Michalski and Euler 2008). Survival during youth is often influenced by the reception of parental resources – these resources refer not

only to food but emotional warmth and security as well.

Because parental resources are finite, siblings may compete with their fellow siblings for these parental resources. These competitive behaviors may manifest in the form of one sibling exaggerating his/her need for parental resources, even at the expense of another sibling (Michalski and Euler 2008). Dunn and Kenrick (1982) found that children may engage in less developmentally mature behaviors (e.g., acting significantly younger than their chronological age) once a younger sibling is born. This behavioral regression is believed to occur as a means of diverting parental resources to one's self instead of to the newborn sibling.

Birth Order

Birth order refers to the chronological position, relative to one's siblings, in which one was born. For example, a firstborn child refers to an individual who was born before all other siblings. A later-born child refers to an individual who was born after one or more siblings. Many individuals have theorized that differences in birth order – due to variance in selective pressure from the environment, such as parental care and attention – may lead to differences in personality between siblings (Sulloway 1995, 1996). More than 200 studies have been conducted on this subject.

Frank Sulloway theorized that birth order may account for many differences in the five-factor model of personality – extraversion, conscientiousness, agreeableness, neuroticism, and openness (McCrae and Costa 1987) – between siblings. According to birth order theory, firstborn children will possess higher levels of extraversion, conscientiousness, and neuroticism than their later-born siblings. Firstborn children will also possess lower levels of agreeableness and openness than their later-born siblings.

Sulloway's (1995) meta-analysis of 196 birth order studies found support for this relationship

between birth order and the five-factor model of personality. Specifically, firstborn siblings were more talkative, more assertive, more responsible, more organized, more achievement-oriented, more anxious, more fearful, and more neurotic than their later-born siblings – indicating higher levels of extraversion, conscientiousness, and neuroticism. Also, firstborns were less approachable, less easygoing, less independent, and more traditional than their later-born siblings – indicating lower levels of agreeableness and openness. However, the relationship between birth order and personality is quite controversial. While many studies have found support for the above-mentioned relationships, many other scientists have been unable to replicate similar findings (Beer and Horn 2000; Freese et al. 1999).

Conclusion

Evolutionary psychology has provided many theories to account for sibling cooperation, rivalry, and differences in personality. While the three theories discussed in this entry – kin selection theory, sibling rivalry, and birth order – provide supported explanations for behavior between siblings, they are not the only theories that account for sibling behavior, nor do they account for all sibling behavior. Evolutionary psychologists continue to conduct research and evaluate all theories related to sibling relationships and behavior.

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Birth Order and Sibling Relationships](#)
- ▶ [Full Siblings Versus Half Siblings](#)
- ▶ [Half-Siblings in Human Evolutionary History](#)
- ▶ [Higher Survival with Older Siblings](#)
- ▶ [Presence of Siblings](#)
- ▶ [Sibling Conflict](#)
- ▶ [Sibling Studies](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)
- ▶ [Sibships](#)

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Siblings Pose Unique Adaptive Problems

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Synonyms

Brother; Sibships; Sister

Definition

Siblings are individuals with mutual parents. Full siblings share both parents, while half-siblings

only share one parent. In consequence, on average 50% of the segregating genes of full siblings are same, whereas for half-siblings the number is 25%. According to kinship selection theory, siblings are expected to behave altruistically toward each other, because the mutual genes imply inclusive fitness benefits of such behavior. However, siblings are also expected to compete for parental resources. The opposing forces of cooperation and conflict strongly define sibling relations.

Introduction

Siblings shape each other's childhood environments significantly, and in a way, each child is born into a different family. While altruistic actions are expected from siblings due to mutual genes, in infancy siblings mostly represent competition for parental resources. A firstborn receives a hundred percent of parental investment for the first few years of life, and the last-born's infancy is not interrupted by new babies. The middle-born, however, have to share parental investment throughout childhood. The number and characteristics of the existing children in the family provide a background for individual development. Accordingly, the existence of siblings, in general, and more specifically birth order effects on developmental outcomes, well-being, and personality have been studied quite extensively from an evolutionary viewpoint.

Birth Order and Development

The sheer existence or nonexistence of siblings profoundly modifies the developmental environment of an individual. A large body of literature associates siblings with negative outcomes. The number of siblings is inversely related to academic achievement and adulthood income in Western contemporary societies and to child survival in preindustrial societies (Lawson et al. 2012; Steelman et al. 2002). This is assumed to be the consequence of parental quality–quantity trade-off: with limited parental resources, each additional child reduces investment in any one

child (see, e.g., Gillespie et al. 2008). Nevertheless, the effects of siblings vary substantially with ordinal position in the sibship. There is an indisputable “firstborn advantage” in almost every outcome that has been studied so far, from reproductive success to education (see, e.g., Steelman et al. 2002). Later-borns are suffering more, while firstborns usually fare equally well as only children.

Some studies suggest that middle-borns differ from other children by, for example, being emotionally less attached to the family (Salmon and Daly 1998). It is hypothesized that such a pattern is indicative of parental investment: firstborns receive exclusive parental investment before other children are born and afterward may receive disproportionate amounts of investment because they have a higher reproductive value (i.e., they have survived some or most of the potential hazards causing child mortality and are closer to starting reproduction; see Sulloway 1996). Last-borns, in turn, as the last baby of the family, receive more investment from the mother in infancy and are usually the last ones to leave the nest. Conversely, middle-borns are forced to share parental investment throughout childhood (Sulloway 1996). However, many studies have not found any distinct middle-born effects on developmental or reproductive outcomes, and their existence is currently under dispute.

Sibling Relationship Quality

As siblings represent less parental resources directed to any one child, the resulting competition for parental resources is likely to cause conflicts among siblings. Accordingly, substantial amounts of sibling bullying are not uncommon in sibling relationships (Wolke et al. 2015). As later-born siblings are more disadvantaged by having siblings than firstborns, it might be hypothesized that later-borns compete more and thus have less positive relationships with siblings than firstborns. Indeed, this seems to be the case, as older siblings, in general, and firstborns, specifically, are more likely to describe their sibling relationships as very good (e.g., Pollet and Nettle

2009). Pollet and Nettle (2009) further hypothesize that the better quality of sibling relationships reported by firstborns is related to them potentially gaining larger inclusive fitness benefits from altruistic behaviors toward siblings in adulthood. Having reached maturity, and started reproduction, a younger individual always has a higher reproductive value than an older one, i.e., more expected years to procreate. As firstborns are always older than later-borns, they benefit more from investing in their younger siblings than vice versa. The existence of older pre-reproductive siblings, actually, seems to be associated with higher survival of younger siblings (Sear and Mace 2008). This possibly reflects altruistic childcare of younger siblings, as older siblings function as “helpers at the nest.”

Niche Picking

Ordinal position in the sibship could also be related to personal characteristics such as personality and ambition. Frank Sulloway (1996) first hypothesized that siblings influence each other’s personality in ways that can be understood from an evolutionary viewpoint. Firstborns, in general, would benefit from being more assertive than later-borns. This is because firstborns are by definition older, bigger, and stronger than others and therefore more readily gain benefits from behaving dominantly. In addition, firstborns are hypothesized to be more conscientious than other members of the sibship, because they often take on the role of a “surrogate parent,” i.e., aid parents in caring for later-born siblings. Firstborns, in a way, can afford to behave altruistically toward siblings, because they generally receive more parental investment. According to Sulloway’s theory, other children adjust to the personality characteristics of existing children with a process called de-identification or niche picking. Being dissimilar than other members of the sibship allegedly decreases competition (Sulloway 1996).

Empirically, birth order effects on personality have been vastly studied. The results, however, are very mixed. Some studies find patterns as hypothesized by Sulloway, with firstborns being

more dominant or conscientious than later-borns (e.g., Paulhus et al. 1999), but many do not (e.g., Rohrer et al. 2015). In the absence of a comprehensive meta-analysis, the jury is still very much out. However, Sulloway's theory on niche picking points out the evolutionary uniqueness of the family environment and sibling constellation for its individual members.

Conclusions

Siblings face the opposing evolutionary forces of competition and cooperation in their interactions with each other. These forces are not, however, met similarly by all members of the sibship. The existing numbers and qualities of children in the family provide a unique environment for each successive child. This environment shapes the characteristics of the members of the sibship and interactions between them, as each individual tries to find a niche in which fitness is maximized.

Cross-References

- [C < Rb](#)
- [Competition for Parental Investment](#)
- [Frank Sulloway \(1996\) On Birth Order](#)
- [Helpers at the Nest](#)
- [Kin Selection](#)
- [Parental Investment](#)
- [Parent-Offspring Conflict](#)
- [Sibling Conflict](#)
- [Sibships](#)

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Sibships

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Synonyms

[Brother](#); [Horizontal family relations](#); [Sibling](#); [Sister](#)

Definition

Siblings are individuals who share parents. Full siblings share both the mother and the father, while half-siblings share only one parent. Through mutual parents, siblings are genetically related to each other. On average, 50% of the segregating genes of full siblings are same, although the range, in principle, is from 0 to 100%. Half-siblings, on average, have 25% of

their segregating genes in common. Stepsiblings are individuals whose parents are in a romantic relationship and who usually live in the same household, but are not genetically related to each other. This entry concentrates on full and half-siblings. Siblings are assumed to share mutual goals through their mutual genes and therefore expected to behave altruistically toward each other. On the other hand, siblings are expected to compete for parental resources.

Introduction

A majority of humans grow up with a sibling or siblings, and relationships with siblings often-times are the longest relationships in an individual's life course. Full siblings share, on average, 50% of their segregating genes, while half-siblings, on average, share 25%. According to the inclusive fitness theory, alternatively called the kin selection hypothesis, genetically related individuals have an incentive to behave altruistically toward each other. That is, helping genetically related individuals is beneficial in terms of one's own fitness, as long as the cost of the altruistic behavior is not too high. Hamilton's (1964) rule, $br > c$, where b is the fitness benefit to the recipient, c is the fitness cost to the actor, and r is the genetic relatedness between the two, sets the boundaries for altruistic behavior. Full siblings represent, alongside of parent-child relations, the greatest genetic similarity between two people, surpassed only by identical twins. Indeed, siblings do seem to help and behave altruistically toward each other (Stewart-Williams 2007), as would be expected from the Hamilton's rule.

Besides genes, siblings share parents. Human beings grow up exceptionally slowly, our big brains take a long time to develop, and human children are dependent on other people providing food and shelter many years after weaning. Although humans seem to practice a great deal of alloparenting or cooperative breeding (meaning that other people than the mother participate in taking care of the child), parents, and mothers especially, are vital for child survival (Sear and Mace 2008). In this sense, siblings represent

competition for parental investment (Trivers 1972) and, as you are always more related to yourself than to your siblings, pose a threat to your own fitness. Sibling relationships are innately characterized by these two opposing forces of altruism and competition (West et al. 2002).

Recognizing Siblings

Human individuals have no direct ways of inferring their genetic relatedness to other individuals. However, in terms of inclusive fitness, recognizing biological kin is important for altruistic behavior to be targeted appropriately. A large body of research has thus concentrated on how genetic kin recognize each other, for example, on how to confirm biological paternity. In terms of siblings, two important recognition mechanisms have been identified. Firstly, the strength of aversion to engage in sexual acts with someone signals genetic relatedness. This phenomenon, called incest aversion, was first defined by Edward Westermarck already in the early twentieth century (Westermarck 1921). Inbreeding (procreating with a genetic relative) is detrimental to fitness, and any genes aiding in avoiding it will have spread in the population. Secondly, co-residence seems to be an important factor in determining siblinghood: length of co-residence in childhood is strongly correlated with incest aversion between two individuals (Lieberman et al. 2007). Other mechanisms that play a role in sibling recognition are phenotypic resemblance and observing your biological mother breastfeed another infant. The latter mechanism, naturally, only works for older siblings, while younger siblings need to rely on other cues. Emotional closeness may function as an additional cue for recognizing siblings as targets of altruism, at least in cases where more reliable cues are missing (Bressan et al. 2009).

Conflict Among Siblings

Conflicts between siblings are extremely common – up to 40% of children report repeated

sibling bullying, that is, being a victim of or perpetrating concurrent physical or verbal aggression toward siblings (Wolke et al. 2015). Sibling rivalry is assumed to be one consequence of the so-called parent–offspring conflict (Trivers 1974). Parent–offspring conflict reflects the contradicting needs of parents and children. It is always in the offspring’s interest to extract a maximum amount of investment from the parents. For the parent, however, parental investment in one child is always traded off with investment in other children, current or potential future ones. Further, a parent may increase their own reproductive success by choosing to invest more in offspring with higher reproductive value, i.e., offspring with higher expected genetic contribution to future generations (Jeon 2008). For the child it is, naturally, utterly unbeneficial to be the one in whom parents invest less. Accordingly, it seems that sibling rivalry is increased when parents treat their children differentially. Parental differential treatment has been associated with more conflictual sibling relations in numerous studies (Volling 2003). Similarly, poorer relationships between a parent and a child are reflected in a more problematic relationship between siblings.

The amount and severity of sibling conflict is also associated with structural features of the sibling dyad, as well as personal characteristics of the siblings. The sex composition of a sibling dyad plays a role, with a dyad of two sisters being most harmonious (Volling 2003). Opposite-sex sibling dyads with an older sister are, on average, more positive and less conflictual than those with an older brother. Generally, younger siblings report less positive sibling relationships than older siblings. Studies concerning such structural features have mostly been conducted on Western industrialized societies, in the context of family sociology or psychology. The focus is generally on the well-being of the family members and, for example, implications for therapeutic interventions. Therefore it is not clear how, for example, the sex composition of the sibling dyad and its impact on the quality of the sibling relationship are related to evolutionary concepts such as parent–offspring conflict. Future research will hopefully shed more light on these matters.

Thus, existing siblings shape the developmental environment of an individual to a great extent. In addition to sex composition, birth intervals between siblings are associated with the quality of the relationship. Shorter birth intervals seem to correlate with poorer relationships (e.g., Milevsky et al. 2005). Presumably this is related to increased competition over parental investment, as two very young children impose greater challenges in caring for them. Also birth order effects on sibling relationship quality, individual development, and characteristics such as personality have been studied extensively.

With substantial divorce rates in Western societies, households with full, half-, and stepsiblings are becoming ever more common. Following Hamilton’s rule, the greater genetic similarity between full siblings compared to half-siblings would suggest greater conflicts between half-siblings: household resources are shared with a more distant relative. Perhaps somewhat surprisingly, the opposite pattern seems to be true, with conflicts between full siblings being more frequent than between half-siblings (e.g., Tanskanen et al. 2017). It has thus been suggested that as two half-siblings often have more parents (three as opposed to two in full siblings) investing in them, this would decrease the competition compared to full siblings (Tanskanen et al. 2017). In addition, it is worth remembering that Hamilton’s rule does not entail conflicts but cooperation: full siblings are expected to behave more altruistically toward each other than half-siblings. This seems to hold true, even in cases where solidarity between half-siblings is strongly culturally imposed (Bressan et al. 2009; Jankowiak and Diderich 2000), even though competition may weaken or override these altruistic impulses (West et al. 2002).

Quality–Quantity Trade-Off

While making reproductive decisions, parents are faced with a quality–quantity trade-off: the number of offspring is inversely related to the amount of resources a parent can invest in any one child. Research showing evidence of consequences of

this trade-off on children in contemporary Western societies is compelling. The number of siblings is negatively associated with individual's cognitive skills, academic performance, and adulthood income (Steelman et al. 2002). The effect of siblings on these measures is generally equal to, or even larger than, the effect of parental education, and it persists even when controlling for parental characteristics such as socioeconomic status or income. Having more siblings also seems to exert negative health effects on children, even in modern conditions with no nutritional impoverishments (Lawson and Mace 2008). On a more proximate level, it has been shown that larger number of siblings is indeed associated with lower parental investment, for example, less parental time spend in an interaction with an individual child (Lawson and Mace 2009).

Although a vast majority of research on siblings has been conducted on Western low-fertility, low-mortality populations, some studies from small-scale subsistence societies have shown similar effects. For example, in an African agropastoralist society, men with more elder brothers marry less optimally and have lower agricultural productivity and lower reproductive success (Gibson and Gurmu 2011). In pre-industrial, high-fertility, high-mortality societies, the number of siblings also significantly decreases child survival (Lawson et al. 2012). Ordinal position in the sibship also plays a role, with firstborns often faring equally well compared to only children and later-borns suffering the most. Firstborns seem to benefit from receiving undivided parental attention for the first couple of years of life. Results comparing only children with firstborns are mixed, some reporting no additional benefits of being an only child (e.g., Falbo and Polit 1986). Why only children would not benefit from monopolizing parental resources remains a puzzle to be tackled by future research.

The negative effects of having siblings seem to be more pronounced in societies where land, property, or other material assets are inherited from the parents (e.g., Gibson and Gurmu 2011). Although it is generally assumed that the trade-off between number and quality of offspring is of more importance in resource-scarce

environments, it seems that better environmental or material conditions actually might steepen the trade-off (e.g., Lawson and Mace 2008, 2009). This pattern has been observed both in developing and industrialized societies. As environmental and/or economic conditions pose less restrictions to child survival, development, and well-being, the maximum amount of parental investment still expected to be beneficial to fitness is increased (e.g., Quinlan 2007). And as parental investment increases, so will the competition over those investments between siblings increase.

Cooperation Between Siblings

Research on siblings has mainly concentrated on conflicts and competition, and less is known about altruistic behavior between siblings. However, despite the overall negative effects of having (especially older) siblings on health, survival, and educational attainment, it seems that siblings may also function as “helpers at the nest.” When siblings are sufficiently old as not to compete for parental resources as much as in early childhood, but still pre-reproductive, their presence seems to improve the survival of younger siblings and increase mother's reproductive success (Sear and Mace 2008). This is especially true for older sisters. In hunter-gatherers, older pre-reproductive siblings seem to provide direct child care as well as nutritional resources to the family. In addition, while a larger number of siblings is detrimental to the “quality” of children in postindustrial societies, it does not seem to translate into poorer reproductive success of those children (Goodman et al. 2012). On the contrary, number of siblings positively correlates with the number of one's own children in low-fertility and low-mortality conditions. In other words, in terms of ultimate fitness, the negative effects of siblings may not be detrimental, at least in affluent environmental conditions.

People express willingness to behave more altruistically toward siblings than other close, non-kin acquaintances (Stewart-Williams 2007). This difference in willingness to engage in altruistic behavior increases as the altruistic behavior

becomes more costly. Siblings also do not expect reciprocity in or gratitude from altruistic behavior toward each other, whereas both are expected from altruistic behaviors toward close friends (Rotkirch et al. 2014). Altruistic behavior in sibling relationships seems to be innate, or taken for granted, while it must be earned in other close relationships.

In modern, postindustrial conditions, the effects of siblings on well-being and development have received some scholarly attention. Positive relationships with siblings (as opposed to more negative ones) seem to provide benefits for individuals, such as higher well-being or fewer internalizing and externalizing problems (Volling 2003). The causal pathways of such associations are difficult to disentangle, but the effects are most likely to be bidirectional. To what extent these positive effects of siblinghood are found in pre-industrial societies remains to be seen. On one hand, positive effects can be expected to exist in such societies as well, as sibling competition in more harsh environmental conditions seems to be less severe. On the other hand, siblings seem to pose more critical threats to individual's survival and health in such conditions, which may annihilate any positive effects of having siblings.

Sibling Relations Throughout the Life Course

Longitudinal studies on sibling relationships are scarce, and most studies on siblings have been conducted on children and adolescents. In addition, the little knowledge of sibling relations in adulthood is based on research in contemporary Western societies. Practically nothing is known of these relationships in, for example, high-fertility and high-mortality societies. However, it is expected that the nature and quality of sibling relationships change with age. Firstly, as children grow older, the need for parental investment diminishes. This should decrease sibling competition. Secondly, as siblings approach their reproductive life span or embark on parenthood, altruistic behavior toward siblings may result in greater inclusive fitness payoffs. Accordingly,

conflicts among siblings do diminish while positive affections stay the same or even increase from childhood to adolescence and early adulthood (e.g., Kim et al. 2006). However, it seems that in adults, age is inversely related to contact frequency and amount of help between siblings – while positive affections may increase (reviewed in White 2001). Being married reduces contact, perceived support, and help among elderly siblings. Somewhat surprisingly, the same applies to having children, contrary to what could be expected from Hamilton's rule. It seems that people allocate their resources toward their own children at the cost of helping siblings and their children (see also White 2001). Childless siblings, however, seem to allocate a great deal of their resources into helping their parenting siblings, especially in young adulthood (Voorpostel et al. 2007). In terms of inclusive fitness, such a pattern is expected.

Losing a spouse is related to strengthening relationships between siblings (White 2001). It seems that in an individual's social network, the innermost circle of significant others has approximately five spots (Dunbar 2003). In adulthood, these places may be filled with members of the nuclear family, but once a place is left vacant, a sibling easily fills it. Results concerning the loss of a parent are more mixed. Some studies report comparable findings to a loss of a spouse, with a parent's death increasing sibling contact (White 2001). The majority of the studies, however, seem to report decreasing emotional closeness between siblings in the face of parental death in adulthood. It may be implied that caring for elderly parents rarely provides any fitness benefits to the caregiver and causes tension in sibling relations. Nevertheless, positive relations with siblings in adulthood are associated with better mental and physical health, at least in Western industrialized societies (see Van Volkom 2006).

Conclusions

From the evolutionary perspective, siblinghood is characterized by two opposing forces: altruism driven by shared genes on the one hand and

conflict and competition driven by shared parents on the other hand. Research evidence concerning competition between siblings, for example, the negative impact of having siblings on individuals' survival, health, and socioeconomic prospects, is compelling. Less is known about altruistic behaviors between siblings. It does seem, however, that siblings behave more altruistically toward each other than toward other close, non-kin acquaintances and that altruism toward siblings is more "automatic" than other types of altruism. As competition for parental resources decreases with children growing up and potential fitness payoffs for altruistic behavior increase, sibling relationships could be expected to improve by age. With limited research on the subject, it seems, however, that the opposite might be true. However, the existence of siblings in the old age, especially if the relationship is positive, seems to have beneficial effects for mental and physical health. The evolutionary meanings and explanations of such findings are yet to be contemplated, especially because research on adult sibling relationships is currently confined to contemporary Western societies. One might only hope that these patterns are enlightened by future research.

Cross-References

- [Competition for Parental Investment](#)
- [Kin Recognition and Classification in Humans](#)
- [Kin Selection](#)
- [Parental Investment](#)
- [Parent-Offspring Conflict](#)
- [Quantity Versus Quality of Offspring](#)
- [Sibling Conflict](#)
- [Siblings Pose Unique Adaptive Problems](#)

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Side Effect

► By-Product

Sidetrack

► Loop Variant, The

Sign Language

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Synonyms

[Visual-gestural language](#); [Visual-spatial language](#)

Definition

A natural language used by the deaf that employs visual means to convey meaning.

Introduction

Sign languages are full-fledged systems of visual-gestural communication that develop spontaneously within communities of deaf people. The Ethnologue database (Lewis et al. 2016) currently includes information on 141 natural sign languages used around the world but there may be more that have not yet been described in the linguistic literature (in 2005, the same source listed only 121 sign languages). As compared to spoken languages, sign languages are still under-researched, in terms of both their grammatical and sociolinguistic properties. What leaves no doubt, though, is that they are structurally and diachronically independent of spoken languages that surround them. The fact that, for instance, American Sign Language (ASL) and British Sign Language (BSL) are not only different, but actually mutually unintelligible shows that sign languages do not derive from spoken languages they are nested within.

Sign Language Acquisition

For most deaf children, the language acquisition process differs quite radically from how the

hearing typically acquire spoken language. A vast majority of deaf individuals (estimated to exceed 90 % – see, e.g., Mitchell and Karchmer 2004) are born into hearing families, which means that their relatives do not use a language that is sensorially accessible to them. Deaf children may, at some stage, start interpreting the movements of the lips, tongue, and face of their hearing family members as meaningful but the lipreading technique does not form a sufficient basis for natural language development. Such a limited input, combined with the fact that a deaf infant's hearing relatives do not usually learn any sign language, results in deaf children often showing delayed development of communicative skills.

Although it is very likely that, throughout the history of mankind, deaf people used various forms of gesturing (often referred to as homesigns, different from sign language in being inconsistent and generally lacking a systematic grammatical structure) as a tool of communicating with the hearing around them, it was only in the second half of the eighteenth century that complex sign languages started to evolve (Eriksson 1998). The ratio of profoundly deaf to hearing newborns is usually estimated to be 0.1 % (one in a thousand). Therefore, apart from very rare situations where an exceptionally high incidence of deafness resulted in the emergence of so-called village or shared sign languages (Nyst 2012), used by both deaf and hearing members of a given community (as in the case of the population of Martha's Vineyard – Groce 1985), most signers acquire sign language through peer-to-peer transmission in schools for the deaf. The first public school for the deaf was founded in the early 1760s by Charles-Michel de l'Épée in Paris, France. In the following decades, educational methods based on sign language started to spread around Europe and North America, which allowed for an unprecedented development of natural sign languages. However, in the second half of the nineteenth century many educators of the deaf adopted the so-called oralist approach, according to which sign languages should be rejected in favor of methods that focus on lipreading and speech training. Oralism

is now generally perceived by the deaf as a vivid example of discrimination (often dubbed as “audism,” i.e. a paternalizing attitude based on the assumption that hearing is central to human experience – Lane 1992).

How important a role deaf schools may play in the emergence of sign languages is manifested by a widely discussed example from Nicaragua. A sign language was born there in the 1970s when children that had been isolated in their families started to participate in a newly established school program. Although they were expected to learn spoken Spanish and lipreading, a signed communication system started to develop among them (with no adult influence), paving the way to what later became a creole-like sign language. Many linguists see this as an argument for the Chomskyan view that linguistic competence is rooted in an innate language faculty (Kegl et al. 1999).

Sign Language Communication

As first demonstrated by Stokoe (1960), sign languages are not based on mimetic gestures (pantomime). Each sign may be analyzed as a bundle of contrastive meaningless features – comparable to the phonemes of spoken languages. Individual words (signs) are composed into sentences in accordance with the rules of grammar. In principle, these basic mechanisms underlying signed communication are not in any significant way different from what happens in spoken languages. However, sign language syntax may be claimed to possess a unique characteristic: unlike the strictly linear syntax of spoken languages it allows for three-dimensionality. The signing space (i.e. the area in front of the signer's body) is exploited syntactically, semantically, and pragmatically in the visual-gestural communication (Perniss 2012). Particular locations in the signing space may be associated with discourse referents, resulting in a mapping of mental spaces onto the structure of a particular utterance. Spoken language words cannot be articulated at different spatial positions but sign language words can. This is



Sign Language, Fig. 1 The use of space in a sign language sentence

illustrated in Fig. 1 (extracted from a corpus of Polish Sign Language, PJM – Rutkowski et al. 2016). The signer is describing a lake surrounded by rocks. Each of the three snapshots of Fig. 1 captures a different location associated with a different rock. A spoken language equivalent of this sentence could include prepositions or other space-referring expressions. In sign languages, signers will typically convey this kind of information by modifying the place of articulation of a given sign.

The spatial aspect of grammar distinguishes natural sign languages from artificial manual codes that have been created around the world

with the aim of representing spoken languages visually (for instance, “Signed Exact English” or “Calqued Lithuanian”). Many hearing educators of the deaf prefer to use manually coded versions of spoken languages because they consider this strategy successful in bridging the gap between the deaf and the language of the hearing majority. However, mirroring the linear organization and the phraseological structure of a spoken language often results in an unnatural hybrid communication system that does not effectively fulfill communicative functions. Apart from lacking the spatial dimension, manually coded systems do not typically make use of nonmanual signals. Natural sign languages are articulated with the whole body of a signer. The hands play the most important role with respect to conveying the lexical basis of meaning but nonmanual signals (such as facial expressions, eye gaze, body leaning, head tilting, shoulder raising, mouthing, etc.) are used as, for instance, grammatical markers and their function is not merely ancillary. Because of their absence, deaf signers often perceive manually coded systems as difficult or even impossible to understand.

Conclusion

Being deaf does not equal being a sign language user. Many deaf children who are given a cochlear implant at an early stage of their lives and do not feel part of the signing community will never develop any fluency in sign language. However, those deaf individuals who use sign as their first and preferred means of communication should be considered members of linguistic minorities in their respective countries. As complex lexicogrammatical systems that allow the unlimited expression of thought, sign languages are full-fledged natural languages, their only unusual characteristic being that in most cases they are not passed on from generation to generation but rather through peer assembly (typically, in deaf schools and communities).

Cross-References

- [Communication and Developmental Milestones](#)
- [Communication, Cues, and Signals](#)
- [Field of Linguistics, The](#)
- [Language](#)
- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Development](#)
- [Noam Chomsky and Linguistics](#)

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Signal Reliability

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Synonyms

[Honest signaling](#)

Definition

Communication occurs when one individual influences the behavior of at least one other individual through the information conveyed by its signals or cues. Whereas cues are often incidental byproducts of individual behavior or physiology that convey information, signals evolved specifically for the function of communicating (see ► [“Communication, Cues, and Signals”](#); Maynard Smith and Harper 2003). A signal is reliable when it is consistently and predictably associated with either the signaler's state or some salient aspect of the environment. In animal species, signals are generally reliable because of strong selection pressure on receivers to ignore or avoid unreliable signals or signalers – unreliable signals are therefore selected against.

Introduction

Communication is often a dyadic interaction between signalers, who produce signals, and receivers, who monitor signals. For decades leading up to the 1970s, the general view of animal communication was that individuals produce reliable signals to benefit both the signaler and the receiver. In his seminal book, *The Behavior of Communicating: an Ethological Approach*,

Smith (1977) developed the notion of communication as sharing of information between signaler and receiver, as a foundational mechanism of social regulation. “An event in which communication occurs through the agency of displays involves the behavior of at least two individuals, a communicator and one or more recipients, usually to their mutual advantage” (Smith 1977, pp. 10–11). Similar definitions of communication describing benefits to both signaler and receiver can be found widely in the ethological literature prior to Smith’s book.

A year after Smith’s book was published, Dawkins and Krebs (1978) argued against the notion of communication being the transfer of information for the general benefit of both signaler and receiver. Instead, they argued that communication is better understood as manipulation of the receiver by the signaler – communication occurs because signals and signaler behavior have evolved to benefit the signaler, often at the expense of the receiver. Under this view, signals are like propaganda, and they have evolved to persuade receivers to the signaler’s advantage. Dawkins and Krebs (1978) argued that deception, dishonesty, and exaggeration were the rule rather than the exception – signals should generally be unreliable so that receivers cannot easily predict signalers’ behavior. Signals are considered unreliable if they are not consistently correlated with either the signaler’s state or the environment.

Although the views advocated by Dawkins and Krebs influenced the field of animal communication for decades to come, research has clearly shown that signals are, by and large, reliable. Variation in signal structure or signal production is often reliably associated with aspects of the signaler or the environment that are important to the receiver and to the signaler. Given that signalers could benefit by manipulating receiver behavior with deceptive or otherwise unreliable signals, why do signalers so regularly produce reliable signals? One of the key reasons is that in many social species, signaler and receiver interests (those related to survival and reproduction) are often aligned with one another, such that both signalers and receivers benefit from honest communication.

Alignment of Signaler and Receiver Interests

Signals are generally correlated with conditions external to receivers and, as such, can provide crucial information to receivers that may cause receivers to alter their behavior. The more highly correlated a signal is to conditions external to receiver, the more reliable the signal is. In cases where interests of signalers and receivers align, a signaler may produce a signal to manipulate the behavior of a receiver, but both signaler and receiver will generally benefit from this communication (Bradbury and Vehrencamp 2011). Signaler and receiver interests are similar in many contexts involving kin selection, food calling, alarm calling (see ► [“Alarm Calls”](#)), mobbing behavior, social cohesion, or begging. As such, signals used in these contexts are generally reliable (Searcy and Nowicki 2005). For example, vervet monkey (*Chlorocebus pygerythrus*) signalers produce different types of alarm calls depending on whether they have detected a leopard, hawk, or snake predator. Upon hearing these signals, receivers will behave motorically in escape as if they had themselves detected the same predator (Seyfarth et al. 1980). Since each different alarm signal is produced exclusively when that predator is in the area, these signals are highly reliable. Individuals signal reliably in this species because of their aligned interests of gaining the fitness benefits that come from social living with the members of their group.

Another important example of reliable signals in the context of aligned interests comes from classic studies of Belding’s ground squirrels (*Spermophilus beldingi*; Sherman 1977). When terrestrial predators are detected, individuals often produce alarm calls, and these calls are costly – compared to a silent ground squirrel, a calling ground squirrel is twice as likely to be detected and attacked by the detected terrestrial predator. Of importance is the relatedness of individuals in the immediate environment of an alarm caller. Alarm callers are frequently reproductive females, and alarm calls are produced by them primarily when their own family members (such as siblings or offspring) are nearby. Despite

the increased costs of alarm calling to the signaler, reliable signaling can evolve through kin selection due to the high levels of relatedness of signaler and receivers in this system.

Prior to the point of parent-offspring conflict (Trivers 1974), the interests of parents and their offspring are clearly aligned with one another. In many altricial animals, young individuals produce “begging” signals when they are hungry. In tree swallows, *Tachycineta bicolor*, hungry nestlings produce begging calls at higher rates than sated nestlings, and playbacks of calls of hungry nestlings lead to more feedings of nestlings near those speakers than playbacks of calls of sated nestlings (Leonard and Horn 2001). Thus, the rate of calling by nestlings in this species, and perhaps other acoustic features of these signals, serves as an honest signal of need and influences parents’ feeding behavior accordingly.

Nonalignment of Signaler and Receiver Interests

In many instances, the interests of signalers and receivers only weakly align or are clearly opposed to one another. This can be observed frequently within certain types of mating system. For example, in mating systems where parental investment is unequal, individuals with higher parental investment (usually females) are typically the more discriminating sex. Individuals of the less discriminating sex (those with lower parental investment; usually males) signal to communicate their reproductive quality. In these mating systems, individuals of the less discriminating sex have the goal of as many matings as possible, to increase reproductive output. Individuals of the more discriminating sex, conversely, have the goal of achieving a quality mating to increase chances of having quality offspring. Therefore, signaler (usually males) and receiver (usually female) interests only weakly align, and we may expect to see dishonest signaling from signalers about their quality. An example of such deceptive signaling occurs in the Asian corn borer moth (*Ostrinia furnacalis*). In this species, moths react to predator bat echolocation signals by freezing.

Male Asian corn borers have evolved an ultrasonic vocal signal they use that also causes females to freeze, thereby increasing the males’ chances of mating with them for longer durations while bypassing the normal mate recognition and courtship sequence of the species (Nakano et al. 2013).

In aggressive conflicts between two individuals over access to a resource, interests of signalers and receivers are typically opposed. In these conflicts, where the goal for one individual is to defeat the other, we might expect to see cases of deceptive, or unreliable, signaling. In such cases, individuals may bluff signals related to their status, condition, quality, or fighting ability. In addition, unreliable signals can occur when an individual would benefit from avoiding an aggressive encounter it would be sure to lose. Such is the case in Augrabies flat lizards (*Platysaurus broadleyi*; Whiting et al. 2009). Some males appear phenotypically like females in terms of body coloration and can therefore better avoid aggressive interactions with territorial males and increase their own chances to reproduce with females attracted to the areas of those territorial males. In this species, the males that mimic females are able to do so visually, thus usually fooling the territorial males. However, they are not able to mimic chemical signals of females and therefore must avoid direct interactions with territorial males (Whiting et al. 2009).

Under the scenarios raised above with regard to nonalignment between signaler and receiver interests, we might expect substantial use of unreliable signals (Dawkins and Krebs 1978). Conversely, research shows dishonest signaling still seems the exception rather than the rule (Searcy and Nowicki 2005). Consider a situation in which a prey individual detects a predator that has detected it. The prey individual might be expected to produce signals that communicate to the predator greater condition, strength, or escape ability on the part of the prey individual than is true. If theory suggests we should see dishonest signaling in cases where signaler and receiver interests are not aligned, why do we typically see reliable signaling?

Why Are Signals Typically Reliable When Signaler and Receiver Interests Do Not Align?

There are several arguments (not necessarily mutually exclusive) for the reliability of signals even in cases where interests of signalers and receivers oppose one another. One straightforward example is the situation of signals that are sufficiently physically constrained that they cannot be faked – these are called index signals. Index signals are typically constrained by either the physical features of the individual producing the signal or by the experience of the signaler (Bradbury and Vehrencamp 2011). For example, male North American bison, *Bison bison*, produce loud and low frequency bellows in inter-male interactions over control of female harems, larger males produce lower frequency bellows than smaller males are able to produce, and lower frequency bellows are associated with greater male fitness (Wyman et al. 2012). Smaller males are not able to produce lower frequency bellows because of the smaller size of their vocal tracts in comparison to larger males, and vocal tract length constrains frequency (pitch) of sounds produced. In our own species, the frequency contours of phonemes (formant frequencies) and the spacing among those contours are strongly correlated with height and weight variation in both women and men (Pisanski et al. 2014). Given that variation in these frequency contours is thought to be derived from variation in human vocal tract length, and vocal tract length is related to body size, these correlations indicate that frequency contours of human phonemes may be index signals. With index signals, signalers have limited ability to choose which signals to produce and cannot bluff a better quality signal. Other common index signals include visual signals on the body of the signaler – in cases where the size of the signal communicates important information to receivers, larger signalers will often possess larger signals than smaller signalers simply by virtue of their differences in body size.

Conventional signals are signals that are typically energetically no-cost or low-cost to produce and are arbitrary in themselves but are

given meaning by the coding scheme used by signalers and receivers (Bradbury and Vehrencamp 2011). In situations where signalers have different interests than receivers and therefore we may expect cheating to occur, receivers react agonistically to signalers when their signals do not match the convention, thus increasing costs for cheaters (Guilford and Dawkins 1995). For example, banded wren, *Thryothorus pleurostictus*, males counter-sing in aggressive interactions with one another. Males have multiple songs in their song repertoires, and males share many songs. A male that counter-sings with the same song its opponent used is using the most aggressive strategy, and the opponent is likely to approach rapidly in escalation. A counter-singer using this aggressive strategy, if it is in relatively poor condition, is likely to be attacked by the opponent (Molles and Vehrencamp 2001). Thus, conventional signals are often reliable, even though they are physiologically inexpensive to produce, because of the costs of retaliation imposed by receivers.

Handicap signals are signals that are costly to produce and proportionally more costly for relatively low quality or poor condition signalers (Bradbury and Vehrencamp 2011; Zahavi 1975). Handicap signals are often tightly linked to the physical attribute about which they communicate. For example, male side-blotched lizards (*Uta stansburiana*) compress their bodies to produce a visual threat display in aggressive interactions with other males. These signals are handicaps because low-quality males cannot produce them as long as high-quality males, and experimental reductions in endurance (through treadmill running) result in decreased production of threat displays (Brandt 2003). Likewise, increased production of threat displays results in decreases in endurance. While the original hypothesis referred to physical, or receiver-independent, costs of signals that are different for low- and high-quality individuals (Zahavi 1975), recent theory points to the importance of social costs even with energetically costly signals (Számadó 2011). Social costs and physiological costs of signaling are not mutually exclusive and may occur together in a system (Tibbetts 2014).

Proximity signals are those given in contexts where signalers interact closely with their opponents. The use of song matching in song sparrows (*Melospiza melodia*) is an example of a proximity signal that predicts the probability of a bird attacking in territorial disputes. Using a model bird and a sophisticated playback technique, researchers demonstrated that these sparrows use type-matching (producing songs that match the type of songs produced by an intruder bird) to reliably indicate their eventual attack on a simulated intruder bird in territory defense. Birds who initially type-matched simulated intruding bird but quickly switched song types as the intruder approached were much less likely to attack the invading mount (Akçay et al. 2013). This signal has costs – previous research has shown receivers are more likely to react aggressively when their songs have been type-matched (Burt et al. 2001), so individuals who type-match in close proximity to the intruder must be prepared for the dispute to escalate. Again, signalers have some degree of choice when making proximity signals but must pay for cheating through additional costs or loss of benefits compared to signalers who signal honestly (Bradbury and Vehrencamp 2011).

Human interactions in social groups are subject to similar pressures to ensure reliability. Displays of wealth, skill, or productivity are signals that represent social capital, which, in many cultures, is essential to secure marriage proposals and alliances. For example, making conspicuous purchases and wearing jewelry signals the stature and wealth of the signaler, particularly for newly wealthy individuals who do not yet have a high reputation (Bird and Smith 2005). These signals are also known as “symbolic capital” and can take the form of displays of favor and generosity. If the cost of the resources shared in such displays is less than the value of the social capital gained by the display, the display is a conventional reliable signal of an individual’s skill in generating resources. Both signalers and receivers benefit from gaining marriages and alliances from those with higher status than themselves, so dishonest signals could be expected. However, the cost to generate the resources required for these displays is prohibitive and limits the ability of a signaler

to bluff. Particularly in cultures where wealth displays are connected to marriages and other interfamily alliances, receivers have ongoing expectations for those that signal wealth such that dishonest displays would be too costly to consistently perform. When signalers cannot meet receivers’ expectations, they incur social and resource costs if they attempt to signal their wealth dishonestly (Bird and Smith 2005).

One last issue to consider for addressing widespread signal reliability is the general principle of strong selection pressure on receivers to avoid being influenced or deceived by unreliable signals (Krebs and Dawkins 1984). If signalers were to constantly cheat when signaling, the communication system between receivers and signalers would break down, since there would be no incentive for receivers to pay attention to signals produced by others if those signals cannot be trusted. Selection pressure on receivers to discriminate more effectively reliable signals from unreliable signals should generate populations of better discriminators. This, in turn, will serve as a strong selection against unreliable signalers.

When Is Deception Expected?

Signalers are generally not able to fake an index signal, meaning that index signals remain reliable because deception is not possible. However, for non-index signals, if a signaler is able to bluff or produce a dishonest signal, they may be expected to do so when the benefits of producing a dishonest signal outweigh the costs. For some conventional, proximity, or handicap signals, costs for producing a dishonest signal may be enforced socially. These socially induced costs are also known as “potential costs,” since the receiver must (1) be aware of the dishonesty and (2) choose to punish the signaler for their dishonesty, otherwise the signaler is rewarded for cheating (Számádó 2011; Webster et al. 2018). Such unreliable or dishonest signals must be rare in the population to persist, however, if selection on receiver discrimination is strong, as mentioned above.

We may also expect dishonest signaling in cases where receivers incur higher costs for ignoring a reliable signal (false negative) than for responding to a dishonest signal (false positive). Forked-tailed drongos (*Dicrurus adsimilis*), for example, forage in mixed-species flocks where other species respond to alarm calls produced by drongos by displaying antipredator behavior. However, drongos sometimes dishonestly produce alarm calls, scaring other species away from food resources that drongos then steal (Flower 2011). Drongos also flexibly use a variety of alarm calls to avoid others detecting their dishonesty (Flower et al. 2014). This dishonesty persists in the signaling system because receivers incur larger costs for ignoring honest alarm calls (they are more likely to be killed by a predator) than they do for responding to dishonest ones (they are more likely to lose a foraging opportunity).

One interesting case of common deception that does not seem to involve the relative false positive and false negative costs mentioned above is that of regenerated claws in male fiddler crabs (*Uca* species; Wilson and Angilletta 2015). Regenerated claws are typically weaker than the original claws, and males with regenerated claws are therefore at a disadvantage if they get into actual fights with other males. Although the regenerated claws in some species look different from original claws, evidence suggests that neither male opponents nor potential female mates can discriminate the two claw types at the typical distances these crabs wave their claws when communicating. It is possible that selection pressure on at least female receivers is not strong enough to select against this unreliable signal, as males with regenerated claws do not sire young at any disadvantage in comparison to males with original claws.

Conclusion

In situations where interests of signalers and receivers are strongly aligned, reliability of signaling systems typically occurs due to those shared interests. In situations where interests of signalers and receivers diverge, reliability of the

signaling system typically occurs due to the fact that receivers have their own interests, and with selection for stronger discrimination ability over generations, populations of receivers will no longer pay attention to a signal if it is routinely dishonest (Laidre and Johnstone 2013). This puts pressure on signalers to signal in a way that can be validated by receivers, and to maintain a reliable signaling system (Laidre and Johnstone 2013), even if they are able to cheat occasionally. For a signal system to be reliable, the signal in question does not need to be honest 100% of the time. Instead, honest signals are “honest on average,” meaning they are reliable enough that receiver benefits more from attending to them than from ignoring them (Laidre and Johnstone 2013). Indeed, the fact that signals are honest on average is what makes deceptive signaling possible, provided it is relatively rare in the population – “reliability is necessary if receivers are ever to respond to a signal at all” (Searcy and Nowicki 2005, p. 224).

Cross-References

- ▶ Alarm Calls
- ▶ Communication, Cues, and Signals
- ▶ Costly Signaling
- ▶ Deceptive Alarm Calls
- ▶ Manipulation and Dishonest Signals

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Signaling

► Communication, Cues, and Signals

Signaling Body Dimensions

► Signals of Body Size

Signaling Theory

► Costly Signaling and Altruism

Signals

- Animal Signalling
- Cues to Infidelity
- Facial Expressions
- Health Cues
- Observations of Sexual Dimorphism
- Social Cognition and Communication in Chimpanzees and Bonobos

Signals of Body Size

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Synonyms

Cues to body size; Cues to height; Cues to size;
Cues to weight; Signaling body dimensions

Definition

The perception of cues related to visual and acoustic body size provides socially relevant information linked to an individual's fitness.

Introduction

The body size of individuals varies and is associated with sexual maturity, health, dominance, strength, and overall genetic quality. Physical size is a crucial determinant of various socially relevant characteristics of an individual across many species. The perception of conspecifics' body size is thus involved in various social contexts including physical confrontations.

The main components of body size are body weight, height, and muscularity. These factors have been shown to be linked to success in physical confrontations. Potential competitors can thus base their fight-or-flight decisions on body size assessments (Sell et al. 2010).

Body size-related cues can be perceived by several modalities. Multimodal perception can provide overlapping information and thus reduce the risk of inaccurate assessment. Alternatively, each modality can provide additional information, thereby helping to increase the accuracy of judgement. Acoustic and visual assessment of others prior to close contact is common in many species, since it helps to reduce the risk inherent in direct

physical contact. Since the accuracy of assessment of physical characteristics solely from visual cues may suffer due to obstacles in the environment, excessive distance, and/or low luminance, acoustic cues can supplement or replace solely visual information.

In humans, assessments of others are initially guided primarily by visual and acoustic cues. Our physical appearance and voices are socially rich stimuli which attract attention and offer plenty of cues to socially relevant qualities.

Acoustic Cues to Body Size

Apart from conveying linguistic information, human voice carries cues to various physical, social, and fitness-related characteristics of speakers such as age, sex, and body size (Pisanski et al. 2014).

Fundamental frequency (F0) and formant frequencies (FF) are the two most studied features of the human voice. According to source-filter model of speech production, which is based on the basic idea that voice/sound is produced by expelling air from the lungs (the source) through vocal folds, vocal tract, and the mouth (the filter) where it is modulated into speech. F0 and FF are anatomically and functionally independent (Fant 1960). Fundamental frequency is determined mainly by the length and the mass of vocal folds, which vibrate during phonation-modulating flow of air expelled from the lungs. Produced sounds are then perceived as having a certain pitch. Increase in the folds' thickness results in a lower F0 and a lower perceived voice pitch.

Formant frequencies (FF), on the other hand, i.e., the spectral characteristics of speaker's voice perceived as the voice timbre, are determined mainly by speaker's supra-laryngeal voice tract length (VTL) and its resonance. Formants are more anatomically constrained than F0 by the length and dimensions of the vocal tract, which is related to skull size and body height (Fitch 2000).

F0 and FF are associated with individuals' stable characteristics due to the exposure to testosterone during development and are

consequently anatomically related to physical size (Rendall et al. 2005). In boys, elevated levels of circulating testosterone during puberty lead to a lengthening and permanent thickening of vocal folds, which result in a lower F0 (Jenkins 1998). Further, the descent of larynx results in a lowering of formants and narrowing of formant dispersion (formants being produced closer together). The acoustic effect of these changes is that the voices of adult men are lower-pitched and deeper or, in other words, more resonant and rather monotonous than the voices of women or prepubescent children. Longer vocal tract and thicker vocal folds thus produce lower FFs and lower F0, which can thus serve as potential cues to a bigger body size.

Research which tested the role of F0 and FF as indicators of size has generally confirmed that both independently predict variation in body size among different species (Pisanski et al. 2014; Rendall et al. 2005), meta-analyses of acoustic predictors of human voice showed only weak or marginally negative relationships between both F0 (accounting for less than 2% of the variance) and FF (accounting for up to 10% of the variance) and the height or weight within each sex (Pisanski et al. 2014).

Listeners demonstrate sensitivity to variations in F0 and FF and a high consistency in associating lower F0 and FFs with larger speakers. Their judgments, however, tend to be incorrect with respect to speakers' actual size (Pisanski et al. 2014). This relatively low accuracy in assessing body size from voice might be due to the presence of other characteristics unrelated to height or weight, which, too, affect the quality of human voice.

Current research indicates that men with a lower voice pitch are significantly stronger than those with high-pitched voices, and that raters are able to estimate strength from vocal cues accurately and independently of their height or weight assessments (Sell et al. 2010). Some studies which investigated the relationship between voice acoustics and muscularity suggest a negative correlation between F0 and men's shoulder-to-hip ratio (i.e., lower FF indicates individuals with larger upper body musculature). Other

studies, however, did not confirm this association (Pisanski et al. 2016).

Human voice also provides cues to speaker's current state. Certain psychological states, such as self-confidence, fear, or rage, can modulate the position of the larynx and change the tension of the vocal folds, thereby affecting also the resulting F0. The F0 can be modulated to deceive others and to disguise or exaggerate the characteristics of an individual (Fitch 2000). This feature is not unique to humans. It has been suggested that its original selective advantage may have been in enabling individuals to simulate the vocalizations of larger conspecifics, thus exaggerating their own size, and reducing the degree to which FF accurately indicate body mass and shape (Pisanski et al. 2016).

Most recently, scholars have been focusing on some less variable voice parameters, such as non-mean-based F0 measures (measuring voice pitch deviation from its baseline), voice jitter (frequency perturbation), shimmer (amplitude perturbation), and harmonic-to-noise ratio (which is related to the mass and oscillating properties of the vocal folds). These characteristics are supposed to be sexually dimorphic, related to body size and shape via shared influence of sex hormones on these vocal properties, and linked to the development and distribution of lipid and muscle mass (Pisanski et al. 2016).

Visual Cues to the Body Size

In many species, direct visual inspection of the physical size of others is the primary determinant of social dominance. It is therefore not surprising that individuals try to appear physically larger to make a more intimidating impression. Interestingly, direct observations of overall body size of others and the effect of nonverbal behavior on the perception of body size have not yet been thoroughly tested in humans. Available evidence suggests that changes in apparent physical size (e.g., elevation by standing on a platform) affect the perceived height of the individual in question (Schwartz et al. 1982). Perceived body height can also be manipulated by altering other

perceptual cues to size, such as the size of background features, which then increase or decrease the apparent size of individuals (Marsh et al. 2009). Moreover, nonverbal cues such as expansive body posture or posture openness can also make the displayer appear physically larger in eyes of others (Marsh et al. 2009).

Based on facial traits, we spontaneously attribute various personality characteristics. High levels of testosterone are thought to be an important determinant of both the body size and changes to the shape of face during puberty, because testosterone has a strong anabolic effect on the musculoskeletal system, thus influencing various features including the volume of lean body mass and differences in muscle strength. Through the mechanism of hormone action, facial morphology thus seems to be connected to both muscularity and overall body size.

Several studies have investigated a relation between testosterone levels and facial appearance. Their aim was to identify visual cues used to estimate height and weight from the face. Generally, taller people are reported to have more elongated faces than shorter ones (Windhager et al. 2011). Facial elongation (full length of the face divided by its width) increases from infancy to adulthood as the lower jaw develops and starts protruding, making the face less round and more oval. Heavier men and women have wider and more square faces, and heavier men have also rounder lower facial regions (Coetzee et al. 2010). These facial shape cues can be quantified by width-to-height ratio, perimeter-to-area ratio, or cheek-to-jaw-width ratio (for a review see Coetzee et al. 2010). Adiposity produces a typical facial shape because large percentage of facial fat is allocated to the cheek area, buccal fat pads, thus providing a visual cue to body size (Coetzee et al. 2009).

Available evidence indicates that people use the abovementioned or related facial cues to assess body weight and height of others, and they are fairly accurate in their judgments. Individuals with wider, squarer faces, and rounder lower faces are correctly judged to be heavier (Coetzee et al. 2010), while people with longer faces are judged as being taller (Re et al. 2013).

We should, however, bear in mind that visual cues in 2D images (portrait photographs) are fairly limited, especially for volumetric weight estimates (Coetzee et al. 2010). Moreover, we do not usually view faces from the perspective of a typical facial stimuli presentation, i.e., a vantage point centered on and aligned with their faces. Humans show relatively significant height dimorphism and since men are typically higher, they view women's faces from slightly above, while women tend to view men's faces from slightly below (Burke and Sulikowski 2010). When this vantage point is manipulated, participants tend to overestimate body weight for faces presented from a lower vantage point and underestimate it for faces presented from a higher vantage point (Schneider et al. 2012).

Conclusion

Assessment of body size is an important part of first impression formation. It is involved in various social interactions including physical confrontation. Most previous research on perception of body size focused on vocal and facial cues. It has been shown that the main vocal parameters affecting the perception of body size are fundamental frequency and formant frequencies. However, attribution of body size based on these vocal cues tends to be inaccurate. On the other hand, people are usually relatively accurate when judging body height and weight from facial images. The main facial cue related to body weight is a rounder lower facial region, while body height is associated with elongation of the face. Interestingly, relatively little is known about behavioral cues to body size. Further, to our best knowledge, no studies have as yet tested cross-modal integration of individual body size-related cues.

Cross-References

- [Aggression](#)
- [Communication, Cues, and Signals](#)
- [Evolution of Fighting Assessment Abilities](#)
- [Fighting Assessment](#)

- Vocal Attractiveness
- Vocal Indicators of Dominance
- Voice Pitch

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Significance of Helping

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Synonyms

Altruism; Caregiving; Cooperation; Prosocial behavior

Definition

Helping is assisting, supporting, or being of benefit to someone (Merriam-Webster definition)

Introduction

What Is Helping?

The Merriam-Webster dictionary defines “helping” as assisting, supporting, or being of benefit to someone. However, other terms can signify helping: altruism, prosocial behavior, cooperation, and caregiving. Nowak (2006) defines a cooperator as someone who benefits others at a cost to themselves. Helping and cooperating can both be seen as prosocial behaviors (Pettygrove et al. 2013; Warneken and Tomasello 2007). In some instances, helping may develop first, before

cooperation (Warneken and Tomasello 2007). Sommerville et al. (2013) found that there are two related helping behaviors that comprise prosocial tendencies: instrumental and informational help. Instrumental help includes providing help in response to something that has happened (e.g., when a helper brings back an item that another person has dropped). Informational help includes providing help by information (e.g., when a helper tells a person where something is if he or she doesn't see it).

Overall, previous studies that explored this topic have suggested that helping begins early in life (Pettygrove et al. 2013; Sommerville et al. 2013; Warneken and Tomasello 2007). It has been found that children are very eager to help adults (Sommerville et al. 2013). Sommerville et al. (2013) found that in most cases, they help adults instrumentally, which means that often-times, it is not even requested. However, research found that they also tend to assist same-aged peers by either helping to reach for a toy or by retrieving it for them even when it was not requested (Hepach et al. 2017). But why would they do it is a whole other issue.

Why Do We Help?

Historically, helping others would have required two main elements: (1) a person's relatedness to the other (i.e., kin selection; Hamilton 1964) and (2) the act of returning a favor (i.e., tit for tat or reciprocal altruism; Trivers 1971). Helping behavior was mostly targeted at a kin due to genetic resemblance (Dawkins 1989; Hamilton 1964). This was also known as family-based altruism (Dawkins 1989; Hamilton 1964). However, in most human-built societies, kin-like altruism had expanded beyond familial genetic resemblance and into communities that were made up of strangers who lived in close proximity to one another (Bowles and Gintis 2004). By creating cooperative communities, who shared food and info, survival was enhanced (Bowles and Gintis 2004). Thus, helping behavior toward "the sick, the wounded, the very young and old" (Trivers 1971, p. 45) offered opportunities for reciprocal altruism and promoted survival. However, reciprocal help was not always a requirement; some

helping behaviors were instrumental, in that they occurred toward other people who were unrelated or unknown to the helper or without any benefit in return (Warneken and Tomasello 2006). This may be because of group affiliations (Over and Carpenter 2009). Over and Carpenter (2009) studied infant's likelihood of helping when primed for affiliation. Results revealed that infants that were primed with affiliation helped the researcher more than when they were primed with individuality. In the latter case, helping behaviors actually decreased (Over and Carpenter 2009).

de Waal (2008) summarized what drives directed altruism (i.e., helping others who were unrelated to the helper). The author provides three scenarios that would motivate one's altruism. One may experience altruistic impulse. This is when one may help someone who is asking for it or is in visible distress. He or she may also experience learned altruism. This is when one may help someone because their helping behavior has been reinforced in the past. Finally, one may experience intentional altruism. This is when one may help someone because they think this action will be repaid for in the future. This could also occur when one may help just for the sake of helping.

From an evolutionary perspective, such altruism should not have been favored because it comes with costs and may reduce one's own fitness (Dawkins 1989). Dawkins' (1989) example of a bird calling for food or for warning illustrates an altruistic behavior; the bird is trying to let others in the flock know that there is food or a predator nearby. The potential cost could be intriguing the interest of the nearby predator and potentially dying. Hence, helping or cooperating does not make sense evolutionary, especially if there are limited opportunities to ensure one's own genetic survival (Dawkins 1989). It is so puzzling that Nowak (2006) states at the end of the article that "natural cooperation" should be a "third fundamental principle of evolution beside mutation and natural selection" (p. 1563). On the other hand, altruistic actions may be adaptive in an indirect way. Ligon and Stacey (1989) showed that in some situations, cooperative breeders, who feed and help non-related offspring, indirectly increase their own personal fitness by building

their personal and social relationships with the other birds. This may then increase their breeding status and ease of emigration to other spots (Ligon and Stacey 1989).

The reason or motivation behind helping behavior may include two mechanisms. First, de Waal (2008) summarizes evidence that suggests that this behavior was indeed evolutionary “selected” but runs via another mechanism of empathy. The author argues that the capacity for empathy started to evolve in parents and offspring dyads and quickly transferred to others who were living in close proximity and were a part of one’s social circle (de Waal 2008). Paciello et al. (2013) showed that even in situations when costs to the helper were high, the role of empathy still prevailed; high empathy yielded helping behavior (an altruistic response). Second, familiarity may be key; if children were familiar with the person requiring help, they were more likely to help him/her (Allen et al. 2018; Wynn et al. 2017). Thus, some evidence suggests that perhaps helping non-related beings is still beneficial.

Who Is More Likely to Help?

Helping behavior is not unique to humans. Both human infants and chimpanzees have the ability to help another person, but as one would expect, chimpanzee’s helping behavior was more limited (Warneken and Tomasello 2006). Interestingly, several studies showed that helping behaviors develop during earlier years of life, in particular around the second year or younger (Pettygrove et al. 2013; Sommerville et al. 2013; Warneken and Tomasello 2007). This suggests that younger children have the capability of helping others. While it has been shown that younger children have helping tendencies, older children (those who were 30 months old) still help more readily (Svetlova et al. 2010). This suggests that helping, although present in young children (as young as 2), may very well increase with age.

One study that explored sociability in helping found that children who were more approachable to the researcher helped more often (Hammond and Carpendale 2015). This could suggest a certain personality dimension that contributes to one’s helping tendencies. However, environmental

factors may also play a role in who is more likely to help. Hepach et al. (2017) found that children who grew up with siblings helped more while those who attended kindergarten helped less. Another research, by Hammond and Carpendale (2015), which examined parental scaffolding, found that mother’s scaffolding increased children’s helping behaviors.

Furthermore, it could be argued that culture shapes helping behavior. For instance, helping, in a caregiving literature, is a female-biased behavior. From an evolutionary perspective, this makes sense as the parental investment theory explains why women are usually more responsible for increased caregiving behaviors (Dawkins 1989; Geary 1998). Other studies also found that females are more empathetic (Ashton et al. 1998; Davis 1983), more altruistic (Ashton and Lee 2007), and better at perspective taking (Batson et al. 2007). This may explain why females provide the bulk of care. However, these are relative, not absolute differences, heavily influenced by cultural norms and ideals (e.g., Barry et al. 1976; West and Zimmerman 1987). For instance, in Hunter-gatherer societies, such as the Baka, males participate in care for their siblings perhaps even more than females (Hirasawa 2005), which, due to its’ paternal investment, ensures offspring survival (Geary 1998). Today, males play a significantly greater role in caregiving. This may be due to the contemporary shift that views males and females more similarly (Fine 2017).

Conclusion

The Significance of Helping

To conclude, Warneken (2015) suggests that it would be possible to highlight the significance of helping by reviewing why this behavior was favored to begin with. Helping the kin or even a group of strangers may be favored because it ensures survival of one’s genes. Furthermore, helping maintains the cohesion of a community and enhances the morality of humanity. Can we imagine a society or a family unit that is characterized by lack of helping, cooperating, or caregiving? The answer is no.

Nowadays, helping behavior is more culturally and developmentally reinforced. For these reasons, some youngsters' helping behavior is not easily accepted. For instance, young carers, children and youth who help ill, disabled, or addicted family members, are less likely to get recognition for their role as helpers (Charles et al. 2009). However, since they help significantly to ensure survival of their family unit, their helping behaviors are indeed adaptive and should be recognized as such (Lakman et al. [under review](#)).

Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Evolution of Cooperation](#)
- [Helping](#)
- [Helping More Likely with Close Kin than More Distant Kin](#)
- [High-Cost Altruistic Helping](#)

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Signs

► Facial Expressions

Silent Ovulation

► Concealed Ovulation

Silly

► Humor Production

Silver Fox Domestication Experiment

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Synonyms

Artificial selection; Domestication; Evolution

Definition

An ongoing, six-decade-long experiment on the domestication of silver foxes in real time.

Beginning in 1959 and continuing to this day, a team of Russian geneticists, led by Lyudmila Trut, has been running one of the most important biology experiments of the twentieth, and now twenty-first, century. The experiment was conceived by Trut's mentor, Dmitry Belyaev, who initiated an experiment to study the process of domestication in real time. Belyaev was especially interested in understanding the domestication of wolves to dogs, but rather than using wolves, he used silver foxes (*Vulpes vulpes*) as his subjects.

As a result of his reading of Darwin's *The Variation of Animals and Plants Under Domestication* (Darwin 1868) and his own interactions with domesticated animals, Belyaev was aware that domesticated species tend to share a suite of characteristics that include floppy ears, short/curly tails, juvenilized facial and body features, reduced stress hormone levels, mottled fur, and relatively long reproductive seasons. That suite of traits has been dubbed the domestication syndrome, and one of Belyaev's interests was why the domestication syndrome exists. We have domesticated species for many reasons, including transportation, food, companionship, and protection; but no matter what domesticated species are selected for, over time, they begin to display traits in the domestication syndrome. Why?

Belyaev hypothesized that the early stages of *all* animal domestication events involved choosing the calmest, most prosocial-toward-human

animals – the tamest animals – and that all of the traits in the domestication syndrome were somehow, though he didn't know how, genetically linked to genes associated with tameness. He and Trut put those ideas to the test (Trut 1999; Trut et al. 2009; Dugatkin and Trut 2017). They and their team developed a scale for scoring tameness. How a fox scored on this scale was the *sole* criteria for selecting foxes to parent the next generation. Every generation they tested hundreds of foxes, and the tamest 10% were selected to parent the next generation.

Starting with almost wild foxes, within six generations, selection based on tame behavior alone produced a subset of foxes that licked the hand of experimenters, could be picked up and petted, whined when humans departed, and wagged their tails when humans approached. In the earliest years of the experiment, the tamest of the foxes made up a very small proportion of the animals in the experiment; today they make up more than 75% of the experimental population.

Selection for tameness also resulted in the emergence of traits in the domestication syndrome. With a decade, some of the domesticated foxes had floppy ears and curly tails. By generation fifteen of the experiment, domesticated foxes had stress hormone levels about half that of wild foxes. Over the course of the experiment, domesticated foxes began to display mottled fur patterns, more juvenilized facial and body shapes, and longer reproductive periods. Social cognition experiments have also found that the domesticated foxes are as good as dogs at following at human gaze.

When Belyaev first hypothesized that selection for tameness would lead to the emergence of traits in the domestication syndrome, he did not have a proposed mechanism. The neural crest cell hypothesis, first proposed in 2014, may provide that mechanism (Wilkins et al. 2014). Very early on in animal development, neural crest cells migrate from the neural crest to glands in the endocrine system, bone, fur, cartilage, brain, and other spots in a developing embryo. The neural crest cell hypothesis proposes that selection for tame behavior reduces the number of migrating neural crest cells, which in turn leads to changes

in fur coloration, facial structure, the strength of cartilage (affecting floppy ears, curly tails, and so on), hormone levels, the length of the reproductive season, and more.

The silver fox domestication experiment is now entering its 60th year at its home at the Institute of Cytology and Genetics in Novosibirsk, Russia. Trut turned 85 years old in 2018 and remains the lead investigator on the work to this day. Belyaev died in 1985.

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Similar Tools Are also Called Slickers and Burnishers in Modern Leather-Work

► [Bone Lissor](#)

Similarity

► [Dyadic Processes](#)

Similarity Selection

► [Specific Friendships](#)

Simile

► Metaphor and Analogy

Simon Baron-Cohen (Darwinian Psychiatry)

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Definition

Dr. Simon Baron-Cohen is a developmental psychopathologist and cognitive neuroscientist, most known for his work with autism. He was born on August 15, 1958, and graduated with his Ph.D. from University College London under the direction of Dr. Uta Frith. He currently works as a Professor of Developmental Psychopathology at the University of Cambridge and is also a Fellow at Trinity College, Cambridge.

Introduction

Dr. Baron-Cohen has made several distinct contributions to the understanding of autism over the course of his career. He articulated the cognitive model associated with “mindblindness” and has more recently proposed the idea that autism is a form of “extreme male brain” associated with male fetal sex hormones and a tendency for “systemizing” (as opposed to empathizing). In addition, he has pioneered unique instruments in the assessment of abilities relevant to autism, including the autism-spectrum quotient (or “AQ”), and an assessment of one’s ability to read emotional states from eyes.

Proposed Cognitive Model from “Mindblindness”

In his 1995 essay “Mindblindness,” Baron-Cohen discusses the idea that autism stems from the inability to perceive social information. This is analogous to the way in which colorblind people have the inability to perceive different wavelengths of light. After introducing this idea, Baron-Cohen proposed a specific array of cognitive modules that allow for mindreading in neurotypical individuals. These are: the Intentionality Detector (ID), the Eye-Direction Detector (EDD), Shared-Attention Mechanism (SAM), and the Theory of Mind Module (ToMM). The model proposed by Baron-Cohen is closely related to the model proposed by Alan Leslie (1994). They cover much of the same ground, but differ in which modules are responsible for which functions.

In Baron-Cohen’s model, the ID is tasked with identifying those objects that, by virtue of their motion, are candidates for having mental states. An animate object will move in a way that is special, at least compared to inanimate objects. An animate will have self-propelled motion: it will ACT, as opposed to simply being acted upon. Also, its motion will have meaningful direction and, therefore, be possible to describe with intentions. An object that moves towards another object or moves away from another object is an animate that the ID mechanism may interpret as having a goal: to approach an object of desire, or to avoid a harmful object. The ID mechanism is proposed to be functional quite early in life, as demonstrated by multiple studies in which infants seem able to interpret behavior as goal-directed based solely on the motion patterns of geometric shapes (Gergely et al. 1995; Hamlin et al. 2007). Importantly, the Intentionality Detector mechanism is proposed to be multimodal, so that animate motion can be detected through sight, touch, or sound.

The Eye Direction Detector

In contrast, the EDD is proposed to be a part of the visual system and sensitive only to eye-like stimuli. The mechanism can be described as having three related functions: the detection of eye stimuli in the

first place, the calculation of the direction of the gaze of those eyes, and the inference that the owner of those eyes is aware of the existence of whatever the eyes are looking at (that is, an agent “sees” the thing towards which the eyes are oriented.)

The Shared Attention Mechanism

Once a brain is capable of identifying agents (ID) and appreciating the things of which the agent is aware (EDD), the output of these functions can be combined into what Baron-Cohen calls “triadic representations.” This is an appreciation of the fact that I, and another agent, can potentially both direct our attention to the same third thing. In this way, importantly, we are able to share information with each other regarding another person or object. Such joint attention is a paramount skill in the transfer of relevant information about the world, and most very young children seem quite keen to establish joint attention. Goals (inferred by the ID) and eye direction (inferred by the EDD) are synthesized by the SAM in order to determine that a person may *want* the thing that they are looking at. (It should be noted that the role of eyes, so central to the functioning of EDD, can be played by other relevant input. Children who live their entire lives without sight nevertheless seem able to develop the inputs that allow SAM To function normally.) However, the SAM is limited in that it can only function when the third object can be confirmed to be present and being perceived, in the moment, by both parties. In order to share information and contemplate things that are not currently being observed, another module is necessary.

The Theory of Mind Mechanism

The Theory of Mind Mechanism is responsible for inferring the “epistemic mental states,” which include things like knowing, believing, deceiving, and wondering. These states capture what is going on inside an organism’s head and are very closely related to what an organism is likely to do. This allows for the representation of things that are not currently present (such as, “John remembers that his car is parked in the Itchy Lot.”) Of course, none of these epistemic mental states can be observed

directly, even with the most modern of neuroimaging techniques. They must all be inferred from the clues present in the environment, such as eye gaze. (That is, if a person appears to be looking longingly at a new bicycle, it can be inferred that the person desires the bicycle and may be willing to engage in a series of actions with the goal of getting it. As such, this person may be willing to contribute to your welfare if you are able to contribute to their goal of owning the bike.) In that sense, the Theory of Mind Mechanism is about a theory, since epistemic states are merely theorized or inferred. We never have direct evidence of their existence. In fact, Baron-Cohen does not commit himself to the actual and literal existence of things like beliefs and desires and is content with the possibility that these things are merely hallucinated in order to help summarize information in a way that helps us to make sense of behavior.

The ID and EDD mechanisms are proposed to feed information to the SAM module, and the outputs of the SAM module are proposed to spur the development of the ToMM module. Thus, an interruption in the development of any one of these could result in a person who is not able to represent epistemic mental states or use them in a predictive “theory-like” way. In Baron-Cohen’s view, this is very much the essence of what it is to be a person with autism.

The Autism Connection

Research into the specific abilities and disabilities of people with autism have revealed a remarkable set of intact abilities, coupled with specific deficits. Autism is not characterized by a general lack of intelligence but by the impairment of functions that seem to interfere with communication and social appropriateness. Baron-Cohen’s own work has suggested that children with autism are quite able to infer an agent’s goals, follow the gaze of their eyes, and even know that the agent will be sad or happy depending on whether or not they get what they want. For these reasons, it is unlikely that autism is characterized by an impairment of either ID or EDD. On the other hand, evidence leads to the conclusion that there are large problems with the SAM, in that children with autism do not

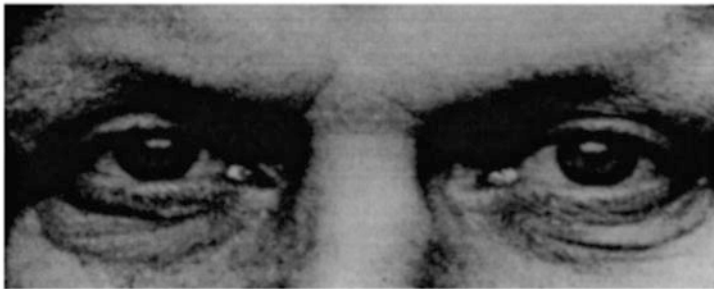
typically attempt to draw others' attention to interesting objects, nor do they seem particularly interested in monitoring the gaze of other people.

Furthermore, the majority of children with autism seem to be impaired in representing epistemic mental states. This prevents them from efficiently dealing with information about what other people know or believe. Autistic children tend to fail the classic False Belief Task, in which one character sees an object being placed at location A but is then unaware of the object's removal to location B. While the neurotypical child will appreciate that the character will look in location A for the object (because she *thinks* the object is in location A), a child with autism will persistently guess that the character will look in location B (where the object actually is). This pattern of response among people with autism makes sense, as a prediction of action towards location A hinges on the representation of the character's epistemic mental state "thinks that the object is in location A".

Eyes and Emotions

Baron-Cohen also describes children with autism as deficient in their ability to infer emotional states from facial expressions. While it may be possible to predict emotions from *circumstances* ("Tommy lost his truck. Now Tommy is sad."), it is something else to be able to infer that Tommy is sad because his mouth is turned down and his eyes are red and squinting. In his work, Baron-Cohen created stimuli in which the only facial features available to express emotions were the eyes, and found that neurotypical males show a deficit in performance relative to females, that is an echo of the deficits in autism. That is, while the average male is a little bit worse than the average female when it comes to reading emotions from a snapshot of eyes, a person with autism is far worse (Fig. 1).

This pattern of "neurotypical male is slightly bad at something on which a person with autism is



An example of a (male) stimulus used: in the first version word choices were serious (correct) vs. playful. In the revised version the word choices were serious (correct), ashamed, alarmed, and bewildered.



A second (female) example from the Eyes Test: in the first version the word choice was reflective (correct) vs. unreflective. In the revised version the word choice was reflective (correct), aghast, irritated, and impatient.

Simon Baron-Cohen (Darwinian Psychiatry), Fig. 1 Examples of the revised Reading the Mind in the Eyes test, from Baron-Cohen et al. (2001b)

quite bad” presents itself repeatedly in the “extreme male brain” theory of autism.

Autism and “Extreme Male Brain”

The extreme male brain theory of autism (Baron-Cohen 2002) is predicated on the measurement of two variables, each of which show significant amounts of individual differences. The first of these is “empathizing,” which is not a new concept. A person high on empathizing will be adept at understanding the emotions, motivations, intentions, and thoughts of others. They will be able to quickly and easily communicate with other people and navigate the social world fluidly. On the other hand, the dimension of “systemizing” involves the attempt to understand physical systems with inputs and outputs in terms of how their parts interact. For instance, if a person were approaching a bicycle with a systemizing approach, they might observe that the chain travels around in a loop when the bicycle is moving. This correlation between the motion of the bike and chain might lead to the further understanding that the chain is transferring power from the pedals to the rear wheel.

While the understanding and prediction of people is *also* the understanding and prediction of a physical system, the system in question is so perversely complex that it calls for a specialized brain mechanism to do the job easily and automatically. In other words, it might be theoretically possible to understand all of the physical inputs, outputs, and processes that go into something like figuring out when you should and shouldn’t tell a dirty joke. However, if we attempted to apply what Daniel Dennett calls the “physical stance” to this problem, it would be too cumbersome to solve. However, through a series of automated shortcuts and assumptions, we can intuitively get the right answer by using what Dennett calls the “intentional stance”: treating a person-object like a special kind of thing that is driven by somewhat mysterious emotional states, desires, and knowledge.

A person high on systemizing may be very, very skilled at understanding the individual parts of an interactive system, but this will not get them

very far at all when trying to deal with the complexity of human behavior.

Unsurprisingly, females are typically found to be higher on empathizing than males. Evidence of this comes from the typically superior female ability to do things like read emotions from faces, take turns, value and display empathy, value relationships, communicate with language, and refrain from violence and aggression. Males, on the other hand, typically excel at tasks that require the scrutinizing of parts, such as: math, physics, engineering, construction, and map reading. They tend to gravitate towards toys and adult occupations that stress these abilities. Males also tend to perform better on specific cognitive tasks that require isolating the perception of a certain part of a system, such as the mental rotation task, Rod and Frame test, and Water-Level task.

It is yet to be determined how much of this difference is due to stable differences between males and females and how much is due to expectations from others. Almost certainly, these two factors resonate and reinforce each other. However, research has established a link between increased levels of fetal testosterone and a reduced tendency to use language that invokes the intentional stance (Knickmeyer et al. 2006).

So, if a male is slightly better at systemizing and slightly worse at empathizing, the extreme of this would be a person who was essentially disabled in terms of empathizing while preserving or even excelling at systemizing. This is what Baron-Cohen sees in people with autism: a severe impairment in the Intentional Stance, often accompanied by enhanced abilities underwritten by the Physical Stance.

Autism Assessment: The “Autism Quotient”

Autism is not necessarily a clean-cut distinction between those with and without the disorder. As the “extreme male brain” conceptualization suggests, if simply being male is a mild version of what it means to have autism, then there must be extreme and less extreme versions of autism.

Baron-Cohen and colleagues set out to design an instrument to quantify this tendency toward autism in normal populations. This instrument became known as the “Autism Quotient” or “AQ” (Baron-Cohen et al. 2001a). The AQ ranges from 0–50 and scores higher than the low 30s are considered to be extremely high, indicating Asperger’s Syndrome or High Functioning Autism.

The instrument is informed by a set of assumptions about the nature of autism, which has led to the assessment of five different areas: social skills, attention switching, attention to detail, communication, and imagination. The AQ shows a reliable difference between men and women, with men scoring higher. Scientists also reliably score higher than nonscientists, with mathematicians scoring higher than other professions.

Intervention

Baron-Cohen has also worked in the applied side of autism research, using an understanding of the interests and deficits common to people who he conceptualizes as more “systemizing.” He has authored DVDs intended to help people with ASD to recognize emotions, began the Cambridge Lifespan Asperger Syndrome Service (CLASS), and has investigated “LEGO therapy,” which uses the highly “systemized” LEGO toy to encourage social skills among individuals with autism.

Conclusion

Simon Baron-Cohen has had several major impacts on the study of autism and related disorders over decades of research, assessment, and intervention. Major contributions such as: the idea of mindblindness, the “extreme male brain” theory, and the Autism Quotient stand as noteworthy contributions to the field.

Lastly, for those who recognize the rather unique surname, Simon Baron-Cohen is, in fact, the cousin of actor and comedian Sacha Baron Cohen.

Cross-References

- [Autism](#)
- [Daniel Dennett on Free Will](#)
- [Intentional Stance](#)
- [Mindblindness](#)
- [Theory of Mind](#)
- [Theory of Mind and Evidence of Brain Modularity](#)

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Simple Phobias

- [Fears and Phobias](#)

Simulating Orgasm

- ▶ [Women Pretending Orgasm](#)

Single Parent

- ▶ [Single-Mother Families](#)

Single Person

- ▶ [Loop Variant, The](#)

Single Trial Learning

- ▶ [Declarative Knowledge](#)

Single-Male Group

- ▶ [Harems](#)

Single-Male Troop

- ▶ [Harems](#)

Single-Male/Multi-female Group

- ▶ [Harems](#)

Single-Mother Families

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Synonyms

[Caregiver](#); [Matriarch](#); [Single parent](#)

Definition

A family system headed by the female parent without the male parent physically in the home; male parent often offers little to no assistance in caregiving activities.

Introduction

Single mothers have been present throughout human history. Today, single-mother families are one of the fastest growing demographics with approximately 9.5 million families in the United States being headed by single mothers (Afifi et al. 2006). Because of the prevalence of single mothers, many researchers have tried to understand why mothers might have to raise their child alone, and the effects single-mother families can have on mother and child well-being. Some explanations of single motherhood are traced to sexual strategies. As with many other species where a mother has more parenting responsibilities, males might choose to mate with multiple women (Trivers 1972). As seen in birds, males might father multiple offspring with multiple partners, but will assist with rearing children with only one partner (Trivers 1972). Therefore, all other sexual partners who yield offspring will be left to care for their young without partner assistance.

While sexual strategies can lead to single-mother families, countries like the United States have also seen an increase in the number of families headed by single mothers because of cultural shifts leading to an increased social acceptance of divorce and single parenthood (Afifi et al. 2006).

However, while some mothers might become single parents because of divorce or partner absence, other mothers might have to raise children alone after the death of a partner or for other reasons. With increased interest in single-mother families, recent research has shown that it is important to make distinction between the causes of single motherhood because the cause for singlehood can have large influences on maternal and child outcomes ranging on maternal mental health, employment, and child behavioral development.

Causes of Single Motherhood and Its Effects on Mental Health and Employment

Mothers and children in two-parent households typically have more advantageous outcomes than children in single-mother households. In two-parent households, having two caregivers allows for more resources to allocate and higher levels of parental investment across children (Trivers 1972). Not having a second caregiver in the household can create strains on resources for in single-mother families that can lead to deleterious outcomes for both the mother and her children (Bilbarz and Gottainer 2000; Trivers 1972). Being a single mother can create emotional strains by increasing a mother's likelihood of developing a psychological disorder and financial strains because the loss of a second income might make it harder for a mother to maintain the basic physical needs of her family.

The absence or loss of a partner can create emotional strains which might limit a mother's ability to care for her offspring. However, the cause of single motherhood can create distinct differences in the mental health of the mother. Comparing married, never-married, and separated/divorced mothers, Affifi et al. (2006) found that the cause for single motherhood can significantly influence a mother's susceptibility to anxiety, mood, and externalizing disorders. Results found that separated/divorced mothers had significantly higher rates of anxiety, mood, and externalizing disorders than never-married mothers. Additionally, never-married mothers exhibited

very similar rates of anxiety, mood, and externalizing behaviors as married mothers who also had significantly lower reported scores than separated/divorced mothers (Afifi et al. 2006). These results could indicate that the social circumstances leading to separation or divorce might either place mothers at risk of developing psychopathology. However, because the present study does not examine the mental health of single mothers who are single due to partner death, this could potentially mean that other situational factors such as grief could further influence the mental health of mothers. The cause of single motherhood might not only influence a mother's emotional well-being, but might also influence her ability to financially provide for her offspring. This could further cause emotional strain and distress for the mother.

In western societies, research indicates evidence that it might be more financially advantageous for a mother to be widowed than to be divorced or never-married. In the United States, many widowed mothers are protected by financial statutes (such as Social Security) to provide some financial security for mothers and children after the death of her husband (Bilbarz and Gottainer 2000). In the case of divorced or non-married partners, the father might be instructed to pay child support, but this is not always guaranteed and can place single mothers and their children in financial jeopardy. While there might be some financial resources available for single mothers and their families, many single mothers, regardless of the reason why they are single, are required to enter the work force to provide for their families (Budig and England 2001). In a study comparing non-mothers to both married and non-married mothers, Budig and England (2001) found that while most mothers experience a 7% wage penalty per child, lifetime financial gain is seen to differ between married and non-married mothers. Reasons for the wage penalty across mothers could be due to extended leave to care for newborns, part-time work, and having to take more time off to care for sick offspring. However, for single or non-married mothers, the lifetime wage penalty is lower because she might have to work full time or forgo leave to ensure that she has the resources needed to provide for her family

(Budig and England 2001). While the financial needs of the family might be met, long periods of maternal absence can have large influences on child outcome.

Single-Mother Households and Child Outcomes

Household environment has a large influence on the developmental trajectory of children. Children who are raised by single mothers might have increased problem behaviors because of financial and emotional strains on the family. For some children of single mothers, this might lead to an increased influence of peer groups which can impact school performance and behavioral development (Steinberg 1987). The absence of the father in the household can also lead to biological changes in the child which can advance sexual maturation and lead to riskier sexual behaviors (Ellis et al. 2003).

Academic performance can have a large influence on later life trajectory by providing individuals with opportunities for financial and social advancement. Children raised by single mothers are seen to have decreases in academic performance compared to children from two-parent families (Lee et al. 2007). However, this effect is different between male and female offspring. In a study comparing families of single mothers to single fathers, Lee et al. (2007) found that high maternal involvement increased academic achievement in male children for reading and English test scores, but for female children, high maternal involvement was related to decreased performance in reading, English, and math scores. The opposite results were found for children of single fathers. Lee et al. (2007) posit that this difference might be due to children viewing their highly involved same-sex parent more as a peer than a parent. This could lead to diminished authority of the mother regarding the academic performance of her female children.

Though highly engaged single mother might have negative influences on female academic development, low parental involvement is typically shown to influence substance use and

antisocial behavior in children (Kuntsche and Silbereisen 2004; Steinberg 1987). In a study of Swedish 9th graders, Kuntsche and Silbereisen (2004) found that adolescents raised in single-parent homes engaged in higher levels of substance use behaviors. The results of this study might be explained by the financial strains caused from single motherhood that can cause a mother to spend extended periods of time away from the home. Extended absences can lead to weakened parent-child relationships and the increased reliance on peers. Steinberg (1987) found that adolescents who were raised in single parent households rated that they were more likely to engage in negative behaviors with peers (e.g., vandalism, drinking). While this could be related to the reliance on peers, these behaviors can also be driven by the parenting style adopted by single parents (Aunola and Nurmi 2005; Steinberg 1987). Single mothers are seen to engage in higher levels of high-control (often referred to as authoritarian) parenting styles (Kuntsche and Silbereisen 2004), and high-control behaviors are associated with higher levels of internalizing and externalizing problems for adolescents (Aunola and Nurmi 2005). Increased internalizing and externalizing behaviors place children at higher risk for engaging in antisocial behaviors. However, as with academic performance, research conducted by Steinberg (1987) and Kuntsche and Silbereisen (2004) indicate that there are sex differences in the outcomes for children of single mothers. Broadly, male children raised by single mothers are seen to engage in higher rates of externalizing behaviors than male children raised in two-parent households; females with highly involved mothers do not (Steinberg 1987; Kuntsche and Silbereisen 2004). Even though males engage in higher levels of risk-taking in general, males from single-mother homes still engaged in higher rates of risky behaviors than male children of two-parent families (Steinberg 1987).

Being raised in a single-mother household might not only increase the risk for externalizing behaviors in children, but father absence is seen to accelerate pubertal development of female children and place them at higher risk for risky sexual

behaviors and teenage pregnancy (Ellis et al. 2003; Quinlan 2003). In a cross-cultural longitudinal study, Ellis et al. (2003) found that females who had absent fathers had significantly earlier menarche, earlier first sexual experiences, and higher pregnancy rates than females of two-parent families. The results of this study found that these effects were magnified in female children who were in father-absent homes *before* they were 5 years of age – indicating that the timing of father absence might also be an important factor of development. However, when examining the effects of timing on internalizing and externalizing behaviors, timing was not a significant predictor, indicating that there might be alternate explanations for these increased behaviors in single-mother families (Ellis et al. 2003).

Conclusions

Single-mother families are one of the fastest growing demographics in society today. Even though single-mother families account for a growing number of families, research indicates that there are significant difficulties and stressors which can affect mothers and their offspring financially, emotionally, and physically. As shown in the research, coming from a single-mother household can place a child at specific risk for many negative outcomes. Further, research examining the timing of father absence on behavioral development might help with the understanding of the developmental outcomes of children raised by single mothers. With that in mind, it is clear that there are certain advantages afforded to offspring of two-parent families, and because the number of single-mother families is increasing, more research needs to be conducted to understand the preventative measures that can be taken to reduce the disparity in outcomes between children of two-parent families and single-mother households.

Cross-References

► Maternal Role

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Single-Subject Experimental Design

► Methods and Enduring Impact of Behaviorism

Sister

- ▶ [Competition for Parental Investment](#)
- ▶ [Siblings Pose Unique Adaptive Problems](#)
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Sisters

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Situational Awareness

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Size

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Size and Dominance

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Synonyms

[Size](#): breadth, circumference, girth, height, length, mass, stature, volume, weight

[Dominance](#): influence, power, prestige, rank, status

Definitions

Size refers to relative organismal magnitude among conspecifics and is typically measured by somatic height, weight, mass, and volume, as well as length, width, and circumference of morphological traits. Among animals, larger body size often facilitates dominance, one's social rank attained via the use of force or threat of force.

Introduction

Size is among the most salient properties of biological organisms. An association of largeness with dominance and smallness with submission exists across species – exemplified by the common behavioral trait of manipulating one's apparent size through expansive or contractive gestures and, in humans, by the pervasive use of size terminology to denote status (e.g., “the high and the mighty” vs. “little people”) (Ellis 1994). In many species, dominance is associated with superior fitness outcomes, particularly among males (Ellis 1995), reflecting a legacy of selection favoring greater size, manipulations of size, and acuity to both. In humans, high social rank and rank-related reproductive benefits are attainable not merely through size and physical coercion, but also via prestige, status earned through perceived merit (Henrich and Gil-White 2001).

Selection for Size

Biological taxa often exhibit phyletic increase in size. This tendency is believed to result from the reproductive importance of organismal size despite costs attendant both to being and becoming large: greater food requirements, thermal stress, and conspicuity to predators, as well as the protracted vulnerability associated with slower growth, or the risky foraging and early reproduction associated with faster growth

(Blanckenhorn 2000). In fact, not only do larger-bodied individuals realize greater fitness than do smaller-bodied conspecifics across phylogenetically distant species, selection is stronger on size than it is on other morphological traits. Possible ecological selection pressures favoring large size include greater capacity to survive environmental variation, increased longevity, more efficient use of heat per unit volume, better ability to engage in or avoid predation, and reduction in mortality from superior resource competition and use (Kingsolver and Pfennig 2004).

Ecological selection pressures may also explain much intraspecific variation in size. As initially suggested by Darwin (1871) and supported more recently in a diverse array of anisogamous reproducers, selection often favors greater female size because of associated increases in fertility: larger females are often better able to procure resources, physiologically invest in offspring (e.g., in mammals via gestation and lactation), and produce ova of greater quality or in greater quantities (Andersson 1994). In some sequential hermaphroditic species, for example, individuals begin life as males but possess the ability to reproduce as females upon reaching a body size at which the costlier investment of female reproduction is advantageous. However, in many species, particularly among birds and mammals, males are larger than females. This is often the result of sexual selection, the evolutionary process that favors traits beneficial in securing mating opportunities (Darwin 1871). Competition for mates is generally more intense among males, for whom greater size may permit physical exclusion of same-sex rivals from mating opportunities and/or increase attractiveness to females (Andersson 1994).

Size and Dominance in Males

In humans, greater body size is associated with better fitness outcomes among men. For example, Mueller and Mazur (2001) found a positive relationship between height and reproductive success in a cohort of male military officers, attributable

to taller men's greater number of wives. Similarly, in a British cohort, Nettle (2002a) found that although taller men did not out-reproduce shorter men, they had more long-term relationships and were less often childless (though very tall men were more likely to be childless and have serious illnesses). Because men's height was better predicted by their fathers' social class than by their own social class, Nettle (2002a) attributed the finding to taller men's greater ability to secure long-term mates. Furthermore, Pawlowski et al. (2000) reported that taller men in their thirties, forties, and fifties were significantly more likely to be married and have children than were shorter men in each age group.

Men's height exceeds women's across populations (Gaulin and Boster 1985) and appears to be the product of sexual selection, a hallmark of which is appreciable sexual dimorphism that emerges at puberty. Males' 1% greater length and similar body fat percentage to females at birth (Wells 2007) becomes 7% greater height (Gustafsson and Lindenfors 2004) and 14% greater body mass in adulthood (Smith and Jungers 1997), largely as a result of males' pubertal increase in testosterone production.

One mechanism through which sexual selection may have favored male height is female mate choice. Females are predicted to be relatively discriminating in their mating decisions, and so the preferences of ancestral females may have shaped male stature. Consistent with this, studies of personal advertisements have shown females, but not males, to prefer tall partners, and taller males, but not taller females, to receive more responses. Similar results have been obtained in studies featuring greater ecological validity. Hill et al. (2013), for instance, found men's height to predict their attractiveness to familiar women when other sexually dimorphic traits were controlled, and in a natural fertility population from The Gambia, Sear (2006) found that while taller men did not realize greater reproductive success than did shorter men, they did have more marriages. This may reflect female mate choice for greater male height, or kin-mediated marriage decisions in which taller men have greater access to resources, possibly

by virtue of higher status. In addition to height, masculine male body morphologies are consistently associated with greater male attractiveness and mating success.

Selection pressures other than female mate choice may also have favored greater male size. For example, in an exploration of mating success among groups of social peers, Hill et al. (2013) found that body size (measured by a composite of weight as well as biceps, chest, and shoulder circumference) predicted number of sex partners in the previous year, a relationship not mediated by attractiveness to females but by physical dominance to males. Thus, men's mating success in this sample was predicted by success in male contest competition, a mechanism of intrasexual rivalry favoring greater size, strength, anatomical weaponry, and bellicosity that facilitates physical exclusion of same-sex rivals from mating opportunities. This research suggests that physical contests among men may have exerted stronger sexual selection pressure on human male traits than has female mate choice (see also Hill et al. 2017; Puts 2016). Indeed, U.S. presidents, many of whom have achieved their rank at least partly via dominance, have tended to be taller during times of societal threat and enjoy a wider margin of victory even with this variable controlled, suggesting that male height may be more valued when the perceived benefits of a dominant leader are believed most in need (McCann 2001).

Intrasexual contests also appear to have influenced male phenotypes among the other great apes (e.g., Wilson et al. 2014), whose male-biased sexual size dimorphism suggests that this trait may be phylogenetically conserved (Plavcan 2012). However, humans are more skeletally sexually dimorphic than their closest extant relatives, the chimpanzees (Gordon et al. 2008). In addition, sexual dimorphism in overall human body mass fails to capture men's appreciably greater muscle mass (Lassek and Gaulin 2009), which would likely have been attenuated in the absence of continued selection favoring it in antecedent hominins. Moreover, male-biased sexual size dimorphism among polygynous primates is

positively related to the intensity of mating competition, even with phylogeny and allometry controlled (Mitani et al. 1996).

Across a wide array of species, body size is associated with male dominance (Ellis 1994), and dominant males realize greater reproductive success (Ellis 1995). Being large or conveying cues to large size is thus an important determinant of fitness outcomes in animals. Indeed, exaggerations of apparent size such as low-frequency vocalizations are prominent among primates, including humans, perhaps because they create the impression of size with less somatic investment (Puts et al. 2014, 2016). In many primate species, dominant males monopolize sexual access to multiple females or disproportionately mate with those near ovulation. Across 13 species from 6 anthropoid genera, for instance, Cowlshaw and Dunbar (1991) found a positive relationship between male dominance rank and mating success with estrous females. Although inferences of fitness outcomes from mating behavior in nonhuman primates can be complicated by paternity uncertainty, genetic research has demonstrated positive relationships between male rank and reproductive success.

Male dominance and fitness also exhibit a consistent relationship in the human ethnographic record. Among the Yanomamo of Venezuela and Brazil, Chagnon (1988) found that *unokais* (warriors, or "men who have killed") realize greater reproductive success than do non-*unokais* as a result of both marriage and bride-theft. Becoming an *unokai*, an encouraged but voluntary duty, confers higher status on men, who list access to females as their primary impetus for killing. By contrast, men who consistently abandon inter-village raiding parties lose status, as evinced by the increased sexual attention from other males that the wives of such men receive. As with all traits, however, there are costs to physical aggression, the optimal level of which is therefore likely to vary across environments. For example, among the Ecuadorian Waorani, "a people even more warlike than the Yanomamo," the most zealous warriors experience poorer measures of fitness than do less zealous warriors (Beckerman et al. 2009).

Status in human males may be achieved not only as dominance via coercion, but also as prestige via elicitation of voluntary deference. Whereas dominant individuals are often feared and avoided, prestigious individuals are sought-after, emulated, and venerated because of their locally valuable knowledge and skills (e.g., in hunting), as well as their willingness to share these (Henrich and Gil-White 2001). For instance, among the Tsimane of Bolivia, von Rueden et al. (2008) found that men's knowledge-based skills and social support impacted the influence and respect they received among community members more than did their body size, though body size was the best predictor of peer assessments of men's ability to win in dyadic physical fights. Moreover, prestige-oriented status is associated with male fitness across small-scale human societies (e.g., Irons 1979). Prestige, however, does not appear to have superseded dominance in importance – both are viable means of acquiring and maintaining status in humans (Cheng et al. 2013). Indeed, among the Tsimane, both dominance and prestige have predicted men's surviving offspring, number of live births, extramarital affairs, number of serial marriages, wives' attractiveness, and number of allies and labor partners (von Rueden et al. 2011).

In addition to being distinct from dominance, prestige exhibits no clear relationship with body size. For instance, while male-biased sexual size dimorphism has been explained as the product of ecological selection via hunting (Plavcan 2012), a predominantly male activity associated with men's fitness in natural fertility populations (Gurven and von Rueden 2006), hunting is the most learning-intensive of all foraging behaviors (Kaplan et al. 2000), and return rates from hunting in small-scale societies often peak long after males peak in physical formidability (Walker et al. 2002). Thus, while hunting may have helped shape certain traits related to men's physical performance (e.g., Apicella 2014), relationships between hunting success and male fitness are most parsimoniously attributed to possession of knowledge-based skills. Moreover, the male-biased sexual size dimorphism inferred among some Pliocene hominin species (Plavcan

2012) reflects a greater antiquity in the human lineage than the emergence of hunting during the Pleistocene, and ecological selection leaves unexplained a suite of men's traits (e.g., facial hair, facial robusticity, and deep voices) that confer little benefit apart from aiding in male contests (Hill et al. 2017).

Size and Dominance in Females

As in males, body size is reproductively consequential in females of many species. In contrast to large males, however, large females often accrue fitness benefits through ecological selection for greater fecundity (Andersson 1994). In mammals, for example, selection favors females capable of gestating, lactating, and provisioning and protecting altricial offspring at least until weaning (Eibl-Eibesfeldt 1989). Human females appear similarly designed to invest physiologically in offspring. Women's body fat is essential for successful ovulatory function (Frisch and McArthur 1974), taller and heavier women have been shown to produce heavier offspring (e.g., Kirchengast et al. 1998), and maternal height is negatively related to offspring mortality, particularly in non-Western populations (e.g., Stulp et al. 2012). In women as well as men, moreover, height and mortality are negatively related (Jousilahti et al. 2000), though extreme height has been associated with reduced fitness and poor health in both sexes (Nettle 2002a, b).

Physiological investment in offspring is contingent on acquisition of resources such as food, to which dominance over same-sex conspecifics often affords females priority. Indeed, dominance and reproductive success are associated in females of many species (Ellis 1995). Across primates, benefits accrued by dominant females include higher-quality diets, earlier reproduction, faster reproductive rate, longer lifespan, and offspring that mature earlier and survive longer (e.g., Fedigan 1983; Harcourt 1987; Pusey et al. 1997).

While dominance and height are associated in females of many species, including humans, the association is often not as strong as it is in males

(Ellis 1994). In nonhuman species, this may reflect constitutional differences among females that permit some to achieve dominance more easily than others, or superior developmental diet and health, particularly in the case of inherited rank. In humans, females may compete more for access to long-term mates likely to furnish limited resources than for direct access to resources. As a result, sexual selection via contest competition has shaped the human female phenotype less than has male mate choice, which often appears designed to capture female physiological investment (Puts 2016).

Conclusion

In humans and across an array of animal species, organismal size facilitates and is positively related to dominance, or coerced social rank. While this relationship exists in both sexes, it is stronger among males, particularly in humans. Large individuals often receive priority of access to the resources most strongly constraining their reproduction: males to mates, food, and resources, females to food and resources. While alternative explanations have been posited, the aggregate of evidence suggests that, in humans, male size and body composition are the products largely of male contest-mediated sexual selection, whereas female size and body composition are the products largely of ecological selection for fecundity as well as male mate-choice mediated sexual selection. These conclusions have received support from diverse methodologies, species, and human populations.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Anatomical Adaptations for Fighting](#)
- ▶ [Assessment of Fighting Ability](#)
- ▶ [Body Attractiveness](#)
- ▶ [Body Fat Percent and Distribution](#)
- ▶ [Body Posture](#)
- ▶ [Change in Male Hunting Returns](#)
- ▶ [Comparative Evidence](#)

- ▶ [Cross-Cultural Studies](#)
- ▶ [Dominance and Health](#)
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- ▶ [Dominance and Testosterone](#)
- ▶ [Dominance in Humans](#)
- ▶ [Evolutionary Standards of Female Attractiveness](#)
- ▶ [Facial Width to Height Ratio and Dominance](#)
- ▶ [Female Mate Choice](#)
- ▶ [Height and Dominance](#)
- ▶ [Indicators and Correlates of Status and Dominance](#)
- ▶ [Intrasexual Rivalry Among Men](#)
- ▶ [Intrasexual Rivalry Among Women](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Male Adaptations to Assess Fighting Ability](#)
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- ▶ [Nonverbal Indicators of Dominance](#)
- ▶ [Resources](#)
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- ▶ [Serotonin and Dominance](#)
- ▶ [Sex Differences](#)
- ▶ [Sex Differences in Ability to Assess Fighting Ability](#)
- ▶ [Sexual Access as Benefit of Victory in War](#)
- ▶ [Sexual Selection via Direct Male-Male Interactions](#)
- ▶ [Shifting Dominance](#)
- ▶ [Social Status and Economic Resources](#)
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- ▶ [Upper Body Strength](#)
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- ▶ [Upper Body Strength from Photo](#)
- ▶ [Vocal Indicators of Dominance](#)
- ▶ [Waist-to-Hip Ratio](#)
- ▶ [Women's Mate Preferences](#)

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Size Dimorphism and Locomotion

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Synonyms

Bipedalism; Human reproduction; Intrasexual competition; Sexual dimorphism; Size dimorphism

Definition

Sexual size dimorphism is defined as the physical size differences between males and females of a species. Whereas body size has traditionally been the most common measure, differences in the size of other features, such as canine teeth, as well as skeletal and cranial features are also used to measure the nature of Sexual size dimorphism in a species.

Introduction

Sexual size dimorphism (SSD) refers to the physical size differences between the sexes. Such size dimorphisms evolve as a result of natural and sexual selection and are closely linked to the nature of social and mating system in that species (Darwin 1871). Three major hypotheses traditionally explain how SSD may evolve: (1) SSD can arise through sexual selection if individuals of a certain size in one sex have better (or worse) reproductive success through mate choice and/or intrasexual competition. (2) SSD can evolve if larger females have better reproductive output than smaller females. (3) SSD can evolve when the sexes have adapted to different ecological niches in order to reduce intersexual competition. Research over the last decade suggest a more

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complex interaction of factors influencing survival (e.g., viability selection), reproduction (fecundity selection), and mating success (sexual selection) that shape the nature of SSD, because males and females often differ in each of these traits. There is considerable interest in understanding how and why SSD evolved in humans. Although intrasexual competition is popularly used to explain human SSD, a variety of factors, including intra- and intersexual competition, locomotion, and reproduction, appear to have contributed to SSD in humans.

Sexual Size Dimorphism in Hominins

Modern human males are on average 7% taller and about 15% heavier than females; they have broader shoulders, stronger musculature, and increased upper body strength compared to females. The modern human male skeleton is also more robust with heavier and larger bones. Male skulls are slightly larger with specific shape variations compared to female skulls. The human pelvis shows marked dimorphism in size and shape reflecting modifications for childbearing in females. Compared to extant nonhuman great apes, humans' SSD levels are low to moderate depending on what is being measured (Plavcan 2012). Most comparative studies use canine teeth and body mass in primates because they are more easily related to theories of sexual selection. Moreover, these traits are shared across primate taxa and thus are useful for comparative studies. Intense male-male competition is characteristic of great ape mating systems where there is selection on fighting performance. During male competition, canine displays are often cited to be aggressive signals; therefore, the lengths of the canines are used as a proxy for the intensity of male-male competition. Canine teeth dimorphism in humans is low compared to other primates. Total body mass is widely accepted to be the best indicator of SSD and also relates to male-male competition since larger males are physically more powerful and more successful in combat. They can also intimidate other males into submission without the need for combat. Compared to primates,

humans are only slightly more dimorphic than gibbons but slightly less dimorphic than chimpanzees (Plavcan 2012). Skeletal features are useful when comparing SSD to fossil data. Skeletal features suggest moderate stature dimorphism in humans compared to chimpanzees; skull SSD estimates are moderate, and postcranial (features other than the skull) estimates slightly exceed that of chimpanzees (Gordon et al. 2008). Overall, low body mass and canine SSD in modern humans suggest a reduction in the nature of male-male competition through human evolution. On the other hand, the moderate levels of SSD inferred from skull and postcranial stature would suggest that multiple factors influenced SSD in human evolution.

SSD in Ancestors of Modern Humans

The scanty human fossil record makes it very difficult to robustly assess SSD through human evolution. As observed in modern humans, most studies find that reduced canine size dimorphism is a typical feature of ancestral hominins (White et al. 2009) reinforcing the notion that male-male competition had reduced from that of chimpanzees. Skull, teeth, and postcranial estimates suggest very little SSD in *Ardipithecus ramidus* (~4.6 million years ago (ma)) (White et al. 2009) suggesting that male-male competition decreased early in hominin evolution. Estimates of SSD vary considerably across members of the genus *Australopithecus* (~4.2 ma), but the consensus indicates strong SSD in *Au. afarensis*, *Au. anamensis*, and *Au. robustus* (Gordon et al. 2008). Some studies claim humanlike levels of SSD (Reno et al. 2010). Size dimorphism appears to be strong in early *Homo* (~3.2 ma) in later *Homo* (see Plavcan 2012), as seen in *H. habilis* and *H. erectus* but then decreases to humanlike levels in later *Homo* (see Plavcan 2012). Overall, evidence suggests an intriguing trend with two major changes occurring through hominin SSD evolution, and both involve changes in female size. Given the apparent lack of SSD in *Ardipithecus*, strong SSD in *Australopithecus* was likely due to a decrease in female size (Gordon

et al. 2008; White et al. 2009; Plavcan 2012), and reducing SSD through later *Homo* likely occurred through substantial increases in female size. Inferring behavior from SSD data is in all likelihood speculative, but male-male competition alone cannot explain SSD evolution in humans.

Bipedalism and SSD: Intrasexual Competition and Male Body Size

Several hypotheses have been proposed to explain why bipedalism evolved in humans, including predation, foraging, thermoregulation, and energetics, but all of them invoke the overarching influence of environmental changes in the Miocene, which resulted in the disappearance of forests, and increased grassland. The demands of ecosystem changes likely influenced hominins to evolve energetically better locomotion to seek food and shelter in increasing savannah habitat and to reduce group sizes and intergroup distances in order to decrease competition for resources. Bipedal locomotion evolved early in hominin evolution. Strong evidence of bipedal features first appear in the pelvis of *Ardipithecus ramidus*, suggesting that members of the genus *Ardipithecus*, whose origins date back to the late Miocene (~5.8 ma), may have been partially bipedal (Haile-Selassie et al. 2012). Habitual bipedalism is widely observed through specializations in the feet, pelvis, and spine of *Australopithecus* (~4.2 ma). The spine reveals modifications to bear lumbar load during pregnancy – a feature not required in quadrupeds. Bipedalism provided a variety of advantages – from use of free hands, enhanced energetic, and ability to traverse craggy terrain – to the evolution of complex social behaviors.

Lack of significant canine dimorphism in hominins suggests that teeth baring was not relevant in competition, but body size must have been because males have maintained larger bodies through human evolution. During fights, all apes strike blows in a bipedal stance. Being able to stand upright not only frees the hands for striking opponents, but it also enhances fight performance by increasing range of motion and generating

more striking power (Carrier 2011). Moreover, humans are able to generate more force when striking downward, than upward, which could significantly affect the success of larger and taller males during combat (Carrier 2011). Being larger and taller would also have its advantages during hunting and obtaining mates. Almost all great apes are aggressive, and male-male competition for females can be intense and violent. Bonobos are an exception with lower violence. Ancestral hominins were no exception even if competition intensity had decreased. Moreover, male competition for mates is exacerbated in polygamous and promiscuous mating systems. Ancestral hominins were mostly polygamous. Even if they were like modern humans with serial monogamy, males would have competed for mates and resources.

Bipedalism and SSD: Selection on Female Size Through Reproduction

Fossil evidence suggests a decreasing trend of SSD through human evolution; SSD in *Australopithecus* resulted from a decrease in female size and then female size increased from early to late *Homo* (Plavcan 2012). If this is true, then clearly there was stronger selection on females relative to males. Theory suggests that there is typically a trade-off between body size, reproduction, and life history. Female fertility and fecundity is particularly important because their rates determine population growth and age structure, which can substantially influence life history traits, especially those associated with reproductive strategies.

In *Australopithecus*, while males may have maintained their size through competition, selection on smaller females were likely associated with early reproduction and fecundity due to early mortality and/or due to severe resource stress. Increasing female size from early to late *Homo* suggests selection favoring larger females either because they are outcompeting smaller females in a time of scarce resources or if larger females produced higher-quality offspring. It is possible that reduced mating competition and increased resource competition characterized later *Homo*. Resource scarcity will increase

mortality and thus exert pressure to decrease rates of early reproduction. Dominant resource-rich groups would have well-nourished females who could produce high-quality offspring. There are also suggestions that substantial ape-like to humanlike life history transitions, such as later age of first births, increased lifespan, and slower life history, all of which would increase female body size, occurred in later *Homo* (Robson and Wood 2008).

Another popular but intensely debated hypothesis, the obstetric dilemma, suggests that the female pelvis faced antagonistic selective pressures of bipedalism and birthing infants with large heads. This indirectly implies that selection may have acted against small statured women who are at higher risk of obstructive labor, which could explain increasing female size. However, recent studies reveal that bipedalism evolved under complex interactions between selection and drift and that a narrow pelvis is not required for bipedalism (Grabowski and Roseman 2015). Recent analyses also reveal broad pelvic canals in *Australopithecines* and even in later *Homo* (Gruss and Schmitt 2015). Moreover, pelvic dimorphism suggestive of any obstetric difficulties is not seen until *H. neanderthalensis*, and it was not until the late Pleistocene that the anatomically narrow pelvic canal evolved in *Homo sapiens* (Gruss and Schmitt 2015).

Another possibility that can influence female-specific changes in body size is maternal mortality in younger and in smaller females. Selection against early reproduction and smaller female size can result from male preference for younger women as mates. Given the shorter lifespan of ancestral hominins, it may not be unreasonable to assume that females reproduced at a relatively early age. If age of first birth in ancestral hominins is anything comparable to that in chimpanzees, which is 12–14 years, and if females of such age were developmentally unprepared for pregnancy (as they are in modern humans), then male mate choice would exacerbate selection against early reproduction, thus contributing not only to the increase in female size, but would also exert selection to extend age of reproduction. If dominant males can monopolize resources and mates,

and if these males preferred younger females, then male mate choice can accelerate the process of selection against smaller-sized females. However, this theory needs to be tested.

Conclusion

Current consensus is that a variety of factors, including sexual selection, natural selection, and environmental change, were involved in shaping human SSD. The magnitude to which each of these factors influenced SSD remains to be ascertained. Moreover, inferring behavior from fossil data is speculative. Early in hominin evolution, bipedalism may have contributed to intense male-male competition by enhancing fight performance, but resource scarcity driven by environmental changes likely influenced changes in hominin life and reproductive history traits. A large part of these changes appear to have occurred through modifications in female fertility and fecundity, which may have resulted in selection for larger females and thus reducing SSD in later hominin lineages. Much of these conclusions remain tenuous but also inspire more research to advance our understanding of human evolution.

Cross-References

- [Adaptation](#)
- [Bipedal Locomotion](#)
- [Reproductive Strategy](#)
- [Sex Differences](#)
- [Sexual Dimorphism](#)
- [Sexual Selection](#)
- [Sexual Selection via Direct Male-Male Interactions](#)
- [Sexual Size Dimorphism](#)

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Skew Theory

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Synonyms

[Optimal skew theory](#); [Reproductive skew theory](#)

Definition

An evolutionary theory attempting to explain the unequal sharing of reproduction among same-sex individuals within social groups.

Introduction

Cooperatively breeding animals vary markedly in reproductive skew, the unequal distribution of direct reproduction among same-sex individuals within social groups. In high-skew groups, such as eusocial ants, honeybees, termites, and meerkats, reproduction is concentrated in one or a few dominant individuals; in low-skew groups, such as some polistine and polybiine wasps and banded mongooses, reproduction is distributed more equitably among group members. Variation in skew frequently occurs both within and across species (Reeve and Ratnieks 1993; Vehrencamp 1983).

Reproductive skew theory aims to predict how members within a social group would partition reproduction in an evolutionarily stable way. To determine the optimal level of skew, it integrates genetic relatedness, ecological constraints on solitary breeding, group-living benefits, and within-group competitive asymmetries into a single theoretical basis (Johnstone 2000; Reeve and Ratnieks 1993). Further, skew models tend to, but not always, assume that each member's payoff of staying in the group should be greater or equal to the payoff of leaving to breed alone or fighting for the sole possession of the nest, thus opening up a new avenue for unraveling the evolution of group size and within-group conflict. Not surprisingly, researchers have boldly claimed that reproductive skew theory may be a good candidate for a general unified theory of social evolution, one that explains all the major features of all social taxa ranging from termite colonies to human societies.

Over two decades, a wide variety of skew models has been devised and the resulting predictions have been tested numerous times. The plethora of model variants with conflicting predictions, however, has attracted considerable skepticism and criticisms (Nonacs and Hager 2011). As a comprehensive literature review over various work and controversies on skew is beyond the aim of this entry, the basic models of reproductive skew and their implications for the humans are presented below.

Models of Reproductive Skew

Reproductive skew models can be classified into three major classes according to their different assumptions about how reproductive sharing is achieved within a social group: transactional models, compromise models, and synthetic models.

Transactional Models

Transactional models of skew assume that one individual has complete control over the partitioning of reproduction but the individual may “yield” a share of reproduction to other group members in order to maintain group stability (Reeve and Ratnieks 1993). Two types of transactional models exist: concession models and restraint models.

First, the concession model assumes that the dominant individual has full control over the reproductive partitioning within the group. Consider a group of two individuals, a dominant and a subordinate. If the dominant is too greedy and try to monopolize all direct reproduction in the group, the subordinate may choose to leave the group and reproduce solitarily. In response to the subordinate’s threat of departure, the dominant may concede just barely enough reproduction to the subordinate as an incentive to stay (Reeve and Ratnieks 1993; Vehrencamp 1983). The minimum share given to the subordinate would decline as (1) the expected reproductive success of a subordinate pursuing the departing option decreases (because, under harsh ecological constraints on solitary breeding, the dominant does not need to “pay” a large staying incentive), (2) the group’s overall productivity increases (i.e., the total size of the pie to be divided between the two has expanded), and (3) the genetic relatedness between the dominant and the subordinate increases (the subordinate’s indirect fitness payoff from remaining in the group increased).

Second, the restraint model assumes that the dominant only control group membership; that is, it has have the ability to evict the subordinate from the group (Johnstone and Cant 1999). It is the subordinate, however, who is assumed to have complete control over reproductive sharing. The subordinate may still exhibit a form of

reproductive restraint in order to avoid ejection from the group; it will thus obtain its maximum share of reproduction that can be tolerated by the dominant. Consequently, the concession and restrain models make exactly opposite predictions about the relationship between the genetic, ecological, and social factors and the level of reproductive skew.

Compromise Models

Compromise models do not incorporate the possibility of group dissolution. In other words, they assume that subordinates could not voluntarily depart the group, nor could the dominant forcefully evict subordinates. Another difference from the transactional models lies in whether any individual is assumed to have full control over the division of reproduction. In compromise models, no individual has complete control. Rather, each group member competes selfishly to gain a higher personal share of reproduction, at a cost to the overall productivity of the group. The partitioning of reproduction is determined by a compromise between the diverging optima of dominant and subordinates (Reeve et al. 1998).

The most well-known variant of this category, i.e., the tug-of-war model of Reeve et al. (1998), assumes that the dominant’s higher competitive ability renders it more efficient in converting its selfish effort to an increased personal share of reproduction. The evolutionarily stable level of skew is solved by finding the selfish efforts of dominants and subordinates in a way that the inclusive fitness of each is simultaneously maximized. The tug-of-war model yields different predictions from those of transactional models. The subordinate’s reproductive share at equilibrium would decline as the subordinate’s relative competitive ability decreases, but it will be quite insensitive to the genetic relatedness between the competitors. Ecological constraints, which were assumed away from the outset, would not affect the division of reproduction.

Synthetic Models

Synthetic models integrate the possibility of both group dissolution and incomplete control into a single framework. Each group member may

exchange reproductive payments to each other in order to maintain group stability, while simultaneously engaging in a tug-of-war competition over the remaining portion of reproduction (Johnstone 2000; Reeve and Shen 2006). Initial models, however, have been harshly criticized for theoretical shortcomings. For instance, it has been formally proved that a mixed strategy that involves both a tug-of-war and reproductive payments is unstable to invasion by a mutant “nicer” strategy that competes less strongly and gives a lesser reproductive payment (Cant and Johnstone 2009). Recent synthetic models attempt to overcome the stability problems of previous analyses, taking seriously the threat of departure/eviction or the power of negotiation.

Skew Theory Applied to Humans

Given that reproductive skew theory aspires to be a unified science of social evolution, it may be fruitfully utilized to elucidate the foundations of human sociality. Summers (2005) applied the classical concession model to the development of social stratification among human males. Recall that the concession model predicts that when group productivity benefits are greater, when the prospects for solitary breeding are lower, and when group members are more closely related, the level of skew within a group will be higher. Summers (2005) suggested that, since our divergence from the chimpanzee lineage, early hunter-gatherer societies were largely egalitarian (i.e., low level of skew) via the collective suppression of a self-assertive dominant individual by a group of subordinates. Around 10,000 years ago, strong ecological constraints on solitary dispersal, combined with the economically storable nature of agricultural crops, led to the formation of despotic preindustrial societies (i.e., high level of skew). For example, the harsh environments surrounding the Nile Valley made possible the development of extreme despotism in ancient Egypt. In the same vein, Betzig (2014) emphasized the role of ecological constraints in shaping despotic civilizations in Mesopotamia, Egypt, India, and China. Kings and emperors collected as many as

100,000 fertile women, whose children were supported by thousands of eunuchs (“sterile castes”). About 500 years ago, modern egalitarian societies emerged, the reason of which was attributed to the relaxation of ecological constraints, i.e., the discovery of two nearly empty continents (Betzig 2014).

In addition to human societies, the reproductive skew framework has been applied to analyze the extended human family. A growing body of evidence indicates that humans have evolved as a cooperatively breeding species, in which care and provisioning from family members from other than mothers were essential for child survival. Cant and Johnstone (2008) applied the tug-of-war model to understand reproductive conflicts between women of different generations. If female dispersal predominantly occurred in ancestral humans, there would be relatedness asymmetries between a mother and her son’s wife in the extended family. Although the mother is related to the offspring of the daughter-in-law, the daughter-in-law, by contrast, is completely unrelated to the mother-in-law’s offspring. Under these circumstances, the evolutionarily stable solution is for the old mother to commit to zero reproduction and allow the daughter-in-law to monopolize reproduction, leading to the evolution of menopause in human females. Empirical studies that tested Cant and Johnstone’s (2008) reproductive conflict model, however, have yielded mixed results.

Conclusion

Models of reproductive skew predict how reproductive conflict among same-sex individuals within a group will be resolved at evolutionary equilibrium, depending upon various factors such as grouping benefits, ecological constraints, genetic relatedness, group size, and competitive ability. The bewildering array of skew models, however, has recently met serious criticisms based on both theoretical and empirical grounds. Nonacs and Hager (2011) reviewed dozens of empirical studies across diverse animal taxa, concluding that neither relatedness nor competitive ability affected skew within a group. It thus

remains to be seen whether skew theory lucidly captures the true causes underlying the evolution of sociality. Nonetheless, skew theory has already done an important contribution on the study of cooperative breeding and reproductive conflict. For instance, the theory has rightfully highlighted that the possibility of group dissolution via departure/eviction has a great influence on how within-group conflict is resolved (Cant and Johnstone 2009). It is apparent that the studies of human kinship would also benefit by making full use of skew framework.

Cross-References

- ▶ [Cooperative Breeding](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Game Theory](#)
- ▶ [Menopause](#)

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Skinner Box, the

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Synonyms

[Lever box](#); [Operant conditioning chamber](#)

Definition

A laboratory apparatus developed by B. F. Skinner in operant conditioning experiments to study animal behavior, which typically contains a lever that delivers reinforcement in the form of food or water upon being pressed.

Introduction

The Skinner box (also known as operant conditioning chamber) was invented by Skinner while developing his theory of operant conditioning as a graduate student at Harvard University in the 1930s. It is used in the experimental study of animal behavior and allows the experimenter to manipulate, observe, and record an animal's behavior in response to environmental stimuli. Reinforcement delivery in the form of food or water is contingent upon a lever being pressed by the animal (usually a rat or pigeon). Responses are recorded on a cumulative recorder. The Skinner box and the cumulative recorder are two of Skinner's most important inventions in the experimental study of behavior and played a fundamental role in the development of operant conditioning theory.

The Skinner Box Design

Skinner may have been inspired to design his operant conditioning chamber by Thorndike's experiments using a puzzle box, which led to the development of Thorndike's Law of Effect (Thorndike 1898, 1911). The Skinner box is a soundproof rectangular box that contains a lever that, upon being pressed by the animal (e.g., rat or pigeon), delivers reinforcement in the form of food or water. In this controlled setting, a researcher is able to manipulate environmental stimuli and obtain a cumulative record of the animal's behavior from a device connected to the Skinner box, known as a cumulative recorder. This device produces a cumulative record in visual form, i.e., a graph that measures the total number of responses since the beginning of the experiment (Skinner 1959). Each response by the animal (rat or pigeon) moves a pen moving horizontally at a slow speed on a piece of paper one notch up, thus indicating vertically the number of cumulative responses recorded up to that point in time (time is measured in minutes and seconds horizontally). This design allowed Skinner to collect information on how different reinforcement schedules affect behavior (Ferster and Skinner 1957).

Uses of the Skinner Box in Research

The Skinner box has been used and is still being used by researchers as an apparatus in various areas of research. Indicative fields include testing the addictive effects of drugs (e.g., (Tirelli 1987; Pinkston and Branch 2004; Weaver and Branch 2008), animal cognition and learning (Shepard and Cooper 1982; Kentaro et al. 2002), memory and learning following brain damage (Nelson et al. 1997), and nutrition and its effects on learning and memory (e.g., Rojas et al. 2010). Researchers have gone as far as designing human Skinner boxes to study complex learning (e.g., Dibbets et al. 2002).

The Evolution of the Skinner Box in the Digital Era

Contemporary Skinner boxes retain the traditional 3D structure, but they are also connected to a computer through an interface. Behavioral responses are being detected electronically and they are recorded by a computer software. The presentation of the reinforcers (e.g., food or water) can also be programed with computer software. Some also include LCD screens to display digital images. Operant conditioning chambers in the digital era have evolved into computer controlled Skinner boxes (see for example Sokolowski and Abramson 2010).

Maintaining animal laboratories with operant conditioning chambers can be expensive (Graham et al. 1994). This poses a challenge for university professors who, in addition to the theory, aspire to give students hands-on experience of operant conditioning principles. To overcome such financial obstacles as well as the ethical dilemma of using animals for teaching purposes, software programs simulating operant conditioning chambers have been developed. Examples include *Sniffy the Virtual Rat* (Graham et al. 1994) and *EverQuest: The Virtual Skinner Box* (Yee 2001). More recently, open source devices such as the ArduiPod Box (Pineño 2014) have been introduced as low-cost alternatives to maintaining an operant conditioning chamber.

Conclusion

The Skinner box, an innovation developed by Skinner in the 1930s, has played a fundamental role in his experimental work on behavior and learning, which ultimately led to the formation of the principles of operant conditioning theory. The Skinner box has been widely used as an apparatus to collect information about animal behavior in response to environmental stimuli and reinforcers in various fields and areas of research. Contemporary versions of the Skinner box include computer-controlled operant conditioning chambers and virtual simulations.

Cross-References

- [Operant Conditioning](#)
- [Positive and Negative Reinforcement and Punishment](#)
- [Reinforcement Schedule](#)
- [Thorndike's Law of Effect](#)

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Sleep-Wake Cycles

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Synonyms

[Circadian rhythm](#); [Master clock](#); [Molecular clock](#)

Definition

An endogenously generated daily cycle of approximately 16 h of wakefulness and 8 h of sleep

Introduction

Aside from nocturnal animals, humans, like many other mammals, sleep during the night, when the sun is below the horizon. Throughout sleep, metabolic processes are slow, activity is minimal, and consciousness shifts to a different state. Wakefulness generally occurs during daylight, characterized by high physical and mental activity, driving the consumption and utilization of large amounts of energy. The first glimpse of a biological driver of the sleep-wake cycle occurred in a fly, where the behavior was significantly altered when a gene was manipulated

(Wager-Smith and Kay 2000). Since then, both biological and psychological research have elucidated a complex feedback system that stimulates alertness in most animals and facilitates sleep. The circadian rhythm is one of the most conserved biological processes across a wide range of animals and is present in almost all human cells, controlled by a central regulator.

Brain and Function

The circadian rhythm is highly interconnected to metabolic processes and is controlled primarily by a regulator, the master clock, in the brain. The region of the master clock is called the supra-chiasmatic nucleus (SCN), within the hypothalamus, and contains about 20,000 neurons. The master clock receives input directed from the optical nerves in the eye, permitting “zeitgebers,” or environmental stimuli that signal daylight, to be perceived. Other signals, highlighting the relationship between organ systems, can stimulate and disrupt the sleep-wake cycle, such as food consumption or stress. The SCN, once stimulated, sends signals to the paraventricular nucleus (PVN) of the hypothalamus and activates the hypothalamic-pituitary-adrenal (HPA) axis. This pathway is responsible for stress signaling through steroidal hormones called glucocorticoids (GCs), as well as energy balance or metabolism (Nader et al. 2010). The PVN produces corticotrophin-releasing hormone (CRH), which is released into the hypophyseal portal system to bind to receptors in the anterior pituitary that initiates the secretion of adrenal-corticotrophic hormone (ACTH) into the bloodstream (Buckley and Schatzberg 2005; Garabedian et al. 2017). This stimulates the synthesis of the GCs cortisol (humans) or cortisone (rodents) from the adrenal cortex and, in turn, negatively regulates the HPA axis to control the concentration of circulatory GCs.

Glucocorticoids inhibit insulin production to prevent glucose from being stored in order to remain available for usage during a period of stress, whether it be exercise, mental focus, or infection. Circulating GCs act upon receptors in

almost all regions of the body except for the SCN itself. The master clock works through two antagonistic, self-regulating sets of oscillating genes, called a positive and negative limb, named for the activation or inhibition of transcription and translation (Zelinski et al. 2014). The clock genes, named CLOCK and BMAL1 (brain and muscle arnt-like 1), bind to form a heterodimer and induce the production of more genes, *Per* (period) and *Cry* (cryptochrome), which, in turn, downregulate CLOCK/BMAL1 and inhibit their own production. CLOCK/BMAL1 also induce another loop of circadian genes with *ROR α* and *REV-ERB α* , which bind to the BMAL1 promotor and counter-balance each other. With diurnal stimuli, this continuous loop leads to the oscillation of these circadian genes and the rhythmic expression of GCs through HPA axis stimulation. Without this complex system, GCs would be continuously released into the circulatory system, simulating a chronic stress state. These genes are present in almost all peripheral cells throughout the body and can be stimulated by GCs which can disrupt their natural metabolic cycle if the HPA axis has been activated in an acute or chronic state.

Disruption

Studies on shift workers detail a disruption in circadian rhythm signaling, including increased concentrations of GCs, into circulation during a period when they are typically suppressed (Karlsson et al. 2001). Along with the research on shift workers, investigations on disturbed light-dark signaling with animal models have correlated the chronic disruption in circadian rhythm signaling and GC patterns to the development of metabolic syndrome (Evans and Davidson 2013). Metabolic syndrome describes a cluster of disorders, such as low HDL cholesterol, visceral obesity, hypertension, insulin resistance, and increased triglycerides. A patient typically requires a diagnosis of at least three disorders to be categorized as metabolic syndrome.

Chronic sleep-wake cycle disruption has been linked to cognitive impairments, especially

with aging, such as depression, Alzheimer's, Parkinson's, and Huntington's disease (Musiek et al. 2015; Mattis and Sehgal 2016; Musiek and Holtzman 2016). Further disruption of sleep-wake cycles shifts the natural pattern of sleep; however, it does not necessarily interfere with sleep characteristics such as rapid eye movement (REM) sleep.

Evolution

Metabolism of resources are required to nourish organs and tissues, with a significant 30% going directly to the brain. The brain is known to process learned events during sleep, enhancing and storing memories as well as maintaining synaptic connections (Vorster and Born 2015). Predatory animals primarily hunt during the day, and as such, the theory behind sleeping at night serves as a multifaceted function – to conserve energy and to consolidate memory during a period when we are no longer active nor are threats to our survival as high (Berger and Phillips 1995). To conserve fewer resources, the master clock integrates the lack of daylight signals, and levels of clock gene expression are mostly inactive. GCs circulate at a significantly lower concentration, and most neural processes slow during sleep, except for survival functions and consolidation processes for memory. Energy expenditure is conserved with digestion slowing, body temperature dropping, and movement all-but-stopping. However, humans are not left totally unprepared to deal with a threat; if a startling situation were to occur, the fight-or-flight system would activate quickly, and energy stores would provide the energy required.

In addition to energy conservation, sleep-wake cycles have evolved to promote memory storage and enhancement (Kavanau 1997; Vorster and Born 2015). Sleep enhances the synaptic connections made during the day, intensifying what was learned. Numerous studies highlight the benefits of sleep; some have shown that subjects are able to recall more nonsensical information if they slept right after a learning session, and others have provided evidence in other learning tasks

and skills. Sleep can be seen in a wide variety of animal species; however, the evolution of memory consolidation in sleep seems to be convergent, considering the neural processes and characteristics of sleep among different animals, such as birds and reptiles, are quite different than those of humans and other mammals.

Conclusion

The evolution of the sleep-wake cycle and the master clock is conserved across many species; even though some have more or less genes involved, the system is intact in its structure and purpose. Not only does the circadian rhythm control metabolic and activity levels, but it also controls physiology, all through rhythmic gene expression. The system has evolved to control homeostasis and to either conserve or produce energy when required, but if dysregulated, it can disturb a cascade of physiological systems, ultimately leading to physical and mental disorders in humans.

Cross-References

► [Co-sleeping](#)

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Smacking

- [Spanking](#)

Small Infants

- [Low Birthweight and Preterm Infants](#)

Small-Band Hunter-Gatherers

- [Hunter-Gatherer Societies as Sources of Data in Evolutionary Psychology](#)

Smarties Task, The

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Synonyms

[Appearance-reality task](#); [Unexpected contents task](#)

Definition

The Smarties Task is a subtype of false-belief tasks that is used to test for theory of mind.

Introduction

The Smarties Task constitutes a by now classical paradigm often used in theory of mind experiments. In this procedure, children are shown a tube of “Smarties” (the brand name of a kind of chocolate candy) and asked to guess its contents. As expected, they typically reply by saying that the tube contains Smarties. Then the experimenter opens the tube, and it turns out that it actually contained an unlikely object (e.g., pencils). At this point, children may be confronted with two different situations: (1) a situation where they should state what another child (who has been waiting outside the room and did not witness the disclosure of the contents of the Smarties tube) would think the tube contained and (2) a situation where the child is asked what he or she initially thought the tube contained (Perner et al. 1987). Crucially, the first situation here requires the child to contrast his/her own current true belief (i.e., “the tube contains pencils”) with the false belief of another *ignorant* agent (i.e., “the tube should contain Smarties”), which is not different from what is found in other false-belief tasks, such as

the Sally-Anne task. The second situation, however, differs from other false-belief paradigms in that it requires the child to contrast his/her current true belief with his/her own past false belief. Perner et al. (1987) reported that children below age 4 failed in the first task where they had to attribute false beliefs to another person, while fewer children in the same age group failed in the second task, which was interpreted to mean that it was more difficult for children to reason about the mental states of others. The authors further explained this difficulty by saying that it must be hard for young children to assign two conflicting truth values to the same proposition (i.e., “the tube contains Smarties”) according to two different perspectives.

Variations

There are different versions of these appearance-reality tasks. While the Smarties Task may be the most famous one, there have been other influential paradigms that were similar to the Smarties Task in their underlying motivations and in what they tested. In a different experiment, for example, children are shown objects that deceptively look like another object at first sight (e.g., a sponge that is painted to look like a rock), and after the true identity of the object is revealed, they are asked to state either (1) what the object *looks like* and what it *really is* (an appearance-reality task, Flavell et al. 1983) or (2) what they thought the object was when they first saw it (a representational change task, Gopnik and Astington 1988). While the first study here focuses on whether children can discriminate between appearance and reality at a conceptual level, the second study is centered upon the question of whether children can scrutinize their erroneous past beliefs in the face of new evidence. The two lines of research converge toward the same findings, however. Flavell et al. (1983) found that 3-year-olds performed poorly in this task, while 4-year-olds were better, and 5-year-olds were virtually adult-like, showing that the appearance-reality distinction had not fully matured by age 3. Gopnik and Astington

(1988), on the other hand, found that 3-year-olds failed in the representational change task, while 5-year-olds succeeded at it. In this task, the object remained the same, while the child’s representation of it had to change (*rock* → *sponge*), so the child was required to ascribe two different representations to the same object over time. The authors attributed younger children’s failure to an inability to consider alternative representations of the same object, which they contend develops at around age 4.

It is notable, however, that notwithstanding the minor differences in the experimental designs and the results that were obtained, researchers’ explanations often point to an incapacity to represent conflicting truth values, perspectives, or representations as the most likely culprit for these error patterns. This suggests that some working memory and inhibitory control limitations might be playing a role in motivating the non-adult-like behavior in these explicit theory of mind tasks. Indeed, some studies have found a relationship between working memory and theory of mind, lending credence to this view (Gordon and Olson 1998; Carlson et al. 2002; Mutter et al. 2006).

Conclusion

Studies that employ the Smarties Task or similar paradigms have consistently found that preschool-aged children often have difficulties in discerning (or at least reporting) the differences between how an object is perceived by two different people, or by the same person at two different time points, or the differences between appearance and reality in general. While it is possible that children experience a conceptual change at this developmental stage whereby they become able to grasp that one object can appear one way but essentially be something else, or that different people have different perspectives, which may cause them to have different perceptions of an objective fact, it is also possible that children’s difficulties with this multifaceted thinking stem from immature general cognitive abilities.

Cross-References

- [False Beliefs](#)
- [False-Belief Test, The](#)
- [Theory of Mind](#)

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Smoother

- [Bone Lissor](#)

Snail

- [Aplysia](#)

Sneak Copulation

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Synonyms

[Hide and hurry](#); [Mate poaching](#); [Opportunistic mating](#); [Sneaking](#); [Surreptitious mating](#)

Definition

Sneak copulations are copulations that take place quickly, where the copulating pair attempts to remain hidden to avoid harassment and prevention of copulation.

Introduction

Sneak copulations occur in the following contexts in primates: 1) as an alternative to consortships (i.e., a short term mate guarding relationship) when consortships are harassed by higher ranking males (typically in species with shorter consortships), where females spend significant time not directly mate guarded (i.e., rhesus macaques *Macaca mulatta* Berard et al. 1994; Japanese macaques *Macaca fuscata* Soltis et al. 1997); 2) as an alternative to consorting when higher ranking males are able to monopolize access to females, typically while the male is distracted (i.e., mandrills *Mandrillus sphinx* Setchell et al. 2005; yellow baboons *Papio hamadryas cynocephalus* Alberts et al. 2006; olive baboons *Papio hamadryas anubis* Danish et al. 2014); and 3) as a means of gaining copulations with a pair bonded female (i.e., humans *Homo sapiens* Schmitt and Buss, 2001, gibbons *Hylobates* spp. Barelli et al. 2013).

Description

In seasonally breeding species, the high degree of female cycle synchrony in these species makes it difficult for males to monopolize access to females and reduces the benefits of mate guarding since mate-guarding males lose other mating opportunities (Berard et al. 1994; Soltis et al. 1997). As a result, females are not consorted all the time; however, lower-ranking males that attempt to consort are typically harassed; sneak copulations allow these males to avoid harassment. As expected with sneak copulations, even human observers may not see them; for example, subordinate male Japanese macaques (*Macaca fuscata*) are rarely observed to mate – but sire approximately half of the offspring (Soltis et al. 1997). In rhesus macaques, 45 % of known conceptions resulted from sneak copulations (Berard et al. 1994).

Males likely have fewer opportunities for sneak copulations when a female is continuously mate guarded (Alberts et al. 2006). Nevertheless, sneak copulations are observed in these species, though typically by adolescent males in the baboons and lower-ranking males in mandrills (Setchell et al. 2005; Alberts et al. 2006; Danish and Palombit 2014). Such copulations typically occur when the male is distracted by monitoring the group or even during an attempt by another male to oust the mate-guarding male. Sneak copulations result in little overall reproductive success in yellow baboons, however, with three adolescent males siring offspring using this tactic (1.4 % of 208 infants) (Alberts et al. 2006). Notably, the baboons live in an open habitat with high visibility, further reducing the success of this tactic; in mandrills, which live in a forest habitat, 27 % of infants are sired by sneak copulations (Setchell et al. 2005).

In species that are characterized by the formation of socially monogamous relationships and pair bonds, females are in longer-term mate-guarding relationships that continue beyond the fertile period (Schmitt and Buss 2001; Barelli et al. 2013). While gibbons and humans often live in pairs, extra-pair matings are observed.

Matings outside of the primary relationship are therefore sneaky by necessity and carry the risk of causing the cuckolded mate to abandon the relationship if discovered. Notably, both individuals engaging in sneak copulations may have primary partners. Although a majority of offspring are sired by the pair-bonded partner, sneak copulations do result in offspring (7 % for gibbons, up to 10 % for humans). In humans, behavior intended to attract a mate from an established pair bond is known as mate poaching. While mate poaching includes an attempt to permanently break the pair bond with the previous partner, it can also be a short-term event, relying on sneaky copulation.

Sneak copulations are considered an alternative mating strategy/tactic, as it is an alternative to the use of individual strength to obtain access to females (Setchell 2008). Low-ranking and extra-group males typically rely on sneak copulations, as they are unable to compete successfully with other males to obtain access to females. Sneak copulations comprised entirely of mating in response to a solicitation by a female are understood better as a female mating strategy. At least sometimes, however, males alter their behavior to take advantage of potential opportunities. Sneak copulations often occur on the periphery of the group, with females moving to the periphery of the group, suggesting the possible importance of female choice in this male strategy (Berard et al. 1994). Males either follow females after being solicited or wait for females on the periphery of the group. It is unlikely for a male to use successfully this strategy without female cooperation, since the success of the strategy is dependent on remaining inconspicuous.

The occurrence of sneak copulations is expected to exert selective pressure on higher-ranking males to more effectively mate guard fertile females (Schmitt and Buss 2001). The costs involved in mate guarding and synchrony of female cycles, however, constrain this counterstrategy. While sneaking generally is less successful than mate guarding, sneaking males avoid the costs of mate guarding and male intrasexual competition (Setchell 2008). Notably,

if sneaking is effective, the benefit to high rank – and therefore selective pressure to achieve such rank – is reduced. In addition, since sneaking results in multiple males mating with a fertile female, postcopulatory selection may be an important factor (Alberts et al. 2006).

Conclusion

Sneak copulations are an alternative mating strategy/tactic with variable fitness benefits; this variation may be due to differences in male effectiveness at mate guarding and habitat visibility (Setchell 2008). Sneak copulations, however, seem to be most effective in species in which high-ranking males are unable to effectively mate guard and the habitat has reduced visibility. Notably, in socially monogamous species, sneak copulations may be part of a mixed strategy, by which males with a primary partner obtain extra matings (Trivers 1972). When mate guarding is effective, sneaking seems to be a case of making the best of a bad job, allowing lower-ranking males to achieve at least minimal reproductive success. Sneaking is expected to promote sperm competition and select for increased mate-guarding behavior in higher-ranking males (Schmitt and Buss 2001; Alberts et al. 2006).

Cross-References

- [Conditional Strategies](#)
- [Condition-Dependent Mating Tactic](#)
- [Dominance Hierarchy](#)
- [Female Sneak Copulation](#)
- [Human Mate Poaching](#)
- [Mate Poaching](#)
- [Multiple Matings](#)
- [Paternity Uncertainty](#)
- [Primate Dominance Hierarchies](#)
- [Primate Sperm Competition](#)
- [Promiscuity](#)
- [Sneak Copulation as an Alternative Mating Strategy](#)
- [Sperm Competition](#)

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Sneak Copulation as an Alternative Mating Strategy

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Synonyms

[Alternative mating tactic](#); [Parasitic male](#); [Sneaker males](#)

Definition

Males that sneak fertilizations with females to circumvent direct competition with dominant males.

Introduction

Sneak copulations often occur as a way to circumvent direct competition with dominant or territorial males during mating. This gives males a chance to gain access to mates and increase their reproductive success, without the costs associated with aggressive interactions. Sneak copulations can be used opportunistically, or they can be the primary behavioral phenotype used by individuals either during a certain stage in their life or throughout their entire lifespan.

Sneaking as a Reproductive Tactics

In systems with alternative reproductive tactics (alternative behavioral phenotypes used to access mates, ARTs), the tactics typically consist of large “bourgeois” (dominant/territorial) males and smaller “parasitic” (sneaker) males (Taborsky 1998). Dominant males often guard territories and/or females within their territory during the mating period in order to prevent cuckolding by other males. In some cases, dominant males will directly compete with other males to maintain these territories or as a way of attracting females. Sneaker males, however, sneak fertilizations with females and avoid aggressive interactions with the dominant males.

Most of the sneaker tactics observed across taxa are likely components of a conditional strategy (Gross 1996). In game theory, a conditional strategy follows a decision rule where individuals that are condition A should perform behavior X, while those that are condition B should perform behavior Y. For instance, if large use a territorial tactic but if small use a sneaking tactic. However, the threshold condition that delineates behavior X and Y is likely to be genetically determined and show individual variation (Tomkins and

Hazel 2007). There are a few cases where a sneaking strategy is associated directly with a genetic polymorphism, such as the marine isopod, but this appears less common.

Sneak copulation behavior can be used opportunistically, associated with a specific life stage, or can be the predominant mating tactic used over the course of an individual's lifetime. One interesting species that exhibits a combination of these scenarios is the sailfin molly (*Poecilia latipinna*). In this species, male size is influenced by copy number variation at the melanocortin 4 receptor (*mc4r*) gene, and male size is highly associated with mating tactic (Smith et al. 2015). Small males predominately sneak fertilizations from unsuspecting females, while larger males predominantly perform courtship displays to attract females for copulation. However, males that are intermediate in size will switch between a sneaking and a courtship tactic, depending on the presence of other males in their environment (Fraser et al. 2014). When no other males are present, intermediate males will adopt courtship behaviors. However, when other males are present, these males will spend more time trying to sneak copulations.

Phenotypic and Life History Differences

In some species with ARTs, individuals may transition from one tactic to another either as they grow or in response to some environmental change. This transition can result in significant phenotypic and behavioral changes. One such example is the black-faced blenny. During the breeding season, sneaker males maintain a camouflage phenotype, while territorial males develop conspicuous coloration, consisting of a bright yellow body and black head. If a territorial male is removed from the area, a sneaker can change his coloration and take over that territory (De Jonge and Videler 1989). Utilizing a sneaking tactic early after reproductive maturation and transitioning into a territorial tactic once the individual can successfully compete for mating opportunities or resources is not unusual and has been observed in a number of species with ARTs.

While the above example included individuals that modify their behavior and morphology in response to an environmental change, some ARTs express these distinct phenotypes during the majority of their life. In dung beetles (*Onthophagus acuminatus*), there are significant differences in both body and thoracic horn size between territorial and sneaker males. Territorial males develop larger horns that are used in competition with other territorial males in order to defend burrows that contain females. However, sneaker males have a smaller body size and their horns are either reduced or even absent. Sneaker males avoid direct interactions with territorial males by digging alternative entrances to the burrow that intersect the main tunnel in order to gain access to the female (Emlen 1997). Body size, horn size, and tactic are dependent on larval diet, which can be experimentally manipulated by altering food quality (Emlen 1994). These territorial and sneaker morphs represent facultative developmental alternatives, where the body size and tactic assumed are regulated by a developmental switchpoint that is maintained throughout their lifetime.

Sneaker males can also have different life history traits compared to dominant males. This is seen in the bluegill sunfish (*Lepomis macrochirus*) and Atlantic salmon (*Salmo salar*). Sneakers of these species exhibit precocious maturation (i.e., they become reproductively mature at an early age). They also invest more heavily in reproduction relative to growth compared to territorial males. In bluegill, the testes of reproductively mature sneaker males represent roughly 4.5% of their total body weight compared to 1.0% for the parental (territorial) males (Gross 1982). Males in the precocious maturing life history do not transition into territorial males as they age. In contrast, they remain smaller than territorial males throughout their life and rely on cuckolding fertilization for their reproductive success. However, the average reproductive success of tactics associated with distinct life histories can be very similar, and these tactics may be maintained at an evolutionary stable equilibrium through frequency-dependent selection (Gross 1984).

Conclusion

Some males use a sneak copulation tactic as a way to increase their mating success while avoiding direct competition with dominant males. In some species, the use of a sneaking tactic can be opportunistic, while in others, this tactic is employed throughout their lifetime. Phenotypic and behavioral differences between males exhibiting a sneaking versus a territorial tactic can be striking. Sneaker males and territorial tactics may also be associated with distinct life histories.

Cross-References

- [Making the Best of a Bad Job](#)
- [Mating Strategy Equilibria](#)

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Sneaker

- [Female Mimics](#)

Sneaker Males

- [Sneak Copulation as an Alternative Mating Strategy](#)

Sneaking

- [Sneak Copulation](#)

Sneaky Mating

- [Female Sneak Copulation](#)

Snivelling

- [Crying](#)

Sobbing

- [Crying](#)

Sobriety

- [Abstinence](#)

Social Aggression

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Synonyms

[Indirect aggression](#); [Peer-to-peer aggression](#); [Relational aggression](#); [Relational bullying](#)

Definition

Social aggression is a broad term that generally includes relational (attempts to damage relationships or exclude others), indirect (behaviors, such as spreading rumors online, which do not occur in the presence of the victim), and nonverbal forms of aggression (e.g., dirty looks) along with verbal insults, the goal being to damage the victim’s self-esteem and social status (Ostrov et al. 2018).

Introduction: Theoretical Perspectives

Social aggression is used interchangeably with relational and indirect aggression throughout the literature; thus, it will be used as a broad term to represent all three forms of aggression. Several theories have been used to explain the development and maintenance of social, or relational, aggression; a few of these are briefly presented here.

Evolutionary theory provides the underlying context for understanding how the pressures placed on humans over time contributed to development of a system in which the expression of aggression serves a purpose, is valued, and

maintains the system (Godleski 2018). From this perspective, social aggression can lead to positive outcomes for the aggressor. Social dominance theory and resource control theory, which both integrate evolutionary theory, have also been linked to social aggression. Social aggression can be used to obtain and maintain social dominance over others within the same social setting (e.g., high school). Resource control theory provides context for why individuals who use social aggression may also demonstrate prosocial behaviors or strategies (Godleski 2018). Specifically, when social aggression is used in conjunction with prosocial behaviors, individuals are more likely to obtain the desired resources while also maintaining social status. The purpose of obtaining social dominance and gaining control of resources varies dependent upon age and setting. Examples include a child who befriends another child and uses coercive strategies (e.g., I won't be your friend unless you. . .) to gain access to something that child has (e.g., a special toy), an adolescent female who gossips and spreads rumors about the popular girl because she wants her boyfriend, and a man who feels threatened by a younger employee, so he attempts to socially isolate him by excluding him from social events and making demeaning comments about him to coworkers.

Who's Involved and What's the Prevalence?

There are several key players when looking at social aggression: the aggressor (i.e., bully), victim (or target), and bully-victim (those who are both socially aggressive and victimized). Additionally, there are bystanders who either watch and do not interfere in the bullying, defend the victims (defenders), or support the aggressor.

Prevalence rates for social aggression and other forms of bullying can be difficult to determine due to factors such as how the behavior is defined, level of frequency (e.g., two to three times in the past month) measured, length of time assessed, and the setting (Smith 2013).

There are some large-scale studies and meta-analyses that provide estimates. Cook et al. (2010) completed a meta-analysis on studies examining school bullying and aggression from several countries, including countries in Europe (42 studies) and the United States (21) and from other countries (16). The results revealed that, averaged across studies, 20% of students had bullied others, 23% of students were victims of bullying, and 8% were both bullies and victims.

The World Health Organization produces large-scale prevalence data from internationally representative samples of students (ages 11, 13, and 15) for school-based bullying based on the Health Behavior in School-aged Children (HBSC) surveys every 4 years. The 2009/2010 survey produced lower prevalence rates than Cook et al. (2010) with only 10.3% of students reporting that they had bullied others and 11.3% reporting being victimized. Data for bully-victims was not provided (Currie et al. 2012).

Through self-report measures and questionnaires, research indicates a steady decline throughout adolescence of those reporting being victims. The same decline cannot be seen when looking at self-reports of those who bully others; rather the type of bullying shifts from more physical in nature to more relational (Smith 2013). In considering sex and gender, boys and girls are closer to equal in the victim category, while boys are more prominent in the bully category. Additionally, the ways in which the bullying occurs may appear different between the sexes. Boys will likely engage in more physical forms of bullying, while girls center on relational bullying often fueled by ongoing feuds or opposing friend groups (Smith 2013).

Effects

Social aggression can have multiple negative effects on both the victims and bullies. Individuals who are aggressive have been shown to have both internalizing (e.g., anxiety, depression) and externalizing (e.g., defiance, impulsivity) behavior issues. Aggressors are more likely to be involved

in crime as adults and display conduct problems throughout adolescence (Holt et al. 2007). Victims have a higher risk of low self-esteem, school avoidance, and depression than their non-bullied peers (Holt et al. 2007). Both youth who are socially aggressive and youth who are victimized exhibit reduced social problem-solving, decreased emotional regulation, and increase peer issues (Leff et al. 2010). However, in some situations relational aggression may lead to popularity indicating that social aggression is a complex issue that needs to be fully understood in order to know how to best intervene (Leff et al. 2010). Those who are bully-victims are at the highest risk. These students may be the “provocative victims” or react strongly and aggressively to their own victimization. Bully-victims tend to be the most stigmatized by their peers and have a greater probability of being referred for psychiatric consultation (Holt et al. 2007).

In addition to those directly involved in the bullying process, there are also those in the roles of bystanders, including defenders and supporters. Research indicates that a student’s role as a bystander is largely influenced by both individual and social factors. Defenders are more likely to display personality traits such as altruism, agreeableness, and a prosocial orientation and often have high self-esteem and productive coping styles. Bystanders who just watch may have a fear of being the next victim or feel uncertain about how to intervene (Nickerson et al. 2008). Many bystanders will express feelings of disgust, sadness, or anger at bullying and aggression, while few do anything to intervene. Understanding the social phenomenon of the bystander effect has been a focal point of research for social psychologists for decades (Nickerson et al. 2008).

In extreme circumstances, experiencing social aggression can lead to school or work avoidance or even suicide if the individual becomes hopeless. Hinduja and Patchin (2010) examined the links between bullying, cyberbullying, and suicide. The authors found that middle school students who were engaged in cyberbullying or in-person bullying as the victim or bully showed increased reports of suicidal ideation and suicide

attempts in comparison to peers that did not experience or engage in cyberbullying or bullying. However, students who were victimized showed the highest rates of suicidal ideation and behaviors (Hinduja and Patchin 2010). It can be argued that the effects of social aggression are just as, if not more than, harmful as physical aggression.

Prevention and Intervention

In general, the programs that target social aggression have numerous important similarities: they are developmentally appropriate for their audience, and they tackle relational aggression from a systemic approach, teach social problem-solving skills and leadership strategies, and take a multilevel approach (such as involving the teachers and/or parents; Cappella and Weinstein 2006; Leff et al. 2010). It is also important to consider factors such as social aggression in romantic relationships and in the cyber-world when identifying an intervention and considering objectives (e.g., what skills are taught). As technology is advancing, social aggression is taking form via cyber or electronic communication. Youth are no longer free from aggression in their own home; instead they can be subjected to these interactions 24/7, necessitating a program that addresses cyber-forms of social aggression (Hinduja and Patchin 2010).

Schools can take a systematic approach to address social aggression by implementing intervention and prevention efforts at three levels: school-wide, in individual classrooms or small groups, and to individuals. The same approach could be used in the work setting implementing interventions across the company, within a department, or for individuals. At the school-wide level, key personnel with knowledge regarding evidence-based interventions, such as the school psychologist and principal, can determine what intervention or prevention programs are appropriate for their school (Leff et al. 2010). It is critical that the program is monitored through data collection to determine its effectiveness. *I Can Problem Solve* is a school-wide program that has

teachers implement a curriculum focusing on teaching prosocial and problem-solving skills. In addition to formal programs, strategies such as increasing supervision at recess, establishing bullying policies and disciplinary measures, and parent training or involvement have been shown to be effective aspects of prevention and intervention (Ttofi and Farrington 2011). Bullying policies and disciplinary measures were found to be correlated with less bullying overall; however, there is no evidence that these policies had positive effects for bullies or victims individually, demonstrating the need for targeted interventions (Ttofi and Farrington 2011).

Intervention can also be implemented at the small group level, which allows for specific interventions (e.g., conflict resolution skills) to meet the needs of identified students. There are many programs that exist to prevent and/or intervene regarding social aggression at this level such as Second Step and Social Aggression Prevention Program (SAPP; Leff et al. 2010). By implementing evidence-based social emotional learning programs such as SAPP, issues related to social aggression can be targeted and addressed. For example, Cappella and Weinstein (2006) examined the effects of implementing SAPP for girls in fifth grade and found increased empathy and increased social problem solving as an outcome of the program. They also found that girls identified as being high-risk for social problems had more positive outcomes (Cappella and Weinstein 2006). Lastly, schools can intervene on an individualized level with individuals involved in social aggression by determining the area of need and selecting an appropriate evidence-based intervention.

Overall, policies addressing bullying and social aggression and prevention and intervention efforts that teach social problem-solving and prosocial leadership and include parent involvement have been shown to have positive outcomes. Generally, the longer and more intense intervention or prevention programs result in greater outcomes (Ttofi and Farrington 2011). Programs that allow people to practice these skills and to be given feedback over a consistent duration of time are essential.

Conclusion

Social aggression is a complex event that is used to manipulate and damage relationships, cuts across settings (e.g., schools, cyberspace), and leads to negative outcomes that range from mild to extreme. While consistent prevalence rates of social aggression are difficult to establish, it is clear that this is a problem affecting many youth and adults and can have negative, even dire, consequences for the individuals involved. Addressing social aggression through evidence-based prevention and intervention efforts, especially for children and adolescents, is of paramount importance.

Cross References

- Bullying
- Cyberbullying
- Gossip, Rumors, and Social Exclusion
- Indirect Aggression
- Relational Aggression
- School Bullying
- Sex Differences in Aggression
- Verbal Derogation Among Women

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Social Anxiety

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Synonyms

Social anxiety disorder; Social phobia

Definition

Social anxiety disorder is a marked fear or anxiety about one or more social situations in which the individual is exposed to possible scrutiny and negative evaluation of others. The social situations almost always provoke fear or anxiety, and the social situations are avoided or endured with intense fear or anxiety (American Psychiatric Association 2013).

Introduction

Other people have been our primary psychological selection forces. As species, hominins were selected socially and sexually, and as such, other people have both been our primary competitors and our greatest resources. We are therefore especially interested in evaluating other people, considering their emotional states, their personality traits, and considering what resources or threats they might be for us.

The need to socially belong is one of the fundamental human motivations (Baumeister and Leary 1995). Hence, we would expect the evolution of psychological adaptations that regulate and express this desire in adaptive ways. Social fear and anxiety might serve the function of inhibiting social behaviors that put humans at social risks, for example, by inhibiting other aspects of human nature, such as mate poaching, stealing, cheating, and murdering. Fear of social sanctions might adaptively inhibit these behaviors (Buss 1990).

For an hyper social species such as humans, losing the support of others or being disliked by other people in our group would have been devastating to our ancestors' fitness (Buss 1990). Ostracism would probably result in becoming an evolutionary dead end. Fear of negative evaluation is therefore not surprisingly something that concerns many, if not most, people. Fear of negative evaluation is naturally the hallmark of social anxiety disorder. However, only 12.1% of the US population develops debilitating symptoms that warrant a diagnosis of social anxiety disorder during their lifetime (Kessler et al. 2005). Furthermore, The risk is higher for females, and the disorder typically has

an early onset, often beginning in childhood or early adolescence (Stein and Stein 2008).

Different Theories of the Evolution of Social Anxiety Disorder

Öhman (1986) proposed one of the earliest, and most comprehensive, models of social anxiety disorder from an evolutionary perspective. His perspective is that we are prepared through selection to fear specific stimuli. In the case of social anxiety, the stimuli are dominant and aggressive conspecifics. Angry faces are therefore important social stimuli. Social anxiety is therefore considered part of a prepared submissiveness learning system.

Trower and Gilbert (1989) also proposed a model of social anxiety in which people evaluate conspecific threats, and that activates a dominance hierarchy mind set. This means that humans have psychological adaptations that assess and protect against hostility from others with submission and appeasement. The idea is hence that social anxiety reduces the chance that social conflicts will escalate into fitness-damaging violence and catastrophic social exclusion. This theory shares some foundations with the social competition hypothesis of depression, namely, to protect against aggression from others.

Finally, Stein and Bouwer (1997) suggested the false appeasement theory of social phobia, which also is about defending against social aggression from others. In this model, social phobia is considered to result from severely exaggerated appeasement displays, especially blushing, when such is not called for by the social context. Social anxiety is hence viewed as a dysregulated activation of otherwise adaptive features.

Leary and Jongman-Sereno (2014) provide an update of one of the most developed accounts of social anxiety disorder from an evolutionary perspective, based on self-presentation theory. This perspective expects social anxiety to be elicited when people are not confident that they will be

able to make the desired good impression on others. The self-presentation perspective may be extended with sociometer theory, where the relational value of others needs to be considered, when predicting when a social context elicits social anxiety.

General Discussion of the Theories

Most of the theories above are based on normal social anxiety being an adaptive, social relationship regulating mechanism, while full-blown social anxiety disorder is a harmful dysfunction. This might be true. However, people seem to be popular even when very low on social anxiety. The social dominance aspect might therefore be relevant, a position most of these approaches promote. The problem of the above theories is largely a lack of correspondence with how social anxiety presents. If the adaptive value of social anxiety is to prevent social ostracism, then we should not find extroverts more socially attractive, and socially anxious people should not be excluding themselves from society and their in-group by having fewer relationships, marrying later, having less education, and receiving fewer promotions. It is important to note that there is little evidence that people who reduce their social anxiety run the risk of social attacks or exclusion. Reducing safety behaviors improves social functioning; avoidance promotes continued anxiety. There is therefore little evidence of adaptive value to current social anxiety disorder (Kennair 2007). The lack of empirical work to convert these theories into practical and evidence-based mental health interventions is a general problem within evolutionary clinical psychology.

Further, as we saw in the introduction, social anxiety disorder is by no means a human universal, which we would expect if social anxiety disorder were in itself an evolved adaptation. Most people do not experience these symptoms during all of their life, even though the social situations that tend to activate crippling fears in people with social anxiety disorder are part of the general human experience.

A Cognitive Therapy Approach

None of the current evolutionary theories of social anxiety disorder have made it fully into mainstream clinical theorizing or practice; they are more or less familiar as just-so stories with little practical value. Current effective treatments such as Clark and Wells (1995) cognitive model stress how patients create exaggerated negative images of themselves based on the intropection of anxiety symptoms. The patient thereafter assumes that peers will evaluate them negatively due to how they appear. To reduce the impact of the anxiety symptoms, patients engage in unhelpful symptom concealing and safety behaviors, including social avoidance. Reducing safety behaviors and providing patients with more realistic feedback of how they appear seem to reduce symptoms efficiently. In addition, the therapist helps the patient discontinue worry about how one appeared in social situations. People with less social anxiety worry less about negative evaluation of others. A normal interest in how others perceive oneself is probably helpful for socially intelligent interaction with others; overly negative assumptions about how others perceive one based on faulty perception and worry are probably not adaptive. Evolutionary approaches might become more relevant if they incorporate the functional knowledge about maintaining mechanisms and efficient treatment within mainstream mental health care.

Conclusion

It is likely that many human emotions and motivations have evolved to solve evolutionary problems that inevitably arise when living in groups. The acquisition of social status, mates, friendships, and other alliances requires adaptive regulations of social emotions and behaviors. The adaptive theories of social anxiety may therefore be useful if they generate testable predictions about human nature that can be a key in understanding why people are vulnerable to develop social anxiety disorder.

Different evolutionary approaches to social anxiety disorder have been proposed focusing on the threat of dominant conspecifics and exaggerated appeasement or submission. These have not largely influenced mainstream mental health care or research. Future evolutionary considerations of social anxiety disorder might benefit from addressing the functional models found in efficient therapy.

Cross-References

- ▶ Adaptations to Avoid Ostracism
- ▶ Anxiety
- ▶ Anxiety Disorders
- ▶ Emotions
- ▶ Evolutionary Clinical Psychology
- ▶ Fears and Phobias
- ▶ Sociometer Theory

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Social Anxiety Disorder

- ▶ [Social Anxiety](#)
- ▶ [Social Disabilities](#)

Social Authority

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Synonyms

[Dominance](#); [Leadership](#); [Power](#); [Social rank](#); [Social status](#)

Definition

Social authority is an individual or institution that has legal power and control in a social system or makes decisions and enforces rules.

Introduction

In hunter-gatherer societies, living in a group is more adaptive than living alone. Groups are better able to cope with natural disasters, such as earthquake and famine, and social problems, such as fighting against intruders and predators, than

individuals. Thus, in the evolutionary past - and in contemporary human societies - being a member of a group had survival value and offered reproductive advantages (Baumeister and Leary 1995; Kenrick et al. 2010). In addition, members of a group may encounter recurrent problems that not every member can solve alone. These problems create pressure and circumstances favorable to the emergence of a social authority composed of experienced individuals who can lead and help other group members to solve problems. Following a social authority may benefit group members.

The Emergence of Social Authority

The situation, processes, and qualities (SPQ) model was originally used to explain the emergence of leadership (Spisak et al. 2011) but can also be used to provide an account of emergence of social authority. The adaptive challenge of social authority comes from the demands of authority “situations” (the S factors). In any situations, there needs authority “processes” (the P factors) to promote the benefits of a group. A social authority process is any behavior related to the exercising of legal power and control or the making of decisions and enforcing of rules. Last, social authority “qualities” (the Q factors) should be considered in order to determine whether there are individuals who can execute these behaviors. This model is consistent with the evolutionary hypothesis of stable individual differences in the emergence of social authority. But future empirical studies should be conducted to test these hypotheses based on the SPQ model.

Conclusion

In summary, an individual’s survival and reproductive opportunities are enhanced by living in a group that obeys a social authority. It should be noted, however, that there is less empirical literature dealing with social authority from an evolutionary perspective than there is in the case of related constructs (e.g., social dominance, status, power and leadership). The evolutionary origins

and functions of social authority are not fully understood. In addition, there is no unified or general evolutionary model of social authority. One way of exploring social authority involves distinguishing it from related concepts (e.g., social dominance, status, power, and leadership). The challenge for evolutionary psychologists is to generate better explanations of social authority.

Cross-References

- [Dominance in Humans](#)
- [Evolution of Culture](#)
- [Men in Positions of Power](#)

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Social Avoidance

- [Social Withdrawal in Childhood](#)

Social Belonging

- [Social Media](#)

Social Bias

- [In-Group–Out-Group Bias](#)

Social Bond

- [Pair-Bonding in Other Mammals](#)

Social Bonding

- [Vocal Grooming](#)

Social Bonds

- [Special Friendships Among Baboons](#)

Social Brain Hypothesis

- [Gossip and Grooming Hypothesis](#)
- [Social Intelligence Hypothesis, The](#)

Social Categorization

- [Groups and Categories](#)

Social Categorization by Age of Faces

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Synonyms

[Age perception](#)

Definition

Chronological age refers to the number of years since birth that an individual has been alive. Age can also be discussed as a category, however, with individuals belonging to a group of people whose chronological age falls within a specified range (i.e., age group). For example, youth as an age group may include anyone with a chronological age between 0 and 30 years old. Ultimately, age groups are social constructs and may vary by culture.

Social categorization refers to the classification of other individuals into particular group memberships based on characteristics deemed meaningful by society. Examples of social categories include age group, sex, and race. Social categorization based on age can lead to stereotypical and evaluative biases. One of the central ways by which we categorize age is through examining the facial characteristics of others.

Introduction

Social categorization is instrumental to our understanding of others and, accordingly, much research has been dedicated to elucidating its mechanisms. Building on theoretical models of face perception, investigations have focused on understanding the categorization of faces based on three fundamental social categories: age, sex, and race. Of the existing research on these social categories, the social cognitive processes specific to age categorization have received the least attention. However, there is reason to believe that age categorization is in many ways distinct from sex and race categorization. For example, over the life span, one's age group changes (e.g., from childhood to young adulthood; young adulthood to middle-age, etc.). This is not typically the case for one's sex or racial group. Age group transitions are reflected in featural changes in the face and body (Wiese et al. 2013). Such featural changes may shape perceptions of someone's age category, ultimately influencing our motivations and experiences with that person. Although we often categorize others based on age through

the perception of particular facial features, the process of age categorization from faces is influenced by additional information available about others, including other social categories.

Categorization by Age of Faces

Faces represent particularly rich sources of information about others. Together with prior knowledge about a person, they can reveal an individual's age, gender, race, identities, emotional states, current mental states, and even general traits such as trustworthiness or dominance. Due to the unique range of knowledge we can extract from them, researchers believe that humans are adapted to become face experts from a young age (see Simion and Di Giorgio 2015 for a review). Possibly as a result of our extensive exposure to and experience with interpreting faces, it is believed that faces may be processed by dedicated neural processing in comparison to other frequently encountered visual objects.

Evidently, it seems that social categorization from faces arises not only as a result of one's experiences, social environment (i.e., social norms, intergroup contact), and attempts to understand others, but is also tied to particular cognitive and neural processes. Indeed, we can categorize others even more efficiently than we can recognize them (Cloutier et al. 2004) and evidence shows that we spontaneously categorize faces by age (and other categories) with little effort (Montepare and Zebrowitz 1998). Furthermore, we are particularly efficient at estimating age from faces based on features such as skin (texture and elasticity) and hair (color and quantity) (Rhodes 2009).

Function of Age Categorization

Although social categorization is relatively efficient, categorization based on age is not inevitable when we encounter others. Perceivers may categorize an individual based on one category in lieu of another, and doing so may have particular evolutionary functions. For example, whether a

perceiver preferentially attends to someone's age or sex depends on which social category (i.e., age or sex) is more important in shaping our behavior toward that person. For example, young adult perceivers spontaneously attend more to age when categorizing infants, but attend more to sex when categorizing young and old adults (Cloutier et al. 2014). Given that sexual maturation of facial features does not occur until well beyond infancy and that infants' age should guide adult behaviors towards them to a greater extent than their sex, knowing the infant's age can be more useful than knowing the infant's sex. In contrast, perceivers may primarily attend to the sex of younger adults as it represents the age period when reproduction is most likely. Thus, the social category we primarily attend to may depend on which is most functional (i.e., useful to know). As a consequence, the ability to categorize based on age may provide the means for determining who requires care (e.g., infants, children, elderly) and when reproduction is viable (e.g., young adulthood) (Neuberg and Sng 2013).

Consequences of Age Categorization

Even if social categorization allows us to efficiently navigate our social environment, it is not without negative consequences. While categorization from faces can be quite accurate and faces themselves provide perceivers with a wide range of information, the information we infer may not always be correct. That is, humans can be prone to error when forming impressions about others from faces. Not only do we tend to have better recognition for faces of people from our own age group (known as the Own-Age Bias; Wiese et al. 2013), but we also often exhibit evaluative and stereotypical biases towards other-age individuals. Generally, older individuals are perceived negatively and stereotyped as low in cognitive ability and competence (Cuddy and Fiske 2002). In contrast, young people are generally perceived as possessing greater ability and promise than older people. These stereotypes often emerge and are applied unintentionally, yet can have

negative external consequences for the members of a given social group. Discrimination can emerge against elderly individuals systematically (i.e., medical or work settings; see Cuddy and Fiske 2002 for review) as well as on an individual level (e.g., interactions with younger family members or caretakers; Ryan et al. 1995).

Because faces provide information about multiple social categories and traits, it is important to consider how age categorization unfolds when other attributes of the person are known. As is the case with evaluative biases, stereotypic age biases can change as a function of the race or gender of the perceived individual. Thus, stereotypes associated with any one dimension alone may or may not apply to different-age individuals. Rather, stereotype activation, in addition to categorization, is sensitive to the context and social expectations we have about others.

Conclusion

While the exact functional constraints shaping age categorization remain to be determined, it is without a doubt one of the social cognitive tools recruited to help us make sense of our social environment. We can efficiently and accurately extract age from facial cues, and the process of age categorization subsequently impacts our evaluations, judgments, and interactions with others. Nonetheless, age categorization and its social consequences can be highly influenced by context and other category memberships such as sex and race. Given that aging is an unavoidable aspect of the human condition, it is necessary to continue investigating age categorization in order to better understand its function, its impact on person perception and evaluation, and the consequences it has for others.

Cross-References

- [Categorization by Age](#)
- [Categorization by Sex](#)
- [Salience of Category](#)

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Social Categorization by Race

- Race as a Social Badge (Kurzban)

Social Change

- Rite of Passage

Social Closeness

- Emotional Closeness Predicted by Relatedness

Social Cognition

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Synonyms

Social information processing

Definition

Processing information on other agents, their relations and interactions, necessary for social behavior and group living.

Introduction

Social cognition is a broad range of processes underlying agents' ability to identify, represent, and respond to other agents and groups, their behaviors, intentions, and relations. It covers many aspects of human cognition, such as perception, memory, attention, to the extent that they refer to social stimuli, but also deals with some more specific phenomena: social categorization, biases and stereotypes, imitation, Theory of Mind, or emotions. In a broad sense, social cognition encompasses affective processes as well perception, memory, or reasoning. The traditional division between cognitive and affective sides of human subjectivity was challenged by Damasio (1994) and is currently not considered as a fundamental and objective division. Instead, they can be seen as a set of closely connected and interdependent processes. As opposed to behaviorism, which considered human mind as a “black box,” the theory of social cognition seeks to

identify those processes and mechanisms, which serve as an intermediary between two objective and observable sets of phenomena: that of the brain (and sometimes body) functioning, and that of behavior.

Although social cognition is only a part of cognitive abilities, it is considered as a special domain, which is responsible to many uniquely human abilities and the foundation of human social life. Currently, there are several key issues in the study of human social cognition: its evolutionary origin, the relations between sociality, and the evolution of cognition; the uniqueness of human social cognition; the composition and structure of social cognition. Below, these issues are considered in more details.

Social Cognition as an Adaptation

The key assumption of evolutionary psychology is that all sustainable aspects of human mind and behavior evolved as the adaptations to specific environmental challenges. The same is true about social cognition. According to evolutionary perspective, any specific social cognitive ability, which can be identified in humans or other species, such as communication, imitation, social categorization, etc. should be considered as a response to ecological or social environment and problems of their ancestors. These abilities are supposed to increase individuals' and/or groups' fitness and, in the long run, reproductive ability.

Although the general idea of adaptive advantages of social cognition is widely accepted, there is no consensus regarding the exact list of challenges and selective pressures fostering the evolution of specific cognitive abilities as well as on the very list of such abilities. Some researchers only point to cooperation and competition as two main tasks involving the need for specialized social cognition skills (Platt et al. 2016). Others discuss a wider and more complicated range of social domains, in which evolutionary pressures toward the development of social cognition exist. According to Kaschak and Maner (2009), there are four such domains challenges:

1. Self-protection. The fundamental need for protection includes protection from social threats, i.e., other individuals or groups, and, correspondingly, the need for abilities to rapidly identify and evaluate such threats.
2. Social affiliation. Living in groups implies social inclusion, cooperation, and social exchange, which require the ability to identify interpersonal relations and group membership, and control for possible social exclusion.
3. Mating. Mate selection and protection of relatively long-term relationships, necessary for successful reproductive strategies, foster the abilities to identify and evaluate potential mates and rivals.
4. Status/Power. The necessity to increase access for resources and avoid conflicts with more powerful individuals may lead to the development of cognitive skills of fast and accurate recognition of social hierarchy.

A slightly different list is provided by Ackerman et al. (2012). In addition to four challenges similar to those described by Kaschak and Maner (interpersonal aggression, affiliation, status, and mating), they add two more:

5. Disease avoidance. Potential dangers of social contacts are not limited to violence and aggression but also include contagious diseases. The ability to correctly identify cues of potential risks to one's health can thus be considered as another element of social cognition.
6. Inclusive fitness. Authors consider kinship as a special type of social relationship, differing from affiliation and requiring specific psychological mechanisms, fostering unconditional altruism, and prosocial behavior.

It can be seen that these extended lists of evolutionary challenges are not unique for humans or even other "social" species. Many species have to manage kinship or power relations, not to say of self-protection or mate behavior. At the same time, there is a wide consensus that humans' abilities for social cognition are far more advanced than that of other species including primates. This means that applying evolutionary arguments to human social cognition, one needs to argue that

their early ancestors faced some unique combination of selective pressures or that some emerged new adaptations gave them important advantages in comparison to other species. These two possible factors underlying the uniqueness of human social cognitions are not necessarily contradicting and may reinforce each other.

When evolutionary psychologists try to identify specific features of human social life as a source of unique social cognition ability, they mainly point to its enormous complexity (Freeberg et al. 2019; Dos Santos and West 2018). This complexity is not simply the size of groups, in which humans live. Many species live in groups including hundreds and thousands individuals. What is more important is the diversity of individuals and group types, their complex internal structures, and the multitude of relationships within and between groups. Even in archaic human societies, individuals have to correctly represent this complexity to solve practical problems. For example, the universal task of self-protection needs advanced cognitive skills in complex groups as compared to simple ones. To correctly evaluate the potential threats from other individuals, one has to take into account not only their physical conditions and current activities but also relations to others, possibility to recruit allies, affiliation with the different groups, long-term goals and strategies, and the needs for cooperation. Additionally, human affiliation and hierarchy are multidimensional, diverse and flexible. Any individual can be affiliated with numerous groups: families, clans, political or religious organizations, local communities, work- or hobby-related groups, contextual associations, etc. Even the basic kinship relations in archaic societies are subjectively complex and managed by fine-grained sets of rules, albeit implicit (Bourdieu 1980). Social hierarchies are based on various types of unequally distributed resources: physical ability, money, competences, political power, reputation, and so on. To manage the diversity of social affiliations and hierarchies, one has to properly recognize and represent them as well as construct complex models of interactions including this diversity. As a result, some researchers propose that the very notion of social complexity

should include the use of cognition as its defining feature (Bergman and Beehner 2015).

Although navigating the complex social world of human societies is cognitively challenging and requires exceptional skills, this doesn't mean that human social cognition is a direct consequence of this complexity. The very development of such complex societies would be impossible without appropriate social abilities. Thus, it would be more accurate to say that human social cognition evolved in interaction with the evolution of societies and culture (Dos Santos and West 2018). The unique social environment of human societies is thus insufficient to describe the uniqueness of human social cognition as such.

Sociality and the Evolution of Human Cognition: Four Hypotheses

In explaining what is uniquely human in the cognition of our specie, or arguing the very existence of such uniqueness, two general approaches can be proposed: general and adapted (specialized) intelligence (Herrmann et al. 2007). The first one implies that the evolution of humans and primates in general are associated with increased general cognitive skills resulted from larger brain-to-body size ratio. Larger brains allow to store more information, make more complicated and efficient computations, predict and plan better, and learn faster. Although larger brains are more energy-consuming, they provide benefits in solving practical daily tasks such as foraging, navigation, self-protection, and so on. According to this view, human social cognition might be simply a by-product of such greater cognitive abilities as they allow to better recognize and store information about different social agents, reconstruct their goals and develop own strategies, operate with cultural symbols, etc.

In support of the general intelligence hypothesis, Reader et al. (2011) analyzed data on 62 primate species and found that various ecological, technical, and social capabilities, such as social learning, innovation, and tool use, coevolved and are all a part of a composite measure of general intelligence. They also revealed that high level of

general intelligence evolved independently in four different lineages (capuchin, baboon, macaque, and apes) in response to various ecological contexts, and that social complexity was not a good predictor of both general intelligence measure and laboratory cognitive performance.

Alternative approach suggests that the evolution of exceptional cognitive abilities of humans is a result of more specialized adaptations. There are three main hypotheses specifying these adaptations, not necessarily mutually exclusive: ecological, social, and cultural intelligence.

The ecological intelligence hypothesis explains the evolution of human cognition as a response to specific ecological contexts, in which our ancestors lived. This hypothesis is in line with the fact that many different species developed very advanced, highly specialized cognitive skills necessary to solve specific tasks. Ethologists provide numerous examples of exceptional capabilities of many non-primate species including birds, fishes, lizards, and insects, in perception, memory, navigation, computation, learning, or communication tasks (Shettleworth 2010). In these specific tasks, they can easily outperform humans or other primates.

When speaking about primates, their specific cognitive capabilities are typically associated with foraging demands and particularly the use of tools and object manipulations (Parker and Gibson 1977; Rosati 2017). The initial argument was that primate species living in more demanding ecological contexts developed adaptations necessary to use tools and manipulate objects for feeding purposes. Recent studies focused on a more extended list of capabilities necessary to exploit rare and high-value food resources by primates (MacLean 2016; Rosati 2017). For example, Rosati (2017) compared cognitive performance and ecological contexts of two primate species, which are closest human relatives, bonobos and chimpanzees. Having equally complex social organizations, they demonstrate important differences in cognitive abilities and behavior. Particularly, chimpanzees have better spatial memory, larger preference for delayed rewards, and larger preference for more rewarding but risky choice. The two species are also characterized by several

social features: chimpanzees are more aggressive and have more intense male-to-male bonds, whereas bonobos rely more on female bonds and are more tolerant.

These differences, both cognitive and social, are thought to result from various ecological pressures and feeding demands. Briefly, chimpanzees live in more demanding environment and depend on more patchy fruit resources. On the contrary, the bonobo's diet is based on more evenly distributed food resources (herbs). Chimpanzees' feeding strategies, to be successful, should be based on spatial memory and more costly behaviors, including the use of tools and hunting. Importantly, ecological factors are considered as the source of both nonsocial and social cognitive abilities and behavior. Chimpanzees' ecological context demands a more individualistic behavior with greater feeding competition, although still allowing for contextual cooperation. In turn, bonobos, with their reduced aggression and intolerance, are more cooperative. Comparing bonobos and chimpanzees is crucial for understanding human social cognition, as these two living species are considered as the best models for the reconstruction of the last common ancestors of humans and other apes. Although both species share distinctive features of human social cognition, increased cooperative abilities and communication skills seem to be especially crucial for human sociality (MacLean 2016). What is important for the ecological intelligence hypothesis is the assumption that the initial drive for the necessary adaptations, including hormonal regulation, sexual dimorphism, or social cognition, was the ecological context and selective forces, which were, in fact, nonsocial by nature.

Comparative analysis regarding six species of lemurs also showed the interrelation between specific ecological context, types of sociality, and cognitive differences (Rosati 2017). Particularly, species relying on more frugivorous diet have significantly better spatial memory and motor control as compared to species with more folivorous diet. At the same time, as regards specifically social cognition, purely ecological explanations may seem incomplete. Some lemur species relying on mixed diet were found

to differ in some aspects of social cognition depending on the type of sociality: ring-tailed lemurs living in large groups have significantly better gaze following and transitive interference capabilities as compared to mongoose lemurs living in pairbonds (Rosati 2017). Thus, contemporary views on ecological intelligence confirms the significance of nonsocial ecological factors in the evolution of human cognition but also bridge the gap with the main rival hypothesis, that of social intelligence.

The social intelligence hypothesis (also known as Machiavellian intelligence) is the major alternative to both the general and ecological intelligence hypotheses. It argues that it is exactly the social environment and social complexity, which is responsible for unique cognitive capabilities of higher primates and especially humans. Studies of primates, conducted in the second half of twentieth century challenged the view that the evolution of human mind was primarily associated with tool making and use. They showed that primates had complex and diverse social life and shared many specific social features which were traditionally thought as uniquely human, such as establishing coalitions, deception, reconciliation of relationships after conflicts, reciprocation of help in contests, and other (Byrne 1996). As a result of these studies, a new theoretical framework explaining the origin of human cognition emerged under the umbrella term “Machiavellian Intelligence” (Byrne and Whiten 1988; Whiten and Byrne 1997). Richard Byrne and Andrew Whiten, two main proponents of this approach, describe its core idea as “the implication that possession of the cognitive capability we call ‘intelligence’ is linked with social living and the problems of complexity it can pose” (Whiten and Byrne 1997, p. 1). The term “Machiavellian” is used to stress that human social behavior is not simply based on self-interest but also that in pursuing own goals individuals develop complex and elaborated strategies, in which this self-interest can be well camouflaged and presented as altruistic behavior. This means that social life fostering cooperation and prosocial behavior can be more efficient in terms of reproductive success than more obviously egoistic

behavior, when individuals live in complex groups with high degree of interdependence.

Proponents of the Machiavellian Intelligence hypothesis agree that the ecological context poses serious problems which can favor specific cognitive adaptations. However, they stress that the social environment has some unique features triggering faster cognitive evolution. Unlike most nonsocial environmental pressures, changes in cognitive abilities directly change the social environment itself. Increased intelligence among some social agents gives them advantages in competition, thus leading to increasing cognitive capabilities across the whole population.

Social complexity is the key factor affecting the evolution of the social intelligence. It is not reduced to the number of individuals in a group but rather deals with the complexity of social relations among them and the variety of social behaviors expressed by individuals. Species living in relatively complex social environments, often use subtle social tactics. For example, a female baboon can spend time and efforts for grooming a sole male to establish affiliative relations with him, with the goal of receiving support in further contests (Byrne 1996, p. 174). Different forms of complex social tactics of establishing short- or long-term alliances, hierarchies, competition involving third parties, deception, and others were found in both primates and other species such as zebras, lions, hyenas, dolphins, etc. Such tactics would not be possible without specific cognitive abilities: correct identification of conspecifics, their position in a social structure, good memory for their personal histories, attention for social information, and visual perception. Social complexity is thus thought to select for better memory, effective learning, and processing of social information (Byrne 1996, p. 175).

Further development of the approach was the idea of the “social brain.” According to it, greater social complexity requires more computational capabilities, which, in turn, need larger brain and brain-to-body size ratio. Of a special importance are neocortical areas of the brain involved in cognitive mechanisms of reasoning and consciousness, which are crucial for social cognition. An analysis performed by several researchers,

particularly Robin Dunbar, showed a relative neocortical size in 24 anthropoid primates as strongly correlated with the group size (Dunbar 1998). Importantly, the neocortical size was not correlated with the type of diet or other possible indexes corresponding to the logic of the ecological intelligence hypothesis. The social brain hypothesis implies that the brain, and especially neocortex size, determines the information-processing capacity necessary to maintain complex social relations and the cohesion of a group. The so-called Dunbar number (roughly equal to 150) determines the number of social contacts, which can be effectively managed by the human brain.

Equally important for the social brain hypothesis is the idea that the brain size as such is not sufficient to understand the evolution of human cognition. The type of cognitive processes supported by it is even more important. The social brain is not simply about memory; the key specialization of neocortical areas is mental representation capabilities, and especially “theory of mind,” i.e., the ability to understand and reconstruct others’ mental states and intentions. Such abilities, more developed in apes than in monkeys, are a distinctive feature of human cognition and are necessary to develop fine-grained strategies of the “Machiavellian” type.

Although now widely accepted, the social intelligence hypothesis is not free from criticism. Kay Holekamp (2007), comparing various species, points to several problems of this theory. For example, some non-primate species, such as spotted hyenas, live in as large and complex social groups as many primates and demonstrate the comparative variety of social capabilities including processing complex social information, memory for conspecifics, their affiliations and rank, reconciliation after contests, and so on. At the same time, the primates’ greater intelligence, cognitive flexibility, and learning capabilities may indicate that such social complexity is not sufficient to explain the cognitive evolution. Other facts also seem to contradict the social intelligence hypothesis. Bears, which are solitary species, have larger brain and neocortex, are more innovative and flexible as compared to most gregarious

carnivores, e.g., hyenas. Even more remarkable is the fact that great apes have some unique cognitive capabilities (social learning and mentalizing) as compared to monkeys, although they live in groups of similar size and complexity. Recognizing these facts, the proponents of the social intelligence idea hypothesized that other, nonsocial selective pressures (e.g., the need for greater representational abilities to manage more complex feeding environment) might contribute to the cognitive evolution of primates and humans (Byrne 1996). As a result, integrative views on cognitive evolution recognizing both social and ecological factors are currently considered as a more appropriate explanation (Holekamp 2007; Rosati 2017).

The Cultural Intelligence Hypothesis can be considered as an advanced version of the social intelligence hypothesis, focused almost exclusively on the evolution of human mind. Some researchers use the term “ultra-sociality” to stress the exceptional cooperative abilities necessary to maintain human societies (Tomasello 2014). The evolution of human cooperation is considered as a two-step process. First, ecological pressures associated with reduced availability of food resources forces early humans to cooperate intensively. Second, such cooperation extended beyond kinship and included larger social groups. In turn, the need to cooperate within large groups required large-scale solidarity and identification. Such large social groups are in fact cultural groups as their existence relies upon symbols and institutions, which mediate and structure social interactions. Living in cultural groups requires specific skills to learn and operate with symbolic objects necessary to interact with others and acquire knowledge (Tomasello 1999). The hallmark of human symbolic communication and learning abilities is language. Although human language shares many common elements with animals’ communication systems at the neural level (Seyfarth and Cheney 2014), it is significantly more complex, and culture is thought to stimulate fast biological adaptations for the development of language (Thompson et al. 2016).

The cultural intelligence hypothesis argues that early symbolic cognition necessary to live in large

cultural groups are responsible for human exceptional cognitive abilities in general. To test this hypothesis, an international group of researchers compared performance of human 2.5 years children, chimpanzees, and orangutans in a large set of physical and social cognition tests (Herrmann et al. 2007). They found that, across various tasks in the domain of physical cognition (e.g., locating a reward, discriminating quantities, tool use), chimpanzees and human children did not differ in their performance, and orangutans performed only slightly worse. On the contrary, in the social domain (e.g., social learning, understanding communicative cues, gaze following, etc.) human children significantly outperformed both species of apes. The results were interpreted as supporting the cultural intelligence hypothesis and contradicting the general intelligence hypothesis. If the later was true, we might expect that human children would outperform apes in both social and physical cognition tasks. Authors supposed that the crucial developments of social cognition occurred not earlier than one million years ago and became the response to the needs of complex forms of cooperation during foraging. Again, confirming the potential role of nonsocial ecological factors in the development of human sociality, the cultural intelligence hypothesis is not incompatible with other versions of the adaptive intelligence approach.

Uniquely Human Social Cognition

The approaches explaining the evolution of human mind, briefly described above, differ in the role they ascribe to social environment as a driving force of this evolution. Among them, the cultural intelligence hypothesis is the most interested in understanding those aspects of cognition, which make humans unique specie. Comparative research in the evolutionary biology revealed that social cognition is widespread in the nature and many cognitive abilities traditionally considered as uniquely human are shared by different primate and non-primate species. At the same time, the difference between the complexity of human societies and animal group living is enormous. This

poses an important question of what exactly are those social cognitive abilities, which support the human “ultra-sociality.”

The cultural intelligence hypothesis was the closest to answering this question. The study by Herrmann et al. (2007) mentioned above not only concluded that human children are better in social cognition tasks than great apes but also specified the nature of these differing capabilities. In only one of six social tasks used by the researchers, there was no difference in performance. In this task, participants had to make a pointing gesture to receive a hidden reward. In all other five tasks human children performed better, and the difference was especially high in a social learning task (learning how to solve a problem by observing how is it solved by another individual). These results indicate that the ability to learn from others and, to a lesser extent, to identify their internal states and communicative abilities are especially important to deal with the social complexity of human societies.

Rebecca Saxe identifies two aspects of social cognition, which are assumed to develop in childhood and be responsible for complex social behavior: attention to faces and the representation of triadic relations (Saxe 2006). First, although sensitivity to faces and basic skills of mentalizing are common for both humans and apes, the ability to differentiate between the actual state of affairs and its representation by others develops only in humans. This means that the ability to represent and reconstruct others’ representations (rather than simply goals or intentions) is a uniquely human aspect of social cognition. The second distinctive feature is the ability to represent triadic relations between Oneself, the Other, and an Object: unlike apes, human children are able to understand others’ communicative gestures (e.g., when the Other points to a hidden reward). According to Saxe (2006), these uniquely human aspects of human cognition are supported by two specialized brain systems: temporoparietal junction (Theory of Mind construction) and medial prefrontal cortex (triadic attention).

The black-and-white view on the mentalizing abilities as uniquely human was recently challenged, when advanced forms of mentalizing

were found in apes and other primates in more natural competitive contexts (MacLean 2016). The abilities for deception and manipulating others are consistent with the Machiavellian Intelligence hypothesis and are thought to be crucial when competition is sharpened. Instead, researchers supposed that what is more specific for human is a combination of perspective-taking skills with a cooperative motivation to share one’s mental states with others, i.e., advanced communication (Tomasello et al. 2005; MacLean 2016).

Exceptional cooperative needs and interdependence of human societies, as well as living in large groups, stressed by the cultural intelligence hypothesis, have three important consequences for human social cognition (Tomasello 2014). First, to cooperate in socially complex and diverse contexts, humans must be able to construct alternative perspectives and representations of a situation, which can even be contradictory. Second, to develop long-term cooperative strategies, they must be able to make recursive social judgments and reconstruct others’ perceptions of one’s mental states and intentions. Third, they must be able to represent group norms and evaluates own and others’ behavior in terms of them, – which is a direct consequence of high interdependence between individuals. Moral reasoning is thus a necessary aspect of human social cognition and rationality necessary to cooperate in large groups.

The Structure of Social Cognition

What the evolutionary approaches share is the assumption that all human cognitive abilities including social ones should be understood as adaptations to specific situations, in which our ancestors lived. Correspondingly, it is reasonably to consider any specific element of social cognition as an adaptive response to specific evolutionary challenge. The structure of social cognition, i.e., its specific elements, processed and/or abilities, should thus reflect the nature of ecological and social problems typical in the earlier stages of human and/or primates ontogeny. One attempt to describe the structure of social cognition as a set

Social Cognition, Table 1 Correspondence between evolutionary problems and the structure of social cognition. (Adapted from Kaschak and Maner 2009, p. 1237)

Social domain	Evolutionary problems	Social cognitive processes
Self-protection	Avoiding social threats	Automatic and fast attention to angry faces and other cues of social threat
Affiliation	Gaining acceptance by a group; regulating social exchange; helping others with minimal costs	Identifying with a group, estimating degree of social closeness (e.g., kinship-based); vigilance to potential cues of social exclusion
Mating	Evaluation and selection of mating partners; relationship protection	Sensitivity and attention to physical attractiveness; vigilance to attractive rivals
Social hierarchy	Gaining high status; avoiding conflicts with high-ranked individuals	Representation of hierarchical relations and attention to status symbols

of adaptive responses was provided by M. Kaschak and J. Maner (see Table 1).

Although attempts to directly deduce the expected social cognitive processes from the retrospectively reconstructed evolutionary challenges can be useful, this is not the only possible way to understand the composition of social cognition. Studies in social psychology and social neuroscience provide a view on human social cognition without a direct reference to the problem of its evolutionary origin.

At present, there is no consensus in social psychology and social neuroscience on the exact list and interrelations of social cognitive processes as well as the degree of their specificity for the “social” realm. Many researchers provide significantly varying accounts on what social cognition consists of and on the scope of phenomena covered by this term.

For example, Fiske et al. (2007) proposed that social cognition can be understood in terms of two underlying fundamental dimensions: warmth and

competence. These dimensions reflect the perception of key issues of social life, competition/cooperation, and status. Jointly, the two dimensions describe representation of any social agent and specific emotions and behaviors toward them. This approach considers the basis of social cognition in social perception. Even more importantly, the fundamental aspects of social cognition are thought as typological, i.e., social agents are perceived in terms of their common, universal traits rather than their individuality, intentions and goals.

Other researchers extend the domain of social cognition far beyond such typological processes. A review by Happé et al. (2017, pp. 244–245) describes several such taxonomies:

- Individual recognition, knowledge of others' relationships, and theory of mind (Seyfarth and Cheney)
- Affiliation/attachment, social communication, self-perception, perception and understanding of others (National Institute of Mental Health)
- Affiliation, agent identification, emotion processing, empathy, individuals' information store, mental state attribution, self-processing social hierarchy mapping, social policing, ingroup/outgroup categorization (Happé & Frith)

The authors themselves described eight elements of social cognition (Happé et al. (2017, p. 247):

- Affiliation and social motivation (regulating approach-avoidance behavior)
- Agent recognition (identifying others' individuality)
- Motion perception, action recognition, and imitation (identification of actions made by others)
- Emotion recognition
- Empathy (mirroring emotional states of others)
- Social attention (conscious or automatic)
- Social learning (learning from others)
- Theory of mind

This list of cognitive processes used by the authors is obviously incomplete, as it does not include such important elements of social

cognition as the representation of social hierarchies or social judgments. However, the authors used this list not to reconstruct the general structure of social cognition but rather to illustrate how the different processes can be related to each other. For example, imitation, empathy, and theory of mind can all recruit one common process, self-other distinction, which can be thus considered as their foundation.

Another theory, considering social cognition as a construction of subjective social reality, distinguishes between the three general elements: direct input of social information from a given situation (e.g., by observing others' behavior); extracting relevant information from memory; variety of operations, both automatic and controlled, performed with these two types of input information (Greifeneder et al. 2018). Whereas many other psychologists and neuroscientists study basic, lower-level processing of social information, the authors are more focused on high-level social cognition involving complex social constructs and operations, such as stereotypes, scripts, priming, social judgments, etc.

Unlike psychologists, social neuroscientists attempt to identify key elements of social cognition by distinguishing underlying neural systems and processes. For example, according to Gallese et al. (2004), there are two similar but distinct neural mechanisms based on mirror neurons (specific type of neurons, which are activated both when an individual perceives others' actions and perform the same actions) involved in social cognition. They are responsible for our understanding others' actions and emotions. In its core, social cognition is fundamentally individuated, whereas any typological representations (e.g., representation of social groups or status) should be considered as relying upon these basic abilities to imitate other individuals.

An integrative model proposed by Yang et al. (2015) identifies three basic components in the neural system of social information processing: social perception (decoding others' mental states based on face expressions and behavioral signals); action perception (imitating others' actions with the mirror neuron systems); and theory of mind (high-level cognitive ability to represent other's

mental states and intentions necessary for strategic planning).

One of the most detailed map of social cognitive processes is provided by Lieberman (2007) who identified four broad areas of social cognition processed by distinguishable neural systems:

- Understanding others (representation of psychological states and traits of others; empathy)
- Understanding oneself (visual self-recognition; recognition of own body and movements; self-reflection on present and past experiences; self-concept)
- Self-regulation (impulse control; reappraisal of emotional events; expressing feelings with words; unintentional self-regulation in placebo effect)
- Self-other interface (imitation; understanding oneself by referring to one's theory of others' minds; implicit and explicit attitudes; regulating prejudice and attitude change; social connection and rejection; social and moral reasoning; fairness and trust)

In this view, social cognitive processes do not include some lower-level processes mentioned by other theorist (e.g., social attention) but include executive functions (behavioral control and decision-making), which are typically excluded from the concept of social cognition. In sum, both psychological and neuroscience approaches are very diverse in their understanding of what social cognition is about. Currently, achieving consensus on the nature and structure of social cognition remains to be an unresolved task.

There are two other issues discussed by researchers and necessary for our understanding of the mechanisms and structure of social cognition. These issues are the relations between:

- Domain-specific and domain-general aspects of social cognition
- Automatic and controlled mechanisms of social cognition (Happé et al. 2017).

Both issues are directly related to the discussions on the nature and evolution of social cognition. The first question is whether social cognition

is based on general or specialized processes – the question directly related to the debate between general- and specialized-intelligence hypotheses. The current state of knowledge gives no univocal answer to the question. The studies in social cognitive neuroscience provide evidence that at least some elements of social cognition are based on highly specialized neural systems or mechanisms. Examples include the mirror neurons (action and emotion recognition), temporoparietal junction (theory of mind), fusiform face area (sensitivity to faces), etc. At the same time, methodological constraints of contemporary neuroscience do not allow to evaluate the degree of putative specialization of such systems.

The answer to the second question seems to be more definite. A wide range of the so-called dual process (dual systems) theories arguably differentiate between the two types of cognitive processes equally important for social cognition (Lieberman 2007; Evans 2008; De Neys 2018). The first system (system 1) is fast, automatic, implicit, and mandatory whereas the second (system 2) is slow, controlled, explicit, nonmandatory and of limited capacity. The interaction between the two systems can be found in many domains of social cognition including mentalizing, social perception, social categorization, although the mechanisms of such interaction can be more complex than previously suggested (De Neys 2018).

An example of the two systems interaction is the time-course of perception of the different types of social stimuli. In an experiment by Cunningham et al. (2004) White participants observed Black and White faces for two time periods corresponding to subconscious (30 ms) and conscious (525 ms) cognition. The amygdala, a part of the neural System 1, was activated more to the Black faces in the first condition whereas in the second condition (525 ms), its activity was reduced and the frontal cortical regions, responsible for the controlled processes, became active instead. This proves that both types of processes are involved in social perception and interact. A more complex and non-trivial example is the study by Freeman et al. (2010). They investigated how the brain responds to a set of faces, which were artificially transformed to represent a

continuity of sexually dimorphic faces, ranging from masculine to feminine. They found that whereas the fusiform gyrus, known to be responsible to visual perception of social stimuli, responded continually, depending to the degree of dimorphism, another brain area, orbitofrontal cortex, responded to faces in a discrete manner, encoding them as either males or females. These and other findings support the view that the dual process view on social cognition is useful, although the exact nature of the two systems functioning and interaction is yet to be studied.

Conclusion

There are no doubts that living in a complex social world requires multiple and advanced social cognitive abilities necessary to accurately represent this complexity, build short- and long-term relationships and determine appropriate behavior in various contexts. Although there is a general agreement that human social cognitive abilities evolved altogether with the evolution of sociality itself, the role of different factors and especially the balance between competition and cooperation remains debatable. The range and composition of phenomena described as social cognition by researchers remains equally diverse and often contradictory. Whereas some researchers focus on more basic, low-level social information processing, such as attention and visual perception of individual social agents, others pay more attention to higher-level constructs and operations, which include typologizations and abstract representation of the social world, strategic planning, and decision-making. Many of the more complicated aspects of social knowledge (e.g., ideologies, moral reasoning, strategies of self-identification) are normally discussed within philosophy, sociology, political studies, and other social sciences and remain beyond the studies in social and especially evolutionary psychology.

Key issues in contemporary studies include identification of specific neural systems and processes responsible for various aspects and types of social cognition as well as their interrelations and interactions. There are good reasons to think that

at least some social abilities are supported by specialized, domain-specific systems, although the degree of their specialization and contribution to complex, especially explicit social cognition remains a matter of discussions. Another increasingly important line of research is the studies of culturally conditioned neural processing of social information. Studies in cultural neuroscience show that many key social cognitive processes such as self-other distinction, social attention, memory, mentalizing are processed differently in various cultures at the neural level (Oyserman et al. 2014; Han and Humphreys 2016). Further studies in this direction are a promising step in understanding the evolution of social cognition as reflecting the evolutionary pressures from the interrelated ecological and cultural contexts.

Cross-References

- [Communication and Social Cognition](#)
- [Cooperation and Social Cognition](#)
- [Social Learning and Social Cognition](#)
- [Social Neuroscience of Self-Categorization](#)
- [Theory of Mind and Nonhuman Intelligence](#)

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Social Cognition and Communication in Chimpanzees and Bonobos

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Synonyms

Cooperation; Facial expressions; Gestures; Mental processes; *Pan*; Signals; Social knowledge; Social learning and culture; Theory of mind; Vocalizations

Definition

Social cognition: mental processes involved in the acquisition and interpretation of information about the social world; communication: exchange of information between at least two individuals, where acts achieve their ends indirectly.

Introduction

The study of our closest living relatives, chimpanzees and bonobos, has been of interest to humans for well over a century. Darwin recognized the apparent similarities in our expressions in his 1872 book “The Expression of Emotions in Man and Animals.” More systematic research on their social cognition and communication in captivity started in the early 1900s, before they were recognized as separate species, with Köhler’s studies of chimpanzee intelligence (Köhler 2018), and was extended to wild chimpanzee populations in the 1960s with Goodall’s work in Gombe (Goodall 1986) and wild bonobo populations in the 1970s with Kano’s work (Kano 1992). However, unlike the crop of long-term chimpanzee research sites taking off at the

same time, repeated civil wars and limited infrastructure in the Democratic Republic of Congo delayed the study of wild bonobo behavior for decades. Even today, there remain relatively few places, in the wild or captivity, where it is possible to study bonobo behavior. Besides, what is the point? Research on these highly social long-lived species taken decades, in chimpanzees, we already have a *closest living relative* to compare ourselves against. Do we really need another one? The answer is of course, yes, and for all their obvious and more subtle similarities, there are equally obvious and subtle differences between them that are only starting to become apparent.

Both species live in large social groups and need to be able to acquire, interpret, and act on information about social relationships, including kinship, alliances, and dominance. Growing up in a social environment offers a range of ways in which you can gain social information and other benefits from those around you, whether kin or non-kin. The opportunity to learn, for example, about your physical environment: where is food? What is food? How to access or process food? In social-living species, an individual’s socio-emotional development depends on the opportunity to interact with others and form stable relationships, with profound life-long negative repercussions following atypical early social loss or isolation.

Today, the behavioral plasticity found within the species and subspecies that make up the *Pan* genus challenges the now outdated distinctions made between the *violent* chimpanzee and the peaceful *hippy* bonobo. However, there remain important differences in their social relationships, including in dominance, tolerance, and female cohesion, all of which impact the socio-cognitive tool kit they employ in their day-to-day lives. Direct comparisons within *Pan* species allows us to better understand them as modern species, but an understanding of within species flexibility and between species distinctions are also important for a more grounded discussion of the socio-cognitive suite of abilities present in our common ancestor.

The Species

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) belong to the genus *Pan*. Both equally proximate to us in their genealogy, our lineage diverged from the *Pan* lineage around 5–8 Mya; chimpanzees and bonobos diverged from one another around 1–2 Mya, after which chimpanzees split into several subspecies. Recent studies suggest that bonobos may have evolved from an ancestral *Pan* population that crossed the Congo River at a time of drought (Takemoto et al. 2017).

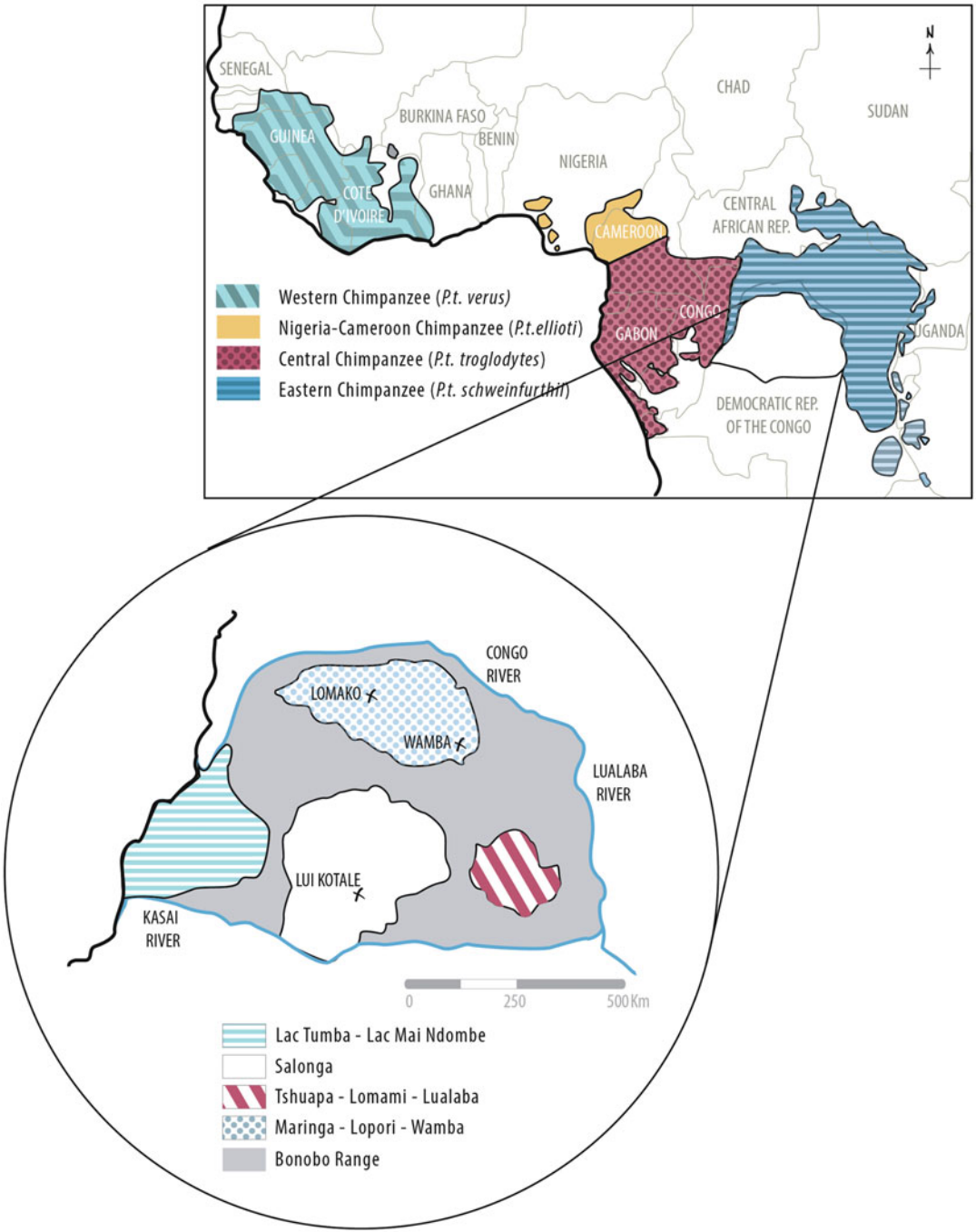
Today, chimpanzees are listed as an Endangered Species (IUCN 2018), but despite this status, they represent the most abundant and widespread of the nonhuman great apes, typically occupying primary and secondary forest, but also grassland and savanna woodland. In the wild, chimpanzees are found across equatorial Africa, with a discontinuous distribution from southern Senegal across the forested belt north of the Congo River to western Tanzania and into western Uganda. The four formally recognized subspecies – Western Chimpanzee (*Pan troglodytes verus*); Nigeria-Cameroon Chimpanzee (*P. t. ellioti*); Central Chimpanzee (*P. t. troglodytes*); and Eastern Chimpanzee (*P. t. schweinfurthii*) – occupy mutually exclusive geographical ranges (Fig 1). Morphological differences across the four subspecies are relatively minor but they show substantial diversity in behavior from tool use and hunting, to female cohesion and the use of lethal aggression. Although part of this diversity can be explained as the result of variation in local ecology, for example, in the availability of particular foods or tool materials, other striking social and cultural differences persist, even where there is little evidence for ecological or genetic variation (Whiten et al. 1999).

Bonobos (*Pan paniscus*, Bilia or Mokonbusu) are also listed as an Endangered Species (IUCN 2018). Previously named *pygmy* chimpanzees, they are slightly smaller and more gracile, and display less sexual dimorphism in maturity. In the wild, bonobos are confined to the primary

and secondary rainforests of the Democratic Republic of Congo (Fig. 1). Their geographical range extends from the Lualaba River in the east to the Kasai and Sankuru rivers in the south, and the Congo River in the north, which forms a biogeographical barrier separating them from chimpanzees. Bonobos occupy forest-savannah mosaics that include tropical forest, dry forest, swamp forest, savannah woodland, and marshy grassland. Like chimpanzees, bonobo populations have experienced significant decline over recent decades, mainly due to habitat loss and poaching for the commercial bushmeat trade. Bonobos have no recognized subspecies: the constraints of the riverine barriers limit the gene flow between populations, which appear relatively stable. However, four strongholds have been identified: Maringa-Lopori-Wamba in the northern block (Lue Scientific Reserve, Lomako, Yokokala Faunal Reserve and Kokolopori Bonobo Reserve), Tshuapa-Lomami-Lualaba in the eastern block (Sankuru Natural Reserve), Salonga in the southern block (Salonga National Park), and Lac Tumba – Lac Mai Ndombe in the western block (Tumba-Lediima Natural Reserve) (Fig. 1).

Chimpanzees and bonobos are both diurnal and semiterrestrial. A large part of their typical activity budget includes foraging, feeding, and resting. Both species build sleeping nests in trees at night. Chimpanzee and bonobo females exhibit extended sexual swellings related to their estrous cycle, with a maximal swelling occurring near ovulation. While both species' maximal swelling is extended sufficiently to conceal the precise timing of ovulation, favoring a promiscuous mating strategy, this period lasts longer in bonobos and may lead to greater uncertainty about paternity (Boesch et al. 2002).

Chimpanzees and bonobos are omnivorous and opportunistic feeders. Their diet consists mainly of fruit supplemented with vegetation, seeds, roots, pith, and bark, but both species also eat honey, eggs, soil, resin, invertebrates, and vertebrates. Some of the variation found within and between species is likely driven by different necessities and opportunities related to the abundance of available food resources;



Social Cognition and Communication in Chimpanzees and Bonobos, Fig 1. Distribution of the genus *Pan*, including the four strongholds of bonobos and the four subspecies of chimpanzee. (Image credit Leonor Lavradio)

however, variation could also reflect individual selectivity. Chimpanzees, for example, are prolific hunters, with variation between even neighboring

communities in techniques and prey species. Both species hunt opportunistically and in groups. In chimpanzees, group hunting is more often

initiated by males, whereas in bonobos, females take a more active role and receive a larger share of meat (Boesch et al. 2002; Surbeck and Hohmann 2008). In contrast to bonobos, chimpanzees are skillful extractive foragers, frequently employing tools such as stones, sticks, and soft vegetation to extract and eat termites, ants, honey, nuts, and small mammals, again with cultural variation across populations and communities (e.g., Whiten et al. 1999).

Systematic research has been conducted with wild chimpanzees since the 1960s, focused at six long-term study sites each with over 30 years of continuous study: Gombe and Mahale in Tanzania, Sonso and Kanyawara in Uganda, Tai in Ivory Coast, and Bossou in Guinea. More recently, research has diversified, with at least 120 active field sites (Gruber and Clay 2016). Research in bonobos living in their natural habitat has been conducted in considerably fewer field sites. Long-term studies started in the 1970s in two field sites: Wamba and Lomako (Fig. 1), with Lui Kotale established in 2002. Research has been more regularly interrupted due to extended political instability and widespread epidemics, such as Ebola, but today, as in chimpanzees, the number of groups under study is starting to expand. As with wild populations, research opportunities in captive environments have also expanded, including both zoos and sanctuaries around the world, but in particular within an increasing number of semi-free-ranging sanctuaries in Africa.

Social Development and Behavior

Chimpanzees and bonobos live in multimale-multifemale fission-fusion societies, forming dynamic subgroups during the day (Goodall 1986; Kano 1992). They can live for over 50 years, with estimated generation times of around 25 years in both species. In some aspects, bonobos' social and physical development occurs more slowly than in chimpanzees with some apparently *juvenile* characteristics preserved into adulthood, such as high levels of play and non-conceptive sexual behavior, increased tolerance,

and decreased aggression. In other aspects, such as sexual development, time of emigration, and first reproduction, bonobos are more precocious. In chimpanzees and bonobos, males are the philopatric sex, remaining in their natal community, whereas females typically migrate to other groups when reaching maturity: at around 11–13 years in chimpanzees and 6–10 in bonobos (Gruber and Clay 2016). However, in chimpanzees, all mature males typically outrank all mature females and express a typically linear hierarchy, particularly among the highest ranked individuals, although the relative *steepness* or apparently despotic as opposed to egalitarian nature of these male hierarchies can vary between communities (Kaburu and Newton-Fisher 2015). In contrast, the highest ranked individuals in bonobo communities are typically mature females, and the overall pattern is more flexible, with some males having similar or higher ranks than some mature females (Boesch et al. 2002).

Chimpanzees are territorial and compete aggressively, at times lethally, over territorial space. In contrast, bonobos occupy more flexible *territories* in which there can be large overlap in areas of use between adjacent communities and positive intergroup encounters that may last for days. Chimpanzee males are highly gregarious and tend to establish strong bonds with other males, with whom they often share food, cooperate in shared activities such as boundary patrols, and support each other in social conflicts (Goodall 1986). Male bonobos do not typically form strong non-kin alliances or offer regular support to other males in agonistic contexts. Here, females are the more gregarious sex, and male sociability is more typically characterized by stable bonds with their mothers and other females in their communities (Kano 1992). Nevertheless, despite these broad-stroke differences in typical species behavior, there is striking variation within species, even in fundamental aspects of social behavior. For example, West African chimpanzees show low levels of lethal aggression and high levels of female gregariousness more reminiscent of bonobo communities than of their closer phylogenetic relatives, East African chimpanzees (Gruber and Clay 2016).

Social Cognition

Cooperation

Cooperation among relatives conveys benefits for individual fitness. Therefore, in philopatric species, such as chimpanzees and bonobos, more cooperation is expected among males. While bonobos are typically thought of as more *cooperative*, male chimpanzees cooperate across diverse contexts including high-risk high-cost behavior such as within-group coalitions, cooperative hunting, meat sharing, and territorial boundary patrolling. Both coalitionary behavior (two or more individuals cooperating to direct aggression toward others) and territorial boundary patrolling may result in severe injuries or even deaths within and between groups. In cooperative hunting, individuals may search for monkeys up to hours, time in which they may travel extended distances and forgo other opportunities to feed. These costs should be outweighed by the associated benefits, at least over individual lifetimes. So, for example, group hunting only appears to be stable in communities where the meat consumption per individual is higher than alternative individualistic hunting strategies. Males may also use meat sharing to strengthen their social bonds with other males or in a meat-for-sex exchange in females (Boesch et al. 2002). Similarly, despite lower levels of relatedness between females, in bonobos, it is females who primarily hunt for and share meat (Surbeck and Hohmann 2008).

Captive studies allow for more controlled exploration of the different factors that lead to cooperation. Both chimpanzees and bonobos work with conspecifics to solve cooperative tasks and show an understanding of the role that their partner's play in achieving them. However, differences in the social structure of both species may impact the ways in which they cooperate. In experimental settings, bonobos outperformed chimpanzees in cooperative tasks to achieve food rewards. One hypothesis argues that bonobos evolved in an environment with abundant resources and consequently with reduced feeding competition, leading to greater social tolerance than in chimpanzees (Hare et al. 2012). Similarly,

differences in ecology and demography may explain some variation found across communities within species, suggesting species differences may be more of degree than kind, and that caution should be used when extrapolating from any single population, particularly from captive ones given their unique socio-ecological environment.

Theory of Mind

Having a *theory of mind* (ToM) refers to the ability to assign mental states to other individuals (Premack and Woodruff 1978) and was long believed to be unique to humans. In human children, it is typically thought to be fully developed by around 4 years old but implicit understanding may be present from a much younger age (Schmelz and Call 2018). The cognitive capacity to understand others' mental states may be adaptive for many social-living species, as it may help them to predict others' behaviors, and over recent decades, ToM research has been extended to other primates and other animals (see Krupenye and Call 2019 for a review). Much of this work has focused on individual's ability to identify others' goals and intentions, and to understand others' perception and knowledge, including, for example, subjective desires and false beliefs (Krupenye et al. 2016). A significant challenge to investigating ToM is that most methods for doing so require at least some language use, providing challenges to our ability to explore the capacity not only in preverbal children but also in other species. As a result, it was unclear for many years to what extent the capacity to understand that other individuals have their own mental states was exclusively human, or whether its absence in other species was a reflection of our inability to detect it.

A major breakthrough in this field was the use of methods that take into account the socio-ecological perspective of the species being tested. In their 2000 study, Hare et al. asked "Do chimpanzees know what others do and do not see?" While not a direct investigation of ToM, understanding another's visual perspective is likely a key precursor to understanding another's state of mind. Crucially, rather than the many

cooperative paradigms used in the past, which require two individuals to work together to achieve a food reward, this study took into account chimpanzees' typically competitive approach to food and measured their abilities in an ecologically relevant paradigm. In doing so, they provided both the first consistent body of evidence for this capacity and, perhaps more importantly, a methodology that allowed the next generation of research to move forward in exploring other species' understanding of each other's minds. Over the past two decades, a body of work has built up supporting the existence of ToM in other ape species. Chimpanzees and bonobos seem to be able to interpret others' actions as goal directed and have a basic understanding of what others know and perceive. Experimental studies conducted in captivity and in the wild have shown that chimpanzees were able to distinguish between knowledgeable and ignorant individuals. Moreover, some experimental studies have shown that chimpanzees can reason about others' intentions, distinguishing situations such as: unwillingness to share from inability to share food; actions done on purpose or by accident; or a food thief from an innocent receiver of stolen food (Schmelz and Call 2018).

However, it remains unclear to what extent chimpanzees and bonobos are able to hold, and attribute to others, shared goals and intentions. Understanding *false belief* is the ability to understand that another individual may hold a belief that differs from reality. In the classic test of this capacity, a child watches while puppets place a chocolate in a cupboard, and then – when one of them is out of the room – the other moves the chocolate (Wimmer and Perner 1983). Being able to tell that, despite they themselves knowing the *true* location, that the puppet who was out of the room still believes it to be in the original (now *false*) location, shows the capacity to recognize that others' perspectives may differ from your own. Recent evidence using modern eye-tracking methods suggests that apes may be sensitive not just to others' knowledge but also to their, potentially *false beliefs* (Krupenye et al. 2016).

Recent work investigating ToM in chimpanzees and bonobos is not without critique. Non-mentalistic hypotheses can also be invoked to explain behaviors argued to represent evidence for theory of mind: for example, abilities such as self-recognition, deception, and perspective-taking can be explained by other processes like associative learning or even inferences about observable features of the situation rather than mental states. In false-beliefs tasks, successful performances could be also explained if subjects had learned heuristic rules of thumb “agents tend to search for things where they last saw them,” or that “the agent may found the object without fully representing that the actor believed that the object was in that location” (Krupenye and Call 2019; Schmelz and Call 2018).

To date, while there are still critiques to address, the trend of support is for increasing diverse evidence in favor of chimpanzee and bonobo's capacity to attribute psychological states to others and to understand others' perception, knowledge, and goals. These abilities are still less explored in bonobos than in chimpanzees, and there are hints they may differ in interesting ways; for example, bonobos appear to be less willing to cooperate when food, as opposed to food and social contact, is the only reward (Tan and Hare 2013). A more nuanced understanding of the differences between these two species requires not only testing the two species under similar conditions but also diversifying testing approaches so that they take into account the ways in which bonobo ToM may be expressed.

Social Learning and Culture

Where physical environments offer different problems and opportunities, differences in population behavior may result from adaptation to local ecology. However, population-specific behavioral traditions, in the absence of genetic or ecological variation, are an indication of potential cultural variation (Whiten et al. 1999). Comparing apparently cultural behavior in chimpanzees and bonobos provides fewer examples of cultural traditions in bonobos; however, as long-term research is needed to detect often subtle variation,

the more limited range of sites and the fewer cumulative years of study available impacts our ability to confidently describe the expression of bonobo cultural behavior (Hohmann and Fruth 2003).

Of the 65 behavioral patterns that Whiten and colleagues listed as candidates for cultural behaviors in chimpanzees in 1999, 14 were described in review of bonobo behavior (Hohmann and Fruth 2003); and others are regularly being added as research expands (Furuichi et al. 2015). The hand clasp is one example of a shared behavioral pattern across both species that appears to then vary in its use between populations within species. Here, two individuals sit facing one another, raise an arm, and clasp each other's hand overhead while engaging in mutual grooming. East African chimpanzees often engage in this behavior at Mahale but not in Gombe, and hand clasping occurs in some western chimpanzees' sites such as at Tai, but not in others, such as Bossou. Hand-clasp grooming has been described for some bonobo populations, such as Lomako (Hohmann and Fruth 2003).

A particular source of apparent divergence in chimpanzee and bonobo cultural behavior is in extractive-foraging techniques. Chimpanzees employ a wide range of diverse tools, from sticks, and stones, to leaves and moss to extract food from a wide range of sources, with extensive study of group-specific cultural differences. In contrast, in bonobos, only leaf- and moss-sponge tools for drinking water have been described to date (Hohmann and Fruth 2003). At present, the definitions and criteria imposed by the current methods to detect cultural behaviors in nonhuman animals are far more restrictive than the ones established for humans and, as a result, the size of the cultural repertoire of other species, particularly with regards to nonmaterial culture, may be being significantly underestimated. Schuppli and van Schaik (2019) have proposed a new method taking into account cultural adaptations to local ecological contexts, and even cultural universals. Developing the current methodologies used to study social learning may allow us to detect more candidates for cultural behavior in the future.

Communication

Gestures

Chimpanzees and bonobos use gestures in a flexible and intentional way to achieve a social goal (Graham et al. 2018; Hobaiter and Byrne 2011). At its simplest, in intentional communication, rather than broadcast a stimulus-driven signal, the signaler must choose to deploy a signal with the aim of changing the behavior of a specific recipient. While we have no direct access to the signaler's cognitive processes, we can employ reliable behavioral cues adapted from the study of intentional communication in preverbal human infants; for example, selecting the modality of signal appropriate for the recipient's visual attention, waiting for the recipient to respond, or persisting and elaborating based on the recipient's behavior. While the majority of the gestures are used to get help from another individual in attaining a physical goal, there is some evidence from studies of captive and wild apes that they may be able to express additional linguistic features such as reference (Liebal et al. 2014).

The gestural repertoires of bonobos and chimpanzees are large, containing over 80 distinct signals, but overlap almost entirely between the two species. Usually these repertoires are described in terms of their physical features, which may include the body part involved and the type of the movement (e.g., *arm raise*, *leg swing*), and are then grouped according to sensory modalities involved in perceiving the signal: silent gestures – those that create no sound or physical contact when made (also referred to as visual gestures, although all gestures contain visual information); contact gestures – those that include physical contact between the social partners (sometimes also referred to as tactile gestures); and audible gestures – those in which the production of the gesture necessarily includes an audible component. Ape signalers take the ability of the recipient to receive visual information into account when selecting from within their large repertoires, for example, using silent gestures when in full-sight, and contact or audible gestures when out-of-sight of the recipient (Hobaiter and Byrne 2011; Liebal et al. 2014).

Differences between chimpanzees and bonobos in their use of gesture appear to be related to species-specific differences in their sociality. Bonobos seem to gaze more frequently before they start signaling, and they are very proactive – often responding before the signaler finishes their communication. Chimpanzees adjust their body orientation toward recipients and engage in more time-consuming communicative negotiations that may involve longer periods of response-waiting and gestural sequences (Fröhlich et al. 2016). The gestures reported for bonobos that are apparently absent or rare in chimpanzees are typically used in sexual contexts, whereas those reported only for chimpanzees are more often related with male displays and dominance. Gestures are flexible and the same gesture can be employed to achieve multiple goals or multiple gestures used towards the same goal. Bonobo gestures appear to be more tightly associated with just one or two meanings, while there is greater flexibility in a larger proportion of the chimpanzee repertoire (Graham et al. 2018). Nevertheless, the description of gestural repertoires takes truly large datasets; group differences described in early studies were likely the result of under-sampling and, until more data are available on bonobos or a greater range of chimpanzee populations, apparent differences (or similarities) should be treated with caution. For example, variation in the frequency with which the two species engage in sexual and competitive behavior may create fewer opportunities to observe specific gesture types, which may be present in the species-repertoire but rarely employed (Graham et al. 2018). Bonobos employ tactile gestures more frequently, perhaps as a result of the higher degree of social tolerance and lower rates of physical aggression. However, to date, there has been little direct comparison of the two species within a single study method, and only wider and consistent data collection across communities, species, and subspecies will allow us to better understand their variability.

While the onset of bonobos' socio-cognitive abilities is typically a little later than their onset in chimpanzees; both species start using gestures to communicate at approximately the same time (Schneider et al. 2012). Around 9–10 months,

they begin using gestures in interactions with their mothers, with silent and contact gestures emerging earlier than audible ones. As they start to interact with other members of the group, both species tend to use fewer contact and more silent gestures (Schneider et al. 2012). How apes acquire their gestures is still debated. Striking similarities found within and between groups of the same species and even across different species of apes suggests that the available repertoires of signal types may be genetically determined and potentially present in *Pan* or even Hominidae common ancestors (Hobaiter and Byrne 2011). However, other mechanisms such as individual and social learning may play a role in the acquisition of some specific gestures; for example, conventionalization or ontogenetic ritualization (Tomasello and Call 1997), or social negotiation (Pika and Fröhlich 2019), and even where gestures are acquired as part of a biological repertoire, how they are used in day-to-day interactions is likely learned and adapted to the behavior of their social partners (Bard and Leavens 2014).

Vocalizations

Early studies suggested that vocalizations were tightly associated with emotional states and involved a lower degree of voluntary control in their production. However, more recent research suggests a higher degree of flexibility in the way that the signal can be produced and perceived. Both species seem to be able to modify their production of vocalizations in response to the presence of particular others, for example, close social partners or high-ranking individuals, and in a variety of contexts, in ways that suggest a degree of voluntary control (Liebal et al. 2014).

The vocal repertoire of chimpanzees and bonobos contains around 15 broad signal types and includes signals that sound alike in both species and that are used in similar social contexts, such as *panting-laugh* or the *pout moan* (e.g., Bermejo and Omedes 1999; Crockford and Boesch 2005). Nevertheless, the general acoustic structure of the two species' repertoire is dramatically different, with particularly significant variation in pitch (De Waal 1988). Variants of the same type of

vocalizations such as *grunts*, *screams*, *hoots*, and *barks* are used in both species but sometimes differ in duration, rhythm, or other acoustic features. For example, the *greeting grunt* in bonobos serves a similar function as the *pant-grunt* in chimpanzees but has a slower rhythm and lacks emphasis on the in-breath. Vocal repertoires also include species-specific vocalizations such as *hoos* in chimpanzees and *peeps* in bonobos. Both apes can combine discrete calls to form longer vocal sequences and combine vocalizations with other type of signals such as gestures and facial expressions (Bermejo and Omedes 1999; Crockford and Boesch 2005).

A particular challenge in describing both species' calls and *repertoires* is that their vocal signals are highly graded, with many sub-types and significant ambiguity between them. This ambiguity may allow social information to be transmitted through nuanced changes in acoustic structure. For example, information on the caller identity, age, social status, and their behavioral context, is encoded in chimpanzee calls such as *pant-hoots*, *screams*, and *whimpers* (e.g., Fedurek et al. 2016). Chimpanzees also encode information about perceived food quality through variation in a single call spectrum (*food grunts*). In contrast, bonobos produce sequences of different vocalizations such as *barks*, *peeps*, *peep-yelps*, *yelps*, and *grunts*, when interacting with food, and information about food quality appears to be encoded in the overall structure, although the specific patterns of association remain unclear (Clay and Zuberbühler 2009).

There is increasing evidence for flexibility in both chimpanzee and bonobo vocal production. Where two groups were combined in captivity, immigrant chimpanzees appeared to accommodate the structure of their food calls to match those of the resident chimpanzees. Both bonobos and chimpanzees appear to adjust the structure of their long-distance calls to match those of calling partners within their community. The ability to converge on some acoustic properties of group members' calls suggests the potential for group-specific *dialects*, where parallel convergence in

different groups occurs in different directions. For example, in West African chimpanzees, there is some evidence that the acoustic structure of long-distance *pant-hoots* from chimpanzees in the same forest varies so that groups that neighbor each other's territory are more acoustically distinct than groups who are further apart (Crockford et al. 2004).

Facial Expressions

Facial expressions convey abundant and diverse information about individual motivations and emotions and play a crucial role in coordinating social interactions. Facial expressions are tightly connected with the expression of emotional states – the presence of emotions such as fear, pleasure, distress, or excitement are typically seen as a necessary implicit component when defining facial expressions – and there remains significant debate about whether they are under voluntary control.

The facial musculature of humans, chimpanzees, and bonobos are very similar, but it does not follow that the same combination of physical components represents the same affective state. A standardized coding system based on muscle movements was developed for humans (The Facial Action Coding System: FACS) and later adapted for chimpanzees (The ChimpFACS) and other primates (e.g., MaqFACS, GibbonFACS, and OrangFACS). These Facial Action Coding Systems identify the minimal units of facial movement, referred to as *Action Units*, with each *expression* consisting of a unique combination of action units. Fifteen *Action Units* making up 9 facial expressions were identified for chimpanzees including: *bared-teeth display*, *relaxed open-mouth face* (also known as *play face*), *pant-hoot*, *scream*, *alert face*, *pout*, *whimper*, *neutral*, and an *ambiguous* category used for the facial expressions that could not be easily classified (Parr et al. 2007).

Higher high levels of face-to-face interaction and eye contact in bonobos has been used to argue that they may prioritize facial signals; however, their repertoire of facial expressions matches

those found in chimpanzees; although they show differences in duration, intensity, and how often they are used. During play, chimpanzees are more likely to use the partial form of the *relaxed open mouth*, while bonobos are more likely to use the full form, with both upper and lower teeth exposed. The chimpanzee *pout* is morphologically similar to the bonobo *silent pout*, but while the chimpanzee *pout* is associated with frustration after a rejection, the bonobo *silent pout* occurs in relaxed grooming sessions (De Waal 1988).

Conclusion

The last common ancestor of humans and *Pan*, and of chimpanzees and bonobos likely lived in large social groups, with a fission-fusion hierarchical social system. Different ecological challenges after the divergence of chimpanzees and bonobos may have dictated distinct social dynamics that favored the development of specific socio-cognitive skills in each species, but both species retain substantial flexibility and the differences expressed remain sensitive to population- and community-specific socio-ecological niches. Studying a large number of groups is important to describe the diversity within a species in order to avoid misleading generalizations of certain traits, abilities, or behaviors present in a subset being attributed to the whole species. While current models of human evolution are frequently based on a limited number of chimpanzee groups, the research landscape is diversifying allowing us to better describe both modern bonobo and chimpanzee species behavior, and more accurately describe the evolutionary trajectory along both the *Pan* and *Homo* lineages.

Cross-References

- ▶ Alarm Calling upon Predator Detection
- ▶ Alarm Calling
- ▶ Cooperation Among Nonchimpanzee, Nonhuman Primates

- ▶ Cooperative Alliances
- ▶ Cooperative Hunting
- ▶ Frans de Waal's (1982), *Chimpanzee Politics*
- ▶ Evolution of Culture
- ▶ Manipulation and Dishonest Signals
- ▶ Social Cognition

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Social Communication

► Eye Contact with Adults Versus Babies

Social Communication Disorder

► Social Disabilities

Social Comparison

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Synonyms

[Comparison](#); [Competition](#); [Evaluation](#)

Definition

The evolutionary perspective argues that social comparison facilitated us in assessing our abilities and competition.

Introduction

Comparing oneself with others is central to the social life of humans and it is a particularly complex phenomenon. While engaging in social comparison can lead to positive outcomes, such as increased levels of hope and inspiration (Wood 1989), enhanced subjective well-being (Wills 1981), and a more positive self-view (Collins 2000), it can also result in dissatisfaction (Emmons and Diener 1985) and feelings of deprivation (Crosby 1976; Smith et al. 2012; Callan et al. 2015). Given the mass of information people are exposed to in modern societies, social comparisons occur more spontaneously than ever before. The wealth of social information afforded by technology, the Internet, and most evidently, social media, have amplified the frequency and intensity at which social comparisons occur. This holds important implications for the self-evaluations and well-being of people in modern times.

This entry reviews the social comparison theory from an evolutionary perspective, highlighting *why* humans engage in social comparison despite potentially experiencing negative feelings when comparing themselves to others. In doing so, this entry also demonstrates how social media interacts with our evolved psychology to result in

excessive social comparisons, which in turn brings about the various effects on behaviors and well-being that is observed today.

Theory of Social Comparison

Social comparison theory posits that as humans, we compare ourselves to others as we have an innate desire to evaluate our opinions and abilities (Festinger 1954). In doing so, we derive at various outcomes, including having an accurate self-portrayal (Festinger 1954), aspirations to improve our skills or abilities (Wood 1989), and protecting or enhancing our self-esteem (Wills 1981; Wood 1989; Tesser et al. 2000).

The process of social comparison can be grouped into two broad categories: upward social comparison and downward social comparison. Upward social comparison occurs when we compare ourselves to others who are better than us in certain aspects. Typically, upward comparison provides aspirations and motivations which elicit behaviors aimed at improving oneself to be more like the standard of the comparison target (Wheeler 1966; Thornton and Arrowood 1966; Taylor and Lobel 1989). However, upwards social comparison also brings about lowered self-esteem (Wheeler and Miyake 1992), worsened mood states (Gibbons 1986), feelings of deprivation (Crosby 1976; Smith et al. 2012; Callan et al. 2015), and dissatisfaction (Emmons and Diener 1985).

In contrast, downward social comparison occurs when we compare ourselves to others who are less fortunate or worse-off than us. Downward comparison is usually employed when one seeks to protect or enhance self-esteem as such comparisons result in enhanced mood and more positive evaluations of the self (Wills 1981; Pyszczynski et al. 1985). While there exists different motivational states for each type of social comparison (Brown 1991; Sedikides 1993; Collins 1996), and moderators which would influence the outcomes of each type of social comparison (Collins 1996), such as self-esteem (Wheeler and Miyake 1992), group identity (Major et al. 1993), and closeness of comparison target

(Brewer and Weber 1994), these discussions is not within the scope of this entry. Instead, the focus on this entry centers itself on the evolutionary perspective of the social comparison process.

Social Comparison – An Evolutionary Perspective

Human psychology and behaviors are the products of our evolved psychological mechanisms, which are adaptations that has resulted from successfully overcoming obstacles that threaten survival and reproduction. Both the need to survive and the need to reproduce are adaptive problems, and humans have evolved a range of psychological mechanisms over the course of evolutionary history designed to optimize solutions to these problems. For example, to survive, one would need to form alliances with others and defend against enemies. The operation of psychological mechanisms that function to identify parties to form alliances with results in cooperative behaviors that initiate the forming of an alliance. Similarly, to achieve reproduce success, one would have to acquire reproductively viable mates; psychological mechanisms function to identify and pursue mates with high quality reproductive traits in order to increase reproductive success. Psychological mechanisms engage adaptive behaviors that serve to increase the chances of survival and reproductive success. Social comparison is a psychological mechanism that inhibits or facilitates subsequent behaviors.

From an evolutionary perspective, social comparison served several functions that aided in survival and reproductive success. Comparing oneself with others allowed for humans to determine the social ranking of themselves relative to others (Gilbert and Allan 1994). Individuals who were higher in the social hierarchy make better allies as they tend to have more resources and breeding opportunities than those who were lower in the social hierarchy. As such, when one recognizes themselves to be lower in the social hierarchy, they behave in ways that signal that they are not in an aggressive state of mind and are not seeking any challenge. Such submissive behaviors will not be evident in individuals who identify themselves to be higher in the social

hierarchy, who were more likely to exhibit assertive displays (Gilbert and Allan 1994).

Social comparison also afforded the assessment of competition, which was vital for out-competing others who are after the same pool of resources (Trivers 1985). This judgment of relative probabilities of success decides subsequent behavior and is best evidenced in the mating context.

Social Comparison in Mating

To ensure reproductive success, one must, first, possess traits preferred by the opposite sex, and two, ensure that the traits they possess are better than others who are also competing for the same pool of mates. Social comparison facilitates this process as it allowed one to identify the qualities that are deemed attractive by the opposite sex and recognize one's standing in the mating competition. Men and women evolved to prefer different traits in their mates due to the different adaptive problems they have faced in the ancestral past. As men's reproduction is constrained by the declining fertility of women, men tend to prefer traits that signal high reproductive value in women such as physical attractiveness (Buss 1989) and a low waist-to-hip ratio (Buss and Schmitt 1993). In contrast, women required protection and resources for her and her offspring, and as a result, women evolved to prefer men with social status as this was ancestrally an indicator of physical strength and is related to their ability to provide resources (Buss 1989; Buss and Schmitt 1993). Because these key traits are sort after by other same-sex individuals, knowing one's relative standing in the competition enable them to direct effort to obtain favorable attention (Gilbert et al. 1995), such as improving on the quality of these key traits, should they fall short.

Even though competition for mates is more evident among men as a result of their ability to achieve greater reproductive success with increased mating events (Darwin 1871), women also participate in this competition for mates – especially when there are more women than men (Stone et al. 2007). In current times, social media and its reach of over a million users has induced the social comparison process excessively. Both

men and women now perceive that they are competing for mates against an extremely large pool of competitors. Additionally, dense human populations (Sng et al. 2017) consisting of different ethnic groups (Kanazawa and Li 2015) in modern environments obstruct the effective operation of social comparisons. As a result, maladaptive consequences are now commonly associated with social comparisons.

Social Comparison in the Modern World

Evolutionary Mismatch

The modern environment, characteristically consisting of technological gadgets and cosmopolitan-ness, is quite different from the environment in which our psychological mechanisms have evolved. This results in a mismatch between the modern environment and our evolved psychological mechanisms (Li et al. 2018; Tooby and Cosmides 1990). The consequence of such mismatch is that psychological mechanisms that were adaptive in the ancestral environment are now producing maladaptive outcomes. One of the most commonly cited examples is our preference for sugary and fatty food; where such food provided superior nutrition and calories to humans in the Pleistocene environment where humans have evolved from (Barkow et al. 1992). However, now with most food producers manufacturing foods high in sugar and fat, and our evolved preference for such food type still in operation, this has resulted in obesity (Buss 1995). Such a framework allows us to understand how evolved psychological mechanisms that were once adaptive produce maladaptive outcomes in modern contexts.

Social Media and Modern Societies

Social media, broadly referred to as platforms allowing for the production and sharing of content online including social networking sites and weblogs, is an integral part of everyday life in our modern societies. Social media has afforded us many opportunities for forming new social bonds and maintaining existing ones (Boyd and Ellison 2007; Manago et al. 2012). One

characteristic of social media is that it allows users to create their personal profiles, and thereby, present information about themselves. More often than not, users present themselves in positively on their profiles by including self-promotional and socially desirable contents, such as their accomplishments and possession of consumer goods (Zhao et al. 2008; Mehdizadeh 2010; Rosenberg and Egbert 2011; Nadkarni and Hofmann 2012). Social media users spend a lot of time on social media browsing profiles more so than engaging in interactions with others (Joinson 2008; Pempek et al. 2009). The consequence of such online behaviors typically triggers social comparisons, especially when they view posts and photos of others (Lee 2014). Since most profiles reflect the best aspects of users' lives, most users end up comparing themselves to those who are perceived to be better than them (Chou and Edge 2012; Feinstein et al. 2013).

Upward social comparison leads to positive feelings about the self, but this usually happens when one subjects themselves to it by choice (Nosanchuk and Erickson 1985; Collins 1996). With the massive amount social information users are constantly bombarded with on social media, users would be forced to engage in upward social comparisons. Moreover, with digital and physical enhancements, the competition users face also "possess" traits of levels that are surpassingly high, leading them to perceive that there is hardly a way to out-compete others. Such chronic comparisons have been associated with maladaptive outcomes, including depression (Feinstein et al. 2013), self-esteem declines (Kalpidou et al. 2011; Lee 2014; Vogel et al. 2014; Gonzales and Hancock 2011), negative self-evaluations (Haferkamp and Krämer 2011), and lower levels of well-being (Kross et al. 2013).

Finally, modern societies usually consist of multiethnic individuals (Kanazawa and Li 2015). Living with people of different ethnicity is unheard of in ancestral times – humans lived in ethnically homogenous groups (Oppenheimer 2004). Hence, they are usually perceived as potential threats and the well-being of individuals living in such environments is usually low (Kanazawa and Li 2015; Li and Kanazawa

2016). More importantly, with individuals who look different, speak different, and endorse different values, it complicates how one selects the target of social comparison, which may subsequently lead to an unstable evaluation of the self (Festinger 1954).

Conclusion

We compare ourselves to others in order to derive an accurate evaluation of ourselves, to make ourselves feel better, or to inspire us to become more like those we hold our comparisons too. While these strategies should generally serve to increase our well-being, the society we live in and our copious use of social media has made social comparisons unbearable. Modern environments, with populations consisting of different ethnicities, makes establishing a similar comparison target difficult. Moreover, with an explosion of social information where people tend to portray achievements and possessions that signal a high-quality life, we are subjected to an illusion where we perceive an overwhelming number of competitors that is impossible to out-compete. As a consequence, social comparisons bring about several undesirable outcomes including more negative evaluations of the self and lower levels of self-esteem and well-being.

Cross-References

- [Evolutionary Mismatch](#)
- [Intrasexual Competition](#)
- [Self-Evaluation](#)
- [Social Media](#)

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Social Competence

► Social Skills

Social Complexity Hypothesis

► Social Intelligence Hypothesis, The

Social Conditions

► Social Context

Social Consequences of Initiating Gossip

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Synonyms

Benefits of gossip; Evaluative conversation; Implications of gossip; Negative effects of gossip; Talking about others

Definition

The social implications and effects of initiating evaluative conversation about a third party who is not present for the discussion.

Introduction

Gossip is defined as the sharing of evaluative information, either positive or negative, about others who are not present for the conversation

(Beersma and Van Kleef 2011, 2012; Farley 2011; Foster 2004). Gossip is heavily incorporated in humans' interactions and is estimated to comprise between 65% and 90% of people's everyday conversations (Beersma and Van Kleef 2012). Research has also demonstrated that even 4- and 5-year-old children engage in gossip as a means of learning about their environments (Baumeister et al. 2004). While gossip is often perceived as malicious, condemnable behavior (Beersma and Van Kleef 2012), evolutionary psychological research has demonstrated that there are numerous positive consequences that arise from initiating gossip, such as providing and gathering useful information, protecting a group from self-serving and free-riding behavior, strengthening bonds, and heightening one's social status (Baumeister et al. 2004; Beersma and Van Kleef 2011, 2012; Ben-Ze'ev 1994; Dunbar 2004; Enquist and Leimar 1993; Farley 2011; Foster 2004).

Providing and Gathering Information

Gossip is an efficient and effective way for people to share and receive information about the individuals/situations to which the gossip refers (Beersma and Van Kleef 2012; Ben-Ze'ev 1994; Foster 2004). Providing and gathering knowledge has consistently been identified as a significant reason that people engage in gossip with others (Beersma and Van Kleef 2012; Dunbar 2004). Instigating gossip about others' successes, as well as trials and tribulations, reveals potentially useful information to the receiver of the gossip to help them navigate and understand their environment. It is a powerful means of passing along practical information about the norms and standards of a culture or society that may not be learned otherwise (Baumeister et al. 2004; Ben-Ze'ev 1994). For example, a mother might tell her child a story about someone she knows who began using drugs and ultimately ruined their life in order to convey to her child the potentially lifesaving information that drugs are harmful and should be avoided. In this instance, commencing "gossip" in the form of storytelling about others

serves the purpose of teaching valuable lessons that may not be absorbed as effectively otherwise (Baumeister et al. 2004; Beersma and Van Kleef 2012).

Group Protection

Gossiping with others allows one to caution group members against those who deviate from group norms (“norm violators”) or take advantage of a group. When working in groups, it is common for some members to not contribute to the work but still receive the benefits – this is commonly referred to as “free-riding,” as such individuals share the success/benefits of the group work without actually assisting (Beersma and Van Kleef 2012). Gossip serves an important evolutionary function in protecting against such norm-violating behavior (Beersma and Van Kleef 2012; Enquist and Leimar 1993). Researchers Beersma and Van Kleef (2011) found that when participants in a study were told that the other group members would gossip about their participation, they contributed more to the group, consequently decreasing their free-riding and self-serving behavior. In this instance, initiating gossip functions to protect a group against those who wish to take advantage by enforcing the group’s norms and expectations and subsequently decreasing self-serving behaviors by members of the group (Beersma and Van Kleef 2011, 2012).

Strengthening Bonds

Initiating gossip can allow one to strengthen their relationship with the person whom they gossip (Foster 2004). Gossiping together allows the individuals participating to spend time together in the conversation, serving as a mechanism for social bonding (Baumeister et al. 2004; Dunbar 2004). Initiating gossip “communicates alliances, increases the intimacy of social bonds, and delineates the distinctions between the in-group and out-group” (Farley 2011). Furthermore, one who initiates gossip shares information that could be

useful or pertinent to the receiver, strengthening their social bond (Baumeister et al. 2004; Dunbar 2004).

Social Status

Gossip has the potential to increase or decrease one’s social status (Baumeister et al. 2004; Farley 2011). Research has found that those who instigate gossip may be seen as having an elevated social status because they are demonstrating that they comprehend social rules or regulations that may be unknown to or not understood by the receiver of the gossip. In other words, the individual who shares the gossip is perceived as having knowledge or understanding that is not possessed by the receiving party (Baumeister et al. 2004; Foster 2004). Furthermore, the instigator of gossip is perceived as having more social influence by being aware of their environment and changes within it and consequently sharing this information with others (Dunbar 2004; Farley 2011). However, engaging in too much gossip, or gossip that is negative about the target, can have undesirable effects. Farley (2011) found that people who engage in gossip frequently are perceived as less powerful and likeable compared to individuals who do not gossip as frequently. The same findings were true of those who gossip about others in a negative sense compared to in a positive regard (i.e., critiquing someone’s appearance versus complimenting it). Thus, this study revealed that individuals who engaged in high-frequency, negative gossip were perceived as being the least socially powerful and likeable compared to other types of gossipers (i.e., low-frequency, positive gossipers) (Farley 2011).

Gossip also has the potential to influence the social status of the target of such gossip. One who instigates gossip has the power to manipulate the target’s reputation by spreading information about that person. The gossipier has the potential to paint an influential, negative picture of the target, which can potentially induce social exclusion, a highly undesirable consequence for the target of the gossip (Beersma and Van Kleef 2011).

Conclusion

Research has demonstrated that gossip can have a number of positive, beneficial social consequences, such as a means of providing and gathering information about others, defending against self-serving behaviors within groups, fortifying relationships between individuals, increasing one's social status, or even decreasing the social status of someone else. However, too much gossip with a negative connotation can ultimately lead one to be portrayed as unlikeable and unpowerful. Initiating gossip can have undeniably advantageous consequences when one is mindful of the type of gossip they engage in and how often they do so.

Cross-References

- [Alliances](#)
- [Evolutionary Social Psychology](#)
- [Gossip and Indirect Reciprocity](#)

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Social Constructionism

- [Blank Slate, The](#)
- [Standard Social Science Model](#)

Social Context

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Synonyms

[Environment](#); [Social conditions](#); [Social/contextual factors](#)

Definitions

Social contexts, Microsystem, Mesosystem, Exosystem, Macrosystem, and Chronosystem.

Introduction

According to the APA (2018), social context refers to the situational circumstances or conditions that exist in the social environment of individuals. These circumstances, directly or indirectly, influence individuals' developmental outcomes, behaviors, thoughts, and feelings, as individuals spend an incredible amount of time, energy, and effort in interacting with the elements of social contexts (Bronfenbrenner 2009). These interactions can be both passive and active

(reciprocal) and the influences of the elements can be both direct and indirect, thereby making social context a dynamic environment.

Bronfenbrenner (2009) highlighted and expanded on the role of the social environment in his PPCT model of Bio-Ecological Theory. He suggested that the five systems, namely, *micro, meso, exo, macro, and chrono*, along with their elements, make up the environment (aka social context) of an individual. Bidirectional interactions and exchanges within and between systems and elements are known as *proximal processes*, and these *processes* contribute to the dynamic aspects of the environment. For example, the social context of a child “A” raised in a high SES with access to quality resources in a two-parent family is in contrast with a child “B” who is raised in a low SES, by a single-parent family and lives in a risky neighborhood. These proximal processes in *microsystem* and rippling effect of the outer systems such as strenuous work environment of the parent, lack of medical facilities, and resources in the community along with marginalizing and discriminatory practices based on race, class, sex, and gender can negatively influence the developmental trajectory of child “B.”

Although, understanding social contexts assists in predicting individual or group outcomes; the role of social context is not limited to precise conceptualization and examination of the developmental outcomes. In fact, a thorough examination of the social context guides the construction of best practices for research and interventions. Given below is a brief description of the implications of social context for individual outcomes, research practices, and interventions.

Implications for developmental outcomes.

Social/contextual factors, along with biological factors, dictate the cumulative effects on the momentum and direction of the developmental outcomes of an individual. Schriber and Guyer (2015) applied neurobiological susceptibility models to provide a rationale for the differential outcomes of interventions among adolescents. The researcher suggested that certain biological factors in the brain confer higher susceptibility to environmental influences, forging these

adolescents to be more responsive to interventions than their age mates. In addition to greater susceptibility to environmental influences, adolescents who experience warm and supportive environments have more significant gains in comparison to those who are neither context-sensitive and nor have a positive environment around them. Notably, the authors emphasized the role of sensitive periods and concluded that interdisciplinary lens is crucial to draw accurate conclusions regarding the effects of social context on developmental outcomes.

Implications for research and interventions.

Social context not only helps in understanding the complexity of the social issue in terms of the gravity of the situation, but it also identifies and clarifies the role of related moderators and mediators that must be accounted for while analyzing data and deciding appropriate levels for prevention and intervention programs (Glisson and Schoenwald 2005). To illustrate, Alegria et al. (2019) conducted longitudinal research to study the impact of having a “minority status” on mental health outcomes of 1863 Puerto Rican and South Bronx youth. Overall, the research team concluded that higher perceptions of minority status are related to higher manifestations of anxiety and depressive disorders. However, mental outcomes were moderated by positive social relationships, and mental health outcomes were mediated by social stress related to discrimination, more so among South Bronx youth than Puerto Rican youth.

Based on the above-stated findings, most investigators would suggest interventions at the individual level for South Bronx youth; but Alegria et al. (2019) recommended interventions at the community level as in the presence of substantial community-level risk factors; individual-level support systems may eventually become ineffective. In comparison to Puerto Rican, South Bronx youth was characterized by a substantially higher number of single-parent families, violence, and perceptions of discrimination and unfair treatment. The South Bronx youth also reported a weaker ethnic identity and poor relationships with family and peers. Therefore, investigation of the social context of different outcomes and its interpretation in the light of research

findings are warranted. Only after assessing all the main, moderating, and mediating effects of social context, accurate conclusions for research findings and program components can be drawn (Glisson and Schoenwald 2005).

Social context also offers insights into the long-term impacts of prevention and intervention programs. To elaborate, Miklikowska et al. (2019) refuted the previous studies that suggested parent-based interventions to diminish prejudice against immigrants in Sweden. Previous findings were based on moderate-positive correlations between adolescents' and parents' prejudicial attitudes. Miklikowska et al., after investigating the social context of Swedish youth, suggested that even though pro-immigrant environment at home may diminish prejudicial attitudes among youth, yet the effects of the intervention will not be long-term without integrating peers' prejudicial attitudes in the equation. Positive contact with ethnically diverse peers may not only lower prejudice but may also cancel out the negative impact of anti-immigrant messages from parents.

Conclusion

To conclude, social contexts play a vital role in determining life course trajectories (Stokes 2018), and therefore the integration of social context in research and practice is warranted to understand human motivations that direct them to a specific direction or make them more amenable to change.

Cross-References

- [Social Development](#)
- [Social Roles](#)

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Social Contract Rule Violation

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Synonyms

[Cheater detection](#); [Social reasoning](#)

Definition

When an individual in a social exchange with another “cheats,” by taking a benefit without incurring a cost and/or returning the favor to another.

Introduction

One of the founding principles of Evolutionary Psychology is that the human mind consists

of domain-specific modules that have been shaped by evolution. This modular view of the mind suggests that our ancestors were able to use these modules to help solve specific problems they encountered in their environment. Possibly the most well-known example of such a module is one dedicated to reasoning about social contracts (Cosmides 1989; Cosmides and Tooby 1992). In such contracts, there will be a rule about how an individual is expected to behave (e.g., “if you take a benefit from another individual, then you must return the favor in some form”), and when entering such an exchange each individual is aware of this. According to Cosmides and Tooby (1992), individuals who violate such rules (i.e., “cheats” who take a benefit without incurring a cost or returning the favor) need to be avoided as partners in social contracts, as they will be exploitative and costly with no benefit. Therefore, a “cheater detection” module has evolved in humans which makes us very good at detecting and remembering individuals who cheat in social contracts.

Cosmides and Tooby (1992) provide evidence of this heightened ability to detect cheats in social contracts using the Wason Card Selection Task (Wason 1966). In the standard format of this game, individuals are presented with four cards lying down and are told that each card has a number on one side and a letter on the other. An example of the four cards can be seen in Fig. 1.

Individuals are then asked which cards they would need to turn over to see if the following rule is correct: “If there is an even number on one side, then there is a vowel on the other.” In this abstract version of the task, few people choose the correct options (the “4” and the “D” card), in fact only about 25% get it right.

However, this changes when the original abstract version of the task is replaced by one that features a social contract (Cosmides and Tooby 1992). For example, in the following version individuals were again presented with four cards but were now told that each card has a drink on one side and a person’s age on the other. An example of this social contract version of the task can be seen in Fig. 2.



Social Contract Rule Violation, Fig. 1 The abstract version of the Wason Selection task



Social Contract Rule Violation, Fig. 2 A social contract version of the Wason selection task

Individuals were told to imagine they were working in a bar and had to ensure that the following social contract was upheld: “If a person is drinking alcohol, then they must be twenty-one years old or older.” Compared to the abstract version of the task, a majority of people (approximately 90%) answered correctly (the “Beer” and the “18” card). So why such a difference in accuracy, if the underlying reasoning logic for the two tasks were the same? Cosmides and Tooby (1992) suggest that as the latter version involved a social contract, it activated individuals’ “cheater detection” module, meaning they were better able to spot cheaters here. In other words, drinking alcohol can be considered a social contract, where individuals must incur a cost (i.e., being twenty-one or older) in order to gain a benefit (i.e., drinking alcohol). Therefore, we are better able to identify violations of this rule, which is someone taking the benefit (drinking beer) without incurring the costs (being aged 18), and select those cards accordingly more readily.

Further evidence of the existence of heightened ability to detect social contract rule violation comes when novel or unusual social contracts are used. For example, Cosmides and Tooby (1992) also presented individuals with a similar card task but with a different social contract rule for them to check; “if you get married, you must have a tattoo on your forehead.” Even though this was novel for individuals (compared to the drinking alcohol/age

rule), accuracy here was still very high (approximately 75% picked the correct cards). Also, when tested cross culturally, it has been found that performance is similar, which suggests that an ability to detect social rule violators is universal. For example, Sugiyama et al. (2002) found that among the Shiwiar tribe in Ecuador, performance on the social contract versions of the selection (86% selected the correct cards) was very similar to that of the original US sample. This evidence highlights that it is not familiarity with a social contract rule that causes heightened detection of social rule violators but an underlying evolved ability humans have to recognize a social contract whether it is familiar or novel that allows us to detect cheats quickly and accurately.

Evidence also exists that reasoning relating to social contract rule violation is separate to that of similar cognitive abilities. For example, Stone et al. (2002) found that patients with brain damage performed normally on abstract versions of the Wason Selection task, but poorly on versions that involved social contracts. Also, due to the high costs involved in social contracts, the role of emotions in reasoning about social contracts has been shown to be important (Reis et al. 2007) and violations of social contracts elicit anger as the predominant emotion (Fiddick 2004). Finally, recent evidence exploring personality traits as predictors of social contract reasoning has shown that conscientiousness (and to a lesser extent trust) correlates with social contract reasoning abilities (Brase et al. 2019), further showing how human reasoning is affected by social contexts.

Conclusion

By showing that humans would have faced the problem of who to trust in social exchanges, and that we have evolved an ability to understand these social rules, researchers such as Cosmides and Tooby have shown how our cognition can be tuned to certain topics. These topics were relevant in our evolution, and our better reasoning with these than with more abstract topics suggests our minds are built for specific, not general problem-solving.

Cross-References

- [Cheater Detection](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)
- [Memory Enhanced for Cheaters Versus Non-cheaters](#)
- [Wason \(1966\) Selection Task](#)

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Social Cooperation

- [Recall of Cheaters](#)

Social Cues

- [Altruism and Watching Eyes](#)

Social Customs

- [Social Values](#)

Social Darwinism

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Synonyms

[Social evolution](#); [Survival of the fittest](#)

Definition

The application of Darwinian biology and evolutionary principles to human social theory.

Introduction

In the broadest sense, the term *social Darwinism* has been used to refer to any effort made toward applying concepts from Darwin's theory of evolution by natural selection to social theory, political systems, economics, and other domains of human social life (Dickens 2000). However, social Darwinism is likely best known for its infamous association with early twentieth century political ideologies targeted at "improving the human race." Darwin's ideas were used to justify eugenics (Nourse 2016), race war (Barondess 1998), imperialism (Leonard 2009), and a variety of economic political ideologies (Hawkins 1997). However, these ideas were often based on misinterpretations of Darwin's original ideas and the

process of natural selection. Some have argued that early academics who have since become associated with nefarious applications of social Darwinism (e.g., Herbert Spencer, William Graham Sumner, Richard Hofstadter) were often misinterpreted or misrepresented (Hodgson 2004; Leonard 2009). Moreover, earlier work did not incorporate many contemporary discoveries within evolutionary biology that have since replaced some of Darwin's original ideas (e.g., Fodor and Piatelli-Palmarini 2011).

Natural Selection

Perhaps one of the most widely misinterpreted concepts within the theory of evolution was the phrase "survival of the fittest." The lay understanding of this phrase (i.e., "the strongest individuals survive") has been the mantra for social and political policies aimed at favoring one group of individuals over another (e.g., Barondess 1998). However, this understanding of the phrase is inaccurate. In evolutionary biology, "survival of the fittest" is a catchy and succinct way of describing one of the central processes of evolution: natural selection. Natural selection occurs when variation in a heritable trait (e.g., intelligence) leads to differential reproduction within a population of individuals. For example, individuals who were relatively more intelligent may have been better at adapting to new situations, inventing creative solutions to novel problems, and attracting potential mates. Therefore, more intelligent individuals would have experienced greater reproductive success compared to less intelligent individuals. Over several generations, if intelligence consistently conferred this reproductive advantage, intelligent individuals would have begun to outnumber relatively less intelligent individuals in the population. In this example, the process of natural selection thereby leads to the survival (i.e., consistent and continued reproductive success) of the fittest (i.e., individuals who possess a trait which confers a reproductive advantage over competitors). Therefore, "fittest" does not necessarily equate to "strongest." In fact, some adaptations for physical strength could be

detrimental to an organism's reproductive success if, for example, diverting somatic resources to muscle development were to become an inefficient use of the body's resources.

Relatedly, there are no traits that are inherently better than other traits. A common justification for the use of eugenics (Nourse 2016) was that the human race could be improved by artificially selecting traits which were believed to be genetically superior (e.g., blonde hair and blue eyes). However, this presumes knowledge of which traits will confer a reproductive advantage. A trait only benefits an individual's reproductive success insofar as it helps the organism adapt to current environmental conditions. Returning to the example of strength, within environments where same-sex competition between males is intense, physical prowess may increase competitive success and thereby reproductive success. Likewise, physical strength might allow individuals to manipulate large objects or protect kin, friends, and mates. In this sense, one could argue that physical prowess should be artificially selected for inclusion in future human populations. However, having less physical strength may also increase reproductive success within particular environments. Greater physical strength typically entails more muscle mass and therefore greater body size, which may slow an individual down or make an organism conspicuous and more likely to be preyed upon. Genes coding for greater physical strength may also inadvertently affect the expression of other traits, such as circulating levels of testosterone and behavioral aggression. In this way, something that is typically seen as "better" (i.e., strength) may actually contribute negatively to an organism's overall fitness within a particular environment. This is only one example, but the basic logic may be applied to a variety of potential traits. Those who applied this logic to social and political theory were not concerned with reproductive success, *per se*, as much as with optimizing various aspects of human social, political, and economic systems (Dickens 2000; Hawkins 1997). However, applying evolutionary logic in this way is similarly flawed in these contexts. People, and social systems, are the products of multiple intersecting processes and traits.

Altering or favoring one trait (e.g., physical strength) without conscientious consideration of this change's impact on related attributes and processes (e.g., behavioral aggression) could have unintended consequences.

Contemporary Social Darwinism

Any version of social Darwinism which has had its origins in these flawed understandings of Darwinian and evolutionary logic has no credibility in current evolutionary science. Yet, some modern social and evolutionary theorists still discuss (and debate) how evolutionary principles might be applied to the study of human social systems (e.g., Dickens 2000; Hodgson and Knudsen 2010; Schubert 2012). This debate includes whether social evolution (i.e., memetic descent and modification) more closely resembles Lamarckian or Darwinian evolution (Hodgson 2001), whether welfare economics may be reformed using evolutionary principles (Schubert 2009), and how an understanding of psychological adaptations can inform various facets of human morality and politics (see Shackelford and Hansen 2016). Unlike its predecessors, contemporary social Darwinism adopts a more nuanced and morally conscientious approach to integrating human social behavior and evolution. Indeed, although social Darwinism has acquired a stigma within many intellectual circles, an understanding of how evolution has shaped human psychology will provide clues about how to optimize the various social, political, and economic systems that have emerged from that psychology.

Cross-References

- ▶ [Dangers of Evolutionary Ethics](#)
- ▶ [Mismatch Between Evolved Morality and Modern World](#)
- ▶ [Moral Concerns](#)
- ▶ [Racism and Prejudice](#)
- ▶ [Science and Morality](#)

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Social Development

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Synonyms

Enculturation; Social habit development; Socialization; Unfolding; Upbringing

Definition

Children develop their sociality according to propensities for cooperation and from their family and community experiences. In precivilized societies, social development occurs naturally as children learn the ways of the community through informal apprenticeship. In civilized societies, social development often involves “socialization,” as adults coercively teach children how to behave.

Introduction

We can contrast two basic forms of societies: civilized and pre- or un-civilized. Civilization has been around for about 10,000 years (about 1% of human genus history). Civilized societies are those that domesticate and control the lives of animals and plants to their own benefit, hoarding resources and constructing hierarchies to keep the social system of controlling resources in place. Civilized nations have been successful technologically but destructive of earth life and biocultural systems as they expand to eliminate and cultivate more and more wilderness areas and land governed by others. They must also ensure their populations conform to the system. Thus, socialization and social development has this as a primary aim.

On the other hand, humanity spent about 95% of its history outside of civilization (Fry 2006). “Uncivilized” societies have continued alongside the civilized to the present day (Lee and Devore 1968). “Uncivilized” groups will be termed “primal” groups here because the social structure is ancient, and they are more in tune with ecological systems, upon whom they traditionally directly rely. The data accessed are mostly from small-band hunter-gatherer bands or nomadic foragers who are immediate-return societies (migratory, with few possessions, no cultivation of plants, no domestication of animals; Woodburn 1982). Because they migrate in particular landscapes according to the availability of food sources like other migratory animals do, primal societies are

careful not to over harvest plants or animals so that these will be available on their next visit to the locale. Social development takes a natural course in these societies, unfolding as the maturational schedule of the child dictates in relation to the pressures of living in the local landscape. The goal is to become a full human being who lives well and responsibly under the local conditions.

In this entry, distinctions are made between the societies that socialize for civilization and those that do not. The two approaches to social development are contrasted in the sections below.

Humanity's Inheritances

Although genes are often the focus of human inheritances, humanity inherits much more, including for example, landscape ecology, cultural practices, maternal microecology, and capacities for self-organization (Kauffman 1993; Oyama et al. 2001). Humans also inherit greater epigenetic plasticity, especially in early life, than other apes (Gómez-Robles et al. 2015).

As all animals do, humans have a nest that evolved to optimize the development of the young. The nest represents “the reliable and repeatable features of stimulation and experience occurring in an organism’s developmental context” (Lickliter and Harshaw 2010, p. 497), a species-typical developmental system that leads to a species-typical outcome. For humans, who are part of the social mammalian line, the early life nest is provided by the mother and her community and includes soothing perinatal experience; nearly constant touch in the first year and extensive affectionate touch thereafter; on request breastfeeding for several years; warm responsiveness to needs from mother and then by a small community of caregivers; self-directed play in the natural world with multi-aged playmates; and positive social support with no physical punishment (Hewlett and Lamb 2005).

Why does the nest matter? At full-term birth (40–42 weeks of gestation), a human baby emerges with only 25% of adult brain volume, which grows especially rapidly in the first year with 90% in place by age five (Trevathan 2011). In fact, newborns look and act like fetuses of other

animals till about 18 months of age. Thus, many physiological and social systems are shaping themselves during the sensitive prenatal and postnatal periods, including the stress response, endocrine systems, neurotransmitters, immune system, and capacities for social engagement (Narvaez et al. 2013b). How well these develop is influenced by the quality of the nest.

In primal societies, the evolved nest is provided without resistance or question – adults cooperate with the needs of the child. A community of responsive caregivers provide what babies and young children need, even sharing breastfeeding (Hrdy 2009). Primal societies display a deep trust in natural processes (Ingold 2005). By providing the evolved nest, they ensure human propensities for cooperation are developed, a leading source for successful evolution (Weiss and Buchanan 2009), especially human evolution (Tomasello et al. 2012).

Civilized societies do not provide the evolved nest, and if a component is provided it is usually partial or degraded. For example, breastfeeding might occur but only for a short duration (less than a year) rather than for an average age weaning of 4 years as found among small-band hunter-gatherers (Hewlett and Lamb 2005). Instead of providing what babies evolved to need, civilized societies display a deep *distrust* in natural processes related to nest components and child raising. Civilized nations tend to work against natural processes instead of with them. The costs to social development are deep and wide, from poor health to poor sociality and the reliance on evolutionarily more primitive brain systems to survive (Narvaez 2014).

Social Development in Primal Societies

How does a child learn to be a human being? Primal societies know it takes some time. In primal societies, children are assumed to be autonomous agents who are learning to be fully human within the community and can take charge of their own learning (for review, see Narvaez 2013). Children follow evolved innate programs that guide them in learning to live within their society, mimicking models, and practicing what they are

motivated to practice at the particular age – as babies, apart from feeding and sleeping, primarily social feeling and social routines for how to start and carry on conversations, share eye gaze and play. Initially, self-regulation and sociality are guided by foundational interactions with adults and other caregivers, shaping physiological systems. For example, responsive care (meeting the needs of the baby in a timely, warm manner) fosters a well-functioning stress response (one that is not easily triggered nor mute from excessive distress) and a well-functioning social engagement system of the vagus nerve (Lupien et al. 2009; Porges 2011, 2017).

Adults provide support without interfering in the unfolding development of the young child. Primal societies avoid coercion at any age, understanding that it can undermine the normal trajectory of development, undermining self-confidence and increasing dependence on others for self-direction. Coercion or punishments are avoided as they can do damage to the developing spirit of a child. Throughout childhood, children learn without schooling, a “natural pedagogy” where younger imitate older and older guide younger and the skilled guide the unskilled through apprenticeship (Rogoff 1990).

Becoming a good human being is the goal among primal societies (Narvaez 2013). What does that look like? Adults are expected to cooperate in all sorts of ways (Hill et al. 2011). For example, they share food and resources without resistance, act with others in mind, enjoy socializing virtually all the time, not coerce others but be highly autonomous; in fact, SBHG adults around the world, no matter their culture, are typically described as independent but also communal, calm, and content but also generous (Ingold 2005). The evolved nest may provide a “cultural commons” for the development of these shared personality characteristics, and sociomoral capacities for relational attunement and communal imagination (Narvaez 2014, 2018). Other social practices are common in these societies. For example, when an individual starts to get a big head (e.g., a successful hunter), the group teases him relentlessly (e.g., “it’s such a tiny animal, we should go find a rabbit instead”) until he bursts into laughter and the puffed-up ego is deflated (Lee 1979).

Optimal social development is expected for individuals in primal societies and their survival may have depended upon it. But fitting well into the human society is not enough to be a good human being. It is expected that grown individuals will act with the biocommunity in mind, the place on the earth in which one’s lifecourse is embedded, and include respect for the wellbeing of entities in the natural world. One must maintain proper relations with all entities (e.g., animals, plants, rivers) in an ongoing dynamic manner, that is, being present and responsive to what is unfolding in the human and other-than-human lifeworlds (Ingold 2005, 2011). Interestingly, the capacity to receptively attend to the living world – its sentience, communications, and relationships – is initially governed by right-brain hemisphere capacities, which develop rapidly in early life, when the evolved nest is especially influential.

Primal societies, including native American tribes, display a companionship orientation to raising children and living on the earth (Narvaez 2014), a place considered sacred and moral (Redfield 1953). Because an individual’s actions are impactful on the wellbeing of the whole biocommunity, they must be taken with respect and awareness. Elders typically display social engagement, wisdom, and communal morality and guide social development of the community through story and ritual (Deloria 2006).

In summary, primal societies provide a species-typical developmental system for raising the young. Even beyond the evolved nest for early childhood, they provide a continuum of support throughout life, including the transition to adulthood and maintaining connection to the cosmos through ritual and trance. It is rare for a child not to develop into full humanity.

Social Development in Civilized Societies

In civilized nations, socialization is often discussed as “the processes whereby naïve individuals are taught the skills, behavior patterns, values, and motivations needed for competent functioning in the culture” (Maccoby 2015, p. 3). Notice the focus on adults “teaching” and

controlling children. It is assumed that children must be pressured into fitting in. This typically involves coercion of some kind (corporal or psychological punishment). Punishment may be needed to overcome the natural egalitarianism and expectation for companionship and respect young children display (Fehr et al. 2008; Trevarthen 2005), making them feel more insecure and more prone to comply with adult directives.

Child raising advice for centuries has advocated harsh treatment in early life, treatment that breaks the spirit of children in order to control them for life (because the early years of experience won't be consciously remembered later; Miller 1983). Civilization has a long history of harsh treatment. Lloyd deMause (1974) described six historical phases reflecting changing parent attitudes towards children, moving from *infanticide* (antiquity to fourth century AD) to emotional or physical *abandonment* (fourth to thirteenth century) to *ambivalence* (fourteenth to seventeenth centuries) where children were beaten into shape, followed by *intrusive* parenting (nineteenth century), when empathy emerged, but there was still a focus on controlling the child in every way, *socialization* (nineteenth to twentieth centuries) to channel impulses – as proposed by psychodynamic theorists who emphasized the control of innate aggressive and sexual impulses, later morphing to a focus on self-regulation – indeed, radical behaviorism emphasized the conditioning of good habits from an early age, like baby independence, because as young adults it would be required (Watson 1928). Finally, deMause identified a *helping* orientation (mid-twentieth century till present) where parents became involved in empathizing with and fulfilling child needs.

Still today, parental control and obedience are dominant goals for young child raising in civilized societies. Note the popular theory of parenting styles proposed by Diana Baumrind (1967), who favors parental control. She distinguished four basic styles: authoritarian (high demandingness, low responsiveness), authoritative (high demandingness, high responsiveness), permissive (low demandingness, high responsiveness), and uninvolved (low demandingness, low responsiveness). Among individualistic societies like the

USA, the authoritative style leads to greater child success as measured by the middle-class values of society (i.e., school achievement, work success) (Baumrind 1971a). However, a subset of families did not fit Baumrind's model (Baumrind 1971b). She called them "harmonious" parents. They were only moderately demanding, highly responsive but also highly tolerant. She noted that preschool girls thrived but that preschool boys seemed feminized in those families (i.e., submissive rather than rebellious). This mode and outcomes are more aligned with primal society.

What does social development look like in a civilized society? There is a great deal of variability in specifics, but gender roles tend to be more rigid than in primal societies; there are often class and racial differences, made explicit, or enforced implicitly; and if a person does not stay within the correct pathway, the individual can be ridiculed or even ostracized and killed (Turiel 2002). So, obedience to prescribed ways of being is a primary aim, wanting for self what society wants for the self and learning to avoid stepping out of bounds. In individualistic, consumerist societies like the USA, the goal for a middle-class child is success in school where entrepreneurial, rebellious, and creative skills (within the confines of the worldview) are encouraged. These lead to a good-paying, high-status job within the system. In contrast, often lower-class children are socialized through the hidden curriculum to follow rules and authority, skills for low-grade factory or service work (Freire 1970; Kozol 1991; Jackson 1968).

Traditional pedagogy holds the view that reasoning and explicit conscious knowledge guide behavior and so adults directly teaching rules of moral behavior is considered an effective way to socialize a child (Dewey 1908). This view of learning has led to all sorts of difficulties, such as incongruence between explicit knowledge about the right way to behave and actual behavior. If the child disobeys the rules, it is considered the child's fault. In reality, children learn from immersed experience – they initially construct their patterns of behavior from the sensorimotor routines that work in their family contexts, using these implicit notions to guide their lives (Varela

1999). Children especially learn from how they are treated, imitating what adults do, not so much what adults might say otherwise to do.

In the late twentieth century, rather than focusing on the development of moral reasoning (Kohlberg 1969), psychology researchers began to focus on the development of prosocial emotions (e.g., empathy) and helping behavior as central to social development (Eisenberg 2000). The social capacities needed include not only self-control (not aggressing against others, not withdrawing) and complying with rules, but sufficient empathy with and sympathy for others and skilled cooperation (flexible getting along). But the trends for the USA as a whole on these characteristics have been going in a downward direction for perhaps 50 years. Many children and adults have difficulty with self-regulation, display low empathy, and lack responsive social skills (Narvaez 2017). Early life stress fosters self-disorganization and physiological systems that are threat reactive, leading to habitual externalizing (aggression toward others) and/or internalizing (depression and withdrawal) (Shonkoff et al. 2012). Children raised outside the evolved nest necessarily represent species atypical development. Many do not reach their potential but are dominated in their sociality by more primitive survival systems.

As a result, psychological science has been examining possible sources of failure and success to socialize children to be cooperative and contributing adult members of civilized society. Interestingly, components of the evolved nest are factors that foster success. The most widely studied is caregiver responsiveness (Maccoby and Martin 1983). Neuroscientific studies are supporting the emphasis on early life relational attunement with caregivers and the development of secure bonding and attachment (Schore 2000). A child treated with reciprocal mutual respect, empathy, and cooperation develops those same characteristics over the long term, including identifying as a moral self (Kochanska 2002; Thompson 2012). When the social ecological contexts coordinate relational support for a child, resilience (avoiding risky behaviors) and thriving are more likely (Bronfenbrenner 1979; Lerner et al. 2003; Scales and Leffert 1999). Other components of the evolved nest also appear to shape

empathy, conscience, and cooperation (Narvaez et al. 2013a, c).

It should be noted that basic aspects of social development like self-control and social interest are impaired by nonsocial factors that occur in developmental contexts, like pollutants (e.g., lead, mercury, plastic), which are released into mother's bodies and children's environments by civilization's practices (e.g., Liu and Lewis 2014).

Optimal social development in civilized societies is contested. Some societies value autonomy, whereas others emphasize community values or respect for a divine order (Jensen 2011). Moreover, as societies have undermined provision of the evolved nest and pathologies have multiplied, there is no agreement on baselines for raising children. If there is interest in the question of baselines for raising young children in advanced societies, there is little agreement on what optimal development looks like. Part of the reason is that science has taken over knowledge systems to such an extent that people feel they cannot "know" something without an experiment to show it. At the same time, science typically prides itself on being value-neutral and does not wish to weigh in on value questions like parenting. Nevertheless, advanced nations are often under the thumb of science-wedded-with-technology which values detachment and machine-treatment of human beings and control of human life by technology (Mumford 1967; Postman 1993), despite the fact that scientific theories have moved to dynamic interactionism (Kauffman 2016). Civilization's system of controls requires conformist human natures and not the free spirits of normal, species-typical human beings (Fromm 1964). As a result of confusion about raising children and the nature of human nature, Westernized societies are looked at askance by traditional societies (Sahlins 2008).

Differences Between Civilized and Primal Societies

There are several key differences between primal and civilized nations that play a role in social development. In civilized societies where childhood experiences vary widely, there is frequent discussion of "nature" versus "nurture" in

determining child outcomes. Of course, this is a false dichotomy for a dynamic system that is a human being, whose self is biosocially constructed (biology is co-constructed by social experience, and social capacities are shaped by that biology; Ingold 2013). In contrast, in primal societies the evolved nest is provided universally to young children. The focus of development is on empowering the child's unique spirit. The basic assumption is that, with proper support, every child will be a cooperative member of society.

Whereas in primal societies, the village raises the children, in civilized nations the initial task and responsibilities reside most often with parents alone (and even with a single parent), at least until schooling. Parents are often isolated, highly stressed and even depressed in individualistic societies, unless government programs build in different types of support (e.g., parental leave after birth, nurse visits, government-subsidized daycare) (Lally 2012). Because parental responsiveness is fundamental to good child outcomes, the lack of support means that children are unlikely to develop their full human potential.

As a result of early life stress, the Westernized world has undermined the development of the right hemisphere, which is scheduled to develop rapidly in the first years (Schore 1994). Lack of appropriate care leads to the underdevelopment of right-hemisphere-directed self-regulatory, social and receptive capacities, which are difficult to repair later. The undermining of right hemisphere development may be cause and consequence of the Western world's capture by left-hemisphere thinking, shaping society to be the detached-from-nature culture it has become (McGilchrist 2009), guided by a worldview that life and the cosmos generally are amoral, disenchanted, and fragmented (rather than moral, sacred, and unified (Four Arrows 2016; Redfield 1953).

In primal societies traditionally, the group focuses on living well in that place on the earth, and it is the elders who have lived experience to guide the community in living well and sustainably in the particular landscape. In civilized nations, rapid technological change means that parents and children are often focused on adopting and managing the latest technologies, and the

children do that better, reversing the roles of who learns from whom. Perhaps as a result of missing elder wisdom, civilization has shifted to values of technological efficiency over human values (Postman 1993). Civilization spends a great deal of energy focusing on preventing immediate bad outcomes for privileged humans, using coercion to enforce norms of hierarchy and obedience to the system, at the expense of biocultural diversity (Christen et al. 2017).

Most research on child social development is done in civilized societies or at least with their constructs about what is important. Baseline assumptions about human nature and about children guide research paradigms and interpretations. Cultures that believe humans are basically evil will think it is necessary to use coercive techniques in parenting and socialization. If you assume humans are naturally selfish and aggressive, then parental control will be considered vital for social development properly carried out, necessary for self control over natural impulses. In contrast, if you think humans are basically good, then you would be more likely to let development occur without too much interference, as in primal societies (Rousseau 1979.) Assuming that humans naturally grow into cooperative community members, you expect cooperation to emerge over the course of development given proper support. When social development goes awry, the explanation will be different depending on the baseline assumptions one has about human propensities. In the first case, not enough force (reinforcement, punishment) was used by adults to shape the child. In the second case, not enough support was provided to allow the natural course of development to take place or trauma was experienced that led the child's development astray.

As noted, over the course of civilization, adult treatment of children has shifted (deMause 1974). Researchers too have shifted in their assumptions, moving increasingly toward the view that children are naturally cooperative with proper support, and that lack of support or trauma can undermine normal social development. The sciences generally are moving to the view that humans, like all living things, self organize around experience (Kauffman 2016). If early experience guides the shaping of

physiological systems and social capacities, social support including the evolved nest, may be necessary for social development as a human being.

Cross-References

- [Alloparenting](#)
- [Attachment Theory](#)
- [Breastfeeding Benefits](#)
- [Co-sleeping](#)
- [Hunter-Gatherer Societies](#)
- [Socialization Processes](#)

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Social Development in Nonhuman Primates

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Synonyms

Growth; Maturation; Primates

Definition

Changes in the social behavior of nonhuman primates from birth to adulthood.

Introduction

Research with nonhuman primates can provide valuable insights into two main aspects of child development: normative development and interindividual variation. These insights can be mainly theoretical, empirical, or both.

Normative Development

Nonhuman primate research can potentially inform many different theoretical and empirical aspects of normative child development, including socio-behavioral development, cognitive

development, communicative development, emotional development, and physiological development as well as various normative aspects of parent-child relationships including attachment, parent-child conflict, and others. Historically, the main contributions of nonhuman primate research to our understanding of normative child development have been in the context of parent-child relationships. Specifically, nonhuman primate research played a pivotal role in John Bowlby's formulation of attachment theory (Bowlby 1969).

Bowlby derived from ethology the notion that a comprehensive theory of attachment should account for this phenomenon at different levels of behavioral analysis: causation (the endogenous conditions and external stimuli that activate attachment), ontogeny (the development of the attachment system in infancy and throughout the life span), function (the adaptive value of the attachment system), and phylogeny (the evolutionary continuity in attachment across humans and the other primates) (Maestripieri 2003). In addition to conceptual contributions to attachment theory, observations of mother-infant interactions in captive rhesus macaques conducted by Robert Hinde and coworkers provided important insights into developmental changes in the attachment system, responses to maternal separation and potential threats, and exploration and secure base phenomena (Hinde 1974). Hinde and coworkers documented the quantitative changes in time spent in contact and proximity and in the mother's and infant's roles in maintaining contact and proximity. These studies revealed that the developmental changes in mother-infant interactions during the first few months of infant life are remarkably similar across different populations and environments, suggesting that there are modal developmental curves for mother-infant interactions that are characteristic of all old-world monkeys. Hinde introduced Bowlby to the work of Harry Harlow, which experimentally demonstrated the primary role of the caregiver as a source of contact/comfort and protection rather than nutrition (Maestripieri 2003). Thus, research on primate behavior played a crucial role in outlining the normative aspects of human attachment theory.

In terms of normative development of attachment in nonhuman primate infants, there is good experimental and observational evidence that monkey infants (1) gradually discriminate their mother, or more generally their primary caregiver, from other individuals, (2) selectively direct their attachment behaviors toward this individual, (3) show distress and anxiety when separated from this individual, (4) use this individual as a secure base for exploring the environment, and (5) as a safe haven when they are frightened or in distress (Maestripieri 2003). Essentially, nonhuman primate infants possess an attachment system whose normative aspects are very similar to those of human attachment. In particular, the attachment system appears to serve a similar biological and social function in nonhuman primate and human infancy and appears to be regulated by similar exogenous and endogenous factors. There may also be some obvious differences, however. The extent to which nonhuman primate infants develop a representational model (i.e., an internal working model) of the caregiver in relation to the self and the external environment is not clear. Other differences between nonhuman primate and human attachment likely involve the ontogeny of the attachment system and the timing with which it and its components mature and/or become activated. The ontogeny of the attachment system, and to some extent also its proximate regulation and adaptive function, is likely to vary not only between humans and other primates but also among the over 300 nonhuman primate species, in relation to the life history of the species and its specific ecological, social, and reproductive adaptations.

In nonhuman primate research, the study of normative attachment processes has also been conducted by examining infant behavioral and physiological responses to separation from the mother (Maestripieri 2003). Early studies focused on the infant's behavioral responses to separation. Such studies documented the occurrence of an initial phase of "protest" followed by a phase of "despair," similar to those observed for institutionalized children. A third phase of detachment observed in children following the reunion with their caregivers has not been observed in

nonhuman primates. Separation studies have gradually incorporated more physiological variables (e.g., heart rate and body temperature, hormones and neurotransmitters, immunological measures) and more sophisticated techniques of measurement. Subsequent developments of this area of research have included postmortem studies of brain anatomy in maternally separated and/or socially deprived monkeys. The rationale underlying the study of infant responses to separation was, at least initially, the notion that the occurrence of a response to separation would provide information about the existence and strength of an attachment bond. Response to separation from the caregiver is an important component of attachment theory, and the occurrence of a separation response may indeed provide evidence of the existence of an attachment relationship. Beyond showing that separation is stressful, however, the contribution made by separation studies to research on normative attachment is unclear.

While research on normative aspects of attachment in nonhuman primates preceded, informed, and even guided human research on normative aspects of attachment, the opposite was true for research on normative aspects of socio-behavioral development, cognitive development, communicative development, emotional development, and physiological development. In these cases, human research typically preceded, informed, and guided nonhuman primate research. Other than showing that some aspects of normative child development are not unique to the human species but are also shared by other primate species, the contributions of nonhuman primate research have not been highly significant.

Interindividual Variation

The contributions of nonhuman primate research to our understanding of interindividual variation in child development have been mainly empirical, not theoretical. Studies of attachment in nonhuman primates have often addressed individual differences in the development and expression of attachment but almost exclusively in the context

of infant behavioral and physiological reactions to maternal separation. For example, these studies have documented variability in the intensity of the “protest” response to separation and in the extent to which such response is followed by withdrawal and depression. It has been shown that individual differences tend to remain consistent across repeated separations and reunions and stable throughout major periods of development. Stable individual differences in behavioral and physiological responses to social separation have also been found among rhesus macaques reared with surrogate mothers, notably peers.

In nonhuman primates, individual differences in response to separation are accounted for by both heritable and experiential factors. Although the study of genetic influences on behavioral development and stress reactivity in nonhuman primates is a relatively new area of research, a growing body of evidence has already accumulated about the importance of gene polymorphisms involved in emotion regulation and, in particular, of *5-HTTLPR* (serotonin transporter), *OPRM1* (opioid receptor), and *DRD4* (dopamine receptor). The effects of these polymorphisms often interact with each other and with early experience, such as exposure to stress in the first few months of life. The mechanisms underlying main genetic effects on behavior or gene-environment interactions are still poorly understood, but research on epigenetics appears to be particularly promising. Although systematic research on the effects of genes and early experience in nonhuman primates has been conducted with a very limited number of species, it is highly likely that the results of this research are generalizable to humans (Coyne and Maestripieri 2016).

A different line of nonhuman primate research has investigated the role of the mother’s own behavior toward the infant, namely, her parenting style, as a source of interindividual variation in both socio-behavioral development and reactivity to stress (Clancy and Hinde 2013). Variation in artificial rearing conditions in the laboratory (e.g., rearing infants with or without their mothers, with peers, and under various conditions of social deprivation or social enrichment) can also affect the

development of behavior and reactivity to stress. Nonhuman primate studies have shown that exposure to variable levels of maternal protectiveness and maternal rejection experienced in early infancy affects variation in infant independence from the mother and infant tendency to explore the environment or respond to challenges at various ages. Infants reared by highly rejecting (or less responsive mothers) mothers generally develop independence at an earlier age (e.g., spend more time out of contact with their mothers, explore the environment more, and play more with their peers) than infants reared by mothers with low-rejection levels. In contrast, infants reared by more protective mothers appear to be delayed in the acquisition of their independence and are relatively fearful and cautious when faced with challenging situations. Effects of maternal style and other aspects of the infant’s early social environment have also been documented with regard to responsiveness to negative visual stimuli (e.g., threatening facial expressions). Studies have shown that rhesus infants reared by more protective mothers and those reared by high-ranking mothers exhibit a stronger attentional bias toward faces with threatening expressions, as opposed to faces with neutral expressions, when compared to infants reared by less protective mothers and those reared by lower-ranking mothers (Coyne and Maestripieri 2016).

The issue of whether these effects of early experience on infant reactivity to the environment also persist into later stages of development and adulthood has been addressed by a few studies, and the results have been mixed (Coyne and Maestripieri 2016). The best evidence for long-term effects of early exposure to variable parenting style in infancy has been provided in the context of intergenerational transmission of parenting style in female monkeys. Here research has shown that there are similarities in maternal rejection rates and in the propensity to display physically abusive parenting behavior between mothers and their adult daughters. Studies of this phenomenon using a cross-fostering experimental design have shown that early experience, rather than genetic similarities between mothers and daughters, plays a crucial role in the

intergenerational transmission of parenting style. However, the contribution of genetic predispositions for particular personality traits or other psychological and behavioral characteristics cannot be ruled out. Although cross-fostering experiments are difficult to conduct in humans, many human longitudinal studies of child development in large pedigreed populations, or in which data on adopted children or twins are available, have confirmed that both early experience and inherited genetic predispositions play an important role in the origin of individual differences in child development. Although non-human primate research could potentially make significant theoretical and empirical contributions to human research on interindividual variation in child development, this potential remains yet to be fully realized.

Conclusion

Nonhuman primate research has contributed in the past to our understanding of many fundamental aspects of early child behavioral development (e.g., the discovery of the attachment system and its role in mother-child relationships and in the acquisition of independence). Thus, in the future, it has the potential to enhance our knowledge of many other aspects of development including, for example, brain-behavior relationships early in life and how these relationships are affected by genes and environment (Coyne and Maestripieri 2016). Nonhuman primate research offers the opportunity to perform biological and environmental manipulations that would be difficult or impossible in humans. It also provides the opportunity to longitudinally investigate developmental processes across an individual's lifespan and generations in a relatively short period of time. Finally, by studying and comparing developmental processes across a number of primate species in relation to their phylogenetic history, non-human primate research can help us understand the extent to which many aspects of human development are unique to our species or shared with other species by virtue of our common evolutionary history.

Cross-References

- [Early Attachment Experiences and Romantic Attachment](#)
- [Individual Differences](#)
- [Physiological Mechanisms](#)

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Social Dilemma

- [Prisoner's Dilemma and Cooperation](#)

Social Disabilities

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Synonyms

[Autism spectrum disorder](#); [Rett syndrome](#); [Social anxiety disorder](#); [Social communication disorder](#)

Definition

Impairment in social functioning including but not limited to anxiety caused by social situations

or lack of ability to form or understand relationships. Autism spectrum disorder is commonly thought of when referring to social disability.

Introduction

There is no specific DSM-V classification of social disability; despite this, there are disorders that negatively influence social behavior and therefore may be considered social disabilities. These disorders, which are often categorized as *pervasive developmental disorders* (PDDs), delay or inhibit the socialization and development of communication in humans (American Psychiatric Association 2013). The PDD category includes disorders such as Autism Spectrum Disorder (ASD) and Rett syndrome. However, there are other disorders, such as social communication disorder and social anxiety disorder that are not considered part of the PDD category but still negatively influence social behavior. This entry will describe the symptoms and potential causes of the following social disabilities: ASD, Rett syndrome, social communication disorder, and social anxiety disorder.

Autism Spectrum Disorder

ASD refers to a continuum of social disability symptoms – listed on the continuum in order of prevalence and severity. Because this spectrum encapsulates a variety of social impairments, ASD may be viewed as the social disability that affects the most people. ASD is considered part of the PDD diagnostic category and contains many disorders that may be considered social disabilities. For instance, individuals on the mild end of the Autism spectrum are often diagnosed as having Asperger's syndrome. Asperger's syndrome differs from ASD in that individuals with Asperger's may attempt social situations but are often perceived as being socially awkward.

Individuals with ASD experience lifelong impairment of social functioning. ASD affects about 1% of the population and is approximately 4.5× more common in boys compared to girls

(American Psychiatric Association 2013; Center for Disease Control and Prevention 2017). There is a wide range of difficulties associated with ASD, ranging from mild social impairment to the inability to care for oneself without assistance. Arguably, one of the most debilitating social impairments caused by ASD is the inability to understand relationships or display social-emotional reciprocity (American Psychiatric Association 2013). Other symptoms common in ASD patients include strong fixated interests, issues with sensory input (e.g., sensitivity to fabric in clothing), and insistence on “sameness” or extreme consistency and familiarity within one's social environment (American Psychiatric Association 2013). It is not unusual for ASD to be comorbid with intellectual disabilities, although some individuals with ASD may have above average intelligence (American Psychiatric Association 2013).

The most commonly used treatment for ASD is Applied Behavioral Analysis (ABA), which rewards positive behaviors and discourages maladaptive behaviors. There is a growing trend within school environments to utilize ABA therapy to treat students with ASD (Center for Disease Control and Prevention 2017). ABA essentially uses operant conditioning to influence behavior, as individuals generally make connections about behaviors and their consequences (Mash and Wolfe 2016).

While there is no known exact cause of ASD, researchers have found several links between ASD and various potential biological and environmental determinants that has helped shed light on the potential cause(s) of ASD. For instance, twin studies have shown that there may be a genetic component, and that the disorder is comorbid with chromosomal disorders such as Down syndrome or Fragile X syndrome (Center for Disease Control and Prevention (2017). Researchers have also found a link between elevated testosterone levels and ASD symptoms – indicating that children with ASD may possess an “extreme male brain” that causes these ASD patients to lack empathy and interest in social relationships (Baron-Cohen 2002). Other data has revealed that children from obese mothers

are at an increased risk of being born with ASD (Li et al. 2016). Scientists across the world continue to research ASD in hopes of finding the exact cause(s) and better treatments.

Rett Syndrome

Rett syndrome is somewhat similar to ASD in presentation. It is a rare neurological developmental disorder that is more prevalent in females; in males, it is normally fatal during infancy, but in rare cases, it may present as a milder form of what occurs in females (Mayo Clinic 2018). Individuals with Rett syndrome develop normally until about 6 months of age; at this time, there is a regression of milestones that marks the beginning of the first of four stages of progression (Mayo Clinic 2018). The second stage occurs between 1 and 4 years of age and features slow head growth, problems with motor skills, continued degeneration of social skills, and hyperventilating or screaming without reason (Mayo Clinic 2018). The third stage is considered a plateau, which may occur between 2 and 10 years. There may be some limited social improvements but seizures generally begin to occur during this time (Mayo Clinic 2018). The fourth and final stage of Rett syndrome generally begins after 10 years of age and features continued motor degeneration (Mayo Clinic 2018).

Experts believe Rett syndrome is caused by random mutations on the MECP2 gene, although some cases appear to be inherited (Mayo Clinic 2018). Researchers suspect the gene interferes with protein production involved in brain development, but the reason for the development of the disorder is unknown (Mayo Clinic 2018). There is no cure for Rett syndrome nor is there a known way to prevent the disorder. Current interventions for the disorder focus on communication and motor skills (Mayo Clinic 2018).

Social Communication Disorder

Social communication disorder, also called social pragmatic disorder, is similar to ASD in nature but

lacks the presence of restricted behavior patterns, interests, or activities (American Psychiatric Association 2013). Key features of social communication disorder include difficulties understanding “rules” of conversation and storytelling, along with difficulty understanding things not explicitly stated (American Psychiatric Association 2013). Diagnosis of the disorder is unusual under the age of 4 years old but may not be realized until adolescence when the individual struggles to understand complex conversation or interactions (American Psychiatric Association 2013). Individuals with social communication disorder may display similarities to social anxiety disorder symptoms, attention-deficit/hyperactivity disorder, and intellectual disabilities. A family history of ASD and specific learning disorder may increase chances of being born with social communication disorder (American Psychiatric Association 2013).

Social Anxiety Disorder

Unlike the preceding disorders, where there is a lack of understanding of social interaction, patients with social anxiety disorder possess an intense and persistent fear of social interaction. For an individual to be diagnosed with social anxiety disorder, his/her fear of social interaction must be out of proportion for the situation; for juvenile patients, their fear of social interaction must not be limited to conversing with adults (American Psychiatric Association 2013). This fear of social interaction is persistent over a long period and causes dysfunction in one’s daily life. However, to be diagnosed with social anxiety disorder, the patient’s fear and anxiety must not be caused by other disabilities such as ASD (American Psychiatric Association 2013).

Social anxiety disorder is more prevalent in women, and onset typically occurs around 13 years of age (American Psychiatric Association 2013). Social anxiety disorder is distinctly different from agoraphobia in that the fear is of judgment by others, not the inability to escape the situation (American Psychiatric

Association 2013). As noted before, social anxiety disorder has similarities to social communication disorder, and these symptoms are also found in children with ASD as well (American Psychiatric Association 2013).

Conclusion

Although this entry focused on four specific social disabilities, it is important to note that social disabilities are not necessarily limited to ASD, Rett syndrome, social communication disorder, and social anxiety disorder. ASD features social difficulties along with stringent interest and insistence on sameness. Rett syndrome presents similar symptoms to ASD but features severe motor degeneration along with the social impairment. Social communication disorder presents with similar social difficulties to ASD but does not feature symptoms such as stringent interest. Social anxiety disorder includes fear of social situations, although there is ability to understand the social situation. There is no ubiquitous system of accommodations in place strictly for individuals with social disabilities in schools. However, school administrations can grant accommodations to socially disabled students if they possess certain comorbid intellectual disorders, learning disabilities, or PDDs.

Cross-References

- [Anxiety](#)
- [Autism](#)
- [Child-Centered Learning](#)
- [Communication and Developmental Milestones](#)
- [Darwinian Psychiatry](#)
- [Disabilities](#)
- [Learning](#)
- [Mindblindness](#)
- [Neonatal Imitation](#)
- [Play and Social Learning](#)
- [School Environment](#)
- [Simon Baron-Cohen \(Darwinian Psychiatry\)](#)
- [Special Case: Autism](#)

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Social Disorganization Theory

- [Sociocultural Theories of Violence](#)

Social Dominance

- [Popular Children](#)
- [Same-Sex Coalitions That Exclude Women](#)

Social Dominance and Sexual Access

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Synonyms

[Reproductive skew](#); [Resource holding potential](#)

Definition

In many social systems, individual access to reproductive opportunities is moderated by dominance status within the social group.

Introduction

Achieving and maintaining dominance status within a group are assumed to be energetically costly and at least in the short term require engagement in conflict or agonistic interactions at the expense of other behaviors. In the long term, however, dominance status is often associated with greater access to food and other resources, as well as greater opportunities for reproduction and ultimately fitness gains. For many species associations between dominance status and reproductive success are clear, although relative importance of access to mates versus other advantages of dominance status (such as food resources or shared parental care) varies within and between species.

Dominance and Resource Holding Potential

Social dominance is commonly associated with resource holding potential (RHP; Parker 1974) such that individuals possessing traits which equip them for success in aggressive or agonistic interactions have greater access to resources. RHP (and by association, dominance) has been framed in the context of conflict over food resources, shelter, and access to mates and reproductive opportunities.

Among the many cases in which social dominance is associated with reproductive success, access to mates is in many cases influenced by dominance status through several behavioral and physiological mechanisms.

Mate Choice

While greater resource holding potential may explain some cases of socially dominant individuals being able to monopolize reproductive opportunities, access to mates may also be moderated through sexual selection and preference for socially dominant individuals. Preference for dominant mates has been suggested to be selected for either due to direct fitness benefits (through resources, protection from harassment) or due to

indirect fitness benefits for offspring such as parental care or good genes. In wide-ranging species, individuals capable of acquiring and maintaining dominance status also have “good genes” which are associated with resource holding potential, elaborate morphological features and behaviors associated with reproduction, and higher overall fitness. In cricket *Gryllus bimaculatus*, dominant males had higher immunocompetence which may explain female preference for them (Rantala and Kortet 2004). In chimpanzees, *Pan troglodytes*, priority of access by dominant males was predictive of reproductive success, but that of subordinate males did frequently reproduce “low-quality” females (Wroblewski et al. 2009). However, in many cases an apparent preference for dominant mates may not solely result from a preference for dominance. For example, Lynch et al. (2012) hypothesized that female preference for large males in the coercively mating mosquito fish (*Gambusia*) may have more to do with avoiding the advances of smaller males than an actual preference for large males.

Glucocorticoids and Their Impact on Reproductive Processes

Glucocorticoid hormones have many important functions in vertebrates but are perhaps best known for their role in stress-response pathways through which glucocorticoids activate and reallocate energy toward skeletal muscles, eyes, and respiration rather than toward functions such as reproduction or digestion – commonly referred to as the “fight or flight” response. In many animal groups, subordinate group members may have chronically elevated glucocorticoid hormone levels which in some cases can inhibit other hormonal pathways associated with reproduction. Thus, either through social dynamics or overt aggressive interactions, the reproductive capacity of subordinate group members can be reduced.

The Importance of Reproductive Skew

Cooperatively breeding societies and many dominance-structured animal groups present a

unique scenario to examine the relationship between dominance and access to mates. A key defining characteristic of cooperatively breeding societies is that dominant individuals have greater access to mates and thus generally greater reproductive success than subordinate group members. Subordinate group members that attempt to reproduce may face harassment, eviction, or infanticide. While reproductive skew is typically high in cooperatively breeding groups, dominant individuals may concede reproductive opportunities to helpful subordinate individuals under the “concessions model” framework which has empirical support in a number of species including gelada baboons (Snyder-Mackler et al. 2012) and the cichlid fish *Neolamprologus pulcher* (Heg et al. 2009).

For many primate and non-primate societies, female social status is associated with reproductive output although this relationship is likely more heavily influenced by social connections rather than access to mates.

Dominance, Sexual Access, and Human Societies

Like in many other animal species, there is abundant evidence that socially dominant humans also have greater reproductive success. For males in both pre-modern and modern civilizations, dominance is associated with reproductive success, although this relationship is likely moderated by resource holding potential and access to resources, and also confounded by wealth and education. Additionally, there is evidence of a role for sexual selection as Havlicek et al. (2005) found female human subjects preferred the odor of “dominant” men during the fertile period – particularly females in stable relationships.

Studies on humans have drawn distinctions between dominance (determined by direct dyadic conflict) and prestige (social status) and found a general trend that heterosexual women prefer males with high prestige rather than dominance (Snyder et al. 2008). However, von Rueden et al. (2010) drew distinctions between dominance and prestige and found that both are important predictors of the number of

within-pair offspring as well as extra-pair affairs in the Tsimane people.

Conclusions

The relationship between dominance and access to mates has been of interest to evolutionary psychologists, primatologists, and behavioral ecologists for decades. In humans and nonhuman animals alike, apparent relationships between dominance and reproductive success have been well documented in many taxa. Having access to mates is one mechanism through which the relationship between dominance and reproductive success could be manifested. In many cases, these relationships may actually have less to do with access to mates and instead be more heavily influenced by differential access to other resources such as food or habitat or other factors such as social stability.

Cross-References

- ▶ [Aggression for Sexual Access](#)
- ▶ [Convergent Evolution of Hyena and Primate Social Systems](#)
- ▶ [Cooperative Breeding](#)
- ▶ [Dominance in Humans](#)
- ▶ [Dominance, Testosterone, and Cortisol](#)
- ▶ [Eusociality](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Fighting Assessment](#)
- ▶ [Helpers at the Nest](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Social Dominance reduces Fighting](#)
- ▶ [Status and Reproductive Success](#)
- ▶ [Status Hierarchies](#)

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Social Dominance Hierarchy

► Dominance Hierarchy

Social Dominance Orientation (SDO)

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Synonyms

Between-group hierarchy; Dominance; Evolutionary political psychology; Political attitudes; Prejudice; Sex differences; Warfare

Definition

Social dominance orientation is a measurement of “the general desire to establish and maintain hierarchically structured intergroup relations regardless of the position of one’s own group (s) within this hierarchy” (Sidanius et al. 2016, p. 152).

Introduction

Human societies tend to structure themselves as group-based social hierarchies such that some groups enjoy greater access to fitness-relevant resources such as prestige, wealth, social status, healthcare, food, homes, mates, and so on. Social dominance theory (SDT, Sidanius and Pratto 1999) asks the questions why and how group-based hierarchies are continuously reproduced, at least among surplus-producing societies. The theoretical framework spans macrostructural, institutional, ideological, social role, individual, and behavioral genetic levels of analysis to address this question and postulates that humans have a predisposition to navigate group-based social structures (Kleppetø et al. 2019; Kunst et al. 2017; Pratto et al. 2006; Sidanius et al. 2016; Sidanius and Pratto 1999).

Conflicts between groups are ubiquitous across history and cultures. Ideologies that justify beliefs about the superiority of dominating groups might serve the function of reducing conflicts by legitimizing the hierarchical status quo (Pratto et al. 1994; Sidanius and Pratto 1999). According to SDT, when these ideologies are widely accepted within a society, they justify discrimination and allow some groups to dominate over others based on their gender, age, and, especially, socially constructed markers of group membership such as class, race, ethnicity, caste, and religion – what SDT coins arbitrary sets. The beliefs and ideologies that justify dominance hierarchies are called hierarchy-enhancing legitimizing myths; examples are the “divine rights of kings,” sexism, and the Protestant work ethic suggesting that you get what you personally deserve (myths in this context mean widely shared ideologies, not implying that they are

false or true). Beliefs that justify flat or egalitarian group structures are called hierarchy-attenuating legitimizing myths, examples being the universal rights of man, socialism, and feminism (Sidanius et al. 2016; Sidanius and Pratto 1999). Importantly, SDT postulates that particular instances of modern group-based discrimination such as racism, classism, sexism, and nationalism are manifestations of more general processes where dominant groups maintain social, economic, and military supremacy over subordinates (Sidanius et al. 2016).

At the individual level of analysis, endorsement of such intergroup dominance hierarchies is reflected in the individual difference of *social dominance orientation* (SDO) (Ho et al. 2015; Pratto et al. 1994) to which we now turn our attention. This general relational motive to enhance versus attenuate between-group hierarchies has proven one of the most robust predictors of intergroup attitudes (Pratto et al. 2006; Sidanius et al. 2016; Sidanius and Pratto 1999), from support for social welfare to ethnic persecution of immigrants (Dunwoody and McFarland 2018; Ho et al. 2012, 2015; Thomsen et al. 2008). Here, we discuss the conceptual and psychometric properties of SDO, and we highlight some key evolutionary forces that might explain SDO's inter-individual variation and mean-level sex differences.

The Construct of Social Dominance Orientation (SDO)

Sidanius et al. (2016, p. 152) define SDO as “the general desire to establish and maintain hierarchically structured intergroup relations regardless of the position of one's own group (s) within this hierarchy.” Since its first introduction in 1994 (Pratto et al. 1994), the SDO scale has gone through several iterations. The most recent version, the SDO7 (Ho et al. 2015), consists of 16 statements (such as “Some groups of people must be kept in their place”), which responders rate their levels of agreement with on 7-point Likert scales. Scores on these items can be averaged to form an SDO score (with half the items being reverse scored). Below we discuss the

dimensionality of SDO and how SDO relates to other variables and constructs.

Dimensionality

SDO was previously considered a unitary construct, but increasingly there is evidence that the construct can be divided into two: dominance (SDO-D) and egalitarianism (SDO-E) (Ho et al. 2012, 2015). SDO-D reflects preferences for active oppression of groups and is most reflective of hostile beliefs such as old-fashioned racism, dehumanization, and support for war (Sidanius et al. 2016). SDO-E, on the other hand, reflects a preference for inequality or at least an opposition to active measures toward reducing inequality. SDO-E is also often labeled “anti-egalitarianism.”

SDO-D and SDO-E have been shown to constitute separate facets of SDO in factor analyses, and they also differ when used as predictors for conceptually relevant variables. In the overview of relations between SDO and other traits below, we discuss correlations for full-scale SDO scores, while noting differences between SDO-D and SDO-E whenever relevant.

Predictive Power of SDO

SDT predicts that SDO will correlate positively with support for hierarchy-enhancing and negatively with hierarchy-attenuating ideologies or legitimizing myths. Consistent with this, SDO has been tied to support for a wide range of attitudes about ideology and politics, including political and, particularly, economic conservatism and support for social welfare and affirmative action (Sidanius and Pratto 1999). And SDO continues to predict emergent current phenomena, such as attitudes toward Syrian refugees and voting for Donald Trump (Dunwoody and McFarland 2018; Sheehy-Skeffington and Thomsen 2019). Most centrally, SDO has been found to consistently predict most kinds of prejudicial attitudes. This includes prejudice against women, the poor, ethnic/racial minorities, LGBTQ people, and immigrants (see Sidanius et al. 2016, for an overview of studies on this). Prejudicial attitudes predicted from having *low* scores on SDO are less studied, though there are indications that they could include prejudice against political conservatives

and against social groups deemed to be privileged (Lucas and Kteily 2018).

SDO has also been explored in relation to personality traits. In particular, SDO has been connected to many personality traits that are socially undesirable (Ho et al. 2015), such as the Dark Triad traits of Machiavellianism, narcissism, and psychopathy, which are particularly strongly linked to SDO-D. Relatedly, SDO-D in particular is inversely correlated with the honesty/humility dimension of the HEXACO personality inventory, which reflects an unwillingness to “get ahead” through dishonest means. Among the Big Five traits, SDO is most strongly related to agreeableness and openness to experience, with both correlations being negative here as well. The Empathic Concern scale is also negatively related to SDO (Lucas and Kteily 2018).

Distinctions Between SDO and Related Constructs

To further clarify what the SDO construct is meant to represent, we here go through three constructs that SDO is related to but importantly distinct from. These are interpersonal dominance, in-group favoritism, and right-wing authoritarianism.

Upon hearing the name “social dominance orientation,” a natural interpretation is that it reflects how oriented someone is toward being interpersonally dominant in social settings. But this is not what SDO is meant to measure, and the discriminant validity of SDO from standard personality measures of interpersonal dominance was established early on (Pratto et al. 1994; Sidanius and Pratto 1999): SDO concerns preferences regarding dominance hierarchies *between groups* in society, and so it is conceptually quite distinct from being interpersonally dominant.

Another misinterpretation of SDO is that it necessarily involves a preference that *one's own group* should be the one to dominate, so that it would correspond to in-group favoritism. Such an interpretation would indeed align with how SDO was originally conceptualized (e.g., Pratto et al. 1994), but contemporary understandings of SDO have shifted away from this to propose that SDO reflects a person's general orientation toward the

idea of hierarchies between groups. Consistent with SDT's prediction of *ideological asymmetry*, this suggests that a black American with a high score on SDO would not desire blacks to dominate whites, but would rather endorse the existing hierarchical status quo, even though this implies that whites continue to have more status and power than blacks (Ho et al. 2015; Sidanius and Pratto 1999). Accordingly, SDO is more positively associated with ethnic identity, perceived ethnic victimization, and other variables related to in-group favoritism among dominant than subordinate groups (Sidanius et al. 2016; Sidanius and Pratto 1999; Thomsen et al. 2010).

SDO is also related to, but yet distinct from, the concept of right-wing authoritarianism (RWA). RWA is manifested in submission to traditional authorities and in aggressive enforcement of established norms and customs. Thus, RWA and SDO are conceptually related, as they both concern attitudes toward hierarchy. Additionally, SDO and RWA tend to correlate quite substantially (usually at about $r = 0.40$), and they are both good predictors of many kinds of prejudicial attitudes.

However, SDO and RWA also have important theoretical and empirical distinctions. The dual-process motivational model of ideological attitudes (Duckitt and Sibley 2010) proposes that RWA reflects needs for social order and stable traditions, which result from seeing the world as a threatening and dangerous place. Thus, people high in RWA should prefer authorities that emphasize order and law and that defend traditional values. High SDO rather implies perceiving society as a competitive jungle, where you need to fight for power and control over others. People high in SDO therefore tend to prefer authorities that favor social inequality and group dominance.

While both RWA and SDO are associated with prejudice toward outgroups, the particular types of prejudice predicted from them are importantly different. According to Duckitt and Sibley (2010), RWA predicts dislike of groups that are socially deviant and/or norm-violating, whereas SDO predicts prejudice against groups that are low in status. For example, Thomsen et al. (2008) demonstrated in Switzerland and Southwestern USA

that for people high in RWA, negative attitudes toward immigrants were mainly provoked by immigrants' refusal to assimilate into the dominant culture and adhere to established norms, thus threatening cultural conventionality. In contrast, SDO predicted aggression toward immigrants that assimilated *too much* into the dominant culture and thus threatened the existing status boundaries.

SDO Is Contingent upon Hierarchical Position but Is also a Stable Trait

There are myriad studies documenting that SDO responds to the hierarchical nature of the context. Perhaps most importantly, it has been shown many times over that one's level of SDO is highly contingent on the placing of one's own group in the hierarchy. Consistent with how SDO only reflects self-interest when measured in dominant groups, people from lower-ranking groups tend to score substantially lower on SDO. For example, the difference in mean SDO between blacks and whites in the USA is substantial (e.g., Ho et al. 2015). It has been found that as the objective, salient, or perceived difference in power between groups becomes larger, so too does the difference in SDO levels between the groups (e.g., Levin 2004).

Consistent with this, in a meta-analysis across 27 countries, the average SDO level among dominant groups corresponded to the macrostructural level of inequality, that is, to the status gap between dominant and subordinates, consistent with dove-hawk type dynamics (Fischer et al. 2012). Accordingly, SDO among dominant groups also correlated across nations with macro-level indicators of poor governance, corruption, lack of rule of law, and democracy, all consistent with the notion that dominant groups are more likely to coercively claim resources the greater the macrostructural inequality. In an independent sample collected across 30 US states, macrostructural inequality (Gini) across states predicted SDO and mediated the effect of SDO on attitudes toward minorities (Kunst et al. 2017).

Just as SDT describes hierarchy-enhancing myths, it also describes hierarchy-enhancing social institutions. These are institutions which serve to uphold and enhance hierarchies, and

the theory predicts not only that people will self-select to hierarchy-enhancing versus hierarchy-attenuating institutions depending on their SDO levels but also that membership in hierarchy-enhancing institutions will lead to corresponding increases in SDO (Sidanius and Pratto 1999). Examples of institutions that have been described to have hierarchy-enhancing elements are the criminal justice system and the police force, housing, labor, healthcare, retail, and education (Sidanius and Pratto 1999).

Consistent with this, Sidanius et al. (1994) found that police officers in LA had higher mean SDO than students and jurors (who represented a random sample of Los Angeles citizens), whereas public defenders (working at the public defenders office, which is a HA institution) were found to be significantly less social dominance-oriented than both students and jurors.

SDO scores can also vary on more of a moment-to-moment basis when one's salient position in the hierarchical context changes. In a study illustrating this, Levin (1997) divided the SDO scale in half and put one half alongside questions about the tensions between Ashkenazi and Mizrahi Jews in Israel and the other half alongside questions about the tensions between Jews and Arabs. In the section on Jew conflict, Ashkenazis (who are seen as higher in status) scored higher on SDO than Mizrachis. But in the section on tensions between Jews and Arabs (where both groups of Jews are higher in status), then both groups of Jews scored higher than in the other condition, and the difference in scores between the groups disappeared.

Interestingly, Levin's (1997) study of contextual influences on SDO also illustrates how SDO also can be seen as a stable trait. Specifically, as has been shown in many studies, SDO has high rank-order stability. This means that people with relatively high scores in one context will be likely to be high scorers in other contexts. Despite the large shifts in mean SDO levels between conditions in Levin's study, correlations between SDO scores from the same participant were still substantial. Levin (2004) conceptually replicated these effects in Northern Ireland among Catholics and Protestants and further demonstrated that the

difference in SDO between dominant and subordinate groups are moderated by personal perception of the nature and size of the status gap.

Recently, Bratt et al. (2016) demonstrated the rank-order stability of SDO and its predictive power on outgroup prejudice over time using latent growth-curve modeling among large samples of Norwegian teenagers and American university students. Thomsen et al. (2010) demonstrated the stable relations of SDO scores across more than 3 years, as well as their longitudinal, cross-lagged effects on perceived white victimhood and prejudice. In summary, SDO does, contrary to the claims of some critics, constitute a *generalized* orientation toward intergroup hierarchy that holds *regardless* of which groups people are instructed to hold in mind when they fill out the SDO scale.

Interpretation of Low SDO Scores

SDO is often skewed toward the lower end of the scale. For instance, in Ho et al.'s (2015) validation study of the SDO7 scale, the average SDO score across six US samples on a 7-point Likert-scale was 2.6, corresponding to a percentage of maximum possible agreement (POMP) score of 27.2 (ranging from 0 to 100), including a representative population sample, the SDO mean of which was 3.0, corresponding to a POMP score of 32.5. Consistent with this, meta-analytical estimates indicated that the mean SDO POMP score across 27 nations was at 25.8, ranging from 15.7 in Switzerland to 63.0 in Japan (Fischer et al. 2012).

This raises issues about how scores are to be categorized. An SDO score of 3.8, for example, is below the scale midpoint of 4, yet it would place you about a standard deviation above the mean in Ho et al.'s samples. So, if you score at 3.8, do you then have high or low SDO? Are you predicted to want to attenuate or amplify hierarchies? Notably, SDO correlates very strongly with the anti-egalitarianism scale ($r = 0.85$ in Lucas and Kteily 2018), which has scores more evenly distributed around its scale midpoint than SDO has. Thus, it could be argued that SDO scores that are high relative to most sample means can be taken to represent opposition to egalitarianism, even if

they are below the midpoint of the scale (see Lucas and Kteily 2018). Plausibly, SDO scores might be shifted downward, e.g., through social desirability bias. If so, then the "true" SDO level of someone scoring 3.8 could be well above 4, and so they would have high SDO in both a relative and an absolute sense. Also, the low scores may simply reflect a general human aversion to strong group hierarchy or a preference for between-group equality, relatively speaking. Indeed, SDO scores would presumably only be shifted downward due to social desirability concerns if there is a widespread normative default expectation of equality (that makes endorsement of between-group dominance socially undesirable). Recent evidence from preverbal human infants suggests this is in fact the case, at least for default expectations of equal resource distribution (see Sheehy-Skeffington and Thomsen 2019).

In any case, although the majority of people may disagree with strong intergroup oppression in absolute terms, the variance between strongly and less strongly disagreeing with between-group hierarchy, as captured by the SDO scale, has proven one of the most robust predictors of intergroup phenomena in political psychology. Social dominance theory attempts to understand how this variance intersects with macrostructure and immediate institutional contexts and social roles to explain the continuous reproduction of the hierarchical status quo (Sidanius and Pratto 1999).

Evolution of Dominance and Egalitarianism

As we have seen, social dominance orientation predicts a plethora of political beliefs and ideologies. In the ethological literature, a concept known as *behavioral syndrome* captures traits that tend to correlate across situations and contexts. Given that SDO correlates with many related political beliefs, can these patterns be described as a behavioral syndrome?

Strategies of dominance and egalitarianism have deep evolutionary roots and can often coexist within the same species. In game theoretical

competitions for dominance, the contests often follow a hawk-dove dynamics where more formidable individuals (hawks) will prevail in such zero-sum conflicts, claiming contested resources, while subordinates (doves) will yield to more formidable opponents, so as to minimize costly fighting and injury. Consistent with the notion of evolved representations and motives for social dominance, greater physical formidability is also associated with greater dominance motives and claiming of societal resources among humans (Petersen et al. 2013). Indeed, even preverbal infants use cues of formidability and predict that the novel agents who are largest, most numerous and have won before will prevail in zero-sum conflict over smaller, less numerous, and previously weaker ones (Thomsen et al. 2011).

Importantly, egalitarian strategies are likely to have evolutionary underpinnings as well. In several primate species, coalitions form among lower-ranked males in order to gain access to fitness-relevant resources guarded by higher-ranking individuals. Furthermore, hunter-gatherers do display levelling mechanisms that keep any one individual from gaining despotic control (Boehm 1999).

If both dominant and egalitarian intergroup strategies, as tapped by low and high SDO, are maintained in human populations, what evolutionary genetic forces maintain them? A recent investigation using genetic sensitive data found that SDO and related political beliefs were all heritable and that the covariation between them are genetic in origin (Kleppestø et al. 2019).

It is possible, then, that both endorsement and opposition to intergroup hierarchies and the social policies that are meant to amplify or attenuate them build on universal adaptations for navigating social hierarchies. Given the enormous variation in available resources across ecological and social contexts throughout human history, it is unlikely that a single optimal level of hierarchy-preference exists. Hence, it is plausible that some kind of balancing selection may maintain the heritable variation in SDO, for example, through migration-selection balance, a process where genetic variation is maintained due to the changing selection pressures over time and space.

This maintenance of genetic variation can occur with personality traits because humans select environments and alliances that match their traits (niche-specialization or active gene-environment correlation). Individuals will then maximize the chance of obtaining fitness-relevant resources such as social alliances and mates.

The extensive evidence that people self-select to areas of study and professional careers that match their levels of SDO in terms of being hierarchy-enhancing or attenuating (e.g. people who are high in SDO are more likely to chose to become police officer and people low in SDO are more likely to chose to become social workers) and also stay longer and do better in these educations and jobs the better this SDO-institution match is (e.g. students with lower SDO get better grades in traditionally hierarchy-attenuating educations), and, finally, also socialize SDO to go up or down according to the hierarchy-enhancing or attenuating nature of the institution (Gatto and Dambrun 2012; Sidanius and Pratto 1999) provide support for this proposal. This also suggests that any heritability of SDO must be understood in its broadest sense to allow for such niche-building gene-environment associations, where SDO leads to the selection of environments that further adjust SDO levels in congruent ways.

Evolution of Sex Differences in Social Dominance Orientation

Across societies men score higher on SDO than women (Lee et al. 2011). Typically this difference is on the magnitude of about half a point on the scale (e.g., ~2.9 for men vs. ~2.5 for women in Ho et al. 2015). In contrast to the differences in scores between ethnic groups, which are thought to be entirely due to contextual factors, this sex difference is argued to be substantially less context dependent. This claim about stable gender differences on SDO is called the “invariance hypothesis” by SDO theoreticians and has been replicated across many cultures (Lee et al. 2011).

Why would the sexes differ in attitudes and behavior related to intergroup aggression? Sexual selection and parental investment theory suggest

that the payoff for costly intergroup aggression might be very different for men and women (Tooby and Cosmides 2010). In mammalian species, the fitness of males is constrained by access to fertile women. For women however, fitness payoffs are not constrained by the availability of fertile males, but rather by the time and resources required for successful gestation and lactation. This pattern gives rise to strong intrasexual competition among men for access to fertile females. This gives rise to men fighting other men individually, but also for *intergroup* competition where men raid, or attempt to dominate, other groups for access to the reproductive resources within them. Furthermore, coalitional aggression has also been observed in closely related primates (Wilson and Wrangham 2003).

Based on this, social dominance theory (Sidanius and Pratto 1999) predicted that intergroup conflict between socially constructed, arbitrary-set alliances (such as race, ethnicity, culture, class, caste, religion) will be a primarily male-on-male phenomena. This implies that the main targets of intergroup oppression will be subordinate males (i.e., in an American context black and Hispanic males; in a European context Muslim/Middle Eastern and African males), and so SDT coined this idea the *subordinate male target hypothesis (SMTH)* (Sidanius and Pratto 1999), described more generally elsewhere as the *male warrior hypothesis* (McDonald et al. 2012). It postulates that men engage in coalitional aggression for direct sexual access but also indirectly for foraging territories, social influence, power, and status, and it may explain why men are much more likely to be both perpetrators and victims of intergroup violence and why men tend to be less egalitarian in their social attitudes, such as SDO.

Indeed, the available evidence strongly suggest that men are more prejudiced, conservative, punitive, and racist than women are (Sidanius and Pratto 1999). Nevertheless, modern expressions of prejudice are probably not adaptations in and of themselves (Navarrete et al. 2010). However, they might have important evolutionary underpinnings, such as the alliance detection system. That is, modern prejudice might be expressions of psychological adaptations that evolved in a context where coalitional aggression was much more

common than it is today (Tooby and Cosmides 2010). Indeed, high degrees of coalitional aggression can be observed among current hunter-gatherer tribes.

SDT argues that men are not just the primary agents of discrimination based on arbitrary-set group differences (such as race), but also the main target of it (Sidanius and Pratto 1999). Experimental psychophysiological evidence on prepared fear-learning supports the proposition that we tend to primarily be wary of outgroup males, rather than females (Navarrete et al. 2009). For women the argument has been made that such outgroup bias is primarily motivated by fear of sexual coercion, while for males it is based on motives for aggression and social dominance (Navarrete et al. 2010). In other words, sex is an important variable in both the amount of prejudice held by individuals but also in who is targeted for discrimination.

Another crucial part of the male warrior hypothesis is that it predicts variation among males in their desire to dominate other groups. That is, men are expected to calibrate their desire for dominance based on their own formidability, leadership ability, available alliances, and other environmental information (Petersen et al. 2013). In fact, the association between physical formidability and SDO holds even when controlling for the time spent lifting weights, suggesting that physical formidability directly drives SDO, rather than the reverse (Price et al. 2017; Sheehy-Skeffington and Thomsen 2019).

Conclusion

Human societies tend to be structured as hierarchies where dominant groups enjoy a greater access to fitness-relevant resources. Social dominance orientation (SDO) measures the degree to which individuals prefer that dominant groups stay on top, or if society should be structured in a more egalitarian fashion. SDO predicts many important attitudes, such as political beliefs, prejudice, and life choices. Men tend to score higher, which might reflect men's sexually selected tendency to be motivated to engage in intrasexual competition for social status, which in turn give

them access to fertile females. Humans are likely to possess adaptations designed for both dominance and egalitarianism.

Cross-References

- [Context, Environment, and Learning in Evolutionary Psychology](#)
- [Dominance in Humans](#)
- [Evolutionary Personality Psychology](#)
- [Female Choice for Men High in SDO](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Political Affiliation](#)
- [Primate Dominance Hierarchies](#)
- [Self-Beneficial Political Attitudes](#)
- [Status and Dominance Hierarchies](#)

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Social Dominance Reduces Fighting

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Synonyms

Loser effects; Resource holding potential; Winner effects

Definition

In certain circumstances, the establishment of dominance relationships may reduce the frequency or intensity of agonistic interactions between individuals within the hierarchy.

Introduction

Dominance relationships within groups typically revolve around access to resources such as food, shelter, and mating opportunities. More dominant individuals typically have greater access to these resources. In many cases, once established, dominance relationships enable individuals with differing dominance status to coexist relatively peacefully without the need for repeated agonistic encounters. While the extent to which conflict is reduced depends on the system and the context of conflict, familiarity with conspecifics does often seem to correlate with reduced aggression.

Conflict and Dominance

Across animal taxa, organisms engage in conflict with one another for resources such as food, shelter, and mates. Success in such conflict is often attributed to resource holding potential (RHP), such that individuals better equipped to acquire and maintain resources have greater access to them (Parker 1974). Conflict between individuals in social groups is often greatest between individuals near one another in size or status which have similar RHP; however in many cases even small size discrepancies can be adequate to predict the outcome of conflict. Conflict can be costly for individuals, and thus mechanisms which serve to establish dominance relationships without physical altercations could be selectively advantageous if it reduces the costs associated with agonistic interactions (Smith and Price 1973).

Dominance relationships have been an important focus of behavioral research in both human and nonhuman animals for quite some time. Selection for dominance hierarchies has been proposed as a possible mechanism

through which perpetual aggressive encounters can be reduced or avoided, although whether this mechanism exists has been questioned and may vary between species and populations. Support for this selective advantage of dominance relationships has been suggested in alpine ibex, *Capra ibex*. Male ibex compete with one another for access to mates; however actual conflict during the rut appears to be lessened through dominance relationships which were established prior to the breeding season (Willisch and Neuhaus 2010). Similarly, for great bustard, *Otis tarda*, dominance status is associated with reduced conflict once it's been established, at least for high-ranking individuals (Magaña et al. 2011).

Often physical features such as size, ornaments, or auditory cues provide honest information about the resource holding potential of individuals. So long as these traits are honest signals of quality, dominance hierarchies within groups may form as a result of these cues in the absence of actual agonistic interactions. While aggression may be reduced in systems with cues, period aggression or "testing" of individuals may be important for maintaining the honesty of the signal and prevent the evolution of cheaters in the system. Indeed, individuals with traits that have been experimentally modified often face severe aggression from conspecifics (Tibbetts 2004). Interestingly, in pukeko (*Porphyrio porphyrio melanotus*), there appears to be feedback between agonistic interactions resulting from experimentally modified cues and the actual trait value (size of a "shield" on their head in this case) of the cue (Dey et al. 2014) such that individuals whose shields were experimentally reduced faced aggression as though they were lower rank and their actual shield size reduced as well.

Winner effects, loser effects, and bystander effects have been proposed as possible mechanisms that explain the dominance relationships emerging from agonistic conflict. Winner effects (individuals being more likely to win subsequent bouts after winning previous encounters) and loser effects (individuals being more likely to lose subsequent bouts following losses in previous encounters) may have important

consequences for emergent social structure, although evidence for each effect varies from system to system. In the green anole, *Anolis carolinensis*, both winner and loser effects may be at least in part moderated through neuroendocrine pathways (Greenberg and Crews 1990). Bystander effects emerge when individuals observe interactions between conspecifics and decide whether and who to engage in agonistic encounters depending on the outcome of the initial conflict (Earley 2010) and further reduce the need for direct conflict to resolve dominance relationships.

One mechanism through which dominance relationships may facilitate reduced aggression is through policing. In many animal societies, the presence of particular group members is associated with reduced conflict in groups, as well as shifts in other group characteristics. In many cases, these "policers" are relatively high-ranking individuals which possess the power to influence group dynamics. In human societies, policing (specifically law enforcement) may similarly reinforce cooperation between individuals (Kümmerli 2011).

Conclusions

In many cases dominance relationships may lead to reduced aggression between individuals and thus reduce risks associated with injury through agonistic encounters. Possible mechanisms through which agonistic interactions could be reduced include familiarity with social partners or honest signals of quality or resource holding potential. Additionally, in many human and non-human animal societies alike, policing (often by high-ranking individuals) may further reduce conflict and facilitate for cooperative interactions between individuals.

Cross-References

- [Aggression for Sexual Access](#)
- [Convergent Evolution of Hyena and Primate Social Systems](#)

- ▶ [Dominance and Testosterone](#)
- ▶ [Dominance in Humans](#)
- ▶ [Dominance, Testosterone, and Cortisol](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Fighting Assessment](#)
- ▶ [Observed Mating Behavior and Women's Long-Term Mating](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Social Dominance and Sexual Access](#)
- ▶ [Status and Reproductive Success](#)
- ▶ [Status Hierarchies](#)

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Social Dominance Structure

- ▶ [Serotonin and Dominance](#)

Social Emotion Evolution

- ▶ [Evolution of Emotion in Social Context](#)

Social Evolution

- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Social Darwinism](#)
- ▶ [Triggering Kin Selection](#)

Social Exchange

- ▶ [Adaptations for Reciprocal Altruism](#)

Social Exchange Algorithms

- ▶ [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)

Social Exchange Among Non-kin

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Synonyms

[Reciprocal altruism, dyadic cooperation among genetically unrelated individuals](#)

Definition

The act of engaging in a social behavior that is beneficial to another individual with the

expectation of a reward in return that outweighs the costs associated with the behavior.

Introduction

Social interactions are among the most fundamental characteristics of human existence. Human beings have lived and interacted in social groups throughout our evolutionary history. Homans (1958) was one of the first scholars to conceptualize social interactions as exchanges between two or more people that have both costs and rewards. Building on this conceptualization, social exchange theory posits that individuals engage in a particular social behavior only if the rewards outweigh the costs.

Social exchange theory is a helpful framework in understanding prosocial behavior, actions performed with the intention of benefiting another individual or group. Social exchange theory argues that one engages in prosocial behavior only if they anticipate higher rewards (e.g., receiving reciprocal help in the future) than costs (e.g., the time associated with help). In a related vein, social exchange is also linked to cooperation, which is integral in ensuring group living. Cooperation inherently brings costs, but when those costs are outweighed by rewards, individuals cooperate and potentially reach benefits they cannot achieve on their own. Cooperation is seen in other animals too (e.g., insects, fish, birds, mammals). Yet this cooperation is typically undertaken with other conspecifics with whom the individual shares genes. Indeed, helping and receiving help from relatives offer adaptive advantage (e.g., work on kin selection and inclusive fitness, see Hamilton 1964). What is unique about human cooperation is that human beings have the capacity to cooperate widely with other conspecifics even when they do not share any genetic material. This ability to cooperate with non-kin on a large scale has been possible thanks to the cognitive skill of engaging in social exchange, and this has ultimately enabled human beings to form cohesive, structured, and efficient groups and build the civilization we have today.

Social Exchange Among Non-kin

Social exchange can take place between two or more individuals in a variety of social settings that do not include kin relationships. Romantic relationships (that may or may not involve producing offspring), friendships, neighbor relationships, colloquial relationships, and business partnerships are common examples. Social exchange can even take place between individuals who do not know each other prior to the exchange.

Such exchanges, however, are known to be less stable than kin relationships as they have a voluntary nature. In such situations, the conditions of the exchange are more likely to be explicit and rely on agreed upon norms (e.g., social contracts; Cosmides and Tooby 1992). Such social exchange requires a highly evolved cognitive capacity that involves perceiving the interaction partner's mental state and intention and calculation of costs and rewards and detecting potential deceit. Hence, social exchange can be mentally taxing. Moreover, it is risky considering selection may favor cheaters who receive help without offering the rewards. Therefore, researchers have posited that human beings have developed sophisticated cognitive mechanisms to detect and exclude cheaters and low-value group members from the social exchange circle (Cosmides and Tooby 1992). Neurobiological evidence supports this; deceit detection has been identified to be executed by specific regions in the brain (i.e., orbitofrontal cortex, temporal pole, and amygdala; Stone et al. 2002).

Reciprocal altruism is central to social exchange among non-kin. Reciprocal altruism (Trivers 1971) refers to engaging in a costly prosocial act when the individual expects that it will be similarly reciprocated in the future. In this framework, the immediate cost of helping is outweighed by the future reward of being reciprocated when one needs help. Such social exchange typically involves *positive* reciprocity, where individual expects a benefit in return of a benefit, but social exchange may also be characterized by *negative* reciprocity, where individual offers help, or halts aggression, in hopes that the other individual will not harm

them in the future. In both cases, over time, both members of the reciprocal relationship will be better off as compared to their initial state. Reciprocal altruism can lead to successful and stable cooperation in social groups that interact frequently with each other and have formed trust based on prior affirmative social exchanges. Probably to ensure this, human beings have strong needs to maintain trust and good social reputation and avoid social exclusion from one's social network (e.g., Panchanathan and Boyd 2004). In addition, social norms sanctioning the punishment of cheaters by cooperators protect the secure environment to ensure that reciprocity is sustainable (e.g., Bornstein and Weisel 2010).

Social exchange among non-kin is argued to have evolved as an adaptation to combat resource scarcity and unpredictability, which characterized our evolutionary history. It is argued that the variability in available resources was combatted with an "insurance" mechanism: "Successful" individuals who have high resources at a given point in time agree to share these resources with the less successful individuals in exchange for receiving their resources when they cannot secure their own in the future. This strategy ensures that the total access to resources of all individuals shows less variability in unpredictable settings (Kaplan et al. 2000). Recent support for this conjecture comes from a study where participants in a virtual setting readily established reciprocal trading relationships in face of unsynchronized variance in resources and hence maximized the average resources each individual has at any given time point (Kaplan et al. 2012).

Conclusion

Social exchange is a crucial mechanism through which individuals judge the costs and benefits of a social interaction and decide whether to engage in it or not. Thanks to this sophisticated cognitive ability, human beings have been able to cooperate with non-kin and form large-scale social groups, which have been the engine of modern life.

In environments characterized by mutual trust and respect for the social norms, social exchange can aid in the advancement of both the individual and the social group.

Cross-References

- [Group Living](#)
- [Prosocial Behavior](#)
- [Reciprocal Altruism](#)
- [Selection for Cooperative Relationships](#)
- [Social Exchange Theory](#)

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Social Exchange Theory

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Definition

A broad conceptual paradigm that aims to predict how social interactions and relationships are built, maintained, and ended.

Introduction

Social exchange theory refers to a broad conceptual paradigm for understanding social interaction, which can be found in a number of social science disciplines including, for example, social psychology, anthropology, management, and sociology. It is therefore not a single theory of social exchange (Barbalet 2017) but can be better thought of as a family of conceptual models (Cropanzano et al. 2017; Cropanzano and Mitchell 2005). These conceptual models aim to predict how social interactions and relationships are built, maintained, and ended (Agnew and Lehmiller 2007). According to social exchange theories, social life involves a series of sequential interactions between two or more parties (individuals or institutions), in which resources, material and nonmaterial, are exchanged (Homans 1958). Over time, these interdependent, reciprocal exchanges have the potential to foster high-quality relationships characterized by loyalty, trust, and mutual commitments.

Background and Principles of Social Exchange Theory

The foundational work for social exchange theory can be found in the writings of scholars like George Homans (1958, 1961), Peter Blau (1964), John Thibaut and Harold Kelley (1959), and Richard Emerson (1962). Homans (1958) conceptualized social behavior as an exchange of activity between

at least two people, which is more or less rewarding or costly. A behavior by one party elicits a reaction in the other party that “either reinforces the original action and therefore encourages its repetition or through punishment dissuades its recurrence” (Barbalet 2017, p. 1). Principles of operant conditioning in behaviorism thus underlie Homan’s approach to social exchange. In contrast, Blau’s (1964) approach builds on neoclassical economic theory and adapts a utilitarian view of human behavior. In his micro-exchange theory, Blau also believes social exchange to be a fundamental process in social life and considers the costs and benefits that accompany a person’s interaction. However, according to Blau’s (1964) utilitarian view, social exchange is characterized by voluntary acts of individuals that are motivated by the returns they are believed to bring. Moreover, albeit rewards might reinforce the behavior of individuals in social exchanges, Blau believes the process of reinforcement to be insufficient to explain the relation that develops between the interacting individuals. He therefore focuses on the emergent properties in interpersonal relations that arise from the reciprocal exchange of benefits between the participants.

Building on this early work different perspectives on social exchange have evolved over the years. These different perspectives, however, share some common features and guiding principles (see Cropanzano and Mitchell 2005): (1) exchange rules; (2) resources exchanged; and (3) interpersonal relationships. First, *exchange rules* reflect the guidelines of exchange processes and guide the behavior of the involved parties. Most research emphasizes the rule of reciprocity, albeit other rules are also relevant for understanding social interaction and exchange relationships. Reciprocity implies repayment in kind such that a positive treatment by one party is reciprocated by the other. While a positive norm of reciprocity has attracted the most attention by far, a negative reciprocity norm can also shape people’s behavior in exchange processes (Cropanzano and Mitchell 2007). For example, experienced harm by one party might be reciprocated. In addition, experienced workplace incivility was found to facilitate

interpersonal deviance, particularly for individuals who were high in both hostile attribution bias and negative reciprocity beliefs (Wu et al. 2014). Some scholars assert that reciprocity is a tendency that is learned by people through the process of socialization, whereas others argue that it is driven by evolutionary considerations and facilitated by cognitive adaptations (e.g., Cosmides and Tooby 2005). In general, it appears that the norm of reciprocity is a universal principle, although the degree with which this principle is applied by individuals and cultures differs. Depending on whether individuals endorse the norm of reciprocity more or less, they are referred to as higher or lower on exchange ideology. For example, in their longitudinal study of conscripts to military service, Pazy and Ganzach (2010) found perceived pre-entry organizational support was positively related to combat choice service, particularly so for conscripts high in exchange ideology. While most research emphasizes reciprocal exchanges that do not require explicit bargaining, other forms such as negotiated agreements do exist (Cropanzano and Mitchell 2007). Negotiated exchanges tend to be more explicit and *quid pro quo*, they are often part of economic transactions and thus less likely to contribute to closer relationships, and they may or may not imply legal or contractual sanctions.

Second, *exchange resources* refer to the types of resources and potential benefits in exchange processes. These are typically classified into economic and socioemotional resources (Cropanzano and Mitchell 2005). Economic resources are commonly tangible and meet the individual's financial needs (e.g., money, goods, etc.). In contrast, socioeconomic resources are commonly not tangible and yield symbolic value (e.g., loyalty, love, etc.). The receipt of socioeconomic benefits further conveys the message to its beneficiary that he/she is valued and respected.

Finally, a common feature of social exchange theories is the focus on the development of *social exchange relationships*. The focus on interpersonal connections is particularly relevant to the study of workplace relationships in management and

organization science. According to Blau (1964), individuals either engage in economic exchange or social exchange with other parties. Economic exchange relationships entail clearly specified benefits of short-term financial and material nature, whereas social exchange relationships are characterized by unspecified obligations of socioemotional nature. Social exchange relations, thus, bear a greater risk that a favor demonstrated by one party is not returned and therefore require a certain level of trust at the beginning. Over time, mutually benefiting reciprocal exchanges foster positive, enduring relationships characterized by loyalty, trust, and commitment, whereas economic exchange relations do not. For example, employees who perceive their employers providing organizational support and caring about them, reciprocate with more positive work attitudes (e.g., commitment) and higher levels of extra-role performance.

Conclusion

Social exchange theory has emerged as one of the most prominent theoretical perspectives for understanding social interactions and relationships in the field of social sciences. It has become an integral part of theories such as psychological contracts, organizational justice, organizational support, and leader-member exchange, and social networks. Nevertheless, social exchange theory has its limitations. Individual self-interest, for example, is not the only possible reason for social exchange; other exchange rules do exist (e.g., altruism, competition) but have been less researched. In addition, social exchange is rarely an isolated event but rather implies a multitude of social exchanges in which actors are engaged simultaneously (Barbarlet 2017). Most recently, scholars have also criticized the lack of sufficient theoretical precision (e.g., overlapping constructs), which might undermine the utility of social exchange theory (Cropanzano et al. 2017). Social exchange theory, however, remains a powerful conceptual framework that explains how reciprocal transactions foster and maintain social relationships and – when mutually beneficial for

the involved parties – contribute toward high-quality relationships over time.

Cross-References

- [Adaptation](#)
- [Altruism](#)
- [Positive and Negative Reinforcement and Punishment](#)
- [Reinforcement Schedule](#)
- [Resources](#)
- [Strong Reciprocity](#)

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Social Exclusion

- [Adaptations to Avoid Ostracism](#)
- [Humor and Ostracism](#)
- [Peer Rejection, Gender Differences in Response to](#)

Social Exclusion or Rejection

- [Sociometer Theory](#)

Social Factors and Crime

- [Criminology](#)

Social Grooming

- [Cooperative Grooming](#)

Social Groups

- [Human Groups](#)

Social Habit Development

- [Social Development](#)

Social Hierarchies

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Synonyms

Group organization; Social rank; Social status;
Social structure; Status hierarchy

Definition

Social groups often are organized hierarchically, such that higher-ranking group members have greater control over valued group resources than other group members. Higher-ranking individuals also enjoy relatively more freedom to act in accordance with their own goals and desires and have greater capacity to exert their will over lower-ranking group members. Ultimately, these proximate advantages yield fitness benefits for high-ranking individuals and their offspring and help lower-ranking group members by allowing them to benefit from the increased overall prosperity of the group.

Introduction

Across many group-living species, to include primates, social hierarchies exist in which high-ranking individuals control a disproportionate amount of resources and influence in the group (Maner and Case 2016). The ubiquity of hierarchy among social species is likely due to its evolutionary benefits for both the individual and, potentially, the group (Maner and Case 2016; Van Vugt 2006). These individual- and group-level benefits are theorized to have perpetuated the existence of hierarchically arranged groups throughout evolutionary history. The study of humans and nonhuman animals has revealed some functionally specific behavioral and

psychological capacities that facilitate individuals' ability to navigate social hierarchies (Cheng et al. 2013). Other work has identified some of the key fitness benefits experienced by groups with hierarchical structures (Powers and Lehmann 2014; Van Vugt 2006). Together, these complimentary streams of research provide compelling evidence for the evolutionary advantage of social hierarchy.

Individual-Level Fitness Benefits of Social Hierarchy

Social hierarchies provide ample opportunities for individuals to accrue both direct and indirect fitness benefits. Regarding direct benefits, high-ranking individuals tend to receive specific perks unavailable to those lower in the hierarchy, such as a disproportionately large share of a group-produced good (von Rueden and van Vugt 2015). Importantly, these benefits come to high-ranking individuals without resistance from lower-ranking group members. That is, high-ranking individuals do not have to continuously achieve their rank on a case-by-case basis, but rather, their reputation remains stable over time within the group thus affording the accumulation of fitness benefits (Henrich and Gil-White 2001).

Beyond receiving additional benefits, high-ranking individuals also are subject to fewer constraints than low-ranking group members. For example, high-ranking members in certain small-scale societies sometimes have rights to polygyny that low-ranking members do not (von Rueden and van Vugt 2015). This combination of increased access to fitness-enhancing resources and decreased social constraints provide high-ranking individuals with easier routes to evolutionary success than their low-ranking counterparts.

In addition to the direct benefits awarded to high-ranking individuals, they are awarded indirect benefits as well. Specifically, high-ranking individuals receive higher social status, represented by things such as deference from lower-ranking group members and increased

mate value, ultimately leading to tangible fitness advantages. Specifically, von Rueden and van Vugt (2015) found that social status in small-scale societies was positively associated with reproductive success. Notably, this association remains when material resources are equal between high- and low-ranking individuals. For example, among the Tsimane of Bolivia, leaders of fishing excursions do not take more fish than others, but they do enjoy greater reproductive success and social support than lower-ranking individuals (Glowacki and von Rueden 2015).

Dominance and Prestige: Two Evolved Mechanisms to Navigate Social Hierarchies

Because social hierarchies have been a prominent feature of many social groups throughout evolutionary history and provide immense opportunity for fitness benefits, many species possess behavioral repertoires designed to successfully navigate social hierarchies. Scholars have classified these behavioral repertoires into two categories: a socially coercive strategy in which higher rank is acquired through actual or threatened aggression – the dominance strategy – and a more pro-social strategy – the prestige strategy – in which elevated social standing is achieved by demonstrating group-valued skills and expertise.

One key difference between the dominance- and prestige-based strategies is the route through which deference is conferred. Individuals who employ the dominance strategy use aggression and intimidation to demand deference from subordinates (Cheng et al. 2013). Importantly, their tactics can often be more subtle than direct physical aggression, such as manipulating control of a valuable resource. For example, dominant leaders have been observed to monopolize control over resources such as useful information and access to valuable social partners (Maner and Case 2016). Through anti-social means such as these, dominant individuals are able to establish and protect their high-ranking positions and, as such, are able to reap the fitness benefits associated with those positions.

In contrast to the dominance strategy is the prestige strategy – another viable route through which individuals can navigate their group's hierarchy. The prestige strategy involves receiving freely conferred deference from subordinates by demonstrating one's worth to the group (Henrich and Gil-White 2001; Maner and Case 2016). In essence, subordinates trade their deference for access to the prestigious individual with the goal of learning his or her valuable skills. Prestige is a strategy primarily observed in humans that requires advanced cognitive abilities such as ranking the skills of others and preferentially copying those who rank highest. These learning capacities allow prestigious individuals to maintain high social rank well past their physical primes, as evidenced by the high status of the elderly that is much more common in humans than in other species. Crucially, it is not enough to have valuable skills and abilities; leaders must also be willing to share their expertise with the group to garner prestige (Sugiyama and Sugiyama 2003). Thus, prestigious leaders help the group by acting as a model for others to follow.

Furthermore, prestigious individuals differ from dominants in how they obtain and maintain influence over others. Prestigious individuals' opinions are given great consideration and typically are followed, but deference is not required as it is for dominants. For instance, among the Nyangatom, a nomadic group in East Africa, unresolved conflicts can be presented to the council of elders for mediation. Although their word is not binding, to not follow it would likely result in social consequences from other group members, such as exclusion from group activities (Glowacki and von Rueden 2015). By garnering rewards through prosocial behaviors that benefit the group, prestigious individuals procure a fitness advantage over lower-ranking individuals.

Group-Level Fitness Benefits

Given the numerous fitness advantages enjoyed by those with high social rank, why do some group members choose to follow? Throughout phylogenetic history, between-group

selection pressures, such as intergroup conflict, were sometimes stronger than within-group selection pressures. As such, groups that could collectively work together to produce the best outcomes for the entire group had an advantage over groups that were unable to coordinate their actions (Van Vugt 2006).

Hierarchically structured groups are best able to act collectively to reach a common goal that benefits everyone (Glowacki and von Rueden 2015). Indeed, even in egalitarian groups, task-based hierarchies sometimes emerge to facilitate collective action for a common good (e.g., Powers and Lehmann 2014). One of the key reasons collective action can fail is because group members known as “free-riders” enjoy the common good without themselves contributing to its production. Because punishing and deterring free-riding is one of the primary functions served by high-ranking group members (Lukaszewski et al. 2016), hierarchically arranged groups historically were more efficient than egalitarian groups at carrying out the types of collective action required to outcompete intergroup rivals.

Because hierarchically structured groups can outcompete groups with more egalitarian structures, individual members of those hierarchical groups tend to personally prosper – they enjoy elevated resource potential and reproductive success. This is one reason social hierarchy can become cemented into a group (Powers and Lehmann 2014). Moreover, because members of groups become dependent on the common good produced by hierarchical groups, they tend to remain in those groups, even when they themselves hold a lower-ranking (and less desirable) position within the group’s hierarchy (Powers and Lehmann 2014). Thus, by increasing the productivity of the group as well as group members’ dependence on the group, social hierarchy can create powerful, cohesive groups that are better equipped to survive than egalitarian groups.

As well as being better equipped to survive at their current size, groups that are organized hierarchically also are better equipped to expand in number compared to egalitarian groups. After

the advent of agriculture, human groups grew in size in response to the increase in available resources but, simultaneously, those resources became more easily monopolized than ever before, leading to increased intragroup competition and free-riding. Because egalitarian groups are less equipped than hierarchically arranged groups to discourage free-riding, groups without social hierarchy had an especially difficult time maintaining their prosperity. In contrast, groups with stringent social hierarchies experienced unprecedented levels of cooperation and coordination, allowing them to expand even further in size (Richerson and Boyd 1999).

Conclusion

Compared to more egalitarian social structures, social hierarchies provide greater opportunities for group-level fitness advantages through leader-follower dynamics that promote collective action and conflict resolution. Nonetheless, not all group members benefit equally from social hierarchy due to the stark contrast in individual-level fitness advantages at different levels of the hierarchy. To capitalize on hierarchically arranged groups, humans and other social organisms employ functional strategies, namely, dominance and prestige, to help them successfully navigate those hierarchies, ultimately maximizing their ability to survive and reproduce. Due to the evolutionary benefits available to members of hierarchically structured groups, it is no surprise that social hierarchy has pervaded almost every human society.

Cross-References

- ▶ [Examples of Group Selection](#)
- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Humans: Within-Group Conflicts](#)
- ▶ [Language and Economic Cooperation](#)
- ▶ [Living in Groups](#)
- ▶ [Nonhuman Primates: Between-Group Conflicts](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)

- ▶ Polygyny and Male Risk-Taking for Status
- ▶ Primate Dominance Hierarchies
- ▶ Service-for-Prestige Theory of Leader-Follower Relations
- ▶ Status and Reproductive Success

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Social Hierarchy

- ▶ Alpha, Beta, and Gamma Males
- ▶ Dominance Hierarchy
- ▶ Higher Status in Group
- ▶ History of Dominance Theory
- ▶ Men's Egoistic Dominant Acts
- ▶ Serotonin and Dominance
- ▶ Status and Redistribution of Resources
- ▶ Status Competition and Peer Relationships in Childhood
- ▶ Women's Prosocial Dominant Acts

Social Hypotheses of Homophobia

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Synonyms

Homonegativity; Sexual prejudice

Definition

An umbrella term for a negative (attitudinal, affective, or behavioral) response towards homosexuality and homosexuals.

Introduction

Following societal change in thinking about the status of homosexuality and its politically motivated removal from the *Diagnostic and Statistical Manual of Mental Disorders* in 1974, research on the origin of homosexuality declined and was replaced by studies on homophobia. The term

homophobia, defined as “the dread of being in close quarters with homosexuals – and in the case of homosexuals themselves, self-loathing” (Weinberg 1972, p. 4), has been repeatedly criticized for its inherent evaluation of the response as (fundamentally) fear-based, pathological, irrational, and even unscientific (e.g., O'Donohue and Caselles 1993). As a consequence, a variety of broad and narrow re-definitions of the term as well as alternative terms, among others, *homonegativity*, *homosexism*, and *sexual prejudice*, (Herek and McLemore 2013; O'Donohue and Caselles 1993), emerged. Accompanied by several theoretically and methodologically diverging measures, this conglomeration of neologisms for the same, a fraction of the same, or a similar construct has been impeded the investigation of homophobia and its underlying mechanisms because of questionable validity of comparisons across studies. Nonetheless, several socially rooted factors associated with negative responses (of heterosexuals) towards homosexuality and homosexuals in the Western civilization could be repeatedly and robustly identified, allowing for the following formulation of social hypotheses of homophobia.

Religiosity, Fundamentalism, and Right-Wing Authoritarianism

A majority of studies, mostly relying on occidental samples, found a positive association between (Christian) religiosity and homophobia, which has been also reported for Muslims (e.g., Anderson and Koc 2015). Herek and McLemore (2013) interpreted this correlation in terms of three psychological functions: (1) The maintenance and strengthening of one's religious identity, which relies on a specific value system and moral conviction; (2) the reinforcement of the affiliation with one's religious group; and (3) the countering of one's experienced insecurities by (re-)affirming one's compliance with normative order due to an “unequivocal obedience to religious authority, strict conformity to religious teachings, feelings of moral superiority over outgroups, and self-righteousness” (i.e., fundamentalism; p. 10).

Especially the latter two functions might have been phylogenetically advantageous, since they enhance ingroup cohesion, which might have been critical for the group's survival.

However, these functions neither apply to every highly religious heterosexual person nor is every highly religious person invariably homophobic. On the contrary, several findings suggest that some highly religious individuals accept homosexuals (e.g., Hunsberger and Jackson 2005). These individual differences may be attributable to right-wing authoritarianism (RWA), a personality characteristic found to be positively associated with both homophobia and religious fundamentalism (Altemeyer and Hunsberger 1992). RWA is characterized by allegiance to established authorities, antagonism towards societal minorities, and conformity with conservative values and traditions. It has been argued that highly authoritarian individuals, who also tend to be religiously fundamentalist, condemn any form of nonconformist, non-heteronormative life style as a consequence of their vehement advocacy of conservatism and traditionalism, resulting in homophobic tendencies (Nagoshi et al. 2008). Yet, the correlation between religiosity and homophobia has been found to persist even when controlling for RWA (Johnson et al. 2011), supporting an association between religiosity and homophobia independent of authoritarian tendencies. In summary, previous and current research suggests that homophobia is positively associated with rudimental beliefs and social attitudes including religiosity (hypothesis 1), fundamentalism (hypothesis 2), and right-wing authoritarianism (hypothesis 3).

Gender, Gender Role, and Masculinity

Men have been consistently observed to be more homophobic than women and to hold more negative attitudes towards homosexual men than homosexual women (Herek and McLemore 2013). This gender difference and the differentiation regarding the homosexual's gender have been argued to be created as a consequence of the sociocultural pressure of adhering to a specific

gender role. While women also face gender role expectations, men are confronted with more (ingroup-)dynamic, inflexible, and sensitive societal ideals of masculinity that have to be proven on a regular basis in order to achieve acceptance by other male heterosexuals (Herek and McLemore 2013). Consequences of failing the expression of masculinity are, among others, being labeled homosexual (e.g., Bosson and Vandello 2011) and aggressive behavior against oneself (e.g., Parrott 2009). As Herek and McLemore (2013) put it, “sexual prejudice is often a strategy for men to demonstrate—both to others and themselves—their ability to meet cultural expectations about masculinity” (p. 14).

From an evolutionary psychological point of view, expressing one’s masculinity might have been fruitful for attracting potential mating partners, because aggressively demonstrated strength and superiority over (apparently) physically weaker males might have appeared as an improvement of the individual fitness and, thus, the chances of the offspring’s survival. In other words, natural selection might have contributed to the continuance of homophobia (see ► [Genetic Hypotheses of Homophobia](#)). In summary, research suggests three further hypotheses: In face of different social role expectations, Heterosexual men display more homophobic responses than heterosexual women (hypothesis 4), hold more negative attitudes towards homosexual men than towards homosexual women (hypothesis 5), and would show more homophobic responses if their masculinity is threatened (hypothesis 6).

Are Heterosexual Homophobes Secretly Attracted to Homosexuals?

Research on the popular belief that male heterosexual homophobes are as a matter of fact closet-homosexuals who either try to conceal their own and true sexual attraction towards men or use such an attitudinal stance as a solution for an inner conflict with their world view (i.e., as a defensive reaction, see above) remains inconclusive (Herek and McLemore 2013). As

Herek and McLemore pointed out, although several studies apparently showed same-sex attraction in self-proclaimed homophobic heterosexual men, this interpretation is debatable due to methodological limitations. While it cannot be fully excluded that homophobia also serves as a defensive function for some undisclosed homosexual men, current research generally does not support this notion.

Homophobia as a Culturally Driven Phenomenon?

Herek and McLemore propose that homophobia is a cultural rather than a primarily psychologically established phenomenon. According to them, cultural institutions, for example religious denominations, uphold a (self-defining) homophobic doctrine. Along with political and juridical decisions, these cultural institutions define and structure the social environment in which the individual is placed. They distribute power and status among groups, subsequently specifying more and less desirable group affiliations. The individual naturally strives for the satisfaction of critical psychological needs (see above) as well as an opportune group affiliation, which culminates in the internalization of the externalized stigma. The political development in the Western society in the last 40 years proves this account to be somewhat accurate, as can be observed in decreased criminal offenses against homosexuals and the overall more favorable opinion towards homosexuality.

This might be partly explained by Allport’s (1954) Intergroup Contact Theory, which states that positive intergroup contact can diminish prejudice. Through the change in the societal perception of homosexuals, the subsequent inclusion of homosexuals in the “inner circle,” and the increase of the salience of homosexuals in everyday situations and selective institutions (e.g., student clubs representing homosexuals), the higher probability of a positive (less stigmatized) contact with homosexuals might lead to an additional decrease in homophobia. The contact hypothesis has been supported for antigay attitudes (e.g.,

Herek and Capitanio 1996). In other words, positive contact with homosexuals is correlated with a decrease in homophobic tendencies in heterosexuals (hypothesis 7).

Still, the development towards more political correctness and a heightened chance in positive contact with homosexuals does not cover latent signs of homophobic tendencies like the ongoing pejorative use of homosexuality or the prevalent stigmatization of homosexuals in sports, which alludes to an underlying, more visceral, and phylogenetic aspect of homophobia beyond a mere cultural stigma.

Conclusion

To sum up, homophobia remains a multifaceted, complex phenomenon, rooted both in cultural, social, evolutionary, and differential psychological mechanisms. Although current research suggests that religiosity, religious fundamentalism, authoritarianism, male gender role expectations, and masculinity play a major role in the development of homophobia and that sociocultural acceptance of homosexuals as well as positive contact are associated with less homophobia, measures beyond self-rated attitudes towards homosexuality or homosexuals have to be developed to measure homophobia (e.g., implicit measures) more objectively and accurately (i.e., to control for socially desirable responding) to fully grasp the sources of homophobia. Moreover, research on homophobia has to further expand to non-Western societies in order to distinguish religious from cultural influences on homophobia and clarify the function(s) of homophobia. A distinct and elaborate definition of homophobia is necessary, especially for the better understanding of the link between negative attitudinal, affective, and behavioral responses towards homosexuality and homosexuals. It is only by finding an enlightened and globally functional conceptualization that discrimination of sexual minorities like homosexuals can be fully understood and diminished on an international level.

Cross-References

► Genetic Hypotheses of Homophobia

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Social Identity

- [Groups and Categories](#)
- [Honor Code](#)

Social Identity Formation

- [Self-Concept](#)

Social Inclusion or Acceptance

- [Sociometer Theory](#)

Social Information Processing

- [Social Cognition](#)

Social Intelligence Hypothesis, The

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Synonyms

[Machiavellian intelligence hypothesis](#); [Social brain hypothesis](#); [Social complexity hypothesis](#)

Definition

The social intelligence hypothesis is a scientific hypothesis proposing that social complexity was the main selective force shaping the evolution of sophisticated intelligence and large brains in extant animals.

Introduction

The social intelligence hypothesis (SIH) is a popular hypothesis that purports to explain the evolution of large brains and sophisticated cognitive abilities. The SIH proposes that social complexity is cognitively demanding and is thus the key selective pressure affecting brain size and, by extension, intelligence (Dunbar 1998; Humphrey 1976; Jolly 1966). The SIH was originally developed to explain the large brains and intelligent behavior of primates compared to other animals (Dunbar 1998). It has also found support across many mammal and bird species to explain variation in both brain size and cognitive abilities (Dunbar and Shultz 2007; Shultz and Dunbar 2010). Though often pitted against “ecological” hypotheses, which emphasize the role of diet and environmental challenges in brain evolution, proponents of the SIH often claim that the two are not mutually exclusive. Instead, they propose that ecological problems are solved socially, not individually, and that ecological selection thus acts indirectly on brain size through selection for social intelligence (Dunbar and Shultz 2007). More conservative forms of the SIH simply posit that more complex social groups favor specialized social cognition. But ultimately, the SIH suggests that the primary function of intelligence is in the social domain.

Origins of the SIH

The SIH was originally formulated based on the observation that primates in general, and great apes in particular, have unusually large brains and uniquely complex social systems. The origins of the social intelligence hypothesis are usually credited to Humphrey (1976). Though Chance

and Mead (1953) and Jolly (1966) had previously developed similar ideas, they were not as widely read or detailed as Humphrey's (1976) work. Chance and Mead (1953) suggested that male-male competition for access to mates in primates may have been a strong driving force in the evolution of the human cortex. Years later, after observing that lemurs have quite complex societies, but do not show the intelligence displayed by simiiforme primates (monkeys and great apes) when dealing with the physical world, Jolly (1966) suggested that social complexity preceded and defined the nature of general intelligence. Independently, Humphrey (1976) suggested that the social realm offers far more opportunity for cognitive challenges than the physical world. He observed that, although primates did not need to be particularly strong innovators, their survival required a high level of practical knowledge about their environment and that this knowledge was acquired socially. This type of society, with mixed age and sex members, creates a degree of complexity where social intelligence can have large payoffs, ultimately leading to the development of culture and human intelligence.

Eventually, with advent of empirical data relating social complexity, social intelligence, and brain size, the SIH became the most popular hypothesis for the evolution of intelligence. Overall, the SIH makes four key predictions: (1) social complexity is the main selective force behind enlarged brains and general intelligence, (2) complex social groups select for greater social intelligence than less complex groups, (3) social intelligence may be transferred for use in the physical domain, and (4) large brains and intelligence are primarily used for solving social problems.

Social Intelligence in Primates

Primates possess many sophisticated socio-cognitive skills (Barrett et al. 2003; de Waal 1982; Seyfarth and Cheney 2012). For example, in complex primate societies, keeping track of relationships among other individuals is critical for access to mates and food resources. Two social cognitive skills of particular interest are recognition of third-party relationships and theory of

mind. Not only do primates recognize other individuals in their group and understand their own relationships to those individuals, but they also recognize the relationships between group members to whom they themselves are unrelated; this entails recognizing third-party relationships. This skill is particularly interesting because, although remembering as many as 100 other individuals in a primate group may be difficult, the number of pair-wise relationships that are possible, even in small groups, is combinatorially massive and thus intellectually challenging (Seyfarth and Cheney 2015). Theory of mind, which is the ability to recognize mental states in other individuals, is an advanced cognitive skill that helps predict the actions of others. Theory of mind likely came about as a result of social pressures in humans, but the rudiments of this ability appear to exist in the great apes (Call and Tomasello 2008). For a more complete summary of primate social intelligence, see Barrett et al. (2003), Cheney and Seyfarth (1985), and Seyfarth and Cheney (2012). Today, a vast number of social cognitive skills have been observed in primates such as reconciliation, reciprocity cooperation, and communication to name a few. In general, the great apes appear to outperform monkeys, which correlates with the greater brain size observed in great apes. The presence of sophisticated social cognition suggests a strong degree of selective pressure for such skills, and these skills are related to fitness in primates (Seyfarth and Cheney 2015). This research supports the idea that selection has favored the evolution of social intelligence.

Social Correlates with Brain Size in Primates

Interest in the SIH grew with the advent of research that correlated specific measures of social complexity with measurements of brain size in primates. Group size was the first quantitative measure of social complexity, and it was correlated with a quantitative measure of brain size (Dunbar 1998). Group size was chosen as the key measure of social complexity because primates interact individually, in potentially fitness-affecting ways, with every member of their groups, and because it is an easy number to obtain for most species. The ratio of the neocortex

to the rest of the brain was preferred in much of the research on the SIH because body size is a much more evolutionary labile trait than brain size. Other measures that were also related to neocortex ratio include tactical deception, grooming clique size, rates of social play, type of mating system, and the presence of long-term stable social bonds (Dunbar 1998; Dunbar and Shultz 2007). Rates of social learning have also been associated with multiple measures of brain size (Reader and Laland 2002).

Defining Social Complexity

Most of the aforementioned studies relating brain size to some aspect of primate sociality also purported to identify the factor that makes primate groups socially complex. Group size remains the most popular measure of social complexity across all species despite its shortcomings, and no other measure has quite been able to replace it, despite varied proposals regarding what makes an animal society complex. Other measures of social complexity that have been studied are fission-fusion dynamics, complex alliances, presence of a linear dominance hierarchy, transactional interactions, or even crèches (for a review and critique, see Bergman and Beehner 2015). de Waal and Tyack (2009, p. 1) suggest that a commonality underlying various research on social complexity is the idea that individual animals must “keep track of interactions with other individuals with whom they must compete and cooperate.” Complex groups are those in which there are many such individuals; simple groups are those in which individual members are largely anonymous.

Primates certainly appear to possess sophisticated social intelligence, but social intelligence itself might be the cause of social complexity, which creates a level of circularity (Gigerenzer 1997). However, others argue that one *must* include social intelligence in the definition of social complexity, because social complexity is hypothesized to be cognitively demanding (Bergman and Beehner 2015). Thus, when researchers attempt to define social complexity, they should attempt to identify the cognitively demanding features of a social group. Using this logic, Bergman and Beehner (2015, p. 204)

suggested that social complexity should be defined as “the number of differentiated relationships that members of a species have with conspecifics.” This definition provides an objective and easy to quantify metric where cognition is clearly required to differentiate group members. Unfortunately, no definition of social complexity has been agreed upon to date; this is a major shortcoming of the SIH because social complexity is *the* key independent variable of the SIH.

Summary: Primates Are Specialized for Social Intelligence

Overall there is good evidence supporting the SIH in primates. Primates possess sophisticated social intelligence, many measures of social complexity correlate with brain size, and primate intelligence appears to be highly social in nature. Specific neurons and multiple brain regions have been found in primates that are specialized to respond to social features of the environment; this supports the idea that social complexity among primates favored “social brains” (Brothers 1990; Frith 2007). In addition to possessing sophisticated social intelligence and complex societies, primates excel at technical skills which require general intelligence (Byrne 1995; Reader et al. 2011). However, the causal relationship between these variables is unclear, and there is a dearth of evidence suggesting that social complexity leads to general intelligence in addition to social intelligence. In sum, primates appear to have social brains, and it also appears that their social complexity does relate to social intelligence, but this social intelligence may be more modularized than the SIH predicts. Research on the SIH is limited outside of primates, and support is much more mixed in non-primate taxa.

Testing the SIH in Non-primates

Mammals

Group size does not explain variation in brain size in carnivores (Finarelli and Flynn 2009), instead the hunting of large vertebrate prey best explains brain size (Swanson et al. 2012), nor does physical problem-solving skill relate to sociality in carnivores (Benson-Amram et al. 2016).

Extensive research on spotted hyenas, which have societies that exhibit convergent evolution with those of cercopithecine primates, provide an interesting case study into the evolution of social intelligence (Holekamp et al. 2007). They exhibit comparable social cognitive skills on every measure tested, including the recognition of third-party relationships, and compared to other hyenids, they have larger brains, are more social, and are better at tasks of physical problem-solving (Holekamp et al. 2015). Taken together, the data from Hyaenidae strongly support the SIH. However, compared to cercopithecine primates, spotted hyenas are small brained and poor physical problem solvers which contradicts many predictions of the SIH when considering their convergent sociality. In bats, living in stable social groups and smaller teste size were associated with an increase in brain size (Barton and Dunbar 1997; Pitnick et al. 2006). Within gregarious ungulates, those that live in stable year-round groups of at least six individuals had the largest brains (Pérez-Barbería and Gordon 2005). Another study found that monogamous ungulates that lived in mixed habitats had the largest relative brain sizes. Elephants are some of the largest brained and longest lived mammals; they are extremely social, forming differentiated relationships with many individuals. Like primates, elephants use tools and may have the rudiments of theory of mind (Hart et al. 2008). In cetaceans, pod size and relative brain size are associated (Marino 2002). Cetaceans also exhibit remarkable convergence with primates of cognitive abilities in both social and physical domains (Marino 2002; Marino et al. 2007). As cetaceans are among the largest brained mammals, this convergence strongly supports the SIH. A large study that included data from both the mammalian fossil record and extant species showed that increases in brain size in mammalian taxa across evolutionary time were associated with greater proportions of species, but not all species, within those taxa living in stable bonded groups (Shultz and Dunbar 2010). This provides some support for the SIH but does not explain the fact that many extant mammalian species with large brains are *not* social (Holekamp and Benson-

Amram 2017). In sum, varied measures of social complexity sometimes correlate with brain size in mammals, but this relationship is not consistent, and there are notable exceptions to this relationship (e.g., bears).

Birds

Birds are capable of many of same feats of social cognition and tool use as primates (Emery and Clayton 2004; Marler 1996). Beauchamp and Fernández-Juricic (2004) found no relationship between either mean or maximum flock size in birds and forebrain size, possibly because flock size is not a stable trait in most bird species. However, Burish et al. (2004) found that telencephalic volume fraction, a measure similar to neocortex ratios in primates, was related to a categorical measure of social complexity. Corvids, in particular among birds, appear to show convergent evolution with apes when it comes to brains and intelligence. Though corvids have smaller overall brain sizes, their relative brain to body size ratio is almost the same as that in chimpanzees (Emery and Clayton 2004).

In a large study that included several mammalian and bird taxa pair-bonding was found to be the strongest predictor of brain size. One explanation for why pair-bonding, as opposed to group size, is related to brain size outside of primates is because any groupings larger than a pair-bond in non-primates could be temporary aggregations or involve undifferentiated relationships (Dunbar and Shultz 2007). That is, primate relationships might be uniquely bonded such that group size approximates the number of bonded relationships only in primates. However, we now know that many species outside of primates do form stable bonds outside of pair-bonds (e.g., spotted hyenas or elephants). In addition, recent research that specifically examined bird species that *do* live in long-term stable groups found that stable groupings larger than the pair-bond were associated with smaller brains (Fedorova et al. 2017) contradicting the idea that long-term stable bonds might be the main cause of social complexity and larger brains.

Fish

Fish have both relatively and absolutely small brains, but fish have been shown to exhibit social intelligence with a diverse array of social cognitive skills documented, including reciprocation, transitive inference, coordination and cooperation, and the ability to remember past interactions with other individuals (Bshary et al. 2014). This research suggests that relatively simple brains can accomplish many of the same feats seen as intelligent in primates, which at the least suggests that a closer look at the rules governing social behavior may be required to measure social intelligence. That is, not all complex social behavior may be indicative of social intelligence. However, in one clade of fish, increased telencephalic size was related to monogamy (Pollen et al. 2007) which, similar to findings in birds, suggests pair-bonds may be related to relative increases in brain size.

Invertebrates

Insects possess remarkably miniaturized brains but can also show highly sophisticated social skills, among other cognitive abilities. This research suggests that brain structure or function may be more important to social intelligence than brain size (Lihoreau et al. 2012). Octopuses also provide an interesting case study. They are large brained relative to other invertebrates and show high general intelligence; they use tools, differentiate individual humans, and show advanced performance on a variety of cognitive tests (Darmaillacq et al. 2014); however they are strictly solitary. Overall, invertebrates possess a rich repertoire of cognitive abilities, which challenges the assumption of the SIH that complex cognition requires a large brain (for a full review of invertebrate cognition, see Roth 2013).

Conclusion

Overall, the SIH explains substantial variation in cognition and brain size within primates, particularly between monkeys and apes. Primates, including humans, do appear to have brains specialized for social cognition, and primate intelligence may be primarily social. Outside of

primates, both support and opposition have been found for the SIH; it is not yet clear what the major selective force favoring large brains and intelligence might be outside of primates, though sociability may have played a role. Certainly, the SIH has drawn attention to the fact that cognition in the social realm is both varied and complex and has a strong impact on fitness and daily lives of animals as well as highlighting the role sociability may have had in human brain evolution. Humans, as well as possessing high general intelligence, are largely unique in the realm of social cognition with regard to our language and culture.

However, the SIH still faces several serious challenges in addition to the described challenges defining social complexity. The SIH has yet to adequately account for grade shifts between different taxa. When comparing brain size to body size, or some other scaling variable, there are marked differences in the y-intercepts or slopes of the regression lines for different taxa. These grade shifts can bias measures of relative brain size and are often not taken into account when comparing measures of brain size to measures of social complexity. For example, orangutans are relatively solitary compared to other apes, but also large brained, in part because the great ape lineage lays on a higher grade than other primates (also see Finarelli and Flynn 2009). A recent paper that reanalyzed the data from primates using updated phylogenies and a larger number of species found no relationship between several measures of social complexity and brain size. Instead, frugivory was the strongest predictor of brain size (DeCasien et al. 2017). Frugivory may require both technical skill through the extractive foraging of fruits and seeds and increased spatial cognitive abilities for remembering when and where to find ripe fruit; this would tend to support ecological hypotheses for brain evolution rather than the SIH (Parker 2015). This finding highlights the fact that the SIH cannot explain general intelligence. Though the SIH hypothesizes that social intelligence may be used to solve physical problems, it seems that social intelligence instead is quite specialized; there is little evidence for transference between social and general intelligence. Though specialized social skills are related

to size of certain brain areas, there is a lack of research that directly relates social intelligence to brain size.

Despite these problems, the SIH currently remains one of the most popular hypotheses for the evolution of intelligence. Overall, there is ample evidence to support the claim that social complexity, large brains, and intelligence are strongly associated in many taxa. Just why or how they are related, and what selective pressures are involved when they are not related, must still be determined.

Cross-References

- Bird Tool Use
- Brain Size and Intelligence
- Cephalopod Tool Use
- Cognitive Buffer Hypothesis, The
- Communication and Social Cognition
- Convergent Evolution of Hyena and Primate Social Systems
- Convergent Evolution of Intelligence
- Convergent Evolution of Intelligence Between Corvids and Primates
- Cultural Intelligence Hypothesis, The
- Evolution of Intelligence, The
- Evolution of the Brain, The
- Extractive Foraging Hypothesis, The (Parker and Gibson 1997, 2015)
- General Intelligence Factor *G* (Reader, Hager, and Laland, 2011)
- Nonhuman Intelligence
- Primate Tool Use
- Relative Brain Size, Encephalization Quotient
- Social Learning and Social Cognition
- Social Tool
- Technical Intelligence Hypothesis, The
- Theory of Mind and Nonhuman Intelligence
- Vygotskian Intelligence Hypothesis, The (Moll Et Al., 2007)

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Social Interaction

► Interactive Language Development

Social Interaction Source

► [Yo-he-ho](#)

Social Isolation

► [Social Withdrawal in Childhood](#)

Social Knowledge

► [Social Cognition and Communication in Chimpanzees and Bonobos](#)

Social Learning

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Definition

In humans, social learning can take many forms. It can occur within academe, outside academe, as group learning and individual learning. We have evolved as social and learning beings.

Introduction

It may be stated that the role of evolution (Darwin 1859) has not been embraced widely by researchers in psychology and social scientists. However, increasingly, a number of contemporary scholars have suggested that the evolutionary process enables a better understanding of human cognition and socialization (e.g., Geary and Berch 2016; Bjorklund and Ellis 2014; Sweller 2008; Wellman 2014). To discuss the numerous ideologies of evolutionary psychology and their associations with social theories is beyond the limits of

this chapter, therefore, it will concentrate on two major perspectives. These are from Sweller's cognitive load theory and Geary's evolutionary cognition theory. They provide evidence from an evolutionary standpoint of how our memory system and cognitive abilities developed and the implications for learning. These are not the only way to look at the domains but they do provide some compelling evidence.

Cognitive Load Theory

Cognitive load theory (Sweller 2016) is a cognition theory originating in the mid-1970s related to our human memory system structures. Since its foundation, the theory has provided a framework for thousands of empirical studies in educational psychology and instructional design.

The theory is based upon substantial evidence that we acquire and process information via a very small, limited, finite working memory. It has been demonstrated that the recall limit after being shown novel information (e.g., a set of numbers or letters) is seven plus or minus two items (Miller 1956). Later research suggests it is possibly less at four plus or minus one (Cowan 2001). Furthermore, Peterson and Peterson (1959) established that the duration of working memory recall of items is only up to 20 s.

Without a strategy to process the held items, the novel information is lost forever. This is on the proviso that there is no strategy available such as grouping into meaningful blocks or chunks (Miller 1956). As an example, when faced with the task of recalling a random ten digit number (such as a new cell phone number), recall fails after around the first seven to nine digits then may only be retained for the limited time. Fortunately, working memory does interact with, as far as we know, an unlimited capacity long-term memory (Ericsson and Kintsch 1995).

Long-term memory is composed of prior knowledge in the form of hierarchical organized networks of the schema (Miller 1956). De Groot's foundational research with chess masters versus chess novices indicated that master chess players do not have a larger memory system compared to

novice or *weekend* chess players but more schemas in the form of previously remembered chess board configurations (see De Groot 1965 for a full description).

An Update of the Theory Aligned with Evolutionary Psychology

As aforementioned, cognitive load theory is based on the premise that if the characteristics of working memory capacity and duration limitations are ignored when instructional design procedures are developed, an incomplete, or failure of learning will result (Sweller 2016). When the theory was developing, it was based on the interactions between working and long-term memory. These interactions are still completely valid. However, it was not established that there was an association with the theories of evolution. Evolutionary cognition theories mapped against what we now know about contemporary cognitive architecture has been able to afford context and given substantial explanatory power to cognitive load theory and provide a wider range of hypotheses. Sweller is not unique in his analysis of cognition linked with evolution it has been comprehensively elaborated on by others such as Geary (2005), Campbell (1960), and Darwin (1859). Critically for this chapter, a latter reinterpretation of cognitive load theory by Sweller and Sweller (2006) specifically uses five principles aligned with evolution theory. These are the *information store principle*, the *borrowing and reorganizing principle*, the *randomness as genesis principle*, the *narrow limits of change principle*, and the *environmental organizing and linking principle*.

The *information store principle* indicates a very large knowledge base is essential. In nature, the storage facility is genomes which are also immense in holding of genetic information. Although there is no agreed information unit size for a particular genome capacity, it is in the thousands of smaller genomes and much more for larger genomes (Stotz and Griffiths 2004). So too for the store of human long-term memory as it has, as far as we are aware, an unlimited capacity for holding information. Our long-term memory

holds so much that if we were asked to write down all our knowledge, the task would probably be endless. As humans, we can hold simple information from minimal concepts such as an exclamation mark and a comma. We retain that a lemon is yellow and an egg is oval. We also hold larger procedural networks of how to use a pen, drive a vehicle, write a computer program, or read a spreadsheet. All this knowledge plus vastly more is retained in our long-term memory.

The *borrowing and reorganizing principle* for natural information systems is attained during either asexual or sexual reproduction. Prior hereditary lines are the providers of the information. In the case of sexual reproduction, that information is necessarily reorganized as an essential part of the process. Genetic information does not replicate to the identical. For example, offspring are usually similar but not an indistinguishable duplicate of their parents. Likewise in an equivalent process, the majority of the acquired knowledge kept in long-term memory is not a reproduction of the borrowed information and is always changed in some way. Sophisticated communication is an indication of how humans have evolved to acquire most of their information from each other. A learner borrows knowledge by observation, listening, and reading from what others write. Almost all we know is borrowed knowledge. We emulate what others do (Bandura 1986). We imitate other's gestures from infancy. For example, a child comes to understand that "clapping" is used as a signal of appreciation (at least in Western society). In addition, we listen to information from family members and the media. We utilize text to increase our knowledge in a domain. This process involves reorganization, in that new material must be combined with previous material stored in long-term memory using a constructive and reconstructive process.

Unique information is also created from the evolutionary process. Natural selection does so by a random mutation, which is a necessity and the primary source of all biological differences. Similarly, the *randomness as genesis principle* is based on the foundation that, if knowledge cannot be borrowed from others, learners have to randomly create new knowledge and test it for

value during problem solving. When faced with a novel problem all we can do is test it against previous learnt knowledge retained in long-term memory. This in turn generates new knowledge that we deem is either effective or ineffective. Effective new knowledge if, of use, can be retained in long-term memory while ineffective new knowledge is discarded.

To illustrate, if faced with four potential trails while being lost on a walk, we can only choose one and proceed. If it is ineffective we will turn back and choose one of the three remaining trails. The strategy will continue on until we discover the correct trail. The productive trail is retained in long-term memory and the others discarded. Clearly a random generate and testing procedure could result in an unworkable number of possible outcomes if there were too many trails. As another example, consider that there are two elements of A and B that need to be combined but there is no prior knowledge available of the correct combination. Using a random generate and test procedure, the permutations for A and B are 2. A combination of A, B, C, and D is more difficult to determine as the permutations are 24. For 7 letters, the total is 5040 permutations. If we must deal with 10 elements, there are 3,628,800 permutations. This has the task of problem-solving essentially unmanageable. Due to the number of possibilities, the combination of just 10 items, or even 7, will take much longer and clearly be beyond the limited capacity and duration of working memory.

Evolution by natural selection as well imposes restrictions on the possible generating number of mutations. A genome is generally limited in the number of changes to its genetic composition. Variations are usually slow and incremental as too many alterations could be unproductive or fatal. Genetic mutations thus are slight and occur over a prolonged and measured period. Similarly, the *narrow limits of change principle* is a safeguard that variations to long-term memory are minor and incremental due to the very limited capacity and duration of working memory. The quantity of randomly created new knowledge has to be restricted to preserve the functionality of the information stored in long-term memory.

The *environmental organizing and linking principle* endorses the previous four principles outlined. In nature, this final principle assures that a change is suitable for the prevailing environment. The environment does influence fluctuations to the information store however, the eventual goal of this store is to permit adaptive functioning in the given environment. The epigenetic system here is the stable governor and can turn genes on and off after cell division. Regardless, it does so evenly. The environmental organizing and linking principle similarly show that working memory is restricted when processing novel information, it has however much extensive, unidentified boundaries when processing known information imported from long-term memory.

The Link Between Cognitive Load Theory and Geary's Evolutionary Cognition Theory

The updating of cognitive load theory and implications for instructional design is due to the relationship with Geary's theory. Many aspects of Geary's thesis have been implemented and supported by contemporary cognitive load theory research. In addition, previous theoretical problems with cognitive theory insofar as findings have been clarified. Geary (2006) and Geary and Berch (2016) suggest evolved and nonevolved abilities have equivalency between natural selection and human learning to provide instructional procedures. Some knowledge is inherent and will need no instruction. Geary divides knowledge into what is known as *biological primary knowledge* and *biological secondary knowledge*. The two categories align with Sweller's theory in that it is only biological secondary knowledge that requires an awareness of the constructs of our memory system and implications for instructional design. This will be explained in the following section.

Biological Primary Knowledge

Biological primary knowledge tends to be concerned with generic skills that are essential to

human functioning. It is knowledge that we need to function at least basically in a society. It can be termed a *cultural knowledge*. Clearly, there are numerous adaptive difficulties accompanying a navigating of the social world. Humans have to maintain allies, manage status hierarchies, cope with the competing interests of others, interact with groups and other group members, coordinate social activities, and participate in joint decision-making. Humans have to create favorable conditions using others to their benefit and avoid being used by others for gain.

As well, they have to deal with the realities of the physical world. This is exactly what happens in the natural world (Geary and Berch 2016). A species has to cope with the competing interests of other species, create their own habitats, share their own habitats, and avoid certain habitats of other species. Species need to utilize other species by hunting and evade being used by others by avoiding becoming quarry.

We too as humans have evolved to acquire this knowledge automatically. To reiterate, it is that knowledge we really do not need to be explicitly taught. The capacity to learn our first language is a necessity for our species, and it is required of us to communicate verbally. The commencement of speech is an example (Kuhl 2000). The ability of toddlers with virtually no training to learn and be motivated to learn their first language (to the extent of at least being understandable) by listening is biological primary knowledge. An infant does not need instruction to utter sounds as it will make its first sounds independently. To teach a child to make a word needs to consider the physical mechanics needed to make the sound of the word. It requires a concurrent arrangement of lips, tongue, breath, and voice (Sweller 2008). Yet, without any explicit instruction, a child can independently verbalize this word and others at some stage of its development.

To be mobile is crucial and a child does not need to be taught how to rise upon its legs and take its first steps. Similarly, the recognition of faces (Bentin et al. 1999) is essential and a child has no need to be explicitly taught to distinguish parents, caregivers, family, or friends. As well, a child is able to read emotions from facial expressions and

can follow the gazes and gestures of others (Herrmann et al. 2007). In agreement is Bandura (1986), who states that the knowledge to imitate is a skill that has no need to be taught. Imitation is exhibited at an early age where young children will commence to frequently imitate the *other* without instruction. Although Piaget demonstrated this to occur at a later age of around two onwards (Piaget 1951), it is shown to commence as early as 6 weeks where babies imitated facial expressions of the mother (Meltzoff and Keith Moore 1994).

Biological Secondary Knowledge

The second category of biological secondary knowledge is information where instruction is certainly required. This class of knowledge is different from the first of biological primary knowledge as it is culturally specific (Sweller in Geary and Berch 2016). To be literate and numerate are skills that are needed to be explicitly taught. Educational institutions teach biological secondary knowledge to the members of its society to enable full and successful participation in that society. For example, academe usually instructs in language, mathematics, science, history, geography, and economics among other subjects in a curriculum. The knowledge within these domains are not automatically inherent in the genesis and progression of the human mind and therefore needs instruction.

Pronumerals and algebra as well are examples of biological secondary knowledge. That the pronumeral a can have a value for one equation and another value for an alternative equation must be specifically taught as well as the procedures to solve equations. We are not genetically programmed to spontaneously comprehend these type of mathematical constructs. In English, to comprehend that within our grammatical rules, a sentence must have a subject, is not a tacit construct for us. As infants, we may be able to learn to speak our first language by simply listening as it is biological primary knowledge. However to speak our language fluently, as required by our society, requires the biological secondary knowledge of the rules of grammar. An infant's biological

primary knowledge attained expression of *Me want drink* is not a grammatical sentence.

David Geary's categorization of knowledge is a logical proposition. The connection between the second category of biological secondary knowledge then has implications for learning and the role of explicit instruction.

Discovery Learning Versus Explicit Instruction?

For at least a half a century, there has been an energetic belief in many educational circles that we learn more efficiently by a *discovery* approach. Exemplified by Jerome Bruner in Bruner 1961 and Seymour Papert (1980), the philosophy has had many variants where labels such as *discovery learning*, *problem-based learning*, *inquiry learning*, *constructivist learning*, and *experiential learning* are exemplified (see Kirschner et al. 2006). The Piagetian theory of the construction of knowledge is also related here. The terminology tends to signify the same constructivist/discovery view point of emphasizing *minimally guided instruction* for the learner. It seems that a driver for the movement is an argument that travels along the following lines:

An immense amount of information and knowledge is learnt *outside* educational institutions. Furthermore, this information and knowledge are accumulated with ease and without intervention of an instructor. If this information is absorbed without structured, explicit methods and is successful, then it must be a useful paradigm. Moreover, the artificial methods by which we teach such as guided or direct instruction and transmission from a teacher must be insufficient. Certainly, the argument goes, current teaching methods are not exemplified by students learning syllabus content with ease and without intervention. So, we must then utilize the way information is absorbed in the *outside* world for use *inside* the educational institutions. If people learn by being *immersed* in a society/culture we can then immerse students in a subject or topic and thus somehow they will accrue the required knowledge and more importantly obtain *understanding*.

A common example of the unguided method is in science instruction. Students are placed in inquiry learning contexts and have to discover recognized principles by demonstrating the investigatory attributes of professional researchers (Van Joolingen et al. 2005). Another illustration is where university medical students in problem-based learning (PBL) courses are urged to find solutions for patients' common conditions using problem-solving techniques (Schmidt 2000). Guided, direct instruction and rote learning were deemed to be unproductive. Yet, what has been outlined in this chapter regarding secondary biological information and its processing by our cognitive architecture makes clear that having one discover information alone is not efficient. There are too many possibilities for a discovery path which may overload working memory.

There is no compelling empirical evidence that discovery approaches are efficient methods of learning in spite of decades of research. In stark contrast, there is a large body of evidence from numerous controlled empirical experiments that the epitome of direct instruction, that is worked examples, are substantially superior as instruction (see Renkl 2005). A worked example is a step by step guide given to novices in a domain that shows the solution to a problem. The alternative would have a learner discover the answer.

Consider the following algebra problem: $a + b = d$ solve for b where $a = 3$ and $b = 4$. A full worked example would give a step by step guide in perhaps less than 8 steps. However, a novice with minimal prior knowledge in the domain may not find a solution at all, or at least take some time to *discover* a correct solution. The reason for this is our human cognitive architecture. Working memory may be faced with numerous possible solution paths and be overloaded resulting in a learning failure.

Research on the traditional use of worked examples has shown that usually one or two worked examples are given then they are followed by a number of similar problems to solve. This is ineffective, and instead, it is more productive to have many worked examples initially, then followed, by similar problems to solve (Sweller and Cooper 1985).

As another example of the debate, *rote learning* is a strategy that within a discovery learning philosophy is frowned upon. Discovery type learning appears to use the rationale that better *understanding* within the learner is developed and certainly no understanding will ever develop by *rote learning*. A problem with this premise is that *understanding* is not defined (Sweller 2008). We know that the way our human memory system operates is critical for learning so it would be now used to look at what we mean by *understanding* as well as *rote learning* and how they could be placed within the operation of this system.

Although this may not be evident under a discovery learning philosophy, both understanding and rote learning are crucially dependent on our long-term memory store (Sweller 2008). Elementary math learning of tables by novices is an illustration of rote learning in early education. If a child can rote learn that $5 \times 9 = 45$; that knowledge is then stored in long-term memory. If the child can also understand that $\times$ means repeated addition so that $9 + 9 + 9 + 9 + 9 = 45$; this too can be stored in long-term memory. It is not the case that the first is stored and the second is not. What is more important is the differences between the two in the structure of the learning content. Learning with understanding requires large amounts of connected information stored in long-term memory. To make those connections imposes a huge amount of cognitive load on working memory during initial processing to have them stored in long-term memory. Thus as an alternative strategy, novice learners will rote learn (Sweller 2008). Learning with *understanding* does not negate the function of long-term or working memory. It means that learning with understanding results in a large amount of linked information needed to be stored in long-term memory. This linked information has features that are difficult to process in working memory. If we return back to the algebra worked example illustration previously as researched by Sweller and Cooper (1985), the continued processing of a number of worked examples initially results in more linked knowledge. This is then stored in long-term memory and therefore resulting in better *understanding* of, in this case, basic algebra.

Schooling, Observation, and Learning

An integral feature of social learning theory is people's observation of another (the model). The observation takes part within the context of social interactions and experiences. A model carrying out a behavior and the significance of that behavior is recalled with the order of events. The information is then utilized to guide following behaviors (Bandura 1986). Humans do not learn new behaviors merely by testing them and having a resultant achievement or failure. Observing a model can also prompt the viewer to engage in behavior they already learned. To be able to reproduce the actions of others including reproducing the *learning* of others could be viewed as the survival of a species. Educational institutions such as schools, colleges, and universities were set up for this reason. Too, they are not only considered as sites for social learning but also "content" learning. As previously outlined, almost all we know has been directly perceived or learnt through another person or group. Geary's category of biologically secondary knowledge covers the types of information that is found in every syllabus area within an educational institution. School was devised for the teaching of biologically secondary knowledge. This category of knowledge is unlike primary knowledge and is not likely to be attained without the constructs and tasks established in educational institutions (Sweller 2015).

Domain General and Domain-Specific Knowledge

According to Sweller (2015), knowledge that is *domain general* can be considered as *generic* and is aligned with Geary's biological primary knowledge. As outlined previously, they are essential human functioning skills that we have genetically attained without instruction. When solving any problem, the looking at differences between the goal and initial state of the problem and minimizing these differences is a first general problem-solving heuristic (Newell and Simon 1972). For example, when faced with a novel problem in

direction, we automatically look for differences in the present state of where we are, compared to the goal state of where we wish to go. We just do not inertly stand there. The knowledge is generic, essential for the survival of our species and does not have to be taught. A secondary response of studying the position of the sun or stars if possible as direction indicators is an example of *domain-specific knowledge* and has to be attained by prior instruction. Other examples of domain-specific knowledge are mathematical operations, the grammar of a language, chemistry principles, and computer coding or medical procedures. These too require detailed training. Educational institutions were established to address the need to teach domain-specific knowledge (which really can be considered biologically secondary knowledge). The chapter will now outline a cognitive load effect related to socialization.

A Collective Memory Through Socialization

Pass and Sweller (2012) state that from the viewpoint of evolution, natural selection supports the “fittest.” According to Brem et al. (2003), self-interest would appear to be a dominating and predisposing force for an individual. Furthermore, Richard Dawkins even labeled this tendency the “selfish gene” (Dawkins 1989). Although this argument of selfishness is questioned due to definitions (see Hawley 2016 for a fuller account), co-operation has the potential of strengthening the group with joint available resources rather than an individual working independently.

The use of group work in educational institutions is common. Group work can be defined as a small group of students who collaborate to learn and complete tasks. Humans working as a group in many situations can provide an individual with information more expediently, than trying to obtain that information without support from a group. In a group, detailed individual knowledge is not a requirement. Clearly, the group can access more resources than when working individually. A team of collaborating learners may

well be able to solve complex problems that may be insolvable for an individual learner (Pass and Sweller 2012).

Paas and Sweller have completed research related to this termed the “collaborative learning effect.” Recall, the borrowing and reorganizing principle (Sweller and Sweller 2006) where borrowing and reorganizing information from others is the main source of our knowledge. Correlated with this principle, is that rather than acquiring information alone, information can be better learned by us from an instructor or via instructional materials.

The collaborative learning effect is where during shared learning, that information can be obtained from other sufficiently knowledgeable people engaged in the same task (Pass and Sweller 2012). The effect has been demonstrated in cognitive load research comparing an individual to collaborative learning environments. The Pass and Sweller contribution is more empirically specific than that of Vygotsky and his construct of the *Zone of Proximal Development* (Vygotsky 1962), where terminology and specific outcomes have been accused by some critics as vague.

A detailed examination of group work from a cognitive load perspective will be now outlined: A co-joined working memory has the potential to increase the ability of the group producing a larger working memory. The elements of information necessary for a learning task can be divided between group members so memory load is shared by the group cognitive capacity. Note that *general* communication and coordination between the group members is a requirement as well; however, this is a biological primary knowledge process that has evolved and is not needed to be learned. Whereas the content of the learning task is biological secondary knowledge. Yet the collaboration (group work) versus independent (working alone) approach has two contrary consequences (Paas and Sweller 2012).

Firstly, a substantial working memory load can be inflicted by the learning material (the biologically secondary information). However, that can be shared over several cooperating members so that they have to devote less cognitive effort than

if they were learning alone. As a result, a large reduction in a singular working memory load can be distributed among group members. Secondly, by dividing the work the communication and coordination processes (group interactions) require the group members to invest an additional cognitive effort, which is an effort that individuals do not have to exert.

This cost of group interactions can be further divided into two categories of biologically primary knowledge or biologically secondary knowledge. The working memory costs of general group interactions may be minor because they are biologically primary. In contrast, the working memory costs of the task-specific group interactions may be considered because they are biologically secondary information. Consequently, a prospective advantage of group learning may only be evident if the working memory costs are largely biologically primary. According to Serfaty et al. (1998), the working memory costs of task-specific communication and coordination processes can be reduced by teaching those processes or by working in carefully designed learning settings.

Conclusion

From this chapter, evidence has been presented that our memory system has proceeded through evolution and developed to make us what we are. As outlined in the Introduction, these perspectives from David Geary, John Sweller, and others are not the only way to look at the domains but undoubtedly compelling ones. The interactions between evolution and our human cognitive architecture may enable a better understanding of why, what, and how we learn in both a social and educational context.

Cross-References

- Cultural Transmission
- Learning Versus Imitation

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Social Learning and Culture

► [Social Cognition and Communication in Chimpanzees and Bonobos](#)

Social Learning and Social Cognition

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Synonyms

[Cognition](#); [Culture](#); [Language](#); [Pragmatics](#)

Definition

Social learning as posited by Bandura (1977) states that all individuals learn from each other by means of observation, modeling, and imitation. Cognitive learning theory states that mental processes (i.e., learning) are influenced by both intrinsic and extrinsic factors. Social cognitive theory states that learning is directly associated with observing others and engaging in social interactions.

Introduction

The three basic types of learning theories include behaviorism (e.g., Skinner), social constructivism (e.g., Vygotsky), and cognitive constructivism

(e.g., Piaget). Within social constructivism one finds social learning theory, and within cognitive constructivism one finds cognitive learning theory.

Social learning theory as posited by Bandura (1977) states that all individuals learn from each other by means of observation, modeling, and imitation. Bandura's model includes attention, memory, and motivation as factors in learning. It has been said that social learning theory is a bridge between behaviorism and cognitive learning theories. Bandura believed in "reciprocal determinism" or when individuals jointly learn from each other.

Cognitive learning theory has grown out of cognitivism (Piaget) where learning occurs internally in response to experiences. Cognitive learning theory states that mental processes (i.e., learning) are influenced by both intrinsic and extrinsic factors. What occurs within the learner is as important as to what occurs in the environment. Cognitive learning theory encompasses social cognitive theory and social behavioral theory (Bandura 1977). Social cognitive theory states that learning is directly associated with observing others and engaging in social interactions.

Social learning and social cognition encompass many overlapping layers of cognition, social learning, language, and culture. Because these layers are overlapping, it is impossible to determine causal factors among them. However, it should be noted that language is central to all of these layers. Consequently, discussion will focus on the following: (a) language and social cognition, (b) language and social learning, and (c) language and culture.

Language and Social Cognition

Language and social cognition are inseparable. Mathew and Raja (2015) stated that, "Any account of human social cognition cannot get away from language" (p. 6). Social cognition (SC) is the way that one perceives, interprets, analyzes, and uses information about the social world in which we live. Mathew and Raja also stated that, "SC and language together, probably formed an evolutionary cycle where in advances in one could feed advances in the other, and it is unclear what human cognition would be like

without the powerful cultural augmentation that language provides" (p. 7). Social cognition will hereinafter be referred to as simply cognition.

Opposing views of the roles of cognition, language, and culture have emerged over the last 100 years. Fundamental to this review are brief discussions of the philosophical viewpoints of Cognitive Development Theory (e.g., Piaget), Social Interactionist Theory (e.g., Vygotsky), Universal Grammar or Universalist view (e.g., Chomsky), Nativist view (e.g., Pinker), Linguistic Relativity (e.g., Whorf), and Cultural Psychology (e.g., Markus, Shweder, or Rogoff).

Piaget's Cognitive Development Theory (also known as cognitivism) sequences learning according to different developmental stages (sensory motor, preoperational, childhood, concrete operational, and formal operational) (Piaget 1926). Children take an active role in learning and are not just passive learners. Initially children learn through manipulating their environment and sensory exploration (sensory motor phase). During the preoperational phase, children begin to think with words and symbols. In the concrete operational phase, children begin to think logically and their thoughts become more organized. It is not until the Formal Operations stage that children begin to think abstractly. Hence, Piaget's approach focuses on early learning and sequential development of cognitive processes. Other cognitivists include Vygotsky and Bruner.

On the "other end" of the philosophy continuum, one finds Social Interactionist Theory that incorporates aspects of developmental theory (Piaget 1926) and information processing model (MacWhinney 2005). Vygotsky was an early proponent (1962) of the idea that social interaction with others, particularly more experienced language users, plays an important role in language learning. Vygotsky suggested that social interaction is key to learning and consequently he proposed the zone of proximal development (ZPD). ZPD is the difference between what a learner can do and she/he cannot. The zone of proximal development is the area where a learner needs assistance from someone with higher skills. This is accomplished through scaffolding. Scaffolding is the process of encouraging learners through

progressive stepwise levels. Scaffolding was coined by Jerome Bruner and attributed to Vygotskian learning. The ZPD and scaffolding encompass Vygotsky's social and cognitive learning.

Noam Chomsky is best known for his belief in universal grammar and consequently the Universalist view of cognition (Chomsky 2006), i.e., language principles are innate and fixed (nativist view). According to Chomsky, the ability to learn grammar and language is hard wired into everyone's brain. In addition, language ability develops without being taught and in the absence of external stimuli (i.e., poverty of stimulus). The Universalist view grew out of universal grammar and espouses the belief that all human beings share a common set of cognitive abilities and that cultural variabilities and influences are nonexistent or negligible (Pinker 2002).

The separation of cognition and language and how language is acquired is still debated. However, most researchers will agree that cognition and language are inseparable and intertwined (i.e., whether a weak or strong connection exists). The role of language and culture has also been extensively disputed. The theory of Linguistic Relativity is discussed next.

The theory of Linguistic Relativity suggests that language affects how individuals see and construct their world (Lucy 1997). Lucy defines linguistic relativity as, "The linguistic relativity hypothesis, the proposal that the particular language we speak influences the way we think about reality, forms one part of the broader question of how language influences thought" (p. 291). Linguistic Relativity evolved from the earlier works of Benjamin Whorf (1956). Whorf believed that difference in language grammars and how the languages are used affects the manner and way in which speakers perceive the world and their environment. One can postulate that language is constructed and learned and therefore, a reflection of culture (Lucy 1997).

Cultural Psychology as defined by Shweder (1991) is the manner in which culture expresses and changes the mind resulting in cultural and ethnic diversity. This approach presumes that culture and cognition are inseparable and consequently, cognitive theories in one culture will

have less relevance in another culture. Markus (2013) stated that

Cultural psychology builds on one of the most fundamental ideas in psychology: The products of the mind are a function of the social communities that people are part of. Cultural psychology is an effort to recognize human nature and the different ways of being human (lines 8–9).

Rogoff (2003) states that all children approach developmental learning stages according to the cultural practices in which they have participated. Cultural practices are transmitted through language and social learning.

Language and Social Learning

Acquiring information from interacting and observing others is social learning (Crivello et al. 2018). Most learning takes place in social contexts (Vygotsky 1962). Consequently, social learning leads to enhanced cognitive, attentional bases, social reciprocity, and social communication. Language is the medium by which social learning occurs. Language for social learning and social interaction is pragmatics.

Pragmatics consists of the ability to use language socially and appropriately in given situations (Hymes 1972). Pragmatics is also concerned with how language is used and interpreted. It is thus the study of speaker-listener interactions.

Pragmatics consists of intentions on the part of the speaker to communicate a message. Speakers must have a reason to communicate (i.e., intent). This purpose to communicate occurs early in infancy in the form of nonverbal communications (e.g., smiles, coos) and develops into more meaningful exchanges with the onset of gestures combined with symbolic words. The purpose of a message is illocutionary intent. The actual message (nonverbal and verbal) is referred to locutionary language and the effect it has on the listener is the perlocutionary effect. All speakers must possess presuppositional knowledge of the listener (i.e., what background knowledge must the listener have so that the message is understood?). Children are unable to acquire presuppositional knowledge until they are able to take the perspectives of others (i.e., neo-egocentrism) and the ability to consider several aspects simultaneously (i.e., decentration).

Pragmatics is context specific, i.e., environmental context influences language interactions. And language is also capable of influencing the contextual environment (Hymes 1972). Bates (1976) stated that pragmatics occupies the interface among linguistic, cognitive, and social development. In sum, pragmatics parallels both social learning and cultural learning (i.e., acculturation).

Social Interaction is Cultural Interaction

Social interaction and cultural interaction are governed by rules of communication, which in turn are governed by language. In order to understand social interaction and cultural interaction, one must understand how culture and language (i.e., the symbolic representation of culture that holds meaning to a given group of individuals) are mediated through social interaction (Gibbons 2012). Culture and language define and determine how social interactions impact how individuals interpret their world (i.e., social interaction behaviors and value systems) and how individuals communicate.

Language can designate, associate, denote, or connote meaning (Brice and Brice 2009) and is expressed verbally via oral and written narratives as well as nonverbally through gestures, eye contact, and body language. Cultural variations exist in how language is expressed and used within different contexts. For example, verbal expression of emotions in Western culture may be considered appropriate, while in Eastern cultures this can be viewed as immature and disruptive to social harmony (Fernández et al. 2000). In the nonverbal language domain, some argue that facial expression of emotions is not culturally universal and may contain distinctive nonverbal “accents” and “dialects.” Tuning into these fine distinctions is important in understanding and interacting with culturally and linguistically diverse (CLD) individuals. Therefore, social interaction is complex and dictated by cultural variation, beliefs, and values.

Language and Culture

Defining culture is a complicated endeavor given its variation across domains and purpose, which is embodied within a historical context. An anthropological definition of culture is “that complex

whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society” (Tylor 1871, p. 1). Culture is also defined by Roseberry-McKibbin (2007) as, “Simply, culture is a dynamic set of values and belief systems that shape the behavior of individuals from various groups and communities” (p. 104).

Culture can be defined according to various continuums of behavior, individualistic vs. collectivistic cultures, loose cultures vs. tight cultures, low context vs. high context communication styles, and horizontal vs. vertical cultures (Triandis 2001). These continuums are not absolute; for example, individuals from collectivistic cultures can display behaviors that are individualistic. It is best to think of these continuums as ranges of behavior.

Individualistic Versus Collectivistic Cultures

Ting-Toomey and Chung (2012) refer to individualism as the broad value of tendencies of a culture to emphasize the importance of individual over group identity, individual over group rights, and individual needs over group needs. In contrast collectivism refers to the broad value of tendencies of a culture to emphasize the importance of the “we” identity over the “I” identity, group obligations over individual rights, and in-group-oriented needs over individual wants and desires.

Hence, individualistic cultures define the self as independent or apart from the group. The focus is on the person and less on the group (Ting-Toomey and Chung 2012). Individualistic cultures rely on internal and personal attributes to explain behaviors, e.g., Diego seeks the teacher’s approval because he needs reassurance. Individualistic cultures also emphasize the “autonomous self” (Ting-Toomey and Chung 2012), the outer portrayal of oneself (i.e., face) is self-oriented and self-driven (Triandis 2001). Individualistic cultures stress direct communication. An example of direct communication is when strangers establish relationships and communicate more openly and freely.

In contrast, collectivistic cultures value indirect communication, social interactions, and non-confrontations. Individuals from a collectivistic culture define themselves as part of a group and belonging to the group (Gudykunst 2003; Triandis

2001). Group participation and cohesion are of paramount importance (Brice and Campbell 1999). Behaviors are explained by collectivistic norms or standards of expected behavior, e.g. Diego seeks teacher approval because the close relationship to the teacher indicates his participation in the group. Collectivistic cultures emphasize “face” or being other-group oriented (Gudykunst 2003). Membership in the group gives one the right to become involved in the affairs of others, e.g., teachers or school psychologists may intercede on a student’s behalf. Examples of collectivistic cultures include many Latino cultures, Asian cultures, Middle Eastern cultures, African cultures.

Loose Versus Tight Cultures

Tight cultures have strong societal norms and low tolerances for deviant behavior (Gelfand et al. 2011). Collectivistic and tight cultures demonstrate a strong distinction between ingroup and outgroup members. Gelfand et al. (2011) also distinguish loose cultures as having weak norms and a high tolerance for deviant behaviors. Membership in collectivistic loose cultures tends to be less restrictive.

Loose cultures and individualistic cultures are a part of the same continuum, whereas tight cultures are associated with collectivistic cultures (Brice and Campbell 1999). Looseness carries the connotation of creativity. This is evidenced in language via word puns and humor. However, not all cultures will exhibit all behaviors consistent with either end of the individualistic/collectivistic or tight/loose distinctions. For example, Cuban culture exhibits traits of creative language use and puns although Cuban culture tends to exist along the collectivistic tight end of the continuum (Brice 2002).

According to Gelfand et al. (2011), the USA is considered to be a loose culture, while Japan is considered to be a tight culture. In comparing Japanese and US American ingroup vs. outgroup standings, Whitting (1989) uses American vs. Japanese baseball as a means of cultural contrasts. The point of ingroup vs. outgroup membership is illustrated when he quotes an American baseball manager in Japan, “All the managers manage differently here. I mean they manage Japanese

style. And I do it more or less U.S. Style. So I’m the one that’s different really” (p. 143). Whitting also exemplifies this point by stating that, “Many Japanese will argue that a foreigner should never be allowed to manage a Japanese baseball team” (p. 143).

Low Context Versus High Context Communication

Hall (1983) initially introduced the concepts of low-context and high-context communication. Low-context communication relies less on the contextual environment for understanding the intent of the message; instead, the majority of the message is found in mostly just the words (e.g., print or formal communication such as speeches). Interaction between the speaker and listener is typically reduced. Low-context communication reflects a logical and linear approach. The direct verbal interactions, overt communicative intentions, and sender-oriented values seen in low context communication are typically found in individualistic cultures (Ting-Toomey and Chung 2012). Low-context cultures tend to attribute one’s behavior to the individual’s personality.

High-context communication attributes behavior according to the situation or factors that are external to the person, i.e., an external locus of control or where one places responsibility for actions (i.e., within oneself or outside of oneself) (Brice and Campbell 1999). High-context communication can be depicted as a spiral communication approach that uses indirect styles of speech, and includes many indirectly related conversations. Verbal negotiations and use of subtle nonverbal nuances are key points. Whereas in low-context communication messages are direct and “to the point.” High context communication is seen in many Hispanic cultures. Brice (2002) in examining communication styles of Cuban-Americans stated that Cuban-Americans exhibit a more indirect communication style, i.e., more spiral as opposed to more linear. Discussion of family, friends, employment, etc., almost always precedes formal topic discussions.

Horizontal Versus Vertical Cultures

Another feature of cultures is the horizontal vs. vertical distinction. A collectivistic or

individualistic culture may be either more horizontal or vertical on this continuum. The horizontal orientation emphasizes that individuals are similar, equal, or parallel on most aspects especially those involving rank or status. In contrast, vertical orientations emphasize rank, privileges of rank, and inequalities associated with rank. (Triandis 2001). Hence, four possibilities exist when combining the collectivistic vs. individualistic and horizontal vs. vertical distinctions: (a) collectivistic horizontal (group/same), (b) collectivistic vertical (group/rank), (c) individualistic horizontal (individual/same), and (d) individualistic vertical (individual/rank).

Individuals from a collectivistic horizontal (group/same) culture accentuate group values, social cohesion, cooperation, and equality among members. Israeli kibbutzim members both are group oriented and membership equality. Triandis (2001) stated that individuals from a collectivistic horizontal background do not want to stand out nor dominate others in a group, and that community needs are valued more than individual needs.

Collectivistic vertical cultures (group/rank) are exemplified by traits of belonging to the group, yet maintaining rank and class distinctions. In Japanese language and culture, the word and concept of “*giri*” signifies honor, duty, obligation, and burden all into one. One is bound to the group and also bound to superiors in fulfilling one’s duty (e.g., to the family and to one’s parents/grandparents) over one’s individual wishes and desires. A hierarchical model is also evident in language and how it is used (e.g., honorifics or the etiquette found in how one addresses another individual based on rank, status, and/or hierarchy). For example, in the Japanese language and culture, one may use the affix “*san*” added to another person’s name that is in the same social station as oneself. “*Sama*” is generally reserved for more elder family members (e.g., *otosama* – father; *okasama* – mother). “*Chan*” may be used as a form of endearment, primarily for children. “*Sempai*” (mentor) is used in workplaces for those with seniority. However, “*kouhai*” is the opposite of “*sempai*” denoting someone of a lower social rank. It is considered rude to employ such a term in speaking with that individual.

Individualistic horizontal cultures (individual/same) place an emphasis on uniqueness and sameness. Sweden and Finland are examples. Communication is respectful but more informal as all individuals are seen as the same. Initiating conversations and maintaining conversations is not burdensome. What may be seen as intrusive in a rank oriented culture is seen as typical in a horizontal culture. Parents and grandparents do not live with their offspring children. Living independently is a valued trait. Individual horizontal cultures are often seen in democratic socialistic governments (especially, the Scandinavian countries).

Individualistic vertical cultures (individual/rank) are focused on self-achievements and obtaining status. Persons from such a culture (e.g., middle and upper SES individuals from the USA) behave in ways to “stick out” or be recognized on one’s individual merits that place one at a higher social status. Taking “selfies” and/or posting on Facebook illustrate the importance of “I” and how to stand out from others. Rank is seen in the form of titles (e.g., Instructor, Lecturer, Assistant Professor, Associate Professor, Professor). The CEO of a company or Dean of a College have the expected honor of having more “talk-time” in a meeting than the employees. Those in superior positions may be allowed to be more direct or blunt in communication.

It can be argued that language and culture are, in essence, inseparable. Dumitrescu (2012) stated that

The inextricable relationship between language and culture has been confirmed by linguistic anthropologists, who have come to the conclusion that language learning is coextensive with culture learning . . . language learning cannot be distinguished from the process of enculturation to which every member of a society is exposed from early childhood (p. 161).

Language is highly intertwined with culture, as it is both a by-product and a constructing mechanism of culture making it difficult to separate the two. In addition, culture also impacts language and how we interact. For example, the word “meal” can be differentiated into breakfast, lunch, and dinner in western cultures. However, there may be no differentiations in other cultures. This distinction of dividing meals into three

different times may not be reflected in agricultural or nomadic cultures. Culture impacts perception, which then influences language, and language which then influences interaction.

In essence, culture shapes how people live, interact, and interpret the world around them as well as what people value. For example, one culture may value independence and autonomy, while another values dependence and cooperation. Culture or shared patterns of behavior, thoughts, feelings, attitudes, and values may differ according to membership of racial, ethnic, religious, or social groups. Furthermore, culture can also differentiate between gender, class, physical and mental abilities, religious and spiritual beliefs, sexual orientation, and/or age.

Conclusion

The three main schools of learning include behaviorism (e.g., Skinner), social constructivism (e.g., Vygotsky), and cognitive constructivism (e.g., Piaget). As a result, the latter two theories have evolved into social learning theory from social constructivism and cognitive learning theory from cognitive constructivism. The key elements of these theories have endorsed social interaction and learning occurring internally in response to experiences. At the key to all learning is the ability to use language in interaction with others and to use language to acquire knowledge.

Hence, language underlies all aspects of social cognition, social learning, and culture. After a certain developmental period when language becomes a child's main means of communication (e.g., in typically developing children, this will occur between three and 4 years of age), then language and cognition become inseparable (Brown and Lenneberg 1954). Learning is mediated through language and social interaction. Social interaction is evident in the child's early life. The Whorf (1956) hypothesis states that language orients learners to specific ways of seeing the world. Duquette (1991) stated that "there is more in the home culture that reflects to language development than might at first appear. In fact,

culture may be to language what language is to speech because they involve each other" (p. 131). Language and culture also appear to be highly intertwined. In sum, language is the key to all learning.

Cross-References

- [Cross-cultural Expression](#)
- [Grammaticalization Theory](#)
- [Intelligence Versus Natural Selection](#)
- [Language Development](#)
- [Pinker's \(1994\) The Language Instinct](#)
- [Sensorimotor Play](#)
- [Social Learning](#)

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Social Learning in Mate Choice

► Mate Choice Copying

Social Learning of Mate Preferences

► Mate Choice Copying

Social Learning Theory

► Sociocultural Theories of Violence

Social Media

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Synonyms

Evolutionary mismatch; Social belonging; Social monitoring; Well-being

Definition

The evolutionary perspective argues evolutionary mismatch, well-being, social belonging, social monitoring that social media exploits people's evolved psychological mechanisms for social belonging and monitoring, thus explaining why people continue to use social media widely despite its potential harmful effects.

Introduction

Social media broadly refers to platforms that allow for the production and sharing of content online, which include collaborative projects (e.g.,

Wikipedia), weblogs (e.g., YouTube), and social networking sites (e.g., Facebook, Instagram). On the one hand, social media can facilitate the expansion and maintenance of social networks, thereby bringing about improved psychological well-being and life satisfaction (Kim and Lee 2011; Valenzuela et al. 2009) as well as reduced stress via perceived social support (Nabi et al. 2013). On the other hand, a host of nontrivial adverse effects also accompany its usage, such as negative mood (Sagioglou and Greitemeyer 2014), low self-esteem (Neira and Barber 2014), and depression (Morrison and Gore 2010).

As the virtual engagement with others on social media increasingly becomes an integral part of everyday life and carries real-life consequences for its users, the effects of social media and the factors that drive its usage have become key public concerns and received notable research attention (e.g., Kim et al. 2009; Morrison and Gore 2010; Nabi et al. 2013; Neira and Barber 2014; Valenzuela et al. 2009). The current entry reviews some contemporary explanations of social media usage, highlights their explanatory shortcomings, and demonstrates how an evolutionary perspective can address these gaps.

Current Theories of Social Media Usage and Effects

Several theories have been proposed to explain people's extensive use of social media. The cognitive-behavioral model of pathological Internet use (Davis 2001) suggests that positive reinforcements, such as receiving likes, positive comments, and other sources of social validation, entice people to continue using social media. When coupled with underlying psychopathology (e.g., social anxiety, low self-esteem, depression), problematic outcomes occur, including excessive social media use and maladaptive cognitions. Maladaptive cognitions refer to distorted thoughts involving self-doubt and negative self-appraisal, such as "I am only good online" or "nobody loves me offline." Empirical support for this model is evinced from the documented associations between depression and pathological Internet use

(Shapira et al. 2000; Caplan 2005). The socio-cognitive model of Internet addiction (LaRose et al. 2003) offers a similar explanation and proposes that because Internet use can be psychologically rewarding, people are incentivized to continue using it. When combined with low self-regulation and high self-efficacy, habitual Internet use can develop, resulting in extensive social media usage. Finally, the social skill model (Caplan 2005) posits that people engage in social media activity because they perceive online social interactions more favorably than in-person, face-to-face interactions. Over time, this preference for online social interactions results in compulsive social media use. According to this model, people are more likely to have or develop this preference if they perceive themselves as lacking self-presentational skills (McKenna and Bargh 1999) or if they believe that "one is safer, more efficacious, more confident, and more comfortable with online interpersonal interactions and relationships" (Caplan 2005, p. 629).

These theories are useful in elucidating the "how's" and "what's" of social media, thus shedding light on the precursors and outcomes associated with social media use. However, they are inadequate in addressing the fundamental "why" questions, such as why human beings would be so amenable to social media in the first place or why excessive social media use can be harmful. In the following sections, we apply an evolutionary analysis to social media and describe how social media interacts with our evolved psychology, which in turn gives rise to its various effects on human behavior and well-being. In so doing, we also demonstrate how an evolutionary perspective can address fundamental questions associated with social media usage and its effects.

The Evolutionary Basis of Social Media Use and Effects

From an evolutionary perspective, human behaviors are the products of psychological adaptations that evolved to solve recurrent survival and reproductive challenges. Because humans rely heavily on social groups to meet their survival and

reproductive needs, individuals who get ousted from their groups face a tremendous survival disadvantage. As such, our psychology is adapted to facilitate behaviors that increase the likelihood of social inclusion and reduce the likelihood of social exclusion. The need to belong and desire for social acceptance may have evolved in humans to motivate affiliative behaviors and increase the likelihood of being included in groups (Buss 1990).

In order to enact adaptive behaviors to maintain or protect inclusionary status, humans may have also evolved a social monitoring system to detect cues signaling important social information, such as indicators of social approval or rejection (Pickett and Gardner 2005), which then trigger the psychological mechanisms responsible for producing appropriate adaptive behavioral responses. For example, self-esteem has been argued to be an internal gauge that signals how well liked or socially accepted a person is (Leary et al. 1995). When people detect that they have been socially rejected or excluded, their self-esteem correspondingly decreases. This aversive psychological experience adaptively activates compensating behaviors that may appear aimed at restoring self-esteem on the surface, but are more fundamentally aimed at repairing their social acceptability. Hence, the social monitoring system plays a critical role in detecting social information that conveys the status of social relationships and acceptance in social groups.

Social Media Hijacks Our Evolved Social Psychology

People's amenability to social media can be understood in terms of social media's function as an outlet for people to satisfy their evolved social needs. In a small ancestral village, events that occurred to a person would be maximally only three degrees of separation away from anybody else in that village (Christakis and Fowler 2009). Thus, any social information was likely to be self-relevant and important because of the small size of a village community, and we likely evolved to be highly sensitive to all kinds of social information (Yong and Li 2018). Social media, in particular, social networking sites such as Facebook,

MySpace, and LinkedIn, capitalizes on our tendency to assume that all social information is important. The vast amount of readily available social information on social media triggers people's evolved psychology to attend to such information and can cause social media users to spend copious amounts of time on social media. For instance, a study found that students spent more time observing content on Facebook rather than actually posting content (Pempek et al. 2009), thus suggesting that social media sites feed people's need to monitor social information.

Because of the need to rely on others for survival, early humans evolved to instinctively forge ties with others, and the careful (and successful) maintenance of strong ties was also likely possible given the small population of an ancestral village (approximately 100–230 people; Dunbar 1992). Thus, the need to belong and build relationships can motivate people's social media use (Nadkarni and Hofmann 2012). Social media sites enable users to form new friendships, maintain existing relationships, and interact with other people in a wide variety of ways with unprecedented convenience. As such, Facebook users aged 18–24 years old have, on average, more “friends” than an ancestral person would have encountered in an entire lifetime (Blease 2015). Due to the large size of online social networks, the ties between social media users and most of their connections are typically latent (i.e., individuals only have passing awareness of each other) or weak (i.e., individuals only seek each other occasionally for information or other forms of trivial support; Ellison et al. 2011). Yet, we likely evolved to treat our large but weak online social networks with as much attention as ancestral humans would have given their strong but small social networks. Thus, the amount of effort put into maintaining a social network of the size faced by our ancestors may have been more manageable than that faced by modern humans, causing social media users to spend an unnecessarily substantial amount of time and effort upkeeping their online connections.

Social media also capitalizes on our evolved need for social validation. Social media sites often incorporate the use of “like” buttons as a means

for users to quickly provide social feedback. Because such likes directly reflect social approval, people can rely on likes to monitor their inclusionary status and how socially accepted they are. A study that experimentally manipulated the number of likes received by participants for a personal photograph found that people who received a greater number of likes reported higher levels of self-esteem (Burrow and Rainone 2017). The ostensible display of the number of followers one has also serves as another proxy for social inclusion and popularity. This is further glorified by Instagram's coveted "blue tick," which is usually conferred to users with a substantial amount of followers and influence, such as celebrities, influencers, and politicians.

One commonly cited reason for the extensive use of social media is the "fear of missing out" (FOMO; Przybylski et al. 2013), which is defined as a preoccupation over whether others might be having rewarding experiences in one's absence. As such, people can feel compelled to stay connected on social media to find out what others are doing. This apprehension is arguably indicative of the social monitoring system at work, whereby social media users constantly monitor for cues to social inclusion or social exclusion from network acquaintances. FOMO has been found to be associated with the activation of the right middle temporal gyrus, a brain region involved in the processing of social inclusion cues (Lai et al. 2016), thus suggesting that individuals are on the lookout as to whether they are still included in their social groups.

The foregoing analysis shows that our proclivity toward social media use and vulnerability to overuse can be understood within the context of our evolved psychology to socially belong and monitor for social information. As opposed to other theories that implicate addiction or other forms of psychopathology, the evolutionary perspective instead suggests that because social media exploits common features of normal human psychology, obsessive social media use can also occur in well-adjusted, psychologically healthy individuals, thus accounting for its widespread contemporary use.

Harmful Outcomes of Social Media Use

The evolutionary approach can also be used to shed light on the harms that may emerge from excessive social media activity and why, despite these harms, people still persist in using social media.

Through comments or likes, social media presents users with opportunities to quickly gauge social approval. However, people who post content on social media are exposed to both the possibility of receiving many likes as well as the possibility of receiving very few or no likes at all. As people tend to be more sensitive to negative information, social media users can inadvertently be more affected by not having enough likes compared with having enough likes, resulting in poorer mood and lowered self-esteem (Burrow and Rainone 2017). The desire to gain likes and other positive feedback may also prompt an obsession with the sharing of content that leads to unhealthy self-image, such as photographs of oneself in skimpy clothing or engaging in sensational or scandalous activity, which may garner more attention (Chua and Chang 2016).

Social media can also induce envy and self-dissatisfaction in users due to social comparison. As social media users tend to carefully select and curate the things they upload on social media platforms, social media tends to portray only the most perfect aspects of people's lives, such as flattering photographs, nice holidays, and work success (Siibak 2009). Our evolved psychological tendency to crave and digest social information takes the information we see on social media seriously and makes us compare ourselves to those we see on social media. As social media sites continually present information about how good-looking others are or how well others are doing, avid social media users are apt to experience envy and dissatisfaction with various aspects of their own lives (Yong and Li 2018).

By being a source of more information than people are evolved to need, social media can also trigger excessive jealousy. Increased Facebook use has been found to be associated with elevated jealousy due to a feedback loop, whereby using Facebook exposes people to ambiguous information about their partner that they may otherwise not have known, which then motivates further use

to seek more information that may be unwittingly self-confirming (Muisse et al. 2009). Texts on social media are often ambiguous because they are devoid of emotional cues. For instance, a neutral message left by a man on a woman's public post on Facebook, such as "hey how r u," can be misinterpreted to be more flirtatious than it really is by the woman's jealous partner.

People still persist in their use of social media despite its deleterious effects. From an evolutionary mismatch perspective, this is unsurprising because social media represents a modern stimulus that efficiently hijacks our evolved psychological mechanisms, which are adapted to respond to stimuli in ancestral conditions (Li et al. 2018). Just as how our tastes for sweet things, which evolved to adaptively impel humans to eat fruits and other natural foods high in calories and nutrients, are now inducing people to ingest modern foods manufactured with high levels of sugars (e.g., candy bars, soda), likewise modern humans cannot help but continue responding to social media in the ways that they do, to their own detriment.

Conclusion

The use of social media in the modern world can be a puzzling phenomenon, especially if we consider that people continue to use and participate in social media activity despite its negative effects. The evolutionary approach, which considers how social media hijacks our evolved psychology for social belonging and monitoring, can facilitate a better understanding of the widespread use and effects of social media. This awareness of the fundamental mechanisms that underlie social media use can encourage future research on the factors that may regulate excessive social media use, such as users' social media network size or other offline activities that may engage people's need to belong in relatively healthier ways.

Cross-References

- [Evolutionary Mismatch](#)
- [Group Size](#)

- [Human Groups](#)
- [Living in Groups](#)
- [Mate Value Inflation](#)
- [Self-Esteem as a Status-Tracking Mechanism](#)
- [Self-Esteem Reflects Assessments of Valuation](#)
- [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- [Social Anxiety](#)
- [Social Comparison](#)

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Social Monitoring

► Social Media

Social Monogamy

► Evolution of Long-Term Pair-Bonding in Humans

Social Networks

► Peer Socialization

Social Neuroscience of Self-Categorization

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Synonyms

Social neuroscience of social identity

Definition

The study of neural processes underlying representation of social group membership.

Introduction

Self-categorization is a cognitive process of perceiving both oneself and others in terms of collective entities (social groups or categories) rather than in terms of individual characteristics and personality. Development of new methods of the brain research allows studying self-categorization at the neural level. Self-categorization became one of the key issues in a new scientific discipline, social neuroscience, which is an interdisciplinary field of research on the intersection of neuroscience and social psychology studying neural basis and mechanisms of social cognition, emotions, and behaviors.

Self-categorization in Social Psychology

Self-categorization refers to social categorization, i.e., classifying individuals into social groups or categories, from an ego-centric perspective. This means that not only social world is classified and typified during social categorization but also that an individual is positioned in this social world and describes him/herself in terms of membership in specific social groups or categories such as ethnicity, race, gender, age, political preferences, family. The outcome of self-categorization is the formation of specific social identity, which is a part of the self-concept, representing knowledge and feelings of their group as well as its psychological value. Key theories of social psychology, namely, Social Identity Theory and Self-Categorization Theory (Turner and Reynolds 2003), treat self-categorization and social identity as the basis of intergroup relations and associated perceptions, attitudes, and behaviors.

During social categorization, individuals tend to focus on similarities within groups and differences between groups, thus maintaining and reinforcing group boundaries. Studies in social

psychology showed that individuals differently respond to social groups with which they associate themselves, i.e., ingroups, and all other, i.e., outgroups. These effects include asymmetrical responses to in- and outgroups at cognitive, affective, and behavioral level. Perceived group differences affect attention, memory, judgments, evaluations, empathy, motor predispositions, and allocation of resources. Social psychology treats these asymmetries as a source of many problematic aspects of intergroup relations such as prejudice, discrimination, intergroup conflicts.

Evolutionary, social categorization is considered as an important tool for social species. Living in collectives requires ability to make fast and accurate identification of social agents and infer their intentions. Establishing alliances is crucial for survival and the necessity to detect allies should lead to development of effective skills in social cognition. Affiliation with a group is necessary to satisfy social needs such as sense of belonging and self-esteem. Studies in primatology show that nonhuman primates have well-developed social cognitive skills and share basic predisposition to form and detect various social groups as well as form preferences for the members of their own group, the so-called ingroup favoritism.

The Social Neuroscience Approach to Self-categorization

Evolutionary significance of social categorization implies that the ability to effectively classify and automatically respond to different types of social objects must be supported by specialized biological systems and mechanisms: genetic, physiological, and neural. The progress in neuroscience provided social psychologists with new research tools to study social categorization. Among them, functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) became the two most actively used. Whereas the first one helps to identify neural systems involved in various aspects of social categorization, the second one allows effective tracing the time-course of social cognitive and affective responses during social

categorization. Other research methods that can be used in social neuroscience of self-categorization include magnetoencephalography, transcranial magnetic stimulation, administration of “social” hormones such as oxytocin and testosterone, lesion studies, animal models, and some other.

The Brain Structures Involved in Neural Processing of Self-categorization

Studies in social neuroscience revealed several brain regions, which are especially important for social categorization and representation of social identity (Cikara and Van Bavel 2014; Molenberghs 2013; Shkurko 2013).

Amygdala, a part of the brain’s limbic structure, was initially associated with fear conditioning and fast negative response to the members of racial outgroups. Later studies showed that it can be selectively activated in response to ingroup member as well. Currently, the role of amygdala in social categorization is associated with the detection and emotional arousal in response of socially relevant stimuli. In different contexts, both in- and outgroups can be motivationally significant and evoke selective activation of amygdala.

Medial prefrontal cortex (mPFC), a frontal part of the cerebral cortex, is involved in several higher-order social cognitive processes which include mentalizing (taking the perspective of other individuals), processing self-relevant information, and cognitive empathy. Particularly, mPFC demonstrates greater activation in response to ingroup members and self-referential thinking as compared to mentalizing about outgroup members, thus supporting the view that social identity is a part of individuals’ self-concept. Extreme outgroups such as homeless people, on the contrary, may not elicit activation of mPFC during mentalizing tasks, thus indicating “dehumanization” of such social groups.

Anterior cingulate cortex (ACC) plays an important role in affective regulation. Specifically, parts of this brain structure were found to support affective empathy toward ingroup members and suppression of negative emotions in response to outgroup members.

Temporoparietal junction (TPJ) is important for mentalizing and may be involved in the construction of ingroup via perceived similarity with oneself and result in greater ingroup bias.

Fusiform gyrus (FG) and *fusiform face area* (FFA) are traditionally associated with perceptual expertise and sensitivity to facial stimuli, which are one the most important source of socially relevant information. Activation in FFA is associated with the better memory for ingroup faces. This finding is consistent with the idea that self-categorization lead to greater attention and individuation of ingroup members. There is evidence that FG is flexibly involved in social categorization and is subject to top-down regulation of social stimuli perception (Freeman et al. 2010). Particularly, preexistent high-level knowledge of social categories may modulate perception of social sensory input.

The human reward processing system, which includes *ventral striatum* (VS), *dorsal striatum* (DS), and *orbitofrontal cortex* (OFC), is also involved in several aspects of social categorization. Being sensitive to social status information and representing the value of subjectively rewarding stimuli, these regions are important for situations in which group perception is associated with the differences in status or involved in competitive relations. For example, in the context of intergroup competition, VS is activated in response to outgroup failures or misfortune, thus indicating their subjective value (*schadenfreude*) and group-based modulation of empathetic responses (Cikara et al. 2014; Hein et al. 2014). Some studies show that OFC can encode the value of pro-social, cooperative behavior and thus can be involved in mitigating discriminating behavior.

Insula is believed to be a part of the “pain matrix” and is involved in processing negative emotions during social categorization, although its exact role and group selectivity is not clear. For example, left anterior insula was especially responsive to the pain of ingroup members. At the same time, other studies reported activation of the right insula in response to outgroup members and its role in modulation of discriminatory behavior toward them.

Identification of the brain systems involved in social categorization is mainly the result of using fMRI technique. However, studies of hormones become increasingly important in revealing neural mechanisms related to social identity and intergroup behavior. For example, a neurohormone oxytocin known for its role in social affiliation can be sensitive to group membership. Particularly, in the social contexts in which social identity is salient, oxytocin is associated with greater ingroup love (but not outgroup hate). Exogenous administration of oxytocin and some drugs such as propranolol are considered as possible tools for interventions aimed at reducing intergroup conflicts and other negative consequences of social categorization.

Neural Processing of Self-categorization: Key Findings

Contemporary social neuroscience provide evidence supporting several important conclusions on the neural processing of self-categorization and social identity:

1. Social groups are represented in the brain differently. Those groups with which an individual identifies him/herself evoke different neural responses as compared to other groups. Moreover, different ingroups and outgroups can also evoke different neural responses.
2. The social brain evolved to support fast and effortless reaction to different social groups. Both EEG and fMRI studies showed that the brain can detect group membership of perceived social agents within first two hundred millisecond, i.e., classify them automatically.
3. Asymmetrical neural responses to ingroups and outgroups were found in regard to many different cognitive, affective, and behavioral domains: visual perception, attention, memory, mentalizing, empathy, motor predispositions, judgments, evaluation, and economic decision-making.
4. Effects of social categorization on perception, cognition, evaluation, and behavior occur even when group boundaries are based on trivial situational and arbitrary criteria, i.e., in the so-called “minimal groups.” These effects include better face recognition of ingroup members, biased judgments, and ingroup favoritism. This means that the social brain evolved not only to facilitate fast identification of social groups but also to support cognitive biases, prejudice, and discriminatory behavior in favor of the group to which individuals belong.
5. Despite the importance of automatic neural responses supported by the limbic system, social categorization in humans is subject to cognitive and affective regulation processed by evolutionary more recent prefrontal cortical areas of the brain. Moreover, there is evidence that neural processing of social categorization is bidirectional and combine continual representation of actual perceptual stimuli, particularly in FFA, with higher-order discrete categories represented in other cortical regions, particularly OFC (Freeman et al. 2010).
6. The neural representation of social identity and group-related effects can be flexibly tuned and reconfigured in response to changes in the context, social roles taken by individual, and tasks performed. When a new identity becomes contextually salient, other identities (e.g., race) even evoking automatic biased responses can become overridden and their negative effects can be diminished.
7. Neural processing of self-categorization and social identity is culturally conditioned. Individuals from different cultures, e.g., individualistic and collectivistic, demonstrate differences in the representation of ingroups and various aspects of ingroup bias. For example, collectivists more than individualists involve activity in mPFC and left TPJ during representation of the personal self thus probably indicating a greater role of social identity and perspective-taking in the construction of the self (Sul et al. 2012).

Conclusion

The human brain evolved to effectively manage complex social relations and support group-based

thinking, emotions, and behaviors. Studies in social neuroscience showed that there are no single neural system which could be directly associated with the representation of social identity and self-categorization effects. Instead, multiple systems are involved in various aspects of social categorization in a flexible and context-dependent manner. As a result, the brain is tuned for both biased and discriminatory reactions to the members of the social groups, and cognitive mechanisms supporting egalitarian responses and strategic manipulations with social identities to better fit the situation and the task needs.

Cross-References

- [Brain Imaging](#)
- [In-Group–Out-Group Bias](#)
- [In-group Versus Out-group](#)
- [Same-Different Categorization](#)

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Social Neuroscience of Social Identity

- [Social Neuroscience of Self-Categorization](#)

Social Norm

- [Norms](#)

Social Norm Violation

- [Recall of Cheaters](#)

Social Norms

- [Social Values](#)

Social Organization

- [Groups and Categories](#)
- [Human Enculturation](#)

Social Outcomes and Sex Ratio

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Synonyms

[Behavioral adaptations to variation in human sex ratios](#); [Consequences of imbalanced sex ratios](#)

Definition

Social outcomes that are associated with variation in the relative share of men and women active on a mating market.

Introduction

An imbalanced sex ratio, that is, a male or female surplus on the mating market, may occur due to sex-selective fertility, mortality, or migration dynamics (Dyson 2012). For instance, in parts of Asia and Europe, continued son preference, fertility decline (in the case of China's one-child policy legally prescribed), and the spread of ultrasound technology facilitating sex-selective abortions are seen as the main contributors to a trend of demographic "masculinization" (Guilmoto 2009; Hudson and Den Boer 2005). In 2004, for instance, the nationwide average for the sex ratio at birth was at about 120 and 112 boys per 100 girls born in China and India, respectively. In some provinces it was even higher, thus clearly exceeding the ratio of about 105 boys per 100 said to be the "natural" sex ratio (Guilmoto 2009; Hudson and Den Boer 2005). As the cohorts affected by such imbalanced sex ratios at birth have been maturing and reaching adulthood, many young men – sometimes referred to as "bare branches" – have found it difficult to find a partner (Hudson and Den Boer 2005). Another instance is a clear pattern of sex-selective migration that has been documented for regions across Europe: Women are more likely to migrate from rural areas to the cities for better educational and occupational opportunities than men, resulting in a wide range of sex ratios across these regions (Filser and Schnettler 2018; Wiest et al. 2013). Yet, in other cases of *international* migration, migration patterns are sometimes dominated by men or don't show a clear sex-selective pattern (Dyson 2012).

Scholars from various disciplines, including evolutionary biology and psychology, family sociology, and demography, have argued for a potential link between sex ratios and a range of social outcomes. Empirical research in these only partially overlapping literatures has demonstrated such associations with multiple such outcomes

and on various geographic scales (Dyson 2012; Filser and Schnettler 2018; Guilmoto 2009). Social consequences that have been linked theoretically or empirically with sex ratios include couple bargaining, economic decision-making, female labor force participation, female pubertal maturation, fertility and fertility preferences, gender roles, marriage and relationship dissolution, as well as sexual norms and preferences (e.g., Bauer and Kneip 2013; Dyson 2012; Filser and Schnettler 2018; Gay and Boehnke 2017; Guttentag and Secord 1983). Yet arguably the most severe consequence that scholars predict and one that has received most scholarly and public attention is that male-biased sex ratios may contribute to higher rates of violent crimes and prostitution, and regional destabilization (Dyson 2012; Filser and Schnettler 2018; Hudson and Den Boer 2005; Schacht et al. 2014). However, the variety of disciplines involved in sex ratio research has resulted in a fragmented and sometimes contradictory literature.

Potential Mechanisms

Why should any consequences of imbalanced sex ratios and social outcomes be expected at all? The main argument is that the surplus of one sex on the mating market increases competition among individuals of the abundant sex and allows individuals of the scarcer sex to be more selective in their partner choice. In addition, dyadic power in an existing relationship is considered to be affected by sex ratio-dependent opportunity costs. Thus, whether an individual decides to cater to a partner's preferences or to end the relationship is co-determined by the number of alternative relationships. The numerical balance of men and women on the mating market in turn affects this number of alternatives. A favorable sex ratio, i.e., a shortage of one's own sex, makes finding an alternative partner more likely than an unfavorable shortage of individuals of the opposite sex. Following this logic, an argument can be made, that the prevalence of any behavioral adjustment that would allow individuals of the abundant sex to improve their chances on the mating market, or to retain their partner in an existing relationship,

might be associated with sex ratio imbalances (Filser and Schnettler 2018; Guttentag and Secord 1983).

Whereas this supposed relationship, on a very coarse level, seems to be agreed upon by most authors, there are considerable differences when it comes to detail. In fact, this leads to diametrical predictions with regard to the purported association between sex ratios and violent crime: Some authors propose that an increase in the sex ratio should go along with an *increase* in violent crimes. Others argue that an increase in the sex ratio should go along with a *decrease* in violent crimes. On both sides of the argument, authors draw on parental investment theory (► [“Parental Investment and Sexual Selection”](#)): Due to a differential in (potential) reproductive variance between males and females, sexual selection is thought to have favored a stronger preference for long-term mating and signals for parental investment in females as compared to men. Now the two sides of the argument differ in their emphasis on what follows from this. On the one hand, scholars who propose a positive association between sex ratios and violent crime argue that females, due to their comparatively higher selectivity in partner choice, are to be considered a scarce resource. This in turn favored mate seeking and competitiveness in males. Increasing sex ratios are thus expected to imply more (violent) mating competition. On the other hand, scholars who propose a negative association emphasize that in a high sex ratio context males should compete for female partners by meeting female preferences, that is, by signaling long-term mating and parental investment potential. In this view, violence appears to be a counterproductive strategy for finding a mating partner, because women might choose men with resources over physically dominant males (Schacht et al. 2014).

Methodological Issues

If the theory on sex ratio outcomes is so divided, has at least empirical research been able to settle this issue? Not quite! In fact, some authors find a positive, some a negative, and some a null-finding with regard to the association of sex ratios and

violent crimes (Filser and Schnettler 2018; Schacht et al. 2014). A number of methodological and data-related issues of previous studies may contribute to this inconclusiveness: Some studies compare sex ratio associations between countries which implies that entire countries are operationalized as potential mating markets. This may, however, be inappropriate given a considerable within-country variation in sex ratios (e.g., between rural and urban regions) in many countries. In addition, almost all studies correlate sex ratios and social outcome indicators on the aggregate level, thereby risking an ecological fallacy. Most research has also been limited by cross-sectional research designs. Longitudinal research designs would improve the ability to establish a potential causal link between sex ratios and social outcomes (Filser and Schnettler 2018).

Conclusion

Imbalanced sex ratios have been linked to a wide variety of social outcomes. Of these purported associations, only few have received as much attention as the potential correlation between sex ratios and violent crimes. Nevertheless, theoretical predictions and empirical evidence of this association remain contradictory.

Overall, our understanding of consequences of sex ratio imbalances is still emergent even for relatively well-studied potential outcomes of imbalanced sex ratios. For instance, a number of studies have addressed the association between sex ratios and mating behavior, yet empirical evidence seems inconclusive as well (► [“Sex Ratio and Men’s Long-Term Mating”](#)). Therefore, it seems particularly premature to draw conclusions on associations of sex ratios with other social outcomes in cases where empirical evidence consists of a single or only a few studies. Thus, more research is necessary to substantiate which social outcomes are associated with sex ratios and how strong these associations are. This should include replication studies to test if the same associations hold with data from other social and cultural contexts, data sources, and research designs.

To maximize the insight of future studies, researchers should seek to follow a few

recommendations. Whenever possible, individual-level data should be used: For example, in the case of violent offending, data on individual-level offending should have priority over aggregate crime rates. Second, different operationalizations of mating markets should be tested and compared. How robust are findings to these different operationalizations? Finally, longitudinal research designs should be given priority over cross-sectional designs. After all, if the sex ratio can be considered a cause of a particular social outcome, its measurement needs to precede the measurement of the social outcome of interest. The issue of migration illustrates this well: Sex-selective migration affects sex ratios, but imbalanced sex ratios may themselves drive sex-selective migration (Dyson 2012; Wiest et al. 2013). To disentangle such a potentially bidirectional causal link cannot be resolved with cross-sectional observational data.

In addition to studies that document statistical associations, ideally with improved research designs, research is needed that closely focuses on the potential mechanisms involved therein. Little is known, for instance, about if and to what degree local sex ratio imbalances on mating markets are actually perceived as such by individuals active on those markets and how this affects their behavior (Filser and Preetz 2019). Although some studies have tested the sensitivity of individuals to sex ratio variation in materials presented to participants in a lab setting, little is known about the external validity of these findings: Does this sensitivity, for instance, only apply to micro-situational contexts (e.g., the sex ratio in a room, at a party, or in a business meeting), or does this sensitivity generalize to larger contexts like marriage markets? A recent study compares subjective and objective sex ratios at various geographical scales and with different operationalizations of the sex ratio. It finds no association between the two (Filser and Preetz 2019).

The distinction between perceptions of sex ratios on a situational versus larger context is relevant with regard to the underlying mechanisms. A common assumption is that individuals do in fact perceive if they are on a highly competitive mating market and adjust their behavior accordingly, e.g., by acting more aggressively or

by adjusting more strongly to the (perceived) preferences of potential mating partners (Schacht et al. 2014). Another potential explanation would see individuals more or less ignorant toward sex ratio imbalances in their respective regions. However, these imbalances would imply that individuals are selected with a certain probability into social situations that are themselves characterized by a similar numerical imbalance between men and women. Only in these situational contexts would individuals actually perceive the (situational) sex ratio imbalance, which could in turn induce behavioral responses. Taylor (2014) showed experimentally that the co-presence of another man increased cortisol levels in male participants when solving a competitive task. This finding may be interpreted as preliminary evidence that (male) individuals respond to differences in the sex composition of their immediate social context.

Cross-References

- [Local Sex Ratio](#)
- [Reproductive Variance](#)
- [Parental Investment and Sexual Selection](#)
- [Sex Ratio](#)
- [Sex Ratio and Men's Long-Term Mating](#)

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Social Partner Choice

- [Reciprocal Altruism \(Middle-Level Theory in Evolutionary Psychology\)](#)

Social Phobia

- [Social Anxiety](#)

Social Play

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Synonyms

[Human play](#); [Play with others](#); [Social playing](#)

Definition

In most mammalian species including humans, Social Play describes playful activities, such as tumbling, chasing, and making faces, among two or more individuals that support the development of mutually beneficial connections between them.

Introduction

Social play involves a variety of playful activities that are directed towards other people (Pellis and Pellis 2007), involving at the very least two interacting players exhibiting behaviors that highlight the context of the relationship between them (Gleason 2017). For young primates, social play is the stage that involves making use of their peers for the purpose of social exploration characterized by at least two basic social play patterns: rough-and-tumble play or contact play, e.g., wrestling, pulling, biting, and rolling, and, approach-withdrawal or noncontact play, i.e., taking turns swiftly chasing back and forth each other across an area, with regular interchange between the roles of leader and follower (Harlow 1969). Some additional expressions of social play in both humans and animals include chasing, play-fighting, and peek-a-boo while more cognitively sophisticated forms found largely in human children include sociodramatic and construction play (Graham and Burghardt 2010).

Social Play – An Overview

To engage in social play, a very common mammalian activity (Durand and Schank 2015), at least two individuals are needed which are commonly from, but not limited to, the same species (Graham and Burghardt 2010). Another definition views social play as a “state of engagement” where both partners alternate behaviors that they modify each time based on each other’s reactions in a successive order, hence, these behaviors meet two criteria where on one hand they are alternating and contingent on each other and on the other hand they appear to be nonliteral or abstract

(Garvey 1974). For example, in play-fighting the attacker might intentionally let his guard down, something unlikely to happen in a real fight, so that the defender can counterattack (Pellis et al. 2010).

When at least two children are alone in a room together there are four possible “play” states that can take place: (a) social non-play (a joint activity that does not involve play, e.g., work together to fix a toy that was broken), (b) non-social non-play (e.g., even though they are in the same room, they explore independently), (c) non-social play (e.g., play acting imaginative scenarios independently, e.g., one is playing the doctor and the other is playing the cook), (d) social play (collaboratively playing together, e.g., hide and seek) (Garvey 1974). There is additional support from behavioral studies and observations with juvenile rats which differentiate social type behaviors as between related and unrelated to play (Vanderschuren et al. 1997). According to Burghardt (2011), there are five criteria that describe play behavior, which state that: “Play (1) is incompletely functional in the context in which it appears; (2) spontaneous, pleasurable, rewarding, or voluntary; (3) differs from other more serious behaviors in form (e.g., exaggerated) or timing (e.g., occurring early in life before the more serious version is needed); (4) is repeated, but not in abnormal and unvarying stereotypic form (e.g., distressed rocking or pacing); and (5) is initiated in the absence of acute or chronic stress.”

One of the most common forms of social play found in animals is rough-and-tumble play also called play-fighting and accounts roughly for 10% of play activities in human children (Pellis et al. 2010). Rough-and-tumble play or play fighting is a competitive form of social play with the most amount of research (Pellis and Pellis 2007). The differences between play-fighting and actual fighting lay in five specific details: (a) during play-fighting there is no competition for vital resources, (b) the players show restraint and avoid doing serious, if any, harm, (c) there are reversing roles between the two players of attack, defense, and counterattack, (d) the act brings both parties closer together, and (e) for humans and many other species, play is communicated

through distinctive signs from the face and body (Pellis et al. 2010). Despite the similarities to other sexual or aggressive behaviors, these differences that describe social play postulate it a distinct category of behavior and not only a precursor of adult type behaviors (Vanderschuren et al. 1997).

According to Bekoff (2001), because of the similarities with aggressive behaviors, play needs to be communicated to the social partner beforehand in an effort to reach a consensus on the activity avoiding the chance for it to be interpreted as a threat (e.g., perceived as an intention to fight or predation). Exaggerating normal behavior or the use of plain old smiles and giggles can reflect the intent to play and that the presented play activity or behavior is neither threatening nor meant to be taken literally (Garvey 1974). What is more, Bekoff (2001) expresses the value of “role-reversing” (where the dominant individual voluntarily behaves in a manner unlikely to transpire in real events, e.g., rolling over) and “self-handicapping” (e.g., biting less intensely) in social play to balance the scales of power and make their intention of continuing to play known to their partner. These actions have the added benefit of allowing juveniles the opportunity to practice and learn valuable skills that would otherwise cost them their survival if not properly mastered (e.g., practicing counterattacks during play-fighting that will be extremely valuable in a real fight happening in the future).

Bekoff (2001) further proposed that in a sense social play may have facilitated the evolution of social morality, specifically the value in playing fairly during a game where innocence in play and forgiveness of any transgressions prevails over competition while allowing to safely practice cooperative skills – especially to younger players still on the learning curve and not thus far perceived as anyone’s adversary. Through social play, rules for social conduct have evolved, practiced, and learned to monitor acceptable and unacceptable behaviors and establish the grounds for social morality to be generalized across other real-life situations. Also, this social conduct assists the development of trust placed from one partner to another as well as the development of a preference to finding partners that play fairly quite possibly extending to represent the integrity and stability of

a group of individuals. In addition, the author explains that for the duration of the “socialization period,” a short but critical time interval during the early development, self-responsibility about one’s own welfare is waived so that social skills development happens at a faster pace while social play deprivation during this critical time period can result in unwanted consequences.

Eckerman et al. (1975) separated 60 children in three different age groups; 10–12, 16–18, and 22–24 months of age (10 pairs each) and observed them during a novel play setting with both mothers and peers present. They found that children between 10 and 12 months of age preferred solitary play; from 16 to 18 months of age, children chose to play more with their mothers; and from 22 to 24 months, children preferred to play more with their peers. In other words, similar to Harlow’s (1969) reports with young primates as age increases and social play interaction begins to involve more people, the children’s preference turns to their peers rather than their parents. Additionally, Eckerman et al. (1975) observed that by the second year of life, children’s behaviors towards other children closely resembled those cultivated through contact with significant adult figures in their lives such as “smile, laugh, vocalize and gesture to one another, show and offer toys, imitate each other, struggle, and engage in reciprocal play” rather than those learned during play with inanimate objects. Possible explanations behind these sex differences in social play may very well lay in the different prenatal hormonal exposures between males and females (Meaney 1988) or the aftermath of the many discrepancies different cultures have between them (Michael and Crook 1973). Despite the fact that there are relatively few data regarding the survival and reproductive benefits of social play, it is widely accepted that both short-term and long-term benefits among different age groups, species, and sexes deviate (age and sex differences exist even within the same species) (Bekoff 2001). Additionally, Meaney et al. (1985) reported a large number of studies to illustrate that sex differences do exist in mammalian species’ social play, yet, the authors caution that these differences are not universal for all species. For instance, they

provided research-based evidence from several studies which indicated that males prefer and engage more intensely in play-fighting than females even though their play is not qualitatively different; during chase-play, males tend to be the most frequent chasers and play-mothering (e.g., play acting with baby dolls) is far more prominent in female social play.

Social competency’s development is favored through the play-fighting interaction (Pellis and Pellis 2007) and social play may represent an extension of a social learning process in young mammals where they learn and practice new skills with their peers (Meaney 1988). Evidence suggests that autistic children can demonstrate successful social adaptation by incorporating their thematic ritualistic activities (i.e., repetitive behaviors) in social play interactions with their siblings, leading to social skills and affect improvement sustained to at least a 3-month follow-up measure (Baker 2000). Durand and Schank (2015) proposed a theoretical model where social play evolved because it allows juveniles to practice cooperation for a common goal and retain this skill as adults. However, they stress that for it to be adaptive, the potential fitness costs of social play, such as increased risk of predation, injury, energy, and foraging loss, must be significantly less than the long term benefits.

Social Play Interactions During Childhood

A critical developmental stage of childhood during the preschool years (before the age of 6) involves building a strong foundation of social competence through the initiation and maintenance of positive social interactions that facilitate later school success (Veiga et al. 2016). Even in the early stages of infancy, some form of social play begins from mutually playful interactions between newborns and their primary caregivers; however, once peer interactions commence this adult-infant social play synergy will eventually lose its precedence and be replaced by other children (Whaley 1990). Having said that, for infants social play begins from their first smiles and once

they are more communicatively adept it takes the form of babbling and cooing with their primary caregivers which empowers them to learn social rules through an adult-infant socialization and cultivate essential skills such as turn taking and role repetition (Frost et al. 2011, pp. 111–112).

Frost et al. (2011, pp. 151–152) defined six categories of observable social play behaviors based on the work of Parten (1932) that describe the development of social play in preschoolers. These categories include: “unoccupied behavior” – child is not playing but is mobile, active, and observes the room; “onlooker behavior” – the child is not playing and mostly observes his/her peers playing and may occasionally speak to them; “solitary play” – around 2–3 years of age, the child plays with his/her own toys by himself but does not engage other children and uses different toys than the other children; “parallel play” – the child uses the same toys as other children and plays beside but not with them; “associative play” – children play together in a common activity without sacrificing individual interests for a common group goal; and “cooperative play” – group play characterized of shared goals that are negotiated and comparable to adult situations. Additionally, they emphasize that children may progress in and out of these stages at a faster pace because contemporary child care is more advanced and readily available than the early 1930s.

According to Veiga et al. (2016), there are distinguishable variations and patterns that can be seen while observing children play, e.g., “children jump, use objects to facilitate pretend play, chase one another, pretend to be someone else and so on,” which can be further separated into four distinctive forms of play: fantasy play (begins around the age of two and involves playing with an object using imaginative thinking rather than the objects’ actual properties), role play (begins around the third year of life and involves play acting imaginative scenarios with peers) – both described as an extension of pretend play, and exercise play (starts during the first year and increasingly peaks during the fifth year of life and involves the child playing using motor skill-

based activities such as running or hopping) and, finally, rough-and-tumble play (peaks in frequency around 6–10 years of age and involves behaviors that may appear aggressive, such as chasing or wrestling, but in the context of play are socially important) – both described as an extension of physical play. Furthermore, there are different relationships between different types of play and different cognitive abilities; e.g., group pretend play promoted increased use of adjectives and prepositions in children’s speech in contrast to solitary or dyadic play, while tabletop toys decreased children’s performance on creativity tasks conceivably because they are usually played in solitary or in pairs and they do not favor creative thinking (Holmes et al. 2017).

Adults and siblings offer different supporting roles during play activities with children on the grounds that adults provide structured play activities with increasing difficulty, much like a scaffolding, that allows children to practice and develop more complex play whereas siblings provide a play partner for the toddlers where they can use and master the skills they have developed (Frost et al. 2011, p. 113). Nevertheless, children often participate in social play with seemingly no one present in the room with them. Gleason (2017) elaborated on the unique ability of humans due to their highly evolved cognitive functioning to reap benefits from social play through the act of imagination and fantasy alone. The author explained that children play with their imaginary companions to practice skills, experience positive and negative emotions, experiment and rehearse real life events in a relationship, with no considerable risks to their well-being, leading to a more adaptive social development. Instead of only playing with real partners, children gain the added advantage of being able to create a personally customized partner capable of suiting their needs which opens the door for higher social competence, emotional regulation, and interpersonal skills development. What is more, the author suggested that from an evolutionary standpoint, imaginary companions cannot be explained from having benefits to evolutionary fitness since not all children create them and yet they typically develop the necessary social skills to

form healthy relationships. In turn, considering that usually children use imaginary companions in direct relevance to relationships with their significant others, imaginary companions are probably an adaptation by-product from the evolution of imagination and the highly evolved neurobiological systems that promote relationship formation.

The choice of play materials, ranging from toys meant to be played alone to toys that are best utilized with the company of others places a significant impact to children's social behaviors (Quilitch and Risley 1973; Ivory and McCollum 1999). Providing either "isolate" or "social" toys to children of 7-years age average revealed a 16–78% preference in social play activities, respectively. This data illustrates that in order to maximize therapeutic benefits for children with social deficits (e.g., autism), practitioners could incorporate play materials into therapy that promote social and cooperative play (Quilitch and Risley 1973). Lastly, there are considerable developmental benefits for children engaging in social play, for instance, the storytelling of children was more enriched with verbs after the engagement in pretend play (Holmes et al. 2017), exercise play at the school's playground during preschool years facilitates later development of social competence (Veiga et al. 2016), and social play can accurately predict greater involvement in the outdoor preschool environment (Miranda et al. 2017).

Massively Multiplayer Online Games

A more recent form of social play emerged because of the popular use of the internet which equipped video gaming with a social component creating the growing phenomenon of Massively Multiplayer Online Games (MMOGs). Online social play causes a shift in the play setting from a real world to a virtual world setting that comes with its own set of challenges for the unacquainted and yet semantically interacting online players (Frost et al. 2011, p. 366). Ducheneaut et al. (2006) examined one of the most popular MMOGs, World of Warcraft (WoW), and indicated that even though MMOGs create a distinct

social environment at least in the early stages of the game, players use others as their audience for their achievements in the game instead of interacting in cooperative activities with them. Additionally, they suggest that MMOGs act as a "virtual Skinner box" where the player's actions are reinforced getting them hooked to the online game, making WoW an excellent example of how operant conditioning coupled with a social environment that emphasizes success versus failure can in fact become highly addictive. Massively Multiplayer Online Role-Playing Games (MMORPGs) have many features similar to single player games (Ducheneaut and Moore 2004) yet their social nature enables players to experience collaborative activities that hone their teamwork skills (Cole and Griffiths 2007) and rewards them by seeking and gaining reputation within a virtually constructed social community (Yee 2002).

A recent study found that adults aged over 55 years were able to develop meaningful relationships with their online World of Warcraft friends. However, their difficulty was to extent this online friendships and incorporate them into their real lives, possibly because of the long distance between them or a general difficulty to transform online friendships to real life ones (Zhang and Kaufman 2017). In addition, research into MMORPGs revealed that for people who are uncomfortable with parts of their self-image (e.g., appearance, gender, sexuality, age, etc.), the social environment created by MMORPGs can facilitate their ability to express genuinely and additionally provide them with a great opportunity to create lasting and meaningful friendships or partners (Cole and Griffiths 2007). This evidence may suggest that MMOGs are the next step of social play evolution where children and adults could practice basic skills of social interaction safely and at a low personal cost in a virtual world.

The Neurobiology of Social Play Behavior

Observational studies indicate that generally species with more developed forebrains exhibit more

frequent and complex forms of play (Pellis et al. 1992). Social play possesses significant merits in social development and some of its numerous functions illustrated by experiments using play deprivation include: social group organization or building ties between group members, to facilitate the development (on a cognitive level) of the ability to express and understand communicative signals between conspecifics which may in turn improve their ability to cope with social conflicts, and offer an opportunity to practice a variety of behaviors in a sequence in an effort to find out the ones that are most compatible to each other and eventually form advanced combinations (Vanderschuren et al. 1997).

Characterized by its inherent reward value, and because the power reward has positively reinforcing behaviors, social play can act as a well-used behavior learning incentive in animal studies (Vanderschuren et al. 1997). On account of this existing biological reward system which is influenced by social play behaviors, social play is expressed differently based on the pleasure and motivation experienced during the activity (Achterberg et al. 2016). Survival of the species depends on behaviors that are considered as naturally rewarding some of which include feeding, drinking, and sexual reproduction (Vanderschuren et al. 1997).

Motivation and incentives in social play are affected by dopaminergic neurotransmission (Achterberg et al. 2016) which is concurrent with research showing that the rewards gained from social play behaviors is underlined by an activation of the opioid and dopamine systems in the brain (Vanderschuren et al. 1997). In conjunction with this, research-based evidence illustrate that social behaviors increase after opioid drug treatments; however, social play is not guaranteed to increase from the stimulation of dopaminergic neurotransmission even though forebrain dopamine levels appear to increase during social play activities (Vanderschuren et al. 1997). Achterberg et al. (2016) examined the different effects of dopaminergic and noradrenergic signaling using an operant conditioning task and two psychostimulant drugs (methylphenidate and cocaine) on the social play behaviors of rats

and found that while dopamine acts as a stimulant in social play's motivation, it shows no influence over its expression; however, noradrenaline affects negatively the motivation and alters the expression of social play behavior. Evidence such as these indicates that social play is an independent category of behavior not only because of distinctive behaviors found only in such an engagement but because of specific neurobiological pathways triggered during social play (Vanderschuren et al. 1997).

To investigate the neural mechanisms during play, intact and decorticated rats were compared, indicating that those with removed cortices attacked and defended during play-fighting as frequently as their intact or decorticated pairs, hence a subcortical mechanism's involvement was proposed (Pellis et al. 1992). Pellis et al. (2010) discussed evidence of several studies to show the effects of the subcortical structure, amygdala, on regulating social behavior. They argued on research showing that play-fighting frequency as well as social recognition is impaired in rats with amygdala damage and that organisms with larger amygdala exhibit more play behaviors. They further explain that amygdala's role in monitoring fear and impulses during play fighting is essential since an animal's fear can prevent it from accepting another conspecifics' intention to play and minimizes social contact or inhibits them from controlling their impulses making them for unreliable play partners. Conversely, there is another perspective which views that a larger brain affects the production of more complex forms of play indirectly by extending the period of development and growth allowing for more play opportunities to occur (Pellis et al. 1992). In addition, there are some implications of mirror neurons firing when individuals share their intentions to partake in a social interaction (e.g., play), but it still warrants more research (Bekoff 2001). Lastly, some alterations of the amygdala have been shown in autistic people, which might offer an explanation for the difficulties they face with social contact consequentially causing individuals with autism to demonstrate poor social play (Pellis et al. 2010).

Conclusion

In response to social play's positive impact on social and cognitive development (Achterberg et al. 2016), evolutionary forces may have facilitated through positive selection the continuation of genes coding for a predisposition in the human species to engage in social play activities to increase fitness (i.e., individual reproductive success that also reflects the adaptation degree of an organism to its habitat) and therefore improve chances of survival. For instance, similar to primates' rough-and-tumble play, young human children engage in this type of social play with similar patterns since it increases chances of survival by enabling them to experience the sensation of being the dominant individual which in turn endorses self-confidence in future social interactions (Frost et al. 2011, pp. 150–151). Some other benefits of social play include advanced language abilities in children (Holmes et al. 2017) as well as opportunities to foster their creativity (Frost et al. 2011, p. 163).

Even though there are significant findings from several studies about the many benefits of social play, there are important limitations in the applicability of the results. Not surprisingly, most research on social play, especially in play-fighting, is carried using nonhuman animals that are most often of the rat species, mainly because of the practical (Pellis and Pellis 2007) and ethical limitations in conducting such experiments with human subjects which may in turn commend using caution when generalizing these same finding onto the human species. Additionally, it is worth noting that some researchers have advised that even if a child engages frequently in social play activities, it does not in any way guarantee a socially competent or maladjustment free adolescence (Frost et al. 2011, p. 194). Nevertheless, these limitations aim to increase awareness for more creative experimental testing and should not undermine the aforementioned developmental and evolutionary benefits of social play or the importance of informing adults and schools about the advantages in encouraging social play engagement in children.

Cross-References

- [Classical Conditioning](#)
- [Communication, Cues, and Signals](#)
- [Cooperation](#)
- [Evolution of the Brain, The](#)
- [Human Storytelling](#)
- [Moral Instincts](#)
- [Natural Selection](#)
- [Operant Conditioning](#)
- [Peer Pressure](#)
- [Play and Tool Use](#)
- [Social Learning](#)
- [Team Sport](#)

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Social Playing

- [Social Play](#)

Social Problem Solving

- [Problem Solving](#)

Social Psychologist

- [Douglas Kenrick](#)

Social Psychology

- [Evolutionary Social Psychology](#)

Social Rank

- [Higher Status in Group](#)
- [Men in Positions of Power](#)
- [Self-Esteem and Social Status: Dominance Theory and Hierometer Theory?](#)
- [Social Authority](#)
- [Social Hierarchies](#)
- [Social Reasoning Affected by Rank \(Mealey, Daood, Krage, 1996\)](#)

Social Rank and Fitness

- [Status and Reproductive Success](#)
-

Social Ranking

- [Status and Dominance Hierarchies](#)
-

Social Reasoning

- [Emergence of Deontic Reasoning](#)
 - [Social Contract Rule Violation](#)
-

Social Reasoning Affected by Rank (Mealey, Daood, Krage, 1996)

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Synonyms

[Cheater detection](#); [Dominance](#); [Reasoning about social norms](#); [Social exchange algorithms](#); [Social rank](#)

Definition

The influence of the social status of a person within a group or society on cheater detection and memory for cheaters.

Introduction

Most human societies and primate groups are pervaded by social dominance hierarchies. It is

therefore plausible to assume that our cognitive system is shaped by selective pressures that require the individuals to adapt to the hierarchical organization of these social environments. Specifically, dominance theory (Cummins 1998, 1999, 2005) implies that the reasoning about social norms is affected by social rank. This hypothesis seems quite reasonable considering that social dominance hierarchies can be defined as a set of explicit or implicit social norms that define who is allowed to gain access to valuable resources (such as mates or food) and who is not. A social dominance hierarchy can only be maintained if the individuals in the group learn and follow the explicit or implicit rules that determine which behaviors are permitted, prohibited, or obligated for each individual, depending on the individual's social rank (Cummins 1998, 1999, 2005). This theory leads to the hypothesis that social rank may affect social reasoning (Cummins 1999) and, in particular, memory for cheaters (Mealey et al. 1996). This hypothesis needs to be empirically tested.

Dominance Theory

Following norms and helping others is one way to build alliances that help to gain and to maintain a high social rank in a group or society. High-ranking individuals have to share resources and have to fulfill reciprocal obligations to avoid losing important allies and, thereby, their status. Individuals with a low social rank, in contrast, may try to increase their limited access to valuable resources by cheating and by violating the social norms that deprive them of those resources. Given that the individuals with high social rank usually benefit most from the organization of the society, they are often responsible for enforcing the social norms that grant them privileged access to resources and for punishing the violation of these norms. Low-ranking individuals, in contrast, are lacking the resources to punish high-ranking individuals. Based on this reasoning, dominance theory (Cummins 1998, 1999, 2005) predicts that high-ranking individuals monitor the behavior of low-ranking individuals and are

highly vigilant against norm violations of low-ranking individuals, but not vice versa. In fact, the theory implies that cheater detection is a cognitive adaptation that serves to maintain social dominance hierarchies. A clear prediction that can be derived from this framework is that people should be more prone to detect the cheating of lower-ranking individuals in comparison to the cheating of higher-ranking individuals (Cummins 1999).

Although the above hypothesis is well grounded in a functional-evolutionary framework, it would not be right to uncritically accept this hypothesis based on plausible-sounding evolutionary arguments alone. Hypotheses in evolutionary psychology are tested in a similar manner as hypotheses in other areas of psychology and have to receive support from empirical tests before they should be accepted. It is useful to be aware that alternative hypotheses about the relationship between social rank and social reasoning are possible as well. A possibility that should be seriously considered is that social norms apply equally to high-ranking and low-ranking individuals. Consider, for example, the dictator game: In this game, the distribution of power is maximally unequal. One player, the dictator, receives a certain amount of money and has to decide how to split this money between him- or herself and the recipient. The recipient is entirely powerless and has to accept the offer of the dictator no matter how small. The dictator game can be viewed as a model of situations with extreme differences in social rank because the dictator has access to all of the resources and the recipient has nothing. Nevertheless, people generally judge an equal split between the two players to be most socially appropriate (Krupka and Weber 2013), suggesting that fairness norms are equally applicable to persons with high and low social rank. It is even possible to postulate that cheater detection should be higher when tracking the wrongdoings of high-ranking individuals (e.g., politicians with high political power), which would be directly opposed to the predictions outlined above. Some studies have indeed found positive associations between social rank and norm violations (Piff et al. 2012; but see Francis 2012). Despite this evidence to the

contrary, high-ranking individuals (e.g., professors) are often expected to be moral role models for lower-ranking individuals (e.g., students) and may therefore be judged by harsher standards. Accordingly, it is also possible to postulate that high-ranking individuals should show a noblesse oblige effect and should be more generous and forgiving against low-ranking individuals than vice versa (Fiddick et al. 2013). Hence, the hypothesis that people should be more vigilant against the cheating of low-ranking individuals in comparison to that of high-ranking individuals is a plausible possibility, but the opposite is equally plausible.

Is Social Reasoning Affected by Social Rank?

To test the prediction of dominance theory that people are better at detecting norm violations of lower-ranking individuals, Cummins (1999) used a deontic version of the Wason Selection Task. In the classical version of the task (Wason 1968), participants see four cards with a letter on one side and a number on the other (upper panel of Fig. 1). The visible sides of the cards show “A,” “B,” “4,” and “7.” Participants are required to select the cards they have to flip over to test the rule “If a card shows a consonant on one side, then

B	A	7	4
Borrowed the car	Did not borrow the car	Filled up the tank with gas	Did not fill up the tank with gas

Social Reasoning Affected by Rank (Mealey, Daoood, Krage, 1996), Fig. 1 Examples for the Wason Selection Task. In its original version (*upper panel*), participants see four cards and are asked: Which cards do you have to turn over to test the truth of the rule *If a card shows a consonant on one side, then there is an odd number on the other?* In the deontic version of the task (*lower panel*), participants are asked: Which of the cards do you have to turn over to see whether someone breaks the rule *If you borrow my car, then you have to fill up the tank with gas?*

there is an odd number on the other.” The correct solution is to pick the two cards that allow for a falsification of the rule (“B” and “4”). An interesting aspect of this task is that the majority of participants fail to solve the task correctly, suggesting that humans are not very good at (and not biologically prepared to) thinking about abstract logical problems. Another interesting observation (Cosmides and Tooby 2005) is that people are much better at solving the task when confronted with the more natural task of detecting cheaters that violate social rules such as “If you borrow my car, then you have to fill up the tank with gas” (lower panel of Fig. 1).

In Cummins’ (1999) deontic version of the Wason Selection Task, participants were required to test whether a resident assistant or a student showed compliance with the rule “If someone is assigned to lead a study session, that person is required to tape-record the session.” In a control condition, participants were told to imagine that they overheard a resident assistant’s or student’s statement “If I am assigned to lead a study session, I always tape record the session.”, and were asked to test the truth of the statement. Half of the participants were cued into the perspective of a resident assistant, and the other half were cued into the perspective of a student. Half of each group was instructed that they were checking on a resident assistant, and the other half were told that they were checking on a student. Reasoning was affected by rank, but only in the deontic version of the task. Participants were more likely to show evidence of a “look-for-cheaters” strategy when they were cued into the perspective of a resident assistant checking on students (65 % correct answers) in comparison to all other conditions (15–20 % correct answers). This confirms the prediction of dominance theory that high-status individuals are vigilant against norm violations of low-status individuals. Cummins (1999) interpreted these findings as evidence of a biological adaptation to social dominance hierarchies.

However, a plausible alternative to this interpretation is that Cummins’ (1999) manipulation had served as an implicit cue to monitor the compliance with the rule. Enforcing social norms and confronting norm violations of students is an

integral part of the role of a resident assistant, but not of fellow students. It seems possible that the effect was not due to differences in social rank but was rather due to the participants being aware of the fact that resident assistants are supposed to monitor the students’ compliance with norms. It seems therefore unnecessary to postulate a domain-specific mechanism for reasoning about social dominance hierarchies when the results can be attributed so easily to general learning mechanisms that allow individuals to acquire knowledge about the world, including knowledge about specific behaviors required by social roles. Therefore, additional research is needed to test whether these effects are indeed due to the influence of social rank rather than to the specific scenario realized in the study of Cummins (1999).

In a follow-up review, Fiddick and Cummins (2001) summarized several studies in which social status was unintentionally manipulated. Specifically, Gigerenzer and Hug (1992) required participants to take the perspective of high-ranking or low-ranking individuals when reasoning about rules. For example, participants were cued into the perspective of an employer or of an employee when reasoning about the rule “If an employee works on the weekend, then that person gets a day off during the week.” Fiddick and Cummins note that the findings reported by Gigerenzer and Hug (1992) do not provide consistent evidence of an influence of social rank on social reasoning. There was no significant effect of social rank on performance in the day-off problem (75 % detection of high-status cheaters and 61 % detection of low-status cheaters) and in a similar pension problem (64 % detection of high-status cheaters and 70 % detection of low-status cheaters). Only in one of three problems, the subsidy problem (“If a home owner gets a subsidy, then that person must have installed a modern heating system”), a significant effect of perspective was found (81 % detection of low-status cheaters and 59 % detection of high-status cheaters) although the subsidy problem was the problem with the least pronounced differences in social rank (house owner vs. environmental officer). However, the latter effect should not be over-interpreted given that Holyoak and Cheng (1995)

have obtained no effect of social rank using the same scenario.

Fiddick and Cummins (2001) used another variant of the Wason Selection Task in which they required participants to look for violations of the rule “If you pay for the gas, I’ll drive you to work.” Participants were either asked to take the perspective of a high-ranking individual (a boss) or of a low-ranking individual (an employee). The study demonstrated a high degree of intercultural variability in the effects of social rank on performance in the Wason Selection Task. In Germany, no significant effects of rank were obtained. In California, participants were better when monitoring the compliance of high-status individuals (70 % correct answers) than when monitoring the compliance of low-status individuals (45 % correct answers). This effect is in the opposite direction of what was predicted by Cummins (1999). The high cultural variability in the findings that has been identified by Fiddick and Cummins (2001) is challenging for the interpretation of the findings in terms of an evolutionary adaptation.

In another series of experiments, Fiddick and Cummins (2007) used a ledger task in which they confronted participants with different degrees of compliance on the part of the gas-paying partner and required them to indicate (1) how likely they would want to continue the car-sharing arrangement and (2) to what degree the arrangement was seen as fair or unfair. Again, participants were required to take the perspective of either a high-ranking individual (a boss) or a low-ranking individual (his or her employee). Participants cued into the perspective of a high-ranking individual were more tolerant of cheating than participants cued into the perspective of a low-ranking individual, which is again inconsistent with the original hypothesis that high-ranking individuals should be more, not less, vigilant against cheating of lower-ranking individuals (Cummins 1999). The results seem to be quite robust (Fiddick et al. 2013), but they are difficult to interpret. Fiddick and Cummins (2001) explained the discrepancy to earlier findings by arguing that the earlier findings (Cummins 1999) are about monitoring the compliance with social norms, while the

car-sharing scenario is about a reciprocal personal exchange. However, it is questionable whether these two can be clearly separated when reasoning about work-related activities that concern the employer-employee relationship. Somewhat puzzling, the noblesse oblige effect could not be attributed to an asymmetrical perception of the costs and benefits of the car-sharing arrangement for the employer and the employee, and it is unrelated to differences in income. When the individuals in the scenario were described as boss and employee, but not each other’s boss and employee, the effect vanished. This suggests that the underlying causes for the effect may lie in the specific relationship between a boss and his or her employee when performing work-related activities (paying the other person money for getting back and forth to work) rather than in differences between high-ranking and low-ranking individuals per se. It is an open empirical question whether these findings would generalize to other agreements between a boss and his or her employee and other asymmetrical social relationships.

Is Memory for Cheaters Affected by Social Rank?

Given that the research in the Wason Selection Task does not provide a clear picture, it seems necessary to test the influence of social rank on cheater detection in other paradigms. Fortunately, such evidence is available. Social rank was manipulated in studies of memory for cheaters, which provides an additional test of the hypothesis that processing information about cheaters is affected by social rank. In their pioneering study, Mealey et al. (1996) examined old-new face recognition for faces of cheaters, neutral, and trustworthy persons. They were primarily interested in testing the hypothesis that memory for cheaters is enhanced over memory for other types of faces, but they also included a manipulation of social rank by pairing the faces with high-status professions (e.g., a bishop) or low-status professions (e.g., a cashier). Interestingly, their initial hypothesis was that faces of high-ranking cheaters

should be attended, encoded, and recognized with a higher probability than the faces of low-ranking cheaters. Their reasoning was that the behavior of more powerful individuals is less constrained by situational factors, which means that the cheating of those individuals can be more readily attributed to internal character flaws. One may add that the cheating of a high-ranking individual (e.g., of an influential politician) may have more devastating consequences than the cheating of a low-ranking individual, simply because high-ranking individuals are more influential, and their decisions may be more likely to affect a larger number of people to a greater extent than those of low-ranking individuals.

Inconsistent with this *a priori* hypothesis, Mealey et al. (1996) found that the interaction was in the opposite direction of what was predicted. Furthermore, the results are less compelling than often claimed. Only the recognition of individuals with a low social rank was modulated by whether the face was paired with cheating, neutral, or trustworthy behavior. Even though this effect is often interpreted as evidence for (far) better memory for faces of cheaters (Cummins 1998), the difference between the cheater condition and the neutral control condition was much smaller than the difference between the neutral control condition and the trustworthy condition. Post hoc tests were not reported, but it is possible to conclude from the descriptive pattern of results that the effect was mainly driven by a decreased recognition of trustworthy individuals with a low social rank rather than by an enhanced recognition of cheaters with a low social rank, relative to a low-status neutral control condition, which is hard to reconcile with a functional perspective on memory for social interaction partners. As a post hoc explanation for the absence of any effect of behavior on the recognition of individuals with a high social rank, Mealey et al. proposed that the high attractiveness of the high-ranking individuals may have caused participants to ignore their untrustworthy behaviors. This interpretation was seemingly supported by the fact that female participants showed a descriptive tendency toward a better recognition of trustworthy individuals with a high social rank,

but this finding cannot be meaningfully interpreted because the three-way interaction between social status, behavior, and participant gender was not significant. Even if this problem is ignored, it remains debatable whether women should ignore the untrustworthy behaviors of attractive mating partners entirely. More important in the present context is that the pattern of results reported by Mealey et al. has been cited as supporting evidence for the assumption of dominance theory (Cummins 1999) that the cheating of low-ranking individuals should be monitored more closely (Cummins 1998, 1999, 2005).

Given the unexpected nature of Mealey et al.'s (1996) findings, it seems problematic to base strong conclusions on this single study. Fortunately there are several attempts to reproduce Mealey et al.'s findings that provide a clearer picture. Barclay and Lalumière (2006) repeated the study in two experiments ($N = 179$ and $N = 49$) and found no effect of social status, no effect of behavior, and no interaction between these two variables on face recognition in either of the experiments. Similarly, Mehl and Buchner (2008) found no evidence of a recognition advantage for faces of cheaters, no effect of social status, and no interaction between these variables in two experiments ($N = 96$ and $N = 123$). In a third experiment ($N = 64$), they found a small effect of social status (the faces of high-ranking individuals were recognized somewhat better than the faces of low-ranking individuals), but the effect was descriptively small. The interaction between social status and behavior was not replicated once again. In light of these failed replications, the findings of Mealey et al. should not be regarded as convincing evidence in favor of dominance theory (Cummins 1999).

Buchner et al. (2009) have argued that the null findings summarized in the previous paragraph are not necessarily problematic for any theory about cheater detection because recognizing faces as familiar cannot help to avoid cheaters and therefore does not provide an evolutionary benefit when the source or context in which the face was encountered is forgotten. What is required instead is the ability to remember that a particular person was associated with a history of

cheating. Indeed, source memory for faces of cheaters – that is, the ability to remember that an individual's face belongs to a cheater – was found to be enhanced in comparison to source memory for trustworthy or irrelevant individuals (see Bell and Buchner 2012, for a review). Most relevant in the present context, the source memory advantage for cheaters was not affected by social rank: Source memory did not differ between high-ranking and low-ranking individuals at all. This finding provides compelling evidence that people are equally interested in the cheating of high-ranking and low-ranking individuals.

Conclusion

In essence, then, there is as yet no reliable evidence that reasoning about social norms or memory for cheaters is affected by social rank. One study (Cummins 1999) demonstrates that high-ranking individuals may be more vigilant against the cheating of low-ranking individuals, but this finding can be attributed to the fact that some social roles with leadership status imply the duty to enforce social norms on others, which may affect the behavior of participants assigned to those roles accordingly. Other studies (Fiddick and Cummins 2007; Fiddick et al. 2013) show that high-ranking individuals are more tolerant of the cheating of low-status persons, but this finding may have to be attributed to the specific relationship between a boss and his or her employee rather than to status differences per se (Fiddick and Cummins 2007). Other lines of research either show a highly inconsistent pattern (Fiddick and Cummins 2001) or have demonstrated that social rank has no effects at all (Barclay and Lalumière 2006; Buchner et al. 2009; Mehl and Buchner 2008). In sum, the results seem to suggest that the relationship between social rank and social reasoning is determined by the specific situation. Although the idea that people may be biologically prepared to deal with social dominance hierarchies sounds quite plausible, the available evidence suggests that this does not necessarily include specialized modules for reasoning about norm violations or

memory for cheaters. More research is necessary to gain a deeper understanding of the conditions under which the processing of exchange-related information is affected by social hierarchies.

Cross-References

- [Dominance and Threat or Use of Force](#)
- [Dominance Hierarchies](#)
- [Dominance Theory \(Cummins\)](#)
- [Effect of Status on Social Reasoning \(Cummins 1998\)](#)
- [Memory Enhanced for Cheaters Versus Non-Cheaters](#)
- [Rule Violations Checked if High Status](#)
- [Rule Violations Not Checked if Low Status](#)
- [Status and Dominance Hierarchies](#)
- [Strength and Anger-Proneness](#)

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Social Rejection

- ▶ [Peer Rejection, Gender Differences in Response to](#)
- ▶ [Peer Rejection, Sex Differences in Initiation of](#)

Social Relations Theory (Fiske)

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Synonyms

[Moral relationships](#); [Social structure](#)

Definition

A set of psychological models centering on social relationships.

Introduction

Much of social psychology examines human behavior as a product between the individual and the situation. This focus led to many distinct findings that some argue were poorly explained (see Fiske 1991). With no overarching theory to guide them, most studies were presented as individual findings, unconnected to other findings within social psychology. To remedy this, some social psychologists had proposed unified theories of social psychology. However, these theories assumed humans thought of other humans as if they were inanimate objects (Fiske 1991). To counter this, Fiske (1992) proposed a unified theory of social relations that could help explain many findings in social psychology. This theory presented four psychological models that focus on human social relations: communal sharing, authority ranking, equality matching, and market pricing.

Communal Sharing

Communal sharing relationships are created through the notion that everyone within a communal group are both equal to one another and bound to one another. In this model, members of a group treat each other relatively the same, and

relationships are focused on disregarding individual differences and embracing commonalities. A key feature of these relationships is the belief that some immutable substance is shared across the group (e.g., genes, spirit). This psychological model is most often found in kinship ties, but can be seen in many ethnic identities or other such tightly bound groups. A common example of communal sharing groups is found in hunting and gathering societies. In these societies the whole group shares the meat of animals killed, and tools are shared freely (Marshall 1961). An important aspect of this form of sharing is the communality of land; land cannot be bought or sold, and it frequently becomes closely associated with the group living on it (Elias 1956).

One key feature of communal sharing relationships is the division of those outside the communal group into different classes that can be compared. For example, non-kin may be divided as neighbors and non-neighbors. Neighbors may receive the same resource support as kin, whereas non-neighbors may not, but both groups are socially equivalent for the purposes of alliance building in times of conflict. This type of psychological model may be especially useful when needing to keep track of large numbers of others while maintaining an in-group bias.

Authority Ranking

Authority ranking relationships function by building asymmetrical relationships among others who are ordered in a linear and hierarchical structure. These relationships are defined by a salience of one's rank compared to those around them, namely, determining if others are higher or lower than oneself in the status hierarchy. Individuals with a higher rank tend to have higher prestige, privileges, and deference by those below, whereas those with a lower rank are generally entitled to protection by those above them. These differences can be seen in the explicit rhetoric used, and the space granted, to those with more status in Western societies; those higher in rank are referred to as "higher-ups" and to be knocked down is to be "belittled." Moreover, those with more power are

given offices on higher floors with more space, whereas being sent to work in a basement is an insult.

A key feature of these relationships is the linearity of the ordering; no two individual can have the same status, and status is seen as unidimensional. For example, if person A is said to have a status equal to or greater than person B and if person B also has status equal to or greater than person A, then person A and B must be the same person. This means there are no branches or loops in an authority ranking relationship; the order among a group using such a relationship must be perfectly linear. Thus, this theory states that when individuals think in a linearly structured relationship model, they treat higher ranks as better.

Equality Matching

Equality matching relationships are based on an egalitarian form of justice, where retribution equals the harm. The main concern for those in such a relationship is balance. This is similar to a communal sharing relationship, except the focus of such sharing is on reciprocity, not care. In other words, everyone shares as a consequence of the threat of retribution, not because they feel any special affinity for those they are sharing with. As there are no assurances that everyone will pull their full weight in these relationships, individuals spend more time ensuring a one-for-one relationship to try and catch potential cheaters/freeloaders as soon as possible. Some common forms of these relationships are car pools or baby-sitting cooperatives. If a deficit is noticed, the cheater may be expected to give more to equalize the balance. For example, if an individual claims to be injured and cannot work a communal field one day, they may be expected to work the field alone the next time the group takes a day off.

Two key features of these relationships are linearity of debt and irrelevance of order. The first feature refers to the way humans conceptualize equality, stating that a debt of two carpool trips is exactly one step worse than a debt of one carpool trip, which is exactly one step worse than no debt. This second feature of these

relationships, the irrelevance of order, states that the way a debt is gained is irrelevant to the requirements for paying off the debt. For example, failing to carpool twice, carpooling once, and then failing to do so three more times are no worse than failing to do so three times, carpooling once, and then failing to do so two more times. Either way you have failed to balance your debt four times.

Market Pricing

Market pricing relationships focus on proportionality in social relationships. This means that everything in consideration is condensed into a single value that allows for comparisons to others. There are many such metrics, such as social value or money. As in the equality matching model, these ratios are linear, but unlike in equality matching model, the values can be compared to non-like concepts. For example, if two individuals in the carpool group were also in a group that watched each other's children, one failure to carpool would have no direct relationship to one failure to care for children. However, in market pricing relationships, you can compare these things. For example, if you owe someone a horse but all you own are dogs, each dog has a value so there will be some number of dogs whose collective value is worth more than the value of the horse you owe.

Conclusion

Fiske (1992) presented one of the most comprehensive and, for its time, novel approaches to a unified theory of social psychology seen in academia. By supporting his research with numerous cultural studies using a varied methodology, Fiske demonstrated that his theory not only accounted for many of the findings within social psychology, but that his theory could also be applied in cross-cultural research. In particular, he demonstrated a theory that was flexible enough to account for massive cultural differences without violating previous findings within social psychology.

Cross-References

- [Cultural and Moral Relativism](#)
- [Evolution of Cooperation](#)

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Social Relationships

- [Cost of Same-Sex Friendships](#)
- [Same-Sex Friend](#)

Social Reputation

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Synonyms

[Social standing](#); [Social stature](#); [Social status](#)

Definition

Social reputation refers to the global impression that individuals within a community hold regarding a particular target individual. From an evolutionary perspective, we can think of one's social reputation as largely existing on a continuum with selfish on one end and other-oriented on the other.

Introduction

From an evolutionary perspective, the issue of reputation is initially something of a conundrum. That is, evolution generally selects for attributes of organisms that primarily and ultimately facilitate one's own probability of survival and/or reproduction (Dawkins 1976). To understand the relevance of one's social reputation from an evolutionary perspective, we need an understanding of the fact that humans evolved in contexts in which we interacted with the same other individuals repeatedly over long periods of time in small-scale societal conditions (Dunbar 1992). Further, a hallmark of being human pertains to the fact that these social conditions included a mixture of kin and nonkin. In such circumstances, reciprocal altruism (see Trivers 1971), or helping others with an implicit expectation of help back at a future point, can evolve to be a very powerful force in shaping social psychological phenomena.

In fact, reciprocal altruism ends up being a foundational aspect of what it means to be human, and this concept can help us understand a broad suite of cognitive and emotional processes in humans (see Geher 2014). For instance, we can understand guilt in terms of the fact that this emotion emerges when people fail to reciprocate altruistic acts within one's social circle. Similarly, apologetic behavior can be understood as having the function of staying connected with others after some sort of transgression. From this perspective, we can see how cultivating a reputation as a pro-social individual (i.e., an altruist) can ultimately have benefits that flow back to oneself within the context of his or her social circle. On the other hand, having a reputation as someone who is selfish and not trustworthy could have very damaging consequences for oneself.

The Social Ecology of the Environment of Evolutionary Adaptedness

Prior to the advent of agriculture, our ancestors lived in small, nomadic societies in numbers rarely exceeding 150 (Dunbar 1992). And in these small groups of individuals whom you

would spend your whole life interacting with, about half were kin (i.e., genetically related individuals) and half were nonkin whom one interacted with regularly. An implication of this feature of the ancestral human social ecology is that human psychological processes were shaped to deal with about 150 total individuals, a number now referred to as *Dunbar's number*.

The importance and relevance of Dunbar's number is that our minds evolved for small-scale living and interactions. Further, because of our evolved affinity toward small-scale social groups, things like social reputation weigh heavily on our livelihood.

Reciprocal Altruism

In a social world in which an individual is surrounded by the same conspecifics (i.e., members of the same species) repeatedly over time, it is possible that reciprocal altruism could evolve. This is because that in such a context, helping others with an expectation of help in return is possible. In his classic treatise on reciprocal altruism, Trivers (1971) discusses three specific preconditions that must exist in a species for reciprocal altruism to be mathematically possible (as it would have to ultimately pay off in survival and/or reproductive benefits for oneself given how natural selection operates). These three conditions are as follows:

1. The social ecology of the species must be such that individuals live in small groups comprised of the same individuals.
2. The lifespan of the species must be relatively long (so that altruistic behavior has a chance of being paid back).
3. The members of the species must be able to recognize specific conspecifics as individuals (so that an individual is able to differentially reciprocate based on who is who).

Humans fit these criteria to a tee (see Trivers 1985). So it is not surprising that reciprocal altruism is a foundational feature of the human social world.

In a world in which reciprocal altruism is ubiquitous, you have to watch yourself. If you never help anyone, then you might be ostracized and shunned. Even hated. If you help anyone at any point with zero discrimination as to who has helped you in the past, you risk being seen as someone who others might take advantage of.

In their classic work on the cognitive psychology of cheater detection, Cosmides and Tooby (1992) provided strong evidence demonstrating that human logic-based reasoning is enhanced when we are primed to think about a scenario in which someone might be trying to cheat others in a social context. In other words, when we are primed to think about if someone is failing to reciprocate altruism, our minds seem particularly astute. This general finding fits strongly with the idea that reciprocal altruism is a foundational part of the human social world. Our evolved psychology is filled with adaptations that were shaped by the fact of reciprocal altruism.

The Emergence of Social Reputation

Cultivating a reputation as a trustworthy altruist within one's community has both potential long- and short-term benefits aiding one's capacity for survival and reproductive success. In fact, pro-social, other-oriented personality traits (e.g., empathy, kindness, high agreeableness) are highly attractive and sought-after in potential mates (see Buss 2003). Nesse (2007) argues that the unique, and sometimes extreme, altruistic tendencies of humans evolved due to mating competition and is possibly a result of runaway social selection processes. This *competitive altruism* has been found to be a successful courtship display used to attract others (Barclay 2010), specifically when these signals are socially conspicuous, serving to bolster one's social reputation.

While cultivating a reputation as an altruist is one clear social strategy in humans, there are clearly a plurality of social strategies that exist in our species. For instance, one may take another avenue for evolutionary success and instead choose to maintain his or her social reputation as a dark, confident, powerful, and fear-inducing individual. Such a dark strategy may be successful in certain

contexts. However, when it comes to human evolved social psychology, any behavioral strategy comes with a variety of costs and benefits.

One empirical study supporting the competitive aspects and direct effects that altruistic behavior has on one's social reputation found that participants chose costlier signals and helped more, to essentially "show off," when the altruistic behavior was public, rather than anonymous (Bereczkei et al. 2010). Public displays of altruism, even if costly, appear to have an overall payoff in terms of social recognition, prestige, and popularity. In other words, altruistic behavior may partly be about cultivating a positive social reputation.

Conclusion

Under ancestral conditions, humans evolved in small-scale societies, surrounded by the same others for the lion's share of their lives (Dunbar 1992). Related to this kind of social ecology, reciprocal altruism evolved as a basic aspect of how humans interact with one another. In such a social world, there are clear benefits to oneself that follow from helping others – especially in publicly observable contexts (see Barclay 2010).

While taking a selfish approach to life as a human may have various immediate kinds of pay-offs, being tagged as selfish in terms of one's social reputation within the group can actually be quite deleterious to one's life. Across one's entire social life, social reputation matters. And the evolutionary perspective helps us understand why.

Cross-References

- [Altruism](#)
- [Cooperation](#)
- [Reciprocal Altruism](#)

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Social Responsibility

► Civic Duty

Social Roles

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Synonyms

Role; Roles

Definition

A socially defined pattern of behavior that is expected of a person who occupies a certain social position or belongs to a particular social category.

Introduction

Social roles are a socially defined pattern of behavior that is expected of persons who occupy

a certain social position or belong to a particular social category. The construct of social roles is central to the social sciences, and it came into general use during the 1920s and 1930s by analogy to the theatre. Social life occurs as performances by social actors, who are constrained by the scripts of their roles; the same actor can perform very different roles in different plays, and different actors can perform the same role quite similarly (Biddle 1986).

Types of Roles and Role Theory

At an individual level, roles function as schemas, that is, mental concepts that inform a person about how to behave in a particular role or situation. In addition, these role schemas are important structures at societal level as they tend to be consensual, (i.e., shared by members of society), and all persons in a society can be expected to support these shared behavioral expectations. Roles are therefore aspects of social structure that can be regarded as “persisting and bounded patterns of behavior and interaction among people or positions” (House 1995, p. 390). Different types of roles can be distinguished from each other (see Turner 2001). *Basic* roles, which are based on membership in general social categories (e.g., gender, age, ethnicity), have great generality because they affect all portions of an individual’s daily life. In contrast, *position* or *status* roles, which are based on, for example, occupations (e.g., firefighter, nurse) and family relationships (e.g., father, daughter), are primarily important for one’s behavior in particular settings (e.g., organizational work-context) or in a particular group. *Functional group* roles, like “mediator,” “counselor,” and “devil’s advocate,” develop informally as individuals adopt situational identities during social interaction in a group setting. Finally, *value* roles, such as “saint,” “hero,” and “villain,” emerge in the context of very positively or negatively valued behavior. It is also important to note that social roles can be either ascribed (e.g., gender, age) or achieved (e.g., parent, doctor).

Role theory is concerned “with the organization of social behavior at both the individual and collective levels” (Turner 2002, p. 233). Individual behavior in social contexts, tasks, and responsibilities in work groups and organizations,

as well as participation in society are organized into social roles. The role construct implies that individuals, who occupy the same social position within a social structure (e.g., organization, family), or who belong to the same general societal category (e.g., as men, as African Americans), are subject to the same situational constraints that help maintain their characteristic patterns of behavior. These constraints stem from the mental schemas for roles, for example, schemas for the daughter role, the doctor role, or the hero role, which people in their society share. As these schemas entail shared norms for appropriate conduct in these roles, “all persons in the system can be counted on to support those norms with sanctions” (Biddle 1986, p. 76). Role theory thus contributes to our understanding of the relationships among the micro-, meso-, and macrolevels of society.

Approaches to role theory can be broadly categorized via their most important distinguishing characteristic; they are either *structural* or *interactional*. Structural theories, building on Linton (1936), focus on the collective level and view roles as a set of expected behaviors, which are linked to positions in organizations and statuses in society. Individuals play their assigned parts in scripts written by culture with minimal improvisation. However, a somewhat more dynamic approach to structural theory put forward by R. Merton (1957) grants role incumbents (e.g., nurses) the option to act out different roles in response to the varied expectations of different people of importance (e.g., doctors, patients, family members of patients, fellow nurses). These different roles which emerge from varied expectations toward the role occupant are labelled a *role-set*. In contrast, interactional theories, building on G. H. Mead, shift the focus on social stability to social change, social structures to social processes, and on conformity to role-making (Turner 1962). Scripts only broadly determine the behaviors of the actors; during performances, the role incumbent improvises and develops and changes the scripts in a way that combines elements of creativity with conformity. Human agency and creativity in shaping social structures are seen as critical to social life as are

social constraint and conformity. While the classification into structural or interactional approaches is the most critical one, Biddle (1986) distinguishes three additional subsets of role theories including functional role theory, oriented to analyses of stability in social systems; organizational role theory, which focuses on role conflict in formal organizations; and cognitive role theory, which studies role expectation-behavior relations.

Multiple Roles and Psychological Adjustment

Basic roles, like those attached to gender and age identities, coexist with specific roles, like family and occupational roles, and are relevant to a wide variety of situations, including social interactions that are also structured by these specific roles. In the workplace, for example, a nurse or firefighter holds a particular role defined by occupation but is, at the same time, a man or woman and, therefore, also acts in accordance with his or her gender role, i.e., shared expectations that apply to individuals based on their socially identified sex. Social role theory (Eagly et al. 2000) posits that in the presence of typically very constraining role information, gender roles become less influential determinants of a person's behavior. More generally, research suggests that people combine or average the expectations linked to specific roles and more basic roles, like gender roles. Experimental evidence has further shown that men's and women's occupancy of the same role reduced or even eliminated gender-stereotypical trait judgments (Bosak et al. 2008, 2012). Eagly et al. (2000) conclude that specific social roles (e.g., occupational roles) mainly influence how the tasks required by the role are accomplished by individuals, regardless of their basic roles. In contrast, basic roles (e.g., one's gender or sexual orientation) might “spill over” to impact the discretionary behaviors that are not required by the more specific social roles.

The coexistence of multiple social roles is also critical to the psychology of adjustment. A key concept is role conflict, which can be defined as

“the concurrent appearance of two or more incompatible expectations for the behavior of a person” (Biddle 1986, p. 82). With *intrarole* conflict, the role incumbent must reconcile incompatible expectations and demands associated with the role. For example, an employee might experience intrarole conflict when being asked to complete a task for each of his or her supervisors at the same time. With *interrole* conflict, the role incumbent must manage contradictory expectations associated with different roles. For example, the interface between work and family demands can be a significant cause of interrole conflict. Because of role conflict, role strain, i.e., the felt difficulty in fulfilling role obligations (Goode 1960), may emerge. In addition to role conflict, other structural conditions that might cause problems in social systems include, for example, role ambiguity, i.e., a condition in which the role lacks specificity or complete information to guide behavior, and role overload, i.e., a condition in which a person faces too many expectations. In general, research suggests that, in work settings, these demands are associated with stress, burnout, and higher intention to quit. For example, a recent study conducted in a Canadian hospital found that job demands, (i.e., role conflict, role overload), were positively associated with burnout among hospital staff, (i.e., emotional exhaustion and depersonalization), and that staff perceptions of human resources practices (including empowerment, information-sharing, training, and non-monetary recognition practices) reduced the perceived demands and, in return, burnout (Kilroy et al. 2016).

The conflict perspective was challenged by Sieber (1974) who advanced the idea of *role accumulation* according to which the advantages of pursuing multiple roles might accumulate more substantially than the disadvantages, to the incumbent's benefit. According to the role enhancement perspective, a larger number of roles will increase an individual's resources, social connections, power, prestige, and emotional gratification (Marks 1977; Sieber 1974; Thoits 1983). This shift in focus from investigating the negative consequences of combining multiple roles (e.g., being both a parent and an employee) to its

positive consequences has been particularly prominent in research on the work/nonwork interface – as evidenced by Greenhaus and Powell (2006)'s model of work-family enrichment. These scholars defined work-family enrichment as “the extent to which experiences in one role improve the quality of life in the other role” (p. 73) and propose that enrichment is bidirectional.

Conclusion

Social roles can be understood as a socially defined pattern of behavior enacted by a person in a particular social position or belonging to a particular social category. Different roles (e.g., basic roles, position roles) can be distinguished from each other and they combine, in the form of multiple roles, to influence people's behavior. The coexistence of multiple social roles has important implications for individual's psychological adjustment and well-being, although the two competing perspectives – i.e., role strain perspective versus role enhancement perspective – differ in their propositions of and explanations for the effects of multiple roles on well-being.

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Social Sanctions

- [Procedures for Dealing with Bullies](#)

Social Science

- [Psychology](#)

Social Signal

- [Color Red](#)

Social Signals

- [Sex Differences in Emotional Communication](#)

Social Skills

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Synonyms

[Cooperation](#); [Social competence](#)

Definition

Social skills form a set of behaviors emitted in social interactions, which can contribute positively to relationships between peers and to the development of a relationship considered to be satisfactory according to a particular context.

Introduction

Social interaction is recognized as extremely important for the survival of the human species. Although competition was fundamental to evolution, cooperation was also significant in terms of building society (Yamamoto et al. 2018).

Main Text

The expression of feelings, attitudes, desires, opinions, or rights of a given person, in a manner that is appropriate to the situation in which they are, is an important factor for achieving social competence (Caballo 2006). It also involves respect for these behaviors when expressed by another person in order to reach a resolution of an immediate problem or to prevent future adversities. In addition, there are behaviors that permeate everyday circumstances in different areas of a subject's life, including, according to Del Prette

and Del Prette (2001), communication skills, such as starting, holding, and ending a conversation; civility (how to present oneself, greet someone, thank someone, etc.); exercising rights and citizenship, such as expressing opinions, agreeing, disagreeing, apologizing, admitting failures, interacting with authorities, ending relationships, expressing dislike, etc.; and work, such as speaking in public, solving problems, making decisions, mediating conflicts, etc.

Childhood is a crucial period for the elaboration of social skills, because it is the phase in which children are invited to develop a satisfactory repertoire for the construction of healthy bonds (Schneider et al. 2016). Parental educational practices have a powerful influence on the development of children's social skills, and they extend the skills they learn to other social environments. An experiment conducted by Warneken and Tomasello (2006) found that children as young as 18 months of age were able to choose behaviors to help a stranger rather than help themselves. This choice can be understood both from the nonverbal behaviors learned early on through parental practices and from gene predisposition to prosocial actions (Penner et al. 2005; Del Prette et al. 2013).

Although they can contribute, the genes related to prosocial behaviors are not enough for the development of good social skills. Oxytocin, a hormone secreted by the hypothalamus and considered the biological substrate of empathy, seems to positively influence prosocial behaviors such as cooperation, generosity, and reciprocity (Barraza et al. 2011; Thompson et al. 2013). The behavior of helping a stranger who is suffering can be explained by the neural empathy mechanism that favors the observer to create a representation of the emotional experience of others, increasing the possibility of helping (Preston and De Waal 2002).

Just as there are benefits derived from good SK, failures in the development of this area can lead to several and significant losses in a person's life. Non-skillful social behavior may make it difficult to create bonds and, consequently, to form a support network. From this, Del Prette et al. (2013) put social isolation as a risk factor

for early death. In addition, the same authors report that individuals with SK deficits may be considered more vulnerable to psychiatric disorders in general.

Conclusion

Humans are essentially social beings, and, in this sense, the ability to maintain themselves in social interactions seems to have a protective even now. The studies presented have demonstrated the importance of social skills, as well as the presence of biological mechanisms in prosocial behaviors.

Cross-References

- [Cooperation and Social Cognition](#)
- [Peer Competition and Cooperation](#)
- [Social Development](#)
- [Social Learning](#)

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- [Social Hierarchies](#)
- [Social Reputation](#)
- [Status and Redistribution of Resources](#)
- [Women's Prosocial Dominant Acts](#)

Social Source Memory

- [Memory Enhanced for Cheaters Versus Non-cheaters](#)

Social Standing

- [Sex Differences in Pursuit](#)
- [Social Reputation](#)
- [Social Status and Economic Resources](#)

Social Stature

- [Social Reputation](#)

Social Status

- [Dominance and Health](#)
- [Dominance and Testosterone](#)
- [Dominance in Humans](#)
- [Dominance, Testosterone, and Cortisol](#)
- [Emergence of Social Reasoning About Hierarchies](#)
- [Facial Width to Height Ratio and Dominance](#)
- [Function of Dominance](#)
- [Higher Status in Group](#)
- [Men in Positions of Power](#)
- [Men's Egoistic Dominant Acts](#)
- [Social Authority](#)

Social Status and Economic Resources

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Synonyms

[Dominance](#); [Economic resources: wealth](#); [Financial prospects](#); [Foraging ability](#); [Hunting ability](#); [Social standing](#); [Social status: prestige](#)

Definition

Social status: a person's standing within the hierarchy of a community or society; economic resources: the ability to provide food directly through foraging or indirectly through money.

Introduction

Only 3–5 % of mammalian species have long-term pair bonds between males and females and paternal care (Clutton-Brock 1991). Among great apes, the species most closely related to our own, in no species do fathers provide food for their offspring (Gray and Anderson 2010). Pair-bonding seems to have evolved in humans in part to facilitate paternal provisioning (Quinlan and Quinlan 2007). Forager men provide an average of 64 % of food, and in the USA married fathers provide more money for their family than mothers in about 75 % of households (Wang et al. 2013). This suggests that women have an

evolved preference for men offering resources, particularly when choosing long-term partners.

Preference for Social Status

Women display a preference for high social status in potential long-term mates across cultures (Buss 1989). Von Rueden et al. (2010) revealed that in a small-scale forager-horticulturalist society more similar to the societies in which humans evolved than industrialized societies, high-status men had more children within their marriages, and those children were less likely to die before reaching adulthood either because of genetic quality, better access to resources or both. This suggests that high status positively affects men's wives' reproductive success. Furthermore, a study of 186 pre-industrial societies demonstrated that women value social status in men because of the benefits it brings to their mutual children: high-status men have more wives and are better able to feed their children (Betzig 1986).

Women in industrialized societies also prefer high-status men as long-term mates. Buss' (1989) study of 37 industrialized nations across the globe found that women value ambition-industriousness more than men in 78 % of the countries sampled, and in only one country did men value the same trait more than women. Recent studies have shown that social status is a necessity for women selecting a long-term mate: it is highly valued when scarce, but diminishes in value once sufficient levels of it are obtained (Li, Valentine, & Patel, 2011). A series of speed-dating studies demonstrated that this preference is not merely theoretical; women prioritize social status when choosing long-term mates in a live-interactive setting (Li et al. 2013).

Preference for Economic Resources

If women select men with high social status because of the resources that such men can provide women and their future children, then a more direct preference for men with resources should

also be evident. Indeed, it is. Among the Hadza foragers, good foraging ability was the most common trait that women listed as being important in a spouse (Marlowe 2004). Furthermore, in the 37-nation study discussed above, women value "good financial prospect" more than men in 36 of the 37 cultures sampled. In a nationally representative US sample, these results were conceptually replicated: women were found to be more willing to marry someone who earns more than them and less willing to marry someone who earns less than them compared to men (Sprecher et al. 1994). Similarly, women value earning capacity more than men at every level of involvement, and a higher earning capacity is required at each stage of commitment (dating, sexual relations, steady dating, and marriage; Kenrick et al. 1990). Just as we saw with social status, there is also real-world evidence that women prefer men with more resources as long-term mates. Income significantly predicts how many replies men receive from personal ads (Baize and Schroeder 1995).

Conclusion

The survival of the fittest has favored women who select mates who give them the most benefits with the fewest costs. One benefit men can bestow upon women is resources. Women prefer men who can provide resources and men who have high status, a signal of the ability to provide resources as long-term mates. This preference has been found in both preindustrial and postindustrial countries and has been demonstrated in studies with high ecological validity. However, that does not mean that this preference is insensitive to context. Women's personal resources and women's mate value can impact the extent to which social status and resources are prioritized (Zentner, this volume; Edlund and Beck, this volume).

Cross-References

- [Women's Mate Value](#)
- [Women's Personal Resources](#)

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Social Status: Prestige

- [Social Status and Economic Resources](#)

Social Structure

- [Social Hierarchies](#)
- [Social Relations Theory \(Fiske\)](#)

Social Support

- [Coalitional Relationships](#)

Social Thinking

- [Communication and Social Cognition](#)

Social Tool

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Definition

A tool directed toward another animal (social target) or the use of another animal as a tool (social means).

Introduction

Tool use in nonhuman animals takes many forms. Social tool use consists of two different categories. Social-target tool use involves an animal using a tool toward or for the purpose of another animal. For instance, a male gila woodpecker often fed his offspring with honey, but this proved difficult when the honey was thinned down. He then removed pieces of bark and dipped them in the honey, which allowed him to transport it to his offspring. Thus, the bark was a tool that functioned to transport a liquid to a social target. The second category is social-means tool use: using another animal as a tool. For example, African elephant bulls have been observed to pick up and throw young bulls at fences, which broke and consequently enabled the bulls to pass. The young bulls were used as throwing tools. Some cases involve both social-target and social-means tool use, such as when a chimpanzee hits another

chimpanzee with a dead colobus monkey (examples from Shumaker et al. 2011).

Based on Shumaker et al.'s (2011) general definition of tool use, social-target tool use is the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another animal (not the user itself), when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool. Social-means tool use is the external employment of another manipulable animal (the tool) to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.

The majority of tool-use modes can be social-target tools and social-means tools. Some modes even require a social target, such as using a tool to stab, beat or entice others. Tools can also be used to create or augment a display, which clearly has a social component. However, our definition excludes certain behaviors that are sometimes regarded as social tool use (e.g., Johnson 2010; Völter et al. 2015) because the tool is not physically manipulated by the user. Examples of excluded behaviors are social learning of tool use, material culture, recruitment, communication, deception, tool sharing, and cooperation. Nonetheless, this distinction is not absolute and is only based on their typical aspects. For instance, communication may involve social tool use when an object is used to create or augment a social display.

Social-Target Tool Use

One of the most common types of social-target tool use is agonistic dropping or throwing. Some bird species and most primates appear to do this, with the exception of prosimians (Hunt et al. 2013; Shumaker et al. 2011). It is sometimes argued that only aimed throwing and dropping should be considered tool use, but this is often difficult to determine. Moreover, throwing and dropping may have the same function whether

aimed or not; they can effectively intimidate, threaten, or displace others (Osvath and Karvonen 2012). Some unaimed dropping and throwing appears to be stereotyped displacement, or originates from it, which could then have developed into aimed social-target tool use (Hunt et al. 2013).

Social-target throwing may also arise through complex cognitive abilities. Some chimpanzees pile feces or wet chow to later throw at visitors (Hopkins et al. 2012). A zoo-housed male frequently planned for future stone throwing by collecting stones and caching them while he was calm and no visitors were present. Later during the day he would retrieve and throw these stones at visitors during dominance displays. He also innovated this behavior, most notably through tactical deception. For example, he chipped off concrete projectiles but desisted throwing them because the visitors were told to back away. When the group returned 3 h later, the chimpanzee calmly picked up an apple from the surrounding moat while holding two projectiles (see Fig. 1). He suddenly threw one when within range of the group. The nonchalant behavior preceding the throw follows the deceptive strategy of creating a neutral image. Deception was also evident from his frequent concealing of projectiles when no visitors were present (Osvath and Karvonen 2012). Such inhibition of a prepotent social response that will be more effective in the future can be highly advantageous for animals living in groups with a hierarchical structure (Parker and Gibson 1977).

Not all chimpanzees are habitual projectile throwers. Only 39 out of 91 chimpanzees threw consistently in one group. Those that did had greater cortical connectivity in areas of the brain that are associated with motor control and speech production in humans. These differences were mainly present in the brain hemisphere opposite to their preferred throwing hand, which was also the hand they mostly used in other tool tasks and gestural communication. This contralateral brain-limb association is likewise typical for humans. Chimpanzees that had learned to throw scored better on tests of communicative abilities than those that did not. There were no differences in performance on other tests of social and physical



Social Tool, Fig. 1 Deception by a male chimpanzee preparing for social-target tool use. He holds two projectiles in his left hand and calmly picks an apple from the moat. He then approaches the visitors and suddenly throws the projectiles toward them. Reproduced from Osvath M,

Karvonen E (2012) Spontaneous Innovation for Future Deception in a Male Chimpanzee. *PLoS ONE* 7(5): e36782. doi:10.1371/journal.pone.0036782. Photo: Tomas Persson. License: CC BY 4.0 <https://creativecommons.org/licenses/by/4.0>

cognition. Both throwing and gestural communication serve to alter the behavior of others, although it is unclear whether one is the result of the other (Hopkins et al. 2012).

Social-Means Tool Use

Using another animal as a tool seems to be rarer than social-target tool use. In one case, a large troop of Japanese macaques was provided with food in a long transparent tube. They were conditioned to use stick tools, and some learned to throw stones to push the food out. Other macaques often waited at the far end of the tube so they could steal the food if a tool user threw a stone against it. The tube was wide enough for infants to enter, and two females pulled back theirs if they spontaneously crawled into the tube and collected the food. Another female used all four of her infants as social-means tools by actively pushing them into the tube and pulling them back once they retrieved the food. The advantages of this tool use are that the tool was always available, in contrast to sticks and stones that could be buried under snow, and that scroungers could not wait at the other end of the tube to steal the food (Tokida et al. 1994).

Orangutans can also use their offspring as social tools. In one experiment food was placed behind a barrier with holes too small for the hands

of adults. Each of three orangutan females frequently used their juvenile offspring as tools by moving them toward the barrier, pushing their hands through a hole, or pulling their arms once they grabbed the food. Similarly, when food was placed behind a small door opening, the mothers pushed the juveniles through, held on to their limbs, and pulled them back as soon as they retrieved the food. They then took the food from them. Similar results were found when the goal was a tool that could be used to retrieve inaccessible food, which shows that orangutans can use tools sequentially with the first tool being a social-means tool. In forced choice experiments, the juveniles preferred to take the food but were often coerced by their mothers to take a tool that they then used to retrieve preferred food. They were also sometimes moved through the narrow door opening if they could use a tool there to obtain food for themselves and their mothers (Völter et al. 2015). Orangutans also throw objects at dogs and even pull humans toward a goal so they can use them as ladders (Köhler 1993). These experiments show that orangutans can adjust their behavior flexibly by using others as social tools.

Social-Means-Target Tool Use

A triadic interaction is necessary when both social tool use types are combined. The user manipulates

another animal as a tool to affect a third animal in social-means-target tool use. However, it does not follow that all triadic interactions involve social tool use, as some researchers have claimed (e.g., Johnson 2010), when the user does not physically manipulate the tool. One type of triadic interaction that does involve social tool use is *agonistic buffering*, in which an animal uses another animal as a tool to discourage attacks from an aggressive target. Primates such as macaques, baboons, bonobos, and chimpanzees sometimes hold infants to inhibit potentially agonistic interactions. In some cases they instead used infants to get third parties to follow them or elicit affiliation from them (Johnson 2010; Parker and Gibson 1977; Shumaker et al. 2011).

A very different kind of social-means-target tool use is found in boxer crabs. They hold small stinging anemones in their claws and use them to catch food. They also use these anemones as protection against threats or as weapons in fights with other crabs. This behavior mostly encompasses twitching, waving, and extending the anemones. Contacting other crabs with anemones only rarely occurs. Fights are often ritualized in many animal species, which include the weapon use of boxer crabs that could inflict serious damage on contact (Karplus et al. 1998).

Conclusion

Social tool use can involve cognitive complexity that is traditionally only associated with nonsocial tool use. Although learning socially to use tools and the psychological manipulation of others are interesting behavioral categories, they should be seen as distinct from social tool use because the user exerts no direct physical control over the purported tool, which is instead regarded as a self-propelled agent. With our operational definition, social tool use can be investigated as being both a social and tool-related behavior, which offers unique avenues for future research.

Cross-References

► [Evolution of Tool Use](#)

► [Nonhuman Tool Use](#)
 ► [Primate Tool Use](#)
 ► [What Makes a Tool](#)

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Social Value

► [Self-Esteem Tracks Social Evaluation and Relational Value](#)

Social Values

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Synonyms

Community principles; Cultural doctrines; Cultural elements; Ethics; Moral codes; Social customs; Social norms

Definition

Moral codes that characterize human societies; cultural elements that bring together a group of individuals and render humans as the only species to be separated qualitatively from animals on the basis of social order and community.

Introduction

Societies seek to establish congruence between social values associated with their activities and the norms of acceptable behavior in a larger social system. Values foster harmony within a human society and function as the foundation of organizational legitimacy. Absence or violation of cultural, common values leads to disparity that can threaten congruence and undermine unity within a society. As communication is a vital component in the realm of enculturation, language appeared to develop in parallel with human cultural values. Human species evolved over generations, and communication became more complex. Arbitrary cultural meanings are found to be assigned to rites of passage and initiations of individuals in communities, as well as animate and inanimate objects. Interpretively, this allows for a vivid evidence that early culture rituals were occurring,

enriching the notion of human civilization that was continuously on the rise.

Emergence of Identity Within Culture

In developing their sense of identity, people identify successively with values of influence over their well-being. The primary process involved in identity development is one of enculturation of cultural elements (Berry 1980). Enculturation references the agentic individual's process of identification with whatever cultural elements of influential others are accessible to the person (Weinreich 1983). In the main, the young child identifies with mother and father in the first instance but identifying only with limited aspects of them apprehended from the child's perspective (Mikhail 2011). Subsequently, the person as older child, adolescent, and then young adult successively identifies with members within their direct environment, and beyond with agents of the wider community, and part-identifies with their salient features according to increasing levels of comprehension (Erikson 1950, 1968). As a consequence, over a formative period, the child who becomes the adult migrant will have enculturated major aspects of heritage culture including some elements that are incompatible with others, since cultures are not entirely monolithic (Wrangham 1987). According to ISA, identity is a modification of earlier ones and emphasizes people's construal of their biographical past and their aspirations for the future. For human species, their biographical past scenarios can be located in their heritage locations and cultures (Boesch 2007), while their future aspirations entail considerations about their intended modes of engaging with their receiving communities (Weinreich 2003).

Embodiment of the Self in the Community

Rites of Passage

A rite of passage is a ceremony and marks the transition from one phase of life to another. It

plays a critical role in the evolution of human civilization as it defines the common values of a society (Tooby and Cosmides 2005). A rite of passage manages to conserve social order and the sense of community among the members of a group who come together to celebrate an occasion and practice traditions and customs on the foundation of shared social values (Yamamoto and Tanaka 2009). Rites of passage are characterized by the ordeals with which a youth is formally invested with adult status in a community. Intriguingly, these rituals and ceremonies allow adults to transition into new life roles along the path of adulthood, all the way into meaningful elderhood. When humans design rite of passage experiences, they work to assure that initiates come out of the experience with a new and empowering story that helps them take responsibility for the decisions that set the course of their future (Sober and Wilson 1998). Members of social group initiates create the story of who they are and the kind of life they wish to build based within the exploration of their own personal values (Haidt 2003). Initiates are encouraged to select the story that connects them to their community. Through this self-exploration, they emerge with a stronger sense of personal responsibility to all aspects of their lives, stretching all the way out to the larger world of which they are a part of (Carrithers et al. 1985). Consequently, both the community and the initiate benefit from a rite of passage. An intentional rite of passage experience provides the space for the community to transmit its core values and ethics and confer the role responsibilities appropriate to the initiate's stage of life (Frank 1988), hence, insuring cultural continuity and knitting together of the generations.

The Role of Honor Code

A fundamental aspect of culture is its embodiment of the societal processes of substantial groups of people who perceive themselves as belonging to a commonality of values and beliefs, moral imperatives and religious beliefs, dress and behavior, history, and modes of living, whereby one group is culturally distinctive from another (Henry 2008). From evolutionary

perspective, Honor Codes appear to maintain cohesive order within communities. The role of an Honor Code is to encompass a set of ideals in a society and govern accordingly a group of individuals that abide by moral rules. It is based on what constitutes honorable behavior among group members, and its use depends on the notion that individuals within the group can be trusted to act honorably (Locke 2014). In many cultures, an Honor Code exists parallelly to ethics that require proper compliance according to societal rules, by members who seek to be recognized for their individuality and be inviolably included in community. Punishments upon disregard of the Honor Code underline that values-driven individuals ought to be more successful within a society.

Development Levels for Compliance and Ethics

From evolutionary perspective, crucial components that characterize Honor Codes of human societies appear to be diachronic as they influence critically the man of today who seems to adhere to values that had always fostered healthy functions in communities since ancient times (Hagan and Hammerstein 2006). Modern society has adopted these values and incorporated them into organizational Honor Codes. Foundation level programs set the basis for establishing a healthy organizational culture and preventing, detecting, and resolving legal and regulatory compliance violations (Shafer-Landau 2012). The behavioral focus is on compliance and the business focus is on the organization. Transformation level programs support a shift from a compliance focus to a compliance and ethics focus. The behavioral focus is on compliance and ethics promoted by values-based leadership. The business focus is on the organization and primary stakeholders which might be customers, suppliers, investors, financiers, and communities in operating area. Sustainability level programs foster aspirational behavior and contribute to the organization's continued success. The behavioral focus for this level is on compliance, ethics and honor, collaboration, and meaning, all promoted by values based on

leadership. Hence, the business focus is on the organization, primary stakeholders and secondary stakeholders which might be special interest groups, media, government, competitors, consumer advocates, and global society (Henry 2008).

Conclusion

The continuous process of human enculturation is the foundation of the person's identification as well as the coexistence of mixed cultural elements within the person's identity. Ultimately, the goal is the creation of elemental identification that is characterized by common social values and is expressed within social boundaries and moral incentives. The values of shared ethics, Honor Codes, and rites of passage appear to be among some of the most crucial components to maintain social norms and community order intact in human communities. The purpose of social values is not to cultivate individuals who blindly appraise ideals of a rather unknown cultural history. The concept of culture is not only characterized by participation of the individual in community but also by the separation from the massive group in an attempt to acquire identity and authentically accustom by the values that define the broader society they live in. The goal is a new emerging self that can actively engage in rituals and celebrate ideals while she or he questions the nature of traditions and seeks to gain knowledge regarding the historical background that determines their identity.

Cross-References

- ▶ [Honor Code](#)
- ▶ [Human Enculturation](#)
- ▶ [Moral Emotions](#)
- ▶ [Morality](#)
- ▶ [Normative Ethics](#)
- ▶ [Rite of Passage](#)
- ▶ [Spiritualism](#)

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Social Withdrawal in Childhood

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Synonyms

Preference for solitude; Social avoidance; Social isolation

Definition

Process whereby children remove themselves from opportunities for social interaction and engage in solitary activities in the presence of peers.

Introduction

Interacting with others is an integral part of childhood. Making new friends, playing with a group of peers, and being liked and accepted by classmates all represent critical and formative experiences for children. For most children and adolescents, the considerable amount of time spent in the presence of peers is not only perceived as enjoyable and fulfilling but also serves to provide opportunities to learn and refine important social, emotional, cognitive, and linguistic skills. Notwithstanding, some children still choose to engage in solitary activities in lieu of social interaction with peers. Social withdrawal refers to the process of removing oneself from opportunities to interact with others (Rubin et al. 2009). The concept of social withdrawal extends beyond the broad notion of a physical separation from others and involves a complex combination of motivational, emotional, and cognitive factors. For example, for some children, social interaction may elicit powerful feelings of anxiety. In contrast, others may seek out

solitude for its own enjoyment. Regardless of the underlying reasons for not engaging with peers, social withdrawal is implicated in social maladjustment across childhood, and *excessive* social isolation may have severe consequences for children's social, emotional, and psychological well-being.

Defining Social Withdrawal

Social withdrawal is an umbrella term that encapsulates a range of behaviors and motivations associated with removing oneself from opportunities for social interaction (Rubin et al. 2009). This construct is meant to be distinct from the process of *active isolation*, whereby children are ostracized or excluded by peers (thus preventing them from engaging in social interactions) (Rubin and Mills 1988). However, these appear to be transactional processes that influence each other over time (Rubin et al. 1991). For example, individuals may respond to social ostracism by seeking out solitude (Ren et al. 2016). Likewise, socially withdrawn behaviors may elicit negative peer responses, including peer rejection and victimization (Coplan et al. 2015b).

Children may be motivated to withdraw from others for a variety of reasons, which can have specific implications for their social adjustment and well-being. For instance, some socially withdrawn children experience elevated fear, anxiety, and self-consciousness in social situations and may avoid social interaction to alleviate these negative emotions (Crozier 1995). Alternatively, other children engage in solitary activities, not out of social wariness, but because they find solitude intrinsically rewarding and enjoyable (Coplan and Weeks 2010). Notwithstanding these underlying motivations, there is reason to be concerned about social withdrawal in childhood. From an evolutionary perspective, social interaction is adaptive because it facilitates social bonding and individual happiness. Consequently, frequent social withdrawal in childhood is viewed as *maladaptive* because it may pose substantial risks for children's socio-emotional adjustment and well-being.

Social Withdrawal as Evolutionarily Maladaptive

A strong case has been made for considering childhood social withdrawal as evolutionarily maladaptive. In this section, we consider these arguments at both the level of the species (e.g., notions of natural and sexual selection) and the individual (e.g., concurrent and predictive implications for the child).

Survival and Reproduction

Humans are fundamentally social beings, capable of forming complex social hierarchies and intimate social bonds. This penchant for social interaction is considered to have been an essential ingredient for the survival and proliferation of our species (Campbell 1983). Cooperation promotes survival, resource exchange, and abundance and fuels the growth of large-scale communities (see Reeve, ► [Evolution of Cooperation](#)). Additionally, interpersonal communication fosters intimacy and trustworthiness (see Scalise Sugiyama, ► [Gossip and Grooming Hypothesis](#)). Failing to partake in social rituals may result in reduced social status in the community or outright ostracization.

Moreover, as evidenced among human and many nonhuman species (e.g., great apes), a disposition toward social dominance and assertiveness is favorable to siring offspring, thus increasing the prevalence of such traits in the population (see Moore, Starkey, & Benjamin, ► [Dominance in Humans](#)). Those lacking such traits would have diminished access to resources (e.g., food and protection) and fewer opportunities to mate due to decreased sexual competitiveness (particularly under stressful circumstances, e.g., Boyce et al. 1998). Taken together, evolutionary reasoning supports the view that sociability and assertiveness are assets for both an organism's survival and their ability to reproduce and pass on their genes.

Childhood Peer Interactions and Relationships

Social withdrawal is also viewed as maladaptive because of its potentially adverse impact on

children's interactions and relationships with peers. Children's early peer interactions lay the groundwork for the acquisition of social competencies, while the formation of peer relationships further strengthens social skills and facilitates optimal adjustment (Rubin et al. 2015). As such, children who consistently eschew opportunities to play with others in favor of solitary play may miss out on formative social experiences integral to the development of social skills (Rubin et al. 2009). This may contribute to further social isolation as these children may lack confidence in their abilities to engage with peers.

Moreover, socially withdrawn children tend to garner more negative reactions from peers. Social expectations and norms regarding the quantity (and quality) of peer interactions rise steadily from early childhood to adolescence (Rubin et al. 2015). By late childhood, peer interaction is clearly the norm. For example, Coplan et al. (2015b) observed children in grades 4–7 in the schoolyard over recess and lunch and reported that, on average, children interacted with a peer or peers more than 90% of the time. Thus, withdrawing from the peer group in this context is likely to be viewed as socially deviant. Societal expectations and norms regarding social interactions may help explain why withdrawal appears to be more problematic for boys compared to girls (Doey et al. 2014). Indeed, shy boys tend to garner more negative responses from peers and experience more peer exclusion and rejection (Gazelle and Ladd 2003; Spangler and Gazelle 2009). It is hypothesized that withdrawn behaviors violate typical gender norms ascribing assertiveness and dominance among boys, contributing to more negative reactions from peers (Doey et al. 2014).

It should not be surprising that socially withdrawn children are often isolated by peers (Spangler and Gazelle 2009). This can lead to a transactional process whereby peer rejection and exclusion exacerbate children's retreat into social withdrawal, which in turn serves to further promote negative peer experiences (Rubin et al. 1991). Moreover, when socially withdrawn children do form friendships, these relationships tend to be of lesser quality as compared to their more sociable counterparts (Pedersen et al. 2007; Rubin

et al. 2006). This also appears to hold true in the context of romantic relationships, with socially withdrawn adolescents having fewer and less intense romantic partnerships (Boisvert and Poulin 2016).

Peer difficulties among socially withdrawn children also extend beyond isolation and rejection to more overt victimization (Hanish and Guerra 2004). Victimizers may view socially withdrawn children as “easy targets” given that they are sometimes perceived to be physically “weak” and less likely to retaliate when confronted (Rubin et al. 2006). Additionally, deficiencies in social skills may expose these children to further mockery and ridicule, thus perpetuating a reciprocal relation between social withdrawal and peer rejection (Greco and Morris 2001).

Taken together, social withdrawal appears to have an adverse effect on how children interact with and are treated by their peers. Particularly in late childhood where peer play is especially prevalent (Coplan et al. 2015b), solitude is likely to be perceived as atypical. In addition, frequent bouts of solitary play may hinder the acquisition and refinement of social competencies necessary for forming relationships with peers.

Happiness, Health, and Individual Well-Being

A final reason that social withdrawal may be maladaptive is that, overall, time spent with others makes us happier and healthier than time spent in solitude (see Coplan et al. *in press-b*, for a recent review). For example, simply being alone is associated with elevated levels of the hormone cortisol, which is implicated in feelings of stress (Matias et al. 2011). Moreover, most people just do not like spending time in solitude. Indeed, in a series of recent experiments, Wilson et al. (2014) demonstrated that most university students opt to self-administer electric shocks instead of being left alone with their thoughts for 15 min. Further, frequent solitude is tied to feelings of loneliness (Hawkley and Cacioppo 2010). Loneliness arises from a perceived dissatisfaction with the quantity and/or quality of one’s social relations (Cacioppo et al. 2015). Socially withdrawn children may become increasingly lonely with age as they develop more sophisticated self-concepts based

on their relative social standing among peers (Lempinen et al. 2017; Qualter et al. 2015). Loneliness can also have long-term detrimental consequences for one’s physical and mental health. Indeed, loneliness is associated with heightened cardiovascular problems, substance abuse, and mortality, as well as depression and chronic stress (Hawkley and Cacioppo 2010).

In contrast, interacting with others is generally associated with positive moods (Vittengl and Holt 2000). Experimental evidence suggests that social situations are perceived as more satisfying and enjoyable compared to nonsocial situations (Epley and Schroeder 2014; Sandstrom and Dunn 2013). Furthermore, even dispositionally introverted individuals report substantial positive feelings following social interaction (Zelenski et al. 2013). Scholars have historically espoused the view that humans have an innate psychological *need* to interact with others (Baumeister and Leary 1995; Maslow 1943), and people report greater life satisfaction and meaningfulness when they regularly engage in social interaction and partake in social activities (Demir et al. 2011). Similarly, children who have frequent, positive interactions with family and peers report greater happiness and a more positive self-concept compared to children who have fewer social interactions (Holder and Coleman 2009). Thus, the potential negative effects of social withdrawal on happiness and well-being are twofold: (1) being alone is associated with momentary decreases in happiness, and (2) excessive solitude is linked with loneliness and appears to have severe consequences for health and well-being.

Can Certain Subtypes of Social Withdrawal Be Adaptive?

To this point, we have focused on the myriad of potential reasons why the broad construct of social withdrawal might be considered evolutionarily maladaptive in childhood. However, as we have noted, social withdrawal itself is a multifaceted phenomenon that is now widely considered as comprising varying emotional and motivational substrates (Coplan et al. 2015a). Simply

stated, there are several different *reasons* why children might withdraw from opportunities for social interaction, and these varying motivations can have substantially different implications for children's social adjustment and well-being. For example, some children may socially withdraw because they experience unpleasant feelings in unfamiliar social situations. Children who are *shy* experience fear and wariness toward social novelty, as well as self-consciousness in situations of perceived social evaluation (Coplan et al. 2004). Shy children are also thought to experience an *approach-avoidance conflict*, whereby their desire to engage in social interaction is simultaneously inhibited by fear and anxiety (Asendorpf 1990). Shy children often have difficulty integrating into peer groups and may, instead, engage in onlooking behaviors during instances of peer play (i.e., watching without joining in) (Coplan et al. 1994).

Shyness is a risk factor for social adjustment difficulties throughout childhood and adolescence (Rubin et al. 2009). In particular, shy children are more prone to *internalizing problems* (Karevold et al. 2012), which involve retreating from one's environment and engaging in inwardly focused behaviors (Achenbach and Edelbrock 1981). Overall, as compared to their more sociable counterparts, shy children are more likely to experience anxious and depressive symptomology, as well as feelings of loneliness and low self-worth. Indeed, extreme shyness in childhood is one of the best predictors of later social anxiety disorder (Clauss and Blackford 2012).

Shyness, as a trait, is relatively enduring within the population, with estimates suggesting that roughly 15% of children are born with a predisposition toward heightened wariness (i.e., behavioral inhibition; Kagan et al. 1988), which is a precursor for social withdrawal (Chronis-Tuscano et al. 2009). Evolutionarily speaking, socially withdrawn traits would not likely have evolved to exist in humans if they were completely detrimental. One often cited advantage of heightened wariness is its survival value. Among animals across a range of taxa, shy-like traits (i.e., greater reactivity to novel stimuli) promote behaviors that reduce the likelihood of predation (Verbeek et al.

1994). Organisms predisposed to flee from potentially threatening situations had a greater chance of avoiding predation and passing on these genes. As such, heightened sensitivity to novelty is suggested to have evolved as a survival strategy (LeDoux 2000).

To a certain extent, this is evident among infants and toddlers exhibiting stranger anxiety – a tendency to avoid unfamiliar others (Mangelsdorf et al. 1995). As another example, Colonnese et al. (2014) suggest that certain behavioral displays of shyness such as a *coy* smile (i.e., the combination of smiling, avoiding eye contact, and tilting the head) can serve an adaptive function by reducing social tensions in potentially stressful situations (e.g., encountering a stranger). However, avoiding threatening situations is not synonymous with avoiding social interaction, and it has been argued that social withdrawal emerged as a *by-product* of evolutionarily driven mechanisms for heightened threat detection (LeDoux 2000).

Notwithstanding, some children may also socially withdraw because of an intrinsic, non-fearful preference for solitude. This type of social withdrawal is referred to as *unsociability*, *social disinterest*, and/or *affinity for aloneness* and is believed to be a relatively benign form of social withdrawal (Asendorpf 1990; Coplan et al. 2004). Moreover, emerging evidence suggests that non-fearful solitude seeking may be adaptive for some aspects of individual well-being, particularly among adolescents and young adults (Goossens 2014).

Although direct empirical evidence remains sparse (Coplan et al. in press-b), it continues to be argued that spending time alone can also promote intellectual, creative, and spiritual growth while reducing stress and anxiety (Korpela and Staats 2014; Long et al. 2003). In childhood, occasional solitary play promotes regulatory and exploratory behaviors, as well as facilitating identity formation (Galanaki et al. 2015; Katz and Buchholz 1999). Preschool children who engage in more constructive forms of solitary play score higher on measures of creativity and divergent thinking (Lloyd and Howe 2003). Moreover, researchers speculate that the benefits associated

with solitude become more salient over time in concordance with developments in identity and peer relations (Larson 1997). In early childhood, stronger social pressures to engage in group play may undermine the potential benefits of solitude, but advantages of spending time alone may emerge among older children with increasing positive and sophisticated views of solitude.

Despite these assertions, it remains unclear as to whether the proposed benefits (or lack thereof) of solitude in childhood can be attributed to those with a *trait-level* affinity for solitude, compared to the actual state of being alone. Excessive social withdrawal in children, regardless of whether it is motivated by an affinity for solitude, still warrants concern as it poses significant risks for children's social adjustment and well-being. Children who perpetually choose solitary play in place of peer interaction may fall behind in their development of social skills compared to their more sociable counterparts (Rubin et al. 2015).

Future Directions: Considering Context

Until now, this summary has largely focused on social withdrawal within the broader context of adaptive versus maladaptive outcomes in childhood and how these may vary as a function of children's social motivations. However, environmental and social contexts also play integral roles in defining attitudes toward socially withdrawn behaviors, which ultimately impact outcomes associated with social withdrawal. This final section addresses (1) the role of culture in children's social withdrawal and (2) how computer-mediated communication (e.g., texting, social networking, etc.) is actively changing the meaning of solitude and its implications for socially withdrawn children.

Culture

Research on social withdrawal and its concomitants was traditionally limited to predominately affluent Western populations. However, there is burgeoning interest in the meaning and socio-emotional impact of childhood social withdrawal across cultures. Culture plays an important role in

shaping attitudes and beliefs about social behaviors (Chen and French 2008). As such, certain cultures may view socially withdrawn behaviors in children more or less positively, which in turn can influence its implications for socio-emotional adjustment and well-being.

For example, traditional Chinese society values group harmony and cohesion over assertiveness and independence, which helps to explain why Chinese parents, teachers, and peers have historically been more accepting of children's shyness (Chen et al. 1995; Oyserman et al. 2002). Consequently, shyness was formerly associated with greater academic success and led to comparatively fewer instances of peer rejection (Chen et al. 1995). However, ongoing shifts in China's economic and political landscape (e.g., amplified pressures to compete in a Western dominated economy) have placed heightened value on assertiveness, particularly in urban Chinese societies (Chen et al. 2005). Consistent with Western cultures, shyness in Chinese children is currently linked with peer difficulties and internalizing problems (e.g., Coplan et al. 2017). However, in contrast to Western society, unsociability (i.e., a non-fearful preference for solitude) is also associated with social adjustment issues among Chinese children (Liu et al. 2015). Indeed, despite an increased value of assertiveness, interdependence and group affiliation remain core values in Chinese culture, such that a preference for solitude may be discouraged for deviating from entrenched societal norms (Chen and French 2008). Thus, cultural context exerts considerable influence on our attitudes and beliefs about social withdrawal, which in turn effects how family and peers respond to socially withdrawn children.

Computer-Mediated Communication

Advances in communication technology also have considerable import on our understanding of social withdrawal and its developmental significance. Among older children and adolescents (and increasingly among younger children), conversing and networking with peers via online social media platforms and text messaging are pervasive in developed countries and proliferating in developing countries. A recent poll of

adolescents in the USA indicated that roughly 90% of adolescents have access to a mobile phone and almost 25% report using these devices constantly (Lenhart 2015). It thus appears typical for older children and adolescents to be *physically* isolated yet actively communicating with peers across any number of media platforms. This has prompted a conceptual reconfiguration of the definition of social withdrawal to expand beyond face-to-face communication.

The impact of social media and online communication among socially withdrawn children remains largely unexplored. Some have argued that online communication may exacerbate social withdrawal and impede the development of social skills that are otherwise acquired via in-person interaction (Hamburger and Ben-Artzi 2000; Kraut et al. 1998). According to this perspective, socially withdrawn children may resort to online communication as a sort of crutch in place of in vivo social interaction, which further isolates them.

More recently, however, researchers have acknowledged some potential benefits of online communication for individuals less comfortable engaging in face-to-face interaction (e.g., Madell and Muncer 2007). Socially anxious and withdrawn children tend to gravitate toward online communication relative to their more sociable peers (Valkenburg and Peter 2007). One likely reason for this is that online communication lacks much of the immediacy of in-person communication, which provides users with a greater sense of control (Madell and Muncer 2007). The traditional conversational tempo of face-to-face communication (i.e., immediate back and forth responding) is far less constrained online, and the lack of physical proximity offers an additional veil of control. In short, socially withdrawn children may find solace in some forms of online communication because they can take more time deciding what they want to say.

Another difference between in-person and online communication is anonymity. Of course, many forms of online communication are not anonymous (e.g., social media platforms). Nevertheless, the Internet is teeming with forms of online communication that permit a great deal of

anonymity (e.g., blogs, forums, chat rooms, etc.). There currently exists a proliferating culture of online gaming that allows individuals to interact anonymously with strangers from around the world. This anonymity may reduce the inhibitions of socially anxious children and provide them with a greater sense of interpersonal mastery (Kowert et al. 2014). However, excessive online gaming can come at a cost in the form of online gaming addiction (Kuss and Griffiths 2012). Moreover, among young adults, socially avoidant tendencies are associated with problematic media use, including excessive video gaming, online gambling, and consuming pornography (Nelson et al. 2016). Indeed, risk factors associated with obsessive, problematic gaming among children and adolescents (e.g., loneliness, depression, social anxiety) are comorbid with social withdrawal (Carrass et al. 2017). Overall, these findings indicate that measured use of online communication may offer some advantages for socially withdrawn children but should not be used as a replacement for in-person social interaction.

Conclusions

Scholars have suggested that humans are distinctively *ultrasocial* as compared to other species (e.g., Campbell 1983) and that this proclivity for social interaction has endowed humans with an evolutionary advantage for cooperation and colonization (Tooby and Cosmides 1996). Nevertheless, high sociability is evidently not an *essential* human trait, as a substantial portion of children and adults often refrain from interacting with others in favor of solitary activities. Current research continues to elucidate the motivations behind children's social withdrawal and the consequences that go along with different reasons for spending time alone in childhood.

Moving forward, the development of social withdrawal and its concomitants continues to be an active area of empirical inquiry. Researchers are continuing to address the clinical implications of excessive withdrawal and social anxiety. Interventions such as social skills training and peer

pairing have shown promise as effective techniques for promoting peer interactions and social competence among severely withdrawn children (see Coplan et al. [in press-a](#), for a recent review).

Perhaps most notably, insights into the potential benefits of solitude for children may reshape our understanding of the relative adaptiveness of socially withdrawn behaviors. Moreover, societal changes and advances in technology are constantly modifying our understanding of what it means to be *alone*. Opportunities abound for social interaction across an ever-changing plethora of media platforms, and children are increasingly exposed to such modalities earlier in their development. These changes in addition to social and cultural shifts will certainly impact children's beliefs and outcomes associated with social withdrawal.

Cross-References

- [Loneliness in Modern Life](#)
- [Peer Socialization](#)
- [Social Anxiety](#)
- [Social Development](#)

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Social/Contextual Factors

► Social Context

Sociality

- Baringa's (1996) Crayfish
- Eusociality
- Group Living
- Grouping and Predation
- Personality, Gender, and Culture

Socialization

- ▶ [Human Enculturation](#)
- ▶ [Peer Groups](#)
- ▶ [Social Development](#)

Socialization Processes

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Synonyms

[Child-rearing](#); [Parenting](#); [Social development](#)

Definition

Socialization refers to the ways in which new members of a group are assisted by older, more experienced, members to learn the values, attitudes, and appropriate behaviors of the group.

Introduction

Whenever they move into a new group, humans need to learn what is appropriate behavior in that group. This process of socialization goes on throughout the lifespan: Children learn how to behave in the home, at school, and while interacting with peers. As they become adolescents and adults, they move into new school settings and the workplace. As well they have to learn how to be marital partners, parents, and how, finally, to behave as an older member of society.

Most research has focused on socialization during childhood, as well as on the role of parents in that socialization. The focus on children reflects the fact that so much must be learned in this context, including regulation of emotions such as distress and anger, social competence, not

harming others, helping others, and understanding the perspective of others. The focus on parents reflects the fact that parents are biologically prepared to care for their offspring and that they are generally assigned the task by society. This entry will deal with children and parents, although it should be noted that other agents of socialization include teachers, peers, and siblings, where the same processes are operating.

Features of Socialization in Childhood

The Role of the Child

Socialization is not a one-way street, with the direction from parent to child. Children also influence their parents (Kuczynski and De Mol 2015). Thus it is not infrequently found that children's behavior produces change in the socializer's behavior. The change can be of either a positive or negative nature. A child's disobedience may lead to anger on the part of the parent, with that anger only serving to increase the disobedience. Or the disobedience may lead to a reconsideration of socialization strategies and choice of one that has a better chance of succeeding. The child's active role is reflected as well in the fact that children do not accept the teachings of the socializing agent as a whole. Values are not transmitted but, rather, are constructed as the child weighs a variety of choices (Bandura 1977). As children experience the negative impact of hurtful behavior on themselves, for example, they develop a sense of morality that includes not hurting others. As another example, children can change the values of their parents as they come in contact with other agents of socialization and other influences (Kuczynski and De Mol 2015).

The bidirectional nature of socialization is also evident in the fact that a given approach to socialization is not effective for every child. Effectiveness depends on a number of variables including the child's sex, age, temperament, mood, nature of the act, and previous history with the socializing agent (Grusec and Goodnow 1994). Fearful children, for example, are more likely to be negatively impacted by harsh parenting than are fearless ones (Bates and Pettit 2015). As other examples,

reasons for why a particular behavior is unacceptable must be matched with the cognitive abilities of the child, and the negative impact of physical punishment is lessened in countries where this form of punishment is more normative (Lansford et al. 2005).

Related to the fact that individual differences alter the impact of an intervention is the fact that a child's genetic makeup interacts with socialization experiences to produce different outcomes. As one example, Caspi et al. (2003) showed that child maltreatment was associated with subsequent depression, but only in individuals who had a short allele of the serotonin transporter (5-HTT) gene.

The Nature of Values

Values can be placed in two major categories. Intrinsic values include aspirations for personal growth, meaningful relationships, social responsibility, and physical health. Extrinsic values include financial success, physical attractiveness, and social recognition. Individuals who rate themselves higher on intrinsic values report greater feelings of psychological well-being than those who rate themselves higher on extrinsic values (Kasser and Ryan 1996). One explanation for this result is that people need to feel their behavior is self-determined rather than directed by others. Because extrinsic values depend on the reactions and evaluations of others they run counter to this basic need (Ryan and Deci 2000, 2017).

Schwartz (1992) has distinguished between self-transcendence and self-enhancement values. The former include tolerance, the protection of people and nature, and the preservation and enhancement of others. Self-enhancement values include status, prestige, control over people and resources, and personal success. The two sets of values are negatively correlated, with self-transcendence values generally valued more highly in many different countries.

Intuitive Morality

There is a substantial body of evidence that babies have a basic awareness of prosocial and moral values, that is, of concern for others and dislike of harm to others (Hamlin 2013; Warneken and

Tomasello 2015). As early as the first year of life infants show concern when others are distressed. As an example, they show pupil dilation, an indication of tension, when they see someone who needs help, with the tension reduced when help is received (Hepach et al. 2012). Infants at 6 months of age look longer at and are more likely to reach out to a puppet who helps another puppet trying to climb a hill than they look at and reach out to one who pushes the climber down the hill (Hamlin and Wynn 2011). This apparently innate predisposition is said to stem from ecological conditions faced by our ancestors that required collaboration in order to survive (Warneken and Tomasello 2015). Cooperative behavior, therefore, increased reproductive fitness. Moreover, cooperative behavior often required curbing selfish goals or even personal sacrifice, thereby facilitating the development of a moral sense, that is, a sense of what is right or proper. The fact that babies come equipped with prosocial tendencies, however, does not negate the central role of socialization which can shape those tendencies in a multiple set of directions.

Domains of Socialization

Adults socialize children in a variety of ways. Building on the work of Bugental (2000), Grusec and Davidov (2010) proposed five domains or contexts in which parenting could occur. Each domain involves a different need on the part of the child, a different relationship between parent and child, and different kinds of parenting action. The first two domains, protection and reciprocity, include the building of a caring and responsive relationship between parent and child. This relationship facilitates the acquisition of specific values that are learned in the remaining domains – control, guided learning, and observational learning/group participation.

With respect to the protection domain, humans have evolved to seek a safe haven and nurturing when they are in distress or danger. In turn, parents have evolved to provide that safe haven. Thus the child's attachment system and the adult's caregiving system are complementary and have evolved in parallel. When either system is activated child and caregiver move closer together so

that protection is enhanced (Bowlby 1969/1982). When the system is not activated children can explore their world, knowing that they have a secure base to which they can return.

Appropriate responses to children's distress change with age. Holding is suitable for a baby. Young children may profit from a discussion of emotions. Ultimately the goal is to teach children how to cope with distress on their own. "Not-too-nice parenting" (Bates and Petit 2015) is one way in which this is accomplished. In this approach to socialization, parents are not excessively sensitive and responsive (see, for example, Degnan et al. 2008), and they respond to children's emotions by listening, accepting, querying, and complying rather than engaging in overindulgent helping and comforting or even simple distraction (Morris et al. 2011).

One important outcome of caregiver reactions to children's distress is the development of behavior that is helpful and comforting to others. Parents who try to help their children alleviate feelings of distress, or who help them find ways to problem solve and deal with challenging issues, facilitate children's coping with their own emotions, including the empathic distress they feel for others. In this way, children are able to act prosocially in response to the negative emotions of others rather than being overwhelmed and immobilized by their own distress (Eisenberg 2010). Toddlers of mothers who were supportive were found to comfort an adult who had "accidentally" hurt herself by, for example, patting her or getting the mother's attention. Children with mothers who were less supportive tended to go to the mother, touch her, hold their arms out to be picked up, or buried their heads in her lap (Eisenberg et al. *in press*).

The next domain, reciprocity, emerges from the human tendency to reciprocate favors, a characteristic that, like protection, contributes to survival and reproductive success (Trevvarthen et al. 1999). Reciprocity occurs not only with kin but with unrelated individuals as well. In this domain, the relationship is one of equality where children have an equal say in how the interaction will proceed. When parents respond to their children's reasonable requests they set up conditions where

their children, in turn, will respond to their parents' (reasonable) requests. Most importantly, this compliance is willingly given rather than a result of parental pressure. Play is one example of a reciprocal interaction, provided socializing agents refrain from assuming a didactic role. When play is jointly managed, and there is shared positive affect between adult and child, children show higher levels of peer competence and prosocial behavior as well as less antisocial behavior (for example, Lindsey et al. 2010).

In the control domain, children experience consequences in the form of discipline or punishment for antisocial actions and reward for prosocial actions. Additionally, they need to internalize the values associated with those actions, that is, believe that those actions are intrinsically motivated or inherently correct. Otherwise, they would have to be under constant surveillance to make sure they behaved in accord with societal rules and regulations. Researchers have demonstrated that internalization is most likely to be achieved when agents of socialization use a combination of punishment and reasoning, make rules clear, and enforce them consistently (Grusec and Goodnow 1994). Additionally, the punishment must be just sufficient to capture the child's attention and just sufficient to motivate a change in behavior. Otherwise, positive action can be attributed to external pressure rather than an understanding of why one particular action is more appropriate or more moral than another (Grusec and Goodnow 1994; Grusec and Davidov *in press*). In the former case not only is compliance with societal dictates not given willingly, but it can lead to reactance, that is, a desire to do the opposite of what is required. Reactance occurs because of the human need for autonomy or choice which is thwarted when too much external pressure is applied (Ryan and Deci 2017). Also to be noted is that discipline is most effective when it is administered by parents who have a positive and warm relationship with their children (Grusec and Goodnow 1994).

Punishment involves a variety of consequences, including verbal disapproval, withdrawal of love, withdrawal of material rewards and privileges, time-out, and corporal

punishment. Considerable debate has centered around the question of whether corporal punishment in the form of spanking or hitting on the buttocks or extremities with an open hand is harmful (let alone ineffective). In a review of a considerable body of research, Gershoff and Grogan-Kaylor (2016) reported strong evidence that corporal punishment is not only associated with, but leads to, children's externalizing problems.

Socialization in the control domain has its challenges. For example, it often occurs in the context of high levels of arousal on the part of both child and parent. When parent and child are angry it can be difficult for the parent to function effectively or for the child to listen and accept. The guided learning and observational learning domains present fewer of these sorts of challenges.

Socialization in the guided learning domain is important because humans have limited physical prowess and so, in order to survive, they must rely on the learning of intellectual skills. The human capacity for language allows for the teaching of complex skills and the relatively long period of dependence the young have on their parents allows time for this teaching. In this domain, the relationship is one between teacher and student. Importantly, teaching must be done within the child's zone of proximal development (Vygotsky 1978), so that teachers help children solve problems they are not quite ready to solve independently, with constant alterations to match the child's changing skill level. Eventually, a shared understanding is achieved and the particular lesson is said to be internalized. The process is an interactive one, with discussion and exchange of views leading to better mastery of the task (Haden et al. 2001). In this domain, children can learn about values and associated actions, as well as about the nature of emotions and how to express and manage them (Denham et al. 2015).

Guided learning is an important element in moral development. Even very young children engage in conversations about moral values with their parents, often taking the lead in these conversations (Wright and Bartsch 2008). The most successful conversations are those where parents elicit their children's opinion and check for

understanding, as well as being supportive and not negative (Walker et al. 2000). Parents who are high in generativity, who see the training of future generations as an important part of their functioning, are particularly likely to engage in guided learning, that is, story-telling that deals with suffering, growth, and kindness of others (McAdams 2004).

Finally, the group participation domain includes modeling of others' behavior as well as participation in positive social behavior with other group members. Adoption and valuing of group practices and symbols is important from an evolutionary perspective because it identifies the individual as a member of the in-group, where good treatment is more likely (Brewer and Gardner 1996). These practices are very frequently learned through observation of others, a procedure Bandura and Walters (1963) identified as the basic form of human learning. Through watching others, children learn values and how to behave (or not to behave) in accord with those values. Socializing agents, in turn, try to control the models to which their children are exposed by selecting the neighborhoods in which they live, monitoring their access to media, and encouraging their interaction with peers whose values they consider appropriate.

As well as learning about appropriate behavior through watching others, children also learn it from engaging in routines and rituals. Examples of routines are helping out around the house or engaging in value-related activities such as volunteer work. Social conventions such as ways of dressing and table manners are also carried out in a routine way so that, with repetition, they come to be viewed simply as the way things must be done. Rituals are activities such as holiday celebrations or family get-togethers that reflect group membership and values, and thereby enhance feelings of being part of the group and engaging in activities with the group.

Conclusion

Effective socialization involves both a positive relationship with the agent of socialization as

well as the learning of specific values and standards of behavior. There is no one effective way in which to help children become well-functioning members of their social group. Parents act as protectors, playmates, disciplinarians, teachers, and fellow group members and need to act in accord with that particular role. Whichever role they need to assume depends on sensitivity to the child's current state.

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Sociobiology Controversy

- [Sociobiology Wars, The](#)

Sociobiology Debate

- [Sociobiology Wars, The](#)

Sociobiology Wars, The

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Synonyms

[Sociobiology controversy](#); [Sociobiology debate](#)

Definition

The heated controversy that followed the publication of Wilson's book *Sociobiology: The New Synthesis* and involved Wilson himself as well as critics in biology and the social sciences.

Introduction

More than 40 years ago, in 1975, biologist Edward Osborne Wilson (► [E. O. Wilson](#)) published his book *Sociobiology: The New Synthesis*. It was an attempt to bring together research on animal social behavior in one place, consolidating theory and empirical evidence from several subfields in biology, including ethology, population biology, and zoology. What later led to the “sociobiology wars,” or the “sociobiology debate,” was not Wilson's aim to foster cross-species comparisons of social behavior with that book and thereby advance the study of animal behavior. Even though contained in only the last of a total of 27 chapters, titled: “Man: from sociobiology to sociology,” it was rather his explicit aim to extend this approach to human behavior – and his ambition to thereby lay the ground for a potential integration of the social sciences into the field of evolutionary biology. This appeared justified given the seemingly gradual distinction of human from animal behavior (Schnettler 2010). In this entry, we will take a look at what was at issue in the ensuing debate, what it meant for the integration of evolutionary and social sciences in the upcoming years, and how similar issues have been debated and applied in more recent years.

Dissecting the Sociobiology Debate

Based on many interviews and her reading of the publications and other written exchanges between the relevant protagonists, Swedish sociologist and historian of science Ullica Segerstråle provides arguably the most in-depth account of the sociobiology debate in her book *Defenders of the truth: The Battle for Science in the Sociobiology Debate and Beyond* and in a number of journal articles

(e.g., Segerstråle 2000, 2001). She dissects how the exchange between Wilson and his critics got started and why the sociobiology debate, which “raged throughout the 1970s and 1980s” (Laland and Brown 2002, p. 4) turned, at times, so acrimonious and personal. One of the most dramatic events that illustrates well how heated the debate had gotten was when at “the 1978 meeting of the American Association for the Advancement of Science in Washington [...] a group of activists from the International Committee against racism poured a pitcher of ice-water in Wilson’s neck, shouting: ‘Racist Wilson, you can’t hide, we charge you with genocide!’ and ‘Wilson, you are all wet!’” (Segerstråle 2001, p. 549).

As the description of this scene illustrates, one of the central and loudly voiced accusations against Wilson was that he followed a conservative political and even racist agenda with his sociobiology. These and other accusations and criticisms (e.g., naïve adaptationism, genetic determinism) were originally brought forward by his Harvard colleagues, famously including Stephen J. Gould and Richard Lewontin (► [Richard Lewontin and Stephen Jay Gould](#)), who were among the members of the critical Sociobiology Study Group which at some point published a critical letter about Sociobiology in the *New York Review of Books* (Segerstråle 2001). From her empirical material, Segerstråle (2001) concludes that it was in fact a mix of motives that fueled the sociobiology debate. These were introduced by what she called two different types of “Trojan horses,” a term that she uses to highlight that, in the sociobiology wars, moral goals were hidden behind scientific arguments and vice versa: “On the one hand, the protagonists used political rhetoric to generate attention for their own scientific agenda. On the other hand, and with an eye on historical misuses of Darwinism in the form of Social Darwinism, they used scientific arguments to thwart sociobiology and thereby reduce the potential risk of a renewed political instrumentalization of evolutionary theory by others” (Schnettler 2010, p. 19; Segerstråle 1986).

Given the extremely politicized atmosphere of the sociobiology debate, it might come with no surprise that the reactions to sociobiology

included some distortions of Wilson’s writings and that the criticisms were therefore at least in part unjustified (Schnettler 2010; Segerstråle 2000). A quote of one of the few scientists at the time who took the middle ground in the sociobiology debate, John Maynard Smith (Laland and Brown 2002), illustrates how polarized the opposing protagonists in the debate had gotten: “I find that if I talk to Dick Lewontin or Steve Gould for an hour or two, I become a real sociobiologist, and if I talk to someone like Wilson or Trivers for an hour or two, I become wildly hostile to it” (interview excerpt, quoted in Segerstråle 2000, p. 241).

Evolutionary Psychology, the New Sociobiology?

Despite the heated atmosphere of the sociobiology debate, scientists were able to continue working on animal and human behavior from within an evolutionary framework somewhat under the radar by using different field labels. New fields like ► [human behavioral ecology](#), evolutionary psychology, and ► [dual inheritance theory](#) had emerged that could all be considered descendants of sociobiology (Laland and Brown 2002; Schnettler 2010). Of these, evolutionary psychology, which had been established as a new paradigm in the late 1980s and early 1990s, became quite popular but in the following years drew some of the same criticism as sociobiology had drawn earlier, yet in a quieter and somewhat less politicized way (ebd., see also Freese 2002).

Sociobiology and Sociology

It was not only from within his own discipline and even university department that Wilson was criticized. Strong criticism was also expressed by the social sciences, not least because of Wilson’s ambition to ultimately subsume the social sciences as a branch of biology (Laland and Brown 2002). The reservations against sociobiology, in fact against any biological explanation to human behavior, have long persisted in sociology. This

only recently started to change. Now it was suddenly sociology that got increasingly criticized for disregarding new developments in the evolutionary theory of human behavior (► [Crisis in Sociology](#)). Some even went so far as to diagnose sociology with a veritable “biophobia” (Barkow 2006, p. 10). And this neglect of biological approaches to human behavior was also increasingly seen problematic from within sociology (e.g., Freese et al. 2003; Schnettler 2010). In recent years, however, sociology has increasingly opened toward integrating biological explanations into their explanatory repertoire as labels of new fields of study like “sociogenomics,” “neurosociology,” or “evolutionary sociology” illustrate (Conley et al. 2014; Machalek and Martin 2004; von Scheve 2011).

Cross-References

- [Crisis in Sociology](#)
- [Dual Inheritance Theory](#)
- [E. O. Wilson](#)
- [Human Behavioral Ecology](#)
- [John Maynard Smith](#)
- [Richard Lewontin and Stephen Jay Gould](#)

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Sociocultural Theories of Language

- [Modern Theories of Language](#)

Sociocultural Theories of Violence

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Synonyms

[Code of the streets](#); [Collective efficacy](#); [Culture of honor](#); [Institutional anomie theory](#); [Social disorganization theory](#); [Social learning theory](#); [Strain theory](#); [The civilizing process](#)

Definition

Sociocultural theories of violence focus on how violence can be explained through a combination of features of the cultural environment and aspects of specific social structures and institutions.

Introduction

Violence in its myriad forms is an endemic feature of human societies. Globally, in 2012 approximately 437,000 individuals were the victims of homicide (United Nations Office of Drugs and Crime 2013), just under 40,000 were casualties of armed conflict (Pettersson and Wallensteen 2015), and many more individuals suffered from the consequences of nonlethal interpersonal and collective violence. Rates of violence do, however, vary quite substantially between nation-states, different regions, and different neighborhoods. They also vary over time: violence is more common during some historical periods compared to others (Eisner 2014). One challenge for theories of violence is to explain not only why violence occurs and the contextual factors that make violence more or less likely but also to account for the substantial *variation* that is found in violent offending in different locations and during different time periods. Sociocultural theories of violence are especially salient for addressing this particular challenge (Durrant and Ward 2015). Very broadly speaking, two different types of explanation have been developed by social scientists to account for regional and historical variations in violent offending. First, *cultural approaches* focus on how specific beliefs, norms, values, and attitudes might influence the expression of violence. Second, *social-structural approaches* explore how social-structural characteristics such as poverty, inequality and political legitimacy, and particular *social institutions* shape the expression of violence in society. In order to keep this review to a manageable length, the focus will be on theoretical attempts to explain interpersonal violence; thus sociocultural approaches to understanding collective violence such as war, terrorism, and genocide will be excluded.

Cultural Approaches

There is no universally agreed upon definition of “culture,” but broadly speaking culture refers to shared patterns of norms, values, beliefs, practices, and institutions that help to distinguish

among different social groups. These shared patterns, furthermore, arise through a process of social or cultural learning as individuals who are embedded in particular social groups acquire the relevant values, norms, and practices of those groups during their development. Although clearly developmental outcomes are shaped by both biological and cultural factors and their interactions, many social scientists focus on the way that the acquired values, norms, beliefs, and practices can influence behavior, including the expression of violence.

Social Learning Theory

The central idea of social learning theory is relatively straightforward: humans acquire their specific attitudes, beliefs, norms, and behaviors through a process of social learning. Individuals learn not only from their own experiences with the world but also through the observation of others – or what Albert Bandura (1973) terms *vicarious learning*. Whether or not a given behavior is learned by an individual depends both on the outcome of that behavior and, for vicarious learning, on the status of the observed individuals (who are referred to as “models”). Behavior is more likely to be learned if it (a) results in (or is observed to result in) positive outcomes for the individual and (b) if the observed individual is high in status and shares similar characteristics to the observer. Social learning explanations have played a prominent role in understanding the development of aggression and violence (Akers 1977; Bandura 1973).

In a classic study in social psychology, Bandura and colleagues demonstrated that when young children observed an adult engaging in aggressive behaviors toward a large, inflatable “bobo” doll, then they were more likely to behave aggressively toward the doll – including imitating the very same behaviors observed in the adults – than were children who had witnessed adults engage in nonaggressive actions (Bandura et al. 1961). These studies and others like them suggest that aggressive acts can be learned through the observation of others’ behaviors. The idea that violence and other criminal behaviors arise through social learning from others also features

in several prominent criminological theories. Sutherland's (e.g., Sutherland and Cressey 1974) idea of differential association is premised, for instance, on the idea that criminal behavior is essentially learned and that individual differences in criminal behavior arise through different patterns of associations with others. Similarly, Akers (1977) argued that crime is learned through social interactions with others such that in social environments where criminal behavior is positively reinforced, it is more likely to be repeated.

A social learning approach to understanding violence has been particularly relevant in explaining how growing up in a family environment with high levels of violence can subsequently elevate the risk for aggressive and violent behavior. The *intergenerational transmission of violent offending* is now well documented as children who are exposed to violence in the home are more likely to engage in violent offending than those who do not. This suggests that, in part at least, their violent behavior is the result of social learning processes (Van de Wijer et al. 2014; Widom 1989). There is also an accumulating body of evidence that suggests that exposure to violent films, video games, and other violent media elevates the risk for aggression and violence as a result of social learning (e.g., Anderson et al. 2015), although others have disputed this conclusion (e.g., Ferguson 2015) and media effects may be relatively small in magnitude. In sum, the human capacity for social learning is an important characteristic that can help us to understand the development of violent behavior. Social learning theory also provides the theoretical base that other sociocultural explanations rely on to account for variation in offending across time and space.

Subcultures of Violence Theory

If violent behavior is, in part, socially learned from interactions with others, it follows fairly straightforwardly that some social environments may promote the development of violence more than others. In particular, social environments in which violence is more frequent and in which attitudes toward violence in particular situations are more positive should foster the development

of norms, values, and behaviors that are favorable to the use of violence. According to Wolfgang and Ferracuti's (1967) *subcultures of violence theory*, there exist certain social groups or subcultures in society which differ from the culture of mainstream society. In these social groups – which are typically more socially disadvantaged – violence can be viewed as a legitimate or even obligatory response to particular social situations, especially those that entail the maintenance of respect or social status. The development of these subcultures of violence is strongly shaped by prevailing social-structural features of society but is subsequently acquired by members of the subculture through social learning processes.

The subcultures of violence theory have been further developed in the work of Elijah Anderson (1994, 1999) who argued that the high rates of violence among, in particular, socially disadvantaged African-American males can be attributed to their inculcation into what he refers to as the “code of the streets” “which amounts to a set of informal rules for governing interpersonal public behavior, including violence” (Anderson 1994, p. 82). Of particular note is the way that this “code” dictates (or, at least, socially endorses) the use of violence in response to threats to status or “face”: individuals inculcated into the code of the streets learn to adopt a tough, no-nonsense, persona and the willingness to use violence to resolve disputes and to respond to social threats. Why has this “code” developed and how might it potentially be “adaptive” in particular social contexts? According to Anderson (1999), the specific set of attitudes, norms, and practices relating to violence emerges as a response to social-structural contexts characterized by high levels of poverty, low unemployment, and a lack of reliable third-party reinforcement of social norms (e.g., the police). As a result, status becomes a precious commodity, and individuals are required to resolve their own disputes and conflicts. The threat and use of violence, thus, becomes an effective method of obtaining status and resources. Because children develop in this particular cultural milieu, they come to learn rules, norms, and beliefs that are conducive to the use of violence in

particular contexts, thus perpetuating this subculture of violence.

Support for Anderson's subculture of violence theory has come from a number of studies. Stewart and Simons (2010), for example, conducted a longitudinal study of African-American youth and their caregivers in low-income neighborhoods in Iowa and Georgia. The self-reported violence of youth was measured at two time points along with a measure of neighborhood street culture completed by caregivers which tapped into the key constructs of Anderson's "code of the streets" (e.g., "When someone disrespects, it is important that you use physical force or aggression to teach him or her not to disrespect you," and "People will take advantage of you if you don't let them know how tough you are"). The results largely supported Anderson's thesis: individuals who lived in neighborhoods where the code of the streets was more strongly endorsed were more likely to report aggressive and violent behavior, after controlling for other relevant factors. Interestingly, although the code of the streets was initially developed in the specific context of disadvantaged African-American communities in the United States, it has since been extended to other cultural contexts such as street children in the Ukraine (Naterer 2015) and socially disadvantaged communities in Scotland (Holligan 2015). This suggests that something like the set of values, norms, and behaviors that are reflected in the "code of the streets" may be a fairly robust human (especially male) response to a particular set of social contexts such as those characterized by a weak criminal justice system and a lack of legitimate routes to obtain status. A very similar idea is presented in culture of honor thesis developed by Nisbett and colleagues (1993; Nisbett and Cohen 1996).

The Culture of Honor Thesis

Regional differences in homicide rates in the United States are well recognized. In particular, homicide is more prevalent in the Southern, compared to the Northern states. Why might this be the case? Various factors have been proposed over the years including differences in poverty, income inequality, temperature, and the legacy of slavery.

However, according to the culture of honor thesis, the difference in homicide rates can be largely accounted for by cultural factors (Nisbett 1993; Nisbett and Cohen 1996). The culture of honor thesis rests on three key foundations. First, although the human capacity for aggression and violence may be the result of evolutionary processes, its expression is strongly shaped by specific ecological contexts. Of particular relevance to the culture of honor thesis is the idea that individuals whose livelihood is primarily based around the herding of domestic animals like sheep, pigs, and cattle are more likely to use violence and the threat of violence to maintain their status and reputation compared to individuals who primarily engage in farming. Because the wealth of herders is invested in their livestock, they face a greater risk of their livelihood being stolen by others. They are also more likely to live in regions that are sparsely populated and hence not readily subject to the rule of law. This means that herders need to be able to resolve their own disputes and, ideally, prevent theft from others by cultivating "a posture of extreme vigilance toward any act that might be perceived as threatening in any way, and respond with sufficient force to frighten the offender and the community into recognizing that they are not be trifled with" (Nisbett 1993, p. 442). Farmers, on the other hand, according to Nisbett and Cohen (1996), are more likely to form tight knit and cohesive communities involving the sharing of resources and to live in regions where the effective rule of law is more likely to be in place.

The second component of the culture of honor thesis rests of the particular pattern of immigration from the United Kingdom to the United States. The Northern states of the Eastern Seaboard were primarily settled by farmers from England, Holland, and elsewhere, while the Southern states attracted more settlers from Scotland and Ireland whose economy was largely based on herding. These settlers relocated to southern and western frontiers and continued a livelihood largely based on herding and hunting (Nisbett 1993). These different settlement patterns meant that cultural values relating to violence and honor also differed in the different regions: in the American South, a

culture of honor persisted, whereby individuals (mainly men) believe that violence is the appropriate – perhaps expected – response to threats to the reputation of the self or family. The third component of the culture of honor thesis rests on the assumption that these particular values, norms, and beliefs are more common today in the American South as a result of their ongoing socialization in subsequent generations.

The culture of honor thesis, then, predicts that certain forms of violence, and norms related to violence in particular contexts, will be more common in Southern regions of the United States. In particular, it is argued that dispute-related homicides (as opposed to purely instrumental homicides such as might occur in robberies) will be more prevalent. What evidence is there in support of this idea? Generally speaking it appears that regional patterns in dispute-related homicide support this hypothesis. Such homicides are more prevalent in Southern states and in locations where there is a relatively greater proportion of white men who were born in the South and hence likely to be inculcated with the culture of honor (e.g., Ousey and Lee 2010). Moreover, counties with a greater proportion of Scottish and Irish immigrants in the nineteenth century have higher rates of dispute-related homicides (Baller et al. 2009). Experimental research also supports the idea that Southern men possess different norms regarding the appropriate response to insults and threats and demonstrate more aggressive behavior in response to such threats along with heightened physiological arousal (Cohen et al. 1996).

Although the culture of honor thesis was developed to explain regional differences in the use of violence in the United States, the underlying mechanisms that account for the different use of violence are likely to be more widely applicable. The use of violence can often be a viable strategy for obtaining desirable outcomes, but it also entails risk. Individuals who are more likely to use violence also place themselves in contexts where they are more likely to experience harm themselves from the retaliation by others. Thus violence is a context-dependent strategy: to the extent that values, norms, and beliefs regarding violence shape its use, these should be more

common in certain contexts rather than others. According to a recent model developed by Nowak et al. (2016), honor cultures reliably emerge in particular social contexts: when institutions that regulate third-party conflicts (e.g., an effective criminal justice system) are absent. Under such contexts, the use of violence is effective despite the costs that it might entail to individuals. The culture of honor thesis, thus, might reflect more general processes that emerge in a range of different cultural contexts even though the main focus has been in explaining regional differences in the United States (also see Daly 2016, for a thoughtful critique of the culture of honor thesis as applied to differences in homicide rates in the United States).

The Civilizing Process

The prevalence of violence also varies – and varies quite substantially – over time. This is most evident from the precipitous fall in homicide rates in Europe over the last 500 years, from an average of around 30 homicides per 100,000 people in the fifteenth century to a mean of around 1 per 100,000 in the twentieth century – a 30-fold decline (Eisner 2014). Homicide rates have also fluctuated quite dramatically in many Western countries over the last 50–60 years. In the United States, for instance, homicide rates that were low in the 1950s gradually increased in the 1960s and 1970s, reaching a peak in the late 1980s and early 1990s before declining again (e.g., Farrell et al. 2014). If we accept that homicide rates are a pretty reliable general indicator of the overall prevalence of violence in society, then it is clear from the historical record that violence is more common in some historical periods compared to others.

There have been many attempts to explain patterns of violence (and other types of crime) over time, with no widely accepted set of explanations (see Eisner 2013, 2014; Pinker 2011). It is likely that there are many factors relevant to understanding temporal patterns in violence, but the sociologist Norbert Elias' (1939/2000) theory of the “civilizing process” provides a useful starting point. The main interest of Elias was to account for changes in “civilized” behavior such as those relating to manners and personality over

time, but the key processes that he emphasized are also broadly relevant for understanding shifts in the use and acceptance of violence.

The starting point for the shift in violence in Western society is linked to two key social-structural changes (Eisner 2014). First, the expanding power of the state meant that increasingly disputes were resolved by legitimate third parties rather than individuals and their families, reducing the need for individuals to take matters into their own hands. Second, the expansion of trade and the market economy created dense networks of exchange that encouraged reciprocal interdependencies among people. In turn, these changes promoted the importance of self-control and a growing distaste for the use of force to resolve conflicts. For Elias, these changes first occurred among elites. Then, as others imitated the beliefs and practices of high-status individuals' relevant norms, beliefs and attitudes spread throughout the population, leading to wholesale shifts in violent-related norms, values, and beliefs and a decline in violent crime. Although such shifts are theorized to occur relatively slowly to account for the decline in homicide in Europe since the fifteenth century, changes in cultural values may also occur more rapidly and can potentially account for the fluctuations in violent crime witnessed in many Western countries over the last 50–60 years (Eisner 2014; Pinker 2011).

Social-Structural Approaches

There is an extensive amount of research that has examined the social-structural correlates of violence, with a particular focus on homicide. In an early study conducted in the United States, it was found that resource deprivation, population structure (size and density of population), and divorce rate significantly predicted variation in homicide rates across states, cities, and metropolitan areas (Land et al. 1990). Subsequent research has uncovered a range of social-structural correlates with poverty and income inequality, the ones that most reliably predict variation in homicide rates (e.g., Nivette 2011), although a range of other factors such as population structure and growth

are also important (Nivette 2011). Two prominent theoretical traditions in criminology – social disorganization theory and strain theory – have been employed to account for these findings and are useful in helping us to understand the social-structural factors that contribute to violence in society.

Social Disorganization Theory

According to the central tenets of social disorganization theory, neighborhoods and communities in which there is significant social disadvantage and a high turnover of residents, which are ethnically diverse, tend to be less socially cohesive because there is a lack of agreement over appropriate norms and values for the informal control of behavior. Crime rates remain high over time even in the face of substantial changes in the population of such communities as, via social learning, individuals acquire the norms, attitude, and values that are characteristic of such communities. Robert Sampson's (Sampson 2012; Sampson et al. 1997) theory of *collective efficacy* represents the most prominent contemporary approach within the social disorganization tradition. The term "collective efficacy" was developed to characterize the degree of social cohesion that is found within a given community. Communities that are high in collective efficacy are characterized by individuals who share certain norms, values, and beliefs about behavior and are willing to enforce these in order to maintain social control and to reduce violence. Thus, "the differential ability of neighborhoods to realize the common values of residents and maintain effective social controls is a major source of neighborhood variation in violence" (Sampson et al. 1997, p. 918).

The theory of collective efficacy can, therefore, in principle, help us to understand some of the variation in violent offending that is found between neighborhoods or communities. A number of studies in the United States and elsewhere have largely supported the underlying assumptions of collective efficacy theory (Armstrong et al. 2015; Mazerolle et al. 2010; Sampson et al. 1997; Sutherland et al. 2013). For example, Sampson et al. (1997) conducted a survey of over 8700 residents in 343 neighborhoods

in Chicago measuring participants' perceptions of both collective efficacy and the frequency of violence in the neighborhood in which they reside. Results indicated that neighborhoods varied significantly in terms of perceptions of collective efficacy which, in turn, was significantly associated with the prevalence of neighborhood violence. In a more recent study by Sutherland et al. (2013) involving 60,000 individuals in 4700 neighborhoods in London perceptions of neighborhood collective efficacy significantly predicted police recorded rates of violence crime, although the relationship was relatively small in magnitude. It is reasonable to conclude at this stage that a community's level of social cohesion or collective efficacy does appear to have an influence on the prevalence of violence in that community and can potentially explain variations in the prevalence of violence that is found among neighborhoods and communities. Sampson (2012) has also argued that shifts in collective efficacy over time can also account, in part, for changes in the rate of violent crime over time and may be one factor that is implicated in the overall decline in violent offending in the United States since the early 1990s.

Strain Theory

The sociologist Robert Merton (1938) argued that crime, in general, largely emerged in response to particular social-structural and cultural contexts. In particular he highlighted how the cultural values underpinning the "American dream" of economic success and prosperity were not available to everyone in American society as many individuals are impeded from fulfilling this vision due to poverty and barriers to social mobility. As a result, Merton argued, criminal behavior – including the use of violence – can often be viewed as an adaptive strategy to mitigate the strain brought about by the failure to achieve culturally prescribed goals. This basic idea has been subsequently developed by criminologists working in the strain tradition, including Agnew (1992, 2007) and Messner and colleagues (2012; Messner and Rosenfeld 2013).

Agnew's *general strain theory* builds on earlier theoretical work in the strain tradition by

emphasizing how an individual's response to strain can vary depending on a range of factors including the nature of the strain (whether it is unjust, its magnitude or impact, and how controllable it is) and their individual perceptions of that strain. For Agnew (1992), although social-structural factors are an important distal source of strain, it is the experience of negative relationships with others that can result in negative emotional states such as anger and frustration which, in turn, can lead to various forms of violent and non-violent offending. Although general strain theory has been employed to explain offending in general, Agnew (2007) has also argued that it can account for both individual and community variation in violent offending. More recently, Agnew has expanded the scope of his theory to other forms of violence, including terrorism (Agnew 2010).

Messner's *institutional anomie theory* following the pioneering work of Merton highlights the way in which American cultural values and the institutional structure of American society reinforce a set of culturally prescribed values focusing on economic success and prosperity while at the same time excluding many individuals in society from their attainment. The relatively high rates of crime that are found in American society thus are the result of "... dominant cultural values that extol the virtues of competitive individual achievement and wealth accumulation at the expense of values that emphasize noneconomic forms of achievement, collective solidarity, and the common good" (Messner et al. 2013, p. 411). Thus, one central idea of institutional anomie theory is that certain types of "institutional configurations" (Messner 2012, p. 11), particularly those that elevate the role of the economy above all else, are more conducive to generating anomie which, in turn, elevates the risk for violence.

Conclusions

Understanding violence requires that we consider a range of different theoretical approaches drawn from different levels of analysis. Ultimately, in order to provide a complete explanation, we

need to consider (a) the evolutionary functions and history of violence, (b) how violence emerges during human development, (c) the proximal psychological and physiological mechanisms that give rise to violent behavior, and (d) the specific situational contexts that make violence more likely (Durrant and Ward 2015). Because the prevalence of violence varies quite substantially among different neighborhoods, communities, regions, and countries, over time we also need to consider how features of the cultural and social-structural environment make violence more or less likely. A number of specific cultural and social-structural explanations for violence have been considered in this article.

Cultural approaches to explaining violence focus on how particular norms, values, practices, and beliefs can influence the likelihood of violence. Thus, according to the subcultures of violence hypothesis, some subcultural groups hold norms that are favorable to the use of violence, especially in situations that involve a threat to reputation or status. Similarly, according to the culture of honor hypothesis, regional variations in violence in the United States can be explained, in part, due to cultural differences in beliefs about normative responses to threats to honor and reputation that have their historical origin in herding communities in the United Kingdom. More generally, cultures of honor tend to arise when there is a lack of third-party enforcement of social norms, resulting in the need for individuals to use violence as a way of settling disputes and deterring victimization. Ultimately the cultural factors that can influence violence arise through the social learning on norms, values, and practices from relevant individuals in the community.

Social-structural approaches to explaining violence focus on the particular role of social institutions. Theories that have emerged from the social disorganization perspective highlight the importance of social cohesion or collective efficacy in accounting for neighborhood variation in violent offending. Work in the strain tradition emphasizes the way that social institutions affect individuals in ways that can make offending more likely by increasing strains. Agnew's general strain theory focuses more on individual differences in

response to strains, whereas Messner's institutional anomie theory attempts to account for the high rates of violent crime in American society by noting the highly competitive, economically oriented nature of America's dominant cultural values and social institutions.

Cross-References

- [Aggression](#)
- [Criminology](#)
- [Culture of Honor and Retaliation](#)
- [Social Learning](#)
- [Steven Pinker](#)
- [Violence](#)

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Socioeconomic Flattening

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Sociometer

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Sociometer Theory

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Synonyms

[Interpersonal relationships](#); [Mating sociometer](#); [Self-esteem](#); [Self-esteem feelings](#); [Self-evaluation](#); [Social exclusion or rejection](#); [Social inclusion or acceptance](#); [State self-esteem](#); [Trait self-esteem](#)

Definition

The *self-esteem* refers to a person's appraisal of his or her value. *Global self-esteem* denotes a global value judgment about the self, whereas *domain-specific self-esteem* involves appraisals of one's value in a particular area. Self-esteem is, by definition, a subjective judgment and, thus, may or may not directly reflect one's objective talents or accomplishment (Leary and Baumeister 2000). Importantly, self-esteem is an affectively laden self-evaluation. *Self-evaluations* are assessments of one's behavior or attributes along evaluative dimensions (e.g., good-bad). Some self-evaluations are dispassionate, whereas others are affectively laden. There are two monitoring systems – one immediate and one long term – corresponding to the common distinction between state and trait self-esteem. *Trait self-esteem* is a person's long-term, typical, affectively laden self-evaluation. *State self-esteem*, also called *self-esteem feelings*, refers to a person's affectively laden self-evaluation in a particular situation (Heatherton and Polivy 1991). The self-esteem system is essentially a *sociometer* that monitors the quality of an individual's *interpersonal relationships* and motivates behaviors that help the person to maintain a minimum level of acceptance by other people (Leary and Downs 1995). Although considerable research has identified types of events that raise and lower self-esteem, sociometer theory offers a novel perspective on why these particular factors have their effects. According to the theory, things that affect self-esteem do so via their perceived association with *social inclusion* and *exclusion*.

Introduction

The fact that people are highly and pervasively motivated to protect and enhance their self-esteem suggests that self-esteem must somehow be linked to some important and highly desirable outcome. This entry focuses on two pertinent issues in the literature on *sociometer theory* on self-esteem.

- (A) What is the self-esteem and what is the function of the self-esteem?
- (B) What is the sociometer theory and what is the extension of sociometer theory?

The Nature of Self-Esteem and Its Function

The human organism is characterized by a basic need to belong – a fundamental motivation to form and maintain at least a handful of meaningful social attachments. The power and importance of this motivation are sufficient to think that people might well possess an internal meter to monitor such relationships. Indeed, when something is extremely important to an organism's well-being, internal mechanisms tend to develop for monitoring it. For example, pain serves to signal the possibility of damage to the body, and hunger and satiety monitor how well the person is obtaining nutrition and sustenance (Leary and Baumeister 2000; Zhang and Cao 2011; Zhang and Li 2009).

The central tenet of sociometer theory is that the self-esteem system monitors the quality of an individual's actual and potential relationships – specially the degree to which other people value their relationships with the individual. People do not always seek to be explicitly accepted but rather relational appreciation – the sense that other people regard their relationships with the individual as valuable, important, and close. When low relational evaluation, and particularly relational devaluation is experienced, the sociometer evokes emotional distress as an alarm signal and motivates behaviors to gain, maintain, and restore relational appreciation (Leary and Baumeister 2000).

According to Leary and Baumeister (2000), self-esteem not only signals one's relational value in the immediate situation but reflects the general outlook for relational appreciation and social belongingness in future encounters and relationships. There are two monitoring systems – one immediate and one long term – correspond to the common distinction between state and trait self-esteem. State self-esteem monitors the

person's current relational value and, thus, the degree to which he or she is likely to be accepted and included versus rejected and excluded by other people in the immediate situation (Leary and Downs 1995). The state self-esteem system monitors the person's behavior and social environment for cues relevant to relational evaluation and responds with affective and motivational consequences when cues relevant to exclusion and detection. Trait self-esteem, in contrast, involves the assessment of the degree to which one is the sort of person who generally will be valued by desirable groups and relationship partners. It is a subjective sense of one's potential for social inclusion versus exclusion over the long run.

Several properties of the self-esteem system can be proposed on the basis of the sociometer function. First, the system should be highly sensitive to indications that one's social inclusion or acceptance is in danger. Second, it should operate continuously at an unconscious or preattentive level so that relational devaluation would be detected no matter what else the person is doing. Third, assuming that most people have at least the minimum amount of social acceptance they need most of the time, the system should be more sensitive to relational devaluation than to relational appreciation. Even though social inclusion is of paramount importance to their physical and psychological well-being, people do not possess the cognitive capacity to constantly monitor other's reactions to them at a conscious level. Thus, a system for monitoring relational appreciation and devaluation would have to function automatically, probably at a preconscious level (Cherry 1953; Schneider and Shiffrin 1977). The primary advantage of automatic system is their efficiency. Assessing real and potential belongingness is important to human well-being, but to consciously think through the implications of all interpersonal transactions and social experiences to assess their implications for belongingness would interfere with the person's ability to process other information. Therefore, a mechanism for monitoring one's global desirability for groups and relationships would need to be automatic.

The Mating Sociometer

In an extension of sociometer theory, Kirkpatrick and Ellis (2001, 2006) proposed that there were multiple sociometers associated with functionally distinct social-psychological systems and that these sociometers had multiple functions (in terms of guiding day-to-day decision-making and behavioral strategies). One of these proposed functions was guiding adaptive relationship choices.

In the context of developing social relationships in different social domains (e.g., the mating domain, the friendship domain, the work domain), individuals faced the problem of adaptively calibrating their levels of aspiration. Natural selection should act against individuals who either invested too heavily in social relationships that were substantially lower in value than they can command on the social marketplace and thus failed to get a fair return on the value they bring to the relationships, or wasted investment pursuing social relationships that were higher in value than what they could realistically obtain and protect. Accordingly, Kirkpatrick and Ellis (2001) hypothesized that an important function of self-esteem was to guide individuals to approach social relationships that were of relatively high quality yet defensible given one's own social value. Their model posited that experiences of social acceptance and rejection fed into domain-specific sociometers, causing alterations in state self-esteem in the relevant social domain, which, in turn, affected aspiration levels in approaching new relationships in that domain (Zhang et al. 2015).

Conclusion

The self-esteem operates as an internal measure of one's potential for inclusion in desirable groups and relationships. It is thus essentially a meter that serves to monitor, regulate, and maintain interpersonal attachments, and it is designed to motivate behaviors to increase inclusion and forestall rejection. Self-esteem will be based on whatever criteria those important groups use to include or exclude individuals. These criteria will primarily

involve some combination of competence, likability, attractiveness, and trustworthiness (or moral character in general). State self-esteem will respond to immediate cues relevant to relational evaluation, including particular episodes of acceptance and rejection, whereas trait self-esteem will be a relatively stable appraisal of one's relational value in general (Leary and Baumeister 2000).

As a sociometer, the self-esteem system is likely to monitor the environment constantly for cues or signals that pertain to one's inclusionary status, and so automatic, preattentive processing is likely involved. Assuming that most people have some social ties most of the time, the danger of losing attachments is more urgent than the appeal of forming new ones, and so the sociometer should be especially attuned to cues that connote devaluation, rejection, exclusion, or any broadly undesirable aspect of the self. When the monitoring system detects cues suggesting that one may be rejected now or in the future, the sociometer triggers negative effect as a warning to take preventive or remedial action (Leary and Baumeister 2000).

The sociometer is tied both to specific changes in actual interpersonal relationships and to the possibility of future changes. Thus, for example, a bad test score could trigger a loss of self-esteem and resultant anxiety because it suggests a lack of competence that could make one less appealing to others (for instance, as an employee or as a provider in a close relationship). The salience, pervasiveness, and emotional power of the sociometer most likely entail it acquiring a degree of functional autonomy in the sense that people may become concerned about self-esteem without always noting the link to belongingness (Leary and Baumeister 2000).

In brief, the sociometer theory provides a broader, more parsimonious explanation of what is currently known about self-esteem.

Cross-References

- [Changes in Self-Esteem Motivate Behavioral Changes](#)

- [Self-Esteem as a Status-Tracking Mechanism](#)
- [Self-Esteem as Manipulative Status Communication](#)
- [Self-Esteem Tracks Mate Value](#)
- [Self-Esteem Tracks Social Evaluation and Relational Value](#)
- [Sex-Specific Link Between Self-Esteem and Mate Value](#)

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Sociometric Status

- [Higher Status in Group](#)

Sociomoral Emotion

- [Sacredness/Purity/Disgust](#)

Sociopathy

- [Psychopathy](#)
- [Psychopathy \(Mealey\)](#)

Sociosexual Behavior in Primates

- [Primate Sexuality](#)

Sociosexual Orientation

- [Sociosexuality](#)

Sociosexuality

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Synonyms

Promiscuity; Sexuality; Sociosexual orientation;
Unrestricted sexuality

Definition

Sociosexuality refers to individual differences in willingness to engage in casual, uncommitted sexual relationships (Simpson and Gangestad 1991).

Introduction

Two early comprehensive surveys of the sexual behaviors of North American men (Kinsey et al. 1948) and women (Kinsey et al. 1953) showed that people significantly differ on several attitudes and behaviors related to casual, uncommitted sexual relationships. To describe individual differences in sexual permissiveness and promiscuity, Kinsey and his colleagues were the first to introduce the term sociosexuality. With the exception of research on general sex drive, the majority of early research on sociosexuality was atheoretical. Other shortcomings of this research are that they did not conceptualize sociosexuality in the context of ongoing relationship and did not differentiate between sexual behaviors in committed and uncommitted relationships (Simpson et al. 2004). The scientific interest on this issue largely increased after the construction of the Sociosexual Orientation Inventory (SOI), a valid and theoretically informed measure of sociosexuality (Simpson and Gangestad 1991). Individuals with lower scores on this measure tend to have sex exclusively in emotionally close and committed relationships (restricted sociosexuality), whereas

those with higher scores tend to have sexual relationships with low commitment and investment, often after short acquaintance and with different partners (unrestricted sociosexuality).

Research consistently showed that men display more permissive sociosexual attitudes, fantasize more often about having sex with different partners, and engage in more unrestricted sexual behaviors than women. However, on almost all indicators of sociosexuality, the variability in responses within each sex is greater than that between sexes (Simpson and Gangestad 1991). Phenotypic variations in sociosexuality are substantially influenced by genes (almost 50%) and non-shared environment, and the same genes operate in males and females (Bailey et al. 2000).

Sociosexuality Measures

Among several measures of sociosexuality, the most frequently used is the Sociosexual Orientation Inventory (SOI; Simpson and Gangestad 1991). It consists of seven items that describe actual sexual behaviors (“With how many different partners have you had sex (sexual intercourse) within the past year?” and “With how many different partners have you had sex on one and only one occasion?”), anticipated (future) sexual behavior (“How many different partners do you foresee yourself having sex with during the next five years?”), frequency of cognitions about sexual behaviors (“How often do you fantasize about having sex with someone other than your current dating partner?”), and three items describing attitudes about casual sex (“Sex without love is OK”, “I can imagine myself being comfortable and enjoying ‘casual’ sex with different partners.”, and “I would have to be closely attached to someone (both emotionally and psychologically) before I could feel comfortable and fully enjoy having sex with him or her.”). Because sociosexual behaviors, attitudes, and preferences are relatively highly interdependent, they could be different manifestations of individual differences in global sociosexuality (Simpson and Gangestad 1991). Previous research shows that this measure has sound psychometric properties and is most frequently used as unidimensional, with higher scores denoting unrestricted sociosexuality

(Simpson and Gangestad 1991). However, some findings suggested that the SOI may not be unidimensional, but instead supported a two-factor structure accounting for behavioral and attitudinal sociosexuality (Webster and Bryan 2007).

In order to overcome some limitations of SOI such as its unclear structure, sometimes low internal consistency, open response items that lead to exaggerated responses, different scoring methods, and the formulation of one item that makes the SOI inappropriate for singles, the Revised Sociosexual Orientation Inventory (SOI-R) was developed (Penke and Asendorpf 2008). It consists of nine items, three for each of the three facets: past behavioral experiences referring to the number of casual and changing sex partners, the attitude toward uncommitted sex, and sociosexual desire, which represents a motivational state characterized by heightened sexual interest often associated with sexual arousal and sexual fantasies. Unrestricted sociosexual desire is conceptualized as a sexual attraction toward potential mates to whom no committed romantic relationship exists (Penke and Asendorpf 2008). Although SOI-R full-scale score and the SOI showed very similar relationships to the established correlates of sociosexuality, the results concerning three SOI-R facets show highly distinctive pattern of relationships, which may suggest that past behavioral experiences, the attitude toward uncommitted sex, and sociosexual desire are unique components of sociosexuality (Penke and Asendorpf 2008).

Empirical studies on the conditional expression of long- and short-term mating strategies showed that although men and women do not differ in their interest in long-term sexual partners, men show more interest in short-term partners than women (Buss and Schmitt 1993). Because SOI measures individual variations in the desire for short-term sexual relationships more than for long-term committed relationships, Jackson and Kirkpatrick (2007) proposed that two-dimensional model of sociosexuality that discriminates between long- and short-term sociosexual attitudes would be more appropriate than unidimensional. Accordingly, they developed a scale of human mating strategies consisting of three

factors, short-term mating orientation, long-term mating orientation, and previous sexual behavior. Their results showed that long- and short-term dimensions were largely independent and that they correlated differentially with other theoretically relevant variables (Jackson and Kirkpatrick 2007).

Theories of Sociosexuality

Several not mutually exclusive but rather complementary theoretical models are particularly useful for understanding variations in restricted versus unrestricted sociosexual orientation in men and women. One of them is life history theory (LHT) which proposes that all organisms must allocate certain amounts of their total available resources over the life span into somatic effort (e.g., growth and development of the body) and reproductive effort (e.g., mating and parenting effort) (Stearns 1992). Organisms living in harsh, unpredictable, and uncontrollable environments evolve “fast” life history strategies, allocating resources preferentially to reproductive and mating effort (r-selected organisms), whereas those living in predictable, stable, relatively safe, and controllable environments evolve “slow” life history strategies, allocating resources preferentially to somatic and parental effort (K-selected organisms) (Stearns 1992). Developmental theories based on LHT, such as psychosocial acceleration theory, propose that stressful and supportive environments influence family dynamics, especially parent-child and marital/pair-bond relations (Belsky 2012). Early experiences related to sensitivity and consistency of parenting, harsh or mild environments, and economic situation provide children with information about the kinds of environments they would most likely encounter during their lives and eventually lead to two different mating strategies, unrestricted, short-term and restricted, long-term orientation (Belsky et al. 1991). A variant of this model states that high stress and inadequate resources reflected in local mortality rates may also accelerate reproductive development (Chisholm 1996). Although many studies supported psychosocial acceleration theory, it does not adequately explain why men are more prone to short-term, unrestricted

reproductive strategies and women to long-term, restricted reproductive strategies (Simpson et al. 2004).

The explanation of different sexual reproductive strategies in men and women proposed by sexual strategies theory (SST; Buss and Schmitt 1993) is based on Trivers' (1972) parental investment theory. Because women tend to invest more in their offspring and tend to have relatively smaller number of children, they should be more selective and discriminating when choosing mates, whereas men, who have usually lower initial parental investment and may have larger numbers of offspring, should be less discriminating and more inclined to compete for mates (Trivers 1972). According to SST, during human evolution men and women have evolved different mating strategies that have helped them to solve specific adaptive problems related to reproduction. As mating strategies are context dependent, SST explains conditions within which men and women may benefit from adopting short-term (i.e., unrestricted), long-term (i.e., restricted), and a mix of these mating strategies (Buss and Schmitt 1993). Because of differences in minimal parental investment and potential number of offspring, short-term mating strategies (i.e., unrestricted sociosexuality) should be more beneficial for men than for women. Despite considerable support, SST does not fully explain why there is a greater variability in sociosexuality within both men and women than between them (Simpson et al. 2004).

According to the strategic pluralism model (SPM; Gangestad and Simpson 2000), within and between sex variations in mating strategies may be explained by principles of "good-genes" and "good-parenting" sexual selection as well as by local environmental conditions. When evaluating men as their potential mates, women evolved to make trade-offs between two dimensions: the degree of their health/viability ("good genes") and the level of their commitment/investment in the relationship and offspring ("good parenting") (Gangestad and Simpson 2000). These trade-offs depend on women's attributes such as health and physical attractiveness, as well as environmental demands such as

harshness/benignity and resourcefulness. For example, when environments are nondemanding and women have sufficient resources, their sociosexuality increases and becomes more unrestricted because they can expand additional effort to obtain access to genetically more viable men (Gangestad and Simpson 2000).

The restrictive orientation has been probably designed to facilitate paternal investment in offspring, whereas the unrestricted orientation has probably served to promote the reproductive success of offspring, particularly sons. These two global mating orientations may have evolved and been maintained through frequency-dependent selection (Gangestad and Simpson 1990). More genetically viable men may be reproductively successful without heavy investment and therefore will tend to use unrestrictive, short-term mating strategy, whereas those less viable should invest more heavily, and therefore they will use restrictive, long-term mating strategy. Although the model proposes that women's sociosexuality are more dependent on environmental demands than men's, in more demanding environments the need for biparental care increases, and therefore, restrictive, long-term mating strategy is more appropriate for both men and women. Taken together, this model postulates that men and women have a repertoire of alternative mating strategies whose adoption is under the influence of personal attributes and local environments and explains why sociosexuality is more variable within women and men than between them (Simpson et al. 2004). Research confirms that SPM is well-supported evolutionary perspective on sociosexual variation across cultures (Schmitt 2005b).

Sex ratio theory (SRT; Pedersen 1991) seeks to explain sex and cultural differences in sociosexuality. According to this theory, operational sex ratio is high when local culture includes relatively more marriage-age men than marriage-age women (usually between 15 and 49 years) and low when there are relatively more women than men (Pedersen 1991). Although there are often variations in sex ratio across cultures and historical times, women generally have a slight tendency to outnumber men mainly because of men's

greater mortality rate. Because in cultures with low sex ratio (i.e., men are more scarce than women), men can afford to be more promiscuous (i.e., show higher levels of sociosexuality), and because of mating market forces, the whole culture becomes more sociosexually unrestricted. Conversely, cultures with high sex ratios (i.e., more men than women) are associated with reduced levels of sociosexuality, because these cultures are driven more by women's than by men's sexual desires (Schmitt 2005b). Findings of two extensive cross-cultural research supported the key hypothesis of the SRT (Lippa 2009; Schmitt 2005b).

Social structural or biosocial theory (Wood and Eagly 2002) proposes that sex differences in psychological characteristics such as sociosexuality do not result from evolved psychological dispositions, but rather from social and cultural factors. According to this theory, the proximate causes of sex differences are social structure (e.g., greater male than female power, patriarchy), social roles (e.g., men as workers, women as housekeepers), and the gender ideologies behind patriarchal social structures and social roles. Because all modern societies display patriarchal social structures, although to varying degrees, they all show unidirectional sex differences in sociosexuality (Eagly and Wood 2005). Therefore, sex role socialization is sensitive to local economic and sociopolitical environments leading to sex differences in mating behaviors. In more patriarchal societies with traditional sex role ideologies, men's sociosexuality should be much higher than women's, whereas in societies with higher levels of gender equality and economic development, sex differences in sociosexuality should be weaker, which was supported by some large cross-cultural research (Lippa 2009; Schmitt 2005b).

Cross-Cultural Differences in Sociosexuality

Sex differences in sociosexuality are generally large and cross-culturally universal. Two large cross-cultural studies that included 48 (Schmitt 2005b) and 53 nations (Lippa 2009) found that in every culture, men were more unrestricted than women (average d in both studies was 0.74).

However, several mutually related factors moderate the degree of sex differences in sociosexuality. They are larger in more demanding reproductive environments (e.g., higher stress, fewer resources, higher mortality rate) and smaller in undemanding environments and cultures with higher economic development and political and gender equality (Schmitt 2005b). In cultures with more gender inequality, levels of sociosexuality in both men and women decreased although more sharply in women (Lippa 2009). Countries also differ substantially in the mean level of sociosexuality. Those with the lowest level of sociosexuality were from East and South Asia (e.g., Taiwan, Bangladesh, South Korea) and Africa (e.g., Zimbabwe, Botswana, Ethiopia), whereas those with the highest levels were from Europe (e.g., Finland, Slovenia, Lithuania), indicating that people are more sexually restricted when reproductive demands are higher and more stressful (Schmitt 2005b).

One aspect of environmental threat is a potential danger posed by infectious diseases. Namely, when pathogen transmission is highly probable, people exhibit more careful and cautious behavioral styles. Research supports the hypothesis that in regions with historically higher prevalence of infectious diseases, people show lower levels of sociosexuality. This tendency is more strongly pronounced in women than men because women face relatively higher parental investment costs than men, and, therefore, they might be more sensitive to the signals of increased costs related to unrestricted sexual behaviors (Schaller and Murray 2008). It seems that only those parasites which have the capacity for human-to-human transmission provoke threats affecting sociosexuality, whereas no such relationship was found for parasites infecting animals (Thornhill et al. 2010).

As already mentioned, sex ratio can also produce cross-cultural differences in sociosexuality. Research across 48 nations showed that sex ratios were significantly negatively related to national sociosexuality levels ($r = -0.45$). Low sex ratio (more women than men) and high sociosexuality levels were especially evident in Baltic countries, whereas high sex ratio (more men than women)

and low sociosexuality levels were evident in some Asian cultures such as Hong Kong, Bangladesh, and Taiwan (Schmitt 2005b).

Sociosexuality and Other Individual Differences

Research shows that sociosexuality is related to various psychological constructs such as personality traits and attachment styles. One of the earliest studies shows that sociosexuality was related to two higher-order personality dimensions labeled extraversion and lack of constraint and that individuals with unrestricted sociosexuality were more extraverted, aggressive, disinhibited, and more likely to lack control than those with restricted sociosexuality (Gangestad and Simpson 1990). In a large cross-cultural study encompassing 46 nations, extraversion was associated with unrestricted sociosexuality worldwide as well as across almost all 10 major world regions in both men and women (Schmitt and Shackelford 2008). Somewhat less consistent across world regions were the relations of higher agreeableness and conscientiousness with unrestricted sociosexuality. Compared to the other five-factor personality traits, neuroticism showed the lowest correlations with sociosexuality worldwide, with unrestricted sociosexuality associated with lower levels of neuroticism only in men. Openness showed positive correlations with unrestricted sociosexuality worldwide in both men and women, but these links were somewhat inconsistent, depending on sex and world region (Schmitt and Shackelford 2008). Additionally, honesty-humility factor of the HEXACO model was moderately positively related to restricted sociosexuality (Bourdage et al. 2007). Majority of the significant correlations between sociosexuality and abovementioned personality traits were low to medium. Sociosexuality was somewhat more highly related to the dark triad, a constellation of three subclinical antisocial personality traits – psychopathy, Machiavellianism, and narcissism. Psychopathy is characterized by callous affect, remorseless manipulation, and exploitativeness, narcissism by dominance, exhibitionism, exploitation, and feelings of superiority and entitlement, while Machiavellianism refers to

manipulativeness, insincerity, and callousness. All three dimensions as well as the composite of the dark triad measures showed moderate positive correlations with unrestricted sociosexuality and other indicators of short-term mating (Jonason et al. 2009). In a large cross-cultural survey across 53 nations and 11 world regions, narcissism positively correlated with self-reported unrestricted sociosexuality worldwide and across almost all major world regions. These relationships were especially pronounced with the socially maladjusted facets of narcissism, exhibitionism, exploitativeness, and entitlement (Schmitt et al. 2017). It seems that the dark triad traits and unrestricted sociosexuality are parts of fast life history strategy facilitating short-term sexual strategies. Regarding other personality traits, sensation seeking showed positive relationships with all three aspects of sociosexuality measured by SOI-R, whereas social inhibitedness (shyness) showed negative relationships with sociosexual behavior and attitude but not with sociosexual desire (Penke and Asendorpf 2008). Individuals with unrestricted sociosexuality also tend to be more impulsive and masculine and higher in self-monitoring (Simpson et al. 2004), as well as evening chronotype (Marvel-Cohen et al. 2018). As could be expected, sociosexuality was strongly related to the three scales from the Sexy Seven, instrument that measures sex-specific and evolution-relevant dimensions of individual differences (Schmitt and Buss 2000). Restricted sociosexuality was related to relationship exclusivity (low promiscuity and adultery) and sexual restraint (abstinence and prudishness), whereas unrestricted sociosexuality with erotophilic disposition (obscenity, indecency, and lust) (Bourdage et al. 2007).

Sociosexuality was also examined in relation to attachment styles. Namely, attachment theory states that early children's experiences with their primary caregivers are internalized into a framework of thoughts, feelings, and expectations regarding relationships, which continue to affect individuals' interpersonal relationships throughout their lives (Bowlby 1969/1982). Three primary attachment orientations have been determined as the most important in infant-caregiver and adult

romantic relationships: secure attachment orientation and two insecure orientations, avoidant and anxious. Securely attached individuals believe they are worthy of love and that others are trustworthy and will support them when needed. Avoidantly attached individuals believe that others are untrustworthy and experience distress when they must depend upon others, whereas anxiously attached individuals believe that they are not worthy of love and care from others and fear that others will not be supportive or will abandon them in the times of need. Research showed that secure attachment orientation was related to more restricted sociosexuality (Brennan and Shaver 1995) and that it mediated the relationship between early environments and sociosexuality in early adulthood. Namely, it seems that more predictable, stable early environments facilitate higher-quality parental care and secure attachment orientation, which results in more restricted sociosexuality in early adulthood (Szepeswol et al. 2017). On the other hand, insecure attachment, especially avoidant orientation, was related to unrestricted sociosexuality (Brennan and Shaver 1995). Dismissing attachment was cross-culturally related to unrestricted sociosexuality in most world regions and in both sexes, whereas preoccupied, fearful, and secure attachment generally showed low and inconsistent relations with sociosexuality across gender and world regions (Schmitt 2005a). However, many relationships obtained between attachment and sociosexuality were relatively small and most frequently found in Westernized cultures (Schmitt and Jonason 2015).

To summarize, individuals with unrestricted sociosexuality tend to be more extraverted and open to experience, less agreeable and conscientious, more aggressive, disinhibited, impulsive and masculine, as well as higher sensation-seekers. They also tend to be higher on all dark triad traits and personality attributes related to erotophilia, more avoidantly attached, and evening chronotype. On the other hand, sociosexually restricted individuals could be described as more introverted, agreeable, conscientious, inhibited, honest and humble, as well as less aggressive, impulsive, and less open to

experience. They also tend to be lower on all dark triad traits and higher on personality attributes related to relationship exclusivity and sexual restraint as well as more securely attached and morning chronotype. Personality characteristics related to unrestricted sociosexuality are likely to facilitate successful pursuit of short-term mating strategies, while those related to restricted sociosexuality may be helpful in effective enactment of long-term mating strategies (Simpson et al. 2004).

Sociosexuality and Mating Behavior

Global sociosexuality as well as its components show moderate to strong associations with a wide range of mating behaviors. It was found that persons with restricted sociosexuality have a tendency to be more attracted by potential partners' attributes such as loyalty, faithfulness, and responsibility, as well as personal compatibility with them, characteristics that usually facilitate and help to maintain stable, committed, and long-term relationships. Those with unrestricted sociosexuality tend to be more attracted by physical/sexual appeal and social visibility of their potential partners, which are important features for initiating and developing short-term relationships (Simpson et al. 2004). Sexually unrestricted persons seem to be especially sensitive to physical characteristics that signal reproductive value of a potential partner. For example, unrestricted women prefer men with more masculine bodies (Provost et al. 2006), and sexually unrestricted men prefer women with low waist-to-hip ratio, an indicator of women's fertility (Price et al. 2013).

It should be noted that people could validly assess sociosexuality of previously unacquainted individuals on the bases of their nonverbal behavior and that men assess sociosexuality more accurately in women than women do in men. Unrestricted men are more likely to smile, display head cants, flirtatious glances, and are perceived as socially engaging and dominant, whereas unrestricted women are more likely to lean forward and cant their heads (Simpson et al. 1993). Relatedly, unrestricted people were more attracted to potential dating partners who display flirtatious

glances, intermittent gaze aversions, and head cants (Simpson et al. 2004).

Unrestricted persons are more likely to get involved in extra-pair sexual relationships and exhibit a pattern of sexually assertive behaviors such as more frequent flirting and engaging in socially dominant behaviors (e.g., maintaining eye contact and close physical proximity during social interactions), along with chronic, heightened responsiveness to situational sexual cues (Penke and Asendorpf 2008; Simpson et al. 2004). In both sexes, unrestricted sociosexuality was linked to different mate poaching experiences such as mate poaching attempts, being the target of mate poaching attempts, and being successfully poached (Grundler et al. 2013). Therefore, positive links between unrestricted sociosexuality, especially perceived sociosexuality of one's partner and mate retention behaviors, are not unexpected (Kardum et al. 2006). Additionally, unrestricted sociosexuality, especially sociosexual desire, was negatively related to relationship quality, commitment, investment, and fidelity, and it predicted relationship dissolution and sexual involvement with new partners (Penke and Asendorpf 2008). However, it seems that if unrestricted persons have romantic relationships in which they agree with partners about the possibility to satisfy their need for sex with other people, their relationship quality will not be negatively affected (Rodrigues et al. 2016). It should be mentioned that many mating behaviors could be related to some specific components of sociosexuality. For example, sociosexual attitude was the only component that did not contribute to the prediction of future sexual behavior and relationship outcomes (Penke and Asendorpf 2008).

Sociosexuality is also associated with not so obvious although theoretically meaningful outcomes. For example, because men tend to exhibit greater variability in their total number of offspring than women do, SPM predicts that genetically predisposed unrestricted women typically should have benefited from having relatively more sons ("sexy son" hypothesis), while genetically predisposed restricted ones should have benefited from having relatively more daughters, which was supported in three studies (Gangestad and Simpson 1990).

Conclusion

Over the last several decades, the study of individual differences in sociosexuality as well as its underlying mechanisms greatly advanced our understanding of the important aspects of interpersonal relationships, i.e., sex and sexuality. Sociosexuality is especially relevant in explaining gender and cross-cultural differences in sexuality and their implications, as well as how social and physical environmental factors affect reproductive behavior. These advances were possible because the concept of sociosexuality is theoretically well-grounded and has clear and valid operationalizations. The abundance of studies embedded sociosexuality within a nomological network of relations with a wide range of other individual difference variables and consequential mating behavior, showing fundamental differences between short- and long-term mating strategies.

Cross-References

- ▶ [Environmental Harshness](#)
- ▶ [Infidelity](#)
- ▶ [Life History Theory](#)
- ▶ [Randy Thornhill](#)
- ▶ [Relationship Between Sexuality and Gender](#)
- ▶ [Relationship Choices and Sexuality](#)
- ▶ [Sex Differences in Long-Term Mating Preferences](#)
- ▶ [Sex Differences in Short-Term Mating Preferences](#)
- ▶ [Sex Ratio](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)

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Sociosexuality and Sexual Conflict in Mating Strategies

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Synonyms

Error management theory; Mating strategies; Sex differences; Sexual conflict; Sociosexuality

Definition

Men and women differ in terms of their sociosexuality, or evolved preferences for whether and how soon to have sexual relations. Reflecting these differences, the sexes often come into sexual conflict.

Introduction

Sociosexual orientation, or sociosexuality, is a construct reflecting an individual's tendency to engage in casual, uncommitted sexual relationships. It is commonly measured by the Sociosexual Orientation Inventory (SOI) (Simpson and Gangestad 1991), which measures both behavioral elements – past number of partners, predicted number of future partners, number of one-night stands, frequency of sexual fantasies – as well as attitudes toward engaging in casual, uncommitted sex. Individuals with a restricted sociosexual orientation are more likely to insist on commitment and closeness in a relationship before engaging in sex and to pursue a long-term mating strategy, while those with an unrestricted sociosexual orientation are more likely to be comfortable engaging in sex without commitment or closeness and to pursue a short-term mating strategy.

Sex Differences in Sociosexuality

On average, men have evolved to have a more unrestricted sociosexual orientation than women. This difference can be traced back to Trivers' (1972) theory of parental investment and sexual selection. That is, men are biologically required to invest much less than women in their offspring. Men only need to contribute a few sex cells and a few minutes of their time, while women must go through 9 months of pregnancy before the offspring is born and, in natural settings, several years of post-birth lactation. Because of these key differences, men have more to gain than women – in terms of reproductive fitness – from having frequent sex with several partners; such behavior leads to a direct increase in the number of offspring produced while incurring relatively little cost for men, but not women. As such, men have evolved to have a greater desire for casual sex than women. In contrast, ancestral women would have faced a high cost if offspring were produced as a result of uncommitted sex as they would have to go through a long period of gestation and ensure the survival of the offspring without any help from a reliable and resourceful father. This high cost of casual, uncommitted sex has resulted in women evolving a more restricted sociosexual orientation as compared to men.

Consistent with the theory, a worldwide study spanning 48 nations revealed that sex differences in sociosexuality in the predicted direction were large and were universal across cultures (Schmitt 2005). Due to their relatively unrestricted sociosexuality, men prefer to engage in sex sooner than women and pursue it more persistently and aggressively. Indeed, men are more willing to have sex than women at every time interval of knowing a potential mate up to 5 years (Buss and Schmitt 1993). Only at 5 years of acquaintanceship are women, who require investment and commitment from their partner, equally likely interested in engaging in sex. The result of these opposing sexual strategies and sex differences in sociosexuality lead to much potential sexual conflict between men and women, including conflict over the occurrence and timing of sex and much of the sexual aggression that occurs.

Conflict About the Occurrence and Timing of Sex

A major source of sexual conflict concerns decisions over *whether* sex will occur and *when* it will occur. As described above, men, on average, have evolved to desire to have sex with more partners sooner and without significant prior investment, while women, on average, have evolved to prefer less partners and to grant sexual access upon having obtained proof of resources and commitment. These different and somewhat opposing strategies are associated with different cognitive biases and deceptive tactics on the part of both sexes (Haselton and Buss 2000).

Regarding biases, because individuals are typically uncertain about the feelings and intentions of potential mates, they have to make judgments one way or the other. Regarding perceptions of sexual interest, there are two types of errors that can be made: falsely inferring sexual interest when there is none and failing to detect sexual interest when it exists. According to error management theory (Haselton and Buss 2000), the reproductive costs of these two errors are unlikely to be identical. Therefore, selection pressures would have produced cognitive biases that aim to avoid incurring the more costly error. Which is the more costly error differs for men and women. For men, missing an actual sexual opportunity (and thus, missing an opportunity to increase reproductive fitness) is generally costlier than pursuing a nonexistent sexual opportunity (which may waste a degree of time and energy). Hence, men may have evolved to overestimate the amount of sexual interest a woman has in them. As a result of this bias, men will miss less sexual opportunities that exist but will also make a number of unwanted sexual advances toward women who are not actually interested. Consistent with this reasoning, men perceive more sexual intent in opposite-sex interactions than women do, and women more than men experience their own friendliness as being misperceived as a sexual invitation (e.g., Abbey 1982). Indeed, a lot of unwanted male sexual attention occurs in the modern workplace, resulting in the filing of sexual harassment claims from mostly women.

An interesting real-world example of this occurred when a supermarket chain instructed their employees to smile at and make eye contact and pleasant conversation with their customers. Female employees became the target of unwanted sexual comments, come-ons, and pursuits because male (but not female) customers had perceived the friendly behavior as signaling sexual interest. It should be noted that it is not entirely clear whether, in this and other instances of conflict, men are overperceiving sexual interest or whether women are deceiving. In this case, the employees were not actually behaving naturally but in accordance to company instructions. Furthermore, if the employees' behaviors had been freely chosen rather than instructed by the company, the behaviors (which clearly stand out from the usual impersonal and less friendly service provided by most cashiers) could arguably indicate a level of potential interest or an attempt to feign sexual interest. If so, then rather than simply concluding that men are overperceiving, it may be more accurate to say that men were responding to cues that would normally be put forth when women actually want to signal sexual interest. These competing possibilities have yet to be thoroughly examined. At any rate, the sex difference is clear: male but not female customers' behavior indicated perceptions of sexual interest.

In contrast, women face a different kind of error asymmetry: consenting to sex without commitment tends to be a more costly error for women than waiting a longer time for sexual relations to commence, thus making women more susceptible to the commitment skepticism bias, where they tend to underestimate a man's actual level of commitment early in courtship (Haselton and Buss 2000). Such underestimation tends to encourage further escalation of commitment from male partners before sex occurs.

In conjunction with these cognitive biases, the sexes also engage in the use of deceptive tactics to further their own respective strategies. For instance, men often exaggerate the depth of their feelings to indicate commitment and thus, to speed up the occurrence of sex. A study of college men and women found that 71% of men reported having ever exaggerated their feelings to get sex,

while only 39% of women had done so. On the other hand, more women than men admit manipulating perceived sexual access. That is, women more than men report using their sexuality, such as smiling and flirting, to get favors from the opposite sex even though they have no sexual interest. Moreover, more women than men report engaging in sexual withholding, where they delay the occurrence of sex in order to increase men's investment and commitment.

Sexual Aggression

Although some conflicts are benign, consisting of annoyances and temporary misunderstandings, the opposing sexual strategies of men and women as a result of their differing sociosexual orientations can sometimes result in more serious forms of conflict, including sexual aggression and rape. Because of men's evolved desire to have sex sooner and without the need for significant investment and women's evolved reluctance and need for commitment, men may sometimes resort to forcing their sexual interest on reluctant women. These acts of sexual aggression can be directed towards single women, or a man's current partner. Victims are disproportionately concentrated among young and physically attractive women, indicating that male sexual aggression is primarily aimed at generating reproductive fitness. Women are also more likely to experience greater distress from sexual aggression than men, citing it as more upsetting than verbal or nonsexual physical abuse (Buss 1989). The conflict of sexual aggression is made even worse by the fact that men underestimate how upsetting sexually aggressive acts are to women, which may incline some men to engage in such behaviors more often.

Rape occurs when sexual aggression involves forced sexual intercourse. A controversial issue in evolutionary psychology is whether rape is an adaptation designed to obtain sexual access when consensual opportunities are lacking (Thornhill and Palmer 2000). In one study, 35% of men indicated that they would consider forcing sex on a woman against her will if there was no chance of getting caught. Victims of rape also tend

to be young and fertile women, and the pregnancy rate associated with rape is higher than the rate for consensual sex. Although these findings support the perspective that rape is an adaptation, they do not sufficiently distinguish from the alternative perspective that rape is a by-product of other evolved mechanisms, such as a desire for sexual variety and greater physical aggression. Regardless of which perspective is more accurate, rape has occurred throughout human history and as such, women have also been hypothesized to have evolved anti-rape adaptations, such as making alliances with male friends for protection, avoiding risky activities during ovulation, and experiencing psychological pain from rape to avoid it in future. However, research on women's evolved defenses against rape is still in its infancy and more work is needed in this area.

Individual Differences

Although men have tended to evolve different sociosexualities than women have, not all men are higher on sociosexuality than all women. There are important within-sex differences. For example, asymmetry is negatively correlated with sociosexuality (Gangestad and Simpson 2000). For men who are lacking in attributes that women find attractive in short-term mates, such as facial symmetry, the costs of pursuing a short-term mating strategy are likely to outweigh the benefits. It would be more beneficial for these men to embrace a more restricted sociosexual orientation and thus, invest heavily in a long-term mating strategy and a single mate's offspring. Such within-sex differences in sociosexuality also lead to within-sex differences in some areas of sexual conflict. For example, men who are more inclined to pursue a short-term mating strategy are more susceptible to the sexual overperception bias (Lenton et al. 2007) and are therefore more likely to get involved in conflicts about sexual access and whether sex will occur.

Furthermore, the magnitude of these sex differences tends to vary across cultures (Schmitt 2005). In cultures where the environment is more demanding (e.g., fewer resources, higher

mortality), sex differences in sociosexuality have been found to be larger, presumably because women are more monogamous in response to the environmental demands for better offspring care. Men, on the other hand, may still benefit from short-term mating, regardless of environmental influences. Cultures with more traditional sex role ideologies may also have larger sex differences in sociosexuality. Women are more constrained in these societies economically, politically, and reproductively, which promotes a more restricted sociosexual orientation as compared to men.

Conclusion

This entry has described the link between sex differences in sociosexual orientation – the degree to which people seek sexual relations without commitment – and key sexual conflict dynamics. Future research, guided by an evolutionary perspective on sex and within-sex differences in sociosexuality and sexual conflicts, is needed to shed further light on the dynamics of human mating as well as provide insights on how to prevent sexual conflict.

Cross-References

- ▶ [Environmental Harshness/Mortality](#)
- ▶ [Evolution of Desire, The](#)
- ▶ [Evolution of Female Resistance](#)
- ▶ [False Negatives](#)
- ▶ [False Positives](#)
- ▶ [Female Infidelity](#)
- ▶ [Female Manipulation of Men](#)
- ▶ [Female Mate Choice](#)
- ▶ [Fluctuating Asymmetry](#)
- ▶ [Forced Copulation](#)
- ▶ [Hookup Culture](#)
- ▶ [Impersonal Sex](#)
- ▶ [Limited Reproductive Potential](#)
- ▶ [Local Sexual Practice](#)
- ▶ [Male Friendship](#)
- ▶ [Maternal Investment](#)
- ▶ [Obligatory Parental Investment](#)

- Parental Investment and Sexual Selection
- Perceiving Sexual Intent
- Perceptions of Infidelity
- Randy Thornhill
- Rape
- Reproductive Frequency
- Reproductive Timing
- Reproductive Value
- Sex Differences in Commitment Skepticism
- Sex Differences in Inferring Sexual Interest
- Sex Differences in Long-Term Mating Preferences
- Sex Differences in Same-Sex Aggression
- Sex Differences in Short-Term Mating Preferences
- Sex Ratio
- Sexual Coercion
- Sexual Coercion and Violence
- Sexual Conflict and Sex Differences in Parental Investment
- Sexual Conflict in Mating Strategies
- Sexual Harassment
- Sexual Receptivity
- Sexual Strategies Theory
- Short-Term Mating
- Social Status and Economic Resources
- Sociosexual Orientation
- Sociosexuality
- Steve Gangestad
- Violation of Long-Term Mate Preferences
- Violation of Short-Term Mating Preferences

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Solidarity

- Consolidating Familial Power

Solitude

- Loneliness in Modern Life

Solution to Paternity Uncertainty

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Synonyms

Anti-cuckoldry tactics; Paternal assurance tactics

Definition

Due to internal fertilization, human males cannot be sure that they are investing in their own biological children. As a result, men have developed solutions to this issue: anti-cuckoldry, or paternal assurance, tactics.

Introduction

Because of internal fertilization, human males cannot be sure that the children they invest in are biologically related to them. The threat of cuckoldry was examined thoroughly by Anderson (2006); the incidence of nonpaternity rates from paternity testing laboratories (involving samples that in some cases were in the thousands) ranged from 14.3% to 55.6%. Anderson partitioned the incidence of nonpaternity into males with high paternity confidence (i.e., males who had no reason to question their paternity) and those with low paternity confidence. Among those with high paternity confidence, the incidence of nonpaternity was approximately 2%. For those with low paternity confidence, however, the incidence of nonpaternity was 30%. First, this shows that cuckoldry can be a significant factor in male reproduction. Second, this shows that men question their paternity and attempt to determine paternity to make investment decisions. They also engage in various tactics to increase their paternity confidence.

Paternal Assurance Tactics

Gallup and Burch (2006) created a model to describe the motivations for, and ways in which, men attempt to solve the problem of paternal uncertainty. The model outlines four categories of tactics: insemination prevention, counter insemination, pregnancy termination, and postpartum investment. Each of these categories of strategies is implemented by men in sequence and according to context.

Insemination Prevention

The first and most obvious paternal assurance tactics are those that involve *insemination prevention strategies*. Common tactics for insemination prevention involve keeping women away from other men, particularly if it is unmonitored. This can begin even as women are still girls as this will not only affect their marriageability and their family's reputation in several cultures. A woman who is unfaithful to her husband puts her children's livelihoods in danger, but also may be perceived to be possessing a heritable trait, leaving her mother's fidelity, and therefore her father's paternity, in doubt. Because of this, parents may be just as invested in perceived female purity as prospective mates (Burch 2019, *in press*).

To insure that the female partner has previously avoided men and is not predisposed to seek them out, men often insist on virginity or little sexual experience (Espin 2018; Bekker et al. 1996). This idea, that low promiscuity becomes low infidelity after marriage, was supported by Essock-Vitale and McGuire (1985) who found that among adult women, promiscuity prior to marriage was also a predictor of infidelity once women were married. Other attempts to prevent infidelity or insemination by other males include physically restricting female sexuality through mechanical means like chastity belts, or surgical means like female genital mutilation and infibulation (see Daly et al. 1982, for review). It is important to note that these strategies are implemented as girls grow into sexual maturity, ensuring their virginity for future husbands, and used by those husbands throughout their marriages.

The most widely researched insemination prevention tactic is mate guarding, motivated by male sexual jealousy (Daly and Wilson 1988). What is sexual jealousy other than the fear of cuckoldry? Sexual jealousy can manifest itself in indirect monitoring of the female partner (checking mileage on the family car, checking phones and other devices, asking others to monitor or report on her behavior), limiting the number of places the female is allowed to go alone (or "unsupervised"), restricting her resources so

she cannot venture out, separating her from family and friends, or creating conflict when she violates these restrictions (see Buss 2002 for review). Jealousy can (and often does) escalate into severe isolation and abuse. Sexual jealousy has been described as one of the most frequent motivators of domestic assault (Wilson and Daly 1996).

Counter Insemination Strategies

However, if these mechanisms fail and insemination of the female occurs as a consequence of extrapair copulation, *counter insemination strategies*, such as sperm competition (Baker and Bellis 1995; Birkhead 2000) and semen displacement (Gallup et al. 2003) are then implemented.

Sperm competition refers to the competition between the ejaculates of two different men when a woman mates with more than one man within a small window (given the lifespan of sperm, this is typically less than 48 h but can extend days) (Baker and Bellis 1995). Baker and Bellis (1993) surveyed over three thousand women through a British magazine and found that one-half of women had double mated within their first 500 copulations, and over 80% had double mated by the time they had experienced 3000 copulations. Approximately 30% of women reported having been inseminated by two males within 24 h on one or more occasions.

If and when double mating occurs, males have developed strategies to compete against rival males. First of all, jealous men are more likely to insist on frequent sex with their partners, essentially putting their sperm into competition with suspected rivals (Shackelford et al. 2007). Men have also insisted or even forced their partners into sex when they have suspected infidelity (Goetz and Shackelford 2006). In addition, there is evidence that not only do men make sure their sperm are in competition when they suspect infidelity but they also put

more sperm in competition. Kilgallon and Simmons (2005) found that when men were shown pictures designed to simulate sperm competition, such as sexually explicit images of two men and a woman, they had significantly higher proportions of mobile sperm in their ejaculates. Men who masturbate while watching pornography of other men having sex with women produce greater volumes of seminal plasma, higher sperm counts, higher percentages of morphologically normal sperm, and greater sperm motility (Yamamoto et al. 2000).

Another counter insemination strategy would be to remove the sperm of rival males from the female reproductive tract. As odd as this sounds, semen displacement is an evolved feature of human penile morphology, where semen from rival males is displaced from the cervical area of the vagina by the coronal ridge of the glans of the penis through thrusting during sex. After displacing the rival semen, the resident male can then ejaculate at the cervical end of his partner's vagina. If semen displacement was a mechanism to prevent insemination by rival males, thrusting (and therefore displacement) would be increased in situations where men suspected infidelity. Gallup et al. (2003) found that following allegations of female infidelity or periods of separation, the majority of males and females reported increase in both the depth and vigor of thrusting. This would enhance the magnitude of semen displacement.

Pregnancy Termination Strategies

If a man suspects infidelity and his female partner becomes pregnant, he may suspect that the child is not his. This may be evidence that his insemination prevention and counter insemination strategies have failed, and the pregnancy would be potential cuckoldry. At this stage, men may employ *pregnancy termination strategies*. Pregnancy termination can occur through chemical (semen composition) or physical (abuse) means.

It is important to note that suspicions of cuckoldry may not be founded, but this does diminish male behavior. Just as with sexual jealousy and paternal resemblance (see below), it is the perception that motivates the tactics. For example, Campbell et al. (1992) found that regardless of actual paternity, men still suspected their partners had been unfaithful, and this resulted in physical abuse during their pregnancies. Likewise, Burch and Gallup (2004) found that among men convicted of domestic violence, the frequency and severity of abuse men doubled when the woman was pregnant. Men reported that sexual jealousy was the prime motivator of violent incidents. The men who abused their pregnant partners reported greater sexual jealousy and questioned the paternity of the unborn child. Physical abuse directed toward their pregnant partner's abdomen was common, making the purpose of the abuse clear.

Interestingly pregnancy termination attempts can also be chemical in nature. For example, it appears that repeated exposure to the biological father's semen may be a factor in pregnancy maintenance. Women who have limited exposure to the biological father's semen are at an elevated risk for preeclampsia (Robertson et al. 2003), a contributing factor to maternal mortality and a major cause of perinatal morbidity and mortality (Klonoff-Cohen et al. 1989). Treating women who suffer recurrent miscarriages with seminal plasma also improves pregnancy success (Stern and Coulam 1993), and the risk of preeclampsia is reduced by repeated semen exposure over time (Klonoff-Cohen et al. 1989). Dekker et al. (1998) identified changes in "paternity" as playing a role in preeclampsia. Additionally, live birth rates in couples undergoing in vitro fertilization are significantly improved when they engage in intercourse prior to embryo transfer (Tremellen et al. 2000). In other words, pregnancies from a resident male are more successful and seminal plasma is a clear mechanism.

As would be expected following this model, men who attempt to prevent cuckoldry and

suspect that a pregnancy may not be theirs would likewise suspect children in the family may not be related to them and may in fact be cuckoldry in action. As a way to solve this problem of paternal uncertainty, males will look for cues to paternity and engage in postpartum investment strategies, detecting cues to certainty and making investments in children according to those cues.

Postpartum Investment Strategies

Just as during pregnancy, men may not believe the children in the home are theirs. According to the model, men unsure of their paternity may see children as evidence that insemination prevention strategies, counter insemination strategies, and pregnancy termination strategies have all failed. It is also important to note that men may be engaging in postpartum investment strategies with existing children, while engaging in any of the other strategies with the female partner at the same time. For example, he may be mate guarding his partner but also using cues from his children to make decisions about his children. He may also use cues from his children to make decisions about this partner, and vice versa (see below). A father may also have a higher paternity confidence with one child and lower with another, based on previous circumstances or partner behavior. But most of all, men will look to cues in the children themselves to determine investment, investing the most in those that provided the greatest paternal certainty. Paternal investment could range from significant investment, to indifference, neglect, abuse, abandonment, and even infanticide (Daly and Wilson 1996).

Using paternal resemblance as a cue and making investment decisions based on it is a significant postpartum investment strategy, an attempt to solve the problem of paternal uncertainty. Burch and Gallup (2000) asked abusive men to report how much they thought each child in their home resembled them, then asked questions regarding

child and partner investment. The more the abusive men thought a given child resembled them, the better they rated their relationship, and the better the child was treated. The more the men thought their children resembled them, the less violence and abuse they inflicted on their female partners as well, showing that these strategies and cues are interrelated.

Platak et al. (2002) created a more controlled study, but examining the reactions of male and female college students to morphed images of children's faces. The children's pictures were digitally morphed with either images of the subjects themselves or one of four other people of the same sex, then subjects were presented with hypothetical parental investment scenarios and asked to choose which child's picture they would invest in. Males chose their own morphed picture more often than females in almost every positive investment category and less often in almost every negative investment category. Platak et al. (2003) investigated whether this effect was caused by a greater ability in males to detect resemblance. There is no sex difference in the ability to detect resemblance, but males were far more likely than females to make investment decisions based on resemblance. Thus the literature overwhelmingly implicates a male specific effect of resemblance in child investment. Indeed, males who committed infanticide cited a lack of resemblance implying non-paternity as a reason (Daly and Wilson 1984). Resemblance has been implicated in the father/child relationship (Apicella and Marlowe 2004), with perceived child resemblance valued more highly by men (Volk and Quinsey 2002).

As evidence that these strategies are attempted solutions to paternal uncertainty, these male behaviors shift dramatically with knowledge of paternity. Burch and Gallup (2000) found that the presence of children that were explicitly *unrelated* to the male (e.g., children from a female's previous relationship or a stepchild) greatly increased the amount of violence in the home. In this situation, paternity (or nonpaternity in this case) is certain. Daly and Wilson assembled

cross cultural evidence showing that non-biological parents are as much as 100 times more likely to kill their children than biological parents (Daly and Wilson 1985, 1996, 1998).

Conclusion

Paternal uncertainty has an enormous and varied impact on male behavior and investment. This is just a brief overview of these paternal assurance strategies and how each has evolved to solve the problem of paternal uncertainty (each strategy can be, and is, reviewed in more detail, particularly ► [Sexual Jealousy](#), ► [Sperm Competition Theory](#), and ► [Resemblance](#)). Men use these strategies according to level of uncertainty, suspicion of infidelity, and other contextual factors (for example, a man may choose to not invest in any of his children, regardless of resemblance, and focus reproductive efforts on insemination and not child investment) as solutions to paternal uncertainty, attempting to maximize fitness by making the correct reproductive decisions.

Cross-References

- [Cuckoldry](#)
- [Fitness Benefits of Mate Guarding for Males](#)
- [Resemblance](#)
- [Sexual Jealousy](#)
- [Sperm Competition Theory](#)

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Somatic Maintenance

- ▶ [Darwinian Medicine and Survival Problems](#)

Somatosensory System

- ▶ [Proprioception](#)

Son/Daughter

- ▶ [Offspring Sex](#)

Soprano

- ▶ [Music and Hormones](#)

Sororicide

- ▶ [Siblicide](#)

Sound Generation

- ▶ [Distinguishing the Direction of Sounds](#)

Sound Perception

- ▶ [Evolution of Hearing and Balance](#)

Soundwaves Direction

- ▶ [Distinguishing the Direction of Sounds](#)

Sour

- ▶ [Taste](#)

Source Memory

- ▶ [Recall of Cheaters](#)

Source Memory Advantage for Faces of Cheaters

- ▶ [Memory Enhanced for Cheaters Versus Non-cheaters](#)

Southern Cultures of Violence

- ▶ [Culture of Honor and Nepotism](#)

Space, Time, and Number

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Synonyms

Numerical cognition; Quantity representation;
Spatial processing; Temporal processing

Definition

Representations of discrete and continuous quantities.

Introduction

How many cookies are on that plate? How big are they? How many seconds will it take to devour them? From infancy to adulthood and across human and nonhuman species, the ability to quantify space, time, and number has been shown to be critical for basic processes including foraging, language acquisition, and basic learning, but also for the acquisition of more complex processing such as formal mathematics. Because representations of time, space, and number are not tied to any one sensory modality (e.g., different durations, set sizes, or dimensions of space can be seen, heard, or felt), these quantities are uniquely abstract in nature and omnipresent throughout our daily experiences. While the ability to represent exact quantities symbolically (i.e., denoting quantity information using language (*four seconds*) or Arabic numerals (25.8)) does not occur until later in human life, the ability to represent these abstract quantities in an approximate nonsymbolic manner has been demonstrated in preverbal infants (e.g., Lourenco and Longo 2010) and in a variety of nonverbal nonhuman species (see Gallistel 1990), providing substantial evidence that these representations are not linguistically dependent. This entry highlights the key features of space, time, and number

representation, considering current proposals regarding the format of these representations.

Key Features of Space, Time, and Number

Adherence to Weber's Law

It has long been noted that temporal, numerical, and spatial quantity (i.e., length or area) discriminations adhere to Weber's law, such that the speed and/or accuracy of the discriminability of two values, be they durations, areas, or numbers, is dependent upon their ratio (e.g., Stevens 1957). For example, the ease with which a set of 10 items is discriminated from a set of 20 is comparable to the ease with which a set of 40 items is discriminated from a set of 80, since both comparisons involve a 1:2 ratio change. This ratio dependence of quantity discriminations has been demonstrated across a variety of nonhuman species (see Gallistel 1990) and across human development (see Feigenson 2005). To account for the Weber-like characteristic of quantity discriminations, it has been proposed that spatial, temporal, and numerical quantities (both symbolic and nonsymbolic) are represented via a noisy (i.e., imprecise) analog mental magnitude system (Meck and Church 1983). In the numerical cognition literature, this system is frequently referred to as the approximate number system or ANS (Feigenson et al. 2013).

Increasing Precision Throughout Development

Quantity discriminations obey Weber's law throughout development; however, evidence also reveals that the precision of these discriminations increases with age (e.g., Odic et al. 2013; Droit-Volet et al. 2008). In infancy, a comparable developmental trajectory for spatial, temporal, and numerical discriminations has been found, with 6-month-old infants consistently discriminating changes involving a 1:2 ratio change, but not a 2:3 ratio change, and 10-month-olds successfully discriminating a 2:3 but not a 3:4 ratio change for time and number (see Feigenson 2005). However, in older children, the ease with which these

quantities can be discriminated differs, with evidence suggesting that area acuity is higher than that of numerical acuity (Odic et al. 2013), with timing acuity being even lower (Droit-Volet et al. 2008). Given links between representational acuity and formal math abilities, it is important to understand the source of this developmental change, yet more work is needed.

Neural Activation

While some evidence demonstrates overlapping intraparietal sulcus (IPS) activation during estimation of time, space, and number (e.g., Dormal and Pesenti 2012), other studies provide evidence for distinct neural activations across these quantities (e.g., Mattell and Meck 2004). An overwhelming amount of evidence suggests that the IPS is relevant for numerical and spatial tasks. For example, when participants are asked to judge the numerosness of a display and/or the length of a line, then activation in the IPS occurs (Dormal and Pesenti 2012). It is not clear whether the IPS is implicated in timing though. In fact, substantial evidence from drug, lesion, clinical, and imaging studies in both rodents and humans points to the basal ganglia as the center of interval timing (see Mattell and Meck 2004), suggesting a neural dissociation between space, time, and number.

Despite evidence suggesting distinct neural activation patterns across representations of space, time, and number, there are striking comorbidities of temporal, spatial, and numerical deficits found in many disorders. For example, patients with genetic disorders such as Turner syndrome, fragile X, and chromosome 22q11.2 deletion syndrome also experience deficits in mathematical, spatial, and temporal processing (Vicario et al. 2013). Individuals with left neglect, a condition in which individuals struggle attending to or experience a lack of awareness of space, also exhibit difficulties accurately estimating time and show disrupted numerical processing (see Dormal and Pesenti 2012). Together, these consistencies across clinical populations hint at some degree of neural overlap.

Representing Small Versus Large Values: Two Distinct Systems

Substantial evidence points to breaks in the mental timeline and the mental number line, such that representations of smaller values may be represented in a distinctly different fashion than those of larger values (see Buhusi and Cordes 2011). Distinct neural activation patterns and different behavioral patterns when timing short (subsecond; i.e., <1 s) compared to long (suprasecond) durations in both animals and humans have suggested the presence of two separate timing systems (Gooch et al. 2011). Relatedly, there is also evidence that number is represented via two distinct systems: one for small sets (less than 4 or 5) and another for large sets (>4 or 5). Separate neurological structures have been implicated during estimation of small relative to large sets (Ansari et al. 2006). Most strikingly, substantial behavioral data reveal remarkable dissociations when young infants discriminate small from large sets (see Posid and Cordes 2015). There is no evidence to date, however, in support of distinct systems for representing small and large spatial extent.

Cross-Domain Interference

Other work has explored how these quantity representations may be altered by the presence of other quantitative information (a question of the relative dependence of quantity representation; see Dormal and Pesenti 2013). Results of these studies have generally revealed adult abilities to track spatial, temporal, or numerical information to be altered by the presence of other numerical and spatial information, but not temporal information (e.g., Dormal et al. 2006; Merritt et al. 2010). For example, Dormal and Pesenti (2013) designed a three-dimensional Stroop task in which participants were presented with two arrays of dots, which differed in number of dots, spatial extent (length of the array), and duration of presentation. Participants were either asked to judge (1) which array was more numerous, (2) which was physically longer, or (3) which was presented for the longer duration (between subjects). Results revealed that both the relative numerosness and

length of the arrays significantly interfered with temporal judgments. Temporal cues, however, did not significantly impact either numerosity or length judgments (Dormal and Pesenti 2013).

Cross-Domain Transfer

A number of studies have reported spontaneous cross-domain transfer, in which animals, preverbal infants, and adults have spontaneously applied rules learned in one quantitative domain to a novel quantity. Cross-domain transfer has been shown as early as infancy (e.g., Lourenco and Longo 2010) and across nonhuman species (Meck and Church 1983). The first evidence of cross-domain transfer was demonstrated when rats were trained to discriminate between two distinct durations (2 s vs. 8 s). During the test trials, rats were presented with ambiguous stimuli that were always 4 s long (the geometric mean of the two trained standards), but varied in number. The rats spontaneously responded on the task as if they had originally been trained with numerical stimuli, classifying stimuli involving larger numbers in the same way in which they originally classified longer durations, producing overlapping response distributions for temporal and numerical judgments (Meck and Church 1983). More recent studies with human infants have also revealed the spontaneous generalization of a pattern or rule in one domain (i.e., increasing numerical values) to another domain (i.e., increasing line lengths). For example, when infants were shown that larger objects had certain features (i.e., objects were black with stripes) relative to smaller objects (i.e., objects were white with dots), infants expected this rule to generalize to numerosity and duration (Lourenco and Longo 2010). It has been argued that these findings suggest that infants treat time, space, and number as falling along a single dimension.

Other work on cross-domain mappings has pointed to a privileged relationship between space and number. Some work suggests that number may be inherently mapped in an increasing order from left to right. The Spatial Numerical Association of Responses Codes (SNARC) effect, a phenomenon in which smaller numerical values

are associated with the left and larger numerical values are associated with the right, has been demonstrated in children and adults (Dehaene et al. 1993). For example, when asked to judge the parity of a digit (odd/even), participants are faster to respond with the left hand when the numerical value of the digit is small compared to when it is large and faster to respond with the right hand when the numerical value of the digit is large compared to when it is small (Dehaene et al. 1993). Although this SNARC effect seems to track with the direction of reading in the culture, such that individuals in cultures that read from right to left exhibit a reverse SNARC effect (Dehaene et al. 1993), more recent work has suggested that the SNARC effect may not be culturally dependent and instead reflect evolutionarily derived natural proclivities. For example, Rugani et al. (2015) trained chicks to retrieve food from behind a panel depicting an array of dots, always with the same standard number (5). Then, during test, the chicks were presented with two side-by-side panels, both displaying the same set size (i.e., 10 dots). When the number of dots on the card was larger than the trained standard, chicks were significantly more likely to retrieve food from behind the right panel. On the other hand, when the number of dots on the card was smaller than the trained standard, chicks were more likely to go to the left panel. This robust pattern provides some of the first evidence to suggest that number, even in nonhuman species, may be represented in a left-to-right orientation in the mind.

Basic Quantitative Processing and Academic Achievement

A significant amount of work has shown a relationship between our approximate sense of number and formal math abilities (for a review, see: Feigenson et al. 2013, but also see: Gilmore et al. 2013). The predictive relationship between numerical acuity and math achievement appears to be bidirectional, with preschoolers' numerical acuity predicting math abilities at age 6 and formal math abilities in kindergarten predicting numerical acuity at 14 years of age (see Feigenson

et al. 2013). While most of this work is correlational, some training studies have pointed to a causal relationship between our approximate number system and formal math abilities (e.g., Wang et al. 2016).

The strength of the relationship between numerical acuity and math achievement, relative to that of other numerical abilities and math abilities, has been called into question, however (e.g., Gilmore et al 2013; Skagerlund and Traff 2015). For example, Skagerlund and Traff (2015) investigated basic quantity processing and formal math abilities in 8–10-year-olds and found that symbolic number comparison, but *not* nonsymbolic numerical discrimination, predicted formal math abilities. The authors suggest that once children become comfortable with the symbolic nature of mathematics, the importance of the approximate number sense becomes less indicative of formal math ability.

Spatial abilities, including mental rotation and quantitative spatial tasks, are also predictive of formal math abilities (for a review: Mix and Cheng 2012). In one study, adults completed an approximate number judgment task, an approximate surface area judgment task, and a set of standardized math assessments. Results revealed that adults' abilities to discriminate both number and surface area were correlated with formal math abilities (Lourenco et al. 2012). Other work ties spatial processing specifically to mathematical equation solving (Skagerlund and Traff 2015).

Most recently, timing abilities have also been linked to formal math achievement (e.g., Skagerlund and Traff 2015). For example, temporal discrimination abilities have been found to predict calculation skills in children (Skagerlund and Traff 2015). However, the link between nonsymbolic magnitude processing and mathematical abilities is not robust (see Agrillo et al. 2013), and thus more work is needed to fully understand the relationship between basic quantitative processing – including nonsymbolic temporal, spatial, and numerical processing – and formal mathematics.

Does a Common Magnitude System Exist?

Some researchers have suggested that a single common cognitive system may be responsible

for processing space, time, and number (e.g., Meck and Church 1983; Walsh 2003), in which spatial, temporal, and numeric magnitudes may be processed identically within a single neural locus. Proponents of a common magnitude system have cited identical behavioral signatures (i.e., adherence to Weber's law), common developmental trajectories, some evidence of neural overlap, cross-domain transfer, and quantity interference as support in favor of a single quantity processing system (e.g., Walsh 2003).

Despite the remarkable similarities across spatial, temporal, and numerical processing identified, other researchers have identified a number of inconsistencies calling into question the idea of a common magnitude system. For example, despite seemingly similar discrimination patterns across infancy, other work has revealed dissociations between temporal, numerical, and spatial discrimination abilities across individuals (e.g., Odic et al. 2013; Young and Cordes 2013). Moreover, the relatively limited evidence in support of neurobiological overlap across representations of quantity, striking dissociations across temporal and numerical biases (Young and Cordes 2013), and findings suggesting that spatial, temporal, and numerical abilities may each uniquely predict (or not) distinct aspects of formal math abilities (Agrillo et al. 2013; Skagerlund and Traff 2015), have caused some to rethink claims of a common system. As such, it has been posited that space, time, and number may instead be represented by three distinct, yet similar, cognitive systems.

More recently, Newcombe (2014) suggested an alternative to the common magnitude account in which development may begin with reliance upon a single system; however, over the course of development, the system diverges into three (or more) separable systems later. Findings of comparable spatial, temporal, and numerical acuity in infancy but not childhood provide support of this notion (see Feigenson 2005; Odic et al. 2013). Further, the substantial evidence of cross-domain transfer in preverbal infants, incapable of verbalizing their strategies on the task, points to the presence of a single magnitude system (Lourenco and Longo 2010). More work is needed to assess the plausibility of a developmental divergence model. Future

work may employ developmental designs to confirm the overlap in space, time, and number in infancy and determine at what point in development these quantities are no longer represented by a common system. Even if a common magnitude system is present in infancy, the implications of such a system are unclear. Are there benefits for representing space, time, and number with a single system? Does using a single system to process quantity free up other cognitive resources for the purposes of other processes? What would provoke divergence across development?

Conclusion

Whether we are choosing the single largest cookie, picking the plate with the most cookies, or estimating how long it takes us to devour the treats; space, time, and number shape our daily life. These quantities adhere to Weber's law and follow similar developmental trajectories, at least in infancy. Further, cross-domain transfer and interference suggest commonalities between magnitude representations. Important differences in these representations do exist, such that unique neural activations are related to specific quantities and emotions impact quantities differentially. In addition, each quantity appears to predict different aspects of formal math. While prominent theories posit that quantities are represented by a common magnitude system (e.g., Walsh 2003), others contend that the evidence supports the existence of separate systems (Agrillo et al. 2013; Odic et al. 2013). Opportunities for research in the realm of space, time, and number are rich as they will continue to inform our understanding of quantity processing, both in the service of understanding the basic processes these quantity representations subserve and in understanding the link to formal mathematical understanding.

Cross-References

- [Cognitive Development](#)
- [Quantity Estimation](#)
- [Spatial Reasoning](#)

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Spandrel

- [By-Product](#)
- [By-Products of Adaptations](#)
- [Evolutionary By-Products](#)

Spandrels

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Synonyms

[Historical contingency](#); [Nonadaptive hypotheses](#)

Definition

In evolutionary biology, an unnecessary adaptive hypothesis for the presence of a trait that is better explained using different levels of analysis.

Introduction

As the field of evolutionary biology and, in particular, behavioral ecology flourished in the 1960s and 1970s, some practitioners became concerned with a perceived over-exuberance in seeking adaptive explanations for every trait and behavior. In “The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme”, Gould and Lewontin (1979) discussed the limits of natural selection in explaining the function of organismal phenotypes. This influential paper launched a debate about how biologists should ask questions that continues to this day.

In “Spandrels,” Gould and Lewontin proposed that the misuse of and overreliance on adaptive hypotheses for the function of traits stemmed from two related problems. First, they argued against an over-dissection (“atomizing”) of organisms into individual components to be studied in isolation rather than as part of a connected whole. Second they believed that hypotheses based on historical contingencies or developmental constraints were rarely considered as legitimate alternatives to explanations based on naturally selected function. A consequence of these perceived shortcomings was that it became difficult

or impossible to reject a functional (i.e., argument based upon a naturally selected fitness advantage) explanation for the presence of a trait, since when researchers failed to find support for one functional hypothesis, they were tempted to assume the correct functional hypothesis had yet to be tested, rather than considering nonadaptive hypotheses. Gould and Lewontin proposed that integrative studies (which they link to the idea of a bauplan, the organismal blueprint or assemblage of traits that make up a generalized body plan) that emphasize the way traits comprise the design of a whole organism – how it is built over developmental and evolutionary time – are more appropriate for finding and testing these alternatives.

By way of analogy, these authors open “The spandrels of San Marco” with a description of a grand cathedral containing spandrels, architectural elements at the junction of perpendicular arches supporting a dome (Gould 1997). These features are frequently embellished and elaborated, which could lead to functional interpretations for the existence of spandrels that rely on their decorative nature. However, Gould and Lewontin argue that spandrels are best explained as necessary by-products of the structural connection of two arches and can therefore only be fully understood by considering the engineering and construction requirements of the dome as a whole. This has led to the term “spandrel” in evolutionary biology as shorthand for the application of a (potentially incorrect) functional explanation for a trait’s existence that can be (better) explained at another level of analysis.

The publication of “The spandrels of San Marco” prompted a range of responses that included rhetorical critiques, substantive arguments, and even accusations that the “Spandrels” paper was a politically motivated attack on human sociobiology (Borgia 1994; Queller 1995). These replies found “Spandrels” too divisive while minimizing the powerful role of natural selection that most evolutionary biologists accept. While in most cases the rhetorical attacks have subsided, debates about the primacy of functional explanations for adaptations continue. For example,

“adaptationists” (e.g., Reeve and Sherman 1993) tend to place more emphasis on searching for functional advantages conferred by traits while also stressing that functional hypotheses are complementary and not alternatives to hypotheses pitched at mechanistic, developmental, or historical levels of analysis. Importantly, they refute a major premise of “Spandrels” – that behavioral ecologists view all traits as optimally designed. In turn, others (e.g., Autumn et al. 2002) have refined the scientific arguments put forward in “Spandrels” to advocate for an explicitly integrative view of the study of adaptations. As an example, consider the preference of female túngara frogs (*Physalaemus pustulosus*) for males that produce lower-frequency “chuck” calls. Although females benefit from this behavior by obtaining increased fertilization success from mating with larger males with lower-pitched calls, nonadaptive explanations based upon mechanism and phylogenetic history suggest that current functional advantage is unimportant for understanding female preference for lower-pitched calls. Specifically, the female preference for “chucks” and patterns of auditory sensitivity that result in better detection of lower-frequency chucks appears to have evolved prior to the evolution of the “chuck” calls themselves (reviewed in Autumn et al. 2002).

Additional debates focus on the proper form of null models for studies of trait evolution. For example, are there null expectations for the evolution of sexually selected traits and their corresponding preferences that can be seen as nonadaptive (Prum 2010)? Null or neutral models have become central to other biological disciplines such as population genetics and ecology (e.g., Hubbell 2001); in some ways, the “Spandrels” critique can be seen as a precursor to this conceptual development in behavioral ecology.

Conclusion

Although rhetorically unsavory and scientifically unconvincing to many, “The spandrels of San

Marco” served as a warning for behavioral ecologists to ensure their hypotheses are falsifiable, and that nonadaptive hypotheses based on mechanism, developmental constraint, or history should be considered when appropriate functional hypotheses fail to find support. These propositions are not controversial. However, debate continues as to how often we expect existing traits to offer a fitness advantage, and whether demonstrating a fitness advantage is sufficient to suggest that a trait is an adaptation.

Cross-References

- [Adaptations: Product of Evolution](#)
- [Biological Function](#)
- [Maladaptations](#)

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Spanking

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Synonyms

[Corporal punishment](#); [Lashing](#); [Paddling](#); [Physical discipline](#); [Physical punishment](#); [Smacking](#); [Swatting](#); [Whipping](#)

Definition

Spanking is a form of corporal punishment. The United Nations Committee on the Rights of the Child defines spanking as a form of punishment that uses physical force with the intent to cause pain or discomfort (2007). Merriam-Webster online dictionary defines *Spank* (n.d.) as a verb as striking someone with an open hand (often on the buttocks; e.g., she would spank him for misbehaving). Spank as a noun is defined as the actual strike on the buttocks itself (e.g., he received a quick spank).

Introduction

Spanking is a form of corporal punishment or physical discipline that is sometimes used by parents, caregivers, and even educators as a tool for addressing inappropriate behavior. It is often used to reduce undesirable behaviors and encourage more appropriate behaviors. It is a form of discipline that has been around for thousands of years and has been used across countries and continents. The effectiveness of spanking is often hotly debated, as is its potential to change from physical discipline to physical abuse. Historically, deference to parental authority contributed to society’s lack of opinion or intervention regarding spanking. However, as children’s rights were recognized and documented, corporal punishment was examined more closely, and the use of spanking

began to be questioned. There are several studies that have examined topics such as the long- and short-term impact of spanking on children, factors that contribute to the use (or not) of spanking as a discipline strategy, and alternative discipline interventions that more effectively address undesirable behaviors. In more recent years, corporal punishment, including spanking, has been considered a public health issue due to the various negative health outcomes that have been associated with it (Gershoff and Grogan-Kaylor 2016). This speaks to the current critical need for parental education about the effects of spanking on children and alternative discipline strategies.

A Historical Perspective

Historically, across civilizations, child protection was not considered a governmental issue but rather was left to individual families. The administration of discipline of children was assumed to be the role and right of the parent. In the United States, animal protection laws preceded and contributed to the development of child protection laws (Lebow and Cherney 2015). In general, societies believed that it was a family's right to determine how to discipline their children, which made individuals hesitant to interfere or intervene. In some countries, this view has largely persisted; however, in other countries, there have been bans on corporal punishment, including spanking.

In 2008, Gershoff compiled a comprehensive document, *Report on Physical Punishment in the United States: What Research Tells Us About Its Effects on Children*, on the status of spanking and its effects on youth. The report provides comprehensive review of the existing literature (at that time) on the effects of physical punishment, including spanking, on children. The document was created to provide information for a variety of individuals who care for, interact with, provide services to, develop services for, or in some way impact children. It was also created for the children themselves. Gershoff's (2008) synthesizing of the literature revealed four distinct conclusions (p. 7):

- There is little research evidence that physical punishment improves children's behavior in the long term.

- There is substantial research evidence that physical punishment makes it more, not less, likely that children will be defiant and aggressive in the future.
- There is clear research evidence that physical punishment puts children at risk for negative outcomes, including increased mental health problems.
- There is consistent evidence that children who are physically punished are at greater risk of serious injury and physical abuse.

As will be illustrated, Gershoff's (2008) findings are still relevant and consistent with findings from research that has since been conducted. It begs the question then, why is spanking still an accepted discipline practice? Do the perceived benefits outweigh the empirically based negative implications of spanking?

Theoretical Framework

There is one theory that has emerged in research to provide understanding about the use of spanking or corporal punishment as a discipline practice, despite overwhelming evidence that suggests it is not an effective tool. The *Theory of Planned Behavior* (TPB) essentially suggests that an individual's intentions and behaviors are a function of three factors: one being personal, one tied to social influence, and the final related to control (Ajzen 2005, p. 117). The personal aspect is one's "*attitude toward the behavior*," be it positive or negative, while the social influence aspect relates to "perception of social pressure to perform or not perform the behavior" (Ajzen 2005, p. 118). So, an individual who was spanked and perceives that they "turned out okay" might view spanking as an acceptable form of discipline. The third element is "*perceived behavioral control*," or the "...sense of self-efficacy or ability to perform the behavior of interest" (Ajzen 2005, p. 118). The individual believes that they are capable of and have opportunities to engage in a behavior. For example, a parent may intend to use spanking as a form of discipline when they view it positively, see it as effective, believe it to be an acceptable practice (e.g., their own experiences, friends who use spanking to discipline), and feel confident they

can use spanking to discipline their child. Generally, when a parent expects positive outcomes from using spanking (e.g., respect from child, improved child behavior), this predicts a more favorable attitude towards spanking and an increased likelihood of using spanking as a form of discipline. Similarly, perceived social support for spanking (e.g., personal experience and outcomes; or local, familial, or cultural norms or acceptance) can also influence the likelihood of using spanking (Taylor et al. 2017).

In a recent study, Flemming and Borrego (2019) surveyed undergraduate students to examine if discipline acceptability could influence the effect of past discipline experiences on future discipline intent; both aggressive and positive discipline practices were evaluated. Acceptability of aggressive discipline practices was indeed found to affect the relationship between discipline experiences and intent. This was also true for positive discipline practices, though a direct effect between positive discipline experiences and intentions suggests that additional factors may also influence the relationship between these two constructs. The findings of this study suggest that TPB is a useful framework for exploring and understanding the use of corporal punishment or spanking, as well as identifying prevention and intervention strategies.

What Is Spanking?

The definition of spanking is inconsistent across entities and researchers, creating challenges in accurately measuring it. Further complicating matters, different terms are sometimes used interchangeably with spanking, such as corporal punishment or smacking. The United Nations (2007) defines corporal punishment as “any punishment in which physical force is used and intended to cause some degree of pain or discomfort” (p. 4). The expanded definition includes the use of an implement (e.g., a whip, stick, belt, or wooden spoon), physical aggression (e.g., pinching, kicking, biting), and other severe and degrading behaviors (e.g., burning, forced ingestion of a substance). Alternatively, some researchers define spanking as non-injurious,

open-handed hitting of the extremities or buttocks with the intention of modifying child behavior (Gershoff and Grogan-Kaylor 2016). These varying definitions complicate discussions about physical punishment. A helpful definition is to consider spanking a form of physical discipline or corporal punishment that uses physical force with the intention of causing a child to experience pain but not injury for the purpose of correcting inappropriate behavior. Spanking is usually differentiated from physical abuse in that physical abuse is use of excessive force that results in injury. However, guidelines for what constitutes *injury* and *excessive force* are often unclear.

Prevalence of Spanking

UNICEF (2014) compiled data on violence against youth, including corporal punishment, from over 190 countries in its publication *Hidden in plain sight: A statistical analysis of violence against children*. The report states that physical discipline from caregivers, including spanking, is experienced by roughly 6 out of 10 children between the ages of 2 and 14 worldwide (p. 97). Spanking was found to be the most common form of physical discipline with about 44% of youth experiencing it. Children ages 5–9 were the most likely to experience violent discipline (which includes violent psychological aggression), though both younger children (ages 2–4) and older children (ages 10–14) were still highly likely to experience some type of physical discipline. It is important to point out that the majority of youth experience both violent discipline and nonviolent discipline (e.g., explaining why behavior is wrong, taking away privileges, redirecting the child).

The International Dating Violence Study gives additional insight into the disciplinary practices of 32 nations. The average amount of adults who recall receiving corporal punishment “a lot” before age 12 was 52.3%. (This data probably does not reflect rates for ages below 5, of which adults have few memories). Taiwan, Tanzania, and South Africa reported rates of corporal punishment over 70%, while New Zealand, Belgium, and the Netherlands were under 20% (Straus et al. 2014).

In the United States, spanking is also a common childhood experience. Corporal punishment in the home is legal, and corporal punishment in the school context is legal in 19 of the 50 states (Global Initiative to end all Corporal Punishment of Children [Global Initiative] 2020b). It is estimated that more than 90% of parents in the United States spank or slap toddlers, with over 30% of these parents reporting the spanking of infants. Spanking continues at a rate of over 50% until age 12 and only drops to 25% by age 16 (Straus et al. 2014). Unfortunately, there is evidence that the majority of substantiated cases of abuse in the United States occur within the context of spanking to correct behavior (Gershoff and Grogan-Kaylor 2016; Straus et al. 2014).

To Spank or Not to Spank: Effects of Spanking

The harmful effects of spanking have been the focus of intense research for several decades. Determining a cause and effect relationship is difficult as experimental designs would often be unethical, and much of the research which examines the effects of spanking is correlational. However, several meta-analyses reviewed many of these studies (e.g., Gershoff and Grogan-Kaylor 2016). There are also longitudinal studies which provide stronger evidence of the relationship between spanking and other externalizing and internalizing behaviors (e.g., Gershoff and Grogan-Kaylor 2016; Mulvaney and Mebert 2007). Overall, the research confirms the association of corporal punishment with increased externalizing and internalizing behaviors. Gershoff and Grogan-Kaylor's (2016) meta-analysis attempted to differentiate between open-handed spanking and more severe forms of physical punishment, and still spanking was associated with more aggression, antisocial behavior, externalizing and internalizing problems, mental health problems, and lower cognitive ability. Additionally, the negative outcomes for corporal punishment are similar in magnitude and direction with physical abuse (Gershoff and Grogan-Kaylor 2016; King et al. 2018).

Externalizing Effects

Corporal punishment, including spanking, is associated with increases in aggression and other externalizing problems such as lying, bullying others, property damage, and cheating (Straus et al. 2014). Immediate compliance and self-control have had a small but positive association with corporal punishment in a few North American studies; however, similar results are also gained through nonviolent disciplinary tactics such as time-outs (Gershoff and Grogan-Kaylor 2016; Straus et al. 2014).

Several longitudinal studies demonstrate increased odds for aggression and antisocial behavior later in childhood, adolescence, and adulthood across North America, Europe, and Asia (Rebellion and Straus 2017; Mulvaney and Mebert 2007). Indeed, these associations remain even after accounting for moderating variables such as race, difficult child temperament, maternal depression, and family income. Research confirms a dose-response relationship. That is, the more frequent the spanking, the higher the odds of externalizing issues (Afifi et al. 2006). In contrast, children who experience no corporal punishment tend to be better behaved, have better relationships with their caregivers, and are less likely to commit crimes or experience addiction (Straus et al. 2014).

Internalizing Effects

According to one US study (Afifi et al. 2012), 2–5% of Axis I disorders (such as major depressive disorder and generalized anxiety disorder) and 4–7% of Axis II disorders (such as borderline or narcissistic personality disorder) can be attributed to the effects of harsh physical punishment (e.g., being pushed, grabbed, shoved, slapped, or hit) even when adjustments are made for family dysfunction and sociodemographic variables such as race and level of education. Similarly, Afifi et al. (2006) found increased odds of experiencing major depression, alcohol abuse, or alcohol dependence. This suggests that corporal punishment practices are potentially inconsistent with the promotion of mental health and well-being. While these findings are from one study, they highlight the importance of considering both the

(potential) short- and long-term impacts of corporal punishment.

Cognitive Effects

Research has found that spanking, and other forms of corporal punishment, increases the odds of lower academic achievement and is associated with failing to keep up with average development of cognitive ability (Straus et al. 2014). It is thought that corporal punishment is a frightening and threatening experience for children that occurs over a long period of time. This stress may disrupt cognitive growth. Furthermore, parents who regularly use spanking as their main form of discipline may be less likely to use cognitive-enhancing verbal explanations when punishing (Straus et al. 2014). Data from the National Longitudinal Study of Youth suggests that young children who do not experience corporal punishment between ages 2–4 increase cognitive ability faster (when assessed 4 years later) than those who have not been spanked (Straus and Paschall 2009). Examining the effects on cognitive ability from a different perspective, Mackenzie et al. (2013) found a negative association between paternal corporal punishment at age 5 and receptive vocabulary in children at age 9. Their longitudinal study also found that spanking at age 1 predicted lower Bayley mental development scores at age 3 (Mackenzie et al. 2013). The research examining the impact of spanking and related corporal punishment indicates that, contrary to popular belief, spanking young children can indeed be harmful to children both in their emotional and cognitive development.

Cultural Considerations on Spanking as a Disciplinary Practice

Cultural factors are important to consider regarding the use of spanking by parents. Many aspects of culture have been researched regarding potential impact on the frequency of use of spanking, as well as on the outcomes of spanking for children. Understanding the relationship between spanking and culture is complex and difficult due to a

multitude of factors, including how researchers define relevant terms such as corporal punishment, spanking, and culture, as well as how confounding variables like socioeconomic status, high-risk populations, education level, and domestic violence may influence research (Gibson and Fagan 2018; Ragavan et al. 2019).

Despite these complicating factors, most literature agrees that spanking is still a frequently used disciplinary technique by parents around the world. Ripoll-Nunez and Rohner (2006) found that 75% of the world's societies use corporal punishment at least occasionally, although the frequency with which spanking is used varies greatly, with only 20% of societies using it often. Research also shows that the negative effects of spanking can be generalized across all countries and societies. In a study of 62 countries, 59 had a negative relationship between the use of spanking and socioemotional development (Pace et al. 2019). Among both high- and low-income countries, spanking is shown to be associated with internalizing and externalizing behavior problems, although the strength of this association appears to be weaker in countries where spanking is more culturally normative (Lansford 2010; Lansford and Dodge 2008; Pace et al. 2019; Wang et al. 2018). This weaker correlation with detrimental outcomes for children may be explained in part by a cultural normativeness perspective, which purports that negative effects may be lesser because a child perceives that spanking is widely accepted in their cultural group. Hence, being spanked may not signify that they are being rejected by their parents or treated in an unduly harsh way (Gershoff and Grogan-Kaylor 2016). Noteworthy, however, is research that also suggests that there is a global association between more frequent use of spanking in a culture and higher levels of societal violence (Lansford 2010; Lansford and Dodge 2008).

Other cultural factors have been shown to predict use of spanking. Household composition is one such factor, where single-parent households are more likely to use corporal punishment than extended-family households (Ripoll-Nunez and Rohner 2006). Immigrant status may also influence likelihood to spank. Ragavan et al. (2019)

report that Latino mothers are less likely to spank if they are first-generation immigrants. This may be because they have had fewer adverse childhood experiences, because they were spanked less themselves (e.g., immigrated from countries where spanking was less normative), or because they have more community- and relationship-level buffers like social support. Religious factors can also influence use of spanking. In the West, conservative Protestantism supports the use of corporal punishment and can even suggest that a parent refraining from the use of spanking may be detrimental to the child (Ripoll-Nunez and Rohner 2006). Furthermore, in Eastern and Western societies alike, the use of corporal punishment is shown to be transmitted across generations. For example, Wang et al. (2018) studied the intergenerational transmission of parenting in Chinese families, where corporal punishment has long been the norm. The intergenerational transmission of parenting is the process (either intentional or unintentional) whereby an earlier generation psychologically influences the parenting attitudes and behaviors of the following generation. This transmission of corporal punishment across generations may be universal in both Western and Eastern societies. People who experienced corporal punishment as children are more likely to approve of the use of spanking as a disciplinary technique and are therefore more likely to employ this technique themselves when faced with their child's misbehavior (Wang et al. 2018).

Within the United States, in particular, culture also plays an important role in understanding the frequency, effects, and prevention of spanking as a disciplinary technique. Much of the research shows that cultural groups tend to influence the frequency with which parents use spanking. In some cultural groups, including the American South, lower SES families, and conservative Christian Evangelical Christianity, spanking is found to be more normative (Lansford and Dodge 2008). Additionally, many studies indicate greater use of corporal punishment in Black families than in White families (Gershoff and Grogan-Kaylor 2016). Data is conflicted regarding the use of spanking in Latino families, with some studies reporting as high as 73% of Latino families using

spanking (e.g., Klevens et al. 2019), and some reporting rates of spanking in Latino families to be less than that of White families (e.g., Ma and Klein 2018). Differences in the use of corporal punishment between racial and ethnic groups have been found to be associated with parental stress, parents' cognitive-emotional processing of children's misbehavior, negative perceptions of the child, beliefs regarding the effectiveness of corporal punishment, the level of importance placed on obedience, and positive attitudes regarding corporal punishment (Klevens et al. 2019). For example, in many Black families, the cultural value of deference to adults is highly esteemed, and therefore, corporal punishment can be considered necessary to correct disrespect. Furthermore, in the United States, a national history of racial discrimination and institutionalized social and economic segregation of Black communities may influence Black parents in low-income neighborhoods to employ parenting techniques such as spanking in order to better prepare their children for the environmental challenges and physical dangers they may face. Other researchers have found that, in Hispanic families, cohesiveness, respect, family harmony, and the mother's role as a caring and nurturing parental figure are highly esteemed values that may contribute to the reported lower rates of spanking in some studies (Ma and Klein 2018).

However, regardless of how culture affects the frequency of spanking among various racial or ethnic groups, most of the literature concludes that the detrimental effects of spanking on children remain consistent (Ma and Klein 2018). Gershoff et al. (2012) studied four racial or ethnic groups in the United States (Hispanic, Asian, White, and Black) and found that, despite differences in the frequency of use of spanking, there were no differences in how spanking predicted an increase in children's behavior problems. Growing research continues to highlight the similarities, not differences, in the association between spanking and adverse child outcomes. This data for cultural groups within the United States appears to contradict cultural normativeness theory, as spanking is associated with the same negative outcomes for all children, regardless of racial or ethnic differences (Gershoff and Grogan-Kaylor 2016).

Alternative Strategies

Regardless of the reason for the use of spanking (e.g., personal history, cultural, contextual), a robust body of research has demonstrated both the ineffectiveness of spanking, as well as the potential harm it can cause. Despite this, parents and even school staff continue to use spanking as a disciplinary practice. This signifies the need for general education and support in identifying positive discipline practices that are effective and support child development. Parents and others who work with children would benefit from education about the potential short- and long-term effects of spanking, as well as alternative nonviolent discipline practices that have demonstrated effectiveness in addressing behavioral issues. Schools that use corporal punishment would also benefit from this information. Finally, families and educators would benefit from preventative strategies that aim to teach desired behaviors and coping skills.

Build Knowledge and Awareness

Research shows that people are more likely to use corporal punishment if they believe that professionals approve of its use (Taylor et al. 2018). Therefore, professionals such as pediatricians, clergy, and mental health clinicians can play a significant role in providing guidance about child discipline practices. These professionals can help to educate parents at office, clinic, or home visits in ways that are culturally sensitive and empirically informed (Gershoff and Grogan-Kaylor 2016). Pediatricians are especially well-poised to provide guidance on child discipline and can give input on the latest research findings regarding the effects of spanking, providing empirically based information rather than personal perspective, on this issue.

These professionals should have the training to provide parents with accurate information regarding the effectiveness, or lack thereof, of spanking, potential outcomes of spanking, typical child development and the impact of spanking, and alternative appropriate disciplinary techniques. Positive alternatives to corporal punishment can include strategies to reinforce (and increase) the

desired behavior, such as clarifying expectations and consequences beforehand and praising for good behavior; and strategies to reduce the undesired behavior such as redirection, removal of dangerous objects, ignoring the behavior, reasoning, taking away privileges, and time-outs to address the undesirable behaviors (Klevens et al. 2019).

Early Education and Intervention

Changing the expected outcome of spanking is also critical to decreasing its use (Taylor and Hamvas 2011). This can be accomplished in a variety of ways. At prenatal and newborn visits, healthcare providers can give information regarding the potential harms of spanking, particularly for 1-year old children (Ragavan et al. 2019). Additionally, providers can create spanking prevention anticipatory guidance interventions which help guide discussions on positive parenting, the harms of spanking, and even in-office training on appropriate discipline choices like time-outs (Ragavan et al. 2019; Sege et al. 2018). Wang et al. (2018) suggests that prevention should also specifically focus on targeting parents who received corporal punishment themselves as children. Exploring and modifying beliefs regarding parental childhood experiences and expected outcomes of spanking may reduce intergenerational transmission of corporal punishment. Teaching parents that corporal punishment is ineffective and possibly harmful for child development, as well as supporting them in the learning and mastery of more appropriate and effective alternative disciplinary methods, could prove to be uniquely effective in reducing the approval of and use of spanking as a parenting technique (Wang et al. 2018). Evidence suggests that these types of parent education interventions are effective in reducing the use of spanking by parents in diverse cultures within the United States, as well as in countries around the world (Gershoff and Grogan-Kaylor 2016).

Gershoff et al. (2017) conducted a review of promising programs and strategies that can be used to change parents' use of physical punishment, such as spanking. One program the authors identified for parents with young children

(suggested ages 1 through 7) is *Play Nicely*. *Play Nicely* is an interactive multimedia program that originally was developed for parents to use in a clinic or primary care setting but now is available online (website: play-nicely.org). The program uses short educational videos (ranging from roughly 5–10 min) that include common parent-child conflict issues and asks users to choose the best solution from a menu of options that includes both physical (e.g., spanking) and nonviolent forms of discipline; feedback is given about the response (e.g., great option, there are better options). In a review of the literature, Gershoff et al. (2017) found that parents who completed the Play Nicely program were less likely to endorse spanking and less likely to have an intention to use spanking in their discipline practices.

Laws and Social Norms

Finally, enacting legal reform and changing social norms can also be effective strategies in the effort to reduce and prevent the use of spanking (Lansford 2010). Perceived social norms are the strongest predictor of having a positive attitude towards spanking (Sege et al. 2018). In order to change social perception of the acceptability of corporal punishment, many countries worldwide are moving to outlaw spanking as a parenting practice. Legal bans on spanking are currently present in 54 countries. Research has shown that bans are correlated with reduction in use by caregivers (Pace et al. 2019). In many cases, the primary purpose of legal banning is not to criminalize parents' behavior but to shift public perception and understanding (Ripoll-Nunez and Rohner 2006). Countries such as Sweden and Finland have accompanied their laws prohibiting spanking with national campaigns to decrease the perceived social acceptability of spanking (Global Initiative 2020a; Ripoll-Nunez and Rohner 2006). However, some argue that given the continued support for spanking in the United States, as well as the fact that the United States is the only country not to ratify the UN Convention on the Rights of the Child, a legal ban on spanking may not be a likely method of reducing the use of corporal punishment within the United States

(Gershoff and Grogan-Kaylor 2016). Mass media campaigns, though, show great promise for shifting public approval of corporal punishment. For example, the Triple P – Positive Parenting Program – is a multitiered intervention which includes a public education campaign (Gershoff and Grogan-Kaylor 2016). Triple P – is used in more than 25 countries and has been shown to be effective across cultures, socioeconomic groups, and household structures.

Conclusion

Spanking is a complex and often controversial issue and is a topic that many people have strong opinions about. In fact, it is a topic that can be polarizing within families and among friends. The controversy surrounding spanking can create challenges in having productive conversations about whether or not spanking as a discipline practice should be supported or condemned. Many individuals might believe that it is a parent's decision and not to be commented upon by outsiders, while others might believe that it should be a community decision. Still others, such as some religious schools, deem it their right, and even responsibility, to use spanking or other forms of corporal punishment as a means of discipline.

The research examining spanking and corporal punishment illustrates the potential for a negative impact with relation to externalizing behaviors, internalizing behaviors (e.g., social and emotional development), and cognitive development and growth. These negative outcomes can occur and persist both in the short-term and over the long-term. It is critical that empirical research related to spanking and corporal punishment is disseminated much more widely so that it is accessible to all individuals. Professionals, such as pediatricians, mental health professionals, or clergy, might not need to tell parents whether or not they should spank their child, but they should at the very least inform parents about the effectiveness (or lack thereof) and the potential outcomes (overwhelmingly negative) of spanking. These professionals then have an opportunity, and one could argue a responsibility, to provide parents

with alternative discipline practices to address the behaviors of concern. Additionally, they should check in with parents about how effective their discipline practices, spanking or otherwise, are at addressing behavioral concerns.

The critical importance of considering the implications and impact of spanking before implementing it as a discipline practice, and even during, cannot be understated. Despite this, spanking is a practice that is often given little thought with regard to the potential negative effects on internalizing behaviors, externalizing behaviors, or cognitive development and growth. It is unclear how parents determine if the practice of spanking is effective, nor if they weigh the value of its effectiveness on a specific behavior or behaviors compared to the negative outcomes that most likely co-occur with any perceived benefits.

The Global Initiative's (2020a) report on corporal punishment indicates that 58 countries have *prohibited* all corporal punishment of children and 30 states (or countries) have *committed* to prohibiting all corporal punishment. Please note that the report refers to countries as states. Examining the percentage of the global child population that is fully protected in law from corporal punishment, 12% of youth are fully protected, 78% are fully protected in some settings outside of the home, and 10% of youth are not protected in any setting. If we believe that children should have rights, particularly the right to protect their body, it is alarming to see the very limited protections that have been enacted to ensure those rights. Contextualizing this information in the context of how we view our children's rights, this data suggests that the overwhelming majority of youth globally are not fully protected from experiencing corporal punishment and therefore have limited say over what happens to their body in relation to discipline, physical discipline in particular.

While spanking is viewed by some as perhaps a less harsh or less harmful form of corporal punishment, a large body of research suggests otherwise. It is important to acknowledge that physical discipline, including spanking, does more than just physical harm. The effects beyond those that are physical may not easily be observed

or understood by parents or caregivers who use physical punishments. This again speaks to the critical need for more education about alternative strategies, dissemination of empirical evidence, and more open conversations about spanking. In addition to a wealth of evidence on the negative effects of spanking, there is much research that supports alternative and nonviolent discipline strategies to address behavioral concerns.

Cross-References

- Corporal Punishment
- Evolution of Punishment
- Physical Punishment

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Spatial Abilities

- ▶ [Sex Differences in Navigation](#)
- ▶ [Unknown Territory](#)

Spatial Mapping

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Synonyms

[Cognitive map](#); [Mental map](#); [Spatial navigation](#); [Spatial reasoning](#)

Definition

Spatial mapping is the ability to use a combination of external and internally-generated information (e.g., vision and proprioception) to construct a mental representation of the surrounding environment. It is shared by a wide range of species, from fish to humans, and thought to have ancient evolutionary origins.

Introduction

One of the most crucial cognitive abilities of any navigating individual is to form a *mental map* of its surrounding environment and to figure out how to get from one place to another. Everyday excursions, such as hunting and foraging, can take an individual on a complex path away from home, along which one can easily become disoriented and lost. An external, world-based representation of the environment provides the navigator with the capacity to not only compute one's own location in space but also plan multiple possible routes to one's destination. Such an ability is highly adaptive for the behavioral flexibility it provides,

as goals and paths that are subject to change for a variety of reasons. While it has been argued for many decades that we (and other animals) do indeed possess such *allocentric* representations (Tolman 1948), the precise nature of such spatial computations and their neural underpinnings have only come into light more recently.

Environmental Influences on Spatial Mapping

An important characteristic of our spatial mapping ability is that it relies heavily on calculations of geometric relationships defined by the large-scale structure of the environment (Gallistel 1990). For instance, a disoriented child is able to use distance relationships according to the walls of a room to reliably find her way to a goal location, while being unable to use those same geometric properties when provided by an array of freestanding objects or 2D lines. Objects and surface markings such as colors and texture are used effectively as *beacons*, or direct cues to location, but evidence suggests that relative spatial locations are mapped primarily with respect to extended 3D structures (e.g., boundaries). This pattern emerges early in development and persists until middle childhood, when performance changes with the acquisition of abstract representations of space. It is shared by nonhuman animals, including birds and fish, and proposed to serve as one of the core components of Euclidean geometric concepts in humans (Spelke and Lee 2012).

Why might children have a representation of space that is more attuned to particular properties of the environment over others? There are several possible reasons that could explain the primacy of extended surfaces in spatial encoding. One advantage to representing the 3D structure of the environment is that unlike natural objects and their featural properties (e.g., color, texture, odors), the geometric shape of the terrain is a stable, reliable source of information that does not change significantly throughout the year. Another advantage is that large, extended structures are easier and faster to process globally and does not take up a lot of attentional or perceptual resources.

A third possibility is that because the sensory system is inundated with spatial information, it is much more computationally efficient to organize the input into large-scale 3D layouts and to encode locations with respect to those layouts, rather than to process all of the information (e.g., as in a pixel-by-pixel visual-matching strategy).

Neural Correlates of Spatial Mapping

Spatial mapping abilities would not only have been adaptive to ancestral hominid species but to all animals, long before humans existed. Therefore, to understand the origins of such mechanisms, we must look very far back into our evolutionary history. Most scientists across the field of psychological and brain sciences agree that through a process of natural selection we have been endowed with neural mechanisms that enable us to encode and remember information about spatial location. Nested deep within the medial temporal lobes of the brain, the hippocampus has been identified to be the hub of spatial representation and memory. It is an evolutionarily ancient part of the brain, present across all vertebrates, and it is not coincidentally adjacent to areas such as the amygdala and ventral tegmental pathways which color our memories with emotional valence and reward processes. Although there is some variability in its anatomical characteristics, the functional specialization of the hippocampus for spatial mapping is preserved across species far and wide across the phylogenetic tree. For instance, when the hippocampus is removed or damaged, subjects' ability to compute spatial relationships is severely impaired, while their ability to learn direct cues or to use beacons remains intact (Rodríguez et al. 2002).

In 2014, the Nobel Prize in Physiology and Medicine was awarded to three scientists – John O'Keefe, Edward Moser, and May-Britt Moser – who identified the neural bases of spatial mapping in the rodent hippocampal formation at the single-cell level. O'Keefe's characterization of *place cells* that increase their synaptic activity at specific locations in space (regardless of facing direction of the animal) (O'Keefe and Dostrovsky 1971)

and the Mosers' discovery of *grid cells* that activate in regularly spaced honeycomb-like tiled pattern across the environment (Hafting et al. 2005) provided scientists with a window into the neural processes underlying metric representations of space. Directional and environmental input to place mapping are provided by *head-direction cells* that encode the direction of an animal's heading and *boundary cells* that specifically encode extended 3D structures. These four types of spatial representations are said to provide, at least in part, the basis for a mental mapping, position-tracking system (Barry and Burgess 2014).

The discovery of spatially selective cells in the rat brain is particularly impactful because of its analogy in the human brain and its implications for the way the human mind organizes and processes information. Scientists are currently investigating the extent to which the representations of what is currently known to be spatial cells might serve a more general function, as in encoding other metric quantities such as or even abstract conceptual relations (Macdonald et al. 2011; Constantinescu et al. 2016). With improved methodologies in studying the human brain, it is also possible to investigate whether the mechanisms originally evolved for spatial navigation and memory might subserve higher-level human cognition, such as imagination and abstract thinking (Jacobs and Lee 2016).

Conclusion

The organization of spatial information in the form of a boundary-based mental map is fundamental to a wide variety of distantly related species. Striking behavioral similarities in spatial memory tasks and shared hippocampal neural correlates of those behaviors suggest that spatial mapping has an ancient evolutionary origin. At the same time, however, the vast range of habitats and modalities of perception and locomotion across animals indicate that there must be a divergence of specialized spatial mechanisms in addition to those that are shared and of common descent. Future research must shed light on such differences and the evolution of our own human reasoning about space.

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Spatial Navigation

► Spatial Mapping

Spatial Processing

► Space, Time, and Number

Spatial Reasoning

► Spatial Mapping

Special

► Why Humans Are Unique

Special Case of Bonobos and Female Counter-Adaptations to Rape

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Synonyms

[Female-female alliances](#); [Matriarchal](#); [Sexual access](#); [Sexual assault](#); [Sexual coercion](#)

Definition

Within the social structure of bonobos, also called pygmy chimpanzees, the female dominance hierarchy and female-female alliances effectively prevent sexual coercion and dominance of females by males.

Introduction

Sexual coercion is the use or threat of force by males to increase mating opportunities with likely fertile females (Smuts and Smuts 1993). Sexual coercion is a subset of male aggression and is commonly expressed through forced copulation and other violent behaviors. Sexual conflict in the form of sexual coercion may be an inevitable consequence of the divergent evolutionary interests of males and females, where females are more interested in mate quality while males are more interested in mate quantity (Hosken and Stockley 2005).

Evolutionary biologist Robert Trivers' parental investment theory (PIT) offers an explanation for how sexual conflict influences how the sexes evolve and interact. PIT holds that males are

more indiscriminate than females when it comes to selecting sexual partners (Trivers 1974). Particularly in mammals, the reproductive success of females is limited by the time and resources needed to raise offspring so they take greater care in choosing a mate that provides good genes and parental care (Smuts and Smuts 1993). This creates conflict since females are not always receptive to mating. Conflict is mitigated when males court females with “nuptial gifts,” protection, or help in rearing young. However, these offerings are costly. As a lower cost alternative, males may use coercion to overcome female reluctance to mate.

While animals use aggression in nonsexual contexts, aggression and sexual coercion are heavily intertwined in the evolution of sex (Arnqvist and Rowe 2013). Sexually coercive behaviors, which include physical attack, violent restraint, and forced copulation, are surprisingly common and are especially prominent in primates (Parish et al. 2000). Previous studies of baboons and chimpanzees revealed that males behave more aggressively towards fertile females, which shows how this type of behavior is focused on reproductive goals (Baniel et al. 2017). Males attempt to monopolize sexual access to females around ovulation, increasing their chance of reproducing. If these mating behaviors increase reproductive success, then they will be selected for (Smuts and Smuts 1993). Additionally, females ideally seek mates whose genes produce the most reproductively successful male offspring. If sexually coercive and aggressive behaviors yield this, females may be incentivized to allow male aggressors to mate with them, leading to a self-reinforcing sexual selective cycle that is difficult to disrupt.

Special Case of Sexual Coercion in Bonobos

Bonobos have managed to break this cycle indicated by the overall lack of sexual coercion. Male bonobos exhibit limited aggression, which starkly contrasts with the intense aggression reported in male chimpanzees (Smuts and Smuts 1993). Male aggression towards females is rare and is almost

never followed by copulation (Hohmann and Fruth 2003). Because it does not lead to sex or offspring, sexual coercion is not a successful mating strategy for male bonobos. Female targets of male aggression also suffer serious injury after being subject to physical violence (Parish et al. 2000). Thus, female bonobos have developed counter-adaptations to resist sexual coercion, which is highly instructive of the mechanisms that species can employ to manage sexual aggression as a reproductive strategy.

Socio-Spatial Interactions and Social Structure of Bonobos

To understand how and why bonobos are less aggressive than other primates, it is important to examine their socio-spatial interactions. A key aspect of bonobos' social structure is how they form and maintain stable relationships. Less aggression and more matings have been observed when males and females harmoniously engage in close association (Hohmann and Fruth 2003). Since aggression is incompatible with intersexual bonding, males have adapted alternative ways to enhance mating opportunities. Female bonobos benefit from these associations since aggression is prevented while males able to maintain friendly relations with females benefit with improved reproductive success (Wrangham 1993).

These mutually beneficial stable parties may have formed due to bonobos' feeding ecology, which is less competitive than those of other primate species (Hare et al. 2012). Bonobos' habitats exhibit high food density, decreasing the need for competition. Females will routinely feed and travel together, while males are deferent and yield feeding priority to females (Hohmann and Fruth 2003). This may reflect a strategy to increase reproductive success, since females would potentially choose mates based on this deference (White and Wood 2007). This type of deferent behavior is connected to a larger social hierarchy where females consistently dominate males. Within bonobo parties, social relationships are centered around females, which are further structured by a linear, but not unidirectional, despotic rank order (Parish et al. 2000). As a result,

the bonds females share with one another allow them to routinely dominate males beyond just feeding priorities.

Patterns of female coalition formation can be explained by the kin selection theory, where females stay within their natal groups and close kin throughout their lives (Tokuyama and Furuichi 2016). These relationships are critical in shaping social relationships in primates. Female bonobos break from this model by dispersing from their natal groups and forming new coalitions with nonrelatives. These coalitions often do not direct aggression towards other females but males become a target when they exhibit aggressive behavior, especially towards females. This has been observed in both wild and captive bonobo populations, which suggests that female coalitions evolved as a counter-adaptation to cope with intersex competition. Groups of bonobos, which usually include males, headed by females have been seen to charge at both resident and unfamiliar males. Males may risk retaliation from females who are supported by their coalitions and male allies when they attempt to coercively mate.

Role of Nonconceptive Sex and Less Honest Signals About Ovulation

The fact that adult female bonobos that form coalitions outside of their natal groups implies that females replace kinship bonds with social cooperation. Nonconceptive sexual activity is the key to forming new bonds (Hashimoto 1997). Bonobos are the most nonprocreative sexually active nonhuman primate. Male and female bonobos regularly employ genital contact to establish and regulate social relationships. This occurs in most age-sex combinations, even among juveniles. The hypersexuality of bonobos is unique and functions to develop and nurture social relationships, preventing aggression and repairing broken alliances.

In the context of female counter-adaptations to rape, nonprocreative sex can be used for paternity confusion and communication (Wrangham 1993). Paternity confusion refers to interactions where

the female is not fertile but the male acts as if she were. Females benefit from this since they can recruit male aid and prevent potential harm directed towards her offspring while males benefit since there is a slight chance of conception. These sex acts also communicate to third parties the type of bond present between sex partners. For example, female-female sexual activity may communicate that an important alliance has been formed, thereby inhibiting male aggression.

Primate sexual swellings and female receptivity also influence how bonobos navigate mating strategies (Douglas et al. 2016). Sexual swellings typically signal female fertility, which males use to pinpoint ovulation so they can act accordingly to maximize reproductive success. Female bonobos express regular sexual swellings during cycles where ovulation does not occur, making them less reliable indicators of ovulation in comparison to other primates. Due to their variability in swellings, males cannot accurately predict the fertility of potential mates. In species where the timing of ovulation is more predictable, males may mate guard fertile females, a form of indirect sexual coercion, and constrain their ability to mate with others. The variability of female bonobos' swellings may constrain mate-guarding efforts by males and moderate inter-male sexual competition, reducing sexual coercion (Surbeck et al. 2017). This may be akin to concealed ovulation in humans, arguing that these could be adaptations aimed, in part, at the reduction of sex-based aggression.

Self-Domestication Hypothesis

The self-domestication hypothesis offers another explanation for the reduced aggression and lack of sexual coercion observed in bonobos, positing that natural selection against aggression leads to a series of phenotypic changes in some wild animals, similar to the changes experienced by captive animals bred for domestication (Hare et al. 2012). Experiments in domesticated mammals indicate that selection against aggression also brings about a "syndrome" called neotany in which adults retain some aspects of characteristically juvenile

morphology, physiology, and behavior. For example, less aggressive wolves may have gained a selective advantage by being more willing to explore the niche of lives with humans and therefore would have been better able to exploit novel ecological opportunities.

This hypothesis may explain differences observed in wild species with low levels of aggression (Hare et al. 2012). Bonobos, for example, geographically diverged from their chimpanzee-like ancestors approximately 1 million years ago. They had larger niche ranges, more high-quality food available, and lacked competition from other species. The unique social structure and feeding ecology of bonobos may have led to selection against male aggression. Less aggressive males who allied with females and their coalitions were more successful than their aggressive counterparts. Natural selection would have favored males with more juvenilized behavior, characterized by increased adult play and decreased predatory motivation. This is also accompanied by morphological changes such as smaller canine teeth and a juvenilized cranium. Thus, self-domestication may provide insight into the selective forces that allowed female bonobos to establish systematic dominance over males.

Conclusion

The combination of habitat and feeding ecology, female dominance, hypersexuality, and variation in ovulation signals has influenced the psychological evolution of bonobos. These factors have worked in tandem to select against certain behaviors which, in turn, has led to an overall reduction in aggression and sexual coercion amongst bonobos. Evidence for the self-domestication hypothesis grows stronger as more powerful phylogenetic tests are applied to more species that also show reduced aggression and higher social tolerance.

Furthermore, female coalitions have been considered especially paramount for shaping the social lives of bonobos and understanding the scarcity of forced copulation. In humans, males commonly seek to control female sexuality and pursue reproduction through violence. Examining

how female bonobos have developed counter-strategies for sexual coercion shows that above all, strengthening female social alliances and recruiting male allies can decrease vulnerability to male aggression and sexual coercion.

Cross-References

- [Rape](#)
- [Sexual Coercion](#)
- [Sexual Coercion and Violence](#)
- [Sexual Harassment](#)
- [Types of Sexual Coercion](#)

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Special Case: Autism

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Synonyms

ASD; Autism spectrum disorder; Autistic disorder

Definition

A neurodevelopmental disorder with two main diagnostic criteria: (a) persistent deficits in social communication and social interaction and (b) restricted, repetitive patterns of behavior, interests, or activities.

Introduction

Autism is a neurodevelopmental disorder with two main diagnostic criteria: (a) persistent deficits in social communication and social interaction and (b) restricted, repetitive patterns of behavior, interests, or activities. Autism has been associated frequently with an impaired Theory of Mind. Theory of Mind is defined as the realization that other people may have different beliefs, knowledge, thoughts, feelings, and emotions from one's own. A seminal article on the association between autism and Theory of Mind was published in 1985

and addressed the question: *Does the autistic child have a Theory of Mind?* (Baron-Cohen et al. 1985). The article revealed that children diagnosed with autism fail to assign beliefs to others and are unable to predict others' behavior, in contrast to nondiagnosed controls and children with Down syndrome. Because the children with autism were not mentally retarded, in contrast to the children with Down syndrome, it was concluded that the impairment in Theory of Mind was independent of the level of intelligence. This suggests that children with autism have a domain-specific impairment in Theory of Mind. This has been called the *mindblindness theory of autism* (Baron-Cohen 1995).

Extreme Male Brain Theory of Autism

Baron-Cohen extended this finding into the *extreme male brain theory of autism* (also called the *empathizing–systemizing theory*, Baron-Cohen 2009). A male brain refers to individuals in whom systemizing is significantly better developed than empathizing. Systemizing is defined as the drive to analyze the working of systems and to derive their underlying rules. Systemizing is closely related to capabilities necessary for engineering. Empathizing refers to the drive to identify another one's emotions and thoughts and to give an appropriate response. Empathizing is closely related to capabilities necessary for nursing and taking care of children and overlaps with Theory of Mind. A female brain refers to individuals in whom empathizing is significantly better developed than systemizing. Consistent with this typology, research revealed that 54% of the male participants were significantly better at systemizing than at empathizing (compared to 17% of the female participants) and that 44% of the females were significantly better at empathizing than at systemizing (compared to 17% of the males) (Goldenfeld et al. 2005). From an evolutionary perspective, Baron-Cohen has argued that good systemizing is associated with using and making tools, and hunting and tracking, and low empathizing with tolerating solitude and aggression, which are considered to be important

characteristics of males in ancient times. Good empathizing is associated with mothering and making friends, which were important skills for females in our evolutionary past.

Baron-Cohen (2009) considers autism as a case of an extreme male brain, i.e., the extreme of a normal male profile. Empirical results revealed that 47% of the people diagnosed with autism showed an extreme difference in scores on systemizing and empathizing tasks, compared to 6% of male controls and 0% of female controls (Goldenfeld et al. 2005). Because of the overlap between empathy and Theory of Mind, these results are consistent with the mindblindness theory of autism. Moreover, the theory has also been supported by neuroscientific studies, showing that activity in brain areas associated with Theory of Mind is reduced in people with autism compared to controls (e.g., Kana et al. 2016).

Alternatives to the Mindblindness Theory of Autism

Despite the empirical evidence, the mindblindness theory of autism has not remained unchallenged. Most notably, some researchers have argued that a deficit in executive functioning, rather than a deficit in Theory of Mind, is the core of autism (for a review, see Russo et al. 2007). Executive functioning is set of cognitive processes – including attention, inhibition, working memory, and cognitive flexibility – whereby behavior is directed and controlled in order to achieve desired behavior. Others have argued for weak central coherence, i.e., reduced global processing and increased local processing, as the core of autism (for a review, see Happé and Booth 2008). In a longitudinal study on children with autism, Pellicano (2010) showed that individual differences in executive functioning and central coherence predicted performance on Theory of Mind tasks 3 years later, independent of early performance on Theory of Mind tasks. Predictions in the opposite direction were nonsignificant. The author concluded that deficits in Theory of Mind are the result of earlier, more domain-general deficits, rather than the cause of autism.

White (2013) proposed an alternative interpretation; she argued that people with autism have difficulties with executive function tasks, because they do not understand the experimenter's implicit expectations for the task. She called this an impairment in Inferring Implicit Information (the *Triple I impairment hypothesis*). People with autism tend to fail on executive function tasks that are open-ended, unguided, and ill-structured, such as card sorting tasks, whereas they perform well on tasks that are explicit, logical, and constrained, such as the classic Stroop task (for references, see White). This hypothesis is consistent with the mindblindness theory of autism. Other authors have argued that, because of the heterogeneity of the symptoms of autism, it is unlikely that this disorder is caused by a single factor. They argue for different, independent factors to explain the different symptoms of autism. This has been called the *fractionation of autism* (Brundson and Happé 2014).

Conclusion

To conclude, there is ample empirical evidence for the hypothesis that autism is associated with deficits in Theory of Mind. However, it remains inconclusive whether Theory of Mind is the core of autism or whether the observed Theory of Mind deficits are the result of other impairments.

Cross-References

- [Cognitive Development](#)
- [Domain Specificity](#)
- [Empathy](#)
- [Evolutionary Clinical Psychology](#)
- [Evolutionary Cognitive Psychology](#)
- [Executive Functioning](#)
- [Sex Differences](#)
- [Sex Differences in Cognitive Development](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Simon Baron-Cohen \(Darwinian Psychiatry\)](#)
- [Social Cognition](#)
- [Theory of Mind](#)
- [Theory of Mind and Evidence of Brain Modularity](#)

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Special Friendships Among Baboons

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Synonyms

Pair bonding; Social bonds; Special relationships

Definition

Baboons (*Papio* spp.) form long-term, nonsexual social bonds between unrelated males and asexual females known as “friendships.”

Introduction

Persistent social bonds between group members known as “friendships” have been described in numerous mammals (e.g., capuchin monkeys, *Cebus* spp.; elephants, *Loxodonta africana*; spotted hyenas, *Crocuta crocuta*; dolphins, *Tursiops aduncus*) (reviewed in Seyfarth and Cheney 2012). Typically, these friendships refer to long-term bonds between nonkin that transcend associations formed in sexual contexts (e.g., during mating periods or consortships). Unlike affiliations with other group members, friendships are broadly characterized by high rates of association in close spatial proximity; positive, non-harmful social interactions; and mutual tolerance and physical, emotional, and/or social support (Silk 2002; Palombit 2017).

Long-term social bonds between males and females are not commonly observed in many mammals outside of pair-living or small group-living species. Under these social structures, limited reproductive opportunities and high parental certainty should select for increased investment in mating and parenting efforts by males, resulting in the formation of heterosexual pair bonds. In contrast, primates typically live in large, multi-male, multi-female social groups that provide more mating opportunities and lower rates of paternity certainty. Nonetheless, the formation of heterosexual friendships has been observed in a number of primate species (e.g., chimpanzees, *Pan troglodytes*; Assamese macaques, *Macaca assamensis*; Japanese macaques, *M. fuscata*; rhesus macaques, *M. mulatta*; chacma baboons, *Papio ursinus*; olive baboons, *P. anubis*; yellow baboons, *P. cynocephalus*) (Seyfarth and Cheney 2012). Establishing the adaptive benefits of maintaining such male-female bonds in polygynous and polygynandrous species has become a question of interest in both behavioral ecological and

anthropological theories. Furthermore, given the likely multi-male multi-female social structures exhibited by early hominins, testing hypotheses of how heterosexual friendships have evolved in similar social structures in extant primates can inform on how the strong male-female pair bonding found in modern humans may have first evolved.

Male-Female Friendships in Baboons

Baboons are polygynandrous, mostly female philopatric monkeys that live in multi-male, multi-female groups, and exhibit separate linear dominance hierarchies for each sex. These species provide some of the best-studied examples of friendship in nonhuman primates. The term “friendship” in baboons primarily refers to the social bonds formed between adult males and females that persist beyond the periovulatory period – in contrast to the short-term consortships formed between males and females in estrus. Under the above definition of friendship, positive social interactions between male and female baboon friends include increased rates of mutual grooming, vocalizing, and female tolerance of male alloparenting (Palombit 2017). Friendships are common throughout groups of chacma and olive and yellow baboons in southern and eastern Africa, respectively, although some dynamics vary within groups and between populations (reviewed in Palombit 2017). For example, while it is common for nearly all adult females in a group to have male friends, the opposite is not true – not all males have female friends at any one time. The number of friendships a female engages in can vary both between females and populations – chacma baboon females typically have only one friend, but in olive baboons the number of friendships can extend to three or more simultaneous friendships. In groups where females exhibit multiple concurrent friendships, the number of friendships may also be positively correlated with dominance rank. Similarly, in some yellow and chacma baboon populations, females are more likely to preferentially select male friends with equal or higher dominance

ranks to their own. The instigator of a friendship also varies between populations. In olive baboons, males are the primary maintainers of friendships by initiating grooming bouts and reducing spatial proximity – in contrast to chacma baboons, where females invest a greater effort into maintaining associations (Shur 2008).

Adaptive Benefits of Friendships for Female Baboons

The pervasiveness of heterosexual friendships among multiple baboon species suggests a substantial adaptive significance to the formation of these bonds. For example, infanticide by males is a well-documented reproductive strategy in non-human primates, particularly in immigrating individuals. By killing an unweaned infant, a male can cause the mother to resume cycling sooner, therefore increasing the number of opportunities for fertilization by the infanticidal male. Evidence from two different methodologies support the hypothesis that for female baboons, a key benefit of friendship with a male is protection against infanticide. First, in a study of chacma baboons during which infanticide was a substantial cause of infant mortality (e.g., 38% of infant deaths), playback experiments found that both male and female friends reacted more strongly to the distress vocalizations of friends under attack compared to non-friends (Palombit 1997). Moreover, male friends responded more strongly to the calls of females with infants compared to females following the death of their infant or when recordings included the calls of a potentially infanticidal male. Second, hormonal analyses of chacma baboon stress responses found that while females experienced higher glucocorticoid levels when their group was taken over by an immigrant male, these levels were significantly lower in lactating females with male friends compared to those without (Beehner et al. 2005). Conversely, males with female friends exhibited increased glucocorticoid levels, but males without friends did not. As such, behavioral and physiological responses in both sexes to behavioral cues in friends and the presence of infanticidal males

suggest that female chacma baboons benefit from the active defense of their infants by male friends.

In baboon populations where infanticide by males is less common (e.g., yellow and olive baboons), friendships are expected to protect against nonlethal harassment. A repeat of the playback experiments conducted in chacma baboons found similar results. Despite a substantially lower risk of infanticide, male olive baboons demonstrated similar protective responses toward female friends in distress. In these cases, female baboons appear to benefit from male friends who can defend them from aggression from other group members targeting themselves or their infants (Nguyen et al. 2009; reviewed in Palombit 2017). More specifically, females benefit from greater protection afforded by higher-ranking male friends, because these males can defend against a higher number of lower-ranking males (Shur 2008). This protection should have a direct fitness benefit, as demonstrated by studies that have shown adult females and infants of mothers who are more closely socially integrated to conspecifics of either sex live longer (e.g., Alberts 2019).

Adaptive Benefits of Friendships for Male Baboons

For male baboons, benefits can be grouped under two hypotheses. Under the parental effort hypothesis, males that have sired the infants of female friends should maintain associations in order to protect their offspring and improve infant survivorship. Paternal care by friends is especially prevalent in populations where paternal certainty is higher, because males are more likely to invest in infant protection, even extending to male friends protecting the unborn offspring of pregnant females, which may be susceptible to abortion induced by immigrant males (Baniel et al. 2016; Städele et al. 2019).

Under the mating effort hypothesis, males should benefit from maintaining heterosexual friendships through increased likelihood that a female will select a male friend to sire subsequent offspring. As such, this hypothesis overlaps with

the previous hypothesis of parental effort in that most examples of paternal care likely reflect a form of mating effort if infant care by a male positively influences female mate choice. Nguyen et al. (2009) and Baniel et al. (2016) found no evidence that friendships generate future mating opportunities for males of any relation to infants after their female friends had weaned and resumed cycling. It is possible however that the effect of prior friendships on mating opportunities may vary between males that have sired their friend's offspring and those that have not (Städele et al. 2019) or if increased mating opportunities occur with the same female friend or a different non-friend (Palombit 2017). Moreover, both the aforementioned studies were conducted in yellow and chacma baboons, respectively. In these species, female mate choice may influence male mating success to a lesser extent compared to male dominance rank (e.g., compared to olive baboons). Städele et al. (2019) found a positive relationship between heterosexual sociality and subsequent male mating success in olive baboons, although there was no effect when considering (1) males who had sired the current infant and (2) lactating females (as opposed to cycling females without sexual swellings). In olive baboons, there is therefore likely a complex interaction between the effects of male friendships and rank on female mate choice, although a female's friendships may have a greater influence than male rank compared to other baboon species.

Conclusion

The conspicuousness of male-female friendships in baboons provides an excellent window into the evolutionary significance of sociality among non-kin in nonhuman primates. While several questions have yet to be explored – for example, the effect of friends in deterring predators and for males the possibility that friends facilitate access to grooming networks or infants for use in agonistic interactions – current data already indicate key selective pressures in baboons through which such stable pair bonds may have evolved. In particular, hypotheses of male mating and parental

effort reflect predictions for the origins of pair bonds in early hominins and subsequently modern humans. As such, studies of friendship in baboons, among other nonhuman primates, can provide useful models for inferring ecological and social determinants of human behavior that are not retained in the fossil record.

Cross-References

- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation and Social Cognition](#)
- ▶ [Infanticide in Nonhumans](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Nonhuman Primates: Within-Group Conflicts](#)
- ▶ [Paternal Care](#)
- ▶ [Primate Cooperation](#)
- ▶ [Primate Dominance Hierarchies](#)

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Special Relationships

- ▶ [Special Friendships Among Baboons](#)

Special Resemblance

- ▶ [Masquerade](#)

Specialization

- ▶ [Evidence for Modularity](#)

Specialized Cognitive Skills

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Synonyms

[Cognitive specialization](#); [Functional specialization](#)

Definition

“Specialized Cognitive Skills” refer to a set of skills that pertain to specific behaviors and are a product of natural selection and transmission to one’s offspring. These skills are refined over time

to allow for maximum benefit to the individual organism and to facilitate adaptive survival. Some examples of such skills include theory of mind, altruism, sensorimotor skills, and language.

Introduction

The ability to understand someone's intentions, to empathize, or to sympathize is a product of one's environment as well as neurobiological processes responsible for making unique connections in the brain over time. Alternatively, the brain's ability to remember information and make decisions is also a product of one's environment as well as neurobiological processes. Together, these skills represent processes that are interdependent of one another. From an evolutionary perspective, these processes represent both cognitive specialization and functional specialization (Povinelli and Preuss 1995). Cognitive specialization (also referred to as specialized functions) is a result of the brain's ability to be modular, with specific cognitive domains responsible for processing specific types of information (Fodor 1983; Caramazza and Coltheart 2006). Functional specialization refers to the actual neurobiological processes that occur to facilitate cognitive processes (Mahon and Cantlon 2011).

One of the most debated topics regarding specialized cognitive skills is the mapping, or how cognitive processes relate to brain activity (Mahon and Cantlon 2011). To date, two theoretical paradigms attempt to explain this association; however, both are contrasting in nature: the *reverse inference* and *forward inference* approaches (Poldrack 2011; Henson 2006). The reverse inference approach asserts that due to a specific activation in a given brain region, a specific cognitive process emerges (Poldrack 2011). Conversely, the forward inference approach asserts that when a given brain region is activated, a specific cognitive process may occur; however, this same brain region might also recruit an additional cognitive process simultaneously (Henson 2006).

From an evolutionary perspective, cognitive specialization and functional specialization are

both a result of neuroplasticity (i.e., the brain's ability to reorganize and adapt), meaning, they depend on information reorganization, accommodation, and assimilation on a neurobiological level to execute cognitive skills such as theory of mind (ToM), trust, and language and to make use of heuristics in social interactions. Specialized cognitive skills are best understood in the context of social interactions and how they influence an organism's ability to acquire, develop, and evolve these skills in order to ensure survival (Povinelli and Preuss 1995).

Social Cognition and Specialized Cognitive Skills

Adaptive functioning in one's environment is central to the acquisition, development, and evolution of specialized cognitive skills. Such skills are integral when an individual attempts to make sense of their environment, learns, forms judgments, makes decisions, communicates with others, and regulates behaviors. For example, *alexithymia* is a subclinical phenomenon that results in a lack of emotional awareness; specifically, an individual may struggle with identifying feelings within themselves, describing feelings to others, have a restricted imaginative process, and have an external locus of control (Sifneos 1973; Taylor et al. 1999). In context to social cognition, alexithymia is the antithesis of optimal learning, decision-making, communication, and behavior regulation as many who struggle with this condition often experience low levels of happiness and life satisfaction (Timoney and Holder 2013).

The evolution of specialized cognitive skills has been extensively studied using primates, namely, due to their similar cortical cytoarchitecture relative to *Homo sapiens*. For example, the concept of *cooperation* was demonstrated by chimpanzees that reacted to release fellow primates from their enclosure in order to collaborate on a specific task (Gilby et al. 2008.; Melis et al. 2006). The "seeing-knowing" link, aka *theory of mind*, was demonstrated in a group of chimpanzees that observed the gaze of a fellow primate when they were interested in the whereabouts of

another (Premack and Woodruff 1978; Call and Santos 2012; Whiten 2013; Krupenye et al. 2016). These examples refute the notion that only *Homo sapiens* are capable of higher-order perception and decision-making skills in context to a social environment.

Specialized Cognitive Skills and Functional Systems Theory

Functional systems theory (FST) is a theory proposed by Russian biologist and physiologist, Pyotr Anokhin (Anokhin 1974; Red'ko et al. 2004). The theory outlines how various organ systems, including the brain, work in an interrelated fashion and adapt as a result of environmental and neurobiological sensory input and actions (Red'ko et al. 2004). This theory contrasts with the reflexive theory which surmised that behavior was a result of a series of stimulus and responses that followed a linear trajectory (Red'ko et al. 2004). Some examples of FST include swimming, running, swallowing, etc. These examples portray a rather complex orchestration of interrelated anatomical systems cooperating to achieve synchronous activation, and ultimately, leading to a specific behavior or activity (Red'ko et al. 2004).

As humans evolve, so do our behaviors; as such, our behaviors require us to adapt and assimilate new information in order to achieve our goals and execute behaviors. According to FST, there are eight stages for which an organism acquires information and assimilates it to achieve a desired goal or behavior: (1) afferent synthesis, (2) decision-making, (3) generation of the acceptor of the action result, (4) generation of the action program, (5) performance of an action/behavior, (6) attainment of the result, (7) backward afferentation (feedback), and (8) comparison of the result with its model (Red'ko et al. 2004). However, these steps can be broken down into five basic hierarchies: (1) *afferent synthesis* (excitement of the central nervous system), (2) *decision-making*, (3) *action*, (4) *evaluation of results*, and (5) *meeting the needs*. Each of these steps are integral in an organism's ability to

understand language or other forms of communication (e.g., intentions of others), compare the situation and results to goals and previously acquired information, and generate a response such as an emotion or behavior (Red'ko et al. 2004).

Evolutionary Cognitive Neuroscience

To better understand cognitive specialization or skills, one must look at the neural substrates, neurotransmission, and cerebral architecture that are involved in functional specialization. As previously mentioned, functional specialization refers to specific functions of the brain that facilitate cognitive specialization (Povinelli and Preuss 1995; Mahon and Cantlon 2011). When one considers the multitude of cognitive processes involved in a social environment, concepts such as orientation, attention, and social responses come to mind. To underscore these processes, Blumstein et al. (2010) developed a framework of social cognitive neuroscience that explains the interrelationship among brain regions, genes, and brain development as they relate to social perception, attention, decision-making, and social responses.

The framework developed by Blumstein et al. (2010) asserts that social behaviors are mediated by a complex system of neural mechanisms that have evolved over time. The authors iterate that these mechanisms operate on *divergence* (e.g., temporal variations in neuroendocrine mechanisms), *convergence* (e.g., combined functioning of different systems), and *conservation of function* (e.g., use of glucocorticoids to aid in mobilization for fight or flight). The model proposed by Blumstein et al. (2010) was refined by Kosciak and Tranel (2012) with their addition of the *Inferential Brain Hypothesis (IBH)*. This hypothesis asserts that social processes shifted over time resulting in a change from evaluating stimuli based on its intrinsic properties to making inferences of the stimuli based on properties independent of the stimuli (Kosciak and Tranel 2012). The IBH approach helps explain why human brains tend to be much larger than other mammalian brains.

Conclusion

The human brain has evolved to accommodate the ever-expanding amounts of sensory information we come in contact with on a daily basis. The ability for an organism to acquire information, integrate it, and enact a goal-directed behavior is a product of both cognitive and functional specialization. Due to a modular neural system, the human brain is able to process vast amounts of information with specific brain regions dedicated to processing domain-specific stimuli. As a result, the human brain possesses the ability to create higher-ordered meaning from seemingly simplistic information input. Such higher-ordered processes include perspective-taking (aka “theory of mind”), linguistic development, socialization, altruism, and even sensorimotor behaviors. As mankind evolves, so will our brains; some types of sensory input and analysis may become more irrelevant as genetics may alter our neurobiology as a result of habituated responses and natural selection.

Cross-References

- [Domain Specificity](#)
- [Evidence of Brain Modularity](#)

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Species Concepts

- [Early Definitions of Species](#)

Species Definitions

- [Early Definitions of Species](#)

Specific Brain Damage

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Synonyms

Blast injury; Brain lesion; Concussion; Contusion; Head injury; Localized damage; Non-penetrating injury; Penetrating injury; Rotation injury; Traumatic brain injury

Definition

“Specific brain damage” describes the destruction or decay of neurons leading to alterations in cognitive, emotional, and/or behavioral functioning as a result of an acquired or neurodegenerative syndrome. Damage may include focal, local, diffuse, or global neuropsychological impairment involving language, attention and concentration, learning and memory, executive functioning, and visuospatial functioning.

Introduction

The concept of specific brain damage and the resulting neuropsychological alterations associated with it have been documented since the advent of the Edwin Smith Papyrus in ancient Egypt. The Egyptians noted aspects of basic neuroanatomy such as the meninges, cerebrospinal fluid, and the overall cranial structure, as well as notions of abnormal brain functioning such as paralysis due to trauma. From an evolutionary perspective, *Homo sapiens*’ brain has by far the most complex arrangement of cerebral processes than any other mammal. Over time, the hominid brain has evolved to account for the demands in its environment. Different from its predecessor *Homo heidelbergensis* and *Homo neanderthalensis* whose brains measured to be approximately 1100–1200 cm³, *Homo sapiens*’ brain measures at 1400 cm³ to accommodate for

larger brain volume due to the emergence of the neocortex. This brings into question, at what level of the brain (allocortex or neocortex) is most impacted or preserved in the event of damage to the brain? What dysfunction is likely observed when damage occurs at either level?

In the 1800s, brain lesion studies helped elucidate the relative anatomical-physiological relationship of various brain functions as a result of specific damage to a given brain region. Around the same time, the now defunct practice of *phrenology* became prominent due in part to the theories of brain functioning proposed by Franz Joseph Gall. Phrenology sought to account for an individual’s intellectual abilities relative to one’s brain size. Essentially, a person’s intellectual abilities were thought to be proportional to a given brain region which could then be observed based on unique geometric-surface differences of a person’s cranium. Present day approaches in detecting specific brain damage include the use of radiological images such as *computed tomography*, *positron emission tomography*, and *magnetic resonance imaging*, and electrophysiological tools such as *evoked potentials* and *event-related potentials*, as well as neuropsychological assessment.

Brief History of Brain Damage and Neuroimaging

One of the first historical antecedents in delineating brain damage can be traced back to the nineteenth century Italian physiologist, Angelo Mosso who monitored pulsations in the brains of adults by surgically trepanning their skulls. After having his patients engage in mental math calculations, he observed an increase in cerebral pulsations via increased blood flow that led him to conclude blood flows according to function; this technique was named the “human circulation balance” (Mosso 1881). However, this relationship was not formally analyzed and determined until 1890 when Charles Roy and Charles Sherrington expanded upon Mosso’s research (Roy and Sherrington 1890). To understand brain damage, it is better to understand it via the perspective of those who theorized how the brain worked in the

first place. This “what” question eventually propelled the field of neuroradiology by systematically testing hypotheses to determine the “how and why.” The two primary schools of thought were proposed by William James in 1890 (externally driven) and Graham Brown (intrinsically driven) between the years of 1911–1915.

Upon reading Mosso’s work on the human circulation balance, James had postulated that the brain worked as an extravagant “input/output” system driven to meet the demands of one’s environment. In essence, he believed that movement/action was a simple coordination between the sensory demands being imposed on a person whereby a complex system would naturally respond with appropriate action (James 1950 [1890]). Eventually, James’s theory would encourage a neurophysiologist by the name of Charles Sherrington to study the central reflex arc and the corresponding synaptic transmission and integration that drove such reflexes (Sherrington 1907).

In contrast to James’s theory, Graham Brown postulated that organization in the central nervous system was “self-referencing.” He believed that neuronal circuits provided the drive for transmission generation needed to initiate organized movement (Brown 1911, 1914, 1915). This theory led Brown to further assert that movement is intrinsically generated in the absence of sensory input (Brown 1915). In Brown’s pursuit to distinguish functionality, he examined spinal cord reflexology and found that locomotion within the spinal cord operated via autonomous neural networks on one side of the spinal cord that activated muscle movement, while on the other side, it inhibited opposite limbs. He described this process as a “half-paired center” (Brown 1914). Today, we know that he was referencing the various laminae within the spinal cord itself, specifically, the posterior/dorsal column for afferent signal integration and the anterior/ventral column for efferent signal transduction, respectively. Brown’s views of central nervous system organization and research would eventually serve as the basis for much of the modern advances in neuroimaging analysis and detection of neuropathology.

Neuroimaging would finally get its “boost” in 1948 when Seymour Kety and his colleagues at

the University of Pennsylvania measured cerebral blood flow as a result of specific functioning. Kety and his colleagues measured whole-brain activity by using an in-vivo tissue technique on animal subjects called autoradiography, an image on an x-ray film produced by the pattern of decay emissions (e.g., beta particles) from a distribution of a radioactive substance. Kety’s quantitative element would eventually be used in the development of the positron emission tomography scan (Kety and Schmidt 1948).

Up until 1986, it was thought that blood flow was a direct response to the brain’s need for oxygen to metabolize glucose into carbon dioxide and into water for the production of energy. It was thought that functional increases in oxygenated blood changed the ratio of oxy vs. deoxyhemoglobin. It was later discovered by Ray Cooper and his colleagues at the Burden Neurological Institute that patients undergoing evaluation for surgery due to epilepsy showed task-induced focal increases in oxygen availability, an indicator that blood flow increased more than oxygen consumption (Cooper et al. 1975). This discovery would later become the foundation for a contrast agent known as blood oxygen level dependent (BOLD) and eventually used as an adjunct measurement in magnetic resonance imaging.

Methods in the Detection of Specific Brain Damage

While trepanning, phrenology, and brain lesions served as a rudimentary and even barbaric approach to detecting specific brain damage, they laid the groundwork for more modern approaches. Current trends in detecting brain damage include the use of computed tomography, positron emission tomography, magnetic resonance imaging, electrophysiological techniques, and neuropsychological assessment. Each approach adds a unique and highly important element in detecting brain damage on both a structural and functional level. By combining neuroimaging, electrophysiological techniques and neuropsychological assessment, clinicians are better able to determine both structural and functional aspects of an individual’s brain functioning.

Computed Tomography

Before PET and MRI, the X-ray computed tomography (CT) or computerized axial tomography (CAT) was the first modern imaging technique to be used in clinical practice. This technique was first theorized and tested by William Oldendorf in 1958 and created by Godfrey Hounsfield in 1967, and was adapted for hospital use in 1971. It operates by passing a highly focused X-ray beam through an object and recording the object's attenuated response and produces a three-dimensional transaxially tomographic image of that object. Prior to the CT was a more invasive technique called pneumoencephalography, a process that localized mass lesions via removing spinal fluid and replacing it with air to determine the rate of ascension into the ventricles when the patient was in an upright position (Raichle 2000). The patient would be manipulated in space while strapped into a bed or chair so X-ray images could be taken. The CT was the first imaging technique developed; however, it was an anatomical tool that left out the functional characteristics of the brain.

Magnetic Resonance Imaging

The theoretical principles behind magnetic imaging (MRI) were discovered by Raymond Damadian, Felix Bloch, and Edward Purcell in 1946 (Kevles 1997); however, it was not until 1973 when Paul Lauterbur devised a strategy to adapt the applications of nuclear magnetic resonance (NMR) and incorporated it with the capabilities of CT imaging to create what is now known as MRI (Lauterbur 1973). The basis of MRI is complex, but the core principles include measuring the activity and behavior of atoms (protons) in water within a magnetic field. Within a strong magnetic field, protons behave like smaller magnets that align within the magnetic field; when these magnets are disturbed from their equilibrium state by a radio frequency pulse, the X-ray captures these changes over time as these time-dependent changes occur as a function of proton fluctuations within tissue.

Positron Emission Tomography

Seymour Kety implemented a technique using radiographic imaging to determine the attenuation

of emission decay within tissue that would later give rise to the positron emission tomography (PET). In 1951, the idea of measuring the decay of a group of radionuclides and its positron emissions was first suggested by David Kuhl and his colleagues at the University of Pennsylvania. It was theorized that transverse sections of the body could be reconstructed by measuring the attenuation of highly focused X-ray beams projected through the section, then, further localization could be achieved by distributing radionuclides in that section and measure the decay of positron emission which would accurately and quantitatively reconstruct the selected section (Wrenn et al. 1951).

Electrophysiological Techniques

While neuroimaging examines the structural aspects of the brain, electrophysiological techniques examine the relative electrical impulses given off by communicating neurons throughout the brain. The concept of *electrodiagnosis* is concerned with measuring action potentials across the brain; such potentials are a product of intracellular processes involving ion channels that mediate such potentials. Abnormal functioning in these ion channels may lead to irregular or even absent action potentials. Common electrodiagnostic procedures include the electroencephalogram (EEG), evoked potential (EP), and event-related potential (ERP). Invented in 1875 by Richard Caton, the EEG records “surface activity” via specifically placed electrodes that measure relative action potentials in a given brain region. Common reasons for the use of EEG include seizure disorder, sleep disorder, and to determine brain death.

Some adjunctive measures to EEG that examine activity-specific action potentials include EP and ERP. The ERP measures brain waves attributed to a specific cognitive, sensory, or motor event. Measured wavelengths may be singular or multiple, indicating the relative time in signal transduction across the cerebrum. Alternatively, EP measures wavelengths that are attributed to peripheral nerve activity and can be recorded from peripheral nerves, the spinal cord, or the cerebral cortex. Three types of EP include

(1) somatosensory evoked potentials (SSEP), which measure wavelength activity from the upper and lower extremities in peripheral nerves, (2) visual evoked potentials (VEP), which measure cortical wavelength activity attributed to visual input, and (3) brainstem auditory evoked potentials (BAEP), which measure cortical wavelength activity attributed to auditory input.

Neuropsychological Assessment

The advent of clinical neuropsychology and neuropsychological assessment began in the twentieth century with its focus on delineating brain-behavior relationships after the onset of brain damage. The concept of “brain-behavioral relationship” refers to the identification of behavioral, emotional, cognitive, and physical outcomes as a result of damage to part(s) of the brain. The neuropsychological assessment provides a wealth of information to referral sources (e.g., neurologists, neurosurgeons, psychiatrists, lawyers, etc.) where other approaches of detecting brain damage may lack (i.e., neuroimaging and electrophysiological techniques). In context to medicine, the overarching concept behind a neuropsychological assessment is focused on (1) diagnosis, (2) describing the neuropsychological status of an individual, (3) planning appropriate treatments, and (4) tracking efficacy of applied treatment(s). Tests are usually paper and pencil-based; however, there has been an increase in the development of computer/tablet-based measures. Such measures “tap into” various cognitive domains (e.g., attention, language, etc.) that provide the clinician insight into the patients’ relative strengths and weaknesses in a given cognitive domain.

While neuroimaging and electrophysiological techniques can identify temporal and spatial elements of cerebral functioning, they cannot describe exactly “what” is impaired or preserved following an injury to the brain. For example, while Broca’s area is responsible for the motor, or efferent aspects of speech, each person differs ever-so-slightly in where their Broca’s area is located. Thus, not everyone who sustains damage to the left posterior inferior frontal gyrus will necessarily present with a prototypical Broca’s aphasia. This example holds true to other aspects

of the brain that mediate other cognitive functions such as attention, visuospatial functioning, memory, etc. Common approaches in neuropsychological assessment make use of either a (1) “fixed battery” approach or (2) “flexible battery” approach. A “fixed battery” refers to a series of tests that measure various cognitive functions that are uniformly applied to every patient regardless of their presenting problem (e.g., stroke, TBI, etc.). Conversely, a “flexible battery” refers to a series of tests that measure various cognitive functions that are independently selected relative to each patient’s presenting problem. While the “fixed battery approach” tends to be favored among researchers, both approaches in measurement are routinely practiced in clinical settings.

Types of Brain Damage

Specific brain damage can be thought of as being acquired brain injuries, consisting of two types: (1) traumatic brain injuries and (2) nontraumatic brain injuries. Both types of damage are specific in nature, meaning, that they are unique in terms of the pathophysiology that underlie them, and the alterations in neurocognitive functioning specific to the neural damage.

Acquired Brain Injuries

Acquired brain injuries (ABI) can be broken down into two categories: (1) *traumatic brain injuries* and (2) *nontraumatic brain injuries*. Both taxonomies of ABIs may result in little to significant alterations in cognitive, emotional, physical, and behavioral functioning. ABIs may be acute or chronic in nature lasting as little as hours and as long as years. A *traumatic brain injury* (TBI) can be defined as “a disruption in normal brain function caused by external mechanical force” (Gómez-de-Regil et al. 2019). A TBI is often associated with alterations in brain function that could lead to a period of reduced or complete loss of consciousness, post-traumatic amnesia (i.e., a state of disorientation to time, place, and person), and reduced memory abilities for events immediately before the accident (i.e., retrograde amnesia), or events after the accident (i.e., anterograde amnesia)

(Gómez-de-Regil et al. 2019). Etiologies of TBI include falls, motor-vehicle accidents, strikes or blows to the head, assaults, projectiles (e.g., firearms), and “shaken-baby syndrome” in young children. Traumatic brain injuries can be conceptualized as being focal or diffuse. However, most TBIs are heterogenous, often presenting with both focal and diffuse injuries (Greenfield et al. 2008). Associated neurocognitive difficulties include impaired processing speed, executive functioning and personality, visuospatial functioning, language, orientation, and attention.

A *nontraumatic brain injury* (nTBI) is differentiated from a TBI by the fact that the underlying neuropathology is a result of an internal dysfunction rather than an external force being applied to the cranium as in the case of a TBI. The most common forms of nTBI include stroke, infectious disease, seizure, electric shock, tumors, toxic exposure and neurotoxic poisoning, anoxia, metabolic disorders, hydrocephalus, and drug overdose. The effects of an nTBI are similar to a TBI; however, most TBIs tend to affect focal areas while nTBIs tend to affect multiple areas due to the spread of cellular necrosis (Greenwald et al. 2003). Both TBIs and nTBIs range in severity from mild, moderate, and severe as determined by the Glasgow Coma Scale (GCS).

Another important aspect in conceptualizing the pathophysiology of an ABI is whether the injury was primary or secondary, meaning, the insult to the brain was affected directly or indirectly (Graham et al. 2002). Primary injuries result from external mechanical forces that produce deformation of brain tissue and disrupt normal brain function. Common causes of a primary injury are acceleration-deceleration forces, rotational forces, forces generated by blast winds, blunt impact, and penetration of projectile objects. As a result, such an injury can produce damage to neurons, axons, dendrites, glia, and blood vessels. Damage to these aspects of the brain will also result in a cascade of other processes such as focal, multifocal, or diffuse patterns of alterations in cellular, inflammatory, mitochondrial, neurochemical, and metabolic functioning (Graham et al. 2002). Alternatively, a secondary injury occurs as a result of a complication with the

primary injury. Secondary injuries often initiate within hours of the primary injury and include ischemic and hypoxic damage, cerebral edema, increased intracranial pressure, hydrocephalus, and infection, all of which may be reversible (Graham et al. 2002).

Evolution of Pain and Neuroplasticity

Trauma to the central nervous system can evoke pain, an evolutionary function that provides warning to an individual in connection with the accident and onset of disease or trauma. In some instances, individuals possess genetic abnormalities that prohibit them from experiencing pain (i.e., congenital analgesia); as a result, they tend to live shorter lives compared to individuals who possess pain receptors. Darwinian evolution suggests that pain perception has evolved over time in response to *Homo sapiens*’ encounters with their environment. Such encounters would elicit specific nociceptive responses unique to the painful stimulus in question. In other words, this is classified as “good pain” as it either promotes survival or favors the fittest in some manner. Conversely, “bad pain” is not beneficial to *Homo sapiens*’ survival; essentially, pain neither promotes survival nor favors the “fittest.” Some examples of bad pain are chronic neuropathic pain and chronic migraines, conditions that emulate a kind of autoimmune response within the central nervous system. For whatever the reason, evolution has yet to improve the immune system’s response to eliminate such forms of bad pain.

Related to pain is neuroplasticity, a process where the brain is able to adapt and accommodate its structure and function both post-injury and in non-injurious situations. The concept of neuroplasticity thus negates the assumption that the brain is hardwired and functions in a fixed manner. Neuroplasticity occurs both within the brain and spinal cord, mediating both “beneficial” and “harmful” neuroplasticity. Beneficial neuroplasticity mediates neural and spinal mechanisms to adapt to changing demands in the central nervous system. Harmful neuroplasticity can lead to chronic diseases such as central neuropathic pain, tinnitus, spasm, and spasticity, and

is also involved in mediating low back pain, fibromyalgia, and chronic fatigue syndrome.

From an evolutionary perspective, chronic pain conditions are relative to *Homo sapiens*; the structure of our brains have changed compared to the *Homo neanderthalensis*. Specifically, *Homo sapiens* have enlarged primary, secondary, and association visual cortices (V1, V2, V3, V5), as well as greater volume in the temporal and parietal lobes (Pearce et al. 2013). These structures and their related cognitive processes of visuospatial organization, language, and learning and memory are integral in how pain is perceived. Thus, with greater aptitude in these respective cognitive processes, it is understandable that we are more likely to experience chronic pain conditions.

Conclusion

The preceding sections outlined how humanity has identified and tracked specific brain damage over time. This entry has discussed the advent and role of modern techniques in identifying brain damage, specifically the use of various neuroimaging and electrophysiological techniques as well as neuropsychological assessment in providing a holistic perspective in the functional impairments derived from damage to the brain. *Homo sapiens* have undergone cerebral changes as a product of natural selection. It has been well-established that there are some cerebral functions that have been selectively eliminated or bolstered as a result of changes in *Homo sapiens* environment. For example, the orbitofrontal cortex and olfactory bulbs have enlarged compared to our *Homo neanderthalensis* counterpart. Thus, olfaction may have greatly improved as a result of such evolutionary changes. Due to these evolutionary changes, an acquired brain injury affects *Homo sapiens* in a unique manner due to our higher-ordered cognitive processes that grew out of necessity related to environmental demands. Our brains have evolved to experience pain as a result of structural changes involved in the perception of pain. Over time, neuroplasticity has mediated both adaptive and maladaptive alterations in neural functioning that allow us to experience pain, but also to recover from specific brain injuries.

Cross-References

- Adaptive Plasticity
- Aplysia
- Brain Development
- Brain Imaging
- Brain Lesion Studies
- Evidence for Modularity
- fMRI
- Habituation
- Kindling
- Long-Term Potentiation
- Spontaneous Recovery

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Specific Friendships

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Synonyms

Cooperative alliances; Covariance of partner phenotypes; Homophily; Need-based support; Nonexploitative partners; Nonsexual social selection; Same-sex friendships; Similarity selection; Stable cooperation; True friends

Definition

Friendships among nonkin individuals pose benefits related to survival and reproduction. However, dyadic relationships between any two

individuals are not beneficial because of possibilities to exploit others. Selecting partners who are trustworthy is beneficial compared to forming bonds with exploitative partners. The likelihood that mutually nonexploitative and trustworthy friendships are especially beneficial is supported by the observation that individuals with non-exploitative personality traits tend to form stronger dyadic ties.

Introduction

Universally occurring friendships among nonkin humans are founded on need-based support (Hruschka 2010). Need-based support entails a commitment to support one another in situations that warrant assistance. It can be understood as a risk-pooling alliance to mitigate future uncertainties and predicaments (DeScioli and Kurzban 2009). Because predicaments tend to occur rarely and randomly, and there are few possibilities, if any, to prove *true friendship* by offering support in a time of need (Smith and Ohtsubo, Cross-reference), uncertainty regarding the commitment of the partner also characterizes friendships. In other words, a friend may not be a true friend (one who respects the coalition by helping) but instead a “fair-weather friend” (an exploiter or defector) (Smith and Ohtsubo, Cross-reference). Proposed solutions for this uncertainty include feelings of mutual dyadic irreplaceability that result, for example, from a runaway-like dyadic commitment process (Tooby and Cosmides 1996). Through the results of studies that have considered associations between personality and real-life dyadic relationships, this entry introduces the view that partner selection based on non-exploitative personality traits may be important for explaining the formation of beneficial friendships.

Nonexploitative Personality Traits

Personality traits refer to temporally stable behaviors, feelings, and cognitions through which individuals differ from one another. Traits are moderately heritable as well as moderately

observable by others. Because there are numerous personality traits, they are described by models of personality structure that combine sets of traits under a more parsimonious set of broader traits (factors) based on trait covariation. These broad trait factors are descriptive summaries of various intercorrelated traits, each of which may also have unique etiologies. An important property of personality traits is that they are envisioned as dimensional continuums that range from one pole to another, and these poles are oppositional to each other (e.g., introversion versus extraversion, agreeableness versus disagreeableness).

Current personality models often encompass or especially describe personality traits that span from *dark* to *bright*. These traits are considered highly relevant with regard to interpersonal cooperation and exploitation. Specifically, the dark ends of these personality trait continuums describe interpersonally malevolent, selfish, and exploitive behaviors, whereas the bright ends correspond to cooperative, humble, and non-exploitative tendencies, which are hereafter referred to in general as nonexploitative personality traits. One popular model of personality that encompasses such traits is the honesty-humility, emotionality, extraversion, agreeableness, conscientiousness, and openness to experience (HEXACO) model, which incorporates six broad personality factors. Of these factors, honesty-humility is descriptive of nonexploitation at the high end of the trait and of exploitation at the low end (Ashton and Lee 2007). Another personality trait model, the dark triad, focuses on three types of (non)exploitative personality traits, namely, Narcissism, Machiavellianism, and psychopathy. In this model, high scores indicate exploitation in interpersonal relationships and contexts, while low scores signify nonexploitation. The common variance among these three dark triad traits is also perfectly shared with the honesty-humility element of HEXACO, which suggests their engagement with identical personality phenomena (Hodson et al. 2018). In other words, high scores on honesty-humility and low scores on all dark triad traits are similarly descriptive of an interpersonally nonexploitative personality.

Behaviors in economic games have also illuminated the relevance of these traits for non-exploitation. Honesty-humility predicts active cooperation in dictator and public goods games when it is possible to exploit others (Hilbig et al. 2013). In addition, the trait has been associated with unconditional kindness and trustworthiness in the trust game: independent of how much money a trustor initially gives to a trustee, trustees who were high in honesty-humility returned the highest proportion, and trustees who were low in honesty-humility returned the lowest proportion to trustor (Thielmann and Hilbig 2015). Thus, individuals with a nonexploitative personality also behave accordingly in economical experiments.

Nonexploitative Personality Traits and Friendships

In the case that there are individual differences in personality traits and opportunities to select friends, it is beneficial to choose friends who are nonexploitative. This stands irrespectively of the personality of the actor; trustworthy cooperators are generally preferred. However, unconditional kindness and cooperation might be especially costly (i.e., easy to exploit) if these individuals did not often form friendship coalitions with similar companions who are also nonexploitative. This has also been the general observation in studies of real-life friends; friends tend to be similar in honesty-humility while not systematically similar (or dissimilar) in other broad personality traits (Lee et al. 2009). However, this observation of friendship similarity in honesty-humility is not a sufficient indication that two nonexploitative individuals tend to form friendship relations with each other. Friendship similarity applies to the entire trait continuum on the range from low to high honesty-humility, and it therefore conveys with comparable weight that those who are low in honesty-humility (exploitative personalities) are likely to be friends with each other. However, friendships between individuals with low honesty-humility would be inconsistent with the concept of friendships as beneficial in terms of need-based support, as support following

the occurrence of a predicament is unlikely in relationships of individuals with exploitative personalities.

In addition to examining the similarity of friends in nonexploitative personality trait dimensions, examinations of similarity-based attraction and formation of dyadic relationships have demonstrated that dyadic similarities in two other dark personality traits, namely, manipulateness and egotism, are associated with mutual liking among male military cadets (Ilmarinen et al. 2016). This finding corresponds well to the friendship similarities observed for honesty-humility of HEXACO given that the manipulateness and egotism of the supernumerary personality inventory also occupy the same nonexploitative locations in personality space with honesty-humility (Lee et al. 2005). Further examinations of this association have revealed that the similarity-attraction pattern among military cadets was not present along the entire trait continuum but instead only at the low ends of both manipulateness and egotism (Ilmarinen et al. 2016). Thus, dyadic similarity in personality is only associated with friendships at the nonexploitative ends of these personality trait continuums. This finding highlights that if there are individual differences in nonexploitative personality traits, and if individuals can select partners according to these traits, then similarities in kindness and trustworthiness are likely to influence the formation of dyadic relationships.

However, it remains unknown exactly how nonexploitative personality traits and partner selection can impact the friendship formation process to produce dyadic ties between cooperative individuals. In friendships, feelings of mutual irreplaceability – the end result of a pattern that some have suggested is essential for the evolution of friendships (Tooby and Cosmides 1996) – can result from a runaway-like process or from gradually raising the stakes (risks and benefits) in the dyadic relationship (Smith and Ohtsubo). In view of this, it is possible that partner selection initiates these processes according to individual differences in nonexploitative personality traits. This selection could be enabled, for example, through honest and perceivable signals of trust and caring for others that these individuals project in

interpersonal contexts. The active cooperation and unconditional kindness that are associated with these traits in economic games also support this idea (Hilbig et al. 2013; Thielmann and Hilbig 2015). This partner selection and the benefits of friendships may present additional significance for explaining the evolution of these nonexploitative personality traits. More work is nevertheless needed to understand how this similarity-based friendship formation in nonexploitative personality traits comes to fruition.

Conclusion

The understanding that human friendships are based on the provision of help in times of predicaments suggests that an ability to select nonexploitative partners is beneficial. Real-life friendships confirm this pattern, as individuals who are similar in nonexploitative personalities are likely to have the strongest dyadic relationships. Through trustworthiness and mutual commitment, these connections have the power to become relationships that are characterized by mutual feelings of irreplaceability, i.e., specifically beneficial friendships.

Cross-References

- ▶ [Cost of Same-Sex Friendships](#)
- ▶ [Fair-Weather Friends Versus True Friends](#)
- ▶ [Gender of Friend](#)
- ▶ [Same-Sex Relationships](#)

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Specific Phobias

- [Fears and Phobias](#)

Speech

- [Vocal Communication](#)

Speech Amplitude

- [Speech Volume](#)

Speech Intensity

- [Speech Volume](#)

Speech Loudness

- [Speech Volume](#)

Speech Volume

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Synonyms

[Speech amplitude](#); [Speech intensity](#); [Speech loudness](#); [Vocal amplitude](#); [Vocal intensity](#); [Vocal loudness](#)

Definition

The psychoacoustic terms “loudness” or “volume” are primarily influenced by the amplitude vibration (or intensity) of a sound wave. Measured in decibels, these terms assess power per unit of area in a vocalization.

Introduction

Human speech is a complex, multidimensional signal used by listeners to make a variety of fitness-relevant decisions. Evolutionary signaling theory predicts that listeners have been selected to attend to those acoustic signals that reveal (on average) honest or accurate information about the signaler (Searcy and Nowicki 2005). Evolutionary psychologists have primarily focused on a single component of speech – fundamental frequency (i.e., the primary determinant

of perceived pitch) – and its information value in intrasexual competitive contexts. For instance, a number of studies have shown that lower fundamental frequency increases perceptions of physical and social dominance (e.g., Hodges-Simeon et al. 2010). Several other components of the voice (including formant frequencies) have been investigated from an evolutionary perspective; however, few studies have examined the information content of *acoustic loudness* in order to elucidate the selection pressures that have acted on this particular aspect of the human voice (cf. Hodges-Simeon et al. 2010).

The psychoacoustic terms “loudness” or “volume” are primarily influenced by the amplitude vibration (or intensity) of a sound wave. Measured in decibels, these terms assess power per unit of area in a vocalization (Baken 1987). Because amplitude is a function of the burst of air that leaves the vocal folds, factors such as lung pressure, lung volume, torso musculature, and vocal fold size contribute to an individual’s vocal loudness (Baken 1987). Therefore, larger and stronger organisms possess the capacity to produce louder sounds, and it is this association that should make loudness a valuable signal in intersexual competition.

Among several nonhuman animals, vocal amplitude is a component of acoustic dominance displays (Soltis et al. 2009). For example, female African elephants produce increased amplitudes along with other vocal cues (e.g., longer duration and steadier fundamental frequencies) when engaging in dominance interactions (Soltis et al. 2009). Conspecifics likely attend to louder vocalizations as a signal of larger body size; however, little research has examined the relationship between loudness and body size or strength. In many territorial primate species, “loud calls” are long-distance vocalizations that serve to protect and increase territory size (and therefore resource and mating access) among males.

Loudness may also play a role in dominance assessments among humans; however, research is somewhat conflicting. Aronvitch (1976) found that both males and females make judgments of others’ dominance based on loudness. Further,

men speak with a louder volume than women (Kimble and Musgrove 1988). Several other studies (Hodges-Simeon et al. 2010; Kimble and Musgrove 1988; Page and Balloun 1978), however, found no association between loudness and judgments of dominance. These inconsistent findings may stem from variable interpretations of the word “dominant” across different studies. Several researchers have suggested that there are two routes to attain status: *physical dominance or dominance*, which is attained using force or the threat of force, and *social dominance or prestige*, which is attained with social acumen, intelligence, and unique skill sets (Henrich and Gil-White 2001).

Research suggests that vocal loudness may be associated with the use or threat of physical force in order to achieve physical dominance. For instance, several studies show that loudness contributes to perceptions of aggressiveness. In one study, researchers manipulated recordings of a female speaker’s vocal intensity, which were rated by male and female college students (Page and Balloun 1978). Results showed that loudness had a significant effect on ratings of aggressiveness, but not on dominance or self-assurance. In another study (Rose and Tryon 1979), actors produced vocalizations at three different intensities (68 dB, 76, and 84 dB). Raters assessed on a scale from 0 to 20 (sub-assertive 0–5, assertive 5–15, and aggressive 15–20). Quieter vocalizations (68 dB) were rated as sub-assertive, whereas those at the 76 dB level were rated as assertive, and loud speakers as aggressive. Results of these studies suggest that listeners may attend to speech loudness in order to assess the speaker’s motivation and intention to engage in conflict. Further, those that are motivated to engage in competition are usually confident in their ability to compete. Kimble and Seidel (1991) asked students to respond to trivia and rate how confident they felt with their answers. Those who felt more confident answered more loudly and with greater speed.

The study of perceived loudness is complicated by an interaction with fundamental frequency, that is, those with lower frequency voices are perceived as louder even when amplitude stays constant

(Baken 1987). Hodges-Simeon et al. (2010) analyzed five vocal parameters of male voices (i.e., mean F_0 , F_0 variation, loudness, utterance duration, and formant dispersion) and then used multivariate methods to assess the independent effects of these different acoustic variables on intra- and intersexual competition (i.e., ratings of attractiveness by females and physical and social dominance by males). Of these parameters, high vocal intensity significantly predicted female ratings of male vocal attractiveness – after controlling for mean F_0 , F_0 variation, duration, and formant dispersion.

Conclusion

Humans – like other animals – use complex acoustic signals when assessing potential mates or rivals, which are then used to make fitness-relevant decisions. Future studies on vocal loudness and dominance should distinguish the different routes to achieve status and use multivariate methods to tease out the independent effects of different vocal parameters on social perceptions.

Cross-References

- [Dominance in Humans](#)
- [Height and Dominance](#)
- [Indicators and Correlates of Status and Dominance](#)
- [Nonverbal Indicators of Dominance](#)
- [Signals of Body Size](#)
- [Size and Dominance](#)
- [Status and Dominance Hierarchies](#)
- [Vocal Attractiveness](#)
- [Vocal Competition](#)
- [Vocal Communication](#)
- [Vocal Indicators of Dominance](#)

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Sperm

- [Production of Eggs and Sperm](#)

Sperm Allocation

- [Sperm Competition](#)
- [Sperm Competition Theory](#)

Sperm Choice

- [Cryptic Female Choice](#)

Sperm Competition

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Synonyms

Competitive mating, Sperm allocation

Definition

Competition within a single female between the sperm of multiple males for the fertilization of the ova (Parker 1970).

Introduction

“Winning” sperm competition is largely dependent on a lottery principle. That is, the more sperm a male produces, the more likely it is he will win the competition. Thus, the most fundamental prediction generated from sperm competition theory is that males will produce and ejaculate more sperm as the risk of sperm competition increases (Parker 1982). As the proportion of time a couple spends apart since their last copulation increases, the probability that a man’s partner has been unfaithful, and inseminated by another male, logically increases. Producing more sperm in an ejaculate during copulation following a period of time spent apart from a partner may function to outnumber or outcompete sperm from rival men that may be present in the reproductive tract of the woman. Baker and Bellis (1989, 1993) demonstrated that as men spent more time apart from their partner since their last copulation, the men increased the number of sperm produced in the ejaculate at the couple’s next copulation. Researchers have also identified many possible psychological adaptations to the adaptive problem of sperm competition.

Psychological Adaptations to Sperm Competition

Shackelford and colleagues (2002) were the first to document psychological adaptations that function to decrease the likelihood that a rival man’s sperm will fertilize a partner’s ovum. They found that a man who spends a greater proportion of time apart from his partner since the couple’s last copulation rates his partner as more attractive, reports that other men find his partner more attractive, reports greater interest in copulating with his partner, and reports that his partner is more interested in copulating with him. These effects were independent of relationship satisfaction, total time since last copulation, and total time spent apart. This rules out several alternative explanations for their findings such as “men are simply sexually frustrated.” These perceptual changes may motivate men to copulate as soon as possible with their partner, thus entering their sperm into competition with any sperm from a rival male.

In order to avoid sperm competition or in order to compete more effectively, men may have evolved mate preferences that function to select as short-term sexual partners women who suggest a lower risk of sperm competition currently or in the future. Shackelford and colleagues (2004) found that men’s reported likelihood of pursuing a short-term sexual relationship was lowest when imagining that the potential short-term partner is married, moderate when imagining she is not married but involved in casual sexual relationships, and highest when imagining that she is not married and not involved in any casual sexual relationships. Shackelford and colleagues (2004) interpret these findings to suggest that when selecting short-term sexual partners, men may do so in part to avoid sperm competition.

Sperm Competition and Pornography

Pound (2002) argued that men should find cues of increased sperm competition risk to be sexually arousing because frequent copulation can be an effective method of paternity assurance. Thus,

Pound (2002) hypothesized that men would be particularly aroused by pornography that provides cues of sperm competition. An online survey measuring self-reported preferences as well as an online preference study that unobtrusively examined preferences for particular images also demonstrated results in support of the hypothesis. Pound (2002) argued that the most parsimonious explanation for these findings was that male arousal in response to visual cues of sperm competition risk reflects evolved psychological mechanisms that would motivate adaptive copulatory behaviors in ancestral males exposed to cues of sperm competition risk or female promiscuity. That is, while men may *prefer* cues that indicate no sperm competition risk, they may be especially sexually aroused if they are exposed to said cues. This arousal would facilitate copulating sooner and entering into competition with rival male sperm that may be present.

Subsequent research has also supported Pound's (2002) hypothesis. For example, Kilgallon and Simmons (2005) provided experimental evidence that men who viewed images depicting cues to sperm competition produced more competitive ejaculates than men viewing comparable images in which cues to sperm competition were absent. Recent research by McKibbin et al. (2013) also appears to corroborate Pound's (2002) hypothesis. They demonstrated that men's purchases of pornographic DVDs appear to be influenced by their evolved psychological mechanisms for sperm competition. That is, DVDs depicting cues to sperm competition sold better than those that did not.

Sperm Competition and Female Orgasm

McKibbin et al. (2010) demonstrated an effect of sperm competition on men's interest in partner orgasm. Because orgasm may bias retention of a particular male's sperm (Baker and Bellis 1995), men may benefit by ensuring their partner experiences orgasm with them. McKibbin and colleagues demonstrated that men under greater risk of sperm competition, relative to men under lesser risk of sperm competition, are particularly interested

in ensuring their partner experiences orgasm. In this way, men may be able to ensure their sperm experiences selective uptake, rather than a rival's sperm.

Conclusion

In conclusion, sperm competition theory has provided to researchers a wealth of useful predictions regarding male psychology in particular. Their findings have implications for understanding relationship dynamics, extra-pair copulations, and many other aspects of male psychology.

Cross-References

- ▶ [Female Orgasm](#)
- ▶ [Infidelity](#)
- ▶ [In-Pair Copulation](#)
- ▶ [Semen from In-Pair Partner](#)
- ▶ [Sexual Coercion](#)
- ▶ [Sexual Selection via Direct Male-Male Interactions](#)
- ▶ [Sperm Competition: Evidence in Nonhumans](#)
- ▶ [Sperm Competition Risk and Partner Abuse](#)
- ▶ [Sperm Competition Theory](#)

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Sperm Competition in Birds

► Avian Sperm Competition

Sperm Competition Risk and Partner Abuse

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Sperm competition is when spermatozoa from at least two males compete for fertilization, which occurs when a female mates with more than one male in one reproductive cycle. Multiple mating within a reproductive cycle can be costly to females, such as increasing exposure to predators and partner retribution. Recent research suggests there may also be various benefits, including mating with males with better genes, gaining additional resources, confusing paternity to improve offspring safety, enhanced status, diversifying genes, increasing social networks for employment, and replacing a low-quality

mate (reviewed in Mulder and Rauch 2009; Wilson and Daly 1992).

Sperm competition creates a selection pressure that leads to traits that either assist males with successful competition for fertilization or females with choice in paternity. Evidence for such an evolutionary process has been studied in a wide variety of species, including fish (e.g., Stockley et al. 1997), insects (e.g., Parker 1970), birds (Dunn et al. 2001), and mammals (Gomendio and Roldan 1991) by considering how physical, physiological, and behavioral traits could have evolved in response to such competition.

Although early applications of sperm competition to humans have been criticized, there has been increased attention to empirical and theoretical work in this area (Shackelford et al. 2002, 2016; Simmons et al. 2004). One area of human sperm competition that received significant attention is in the context of cuckoldry risk – in species that form pair bonds, this risk occurs when females engage in extra-pair copulation and males unknowingly raise unrelated offspring. Forced in-pair copulation (see ► “Partner Rape” entry) has been hypothesized to function by minimizing the risk of cuckoldry by engaging in sperm competition. Several studies have confirmed an association between female infidelity risk and various forms of male sexual coerciveness towards a partner, including partner rape (Camilleri and Quinsey 2009; Goetz and Shackelford 2009, 2006; Starratt et al. 2008). In particular, the association between infidelity risk and sexual coercion appears to be true only among men, and this association is strongest when there are more recent cues to infidelity (Camilleri and Quinsey 2009).

Other behaviors may have evolved to prevent the need to engage in sperm competition. For example, *herding* (i.e., aggressive separation of women from other men), *sequestration* (i.e., aggressive removal of women from their social group), and *harassment* (i.e., persistent sexual pursuit) may function by minimizing women’s opportunities for extra-pair copulations (see Camilleri and Quinsey 2012). Some evidence supports this notion that female-directed intimate partner violence may be a way to coercively

control a partner's reproductive options. Violent men were more likely to engage in actions that limited the autonomy of their partner (Wilson et al. 1995), sexual jealousy is associated with wife assault recidivism, and infidelity risk is associated with nonsexual intimate partner violence (Hilton et al. 2004).

In summary, some variation in partner-directed abuse may be explained as an evolved response to sperm competition. Though much of the research on sperm competition has focused on nonhuman animals, some scholars are testing its application to human psychology. In particular, abusive actions, such as intimate partner sexual and physical violence, may be an adaptive response to cuckoldry risk by engaging in – or preventing the need for – sperm competition.

Cross-References

- [Cuckoldry](#)
- [Partner Rape](#)
- [Sperm Competition](#)

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Sperm Competition Tactics

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Synonyms

[Adaptations to sperm competition](#); [Anti-cuckoldry tactics](#)

Definition

Sperm competition tactics refer to a suite of behaviors designed to reduce the chances of a male being cuckolded.

Introduction

Sperm competition occurs when sperm from two or more males occupy the reproductive tract of the same female simultaneously and therefore compete to fertilize ova (Pham and Shackelford 2015). Across most species, including humans, male reproductive success can be enhanced either through preventing sperm competition or winning sperm competition and achieving paternity. Failure at sperm competition, when it occurs, can result in failure to pass one's genes to the next generation and waste time and resources on biologically unrelated offspring. Therefore, males of many species have evolved tactics to both prevent sperm competition from occurring in the first place and to aid in successful fertilization in the event of sperm competition (Pham and Shackelford 2015).

Precopulatory Tactics

Before the point of copulation with a mate, sperm competition can be prevented or at least reduced. This is mainly achieved through guarding a mate from other males in various ways (Parker 1974). For example, in nonhuman animals with little paternal investment, deer engage in male-male combat with their antlers to ward off any rival males near a female of interest (Kodric-Brown and Brown 1984). Similarly, male elephant seals fight one another to gain access to a harem of females (Haley et al. 1994). Theoretical models have been applied to predict the degree of precopulatory mate guarding males will engage in, with the general finding that as the encounter rate of receptive females increases, the amount of mate guarding decreases. This is due to the possibility of missed mating opportunities. Males can increase reproductive success through

mating with multiple females within one breeding season, if that is possible. If there are limited receptive females, however, male intrasexual competition for the small pool of females will be more intense, and mate guarding is a better strategy to avoid sperm competition (Parker 1974).

Humans form monogamous pair-bonds and demonstrate heavy paternal investment, therefore sperm competition and cuckoldry is more costly to male reproductive success. Psychological tactics have then evolved to avoid sperm competition even before relationship initiation (Pham and Shackelford 2015). When men are selecting a mate, even for the short-term, they exhibit a strong preference for women who display the lowest risk of sperm competition. For example, when measuring arousal between the options of married women, those in casual sexual relationships, and women not engaged in any type of sexual relationship, men consistently show the highest arousal for women who are not currently engaged in a sexually active relationship (Shackelford et al. 2004). Similarly, Mogilski and colleagues (2014) found that men place sexual fidelity in the ideal long-term mate as a higher priority than other desired qualities such as physical attractiveness and emotional investment.

Postcopulatory Tactics

In nonhuman animals, several evolved postcopulatory sperm competition tactics have been observed. Male animals of many species, including insects, primates, and rodents, practice ejaculate adjustment, which refers to adjusting the number of sperm per insemination depending on the current risk of sperm competition. Males often rely on environmental cues to estimate sperm competition risk for this purpose. For instance, if a male notices that many other rival males are near a receptive female, he will inseminate more sperm during copulation with her than if he notices few or no rival males to give himself an advantage in the likely event of sperm competition. Increasing sperm count could outnumber the amount of

sperm from rival males in the female's reproductive tract to facilitate fertilization success (Pham and Shackelford 2015). Another tactic commonly observed in male insects (e.g., dung flies) is to interrupt coitus before the rival has a chance to ejaculate, usually by physically knocking him off of the female and to take that male's place to inseminate the female instead (Parker 1970). Also seen in insects, such as damselflies, is the tactic of semen displacement using specialized appendages (often attached to the penis) to scrape out any rival sperm from a previous copulation before the male ejaculates his own sperm into a female's reproductive tract (Waage 1979). Semen displacement can also be achieved via delayed ejaculation, in which the male copulates longer than normal to displace any previously deposited sperm with his penis before he ejaculates. In many species, prolonged copulation also serves to guard females they have recently copulated with to prevent sperm competition, and in some species, males will physically attach themselves to the female for long periods post-insemination to prevent her from contact with other males (McLain 1989).

In humans, there are similarities in sperm competition tactics used by men. Because sperm competition in humans is most likely to occur via female infidelity, men in long-term relationships attempt to keep a steady supply of sperm in their partner's reproductive tract. To achieve this, men engage in frequent in-pair copulation with their regular partner (Pham and Shackelford 2015). Not only do men try to ensure the presence of their sperm in their partner's reproductive tract at any given time, there is some evidence that men engage in ejaculate adjustment based on objective sperm competition risk. That is, men in long-term relationships inseminate more sperm per copulation with their regular partner as time apart from their partner since the couple's last copulation increases. This increased time away from one's partner objectively signals an increased risk of sperm competition (time for which her whereabouts cannot be accounted; Baker and Bellis 1993). Another tactic reported by both men and their regular female partners during copulation is possible semen displacement through deeper

thrusting when men perceive high risk of sperm competition (Pham and Shackelford 2015).

There is also evidence that men engage in postcopulatory mate guarding, albeit mainly with psychological tactics. Specifically, men in committed, sexually exclusive relationships exhibit jealousy when they suspect their partner has committed infidelity. Male jealousy motivates men to discourage infidelity through performing a range of behaviors including monitoring a mate's whereabouts, forbidding her to spend time with others without him present, and threatening to punish infidelity. In extreme cases, men will physically abuse partners who have been unfaithful or rape an unfaithful partner to quickly introduce his sperm to compete with the rival's. Additionally, male sexual jealousy is the number one cited motive for husbands to murder their wives (Kaighobadi et al. 2009).

Conclusion

Throughout evolutionary history, males of many species have faced the recurring problem of sperm competition. Like ancestral problems in other domains, tactics and strategies have evolved to avoid or reduce the likelihood of sperm competition. These tactics fall in two general categories: precopulatory and postcopulatory. Among non-human animals, mate guarding through physical male-male competition is a common precopulatory tactic to avoid sperm competition while ejaculate adjustment and semen displacement are more commonly used postcopulatory tactics. In humans, precopulatory tactics involve mate preferences designed to avoid high sperm competition risk. Postcopulatory tactics include frequent in-pair copulation, ejaculate adjustment, semen displacement, and behaviors stemming from male sexual jealousy.

Cross-References

- [History of Sperm Competition in Humans](#)
- [Physiological Evidence for Human Sperm Competition](#)

- ▶ [Psychological Evidence for Human Sperm Competition](#)
- ▶ [Sperm Competition](#)
- ▶ [Sperm Competition: Evidence in Nonhumans](#)
- ▶ [Sperm Competition Risk and Partner Abuse](#)

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Sperm Competition Theory

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Synonyms

[Male-male competition](#); [Postcopulatory sexual selection](#); [Sperm allocation](#); [Sperm expenditure](#); [Strategic ejaculation](#)

Definition

Sperm competition is an intrasexual process in which the sperm from two or more males compete to fertilize a female's ova.

Introduction

Darwin's classic view of sexual selection holds that, controlling for differences in survivorship, variation in the reproductive success of the members of one sex can be attributed to two main processes. First, the members of one sex (usually females) preferentially choose to mate with certain members of the opposite sex (usually males), leading to the evolution of sexual “ornaments,” “seductive” traits, and sexual “advertisements.” Second, members of one sex (usually males) directly compete against each other for access to sexually receptive members of the opposite sex (usually females), leading to the evolution of weaponry. These processes are commonly referred to as female mate choice (or intersexual sexual selection) and male-male competition (intrasexual sexual selection), respectively. Darwin's description of these processes extended no further than the precopulatory stage. In 1970,

however, Geoff Parker (1970) recognized that male-male sexual competition can continue after copulation: if a female mates with more than one male during her receptive period, as is the case in most animal species, then sperm from different males can compete for access to the same set of eggs. And, by analogy with female mate choice, females could also use various mechanisms to bias paternity towards preferred males (so-called cryptic female choice).

Over the last three decades, numerous studies have investigated which male traits are favored by postcopulatory sexual selection (i.e., sperm competition and cryptic female choice). Candidate traits include aspects of the size or shape of genitalia, grasping or clasping structures used during mating, courtship behaviors during and immediately after copulation, mate guarding after mating (to reduce the chances that the female remates), seminal proteins, and other chemicals transferred to females during mating (Leonard and Cordoba-Aguilar 2010; Perry et al. 2013; Peretti and Aisenberg 2015). Here, we focus on the evolution of the sperm component of ejaculates, more specifically the number, type, and quality of the sperm.

Sperm Quantity: The Numbers Game

The single best predictor of male fertilization success under sperm competition is to inseminate more sperm than your rival. Indeed, almost all the current theoretical models developed to study “sperm competition games” (Parker 1998; Parker and Pizzari 2010) explore evolutionary stable strategies for investment into numerical sperm production and maximizing the retention of sperm by females. More importantly, game theory models suggest that increases in sperm size that decrease sperm number will only be favored under restrictive conditions (Snook 2005). Below we describe game theory models that predict ejaculate size and then, where applicable, review the evidence from: cross species comparisons (phylogenetic comparative analyses); creating a scenario in the laboratory, such as variation in the level of multiple mating by females

that should affect the strength of sexual selection, and then watching evolution unfold (experimental evolution); studies of changes in ejaculate size under different conditions, such as mating with a virgin or nonvirgin female (phenotypic plasticity studies); and studies of differences in sperm production and ejaculation strategies between different male mating types, such as large, socially dominant males and smaller, “sneaky” males.

Game Theory Models of Ejaculate Size and Expenditure

Mathematical models – predominantly gametheory models – have provided a solid base from which to predict the evolutionary stable strategy (ESS) (i.e., the most profitable outcome given the decisions taken by other males in the population) for ejaculate expenditure (E) or ejaculate size (s). These models cover a wide range of biological scenarios, and, for example, vary in whether fertilization is external or internal; whether male-female interactions affect sperm survival; whether or not competing males are related; the extent to which sperm properties (e.g., size, survival, swimming speed) or other ejaculate chemicals affect fertilization success; whether there is an effect of females being virgins or having already mated; whether females vary in quality; whether males vary in the individual costs associated with mating and/or in the resources they have available to invest in reproduction; whether males switch between different mating roles or have a fixed mating role for life (i.e., social mates vs. unpaired males), when roles differ in how initial ejaculate size translates into relative fertilization success (i.e., favored and disfavored mating role with respect to the likelihood that a given sperm will end up fertilizing an egg); whether males have perfect or imperfect information about the risk of sperm competition; how males respond when the risk of sperm competition or the intensity of sperm competition is above or below the population average; and, finally, whether the model allows feedback so that ejaculate size affects the mean level of sperm competition (Parker 1998; Simmons 2001; Parker and Pizzari 2010).

Most mathematical models assume that a male has a fixed amount of resources R that are allocated to reproduction. These resources can be divided between investment into obtaining mates (where C is the cost of mating) and investment into larger ejaculates (where D is the cost per unit of ejaculate). A male's lifetime fitness is the product of the number of times he mates and his average fertilization success per mating. The ESS is the ejaculate size (s^*) that maximizes lifetime fitness when all males pursue the same investment strategy in the equivalent mating context (i.e., the strategy can include tailoring the ejaculate size to the specific mating context, such as a virgin vs. nonvirgin female). Clearly, mating success will increase under precopulatory sexual selection as more resources are devoted to traits that increase access to mates (e.g., weapons or ornaments) (Parker et al. 2013); while a larger-sized ejaculate will increase a male's average fertilization success under sperm competition.

The models vary in how ejaculate size predicts relative fertilization success. The simplest models assume a raffle-like process, whereby a male's relative numeric share of the competing sperm determines his success: the more sperm per ejaculate, the higher a male's fertilization success ("fair raffle"). Modifications to this assumption are then made to account for cases where the raffle is "loaded" so that certain mating roles have a higher likelihood of fertilizing eggs. That is, some male's sperm are more likely to enter the "fertilization set" of sperm that can then compete for eggs in a raffle-like manner. This differential likelihood of fertilization could arise due to: mating order effects (e.g., first or last-male sperm precedence), temporal effects (e.g., if sperm are steadily lost from the female's reproductive tract after ejaculation, then mating shortly before eggs are fertilized is advantageous), or positional effects (e.g., guarders release sperm closer to the eggs and/or moment of egg release than do sneakers). With a few exceptions, the models do not assume that females favor fertilization by specific males (i.e., there is no cryptic female choice).

If there were no constraints, males would produce an infinitely large ejaculate to numerically swamp their rivals. But because sperm production

incurs nontrivial costs males should facultatively adjust their investment in ejaculates depending on the likely benefits (Wedell et al. 2002). This facultative adjustment in sperm production (or generation of specific sperm traits) is known as "strategic ejaculation." Given finite resources, males should also experience an energetic trade-off between ejaculate expenditure and investing in morphological and behavioral traits that increase mate acquisition (Parker et al. 2013). Indeed, males are known to become sperm depleted, so there is a demonstrable direct trade-off between the number of matings per unit time and fertilization success per mating under sperm competition. For simplicity, most models assume that all males have the same resources R available to invest into reproduction and pay the same costs for ejaculate production or to obtain a mating. The main exception is in models where males are divided into two discrete classes that vary in the average level of sperm competition they experience so that the ESS for each class is predicted. Recently, however, models have been developed that allow for continuous variation among males in available resources and/or variation in the costs paid to elevate mating rate/ejaculate size (Parker and Pizzari 2010). Lower costs of mating lead to a reduced investment in ejaculates because the comparative rate of return from increasing the mating rate more than compensates for a lower fertilization rate per mating.

Broadly speaking, sperm competition game models are divided into those that consider sperm competition risk (whether or not it occurs) or intensity (the number of ejaculates competing for a set of eggs). The "risk" models investigate the effect of variation in q (the probability that two ejaculates compete). Note that early models use an alternate formulation with p , which is the probability that an ejaculating male will face sperm competition from another male [$p = 2q/(1-q)$] (Parker 1998). Risk models are usually envisaged in terms of internal fertilizers and the likelihood that a female will mate twice, while "intensity" models are framed in terms of external fertilization and variation in the number of males (N) ejaculating when a female spawns. They can, however, be applied to both fertilization

modes. Treating risk and intensity separately is a mathematical convenience as the two actually “overlap” (e.g., they should produce the same predictions when $q = 1$ and $N = 2$). Williams et al. (2005) argue that the distinction between the intensity and risk of sperm competition is untenable because the two factors depend on the mean and variance in female mating rate. Risk and intensity are not independent variables if they covary, as is the case, for example, when the number of matings per female approximates a Poisson distribution (see also Fromhage et al. 2008). Engqvist and Reinhold (2005) provided a concise, cautionary account of why treating risk and intensity as independent is problematic when empirically testing models. Their main point is that assumptions have to be made about whether an experiment alters the perceived risk *or* intensity of immediate sperm competition *and/or* the future expectation of the mean level of sperm competition. That is, an experimental treatment with more males per female increases the immediate intensity of sperm competition and the likelihood that a female will mate with at least two males (i.e., risk).

The main prediction of both risk and intensity models is that as the mean risk or mean intensity of sperm competition increases the proportion of the total reproductive effort per mating devoted to ejaculate expenditure ($E = Ds/(Ds + C)$) increases. The rate of increase in E is, however, linear as risk increases but asymptotic as intensity increases (Parker and Ball 2005). E is an index of sperm demand and often estimated empirically by calculating relative testis size (Parker 2016) (i.e., assuming that testis size is a measure of sperm production capacity). The optimal value of E with a fair raffle is $E^* = q/2$ or $(N-1)/N$ (Parker 1998; Parker 2016). This predicts that the mean value of E will be greater in species with a higher mean level of sperm competition. However, if there is a loaded raffle, the payoff to investing in a given mating decreases so that E^* (total reproductive effort) should decline (Parker and Pizzari 2010). Consequently, in taxa where there is strong first or last male fertilization advantage, variation in the risk of sperm competition among species should have little effect on E^* . If a male is in the favored

position, he already has high fertilization success so there is little to be gained by investing more into the ejaculate, and if he is in the unfavorable position, the large amount of additional sperm he would have to produce to substantially increase his fertilization success becomes prohibitively expensive. Relative ejaculate allocation should therefore be lower under the loaded raffle versus a fair raffle.

The magnitude of E^* depends on whether males occupy roles randomly or consistently (although this is obviously an analysis of the extremes of a continuum). If roles are random, males produce the same-sized ejaculate even when they are in the disfavored role (e.g., mating second when there is sperm precedence) ($E^*_{\text{favored}} = E^*_{\text{disfavored}}$). This occurs because the benefits of increasing ejaculate size when a male is in the disfavored role (to counter the lower share of paternity) exactly balance the costs of so doing (fewer resources to invest in future matings where there is an equal chance of being in the favored role). In contrast, when roles are nonrandom, as in the case of alternative mating morphs, there is selection for males in the disfavored role to produce larger ejaculates (Parker 1998; Parker and Pizzari 2010) ($E^*_{\text{favored}} < E^*_{\text{disfavored}}$), assuming that the costs of sperm production do not differ between roles.

An asymmetry among males in the information that they have about q should affect E^* . Parker (1998) and Parker and Pizzari (2010) envisaged two scenarios: each male mates with his social mate and engages in an extrapair copulation (EPC) with some fixed probability or males either play the role of guarder or sneaker. In both cases, certain males (sneakers or those performing an EPC) “know” that there will be sperm competition once they ejaculate ($q = 1$), while other males only know the average risk of sperm competition (mean q). The predicted E^* is greater for males that know there will be sperm competition (e.g., sneakers), although the difference in E^* will be vanishingly small when the probability that mating involves a sneak is very high (i.e., as mean q approaches 1). Finally, males might have information about whether q is above or below average for a specific mating event (i.e., an opportunity for

strategic ejaculation). This has been modeled in the context of a female's mating status or propensity to remate, but it is also relevant when males can use social cues (e.g., the presence of rivals) to estimate the likelihood of sperm competition. If the likelihood that a female mates twice is q then when a male has perfect information about a female, E^* varies between the minimum required to fertilize her eggs if she will mate once and $(1 + q)/4$ when she will definitely mate twice. More realistically, if males can distinguish between virgins (some of whom will not remate) and mated females then for all mean values of q (except 0 and 1 where the likelihood of remating is known) E^* is greater when mating to a mated female ($q/[1 + q]$) than a virgin female ($q/2/[1 + q]$) because the expected level of sperm competition is higher (Parker and Pizzari 2010; but see Kelly and Jennions 2011).

In species where most breeding events involve sperm competition (i.e., most females mate multiply or group spawn so that $q \approx 1$) within-species "intensity" models predict how ejaculate size changes with the number of males (N) per spawning event. Unlike the case for an increase in sperm competition risk within a species, or of mean risk/intensity across species, the prediction is that E^*_i decreases as the number of males competing in a given reproductive event increases beyond two. For example, if males have perfect information about the number of rivals, N_i , and the distribution of males per reproductive event follows a Poisson distribution with mean N_m then $E^*_i = N_m(N_i - 1)/N_i^2$. There is an increase in E^*_i as N_i goes from a solitary male without sperm competition so that s^* is the minimum required to fertilize eggs to a maximum when there are two males (i.e., the risk of sperm competition q goes from 0 to 1), but thereafter as N_i increases, E^*_i declines. This occurs because the value of each sperm released is diminished: the number of eggs available remains constant while the total number of sperm (due to the participation of more competitors) increases. Consequently, the marginal returns from the release of additional sperm are reduced, so the optimal ejaculate size is smaller (Parker 1998). In short, males are better off "saving" sperm for a future breeding event with fewer

competitors. Despite this decline in ejaculate size, however, after taking into account the greater number of matings that males must be engaging in when the intensity of sperm competition is higher, the mean investment in sperm expenditure E^* still increases with the average intensity of sperm competition (i.e., N_m) (Parker 2016).

At the within-species level, several models have investigated how mating roles and/or other predictable deviations of q or N from the species/population mean affect the optimal ejaculate size (s^*) for a given mating event. For simplicity, "risk" models consider cases where there are only two mating roles (favored and disfavored), males "know" their mating role and females mate at most twice. The focus is therefore on s^* when the probability that sperm competition is present or absent changes. Results are, however, usually presented in terms of E^* because it is a unitless parameter useful for comparison across species or morphs. In addition, relative testes size is a measurable trait that is assumed to be positively correlated with E^* if there is selection for larger testes size when the product of the "sperm demand" per mating and the mating rate is higher. Relative testes size can, therefore, be used to test predictions about E^* only in cases where E^* represents the mean sperm allocation for a species or population (Parker and Pizzari 2010).

Parker and colleagues' early models did not consider how, given limited resources and a cost to mating, increasing s^* will decrease the maximum number of matings in which a male can participate ($R = N_m(s + C)$, where N_m = number of matings) which lowers the mean intensity (i.e., N_m). Crucially, this also changes the variance in the number of mates per female, hence the likelihood of sperm competition (i.e., q) thereby creating a feedback loop that affects s^* (Williams et al. 2005). Given the feedback affects both N and q , sperm competition risk and intensity cannot be separated. Williams et al. (2005) allowed the sperm allocation strategy to evolve by varying the resources available for reproduction. They then explored the consequences for mean s^* under various scenarios (E^* was not presented). For simplicity, they did not model strategic ejaculation and only explored cases where ejaculate

size per mating was constant across a male's lifespan (i.e., evolution in response to mean sperm competition level). Their model produced two novel predictions that differed from those of earlier models. First, in populations/species where the total resources that males can allocate to reproduction R increase, s^* increases. Greater R increases the maximum number of matings per male, which increases the number of multiply mated females (and hence sperm competition), which elevates s^* . Second, in agreement with Parker (1998; Parker and Pizzari 2010) the model predicted that s^* increases as the cost of mating increases when there is a fair raffle, however, with a strong mating order effect s^* actually decreases. This occurs because a higher mating cost initially selects for a larger ejaculate, but this decreases the number of matings per male, which lowers sperm competition levels and favors a smaller ejaculate. The relative strength of the two opposing forces of selection on s^* depends on the fairness of the raffle. When the raffle is loaded, the gains from a higher mating rate can outweigh those from greater fertilization success per mating. The wider implication of these results is that variation in mating costs among populations/species could, somewhat counter-intuitively, lead to greater sperm competition risk/intensity being associated with lower s^* .

More recently, Fromhage et al. (2008) pointed out that an implicit assumption in Williams et al.'s model is that males determine the female mating rate which generates the feedback between the level of sperm competition and s^* . Fromhage et al. (2008) therefore modeled the effects of variation in female resistance to unwanted mating attempts. Encouragingly, their model captures the essence of the models of Williams et al. and Parker and colleagues. They show that these earlier models produce results that lie at the ends of a continuum. When female resistance is absent, they obtain comparable results to Williams et al. (2005), and when resistance is strong they produce results comparable to those of Parker's classic models. For example, when female resistance to excessive mating is strong, s^* tends to increase with greater mating costs. The model also shows that as the mean risk of sperm competition

(q) increases s^* can increase, decrease, or remain unchanged depending on the level of female resistance. As the mean intensity of sperm competition (N) increases s^* can decrease or reach a maximum at an intermediate level of N that depends on the level of female resistance. Even so, the classic predictions that E^* decreases with greater mating costs and increases with a greater risk or intensity of sperm competition holds regardless of the level of female resistance. Finally, Engqvist and Reinhold (2007) produced a model predicting that variation among males in their sperm reserves creates a difference in the direction of the relationship between ejaculate size and sperm competition intensity: the relationship is negative for males with small reserves and positive for those with large reserves.

Resolving Areas of Confusion

The development of numerous sperm competition game models has generated confusion about what predictions should be made when conducting empirical studies of strategic ejaculation (Engqvist and Reinhold 2005; Parker and Pizzari 2010). The most obvious concern is to make sure that the predictions being tested are not derived from a model referring to the mean level of sperm competition (i.e., a species-level model). More specifically, there is sometimes a failure to answer two key questions to ensure that the correct prediction is tested: (i) What is the measure of ejaculate expenditure (i.e., s or E)? and (ii) Does the scenario or experiment involve a change in the risk *or* the intensity of sperm competition?

- (i) A distinction must be drawn between ejaculate size s and relative expenditure on ejaculates per mating E . Species-level risk and intensity models make different predictions about how ejaculate size changes with sperm competition: E (and relative testis size) increases as the mean levels of sperm competition risk and intensity increase (Parker and Ball 2005); however, ejaculate size (s) increases with the mean risk of sperm competition ($s^* \propto q/(1+q)$) but declines with intensity when the mean number of competitors (N) increases beyond two males

($s^* \propto (N-1)/N^2$) (Parker and Ball 2005). Fromhage et al. (2008) extended these models by varying the cost of mating and by including female resistance to excessive matings, which influences risk levels by modifying the variance in female mate number. They predict that s^* can increase, decrease, or remain unchanged depending on the level of female mating resistance (Fig. 2a in Fromhage et al. 2008). Similarly, when the cost of mating varies, s^* either decreases or reaches an intermediate peak then decreases as N increases. Predictions about ejaculate size changes are therefore less straightforward than they once appeared. Even so, Fromhage et al. (2008) support the standard prediction that E increases as sperm competition risk or intensity increases.

- (ii) The conceptual distinction between the “risk” and “intensity” of sperm competition is theoretically worrisome and might be empirically intractable. For example, intensity models show that ejaculate size increases when there is a shift from no rival to one rival male and then declines as additional competitors participate. However, the very possibility of there being no rival means that there is a probability that can be attached to whether or not sperm competition occurs (i.e., the risk is less than 100%). Parker (1998) has noted that risk and intensity models represent two extremes and that one would ideally use a probability distribution of the number of competing ejaculates per breeding event. Unfortunately, this has to be calculated empirically or based on assumptions about how males and females interact (e.g., the use of Poisson distributions by Williams et al. (2005) who assume that males control whether mating occurs).

Engqvist and Reinhold (2005) highlighted that there is currently a theoretical grey area where the risk and intensity models meet. We know ejaculate size will increase with a greater risk of sperm competition, but once sperm competition is certain it will decline as the intensity increases. The question is therefore one of determining the

position of the “peak” ejaculate size. This is an important question because it can be almost impossible in experiments to know whether a manipulation (e.g., the presence/removal of a rival male) has altered the focal male’s perception of the risk and/or the likely intensity of sperm competition. First, varying the number of potential competitors could alter both factors if the likelihood that a given male competes is less than one (Pitfall2 in Engqvist and Reinhold 2005). Second, a manipulation might affect the focal male’s perception not only of the immediate risk/intensity of sperm competition but also of the future mean risk/intensity (Pitfall1 in Engqvist and Reinhold 2005). This is problematic because changes in the immediate and the future intensity of sperm competition create opposing selection on ejaculate size. An increased future (hence mean) value generally selects for larger ejaculates (Fromhage et al. 2008; Parker and Pizzari 2010), while an increased immediate value selects for a smaller ejaculate (Parker 1998). The combination of uncertain theoretical predictions at the risk/intensity interface and practical problems in designed experiments makes it difficult to design experiments to test specific models of strategic ejaculation. In practice, using meta-analyses to summarize the empirical results obtained for specific experimental designs might provide insights into how different set-ups affect male’s perception of sperm competition levels.

Evidence that Sperm Competition Favors Greater Sperm Production

The most widely invoked evidence that sexual selection favors greater sperm numbers comes from comparative studies. Sperm production is usually defined as the proportion of reproductive resources invested into ejaculates (E) and is often empirically measured as relative testes size (i.e., corrected for body size) (Parker 2016). Ejaculate size (s) and relative testes size need not evolve in the same direction across species, although earlier game theory models did not make this clear (Parker 2016). The ESS for ejaculate size depends on the level of sperm competition, which depends

on how often females mate. The ESS for sperm production, hence E , depends on ejaculate size and the male mating rate. But, given that every mating involves a male and female, if males mate more often, so do females. This means that the male mating rate and ejaculate size are linked because the higher the male mating rate the greater the level of sperm competition.

The crucial factor in determining whether there is a positive correlation in changes in relative testes size and ejaculate size across species is whether variation in sperm competition is mainly associated with the risk of its occurrence or the intensity of competition. As described earlier, the marginal returns (i.e., change in fertilization success) with each additional sperm diminish as the number of rival sperm (i.e., number of rivals) increases – so the ESS ejaculate size actually decreases as the intensity of sperm competition increases. In contrast, the returns on each additional sperm continue to increase monotonically as the risk of rival sperm being presented increases – so the ESS ejaculate size increases with the risk of sperm competition. The net result is the prediction that ejaculate size will increase with greater *risk* but decline when the *intensity* of sperm competition increases (a prediction that is often assumed only to apply within-species) (Parker 1998; Parker and Pizzari 2010). Predictions about the species level relationship between ejaculate size and sperm competition, therefore, depends on whether the general level of sperm competition is low or high. Many researchers are seemingly unaware of this prediction, perhaps because it was not clearly stated in Parker's early papers. In contrast, the ESS for sperm production, hence E , increases with the level of sperm competition regardless of whether there is a change in the risk or intensity of sperm competition. Even though it depends on both ejaculate size and the male mating rate the effect of the later is more important.

The distinction between relative expenditure and ejaculate size should be borne in mind when interpreting studies of relative testes size. Relative testes size is a common index of ejaculate expenditure, and there is good evidence that larger testes, with a presumably greater mass of sperm

producing tissue, increase sperm production (sperm per unit time) (Parker 2016). This relationship is reassuring given that simple measures of testes mass do not take into account the potential for mass independent variation in sperm production (i.e., production rate per unit volume), changes in the ratio of sperm-producing tissue to other tissue types, and any effects of sperm size on testes size (Parker 2016). In contrast, the relationship between relative testes size and individual ejaculate size (corrected for body size) is less certain. For example, sperm number per ejaculate can be increased via changes in the social environment without a change in testes size in mice (Ramm and Stockley 2009) and, more generally, this is always the case whenever there is strategic ejaculation and ejaculate size changes in response to the local mating context. Ideally, studies investigating selection on ejaculate size need to directly count the number of sperm per ejaculate rather than use static measures such as testes size or even rely on proxy measures such as ejaculate volume. In short, testes size could increase under sexual selection to produce more ejaculates of the same (or even of a smaller) size, rather than selection to produce both more *and* larger ejaculates. It is inappropriate to use relative testes size to test predictions about ejaculate size, although this is a commonplace inference.

1. Comparative studies

Researchers use the comparative method to investigate the relationship across species or populations between sperm traits and estimates of sperm competition. Species differ greatly in how males allocate resources to traits that increase precopulatory success versus postcopulatory success (Parker et al. 2013). Consequently, it is possible that greater sperm competition might not lead to greater relative testis size if sexual selection strongly favors male investment in precopulatory traits (Lüpold et al. 2014). Therefore, negative phenotypic correlations that are seen within species might not occur at the species-level (Fitzpatrick et al. 2009) or might vary even among related taxa (e.g., Immler and Birkhead 2007).

Comparative analyses across a wide array of taxa show that relative testes size is greater in species that experience higher levels of sperm competition. This is true for estimates of sperm competition based on social group size, rates of extrapair paternity, direct evidence for sneak matings, measures of individual mating rates, female propensity to remate, frequency of sneak males, and so on (Parker 2016). Similar patterns are also seen among populations within a species. For example, relative testes size increases with the level of polyandry in house mice (Firman and Simmons 2008). It has been suggested, however, that a positive relationship between testes size and sperm competition is less likely in invertebrates, especially insects, as more complex sperm storage and the evolution of mechanisms for sperm displacement and removal reduce the importance of the number of sperm inseminated per male in determining paternity (Simmons 2001).

The consistent weakness of all comparative analyses is that while correlations can be detected, causation can only be inferred: experiments are needed to determine causality. Even so, the comparative method has been fruitful. The testis size-sperm competition relationship is sufficiently well established that many studies now use relative testes size as a surrogate measure of the level of sperm competition (Parker and Pizzari 2010; Parker 2016). Even so, some researchers have pointed out there are assumptions, methodological and analytical problems, and potential pitfalls associated with the use of testes size in comparative analyses (Calhim and Birkhead 2007). Ideally, future studies will better distinguish between the sperm producing and non-sperm-producing component of testes, control for ecological factors unrelated to sperm competition that might influence testes size and spermatogenesis, and take into account that sperm production rate can vary per unit mass of testes (Ramm and Schärer 2014; Giannakara et al. 2016).

Comparative studies that directly report on the relationship between ejaculate size (or a proxy thereof other than relative testes size) and level of sperm competition are rare. A comparison of 15 species of *Cataglyphis* desert ants showed that males in species experiencing greater sperm

competition (the number of males that contribute to offspring production by a queen) produce more sperm (after controlling for male size) (Aron et al. 2016). One conceptual issue with such studies is whether testes mass should be controlled. So doing could obscure a relationship between sperm competition and ejaculate size if the main mechanism by which ejaculate size is increased is through the development of larger testes size (as opposed to an increase in sperm production per unit volume of testes).

2. Experimental evolution

Experimental evolution studies of the effects of sperm competition generally involve establishing selection lines in which each successive generation is derived from females that are either forced to mate monogamously (i.e., no sperm competition, cryptic female choice, or sexual conflict) or from females that are allowed to mate with several males (polyandrous). The resultant evolution of male traits after several generations is recorded and any divergence between selection lines, beyond that expected by drift, is attributed to postcopulatory sexual selection and/or removal of sexual conflict over mating rates. Most experimental evolution studies have reported fairly large changes in at least some aspects of ejaculate production. This implies that there is active selection against traits favored by postcopulatory sexual selection in monogamous lines, presumably because such traits are costly. Comparison of monandrous and polyandrous selection lines has, for example, shown the evolution of smaller relative testes size (Gay et al. 2009) and fewer sperm (Firman and Simmons 2011) in monogamous lines.

3. Comparison of mating tactics or social status

Parker (1990; see also: Parker 2016) used game theory models to predict that when there is competition for mates, males in the favored behavioral role, who are less likely to be subject to sperm competition or have an inherent advantage under sperm competition (i.e., there is a loaded raffle), should invest fewer sperm per

ejaculate or have smaller relative testis size than those in the disfavored role (i.e., sneaks). This could lead to permanent differences in investment in ejaculates when males pursue distinct mating or reproductive tactics. Males that consistently pursue a minor strategy (e.g., “sneaker” or “satellite”) always release sperm when another male is present (or has already mated) and therefore have a greater average risk or intensity of sperm competition than those pursuing the major strategy (e.g., a territorial male), who will sometimes mate in the absence of sperm competition. Major males should, therefore, invest more heavily into the production of competitive ejaculates (Parker 1990). A caveat is that the predicted difference depends on the frequency of minors: if they are sufficiently abundant then the risk/intensity of sperm competition experienced is likely to be almost identical for all males. The same argument can be extended from discrete morphs to continuous variation in male social status (e.g., when dominant males are more likely to have exclusive access to females and therefore suffer a lower risk of sperm competition than subordinate males). The use of evidence from morphs or social rank is based on “all else being equal” assumptions about trade-offs between investment into ejaculates and other traits that might not hold. For example, dominant males with access to many females might be at greater risk of sperm depletion and therefore have to trade-off ejaculate size against the total number of matings; or morphs might differ in the fitness returns from investment in traits that increase mating opportunities as opposed to relative fertilization success; or guarder males might invest more heavily in mate guarding to reduce sperm competition than in testes size to increase success under sperm competition; or males that pay a lower cost to obtain a mate (e.g., attractive males) might invest fewer sperm per mating (Parker and Pizzari 2010).

The evolution of differences in sperm expenditure between discrete mating types has mainly been studied in insects and fish, while studies of frogs, birds, and mammals have mainly looked at continuous variation in traits that might affect the extent to which males are in the favored role (Birkhead and Møller 1998; Simmons 2001;

Parker and Pizzari 2010). Simmons et al. (2007b) used *Onthophagus* dung beetles to test the prediction that across species male expenditure on the ejaculate should increase with increasing probability of a sneak mating. Their comparative analysis showed that as predicted smaller, sneaker males (“minors”) have relatively larger testes than guarding males (“majors”) in 14 of 16 species, and in nine species the difference is statistically significant. Many studies on fish show that sneakers have larger relative testes size and/or higher sperm density per ejaculate (Pitnick et al. 2009a). If sperm density is higher then, assuming ejaculate volume is the same, this will lead to larger ejaculate size (defined as total sperm count).

Several studies have examined body condition, body size, or social status as traits that might affect male access to females, hence being in the favored role. For example, in the frog *Crinia georgiana* larger males more often tend to amplex with females during mating, while smaller males tend to be sneakers occupying a more peripheral position. These mating roles are, however, plastic so the same male might find himself in both situations. One study found no difference in relative testes size or ejaculate volume between males captured as guarders or sneakers (Byrne 2004) and a follow-up study confirmed that there was also no difference in ejaculate size between large and small males (Hettyey and Roberts 2007). In contrast, in Arctic charr, subordinate males have larger ejaculates than dominant males (Rudolfson et al. 2006).

4. Phenotypic plasticity in the form of strategic ejaculation

Evidence of phenotypic plasticity in sperm traits in response to variation in known costs and benefits (i.e., costs of producing a different ejaculate weighed against the benefit of the likely number of offspring that will be sired by the focal male) provides the most powerful argument for the extent to which postcopulatory sexual selection favors specific ejaculate traits (Wedell et al. 2002). Selection can sometimes favor facultative or strategic adjustment of ejaculate traits by

males in different mating contexts (delBarco-Trillo 2011; Kelly and Jennions 2011). The key underlying premise of strategic ejaculation is that producing more sperm or generating specific aspects of individual sperm (e.g., tail length) is sufficiently costly that males can profit from adjusting investment into ejaculates depending on the likely net benefits. The secondary premise is, as with all cases of adaptive phenotypic plasticity, that males have informative cues about the costs/benefit of a given level of investment and that the costs of changing their phenotype are sufficiently low to make this worthwhile. The meta-analysis of empirical studies suggests that the rate of return from an ejaculate depends on the number of unfertilized eggs available (e.g., female size) and the risk of sperm competition (Kelly and Jennions 2011). There is less evidence, however, that males allocate fewer sperm when more rivals are present or transfer less sperm when mating with virgin females (Kelly and Jennions 2011).

Is Sperm Quality Sexually Selected?

Although relative sperm number is often the best predictor of a male's fertilization success, even after controlling for mating order effects (i.e., first or last male sperm priority), it still only accounts for a modest proportion of the total variance in success (Snook 2005). If this is not solely attributable to measurement error, then much remains unexplained. One possibility is that certain sperm traits affect fertilization success. There is tremendous variation in sperm morphology and movement among related species, among populations of the same species, and even among males within a population (Pitnick et al. 2009a). Why? One suggestion is that variation in sperm morphology might arise due to cryptic female choice (i.e., male-female interactions and sperm selection), which partly determines males' fertilization success (Pitnick et al. 2009b).

Sperm traits that are potentially under sexual selection when females mate multiply include: sperm viability or longevity; swimming speed/motility; sperm size or length (often measured as

total length, but this can be subdivided into different components such as tail, midpiece, and head length); and sperm type (heteromorphism). These sperm traits (whose expression is sometimes mediated by changes in seminal fluid composition) are often collectively referred to as "sperm quality," which is a measure of fertilization success controlling for sperm number (Birkhead and Møller 1998). The available evidence varies widely for the influence of each trait on ejaculate competitiveness. Here, we consider four main aspects of sperm: longevity, speed, size, and shape/type. As with selection on sperm number, we present evidence that these traits are under selection from: within species studies (i.e., correlations between the focal trait and fertilization success under sperm competition); comparative analyses; experimental evolution (monandry vs. polyandry); comparison of mating types; and studies of adaptive phenotypic plasticity.

1. *Sperm viability or longevity*

Sperm viability is the proportion of live sperm in an ejaculate. Hunter and Birkhead (2002) found that, within seven pairs of closely related species of insect, the species with a higher estimated level of sperm competition tended to have greater sperm viability. Similarly, Fitzpatrick et al. (2009) found that across 29 species of African cichlid fish sperm longevity was greater in species with a higher risk of sperm competition. All else being equal this makes sense as the more sperm that are alive, the greater the likelihood of increased fertilization success relative to a rival. This does, however, imply that there is a cost to increasing longevity. For example, it has been suggested that in external fertilizers (where fertilization occurs shortly after ejaculation) males trade-off reduced sperm longevity against other traits that allow sperm to reach the eggs more rapidly (Pizzari and Parker 2009). It is important to note, however, that the majority of studies investigating the effect of sperm quality on fitness are correlational. Thus, sperm longevity, for example, might always have the same functional effect, but be obscured by variation in other sperm/ejaculate traits that effect fertilization

success, but do so differently across species (e.g., sperm size is probably more important in some species than others), and that affect resource allocation to sperm longevity. Unfortunately, the challenge of experimentally manipulating individual sperm traits is enormous. Causality therefore has to be inferred based on correlations and other indirect types of evidence.

Sperm viability and longevity appear to be phenotypically plastic traits that males can adjust in response to social changes that should affect sperm competition levels. For example, in *T. oceanicus*, sperm viability is a good predictor of a male's relative fertilization success (Garcia-Gonzalez and Simmons 2005). Males produced ejaculates with an intermediate level of sperm viability when mated to virgin females, higher sperm viability when mated to a once mated female, and far lower sperm viability when mated to an already multiply-mated female (Thomas and Simmons 2007). This variation in sperm viability is assumed to be a response to male assessment of how many times a female has already mated based on chemical cues left by previous males. In addition, there is evidence that males adjust sperm viability based on cues about the future level of sperm competition, such as the number of rival males they encounter before mating (Simmons et al. 2007a).

2. Sperm swimming speed and motility

One might predict that sexual selection favors fast swimming sperm that reach unfertilized eggs before the sperm of rivals (Pizzari and Parker 2009). In practice, predictions about the association between sperm swimming speed and sperm competition are complicated by potential trade-offs with longevity and/or size that can also be under selection, although the nature of any such trade-offs remains uncertain (Pizzari and Parker 2009). If fertilization is delayed (e.g., due to sperm storage in internal fertilizers), then selection might actually favor slower sperm (if this increases survival time in the female reproductive tract) or faster sperm (to more rapidly reach female sperm storage organs where survival rates are higher). In external fertilizers, however,

it is generally assumed that swimming speed is more important than longevity.

In a comparative analyses of 29 African cichlid fish there is evidence that species with a higher level of sperm competition have faster swimming sperm (Fitzpatrick et al. 2009); the same was true in a study looking at 42 temperate passerine bird species (Kleven et al. 2009). However, another bird study found no relationship between swimming speed and level of sperm competition across 40 species, although sperm length was positively correlated with both traits (Lüpold et al. 2009). The evidence from within-species studies is also ambiguous. A few studies in birds and fish have shown that relative fertilization success is positively related to greater sperm motility within species (Pizzari and Parker 2009). Meanwhile, slower swimming speed and a higher proportion of motile sperm increase relative fertilization success in the myobatrachid frog *Crinia georgiana* (Dziminski et al. 2009). At present, the general relationship within species between sperm speed or motility and fertilization success remains uncertain. Another line of evidence is to look for differences in sperm traits between discrete mating types in fishes (e.g., sneakers and territorial males). These data provide some evidence that sperm motility and/or velocity are under selection. Sneaker males, who tend to experience more intense sperm competition than territorial males, tend to have faster swimming or more motile sperm than males using other reproductive tactics, but the relationship is weak (Pitnick et al. 2009a).

There are very few studies that test whether sperm motility or velocity are phenotypically plastic traits that males adjust in response to social changes that affect the level of sperm competition. In humans, sperm motility increased when men were exposed to images suggestive of greater sperm competition (Kilgallon and Simmons 2005); but we need more studies that experimentally manipulate variables associated with greater sperm competition levels (e.g., population density, lower social status) to see if and when this leads to the production of more motile sperm. Ideally researchers should directly measure sperm speed rather than infer it from other traits because we still do not know what properties of a

sperm increase its swimming speed (e.g., the optimal ratio of head to midpiece to tail length) (Simpson et al. 2014).

3. *Sperm length or size*

The number of sperm in an ejaculate is usually several orders of magnitude greater than the available number of unfertilized eggs. This presumably reflects strong sexual selection under sperm competition for greater numerical representation of sperm (Gage and Morrow 2003). Given a fixed investment into each ejaculate, it is therefore predicted that sperm will be tiny because of a trade-off between size and number (Pizzari and Parker 2009). If relative sperm number is the major predictor of male fertilization success under sperm competition then any gains from greater sperm size (e.g., higher zygote survival due a greater male parental investment) are likely to be outweighed by the decline in the total number of eggs fertilized. Intriguingly, however, evidence for a size-number trade-off from comparative studies across species or population or even from within-species correlations is ambiguous (Snook 2005; Pizzari and Parker 2009). This is not really surprising though as confounding variables (e.g., variation in total resources among males when looking at within species patterns) can easily obscure genuine causal relationships between traits, such as a resource trade-off (Reznick et al. 2000). Although there are very restrictive conditions under which larger sperm size might be under natural selection for fertilization efficiency (Snook 2005; Pizzari and Parker 2009), it is more plausible that sexual selection favors greater sperm size. For example, larger sperm might be better able to displace rival sperm, or avoid being displaced from female sperm storage organs, thereby increasing a male's numerical representation of sperm at the time of fertilization. This could lead to coevolution of sperm size and the dimensions of female sperm storage organs (Pitnick et al. 2009b).

In many cases, it is assumed that sperm size is indirectly favored because it has a functional effect on other traits that are the target of sexual selection. For example, selection might favor

faster-swimming sperm, which can be achieved by an increase in sperm size (Snook 2005; Pizzari and Parker 2009). Similarly, larger sperm might be indirectly selected for if this increases longevity, and longevity elevates fertilization success when there is a delay between insemination and fertilization (Snook 2005; Pizzari and Parker 2009). Correlational studies have shown, however, that a size-longevity relationship can be positive, negative, or absent (Snook 2005; Pizzari and Parker 2009). Alternatively, even smaller than usual sperm might be favored if fertilization occurs shortly after ejaculation so that longevity has less effect on male fitness than the number of sperm released. Consequently, current models predict sexual selection for either longer or shorter sperm depending on: the fertilization mode (e.g., external vs. internal fertilization); delay between insemination and mating; how sperm size affects longevity or swimming speed; whether female-sperm interactions favor larger or smaller sperm; and the extent to which the number of competing sperm affects the competitiveness of different sized sperm (Snook 2005; Pizzari and Parker 2009).

The relationship between sperm length and relative fertilization success varies widely across species from significantly positive to negative. It is worth noting that stronger postcopulatory sexual selection is associated with reduced variation within and among males in sperm length, suggesting stronger stabilizing selection on sperm size (Pizzari and Parker 2009). Interestingly, this conflicts with the general view that secondary sexual traits show higher variation among males than other traits, a pattern which is usually attributed to condition-dependent expression. The implication is therefore that sperm quality traits are less often condition-dependent, although the available evidence is ambiguous (Lüpold et al. 2016).

In experimental evolution studies, the elimination of sperm competition through enforced monandry does not generally lead to the predicted evolution of shorter (less costly) sperm (Pitnick et al. 2009a), although it did lead to a significant decrease in sperm size in at least one hermaphrodite species with high and low rates of selfing (LaMunyon and Ward 2002).

Strategic ejaculation of different sized sperm in response to a change in the likelihood of sperm competition has, to our knowledge, been reported once only. In the ascidian *S. plicata*, experimental manipulation of adult densities (presumably increasing sperm competition levels) resulted in the production of larger sperm at higher adult densities (Crean and Marshall 2008). This is opposite to the predicted response given a size-number trade-off (Parker 1998; Pizzari and Parker 2009). One suggestion is that the result reflects selection to reduce polyspermy (zygote failure because too many sperm enter the egg), which occurs in some broadcast spawners, such as *S. plicata*. However, reduced sperm production would only be selected for if polyspermy arises partly due to multiple sperm from the same male entering a given egg (otherwise males that produce fewer sperm would increase the relative success of other males at a cost to their own chances of fertilizing fewer eggs).

More generally, there is evidence that environmental factors affect sperm size. For example, sperm length increases at higher temperatures and decreases with greater larval density (Pitnick et al. 2009a). There is, however, little evidence that diet affects sperm size. To date, none of these environmental factors (with the possible exception of larval density) have been shown to predict the future level of sperm competition. Nonetheless, these studies suggest that phenotypic plasticity in sperm size is at least possible, albeit that this is probably due to longer-term developmental changes in males rather than the rapid changes in sperm production mechanisms. Perhaps the best evidence that strategic ejaculation of different sized sperm is possible comes from studies showing a difference in sperm size between successive ejaculates from the same male, which might be related to the risk of sperm competition (Pitnick et al. 2009a).

Comparisons of mating types provide weak support for the claim that sperm size is under strong sexual selection. Studies comparing sperm length between males using different mating tactics reveal no differences in several species of fish and insects (Snook 2005).

4. Sperm type

The most extreme within-species variation in sperm types occurs when males produce both fertile (eusperm) and infertile sperm (parasperm). The later are often considerably shorter than the former. Parasperm have been intensively studied in Lepidoptera, but discrete sperm types have been reported in many other taxa, ranging from rotifers to fish (Pitnick et al. 2009a). A variety of hypotheses for the existence of discrete sperm types have been formulated (Pizzari and Parker 2009). Some of these explanations invoke natural selection for improved fertilization rates or that infertile sperm are simply a way to transfer nutrients to females that are a form of male parental investment. However, many explanations assume that sexual selection favors the division of labor between distinct sperm types to increase ejaculate competitiveness (either offensive or defensive). Unfortunately, experimental tests of these hypotheses are largely lacking (Pitnick et al. 2009a). Some studies have, however, begun to elucidate how parasperm and eusperm interact to increase fertilization success (Pitnick et al. 2009a).

Some of the most convincing evidence that parasperm evolved under sexual selection comes from studies testing for facultative adjustment in the proportion of parasperm in ejaculates in response to the level of sperm competition. For example, male moths (*P. interpunctella*) transfer more eupyrene but not more apyrene sperm to mated females (i.e., when sperm competition is inevitable) (Cook and Gage 1995). Long-term studies – that might reflect developmental shifts rather than short-term strategic ejaculation – also show that the snail *Viviparus ater* increases the proportion of non-fertilizing, oligopyrene sperm when the sex ratio is male-biased so that the risk of sperm competition is higher (Oppliger et al. 1998).

Conclusion

Our focus here has been on sperm competition in nonhuman animals. We have highlighted several

intriguing and exciting discoveries in sperm competition research while also highlighting many of its associated problems and pitfalls. Importantly, these problems arise in studies using simple animal model systems in experimentally controlled situations. We therefore urge caution to those studying sperm competition in humans; it is imperative that investigators carefully consider how hypotheses are tested, how variables are measured, and how results are interpreted.

Cross-References

- [Copulatory Plugs](#)
- [Mate Preferences](#)
- [Mating Systems](#)
- [Phenotype Linked Fertility Hypothesis, The](#)
- [Polyandry](#)
- [Precopulatory Intrasexual Competition](#)
- [Reproductive Strategies](#)
- [Robin Baker and Mark Bellis](#)
- [Sexual Selection via Direct Male-Male Interactions](#)
- [Sneak Copulation](#)
- [Sperm Competition](#)

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Sperm Competition: Evidence in Nonhumans

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Synonyms

Post-copulatory Sexual Selection; Sexual promiscuity; Sperm competition

Definition

Sperm competition arises when the sperm of two or more males compete to fertilize a given set of ova. This broad definition includes both competition between sperm of two or more males within the body of a single female (internal fertilizers) and processes observed when fertilization takes place outside the female body (external fertilizers), as in most bony fishes or amphibians

(Parker 1998). It is worth noting that, in a broader sense, gamete competition occurs in most sexually reproducing organisms. In plants, for example, pollen (male gametes) of several individuals may compete to fertilize the same set of female gametes which, in principle, follows the classic sperm competition scenario described in animals (Delph and Havens 1998).

Introduction

The term “sperm competition” was first defined by Geoffrey Parker based on his seminal work on mating strategies in *Scatophaga* flies (Parker 1970). He realized that mate choice and sexual selection continue long after copulation in this insect, which led to our present understanding of postcopulatory sexual selection processes by revealing the – until then hidden – components of variation in male reproductive fitness. The evidence for sperm competition has been accumulating ever since. Not only have follow-up studies identified extraordinary variation in the levels of sperm competition among species, they have also uncovered a plethora of behavioral, morphological, physiological, and molecular adaptations that have evolved in males and females in response to sperm competition. In males, such adaptations could include differences in ejaculate load and sperm size or shape (Pizzari and Parker 2009), while various sperm storage organs may evolve in polyandric females to facilitate sperm competition and choice of the most viable sperm. Moreover, postcopulatory sexual selection, including sperm competition, has been identified as potential mechanism leading to the emergence of prezygotic barriers to gene flow between populations, and hence speciation (e.g., Howard et al. 2009). Mechanisms of sperm competition could involve male precedence or displacement, where the sperm’s ability to outcompete the sperm of other males depends on the order in which males mate with a given female, or could simply depend on the amount of ejaculate (sperm number) from each male, that is, a fair-raffle scenario with “more tickets in the raffle” being the winner (reviewed in Parker 1998).

As mentioned above, there is tremendous variation in the level of sperm competition across species, and even across populations of the same species. Approaches to studying levels of sperm competition include analysis of unexpected segregation of paternal heritable traits in offspring, behavioral observations and deviance in estimated heritability between paternal and maternal genotypes (e.g., Griffith et al. 2002). In addition, phenotypic traits known to evolve in response to varying levels of sperm competition (usually relative testis mass) may be used as surrogates for levels of sperm competition in given species or populations (Soulsbury 2010). In recent years, however, sperm competition levels have typically been estimated via molecular analysis of paternity. Paternity analysis, which uses the DNA of offspring to identify the number of putative genetic fathers, only became possible due to rapid progress in molecular testing over the last two decades of the twentieth century, the so-called parenting revolution. Below, I provide an overview of sperm competition, based on a range of more-or-less direct sources of evidence, and its evolutionary consequences across the animal kingdom, focusing on well-known model systems.

Sperm Competition in Invertebrates

In invertebrates, evidence for sperm competition has been accumulating since the 1970s (Parker 1970). Interestingly, in some invertebrate groups, such as some corals, flatworms, and sea slugs, sex roles are not well defined. Typically, these organisms are simultaneous hermaphrodites, with male and female gonads occurring in each individual. Alternating the role of sperm exchange is relatively common in this system and insemination is reciprocal. Donors provide sperm and receivers ova; however, mating conflicts often arise concerning an individual's role (donor or receiver) due to advantages gained by being the sperm donor (Michiels 1998). Given the low population density of most hermaphrodites, there is only limited space for sperm competition to occur. Some species, however, are able to "mate multiply." In sea slugs and some flatworm species, for example,

autosperm (own sperm) are donated to one partner and allosperm received from another partner. In the nematode *Caenorhabditis elegans*, while hermaphrodites typically use their own sperm for fertilization (selfing), the sperm of rarely occurring males outcompete the hermaphrodite's own sperm.

Control over mating leads to some bizarre adaptations. In *Macrostomum* flatworms, who practice reciprocal mating, bristles have evolved on the sperm's surface, ensuring that sperm are not ejected and are utilized by a reciprocally copulating partner. On the other hand, where there is no "female" control over the fate of ejaculated sperm, such as when mating occurs via hypodermic (traumatic) insemination, the sperm lack bristles and are small and highly motile (Schärer et al. 2011). In the latter case, more donors tend to provide sperm, which compete over fertilization within the body of the recipient, another example of fair-raffle sperm competition favoring small and more numerous spermatozoa.

Molluscs provide some notable examples of hermaphroditism. In this group, several types of sperm are sometimes produced by a single individual. While eupyrene sperm carry DNA and are responsible for fertilization of the ova, the role of apyrene or oligopyrene sperm remains less clear, though they may play a role during sperm competition. The occurrence of sperm storage organs indicates that sperm competition could be common in this group (Baur 1998). Evidence for multiple paternity exists in mussels, though examples of parentage analysis are rare. Gonochorism, with individuals having just male or female reproductive organs, is typical in Cephalopods. Both sperm storage and mate guarding occur in this group and most cephalopod species analyzed to date appear to mate multiply. In dumpling squid *Euprymna tasmanica*, for example, all clutches laid naturally had multiple paternity, with 2–4 males siring the clutch. Females of this species store sperm for extended periods, multiple paternity resulting from females mating between layings with different partners (Squires et al. 2013). "Last sperm precedence" appears to occur in squid, whereby the later copulating male sires a disproportional number of offspring.

Spiders and other Arachnida serve as a popular model group for sexual selection (reviewed in Elgar 1998). Interestingly, there appears to be evidence for first male precedence in some spider species, while last male sperm precedence clearly occurs in other arachnids. Several adaptations that have evolved in spiders would appear congruent with the existence of sperm competition in this group. Male spiders, for example, may transfer substances in the seminal fluid that interfere with female receptivity, or plug females with secretions or genital (pedipalps) fragments, making the female less accessible to subsequent males. In some spider species, females possess paired sperm storage organs (spermathecae), facilitating separate sperm storage from different males.

Insects are among the most intensely studied group as regards sperm competition and post-copulatory selection mechanisms, including the original work on *Scatophaga* flies (Parker 1970) that defined the term “sperm competition.” As in other arthropods, sperm storage organs have also evolved in insects. Moreover, most insect females will accept copulation with another male before the stored sperm are exhausted. Hence, a temporal and spatial overlap of sperm from different males often occurs within the female sperm storage organs, providing opportunities for sperm competition. Indeed, a plethora of adaptations appears to have evolved in insects in response to sperm competition. Males of some species deliver their sperm in “spermatodoses” that may overlay the sperm of other males in the female spermatheca. “Sperm displacement” could be achieved by flushing female sperm-storage organs with their own ejaculate, thus effectively removing spermatozoa of competing males. The penises of some beetles and Odonates have adaptations for removing sperm from the female spermatheca (Simmons and Siva-Jothy 1998). Mating plugs have also evolved in some insect species to prevent other males from removing the preceding male’s sperm. In general, mixed sperm utilization (including fair-affle scenarios) and second male precedence are the most common patterns of sperm utilization observed in insects (reviewed in Simmons and Siva-Jothy 1998). In just a few species, males

and females form pair associations during the reproductive season and exhibit biparental care. Males of these species tend to copulate with their partners frequently in order to avoid the risk of sperm competition. Despite this, multiple female mating remains common. For example, in the horned passalus *Odontotaenius disjunctus*, a socially monogamous beetle exhibiting biparental care, 54% of offspring in 70% of nests are sired by extra-pair males (Dillard 2016).

Sperm competition appears to be associated with ejaculate properties in insects, such that males of polyandrous species (where females mate with multiple males) have more viable sperm than males of monandrous species (Hunter and Birkhead 2002). In the same vein, within- and between-male variation in sperm length appears to be reduced in polyandrous species, indicating that stabilizing selection on sperm length occurs in species where females store spermatozoa in specialized organs after copulation (e.g., see discussion below concerning birds). In several insect species, larger sperm outcompete smaller rival sperm, possibly through enhanced displacement. This may lead to the evolution of very large sperm in some insects, a notable example being fruit flies of the genus *Drosophila*, in which more promiscuous species produce longer sperm and males generally produce just a few truly gigantic sperm. In *Drosophila bifurca*, a small fly with body length of less than 3 mm, sperm can be up to 5.8 cm long, 1000 times longer than a human sperm and by far the longest sperm on Earth! Sperm size in fruit flies can be considered a classic Fisherian trait (somewhat like a peacock’s tail), evolving through runaway coevolution between length of sperm and the size of the female’s receptive organs (Lüpold et al. 2016). Several *Drosophila* species have evolved a process known as “traumatic insemination.” This unusual method of male-female interaction, whereby the male pierces female abdomen and injects sperm directly into her abdominal cavity, has also been detected in several other unrelated insect groups such as bed bugs (*Cimex*), where it may have evolved as a result of sexual conflict for control of insemination (see Tatarnic et al. 2014 for further discussion).

Sperm Competition in Vertebrates

Both internal and external modes of fertilization occur in vertebrates and evidence of sperm competition is apparent in both. Most fishlike vertebrates and amphibians are external fertilizers, with sperm reaching the ova outside the female; indeed, this process is typical for aquatic species. In most fishes, external fertilization provides an opportunity for ova to be fertilized by multiple males simultaneously (reviewed in Petersen and Warner 1998) as several males may release sperm during the spawning event. Many species even display parasitic spawning. External fertilization in fishes may encourage subordinate males to adopt an alternative reproductive tactic such as sneaking during mating. Sneaker males tend to be smaller and less conspicuous than dominant androgynous males and may “steal” fertilizations from dominant males during spawning. The presence of male sneakers may be beneficial to females, indeed females often fail to show sneaker avoidance (reviewed in Reichard et al. 2007). Even in fish species where fertilization is internal and offspring are carried in body cavities, the proportion of broods sired by multiple males can reach up to 100% (reviewed in Coleman and Jones 2011). In contrast, multiple paternity is absent in fish species such as seahorses (*Hippocampus*) where male pregnancy occurs. Sperm competition is also less intense in species where males build and defend nests (Coleman and Jones 2011). Sharks and other Elasmobranchs are strictly internal fertilizers, the ova being fertilized within the female reproductive organs. Although their reproductive biology is still poorly known, recent studies have confirmed that multiple paternity, and hence sperm competition, is common in several shark species (reviewed in Fitzpatrick et al. 2012).

Evidence for sperm competition has also been documented in various amphibians fertilizing internally and externally. In some internally fertilizing salamanders, females store sperm for a prolonged period, opening space for the sperm of several males to compete within the female body. In red-backed salamanders *Plethodon cinereus*, a terrestrial and socially monogamous

species, over 80% of clutches are sired by more than one male (Liebold et al. 2006). Likewise, sperm competition is intense in externally fertilizing frogs and toads, in which the clutches of single females also display multiple paternity (e.g., Laurila and Seppä 1998). Unlike fish, simultaneous sperm release is uncommon in frogs and toads.

Living amniotes include the sauropsids (reptiles and birds) and synapsids (mammals), all of which are internal fertilizers. Regarding sperm competition, the major focus has been on birds and mammals, while reptiles remain somewhat neglected. This has now changed, however, and recent estimates in reptiles suggest multiple paternity occurs in over 50% of clutches (reviewed in Uller and Olsson 2008). Sperm competition in reptiles can arise through females mating with more than one male during a single reproductive cycle in combination with the ability to store sperm from several males over several reproductive cycles (up to several months in some species). Sperm storage organs in reptiles appear to be less differentiated than in arthropods but still allow for long-term sperm storage. In general, turtles appear to have lower levels of multiple paternity than lizards and other squamates. The proportion of clutches with multiple paternity varies considerably among reptiles, ranging from genetic monandry (as in leatherback turtles *Dermochelys coriacea*) to complete genetic polyandry (some snakes), with 100% of clutches containing multiple paternity. Multiple paternity, with over 30% of clutches sired by more than one male, also occurs in crocodiles, the closest living relatives of birds.

From the very beginning, birds have been at the center of paternity-oriented research (Griffith et al. 2002), possibly as their social systems resemble those of humans (i.e., the prevalence of social monogamy). This despite the fact that levels of sperm competition could actually be higher in some other vertebrate groups, such as reptiles, bony fish, or mammals (Coleman and Jones 2011). Since the late 1980s, more than 30,000 offspring of around 200 avian species have been screened for paternity status. As in some reptiles, female birds are capable of storing sperm over time in specialized organs known as

“sperm storage tubules” (SSTs), situated at the uterovaginal joint. For a given species, SSTs will typically be three times longer than the sperm cell, indicating intimate coevolution between sperm length and female sperm storage organ (Birkhead 1998). Interestingly, as the sperm of different males must find space when fitting into the SST, balancing selection on sperm size should be stronger in species with a high risk of sperm competition. Indeed, as in some insects, sperm length variation between males in polyandrous (promiscuous) species is reduced compared to species with relaxed sperm competition (Kleven et al. 2008).

Levels of sperm competition in birds are typically inferred based on paternity studies. Given that social monogamy prevails, multiple paternity in birds is often termed “extra-pair paternity” (EPP). Up to 80% of all offspring in some small passerines (e.g., Australian fairy-wrens [*Malurus*]) may display EPP. On the other hand, EPP is almost absent in 10% of avian species, particularly in large-bodied and long-lived species with substantial male contribution to parental care, such as owls, birds-of-prey, and seabirds. EPP affects around 19% of broods in socially monogamous species, with around 11% of offspring resulting from EPP (Griffith et al. 2002). As in other taxa, the ejaculate of highly promiscuous species (such as the polygynous Galliformes) is selected for high quality, whereas the ejaculate of genetically monogamous species with relaxed or absent sperm competition (such as owls, falcons, or penguins) often contains a large proportion of abnormal or immature sperm. Moreover, the ejaculate of promiscuous species will contain longer and faster sperm cells. Mate guarding and frequent within-pair copulations to ensure control over paternity are also typical of promiscuous avian species (Birkhead 1998). Moreover, differential sperm allocation has been demonstrated in some bird species. In the jungle fowl (*Gallus gallus*), for example, cocks allocate sperm supplies differentially based on female quality, her level of polyandry, the number of partners available and the male’s own perceived quality (e.g., Cornwallis and Birkhead 2007).

Sperm competition is widespread in mammals, including primates, with some 35% of litters containing offspring sired by more than one male. In fact, multiple paternity levels seem to be higher in mammals than in birds (Coleman and Jones 2011) but may vary in space and time. To date, no genetic polyandry has been detected in only few mammalian species (reviewed in Huck et al. 2014). Relative testes mass, which has traditionally been used as a proxy for sperm competition levels in mammals (reviewed in Soulsbury 2010), tends to be greater in spontaneously ovulating species than those where males induce ovulation (i.e., ovulation is triggered by copulation), such as some cats, hares, and rodents. Spontaneous ovulators also tend to have higher sperm concentrations and produce ejaculates with a greater number of sperm, which is in line with the hypothesis that intense sperm competition selects for more competitive ejaculate across species. As in other groups, mammalian sperm morphology is clearly shaped by postcopulatory processes, with some exceptional examples. In the muricid rodents (Muroidea), for example, hooks have evolved on the sperm head as a response to intense sperm competition. Sperm cells use these hooks to form groups sometimes comprising hundreds or even thousands of sperm cells, commonly known as “sperm trains.” These “trains” move faster within the female reproductive tract than single sperms, thus allowing the sperm to reach the ova before that of other males. An important prerequisite for this unusual form of cooperation is that the sperm cells of particular males recognize each other and avoid forming trains with genetically unrelated sperm (Fisher and Hoekstra 2010).

In four marsupial species, “suicidal reproduction” (semelparity) has evolved in response to sperm competition. In such cases, an extreme burst of steroid hormones facilitates male investment into sperm production and ejaculate quality. Excessively high testosterone levels lead to the collapse of the immune system, however, and reproducing males die very soon after the mating season (Fisher et al. 2013). As males typically live for only 1 year, even without breeding, they are unlikely to mate in the following season; hence,

such a lethal investment into ejaculate quality is adaptive. It has also been shown experimentally that sperm competition in these marsupials enables females to improve offspring survival and own lifetime fitness by mating promiscuously. Though rare, this system provides a clear example of indirect benefits gained by promiscuous females from polyandry.

Conclusion

There is now solid evidence that multiple paternity is common in animals. Indeed, today, genetic monogamy is only rarely detected in paternity studies (e.g., Huck et al. 2014). It should be noted, however, that while the presence of multiple paternity indicates that sperm competition occurs, its absence is no proof that sperm competition is absent (Parker 1998). How then does female reproductive promiscuity evolve and how is it maintained? Traditionally, adaptive explanations for female promiscuity have suggested that females gain direct (material) or indirect benefits in terms of improved genetic diversity or genetic quality of offspring by mating with multiple males. Social aspects, including avoidance of infanticide by mating with multiple males, should also be considered, particularly for some taxonomic groups. Unfortunately, the indirect benefits resulting from female promiscuity are difficult to study. In birds, for example, there is no clear consensus as to whether sexual promiscuity is adaptive and beneficial to females (Forstmeier et al. 2014). On the other hand, the existence of sexual promiscuity could result in costs to females, such as sexual harassment from males, forced copulations, or disease transfer. Some of these costs also apply to males, yet mating with multiple mates appears to have an obvious net positive effect on male fitness (Trivers 1972).

We are far from resolving the enigma of genetic polyandry in animal populations and its evolutionary significance. Interestingly, one recent study has indicated that extinction risk following a genetic bottleneck is lower in promiscuous populations (Lumley et al. 2015), implying that, under certain circumstances, sexual promiscuity may be an important mechanism of mate

choice with similar effects on population genetic quality as those proposed for the sexual mode of reproduction itself.

Cross-References

- [Avian Sperm Competition](#)
- [Counteradaptations/Female Counterstrategies](#)
- [Ejaculate Adjustment](#)
- [Insect Sperm Competition](#)
- [Sperm Competition Theory](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)

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Sperm Expenditure

► Sperm Competition Theory

Sperm Plug

► Copulatory Plugs

Sperm Storage

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Definition

Female sperm storage is a biological process where sperm is temporarily retained within a specific part of the female reproductive tract before the oocyte, or egg, is fertilized.

Introduction

Female sperm storage often occurs when sperm cells are transferred into a female during mating. This form of sexual selection has evolved to ensure that conception occurs at different times and/or in different environments. Sperm storage is an essential step in reproduction and is often required for successful fertilization.

Sperm

On average a male can produce 1500 sperm per second (Baker and Bellis 1993). The average male can ejaculate anywhere from 280 to 500 million sperm per ejaculation (Moore et al. 2015). The chances of fertilization appear high; however, there are many obstacles sperm encounters during the process of conception. The underlying evolutionary processes affecting successful male fertility are determined by the sperm's ability to survive within the female reproductive tract.

Variables Necessary for Survival

Individual longevity of sperm and the internal metabolic capacity of sperm are essential for survival. The anatomy of sperm influences the survival and probability of fertilization. A sperm's speed and length play an imperative role in sperm competition. The tail of the sperm helps propel them toward the cervix and into the fallopian tube to wait for egg fertilization. Semen or seminal fluid is the nourishing fluid that surrounds and protects the sperm before entering the cervix (Moore et al. 2015). Seminal fluid is necessary for sperm survival; without semen, sperm would have a zero probability of conception. The environment of the vagina including body temperature, pH levels, and relative acidity determines the survival and storage of sperm (2015). The components in seminal fluid counterbalance the acidic environment of the vagina.

Fertile cervical fluid is essential for sperm to survive and necessary for conception. The presence, quantity, and quality of female cervical mucus affect the internal metabolic capacity

of sperm (Wilcox et al. 1995). Since the vaginal environment is typically highly acidic, the presence of fertile cervical fluid is necessary for conception. Cervical fluid allows the sperm to easily swim into the cervix. Without fertile cervical mucus, the sperm would rapidly die and the potential success of conception reduces to a few hours during the peak of ovulation (Wilcox et al. 1995).

Once the sperm reaches the fallopian tube, the sperm awaits the opportunity to fertilize an egg. Sperm can potentially survive for up to 5 days in the female reproductive tract (Wilcox et al. 1995). Only a minimal number of sperm will even survive the long journey through the female reproductive tract.

The evolution of female sperm storage ensures high rates of fertilization and mating success within the reproduction of the human species. This type of natural selection assists in the fertilization and conception of mammals faced with a plethora of deterrents.

The Penis as a Sperm Displacement Device

If a female's egg comes into contact with male A's sperm, male B can still fertilize that same egg within up to 5 days, depending on the female's cervical fluid acidity. There is a growing body of literature showing the human penis as a way to remove existing sperm from the female's vagina, to interrupt the storage of another male's sperm. Recent work has shown a replication of this hypothesis, with artificial penises, vaginas, and sperm showing a similar effect. This behavior is seen not only in humans, but in animals as well, even in birds such as chickens, perhaps giving us a greater understanding how the penis came to be shaped evolutionarily (Gallup et al. 2003).

Conclusion

In conclusion, female sperm storage is an essential means of eventual fertilization. Fertilization, therefore, is a key component of evolution, as the only way any species can continue is through survival and reproduction.

Cross-References

- ▶ [Life Expectancy and Reproduction](#)
- ▶ [Observed Mating Behavior and Women’s Long-Term Mating](#)
- ▶ [Sexual Reproduction](#)

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Sphragis

- ▶ [Copulatory Plugs](#)

Spicy Food in Hotter Countries

- ▶ [Climate and Use of Spices](#)

Spillover Effects

- ▶ [Externalities](#)

Spillovers

- ▶ [Externalities](#)

Spiritism

- ▶ [Spiritualism](#)

Spirits

- ▶ [Spiritualism](#)

Spiritualism

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Synonyms

[After life](#); [Beliefs](#); [Spiritism](#); [Spirits](#)

Definition

Spiritualism is a belief that the deceased souls have the ability to communicate with the living with the help of a medium.

Introduction

Spiritualism propagates that the souls of the dead have both the capacity and the tendency to interact with the living. Spiritualists believe that spirits continue to evolve in the spirits world. Since they can communicate with the deceased souls and they considered the spirits superior than humans, they believe that spirits can give us the information and the knowledge about ethical issues, as well as to answer any questions related to God. Many spiritualists seek spiritual guidance to help them with their personal growth in life (Carroll 1997; Braude 2001). Kardec (1996) proposed spiritism, in which he emphasized the process of reincarnation.

The first case reported of a living to communicate with a spirit was in 1848. The Fox sisters, Margaret and Kate, moved with their family to a cottage, until their house was built in a nearby land. Since the first days they moved in the cottage, the whole family was listening to bizarre noises, with the two girls reporting the presence of unusual voices and movements. One day, while their father was searching the house to find out from where all these noises are coming from, Kate observed that when her father knocked a wall or a door, there was a reply. So she realized that someone was trying to communicate with them. Soon after, the Fox sisters became popular for their mediumistic powers and they were giving performances of their gift. The news of their supernatural communication with the spirits spread in the world and the movement of spiritualism commenced (The haunted museum n.d.). The notion of spiritualism developed for many years through magazines, preaching, and tours by highly skilled mediums. With respect to evolution, both evolutionary theories as well as spiritualism believe in the gradual progression of society. Yet, the postulation that the humans derive from the animals has been viewed by Spiritualists as threatening to the belief of immortality of the mankind. Spiritualists' view of evolution is that life does not stop with death. It goes beyond death in new spheres of spiritual existence. According to Spiritualists, Darwin's evolutionary theory does not adequately explain human evolution. It has been postulated that Darwin's theory only partly explains human evolution, and Spiritualism fills in this gap, since even if the origins of the mankind could derive from animal creation, still the inherent cause of the development is Spiritual.

Conclusion

Spiritualism is a movement in which the spiritualists communicate with the spirits of dead people with the help of mediums. Its believers argue that by interacting with the spirits, they could establish the validity of a person's survival after their demise. Today, although there are some people who believe in life after death, it is not quite widespread.

Cross-References

- [Honor Code](#)
- [Human Enculturation](#)
- [Rite of Passage](#)

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Spirituality

- [Joseph Henrich on Religion](#)
- [Religious Beliefs](#)

Split-Brain Patients

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Synonyms

[Callosotomized patients](#); [Callosotomy patients](#)

Definition

The expression "split-brain" was first used in the 1960s by Roger W. Sperry of the California

Institute of Technology (Sperry 1961), referring to those animals who had undergone the surgical resection of the *corpus callosum* (CC), the largest nerve bundle connecting the left and right cerebral hemispheres (the surgery is called callosotomy). In some cases, the expression is specifically used to refer to the resection of all of the cortical commissures (commissurotomy; here both callosotomy and commissurotomy are used without further distinctions; for a deeper differentiation, see Corballis 1995). Thus, the expression “split-brain patients” is used to refer to such patients who usually suffer a very disabling form of epilepsy which does not respond to pharmacological treatment, so much so that the surgical resection of the callosal fibers is performed to prevent the spreading of seizures across the two sides of the brain. Sometimes, the callosal fibers are sectioned in the presence of a brain tumor. The hemispheric disconnection can be complete (involving all of the callosal portions) or partial (involving only a portion of the CC; Fig. 1). A difference has to be underlined between split-brain patients, who receive the surgical resection of the CC, and acallosal patients, in whom the callosal fibers are absent from birth.

Introduction

The first callosal resections in humans were performed in 1940, in a group of 26 epileptic patients at the University of Rochester, by the neurosurgeon William P. Van Wagenen. Tested by the neurologist Andrew J. Akelaitis, these patients showed a decrease in epileptic activity, but Akelaitis did not notice marked behavioral or cognitive disorders as a consequence of the surgery.

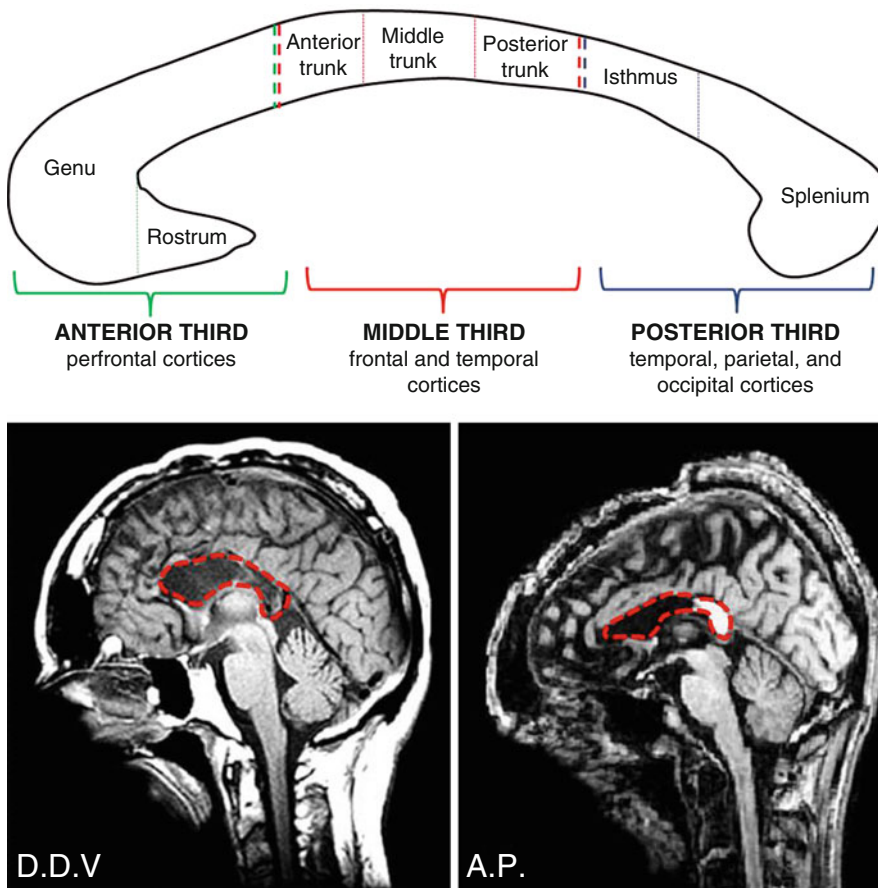
A different frame emerged, however, from the commissurotomies performed on monkeys, rats, and cats in the 1970s at Caltech (California Institute of Technology), revealing that the resection of the interhemispheric fibers prevented the information exchange between the left and the right side of the animals' brain. In those years, Philip J. Vogel and Joseph Bogen were successful in reducing the epileptic activity of a man by

means of commissurotomy, starting from the assumption that only a complete interhemispheric surgery disconnecting all the cortical commissures would interrupt the epileptic propagation. In fact, besides the CC, other minor commissures in the human brain exist, such as the anterior commissure, the hippocampal commissure, the posterior commissure, and the intercollicular commissure.

In this context, Michael S. Gazzaniga started his research on the “Caltech patients”, working in Sperry's lab (see Gazzaniga 2015). In this same lab, Ron Myers had noticed some behavioral abnormality in split-brain animals (e.g., after the surgery, the monkey's hands seemed to become independent from one another), and Gazzaniga was interested in assessing whether a callosal disconnection would truly lead to a lack of behavioral and cognitive effects in humans. Under the supervision of Sperry, Gazzaniga performed a large number of experiments aimed at answering this question, and the results of those experiments represent a milestone of the cognitive neurosciences even today. Indeed, those works revealed effects of hemispheric imbalance that were completely unknown, to the point that in 1981, Sperry was awarded the Nobel Prize in Physiology or Medicine for the discoveries on the functional specialization of the cerebral hemispheres. From then on, the “split-brain literature” would reveal the coexistence of two minds in a single brain.

Hemispheric Asymmetry and the Divided Brain

The assumption at the basis of the split-brain studies is the crossed organization of the human sensory and motor systems, meaning that (i) stimuli presented to the left side of the body are directly projected to the right hemisphere and vice versa (Fig. 2) and (ii) motor commands from the right hemisphere directly control the left half of the body, and vice versa. Once a stimulus reaches the contralateral hemisphere, the cortical commissures ensure that the information also reaches the hemisphere ipsilateral to the stimulus (e.g., left eye: left hemisphere), by means of an



Split-Brain Patients, Fig. 1 *Upper panel:* schematic representation of the functional portions of the corpus callosum and their cortical connections. *Lower panel:* mid-sagittal MRI of two split-brain patients. On the left,

D.D.V.'s brain, showing the complete absence of callosal fibers; on the right, A.P.'s brain, showing a callosal section saving the splenium

indirect pathway involving the CC. In the split-brain patients, this latter pathway is abolished, due to the resection of the callosal (or commissural) fibers, and thus only the contralateral hemisphere receives sensory information. Due to this peculiarity of brain organization, in humans the response of each disconnected hemisphere can be investigated by using some special artifices.

One of the most exploited paradigms for the investigation of visual asymmetries is the divided visual field paradigm, i.e., the very rapid (tachistoscopic) presentation of a visual stimulus in a single visual hemifield. Starting from the direct contralateral projections of the visual pathways, a left-hemispheric dominance for linguistic processing has been largely shown in the healthy

population, confirmed by rich evidence in neurological patients with unilateral lesions. This left-hemispheric superiority for linguistic processing was confirmed in split-brain patients, but a deeper exploration in this domain also revealed an unexpected result: as reviewed for the first time by Gazzaniga in 1975, the right disconnected hemisphere of split-brain patients can process verbal stimuli "without awareness". In particular, when a word was flashed in the left visual field of a split-brain patient, the patient was unable to read the word, referring not having seen the stimulus. However, when asked to retrieve an object from a series of objects placed out of view by using the left hand (directly controlled by the right "speechless" hemisphere), the patient was able to select

the appropriate object, corresponding to the word seen by the right hemisphere. This evidence suggested for the first time that the right hemisphere can, to some extent, process linguistic information.

Besides the well-known left-/right-hemispheric dominance for linguistic/spatial abilities, a further dichotomy was proposed by Corballis (1995) as regards visual abilities and attentional resources. According to this perspective, the two cerebral hemispheres control two “visual systems”, each with its perceptual and attentional subsystems: a voluntary “spotlight”, location-based attentional system, integrated interhemispherically by means of subcortical *nuclei* (such as the pulvinar), and an automatic, object-based attentional system, hemisphere-specific and based on a fine-gradient cortical analysis. Corballis reviewed a number of evidence in support of this distinction that could be referred to the well-known distinction between the “what and where” routes of the visual system: the subcortical network would be responsible for position and movement analyses, and it would be shared by the two hemispheres, so much so that split-brain patients would be able to compare the position of two visual stimuli simultaneously presented in both visual fields. On the other hand, the cortical network would be responsible for shape, color, and form analyses, and it would be separated in split-brain patients, who would not be able to compare these attributes when simultaneously presented in both visual fields. The author concluded that the what (cortical) system is not integrated across the hemispheres and that it enables two relatively independent attentional systems in the divided brain.

Concerning the relationship between attentional processes and the auditory system, Hugdahl (2003) reviewed evidence according to which callosal fibers play a central role in orienting the attentional resources: the author claimed that the CC is not only an automatic route for the exchange of sensory information between the cerebral hemispheres but it also allows for the dynamic interhemispheric interaction due to both bottom-up and top-down sensory processing. The paradigm most exploited to investigate cerebral asymmetries in the auditory modality is the

dichotic listening task, in which two different auditory percepts (often syllables) are simultaneously presented in the two ears. By using this paradigm, a Right Ear Advantage (REA) effect has been shown in healthy listeners, and this effect has been explained by referring to the predominance of the contralateral versus the ipsilateral auditory pathway (see Fig. 2) and to the left-hemispheric superiority for language processing. Hugdahl (2003) reviewed the evidence according to which the REA effect could be reversed by asking participants to explicitly pay attention to the left ear. The author described results showing that the callosal projections could modulate this asymmetry, and thus in case of callosotomy, a left ear extinction appears, due to the absence of interhemispheric auditory exchange. Finally, the author reported a significant correlation between left ear performance and callosal size, specifically referring to the posterior portion of the CC, containing the auditory fibers.

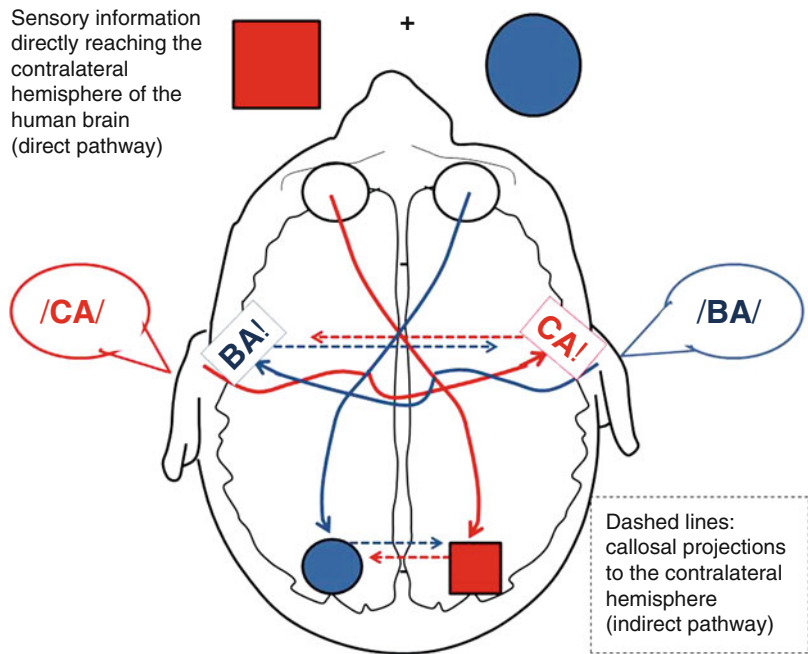
Concluding, as suggested by Gazzaniga (2000), the CC is possibly one of the bases for the development of the complexity in our brain, in the sense that it allows for the genesis of specialized neural circuits in the brain, separately in each hemisphere. This process would have evolved by addressing extant cortical areas at reorganizing in novel ways, while preserving existing functions, and avoiding redundant systems. Despite these interhemispheric differences, however, we always experience a totally integrated sense of presence.

Conclusion

The resection of callosal fibers is a neurosurgical treatment of epilepsy and other brain pathologies which has mostly been abandoned today, thanks to the development of more efficient pharmacological therapies than those available in the past decades. The evidence collected with split-brain patients, however, allowed neuroscientists to discover many details about the integrative function of the nervous system. Despite the rareness of such treatment, split-brain patients still constitute a unique opportunity to test some hypotheses

Split-Brain Patients,

Fig. 2 Schematic representation of the direct contralateral projections of the human sensory systems (only visual and auditory pathways are represented, but contralateral projections also involve tactile, proprioceptive, and olfactory systems). *Dashed lines* represent the indirect callosal projections to the hemisphere ipsilateral to the stimulus



about hemispheric cooperation/imbalance. The literature on split-brain patients has narrowed and narrowed in the new millennium, but the few surviving split-brain patients still constitute a very interesting research sample for neuroscientists. Besides the evidence collected in decades in the USA (mainly in California, Connecticut, Massachusetts, New Hampshire, Ohio), a limited number of split-brain patients are still being tested in Italy, both from a cognitive and a neuropsychological point of view (see Prete et al. 2015) and from a morphological and functional point of view (see Polonara et al. 2015). These recent studies are even revealing novel perspectives on hemispheric lateralization, for instance, in emotion processing (Prete et al. 2015), as well as an innovative point of view about the functional role of callosal projections, which seem to be constituted not only by white matter but also seem to be the place of neuronal activation (Polonara et al. 2015). To conclude, despite the exceptionality of such a neurological condition, neither sophisticated behavioral paradigms nor neuroimaging techniques can fully replace the testing of the two disconnected cerebral hemispheres in split-brain patients (see Doron and Gazzaniga 2008).

Cross-References

- [Evolution of Mammalian Vision, The](#)
- [Human Visual Neurobiology](#)

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Spontaneous Abortion and Maternal-Fetal Conflict

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Synonyms

[Miscarriage](#)

Definition

Unexpected loss of a fetus before the 20th week of gestation.

Introduction

Evolutionary conflict occurs when natural selection acts in opposing directions on different genes involved in an interaction (Burt and Trivers 2008). Conflict can be found at all levels of organization, from conflict between species, to conflict between individuals within a species, to conflict within an individual itself. Most of these forms of conflict revolve around competition for resources and

differences in optimal resource allocation among individuals. Between genetic relatives, what is beneficial to one relative may not be beneficial, and may even be detrimental, to another. This situation occurs when there is an unequal probability that genes from one individual will be shared with another. For example, if a mother invests abundant resources in one embryo, it benefits both that embryo and, due to shared genes, the mother herself; however it will detract from the mother's ability to invest in other offspring. From the maternal perspective, she shares half her genes with each of her children, so she benefits optimally from maximizing her reproductive output. However, from the perspective of any one child, there is a lower probability that a gene found in that child's genome will be present in other siblings (although there is a 50 % probability that a maternal gene found in one sibling will be found in the other, the sibs may not be paternally related, thereby reducing their probability of genetic similarity) (Trivers 1974). Therefore there is an unequal benefit for the child relative to the mother when she allocates resources to any one child versus conserving resources for other potential offspring. These situations produce what is known as maternal-offspring conflict.

One of the earliest opportunities for maternal-offspring conflict arises when the mother physiologically “decides” whether or not to carry the child. While it is often in the best interest of genes found in the fetus to be carried to term, this comes at the cost of reducing the mother's future reproductive resources. This creates a “conflict zone,” whereby it might benefit the mother to abort this fetus in the interest of conserving her resources for future reproductive episodes.

Spontaneous Abortion in Other Mammals

Many mammals exhibit spontaneous abortion when the likelihood of infanticide is high. For example, a phenomenon known as the Bruce effect has been demonstrated in several rodent species, both in the lab and in the wild (Bruce 1960; Marashi and Rüllicke 2012). The Bruce

effect describes a striking result: recently impregnated females will undergo spontaneous abortion in the presence of a strange male. While this has been most extensively studied in rodents, a study conducted on wild geladas showed that spontaneous abortions occurred in 80 % of pregnancies when a new dominant male took over (Roberts et al. 2012). This is in line with what we would expect given that gelada males employ infanticide quite readily as a reproductive strategy, with almost 60 % of infant deaths occurring upon male replacement (Beehner and Bergman 2008). Furthermore, data on inter-birth intervals (IBIs) over time indicate that females who terminated a pregnancy had a comparable average IBI to the overall population, both of which were significantly shorter than the IBIs of females whose infant was killed by infanticide (Roberts et al. 2012). This provides further support to our understanding of spontaneous abortion as an adaptive strategy that boosts reproductive output of females.

Early Decision Making

Pregnancy is a long, expensive process. It would be extremely costly for a mother to carry an unfit embryo to term if the chances of survival and reproductive success of that offspring will be low after birth. However, there is a maternal expenditure of resources already committed to the pregnancy at the time of miscarriage; therefore any adaptive miscarriage is likely to occur as early in development as possible (Haig 1993). In humans, about 20 % of conceptions result in miscarriage before the first expected menstrual period (Ellish et al. 1996). Up to 83 % of first-trimester spontaneous abortions have been found to have chromosomal abnormalities (Strom et al. 1992), supporting our understanding of early-term miscarriage as an evolved “quality control” strategy (Haig 1993).

Fetal Response

The fetus has evolved certain defenses in response to this maternal pressure. In the case of humans,

the fetus has taken over partial control of its own fate by way of hormonal control. Before implantation human embryos already begin to secrete human chorionic gonadotropin (hCG). By the time of implantation, placental secretion of hCG into the maternal blood stream has appropriated maternal pituitary control. This prevents early regression of the corpus luteum (CL), without which an early-stage human pregnancy will miscarry (Haig 1993). Placental hCG also stimulates progesterone production, which allows the pregnancy to go to term beyond the eighth week even if the CL is removed. In this way the human fetus attempts to take control of its own fate, to the potential detriment of the mom (Haig 1993).

Conclusion

Genes found in both the mother and the fetus would benefit from increased investment in healthy sibs as opposed to maternal investment in a child unlikely to survive and reproduce. However, there is a zone of conflict in which it would be in the mom’s best interest to abort, but in baby’s best interest to be born. Both individuals have evolved mechanisms to respond to the pressures brought on by this discrepancy.

Cross-References

- [Maternal-Fetal Conflict](#)
- [Parent-Offspring Conflict](#)

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Spontaneous Language

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Synonyms

Creolization; Grammaticalization; Language acquisition; Origin of language

Definition

Spontaneous language is the phenomenon in which all or part of a language is constructed based on innate assumptions combined with input from an environment that underspecifies the language. Input signals may be the product of a language or have a less formal source. The resulting language is consistent with the input, though it may not exactly reflect the process by which the input was generated.

Introduction

Natural human language is a complex phenomenon, with individual and communal components.

It consists of highly structured signals with rich semantics, transmitted through vocalizations, facial expressions, and manual gestures. Normal individuals each have a body of knowledge about their native language called I-language. At the community level, an E-language is the amalgam of the I-languages of all individuals and may not exactly match any individual's I-language.

I-languages are constructed instinctively and spontaneously by children as they acquire their native language, based on innate assumptions and primary linguistic data (PLD). Normally drawn from an E-language, PLD consists of gestures, utterances, and the contexts in which they are experienced. The innate assumptions, called universal grammar (UG), limit natively acquired languages to a learnable subset of all mathematically possible languages. Consequently, children receiving PLD from the same environment acquire similar I-languages, which in turn perpetuates the E-language.

The exact composition of UG is uncertain. The term UG is often associated with the principles-and-parameters (P&P) system of generative syntax and a nativist model of acquisition, which posits extensive innate knowledge of specific grammatical rules (Lightfoot 1999). An alternative is to suppose that only the most basic rules are innate and others are acquired as compound templates (Tomasello 2005; Jackendoff 2002).

The native language acquisition process in a child's brain is based on inference from experience and is not programmable. That is, if an adult explains a grammatical rule to a young child, the child cannot incorporate it into his or her language immediately the way an adult learning a second language might. Rather, the child must find evidence for the rule in the PLD and incorporate it instinctively.

There are circumstances other than routine native language acquisition under which an I- or E-language spontaneously forms. Section 2 describes language change and diversification, in which new languages emerge from the PLD of existing languages. Section 3 describes creolization, in which children construct a full language from highly impoverished PLD. The biological origin of language is discussed in section

4. Iterated learning experiments, in which human subjects or agents in a computer simulations must construct a communication system from scratch, have become a popular tool for studying language origins. These are discussed in section 5.

Language Change and Diversification

E-languages naturally have a spontaneous component (Labov 1994). Some signals and meanings drop out of use. New ones are continually invented and added to the cultural environment. Some of these innovations become widespread and others do not. The collective decision to adopt or abandon a signal or meaning depends on many social factors, such as the extent to which the community or a subcommunity associates some favored status with the signal or meaning. The sex, status, and friendship networks of those who initiate an innovation are important factors in its spread. In addition to the lexicon, grammar is subject to natural, spontaneous changes. The accumulation of such changes can transform a language drastically. For example, Old English as spoken prior to the twelfth century must be learned as a foreign language by native speakers of Modern English despite the unbroken chain of acquisition.

Language change can lead to diversification. For example, the Romance languages, including Italian, French, Spanish, and others, developed from regional dialects of Latin that diverged over centuries.

Language changes can sometimes be attributed to a specific nonlinguistic event, especially contact with another culture (Trask 1996). English borrowed many words from French during the Norman conquest in the eleventh century. However, some changes appear to happen spontaneously, in the sense that there is no nonlinguistic driving force. For example, the sound systems of languages are in constant flux. Vowel shifts, such as those that occurred over centuries in English and Greek, seem to arise directly from speech and language acquisition. More complex changes called reanalysis and grammaticalization affect morphology and syntax. These arise from inherent ambiguities in language. For example, the

definite article “the” in Modern English arose from an Old English demonstrative, and the indefinite article “a/an” came from a word meaning “one.”

Creolization

A pidgin is an artificial language constructed by societies in contact for which no natural language suffices for communication. Most pidgins originated during the colonial era as a tool for trade, or by culturally mixed slave communities. They generally lack agreement morphology and complex syntax such as embedded clauses. Their vocabulary is minimal and utilitarian. A creole is a natural language that appears to have been derived by simplifying the phonology and lexicon of another language and imposing a simplified but fully expressive grammar with recursion, minimal inflectional morphology, and regular derivational morphology. Creoles arise when children extract PLD from a pidgin, and spontaneously complete it to a natural language, a process called creolization (Bickerton 2008), though some linguists disagree with this characterization. Creole grammars are generally more similar to each other than to those of their parent languages, which suggests that this kind of grammar might reflect some default state of the language acquisition process.

Sign languages can also form via creolization. If isolated from other signers, deaf children develop an ad hoc gesture system called home sign for communicating with their hearing family members. When isolated deaf people form a community, they share their home signs. Deaf children entering such communities treat these gestures as PLD and develop it into a complete sign language analogous to a spoken creole. A well-documented case of spontaneous sign language formation occurred when the first school for the deaf opened in Nicaragua (Senghas and Coppola 2001).

Biological Origin of the Language Faculty

It is generally accepted by the scientific community that a combination of genetic mutations and

natural selection led to the spontaneous evolution of the language faculty among hominins (Tallerman and Gibson 2012; Hauser et al. 2002).

The human language faculty is distinct from the communication abilities of the other great apes. Although chimpanzees and gorillas have been successfully taught to use signs and other forms of communication, the process is laborious, and the subject animals never develop human-like syntax and fluency. The human language faculty must have evolved sometime after hominins and chimpanzees diverged 4–8 million years ago.

Little physical evidence related to the biological history of human language is available, and it is indirect and difficult to interpret. The oldest known artifacts with writing are only a few thousand years old, which is too recent to be informative. Fossils yield only indirect information about brain and vocal tract anatomy. There is physical evidence of artifact use and cultural practices of hominins, but the extent to which these behaviors may reliably serve as proxies for language ability is uncertain. Genetic evidence is also elusive. The genes involved in language must have experienced mutations and selective sweeps since the divergence of chimpanzees and hominins. There are statistical tests for identifying genes that have experienced such events; however, they are controversial and of limited inferential power (That said, the regulatory gene *FOXP2* has been identified as affecting language. Its function is not well understood.) Consequently, investigations into the biological history of human language consist primarily of identification of general principles, formulation of plausible scenarios, testing of hypotheses via simulation, and informed speculation.

Neanderthals probably had some form of language. They were genetically similar enough to modern humans to interbreed, and fossil evidence suggests that the Neanderthal vocal tract was similar to that of modern humans. That would place the origin of language prior to the divergence of the two species about 500,000 years ago.

There are two hypotheses about the timescale of the origin of language. Originating from the observation that the language faculty is difficult to divide into smaller features that could have plausibly been selected for independently, the saltational or sudden hypothesis is that the

transition from a prelinguistic ancestor species happened relatively rapidly and is possibly due to a single evolutionary event. However, organisms normally evolve new features by accumulating modifications to existing features, and it is unlikely that one mutation would construct a complete language faculty from essentially nothing. A more biologically plausible gradual hypothesis is that the language faculty arose in several steps, accompanied by a sequence of protolanguages.

A plausible gradual scenario is as follows. The ability to observe and mimic complex sequences of gestures improved. Societies became large and complex. Cognitive functions that originally served to keep track of personalities, intentions, dominance, and friendships were exapted to form a theory of mind. Hominin intelligence was increased by extending the period of brain growth after birth, resulting in a long childhood and more opportunities for learning. Communal activities such as rearing children, producing tools, acquiring food, and finding mates were facilitated by communication. A protolanguage faculty formed and further mutations improved it. A theoretical challenge is that social structure, hunting, foraging, child-rearing, culture, and E-languages all had to change along with the language faculty. Improvements in one of these areas became possible only after improvements in some of the others.

The composition of protolanguage is lost to history. It is possible that early child language reflects protolanguage, in which case it would have consisted largely of short phrases of one to three protowords and gestures primarily expressing requests, general intentions, and attempts to bring something to another individual's attention. Much of the meaning would have to be extracted from context and assumptions shared between speaker and hearer. The recursive nature of syntax, in which entire sentences can be nested within a sentence, is generally thought to be a recent addition to the language faculty.

Iterated Learning Experiments

In light of the limited data, investigations into the origins of language often include simulations.

A popular paradigm is iterated learning (Lyon et al. 2007, Chap. 13). Subjects (humans or computer programs) are placed in a scenario where communication is required, but no natural language is available. Subjects must produce signals and develop a mapping from signals to meanings. Repeatedly, another generation of subjects replaces all or part of the existing generation. Each generation receives some information about how the previous generation used signals, and are asked to perform the same kind of task. The communication system evolves in a cultural sense, and its trajectory reveals something about how a natural or artificial learning process interacts with communication in use. Rules for forming structured signals can form spontaneously.

Iterated learning experiments have been performed on these topics, among others: the acquisition, persistence, and loss of irregular versus regular morphology; how structure in signals reflects structure in meanings; the effect of an expectation by the learner that signals have structure; differences between adult learners and child learners; and the formation and perception of signal-mediated social status. Uncertainty remains about how well these experiments reflect natural language formation.

Conclusion

Human language has many spontaneous aspects. Children learn native I-languages instinctively. Adults introduce variation into communal E-languages. This combination of use and learning causes languages to change and diverge. New creole languages can be formed from highly impoverished primary linguistic data. The language faculty is thought to have evolved in hominins prior to the divergence of modern humans and Neanderthals, likely due to many mutations that improved intelligence, learning, motor control, and social structure. Humans and automated learning processes can construct sophisticated dynamic communication systems via iterated learning.

Cross-References

- [Communication and Social Cognition](#)
- [Interactive Language Development](#)
- [Language Acquisition](#)
- [Michael Tomasello](#)
- [Modeling Language Transmission](#)
- [Noam Chomsky](#)
- [Pidgins and Creoles](#)
- [Sign Language](#)
- [Steven Pinker](#)

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Spontaneous Problem-Solving

- [Role of Experience in Tool Use](#)

Spontaneous Recovery

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Definition

The recovery of a habituated response.

Introduction

Spontaneous recovery is a phenomenon encountered within non-associative learning processes.

The Process of Spontaneous Recovery

In a series of experiments undergone by Rankin and Broster (1992) on the nematode *Caenorhabditis elegans*, mechanical stimuli were delivered at four interstimulus intervals (2, 10, 30, and 60 s) in order to investigate the effect of interstimulus intervals in the development and maintenance of habituation. Results indicated that recovery from habituation was dependent on some factors. One of these factors is the length of interstimulus intervals; it was observed that recovery from habituation was faster when short interstimulus intervals were applied rather than longer interstimulus intervals. That is, long-term habituation prevents recovery. Also, the rate of recovery varied according to which response level each subject exhibited on the habituation curve. The recovery of animals on the lowest response level appeared to be determined by interstimulus interval and not by the further addition of stimuli. Interstimulus interval recovery rates did not differ even though the number of stimuli the worms received was significantly bigger (60 vs. 10) in the second group. In short what was evident is that

the frequency of stimulation during habituation training was the one to determine the rate of spontaneous recovery.

Moreover, Rankin et al. (2009) upon revisiting the characteristics of habituation, originally described by Thompson and Spencer (1966), revised a point concerning spontaneous recovery. It is described in the characteristics that when a sequence of stimulus presentations is interrupted, the object at hand will return to its earlier stage, and the behavior will recover over time. Rankin and colleagues (2009) revised this characteristic by adding that sometimes the response recovers completely, but sometimes it recovers only partially depending on the time frame that recovery was examined.

Further, when stimulus presentations and spontaneous recoveries are given repeatedly, the phenomenon of *potentiation of habituation* is observed. Here, the decrement in response that follows spontaneous recovery (i.e., habituation) becomes gradually more rapid with each application of spontaneous recovery. Moreover, the process of spontaneous recovery can be disrupted with the presentation of a new, strong stimulus, that is, sensitization.

Lastly, it is crucial to note the importance of spontaneous recovery; it is the second way, with stimulus discrimination being the first way, to distinguish sensory adaptation and fatigue from habituation. With regards to learning, this process demonstrates that even though a response might disappear, it does not necessarily mean that it has been withdrawn from memory and that it will never reoccur.

Conclusion

Experiments on the lowest living forms illustrate the phenomenon of spontaneous recovery and those indicate that spontaneous recovery is highly determined by the frequency of stimulus presentation. These experiments provided a special insight on the underlying processes of habituation.

Cross-References

- ▶ [Habituation](#)
- ▶ [Interstimulus Interval](#)
- ▶ [Sensitization](#)

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Sports

- ▶ [Physical Health](#)
- ▶ [Team Sport](#)

Spousal Abuse and Homicide: Byproduct Theory (Daly and Wilson)

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Synonyms

[Intimate Partner Violence](#); [Intimate Partner Homicide](#)

Though most homicides are perpetrated by men against other men, women are disproportionately the victims of spousal homicide. Globally, 39% of

all homicides of women are by an intimate partner, whereas 6.28% of all homicides of men are by an intimate partner (Stöckl et al. 2013). Daly and Wilson proposed that uxoricide (i.e., killing of female spouse) is a byproduct of male sexual proprietariness. Male sexual proprietariness is a tendency for men to believe they own or are entitled to their intimate partner. Such beliefs would have been an adaptive response to competition with rival males. Men can increase their reproductive success through mate number, which creates a high degree of competition between men for access to mates. Men who were able to limit their intimate partner's mating opportunities with rivals would have been more successful than men who did not. Having a partner who engages in extra-pair mating introduces a cost – investing resources and time in raising offspring who are not genetically related (known as cuckoldry risk). Daly and Wilson suggest that intimate partner violence may function by limiting a partner's extra-pair opportunities through coercive control to reduce the risk of cuckoldry and that uxoricide is a byproduct of such actions.

A trait is considered to be a byproduct if it is not-adaptive because it does not solve any reproductive or survival problems (Buss et al. 1998). Daly and Wilson (1988) argue that in order for spousal homicide to be an adaptation, it requires a clear reproductive or sexual benefit, but if a husband kills his wife, it prevents any future reproductive success and presents additional costs such as retribution from the victim's family, loss of caregiver to any current offspring, and gaining a reputation as a murderer which hinders the acquisition of new mates. They therefore suggest that spousal homicide is not an adaptation, but a byproduct of male sexual proprietariness because many incidents of uxoricide occur in the context of sexual jealousy or loss of a partner to a rival (c.f. chapter "[Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)").

Daly and Wilson's hypothesis of homicide as an evolutionary byproduct explains many of the identified risk factors and demographics associated with patterns of spousal homicide rates. It explains that younger women are at higher risk

of being victims of uxoricide because there is greater competition among men for partners with higher reproductive value. Estrangement is also a risk factor because it results in losing a partner to a rival, creating a higher degree of conflict. The byproduct hypothesis also explains socio-economic status as a correlate of spousal homicide because men of lower socio-economic status may be more prone to losing a partner to a higher-status male. The prevalence of ethnic minorities as perpetrators is not explained by evolutionary principles, but Campbell et al. (2007) suggest that this pattern could be due to higher rates of unemployment among ethnic minorities in the USA. Using coercive tactics may mitigate these various conditions that increase the risk of losing a partner to a rival, but they also risk more severe actions, including homicide.

Conclusion

Spousal homicide has been hypothesized to be a by-product of male sexual proprietariness, when spousal abuse may function by limiting men's sexual partner's mating option.

Cross-References

- [Spousal Abuse and Homicide: Evolved Homicide Module Theory \(Buss\) \[Spousal Homicide\]](#)

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Spousal Abuse and Homicide: Evolved Homicide Module Theory (Buss) [Spousal Homicide]

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Synonyms

[Intimate partner violence](#); [Partner abuse](#)

Definition

Spousal abuse is when someone use physical violence, sexual violence, stalking, psychological aggression, or coercive acts toward a current or former intimate partner.

Introduction

Intimate partner violence (also called partner abuse) is when someone uses physical violence, sexual violence, stalking, psychological aggression, or coercive acts toward a current or former intimate partner (Centers for Disease Control and Prevention 2018). Intimate partner violence is often habitual and can escalate, resulting in serious injury or homicide (Focht 2018). *Evolved Homicide Module Theory* (also referred to as ► [“Homicide Adaptation Theory”](#), see entry) provides an explanation for why intimate partner violence may result in homicide by suggesting that homicide evolved through natural selection by ultimately providing fitness benefits while minimizing costs (Duntley and Buss 2011).

An adaptation is any change in the structure or function of a phenotype through natural selection by better equipping the organism to survive and reproduce. Generally, homicide may be an adaptation because it functions by resolving conflict. For example, homicide may increase fitness by preventing one's own premature death, acquiring resources, reducing the number of rivals for

oneself and one's children, avoiding investing in stepchildren, and developing an aggressive reputation to prevent challenges from rivals (Duntley and Buss 2011). Spousal homicide may therefore be functional. Buss (2006) suggested that in addition to losing a partner, cuckoldry provides a major cost, and such a cost is compounded by a rival's reproductive gains. Under these circumstances, it is theorized that killing a spouse reduces the fitness of rivals while maintaining a reputation that one is not to be exploited. Supporting this hypothesis are the number of intimate partner homicides that are preceded by sexual jealousy or intimate partners leaving the relationship (Buss 2006; Shackelford et al. 2003). There is also some suggestion that women may have evolved anti-homicide defenses, but these ideas have not been fully explored or tested.

A potential challenge to the spousal homicide as an adaptation hypothesis are the steep costs associated with such actions, including losing a reproductive partner, removal of a caregiver to one's offspring, gaining a reputation as a murderer, and familial retribution.

Although men account for most spousal homicides, in some areas women account for almost as many spousal homicides (Wilson and Daly 1992). The motivation behind women's killing of men are not the same as men's – most instances of women's spousal murder is in self-defense from an abusive partner (Wilson and Daly 1992). Daly and Wilson suggested that spousal homicide is a byproduct of male sexual proprietariness, which is when aggressive autonomy-limiting actions are used to prevent cuckoldry. Spousal homicides are therefore nonadaptive, extreme manifestations of men's coercive control (see ► “Spousal Abuse and Homicide: Byproduct Theory (Daly and Wilson)” entry). Women's killing of men seems to be in response to men's aggression toward them. Very little theoretical or empirical work, however, has considered these cases.

Conclusion

Spousal homicide has been hypothesized to function as an adaptation to reduce reproductive success of rivals while maintaining one's status of not

being a cuckold. It is not yet clear whether spousal homicide evolved as an adaptation, or is a by-product of male sexual proprietariness.

Cross-References

- [Spousal Abuse and Homicide: Byproduct Theory \(Daly and Wilson\)](#)

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Squirrel Family *Sciuridae*

- [Alarm Calling upon Predator Detection](#)
- [Predator Confusion Hypothesis](#)

SSSM

- [Standard Social Science Model](#)

Stable Cooperation

- [Specific Friendships](#)

Stages of Development

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Synonyms

[Developmental stage](#); [Life cycle](#)

Definition

Phases that all individuals pass through in a normal lifetime.

Introduction

The fact that humans progress through a set of distinctive stages over the life course is readily observed in others and subjectively experienced. However, the number and definition of those stages have shifted over the course of the Western tradition from 3 to as many as 12 distinct stages, making it clear that the classification of life stages is in part a cultural representation (Mintz 1993). Erik Erikson (Erikson and Erikson 1987) proposed seven life stages, including infancy, toddlerhood, middle childhood, adolescence, and young, middle, and old age, based on psychosocial identity, representing the most widely known cultural model of the life course for the late twenty-first century.

Yet, Erikson leaves out fetal development, a stage only visible to the casual observer from the outside, emphasizing Erikson's life stages as based on subjective experience. But increasingly the use of noninvasive techniques such as ultrasound imaging has made prenatal development accessible to observation. In fact, a more sophisticated understanding of the biology of development has given us a picture of the species-specific processes underlying life stages that go beyond well-defined social roles and individual psychology.

This entry on life stages outlines phases of the human life course based on overlapping biological, psychological, and social elements. Importantly, the advent of brain imaging techniques means that in addition to physical traits used to define life stages, we can add changes in the brain to the developmental picture. Given that the brain is both part of the body and the locus of behavior, this brings us closer to an integrated biopsychosocial model. Steroid hormones provide an additional link between development, brain, and behavior.

Below I list eight different life stages, including fetus, infancy, early and middle childhood, adolescence, and young, middle, and old age. I describe key aspects of their biological underpinnings, and brain correlates along with some psychological components and social interaction. Because the biopsychosocial model implicit in my discussion comes most clearly into evolutionary perspective with comparison to our closest relatives the great apes, I also compare human life history with the relevant findings among chimpanzees the species for whom we have the most information.

Prenatal Stage. Fetal development is traditionally subdivided into three phases, or trimesters, each characterized by different elements of prenatal growth and/or development. The first trimester is defined by the development of a complete organism from the initial undifferentiated ball of cells. The second trimester is defined by the development of organ systems. The fetus is now potentially viable outside the womb. The third trimester is defined by growth of the fetus. It is at this point that the brain becomes a large part of the fetus energy demands on the mother.

Though difficult to observe directly, fetal development is important because being first it has the capacity to effect all other life stages, through prenatal programming, i.e., setting the fundamental conditions for all subsequent development. Hormones are one important such mechanism. Much of the focus has been on the hypothalamic pituitary axis (HPA) which mediates the effects of prenatal stress on cortisol reactivity during infancy and later in life (Howland et al. 2017). Androgens also play a role. For instance, females with congenital adrenal

hyperplasia which exposed them to high level of DHEA, a weak androgen, in utero show increased aggression and activity levels. Whether such results can be extended to the larger populations is unclear (Hines et al. 2015). Separately, infants born premature or at very low birth weights show reduction in executive function (van Houdt et al. 2019), reflecting disrupted development of the prefrontal cortex with implications for lifelong intelligence and social behavior.

Infancy. The infant stage extends from birth to weaning and is characterized by rapid but declining somatic growth (Bogin 1999). Exclusive breastfeeding is sufficient for the infant's energetic needs for the first 6 months after which the diet must be supplemented with supplementary foods. In subsistence societies the average age of weaning is about 3 years. Hence 3 years marks a milestone in the degree of direct comforting nutritional physical contact with the mother and signals increasing interaction with others. During this stage the brain is growing rapidly in size, and the limbic system is developing.

Mother-infant interaction is central to infancy and leads to attachment as defined by John Bowlby (1982). The nature of such attachment shapes the internal model the infant develops of itself with important implications for all personal relationships formed after infancy. Secure attachment develops when an infant feels love and positive regard and avoidant when it feels unloved and rejected, and resistant attachment is based on the infant feeling angry and confused.

One important element of maternal behavior is a high pitched emotional voice referred to as motherese. Motherese appears to peak at around 7 months, just when the infant can be put down for longer periods of time. Variation in receptive and expressive language is related to the size of the amygdala suggesting that the infant's early experience of security with the mother has an important effect on the development of basic cognitive skills.

Infancy is also defined by the rapid development of two defining human skills, bipedal walking and spoken language. Walking generally starts around 9–12 months, developing from crawling. Language itself develops starting around 1 year,

though it follows a long period of vocalization. Once initiated early language development progresses at a dizzying rate, as any parent can attest.

Childhood. Childhood is defined as the period between weaning and the onset of puberty, thus stretching from the age of 3 to 12 years. However, such a long period includes at least two distinct phases: early childhood defined as age 3–6 years and middle childhood from 6 to 12 years. Some authors separate late childhood, defined as between the ages of 10 to 12 as a third stage.

Early childhood is associated with continued growth of the brain with volume reaching 95% of adult values by age 7. This is also a period of increased synaptogenesis with increased energetic demands. Brain glucose utilization peaks around 5 years (Kuzawa et al. 2014). Somatic growth is slow and linear (Bogin 1999), suggesting a possible trade-off with brain growth. There is a rapid development of motor skills.

Psychologically early childhood is associated with continued cognitive development, including refinements of language, executive control, and sense of self. Because cognitive development continues processes started during infancy and the energetic demands of the brain start increasing at birth and continue until the age of 5, and because 5 years is the cutoff for kindergarten, sometimes infancy and early childhood are combined in a single stage referred to as “under-5 s.” This breaks down the assumption of a discrete age-related boundary between early and middle childhood and leads to what is known as the 5 to 8 transition discussed below.

Middle Childhood. Entry into middle childhood is associated with the 5 to 8 transition, termed the age of reason and responsibility by Sheldon White (White 1996) because it is the beginning of children's capacity to reason and act according to social rules. This shift is recognized in the Catholic Church by the rite of confirmation which marks the child's capacity for moral reasoning and in our larger culture by the beginning of formal schooling which marks the child's ability to learn and retain knowledge. In fact, Lancy and Grove (2011) report that some societies say that before the age of 6, children are stupid and have no common sense. Given that common sense

is by its nature culturally defined, this statement captures the onset of socialization during this stage.

In terms of cognitive development, middle childhood is associated with the onset of metallization or the capacity to think about thoughts, a key human cultural capacity, associated with the development of the right temporoparietal junction (Saxe et al. 2009). It also marks the beginning of a long process of cortical maturation that stretches into the mid-20s (Gogtay et al. 2004) which underlies the capacity for cognitive development throughout childhood and into young adulthood (Shaw et al. 2006). Middle childhood is also marked by adrenarche, or the onset of production of adrenal androgens, which has been related to the maturation of the tempoparietal junction from the age of 7 to 12 years (Nguyen et al. 2013).

Adolescence. Adolescence (12 to 18 years) serves as a good example of the overlapping of cultural, social, and biological levels of human life stages. Biologically, adolescence is defined by puberty and reproductive maturation, while adolescence as a social category is the transition from childhood dependence to adult independence including such things as entry in high school and being just competent for driving, drinking, and military service. Culturally, adolescence also includes the onset of family formation and reproduction. It is important to recognize that unlike early life stages which involve subtle physical and behavioral changes most recognizable to those familiar with the developing child, puberty is easily recognized by a wide range of others. Secondary sexual characteristics are obvious signals that invite a response by others, whether as a possible sexual partner, as a physically mature adult, or as potential troublemakers.

Puberty itself is variable in timing with some individuals starting to show the earliest development of secondary sexual characteristics by the age of 10 and some not until 15 years. In addition, on average boys mature about 2 years later than girls. Gonadal maturation is associated with the rise in testosterone in males and estrogen and progesterone in females. These hormones lead to the development of secondary sexual characteristics such as the development of breasts and hip

among girls and facial hair and voice changes in boys. In addition, rising hormone levels are associated with a growth spurt in height. The spurt is fueled by the effects of androgens on bone growth and cutoff by rising estrogens, meaning that girls not only stop growing earlier than boys but on average attain shorter adult heights than do boys (Bogin 1999).

Behaviorally, increases in testosterone have also been associated with increased sexual behavior in both boys and girls even when controlled for pubertal stage (Halpern et al. 1997, 1998). This suggests that changes in individual sexual motivation play a role in sexual initiation in both sexes, alongside social factors such as SES, ethnicity, and religiosity (Halpern et al. 1994).

In addition to sexual behavior, adolescents and especially male adolescents are well-known for high levels of risk-taking and antisocial behavior. Such risk-taking appears to represent the differential timing of increases in cognitive capacity and social maturity. Steinberg (Steinberg et al. 2008) documents a more or less continuous increases in intellectual capacity from 10 years into the late 20s, while measures of psychosocial maturity plateau from 10 to 21 years and only then begin to climb throughout the 20s. More detailed measures show that planning ahead actually reaches a nadir in mid-puberty and then increases into the 20s (Steinberg 2010).

Adulthood. Adulthood is the species defining life stage, with adults recognized as fully functioning members of society in terms of both production and reproduction. Yet, the biological underpinnings of reproduction and production vary across adulthood. As soon as adulthood is reached, individuals start undergoing senescence, defined as declining functional capacity, including the soma, brain, and reproduction, but may continue to increase their knowledge, social networks, and status.

In contrast to development which is a highly orchestrated interplay of somatic, cognitive, and reproduction process with a defined length of time in order to maximize the possibility of reproduction, senescence reflects a much less controlled devolution of bodily function resulting in greater individual variation in the process. Thus

environmental factors such as activity, education, and social support are important determinants of the rate of senescence.

Adulthood is usually divided in three stages: young adulthood (20–40), middle age (40–60 years), and old age (60 onward). It is important to recognize that the age boundaries are as much for the purpose of definition as they are specific events and that the relationship between the biological and social definition of the stages can be fuzzy. For instance, if adulthood is defined as the end of puberty, it can be said to start at 18 years. On the other hand, if adulthood is defined as being held legally accountable for one's actions, then adulthood starts at 21 years. In another example, the onset of old age is 60 years when defined by an increasing rate of senescence decline both physically and cognitively, but 65 if defined by retirement and a decrease in economic productivity.

Socially, young adulthood is defined by employment, family formation, and reproduction. Thus this stage may be the stage most directly associated with changes in economic structures across cultures and at the same time the one most subject to cultural categorization. In many subsistence societies, the onset of these activities may be more or less synchronous with physical maturity with food production by the male necessary for family formation and reproduction, though not always in that order.

On the other hand, the lengthening of education and the delay in careers and marriage in industrialized societies mean that these activities are no longer closely tied to physical maturity. Hence Jeffery Arnett (2000) has suggested an additional stage which he refers to as emerging adulthood. Emerging adulthood is considered to result from ongoing social changes in education and career development that put off family formation and hence fully recognized adulthood.

However, recent findings demonstrate that maturation of the brain cortex continues to develop into the mid-20s (Gogtay et al. 2004), suggesting an underlying biological basis for such a stage. Coupled with the increases in psychosocial maturity in the 20s mentioned above, such changes in the brain suggest that emerging

adulthood is not simply a novel product of social change but a more biologically defined aspect of entry into the young adult stage.

At the other end of young adulthood, the transition to middle age is defined by the end of family formation. The average age of last reproduction for women is around 40 years, though fertility has been declining since the early 30s. In men there is much less evidence for a decline in reproductive capacity, but in monogamous relationships reproduction itself is tied to the women's age. While physical and cognitive functions decline in both men and women throughout young adulthood, the decline itself does not define the life stage.

Middle adulthood (40–60 years) is marked by important changes in the nature of family, along with increased economic productivity. Children born during young adulthood will now be in young adulthood themselves, shifting the nature of continued parental concerns and help. At the same time, aging parents may require everyday support for themselves. No wonder Erikson characterized this stage as one of caring.

Some research suggests a plateau in decline of cognitive functions during this stage including men such as word recall, matrix reasoning, spatial relations, and pattern comparison in both men and women during this stage.

Biologically, old age (60+ years) is defined by an increasing rate of senescence. This includes increasing decline in muscle mass in men and fluid intelligence in both sexes. The cognitive changes are underlain by changes in the brain, most notably a decline in white matter starting around the age of 50. Cognitively, the decline in fluid intelligences is countered by an increase in crystallized intelligence. This is notable in occupations characterized by knowledge production such as academics where some individuals remain productive well into old age. However, socially old age is marked by a loss of productivity, signaled by a retirement age of 65.

More generally old age is marked by an increase in wisdom along with increasing physical frailty. The fact that among hunter-gatherers some individuals live into their 80s indicates that this is a normal phase of the human life cycle and not simply an artifact of our modern conditions.

Those individuals who manage to survive into later age have been successful in doing so. Thus the result of their experience is not just accumulated cultural knowledge but by definition wisdom. Nonetheless, for many the last stage of old age will be defined as loss of self-sufficiency and an involuntary withdrawal from the social world as friends die. What is left but to concentrate on one's self and the inevitability of death?

This brings us to one of the most distinctive elements of the human life cycle: menopause. The complete cessation of reproductive function before death is rare among mammals. Thus human menopause raises the question of how such a state can be produced by natural selection. The grandmother hypothesis (Hawkes 2003) suggests that human females remain alive past their reproductive years because they provide help to their daughter's offspring. The grandchildren's survival then promotes selection for the genes underlying longevity. Whether this selection pressure is sufficient to generate a post-reproductive life span of 40 or more years among ancestral hunter-gathers is unclear. On the other hand, it does appear that grandmothers do result in more offspring surviving in some societies where the hypothesis has been tested.

Comparative Biology. Human life stages come into clearer evolutionary perspective when contrasted with our closest relatives, the great apes, in particular chimpanzees, for whom we have quite a bit of information. At about 250 days, gestation in the chimp is roughly the same length as for humans, suggesting similar prenatal development. Development of the brain in human is much more rapid during the last trimester compared to chimpanzees (Sakai et al. 2012). This suggests that continued brain development during the last trimester represents a relatively recent evolutionary phenomenon and may be important to the development of the brain after birth as well.

Weaning in chimpanzees is at about 5 years of age and reproductive maturation for females at close to 12 years (Walker et al. 2018). Thus the development of early childhood in human reflects an additional life stage inserted into the ancestral pattern. Such a change has two important

implications. First of all human infants spend less time with their mothers and more with other family members. In addition the prolonged period of development from weaning to puberty is associated with slower somatic growth rates (Walker et al. 2006) that allows for an extended period of brain maturation. In turn extended development suggests that the human brain can be shaped by environmental inputs during childhood increasing the importance of learning.

Comparison of the timing of reproduction among adult female humans with those of chimps is instructive about the evolutionary origins of human old age. Human females mature later but have higher age-specific fertility throughout their peak reproductive years, but the average age at last birth is close to 40 about the same age as human females (Hawkes 2010). Yet, even among hunter-gatherers, human females continue to live for up to 40 more years, while female chimpanzees rarely outlive the end of their reproductive capacity (Hill et al. 2001).

Importantly, a comparison of humans and chimps reveals that humans show a decrease in brain volume with age while chimpanzees do not, suggesting that the human brain undergoes senescent decline as a result of our extended life span (Sherwood et al. 2011), just as the human body does. In contrast, the chimpanzee brain appears to maintain more or less function until bodily and reproductive demise around the age of 50 years.

Interestingly, life satisfaction among captive great apes including chimpanzees shows a u-shaped curve with lowest levels during middle age (Weiss et al. 2012) just as it does among humans (Blanchflower and Oswald 2008). The authors characterize the nadir in life satisfaction as a midlife crisis, but it seems more accurate to point out that it reflects important changes in the demands of raising offspring.

Conclusion

Life stages are a cultural categorization of the inevitable changes experienced by individuals over their lifespan. While life stages represent culturally defined categories, current thinking

emphasizes eight distinct stages, including prenatal, infancy, early and middle childhood, adolescence, and young, middle, and old adulthood, characterized by biological, psychological, and social dimensions. An increasing understanding of the brain and hormonal changes provides a species-specific biological underpinning for these stages. Comparison with chimpanzees suggests the emergence of two new life stages in the last six million years of hominid evolution. These include the insertion of an early childhood phase between infancy and middle childhood that is characterized by continued development of the brain no longer dependent on the mothers the context of close relatives. It also includes old age, most clearly demonstrated by an extended postmenopausal female life stage.

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Stages of Life

- [Rite of Passage](#)

Stalking

- [Circumventing Mate Choice](#)
- [Female Age as a Predictor of Men's Aggression Against Women](#)

Stammering

- [Stuttering](#)

Stamping In

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Standard

- [Norms](#)

Standard Model

- [Standard Social Science Model](#)

Standard Social Science Model

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Synonyms

[Blank slate](#); [Cultural determinism](#); [Relativism](#); [Social constructionism](#); [SSSM](#); [Standard model](#)

Definition

The concept of Standard Social Science Model (SSSM) is used for description of the basic theoretical assumptions that determine the specific focus of consideration of social and cultural phenomena in psychology and social science for twentieth century. The core of SSSM is formed by the idea about the human mind as a blank slate and the related concept on exclusive role of the social world and culture in the formation of its content.

Introduction

The concept of Standard Social Science Model was first introduced by John Tooby and Leda Cosmides in 1992 (Tooby and Cosmides 1992, 1997) for identifying the epistemological framework of

social science and psychological studies of the twentieth century. According to them, its representatives are excessive concentrated on the social and cultural factors while denying any influence of biological one in their research. Tooby and Cosmides determined this view as a source of separation between social and natural sciences and one of the major obstacles for social science progress now. Moreover, social scholars used the idea on the sufficiency of social factors for the explanation of human behavior (such view is especially strong in sociology starting from sociologism of Emile Durkheim) as the way to establish and then to maintain disciplinary autonomy.

Tooby and Cosmides (1992) put into the core of SSSM an idea of the human mind as a blank slate (or, in Latin, as British philosopher of the seventeenth century John Locke said “*tabula rasa*”), i.e., the proposition that humans are born without any predispositions toward certain social perception, social cognition, and social behavior. Pinker (2016) also argued that the blank slate is accompanied by two other doctrines such as the concept of Noble Savage (J.-J. Rousseau, T. Hobbes) and the concept of the Ghost in the Machine (R. Descartes). Thus, the next logically related idea is that social factors and culture determine how and what we percept and learn and how we behave. Pinker also put this idea in relativist framework as SSSM supports the idea on the connection between variations in culture and the content of the human minds. At last, SSSM also proposed that human mind has no evolved structure, considering it as an externally programmed general-purpose device for learning.

According to Steven Pinker (2016), SSSM began to dominate in the intellectual life since the 1920s. He named among the most famous founders and supporters of SSSM anthropologist Margaret Mead, behaviorist psychologist John Watson and Burrhus R. Skinner (Pinker 2007). To this list, we can also add one of the fathers of social interactionism George H. Mead, who is considered as a social behaviorist. Besides, Pinker named such modern scientists from different disciplines as Richard Lewontin, Stephen Jay Gould, Steven Rose, and Leo Kamin as proponents of SSSM.

This entry describes the main assumptions of SSSM as they described by Tooby and Cosmides (1992), as well as reflected in the context of critical consideration of Pinker (2016, 2007). It is also considered the alternative nativist models proposed by them that largely supported by the recent progress in the studies of neurobiological mechanisms of the social behavior and the development of evolutionary psychology. At the end of the entries, some critical views on the dichotomy between Standard Social Science Model and the alternative Integrative Causal Model are discussed.

The Main Assumptions of Standard Social Science Model

Analyzing considerations that motivated the advocates of SSSM, Tooby and Cosmides identified the main features of the social sciences view in this framework (Tooby and Cosmides 1992, pp. 25–31):

1. The psychic unity of humankind. According to this note, the human infants all around the world are born identical in their basic human design and the development potential. As genetic variation cannot explain the extreme differences in thought and behavior between groups and the similarity within groups, social scholars put social factors and culture into first place. They forward these factors as responsible for inter-group differences.
2. Human nature has no casual significance in mental organization, social arrangements, culture, and so on. According to Tooby and Cosmides, this statement looks as a result of the logical trick.

Thus, the supporters of SSSM conclude that evolved structure of the human mind has no influence on inter-group differences in mental and social organization in adults as infants have the same biological nature.

3. The humans acquire knowledge, patterned social behavior, etc. from outside in the process of their development (SSSM considers only ability to learn among infants). In this, the external factors are considered only

source for human mental transformation. This statement is deduced from the lack of any complex mental organization in infants in comparison with adults.

4. Social world is the cause for mental organization of the adults. Such conclusion is based on two propositions. First, what we see as a mental organization in the infants is “innate,” i.e., inborn or genetically determined, etc., while in adults, it is formed under the influence of environmental factors. Thus, SSSM states cultural phenomena, fundamentally, have no heredity and are only acquired. Second, based on the deprivation thought experiments, SSSM supports that humans without being programmed by culture demonstrate “virtually ungovernable, a mere chaos of pointless acts and exploding emotions, his experience virtually shapeless” (Tooby and Cosmides 1992, p. 26). Once the factor of culture appears, the individuals change and become socially organized and predicted. This leads the supporters of SSSM to conclusion on the fundamental role of culture in the shaping of mental organization in adults.
5. There is overwhelmingly or entirely one direction of causation: socially organized environment and culture precede the existence of the individuals and are external to them; they determine or construct them. At the same time, this influence is unidirectional – when we are born, we find certain social and cultural circumstances. From this, the advocates of SSSM conclude that the individual (mind) cannot create the social world and only follow its settings, the last create the individual (mind). Individuals are in the situation of social coercivity (for the first time, this idea was clearly formulated by Emile Durkheim in 1895 in his work *The Rules of Sociological Method*, who said about coercion considering crucial influence of social facts on the individuals). As Tooby and Cosmides exemplify, according to SSSM, we have no choice what native language to learn or we cannot to create new language. Moreover, from the observation of the strong influence of sociocultural or political processes in modern society on the individuals in contrast to the influence of the individuals on them, the supporters of SSSM conclude that “the sociocultural world is the actor (the cause or the prior state that determines the subsequent state)” (Tooby and Cosmides 1992, p. 26).
6. As culture is the only one that has a matter in shaping the human mind and behavior, then it only deserves our examination. SSSM interprets culture in different ways, for example, as economic relations, political regimes, meaningful symbolic system, social relations, social institutes and norms, traditions, knowledge, and so on. At the same time, it is always considered as nonbiological entity (nonbiological in its origin and its nature). Interesting moment here is that not only the above staff of culture is external to the individuals, but is also such psychological phenomena as thinking too. The last means that our thinking is to a large extent social and public, consists of significant culturally determined symbols and in the most part of the words (this idea is well elaborated on by George H. Mead).
7. The individual is not a creator of a complex and significant organization in the social world. As Durkheim noted “once the individual is ruled out, only society remains” (Durkheim 1982, p.182). Such position is marked now as sociological realism (contrary to social nominalism). In sociological realism, the “collective concepts” such as society, social class, state, social organization, etc. capture the real existence of supra-individual phenomena. They are considered as more than the sum of the individuals. Advocates of social realism believe in objective regularities in the social world and its independence from the individuals.
8. Sociocultural phenomena are generated by other phenomena at the sociocultural level. Thus, sociocultural reality is a reality *sui generis*, which can be explained in the terms of itself. Such position was forwarded by many social scholars in different disciplines. Thus, Durkheim developed sociological

conception named sociologism, which includes ontological and methodological aspects. In ontological sense, society was analyzed as a special kind of reality that cannot be reduced to its other types. He insisted on the top priority of social reality over the individuals (i.e., over biopsychic reality that is implemented in the individuals). Methodological aspect of sociologism includes guiding principle for social science studies. According to this principle, social facts must be explained only by other social facts, without any references to psychic phenomena, or something like that. In Durkheim's view, it is quite enough for understanding the social phenomena. It is also important that he considered social facts as things: they exist independent from the individuals, but influence on them.

9. Human nature (the evolved architecture of the human mind) is only a necessary condition for the organization of social life; however, it does not play any notable role in its configuration. The role of the human nature (or human mind) is only in the ability for learning and incorporating the culture. Moreover, the human mind is formless, malleable, and plastic phenomenon that is enough, easily formed by sociocultural factors in the process of socialization. Then, the human mind is considered as a general-purpose computer that is programmed for learning certain types of behavior by culture and so controlled by outside mechanisms. In SSSM, this idea is connected with a view on the human mind as an empty vessel, which is waiting to be filled by knowledge, social norms, behavioral patterns, and so on. Thus, the mind itself is not a problem or subject of investigation in SSSM. The main problem is cultural or social circumstances that determine it.
10. Learning is the basic mechanism of incorporation of "the culturally manufactured pre-existing complex organization outside of the individual" (Tooby and Cosmides 1992, p. 30) into the human. Consequently, the role of psychology is to provide knowledge about the process of such learning. In such

perspective, the human mind, if it is at all inborn equipped, must have such mechanisms or structure that enable individuals to absorb any environmental influences. At the same time, the human mind organization could not shape the content of culture or even be predisposed to the certain selection of cultural inputs (e.g., what to learn and what not). According to Tooby and Cosmides, the psychological studies of the general laws of learning (and underlying cognitive processes) had positive effects on the bringing psychology and natural sciences closer together.

As Hampton (2004) summarized, the SSSM states "(a) that mind, aside its capacity to learn, is a tabula rasa; (b) that culture is the cause of mental content; (c) that culture is independent of mind; and (d) that psychology should be concerned with the study of enculturation" (Hampton 2004, p. 17).

Steven Pinker, modern advocacy of evolutionary psychology and the computational theory of mind, refers to the concept of Standard Social Science Model to advance his own an alternative view on the human nature (about this below). He describes SSSM as a relativist perspective in which the human nature is lacking universal essence, i.e., its content is very malleable and varies according to culture, society, and historical situation and does not possess fixed structure. In popular-science book "The Language Instinct" (2007), Pinker lists the significant points of SSSM, which he finds problematic:

1. Human behavior (in contrast to animal) is determined by only "free from biological constraints" culture, which can vary "arbitrarily and without limit" (Pinker 1994, p. 406).
2. A few reflexes and an ability to learn are only inborn human infants who learn the culture in the process of socialization (Pinker 1994, p. 406).

For Pinker, "SSSM has not only been the foundation of the study of humankind within the academy, but serves as the secular ideology of our age, the position on human nature that any decent person should hold" (Pinker 1994, p. 406).

SSSM is considered as an alternative to “biological determinism” that is treated as having harmful social effects contributing to different forms of social discriminations, supporting social inequality, promoting racist or imperialist ideologies, and initiated such horrors of the twentieth century as human forced sterilization and genocide.

Such taboo on human nature “put blinkers on researchers” and “turned any discussion of it into a heresy that must be stamped out” (Pinker 2016, p. xi). In “The Blank Slate: The Modern Denial of Human Nature” (2016) Pinker also proposed that different types of fear such as the fear of inequality, the fear of imperfectability, the fear of determinism, and the fear of nihilism are the sources of the notion that human mind does not have innate traits. He also called for “realistic biologically informed humanism” considering many negative social and political effects of the elimination of human nature as an important basis for social decision-making.

The philosophers Mallon and Stich (2000) use the term of “social constructionism” as a label for those who advocate the most assumptions of SSSM, but do it in more constructive manner. As they said, all SSSM followers are social constructionists, though not all social constructionists share every aspect of SSSM. Social constructionists do not deny innate “mental endowment imposes some constraints on what we can learn and what we can do” (Mallon and Stich 2000, p. 134); however, they believe that for “explaining the diversity of psychological phenomena like emotions, beliefs, and preferences, differences in the surrounding culture loom large” (Mallon and Stich 2000, p. 134). The different aspects of social constructionism and six graduations (historical, ironic, reformist, unmasking, rebellious, revolutionary) of the using of construction ideas are analyzed by Hacking (1999).

Alternative Integrated Model

Tooby and Cosmides (1992) critically estimate the basic ideas of Standard Social Science Model.

The central points of Tooby and Cosmides’ critiques of SSSM are (1) its isolationism, i.e.,

SSSM has failed to integrate itself with other sciences or even to acknowledge the necessity to be consistent and compatible with them, (2) its neglect to biology that is mostly motivated by moral and political concerns, and (3) its requirement an impossible psychology, “it posits theories of the human mind that cannot account for abilities we are already known to possess, and that also never could have evolved” (Scher and Rausche 2003, p. 233). Thus, they criticize SSSM for abandonment of any biological influences in the human mind and social behavior and for overestimation of the environmental factors. They also note that SSSM is one of the key factors of a lack of progress in social science now.

Indeed, recently biosociological sub-disciplines such as neurosociology, evolutionary sociology, social studies of genomics, etc. have started to develop. Their representatives try to incorporate biological variables into the sociological conceptions and theorizing, considering different dimensions of social behavior at micro- and macro- levels in the terms of the evolved adaptations strictly embedded in the neural activity of the human brain. The social scholars of these new areas talk about great difficulties to make sociology close to biological sciences. Many of them faced misunderstanding, difficulties in the publication of their research results and even discrimination from the colleagues (e.g., Kalkhoff et al. 2012; Massey 2013; Udry 2001). Such oppressive reaction is mostly determined by biophobia that is widespread in the sociological community. Biophobia means unjustified avoidance of using biological variables in the sociological studies, intolerant attitudes toward those who conduct such research. The causes of biophobia are rooted precisely in the basic assumptions of SSSM. Ellis (1996) determine such causes as semantic factors (i.e., “tendency to equate sociological with social causes”), lack of training in biology, exclusive focus on humans, and moral or political factors. The latter “involves a strong moral/ideological commitment to human equality that prevents many sociologists from considering the possibility of biologically based causes of individual and especially group differences in behavior” (Ellis 1996, p. 24). Moreover, biophobia (or as Ellis

also put “pure environmentalism”) lead to theoretical sterility and sociology’s decline (Ellis 1996). Sociologists conducting bisociological research certainly challenge the fundamental principles of sociological science. As Machalek and Martin (2015) emphasize, they had to adjust SSSM which supports a simplified dualism – learning vs. instinct, culture vs. biology, social vs. psychological factors of human behavior. Thus, the representatives of evolutionary sociology question the possibility to find the causes of social behavior exclusively in the social structure. They reduce the level of significance of the cultural factor in the determination of social behavior. The obtained results (e.g., Hopcroft 2018; Turner and Machalek 2018) are also clearly demonstrated that there are evolved biological predispositions to organizing themselves into social rank-ordered systems, male dominance, territoriality, aggression, sexual and reproduction social behaviors, emotionally based social relations, etc.

Thus, due to recent advancement in the studies of the evolved neurobiological mechanisms of social cognition, social perception, and social behavior in evolutionary psychology, cognitive and development psychology, as well as neurobiology and the related disciplines, the changes have taken place. These changes potentially can lead to formulate more balanced and complete epistemological basis for social science (as we can already see in the biosociological research).

Tooby and Cosmides (1992) proposed the Integrated Causal Model (ICM) on the position of SSSM, also known as Integrated Model (IM), where they merged biological and cultural factors considering the human mind and behavior in the terms of the evolved mechanisms, as well behavioral and psychological adaptations.

According to Tooby and Cosmides, only the first idea of SSSM about the biological identity in the infant design and development potential is correct. Therefore, it is included into the ICM without modification. This note is supported by the Human Genome Project and recent studies which highlighted the basic genetic similarity of all humans. Thus, “genetic variation does not explain why human groups dramatically differ from each other in thought and behavior” (Tooby and Cosmides (1992, p. 25).

The Integrated Causal Model includes the following main assumptions:

1. The human mind is a set of evolved information-processing mechanisms which have neurophysiological basis.
2. These mechanisms are adaptations obtained by the humans in the process of evolution and contributed to their survival.
3. The information-processing mechanisms of the human mind is specialized on solving particular adaptive problems.
4. Largely due to such specialization, they have content-specific structure.
5. According to this content specialization, the human mind produced specific content of the culture.
6. Such generated cultural content is then adopted or modified by psychological mechanisms in accordance with specific environment (Tooby and Cosmides 1992, p. 24).

Close to the Integrated Causal Model, the alternative perspectives have been developed by Pinker and some other nativist scientists. As Rosenberg notes, they treat the mind as “a package of a large number of different special-purpose instruments, each with its own independent domain of operation, each the developmental result of a distinct package of genes that were selected for by the evolutionary environment from which *Homo sapiens* and its immediate ancestors emerged”. (Rosenberg 2016, p. 226). Again, in contrast to SSSM, in nativist models (ICM is among such models too), the human mind/brain is modulated, structured and hardwired by the environment (including social setting and culture) under pressure of evolutionary factors. The humans at birth have already hardwired brain (consists of functionally specialized modules) that predisposed them to certain social perception, cognition, and behavior.

Thus, the human mind as a blank slate is replaced by the human mind as a set of the evolved adaptations strictly associated with neurophysiological processes. These adaptations reflect in the mind in the form of functionally structured information-processing mechanisms.

In contrast to SSSM, in alternative models, the human mind is a content specialized (not generally-purpose and only specialized for learning) machine. Then, ICM contrasts the note about human behavior as derived from the interactions between evolved psychological mechanisms and environmental (including, of course, cultural and social) factors with the idea about the human mind as culturally programmed in the process of learning. Further, culture has influence not only on the human nature, but at the same time it is also constructed by it. At last, the consideration of biological factors of human behavior is considered as important for its understanding in the alternative integrated models, but is not in the SSSM.

Criticism of the View on Social Science Through the Lens of SSSM

Richardson (2007) criticizes Tooby and Cosmides for that they proposed false dichotomy between “manifestly untenable view and their own” (Richardson 2007, p. 176) counterposing SSSM and ICM. According to him, in fact, Tooby and Cosmides had not proposed alternative as SSSM in their description is not in accordance with the real situation in social sciences and is not supported by scholars in the twentieth century. Richardson notes that hardly anybody really share the view on human mind as “general-purpose cognitive mechanisms, which lack any nativist element whatsoever” and that “no differences between individuals and no biological contribution to individual or social development” (Richardson 2007, p. 176).

Another line of critique is the interpretation of the political decision-making as a consequence of the implicitly or explicitly adapted SSSM view. Such critique is in Sampson’s work (2009), who based it on the dissection of the Pinker’s version of SSSM (“the idea that the mind is like a passive camera film”) and its role in society and science. Sampson (2009) says that the statement about domination of the SSSM as a “secular ideology” is untenable at least relative to some cultures (he said about Britain). Thus, he notes that in the

twentieth century (until 1990s) in education sphere, an idea about existing of natural children bents that need development are prevailed. Besides, although SSSM perhaps promotes to overcoming the role differences between sexes, women movements also began in the late 1960s (not as Pinker put it in the 1920th) and has become an influence only in the last decades, in the period when SSSM was started to be replaced by nativism philosophy. Therefore, they cannot be considered as practical implementation of the SSSM idea on the biological emptiness of the human mind. Sampson (2009) also ironized that the greatest founders (M. Mead, Watson) and advocates (Skinner) of SSSM (as Pinker point out) are hardly among the most influential thinkers of the twentieth century. At last, he (as well as Richardson (2007)) blames Pinker in “an appallingly crude version of empiricism – not a version that any serious thinker is likely to defend” (Sampson 2009, p. 132).

Neil Levy (2004) also says about overestimation of the role of SSSM in the intellectual life, as it was described by Pinker and his misleading in attributing Skinner to this view. According to Levy, “even behaviorists believe that the human mind has in-built learning mechanisms and preferences” (Levy 2004, p. 461). Without denying the differences between the basic assumptions of evolutionary psychology and SSSM, he emphasizes that nobody really shares the ideas of only one of the sides of the nature-nurture debates, at least in its extreme forms. Thus, everyone agrees that genetic factors influence the behavioral and psychic traits of the human in a probabilistic way, in accordance with the features of the environment (Levy 2004).

Hilary Rose (2001) emphasizes that Tooby and Cosmides in their assertions perverse the situation in sociological and anthropological studies considering it as concentrated on the nature-nurture debate. However, according to Rose, sociology and anthropology have not been at all very interested in the heritability factor over the last 50 years. The nature-nurture debate was rather a question for “Anglo-Saxon” psychometrics” (Galton, etc.) which aimed at measuring the so-called hereditary genius. Rose also surprised

about the adherents of SSSM how they were determined by Tooby and Cosmides. This especially concerns evolutionary paleontologist Stephen Jay Gould, the population genetics Richard Lewontin, the neurobiologist Steven Rose, and the psychologist Leo Kamin. The latter three scholars developed an alternative dialectical conception (opposite to biological determinism) considering dialectical relation between biological organism and environment. According to Rose, their dialectical view is more adequate than the Integrative Model of Tooby and Cosmides.

Thus, the main points of criticism concern how Tooby and Cosmides, as well as Pinker put the assumptions of SSSM into the intellectual framework of the twentieth century rather than its content. According to the aforementioned scholars, they do not correctly reflect on the mainstream ideas dominated in social sciences and reduced it to nature-nurture debate.

Conclusion

Standard Social Science Model is a concept used for describing the specific view of those social scholars and psychologists who give top priority to social and cultural factors in the formation of human mind and thus eliminate any evolved predispositions as well as biological factors in their considerations. SSSM is considered not only as a set of basic principles for social science studies but also as a theoretical basis for the dominant secular ideology. The major assumption lying in the foundation of SSSM is the human mind as a blank slate or *tabula rasa* in the term of philosopher John Locke. The human mind has no innate traits and its biological nature is unimportant for understanding human behavior.

SSSM was developed as an opposition to biological determinism and extremely dominant in social sciences in the twentieth century. But situation recently changes largely due to the progress in evolutionary psychology, and the related disciplines. Its development has been made possible after approving the idea on the evolutionary nature not only the human body but also the mind which is considered as connected with evolved neurophysiological basis.

Based on this idea, the authors of the concept “Standard Social Science Model” Tooby and Cosmides proposed the alternative view for social sciences. They named it the Integrated Causal Model. Thus, Tooby and Cosmides replaced the idea on the human mind as a blank slate by the note on the human mind as a set of evolved adaptations which contributed to the survival of our ancestors. Then, to the human mind as a general-purpose device, they contrasted the functional specialized information-processing mechanisms. At last, the assumption about independence of culture from any influences of the human biological nature was replaced by the idea of its dependence on the content-specific structure of the human mind which is specialized on solving different adaptive problems. Besides, based on the recent findings in neurobiology, the Integrated Causal Model takes as a starting point an idea that evolved information-processing mechanisms of the human mind strongly associated with neurophysiological activity. The similar ideas are also forwarded in other alternative nativist models (e.g., by Pinker).

Some modern scholars (e.g., Rose, Richardson, Levy, and Sampson) criticize the authors of the concept of Social Science Standard Model for that they formulated a simplified view on the basis of social science when considered it as only focused on the dichotomy nature vs. nurture. They also point on the overestimation of the importance of SSSM for the development of social science and intellectual life, as well as for creating the theoretical basis for secular ideology in modern society.

Nevertheless, despite the above criticism, the concept of Standard Social Science Model allows to more clearly fix the problem concerning different epistemological strategies for consideration of the human mind and behavior, as well as to see the effects that have such strategies in science and society.

Cross-References

- [B. F. Skinner and Behaviorism](#)
- [Biosociology](#)
- [Blank Slate, The](#)

- [Founders of Evolutionary Psychology](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)
- [Pinker's \(1994\) The Language Instinct](#)
- [Steven Pinker](#)

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Standard Social Science Model, Tabula Rasa, Empiricism, Environmentalism

- [Blank Slate, The](#)

Standing Tall

- [Big Man](#)

Stanford-Binet Intelligence Scales

- [Intelligence Testing](#)

State Self-Esteem

- [Sociometer Theory](#)

State-Sanctioned Punishment as Deterrent to Violence

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Synonyms

Criminal justice system; Norms and social contract; Punishment

Definition

State punishment is an administrative system of punishments which functions are deterrence, retribution, communication, incapacitation, or rehabilitation of criminal offenders.

Introduction

Aggression is any form of behavior that goals to harm or injure (Baron 1977), while the violence is an aggression that has extreme harm as its aim (Anderson and Bushman 2002). Aggression mechanisms have emerged as solutions to a host of distinct adaptive problems, such as retaliate against or punish group members who violate social and moral norms (Buss and Shackelford 1997; Durrant and Ward 2015). The social structural and cultural factors play a role in the nature and form of punishment and how these have changed over time (Durrant and Ward 2015). Punishment can be defined as the intentional infliction of sanctions by the state on who have unjustifiably harmed other people (Boonin 2008). In addition, Miller and Vidmar (1981) suggest that punishment is a negative sanction intentionally applied to someone who is perceived to have violated a law, a rule, a norm, or an expectation. From an evolutionary perspective, the ultimate function

of punishment is to communicate to group members or outside kin offenders the appropriate behavior according to the social norms and to deter these future aggressions from occurring (Durrant and Ward 2015). Punishment remains the central tool of dealing with normative violations and criminal offenders in modern societies.

State-Sanctioned Punishment

Criminal justice system, as an institution that provides the administration of punishment, can provide signals as to the normative boundaries of human social behavior. It also serves to put limits in the extent of offending acts (Carlsmith 2008; Durant and Ward 2015). Indeed, this tendency to punish who transgress social norms is arguably a universal feature of all human societies (Hoffman 2014). Changes in legal practices have an important role to play in the violence context (Durant and Ward 2015).

The mechanisms underlying punishment are related to altruistic and cooperative processes. Punishment's mechanisms are evolutionary adaptations that have been selected because of their enhanced biological fitness by sanctioning group members who violate the norms, promoting cooperative actions and cohesion of the group. Also, punishment increases the likelihood to communicate a model of appropriate behavior to the offender and to other members and express disapproval to a criminal conviction (Durant and Ward 2015).

According to criminal justice literature, punishment functions are deterrence, retribution, communication, incapacitation, or rehabilitation of criminal offenders. The type of punishment depends on the justice paradigm, but in general, the punishment for criminal offenders is the prison sentence that operationalizes the severity of the punishment in years of imprisonment. The legal system is responsible for protecting citizen interests and rights (Durrant and Ward 2015). A state-sanctioned punishment is increased by the power of centralized governments that remove the punishment from the hands of the aggrieved and place it instead in the hands of objective and neutral legal systems (McCullough 2008).

Conclusion

When the state legitimates the law and has the power to apply punitive sanctions with enough severity, violence tends to decrease (McCullough 2008). The states that are most efficient at controlling violence and retaliation are those that are effective at enforcing the law, protecting their citizens from harm, and punishing violators (McCullough 2008). State-sanction punishment should have the functions of protection and defense of citizens and punish norm violators. As the sociologist Norbert Elias (1969) wrote, “When a monopoly of force is formed, pacified social spaces are created which are normally free from acts of violence.”

Cross-References

- [Altruistic Punishment](#)
- [Evolution of Punishment](#)
- [Mechanisms to Detect and Punish Cheaters](#)
- [Norms](#)
- [Violence](#)
- [Violence as Coercive Control](#)
- [Wild Justice](#)

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State-Sanctioned Punishment as Substitute for Tribal Vengeance

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Synonyms

[Punishment](#); [Retaliation](#); [Revenge](#)

Definition

State punishment is an administrative system of punishments that mediate conflicts between aggressors and victims and replaced the previous sanction of tribal revenge.

Introduction

Revenge is considered a taboo in modern societies, but blood revenge is one of the most commonly cited causes of violence and warfare in tribal societies (Chagnon 1988). Evolutionary psychology considers that revenge could be transmitted by primary mechanisms and by cultural transmission, assuming that revenge is a built-in feature of human nature (McCullough 2008).

The definition of revenge is similar to biologists' definition of punishment. Clutton-Brock and Parker (1995) define punishment as a costly imposition of costs that results in delayed benefits for the punisher. McCullough et al. (2013) claimed

that revenge is defined when the imposition of costs at a cost is only a response to an imposition of harm or a benefit-withholding that was caused by a mechanism designed to deter cost-impositions or benefit-withholdings in the future.

Evolution of Punishment

Tribal revenge can mean retaliatory killing, revenge raid on the members on the current community of the initial killer (Chagnon 1988). Using selection thinking, the propensity of revenge may have been selected because it helped to deter individuals who aggressed against ancestral humans from harming them a second time, to deter some would-be aggressors, and for punishing members of the social group who failed to pitch in to the common good (McCullough 2008).

“Evolution of Punishment,” by A. Warren Stearns (1936), helps to understand how this tribal vengeance was substituted by state-sanctioned punishments. Stearns assumes that in this early period, known as private vengeance, the fundamental purpose of punishment had to do with defense of private groups and family members, and the immediate motivation was an aggression or offense. In those tribal societies, every kin-based group had its codes and conventions based on vengeance (Blick 1988). But, these punishments could also engage the members in paybacks with no due process and without proportionality, causing the cycle of revenge (Stearns 1936; Walen 2016).

The development of complex codes of punishment and justice is concomitant with the beginnings of organized societies, e.g., Chinese and Hebrew people. This private justice period is marked by the governmental intervention to regulate the retaliation, protecting the individuals from excessive or unjust vengeance (Stearns 1936). The “eye for an eye, and tooth for a tooth” law was the beginning of a rising political state. Justice appeared as an abstract sanction that transferred the responsibility of punishment, previously belonging to the kin, to the state. Besides deterrence function, the punishment began to have a preventive function, following the idea that the more severe the punishment, the greater its effect (Stearns 1936).

Justice theories started to substantiate a deterrence and teaching purpose for the punishment, applying proportionality of punishment as the modern substitute for the primitive practice of private vengeance. The current state of public vengeance is arranged by the mediation of conflicts between offender and victim by the modern criminal justice system, establishing and measuring punishment (Walen 2016).

Revenge by individuals or extended kin groups was replaced by formal adjudication in societies with favorable resource bases and vertical inheritance (McCullough et al. 2013). According to Boonin (2008), punishment in the criminal justice system is intentional, directed toward a particular end, retributive, and harmful and expresses disapproval or censure, resulting in suffering or deprivation to the offender. State-sanctioned punishment follows a violation of important social norms that protect common interests of political community (Walen 2016).

Conclusion

The evolution of tribal vengeance to state-sanctioned punishment follows the development of societies as a complex political system (Walen 2016). The main purpose of revenge system is to deter an aggressor or would-be aggressors from imposing future costs to the victim (McCullough 2008; McCullough et al. 2013), whereas criminal justice system serves as an institution that administers punishment. Tribal vengeance punishment was applied in the victim-aggressor context within a close kin relationship and without clear rules of magnitude of punishment. State-sanctioned punishment is based on the socially built idea of justice as the mediator of the conflict, responsible for applying the punishment according to societal norms and the law (McCullough 2008; Roberts and Murray 2013). It is plausible to assume the individuals would stand to benefit from the social stability that comes from replacing revenge with other means of sanctioning as the punishment by the representatives of social institutions (McCullough 2008; Ward and Salmon 2009).

Cross-References

- Ability and Willingness of Victim to Retaliate
- Aggression
- Costs of Aggression
- Culture of Honor and Retaliation
- Evolution of Punishment
- Motivates Punishment

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Statistical Summary

- Summary Representation

Status

- Dominance and Health
- Dominance and Testosterone
- Dominance in Humans
- Dominance, Testosterone, and Cortisol
- Dominant Acts Expressed (Buss 1981)

- Function of Dominance
- Indicators and Correlates of Status and Dominance
- Redistribution Preferences and Low Socioeconomic Status
- Reputation as a Context for Men's Aggression Against Men
- Rule Violations Checked If High Status
- Rule Violations Not Checked If Low Status
- Status Hierarchies
- Vocal Indicators of Dominance

Status Acquisition

- Status Competition

Status and Dominance Hierarchies

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Synonyms

Social Ranking

Definition

A social structure in which some individuals have priority of access to resources relative to others.

Introduction

In most species (including humans), competition and cooperation among members of a social group produces a complex social structure called a **status (or dominance) hierarchy** in which some individuals have regular priority

Denise D. Cummins is retired.

of access to resources and fertile mates in competitive situations. These individuals are referred to as high status (or high ranking). Individuals who have lower priority of access are called subordinate or low status. In its most developed form, the dominance hierarchy is transitive, meaning that if A has priority over B and B has priority over C, then A has priority over C and so on.

Because of their privileged access to resources, higher-status individuals are less likely to die of predation or starvation and more likely to leave living offspring. Among species in which status is unstable, the level of reproductive success achieved by any individual is directly related to the length of time during which that individual is high ranking. Accordingly, there is a direct relationship between status and *inclusive fitness* (reproductive success of individuals and their closely related kin).

In small-scale human societies, men's social status is positively associated with various indices of reproductive success such as number of mates and surviving offspring (von Rueden 2014). In large-scale, modern human societies, status is highly correlated with potential fertility (as estimated from copulation frequency), accounting for as much as 62 % of the variance in this proximate component of fitness (Pérusse 1993). This value is comparable to that found in small-scale societies.

Types of Status Hierarchies

According to an influential model of hierarchical sociality, there are two systems of status – “two ways to the top” (Henrich and Gil-White 2001). In the **dominance** route, physical intimidation and coercive power are used to achieve high-status positions. In the **prestige** route, skills and knowledge translate into social influence and social status. Among species in which rank is unstable (as opposed to fixed and inherited), status in both types of hierarchy depends on individual differences in physical characteristics and social cognition acumen.

Physical Correlates of Status

Physical size. Physical size and rank are correlated in many species, with larger individuals tending to be higher ranking (Ellis 1995). Successful leaders in both small-scale and large-scale modern human societies tend to be taller than average and to possess more masculine facial and vocal characteristics (Mayew et al. 2013; Stulp et al. 2013).

Age. Adolescent chimpanzees are subordinate to all adult males, and status striving among males typically involves younger males challenging older ones. Rank declines with physical age, but alphas may maintain high-ranking positions through coalitions with other males.

In small-scale human societies, older adults typically fill leadership roles. This is primarily because they have had more time to accrue task-relevant knowledge and interpersonal skills and have larger adult kinship networks. During times of institutional change or informational obsolescence, however, younger individuals are more likely to hold leadership roles.

Gender. Female dominance over males is rare among mammals, being reliably observed only in hyenas, horses, bonobo chimpanzees (*Pan paniscus*), and certain species of monkeys, such as macaques and vervet monkeys.

Leadership positions in small-scale human societies typically are held by men. Women's opportunities tend to be limited by demands of caring for multiple dependent offspring, who spend more time as prereproductives than any other species. These caregiving demands limit opportunities for networking beyond the extended family.

Hormone-dependent social interaction styles. Status correlates with levels of sex hormones and cortisol in many species of primates, including humans. Higher testosterone levels are associated with higher social rank in nonhuman primate males and human males (Sherman et al. 2015). In female chimpanzees, higher levels of circulating estradiol are associated with higher status; in human females, it correlates positively with measures of implicit dominance motives (Stanton and Edelman 2009).

Eisenegger et al. (2011) provide detailed summaries of research on the relationship between testosterone levels and dominance or status behaviors. They report that salivary testosterone levels correlate with implicit measures of power motivation, increased vigilance for status threats, and high-risk tolerance. They also report that single-dose administration of testosterone reduces subconscious fear and fear-potentiated startle response, reduces trust in economic games, reduces cognitive empathy, and increases social cooperation.

Cortisol inhibits the impact of testosterone, and the interplay of these two hormones has been found to regulate status-related behaviors (Mehta and Josephs 2010): Across two studies of leadership and competitive behavior, testosterone was found to positively correlate with dominance, but only in individuals with low cortisol. In individuals with high cortisol, the relation between testosterone and dominance was blocked or reversed, particularly following social defeat. These findings suggest that high testosterone levels facilitate status attainment only when cortisol is low. When cortisol is high, the impact of testosterone is blunted.

These findings were replicated in a study based on 78 male executives (Sherman et al. 2016). Despite the myriad nonhormonal factors that determine organizational promotion, the executives' hierarchical position in their organizations could be accurately predicted from their endogenous testosterone and cortisol levels: Testosterone positively predicted executives' number of subordinates, but only among low-cortisol executives.

Numerous studies have also found that the relationship between hormone levels and status is bidirectional, that is, changes in status can have profound impact on testosterone, cortisol, and serotonin levels. Following contests of rank among nonhuman primates, defeated males exhibit a drop in testosterone levels, while winners' levels rises; serotonin levels rise in subordinates who improve their social status. Among humans, male winners typically show elevated testosterone levels relative to losers; this is true even when the competition involves little physical

action, as in chess competitions or contests in reaction time (see Eisenegger et al. 2011).

Compared to socially dominant individuals, subordinate or submissive individuals have higher baseline cortisol levels and display greater changes in physiological stress indices during conflict and slower recovery from conflict-induced changes in cardiovascular activity measures. The reason for this may lie in the diminished power lower-ranking individuals possess to control events in their everyday lives.

Social Skills, Reputation, and Social Capital

Among male primates, rank within the dominance hierarchy is acquired and maintained through dyadic aggression, and alliances determine the fate of outranked individuals. Importantly, these alliances are formed and maintained through cooperative effort or, more precisely, through the formation of reciprocal obligations. During agonistic encounters, individuals typically call for help, and *non-kin* allies are more likely to supply that help if the individual in question has groomed them, shared food with them, or assisted them in agonistic encounters in the past. Similarly, they punish noncooperators by directly aggressing against them when they themselves request help, failing to come to their aid, or by misinforming or failing to inform them about the location of food.

What counts as sufficient reciprocation also depends on rank. Among those close in rank, the rate of intervention by individual A on behalf of B is proportional to the rate of intervention of B on behalf of A. But high-ranking individuals need not to reciprocate as often as subordinates in order to maintain an alliance. The most frequent explanation given for this is that greater benefits derive from their interventions due to their priority of access to physical and social resources. Accordingly, nonhuman primates often focus their alliance-building efforts on higher-status individuals. For example, baboons, macaques, and vervet monkeys form matrilineal hierarchies in which any female is dominant to all the females

that are subordinate to her mother, and she is subordinate to all the females that are dominant to her mother (Cheney and Seyfarth 1990). During agonistic encounters, support is typically given to the higher-ranking females who in turn intervene in conflicts when they themselves are dominant to the target of the aggression. By aiding higher-ranking females, lower-ranking females form strong alliances based on reciprocal obligations that enable them to move up in rank.

In small-scale human societies, men with large kinship networks are more likely to gain political influence, but social support from non-kin is also instrumental in the acquisition and maintenance of status (see von Rueden 2014). Among Tsimane men, influence within small groups and at the level of the community depends on social support from non-kin as well as kin, and the formation of such alliances depends on cooperation through activities such as food sharing. To express commitment to food sharing, some societies, such as the Ache of Paraguay and Hadza of Tanzania, consider it taboo for hunters to consume portions of their own kills or to brag about their hunting prowess. Instead, successful hunters are expected to deprecate their own achievements and to share meat generously. Doing so not only facilitates alliance formation but signals quality as a mating partner.

Henrich et al. (2005) conducted a cross-cultural study on social decision-making involving 15 small-scale horticultural, foraging, and pastoral cultures in Africa, South America, and Asia. The tasks involved economic games in which participants are given an opportunity to cooperate with or exploit others in economic transactions. A cornerstone of economic theory is that rational agents are self-interested, that is, when making choices about allocations of resources, rational agents make choices that maximize benefits to themselves. But that is not what the researchers found. The rational self-interest model failed to a large degree in all of the societies. For example, in the ultimatum game, one party proposes how to divide a resource (proposer), and the other party is allowed to accept or reject the offer (responder). If the offer is accepted, the resource is divided as agreed. If the offer is rejected, no one gets anything. Many

ultimatum proposers among the Au and Gnao of Papua New Guinea offered their partners more than half, but they were frequently rejected. The authors interpreted this pattern of behavior as a reflection of status seeking through gift giving, which is common throughout Melanesia. In these societies, accepting gifts implies a strong obligation to reciprocate, and reciprocation often takes the form of political alliances.

More than a decade of research in large-scale industrialized societies has also challenged the legitimacy of the “rational agent” model as a descriptive model of human behavior. People do not always seek outcomes that maximize benefits for themselves. Instead, our choices appear to be equally motivated by concerns about fairness, equity, and reciprocity. The modal response in studies based on economic games is to trust with the expectation of reciprocity, and failures to reciprocate are met with retaliation in subsequent games. In fact, players and observers are willing to pay a penalty for the opportunity to punish nonreciprocators (Fehr and Fischbacher 2004). In order to accommodate these results, normative theories have been proposed in which reciprocity, altruism/spite, and inequity aversion play prominent roles. When viewed from these theoretical perspectives, individuals enter economic transactions with normative standards of fairness, and their decisions are guided in large part by distance from the expected normative division. Behavior that departs significantly from these norms elicits retaliatory, spiteful, or other apparently “irrational” response profiles that depart significantly from predictions based on simple self-interest.

Even here, however, the impact of relative status looms large, as does the way in which status is achieved. When the role of proposer is awarded arbitrarily, proposers behave fairly toward their transactional partners (offering close to 50 %), and responders typically reject unfair offers. But when told transactional roles have been assigned on the basis of performance on competitive outcome (e.g., score on a trivia test), exploitation becomes the modal response: High-ranking individuals offer their low-ranking partners less and low-ranking responders are willing to accept less (Hoffman et al. 1996).

When status is awarded on the basis of prestige, however, high-ranking individuals behave more generously toward low-ranking transactional partners, a norm referred to as *noblesse oblige*. Fiddick et al. (2013) investigated tolerance toward nonreciprocation in participants from seven countries that vary along hierarchical and individualist/collectivist social dimensions. They found strong and converging evidence of *noblesse oblige* in all seven countries. Compared with participants who adopted an employee perspective, those who adopted a boss perspective were far more willing to continue a reciprocal arrangement despite significant noncompliance, were more likely to feel they had been treated fairly, felt less animosity toward their cheating partners, and believed they got the better deal because they felt they bore less cost and received higher value from the arrangement. These results obtain even when the employee was described as having higher income than the boss (due to sales commissions) (Fiddick and Cummins 2007). The authors interpret this pattern of results to mean that *noblesse oblige* is a cross-cultural norm whose function is to honestly signal phenotypic quality through costly displays which enhance reproductive success, successful alliance formation, and enhanced feelings of internal satisfaction (utility). Alternately, high-status individuals might be more altruistic not because of costly signaling but because their reputations are more easily damaged owing to more intensive scrutiny.

Social Cognition and Status Acquisition

Status hierarchies are rarely static structures. They are instead dynamic structures in which individuals vie for control of resources. Higher-ranking individuals defend their privileged access to resources by detecting and punishing acts that threaten privileged access, while lower-ranking individuals attempt to engage in forbidden activities in order to secure a larger share of resources. In order to survive, an individual must be capable of performing – on a nearly continual basis – the following cognitive tasks: (a) making rank and kinship discriminations, (b) recognizing what is

forbidden and what is permitted based on one's rank (social norm cognition), and (c) deciding whether to engage in or refrain from activities (reciprocity, “mind reading”) that will allow one to move up in rank (i.e., garner a larger share of resources). These are the reasoning problems that impact most directly on survival and reproductive success.

Investigations of social interactions in a variety of species (including humans) have found that those who achieve high status are those who are particularly adept at these types of social cognition. In other words, *selection favors those who have social and political intelligence*.

Rank discrimination. Nonhuman primates readily make kinship and rank discriminations among individuals in their social groups, a skill that depends on transitive reasoning when all possible dyadic interactions are not directly witnessed (Cheney and Seyfarth 1990, pp. 91–96). (They infer that A is dominant to C given that they have witnessed interactions in which A is dominant to B and B is dominant to C.) In contrast, they can perform transitive inference on object-oriented tasks only after considerable drilling with paired stimuli (Gillan 1981).

Human infants as young as 10 months of age can infer dominance hierarchies from observing interactions between similarly sized actors (Gazes et al. 2015). Status hierarchies are apparent in the play groups of preschool children as young as 2 years of age (Strayer and Trudel 1984), and the transitive relations can be reliably reported verbally by 4-year-olds. Yet, like other primates, children can perform object-based transitive reasoning only if they are extensively drilled on the object pairs upon which the inference is to be performed. Truly content-free transitive reasoning does not reliably appear until 6 years of age. As early as 3 years of age, preschoolers are able to infer dominance not only from physical supremacy but also from decision power, age, and resources (Charafeddine et al. (2015)). They also have expectations regarding the ways in which a dominant and a subordinate individual are likely to differ in that they expect an individual who imposes his choice on another to exhibit higher competence in games and to have more resources.

Children also prefer to associate with and imitate high status as opposed to low-status individuals.

Santamaria-Garcia et al. (2015) combined event-related potentials (ERP) and structural magnetic resonance imaging (MRI) to reveal the neuroanatomical substrates of early status recognition. Participants performed a task either with a superior or with an inferior player. The pattern of ERP and imaging results indicated early recognition of social hierarchies through activation of a network involved in the automatic recognition of social identity.

These results indicate that rank discrimination cognition emerges early in development and functions fluidly as an automatic cognitive process through adulthood.

Social norms. From a cognitive standpoint, a social hierarchy is, essentially, *a set of social norms that constrain the behavior of individuals depending on their rank* (Cummins 1998). Norms are socially constructed objects that are created by agents to direct the behavior of other agents over whom they have authority. They prescribe constraints on social behavior that dictate what is permitted and obligated. An agent succeeds in creating a norm depending on whether the agent has the authority to do so.

In animal societies, these “social norms” are implicit yet reflected in virtually every activity, including who is allowed to sit next to, play with, share food with, groom, or mate with whom. In order to avoid punishment (or ostracism, which can mean death due to predation or starvation), individuals must learn what is *permitted*, what is *forbidden*, and what is *obligated given their place in the hierarchy*. High-ranking individuals monitor the behavior of subordinates in order to protect their privileged access to resources. High-status individuals typically take on the role of enforcing these implicit “social norms,” aggressing against those who violate them and breaking up disputes between lower-ranking individuals (Boehm 1999).

All human societies depend on social norms to regulate daily interactions. These norms may be implicit or explicitly codified as regulations or laws. Social norm reasoning has been found to emerge early in human cognitive development;

very young children show a marked *precocity* for acquiring social rules and monitoring compliance with them (see Cummins 2013). Children as young as 3 years of age do not just follow social norms; they actively enforce them on others – even when serving as spectators rather than players in the game. They do not need to be explicitly instructed about the rules by an authority, but they do need to see that an authority expects such behavior. When asked to test compliance with social rules, 3-year-olds also spontaneously seek out potential rule violations, readily distinguish rule-violating behavior from compliant behavior, and provide cogent explanations as to why violating instances constitute violations of the rule. In fact, their performance is equivalent to adults on these social reasoning tasks. In contrast, when asked to perform a nonsocial task of apparent equal complexity (test the truth of a rule rather than monitor compliance), children and adults fail to seek out potentially falsifying evidence, often fail to distinguish confirming from falsifying instances, and cannot give coherent justifications for their decisions.

These studies indicate that the average 3-year-old has as firm a grasp on the implications of socially prescriptive rules as the average adult, while the average adult fails to grasp the normative rules for testing the truth of rules or hypotheses.

Mind reading. Unlike objects, agents move of their own volition and are motivated by internal states that are not directly perceivable by others. As a result, successful cooperation and competition frequently depends on forecasting the behavior of others, a skill referred to as “mind reading” by the ethologists. In psychology, the term “theory of mind” is used to refer to the ability to not only forecast behavior but to attribute mental states (beliefs, intents, desires, knowledge) to oneself and others and to understand that others have beliefs, desires, intentions, and perspectives that are different from one’s own.

A singular cognitive skill that relies on mental attribution is **deception**. A successful deception creates a false belief in the one deceived. Subordinates in primate hierarchies engage in deceptive behavior that improves their access to

resources (Byrne 1995). For example, they conceal objects or behaviors from others by hiding them from view, acting quietly so as not to attract attention, avoiding looking at desirable objects themselves, or distracting attention away from the desired object or forbidden behaviors. This behavior allows subordinates to garner a larger share of resources immediately or to increase the probability of future rewards if the deception involves surreptitious food sharing or grooming to form alliances that can be called upon during contests of rank.

The neocortex ratio expresses the relative volume of the neocortex compared to the volume of the rest of the brain. It correlates with the mean group sizes that characterize primate species, with larger group sizes corresponding to greater neocortical volume. This ratio correlates with the prevalence of tactical deception observed across primate species (Byrne 1995, pp. 219–221). Not surprisingly, species that show the greatest capacity for this type of deception (such as common chimpanzees) also have the most unstable hierarchies. Greater cognitive skill mitigates the impact of physical size and strength in dominance acquisition and maintenance. It is difficult to physically dominate individuals who have the cognitive wherewithal to outwit you and to form stealth alliances with others. In order to dominate such individuals, one must have the cognitive wherewithal to recognize and thwart acts of deception whose target is flouting norms concerning privileged access to resources.

The manner in which mind reading is successfully deployed to acquire and maintain status depends on the size of the social group; the larger the group, the more likely deception will succeed. For example, the ability to persuade through oratory is typically requisite for gaining political influence within small-scale societies, even those that seemingly lack formal authority, such as the !Kung and the Semai of Malaysia. But in such societies, trustworthiness, generosity, and fairness are integral to leader emergence and effectiveness (von Rueden et al. 2014). Accordingly, most have developed norms and traditions regarding leadership that depend on demonstrating these qualities, thereby protecting members against exploitation

by leaders. For example, although hunting prowess is a ubiquitous determiner of male social status in human small-scale societies, meat-sharing generosity determines coalitional support and hence stability of political leadership (von Rueden et al. 2014). Generosity must be carefully deployed to signal less about their wealth and more about its use to benefit the community. This usually means that generosity must be combined with obvious signs of humility to avoid sewing distrust rather than affiliation.

As Boehm (1999) observes, the egalitarianism of small-scale societies is often misconstrued as an absence of dominance motivations (or status striving) on the part of group members. Yet, as von Rueden and van Vugt (2015) point out, leaders in these societies may orchestrate collective actions that produce goods more beneficial to themselves and their kin. For example, wealthy Barabaig pastoralists enforce conservation of grazing land because their larger herds stand to benefit the most. They may also claim a fee for their services through a greater share of normatively regulated benefits (e.g., rights to polygyny). Instead, small-scale society egalitarianism is better understood as an active leveling of would-be dominants through norms compelling humility and coordinated punishment of aggrandizers (Boehm 1999). In short, leaders must carefully manage perceptions of their generosity and fairness or risk censure, ostracism, or even execution.

While small-scale human societies frequently institute norms that proscribe deceptive exploitation, modern large-scale societies frequently fall prey to (and even reward) such behavior. For example, the GLOBE surveys on leadership in 62 modern large-scale societies show that integrity is a universally highly valued leader trait (Den Hartog et al. 1999). Yet in these societies, individuals who are perceived and rated as socially dominant are better at deceiving others, persuading others, and interpreting others' intentions. von Rueden and van Vugt (2015) present a comprehensive review of research on large-scale industrial societies which indicates that individuals who are narcissistic or overconfident are often selected as leaders despite null or even negative consequences for groups. They point out that in these

contexts, overconfident and narcissistic leaders are often mistaken for competent and agreeable leaders because they are persuasive, charming, and sociable. Deceptive traits associated with psychopathy may be socially adaptive in the short run in large populations of altruistic and trusting individuals.

Sex Differences in Status Striving

Among mammals, females necessarily invest more energy in reproduction than do males (e.g., pregnancy and lactation), and females are typically more involved in the care of very young offspring (i.e., infants and toddlers). Comparatively speaking, therefore, female reproduction is limited by access to resources, while male reproduction is limited by access to mates. Female lifelong reproductive success is enhanced by investing in offspring to ensure their survival. For this reason, women traditionally have competed for high-status men who typically control more resources. For example, women in polygynous societies that restrict the avenues women may pursue to obtain resources typically prefer to be one of the many co-wives of a prosperous man than the only wife of a poor one. In western cultures that have legally enforced monogamy and relatively greater financial opportunities available to women, high-status men are nonetheless still preferred as mates and as partners in extramarital affairs (Pérusse 1993).

Intrasexual competition among females has received less attention from researchers than has intrasexual competition among males. This seems partly due to the fact that females compete in far subtler ways than do males. Males tend to use direct confrontation to dominate and subdue potential threats and rivals, while females prefer to use indirect means that can easily go undetected, such as spreading rumors aimed at ruining a potential rival's reputation, excluding, ignoring, and isolating her socially. A 2014 study conducted by the Workplace Bullying Institute found that 30 % of office bullies were women, and these female bullies targeted other women more than two-thirds of the time using indirect

means of aggression. Fisher (2015) proposed that females often prefer low-risk competitive strategies because they typically are the primary caregivers and protectors of offspring.

These sex differences in competitive strategies appear to be rooted in a social proscription against direct and overt female displays of dominance. Such displays diminish women's likability while enhancing men's likability and negatively impact outcomes such as hirability (Williams and Tiedens 2016). Implicit forms of dominance (e.g., eye contact), however, do not negatively impact these factors for females. The authors point out that the effect of dominance on men's and women's perceived competence did not differ, which indicated that these subjective social evaluations obstruct women from adopting leadership roles. In other words, women must seek to dominate rivals without appearing to do so.

These sex differences seem to be facultative rather than obligate in that they are significantly impacted by environmental contingencies. Gneezy et al. (2008) compared female competitive strategies in two distinct societies: the patriarchal Maasai of Tanzania and the matrilineal Khasi of India. Maasai men were apt to compete at roughly twice the rate as Maasai women, but this result was reversed among the Khasi, where women chose the competitive environment more often than Khasi men and even chose to compete more often than Maasai men did in their culture.

Cross-cultural sex differences exist for basic human values relevant to status striving. Men attribute more importance than women do to self-interested values such as power, achievement, and self-direction values, while women attribute more importance than men to other-regarding values such as benevolence and universalism. Power values pertain to the attainment and protection of status, prestige, and dominance over people and resources. Achievement values pertain to personal success through demonstrating competence according to social standards. In contrast, benevolence values motivate people to preserve and enhance the welfare of close others (e.g., offspring and other kin), while universalism values have as their goal promoting the welfare

of all people and for nature. But a reexamination of these factors conducted by Schwartz and Rubel-Lifschitz (2009) indicated that in societies with greater gender equality, both men and women attributed more importance to benevolence, universalism, and self-direction. Increased individual resources of wealth, education, and autonomy that accompany greater gender equality facilitate the expression and attainment of these values.

Conclusion

Status hierarchies are ubiquitous in the societies of human and nonhuman animals. These hierarchies constitute social norms that constrain behavior of individuals depending on their rank, dictating what is permitted or obligated in social interactions. They emerge as a result of individual differences in traits that impact access to resources, with higher-ranking individuals gaining priority of access to resources in competitive situations. Some of these traits that contribute to status acquisition and maintenance are physical in nature, such as size, age, and gender. Others pertain to social skills and cognition, such as skill at forming alliances based on reciprocal obligations, persuasion through oratory, or manipulation of beliefs through deception.

Cross-References

- [Access to Resources](#)
- [Competition for Resources Desired by Females](#)
- [Cooperative Alliances](#)
- [Dominance and Health](#)
- [Dominance in Humans](#)
- [Female Mate Choice](#)
- [Higher Status in Group](#)
- [In Nonhuman Primates](#)
- [Nonhuman Primates](#)
- [Primate Dominance Hierarchies](#)
- [Reciprocal Altruism](#)
- [Reproductive Strategy](#)
- [Resource Competition](#)
- [Resource Defense](#)

- [Sex Differences](#)
- [Sexual Contact and Sexual Disgust](#)
- [Sexual Strategies Theory](#)
- [Social Dominance and Sexual Access](#)
- [Social Status and Economic Resources](#)
- [Status and Redistribution of Resources](#)
- [Status and Reproductive Success](#)

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Status and Redistribution of Resources

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Synonyms

[Social hierarchy](#); [Social status](#)

Definition

This chapter reviews work on the extent to which individual status influences support for the redistribution of scarce resources.

Introduction

Evolution by natural selection depends on competition over scarce resources. Within social groups, however, overt competition or hostility can be costly and ultimately a detriment to the well-being of group members. Accordingly, many primate species have evolved means of minimizing social conflict by imposing simple systems of dominance that determine access to and control over scarce resources. It is to these basic systems of distribution that many psychologists trace systems of status and distribution in human cultures, even if the rules and systems that shape outcomes are comparatively complex.

The present chapter briefly summarizes research on status, reflecting differences in access to and control over resources, and the redistribution of resources. This review highlights that status relations afford a degree of stability that can minimize intragroup conflict, but across species we see that status itself can sometimes motivate conflict by disadvantaged group members seeking to rework the current distribution of outcomes.

Status and Distribution

Status is an evolved means of minimizing competition over scarce resources within members of a species. Rather than needlessly expending effort in constant conflict, status creates implicit social rules regarding which members have control over resources and which do not.

These hierarchical relations are well studied in the context of primate behavior (for a review, see Kappeler and van Schaik 2002). Among many primate species, dominant males typically have greater control over scarce resources, including mates. Accordingly studies consistently find that higher-ranking primates have greater access to mates (Jack and Fedigan 2006; Wroblewski et al. 2009) and that male social rank is therefore a predictor of reproductive success (Gerloff et al. 1999; Widdig et al. 2004).

There is also evidence that female chimpanzees institute their own systems of dominance to control access to prime foraging areas. Dominant females therefore benefit from status because of the direct effects of improved nutrition for reproductive success, including greater infant survival and the production of more offspring (Pusey et al. 1997).

Beyond evidence of status hierarchy in primate societies, there is consistent evidence that status is a motivating factor in human social behavior. Across cultures, people desire status, even if this pursuit has been found to be stronger for males than females (Huberman et al. 2004). Other research has found that males are more sensitive to potential status differentials between themselves and other males (Gutierrez et al. 1999). This sex

difference may be attributable to the fact that human females are more likely to use male status as a marker of mate attractiveness (e.g., Kenrick et al. 1994).

These facts suggest that having status is ultimately adaptive for both the individual and the group. For the individual, the possession of status secures access to resources. While this reality creates disadvantaged group members, status relations provide groups with a degree of stability from which to maintain cooperation without the specter of unending overt competition between dominant and subordinate members. In other words, status creates a stable system for distributing scarce resources without constant conflict.

Status and Redistribution

This is not to say that status relations, or their consequences for the distribution of resources, are immutable. For example, among primate species, subordinate males often form coalitions against the status quo of their group (de Waal 2007). These coalitions allow subordinate males to reclaim a greater share of mates or other scarce resources from dominant group members (Wrangham and Peterson 1996). In these and other cases, coalitions allow members to pursue group-based interests: In some cases, subordinates benefit from upending status relations currently to their disadvantage; in others, dominant members come together to secure their position within a status hierarchy. The remainder of this chapter reviews research and theory about the evolutionary origins of processes related to this motive to seek (or prevent) redistribution on the part of social group members.

Social Dominance

Research on redistribution from an evolutionary perspective often adopts the view that individuals evolved to pursue group-based interests, that is, to achieve and maintain social dominance of other groups (Sidanius and Kurzban 2013; Sidanius and

Pratto 1999). This kind of behavior is well noted in close primate relatives, including research showing that coalitions form to pursue group interests, such as killing out-group males who are rivals for scarce resources (Wrangham 1999).

Social dominance motives have been noted in humans as well and are important individual predictors of attitudes toward resource redistribution. For example, dominant (White) group members who express high trait social dominance orientation tend to be resistant to any effort to upset the economic status quo, even if that hierarchy is not seen as legitimate (Levin et al. 2002). More socially dominant individuals also tend to be less supportive of social policies that ameliorate hierarchy in society, including unemployment benefits and public health care (Pratto et al. 1994).

If this motive to promote group-based interests is evolved, it would be expected that humans are highly sensitive to cues indicating a target's coalitional status as either a potential collaborator or competitor. Although race is a common line along which social group boundaries are drawn, research shows that individuals encode information about coalitional affiliation more strongly than race when there are clear group cues (Kurzban et al. 2001). This research promotes the idea that race and other salient group categories are of secondary importance to coalitional status and indeed may be relied upon primarily as heuristic judgments to assess the extent to which others may be expected to cooperate in the promotion of group interests.

Strategies for (Re)distribution

Other research has explored how evolutionary processes may have shaped the strategies that subordinate (vs. dominant) group members use to promote (vs. prevent) redistribution of resources. For example, group-based competition over scarce resources sometimes requires a degree of cooperation among in-group members. This cooperation is sometimes secured through social exchange: In one comprehensive review of food sharing behavior (Jaeggi and van Schaik 2011), the authors find evidence that many primate species share food among adults and that this food sharing behavior

is particularly likely among species that form coalitions. While food sharing with kin (e.g., offspring) is common in most primate species, exchange between adults is most likely when there are opportunities to attract mates with exchange or when food can be given to garner coalitional support to challenge (or preserve) status relations.

This research suggests that direct redistribution of resources to disadvantaged group members may be an evolved strategy for self-promotion to the extent that redistribution builds a coalition. Humans similarly balance prosocial motives with self-promotion to navigate status hierarchies. Research on status in children finds that those best able to garner and maintain status enact a combination of both coercive and prosocial strategies (Hawley 2003a, b). This dual focus allows individuals to both directly promote self-interest and at the same time mitigate the social costs of purely coercive or dominant social strategies through prosocial gestures.

How do individuals balance these self-promoting and prosocial strategies to effectively gain status and resources? Prior research finds that resource competition can trigger cooperation-seeking strategies but only when individuals lack the ability to compete on their own. This pattern has been found with male chimpanzees, for whom the probability of forming a coalition to protect access to mates was directly proportional to an individual chimpanzee's control over female mates (Watts 1998). As males lost control over access to mates, they formed increasingly powerful coalitions to restore shared dominance.

Other research has replicated this pattern in humans, showing that the use of competitive or cooperative strategies depends primarily on individual competitiveness (Benenson et al. 2009). In one study, individuals played a decision-making game in which they ostensibly played with a partner and a competitor. Each player was assigned a strength (i.e., a probability of winning a round) and given the option of playing the game alone, with the partner who would take a percentage of their winnings, or they could accept a guaranteed lesser payout. As an individual's strength in the game, that is, the probability of winning a round, increased, so did the percentage of individuals

opting for the competitive strategy. In contrast, as individual strength decreased, there was a marked preference for coalition formation.

Other research supports this view using measures of individual social status (Brown-Iannuzzi et al. 2015). Specifically, those who are wealthier are less likely to support policies that redistribute wealth, including spending on social programs. These effects were observed even on merely subjective differences in wealth: That is, merely feeling richer caused people to be less supportive of wealth redistribution.

Other research finds that strength, reflected by measured muscle mass, interacts with male status to shape support for redistribution (Petersen et al. 2013). The researchers assessed strength with a measure of bicep circumference and found that among lower-status men, physical strength was highly predictive of support for redistribution. In contrast, among higher-status men, this relationship reversed with stronger men expressing greater hostility toward redistributive policies. Notably, these findings replicated across three cultures (the USA, Denmark, Argentina), suggesting that they are unlikely to be due merely to cultural factors.

The latter findings suggest that individual competitiveness motivates individuals to support redistributive policies in their interest, while those who are less competitive are more willing to tolerate the status quo. The researchers note that this finding supports the asymmetric war of attrition model (Hammerstein and Parker 1982) in which those with the means to fight for access to resources should be willing to pursue conflict, while those without will cede resources to fight another day.

Not all attempts to seek redistribution are based on overt conflict however. Other research has considered the use of deception as a means of balancing the social scales. Recent research with chimpanzees finds, for example, that subordinates are aware of what a dominant member knows about the location of food and that they use this information to their advantage (Hare et al. 2000; Tomasello et al. 2003). Specifically, when subordinates saw food that was hidden from a dominant chimpanzee's line of sight, they pursued this food rather than attempting a direct challenge over food known to both parties. Importantly, this

preference was not observed when the subordinate saw that the dominant member witnessed the placement of this hidden food.

Criticism of Evolutionary Perspectives on Status and Redistribution

One popular criticism of evolutionary perspectives on status and redistribution is as follows: If the motive for social dominance is innate, then social dominance and intergroup conflict seem to be a biological inevitability (Turner and Reynolds 2003). After all, if conflict over status disparity is instinctive, some see the implication that equality is impossible and efforts at intergroup harmony as misguided. Other criticisms of social dominance approaches stem from the perceived assumption that group members primarily pursue their self-interests given that status is adaptive for group members (Jost et al. 2004). In other words, some see social dominance approaches as implying that group members will primarily pursue self-interest, despite evidence that subordinate group members sometimes legitimize social systems that work to their disadvantage.

In defense of an evolutionary approach to understanding status and redistribution, Sidanius et al. (2004) note that evolved tendencies must be considered subject to modification and variation in light of environment. In short, whatever evolved motives exist that incline individuals to pursue status or to upset hierarchy in the pursuit of self-interest must pass through the filter of current social pressures and cultural rules. This can create situations in which social groups support distributive policies against their own interests if, for example, there are cultural ideologies or political systems that override biological dispositions.

Conclusion

This chapter has reviewed evolutionary psychological theory and research on status and redistribution. In broad strokes, this research finds that status is an evolved mechanism that minimizes conflict in social groups and that affords

individual members specific advantages. However, status relations are often fluid, and research finds consistent evidence for evolved strategies aimed at either challenging or preserving the disparities inherent in status relations.

This research often takes the assumption that humans have evolved a motive for social dominance which motivates them to pursue the interests of themselves and their groups. Broadly this work finds that some individuals pursue (vs. prevent) redistribution by adopting competitive strategies, particularly when they are most able to challenge (vs. defend) the status quo. Other strategies include the use of deception to gain comparative advantages over high-status members or the formation of coalitions that can upset status relations. This work points to an important role of evolutionary processes in the psychology of status and redistribution, even if these phenomena ultimately involve factors that may moderate the expression of evolved traits.

Cross-References

- [Indicators and Correlates of Status and Dominance](#)
- [Social Status and Economic Resources](#)
- [Status and Dominance Hierarchies](#)

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Status and Reproductive Success

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Synonyms

Male-male competition; Reproductive skew; Social rank and fitness; Status competition

Definition

The common statistical association between accessing greater positions of relative social rank within a group and measures of evolutionary fitness.

Introduction

Social status seems to be a key component of social organization among small-scale human societies. Status is often defined as relative access to contested resources within a social group (Henrich and Gil-White 2001). More broadly, it can be conceptualized as access to social power and influence or the ability to advance one's aims and interests when they conflict with the goals or motives of others. The purpose of this entry is to provide a general introduction to the concept of social status and detailed results from research studies among two small-scale societies on the link between status and reproductive success, as well as citing summarizing research which provides context on the prevalence of finding this association when investigated.

Status and Reproductive Success in Small-Scale Societies

Even among the most egalitarian extant hunter-gatherer societies, relative status differences can be found in contexts of situational leadership. These instances illustrate the concept of prestige-based status, whereby individuals freely confer individuals, often in the role of leaders, with their influence because they possess knowledge, skills, or experience that assist leaders in coordination of group-beneficial collective action (Henrich and Gil-White 2001; Hooper et al. 2010). A key distinction exists between status that is derived from prestige with status which is derived from dominance. In contrast to prestige, dominance is status or deference given by subordinates to avoid physical costs during interactions with a dominant individual (Henrich and Gil-White 2001).

Research conducted among small-scale societies provides empirical support for the link

between accessing social status and increasing proximate measures of reproductive success. Among the Tsimane forager-horticulturalists of the Bolivian Amazon, high-status men were discovered to enhance their fitness via multiple pathways (von Rueden et al. 2011). Both prestigious and dominant men were found to possess more allies and have higher fertility, more extramarital affairs, more attractive wives, and a higher probability of remarrying if divorced or widowed (von Rueden et al. 2011). However, there were some differences in how prestigious and dominant men were achieving higher relative fitness. Prestigious men were found to have offspring with lower childhood mortality, marry at earlier ages, and have wives who begin reproducing at earlier ages, while dominant men did not. However, dominant men were found to marry younger women and have wives who spend more time caring for offspring, while prestigious men did not (von Rueden et al. 2011). Another well-known case is that of Yanomamo who can acquire the special signifier and cultural status of *unokai*. *Unokai* are men who have been recognized as having gone on a raid against another village and killed an enemy. In comparison with non-*unokai* men, *unokai* were found to have approximately twice as many wives and three times as many children (Chagnon 1988). This research has long been controversial and contested, but a recent reanalysis with a more informed statistical model and proper controls replicates the original finding (Macfarlan 2015). Specifically, *unokai* are enhancing their relative fitness by engaging in a system of marriage exchange with their co-*unokai*, i.e., men who participate in raids together. Nearly half of all co-*unokai* dyads married women from each other's patriline, providing a mechanism to explain the finding that they have more wives and therefore children than men, non-*unokai*, who don't participate in this large system of raiding and wife exchange (Macfarlan et al. 2014).

The Tsimane and Yanomamo are just two cases which support a link between status and reproductive success. Elsewhere, von Rueden has summarized a near exhaustive list of relevant data which tests this association in small-scale societies (2014).

He notes that 71% of studies that tested for it found a relationship between higher status and more surviving offspring, while 78% of studies that tested for it found a relationship between higher status and greater fertility and that 67% of relevant studies detected an association between higher status and lower offspring mortality (von Rueden 2014). The association between social rank or status and reproductive success characterizes male primates generally, including humans in small-scale societies (von Rueden and Jaeggi 2016). Interestingly the strength of the association between higher status and higher fitness is broadly consistent across foraging, horticultural, pastoralist, and agricultural societies (von Rueden and Jaeggi 2016).

Conclusion

Taken together, this empirical evidence supports the notion that there exists in human psychology an evolved desire or taste for achieving heightened social status since in small-scale social contexts it is reliably predictive of fitness enhancing outcomes.

Cross-References

- Polygyny and Male Risk-Taking for Status
- Social Dominance and Sexual Access
- Status Competition

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Status and Wealth

► Resources

Status Competition

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Synonyms

[Intra-sexual competition](#); [Male-male competition](#); [Status acquisition](#); [Status striving](#)

Definition

Status is defined as an individual's relative access to contested resources in a group (Henrich & Gil-White, 2001). Status can be more broadly

conceptualized as an individual's influence in pursuing their interests and goals when they conflict with the motivations and interests of others. Status competition is comprised of all the behaviors and strategies which individuals use as they vie for more relative influence and status.

Introduction

Potential status differentials among individuals are an important aspect of political dynamics in small-scale societies generally. This entry will present the evolutionary logic underpinning status competition, its general relevance to human evolution and social organization, and empirical studies on its overt expression in small-scale societies.

Status differences are considered a near human universal, that is, it occurs in some form, degree, and context in almost every society known ethnographically (von Rueden 2014). Acquiring status appears to be a viable strategy for achieving enhanced reproductive success assuming that when individuals have greater ability to pursue their interests, they make decisions that have fitness enhancing effects. This assumption is supported by an interspecific and cross-cultural analysis that greater status is associated with enhanced individual reproductive success in men and male nonhuman primates (von Rueden and Jaeggi 2016). This relationship is consistent in degree for humans across forager, horticulturalist, agriculturalist, and pastoralist societies (von Rueden and Jaeggi 2016). This general importance of status in achieving reproductive success therefore sets up the competitive contexts in which individuals strive to acquire status.

Status competition has been an important influence on human evolution. While human sexual dimorphism is notably reduced relative to older hominin species, indicating less dyadic male-male competition for mate access, our evolved system of status competition importantly involves alliance building that attenuates how social power is distributed (Boehm 1999). This is the case even among the most assertively egalitarian mobile foraging societies. Christopher Boehm notes that group-wide coalitions are a social mechanism that

guards against authoritarian social behaviors among individuals in a band (1999). This in and of itself is an example of status competition. Any incipient authoritarian individual who strived to acquire disproportionate social power over others were often killed in response in order to deny them the social power they tried to wield. Status competition should therefore be recognized as occurring even if allies form bottom-up revolutionary coalitions to maintain an approximately egalitarian distribution of social power (Boehm 1999). However, these dynamics and tendencies do importantly become altered in other types of small-scale social organization where status striving is less constrained and guarded against than in egalitarian foragers. The next paragraph presents some empirical data regarding status competition in several of these types of small-scale contexts.

As noted, alliances between individuals drastically attenuate the importance of body size and formidability in dyadic male-male competition. That is, it is unlikely that one individual can successfully compete against two individuals who are in alliance and support one another in a coalition. The importance of alliances and coalitional support in acquiring status is supported by several studies. Among Tsimane hunter-horticulturalists, men who have greater social support via central positions in kinship networks and more allies achieve greater reputations for various forms of status, such as perceived ability to win in a dyadic fight, getting their way in a group context, community-wide influence, and overall respect (von Rueden et al. 2008). This acquisition of status among the Tsimane is also a fitness enhancing strategy (von Rueden et al. 2011). Prestigious and dominant Tsimane men were found to have more allies and were observed to have higher fertility, more extra-marital affairs, more attractive wives, and more likely to remarry if divorced or widowed (von Rueden et al. 2011).

Yanomamö men have been found to strive to acquire the culturally significant status of *unokai*. A man becomes an *unokai* when he is recognized as participating in a raid against an enemy village and successfully kills someone (Chagnon 1988). Being an *unokai* has notable fitness enhancing effects; compared to non-*unokai*, *unokai* have twice as many wives and three times as many

children (Chagnon 1988). Importantly, these effects remain robust when a more sophisticated analysis with proper controls for confounding variables is used (Macfarlan 2015). More recent research has revealed how men achieve enhanced fitness via alliance building by co-participation in raids. Among all co-*unokai*, men who participated and killed during a raid together, nearly half eventually engaged in some type of marriage exchange of women from each other's patriline (Macfarlan et al. 2014), which provides the mechanism by which *unokai* acquire more wives than non-*unokai* (Chagnon 1988).

Similar patterns are observed among other Amazonian hunter-horticultural groups, such as the co-residing Achuar and Quichua of Conambo, Ecuador. Patton shows that men strive for status by developing reputations as willing and capable warriors (2000). Importantly, the association between warriorship and status is mediated by coalitional membership; individuals allocate social status to reputable warriors from their own but not the opposing political coalition in Conambo (Patton 2000). This relationship can also be shown at the level of dyadic alliances; men are biased to give more status to men of their own coalition with which they are more strongly allied (Patton 2005). These results support that men strive and compete for status allocated by other coalition members and allies by engaging in coalitional conflict on their behalf. And in this particular context of Conambo, having more status than similarly aged men was found to be associated with women's perceptions of male attractiveness (Escasa et al. 2010). While, developing a heightened reputation of warriorship is associated with being considered a better potential son-in-law by other men (Patton 2005). These studies present data on quite overt forms of status competition, but status striving also takes nonviolent forms involving more nuanced dynamics of reputation formation, cooperation, and relationship formation.

Conclusion

Social status is indicative of a greater ability to pursue one's interests. The persistent link between greater social status and measures of fitness

therefore support the evolutionary and adaptive basis of status striving. Further, ethnographic case studies support that status acquisition is affected by and occurs in political contexts of alliance building and coalitional competition.

Cross-References

- [Alliance Formation Theory](#)
- [Cooperative Alliances](#)
- [Status and Dominance Hierarchies](#)
- [Status and Reproductive Success](#)
- [Status Hierarchies](#)

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Status Competition and Peer Relationships in Childhood

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Synonyms

[Dominance](#); [Popularity](#); [Power](#); [Prestige](#); [Reputation](#); [Social hierarchy](#)

Definition

Status competition is the contest or rivalry between two or more individuals over the pursuit of influence, deference, attention, and associated resources. Peer relationships are associations between two or more individuals that may vary in closeness and duration and which reflect and sometimes lead to the creation of friendships, partnerships, allegiances, and group membership.

Introduction

While the underlying fabric and structures of human groups are diverse, two processes seem

ubiquitous to social life: individuals desire affiliation with others and form social hierarchies. From the formal social organization of businesses to the relationships within some of the most egalitarian societies that lack formal structures of power (reviewed in Cheng et al. 2014), individuals assort hierarchically, with people occupying different strata within a group based on their standing in multiple culturally valued domains (Henrich and Gil-White 2001). The reason for the universality of both processes is that their presence provides a solution to the competition over relatively scarce social, sexual, and material resources that characterize most group-living species. These processes not only reduce costly conflict, aggression, and warfare, but may also generate and sustain cooperation within a group (Henrich et al. 2015). Although these relationships are present and important during adulthood, an understanding of the social world, and the positions that individuals occupy within that world, develops during childhood as early as in the first few months after birth.

Both the desire for peer relationships and status competition are present throughout the developmental periods of human life, although they take different forms and serve diverse purposes during each developmental stage. However, the means by which individuals both attain social status and successfully manage peer relationships seem to fall into two routes across a range of developmental periods: dominance and prestige (Cheng et al. 2010; Sijtsema et al. 2009; Hawley 2002). The vast and growing body of research supporting the dual model of social hierarchy during childhood suggests that prestige and dominance have distinct outcomes for different dimensions of status and that their efficacy is governed by the period of development and the group's social norms. The current entry surmises (1) the different types of status and peer relations in childhood and further outlines (2) the pathways to attaining status and managing peer relationships during childhood.

Social Hierarchy During Childhood

Children have an innate disposition towards social hierarchy. Evidence suggests that beginning in the

earliest years of life, even during preverbal periods, infants are remarkably skilled in recognizing and inferring relative social rank. For example, they make transitive rank inferences (e.g., if Ian is lower in rank than Jess and Jess is lower in rank than Harry, then Ian is lower in rank than Harry; Gazes et al. 2017) and show an expectation for these relationships to be stable over time (Mascaro and Csibra 2012). Moreover, infants as young as 10 months old use physical size to predict the results of conflicts of interest, specifically revealing an expectation for larger agents to win dominance contests (Thomsen et al. 2011). Given these exceptional abilities in forming rank-related mental representations, it is perhaps not surprising that preschoolers observe and react accordingly to the complex hierarchical dynamics of their group (e.g., subordinate peers defer to their dominant counterparts: Hawley 1999).

Although the valued resources that individuals compete over are often different to those during adulthood, status is of paramount importance during development, especially in adolescence (Cillessen and Rose 2005). High status children wield considerable power and influence and have access to valued social and material resources within their group (Hawley 1999). This power over resources continues into adolescence, with status being of principal importance for individuals and members of a peer system aspiring to befriend and imitate popular adolescents (Adler and Adler 1998). Moreover, these popular adolescents display greater emotional wellbeing, reporting fewer cases of anxiety and depression (Rodkin et al. 2000). During adulthood, an individual's relative standing within their hierarchy is equally important, as it impacts both social and reproductive success (McDougall and Vallancourt 2015; von Rueden et al. 2010). Status competitions are thus widespread across societies and social settings and highly prevalent across the lifespan.

Social Status

Although there is agreement on the importance of the individual rewards and group benefits of social status during childhood, there has been a divergence in theoretical conceptions of what it means

to be high in status. The current section outlines three measures of status. The first two measures are commonly used in Developmental Psychology: popularity, or social prominence, and social preference, also termed sociometric popularity (see Parkhurst and Hopmeyer 1998; Cillessen and Marks 2011 for a review). These two measures of status have a strong overlap during early childhood, but their association gradually decreases over time and they become distinct (Cillessen and Rose 2005). The third measure of status discussed, social rank, explicitly captures an individual's perceived social influence and agency. These distinct but overlapping conceptions of status are important, as they describe distinct dimensions of status during childhood, which have different antecedents and may produce divergent outcomes for both groups and individuals (reviewed in Mayeux et al. 2011).

Popularity

As a child, negotiating one's way through the hierarchies of the classroom, playground, and household can be difficult. Ethnographic accounts and evidence from classroom settings indicate that developmental hierarchies – especially those during adolescence – are competitive, with individuals struggling against one another to attain and defend their popularity and position within a group (Merten 1997). Popularity is defined as an individual's (or groups'/cliques') social centrality and eminence among their peers (Adler and Adler 1998). Popularity reflects an individual's reputation, signposting their impact, prominence, social influence, and power within a group (reviewed in Asher and McDonald 2009).

Popularity during child development is complex and is often governed by a combination of physical attributes, such as attractiveness and athletic ability (Dijkstra et al. 2009) and relational behaviors (e.g., assertiveness or kindness: Rodkin et al. 2000). In addition to these, the social structures of a group and social network processes have bearing on popularity during development. Evidence suggests that individuals assort and affiliate with those similar to themselves (sometimes called homophily), and this preference is also seen among children, who form friendships and

playgroups at higher rates with other children who share similar demographic traits (McPherson et al. 2001). However, two processes may govern similarity based on popularity over time: selection and influence. Selection refers to individuals preferentially choosing to associate with those similar to themselves on a given dimension (e.g., same-sex friendships), whereas influence denotes a subsequent gradual shift towards similarity between proximate individuals (some of whom may have been initially brought together through selection processes; reviewed in Steglich et al. 2010). Both selection and influence operate with regard to popularity during development (Dijkstra et al. 2013). Less popular individuals attempt to gain status by association with popular conspecifics (via influence processes), and popular individuals often try to maintain their status by preferentially selecting those similar in popularity as they risk their popularity decreasing via influence processes of being associated with those less popular.

Why do children and adolescents place such high emphasis on popularity? After all, popularity is not easily obtainable and being popular can be seen as a double-edged sword as it is also associated with a number of harmful outcomes, such as increased health risk-taking behavior and potentially poor academic outcomes (Mayeux et al. 2008). However, popular children attain a vast array of benefits. Highly popular children have greater access to a group's valued social, material, and informational resources (Reviewed in Hawley 1999). Popular children are believed to dictate the desirability of behavioral patterns within a classroom and are sought after as friends (Ellis and Zarbatany 2007). In contrast, being unpopular has a considerable, deleterious impact on children due to its relationship with victimization, which is associated with mental health disorders (Arseneault et al. 2006), poor academic functioning (Schwartz et al. 2005), reduced physical quality of life (Bogart et al. 2014), and in extreme cases even suicide (Bearman and Moody 2004). It seems that these “controversial” children, who are perceived as being popular, but relatively disliked, have great social power and influence among their peers (Coie et al. 1982).

Social Preference

In contrast to perceived popularity, status based on social preference – for example, as assessed using nominations of likability (Cillessen and Marks 2011) – has a weaker association with power and influence in children. Social preference represents a form of status that is founded on personal sentiment (Bukowski 2011). However, social preference (or sociometric status) is a somewhat controversial measure of status that is limited only to studies among children, as its relation to status outcomes is ambiguous and a finer distinction between likability, or warmth, and status has been drawn in studies during adulthood. It seems that it may be less complex, and less risky, to be socially preferred than to be popular, with the strongest antecedent of social preference being prosociality (Rodkin et al. 2000). Social preference seems to be rooted in relational intimacy, with prosocial and socially preferred individuals having closer friendships and a greater number of friendship nominations to those not socially preferred (Gest et al. 2001). These socially accepted individuals seem to be likeable and driven by communal goals, wishing to forge close relationships with their peers (Ojanen et al. 2005).

There are abounding benefits, and relatively few negative consequences, of childhood status derived from social preference. Socially preferred children do not come across as much adversity (e.g., bullying) as those who are not socially preferred, and social preference is not associated with risk-taking behavior (Buhs and Ladd 2001). Rather, being socially preferred is associated with cooperation among children, with likeable children holding the development of interpersonal skills as highly important (Rubin et al. 2007). Moreover, high social preference is associated with a strong sense of group belongingness and social support and has long-term benefits for a child's mental health and academic functioning (Ladd and Kochenderfer-Ladd 2016).

Social Rank

Akin to the concepts of popularity and social preference, a third conceptualization of status that has been studied within adult populations,

termed social rank, has been captured using peer-ratings (see Cheng et al. 2010; Cheng et al. 2013). This measure captures an individual's perceived social influence within a group and their perceived agency (Wiggins et al. 1988). Both social influence and agency reflect an individual's power, control, and status, which are central dimensions of an individual's social rank. To date, this measure has not commonly been used to measure status during childhood (the exception being an adapted version by Redhead 2016), and thus, little is known about how this form of status relates to important developmental outcomes, such as academic functioning, friendship, and health. Given the similarity of the construct to the dimension of popularity, such as increased social influence and power, and its distinction with likability (Cheng et al. 2013), similar developmental outcomes are expected. Additional research is needed to further understand how it operates during childhood.

The Routes to Social Status

Social asymmetries are multidimensional and relative status arises from two distinct systems of rank allocation: prestige and dominance (reviewed in Cheng et al. 2013). Although there are many factors that impact a child's status and behaviour, such as family dynamics and parental influences (Lukasewski 2015; Kapetanovic et al. 2017), the current focus is on the contributions of personality, behavioral disposition, and individual differences. A large body of research focuses on the unique relationships that specific determinants of social status, such as aggression and prosociality, have with popularity and social preference during childhood. However, the current entry emphasizes that these dimensions comprise two psychological profiles, prestige and dominance, that broadly predict an individual's status. It is important to note that the effects of prestige and dominance on social status and peer relationships discussed may be moderated by a group's norms, with dimensions relating to the two routes to status potentially having fluctuating efficacy based on the peer ecology (Laninga-Wijnen et al. 2017).

Dominance

Dominance is a rank acquisition system that is centered on the use of intimidation and coercion. Individuals strategically advertise their ability and propensity to inflict harm (either physical, material, or psychological), which urges others to yield to their will (Henrich and Gil-White 2001). Dominance is often associated with physical strength and size, as these are physiological cues to an individual's ability to triumph during agonistic conflicts or inflict harm (Archer 1988). As shown in Table 1, a dominance psychological profile is characterized by aggression, disagreeableness, narcissism, and manipulative tendencies, all of which aid in an individual's ability to propagate fear and coerce their peers (see Cheng et al. 2010). It is common for individuals high in dominance to have egocentric goals, aiming to increase their power and reach their social and material goals with little consideration about others (also referred to as "agentic goals": Sijtsema et al. 2009).

While aggression is an essential facet of dominance, children employ dual forms of aggression and these have divergent implications for their relative status with peers (reviewed in Dodge and Coie 1987). The first form of aggression, reactive aggression, is a response to anger, provocation, and frustration, which may have either positive or negative effects on status, depending on context, and is often associated with behavioral difficulties (Crick and Dodge 1996). Conversely, proactive aggression is a behavior that is a deliberate route for individuals to attain agentic goals and often has a positive effect on status during childhood (Pellegrini et al. 1999). The most pronounced form of proactive aggression during childhood is bullying, defined as repeated aggressive acts towards a peer, often lesser in size, status, or with fewer alliances (Olweus 1978). Bullying pervades cultures and species and can persist into adulthood (Volk et al. 2016). Those with more direct status-striving goals are most likely to be bullies and bullying does indeed increase an individual's popularity, even though bullies are as socially rejected by others in their group as their victims are (Sijtsema et al. 2009). It seems that if a

child were to perform aggressive acts with socio-political aptitude, just as the reminders of power often seen in dominance hierarchies among non-human primates, they accrue status, social influence, and positive attention (Hawley 1999).

The relationship that dominance has with status during childhood indicates those high in dominance are met with several benefits and costs. Aggressive adolescent males are perceived as highly attractive by the opposite sex and are high in status (Pellegrini and Long 2003). Among a group of children and young adults in Romanian state care, both males and females perceived as high in dominance were also perceived as high in social rank, were nominated more as friends, and had disproportionate control over the group's resources (Redhead 2016), of which has also been found in western classroom settings (Hawley 2002). However, the friendships that these individuals have tend to be low quality (Hawley et al. 2007). Children behaving aggressively receive greater visual attention from their peers, which is considered an indicator of social rank (La Freniere and Charlesworth 1983). Dominance-related behaviors seem most utilized and effective during periods of transition (e.g., between primary and middle or junior high school) and decrease across school years once hierarchies begin to stabilize (Pellegrini and Long 2002). Overall, as depicted in Fig. 1, current evidence suggests that dominance makes for popular and high-ranking, but disliked, children.

Prestige

Social learning is essential to human culture and individuals selectively learn from others based on a number of cues, of which are present during childhood (reviewed in Wood et al. 2013). Experiments assessing the microevolution of cultural traditions among children have repeatedly shown that the majority of children selectively learn from others, becoming followers to and imitating knowledgeable peers, while a minority may still produce innovations that create meaningful group differences (Whiten and Flynn 2010). Children may preferentially learn from peers similar to themselves on given attributes, peers high in

status, and to older individuals. Cues to a peer's competence and reliability also effectively govern children's learning. This discriminates social learning, biased towards deferring to and imitating those perceived as competent and knowledgeable, is termed prestige-biased social learning (Henrich and Gil-White 2001), and individuals possessing a prestigious psychological profile, or cuing prestige, are preferentially attended to by children (Chudek et al. 2012).

Prestige is a system of rank acquisition where individuals possessing skills in a culturally valued domain are provided freely conferred deference from peers through respect and admiration. Prestigious individuals not only have to cue an ability, but also a willingness to provide informational knowledge and help. Therefore, prestige is not solely dependent on competence, but also a moral, prosocial reputation (see Bai 2017; note that the current entry presents morality and

prosociality as traits that partially confer prestige). As shown in Table 1, individuals high in a prestige psychological profile are perceived as being agreeable, conscientious, agentic, and high in genuine self-esteem (see Cheng et al. 2010). Moreover, individuals high in prestige are characterized by behavioral tendencies that are antithetic to dominance and are perceived as highly cooperative, socially skilled, and capable advice-givers (Cheng et al. 2010). The social goals of individuals high in prestige are further distinct from those of dominants, with individuals possessing dimensions of prestige reporting an intrinsic motivation to pursue friendships with others (Hawley et al. 2007).

Given the association to social learning, and previous research consistently presenting a positive relationship of prosociality with status, prestige makes likable, socially accepted and, to some extent, popular children. The popularity of an

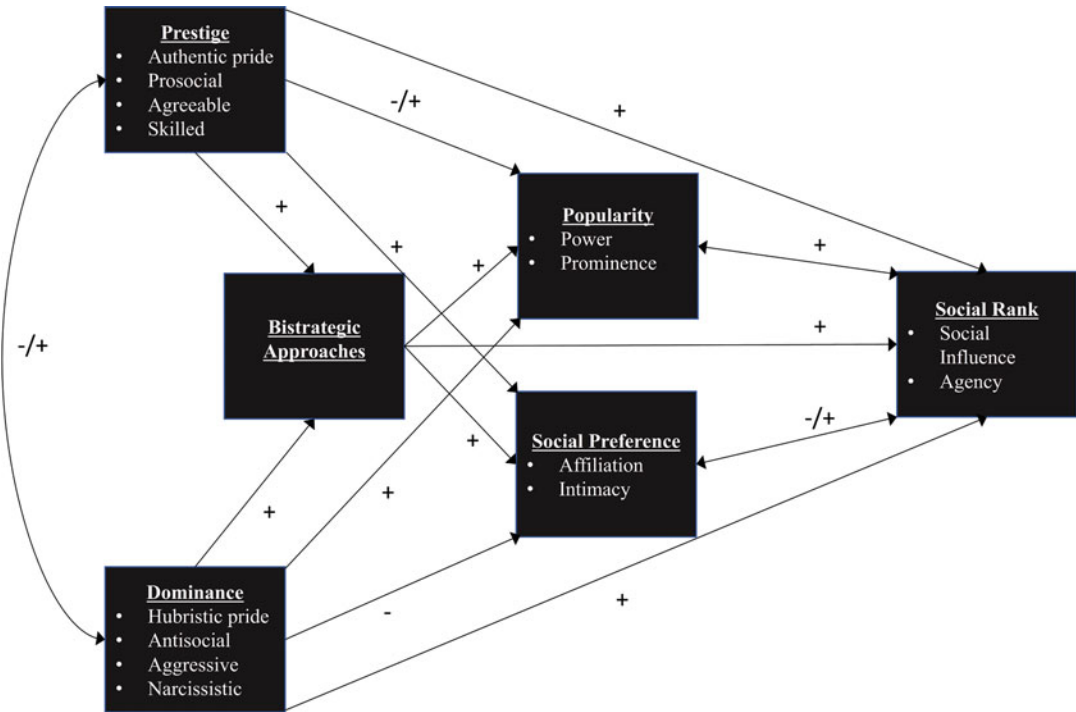
Status Competition and Peer Relationships in Childhood, Table 1 Relationships that peer-rated dominance and peer-rated prestige have with self-rated traits and peer-rated abilities

	Peer-rated dominance	Peer-rated prestige
Self-rated traits and attributes		
Genuine self-esteem	0	+
Narcissistic self-aggrandizement	+	0
Social acceptance	0	+
Aggression	+	0
Extraversion	+	0
Agreeableness	—	0
Conscientiousness	0	+
Neuroticism	0	0
Openness	0	0
Agency	+	+
Communion	0	0
GPA	—	+
Peer-rated abilities		
Advice-giving	0	+
Intellectual	0	+
Athletic	+	+
Social skills	0/+	+
Altruism	—	+
Cooperativeness	—	+
Helpfulness	—	+
Ethicality	—	+
Morality	—	+
Leadership	+	+

individual perceived high in prestige is potentially not as strong as with aggression (Ellis et al. 2012). However, these individuals are accepted by their peers and perform well academically (Padilla-Walker and Carlo 2014). Among a group of children and young adults in Romanian state care, individuals perceived by their peers as being highly prestigious were high in social rank, more central in networks of cooperation (i.e., toy and resource sharing), and received high numbers of friendship nominations (Redhead 2016). Those perceived as high in prestige-related facets are often advice-givers (Hawley 2002) and enjoy the resource-related benefits of long-term friendships (Pellegrini et al. 1999). Furthermore, research suggests that individuals high in prestige-related facets have greater social support, receiving greater numbers of reciprocated friendships, of which are high in intimacy and low in conflict (Hawley et al. 2007). These prestige-related behaviors exhibit an increase between childhood and adolescence and are somewhat stable

strategies throughout adolescence (Eisenberg et al. 2009). As with adults, evidence suggests that the behaviors associated with prestige increase a childhood group’s ability to cooperatively and collaboratively learn (Padilla-Walker and Carlo 2014). Overall, as shown in Fig. 1, prestige provides distinct hierarchical benefits to dominance for both groups and individuals during childhood, bolstering a child’s social acceptance but not necessarily their popularity.

Although research directly assessing the effects of prestige and dominance on social status has illustrated that the two profiles are either uncorrelated (Cheng et al. 2010; Cheng et al. 2013) or negatively related (Redhead 2016), work within developmental psychology indicates that there may be bi-strategic approaches (i.e., the deployment of both prestige and dominance simultaneously) to status acquisition. A number of studies have suggested that these bi-strategists may have found the optimal route to “getting ahead and getting along” (Hawley 1999). A specific



Status Competition and Peer Relationships in Childhood, Fig. 1 Relationships between prestige, dominance, and dimensions of social status during childhood. Arrows

indicate the theoretical directionality of the effect and plus/minus symbols illustrate whether the effect is positive or negative

form of social competence characterizes these bi-strategists. They understand social rules and have a similar profile to prestige. However, they also utilize aggressive, forceful acts and view relationships as avenues to resource acquisition (Hawley et al. 2007). As shown in Fig. 1, through the positive association with both popularity and social acceptance, bi-strategists enjoy intimate relationships (Hawley et al. 2007) and maintain high status reputations (Cillessen and Rose 2005).

Conclusion

There are two routes to attaining social status and managing peer relationship during childhood: prestige and dominance. As shown in Fig. 1, prestige-related behaviors and traits are strongly associated with social acceptance and social rank, while evidence indicates that those related to dominance are associated with a child's perceived popularity and social rank. These different associations with status allot distinct benefits and costs related to prestige and dominance during childhood. While there is an expansive body of research assessing the impact of certain dimensions of prestige and dominance during childhood, there is limited empirical evidence directly testing the dual model of social hierarchy in a developmental context, of which provides a fruitful platform for future research.

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Status Gradient

► Greater Risk-Taking and Status

Status Hierarchies

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Synonyms

[Dominance](#); [Hierarchies](#); [Status](#)

Definition

Social hierarchies are emergent social structures demarcating the relative power, status, and dominance of individuals and groups with respect to their ability to access fitness-enhancing resources.

Introduction

Social hierarchies are a fundamental part of social life among humans and many other social species. Dominance orders reflect differences in superiority of access to fitness-enhancing resources, including food, territory, and mates. Evidence for elementary dominance orders exist for dragonflies, pecking orders exist for chickens, and complex and often fluid dominance orders exist for primates, including humans. Human hierarchies may be more complex than those in other species, but all hierarchies ultimately reflect individual differences in the ability to gain and maintain access to fitness-enhancing resources. The intensity of competition for resources varies across species and explains species-typical differences in social hierarchies. Chimps, for example, have tyrannical male-led hierarchies in which alpha males command disproportionate access to resources and mates. Once sexual maturity is reached, male chimps tyrannize female conspecifics before attempting to establish dominance over other males. This process involves aggressive posturing and physical violence. Bonobos, on the other hand, have evolved matriarchal hierarchies that produce much less dominance competition, particularly between males and females. Ritualized sex – both homo- and homosexual – is used to regulate bonobo hierarchies.

Hierarchies suffuse human social relations. A key part of social life is finding access to mates, and for this reason, human hierarchies reflect processes of sexual selection. Humans have many tactics for negotiating their positions in hierarchies, including gossip, direct and indirect forms of aggression, displays of creativity, as well as more cooperative tactics, such as forming

coalitions with those with shared interests. Hierarchies are mediated by hormones, which both reflect and reinforce individual positions in hierarchies. Finally, individuals who are lower in social hierarchies are likely to suffer from health problems and die younger than those at the top of hierarchies. Given that hierarchies are critical to human life, it is not surprising that aggression is strongly connected with competition over positions in hierarchies. In what follows, these and other key facets of hierarchies for human social life are explored.

Evolution and Social Hierarchies

Male Armaments and Female Choice

Secondary sex characteristics such as muscular bodies and low-pitched voices were designed for effective male intrasexual competition, to intimidate or defeat rivals and obtain high-quality mates. However, these armaments may also be particularly desirable to females insofar as they are honest signals of health and virility. The immunocompetence handicap hypothesis maintains that male armaments such as muscularity are honest signals of health, a well-functioning immune system, and superior genetic quality. The signal is kept honest (i.e., reliable) because the reproductive hormones used to make and maintain them (i.e., testosterone) suppress immune function and increase disease rates. As such, high- but not low-quality males can risk high levels of testosterone and advertise this through exaggerated secondary sexual characteristics.

Short-term strategizing females are particularly attuned to these signals of mate quality – they generally prefer dominant males who possess traits that confer high-quality genes to their offspring. Strong, muscular men generally have more sexual partners and start having sex earlier in life, and short-term strategizing females prefer muscular, socially dominant men. Muscle mass is moderately heritable, suggesting that short-term strategizing females may find these traits attractive because they will be passed on to offspring, increasing inclusive fitness. More generally,

females prefer dominant male behaviors (i.e., social presence, direct intrasexual competitiveness) and find males with dominant facial features, bodily features, and vocal masculinity sexually attractive, especially when fertile. Male faces rated by women as more dominant, attractive, and masculine also tend to have greater strength, suggesting that those with attractive, masculine facial features (e.g., pronounced jaws, cheekbones, and brow ridges) may occupy the top tiers of hierarchies due to their physical dominance and formidability. Indeed, a study of military cadets found that those with more masculine, dominant faces were likely to occupy a higher rank within the military academy in West Point during junior and senior years (Mazur et al. 1984).

Ultimately, short-term strategizing females may have developed a preference for dominant behaviors and armaments like muscularity to maximize their chances of mating with socially dominant, high-status males to confer material and genetic resources to their offspring in the short term. However, females generally do not prefer dominance and aggressiveness in long-term mates. Individuals perceived to be highly aggressive and domineering are also rated as more promiscuous and less desirable as spouses. Indeed, short-term strategizing men who allocate more resources to mating versus parenting are higher in testosterone (Archer 2006), suggesting that masculine men with elaborate armaments may be promiscuous and therefore undesirable long-term mates. Masculine, physically attractive men are more successful at mate poaching and have more extra-pair copulations (Gangestad and Thornhill 1997), rendering them particularly suitable for short-term rather than long-term mating. Further, while effect sizes are small, it has been shown that men with high testosterone levels tend to occupy lower status (e.g., blue collar rather than white collar) occupations due to greater antisocial behavior, lower intelligence, and fewer years of schooling, further suggesting somewhat limited parental investment abilities. Thus, while male intrasexual competition led to the development of male secondary sexual characteristics to defeat rivals, a strong female preference for these characteristics among short-term (but not long-term)

strategists likely aided in their propagation and elaboration.

Status Cues and Female Choice

Status competition is intertwined with male intrasexual competition, as females – particularly long-term strategists – value cues to resource acquisition abilities and status, including males' achievements and ambition, older age, character, socioeconomic status, and even height, which is a cue to physical health and social dominance. Given the importance of male status striving and resource acquisition to females, insults directed at males' poor financial prospects are particularly effective in undercutting male rivals in intrasexual mate competition. In Buss and Dedden (1990), undergraduates rated the following status-related insults among the most effective in making a rival male appear undesirable to a female: the rival's financial resources (saying "he is poor"), his strength ("I can defeat him physically"), his ambition ("he has no goals"), and his social connectedness ("he is unpopular"). Unsurprisingly, men experience jealousy when facing wealthy, high-status males, and females are more envious of fellow females with wealthy, resource-rich husbands who can provide for them and their offspring in the long term.

Female Intrasexual Competition and Status

Comparative evidence suggests that female intrasexual competition contributes to dominance behaviors and status striving among women. Among female primates, those with higher-status positions often have superior mating opportunities and can suppress the fertility of subordinates. However, some have argued that status striving is not as important for human females as for males in a mate competition context. Human females at the top of the hierarchy do not necessarily receive the substantial reproductive benefits from social status that males do, as dominant females are generally not rated as more attractive or desirable to potential male mates. Ultimately, status striving – particularly through aggressive means – is likely more strongly implicated in mate competition processes for human males than for females.

Attaining and Maintaining Social Status

Aggressive Tactics

Direct and indirect forms of aggression can be used to maintain or enhance social position. Direct aggression includes physical fighting (e.g., punching, kicking), as well as verbally assaulting individuals with whom one is competing (e.g., using personal insults or racial slurs). Among honor cultures, such as those in the American south, people are more likely to use direct aggression and violence to protect their threatened social standing (i.e., when insulted) and to maintain a sense of justice (Nisbett and Cohen 1996). Relative to females, males are more likely to use aggression and displays of athleticism as status-striving tactics, whereas females tend to solicit aid from others and enhance their appearance to move up the social ladder (Kyl-Heku and Buss 1996), which aligns with extant research and theorizing on sex differences in aggression and mate competition tactics.

Indirect aggression consists of covert social manipulation and includes tactics such as rumor spreading, malicious gossip, and social exclusion. Ultimately, aggression is a strategy to enhance the aggressor's status, reputation, and hence their survival and reproductive prospects. Indeed, perpetrators of indirect aggression are generally seen as popular, high status, and central in their social networks.

Cooperative Tactics

Beyond aggression, there exist a variety of pro-social status-striving tactics that are more cooperative and less antagonistic in nature. Kyl-Heku and Buss (1996) found several commonly reported tactics for negotiating status hierarchies, among them industriousness/knowledge, social display/networking, aid accrual, and autonomy. The use of certain tactics, such as industriousness (e.g., working hard), significantly predicted increased academic degrees, promotions, and higher salary, suggesting that they can be effective in attaining high status. Additional self-presentation-based strategies identified in the

literature include obtaining and displaying resources and demonstrations of sacrifice and loyalty to the in-group.

Within groups, higher status can be attained when one makes substantial contributions to the group and its performance, as when devoting time and effort to group goals and providing expertise. This type of status striving is driven by prestige – possessing and sharing culturally relevant knowledge and skills – rather than by physical dominance. Coalition formation with fellow in-group members or with other groups can also help individuals and groups maintain and improve their relative positions within a hierarchy. Indeed, Simpson and Macy (2001) found that when low-power individuals were given the opportunity to form a coalition with one another, their bargaining status, and total earnings in an economic game increased.

Communication Tactics

Mazur (1985) suggests that verbal and nonverbal conversational style signals social status. For instance, dominant, higher testosterone individuals generally use more direct eye contact when speaking, more frequently interrupt lower-status individuals, speak loudly or angrily, set the mood and pace of the conversation, introduce and terminate topics of conversation, and have more expansive nonverbal postures (e.g., hands on hips, legs spread apart). Nonverbal cues such as facial expressiveness and successful interruptions have also been found to associate positively with social standing. Using these strategies could help an individual maintain their high social standing or attain a higher position, provided they can legitimately occupy that position. Stress management abilities while speaking with others may also help solidify individuals' positions within a hierarchy. High-status individuals have a lesser stress reaction (e.g., lower pulse rate) during speaking than lower-status individuals, suggesting they may be more comfortable asserting themselves in social scenarios and can more effectively manage social stressors than their subordinates (Mazur et al. 2015).

Hierarchies and Hormones

Research has focused on the role of testosterone (T) in mediating aggression and physical dominance, particularly among men. Individuals use aggression as a forceful means of attaining or maintaining status or of defending a threatened position within a hierarchy. Indeed, Griskevicius et al. (2009) found that status motives contribute to increased aggression among both males and females, although males tend to use direct forms of aggression (e.g., hitting, yelling), whereas females prefer more indirect forms of aggression (e.g., malicious gossip, social exclusion). Across many species including humans, modest associations between testosterone levels and aggression have been reported. However, the testosterone-aggression link is debated, and some argue that testosterone is more directly connected with dominance signaling than with aggression per se (see Mazur et al. 2015). Regardless, links between testosterone and the development of male armaments suggest that hormones are strongly implicated in intrasexual competition and status-striving behaviors, aggressive or otherwise.

Testosterone and Armaments

Testosterone causes the development of secondary sexual characteristics, including increases in muscle mass, more robust brow ridges, high cheekbones, facial and body hair, and a lower fundamental vocal frequency. These physical traits play a role in signaling dominance and aid in successful fighting. In humans, greater strength is associated with higher testosterone in men, and muscle mass is associated with men's higher testosterone levels (Bhasin 2003). Additionally, males with lower-pitched voices (a trait associated with higher T) are perceived as more physically dominant than those with higher-pitched voices. Thus, testosterone contributes to the development of male secondary sex characteristics, and these characteristics contribute to perceptions of male dominance and status.

Testosterone and Dominance

Comparative evidence supports the testosterone-dominance link. For instance, testosterone removal

(through castration) has been shown to decrease aggressiveness and social dominance in rats. In a study of rhesus monkeys undergoing group reformation, the new alpha male experienced testosterone increases, while the previous alpha male, newly subordinate, experienced an 80% drop in testosterone levels (Rose et al. 1975). In a study of human teenage males, testosterone levels were positively associated with leadership capacities among those with nondeviant (rather than deviant) peers, suggesting that there is an interaction between T, social groups, and dominance (Rowe et al. 2004). In their examination of data from US Army veterans, Mazur and Booth (2014) found that testosterone is linked to aggressive and dominant behavior, including juvenile delinquency, violence, and vagrancy, as well as alcohol and drug use.

Testosterone and Competition

While higher testosterone can contribute to higher social standing within a hierarchy, higher social status can also contribute to testosterone increases, creating a status-testosterone feedback loop that may keep dominant, high testosterone individuals at the top of the hierarchy and lower testosterone individuals at the bottom. Among nonhuman primates and among university wrestlers, male tennis players, and chess players, victors in competition experience greater increases in testosterone levels than those who are defeated in competition, who sometimes experience decreases in testosterone. Even merely visualizing a future victory in a dominance contest or anticipating future competition can increase human males' testosterone levels in certain situations. The comparatively higher testosterone levels of victors could help them win future contests using aggression and dominance behaviors, thereby aiding in effective status maintenance and status striving. In line with this reasoning, Carré et al. (2013) found that male victors experienced increases in T, and this T reactivity after competition was a mediator between winning and later aggressive behavior among males.

Female Hormones

Among females, hormones including estradiol and testosterone have been linked to status striving. For human females, estradiol may serve a function analogous to testosterone, as it is linked to dominance in women and has been shown to increase following victory in a contest for those with high-power motivation (Stanton and Schultheiss 2007). Further, women with higher estradiol levels tend to have higher implicit power motivation.

Testosterone may also be associated with dominance and high status in females, particularly among those high in basal cortisol. Examining female college athletes, Edwards and Castro (2013) found that those competing had higher T levels than those on the sidelines. Further, higher testosterone before a game was associated with occupying a higher-status position on the team, but only among females who had relatively low cortisol levels prior to the game. Zilioli et al. (2014) found that when the outcome of a competition between females is uncertain, competitors experience a T boost, perhaps due to the possibility of future victory. Finally, females with congenital adrenal hyperplasia (CAH), a condition involving abnormally high prenatal androgen exposure, have been found to engage in higher levels of direct aggression relative to non-CAH females (Pasterski et al. 2007). Overall, the links between hormones and dominance behaviors in competitive contexts suggest that hormones shape hierarchy structure, and hierarchy structure shapes hormone levels among both males and females.

Hierarchies and Health

High status confers many potential fitness benefits to humans and nonhuman primates, including longer life and better health, more mating opportunities, and material resources (Ellis 1995). These detrimental effects of lower status exist along a continuum, with those in lower socioeconomic status (SES) positions experiencing more negative outcomes than those on top. Indeed, lower status is associated with physical and mental health problems. In stable hierarchies with

extreme inequality, adverse health outcomes such as physical and psychological stress are particularly likely for those at the bottom, who receive the least social support and resources (reviewed by Abbott et al. 2003). While individual differences exist, occupying the lowest rungs of the social ladder can contribute to chronic stress, particularly in steep and stable hierarchies. Chronic stress, in turn, is associated with immune suppression, hypertension, high cholesterol levels, testicular atrophy, increased risk of miscarriage, and increased risk of developing heart disease (Brunner et al. 2002), diabetes, and stroke. Among humans, lower SES contributes to higher infant mortality, decreased likelihood of using many types of health care (e.g., vaccinations and dentist visits), and higher heart disease and stroke mortality (CDC 2009).

These SES-based health disparities persist among employed individuals with health-care access, indicating they do not arise from differential access to health care. Those on the lower rungs of the social ladder are more likely to smoke, drink excessively, have sedentary lifestyles, poor diets, and fewer preventative health opportunities such as health club memberships and safe parks. However, these lifestyle factors account for only a third of the SES gradient in health outcomes (Sapolsky 2004).

Employment Rank

Working a low-status job is associated with a host of adverse health outcomes. For instance, having a low-status career is associated with low heart rate variability (HRV), which is a predictor of heart disease (Hemingway et al. 2005). Lower HRVs have also been found among individuals with small social networks, depression, and low job control (e.g., an unstable position within the hierarchy) relative to those with more social support and job control. In the classic Whitehall studies, employment rank was positively associated with disease mortality – including heart disease mortality – among British civil servants (Marmot et al. 1978). These detrimental effects of low-status positions may stem from a high ratio of costs relative to benefits in the workplace. Indeed, a high cost-reward ratio at work is associated with

an increase in coronary heart disease, poor mental health, and poor physical health.

Comparative Evidence

Nonhuman primates at the bottom of social hierarchies do not always experience the chronic stress responses that humans do. Among some primates, those at the bottom of hierarchies actually exhibit lower cortisol levels than those at the top. Some reasons for this are that primate social structures are diverse – not all consist of highly unequal hierarchies with stable boundaries, and primates engage in reconciliation and peacemaking behaviors that may support those in the lower rungs of the social ladder (see Abbott et al. 2003).

Despite this, in some species, subordinate primates experience worse health outcomes than those at the top of the hierarchy. For instance, in some primate groups, those occupying the lower rungs have higher cortisol, particularly when they are experiencing more stressors and a lack of social support (Abbott et al. 2003). Among female primates, high status is associated with getting pregnant more quickly, higher offspring survival rates, and less aggression from fellow females (Hrdy 1981). In turn, among low-status female primates, ovulation can be suppressed by stress brought on by aggressive, high-status females. High-status females can also contribute to lengthening of the menstrual cycle, maturational delay, and spontaneous abortion in subordinate females (Hrdy 1981). Among both humans and nonhuman primates, high-status females are likely to mate with high-status males, thereby conferring the good genes and superior health to her offspring.

Conclusion

Hierarchies emerge from competition over fitness-relevant resources. Given that such competition is integral to reproductive fitness, it should be no surprise that hierarchical social structures are found across social species. It appears that humans and other animals have adaptations to negotiate hierarchies – to maintain position and to strive for higher-status positions, for instance. Occupying a dominant, high-status

position confers numerous survival and reproductive benefits, including access to high-quality mates. Hierarchies are formed partially on the basis of hormonal biochemistry interacting with the social environment. One's social position can, in turn, shape physiology and subsequent dominance behavior. Social hierarchies have a profound influence on health, affecting mortality and morbidity for a variety of diseases, and shape psychological well-being. Given the plethora of benefits that high status confers, individuals strive to maintain their high status and improve their social rank using a variety of context-dependent strategies, including both aggressive and cooperative tactics.

Cross-References

- Aggression
- Health
- Mating
- Physiology
- Sexual Selection
- Testosterone

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Status Hierarchy

- [Men in Positions of Power](#)
- [Social Hierarchies](#)

Status Striving

- [Status Competition](#)

Status Symbol

- [Color Red](#)

Status-Leveling

- [Downfall of “Tall Poppies”](#)

Steady Future

- [Good Health and Stable Future](#)

Stepchildren

- [Presence of Children](#)

Stepfamilies

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Synonyms

[Amalgamated families](#); [Blended family](#); [Bonus family](#)

Definition

Stepfamily is defined as “a unit that is created when two adults form a household in which one or both brings a child from a previous relationship” (DiVerniero 2011, p. 3).

Introduction

There are many different types of stepfamilies. According to Papernow (2018), “Stepfamilies come in many forms. Stepouples may be married, or unmarried” (p. 3). For example, a family that is shaped by two individuals and only one of them has children is called a “simple” stepfamily. A different type of stepfamily includes an adult who is either married to or cohabitating with another adult, and both adults have children; these are called “complex” families. A stepfamily is created once a parent takes a new partner, by living together, or due to divorce. Previous paternal relationships may have ended in divorce, death, or breakup in the case of unmarried couples. The divorce average has fallen in the United States, with the exception of those more than 50 years of age, with the rate doubling between 1990 and 2010 (Brown and Lin 2012).

Thus, the increasing numbers of new couples are over the age of 50, some with adult children and even grandchildren. All these stepfamilies face five challenges for intimate relationships (Papernow 2013). This entry will describe the stepfamily, explore the challenges that face stepfamilies, and examine the myths and realities regarding stepfamilies.

Challenges Faced in the Stepfamily

The first challenge faced by stepfamilies is that insider/outsider positions are intense and stubborn. The strong fetters of the family, common history, and common values in the structure of parents and children create the bonds for strong parent-child relationships. However, the parents can become torn between the needs of their children and their partners. Culture also plays a role in the formation of this challenge. The Anglo-European family standards draw firm boundaries around the nuclear family, setting a context for competition. By contrast, African American traditions in “childcare” and “informal adoption” support cross-family cooperation (Gonzalez et al. 2014). These differences may explain the discovery that adolescent black-stepchildren in many large samples of married stepfamilies show more resilience than their white counterparts (Adler-Baeder et al. 2010).

Cultural standards can also restrict, or support, the participation of nonresident fathers. In Japanese and Latin stepfamilies, nonresident parents are often excluded, even from the family conversation (Papernow 2013). In the United States, nonresident Latino parents have significantly lower levels of post-divorce involvement than Anglo-American or African American parents (Stykes 2012). In sharp contrast, non-African American parents, both married and single, keep participation higher than Anglo-Latin parents through a variety of measures (Papernow 2013). The lack of data available across cultures suggests the existence of marginalized stepparents in cultures where the “nuclear family ideology” is very strong. Second wives in Hong Kong, for example, are referred to as “worn shoes” (Papernow 2015).

Therefore, there are many factors that impact the insider/outsider positions within stepfamily relationships.

The second challenge faced involves children struggling with losses, loyalty binds, and changes. According to a study conducted by the American Academy of Child and Adolescent Psychiatry (AACAP) (2015), it takes one to 2 years for amalgamated families to regulate and adjust to the changes. However, couples who are practical in reducing and tackling potential matters will create adjustment efficiently. Sibling rivalry is an example of a big challenge in a stepfamily. Children do not like to share parents. In fact, while a new relationship is a wonderful gift for adults, children – even adult children – often experience their stepfamily as yet another set of losses (Cartwright 2008). This problem can be solved if the husband and wife talk peacefully to resolve the issue and never blame each other. Everyone desires attention in a stepfamily. When the number of children increases in the family, the children feel that they are not obtaining the attention they are accustomed to getting. Additionally, amalgamated families generally have less time and cash for every child’s extracurricular activities or for family outings due to the increase in the size of the family. This problem can be sorted out by giving each child some positive time.

The third challenge involves dividing parenting tasks between parents and stepparents. “Stepfamilies by their very nature are complex and infinitely varied” (Papernow 2013, p. 3). Therefore, stepparent discipline often becomes a challenge. However, previous research has convincingly demonstrated that biological parents must retain control of discipline issues so that children and their parents can have a satisfactory relationship (Pylyser et al. 2018). Whereas once the biological parents’ partner was somebody to have fun with, they become an authority figure, which may cause some issues within the home. However, an amalgamated family remains simply a family despite the existence of such issues. Although there can be growing pains, squabbles and some moments of discord, everybody can eventually go on with the new state of affairs (Morin 2019). As the nature and complexity on

the part of stepfamily relationship have effects on stepparent discipline, the parenting tasks in the family need to be maintained to overcome relationship mismatches.

A fourth challenge can be connected to a new family culture which must be formulated in the presence of already established cultures. This is a challenge which step families experience when the two parents come from different ethnic and sociological backgrounds. It is represented in the family members' common understanding about noise, chaos, holiday rights, money, etc., and it exists in parent-child relationships rather than the relationships between spouses. The differences, large and small, saturate daily life. Successful families slowly adopt a new family culture while respecting and honoring the traditions, values, and family customs in place.

The fifth challenge involves Ex-spouses (other parents) who are part of the family. Children have another parent, alive or dead, who was nurtured or abused, outside the nuclear family. Children's well-being is the highest with positive parental behavior, joint cooperation with parenting, and when children feel safe with all adults in their lives (Papernow 2013). This challenge is considered as having the least impact on the new family, as it is often avoided by explaining that there were no other choices than starting a new family. Also, children seem to grow out of making complaints about their loss of an ex-member of a family once they understand the new situation. Finally, despite all the challenges that seem to occur along with the formations of stepfamilies, still there are many new families are formed every day and still parents believe this type of family is a better solution to the traditional family breakdowns and relationship failures.

Many children that stay with their foster parents have faced injustices. Typically, stepparents have abused children that are not of their own genetic makeup. When children stay in a household without any genetic parent, the stepparents tend to mishandle them and instead, focus on their own genetic tree that they expect to extend to further generations. Abuse of stepchildren is rampant as compared to that of children living with their genetic parents. They foster parents tend to

include violence and aggression in modeling stepchildren, especially those that are not their blood relatives (Skånland 2012). However, even genetic fathers kill their own children and subject some of them to social injustices including sexual violence. For example, genetic fathers killed 178 children aged below 5 years between 1974 and 1990 based on a study conducted by Daly and Wilson (1983). About 67 stepchildren were killed by their foster parent although the risk of being killed by a stepfather is still higher than that of being killed by genetic parents. Additionally, children living with single parents, either genetic or stepparent, are at higher risks of physical, sexual, and emotional abuse as compared to when those parents are living with their biological offspring. Consequently, research proves that stepchildren are often injured as compared to biological children since the abuse rates among the latter group have declined in recent years. Also, children living with disadvantaged families, specifically those experiencing abject poverty, experience abuse as compared to those in socio-economically advantaged homes (Skånland 2012). This implies that children living with stepparents are at higher risks of abuse and poverty is a major contributor to the increased risk. Other than poverty, age is equally a perpetrator of child abuse since evidence proves that younger parents abuse both genetic and nongenetic children as compared to the aged.

Myths and Reality about Stepfamily

In modern America, one in three people are a part of a stepfamily. There are a lot of misconceptions and myths about stepfamilies. Professionals have not paid much attention to the requirements and problems faced by these families. The most common myth in society is the Wicked Stepmother. Whether it is fairy tales of centuries past or modern cinematic plots, this stereotype continues to dominate society's thinking about mothers (Christian 2005).

There is also the myth that a partner in a stepfamily works to fit in someone else's role in order to recreate the first family, which is not true

(Jacobson 1979). The reality is that stepparents build their family in keeping with their own values and background. The thought that stepparents are always bad and evil is far from reality. The truth is that stepparents need a cheerful, healthy family like anyone else. Stepparents are not universally evil people. This does not, of course, mean that every parent is great or that they never do any wrong. The perception that partners decide to form a stepfamily for their own gains is false and ignores the tremendous modification and sacrifices they are doing to settle in with their new family. TV shows, fiction, and films portray ex-parents as adversaries, always in disagreement (Jacobson 1979). The fact is that a stepfamily is a way to lead a peaceful and respectful life in many cases where marriages are not successful and lack compatibility. It is in the interest of both children and adults to be in a civilized stepfamily rather than to drag on in the unhappy relationship, everyday confrontations, violence, and unpleasant situations.

Another myth is that co-parenting is the sole method for families. The truth is within the high-conflict situation in the family, parallel parenting will be the foremost effective selection for families (Jacobson 1979). It is often said that the kids in stepfamilies cannot love all of their parents-biological and stepparents. In reality, if children are treated well, inspired, and educated to have compassion for all, they will overtly love all adults in their family. Children who are not treated well in stepfamilies can feel extreme anxiety and stress concerning their family dynamic. However, children who are motivated to have positive, loving relationships with all live happily in the stepfamily (Jacobson 1979).

Conclusion

In spite of the arguments that are warning about growing lack in success of second and later marriages, there are several stepfamilies who have reached some extent where members of the family can actually say they have achieved happiness. Wilson (2014) argues that the cultural expectations surrounding mothers and wives began to

improve in the early nineteenth century. Following developments in children's literature and educational literature, Wilson claims that the growing cultural importance of domestic life, as well as the belief in the potential for personal reform promoted by the Second Great Awakening, led to a revision of the qualities and roles of the stepmother.

The importance of school-family-community (SFC) partnerships have long been established; but, a lot of analysis, practices, and policies are required to perceive and support numerous socio-cultural contexts of children coming from stepfamilies who experience an educational set back due to the changed environment. Families may openly discuss the problems and stresses that they observe in the newly created stepfamily. With the use of Epstein's model on SFC partnerships, strains faced by children and stepfamilies can be addressed by the following: parenting, communication, volunteering, earning at home, and cooperation with the community (Epstein, Sanders, Sheldon, Simon, Salinas, Jansorn, Hutchins, 218). Cultural disparities, educational problems, and other constraints should be openly shared by all stakeholders. Respect towards each other, trust and appreciation of observations made by parents and school authorities should be ensured. When a strong partnership is developed students' educational and nonacademic outcomes are improved (Paik et al. 2019). The increasing numbers of new step families contain couples of different ages in addition they include children of school ages and some with adult children. All these stepfamilies need to be integrated in community programs in order to avoid the children being trapped in evolving intimate relationships as a result of the new form of familial structures. This entry provided a description of this new social symptom known as the stepfamily, and it examined the challenges, presenting some of the myths and misconceptions about such a sociological phenomenon.

Cross-References

► [Two-Parent Families](#)

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Step-Parenting

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Definition

(Co)parenting of a partner’s child which is not one’s biological child.

Introduction

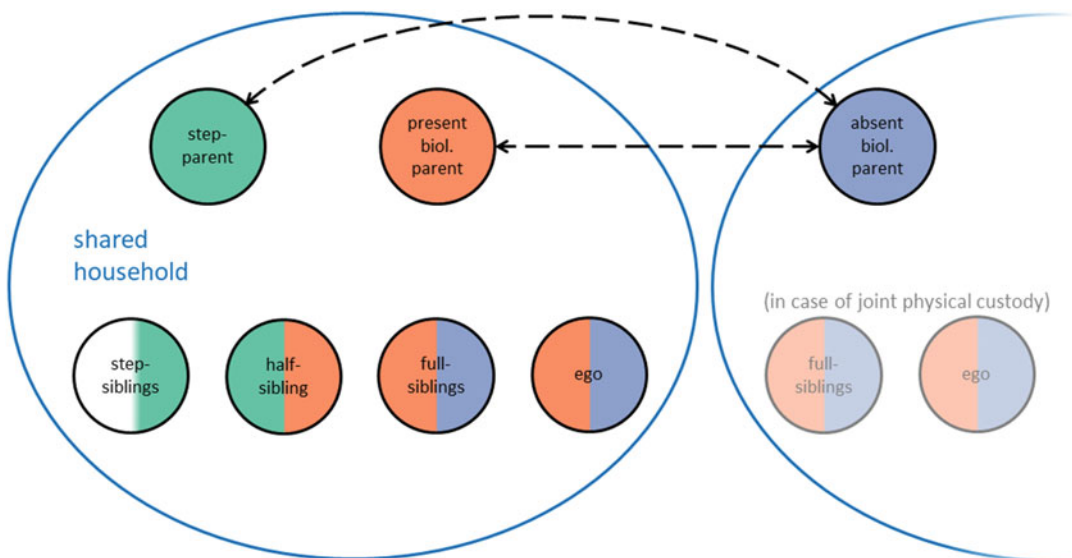
Step-parenting takes on many different forms and may have different causes. Historically and across societies, there is variation in what constitutes the most common causes for stepfamily formation: Whereas in modern industrial societies increasing rates of separation and divorce along with re-partnering and multiple-partner fertility have been major drivers for the formation of stepfamilies (Steinbach 2010), historically stepfamilies were mostly formed after the death of one biological parent, often out of economic necessity (Hill and Kopp 2013, p. 33).

In both cases, what constitutes a stepfamily – from the perspective of a child – is that children share the household with one biological parent and his or her current partner who is not a biological parent. Possibly, and this is more characteristic for modern stepfamilies, the child has a second parental home where the other biological parent

lives with or without a new partner who would constitute a second stepparent. If one or both biological parents have additional children with their new partners and/or the stepparents have children from (a) previous relationship(s), half- and/or stepsiblings may be present in one or both households (Schnettler and Steinbach 2011). Stepfamilies can thus be characterized by various degrees of family and household complexity (Thomson 2014). Recent research on stepfamilies reflects on the importance of these multiple-household family structures with regard to potential outcomes for children (e.g., Brown et al. 2015; Schnettler and Steinbach 2011), especially at a time when joint parental custody is on the rise with, in some cases, an equal share of time spent in either of the two parental homes (Steinbach 2019) (Fig. 1).

The presence of a stepparent does not necessarily contribute to the well-being of the child to the same degree as the presence of two biological parents. Research shows overwhelming evidence for the existence of a so-called stepgap (Delongis and Preece 2002), that is, a mean difference in

outcomes between children living with and without stepparents on a range of indicators, in both contemporary as well as historical societies. This includes a range of subjective outcome indicators like children's assessment of their relationship with their parents and a range of objective measures like parental investment of time and money, children's academic achievement, psychological adjustment, child abuse and mistreatment, behavioral problems, and even cortisol levels as indicator of social stress (Anderson et al. 1999a, b; Brown and Rinelli 2010; Coleman et al. 2000; Daly and Wilson 1985; Flinn and England 1995; Hamilton et al. 2007). The direction of the stepgap is usually such that, on average, children living in a stepfamily have worse outcomes than children living with two-biological-parent families. Although part of the stepgap may be attributed to between-family differences (e.g., Buller 2005), Schnettler and Steinbach (2011) show that a stepgap persists after taking differences between families into account. In their study, the stepgap in subjective assessments of the child-parent



Step-Parenting, Fig. 1 Schematic illustration of a stepfamily from the perspective of a child (ego). Genetic relatedness is indicated by colors. The relationship of the absent biological parent to his or her children (ego and full siblings) might be of similar importance as the relationships between the absent biological parent with the present biological parent and with the present stepparent (indicated by

dashed lines). Likewise, the sibling composition in either household is of importance. The stepparent's behavior toward ego might be different if the stepparent has biological children with ego's present biological parent (half-siblings to ego) or if children of the stepparent from a former relationship (stepsiblings) are present in one of the two households of the two biological parents, too

relationship even roughly follows a gradient along the lines of genetic similarity in sibling dyads, based on pairs of monozygotic and dizygotic twins, full-, half-, and stepsiblings from the US Adolescent Health Study.

Nevertheless, the persistence of a stepgap in studies using a within-family research design is no proof that the difference is biologically hardwired (Schnettler and Steinbach 2011). Theories in evolutionary biology provide reasoning for why parents would be biased in their investment toward biological versus stepchildren. One central such reason would be (the lack of) genetic relatedness that – according to kin selection theory – should play a decisive role in steering parental investment patterns and other forms of altruistic behavior. Yet, there are also conditions under which, even from an evolutionary perspective, parents may strategically provide investment to their stepchildren. Furthermore, as evolutionary psychology has amply demonstrated regarding other adaptive problems in human behavior, psychological mechanisms that have evolved in an ancestral environment may prove maladaptive in the modern environment (Barkow et al. 1992). There may exist social contextual conditions in which we would expect smaller or nonexistent differences in stepparent- versus biological parent-child ties, even though evolutionary biology predicts that preferential treatment of biological kin is adaptive. Genetic relatedness is but the ultimate evolutionary explanation, relating to underlying mechanisms. More direct, proximate mechanisms may involve co-residence duration, similarity in looks (phenotypical similarity), or similarity in smell (olfactory cues) that all affect how children are treated and which can result in different treatment of biological vis-à-vis stepchildren. In this interplay of multiple potential mechanisms lies the possibility that the size of the stepgap is malleable by contextual differences, such as differences across time and space in the likelihood that stepparents and stepchildren live together in one household. Such differences provide potential leverage for policy-making that aims at improving parent-child relationships in stepfamilies.

Previous research has investigated different potential mechanisms for this stepgap: The

majority of studies with a background in the social sciences as well as in psychology has focused on stressors associated with parental separation or death and with life in (complex) post-separation families, and on stepfamily selectivity. Evolutionary research, on the other hand, has emphasized the evolved motivational and behavioral patterns which may play an important role in producing the stepgap.

Step-Parenting in the (Standard) Social Sciences

Family research offers two major hypotheses on potential causes of the stepgap: the selection hypothesis and the stress-mediation hypothesis (Coleman et al. 2000; Hadfield et al. 2018). According to the selection hypothesis, “multiple transitions and negative child outcomes may be associated with each other through common causal factors reflected in the parents’ antecedent behaviors and attributes” (Fomby and Cherlin 2007, p. 181; cited in Hadfield et al. 2018). Multiple transitions are (repeated) parental separation and re-partnering events that produce more or less complex types of stepfamilies. In this view, it is unobserved heterogeneity between different family types which is also responsible for the stepgap in developmental outcomes. Better data availability in the form of repeated measures over time and for siblings in the same families has made it possible to test this hypothesis empirically. One study using longitudinal data, for instance, shows that parental attention after the birth of a new biological child shifts from older children to the newborn roughly to the same degree in two-biological-parent families and stepfamilies (Stewart 2005). This seems to imply that the stepgap may partially be driven by a birth-order or age effect. Yet, in a within-family comparison of siblings living in the same families in the USA, Schnettler and Steinbach (2011) find that the stepgap in adolescents’ perceived parental closeness and care persists even after taking into account children’s age, other relevant factors that can vary within families, and, most importantly, after applying family fixed effects to control for

unobserved heterogeneity between families. Arránz-Becker et al. (2013) also find a persisting stepgap after inclusion of family fixed effects in their statistical models, in this case applied to parents' emotional closeness to their mostly adult children in Germany.

Both studies also reveal a number of moderating factors that narrow the stepgap. These are, most importantly, relationship duration, the amount of family resources, and the importance of norms of familism. Yet, in both studies, a considerable stepgap persists even after taking these moderating factors into account (Arránz-Becker et al. 2013; Schnettler and Steinbach 2011). Together, these studies thus provide evidence that unobserved heterogeneity seems not to be the sole explanation for the stepgap, at least with regard to the particular indicators studied. This is consistent with studies using fixed-effects models to control for unobservable factors across time, siblings, or families with regard to the effects of divorce. Here, too, a central conclusion is that effect sizes decrease after taking into account unobserved heterogeneity, but moderate associations between divorce and outcomes persist on a range of measures (Amato and Anthony 2014).

Different from the selection hypothesis, the stress mediation hypothesis attributes a causal role of family transitions (separation, re-partnering) to developmental outcomes for children and adolescents growing up in stepfamilies. Living in a stepfamily implies that the parents of a focal child or adolescent have at least once separated or divorced and formed a new relationship. According to the hypothesis, each family transition creates stress which can accumulate across multiple transitions and negatively affect developmental outcomes in those affected by these (multiple) stressors (Hadfield et al. 2018). An enormous amount of literature on the consequences of divorce shows that relationship instability and divorce can harm development in manifold ways and with persistent, adverse effects into adulthood (Amato 2001; Amato and Anthony 2014; Patterson 2001). A recent review that covers 39 articles published over the preceding decade that specifically test the instability hypothesis also generally shows support for the

instability hypothesis. But mixed results with regard to certain transitions, groups, and outcomes point toward additional explanatory factors that may be at play but are not yet well understood (Hadfield et al. 2018, p. 20).

Recently, researchers in the social sciences have increasingly focused on the complexity of family constellations across households at a given time as one such overlooked factor (cf. Schnettler and Steinbach 2011, p. 190). One might argue that the specific family and household structure of a child adds another set of potential stressors that contributes to the link between family type and developmental outcomes. Navigating family relationships across households may be stressful merely because it is more demanding to organize life across two more or less geographically distant households than it would be to organize daily life in one household. In addition, communicating and negotiating the demands of the parent living in either household may be emotionally taxing, a challenge that arguably becomes more difficult as additional relationships are involved, e.g., toward stepparents and step-siblings in the main and secondary parental home. This reasoning may be used to extend the instability hypothesis toward an instability-complexity hypothesis: multiple family transitions and the degree of complexity of cross-household family constellations both provide independent and additive sources of stress that may cumulate and affect developmental outcomes of children and adolescents.

The Evolutionary Approach to Understanding Stepparental Behavior

In the standard social science approach, the stepgap is interpreted mainly as the consequence of various stressors stemming from characteristics of the family environment (see above). In contrast, sciences that explicitly draw on Darwinian evolutionary theory see evolved anthropological inclinations as the driving forces behind the stepgap. Kin selection theory (► [“Kin Selection”](#)) explains why biological children usually receive significant parental investment and why parents truly exhibit an interest in their children's

prosperity. For the same ultimate causes, that is, the absence of (personal or inclusive) fitness benefits, stepparents do not have kin-altruistic interests in their non-genetically related stepchildren. In general, parental investment can be understood as any kind of resource transfer from parents to their offspring. Parents usually do not receive economic or social net-benefits for taking over the tasks of parenting (Lee and Kramer 2004), but when investment occurs for biological offspring, altruistic behavior can increase direct fitness, also known as personal fitness.

In contemporary industrialized countries, step-parenting occurs most commonly due to parental separation or divorce. However, in historical Europe as well as in societies in Sub-Saharan Africa, stepparental relationships are mostly due to parental death (Bock and Johnson 2008). The tasks of parenting are then often taken up by adult kin, like grandparents, biological aunts, and uncles who adopt their grandchildren, nieces, or nephews. For these cases, inclusive fitness theory predicts that stepchildren receive more care and attention than stepchildren would do on average. This is because they are biologically related to their stepparents. However, due to their lower genetic relatedness and the absence of direct fitness benefits, the theory still predicts them to receive less care and attention, on average, than children would usually receive from their biological parents.

Whereas kin selection theory argues on the level of ultimate causality, there is also research on the proximate mechanisms that may be involved in mediating parental investment: It is expected that natural selection has favored such mechanisms that (a) increase the likelihood of having biological offspring, e.g., by means of sexual desire or an emotional desire to have children (cf. Foster 2000), (b) make adults attend and respond to the needs of infants (see ► [“John Bowlby and Attachment Theory”](#)), and (c) allow individuals to reliably recognize and to direct investment toward close biological kin (► [“Kin Recognition”](#)). The evolved proximate mechanisms therefore will reduce the likelihood that stepparental altruistic behavior is exhibited toward non-genetically related children.

When it comes to stepparental investment specifically, one central point of debate with regard to potential mechanisms has been the question as to whether the stepgap is merely the result of higher (step-)parental investment in favor of biological over stepchildren or whether stepparents actively disadvantage their stepchildren in the household. Research on this topic has been inspired by Daly and Wilson (1985, 1999) who were among the first to make an argument for the latter and to name the tendency toward disadvantaging stepchildren the “Cinderella effect,” alluding to Cinderella’s bad treatment by her stepmother in the fairy tale of the same name by Brothers Grimm. They supported their argument empirically with a study using data from the American Humane Association. Here, they compared the risk of fatal child abuse in households with and without the presence of a stepparent and showed that the risk was indeed higher in households where a stepparent was present. Although their foundational work in this area has provoked many, partly justified, methodological criticisms (see, e.g., Buller 2005), further research around the globe replicated Daly’s and Wilson’s finding, even after considering a variety of relevant context factors (e.g., Anderson et al. 1999a, b). In this regard, the sequence of events resembles that in the social scientific literature cited above. Yet, the interpretation of results has been different: Whereas social scientists have tended to see the remaining stepgap as the result of yet unexplained contextual factors (e.g., hitherto unmeasured forms of stress in complex family and household constellations), evolutionary psychologists have interpreted the residual stepgap as a potential result of the “Cinderella effect,” and there has been a heated debate on whether this effect can be understood as an unconditional (“hardwired”) human trait.

The discussion of the “Cinderella effect” in Darwinian psychology has largely ignored potential variability in the origins of stepfamilies across time, place, and population segments. However, as we have already pointed out above, stepfamilies can be the result of divorce and remarriage. Or they can be the result of parental death and remarriage. In that case, the formation of a

stepfamily can indicate normalization after a severe family crisis (Anderson et al. 1996), whereas step-parenting due to divorce might indicate a family environment in which parental motivation to care is reduced and in which parents and children are exposed to a set of potential stressors (see above). Willführ and Gagnon (2013) illustrate the conditionality of parental motivations to invest in or even actively disadvantage their stepchildren. They investigated the consequences of parental death and remarriage in the historical Krummhörn region in Germany (1720–1874) and in the historical St. Lawrence Valley (1670–1799). In the Krummhörn region, the presence of a stepmother was associated with increased offspring mortality to a similar extent as the death of a mother, whereas the remarriage of the father was a neutral event for his children from a previous marriage. The differential effect of the stepmother can be explained by the different socioeconomic contexts: Although the population of the St. Lawrence Valley was expanding, individuals were competing less for an inheritance (e.g., the parental farm), as land was abundantly available for the French settlers who benefitted from large family sizes. In contrast, the Krummhörn region was demographically saturated and there is evidence for increased sibling competition. By disadvantaging the children of her husband's former marriage, the stepmother intervened for the benefit of her own children. The conclusion of this study is that a stepparent's behavior is conditional on socioeconomic context and depends on whether reproductive interests are narrowed by one partner's former reproduction.

Overall, we can understand the treatment of stepchildren as an expression of an opportunistic strategy which is characterized by a trade-off (cost-benefit calculation). This trade-off is dependent on the socio-environmental context: If the benefits for the stepparent prevail over the costs, stepchildren can expect to receive a certain amount of stepparental investment even if the stepparent does not have an altruistic interest in a stepchild's prosperity. An illustration for this trade-off in modern stepfamilies would be a case of overdue alimony payments by the absent biological parent. Depending on the amount of

financial resources in the newly formed stepfamily, overdue or withheld alimony payments by the absent biological parent may to a higher or lesser degree mean a financial burden for the stepparent and thus enhance conflict potential within this newly formed stepfamily.

Whereas much of the literature on parental investment in stepfamilies focuses on disadvantages, it is worth noting that stepparental investment is – under certain conditions – consistent with evolutionary theory. Although kin-selection theory predicts that stepparents are not altruistically interested in their genetically unrelated stepchildren because of the absence of fitness benefits, there may be other evolved motivations why stepparents display parental investment toward their stepchildren. One such case is when the motivation to invest may be part of a mating or mate-retention effort (Anderson et al. 1999a, b). Another case could be stepparental investment as a signaling effort, e.g., to earn reputation in one's social network in social contexts where stepparental investment is highly encouraged by social norms. Finally, if one considers that many individuals display a desire to have and care for children – a desire that itself may be an evolved motivation (Foster 2000; Rotkirch 2007) – step-parenting may be one way to fulfill this desire, especially for individuals unable to have biological children.

Conclusion

From this review of the literature on step-parenting, it becomes apparent that the (evolutionary) biological, psychological, and social scientific literature focus on different aspects of step-parenting. Whereas both the evolutionary and social sciences have empirically established the stepgap and then shown that it gets smaller with better methodological designs and better data, they have highlighted different potential explanations for the remaining stepgap. Evolutionary biology and psychology aim at explaining different motivations for parents to invest in their biological children and stepchildren. The social scientific literature,

however, has focused mainly on explaining the stepgap by means of contextual factors like family resources and stressors across different family types. We argue that these approaches are not necessarily at odds with each other but complement each other in central aspects. In order to integrate them we need to engage with these various theories on a more fine-grained level and build new, interdisciplinary models that integrate motivational and contextual factors. Also, new types of data collection will be necessary that combine contextual variables along with biologically relevant variables. Human life courses are neither solely affected by evolved inclinations and individual motivations nor are these anthropological inclinations hardwired to a degree that makes them unmodifiable to environmental influences.

Cross-References

- [John Bowlby and Attachment Theory](#)
- [Kin Recognition](#)
- [Kin Selection](#)

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Stepparents

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Synonyms

Non-biological parents

Definition

An adult person (man or woman) becomes a stepparent if he/she lives together in a romantic relationship (e.g., marriage) with a partner

who already has one or more biological children from a previous relationship. Stepparents must be differentiated from adoptive parents, as the latter raise children who are not biologically related to any of the two parents.

Introduction

The possibility of becoming a stepparent is not exclusive to people in modern societies. In some bird and primate species (e.g., olive baboons), it has also been observed that a new partner helped raise the offspring of a female (Rohwer 1986; Smuts 1985, cited in Anderson 2011). Even in pre-industrial societies many families exist in which children live together with the mother and her new partner after the father's death or when the parents' relationship ends for any other reason. In the Middle Ages in Western societies, stepmothers were more prevalent because of the common remarriage of fathers after their wives' death due to perinatal complications. In today's Western societies, in contrast, the number of stepfathers significantly exceeds that of stepmothers. The reason for this is that after divorce children usually stay with the mother. Some calculations show that 30% of American children live with a stepparent, typically with a stepfather (Bumpass et al. 1995, cited in Anderson 2011). This rate in Europe varies between 1.1% and 11.4% (Heuviline et al. 2003, cited in Anderson 2011).

Stepparents and Evolution

According to Miller (2001), in hominid predecessors of *H. sapiens* monogamous relationships lasted for a couple of years. After this period pairs split up and formed new exclusive relationships. In this mating pattern, also called *serial monogamy*, children usually stayed with the mother. However, mating behavior was combined with parenting behavior both in males and females. Partner choice of males was influenced

by their impression of maternal competence of available females, as a sign of their capability to care for the males' future offspring. Similarly, hominid females with an offspring paid attention to potential mates' willingness to cooperate in child raising and probably were influenced by the attraction of their children toward these males as well. Female partner choice, therefore, was intertwined with children's choice. Nevertheless, the courting effort of hominid males was directed partly on the offspring of potential sexual partners. Hence the presence of children around reproductively active adults might have had a major effect on sexual selection.

Stepparents and Parental Care

The majority of stepparents not only tolerate but also support their stepchildren. At first sight this could seem a violation of *Hamilton's rule*. However, in light of the above evolutionary considerations, this behavior is reasonable. Stepfathers' willingness to invest in their stepchildren increases their attractiveness and enhances the quality and stability of the relationship between partners as well (Lancaster and Kaplan 2000). Nevertheless, not surprisingly, biological fathers invest more in their biological children than stepfathers all around the world. Biological children, in general, have an advantage over stepchildren. Stepfathers spend less time with their stepchildren, provide less financial support (Anderson et al. 1999a), and communicate and play less with them (Marlowe 2005). Studies with 5–12-year-old children showed that co-residence is also a significant factor of parental support (Anderson et al. 1999a, b). Stepfathers and biological fathers support children living in the same household to a similar extent, irrespective of genetic relatedness. Investment by stepfathers correlates positively with the time spent together in the family. Although some stepparents might have negative feelings toward stepchildren at the beginning,

there is a good chance that positive experiences will change these so that stepchildren will be treated similarly to biological ones (Marsiglio 1991).

Stepparents and Child Abuse

In contrast to the quite frequent occurrence of infanticide in the animal kingdom, human infanticide is relatively rare, although prevalent. Daly and Wilson (1985) showed that in those North American families where at least one of the parents is a stepparent, the likelihood of child abuse is 30–40 times higher than in families where all members are genetically related. In the case of infanticide, this figure is 70–100 (Daly and Wilson 1994). Regarding the way of perpetration, it was found that biological fathers choose a quicker and less painful method of murder. This holds for the difference between stepmothers and biological mothers as well (Weekes-Shackelford and Shackelford 2004).

Conclusions

The presence of a stepparent in the family might have been a frequent feature of the environment of our hominid ancestors. Even though the enhancement of inclusive fitness is considered a major goal in evolution that affects allocation of resources and competition among conspecifics, sexual selection might divert individual strategies from focusing only to direct reproductive benefits. Serial monogamy, for instance, creates circumstances under which parenting effort directed toward genetically unrelated juveniles is in fact not only beneficial but downright necessary in terms of reproductive fitness. Thus, the behavior of human stepparents is characterized much less by causing disadvantages to stepchildren, and more by showing the same amount of care as for biological relatives, than it is typical in other animal species.

Cross-References

- ▶ [Half-Siblings in Human Evolutionary History](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Kin Selection Theory](#)
- ▶ [Mate Preferences After Having Children](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Parent-Offspring Conflict](#)
- ▶ [Siblings](#)
- ▶ [Stepfamilies](#)

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Stereotyped Vocalizations

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Synonyms

[Larynx](#); [Oral cavity](#); [Pharynx](#); [Voice box](#)

Definition

Stereotyped vocalization: Evolved, species-typical vocal act with signal character.

Introduction

How did human communication evolve from an animal-like vocal system to spoken language? Research on primate communication in particular has produced a wealth of data, which highlight the various evolutionary continuities and discontinuities between animal and human communication. Research topics include the mechanisms and flexibility of sound production, how different call units are assembled into complex utterances, how meaning is extracted from vocal structures, and how the psychological mechanisms underlying animal call production and comprehension

compare to those of humans. The purpose of this chapter is to present the state-of-the-art of these various strands of research and to show how methodological tools of linguistics can help decipher animal communication.

Animal Vocal Behavior

Vocal Control

Mammalian vocalizations are produced by a larynx that oscillates in response to airflow from the lungs. This creates a basic acoustic signal further shaped by the supra-laryngeal vocal tract. Many species can actively change the geometry of their vocal tracts, which determines the call's resonance properties and acoustic quality. Within the primates, humans are somewhat special in that the larynx is in a permanently low position, which results in a characteristic perpendicular two-tube vocal tract. There has been much debate as to whether this anatomical specialization is crucial for speech production, but current opinion suggests that this is not essential. Humans are also unusual in their high degree of motor control of both larynx and vocal tract, mostly due to specialized cortical innervations (Ackermann et al. 2014). Great apes also have relatively good motor control over the facial musculature, including some of the speech articulators, suggesting that the transition to speech was largely due to control of the larynx (Lameira et al. 2014). One consequence of the lack of voluntary control over sound production is that nonhuman primates are essentially prevented from acquiring new sound patterns by vocal learning. As a result, each species communicates by means of species-specific vocal repertoires that develop under relatively strong genetic control.

Acoustic Flexibility in Animal Calls

Although the differences to humans are vast, primates exhibit limited vocal flexibility in some call types. At the most basic level, many call types carry individual signatures, which enable receivers to extract identity information. For

example, chimpanzees (*Pan troglodytes*) recognize each other by their pant hoot vocalizations, a long-distance signal, and discriminate the calls of neighboring males from the calls of unknown stranger males (Herbinger et al. 2009). Another interesting example is found in bottle-nosed dolphins (*Tursiops truncatus*) where individuals match each other's individual signature whistles, although they are not produced by the larynx (King and Janik 2013). Although there is widespread evidence for individually distinct calls, not all call types convey identity cues, Gelada baboons (*Theropithecus gelada*) being a striking example (Bergman 2010). In several primates, there is also evidence for acoustic convergence, usually within the contact calls. The general pattern is that calls of closely affiliated individuals are more similar to each other than calls of less affiliated group members. Another source of acoustic flexibility is found in calls given to external events as, for example, in Japanese macaque (*Macaca fuscata*) and chimpanzee food calls, Rhesus macaque (*Macaca mulatta*) and chimpanzee agonistic calls, or baboon (*Papio ursinus*) alarm barks (Zuberbühler 2015). A related but somewhat more complex way of creating acoustic variation is by assembling discrete acoustic units within the same calls. For example, male Campbell's monkeys (*Cercopithecus campbelli*) combine three basic alarm calls with an acoustically invariable vocal suffix. Suffixes are typically given to situations that do not warrant direct or strong antipredator responses, while unsuffixed calls are almost always given to dangerous predators, such as leopards or crowned eagles. Diana monkeys (*Cercopithecus diana*), a frequent association partner of Campbell's monkeys, discriminate this subtle feature, suggesting that suffixation is an evolved function in primate communication. Another relevant example is Diana monkey contact calls, which consist of individually distinct arched structures that convey identity information, which are regularly combined with three other call types linked with specific external events (Zuberbühler 2015).

Animal Call Sequences

In a number of species, semantically relevant units can be at the level of call sequences, rather than individual calls (Kershenbaum et al. 2016). A recent example is the vocal system of pied babblers (*Turdoides bicolor*), a social passerine that combines alert and recruitment calls into sequences when encountering terrestrial predators. Recipients respond differently to sequences than components calls, and it has been argued, controversially, that these birds show compositionality, as they communicate both context and requested action (Engesser et al. 2016; but see Schlenker et al. 2016). Related examples in primates are the call sequences of black-and-white Colobus monkeys (*Colobus guereza*), with sequence length and structure relating to predator type. In putty-nosed monkeys (*Cercopithecus nictitans*) call combinations encode both predator class and travel intention and in Campbell's monkeys predatory and non-predatory dangers (Schlenker et al. 2016). For apes, gibbon duet songs broadcast social information relevant to neighboring individuals but lar gibbons (*Hylobates lar*) also sing when encountering predators. Predator-induced songs and duet songs are assembled from the same unit repertoire but according to different patterns. Another example is bonobos producing sequences of acoustically variable calls when finding food, which are linked to the value of the food, something that listeners use to base their foraging decisions (Zuberbühler 2015).

Meaning in Animal Calls

There is overwhelming evidence that primates can extract information from others' calls, sometimes by taking into account the pragmatic context or reason for calling. The basic pattern is that specific events tend to trigger specific vocal responses, which are recognized and interpreted by listeners, a sort of by-product semantics. Hence, one hypothesis is that there is a profound discrepancy between signalers (uttering vocalizations for specific functions, e.g., to recruit a nearby ally), and recipients, who can infer the call causing events, even if not participating in the event. According to this model, nonhuman primate communication is

profoundly different from human language, where speakers are interlinked at a deep psychological level. Humans communicate, verbally or nonverbally, to be understood and have repair mechanisms in case of failure. Recipients, on the other hand, assume that signalers intend to communicate something meaningful and use common ground to infer meaning, beyond signal-event contingencies and direct linguistic meaning. An important problem in current research is therefore the degree to which primates communicate "intentionally," i.e., with the goal of informing about events relevant to their listeners and whether they experience an intention to be understood.

Recent research on call meaning has focused on three main questions: (i) what is the referential content or meaning of individual calls? (ii) How are the meanings of individual calls combined? (iii) Is the meaning of calls sometimes enriched by "pragmatic" principles of competition, notably an "informativity principle" whereby a more informative call is preferred whenever possible over a less informative one?

Campbell's monkeys afford a rich case study (Schlenker et al. 2016). Males use a call *krak* to raise leopard alerts and *hok* for raptor alerts, as well as suffixed *krak-oo* for alerts of all sorts and *hok-oo* for non-ground alerts. The challenge is to assign meanings to *krak*, *hok*, and *-oo*. Further complexity is added by Campbell's call use in another habitat, Tiwai Island, Sierra Leone, where leopards have not been seen for decades. Although both monkey populations produce the same call types, there are relevant differences in call use. On Tiwai, *krak* raises unspecific alerts (as does *krak-oo*), rather than specific leopard alerts, possibly a case of limited "dialectal" variation: *krak* has a leopard meaning in Tai and a general meaning on Tiwai. On an alternative theory, the "informativity principle" plays a key role: *hok* has a meaning of aerial alert, and *-oo* weakens the resulting alert, hence *hok-oo* is used for non-serious aerial alerts. *Hok* is further enriched by competition with the (more informative) call *hok-oo*, which explains why *hok* comes to be used for serious aerial alerts – hence raptors. *Krak* has a meaning of (general) alert at both sites, hence *krak-oo* is used for nonserious alerts.

By the “informativity principle,” the meaning of *krak* is further enriched by competition with *krak-oo* (“there is a nonserious alert”) and *hok* (“there is an aerial alert”). In the end, *krak* can only be used for *serious (not krak-oo) ground (not hok) disturbances* – hence the leopard uses in Tai. On Tiwai, the “informativity principle” would yield a useless meaning due to the absence of serious ground predators, hence *krak* retains its basic meaning.

The debate on the meaning of Campbell’s calls is still open, but several species might provide independent evidence for the “informativity principle.” Often calls are used in highly heterogeneous contexts and seem to have a general alert meaning; but in the event of a specific threat for which there is a precise call the more informative call trumps the general one.

Concerning call combination, a key question is whether call sequences are “compositional,” which is the case if *their meaning can be systematically derived from that of their parts*. As mentioned, in black-and-white Colobus monkeys, putty-nosed monkeys, and titi monkeys, some sequences seem to be interpreted “wholesale” and thus to present challenges to compositionality. Three general research directions are currently explored (Schlenker et al. 2016): (i) some call sequences might indeed be irreducible to the meaning of their component parts (possibly in Colobus and putty-nosed monkeys); (ii) sometimes a compositional analysis can be maintained if call meanings are taken to be very weak, and to be enriched by some competition principles; (iii) sometimes the complexity of the call sequence might reflect the caller’s changing perceptions as the events unfold.

Intentionality in Animal Communication

In great apes, there is evidence that signalers are aware of the social consequences of some of their signals, but there is no strong evidence that they also actively inform others or take their mental states into account during call production. Signal production may be based on simple social categories, such as dominance or affiliation, rather than the shared history with individual recipients and their momentary mental states, such as knowledge or ignorance. Although primates can perceive

others as goal-directed agents, they may not consider their mental states, such as beliefs or knowledge, when addressing them. Related to this, primates are not generally motivated to use communication in a cooperative way to inform others about facts or events relevant to them. Noteworthy exceptions are studies on predator encounters where signalers, especially adult males, appear to be concerned about the wellbeing of others (Zuberbühler 2015). Other forms of seemingly altruistic signaling, such as when encountering food, can be explained by callers trying to avoid negative consequences if failing to advertise the event.

Conclusion

Many social animals, including humans, possess a repertoire of species-specific vocalizations, with different calls produced to more or less specific events. However, humans have evolved an additional layer of vocal control, characterized by highly coordinated movements of the jaws, lips, and tongue in union with controlled laryngeal sound production. Nevertheless, recent work on nonhuman primate calls has shown some acoustic flexibility within individual calls and also at the level of call sequences.

The default model is that animal signals serve evolved biological and social functions, e.g., to dissuade predators, to recruit others, or to induce competition for copulation calls, but these contingencies are readily absorbed and actively interpreted by listeners, a sort of by-product semantics. Several studies have further shown that receivers attend to subtle acoustic variation within some call types in ways that suggest that they are meaningful to them. Progress has also been made by applying linguistic theory to the study of primate call sequences, in particular to assess the respective roles of call meaning, principles of call combination, and potential rules of competition among calls.

Another major theme in animal communication is whether nonhuman individuals produce signals with an intention to inform others. Here, the evidence is relatively weak, with only a

handful studies suggesting that callers monitor whether others have perceived or understood their signals or show concern to provide information that is relevant for their recipients. Studies on ape gestural communication, however, suggest that basic mental state attribution is within the cognitive realm of primates and can play a role in communication.

To conclude, although differences are vast, human vocal communication, including spoken language, is the result of evolutionary continuity with relevant precursors seen in nonhuman primates in almost every relevant capacity.

Cross-References

- [Vocal Communication](#)
- [Vocal Competition](#)

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Stereotypes

- [Avoiding Stigmatization](#)

Steroid Hormone

- [Testosterone](#)

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Synonyms

[Handicap hypothesis](#); [Hard to fake signaling](#);
[Intra-sexual signaling](#)

Definition

Sexual signaling refers to the ways that members of one sex signal their mate quality to members of the opposite sex.

Introduction

Steve Gangestad, Distinguished Professor, Evolutionary-Developmental Area Head University of New Mexico, is a psychologist at UNM, where he is best known for his work on evolution and development using quantitative methods. For many years he has been working with collaborators – notably Randy Thornhill – on the question of whether, in humans, female estrus is (as some scholars aver) truly lost. Typically, primates advertise their fertile phase through conspicuous displays. Humans do not do this. However, Gangestad has argued that a raft of behaviors indicate that estrus is concealed in humans rather than lost. This implies that there are two distinct types of sexual behavior in women. The first, during the fertile phase and the second – extended sexuality – during the non-fertile phase. Humans are not unique in having sex outside of fertile phases (bonobos and cetaceans also do this Gangestad et al. 2015), and Gangestad's work aims to root the study of human sexuality within the general phylogeny of vertebrates (Thornhill and Gangestad 2008).

Sexual Hide and Seek

For organisms to be able to transmit mate quality to potential partners in ways that might fall under selection (intra-sexual selection), it must be a hard to fake signal. There are a variety of ways for members of a species to honestly signal their quality to potential mates (Zahavi 1975; Gangestad and Thornhill 1997). Using peer report of attractive qualities in others, rather than the more usual self-report, Gangestad (Speed and Gangestad 1997) showed that sexually popular males are physically attractive, seen as trendsetters, and outgoing. Attractiveness in females also emphasized physical attraction and trendsetting. Surprisingly, earning potential did not feature in this population as a marker of attraction.

While all cultures value facial attractiveness, it is not immediately obvious why this should be. If such attraction were an entirely capricious thing, then it would imply that such qualities do not reliably covary with any underlying features in

potential mates. This is unlikely. Gangestad's work has shown repeatedly that in general, healthy mates are preferred and indicators of such things (such as clear skin and eyes and lustrous hair are universally valued (Thornhill and Gangestad 1999a)). Facial symmetry also seems to be a marker of genetic quality given that such symmetry reliably indicated resistance to developmental pathogens that would have resulted in asymmetry over evolved time, although the support for this hypothesis is more mixed.

Smell also indicates partner quality, perhaps in terms of compatibility. While human males seem largely unaware of the importance of this marker, human females regularly report that partner general attractiveness and partner smell covary (Thornhill and Gangestad 1999b). Indeed, an attractive partner smell was the leading predictor of orgasmic response in females – which may contribute to fertility (Thornhill and Gangestad 1999b; King and Belsky 2012). It is, however, unclear as yet as to whether attractiveness in partner smell results from an honest signal of general quality (e.g., that attractive scent covaries with symmetry) or signals specific major histocompatibility between the sexual partners. That the incidence of female orgasm seems to increase with extra-pair copulations, lends credence to the view that there is a sperm-selection function at work.

As noted above, a standard textbook view has been that human female primates are unique in having concealed ovulation. One of the figures chiefly responsible for revising this view has been Steve Gangestad. As he has shown in a variety of ways, it is more appropriate to think of ovulation as being guarded rather than completely covert. Not only does women's behavior become more overtly sexual and assertive during their fertile phase, but their partners seem alert to this on some level, increasing their levels of mate-guarding behaviors (Thornhill et al. 1995; Gangestad et al. 2014).

Conclusion

It is trivially true to say that humans are a unique species – uniqueness is built into the definition of a species. However, some mistake uniqueness for

immunity to the normal rules of natural and sexual selection. Gangestad's (and others) work on sexual signaling shows that humans are complex sexual strategists – just like any sexually reproducing species. Furthermore, he has shown that attention to evolutionary theory generates a range of falsifiable hypotheses about human behavior. For example, it is still an open question whether general symmetry (indicating developmental stability and hence immunocompetence) or specific markers of histocompatibility are being signaled in terms of mate preference. This alone gives the lie to oft-repeated canard that evolutionary hypotheses are fundamentally untestable. On the contrary – humans are rapidly being shown to have a range of complex strategic responses to mate selection utterly in keeping with their evolved natures.

Cross-References

- [Fluctuating Asymmetry](#)
- [Infidelity](#)
- [Mate Retention](#)
- [Personality and Mate Poaching](#)
- [Sociosexuality](#)

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Steven Pinker

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Steven Pinker (1954–) is a Canadian-American experimental psychologist and public figure. He is considered one of the most influential living figures in science and a leading expert on language and the mind.

He is known to general audiences as the author of numerous books ranging in subject from the mind and brain to human nature, violence, and language, including *The Language Instinct: How the Mind Creates Language* (1994), *How the Mind Works* (1997), *The Blank Slate: The Modern Denial of Human Nature* (2002), and *The Better Angels of Our Nature: Why Violence Has Declined* (2011).

Pinker is the Johnstone Family Professor of Psychology at Harvard University. Until 2003, he taught at the Massachusetts Institute of Technology, serving also as Director of the McDonnell-Pew Center for Cognitive Neuroscience (1994–99) and earlier as Co-Director of the Center for Cognitive Science (1985–84). He frequently appears on public debate panels (2005) and discussions and writes for numerous publications including *The New York Times*, *The Atlantic*, and *Time* magazine.

Education and Research on Visual Cognition

Pinker received his Bachelor of Arts in experimental psychology from McGill University (1976) before earning his doctorate from Harvard University (1979). Pinker's doctoral research, carried out under the supervision of Stephen Kosslyn, focused on visual cognition and the mental representation of objects in three-dimensional space.

Research on Language

Pinker completed his postdoctoral fellowship at MIT under the mentorship of linguist Joan Bresnan, previously a student of Noam Chomsky. This and subsequent research led to the publication of two technical texts: *Language Learnability and Language Development* (1984), in which Pinker presents a theory of how children acquire words and grammatical structures; and *Learnability and Cognition* (1984), focusing on syntax and the behavior of words, notably verbs, as well as the implications of these findings for our understanding of how the mind represents language.

In 1994, Pinker published *The Language Instinct*, in which he argues for the innateness theory of language. Inspired in part by the work of linguist Noam Chomsky, *The Language Instinct* presents wide-ranging evidence from cognitive neuroscience, developmental and experimental psychology, and linguistics for the theory that the ability to acquire grammar and new words is innate.

For both Pinker and Chomsky, the common logic underlying the world's languages, and the surprising speed and skill with which children acquire their native language, learn the meanings of words, and generalize grammatical rules are all evidence in favor of a universal grammar. Indeed, nearly every sentence a child hears or speaks is a unique arrangement of words; language must therefore be represented in the mind as a discrete combinatorial system, where a finite number of units can be combined in an infinite variety of ways. Universal grammar would explain the

“linguistic genius” demonstrated by children when faced with such an overwhelming influx of information.

Pinker moreover asserts that the apparently unique existence of the language faculty in modern humans can be explained with the Darwinian theory of evolution and natural selection.

In later books, notably *The Blank Slate*, Pinker applies the view that humans are born with certain innate cognitive capacities to human nature and cognition more broadly, opposing the notion of the “blank slate,” whereby the mind is a general-purpose learning machine, and human nature is purely a product of the individual's environment.

Pinker further discusses the mental representation of language and elements of language, such as word origins and word structure, in *The Stuff of Thought* (2008) and *Words and Rules* (1999).

Research on Violence

In his 2011 book, *The Better Angels of Our Nature*, Pinker argues that we are living in perhaps the most peaceful period in human history. He presents evidence that violence of all kinds has declined since our prehistory, drawing on extensive data drawn from research in the social, political, and historical sciences, as well as from cognitive science.

Pinker lists six major movements in the decline of violence:

1. The Pacification Process, in which nomadic communities formed agricultural societies, which grew into the first nation-states.
2. The Civilizing Process, in which rulers consolidated smaller, belligerent, feudal territories into larger kingdoms and commercial, cosmopolitan, and industrial forces incentivized peaceful exchange between members of the society.
3. The Humanitarian Revolution, exemplified by the eighteenth- and nineteenth-century European Enlightenment, and notable for major advances in secularism and humanitarianism. This era saw the widespread abolition of judicial torture, capital and corporal

punishment, slavery, and other previously state-sanctioned cruelties.

4. The Long Peace, or the unprecedented decline in warfare and violence since the end of World War II.
5. The New Peace, the further decline in organized conflict since the end of the Cold War in 1989.
6. The Rights Revolutions, the multiple civil, women's, children's and animal rights movements in the twentieth and twenty-first centuries that lowered our tolerance for hate crimes, domestic violence, child abuse, and animal cruelty.

According to Pinker, the exogenous causes of these historical trends can be attributed first to the rise of nation-states and the consolidation of power in centralized governments. Borrowing from Thomas Hobbes's political philosophy, he calls this the "Leviathan": as states gained a monopoly on the legitimate use of violence, levels of violence between individuals decreased.

Second, the rise of commerce incentivized cooperation and communication between individuals, rendering one's trading partners more valuable alive than dead. The zero-sum game of plunder thus gave way to the positive-sum game of trade.

A third factor is what Pinker calls the "Escalator of Reason," in which a confluence of events, such as the advent of the printing press and the consequent of the growth of literacy, as well as technological innovations that facilitated travel and the sharing of information between distant places and peoples raised general awareness about the world, lowered belief in superstitious doctrines, and encouraged the flourishing of rational thought. Together, these forces rendered practices such as witch-hunts and heresy trials, as well as torture and slavery less and less justifiable.

Lastly, Pinker argues that reasoning about the common experience of pleasure and pain, the discovery of the mutual benefits of nonviolence and other forms of cooperation, and repeated interaction with other groups widens the circle of people for whom we feel empathy or concern. Borrowing from philosopher Peter Singer, Pinker

calls this concentric form of moral progress the "Expanding Circle."

On Writing

Pinker has expressed criticism for traditional style manuals which impute arbitrary rules of language use that "force writers into fuzzy, clumsy, wordy, ambiguous, incomprehensible prose, in which certain thoughts are not expressible at all" (2007). In 2014, Pinker published his own style guide, *The Sense of Style: The Thinking Person's Guide to Writing in the twenty-first Century* (2014).

Awards

Pinker has received numerous awards for his scientific research, as well as for his books. In 2016, he was nominated to the National Academy of Sciences. He has also received awards from the American Psychological Association, the National Academy of Sciences, and the Royal Institution in Great Britain.

Cross-References

- [Noam Chomsky](#)
- [Pinker's \(1994\) *The Language Instinct*](#)
- [Steven Pinker and Language Development](#)
- [Words and Rules](#)

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Steven Pinker and Language Development

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Synonyms

Language instinct; Nativist approach; Psycholinguistics

Definition

A description of Steven Pinker’s scholarly work on language development and psycholinguistics.

Introduction

Steven Pinker was born in Montreal, Quebec, Canada, in 1954 and is a prominent psychologist, linguist, and professor in the Department of Psychology at Harvard. He is well-known as a popular science author and an advocate for science, especially evolutionary psychology (for which he won the Richard Dawkins Award in 2013). He is also a major proponent of the information processing metaphor of the mind and frames human language development in terms of evolved psychological mechanisms operating like software on the hardware of the physical brain.

Pinker’s published research on psycholinguistics is highly influential. For instance, a 1988 paper challenging the popular connectionist theory of regular and irregular phenomena in language (Pinker and Prince 1988) has over 1900 citations to date.

He has also written major review papers on language development processes (e.g., Pinker 1979). Additional areas in which Pinker has contributed to our knowledge on language development include the neurological bases of grammar, the use of euphemism, irony, and innuendo. He has written two technical books that proposed a general theory of language acquisition and applied it to children’s learning of verbs.

In several books written for a mass audience, Pinker has provided a litany of evidence, from both his own original research and from the field of psycholinguistics more broadly, regarding the existence of innate mental modules for language acquisition shaped by natural selection. Of his seven books, six include psycholinguistics as a primary or major theme: *The Language Instinct* (1994), *How the Mind Works* (1997), *Words and Rules* (1999), *The Blank Slate* (2002), *The Stuff of Thought* (2007), and *The Sense of Style* (2014). Pinker’s other book, *The Better Angels of Our Nature* (2011), reviews myriad evidence of exponential decline of violence per capita over millennia, centuries, and decades, and he suggests six major causal factors that explain this decline.

The following sections outline some of the key points of each of Pinker’s other six books, especially in regards to psycholinguistics and language development.

The Language Instinct (1994)

In *The Language Instinct*, Pinker asserts that the human capacity for language acquisition is innate. In many ways, Pinker agrees with Noam Chomsky’s theory of universal grammar, which states that language is hard-wired in the brain; that language skills develop naturally without instruction, rewards, or punishments; and that properties shared by all human languages demonstrate that it is a universal human trait. He does, however, consider himself more credulous than Chomsky regarding the ability of the theory of evolution by natural selection to explain our innate language capacities.

Pinker refutes purely behavioristic conceptions of language acquisition. For instance, Pinker

illustrates that children learn a great deal about language without instruction, which he claims is at odds with common conceptions of language learning. In addition, he criticizes common assertions that the typical person has poor grammar and that language is degenerating over time. He also provides evidence against certain academic linguistic theories such as the Whorfian Hypothesis (also known as linguistic relativity), which states that the properties of a specific language affects how its speakers can perceive and talk about the world. He is especially critical of the “strong version” of this hypothesis: that language determines thought. For instance, one could claim, based on the strong version of the Whorfian Hypothesis, that a speaker whose native language has no word for “rebellion” would be able to express or perhaps even have thoughts of rebellion. Pinker argues in *The Language Instinct* that thought is independent of language and asserts “the more you examine Whorf’s arguments, the less sense they make” (p. 60).

Pinker views language as unique to humans and as an ability that allowed our ancestors to adapt to selection pressures whereby hunter-gatherers who could more effectively communicate with each other would have a survival advantage over those who could not. And because language capacity evolved as the result of a domain-specific selection pressure, Pinker asserts that it is a unique mental module rather than a component of a more domain-general skill such as general cognitive ability. Research supports such a view by demonstrating a double dissociation between brain injuries resulting in loss of language abilities and those resulting in loss of general cognitive ability (e.g., Dunn and Kirsner 2003). For example, a condition known as Specific Language Impairment results in impairment of language skills without impairment of cognitive ability (van der Lely 2005), and a condition known as Williams Syndrome results in impairment of cognitive abilities but not a direct impairment of language (e.g., Bellugi et al. 1988).

That language is a product of natural selection and an innate part of human nature means that it is not the direct product of human culture; it is not a human invention in the same way as the wheel or

the computer. Language is universal across all human cultures whereas human inventions are not. Pinker asserts that the universal sequence of language acquisition – wherein children first demonstrate language through babbling, then holophrases (single words expressing an entire thought), and other intermediate stages before, achieving mature language skills – is apparent even in deaf individuals. He cites research evidence of “manual babbling” (babbling with hand gestures) in deaf infants (e.g., Petitto and Marentette 1991).

Additionally, Pinker points to so-called critical periods in language development (age ranges during which a child must have a certain experience in order for language skills to develop normally) such as those detailed by Kuhl et al. (2003). Such specialized and rapid learning processes are not explainable by operant conditioning or formal instruction.

Pinker claims that these findings as well as the natural development and acquisition of language skills in the absence of formal instruction are indicative of the innateness of spoken language.

How the Mind Works (1997)

The Language Instinct: How the Mind Creates Language (1994) played a vital role in refuting many myths regarding the development of language abilities. Pinker argued against the behaviorist perspective that language acquisition was primarily or entirely the result of operant conditioning process and presented substantial evidence to attest to the fact that, despite its complexity, understanding and using spoken language is a relatively easy accomplishment for most children. Language acquisition is largely dependent on evolved psychological mechanisms, which result in a predictable developmental sequence of language abilities.

In *How the Mind Works* (1997), Pinker extends his work on language from *The Language Instinct* while simultaneously broadening the focus to include myriad other areas of psychology and cognitive science: vision and the senses, emotion and affect, ideology, sexual attraction and love,

gender roles and identity, learning, judgment and decision making, social behavior, and much more. Pinker's expansion of his range of topics is necessary to address the goal of *How the Mind Works*: to attempt to explain the many functions of the mind, including those that are poorly understood, in evolutionary terms. Or, as Pinker himself puts near the end of his book, "To get you to step outside your own mind for a moment and see your thoughts and feelings as magnificent contrivances of the natural world rather than as the only way that things could be" (p. 563). The work is largely inspired by and uses the frameworks of cognitive psychology and evolutionary psychology, and Pinker highly utilizes the work of prominent evolutionary psychologists such as John Tooby and Leda Cosmides.

Pinker's two main assertions in *How the Mind Works* are taken from cognitive and evolutionary psychology. First, Pinker utilizes the information processing metaphor from cognitive psychology/cognitive science, which posits that the human mind is like a computer, which utilizes sets of algorithms ("modules" or "programs") to process data and produce behavioral output. Second, Pinker asserts that these mental programs represent evolved psychological mechanisms that were crafted by natural selection to efficiently solve specific adaptive challenges: acquiring language, choosing mates, avoiding danger, etc. Pinker even uses an evolutionary framework to explain negative emotional states such as sadness, which may elicit social support when we need it most, and disgust, which motivates us to avoid contamination by potentially lethal pathogens. Because natural selection results in evolved psychological mechanisms that on average improve the odds of an organism passing on its genes, Pinker's viewpoint explains why our minds are often predisposed to believe things that are untrue but that enhance our ability to survive and reproduce.

Towards the end of *How the Mind Works*, Pinker poses the question "[I]f the mind is a system of organs designed by natural selection, why should we ever have expected it to comprehend all mysteries, to grasp all truths?" (p. 563) Indeed, a mind that evolved to efficiently navigate the

relatively small-scale social dynamics and primitive survival pressures of our early human ancestors should not be expected to easily grasp macroeconomics, geopolitics, or the mysteries of the cosmos.

Words and Rules (1999)

In *Words and Rules* (1999), Pinker uses a single phenomenon, the form and frequency of grammatical errors, and analyzes it from as many angles as possible in order to make a more general point regarding the nature of language and mind. His analysis provides evidence for his view of language development as emerging from evolved psychological mechanisms.

The title of the book refers to how Pinker contends language is organized in human minds. He states that words in our "mental dictionaries" are sometimes stored as unique semantic entries, but that others are constructed using morphological rules. For instance, once a child learns the basic rules for creating plural forms of nouns or the past tense of a verb, they would not need to create new mental dictionary entries, so "horses" and "baked" would be created and stored as extensions of "horse" and "bake," respectively without the creation of unique semantic entries. However, this sometimes leads to mistakes when a word has an irregular pluralization (e.g., "deer" rather than "deers" and "geese" rather than "gooses") or irregular conjugation (e.g., "swam" rather than "swimmed" and "built" rather than "builded"). Pinker thinks that forms of irregular verbs must be memorized directly rather than automatically connected to their present tense forms.

The Blank Slate (2002)

In *The Blank Slate*, Pinker argues more broadly against the misconception that human beings are "blank slates" or tabula rasa that are born without any innate predispositions. This involves again referring to his findings and the findings of other psycholinguists demonstrating innate learning mechanisms for language acquisition.

The Stuff of Thought (2007)

In *The Stuff of Thought* (subtitled: *Language As a Window into Human Nature*), Pinker examines the ways in which our words and thoughts are associated both with each other and to our experience of the world around us and again utilizes language to explore human nature and innate predispositions.

One major focus in the book is Pinker's assertion of the two things that language must do: (1) communicate a message from speaker to audience and (2) establish, preserve, or negotiate the nature of the relationship between the speaker and the audience. Because of this, we often observe differences between the surface meaning of an expression and its deeper meaning. For instance, common expressions such as "If you could keep the music down, that would be great" function as requests even though no overt request (e.g., "Would you please keep the music down?") or demand (e.g., "Keep the damn music down.") is made. It also serves to avoid sending the message that the requester is in a position of authority over the other person as a direct demand would and is thus perceived as more polite. Pinker explains that on one hand, the requester does indeed want something, while on the other you do not want to be perceived as bossing other people around, so you end up uttering a sentence that sounds like a hypothetical musing or like complete nonsense, but it functions effectively as a request and as a social negotiation.

The Sense of Style

Pinker's seventh book, *The Sense of Style* (2014), is a guide to writing nonfiction with a style that is appropriate for producing maximum comprehension in general audiences. Using evidence from psychology and cognitive science, Pinker explains why much of today's popular science writing is difficult for readers to understand and offers his own advice for how to avoid such pitfalls.

Conclusion

Stephen Pinker's work on language development includes both compelling original research as well as perhaps the best examples of summarizing the nativist approach to language for a general audience. In addition, his work integrates nativist theories on language into broader examinations of evolutionary psychology.

Cross-References

- [How the Mind Works](#)
- [Pinker's \(1994\) The Language Instinct](#)

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Steven Pinker *How the Mind Works*

► [How the Mind Works](#)

Steven Pinker on Genetic Determinism

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Synonyms

[Biological determinism](#)

Definition

Genetic determinism is an emerging idea in the genetic field that suggests that there are genetic predictors for behavior traits.

Introduction

Experimental psychologist Steven Pinker volunteered to submit his DNA to kick off George Church's Personal Genome Project (P.G.P.). The P.G.P. sought to create an online database of 100,000 people's genomes and traits to allow global engagement of geneticists. Pinker explains that increased interest in globalizing genetics and making access greater is leading to a rise in consumer genetics. Consumer genetics refers to commercially available genetic testing that can explain who each person is via their own genetic code. These genetic kits can vary in depth of information and offer consumers data on their ancestry, traits, and disease risk (Pinker 2009).

Benefits

Personal genomics allows everyday people to access information about their disease risk and other health factors. This information could lead to a future of personalized medicine with regimens and drugs that are established based on a patient's individualized gene code and needs, thus reducing the need for trial and error testing or prevention screening. The information would also shift the healthcare debate in a direction toward national health insurance by changing the way we view preexisting conditions and how insurers cover them, along with how customers purchase insurance plans (Pinker 2009). Additionally, by being knowledgeable of genetic history, individuals can make informed choices regarding the risks of passing along hereditary diseases during reproduction.

Understanding one's genetics also allows for greater understanding of one's personality. Genetic makeup plays a huge role in understanding what shapes a person beyond their environment. The variations in human genes are inevitably what causes human behavioral traits, which explains why people who are biologically related are more similar than unrelated people. This can especially be seen in instances of biological versus adopted siblings. The intensity of this similarity can also be seen in identical twins compared to fraternal twins or siblings, where identical twins with identical genetic makeup are much more similar in personality than twins or siblings that share only related genetic makeup according to Pinker (2009). Furthermore, understanding the underlying genetic causes of personality will allow greater understanding of how environment affects personality in comparison (Pinker 2009).

Genetic Determinism of Psychological Traits

Neuroscience and genetic testing express the link between genetic makeup and psychological traits such as intelligence. Genetic predisposition for certain levels of intelligence can be seen when

comparing identical twins raised together or that were separated at birth (Pinker 2006). The possible explanation for why humans differ in intelligence is mutation-selection. Unlike personality, where different personality traits have different values in society, higher intelligence is universally valued. Intelligence is also made up of a wide network of brain areas, along with physical well-being and health, and thus is dependent on a wide variety of genes that can be affected by mutation. These mutations may, in turn, cause decreased levels of intelligence (Pinker 2009).

Genetic testing can be used to determine how dopamine receptors affect specific personality traits. Since dopamine is associated with wanting, satisfaction, and attention, the receptors evident in the gene code could adjust personality traits accordingly. While one form of the receptor could make a person novelty seeking and extraverted, a less effective version of the receptor would predispose a person for substance abuse and obesity due to impulsivity (Pinker 2009). Testing has further expanded to serotonin as well by looking at the genes in charge of SERT, the serotonin transporter, and its link to anxiety and depression. There are a variety of genes that match up with the lengths of the SERT in the human body, and the varying lengths are linked to how affectively the SERT work to transport serotonin (Pinker 2009). Pinker explains that knowing the genetic makeup of our personality leads to fear of determinism – that behaviors and traits will be blamed on genetics instead of holding actions and free will accountable. Furthermore, the fear that boiling human behavior down to just the gene code creates a sense of nihilism (Baer et al. 2008; Pinker 2006). Despite this, Pinker states that understanding the science of human nature only furthers our relation to the moral nature of human kind and expands the understanding of human individuality (Pinker 2006).

Pitfalls

Pinker discusses that the costs of personal genome testing are high, ranging from \$400 for 23andMe to \$99,500 for Knome (Pinker 2009). These initial high costs are due to the infancy of the technology,

and as it matures and becomes more popular, Pinker hypothesized that the prices would become much more accessible. The accessibility, however, lends itself to future political issues. George Bush signed the Genetic Information Nondiscrimination Act in 2008 in order to make job or health insurance discrimination due to genetic information illegal and several states are taking action against genetic companies saying they're overstepping by ordering tests only doctors can order (Pinker 2009). As accessibility increases, new abuses of genetic data will likely arise, and more political restrictions to prevent this will follow. Furthermore, there will likely be "paternalistic measures" to prevent genetic testing from gaining momentum, but Pinker believes people's desire to know this information will not allow the industry to remain stifled (Pinker 2009).

Conclusion

According to Steven Pinker, despite the potential financial and ethical drawbacks, genetic determinism offers endless future possibilities of global genetics and provides the opportunity for individuals to personally become active agents in their genetic potential (regarding reproduction and insurance/medication).

Cross-References

- Genetic Determinism
- Steven Pinker

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Steven Pinker on Language

- [Language Instinct, The](#)
- [Pinker's \(1994\) The Language Instinct](#)

Steven Pinker on Universal Grammar

- [Language Instinct, The](#)
- [Pinker's \(1994\) The Language Instinct](#)

Stick Tools for Foraging

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Synonyms

[Pounding tools](#); [Probing tools](#)

Definition

Use of sticks as probes or pounding tools to reach or process food items.

Introduction

Tool use is defined as the employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool (Shumaker et al. 2011). It was once seen as an exclusively and defining human trait, but is, in fact, widespread throughout the animal kingdom, and does not necessarily imply complex

cognition or learning, but can result from stereotyped, species-specific behaviors.

Sticks can be employed as tools by nonhuman animals, from insects to primates, in a variety of contexts, and from play and exploratory behavior to bodily care, as weapons or as props in communicative displays.

The use of sticks in foraging contexts is present in the behavioral repertoire of avian and primate species, but has been, more rarely, observed in other animal taxa, such as crocodilian reptiles (which use sticks as lures to attract avian prey). Sticks can be used to manipulate prey or to dislodge it from nests, tree holes, or rock crevices.

Probe Tool Use in Birds

Woodpecker finches (*Cactospiza pallida*) inhabiting the drier vegetation zones in the coasts of the Galapagos Islands use modified twigs or cactus spines as probes to pry arthropods out of tree holes (in humid areas, where food is more abundant and seasonally more predictable, they rarely use tools; Tebbich et al. 2002).

The most renowned probe-tool-using birds, though, are corvid species, most notably, the New Caledonian crows (*Corvus moneduloides*), from New Zealand. In the wild, they extract beetle larvae from wood using probes with “hooked” ends made (by trimming and sculpting) from sticks or leaf stems or with the aid of “stepped tools” made from the leaves of *Pandanus*, cut in tapering shapes, with the leaves’ barbs used as hooks (Hunt and Gray 2003).

The role of social learning in bird tool use is still unclear. In the case of woodpecker finches, experiments showed that this behavior depends on very specific learning dispositions, involving trial-and-error learning during an early sensitive phase. Though field studies with New Caledonian crows suggest some culturally based local variation, experimental laboratory studies with hand-reared juvenile crows, without discarding individual and cultural transmission, point to a greater role of inherited species-typical action patterns (Kenward et al. 2006).

Probe Use in Nonhuman Primates

Although captive primates may exhibit sophisticated object manipulation (spontaneously or in experimental settings), such as combining sticks to get out-of-reach food (as the chimpanzees in Koehler classic experiment), the spontaneous and *customary* (shown by most or all relevant individuals) or *habitual* (shown by at least several relevant individuals) use of tools by wild primate populations seems restricted to a few species, its discontinuous occurrence apparently reflecting convergent evolution (due to a conjunction of social, cognitive, and ecological conditions), rather than phylogenetic proximity. Nonhuman primates' lithic tools do not typically involve the modification of raw materials; probe tools, on the other hand, are frequently manufactured – sticks being modified by the trimming of side branches and leaves, by peeling the bark, and/or by shaping the points. The customary use of sticks as probing or pounding tools for foraging has been observed in some populations of apes (chimpanzees and orangutans) and New World monkeys (bearded capuchin monkeys).

Probe Tool Use in Bearded Capuchin Monkeys

The use of lithic tools is widespread among savanna populations of tufted capuchin monkeys (*Sapajus* spp.). The customary use of stick probes, though, has so far been only observed in the population of bearded capuchins (*S. libidinosus*) inhabiting the Serra da Capivara National Park, in northeastern Brazil (although there are a couple of anecdotal reports from other sites). These sticks are used to probe for water, or insects in their nests, to poke dangerous animals, or to dislodge small vertebrate prey from rock crevices. Probing tools usually undergo some modification steps (peeling, trimming of side branches and leaves) and may occasionally be used in association with stone tools. For reasons yet unclear, there is a strong gender bias, probe use being an almost exclusively male activity in this population (Falótico and Ottoni 2014).

Probe Tool Use in Orangutans

Wild orangutan populations in a few swamp sites, such as Suaq Balimbing in Sumatra (*Pongo*

abelii) and Gunung Palung in Borneo (*Pongo pygmaeus*), exhibit customary use of stick tools to extract honey from bee nests or (in some Sumatran populations only, absent in Borneo) to open *Neesia* fruits and remove irritating hairy material. Though orangutans are usually very dexterous in captive or semi-free (rehabilitation) conditions, probe tool use is only observed, in the wild, in atypically gregarious and tolerant social contexts, which strongly argues for its socially biased learning and, therefore, its traditional nature: van Schaik and colleagues (2003) believe that neither genetics nor ecology suffice to explain the distribution of tool use in wild orangutans.

Probe and Pounding Stick Tools Use in Chimpanzees

Leaf petioles are used by Bossou chimpanzees in the extraction of oil palm shoots' material by "pestle pounding," and sticks are used to break termite nests and beehives, to access the insects or honey, by many populations.

The use of stick tools in termite and driver ant fishing is customary in many chimpanzee populations in eastern Africa. Termite fishing frequently involves the associative use of two sticks, one to perforate the termite nests' walls (thicker, blunt ended) and another thinner one (with a brush-shaped tip) for fishing the insects. It has been reported in more than 20 populations, including Bossou, Gombe, Fongoli, and Mahale K and B communities (but it is absent in the Mahale M community and is not habitual in Bossou).

Driver ant (*Dorylus* spp.) "dippers" usually employ a "pull-through" technique (gathering the ants from the stick with a hand; Gombe, Bossou) or "direct mouthing" (taking the ant-laden stick directly to the mouth; Taï, Bossou). Carpenter ants (*Camponotus* spp.) "fishing" in trees was first observed in Mahale, then appeared as an innovation in Gombe.

Chimpanzees from Fongoli (Senegal) use sticks as spears to hunt vertebrate prey such as bushbabies (*Galago senegalensis*). Sticks and twigs are also used to probe honeybee nests, to extract water from holes, and the marrow from *Colobus* monkeys' bones.

Conclusion

To examine the potentially cultural nature of behavioral variation between chimpanzee populations, Whiten et al. (1999) compared the repertoires of seven long-term field studies, trying to sort out variation explainable by genetic differences or by particular environmental pressures or affordances (including the availability of the necessary materials). Interpopulation differences in 39 behavioral patterns (including tool use for food acquisition and processing) seemed not due to genetics or ecology and were thus considered as cultural variations. This comparative method can be useful for the detection of potential cultural traits, but, by itself, can be prone to “false positives” (and “false negatives”); therefore, supplementary developmental (and experimental) studies focusing the role of socially biased learning are necessary. One example is the above-mentioned regional variation in use of sticks to gather driver ants. It was initially considered an evidence of cultural variation; subsequent observations suggested that those different techniques could be explained by differences in the behavior of the distinct ant species available in each site. Further investigation pointed to a more complex scenario, involving both environmental causes (ant behavior) and socially learned components (Schöning et al. 2008).

The different approaches by chimpanzees from populations with different toolkits, when facing a probe-related experimental task (Gruber et al. 2009), also suggest a cultural bias in their problem-solving abilities: only the group exhibiting customary probe use solved the task. In a similar study, Serra da Capivara capuchin monkeys readily solved a probe-using task, while monkeys from a non-probe-using population (Fazenda Boa Vista), 350 km away, did not (Cardoso and Ottoni 2016).

Though there is plenty of evidence of social biases in individual learning (usually involving the curiosity of youngsters and the tolerance of adults), reports on the occurrence of some form “teaching” among nonhuman primates are virtually nonexistent. Christophe Boesch reported the observation of a chimpanzee mother from the Tâi

Forest (Ivory Coast) correcting their infants’ handling of wooden hammer tools. In the case of termite fishing, a gender bias in the performance of young chimpanzees suggests an effect of the close observation of their mothers’ behavior (females spend more time with the mothers than males and become proficient probers at younger ages), and a recent study has conveyed evidence of “functional teaching” (or “scaffolding”), with mothers donating probes to their infants (Musgrave et al. 2016).

Cross-References

- ▶ [Bird Tool Use](#)
- ▶ [Fish, Amphibian, and Reptile Tool Use](#)
- ▶ [Innate and Learned Tool Use](#)
- ▶ [Nonhuman Tool Use](#)
- ▶ [Primate Tool Use](#)
- ▶ [Sequential Tool Use](#)
- ▶ [Social Learning](#)
- ▶ [Tool Manufacturing](#)
- ▶ [Tool Use](#)

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Stigma

- [Facial Disfigurement](#)
- [Out-Group Members](#)

Stigmatization and Ostracism

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Definition

Stigmatism refers to any characteristic that causes people to be labeled as undesirable. People often ignore, exclude, or ostracize those who are stigmatized.

Introduction

Humans have a need to belong. Our communities provide us the emotional support we need to thrive. But sometimes an individual or community decides to ostracize someone.

From an evolutionary perspective, it is adaptive to avoid people who seem sickly because

they could spread a harmful disease (Kurzban and Leary 2001). Others can threaten our general well-being, such as free riders (Trivers 1971). Finally, to survive and thrive, it aids an advantaged group to keep resources to themselves – it is often not to their direct benefit to share their goods with a less advantaged outgroup (Sidanius 1993).

Disease-ridden cheaters are not the only people we ostracize. Looks alone can lead to stigmatization and ostracism. Obese people face stigma because many perceive them as lazy (Hebl and Heatherton 1998). Sometimes people automatically judge stigmatized people (Smart Richman and Leary 2009). Racial stereotypes can lead to ostracism because one group seeks to keep a social advantage within their own group (Lareau and Horvat 1999).

Getting left out hurts (Leary and Springer 2001). The pain of ostracism can cause people to act out in ways that are maladaptive. Anger is a common response to social rejection, even though it does not help repair social bonds (Leary et al. 2006). Lashing out at those who ostracize us might be adaptive in our evolutionary past, but vengeful outbursts are maladaptive in modern times (Smart Richman and Leary 2009). Likewise, withdrawing further from the social group may give a person time to nurse wounds, but it hardly repairs the social bond (Vangelisti et al. 2005).

Conclusion

Humans have fundamental motivations to be liked and included. Stigma and ostracism threaten these motivations. Undesirable or dissimilar traits can encourage us to favor our own group members and ostracize others. By understanding stigmatization and ostracism, psychologists can understand how to promote acceptance and inclusion.

Cross-References

- [Adaptations to Avoid Ostracism](#)
- [Avoiding Stigmatization](#)

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Stimulation of Partner's Genitalia and Having Partner Stimulate Genitalia

► Sexual Behavior

Stimulus Generalization and Discrimination

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Definition

Stimulus generalization refers to a set of stimuli sharing similar properties with the original stimulus

that provoked a response. *Stimulus discrimination* is the ability of an organism to respond only to the original stimulus, and not to other similar stimuli.

Introduction

The concepts of stimulus generalization and stimulus discrimination are encountered within the context of associative and non-associative learning.

Differentiation of Stimulus Generalization and Stimulus Discrimination Concepts

Both concepts are inherent mechanisms in the processes of associative and non-associative learning, and for both processes to take place, it is essential that a stimulus model should be stored in memory in order for comparisons with new stimuli to take place.

To begin with, generalization occurs when an organism produces the same response to different stimuli. Stimuli who exhibit analogous properties to the original are more likely to provoke a response: habituation. There could be variations in terms of the level of pitch, brightness, loudness, and so on; however, if these variations deviate significantly from the properties of the original stimulus, generalization will not occur; hence, it is more likely that habituation will not occur either Teyler, Chiaia, DiScenna, Roemer (1984). Stimulus generalization of habituation can only be determined when a second habituation series is done with the use of a novel stimulus. With a comparison of the rates of habituation between the original and the novel stimulus, the amount of generalization will be demonstrated. More rapid habituation in the second series would be indicative of generalization whereas similar rates between the two series would be indicative of a lack of generalization Petrinovich and Widaman (1984).

On the other hand, if stimuli are rather dissimilar than similar, the opposite process of stimulus generalization, the so-called *stimulus discrimination* will be activated. In *stimulus discrimination*, the organism shows the ability to differentiate

between similar stimuli and only to respond to a specific stimulus, hence the organism responds differently to the two stimuli. *Stimulus discrimination* is particularly important in the process of habituation, as it can be used to dismiss sensory adaptation and fatigue as an alternative explanation of the occurrence of habituation. Further, *dishabituation* is indicative of the ability to discriminate, therefore ending habituation Thompson and Spencer (1966). It is important to clarify, however, that dishabituation occurs due to repetitive stimulation of a completely irrelevant stimulus and should not be thought of as the same as stimulus discrimination. Finally, stimulus generalization is useful because it allows for learning to take place quickly in new situations that share similarities with past experiences and promotes the transfer of skills into similar situations thus saving time and effort. Stimulus discrimination offers assistance in a practical level as well.

There are well-known experiments undergone within the concept of conditioning (Pavlov's and Watson's experiments) that illustrate the stimulus generalization and the stimulus discrimination concepts more elaborately.

Conclusion

Stimulus generalization and discrimination are crucial processes in learning and both are of paramount importance to adaptation. Clearly, any organism that lacks such abilities would have minimal chances of survival.

Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Habituation](#)
- [Little Albert](#)
- [Non-associative Learning](#)

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Stochastic Environment

- [Environmental Unpredictability](#)

Stochastic Phenotype Switching

- [Environmental Unpredictability and Betting](#)

Stone Hammers

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Synonyms

“Hammer” and “anvil” stones; Percussive lithic tools

Definition

Use of stones as percussive tools.

Introduction

Tool use, per Beck's definition (Shumaker et al. 2011), is the employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or

condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.

Once conceived as an exclusively and defining human trait, the use of tools is, in fact, widespread in the animal kingdom, from *Ariadna* spiders, which use tiny quartz pebbles as web enhancements, to the complex and variable toolkits of a few primate species in the wild. Therefore, tool use does not necessarily imply complex cognition or social learning and can result from stereotyped, species-specific behaviors. Though spontaneous tool use in the wild is usually associated with foraging activities, tools may be employed in a variety of contexts, such as exploration, bodily care, play, aggression, or communication.

There is at least one report of “hammer” stones used by an insect: digger wasps (*Ammophila* and *Sphex*) hammer the closure of their egg-filled burrows with small pebbles. Among vertebrates, the use of lithic tools has been observed in bird and mammal species, which may employ them in a variety of ways, from dropping on aggression targets to using them as “hammers,” “hoes,” “blades,” or “projectiles.”

Use of Stone Hammers in Birds

Egyptian vultures (*Neophron percnopterus*) may kill lizards or break ostrich eggs to consume their contents, using stones they raise in their beaks. There are reports of American crows using rocks (held in their talons) to hammer acorns and of a captive bald eagle doing the same to predate crickets and scorpions.

Use of (Passive) Stone “Hammers” in a Non-primate Mammal

Among non-primate mammals, there is at least one, well-known case of percussive stone tool use: sea otters (*Enhydra lutris*) crack mollusk shells by hammering them with their hands against “anvil” stones resting on their chests. This is a very flexible behavior, with great

individual and intergroup variation – much of which seems to be explained by the type of prey consumed. There seems to be also a strong innate predisposition to use tools, since captive sea otters’ pups exhibited this behavior without previous experience. On the other hand, there is evidence of matrilineal transmission of food preferences, which, along with the observation of other skilled individuals, might facilitate the social transmission of this behavioral pattern (Fujii et al. 2015).

Use of Stone Hammers in Nonhuman Primates

The spontaneous and *customary* (shown by most or all relevant individuals) or *habitual* (shown by at least several relevant individuals) use of lithic tools by wild nonhuman primates seems to reflect convergent evolution rather than phylogenetic proximity, being apparently restricted to populations of a few species: chimpanzees, tufted capuchin monkeys, and long-tailed macaques. The known cases of wild nonhuman primates’ stone tool use do not involve *manufacture* (modification of raw materials). *Secondary* tools (tools produced with the use of other tools), though, have been observed, as well as the *associative use* (of more than one tool combined in the same task), in the *tool sets* of stone “hammers” and “anvils” or in the combined use of stone “hammers” and stick probes in a single task.

Tufted Capuchin Monkeys (*Sapajus* sp.)

The use of stones as “hammers” by tufted capuchin monkeys (to crack open palm nuts) was initially studied in semi-free-ranging groups in Brazilian urban parks. Although tool use (lithic or otherwise) seems virtually absent in forest populations, surveys of wild groups in central-western Brazil have shown that, for savannah populations, the use of tools to crack open hard food is rather the rule than the exception, stone “hammers” being associated with stone or wooden “anvils.” The degree of terrestriality – rather than food scarcity – is, apparently, a stronger predictor of the use of stone “hammers” to process defended food in present populations – although

the evolutionary history of tufted capuchin monkeys, occupying savannah environments in times of intense climatic change, suggests a role for hard-shelled fruit as fallback food in the past. The first direct and systematic observations of stone-aided encapsulated food processing in the wild were done with two populations of bearded capuchin monkeys (*Sapajus libidinosus*) in the state of Piauí (northeastern Brazil), in Fazenda Boa Vista, and in Serra da Capivara National Park (Otoni and Izar 2008). In Serra da Capivara, the monkeys exhibit an atypically complex toolkit (including stones and sticks); stone tools are employed not only for cracking nuts but also for digging roots and arthropods' nests and, in one group, as part of females' estrus display (Falótico and Otoni 2016). The broader distribution of stone tool use (as compared to the use of stick probes) among capuchin monkeys' populations may be due to the lasting remains of nut-cracking activity (the "nut-cracking sites"), which enhance the opportunities for delayed socially biased learning, by "local enhancement."

Long-Tailed Macaques (*Macaca Fascicularis*)

Most reports of tool use by Old World monkeys refer to cercopithecines. Small stones are handled in play situations by some populations of Japanese monkeys (*Macaca fuscata*). There are anecdotal reports of the use of stones by macaques and baboons to smash scorpions and about captives using percussive tools in a variety of ways.

The only Old World species where customary use of stone tools has been observed in the wild, though, are long-tailed macaques. The Burmese subspecies (*M. fascicularis aurea*) employ stones to detach or break oysters, gastropods, crabs, and fruit. They transport stones of up to 2 kg and use them as "hammers" to smash open food or as "axes" to extract shellfish from beach rocks – selecting the proper shape according to the usage (Gumert et al. 2009).

Chimpanzees (*Pan Troglodytes*) and Other Apes

Tool-aided problem solving by captive chimpanzees has been extensively observed in a variety of contexts, experimental or not, since Koehler and

Yerkes studies in the 1920s. Orangutans, gorillas, and bonobos, too, frequently exhibit the use of percussive tools in captivity (or rehabilitation) conditions. Kanzi, a symbol-language-proficient bonobo, even produced blades by flaking stones. The customary use of stone tools by apes in the wild, though, seems restricted to chimpanzees.

Wild chimpanzees modify and use as tools a wide range of objects, mostly in foraging, but also in communicative, bodily care, or other contexts. Tool-aided nut cracking had already been reported in the nineteenth century, but the first long-term field studies in the 1960s revealed not only the complexity of their social life but also their technical skills – and a lot of interpopulation variation (McGrew 1992). The customary use of stone or wooden "hammers" for nut cracking is common in West Africa (Guinea, Ivory Coast, Liberia, and Sierra Leone), though techniques and materials vary, but is virtually absent in Central and East Africa – even where nuts and stones are also available. In the Taï forest (and other sites), wooden or stone "hammers" are usually employed to crack *Coula* nuts. For the harder *Panda* nuts, stone "hammers" are the preferred choice. Diécké chimpanzees and other populations crack these nuts with stone hammers and stone or wooden "anvils." In Bossou, where nut-cracking behavior is studied in a "field laboratory," chimpanzees crack softer palm nuts with smaller stone tools. They may employ different techniques to level the "anvil" stones, turning or repositioning them (Matsuzawa et al. 2011).

Conclusion

The study of tool use in wild nonhuman primates has had a central role in the development of "cultural primatology," since interpopulation variation is not usually explained away by genetic differences or environmental constraints and affordances. The "comparative approach" (Whiten et al. 1999) cannot, by itself, establish the "cultural" nature of nonhuman primates' tool use but has paved the way to further longitudinal and experimental studies that examined the role of socially biased learning in the individual

acquisition of local behavioral variants, thus supporting the characterization of tool use repertoires as behavioral traditions.

Furthermore, since the use of lithic tools leaves lasting remains, archeological techniques can be applied in the search of ancient evidence of non-human primates' technology. Archeological evidence has already shown that Tāi chimpanzees have been using stones as “hammers” and “anvils” for nut cracking for at least 4,300 years (Mercader et al. 2007) – and that bearded capuchin monkeys have been using stone “hammers” to process cashew nuts for at least 700 years (Haslam et al. 2016).

Cross-References

- ▶ [Bird Tool Use](#)
- ▶ [Fish, Amphibian, and Reptile Tool Use](#)
- ▶ [Innate and Learned Tool Use](#)
- ▶ [Nonhuman Tool Use](#)
- ▶ [Primate Tool Use](#)
- ▶ [Sequential Tool Use](#)
- ▶ [Tool Use](#)
- ▶ [Tool Manufacturing](#)

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Stopping Early Hypothesis

- ▶ [Grandmother Hypothesis of Menopause](#)

Stopping-Early Hypothesis

- ▶ [Grandmother Hypothesis, The](#)

Story

- ▶ [Human Storytelling](#)

Storyteller

- ▶ [Human Storytelling](#)

Storytelling

- ▶ [Fiction](#)
- ▶ [Narrative](#)

Strain Theory

- ▶ [Sociocultural Theories of Violence](#)

Stranger Anxiety

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Synonyms

Anxiety of strangers; Fear of strangers

Definition

Anxiety response on encounter with strangers during early infancy and childhood.

Introduction

Human being is a social animal. Human interact with its environment in an intricate manner. The part of the environment that is repeatedly and consistently exposed to the individual becomes familiar over a period of time and the part of the environment that is never to rarely exposed remains unfamiliar to the individual. When it comes to human interaction, classically the unfamiliar persons were recognized as strangers. However, an individual may not interact with all the individuals with whom, he/she is repeatedly exposed; these individuals were called as familiar strangers (Agnel 1999; Paulos and Goodman 2004).

When anxiety is discussed from the developmental perspectives of an individual, anxiety to specific environmental stimuli or environmental change develops during the late part of the first year of life (Scher and Harel 2008). The specific environmental stimuli or environmental changes are exposure to a stranger (stranger anxiety) or being separated from an attachment figure like parents or caregivers (separation anxiety).

Evidences suggest that maternal depression can attribute to the development of stranger

anxiety in the child (Gartstein et al. 2010). The children, who develop anxiety with strangers, are often seen to have internalizing response. They often experience anxiety and guilt, avoid situations, and remain withdrawn to self (Baker et al. 2012). Various factors (temperament of the baby, nature of mother-baby attachment, gender of the stranger, context of exposure with the stranger, as well as availability of any attachment figure) play pivotal role in development of stranger anxiety in an infant (Tsola and Anastassiou-Hadjicharalambous 2011).

Evolution of Stranger Anxiety

The stranger anxiety has been found to have an ontogenic adaptation, i.e., the development of stranger anxiety during the origin of human species. Since ancient times males of different cultures have been found to deliberately kill out-group infants. The out-group male infants were killed to reduce the potential out-group male competitors and female infants were killed to reduce the possible reproductive resource for out-group males and their kin. It has also been observed that during those times more of male infants were killed as compared to the female infants. A tribe of Brazil have been found to kill boys more so as to reduce the warrior population of out-group tribe (Chagnon 1983). It has also been observed that langurs, a primate species, tend to target more of out-group male infants as compared to female infants (Hamai et al. 1992). Thus, the individuals are predisposed to have fear of strangers as this helps in protecting them from the stranger violence that was present in the ancient times.

Anxiety to strangers also has a protective role from the evolutionary perspective. Anxiety is an alarming response to the individual to get aware of the unknown (stranger), who may possess threat. So, stranger anxiety enables an individual to combat threat from stranger. Similarly, during the course of cognitive development, social cognition and abstract reasoning develops late during the childhood; infants and toddlers are deficit in these cognitive functions. Deficits in social cognition and abstract reasoning might result in

development of stranger anxiety. An infant or child with concrete thinking may perceive an unknown individual in more threatening way and due to deficits of social cognition may not be able to anticipate and predict the reality.

This stranger anxiety has been found to reduce as the infant grows because of two reasons: habituation and executive inhibition (Hahn-Holbrook et al. 2010). As children grow, they tend to come in contact with many strangers. Parents help the infant in socializing with strangers. Thus, as the child gets exposed to various strangers, the fear of strangers reduces. Executive inhibition has been found to be inversely related to stranger anxiety. It develops during the 10–12 months when stranger anxiety generally reduces (Diamond 2006).

Implications of Stranger Anxiety

Evidences suggest that early life (infancy) stranger anxiety can be a predictors of development of separation anxiety disorder in children (Lavallee et al. 2011). Stranger anxiety explains a failure in communication process with a stranger. The anxiety responses are often inhibited during effective communications with strangers (Duronto et al. 2005). Stranger anxiety also predicts the avoidance behavior during communication. Extreme degree of fear to stranger also predicts about future risk of development of separation anxiety disorder (Brooker et al. 2013).

Evidences suggest Respiratory Sinus Arrhythmia (RSA) has association with fear and anxiety experience in young children. Successful regulation of anxiety and fear during interaction with stranger results in suppression of RSA (Brooker et al. 2013).

Conclusion

Stranger anxiety is an important mental phenomenon in early age, which has developmental significance. Persistence of stranger anxiety and more severe form of stranger anxiety may be considered as abnormal, which may predict the future risk of development of anxiety disorders.

Cross-References

► Anxiety of Strangers

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Stranger Sex

► Casual Sex

Strategic Aggression

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Synonyms

Calculated; Evolutionary aggression; Hostility; Organized; Planned; Proactive aggression; Tactical; Violence

Definition

Strategic aggression is an organized set of tactical and calculated sequences of actions that may increase the probability of enhanced evolutionary fitness and reproductive success.

Introduction

Historically, aggressive tendencies have been a fundamental characteristic among mammals. Strategic aggression specifically is an adaptive trait leading to an increased chance of reproduction and survival of the fittest. In humans, functional strategic aggression was used by hunter gatherer tribes for acquiring resources and improving social standing (Hawley et al. 2013).

Aggressive behavior functions as a set of evolved responses to frequent evolutionary problems such as fending off danger and actively competing for resources (Archer 2001).

Strategic aggression, synonymously known as proactive aggression, is conducive to predatory behavior because it does not show overt signs of threat. The adaptive benefits of strategic aggression are distinguishable from reactive aggression in that reactive aggression is associated with high physiological arousal including verbal (i.e., threats) and non-verbal (i.e., body language/posturing) communication of intent and utilizes immediate ways to protect one's own well-being. By contrast, proactive aggression is characterized by low physiological arousal, a lack of social communication, and targeting of vulnerable body parts. Proactive aggression applies specific strategies in order to obtain valuable resources in a tactical manner (Wrangham 2017).

Sex Differences

From an evolutionary perspective, strategic aggression was demonstrated through both cooperative and competitive means. In this aspect, males experienced more adaptive benefits than females from planned aggressive behavior. Males in nomadic tribes of hominids and early humans had to compete with one another for access to mates and valuable resources that bolstered their likelihood of survival and reproductive success (Klasios 2019). Additionally, it was the physically larger males who were responsible for most of the hunting to acquire meat for the tribe. Hunting was often a cooperative effort, especially when targeting larger animals such as mammoths or buffalo (Sheets-Johnstone 1986). Thus, males with greater ability to successfully plan both kinds of aggressive acts experienced increased fitness and improved their probability of passing on genes rich with strategic aggressive behavior.

The human history of adaptive strategic aggression in males resulted in lasting sex differences that remain today across cultures. For instance, males commit the vast majority of all

homicides (87%) and are also the majority of homicide victims (75%) globally (Duntley and Buss 2011). This suggests a large prevalence of male-on-male violence likely stemming from many of the same evolutionary problems: competition for mating opportunities and favorable resources.

Then and Now

From an evolutionary perspective, the advancement of survival and reproductive success through strategic aggressive means (i.e., hunting and interpersonal skills) became an adaptive quality that promoted evolutionary fitness via ancestral selection pressures. The current implications involving strategic aggression are still influenced by survival of the fittest; however, the emphasis now is placed on more covert acts on aggression rather than directly hurting others. Certain types of violence were adaptive in ancestral conditions that now negatively impact individuals (Klasios 2019). Whereas simply harming a rival could have solved an evolutionary conundrum in previous generations, the consequences of committing a similar act today often result in unfavorable outcomes that decrease fitness. For example, the development of preventative regulations and law enforcement has expanded the evolutionary costs of violent behavior. The present-day consequences of these acts often include incarceration or fines, both of which reduce resources and mating opportunities. While there are still instances today in which acts of direct planned violence may avoid evolutionary costs and serve as adaptive behaviors, covert forms of strategic aggression have also evolved over time with the purpose of avoiding the newer maladaptive costs now associated with violent actions.

Conclusion

In conclusion, strategic aggression represents calculated aggressive tactics individuals use while interacting with others (Archer 2001). These tactics include forcibly acquiring adaptive resources and

involve elements of competition as a way of advancing oneself in an organizational setting. If perceived challenges arise toward a potential rival, hostile strategies may enhance the likelihood of success. While the specific strategies incorporating hostile behavior to obtain a desired goal have changed over time, the evolutionary mechanisms underlying proactive aggression remain intact.

Cross-References

- [Aggression](#)
- [Costs of Aggression](#)
- [Development of Aggression](#)
- [Homicide by Design](#)
- [Indirect Aggression](#)
- [Relational Aggression](#)
- [Social Aggression](#)
- [Variability of Aggression](#)

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Strategic Ejaculate Investment

- [Male Prudence and Sperm Limits](#)

Strategic Ejaculation

- [Sperm Competition Theory](#)

Strategic Interference

- [Sexual Conflict in Mating Strategies](#)
- [Violation of Short-Term Mating Preferences](#)

Strategic Pluralism Theory

- [Mating Strategies](#)

Strategies

- [Procedures for Dealing with Bullies](#)

Strategies for Navigating Social Rank Hierarchies

- [Adaptations for Navigating Social Hierarchies](#)

Strategies for Successful Cooperation

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Synonyms

[Core design principles](#); [Evolution of cooperation](#)

Definition

Strategies for successful cooperation are the mechanisms by which cooperation, the act of

engaging in a behavior which benefits another, is able to evolve and persist.

Introduction

Cooperation, the act of bestowing a benefit upon another, encompasses both mutually beneficial and altruistic behaviors (West et al. 2011, 2007a, b). The evolution of cooperation in a world characterized by competition over scarce resources is generally regarded as puzzling (Ben-Ner and Putterman 2000; Lewis and Dumbrell 2013; Nowak 2006; Rand and Nowak 2013; West et al. 2011), yet cooperative behaviors are frequently observed across human and nonhuman species (Jaeggi et al. 2010; Phillips and Dykhuizen 2015; West et al. 2007a). Cooperation evolved and has been maintained through mechanisms which trigger the behavior under conditions which, on average, foster a positive net benefit. Strategies for successful cooperation should, and do, make best use of evolved mechanisms and predispositions to increase the prevalence of cooperation in modern human societies.

Defining Cooperation

A proper discussion of cooperation requires first a clear definition. Although many authors speak of cooperation as either distinct from or interchangeable with altruism (Barclay 2013; Jaeggi et al. 2010; Phillips and Dykhuizen 2015) or adopt that cooperation is universally costly to the cooperator (Lewis and Dumbrell 2013; Nowak 2006; Rand and Nowak 2013), still others define altruism and mutually beneficial behavior as subsets of cooperation (West et al. 2011, 2007a, b). It is the latter definition that is used herein. Under this definition, a cooperative behavior is simply any act that provides benefit to another. Mutually beneficial cooperation is advantageous to both actor and recipient, while altruistic cooperation aids the recipient at net cost to the cooperator. Cooperation is typically characterized as, at best, neutral for the cooperator because natural selection works on relative, rather than absolute, fitness. Any single

cooperative behavior is generally observed to advantage the recipient in excess of the actor. Yet, despite the implied fitness disadvantage, cooperation is frequently witnessed across human and nonhuman species (Phillips and Dykhuizen 2015; West et al. 2007a). The challenge, then, is to explain why and how natural selection might favor cooperation or individuals might consciously resolve to engage in cooperative behavior.

Adaptive Problems and the Evolution of Cooperation

Like any fitness-relevant trait, cooperation evolved as a solution to adaptive problems, problems which generations of humans had to overcome to reproduce and survive (Cosmides and Tooby 1994). Evolutionary theory asserts that the propensity to exhibit a trait or behavior must only improve fitness *on average*, not at every instance in which it is employed (West et al. 2011). Thus, the simplest, yet not quite satisfying, answer to the riddle of cooperation is that cooperation provided a fitness advantage over noncooperation, on average, in the ancestral environment, given the recurrent problems posed by environmental characteristics.

Humans are widely believed to have evolved in small groups (Ben-Ner and Putterman 2000; Cosmides and Tooby 1994; Gowdy and Krall 2016; Phillips and Dykhuizen 2015; Richerson et al. 2016; West et al. 2007b). Our modern social behaviors are a function of that evolutionary history, regardless of any contrasts between the adaptive problems presented by life within small groups and those presented by the current environment (Cosmides and Tooby 2013; Henrich et al. 2010; Phillips and Dykhuizen 2015). Although it is not possible to precisely identify the adaptive problems encountered by our ancestors, the class of problems can be surmised to be those for which cooperation was a potential solution.

The abovementioned mystery of the evolution of cooperation is only interesting and relevant if the ancestral environment could not support unconditional cooperation. Although it is generally agreed that unconditional cooperation is

likely, if not destined, to fail (Cosmides and Tooby 2013; Nowak 2006), unconditional cooperation could evolve and persist given a particularly harsh environment. The interdependence hypothesis (Tomasello et al. 2012) puts forth that collaboration was necessary for survival in harsh ancestral environments. Agent-based models of cooperation have confirmed that interdependence, modeled as a large cost of not finding a cooperative partner, can allow for the evolution and persistence of cooperation (Smaldino et al. 2013). Interdependence is also modeled in games such as the “stag hunt,” an evolutionary game of coordination (Lewis and Dumbrell 2013), in which players can either hunt alone or together. In a particularly harsh environment, payoffs in this game would make hunting alone a poor choice.

The mechanisms that encourage cooperative behavior at present may well be different from those mechanisms which allowed for cooperation to evolve within the ancestral environment (Burkart et al. 2014). More often than not, and especially in modern society, the fitness advantage provided by cooperation is vulnerable to noncooperative strategies capable of taking a “free ride” on the cooperation of others. Given these vulnerabilities, the characteristics of our human ancestors, and the adaptive problems posed by their environment, particular mechanisms were differentially successful at maintaining cooperative behavior (Jaeggi et al. 2010; West et al. 2011) because they signaled the need to use cooperation judiciously.

The formulation of strategies for successful cooperation in modern society is aided by addressing two questions: (i) in the absence of an environment capable of producing sufficient interdependence such that unconditional cooperation is the norm, what are the solutions or mechanisms that have developed to allow cooperative behavior to persist despite the existence of noncooperative strategies in the population? and (ii) how can this knowledge be used to manipulate a situation for the purpose of increasing the probability of cooperation? This paper provides a brief overview of answers to both questions. First, proximate mechanisms widely acknowledged to support the evolution of cooperation are reviewed.

Next, connections between these mechanisms and Elinor Ostrom's core design principles (Ostrom 1990; Wilson et al. 2013) are explored. The paper concludes with suggestions for creating successful strategies for cooperation which build upon both the proximate mechanisms for the evolution of unconditional and conditional cooperation and Ostrom's work.

Proximate Mechanisms for the Evolution of Cooperation

The decision to cooperate, to benefit a recipient, sometimes at cost to oneself, can be deliberative or automatic. Although deliberative acts likely involve a conscious weighing of benefits and costs, automatic or instinctive, cooperation does not require conscious decision-making (Bear and Rand 2016; Lotito et al. 2013). Rather, the propensity to produce a cooperative behavior is at least partially the result of benefit-cost analyses performed by natural selection on an evolutionary time scale. Just as in any benefit-cost analysis there is not likely to be one single cost or benefit that drives the direction of the net benefit of a proposal, there is no reason to believe that there is one particular mechanism solely responsible for the evolution of cooperation. The following discusses a number of popular mechanisms cited as contributing to the evolution and maintenance of cooperation, starting with an explanation of each of the "five rules" (Nowak 2006).

The Five Rules

Five mechanisms are widely acknowledged to allow natural selection to produce cooperation in environments in which both cooperation and non-cooperation exist as strategies: direct reciprocity, indirect reciprocity, spatial selection, multilevel selection, and kin selection (Nowak 2006, 2012; Rand and Nowak 2013). Although Nowak and his colleagues are credited with the synthesis of these mechanisms, each mechanism is widely studied by numerous other researchers. Of note is that some scholars see little difference in the underlying structure of these mechanisms (Fletcher and Zwick 2006; Nee 1989; West et al. 2007a). The unifying rationale for the success of each of the five mechanisms is that the expected benefits of

the act outweigh the costs whenever there is a high probability of being a recipient of a similar benefit in the future, whether directly from the initial recipient or through network or group channels.

Kin selection as formalized by Hamilton (1964) states that cooperation can evolve through natural selection given that the relatedness between the actor and the recipient is greater than the cost-to-benefit ratio, where the cost is borne by the actor and the benefit is received by the recipient. Also referred to as inclusive fitness, kin selection is useful in explaining cooperative behavior amongst genetic (or cultural) relatives, assuming that kin discrimination is possible.

But, an adequate theory of cooperation must also explain the high degree to which humans cooperate with non-kin. Direct reciprocity, or reciprocal altruism (a name notably inconsistent with the definition of altruism expressed here), encourages the evolution of cooperation between non-kin in that individuals are more likely to cooperate with those who have cooperated with them in the past (Axelrod and Hamilton 1981; Nowak 2006, 2012; Trivers 1971; West et al. 2011, 2007a). Specifically, direct reciprocity can evolve when the cost-benefit ratio of the act is less than the probability of future interaction between the two individuals (Nowak 2006). Direct reciprocity is consistent with evidence that individuals demonstrate neural activity associated with reinforcement learning when tracking the past behavior of partners in an economic game (Stallen and Sanfey 2013). It has also been suggested that uncertainty as to the probability of encountering a partner in the future can allow direct reciprocity to produce cooperative behavior in one-shot games. This effect occurs due to the potential to incur the high costs associated with prior noncooperation should interaction between the parties unexpectedly occur in the future (Delton et al. 2011).

Indirect reciprocity expresses cooperation as a function of a process in which individuals help those who have a reputation for being cooperative (Nowak 2006). That social behavior is influenced by the presence of an audience (Jaeggi et al. 2010) provides support for indirect reciprocity as a mechanism for encouraging cooperation. In both

direct and indirect reciprocity, cooperation can evolve and persist because it is conditional upon the likelihood of receipt of future payoffs.

Likewise, spatial selection and network reciprocity can produce cooperation because structured populations have the potential to shield individuals who frequently express a cooperative trait from those who frequently engage in noncooperative behaviors (Nowak 2006; Rand and Nowak 2013). Spatial selection modeled on dynamic networks is similar to indirect and direct reciprocity in that the individual can decide to break the links it shares with noncooperators (Rand and Nowak 2013).

In cultural group selection, an oft-cited source of human pro-social behavior (Boyd and Richerson 2009; Boyd et al. 2011; Richerson et al. 2016; Waring et al. 2017), differences in the cultural characteristics and practices of human groups can be exploited by an evolutionary process much in the same way that natural selection acts upon genetic variation. Group selection requires a high degree of variation between groups relative to the variation within groups and sufficient competition or conflict between groups. The adaptive problems that allow for cooperation through group selection are likely to have been those in which groups consisting of a large proportion of cooperators were able to produce an effective solution or otherwise out-compete groups of noncooperators. The debate about the magnitude of the role of cultural group selection in the evolution of cooperation is well documented in Richerson et al. (2016). Like the four previously described mechanisms, group selection allows the benefits of cooperation to fall disproportionately on the cooperators, if not immediately, at least in the long run.

Additional Potential Mechanisms for the Evolution of Cooperation

Natural selection works on relative differences in reproduction and survival; thus, many researchers have focused on aspects of the ancestral environment which are directly relevant to reproductive success and procurement of sustenance and protection. Cooperative breeding (Burkart et al. 2014) and the signaling of potential parental

investment (Phillips and Dykhuizen 2015) have been hypothesized as potential origins of cooperation. Variance of resource procurement as a function of luck has also been cited as a potential source of cooperation (Cosmides and Tooby 1994).

Burkart et al. assert that allomaternal care is the best predictor of proactive prosociality in human and nonhuman primates, a finding that suggests that the ancestral environment presented problems for which care for offspring provided by non-mothers was a preferred solution. Agent-based simulations demonstrate that the presence of cooperative breeding can be explained at least in part by environmental harshness (Smaldino et al. 2013).

Allomaternal care can also be explained by theories of costly signaling. One hypothesis is that altruistic behavior displayed by males served as a costly, and thereby honest, signal of likelihood to care for offspring (Phillips and Dykhuizen 2015). Here, the costliness of altruistic behavior, a behavior which benefits the recipient at a cost to the cooperator, is essential to the evolution of cooperation, rather than a dilemma that must be solved. However, that the cooperative behavior has potentially significant benefits calls into question its categorization as altruistic as opposed to mutually beneficial.

Many of the principles of sexual selection can be applied to partner choice more generally (Barclay 2013). Cooperative behavior may be used as a costly signal to attract partners in other contexts such as in the choosing of allies or hunting partners. Individuals who witness or receive information about the cooperative behavior of a potential partner may be more inclined to initiate an interaction. The possibility for partner choice is also a necessary precondition for direct and indirect reciprocity.

An additional factor which may have affected the relative net benefits of cooperation was the development of extrasomatic weaponry, weapons that are external to the human form (Phillips and Dykhuizen 2015; Phillips et al. 2014). Prior to the advent of extrasomatic weapons, individuals could use signals of their strength and superiority to avoid potentially costly conflict in which even

the winner was likely to be injured. The development of weaponry, however, allowed individuals the ability to cause harm to another at little to no cost to themselves. Under these conditions, there is selection for the display of cooperative traits that might allow individuals to avoid conflict.

Core Design Principles

Humans can explicitly learn from the mechanisms which allowed natural selection to produce cooperation to consciously develop institutions, policies, and practices that foster cooperation. At the same time, humans are also predisposed to cooperate in specific contexts and make choices with machinery forged by natural selection (Hodgson and Knudsen 2010, p. 50). For these reasons, it is not surprising to find a marked relationship between the previously discussed evolved mechanisms which can produce cooperation and the core design principles as developed and refined by Elinor Ostrom and colleagues (Ostrom 1990; Wilson et al. 2013). The core design principles, a set of eight guidelines for creating successful common pool resource management groups, are readily generalizable to both dyads and collectives.

The core design principles were developed through empirical research that involved the creation of a database of common pool resource organizations from around the world. Ostrom studied the characteristics of those groups which were able to overcome the “tragedy of the commons” (Hardin 1968) and distilled her findings to produce the eight principles briefly described below (Wilson et al. 2013). First, the groups employed clearly defined boundaries. This applied both to the members of the group (it was clear who was a part of the organization and who was not) as well as the resource. Second, groups used the benefits principle, creating proportionality between benefits enjoyed and costs incurred by members. Third, successful groups allowed members to develop group rules and to make decision by consensus. Fourth, members were involved in low-cost monitoring of the behaviors of other group members. Fifth, punishment was used, but was graduated in its severity. Sixth, conflicts

between members were dealt with quickly and fairly. Seventh, groups were seen as having decision-making authority. And finally, nested hierarchies, or polycentric governance, were used when the systems to be managed were large in scale or scope.

Each of these principles connects in some way to mechanisms which allow for the evolution of cooperation. For example, well-defined boundaries, proportionality, group rule development, monitoring, and sanctions help to focus the benefits of cooperation on group members and to ensure individuals that conditions are favorable for the expression of the cooperation trait, i.e., that free riding will not be rewarded. Application of these principles to improve cooperation in other domains is underway (Wilson et al. 2013) but deserves additional attention.

Conclusion

Knowing what signals commonly trigger both cooperation and non-cooperation can assist in designing policy to better achieve desired societal aims. (Stallen and Sanfey 2013, pp. 301–302)

Cooperation can evolve when either environmental conditions are suitable to permit unconditional cooperation or when, in the absence of such an environment, mechanisms exist that cue conditional cooperation. The core design principles provide a comprehensive framework for successful collective action in the latter situation. They implement widely researched mechanisms for the evolution of cooperation in the context of common pool resource management, providing strong empirical evidence for the effectiveness of the mechanisms in the real world.

Strategies that can alter the environment to make it more amenable to unconditional cooperation are more complicated, but worth pursuing. Two potential pathways are through emphasis on interconnectedness and appreciation of the large role that luck plays in life circumstances. Effective and precise methods for invoking these two concepts should be the focus of future research in cooperation.

Cross-References

- [Altruism Among Nonkin](#)
- [Cooperative Breeding](#)
- [Evolution of Cooperation](#)
- [Evolution of Reciprocal Altruism](#)
- [Prisoner's Dilemma and Cooperation](#)
- [Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reciprocal Altruism and Group Living](#)

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Streetwalking

- [Prostitution](#)

Strength

- [Attractiveness and Anger-Proneness](#)
- [Hollywood Actors](#)

Strength and Anger-Proneness

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Synonyms

[Aggression](#); [Antisocial behavior](#); [Physique](#)

Definition

Physical strength has a positive association with levels of aggression.

Introduction

Physical strength has always been a desirable characteristic among humans, particularly males. It has long been suspected that males developed greater physical strength in order to compete in direct confrontations for mates. As such, male's upper body strength tends to exceed that of females (Isen et al. 2015; Darwin 1871; Sell et al. 2012). These traits of physical strength are meant to intimidate rivals. However, physical strength is not as useful for males if they do not also possess psychological and behavioral adaptations that encourage engagement in conflict. Thus, a male that is not only physically strong but also has the psychological need for battle will be the most fit (Isen et al. 2015). Accordingly, it is logical for a relationship to exist between physical strength and aggression.

The Link Between Physical Strength and Aggression

There is evidence in the field of evolutionary psychology, as well as related fields, that there is a positive association between physical strength and aggression. For example, Gallup and colleagues (2007) found that handgrip strength among males predicted past aggressive behavior, with males that have more handgrip strength having higher levels of past aggressive behavior. They also found that the males who had stronger handgrips were more likely to have broad shoulders (Gallup et al. 2007). Similarly, stronger men tend to report more successful resolving of conflicts in their favor than weaker men. They are also more likely to get angered easily and more frequently (Sell et al. 2009).

Research also suggests that particular body types are overrepresented in prisoners and delinquents. William Sheldon (1949) studied males between the ages of 15 and 21 to determine whether a link existed between physique, temperament, and delinquency. He found that there were three predominant body types: endomorphs (soft and round build), mesomorphs (muscular and athletic build), and ectomorphs (skinny and fragile build). Within his sample, the mesomorphic body type was the most likely to engage in delinquency (Sheldon 1949). Sheldon's findings were supported by (Glueck and Glueck 1956), who conducted a study comparing male delinquents to nondelinquents. They found that the delinquent group tended to have wider chests, bigger forearms and upper arms, and larger and broader waists than nondelinquents. Additionally, only 31% of the nondelinquents were found to have a mesomorphic build, while 60% of the delinquent group had a mesomorphic build (Glueck and Glueck 1956).

What Explains the Relationship Between Strength and Aggression?

Since the link between physical strength and aggression appears well established, it is important to determine what causes this relationship. There are currently several explanations for this

association that take somewhat opposing viewpoints. The first explanation, the facultative-calibration view, asserts that physical characteristics of strength precede aggressive behaviors. Accordingly, stronger men receive positive reinforcement when engaging in physical activities, which reinforces the use of aggressive behavior. Thus, strong men have a desire to participate in physical challenges because they have the ability to compete well (Lukaszewski and Roney 2011; Isen et al. 2015). Several predictions from this hypothesis have been tested empirically with results being quite supportive (Sell et al. 2009).

A secondary explanation takes a contrasting position by stating that more aggressive individuals choose to take greater stock in developing physical strength. This hypothesis posits that males who are more aggressive often attempt to increase their physical strength through various forms of exercise (Isen et al. 2015). Support for this explanation can be found in the large body of literature which suggests that aggression is a very stable trait throughout the life of an individual (Huesmann et al. 1984). This line of research asserts that an aggressive child will grow into an aggressive adult, regardless of his physique as a child. A recent study tested this theory by examining boys at age 11 and following them until the age of 17. This study found that antisocial behaviors, such as fighting, tend to precede the appearance of physical strength characteristics. In fact, boys with increased antisocial behaviors in childhood had larger gains in physical strength between the ages of 11 and 17 than boys who did not display antisocial behaviors in childhood (Isen et al. 2015).

The third explanation, the neuroandrogenic hypothesis, is a middle ground between the above two explanations. This framework argues that there is no causal relationship between strength and aggression. Instead they both co-occur because of common biological factors that masculinize the body's physical structure and the brain, independently. Research has found that testosterone exposure affects both physical development and brain functioning, which supports the idea that aggression and physical strength develop independently but around the same time (Ellis et al. 2008).

Conclusion

The physical ability to defeat one's rivals has always been an important trait for males to have. Since physical strength would be relatively meaningless without the internal desire to use that physical ability, it is logical that there evolved to be a relationship between strength and aggression. The positive association between a male's physical strength and their levels of aggression is well established; however, the causal mechanism behind this relationship is not yet known. It is plausible that males with strong physiques are socialized into aggressive behaviors because of their appearance. On the other hand, aggressive males may greatly emphasize increasing their physical strength. There may also be no causal relationship between strength and aggression, but rather both are caused by biological factors.

Cross-References

- [Physical Aggression](#)
- [Recalibration Theory of Anger](#)
- [Sex Differences in Anger Proneness](#)
- [Upper Body Strength and Fighting Ability](#)

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Stress

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Synonyms

[Stress reactivity](#); [Stress response](#); [Stressor](#)

Definition

Stress generally describes the process by which an organism perceives and responds to events – often called stressors – that are judged to be harmful, threatening, or challenging. Stressors describe demanding events or situations that trigger coping adjustments in an organism.

Introduction

Through a variety of mechanisms, the stress response regulates a wide range of physiological and behavioral processes that include bodily growth, metabolism, reproductive functioning, attention and memory, learning, aggression,

risk-taking, caregiving, among others (for review, see Del Giudice et al. 2013). For example, neurobiological mechanisms underlying the stress response include hierarchical, coordinated action of the autonomic nervous system and the hypothalamic–pituitary–adrenal axis (HPA), as well as feedback loops with cortical brain structures. Natural selection has shaped the stress response to increase the ability of organisms to cope with environmental stressors, with stress-related response mechanisms emerging early in the history of life.

Functions of the Stress Response

The stress system is a highly complex, sophisticated, and carefully regulated adaptation that has been shaped by natural selection because it gives a selective advantage. The stress response serves several vital functions and the advantages associated with those functions must be substantial in order to outweigh the significant costs. The first essential function of the stress response includes coordinating an organism's physiological and behavioral response to threats and opportunities in the environment. This includes events that have fitness-relevant consequences for the organism, requiring the organism to make adjustments in an effort to respond effectively. Environmental opportunities may reflect novel or unexpected events, as well as situations that are pleasurable (e.g., signs of sexual availability in a potential mate; see Del Giudice et al. 2013). Challenges in the environment that require adjusting in the whole organism are often referred to as allostasis (McEwen 1998; McEwen and Wingfield 2003; Sterling and Eyer 1988). The stress response mediates this process by coordinating brain-body changes in response to environmental stressors that may be either acute or chronic.

A second function of the stress response includes the encoding and filtering of environmental information. Information about the external environment is received through limbic structures, and interaction with other neuroendocrine systems (e.g., the HPG axis and the immune

system; see Herman et al. 2003) yields complex information that can be utilized by the organism. When the stress response and associated neurobiological systems are activated, useful information is provided related to the probability, type, and severity of threats and opportunities in the environment. This information may be encoded as part of the stress response and can provide a useful type of “summary” of key dimensions of the environment, such as extrinsic morbidity–mortality and unpredictability (Del Giudice et al. 2013).

A third critical function of the stress response extends beyond responding to immediate environmental challenges, and rather, involves the regulation of several traits and behaviors that are relevant to life history (for review of Life History Theory, see Ellis et al. 2009; Hill 1993). For example, baseline activity and responsiveness of the stress response is associated with individual differences in several life history-relevant domains such as competitive risk-taking, learning, self-regulation, attachment, affiliation, reproductive functioning, and caregiving (for review, see Del Giudice et al. 2011).

Phylogeny of the Stress Response

Comparisons across species can provide insight concerning the phylogeny of the stress response. All vertebrate species possess the molecule proopiomelanocortin (POMC), which serves as a precursor to both adrenocorticotrophic hormone (ACTH) and opiate-like peptides – molecules with related functions. Human ACTH shares similar peptide sequences to mammals, amphibians, reptiles, and insects, among others. ACTH is also closely associated with various signaling molecules such as corticotropin releasing hormone (CRH), biogenic amines, steroids, cytokines, and nitric oxide. The genetic sequences for these molecules have been conserved over hundreds of millions of years and serve closely related functions, particularly those involving defense. The small degree of change that has taken place in such molecules over time suggests that they provide many essential functions, creating a strong selective force against

mutations that would otherwise result in a sequence change (Nesse et al. 2010).

As with any trait, the stress response is associated with cost-benefit trade-offs. The trade-off between the long-term costs and the immediate benefits of a relatively quick, intense, or prolonged stress response, ultimately shape the mechanisms that regulate the responsiveness of the stress system. Cost-benefit trade-offs are associated with an organism's resiliency to the effects of stress on physiology or behavior, with neuroendocrine habituation to repeated stressors, and even maternal care (for discussion, see Nesse et al. 2010). Despite the significant costs associated with the stress response, natural selection has shaped this trait because it confers a selective advantage that is greater.

Sex Differences

It is probable that sex differences in biological and behavioral responses to stress arose during human evolutionary history. In the context of life history trade-offs, the associated costs and benefits for males and females are not equal, and thus, life history strategies show consistent sex differences. On average, faster strategies are associated with males who invest more in mating effort – in contrast to parenting effort – than women. The extent to which sex differences in life history-related behavior are expressed, however, depends in part on conditions of the local environment. At the slow end of the life history continuum, males and females engage in high parental investment, and the interests of both sexes focus on long-term, committed pair bonds; in this context, sex differences in behavior are thus expected to be relatively small. However, as life history strategies become faster, sexual competition is enhanced, and sex differences in competitive strategies are expected to be more apparent. Males are also expected to be overrepresented as high-risk, low-investment strategists due to the greater potential benefits of extreme mating-oriented behavior (for review, see Del Giudice et al. 2011, 2013).

It has also been argued (Taylor et al. 2000) that while the nervous system response associated with stress is virtually identical for men and women, there are sex differences in the neuroendocrine and behavioral response to stress that arose over the course of human evolution. It has been proposed that the stress response in women is best characterized as “tend-and-befriend,” where tending involves nurturing activities that are designed to protect the self and offspring, promote safety, and reduce distress. Befriending involves the creation and maintenance of social networks that may contribute to this process. The biobehavioral mechanism underlying the tend-and-befriend pattern is thought to draw on the attachment-caregiving system, with neuroendocrine evidence strongly implicating the hormone oxytocin in conjunction with female reproductive hormones and endogenous opioid peptide mechanisms. Alternatively, the stress response of men is thought to be more typical of the classic “fight-or-flight” pattern, where behavioral responses to environmental stressors involve either fighting or fleeing.

Conclusion

The stress response involves the process through which an organism perceives and responds to events that are harmful, threatening, or challenging as part of an adaptive coping effort. The stress response involves hierarchical, coordinated action between several neurobiological systems. Elements of the stress response are conserved across vertebrates, suggesting that the molecules supporting this response served many important functions. As with any trait, the stress response is associated with cost-benefit trade-offs. The stress response serves multiple critical functions: shaping of the allostatic response, the encoding and filtering of environmental information, and the regulation of several life history-relevant traits and behaviors. Finally, it is likely that sex differences in biological and behavioral responses to stress arose during human evolutionary history.

Cross-References

- [Correlates of Fear](#)
- [Increased Cortisol](#)

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Stress and Cortisol

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Definition and Synonyms

Stress, initially described as a physical force, claimed its new meaning as a psychological, physiological, or chemical impact on an individual that changes the body's homeostasis (Chrousos 2009). Examples of stress include strife in the workplace, toxic chemical exposures (e.g., asbestos), and traumatic experiences, such as a house fire. When an individual undergoes stress, the body has its own mechanisms in store to adapt. Chrousos described the adaptation: “When any stressor exceeds a certain severity or temporal threshold, the adaptive homeostatic systems of the organism activate compensatory responses that functionally correspond to the stressor” (2009, p. 374). Researches have yet to explore all the effects of stress on the body; however, they have found a link between stress and cortisol. Cortisol is a hormone secreted by two, golf ball sized glands sitting above the kidneys, the adrenals. Cortisol not only resides within the adrenal glands but also travels throughout the body within the bloodstream (Staufenbiel et al. 2013). Individuals may not detect the effect that cortisol has on everyday bodily function. Researchers have found that stress can alter the way that cortisol is released, used, and stored.

Introduction

Stress is often discussed as a mental tension caused by environmental pressure on the brain and the body. One key factor in the body's response to stress is a hormone called cortisol.

Not only does cortisol aid in adapting the body at that exact moment, but it has longer effects. Cortisol affects other bodily systems and parts, all of which reveal stress as a substantial factor in daily function.

Physiology of Cortisol in the Body

A set of adrenal glands produce the glucocorticoid hormone, cortisol (McEwen 2008). Before the adrenals produce and release cortisol, several things must occur. First, an outside stressor is sensed by an individual. After sensory neurons receive the stimuli and it exceeds the stressor threshold, the impulse is sent to the hypothalamus, a region of the brain dedicated to the autonomic nervous system and homeostatic bodily systems. The hypothalamus releases corticotrophin to the pituitary gland, a pea-sized gland in the brain. The pituitary then produces adrenocorticotrophic hormone (ACTH) and releases it into the bloodstream down to the adrenal glands. The glands release epinephrine and catecholamine, creating the “adrenaline” response individuals may get when presented with a stressor. The adrenals also release norepinephrine, which stimulates the liver (Lee et al. 2015). The hypothalamus, pituitary, adrenal process is often called the “HPA axis” or “HPA loop” (Gómez-Gallego and Gómez-García 2018).

Effects of Cortisol

Researchers found that there are many effects on cortisol of the body. Because the HPA axis involves neurological mechanisms that are responsible for homeostasis throughout the body, cortisol plays a major role in our body’s maintenance. Generally, cortisol can increase sugar within the bloodstream and increase the accessibility of repairing materials throughout the body. Cortisol can also affect an individual’s immunity, digestive system, and reproductive system, depending on levels and cortisol use (Chrousos 2009).

In stressful, flight or fight situations, through the HPA axis, cortisol and adrenaline levels will

rise, and naturally and typically, fall back down to a baseline state through feedback from the hypothalamus and the hippocampus. Researchers have found that when stressors are prolonged, cortisol levels rise; however, it may not come back down to that baseline. Cortisol may stay in the bloodstream and circulate in the body, even after the stressors have been removed. Researchers saw that this acute state can contribute/cause anxiety, depression, heart disease, gastrointestinal diseases/problems, metabolism problems/weight gain, other endocrine/reproductive difficulties, and circadian rhythm (Fogelman and Canli 2018).

Chrousos (2009) listed the effects of both effects of hypo and hypercortisolism and change in the HPA axis. Increased activity conditions include: depression, anorexia, obsessive-compulsive disorder, panic disorder, excessive exercise, alcoholism, diabetes mellitus, obesity, and hyperthyroidism. Decreased activity include: adrenal insufficiency, depression, fatigue, fibromyalgia, premenstrual tension syndrome, hypothyroidism, rheumatoid arthritis, asthma, and eczema.

There are two more well-known diseases related to cortisol levels: Cushing’s syndrome and Addison’s disease. One of them, due to hypercortisolism is called Cushing’s syndrome. Symptoms of Cushing’s syndrome include: weight gain, round face, thin arms and legs, and easy bruising. Individuals may also experience difficulties with reproductive systems, such as irregular menstruation or amenorrhea (Krieger 1983). The other, Addison’s disease, is due to hypocortisolism (i.e., sparse cortisol). Symptoms of Addison’s disease include: fatigue, weight loss, hyperpigmentation, low blood pressure, abdominal pain, and salt craving (Levine et al. 2007).

Diagnostic Measures of Cortisol

Researchers and physicians may test cortisol various ways; however, each way measures cortisol in different areas. Cortisol may be found bound, unbound (free), or both unbound and bound (total). Bound cortisol is attached to “sex-hormone-binding” globin. Unbound cortisol is also found in the blood stream, not connected to

anything. Total cortisol is the combination of bound and unbound cortisol (Levine et al. 2007). Based on what the researcher or physician is looking for, an individual may use hair or saliva samples, urine testing, or blood samples to check cortisol levels (Levine et al. 2007).

In order to begin a blood test, a health professional will take two separate blood samples, one in the morning and in the evening to record change in cortisol levels at different parts of the day. Blood would then be sent to a lab to analyze. Blood cortisol testing can test total cortisol levels (Levine et al. 2007).

The last three samples are less invasive. Salivary and urine samples can also test unbound cortisol (Hellhammer et al. 2009). Both samples can be taken throughout the day depending on the researcher and/or physician's instructions. The last form of testing is taking a hair sample. Because hair is made from capillaries from the skin, blood from the hair can be examined over time. The samples can be taken and sent to a lab for testing (Lee et al. 2015).

Treatment of Stress and Cortisol

Physicians and professionals recommend a variety of treatment approaches to reduce stress and aid in lowering hypercortisolism. Typically, yoga, meditation, and enjoyable activities are recommended. Sullivan, Carberry, Evans, Hall, & Nepocatych described in a recent study, how individuals who participated in a type of restorative yoga had decreased cortisol directly after the class (Sullivan et al. 2017).

Treatment varies for everyone. Some may eventually partake in counseling or therapy. Others may need to lower their stress input to get the body back to homeostasis. Those individuals may need to identify whatever stressor is present and eliminate it or learn how to adapt or change it so that stress is lowered. Sometimes a stressor is physiologically inherent, meaning it is already present in the body. Stress within the body can increase cortisol levels. Seeing a physician about concerns of heightened cortisol levels may be suggested for this individual.

Conclusion

Stress not only changes the way the body functions, but also has long-lasting effects on the body's systems. Managing stress as well as attending the body's response to stressors could aid in cortisol regulation. Awareness of diagnostic methods also increases awareness as well.

Cross-References

- [Cortisol Affords Immediate Action and Alertness](#)

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Stress Hormones

► [Dominance, Testosterone, and Cortisol](#)

Stress Reactivity

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Synonyms

[Arousability](#); [Stress response](#); [Threat reactive](#)

Definition

The physiological response involved when faced with a stressor (e.g., interpersonal conflicts, psychosocial, threats), which are based on individual differences.

Introduction

Life History (LH) Theory is a mid-level evolutionary framework used to explain phenotypic variation (e.g., sexual maturation, impulsivity, offspring number) based on developmental exposure to environmental cues (e.g., risks of morbidity and mortality) (Charnov 1993; Stearns 1992). Essentially, exposure to early life adversity leads to systematic differences in response to negative events, which are adaptive for varying environments. From this standpoint, individuals in less affluent areas theoretically adopt “fast” LH

strategies (as opposed to “slow” LH strategies) and are prone to engaging in risky behaviors, employing short-term mating tactics, bearing more offspring, and having higher incidences of mental illness (Charnov 1993; Hurst and Kavanagh 2016; Promislow and Harvey 1990). Reasons for expending resources sooner are due to a lowered survivability and thus an inability to pass down genes to the next generation.

These context-dependent trade-offs are regulated by a sequence of hormonal (i.e., cortisol) and immunological cascades that ultimately influence gene expression (Boyce and Ellis 2005; Shalev and Belsky 2016). Due to the highly conserved pathways involving neuroendocrine mechanisms, it is therefore important to outline the basic biological pathways involved to gain a better understanding regarding the function of stress reactivity and how the body has adapted mechanisms to prepare individuals to respond to threatening or challenging situations (Boyce and Ellis 2005). Additionally, a heightened state of arousal is necessary for unfavorable conditions and will be thoroughly explained as it relates to mortality and longevity.

Hypothalamic-Pituitary-Adrenal (HPA) Axis

The hypothalamic-pituitary-adrenal (HPA) axis plays a crucial role in stress reactivity and regulates other processes such as the immune system, mood, sexual drive, metabolism, and energy. Once activated by a stressor (an agent that causes stress to an organism), the HPA axis then triggers a biological cascade, one that works in conjunction with the central nervous system and the endocrine system. In its basic form, the hypothalamus will release corticotropin-releasing hormone (CRH), then stimulating the release of adrenocorticotrophic hormone (ACTH) located on the anterior lobe of the pituitary gland, which will then secrete glucocorticoids (specifically cortisol, the stress hormone) found in the adrenal cortex. Cortisol will eventually inhibit the activation of the hypothalamus and the pituitary gland once the stressor has passed, functioning as a negative

feedback loop. Cortisol's main role is to regulate energy homeostasis and activate physiological arousal states in response to stress-induced situations. Dysregulation within the system (e.g., chronic stressors) leads to problems surrounding immune functioning (i.e., hyperactivity and immunosuppression), which has been termed as allostatic load (Ellis and Del Giudice 2014). Over time, allostatic load can have detrimental consequences to individuals' health, accelerating morbidity and mortality.

Adaptive Calibration Model

A growing interest within the field has sought to examine the adaptive functionality of immunology as it relates to human ecology. Researchers have argued that prolonged exposure to stressful environments incur physiological harm that is said to be maladaptive, giving rise to disease and other downstream health consequences (see Miller et al. 2011). To this end, the allostatic load model has been the most widely accepted approach to understanding stress reactivity. It has been integral in explaining the pathological effects with regard to dysregulation in the autonomic, neuroendocrine, metabolic, and immune system (Ellis and Del Giudice 2014). Recent theoretical approaches, however, have proposed an alternative viewpoint that aims to conceptualize why these mechanisms have remained throughout human evolution. This approach is called the adaptive calibration model, which is rooted in LH Theory (Ellis and Del Giudice 2014).

The adaptive calibration model is, in essence, an extension and revision to the allostatic load model with a focus on the functionality and a positive take of the stress response system. From an evolutionary perspective, it can provide why phenotypic variation in stress reactivity exists, all of which has been shaped by natural selection (Ellis and Del Giudice 2014). It stands to reason that certain traits were selected for those with chronic exposure to adverse environments. For example, this model has the flexibility to explain why some individuals are able to respond to stressors more quickly than others. Additionally, this model was

heavily influenced by Belsky et al. (1991) who first highlighted the importance of early life adversity, indexed by parental conflict, which served as a proxy for morbidity and mortality.

Psychosocial Acceleration Theory

In their seminal study, Belsky et al. (1991) advanced the field by incorporating a psychosocial element with LH Theory. They began addressing the development of LH strategies (e.g., attachment styles, precarious behaviors, sexual maturation, parental investment), all of which were impacted by harsh early childhood conditions. Their important contribution documented the consequences of father absence and its relationship to reproductive timing, which they described as the psychosocial acceleration theory. The work by Belsky et al. (1991) paved the way for future developmental research using LH Theory as its theoretical framework. Since then, studies focusing on reproductive timing in females have illustrated early childhood adversity to be related to earlier onset of menarche in females, with these individuals adopting behaviors consistent with fast LH strategies (Chisholm et al. 2005; Ellis 2004). Others within the field of developmental psychopathology have also found converging evidence that demonstrates an association between early childhood poverty, maltreatment, and attachment styles later predicting heightened cortisol levels (see Fearon et al. 2016). Recent emergence of evolutionary LH models, however, has suggested that there are two intersecting ecology dimensions: harshness and unpredictability.

Harshness and Unpredictability Dimensions

Harshness is defined as age-related risks for death and disease, whereas unpredictability is defined as the variability at which harshness occurs (Ellis et al. 2009). To test this model, Simpson et al. (2012) sought to evaluate whether early childhood environmental cues, distinguishing

between harshness and unpredictability, predicted precarious behaviors in adulthood. He used longitudinal data to provide evidence that those experiencing unpredictable environments such as changes in residence, employment, and cohabitation status during early childhood (ages 0–5 years old) engaged in riskier sexual behavior and delinquency in early adulthood. Although early childhood environmental harshness did not predict behaviors in early adulthood, studies have shown that both dimensions of environment do indeed provide predictive power in later life (Brumbach et al. 2009; Belsky et al. 2012). These studies suggest that those engaging in these riskier behaviors may require more heightened stress reactivity due to their more perilous activities.

Under a LH perspective, researchers have also emphasized that exerting resources toward the immune system is energetically costly and is largely influenced by an individual's ecology (McDade 2003). Thus, redirecting resources toward reproductive effort, as opposed to maintenance, may be more advantageous under a harsh or unpredictable environment in order to maximize fitness benefits.

Hypervigilance and Psychopathology

While it appears that the accumulation of stress can trigger psychopathological disorders such as anxiety and depression, these mental processes may prove to be context-dependent and central to survival (Frankenhuis and Del Giudice 2012; Nesse 2000). For instance, depressive symptoms appear to serve as a buffer for self-preservation and may have evolved as an adaptive strategy for individuals living in stressful and adverse environments to “prepare for the worse.” Likewise, individuals experiencing anxiety enables them to be alert in situations where alertness and vigilance are favorable attributes that will likely help aid in survival. While it is costly to maintain a heightened state of arousal, it is likely more costly to be unprepared in a situation where the risk for mortality and morbidity are high. These situations are specific to stressful and unpredictable conditions, which are typical to individuals experiencing

discrimination, violence, and disorder. While it is reasonable that threat sensitivity may be the underlying cause to explain the symptomology of psychopathological disorders, it is clear that prolonged and rampant symptoms can eventually lead to mental illness such as major depressive disorder. It is when individuals resort to behaviors and negative thoughts that induce chronic stress, that these symptoms no longer become favorable (Nesse 2000).

Previous research has provided explanations as to why these traits have evolved. Lacking within the literature, however, is empirical evidence clearly justifying potential mechanisms involved with the onset of psychopathological symptoms. A recent study sought to bridge the gap within the literature by exploring the relationship between LH strategies, environmental stressors, psychopathological symptomology, and associated behaviors such as aggression and self-harm (Hurst and Kavanagh 2016). Drawing from various community-based samples, these researchers found a relationship between higher symptomology count and poor parental support correlating with fast LH individuals. These results are in line with previous work by others who have posulated that higher levels of depression are associated with individuals experiencing environmental adversity, all believed to be characteristic of a fast LH strategy (Hurst and Kavanagh 2016). As stated above, it makes logical sense to be hypervigilant particularly in harsh and/or unpredictable ecologies since the future remains uncertain.

Psychosocial Acceleration Theory Revisited

More than two decades has passed since the introduction of the psychosocial acceleration theory. It has gone on to inform countless research studies and other theoretical frameworks. With time, researchers now have a better understanding of the cumulative effects stress has on reproductive success and other LH strategies. To this end, Shalev and Belsky (2016) revisited the psychosocial acceleration theory and proposed its integration with evolutionary theories of aging, focusing

on the downstream consequences of stress on the biological marker of aging, telomeres.

Telomere lengths are repeated nucleotides (TTAGGG) found at the end of each DNA chromosome and serve as protective caps during the DNA replication process (Bodnar 2009). It is a highly conserved sequence whose function is thought to reduce the risk of morbidity and mortality (Monaghan 2010). Much of the literature to date has focused on role of telomere lengths and cancer, but recent studies have now called on evolutionary theories and the integration of physiology and ecology to explain the effects of oxidative stress on development and health (Monaghan et al. 2008; Selman et al. 2012). Furthermore, oxidative stress, which stems from growth and environment, is a metabolic process that occurs when the ratio between free floating radicals (generally unstable) to antioxidants (neutralizes free radicals) are disproportional. These free radicals trigger a chain of reactions that leaves a trail of unstable molecules in its wake and causes extensive damage to cells. Thus, oxidative damage may be one of the factors responsible for the wide variation in telomere loss and may in fact accelerate the rate of senescence (Monaghan et al. 2008).

Previous research suggests that psychosocial stress can alter the rate of telomere loss (Monaghan et al. 2008). Acute stressors have the ability to enhance survival and slow the rate of senescence because the HPA axis is activated for a brief amount of time. However, those living in stressful environments typically engage in chronic stressors and have shorter telomere lengths compared to those living in low stress environments (Epel et al. 2004; Kotrschal et al. 2007; Nettle et al. 2015). Environmental factors have the ability to disrupt the body's defense mechanisms, which ultimately affects the variability in mortality rates (Monaghan et al. 2008).

By combining the psychosocial acceleration theory and research regarding telomere lengths, Shalev and Belsky (2016) proposed a two-hit developmental model of accelerated aging. This model posits that early life adversity and early maturation (leading to earlier reproductive behaviors) interact to predict accelerated aging due to a

fundamental cost-benefits analysis. This interaction is also mediated by biological processes central to the stress profile (i.e., HPA axis, inflammation, metabolism). Early life stress leads to an increased stress reactivity associated with physical health and psychological consequences (as previously mentioned), which likely decreases the lifespan. Additionally, early reproductive behavior requires an extensive amount of energy, which then takes away any kind of somatic maintenance and contributes to a decrease in longevity. If the primary goal is to reproduce, then individuals may incur these costs regardless, in order to ensure the success of passing down genes to the next generation. Thus, the rationale behind the two-hit developmental model of accelerated aging provides a detailed mechanistic approach mapping out the long-term effects from early childhood stress (Shalev and Belsky 2016).

Conclusion

Overall, a LH perspective offers an alternative approach to understand the adaptive function of stress reactivity as it relates to physical health, psychosocial stress, psychological disorders, and accelerated aging. A recent review examining glucocorticoids and its correlates between LH trade-offs through reproduction and survival concluded that this relationship is more complex than previously thought and the evidence to suggest its associations offer equivocal evidence, at best (Crespi et al. 2013). In a field that has capitalized on various theoretical models, future directions should seek to provide empirical evidence for these models. In conclusion, there is much work to be done regarding stress reactivity under the umbrella of LH Theory and many exciting questions that remain unanswered.

Cross-References

- [Bruce J. Ellis](#)
- [Cortisol Affords Immediate Action and Alertness](#)
- [Early Childhood and Adolescence](#)

- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
- [Fast Versus Slow Strategies](#)
- [Father Absence and Stress Reactivity](#)
- [Increased Cortisol](#)
- [Jay Belsky](#)
- [Life History Strategies](#)
- [Life History Theory](#)
- [Stress](#)
- [Stress and Cortisol](#)
- [Tend and Befriend Adaptations](#)

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Stress Reduction and Mental Health

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Synonyms

Anxiety; Green exercise; Meditation; Mindfulness; Positive psychology

Introduction

Approximately 18% of persons in modern societies experience a mental illness that would meet standard diagnostic criteria of the DSM in any given year; anxiety and mood disorders are the most prevalent (National Institute of Mental Health 2017). Prevention and improvement of mental health status has been the subject of considerable research. Empirical investigation supports several lifestyle interventions that reduce stress and appear to generally benefit overall mental health. These interventions include meditation, exercise, and attention shifts to positive events.

Evolutionary psychologists generally conceptualize mood and emotions as evolved mechanisms to influence behavioral tendencies. Modern life often features combinations of multitasking, serial relocations, high levels of noise, and a sedentary lifestyle, things that would be uncommon or which would be associated with upheaval or illness in hunter-gatherer societies. Modern, industrialized lifestyles may present challenges for the evolved adaptations of the mind

that increase general levels of stress and present risk to well-being. Subjective feelings of stress and mood disorders may be partially a mismatch of evolved mechanisms to expected environments compared with the challenges of modern life (Grinde 2002). Research exists that may provide guidance on alleviating the high levels of anxiety, stress, and negative mood found in modern society.

Meditation and mindfulness. Meditation and mindfulness-based stress reduction (MBSR) appear to reduce stress and increase physical and mental well-being (Krisanaprakornkit et al. 2006). MBSR and the similar mindfulness-based cognitive therapy feature the practice and acquisition of nonjudgmental awareness of current perceptible mental states through focused training. Common techniques include focus on breath awareness under a set of specific instructions designed to increase the narrowness of attention. A meta-analysis of 115 randomized clinical trials (over 8000 total participants) provided evidence of a clear benefit on stress reduction as well as alleviation of depression and improvement in quality of life (Gotink et al. 2015). Earlier research and meta-analyses has also found evidence that mindfulness-based techniques reduce stress and benefit mental health (Grossman et al. 2004).

Green Exercise. Researchers have considered the effects of exposure to nature on mental health. The effect of exercise in the presence of nature (something modern society tends to lack but would be common in environments of evolutionary adaptation) has also been found to reduce stress and improve mental health. A meta-analysis of 10 studies (over 1000 participants) found that exercise in nature improved both general mood and measures of self-esteem (Barton and Pretty 2010). Interestingly, there was evidence that inclusion of water features (e.g., an ocean front or a stream) resulted in greater effect sizes. It appears that the level of the color green itself in a natural setting predicts better mood and tends to lower an individual's perceptual awareness of physical exertion, even when actively exercising (Akers et al. 2012).

Gratitude expressions. Investigations sometimes grouped under the heading "Positive

This article is an overview to empirically-validated behaviors and life-style interventions that impact mental health, broadly defined. Effects related to diet, conventional therapy, and/or medical interventions are not included in this section. Theoretical connections regarding the risk of mental illness related to mismatch between environmental of evolutionary adaptation and modern life are mentioned.

Psychology” are also relevant. By investigating which kinds of activities increase positive emotions, the outcomes measured in such research have also spoken to mental health overall. Interestingly, there is evidence that becoming more aware of and expressing gratitude causes large increases in outcomes related to mental health. Specifically, Seligman and colleagues (2005) assigned participants to placebo or active conditions and found effects on mental health. Daily journaling about specific good events in a day including thoughts about likely causes of those good things, and writing and delivering letters expressing gratefulness to someone who had shown them kindness significantly decreased feelings of depression, and improved feelings of self-esteem. Such reflections may be relatively absent in modern society but appear to be important to mental health.

Conclusion

Evolutionary psychology offers concrete advice of theoretical understanding regarding stress reduction and mental health.

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Stress Response

- Increased Cortisol
- Stress
- Stress Reactivity

Stress Response System

- Father Absence and Stress Reactivity

Stressor

- Stress

Strike Back

- Ability and Willingness of Victim to Retaliate

Strong Negative Reciprocity

- Altruistic Punishment
- Altruistic Punishment and Strong Reciprocity

Strong Reciprocity

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Synonyms

Altruistic rewarding and punishment; Costly rewarding and punishment; Indirect reciprocity

Definition

A combination of a tendency to reward others for cooperation and of a willingness to impose sanctions on norm violators at the strong reciprocator's own cost, even in the absence of future material return.

Introduction

The theory of strong reciprocity is regarded today as one of the most influential attempts at explaining the evolution of human cooperation and altruism (Bowles and Gintis 2011; Fehr and Fischbacher 2003, 2004; Fehr et al. 2002; Fehr and Gaechter 2002; Fehr and Gintis 2008b; Fehr and Henrich 2002; Fehr and Rockenbach 2004; Fowler 2005; Gintis et al. 2003, 2008b; McElreath et al. 2003). Strong reciprocity may take both positive and negative forms. A person is a strong *positive* reciprocator if he/she is willing to sacrifice resources to reward someone else who cooperates, that is, to practice *altruistic rewarding*. In the case of strong *negative* reciprocity, the individual who prefers cooperation is willing to sacrifice resources in order to punish or sanction those who free ride on others, thus practicing *altruistic punishment*. These forms of behavior cannot be explained by self-interest and point to the existence and motivating role of *other-regarding preferences* and *moral norms* in human social exchanges (Gintis 2000, 2008, 2009; Gintis et al. 2008b).

Experimental Evidence

Strong reciprocity has been widely documented in multilateral experimental situations. These typically resemble *social dilemmas*: *n*-person situations in which everyone would gain by cooperation but each individual has an incentive to gain at the expense of the others. The behavior that would be beneficial for all is less profitable for the individual than the selfish alternative, yet it would severely harm the interests of the community if everyone followed self-regarding strategies (Gintis 2009; Van Lange et al. 2007; Van Lange and Joireman 2008; Van Vugt and Van Lange 2006). The *public goods game* is one of the most widely applicable models for such dilemmas (Bowles and Gintis 2011; Camerer and Fehr 2004; Fehr and Gächter 2002; Gintis et al. 2003). This game typically consists of more than one round, in groups of $2 + n$ players. In each round, the players are provided with a certain amount of money, and they have to decide how much of it (if any) to contribute to a common account (i.e., the public good) and how much to keep in their own private account. The individual contributions are summed up and multiplied by a factor of usually three. The resulting sum is then equally divided and added to the players' private accounts, independently of their individual contributions. In public goods games without costly punishment opportunity, the amount contributed to the public good gradually declines over time, which can be explained by the fact that those players who are inclined toward strong positive reciprocity do not cooperate at any cost – their cooperation is conditioned by the other group members' behavior. In the absence of other options, they signal their dislike of the free riders' strategy by lowering their own contributions. If, however, the players are given the option to use targeted, costly punishment against each other, the game unfolds differently. Sanctioning behavior follows the principles of strong negative reciprocity; the players who impose punishment even at their own expense are those who have an initially cooperative approach to the situation; sanctions are used against those participants who contribute nothing or only substandard amounts to the public

good; and, the existence of punishment opportunities results in a stable and high level of contributions, thus re-establishing cooperation. Thus, by acting to raise the level of contributions to the public good, altruistic punishment itself serves as a so-called second-order public good (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Fehr and Gächter 2002).

Strong reciprocity has been widely observed in dyadic experimental setups, as well. In the *ultimatum game*, two players decide over the division of a fixed sum of money. Player A can make one proposal to player B, who can accept or reject it. If B accepts the proposal, the money is shared accordingly; if B rejects, both players receive nothing. Since the game is one-shot and anonymous, the self-interested outcome would be for player A to offer the lowest possible amount and for B never to reject. However, this outcome is almost never achieved: player Bs typically reject offers lower than 30%, regarding them as unfair, and, anticipating this, player As typically offer around 50% (Fehr and Fischbacher 2005; Gintis et al. 2003).

In the ultimatum game, player Bs are directly affected by player As' proposal. There is evidence, however, that a number of people are willing to employ altruistic punishment against those who behave uncooperatively toward a third person (Fehr and Fischbacher 2004). In the *third-party punishment game*, players A and B take part in a *dictator game*. It has the same structure as the ultimatum game, except that here player B has no option of rejecting A's proposal; she/he has to accept whatever is offered. The game is anonymously observed by player C, who is not affected by payer A's decisions. However, C is endowed by a fixed sum of money and has the opportunity to impose a fee upon A after witnessing A's offer. The fee is costly, for the one-third of the decided amount is deducted from C's initial endowment. Nevertheless, in the experiment (Fehr and Fischbacher 2004), 55% of Cs punished A for offers below 50%, and the amount of punishment increased with the perceived unfairness of the offer. This tendency of

disinterested third parties to use altruistic punishment is in line with the supposed role of strong negative reciprocity as a norm enforcement device in real-life situations, e.g., in the upholding of food sharing norms in hunter-gatherer societies (Bowles and Gintis 2011; Fehr and Fischbacher 2005).

Proximate Mechanisms

It has been suggested that in the experimental scenarios described above, the sole motivation for sanctioning behavior is the punishers' desire to maximize their payoffs relative to the punished individuals (Price et al. 2002). However, there is evidence indicating that this is not the case. In a prisoner's dilemma experiment by Falk et al. (2005), the cost of punishment was the same for the punisher and the punished player, so it was not possible to influence and affect the difference in payoffs via sanctioning. However, almost 60% of players who cooperated in the game imposed substantial amounts of punishment on defectors. Moreover, strong reciprocity has been observed in one-shot experimental scenarios where costly rewarding or punishment holds no possibility of long-term economical benefits for the strong reciprocator. It seems that strong reciprocity is to a large extent motivated by the negative emotions strong reciprocators feel when observing unfair decisions and the positive emotions induced by their own sanctioning behavior as well as by their cooperating with other cooperators (Bowles and Gintis 2011; Declerck et al. 2013; Fehr et al. 2002; Fehr and Camerer 2007; Rilling et al. 2002). Studies combining neuroimaging methods with economic games have shown that both first-person and third-person punishment behavior activate reward-related brain regions (De Quervain et al. 2004; Strobel et al. 2011). Thus it seems that humans are endowed with proximate mechanisms in the form of social preferences and moral emotions that render both strong positive and strong negative reciprocity pleasurable even when it yields no financial gains.

Evolutionary Origins

Costly punishment might feel good, yet the finding that it is not the most economically beneficial strategy in public goods games (high contributors, who neither receive nor give out punishments, are the most successful) raises the question of the possible evolutionary origins of such an altruistic strategy. The answer may be found in the theories of multilevel selection and gene-culture coevolution. According to the literature (Bowles and Gintis 2011; Gintis et al. 2003), in the relevant evolutionary period of the Pleistocene, intergroup competition constituted a formidable force in the dynamics of human evolution. Human groups often had to face dispersal or extinction threats due to wars, famines, environmental disasters, etc. Groups with a relatively high proportion of strong reciprocators enforcing cooperation norms were much more likely to survive such events. Moreover, humans have unique cognitive and emotional capabilities enabling us to create and communicate social norms, among them norms of altruism, cooperation, and the suppression of within-group competition. In such circumstances, within-group selection forces acting against strong reciprocators weaken to the extent that eventually they invade a population of self-regarding types (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003; Richerson and Boyd 2004). The use of moralistic punishment as a norm enforcement device may spread among the members of an entire population through the mechanism of conformist transmission, the behavioral norm of imitating the most successful members in a community (Bowles and Gintis 2011; Richerson and Boyd 2004).

It is worth noting that strong positive reciprocity seems to be evolutionarily less stable than strong negative reciprocity. Whereas the costs of altruistic punishment decline as the number of free riders in a group diminishes, the cost of altruistic rewarding is independent of the number of free riders. Thus, when strong negative reciprocators are common in a group, there are only weak selection forces operating against them, and their

presence allows cooperation to become a stable strategy even within larger groups (Gintis et al. 2003).

The above claims are disputed by those who hold that strong reciprocity is a maladaptive behavior stemming from the differences between the environments relevant for human evolutionary history and those of contemporary modern societies and of the experimental situations. Specifically, this argument states that the human mind is not adapted to deal with anonymous, one-shot scenarios among strangers and treats them as if they were unanimous, repeated interactions among acquaintances. However, there is ample evidence that humans are able to distinguish between friends and strangers and between one-time and repeated interactions and to change their behavior accordingly. Thus, it seems unlikely that the maladaptation theory can account for strongly reciprocal behavior (Fehr and Henrich 2002; Gintis et al. 2003).

Conclusions

Strong reciprocity, the propensity to sacrifice resources in order to reward cooperation and punish free riding, is a well-documented factor in experimental scenarios and may have played a crucial role in the evolution of human cooperation itself. The main motivation behind this behavior lies in proximate mechanisms shaped by evolutionary forces and conditions that rendered this behavior, in spite of its costs, invaluable in the upholding of social norms.

Cross-References

- ▶ [Altruistic Punishment](#)
- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Costs of Punishing](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Game Theory](#)
- ▶ [Gene-Culture Coevolution](#)
- ▶ [Multilevel Selection Theory](#)

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Structure

► Gestalt Theory

Student-Centered Learning

► [Child-Centered Learning](#)

Studies on Adaptation of Human Behavior and Behavioral Outcomes

► [Human Behavioral Ecology](#)

Study of Animal Minds

► [Cognitive Ethology](#)

Study of Dunnock Mating, The

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Synonyms

[Dunnock breeding system](#); [Hedge sparrow mating system](#)

Definition

The study of natural history, behavioral ecology, and evolution of dunnocks, *Prunella modularis*, with respect to their intriguing mating behaviors.

Introduction

A mating system is a description of the processes by which males and females acquire mates. Mating systems are generally stable within and among populations of a species. For instance, most avian species could be described as socially monogamous, meaning that males and females form pairs during the breeding season to mate and, occasionally, to raise young together. Within this typical bird population, most individuals would breed as pairs.

At least since the 1950s (Campbell 1952), bird watchers and researchers suspected that a little dull brown bird, the dunnock, *Prunella modularis*, would hold some surprises about their mating behaviors. But it was not until the 1980s that studies using color-banded individuals (i.e., marked with a unique combination of colored plastic rings on their legs) provided insights about the curious mating behaviors of dunnocks. These studies (Birkhead 1981; Karanja 1982) confirmed what was suspected since at least the 1950s; dunnocks presented considerable variation in mating combinations. Far from the usual monogamous bird species, dunnocks presented within-population variation in mating patterns. Dunnocks breed as pairs (monogamy), groups of a male with two females (polygyny), a female with two or more males (polyandry), or even groups of two or more males sharing several females (polygynandry) (see Davies 1992). Such within-population variation in mating patterns is unique across animals, making the dunnock an interesting study system for understanding the evolution of mating systems.

Dunnocks are also known for a peculiar sexual behavior, first described in 1902 by the ornithologist Edmund Selous. The behavior – named cloaca pecking – is part of the precopulation display performed before a copulation attempt. During this display, the male hops around behind the female while she shudders her wings and raises her tail to expose her cloaca (see Davies (1992) for a thorough description). The male will then peck at the female's cloaca several times within a minute before he copulates with her.

Occasionally, the female will dip her abdomen and eject a droplet of sperm. Males only copulate after females eject this droplet. Nick Davies (see Davies 1992) interprets the behavior as a female attempt to convince the male that he has a chance of gaining paternity. Consequently, encouraging him to stay with the female and provide care toward her young. Davies' interpretation makes sense because social polyandry is a common mating strategy in dunnocks. That is, in social polyandry, females are simultaneously paired with two or more males that copulate with her.

Once these naturalistic studies identified that dunnocks possessed a variable mating system – that is, one in which there was variation in the mating compositions – the focus shifted toward hypothesis-driven studies based on theory. Davies, who was one of the founders of the field of Behavioral Ecology, employed evolutionary theory to investigating the variable mating system of dunnocks (see Davies 1992). The long-term study by Davies in England has helped us to understand many aspects concerning dunnock mating behavior and contributed to the field of behavioral ecology in general. For instance, Davies' study provided understanding of parental investment and sexual conflict theories (see the section "[Cross-References](#)"). Davies' studies have become a textbook example of mating systems. More recently, another study – using an introduced population in New Zealand (see Santos (2012) for details about the introduction history of dunnocks) – has also investigated the mating system of dunnocks to address behavioral and evolutionary questions. These recent studies have found several new facts and unexpected insights into dunnock mating behavior (see below).

Variable Mating System

The Cambridge (see Davies 1992 for details) and the Dunedin (Santos et al. 2015 and references therein) studies provide information on the formation of the different mating types. Apparently, the mating combinations are a consequence of variation in male and female territory size,

and competitive ability of individual birds. Unlike other birds, female dunnocks do not choose males based on their territories or territorial attributes. Females appear to choose their breeding territories independently of males, and female settlement is based on competition with other females for space. Thus, a mating combination – for instance, monogamy – is the result of a small female territory and a male with enough competitive ability to ward off male intruders. Social polyandry is likely to result from a large female territory that overlaps with at least the territories of two males. These males, in turn, chase the female around her territory, while fighting with each other. These male-male interactions result in a dominance hierarchy, and then these males coalesce their territories.

In the Cambridge study, territory size was different between polyandry (0.71 hectares) and monogamy (0.28 hectares). Meanwhile, in the Dunedin study, polyandrous and monogamous groups had similar-sized territories (0.24 hectares) (Santos and Nakagawa 2013). Thus, it seems that while in Cambridge female territory size is an important characteristic shaping the variable mating system, in Dunedin it seems that female territory size may play a smaller role.

Both studied populations presented male-biased adult sex ratios, that is, there were more adult males alive during the breeding season than adult females. In Cambridge, males represented 54.5% of adults, while in Dunedin males represented 57% of breeding adults. Compared to the Cambridge and four other dunnock studies (Davies 1992), the Dunedin population had the highest density of males per hectare, averaging 5 males/hectare, while the Cambridge population averaged 2.6 males/hectare. These demographic differences are probably associated with differences in the frequency of the within-population mating combinations. For instance, in Dunedin – with high male density and skewed sex ratio – territories are small, and social monogamy and polyandry are the predominant mating combinations.

In evolutionary terms, the different mating combinations yield different fitness payoffs to males and females. In species like the dunnock, in which males feed the nestlings, the fitness

consequences of the mating combinations are important to breeding individuals. From a fitness perspective, polyandry is the optimal breeding situation for females because multiple males provide care. Yet from a male perspective, sharing the same female with another male is not optimal. Theoretically, this occurs because a male may lose paternity to his co-breeding male partner. Dunnock mating systems, therefore, are an example of sexual conflict. The development of genetic analyses allowed for the investigation of maternity, paternity, and relatedness between individuals, yielding insights into the consequences of the sexual conflict in dunnocks.

The Genetic Eyepiece

In 1989, Burke and collaborators (Burke et al. 1989) applied a technique called DNA fingerprinting to dunnocks from Cambridge to investigate the relationship between the mating behavior of birds from the different mating combinations and genetic paternity. In social monogamy, all chicks were sired by the resident male. In the polyandrous groups, in which the male hierarchy dictates mating access to females, the dominant and subordinate males split the paternity of broods almost evenly. These findings showed that even with little mating access to the female, subordinate males could gain paternity in polyandrous groups.

Santos and colleagues (Santos et al. 2015) also investigated how paternity was distributed among dunnock broods in Dunedin. In this study, the authors used microsatellite markers to generate individual genetic profiles used to assess paternity and relatedness among dunnocks. The Dunedin study revealed differences in the genetic mating system of dunnocks. While in Cambridge there was little evidence of extra-pair or extra-group paternity – offspring that were sired by males other than the males from the social breeding group – in Dunedin, extra-pair and extra-group paternity was abundant. Extra-group paternity occurred both in socially monogamous and socially polyandrous groups. Over 30% of broods from socially monogamous pairs had at least one chick that was sired by an extra-pair male, while 17% of

broods from socially polyandrous groups had at least one extra-group young (Santos et al. 2015). These data suggest that (i) males in socially monogamous pairs are not as efficient in guarding their mates against intruders as two or more males in socially polyandrous groups; and (ii) females in socially monogamous pairs have more opportunities to leave their territories and engage in extra-pair copulations than socially polyandrous females.

The paternity data from the Dunedin study also changed how we interpreted the reproductive payoffs from a male perspective. Davies and collaborators showed that males had highest reproductive success with polygyny, less with monogamy, and least with polyandry (summarized in Davies 1992). This is the theoretical expectation when males do not lose paternity to extra-pair males. However, in Dunedin, extra-pair or extra-group paternity accounts for the paternity of 23% of young in social monogamy and 10% of young in social polyandry. Considering all the paternity lost and gained by including extra-pair or extra-group paternity in the estimates, Santos and collaborators (2015) showed that the number of young fledged per breeding attempt was similar among three types of males: socially monogamous, alpha, and beta co-breeding males. Thus, from a male perspective, sharing a female with another male in a socially polyandrous group is not such a bad reproductive tactic.

Moreover, the Dunedin study has also showed that when females engage in multiple mating that leads to mixed-paternity clutches, they avoid negative effects caused by inbreeding. Additionally, an increase in the relatedness between breeding males and females in social monogamy decreases hatching success of the eggs. The relatedness between individuals had another biologically relevant consequence. Many male coalitions in polyandrous groups were closely related in Dunedin; that is, their relatedness estimates ranged from cousins to offspring/full-sibling. The consequence of breeding together for these closely related males is that they also gain indirect fitness benefits (estimated at approximately 5% of their direct reproductive success). In Cambridge,

through detailed observations, Davies and colleagues did not observe any instance of closely related individuals breeding together.

Personality and Its Implication for Dunnock Mating

Another study in Dunedin has investigated the relationship between “personality” genes and behavior. Among other findings, Holtmann and collaborators (2016) found significant allele effects for the association between the mating status of a dunnock and its genotype at two “personality” genes. These genes are the serotonin transporter gene (*SERT*), for which allelic variation has been associated with several behavioral phenotypes in other species, and the dopamine D4 receptor gene (*DRD4*), in which variation is associated with exploratory behavior and activity in vertebrates. Mating status was defined as the individual’s social mating composition. This study classified individuals into four mating statuses: (i) monogamous females, (ii) monogamous males, (iii) polyandrous females, and (iv) co-breeding males. These categories represent the different degrees of promiscuity exhibited by individuals. Individual mating status was repeatable across three breeding seasons, meaning that birds were consistent with respect to their mating categories. The intra-class correlation (i.e., repeatability) of male mating status was on average of 73%, while female mating status had an intra-class correlation of 60%. Notably, males that were homozygous for two *SERT* alleles (namely SNP840 and SNP966, see Holtmann et al. 2016) were on average 27% more likely to form a coalition with a co-breeding male than heterozygous males at these alleles. Overall, these findings indicate that genomic information will become an increasingly important tool in the study of mating systems.

Conclusion

The study of dunnock mating started with curious naturalistic observations. When these naturalistic

observations were acknowledged and studied in a systematic manner, dunnocks became a textbook example of a unique mating system and shed light on several important theoretical areas. It is through the combination of naturalistic observations, a theoretical foundation to stimulate study questions, and long-term studies that what could have been an anecdotal observation of a little brown bird became an essential asset in behavioral ecology and evolutionary biology.

Cross-References

- ▶ [Cooperative Breeding](#)
- ▶ [Observed Mating Behavior and Women’s Long-Term Mating](#)
- ▶ [Polygamy \(Behavioral Ecology\)](#)
- ▶ [Seeking Extra-Pair Partners](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)

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Study of Instinct, The

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Synonyms

Genetic codification of behavior; Innate; Nativism

Definition

Patterns of behavior that emerge in the absence of relevant related experience, usually taken to be species-specific and genetically encoded.

Introduction

Historically, the study of behavior has been centered around a strong opposition between instinct (or nature) and learning (or nurture). The “instinct” concept was (and still is) adopted in many fields (Psychology, Ethology, Biology, Linguistics, etc.) as an explanation for the complex behavioral patterns exhibited by most species; when in the absence of relevant external influences, these appear to be internally driven. It is routinely suggested that such cases point to some kind of internalized knowledge. In contrast, learned behaviors are those thought of as being acquired from externally experienced models.

The following paragraphs first introduce the conceptual bases of the “instinct” concept as originally elaborated within the ethological tradition,

and then go on to explain the many shortcomings of the concept that have been alluded by the developmentalist alternative to that tradition.

Arguments for the “Instinct” Concept

The “instinct” concept has a long pedigree. It played an important role in the early evolutionary approaches to the psychological makeup of species by the likes of Erasmus Darwin, Pierre Jean George Cabanis, Jean-Baptiste Lamarck, or Charles Darwin, but its definitive incorporation into the natural sciences is mostly due to the European ethological tradition and the influential figure of Konrad Lorenz. This ethological trend transformed the classical, mostly metaphysical nativist stance into a theory of instincts, that is, of the behavioral reflexes of an evolved species-specific genotype.

According to this tradition, genes play a central role in the explanation of inborn behaviors. In the words of Lorenz, instincts are “a certain type of innate, genetically determined behavior patterns” (Lorenz 1950, p. 221). Correspondingly, a gap is said to exist that distinguishes genetically and experientially determined behaviors – i.e., instinctive and learned conducts. Within this conceptual frame, instinctive behaviors are species-specific in the same sense as morphological features like dentition or claws (Lorenz 1950, p. 238), since they all belong to a pre-specified functional plan of the species.

Instincts are believed to exhibit intrinsic design qualities, for which natural selection is the only reasonable source of explanation (Lorenz 1965). As a matter of fact, ethologists pioneered the application of Darwin’s theory in recent times, following a path that Darwin himself had opened. Furthermore, instincts typically manifest “critical period” effects, and they fix and become endurable in the absence of correlating perdurable stimuli. Instincts may take some time to show up for the first time but, according to Lorenz, far from being the result of a period required for learning the corresponding behavior, such delays are due to mismatches between the instincts themselves and the maturation of the organic systems in charge of their execution.

Lorenz always held a geneticist stance regarding the causal explanation of instincts. However, in the 1960s, he partially qualified his position, clarifying that what is in fact innate are not the behaviors themselves, but the information that underlies them. From that point on, innate features were defined as “coded information stored in the genes” (Lorenz 1965, p. 20), so “organs or behavior patterns must not be called innate” (Lorenz 1965, p. 34). Within this reframing, Lorenz also reformulated the “instinct” versus “learning” distinction, now asserting that the difference refers to the different timescales within which the corresponding sources of information act: instincts correspond to adaptive information which is stored in the genome by natural selection, and learning corresponds to adaptive information which is directly provided by the environment and assimilated during the life cycle. Instincts thus develop under strict genetic control (Lorenz 1965, p. 103).

Such a gene-centric turn is certainly neo-Darwinian in spirit, as it adheres to the usual logic according to which “the genes of an organism are present at its conception, and so its innate traits are also present at the conception, even though only in coded form” (Mameli and Bateson 2011, p. 438). Actually, Lorenz adhered to the notion of a “genetic program” that contains a draft of the whole developmental process of a given organism: “What rules ontogeny, in bodily as well as in behavioral development, is obviously the hereditary blueprint contained in the genome and not the environmental circumstances indispensable to its realization. It is not the bricks and the mortar which rule the building of a cathedral but a plan which has been conceived by an architect” (Lorenz 1965, p. 42).

The “Instinct” Concept: Arguments Against

The notions of “nativism” and “instinct” are not straightforward ones, for they actually mix distinct nonequivalent meanings (Lorenzo and Longa 2018). If anything, they might be treated as conceptual clutters, in the sense of Mameli and

Bateson (2011). Moreover, an increasingly influential developmentalist trend rejects these notions because (1) nothing organic can avoid some kind of constructive developmental path, and because (2) they discourage the study of such paths (Blumberg 2005; Moore 2001). In the critical words of Blumberg, “why discuss development when all of the interesting behaviors are inborn, programmed in the genes, preordained!” (Blumberg 2005, p. 13).

The idea of instinct disdains, according to the same trend, the far-from-trivial influence of prenatal experience on mature capacities. Zing-Ying Kuo famously showed that the pecking behavior of chickens is grounded on the prenatal activity of the embryos, where every single component piece of the total behavior (head movement, bill opening and closing, swallowing, etc.) is already attested. Thus, according to Kuo, “the development of behavior is a gradual and continuous process, and not a sudden manifestation of instincts” (Kuo 1932, p. 109). In a similar vein, Gottlieb showed that prenatal experience paves the way for postnatal conducts (Gottlieb 1997): e.g., birds fostered in incubators show a preference for the maternal calls, because chicks practice similar calls before hatching.

Daniel Lehrman criticized the relevance with which Lorenz credited isolation experiments, which are based on the logic that if an animal bred in isolation exhibits a certain behavior, such behavior must be impressed on the genome. According to Lehrman, such experiments discard only some influences (e.g., frank learning or learning from conspecifics), but not others, somehow less obvious. Thus, he concluded that “The important question is not ‘Is the animal isolated?’, but ‘From what is the animal isolated?’” (Lehrman 1953, p. 343). Experiments based on this logic offer little information regarding the factors actually involved and regarding the comprehension of what development ultimately is. Many so-called instinctive behaviors are simply due to the fact that conspecifics develop in the same environment and share the same action system (Kuo 1921; Lehrman 1953).

In any event, the central point of the developmentalists’ criticism has to do with the

instinctivists' dismissing the idea that development means "the increase of complexity" (Kuo 1921, p. 663), an objection also raised by Lehrman (1953). According to Lorenz, the development of behavior follows inflexible and immutable paths, strictly fixed and informed by the genes. He claimed that development was simply a progression toward the revelation of the instinctive conduct, and not a historical process during which behavioral repertoires are constructed. Lehrman argued against this view, because it ignores the fact that rich interactions between organism-internal processes and the environment occur at every developmental stage, creating qualitatively new, or emergent, properties. In his own words, "The interaction out of which the organism develops is not one, as is often said, between heredity and environment. It is between organism and environment!" (Lehrman 1953, p. 345). Indeed, the genes-environment interactions are mediated by many structural components and levels at different developmental stages. Centering the causal explanation of development on just two factors entails neglecting a plethora of other equally relevant ones.

To close, developmental biology shows that the idea that the genes crucially inform development is misguided: "DNA does only one thing: It provides the information needed to produce proteins" (Moore 2001, p. 73). The effect of the genes on the phenotypic outcomes are very indirect, almost negligible if one does not take into account the contribution of the remaining factors that mediate between the genes and the traits.

Attending to all previous reasons, Blumberg concludes that the "instinct" concept "is an illusion" (Blumberg 2005, p. xiv).

Conclusion

How do morphologies and behaviors take shape? Where do they come from? Where do they obtain the information required to attain a steady state? On the one hand, neo-Darwinism relies on an answer to these questions in line with classical preformationist stances, according to which forms are preformed (nowadays,

programmed) in the genome. On the other hand, current developmentalism defends that no single organic trait can preexist their own development and that shape emerges dynamically through qualitative changes. The issue is not a closed one, neither in the case of anatomical nor behavioral traits.

Cross-References

- [Development](#)
- [Environmental Influences](#)
- [Fetus Development](#)
- [Nativism](#)
- [Nature Versus Nurture](#)
- [Newborn Behavior](#)
- [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Stumble

► Stuttering

Stuttering

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Synonyms

Stammering; Stumble

Definition

Stuttering is a disorder of verbal fluency characterized by repetitions and prolongations of sounds and syllables.

Introduction

Effortless concatenation of words with proper cadence and stress pattern to produce utterances is a much taken-for-granted skill. In roughly 1 % of the general population who stutter, this skill is compromised with negative consequences on educational, vocational, and social life.

Developmental Stuttering

Stuttering typically begins during early childhood years between the ages of 2–5 years – a period of rapid growth, especially in language and speech. Most children within the age group occasionally (or intermittently) repeat monosyllabic words (But- but), initial sounds, and syllables of words (ka- car) (collectively called part-word repetition) before producing the target word. Very rarely,

they may prolong initial sounds of words. Clinicians consider both the type and frequency of these occurrences (called disfluencies) and other speech-related features in the context of family history to diagnose the problem of Developmental Stuttering (DS) (Ambrose and Yairi 1999).

Repetitions and prolongations are considered core features of DS (Wingate 1964). Ambrose and Yairi (1999) have shown that the onset of stuttering is typically gradual; however, in a small minority it is sudden; also, onset is characterized by repetitions of initial sounds, syllables, and monosyllabic words. The other defining feature, namely prolongation of initial sounds of words, is generally considered to be red flag for persistency. There is a consensus, based on many studies (Ambrose and Yairi 1999; Mansson 2005) that in nearly 80 % of children DS is self-limiting, that is, recovery occurs naturally or without formal intervention, within a short span after onset (2–5 years). The remaining 20 % who persist continue to stutter and may exhibit a variety of speech and nonspeech (behavioral, emotional) concomitants that need special therapeutic attention from speech-language pathologists. The incidence of stuttering tapers off considerably after the age of 5 years. The challenge to both researchers and clinicians is to arrive at a list of empirically verified criteria that reliably sort out those in whom the disorder is self-limiting and those in whom it is not. A rough outline of an answer to this question is emerging. Thus, recent research indicates that in children who produce multiple irregularly paced repetitions of the initial sound or syllables of words prolongation of the initial sounds are likely to persist (Ambrose and Yairi 1995). A discerning clinician will take into account these findings along with frequency of disfluencies, family history of persistent, and recovery from it to treat/ manage the disorder.

When clinicians refer to stuttering, they generally refer to children with Developmental Stuttering (DS) or older children and adults with Persistent Developmental Stuttering (PDS). Fluent speech can also be disrupted because of brain injury or psychological causes including malingering for financial reasons (financial compensation following accidents). This group is called Acquired Stuttering (AS). These individuals

exhibit many of the defining features of DS; however, they differ from DS in terms of location of disfluencies in sentences as well as how individual disfluencies are produced. Research in this area is very preliminary because AS is very sporadic (Viswanath 2010).

The proximal causes of speech fluency breakdown during stuttering have been investigated using a variety of methods – EMG, aerodynamic, and acoustic representing multiple levels of production process. These investigations reveal the dynamics underlying stuttering episodes (e.g., Viswanath and Neel 1995) but also have shown that imperceptible but significant deviations in speech gestural coordination (temporal and spatial) exists even when stutterers are perceptibly fluent. The tenuous fluency may arguably be the basis of fully elaborated perceivable intermittent interruptions we call stuttering (Viswanath and Rosenfield 2000) and presents assessment challenges to clinicians.

The more distal causes of stuttering, in a sense more fundamental, is the role of genetics and the brain mechanisms underlying stuttering. A general outline of the role of genetics in the development, natural recovery, and persistence is slowly emerging. It was known for a long time that stuttering runs in the families and that boys with DS outnumber girls with DS (3:1). DS aggregates in multigenerational families in rates greater than general population prevalence of 1 %. However, studies of such multigenerational pedigrees showed that the pattern of transmission (so-called segregation pattern) did not fit into one of the well-known, simple inheritance patterns discovered by Mendel. There are studies of multigenerational families (e.g., Viswanath et al. 2004; Ambrose et al. 1997) that suggest a model where a single dominant gene in a multifactorial context (other genes and environment) may be the best account for the disorder. There have been several recent successful attempts to locate the putative gene (s) on chromosomes using linkage and other more recent techniques in genomic science (e.g., Riaz et al. 2005).

A coherent account about stuttering must address the issue of brain mechanism underlying the intermittent disfluencies that we call stuttering events. Recent applications of neuroimaging

techniques – PET (Positron Emission Tomography), Functional Magnetic Resonance Imaging (fMRI), Magneto-Encephalography (MEG) – have revealed tantalizing differences between PDS and fluent speakers in how the brain implements the task of speaking. The activation patterns and the areas of activation in the two hemispheres, basal ganglia and cerebellum, differ between PDS and fluent speakers; stutterers tend to get “normalized” when immediate fluency is induced by such techniques as Choral speech, speaking in unison with metronome beats, or masking noise. Volumetric MRI – that is useful to study fine-grained anatomical differences – has shown gyral pattern differences between the PDS and normal controls around Peri-sylvian fissure in left hemisphere. Perisylvian areas in the left hemisphere is intimately involved in language and speech processing. All these findings are preliminary – they provide an impetus for developing models of mechanism of stuttering events (Ingham et al. 2003). A coherent and complete account will also provide the pathway(s) from gene (s) and its products (proteins coded) and products’ effect on brain development and functioning that leads to atypical functioning and observable disfluencies.

In the absence of understanding of causal basis of the disorder, current approaches to therapy focus on using behavioral (symptom management) and cognitive therapy techniques. There is generally a consensus that early intervention in young children is preferable to no treatment despite high rates of natural recovery. Modalities of therapy with adolescent and adult stutterers vary with the nature of behavioral and emotional overlay an individual presents. Techniques to modify disfluencies by altering speech pattern coupled with behavioral techniques to eliminate avoidance and escape behaviors that persistent developmental stutterers exhibit is the main focus of therapies in adults.

Conclusion

Stuttering is an early childhood disorder that emerges during rapid growth of language and speech. Recent research shows that it is a

biologically inherited disorder with significant learning component. Eighty percent naturally recover; in the remaining 20 % it becomes persistent disorder with negative impact on vocational and personal life.

Cross-References

- [Brain Imaging](#)
- [Broca's and Wernicke's Areas](#)
- [Communication and Developmental Milestones](#)
- [Critical Period](#)
- [Genetic Predispositions](#)
- [Learning](#)

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Subcultural Theory

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Synonyms

[Culture Subdivision](#); [Subgroup](#)

Definition

A cultural subgroup within a larger culture is defined as having some behaviors, beliefs, or interests different from the mainstream culture.

Introduction

The concept of *subculture* was initially developed in sociology and anthropology (Berzano and Genova 2015). *Counterculture*, on the other hand, refers to a particular type of subculture whose values and behaviors differ substantially from those of mainstream culture, being in opposition to mainstream culture values and behaviors (Hirsch et al. 2002). An example of counterculture may be the hippie subculture during the 1960s and 1970s.

Subculture Characteristics

The concept of subculture began during the early twentieth century. It is related to Durkheim's

sociology (Durkheim 1895) and the so-called Chicago School (Park and Burgess 1921). This concept has been used by a diversity of disciplines, including sociology, anthropology, psychology, and criminology. However, it has been most influential in sociology and criminology as a major explanatory tool to comprehend deviant behaviors (Blackman 2014).

A diversity of subcultures have been described, including subcultures according the age (e.g., youth subculture, aging subculture), gender, place of living, professional activity, illegal groups, economic status, educational level, and others. Nonetheless, the concept of subculture has been frequently used to interpret deviant behaviors. Within criminology, the concept of subculture has been usually interpreted as dysfunctional, inappropriate, and delinquent.

During the 1970s, the Centre for Contemporary Cultural Studies (CCCS) (Hall and Jefferson 1975) redefined the analysis of subcultural studies, youth, and deviance. The new approach on deviant behavior interpreted subcultures in terms of their engagement in resistance and social opposition. Different studies, particularly in England and the USA, have analyzed the characteristics of youth subcultures particularly with regard to deviant behaviors (Blackman 2005; Williams 2007). Currently, and given our contemporary technological conditions, it has been suggested that diverse social media (internet, virtual reality, games, etc.) have promoted the emergence and development of diverse new subcultures among the young generation (Zhao et al. 2017). Gender, ethnic, and even hobbies preference subcultures have been described in youngsters (Hollingworth 2015).

Other studies have emphasized the regional subcultures. As an illustration, Neapolitan (1994) analyzed the Latin American subculture of violence, and relate it with cultural values that have evolved out of the history of colonization and subjugation that is shared by most Latin American nations.

A subculture of education has been proposed since long time ago (Vygotsky 1930/1980). Education develops some specific values and reinforces certain patterns of behavior, and

hence, a subculture of education can be distinguished. Recently, Venuleo et al. (2016) tested the hypothesis that educational subculture in terms of which students interpret their role and their educational setting affect the probability of dropping out of higher education. Results demonstrated that the probability of dropping out is significantly associated with students' educational subculture – but not with their incoming level of knowledge and skills. Similarly, diverse living characteristics in different working and socioeconomic conditions are correlated with some specific values and behaviors. Riessman and Miller (2017), as an illustration, analyzed the working-class subculture. The nature of the conditions of working-class lives (jobs, opportunities, and family structure) affects values, attitudes, and behaviors. As an important element, coping with, the instability threats becomes a dominant activity and core element within the working-class family; specific practices, such as mutual aid and cooperation, extended family perspectives, are important as coping mechanisms found in this working-class subculture.

Similarly, a subculture of poverty has been described in anthropology (Lewis 1959; Wilson 2016). This subculture has some very specific values including helplessness, the search for immediate gratification, dependency, marginality, and powerlessness. The notion of a subculture of poverty, however, sometimes has been considered to be simplistic.

Conclusion

In every culture, variations are observed. When some behaviors, beliefs, and values are different enough from the mainstream culture, we can refer to a subculture. The concept of subculture began in sociology during the early twentieth century and has been sometimes associated with deviant and delinquent behaviors. However, diverse subcultures can be distinguished departing from different social, anthropological, and psychological variables: age subcultures, gender subcultures, professional subcultures, regional subcultures, etc.

Cross-References

- ▶ [Cultural Intelligence Hypothesis, The](#)
- ▶ [Cultural Universals](#)
- ▶ [Cross-cultural Similarities](#)
- ▶ [Cross-Cultural Pattern](#)

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Subgroup

- ▶ [Subcultural Theory](#)

Subjective Arousal

- ▶ [Sexual Arousal](#)

Subjectivity

- ▶ [Meaning Making and the Self](#)

Submission

- ▶ [Primate Dominance Hierarchies](#)

Subordinate Behavioral Tactics

- ▶ [Salter, Grammer, and Rokowski \(2005\)](#)

Substance Abuse

- ▶ [Substance Use Disorder](#)

Substance Addiction

- ▶ [Substance Use Disorder](#)

Substance Dependence

► [Substance Use Disorder](#)

Substance Misuse

► [Substance Use Disorder](#)

Substance Use Disorder

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Synonyms

[Drug abuse](#); [Drug addiction](#); [Drug dependence](#); [Drug misuse](#); [Substance abuse](#); [Substance addiction](#); [Substance dependence](#); [Substance misuse](#)

Definition

A class of mental disorders characterized by compulsive seeking and use of mind-altering substances despite experiencing severe negative consequences.

Introduction

The nature of substance use disorders (SUDs) has changed exponentially over the years with the development of novel and highly potent synthetic formulations and creative methods of ingesting substances to achieve a variety of euphoric effects (Lovrecic et al. 2019; United Nations Office on Drugs and Crime 2017). The global burden of SUDs has reached epidemic proportions for some classes of substances with unprecedented deaths from opioids prompting the declaration of a public health epidemic in the United States (Kanouze and Compton 2015; Kolodny et al. 2015; Rudd et al. 2016; United Nations Office on Drugs and Crime 2017). Integrated biopsychosocial models of the development and perpetuation of SUDs have enhanced our understanding of what many in the scientific community consider a chronic and progressive brain disease (NIDA 2018; Volkow et al. 2016). While effective pharmacological, motivational, and cognitive-behavioral interventions for SUDs exist and are widely available (Carroll and Kiluk 2016), the SUD problem persists and does not seem to be going away any time soon. Evolutionary theories may add a much-needed perspective to help understand and inform the prevention and treatment of SUDs.

This entry reviews three major evolutionary theories of SUDs (i.e., Mismatch Theory, Life History Theory, and False Fitness Theory) directed at understanding how our ancestors used substances to solve problems and protect the species, the mechanisms that evolved to make modern human beings susceptible to SUDs, and reasons natural selection has not eliminated vulnerabilities to developing SUDs. The entry also applies the evolutionary perspectives outlined above to understanding the ontology of SUDs and the major proximal processes, mechanisms, and behaviors associated with compulsive drug seeking.

Evolutionary Benefits of Naturally Occurring Substances

According to Hagen and Sullivan (2018), humans evolved adaptations for detecting, avoiding, and

neutralizing plant toxins through a billion-year arms race with their defenses. For millions of years, our primate ancestors fed on plants that leveraged toxins to ward off predators. Today, humans are armed against plant toxins with defenses such as bitter taste; tissue barriers (e.g., in the gastrointestinal tract); and nausea, vomiting, and conditioned taste aversion. These systems could only have evolved given a long evolutionary history of human exposure to and interaction with plant toxins. That humans correctly identify drugs as aversive toxins, yet find them rewarding enough to seek out and consume, is “the paradox of drug reward” (Hagen et al. 2009; Sullivan and Hagen 2002; Sullivan et al. 2008). Below we review some of the possible fitness benefits of various psychoactive substances in response to this paradox.

First, humans may have evolved to metabolize alcohol through consuming overly ripe and fermented fruits (Dudley 2002). Continued ingestion of overly ripe and fermented fruits and psychotropic plant substances at low, nontoxic doses may have enhanced physical health, performance/endurance, cognitive functioning, and social relationships (for reviews see Davis 2014; Dudley 2002; St John-Smith et al. 2013). Indeed, alcohol improves mood, induces mild euphoria, and increases confidence, sociability, communication and intimacy (helpful for mating/reproduction); moreover, it is an anxiolytic, aids in sleep, and serves as an antibiotic and, in the past, an anesthetic (for reviews see Davis 2014; Nace 2016; St John-Smith et al. 2013).

Cocaine, caffeine, and nicotine increase energy, stamina, alertness, and attention, which may have afforded an advantage in hunting, foraging, and protecting next of kin (Davis 2014; Juliano and Raglan 2016). Cocaine may have also served as a local anesthetic and an appetite suppressant during times of famine, and opioids, found naturally only in trace amounts, may have served as a pain reliever and sleep aid (for a review see Davis 2014). Hallucinogens may have facilitated group cohesion and bonding (St John-Smith et al. 2013). Moreover, people may have deliberately sought compounds found in psychotropic plants for medicinal purposes

(Ben Amar 2006; Davis 2014). Tobacco and cannabis may have helped ancestral humans reduce pathogen load, and consumption of plant neurotoxins may have prevented or treated macro-parasite infections (Hagen et al. 2013). For example, both tobacco and cannabis use appear to ward off helminths (Roulette et al. 2014, 2016).

From an evolutionary perspective, our ancestors may have been able to maximize fitness and survival success by ingesting naturally occurring substances at low levels that did not result in impairment or harm. However, modern technological advances in the production and administration of highly potent substances have led to an evolutionary mismatch and the development of SUDs, which “has no adaptive value” (Hill et al. 2017, p. 142).

Evolutionary Mismatch

According to mismatch theory, pathology stems from the adverse effects of modern environments on evolved traits that were once adaptive (Li et al. 2018). Human intelligence has led to innovations in every facet of life – medicine, technology, food production, transportation, climate control, leisure, etc. (Buss 2000). The human capacity for innovation has extended our longevity, dominance over other species, and has led to the massive migration and propagation of our species. Unfortunately, some innovations have resulted in many unintended consequences including propagating the public health crisis of SUDs (Buss 2000).

Synthetic opioids, initially conceived with the intention of alleviating chronic pain, have morphed into deadly addictions in vulnerable individuals. The development of syringes to deliver medications has contributed to more addictive and lethal means of ingesting addictive substances. Modern-day manufacturing and distribution of substances (e.g., distillation and purification of alcohol; engineering of synthetic drugs without plant cultivation) has led to a major strain on what our ancient brains were naturally evolved to handle (Davis 2014; St John-Smith et al. 2013; Li et al. 2018; Nesse 2002; United Nations Office

on Drugs and Crime 2017). Technological advances and the development of virtual online pharmacies have promoted aggressive and sophisticated marketing techniques, flooding global markets with hundreds of highly potent novel psychoactive substances, including synthetic amphetamines and cannabinoids (Dignam 2017; Schifano 2018).

The change from an ancient environment of very limited resources to a modern world where basic needs are generally satisfied and hedonic desires are easily fulfilled has taxed self-control abilities that were untested or unnecessary in ancient times (Lende 2008). The higher potency of manufactured substances has bypassed defenses or regulatory mechanisms that would have protected our ancestors from developing SUDs. Moreover, insofar as the modern world presents with novel psychosocial stressors, widely available substances may be regularly turned to as a fast acting, albeit maladaptive, coping mechanism, and reward during times of stress (Lende 2008). Indeed, Nesse (2002) has suggested that SUDs may be “a disease of civilization” (p. 471).

Life History Theory

In evolutionary biology, fitness is the average contribution of a genotype or phenotype to the gene pool of the next generation. Life history theory is a framework of trade-offs used by evolutionary biologists to explain differences between species in the manner by which they optimize fitness given the challenges of their particular ecologies (Stearns 1976, 1989). The basic logic of life history theory is that because resources are finite, investments in fitness components (e.g., size at birth, growth, age and size at maturity, number of offspring, rates of survival, and lifespan) trade off against each other. For instance, investments in offspring quantity trade off against offspring quality. Life histories are life course patterns of investments in fitness components that emerge from trade-offs and are often conceptualized as falling along a fast-slow continuum. Whereas mice follow a faster life history trajectory and reproduce early, produce many

offspring, and engage in little parenting, elephants follow a slower trajectory and reproduce relatively late, have few offspring, and parent more extensively.

As recently described by Richardson et al. (2018), life history theory has also been leveraged to explain differences within species in terms of genetic differences as well as developmental plasticity (i.e., differences in developmental trajectories due to early environmental conditions). Applied to humans, the logic of tradeoffs has been used to explain the co-occurrence of investments in traits and behaviors that seem to optimize fitness in harsh and unpredictable environments (e.g., earlier puberty and sexual debut, lesser parenting effort, as well as greater aggression, risk-taking, mating effort), as well as the opposite pattern of investments, which seems to optimize fitness given safe and predictable conditions (e.g., later puberty and sexual debut, greater parenting effort, and lesser aggression, risk-taking, and mating effort). Mirroring the fast-slow continuum between species, the former has been termed a faster life history strategy in human research and the latter a slower life history strategy (Figueredo et al. 2006). Research has confirmed that faster life history strategies reflect harsher and more unpredictable early environments (for a review, see Ellis et al. 2009), although it is not yet clear to what extent this is due to gene-environment correlation and/or causal effects of early environment that change developmental trajectories (Barbaro et al. 2017; Richardson et al. 2018).

Research suggests that internal working models mediate the development of faster or slower life histories in humans. In particular, unpredictability schemas (e.g., belief the world is chaotic and unpredictable; Hill et al. 1997; Ross and Hill 2002; De Baca et al. 2016), present time perspective (Chisholm 1999; Copping et al. 2014; Kruger et al. 2008), and shorter life expectancies (Chisholm et al. 2005) seem to translate harshness and unpredictability into faster trajectories. In light of evidence that (a) faster strategies seem mediated by a focus on short-term survival and reproduction, (b) psychoactive substances provide the experience that substances and related stimuli are of great and immediate biological

importance, and (c) the costs associated with severe use are often realized over a longer term, researchers suggested that faster life history strategists are likely more vulnerable to SUDs (Hill and Chow 2002; Lende and Smith 2002; Richardson and Hardesty 2012). Subsequently, studies confirmed that greater substance use frequency and severity reflects lower levels on a dimension subsuming somatic, parental, and community integrative effort, and higher levels on a dimension subsuming indicators of mating competition (e.g., risk-taking, aggression, delinquency, and greater numbers of sexual partners; Richardson et al. 2014, 2016, 2017a, b, c).

Finally, applications of life history theory to the development and maintenance of SUDs also predict a shift of resource allocation with age toward parenting and nurturing of relationships and away from reproductive and survival goals (Hill and Chow 2002; Durrant et al. 2009). Risk taking behavior, which could be advantageous in mating competition, is expected to peak during young adulthood and decrease with age as individuals mature, obtain resources/status, and develop greater concerns for family welfare and long-term health/survival (Durrant et al. 2009; Hill and Chow 2002). This appears to be the case with SUD, which peaks in young adulthood and then subsides thereafter (Park et al. 2006). Young adult men, relative to women and older men, also engage in the highest levels of risky drinking; from an evolutionary perspective, this has much to do with competition for mates, which is more salient for young men than it is for women or older men (Hill and Chow 2002; Park et al. 2006).

False Fitness Theory

Emotions evolved to serve an adaptive purpose (Al-Shawaf et al. 2015; Buss 2000). Even those emotions that are subjectively experienced as aversive and unwanted are necessary (Buss 2000; Nesse 1994). Anxiety and fear potentiate action tendencies directed at avoiding or escaping from threats; anger promotes aggressive actions that can ward off danger and facilitate competition

for mates; disgust and disgust-related emotions (i.e., guilt, shame, embarrassment) mitigate eating spoiled/toxic foods and repeating noxious behaviors that could result in expulsion from a social group, and jealousy may signal threats to sexual or emotional bonds (Al-Shawaf et al. 2015; Buss 2000). Moreover, emotions that tend to be more pleasant, such as happiness, joy, excitement, and love, likely evolved to motivate various goal pursuits and enhance social bonds, which can enhance longevity, survival, and reproduction (Al-Shawaf et al. 2015). Finally, all emotions serve an invaluable communicative function (Tracy et al. 2015). Given that emotions function to reinforce behaviors that promote survival, circumventing natural emotional responses through substances have a deleterious impact, including giving a false sense of fitness.

In modern society, where unrealistic expectations of success are ubiquitous and self-concept is easily diminished (Buss 2000), self-medication and happiness-seeking through substance use can impair the brain's ability to detect real successes or threats, which can impair adaptive behavior (St John-Smith et al. 2013; Panksepp et al. 2002). Through substance use, humans have learned to directly stimulate pleasure pathways and bypass the natural function of positive emotions, which are meant to signal a reproductive or survival benefit; by doing so, substance use seems to create a sense of fitness where one does not truly exist (Nesse 2002; Sullivan and Hagen 2002). Moreover, substance-induced euphoria signals pathological wanting, signaling to the brain that substance use deserves the utmost attention, even when other goals such as finding food, resting, or caring for a loved one are more important and require forethought and attention (Durrant et al. 2009; St John-Smith et al. 2013; Panksepp et al. 2002). The prominent position that substance use can assume in an individual's life may disrupt relationships, childcare responsibilities, health maintenance, and other important goal-directed behavior. For example, when substance use interferes with experiencing positive feelings and attachment toward a child, the child is more vulnerable to neglect and abuse. Moreover, substance use can override necessary, albeit

unpleasant, emotions like disgust that can reduce the likelihood of engaging in otherwise repugnant acts (e.g., using contaminated needles). In sum, the false fitness effects of substances may disrupt threat detection, learning, coping, self-regulation, and the goal-directed behavior necessary for effective functioning.

Neurobiological Perspective

In the ancestral environment, moderate dosing of psychoactive toxins would have allowed for optimal activation of reward-related brain systems that supported behaviors integral for survival. The same neural systems in a contemporary environment may serve to “prime” the modern brain for addictive behaviors within certain contexts. As already discussed, these may include environments where synthetic drugs with high potency are readily available (Mismatch Theory), where chaotic home environments elicit impulsive behavioral traits (Life History Theory), or where a decoupling of emotional systems from environmental threats and successes allow individuals to bypass normal information processing systems (False Fitness Theory). Notably, advances in both neuropsychological and comparative research can help to support these evolutionary theories of addiction.

Initial support for these enduring physiological changes is provided by comparative evidence, which shows that the mesolimbic dopaminergic reward and opioid and endocannabinoid systems have been preserved, both anatomically and functionally, across phyla. In particular, the role of dopamine in modulating motivational responses to natural rewards is highly conserved and still observed even in worms and flies, which evolved 1–2 billion years ago (Nestler 2005). Moreover, amphibians and bony fish possess a developed opioid system for the purposes of pain perception (Dreborg et al. 2008; Sneddon 2004; Stevens 2004). In humans, research demonstrates that the same mu receptor that mediates motivation for opioids and narcotics may have enhanced mammalian social bonding over the course of evolution (Panksepp et al. 2002). Finally, an ancient

endocannabinoid system signals important functions throughout vertebrates, such as feeding, learning, locomotor control (Elphick 2012), and male fertility (Fasano et al. 2009).

The complex coordination between these reward learning and regulatory brain systems (e.g., NAc, extended amygdala, VTA, PFC, lateral habenula) seems to be preserved across rodents and primates (Scaplen and Kaun 2016). They also play a proximal role in the transition from controlled to compulsive drug seeking in humans (Koob and Volkow 2010, 2016). For example, nearly all drug intoxication is accompanied by the release of dopamine and opioid peptides into the ventral striatum (Mitchell et al. 2012; Volkow et al. 2007; Koob 2015). This serves to elicit appetitive, positive affective emotions (Baldo and Kelley 2007; Burgdorf and Panksepp 2006), high incentive salience (Berridge and Robinson 1998) and to reinforce drug consumption via stimulus-response and conditioned learning processes (Delgado 2007; Daniel and Pollmann 2014). The transition over time of these corticolimbic circuits from prefrontal to striatal control over drug seeking characterizes the move from associative learning to habit formation in individuals with SUDs (Everitt and Robbins 2005, 2013) and is causally linked to the development of addiction (Giuliano et al. 2019; Everitt and Robbins 2016).

In our evolutionary past, habit formation would have been essential for animal and human life (Newlin and Strubler 2007). Interestingly, habit formation circuitry – a mesolimbic system with dopaminergic neurons ascending from the midbrain to a dorsal and ventral striatal complex – has been observed in nonmammalian vertebrates (Nesse and Berridge 1997). While there may be some functional variation within these systems across phyla, findings hold some support for the idea that habit formation circuitry may reflect a preserved system once critical for the development of flexible goal-oriented behaviors, including the acquisition of feeding patterns and foraging (Hodgson 2008; Newlin and Strubler 2007), within an unpredictable and chaotic landscape (Doebeli and Ispolatov 2013).

While the acquisition of survival-related habitual behavioral patterns may have necessitated a progressive transition from prefrontal to striatal control (Everitt and Robbins 2013), natural limitations within the ancestral environment (sparsity of drugs, less potency, positive reinforcement of legitimate fitness) were likely to have provided the regulatory parameters to render substance use adaptive (Saah 2005). In contrast, in our modern environment, thwarting natural selection processes can render these latent processes a liability. Hypofrontality in emotional and cognitive regulatory systems and sensitization of limbic circuits underlying conditioned responses often culminate in a loss of control over enhanced drug salience (Volkow and Boyle 2018).

Negative reinforcement processes are also triggered by the majority of drugs through acutely stimulating core stress system activity within the extended amygdala and habenula, via elevated release of hypothalamic CRF, HPA axis markers, NE, and dynorphin (Koob and Volkow 2016; Koob 2009; Wemm and Sinha 2019). This engagement of the stress systems modifies reward-related behavior through stimulation of mesencephalic dopaminergic transmission (Piazza and Le Moal 1997). Importantly, elevations in core stress system sensitivity and the persistent nature of an enhanced dysphoria and anxiety underlie the propensity for individuals to misuse many drugs of abuse including cocaine, alcohol, opioids, and nicotine (Fox and Sinha 2009; McKay 2011; Sinha 2008; Fox et al. 2007; Cosci et al. 2011). Moreover, activation of the stress response also represents an evolutionarily conserved neural response, with a substantial survival value, including initiating fight or flight behavior in the face of predators, faster reaction time, and increased cognitive acuity from sympathetic arousal (Nesse et al. 2007).

The selective advantage afforded by the stress response is also evidenced by the fact that despite the high health-related costs associated with chronic stress reactivity, it has been preserved by natural selection. This is further exemplified by the fact that all vertebrates produce corticosterone (Raff 2016), peptide sequences similar to human ACTH are observed across phyla (Nesse and Young 2000), and the upregulation of basal stress

hormones has been shown to be a phylogenetically common response to stressful circumstances (Adamo and Baker 2011), and one that is also linked to attenuated predation (Adamo et al. 2013). In view of this, the ability of many psychoactive agents to increase energy and attentional acuity, by activating HPA and autonomic stress systems (Tsigos et al. 2016), may again have represented immense survival value in our ancestors.

In a contemporary society, persistent activation of these evolved circuits may culminate in a dampened motivation for nondrug rewards, an enhanced dysphoric emotional state, and an overriding of prefrontal control networks. In short, the human brain may be “primed” for addiction (Durrant et al. 2009; Lewis 2015). Whereas our ancient brain circuitry can predispose modern humans to addiction, it does so by permitting the flexibility to develop goal-related behaviors. Dysregulations within these systems reflect neuroplastic adaptations that, in the case of addiction, are associated with highly maladaptive behaviors. In other words, addiction is an extreme consequence of a normal functioning brain. An evolutionary psychobiological approach to addiction may provide a picture of a disorder rather than a disease (Henden and Gjelsvik 2017) somewhat akin to a “biological hangover.” Conceptualizing addiction in this way may serve to bridge the divide between conceptualizing addiction as an incurable condition or one that can be overcome by a sense of agency and personal responsibility.

Conclusion

Accounts of human substance use from an evolutionary psychology perspective are integrated with neurobiological findings to understand SUDs as a modern societal ill. Cognitions and behaviors associated with a fast life history maintain vulnerability for SUDs in a modern world that does not reward such traits. In addition, because the human brain did not evolve to process widely available, frequently used, and highly potent substances, an evolutionary mismatch may contribute to the development and maintenance of substance use disorders. Moreover, emotional systems that

evolved to signal threats and to actuate adaptive, goal-directed behavior are out of step with SUDs that signal fitness where fitness does not exist. In an age of sophisticated drug manufacturing, including rapidly advancing synthetic substances, the SUD problem is expected to persist.

While genetic variability has certainly contributed to vulnerabilities that facilitate maladaptive drug seeking, Hill and Newlin (2002, p. 378) caution against using evolutionary theory to support ideas of a “genetic determinism” where it may be wrongly presumed that experience does not influence behavior. Indeed, it is well known that learning is a primary component of behavior and that experience influences gene expression including whether genes are expressed at all (National Scientific Council on the Developing Child 2010). As such, the continued development of cognitive and behavioral therapies that strengthen brain areas involved with self-control combined with policy focused on reducing availability of substances and preventing early life adversities may help to curb the SUD problem. Moreover, a focus on enhancing dimensions of slow life history and curbing those indicative of a fast life history may help to prevent and treat SUDs (Richardson et al. 2019).

An evolutionary approach may also help to reduce stigma and encourage individuals with SUDs to seek treatment. Therapists may benefit from acknowledging that the brain is wired for habit formation and that habit patterns are commonly beneficial and at times necessary for survival. At the same time, therapists can communicate that, even though ingestion of toxins in very low doses may have at one time had fitness benefits, modern developments including the development and wide availability of potent substances that create a false sense of fitness have warped any benefit of this habit system and have, in fact, caused major brain and behavioral disruptions.

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Substantive Ethics

► Philosophical Foundations for a Modern Morality

Sufferer

- Victims Mostly Men
- Victims of Violence

Suicidal Enactment

- Death by Suicide

Suicidality

► Death by Suicide

Suicide

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Synonyms

Self-destruction; To kill yourself

Definition

Suicide is defined as an intentional, self-inflicted death.

Introduction

Suicide is a social phenomenon that can be described as an issue of public health. According to the World Health Organization (WHO 2019a), suicide kills over 800 thousand people worldwide, which translates to one death every 40 s. In 2016, suicide was marked as the 18th leading cause of death in the world, accounting for 1.4% of all deaths. Among those between 15 and 29 years of age, it is the principal cause of death. Other statistics reveal diverse aspects of suicide. For example, suicide is more prevalent among males who usually use more lethal methods. However, women engage in more suicide attempts than do men.

WHO's mortality database allows a broad vision of deaths reported by each country as a suicide. Considering the last reported number, provided between 2014 and 2016, the largest amount of deaths by suicide is found in the United States of America, with over 44 thousand deaths. Japan comes in second, with more than 23 thousand deaths, and Brazil comes next, with more

than 11 thousand deaths by suicide. In addition, France, Mexico, and the United Kingdom reported over 8, 6, and 4 thousand deaths by suicide, respectively (WHO 2019b).

Despite the statistics, the answer to the big question remains a debate in all related science and research fields: why do people want to take their own lives? Aiming to answer this question, many theorists and science fields have attempted to explain suicide in a range of different perspectives. Currently, the theme "suicide" is investigated from diverse angles in suicidology – the field of science dedicated to studying and investigating suicide and suicide-related thoughts and behaviors.

O'Connor and Nock (2014) argue that the most grounded research into suicide began in the 1950s and grew substantially in the last 25 years. The authors list the most prominent contemporary theories on suicide, beginning with the cubic model of suicide by Shneidman (1985), including models as the interpersonal-psychological model of suicide by Joiner (2005) and the cognitive model of suicidal behavior by Wenzel and Beck (2008), and end with ideation-for-action theories – a group of more recent suicide theories (for a brief review of the mentioned theories, see O'Connor and Nock 2014). Another group of recent theories deserves to be emphasized, given that they promise to make a difference toward a better understanding of suicide. These theories are united in what literature has been calling the "Ideation to Action Framework" (Klonsky et al. 2018). Basically, it includes four main propositions so far: Interpersonal Theory (IPT), Integrated Motivational Volitional Model (IMV), Three-Step Theory (3ST), and Fluid Vulnerability Theory (FVT). The major difference between these theories and the ones proposed before them is that these theories understand suicide as two different phenomena instead of just one. Specifically, they divide the concept of suicide into (a) the development of suicidal ideation and (b) the progression from suicide desire to attempts (Klonsky et al. 2018).

Although the Ideation to Action Framework is a new way of conceptualizing suicide, it is already backed up by scientific evidence. According to Klonsky et al. (2018), evidence gathered so far allows researchers to draw some important

conclusions. For example, attempters are distinguished from ideators by their capability for suicide, and pain and hopelessness motivate suicidal desire more than other factors. Nonetheless, as outlined by Aubin et al. (2013), suicide can be understood from the lenses of diverse perspectives. For example, biological theories suggest that suicidal behavior occurs from a combination of biological vulnerability and a psychosocial stressor. Systemic or developmental theories propose that disturbed social forces and family systems are crucial for understanding suicide. Cognitive theories combine a more extensive range of theories and important correlated constructs. For example, cognitive-behavioral theories emphasize the roles of hopelessness, the emotional dysregulation, and the perception of entrapment, among other cognitions (Aubin et al. 2013).

This entry aims to sum up how suicide has been studied from an evolutionary perspective. Specifically, we begin by reviewing the current position of researchers investigating suicide in nonhuman species. After that, we discuss how is it possible for behavior such as killing yourself to be selected for and maintained in humans. It is important to highlight that there we do not aim to cease the debate regarding this theme or present all the existent perspectives in the literature, but instead highlight the complexity of suicide.

Suicide from an Evolutionary Perspective

Through an evolutionary lens, suicide does not appear to make sense at first glance. If this was a romantic novel, suicide would be described as the point where “the plot thickens,” given that the most natural and primal urge of humans is disregarded: the instinct of survival and reproduction. Suicide in this field can be described as a choice to zero out your fitness. Even so, it is a topic with valid theoretical hypotheses behind it. Mainly, evolutionary theorists stress that the goal of evolutionary psychology is to provide clues on ultimate causation and thus explore why the phenomenon exists (Aubin et al. 2013).

There is still a lot of debate toward the premise that suicide can be found in both humans and non-human animals, the major goal being to answer: can nonhuman species commit suicide? Peña-Guzmán (2017) argued positively on this issue; Soper and Shackelford (2018) argued in response that when it comes to other species, suicide is not found due to cognitive limitations of nonhuman species and evolutionary mechanisms that would have already eliminated any suicide genes – had they ever existed. Soper and Shackelford (2018) contend that there is not enough evidence to support suicide in nonhumans and the behaviors described by some as suicide are, in fact, a result of risk-taking behaviors selected by the environment or a sacrifice of their soma in accordance to algorithms of inclusive fitness. In both cases, the main argument is that once the animal has ended its reproductive and protective roles, it has nothing to lose. Therefore, the fact that in some species members die by defending their colonies or in other species they die after their reproductive life is over would not, arguably, qualify as a suicide.

Despite this issue, suicide in humans is an undeniable phenomenon. Hence, in 2013, Aubin and colleagues outlined the main theoretical propositions regarding suicide from an evolutionary perspective: the bargaining hypothesis, the altruistic suicide hypothesis, and the parasite manipulation hypothesis. The bargaining hypothesis posits that suicide attempts function as a gamble, with support by the fact that most attempts are nonfatal. According to this hypothesis, suicidal behavior is a cry for help to a community, which would act as a signal that if assistance or change is not provided in face of a conflict, it will have evolutionarily cost for the community. The gamble consists of measuring the expression of need, because the false exaggeration of need often results in no help, as the honest signal of need usually motivates people with pre-existing interests to help in order to avoid a fatal outcome.

The altruistic suicide hypothesis is based on a mathematical formula developed by De Catanzaro (1991). It affirms that it is possible to assess the residual capacity of an individual to influence his inclusive fitness. In other words, this measure is believed to predict the degree to which self-

preservation is optimally expressed. Regarding suicide, it has been shown that the association of burdensomeness toward kin and low residual reproductive potential can lead to negative values. Basically, suicide may be seen as an altruistic self-destructive (i.e., suicide for the good of the group) behavior when a person is of negative value, according to this hypothesis. Support for this position has been found in a wide variety of organisms, such as unicellular organisms, parasites, and possible in mammals (Aubin et al. 2013; Taylor-Brown and Hurd 2013). In nonhuman animals, the self-sacrifice persists because of its positive impact on the fitness of the colony's reproductive individuals. For example, suicidal defense behaviors can be a consequence of engaging in combat to defend the colony, as a way to rid the nest of an enemy, and even as an altruistic self-removal by sick or contaminated individuals to (presumably) diminish the risk of contamination in the nest. Under this view, human suicide can also be an act of altruism in cases that the reproductive value of an individual is low. In fact, social isolation and perceived burdensomeness toward family has been correlated with suicidal ideation (Shorter and Rueppell 2012). Historically, suicide in old cultures (e.g., Inuits) has been considered altruistic in cases where someone was old or ill and would kill themselves or ask to be killed in order to not be a burden in times of poor hunting. At an individual level, if someone perceives themselves to be a burden, the act of killing themselves might be motivated by the same altruistic principle.

And lastly, the parasite manipulation hypothesis is grounded in literature on modifications induced by a parasite on host behavior. Like in the animal field, humans can also be infected with parasites that have an ability to modify human behavior, and this hypothesis suggests that such parasitic behavioral modifications are what cause suicide. Nonetheless, this is just a hypothetical scenario. For example, Aubin et al. (2013) argue that the *T. gondii* parasite can present a possible explanation for suicide. *T. gondii* is an intracellular protozoan that can infect all mammals, including humans, and its infection in humans was found to be related to mental disorders and behavioral alterations (often subtle), like altered

personality profiles (reviewed by Aubin et al. 2013). This evidence contributes to the assumption that suicide may be caused or increased by such parasite behavioral manipulations.

The Study of Clusters in Suicidal Behavior

“Suicide clusters” refer to multiple suicidal behaviors or completed suicides that occur within a relatively short time frame and/or within a specific geographical area (e.g., Zenere 2009), although the definition of a cluster varies widely with regard to the number of deaths and the temporal proximity in which they must occur. The study of suicide clusters covers suicide's apparent contagion characteristics, specifically studies about the “Werther effect” (i.e., the increase in suicides after a widely publicized suicide) and the different types of clusters known in the literature (for a review, see Haw et al. 2013). As the understanding of suicide clusters advances, evolutionary psychology also contributes to this field with the notion of suicide copycats. This concept refers to the tendency that humans copy each other, especially those who are seen as persons of success, and this tendency may lead to the spread of biologically maladaptive traits like suicide (Mesoudi 2018).

In short, two main types of clusters are widely studied: mass clusters, which are a phenomenon that occurs in a restricted period of time after the media disclosure of real or fictional suicides, and point clusters, which are characterized by a high number of suicides occurring in a small geographical area or institution over a relatively short period of time. More recently, another type of cluster is mentioned: echo clusters. Echo clusters are defined as geographic locations that gather many suicides over long periods of time, such as the Golden Gate Bridge (Haw et al. 2013).

Risk and Protective Factors of Suicide

It is very common for researchers in suicidology to investigate risk factors related to suicidal

behaviors. Protective factors, although less common, are also investigated by some researchers. For example, using principles from research into suicide clusters (e.g., Brent et al. 1989; Haw 1994), it was found common for cluster participants to have a history of suicidal ideation and a previous diagnosis of a mental disorder. Proximity to the original victim in the cluster also predicted a more rapid onset of suicide symptoms (Gould et al. 1989). In this way, the study of clusters contributes to the investigation of the contagion of the phenomenon, endorsing the importance of variables that can be configured as possible risk and protective factors.

Usually, the published material on risk and protective factors are concerned in identifying what figures as a risk/protective factor in different populations or specific phenomena. For instance, Gvion and Levi-Belz (2018) conducted a systematic review of the psychological risk factors for serious suicide attempts and identified that interpersonal problems, impulsivity, and aggression seem to facilitate the occurrence of serious suicide attempts. However, risk factors can also be explained by considering evolutionary psychology's propositions, as noted by Aubin et al. (2013). What is called a "risk factor" can also be understood as nonadaptive by-products of evolved mechanisms that malfunction. For example, mental disorders are often present in suicide cases, and evolution has shown that negative emotional states can be useful in accomplishing a diversity of goals, such as expressing a need for help or signaling the act of yielding in a hierarchy conflict. Even so, it can also lead to the inhibition of certain behaviors that can protect the organism, such as the fact that sadness, pessimism, and lack of motivation can inhibit actions in the absence of a practical plan or in dangerous or futile challenges to dominant figures.

Similarly, to those risk factors used as examples, evolutionary psychology has tackled a great number of risk factors described by literature and joined it with its functional explanation. This includes specific behaviors associated with depression and suicide, such as crying (which elicits empathy and may increase social support), and specific markers, such as negative cognitive bias (which is likely to result in an overvaluation of perceived

burdensomeness and increase the risk of altruistic suicidal behavior; Aubin et al. 2013). Even though risk factors offer a useful way to work within suicidology, theories about the phenomenon of suicide are also abundant in today's literature.

Conclusion

Suicide is a worldly health problem. Different perspectives of studying and trying to explain this human behavior, collectively, converge within suicidology. Cognitive theories have been the focus of research fields and interventions; however, an evolutionary perspective may provide a deeper understanding of the adaptive significance of suicide and contribute to the creation of prevention strategies. For example, considering the promising theories within the Ideation to Action Framework, reduction of perceived burdensomeness and hopelessness in the mating arena might represent an effective prevention strategy.

Cross-References

- [Assisted Suicide](#)
- [Death by Suicide](#)
- [Factors Associated with Suicide](#)
- [Kin Selective Suicide](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)

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Suicide (Evolutionary Clinical Psychology)

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Synonyms

Self-harm; self-injury

Introduction

Suicidal behavior is a universal human phenomenon. Globally, suicide accounts for more deaths than all wars and homicides combined (Lozano et al. 2013). However, evolutionary theorists have for many decades largely overlooked suicidal behavior reasonably regarding the act as pathological or a byproduct of other mechanisms. However, given the universality and commonality of suicidal behavior, self-destructive behavior in all its forms is worth investigating from an evolutionary perspective. Two promising evolutionary theories of suicidal behavior are the inclusive fitness model (1981, 1984, 1991, 1995) and the bargaining model (Syme et al. 2016).

The Inclusive Fitness Model

The inclusive fitness model of suicide, developed by psychologist Denys deCatanzaro, takes an adaptationist view suicide wherein willful self-destruction is a means of increasing one's inclusive fitness. According to the model, suicide will be adaptive when an individual has low reproductive potential and is imposing net costs of genetic kin, such as in the case of a debilitating illness (1981, 1984, 1991, 1995).

There is evidence for the inclusive fitness of model from different areas of research. For example, there are examples of self-sacrifice for the benefit of genetically related individuals in non-human species such as sterile castes of the order Hymenoptera for the purpose of colony defense (Preti 2007). In *E. coli*, self-sacrifice appears to limit the transmission of a bacteriophage to even distantly related organisms (Refardt et al. 2013).

There is some evidence that low reproductive potential and burdensomeness map on to suicide. Cross-national statistics on suicide completions in the West demonstrate that the risk of suicide death increases with age as reproductive potential decreases and as the potential of being a burden on kin due to illness increases (Shah 2007). Moreover, suicidal ideation often corresponds to the perception of being “better off dead” or making others “better off.” There is an association

between chronic pain, a possible cue of burdensomeness, and suicide (e.g., Ratcliffe et al. 2008).

Investigators have tested the inclusive fitness model directly. In a study conducted deCatanzaro (1995), self-reports of low reproductive prospects and low valuations of one's worth to their family correlated with suicidal ideation. In a test of the inclusive fitness model against 53 distinct geographically diverse cultures in the ethnographic record, Syme et al. (2016) found that evidence for deCatanzaro's inclusive fitness model increased as a function of latitude. Thus, there was greater evidence for inclusive fitness model suicides in resource-scarce environments such as the Arctic where the provisioning of nonreproductive and infirm kin can be costly. Finally, according to Brown et al. (2009), low measures of health and low satisfaction in romantic relationships were associated self-destructive motivation among college students. In this same study, the researchers also found an inverse relationship between maternal age and self-destructive motivation, indicating that the reproductive value of kin might moderate the desire for suicide.

Clinical psychologist Thomas Joiner developed a model deemed the interpersonal theory of suicide that was partially informed by deCatanzaro's work. Joiner and his colleagues contend that a lack of belongingness, a sense of burdensomeness, and an acquired ability for suicide (e.g., self-harm, violence) lead to suicide completions (Van Orden et al. 2010). This model, while potentially illuminating in the clinical context, does not provide a complete evolutionary explanation for suicidal behavior and lacks appropriate modeling that demonstrates how such traits could be maintained by natural selection.

Kin directed suicide might explain some but not all cases of suicidal behavior. deCatanzaro (1995) noted that novel technology, such as guns and cars, could cause suicide death even in individuals with otherwise high reproductive potential and low burdensomeness. In such cases, the evolved human mind fails to take into its calculations the high lethality of these technologies. Furthermore, the vast majority of suicidal behavior is, in fact, nonlethal. For example, among US

females, there are about 400 suicide attempts for every one suicide completion (see Syme et al. 2016). Thus, much suicidal behavior occurs among young, healthy individuals who are not burdening their kin.

The Bargaining Model

The bargaining model is game theoretic model of suicidal behavior that was developed by anthropologist Edward Hagen and was originally applied to depression (Hagen 1999, 2003). This model of suicidal behavior sees nonlethal suicide attempt as a costly signal of need that will occur in the face of a severe fitness threat and a conflict of interest between the victim and social partners who are otherwise interested in his or her fitness. The suicide victim will likely have high reproductive potential such that the loss of this individual within the kin network represents a loss of fitness. Suicidal behavior is therefore a means for the powerless to strike back at powerful others in the face of injustice and conflict.

The employment of suicidal gestures as a means for relatively powerless individuals to protest or seek revenge on others is well documented in the ethnographic record. Among the Trobrianders, for example, suicide acted as a protest when one was falsely accused of a wrongdoing (Malinowski 1926). The Huron-Iroquois similarly regarded suicide as means to harm others in the event of a dispute (Fenton 1941). Women in regions as distinct as Afghanistan and Papua New Guinea engage in suicidal behavior (SB) to attack oppressive males, typically fathers and husbands who mistreat them (Billaud 2012; Johnson 1981). Among the Chuukese, suicide also communicates anger and dysphoria and calls attention to social tension (Hezel 1987). These accounts bear a similarity to "cry for help" models developed by psychiatrists and psychologists in the mid-twentieth century such as Stengel (1952) as well as Farberow and Shneidman (1961). However, despite far-reaching empirical support for these models, terminologies such as "cry for help" have fallen out of favor in professional fears due to valid concerns that such framing trivializes

nonlethal suicide attempts. On the other hand, the bargaining model, far from trivializing suicidal behavior, in fact, argues that it is an honest signal of social need.

Syme et al. (2016) tested the bargaining model against 53 cultures in the ethnographic record. In sum, suicidal behavior by young, healthy individuals in the face of a social conflict and severe fitness threat was common across cultural regions, though more research is necessary to confirm if this model is indeed operating in some instances. If the bargaining model is true, then this has critical implications for treating suicidal patients. Specifically, this would suggest that patients would be best treated socially rather than pharmacologically.

Conclusion

Multiple evolutionary models of suicidal behavior hold up against tests of these theories in different contexts. Suicidal behavior is, thus, a highly heterogeneous phenomenon. More research is needed, however, to confirm these theories. The inclusive fitness model might operate in resource-scarce environments that limit the ability of others to provision infirm family members. Features of the bargaining model, on the other hand, are common across diverse cultures. Social conflict, powerlessness, and fitness threats frequently precede suicidal gestures in a range of social and environmental contexts. The characteristics of suicide victims in each model are distinct. Whereas the inclusive fitness model will tend to apply to older individuals, the bargaining model concerns younger individuals with high reproductive potential. Thus, rather than competing, these two models might coexist.

Cross-References

- [Benefits to Kin](#)
- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)

- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide Terrorism](#)
- [Unemployed](#)
- [Young](#)

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Suicide as Kin-Directed Altruism

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Synonyms

[Inclusive fitness model of suicide](#)

Definition

The inclusive fitness model of suicide asserts that willful self-sacrifice can be maintained by natural selection when one has low reproductive potential and imposes costs on genetic kin.

Introduction

The inclusive fitness model of suicide, developed by psychologist Denys deCatanzaro, takes an adaptationist view of suicide wherein willful self-destruction is a means of increasing one's inclusive fitness. According to the model, suicide will be adaptive when an individual has low reproductive potential and is imposing net costs of genetic kin, such as in the case of a debilitating

illness (1981, 1984, 1991, 1995). Focusing on suicide completion, this model is contrasted with other evolutionary models of suicidal behavior that concern nonlethal suicide attempts (e.g., the bargaining model, see Syme et al. 2016).

Research on Suicide as Kin-directed Altruism

There is evidence for the inclusive fitness of model from different areas of research. For example, there are examples of self-sacrifice for the benefit of genetically related individuals in non-human species such as sterile castes of the order Hymenoptera for the purpose of colony defense (Preti 2007). In *E. coli*, self-sacrifice appears to limit the transmission of a bacteriophage to even distantly related organisms (Refardt et al. 2013).

There is some evidence that low reproductive potential and burdensomeness map on to suicide. Cross-national statistics on suicide completions in the West demonstrate that the risk of suicide death increases with age as reproductive potential decreases and as the potential of being a burden on kin due to illness increases (Shah 2007). Moreover, suicidal ideation often corresponds to the perception of being “better off dead” or making others “better off.” There is an association between chronic pain, a possible cue of burdensomeness, and suicide (e.g., Ratcliffe et al. 2008).

Investigators have tested the inclusive fitness model directly. In a study conducted deCatanzaro (1995), self-reports of low reproductive prospects and low valuations of one's worth to their family correlated with suicidal ideation. In a test of the inclusive fitness model against 53 distinct geographically diverse cultures in the ethnographic record, Syme et al. (2016) found that evidence for deCatanzaro's inclusive fitness model increased as a function of latitude. Thus, there was greater evidence for inclusive fitness model suicides in resource-scarce environments such as the Arctic where the provisioning of non-reproductive and infirm kin can be costly. Finally, according to Brown et al. (2009), low measures of health and low satisfaction in romantic relationships were associated self-destructive motivation among college students. In this same study, the

researchers also found an inverse relationship between maternal age and self-destructive motivation, indicating that the reproductive value of kin might moderate the desire for suicide.

Kin directed altruism as a motivation for suicide might explain some but not all cases of suicidal behavior. deCatanzaro (1995) noted that novel technology, such as guns and cars, could cause suicide death even in individuals with otherwise high reproductive potential and low burdensomeness. In such cases, the evolved human mind fails to take into its calculations the high lethality of these technologies. Furthermore, the vast majority of suicidal behavior is, in fact, nonlethal. For example, among US females, there are about 400 suicide attempts for every one suicide completion (see Syme et al. 2016). Thus, much suicidal behavior occurs among young, healthy individuals who are not burdening their kin.

Conclusion

Though there is considerable support for the inclusive fitness model of suicide, not all cases of suicidal behavior correspond to the necessary conditions of the model. Suicidal behaviors are heterogeneous phenomena that might not fit under one evolutionary model.

Cross-References

- [Benefits to Kin](#)
- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Unemployed](#)
- [Young](#)

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Suicide Bombers

- [Suicide Terrorism](#)

Suicide Terrorism

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Synonyms

[Martyrdom](#); [Religious terrorism](#); [Suicide bombers](#); [Terrorism](#); [Violent extremism](#)

Definition

Suicide terrorism, which is usually tied to a non-state organization, is the act of sacrificing one's life in an effort to harm, damage, or destroy members of an out-group, for political and social objectives.

Introduction

Although suicide terrorism is not a particularly modern phenomenon, research on its underlying causes flourished since the September 11 terrorist attacks. Some scholars have turned to the principles of evolutionary psychology in an attempt to shed light on suicide terrorism. Before delving into the topic of suicide terrorism from an evolutionary perspective, we briefly define some of the relevant terms in evolutionary psychology and examine the phenomenon of terrorism more generally. Following this, a brief summary of some of the psychological factors implicated in terrorism will be provided. Finally, three of the dominant explanations for suicide terrorism from an evolutionary psychological perspective will be presented, as well as an integration of research from the fields of psychology and evolutionary psychology.

Relevant Concepts in Evolutionary Psychology

Before examining terrorism and suicide terrorism from an evolutionary psychological perspective, a review some of the relevant key concepts in evolutionary psychology is warranted. Central to the concept of evolution is the notion that organisms have evolved by way of natural selection. During our evolutionary history, humans have ultimately differed in their ability to survive and reproduce. Certain factors in our ancestral environment – known as the *environment of evolutionary adaptiveness* – have led to the selection of *psychological mechanisms* which produce certain patterns of behavior (Cosmides and Tooby 1987). These evolved mechanisms can be seen as psychological adaptations, in the form of information-processing circuits in our brains which produce

specific behavioral patterns (Cosmides and Tooby 1987). Importantly, these psychological mechanisms evolved because they solved specific adaptive problems related to survival and reproduction. In other words, psychological mechanisms which facilitated greater chance of survival and reproductive success in the given environment were selected for, whereas those which did not increase the chance of survival and reproductive success decreased or were eliminated from the gene pool. It follows that these evolved psychological mechanisms generally lead humans to behave in ways which are adaptive, such as avoiding harm and attracting mates in order to produce healthy offspring. However, behaviors do not always evolve because they are adaptive; they can also evolve as a *by-product* of an adaptive mechanism. A by-product is a trait that evolved not because it was selectively advantageous but because it was linked to another trait which was reproductively advantageous. In other words, certain behaviors might be triggered because they “tap into” adaptive psychological mechanisms.

During human evolution, individuals have also engaged in helping behavior that appears to have no direct adaptive benefit for themselves and in many cases can be costly or dangerous to the individual. Within the field of evolutionary psychology, this phenomenon is referred to as *altruism*. Altruistic behavior is characterized by self-sacrificial, costly, helping behavior in the absence of apparent external rewards. However, it is widely debated whether prosocial behaviors can ever be truly selfless or altruistic. Moreover, scholars have argued that in many cases, individuals engage in helping behaviors with the expectation that the favor will be directly reciprocated by the beneficiary of the favor (*direct reciprocity*) or that they will be helped or rewarded indirectly by other individuals (*indirect reciprocity*) (Trivers 1971), due to an enhanced reputation for helping. Others have proposed that in general, individuals act in order to maximize the fitness of their kin. *Kin selection theory* arose from Hamilton's (1964) model of inclusive fitness, where he proposed that an individual engages in altruistic behavior if the benefits of the behavior

for genetic relatives outweigh the costs to the individual. In mathematical terms, Hamilton proposed that natural selection will favor the gene for altruism whenever $r \times b > c$, where r = the degree of genetic relatedness, c = costs, and b = benefits.

The aforementioned models of altruism will be discussed again later in this entry, when assessing how these models might relate to the phenomenon of suicide terrorism. It is important to note that these models, which are based on an evolutionary psychological perspective, focus on the fitness consequences of behavior, also known as *ultimate* explanations of behavior (Scott-Phillips et al. 2011). In contrast, *proximate* explanations of behavior refer to more direct causal triggers of a behavior (Scott-Phillips et al. 2011). While it is virtually impossible to directly test evolutionary models of behavior empirically, and even more difficult to do so in the context of terrorism and suicide terrorism, one can examine whether evolutionary explanations converge with widely accepted psychological explanations for this type of behavior. Thus, in the sections that follow, a brief overview of terrorism and suicide terrorism and their modern-day manifestations, and some of the psychological factors implicated in terrorism behavior more generally, will be outlined.

These factors can be seen as proximate explanations, which can later be examined in relation to their fitness benefits (i.e., ultimate explanations). Subsequently, we will provide perspectives on these behaviors from the field of evolutionary psychology and examine how current research evidence converges with different evolutionary psychological models.

Terrorism and Suicide Terrorism: A Brief Summary

The definition of terrorism has been the subject of much of debate, and leading scholars in the field of terrorism have yet to agree upon a specific definition. One common theme in ongoing debates about what constitutes terrorism centers on whether the definition should include acts of violence perpetrated by state actors (i.e., state-sponsored terrorism). Because the majority of research and theorizing about the underlying causes of terrorism tend to focus on the violence

perpetrated by non-state actors/organizations, this entry will largely focus on this subcategory of terrorism.

Thus, terrorism can be defined as the “symbolic use of violence by nonstate actors with social and political (hence not purely criminal) objectives intended to intimidate, frighten, or coerce a wider audience than the direct (instrumental) targets of the attack” (Kruglanski and Fishman 2009, p3). Historically, many terrorist organizations have emerged in response to ongoing ethnic/religious conflicts (sometimes with regard to claims to land) and often involving the oppression of specific minority groups. Although there are instances of “lone actor terrorism,” the majority of terrorist attacks are connected to terrorist organizations, which can be roughly categorized as Jihadist, ethno-nationalist/separatist, right-wing, left-wing and anarchist, and single-issue terrorism (e.g., anti-abortion terrorists).

Suicide terrorism is a more extreme extension of this tactic whereby the perpetrators of the attack are aware that they will lose their life as a direct result of harming or destroying the target. Suicide attacks are not a particularly new phenomenon and have long been considered a “weapon of the weak,” often employed when previously employed tactics have failed to achieve their goals. For example, suicide attacks were adopted by Japan during World War II, in the form of the kamikaze attacks, whereby pilots crashed explosive missiles into Allied naval vessels (Orbell and Morikawa 2011). Although these kamikaze attacks would be classified as an instance of a state-sponsored suicide terrorist mission, the majority of suicide attacks in modern times are perpetrated by non-state terrorist organizations. Notably, the rise of religious fundamentalist terrorism in the last several decades has coincided with the increased use of suicide terrorism as a strategy employed by Jihadist organizations/Islamist militant groups including Al-Qaeda, Boko Haram, ISIS, Hezbollah, and Palestinian Islamic Jihad. In 2017, suicide bombings occurred in 27 different countries and were tied to 37 different Islamist militant groups (Global Extremism Monitor 2017). However, suicide terrorism has

also been adopted by nonreligious groups such as the Liberation Tigers of Tamil Eelam (LTTE) (Moghadam 2006).

Although the actual act of suicide terrorism can take many different forms, the most common form is suicide bombing whereby the “agent” of suicide terrorism agrees to be strapped to an explosive device (or drive a vehicle carrying explosive devices), which is subsequently detonated once the agent has reached its target or target population. This particular type of suicide terrorism gained popularity among Islamist militant groups in Palestine (i.e., Hamas) and Lebanon (i.e., Hezbollah) in their violent conflicts with the state of Israel. Two of the most high-profile suicide terrorist attacks against the West were the September 11 attacks and the London bombings in 2005. While the terrorist organization Al-Qaeda was responsible for the September 11 attacks, it still remains unclear whether the men behind the London bombings had “self-radicalized” or were in fact tied to terrorist organizations. Most recently, the United States is witnessing a spate of what some consider white nationalist terrorism, typically perpetrated by lone male actors who have been radicalized on Internet message boards and other websites. The section which follows will examine some of the key theories and findings from the field of psychology, providing several explanations regarding the psychological underpinnings of suicide terrorism and terrorism more generally.

Psychological Perspectives on Terrorism and Suicide Terrorism

Despite the general consensus that the field of terrorism studies would benefit from an enhanced understanding of the psychology behind terrorism, the literature on terrorism from a psychological perspective has been subject to much critique. For obvious practical and ethical reason including the difficulties and dangers in gaining access to terrorist organizations or former terrorists and the inherent difficulties in planning prospective studies, there has been a lack of theory-driven empirical research. Moreover, the majority of research focusing on the association between psychology and terrorism has been characterized by theorizing

or speculation based on anecdotal observations (see Victoroff 2005 for a review).

One line of psychological research has focused on potential individual factors that may characterize terrorists. Early work on the psychology of terrorists was dominated by the preconception of the “terrorist as mentally ill.” However, in recent years, terrorism scholars generally agree that individuals involved in group-based terrorism are not mentally ill but “ordinary and unremarkable in psychological terms” (Silke 2008, p 118). Indeed, some scholars have suggested that there is no clear relationship between involvement in terrorism and psychopathology or personality traits (i.e., Horgan 2003). However, recently, a growing body of evidence suggests that a subjective sense of humiliation – which appears to underlie motivations to act out of revenge – is common among individuals who have been involved in group-based terrorism (Silke 2008).

Kruglanski and Fishman (2009) have proposed that terrorists – and suicide bombers in particular – seek to gain personal significance, which can be prompted by the loss of significance. This loss of significance can be attributed to feelings of humiliation, feelings of discrimination, or feelings of disenfranchisement. According to this theory, opportunities for significance gain may become apparent when one’s group experiences defeat or humiliation at the hands of an enemy (Kruglanski and Fishman 2009). Thus, what could originally be conceived of as an individual motivating factor is also tied to the psychology of belonging to a group. Specifically, an individual’s feelings of humiliation and motivations for revenge (or the quest for significance) are in many cases tied to the feeling that one’s social group has been treated unjustly (see Silke 2008). Notably, among Muslim diaspora, feelings of group-based anger, group-based injustice, and group-based relative deprivation have been found to predict violent intentions to defend Muslims (Obaidi et al. 2019). Hence, individual differences in emotions appear to be one area in which individual-level factors are linked to group-level factors.

Given that terrorism is often linked to organizations that mobilize ethnic or religious identity, there is a general consensus that terrorism tends to

be a group-based phenomenon. As Kruglanski and Fishman (2009) point out, “membership in a terrorist group may expose individuals to a unique social reality that condones violence, removes the anticipatory anxiety and guilt restraining one from harming innocents, stemming from societal norms that prohibit such behaviors” (p 16). In social psychological terminology, terrorism can be conceptualized as a violent form of intergroup conflict or nonnormative collective action triggered by perceived injustices perpetrated against one’s group. This view is supported by anecdotal evidence in the form of the justifications given by the leaders of some of the world’s most high-profile terrorist attacks. For example, Osama bin Laden (the former leader of Al-Qaeda, who was behind the September 11 attacks) and Mohamed Sidiq Khan (orchestrator of the London bombings in 2005) both expressed a sense of injustice against Muslims around the world by the hands of the West and the need to avenge these injustices (BBC News 2005; The Guardian 2002).

Terrorism from an Evolutionary Psychological Perspective

As stated in the section above, feelings of humiliation and motivations to take revenge are two individual psychological factors which appear to be implicated in terrorist motivations. Both humiliation and revenge might in fact be evolutionarily adaptive. Revenge can be defined as “an aggressive act that is often justified by the pursuit of equity” (Stillwell et al. 2008). From an evolutionary perspective, revenge can be considered a form of retaliation to perceived transgressions from one or more individuals, which functions to reduce the likelihood that the transgressor (i.e., target of retaliation) will engage in the same injurious transgressions in the future, hence leading to fitness gains (Clutton-Brock and Parker 1995). It has also been proposed that readiness to retaliate against transgressors could be partly due to concerns about one’s social reputation, which is important in primate and human societies (Clutton-Brock and Parker 1995). Moreover, the construct of humiliation is arguably linked to one’s social standing. Humiliation can be defined as “the experience of some form of ridicule, scorn,

contempt, or other degrading treatment at the hands of others” (Klein 1991, p.94). In this way, humiliation and revenge might have operated in concert with one another in ancestral environments, such that perceived transgressions are subjectively experienced as feelings of humiliation, which might trigger a motivation for revenge (i.e., retaliation), in an effort to deter the transgressor from committing further transgressions, or due to reputational concerns. In many instances, these transgressions might have been perpetrated by members of other social groups or tribes. Thus, acts of revenge can be considered as prosocial or even altruistic, if the individual stands to suffer and their group stands to gain. Indeed, some known terrorists have described themselves as behaving altruistically, for the best interests of their group (Victoroff 2005).

A dominant perspective with its roots in evolutionary psychology holds that the tendency for costly cooperation benefiting members of one’s in-group (i.e., altruism), and spite and aggression towards members of other groups (i.e., out-group hostility, parochialism), might have evolved simultaneously, a term which has been more recently coined “parochial altruism” (Choi and Bowles 2007). While there are other perspectives regarding the origins of in-group cooperation (e.g., Brewer 2007), researchers making use of game theoretic analysis agent-based simulations provide some evidence that altruism and parochialism could have evolved jointly (Choi and Bowles 2007).

In order to identify who should reap the benefits of group membership (i.e., cooperativeness and altruism) or be subject to out-group hostility (i.e., parochialism), humans developed the ability to group humans into rigid social categories, such as “Us” versus “Them” (Zmigrod et al. 2019). Although such rigid social categorization occurs to varying degrees for all humans, some humans are more rigid in their categorizations. Recent research suggests that such rigid social categorization which may underlie parochial altruism could more broadly reflect the individual tendency for rigidity in classification of stimuli more generally (Zmigrod et al. 2019). Specifically, Zmigrod et al. (2019) found that

individuals who have a greater propensity towards rigid evaluations of stimuli are more willing to endorse ideological out-group violence and more willing to engage in self-sacrificial behavior in order to benefit their in-group (Zmigrod et al. 2019). While engagement in terrorist acts more generally could be considered a form of warfare or intergroup aggression and thus understood as a manifestation of parochial altruism, suicide terrorism needs to be examined as a phenomenon slightly distinct from non-suicide acts of terrorism. In many ways, suicide terrorism could be considered the ultimate form of altruism.

Suicide Terrorism as Altruism

Suicide terrorism, which involves laying down one's life for the sake of the organization and its goals, is considered the ultimate form of self-sacrifice. Such behavior is initially puzzling for both laypeople and evolutionary psychologists, since it appears to be maladaptive and at odds with the evolutionary instinct to survive. However, despite the destructive nature of suicide terrorism, many scholars have viewed it as a form of suicide terrorism to other forms of self-sacrificial helping behavior and examined whether suicide terrorism is a form of altruism (Liddle et al. 2011; Orbell and Morikawa 2011; Qirko 2009). Indeed, in Palestine, suicide bombers are referred to as a *shaheed* (martyr) and deemed heroes in their communities because they have sacrificed themselves to destroy their enemy. This concept of martyrdom and self-sacrifice is also prominent among the Tamil society in Sri Lanka, with members of the LTTE's suicide squad (the Black Tigers) honored and revered after death (Moghadam 2006). Because of this element of self-sacrifice in order to benefit their group/organization, several scholars have examined whether altruism could possibly shed light on the adaptive functions of suicide terrorism. Thus, scholars have attempted to apply models of altruism to the context of suicide terrorism, assessing the plausibility of these models by examining the available evidence surrounding the perpetrators of suicide terrorism and the terrorist organizations that lie behind these attacks.

Suicide Terrorism as Direct or Indirect Reciprocal Altruism

One of the most popular – and perhaps most straightforward – explanations for altruistic behavior more generally is that individuals are willing to engage in costly or self-sacrificial behavior to help nonkin (individuals they are not genetically related to), because they expect the favor to be directly or indirectly reciprocated (Trivers 1971).

Whereas direct reciprocity occurs when individuals help those who help them, indirect reciprocity occurs when individuals help those who help others, due to an enhanced reputation for helping. Some scholars have been quick to conclude that reciprocity – whether direct or indirect – is unlikely to be the primary motivator in suicide attacks, since one needs to remain alive in order to receive any subsequent help or rewards. Qirko (2009), for example, has suggested that a suicide attack leads to the ultimate loss for the agent of suicide terrorism, with no further opportunities for compensation of the costly act of suicide. However, Qirko and other scholars (i.e., Tullberg 2004) have also acknowledged the possibility that in the minds of the agents of suicide terrorism, an unspoken and “illusory” reciprocal contract is made with the terrorist organization. In evolutionary psychological terminology, suicide terrorism could therefore be understood in terms of indirect reciprocal altruism, contingent on the agents of suicide terrorism believing they will receive subsequent rewards as a direct result of their ultimate sacrifice for the cause.

Specifically, some terrorist organizations, notably Islamist militant organizations, refer to suicide terrorists as martyrs. Within these contexts, martyrs are assigned a special status. In fact, martyrs are promised great rewards in the afterlife. For example, it is reported that Hamas suicide bombers have been promised entry to paradise upon death, accompanied by many other rewards including access to dozens of virgins (Tullberg 2004). Support for the notion of this illusory reciprocal contract comes from research which has shown that Palestinian suicide bombers do not believe they are really dying when they undertake their suicide bombing mission (Kershner

2001). Further evidence for this illusory reciprocal contract is that one motivation shown to be important among Palestinian suicide bombers is the prospect of receiving rewards in the afterlife (Hafez 2006). The fact that many religions stress the existence of the afterlife is one reason why scholars have argued that religious belief is a predictor of suicide terrorism. Liddle et al. (2011) reason that without the belief in the afterlife, and the accompanying belief that one will receive rewards in the afterlife, potential suicide terrorists would be likely to judge the costs of suicide (i.e., death) as far too costly to engage in Liddle et al. (2011). However, the existence of secular (i.e., nonreligious) terrorist organizations, which employ suicide terrorism as a strategy, as the LTTE in Sri Lanka, would appear to contradict the reciprocal altruism account, as well as the supposed key role of religious belief in the existence of suicide terrorism. In other words, the fact that some perpetrators of suicide terrorism act on behalf of nonreligious organizations would imply that such individuals do not hold beliefs about the afterlife, suggesting that the account of an illusory reciprocal contract involving rewards in the afterlife is not valid. Although acknowledging the existence of nonreligious terror organizations, Liddle et al. (2011) argue that the existence of suicide terrorists tied to secular terrorist organizations does not rule out the notion that these suicide bombers believe (or believed in) life after death. Nevertheless, from an evolutionary psychological standpoint, other alternative explanations based on the evolutionary principles of kin selection appear to provide more plausible explanations for the existence of suicide terrorism.

Suicide Terrorism and Kin Selection

Although the act of taking one's life would initially appear to be maladaptive, it could be considered adaptive if one shifts the focus from the individual to the individual's genes. Hence, an alternative explanation rooted in evolutionary psychology is the notion that suicide terrorism is a form of *kin selection*. The act of kin selection occurs when an individual engages in a behavior which leads to benefits for their (genetic) relatives, even when this behavior is costly for the

individual in terms of survival and reproduction (Hamilton 1964). In this line of reasoning, the seemingly maladaptive behavior is adaptive because close relatives share many of the same genes, and by helping related kin to reproduce (by engaging in the altruistic behavior), individuals may increase the frequency of these shared altruistic genes in the next generation.

Applying the kin selection model, engagement in suicide terrorism missions might be adaptive because the family of the suicide terrorist could reap rewards after the individual dies. Several scholars have examined the possibility that individuals engage in suicide terrorism due to kin selection (i.e., Lankford 2015; Liddle et al. 2011; Qirko 2009). Some scholars even suggest that suicide terrorism might in fact be adapted (Liddle et al. 2011; Qirko 2009), since in many cases the relatives of suicide terrorists receive both tangible and intangible rewards. Given that Islam holds that martyrs are awarded a special status and referred to as heroes, relatives of suicide bombers are greatly honored by their community and receive monetary rewards from one or more organizations. For example, reports from several different sources have revealed that Hamas and Hezbollah compensate the family members of suicide bombers with lump-sum payments (Levitt 2005). Moreover, there are even funds which have been initiated, with the sole purpose of dealing out payments to family members of suicide bombers (Levitt 2005). The cost of dying which is the inevitable result of carrying out a suicide attack could technically be offset by the fitness benefits for the genetic relatives. In this line of thinking, several scholars have suggested that when suicide bombers willingly take their lives in order to destroy or harm the organization's targets, the benefits that family members subsequently receive after the attack could mean that this act increases the likelihood that their shared genes are passed onto future generations (Liddle et al. 2011).

An alternative application of the kin selection model to the context of suicide terrorism stems from the observation that terror organizations often recruit family members (usually brothers) or friends of pre-existing members. For example,

Sageman (2008) drew attention to the fact that 70% of individuals who joined Al-Qaeda joined with friends, with 20% joining with family. According to this line of thinking, suicide terrorists might not be sacrificing themselves for the collective good nor attempting to accrue benefits for their relatives. Rather, they might actually be attempting to protect their relatives or close friends from harm. However, an alternative evolutionary psychological explanation stemming from the kin selection model suggests that the phenomenon of suicide terrorism has evolved as a by-product of kin selection, namely, induced or fictive kinship.

Suicide Terrorism as Induced Altruism/Fictive Kinship

Given that the kin of suicide terrorists do not always accrue benefits for their genetic relatives, an alternative explanation – with its roots in kin selection theory – has been proposed. According to Qirko (2004), where genetic relatives of suicide terrorists do not stand to benefit as a direct result of the suicide attack, individuals can be induced to act altruistically in order to benefit the terrorist organization to which they belong (Qirko 2004). According to this view, the same psychological mechanisms which initially evolved to prompt individuals to help their genetic kin are “hijacked” (Qirko 2004). That is, terrorist organizations make use of *kin recognition cues* – cues which allow individuals to distinguish between kin and non-kin – such as physical proximity, phenotypical similarity, and reference to individuals in kin terms (Qirko 2004). In this line of thinking, manipulation of kinship recognition cues induces some individuals to sacrifice themselves for their organization, because members of the terrorist organization essentially become “fictive kin” (Qirko 2004).

Qirko (2004) hypothesized that when one examines terrorist organizations, the cues of physical proximity, phenotypic similarity, and use of kinship terms should be evident in organizational practices. Indeed, there are some contexts in which manipulation of these kinship recognition cues appears to have been adopted. In many cases,

new recruits to terrorist organizations are placed in small groups or cells which promote close physical proximity (Atran 2003). Recruits are also given a uniform in the form of new clothes and accessories and encouraged to wear these, hence increasing phenotypic similarity (Atran 2003). Furthermore, terrorist organizations appear to make use of kinship terms when referring to the organization or members of the organization. Sometimes the organization is referred to as the individual’s new “family,” with individuals within the same group or cell often described as “brothers” (Atran 2003).

Critique of the Evolutionary Psychological Explanations of Suicide Terrorism

Evolutionary psychological explanations of suicide terrorism have also been subject to critique. In particular, the kin selection explanation of suicide terrorism has been criticized on several grounds. For example, Lankford (2015) argues that intentional self-sacrifice is maladaptive and would not have been selected for. To support his argument, Lankford argues that while some animals engage in costly and potentially risky behavior to save/benefit their kin, intentional self-sacrifice – where the animal dies as a direct result of the altruistic behavior – does not appear to be common in the animal kingdom (see Lankford 2015).

Moreover, the observations that the families of some suicide terrorists often come from middle-class backgrounds, do not appear to be in need of money, and do not always receive benefits or increased social status have been interpreted as anecdotal evidence refuting the kin selection explanations (Lankford 2015). Lankford (2015) also argues that the fictive kin interpretation of suicide terrorism is problematic since some individuals decide to become a suicide terrorist before joining a terrorist organization. In an attempt to consolidate the fictive kin interpretation with Lankford’s observation, it is possible that for some individuals, the global Muslim community

(referred to as the *Ummah* among Muslims) – not just members of one’s terrorist organization – are perceived as fictive kin. This explanation could shed light on why some individuals decide to become a suicide terrorist before joining a terrorist organization (i.e., the perpetrators of the London 2005 suicide bombings). Moreover, the notion of the global Muslim community as fictive kin could also explain why perceived injustice against Muslims around the world appears to have been a central motivating factor underlying the September 11 attacks and the London bombings.

Multiple Causes of Suicide Terrorism and the Need for Empirical Psychological Research

This review of current psychological and evolutionary psychological perspectives on terrorism and suicide terrorism suggests that there are multiple explanations for these phenomena. The aforementioned explanations represent some of the most dominant accounts and are by no means exhaustive. Despite a preoccupation with identifying the causes of terrorism in an effort to inform counterterrorism strategies, there is currently no consensus among academics about which explanation is best or most “true.” Psychological factors, which are partly rooted in our evolutionary psychology, provide plausible explanations for why some individuals engage in acts of terrorism and suicide terrorism, but there are likely multiple causes or risk factors which might trigger specific evolved psychological mechanisms in different contexts. For example, if an individual has close family members or friends who have been killed by their “enemy,” negative emotions and a desire for revenge, which appear to be evolutionary adaptive, might be a sufficient motivation to engage in terrorism or suicide terrorism.

In other instances, individuals might be motivated by the prospects of personal rewards in the afterlife, personal significance gain, or benefits for their family. Other individuals might have undergone long periods of indoctrination, thus being exposed to manipulation of kinship cues, thereby strengthening a sense of commitment to the terrorist organization and its goals. The observation that many individuals involved in terrorism have

not personally experienced state oppression or military intervention by the West, but claim to be avenging the atrocities perpetrated against Muslims elsewhere, suggests that group identification processes might also play a key role. The diversity of explanations regarding the psychological underpinnings of suicide terrorism and terrorism more generally suggests that there are different types or subgroups of terrorists and suicide terrorist and hence different pathways to involvement in terrorism. Although there might be certain evolved (universal) psychological mechanisms which can shed light on many aspects of engagement in suicide terrorism, a combination of individual, social, and structural factors is likely to interact with these evolved psychological mechanisms to pave the way towards involvement in terrorist organizations and engagement in suicide terrorism.

It is important to remember that much of the early research on terrorism and suicide terrorism has been largely based on theorizing and anecdotal evidence. This means that psychological research has yet to meet the increasing and current demands for terrorism research. However, the logistical and ethical problems in gaining access to terrorist organizations or former terrorists need not preclude future investigation of the psychological underpinnings of suicide terrorism. In recent years, there has been a growing recognition among researchers within the fields of social and cognitive psychology that theory-driven research examining the propensity for intergroup violence and self-sacrificial altruistic behavior can be examined in large, population-based studies (i.e., Obaidi et al. 2019; Zmigrod et al. 2019). One advantage of examining such propensities for intergroup violence and self-sacrificial behavior, among large population samples, is that this approach enables researchers to control for key confounding variables and enables them to use a range of validated scales or tests. Obviously, findings from such population-based studies must be interpreted in light of the existing research on suicide terrorists and terrorist organizations, and the converging validity of the findings would need to be assessed.

Conclusion

Scholars have examined whether suicide terrorism and terrorism more generally might be partly attributable to evolved psychological mechanisms. These scholars have considered how violent group behavior and intentional self-sacrificial behavior could be conceived of as adaptive. Terrorism and suicide terrorism in particular are often connected to non-state organizations with specific political goals, often in response to perceived oppression or existing ethnic or religious conflicts. As such, from a psychological perspective, terrorism can be considered a manifestation of revenge triggered by negative emotions (i.e., humiliation, anger), often tied not only to personal experiences but to the experiences of one's social group. From this perspective, terrorism can therefore be understood as a form of violent collective action to defend one's social group/organization. While revenge and violent collective action might initially be perceived as evolutionarily maladaptive, some scholars have considered whether suicide terrorism could be a form of altruism, thus, drawing on existing models of altruism from the field of evolutionary psychology. Specifically, suicide terrorism has been interpreted as a form of indirect reciprocal altruism, contingent on an illusory contract between the potential agent of suicide terrorism and the organization. An alternative explanation draws from kin selection theory and assumes that individuals engage in suicide terrorism in order to gain benefits for their (genetic) relatives, hence increasing the likelihood that their genes will be passed onto future generations. Others have suggested that suicide terrorism might have evolved as a by-product of kin selection, such that the presence of kin recognition cues might trigger individuals to perceive members of their terrorist organization as "fictive kin."

Evolutionary psychological explanations of suicide terrorism have been criticized on the grounds that intentional self-sacrifice is not common among animals and that this behavior would not have been selected for. Furthermore, some anecdotal evidence suggests that for some individuals who have engaged in suicide attacks, potential benefits for kin do not appear to be a motivating factor. The aforementioned frameworks provide some

plausible explanations regarding the psychological mechanisms underlying involvement in terrorist organizations and engagement in suicide terrorism. However, much of the research on suicide terrorism – and terrorism in general – is based purely on theorizing and observations of individuals who have been involved in terrorist organizations. It is likely that there are multiple causes or risk factors for engagement in suicide terrorism and involvement in terrorist organizations, which influence certain individuals under certain conditions. However, a proper understanding of the complex interplay between different psychological mechanisms behind suicide terrorism and terrorism more generally will require more rigorous empirical research examining the personality, social, and evolutionary psychological underpinnings of intergroup violence and self-sacrifice. One approach to reach a more nuanced and systematic understanding of the role of these diverse psychological underpinnings is to examine the key psychological factors – and how they may interact – in large population-based samples, which should in turn be interpreted in light of existing evidence on terrorists. Only when the results of many empirical, population-based studies converge with existing evidence on actual terrorists can more definitive conclusions be made regarding the role of specific psychological mechanisms underlying involvement in terrorist organizations and engagement in suicide terrorism.

Cross-References

- [Kin Recognition](#)
- [Kinship Psychology Manipulations](#)
- [Suicide as Kin-Directed Altruism](#)
- [Triggering Kin Selection](#)

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Summary Representation

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Synonyms

Ensemble representation; Incidental encoding; Statistical summary; Visual awareness; Visual statistical representation

Definition

The phenomenon of readily deriving information from the natural world through the visual system that often lies outside consciousness.

Introduction

Humans are sensitive to the summary statistics of the visual world. They derive this information

from complex scenes, often without explicit awareness. The visual system is susceptible to summary statistical stimuli about group or ensemble characteristics in the natural world. The summary statistics are derived across a host of visual domains, ranging from average orientation to the average expression from crowds of faces. The ease with which people can detect an outlier suggests their representations of categories of objects incorporate some notion of what is average and of the upper and lower limits in the normal variability within the dimension in question. When viewing a set of objects, a particularly large or small member of the set will stand out and will be readily detected (Hodsoll and Humphreys 2001).

Memory and Personality Traits

Not only can one have knowledge about the circumstances of one's life, but one can also have semantic knowledge about one's own personality traits. Klein and Loftus and their colleagues (Klein et al. 2001) proposed and tested a model of the relation between memories of personal experiences and trait conceptions of self. Their model incorporated the following three features. First, long-term knowledge of one's traits is abstracted from multiple experiences with trait-relevant behaviors and represented in semantic memory in summary form. Second, trait judgments about the self are made by accessing these summary representations without reference to the behavioral episodes from which they were derived. And third, summary trait representations are functionally independent of memories of trait-relevant behavioral episodes. There now is ample evidence that people form summary representations of their own personality traits and retrieve these when asked to decide whether a particular trait describes them. Equally important, a large body of evidence shows that people maintain detailed stores of behavioral episodes they have experienced.

Scope Hypothesis

According to the scope hypothesis, deciding whether a trait is self-descriptive activates a

summary representation and episodes inconsistent with the trait being asked about. The decision context should determine when boundary conditions are needed, and which kinds of episodes would be relevant. Because decisions regarding personality traits are not amenable to all-or-none answers, it would be reasonable to assume that the trait summary takes a quasi-quantitative form.

Thus, when the individual is asked if a certain trait describes them, possible answers might be "usually," "sometimes," or "rarely." Boundary conditions would be episodes in which the behavior did not meet the criteria for that trait. This should be true for any level the trait summary specifies, even "rarely." This is because the decision context calls for a generalization about it; the function of activating episodes is to place boundary conditions on that generalization. The issue is, "How often is Person Y friendly, and under what conditions is she or he not?" The decision rule activated is designed to make a judgment about the trait being asked about, whether the question originates with another person or with the individual making the judgment.

Different decision rules are designed to retrieve different kinds of information from memory. The type of decision being made matters, because that determines which search engine gets activated, which will determine which array of memory systems gets searched. When asked to trait-categorize their own behavior, subjects should retrieve a trait summary and episodes inconsistent with the trait they are being asked about.

The Statistical Nature of Summary Representation

Research suggests that when subjects attend to a particular dimension of a set of items presented over an extended duration, they quickly learn about the central tendency of the set. However, it is unclear whether such learning can occur incidentally, when subjects are not attending to the relevant dimension of the set. Chris Oriet and Kadie Hozempa (2016) studied incidental summary representation over time exploring whether subjects could reproduce global statistical properties of a set presented over an extended duration

when oriented to task-irrelevant properties of the set. Subjects were tested for their memory of its mean, its smallest and largest exemplars, the direction of its skew, and the relative distribution of the items. Subjects were able to accurately recall the average size circle, as well as the upper and lower boundaries of a set of 4200 circles displayed over an extended period. This suggests that even without intending to do so, they were encoding and updating a statistical summary representation of a task-irrelevant attribute of the circles over time. Such incidental encoding of statistical properties of sets is thus a plausible mechanism for establishing a representation of typically in category membership.

Change Blindness

The failure to notice differences in sequential scenes or images is a well-established phenomenon, suggesting that humans have a limited visual awareness from one moment to the next (Mitroff et al. 2002; Rensink et al. 1997). Although, on the surface, change blindness seems to suggest a sparse visual representation, an abundance of recent research has supported the notion that a failure to represent visual information is unlikely to drive this phenomenon. Much of the incoming visual input is preserved in spite of change detection failures (Beck and Levin 2003; Hollingworth 2003). For instance, Beck and Levin (2003) showed that observers could identify an object change in the absence of a durable representation of that object. Mitroff et al. (2004) demonstrated that this durable representation could potentially be used to aid in object identification. Hollingworth and Henderson (2004) found that visual scene information was preserved even when observers failed to detect a rotation in the scene. Research suggests that despite the limited conscious access revealed by change detection experiments, the “gist” of a scene remains accessible (Oliva and Torralba 2001; Potter 1976; Thorpe et al. 1996).

Given the fundamental and ubiquitous nature of summary statistical representation, Jason Haberman and David Whitney (2011) tested whether this kind of information is subject to the

attentional constraints imposed by change blindness. They showed that information regarding the summary statistics of a scene is available despite limited conscious access. In a novel experiment, they found that while observers can suffer from change blindness (i.e., not localize where change occurred between two views of the same scene), observers could nevertheless accurately report changes in the summary statistics about the very same scene. In the experiment, observers saw two successively presented sets of 16 faces that varied in expression. Four of the faces in the first set changed from one emotional extreme to another in the second set. Observers performed poorly when asked to locate any of the faces that changed (changed blindness). However, when asked about the ensemble (which set was happier, on average), observer performance remained high. Observers were sensitive to the average expression even when they failed to localize any specific object change. That is, even when observers could not locate the very faces driving the change in average expression between the two sets, they nonetheless derived a precise ensemble representation. Thus, the visual system may be optimized to process summary statistics in an efficient manner, allowing it to operate despite minimal conscious access to the information presented.

The Role of Attention

As the perceptual phenomenon occurs when a change in a visual stimulus is introduced, the observer does not notice it. Observers often fail to notice major differences introduced into an image while it flickers off and on repeatedly. Researchers have found that shifting a person's attention, such as causing distraction, leads to increased change blindness. There is already evidence that summary statistical information operates beyond the focus of attention (Alvarez and Oliva 2008). Nonetheless, this has only been demonstrated with low-level features, such as features thought to be analyzed at the earliest stages of cortical visual processing, including orientation, contrast, and motion direction, which are expected to be processed in parallel (Watamaniuk and McKee 1998).

Conclusion

Information taken in by the human visual system allows individuals to form statistical representations of sets of items. One's knowledge of natural categories includes statistical information, such as average size of category members and the upper and lower boundaries of the set. An abundance of research suggests that subjects can represent statistical properties of small sets of items presented simultaneously or over a period of a few seconds. It is also argued that statistical properties can be extracted for sets of items encountered over time, when subjects attend to the measured attribute. This type of statistical summary learning appears to occur without conscious intent.

Cross-References

- [Attention](#)
- [Personality Traits](#)
- [Scope Hypothesis, The](#)

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Superior Longitudinal Folliculus

- [Dorsal Stream, The](#)

Superiority

- [Dominance and Threat or Use of Force](#)

Super-K

- [K-Factor \(Figueredo\)](#)

Supernormal Sign Stimulus

- [Supernormal Stimuli \(Konrad Lorenz\)](#)

Supernormal Stimuli

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Definition

Supernormal stimuli are any stimuli that elicit an instinctual reaction more strongly than does the stimulus for which the instinct evolved.

Introduction

Ethologist Niko Tinbergen won the 1973 Nobel Prize in Biology for his research on instinctive behavior in animals. Tinbergen used various dummies to elicit nurturing, mating, and fighting behaviors. He and his students constructed fake eggs which birds would sit on, artificial female butterflies which male butterflies courted, and models of male fish which other males attacked. Some of the dummies were ingeniously *unrealistic* to elucidate exactly what characteristics triggered the behaviors. Territorial male stickleback fish will not attack a fish-shaped model if its belly isn't red, but they violently pursue some very unfish-like models when the underside is red.

Perhaps the most interesting of Tinbergen's discoveries is that dummies can be devised which surpass the power of any natural stimuli. Tinbergen coined the phrase *supernormal stimuli* for these dummies that elicit stronger responses than occur naturally.

Animal Research

The supernormal stimuli which eventually received the most study were decorated plaster eggs. Tinbergen found that most bird species preferred eggs that were larger than their own and ones which had exaggerated colors or markings. The oystercatcher, which lays small brown-specked eggs, will ignore them in favor of a giant brown plaster egg the size of the bird itself.

Song birds abandon their pale blue eggs dappled with gray to hop on a black polka-dotted Day-Glo blue dummy so large that they continuously slide off and have to climb back on. Ground-nesting birds will retrieve eggs dislodged from the nest, rolling them back into place. When given a choice between its own egg and a *volleyball*, the greylag goose ignores the egg and tries valiantly to roll the volleyball into the nest.

Tinbergen noted that there's at least one bird which has evolved to be essentially a supernormal stimuli to other species. The cuckoo lays its egg in another bird's nest, where the unsuspecting foster parents incubate and feed it, leaving the mother cuckoo free to fly off to lay more eggs. The baby cuckoo is actually given preferential treatment over the host's offspring. The cuckoo egg is usually larger than the host's so it is sat on more consistently than the other eggs in the nest. When hatched, the young cuckoo's wider throat acts as stronger stimuli to the feeding mother than her own chicks.

He studied butterflies and found that marks on the torso of the female and its vibratory movements were the sole mating releasers – he could construct dummy butterfly torsos with brighter stripes and more regular movements. Males would ignore a live, receptive female to mount cardboard cylinders that didn't even need wings!

Tinbergen also studied the stickleback fish whose males are highly territorial. He and students spent hours leaning over the tanks, “swimming” the dummies around. At first these were just dead fish on wires, later they carved and painted wooden ones. Systematically varying the wooden models, they established that it was redness of the underbelly that signaled “male-to-attack.” Sticklebacks didn't attack a realistically shaped model if its belly wasn't red, but violently pursued *very* unfish-like shapes with red undersides. Males in aquariums by the window went into attack mode when a red *postal van* drove by.

Color wasn't the determinant for detecting females; males escorted carved wooden models to the nest if they had the curved belly of an egg-bearing female. They preferred the model with the roundest stomach.

The stickleback models could easily be made to be supernormal. Male sticklebacks ignored a real male to fight a dummy brighter red than any natural fish. They'd choose to escort an exaggeratedly round-bellied model over a real egg-bearing female. For every species and instinct Tinbergen studied, he could successfully produce supernormal stimuli once the eliciting releasers such as shapes, colors, and scale were discovered.

Human Implications

Tinbergen made clear in brief comments that he thought supernormal stimuli applied as much to humans as to other species, but he did not develop this as he was usually writing about fish, birds, and insects. More recently, evolutionary psychologists have begun using the term in describing human behavior. Deirdre Barrett points out that while animals encounter supernormal stimuli mostly when experimenters build them, humans produce their own, and in the technological age, they're becoming ubiquitous: candy, pornography, huge-eyed stuffed animals, and diatribes about menacing enemies.

She argues that supernormal stimuli are a driving force in many of today's most pressing problems, including obesity, our addiction to television and video games, and the past century's extraordinarily violent wars. Man-made imitations radically alter what food humans put into their bodies, how sexuality is expressed, and if and how wars are fought. A unique implication for humans when they become aware of supernormal stimuli is to apply logic and willpower to override instincts in a manner a bird on a bright blue egg cannot.

Conclusion

The key point is that *supernormal stimuli reverse the natural relationship between instinct and object*. This makes for an interesting technique in illuminating animal instincts but creates problems for humans who create them prolifically.

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Supernormal Stimuli (Konrad Lorenz)

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Synonyms

[Artificially exaggerated stimulus](#); [Optimally primed stimulus](#); [Super-stimulus](#); [Supernormal sign stimulus](#).

Definition

Supernormal sign stimuli – a term invented by Niko Tinbergen and now usually abbreviated simply as supernormal stimuli (1951, 44) – are exaggerated/heightened imitations of naturally evolved phenomena/objects that exert a stronger attraction/desire on their target audience than the natural phenomena/objects themselves (Barrett 2010, 3). According to Tinbergen, the phenomenon was first reported by O. Koehler and A. Zagarus (1937), but it was then further developed by Tinbergen together with his colleague Konrad Lorenz. An example of a supernormal stimulus from the natural world is the cuckoo egg. Cuckoo eggs appear very similar to those of their host but are usually somewhat larger and/or brighter.

It has been suggested in evolutionary terms that “instances of supernormality may reflect the action of two factors during phylogeny:

(a) asymmetrical selection pressure with respect to responsiveness to the relevant stimulus continuum (e.g., size, speckledness), and (b) independent selection pressures limiting the corresponding properties of the natural stimulus” (Staddon 1975, 541). As explained by Tinbergen, this means that a naturally evolved situation/item is not always stimulus-optimal (1951, 44).

Konrad Lorenz and Niko Tinbergen

Together with Niko Tinbergen (1907–1968), Konrad Lorenz (1903–1989) was one of the two most important founders of the modern ethology movement. Lorenz’s key significance for ethology has been outlined as follows:

The target of [Lorenz’s] investigations was at first the innate motor pattern . . . He investigated the key stimuli that release a specific behavior prior to all experience and studied the phylogenesis and ontogenesis of innate behavior patterns. In the “instinct-learning intercalation” he found a new mode of integration of innate and acquired components of behavior, and in the phenomena of imprinting he discovered an inborn disposition to learn (Eibl-Eibesfeldt 1975, 7).

Lorenz’s use of the instinct concept in ethology was taken up directly and developed by Niko Tinbergen, most significantly in an important book presenting his work on the investigation of innate behavior, *The Study of Instinct* (1951).

In the 1940s/early 1950s, Tinbergen was also studying the behavior of the three-spined stickleback, the most common freshwater fish in Holland. As has been explained about the results of this stickleback behavioral study:

The most interesting of Tinbergen’s discoveries was that dummies could surpass the power of any natural stimuli. Male sticklebacks ignored a real mate to fight a dummy brighter red than any natural fish . . . Tinbergen named the phenomenon of his exaggerated dummies “supernormal [sign] stimuli”. He published papers outlining the concept that instincts were coded for a few traits and amplification of these traits could easily fool animals (Barrett 2010, 12–13)

In fact as Tinbergen readily acknowledged, he did not discover the concept of supernormal stimuli but he did investigate it in more depth than had

previously been undertaken, and he did more explicitly recognize its wider significance for understanding animal behavior.

Examples of Supernormal Stimuli

Some of the specific animal-related examples of supernormal stimuli that have been presented in the literature are: dummy eggs with exaggerated size, color, and markings, e.g., geese eggs and song-bird eggs, that induce preferred brooding behaviors; dummy females with exaggerated sexually selected features that induce preferred mating behaviors; artificial herring gull food-begging stimuli with heightened colors that induce preferred feeding behaviors (Tinbergen and Perdeck 1950); beer-bottles studded with glass beads that induce preferred mating behavior in some beetles; and exaggerated signal behaviors induced by parasites in order to manipulate their baby bird hosts.

Supernormal stimuli are not only relevant to studying animal behavior but are also relevant to understanding the behavior of human beings. For example, it has been hypothesized that one instance of a supernormal stimulus is the waist-to-hip ratios of human females that are most preferred by males:

A possible human analog [of a supernormal stimulus] is men’s sexual preference for very low WHRs [Waist-to-Hip Ratios]. A female WHR of 0.6 – which is within the human female range, but extremely rare – is perceived as more attractive than a WHR of 0.7 (Singh 1994) . . . Perhaps in the human EEA there was no such thing as a woman with too low a WHR . . . [and] selection favored a simple psychological mechanism instantiating the rule “lower is better”, and the maximally attractive WHR thus is supernormally low (Symons 1995, 111).

In fact a large range of sex-related behaviors and associated sexual enhancement products can be interpreted within the framework of the supernormal stimuli concept, including pornography for men and romance novels for women.

Other specific human-related examples of supernormal stimuli that have been discussed in the literature are: women’s high-heeled shoes (Morris et al. 2013); various fast-food items such

as hamburgers and pizzas (Saad 2011); narcotic drugs such as cocaine and heroin (Barrett 2010, 78); and contemporary Islamic terrorist attacks (Geher 2015). All of these examples of supernormal stimuli aim to employ evolved psychological mechanisms and to manipulate them for specific ends by presenting heightened or extreme forms of a preexisting natural phenomenon or behaviors.

For example, high heels work by exaggerating the natural movement of female hips as women walk; fast food works by presenting more concentrated examples of what human beings naturally desire to consume: meat, sugar, and fat; narcotic drugs work by the heightened activation of pre-existing neural pleasure-circuitry in the brain; and contemporary terrorism works by playing on/exaggerating preexisting fears of sudden and uncontrollable predator attacks that produce death or very serious injury.

Pornography and Mirror Neurons

One example of a supernormal stimulus that is viewed by some as having negative effects is pornography. As has been explained:

Sex is an obvious target for supernormal stimuli . . . everything from pornography to advertising models, from plastic surgery to old-fashioned cosmetics, cinched waists, and padded bras can be seen as people amplifying nature's signalling (Barrett 2010, 30).

Pornography acts as a supernormal stimulus (for men) by portraying female sexuality in a heightened or "amplified" form. Contemporary pornography actresses are usually more beautiful than the average woman, they are (in their porn performances at least) more sexually compliant than them, and they are shown as being more frequently available for sex. It can be hypothesized from the "immersive" nature of pornography consumption that it functions in part through the activation of mirror neuron circuits that have evolved in various primates (including Hominids) over evolutionary "deep time."

As has been explained, the term mirror neurons designate "a group of interconnected neurons that fire (differentially) for the observation, execution,

and . . . imitation of goal-directed motor behaviors involving objects" (Wallis and Wright 2009, 283). Mirror neurons, a variety of visuospacial neuron, fire both when an action is being performed by an individual and when the same action is observed being performed by someone else. They can also be activated when one individual observes another individual performing a specific action, and the first individual is also simultaneously performing the same action as the second (Rizzolatti and Fogassi 2007, 179). By this means, these mirror neurons "give the observer access to the goal of the action and thus put [them] in the place of the performer of the action" (Gold and Roskies 2008, 364).

Evidence that mirror neurons are involved in pornography consumption can be deduced from the fact that when some types of male monkey are shown pornographic imagery of other monkeys having sex, their testosterone level can rise by as much as 400%, testosterone levels being directly linked to sex-drive (Winston 2002, 154). The fact that mirror neurons exist in primates and human beings can be taken as evidence that natural selection has, over a significant period of time, favored some types of behaviors that are performed by individuals in imitation of other animals, and that this imitation process sometimes serves the function of a stimulus enhancement (Visalberghi and Frigaszy 1990, 249).

Can Supernormal Stimuli Be Adaptive?

The subtitle of Deidre Barrett's book on *Supernormal Stimuli: How Primal Urges Overran Their Evolutionary Purpose* (2010) could be taken to imply that supernormal stimuli are an inherently negative development. As Barrett explained, "Animals and man are indeed often harmed by what they desire . . . the supernormal stimulus" (Barrett 2010, 136), but they are not inevitably/always so. It is true that supernormal stimuli *can* have negative consequences in some instances but in other instances they might have positive consequences. It is also possible that they can produce both negative and positive consequences simultaneously.

It might also be asked: Can particular supernormal stimuli ever serve an adaptive function in the Darwinian sense? What might an adaptive function of pornography look like? One plausible candidate for an adaptive function of porn is: to facilitate greater understanding of sexual behavior/interaction so as to improve reproductive fitness by means of improved sexual performance. Or, as has been outlined elsewhere, an adaptive function of pornography could be to make its viewers “sexually aroused in a way that they gain new insight into their own sexuality and desires,” other people’s sexuality and desires, and in consequence the full range of human sexuality in all its varied forms (Maes 2012, 17). Mirror neurons may also assist in this process by enabling better understanding of other people’s sexuality and desires.

This hypothesis assumes that sexual satisfaction, in addition to just reproductive success, is something that all human beings value and is therefore a central part of universal human nature. Behaviorally successful sex can be seen to assist in strengthening the relationship bond between couples, this bond being part of a wider need for the development and maintenance of compatibility between sexual partners.

Within the Darwinian framework, achieving sexual pleasure for both sexes is what evolution would select for (Wells 1989), as it leads to greater reproduction rates. As Charles Darwin explained in his autobiography on the link between pleasure and function:

Pleasurable sensations . . . stimulate the whole system to increased action. Hence it has come to pass that most or all sentient beings have been developed in such a manner through natural selection, that pleasurable sensations serve as habitual guides. We see this in the pleasure from exertion . . . of the body or mind, – in the pleasure of our daily meals, and especially in the pleasure derived from sociability and from loving our families (Barlow 2005 [1887], 74–75).

Better promoting the sexual satisfaction/pleasure of a partner can be seen potentially to serve a Darwinian function, as greater happiness promotes better mental health and thereby greater reproductive success. Supernormal stimuli may, therefore, in certain instances serve a positive function.

Conclusion

The concept of supernormal sign stimuli was initially developed by Niki Tinbergen and Konrad Lorenz as part of the mid-twentieth century ethology program, but more recently it has been usefully employed by contemporary evolutionary psychologists such as Donald Symons (1995), Diedre Barrett (2010), and Gad Saad (2011).

Many different contemporary phenomena have been characterized as supernormal stimuli, and it would be possible to suggest that applying the term to one or two of them – contemporary Islamic terrorism, for example – might be stretching the reasoned applicability of the concept beyond its useful limit. However, it is beyond any doubt that most of the other contemporary applications in the literature – high-heeled shoes, fast food, and pornography, for example – are appropriate uses and therefore the supernormal stimuli concept has proved itself to be a very useful and a scientifically valid one.

Even so, despite the sex-positive case outlined in this entry, it will remain controversial to characterize pornography as an adaptation in the Darwinian sense, as even the existence of this supernormal stimulus is controversial for some, as is the hypothesis that pornography functions through the activation of mirror neurons. But, as has been explained: “Control over . . . erotic imagery for social ends is nothing new. It began more than 30,000 years ago, during the last ice age” (Taylor 1996, 96), so critics of pornography might find themselves disappointed if they expect this particular supernormal stimulus to disappear from the transmitted cultural horizon anytime soon.

Cross-References

► [Pornography and Women’s Short-Term Mating](#)

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Supernormal Stimulus

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Synonyms

Artificial stimulus; Supernormality

Definition

An artificial stimulus capable of eliciting an innate, instinctual stimulus-response more powerfully than the original natural stimulus for which the response is adaptively intended.

Introduction

Our minds evolved as a set of psychological mechanisms, each designed by natural selection to solve a particular adaptive problem. Different stimuli activate different mechanisms, thus eliciting different responses. Unfortunately, this also means that our information-processing machinery is prone to certain kinds of errors because natural selection shaped our brains to interpret the world in an adaptive fashion and not necessarily in a truthful manner. As a result, and particularly with the rapid change between our environment of evolutionary adaptedness and today's artificially made environment, some unnatural stimuli can activate the same mechanisms that naturally evolved stimuli do. These unnatural stimuli are referred to as supernormal stimuli, a term coined by early ethologist Nikolaas Tinbergen.

From Early Ethology to Today's Consumerism

Supernormal stimuli mimic and exaggerate response-producing qualities of natural stimuli

beyond the proportions of what was ancestrally possible. They are usually associated with the ability to sway behavioral preferences away from natural stimuli and in favor of artificial constructions. In this way, preferences that would have been beneficial during ancestral conditions may be manipulated to the detriment of an acting organism.

Tinbergen and Perdeck (1951) observed the effects of supernormal stimuli on sea gull behavior when he successfully elicited a behavioral preference toward exaggeratedly bright-red models of an adult gull's beak. Typically, newly hatched chicks are stimulated by a red spot on the mother's beak, as pecking this spot induces regurgitation. Tinbergen then constructed different beaks, each model exhibiting an even bigger spot to the point that some models barely even resembled a beak at all. Chicks recurrently preferred the exaggerated, unrealistic beaks over the models accurate to an adult gull's morphology. Additionally, other animal species showed similar responses. Small songbirds that lay light blue grey-dappled eggs preferred to sit on bright blue black polka-dotted dummies, even when these were so large that their bodies slid off them repeatedly. Similarly, territorial male stickleback fish would attack wooden floats with red undersides, attacking extremely red floats more vigorously than they attacked actual invading males.

Barrett (2010) suggested that supernormal stimuli offer an explanation for several potentially detrimental human behaviors, including the preference for highly concentrated sugars and fats, pornography and breast augmentation, aggressive property defense, and television. These are all examples of stimuli that are naturally sought after and wanted by humans, but are exaggerated from their original forms to be superficially appealing. This is also an example of the *evolutionary mismatch* effect in things such as sugars and fats. In ancestral times, early hominins needed to survive on a very short food supply. Therefore, sugars and fats were extremely valuable given their ability to be stored and thus represent a better chance at survival by being satiated for longer. In addition, they were rare enough that it was

practically impossible to be consumed to excess. Now, we have the ability to simply walk to our local grocery and pick up sugars and fats in exchange for money. Given this ease and simplicity, it is extremely easy to overconsume sugars and fats, whereas it would have been impossible to in ancestral times. The sugar content is also so high compared to what would have been available to our ancestors that it becomes very easy to overindulge, a classic example of supernormal stimuli. The overconsumption then leads to negative impact on our health and to detriments such as heart disease, diabetes, cancer, and so forth. While not all supernormal stimuli are necessarily harmful for our health, sugars and fats are a clear example of how supernormal stimuli can take advantage of consumers and is the basis for much of how products are sold.

Conclusion

Supernormal stimuli are artificial stimuli that elicit an instinctual response more powerfully than a natural stimuli would. This is apparent in birds such as gulls, with their response to a red dot stimuli of any kind being the same as if they actually saw the red dot on their mother's beak. The same effect is apparent in humans and is a basis for consumerism, as much of what sells is a result of our adaptive responses to stimuli being superficially exaggerated to elicit a want to engage with the said product. Things such as sugars and fats, pornography, and television are all examples of things that utilize supernormal stimuli to sell their product and take advantage of humans' natural propensity toward certain stimuli.

Cross-References

- ▶ [Environment of Evolutionary Adaptedness](#)
- ▶ [Evolutionary Mismatch](#)
- ▶ [Exploitation of Psychological Mechanisms](#)
- ▶ [Mismatch](#)
- ▶ [Supernormal Stimuli](#)
- ▶ [Supernormal Stimuli \(Konrad Lorenz\)](#)

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Supernormality

- [Supernormal Stimulus](#)

Super-Stimulus

- [Supernormal Stimuli \(Konrad Lorenz\)](#)

Superstition

- [Religious Beliefs](#)

Supremacy

- [Dominance and Threat or Use of Force](#)

Surreptitious Mating

- [Sneak Copulation](#)

Surroundings

- [Environmental Influences](#)

Surveillance Cues

- [Altruism and Watching Eyes](#)

Survey

- [Self-Reports](#)

Surveys and Questionnaires

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Synonyms

[Census](#); [Interview](#); [Poll](#)

Definition

Research tools that systematically collect information using a variety of methods.

Introduction

Surveys are a systematic way to collect information and data about the same variables for multiple individuals, which can then be compared. While methods of data collection within surveys can vary, questionnaires are commonly used. Questionnaires are a series of questions which are used to collect responses regarding demographics, emotions, behaviors, and/or thoughts. Researchers can choose if they want responses to be made from a set of options, such as in Likert-type scales, or if they want the questions to be open ended, such that the participant formulates their own answer which is often coded to a scale afterward. Surveys and questionnaires can be administered either in person or remotely, using a variety of methods, such as paper and pencil, telephone, electronically through the Internet, or a combination thereof.

There are several benefits to utilizing surveys. One of the most well-known advantages of

surveys is their efficiency in collecting data. Although some methodologies, such as interviews, may have more difficulty in collecting a broader sample, surveys allow for random sampling within particular populations which gives researchers better opportunities to generalize their findings. When considering the costs of distribution and participant compensation, surveys help keep these costs low. Surveys also provide ethical benefits in regards to anonymity. In particular, self-administered questionnaires can give participants an opportunity to feel more comfortable giving information on sensitive topics. Lastly, surveys have the ability to be flexible in regards to the goals of the researcher.

Although surveys are widely used and provide many benefits to both the researcher and participants, there are issues that should be noted. First, participants may not respond to every question that is given to them, leading to the possibility of missing data. The probability of this occurring depends on the methodology used and what information the surveys are asking for. For example, when seeking sensitive information, participants will be more likely to withhold their responses. Secondly, there are various responses that participants can provide that may not accurately reflect the researcher's intentions. This is known as response bias and is described further in the entry Response Bias within this book.

The means by which a survey or questionnaire is initially constructed is paramount to any research using these methods. As mentioned above, surveys and questionnaires, while having many advantages, also have numerous potential weaknesses. Many of these weaknesses can be avoided or at least mitigated if the research tool is constructed carefully and thoughtfully. Before a measure's construction begins, it is extremely important to carefully specify the research question of interest and the hypotheses to be tested, the analyses that will be performed to test these hypotheses, and the construct that is to be measured. Doing so will allow the measure to perform as accurately and efficiently as possible. Other, more specific suggestions are mentioned below.

Keep Your Target Population in Mind

Make sure to consider both the expected abilities and values of your target population when constructing your measure. Doing so includes considering the language proficiency of your target population. The complexity of the language used in your measure must match the abilities of those with whom you are communicating. For research involving undergraduate students, it is likely safe to assume that the participants are fairly advanced in their language skills. For research with younger children or less educated adults, simpler, more straightforward should be employed. Similarly, avoid using jargon whenever possible; you should only use language that you can reasonably expect your target population to be familiar with. Additionally, take care to avoid phrasing your questions in such a way that it could offend your target population. Make sure to use the currently accepted neutral vernacular when referring to any subgroups as well as neutral language when writing about any personal topics (e.g., a participant's religious orientation).

Construct Your Questions Purposefully

Only ask questions that are of theoretical interest to your research. Unimportant questions are taxing for the participants and the researchers alike. Only include "filler" questions if there is good reason to think that the data may be biased without them. Make certain that your questions are unambiguous in their meaning. If different participants interpret the same question in different ways, the validity of your measure can suffer drastically. Avoid "double-barreled" questions that ask more than one thing at a time (e.g., "how likely are you to lease a new car and a new home in the next 12 months?"). Include enough response options to fully cover the potential range of responses. It is possible that this may require you to have one option that reads "other" with a blank space to allow the participants to fill in their own responses. Similarly, the response options should be mutually exclusive; allowing the responses to overlap can confuse participants and reduce the

precision of your data. When possible, measure responses on a continuous scale rather than an ordinal or categorical scale (e.g., do not ask participants to select an age bracket when it is just as simple to ask for a date of birth). This will only serve to increase the quality of the data that is collected and will allow for more sophisticated analyses to be conducted. Present all questions in a neutral way that does not lead the participant to choose any option over another. Lastly, be cognizant of response biases and either construct your questions in such a way to avoid them or employ additional means (e.g., detailed instructions asking your participants to be mindful of how they are responding) to help avoid these potential issues.

Verify That Your Efforts to Avoid Bias Have Been Adequate

While the non-exhaustive set of advice above will help to avoid or mitigate some issues in using surveys and questionnaires, it can be difficult to know if these preventative measures have been enough to ensure your data will be of acceptable quality. Fortunately, there are a variety of ways to assess the reliability and validity of your measure and whether additional refinement is needed. A few of the most widely used techniques will be listed here to guide future research, but a detailed explanation of these methods is beyond the scope of this entry.

Consult experts and previous research. When possible, it can be fruitful to consult experts in the field to request both suggestions and critiques for your instrument at any stage of development. Additionally, it is not always necessary to build a measure completely from the ground up. Consult previously constructed measures, should they exist, and build upon them rather than seeking to completely replace them.

Pilot test your measure. It is valuable in any study, whether surveys and questionnaires are employed or not, to pilot your measure(s) on a small sample of your target population. This can help to identify many of the problems described above, as well as potential errors in measure

implementation (e.g., an online survey unexpectedly skipping a large portion of the questions).

Utilize test-retest techniques. This can easily be done in conjunction with piloting your measure. If responses that are expected to be reliable are shown to not be, then your measure is not ready for implementation in a study.

Employ multitrait-multimethod techniques. Multitrait-multimethod (MTMM) matrices can be used to examine both the convergent and discriminant validity of a measure when compared to other existing measures. Should other measures exist that examine the same construct as your survey or questionnaire as well as ones that measure other distinct constructs, you can use MTMM techniques to assess the content validity of your newly created measure. For an explanation of MTMM matrices and how to implement them, see Campbell and Fiske (1959). For an additional adaptation of these approaches, see Centra (1970).

Conclusion

Surveys and questionnaires are valuable and popular research tools that capitalize on speed and efficiency of data collection across a wide array of participants. These tools also have a number of potential limitations that may not be issues for other measures. As such, researchers must be cognizant of the measures they use and especially those that they create. Mindful construction of the items used can greatly mitigate many of the potential limitations of surveys and questionnaires.

Cross-References

- [Online Survey](#)
- [Response Bias](#)

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Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches

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Synonyms

Benefits of distractibility; Characteristics that help one stays alive; Traits that facilitate continued existence; Usefulness of hyperactivity

Definition

Symptoms of attention deficit hyperactivity disorder (ADHD) are regarded by evolutionary mismatch theorists as prehistorically useful traits that have become broadly nonadaptive in the present world as a result of evolutionary time lags.

Introduction

ADHD is a condition which is generally typified by an enduring tendency for the sufferer to be extremely active, distractible, and impetuous, and that he/she is also prone to be neglectful of his/her tasks at hand (American Psychiatric Association 2013). It is an affliction that has often been associated with a range of adverse consequences (regardless of whether one has received appropriate psychological/psychiatric interventions or not) such as having a greater likelihood of experiencing weight issues, problems with substance abuse, inferior self-respect and psychosocial competence, and

poorer scholastic and career achievements than their healthier counterparts (Shaw et al. 2012). In virtue of these ramifications, many researchers and clinicians have been pulling out all the stops in trying to identify the possible cause (or causes) of ADHD. A variety of mainstream explanations have been advanced, including those that have highlighted the influential impact of distressing experiences in one's early life, the role of genes, and the significance of neurobiological factors (Shelley-Tremblay and Rosen 1996; Swanepoel et al. 2017).

However, because these prevailing hypotheses have mainly focused on clarifying the processes influencing the development of psychological disorders (in this case ADHD) and not why they came about in the first place, there is a real need to take into consideration their evolutionary origins in order to better appreciate the pathogenesis of a disorder such as ADHD (O and Brüne 2019). In this regard, several prominent evolutionary formulations have been proposed with a view to explain the underlying origin of ADHD. These theories are based fundamentally on the premise of evolutionary mismatch, which refers to the phenomenon whereby many modern problems (such as ADHD symptoms) are believed to be a result of genes and cognitive/behavioral mechanisms generally not being capable of evolving expeditiously enough to be acclimatized to a swiftly metamorphosing contemporary world (O 2018).

Leading Evolutionary Mismatch Approaches of ADHD

ADHD Symptoms as Adaptive Hunters' Traits

One such formulation is Hartmann's (1993) notion of ADHD symptoms (e.g., the high amount of energy, impetuousness, and the tendency to quickly shift attention to new stimuli in one's environment) as traits that were helpful for one's survival in a hunting-oriented prehistoric context filled with unpredictability and hazards (as well as opportunities), which are nonetheless regarded as signs of a disorder in the modern world that is more suited for people (or *farmers*) who would prefer greater organization and a more sedentary approach to life. In other words, cognitions and

behaviors typically regarded as ADHD symptoms are posited to be evolved traits useful for prehistoric hunters but are presently mismatched evolutionarily (and hence regarded as problematic) in a farmers-conducive modern world (Hartmann 1993). For instance, the tendency for an individual to shift attention quickly to a new stimulus in one's environment (e.g., a wriggling snake), while doing another task (e.g., preparing a trap) would probably be lifesaving for a prehistoric hunter; however, such a similar distractible tendency might not necessarily be considered beneficial for a child preparing for his/her exams in the much safer present world (especially when the new stimulus is a television program).

Survival Benefits of ADHD Symptoms for Waders

Founded on Morgan's (1972) expanded aquatic ape theory, Shelley-Tremblay and Rosen (1996) put forth a formulation which suggested that individuals with ADHD symptoms were actually more adept at outliving their non-ADHD counterparts during a significant period of prehistory in which *Homo sapiens* were believed to have spent considerable amount of time in water. According to this formulation, children who are more proficient in drawing the attention of their mothers in such conditions (e.g., those with ADHD symptoms who were conceivably very active, especially orally) would be more successful at obtaining food and security from them (as these children could not easily hold on tightly to their caregivers, who have little body hair as an evolved physical reaction to aquatic environments) (Shelley-Tremblay and Rosen 1996). For instance, a mother in that ancestral context might need to pacify the child who is the loudest and is making the most noises first (perhaps by providing some milk or food so that he/she would not attract the unwelcome attention of predators), before feeding her other offspring while in the water (thereby enhancing the survival odds of that child); however, such traits might not be advantageous in the land-based, resource-rich, relatively predator-free present day. In short, ADHD traits might have represented an evolutionarily mismatched set of cognitions and behaviors that is no longer beneficial in the modern, non-aquatic world in which humans generally reside in.

Individuals with ADHD as Better Fighters

Shelley-Tremblay and Rosen (1996) have also suggested that ADHD symptoms might alternatively have evolved as useful traits for physical combats during a period in evolutionary history where humans were believed to have been actively battling with Neanderthals over limited resources, but are predictably much less relevant in the modern, relatively peaceful context. A hyperactive individual would conceivably be a better combatant (and hence more likely to survive a physical fight) than a lethargic one in such conditions; nonetheless, with the advent of laws and law enforcement forces (and therefore a much peaceful environment) in the contemporary world, being a good fighter is generally no longer beneficial nor an essential attribute for one's continued existence.

ADHD Traits Facilitate Swift Reactions

Jensen and colleagues (1997) alternatively contended that ADHD traits were helpful for one's continued existence in certain prehistoric contexts (e.g., especially those that were generally hostile and unpredictable) because those with such traits were more capable of reacting swiftly to (and thus dealing effectively in terms of) surprises and changes in these conditions as opposed to their calmer, more ruminative counterparts. Being capable of noticing and attacking a rabbit rapidly without much forethought for instance (which were more likely among those with ADHD traits than not), might be the difference between survival and death in a hostile prehistoric world where food was infrequently available (Jensen et al. 1997). Such quick reactions might not comparably be as necessary for one's survival in the present context though, especially when most people (at least in industrialized countries) are currently living in largely tranquil conditions with relatively easy access to food (Jensen et al. 1997).

Survival Advantages of ADHD-Associated Capricious Behaviors

In a different vein, Williams and Taylor (2005) propounded that inquisitive behaviors typically exhibited by those with ADHD (especially if they constitute a small proportion of a band) might actually be helpful for the community across prehistory (despite the potential of

incurring some personal harms). Such inquisitiveness was believed to be instrumental in providing conceivably lifesaving knowledge regarding essential tasks (e.g., identifying edible food from those that are inedible or being cognizant of hazards in one's habitat) for one's community in the ancestral period (Williams and Taylor 2005). For instance, other youngsters might have learned to avoid playing with/eating thorny plants (and hence be more likely to avoid injury or even death) after a curious child with ADHD was pricked by one in the prehistoric context. However, given the widespread dissemination of knowledge regarding food (and other survival-related issues) in the present day, coupled with the relative ease of ensuring one's safety on a daily basis (especially for the industrialized part of the modern world), it is logical to assume that (even though the formulation did not explicitly indicate the role of evolutionary mismatch) these inquisitive behaviors are no longer very relevant in enhancing the well-being of a community in the current context.

The Adventurous Nature (and Hence Survivability) of Individuals with ADHD

More recently, Swanepoel et al. (2017) postulated that those who have ADHD traits were better equipped to survive and procreate in the ever-changing prehistoric world because they tended to be more curious, investigative, and enterprising than people without such traits (e.g., eagerly scouting around for alternatives after a natural disaster has rendered one's current residential location uninhabitable). Such traits nevertheless, are believed to run counter to the key philosophy of modern scholastic culture, where students are supposed to be deferential to rules and to pay attention in class while remaining sedentary for long durations (Swanepoel et al. 2017).

Integration of Key Evolutionary Mismatch Approaches

While a number of evolutionary mismatch accounts has been introduced in the literature to explicate ADHD over the years, there are few

research work investigating the veracity of these explanations thus far (Thagaard et al. 2016). However, this does not necessarily suggest that these formulations are misguided or wrong (the few existing investigations have appeared to provide preliminary support for an evolutionary perspective); it merely indicates that additional scientific work are needed to reliably refute or corroborate these approaches (Thagaard et al. 2016). To this end, in order for future research work to accurately evaluate the evolutionary origins of ADHD, it is reasonable to assume that an integrated framework will be a more appropriate focal point as each of these leading approaches has seemingly only addressed one part of the equation. Under such an integrated framework, ADHD symptoms as a whole would conceivably have evolved gradually across different periods of human evolutionary history (e.g., when humans were mainly hunters or waders), or from a variety of different ancestral circumstances (e.g., when humans were required to be competent combatants during tribal warfare – even if they were actually not battling against the Neanderthals, to adapt to harsh and unpredictable conditions by reacting swiftly or be by being adventurous, or to have a small number of inquisitive members in a group who could provide valuable knowledge about environmental hazards).

Conclusion

Symptoms of ADHD have been posited by an assortment of approaches to confer survival benefits in the evolutionary past. These theories differentially suggested why such traits were advantageous for survival in the ancestral context, but are less useful in a modern world that is broadly dissimilar physically and socially to that of the former. Limited amount of empirical work has thus far evaluated the credibility of such approaches and more investigative research is hence undoubtedly needed in the literature. An integrative framework that combines all the heterogeneous explanations appears to be a more comprehensive and accurate account of the (prehistoric) survival advantages of ADHD traits.

Cross-References

- [Benefits of Profound Kinship Connectedness \(and Problems from a Lack Thereof\) Through an Evolutionary Mismatch Lens](#)
- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
- [Perceived Control and Suicide from an Evolutionary Mismatch Perspective](#)
- [Self-Efficacy, Animal Phobias, and Evolutionary Mismatch](#)

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Survival and Death

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Synonyms

[Living and dying](#); [Longevity](#); [Mortality](#); [Survivorship](#)

Definition

The continuation and cessation of being alive, respectively.

Introduction

The world of our ancestors abounded with dangers, from pathogens and predators to jealous lovers and war-minded out-groups. Such repeatedly encountered threats have exerted selective force that favored the evolution of adaptations specific to each type of threat. These adaptations enable continued survival in various ways, such as detection, avoidance, escape, or physical confrontation.

The degree to which an animal is well adapted to survive in its environment was the meaning of *fit* in “survival of the fittest” as used by Charles Darwin and his contemporaries (Darwin 1858/1968). A longer-necked giraffe was more fit in its environment than a shorter-necked giraffe if the longer neck enabled the giraffe to avoid starvation by eating hard-to-reach foods unavailable to its shorter-necked conspecific. Survival is obviously important during natural selection, because an organism has to be alive to reproduce, but biologists have come to realize that reproduction is often more important to natural selection than is survival. That is to say, natural selection favors animals reducing their likelihood of survival when doing so increases their reproductive output

(Williams 1957). Therefore *fitness* has been reconceptualized in terms of offspring produced. Natural selection at its most fundamental is about the propagation of genes into subsequent generations (Dawkins 1976). A key way to propagate genes is by having offspring, but it is not the only way. Considering fitness only in terms of offspring lacks recognition of the importance of helping the survival and reproduction of *genetic* relatives, who carry copies of the same genes. In modern evolutionary theory, the importance of survival and reproduction of genetic relatives is added to one's own reproduction, and together their effects on gene propagation are referred to as *inclusive fitness* (Hamilton 1964). In a sense, then, survival and death are about genes – but critically natural selection works at the level of individual organisms' phenotypes, which is where adaptations can be seen. We might therefore expect adaptations that lead individuals to trade off their own survival if doing so increases the survival of genetic relatives.

Survival – and its conclusion in death – has profound implications for the inclusive fitness of an organism. In most conceivable situations, survival enables – but death ends – the possibility of improving inclusive fitness. Survival and death are therefore central players in the process of natural selection and have been the focus of substantial research by evolutionary psychologists. Adaptations have been hypothesized to have evolved to solve a variety of problems, such as choosing a habitat, navigating the physical world, avoiding predators, avoiding pathogens and toxins, avoiding starvation and dehydration by consuming food and water, cooperating with kin and non-kin, permanently removing fitness threats via homicide, reaping substantial benefits for self and kin through warfare, and enhancing inclusive fitness by committing suicide. Evolutionary psychologists have also proposed explanations for aging and grief. Before considering specific adaptive problems, an overview of life and death in traditional societies provides the contexts that such adaptive problems arise in terms of how long humans naturally live and what dangers we faced at different ages.

Longevity and Causes of Death in Hunter-Gatherers

A cross-cultural review of available data on hunter-gatherers and forager-horticulturalists by Gurven and Kaplan (2007) provided a broad background regarding likely human longevity and causes of death in the environment of evolutionary adaptation. This is important because humans have spent most of our time as hunter-gatherers, and improvements in sanitation, nutrition, and public health have increased longevity in modern societies. For hunter-gatherers who lived to 15 years old, the most common age of death was 72 years, before which people tended to be productive and after which aging was severe. This finding led Gurven and Kaplan (2007) to suggest that “human bodies are designed to function well for about seven decades in the environment in which our species evolved” (p. 322).

Traditional societies vary somewhat regarding rates of mortality, especially mortality from warfare, but overall and compared to closely related species, the observed traditional societies were similar to one another (Gurven and Kaplan 2007). An average of 57 % of hunter-gatherers survived to age 15, and 64 % of those who lived to age 15 were also alive at age 45. Regarding life expectancy, those who survived to 5 years of age could expect to live on average to about 50 years old, those who survived to 15 years old could expect to live to about 55 years old, and those who survived to 45 could expect to live to about 65 years old. These findings indicate that aging (senescence) is not substantially greater in people who live in traditional societies as compared to those living in modern societies, but they reveal the greater number of threats to survival faced by people who live in traditional societies.

In their review, Gurven and Kaplan (2007) also summarized causes of death for people living in traditional societies (see Table 1). Overall, about 70 % of all deaths resulted from illness, 9 % from degenerative diseases, 6 % from warfare, 5 % from homicide, 8 % from accidents (e.g., falls, predation, drowning, burns), and 2 % from other causes. Illness was the major cause of deaths in

Survival and Death, Table 1 Percentages of death by their cause and by age class (summarized from Gurven and Kaplan 2007, p. 341, Table 5)

Cause of death	Age class			Total
	<15 years old	15–59 years old	60+ years old	
Illness	65.3	60.5	54.6	70.1
Degenerative disease	9.5	9.2	28.2	9.2
Accidents	8.1	12.9	10.3	8.1
Violence	17.1	17.4	6.9	12.5

adolescence and adulthood (60 % of deaths). For older adults, illness accounted for 55 % of deaths, degenerative diseases accounted for 28 %, and accidents for 10 %. For children, illness-related diarrhea compounded with malnutrition was especially deadly. Degenerative diseases were also dangerous for infants, accounting for 10 % of their deaths. Warfare, homicide, and accidents varied substantially across groups. Most homicides were infanticides, with homicide (inclusive of infanticide) accounting for 17 % of deaths before 15 years old. Across groups, accidents accounted for about 4 to 13 % of deaths. These rates were observed in contemporary traditional societies, so they might not perfectly reflect those in the ancestral environments in which humans evolved and lived. Gurven and Kaplan (2007) suggest that if systematic differences exist, most likely ancestral populations had less disease (due to greater social isolation) and higher mortality rates from homicide and warfare compared to the hunter-gatherers who have been observed by anthropologists.

The Nonhuman Environment

Habitat Navigation. Given the substantial impact of environmental dangers on survival in traditional societies, choice of habitat is important. The leading explanation for the evolution of human preferences regarding habitat selection is *The Savanna Theory* (Orians and Heerwagen, 1992). It argues that we evolved on the savanna, and therefore our preferences should match resource and danger distribution in that landscape. For example, people should prefer trees because they provided fruits, enabled predator avoidance,

and shaded us from the sun. We should also like plains, wherein large, huntable animals lived. A complementary approach is provided by *prospect-refuge theory* (Appleton 1988). It suggests that people should favor environments that enable the use of “prospect-providing” views, those that allow information gathering regarding such things as potential food or predators, and we should like “refuge-providing” views, those that allow hiding while observing the environment, such as is afforded by a clump of trees.

Another survival issue related to interacting with the physical world is addressed by Russel Jackson’s *evolved navigation theory* (Jackson and Willey 2013). This theory proposes that issues related to navigating the world – such as body-damaging falls from high cliffs, energy expenditure, and predation – have adapted the perceptual system so that it is biased in ways that reduce the likelihood of related mistakes. Such biases have been demonstrated in previously unknown perceptual illusions. For example, a vertical cliff appears longer when viewed from its top than its bottom, thereby enhancing caution at the top. Another example is that the distance toward a cliff edge appears longer than it is – suggesting extra metabolic costs that deter approach – whereas the same distance viewed from the cliff edge appears shorter than it is, enabling withdrawal.

Predators. In our evolutionary past, humans came into contact with predators such as large cats and hyenas (Barret, 2015). We were hunted by them and competed with them over kills. Predators and prey are special components of the environment because they are intentional agents that have adapted to us. Their relevant adaptations, such as cryptic coloration and intentional goals

to find or avoid humans, require specialized psychological mechanisms unlike those for dealing with static threats or opportunities, such as cliffs or ripe fruit. Adaptations that helped avoid predators include abilities to detect predators and predict their behavior (perhaps including “mindreading” abilities), memory and learning systems (such as prepared learning and social learning), and emotion and motivation systems (such as fear and anxiety; Barret 2015). Evidence suggests that even young humans are perceptually tuned to predator–prey interactions and born prepared to learn about potential predators such as snakes or objects that perceptually loom (appear to get closer). Adaptations for predator avoidance and food collection thus provide likely preadaptations for other adaptations, such as the ability to attribute goals and mental states to others (Barret 2015).

Pathogens, Parasites, Poisons, and Toxins.

As mentioned above, illness is the deadliest of the dangers faced by members of traditional societies (Gurven and Kaplan 2007), and so it is likely that selection has favored adaptations to avoid related costs. The emotion of *disgust* is believed to be an adaptation that evolved to help avoid microbes and other sources of disease (Rozin and Todd 2015). It shows many traits that fit with this proposal. It results in nausea and vomiting, which can remove dangerous substances from the body. It also motivates the avoidance and destruction of disgust-eliciting stimuli. Disgust is experienced less in men than women, which likely reflects the value of avoiding pathogens while women cared for and provided food for infants and children (Buss 2015). The heightened disgust of pregnant women is believed to help prevent women from consuming *teratogens* – agents that disrupt fetal development (Sherman and Flaxman 2001).

Evolutionary psychologists have argued that important features of culture are also related to pathogens. In addition to the physiological immune system, evolutionary psychologists argue that humans have a *behavioral immune system* that helps us avoid pathogens (Thornhill and Fincher 2014). The behavioral immune system helps people to avoid pathogens by avoiding and expressing prejudice against situations and

people that exhibit cues of the presence of disease, such as disfigurement or obesity. The behavioral immune system functions at the individual level, but groups of people are exposed to different levels of pathogens. For example, environments near the equator tend to harbor more pathogens and so groups that live there are exposed to more pathogens. Therefore groups are predicted to systematically vary in sociality variables related to pathogen avoidance depending on their degree of exposure to pathogens. More specifically, *parasite stress theory* argues that groups of people who live in areas with more pathogens should be more xenophobic, socially conservative, and exhibit other in-group biases – because these values enable people in those groups to avoid exposure to novel pathogens carried by out-group members (Thornhill and Fincher 2014).

Another way that groups differ is that spices are more commonly used in the cuisines of cultures that have higher levels of endemic pathogens (Sherman and Flaxman 2001). The *antimicrobial hypothesis* explains this pattern as a result of people capitalizing on the antibiotic effects of some spices to kill food-borne pathogens, which were especially likely to be a problem before refrigeration but are still a common danger today. Spices are molecules produced by a plant that are nonessential for the plant’s metabolism, instead having evolved to reduce the likelihood that the plant itself would be consumed by herbivores, bacteria, or other pathogens. Given that many people have an inborn dislike of spices and the culinary preference for spices is sometimes acquired – often through social pressure – it seems likely that the covariation of cultures and spices reflects cultural learning or cultural evolution. On the other hand, humans have inborn preferences for sweet foods (calorie-rich fruit evolved to entice consumers to eat it and spread seeds) and salt (a cellular-function essential) and dislike of bitter and sour foods, which are more likely to contain toxins and pathogens, and a fear of new and therefore potentially dangerous foods (Buss 2015).

Food and Water. Consuming water and appropriate food is a prerequisite for survival and the use of adaptations unrelated to water and food consumption (Tooby and DeVore 1987).

Humans are omnivores, so our ability to consume and digest a variety of foods helps us get the calories and nutrients we need. Being omnivorous also exposes humans to dangers of plant poisons and pathogens in animal tissues (Rozin and Todd 2015). Unique among animals, humans cook our food, aiding consumption and digestion while killing pathogens. Indeed, Richard Wrangham (2009) proposed that cooking food was a central development in the evolution of modern humans and our large brain. Food acquisition has a repeating pattern: hunger, search, capture, preparation, and consumption – with evolved adaptations for each phase (Rozin and Todd 2015).

Two key methods of searching for food are hunting and gathering. Human ancestors hunted regularly starting at least two million years ago, and over evolutionary time, hunting has been increasingly important (Barret 2015). Meat is a nutrient-rich food that provides a substantial proportion of the diet in many traditional societies (Buss 2015). Hunting almost always involves tools, some of which are projectiles that require substantial perceptual and motor skills (Barret 2015). Cross-generational teaching and learning is required for hunting-tool use. Possible adaptations to and consequences of the extreme complexity of human hunting and extractive foraging include growing larger, smarter brains, hunting and cooperating better, extending childhoods (to learn skills) and the overall length of the human life span (due to cross-generational resource sharing), and information-sharing abilities (Kaplan et al., 2000).

Tooby and DeVore (1987) proposed the *hunting hypothesis*, which claims that hunting large game resulted in the evolution of our large brain; home bases; enhanced human abilities for tool construction, tool use, communication, cooperation, and male coalitions; paternal investment in offspring and a resulting reduction in sexual dimorphism; social exchange; and the male–female division of labor. Kristen Hawkes (1991) proposed a largely complementary *show-off hypothesis*, which argues that big-game hunting – which occasionally provides highly nutritious food in such large windfalls that it is (often equitably) shared with others in the local group –

results in fitness benefits for hunters such as prestige, reciprocated food sharing and childcare, and increased sexual opportunities.

In contrast to the prior theories that suggest men’s hunting drove human evolution, Tanner and Zihlman (1976) suggested that women’s gathering played a key role. They argued that tool use developed for increased gathering efficiency, which is important given that in many traditional societies gathered foodstuffs provide the majority of calories and – unlike hunted animals – are a stable source of food. Regardless of its role in driving human evolution, foraging is likely to have selected for abilities related to spatial cognition, search assuming clumped resources, and the distribution of resources (Barret 2015). The ubiquitous division of labor in traditional societies with men hunting and women gathering is believed to have resulted in evolved sex differences in mental abilities, such as men’s tendency to navigate by direction whereas women use landmarks, men’s advantage on mental rotation tasks, and women’s advantage on object recognition and location recall (Buss 2015).

The Human Environment

Parental Investment in Hunter-Gatherer Societies. Human parent–offspring relationships in hunter-gatherer societies are exceptional in many ways. For example, our offspring are exceptionally dependent for a long time, and we address that dependency with parenting strategies unusual in the animal world (Apicella and Crittenden 2015). High mortality rates in children are common in hunter-gatherer societies, with morality rates of one-third to one-half of children dying before age 15 being common (see also Gurven and Kaplan 2007). Human babies are born so large-headed that childbirth is an extremely dangerous activity (Apicella and Crittenden 2015). The trade-off between extended gestational time and the head being larger (and more dangerous) at birth is believed to have resulted in human infants being born effectively as fetuses, with concomitant extended dependency. Human infants are weaned at a relatively young age, compared to

other primates, with an age of weaning about 1.5–2.5 years in hunter-gatherer societies. Human mothers have another child on average 3.5 years after the birth of their prior child, which is much shorter than other apes. Human adolescence is also extended compared to other primates. Explanations for the extended adolescence include that humans need time to learn how to survive in the local ecology or that it is a by-product of evolution of longer life. Human infants do not contribute resources to the group, but even children aged 3 years old in foraging societies contribute by helping in daily food collection. From 6 years of age through adolescence, immature humans can provide up to half of their own daily nutritional needs. Across infancy, childhood, and adolescence, developing humans require substantially more calories than could be provided by their mother alone (in hunter-gatherer societies). This problem is compounded because having multiple dependent offspring at the same time is common, although children help with caring for younger siblings.

Across hunter-gatherer societies, mothers provide the primary care for children, and in many societies fathers provide the second most care. Human males in most hunter-gatherer societies invest in their children, which is especially notable because paternal investment is exceptional among mammals. The degree of direct care, such as infant holding, by fathers varies substantially across hunter-gatherer societies, with the majority of paternal investment taking the form of provisioning. The high dependency of offspring, along with the necessary investment that is larger than the mother alone could provide, is thought to favor monogamy (one man with one woman) and serial monogamy (people forming a series of monogamous relationships) for most hunter-gatherers, with a minority of hunter-gatherer families with exceptional access to resources being polygynous (one man with multiple women). Parental care has been argued to be the reason men and women differ in their food collection specialization (i.e., hunting versus gathering). Hunted food, which comes in large but ancestrally unstorable packages, is often distributed to people outside the nuclear family, limiting the

provisioning of a father directly to his child. However, meat sharing might be unequal such that it disproportionately benefits the hunter's own family, while also enabling a man's child to benefit from successful hunts of other men. Father death has been found to reduce child survivorship in some but not all hunter-gatherer societies.

Cooperative Child-Rearing. Sarah Blaffer Hrdy (2009) argued that cooperative breeding – cooperative groups including nonrelatives providing for children – was a preadaptation that enabled the evolution of other human adaptations. Our ancestors suffered high mortality, especially when young, and young required substantial caloric provisioning but contributed little themselves. Given the high mortality rate of immature humans and mothers raising multiple immature children concurrently for which she alone would be unable to provide, help from others was a necessity. The infant, in turn, would need to read minds to request nurturing from its mother and others. “We have underestimated just how important shared care and provisioning of offspring by group members other than parents have been in shaping prosocial impulses” (p. 20). Hrdy (2009) argues that our empathy is based on child-rearing and that empathy in turn enabled our powerful culture. That is, we were emotionally modern before we evolved our large brains and language.

Within-Group Violence. Humans help raise one another's children, but they also have many conflicts of interest such that group members can be a hindrance rather than a boon to fitness. Joshua Duntley and David Buss proposed *homicide adaptation theory*, which argues that “homicide is the designed outcome of evolved psychological mechanisms” (Duntley 2015, p. 270). Adaptive problems posed by others in the social environment – such as threats to the self and family, having a reputation as being weak, or exposure to others who might exploit your resources – have the potential to be solved by homicide with a finality unlikely to come from causing injuries or signaling threats, which instead leave the competitor alive to cause the same type of problems in the future. Moreover, given that being murdered has long been an issue for humans, Duntley (2015) suggests that humans

have evolved complementary adaptations to avoid being killed, including avoiding situations where killing is likely, defenses against attackers, and ways of reducing death-related costs to relatives. These homicide-avoidance mechanisms, through a feedback system, further honed adaptations that produce homicides.

If people have evolved adaptations to kill others, then the patterns of homicides should make sense in light of evolutionary theory. This proposal was soundly supported by a review of homicide data by Martin Daly and Margo Wilson in their 1988 book, *Homicide*. The most common situation for murder is between “unrelated men, especially young men whose dismal prospects make dangerous escalation of social competition attractive” with a “cross-cultural universality of enormous sex differences in reproductive competition and same-sex homicide” (p. 294). That is to say, homicide is most common among young men because, of all demographic groups, they face the most intense competition with one another for access to resources and mates. Regarding murders within families, most are husbands killing spouses in attempts “to exert control over women and their reproductive capacities” (p. 295). This largely refers to men’s attempts to avoid being cuckolded – raising a child born of their wife that was fathered by another man – or having their mate abandon them. Analyzing ethnographic data of infanticide across cultures, Daly and Wilson found that infanticide occurs in circumstances “in which the child is of inappropriate paternity, is of poor phenotypic quality, or is unlikely to survive for other reasons” (p. 294). Other important factors include mothers being younger (and so having more time remaining in their life span to bear offspring), mothers being single (who have fewer resources, on average, than married mothers), children being young (with fewer resources having already been invested in them), and having a step-parent (who is genetically unrelated). That is, to say, infanticide is most likely when the offspring has an unusually low probability of successfully reaching maturity and competing for resources and mates. In short, the patterns of homicides in modern societies are explained within the framework of evolutionary psychology.

The demographic patterns of homicide victims that Daly and Wilson (1988) observed in modern society share notable consistencies with those reported by Gurven and Kaplan (2007) for traditional societies. In traditional societies with higher homicide rates, victims are disproportionately infants and children. Infanticide is most common in cases of twins, birth defects, perceived weakness, or ambiguous paternity – all situations where the offspring might either be especially burdensome or have a low chance of flourishing. Also, in societies with substantial adult homicide, the most common victims are adult males.

Warfare. Other groups afford dangers analogous to predators: they can sneak attack, ambush, or opportunistically aggress against lone individuals who are away from their group, so adaptations for avoiding predators likely served as preadaptations regarding intergroup conflict (Barret 2015). Like the concern of predators, warfare predates modern humans; it also occurs among chimpanzees and across resource-strapped human societies, from the modern to hunter-gatherers (Tooby and Cosmides 2010). John Tooby and Leda Cosmides (2010) explain warfare as an expression of a highly adapted coalitional psychology that is also reflected in politics, morality, and group psychology. Aggression, they argue, provides benefits by manipulating or eliminating people who are obstacles to increased fitness (e.g., they reside on better territory) or by enhancing bargaining outcomes (e.g., by threatening punishment for lack of compliance). The capacity to inflict costs on others – *formidability* – is greater for groups than individuals, so coalitions amplify the ability to eliminate fitness obstacles and to bargain. Coalitions provide many benefits and so might have been common across many species, but the evolution of coalitions has substantial barriers that have been overcome by few species other than humans. Humans had sufficient preadaptations: we lived with kin and so costs of coalition-member death were offset by inclusive-fitness benefits of related coalition members, we had advanced cognitive abilities such as theory of mind, and we had dangerous weapons that could kill from a distance. Also important was that coalition members could not predict which of them

would pay costs or reap benefits of coalitional warfare. Coalitional and warfare activities in turn drove further selection to hone cognitive and emotional adaptations for forming and maintaining coalitions as well as coordinating activities. For example, theory of mind was modified to perceive a group as if it had an individual mind – a phenomenon known as *entitativity*. Humans evolved adaptations allowing the formation of coalitions at various scales, with high-level coalition formation for conflict between groups being one of the most important due to “the prospect of large gains or huge losses through displacement, expropriation, subordination, or extermination” (p. 208). From this point of view, warfare is just one expression of our evolved adaptations for coalitional attempts to enhance individual fitness.

Other “Life-and-Death” Considerations

Aging. How natural selection could permit aging – the degradation of the body with increasing adult age – was a mystery until Peter Medawar (1952) and George Williams (1957) proposed two now commonly accepted mechanisms. Both mechanisms build on the observation that the strength of selection decreases with age, which in turn results from reduced survivorship over time. The first explanation – *mutation accumulation* – is that natural selection would be unable to eliminate harmful mutations that are expressed so late in life that most animals in wild populations would already have died. In safer environments, animals would live unnaturally long lives, and normally unexpressed genes would cause aging. The second explanation – *antagonistic pleiotropy* – is that natural selection would favor genes that have harmful effects later in life if they also had beneficial effects earlier in life. That is, a trade-off occurs between early-life vigor and reproduction at the cost of late-life survivorship.

Human aging has features that are anomalous given standard individual-selection models of evolution (Hamilton 1966). Most notably, human women lose the ability to reproduce due to menopause beginning at about 40 years of age, but can survive over twice that long. Standard

evolutionary theories would predict rapid aging and death during post-reproductive ages. One explanation for women’s post-reproductive survivorship is the *grandmother hypothesis* – the idea that women increase their inclusive fitness by helping their children and grandchildren to survive and reproduce (Hamilton 1966; Hawkes et al., 1998; Williams 1957). This is consistent with a review of hunter-gatherer societies that found about one-in-four persons in a traditional society would live as a grandparent for 15–20 years (Gurven and Kaplan 2007). In hunter-gatherer societies, grandmothers increase grandchild survivorship and growth and reduce mothers’ workloads (Hrdy 2009). Grandmothers sometimes selectively live in locations where her grandchildren’s father is absent or their daughters need more assistance. Grandmothers rank third, after mothers and fathers, in how much care they provide to children (Apicella and Crittenden 2015).

Another explanation for humans’ extended life span is provided by *embodied capital theory* (Gurven and Kaplan 2007). This theory suggests that humans need substantial time to physically develop and to learn how to hunt and gather during adolescence and that both men and women invest in educating their children and grandchildren (this theory is thus inclusive of, but more general than, the grandmother hypothesis). Productivity is low early in life but it increases across most of adulthood. This theory explains why the human life span evolved to end at about 60 years old: generally at that age, hunter-gatherer children and grandchildren are grown and no longer depend on the tutelage and provisioning of parents or grandparents. A potential caveat for the above theories of human aging was provided by Hill et al., (2007), who argued that for people to benefit from our extended longevity, people actually had to live longer first. They suggested that the initial extension of our life span was due to highly cooperative humans enabling others to survive by sharing food and caring for the sick and injured.

Grief. When a loved one dies, people react with extreme sadness. Arguing that this sadness is not merely a by-product of the attachment

system. Randolph Nesse (2005) proposed that grief is a special kind of sadness that was shaped, perhaps imperfectly, by natural selection. He notes some adaptive features of grief. It is elicited most strongly by the death of relatives, especially those at maximum reproductive value, and by the death of a close, personal relationship partner. When the body of the lost person is not present, grief induces a desire to search, which would have been adaptive ancestrally when someone was merely missing and not (yet) dead. Survivors ruminate about how the death might have been prevented, which could prevent similar losses in the future. The sadness and negative affect may play a role in disengaging from previous goals shared with the lost person that are no longer relevant, as well as pausing to consider how to move forward. Public displays of grief signal to others that one is capable of deep emotional relationships, which might lead others to choose the griever for cooperative endeavors.

Suicide. Denys de Catanzaro (1995) has provided the most thorough analysis of human suicide from an evolutionary perspective. He argues that there can be situations in which there is a trade-off between benefiting oneself versus harming one's kin (and so one's own genetic interests via inclusive fitness; Hamilton 1964). de Catanzaro argued that ψ , the "residual capacity to promote inclusive fitness," is a function of *reproductive value* (likelihood of producing offspring in the future) plus *kin solicitude*, the sum of possible current and future influences on the fitness of genetic relatives (1995, p. 386), with the latter weighted by Hamilton's coefficient of relatedness. Young, healthy individuals would have high ψ values because their reproductive potential would be high, as would their potential to aid relatives. In post-reproductive individuals, ψ could be positive if aiding kin is possible. Critically, for individuals with low or zero reproductive value, being burdensome to relatives could result in kin solicitude being negative, potentially enough to offset any remaining reproductive value, resulting in a negative value for ψ . This would mean the person is costly to his or her own inclusive fitness. When such situations arise, de Catanzaro argues that self-destructive adaptations

might be expressed, such as physiological failures and self-harming, including suicide. Consistent with this proposition, suicide is higher among older individuals, men, people who fail to acquire a romantic partner, the chronically ill, the disgraced, the socially isolated, and those who experience failure. Moreover, suicide ideation positively correlated with perceived burden on family, as did lack of social connections (loneliness) in elders, whereas sexual activity was negatively related to suicide ideation in younger adults.

Conclusion

The evolution of humans has involved the development of adaptations to help avoid death and thereby continue the survival of oneself, one's kin, and one's coalition members. For over a decade at the start of our lives, humans depend on parents and other group members for food and protection from numerous threats. Once we become mature, we face additional dangers related to mating and coalition-related competition within and between groups. We help one another survive to a degree that is extreme in nature, but we also use deadly force to a likewise extreme degree.

Cross-References

- [Child Homicide](#)
- [Child Mortality](#)
- [Culture of Honor](#)
- [Death](#)
- [Death by Suicide](#)
- [Disease Avoidance](#)
- [Disgust](#)
- [Evidence of Intentional Killing](#)
- [Evolved Psychology of Warfare](#)
- [Factors Associated with Suicide](#)
- [Fear Affords Protection](#)
- [Fears](#)
- [Filicide](#)
- [Food Preferences](#)
- [Homicide](#)

- ▶ Homicide Adaptation Theory
- ▶ Homicide by Design
- ▶ Infant Abandonment
- ▶ Infant Survival
- ▶ Infanticide
- ▶ Infanticide and Parenting
- ▶ Kin Selective Suicide
- ▶ Lethal Violence
- ▶ Marital Status and Infanticide
- ▶ Maternal Abandonment and Maternal-Fetal Conflict
- ▶ Morning Sickness
- ▶ Murder
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- ▶ Pathogen Resistance
- ▶ Predictors of Infanticide
- ▶ Same-Sex Homicide
- ▶ Senescence
- ▶ Sex Differences
- ▶ Sex Differences in Death by Filicide
- ▶ Sex Differences in Death by Homicide
- ▶ Siblicide
- ▶ Sociocultural Theories of Violence
- ▶ Spontaneous Abortion and Maternal-Fetal Conflict
- ▶ Spousal Abuse and Homicide: Evolved Homicide Module Theory (Buss) [Spousal Homicide]
- ▶ Status and Redistribution of Resources
- ▶ Stepfamilies
- ▶ Suicide as Kin-Directed Altruism
- ▶ Theory of Senescence
- ▶ Victims of Violence

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Symbiosis and Mutualism

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Synonyms

Symbiotic and mutualistic relationships

Definitions

Symbiosis refers to a close and prolonged association between two organisms of different species. Mutualism refers to mutually beneficial interactions between members of the same or different species. Mutualistic interactions need not necessarily be symbiotic.

Introduction

Symbiotic and mutualistic interactions are important in evolution because they constitute types of interactions between organisms that affect their fitness. These types of interactions and relationships may assume many forms. An increasing number of investigators have suggested that the prevalence and significance of mutualism have been underestimated in research on cooperation (Dugatkin 1997). Accounting for the evolution of mutualism is challenging, because it often is difficult to quantify the short-term and long-term, direct and indirect, costs and benefits of mutual exchanges and to explain how cooperating organisms avoid exploiter and free-rider problems.

Types of Symbiosis

Symbiotic interactions are commonly classified as parasitism, commensalism, amensalism, or

mutualism. In parasitism, one organism in the association benefits while the other is harmed (+ −). An example is a flea feeding off its host. In commensalism, one organism in the association benefits while the other is neither helped nor harmed (+0). For example, spiders benefit from building webs on plants while plants remain unharmed. Amensalism occurs when one organism harms another but is neither harmed nor benefitted as a result (−0), for example, cows crushing grass as they walk. Mutualism occurs when both organisms in an association benefit (+ +).

Mutualism

Mutualism may occur in dyadic or multiindividual interactions. A classic example of mutualism is cleaning symbiosis in fish and shrimp. One species – the cleaner – cleans another species – the client – by removing parasites, often entering into the mouth of the client to perform this service. The cleaner reaps a benefit by obtaining food; the client reaps a benefit by getting cleaned. In certain conditions, such as when the costs of parasite affliction are high, when the supply of cleaner fish is low, and when cleaners and clients form an ongoing symbiotic relationship, the benefits of getting cleaned outweigh the benefits of eating the cleaner fish.

Types of Mutualism

Investigators have distinguished between obligate and facultative mutualism. In obligate mutualism, two organisms in a mutualistic association are dependent on each other for survival. In facultative mutualism, two organisms benefit from each other but are not dependent on their mutualistic association for survival.

Bergstrom et al. (2003) have identified four forms of mutualism that have been extensively studied by biologists:

Protection mutualisms: protection from a third species traded for food (e.g., cleaning)

Transportation mutualisms: food traded for transport of organism or gametes (e.g., pollination)

Nutrition mutualisms: food traded for food or protection, usually symbiotic (e.g., plant-mycorrhizal symbiosis)

Shared benefit mutualisms: aggregations of many species obtaining benefits from shared vigilance or defense (e.g., mixed-species foraging)

Bergstrom et al. (2003) also have offered a classification of the key variables that differ across types of mutualism. These variables include: (a) magnitude of benefits, (b) magnitude of investment, (c) cost of being cheated, (d) potential for sanction, (e) obligacy, (f) specificity, (g) opportunity for choice, (h) population structure, (i) symmetry, (j) duration of association, (k) influence of third parties, and (l) evolutionary rate.

Intraspecies Mutualism

In evolutionary biology and evolutionary psychology, the term “mutualism” has been used to refer to behaviors that benefit two or more members of the same species (Bornstein 2003, pp. 186–187). Some theorists have questioned this use of the term (West et al. 2007), suggesting that the term “mutual benefit” is more appropriate for intraspecies forms of mutualism. Common examples of intraspecies mutualism, or mutual benefit, include group hunting, group defense, coalitions, cooperative breeding, and communal nursing (van Schaik et al. 2006).

Several evolutionary theorists have concluded that mutualism is more prevalent in the animal kingdom than previously assumed: “Mutualism may be the most prevalent form of cooperation; it occurs frequently across a wide variety of taxa” (Stevens et al. 2005); “A growing number of studies show that mutualism has been underestimated because the costs of participating in the cooperative act have been overestimated and the direct benefits of cooperation have probably been underestimated. . .” (Boesch et al. 2006, p. 149).

Synergistic and By-Product Mutualism

Biologists also have drawn a distinction between by-product mutualism and synergistic mutualism. In by-product mutualism, interacting individuals benefit each other incidentally as a by-product of individually selfish (fitness-increasing) behaviors. Examples include groups of individuals clustering together to reduce chances of predation and escape behavior that alerts other group members of danger. In synergistic mutualism, individuals work together or join forces to produce benefits for themselves and their partners. Examples include coalitions and coordinated forms of group hunting and defense.

In contrast to by-product mutualism, for which no special adaptations may be necessary, in synergistic forms of mutualism, individuals may need to acquire adaptations that enable them to coordinate their efforts to maximize their gains. For example, when dolphins engage in group hunting, they implement a division of labor in which one member of the group chases a prey toward other members of the group. Although there has not been much research on adaptations for coordination, such adaptations probably played a significant role in the evolution of the human species.

Mutualism, Reciprocity, and Pseudoreciprocity

It is commonly assumed that mutualism differs from reciprocity because the benefits of mutualism are immediate, whereas the benefits of reciprocity to one partner are delayed (van Schaik and Kappeler 2006, p. 6) – “you scratch my back, *then* I will scratch your back.” However, in simultaneous forms of reciprocity, individuals may exchange goods or services by, in effect, scratching one another’s backs simultaneously or giving with one hand and taking with the other. The essential difference between reciprocity and mutualism is that in reciprocal exchanges the behaviors that benefit recipients are costly to donors, whereas in mutualism, the behaviors that benefit recipients are also beneficial to donors. Several investigators have suggested that many

acts classified as reciprocity may actually constitute incidents of by-product mutualism or pseudo-reciprocity. Pseudoreciprocity occurs when one individual or organism invests in another individual or organism that produces by-products of benefit to the investor. For example, a bird fertilizes a bush that grows tall enough to shade its nest. “The bird’s return benefit is an incidental effect or by-product of a self-promoting act (growth) on the part of the bush” (Leimar and Connor 2003, p. 205).

The Evolution of Mutualism

Mutualism can evolve when the benefits experienced by two or more individuals interacting with one another exceed the benefits of not interacting or defecting. The benefits could be direct (e.g., increased probability of killing prey, improved defense against predators, increased rank, increased access to mates) or indirect (e.g., improved reproductive success of kin).

Theorists such as Scheel and Packer (1991) have suggested that mutualism usually evolves in hostile environments in which two or more individuals are needed to solve survival or reproductive problems. Familiar examples include group defense in humans and other primates, huddling together in penguins, and group hunting and coalitions in humans and chimpanzees. There probably were strong selective pressures for intra-species mutualism in the human species. Early humans lived in hostile environments containing predators (including other humans) and large game. In contrast to other species, in which dyadic mutualism is most common, humans engage in vast amounts of group-level mutualism.

As with other forms of cooperation, cheating, exploitation, and free-riding are obstacles to the evolution of mutualism. It is in each individual’s interest to minimize his or her costs and maximize his or her benefits from mutually beneficial interactions and relationships; however, if one or more participants adopt this strategy, they could fail to produce the resources they need. A related obstacle to the evolution of mutualism is risk avoidance in collaborative activities, such as group hunting

of dangerous prey, group defense, and agonistic coalitions, in which cheaters attempt to avoid the costs of dangerous injuries. To evolve, adaptations for mutualism must be designed in ways that either prevent exploitation and free-riding or ensure that cheaters do not evolve in greater numbers than cooperators do. When two animals have an ongoing exclusive symbiotic relationship, exploiting their partners in ways that reduce their partners’ chances of surviving may be very costly (Bornstein 2003). A common way of guarding against being cheated – in humans and such other animals as cleaner fish – is to reject those who fail to contribute adequately to mutual tasks and replace them with other partners. Other safeguards include reducing the costs of being exploited, avoiding those with a reputation for cheating, forcing cheaters to cooperate, and punishing cheaters in a variety of ways.

Conclusion

Members of many species form symbiotic and mutualistic relationships, and these relationships may assume several different forms. Although the term mutualism originally was invoked to describe a form of cooperation between members of different species, it also has been applied to certain forms of cooperation within species. In by-product forms of mutualism, animals benefit one another incidentally; whereas in synergetic forms of mutualism, animals coordinate their efforts to obtain the benefits they share. Mutualism is sometimes confused with reciprocity and pseudoreciprocity, but it differs in significant ways. Cheating and free-riding may constitute significant obstacles to the evolution of mutualism.

Cross-References

- ▶ [Cooperative Foraging](#)
- ▶ [Cooperative Grooming](#)
- ▶ [Food Sharing](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Reputation](#)

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Symbiotic and Mutualistic Relationships

► Symbiosis and Mutualism

Symbolic Behavior

► Art Production, Appreciation, and Fitness

Symbolic Culture

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Synonyms

[Behavioral modernity](#); [Modern human origins](#)

Definitions

The creation, use, and transfer of symbolic objects, such as the creation of meaningful images and soundscapes, through culturally mediated transmission.

Introduction

Discerning what makes *Homo sapiens* unique among the rest of the species on the planet has been a difficult task, especially as behaviors such as tool use, learning, altruism, and compassion have been reported in nonhuman animals (though not without controversy). What does seem distinctive is our unique symbolic culture, the use and transmission of symbols inter-generationally. To be clear, animals use sound for communication, and some have elaborate systems of information transfer, but only modern humans use symbolic culture to create and recreate the human niche through concepts such as good and evil and political systems. The origin of symbolic culture has been a major research topic for scholars studying human evolution and has been the subject of contentious debate as to when and where it evolved, as well as what makes something symbolic.

Semiosis

The specific meaning a symbol has is bestowed on it by humans. This meaning can only be ascertained by symbolic communication. For this

reason, it is often seen as a marker of modern human origins and a signal as to the use of language. The American anthropologist Leslie White argues that “Human behavior is symbolic behavior; symbolic behavior is human behavior” (White 1940, p. 451). However, what exactly a symbol is has been the subject of intense debate in both anthropology and semiotics, the study of signs. The two key thinkers on this subject are Ferdinand de Saussure (1857–1913) and Charles Peirce (1839–1914). A key difference in the two approaches is that Saussure’s theory was developed to understand linguistic signs, while Peirce saw linguistic signs as part of a more general system. From an evolutionary standpoint, Peirce’s model provides a more nuanced, though more complex, approach (Kissel and Fuentes 2016).

For subscribers of Peircean semiotics, symbols are signs that only stand for their objects due to conventional agreement as to their meaning. For example, the only reason that a red light means “stop” is that everyone agrees that is the meaning, rather than it being linked by causation (such as a weather vane indicating the wind direction) or similarity (a picture of a bicycle stands for that object). Many anthropologists have argued that only humans use symbols (Deacon 1997). Thus, symbolic culture should only be found in *Homo sapiens*. If true, tracking the evolution of symbolic thought allows scientists to better understand how hominins became human.

Evolution of Symbolic Thought

The earliest members of the genus *Homo* date to over 2 million years old, but many of the early examples of this species do not resemble modern humans. Paleontologists have uncovered remains of *H. sapiens* dating to around 195,000 years ago in Eastern Africa, suggesting that anatomically modern humans date to at least this time period. The fossil record is mute on the question of when hominins began to act modern, however. Notably, many researchers suggest there was a time lag between anatomical modernity and behavioral modernity, the so-called sapiens paradox (Renfrew 1996). Recent work has suggested that this paradox is a product of research bias and

preservation issues (McBrearty and Brooks 2000; Shea 2011), while some suggest that these behaviors have their origins before the evolution of modern humans (Bednarik 2008).

Recently, archeologists have concentrated on the material record in the hopes of delineating when and where our ancestors developed the capacity to think symbolically. Various classes of archeological data such as beads made of shell, bone, or stone; the use of ochre as a body decoration or adhesive; engravings on bone, stone, and ochre; hafting and blade technology; bone tools; artwork; the use of exotic materials; and intentional burial have been used to indicate human cognitive advances. How exactly these artifacts indicate symbolic thought has been the subject of much theorizing, and debate remains as to whether these artifacts indicate symbolic thought. Beads, for example, may suggest that the wearer wanted to signal to other’s who they were and where they come from.

One site that has received much attention is Blombos Cave on the Western Cape of South Africa (Henshilwood et al. 2002). The site has preserved remarkable examples of early symbolic expression, such as shell beads and bone tools at ~73,000 years ago and an ochre processing workshop dating to ~100,000 years ago. While Blombos is one of the best-supported sites indicating contemporary capacity for symbolic thought, other earlier examples exist. For example, scientists working with collections from Java, Indonesia, report engraved lines on a clam shell from a 380,000-year-old site associated with *Homo erectus*. Moreover, ochre use is reported at a 200,000-year-old Neanderthal site. Interestingly, the recently described species *Homo naledi*, with a brain size ~40% that of modern humans, may have had an advanced mortuary practice normally believed to only be seen in anatomically modern humans (Berger et al. 2015). This and other finds may indicate that symbolic originated earlier than has previously been suggested.

Conclusions

The relevance of this is that symbolic thought is suggested to be the basis for language and shared

intentionality, which in turn allows for cumulative cultural learning. Humans create, remake, and modify their cultural niche through symbolic thought and intergenerational learning. Furthermore, evidence from Blombos of shifting styles of bead wearing may indicate the use of full-fledged language. If symbolic thought is a prerequisite for language, its archeological indicators can pinpoint the origins of this uniquely human ability. Humans' remarkable evolutionary success can in part be traced to this ability to share and store information extrasomatically. While research has often focused on the role symbolic thought played in the origins of human language, this often overlooks other aspects of symbolic culture, such as the creation of the human ability to create and innovate (Fuentes 2017). This symbolic niche, one which seems to only be occupied by modern humans, is both the result of, and the cause for, human's remarkable evolutionary success. It allowed our ancestors to start as a relatively small population 200,000 years ago and become the cosmopolitan species we are today.

Telling stories around the campfire allows others to share not just subsistence practices but gossip, ideas, thoughts, and cultural knowledge. The power in symbolic culture is that it allows this data transfer to occur with high fidelity. By at least 300,000 years ago, we can see the initial glimmers of these behaviors as human populations experimented with different ways to express themselves. What seems clear is that humans have been experimenting with meaning-making since before *Homo sapiens* evolved. Even the simplest stone tools could, in theory, be imbued with meaning. The challenge is in understanding how humans were able to create these meanings.

Cross-References

- [Evolution of Culture](#)
- [Evolution of Intelligence, The](#)
- [Evolution of Tool Use](#)
- [Hominin Evolution](#)
- [Ritual and Speech Coevolution](#)

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Symbolic Knowledge

- [Declarative Knowledge](#)

Symbolic Signs

- [Arbitrary](#)

Symmetry

- ▶ [Bernhard Fink](#)
- ▶ [John Manning](#)

Syntagmatic Relations

- ▶ [Grammar](#)

Synapse

- ▶ [Early Stage of Brain Development at Birth](#)

Systems

- ▶ [Evolved Physiological Reactions](#)

Tactical

► Strategic Aggression

Tactics to Solve Adaptive Problems of Sperm Competition

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Definition

The ways in which males strategize to maximize their reproductive fitness in a competitive mating context.

Introduction

Males of all sexually reproducing species compete among one another for paternity. For most males in such species, insemination is usually the end point in the reproductive process; most males do not provision and/or care for their offspring.

Paternal Assurance Tactics

However, in species where the offspring are particularly helpless at birth and require protection and provisioning from both parents (which includes some tree nesting birds and a few primates) the possibility of being cuckolded (i.e., duped into caring for offspring sired by other males) adds to the costs of nonpaternity. Human's anchor this latter dimension. Human infants are more helpless at birth and remain parent dependent for longer periods of time than those of any other species. As a consequence, evolution has operated to produce an ensemble of paternal assurance tactics among human males which function to minimize the chances of being cuckolded. Gallup and Burch (2006) have identified four sequentially dependent strategies that men use (wittingly or not) to increase the chances that they share genes in common with their ostensible children. These include *Insemination Prevention Tactics*, which include mate guarding, mate sequestering, mate monitoring, and male sexual jealousy that function to minimize insemination by rival males. If these tactics fail and a female is inseminated by another male, men move to *Counter Insemination Tactics* which function to reduce the chances of conception as a consequence of insemination by other men, such as sperm competition. Should conception occur as a byproduct of having sex with other men, the ground rules change and men resort to *Pregnancy*

Termination Tactics, and in the event of a live birth men shift to *Postpartum Investment Tactics* where investment in children varies in relationship to the proportion of shared genes between the resident male and the child.

Sperm competition is commonly featured in many diverse species as a means of competing for paternity. This can include context specific adjustments to the ejaculate in terms of the number of sperm which take into account the likelihood of insemination by other males. In some species, most notably humans, there also appear to have been mechanical/morphological adaptations to penis morphology which function to displace rival male sperm from the female's reproductive tract and enable the resident male to substitute his sperm for those of his rivals (Gallup et al. 2003).

Conclusion

The evolution of the glans and the coronal ridge at the end of the penis and the resulting semen displacement properties of the human penis have also led to selective pressure for the size of the penis. That is, confronted with the prospect of semen displacement from rival males there was probably selective pressure for longer penises to deposit semen in the least accessible parts of the vagina to minimize displacement. However, that in turn would up the ante for an even longer penis to access and displace semen from the most remote parts of the vagina, creating an evolutionary arms race of sorts. Thus, both the shape/configuration of the penis and the size of the penis in humans appear to have evolved to capitalize on semen displacement as another sperm competition strategy.

Cross-References

- [Genital Evolution](#)
- [Intrasexual Competition](#)
- [Sperm Competition](#)

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Tactics Versus Strategies

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Definition

Strategy refers to a set of behavioral adaptations while *tactics* are the individual actions taken to pursue a strategy (Gangestad and Simpson 2000).

Introduction

In the context of evolutionary behavior, *strategy* refers to a set of adaptations that determine the range of behaviors that an organism may employ (i.e., to fight, flee, or hide). *Tactic* refers to the specific behavior used within that organism's pre-set strategy; for example, fighting or retreating in the face of competitor conflict (Dawkins 1999). The two terms are closely related, often used in conjunction while discussing conflict related to intrasexual and intersexual selection of mates (Taborsky et al. 2008).

Strategies and Tactics

The distinction between strategy and tactic in terms of behavioral ecology can be, at times, ambiguous and difficult to grasp. Various authors (Dawkins 1999; Dominey 1984; Taborsky et al. 2008) have

acknowledged the potential to confuse the terms with one another. In an attempt to limit confusion, Dawkins (1999) prefers to use the word “program” instead of “strategy.” When considering strategy as it relates to behavioral ecology, it may be useful to use Dawkins’ (1999) analogy and conceptualize strategy as a computer program. A code creates a computer program in order to perform a single action within a set of potential actions.

The unseen code programs the set of available responses. In this example, the code and responses are analogous to strategy and tactics, respectively.

While strategy in general refers to rules governing a set of tactics, there is a further sub-categorization of their relationship.

The most basic categorization being a *pure strategy*, in which the strategy determines a single tactic to be used without any alternative (Neff and Svensson 2013). An example of a pure strategy is an organism, when faced with competitors during mating, only has the behavioral tactic to fight, with no alternative tactic available. A further example is Maynard’s (1976) explanation, which uses the game of rock-paper-scissors as an analogy. A pure strategy, in the game of rock-paper-scissors, would be always employing rock, without ever considering or using the two alternative choices.

A *mixed strategy* can employ more than one tactic, such as to fight or to flee when faced with a competitor (Neff and Svensson 2013). A mixed strategy for a given goal applies a tactic based on preset probabilities defined by its genotype, such as choosing to fight in 70% of encounters and choosing to flee in 30% of encounters (Dominey 1984). Alternatively, mixed strategies may be probabilistically assigned a given tactic for their entire lifetime, such as 70% of the species always opting to fight and 30% always opting to flee when facing a competitor (Dominey 1984).

Neither a pure strategy nor a mixed strategy considers aspects of the organism’s environment and conditions as a determinant of an employed tactic. A *conditional strategy* is one in which the tactic used provides the highest chance of reproduction given the context and surroundings of the situation (Neff and Svensson 2013). A key

difference with conditional strategies is the active decision making by the organism given the context, rather than the use of a single behavioral option or probabilistic behavioral option (Gross 1996). An example of conditional strategy is an individual, when faced with a competitor, chooses to fight if larger, but flee if smaller, than the competitor. In other words, the individual decides on tactic based on the current condition. Behavioral ecologists often consider conditional strategies as superior for their ability to fit the changing demands of the environment (Plaistow et al. 2004).

An important note is that an individual’s strategy is goal specific and not species specific. For example, the same individual may have a pure strategy for fighting competitors, a mixed strategy for foraging, and a conditional strategy for attracting a mate.

Conclusion

Though the terms strategy and tactic can be confusing, their distinction is an important one to make in behavioral ecology. The terminology provides a hierarchical framework to understand an organism’s specific behavior – its tactic – as an option within a larger set of adapted behaviors – its strategy. Additionally, the distinction between strategy and tactic is important to the discussion of many related topics, such as behavioral adaptation, sexual selection, evolutionary game theory, and others (Dominey 1984; Smith 1976; Taborsky et al. 2008). A basic understanding of the two terms, and their relationship to one another, provides a fuller understanding of behavioral ecology and several subsections of theory within.

Cross-References

- ▶ Alpha, Beta, and Gamma Males
- ▶ Conditional Strategies
- ▶ Mating Strategy Equilibria
- ▶ Sneak Copulation as an Alternative Mating Strategy

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Talking About Others

► Social Consequences of Initiating Gossip

Tall Poppy

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Synonyms

High achiever; High status individual; Top dog

Definition

The term “tall poppy” refers to a person of high status, elevated above their peers due to their achievement of fortune or fame and/or high levels of achievement.

Introduction

Their higher social position of “tall poppies” differentiates them from others within the social context. This label of “tall poppy” has a negative connotation and is largely used in a derogatory manner in Australia, in New Zealand, and to a lesser extent in the UK.

Tall Poppy Syndrome

The “tall poppy syndrome” refers to the social phenomenon of the desire to cut down such tall poppies (Feather 1989). This is closely tied with the egalitarian values of Australia where there is a belief that no Australian should assume that she/he is any better than other (Peeters 2004). Everyone in society should be of equal status, so the desire to cut down the tall poppy is in fact a desire to level the playing field.

The key scholar in the field of “tall poppies” is Norman Feather, an Emeritus Professor at Flinders University in South Australia. He has examined perceived deservingness and the emotions of envy and resentment, as predictors of whether a “tall poppy” will be cut down to size. When a tall poppy is perceived to be undeserving of their higher status, for example, becoming famous without any real talent, individuals have a greater desire for this type of tall poppy to be cut down (Feather 2012). Strong feelings of jealousy, hostile envy (not benign envy), and resentment are also predictors of the desire to cut down a tall poppy. Benign envy is not associated with desire to cut down a tall poppy, but instead it is viewed as a motivational force that can drive others to improve themselves.

Building on this foundation, Feather has also examined emotional responses to when tall poppies do in fact fall. Some observers will feel sympathy, while others will feel schadenfreude (joy at another person’s misfortune). The specific type of emotion experienced will depend on the type of fall and the perceived deservingness of that fall (Feather 2012). For example, research by Dasborough and Harvey (2017) has shown that individuals feel more schadenfreude in response to a tall poppy being cut down if that

tall poppy was perceived to be unethical while holding the tall poppy status.

Tall poppies have been studied within the context of student academic performance, scholarly contributions by academics, athletic performance, sports teams, employees, entrepreneurs, and politicians (e. g. Feather 1989; 1991; 1994; 2012; Feather and McKee 2014; Feather et al. 1991; Kirkwood 2007). It is more likely in competitive scenarios, where individuals perceive success and high status to be a zero-sum game. Since status is a relative value; for an individual to boost their own social status, it is perceived that another individual must be lower in status. This desire to cut down tall poppies has also been connected to the “queen bee syndrome,” where women undermine the success of other tall poppy women in workplaces (Funk 2004).

Conclusion

The tall poppy syndrome has been seen in various countries, and across a range of contexts. Given that this syndrome may discourage over-achievers, it is something to be aware of. After all, we are more successful if we build up our high achievers and celebrate them, rather than cut these tall poppies down.

Cross-References

- [Envy](#)
- [High Achiever](#)
- [Jealousy](#)
- [Schadenfreude](#)
- [Status](#)

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Tandem Memory Retrieval

- [Scope Hypothesis, The](#)

Taste

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Synonyms

[Bitter](#); [Palatability](#); [Salty](#); [Savory](#); [Savoriness](#); [Sour](#); [Sweet](#)

Definition

The chemosensory system registering the presence of specific molecules in food ingested by humans and other animals.

Introduction

Although humans experience a large number of sensations when consuming food, much of the

enjoyment of food comes from a combination of smell and taste. Technically, taste is derived from receptors on the tongue and on the epiglottis and a few other places within the mouth. Humans appear to be sensitive to four basic tastes including sweet, salty, sour, and bitter. These basic tastes have been identified by their seemingly adaptive purpose and the hard coding that appears to exist for these tastes. More recently, another basic taste has been proposed. This newer taste category is known as umami and can be thought of as “savory.” This is the taste associated with glutamate, which comes from proteins in meat. Including umami as a basic taste is still somewhat controversial, but receptors for glutamate have been found in the gut and digestive tract. The basic tastes appear to have an important function in terms of the ingestion of nutrients and the avoidance of toxic substances. Sweet tastes indicate the presence of glucose, an important source of energy and something vital to survival. Bitter tastes also serve an important adaptive purpose in that the bitter taste signals the presence of potential toxins in food, allowing us to avoid ingesting harmful or toxic substances. The value of the other two tastes are not as clear with sour potentially also allowing for some protection by signaling the presence of acid. The sour taste is associated with weak acids that are not harmful, but the same taste is also associated with stronger acids that could potentially prove harmful. Again, the sour taste could be protective by allowing the rejection of the material before it is ingested. The taste of saltiness also signals an ion important in many biological functions, so being sensitive to the taste of salt would be beneficial and have survival value as well.

Given the survival value of the basic tastes, it is not surprising that we have developed highly sophisticated and specialized receptors for these stimuli. The taste receptor cells are located within taste buds, which are found in small bumps on the tongue and other structures within the mouth and digestive system called papillae. There are four types of papillae on the tongue, including the filiform, fungiform, foliate, and circumvallate papillae. Only the fungiform, foliate, and circumvallate papillae contain taste buds and taste

receptor cells. Of these, the fungiform papillae, so named because of their mushroom shape, are the most numerous and are found in the lateral portions of the anterior two-thirds of the tongue. These papillae contain one or more taste buds per papilla (Smith and Margolskee 2001) with each taste bud containing between 50 and 100 taste receptor cells (Chaudhari and Roper 2010; Roper 2013). The foliate papillae are found on the lateral edge of the tongue at the back of the tongue immediately anterior to the vallate line. The circumvallate papillae are large structures found at the back of the tongue in an inverted “v” shape. In humans, there are between 3 and 13 of these papillae per tongue with between 700 and 3000 taste buds found in the circumvallate papillae (Spielman and Brand 1995).

The taste receptor cells are found in taste buds in an orange-like arrangement of receptor cells. They send tiny projections, called microvilli, through the pore found at the top of each taste bud where they contact the molecules from the tastants that have been dissolved in saliva through the chewing and eating process.

Cells Found in Taste Buds

Chaudhari and Roper (2010) reviewed recent findings on the various cells in each taste bud. They indicate that there are three cells consistently identified that are associated with taste transduction including Type I, Type II, and Type III cells. Although Type I cells are the most abundant, they are also the cells we know the least about (Chaudhari and Roper 2010). They appear to have “extended cytoplasmic lamellae that engulf other cells” (Chaudhari and Roper 2010, p. 288) and serve a function similar to glial cells in the central nervous system. Specifically, Type I cells appear to help terminate synaptic transmission and inhibit the spread of neurotransmitters (Chaudhari and Roper 2010). They have been linked to salty taste transduction via the direct entry of Na⁺ ions through open ionic gates. Type II cells are also referred to as receptor cells, and these cells appear to respond to sweet, bitter, and umami tastants, but are insensitive to sour and

salty tastes (Chaudhari and Roper 2010). These cells are specialized with different cells detecting specific tastes when molecules in the tastants dock on receptor sites (known as G-protein-coupled receptors or GPCRs) on the receptor cell microvilli causing a cascade of activity within the cell resulting in a release of internally stored calcium ions which then cause a release of the neurotransmitter adenosine triphosphate (ATP). ATP then causes action potentials in the sensory neuron closest to the cells. These signals are then sent to higher levels of the brain where they are then interpreted as specific tastes. Interestingly, these receptor cells (Type II) do not make synaptic contact with neurons sending signals to the brain by way of vesicles releasing neurotransmitters. Instead, the resulting release of ATP triggers action potential generation in the neurons communicating with higher levels of the brain. The Type III cells are also known as presynaptic cells. They express proteins associated with synapses and form synaptic junctions with closely associated nerve terminals (Chaudhari and Roper 2010). These cells may play a role in the responses of other cells and send signals from receptor cells to higher levels of the processing system. They also respond directly to sour tastes and indirectly to sweet, bitter, and umami tastes via the neurotransmitter ATP (Chaudhari and Roper 2010). The presynaptic cell also plays an important role in the receiving and integration of information from receptor cells. Thus, unlike the receptor cells, these cells are not finely tuned and respond to a large variety of taste stimuli (Chaudhari and Roper 2010).

Transmission of Signals from Receptors to the Brain

The signals received on the tongue are sent to the brain through three cranial nerves (cranial nerves VII, IX, and X). Specifically, the anterior 2/3 of the tongue is innervated by the chorda tympani branch of the facial nerve (the VIIth cranial nerve). The posterior 1/3 of the tongue is innervated by the glossopharyngeal nerve (cranial nerve IX), while the taste buds found in the soft

palate and the taste buds at the back of the mouth are innervated by the vagus nerve (cranial nerve X). All of these nerves send impulses to the nucleus of the solitary tract of the pons and medulla. From there, the signals travel to the thalamus, where they synapse once more. Then projections go to the primary taste cortex (the insula) and then to the orbitofrontal cortex of the frontal lobe.

Originally, researcher believed that the taste system would show the same specificity of processing found in the visual system and have specific receptors connecting with specific neuronal channels resulting in the perception of specific tastes. This hypothesis was known as the labeled lines hypothesis. However, researchers now believe that the activity in the brain is of a more general nature and is not specific to the different tastes. Researchers now agree that it is the interpretation of a pattern of activation from a variety of taste receptor cells that result in the specific taste being perceived (Chaudhari and Roper 2010; Scott and Giza 2000; Smith et al. 2000).

Genetic Variations in Taste Perception

Researchers (e.g., Bartoshuk 2000; Prutkin et al. 2000) have indicated that individuals have different taste experiences due to both gender and other genetic influences. In particular, there is individual variation in terms of sensitivity to the bitter taste of PROP (6-n-propylthiouracil), which is a thyroid medication, but in low doses serves as a stimulus in taste experiments. Prutkin et al. report that approximately 25% of the population have no ability to taste the bitterness of PROP. An additional 50% of the population experience the taste of PROP as bitter, while the final 25% of the population experience the taste of PROP as extremely bitter. Those who do not experience a bitter taste when tasting PROP are labeled as “nontasters.” Those who perceive bitterness when tasting PROP are labeled as “tasters,” and those who experience PROP as tasting extremely bitter are “supertasters.” The population distribution for the bitter taste of PROP has been linked to genetics, with the ability to taste PROP linked to a

specific recessive gene (Bartoshuk 2000). According to Bartoshuk (2000), supertasters possess both alleles for this tasting gene, while tasters have received only one allele. Nontasters have not received either allele for this tasting gene. Furthermore, Prutkin et al. indicate that the physical manifestation of this genetic difference is found in the number of fungiform papillae on the tongue of supertasters, tasters, and nontasters. Specifically, supertasters have the most fungiform papillae, while nontasters have the fewest, and tasters have a number between these two extremes.

There are many behavioral consequences and outcomes to these genetic differences in the number of fungiform papillae that have been discovered. Supertasters, for instance, tend to experience a unique taste world and have extreme taste sensations on a number of fronts (Prutkin et al. 2000). According to Prutkin et al. (2000), supertasters tend to experience the bitter tastes of many vegetables to a higher degree than tasters and nontasters, so they may avoid eating vegetables, leading to a diet lower in fiber than may be healthy. This may lead to health problems, and supertasters have been found to have a higher incidence of colorectal cancer (Prutkin et al. 2000).

Women are more likely than men to be supertasters and that taste sensitivity varies with hormonal levels with peaks and troughs at various points in the menstrual cycle that tend to differ for different women (Prutkin et al. 2000). In addition, sensitivity to bitter taste also varies over the course of pregnancy with the highest sensitivity in the first trimester, when major organs are forming and when exposure to teratogens may have the largest effect. In effect, this variation in sensitivity to bitter makes the woman in her first trimester of pregnancy the most effective poison detector (Prutkin et al. 2000). Additionally, sensitivity to bitter appears to outlast pregnancy with fewer nontasters among women who have had at least one child than those with no children (Prutkin et al. 2000). Finally, sensitivity to bitter taste appears to diminish after menopause when women are past their childbearing years (Prutkin et al. 2000).

Conclusions

In summary, human taste sensitivity includes four (and possibly more) basic tastes, including sweet, salty, bitter, and sour and encourages consumption of energy- and nutrient-rich foods while encouraging the avoidance of possibly toxic or harmful foods. Supertasters, who are more sensitive to taste and other oral sensations, live in a different taste world from that experienced by nontasters. In addition, taste sensitivity, at least for certain bitter stimuli, is more prominent for women and varies with the menstrual cycle with a peak during the first trimester of pregnancy. Meanwhile, taste contributes only a part of the typical experience of consuming food. Flavor, that aspect of food consumption that we all enjoy most, is made up of the sensation of taste, smell, and the somatosensory experience of the texture of the food. So, while taste plays an important role in allowing us to obtain nutrients and avoid possibly harmful substances, it is only one part of the food consumption experience.

Cross-References

- Food Aversions and Cravings
- Food Preferences

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Taste Preferences

- ▶ [Antimicrobial Hypothesis, The](#)
- ▶ [Frugivory By-Product Hypothesis](#)

Ta-ta

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Synonyms

[Body and hand gestures](#); [Chew-chew theory](#); [Oral gesture theory](#)

Definition

Ta-ta theory states that humans made the first words by tongue movements that mimicked the movement of the hands, face, or other parts of the body and translated them into audio.

Introduction

According to Richard Paget, the *ta-ta* hypothesis supported that speech and the development of

sound were produced to endorse the hand and body movements of the individual. So as to better demonstrate the meaning behind the gestures, these sounds developed different words or combinations of sounds unavoidably leading to speech patterns (Paget 1930). For instance, when a person would say *ta-ta*, he was basically saying goodbye with his tongue. At some point, this theory was even supported by Charles Darwin (Mandavilli 2016). In the literature, there are several theories such as the *oral gesture theory* and the *chew-chew theory* that support the idea that the origin of language begun from early human gestures made from their mouth. It is of paramount importance, though, to understand that it is not feasible to explain the origin of some words using the *ta-ta theory*.

A major drawback of this early theory on the origins of language is the fact that in order for people to be able to communicate between them, they must see each other in person. Also, there must be daylight, or firelight, and with nothing blocking one's view. In the case of hand gestures, it is important that hands are free from doing something else (Meir et al. 2010). Last but not least, in order for this hypothesis to be the origination of communication, it required a number of gestures be in place already for humans to imitate with their mouth gestures, but it didn't explain how these gestures arose in the first place.

Conclusion

Originally hypothesized by Richard Paget, and later supported by Charles Darwin, the *ta-ta theory* suggested that the origin of language commenced from the use of tongue and mouth gestures imitating the movements of the body and hands. As commonly seen in primates, gestures such as hand and body movement are important aspects of communication and collaboration within societies (Paget 1930). In spite of the fact that it is probable like many of the other hypothesis, the cultural roots of various hand gestures states that this is most likely not the cause behind verbal communication.

Cross-References

- [Bow-Wow](#)
- [Ding-Dong](#)
- [Pooh-Pooh](#)

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Tattoos

- [Body Modification](#)
- [Human Ornamentation](#)

Teacher

- [Maryanne Fisher](#)

Teaching Procedures

- [Instructional Design](#)

Team Athletes

- [Team Sport](#)

Team Sport

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Synonyms

[Athletic competition](#); [Sports](#); [Team athletes](#)

Definition

Any sports activity where two or more players cooperate towards achieving a common objective while they compete against an opposing team. Some examples of team sports include, but are not limited to; soccer, baseball, basketball, American football, hockey, volleyball, and handball.

Introduction

Poliakoff (1987) defined sport as “an activity requiring direct physical competition with an opponent(s), has established procedures and rules, and defined criteria for determining victory” (as cited in Lombardo 2012). The direct goal of a sporting engagement is winning the activity regardless of any other extrinsic rewards that follow the victory, such as earning a trophy or a medal; hence, the core nature of the competition still remains unchanged (Lombardo 2012). Whether conceptualized as functional integrated “super-organisms” (Duarte et al. 2012), complex social networks (Ribeiro et al. 2017), or stripped-down to examine evolutionary benefits, such as gaining prestige (De Block and Dewitte 2009), team sport at its essence remains a fun and entertaining activity for everyone involved. At the moment in the USA, baseball, basketball, and American football are the most widespread team sports played (Budd and Egea 2017).

Groups Versus Teams

Weinberg and Gould (2011, p. 160) explain that merely going out with your friends to watch the “game” does not necessarily make you a group for the reason that group members are characterized by both having a mutual interaction and an interdependence for a shared objective as well. Furthermore, they discuss that some of the similarities between groups and teams include: a potential occurrence of mutual romantic attraction between members and all members share a common goal (e.g., all the members in a fitness class may strive towards weight loss and muscle definition). However, even though both groups and teams interact with each other and depend on each other for a common purpose, sports teams additionally exhibit the following four key components: “(a) Collective sense of identity – ‘we-ness’ rather than ‘I-ness’, (b) Distinctive roles – all members know their job, (c) Structured modes of communication – lines of communication, (d) Norms – social rules that guide members on what to do and not do.”

Team Dynamics

An effective way to increase performance, enhance team spirit, and manage conflict between the team members is to promote outcome interdependence (i.e., members realize that the teams successes and failures has an equal positive or negative effect, respectively, on all of them) by communicating constructive feedback to the whole team to reinforce shared responsibility for the team’s performance and outcome (Weinberg and Gould 2011, p. 170).

Weinberg and Gould (2011, pp. 174–177) emphasize the importance of recognizing and inhibiting the effects of social loafing (i.e., the psychological phenomenon where individual members in a group do not use their full effort to achieve a team goal because of motivation loss and responsibility diffusion) in order to maximize individual performance in a sports team. Furthermore, the authors suggest that because studies show that team success is only partially dependent on each

player’s individual skill level, the following practices are needed to boost each player’s individual contribution and eliminate social loafing in a team; coaches need to (1). Help players recognize their unique contributions to the team and assume responsibility and pride for the team’s welfare, (2). Videotaping team practices and games can make individual contributions known to all members showing that individual efforts are identifiable, (3). Videotaping or other observations additionally aid in the identification of possible social loafing occurrences and the situations under which the team is most often prone to social loafing, (4). Discuss social loafing individually with every member of the team and examine their motivation, (5). Cultivate the players’ understanding for their teammate’s unique role and challenges by rotating players to all positions at least for a short duration, and (6). The team can be divided into smaller subgroups where responsibility is more easily recognized and reinforced while still emphasizing on the overall team effort to avoid the formation of social cliques which results in the disruption of team cohesiveness.

Team sports are commonly characterized by the aggression exhibited from both the opposing team players and their fans. To examine aggression in team sports, Coulomb-Cabagno and Rasle (2006) videotaped and observed 180 soccer and handball games from different competitive levels. Their analysis revealed that aggressive behaviors were more common in male rather than female players with larger gender difference found in handball than in soccer, and at higher competitive levels, instrumental aggressive behaviors (i.e., hurting another player during the game to achieve a competitive goal) increase and hostile aggressive behaviors (i.e., hurting another player during the game for the sake of causing him or her harm) decrease.

The Evolution of Sport

Ranging from cave paintings and stone slabs to monuments, traces of athletic events in societies provide evidence that sports have existed in the past, for thousands of years. In 776 BC, the first ever Olympic Games were inaugurated in Greece,

colonization during the early nineteenth and twentieth centuries promoted team and individual sports across the world while the involvement of North America and Western Europe in this historical phenomenon largely structured the rules and format of modern-day sport, while after the innovation of global communication and mass media in the 1960s, sport begun to gain increased popularity as a profession (Budd and Egea 2017).

In ancient societies only men were allowed to participate in sports; however, in contemporary societies even though men still constitute the majority of athletes the advocacy for women's rights has successfully aided in increasing the number of women that participate in sporting competitions (Budd and Egea 2017). Men initially began participating in sports as a low-cost way to develop the necessary skills required for physical rivalry, primitive hunting, and warfare and later evolved as a means to practice and improve their physical abilities, provide grounds for displaying prowess to attract potential mates, hence increase their reproductive success, and finally, an opportunity to evaluate their potential allies and rivals in terms of their strengths and weaknesses so that they can adapt and appropriately interact with them in the future (Lombardo 2012).

One explanation suggests that sport has evolved through culture as a ritualistic way to present individual physical prowess and attract sexual partners (De Block and Dewitte 2009). From a Darwinian perspective, sports evolution is predicated on three aspects that help determine the fittest contestant: "informativeness," "accuracy," and "transparency." A viable sport is "informative" when it adequately assesses the evolutionary qualities (i.e., the ones related to survival and reproduction) of the competitors, such as their strength, dexterity, intellect, agility, etc., "accurate" meaning that the winner possessed maximum level of skill and minimum level of luck which is largely determined by a fair set of rules, and "transparent" when the audience is able to clearly understand and recognize that the winner was more powerful than the other contestants (De Block and Dewitte 2009).

Team sports, not only improve individuals' status in their communities and sexual attraction from the opposite sex but are also tests invented by the human culture to assess other peoples' ability to work together as a team (e.g., teamwork and cooperation skills) and to utilize their leadership and followership skills (De Block and Dewitte 2009). In addition, men mainly because of an overall higher natural physical fitness tend to perform better in sports than women (Lombardo 2012). Lastly, since men and women rather than primarily focusing on the opposite gender's team sports they exhibit great interest in observing their own gender's team sports, it suggests that team sports have not purely evolved to serve mate choice but at least to a certain degree assist in the improvement of one's physical abilities (De Block and Dewitte 2009).

Involvement in Team Sports Matters

Evidence on the positive benefits of team sports involvement illustrate that the social interaction with peers facilitated through team sports promotes social acceptance in a less threatening environment among marginalized adolescents, and the risk for depressive symptoms associated with dissatisfaction about one's own body image is diminished through the social support, improved physical fitness, and the opportunity to appreciate one's current body's physical appearance and capabilities, offered by the participation in team sports (Boone and Leadbeater 2006). Additionally, students who participate in school team sports tend to exercise more and show higher rates of "milk consumption, and healthy self-image, and significantly lower odds for emotional distress, suicidal behaviour, family substance abuse, and physical and sexual abuse victimization" (Harrison and Narayan 2003). An unexpected finding in Harrison and Narayan's (2003) study was that adolescents who were victims of abuse or experienced substance abuse in their families reported less involvement in sports (a partial explanation for this was contemplated

around a tendency for social isolation exhibited from victims of abuse).

A systematic review of 30 published studies reported that the most common psychosocial health benefits related with participation in sports are higher self-esteem, improved social interaction, and fewer depressive symptoms, while team sport participation when compared to individual activities has the added benefits of being associated with better health outcomes, because the social nature of team sports provides social support and promotes social acceptance (Eime et al. 2013). Last but not least, even though women are less likely to participate in team sports than men, they too reap the same benefits from the positive environment cultivated in sports teams once they do join a team (Boone and Leadbeater 2006).

Conclusion

Undeniably sport places a major impact on the economy, is considered by many people their favorite recreational activity, and is widely embraced by the public as a sensible practice for a healthy lifestyle (Budd and Egea 2017). What is more, for adolescents, a positive involvement in team sports offers unique benefits over and above the engagement in any other extracurricular activities (Harrison and Narayan 2003). Admittedly, when all is said and done, the most important fact may very well be that irrespective of gender, age, ethnicity or ability, team sports are a fun and enjoyable activity for everyone, especially during the twenty-first century where there are hundreds of available sports to choose from (Budd and Egea 2017).

Cross-References

- [Combat Sport](#)
- [Cooperation](#)
- [Evolution of the Brain, The](#)
- [Group Size](#)
- [Human Enculturation](#)

- [Moral Instincts](#)
- [Social Play](#)
- [Social Values](#)

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Tearing

- [Crying](#)

Technical Intelligence Hypothesis, The

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Synonyms

[The extractive foraging hypothesis](#)

Definition

The need to efficiently organize behaviors requiring a high number of sequential operations leads to selection for increased intelligence.

Introduction

The technical intelligence hypothesis is one of the most popular explanations for the evolution of human intelligence. It posits that the need to efficiently organize behaviors requiring a high number of operations led to the evolution of increased intelligence (Whiten and Byrne 1997). The hypothesis was first proposed by Byrne and Whiten as an alternative to the social intelligence hypothesis (cf. Byrne and Whiten 1989; Whiten and Byrne 1997), as within primates, great apes appeared to show certain cognitive skills that could not be explained by differences in social organization.

How to Test for the Technical Intelligence Hypothesis?

Testing the validity of the technical intelligence hypothesis is challenging. It first requires to define what we mean by intelligence. Second, it requires an operational measure of a species' ability to

efficiently organize behaviors requiring a high number of sequential operations. Tool use and manufacture and rates of technical innovations in the wild are the measures that have been considered in the literature. Third, it requires characterizing the cognitive skills of species, ideally by considering skills expected to favor tool use and technical innovations (for example, physical cognition skills such as object manipulation, fine motor control and problem-solving), that should have been directly targeted by selection if the technical intelligence hypothesis is true. As the brain is the organ involved in cognition, testing whether species displaying the ability to develop these complex behaviors also have disproportionately larger brains should also inform us on the cognitive demands of technical innovation. Finally, the causality of an eventual association between tool use/technical innovation and (physical) cognitive skills needs to be assessed, which likely is the most challenging step.

Tool Manufacture and the Technical Intelligence Hypothesis

Early attempts to define the unique intelligence of humans were based on the ability to manufacture and use tools (Oakley 1956), with the underlying idea that human intelligence evolved, at least partly, in response to the need to manufacture tools. However, as hominins were and still are both tool manufacturers and highly social, it is very difficult to distinguish between the social and technical intelligence hypotheses considering our clade alone. The discovery that many animals beside humans also manufacture and use tools in the wild allowed researchers to investigate the general importance of tool use in the evolution of intelligence.

Tools are objects that are used as an extension of the body and held directly in the hand or mouth (see Shumaker et al. 2011 for a more complete definition). As to manufacture and use tools, an animal needs to carry out a number of successive steps in an organized order, tool manufacture and use is a good candidate behavior to investigate the technical intelligence hypothesis. Several dozens

of species, from invertebrates to birds and mammals, have been reported manufacturing and using tools in the wild (Shumaker et al. 2011), making it possible to compare encephalization and cognitive skills of tool-using species with closely related non-tool-using ones. In birds, there is a correlation between tool use and both relative brain size (Lefebvre et al. 2002) and brain structures involved in motor control and learning (Iwaniuk et al. 2009). The New Caledonian crow *Corvus moneduloides*, which shows the most sophisticated forms of tool use and manufacture of all birds (Taylor et al. 2007), also displays a larger brain, relative to its body size (Cnotka et al. 2008), and a larger mesopallium (a brain region equivalent to the nonvisual cortex), relative to brain size (Mehlhorn et al. 2010), than other corvids not known to use tools in the wild. In primates, tool use frequency correlates with both absolute and relative brain size, larger brained species using tools more frequently (Reader and Laland 2002). Overall, tool-using species thus seem to display larger brains, suggesting that tool use requires higher intelligence. The next step was thus to test for association between cognitive skills and tool use.

Using tools is expected to require a certain understanding of the physical environment. Physical cognition, rather than other cognitive skills such as general learning, is thus expected to be a tool-related specialization. Under the technical intelligence hypothesis, tool-using species should perform better on physical cognition tasks than non-tool-using species. Comparing performance on physical cognition tasks in tool-using and non-tool-using sister species however yielded contrasting results. In birds, the tool-using New Caledonian crow outperformed the non-tool-using carrion crow in a physical problem (the cane task, whereby an individual has to choose between pulling two hook-shaped tools laid flat on a surface, the spatial relation between the food and the hook being different (inside or outside of the hook); Teschke et al. 2013). However, in the same study, no difference was detected between the tool-using Galapagos woodpecker finch and its non-tool-using sister species, the small tree finch (Teschke et al. 2013). A range of physical

cognition tasks were also tested on both tool-using and non-tool-using primates (especially apes). In a recent review, Taylor and Gray (2014) showed that although some differences exist, they are largely inconsistent. In addition, most if not all such comparative analyses suffer from potential biases in sampling effort: the sample size is too low, at least for one of the species considered, to conclude with regard to the overall species' performance. Finally, biases associated with differences in developmental history also limit the interpretation of these studies. In many studies, individuals from tool-using species born in the wild were compared with individuals from non-tool-using species born in captivity. These differences are likely to condition individuals' response to the tests and may thus strongly bias the results. Aside from the larger brain of tool-using primates and birds, as compared to their non-tool-using sister species, evidence for increased cognitive skills associated with tool use and manufacture is thus scarce and debatable.

Technical Innovations and the Technical Intelligence Hypothesis

Considering tool use behaviors to investigate the technical intelligence hypothesis has some limitations, especially because of the rarity of this kind of behavior in the wild. Comparative analyses on tool use thus traditionally focus on a limited number of species from specific taxonomic groups (e.g., Corvids or Apes). In addition, considering exclusively tool use and manufacture to investigate the technical intelligence hypothesis is likely reductive (Huber and Gajdon 2006), as other behaviors are likely to also require organized, sequential operations. An alternative approach, initiated by Overington et al. (2009), has been to collect data on the incidence of "technical" innovations in wild animals, with the assumption that a higher number of technical innovations in a particular clade reflects a better ability to express behaviors requiring a high number of sequential operations.

An innovation is a solution to a novel problem or a novel solution to an old one (Kummer and

Goodall 1985). To develop an operational measure of a species' innovativeness (or propensity to produce innovations), Lefebvre et al. (1997) scanned ornithological journals for reports of birds' departure from the standard behavioral repertoire of a species. The number of foraging innovations published in these journals for each species was then used as a measure of a species' innovativeness (after correction by potential confounding factors, such as research effort). This database has since been extended to several regions of the world for birds (Lefebvre et al. 2016) and a similar database has also been developed for primates (Reader and Laland 2002).

Using these databases, Overington et al. (2009) and Navarrete et al. (2016) extracted the innovations that could be considered as "technical," to develop an operational measure of technical innovativeness. These studies, and especially the definition of technical innovation they considered, did not directly aim at testing the technical intelligence hypothesis. However, the metrics and methods they developed can inform us on the relevance of this hypothesis. Overington et al. (2009), working on birds, defined technical innovations as reports where the author described the foraging technique itself as novel, regardless of whether the food type was novel or not. In this framework, innovations involving novel techniques, novel parasitic behavior, novel commensal behavior, novel mutualistic behavior, novel prototool behavior, novel true tool behavior, or novel caching behavior were considered as technical innovations. In primates, Navarrete et al. (2016) considered as technical innovations either tool use or innovative extractive foraging behaviors. These innovations do not necessarily imply behaviors requiring a high number of sequential operations and may thus not allow a direct test of the technical intelligence hypothesis. However, they fit with a broader definition of this hypothesis and as such can inform us on how plausible it might be.

In both birds and primates, species with a higher number of technical innovations also have larger brains, relative to their body size (Overington et al. 2009; Navarrete et al. 2016),

in line with the larger brain of tool-using species as compared to non-tool-using ones. In addition, the correlation between rates of technical innovations and brain size is stronger than between brain size and the number of opportunistic innovations (such as the incorporation of new food types in a species diet), also supporting the idea that these technical innovations require higher cognitive abilities. Although these results suggest that the ability to produce complex new behaviors requires a particular combination of cognitive abilities, whether the need to develop such behaviors actually drove the evolution of larger brains, and of a higher technical intelligence, is debatable.

Did Tool Use/Technical Innovations Drive Brain Enlargement and the Evolution of Intelligence?

The technical intelligence hypothesis is an evolutionary theory. It suggests that the use of tools and the need to develop technical innovations led to an increase in encephalization and intelligence. The hypothesis can thus be considered a refinement of the extractive foraging hypothesis (Parker and Gibson 1977), which argues that the need to obtain some embedded or hard-to-eat food might have favored the evolution of large brains.

Under the technical intelligence hypothesis, the innovative ability to organize behaviors requiring a high number of sequential operations is a specialized adaptation. However, there is little evidence that technical problem-solving is a specialized cognitive function. Indeed, the finding that some birds (e.g., rooks *Corvus frugilegus*, Bird and Emery 2009) and primates (e.g., gorillas *Gorilla gorilla*, Mulcahy et al. 2005) that do not use tools in the wild perform well on tool use problems in the laboratory suggests that the special cognitive abilities of tool-using species have preceded the evolution of tool use (Kacelnik 2009).

Alternatively, the ability to innovate in a technical context may not be the direct target of selection, at least in the early stages of evolution. Instead, this ability may appear as an emergent property associated with the evolution of traits

that have evolved for other functions and that, combined, predispose animals to solve problems through technical innovations (Sol 2015; Sol et al. 2016). The evolution of large brains (which may have evolved for other reasons unconnected with technical intelligence) might have facilitated the emergence of the cognitive abilities required for tool use and technical innovations (Sol 2015; Navarrete et al. 2016).

This is particularly likely in long lived, generalist species searching for ecological opportunities, such as chimpanzees and corvids, all known to have the ability to use tools (Ducatez et al. 2014; Sol et al. 2016).

Conclusion

The technical intelligence hypothesis is difficult to test. Defining and measuring technical intelligence is challenging. Yet demonstrating that the need to efficiently organize behaviors requiring a high number of sequential operations has been a major evolutionary pathway toward enhanced intelligence is even more challenging. Current evidence suggests that these complex, technical behaviors emerged in species with relatively large brains. Whether these larger brains are the cause or the consequence of the need for higher technical cognitive abilities remains debatable. More investigations, especially on the differences in physical cognition between phylogenetically related tool-using and non-tool-using species, are needed to better understand the plausibility of the technical intelligence hypothesis.

Cross-References

- ▶ Adaptive Plasticity
- ▶ Advanced Tool Use
- ▶ Bird Tool Use
- ▶ Brain Size and Intelligence
- ▶ Cognitive Changes in Adolescence
- ▶ Communication and Social Cognition
- ▶ Convergent Evolution of Intelligence Between Corvids and Primates
- ▶ Costs and Benefits of a Large Brain

- ▶ Environmental Unpredictability and Bet-Hedging
- ▶ Evolution of Intelligence, The
- ▶ Evolution of the Brain, The
- ▶ Evolution of Tool Use
- ▶ Extractive Foraging Hypothesis, The (Parker and Gibson 1997, 2015)
- ▶ Intelligence Versus Natural Selection
- ▶ Nonhuman Tool Use
- ▶ Primate Tool Use
- ▶ Proto-Tool
- ▶ Social Intelligence Hypothesis, The
- ▶ Tool Manufacturing
- ▶ Tool Use
- ▶ Why Humans are Unique

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Technological Bullying

► Cyberbullying

Teenage Issues

► Adolescent Issues

Teenage Pregnancy

► Adolescent Parenthood

Teleology

► Goal Detection

Telomerase

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Synonyms

[Telomere](#); [Telomeric repeat sequence](#)

Definition

The enzyme that acts to maintain the end of DNA molecules in the chromosomes of eukaryotes.

Introduction

Telomeres are the strands of DNA at the ends of eukaryotic chromosomes. They consist of sequences that repeat, although the specific sequence varies by species of eukaryote. They perform several important functions. One of the

most crucial is the protection of chromosomes from exonuclease enzymes, which are capable of degrading the terminal regions of chromosomes. Additionally, they ensure that the natural repair systems of DNA do not detect the ends of chromosomes and join them together. Therefore, telomeres ensure that chromosomes remain intact and that DNA replicates efficiently and effectively (Moyzis et al. 1988).

Because of the way that DNA replicates, telomeres should get progressively shorter with each successive round of replication. This is because DNA can only be copied in one direction, which causes the other strand to lag behind. Therefore, the second strand can only be copied in fragments, called Okazaki fragments (Pohjanpelto and Hölttä 1996). Often the last Okazaki fragment is not primed, which leads to a difference in length between the two strands of DNA. Additionally, the final Okazaki fragment can be positioned too close to the end of the DNA molecule. Both of these would result in the gradual shortening of DNA molecules, but telomerase counteracts this process by adding to the ends of DNA strands (Harley et al. 1990).

Telomerase is a unique enzyme because its constituents are both protein and RNA. Contained within its RNA sequence is the reverse of the telomeric repeat sequence. Because of this, telomerase is capable of binding to the telomeric repeat sequence and lengthening the lagging strand of DNA. It is through this mechanism that telomeres are maintained throughout the many cell divisions that must occur in order for organisms to survive (Chen et al. 2000).

Empirical Support

Extensive evidence has supported the existence of telomerase. After telomeres were identified, investigations of the mechanism by which they are extended were undertaken. The first investigation of telomerase were carried out by Blackburn and others using yeast as a model organism. This investigation showed a progressive shortening of telomeres across successive generations of yeast cells. It also supported the role of telomerase in counteracting this process (Blackburn et al. 1989).

Building on this work, other researchers have found evidence of telomerase activity in other organisms, most notably humans (Henderson et al. 1990). In humans, telomerase has been implicated in both normal processes such as aging, as well as abnormal processes, such as cancer.

The shortening of telomeres has been shown to be implicated in the normal aging process. In other words, as humans age, their telomeres get shorter. Therefore, the presence of telomerase is important for extending the life span of humans. Many studies have confirmed the link between the length of telomeres and aging (Greider 1990). Telomere length and the functioning of telomerase have also been shown to be related to disorders common in the aging population, such as dementia, as well as disorders that are marked by abnormal aging processes. Related to this, the functioning of telomerase has been shown to be related to these disorders. These disorders have been shown to occur when the telomerase enzyme is defective or when other enzymes related to the process do not function properly. For example, people with progeria, a disorder marked by premature aging, have been shown to have shorter telomeres than other people. This suggests a failure of telomerase to extend telomeres, which contributes to the characteristic features of progeria (Ding and Shen 2008).

Telomerase can also become overactive. This defect has been implicated in the formation of cancer, which is characterized by cells that rapidly divide and do not die. An abundance of telomerase has been seen in cancer cells. The function that telomerase performs in normal cells, which is to help them to divide, helps to support the rapid division of cancer cells. In cancer, telomerase is often over active. As a result of this, telomeres become longer than they normally are, which leads to more divisions of that cell. This excessive cell division gives rise to tumors and other hallmarks of cancer (Shay et al. 2001).

Importance to Evolutionary Psychology

Telomerase can be found in all eukaryotic cells, including animals and plants. This means that it has been conserved throughout the evolution of

eukaryotic organisms. This maintenance over millions of years of evolution points to its importance in maintaining the integrity of DNA. Its importance is likely due to its ability to stave off aging, as evidenced by its expression in diseases of aging. Evolution is predicated on survival and reproduction, so telomerase has direct implications for evolution by supporting these crucial processes.

Evolution occurs as a result of genes mutating as they are passed from one generation to the next. Telomerase ensures that DNA will successfully replicate, which allows organisms to survive and reproduce, which allows genes to pass to the next generation. Therefore, by allowing chromosomes to maintain their structure, telomerase plays an important role in the continued evolution of the human species. Because most, if not all, psychological traits have been shown to have genetic components, they are acted upon by evolution. Therefore, telomerase allows for the evolution of psychological traits by protecting the parts of DNA that contain genes.

Conclusion

Telomerase plays an important role in the maintenance of the telomeres on the ends of chromosomes. Telomeres are important for protecting genes and allowing genetic material to be transmitted from one generation to another. Telomerase lengthens telomeres after DNA replication, which counteracts the shortening of telomeres that occurs during the replication process. Because of this, it plays an important role in the maintenance of life and the passage of genetic information from one generation to the next.

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Telomere

► Telomerase

Telomere Attrition

► Telomere Depletion

Telomere Depletion

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Synonyms

Telomere attrition; Telomere erosion; Telomere shortening

Definition

Telomeres, the protective caps of chromosomes, shorten with cellular division and age. Shortening may be hastened by exposure to environmental factors including psychosocial stress.

Introduction

Telomeres are nucleoprotein structures that buffer and stabilize the ends of all linear eukaryotic chromosomes. They are evolutionary ancient structures that emerged in response to the chromosomal end replication problem. Telomeres shorten with age, and cells with critically short telomeres either die off or cease to replicate. Accordingly, short telomeres are a risk factor for increased morbidity and mortality in humans and are thus likely to have fitness consequences. In addition to age-dependent telomere depletion, there is evidence that environmental factors, including experiences of psychosocial stress, may hasten telomere shortening.

Overview

Telomeres consist of DNA repeats that function to buffer the coding portions of our genomes, as cell division results in the loss of roughly 50–200 base pairs (bp) due to incomplete end replication (Wright et al. 1997). This loss occurs because DNA replication machinery cannot bind to the ends of linear chromosomes, a phenomenon known as the “end replication problem” (Lingner et al. 1995). Once telomeres reach a critical minimal length, cells either cease to divide or die. Accordingly, the inability for tissues to replace cells impairs health and fitness, and short TL is linked with increased disease and mortality risk in humans and other vertebrates (Cawthon et al. 2003; Wilbourn et al. 2018).

While TL shortens with age, the rate of decline is not the same in all individuals. Numerous environmental factors ranging from smoking to psychosocial stress correlate with shorter TL (Astuti et al. 2017; Willis et al. 2018).

Furthermore, associations between environmental factors and TL are observed throughout the human lifespan, with early exposures generally having a larger association with TL than those experienced during adulthood (Mathur et al. 2016; Ridout et al. 2017; Shalev et al. 2012). Even environmental exposures experienced during intrauterine life correlate with postnatal TL, measured both at birth and during young adulthood (Entringer et al. 2011, 2013).

Experimental investigations using both *in vitro* cell lines and animal models have established mechanistic pathways that may connect these environmental factors with accelerated telomere depletion. These pathways include increased inflammation levels, oxidative stress exposure, and chronic stress hormone exposure (Choi et al. 2008; Haussmann et al. 2012; Kawanishi and Oikawa 2004; Nettle et al. 2017). The contribution of each of these pathways to human telomere depletion, however, remains unknown, as our understanding of the effects of environmental factors on TL in humans almost exclusively comes from correlational studies. While most of these studies assume a causal relationship between environmental factors and shorter TL, alternative pathways exist to explain these findings.

What Are Telomeres?

Telomeres are the ends of linear eukaryotic chromosomes. They are nucleoprotein structures that consist of repeated, noncoding DNA bound to the structural protein shelterin. Due to the end replication problem, telomeric DNA shortens with cell division. When cells have critically short telomeric DNA, they are signaled to cease replication. This signal is thought to be mediated through the uncapping of shelterin from short telomeres (Cookson and Laughton 2009; Lendvay et al. 1996).

Cells that undergo rapid division maintain their telomeres with an enzyme called telomerase. Telomerase functions to rebuild short telomeres by adding repeated telomeric DNA to the 3'-end of the chromosome. Next, after telomerase adds enough substrate, DNA polymerase binds and adds the complementary DNA repeats to the telomere (Blackburn 1992). In most human tissues, telomerase is only active during embryonic

development. However, in tissues that continue to proliferate into adulthood, like blood (i.e., leukocyte progenitors), telomerase remains active, albeit at levels that cannot sufficiently maintain TL (Iwama et al. 1998). Both TL and telomerase activity are vital to cellular maintenance, are presumed to have a causal role in health and fitness, and may explain variation in important life history traits.

Telomere Evolution

Telomeres have a deep evolutionary past, as variations of the repeated telomere DNA sequence are present in every major eukaryotic lineage. Ancestral chromosomes like those in prokaryotes and mitochondria are circular; thus, neither have telomeres nor are subject to replicative DNA loss. With the emergence of linear chromosomes, telomeres evolved as a buffer of noncoding DNA to minimize the risk of the end replication problem (Volff and Altenbuchner 2000). Telomerase may have an even deeper origin, possibly dating back to the RNA world (Eickbush 1997).

TL differs widely across taxa, which makes sense considering that eukaryotes face radically different selective pressures and have lifespans that can vary by over five orders of magnitude (Blackburn et al. 2015). Among 61 studied mammalian species, those with longer lifespans tend to have shorter telomeres (Gomes et al. 2011). The shorter telomeres of long-lived mammals generally are subject to cellular aging, while those in shorter-lived mammals are less affected by cellular aging. A theory used to explain this difference is that TL is under relaxed selection in short-lived animals, with other aspects of their life histories subsequently accelerating their aging (e.g., increased metabolic rate and high reproductive burden).

TL also varies within taxa. For example, in humans, females tend to have longer telomeres than males, which is concordant with females' generally longer lifespans (Kimura et al. 2008). In humans, TL is substantially heritable ($h^2 \approx 0.70$) (Broer et al. 2013). Telomere depletion rates may also be heritable, although it is difficult to tease apart the genetic and environmental effects on TL (Monaghan 2010).

Environmental Exposures Correlate with Depleted Telomere Length

In humans, numerous environmental factors correlate with shorter telomeres, including psychosocial stress, smoking, exposure to heavy metals, radiation, and poorer nutrition (Astuti et al. 2017; Lustig et al. 2016; Rafie et al. 2016; Zota et al. 2015). Of these, socioeconomic status (SES) and perceived stress are the most commonly explored (e.g., Tennyson et al. 2018), with many studies reporting weak to moderate correlations indicating shorter TL in low SES, high stressed individuals (Willis et al. 2018). While support for the association between different stress measures and TL varies across studies, one consistently observed trend is that early life stress better predicts TL than adult stress (Mathur et al. 2016; Pepper et al. 2018; Ridout et al. 2017; Willis et al. 2018). This finding may be explained by individuals being more vulnerable to environmental damage early in life because the rate of developmental change and cell turnover in their bodies is at its fastest (Eisenberg 2011; Gavrilov and Gavrilova 2004). Intriguingly, the effect of early life adversity on TL may stretch back to even before birth, as emerging evidence indicates that the intrauterine environment associates with human TL at birth, as well as the rate of telomere depletion during early life and subsequently TL during young adulthood (Entringer et al. 2011, 2013; Escoffier et al. 2018).

Causal Models and Alternative Hypotheses Explaining Correlations

While ample studies show correlations between environmental factors and TL, we still do not know the extent to which they shorten telomeres. One way to better ascertain the mechanisms of telomere depletion is to explore the multiple pathways that may mediate these associations. Some of these proposed pathways include increased inflammation, oxidative damage/stress, and chronic glucocorticoid exposure. Chronic inflammation increases the rate of cell turnover, which subsequently shortens TL (Nettle et al. 2017). Oxidative stress can directly cleave the vulnerable GGG regions of the repeated human telomere DNA sequence (Oikawa and Kawanishi

1999). Chronic exposure to stress hormones is known to both inhibit telomerase and shorten TL (Choi et al. 2008; Haussmann et al. 2012). Since it is unethical to test these pathways experimentally in humans, most of these data exist from either *in vitro* cell line or *in vivo* vertebrate studies. As such, skepticism remains regarding the actual effect of each pathway on human TL.

Bateson and Nettle (2018) recently suggested that much of the telomere literature too readily assumes that the correlations with environmental exposures reflect a simple causal relationship. Life history theory suggests that those faced with an uncertain future may adaptively exhibit more risky behaviors and devalue their future health (Wilson and Daly 1997). Shorter TL predicts poorer health outcomes (Cawthon et al. 2003). Thus, it may be that individuals with shorter telomeres are more likely to engage in behaviors that are detrimental to their health because of facultative adjustments to their life history strategies. Indeed, shorter TL predicts increased impulsivity and risk taking in young and healthy undergraduates (Yim et al. 2016).

Another causal scenario to consider is that a third variable, possibly early life stress, affects both behavior and TL (Bateson and Nettle 2018). Increased exposure to stress early in life predicts both shorter telomeres and an increased likelihood of adopting certain risky behaviors (e.g., smoking and poor diet) (Boonekamp et al. 2013; Lovallo 2011; Manuck and McCaffery 2014; Shalev et al. 2012). As such, there may be TL-independent pathways that mediate the linkage between stress and behavior, a scenario that subsequently relegates TL as a noncausal biomarker.

The Future of the Field and the Need for Longitudinal Research

It has long been assumed that environmental and behavioral factors shorten telomeres. While experimental data shapes our understanding of the pathways that link environment, TL, and biological health, mostly weak to moderate correlative evidence exists from human studies. These results, along with evidence suggesting a noncausal relationship between certain environmental factors and TL (e.g., smoking by Rode

et al. 2014), have led some to question the long-held assumption of causality (Bateson and Nettle 2018). While it is difficult to ethically measure environmentally mediated telomere depletion in humans under experimental conditions, longitudinal research may provide a promising alternative.

By measuring telomere depletion rather than TL, longitudinal studies allow researchers to account for the variable starting telomere lengths observed among human individuals. Thus, they provide the capacity to better resolve issues of causality. To date, however, only limited longitudinal research has been conducted. These studies average between 4 and 5 years between baseline and follow-up and have frequently used potentially biased statistical methodologies (Bateson et al. 2018). Humans are a long-lived species; a lengthier assessment of telomere depletion with better statistical methods will likely offer more resolution and better causal inference. By studying how telomeres change over time, researchers can determine if risky adult behaviors cause telomeres to shorten or if another factor like early life stress both shortens TL and causes risky behaviors. Discovery of the latter would indicate that the correlations used to infer causal pathways between behavior and TL may, in reality, be indirect. By using a longitudinal design, researchers can also test if individuals with shorter telomeres are more likely to engage in risky behaviors. Finally, by better comprehending the factors that shorten telomeres, we can also assess the possible factors that attenuate or even reverse telomere loss. The idea that lifestyle, social solidarity, resilience, and other factors such as religiosity can attenuate telomere depletion is of considerable interest, especially as the causal role of TL in health and fitness is better understood (Hill et al. 2016; Ornish et al. 2013).

Conclusion

Telomeres are ancient structures that emerged early on in the evolution of eukaryotes. As linear chromosomes shorten with cell division and age, telomeres buffer the genome from nucleotide loss and convey protection against the premature

cessation of cellular replication and cell death. In addition to age, environmental factors, including experiences of psychosocial stress, may shorten TL. Short TL subsequently predicts an array of disease phenotypes as well as increased mortality risk. While mostly correlative data exists for humans, novel experimental data collected from both *in vitro* and animal model studies now allow for the proposal and exploration of causal mechanistic pathways. Hypotheses generated by these data will soon be tested in humans as longitudinal studies may finally have enough time between baseline and follow-up to capture meaningful results in such a long-lived species. The results from these studies will allow better inference of causation, as well as improvements of the understanding of how behaviors and lifestyle choices attenuate the effect of stress on TL.

Cross-References

- Development of Adaptations
- Discounting of Future Returns
- Ecology
- Environmental Harshness
- Environmental Harshness/Mortality
- Environmental Risk
- Environmental Unpredictability
- Environmental Unpredictability and Bet-Hedging
- Evolution of Adaptations
- Increasing Longevity
- Life History Strategies
- Life History Theory
- Selection Pressures as a Function of Age
- Stress
- Stress Reactivity
- Telomerase
- Theory of Senescence

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Telomere Erosion

- [Telomere Depletion](#)

Telomere Shortening

- [Telomere Depletion](#)

Telomeric Repeat Sequence

- [Telomerase](#)

Temper

- [Emotional Disposition](#)

Temperament

- [Emotional Disposition](#)
- [Personality](#)
- [Personality, Gender, and Culture](#)

Temperature

- [Regulation of Body Temperature](#)

Temporal Discounting

- [Discounting of Future Returns](#)

Temporal or Spatial Fluctuation

- [Environmental Unpredictability and Bet-Hedging](#)

Temporal Processing

- [Space, Time, and Number](#)

Temptation

- [Prisoner's Dilemma Outcomes](#)

Tend and Befriend Adaptations

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Synonyms

[Affiliation](#); [Stress reactivity](#)

Definition

Under stress, the need to affiliate with others is an adaptation that enhances survival.

Introduction

Taylor et al. (2000) posited a “biobehavioral” (behaviors that have biological underpinnings) hypothesis regarding the survival instincts of human beings, arguing that the fight-or-flight response is a mislabeling of responses to stressors in human females. The tend-and-befriend hypothesis states that under times of stress, females are more likely to utilize behaviors different from fighting or fleeing, i.e., parenting (tending) and affiliative behaviors (befriending) that protect both themselves and their offspring from stress, whereas males exhibit the classic fight-or-flight sympathetic nervous system response to stress.

The theory offers evidence that the biological underpinnings are (1) the hormone oxytocin and (2) the opioid system, which are central actors that facilitate the tending and befriending behaviors of females under stress. Since its publication in 2000, its influence in the conceptualization of sex differences in physiological stress responses and observational research of psychological stress has fundamentally shifted and enhanced the scientific study of the interplay between observed behaviors and the biological underpinnings of those behaviors.

Tend and Befriend Theory

The crux of tend-and-befriend adaptations lies in the argument that the theory of the fight-or-flight responses shown in animals (Cannon 1932) was largely based on male-biased samples in both human and nonhuman animal research. Fighting or fleeing may be advantageous to males when threatened, whereas they may not offer the same advantages to females, particularly for females with offspring under their care. Fighting or fleeing may put the mother and her offspring at risk in a species that show typically higher maternal investment in offspring (meaning time and effort offered in parenting behaviors). Therefore, in response to stress, females will tend to offspring, and as a piggyback onto that biobehavioral system, will befriend other conspecifics (especially other females) for protection/buffering from stress (Taylor et al. 2000). Subsequent conceptualizations have refined the assumptions of tending and befriending adaptations (see Taylor 2012). Human studies, however, are observational in nature. Thus, nonhuman animal research has offered the bulk of support for the theory's claims regarding tending and befriending behaviors (Taylor et al. 2000).

Biological Underpinnings

Oxytocin and brain opioid systems are hypothesized to provide the biological bases of tending and befriending behaviors (Taylor et al. 2000). Oxytocin has been implicated in a wide array of

reproductive and parenting behaviors, stress, and social behaviors (see Carter 2014 for a current, comprehensive review). Evidence indicates that reactivity to stress releases may in fact create both a cascade of biological reactivity markedly different between the sexes and differential adaptive behaviors (tending and befriending vs. fight or flight) to facilitate the reduction of stress and subsequent calming of the biological responses to stress.

Evolutionary Advantages of Tending and Befriending for Females

Taylor et al. (2000) offer the hypothesis that the tending response (and related release of oxytocin) encourages maternal behaviors that facilitate the survival of offspring. As such, the evidence for tending behaviors in mothers are built on the attachment system between mothers and infants (Bowlby 1988). In addition, seeking support under stress (i.e., befriending) would attenuate stress in species whose survival depends on other conspecifics in cooperative groups. Thus, Taylor (2006) argues that “there would be clear survival benefits of a biobehavioral mechanism that signals gaps in social support and prompts affiliation for beneficial communal responses to stress” (p. 275).

Evidence for Tend-and-Befriend Adaptations

In recent years, evidence for (1) patterns in oxytocin and associated stress responses among human females, and (2) sex differences in stress reactivity have been studied in relation to tend-and-befriend adaptations.

Oxytocin and Stress Responses in Human Females
Evidence in human females is mixed regarding the effects of oxytocin on the behaviors of adults at different stages of life. For example, Heinrichs et al. (2001) found a stress response to the Trier Social Stress Test (TSST) regardless of whether lactating mothers held or breastfed their infants; however, cortisol responses were attenuated in breastfeeding mothers whereas oxytocin levels did not vary significantly in response to the stressor. In contrast, older women on hormone therapy showed higher oxytocin levels, and higher baseline oxytocin levels were associated

with greater self-reported relationship stress, but was not significantly related to stress reactivity to the TSST (Taylor et al. 2006). Subsequent conceptualizations (Taylor 2012) highlight differences in baseline oxytocin levels (but not reactivity) as predictive of perceptions and seeking of social support in adult females.

Sex Differences in Stress Reactivity

Although stress responses in the Hypothalamic–Pituitary–Adrenal (HPA) axis may be somewhat similar (via release of the hormone cortisol) in males and females in certain types tasks, the accompanying perceived stress of events may also offer insights into the observed differences in behaviors typically exhibited by males and females in response to those stressful events. For example, both male and female rowers showed significant cortisol responses to a *physical* task (rowing ergometer test); however, pretask cortisol levels in anticipation of the stressor were positively related to team bonding (i.e., befriending behaviors) in females, but social withdrawal (i.e., fleeing) in males (Kivlighan et al. 2005). Female rugby players showed differential patterns of cortisol and testosterone responses after a competition than previous studies of male competitors in team sports, indicating that there may be unique physiological cascades for females after a group-oriented challenge that is simultaneously psychologically and physically stressful to the individuals (Bateup et al. 2002). Additionally, in nonphysical tasks, males and females showed differential patterns of affiliative behaviors in the Ultimatum Game and the Prisoner’s Dilemma (Nickels et al. 2017), and Byrd-Craven and colleagues (Byrd-Craven et al. 2015, 2016) found sex differences in cortisol reactivity to a crying baby or an out-group threat.

Conclusion

Evidence in both human and nonhuman research offers support for tending and befriending behaviors as adaptive for human females, in particular, those who are distressed. The theory does not offer specifics as to the types of stressors that will cause the cascade of events that will

specifically elicit tending and befriending behaviors in females. However, subsequent research indicates that there are complex social and behavioral mechanisms that may trigger differential cascades of biological and behavioral reactions to stress for males and females in group versus individual threats and subsequent responses to those threats.

Since its publication, researchers have offered expanded definitions of tending and befriending behaviors in males (Geary and Flinn 2002), with mixed findings as to the physiological response cascades associated with social stressors between and among human females and males. For example, Berger et al. (2016) found differences among men participating in the TSST for Groups (TSST-G), suggesting fight-or-flight responses may not accurately characterize responses to stress in males. In addition, other researchers (e.g., Carter 2014; Del Giudice et al. 2011) have integrated tend-and-befriend into theoretical frameworks of biological and behavioral responses to a variety of stressors. Its hypotheses regarding behaviors and underlying biological mechanisms in humans offer myriad opportunities to test physiological and subjective measures of stress in both males and females, further informing the understanding of how a variety of stressors may affect humans.

Cross-References

- Sexual Conflict and Sex Differences in Parental Investment
- Stress and Cortisol
- Stress Reactivity

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Tenor

► [Music and Hormones](#)

Tenth Cranial Nerve

► [Polyvagal Theory](#)

Teratogenic Effects of Alcohol Exposure on the Fetus

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Synonyms

[Adverse effects of alcohol in utero](#); [Fetal alcohol syndrome](#); [Fetal malformation](#)

Definition

The harmful effects of alcohol exposure on the developing fetus leading to its malformation.

Introduction

Alcohol is a well-established teratogen. If consumed by the pregnant mother, this can lead to a wide variety of physical and behavioral effects on the fetus. The range of these presentations can be grouped under the term fetal alcohol spectrum disorder (FASD). Within this spectrum, the most severe condition is called fetal alcohol syndrome

(FAS). This term was first formally coined by Jones et al. in 1973 who noted a group of characteristics seen in children born to alcoholic mothers. The incidence of FAS is difficult to measure on a global scale, largely due to the variability in its presentation. It is approximately seen in 0.5–3/1000 live births in the USA and Canada.

Alcohol as a Teratogen

The teratogenic effects of alcohol on the fetus that contribute to a diagnosis of FAS can be sorted into three main groups: growth deficiency, central nervous system (CNS) damage, and craniofacial abnormalities.

Growth

The growth deficiency in FAS can be assessed at any point during life and is defined as pre-/postnatal height or weight below the 10th percentile. This is used to contribute to FAS and partial FAS diagnoses but is not required to diagnose other diseases in FASD, including alcohol-related neurodevelopmental disorder (ARND). It is therefore postulated that growth retardation is a less important teratogenic effect of alcohol exposure during pregnancy (Institute of Medicine 1995). The rapid placental vasoconstrictive effects of ethanol is thought to contribute to the effects of growth deficiency through impaired delivery of oxygen and nutrients to the fetus (Burd et al. 2003).

CNS Damage

CNS damage is the primary feature for FAS diagnosis and can include a range of effects, including structural damage including microcephaly, cerebellar hypoplasia, and corpus callosum agenesis. This can be related to the teratogenic effects of ethanol on the developing fetal brain. The presence of ethanol at high levels lends itself to metabolism through a placental enzyme CYP2E1. This causes oxidation and generation of superoxide radicals which target and damage fetal brain tissue during their development (Gemma et al. 2007). Ethanol has also been shown to disrupt key neuronal developmental molecules such as alpha and

beta-laminins 1 which can contribute to microcephaly and intellectual disability (Minana et al. 2000; Vangipuram et al. 2008). More recent evidence suggests that ethanol can also interfere with trophoblast growth and cellular differentiation, which are both important steps in fetal development. This is seen with reduced levels of interleukins 6 and 13, signalling molecules specifically involved in neuroepithelial cell renewal and therefore contributing to adverse CNS development (Roberson et al. 2012).

Craniofacial Abnormalities

The presence of craniofacial abnormalities in FASD is usually as a consequence of brain damage. This is most likely linked to ethanol inducing uncontrolled cell death in cranial neural crest cells (Cartwright and Smith 1995). The three facial features associated with FAS are:

1. Smooth philtrum – the philtrum is the groove between the upper lip and the nose which is characteristically flattened in FAS.
2. Thin vermilion – thinned upper lip.
3. Small palpebral fissures – decreased eye width.

Alcohol-Related Birth Defects

The effects of alcohol exposure on the fetus can cause many more both defects that are not diagnostic criteria for FAS. These include heart murmurs (most commonly ventricular septal defect), joint position and functional abnormalities including small distal phalanges, kidney abnormalities (such as aplastic, dysplastic, or hypoplastic kidneys), and optic nerve hypoplasia that can lead to reduced visual acuity (Institute of Medicine 1995).

Mechanism of Alcohol Teratogenicity

The teratogenic effects of alcohol on the fetus are obviously a cause for concern. The reason for its adverse effects is due to the interactions between ethanol's pharmacology and the fetal physiology. Ethanol is known to diffuse from the mother's bloodstream, through the placenta, and into the

fetal compartment. Here, ethanol has a slower elimination compared to the mother and accumulates in the amniotic fluid. The enzymatic differences between mother and placenta also contribute to the teratogenic effects of ethanol as its metabolism lends to production of more toxic metabolites. Therefore, alcohol has a prolonged and dangerous effect on the fetus which is an especially vulnerable structure when developing (Gupta et al. 2016).

Conclusion

Alcohol is a known teratogen. Its effects on the fetus are varied and damaging. This is mediated through numerous mechanisms related to prolonged exposure and harmful metabolism of alcohol in the fetus. It can lead to a range of presentations, the most dangerous of which is FAS. This is characterized by growth retardation, CNS damage, and craniofacial abnormalities.

Cross-References

- [Alcohol](#)
- [Brain at Birth](#)
- [Brain Development](#)
- [Fetus Development](#)

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Terminal Altruism

- [Benefits to Kin](#)
- [Manipulation by Others](#)

Territoriality

- [Resource Defense](#)

Terrorism

- [Suicide Terrorism](#)

Terrors

- [Fears](#)

Testable

- [Falsifiability](#)

Testament

- [Will After Death](#)

Testosterone

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Synonyms

[Androgen](#); [Androgenic hormone](#); [Endocrinology](#); [Sex hormone](#); [Steroid hormone](#)

Definition

A steroid hormone present in various species, often in much greater quantities in males than females. In evolutionary psychology and endocrinology, testosterone is thought to play a key role in mediating life history trade-offs.

Introduction

Testosterone is a steroid hormone involved in many bodily processes, including reproductive physiology (e.g., spermatogenesis), morphology (e.g., development of secondary sexual characteristics), psychology (e.g., sexual desire), and behavior (e.g., aggression)—each of which plays an important role in survival and reproduction. Testosterone effects clearly manifest during puberty when its levels rise significantly. However, after puberty, short-lived testosterone fluctuations continue to affect some of these processes (e.g., aggression and sexual desire). Such

fluctuations take place in response to environmental inputs, including changes in temperature, interactions with potential mates, and competitive exchanges. This entry will provide an overview of testosterone by briefly discussing its history and mechanisms (e.g., production, action), followed by a review of theoretical and empirical approaches to understanding how it may be implicated in behavioral processes that are critical to fitness optimization.

History and Mechanisms

The discovery of testosterone's role in understanding behavior is often traced back to one of the first experiments in the field of behavioral endocrinology, published in 1849. In his work, Arnold Berthold castrated two roosters and demonstrated that the removal of the testes suppressed the development of secondary sexual characteristics (e.g., the comb and wattle), aggressive behavior toward other males, and crowing. Interestingly, Berthold castrated two other roosters and found that by reimplanting one testis in the abdominal cavity of each bird (with vascular and neural connections severed), the birds managed to develop the typical characteristics of an intact rooster (e.g., crowing, growth of combs, engaging in confrontations). Because the testes continued to function normally despite being detached from vascular and neural connections, Berthold concluded that the testes must secrete some chemical that influences morphological development and behavioral functioning. Berthold had just discovered testosterone.

Through several enzymatic steps, testosterone is synthesized from cholesterol in numerous tissues, including the testes, ovaries, and adrenal glands. Testosterone secretion is ultimately governed by the hypothalamic-pituitary-gonadal (HPG) axis. In men, testosterone secretion results from a hormonal "cascade," where the pulsatile release of gonadotropin-releasing hormone (GnRH) from the hypothalamus stimulates luteinizing hormone (and follicle-stimulating hormone) from the anterior pituitary gland, which in turn stimulates testosterone pulses from the

Leydig cells in the testes. In women, testosterone is primarily secreted in the ovaries, which contain cells similar to those of the testes.

Regardless of where it originates, testosterone acts on target cells through genomic and non-genomic mechanisms. Genomic mechanisms refer to the ability of unbound testosterone to cross the cell membrane, bind to the androgen receptor found in the cytoplasm of the cell, and migrate to the nucleus, where gene transcription can be activated or repressed. Once in the cell, testosterone can also be converted to other sex steroids, such as estradiol (via enzyme aromatase) or dihydrotestosterone (via enzyme 5- α -reductase), which in turn bind to steroid hormone receptors and affect cell functioning. Genomic mechanisms are considered "slow," meaning that the effects of testosterone take longer to manifest (e.g., >30 min, up to hours, or even days). Non-genomic mechanisms, on the other hand, are rapid effects (e.g., <30 min) that do not involve gene transcription but instead an interaction between testosterone and cell membrane receptors (e.g., GABA_A receptors).

Testosterone and Life History Theory

In evolutionary biology, life history theory refers to the resource trade-offs faced across the lifespan by species trying to maximize reproductive fitness. The premise of life history theory is that resources (e.g., energy, time, nutrients) are limited, and thus when they are invested into one trait to promote fitness, there is less available to invest in other fitness-promoting traits. Testosterone plays a key role in mediating some of the behavioral, physiological, and morphological processes that are inherent to life history trade-offs, such as copulation and courtship, sperm maturation, muscle growth and maintenance, immune function, and metabolism (Hau and Wingfield 2011).

Mating Versus Parenting Trade-Off

One of the most studied life history trade-offs thought to be mediated by testosterone is mating

effort versus parenting effort. Seminal work by John Wingfield (i.e., “The Challenge Hypothesis”; see Wingfield 2017, for review) found seasonal fluctuations of testosterone in avian species. While androgen levels were the lowest during the nonbreeding season, their levels rose at the start of the breeding season. This increase in testosterone was necessary to promote spermatogenesis, the expression of secondary sexual characteristics, and reproductive behavior. During the rest of the breeding season, androgens reached a physiological maximum in response to intrasexual encounters that birds had to face when protecting their territories. One important finding from Wingfield’s work was that the expression of paternal care required temporary decreases in testosterone secretion, providing preliminary evidence for testosterone’s role in mediating mating versus parenting trade-offs.

Following from Wingfield’s work in avian species, research in humans showed that testosterone levels vary as a function of relationship and fatherhood status. For example, Gettler et al. (2011) followed a large sample of men ($N = 624$) for nearly 5 years and examined the extent to which partnering (i.e., married or cohabitating), fatherhood, and paternal caregiving were prospectively associated with testosterone levels. Single and childless men with elevated morning testosterone levels at the beginning of the study were more likely to become newly partnered and newly partnered with children 4.5 years later. Further, men who became newly partnered with children by follow-up showed a greater decline in testosterone from the beginning to the end of the study, when compared with men who remained single and childless throughout the study. Additionally, a comparison of childcare investment showed that fathers who were most involved in the care of their children had significantly lower testosterone at the end of the study than fathers who did not participate in offspring care. Other studies showed that men with higher testosterone tend to experience less satisfactory romantic relationships and higher rates of divorce, while lower testosterone levels have been associated with greater parental involvement (reviewed in Roney and Gettler 2015; see also Zilioli and Bird in press). These

shifts in testosterone may be adaptive: on one hand, reduced levels may promote investment in successful relationships with close others (e.g., less risk of defection, greater care, and likelihood of offspring survival) and, on the other hand, elevated concentrations may promote behavior aimed at securing mates (e.g., mate seeking, extra-pair desires).

Basal (i.e., at rest) levels of testosterone have been found to map onto traits inherent to reproductive success; however, testosterone concentrations are not static. On the contrary, testosterone fluctuates quite rapidly in response to environmental inputs and in patterns that are consistent with the predictions of the life history theory. Specifically, it has been hypothesized that situations involving mating effort directly (such as interactions with a mate) or indirectly (such as intrasexual competition) lead to an increase in testosterone, while interactions involving parenting effort (such as nurturant parent-offspring interactions) lead to suppressed testosterone release or a testosterone decline (Zilioli and Bird in press). Empirical evidence indicates that testosterone is released both in anticipation and in response to competitions (see Carré and Olmstead 2015), in response to mating-relevant stimuli (reviewed in Roney and Gettler 2015), and drops following nurturant interactions with offspring (Kuo et al. 2016). Importantly, these rapid changes in testosterone to various social stimuli (competition, mating, parenting) seem to map onto future behaviors in these same domains. For example, testosterone responses to competition influence the decision to compete again, future competitive performances, aggression, risk-taking, and courtship behaviors (Carré and Olmstead 2015; Zilioli and Bird in press).

How testosterone is influenced by and influences social behaviors can be modified by situational, motivational, and physiological factors. In other words, the *strength* or *direction* of the bidirectional relationship between testosterone and social behavior changes as a function of *moderators*. Briefly, situational moderators refer to external factors that are not easily controlled, such as winning or losing a competition, with experiences of social victory being associated with an increase

in testosterone relative to losing (see Mazur 1985, for this prediction from the “Biosocial Model of Status”; see Geniole et al. 2017, for meta-analysis). Motivational moderators refer to individual differences in psychological variables such as personality (e.g., dominance) or mating preferences (e.g., sociosexual orientation). Finally, physiological moderators refer to the interaction of testosterone with other hormones and signaling molecules, such as cortisol, which has been found to attenuate the relationship between testosterone and behavior (see Mehta and Prasad 2015, for review of this “Dual-Hormone Hypothesis”).

Conclusion

As briefly reviewed, testosterone is implicated in numerous processes that are critical to reproduction and survival, including the expression of secondary sexual characteristics, mate seeking, aggression, and status seeking. From an evolutionary perspective, testosterone’s role in promoting reproductive fitness can be explained largely from the framework of the life history theory, which proposes that species face evolutionary trade-offs (e.g., mating versus parenting) due to the limited availability of resources (e.g., energy, time). Some of these trade-offs are mediated by testosterone. Future work in evolutionary endocrinology and psychology will be needed to shed light on the situational, motivational, and physiological moderators of the relationship between (1) basal testosterone and behavior, (2) exposure to social stimuli and acute testosterone release, and (3) acute testosterone release and social behavior.

Cross-References

- ▶ Digit Ratio
- ▶ Dominance and Testosterone
- ▶ Dominance, Testosterone, and Cortisol
- ▶ Female Mate Choice (Intersexual Selection)
- ▶ Inclusive Fitness
- ▶ Intrasexual Rivalry Among Men
- ▶ Music and Hormones

- ▶ Life History Strategies
- ▶ Life History Theory
- ▶ Parental Effort Versus Mating Effort
- ▶ Parental Investment Theory
- ▶ Secondary Sexual Characteristics
- ▶ Sexual Selection
- ▶ Survival and Reproduction

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Tests of Male Quality

- ▶ [Evolution of Female Resistance](#)

Thanatology

- ▶ [Death](#)
- ▶ [Nonhuman Reactions to Death](#)

Thayer's Law

- ▶ [Countershading](#)

The Big Five

- ▶ [Five-Factor Model](#)

The Breadth of General Evolutionary Theory

- ▶ [Evolutionary Perspective, The](#)

The Causes of War

- ▶ [Evolutionary Theory and the Causes of War](#)

The Civilizing Process

- ▶ [Sociocultural Theories of Violence](#)

The Evolution of Genitalia

- ▶ [Male Qualities and Likelihood of Orgasm](#)

The Extractive Foraging Hypothesis

- ▶ [Technical Intelligence Hypothesis, The](#)

The Four-Card Problem

- ▶ [Wason \(1966\) Selection Task](#)

The Gravity Hypothesis of Sexual Size Dimorphism

- ▶ [Gravity Hypothesis, The](#)

The Handicap Principle

- ▶ [Amotz Zahavi](#)

The Interjectionist Theory

- ▶ [Pooh-Pooh](#)

The Mating Mind

- ▶ [Geoffrey Miller](#)

The Middle Ages

- ▶ [Dark Ages, The](#)

The Musical Protolanguage Model

- ▶ [Darwin on the Origin of Language](#)

The Origin of Species

- ▶ [On the Origin of Species](#)

The Peripheral and Central Auditory System

- ▶ [Evolution of Hearing and Balance](#)

The Preconscious

- ▶ [Unconscious, The](#)

The Procreation Debate

- ▶ [Debating Procreation \(With David Benatar\)](#)

The Psychology of Crime

- ▶ [Criminology](#)

The Red Queen Effect

- ▶ [Red Queen Hypothesis, The](#)

The Sally-Anne Test

- ▶ [False-Belief Test, The](#)

The Science of Strategy

- ▶ [Game Theory](#)

The Sexual Double Standard

- ▶ [Sexual Stigmatization](#)

The Sexual Response Cycle

- ▶ [Four-Stage Model of the Sexual Response](#)

The Size of a Group

- ▶ [Group Size](#)

The Stress Response

- ▶ [Kinship and Cortisol in Caribbean Village \(Flinn et al., 2005\)](#)

The Subconscious

- ▶ [Unconscious, The](#)

The Traveling Sound

- ▶ [Evolution of Hearing and Balance](#)

The Wason Selection Task

- ▶ [Wason \(1966\) Selection Task](#)

The Westermarck Effect

- ▶ [Co-residence and Early Maternal Perinatal Association](#)

The Zone of Proximal Development

- ▶ [Vygotskian Intelligence Hypothesis, The \(Moll Et Al., 2007\)](#)

Theoretical Reasoning

- ▶ [Emergence of Indicative Reasoning](#)

Theories

- ▶ [Evolved Psychology of Warfare](#)

Theories of Language

- ▶ [Darwin on the Origin of Language](#)

Theories of Language Evolution

- ▶ [Müller's Language Hypotheses](#)

Theories of Morality

- ▶ [Philosophical Foundations for a Modern Morality](#)

Theorist

- ▶ [David Haig](#)

Theory of Asymmetric Investment

- ▶ [Parental Investment Theory](#)

Theory of Close Relationships

- ▶ [John Bowlby and Attachment Theory](#)

Theory of Games

- ▶ [Game Theory](#)

Theory of Mind

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Synonyms

[Folk psychology](#); [Mentalizing](#); [Mental-state attribution](#); [Mind reading](#)

Definition

The capacity to predict and interpret behavior by using representations of hidden, causally efficacious mental states.

Introduction

“Theory of mind” consists in the ability to use concepts of intentional mental states, such as beliefs, emotions, intentions, goals, and perceptual states, in order to predict and interpret behavior. Functional magnetic resonance imaging studies have revealed a distinctive network of neural regions that is active during theory-of-mind tasks, including the temporal-parietal junction, the posterior superior temporal sulcus, the medial prefrontal cortex, the precuneus, and the temporal poles (Van Overwalle [2009](#)). Deficits in theory-of-mind abilities, which are common in autism spectrum disorder (Tager-Flusberg [2007](#)), typically correlate with broader difficulties in social understanding.

Many scholars have suggested that theory of mind is an innate adaptation for social cognition, emerging very early in development and playing a crucial role in social learning and the acquisition of language (Baron-Cohen 1997). However, others have argued that theory of mind is the product of largely domain-general learning processes and is acquired gradually over the course of development through social experience (Wellman 2014). A third view argues that humans possess two systems for theory of mind: an innate, domain-specific “implicit” system and a learned, domain-general “explicit” system (Apperly and Butterfill 2009).

The False-Belief Task Controversy

The classic experimental paradigm for testing theory-of-mind abilities in children is the false-belief task (Wimmer and Perner 1983). In the most common version of this task, participants observe an agent place an object in a box and then leave the room. While the first agent is gone, a second agent moves the object to another hidden location. When the first agent returns, the participant is asked to predict where the agent will look for the object (or in some versions of the task, to say where she thinks the object is). The correct answer is “in the box.” In order to pass the task, the participant must represent that the agent has a *belief* about the location of the object that differs from what is really the case and use that representation to accurately predict what she will do next. Similar tasks test the capacity to reason about other mental states, including desires, states of knowledge, perceptual access, and emotions (Wellman and Liu 2004).

Typically, children fail the false-belief task until after their fourth birthday, as do many adults with autism spectrum disorder (Wellman et al. 2001). Since these results were first discovered, there has been controversy over their interpretation. “Constructivists” have argued that children’s shifting performance on this task reflects the emergence of a new concept of *belief*, amounting to a fundamental change in children’s intuitive theory of the social world, analogous to theoretical changes brought on by scientific discovery

(Gopnik and Wellman 1992). Children, in other words, are learning what beliefs are and the circumstances in which people have them. “Nativists,” in contrast, have pointed to the selective deficits on the false-belief task displayed by people with autism spectrum disorder as evidence of an underlying theory-of-mind module, which is selectively impaired in autism (Baron-Cohen 1997). Nativists also argue that younger children’s difficulties on the false-belief task don’t reflect the absence of a concept of belief but rather a performance error due to the immaturity of their domain-general executive capacities. According to this view, the concept of belief is innate, but children can fail to deploy it successfully in certain experimental contexts. Importantly, the nativist view doesn’t have to claim that theory of mind is unaffected by experience and individual learning. Rather, the claim can be that these changes are both constrained and facilitated by a domain-specific, innately channeled, learning mechanism that comes equipped with a few basic mental-state concepts (Carruthers 2015).

Two Views on the Evolution and Development of Theory of Mind

In the background of the nativist approach is a theoretical commitment concerning the importance of theory of mind in the evolution of human social intelligence. On this view, innate adaptations for theory of mind are thought to have emerged early in the hominid line. In the highly social environments of ancestral hominids, accurate prediction and interpretation of the behavior of conspecifics would have been crucial for survival. Accounts of the earliest emergence of theory-of-mind abilities in primates emphasize the adaptive importance of theory of mind in social competition, deception, and manipulation, as individuals sought to gain mating opportunities and to improve their status within their group’s social hierarchy (Byrne and Whiten 1988). This “Machiavellian intelligence” hypothesis is supported by evidence that modern great apes seem to demonstrate at least simple forms of theory-of-mind abilities in competitive but not cooperative experimental contexts (Call and Tomasello 2008).

Accounts of the evolution of more highly developed, and perhaps specifically human, theory-of-mind abilities, in contrast (including capacities to reason about the false beliefs of others), tend to place greater emphasis on the cooperative functions of theory of mind, particularly when coordinating multiple agents in the pursuit of mutually shared goals, such as group hunting and foraging (Tomasello 2014). Inferences about beliefs and intentions are also thought to have played a crucial role in the emergence of early systems of gestural communication, such as pointing and pantomime, which require inferences about mental states on the part of both the communicator and the audience (Scott-Phillips 2014). These cooperative environments are thought to have created an adaptive feedback loop, where selection pressures for more complex theory-of-mind abilities led to more complex forms of cooperation, which created further selection pressures on our theory of mind. Thus, theory of mind is thought to have fueled the evolution of highly complex forms of mutualistic cooperation, in addition to supporting the development of these same social abilities in ontogeny.

Constructivists typically accept that human beings possess some special adaptations for social intelligence but generally deny that these amount to a genuine theory of mind. For example, some constructivists acknowledge that neonates are innately biased to attend to faces and eyes and are innately disposed to engage in imitative behavior (e.g., Meltzoff 2007). According to constructivist accounts, these low-level, noncognitive mechanisms serve as a scaffold for children's early theory-of-mind development by directing their attention toward socially relevant phenomena. The latter then serve as inputs for domain-general learning procedures, such as statistical learning (Ruffman et al. 2012). Many constructivists also believe that children's acquisition of a mature theory of mind depends on exposure to specific linguistic inputs, such as clausal complementation syntax or mental-state vocabulary (e.g., de Villiers and Pyers 2002). Thus, while nativists posit that the ancestral emergence of domain-specific cognitive adaptations for theory of mind made complex forms of cooperation and linguistic

communication possible, constructivists hold that the existence of complex cooperative environments lay the developmental foundation for children to acquire a theory of mind via individual learning, which implies that it is an evolutionarily recent, culturally dependent phenomenon (Heyes and Frith 2014).

Does Theory of Mind Emerge Early or Late in Development?

Support for the constructivist view comes from evidence that theory-of-mind development is influenced by both social experience and language. For instance, having older siblings tends to lead to earlier success on the false-belief task, as do greater amounts of parental mental-state discourse (Ruffman et al. 2012). Strikingly, deaf children who do not learn sign language until later in life also have persistent difficulties on the false-belief task, even in adulthood (Pyers and Senghas 2009). These findings seem incompatible with the nativist's performance-error account of children's performance on the false-belief task, suggesting instead that children's social and linguistic environment plays an important role in determining their theory-of-mind abilities.

In response to these findings, some nativists have argued that they reflect the fact that children must learn how to *apply* their innate theory-of-mind abilities in different social and linguistic contexts and that variations in social environment impact this learning process (Westra 2017). In effect, the suggestion is that younger children fail at the tasks because their grip on discourse pragmatics is weak, leading them to misunderstand the point of the questions they are asked, and it is this that is impacted by social experience.

In support of the nativist view, a large body of evidence has emerged more recently, demonstrating a range of theory-of-mind abilities in children in the first 2 years of life, well before they pass verbal forms of the false-belief task. For example, a number of studies have adapted the classic false-belief task to make it suitable for infants. Importantly, these tasks never ask children to make explicit, verbal predictions. Instead, they rely on

children's spontaneous behaviors to measure their theory-of-mind abilities. For example, one such task presented 15-month-olds with a scene in which an experimenter hid an object in one of two boxes and then left. While the experimenter was absent, the object was moved to the other box. When the experimenter returned, infants either saw her reach toward the first, empty box, or the second box, where the object then was. Results show that infants look far longer when the experimenter reaches for the second box, suggesting that they find this behavior surprising (Onishi and Baillargeon 2005). The infants were seemingly expecting the agent to reach into the box where she *believed* the goal object to be.

Researchers have also designed ways of testing early false-belief competence by exploiting the fact that young children are highly motivated to help other people achieve their goals (Buttelmann et al. 2009). In these tasks, 18-month-olds observe an experimenter place a toy in one of two boxes and close the lid. The experimenter then leaves the room, and the children see a second experimenter move the toy from the first box to the second box. Then the first experimenter returns and begins to struggle with the lid of the first box. The authors predicted that if children understood that the experimenter desired the toy but had a false belief about its location, they should respond by retrieving the toy from the second box. In a true-belief control task in which the first experimenter observes the location change, in contrast, children should instead help the experimenter open the first box, presuming that she must want something inside it. Indeed, this is what they found.

The interpretation of these results, like those of the original false-belief task, has been a subject of great controversy. While nativists have used infant false-belief paradigms to support the claim that the capacity for representing beliefs is innate (Baillargeon et al. 2010), critics of these paradigms have offered various alternative, low-level explanations of the same findings. According to some of these interpretations, infants' successful performance on these tasks may not reflect an abstract concept of belief but rather the tracking of statistical regularities in observable behavior (Ruffman et al. 2012). Nativists have responded

to these criticisms by pointing out that these alternative explanations have tended to be post hoc and have failed to issue in new data (Scott 2014). The nativist framework, in contrast, has generated a continuous stream of new results, employing an ever-widening set of experimental paradigms. However, these debates are currently ongoing.

Can Apes Pass False-Belief Tasks?

We noted in the section "[Two Views on the Evolution and Development of Theory of Mind](#)" that there is evidence that other great apes have at least a simple form of theory of mind, one that allows them to track and reason about the goals and states of knowledge or ignorance of other agents. But until recently, all tests for false-belief understanding in other primates had proven negative (Call and Tomasello 2008). Recently, however, researchers have successfully adapted for use among primates some of the methods for testing false-belief competence in young children, with striking results. In one study, the experimenters showed chimpanzees, bonobos, and orangutans videos depicting an interaction between an actor dressed as a zookeeper and an actor dressed as a gorilla. The videos began by showing the gorilla hitting the zookeeper and then running into one of two haystacks arrayed at either side of the screen. While the zookeeper turned away to fetch a stick (which, in familiarizations, was used to hit the haystack containing the gorilla), the gorilla moved from one haystack to the other. Then the zookeeper turned around with the stick raised, poised to attack. The researchers used an eye tracker to measure whether the apes would look in anticipation toward the actual location of the gorilla or to the location where the zookeeper will think the gorilla is hiding (i.e., anticipating and reasoning from the zookeeper's false belief). The results showed that all three species of ape looked reliably more toward the false-belief location, suggesting that they were indeed tracking the zookeeper's beliefs (Krupenye et al. 2016). In another study, researchers adapted the active helping design of Buttelmann et al. (2009) (see above) for use with chimpanzees, bonobos, and

orangutans. They, too, found that great apes seemed to use information about false beliefs in order to help an experimenter retrieve an object from a locked box (Buttelmann et al. 2017).

Some critics have argued that these results, like the infant false-belief-task results, should not be interpreted in rich, mentalistic terms; instead, we should prefer explanations that only attribute to apes the ability to make predictions about behavior based on low-level, observable regularities, such as the appearance and disappearance of the colored shirt of the zookeeper (Heyes 2017). To test this hypothesis, Krupenye and colleagues designed a control task that matched their original anticipatory looking paradigm but replaced the actors with inanimate colored shapes (Krupenye et al. 2017). They found that, in contrast to the task involving actors, the participants were no more likely to look toward either target location when observing the same interaction between inanimate shapes. This provides compelling evidence that the apes' predictive gaze behavior was specifically sensitive to the social nature of the stimuli, as opposed to its low-level properties. All of these results are, however, quite recent, and further research is necessary before conclusions can confidently be drawn.

Thus, two recent studies seem to show that three other species of great ape are capable of passing false-belief tasks. This result, if it is valid, has striking implications for the debate about the language dependence of theory of mind. If nonlinguistic primates are able to represent beliefs, this casts serious doubt on the claim that such an ability requires linguistic experience, or is uniquely human. These findings also suggest that belief representation may in fact be evolutionarily quite ancient and potentially shared by the last common ancestor of humans, chimpanzees, bonobos, and orangutans.

Such inferences should be drawn cautiously, however: the presence of robust theory-of-mind ability in modern great apes does not necessarily imply that it is an innate adaptation. For it is possible that these apes acquired their abilities through individual learning (and hence that ancestral apes might have done so as well). In other words, even if great apes do reason about false

beliefs, this doesn't necessarily provide support for nativism about theory of mind in human beings. What it does do, however, is undermine the claim that false-belief understanding is specifically dependent on either *linguistic* experience or experience of distinctively human forms of collaboration and joint action.

The two-Systems View

Another set of theorists has attempted to resolve the dispute between nativists and constructivists by proposing an ecumenical solution that incorporates both constructivist and nativist elements (Apperly and Butterfill 2009). According to these "two-systems" accounts, infants' early competence on "implicit" false-belief tasks (and by parity of reasoning, the recent successful performance of other great ape species on similar tasks) does reflect a domain-specific adaptation for tracking mental states. This "implicit" theory-of-mind system is said to be fast, effortless, automatic, and largely encapsulated from executive systems; it also persists unchanged into adulthood and is shared with our nearest primate relatives. Thus, in many respects this implicit mindreading system resembles the kind of domain-specific adaptation posited by nativists. However, two-systems theorists hold that due to its automatic and encapsulated architecture, the implicit mindreading system is subject to "signature limits." In particular, while it can represent beliefs about the *locations* of objects (e.g., "Bill believes that the apple is in the box"), it cannot handle beliefs about the *identity* of objects (e.g., "Bill believes that the apple is really a pear"). This is because the implicit system is thought to *track* beliefs and other mental states without representing them as such and, in particular, without representing the aspectual nature of belief states. (Famously, one can believe that Jocasta is beautiful without believing that one's mother is beautiful, even though Jocasta is in fact one's mother. Here one and the same person is thought about under two different aspects.) The implicit system cannot, therefore, fully capture the richness and flexibility of the mature concept of belief.

In humans, one of the functions of the implicit system is to scaffold the acquisition of a second, parallel, explicit theory-of-mind system that develops much more gradually. This system is said to be slow, effortful, and heavily reliant upon executive resources, such as working memory. It develops gradually via domain-general learning in response to social and linguistic input and only emerges after children's fourth birthday (thus enabling them to pass the explicit false-belief task). Unlike the implicit system, this one isn't subject to signature representational limits. However, because it relies heavily on working memory, it must be directed by top-down goals and is compromised under cognitive load. The explicit mindreading system closely resembles the conception of mindreading posited by constructivists, albeit supported by a relatively more complex set of domain-specific cognitive adaptations. Thus, by adulthood, human beings are said to possess two parallel theory-of-mind systems, each with a distinct information-processing profile.

To test the prediction that the implicit mindreading system is subject to signature limits, two-systems theorists have compared adults' and young children's implicit theory-of-mind predictions in scenarios where agents have false beliefs about either an object's location or its identity (Low and Watts 2013). To test participants' ability to track false beliefs about identity, the experimenters constructed a scenario in which participants were familiarized with an agent who demonstrated a consistent preference for a certain color, always reaching for blue items rather than red items, for example. Next, out of sight of the agent, participants were familiarized with a paper cutout figure that appeared as a red robot from one side and as a blue robot on the other. They then watched as the agent observed what she would have seen as a blue robot enters one of two boxes. Next, unbeknownst to the agent, the figure rotated 180° and moved to the second box while presenting to the agent as a red robot. Because the agent didn't know that the red and blue robots are the same individual, she should believe that there was still a blue robot in the first box. Thus, if participants were tracking beliefs about identity, they should expect the agent to reach toward the first box. However, neither adults

nor children reliably looked in anticipation toward the first box, suggesting that they were insensitive to the agent's beliefs about object identity. Meanwhile, both groups showed correct anticipatory looking on the control task that only involved beliefs about the object's location.

These results provide support the claim that while implicit theory of mind accurately tracks beliefs about the locations of objects, it doesn't track beliefs about the identities of objects. However, critics of this study and others like it have pointed out that the object-identity task, which involves effortful forms of mental rotation, is likely to place additional demands on executive function that are not present in the object-location control task. This makes it unclear whether the relevant failure is due to signature limitations on implicit theory of mind or rather limitations on working memory (Carruthers 2015). It is therefore unclear whether this evidence truly supports a two-systems view. Nevertheless, two-systems accounts of theory of mind have significantly influenced debates about the cognitive architecture of our social cognition abilities.

Conclusion

As can be observed in the debate about the false-belief task, there is considerable disagreement in the literature about the role of theory-of-mind abilities in socio-cognitive development: while nativists believe that theory-of-mind is a basic adaptation that plays an important role in early social learning, constructivists hold that theory of mind is itself the *product* of social learning. These views correspond to distinct narratives about the emergence of theory of mind in the hominid line: if the nativist view is right, then theory of mind is evolutionarily ancient; if the constructivist view is correct, then it is likely to be a far more recent phenomenon. The two-systems view attempts to carve a middle ground between these two camps, allowing that some aspects of theory of mind are indeed evolutionarily ancient and early developing, while others are evolutionarily novel and acquired via social learning. However, the evidence in favor of this view is itself a source of controversy.

Cross-References

- [Autism](#)
- [Communication and social cognition](#)
- [Cultural Intelligence Hypothesis, The](#)
- [Does the Chimpanzee Have Theory of Mind?](#)
- [Evolution of Reciprocal Altruism](#)
- [False Beliefs](#)
- [Michael Tomasello](#)
- [Nativism](#)
- [Simon Baron-Cohen \(Darwinian Psychiatry\)](#)
- [Social Cognition and Communication in Chimpanzees and Bonobos](#)
- [Social Intelligence Hypothesis, The](#)
- [Theory of Mind and Evidence of Brain Modularity](#)
- [Theory of Mind and Nonhuman Intelligence](#)

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Theory of Mind and Evidence of Brain Modularity

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Synonyms

Commonsense psychology; Folk psychology; Mentalizing; Mind reading

Definition

Theory of Mind (ToM) refers to one's cognitive ability to ascribe and regard the mental states of others. Brain modularity refers to the theory that at least some cognitive functions are facilitated by innate neural structures that have been honed and selected through evolution.

Introduction

The term *Theory of Mind* was coined in 1978 by David Premack and Guy Woodruff during their investigation into the capacity of a chimpanzee to “impute mental states,” an ability previously considered to belong solely to the human race (Premack and Woodruff 1978). Since then, countless studies have tested various aspects of ToM ability, and while the existence of such abilities are accepted nearly ubiquitously across the scientific community, the underlying mechanism allowing for ToM remains a point of contention.

Theory of Mind

The ability to compute the mental states – beliefs, desires, knowledge, goals, etc. – of others varies from person to person. Predicting other's behavior using not only physical and visual stimuli but also inferences of such mental states is a skill that develops through time. In 1983 Heinz Wimmer and Josef Perner conducted a study in which

children observed a boy place chocolate in a blue cupboard and then leave the room. While the boy is out, his mother moved the chocolate to a green cupboard. Upon the boy's return, the studies' participants were asked where the boy would look for the chocolate. Eighty-six percent of 6–9 year-old children correctly guessed that the boy would look in the blue cupboard, where he had left it, while 100 % of the 3–4 year-old participants answered that the boy would look in the green cupboard, where the chocolate actually was, even though they knew the mother had moved it without the boy's knowledge. Thus, Wimmer and Perner were able to conclude that ToM ability develops over time, and children under 4 years old likely don't have the ability to predict other's behavior when it requires an understanding of their propositional attitudes (Wimmer and Perner 1983).

The Modularity-Nativist Approach

The concept of modularity became widely popular upon Fodor's publication of *The Modularity of Mind* in 1983, in which he proposed that certain lower mental functions are the result of innate, domain-specific brain structures (modules), analogous to organs, which are relatively isolated and in turn feed into a domain-general central engine (Fodor 1983).

More recently, however, Carruthers made his case for massive modularity, claiming that the entirety of the brain is comprised of a hierarchy of such modules, each responsible for separate mental functions. As evidence for his theory, Carruthers discussed the ability of various brain injuries to hinder certain cognitive functions while leaving others intact (Carruthers 2006). The Modularity-Nativist Approach to Theory of Mind ability relies on this proposed architecture, and the most convincing evidence for it follows Carruthers' train of thought. Simon Baron-Cohen, in 2001, published a review of the cognitive abilities of autistic children which highlighted a relative inability to pass first- and second-order false belief tests, even when other cognitive functions are more developed (Baron-Cohen 1991).

Conclusion

Theory of Mind refers to one's ability to attribute mental states to others and regard them in relation to one's own. Of the different theories attempting to explain ToM, the argument from modularity is of particular interest to evolutionary psychologists, crediting innate neural structures developed through natural selection as the foundation for mentalizing ability.

Cross-References

- [Carruthers on Massive Modularity](#)
- [Does the Chimpanzee Have Theory of Mind?](#)
- [False-Belief Test, The](#)
- [Mindblindness](#)

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Theory of Mind and Nonhuman Intelligence

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Synonyms

[Mental state attribution](#); [Mindreading](#); [Social cognition](#)

Definition

The cognitive ability to predict or explain an individuals' behavior through the attribution of mental states.

Introduction

Comparative cognition researchers have long been interested in the nature of nonhuman animal social capacities. One capacity has received prolonged attention: mindreading, or “theory of mind” as it's also called, is often seen to be the ability to attribute mental states to others in the service of predicting and explaining behavior. This attention is garnered in no small measure from interest into what accounts for the distinctive features of human social cognition and what are the evolutionary origins of those features. This entry surveys: (1) main hypotheses concerning the adaptive value of mindreading, (2) theoretical problems complicating our ability to determine whether nonhuman animals mindread, and finally (3) proposals that mindreading is a plural rather than unitary cognitive system.

Social Intelligence Hypothesis

One intuitive idea is that mindreading evolved in response to social pressures. The Social Intelligence Hypothesis asserts that the ability to reason about the intelligent action of group members affords greater benefits as social settings become more complex (Humphrey 1976; Jolly 1966). Certain social groupings seem to require substantial cognitive control on behalf of group members. Individuals must potentially be able to recognize and track particular individuals, kin relationships, and dominance hierarchies, all of which are subject to rapid changes over time. The Social Intelligence Hypothesis holds that social environments are necessary conditions on the development of social cognitive skills like mindreading. To substantiate this hypothesis, it is important to determine whether nonhuman animals that lack the complexity of social groupings seen in similar species also lack analogous social cognition skills

(Vonk et al. 2015). For instance orangutans, which are relatively solitary in relation to other great apes, are sufficiently similar with regards to social cognitive skills (Herrmann et al. 2007).

Exactly what social cognition skills were selected for is a further question. The ability to reason about others' behavior in social contexts might be useful in out-competing conspecifics. Known under the guise of the "Machiavellian hypothesis," some argue making better predictions of others' future behavior allows for one to manipulate others through various forms of deception (Whiten and Byrne 1988). As individuals gain more sophisticated understanding of social action and greater predictive success, competition becomes tough, thus creating an evolutionary "arms race." This hypothesis interprets the coalition formation and reconciliation behavior found in many primates in terms of long-term strategic responses, though there may be more mundane reasons, such as tracking food locations that promote this behavior (see Barrett and Henzi 2005).

An alternative view, one commensurate with Alison Jolly's initial account, suggests that cooperative social learning, not competition among conspecifics, led to the development of sophisticated social cognitive skills such as mindreading (Andrews 2012a; Heyes and Frith 2014). Social learning is the transmission of information across group members within a social context. While mindreading ability may not be required to engage in forms of social learning in mimicry and imitation, other social cognition skills may be required. For example, imitation might require that agents have (i) a "natural pedagogy" or evolved interpretive biases towards demonstrators and (ii) take a teleological stance, i.e., attribute purpose, design, or function, to others (Csibra and Gergely 2005). Some comparative evidence suggests that over-imitation, or the tendency to imitate demonstrators' behaviors in spite of their causal irrelevancy, is a distinctively human strategy facilitating more rapid social learning of instrumental skills and social conventions (Horner and Whiten 2004). It has been hypothesized then that our species-specific proclivity for high fidelity imitation may be linked to "cumulative cultural transmission": instrumental skills and social conventions are not

only inherited across generations – imitated behaviors may be recombined in novel contexts and in innovative ways (Legare and Neilsen 2015).

The Logical Problem

It is widely held that reasoning about the intentional actions of others is a form of causal reasoning – we attribute unobservable causal determinants of others' behavior in intentional explanations just as we do when we discover what makes simple machines function. This view receives partial support from developmental research on causal reasoning. Alison Gopnik and her colleagues introduced young children to boxes called "blickets" that would light up or make a sound under various parameters, such as when some collection of objects and the device were in direct contact (Gopnik and Sobel 2000). They concluded that not only did children recruit memories of prior interactions when being asked to predict what would make the blicket work, they were sensitive to the potential causal mechanisms at work. While in many cases causal reasoning requires knowledge of the observable states of objects at different times, it sometimes requires the positing of intermediate states that are perceptually opaque yet causally relevant in the assessment of observed events. The perceptually opaque causal determinants in the case of mindreading are internal mental states – the beliefs and desires or perceptions and goals that cause the resultant behavior.

Comparative researchers disagree about the causal reasoning abilities of nonhuman animals. While Penn and Povinelli (2007) claim studies suggest that chimpanzees do not share proficiency at inferring the underlying causal structure of phenomena with humans, other researchers have found evidence of causal reasoning in great apes on a par with that which we find in human children. Völter and Call (2014) show that apes infer causal structures from the coactivation of blicket detectors similarly to young children and can recruit this knowledge in their interventions.

Assuming mindreading is analogous to causal reasoning in the way hinted above, there is further

disagreement as to whether nonhuman animals' social cognitive abilities call upon unobservable intentional states. While evidence suggests that subordinate chimpanzees know what dominant chimpanzees observe when competing over a food source (Hare et al. 2000), whether their behavioral preferences involve the attribution of mental states is hotly contested. Povinelli and Vonk (2003) take issue with these and similar findings, on the grounds they are subject to "the logical problem". Assume we are deciding between two hypotheses regarding a subjects' behavior in a social context. The mindreading hypothesis assumes the subject confers mental states on some conspecific in the service of predicting their future behavioral states. The competing behavior reading hypothesis assumes she confers only behavioral states. If we are limited to the subjects' behavior when deciding between these two hypotheses, it seems just as likely that the subject relies on associations between observable behaviors in predicting the future states of conspecifics as it does that they would rely on the unobservable mental states.

Exactly what the logical problem means for comparative research and whether it can be solved is up for debate. Tomasello and Call (2006) argue that mindreading hypotheses provide the best explanation since they unify a range of very different experiments already demonstrated. Others, while not so sanguine, are hopeful that a novel experimental design could solve the problem (e.g., Lurz 2012; Heyes 2015; Sober 2015, and Bugnyar et al. 2016). Halina (2015) argues that the logical problem is not a unique theoretical dilemma for comparative researchers, so there is no special epistemic burden with regards to disproving competing behavior reading hypotheses. Andrews (2012b) similarly suggests that the logical problem is an ancillary of the philosophical problem of other minds: what justifies my attributions of mental states to others, given that my access to their mental life is always mediated through their behavior? Buckner (2014) evinces that in order to solve the logical problem, there must be a unique causal role for the contents of an agent's mental states to play in determining their action. But which interpretations of the content of

internal mental states are causally efficacious, and how so? Because any observable behavior is compatible with a potentially infinite set of mental attitudes, accurate attribution that would facilitate causal reasoning about observable actions of others appears to be computationally intractable (Zadwizki 2014).

Multiple Systems Hypothesis

Just as one might distinguish between an agent's explicit, reflective, deliberate knowledge from their implicit, heuristic-based, automatic knowledge of the causal structure of some physical system, we might discover multiple processing systems for mindreading. Children can correctly verbally identify and track false beliefs at around 4 years of age. Even though some nonhuman animals consider others' perceptual perspectives, this ability is not on par with children's ability to verbally reason about others' beliefs. That said, testing false belief responsiveness by measuring preferential looking times has some now thinking that preverbal infants have mindreading skills as well (Onishi and Baillargeon 2005). Infants' surprising performance in social contexts means could help make sense of the ontogeny and phylogeny of social cognition. Some conjecture that mindreading is not a unitary process, but rather can be decomposed into unique social cognition skills that have divergent evolutionary and developmental trajectories.

Partial evidence for these views comes from variations in reaction times in belief attribution.

By comparing performance across species and developmental stages, researchers aim to identify "signature limits" which reveal the contours of mindreading abilities (Butterfill and Apperly 2013). Signature limits indicate restrictions on the performance of some relevant tasks and can help to illuminate the mechanisms involved in performing the task (Thompson 2014). For example, while we require additional processing to report on someone's belief; it takes longer to answer questions about a person's belief than it does to answer factual questions about the situation (Back and Apperly 2010). Perspectival

information is different; perceptual information about others' point of view are automatically processed by subjects (Samson et al. 2010). These studies suggest that adults' judgments about the number of objects they could see in a visual scene were slower and more error-prone when the scene contained an irrelevant agent whose visual perspective was different, suggesting that another perspective can cause an indicative interference effect.

If mindreading was not a unitary cognitive system in humans, then nonhuman animal social skills may mirror some aspects of human capacities and not others. Still there are other ways of interpreting limitations on subjects' performance that do not necessitate the ascription of multiple processes. Subjects' performance limitations could be the result of limitations on domain general capacities such as working memory (Carruthers 2016) or infants' preferential looking times may be the result of implicit memory of the visual contact between the agent and the objects and experience with this sort of behavior (Perner 2016).

Conclusion

Investigations into the social cognition skills of nonhuman animals has profited from the prolonged interaction between researchers in developmental psychology, neuroscience, ecology, anthropology, and philosophy. Above we focus on the development of research with regards to mindreading or the ability to reason about others' mental states in the service of predicting and explaining their behavior. Importantly we see the question of what is the nature of mindreading and what is its adaptive value occur in a parallel, piecemeal fashion.

Cross-References

- [Ability to Recognize Individuals](#)
- [Brian Hare](#)
- [Causal Reasoning](#)
- [Cooperation and Social Cognition](#)
- [False-Belief Test, The](#)

- [Emergence of Social Reasoning about Hierarchies](#)
- [Michael Tomasello](#)
- [Nonhuman Primates](#)
- [Predicting Events and Behavior](#)
- [Social Cognition](#)
- [Social Intelligence Hypothesis, The](#)
- [Theory of Mind](#)

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Theory of Moral Development

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Synonyms

Kohlberg's rationalistic theory; Moral development

Definition

Kohlberg's theory of moral development explains how moral development takes place in human animals.

Introduction

The nature and the cognitive and emotional determinants of moral judgment have been empirically studied since the emergence of the science of psychology. Although one of the first systematic theories began with Piaget (1965), the first systematic theory based on empirical research was introduced by Lawrence Kohlberg (1969). Kohlberg's theory is regarded as a rationalist theory since it assumes that the main determinant of moral judgment is rational thinking processes, even though it is thought that emotional or intuitive processes are also involved – at least in part – in moral judgment.

Kohlberg's Three Levels

There are three levels (in a total of six stages) in Kohlberg's theory of moral development in a hierarchical structure. These three levels follow a stable sequence but qualitatively correspond to different types of moral reasoning. The first and primary motivation of the first level

(pre-conventional morality), which includes the first two stages (obedience and punishment; individual interests), is to avoid punishment and attain pleasure. The individual at the first stage does not understand or care that other people can have similar wishes and desires besides their own desires. Thus, the person in this stage acts in an egoist manner. Then, in the second stage, the person realizes that she can differentiate her own desires from the wishes of other people and the authority figures. At the second level (conventional morality), which includes the third and fourth stages (interpersonal; authority), the individual has a motivation that is concerned with mutual relations and expectations. The main motivation of the individuals at this level is to be accepted and socially approved by others and, in this context, to fulfill the orders of those who are hierarchically superior. Therefore, at this level, people define interpersonal relations through their place in society. At the last and third level (the post-conventional morality), the individual develops an autonomous moral conception, while in moral judgment she often refers to a universal set of principles (such as justice and fairness). This stage corresponds to a universal set of moral principles that all people must follow, according to Kohlberg, and moral superiority is characterized as reaching this stage. The normative moral superiority, which a rational human being as in Kant's categorical imperative must achieve as a result of cognitive reasoning, is a sense of universal justice. The individual in this stage sees morality as an end, not as a means.

Assessing Morality

Kohlberg scores people's moral judgments based on how they justify their moral judgments in terms of these three levels (i.e., pre-conventional, conventional, and post-conventional moralities). For example, in the well-known Heinz dilemma, the participant reads the following moral vignette:

A woman was on her deathbed. There was one drug that the doctors thought might save her. It was a form of radium that a druggist in the same town had recently discovered. The drug was expensive to

make, but the druggist was charging ten times what the drug cost him to produce. He paid \$200 for the radium and charged \$2,000 for a small dose of the drug. The sick woman's husband, Heinz, went to everyone he knew to borrow the money, but he could only get together about \$1,000 which is half of what it cost. He told the druggist that his wife was dying and asked him to sell it cheaper or let him pay later. But the druggist said: "No, I discovered the drug and I'm going to make money from it." So Heinz got desperate and broke into the man's laboratory to steal the drug for his wife. Should Heinz have broken into the laboratory to steal the drug for his wife? Why or why not?

According to Kohlberg, the decision of the participant regarding whether Heinz should or should not steal the drug has no theoretical significance. However, it is theoretically important as to how the participant justifies her moral judgment. Someone who says that Heinz should not steal the drug, because if he steals, he must be imprisoned (i.e., avoiding punishment), or Heinz should steal because if his wife lives he will make Heinz a happier person (self-interest) is scored as having pre-conventional morality. Someone who states that Heinz should not steal the drug because the legal rules prohibit it or that Heinz should steal the drug because his wife would expect him to be a good husband is scored as having conventional morality. Someone who says Heinz should steal the drug because everyone has the right to live or Heinz should not take the drug because others may need this medicine and everyone's life is equally important (i.e., universal human rights) is scored as having post-conventional morality.

According to Kohlberg (1971), moral development does not progress only with age (i.e., biological maturity); however, moral reasoning should be related to cognitive reasoning capacity. It has been found that the individuals who scored as having post-conventional morality showed higher performance in some tasks measuring cognitive reasoning (Kuhn et al. 1977). However, the theory of Kohlberg's moral development was later criticized by different theoretical perspectives (cf., Haidt 2001). It is thought that empathy capacity, rather than cognitive development (e.g., Hoffman 1993), may be an important factor in determining moral reasoning. However, Kohlberg (1981) actually believes that the ability to take perspective, a

cognitive capacity, is the fundamental determinant of moral reasoning.

Criticisms of Kohlberg's Theory

The theory of Kohlberg's (1969) moral development has been subjected to a number of criticisms from both theoretical and methodological perspectives. The most important theoretical criticism is the claim of universality of the hierarchical structure proposed by the theory. However, Turiel et al. (1978) showed that the basic assumptions of the theory were supported in a cross-sectional study. Likewise, Nisan and Kohlberg (1982) and then Colby et al. (1983) tested Kohlberg's theory and showed that most of the predictions were supported in a longitudinal design as well. But all of these studies have some certain limitations, such as being based on hypothetical dilemmas to measure moral judgment (see below).

In addition, the argument that rational processes are the main determinant of moral judgment has been criticized (Haidt 2001). In fact, there are two theoretical perspectives on the study of cognitive processes of moral judgment. The first is the Kantian theory, which Kohlberg adopted, which assumes that rational processes are more active than affective processes when making a moral judgment. In this theoretical approach, although emotional forces are – at least in part – involved, the main determinant of moral judgment is essentially rational. So Kohlberg thinks that the goal of a layperson in making a moral judgment is to reach the normatively superior moral principle like a truth-seeking scientist who always tries to find the universal principles of nature. According to this approach, someone with sufficient cognitive reasoning ability is more likely to score on higher levels of morality. The second theoretical approach to the psychological origins of moral judgment is the Humean sentimentalist approach (Haidt 2001). According to this approach, we use our intuitive rather than our rational processes when making a moral judgment. Accordingly, when an event occurs, strong emotions such as disgust or anger emerge that lead us to intuitively conclude that the

situation is morally right or wrong. After the moral judgment, we use our rational processes only for justification of the previous, already made moral judgment. To test this sentimentalist approach of Hume, the Julie and Mark scenario, which is well known in the literature, is used. In this scenario, the participants read the following scenario:

Julie and Mark are brother and sister. They are traveling together in France on summer vacation from college. One night they are staying alone in a cabin near the beach. They decide that it would be interesting and fun if they tried making love. At the very least, it would be a new experience for each of them. Julie was already taking birth control pills, but Mark uses a condom too, just to be safe. They both enjoy making love, but they decide never to do it again. They keep that night as a special secret, which makes them feel even closer to each other. What do you think about that? Was it ok for them to make love?

Although this scenario is defined as a harmless taboo violation (i.e., there is no direct harm behavior in this scenario; but see Royzman et al. 2015 for a counterargument), the majority of respondents automatically describe the incest behavior in the scenario (in which the feeling of disgust is activated) is morally wrong, and, in doing so, they use their intuitive and low-effort thinking styles (Haidt 2001). Only when they are asked why, do they seek to justify their judgment by using their analytic (high-effortful) thinking processes. Overall, Hume's alternative (sentimentalist) theoretical framework, therefore, claims that we, as a lawyer, try to justify our moral decisions rather than to seek the truth, as do scientists when making moral judgments. This is a direct critique of Kohlberg's rationalist view of moral judgment.

Another theoretical criticism is that the moral judgments scored as conventional level always correspond to traditional and conservative values, whereas those judgments scored as post-conventional level are mostly related to liberal values of justice and universalism. Haidt (2012) argues that this hierarchical approach is a natural result of the age of Enlightenment and thus is biased toward Western thinking style. However, according to Haidt and Kesebir (2010), this hierarchical approach suggested by Kohlberg is

simply wrong, because almost every moral principle that Kohlberg proposed has an evolutionary background and is present in every human being. However, the conservative moral values, scored as conventional level, are suppressed by political liberals (and the majority of Western people) by spending cognitive effort, and as a result, they perceive those foundations as morally irrelevant. However, when we look at the rest of the world (i.e., non-WEIRD cultures: Western, educated, industrialized, rich, and democratic cultures; Henrich et al. 2010), those who value universal principles of justice and fairness (i.e., post-conventional morality) constitute only a small minority (see also Shweder et al. 1997). Hence, the theory's view of liberal values as the top and hierarchically superior level of morality is substantially criticized, and it is thought that Kohlberg's theory of moral development is developed in a way that has a direct Western cultural bias. Apart from that, this hierarchical structure is criticized on its own. Rest (1979), for example, claims that some participants were moving backward in stages. However, since Kohlberg considers the development of cognitive development as related to moral development, he claims that the more the cognitive development increases, the greater the moral development.

Another criticism is related to alleged gender bias embedded in Kohlberg's theory of moral development. In the studies of Kohlberg, men generally score higher than women. However, Gilligan (1977) attributed this to the fact that the theory is constantly tested on male samples and that the higher levels are formed by principles such as justice that men value more. In fact, women often focus more on harm principles than on justice, but justice is considered as a higher moral principle in Kohlberg's classification.

In addition to this male-female discussion in terms of Kohlberg's theory of moral development, this can be seen as a methodological limitation as well since Kohlberg often conducted research with male participants. More importantly, however, Kohlberg sought to observe age-related changes using cross-sectional designs. In other words, one-to-one interviews with children of different ages were conducted to understand what

kind of differences there were between different ages instead of conducting longitudinal studies with the same participants. Although later Colby et al. (1983) conducted a 27-year longitudinal study showing that Kohlberg's theoretical approach is supported, there is still some controversy today regarding the validity of the methods used by Kohlberg.

In addition, some limitations of the method he used were later reported. For example, the moral dilemmas that are used are very artificial, which in turn might lead to a serious problem for ecological validity. Rosen (1980) reports that many of the dilemmas used by Kohlberg are very artificial. For example, the Heinz dilemma is very artificial for the children in the sense that the majority of the participants of Kohlberg range between 10 and 17 years of age, who have not been married and have never had a similar dilemma in their lives before. A second limitation of the scenarios used is the use of completely hypothetical scenarios. However, it is known that there can be discrepancies between hypothetical decision-making and real-life behavior, and the participants can sometimes report on the hypothetical scenarios that they will do things that people will not do in real life (Bostyn et al. 2018).

Conclusion

Kohlberg's theory of moral development can be considered as one of the first systematic – and empirically testable – theoretical approaches trying to understand the developmental stages of moral judgment, which is based on Piaget's moral theory. However, as outlined above, this approach is subject to substantial criticism from both the theoretical and the methodological perspectives and gives way to alternative theoretical approaches such as the moral foundations theory (Haidt 2012) and morality as cooperation theory (Curry et al. 2019). However, it is important to note that it maintains its claim to be the richest theoretical approach to date to explain especially how morality develops, which is lacking in the contemporary alternative theoretical approaches. In this respect, alternative theoretical approaches

that emphasize the developmental sequences of moral judgment are needed in the field of moral development.

Cross-References

- [Evolution of Morality](#)
- [Evolved Moral Foundations](#)
- [Morality](#)

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Theory of Reciprocal Altruism

- [Evolution of Cooperation](#)

Theory of Senescence

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Synonyms

[Aging](#)

Definition

The explanation of degradation to the body due to accumulated physiological defects that make an

individual increasingly susceptible to death at older ages as having evolved because natural selection is stronger earlier in life than later, resulting in (a) selection favoring genes that are beneficial during youth even if harmful later in life and (b) the accumulation of mutations that are expressed only at ages after which natural selection is too weak to remove them.

Introduction

Salmon breed once, after which they immediately die (Haldane 1941). Human women cease ovulating (and therefore reproducing) sometimes around 40 years of age but often live to twice that long (Hrды 2011). Some deep-water rockfish have lifespans longer than 200 years (Cailliet et al. 2001). These examples illustrate how diverse aging processes can be across species. Given that natural selection favors genes that enhance fitness, not those that reduce it, “The problem raised by senescence for evolutionists has been to devise a credible theory of this apparently deleterious phenomenon by natural selection” (Charlesworth 1980, p. 214). In 1952, the title of Medawar’s impactful article on aging was *An Unsolved Problem of Biology*. Holliday (2006), published an article titled *Aging is No Longer an Unsolved Problem in Biology* (see also Hayflick 2007). As these titles suggest, scientists now better understand how natural selection results in organisms that age, but some mysteries remain.

Meaning of the Term Senescence

Medawar (1952) distinguished between *aging*, by which he meant getting older in the sense of passage of time, and *senescence*, which he defined as the “change of the bodily faculties and sensibilities and energies which accompanies ageing, and which renders the individual progressively more likely to die from accidental causes of random incidence” (p. 12). Note that by this definition, age-related genetic diseases such as Huntington’s disease would be considered part of senescence, whereas pathogenic diseases such

as AIDS would be the “accidental causes” mentioned by Medawar. Some researchers have also included age-related reduction in fecundity as being part of senescence (Rose and Charlesworth 1980). Rose and colleagues (2012) provided another suggestion that fits well with the perspective of evolutionary psychologists when they defined aging as “neither more nor less than the deterioration of adaptation with adult age” (p. 3).

Reduced Selection Pressure with Increasing Age

Accepted theories of aging build on the insight of Ronald A. Fisher first proposed in 1930 that natural selection should be weaker on organisms as they become older. He based this conclusion on his idea of *reproductive value*: the number of offspring an organism of a specific age is expected to contribute to the next generation summing across the current age to the end of the expected lifespan. By this definition, reproductive value must decrease with age. Older individuals contribute fewer offspring during the remainder of their life, on average, than younger individuals to the next generation; therefore, selection acts with less force with increasing age.

Fisher did not relate the weakening of selection with age to the evolution of aging. This was done first, albeit superficially, by John B. S. Haldane in 1941. Peter B. Medawar, who received a Nobel Prize for unrelated work on organ transplants, provided the first thought-out argument on the matter in 1952. He built an argument that the strength of natural selection should vary across ages using a metaphorical population of potentially immortal test tubes. They are immortal in that they do not deteriorate with age (they are nonsenescent) but they may be killed (broken) by dangers in the environment. If the rate of death due to these dangers is constant across age, as is birth rate, then an age-structured population will result that consists of more young individuals and fewer elders. This is because as individuals get older their cohort will be smaller due to a larger proportion of their fellows having been killed. From this it is clear that even in a population without senescence, relatively fewer

older individuals are expected. Next, note that even though the rate of reproduction is the same for individuals of all ages, younger individuals will contribute more offspring to the next generation merely because there are more of them. Next, Medawar asks the reader to consider if sometimes individuals spontaneously died. Such a death would be a near complete loss of offspring production for young individuals but have little effect on how many offspring older individuals have. We can now see that a gene that caused spontaneous death would be much worse for the lifetime reproduction of younger than older individuals, and therefore that selection should be stronger for genes expressed in the young and weaker for genes whose expression does not happen until late life. In this scenario, selection would drive harmful genes to be expressed later in life (to the extent possible, see also Haldane 1941) until they are expressed at such a late age that so few animals lived sufficiently long for selection to matter.

William D. Hamilton (1966) showed that Fisher's reproductive value was not quite the right mathematical foundation for the evolution of aging. Hamilton's modified analysis identified two complementary *scaling factors* that are alternatives to reproductive value as ways of understanding how the strength of selection differs across age. The *survival factor* estimates how much selection can act on longevity for members of different age groups based on how much individuals in the age groups will contribute to the next generation. The *fecundity factor* estimates how much natural selection can work on the fecundity of different age groups. For Hamilton's factors but not reproductive value, in stable or increasing populations, the strength of selection is greater on younger than older age groups, but for shrinking populations with fewer younger individuals the strength of selection shifts to be stronger on older age groups. A notable feature of these forces is that with sufficient age they reduce to zero, meaning that selection no longer works on mortality or fecundity. Survival or fecundity rates need not themselves be zero, however, so Hamilton's scaling factors predict that aging should stop at sufficiently advanced age (Rose

et al. 2007). This counterintuitive finding has been demonstrated in evolution experiments using flies (Curtsinger et al. 1992) and in demographic data of humans (Vaupel et al. 1988).

Theories of the Evolution of Aging

Ultimate explanations of aging – how it evolved – differ from proximate explanations – how it occurs in the physiology of individuals during the lifespan. Numerous proximate mechanisms have been proposed, including wear and tear, toxin and metabolite build up, planned cell death, somatic DNA damage, free radicals, telomere depletion, and so on (Eisenberg 2012; Warner et al. 1987). Such proximate explanations, however, do not indicate why aging evolved. Moreover, ultimate mechanisms are relevant for species with specialized germ cells (reproductive cells) but not for species that reproduce by cellular fission such as protozoa which can be considered to live indefinitely (Bell 1984). Proximal theories make no such distinctions regarding germ line. Bell (1984) showed that this distinction is important and that evolutionary theories provide value beyond proximal explanations by demonstrating that age correlates with survival rates for invertebrates that reproduce via eggs but not those that reproduce by dividing their body. Comfort (1956) argued that aging is unrelated to evolution because wild animals rarely become elderly, but even in humans the effects of aging can be seen when people are in their thirties (Williams 1957).

Weisman (1891, as cited in Williams 1957) proposed the first theory of the evolution of aging. He argued on the one hand that aging was the same as the breakdown that occurs during mechanical wear and tear and on the other that a death mechanism evolved to remove the costs imposed by the elderly on the group. However, as Medawar (1952) points out, this logic is circular because it first assumes older individuals have aged then explains that aging evolved to remove those burdensome elders. Williams (1957) criticized the theory by arguing that cells are dynamic systems that can repair and replace themselves and so the analogy between aging and wear and

tear was weak at best. Regarding the death mechanism, Williams noted that not only has no death mechanism ever been found but also that Weisman's theory relies on population-level selection and so requires many assumptions that are complicated and therefore far from parsimonious (unlike his own proposal discussed below that relies on individual-level selection).

Haldane (1941) suggested that since selection cannot work after the end of reproduction (due for example to death), ages older than occur in nature have such reduced strength of selection that populations would build up harmful mutations that would be expressed at unnaturally advanced ages. Haldane mentioned this idea briefly, but Medawar (1952) developed it much more substantially. This theory is referred to as the *non-exposure to selection theory* (Nesse 1988) or *mutation accumulation theory* (Carnes et al. 2008). It argues that harmful mutations in germ lines (DNA that is passed to offspring) will not be eliminated by natural selection if they would be expressed only in relatively old individuals that live beyond the species lifespan in the wild. By this theory, when organisms are cared for and protected by their environment (like zoo animals or modern humans), they live unnaturally long lives and therefore express genes that cause aging that is unseen in wild animals. In short, this reduced or absent selection pressure at later ages allows harmful mutations to accumulate in a population. Haldane (1941) suggested that selection would favor modifier genes that postpone to a later age the expression of harmful mutations. Charlesworth (1980), however, argued that such modification seems unlikely given that the expression of mutations expressed late in life is rare and so the force of selection on their modifiers would be weaker than random sampling of genes or their harm might be offset by any beneficial pleiotropic effects.

Nonexposure to selection theory is widely acknowledged as accurate, but another theory is also considered accurate and to explain more aging in the world. It was also mentioned by Medawar in 1952. He suggested that selection would favor genes with beneficial effects early in life even if they had harmful effects later in life

because selection is stronger on younger than older individuals. This explanation, commonly referred to as *antagonistic pleiotropy*, was mentioned by Medawar only in passing but substantially developed not long after by George C. Williams (1957) in the very influential paper, *Pleiotropy, Natural Selection, and the Evolution of Senescence*. This paper, along with that of Medawar, inspired much of the research on senescence that would follow. Williams argued that selection would strongly favor genes whose effects increase the likelihood of survival or reproduction for a large part of an organism's lifetime reproductive capability – even if those same genes were harmful later in life. For example, a genetic effect that facilitated survival during birth has an impact on the whole of an organism's possible reproductive potential and so would undergo strong selection. By contrast, selection would be weaker for harmful genetic effects that arise later in life because they reduce the organism's likelihood of survival or reproduction for the relatively small fraction of the organism's total reproductive potential. The size of the effect of genes on fitness matters as well, but Williams's theory holds if some genetic effects will benefit organisms sufficiently in early life that they are maintained in the population despite fitness costs later in life. And it is these fitness costs later in life that correspond to the degradation of the body that we refer to as senescence.

William D. Hamilton (1966) did a mathematical analysis of factors related to mortality rates and concluded that his analyses were consistent with the arguments of Williams (1957). He also noted that most age-dependent effects are likely to be the onset of effects that continue rather than effects which are active and then deactivated later. He concluded from this analysis that “senescence is an inevitable outcome of evolution” (p. 12) and would be expected even in a population of initially immortal (nonaging) individuals. Those who reproduce earlier would produce a greater proportion of the offspring in the next generation, and so selection would favor earlier reproduction, with a result being that later-life harmful pleiotropic effects would occur (and produce aging).

Brian Charlesworth (1980) noted an additional way that the reduction in the strength of selection with increasing age could influence senescence. In a nonaging population (mortality rates are identical across ages), natural selection would more strongly favor genetic mutations that increase survival likelihood earlier in reproductive life as compared to later in life. This would result in mortality rates being lower earlier in life than later in life – even if the genes did not have harmful pleiotropic effects later in life. By this approach senescence would reflect youthful vigor rather than aged decline.

Thomas B. L. Kirkwood (e.g., Kirkwood and Rose 1991) addressed senescence in a manner complementary to the population genetics approach of Medawar (1952), Williams (1957), and Hamilton (1966). Kirkwood's approach – *disposable soma theory* – considers how an organism should optimally invest resources in body maintenance versus development or reproduction. The theory can be understood by considering various levels of investment in maintenance. At one extreme, the organism invests nothing in bodily maintenance, in which case its body would quickly die from the accumulation of unrepaired defects and bodily damage. The organism therefore should invest some in bodily maintenance. On the other end of the spectrum, an organism that invested exclusively in bodily maintenance might be able to repair all somatic damage and live agelessly. However, such an organism would increase its fitness if it instead invested slightly less in bodily maintenance and instead invested in growth or reproduction. Given this, organisms should invest some resources outside bodily maintenance. Considering organisms which invest less and less in bodily maintenance, a boundary arises where an organism would suffer from senescence if it invested any less in somatic maintenance. Disposable soma theory predicts that such an organism would be better off if it invested less in bodily maintenance than required to enable immortality. This is because such an organism will eventually die from environmental dangers anyways, and so some of the somatic investment would be wasted – and it could instead have been better invested in reproduction or

growth. The certainty of eventual death pushes the optimal amount of investment in somatic repair below that required for indefinite survival, freeing those resources for better use when the organism is more likely to be alive – that is, when it is younger. The common element in this theory and antagonistic pleiotropy is that, in effect, natural selection trades late survival for enhanced early fecundity.

The Apparent Anomaly of Human Post-reproductive Survivorship

Both Williams (1957) and Hamilton (1966) noted that humans outlive basic theoretical predictions that senescence should result in death once an individual can no longer reproduce, as occurs dramatically in salmon (Haldane 1941). Williams and Hamilton explained the extended survivorship as likely resulting from assistance provided by parents and grandparents – an idea now referred to as the *grandmother hypothesis* (Hawkes et al. 1998). Another explanation is that humans invested in *embodied capital* by spending substantial time during an extended adolescence to master how to hunt and gather successfully in the local ecology, an early life investment that pays later in life (Kaplan et al. 2000). Hill and colleagues (Hill et al. 2007) suggest that grandmothing and extended niche-specialization have as a prerequisite an extended adult survivorship, which they suggest is due to human-reduced extrinsic mortality resulting from “food sharing and care of sick and injured individuals” (p. 453). This is consistent with the suggestion of Rose and colleagues (2007) that the evolution of human intelligence allowed us to avoid some early life sources of mortality and thus live longer, resulting in selection for a longer life span, which in turn increased the strength of selection at later ages – thus resulting in a positive feedback loop. This process is unlikely to have occurred in other species and is analogous to humans artificially selecting themselves for longer lives like scientist Michael Rose has done with flies. The evolution of human senescence is still an active area of investigation without a clear consensus.

Evidence

A review of genetics related to aging indicated that numerous genes have been identified that influence lifespan (Moskalev et al. 2014). A common feature of these genes is that they are involved in response to stress. For example, some “genes promote growth and reproduction while suppressing stress resistance” (p. 1071), a trade-off predicted by antagonistic pleiotropy theory. Other genes are responsive to ecological factors including crowding, food availability, temperature, light, and radiation. Still others are involved in dealing with toxins, immunity, basic cellular function, metabolism, and so on. Many of the types of factors for which these genes have evolved thus fit within expectations of antagonistic pleiotropy theory of aging because they are important for survivorship, especially early in life.

In a review of the biological literature, Brian Charlesworth (1980) found support for aging-related effects consistent with weaker selection with advancing ages (Hamilton 1966). First, aging is found in species that separate soma and germ cells but not for example in plants that reproduce vegetatively (Bell 1984). Second, species with greater external mortality tend to age faster. Third, species in which fecundity increases with age, such as in reptiles, sometimes have longer lifespans. Fourth, senescence starts immediately following reproductive maturity. However, survivorship should reduce quickly after reproduction ends due to mutation accumulation, but human females live after menopause. As mentioned above, various explanations have been proposed for this anomaly, such as the grandmother hypothesis. Nesse (1988) compared survivorship across ages with expected survivorship without senescence (i.e., using a constant mortality rate) for various species, and a substantial number of species showed clear evidence of senescence related to antagonistic pleiotropy but none provided clear evidence for mutation accumulation.

Perhaps the strongest evidence in support for the antagonistic pleiotropy theory of aging comes from experimental research with flies by Michael R. Rose and Brian Charlesworth. As reviewed by Kirkwood and Rose (1991), in selection

experiments, one population of *Drosophila* flies were allowed to reproduce without manipulation, whereas in another population the only eggs allowed to be fertilized were those produced late in the lifespan, which notably progressed to older ages over generations. Such experiments showed that experimental selection can indeed extend lifespan, in one case by 29 % over 15 generations, and females in that group reduced the number of eggs laid early in life and increased the number laid in later life. The population selected for old age showed decreased egg production early in life but increased resistance to various stressors, such as starvation, drying out, and environmental alcohol. They could also fly further. Kirkwood and Rose interpret these findings as supporting antagonistic pleiotropy because the health benefits are offset by reduced fecundity early in life.

Conclusion

Theories of the evolution of aging are based on the idea that the strength of selection weakens with increasing age. One theory of the evolution of aging is that mutations that are expressed only at unnaturally old ages would build up in a population and cause aging for individuals living in safer environments. A more prominent theory is that genes that have beneficial effects early in life but harmful effects later in life will be favored by selection and so become common. The later theory has garnished substantial support. In short, natural selection favors investments in the body and reproduction early in life at the cost of later-life survival because organisms are less likely to be alive at later ages.

Cross-References

- ▶ [Age](#)
- ▶ [Disposable Soma Theory](#)
- ▶ [Extrinsic Mortality](#)
- ▶ [Fisher's Reproductive Value](#)
- ▶ [George C. Williams](#)
- ▶ [Grandmother Hypothesis](#)
- ▶ [Grandmother Hypothesis, The](#)

- ▶ [Increased Grandchild Survival](#)
- ▶ [Life History Theory](#)
- ▶ [Menopause Affords Grandparental Investment](#)
- ▶ [Mothers and Maternal Grandmothers and Childhood Survival](#)
- ▶ [Mutation](#)
- ▶ [Mutation Accumulation Theory](#)
- ▶ [Oxidative Stress and Free Radicals](#)
- ▶ [Pleiotropy](#)
- ▶ [Senescence](#)
- ▶ [Telomere Depletion](#)
- ▶ [William Hamilton](#)

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Theory of the Descent

- ▶ [Jean-Baptiste Chevalier de Lamarck](#)

Theory of War

- ▶ [Evolutionary Theory and the Causes of War](#)
- ▶ [War More Likely with Higher Likelihood of Success](#)

Therapeutic Touch

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Synonyms

Biofield therapies

Definition

An alternative therapeutic intervention, which purports to manipulate the energy field of the client through a non-touch technique for relieving the distress.

Introduction

Therapeutic touch is a therapeutic procedure that has been in use for the past few decades. It is a therapy from the alternative system of medicine (O'Mathúna 2016). This technique was developed by Dolores Krieger and Dora Kunz (Straneva 2000). During the “therapeutic touch” procedure, the therapist move his/her hand over the body of the patient to manipulate the energy field and restore the balance of the surface energy field (O'Mathúna 2016). The word “therapeutic touch” is a misnomer, as, during the procedure, there is no actual skin to skin (body to body) contact between the therapist and the client; however, there occurs contact between energy fields of the therapist and client. It is also known as an energy-based treatment modality. It has been considered as an important intervention modality intended to provide holistic care in nursing practice (Hanley et al. 2017). Therapeutic touch is often used for facilitating subjective well-being, comfort, and relaxation to patients with various illnesses (Engebretson and Wardell 2007; Meehan 1998). It has been recognized as a complementary therapy by the National Center for Complementary and Alternative Medicine.

Basis of Therapeutic Touch

Existing evidence explaining the mechanism of action of “therapeutic touch” is not well understood by the current scientific knowledge. Explanations and claims regarding “therapeutic touch” by the therapists and clients still remain controversial due to its nonscientific nature (Meehan 1998). The theoretical explanations about therapeutic touch center around manipulation of energy field of the body of the client by the therapist (Umphred 2013). As per the existing explanatory models, the human body has an open energy field, which remains balanced in state in a healthy individual due to equal distribution in a biological symmetrical body. From this perspective, any imbalance in the body's energy field results in development of illness/disease (Umphred 2013). The ancient Indian as well as Chinese system of medicine emphasizes the existence of a body energy system and its relevance in maintaining the healthy body and mind. On this basis, therapeutic touch technique was founded and gained its popularity.

Clinical Use of “Therapeutic Touch”

The therapeutic touch technique has been used in treatment of various physical illnesses, ranging from wound care to pain, cardiovascular diseases, cancer treatment, as well as terminal illnesses (Monroe 2009; O'Mathúna 2016; Snyder 1997; Tabatabaee et al. 2016; Umphred 2013). In pain management, therapeutic touch was found to be effective, and as there are no risks associated with it, it may be considered as a useful therapeutic intervention in pain management (Monroe 2009). This therapy has been found effective for symptom relief and is hypothesized to work upon the immune system and improve the immune functioning although it is important to note that the evidence for such an effect is not very concrete (Jain et al. 2015).

Similarly, therapeutic touch has been studied in patients with anxiety disorder. A Cochrane database review revealed that the existing evidence in support of therapeutic touch is not sufficient and emphasized that extensive research with sound

methodology is necessary to provide evidence of its efficacy (Robinson et al. 2007). Nevertheless, some evidence suggests that therapeutic touch has been effective in alleviating the mood symptoms and emotional problems among otherwise healthy women with respect to objective standardized inventories and biomarkers (Lafreniere et al. 1999).

Process of Therapeutic Touch

The process of “therapeutic touch” is a soft, non-invasive general and sophisticated approach. It is individualized to meet the needs of the healing partner (client in need of healing). The process of how the therapeutic touch intervention is purported to occur is by transferring of the energies (field of energies that normally surround bodies of living organisms) (Fig. 1). The therapist, who is trained and certified to perform the therapeutic touch, performs this therapy. They attempt to alter the paradigm of their consciousness to enable their hands to pattern the energies of the sick or painful body part. The procedure requires the healer to stand or sit and the client to lie down or sit in relaxed state. The therapist first assesses the energy patterns by moving his/her hands over the receiver from 2 to 6 inches away from the body. Then, the therapist makes hand movements for correcting the imbalance in energy fields so that the energy can flow freely and heal the person internally (Umphred 2013). During the process, the therapist (healer) sweeps the energy over the

body from the area where it is congested. This particular activity is known as “unruffling the energy field” (Umphred 2013). These therapies usually last 20 to 30 minutes followed by a period of rest. By therapeutic touch procedure, the therapist creates a conducive environment which facilitates the process of healing.

Phases of Touch Therapy

The procedure of touch therapy encompasses of the following phases:

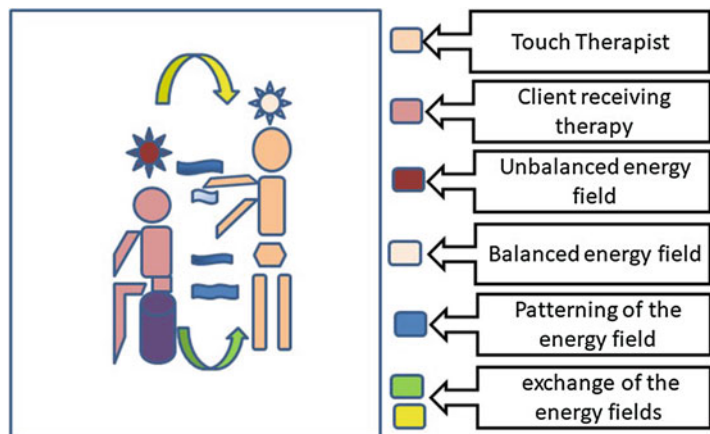
- 1. Centring
- 2. Assessing
- 3. Intervention balancing and rebalancing
- 4. Evaluation and closure

Centring: To bring one’s energy awareness by meditation, guided breathing, imagery, and changing their energy fields to bring a conscious change.

Assessing: Here the therapist assesses the changes in the pattern of the energies by moving his/her hands in 2–6 inches above the body from the head to feet following a rhythm and symmetrical manner. Therapists have reported the feeling of warmth, tingling, and presence of blockade, pulling, and coolness during assessment of clients, which purportedly indicates that deviations in the energy systems are present.

Intervention balancing and rebalancing: In this phase the therapist balances the energy fields

Therapeutic Touch,
Fig. 1 Depiction of a
typical “touch therapy”
session



as per assessment and balances the excess energies and restores lost energy. They make sweeping movements over the areas affected.

Evaluation/closure: The therapist intuitively decides (using their professional expertise) when to terminate the session. The ongoing assessment of the energy fields and continuous feedback from the individuals determine the end of the therapy (Koopsen and Young 2009).

Conclusion

Therapeutic touch is one of the important interventions practiced by nurses as a part of the holistic therapies. It considers individuals as a whole and as having potent ability to heal oneself. Although there is lack of strong scientific evidence on the mechanism of action of the therapy, it has shown promising results in managing pain and promoting healing. There is need of extensive research to understand the basis of this therapy.

Cross-References

► Touch

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Thermal Processing of Food

► Brain Evolution Resulting from Cooking

Thermodynamics

► Psychological Determinism

Thermometer

► Regulation of Body Temperature

Thermoregulation

- Body Temperature Regulation
- Regulation of Body Temperature

Thirteen Misunderstandings About Natural Selection

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Introduction

The theory of evolution by natural selection is the unifying paradigm of biology and indeed of all the life sciences – it explains and integrates a huge diversity of known findings and predicts an astonishing number of new ones (Alcock 2009; Coyne 2009). It has been famously suggested that nothing in biology makes sense except in the light of evolution (Dobzhansky 1973). Prominent philosopher Daniel Dennett has said “If I were to give an award for the single best idea anyone ever had, I’d give it to Darwin, ahead of even Newton and Einstein and everyone else” (Dennett 1996, p. 21). Indeed, scientists, historians of science, and philosophers of science generally regard evolutionary theory as one of the most predictively powerful and explanatorily successful theories in the history of science (Alcock 2009; Coyne 2009; Dawkins 2009; Dennett 1996).

And yet, despite the simplicity of the core idea and its universal acceptance in the scientific community (e.g., Pew Research Center 2015), misunderstandings regarding natural selection abound. Such misconceptions even appear in college textbooks and among students who have taken college-level evolutionary biology courses (Alters and Nelson 2002; Gregory 2009; Nehm and Reilly 2007; Nehm et al. 2008; Winegard et al. 2014). A review of ten textbooks in social psychology revealed at least one factual error

about inclusive fitness theory in *each*, and typically two to three (Park 2007). In this entry, we briefly identify and dispel 13 of the most pervasive misunderstandings of evolutionary theory.

Misunderstanding 1: Natural Selection Is a Random, Chance-Driven Process

Probably the most pervasive misunderstanding about natural selection is that it is a chance process.

In simplified form, evolution takes place in two steps: mutation and natural selection (in reality, the process is more complicated than this). In the first step, random genetic mutations arise. These mutations may turn out to be beneficial, detrimental, or neutral. This step is random, involves no foresight, and does not take into account what the organism “needs” or would benefit from. Indeed, more mutations turn out to be detrimental than beneficial. In the second step, mutations with harmful effects on reproduction are filtered out by natural selection, which acts like a sieve (Dawkins 1982). By contrast, those that have beneficial effects on reproduction are more likely to be passed on and increase in frequency over time.

This second step is quintessentially *non-random*: some mutations make it past natural selection’s filter precisely because they are beneficial, and others fail to make it past the filter precisely because they are harmful. This is the opposite of randomness: it is an orderly and predictable process in which there is a logical connection between the effect a mutation has and its likelihood of making it past the filter of natural selection. By contrast, a random process would be unpredictable and would have no systematic connection between the effects of a mutation and its likelihood of making it into the next generation.

The problem seems to be that people sometimes confuse mutation (which is random) with natural selection (which is not random). To make matters worse, they may conflate one or both of these processes with evolution, which is the *outcome* of these processes (see Misunderstanding #11 for more detail on the distinction between evolution and natural selection).

To avoid these errors, it helps to remember that natural selection is the *nonrandom sorting of randomly mutated genes*. Finally, because natural selection is not random, the process it drives – evolution – is also not random.

The misunderstanding that natural selection is a chance process is particularly pernicious because of its downstream effects. It is nearly impossible that a random, chance-driven process could explain the complexity, utility, and apparent purposiveness of the adaptations we see in the biological world. As a result, falling into the erroneous belief that natural selection is a random process might lead some people to reject evolution altogether on the basis of a conceptual mistake.

Misunderstanding 2: Natural Selection Is Primarily About Survival

It is common to think of natural selection as being primarily about survival, but in truth, it is primarily about reproduction. *Differential reproductive success* – not survival – is the driving engine and the “bottom line” of evolution. It is possible to illustrate this point using both logic and empirical evidence.

To illustrate the point logically, imagine two genes, each of which has two distinct effects (these are called “pleiotropic effects”). Gene A leads the animal in which it resides to live to be 100 years old, but makes it infertile. Gene B leads the animal in which it resides to die at 25 years old, but after having had several offspring. Which gene will have greater representation in the next generation? The answer is that gene B will be well represented, whereas gene A will be entirely absent. This thought experiment helps to demonstrate that when the two conflict, reproduction trumps survival.

It is also possible to illustrate empirically that when survival and reproduction conflict, survival takes the backseat. Examples abound. The peacock’s tail is a massive burden to survival but is crucial in seducing peahens (Darwin 1871; Cronin 1993). Human testosterone is a powerful immunosuppressant but human females are attracted to

testosterone-dependent traits such as a strong jawline and a high shoulder-to-hip ratio (Buss 2015; Al-Shawaf & Lewis 2018). Male redback spiders willingly offer themselves to their mates for cannibalization – they die, but in doing so, they double their paternity relative to noncannibalized males (Andrade 1996, 2003).

In other words, when it comes to evolution, reproduction is more important than survival. Many species take this to an extreme, living only long enough to reproduce and then dying immediately thereafter. This is so common in nature that the phenomenon has a recognized name – *semelparity* – and examples of species that do it range from desert agave plants to butterflies to bamboo plants to Pacific salmon (Quammen 1985). Perhaps even more morbid are those species that successfully reproduce – only to be promptly devoured by their offspring. The matricidal gall midge *Miastor* does this, producing larvae that eat it alive from the inside out (Quammen 1985). The key point is that in evolution, survival is important only insofar as it eventually leads to reproduction. Both logical thought experiments and an abundance of empirical examples illustrate that when survival and reproduction conflict, it is invariably reproduction that wins (Alcock 2009; Dawkins 1976; Hamilton 1964; Williams 1966).

Misunderstanding 3: “Natural Selection” Refers to an Agent That Actively “Selects” the Best Organisms for the Next Generation

“Natural selection” is an unfortunate misnomer. It gives the impression that some kind of causal agent is actively “selecting” traits for inclusion in the next generation. Nothing could be further from the truth: there is no agent and there is no selection. Stated differently, there is no guiding hand in the process of natural selection – the process is blind, mechanistic, and passive.

“Differential reproductive success by virtue of heritable differences in design” is a much more accurate description of the process: some organisms reproduce more than others, and this simple

fact is the key driver of evolution by natural selection. But because “differential reproductive success” is a mouthful, scientists and laypeople alike often use “natural selection” as shorthand. That is perfectly fine as far as it goes, but it is helpful to remember that this is just shorthand for a longer and more cumbersome phrase.

In sum, “differential reproductive success” is a little wordy, but it is more accurate in that it (a) describes what is actually occurring, (b) does not suggest the presence of a hidden causal agent, and (c) does not misleadingly imply some form of active selection. It may therefore be beneficial for readers and writers to bear in mind that “natural selection” is a linguistic shorthand rather than a descriptively accurate term for the process that drives evolutionary change.

Misunderstanding 4: Natural Selection Is Teleological – It Is Working Toward a Goal or Final Purpose

Natural selection does not have a final goal or *telos*. It also has no foresight – in other words, it is impossible for natural selection to take into account future conditions. Though the products of selection can be beautiful and complex, the process itself is blind and mechanistic.

For example, if a certain species of mammal would benefit from evolving a slightly thicker coat of fur, this does not mean that natural selection will guide it toward that goal. First, a beneficial mutation must arise that contributes to said trait. This stage of the process is entirely random and is not affected by what the animal “needs” or would benefit from. In fact, harmful mutations are much more common than beneficial mutations (because there are many more ways to disrupt a functioning biological machine than to improve it). Second, if the new mutation happens to confer a survival or reproductive advantage, natural selection will favor it, and it will tend to increase in frequency as the generations pass. But it is impossible for natural selection to *anticipate future needs* and lead species toward a distant goal state, as natural selection cannot look ahead and does not have goals.

Nor does natural selection inevitably lead to “progress” in the sense of greater intelligence or greater complexity. A common misconception is to think of evolution as progressive – always improving or moving toward greater complexity. In reality, there is no predetermined direction to evolution. Natural selection can easily cause a species to lose complexity when the environment demands it (see e.g., Misunderstanding #6 and Al-Shawaf and Zreik 2017). For example, several species have slowly evolved to lose their sight after moving into pitch-black caves. Since sight is no longer useful in such an environment, natural selection led these species to lose their vision and channel the metabolic resources previously used for sight to other physiological needs such as immune function or cell repair.

Natural selection is a tinkerer, not an engineer (Jacob 1977). An engineer can look ahead to her final goal and implement changes that help her get closer to that final goal. She can also return to the drawing board any time she pleases to fix a mistake. By contrast, natural selection cannot look ahead, has no goal, and can only build adaptations based on the genetic variants already available in the population at the time. In short, natural selection has no *telos* or endgame.

Misunderstanding 5: Natural Selection Favors the Survival of The Species

One of the most common misconceptions about evolution is that natural selection favors the survival of the species. In reality, natural selection works primarily at the level of the gene and the individual bodies in which genes reside – not at the level of groups, subspecies, or species (Hamilton 1964; Williams 1966).

George Williams, one of the most important evolutionary biologists of the twentieth century, showed several decades ago that group selection is theoretically possible – but likely to be extremely rare in nature. For group selection to work, several preconditions must be in place – and these preconditions are themselves very rarely met in nature (Williams 1966). Recent years have witnessed a resurgence of interest in group

selection (e.g., Wilson and Sober 1994; Henrich 2004), but most evolutionary biologists and psychologists agree on the following: (1) group selection is theoretically possible, but (2) genic-level and individual-level selection are considerably stronger than group-level selection, (3) there is no clear empirical evidence that group selection applies to humans, and (4) group selectionist thinking does not appear to have led to any testable new hypotheses (Delton et al. 2011; Krasnow et al. 2012, 2015, 2016; Krasnow and Delton 2012; Pinker 2012). By contrast, orthodox genic-level and individual-level selectionist thinking have led to many hundreds of testable hypotheses, which have in turn led to thousands of empirical studies. This suggests that, unlike genic-level and individual-level thinking, group selectionist thinking may not be especially generative or fruitful as a scientific theory (Alcock 2017).

An important sidenote is worth mentioning: even if group selection turns out to be more widespread in nature than we previously thought, it would still not be the case that adaptations evolve for the good of the *species*. Even dyed-in-the-wool group selectionists are primarily focused on small, local groups – not whole species. It is therefore incorrect, for example, to think we have sex “to perpetuate the species”. We have sex because we are the descendants of ancestors whose sex led to reproduction, and so we inherited their tendency for sexual motivation. An incidental side effect of this is that the species as a whole may sometimes benefit. Outcomes that are beneficial to groups can indeed occur, but they are not the proper biological function of adaptations, they are incidental side effects.

Misunderstanding 6: Natural Selection Builds Perfectly Designed Biological Mechanisms

There are several constraints that limit natural selection’s ability to craft optimally designed mechanisms. These include (a) time lags, (b) historical constraints, (c) constraints due to available genetic variation, (d) unavoidable trade-offs, (e) imperfections at one level due to

selection at a different level, (f) mistakes due to environmental unpredictability, and (g) antagonistic pleiotropy (Al-Shawaf and Zreik 2017; Dawkins 1999). We highlight only three of these in this entry: time lags, historical constraints, and unavoidable trade-offs (for a more thorough discussion, see Al-Shawaf and Zreik 2017).

Time lags refer to the fact that natural selection is a slow and gradual process. Animals are adapted to *past* environments, not current environments (Dawkins 1999). If the environment changes rapidly, natural selection may be too slow to catch up. For example, human taste preferences for fat, sugar, and calorie-dense foods were adaptive when food was scarce during the evolution of our species. By contrast, in today’s world of cheap and ubiquitous fast food, these same taste preferences lead to obesity, type II diabetes, and cardiovascular diseases (Buss 2015). The environment has changed too quickly for the slow, cumulative process of evolution to catch up. Time lags have rendered our previously adaptive taste preferences maladaptive.

A second important constraint on natural selection comes from a species’ *evolutionary history*. Once a species has evolved a certain nervous system or body plan, this constrains what it is capable of evolving next. Given their current body plan, it would be difficult or impossible for elephants to now begin to evolve wings, say, or an exoskeleton. Once a species finds itself on a certain evolutionary trajectory, this limits where it can go next. In other words, the phylogenetic background of a species affects what it is capable of evolving next – history constrains evolution.

Unavoidable trade-offs impose a third constraint on natural selection. Gazelles under predation pressure from wolves may evolve longer legs, enabling them to run faster and increasing their likelihood of escape. But longer leg bones are more brittle and more likely to break. The gazelles therefore face an unavoidable trade-off: longer, more gracile bones with enhanced capacity to flee but increased likelihood of breaking, or shorter, more robust bones with a lower likelihood of escape. The key point is that every adaptation comes with a cost, and this leads to unavoidable trade-offs. Trade-offs, in turn, make it impossible to optimize every parameter simultaneously.

These constraints, along with several others, make it impossible for natural selection to build perfectly designed biological mechanisms (see Al-Shawaf and Zreik 2017; Dawkins 1999, for an extended treatment of the constraints on natural selection). It is because of these constraints on natural selection that we are left with suboptimal designs such as the vertebrate eye (which has a blind spot) and the human esophagus and trachea (whose inelegant setup poses a serious choking hazard). Natural selection can build complex and functional mechanisms. It can even build mechanisms so sophisticated and impressive that engineers are studying them in an attempt to replicate their structure and function in artificial systems (e.g., the luminescence of fireflies, the sonar of bats, and the adhesive abilities of geckos; Bhushan 2009; Kim et al. 2012; Murr 2015). Nonetheless, despite these impressive feats, the constraints on natural selection limit its ability to craft truly optimal biological mechanisms.

Misunderstanding 7: Evolution Implies Genetic Determinism

One of the most widespread misunderstandings is that *evolution implies genetic determinism*. That is, many are under the impression that naturally selected behaviors or psychological mechanisms are genetically determined – that the claim “X is a product of natural selection” is equivalent to the claim “X is genetically determined.” It is emphatically not.

First, evolution by natural selection is an environmentally driven process, and it would not exist at all without the environment. Adaptations (the products of natural selection) require environmental input at every stage of their emergence: (a) initial evolution, (b) ontogenetic development, and (c) immediate activation (Buss 1995). Stated differently, adaptations only evolve in the first place because of an environmental challenge, often referred to as an “adaptive problem” (Buss 1995; Tooby and Cosmides 1992). Subsequently, adaptations require environmental input for their proper development during an organism’s lifespan. And finally, adaptations require environmental

input for their immediate activation in the present. This means that the environment is crucial to every product of evolution at every stage of the evolutionary process.

The second problem with the idea that natural selection implies genetic determinism has to do with the fact that nothing is determined by genes or environment alone. Genes and environment, working together, jointly codetermine every aspect of an organism – from its ears to its personality. Neither genes nor environment is capable of doing this alone. After all, genes are like a recipe for making a body, and environmental input is like the raw ingredients. The ingredients alone are impotent, and the recipe alone is equally impotent (e.g., Dawkins 1976; Ridley 2003). As such, no credible scientist thinks the products of evolution are genetically determined, and the claim that a psychological mechanism is a product of natural selection is *not* in any way equivalent to the claim that it is genetically determined.

It might be worth adding here that the often-misunderstood concept of *heritability* (percentage of variance in a phenotypic trait due to genetics) does not refer to a single individual; it refers to how much of the *differences* between individuals are due to *differences* in their genes as opposed to *differences* in their environments. For example, if the personality trait of extraversion has a heritability of 60%, this does not mean that Bob’s extraversion is 60% due to his genes and 40% due to his environment. Instead, it means that 60% of the *differences* between individuals in their extraversion is due to differences in their genes, and 40% is due to differences in their environments. For a single organism, every single trait is jointly codetermined by genes and environment. This even includes traits with 0% heritability or 100% heritability – there is simply no other way to build an organism. Stated differently, we must distinguish between two levels of analysis: the individual level (in which we are concerned with individual organisms) and the population level (in which we are concerned with the differences between organisms). Partitioning an outcome like height, IQ, or extraversion into percent due to genes and percent due to environment is meaningful at the population level of analysis but

meaningless at the individual level of analysis. A quip by Donald Hebb illustrates this point well: when asked whether nature or nurture makes a greater contribution to personality, he replied, “Well, which contributes more to a rectangle’s area – its length or its width?” (Meaney 2001).

In sum, there are two key points about the relationship between evolution, genes, and environment. First, environmental input is essential to the emergence and activation of all evolved mechanisms. Second, genes and environment jointly codetermine everything from an organism’s morphology to its behavior. For both of these reasons, it is wrong to think that evolution bears any relationship to genetic determinism.

Misunderstanding 8: Adaptations Must Be Present at Birth (or Must Emerge Very Early in Life)

An odd but widespread assumption is that adaptations – the products of natural selection – must be present at birth or must emerge very early in life. Features not present early in life are automatically assumed to be “learned,” not the product of natural selection. One key problem with this line of reasoning is that it mistakenly pits learning and evolution against each other as if they are competing explanations, when in fact they are not (for an extended discussion of the compatibility between learning and evolution, see e.g., Al-Shawaf et al. 2018; Lewis et al. 2017; Symons 1979; Tinbergen 1963). The other key problem is that there is simply no basis for the arbitrary assumption that the products of natural selection must be present at birth.

Teeth and breasts illustrate what is wrong with this principle: they are both adaptations *par excellence*, but they are not present at birth. Instead, they emerge at the appropriate developmental stage of the organism’s life. Natural selection builds adaptations that emerge at the correct point in ontogenetic development, not adaptations that are necessarily present at the moment a baby is born. Teeth and breasts (and pubic hair and facial hair, etc.) emerge later, when they are

needed, during the appropriate life stage. The same goes for walking and bipedalism: newborn infants cannot walk, but nobody doubts that bipedalism is a biological adaptation. Similarly, nobody doubts that flight or vision are exquisite biological adaptations, despite the fact that many newly hatched bird offspring can do neither.

In sum, adaptations – the products of natural selection – can “come online” during the prenatal phase, shortly after birth, or much later in life. There is no theoretically principled reason to stipulate that they must be present at birth. That is not how natural selection works – it works to produce adaptations that come online during the developmental phase in which they are needed, not ones that are present at a particular arbitrarily selected moment.

Misunderstanding 9: The Products of Evolved Mechanisms Are Fixed and Unchangeable

A key misconception is that if a certain behavior is the output of a mechanism built by natural selection, it is fixed and unchangeable. For example, people worry that if there is evidence of an evolutionary basis for aggression, warfare, or sexual infidelity, this somehow means that these undesirable outcomes are inevitable.

In reality, evolved mechanisms are flexible and their outcomes are rarely fixed. All evolved mechanisms require environmental input. Often, changing the input is enough to change the output. For example, all humans have callus-producing mechanisms in their hands. These evolved physiological mechanisms are designed to produce calluses in response to repeated friction of the skin. But this does not mean that the outcome – calluses – is unavoidable: simply remove the friction by wearing gloves, and these mechanisms will no longer produce calluses. By modifying the input, you have successfully changed the output (Buss 2015).

Behaviors produced by natural selection are no more fixed or set in stone than calluses. Indeed, evolved psychological mechanisms are exquisitely context-dependent and environmentally

sensitive (see Al-Shawaf et al. 2018, for an extended treatment of the centrality of context in evolutionary psychology). Even if socially undesirable behaviors such as aggression, warfare, or romantic infidelity have an evolutionary basis, this does not mean that we are stuck with them forever. Indeed, a wealth of evidence shows that war, violence, and other forms of aggression have been steadily declining throughout human history (Pinker 2011). In fact, our best chance of changing or eliminating socially undesirable behaviors will come from understanding them more deeply. Only when we understand the inputs, evolved decision rules, and outputs involved in an undesirable outcome will we have the information necessary to try to change it.

Misunderstanding 10: You Can Use the Principles of Natural Selection to Bypass the Psychological Level of Analysis and Predict Behavior Directly

It is common to think – especially among evolutionists who do not have a background in psychology – that there is nothing wrong with going directly from the principles of natural selection to predictions about behavior, skipping the psychological or information-processing level of analysis. But skipping the level of psychological adaptations – the information-processing machinery built by natural selection – can lead one astray (Cosmides and Tooby 1987).

Consider incest aversion. Studies suggest that the mind uses a few key cues during childhood to tag individuals as siblings, marking them as unsuitable sexual partners. Chief among these are childhood co-residence (years spent growing up with the other child in the same house) and maternal perinatal association (if you are the older sibling, observing your mother breastfeeding the other child). The human mind uses these two key informational inputs to tag someone as a sibling and consequently produces incest aversion at the thought of having sex with them. Normally, siblings encounter these cues during childhood and nonsiblings do not. But sometimes there is a mismatch – and these mismatches are revealing. For

instance, in the phenomenon of Taiwanese minor marriages, a young female child is betrothed to a young male child, and they are both raised by the boy's parents in the boy's parents' house. Because they grow up together in the same household (childhood co-residence), their brains mistakenly tag each other as siblings, producing incest aversion. As a consequence, the individuals involved in Taiwanese minor marriages report less sexual interest in one another, lower fertility rates, lower relationship satisfaction, and higher divorce rates (Lieberman et al. 2007; Lieberman and Symons 1998). In essence, the mind mistakenly coded a nonrelative as a sibling because it received the key informational input of childhood co-residence (Lieberman et al. 2003, 2007).

This process can fail in the opposite way, too: genetic siblings who do not receive the key informational inputs of childhood co-residence and maternal perinatal association may fail to psychologically tag each other as siblings, leaving open the possibility of being sexually attracted to each other later in life. This is exactly what happened to some siblings who were separated at birth, grew up apart, and later in life found each other and fell in love (Childs 1998). This outcome makes no sense unless you take into account the information-processing level of analysis. If you attempt to go directly from the principles of natural selection to behavior, the phenomenon appears incomprehensible – they are genetic siblings, so why are they sexually attracted to each other? By contrast, if you *do not* skip the information-processing level of analysis, the difficulty immediately disappears: these siblings were reared apart, so their minds did not receive the key informational inputs needed to produce incest aversion. That is why they are capable of being sexually attracted to one another.

In short, if you leapfrog the psychological level of analysis and attempt to go directly from the principles of natural selection to statements about behavior, you will make mistakes in both prediction and explanation (Cosmides and Tooby 1987). This brings to mind two quotes from foundational evolutionary thinkers, one by Donald Symons and the other by John Tooby and Leda Cosmides. To paraphrase Don Symons, the

evolutionist should focus on psychology and information processing. When he ignores these in favor of observable behavior, he is like the drunk looking for his key under the lamppost: he knows he dropped it in the dark, but under the lamppost the light is better (Symons 1979).

And as Tooby and Cosmides wrote so eloquently, “The fact that the brain processes information is not an accidental side effect of some metabolic process. The brain was designed by natural selection *to be* a computer. Therefore, if you want to describe its operation in a way that captures its evolved function, you need to think of it as composed of programs that process information” (Tooby and Cosmides 2005, pp. 16–17). In short, if you want to maximize the accuracy of your evolution-based predictions and explanations, you would do well not to skip the information-processing level of analysis.

Misunderstanding 11: Natural Selection Is the Only Driver of Evolutionary Change

Another important misconception is that natural selection is the only driver of evolutionary change. A variant of this misunderstanding is the erroneous belief that the terms “evolution” and “natural selection” are more or less interchangeable.

In reality, evolution is the *outcome*, and there are four evolutionary forces that drive it: mutation, genetic drift, gene flow, and natural selection (e.g., Futuyma and Kirkpatrick 2017). Mutation is a random heritable change in a gene or chromosome and constitutes part of the raw material on which natural selection works. Genetic drift is the random, chance-driven change in allele frequency from one generation to the next. Gene flow, sometimes called admixture or migration, is the movement of genes from one population to another. Natural selection, the fourth evolutionary force and the subject of this entry, is most accurately described as nonrandom differential reproductive success (see Misunderstandings #1 and #2).

To be clear, while natural selection is not the only driver of evolutionary change, it is a key one – and most scientists agree that it is the most

important one (Alcock 2009; Dawkins 1976; Dennett 1996; Williams 1966). It is also the *only* evolutionary force capable of fashioning adaptations or creating the appearance of design, the explication of which is the central explanatory task of evolutionary biology (Darwin 1859; Williams 1966).

This is an important point: while there are four different evolutionary forces, only one of them – natural selection – can create adaptations designed to solve environmental problems. The other three forces can cause evolution – defined as a change in allele frequencies in a population over time – but only natural selection can fashion complex specialized mechanisms like the porcupine’s quills, the turtle’s shell, or the angler fish’s bait, all exquisitely designed to solve key environmental problems in these animals’ lives.

In sum, natural selection is only one of four evolutionary forces, but it is the only one capable of fashioning adaptations.

Misunderstanding 12: Evolutionary Hypotheses Are Primarily Post-Hoc Storytelling – Also Known as “Just-So” Stories

One of the most widespread misunderstandings of evolutionary science – and of evolutionary psychology in particular – is that evolutionary hypotheses are post-hoc storytelling, also known as “just-so stories” (Gould and Lewontin 1979). Nothing could be further from the truth. There are two ways to appreciate why this is a mistake.

First, as in all sciences, evolutionary psychologists can proceed in two ways: using the top-down or bottom-up approach. In the top-down approach to science, researchers generate hypotheses and predictions directly from theory and subsequently go out and test their hypotheses. Since hypotheses and predictions in this approach are made *a priori* on the basis of theory, it is impossible for the top-down approach to be open to the charge of just-so storytelling.

By contrast, in the bottom-up approach, researchers first make an observation, and then generate a hypothesis to explain why that

observation might have occurred. This approach to science is *potentially* open to the charge of post-hoc storytelling, but only if the researcher *stops* after generating a hypothesis and fails to derive or test any new predictions from that hypothesis. Whether or not a proposed explanation counts as just-so storytelling depends entirely on this last step: if the researcher in question simply chooses to believe her hypothesis without generating and testing any novel predictions, then she is guilty of just-so storytelling. If, by contrast, the researcher uses the proposed hypothesis to generate novel, testable predictions, the charge falls flat. A cursory look at published evolutionary psychological papers makes it clear that most evolutionary psychological hypotheses are not open to this accusation, either because they used the top-down approach to generate *a priori* predictions (e.g., see Al-Shawaf 2016), or because they used the bottom-up approach but subsequently generated and tested novel predictions.

A concrete way of remedying the confusion here is simply to list examples where an evolutionary approach started from theory, generated novel hypotheses, and then used those hypotheses to derive new predictions which were subsequently tested in the lab and the field. There are literally hundreds of such examples, and many of them have been included in easy-to-read tables in previous journal articles. We therefore do not replicate them here but instead direct the reader to three articles where they can find plenty of such examples – as well as much more detailed discussions of why evolutionary hypotheses are eminently falsifiable. Key papers that include such tables and discussion are Buss et al. (1998), Ketelaar and Ellis (2000), and Lewis et al. (2017).

The underlying mistake seems to be thinking that if a discipline is partly *historical* in nature (as are the evolutionary sciences), that makes the discipline unfalsifiable and prone to just-so storytelling. But if that were the case, *all* disciplines with a historical component – including, for example, astrophysics, cosmology, and geology – would be exercises in just-so storytelling. This is obviously incorrect. Whether or not a scientific discipline includes a historical component is not relevant in differentiating good science from just-

so storytelling. What *is* relevant is whether the scientists in a given discipline – regardless of whether that discipline includes a historical component – use their hypotheses to *generate novel predictions that can be tested in the present day*. If they skip this crucial step, they may be engaged in just-so storytelling. By contrast, if they use their hypotheses to generate and test novel predictions about previously unobserved phenomena, they are engaged in normal, productive science. It is the latter that characterizes most evolutionary psychological research (for full discussions, see Buss et al. 1998; Confer et al. 2010; Ketelaar and Ellis 2000; Lewis et al. 2017).

Misunderstanding 13: Natural Selection Has Stopped for Our Species, So Humans Are No Longer Evolving

The thirteenth misconception is that humans have stopped evolving because natural selection has ceased operating on our species. This erroneous line of reasoning points out that we have eradicated many diseases, and that modern medicine keeps humans alive when they would have surely died in ancestral populations. There are at least three reasons why this does not warrant the conclusion that humans have stopped evolving.

First, we have not eradicated all diseases. People still die of cardiovascular problems, sexually transmitted diseases, respiratory diseases, cancer, and plenty of other illnesses. Every year, about 800,000 children die from diarrhea-related problems *alone* (Center for Disease Control and Prevention 2015). It is true that WEIRD societies (Western, Educated, Industrialized, Rich, and Democratic; Henrich et al. 2010) have made great medical progress, but as a species, we are far from having eradicated all sources of death and disease. The vast majority of the world still suffers from many illnesses, some of which are fatal. And of course this is to say nothing of warfare, homicide, and other causes of death.

Second, even if we *had* eradicated all sources of disease, this would not imply the cessation of evolution. Recall that it is differential *reproduction*, not survival, that is the bottom line of

Thirteen Misunderstandings About Natural Selection, Table 1 Misunderstandings about natural selection vs. accurate alternatives

Misconception	Accurate alternative
Natural selection is random and so is evolution	Mutation is random, natural selection is nonrandom, and as a consequence, evolution is also nonrandom
Survival is the bottom line of evolution by natural selection	Differential reproduction is the bottom line of evolution by natural selection. Survival is tributary to reproduction, and when the two conflict, reproduction trumps survival
There is an agent doing the “selecting” in natural selection	There is no agent and no active “selection”. The process is blind and passive, and a more accurate term for natural selection would be “differential reproductive success”
Evolution is teleological – the process has a final goal, endgame, or <i>telos</i>	Evolution is not teleological and has no final goal, endgame, or <i>telos</i> . Natural selection is blind and cannot peer into the future
Evolution favors the “survival of the species”	Most evolutionists agree that group selection is a much weaker force than genic-level and individual-level selection. Adaptations do not routinely evolve to benefit groups, and the survival of species is not a goal of evolution
Natural selection builds perfectly designed biological mechanisms	Natural selection builds functional mechanisms that are often impressive but are nonetheless suboptimal. This is because there are several unavoidable constraints on the power of selection (e.g., time lags and trade-offs)
Evolution implies genetic determinism	Evolution does not imply genetic determinism. An evolutionary perspective highlights the centrality of the environment at every stage: the initial evolution of adaptations, their ontogenetic development, and their immediate activation in the present
Adaptations must be present at birth (or must develop very early in life)	Natural selection builds adaptations that “come online” at the appropriate developmental stage of life, not adaptations that are necessarily present at birth. Teeth and breasts illustrate this principle
The products or outputs of adaptations are fixed and unchangeable	Evolved mechanisms are flexible. Because environmental input is crucial to the products of adaptations, it is often possible to change the output by simply modifying the input (e.g., calluses)
You can use the principles of evolution to predict behavior directly, bypassing psychological adaptations	Information processing is the key intervening step between the principles of evolution and predictions about behavior. Skipping this step can lead to errors in both prediction and explanation
Natural selection is the only driver of evolutionary change	There are four drivers of evolutionary change: mutation, migration, genetic drift, and natural selection. Natural selection is very important, and it is the only viable explanation for the structure and function of <i>adaptations</i> , but it is only one of four drivers of evolutionary change
Evolutionary hypotheses are inherently unfalsifiable “just-so” stories	Most evolutionary hypotheses are eminently falsifiable. When researchers use the top-down approach to generate <i>a priori</i> predictions, the “just-so” charge falls flat. When researchers use the bottom-up, observation-driven approach, whether the charge falls flat depends on whether the researchers use their hypotheses to generate novel, testable predictions. For an extended discussion, see Buss et al. 1998; Confer et al. 2010; Ketelaar & Ellis 2000; Lewis et al. 2017
Humans have stopped evolving because natural selection has ceased for our species	Humans are still evolving and natural selection is still ongoing in our species. We have not eradicated all sources of death and disease – and even if we had, the bottom line of evolution is differential reproduction, not survival. As long as some humans still reproduce more than others, natural selection is still ongoing in our species

evolution (see Misunderstanding #2). As long as some humans are still reproducing more than others, natural selection is still operating. This means that, putting survival aside, there are

plenty of sources of selection still operating on our species: mate competition, mate selection, mate retention, romantic infidelity, childrearing, investment in genetic relatives, grandparenting,

altruism, social betrayal, free-riding, status hierarchy negotiation, and more. Eradicating disease does not remove important selection pressures related to social processes, mating processes, and differential reproductive success. Indeed, not only are humans still evolving, but the pace of our evolution has *sped up* over the last 10,000 years (Cochran and Harpending 2009).

Third, it is important to remember that there are three prerequisites for evolution: (1) variation (organisms in a population vary), (2) inheritance (some of this variation is passed on to offspring), and (3) differential reproductive success (as a result, some of these organisms reproduce more than others). As long as ingredient #3 (differential reproductive success) still obtains, natural selection is still operating. And as long as *all three* prerequisites are still in place – as is the case among humans – evolution is still occurring. Consequently, humans are still evolving, and will be for the foreseeable future.

Conclusion

The theory of evolution by natural selection is regarded by scientists as one of the most parsimonious, explanatorily successful, and predictively powerful theories in the history of science (Alcock 2009; Coyne 2009; Dawkins 2009; Dennett 1996; Dobzhansky 1973). Its parsimony and simplicity suggest that it should not be difficult to understand, but misconceptions still abound, even among scientists. There are likely several reasons for this, including insufficient educational exposure to the principles and findings of evolutionary biology as well as social and ideological biases that serve as impediments to understanding (e.g., Von Hippel and Buss 2017). Ironically, some of these errors may also be rooted in the fact that our evolved cognitive systems make it difficult for us to understand evolution correctly (e.g., Evans and Lane 2011; Legare et al. 2013; Shtulman and Schulz 2008).

This entry has tackled what we see as the 13 most important misunderstandings about evolution and natural selection (see Table 1). This list is not exhaustive. For example, due to space

considerations, we were unable to discuss such misunderstandings as the notion that something is good because it is natural, the intuition that natural selection must always lead to change, or the idea that evolution is “just a theory” (e.g., Dawkins 2009). Nevertheless, we have attempted to clear away the most common impediments to an accurate understanding of natural selection. We hope this entry helps readers to avoid these misunderstandings and to think about the process of evolution in a rigorous and clear-headed manner.

Cross-References

- [Adaptations](#)
- [Falsifiability](#)
- [Genetic Determinism](#)
- [George Williams](#)
- [Natural Selection](#)
- [Problems With Group Selection](#)
- [Richard Dawkins on Constraints on Natural Selection](#)
- [The Handicap Principle](#)

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Thomas Cathcart

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Synonyms

Author; Philosopher

Definition

Thomas Cathcart is a New York Times and international bestselling author who specializes in making philosophical reasoning more accessible for public consumption.

Introduction

Thomas Cathcart graduated with a degree in philosophy from Harvard University and went on to

have what he describes as a checkered career of jobs, all the while attending divinity schools. Thomas Cathcart has been a probation officer working the streets of Chicago, has performed similar duties with doctors for medical insurance providers, and was the COO of a hospital while he continued to study philosophy. Later, Cathcart would go on to write several philosophy texts, including his most recent book *The Trolley Problem: or Would you Throw the Fat Guy off the Bridge?: a Philosophical Conundrum* (Cathcart 2013).

Thomas Cathcart has spent his authorial career trying to present major topics in philosophical reasoning in a digestible and accessible manner. Cathcart's first published book, *Plato and a Platypus Walk into a Bar...* (Cathcart and Klein 2008a), utilizes humor and jokes as a method of breaking down and examining issues in a crash course of basic philosophical principals. Similarly, his second book, *Aristotle and an Aardvark Go to Washington* (Cathcart and Klein 2008b), uses a sense of humor and philosophy to digest the political sophistry and fallacious arguments seen in modern American politics. His third book, *Heidegger and a Hippo Walk Through Those Pearly Gates* (Cathcart and Klein 2009), is a historical walk-through of how philosophers from antiquity to today have thought about death. What is clear from Cathcart's writing is that he values making philosophy accessible to the general public.

On his blog on BigThink.com, Cathcart asks the reader the question: Why philosophize? He brings up this question in light of some sobering data that indicates that liberal arts majors (including philosophy) have been decreasing since the 1970s, with the percent of individuals majoring in philosophy today sitting at only 0.7 %. Cathcart compares studying philosophy to children going to summer camp. In this analogy, he asks us to consider the implications of children being asked not to have their cell phones. On the one hand, the camp is designed to allow kids to have natural experiences, and on the other, they would be deprived of devices that they are normally allowed and expected to use in their everyday lives. Cathcart considers his summer

camp experiences as a child, long before cell phones and the Internet were a reality, but where the existence of maps still made the necessity for nature survival training a moot point. At the end, he concludes that summer camp likely has several goals, and one of those goals may simply be to allow kids to have fun, while another goal may be to give kids an opportunity to experience life in the most basic way possible. It is in these experiences, Cathcart says, that we try to form ourselves in some way so that we connect with other people on the most human level. This is why, he argues, we philosophize: to understand how to think critically and in a manner that allows us to connect with other ways of thinking and with other people.

Conclusion

As an author, Thomas Cathcart appears dedicated to making philosophy relevant and accessible in a modern world. His work strives to be humorous while simultaneously asking deep questions about the way humans consider the world around them. The question of why philosophy is important appears to matter a great deal to Thomas Cathcart and his work endeavors to address that question.

Cross-References

- ▶ [Evolution of Morality](#)
- ▶ [Jonathan Haidt](#)
- ▶ [Modern Moral Relativism](#)
- ▶ [Moral Instincts](#)
- ▶ [Morality](#)
- ▶ [Trolley Problem](#)
- ▶ [Trolley Problem, or Would You Throw the Fat Guy off the Bridge?](#)

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Thorndike's Law of Effect

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Synonyms

[Law of Effect](#)

Definition

A theory of learning proposed by Thorndike stating that responses closely followed by satisfaction are firmly connected to that situation and are more likely to be repeated when the situation occurs again. Responses followed by discomfort have their association to the situation weakened and are less likely to occur in similar situations.

Introduction

Thorndike developed a theory of learning through on the basis of this experimental research with animals. He represented the original Stimulus-Response (S-R) framework and considered that learning is the result of associations formed between stimuli and response. He placed emphasis on the role of experience in the strengthening/weakening of S-R connections (Connectionism) and posed that learning happens through trial and error (Ormrod 2016). Some responses eventually dominate because they become associated with satisfaction.

Development of the Theory

Thorndike introduced his theory of learning, termed as Law of Effect in his doctoral

dissertation (Thorndike 1898) undertaken at Columbia University under the supervision of William James. His theory emphasized the role of trial and error in the learning process and on the associations formed between SR connections.

His methodology involved the use of puzzle boxes in which he placed an animal (e.g., a cat). The puzzle box was enclosed but had a door that could be opened by the pressing of a lever inside the box. A hungry animal was placed in the box and a piece of food was left outside the box. Thorndike observed the animal's efforts to escape the puzzle box in order to reach the food and recorded how long it took for each successful escape. The animal would be trying to escape by reaching through the cage and scratching at the bars of the cage. At some point, it would press the lever by accident, and the cage door would open. Thorndike observed that with the repetition of this experiment, the amount of time and effort spent on ineffective activities (reaching and scratching) was reduced and the pressing of the lever occurred sooner. He plotted the escape times in a graph that he called learning curve. While the animals took some time to escape initially, Thorndike found that they became increasingly faster in successive repetitions of the experiment until the escape time stabilized. This resulted in an S-shaped learning curve.

He concluded that responses followed by positive consequences (satisfaction) are more likely to be repeated in a similar situation, whereas responses followed by negative consequences (discomfort) are less likely to re-occur in a similar situation:

"Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur; those which are accompanied or closely followed by discomfort to the animal will, other things being equal, have their connections with that situation weakened, so that, when it recurs, they will be less likely to occur. The greater the satisfaction or discomfort, the greater the strengthening or weakening of the bond (Thorndike 1911, p. 244)

Thorndike described this kind of learning as instrumental conditioning, as a response is likely to be repeated when it is instrumental in producing rewards (Thorndike 1905). Subsequent

experiments led Thorndike to later revise the Law of Effect (Thorndike 1935), as he found that punishment did not weaken S-R connections, it only inhibited their expression. He thus de-emphasized the role of negative consequences and concluded that punishment has an indirect effect on learning as the organism engages in other behaviors (e.g., crying), which interfere with behavior (Ormrod 2016).

Evaluation and Influence of the Theory

Critics of the Law of Effect have focused on the following aspects of the theory: the retroactive working of the effect, its philosophical implication, the identification of the effective conditions that cause learning, and the generality of the law (Waters 1934). Furthermore, the notion of the bond has been contested by subsequent research. Nevin (1999), however, posed that in the light of reanalyzing these findings, this notion remains viable. He concluded that research on resistance to change gives support to Thorndike's view that the strength of the bond depends on the magnitude of the satisfaction received (Nevin 1999).

Thorndike's pioneering experimental work on animal intelligence and the puzzle box methodology he used inspired B. F. Skinner to invent a variation of the puzzle box that he termed operant conditioning chamber (also known as Skinner box) and conduct experiments investigating learning under controlled conditions. This eventually led to the development of one of the most influential learning theories, Skinner's theory of operant conditioning.

Conclusion

Thorndike's theory of learning known as Law of Effect states that responses closely followed by satisfaction are firmly connected to that situation and are more likely to be repeated when the situation occurs again. It stemmed from his pioneering experimental work on animal intelligence. The Law of Effect has been very significant in the development of behavioral learning theory.

Cross-References

- ▶ [Operant Conditioning](#)
- ▶ [Learning Curve](#)
- ▶ [Skinner Box, the](#)

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Threat Avoidance

- ▶ [Children's Antipredator Adaptations](#)

Threat Detection

- ▶ [Anxiety Disorders](#)
- ▶ [Predators as Attention-Grabbing](#)
- ▶ [Selective Attunement to Adaptive Problems](#)

Threat Detection Systems

- ▶ [Anxiety \(Randolph Nesse\)](#)

Threat Reactive

- ▶ [Stress Reactivity](#)

Threat Responses

► [Evolved Physiological Reactions](#)

Threats of Sperm Competition

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Synonyms

[Fear of cuckoldry](#)

Definition

The competition between sperm of rival males when a female engages in double mating. This double mating can result in cuckoldry and so males have evolved several strategies to assure paternity. Sperm competition (in both physiological and behavioral manifestations) is a response to this threat.

Introduction

Sperm competition has been documented in several species, including our own, and reviews of that literature can be found under ► [“Sperm Competition Theory,”](#) ► [“Sperm Competition: Evidence in Nonhumans,”](#) ► [“Human Sperm Competition,”](#) ► [“Opposition to Human Sperm Competition,”](#) and ► [“Tactics to Solve Adaptive Problems of Sperm Competition,”](#) as well as other related entries. While several of these entries provide detailed evidence of the process or its effects on behavior, the impact of such competition or the threat it poses to fitness is usually described in vague terms.

Threat of Cuckoldry

The most widely cited threat from (and motivation for) sperm competition is Cuckoldry Risk (a man

who raises another man’s child rather than his own is investing in an individual that will add nothing to his genetic fitness). What is the extent of this threat? The best available evidence concerning the incidence/risk of cuckoldry comes from a meta-analysis conducted on 67 published papers on paternity testing (Anderson 2006). The rate of nonpaternity ranged from 14.3% to 55.6%. Anderson partitioned the sample into those with high paternity confidence and low paternity confidence and discovered that the average nonpaternity rate was 1.7% for the high paternity confidence group and 29.8% for the low paternity confidence group. What this research indicates is that there is a wide range of cuckoldry incidence in the human species and that males have evolved strategies to detect it. Indeed the men who had reason to question their paternity (low paternity confidence) had cuckoldry rates 15 times higher than the men who had high paternity confidence. This also indicates that men have developed cuckoldry detection strategies across the species. The threat of cuckoldry has loomed large throughout our evolutionary history.

Baker and Bellis (Pioneers of Research on Human Sperm Competition) were among the first to investigate the physiological and behavioral responses to the threat of sperm competition and showed that when men were unable to monitor their partners, their sperm counts increased to meet the possible threat (Baker and Bellis 1993). Other entries have detailed the ► [“Physiological Evidence for Human Sperm Competition,”](#) ► [“Psychological Evidence for Human Sperm Competition”](#) and the exacerbation of these responses in ► [“Sperm Competition Risk and Partner Abuse,”](#) illustrating how sperm competition has been a major facet of male behavior and has major consequences for females. Behaviorally, partner abuse may be the tip of the iceberg as men have evolved counter strategies to sperm competition. Because of the definition of sperm competition, the scope of this review will be limited to the time of potential insemination (the beginning of sperm competition) through pregnancy, as research suggests sperm competition continues to play a role. For consequences/behavioral sequelae of cuckoldry or sperm competition

after birth, see ► [“Paternity Uncertainty and Father-Offspring Conflict.”](#)

Behavioral Responses

Men may respond to sperm competition behaviorally through semen displacement (see ► [“Genital Evolution”](#)). Semen displacement is an evolved feature of human penis morphology, where semen from rival males is displaced from the cervical area of the vagina by the coronal ridge of the glans through deep, vigorous penile thrusting, allowing the resident male to substitute his semen for those of his rivals. Men have also been shown to change their thrusting behavior to increase semen displacement when there are cues of sperm competition (Gallup et al. 2003). This would essentially remove sperm competition by literally removing the rival male's sperm. In addition to semen displacement, men reacting to the threat of sperm competition are more likely to pressure their partners for sex or force sex (Goetz and Shackelford 2006). This would, first, remove the sperm of rival males, and second, deposit sperm from the male partner to compete. It is also assumed, due to the work of Baker and Bellis (1993) that the sperm count of this ejaculate would be much greater.

Postconception Responses

The threat of sperm competition appears to extend past conception, as there appears to be a pregnancy termination strategy males unwittingly employ when sperm from a rival male is present in a pregnant woman's reproductive tract. Tremellen et al. (2000) reported that pregnancy rates were lower among couples who resumed intercourse shortly after undergoing in-vitro fertilization and speculated that coitus-induced intrauterine contractions could have resulted in implantation failure. This adds more depth to the displacement behaviors discussed above, as more vigorous thrusting may interfere with embryo implantation.

There is also the issue of pregnancy complications that occur when another man's seminal fluid is present in the reproductive tract. Dekker et al. (1998) identified changes in paternity (the father of the pregnancy's seminal fluid vs. another male's) as playing a role in preeclampsia. Women who have limited exposure to the father's semen are at an elevated risk for preeclampsia (Robertson et al. 2003) and preeclampsia is more likely in pregnancies from artificial insemination, where sperm are separated from seminal fluid (Koelman et al. 2000). Treating women who suffer recurrent miscarriages with paternal seminal plasma has been found to increase pregnancy success (Stern and Coulam 1993), and the risk of preeclampsia is reduced by repeated semen exposure over time (Klonoff-Cohen et al. 1989). This implies that it is not only exposure to semen that aids in pregnancy maintenance but consistent exposure to the father's semen may also be important. For this to be possible, the body must be able to make the distinction between different ejaculates and react to sperm from the non-paternal (competing) male in a way that threatens the pregnancy. Researchers have yet to discover this mechanism.

This isn't the first time we have seen sperm competition affect semen chemistry, or semen chemistry affect females. In their now classic paper, Chapman et al. (1995) found that sexual activity actually reduced lifespans in female *Drosophila*, due to male seminal fluid products that possessed spermicidal properties. Human ejaculate also contains spermicidal compounds (Jones et al. 1979) and there are also documented effects of human seminal fluid and seminal compounds that affect implantation, immune responses, and other facets of female physiology and psychology (Burch and Gallup Jr. 2006). We do not know the full extent of seminal fluid effects on females, and we also do not know the effect of sperm competition itself (or seminal fluid from two males) in the female reproductive tract. Baker and Bellis (1988) only examined the effect of sperm competition on the sperm who were competing. More research needs to be done on the physiological effects of sperm competition in women.

Postconception responses to sperm competition may also be behavioral. Researchers have long discussed intimate partner abuse during pregnancy and many question why a man would abuse his partner while she was pregnant (Hilberman and Munson 1978). One of the major issues overlooked on this topic is that of sperm competition or cuckoldry. When sperm competition is taken into consideration, it becomes apparent that the father of the pregnancy may suspect cuckoldry and may not believe the child is actually his. In fact, some reports from battered pregnant women suggest that their partner suspected that he was not the child's father, regardless of actual paternity (Campbell et al. 1992). Burch and Gallup (Burch and Gallup Jr 2004) found that among convicted spouse abusers, the frequency and severity of abuse doubled when the woman was pregnant. The men who abused their pregnant partners not only reported greater sexual jealousy, they suspected the unborn child was not theirs and much of the violence was directed at the woman's abdomen.

The Threat of Sperm Competition to Women

This brings up the important point of how sperm competition, and male responses to sperm competition, affects women. Perhaps this is the largest threat of sperm competition, as sexual jealousy and anti-cuckoldry tactics can be dangerous, even lethal to women. Almost half of all instances of homicides of females are perpetrated by their male partners (Fox 2005) and the rates of intimate partner homicide of females are approximately four to five times that of males (Campbell et al. 2007). Sexual jealousy has been described as one of the most frequent motivators of domestic assault (Wilson and Daly 1996) and control of female sexuality has been documented all over the world (Wilson and Daly 1998). It is because male sexual jealousy is a well-documented trigger for violence that some researchers claim that a male partner is the most dangerous person in a woman's life (Browne 1993).

Conclusion

In reviewing the literature, we see that most research on sperm competition is conducted from the male perspective (the goal of preventing cuckoldry); motivation for sexual behavior, semen displacement, sexual jealousy, and paternal uncertainty. However, the vast majority of male responses to sperm competition also have dangerous consequences for women. Male responses to sperm competition can include attempts to shift female physiology, rough sexual behavior, sexual coercion, chemical and physical attempts to terminate pregnancies, sexual jealousy, intimate partner violence, and even homicide.

Cross-References

- ▶ [Cuckoldry Risk](#)
- ▶ [Genital Evolution](#)
- ▶ [Human Sperm Competition](#)
- ▶ [Opposition to Human Sperm Competition](#)
- ▶ [Physiological Evidence for Human Sperm Competition](#)
- ▶ [Psychological Evidence for Human Sperm Competition](#)
- ▶ [Sperm Competition: Evidence in Nonhumans](#)
- ▶ [Sperm Competition Risk and Partner Abuse](#)
- ▶ [Sperm Competition Theory](#)
- ▶ [Tactics to Solve Adaptive Problems of Sperm Competition](#)

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Three Stages of Habitat Selection

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Synonyms

[Environmental aesthetics](#)

Definition

Habitat selection is the process by which organisms choose the places they might occupy and use for some period of time.

Introduction

Choosing a place in which to live is one of the most important decisions most animals make. An evolutionary approach suggests that individuals should evolve an ability to recognize environments in which they function well, to prefer them, and to recognize and avoid less suitable environments (Orians 1980). That is, the neural systems that motivate positive and negative responses to environments are evolutionary outcomes of a complex process that includes perceiving things and spaces, selectively extracting information from them, and reacting to them in terms of their potential utility. Given their diverse ecological needs, the criteria animals use to select habitats vary enormously. These processes do not require conscious evaluations; in the vast majority of species they proceed unconsciously. Human habitat selection, however, does involve

conscious decisions, so investigators have developed concepts that apply uniquely to our species. Habitat selection is usefully conceived as a three-stage process (Orians and Heerwagen 1992). Although the stages may overlap, their identification helps us think more clearly about the entire process.

Stage 1 begins with an encounter with an unfamiliar landscape. Abundant evidence indicates that these initial emotional responses are rapid and unconscious. During this stage an individual decides either to explore the landscape or to move on. If a Stage 1 response is positive, an individual enters Stage 2, during which it explores the area and gathers more information about it. If its exploration and assessment is positive, the individual may decide to stay in the environment. It then enters Stage 3 and makes another set of decisions about how to use that environment.

The assessment process is based on affordance, that is, what the environment offers, both positively and negatively, to an individual if it settles in it (Gibson 1979). Because bad choices were often costly, individuals would have benefited from developing error-detecting mechanisms that check the results of their perceptual calculations.

Stage 1

Although Stage 1 decisions do not require conscious inference, much unconscious processing may occur, especially if the current environment shares features with previously encountered ones (Kaplan 1992). General features of the environment, such as spatial configurations, depth clues, water, and trees (Kaplan and Kaplan 1989), typically trigger people’s rapid Stage 1 responses. Depth clues facilitate rapid assessment of distances. They help determine the time required to cross potentially dangerous open spaces and distances to potential prey or places offering protection. Water and trees provide useful information about food, location of safe sites, and movement

options. In other words, although the rapid responses made at Stage 1 are unconscious, they have evolved to be influenced by elements of the environment that signal its suitability for occupancy.

Our ancestors made many Stage 1 decisions during their lives. Investigators have inferred how our remote ancestors responded and the legacies of their responses by studying how we assess unfamiliar environments today. People quickly and unconsciously draw inferences when shown scenes of unfamiliar landscapes using two types of information (Kaplan 1992). One concerns what we need to know to *understand* and *explore* the scene. The other concerns how much information we need to process to draw *inference*s about it (Table 1).

Coherence refers to the ease with which a person can grasp a scene’s organization. *Legibility* is an assessment of how well one could find one’s way in it without getting lost. A *legible* space is one with a structure that enables individuals to navigate within it and find their way back to the starting point. To assess *complexity* people respond to objects that may tell them about the scene’s resource-richness.

Prospect-Refuge Theory. Aestheticians have long recognized that expansive views (prospects) enhance the attractiveness of landscapes, but an evolutionary perspective was needed to inspire British geographer Jay Appleton to develop prospect/refuge theory (1975). Appleton’s theory uses three features of a landscape – prospect, refuge, and hazard – to explain which features increase the likelihood that the individual will make a positive Stage 1 decision. Appleton conceived his theory while reading a paragraph in Konrad Lorenz’s classic book, *King Solomon’s Ring* (Lorenz 1952) in which, while strolling through a forest on a spring morning, Lorenz approaches a glade, pauses and reflects on how pleasant it is to see without being seen, that is to learn valuable things about an environment while concealed.

Three Stages of Habitat Selection, Table 1 The environmental preference matrix (After Kaplan 1992)

	Understanding	Exploration
Immediate	Coherence	Complexity
Inferred	Legibility	Mystery

Prospect offers a good view or vista. *Refuge* provides cover from which to observe and assess the environment. *Hazard* refers to the risks an individual faces while exploring the environment. These features may be available from the viewer's current position or only after it enters the environment. Elements of prospect-refuge theory are relevant to both our unconscious initial responses to unfamiliar landscapes and for the conscious assessments we make while exploring an area.

Appleton's ideas have influenced investigators across diverse disciplines. Appleton himself suggested that many features of landscape paintings could be understood by assuming that painters wished to induce viewers to imagine entering, exploring, and using the pictured environment. As predicted, he found that most of the landscapes they painted would be easy to explore in low risk ways and that they had places that offered good prospects and refuges (Appleton 1975).

Prospect-refuge theory also predicts that painters should alter actual scenes to emphasize places offering good views and refuges and indicate low risk passages. These predictions were tested by assuming that John Constable's sketches showed the actual scenes and that he made changes in the final paintings (other than those that refined it) to improve the attractiveness of the scenes. As predicted, Constable frequently added houses, people, and animals; he altered vegetation to open views to the horizon or to distant refuges, and made water features more conspicuous. He often added trees to the foreground, framing the picture, creating an impression that the observer was in a refuge where it was possible to see without being seen (Heerwagen and Orians 1993).

Many experiments have shown that although there are regular and meaningful patterns to our rapid evaluations of unfamiliar scenes, we are generally unable to explain our choices. When asked why we like or dislike scenes, we are embarrassed that we cannot explain why (Kaplan 1992), so we invent explanations (Haidt 2006). From an evolutionary perspective, it is not surprising that the brain processes and evaluates that information without our being aware of it.

Sex differences. Men and women should evaluate environments differently because during

most of human evolution men were hunters, women were gatherers. Women are less able to defend themselves when attacked; pregnancy and childcare would have made them especially vulnerable to predators and enemies. Therefore, women should have greater affinity than men for enclosures and protected places. Heerwagen and Orians (1993) tested this prediction by comparing prospect and refuge symbolism and locations of people in paintings by Irish and French female and male landscape painters. Women's paintings had higher refuge symbolism than men's paintings. Although men in the paintings were almost equally divided between prospect and refuge locations, the vast majority of women were within a refuge. Women were more likely than men to place both men and women in refuges. Although the differences are consistent with evolutionary expectations, painters were doubtless influenced by cultural factors as well.

Similar differences exist in the mental maps of men and women in other cultures. An Aivilik hunter's map of Southampton Island accurately shows the island's outline. Women's maps are composed of points that indicate locations of a settlement or trading post (Carpenter et al. 1959). Women in a farmer's market in California were better than men at remembering the locations of booths selling food. They remembered locations of booths selling high caloric density foods particularly well (New et al. 2007).

Stage 2

Cognition may be prominent during Stage 2 when an individual explores the area and gathers more information about it. Environmental features that command attention are primarily those that indicate the resource potential of the area and how safe it would be to use it (Berlyne 1971; Kaplan and Kaplan 1989; Kaplan 1992). But to gain that knowledge, explorers expose themselves to danger.

To avoid trouble while exploring an individual must recognize patterns, determine which ones signal danger, and respond appropriately (Coss and Owings 1985). Neural systems that motivate active escape from, and avoidance of, danger were probably among the first behavioral systems to

evolve in animals. The objects and situations that evoke fear were genuinely dangerous to our ancestors. A fear and learning neural circuit shared by many mammals, located in the amygdala (Öhman and Mineka 2003) yields rapid responses that can be triggered by very few clues (LeDoux 2000). In extreme form, these fears express themselves as persistent, seemingly irrational, phobias: *nature phobias*, *animal phobias*, and *social phobias*.

When we respond to a signal that may indicate danger we can make two kinds of mistakes. We can fail to respond when the danger is real, or we can assume that the danger is real when it is not. A false negative – failure to respond to a dangerous situation – is more costly than a false positive – responding to a situation that turns out to be harmless. The first error could be deadly; the second generally costs only wasting a bit of time and energy. This is why we have a negativity bias (Haselton and Nettle 2006), that is, we are more averse to losses than we are positive to gains (Kahneman 2003). We have more negative than positive emotions and have more words for pain than for good sensations (Rozin and Royzman 2001). We respond faster to threats and unpleasant events than to positive opportunities and pleasurable situations.

Other organisms are sources of food, fiber, and protection, but some of them – predators, parasites, and contaminated food – may be dangerous. Plants with sharp spines or irritating hairs are rooted to one spot, but most animals move around. Many animals are difficult to spot because they behave in ways to avoid being seen. Dangerous animals have been recognized for millennia; they are causes of many phobias, but we did not know of the existence of microorganisms until the twentieth century. We could not have evolved to fear them, but we do experience disgust when we see things that are associated with pathogens – pus, rotting meat, dead bodies, and feces.

Humans have evolved responses to features shared by many dangerous organisms. Predatory mammals have large, pointed canines and claws. Large herbivorous mammals have sharp horns, antlers, or hooves. African savannas are full of plants with sharp thorns and spines that can

puncture skin and eyes. Paying attention to those plants, especially during times of rapid movement, reduces the chance of injury. Richard Coss (2003) videotaped walkers and joggers as they passed two plants, one with sharp spines, the other without them. Both walkers and joggers favored the side of the path where the spiny plant was located; they passed close to it but did not touch it.

Venomous and constricting snakes have long been important vertebrate predators. Even today more than 150,000 people die from snakebites each year, most of them in the tropics. Other than lemurs, which evolved on an island lacking venomous snakes (Madagascar), all primates have an innately based fear of snakes (Isbell 2009). Laboratory-reared monkeys that have never seen a snake become fearful merely by observing other fearful monkeys or by viewing a fearful model monkey on videotape.

Our ancestors benefited from an ability to detect hidden, stationary predators from glimpses of only small parts of them. Special systems for distinguishing the patterns that provide camouflage (stripes, spots, tessellated patterns) and for detecting eyes evolved. We are especially sensitive to tessellated patterns, which are common among snakes but rare elsewhere in nature (Isbell 2009). Nine- to 10-month old human infants do not react differently to snakes than to other animals, but by the age of 1 year, before they begin to walk, infants quickly associate snakes with fear (DeLoache and LoBue 2009). By the age of three, children detect snakes more rapidly than nonthreatening stimuli (flowers, frogs, caterpillars). In contrast, neither children nor adults detect a single frog among flowers better than a single flower among frogs (LaBue and DeLoache 2008).

People of all societies studied by scientists dream about snakes (Mundkur 1983). Dreams of urban New Yorkers, most of whom have never seen a snake are as detailed and emotional as those of Australian aborigines and Zulus, most of whom probably had repeated contact with venomous snakes. Worldwide, snakes and snake-like creatures have mystical significance and are dominant elements of dreams in which animals of any kind appear.

People have perceptual biases that direct their attention to other hazardous situations. For example, uneven ground may be dangerous because a trip can result in an injury that makes it harder to walk; falls of only a meter or two can produce serious injuries. These risks were especially important when our ancestors were pursuing prey or escaping from enemies. Our perceptual system makes vertical surface irregularities seem larger than they are (Jackson and Cormack 2008).

Stage 3

After exploration and assessment, an individual may decide to stay in and use the environment in a variety of ways. It may improve the environment (e.g., dig burrow, build a dam, erect a shelter, clear brush, dig a well) and make decisions about how to use the habitat and the varied patches that comprise it. Which patches should it visit, when, for how long, and for what purpose? These decisions may influence an individual's success over markedly different time frames. A decision about whether to attack a prey item typically affects an individual's behavior for only a few seconds; it may have a minuscule effect on survival and reproductive success. In contrast, a decision about where to build a nest or dig a burrow may influence behavior for a long time and have major fitness consequences.

We can classify information in terms of its relevance to the time frames of major decisions that humans make about how to use an environment (Table 2). Some information signals current events whose significance will quickly pass. Responses to such information must be rapid and decisive. Humans are highly attentive to such information. Other information highlights seasonal environmental changes that are associated with present and future locations of resources. This information is most relevant to decisions, such as when to move a camp that can be made after considerable reflection, evaluation, and discussion.

Assessing the current and long-term food-provisioning capability of an environment is an important part of evaluation during Stage 2 of habitat selection; these assessments also dominate

many Stage 3 decisions. Foraging evolved to be emotionally satisfying because those of our ancestors who did not enjoy seeking food probably left fewer surviving offspring than those who did enjoy it. Also, a successful hunter, by virtue of his success often benefitted socially and sexually (Hawkes 1990). We hunt, fish, and gather berries today even though comparable food is available in stores at much lower prices. Catch-and-release fishing is a rapidly growing sport because many people who do not eat fish nevertheless enjoy fishing!

To find animals, hunters use clues they leave in the form of tracks, feces, damage to vegetation, and remains of kills. Hunters in traditional societies are famous for their remarkable tracking abilities. The skills and predispositions involved in cognitive processing of animal tracks appear to reside in the basic architecture of our brains today. City dwelling people recognize and remember animal tracks more readily than they remember nearly all other types of visual stimuli (Sharps et al. 2002).

A few of the plants humans eat have edible tissues throughout the year. Although they are stationary, remembering the location of specific individuals facilitates when and where to find tender leaves, flowers, and ripe fruits. Leaves vary not only in the hue and saturation of their dominant green color but also in variegated patterns of other colors. A legacy of the value of paying attention to colors of plant tissues is readily apparent during a visit to any modern nursery. Plant breeders have favored mutants of ornamental plants with different overall colors (yellow-green, gray, or blue), variegated patterns, and leaves with different colors on their upper and lower surfaces. Breeders have also favored mutants with leaves that have contrasting colors at times of years when leaves of most plants are green. Mutants of garden trees with atypical leaf colors, even those that produce neither striking flowers nor edible fruits (such as maples), have been strongly favored by plant breeders. Mutants of conifers with yellow, variegated, and blue-gray leaves also are popular among horticulturalists (Orians 2014).

Watching bees visiting flowers helps people find honey, and know where fruits and seeds will be found in the future. In species-rich vegetation,

Three Stages of Habitat Selection, Table 2 Temporal relevance of environmental information

Temporal category	Examples	Decisions affected
Short-term (minutes to hours)	Weather changes (thunder, clouds, wind)	Seeking shelter, initiating or terminating outdoor activities
	Appearance of dangerous animals or enemies	Immediate defensive or evasive actions
	Appearance of prey	Immediate hunting decisions
	Illumination changes	Moving to an appropriate location for spending the night or for daytime foraging
Seasonal	Day-length changes	Shifts of hunting sites, planting, and harvesting of crops
	Vegetation growth	''
	Flowering	''
	Precipitation changes	''
Multiyear changes (decadal)	Vegetation succession	Shifts of hunting sites, movement of villages
	Erosion (river meanders, lake sedimentation)	
Long-term (decades to centuries)	Topography	Constrains many kinds of decisions

flowers greatly aid in identifying plants that otherwise may be difficult to distinguish among masses of similar green leaves. An evolutionary legacy of this value is our fascination with flowers. As far back as we have records people have cultivated and used flowers.

Once found foods might still not be worth pursuing. A normally edible item might be infested with pathogens. Charles Darwin (1872) was the first person to identify the strong relationship between food and disgust. Disgust, which is expressed in all human cultures, is the most powerful reason people reject certain types of food. Disgust is an adaptation that deterred our ancestors from eating animal tissues likely to harbor harmful microorganisms. Microorganisms can multiply rapidly; there is no dose below which it is safe to ingest them. Responses to potential contamination are, appropriately, dose insensitive. Disgust is evolutionarily programmed intuitive microbiology that developed long before people knew that microorganisms existed, much less that they caused diseases. Although plant tissues are generally less nutritious and more difficult to digest than animal tissues, they are much less likely than animal tissues to harbor toxic bacteria. They rarely evoke disgust, but most “inappropriate” foods are plant tissues (Rozin and Haidt 2013).

Conclusion

A rich and expanding literature shows that our varied emotional responses to the physical and biological environment today are, in part, a legacy of the way our ancestors made important Stage 1, 2, and 3 decisions in African savannas and the consequences of those decisions for survival and reproductive success. Environmental challenges were a dominant part of their lives. How they responded to those challenges was often a life-or-death matter.

An evolutionary perspective also suggests why the structure of human thought is binary. Most of the decisions of our ancestors had “either-or” answers. An object or landscape was either to be approached or avoided. A perceived object was either food to be eaten or to be rejected. The appropriate decisions often had to be made quickly. Although taking action requires quick and binary decisions, inputs from the environment are often complex and contradictory. Our brains tend to resolve complex events and inputs into polar categories, which is necessary if appropriate action is to be taken in a timely manner. Claude Lévi-Strauss claimed that all tribal myths are built upon binary opposites (Levi-Strauss 1962). Spatial distinctions in most languages are either-or. The universality of these patterns suggests that polar typology has deep evolutionary roots.

The body of information on human responses to the environment is impressive and growing rapidly, but it is only the beginning of what is certain to become a mature science of the evolutionary psychology of habitat selection. Most tests so far have involved people in only a few cultures. Much more crosscultural and age-related research is needed to determine which of these responses are universal and which are culture-specific.

Cross-References

- [Cross-Cultural Research on Grandparental Investment](#)
- [Defending Against Predator](#)
- [Emotions](#)
- [Hunter-Gatherer Societies](#)

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Thrifty Genotype

► [Calculating Starvation Risk](#)

Time

► [Object Permanence](#)

Tinbergen's Four Questions

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Synonyms

[Levels of explanation](#); [Proximate and ultimate explanations](#); [Tinbergen's four whys](#)

Definition

The four levels of explanation at which Tinbergen (1963) argued that a behaviour can and should be understood.

Introduction

In one of the founding texts of the field of ethology, *On Aims and Methods of Ethology*, Niko

Tinbergen (1963) proposed that a complete understanding of any given behavior necessitates explanation at four different levels (the “four major problems of biology”): causal (or mechanistic), ontogenetic, phylogenetic, and functional. These levels of explanation have variously been referred to as Tinbergen’s four questions and Tinbergen’s four whys. They can be further classified into proximate (causal/mechanistic and ontogenetic) and ultimate (phylogenetic and functional) levels of explanation, distinctions originally proposed by Ernst Mayr (1961). Proximate levels of explanation consider the mechanisms of how a behavior is produced, while ultimate explanation accounts for why, from an evolutionary perspective, the behavior exists (Tinbergen 1963). This entry will define these levels and briefly discuss their significance for evolutionary psychology.

Causal/Mechanistic Explanations

Causal, or mechanistic, explanations for behavior consider the immediate neurophysiological, hormonal, psychobiological, and environmental causes of a given behavior. Such explanations often concern the necessary and sufficient conditions required to produce the behavior. For example, causal/mechanistic explanations for breastfeeding could refer to the roles of prolactin and oxytocin in milk production and letdown, the role of physical stimulation on the breast and nipple that promotes oxytocin production, and the relationships between breastfeeding and a mother’s heightened neurophysiological response to the sound of her own baby crying (Jonas and Woodside 2016).

Ontogenetic Explanations

Ontogenetic explanations for a behavior concern the development of the behavior across the life span, including cognitive development, learning, and other experiential effects. Ontogenetic explanations for breastfeeding might include the role of early mother-infant bonding and the importance of initial breastfeeding attempts (Jonas and Woodside 2016). Ontogenetic explanations also

encompass much more long-term experiential influences on behavior, such as learning experiences surrounding breastfeeding during the mother's own development (Hoddinott and Pill 1999).

Phylogenetic Explanations

Phylogenetic explanations for behavior consider the evolutionary history of the behavior: as it manifests in the extant species in question, and how this has changed over evolutionary time, across multiple speciation events. It frequently includes consideration of exaptations (where structures originally selected for one purpose become co-opted for a different purpose in subsequently evolving forms). Our breastfeeding mother may be understood as breastfeeding her child because humans descended within the mammalian clade and thus inherited the physical (mammary glands, nipples) and physiological (oxytocin and prolactin neuroendocrine pathways) structures that support breastfeeding from ancestors in whom these structures appeared more than 160 mya. A phylogenetic explanation may also consider that mammary glands likely evolved from reptilian abdominal epidermal glands, which were exapted for nutritional purposes as newborn lizards acquired nutrients and immunologic compounds from their secretions (Goldman et al. 1998).

Functional Explanations

Functional explanations of behavior (also referred to as adaptive significance, or current utility, Bateson and Laland 2013) consider the survival value (and ultimately, the reproductive value) of the behavior. They seek to describe the selection pressures that lead to the emergence, shaping, and maintenance of behaviors over evolutionary time. As such, breastfeeding can be understood as evolving in response to selection pressures to provide nutrients and immunocompetence to offspring. In humans, at least, it has also likely been shaped to serve mother-infant bonding functions (Jonas and Woodside 2016).

Tinbergen's Four Questions in Psychology

While much of the discipline of psychology is traditionally focused on proximate explanations of behavior, ultimate, especially functional explanations are the level of explanation most often associated with evolutionary psychology. Tinbergen, however, was clear in his argument that any given behavior can be simultaneously understood at all four levels of explanation, and indeed to fully understand the causes of any behavior, it is necessary to incorporate complete explanations at all four levels (Tinbergen 1963). Indeed, the key insight of Tinbergen's 1963 essay was not simply the content of the four levels of explanation but the complementary and integrative nature of them (Nesse 2013). In spite of its traditionally strong focus on ultimate questions, the discipline of behavioral ecology has more recently shifted toward an appreciation of the importance of integrating explanations across the four levels of explanation (Bateson and Laland 2013). Such integration, however, is still less common within the broader discipline of psychology (Sulikowski and Burke 2015).

Critics of evolutionary psychology (and of adaptive and biological explanations of human behavior more broadly) often mistakenly presume that different levels of explanation are mutually exclusive and competitive. Much confusion, in particular, surrounds the proximate/ultimate distinction. Stephen Jay Gould, for example, argued that "the [*ultimate*] question, 'what is it for?' often diverts attention from the more mundane but often more enlightening [*proximate*] issue 'how is it built?'" (Gould 1981). Rose and Rose (2001) protest that evolutionary psychologists "insist on... ultimate... explanations when proximate ones are so much more explanatory" (p. 4). Persistent misunderstandings about the complementary nature of proximate and ultimate explanations currently impede an integrative application of Tinbergen's four questions to understanding human behavior.

To return to our breastfeeding mother, critics of evolutionary approaches to behavior may argue that an understanding of the behavior may be satisfactorily provided by a description

of the stimulus (her infant crying) and associated neural and hormonal responses to the stimulus [a *causal* explanation] and of the experience and learning surrounding breastfeeding during her own development [ontogeny]. A Tinbergian understanding, however, demands that we also consider the evolutionary history [phylogeny] of breastfeeding, perhaps through the lens of comparative psychology, and the *functional* value of breastfeeding in providing nutrients and immunocompetence benefits to the infant in order to help him survive and develop successfully in order to pass on his mother's genes to the next generation.

Conclusion

While evolutionary psychologists and other researchers who take an evolutionary approach to understanding human behavior provide valuable insight into the ultimate causes of behavior, it has been argued that adopting a formal Tinbergian framework, considering a behavior at all four levels of explanation, can provide a fuller understanding of the behavior in question (Stephen et al. 2017).

Cross-References

- [Adaptation and Natural Selection](#)
- [Controversies in Evolutionary Psychology](#)
- [Development](#)
- [Field of Comparative Psychology, The](#)
- [Spandrels](#)

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Tinbergen's Four Whys

► [Tinbergen's Four Questions](#)

To Afford Protection Against Climate and Weather

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Synonyms

[Apparel](#); [Attire](#); [Garment](#); [Clothing](#) is distinguished from terms like [adornment](#), [costume](#) and [dress](#) which encompass [body painting](#), [cosmetics](#), [scarification](#) and [tattooing](#)

Definition

Humans invented clothes as artificial protection from cold to compensate for the loss of body fur

which became a critical survival issue during the Pleistocene ice ages. The physiological function of clothing as thermal insulation is reviewed, along with archaeological evidence for the development of complex clothes and later textile fabrics as adaptations to changing climates.

Introduction

Adaptation to the thermal environment is crucial to the survival of all living things. Extremes of heat and cold exert selection pressures on animal species, resulting in both biological and behavioral adaptations to climate.

Primates are generally adapted to life in warm climates and early hominins evolved in the tropics of Africa. A number of unusual traits – upright posture, sweating, and the loss of body fur – may reflect adaptation to the dry heat of the African savanna (Ruxton and Wilkinson 2011).

Human evolution is an enigma in this regard. Loss of fur – biological nakedness – deprives a mammal of natural protection against cold weather, yet *Homo sapiens* evolved in the environmental context of the Pleistocene ice ages. Human nakedness mystified Darwin: he could see no advantage in terms of natural selection and suggested it might be a case of sexual selection (Darwin 1871).

Hominins began to spread outside the tropics during warm interglacials. Over the last million years, they developed a series of behavioral adaptations to compensate for their biological vulnerability to cold. The main strategies were control of fire, use of shelter, and the manufacture of clothing. Fire was utilized as early as 800,000 years ago (Walker et al. 2016). While fire and shelter facilitated a hominin presence in cooler climates, only clothes could provide the portable protection necessary for a sustained occupation of cold climates.

Human Cold Tolerance

The human body begins to react to cold at an air temperature of +27 °C (80 °F). At +20 °C, the

metabolic rate begins to climb to generate extra heat, and shivering (a sign of failure) starts at +13 °C. This susceptibility is due mainly to lack of fur: rabbits for example can survive at –45 °C but when shorn, they start to struggle at 0 °C. People can become acclimatized to cold, as seen among those who work in Antarctica: after a few months they manifest an attenuated metabolic response to cold exposure. Clothing plays a paradoxical role: with regular use of clothes from birth, humans habituate to a warm microenvironment and hence become more sensitive to cold. For this reason, hunter-gatherers who are routinely naked have better cold tolerance. The safe naked limit for brief exposure (up to an hour or two) is around 0 °C, extending to as low as –5 °C for foragers like Australian Aborigines who led a traditional lifestyle without clothes. By mammalian standards, human physiological adaptations to cold are distinctly inferior (Jessen 2001).

Hypothermia

The core temperature of the human body must remain within a few degrees of 37 °C. Hypothermia begins at 35 °C and at 33 °C people begin to experience blurred vision and lose consciousness. Below 30 °C is severe hypothermia when blood pressure falls and the heart rate slows, with cardiac arrest inevitable by 15 °C. Depending on variables like age, physical fitness and alcohol consumption, as well as environmental conditions such as wind, survival times for humans with hypothermia vary between 1.5 and 12 hours. At an air temperature of –10 °C, the survival time for people without clothes is 3–6 hours (Dettmeyer et al. 2014).

Frostbite

Frostbite is the other main danger, though it is less commonly fatal. Frostbite primarily affects extremities like fingers, toes, and ears, and it can cause tissue loss and gangrene, which sometimes leads to infection and death from septicaemia. As with hypothermia, the safe exposure times are determined by wind as well as air temperature. At an air temperature of –15 °C and a wind speed of 40 km/h, symptoms of frostbite can develop within 30 minutes (Ducharme and Brajkovic 2005).

Climate Variables

Air temperature and wind are the most salient aspects of climate, along with moisture (rain, snow and humidity); intensity of solar radiation – which varies with latitude – and cloud cover are additional factors. Seasonal and diurnal ranges need to be taken into account when using mean annual values from meteorological data. Also relevant when considering evolutionary adaptations are the likelihood of extreme conditions, which may occur infrequently but which may ultimately determine survival chances.

Temperature

When the temperature of the environment is lower than skin temperature (typically 35 °C), heat is lost from the skin surface to the surroundings. Thermal conductance increases from gaseous to liquid and solid states: water for example has 24 times the thermal conductance of air. Skin cools more rapidly in liquids and more so when in contact with solid surfaces – hence liquids and solids feel colder (and cause more rapid heat loss) than air at the same temperature. This differing conductivity is the basis of thermal insulation with clothes, which trap air near the skin; this is also why moisture is a major problem for clothes.

The thermal comfort zone for modern humans with clothes is generally 21–24 °C. Infants are more susceptible to cold, and when naked they can begin to develop hypothermia at 33 °C.

Wind Chill

Any movement of air against the skin surface removes body heat, and the presence of moisture (either on the skin or in clothes) exacerbates heat loss with wind due to evaporative cooling. At low air temperatures, the cooling effect of wind is exaggerated: even moderate wind speeds increase the dangers at sub-zero air temperatures, as seen with the wind chill index (Osczevski and Bluestein 2005). Superior protection from wind is afforded by fitted (or ‘tailored’) garments.

Environmental Moisture

The thermal conductance of fluids means that moisture in any form compromises the thermal

effectiveness of clothes. Moisture also displaces air, and its evaporation extracts heat from the skin – which is how sweating operates as a cooling mechanism in warm climates. Even in cold climates however, perspiration still occurs and its production increases with physical activity. Higher levels of relative humidity in the environment will reduce the capacity of air to absorb sweat and thus impede the evaporation of sweat. Humidity therefore reduces the cooling capacity of sweating and when wearing clothes, it causes sweat to accumulate. For these reasons, clothing functions best in dry climates.

Clothing Physiology

The insulation value of clothing as protection from cold derives from trapping still air close to the skin surface; all other considerations (such as the material) are secondary. Clothes are of limited value as insulation from heat in hot climates: garments can protect from direct solar radiation but any such benefits are outweighed by impediments to convective and evaporative cooling. To reduce the disadvantages, clothes in warm climates should be loose and made from light woven fabrics, with a minimum number of layers.

Principles

Fitting refers to the shaping of a garment to closely enclose the body. Insulation is further improved with separate cylinders to enclose the limbs (which have a relatively greater surface area and hence higher potential for heat loss). Not only does this result in improved trapping of air, fitting provides more protection from wind penetration and wind chill.

Layers provide additional insulation, since the inner layers are protected from air movement. Modern garments are generally fitted and layers require fitting (at least for inner garments), so the emphasis with cold weather apparel is on layers. Clothing zones are defined based on the minimum number of layers required: the Arctic region for example is designated as a four-layer clothing zone.

Woven fabrics allow perspiration to escape through the material whereas animal skins and

furs are less permeable. Leather may be favored for footwear due to its durability but sweat is always an issue, so running shoes for instance are made from woven material.

Measuring the Thermal Value

Thickness gives an approximate measure of insulation, corresponding to the amount of trapped air. For example, a 50 mm four-layer assemblage can enclose nearly half that radius of trapped air.

Clo units are the commonest scientific measure:

$$1 \text{ clo} = 0.155 \text{ m}^2 \text{ K W}^{-1}$$

(m^2 = surface area, K = °Kelvin, W = watts)

One clo unit corresponds to a typical modern garment assemblage (e.g., shirt and trousers, with underwear) for a person to be comfortable in a room at an air temperature of 21 °C, with modest air movement (0.1 m/s) and low relative humidity (<50 %). In general, each clo unit corresponds to a complete layer of clothes, and a full four-layer ensemble suitable for Arctic winter weather provides ~ 4 clo of insulation.

Climate and Clothing Evolution

Archaeological evidence indicates that hominins began to use simple clothes by the Middle Pleistocene, around 800,000 years ago. The materials were animal skins and furs and the basic Paleolithic technology was the stone hide-scraper. Toolkits dominated by scrapers became more common in middle latitudes as hominins occupied colder environments during glacial episodes from 400,000 years ago.

Complex clothes (fitted garments with the option of multiple layers) required further technological innovation: dedicated cutting tools (stone blades) and hide-piercing implements (awls and later eyed needles, often made from animal bones). These toolkits were a prerogative of *H. sapiens* and complex clothing was developed in cooler parts of Africa during a cold phase 75,000–60,000 years ago. Toolkits with blades and awls accompanied the subsequent spread of

modern humans into northern Eurasia from 45,000 years ago. Complex clothing gave modern humans an advantage over Neanderthals, whose scraper-dominated toolkits suggest they had only simple clothes (Gilligan 2007). By 28,000 years ago as the climate deteriorated towards the Last Glacial Maximum (LGM), modern humans with these clothing-related tools – including eyed needles – had reached northeast Siberia (latitude 70°N), when the average winter temperature is estimated at –50 °C (Kuzmin and Keates [in press](#)).

Textiles became the optimal material for clothes with global warming from 12,000 years ago, notably in agricultural communities where fiber resources such as wool, flax, and cotton were domesticated. Wind penetration was less of an issue whereas the woven structure allowed sweat to disperse (e.g., Tang, Chau, Kan, and Fan 2015) – a critical consideration in climates that were warmer and more humid.

Conclusion

The thermal properties of clothing were crucial to the evolutionary success of hominins, and the development of complex clothes allowed *H. sapiens* to spread into every climate zone on earth. Clothing is a behavioral compensation for biological nakedness and a uniquely human adaptation to past climate change.

Cross-References

- [Clothing](#)
- [Savanna Hypothesis and Landscape Preferences, The](#)

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To Kill Yourself

- [Suicide](#)

To Stop Nursing

- [Weaning and Maternal-Fetal Conflict](#)

Tolerance

- [Primate Dominance Hierarchies](#)

Tool

- [Waterspouts \(Archerfish, Sharks, Rays\)](#)

Tool Behavior

- [Nonhuman Tool Use](#)

Tool Innovation

- [Tool Manufacturing](#)

Tool Manufacturing

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Synonyms

[Creativity](#); [Tool innovation](#); [Toolmaking](#)

Definition

Manipulating an object, by changing or modifying some property of that object, in order to make it function better as a tool.

Introduction

Tool use in animals is rare (despite the multitude of reports in the scientific and nontechnical literature; Shumaker et al. 2011). However, toolmaking is even rarer. Indeed, within the avian taxon, only two species regularly make tools in the wild, and three other species have been observed making tools in an experimental context in captivity. Only woodpecker finches (WF) and New Caledonian crows (NCC) use (some) tools that need to be

either detached or fashioned in some way before use, rather than being found in a perfect state in which they can subsequently be used. There is an argument as to what constitutes tool manufacture. Does removing a spine from a cactus represent toolmaking, or is this a simple environmental manipulation that allows objects to function as tools? A cactus spine is already in a form that aids its eventual use as a tool (i.e., it has a pointed end); the bird does not need to modify the spine in any way for it to function as a probing tool. However, it cannot be used as a tool when it remains attached to its parent cactus plant. Is detaching a spine therefore a case of toolmaking? Shumaker and colleagues (2011) consider it to be. By contrast, consider the less ambiguous case of a stick, either attached to or separated from a larger branch. To become a functional tool, the stick needs to be fashioned in some way (unless it is being used as a fly swat, such as by some elephants). Side twigs need to be removed, the main shaft may need to be shortened or sharpened, or the end sculpted into a hook. These are definitely actions designed to change the original object into something different and so unambiguous toolmaking.

Why do only two species regularly make tools and only within a foraging context (whereas chimpanzees make tools for a variety of purposes)? It is probably the result of the type of tool use employed by other main avian tool users (see Bird Tool-Use). For example, green herons use bait to lure fish, and Egyptian vultures drop stones onto ostrich eggs to break them. In neither case, does an object need to be modified in order to become a functional tool. A piece of bread or an insect can be used as bait, or a stone or rock can be used to crack open an egg; in both cases the original object works well as a tool in its original state (except in the case of maiming the insect so it cannot escape, which does not seem to be a case of toolmaking). NCC and woodpecker finches also use tools that need no modification, such as sticks without hooks, or cactus spines, but importantly they do change other (nonfunctional) objects into (functional) tools, such as turning a *Pandanus* leaf into a probing tool or a stick into a hook.

Likewise, there are three bird species that do not naturally use tools in the wild, but which readily do so in captivity. They each make or modify tools from different materials, but all within the context of acquiring food that is out of reach. The following section will discuss these five examples of avian toolmakers, how they create their different tools, and the advantages of creating or sculpting a tool rather than just using material without any modification.

Avian Toolmakers

Woodpecker Finches

Originally, WF were not thought to make tools, but only use natural found objects in their environment that could function as tools, such as cactus spines and small twigs. However, WF do detach both twigs and cactus spines and modify them (shorten or trim off side branches). Recently, WF were provided with nonnative blackberry bushes, and individuals removed blackberry twigs, using the barbs along the length of the twigs as hooks (Tebbich et al. 2012).

New Caledonian Crows

NCC create three types of tools; *Pandanus* leaf tools and stick tools, either with or without a hooked end (Hunt 1996). Original studies of tool-making extrapolated how they were made through the discovery of tool counterparts (i.e., the shapes left behind in the leaf after the tool had been made and removed) or the tools themselves. However, it was possible to view cases of toolmaking by setting up artificial foraging sites which could be closely observed and recorded. Hunt and Gray (2004a), for example, observed crows making hooked stick tools using a three-stage process. The crow selected the appropriate raw material (i.e., a branch of the correct length) and in the correct location to make a hook (at the fork between two twigs). One twig was removed above the fork in order to leave a hook at one end. This twig was trimmed of side branches and leaves, before sculpting the hooked end, removing small pieces of wood left from the break (see also

Klump et al. 2015, discussing the variety of hook tools based on the raw materials available).

Hunt and Gray (2004b) also observed crows making different tools from *Pandanus* leaves, basically confirming Hunt's (1996) earlier suggestion of how they were made. There are three main subtypes: wide, narrow, and multistep. In each case, a small tear is made at the edge of the leaf, making sure that one side of the tool utilizes part of the natural barbs present along one side of the leaf. Once the initial tear has been made (a small tear for a narrow or multistep tool, a longer tear for a wide tool), a strip down the length of the leaf is pulled (how long is dependent on the tool type); then another tear, either detaching the tool or part of a series of strips; and tears until a multistep tool is created.

Goffin's Cockatoos

A captive Goffin's cockatoo, Figaro, was discovered using a piece of bamboo to rake in a pebble he was playing with. In an experiment, Figaro made a series of tools, pulling long strips of wood from the wooden posts of his aviary in order to retrieve in a cashew nut that had fallen out of reach (Auersperg et al. 2012). In ten trials, he created nine different tools (one tool was ready-made). An assessment of the tools found some conformity in design (although this doesn't necessarily mean that he had a design "in mind" when he made them, rather that this was a constraint of the material and the method for making the tools, which resembled that of *Pandanus* tools made by NCC).

Northern Blue Jays

Similar to Goffin's cockatoos, Northern blue jays also do not use or make tools in the wild, but have been observed doing both in captivity. A caged blue jay was reported tearing strips of newspaper and pushing them through the bars of their cage to rake in food that had dropped out of reach (Jones and Kamil 1973).

Rooks

Rooks have only been observed making tools in captivity. Apart from hooks (see below), rooks

also modify tools to make them functional. For example, rooks were presented with a collapsible platform task (Bird and Emery 2009; see also Bird Tool-Use) in which a weight has to be deposited into a vertical tube to release a platform holding a treat. Four rooks had rapidly learned how the task worked by dropping stones, but then spontaneously dropped heavy sticks or inserted and then pushed down on lighter sticks to achieve the same effect. When rooks were presented with sticks already inserted into the tubes, but with side branches attached to stop them from passing through the vertical tube, they removed only those side pieces that prevented the sticks from becoming functional tools.

Sculpting Wire Hooks

NCC have been observed making hook tools (either using the barbs along the side of *Pandanus* leaves as hooks or fashioning hooks from the cutoff points of detached sticks; Hunt 1996; Hunt and Gray 2002; Klump et al. 2015). However, the discovery that a female NCC called Betty could bend straight pieces of wire into hooks to retrieve a bucket containing meat at the bottom of a tube was a revelation. Betty and her male partner, Abel, were provided with a straight piece of wire and wire already shaped into a hook. Abel stole the hook, but did not use it to retrieve the food. After a number of attempts at using the straight wire to reach the food, Betty then used the corner of the plastic tray the tube was standing in as leverage, to help bend the end of the wire into a hook and then used that end to pull up the bucket (Weir et al. 2002). She did this ten times in a more controlled experiment. Although the hooks were more bent in the wire to a shallow angle than true bends, they were successful in gaining the food. Of most interest is the fact that despite Betty's success in using the hooks, she continued to insert the straight wire, perhaps to spear the piece of meat in the bucket, as this had occasionally been successful.

Although this discovery was stunning, it is inside of the natural capabilities of this species, as they not only fashion hooks but also bend some raw materials into hooks (Klump et al. 2015). Betty had also been provided with a model hook to base her design around. The finding that four captive rooks also bend wire into hooks, however, is more intriguing. How could rooks make tools of this type when they don't even use tools in the wild? The rooks had previous experience of using wooden hooks to retrieve small buckets from the bottom of vertical tubes and had previously inserted sticks (and stones) into tubes resulting in the deposit of a reward. It is possible that despite wire being an unknown substance for making a tool, they could rapidly learn about its properties after inserting it into a tube and trying to use it as a hook. This could have created a small bend, and the feedback from this causes the birds to continue bending the wire until they made a hook. Interestingly, the birds then flipped the hook into a functional orientation before using it successfully (Bird and Emery 2009).

Conclusion

Despite the rarity of bird species that make tools, the case of NCC is presented as one of the most complex forms of tool manufacture of any non-human animal, and the special case of wire bending in both NCC and four rooks demonstrates toolmaking on a par with our early ancestors. Bending an object into a hook has never been observed in any of our primate relatives. Although wire bending, especially in a non-tool-using species, appears remarkable, the fact that only a few birds across a small number of trials did this raises questions about the underlying psychological processes involved in this complex behavior.

Cross-References

- [Bird Tool Use](#)
- [Causal Reasoning](#)

- [Confounding Use of Tools on Physical Tasks](#)
- [Convergent Evolution of Intelligence](#)
- [Convergent Evolution of Intelligence Between Corvids and Primates](#)
- [Corvids](#)
- [Innate and Learned Tool Use](#)
- [Insight](#)
- [Nonhuman Tool Use](#)
- [Role of Experience in Tool Use](#)
- [Stick Tools for Foraging](#)
- [Tool Use](#)
- [What Makes a Tool](#)

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Tool Play

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Definition

Entertaining interaction employing a tool.

Introduction

Primates use natural and human-made items during play. In play, a tool (*sensu* Shumaker et al. 2011) is distinguished from an object by having an immediate and evident purpose. Tool play can be solitary or social. In solitary play an individual plays directly with the tool. In social play more than one individual employ the same tool either to play directly with or as a signal to convey information about a game. Comparatively, there are fewer reports of tool play in monkeys than in great apes.

Evidence from the Wild

The following types of tool play behaviors have been reported for wild primates (Goodall 1986; Sabater Pi et al. 1993; McGrew 2004; Ramsey and McGrew 2005; Nishida et al. 2010; Kahlenberg and Wrangham 2010; Shumaker et al. 2011).

Chimpanzees

During social play chimpanzees drag sticks, aimed throw dead sticks at each other, and use sticks and grass to bat each other. When wrestling, sometimes youngsters use leafy branches to press on a playmate's body. In the "tug-of-war" game, two competing chimpanzees (or seldom two groups) pull an object at the same time but in opposite directions.

To solicit play, the most common behavior is "play-start": an individual invites another to play while holding an object (usually a piece of vegetation, but rarely other object such as a piece of monkey skin or termite mound or an ant nest) in

the mouth (but also in the hand, foot, or groin pocket), teasing and displaying it to the potential play partner, sometimes waving it. This initiates chasing, and roles can be inverted if the partner manages to steal the object. There are other behaviors to invite play: an individual shakes, bites, or folds a branch or "leaf-clips" (tears a leaf while making sound to attract attention) in front of the desired playmate.

As a display to others, chimpanzees perform "leaf-pile pulling", where an individual walks backward while noisily pulling dry leaves with both hands and "leaf-pile pushing", a similar but less common behavior where the leaves are pushed forward instead.

In addition to the common behaviors described above, there are rare reports of social play using tools: subadults were once observed playing together with a blue duiker, and on one occasion an adolescent female used a monkey's tail (leftover from a kill) to tease a juvenile male.

During solitary play, chimpanzees push and rub stones, sticks, twigs, leaves, or food items to tickle themselves ("self-tickle"); play "blindman's bluff" (an individual drapes an object over the face and moves around); drape pieces of vegetation (liana, lichen) on their head or animal skins (baboon, bushbuck) on themselves; and repeatedly throw a stone some distance and get it back. There are also single observations of solitary tool play: once a young male tossed a round fruit into the air and tried to catch it several times (succeeding only once), and an infant used a stick to club an insect.

Chimpanzees treat objects or animals like infant conspecifics, a behavior called "doll play." They hold, cradle, carry, and take into their nest small pieces of vegetation (sticks, logs, woody vines and bark) in a way that resembles maternal behavior toward infants. Similarly, once a female groomed and carried a hyrax and slept with it at night in her nest. In a comparable behavior, two times an adolescent male used a branch in a way that it seemed to symbolize a playmate: he wrestled with the branch, and slapped and mounted it.

Chimpanzees exhibit tool play behaviors that seem related to adult tool use. Infants introduce twigs and grass stems into termite mounds and poke at other objects (e.g., mother's leg) or perform other actions with twigs that are similar to

those involved in termite fishing, sometimes during or after observing their mother termite fish. Infants use sticks to poke ant trails. Individuals show several tool play behaviors related with obtaining water. They insert long objects (such as twigs or grass blades) into water cavities and then suck them. They make a sponge by chewing leaves, and use it to absorb water or “extract” water from what seems imaginary tree holes. Finally, they fold leaves into cups or “leaf-spoons” to get water.

Bonobos

Bonobos exhibit two behaviors to solicit play. The first one is “play-start”, where an individual waves a small branch and runs with it as a signal to be chased by a potential playmate (any other player is later chased if gets and holds the branch). The second one is “leaf-clipping”, where an individual “leaf-clips” and holds the leaves in the mouth while watching the desired playmate.

A stick may function also as a play indicator: one player holds a stick while players wrestle or move without intending to get the stick and not directly playing with it, but if the stick falls, it is retrieved or replaced before reassuming play. Thus the function of the stick seems to be to signal that play is taking place.

Similarly to chimpanzees, bonobos also perform “tug-of-war” and “doll play”, the last one using red-tailed monkeys.

Orangutans

The following tool play behaviors have been reported for orangutans. “Play nests”, where individuals build nests during play with others but without using them for resting. “Snag riding”, where an individual pushes over a snag and rides on it as it drops, holding onto vegetation before it gets to the ground. “Doll play”, where a female makes a leaf bundle, which she treats like an infant, holding it during sleep. In addition, youngsters detach branches and drape them on themselves playfully.

Gorillas

There is only one report of tool play in gorillas: once an adult male used a long-stemmed flower to tickle an infant.

Capuchins

Two games involving tools are reported for white-faced capuchins. The first one is the “hair-passing game”, where one individual bites a tuft of hair from another individual who attempts to get it back. The second is the “toy game”, where one player places an object (stick, leaf, bark fragment, or inedible fruit) in the mouth, while the other tries to get it. Each game differs, but in both either the hair or the object is passed several times from one player to the other, mouth to mouth, until the hair is lost and the object cannot be used. In addition, in one occasion a young capuchin poked another individual with a dead branch he had detached from a tree.

Western Red Colobus

During social play, individuals brake and wave long leaves, sometimes hitting a player with them to stop this individual from getting leaves to use as weapons in the game. As an invitation to play, they manipulate vegetation fragments while looking at the potential playmate and once an individual used a piece of a termite nest to solicit play from a human observer.

Vervet Monkeys

A juvenile tossed and retrieved an empty half-coconut shell several times (Rindal et al. unpublished data).

Interspecies

Chimpanzees and baboons play together “tug-of-war” with vegetation.

Evidence from Free-Ranging Populations

Rhesus Macaques

“Doll-play” behavior was observed in a juvenile female whose mother had an infant: she treated a piece of coconut shell as if it were an infant (Gomez and Martin-Andrade 2005).

Evidence from Captivity

In addition to the wide variety of human objects that enculturated great apes used as tools in play, the following tool play behaviors have been reported for captive primates (Ramsey and McGrew 2005; Gomez and Martin-Andrade 2005; Shumaker et al. 2011; Alexander and Hines 2002; Gruber et al. 2010).

Chimpanzees

During social play chimpanzees throw several objects (including sticks and dirt) at playmates, brandish sticks, use sticks to club each other and employ objects to solicit play (including in “play-start”).

To start social play chimpanzees also use a “peekaboo”-like game, where an individual covers the head with a towel and extends the hands toward a potential play partner, sometimes placing a towel on the face of another individual. Once, a youngster spontaneously began to cover and uncover his face with bedclothes in a “peekaboo” game.

During solitary play chimpanzees balance and climb poles, drape a wide variety of objects on themselves, use elongated pieces of vegetation and nails to probe holes and crevices, use containers to obtain and carry water, play “blindman’s buff” by covering the face with a towel and walking on the ground or in a tree, and exhibit “doll play” behavior. In addition, they have been observed to poke free ranging chickens in a game.

Bonobos

During social play bonobos use different objects (e.g., sticks, branches, paper) to strike and poke other bonobos or humans and drag a variety of objects (including a playmate who holds the object being dragged). To solicit play bonobos hold a stick in the mouth and agitate it, aimed throw objects, or roll a container in front of a potential play partner.

During solitary play bonobos throw and drag various objects, place buckets on the head, play “blindman’s buff” by covering their faces with objects (e.g., paper, branches) and moving around, and sit on an object (e.g., blocks and

balls) pushing their bodies across the floor with their legs. There are also single observations of solitary tool play: one time a female employed a piece of grass to gather ants from the ground, and another female pretended to drink from a bottle without actually ingesting any liquid.

Orangutans

During social or solitary play, orangutans place different objects (fragments of vegetation, cloth, rope, chains, food, and paper) on the head or around the neck. Once, two adolescents played a game taking turns: one individual put a shirt over the partner’s eyes and charged and wrestle him. In exploration, individuals dig with sticks.

Gorillas

Gorillas use branches (and once a piece of straw) for “self-tickling” and cover themselves with many natural and artificial objects during play. In one occasion, an individual used aimed throw during play.

The use of objects as dolls (“doll play”) by female gorillas has been reported several times. They treat objects (such stones, pieces of cloth, balls, shoes, and dolls) in ways similar to how mothers treat their infants.

Gibbons

Apparently playing, one time an individual pointed and threw a banana peel at a conspecific.

Capuchins

There are single observations of tool play in capuchins: a male draped a cloth around his neck, an individual put a bucket on its head, and a pet capuchin employed cloth towels to entice a kitten in play.

Vervet Monkeys

Individuals treat a toy doll in ways similar to how female vervets interact with infants, including performing an inspection of the “anogenital” area of the doll.

Macaques

Tonkean macaques drag branches during play. On one occasion, a rhesus macaque wore cloth pieces

over the head and face during play. Once, playfully, a long tailed macaque spontaneously tossed a rubber ring back to a human.

Conclusion

Tools used by wild primates in play consist mostly of pieces of vegetation, although other natural (such as stones and animals and their products) and rarely artificial (stolen from humans) objects are also used. Captive primates have access to a wide variety of both artificial and natural objects to use as tools, including toys, as a result of enrichment programs. Enculturated great apes use an extensive diversity of objects as tools during play with conspecifics or other species including humans. These apes play with toys in ways that are comparable to how human children play (e.g., they feed, dress, and hairbrush dolls and pretend to eat and drink from empty bowls and cups).

Many of the tool play behaviors exhibited by primates both in the wild and in captivity are cognitively complex. These include imaginary or symbolic (pretense), communication (signals), and those that resemble subsistence tool use (such as termite fishing). Several tool play behaviors are present both in the wild and in captivity in the same species, for example “play-start”, “blindman’s bluff”, and “doll play”. Furthermore, some tool play behaviors are exhibited by all great apes, for example, “doll play”.

In order to unequivocally distinguish tool play from object play, it is essential to be able to infer purposiveness in the behavior (Shumaker et al. 2011). However, this is not always easy to do, and it is likely that tool play is underreported in primates.

Cross-References

- [Evolution of Play](#)
- [Object Play](#)
- [Play and Tool Use](#)
- [Social Play](#)
- [Tool Use](#)

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Tool Use

- [Fish, Amphibian, and Reptile Tool Use](#)

Toolmaking

- [Tool Manufacturing](#)

Tool-Use Tasks

- [Confounding Use of Tools on Physical Tasks](#)

Top Dog

► [Tall Poppy](#)

Tormenting

► [Child Abuse and Bullying](#)

Totemism

► [Ancestor Worship](#)

Touch

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Introduction

As I approach the door to my office, I unzip the pouch where I keep the keys to my office and fumble for my keys. I am engaging in a haptic search where I will use only my sense of touch to locate the keys. Specifically, I am attempting to use the low-threshold mechanoreceptors (LTMRs) of the skin on the tip of my fingers to find the sharp metallic edge of my keys or the soft woven strap that is a part of the key chain holding the keys. In attempting to use only the sense of touch in searching for my keys, I am using the receptors found in the skin, the largest and most versatile organ of the human body which covers an area of approximately 2 m² (McGlone and Reilly 2010). Many times, the search is successful using only the receptors found in my skin. However, sometimes I cannot locate the important signs that distinguish the keys with my sense of touch alone and must resort to other sensory signals to find them (e.g., the sound the keys make as they jingle in the pocket

when I shake my bag, or the blue of the woven band of the keychain when I finally resort to a visual search when all other senses have failed me).

Discriminative Touch

The skin can be broken down into two very large areas including the glabrous, or hairless, skin of the palm and fingertips as well as certain parts of the face and the soles of the feet, and the hairy skin found throughout the rest of the body. The glabrous skin contains four different receptors that are characterized as low-threshold mechanoreceptors (LTMRs) that vary in terms of their adaptive responses to continuous stimulation and the size of their receptive fields – the area of skin to which the cell is responsive. In terms of their adaptive responses, LTMRs show a fast adaptation rate (fast adapting – FA cells) or slow adaptation rate (slow adapting – SA cells). FA cells, which include Meissner's corpuscles and Pacinian corpuscles, respond to deformation of the skin with an initial burst of action potentials that quickly subsides with continued exposure to the stimulus. When the stimulus is removed, there is another burst of action potentials. SA cells, which include Merkel's disks and Ruffini endings, respond with a continuous flow of action potentials during sustained contact with the stimulus. These action potentials subside once the stimulus is removed. In terms of the receptive fields of the LTMRs of the glabrous skin, those close to the surface of the skin (Meissner's corpuscles and Merkel's disks) are the most sensitive and have smaller receptive fields, while those cells deeper in the skin (Pacinian corpuscles and Ruffini endings) are less sensitive and have larger receptive fields. The fast adapting Meissner's corpuscles, with their small receptive fields, will be the most helpful in my haptic search for my keys.

The LTMRs are specialized receptors that effectively transduce mechanical forces contacting the skin into nerve signals that are then sent on to higher levels of the central nervous system. When exposed to vibrations, the LTMRs respond to different vibratory frequencies providing different types of information regarding the stimuli

encountered. The Pacinian corpuscles provide information about vibratory stimuli vibrating at frequencies between 40 Hz and 500 Hz and provide a sense of vibration (McGlone and Reilly 2010). McGlone and Reilly (2010) indicate that Meissner's corpuscles provide a sense of flutter from vibrations in the range between 2 Hz and 40 Hz while the Merckels disks provide a sense of pressure in the 0.4–2.0 Hz range. Finally, a buzzing sensation is provided by the Ruffini end organs from stimuli vibrating in the 100–500 Hz range (McGlone and Reilly 2010).

Abraira and Ginty (2013) indicate that the difference between the Type I (small receptive fields) and Type II (large receptive fields) SA cells is the regularity of their static-phase firing rates. SAI cells demonstrate a more irregular interspike interval than SAII receptors.

The LTMRs of the somatosensory system relay information regarding touch sensations to the brain via axons that synapse with second-order neurons in the dorsal root of the spinal cord or at the level of the brain stem in the dorsal column nuclei (Abraira and Ginty 2013). In the discriminative touch system described up to this point, the fibers running from the receptor cells to the spinal cord are highly myelinated A-beta fibers, whereas in the social touch system that will be discussed below, the fibers connecting the receptors to the spinal cord are lightly myelinated or unmyelinated C-fibers. Both A-beta fibers and C-fibers are believed to transmit noxious or painful stimuli to the spinal cord.

The receptor cells of the touch system are found mostly in the border region between the outer (epidermis) layer and the inner (dermis) layer of the skin. The number of receptors vary greatly depending upon the specific area of the body and the sensitivity of these areas of the skin also vary greatly depending upon the specific receptors found in that area and the types of connections these receptors make with the spinal cord and the brain.

The slowly adapting cells differ in the regularity of their firing rates. Specifically, SAI cells, with their location closer to the surface of the skin, have significantly smaller receptive fields and respond to stimulation with greater

irregularity in their inter-spike rate than found in SAII cells (Abraira and Ginty 2013). These cells respond to mechanical forces on the skin with a continuous, but somewhat irregular response throughout the stimulation (Abraira and Ginty 2013). They respond most effectively to “contact with corners, edges, and curvatures of objects” (Abraira and Ginty 2013, p. 621). They are also very sensitive to the position and velocity of stimuli due to their high spatial resolution (Abraira and Ginty 2013).

Social Touch

In addition to the receptive cells found in the glabrous skin, there are receptive cells found in the hairy skin. While there are many of the same receptor cells in the hairy skin as there are in the glabrous skin, there are also receptors that are found only in this type of skin. These cells have been called C-tactile (CT) receptive cells and connect to the spinal cord with unmyelinated C-fibers (McGlone et al. 2014). Evidence suggests that these receptors are responsible for the pleasant sensation associated with the touch of a loved one or the gentle caress of a caring individual (Ackerley, Saar, McGlone, and Wasling, 2014). Specifically, CT cells respond most effectively to slow stroking motions (in the range of 1–10 cm/s – Ackerley et al. 2014). Research indicates that these receptors respond most effectively to softer stimuli such as a soft brush compared to a harsh or rough surface such as that found on sandpaper (Essick et al. 2010).

The route of the CT receptors to the brain is also different from the route of the LTMRs relaying discriminative touch information. In particular, the unmyelinated C-fibers connecting these cells to the brain use a very slow conduction velocity compared to the myelinated fibers connecting the discriminative cells to the spinal cord. The CT fibers send their signals at a rate less than 2 m/s, whereas the discriminative fibers rates are closer to 60 m/s (Essick et al. 2010). In addition, they connect to different structures within the brain than the cells of the discriminative touch system. Using the mechanical stroke of a soft

brush on the forearm, an area known to have CT innervation and the palm, an area known to be devoid of CT innervation, and measuring brain activation using a PET scanner, McGlone et al. (2012) noticed different areas of activation depending on the types of receptor cells activated. Specifically, a slow stroke on the forearm, activating CT receptors in the forearm that send their signals along unmyelinated C-fibers, results in activity in the posterior insular cortex and the mid-anterior orbital-frontal cortex (OFC). These researchers indicate that stimulation of the palm, which does not have CT receptors, results in activation in the primary and secondary somatosensory cortices that process discriminative touch signals. While such stimulation on the palm is often considered pleasant, McGlone et al. attribute this experience of pleasure on stroking the palm to a learning process. Meanwhile, the stroking of the hairy skin in a way that stimulates the CT receptors causes an innate response in the limbic-related structures of the brain supporting the affective touch hypothesis that “the role of the CT system is to promote emotional, hormonal, and behavioral responses during contextually appropriate intra- and interactive tactile behaviors, such as nurturing and grooming” (McGlone et al. 2012, p. 1787).

The CT system has been linked to the development of social bonds in infants and in the connection between infants and their mother and may develop even before birth (Casio et al. 2019). As the infant develops, touch communication continues to play an important role in the child’s social development. Mothers and their infants interact with each other by touch in 65% of their interactions with these interactions frequently resulting in immediate reductions in both behavioral and physiological reactions to stress (Casio et al. 2019). Such social touch likely plays an important role in the social bonding resulting in successful attachment (Casio et al. 2019). In addition, when this type of touch is missing (for example, when the mother is clinically depressed), its absence can lead to problems. Infants deprived of touch from their caregivers or who actively avoid

it may end up with sensory processing problems such as over sensitivity (Casio et al. 2019). The disordered development of autism may make children overly sensitive to this type of touch which they may perceive as unpleasant causing them to avoid it and miss out on this important aspect of social bonding (Casio et al. 2019). The importance of touch continues throughout development with the connections between the peripheral touch receptors and the brain continuing to develop. Research indicates that the intensity of responses in the portions of the brain receiving the signals increases as the child develops from childhood into adulthood suggesting continued maturation of the social touch circuitry with continued brain development (Casio et al. 2019).

Conclusion

Clearly, touch is an important sensory modality providing important information to the individual about that person’s immediate surroundings. Touch can be used to identify objects when visual and other cues are not available and can aid in the process of object identification when other cues are not sufficient. Social touch plays an important role in human bonding and the development of social skills and human affiliation. The social touch system also appears to be different from discriminative touch with receptor cells found only in hairy skin, with the target of these cells being in different structures within the brain (McGlone et al. 2012). Research is currently underway to fully understand the importance of touch and how it might influence all aspects of life. We can look forward to these important discoveries so that we can better understand our sense of touch and the important information it gives us.

Cross-References

- [Sensorimotor Play](#)
- [Therapeutic Touch](#)

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Towards Methodological Pluralism in Psychological Sciences

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Synonyms

Anthropology; Context – sensitivity; Ecological validity; Human behavioral ecology; Interdisciplinarity; Methodological and phenomenological narrowness; Methodological pluralism; Psychology

Definition

An overreliance on experimental methods in psychology comes with its problems of low context sensitivity, ecological invalidity, and limited scope of study. A move towards interdisciplinarity and methodological pluralism, along with an increased attention to the cultural context of behavior, can give greater validity to its findings, making psychology a more robust science.

Introduction

Gordon W. Allport, in his Presidential address at the 47th Annual Meeting of the American Psychological Association (1939), discussed the results of a survey they had conducted. It showed an increasingly empirical, mechanistic, quantitative, and analytic focus in the field of psychology. He warned against a “slavish subservience” to such a paradigm, pointing out how as a science, psychology, and its researchers ought to also be *rational, qualitative, idiographic*, and even *non-operational* (Allport 1940). Over the years, many researchers have pointed out this narrowness of the experimental methodology, including pioneers in the field such as Solomon Asch, Paul Rozin, Egon Brunswik, Michael Cole, and Ulric Neisser. The father of experimental psychology, Wilhelm Wundt, himself expressed his concerns about the inadequacy of the methods of experimental testing (Cole n.d.). However, a central part of psychology still remains primarily occupied by the experimental paradigm, dictating a quantitative tradition of collecting and interpreting data (Smith et al. 1995).

A major pitfall of such an experimental paradigm is the fact that it takes the human mind outside of its sociocultural environment. Jerome Bruner vociferously stressed upon the importance of culture in our psychological processes (Mattingly et al. 2008). Culture is intimately and inextricably linked with the way we think, feel, process information, interact, make decisions, and behave. Most psychological processes depend on

prior, culturally organized experiences, which differ greatly between societies. However, this relationship gets lost in the current state of psychological methods, which are based on carefully controlled experiments within the laboratory.

A Historical Unity

Psychology and Anthropology: An Important Relationship

Psychology and anthropology have seen some good days of conversation and interaction. Researchers from both the disciplines worked closely together for many years and the fields yielded much influence over each other. Psychologists like Wilhelm Wundt had, among his students, eminent future anthropologists like Franz Boas and Bronislaw Malinowski. Works of Sigmund Freud and his disciple Carl G. Jung was used by anthropologist Bronislaw Malinowski who, via ethnographic data, challenged the universality of Freud's formulation of the Oedipus complex (Bock 1988). Margaret Mead was influenced by Freud's ideas and used material from the Manus Islanders to amend his findings. Anthropologist and linguist, Edward Sapir (known for his linguistic relativity hypothesis) led a course on "The Psychology of Culture" at the University of Chicago (Mattingly et al. 2008). Researchers from both fields were also known to engage in substantial collaborations with each other. Psychologist Jerome Bruner worked in intense collaboration with researchers like Clifford Geertz, Claude Levi-Strauss, and Lev Vygotsky, for multiple years. Bruner taught at both departments of psychology and social relations increasingly attuned to the contributions that anthropological studies were capable of making in psychology. Michael Cole, working on numerical cognition, collaborated with anthropologists to demonstrate the impact of language in symbolization and the importance of culture in cognition (Cole 1967). These collaborations led to an insistence upon a meaning-centered approach in psychology, opposing the reductionist framework of an experiment-only paradigm. An interpretive framework was stressed upon, which turned to

be fundamental in the cognitive revolution of the 1950s (Mattingly et al. 2008).

Cognitive Science

Cognitive science arose as an interdisciplinary field, doing a scientific study of the mind and its processes. One of its great achievements lay in the integration of insights from linguistics, philosophy, anthropology, psychology, neuroscience, and artificial intelligence. This was followed by the emergence of cognitive anthropology in the 1950s, which embraced the idea of culture and understood its implications for mental processes. Cognitive anthropology, like many subfields of cognitive science, studied various theories on the representation of meaning and mental models. With collaboration between anthropologists and psychologists booming, a variety of formal and computational methods for analyzing and representing knowledge were also developed (Bender et al. 2010). However, methodological differences between the fields began to become salient, following a division of labor in the research questions: psychologists started studying *how* people think and anthropologists focused on the *what* (D'Andrade 1981). This led to an unprecedented dissociation of the two disciplines, each establishing themselves as unrelated departments. Eventually, the disciplines grew considerably divorced from each other's insights and developed a distaste for each other's methods: anthropologists were turned off by cognitive psychology's focus on studying undergraduates within highly artificial lab situations, using tightly controlled experiments and ignoring social contexts and real-world relevance; cognitive psychologists started to perceive anthropology as a story-telling enterprise, lacking in experimental rigor and making claims without presenting supporting data (Bender et al. 2010).

A Theoretical Unity

Despite the division of labor, a complete separation of the questions of content (what) and processes (how) of the mind is not possible without losing out on meaningful aspects of human behavior. Given that we grow up, adapt to, and function within a sociocultural world, culture affects not

only *what* people think but *how* they think. Culture provides a common ground for both research programs, and thus, for both disciplines. However, where many anthropologists are deeply involved in the study of culture, contemporary psychologists tend to bypass the mention of culture at all in their studies.

Our social and cultural lives are crucial contributors in the organization of our cognitive processes, making the study of culture in cognition indispensable (Bender et al. 2010). Developmental processes such as autobiographical memory and theory of mind capacities, due to their dependence on cultural environments, vary considerably between societies (Astuti 2015; Mayer and Träuble 2015); studies in linguistic relativity show that languages influence thought, mental processes, and behaviors (Boroditsky 2001); cultural constructs of individualism and collectivism have shown well-documented effects on cognitive processes of perception, reasoning, categorization, and attribution (Kim and Markus 1999; Nisbett et al. 2001).

The Importance of Culture in Cognition

Humans are overwhelmingly submerged in a cultural environment; it stays with us throughout our developmental period right up till we die. No other species is so thoroughly cultural. And indeed, if our brains are organized by experience (including learning), and experience is organized by culture, it naturally follows that culture would be a crucial formative force in the cognitive processes (Bender et al. 2010). Following are two examples demonstrating the importance of taking culture into account, while studying and understanding cognition.

Theory of Mind Theory of mind (ToM) is described as an innate cognitive module by which humans attribute mental states – beliefs, intents, desires, emotions, knowledge, etc. – to oneself and others (Butterfill and Apperly 2013). It is understood to be a universal ability in humans, usually arising at the age of 4 (Huemer et al. 2018). Quite contrary to this, some cultures practice a doctrine, stipulating that it is not possible for any individual to know what is inside other

people's minds and it is morally wrong to do so. This is called the “opacity of mind” doctrine (Robbins and Rumsey 2008). Mayer and Träuble tested ToM capacities in children from Samoa, a culture practicing the opacity of mind doctrine. Using the popular false-belief task paradigm, they found Samoan children to spectacularly fail in comparison with German children (Mayer and Träuble 2015). The experimental results directly suggested that Samoan children lack in ToM capacities or show a developmental delay. However, taking the children's social and cultural contexts into account, much richer inferences can be drawn: (a) Samoan children choose to not ascribe mental states due to the opacity of mind doctrine; (b) “intention” as a concept is irrelevant in Samoa (it is literally impossible to say, “I didn't mean to”), which is what the false-belief task was based on; (c) the children might have been confused by the “easiness” of the task and peculiarity of experimental settings, and indeed one of the children tricked the task itself (Astuti 2015); and (d) receiving instructions from anyone but their parents is unfamiliar to the Samoan children so they stay quiet and thus, fail the task (Mayer and Träuble 2015). Thus, it can be argued that an attention to the cultural environment can not only help in designing better experiments but also in better understanding the mental processes itself.

Visual Information Processing Studies of attention allocation and visual processing in cognitive science are heavily focused on understanding the underlying mechanisms, in an endeavor to find general regularities, if not laws, of visual perception. Egon Brunswik demonstrated the importance of *context* in studying visual processes, such as size perception (Brunswik 1956). More recent studies in visual perception have shown considerable differences between populations, which can be attributed to their cultural backgrounds. A study by Boduroglu, Shah, and Nisbett attempted to study attention allocation by using simple visual change detection tasks (Boduroglu et al. 2009). When shown changing groups of figures, American participants were quick at detecting changes at the center of the

field, whereas East Asian participants were significantly slower. However, the American participants were poorer at detecting changes happening on the periphery, while East Asian were considerably quicker. In such a case of varied results on the same task, culture can be an important explanatory variable: (a) East Asian participants are part of predominantly “collectivistic” cultures, which have complex, interdependent social networks, demanding more holistic cognitive styles; (b) holistic cognitive styles determine a wider focus – with great attention to one’s field and surroundings – explaining their performance in the visual change detection task; and (c) Americans come from social worlds whose ideologies emphasize individuality and independence, leading way to a narrower focus and attention to central objects. Indeed, multiple studies using various tasks have corroborated these findings (Chua et al. 2005; Nisbett and Masuda 2003), indicating a robust influence of culture in visual information processing.

Other examples of psychological and cognitive processes where culture has been seen to exert significant influence include, but are not limited to, attribution (the case of fundamental attribution error; Krull et al. 1999), fairness judgments (Henrich et al. 2005), object categorization (Nisbett and Masuda 2003), sense of morality (Baumard 2016), and even intelligence-testing (Cole n.d.). A complete understanding of human behavior indeed requires an attention to culture and context, along with the study of underlying mechanisms. Geertz called this a “thick description” of a behavior, which takes into account the cultural structures within which behaviors are produced, perceived, and interpreted (Geertz 1973).

A Methodological Disunity

Despite a historical and a theoretical unity, there is no question that psychology and anthropology have moved apart considerably as disciplines, with a major decrease in collaborations and interest towards each other’s findings. A primary reason for such a dissociation can be said to be the methodological differences between the fields. While anthropology studies human behavior

using naturalistic methods like ethnographic fieldwork, participant observation, unstructured and semi-structured interviews, etc. (Bernard 1994); psychology places a major emphasis on quantitative, experimental, and controlled studies in laboratory settings, in order to provide robust predictions (Howitt and Cramer 2007). However, in its urge to be seen as an advanced science, psychology has developed an overreliance on the experimental method, bypassing crucial steps of scientific investigation (Fish 2000). In any natural science study, from physics to biology and even ethology, a general logic of steps is usually followed: systematic observation of phenomena of interest; use of logic and convergent evidence to elaborate that understanding; and choosing investigative methods *in accordance with* the problem/object of study (Fish 2000; Rozin 2001). However, this is not reflected in the view of “science” in psychology, which tries to fit restrictive experimental paradigms and statistical analyses to all objects and phenomena of study, rather than the other way round. In this, they also tend to do away with naturalistic observations and push away anything less-experimental to the realm of less-scientific (Rozin 2001).

Shortcomings of Experimental Methods

Lab-based experiments give researchers the desired control to be able to find robust causal relationships (known as internal validity), provide relevant supporting data, and enhance replicability for verification (Roe and Just 2009). Experimental psychology has long built upon this by expanding procedures, devising new designs and evaluations, but without questioning the underlying framework (Brunswik 1956). The designing of experiments, given the constraints of the lab, and an ignorance of the real-life context of behaviors, has led to serious shortcomings:

Context Impoverishment Behaviors are adapted to specific environments for optimality and derive much of their meaning and function in view of the contexts that they are performed in (cultural environments being one of the main ones). However, as Solomon Asch disapprovingly pointed out, there is a strong tendency in psychology to gain rigor *at the*

expense of context sensitivity (Rozin 2001). Experimental frameworks tend to provide an individual-centered specification of behaviors, stripping away important parts of the context as confounding variables. Despite the experimental control this provides, it leads to a poor understanding of the behavior itself. For example, a wink, when objectively defined, is “the twitching and rapid closing of an eye.” It is only within a given context that one can understand the relevance of said wink – a signal from one friend to another before pulling a prank on the teacher or a covert gesture signaling intimacy between two people standing in a group, etc. (Geertz 1973). Thus, context impoverished explanations not only lack in real-life relevance but also applicability. Moreover, this makes way for undermining the cross-cultural aspects of behaviors (see criticism on psychology as being heavily ethnocentric; Fish 2000).

Low Ecological Validity Ecological validity of an experiment determines the extent to which the experimental setting is representative of real-life context and thus the extent to which the findings can be generalized (Roe and Just 2009). Brunswik (1956) was one of the first to point out the lack of ecological validity in psychology experiments, using the case of perception research. He reproached the psychologist’s preoccupation with studying “narrow-spanning problems of artificially isolated proximal or peripheral technicalities of mediation, which are not representative of larger patterns of life” (Brunswik 1956). While designing experiments, it is important to maintain integrity of the real-life situations that one is trying to study, pay attention to the social and cultural contexts of one’s participants, and take into account the participants’ interpretation of the experimental situation (Neisser 1976). However, most contemporary psychology experiments do not fulfill these requirements of ecological validity. Examples include, playing ultimatum and dictator games with strangers; getting handed a sum of money like windfall, which one then has to divide or put in a common jar; doing a repetitive joint task with a computer; and looking at animated creatures on the screen for judgments of opacity, etc. The concerns extend not only to the

experimental contexts but also the nature of tasks, the stimuli, and instructions given to participants (Schmuckler 2001).

Limited Scope An insistence on studying behaviors in the lab severely limits the range of social and psychological phenomena that can be explored. For example, important social processes like marriage, kinship, friendship, rituals, traditional pedagogical practices, etc. cannot be meaningfully isolated and studied in the lab. This limits the range of processes that psychologists can aim to study and discourages the discovery of new phenomena and creativity. Paul Rozin referred to this as a “phenomenological narrowness” (Rozin 2001).

Moving Towards Methodological Pluralism and Interdisciplinarity

Experiments bring with them a major benefit of providing internal validity and establishing causality, but it does so at the cost of context orientation, ecological validity, and real-life applicability (Roe and Just 2009; Elmes et al. 2011; Smith et al. 1995). Discontent with psychology’s methodological narrowness has led to a slight move away towards real-world studies and an integration with other data collection methods like field experiments, diary studies (Smith et al. 1995), ethnographic approaches and action research, naturalistic observations, and case studies (Elmes et al. 2011). However, such approaches remain relatively scarce and greater efforts need to be made in order to adopt a multimodal approach and move towards interdisciplinarity. The case of human behavioral ecology and evolutionary psychology, two scientific disciplines invested in the study of human behavior, shows how this goal can be meaningfully achieved.

Multimodal Approaches

While lab experiments provide greater rigor in identifying causal relationships, doing experiments in the field, with minimal alterations of the context, can provide ecologically valid results. Developing research schemes by combining lab and field experiments can therefore provide both external and internal validity to findings (Roe and

Just 2009). List exemplified this approach in his study on gift exchange behavior, where he created one research context in the lab and the other in a sports-card market with only minimal alterations (List 2006). By broadening our methodological scope in this manner, the advantages of a “sterile” lab experiment can be combined with context-relevant field data to provide sharper and more convincing results. Additionally, other sources of evidence such as surveys, questionnaires, ethnographies, etc. can be used to provide convergent evidence to strengthen one’s case (Rozin 2001).

Interdisciplinary Collaborations

Psychologists can participate in collaborations with anthropologists and other social scientists, in order to gather relevant information about the cultural contexts. Knowing about the sociocultural environments of one’s study, as well culture-specific behavioral norms relevant to one’s population of interest, can allow researchers to design ecologically valid experiments and make appropriate interpretations from the collected data. For instance, in the case of Samoan children, as suggested by Rita Astuti, knowing about the opacity of mind doctrine and cultural norms of obedience can lead to designing better experiments with the appropriate instructions for the participants. Only then can one be certain that they are *really* studying these children’s Theory of Mind capacities (Astuti 2015; Mayer and Träuble 2015). Anthropologists can have great contributions in psychological studies by providing information on how the cognitive processes of interest are employed in natural environments, and thus, help decide what kinds of hypotheses and design would be relevant to understanding the underlying processes (Bloch 1991).

The Case of Human Behavioral Ecology and Evolutionary Psychology

Many behavioral characteristics that are of interest to psychologists and other behavioral scientists are adaptations that have been shaped by natural selection during the course of our evolutionary history. Evolutionary psychology and (EP) human behavioral ecology (HBE) are the two dominant fields of study that apply evolutionary approaches towards understanding human

behavior, both having arisen from the parent discipline, sociobiology. Where evolutionary psychologists primarily work with the assumption that psychological mechanisms are the main unit on which natural selection operates, HBE considers behavior itself to be the main unit of selection (Durrant and Ward 2015). Both these approaches are crucial, given that any proximate description of a behavior – including psychological mechanisms – cannot be complete without understanding the ultimate explanation – the adaptive value of the behavior within the environmental context (Cronk 1991).

Researchers in these fields stress upon the importance of ecological constraints and natural and social environments for explaining observed behaviors (Nettle et al. 2013). In view of these research goals, the methodological repertoire includes, laboratory experiments, naturalistic observations, ethnographic work, evolutionary modeling, and participant observation. Given this multi-method approach, these fields provide good examples of a scientific study of human behavior, both ecologically valid and sensitive to the context. This is especially true of HBE which often works within departments of anthropology.

The methodology of HBE includes a combination of naturalistic observations and hypothetico-deductive models. Hypothetico-deductive models are built to predict how measurable variations in the social and natural environment affect an individual’s behavior, further affecting the individual’s chances of survival and reproduction (Nettle et al. 2013). Such models are constructed by collecting empirical data from self-report descriptions and surveys, such as national censuses, regular surveys of members of a cohort, and one-off questionnaires (Nettle 2012), as well as interviews and archival research (Winterhalder and Smith 2000). This is followed by formulating testable hypotheses and testing them out using *quantitative* naturalistic observations (Winterhalder and Smith 2000). Such a combination of models and naturalistic observations not only makes the findings more valid but gives the field more methodological rigor, vitality, ecological validity, and broad scope (Nettle et al. 2013). This was demonstrated by Nettle in his study of the relation between parental investment

and socioeconomic factors. He carried out direct observation of parents and children's behavior in natural public spaces, to extend and increase the validity of the conclusions produced by the previous self-report-based studies (Nettle 2012).

Attending to the issue of culture, which is the primary context where all human behavior takes place (as discussed above), participant observation can be another important methodological tool for HBE (Winterhalder and Smith 2000). This method, more regularly used in cultural anthropology, understands *culture as the context* of behavior. It can be described as “a way to collect data in a natural setting by ethnographers, who not only observe but also take part in the common and uncommon activities of the people being studied” (Bernard and Gravlee 2014). Participant observation has added epistemic value for HBE because, in addition to quantitative data collected by naturalistic observations, it allows collection of qualitative data like narratives, audio recording of people telling folktales, videotapes of people making canoes, getting married, having an argument, etc. (Bernard 1994). As Bernard (1994) explains, “quantitative and qualitative data inform each other and produce insights and understanding in a way that cannot be duplicated by either approach alone. Whatever data collection method you choose, participant observation maximizes your chances for making valid statements.” For example, Schnegg claims that participant observation provides information about relationships between people as well as the context in which behavioral data collection took place (Bernard and Gravlee 2014). Interestingly, this is precisely what Nettle (2012) pointed out to be one of the weaknesses of his parental investment study: by making only naturalistic observations, he was not able to infer relationships among the observed individuals and their lives inside their homes, which could have provided important insights to the study.

Conclusion

Maurice Bloch rightly said, “the basis of cognitive science is a combination of different disciplines, each with a contribution to make, but with a single

aim” (Bloch 1991). Understanding human behavior and human lives is no easy task. And psychology is definitely not the only discipline invested in this pursuit. Trying to solve a problem of such complexity by a singular methodological framework can only lead to an incomplete understanding. This entry is not to propagate the view that experimental paradigms should be replaced. Instead, newer avenues for data collection must be explored, and the importance of anthropology and other social sciences in the fields of psychology must be restored.

Cross-References

- [Context, Environment, and Learning in Evolutionary Psychology](#)
- [Cross-Cultural Variation](#)
- [Ecological Influences on Parent–Offspring Conflict](#)
- [Information Processing and the Interdisciplinary Perspective](#)
- [Methods and Enduring Impact of Behaviorism](#)

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Toxic Molecules in Seminal Fluid

► Semen Toxicity

Tradeoff

► Cost-Benefit Analysis

Trade-Off Between Exploration and Exploitation

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You could be reading this or you could be writing that long overdue article. The tradeoff is a natural one and it is the foundation of one of the oldest problems in animal evolution: How should an organism choose between exploiting a resource or exploring to find new resources? This problem is known as the *exploration versus exploitation trade-off* (EvE) and it cuts across domains – in decision research, visual attention, animal foraging, memory search, and computer science, the same basic problem repeatedly surfaces.

The diversity of situations in which this trade-off arises has, in turn, led to a diversity of solutions. In reinforcement learning, rules that achieve appropriate learning rates have elements of exploration intermixed with longer periods of exploitation (Sutton and Barto 1998). Rules such as the *epsilon-greedy algorithm* involve a greedy exploitative component that always chooses options with the highest known payoffs intermixed with some small (epsilon) amount of random exploration. The random exploration prevents the search from being captured indefinitely in local maxima and thus allows the search process to move away from bad initial guesses and to update its predominant choice if the environment starts to change. A similar algorithm based on physical properties of materials in relation to temperature is called *simulated annealing*. Simulated annealing uses “high temperature” phases that allow exploratory search (long distance jumps) through large regions of the search space before “low-temperature” regimes are invoked to exploit local regions of the space (using smaller jump sizes) that were discovered during the high temperature phase (Kirkpatrick et al. 1983). Social insect swarms, such as those of many ants and honeybees, exhibit analogous phases of diffusive and focused search in response to changing

resource distributions (Deneubourg et al. 1986). Finally, both biological evolution and artificial genetic algorithms address the EvE trade-off via altering mutation rates appropriate for moving through the adaptive landscape in smaller and larger steps. In some cases, these mutation rates can be altered in response to environmental changes such as stress – a process called *evolvability* (Gallardo et al. 2007).

Behavioral ecologists have observed this EvE trade-off in animal foraging, in a behavioral strategy called *area-restricted search* (Hills et al. 2013). This search strategy focuses search for resources in rich locations and avoids poor locations. The strategy accomplishes this by using sharp turning angles nearby where other resources have been found in the past and giving up on locations, by turning less sharply, when no resources have been found recently. This process therefore requires memory, as opposed to other search strategies, like Lévy flights, which do not. The amount of evidence needed to modulate between sharp and shallow turning angles depends on multiple factors, but giving up on a location is rarely due to a thorough search. The sensitivity of a search follows directly from what the organism expects to find locally in comparison with its anticipated opportunity cost for looking elsewhere. The anticipated opportunity costs can derive from personal experience or natural selection.

One of the most prominent models of EvE assumes that animals forage in *patches* of resources and are adapted to search optimally in their natural environment by knowing when to leave one patch and move to another. Animals do this by matching the instantaneous rate of resource acquisition within a patch with the long-term expected rate of resource acquisition across all patches. The optimal solution is provided by the *marginal value theorem* (Charnov 1976), and it has been shown to be effective in predicting a wide range of foraging behaviors in animals (Stephens and Krebs 1986) as well as humans (Hills et al. 2012; Pirolli and Card 1999).

From an evolutionary perspective, the EvE tradeoff is likely to be one of the most important

selective forces in the evolution of cognition (Hills et al. 2015). Numerous biological and behavioral aspects of cognition appear to derive from mechanisms that initially evolved to help animals explore in space. For example, the way humans control their attention is both biologically and behaviorally similar to the way many other animals forage in space (Hills 2006). This tells us much about the mind as it suggests that the attentional aspects of cognition are principally a search process (Hills et al. 2010). Moreover, by looking at the evolutionary development of cognitive search capacities, such as the capacity for simulating future action, we begin to explore much deeper questions, such as the evolution of the self (Hills and Buttefill 2015).

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Trade-Off Between Reproductive Fitness and Longevity

► Disposable Soma Theory

Trade-Offs

► Investment Versus Future Payoff

Tradeoffs in Mate Selection

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Synonyms

Mate preferences

Definition

The necessity for males and females to prioritize some qualities over others in potential mates in order to maximize reproductive success.

Introduction

A key factor in mate selection is differential parental investment offered by varying partners. Parental investment can be defined as the time and

resources devoted to raising one's offspring, thereby increasing the offspring's survival and reproductive success but limiting the parent's future reproductive activities (Trivers 1972). According to Trivers, there are sex differences in parental investment, especially in obligate levels of parental investment. In most species, females necessarily invest more in procreation than do males; female sex cells are larger and more metabolically costly, and females are responsible for internal gestation and lactation following birth. The sex whose typical parental investment is greatest will become a limiting resource for the opposite sex; thus, members of the lesser-investing sex will compete to breed with members of the higher investing sex, and members of the higher investing sex will be more selective of mating partners. While humans are included among those species in which reproduction comes at a greater cost to females than to males, human men typically invest a good deal of time and resources into their offspring, which makes them more selective in their mate choice as intention to invest increases.

Strategies for Optimal Reproductive Success

Both men and women have evolved strategies, guided by circumstantial cues, to optimize their investments in mating and child-rearing. In many species, the reproductive success of one sex is directly related to number of partners, but the other sex is limited in reproductive success by internal gestation and lactation. Males usually fall into the first category, females into the second; thus, women are a limited reproductive resource for men. This means that men must put more effort than women into intrasexual competition, or competition with members of the same sex for access to members of the opposite sex. Due to the sex differences in obligate parental investment, men stand to benefit reproductively from securing access to as many partners as possible (Buss 1989). The optimal mating strategy for men, then, is to devote a greater amount of energy to competition for mating access than to parental investment and to seek short-term relationships requiring little investment.

However, because women have fewer reproductive opportunities than men, and because

obtaining a greater number of mates does not create large reproductive gains for women, they should devote more time and energy to parental investment and seek long-term relationships in which their partners are willing and able to invest in offspring (Buss 1989). While short-term mating is more conducive to the optimal male strategy, both men and women engage in short-term mating. Women seeking a partner may use short-term mating to evaluate the quality of a potential long-term partner. Partnered women may also use short-term affairs as a means of obtaining better genes for their offspring from a highly attractive mate, while continuing to receive resources and investment from a long-term partner (Buss and Schmitt 1993). As levels of expected investment in relationship contexts increase, mate preferences and standards may change, and both women and men may be attracted to different qualities in short-term mates than in long-term partners (Gangestad and Simpson 2000), as will be discussed in more detail below.

Sex Differences in Mate Preferences

Research on mate preferences has tended to focus on a stark sex difference: men tend to value attractive mates more so than women, while women tend to value status and resources in mates more so than men (Buss 1989). In line with evolutionary theory, it is adaptive for individuals to be tuned into traits in potential mates that will best support successful production and survival of offspring. A man's value in reaching that goal may be more closely tied with his ability to offer resources to offspring, while a woman's value in doing so may be more related to her health and fertility (Buss 1989). Female fertility can be assessed by visual cues in appearance, which leads men to be more attuned to the physical attractiveness of potential mates. On the other hand, resource acquisition can be assessed by status and earning capacity, which creates in women a preference for these characteristics in potential mates (Symons 1979; Buss 1989).

Trade-offs in Mate Selection

Mate trade-offs can be understood in terms of economics: when given unlimited resources,

people spend freely on luxury items. However, when on a limited budget, people buy necessities first and may spend some leftover money on luxuries. The same principle applies to mate choices: individuals make different mating choices depending on the size of the “budget” at their disposal (Li et al. 2002). When describing an ideal mate, most individuals do not depict perfect 10 s; rather, they calibrate their desired partner traits to their own because this creates realistic mate standards (Campbell et al. 2001). Men desire at least a sufficient level of physical attractiveness in a mate, because women’s physical qualities can indicate their fertility status; although other qualities of women may have effects on child rearing, none of them are reproductively useful if she is not fertile. Likewise, because there is variation in men’s access to resources, and because access to resources affects offspring survival, women should require a minimum level of status or resource acquisition before they consider other traits in a potential mate (Li et al. 2002). Although a sex difference in preferences for physical attractiveness and resource acquisition exists, other traits, like personality and kindness, tend to be equally valued and prioritized by both sexes. Similarly, intelligence seems to be a necessity in a potential partner, as a sufficient amount of intelligence may be necessary for successful parenting (Li et al. 2002). However, the level of each of these characteristics that is considered “sufficient” may vary depending on relationship contexts.

Differences in Preferences Based on Mating Contexts

Strategies and mate standards may vary depending on the mating context and whether the union is intended to be short term or long term (Buss and Schmitt 1993). Both short- and long-term relationships have potential benefits and costs that vary differentially by sex. As previously discussed, men stand to benefit greatly from a series of short-term relationships with as many partners as possible. In short-term mating contexts, then, men should have lower standards for mate qualities. As explained by parental investment theory, women should be more selective of partners due to higher reproductive costs

for women than for men and because women are more likely than men to be the sole parent caring for offspring resulting from a short-term sexual relationship (Trivers 1972). As mating context commitment level decreases, both men and women desire higher levels of partner attractiveness, as good genes for offspring are the main benefit acquirable through short-term relationships (Buunk et al. 2002). However, in long-term relationships, characteristics indicating competence, cooperation, and good parental investment are more highly valued in potential partners (Fletcher et al. 2004).

Conclusion

Biological differences in males and females lead to differences in parenting requirements for men and women. Qualities that suggest good reproductive potential are found most attractive by prospective partners, but some of these qualities also vary between men and women, creating a sex difference in mate preferences. However, these preferences may shift according to the mating context and whether an individual is seeking a mate high in parental or genetic quality. As it is often not feasible to acquire a mate with high marks in both of these categories, men and women alike must make trade-offs in mate selection in order to maximize reproductive success.

Cross-References

- [Fertility](#)
- [Observed Mating Behavior and Women’s Long-Term Mating](#)
- [Reproductive Strategy](#)

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Traditional Life-Expectancy

- [Life Expectancy in Hunter-Gatherers](#)

Training

- [Apprenticeship](#)
- [Exercise](#)

Trait

- [Genetic Predispositions](#)

Trait Anger

- [Anger Proneness](#)
- [Sex Differences in Anger Proneness](#)

Trait Judgment

- [Inceptive and Derived Memory](#)

Trait Self-Esteem

- [Sociometer Theory](#)

Trait Theories

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Synonyms

[Dispositional theories](#)

Definition

Trait theories are the theories in personality psychology whose common denominator is treating traits as key elements in the description of personality. These include Allport’s theory, Cattell’s theory, Gray’s biopsychological theory of personality, Eysenck’s three-factor model, and the five-trait theory of McCrae and Costa. The integrative Big Five trait taxonomy is the most popular and most frequently used.

Introduction

While the representatives of trait theories do not share a common definition of a trait, they agree that it is a disposition to display behaviour in consistent patterns in various situations (Pervin and John 2001). Personality theorists understand traits in two possible ways: either as descriptive summaries or as internal causal properties of behaviours. The authors of the currently

predominant approach define traits as “dimensions of individual differences in tendencies to show consistent patterns of thoughts, feelings, and actions” (Costa and McCrae 1990, p. 23). This prehension includes not only behaviour but also thoughts and feelings. The third crucial term in the definition of traits, besides disposition and consistency, is the stability over time of a given person’s behaviour.

One field of research on personality traits is studying trait heritability. Metaanalyses have shown that the average effect of genetic contributions to individual differences in personality traits ranges from 30% to 50% (Plomin et al. 2008). The evidence for trait heritability is stronger for temperament-related traits (e.g., emotionality according to Buss and Plomin 1984).

Allport’s Theory

Gordon Allport (1937) defined traits as generalized personal tendencies which determine how humans behave in most of situations. This theory distinguishes between three types of traits: cardinal, central, and secondary dispositions. According to Allport, some traits may initiate behaviours. Allport’s theory makes two characteristic assertions with regard to traits. The first assertion is that traits are real entities derived from the nervous system. The second assertion amounts to the statement that apart from common traits there are also traits unique to each person. Simultaneously, Allport did not ignore the role of situation, claiming that traits do not have to be apparent in all situations.

Eysenck’s Theory

According to Hans Eysenck (1990), personality is hierarchically structured. Traits consist of groups of habits and combine into higher-order factors. Eysenck used factor analysis, a statistical method which allows to identify groups and subgroups of correlated behaviours or test items in order to discover the components of personality structure (Pervin and John 2001). By using this technique,

he was able to distinguish the three basic dimensions (so-called superfactors) of personality: (1) extraversion, (2) neuroticism, (3) psychoticism. Eysenck claimed that the individual differences in trait intensities are genetically and biologically determined and reflect differences in neurophysiological functioning. Eysenck’s theory suggests that traits are explanatory concepts. His assumption that the superfactors in a healthy human population are orthogonal (not correlated with one another) was questioned by Gray (1987), among others.

Cattell’s Theory

Raymond Cattell (1965) accounted for a greater number of traits in personality description than other trait theory proponents who used factor analysis. He distinguished surface traits, which can be studied with subjective methods, and source traits, which are the real expression of covariant behaviours and which can only be grasped using factor analysis techniques. To determine the structure of personality, Cattell used three types of observational data: L-data (life data), Q-data (questionnaire data) and T-data (test data). Cattell distinguished among cognitive-ability traits, temperament-stylistic traits, and dynamic traits. He eventually identified 20 personality traits.

The Big Five

The advocates of the Big Five model claim that the number of traits can be reduced to five. Though the names of these traits have not been standardized, the following traits are usually listed: (1) neuroticism (including “a tendency to experience dysphoric effect”), (2) extraversion (including “a preference of companionship and social simulation”), (3) openness to experience (including “a need for variety, novelty, and change”), (4) agreeableness (including “a willingness to defer to others during interpersonal conflict”), and (5) conscientiousness (including “strong sense of purpose and high aspiration level”) (McCrae and Costa Jr 1999, p. 143). The first stage of the personality research which led to

the identification of the five factors used a lexical approach (Goldberg 1990). It was assumed in this approach that there are colloquial names for the majority of universal and important personality traits, which are significant in contacts between people. The authors of the five-factor model of personality which explains the dimensions of the Big Five are Robert McCrae and Paul Costa (1999). They demonstrated that the Big Five structure can also be revealed based on questionnaire studies carried out in various cultural circles. It was found that there is a strong convergence between the results of both lexical and questionnaire studies (McCrae and Costa 1987). McCrae and Costa considered traits as fundamental, biologically determined tendencies. They also accounted for the fact that personality traits can be influenced externally (e.g., by psychoactive substances or traumatic factors) through the biological bases (McCrae and Costa 2008).

Many studies have shown that the Big Five traits are strongly affected by genetic and environmental factors. Both twin and molecular studies reveal genetic determinants of personality traits. The results of molecular analyses are less conclusive compared to twin studies. For instance, there is both evidence for and against a relationship between personality factors measured using the NEO-PI-R questionnaire and polymorphisms within the studied genes (e.g., the Serotonin Transporter Gene – 5-HTTLPR) (Ebstein et al. 2003). Indeed, the results of studies on the potential impact of specific gene polymorphisms on personality traits seem to indicate that individual genes do not have strong effects on the Big Five traits. Some authors (e.g., Bouchard and Loehlin 2001) interpret the genetic influences on personality from an evolutionary perspective. The proponents of the evolutionary approach suggest that some traits may have been more essential for survival than others.

Conclusion

While the representatives of trait theories were united in treating traits as key components of

personality, many differences can be found as well. These differences mostly involve the methods used to determine personality traits and the postulated number of these traits. For instance, Allport employed the lexical approach, while Cattell and Eysenck developed their theories using the methods of factor analysis. McCrae and Costa, in turn, referred to both lexical studies and factor analyses. Currently, some of the most popular models in personality psychology are personality models based on the five-factors idea. Objections to trait theories mostly concern their status as descriptive theories, as the traits do not explain human behaviour.

Cross-References

- [Genetic Predispositions](#)
- [Personality](#)
- [Twin Studies](#)

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Traits

- ▶ [Personality, Gender, and Culture](#)

Traits that Facilitate Continued Existence

- ▶ [Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches](#)

Transformed Information

- ▶ [Inceptive and Derived Memory](#)

Transient Ontogenetic Adaptation

- ▶ [Ontogenetic Adaptations](#)

Transient vs. Non-transient Ontogenetic Adaptations

- ▶ [Ontogenetic Versus Deferred Adaptations](#)

Transition

- ▶ [Rite of Passage](#)

Transmission of Sound

- ▶ [Distinguishing the Direction of Sounds](#)

Transmutations Theory

- ▶ [Jean-Baptiste Chevalier de Lamarck](#)

Transsexualism

- ▶ [Gender Dysphoria](#)

Trap Tasks

- ▶ [Confounding Use of Tools on Physical Tasks](#)

Traumatic Brain Injury

- ▶ [Specific Brain Damage](#)

Traumatic Insemination

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Synonyms

[Copulatory wounding \(pt.\)](#); [Hypodermic impregnation](#); [Hypodermic insemination](#); [Traumatic mating \(pt.\)](#)

Definition

The transfer of sperm through a physically inflicted wound (wound = trauma [Greek]).

Introduction

Traumatic insemination (TI) is a special form of traumatic mating (TM) that refers to cases where routinely “the partner’s intra- or extragenital integument is wounded by specialized devices in the direct context of copulation” (Lange et al. 2013).

This explanation excludes accidental cases of copulatory wounding, which perhaps can happen in any group of animals with internal fertilization. Other forms of TM refer to cases where only seminal fluid, but no sperm, is transferred through the wound, or traumatic penetration with neither sperm nor seminal fluid transferred (Lange et al. 2013).

Far from being a bizarre, even aberrant, behavior, recent systematic reviews (Lange et al. 2013; Tatarnic et al. 2014; Reinhardt et al. 2014) identified both TM and TI as being widespread in the animal kingdom. For example, TM is currently known to have evolved independently approximately 50 times.

Species vary in whether TM occurs inside or outside the genital tract. In some species the trauma is inflicted at a very specific location on the female body; in others, mainly concerning species where only seminal fluids are delivered through a wound, the location is not fixed, and TM can happen anywhere on the female body (Lange et al. 2014). The location the male uses to inject seminal substances might be related to neuronal manipulation (Lange et al. 2014), to bypass the female reproductive tract or to deliver physiologically active substances closer to their target site. Alternatively, the location of trauma infliction may be the result of selection on males, for example, if female responses to sperm have made it advantageous for males to inject sperm at specific sites only.

The trauma is inflicted by a variety of structures, differing in developmental origin, including penis spines, specialized stylet structures, or

spermatophores. In several species, even the chemical lysis of the female skin has been observed, through which sperms are subsequently delivered (Lange et al. 2013). The frequent analogous occurrence of TI strongly suggests a benefit to at least one of the involved parties.

Benefits of TI to Males

TI and TM have generally been discussed in the framework of sexual conflict. It is assumed that males performing TI benefit either by an advantage over other males or by gaining control over aspects of the female reproductive output (Lange et al. 2013; Tatarnic et al. 2014; Reinhardt et al. 2014). It has been suggested that sexual conflict is particularly strong in hermaphrodites because here any intersexual conflict would simultaneously be intragenomic. No direct test of this idea is available, but evolutionary transitions toward TM occurred seven times more often among hermaphrodites than in separate-sex species, relative to their species number (Lange et al. 2013).

TI by males may be a side effect of other male characters under selection, or it may be directly under selection, likely originating from benefits from an ancestral event of accidental copulatory wounding.

Support for the scenario that TI is a side effect of other functions under selection comes from cases where neither sperm nor ejaculate substances are transferred through the wound. The benefit to males would be to tightly anchor their copulatory organs within the reproductive tract of females. Hence, the regular mating traumata result from selection for anchorage, not for wounding itself.

Direct selection for TI may occur in two cases (Lange et al. 2013, for details). First, the adaptive harm hypothesis proposes that TI temporarily increases the female’s output of eggs that are fertilized by the traumatically inseminating male. This hypothesis is based on the concept of terminal investment. The wound generated during TI signals to the female the approaching death and so may lead to a terminal allocation of all remaining resources into reproduction, at the cost of somatic

maintenance. While theoretically plausible, the available empirical evidence, mainly tested in insects, is not supportive.

Second, TI may increase a male's paternity share without acting on the partner's fecundity. This may arise when, by TI, sperm circumvents parts of the hostile female reproductive tract, for example, by being placed closer to the site of fertilization, or if the trauma itself alters the sperm uptake by the respective male. In both cases, males performing TI have an advantage over normally mating males. To test these two scenarios competitively, species would be required that show both types of mating simultaneously – an exceedingly rare case (Reinhardt et al. 2014).

Costs of, and Female Response to, TI

During TI several potentially costly processes occur in the female. Blood loss may weaken the female; the wound may also represent an entry port for microbes, including sexually transmitted diseases, and for molecules in ejaculate fluid. The wound as well as the entry of nonself particles will activate immune and repair cascades which are costly. Several attempts to quantify the costs to females have been made (Reinhardt et al. 2014). However, as TI regularly results in wounds, females are expected to adapt rapidly. Consequently, costs to females measured by observation represent those in the presence of female defense structures and may be low. In fact, current costs to females may only be marginally higher in species with than without TI (Reinhardt et al. 2014). In some insect systems, however, costs can be measured by experimentally circumventing the female defense system. Experimental TI mimicking the ancestral situation in which females have no defense system yet shows costs in the order of 25 % in terms of female lifespan or fecundity.

Following basic coevolutionary theory, females can respond by three different ways to TI, by avoidance, resistance, or tolerance. As females cannot entirely avoid mating, most emphasis has been placed on female resistance

(Holland and Rice 1999). Female resistance reduces the costs to females and consequently the effectiveness of TI. The reduced male success then leads to selection on exaggerated TI traits in males. Recently, the notion of tolerance in sexual conflict has been borrowed from plant-herbivore and host-parasite coevolution (Michels et al. 2015). Under tolerance, females cope with the damage incurred during TI, for example, by sophisticated wound repair but without generating a disadvantage to the male. The consequent lack of selection on males may lead to a stop of coevolution of that particular trait pair. Consequently, other conflict-causing traits in males may be positively selected from the genome and so generate greater trait diversity by tolerance than by resistance (which leads to exaggeration, not diversity).

Benefits of TI to Females

Theoretically, females may benefit from TI if the wounding costs are outweighed by other costs. The female's own immunization, superior performance of sons of traumatically inseminating males, or superior defense by daughters of traumatically inseminating males have been suggested as potential benefits to females. No empirical evidence is available to test these ideas, and several theoretical points also argue against them. For example, indirect benefits are usually small and the quality of sons may be under a trade-off with the quality of daughters.

Evolutionary Trends in TI

Four major evolutionary trends of TI have been identified (Lange et al. 2013; Reinhardt et al. 2014):

- (i) With evolutionary time, the complexity of the organs involved in TI increases in both male and female genitalia. Prime examples are dart-shooting mollusks.
- (ii) In other groups, males evolve simple, needle-like intromittent organs, such as in the Strepsiptera or bedbugs.

- (iii) Thickened or sclerotized tissue evolves at the site of wounding, particularly impressively shown for females across a range of bruchid beetles.
- (iv) The female strategy of tolerance to TI may lead to female defense structures that are open for the male to enter and, therefore, do not represent a trauma anymore.

Traumatic Sexual Intercourse in Humans

Consensual sexual intercourse in humans regularly leads to mucus abrasions or skin lesions; 10% to >50% of women examined showed such symptoms (see references in Reinhardt et al. 2014). As such, sex causes wounds on a regular basis. Why it regularly occurs and possible variation between women, or men, are not clear. Some evidence suggests that sexually inexperienced women may be especially prone to injury (e.g., Tchonzou and Chichom-Mefire 2015). Case studies of genital injuries reported in the medical literature refer to penovaginal disproportion, excessive force, or unusual behavior at coitus (Eke 2002). In whatever way these terms will be defined, it remains unknown whether they are generally associated with traumata during sexual intercourse or remain individual cases. However, such questions are not out of reach of research.

Forensic studies revealed that nonconsensual sex sometimes results in more female genital injuries compared to consensual sex (see references in Reinhardt et al. 2014). However, a standard classification of genital injury after sexual intercourse was developed only recently (Kelly et al. 2013), and it remains unclear whether the differences between studies are real, methodological, or devoted to differences between investigated women. For example, many victims of non-consensual sexual intercourse are outside of reproductive age and may, therefore, differ in responses to injury.

In humans, there is evidence of healing of genital wounds as 36 h after injury fewer wounds were reported than 0–24 h after injury (see references in Reinhardt et al. 2014). If traumata during sexual intercourse occurred regularly in humankind's

past, or in the past of their primate relatives, it is not unlikely that selection acted on rapid wound healing in the genital tract. However, no information is available to compare the speed and efficiency of wound healing inside and outside the genital tract.

Open Questions and Future Research

Most earlier reviews have concluded that TI is understudied and underreported. Arguments that TI is even more frequent than current data suggest include the notion that copulation itself evolved frequently and copulatory organs evolved from many different developmental structures. The resulting evolutionary volatility will frequently generate events of accidental copulatory woundings, which is a likely precursor to TI. Particularly striking in this respect is the frequent and independent evolution of male intromittent organs with spines, hooking or piercing devices, ranging from insects and nematodes to mammals.

In the bedbug family (Cimicidae), two species exist where males traumatically inseminate other males. Since such behavior cannot serve a direct reproductive advantage, a study of these two species might reveal additional functions of TI.

Finally, resurrecting the ancestral state of TI, where females have no defense structure, and then measuring the costs and benefits of TI may be useful for further species. Particularly little is also known about variation across different populations of a species, and nothing on intraindividual differences in wounding or being wounded (Reinhardt et al. 2014).

A special challenge to both the definition and the methods to study TI is posed by the study by Mouginot et al. (2015). These authors show that males impose a dysfunctionalization of the female genitalia after they have mated, that it functions to prevent female remating, and that such behavior may be frequent in spiders. This behavior, for which the authors suggested the term female genital mutilation, is not a case of TI but falls into the realm of TM. While it is clear that it increases a male's paternity share without

acting on female fecundity, other driving evolutionary forces are worth studying.

Conclusion

It is clear that traumatic insemination is a common phenomenon in the animal world. It is one of similar processes subsumed under traumatic mating, which also occurs in humans. Both, male benefits of TI as well as female defense responses warrant further study to understand both evolutionary processes as well as obscure facts related to human reproductive health.

Cross-References

- [Competition for Resources Desired by Females](#)
- [Conflict Between the Sexes](#)
- [Conflict of Mating](#)
- [Copulation](#)
- [Copulatory Intrasexual Competition](#)
- [Differential Reproductive Success](#)
- [Evolutionary Arms Race](#)
- [Forced Copulation](#)
- [Genital Evolution and Sexual Selection](#)
- [Genital Mutilation](#)
- [Human Sexuality](#)
- [Intersexual Selection](#)

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Traumatic Mating (pt.)

- [Traumatic Insemination](#)

Treachery

- [Human Deception](#)

Treatment of Females in Sexual Socialization

- [Sex Differences in Sexual Socialization](#)

Treatment of Males in Sexual Socialization

- [Sex Differences in Sexual Socialization](#)

Trial-and-Error Learning

- [Learning Versus Imitation](#)

Tribal Religion

► Ancestor Worship

Tribalism

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Synonyms

In-group–out-group dynamics; Intergroup conflict; Parochial altruism

Definition

Tribalism is a word that contains a variety of phenomena that relate to loyalty to and favoring of groups to which one belongs. These phenomena include a number of cognitive and behavioral manifestations of that adherence, which can be seen at every level of human social life from the dyadic interaction to the sociopolitical and institutional structure of a nation.

Introduction

All individuals are embedded within a set of concentric social circles. The first circle contains their immediate family members and close friends. Surrounding that is a larger circle of more distant family members and friends, as well as acquaintances. Around that circle is an even larger circle of strangers that belong to the same community and visit the same groups and locations. But this is just the beginning. People also have affiliations such as group membership to a nation, political group, social club, sports team, religion, that create connections between individuals within these different circles as well as between still larger circles that span national boundaries. Therefore,

the human social environment is complex and multifaceted. It contains intersecting and often contrasting loyalties that are at least partly hierarchically arranged. However, one thing is clear from decades of research into how we make groups and cognitively represent them within our social worlds: We tend to prioritize and favor individuals that are closer to us, a tendency known as tribalism (Greene 2013).

This tribal tendency is evident in a wide variety of human behaviors and cognitive mechanisms that works towards the function of cooperating with, and expressing loyalty to one's in-group (i.e., within-group cooperation) or expressing disagreement and hostility toward out-groups (i.e., between-group conflict) (Balliet et al. 2014; Clark et al. 2019; Tajfel 1982). Tribal tendencies manifest in various areas of human social life including politics and warfare, ethnic and racial discrimination, morality, and sports teams. They include in-group favoritism (Balliet et al. 2014; Clark et al. 2019), discrimination and hostility towards out-groups (Balliet et al. 2014; Tajfel and Turner 1979), biased moral reasoning (Ditto et al. 2009; Clark et al. 2019), and ideologically motivated reasoning (Ditto et al. 2018; Kahan 2013). Many of these tribal tendencies are likely rooted in evolutionary theory. Exploring the evolutionary logic of the socio-ecological conditions that make tribal tendencies favorable along with comparative evidence from apes helps to elucidate the forms and functions of human tribalism.

The Origins of Tribalism

The starting point for the evolutionary argument for tribalism is fairly straightforward: Humans almost certainly evolved in contexts where either (but likely both) within-group cooperation and between-group competition (aka intergroup competition) occurred (Tooby et al. 2006; Tooby and Cosmides 2010; Wrangham 1999). In both cases, individuals are pressured for two different but related processes, toward tribalism. In the case of within-group cooperation, groups that are more cohesive, coordinated, and composed of individuals who are committed to shared goals, are more likely to be stronger competitors in intergroup

competition (Tooby and Cosmides 2010). This is especially the case when in-group members penalize free-riding behavior and reward loyalty, which is often the case (Clark et al. 2019). In the case of intergroup competition, individuals who can better identify in-group versus out-group members benefit from intergroup competition (Greene 2013).

Additionally, in order for cooperative groups to be efficient, groups must protect themselves from the exploitation of free riders within the group and from enemies between groups (Tooby et al. 2006). Rewarding cooperators and punishing defectors is one way in which within-group cooperation is maintained. And the ability to distinguish Us from Them, and the tendency to favor Us over Them, is how cooperative groups protect themselves from exploitation from external threats (Greene 2013). Anthropologist Donald Brown identified in-group bias and ethnocentrism as universal in his survey of multiple cultures, which suggests the ubiquity of the Us versus Them mentality (Brown 1991).

The Evolution of Intergroup Conflict

Researchers applying an evolutionary lens to human behavior have argued that tribalism is based on our coalitional psychology – that is, our proclivity to create and support our coalition against other competing coalitions (Tooby and Cosmides 2010; Wrangham 1999). These coalitions can potentially take the form of any kind of group-based formation such as identity-based coalitions (e.g., race and gender), political, and war coalitions, and institutional coalitions. (Pietraszewski et al. 2015; Tooby and Cosmides 2010). Tooby and Cosmides (2010) describe how humans have evolved to join and create alliances and coalitions from the demands of conflict since individuals learned that they could increase their formidability by pooling their strength and formidability into groups.

Perhaps the most obvious implication of tribalism is intergroup conflict and aggression, which reaches its apotheosis in large-scale warfare. While the frequencies of wars have been in decline, war has been a common occurrence

throughout human history (Pinker 2011). Some scholars have taken the ubiquity of wars throughout human history and across time frames, cultural arrangements, forms of government, and demographic factors, to be evidence of war having some evolutionary basis (Wrangham 1999; Wrangham and Glowacki 2012).

The definition of “war” that is being used in this entry is given by Wrangham and Glowacki (2012) as “relationships in which coalition of members of a group seek to inflict bodily harm on one or more members of another group” (p. 8). Therefore, “war” is used interchangeably with “intergroup violence,” and “coalitionary killing.” War-like behavior can be found in chimpanzee intergroup aggression, which has a similar pattern to human war raids (Wrangham 1999). These similar patterns of human and chimpanzee intergroup conflict have led many researchers to study evolutionary parallels between these two species (Wrangham 1999; Wrangham and Glowacki 2012). For example, in both chimpanzees and humans, violence between members of the same species is often coalitionary, where members of the species (usually males) band together and engage in intergroup conflict (Wrangham 1999). The capacity to coalesce into coalitions is a necessary condition for intergroup conflict and war-like behavior. Lethal aggression in most other animals is usually dyadic rather than coalitionary (Wrangham 1999).

Wolves are one of the few non-primate species that engage in coalitionary killing, where there are relatively high rates of intraspecific killings mostly as a consequence of territoriality when rival groups meet at the edges of their territories (Wrangham 1999). Similarly, chimpanzee male groups defend their territories and when members of other groups encroach on their territory engage in hostile aggressive displays and behaviors, which can escalate into fighting and often killing (Wrangham 1999). Interestingly, research has shown that the rates of death from intergroup aggression in chimpanzees is similar to the rates of death in human intergroup aggression in small-scale societies, further adding support to the potential shared evolutionary origins of human and chimpanzee coalitionary aggression (Wrangham et al. 2006).

It is worth keeping in mind, however, that no single evolutionary pathway, or set of psychological adaptations is likely to account for the evolution of intergroup aggression. The evolution of something as complex as intergroup aggression is dependent on a multitude of factors including psychological processes, but also cultural, demographic, and ecological factors (Wilson and Glowacki 2017).

Additionally, the similarities between chimpanzee and human intergroup aggression are going to be limited to the type of human societies that better approximate conditions of chimpanzee societies, such as nonstate, hunter-gatherer groups lacking centralized political control and having independence from other societies (Wrangham and Glowacki 2012). But to fully acknowledge the breadth of human tribalism, it is important to take into account its evolutionary origins, starting from its rudiments we see in our close relatives, the Great Apes. Chimpanzees are mainly being discussed here because, while bonobos and chimpanzees are equally related to humans, evidence indicates that bonobos are in many ways the odd-one out, the one that is most derived compared to the common ancestor of chimpanzees, humans, and bonobos (Muller et al. 2017).

Intergroup Conflict in Humans and Chimpanzees

There is ample evidence that chimpanzees distinguish between in-groups and out-groups, and engage in intergroup conflict (Wilson and Glowacki 2017). Wilson and Glowacki (2017) describe a set of similarities between chimpanzees and humans that have a strong influence on their patterns of intergroup aggression and likely are key features for tribalism more broadly: (1) fission-fusion societies, (2) intergroup hostility, (3) male coalitions, (4) territorial behavior, and (5) coalitionary killings. Wilson and Glowacki (2017) also address striking differences between humans and chimpanzees that likely have had an effect on their development of intergroup aggression: (1) weapons, (2) the types of benefits gained by aggressors, (3) multilevel societies, and (4) language.

Humans likely differ in tribalistic tendencies from chimpanzees because unlike chimpanzee societies, human forager societies possess multiple distinct levels of social organization that form overlapping loyalties and affiliations for individuals. For example, individuals belong to families, collections of multiple families known as bands, and collections of bands that constitute ethnolinguistic groups. Of course in modern developed societies, there are even more layers, such as the nation, the ethnic/race, the cross-national religion, the continent, all of which provide different ways in which humans can and do draw circles around “Us” and exclude “Them.”

The most common form of coalitionary killing is the ambush also known as the lethal raid, which also results in the most deaths from warfare in forager societies (Gat 1999; Wrangham 1999). It is an unusual form of aggression compared to the rest of the animal kingdom because it is proactive rather than reactive and is usually unprovoked (Wrangham 1999). It involves small groups of males getting together and silently and quickly invading enemy territory to attack and then swiftly leave minimizing the potential for danger.

Wrangham (1999) highlights group territoriality and a fission-fusion system along with an asymmetry in power between groups, as being features that favor an evolved behavior of lethal intergroup killing, known as the imbalance-of-power hypothesis. Group territoriality limits access to resources and therefore favors behavior that leads to dominating neighboring groups and a fission-fusion system allows individuals to assess when attack is most likely to be successful (i.e., when the power asymmetry is in favor of the aggressors) (Wrangham 1999; Wrangham and Glowacki 2012). Doing so, increases reproductive and survival benefits to the successors as they now have greater access to food and potentially mates (Wilson and Glowacki 2017). Wrangham and Glowacki (2012) assess warfare among nomadic hunter-gatherers and compare them to the chimpanzee model expectations, which are hostility to other groups, attacking out-group members and doing so when safe, and benefitting from such attacks. They find many consistencies between human intergroup conflict and the chimpanzee model, suggesting the

model provides an accurate foundation for understanding the biological and cultural evolution of war (Wrangham and Glowacki 2012).

Tribalism in Social Perception: In-Groups Versus Out-Groups

The degree of human tribalism present in human nature is evidenced by how early on we begin to slice our social worlds based on morally relevant behaviors. In an experiment of social evaluation of behavior, researchers demonstrated that long before infants can walk or talk, they are making value judgments about appealing and aversive individuals (Hamlin et al. 2007). The researchers show that 6-month-old infants prefer helping individuals over hindering individuals, prefer helping individuals over neutral individuals, and prefer neutral individuals over hindering individuals.

They show this with the use of geometric shapes with googly eyes where a red circle attempts to climb a hill and is either pushed up the hill by a nice triangle (helper) or pushed down the hill by a mean square (hinderer). Importantly, in one of their experiments, they run the same set up but without the eyes and without self-propelled motion to take the animateness out of the shapes. In this case, the pushing up or pushing down of the red circle can no longer be called “helping” and “hindering,” respectively, and so, the interaction of shapes is no longer social. And strikingly, in this case, infants do not choose the pusher-up shape significantly more than the pusher-down shape. Their choosing behavior differs significantly from the first experiment that used animated shapes (Hamlin et al. 2007).

This result shows that infants are not just making mere perceptual preferences but are making social evaluations in particular. Additionally, the fact that such social evaluatory behavior emerges so early in life suggests how important cognitive mechanisms of social evaluation are and how fundamental they are to perceiving and slicing our social worlds based on valuations of agentic behavior. While this social preference in itself is not evidence of tribalism in infants, it does show that categorizing morally relevant behavior is a

fundamental process of social evaluation, which later on in life becomes a key feature in forming and joining tribal alliances (Pietraszewski 2016; Tooby and Cosmides 2010).

An important feature of human social life is that people sometimes discriminate between in-group and out-group members. They tend to evaluate in-group members more positively than out-group members, reward in-group members more than out-group members, and work harder to accomplish in-group goals (Tajfel 1982). The favoring of in-groups is often likely to be an impediment to organizations, communities, and societies, which to a large degree rely on in-group–out-group cooperation and coordination around common goals.

On the other hand, in-group favoritism may help the overall functioning of a group and promote the in-group individual’s long-term benefits including increased survival and reproductive benefits, because cooperating with groups is often necessary to achieve social goals that are necessary for human life (Clark et al. 2019). Favoring in-groups and disfavoring out-groups creates intergroup bias and conflict (Balliet et al. 2014; Schiller et al. 2014). This can lead to hostile tensions and competition between groups that express themselves in different domains of social life, such as war and politics (Pietraszewski et al. 2015; Wrangham 1999).

Evidence from studies using the implicit association test have shown how rapidly and automatically people assign negative qualities to out-group members, for example, people of a different race and gender (Greenwald et al. 1998). But these studies have not only shown how inclined humans are to assign negative qualities to out-group members but also how automatically we slice the social world into Us and Thems in the first place. These studies show how automatically and unconsciously people are perceiving (and inventing) group differences and imbuing these differences with meaning. However, one has to take some of these studies with a grain of salt as some have failed to replicate in recent years (Boniecki and Jacks 2002), and some researchers have advocated caution in interpreting these overt, explicit discrimination and prejudice from evidence of

implicit associations (Arkes and Tetlock 2004; Boniecki and Jacks 2002).

Many social psychology studies have examined the nature of cooperation and competition with in-groups and out-groups (Schiller et al. 2014; Tajfel 1982). Such research has assessed how intergroup bias manifests in decision-making, trust, reciprocation behavior, and rewarding in-group versus out-group members (Balliet et al. 2014). However, research has been divided over the question of how intergroup discrimination emerges. Some studies have stressed the importance of in-group favoritism while others have stressed the importance of the presence of out-groups against whom in-groups can aggress. It is also plausible that both are at play (Balliet et al. 2014).

Theories of Social Cooperation

Findings from classic studies in social psychology have shown that people will engage in intergroup discrimination to, for example, maximize differences in rewards between in-groups and out-groups (Tajfel et al. 1971; Balliet et al. 2014). Tajfel and colleagues pioneered the use of what is called the minimal group paradigm, which are the minimal conditions that would create in-group behavior, to study in-group–out-group dynamics (Hogg 2016; Tajfel et al. 1971). In such conditions, group adherence alone is enough to create intergroup discrimination even when members are randomly assigned to groups, have no personal connection or information about the members of one's in-group or out-group, and no communication with them (Hogg 2016). This central finding has stood the test of time and has been replicated numerous times with varying methodological procedures, across a variety of participant characteristics (Hogg 2016).

Balliet et al. (2014) conducted a meta-analysis of intergroup discrimination and in-group favoritism in cooperation and assessed multiple predictions from two theoretical perspectives. One is social identity theory (SIT) (Tajfel and Turner 1979) and the other is bounded generalized reciprocity (BGR) (Yamagishi et al. 1999). They offer

predictions regarding moderating conditions of intergroup discrimination. For example, BGR stresses the importance of indirect reciprocity and the importance of reputation in cooperation where the theory predicts that in-group favoritism should occur in the absence of an out-group. However, SIT relies on the presence of an out-group to make the in-group categorization meaningful. Balliet et al. (2014) assesses competing and shared hypotheses between these two theories. The study also weighs in on the question of whether intergroup discrimination is the result of in-group favoritism or out-group derogation.

While the meta-analysis found support for both theories in explaining intergroup discrimination, it did support more predictions that were in line with BGR. For instance, in contrast to this prediction of SIT, people do cooperate more with in-group members compared to unclassified strangers, suggesting that the presence of an out-group is unnecessary for in-group favoritism to emerge. This finding also supports BGR in that mere cues of in-group membership elicited enhanced cooperation toward in-group members. Balliet et al. (2014) also found that the possibility of direct reciprocity weakened in-group favoritism. In-group favoritism in cooperative decision-making rests on expectations of indirect reciprocity within one's in-group and is weakened by expectations of direct reciprocity. They show that there was a significant difference between social dilemmas and trust games, with weakened in-group favoritism in the latter, supporting the BGR perspective.

Tribalism in the Modern Day

Much of tribalism in the modern day is in the form of political conflict, which has arguably increased in the wake of the 2016 American Presidential election with the rise of both left- and right-wing extremist groups, if not in actual numbers, at least in popularity in the media. A recent meta-analysis examined the question of whether liberals or conservatives tend to be more politically biased in the following way: selectively evaluating information more favorably when it supports one's political

beliefs than when it challenges them (Ditto et al. 2018). The meta-analysis examined over 51 experimental studies on partisan bias involving over 18,000 participants. Ditto et al. (2018) found evidence for roughly equal levels of partisan bias among liberal and conservative participants across the studies, and across various methodologies.

Engaging in such biased information processing is just one of the many forms of cognitive biases that take on a tribal function. Evaluating information more favorably when it aligns with one's group affiliation is a way to display loyalty to the groups to which one belongs and as well as denounce a rival group. It also likely leads one astray from an accurate understanding of reality since information is being selectively processed and evaluated on the basis of group loyalty rather than truth.

Kahan et al. (2017) found that subjects highest in numeracy – the ability to understand and make use of quantitative data – were better able to solve a difficult apolitical problem compared to people lower in numeracy. However, individuals high in numeracy were also poorer performers when the same data was politicized – that is, presented as the results from a study on gun control. These tribal differences in the political realm map onto differences in moral values between Democrats and Republicans that have been examined by moral psychologists (Graham et al. 2009; Haidt and Graham 2007).

Tribalism and the Coronavirus Pandemic

At the time of this writing, the world has been experiencing the coronavirus (COVID-19) pandemic, to which the response in the United States has been tribal. In other words, an inherently apolitical and amoral infectious disease has come to be perceived politically and morally. This is because the objective existence of the pandemic has been refracted through the lens of subjective, biased, ignorant, tribal human perception.

On the face of it, one ought to doubt that a virus, which infects, spreads, and kills individuals regardless of their socioeconomic status or political affiliation would come to be perceived and

treated differently by certain individuals. On the contrary, the doubtful would be proven wrong. In this case, the relevant tribes to which these individuals with differing information about the coronavirus pandemic belong are political tribes, which can be loosely categorized as conservative on one side and liberal on the other. Indeed, since the outbreak began in the United States, these two tribes, as represented in the government and in the media, have been espousing divergent information about the threat that COVID-19 poses to the American people. The cloud of misinformation has grown to include the severity of the virus, recommendations for how to slow the spread, and the relative importance of preventing deaths at the expense of harming the economy.

A recent NYTimes Op-ed displayed the extent of this political bifurcation in American political life (Plott 2020). The article shows how at least some of President Donald Trump's supporters perceived Trump's response to the coronavirus threat in a very different way than others. While many others took Trump's response to be an unambiguous dismissal of the coronavirus threat to the United States, they instead saw it as Trump's attempt to "stay positive and not incite panic" (Plott 2020).

Recent research shows that, indeed, political tribalism plays a significant role in explaining the reaction of the American public to the coronavirus threat. Specifically, political partisanship better accounts for the differentiation between Americans' health behaviors and policy preferences in regards to COVID-19 than any other factor tested, such as race, marital status, age, income, education, and region of residence (Gadarian et al. 2020). In particular, Gadarian, Goodman, and Pepinsky (2020) show that Democrats are more likely than Republicans to report having adopted a set of health behaviors, such as frequent hand washing, that collectively reflect social distancing. Democrats also reported showing more worrying attitudes towards COVID-19, such as there not being enough testing and that they, along with their friends, will get sick. In contrast to Democrats, Republicans are more likely to support policies restricting trade and movement across borders, whereas Democrats are more likely to

report conforming to CDC-recommended behavior, changing their personal health behaviors, and supporting more socializing policies in response to COVID-19 (Gadarian et al. 2020).

Zooming out from the tribal response to the coronavirus pandemic within the United States, we can also view how differences between cultures in the degree of within-group cooperation and norm-enforcements encourage different responses to the pandemic. Research shows that in addition to government efficiency, the adoption of cooperative norms is essential for the effective response to a collective threat, such as the coronavirus pandemic (Gelfand et al. 2020). In other words, societies that are better able to deal with collective threats not only have governments that can efficiently coordinate institutions to allocate resources to solving collective problems, but also possess cultural and social norms that encourage cooperative norms and punish deviation from those norms (Gelfand et al. 2020). These are often known as “tight” cultures, which overlap with collectivist cultures such as China, as opposed to loose or individualist cultures, such as the United States.

This operationalization of cooperation within cultures is highly related to tribalism, since tight or collectivist cultures do possess more behaviors and tendencies that relate to valuing, favoring, and supporting their in-groups, which often comprise of familial, ethnic, and ethnolinguistic ties (Gelfand et al. 2020). These cultural and social differences between countries in dealing with the coronavirus have very real effects on the rates of infection and mortality for individuals (Gelfand et al. 2020). Indeed, Gelfand et al. (2020) found that nations with higher levels of government efficiency and cultural tightness have lower infection and mortality rates compared to looser cultures with less government efficiency.

Conclusion

In many ways, tribal behavior taps into what Pinker (2011) refers to as our inner demons, which form the main portion of this work. However, there is a bright side to the fact that humans

are tribal creatures. Because we can create tribal identities and categorizations so readily and quickly around a variety of different concepts, we can also leave them quickly and reform and expand them to include more in-group members. Perhaps this process of greater inclusivity is behind what moral philosopher Peter Singer referred to as the expanding circle of empathy (Singer 1981) and one of the reasons behind what some scholars have attributed the decline of violence to (Pinker 2011). As we face new challenges and become a more interconnected species, understanding our tribal nature becomes increasingly important. Only then can we hope to counteract its negative features.

Cross-References

- [Conflict](#)
- [Cooperation](#)
- [In-Group Versus Out-Group](#)
- [Moral Tribes](#)
- [Prejudice as an Expression of Tribalism](#)
- [War](#)

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Tribalism in Moral Tribes

► Prejudice as an Expression of Tribalism

Tribes

► In-Group Versus Out-Group

Trickery

► Human Deception

Triggering Kin Selection

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Synonyms

Inclusive fitness; Social evolution

Definition

The mechanisms that promote kin selection, which is the process whereby traits and behaviors evolve because of their impact on the reproductive success of their bearer's close relatives.

Introduction

Charles Darwin's theory of evolution by means of natural selection set the stage for explaining the appearance of organismal design in the natural world (Darwin 1859), a problem that was famously outlined by William Paley in his book *Natural Theology*: if a watch requires a watchmaker, then organismal design requires a *designer*, to put it simply. In his influential book *On The Origin of Species*, Darwin argued that organismal design is the product of a process he called natural selection, a process that occurs whenever populations show variation among individuals, when this variation is associated with reproductive success and is at least partially inherited from parents to offspring (Darwin

1859). Characters that confer a survival or reproductive advantage upon their bearers are passed on from parents to offspring, and their frequency gradually increases in the population, a process that over long timescales leads to the accumulation of beneficial characters in a population and to organisms being adapted to their environment.

A major puzzle that remained in the wake of Charles Darwin's theory of natural selection was the evolution of altruism. In a world where individuals strive to pass on copies of their genes to future generations, it is difficult to explain why in some cases individuals seem to be designed to voluntarily give up some (if not all) of their own reproduction to help with the reproduction of their social partners. Darwin himself discussed the problem of altruism in *On The Origin of Species* as one of the special difficulties faced by his theory of natural selection. In this *Origin's* passage, he employed a kin selection argument to explain altruism, where he focused on the evolution of sterile castes in social insects. If natural selection works by the transmission of beneficial characters from parents to offspring, he reasoned, how could insect workers, who do not reproduce, transmit their altruistic characters to the next generation? He argued by analogy. Tasteful vegetables are destroyed when cooked, yet horticulturalists can cultivate these tasty variants repeatedly by choosing seeds from the same stock; likewise, tasty meat can be produced again by choosing animals from the same family. Darwin concluded that sterile workers had their origin in a similar process, in which "family" selection operates so that worker traits are passed on to the next generation by the reproductive individuals in the family (i.e., the queens), even if these reproductive individuals do not express the worker traits themselves.

In 1930, Ronald A. Fisher also pondered about the problem of altruism when he discussed the evolution of distastefulness in insects (Fisher 1930). He realized how distastefulness could provide a benefit to a species at large: a predator upon experiencing the distastefulness of an individual would learn to avoid preying upon other individuals of the same species. However, how could distastefulness evolve

by individual selection, he wondered. Fisher also employed a kin selection argument arguing that the selective advantage of distastefulness could be shared among a group of relatives, who are likely to carry and pass on the distastefulness character of the victim. Later, the geneticist J. B. S. Haldane also considered the problem of altruism (Haldane 1955). Haldane questioned why anyone would put her own life in jeopardy by jumping into a river to save a drowning child. He argued that if the two persons were related, helping could indeed be the optimal behavior. While Darwin, Fisher, and Haldane provided us with important insights into the problem of altruism and kin selection, they were unable to provide a comprehensive and general explanation for altruism.

It was William D. Hamilton's theory of inclusive fitness that finally provided a general framework for understanding the problem of altruism in particular and social behavior in general (Hamilton 1964). Inclusive fitness theory posits that individuals are willing to sacrifice some of their own reproduction if by doing so they help genetic relatives passing on copies of their own genes to future generations. This idea is encapsulated in the inequality $-c + br > 0$, which is widely known as Hamilton's rule and where c is the cost paid by the actor, b is the benefit provided to the recipient, and r is the relatedness between the actor and the recipient of the behavior. Altruism evolves if the benefit and relatedness are sufficiently high, and the cost is sufficiently low. Hamilton's inclusive fitness theory expands Darwin's concept of fitness and defines two paths through which individuals can generate fitness: direct (i.e., $-c$) and indirect fitness (i.e., rb). Kin selection operates when a behavior evolves because it increases the indirect component of an individual's inclusive fitness. The term kin selection itself owes its origin to John Maynard Smith (1964) and is widely used because the most common form of generating indirect fitness benefits is when social partners share a recent common ancestor.

Kin Selection and Hamilton's Rule

Ultimately, evolution is defined as the change in gene frequency over time, which can occur

through natural selection but can also occur through other nonadaptive processes such as migration, mutation, and genetic drift. The Price equation provides a general description of an evolving population, which can be used to formulate the foundations of kin selection theory (Price 1970; Queller 1992; Frank 1997; Gardner et al. 2011). The Price equation framework is based on the mapping between two populations, usually denominated by the parental and offspring populations. Parents are characterized by their breeding value (i.e., the heritable component of their phenotype) and their number of offspring, and offspring are characterized by their breeding value. The Price equation focuses on the change in average breeding value (i.e., $\Delta\bar{g}$) from one generation to the next. Total change in breeding value can be either due to natural selection (NS) or transmission. Here we are interested in adaptive evolution, and therefore we will focus on the natural selection component of the Price equation. The average change in breeding value from one generation to the next owing to natural selection is then given by

$$\Delta_{\text{NS}}\bar{g} = \text{Cov}(w, g), \quad (1)$$

where w is the relative fitness of a focal individual, where g is its breeding value, and where the covariance is taken across all individuals in the population. If we expand the Price equation we get $\Delta_{\text{NS}}\bar{g} = \beta_{w,g}\text{Var}(g)$, where $\beta_{w,g} = \text{Cov}(w, g)/\text{Var}(g)$ is the regression coefficient of fitness on the breeding value of the focal individual. This provides a mathematical expression of the three principles that must be satisfied if natural selection is to occur: there must be heritable variation in the population (i.e., $\text{Var}(g) > 0$), and heritable variation must be associated with fitness (i.e., $\beta_{w,g} \neq 0$).

In a social context, however, the fitness of a focal individual depends not only on her own breeding value (g) but also on the breeding value of her social partner(s) (G). In such cases, the regression coefficient $\beta_{w,g}$ can be partitioned into two components by using partial regression coefficients. The Price equation becomes

$$\Delta_{\text{NS}}\bar{g} = \left(\beta_{w.g|G} + \beta_{w.g|G} \frac{\text{Cov}(g, G)}{\text{Var}(g)} \right) \text{Var}(g) \quad (2)$$

where $\beta_{w.g|G}$ is the regression coefficient of an actor's fitness on an actor's breeding value, holding the social partner's breeding value constant; $\beta_{w.g|G}$ is the regression coefficient of a recipient's fitness on an actor's breeding value, holding the social partner's breeding value constant; and $\text{Cov}(g, G)/\text{Var}(g)$ is the regression coefficient between an actor's breeding value and a recipient's breeding value. We thus arrive at Hamilton's rule, the condition for the evolution of a social trait, which is given by

$$-c + br > 0 \quad (3)$$

where the cost to the actor is $c = -\beta_{w.g|G}$, the benefit to the recipient is $b = \beta_{w.g|G}$, and the coefficient of relatedness is $r = \text{Cov}(g, G)/\text{Var}(g)$ and where we assume that there is heritable variation in the population (i.e., $\text{Var}(g) > 0$).

Hamilton's rule extends the concept of Darwinian fitness to include the effects of a focal actor on the fitness of her social partners by partitioning fitness into direct ($-c$) and indirect fitness (br). Hamilton's rule not only establishes the direction of selection but it also provides a causal model of how fitness is achieved by a focal actor. Both Eqs. 1 and 2 offer an answer to which breeding values evolve; however, they presuppose different underlying causal models (see Fig. 1).

Hamilton's rule allows for the classification of any social behavior, which can be defined

according to its effect on the fitness of actors and recipients (Hamilton 1964; West et al. 2007; see Table 1). If the behavior is costly to the actor (i.e., $c > 0$) and beneficial to the recipient (i.e., $b > 0$), the behavior is called altruistic. If the behavior provides a benefit to the actor (i.e., $c < 0$) and a benefit to the recipient (i.e., $b > 0$), the behavior is classified as mutually beneficial. If the behavior is costly to the actor (i.e., $c > 0$) and costly to the recipient (i.e., $b < 0$), the behavior is spiteful. Finally, if the behavior provides a benefit to the actor (i.e., $c < 0$) and is costly to the recipient (i.e., $b < 0$), the behavior is defined as selfish.

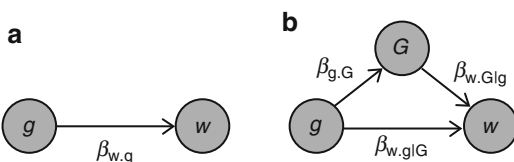
The Triggers of Kin Selection

Kin selection requires that social interactions occur among related individuals, a scenario that can be generated by three main mechanisms. First, kin discrimination generates high relatedness between social partners owing to a recent common ancestor (Hamilton 1964). Second, the greenbeard effect generates high relatedness at the locus of interest between social partners, irrespective of their genealogical ancestry (Hamilton 1964; Dawkins 1976). Finally, population viscosity, in which individuals tend to remain near their place of birth, generates high relatedness among neighbors, which may even favor unconditional expression of altruistic behavior (Hamilton 1964).

Kin Recognition

Kin recognition occurs whenever individuals are able to discriminate genealogical relatives and requires that individuals are able to identify close relatives among their social partners and direct their social behavior toward these relatives. There are two possible kin recognition mechanisms: genetic and environmental kin discrimination.

Genetic kin discrimination – Genetic kin discrimination relies on the identification of a social partner's trait, which once compared with a template carried by the focal individual can provide a correct prediction of kinship between the two individuals. This requires genetic polymorphism in the population at the



Triggering Kin Selection, Fig. 1 The underlying causal models of Darwinian fitness (panel a) and inclusive fitness (panel b). Inclusive fitness partitions fitness into a direct fitness component ($-c = \beta_{w.g|G}$) and an indirect fitness component ($rb = \beta_{g,G}\beta_{w.g|G}$)

Triggering Kin Selection,
Table 1 Classification of social behaviors according to their effects on the actor and on the recipient of the social behavior

		Effect on recipient	
		$b > 0$	$b < 0$
Effect on actor	$c > 0$	Altruistic	Spiteful
	$c < 0$	Mutually beneficial	Selfish

locus of interest so that there is selective pressure for genetic recognition mechanisms. The selective advantage provided by genetic kin discrimination, however, may lead to the erosion of the polymorphism in the population, which, in turn, selects against genetic recognition mechanisms. Due to this evolutionary instability, it is thought that genetic kin discrimination is relatively rare in nature. Despite this, a few cases of genetic kin discrimination have been identified in the natural world.

Dictyostelium purpureum is a microorganism that usually lives solitarily foraging for bacteria in the soil of forests. When they run out of food, they aggregate to form multicellular mobile slugs that move toward the soil surface. Upon reaching the soil surface, a fraction of cells differentiate and become spore cells, while the other fraction self-sacrifices themselves to form a stalk that enables spore cells to disperse and colonize other areas. This extreme altruistic behavior may be rendered evolutionary unstable if cheater lineages, which preferentially differentiate into spore cells while contributing little to the stalk of the fruiting body, emerge in the population. Mehdiabadi et al. (2006) found that genetic kin discrimination may be responsible for the stability of cooperation in *D. purpureum*. When two lineages are mixed together to form fruiting bodies, lineages seem to recognize each other so that each fruiting body ends up with a very high proportion of cells belonging to a single clone. Later studies have found that the *lag* gene family may account for the discrimination mechanism in *D. purpureum* (Benabentos et al. 2009). It has been shown that *lagB1* and *lagC1* are highly polymorphic in natural populations and that deleting these genes caused these strains to segregate with wild-type cells.

Environmental kin recognition – Environmental kin recognition occurs whenever individuals

learn to recognize each other owing to a shared environment. Individuals that share an environment early in life, for instance, are likely to be relatives, and therefore any cue associated with this early-life shared environment is likely to accurately identify a social partner as a close relative later in life.

Environmental kin discrimination has been identified as a factor that stabilizes cooperation in long-tailed tits. Long-tailed tits are a cooperative breeding species in which individuals who fail to breed may become helpers at someone else’s nest. First, it has been shown that helpers are often found in the nest of close relatives (Russell et al. 2001). Furthermore, individuals who fail to breed only become helpers if they are able to find breeders who are close relatives. In addition, when, in an experimental setup, failed breeders were given the choice between nests of unrelated and related individuals, they often chose the nest of related individuals. A later study revealed that vocalizations play a key role in the underlying kin discrimination mechanism used by long-tailed tits. Vocalizations differ across families, and because they are learned early in the life of long-tailed tits when parents are provisioning young, they are reliable cues of kinship and allow individuals to discriminate between kin and non-kin later in life (Sharp et al. 2005).

The Greenbeard Effect

The greenbeard effect occurs whenever a gene or a cluster of tightly linked genes expresses an identifiable phenotype (i.e., the greenbeard), it is able to identify the greenbeard in other individuals, and it is able to direct its cooperative behavior toward them. The greenbeard effect is thought to be rare in nature because they are prone to invasion by individuals who display the greenbeard but do not perform the altruistic behavior. Despite

this, there are some examples of the greenbeard effect in the natural world, especially in microorganisms and insects.

The eukaryotic microorganism *Dictyostelium discoideum* has a life cycle similar to that of *D. purpureum* as outlined above. When *D. discoideum* cells run out of food, they also form a multicellular fruiting body, in which around 20% of cells self-sacrifice themselves to form the stalk of the fruiting body. Because multicellular cells develop from the aggregation of potentially different clones, the cooperative behavior of slime mold cells may become evolutionarily unstable owing to the invasion of cheater lineages that preferentially place themselves in the fruiting body, but do not contribute to the stalk supporting it. Queller et al. (2003) found that the *csA* gene acts as a greenbeard and therefore stabilizes the cooperative behavior in *D. discoideum*. The *csA* gene encodes the gp80 cell adhesion protein that is anchored to the surface of cells. These proteins bind to gp80 proteins in other cells, and therefore during the cooperative swarming of the multicellular body, they leave behind most of the cheater cells that do not produce gp80 proteins.

Population Viscosity

Population viscosity is when individuals tend to remain near their place of birth. Hamilton suggested that population viscosity could play an important role in the evolution of cooperative behavior because it does not require any sophisticated recognition mechanism to generate high relatedness among social partners (Hamilton 1964). Population viscosity, however, also generates competition for resources among close relatives, which may offset some or all of the positive effects of population viscosity on the evolution of cooperation.

An empirical test of how population viscosity influences the evolution of cooperation has been developed using experimental evolution in microorganisms. The pathogenic bacterium *Pseudomonas aeruginosa* relies on iron to grow. Iron is a major limiting factor to *P. aeruginosa* because Fe (III), the most common form of iron in nature, is insoluble and not readily accessible to them.

P. aeruginosa were able to find a solution to this problem. They secrete siderophores that bind to Fe(III) making it suitable for their metabolism. Siderophore production is a cooperative trait because it is costly to manufacture, while its end product is publicly available. Griffin et al. (2004) manipulated the dispersal patterns of different lineages and found that the production of siderophores is favored when close relatives interact with each other, and competition is global (i.e., competition is not among close relatives). Moreover, they found that when both social interactions and competition occur among relatives, cooperation did not evolve.

Kin Selection at Work

The Monogamy Hypothesis

The key prediction of inclusive fitness is that altruism is more likely to evolve when social partners are close relatives. This has led to the hypothesis that lifetime monogamy could be a crucial factor in the evolution of eusociality (Boomsma 2009). In eusocial species, there is a reproductive division of labor in which workers forgo reproduction to help reproductives (i.e., the queens). Lifetime monogamy is thought to promote eusociality because when females mate with a single male the relatedness between siblings is equal to the relatedness between mothers and their own offspring. As a result, the slightest benefit provided by altruism may be sufficient to make offspring forego their own reproduction and help their parents raise their siblings. One problem with the monogamy hypothesis, however, is that in many extant eusocial species promiscuity, rather than monogamy, is common, which suggests that monogamy is not necessary for the evolution of eusociality. To test the monogamy hypothesis, it is thus crucial to understand if promiscuity is an ancestral or a derived trait of eusociality (Boomsma 2009). Hughes et al. (2008) found that the ancestral state of all eusocial species is in fact monogamy, which provides a strong support for the role of relatedness in the evolution of eusociality, in particular, and altruism, in general.

Coalitions in Wild Turkeys

In some cases, it is possible to directly measure the different variables in Hamilton's rule. Wild turkeys (*Meleagris gallopavo*) provide a notable example where kin selection has been directly tested. During the breeding season, male wild turkeys display in an attempt to attract their female counterparts. Male turkeys can either display solitarily or in coalitions of two to four males. Only the dominant male in the coalition mates; thus, it is puzzling why subordinate males are willing to join a coalition and forego mating opportunities instead of displaying solitarily. Krakauer (2005) found that subordinate males had a significant positive effect on the number of matings and offspring fathered by the dominant male. Specifically, Krakauer found that dominant males had on average 6.1 offspring, while solitary males had on average 0.9 offspring. Furthermore, Krakauer found that the relatedness between dominant and subordinate males was significantly higher than the relatedness between two random males in the population (i.e., $r = 0.42$). If we replace these values in Hamilton's rule, we get $-c + br = -0.9 + 6.1 \times 0.42 = 1.7 > 0$, which shows that kin selection is able to explain why subordinate male turkeys are willing to join coalitions.

Kin Selection and Class Structure

Most of the kin selection theory assumes that the quality of individuals is identical within a population. More recently, however, there has been a growing interest in understanding kin selection when individuals vary in quality (e.g., Rodrigues and Gardner 2013, 2016). Variation in quality may occur whenever individuals differ in a life history or social trait, such as size, weight, social status, or nutritional state. To illustrate how individual quality may affect social evolution, let us consider the evolution of dispersal, a classic kin selection problem (Hamilton and May 1971). Dispersal evolves through kin selection whenever it carries a cost to the dispersing individuals, when dispersal frees up resources in the disperser's natal patch, and when these resources are utilized by the disperser's close relatives (Hamilton and May

1971, reviewed in Rodrigues and Gardner 2016). In such cases, Hamilton's rule, the condition for the evolution of altruistic dispersal, is given by

$$-v + (1 - k)v + vhr > 0 \quad (4)$$

where v is the expected reproductive success of an offspring that remains in the natal patch, k is the cost of dispersal, h is the probability that a native offspring wins a breeding site, and r is the relatedness among native offspring within a patch. The left-hand side of Hamilton's rule readily yields a kin selection interpretation of the behavior. First, a disperser pays a fitness cost v . Second, a disperser successfully arrives at a patch with probability $1 - k$, in which case it derives a fitness benefit of v . Finally, the value of the amount of resources freed up by a disperser is v , which goes to a native individual with probability h , whose relatedness to the disperser is r . The first two terms thus represent the marginal direct fitness of the behavior, while the third term represents the marginal indirect fitness. Let us now consider that there is class structure in the population, with a high-ranking more fecund female (denoted by H) and a low-ranking less fecund female (denoted by L) in each patch, which is often the case in many species ranging from mammals to insects. Under this scenario, offspring of the high-ranking mothers find themselves surrounded by more siblings than offspring of the low-ranking mothers, and therefore it is likely that they express different dispersal behavior (Rodrigues and Gardner 2016). The condition for the evolution of altruistic dispersal is given then by

$$-v + (1 - k)v + v\bar{r}_i > 0 \quad (5)$$

where $\bar{r}_i$ is the average relatedness between the disperser (whose mother has rank " i ") and those who remain in the patch, with $i \in \{H, L\}$. Because offspring of high-ranking mothers have more siblings, we have $r_H > r_L$, which means that offspring of high-ranking mothers are selected to disperse more often than offspring of low-ranking mothers. Surprisingly, Rodrigues and Gardner (2016) found that the number of offspring that remain in the patch is exactly the

same irrespective of the mother's quality (i.e., the "constant philopater hypothesis").

A particular case of class-structured populations is when diploid individuals reproduce sexually. Sex structure is an important factor in the analysis of the evolution of social dispersal of females and males in human populations. Nitsch et al. (2016) studied the evolution of human sex-specific dispersal in preindustrial Finland, where they have analyzed how the presence of same-sex and opposite-sex elder siblings influenced the dispersal behavior of later-born siblings. They found that the presence of same-sex elder siblings have a strong effect on the dispersal behavior of later-born siblings, while the presence of opposite-sex siblings has a weaker effect. Specifically, they have shown that younger siblings tend to disperse more when there are older siblings present in the population.

Summary

Kin selection is a process by which traits evolve owing to their effect on the fitness of their bearer's relatives. These indirect fitness effects can be generated through three different mechanisms. Kin discrimination leads to interactions among individuals who share a recent common ancestor. Kin discrimination can be genetic, in which individuals are able to recognize kin through a genetic template, or environmental, in which recognition emerges from cues associated with a shared environment. The greenbeard effect allows for altruism among genetic relatives, irrespective of their genealogical ancestry. Finally, population viscosity leads to neighboring individuals being close relatives, and therefore it may even allow for the evolution of indiscriminate altruism. Kin selection occurs at all levels of biological organization, and it is key for the evolution of cooperative behavior, from the evolution of sterile castes in eusocial insects to the evolution of parental care. Finally, kin selection also plays a crucial role in the evolution of major evolutionary transitions, such as the evolution of multicellularity, in which lower level biological units cooperate to form a cohesive and functional higher level biological unit (Fisher et al. 2013).

Cross-References

- Genetic Relatedness
- Hamilton's Rule
- Inclusive Fitness
- Viscous Population

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Trivers-Willard Effect

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Trivers-Willard Hypothesis

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Definition

Hypothesis that natural selection favors parental ability to alter offspring sex in the direction that maximizes their own reproductive success.

Introduction

Trivers and Willard (1973) proposed that in order to maximize their own long-term reproductive

success, it would advantage parents if they could alter the sexes of their offspring. More than 40 years of research have attempted to confirm this hypothesis, but with mixed results. In humans, several lines of evidence suggest that parents who exhibit characteristics associated with increased male reproductive success have more sons than those who do not. Dominance, in particular, provides both an adaptive and plausible characteristic by which the Trivers-Willard hypothesis might operate. Evidence in support of this possibility comes from four areas: (1) offspring sex ratios of fathers demonstrating characteristics of dominance, (2) offspring sex ratios of mothers demonstrating characteristics of dominance, (3) parental hormones and offspring sex ratios, and (4) assortative mating and offspring sex ratios.

Parental Variation of Offspring Sex

In their seminal article, Trivers and Willard (1973) hypothesized that natural selection should favor parental ability to alter the sexes of their offspring in the direction that maximized their own reproductive success. Now widely known as the Trivers-Willard hypothesis (TWH), their paper proposed that mothers and fathers in good condition (i.e., those who possessed some characteristic or trait ultimately favoring male future reproductive success relative to female reproductive success) should produce more sons. Those sons, in turn, would inherit their parent's good condition and thus obtain greater access than other males to female mates and thus produce more offspring. In contrast, parents in poor condition would maximize their reproductive success by having daughters. The reasoning here is that inheritance of poorer condition would have less impact on a daughter's access to mates than it would for a son's, and her production of offspring would remain relatively stable.

The TWH relies on three assumptions: (1) that parental condition during parental investment reflects the condition of the offspring at the end of parental investment, (2) that this variation in offspring condition persists into adulthood, and

(3) that offspring condition preferentially aids male reproductive success compared to female reproductive success. Using a hypothetical population of caribou as a working example, Trivers and Willard (1973) focused largely on maternal condition (i.e., body weight). They argued that assuming that mothers with higher body weight are better able to provide nutrition to their calves, they would be better suited to have a son. The nutrition a son received would, theoretically, render him larger, stronger, and healthier than other calves. Assuming that he retained these traits until adulthood, the son should be more successful in competitions with other males for female mates, thus producing more grand offspring for his mother. Of course, this example also assumes that large body size, strength, and health are more strongly associated with male compared to female reproductive success in adulthood, thus facilitating greater reproductive benefit for a male than a female offspring.

It is important to note that the TWH is a *theoretical* evolutionary hypothesis focused on ultimate rather than proximate causes of sex ratio variation. In other words, the authors did not propose any explicit mechanisms by which parental ability to vary offspring sex might occur. They also did not provide an exact definition of parental “condition.” As variation in environments, mating systems, and ecological characteristics of animal populations occur, this information is also variable, but it is not crucial for understanding of the underlying principle of how the TWH would operate.

The open-ended nature of the TWH, however, is likely why despite its simplicity and elegance, results from more than 40 years of research have failed to generate consistent evidence that parental condition does, in fact, lead to biased offspring sex ratios. Although variation in maternal condition has been associated with male-biased offspring sex ratios in several mammalian species including humans, this is not always the case (for reviews, see Brown 2001; Brown and Silk 2002; Clutton-Brock and Iason 1986; Hardy 1997; Hewison and Gaillard 1999; Hiraiwa-Hasegawa 1993). One possible reason for the discrepancy is that many researchers have focused

on parental investment (i.e., provision of resources to offspring after birth), whereas many others have focused on either primary (i.e., number of males and females at conception) or secondary sex ratios (i.e., number of males and females at birth). Similarly, because there is no explicit definition of “condition,” researchers have looked largely at physiological rather than behavioral indicators of quality, such as age, physical size, and nutritional status. In addition, virtually all research investigating the TWH has focused on maternal status, allowing no potential influence for paternal condition on offspring sex. When contributing sources of variance are considered, however, a clearer picture of TWH operation in mammals begins to emerge.

In a meta-analysis of the literature involving ungulates, Sheldon and West (2004) found only marginal support for the TWH. However, when they analyzed studies that looked specifically at maternal behavioral dominance (i.e., a female’s ability to compete for resources), they found effect sizes four times larger than those looking at physiological indicators. Although exclusive to ungulates, those results suggest that maternal rank could be more than a simple proxy for physiological status, as has been assumed in much of the research with nonhuman primates. Indeed, Cameron (2004) found significant heterogeneity among studies that looked at maternal dominance and offspring sex for mammals. This suggests that the factors defining favorable “condition” may be considerably more complex than simply physical parameters, such as weight or body size. For example, epigenetic influences, such as parental behavior, could impose reproductive benefits on offspring through social interaction.

Another important factor is whether parental condition at conception, birth, or after birth (i.e., parental investment) is studied as part of the TWH. Although Trivers and Willard (1973) used the illustration of a female nursing of her calf as increasing its size, they did not specify that the mechanism through which parent condition might benefit offspring should necessarily be post-conception. In fact, the evidence in support of facultative adjustment of offspring sex *peri-conception* is much more convincing. Both

Sheldon and West (2004) and Cameron (2004) have demonstrated substantially larger effect sizes from studies evaluating maternal condition around the time of conception compared to post-conception. This suggests that any parental manipulation of offspring sex may be the result of preexisting differences prior to sex determination and therefore variable and dependent on environmental factors.

Offspring Sex Ratios and Characteristics of Dominance in Fathers

A variety of physiological and behavioral characteristics associated with both dominance and increased male, but not female, reproductive success (reviewed in Campbell 1999; Puts 2010; Puts et al. 2012) have been identified for fathers who have more sons. For example, more sons have been observed in families of fathers who are heavier and taller compared to fathers who are lighter and shorter (Kanazawa 2005; but see Gelman 2007 and response in Kanazawa and Reyniers 2009; Manning et al. 1996). This suggests that physical indicators of dominance may be associated with more male offspring in men.

Interestingly, indicators of paternal dominance behavior are also associated with more sons than daughters. Cameron and Delerum (2009) showed that male billionaires, as well as sons of male billionaires, had significantly more sons than daughters. They also had more sons than would be expected in the general population. Although it is possible that this finding more appropriately supports parental investment in offspring (i.e., provision of resources such as food, shelter, health care) rather than parental dominance traits as affecting primary sex ratios, additional evidence showing temporal changes in offspring sex ratios (i.e., from male-biased to balanced) of US presidents (Betzig and Weber 1995) suggests that psychological influences are more likely. In addition, lower (i.e., more masculine) 2D:4D ratios, which have been shown to indicate men's dominance and masculinity (Neave et al. 2003), as well as correlate positively with self-reported attractiveness in men (Manning and Quinton 2007), have been found in fathers with higher sex ratios (i.e., more sons than daughters) (Manning et al. 2002).

Further, both unrestricted attitudes toward sexuality (e.g., favoring promiscuity) (Kanazawa and Apari 2009) and violent (i.e., aggressive) behavior, both of which are involved in men's social hierarchies, also predict more sons (Kanazawa 2006). Indeed, fathers who score higher on measures of behavioral dominance are also more likely to have a first-born son than daughter (Palmer-Hague and Watson 2016a). Taken together, various studies suggest that both physical and behavior markers of a male's capacity to be dominant may be correlated with a tendency for him to sire more sons as predicted by the TWH.

Offspring Sex Ratios and Characteristics of Dominance in Mothers

The TWH predicted that maternal influences could also bias offspring sex ratios. Indeed, dominance characteristics in mothers do appear to bias offspring sex ratios in ways congruent with the hypothesis. Physical features such as female body size are related to higher (i.e., more males) offspring sex ratios. Taller and heavier mothers also have more sons than shorter and lighter mothers (Kanazawa 2005; but see Gelman 2007 and response in Kanazawa and Reyniers 2009; Manning et al. 1996). Women with greater muscle mass in their upper arms – a proxy for nutritional status (i.e., greater resource acquisition ability) – also have more sons (Gibson and Mace 2003). Although larger size is indicative of physical characteristics, such as glucose availability or nutritional stores, a large body of evidence suggests that these factors are all also functionally related to maternal dominance.

Women who score higher on behavioral dominance measures are significantly more likely to have a son than women who score lower (Akande 1999; Grant 1990, 1994; Palmer-Hague and Watson 2016a). In addition, lower-ranking co-wives (i.e., lower status) in Rwandan marriages do have more daughters than higher-ranking co-wives (Pollett et al. 2009), suggesting that maternal dominance is functional in determining offspring sex. Interestingly, Gangestad and Simpson (1990) found that more extraverted, less behaviorally restrained women had more sons than those who

were less extraverted and more behaviorally restrained. Women who exhibit high ranking in social hierarchy, therefore, are not only likely to have increased access to resources important for offspring survival (e.g., food) but also to exhibit behaviors relevant to interpersonal competition and status. This would preferentially benefit sons compared to daughters when it comes to accessing mates.

Parental Hormones and Offspring Sex Ratios

Variation in male and female reproductive hormones is a plausible mechanism for altering offspring sex. As decades of research in social neuroendocrinology indicate, reciprocal relationships exist between hormones, behavior, and the environment. For example, hormonal response to competition and interpersonal challenge (e.g., increases in testosterone with successful interaction), variation in nutrition and caloric availability (e.g., increases in cortisol in response to low calorie diets), and motherhood (e.g., increases in prolactin in response to infant feeding) are all examples where hormone levels change in response to the environment. In turn, these changes can alter an individual's physiology (e.g., testosterone increases vigor and muscularity), behavior (e.g., success in competition), and future experience (i.e., willingness to engage in competition) (reviewed in Hamilton et al. 2015). Although an exact mechanism remains to be identified, there is support for the role of periconception parental hormones in providing a pathway through which dominance can alter offspring sex as predicted by the TWH.

James (1980, 1986) first theorized that increased levels of parental estrogen (E) and testosterone (T) increase the probability of conceiving sons and increased levels of gonadotropins (i.e., luteinizing hormone (LH) and follicle-stimulating hormone (FSH)) increase the probability of conceiving daughters. Although several lines of correlational evidence from epidemiology support of this hypothesis (James 1996, 2008), the process by which paternal hormones could actually alter the probability of a male or female offspring being conceived remains unclear. One possibility is that paternal hormones manipulate

the proportions of X- and Y-chromosome-bearing sperm in seminal fluid (see Edwards and Cameron 2014), but this remains to be investigated.

In contrast, the maternal dominance hypothesis (Grant 1998) predicts that more dominant women can increase their reproductive success by producing sons, and higher levels of endogenous testosterone in these women favor conception of males over females. Specifically, this hypothesis predicts that maternal dominance (i.e., a combination of inherent female traits (e.g., influential, authoritative) that facilitates the changing of another's view or actions) during the period of parental investment is crucial for her son's reproductive success in adulthood. In other words, to some degree, her sons eventually display dominant behavior in response to her dominant interactions with them and others. By producing a dominant son who will successfully outcompete other males for mates, rather than a dominant daughter whose reproductive success will be unaffected, she can enhance her own fitness.

The maternal dominance hypothesis proposes that endogenous maternal testosterone at the time of conception facilitates the reception of a Y-chromosome-bearing sperm by the woman's ovum. This has been demonstrated in bovine ova contained in follicles with elevated fluid testosterone concentrations (Grant and Irwin 2005). Similarly, female rhesus macaques that gave birth to sons were not only more behaviorally dominant (i.e., more successful in displacing conspecifics in direct interactions for food) but also had higher preconception testosterone levels (Grant et al. 2011). Dominance behavior can be both stable and persistent (i.e., a trait) and variable and transient depending on environmental circumstances (i.e., a state). Thus, the maternal dominance hypothesis also explains how the probability of a given woman having either a male or female offspring can vary with each conception.

Although yet to be directly investigated, the maternal dominance hypothesis could also relate to paternal manipulation of offspring sex ratio. For example, more dominant women might choose to mate with more dominant men to facilitate the provision of certain characteristics in her

son (i.e., “good genes”). Interestingly, this would introduce a potential combined parental influence on the production of male or female offspring.

Assortative Mating and Offspring Sex Ratio

Assortative mating based on characteristics that would enhance the reproductive success of male or female offspring presents another possible mechanism through which the TWH might operate. Recent evidence suggests that women who score higher in self-reported dominance (i.e., possessing characteristics that facilitate the changing of another’s views or actions, such as influential or authoritative) are more likely to predict they will have sons (Palmer-Hague et al. 2013). In addition, Palmer-Hague and Watson (2016b) found that women who scored higher in self-reported dominance and predicted they would have sons were also more likely to choose a male described as behaviorally dominant as a potential mate. Retrospective analyses of parents reveal that those scoring higher on measures of behavioral dominance were more likely to have had a firstborn son than a firstborn daughter (Palmer-Hague and Watson 2016a). These results suggest not only that there is some mechanism by which women can evaluate which sex of offspring they are most likely to produce at a given point in time but also that they might differentially choose mates to enhance the reproductive success of this offspring, based on its sex. Similar results were not found for men (Palmer-Hague et al. 2013; Palmer-Hague and Watson 2016b). Thus, manipulation of offspring sex might be under exclusive control of mothers.

Conclusion

In humans, evidence supports the idea that parents can to some extent manipulate their own offspring sex ratio as predicted by TWH. This appears to involve processes related to the expression, attainment, and evaluation of dominance (i.e., condition) by both men and women and that underlying hormonal processes could facilitate conception of either sons or daughters. Testosterone, which is related to a variety of physical and behavioral

characteristics associated with dominance and may actually facilitate the conception of sons, is a plausible candidate.

Cross-References

- [Dominance and Testosterone](#)
- [Dominance in Humans](#)
- [Female Mate Choice](#)
- [Male Mate Choice](#)
- [Male-Male Competition](#)
- [Mate Preferences](#)
- [Observed Mating Behavior and Women’s Long-Term Mating](#)
- [Parental Investment and Sexual Selection](#)
- [Sexual Selection](#)
- [Testosterone](#)
- [Women’s Mate Preferences](#)

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Or Would You Throw the Fat Man Off the Bridge? A Philosophical Conundrum (Cathcart 2013), the trolley problem is discussed and dissected in its most classic version and several other versions (e.g., the fat man version). These discussions revolve around a fictional court case where a jury is presented with arguments derived from moral philosophy to judge the trolley problem and several alternative versions. The book delves into other broad topics that have implications for ethics and moral reasoning.

Trolley Problem

- [Psychology](#)
- [Would You Kill the Fat Man?](#)

Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?

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Synonyms

[Book](#); [Moral philosophy](#); [Thomas Cathcart](#); [Trolleyology](#)

Definition

Thomas Cathcart's book, *The Trolley Problem, Or Would You Throw the Fat Man Off the Bridge?: A Philosophical Conundrum*, is an examination of the famous trolley problem and why this is important to philosophers, scientists, and lay people alike.

Introduction

The trolley problem is a philosophical thought experiment that has existed in several iterations. In Thomas Cathcart's book *The Trolley Problem*,

Thomas Cathcart's book, *The Trolley Problem, Or Would You Throw the Fat Man Off the Bridge?: A Philosophical Conundrum* (2013), is primarily about the famous trolley problem, but it also proposes other issues, such as the difference between moral intuition and moral reasoning, the difference between utilitarian and deontological morals, what the naturalistic fallacy is, what an analogy is for, and basic information about classic philosophers. Thomas Cathcart's approach is to present the famous trolley problem in a unique circumstance. The trolley problem asks the reader to imagine that they find themselves standing at a railway switch with a tough choice to make. A trolley is barreling down the tracks toward a group of five people. Those five people will most definitely be killed if the trolley collides with them. Fortunately, the railway switch will divert the trolley down a separate rail line. Unfortunately, a lone individual stands on that stretch of rail. The reader is in a difficult position: if they do nothing, they allow five people to be killed, but if they act, they doom someone else who is otherwise innocent to die. This problem is so infamous that the study of it and other similar problems has been dubbed *trolleyology*. At its core, trolleyology is an exercise in understanding how people come to a conclusion about what they would do if they were standing at the rail switch. Will they pull it or will they leave it alone?

The Trolley Problem presents this classic dilemma as if a woman named Daphne Jones in San Francisco was actually presented with such a situation and she chooses to pull the switch, killing one man to save the lives of five. In this scenario, the case is being brought before the

Court of Public Opinion, a fictional court that establishes precedent based on the opinions of a large number of people (similar to a survey) to determine if Daphne Jones should be praised for making a tough choice to save the greatest number of people or admonished as someone who played God. The remainder of the book is presented as a series of different people, all of whom have different perspectives, backgrounds, and professions, making the case for why they believe that Daphne Jones is either innocent or guilty.

To Pull or Not to Pull the Switch

According to Thomas Cathcart (2013), the argument in favor of pulling the switch to sacrifice one person to save five others is often argued from a utilitarian perspective. Utilitarianism is a branch of moral reasoning that claims that all actions should be assessed for the amount of utility that they possess. In other words, does an action cause the greatest amount of happiness compared to alternatives? In this case, pulling the switch represents an action which maximizes utility because it results in a situation where five people are spared at the expense of one, whereas the alternative is a situation where five perish and one will survive. The counterargument is presented as the deontological perspective, where actions are assessed as rules that we should follow. According to Thomas Cathcart (2013), the deontological perspective dates back to Immanuel Kant, and the logic of it follows that if an action is being considered, first consider a world where that action was utilized in every possible situation. In other words, the deontological perspective applied to the trolley problem presupposes a world where people are always willing to sacrifice the lives of a few people to save the lives of more people. The reason that the deontological perspective is an argument against pulling the switch is because there is no rule that the bystander should interfere in the trolley scenario and the act of interfering presupposes that the bystander needed to interfere to do good.

As Thomas Cathcart lays out this discussion, he opens the door to several other big questions. First, this brings up the question of what “good” means. According to Cathcart (and other classical

philosophers; reviewed in Cathcart 2013), it is impossible to define what good means. While it is often clear when one option is better than another, to say that one is the good choice and another is bad requires an enormous amount of perspective. Next, it opens the door to several other versions of the trolley problem. For example, what if instead of pulling a switch to stop the trolley, the only option afforded to the bystander was to push a nearby fat man onto the tracks so that the trolley would be stopped by his mass? Cathcart identifies that in most studies of the original trolley problem, over 90 % of those surveyed believe that pulling the switch is the correct choice. In this iteration of the trolley problem, 10 % or less of those surveyed believe that they should push the fat man onto the tracks. It is in these differences where the interesting psychological phenomena occur.

After establishing that people predominantly support pulling the switch, but not pushing the fat man, Cathcart (2013) notes that these results are consistent across gender, age, level of education, and even exposure to moral philosophy in general. However, the reasoning that people give for supporting pulling the switch changes along these same lines. For example, women are more likely to think about the relationship that they have with the people involved in the scenario, whereas men are more likely to be utilitarian in their approach. Women tend to consider how the decision will impact the family and friends of those involved. If the scenario is manipulated so that their relatives are the people in the way of the trolley, they will be even more likely to want to sacrifice someone else. Men, on the other hand, tend to make the decision as a form of moral calculus, identifying the option that results in the fewest casualties and going with that option. Further, when modern, young people are asked why they would pull the switch or why they would not push the fat man, their analysis boils down to an intuitive, gut feeling. Cathcart implies that this lack of ability for modern young adults to walk through their moral reasoning is a unique phenomenon. Indeed, when older individuals are faced with similar moral dilemmas, they tend to put effort into explaining why they believe one

choice is correct (i.e., it seems unfair to push the fat man off the bridge because he was not involved in the trolley incident at all), whereas younger individuals tend to rely more on their gut reaction (i.e., it just feels wrong to push him).

Why the Trolley Problem Matters

This brings up another interesting discussion in *The Trolley Problem* in a chapter where a psychologist gives their opinion: the psychologist argues that human beings are more likely to have a reaction that is deeply tied to our emotions and less so to our reasoning. The psychologist further explains that evolution may have “hardwired” this type of moral intuition into our brains. Research has supported this sentiment. In an unpublished study, Haidt and colleagues (2000) found that participants are more likely to respond in a morally intuitive way than they are to use moral reasoning to come to a conclusion. Participants were asked to judge a male and female pair of siblings who decided to have sex while on vacation. Most participants react to the story negatively, chastising the siblings. When asked to elaborate, most participants will cite the dangers of producing incestuous offspring and how incest can damage families. When this scenario is presented in such a manner so that the siblings use contraceptives and that the incest remains a one-time event that does not damage the family, participants still find issue with the scenario. This phenomenon is further elaborated in Haidt (2001), which outlined how most people have an emotional, intuitive reaction to things and then later try to rationalize their judgments. This is in direct contrast to most moral reasoning models, which claim that people have an intuition and then reason about their intuition before they come to a judgment. In Haidt’s (2001) updated model, he claims that people intuit a judgment and only reason after they have come to their conclusion.

Similar to this way of thinking, the psychologist in *The Trolley Problem* indicates that most people will have an emotional, intuitive reaction to reach their conclusion on how to judge Daphne Jones, the woman who pulled the switch. Thomas Cathcart indicates that while this may be true, this is not necessarily right and would be considered

committing the *naturalistic fallacy* (i.e., when someone commits the error of assuming that because something is natural, it must be right). Specifically, while it may be true that people often intuit a judgment, to say that this judgment is valid because it is an intuition would be committing the naturalistic fallacy.

One of the goals of Thomas Cathcart is to expound upon the positive virtues of moral reasoning and philosophy. Near the end of the book, Cathcart (2013) argues in favor of moral reasoning by bringing up social issues like gay marriage. Before gay marriage was legalized in the United States, many people would intuit that marriage was between a man and a woman, and it was only through rigorous debate and discussion of ethics that we came to change marriage laws in the United States. As Cathcart puts it, one side was able to philosophize better than the other. So, although humans may have a moral intuition that they rely heavily upon, humans can also reason and critically think about an issue to alter their judgment. This sentiment is of particular interest to psychologists who may be interested in judgment, decision-making, and moral reasoning.

Another goal of *The Trolley Problem* is to explain the merits of discussing thought experiments like the titular scenario. Although the trolley problem itself may not be the most ecologically valid situation, it has the potential to reveal multiple facets of human thought and reasoning. In other words, humans are rarely faced with situations as dire and with such clear consequences as the trolley problem, but it can reveal what someone values. Cathcart (2013) writes that while these topics may not be the most realistic, but what they do accomplish is opening up avenues for discussion that could potentially expand our understanding of moral issues.

What Others Think

Reviews from popular periodicals have praised *The Trolley Problem* for its clarity and the light-hearted (but not oversimplified) manner in which it is presented (Akst 2013; Bakewell 2013). While some have criticized the book for the cumbersome cover story of the trial (Bakewell 2013), reviewers

have focused on the efforts of Thomas Cathcart to simultaneously give an introduction to moral philosophy and present a classic thought experiment, and to write about philosophy in such an accessible fashion (Akst 2013).

Conclusion

The Trolley Problem is an excellent introduction to the nominal moral conundrum. Cathcart presents it in both its historical context and outlines the modern versions that continue to push the bounds on moral reasoning. Even though numerous perspectives are proposed as to whether or not someone would condone pulling the switch, this is not a question where there is a truly correct answer. Thomas Cathcart's (2013) exploration is an extensive and succinct account of the trolley problem that helps to explore the moral reasoning that philosophers have discussed throughout the history.

Cross-References

- [Evolution of Morality](#)
- [Jonathan Haidt](#)
- [Modern Moral Relativism](#)
- [Moral Instincts](#)
- [Morality](#)
- [Thomas Cathcart](#)
- [Trolley Problem](#)

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Trolley Problem, The

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Synonyms

[Runaway tram](#)

Definition

The trolley problem is a moral thought experiment involving a trolley on course to kill some number of people. The trolley can be redirected or stopped with varying consequences and with a known benefit depending on the variation of the problem itself.

Introduction

The trolley problem is a moral dilemma used first by philosophers starting in 1967 and then adopted by psychologists to examine moral thinking in humans (Cathcart 2013). The original problem was made by Philippa Foot in a philosophical paper about abortion and the doctrine of the double effect. The problem was presented as multiple variations of a scenario in which someone had to make a choice of killing one to save five. The template scenario involved flipping a switch to change the tram to a different track. These scenarios were intended to enact the doctrine of the double effect, where good consequences with bad side effects are approvable as long as the bad side effects were not intended (1967). The original trolley problem is stated as such:

...To make the parallel as close as possible it may rather be supposed that he is the driver of a runaway tram which he can only steer from one narrow track on to another; five men are working on one track and one man on the other; anyone on the track he enters is bound to be killed. . . (Foot 1967)

The Trolley Problem in Research and Variations

There are many variations of the trolley problem that change single or multiple aspects of the dilemma. The two most common variations are the “loop variant” and “fat man variant.” The loop variation remains similar to the original problem as stated by Philippa Foot, where the participant is given the option to either allow the trolley to continue on its current path which will kill five people or pull a lever redirecting the trolley onto a track which has one person on the track. Whereas the fat man variation usually does not involve a lever, but instead a fat man or large man with a backpack. The fat man variation is generally stated as such:

You are standing near a trolley track, there is a trolley heading down the track toward five workers who are unaware of the trolley and whom will die if nothing is done. There is a fat man next to you, large enough to stop the trolley if pushed onto the tracks; this will kill the fat man. Do you stop the trolley by pushing the fat man onto the tracks or let the trolley hit the five workers on the track? (Cathcart 2013)

These two variations have the same outcome, but drastically different responses, which change further when details about the problem or participants are altered, for example, by adding descriptions of the possible victims of the trolley (Bleske-Rechek et al. 2010) and when participants are psychopaths/sociopaths (Greene 2013). Participants of the basic lever problem will generally choose to pull the lever, whereas in the fat man problem, they do nothing. This is most likely due to spacial and social reasoning, in that pulling a lever to kill one and save five physically separates the participant from the death of the one. In the fat man problem, however, the physical action of pushing a man to his death, even to save five, is associated with murder (Greene 2013).

Bleske-Rechek et al. (2010) at the University of Wisconsin investigated the trolley problem using different descriptions of the man on the looped track. They tested this by replacing the man in the loop variant with relatives of varying genetic relatedness (0–0.5), people of varying ages (2–70), and people of reproductive

opportunities or current mates. They found that when younger, more related people or mates were standing next to the participant in the scenario, the hypothetical person was less likely to be sacrificed for the five (Bleske-Rechek et al. 2010). Results matched inclusive fitness theory; people will prioritize saving themselves, genetic relatives, the young, and potential or current mates over anyone else, even if saving the one relative, kid, or potential mate means allowing five people to die. This evidence, according to Bleske-Rechek et al. (2010), suggests that human moral thinking is deeply seated in our evolutionary history. However, some researchers disagree that hypothetical situations are enough to trigger evolved mechanisms (discussed in Bleske-Rechek et al. 2010).

Another study by Navarrete et al. (2012) used virtual reality headsets with audio to test a realistic example of the trolley problem. In this study, participants were allowed to acclimate to the headset and controls. Participants were positioned on a virtual bridge near the track in a steep ravine and were told that a runaway train car was quickly rolling down the tracks. They are also told that people often use the tracks as a way of travel and due to the nature of the ravine that they will not be able to see or hear the train car until it is too late. From this point, the participant can see, and shortly after hear, the train car barreling down the track. Around the same time, five animated white men begin walking on the main track and one white man begins walking on the track. If participants did not act, the five white men were run down (accompanied by loud screams). However, those who pulled the lever to switch the train car onto a side track killed only one person. Approximately 89.5% of participants chose a utilitarian response, killing the one. Similarly, in his book *Moral Tribes*, Greene (2013) takes an in-depth evolutionary approach to the trolley problem and its variations. He shows that only 20% of people are willing to push a man onto the tracks to save the five workmen. Nevertheless, over 80% of people were willing to switch the trolley onto the second track with one person. Pushing the man with a backpack or the fat man saves the most lives, but people have a negative emotional reaction to this choice. When there is an

option to pull a lever and switch the train onto other tracks, this negative emotional response is weakened (Greene 2013). Greene argues (see also Singer 2005) that pushing the man onto the track is a personally direct action, whereas pulling a lever is an indirect and distant action, and this pushing that man is more distressing than pulling the lever. Greene (2013) provided support for his hypothesis by administering the trolley problem to psychopaths/sociopaths, who showed considerably less variance when choosing to sacrifice the man to save the five (i.e., demonstrated less empathy by tending to logically choose to sacrifice the one and save the five regardless of the circumstances).

Cross-Cultural Trolley Problem

A study by Gold et al. (2014) examined the trolley problem cross-culturally using a real-life example based off the trolley problem that involved orphans and food. The study comprised 45 British participants (24 women), 61 Chinese participants (54 women), and 63 other international participants (i.e., “foreigners,” 46 women). A slightly altered trolley problem was given that involved an 18-s animation of a large ball rolling toward a group of five orphans. They were given the option to flip a switch in order to redirect the ball toward a single orphan, but instead of the children dying as per the original problem, they would simply not be given a meal if run over by the ball. They found that 80% of British participants and 69.35% of the foreigners flipped the switch, denying the one orphan a meal instead of five, whereas only 49.18% of Chinese participants flipped the switch (Gold et al. 2014). Similar research has also found that 76.36% of British participants and 64.44% of Chinese participants (who rated similarly on measures of moral judgments) flipped the switch to save five orphans from the trolley and sacrifice one when using the original problem, with both sets of participants mostly citing utilitarian reasoning (e.g., “the greater good”) for why they flipped the switch (Gold et al. 2014). As for participants who did not flip the switch in either the orphan meal variation or original trolley problem,

the British participants generally voiced that they did not want the responsibility of deciding someone’s fate, whereas Chinese participants similarly claimed they did not want to alter destiny/fate (Gold et al. 2014). More specifically, British participants who did not pull the switch either felt a strong negative emotional response to the idea of either killing the one man or not feeding the one child. For the Chinese participants, however, they felt pulling the switch was not their responsibility to begin with (i.e., pulling the switch was outside their control). Therefore, differences in results can possibly be contributed to cultural beliefs or upbringings (Gold et al. 2014).

Conclusion

The trolley problem can and has been used to analyze moral thinking from an evolutionary perspective in humans. Since the original problem was proposed by Foot, many variations of the trolley problem have spawned. The overall problem can be used in research to test moral thinking in humans from an evolutionary or more generally social perspective. In the loop variation where participants may pull a lever to redirect the trolley onto a second track to kill one person and save five, 80% or more of participants tend to logically save the majority, unless the one being killed is a genetic relative, child, or mate (Bleske-Rechek et al. 2010). In the fat man variation where participants are given the option to push or drop a fat man onto the tracks to save five from the trolley, only 20% or fewer participants choose to sacrifice one person to save many, with the exception of those low in empathy (i.e., psychopaths/sociopaths; Greene 2013). Results support evolutionary theories of moral reasoning (see, e.g., Bleske-Rechek et al. 2010) and provide important insight into human social behavior in general.

Cross-References

- [Fat Man, The](#)
- [Loop Variant, The](#)
- [Morality](#)

- [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)
- [Utilitarianism](#)

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Trolleyology

- [Psychology](#)
- [Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?](#)

True Friends

- [Specific Friendships](#)

Trust

- [Gossip and Indirect Reciprocity](#)

Tu Quoque, Argumentum Ad hominem, Character Attack

- [Ad Hominem](#)

Tumor

- [Cancer](#)

Twin Studies

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Synonyms

[Behavioural genetics](#); [Biometrical modelling](#);
[Classical twin design](#); [Heritability](#)

Definition

Comparing similarity of identical and nonidentical twin pairs to estimate genetic and environmental influence on trait variation.

Introduction

Twin studies allow researchers to investigate the nature versus nurture question: are our individual characteristics due to genes or upbringing? Twin studies have long contributed to psychological science, but have only recently been applied to evolutionary psychological questions.

The classical twin design is basically a natural experiment: twins pairs are born either genetically identical (sharing all their genes), or nonidentical (sharing on average half of their segregating

genes, like normal siblings). If a trait is more similar among identical twin pairs than among nonidentical twin pairs, it can be inferred that the trait is influenced by genetic factors.

Quantifying Genetic and Environmental Influences on Trait Variation and Covariation

Inferring a genetic influence on a trait does not imply that other factors do not also play a role – invariably they do. Structural equation modelling can be used to estimate the proportion of a trait's variation that can be explained by genetic factors, aspects of the environment that twins share (e.g., early home environment), and residual factors (e.g., idiosyncratic experiences, random biological effects, and measurement error). This partitioning is possible because these different sources of variation predict different patterns of twin correlations. If genetic factors were the only source of trait variation, we would expect a twin correlation of 1 for identical pairs and 0.5 for nonidentical pairs, in line with their respective genetic similarities. If shared environment were the only source of variance in a trait, we would expect a twin correlation of 1 for both identical and nonidentical pairs, since both fully share the shared environment, by definition. Residual factors are uncorrelated in both identical and nonidentical pairs, by definition, so if they were the only source of variance we would expect both identical and nonidentical twins to be uncorrelated. Maximum likelihood structural equation modelling estimates the combination of genetic, shared environmental, and residual influences that best matches the observed twin pair correlations. Statistical confidence intervals around the estimates can be calculated, and age and sex effects can be estimated and controlled for.

These methods lend themselves to multivariate extension as well. Analysing two or more traits together enables estimating the relative contribution of genetic and other influences to correlation *between* traits as well as to variation in each individual trait. For example, the genetic correlation

between two traits can be estimated – an index of the extent to which the genetic influence on two traits overlaps.

The reader can find in-depth treatments of the methods and assumptions underlying the classical twin design elsewhere. Neale and Maes (2004) provide a comprehensive book-length treatment, Posthuma et al. (2003) provide a good overview journal article format, and Verweij et al. (2012a) provide step-by-step demonstration of heritability estimation in OpenMx, a popular program for analysing twin data.

Twin Studies and Evolutionary Psychology

Evolutionary psychology and behavioural genetics two fields that developed largely in isolation from each other. Their separation was due in part to the fundamentally different focus of each field. Behavioural genetics focuses only on differences between individuals, while evolutionary psychology has traditionally focussed on characteristics universal to all humans or all men/women. However, the subjects of the two fields are integral to each other: genetic variation in traits allows them to evolve, and evolution shapes the structure of genetic variation and covariation in traits. As such, in the last decade the fields have begun to integrate (Zietsch et al. 2015a).

A simple and profound message for evolutionary psychology in the findings of twins studies is that, for almost all human traits, individual differences are in large part due to genetic differences between people (on average accounting for 50 % of the total variance) and not due to differences in their upbringing (on average accounting for 0 % of total variance) (Polderman et al. 2015). This principle contrasts with a conventional wisdom of evolutionary psychology: that important behavioral characteristics will be fairly universal at the genetic level (i.e., exhibit low or zero heritability). Many evolutionary psychological theories are based on the premise that individual differences are caused by universal psychological mechanisms that calibrate traits to aspects of the early environment or other aspects of the individual.

These theories are often incompatible with the findings of twin studies (Zietsch 2016).

Given the pervasive genetic variation in human behavioral traits, a goal of evolutionary psychology should be to understand the evolutionary basis of this variation. Such widespread genetic variation is a conundrum, central to evolutionary biology as well, because natural selection normally winnows away genetic variation, favouring only the optimal genotype. Twin studies provide an avenue for addressing this problem.

A striking example of the conundrum is the Darwinian paradox of homosexuality. Twin studies have shown a substantial genetic basis to variation in sexual orientation, so the question is: how are the genes predisposing to homosexuality maintained in the population when homosexuality reduces reproductive success? A twin study by Zietsch et al. (2008) provided a potential answer. It showed evidence suggesting that the genes predisposing to homosexuality *increase* the mating success of heterosexual carriers of those genes. This mechanism for maintaining genetic variation in a population is called *antagonistic pleiotropy* – meaning that the same genes have multiple effects (pleiotropy) with opposite (antagonistic) consequences for fitness.

Another example of the genetic variation conundrum is the wide variation in women's preference for facial masculinity in a partner. The dominant evolutionary psychological theory explaining this variation has been that universal psychological mechanisms calibrate women's facial masculinity preference to aspects of the environment or to their own characteristics (such as attractiveness). However, Zietsch et al. (2015b) showed that these putative calibration effects were tiny (accounting for less than 1 % of variation in the preference), whereas genetic factors accounted for around 40 % of the variation. Lee et al. (2014) provide a clue to why this genetic variation may be maintained in the population: they showed that the genes that increase facial masculinity in males also decrease the attractiveness of female relatives. Therefore, even if there is a genetic advantage in choosing a masculine-faced father for male offspring, such a choice may be disadvantageous for female offspring, potentially neutralising the fitness

consequences of women's preferences for masculine or feminine faces.

A final example of the genetic variation conundrum can be seen in personality traits, which have been shown by twin studies to be substantially heritable (Polderman et al. 2015). Again the question is why this genetic variation persists. Using results from twin studies, along with new genome-based methods, Verweij et al. (2012b) showed that the genetic variants underlying personality traits are likely to be low-frequency and directionally dominant (i.e., dominant or recessive in a biased direction with respect to fitness). Given prior evolutionary-genetic modelling, these findings suggest that genetic variation is maintained by a balance between selection on the one hand and accumulation of random mutations on the other (i.e., *mutation-selection balance*).

Conclusions

Twin studies are powerful tools for investigating the genetic and environmental sources of human individual differences. Decades of twin research have shown that virtually all traits exhibit substantial genetic variation, whereas upbringing contributes surprisingly little. Recent and future twin studies can advance the important goal of understanding the evolutionary basis of this genetic variation.

Cross-References

- Genetic Influences of Puberty
- Heritability
- Homosexuality Paradox, The

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Two-Parent Families

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Synonyms

Cohabitation; Father presence; Intact families; Same-gender parents; Stepfamilies

Definition

Families in which offspring receive direct care, support (financial, emotional), and/or other resources (e.g., energetic, social) from two co-residential parents or caregivers.

Introduction

In the United States, it is becoming increasingly common for children to be reared outside of what was once viewed as the “traditional” family context: co-residence with the biological parents (e.g., Fedewa et al. 2015; Hemovich et al. 2011). Understanding the consequences of rearing children within a variety of family structures is of interest to social scientists across disciplines. Here, we consider average differences in children’s outcomes across two- and single-parent families; intervening factors that contribute to these average differences (where they exist); and variation in parental behavior and children’s health and well-being within two-parent families.

Two-Parent Versus Single-Parent Families

There is a widespread belief that growing up in a two-parent family is preferable to growing up with a single parent. The empirical literature across psychology, sociology, and family studies is replete with research documenting average differences between children reared across these dichotomized contexts. The narrative that has emerged is that children and adolescents reared in stably intact families with their biological mother and father are more socially competent, achieve more academically, and enjoy better physical and mental health compared to youth reared in biologically divorced, separated, or single-parent families (e.g., Geary 2007; Hemovich et al. 2011; McLanahan et al. 2013). There is some evidence that these disparities become more pronounced when the parental divorce or separation occurs early in a child’s life (McLanahan et al. 2013).

Due to men's paternity uncertainty and lower minimum obligatory investment in reproduction compared to women, paternal investment is more sensitive to socioecological factors, and thus more variable in quantity and quality, than maternal investment (Geary 2007). These conditions render biological father absence statistically more prevalent than biological mother absence. In this context, the focal comparison in many studies of family structure is between children reared in intact, two-parent families and those reared by single mothers. Though less common, research also documents developmental challenges related to growing up without one's mother or in a single-father (versus two-parent) home (e.g., substance use; Hemovich et al. 2011). The apparent advantages of dual parenting have been observed regardless of parent gender, with children reared by same-gender parents (two mothers or two fathers) enjoying cognitive outcomes, peer relationships, and mental health that are comparable (or, in some cases, superior) to peers reared by biological parents of different genders (e.g., Fedewa et al. 2015).

A variety of explanations have been offered for the average differences in child outcomes across two-parent and single-parent families, including (but not limited to) differences in income, parental monitoring, and parent-child relationship quality (e.g., Hemovich et al. 2011). From a functional perspective, psychosocial stress that accompanies parental dissolution may guide children toward developmental and behavioral pathways that promote fitness under stressful-unsupportive versus benign-supportive conditions. On this view, for instance, daughters who experience father absence are posited to demonstrate early and short-term sexual behavior to prepare for environments in which male investment in partners and offspring is relatively low (Draper and Harpending 1982). Others note that observed relationships of this kind (e.g., between family environments and children's development) are influenced by shared genetics, as absent fathers may be more likely to transmit genes for impulsivity and risk taking to their children than are fathers who remain present (e.g., Schlomer et al. 2018).

Social scientists have taken deliberate steps in an attempt to examine potential causal influences of

father-absent family structures while accounting for environmental and genetic confounds. McLanahan et al. (2013) reviewed studies that implemented causally informed research designs (e.g., longitudinal studies, natural experiments) to test for effects of father absence on children's outcomes across the life course. They found that when rigorous designs were implemented, father absence (versus presence) predicted lower high school graduation rates, increased externalizing problems and substance use, and worse mental health as adults. (However, the effect sizes documented in these studies were generally smaller than those obtained using cross-sectional designs.) Others have begun to explore the possibility that outcomes often considered as resulting from family structure reflect interactions between genetic risk factors and environmental exposures to father-absent environments (e.g., Schlomer et al. 2018).

Variation in Parental Identity and Quality of Investment

Whether observed relationships between family structure and children's outcomes are viewed through the lens of conditional adaptation, shared genetics, or socially transmitted dysfunction, the "effects" of being reared in two- versus one-parent families undoubtedly are more complex than average differences between children reared in such families might suggest. Although the experiences of children growing up in single- versus two-parent homes may be qualitatively different, the effects of different family structures (and the purported benefits of living in two-parent families) may depend on which parents are present in the home, their relationship with each other, and what these parents do while they are present (i.e., the quality of their behavior). In other words, children's outcomes are likely to reflect the fact that not all two-parent family contexts are equivalent.

Stepparent families (two-parent families in which a child is reared by one biological and one non-biological parent) have earned an overall negative reputation across diverse empirical literatures. Children residing in stepfamily households demonstrate reduced academic achievement,

psychological well-being, and social competencies compared to children residing in intact biological families (reviewed in Amato and Sobolewski 2004). Children reared by cohabiting (but unmarried) biological parents often exhibit outcomes that are comparable to children reared within stepfamilies (Brown 2004). Further, children living with one biological and one non-biological parent, whether married or unmarried, are more likely to experience multiple forms of victimization (e.g., maltreatment, physical or sexual abuse) relative to children living with two biological or adoptive parents (Turner et al. 2013).

These baseline disparities between children reared in biologically intact versus stepparent or cohabiting families may be driven in part by differences in the quality of family relationships across these contexts. Interactions within stepfamily structures are more discordant than those within biologically intact families, and children in these families experience greater exposure to parental conflict, substance abuse, and psychiatric disorders (e.g., McLanahan et al. 2013; Turner et al. 2013). The relationships between parents and their stepchildren also are qualitatively different than those between parents and their biological children. Stepfathers, specifically, spend less time with and are less emotionally close to their stepchildren than are co-resident biological fathers (Amato and Sobolewski 2004). However, when children and stepparents are able to develop close bonds, children do seem to benefit from the presence of the second parent (Amato and Sobolewski 2004).

Variation in the quality of parenting provided by the biological parents also has a powerful influence on children. DelPriore et al. (2017) tested for the effects of father-daughter relationship quality on daughters' risky sexual behavior and related outcomes between and within families. The results suggested that daughters who had high-quality (warm, supportive) relationships with their fathers while growing up received more parental monitoring, were less likely to affiliate with sexually promiscuous peers, and engaged in less risky sexual behavior during adolescence compared to daughters who reported lower-quality relationships with their fathers. Further, in a study by Jaffee et al.

(2003), the prolonged presence of fathers who engaged in high amounts of antisocial (e.g., illegal, aggressive, and impulsive) behavior predicted increases in children's conduct problems. In such this case, the two-parent family structure may do more harm than good, conferring upon children both genes and environments that encourage socially undesirable behavior. Although consistently higher (and often less variable) than paternal care, quality of maternal care also matters for children. Goodman et al. (2011) conducted a meta-analysis exploring possible effects of maternal depression. They found that children living with a depressed mother exhibited higher rates of emotional and behavioral issues (e.g., anxiety, aggression) throughout childhood compared to children residing with mothers who did not meet criteria for a depressive disorder. This relationship was strongest for young children, suggesting a decline in sensitivity to maternal quality in later adolescence.

Conclusion

Growing up in a stably intact family, whether with different- or same-sex parents, forecasts a number of socially desirable outcomes for children and youth. However, simply being reared in a two-parent family is not sufficient to guarantee children's health and well-being. The benefits of co-residing with two parents often depend on the nature of the relationship between the parents and the quality of caregiving provided. To the extent that marital relationships that remain intact are characterized by high-quality (warm, supportive, low-conflict) relationships between parents and their children, one might expect that these families will allow most children to reach their potential. Children's genes and environments may collaborate to foster health and well-being in such contexts. However, to the extent that living in a two-parent family keeps children in close proximity to a biological parent or stepparent who is emotionally cold or violent, who abuses drugs or alcohol, or who suffers from other mental health issues, the benefits of dual parenting may be overstated.

Cross-References

- [Children Without Paternal Investment](#)
- [Father Absence](#)
- [Father-Absence and Stepfather Presence](#)
- [Paternal Investment](#)
- [Paternal Investment Relative to Maternal Investment](#)
- [Step-Parenting](#)

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Type III Diabetes

- [Gestational Diabetes and Maternal-Fetal Conflict](#)

Types of Crying

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Synonyms

[Crying diversity](#); [Crying versatility](#)

Definition

Qualitatively different forms of weeping and/or shedding tears.

The range of expressions of emotion associated with shedding of tears from the eyes.

Introduction

Crying is generally understood as shedding tears in response to some emotional state or reaction, more specifically known as weeping. Relevant terms are bawling, blubbering, moaning, sniveling, sobbing, tearing, wailing, weeping, and whimpering, as well as tremor, convulsions, irregular and interrupted breathing, specific facial expressions, and the “lump in the throat” sensation. Accordingly, weeping is often accompanied by vocal emissions, as the term crying implies. Here, we list different types of behaviors that are subsumed under the rubric of emotional crying

and attempt to provide a brief description of their use and etiology. The alternative is reflexive crying, which is defined either as crying because someone else is crying (reviewed in Eisenberg and Lennon 1983, pp. 105–107) or as a response to wind, cold, smoke, and other chemical and physical irritants (Bindra 1972; Bellieni 2017). The latter type of reflexive crying allows the eye to wash away the objects or toxins which have irritated it. Lacrimation is a technical term for tearing as such.

Watery Eyes

Even a small excess of lacrimal fluid may be visible from a few meters' distance, providing a signal of emotional upset. The receiver of this signal typically reflects on her role in the emotional reaction, prompting a change in her behavior, such as apologizing, backing off, withdrawing, or comforting the crier (Hendriks et al. 2008; for a review, see Miceli and Castelfranchi 2003). It has been suggested that blurring the vision with tears handicaps aggressive action and thus serves as a signal of submission, or that it is a way of expressing helplessness and so eliciting an altruistic response (Williams and Morris 1996). Across two measurements in 1981 and 1996, more than half of all crying events for males fitted the description "red eyes and a tear or two" but only one third of events for females, while sobbing, shaking, and bawling constituted more than half of all crying events for females but only one sixth for males (Lombardo et al. 2001). Likewise, 71% of males' crying episodes featured watery eyes, but only about half of females' episodes, according to a diary study (Frey et al. 1983).

Flowing Tears and Facial Expressions

This is where the excess leads to tears running down the cheek, which can occur both in isolation and with any range of additional behaviors. These include a particular set of facial expressions. The corrugator supercilii muscles narrow the eyebrows and wrinkles the forehead, which is

commonly accompanied by grimacing due to excitations of several facial muscle groups, particularly in the cheeks and chin, including, for example, a lowered and extended lower lip. These specific "crying faces" have not been systematically studied, although they might have significant communicative features.

Vocal Emissions

Crying is sometimes associated with extremely strong emotions of despair, a despondent state in which the person seems oblivious to the external world and has no or little control over her behavior. From this end of the spectrum to silent flowing tears, there may be, in decreasing order of intensity, bawling, moaning, and wailing, as might also be reactions to physical pain, followed by whimpering and snivelling, which is characterized by vocal emissions of moderate loudness, often combined with sounds produced by airflow through fluid in the nasal cavity. Blubbering and sobbing are mainly characterized by sounds produced by airflow through the respiratory passage, more specifically convulsive inhaling and exhaling, but may also include softer vocal sounds. Sobbing is specifically related to the irregular and interrupted breathing that is typical of more intense crying and which constitutes around 10–15 percent of all crying episodes (Frey et al. 1983). This proportion may be substantially larger in females (Lombardo et al. 2001). Convulsions and tremors may furthermore be extended to the whole body, including writhing and kicking.

Tears of Sadness and Pain

Sorrow is the archetypical cause of crying, the type of which tends to be long-lasting, difficult to stop once commenced, and to preclude the crier from any other activity. It strongly impacts the crier, but to a lesser extent those who might observe the crier. Such crying can last from a few minutes to several hours, in which case it tends to wax and wane over the longer intervals (Bindra 1972; Williams and Morris 1996). It is associated with extremely negative situations

such as the loss or threat of loss of a loved one, severe personal failures, or self-pity. When caused by physical pain, crying is more rhythmic. There has been considerable speculation that crying in these situations has beneficial effects, in accord with ancient notions to that end in folk psychology (Bylsma et al. 2008), and entails some sort of positive effect or catharsis (for reviews, see Rottenberg et al. 2008a; Stougie et al. 2004). It has been proposed that the relatively rhythmic nature as well as the soothing effect of the tears on the cheeks may serve to calm the crier down (Bellieni 2017).

Tears of Need

Rhythmic crying is generally heard from hungry babies, which mothers will do almost anything to placate. This kind of crying seems clearly to serve an adaptive function to elicit assistance, as the hearer is desperate to stop it, and has been suggested to directly increase maternal milk supply, through the so-called milk let down reflex (Zeifman 2001). It has also been speculated that this effect is so strong that it can be counterproductive under conditions of excessive crying, such as colic, or when the child otherwise remains unsatisfied, in which case it may suffer abuse and even death at the hands of its caretakers (Barr 1990). In adults, hunger, cold, and other threatening states may also elicit crying, even to the extent of “fake crying” (Vingerhoets et al. 2016). As noted above, crying may similarly have evolved in order to signal submission to an aggressor as well as to stabilize the mood of the crier via the release of stress hormones, evoked by a feeling of loss of control. In most people, crying of a similar kind can be evoked empathetically, at the sight of the suffering of another or at the sight of their sadness, though this will be qualitatively different again and will tend to involve tears without actual crying.

Tears of Joy

It may seem contradictory that a considerable proportion of crying episodes is associated with

positive emotions (Bylsma et al. 2008). Typical elicitors of tears of joy are empathy (Rottenberg et al. 2008b), elation (Bindra 1972), and pathos (Lombardo et al. 2001), all of which may reasonably be associated with pride, in-group favoritism, and rites of passage. Even funerals may fit this pattern, as the ceremony expands upon the character, virtues, and achievements of the deceased, which naturally extends to some extent to the relatives and friends present. Other typical examples include weddings, when children receive their exam results, and other manifestations of accomplishment, such as experiencing profound artistic works. For example, weeping and “chills” are frequently experienced when listening to some kinds of music (Gabrielsson 2011; Sloboda and O'Neill 2001).

Conclusions

There is much theorizing on the types of crying, and it has been suggested that different evolutionary explanations apply for qualitatively different kinds of crying (Efran and Spangler 1979; Vingerhoets et al. 2001). Indeed, it has been found that there are consistent sets of circumstances, such as the death of a loved one, in which people cry due to sadness, just as there are consistent sets of circumstances in which people will cry due to joy, such as the wedding of one to whom one is close. It has been proposed that this kind of crying results from the way in which overwhelmingly positive feelings interfere with the body's epistasis, meaning that something has to be done in order to stabilize the body. Crying may achieve this by releasing hormones that bring the person down toward a manageable level of joy (Bellieni, 2017). Consistent with the idea that crying constitutes loss of control, people are most likely to cry alone and then decreasingly likely to cry in front of people the less close they feel to them, presumably because crying evinces their vulnerability to an emotional loss of control. There may also be a broader group dimension to crying in front of others, both to positive and negative events. If it is evoked publically, including at the clichéd funeral and wedding, it can be

seen as signalling empathy and selflessness and would thus be of adaptive value.

Cross-References

- [Communication, Cues, and Signals](#)
- [Crying](#)
- [Facial Expressions](#)
- [Sex Differences](#)
- [Sex Differences in Crying](#)
- [Sex Differences in Emotional Communication](#)

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Types of Sexual Coercion

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Synonyms

[Direct sexual coercion](#); [Forced copulation](#); [Herding](#); [Indirect sexual coercion](#); [Punishment](#); [Sequestration](#); [Sexual harassment](#); [Sexual intimidation](#)

Definition

According to Smuts and Smuts (1993), sexual coercion concerns the use, or threat of use of force, increasing the chances the targeted female will mate with the attacking male. Alternatively, sexual coercion also decreases the likelihood the female will copulate with other males. In both

instances, the female experiences significant fitness costs due to the sexual male's aggression.

Introduction

Although males and females are known to align their reproductive interest (as predicted by sexual selection theory), it is not uncommon for one sex to attempt to increase its fitness at the expense of the other (i.e., sexual conflict). The incompatibility in fitness goals is facilitated by the asymmetry observed in parental investment (Trivers 1972). Resource availability limits the reproductive success of females, whereas the number of reproductively available females restricts males' fitness (Muller et al. 2009a). Therefore, males invest more in mating effort, seeking multiple sexual partners, and fending off rivals rather than allocating resources to parental effort. Since females accrue most of the costs associated with reproduction, females tend to be more selective when relative to males choosing a mate. Female mate bias, however, is not only reflected in their degree of preference for males displaying a particular trait. Resistance against the advances of males exhibiting unattractive characteristics (Watson-Capps 2009) also exemplifies the cognitive and behavioral mechanisms females employ to protect their reproductive interests. Female preference selects in favor of a trait, while resistance selects against it (Watson-Capps 2009). These socio-ecological forces generate higher reproductive variance in males than in females.

Consequently, unattractive males may use force or threat of force to overcome the female's resistance, increasing the probability the targeted female will mate with the aggressor. Sexual coercion is thus a subcategory of sexual conflict (Watson-Capps 2009). Depending on the nature of the interaction, sexual coercion can be further subdivided into direct and indirect.

Direct Sexual Coercion

Direct sexual coercion refers to the employment of force destined to increase the likelihood a male will mate with a female despite the female's

resistance (Muller et al. 2009a). The literature classifies direct sexual coercion into intimidation, harassment, and forced copulations. Harassment involves the male's mating insistence despite the female's refusal. The repetitive nature of the behavior eventually leads to the female's submission. Intimidation, alternatively, describes instances in which the male will attack the refusing female, as a form of retribution, increasing the female's acceptance toward the male's advances (Muller et al. 2009a). Finally, forced copulation refers to the male's aggressively restraining the female, leading to an imminent mount (Clutton-Brock and Parker 1995; Muller et al. 2009a). Some authors also consider infanticide, the elimination of infants with the aim of increasing the chances the targeted mother will mate with the attacker, as another manifestation of sexual coercion (Watson-Capps 2009).

Intimidation occurs in several primate species. For example, chimpanzee males will attack females to facilitate the establishment of a sexual consortship (Clutton-Brock and Parker 1995). Even though most of the times, aggression against female chimpanzees transpires in the absence of any clear behavioral or physiological immediate cue (e.g., the targeted female did not exhibit a sexual swelling; Clutton-Brock and Parker 1995), it is not uncommon for the victim to copulate with the aggressor (Clutton-Brock and Parker 1995). In Japanese macaques (*Macaca fuscata*), females who are frequently the target of aggression are also more likely to mate with the aggressors rather than with less aggressive males (Clutton-Brock and Parker 1995).

Harassment is found across various taxa. For example, in fallow deer (*Dama dama*), males chase and insistently try to copulate with females (Clutton-Brock and Parker 1995). Similarly, due to the considerable sexual dimorphism in elephant seals (*Mirounga angustirostris*), male's mating attempts leads to female injury (Clutton-Brock and Parker 1995). In avian species, female ducks face the risk of drowning due to male intrasexual competition (Clutton-Brock and Parker 1995). In nonhuman primates, such as chimpanzees it is not uncommon for males to employ harassment to increase the likelihood of future copulations (Muller et al. 2009b).

Although forced copulations occur in several vertebrate and invertebrate species (Clutton-Brock and Parker 1995; McKinney and Evarts 1998), relative to other forms of sexual coercion, this particular sexual coercion is less prevalent in nonhumans primates. For example, male mountain gorillas (*Gorilla beringei*), and male chimpanzees (*Pan troglodytes*) rarely restraint females during mating (Muller et al. 2009b; Robbins 2009). Orangutans' (*Pongo pygmaeus*) behavior, however, stands in contrast to this general pattern. It is worth noting that even though initial primatological reports suggested unflanged males, that is, small individuals lacking cheek flanges, employed forced copulations, current evidence indicates that this behavior is part of a general mating strategy of male orangutans (Knott 2009). The female's resistance is dependent on the time of the mating during the estrous cycle. Females reject flanged males if the copulation attempt occurs when the female is not ovulating, as well as unflanged males if they seek to mate during the ovulatory stage (Knott 2009). As a tactic destined to confuse paternity, and decrease the risk of infanticide, females do copulate with unattractive males outside of the ovulatory days (Knott 2009).

Indirect Sexual Coercion

Also conceptualized as coercive mate guarding (Muller et al. 2009a), indirect sexual coercion decreases the likelihood the female will mate with another male (Muller et al. 2009a). Herding, sequestration, and punishment are the main subclasses of indirect sexual coercion. Concerning herding, the guarding male uses aggression to separate the female from competing males. This strategy restores the physical proximity between the guarding male and the female (Muller et al. 2009a). Sequestration occurs when the male uses force to separate the female from the core group, decreasing the likelihood the female will mate with other males, for example, before or during ovulation (Muller et al. 2009a). Punishment is defined as the male's aggression against a female due to her association or mating with other males. This expression of coercive mate guarding,

decreases the risk the female's behavior will repeat in the future (Muller et al. 2009a). Dominant males employ punishment to decrease the risk of females copulating with other males. High-ranking male chimpanzees, for example, target females who associate with other males (Muller et al. 2009b). After a takeover, male hamadryas baboons (*Papio hamadryas*) employ neck bites, nonlethal aggression directed at the nape of the female's neck, to increase the level of female submission. Females experience lower rates of aggression if they are physically close to the male and spend time grooming him (Swedell and Schreier 2009).

Species living in fission–fusion societies, where females spend time alone, are especially vulnerable to herding. In bottlenose dolphins (*Tursiops truncatus*), males are known to form nested alliances restricting the female's free movement (Connor and Vollmer 2009). Primate species living under a fission–fusion structure, such as chimpanzees, also employ herding as part of the establishment of consortships with fertile females (Muller et al. 2009b). Herding in chimpanzees and bottlenose dolphins is suspected to be the product of convergent evolution in life history traits, and social complexity. Both species exhibit slow life history traits and large brain size. Elements necessary for the maintenance of sophisticated political lives include males developing coalitions and alliances, which can be used to coerce females (Connor and Vollmer 2009). Although males of various mammalian species use sequestration, such as in bottlenose dolphins (Connor and Vollmer 2009), in nonhuman primates, this strategy is limited to a few taxa including chimpanzees and Hamadryas baboons (Muller et al. 2009a).

Sexual Coercion in Humans

The plasticity and flexibility of human mating strategies are also evident in the presence of different expressions of sexual coercion. Concerning direct sexual coercion, several studies had found evidence of harassment, intimidation, and forced copulations (Camilleri and Quinsey 2012). Similarly, indicators of indirect sexual coercion, such as sequestration, herding, and punishment are also

reported across human societies (Camilleri and Quinsey 2012). Intimate partner violence (and interpersonal aggression generally) is often divided into several highly intercorrelated categories (Figueredo et al. 2018): (1) verbal/psychological; (2) physical; (3) escalated/life-threatening; and (4) sexual. They have nevertheless been repeatedly shown to represent convergent indicators of a single latent construct (Figueredo and McCloskey 1993; McCloskey et al. 1995). As such, it is probably better to think of these categories as taxonomies of behaviors than as taxonomies of perpetrators, as the same perpetrators are often likely to engage in several of these behaviors. It is also likely that the distribution of offenders might reflect differences in the relative severities of aggression levels represented by the categories, aligned along a continuum. Thus, offenders with a lower level of aggressiveness might only engage in verbal/psychological abuse; offenders with a somewhat higher level might engage in both verbal/psychological and physical abuse; offenders with an even higher level might engage in verbal/psychological, physical, and escalated/life-threatening abuse. It is unclear where sexual abuse would fall on this continuum, as it is so often combined with the other behaviors. Nevertheless, such a quantitative model is in need of development and validation.

Conclusion

Driven by the twin sexual selective pressures of intrasexual competition and intersexual selection, sexual coercion stands reconceptualized as a special case of sexual conflict, which occurs when the fitness interest between the sexes is unaligned. Sexual coercion is further subdivided into (1) direct coercion, wherein the male's use of force against a female increases the probability of copulation despite the female's resistance, evidenced in forced copulations, sexual intimidation, and sexual harassment; and (2) indirect sexual coercion, reflected in instances of sequestration, herding and punishment, where the male coercion functions to decrease the likelihood the female will copulate with other males.

Cross-References

- [Aggression for Sexual Access](#)
- [Life History Theory and Rape](#)
- [Nonhuman Sexual Conflict](#)
- [Sexual Conflict Theory](#)
- [Sexual Harassment](#)

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U

UG

- [Universal Grammar](#)

Ultimate Behavior

- [Alarm Calling upon Predator Detection](#)

Ultimatum

- [Dominance and Threat or Use of Force](#)

Uncertainty Monitoring

- [Metacognition](#)

Uncertainty of Biological Kinship

- [Relational Uncertainty](#)

Uncommitted Mating

- [Lowering Partner Standards in a Short-Term Mating Context](#)

Uncommitted Sexual Encounters

- [Casual Sex](#)

Unconditional Response

- [Unconditioned Response](#)

Unconditional Stimulus

- [Unconditioned Stimulus](#)

Unconditioned Reflex

- [Unconditioned Response](#)
- [Unconditioned Stimulus](#)

Unconditioned Response

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Synonyms

Reflexive response; Unconditional response; Unconditioned reflex

Definition

An unconditioned response is a response that is reflexive and involuntary in nature, which is reliably induced every time an organism comes across to biologically significant stimuli.

Introduction

Living organisms are naturally endowed with a variety of unconditioned responses that prepare them to interact with their environment in an adaptive and usually favorable manner (Baum 2017). Organisms do not have to learn these responses since they biologically received them. These type of responses (i.e., unconditioned responses) appear when an organism comes across stimuli which automatically, and naturally, trigger them (Thines 1987). For instance, a puff of air to an individual's eye area automatically induces a response of an eyeblink (Shanks 1995). The person has not learned to respond with an eyeblink in the presence of this stimulus (i.e., puff of air); he/she naturally and automatically exhibits this response to adapt to the environmental conditions and increases the chance to survive (Thines 1987). The responses that do not need to be learned and are exhibited naturally and automatically by living beings in reaction to a variety of biologically as well as environmentally relevant stimuli are widely known as unconditioned responses. In addition, unconditioned responses are reflexive as well as involuntary in nature and are reliably induced by unconditioned

stimuli (McSweeney and Murphy 2014). The scientific community has obtained valuable knowledge related to unconditioned responses through the outstanding work of a Russian physiologist named Ivan Petrovich Pavlov on a type of learning that is widely known as Pavlovian, classical, or respondent conditioning (Thines 1987).

The Nature of Unconditioned Responses

Natural selection has significantly influenced the development and preservation of unconditioned responses. It has been consistently proposed that unconditioned responses are significantly associated with well-being maintenance, reproduction, and survival enchantment (Baum 2017). For example, eyeblink, shiver, sneeze, and adrenaline release in threatening situations as well as sexual excitement constitute unconditioned responses that seem to be always significantly associated with the preservation and enhancement of healthiness, survival, and reproduction (Ramnero and Torneke 2011). In addition, it has been proposed that people who consistently displayed these unconditioned responses were healthier, reproduced more, and thus enjoyed enhanced survival abilities compared to the people whom unconditioned responses were weak or nonexistent (Baum 2017).

In this sense, over the breeding of multiple generations, the genotypes that promoted a consistent reflexive system would be inclined to enhance reproduction and survival in the prevailing environment more often, up until the maximal fitness is achieved. In other words, the unconditioned responses that living organisms exhibit nowadays are the product of natural selection over the course of long periods of time (Baum 2017). Yet, even though these type of responses improved and persevered fitness in the past, there is no evidence that ensures that the same type of responses would continue to help humans and other living organisms to keep improving and preserving fitness in today's environmental dynamics (Ramnero and Torneke 2011). For example, if the present environmental conditions have significantly altered from the ones that

favored the selection of these types of responses in the past, selection would be enforced to develop new behavioral responses.

Unconditioned Response and Its Role in Classical Conditioning

Ivan Petrovich Pavlov, the founder of classical conditioning through his work on the gastrointestinal system, shed light on the way that living creatures could respond to the associative bonds that are formed between unconditioned stimuli and environmental dynamics enabling them to achieve learning that enhance their capacity for adaption and survival (Ramnero and Torneke 2011). Specifically, I. P. Pavlov examined the alternations of dog's saliva and digestive fluid secretion through their mouth and stomach while feeding. Dogs have an automatic response to the sight of food, that is, they secrete saliva and digestive fluid. Dogs do not have to learn this response since they biologically received it. Yet, at some point, during the course of the experimental procedure that I. P. Pavlov set in order to observe the alternations of dog's saliva and digestive fluid secretion in response to feeding, he observed that the subject's (i.e., dog's) saliva and digestive fluid were also secreted every time he and his associate arrived at the laboratory. Consequently, I. P. Pavlov decided to experimentally examine the functional mechanisms and structures that let the dogs to also secrete saliva and digestive fluid in his presence rather than exclusively to the presence of food in response to which the dogs reflexively secrete saliva and digestive fluid (Spence 1978).

Ultimately, I. P. Pavlov came to the conclusion that the food was associated with the occurrence of his associate by the subjects (i.e., dogs) as the two stimuli had been repeatedly paired. Specifically, the sound of the bell which at the beginning was a neutral stimulus, that is, a stimulus that did not elicit a particular response, acquired the capacity to elicit a response that was qualitatively similar to the one that the food naturally and automatically elicited. The response of the dogs became classically conditioned and respectively

the sound of the bell turned into a conditioned stimulus. Consequently, the new response that was learned as a reaction to the sound of the bell is named conditioned response (Spence 1978).

The Discrepancy Between Unconditioned and Conditioned Responses

Ivan Petrovich Pavlov had proposed through his work on conditioned reflexes that the same response that was elicited by an unconditioned stimulus could also be elicited by a conditioned stimulus through its association with an unconditioned stimulus (McSweeney and Murphy 2014). However, it quickly became clear that conditioned responses are of lower intensity than unconditioned responses. In addition, research related to classical conditioning after I. P. Pavlov's work has reliably proposed that the unconditioned response and the conditioned response are not the same responses, but they are usually qualitatively similar. Yet, this could be significantly different. Specifically, it has been cited that I. P. Pavlov's dogs did not confuse the sound of the bell with nutriment, but they responded to the association among the sound of the bell and nutriment that consistently presented right after the first (Ramnero and Torneke 2011). In addition, the unconditioned response as well as the conditioned response are not limited to the secretion of saliva. Specifically, the secretion of saliva constitutes just a part of a multifaceted response through which the body of the dog is being prepared for obtaining nutriment (Staddon 2014).

Emotional Reactions Based on Unconditioned Responses

Research related to classical conditioning has consistently suggested that affective responses are governed by unconditioned responses, which have been shaped through evolutionary history to help humans to adapt and survive (Baum 2017). Research related to the affective reactions

that are based on unconditioned responses has consistently suggested that humans possess a physiological system that responds to specific unconditioned stimulus. However, the scientific knowledge related to the environmental conditions (unconditioned stimuli) that induce affective reactions is limited. Specifically, the research related to the mechanism and/or conditions that induce such affective responses has not been yet fruitful. This is because, the majority of research studies have included adults as participants, yet, an adult person plausibly has a long-term history of learning (McSweeney and Murphy 2014). However, it has been consistently cited that there are numerous stimuli that are not learned (unconditioned stimuli) yet induce some affective responses. For instance, the affective response of fear can be naturally induced by unconditioned stimulus such as clamorous sound, objects getting near fast, loud noises, and specific facial expressions of other individuals (Thines 1987). Through the lens of an evolutionary perspective, it is not plausible to presume that there is just one kind of stimulus that is able to induce, for instance, fear or anger. That is, if these emotional responses ought to enhance adaption, and thus help an organism to survive, they must be triggered in numerous settings, yet the discrepancy between the stimulus would not have to be very high to have an influence early in a person's life (Baum 2017).

Cross-References

- [Associative Learning](#)
- [Classical Conditioning](#)
- [Conditioned Response](#)
- [Conditioned Stimulus](#)
- [John Watson](#)
- [Unconditioned Stimulus](#)

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Unconditioned Stimulus

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Synonyms

[Biologically significant stimulus](#); [Unconditional stimulus](#); [Unconditioned reflex](#)

Definition

Unconditioned stimulus is any stimulus that has the capacity to reflexively induce a biological reaction which usually enhances adaption and survival.

Introduction

Living organisms are endowed with a number of responses to unconditional stimuli to prepare them to adapt and survive (Baum 2017). Unconditional stimuli refer to any stimuli which naturally and automatically induce innate reactions, that is, reactions that are not learned by living beings; they are biologically endowed to them to be able to respond to unconditioned stimuli (McSweeney and Murphy 2014). The reactions that are induced by unconditioned stimuli are referred to as unconditioned responses since they arise automatically and naturally. For instance, an individual who receives a puff of air in the eye area responds with an eyeblink. The puff of air

constitutes an unconditioned stimulus and respectively the eyeblink an unconditioned response. When a puff of air moves toward the eye area, people blink (Shanks 1995). They do not need to learn this response as they are biologically prepared to do it (Thines 1987). The eyeblink biologically operates to safeguard the eye.

Classical Conditioning and Unconditioned Stimuli

In the most well-known experimental study of Ivan Petrovich Pavlov that was conducted with dogs, the aroma of food was the unconditioned stimulus. Specifically, in this experimental study the dogs were smelling the aroma of the food and in response they automatically as well as naturally began to secrete saliva and digestive fluid. The natural, that is, the unlearned, contingency of a stimulus that evokes a response in that trial was the relationship among food and salivation which represents the contingency of an unconditioned stimulus and an unconditioned response. The term stimulus denotes an event that precedes the response that is investigated (Spence 1978).

Emotional Reactions Based on Unconditioned Responses

Research related to classical conditioning has consistently suggested that affective responses are governed by unconditioned responses, which have been shaped through evolutionary history so that to help humans to adapt and survive (Baum 2017). Research related to the affective reactions that are based on unconditioned responses has consistently suggested that humans possess a physiological system that responds to specific unconditioned stimulus. However, the scientific knowledge related to the environmental conditions (unconditioned stimuli) that induce affective reactions is limited (Schachtman 2011). Specifically, the research related to the mechanism and/or conditions that induce such affective responses has not been yet fruitful. This is because, the majority of research studies have included adults as

participants, yet, an adult person plausibly has a long-term history of learning (McSweeney and Murphy 2014). However, it has been consistently cited that there are numerous stimuli that are not learned (unconditioned stimuli) yet induce some affective responses. For instance, the affective response of fear can be naturally induced by unconditioned stimulus such as clamorous sound, objects getting near fast, loud noises, and specific facial expressions of other individuals (Ramnero and Torneke 2011). Through the lens of an evolutionary perspective, it is not plausible to presume that there is just one kind of stimulus that is able to induce, for instance, fear or anger. That is, if these emotional responses ought to enhance adaption, and thus help an organism to survive, they must be triggered in numerous settings, yet the discrepancy between the stimulus would not have to be very high to have an influence early in a person's life (Baum 2017).

Cross-References

- [Associative Learning](#)
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- [Conditioned Stimulus](#)
- [John Watson](#)
- [Unconditioned Response](#)

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Unconscious, The

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Synonyms

The preconscious; The subconscious

Definition

Mental processes, including inferences, judgments, motivations, and internal conflicts, of which the individual is not consciously aware.

Introduction

The concept of the unconscious mind first became widely known in Freud's work, where it plays a central role in all human activity as an unseen cause or motivation. Although much of Freud's theory has long since dropped out of favor in the scientific psychological community, the central notion that we are often not consciously aware of our own motivations, and that those motivations are often sexual, or perhaps repressed memories of long-forgotten trauma, continues to broadly impact popular culture into the twenty-first century.

Unconscious Conflict

As the *id*, the most primitive part of the human personality, comprising our basic instincts and biological drives for food and drink as well as the sex drive, cannot delay gratification, those fundamental drives inevitably come into conflict with societal rules and laws, internalized as the *superego*. The *ego*'s ability to resolve those conflicts is not perfect, thus leading to feelings of anxiety and guilt which motivate much of what we do. As the *id* and *superego* are both part of the unconscious mind, this conflict, according to Freud, is also entirely unconscious.

A foundational notion of psychoanalytic theory, therefore, is that much of what drives human activity is not directly accessible to the conscious mind and must be discovered indirectly. His favorite means of accessing his patients' unconscious motivations was via dream analysis.

Dreams: The Royal Road to the Unconscious

Freud argued that the primary function of all dreams is wish fulfillment, including fulfillment of the secret desires which we cannot admit even to ourselves on a conscious level.

Understanding our dreams, therefore, requires recognizing that they have become distorted in order to conceal the underlying wishes. The surface content, or *manifest content*, is a heavily disguised version of unconscious wishes and desires, which he called the *latent content*. Understanding the contents of the subject's unconscious mind therefore requires correct interpretation of the symbolic meaning of that individual's dreams.

According to Freud, many of our unconscious motivations are so unacceptable to us that they create a great deal of intrapsychic conflict between the ego and the unconscious parts of the mind. The only way to alleviate the tension and anxiety resulting from that conflict is to allow the forbidden content to surface, though heavily disguised, in dreams. The disguise is necessary because even in dreams, the individual's resistance to these unacceptable impulses remains too strong to acknowledge them directly. The dream's real significance is completely concealed from the dreamer, and dreamers are unable to grasp the actual meaning of their dreams without the help and guidance of the psychoanalyst.

Unconscious Sexual Motivation

Freud was of course notorious for his emphasis on sexuality in his descriptions of the conflicts that roil the unconscious mind. His dream analyses often emphasize the hidden sexual content of dreams, which is unsurprising given the central place occupied by sexuality in his explanation of

mental illness. He famously described the Oedipus complex, an unconscious struggle over a child's desire for the opposite-sex parent, as the "nuclear complex" of all neurosis, arguing that adult mental life simply cannot be understood without analysis of this unconscious conflict from early childhood.

The Parapraxes (or Freudian Slips)

Parapraxis is a Greek term that translators of Freud (although, interestingly, the term does not appear in the original German text, so it was never actually used by Freud—the term he actually used, *Fehlleistungen*, may have been considered too challenging for the Anglophone audience) used to refer to the notion that errors in speaking can reveal the speaker's hidden, unconscious concerns, wishes, or conflicts, just as surely as they can be discerned in dreams. In popular culture, the concept has become so associated with Freud that the common term for such an error is a *Freudian slip*. A widely reported example of such a slip, which caused much mirth among political reporters on American television, occurred when Condoleezza Rice, in her role as National Security Advisor to President George W. Bush, referred in a press conference to a conversation with her boss, beginning, "As I was telling my husb—," stopping herself before completing the thought. This was widely reported in a way heavily influenced by Freud, as a sign of buried sexual tension in their professional relationship, and is easily found via a Google search for *Condoleezza Rice Freudian slip*.

The Cognitive Unconscious

Although Freud's version of the unconscious mind has largely disappeared from scientific psychology, the notion that many of our mental processes occur without conscious awareness is central to modern cognitive and social psychology. Slips of the tongue (no longer called Freudian slips) are actually still studied, as they can reveal useful information regarding how word meanings and word sounds are stored in the brain.

According to recent cognitive research, more than 80% of slips share an initial sound with the intended word, and more than 70% of word endings are identical or very similar as well. While not as immediately intriguing as the notion that a slip indicates hidden sexual desire, this information has led to the modern understanding of the extent to which words are stored in memory in an *echoic* store (by sound) rather than an *iconic* (visual; stored according to similarities in how the words *look*) store. This in turn provides an explanation of the tip-of-the-tongue phenomenon, in which it is often possible to remember the initial or final sounds in a word while being nonetheless unable to recall the word completely. This happens because, since words are stored by sound, sometimes the attempt to retrieve a word activates traces of similar-sounding words, but not the desired word, leading to either a tip-of-the-tongue error (failure to retrieve the word) or the production of a wrong word which was triggered by the search for the correct one (a slip of the tongue, but not Freudian in nature). From both perspectives, complex unconscious processes are involved, but the unconscious processes proposed by more scientifically minded psychologists are quite different from those suggested by Freud.

Cross-References

- [Freud on Sex](#)
- [Freud's Psychoanalytic Theory](#)
- [Infancy](#)
- [Psychodynamic Foundations](#)
- [Sexuality](#)

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Unconstrained Vision of Human nature

- [Blank Slate, The](#)

Uncontrollability

- [Learned Helplessness from an Evolutionary Mismatch Perspective](#)
-

Under-5 Mortality

- [Child Mortality](#)
-

Undereducated

- [Redistribution Preferences and Low Socioeconomic Status](#)
-

Underemployed

- [Redistribution Preferences and Low Socioeconomic Status](#)
-

Understanding

- [Attention and Perception](#)
-

Understanding Human Gaze

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Introduction

The ability to detect the focus of an individual's visual attention can provide rich information about the location of important objects in the

larger environment, as well as about that individual's internal psychological states. Detecting and using such information about gaze direction is a foundational component of human social behavior. For example, even young infants are sensitive to the direction of other's gaze (Flom et al. 2007) and begin to follow gaze geometrically to objects beyond their immediate view in the second year of life. Humans also utilize eye contact as a cue of joint attention – that two individuals are together looking at the same thing. This skill thus allows humans to engage in a variety of potentially species-unique social behaviors, including communication about cultural knowledge (Csibra and Gergely 2009). Finally, our ability to attend to the same stimuli as other individuals is vital to normal social development, providing a scaffold for the development of other abilities such as theory of mind and language acquisition.

Yet despite these links to many complex abilities in humans, sensitivity to gaze is not unique to our species (Rosati and Hare 2009). In fact, gaze-following is widespread across the primate order, as well as in other social mammals and even in some reptiles. Yet these gaze-sensitive behaviors are not necessarily underpinned by the same cognitive processes across species. Comparative cognition researchers are therefore faced with two related questions. First, what are the psychological bases for this skill, and how do they differ across taxa? Second, why does gaze-following appear to contribute to the emergence of complex social cognitive traits in some taxa, such as humans, but not necessarily in others? By answering these questions, we can begin to understand the evolutionary origins of human-unique social cognition.

Psychological Basis of Gaze-Following Across Primate Species

Gaze-following is phylogenetically widespread in primates (Rosati and Hare 2009; Shepherd 2010). Representatives of all major primate groups follow the gaze of others in some situations, including great apes, many Old World monkey species, New World monkey species, and even some lemur species.

However, several aspects of gaze-following behavior differ across taxa. A key distinction is the degree to which gaze-following behavior relies upon more reflexive mechanisms that drive individuals to co-orient – looking in the same direction as others without really understanding why – versus whether gaze-following stems from the attribution of a mental state to another individual. In the first situation, individuals may learn through trial-and-error experience that they gain useful information when they look in the same direction as others, whereas in the latter individuals actually understand that others are looking somewhere because there is something interesting in that direction to see.

As in humans, gaze-following in apes appears to sometimes involve mental state attribution (Call and Tomasello 2008). One piece of evidence comes from experiments using geometric gaze-following (Okamoto-Barth et al. 2007). Within these paradigms, the object that the actor looks at is not within the subject's immediate line of sight, so the subject must move and reorient their position in order to observe the focus of the actor's gaze. Thus, geometrical gaze-following requires the ability to generalize between their own egocentric perspective and that of the actor. The fact that chimpanzees, bonobos, gorillas, and orangutans (see, e.g., Okamoto-Barth et al. 2007) will move in order to view what the observer is looking at makes it unlikely that the behavior is the result of a simple rule to turn their head when other individuals do. Rather this appears to be a more flexible response where the apes are trying to ascertain what the other can see. Moreover, chimpanzees in particular robustly use information about both humans' and conspecifics' current or past visual perspective in competitive contexts (Call and Tomasello 2008). This provides strong evidence that at least some apes can use information about where others are looking to infer their subjective perceptions and knowledge. Along the same lines, rhesus monkeys seem to use information about other's visual perspective during competitive interactions, as well as to predict how others will act (Martin and Santos 2016).

However, there is increasing evidence that gaze-following may be more reflexive and egocentric in other primate species. First, several

monkey species are unable to incorporate gaze information to predict the behavior of humans or conspecifics based on where they were looking previously. Second, unlike chimpanzees or rhesus macaques, several other species do not seem to use information about what others can see in competitive contexts, including capuchins and common marmosets. Finally, while some lemurs have been shown to co-orient with conspecifics during their natural interactions, they may fail to follow the gaze of a human demonstrator in more controlled contexts. However, this may vary across even closely related species: whereas ring-tailed lemurs show a basic gaze-following response to human gazing and also use information about where a human competitor is looking when deciding whether to approach a contested piece of food, several other species of lemur do not (Sandel et al. 2011). Taken together, this suggests that some instances of gaze-following behavior in monkey and strepsirrhine primate species – which can appear behaviorally similar to great ape gaze-following in many respects – might in fact be due to quite different cognitive processes.

A final piece of evidence that the cognitive basis of gaze-following may differ across species comes from studies that compare the ontogeny of these behaviors. In humans, reliable gaze-following emerges within the first year of life. Across nonhuman primates, however, there is quite some variability. In nonhuman apes, gaze-following emerges around 3 to 4 years. In pig-tailed macaques, gaze-following may not emerge until adulthood – leading to the hypothesis that nonhumans require a much longer period of social experience to acquire this behavior. Yet closely related rhesus macaques exhibit gaze-following behavior during infancy, more like humans (Rosati et al. 2016). Overall, this suggests that gaze-following in different species may depend on different social experiences or underlying cognitive mechanisms. Further comparative work examining the ontogeny of social cognition can help elucidate why some species develop social cognitive skills at a different pace and why species may develop certain social cognitive skills but not others.

The Adaptive Value of Gaze-Following

Gaze-following and other gaze-sensitive behaviors appear to be biologically important, given that this skill has evolved in many taxa. In general, this social response may allow diverse species to engage in several important behaviors such as avoiding predators and locating food items in the environment. Yet the cognitive basis of gaze-following differs between species: in humans and other great apes, the ability to model another individual's mental states seems to drive gaze-following, whereas in other species gaze-following may be more egocentric. There are two main evolutionary hypotheses accounting for this variation, and in particular why mind-reading abilities might emerge in some species but not others.

One influential idea is that social competition drives the evolution of theory of mind abilities. If animals can think about other's visual perspective in competitive contexts, this enables more sophisticated deception and counter-deception. This hypothesis is supported by the fact that many primates seem to show their most sophisticated abilities to think about the direction of other's gaze in competitive situations. In contrast, many nonhuman species have difficulty using gaze cues in more cooperative situations, such as "object choice" paradigms in which a human helpfully looks at the location of a hidden food item to communicate this information. In fact, many diverse primate species fail to use such cues.

Yet gaze-following may hold a different adaptive role in humans (Tomasello and Carpenter 2007). Our species may follow gaze to enable successful *cooperative* behaviors. Humans are especially reliant on eyes in gaze-following situations, and eyes subsequently evolved a new social function in human evolution, to support cooperative (mutualistic) social interactions. The "cooperative eye hypothesis" posits that our species' unique eye morphology is an adaptation allowing individuals to view each other's gaze direction with greater precision, enabling these cooperative behaviors. These morphological changes include a white sclera with high contrast to the iris, along with an enlargement of the visible part of the sclera,

and they may explain why humans are especially sensitive to eye direction (compared to face direction or whole-body cues) relative to other species. These changes may allow humans to engage in large-scale cooperative behaviors between non-kin, which appear to be human unique.

More generally, humans appear to be uniquely motivated to participate in "joint attentional interactions," collaborative interactions where the actors usually monitor each other's visual attention in order to better coordinate. Building on this proposal, Csibra and Gergely (2009) have argued that eye contact is a type of cue that humans use to mark the transfer of pedagogical information. In response to such pedagogical cues, infants infer that the information that follows will be culturally relevant information about their social world (Csibra and Gergely 2009). This theory predicts that other species lacking human-like culture and teaching will not respond to such ostensive cues in the way that humans do. However, it remains untested whether other primates do in fact exhibit any similarities with humans in their responses to such cues.

Conclusions

Why are so many species sensitive to gaze direction? Gaze direction information may be useful because other individuals tend to gaze at biologically relevant stimuli, because this information allows an individual to make inferences about another individual's mental state, because gaze is used as an explicitly communicative signal, or because information about gaze direction helps to scaffold the development of other cognitive skills. It is likely that the adaptive purpose of gaze sensitivity varies between taxa, despite the superficial similarity of gaze-following behaviors in many species. Therefore, comparative analysis of the cognitive basis of these skills can illuminate the selective pressures that have resulted in divergent social cognitive skills across taxa. This is of particular importance in light of the hypothesis that the evolutionary origins of human-unique social cognition can be understood as the result of a selective pressure resulting from cooperative

interactions or unique patterns of sociocultural learning. If so, human gaze sensitivity might be uniquely adapted to support such behaviors, for instance, via involvement in processes such as joint attentional interactions or pedagogical learning. Gaze sensitivity therefore provides a window into the selective pressures that have characterized social cognitive evolution between taxa, which may enable researchers to begin to uncover the roots of human-unique cognition.

Cross-References

- ▶ [Cooperation and Social Cognition](#)
- ▶ [Evolutionary Social Psychology](#)
- ▶ [Evolution of Human Sociality, The](#)
- ▶ [Humans as Social Primates](#)
- ▶ [Social Development in Nonhuman Primates](#)
- ▶ [Social Intelligence Hypothesis, The](#)

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Understanding Human Points

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Synonyms

[Declarative communication](#); [Domestication hypothesis](#); [Gestural communication](#); [Object choice task](#); [Ostensive communication](#)

Definition

The comprehension of human gestures, specifically points, as referential and communicative symbols.

Introduction

The main question to be addressed in this chapter is are nonhuman animals capable of understanding human-given points as communicative symbols? Are they capable of understanding the referential intention of the act of pointing? To truly answer these questions, it is first necessary to discuss how *humans* grow to understand the referential and communicative nature of points. Many argue that this capacity is not innate but develops gradually as the child gains experience with both seeing and performing the action as well as with the advances in theory of mind that occur with age (Woodward and Guajardo 2002). To be able to successfully follow a point given by another individual, the point-receiver must first understand that the point is communicative – conveys information – as well as then understand that the action of the pointer was performed intentionally, with purpose and direction. The information conveyed in the point must then be extracted by inference (Moore 2016); it could be simply directing attention to a specific aspect of the environment, it could be part of a more complex set of cues directing the receiver to perform a sequence of actions with the referent of the point, and so

on. The communicative *context* in which the point was given must be considered by the receiver in order to extract the information accurately. This task becomes more complicated if the point referent is ambiguous or the point is poor quality (e.g., in the general direction of the referent, but fleeting and nonspecific). Per Woodward and Guajardo's (2002) work, the idea that a point is object directed, emerges between 9 and 12 months of age. This work was supported by Pfandler et al. (2013) who demonstrated that the comprehension of points by human infants showed a developmental trajectory between birth and 18 months, suggesting that experience with the pointing action and advances in theory of mind are important to the understanding of points.

Pointing in Nonhuman Animals

The task, then, becomes increasingly difficult for nonhuman animals. Broadly speaking, one task has been used predominately to test animals' abilities to follow human points in most comparative research: the object-choice task. The task is simple to perform by experimenters and yields easy to quantify responses from the animals, in most cases. The basic experimental design places the experimenter equidistance between (or behind) two occluders (e.g., opaque cups or buckets). The experimenter then places a desired item (e.g., food or a toy) under one occluder, being careful to also falsely bait the other occluder either before or after truly baiting so that the animal cannot use any alternate strategy to locate the hidden object. The experimenter then points (or gestures in some manner) to the location of the hidden object and waits for the animal to indicate their choice of location – either the correct occluder where the object is hidden or the incorrect occluder where the object is not located. A choice for the animal can be indicated by touching the occluder with their hand/finger, nose, or paw, by direction of gaze, or coming within a certain distance of the occluder. If the animal chooses the correct location, the experimenter then rewards the choice by giving the object to the animal. Many variations of type of point or

combination of visual cues (e.g., gazing in the direction of the correct occluder while pointing) can be utilized. This method is also used in work with human infants.

In human infants, gains in theory of mind are vital to understanding points. Research on theory of mind in nonhuman animals, however, has led to contradictory conclusions. Some researchers would argue that even in our closest evolutionary relatives, primates, evidence is limited, if present at all, rendering the possibility of them understanding human points improbable. Tomasello et al. (1997) and Povinelli et al. (1997) independently concluded that apes were unsuccessful at completing the object choice task, thus incapable of understanding human points. They argue that apes lack the ability to understand the intentionality behind the communicative gesture, despite demonstrating a use of basic gestures in the wild to communicate with group members. Why might they be able to follow gestures given by conspecifics but fail at demonstrating the skill with human pointers? It could be argued that nonhuman primates do not see humans as communicative partners; therefore, they cannot extract the communicative intent from the gesture; the communicative goal is lost in interspecies translation.

If our closest living relatives are incapable of following human-given points by this argument, then what species could be capable? The answer, according to Hare et al. (2002), is domesticated dogs. If apes do not see humans as communicative partners, it could be because of lack of the need for interspecies cooperation. Domesticated dogs, however, have been bred for over 10,000 years to work cooperatively with humans and, therefore, may possess the abilities not shown in apes by necessity. Hare et al. (2002) proposed an explanation for why domesticated dogs appear to show a heightened ability to understand human points over apes in the *domestication hypothesis*, stating, "selection pressure on dogs during the process of domestication [resulted in] specific skills of social cognition and communication with humans" (p. 1635).

Support for an evolutionary predisposition for understanding human communicative gestures has been shown in work looking at the ontogeny

of point following, finding that even very young puppies (less than 1 month of age) could follow human points. These results suggest that experience with humans as communicative partners is not necessary for puppies to understand the communicative and referential nature of points; instead, this ability is a result of selective pressures during domestication (Gasci et al. 2009; Hare et al. 2002). Further support for the domestication hypothesis can be found when comparing the performance of domesticated dogs to that of wolves. As all living domesticated dog breeds were bred from wolves, genetically, these two groups are very similar, but both have experienced different selective pressures in their evolutionary histories. If wolves demonstrate similar capacities to domesticated dogs, it would undermine the premises of the domestication hypothesis. However, the results of tests comparing wolves and dogs on point following tasks found that wolves were not successful on the object-choice task, regardless of their exposure to humans as many of these studies were conducted with captive wolves in sanctuaries and rehabilitation facilities (Gasci et al. 2009; Hare et al. 2002). Even wolf puppies raised with humans took significantly longer than domestic puppies to learn to follow human points (Gasci et al. 2009), supporting the premises of the domestication hypothesis and further explaining why apes notoriously are unsuccessful at using human communicative cues. Importantly, though, Gasci and colleagues' (2009) discovery that while it took longer for wolf pups to learn to follow human points, that skill could be *taught*, suggesting that perhaps evolutionary history is not the entire story when it comes to social cognition, a topic to be discussed further in the next section of this chapter.

As it is in all of science, there was not universal acceptance of the premises of and evidence for the domestication hypothesis. Two areas of contention focused on (1) the assertion that selective pressures in the evolutionary history of a species are more important than the environment in which they developed (ontological pressures) and (2) discrepancies between the object-choice methodologies being used to compare performance between species. Starting with the first concern, very little

in nature is the result of one type of selective pressure. Domestication, granted, is a multi-dimensional pressure, but after thousands of years of other selective pressures and, importantly, differential ontological contexts, assuming the cognitive toolkits remain entirely conserved seems highly unlikely. Notably, not all dog breeds were designed for cooperatively working with humans; some breeds were simply bred for companionship and aesthetics, suggesting that the ability of all dog breeds to follow points in a cooperative setting would not be necessary and, therefore, may not be conserved. Udell et al. (2008) tested point following using an object-choice task with domesticated dogs housed in animal shelters, varying tremendously in their exposure to humans as social partners, to human-reared wolves, who had been raised since puppies with humans. They found that highly socialized wolves outperformed under-socialized dogs consistently, supporting that ontological forces can make as much of an impact on the social cognitive skills of animals as can their evolutionary histories. In further support, the importance of rearing environments and exposure to humans as communicative partners comes from work with apes (bonobos and chimpanzees), finding that those animals raised in highly enculturated environments (long-term exposure to humans as communicative partners) *could* follow human given points, whereas those raised with less exposure to humans in traditional housing facilities struggled to comprehend points (Lyn et al. 2010). These results indicate that experience with humans as communicative partners during development shapes their abilities to follow human points; therefore, the skill is learned not necessarily entirely evolutionarily based.

The second concern with the studies supporting the domestication hypothesis centers around methodologies. While the object-choice task is similar in nature, minor adjustments to the experimental set up can make a major difference for the animals' abilities to follow the points. Udell et al. (2013) discuss that the distance between the two occluders (proximal [close together] or distal [far apart]) and the type of point used (dynamic [moving] or static, proximal

[close to the occluder] or distal [far away from the occluder], momentary [fleeting] or constant) can all make a major difference in the way the point is interpreted by the animal. Previous failures to succeed at the task may not be the result of an inability to follow points, but confusion based on the task design itself. For instance, dogs were not equally successful at all varying point types, suggesting that experimental set up is important and experience with pointing allows for the dogs to continually learn and adapt to the cues, improving their performance after exposure (Udell et al. 2013). Importantly for comparison purposes, much of the research conducted with apes (e.g., Povinelli et al. 1997) used a single type of point – static, proximal occluder position (within 3 ft [0.9 m], distal point position (1 ft [0.3 m] or more from the occluder). This point type places the experimenter *behind* the point referent; therefore, the point is displaced from the object, making it difficult for the animal to trace the sight line from the point to the referent. In addition, due to safety concerns, there is always a barrier between the ape and the experimenter, which also could obstruct the apes' ability to trace line of sight or physically align themselves from the frame of reference of the pointer. Using varied point types with dogs and testing them without barriers between the pointer and the animal could lead to improved performance without any evolutionary history effects. Truly comparative work, using the exact same methodologies between species, is necessary to rule out these possibilities.

Conclusion

Research looking at the abilities of nonhuman animal species to understand the communicative and referential nature of human points is ongoing, looking at many other species, both domesticated and nondomesticated, to elucidate the evolutionary history of the ability. It is an important skill to study as it provides knowledge of the perspective taking, social cognition, and theory of mind abilities of other species. In addition, it allows for the study of how exposure to humans in captive environments has shaped the cognitive toolkits present

in a wide variety of species. Discovering the phylogenetic roots of this ability also provides great insight into the evolution of human language, particularly ostensive communication (Moore 2016).

Cross-References

- [Communication and Social Cognition](#)
- [Convergent Evolution of Dog and Human Social Cognition](#)
- [Cooperation and Social Cognition](#)
- [Nonhuman Intelligence](#)
- [Social Cognition](#)
- [Social Learning and Social Cognition](#)

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Undesirable

► [Antisocial Behavior](#)

Undetected Extra-Pair Copulation

► [Female Sneak Copulation](#)

Undisclosed Ovulation

► [Concealed Ovulation](#)

Uneducated

► [Redistribution Preferences and Low Socioeconomic Status](#)

Unemployed

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Synonyms

[Low-status males](#)

Definition

Some evolutionary theorists link suicide terrorism to low-status males, which in many societies translates into lack of employment or underemployment.

Introduction

One theory of suicide terrorism proposes that attackers will tend to be young males with poor mating prospects. Contending that the sanctioning of polygyny in Islam excludes young, low-status males in some Muslim societies from the mating market, Kanazawa (2007) concludes that suicide terrorism is a byproduct of intrasexual competition. Male reproductive success is constrained by access to mates, and males with higher social status are more likely to be polygynous and/or have greater reproductive success (Chagnon 1988; Turke and Betzig 1985). In modern industrial or postindustrial societies, a positive employment status and high income is associated with greater access to mates and higher reproductive success in males (Hopcroft 2006). Mating competition among males increases risk-taking and aggressive behavior (Wilson and Daly 1985); thus, Kanazawa argues that suicide terrorism relies on the activation of mechanisms associated with intrasexual competition and sexual access manipulations. This theory is not supported by empirical evidence (see ► [Sexual Access Manipulation](#); ► [Young](#)). There is no evidence that unemployment is associated with suicide terrorism at the individual level.

Low Social Status Not Associated with Suicide Terrorism

The data contradict the claim that suicide terrorists have significantly lower status than other males in the populations from which they come in terms of income, education, and employment (Atran 2003; Berrebi 2003). According to Berrebi (2003), suicide attackers in the West Bank and Gaza Strip

came from wealthier families and were more likely to have a high school education compared to the general Palestinian population. Krueger and Maleckova (2003) found similar results among Hezbollah suicide terrorists, concluding that poverty and low educational attainment are not risk factors suicide terrorism at the level of the individual. On the other hand, Atran (2003) suggests that a relative loss of employment and economic opportunities among the educated might be a precipitating factor in suicide terrorism, reporting that a rise in unemployment and wage decreases among college graduates corresponded with the rise of the First Palestinian Intifada. Other studies such as Saleh (2004) have found a correlation between unemployment rates in the occupied territories of Palestine and terrorist attacks in those regions.

Conclusion

Studies indicate that suicide attackers are not low-status males, and though they are typically unmarried, there is no evidence that they would have remained unmarried if they lived to mate and reproduce. Suicide attackers tend to have middle class backgrounds and high education levels. However, terrorism is associated with regional poverty. In sum, suicide terrorists typically come from poor regions but tend to be better off in terms of wealth and education compared to others in their local communities.

Cross-References

- Benefits to Kin
- Denis Decatanzaro
- Kinship Psychology Manipulations
- Men with Poor Mating Prospects
- Monetary
- Redistribution Preferences and Low Socioeconomic Status
- Reputation
- Sexual Access Manipulation
- Suicide (Evolutionary Clinical Psychology)

- Suicide as Kin-Directed Altruism
- Suicide Terrorism
- Young

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Unique Patterns in the United States

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Synonyms

[Cross-cultural variation in intimate partner violence](#); [Domestic violence](#); [Partner violence](#)

Definition

Counter to what is seen in most countries, women are intimate partner violence perpetrators at a similar rate as are men in the United States. Aggression is modulated by environmentally sensitive brain mechanisms. The United States provides a unique set of societal forces that through these mechanisms promote higher levels of female-initiated intimate partner violence relative to other nations.

Introduction

Traditionally, men have been stereotyped as being perpetrators of intimate partner violence (IPV), whereas women have been depicted as victims. Early research suggested that if women were aggressive toward their male partners, it was in the context of self-defense (e.g., Dobash and Dobash 2004). However, in the last 50 years, research from the United States has suggested that women are just as likely to be the perpetrators of IPV, and in many samples they have been shown to be more aggressive than men (Archer 2000, 2006). In a meta-analysis, Archer (2000) found that women in the United States were slightly more likely to engage in physically aggressive acts than men and to use such acts more frequently. Further, women have been reported to engage in male-directed IPV even when in relationships with nonviolent men (Stets and Straus 1992). Some researchers (e.g., Archer 2006) have suggested that the higher rates of female-to-male-perpetrated aggression are unique to the United States and other Western cultures, a finding that needs explanation. This entry provides an examination of what factors might account for the unusually high use of aggression by women in the United States in the context of IPV.

Sociocultural Factors and IPV Symmetry

Several social factors have been identified as being associated with higher levels of aggression in women in the context of IPV. First, gender equity and empowerment are correlated with patterns of IPV (Archer 2006). Women in both low and highly empowered nations are known to use violence against their male partners, but levels of male-to-female-directed IPV are lower than in countries with lower levels of gender empowerment. Therefore, in the highly gender-empowered United States, women's IPV perpetration levels are higher and men's are lower, resulting in a pattern of gender symmetry. Further, the United States is an individualistic culture, and women are

more likely to be aggressors of IPV in cultures characterized higher on this trait relative to collectivism (Archer 2006). Another factor that seems to promote symmetry in IPV perpetration is economic independence. Archer (2000) reports that lower dependence on men for financial support is associated with lower victimization of women and higher levels of IPV perpetration by women. Many women in the United States work outside of the home, which provides them with economic independence. This economic independence has shifted the social structure in the United States. Women are not only less dependent upon their male partners for support, but they also are less likely to be subjected to the coercive power of their husband's kin. In combination with the Western attitudes prohibiting the use of male-to-female aggression and the resulting decreased fear of retribution for hitting men (e.g., Fiebert and Gonzalez 1997), women in the United States lack some of the constraints preventing women in other countries from engaging in the risky use of physical violence against men.

Weapon availability. In general, men are more likely than women to commit homicide (Daly and Wilson 1988). Further, men commit uxoricide at a much higher rate in the United States relative to other countries, including other Western countries (Wilson and Daly 1998). However, as is true of nonlethal IPV, the sex ratio for spousal killing in the United States is more equal than elsewhere in the world (Wilson and Daly 1992). When women kill their male partners in the United States, they are more likely to use guns than any other weapon (Mize et al. 2009). Men are inherently larger and stronger than women, but the availability of guns in the United States serves to equalize those differences making it easier for women to kill their male partners.

Conclusions

In the United States, men and women are almost equally likely to be the perpetrators of IPV. Trivers (1972) parental investment and sexual selection theories would predict that men would be more likely to use risky competition strategies, including

physical aggression. However, the mechanisms underlying aggression are sensitive to environment and social cues (Goetz 2010). The conglomerate of societal factors that prevail in the United States changes the cost-benefit analysis of aggression for women, altering the social strategies that they use to settle interpersonal conflicts in the context of intimate partner relationships (Cross and Campbell 2013). This is manifested in a more symmetrical pattern of IPV perpetration between men and women in the United States relative to what is seen between the sexes in many other countries.

Cross-References

- [Contexts for Men's Aggression Against Women](#)
- [Contexts for Women's Aggression Against Men](#)
- [Male Sexual Jealousy](#)
- [Men's Suspicions of Partner Infidelity and Women's Defection](#)
- [Violence to Control Women's Sexuality](#)

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Unit of Cultural Transmission

► [Memes](#)

Unit of Imitation

► [Memes](#)

Universal Aspects of Kinship

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Synonyms

[Kinship universals](#); [Panhuman manifestations of genealogical relationships](#)

Definition

Behavioral aspects of kinship found in all human societies.

Introduction

Humans exhibit by far the most extensive and internally differentiated networks of kinship of all animal species. Correlatively the importance of kinship in regulating social life in humans is unequaled in the animal world. If this is not evident in modern state societies in which kin represent a small fraction of an individual's social network, it is salient in small-scale societies, notably in groups of hunter-gatherers whose mode of subsistence characterized our ancestors over 99.5 % of the 2.5 million years of evolution of the genus *Homo*. If only for that reason, kinship is expected to have played a central role in shaping the social life and social cognition of hominins and hence to be deeply ingrained in human nature.

Unsurprisingly from that perspective, cultural anthropology was born with the scientific study of kinship when Lewis Henry Morgan published his *Systems of Consanguinity and Affinity of the Human Family* in 1871. One hundred years later, Robin Fox could still state that “kinship is to anthropology what logic is to philosophy or the nude is to art; it is the basic discipline of the subject” (Fox 1967, p. 10). Why is that? Why is kinship so important in human affairs? The most basic reason is perhaps that kinship is not a domain of social activities like politics, religion, or economics but an *intrinsic* characteristic of relations between individuals determined by how they are connected to each other through parent-child links. That characteristic has some fundamental properties (discussed below), which result in kinship structuring social life at all levels of analysis – social acts, social interactions, enduring social relationships, group structure, and between-group relations – and in virtually all domains, from domestic activities to politics to religious practices.

Given that all aspects of human kinship are extremely variable across cultures, the present focus on the universal aspects of kinship may not be immediately obvious. Diversity is so pronounced that most anthropologists have concentrated on studying cultural particulars and emphasized cultural differences in kinship systems and kin terminologies rather than

similarities. Cultural variation, however, results from universal principles operating in different socioecological contexts, from which it follows that any theory purporting to explain cross-cultural similarities and differences must necessarily integrate information about the universal constraints regulating the observed variation. Accordingly, three broad categories of kinship universals are defined here, which pertain, respectively, to the intrinsic properties of kinship (*intrinsic universals*), the universal characteristics of kin recognition (*kin recognition universals*), and the universal characteristics of certain types of kinship bonds (*relational universals*). Because a substantial fraction of those universals stem from our common evolutionary heritage with other primates, the present review proceeds by distinguishing the features we share with non-human primates from those that are specific to our species.

Intrinsic Kinship Universals

Much of the impact of kinship on social life lies in three of its intrinsic properties: kinship affects an individual’s social motivations, it is a permanent characteristic of dyadic relations, and it engenders genealogical structures. Those properties account for some of the most fundamental kinship universals (Table 1).

As in now overwhelmingly documented throughout the animal kingdom, kinship promotes prosocial behavior between relatives. Kin selection (or inclusive fitness) theory is the primary mechanisms involved. Briefly, when a female

protects her daughter, granddaughter, or sister against an aggressor or a predator, she does not gain any direct (personal) benefits, whether immediate or delayed. On the contrary she incurs costs, but by reducing the likelihood that her kin will be wounded or killed, she obtains indirect fitness benefits amounting to a fraction of the direct benefits accruing to her kin, that fraction being determined by their degree of genetic relatedness – in other words, she increases her inclusive fitness. Kin selection theory thus accounts for the existence of both unilateral and bilateral altruism between relatives.

Kin selection is also expected to favor cooperation between kin, whether mutualistic cooperation (activities in the course of which the participants obtain immediate personal benefits) or reciprocity (the participants obtaining personal benefits, but in alternance). This is because when a female cooperates with a kin, she benefits in two different ways. She obtains the direct (personal) benefits of the cooperative act – as she does when interacting with a nonkin – and she derives the indirect fitness benefits previously mentioned. Thus, other things being equal, such as the competence levels of potential partners (Chapais 2006), cooperation between kin pays more than cooperation between nonkin (Wrangham 1982).

In addition to promoting prosocial behavior, kinship has inhibitory effects on sexual behavior: it decreases levels of sexual attraction between close kin. The avoidance of incest is the rule in humans and other primates (Paul and Kuester 2004; Wolf and Durham 2004; Chapais 2008). Incest avoidance is adaptative owing to the biological costs of inbreeding – the reduction of an

Universal Aspects of Kinship, Table 1 Three intrinsic properties of kinship and the corresponding *intrinsic kinship universals*

Intrinsic properties of kinship	Intrinsic kinship universals
Determines social motives	Kin biases in unilateral/bilateral altruism
	Kin biases in mutualistic cooperation
	Kin biases in reciprocity (social exchange)
	Kin biases in social allegiance
	Incest avoidance
Permanent characteristic of relationship	Enduring bonds between biological kin
	Enduring bonds between affines (in-laws)
Engenders genealogical structures	Kinship structures (e.g., lineages, clans)
	Multigroup kinship networks (alliances)

organism's reproductive success due to a lowering of its fecundity or its offspring's chances of survival (for a review on the costs of inbreeding in nonhuman primates, see Charpentier et al. 2007). The avoidance of incest appears to be mediated through the correlates of close kinship bonds such as developmental familiarity, intimacy, and attachment.

The second intrinsic property of kinship is that it is, by definition, a permanent characteristic of the relation between two individuals. This property, in combination with the first one, means that kinship generates enduring biases in altruism and cooperation between relatives, provided the latter recognize each other as kin and have opportunities of interacting on a regular basis. In other words, kinship is a major source of long-term social relationships. As discussed below, the exact repertoire of kinship bonds found in any species depends on many factors, including which kin live together, whether paternity is recognized or not, and the nature of the criteria used by individuals to differentiate their kin. In nonhuman primates, relationships between kin are limited to those that coreside in the same local group, whereas humans are in a position to maintain relationships with kin living in groups other their own.

Finally, the third property of kinship is that it generates extensive *genealogical structures* within which individuals are connected to each other either lineally or collaterally (definitions below). The interest of genealogical structures lies in their group-level character and hence in their potentially important role in shaping social structure as a whole. Depending on the extent of kin recognition, genealogical structures may translate into *kinship structures*, that is, in consistent patterns of social relationships that map the genealogical structure, such as lineages or clans. If kin living in distinct groups maintain relationships with each other (as in humans), genealogical structures produce multigroup kinship networks.

Kin Recognition Universals

The impact of the three intrinsic properties of kinship on social life depends crucially on which kin are recognized. Humans form

multimale-multifemale groups. Owing to our species' life-history characteristics in terms of longevity, age at sexual maturity, interbirth interval, and other parameters, those groups contain three to five generations of individuals, a configuration that maximizes the diversity of coresident kin types. A description of the domains of kin recognition in other primate species will make it possible to differentiate between shared and uniquely human components and better appraise the magnitude of human kin recognition.

The Evolutionary Background of Human Kin Recognition

The other primate species forming multimale-multifemale groups may be divided into two categories according to their dispersal pattern: *female philopatry* or *male philopatry*. In female philopatric species, females stay and breed in their natal group, whereas males leave around puberty to breed in other groups. This dispersal pattern produces spatially localized and rather extensive, three-generation *matrilines* (the set of individuals descended from a common female ancestor through the female line only) but small *patrilines* (the individuals descended from a common male ancestor through the male line only) because males leave their fathers' group. Reciprocally, in male philopatric species, the males stay put and the females leave, a pattern generating, this time, extensive patrilines but small matrilines. Dispersal patterns thus determine which kin live together and have opportunities of recognizing each other. It should be noted here that the word "recognize" does not mean that nonhuman primates perceive genetic relatedness per se, nor that they necessarily conceptualize kin types; it simply means that they interact preferentially with certain individuals, based on their kinship relations with them. For example, mothers are inferred to recognize their daughters based on the observation that they direct certain types of prosocial behaviors to their daughters (approaches, vocalizations, lactation, ventral and dorsal transport, grooming, protection against aggressors, tolerance at food sites, and so on) at higher rates than they do so with less closely related or unrelated individuals. Kin recognition

thus refers to the differential treatment of individuals belonging to different kin categories.

A few definitions are required at this stage. A *lineal* kinship relationship is a chain of parent-child links connecting two individuals, one of whom is ancestral to the other. The individuals may be related through the maternal line only, e.g., a female to her maternal grandmother (*maternal* kin), or through the paternal line only (*paternal* kin). A *collateral* kinship relationship is a chain of parent-child links connecting two individuals, neither of whom is ancestral to the other, such as siblings, aunts and nieces, and cousins. The *genealogical distance* between two kin refers to the number of parent-child links separating them, for example, two links between a grandmother and a grandchild (lineal distance), and three links between a female and her niece (collateral distance). It is also useful to differentiate between ego's *primary kin* (ego's parents, children, and siblings), *secondary kin* (the primary kin of ego's primary kin, such as ego's grandparents, uncles, and nieces), *tertiary kin* (the primary kin of ego's secondary kin, such as great-grandparents and cousins), *quaternary kin* (the primary kin of ego's tertiary kin, such as second-degree cousins), and so on. Finally, the expression *domain of kin recognition* refers to the set of differentiated kin types from ego's perspective.

Observational and experimental studies indicate that the recognition of maternal kin is widespread and sometimes extensive in nonhuman primates, whereas the recognition of paternal kin is comparatively very limited. In female philopatric species, such as macaques and baboons, a female recognizes a substantial fraction of her coresident maternal kin, including her sisters, brothers, mother, daughters, sons, grandchildren, great-grandchildren, grandmother, great-grandmother, and, less systematically, her aunts and nieces, whereas her cousins and other collateral relatives are treated as nonkin (Chapais 2008). In other words, females recognize their primary kin, some of their secondary kin, but usually not their tertiary kin. The recognition of maternal kin stems from the existence of lifetime bonds between mothers and daughters and

appears to involve primarily familiarity and association-based processes (Rendall 2004). In those species, young females come in contact with their sisters, grandmothers, aunts, and other kin types on a regular basis, thanks to the enduring bonds their mothers maintain with those kin. The mother's mediation sets in motion at least two distinct and complementary processes likely involved in kin recognition (Chapais 2008). First, because the mother spends different amounts of time in proximity with her own mother, sisters, nieces, and so on, her daughter accumulates different levels of developmental familiarity with each of those kin. At the same time, the daughter is in a position to learn the specific characteristics of the relationships her mother maintains with her various relatives in terms of degree of proximity, grooming rates, willingness to protect them against certain individuals, and so on. The capacity of nonhuman primates to recognize the relationships of others is well documented (Seyfarth and Cheney 2012). Importantly, both processes of maternal kin recognition require mothers and daughters to maintain lifetime bonds with each other.

The recognition of maternal kin is also observed in male philopatric species, such as our closest relatives, chimpanzees and bonobos. However, the transfer of females between groups usually limits the domain of kin recognition to primary kin (mother-offspring dyads and maternal siblings) for a male will never meet his mother's kin – they live in other groups – nor the offspring of his emigrated sisters (Chapais 2008; Langergraber et al. 2009). The absence of friendly contacts between groups entails that the recognition of maternal kin is limited to coresident ones (Table 2). For reviews of the influence of maternal kinship on behavior in primates, see Silk (2009), Berman (2011), and Langergraber (2012).

In marked contrast with maternal kinship, paternal kinship is absent or extremely limited in female philopatric species. This is due to two factors. First, males and females have several short-term mating partners (they practice sexual promiscuity) so fathers and offspring cannot recognize each other through the intermediary of an enduring bond between the father and the mother.

Universal Aspects of Kinship, Table 2 The domain of kin recognition in primate species forming multimale-multifemale groups, according to residence patterns and type of kinship

Residence patterns	Maternal kinship	Paternal kinship
Female philopatry in nonhuman primates (e.g., macaques)	Relatively extensive but limited to coresident kin, usually to primary and secondary kin	Absent or very limited owing to sexual promiscuity and male dispersal
Male philopatry in nonhuman primates (e.g., chimpanzees)	Limited to coresident kin, usually to primary kin	Absent or very limited owing to sexual promiscuity
Variable postmarital residence patterns in humans	Extensive (beyond quaternary kin) and includes non-coresident kin	Extensive (beyond quaternary kin) and includes non-coresident kin

However, other mechanisms of kin recognition based on *phenotypic matching* – the capacity to recognize one’s kin based on physical similarities such as odors and physical features between an individual and either self or another kin – may allow individuals to recognize their paternal half-siblings in some species (Widdig 2007; Langergraber 2012). Second, male dispersal in these species entails that males do not grow up with their fathers’ kin and hence have no opportunities of knowing them.

In male philopatric species, by contrast, males do live with their paternal kin and belong to relatively extensive patriline. The available data, however, indicate that paternal kinship is absent or extremely fragmentary in those societies. In chimpanzees, for instance, father-offspring recognition is inconsistent at best (Chapais 2008; Langergraber 2012), which is not surprising given that chimpanzees are highly promiscuous sexually. If individuals cannot recognize their father on a consistent basis, it is unlikely that they recognize their father’s kin, such as their paternal grandfather, uncles, and cousins. Empirical studies also indicate that males do not recognize their paternal half-siblings (Langergraber et al. 2007).

Significantly several of the distinctions made by humans to differentiate their kin are also made by nonhuman primates, though in cognitively much simpler ways, which is precisely what one would expect if the shared criteria had common evolutionary origins. The best way to appraise those criteria in nonhuman primates is to focus on the differentiation of maternal kin in female philopatric species, the context that maximizes the domain of kin recognition (Table 2). Empirical

studies (reviewed in Chapais 2008) indicate that in those species, ego interacts differently with its kin depending on whether (1) ego’s kin is a male or a female; (2) the actor, ego, is a male or a female; (3) ego is younger or older than its kin; (4) ego’s kin belong to an ascending (senior) or descending (junior) generation; (5) the lineal distance between ego and its kin is different; and (6) the collateral distance between ego and its kin is different. The effect of each factor on how ego treats its kin is best appraised when all other criteria are held constant.

The effect of whether ego’s kin is a male or a female is evidenced by the observation that ego interacts differently with its brothers and sisters for in this comparison all other factors are constant: ego’s brother and sister are collateral kin belonging to the same generation, separated from ego by the same genealogical distance, and having similar ages (averaged over many dyads).

The effect of ego’s sex on how ego treats its kin is illustrated by differences in how a male and a female interact with a sister, in which case, the two dyads (brother-sister and sister-sister) are collateral kin that belong to the same generation, share the same genealogical distance, and have similar age differences on average.

Differences in how a female interacts with a younger sister and an older one illustrate the effect of ego’s age relative to its kin. In this situation, the two types of sister dyads are collateral kin of the same sex belonging to the same generation and sharing the same genealogical distance.

Differences in how an adult female interacts with her mother and her daughter shows that she differentiates between individuals belonging to an ascending (senior) or a descending (junior)

generation. To ego, both individuals are lineal kin of the same sex and same genealogical distance. They differ in age, however, which makes it possible that ego's differential treatment might reflect the effect of age rather than generation. This is highly unlikely, however, given that ego has a filial relationship with her mother and a parental one with her daughter, which points to the effect of generation per se.

The effect of genealogical distance between lineal kin is exemplified by differences in how females interact with their mother (one parent-child link) and with their grandmother (two links) and by differences in how they interact with their daughter (one link) and granddaughters (two links). To ego, all those individuals are lineal kin of the same sex. But note that those behavioral differences may also reflect the effect of belonging to an adjacent or a nonadjacent generation in relation to ego (whether ascending or descending).

Finally, the effect of genealogical distance between collateral kin is exemplified by the observation that females have much higher rates of prosocial behavior with their sisters than with their female cousins. From ego's perspective, sisters and cousins are collateral kin belonging to the same sex, generation, and age group, but while sisters are separated from ego by two parent-child links, cousins are by four links.

Importantly, the fact that those factors affect how nonhuman primates interact with their kin does not imply that animals conceptualize sex, relative age, ascending versus descending generations, lineal distance, and collateral distance. It means, minimally, that they use proxies, behavioral and/or phenotypic, that correlate with those factors.

Kin Recognition in Humans

The domains of kin recognition in humans are much more extensive compared to the situation in other primates. They include both maternal and paternal relatives and extend to quaternary kin and beyond (Table 3). This reflects essentially three factors. First, the existence of stable reproductive bonds, whether monogamous or polygynous, allows father and offspring to recognize each other based on their enduring relationship with

the same female – wife to one, mother to the other. This in turn allows individuals to recognize their father's kin and their brother's children. In short, kin recognition is bilateral (bilineal), a uniquely human phenomenon.

Second, kin recognition is independent of whether relatives live in the same group – are coresident – or not, because contrary to the situation in other primates, dispersal from the natal group (i.e., a change of residence at marriage, what anthropologists call *postmarital residence*) does not bring about the end of contact between spatially dispersed kin; the latter keep visiting each other on a regular basis (Rodseth et al. 1991). As a result, ego's actual kinship network includes individuals born and living in other groups. Another important consequence of intergroup visiting is that cross-sex kin, such as fathers and daughters and brothers and sisters, are in position to maintain lifetime bonds with each other. This is usually not possible in other primates forming multimale-multifemale groups because dispersal is strongly sex biased and cross-sex kin cease to interact with each other after they have left their natal group. Intergroup visiting, intergroup kin recognition, lifetime bonds between cross-sex kin, and multigroup kinship networks are uniquely human, cross-culturally universal phenomena. They are also highly consequential ones considering that some classic chestnuts of the anthropology of kinship such as *cross-cousin marriage* (unions between the children of cross-sex siblings), and *avuncular relationships* (special relationships between men and their sisters' sons) require lifetime bonds between cross-sex kin (Chapais 2008, 2014).

Third, thanks to enhanced cognitive abilities, humans differentiate their kin on the basis of a much larger set of criteria and distinctions compared to other species (Table 3). As primates, humans inherited the capacity to recognize their kin based on their degree of developmental familiarity with them and on how their parents interact with different kin. In that vein, the close association between newborns and their mother was found to operate as a specific cue allowing individuals to recognize their younger siblings (Lieberman et al. 2007). Phenotype matching

Universal Aspects of Kinship, Table 3 *Kin recognition universals* classified in relation to four dimensions

Dimensions	Kin recognition universals
Mechanisms of kin recognition	Developmental familiarity with one's kin
	Differentiation of bonds between one's mother and other kin
	Recognition of facial similarities between one's kin
	Recognition of facial similarities between self and kin
	Naming kin
Factors defining domain of kin recognition	Multimale-multifemale groups
	Multigenerational groups
	Stable breeding bonds (father-child recognition)
	Dual-phase residence (pre-/postmarital)
	Exogamy (outmarriage)
	Sex-biased or bisexual postmarital group transfer
	Sex-biased or bisexual postmarital residence
	Postmarital residential variability across groups
	Postmarital residential flexibility within groups
	Intergroup visiting
	Multigroup, multilevel social organization
Domain of kin recognition	Mother-offspring recognition
	Father-offspring recognition
	Recognition of lineal kin
	Recognition of collateral kin
	Recognition of maternal kin beyond quaternary kin
	Recognition of paternal kin beyond quaternary kin
	Recognition of deceased ancestors
	Matrilineal descent (chains of mother-daughter links)
	Patrilineal descent (chains of father-son links)
	Recognition of lineages as entities
	Intergroup kin recognition (i.e., independent of coresidence)
	Lifetime bonds between same-sex kin
	Lifetime bonds between cross-sex kin
	Recognition of kin's spouses (affines)
	Recognition of spouses' kin (affines)
	Recognition of affines independent of coresidence
	Symmetrical recognition of affines (husband's and wife's)
Classification of kin	Kin terminologies
	Classificatory kinship
	Criteria of kin differentiation (minimal)
	Ego's sex
	Kin's sex
	Relative age of kin
	Ascending versus descending generation
	Lineal distance
	Collateral distance
	Lineal versus collateral kin
	Bifurcation

also seems to be at work. Humans are proficient at recognizing physical similarities between kin (e.g., between fathers and their children), including similarities between their own kin, for example, their mother and the latter's sisters. They also appear to recognize similarities between themselves and their kin. Experimental research using computer-graphic software to create images of individuals resembling the participants reveals that humans perceive their "virtual siblings" as more trustworthy than other individuals (DeBruine et al. 2011; for a review of the psychology of human kin recognition, see Park et al. 2008). To those association-based and phenotypic matching mechanisms, the evolution of symbolic communication superimposed the capacity to learn about one's kin based on how these are labeled, no doubt a major step in the extension of the domain of kin recognition among hominins (Jones 2010).

Language-based kin classifications and terminologies are cross-culturally universal (Fox 1967), and, importantly, they translate into the differential treatment of kin types: ego has different kinds of social interactions, rights, prerogatives, and obligations with the members of different kin categories. Anthropologists have documented a large variety of kin terminologies, which they group into a number of broad types – e.g., Hawaiian, Iroquois, Eskimo, Crow, Sudanese, and Omaha – depending on which kin types are differentiated and labeled accordingly or grouped together under the same label. For discussions of kin terminologies and of the principles regulating the observed diversity, see Goodenough (1970), Hage (1997), Kronenfeld (2006), and Jones (2010).

Despite their high degree of diversity, all kin terminologies appear to stem from the same set of universal, often binary, criteria (Table 3), a fact implying that variation reflects different ways of using the same criteria in different cultures. As pointed out earlier, humans make distinctions similar to those made by other primates but with some notable differences. Because we conceptualize those distinctions – that is, because we have concepts about "generation," or "lineal kin" – we may group together several distinct kin types on

the basis of a particular criterion (e.g., membership to the senior generation from ego's perspective), irrespective of several other criteria such as genealogical distance, age, and sex. This is called *classificatory kinship*. Kin terminologies vary markedly in this respect. For example, some terminologies group and label accordingly all members of an ascending generation in relation to all members of a descending one, whereas other terminologies distinguish between kin belonging to odd generations in relation to ego (parents and children) and kin belonging to even generations (grandparents and grandchildren). For a given criterion, humans make finer distinctions compared to other primates. For instance, some kin terminologies take generation distance into account and label differently the members of the first, second, third, fourth, and fifth generation, without regard to sex and ascending versus descending generation (Goodenough 1970). As another example, with respect to collateral distance, many societies differentiate between first-degree, second-degree, and third-degree cousins.

Not only do humans conceptualize the criteria they share with other primates, they also utilize at least two additional ones, namely, whether they are related to an individual through a male or a female and through a marital tie or not. Anthropologists use the term *bifurcation* to refer to the fact that humans classify their kin according to whether they are related to an individual through the mother (maternal relative) or the father (paternal relative). This allows distinctions between mother's brothers and father's brothers, patrilineal and matrilineal cousins, and so on. Bifurcation is not possible in other primates forming multimale-multifemale groups if only because, as we saw, sexual promiscuity prevents systematic father-offspring recognition so that individuals are not in a position to recognize their paternal relatives. This suggests that the bifurcation criterion became operative among hominins only after the evolution of pair-bonding and paternity recognition.

Humans also take into account whether they are related to a kin through a marital tie or not. Anthropologists use the term *affines* (in-laws) to refer to the spouses of one's kin and the kin of

one's spouse. A husband's affines comprise the spouses of his own kin, such as those of his children (daughters- and sons-in-law) and siblings (brothers- and sisters-in-law), and his wife's relatives, such as her parents (father- and mother-in-law) and siblings. The same applies to the wife, who recognizes both the spouses of her kin and her husband's relatives. The recognition of affines is thus symmetrical. Depending on cultures, humans may make several finer distinctions. They may, for example, label affines differently depending on the number of marital ties separating them from ego, whether that number is odd or even, whether the marital ties belong to a junior or senior generation, and so on (Goodenough 1970). Because *exogamy* (marrying out of one's group) is the rule in humans, many of ego's affines reside in groups other than ego's group. The symmetrical recognition of affines thus requires intergroup visiting, which explains why affinal kinship is uniquely human.

Finally, humans recognize deceased kin, including their ancestors, notably because they are told about their existence. This was a prerequisite for the recognition of chains of mother-daughter links including dead female ancestors (*matrilineal descent*) and chains of father-son links including deceased male ancestors (*patrilineal descent*). The recognition of descent in turn was an integral part of the recognition of matriline and patriline as social entities, that is, as entities whose members, by virtue of descent from a common, recollected ancestor, share a number of prerogatives, rights, and duties. Prior to the advent of humanlike conceptualization, matriline and patriline were primate-like patterns of social relationships mapping genealogical structures. With conceptualization, matriline and patriline evolved into *matrilineages* and *patrilineages*, in the anthropological sense of the term: kinship structures recognized as such and constituting political and economic units (e.g., Stone 2014).

Relational Kinship Universals and Their Consequences

Relational kinship universals are defined here as universal characteristics of specific categories of

kinship bonds. As pointed out earlier, the permanent character of kinship links favors the development of enduring social bonds between relatives. Some categories of kinship bonds are found in all cultures even though their exact form and content vary substantially across cultures. Such is the case with relationships between primary kin (parents, children, siblings) and some secondary kin, for example, grandparents and grandchildren. Relationships between more remote kin are often not universal owing to cultural variation in classificatory rules.

Kinship bonds belonging to the same universal category, such as parent-child bonds and sibling bonds, share a number of commonalities or relational kinship universals. Although those panhuman features of kinship bonds necessarily have a general character, their interest lies in the magnitude of their impact on human social life. In fact, much of the *deep structure* of human society – the set of structural principles common to all human societies (Chapais 2008) – stems from the universal characteristics of kinship bonds. Parent-child relationships, perhaps the most consequential of these, will serve to illustrate the idea.

Human children all over the world share the same basic set of needs in terms of physical, emotional, cognitive, and social development. Similarly, all human parents are equipped with the same basic morphological, emotional, and cognitive adaptations to satisfy those needs. This translates into the existence of a universal set of parental propensities toward children. Children needs, however, are not sufficient to apprehend the full scope of parental propensities. One must also take into account the fact that humans have the capacity to exercise *instructional control* over others (Chapais 2014). Compared to other animals, humans are able to orient the behavior of other individuals by telling them what to do and not to do. Among the most important cognitive abilities underlying instructional control are language, which makes it possible to spell out directives, and *theory of mind*, the capacity to know that others have thoughts and beliefs of their own. Other primates lack language and a full-blown theory of mind (Call and Tomasello 2008) so the control of others is noninstructional and limited to

preventing others from doing certain things. After the cognitive underpinnings of instructional control had evolved among hominins, individuals could attempt to orient the thoughts and behavior of others either to satisfy their own self-interest or to help their friends and relatives. The parent-child relationship lent itself particularly well to instructional control given the high degree of physical, emotional, and economic dependence of children in relation to parents.

Table 4 gives a sample of universal parental propensities in humans, the last three of which exemplify the possibility for parents of orienting the behavior of their children in ways that satisfy the parents' own interests independently of whether their children agree or not. It is not assumed here that each propensity has its own dedicated biological mechanism or constitutes a Darwinian adaptation. A parental propensity is rather seen as the emergent product of a number of more elementary components which are themselves universal. These include the three intrinsic properties of kinship previously discussed, the cognitive underpinnings of instructional control, the relevant needs or opportunities underlying the propensity (first column in Table 4), and the fact that the parental response in each type of context benefits parents either directly (personal fitness) or indirectly (inclusive fitness). The reasoning also rests on the assumption that universal propensities are so basic as to be internally generated (individually learned by all parents placed in

similar circumstances). In other words, parental propensities would be intuitive components of parental care rather than cultural inventions – even though the particular expression of any propensity is culturally determined (see Chapais 2016).

The relational universals of parent-child relationships appear to have played a central role in defining the deep structure of human society. For example, the propensity to provision children late into adolescence lies at the origin of the division of labor between parents and of the organization of domestic activities in general. Indeed if it were not for the importance of the costs of raising highly dependent children, mothers and fathers would probably not have been selected to form cooperative partnerships in the context of subsistence activities and hence would not have specialized in different ones. Although the exact form taken by the sexual division of labor is extremely variable across foraging, pastoral, agricultural, and industrial societies, the specialization principle is universal, has deep evolutionary roots visible in chimpanzees (Chapais 2011), and appears to reflect the advantages of dividing tasks between partners, compared to accomplishing similar ones (Gurven and Hill 2009). Sexual specialization in turn is a foundational principle of human social organization.

As another example, the parental propensity to transmit material possessions to children, either during the parents' lifetime or at death, lies at the very foundation of heredity-based social orders or

Universal Aspects of Kinship, Table 4 A sample of *relational kinship universals* pertaining to the human parent-child bond

Universal needs and opportunities afforded by children	Corresponding parental propensities (relational universals)
Environmental threats	Protection against physical threats
Intra and intergroup conflicts	Protection against social threats
Lengthened period of dependence	Long-term provisioning of children
Complex technical environment	Transfer of technical knowledge
Complex social environment	Transfer of social knowledge
Complex ideational environment	Transmission of beliefs
Dependence on material possessions	Transmission of possessions (inheritance)
Conflicts between siblings	Interventions in siblings conflicts
Cooperative nature of subsistence activities	Inducing children to contribute to subsistence
High costs of raising children	Inducing children to take care of their siblings
Selection of marital partner	Orienting children's mate choice

hereditary succession. The transgenerational inheritance of wealth and status among lineal kin is observed in societies in which there is material wealth to be accumulated and transmitted, where it generates various forms of heredity-based socioeconomic stratifications, but is much less salient in many foraging societies where differentials in wealth are much weaker or virtually absent (Borgerhoff Mulder et al. 2009).

A final illustration of the role of relational kinship universals in defining human society concerns the parents' propensity to orient their children's choice of a marital partner. This propensity is perhaps the most basic aspect of the widespread phenomenon of matrimonial exchange (Chapais 2014). Cross-cultural studies indicate that *marital arrangements* – agreements between families about the formation of marital unions – are the rule in hunter-gatherer (Apostolou 2007), horticultural, agricultural, and pastoral societies (Apostolou 2010). Marital arrangements take various cultural forms – sister (or daughter) exchange, prescribed marriages between cross-cousins, levirate (a widow marrying her husband's brother), sororate (a widower marrying his wife's sister), and bride service (service rendered by the groom to the bride's family). However diverse, all forms of marital arrangements share a number of fundamental properties: they are planned and regulated by parents and hence imply the instructional control of children; they are governed by the principle of conditional reciprocity; and they rest on the high value of children as commodities of exchange, a value reflecting the importance of securing a competent spouse in a species in which reproduction involves high levels of parental investment and spousal exchange generates long-lasting alliances between families.

Marital arrangements thus depend crucially on the parental propensity to orient mate choice. But for that propensity to translate into children exchange, two conditions must be met (Chapais 2014): parents must benefit from exchanging children, which appears to be the case in a vast number of societies in which children exchange is a primary means of obtaining spouses, resources, services, and alliances (Apostolou 2007, 2010),

and parents must be in a position to impose their preferences to children, a condition often met in preindustrial societies, where children are economically dependent on their parents, but often not satisfied in Western societies, where children may be financially independent of their parents at an earlier age. When the socioecological context is favorable, parents take control of mate selection, and as result, families become dependent on each other for obtaining spouses; they have no choice but to exchange children.

Conclusion

Throughout the present review, the emphasis has been placed on the universal aspects of kinship, but, as just discussed in relation to the role played by relational universals in generating heredity-based stratifications and marital arrangements, kinship universals help crucially in understanding social phenomena that are *not* cross-culturally universal. The same principle applies to many other social patterns exhibiting a strong kinship component, some of which are secular topics of the anthropology of kinship (e.g., unilineal descent groups, lineage segmentation, avuncular relationships). Universal kinship components are an integral part of each such phenomenon, but because they always interact with many other cultural variables, the outcome is a great deal of cross-cultural diversity. Thus, the interest of universals lies not only in their universality per se as in the role they play as “biological constants” involved in the regulation of highly variable social patterns. Universals are to cross-cultural variation what constants are to mathematical equations: essential components of models and theories purporting to explain variation.

Cross-References

- [Kin Recognition and Classification in Humans](#)
- [Kin Selection](#)
- [Nepotism](#)
- [Special Case: Autism](#)

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Universal Grammar

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Synonyms

Mental grammar; UG

Definition

The innate mental structures that constitute the language faculty in humans.

Introduction

Under the view originally presented by Chomsky (1965), all languages have gross commonalities, even though there exist differences across languages. For instance, all languages have predicates and arguments, and all languages have nouns and verbs. There are also similarities in the realm of syntax, such that languages tend to place the verb and its complement object in a consistent order, though this order is subject to variation across languages. As an example, English exhibits a Subject-Verb-Object constituent order, while Japanese opts for a Subject-Object-Verb order. The relative order of Verb-Object or Object-Verb is due to a parametric choice available to languages. In addition to these parameters that yield differences across languages, Chomsky (1965) claims that there are a set of innate, inviolable principles. These are the components of what Chomsky calls *Universal Grammar*, or UG for short.

The Role of UG in Language Acquisition

The innate principles of Universal Grammar come into play in the process of the child's acquisition of language. It is obvious that certain aspects of

language can be learned from positive evidence, i.e., structures that are present in the ambient language and which the child has access to. For example, individual lexical items must be learned from positive evidence alone. There are, however, certain syntactic structures which exist in languages, but which cannot be learned from positive evidence. These are cases where the child has knowledge about forms that are *ungrammatical* in the language they are acquiring. A prime illustration is the oft-cited example of the coordinate structure constraint (Ross 1967), which prevents questions from being formed by means of the fronting of only one element of a coordinate structure. For example, while "What did you eat your eggs with?" is a licit structure in English, *"What did you eat your eggs and?" is ungrammatical. No child ever produces forms such as the latter at any stage of acquisition. Furthermore, despite the lack of positive evidence (i.e., children never have access to examples of these sentences), children still manage to acquire the ambient language, including the knowledge that coordinate structure constraint violations, and other such structures are ungrammatical. This is presumably a universal cross-linguistic constraint, and it is presumably an innate part of Universal Grammar. This lack of positive evidence is what Chomsky (1980) terms *the poverty of the stimulus*, and what Chomsky (1988) relates to "Plato's problem." Since the child accurately arrives at the correct structures, Chomsky has argued, it must be the case that there are mechanisms that are innate to the child.

Bickerton (1981) has presented evidence that indicates that much the same argument can be applied to creole languages. Creoles are the product of language contact and are not grammars inherited entirely from a single source. Instead, a superstrate and a substrate language are essentially combined into a pidgin – a lingua franca that is grammatically simpler than either of its parent languages. The relative simplicity of pidgins is due to their limited usage, mostly as trade languages. Children who acquire the pidgin as a first language, though, have been observed to provide it with highly structured grammatical scaffolding. The result is a creole, which has a fully developed grammatical system. Bickerton

demonstrated that elements of these grammars must emerge *sui generis*, as there is no positive evidence in the learning environment for these structures. It is presumably Universal Grammar which endows the child with the necessary components to provide this structure to the grammar.

Conclusion

Recent thought in grammatical theory is that Universal Grammar is a human genetic endowment that is inherited (Hauser et al. 2002; Chomsky 2007). Given this biological foundation, this recent approach is often termed “biolinguistics” (though the term is much older). Current thinking is that there is a single syntactic operation, called *Merge*, and that this operation serves as the foundation for Universal Grammar, including its evolutionary beginnings. Contemporary approaches to Minimalist syntax (cf. Chomsky 1995) are dedicated to exploring these issues.

Cross-References

- [Nativism](#)
- [Pinker's \(1994\) The Language Instinct](#)

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Universal Human Fears

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Synonyms

[Aversion](#); [Phobia](#)

Definition

A distressing emotion caused by anticipation or awareness of danger.

Introduction

Darwin states, in his book *The Expression of the Emotions in Man and Animals* which supported the theory of natural selection, that fear is “the most depressing of all the emotions” (Darwin 1872, p. 36). A century later, basic emotion theorists have proposed that certain emotions are innate, in part because they are expressed the same in people around the world (e.g., Ekman 1977). There is growing agreement among researchers that fear is an adaptive emotion that motivates “fight or fly” behavior, ultimately promoting self-protection. This entry is focused on (1) domains of human fear and (2) preparedness learning, (3) perceptual biases, and (4) gender differences to support its evolutionary origin.

Fear is associated with ancient parts of the brain; the amygdala areas, which are located deep and medially within the temporal lobes of the brain, have been involved in fear conditioning in a variety of mammals, including rats, mice, rabbits, and monkeys (for a review, see LeDoux 2012). Almost universal physiological and behavioral responses to fear-related stimuli are escape, avoidance behavior, a stronger heart rate, blood pressure, respiration, and adrenaline and glucocorticoid release. It is suggested that fear-related

responses are adaptive, because they prepare our bodies for a fight or escape from a potential danger. Both types of responses require accelerated metabolism via glucose release by adrenaline and oxygen supply to the muscles by rapid breathing in order to make energy available to the muscles for fight or flight (Marks and Nesse 1994).

Evolutionary psychologists have suggested that fear has developed for mostly ancient threats (e.g., certain animals such as snakes, spiders and rats, heights, storms, darkness, blood, strangers, and separation or leaving the safety of home), but not to current threats (e.g., cigarettes, cars, electrical equipment, or handguns). Three lines of evidence support this idea. First, fear stimuli are nonrandomly distributed and are related to real (albeit ancient) threats (Marks and Nesse 1994). People rarely display, for example, a fear of trees, stones, or the sky which were not harmful to our ancestors, but fears of harmful objects or events are relatively common. Second, Martin Seligman (1971) has proposed that fears reflect evolutionarily prepared learning to fear events and situations that have provided survival threats in our evolutionary past. This can be documented with classic experiments carried out by Cook and Mineka (1990, 1991). Laboratory-reared, but not wild, monkeys do not manifest strong fearful responses to snakes suggesting that their reactions are learned, rather than innate. Monkeys are, however, able to quickly acquire a fear of a predator by observing other monkeys expressing fear in interaction with the predator. When laboratory-reared monkeys observed a wild-reared monkey displaying fear of a live and toy snake, they were rapidly conditioned to fear snakes (Cook and Mineka 1990). In consequent experiments, the laboratory-reared monkeys observed displays of fear in response to toy snakes (predators) and flowers (harmless objects) or to toy crocodiles (predators) and rabbits (harmless objects). Fear responses were conditioned only for predators, but not for flowers and toy rabbits (Cook and Mineka 1991). Since the laboratory-reared monkeys had no previous experiences with the stimuli used in the experiment, these results provide support for an evolutionary basis to the prepared learning (Öhman and Mineka 2001).

Third, common human fears seem to develop at a time when the danger might be encountered. Fears of heights and strangers, for example, emerge in infants at about 6 months of age, when infants begin to crawl away from their mothers thereby increasing the risk of a fall and/or kidnapping. The higher risk of an infant being killed by strangers has been documented both in nonhuman primates as well as in modern humans. At the age of 2 years, when infant exploration begins to be more intense, animal fears and fear of darkness emerge (for a review, see Gullone 2000). Humans, unlike nocturnal animals, have limited vision making them more vulnerable to predators when their visual capacity is limited. Fear of the dark restricts infant mobility thereby decreasing vulnerability to predators. Later, when the young child leaves the home base, agoraphobia, the fear of being in crowds or public places, which makes escape difficult, may develop (Marks and Nesse 1994). The intensity of fears in children tend to decrease with age (Gullone 2000) which can be explained by their higher physical and emotional independence from parents.

Evolutionary Evidence for Fear of Dangerous Animals

Snakes are viewed as prototypical stimuli of common fears of animals (Öhman and Mineka 2001). Snakes are present on all continents except Antarctica, and their putative fossils date back as far as 150 million years. At this time, constrictor snakes were critical predators of the small ancestors of modern placental mammals (Isbell 2009). Note that carnivore predators occurred much later, only about 40–60 million years ago. Transitional primate-like creatures were evolving ca. 65.5 million years ago, and recent primates are still attacked by snakes (Cook and Mineka 1991). This evidence suggests that the evolution of primate defense against predators was influenced by snakes.

The second line of evidence regarding danger from snakes comes from introducing an effective venom – a new powerful weapon in the

predator–prey arms race with primates. Fossils of snakes with venomous fangs from at least the Lower Miocene have been discovered, i.e., far before the first ancestors of *Homo* appeared. This evidence strongly suggests that interactions between snakes and early humans could be expected. Snake bite caused substantial human mortality and disability, although these issues have been largely neglected by health organizations. It is estimated that snake bites cause roughly about 20,000–125,000 deaths worldwide, although these estimates are based on incomplete data (Warrell 2010), partly because reporting is not mandatory in many regions of the world. It can be suggested that snake mortality was much higher in our evolutionary past, when human interaction with nature occurred daily and medical help was highly limited (if any).

The early coexistence of dangerous snakes with their mammalian prey may be the reason why snakes are frequently sources of phobias. Robins and Regier (1991), for example, determined that “bugs, mice, snakes or bats” were the most frequently cited category of phobic fears. Indeed, snakes are traditionally labeled as the least liked animals in a range of surveys on animal fears, while certain other terrestrial predators such as wolves or bears received more positive rankings by people (Schlegel and Rupf 2010; Almeida et al. 2014).

Threatening Objects Promote Visual Attention

Coevolution with snakes as significant primate predators predicts that primates, including humans, should have developed a specific visual sensitivity for snake (i.e., danger) cues that promotes vigilance for an early detection of stimuli to escape and/or avoid potentially a deadly encounter with the predator and hence survive and reproduce (Öhman et al. 2001a). Neurobiological research supports this idea, because amygdala tunes visual brain areas for rapid perception of fear-related stimuli. Furthermore, it seems that specific neurons in the primate brain respond especially quickly to images of snakes (Van Le et al. 2013). Humans, similarly to nonhuman

primates, seem to have no innate fear of snakes (DeLoache and LoBue 2009), but show similar abilities to condition snakes with something fearful (LoBue and DeLoache 2010). Rakison and Derringer (2008) found, for example, that 5-month-old infants look longer at a schematic image of a spider or a snake relative to scrambled versions of the same schematic image and look equally long at nonthreatening images such as flowers.

To support the rapid detection of snakes relative to other non-treating stimuli, Öhman et al. (2001a) compared the detection of a fear-relevant target (a snake or a spider) among eight fear-irrelevant distractors (flowers or mushrooms) with that of a fear-irrelevant target (a flower or a mushroom) among fear-relevant distractors (snakes or spiders). As expected, snakes and spiders were detected more quickly than flowers and mushrooms. These findings were repeatedly reported in a number of studies, involving both children and adults (for a review, see LoBue and Rakison 2013). It can be argued that humans should also be sensitive to a visual detection of the emotional cues in the faces of other members in the social group because significant numbers of violent deaths can be attributed to conflicts between conspecifics – similarly as with chimpanzees. The same paradigm suggesting that fear-relevant stimuli receive rapid detection in order to avoid potential threat, Öhman et al. (2001b) found that threatening faces are detected by humans among neutral faces more quickly than friendly faces, a finding which was successfully replicated by other researchers (for a review, Öhman et al. 2001b; LoBue and Rakison 2013). These findings suggest that there is a clear bias for threat in visual detection tasks.

Gender Differences in Common Fears

Girls exhibit more fears than boys (Arrindell et al. 2003), and at least some of them can emerge very early (Rakison 2009). In particular, girls reported being more fearful of darkness, strange sights and sounds, loneliness, personal relationships, animals, injury, and being kidnapped, robbed, or killed (Gullone 2000; Arrindell

et al. 2003). Boys reported being more fearful of not being good and getting into trouble, nightmares, and imaginary creatures including monsters, gorillas, and dinosaurs (for a review, see Gullone 2000). Gender socialization experiences may contribute to the reporting of fear difference by males and females. Girls may learn that it is permissible to express fears, whereas boys are expected to inhibit fears. Rakison (2009) found, however, that 11-month-old female but not male infants learn rapidly to associate negative facial emotions with fear-relevant stimuli (snakes and spiders) suggesting that socialization need not to be the key factor responsible for gender differences in fearfulness.

Although gender differences in fears were reported in a number of studies, their evolutionary origin is much less clear. Certain researchers have suggested that a higher fear of large carnivore predators in females can be explained by female's lower physical condition compared with the physical condition of males (Røskaft et al. 2003; Prokop and Fančovičová 2013). Indeed, females and children who are physically weaker than males are less likely to survive predatory attacks of large carnivores (Treves and Naughton-Treves 1999). The disease avoidance hypothesis suggests that vulnerability to infectious diseases makes people more sensitive to a potential danger. Indeed, females are more disease vulnerable than males, and more disease-vulnerable people perceive animals as more dangerous than less disease-vulnerable people (Prokop and Fančovičová 2013). These two hypotheses can be viewed as compatible, because disease vulnerability is associated with a poorer perceived physical condition (Prokop and Fančovičová 2013). The parental investment hypothesis proposes that females take care of children and have to be more sensitive to danger in order to protect their offspring (Røskaft et al. 2003). This hypothesis has not received empirical support as yet.

Why Humans Display a Fear of Harmless Stimuli

About 100 years ago, John Watson demonstrated that an infant (9-month-old Little Albert) can be

conditioned to fear a white rat by pairing the presentation of the rat with a loud aversive noise. Upon seeing the rat, Little Albert became extremely distressed, crying and crawling away. Interestingly, Little Albert's fear was later generalized to the sight of several other furry objects, such as a rabbit, a furry dog, and a sealskin coat and even a Santa Claus mask with white cotton balls in the beard. It was later proposed of course that classic conditioning is not the only way one acquires fear. Observations, verbally transmitted information, and some other mechanisms (LoBue 2013) can also develop fear.

This simple example of Little Albert's generalization of fear may explain why humans manifest a fear of certain fear-irrelevant stimuli: harmless snakes (Arrindell et al. 2003) or worm-like invertebrates (Schlegel et al. 2015) are considered dangerous or unlikeable, although they do not pose an actual danger. All of these stimuli are associated with potentially dangerous cues, because they superficially look like dangerous animals. The superficial perception of potentially harmful stimuli is favored by natural selection in order to minimize the likelihood of failing to register the presence of genuine danger (the smoke detector principle, Nesse 2005). Although the avoidance of harmless snake could be perceived as "erroneous" (false-positive error), it is still less risky than erroneous detection of a truly harmful snake (false-negative error). That is, predictions guided by the evolutionary theory do not propose that all fears should have reasonable explanations in our ancestral past, but that certain fears can also stem from similarities with fear-relevant stimuli. Finally, some fears are conditioned in everyday life. Children can, for example, easily acquire fear of a medical doctor simply because pain from vaccination is associated with the doctor. The same mechanism can be applied to dogs showing a fear of veterinarians.

Conclusion

The protective emotion of fear was highly beneficial in the ancestral environment where it evolved. Modern society, where the risk of being attacked by a predator is low, may perceive certain fears as

irrational, but a better understanding of our evolutionary past would seem to be helpful in reaching an understanding of our emotions. Comparative research on nonhuman primates and human infants where socialization is minimal seems to be promising in uncovering the origins and adaptive functions of common fears.

Cross-References

- [Evolution](#)
- [Fear](#)
- [Predators](#)

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Universalism

► Cross-Cultural Universality

Universals in Beauty

► Evolutionary Standards of Female Attractiveness

Unknown Territory

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Synonyms

Home ranges; Navigational strategies; Sex differences; Spatial abilities

Definition

Human sex differences in spatial abilities are predicated – in many adaptationist accounts – on males having been subjected to greater selection pressures in one or more domains (e.g., hunting, warfare, mating) to travel extensively throughout unknown territory. Some aspects of extant sex differences – especially in the types of spatial representations and navigational strategies favored by males – may reflect the distinct challenges of traversing large and unfamiliar regions.

Introduction

Many of the adaptationist accounts for sex differences in spatial abilities are motivated by the purportedly greater needs of males than females to travel extensively and through unknown territory. Such accounts differ primarily in their emphasis on which domain of ancestral activities (e.g., hunting, warfare, mating) required males to travel more and consequently greater spatial abilities (Jones et al. 2003). In hunter-gatherer societies, men do commonly have larger home ranges (Ecuyer-Dab and Robert 2004), and their individual success in such fitness-relevant activities has been related to the extent of their travels in some contexts (e.g., Vashro and Cashdan 2015). These adaptationist theories readily anticipate that men's needs to travel more would have selectively enhanced their general abilities to efficiently navigate their larger home range.

Navigating Unfamiliar Areas

It is commonly inferred that males not only traveled more within a large and familiar home range but also ventured more frequently outside their home range into less-familiar – if not entirely unknown – territory. During these longer trips into unfamiliar territory, navigational accuracy would have been even more critical; over greater distances, even small heading errors can compound quickly into large diversions off course. Moreover, the risk of losing one's way in unfamiliar territory is even greater in areas where geographical information cannot be used for course corrections. When moving further from one's home range, established routes between known destinations are soon left behind, and the availability of landmarks for orienting and confirming one's course decreases quickly.

Males' purportedly greater travels in unfamiliar territory may have also been selected for their favoring of navigational strategies that are less reliant on the use of proximal geographical information – in addition to their greater abilities at some basic spatial tasks (Halpern 1992). Males typically employ bird's eye, termed survey,

representations of their spatial environment that are particularly well-suited for navigating new and unfamiliar areas. Further, men prefer to navigate according to cardinal directions, distal landmarks (e.g., mountains), celestial cues (e.g., sun position), and physical distances – strategies that do not rely on environmental information such as proximal landmarks (e.g., water springs) or designated routes (Dabbs et al. 1998; Lawton 1994). These navigational strategies may have proven optimal for pursuing the hypothesized objectives of large game, mating opportunities, or aggressive encounters outside of one's home range. Such ventures would routinely involve their navigation of unfamiliar territory over new, extensive, and wandering paths, while maintaining a sense of relative position to their origin and encountered locations of interest (Dabbs et al. 1998).

Females, however, favor navigational strategies that are heavily reliant on knowledge about their surroundings – particularly the use of routes that are designated, step-by-step, with respect to landmarks for changing or confirming course direction (Lawton 1994). Although route-based navigation is effective for smaller-scale trips, the requisite knowledge and processing requirements grow proportionally – perhaps challengingly so – with increasing distance (Gaulin and FitzGerald 1986). In unfamiliar territories – where fewer proximal landmarks are identifiable – route-based navigation can be considerably less applicable (Ecuyer-Dab and Robert 2004). Whereas males favor navigational strategies that support travel over larger-scale and unfamiliar territory, females favor route-based navigational strategies for which the effectiveness diminishes with increasing distance and decreasing geographical familiarity.

Most evolutionary theories for sex differences in spatial abilities have focused on males' purported needs for greater spatial abilities and strategies to support their navigation through greater and unknown territory (Jones et al. 2003). However, other theories have conversely proposed that female's spatial abilities and preferred navigational strategies reflect their greater needs for navigating smaller and more familiar territorial ranges. In the sexual division of labor hypothesis, women are presumed to have met their nutritional needs

predominantly by gathering immobile plants and capturing small game – activities more proficiently conducted within familiar areas and by revisiting particular locations (e.g., game traps and fruiting trees; Silverman and Eals 1992). The fertility and parental care theory proposes that the greater dependence of offspring on the well-being and parental efforts of the mother acted selectively to contract females' home ranges and decrease their travels into unknown territory during critical reproductive periods (Ecuyer-Dab and Robert 2004). Females' disinclinations for using long-range navigational strategies have putatively functioned to demotivate their traveling extensively and into unknown territory – reducing their exposure to the great risks and energetic expenses of such travels. A number of other influences such as females' lower confidence in their navigational abilities (Picucci et al. 2011) and greater anxiety about navigating (Lawton 1994) and becoming lost (Bryant 1982; Lawton 1994) have also been suggested to deter their travels into unfamiliar territory (Ecuyer-Dab and Robert 2004).

Conclusion

Some of the few reliable sex differences in cognition appear in the domains of spatial reasoning and navigation. The development of these sex differences undoubtedly reflect, to varying degrees, substantial biological and sociocultural factors. However, several distal, originating causes for these differences have been advanced in evolutionary accounts – most of which largely implicate either ancestral differences in women's and men's reproductive roles and strategies or in their primary foraging activities. In many of these accounts, selective pressures functioned to incline males inherently toward larger home ranges and/or to incline females toward smaller home ranges. The needs of males to navigate larger – but familiar – home ranges accounts could have driven some general elaborations and/or enhancements of their spatial abilities. However, selection pressures that were likely far more impactful on males – such as those involved in hunting and

warfare – would have required males to not only travel more extensively, but into unfamiliar and potentially hostile territory. Their needs for venturing into, and returning expeditiously from, unknown areas may have driven further modifications to males' spatial abilities – particularly their preferences for navigational strategies (e.g., survey representations, cardinal directions) that are best-suited for traversing larger and unfamiliar territory.

Cross-References

- [Coalitional Hunting](#)
- [Sex Differences in Navigation](#)

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Unlimited Storage

- [Infinite Storage](#)

Unobservability Hypothesis, The (Vonk and Povinelli, 2006)

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Definition

The unobservability hypothesis (Vonk and Povinelli 2006) stipulates that one essential difference between the cognitive capacities of humans and nonhumans is that humans, but not nonhumans, are capable of reasoning about theoretical entities that cannot take on physical form. Such entities consist of hypothetical constructs such as traits, physical forces, and mental states.

Introduction

Comparative and cognitive researchers have long debated the facets of human cognition that allow for our uniquely human abilities. Scientists quibble over the extent to which human cognition is qualitatively distinct from that of nonhumans (see Penn et al. 2008 and related commentaries), but they cannot feasibly deny that humans stand alone with regard to the capacity to alter their environments, create technology, devise symbolic systems for communication, and so on. What is more contentious is identifying the cognitive trait or suite of traits that allowed for such distinctiveness in the psychological domain.

Testing the Unobservability Hypothesis

Various claims have been made concerning cognitive feats that might be unique to humans. Candidates include imitation/culture, teaching,

deception, theory of mind (ToM), causal reasoning, language, and abstraction. Most of these cognitive processes share the requirement to represent theoreticals or constructs that cannot, in principle, take on physical form. That is, concepts for imagined but unreal entities that could be envisioned, such as Gods and other supernatural beings, do not constitute unobservables, even if such entities have never actually been observed. Vonk and Povinelli's (2006) hypothesis refers strictly to a class of constructs for things that could never be imagined in any perceptual sense. Constructs such as freedom, thought, memory, belief, sameness, and abstraction itself are constructs that exist only as theoreticals. There is evidence that humans reason about such things by virtue of the language that allows for the creation of labels and terminology for these constructs. It is far more difficult to probe for the existence of these constructs in non-human minds that do not have access to the same symbolic systems.

Therefore, one of the challenges with such a hypothesis is that it is difficult to test. Given that researchers must measure real responses to real, observable events and stimuli, and given that unobservable constructs are inferred from observables, it is very difficult, if not impossible to differentiate between cases where animals are responding to observables, and when, alternatively, they have inferred the unobservable force or entity that has given rise to the observable manifestation of such. Take, for example, the most prolifically researched hypothetical construct: ToM. ToM is the capacity to reason about the contents of another's mind (Premack and Woodruff 1978). It is not possible to know another's mental state except through either language, which is restricted to humans, or through inference from observed behaviors, postures, expressions, and other observable phenomenon. Learning to respond appropriately to another's observable indicators of their underlying mental states may come about through associative learning and by inferring potential future outcomes based on past experiences. An animal might come to recognize that another individual with bristling hair, clenched lips, stiff posture, and that is emitting threatening grunts is more likely

to attack compared to another individual with relaxed posture and a playful expression. That conclusion can be based on the observable behaviors and features alone and need not involve the inference of underlying states of anger or calm. However, any experimental test of such inferences necessarily needs to provide the observable cues that would predict the same outcome or there is nothing on which the animal could be expected to make a prediction in the first place. Thus, the existing experimental tests for presence of concepts such as mental states in other beings are necessarily confounded and unable to be diagnostic on the question (Penn & Povinelli 2007, Povinelli and Vonk 2004). The same problem exists with regards to reasoning about physical causal forces and other unobservable constructs.

One particularly promising current direction of research relies upon the notion of appearance reality distinctions and requires apes (in all of the existing tests so far) to reason about another's knowledge based on the idea that the other ape is subject to an illusion that the subject ape is privy to. Thus, the subject ape can predict that a partner will reach for a piece of food that appears to be larger, rather than a piece of food that actually is larger, if the partner is viewing the food through distorting lenses (Lurz and Krachun 2011). Lurz and Krachun (2011) have conducted several such tests, and although these tests have been met with the usual resistance from skeptics (e.g., Buckner 2015 cited in Vonk *in review*), they present a promising new direction for future research, along with the experience projection tasks first proposed by Heyes (1998), and see Povinelli and Vonk (2004) and first conducted by Vonk and Povinelli (2011). Similar to appearance/reality tests, the experience projection tests require an individual to reason about the current psychological experience of another based on previous experience in which the subject themselves experienced the same conditions. For example, subjects might be given experience with artifacts that either block visual access or allow visual access, and then are asked to predict what another individual will do when wearing these artifacts. In Vonk and Povinelli (2011), enculturated chimps were given the chance to employ a species-

specific begging gesture with experimenters wearing buckets that they themselves had previously worn. The experimenters' faces were not visible through either bucket visor, but the chimpanzees had prior experience and should have gestured to the experimenter wearing the bucket that provided visual access rather than to the experimenter wearing the bucket that had not provided visual access. In this study, the chimpanzees behaved equivocally. Karg and colleagues have conducted related studies with more mixed results (Karg et al. 2015). These types of studies remove the association between observable cues and outcomes and link observable cues only to subjective experiences that must be mapped on to other individuals, and thus may circumvent some of the criticisms of other types of paradigms.

However, a remaining challenge with the unobservability hypothesis is that although the hypothesis could theoretically be *disproved* if appropriate experimental procedures were developed and provided evidence for animals possessing such concepts, the hypothesis is difficult to *prove*, because no amount of null results supports the claim that no animal anywhere has the capacity. Systematic and inclusive null results do, however, lend support to the hypothesis when evidence amassed across various hypothetical constructs and contexts leads to the same profound differences in behavior observed between humans and other species. Researchers are also forced to answer the question as to why such an ability would evolve in humans but in no other species and what function it might serve (Vonk in review). Scientists have remained relatively mute on this last point, but it is likely that the capacity is linked to our ability for language and other symbolic systems, which allowed for an extensive communication system unmatched in the animal kingdom.

Conclusion

The extent to which nonhumans represent concepts for unobservables remains uncertain as researchers struggle to make progress with experimental paradigms that will allow for a careful

dissection of processes linked to observable features and those that depend upon an internal representation of an overarching conceptual category subsuming such features (Vonk and Povinelli 2006). However, the idea that humans and nonhumans differ in the extent to which they represent concepts of unobservables remains viable.

Cross-References

- Abstract Concept Formation
- Associative Learning
- Causal Reasoning
- Concept Formation
- Does the Chimpanzee Have Theory of Mind?
- Evolution of Intelligence
- How the Mind Works
- Nonhuman Intelligence
- Non-Human Primates
- Primates
- Same-Different Categorization
- Theory of Mind

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Unokai

► Unokais and the Headmen of the Yanomamö

Unokais and the Headmen of the Yanomamö

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Synonyms

Headmen; Unokai; Yanomami

Definition

Unokais and Headmen are high status members of the Yanomamö tribe, located in the Amazon Basin.

Introduction

Residing within the Amazon Basin is a large tribe of indigenous peoples referred to as the Yanomamö (Sponsel 1998). These primitive people of Brazil and Venezuela were a primary focus of research by anthropologist Napoleon Chagnon (1979; Sponsel 1998). Across 35 years and approximately 25 fieldwork trips to visit the Yanomamö tribe, Chagnon documented much of the social and cultural structure of the group and came to refer to them as, *the fierce people* (Chagnon 2013). This title was chosen to depict the violent and aggressive lifestyle of the Yanomamö (Chagnon 1986a; Lizot 1985). A key illustration of the reverence with which violent behavior is held is the high status that is granted to any member of the group who has killed someone. These individuals are referred to as “unokai” and have among the highest status within the group. Acquiring social status is essential for success within the Yanomamö, particularly for male members, as it translates directly to their mating success. Political leaders within the group (i.e., headman) are also endowed with high social status. This entry will describe the Yanomamö and how status is achieved through violence, success in warfare, and political power, as well as the advantages accrued to those of high status.

Noble Savages

Napoleon Chagnon's first encounter with the Yanomamö tribe was in 1964 when the tribe was not well known and many of its villages had little-to-no contact with the outside world (Chagnon 2013). Chagnon reported that the Yanomamö people were vastly different than his expectations. He had anticipated relatively simple and nonthreatening tribal people. His expectations were to meet the delightful and peaceful humans within their natural state much like what Jean-Jacques Rousseau described in his work, *The Social Contract* (1762/1968). Instead, Chagnon found a tribe of people quite accustomed to violent acts. Early documentation of the Yanomamö describes the tribal people partaking in disturbing and violent

activities including demonstrations of physical aggression, violent raids, and killings. On the basis of his extensive work with the Yanomamö, it was evident to Chagnon that the preconceived notion that humans are innately cooperative and gentle ignores an underlying propensity for violence.

Social Hierarchy

Throughout Chagnon's work with the Yanomamö, a critical observation was the immense inequality that exists among its people. The hierarchy among men in particular has important consequences, as it is a key determinant of mating success, with men at the top of the hierarchy gaining the most mating opportunities. Two positions of high status within the Yanomamö are that of unokai and headman.

The Yanomamö, which make up approximately 25,000 people across roughly 250 villages, operate as a hierarchical society in which females reside at the bottom of the hierarchy and men move up based on status that can be obtained through acts of aggression. A headman who is in charge of the village's politics leads each tribal village and sits at the top of the hierarchy. Chagnon (2013) mentions in his writings that each headman is different in their leadership style. Some are relatively docile in their leadership tactics, while others are belligerent and violent. Individuals are placed into the position of headman according to their lineage; those who have the largest number of kin in the tribe are placed into this position of power. Although this position is typically granted through familial ties, it is also achievable with increased numbers of kin or offspring.

Other highly recognized figures within Yanomamö communities are the unokai, translated as "killed men in war." These high status men have killed another individual in battle or were involved in a severe conflict that led to killing. Like the headmen, unokai are also documented to have a greater number of sexual partners or wives and a subsequently increased number of offspring (Chagnon 1992). These high status positions are

linked to greater opportunity for sexual access to females as they illustrate to their own village honorable actions of force and intensity during warfare. Additionally, anthropological research suggests that much of the violence between tribal villages is the result of competition over resources (Sponsel 1998). The promise of such rewards incentivizes participation in warfare, as one's access to resources can improve one's ability to attract mates. Thus, these individuals are highly regarded in their culture as they take the greatest risks, which serve the function of helping to foster the success and safety of one's group.

Pursuing Status and Mates

A significant benefit for Yanomamö men with high status positions results from their participation in arranged marriages. This marriage system functions as a form of trade among families. For giving a wife, a daughter's family receives some form of payment from the receiving husband. Families look for men with prominent family lineages and men of high status to exchange their daughters with. Yanomami headman and unokai are most highly sought after for marriage. As such, men who are in positions of political power or high-achieved status have the best chance of obtaining a desirable female partner (Chagnon 1988).

In addition to arranged marriage practices, the Yanomamö also practice polygyny, allowing males to have more than one wife. This elevates the level of competition among men and incentivizes the abduction of women across villages. The competition is exacerbated by the fact that there are more males than females in the population, a fact that may be explained by the practice of female infanticide (Chagnon et al. 1979; Owl 1976). Men of high status may monopolize a large share of local females, leaving other men with few mating opportunities. This amplifies competition among men for access to the status and resources that will make them appealing to females. Only those men who are successful stand to pass on their genes to the next generation, and so selection favors aggressive and violent competition in the pursuit of enhancing one's mating

prospects. Actions that are aggressive in nature elevate a man's place in the tribal hierarchy. As one moves up in their position within the tribe, men have access to greater resources, including women.

Conflicts that take place among the Yanomamö range from minor "feats of strength" competitions, such as chest pounding competitions, to extremely violent raids of other villages. Each conflict provides males with the opportunity to illustrate their dominance, and importantly, advance their mating prospects (Chagnon 1988). Within villages, the chest-pounding or club-fighting duels are competitions of will, where males take turns beating one-another until one-person surrenders (Chagnon 1992). The men typically use their open-palms or fists, but occasionally use weaponry such as clubs or axes. Overall, these competitions function to settle disputes between men. However, if death or great injury is the result of these chest duels, divisions within villages can form, leading to the creation of a new enemy village. Ultimately, the males who endure these conflicts receive accolades for their dominance, as they are able to illustrate their strength and usefulness to the group.

When violence escalates to intergroup warfare, men who participate and who are successful in killing members of the rival village are bestowed the great honor of being named a unokai. This is because the killings contribute to a village's reputation for strength. This reputation is important because a group perceived as cowardly or weak will often be attacked. Unokais receive high status within the group and access to more mating opportunities. This incentivizes participation in continued violent and deadly intergroup competition in order to ensure one's place atop the social ladder.

Conclusion

The Yanomamö culture illustrates a tight connection between male status and mating success. Headmen are granted status by virtue of their family and descendants, whereas others engage in extreme violence to fight for their elevated status. In this volatile and conflict prone region,

aggressive behavior is the currency with which men are able to secure reproductive resources. Particularly, in this polygynous society, competition for status and subsequent mating success leads to extreme forms of violence within and across groups.

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Unpopular

- [Rejected Children](#)

Unpredictable Environment

- [Environmental Unpredictability](#)

Unpredictable Environments

- [Harsh Environments](#)

Unrestricted Sexuality

- [Sociosexuality](#)

Unstable Environments

- [Climate and Habitat Diversity](#)

Untruth

- [Fiction](#)

Unusual

- [Why Humans Are Unique](#)

Unwanted Sexual Advance

- [Sexual Harassment](#)

Upbringing

- [Social Development](#)

Upper Body Strength

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Definition

Upper body strength refers to the muscular power of the arms, hands, and chest.

Introduction

The muscular-skeletal system evolved primarily to exert physical force onto the world, as directed by the nervous system. Such a system is – unsurprisingly – used for diverse effects in different species, e.g., mammals use it to expand and compress their lungs for respiratory purposes; virtually all animals use it for movement and to direct the senses. This entry discusses one part of this system in humans: upper body musculature and what its significance has been for human ancestors. In particular, upper body strength has been shown to be an important predictor of fighting ability and thus an aspect of mate value and a correlate of status.

When human ancestors began using bipedal locomotion more regularly, this freed the hands, chest, and arms to specialize in other kinds of muscular movement. Humans are not unique in this. Other bipedal species have evolved shrunken chests which lower their center of gravity and aids in balance (e.g., T-Rex). Other species such as (male) kangaroos have evolved more robust strength in the upper body. Humans are one such species.

For what purpose is this strength used? The answer – of course – is a list rather than an item. The upper body is used to carry altricial infants, fashion and wield tools, process and consume food, climb trees as many primates continue to do, groom, remove parasites, attend to injuries, craft shelters, and so on. Additionally, there are reasons to think that humans used upper body strength in aggression.

How Important Is Upper Body Strength to Aggression?

Technological progress in the modern world has expanded the types of aggression available to humans, e.g., explosives, ballistic missiles, firearms, Tasers, and pepper spray. While human ancestors had fewer options, they did make use of human ingenuity to supplement simple hand-held weaponry. For example, hunter-gatherers have been known to use pathogens (e.g., the Dani laced their arrows with rotting flesh), poisons, and other creative means of rendering

enemies functionless. However, an analysis of ancestral weapons has shown that all muscular-powered weapons used by hominid ancestors were powered by the upper body in particular, e.g., spears, bows, handaxes, clubs, and atlatls (Brues 1959). Additionally, unarmed combat is also heavily reliant on the upper body for punching (Carrier and Morgan 2015), choking, grasping, rending, and gouging.

This means that if human ancestors were fighting, they were doing it largely with their upper bodies. In addition, upper body strength is the most sexually dimorphic kind of strength, with human males having approximately 90 % greater upper body strength than human females, while only having 50 % greater lower body strength (see Lassek and Gaulin 2009). This means that ancestrally, males with weaker upper bodies were reliably killed or rejected by females with such frequency that they were selected out of the gene pool, leaving only the males whose developmental systems magnified their upper body strength in response to testosterone. This selective regime was presumably in place because males are the most aggressive sex and therefore pay a large price for not being able to aggress well.

Thus, upper body strength is greater in the sex that evolved to be skilful at aggression. This suggests that human males' formidable upper bodies evolved – to a large extent – for aggression. Such aggression, however, is not always deployed against other humans. Males are also the sex that engages in the most hunting, particularly big game hunting that would require great upper body strength to kill the target and to transport the meat back to family members and friends (Brown 1991). Is there evidence that upper body strength is particularly relevant to conspecific aggression rather than just hunting?

The answer is “yes.” Evidence from male assessment mechanisms (see ► [“Male Adaptations to Assess Fighting Ability”](#)) shows that such mechanisms are particularly well designed to respond to cues of upper body strength. In other words, a man who has strong legs will not appear as formidable as a man who has strong arms. Even when judging a man's fighting ability from his face or voice, judges return with estimates that

more closely track upper rather than lower body strength. In other words, men with greater upper bodies also have “tougher” looking faces and more formidable sounding voices. This connection cannot be directly causal, e.g., humans do not produce voices with their upper body musculature nor do they lift with their faces, but it does suggest that adaptations that are designed to estimate fighting ability are especially tuned to cues of upper body strength.

What Are the Correlates of Greater Upper Body Strength in Men?

Individual men with greater upper body strength are perceived as – and indeed would have been – better fighters. This has profound implications for human social relationships, because fighting ability is a relevant variable to many kinds of social interactions, specifically any relationships that involve potential aggression either in offense or defense. Not surprisingly, upper body strength in men has been shown to predict many important characteristics.

Research demonstrates that males with more upper body strength feel entitled to better outcomes, set lower thresholds for anger, and are more likely to be involved in aggression (Muñoz-Reyes et al. 2012; Sell et al. 2009, 2016). This has been interpreted in classic game theoretic terms, e.g., animals evolved to calibrate their aspiration levels to their fighting ability (“resource holding power” in evolutionary biological parlance).

Similarly, men with greater upper body strength have been shown to be more attractive to women (Fink et al. 2007) and report more sexual relationships (Sell et al. 2009, 2016; Sneade and Furnham 2016). This has been interpreted as evidence that female mate choice mechanisms are calibrated to seek more dominant males as mates, because they will sire more healthy offspring and be better able to support the female and her children or both. There is evidence of special design for this preference, for example, females who are more fearful of being attacked demonstrate a higher preference for physically formidable males (Ryder et al. 2016).

Conclusion

In conclusion, upper body strength is the kind of strength that is most relevant to ancestral combat. This is presumably why men have much more upper body strength than woman, and why human perceptual systems that estimate fighting ability focus on cues of upper body strength. Men with more upper body strength can leverage it into better treatment, and thus feel more entitlement, set lower thresholds for anger, and are more likely to deploy aggression. Such males are also more attractive to females.

Cross-References

- [Costs of Aggression](#)
- [Sex Differences in Aggression](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Strength and Anger-Proneness](#)
- [Upper Body Strength and Fighting Ability](#)
- [Upper Body Strength from Photo](#)

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Upper Body Strength and Fighting Ability

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Synonyms

Formidability assessment

Definition

Upper body strength is the most reliable indicator of fighting ability in humans.

Introduction

Assessing fighting ability was vital to humans for both natural and sexual selection. Men that could reliably assess fighting ability would have been better equipped to judiciously choose what physical conflicts to enter into, what conflicts to avoid, and when to withdraw. Women too would have benefited from assessing fighting ability accurately by choosing mates with a higher likelihood of successfully protecting them and their offspring. When considering these selection pressures across the scale of evolutionary history, it is quite likely that assessments of fighting ability would have been selected to be accurate and robust.

The best indicator of fighting ability in humans is upper body strength (Sell et al. 2012), which is

fundamentally tied to the musculature of the upper body. Individuals with greater upper body strength were better able to strike, injure, and disable competitors. Accordingly, humans should be able to assess visual cues to muscle mass in an accurate and robust fashion, and those cues should also predict success in conflict. Several lines of work have demonstrated converging support for these ideas.

Empirical Evidence

In terms of accuracy, Sell and colleagues (2009a) demonstrated that judgments of both men's upper body strength and fighting ability from photos correlated strongly with strength as measured by weight lifting equipment. These judgments were accurate at the individual level. Furthermore, strength judgments were almost perfectly correlated with judgments of fighting ability, suggesting that the cognitive program that measures fighting ability is closely tied to strength assessment. More importantly, measured upper body strength also predicted men's self-reported history of fighting and success in conflict (Sell et al. 2009b). However, a major limitation of this work is its reliance on retrospective self-report, which may not accurately reflect real world outcomes. Furthermore, these methods do not directly test what the program was designed to do: to reliably assess the victor of an actual physical fight.

However, there is some direct evidence that addresses whether the program can reliably assess the victor of a fight. This work comes from research on physical fights from mixed martial arts (MMA) competitions. Little et al. (2015) showed untrained individuals facial photographs of MMA fighters who had previously fought against each other. Despite the fact that MMA fighters are an extremely homogenous group (they are all extremely strong and are grouped by weight class), raters were able to guess who won at rates greater than chance (55 %). In addition, these judgments of fighting ability were also strongly correlated with strength judgments, suggesting that strength information was used to decide who would win.

In terms of the robustness of these judgments, there is good reason to believe that the assessment system is quick and sensitive to subtle cues. First, humans make highly accurate assessments of strength and fighting ability in seconds from merely looking at photographs of individuals. These judgments are accurate even when only facial photos are used, which obscure information about the musculature in the upper body. Similarly, humans also accurately assess upper body strength from the voice (Sell et al. 2010), and these assessments provide incremental validity above and beyond what information is gained from visual cues.

Conclusion

In sum, there is strong evidence that the assessment of fighting ability in humans is not only accurate but is also robust. Humans can accurately predict the winners of fights even when competitors are physically similar, and those decisions closely follow judgments of physical strength. Furthermore, accurate judgments of strength and fighting ability can be made even under impoverished circumstances, such as when the body is partially obscured or only voice information is available.

Cross-References

- [Aggression](#)
- [Assessment of Fighting Ability](#)
- [Evolution of Fighting Assessment Abilities](#)
- [Fighting Assessment](#)
- [Intrasexual Competition](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Male-Male Competition](#)
- [Mate Preferences](#)
- [Physical Aggression](#)
- [Psychological Mechanisms](#)
- [Resource Competition](#)
- [Self-Assessment of Fighting Ability](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Signals of Body Size](#)

- [Size and Dominance](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- [Upper Body Strength](#)
- [Upper Body Strength from Photo](#)
- [Vocal Indicators of Dominance](#)

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Upper Body Strength from Photo

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Synonyms

[Formidability assessment](#)

Definition

Humans can reliably assess upper body strength from photographs.

Introduction

Upper body strength is the most reliable cue to fighting ability in humans (Sell et al. 2009). This is at least partially because for most of human history, the most effective fighting tactics involved using the upper body to strike and injure competitors. Given that upper body strength is almost completely determined by the size of the muscles in the upper body (Lassek and Gaulin 2009), upper body musculature is a particularly salient visual cue to an individual's fighting ability. As such, the visual system is well designed to acquire those cues to body size and pass them along to the cognitive program that judges fighting ability.

Empirical Evidence

To test the accuracy of upper body strength assessments, researchers have extensively relied on photographic stimuli. The basic reasoning is that if cues to upper body strength are assessed visually, then humans should be able to accurately assess upper body strength from pictures alone. Sell and colleagues (2009) demonstrated that for men involved in strength training, judgments of upper body strength from full body photographs correlated strongly ($r = .71$) with strength as measured by weight lifting equipment (e.g., arm curl, chest press). These ratings were stable both in aggregate and at the individual level.

In order to isolate what specific cues individuals are tracking when looking at photos, Sell and colleagues (2010) also examined whether humans could accurately assess upper body strength from cues in the face or upper body alone. They also used pictures of individuals who did not engage in strength training, to test the generalizability of these programs. The results definitively showed that raters could accurately assess strength from pictures of the upper body (excluding the face) in both men ($r = .57$) and women ($r = .51$). These cues appear in face as well; raters could accurately assess strength from pictures of the face alone, although the correlations were generally weaker for both men ($r = .39$) and women ($r = .21$).

Furthermore, judgments of strength appear to genuinely track upper body strength, rather than some related cue. For example, when controlling for body size (i.e., height and weight), judgments of men's strength are uniquely predicted by actual upper body strength. Conversely, when controlling for actual upper body strength, measurements of men's height and weight have much smaller and less consistent relationships to judgments of strength. Similarly, judgments of strength from the face (which obscures information about lower and upper body strength) exclusively track upper body strength rather than lower body strength. Thus, there is compelling evidence that humans can track upper body strength and that strength assessment is not a byproduct of a system that tracks some related cue.

Finally, there is evidence that visual cues that indicate upper body strength in humans are species typical. Sell and colleagues found that American raters could accurately judge strength from facial photographs and recordings of voice for American men, Tsimane men from Bolivia, and Andean men from Argentina. These results strongly suggest that strength assessment is an evolved mechanism and not based on culturally transmitted information.

Conclusion

Upper body strength is the single best indicator of fighting ability in humans. Given the importance of accurately assessing the fighting ability of other competitors, humans developed adaptations to reliably assess upper body strength. These adaptations track upper body strength and not some other related cue (e.g., height). The adaptations are also robust, as humans can accurately assess upper body strength from still photographs. Similarly, judgments of upper body strength do not appear to be based on cultural transmission, as Americans can reliably assess the strength of men from other cultural groups.

Cross-References

- [Aggression](#)
- [Assessment of Fighting Ability](#)

- [Evolution of Fighting Assessment Abilities](#)
- [Fighting Assessment](#)
- [Intrasexual Competition](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Male-Male Competition](#)
- [Mate Preferences](#)
- [Physical Aggression](#)
- [Psychological Mechanisms](#)
- [Resource Competition](#)
- [Self-Assessment of Fighting Ability](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Signals of Body Size](#)
- [Size and Dominance](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- [Upper Body Strength](#)
- [Upper Body Strength and Fighting Ability](#)
- [Vocal Indicators of Dominance](#)

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Urban Gangs

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Synonyms

[Intrasexual competition](#); [Intrasexual violence among women](#); [Within-sex competition](#)

Definition

Female membership in gangs provides women with opportunities for affiliation, protection, respect, and mate selection. Women's aggressive behavior within the gang is generally more indirect and less deadly than that of male gang members, typically directed at other females, and used as a means of mate guarding or derogation of one's rivals.

Introduction

Early research on urban gang activity focused primarily on male gang members, only mentioning female members to discuss their appearance or deficiencies as viewed by the male gang members. However, during the 1980s, there was a greater emphasis placed on the motivations underlying women's involvement in gangs. This research suggests that women join gangs for affiliation, protection, respect, and the prospect of finding a mate (Campbell 1991; Molitor 1996). Additionally, a primary focus has been placed on investigating the factors that predict females' engagement in violent behavior within the context of gangs. The research suggests that female-perpetrated gang violence is the result of mate guarding, intrasexual jealousy, defense of one's honor, or pressure exerted by male members (Campbell 1991, 1984). This entry provides an overview of research on female gang members and places the findings in an evolutionary context to help explain women's membership, roles, and aggressive behavior within gangs.

Female Gang Members

There are about 400 gangs in New York City alone with 8000 to 40,000 members in total. Of those members, it is estimated that 10% are female, although some estimate that female members account for as high as 30% of members (Laidler and Hunt 2001). The women who are members of these gangs range in age from 14 to 30. Many are married – often to male gang members – and have children (Campbell 1991). Many

of these women and girls have a lack of education and come from dangerous neighborhoods. Many also have or had an unstable, violent family life, most of which included divorces, remarriages, or girls whose parents were never married. These female gang members were usually members of a gang with both female and male members or in an all-female gang named after the male gang with which they are associated, such as “The Sandman” and “The Sandman Ladies.” There are very few all-female gangs that are not associated with an all-male gang. Before 1980, the female members of gangs were often viewed as playing unimportant or minor roles; however, more recently, their roles within gangs have been more clearly elucidated (Molitor 1996).

Women's Membership and Roles Within Gangs

From an evolutionary perspective, women's membership in gangs can be traced, distally, to mating motivations. Fundamental features of men and women's reproductive physiology have differentially shaped men and women's mating strategies (Trivers 1972). Owing to females' large obligatory investment in offspring (e.g., 9 months of gestation and a long period of breast feeding), lifetime reproductive potential is substantially limited, particularly in comparison to the reproductive capacity of men, who are limited only in their ability to gain access to mating opportunities. As a result, females best optimize their reproductive fitness by selecting high-quality mates, that is, mates who are both willing and able to invest resources into their shared offspring. Indeed, research has shown that women show a strong preference for men of high status who have high income or earning potential (Buss 1989; Buss and Schmitt 1993). In urban environments, women from impoverished backgrounds seeking high-status mates may be drawn to gangs as a means of gaining access to mates who have the ability to acquire high status and access to resources (even if obtained illegally). Partnering with such men may also offer women protection from violence (Snyder et al. 2011).

Descriptive research on women's involvement in gangs is consistent with the idea that it is women of low socioeconomic status who are drawn to gangs. Female gang members are more likely to grow up in poverty and to have been raised in a single-parent home where the mother is the primary caregiver for the family, and the father is absent (Laidler and Hunt 2001). Additionally, many female gang members have backgrounds of physical or sexual abuse (Molidor 1996).

Research is also consistent with the idea that primary motivations for gang membership include the protection, resources, and mating opportunities it provides. Indeed, the "roles" that women play in gangs are often based on their relationships to the male gang members. Research has categorized female gang members as belonging either to the "Good Girls" or "Bad Girls" group. "Good Girls" have brighter prospects for their future. Although they are likely to engage in substance use with the gang, they do so with greater restraint (Campbell 1991; Laidler and Hunt 2001). The "Good Girls" category is further divided into "Independent Women" and "Good Wives." "Independent Women" are members whose membership is temporary, as most hope to attend college and become financially independent. The "Good Wives" also have aspirations to leave the gang; however, they display a strong financial dependence on their boyfriends/husbands within the gang, making it difficult to leave (Campbell 1991).

On the other hand, the female members who fall into the "Bad Girls" group view their membership as long term, often because their options are limited. They tend to have poor money management, do not do well in school, and are at high risk for prostitution and drug addiction (Campbell 1991). Similar to "Good Girls," "Bad Girls" are also divided into two smaller groups: the "Sex Objects" and the "Tomboys." The "Tomboys" generally join in on fights with other gangs and participate in illegal activities, which is atypical in comparison to most female gang members. The male members do not appreciate the willingness of the "Tomboys" to fight, and most male members only accept them through sex, as the

"Tomboys" are generally promiscuous with the male members. However, the women in this group are also able to maintain strong friendships with other female gang members (Campbell 1991), which contrasts sharply with the female relationships of the "Sex Objects."

The women in the "Sex Objects" category are often sexually active with one or more male members of the gang. Sex provides the primary means of their acceptance by the men as most do not have friendships with male gang members outside of sex. Other female gang members distance themselves from these women through othering, gossiping, and judgment of their behavior (Laidler and Hunt 2001). Promiscuous behavior may represent a threat to the other women's ability to secure long-term investment from their male partners. When sex is freely available, there are few incentives for men to invest in long-term relationships. Women's indirect aggression may therefore function as a means of combatting the ease with which men can gain access to short-term mating opportunities (Vaillancourt 2013). Indeed, there are strong norms among female members for ensuring that women dress and act like a respectable woman. Failure to do so results in a loss of esteem by their peers. Being "respectable" includes standing up for themselves, being independent, not engaging in casual sex often, and not letting themselves lose control when under the influence of drugs or alcohol. Female members are typically more judgmental about the respectability of other female members than are the male members and will even engage in fights to defend their respectability or honor (Laidler and Hunt 2001).

Overall, women's relationships with other female members are often exceptionally different than their relationships with the male members. Female relationships are often flimsy and short-lived. Female members in relationships are often very jealous of other women as they typically depend on their partner for financial support. Many female friendships end as a result of disputes over men (Benenson et al. 2013; Campbell 1991). Women's relationships with men may be more long-lasting, though not without their own problems. Although the male members are

protective of the female members (Laidler and Hunt 2001), the women are often physically and sexually abused by them. If a woman is impregnated by a male member, that member often abandons her (Arnocky et al. 2014; Campbell 1991, 2002).

Induction of Female Members

There are many different methods of inducing new female members, depending on the gang. Some women are required to sleep with any gang member who wishes to have sex with her, often to prove that she is heterosexual. A similar type of induction includes the potential female member being coerced into sex with multiple members at a time. Other women are expected to fight many current female members at a time. These potential members are not expected to win these fights, but to prove that they can hold their own in a fight. Other women have to fight one current member of the gang, usually one of the most accomplished fighters. Another way that these women are inducted is by “walking the line,” in which the inductee walks along a line of members who beat her severely. Other times, the potential members are expected to participate in a shooting or a robbery in order to implicate them in the crime and to prove their loyalty to the gang (Campbell 1991; Molitor 1996). These induction methods are similar to hazing practices observed in other groups and which serve the function of fostering loyalty to the group (Aronson and Mills 1959).

There are, however, less violent methods of induction, including women having been associated with the gang from young ages until they are established as gang members, marrying a current gang member, or even being allowed into the gang without any kind of induction or initiation (Campbell 1991; Molitor 1996). It is also possible for gang members to leave the gang. There are two main ways to do so: actively or passively. Most members who actively leave the gang leave due to injuries obtained during a gang-related fight. Members who choose to leave the gang passively often do so by getting married or having children (Campbell 1991).

Violence and Aggression

From an evolutionary perspective, women are expected to engage in less violent aggression than men (Archer 2006; Campbell 1999, 2013). This is due to the large investment that women make in their offspring. Indeed, women are essential to the survival of their offspring in a way that men are not (Sear and Mace 2008). Additionally, there are fewer incentives for women to engage in violent competition. For men, competition with other men serves the function of increasing their mating opportunities, but given women’s low reproductive ceiling, such incentives are much weaker. The reduced benefits, and heightened costs, of engaging in violence for women yield a much lower rate of physical violence among women (Archer 2006). However, women are still motivated to compete with potential mating rivals as a means of protecting an existing relationship from mate poachers, or to attract a potential mate through the derogation of rivals (Arnocky et al. 2014; Benenson 2013). To achieve such ends, women are more likely to use indirect forms of aggression (Campbell 1999). This permits women to compete for the best mates without putting themselves directly in harm’s way.

Although women in gangs are involved in more violence than women who are not members of gangs, they commit fewer violent acts than their male counterparts in the gang. Additionally, much of the violence is directed toward their female competitors. The female gang members are often pressured by male members to commit violent acts (Campbell 1991, 1984). Many of these women would describe the fights as fair, since weapons are often excluded. Instead, most fights include the women using their teeth, nails, or any other body part in order to win the fight, unlike most male fights that use more deadly means of aggression, such as guns (Campbell 1991).

There are different roles that female gang members take part in when using violence. Most women who participate in fights are “Bad Girls.” For example, “Tomboys” use fighting and violence in intergang fights (Campbell 1991; Molitor 1996), while “Sex Objects” fight mostly with other women over jealousies about male

members. When women fight with females outside of their gang, they are mostly fighting with women who are not associated with any gang and the fight occurs without weapons. Another common type of fighting is called integrity fights which occur when a female gang member's honor has been called into question. These fights generally happen in public and are more likely to include weapons. However, overall, most intragang fights occur in private, do not typically have a victim, and generally conclude by both parties voluntarily walking away (Campbell 1984).

Conclusion

Though women's involvement in gangs is less common than that of men, there is now sufficient documentation of women's membership in gangs to begin to understand the underlying motivations for their involvement. Many female members coming from impoverished backgrounds join gangs in order to have access to the opportunities gangs provide for finding a mate who can offer protection and financial security. Women's roles within the gang are often centered around their relationships with the male members. Their dependence on the male members engenders greater competition between female members who seek to protect their partnership from female rivals, thereby leading women to participate in both direct and indirect aggression to derogate rivals of their current or prospective mates. Females tend to use such tactics to find a long-term, financially-stable mate able to support herself and her children (Arnocky et al. 2014; Benenson 2013; Buss 1989; Buss and Schmitt 1993; Campbell 1999, 2013).

Cross-References

- Anne Campbell
- Derogation of Attractiveness Among Women (Intrasexual Rivalry)
- Female-Female Strategies
- Intrasexual Rivalry Among Women

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Urban Sexuality

► Local Sexual Practice

Usage-Based Linguistics

► Modern Theories of Language

Use It or Lose It

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Synonyms

Atrophy; Cognitive decline; Cognitive enhancement; Degenerate; Diminish; Neurogenesis

Definition

Engaging in healthy and serious mental activities can help prevent the loss of cells and cell production (Shors et al. 2012).

Introduction

In recent years, one subject has become a main topic of conversation among cognitive

psychologists: the use-it-or-lose-it theory. This theory suggests that if we do not use a certain function or skill, their loss can be irretrievable or irreversible. It is well-known that cognitive decline naturally occurs after reaching a certain age. In particular, Wilson et al. (2003) have shown that the rate of cognitive decline sharply increases in the last 43 months before death. Potential contributors to cognitive decline may include a reduction of hormonal or trophic support, specific toxin exposure, or activation of the innate immune system by pathogens (Wilson et al. 2003). According to Lustig et al. (2009), a main method of testing the use-it-or-lose-it theory is strategy training. Strategy training usually involves identifying tasks older adults perform poorly on and training them on strategies that may help increase their ability to perform these tasks. Lustig et al.'s earlier work discussed different approaches to testing the use-it-or-lose-it method. Approaches used to test this method include multi-model interventions, strategy training, process-based training, and cardiovascular exercise. The current review expands upon this earlier work, describing several recent findings: some supporting the role of enrichment on buffering cognitive decline and others suggesting small or nonsignificant effects of enriched environments on cognitive decline.

Enriched Environments Can Reduce Cognitive Decline

One way the use-it-or-lose-it theory has been tested is through cognitive performance. Researchers vary in the testing techniques and variables they include in these experiments. In one example, Stine-Morrow et al. (2008) examined two groups of participants: a control group and an experimental group. Participants in the experimental group were given a test for their baseline cognitive performance and then given weekly tasks to train their cognitive function. Once a week, participants would meet at the local community center and have to work together to solve tasks that included processing speed, working memory, inductive reasoning, visual-spatial processing, and divergent thinking. This process continued for 7–8 months,

changing only following breaks in the schedule (e.g., holidays, weather). Their study focused on the effects of an engaged lifestyle on cognitive vitality, with a primary emphasis on fluid ability: the overall composite of variables including inductive reasoning, divergent thinking, and speed. They found a small, but reliable effect in the experimental group after the cognitive intervention training, relative to the control group, who did not participate in the training. However, the researchers noted that, while these group differences were reliable, they were largely limited to the training itself, without a sizable transfer to other task performance or ability. These limitations in transfer are well-documented within the working memory training literature and are not limited to studies with elderly populations (see e.g., Shipstead et al. 2012).

Other researchers have replicated these training benefits. In one recent example, McLaughlin et al. (2018) tested 14 healthy, middle-aged adults, comparing a group of adults completing brain training to another group completing trivia questions. Data were collected over a number of weeks, with participants measured on a variety of cognitive performance variables, ranging from attention to working memory, including speeded components, as well. After six weeks, the authors found significant differences across their two groups, with those in the brain training group seeing improvements in executive function, coupled with decreases in depressive symptoms. These results align with benefits associated with consistent, neurocognitive training.

Similar improvements following cognitive training were reported by Al-Thaqib et al.'s (2018) study, using Lumos Labs' Lumosity brain training as a cognitive training tool. The control group and experimental group were both assessed using the Cambridge Neuropsychological Test Automated Battery (CANTAB) before and after the experiment. Lumosity training – 15 min per day, every day, for 3 weeks – improved cognitive functions including attention and motor speed, compared with healthy control participants. These results largely mimic those described by McLaughlin et al. (2018), with their participants' improvements in executive function. Similar improvements following Lumosity training have

been documented by Mayas et al. (2014). In their study, older adults completing 20-hour-long sessions of Lumosity training showed improvements in alertness and distractibility, relative to a comparable group of older adults who did not participate in Lumosity training. Importantly, the skills they gained through these training exercises also transferred to a novel, oddball task, which differed from the tasks they had completed through Lumosity. These findings, unlike those described by Stine-Morrow et al. (2008), do suggest some amount of skill transfer following brain training.

Researchers have also examined the impact of other, individual differences, variables. One variable of interest is that of gender. In one example, Tun and Lachman (2010) showed that men and women were differentially affected by computer use, with men benefitting more from regular computer use than were women. Together, these studies illustrate some positive outcomes of training programs, with documented advantages observed beyond those of normal, healthy control participants.

Enriched Environments May Not Affect Cognitive Decline

Other findings suggest small or nonsignificant effects of enriched environments. In one example, Shute et al. (2014) had participants play either the Portal 2 video game or engage in Lumosity training. Participants in both conditions completed pretest and posttest measures involving problem-solving, spatial skills, and persistence. Portal 2 participants showed significant increases in all three measurements, relative to Lumosity participants. While Shute et al. did not conduct their experiment with older adults, they, in fact, tested a typical convenience sample of college students. Their results do highlight an important point: Cognitive function is inherently malleable, throughout an adult's lifespan, and these improvements can come from a variety of sources (including those not classically deemed "training interventions"). The authors cite repeated challenges and failures, during gameplay, as an important mechanism underlying their findings.

Meanwhile, Salthouse et al. (2003) *did* examine the effect of challenges on promoting cognitive decline in elderly populations. Their participants, ranging from 20 to 91 years of age, documented weekly activities – rating the cognitive demands of each one – and completed a number of standardized cognitive tests (pertaining to e.g., spatial ability, reasoning, episodic memory, vocabulary). Overall, the authors found little evidence to support mediation *or* moderation of age-related declines following cognitively demanding activities (e.g., preparing tax forms, reading the newspaper). Despite these findings, the authors do recommend that the elderly continue to engage in these activities, despite the potential for weak or nonsignificant effects, simply for enjoyment. Truly, there is no evidence to suggest any harm coming from these activities.

Finally, a review by Salthouse (2006) suggests there may be positive correlations between cognitive training and increases in cognitive function, though there is simply not enough “evidence” to support these claims. Again, despite the lack of evidence supporting training-related decreases in cognitive decline, those who enjoy participating in these activities and games should continue them. The joy from these activities may contribute to a higher quality of life.

Conclusion

Researchers investigating the use-it-or-lose-it theory have published some mixed results. In some cases, researchers find cognitive training activities *may* help slow the process of cognitive decline. However, in other studies there is too little evidence supporting any substantial benefit for elderly participants or that cognitive benefits may arise from other activities not pertaining to cognitive training. Despite these mixed results, researchers are in agreement that these interventions can help elderly populations in important ways, as is the case with the social- and community-based interventions. Whether these interventions translate to some significant cognitive benefit(s) in particular remains unknown. To summarize, further research is needed to find some conclusive answers as to whether training

approaches can help reduce cognitive decline in elderly populations.

Cross-References

- ▶ [Associative Learning](#)
- ▶ [Context, Environment, and Learning in Evolutionary Psychology](#)
- ▶ [Different Functions of Memory](#)
- ▶ [Episodic Memory](#)
- ▶ [Long-term Memory](#)
- ▶ [Mirror Neurons](#)
- ▶ [Neurons in the Cerebral Cortex](#)
- ▶ [Non-associative Learning](#)
- ▶ [Sex Differences in Cognitive Development](#)
- ▶ [Working Memory](#)

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Use of Implements

► Nonhuman Tool Use

Use of Instruments

► Nonhuman Tool Use

Use of Mate Retention Strategies

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Synonyms

Mate guarding; Mate retention

Definition

Mate retention refers to effort aimed at maintaining access to a mate.

Introduction

Mate retention tactics comprise a broad menu of behaviors ranging from acts of kindness and resource provisioning, to vigilance, manipulation, and violence. Mate retention effort often occurs in response to a perceived or actual relationship threat. Sex differences and individual differences exist in the use of specific mate retention tactics, which share the common goal of reducing the probability of partner defection or infidelity. In order to understand the origins of these behaviors, it is necessary to understand the processes that underlie mate selection and the negative implications of partner loss.

Introduction

Trivers (1972) defined parental investment as “any investment by the parent that enhances the offspring’s chances of survival at the cost of the parents’ ability to invest in other offspring” (p. 139). Most often, females invest more in their offspring than do males (Trivers 1972). Males’ amount of obligatory investment to produce offspring (i.e., copulation) is minimal (in terms of energetically “cheap” sperm) relative to the amount of obligatory investment of females, which entails energetically “expensive” gametic production, gestation, lactation, and requisite care after birth (Trivers 1972). Accordingly, females’ reproductive rate is limited compared to males’ reproductive rate, given the number of offspring that a female can produce is limited by the length of gestation; males’ reproductive rate is only limited by the number of fertile females that they can copulate with. In species where females have the greater obligatory parental investment, they are the choosier sex during mate selection (Trivers 1972). In species where males have minimal obligatory parental investment and higher yet more variable reproductive potentials, they compete with one another for access to fertile females (Trivers 1972).

Although females are often the more investing sex, some species do exhibit substantive male parental investment. For example, humans are

considered to be among the less than 5 % of mammals that engage in some form of biparental care (Geary 2000). Men contribute to rearing children by providing resources and protection, educating them, and helping them to form social alliances, often within the context of forming a monogamous (or socially monogamous) pair bond with the mother (Geary 2000). Although paternal investment is not obligatory, there is evidence that when fathers invest in raising their offspring, they are increasing the probability that the child will survive to reproductive age. In pre-industrial societies, paternal investment is associated with a reduction in child mortality (Geary 2000). For example, in the Aché of Paraguay, the child mortality rate for children with fathers who take part in childcare is half the rate for children whose fathers are absent (Geary 2000). Pair bonding can also benefit men's continued sexual access to their partners. Accordingly, ancestral men who exhibited psychological and behavioral mechanisms that facilitated some degree of monogamy and biparental investment may have been more reproductively successful than those who did not, provided that the offspring they were investing in were indeed their own.

The Problem of Infidelity

Generally, infidelity is a problem because it signifies the dissolution of the relationship and the loss of the time, energy, and resources associated with attracting that mate. However, infidelity also poses different adaptive problems for men and women. For men, infidelity represents the possibility of cuckoldry, whereas for women, it signifies the potential for the man's resources to be diverted away from her and her offspring.

Paternity uncertainty. For women, fertilization is internal, guaranteeing that they are the mothers of their offspring. However, men cannot be certain that they are the fathers of their offspring; it is possible that another man could have copulated with and inseminated their mate. Cuckoldry refers to a man unwittingly investing his time and energy rearing offspring that he believes to be his own, but are in fact the offspring of

another man (Buss and Shackelford 1997; Trivers 1972). By raising a child that is not his, a man invests in offspring that do not possess his genes – investment that could instead be allocated to attracting a new mate and producing related offspring. Moreover, men can experience reputational damage when they are cuckolded which may reduce their desirability to prospective mates and further reduce their likelihood of producing offspring. Men experience more jealousy in response to a mate's sexual infidelity than an emotional infidelity, suggesting that they have developed mating strategies that function to alert them to potential cuckoldry.

Diversion of resources. For women, infidelity represents a different adaptive problem – the possibility that her mate may divert his resources away from her and her offspring toward a different woman (Trivers 1972). Losing men's parental investment results in women having to invest significantly more time and resources in order to rear their offspring, effectively reducing the amount of parental investment that each child receives (Trivers 1972). Women experience more jealousy than men in response to a mate's emotional infidelity, ostensibly because men who invest emotionally in another woman are more likely to defect or divert resources from their current relationship. Due to the substantial investment associated with attracting a mate and rearing offspring, it would follow that both men and women would have developed psychological and behavioral adaptations to prevent partner defection.

Jealousy as an adaptive emotion pertinent to mate retention. The prevalence of jealousy in both men and women suggests that infidelity was a problem that ancestral men and women experienced (Buss and Shackelford 1997). Evolutionary psychologists contend that the emotional experience of jealousy is adaptive because it signifies a threat to the relationship and it motivates behaviors geared toward preventing the mate from defecting from the relationship (Buss and Shackelford 1997). Today, male jealousy is frequently cited as a cause of their use of violence in romantic dyads. Jealousy might also relate to women's mate retention efforts. For example,

Arnocky et al. (2012) found that among heterosexual women currently in romantic relationships, jealousy predicted women's use of social aggression toward partners and peers and that physically attractive women reported being the targets of other women's social aggression most often, presumably because they constitute the greatest intrasexual threat to other women.

Why Engage in Costly Mate Retention Efforts?

In order to understand why individuals might engage in costly mate retention tactics, even in the absence of an absolute threat to the relationship, it is important to consider that human decision-making is sometimes biased, such that whenever the costs of errors from two different choices differ in their severity (in terms of reproductive fitness), individuals should be biased toward making the choice which minimizes the cost of the error (Haselton and Buss 2000). From an "error management" perspective, behaviors which might dissuade partners from defecting should be common among humans given the cost of engaging in such behaviors is often less than the cost of failing to maintain a desired pair bond (i.e., losing a reproductively valuable partner). Behaviors that are explicitly or implicitly aimed at maintaining a pair bond are commonly referred to as mate retention tactics. Mate retention tactics encompass a wide range of behaviors that individuals use to prevent partner infidelity and defection.

Taxonomy of Mate Retention Tactics

Conceptually, mate retention tactics can be divided into two broad categories: cost-inflicting behaviors and benefit-provisioning behaviors (Buss 1988). Cost-inflicting mate retention behaviors function to reduce partners' self-esteem and make them feel unworthy of the current relationship or to induce fear and social isolation, all of which might increase the probability of them remaining in the relationship. Conversely,

benefit-provisioning mate retention behaviors function to reduce the likelihood of partner defection by enhancing the partner's satisfaction with the relationship (Buss 1988). Mate retention tactics can also be categorized based on the individual to whom the behaviors are directed. Intrasexual manipulations are behaviors that are directed toward same-sex competitors and function to deter them from attempting to mate with the individual's partner. Intersexual manipulations are behaviors that are directed toward the partner which function to prevent them from straying from the current relationship.

Intrasexual manipulations. Mate retention tactics within this category include public signals of possession and intrasexual negative inducements (Buss 1988). Public signals of possession function to let same-sex competitors know that the individual they may be interested in pursuing is already in a relationship. These tactics include verbal signals of possession (e.g., introducing partner as their wife/husband or girlfriend/boyfriend), physical signals of possession (e.g., holding partner's hand in front of members of the same sex), and possessive ornamentation (e.g., giving partner jewelry to signify to others that they are in a relationship; Buss 1988). Intrasexual negative inducements involve the individual engaging in direct action toward same-sex competitors to deter them from attempting to co-opt their partner. These tactics include derogation of one's own mate to competitors (e.g., telling members of the same sex terrible things about partner so they would not be interested in them), intrasexual threats (e.g., yelling at an individual for looking at their partner), and violence (e.g., hitting someone who made a pass at their partner; Buss 1988).

Intersexual manipulations. Mate retention tactics within this category include direct mate guarding, intersexual negative inducements, and intersexual positive inducements. Acts of direct guarding involve closely monitoring the activities of a mate (Buss 1988). Within the category of direct guarding, there are several strategies including vigilance (e.g., calling a partner at unexpected times to find out what they are doing), concealment of mate (e.g., taking partner away from a social gathering where same-sex competitors are

present), and monopolization of their time (e.g., spending all of their free time with their mate; Buss 1988). Intersexual negative inducements sometimes function to lower the partner's self-esteem so that they do not feel worthy of the current relationship. Intersexual negative inducements include infidelity threat (e.g., flirting with others in front of partner), punishing a mate's infidelity threat (e.g., getting angry with partner for flirting), emotional manipulation (e.g., making the partner feel guilty about talking to members of the opposite sex), commitment manipulation (e.g., demanding a total commitment from partner), and derogation of competitors to one's partner (e.g., insulting same-sex competitors physical appearance in front of one's partner; Buss 1988). Finally, intersexual positive inducements function to increase the partner's satisfaction with the current relationship. They include resource display (e.g., giving gifts to partner), sexual inducements (e.g., giving into partners sexual requests), appearance enhancement (e.g., dressing nicely), emphasize love and caring (e.g., complimenting partner on appearance), and submission and debasement (e.g., doing whatever the partner wishes). The sexes use these tactics with different degrees of frequency and with varying degrees of effectiveness.

Men's Use of Mate Retention Tactics

Based on parental investment theory, men should use mate retention tactics that involve providing their mate with resources, because this would signify that they are able to provide for their mate and any offspring they may have with survival-enhancing resources (Buss 1988; Trivers 1972). In this manner, men are conforming some of their mate retention efforts toward fulfilling the mate preferences of women, who may themselves benefit from an expressed preference for men who are able to provide resources (Trivers 1972). Indeed, Buss (1989) found that across 37 cultures, women reported a stronger preference for resource-provisioning abilities in a mate than did men. In the Aché of Paraguay, a society of hunter-gatherers, men who are better hunters tend to have

greater reproductive success, demonstrating that women may use men's resource-provisioning ability when selecting reproductive partners (Kaplan and Hill 1985). Furthermore, women prefer to mate with men who are older than themselves because these men are more likely to be financially stable and capable of providing resources (Buss 1989). In Buss's (1988) seminal study on men's and women's use of mate retention tactics, men reported engaging in resource display, including acts of gift giving, more often than women. Men who engage in benefit-provisioning mate retention strategies sometimes give their partners gifts when they are trying to secure their commitment (Buss 1988). Men are more likely to offer gifts to their romantic partners than are women (Jonason et al. 2009). Gift giving is a strategy that some men may use when trying to prevent a mate from defecting from a relationship (Jonason et al. 2009). By providing partners with gifts, men may be enhancing their mate value because they are communicating to their partner that they are able to provide resources. Indeed, some research has shown that the probability and value of gift giving is related to indices of individuals' income (Garner and Wagner 1991).

Men who have higher mate value (indexed here by their annual income and status striving) are more likely to use benefit-provisioning mate retention behaviors than men of lower mate value, who tend to resort to using cost-inflicting mate retention strategies with greater frequency. Generally, mate retention tactics that are judged to be most effective for men fall into the category of benefit provisioning and include being kind, caring, affectionate, and complimentary, whereas tactics that are judged to be ineffective fall into the cost-inflicting category and include hitting one's partner and derogating them in front of others (Buss 1988). It is important to note that the frequency and type of mate retention tactics that men use are not static but are under the influence of environmental factors. Two such factors that influence men's mate retention behaviors are partner's attractiveness and partner's fertility.

Partner's youth and attractiveness. Although young and attractive women are highly desirable partners (Buss 1989), forming a relationship with

these women comes at a cost because they are highly sought after by other men and may be more likely to be unfaithful (Hughes and Gallup 2003). Women with lower waist-to-hip ratios (WHRs), a physical trait of women judged by men to be attractive, report cheating on their partner more frequently than do women with higher WHRs (Hughes and Gallup 2003). Moreover, women who perceive themselves to be more attractive than their partner are more likely to flirt with other men and are more resistant to their partner's mate-guarding attempts. Men may use their partner's youth and attractiveness as cues to assess the probability that they will be unfaithful. In support of this, men married to younger and more attractive women engage in more frequent use of mate retention tactics including concealing their partner, emotional manipulation, commitment manipulation, verbal signals of possession, and violence against same-sex competitors, compared to those men married to older and less attractive women (Buss and Shackelford 1997). Men mated to more attractive women also engage in more frequent in-pair copulation (IPC; i.e., they have sex with their romantic partners more often; Kaighobadi and Shackelford 2008). Kaighobadi and Shackelford (2008) suggested that men married to attractive women might copulate with them more frequently as a strategy to prevent them from being cuckolded. By frequently introducing sperm into their partner's reproductive tract, they are enhancing the probability that their partner's offspring are also their own (Goetz et al. 2005).

Partner's fertility. In humans, ovulation is largely concealed; however, there is some evidence that the frequency and intensity of men's mate retention behaviors are influenced by their partner's fertility (Gangestad et al. 2002). Women report that their partners were both more attentive and more proprietary near ovulation (i.e., in the late follicular phase of their menstrual cycle; Gangestad et al. 2002). Men engage in more expressions of love and affection and are more self-assertive when their partner is fertile (Gangestad et al. 2014; Pillsworth and Haselton 2006). The increased frequency and intensity of men's mate retention behaviors during the late follicular phase of their partner's cycles is logical

because this is when they are most susceptible to being cuckolded. In addition to being vigilant about the possibility of mate poachers (i.e., individuals who try and co-opt individuals from existing relationships), men must also be vigilant about their partners straying from the relationship. Women are most interested in engaging in extra-pair copulation (EPC) when they are fertile (Gangestad et al. 2014). This is especially true when women perceive their partner to be less attractive than themselves (Pillsworth and Haselton 2006) and may reflect a dual mating strategy whereby women try and obtain good genes from one man and resources and commitment from the other.

Women's Use of Mate Retention Tactics

Women's mate retention behaviors also align with parental investment theory (Buss 1988; Trivers 1972). Like men, women seem to conform some of their mate retention efforts toward satisfying the mate preferences of the opposite sex. For instance, men have developed a preference for cues to physical attractiveness, which may signal youth and fertility in a partner (Buss 1989; Trivers 1972). Across cultures, men consistently rate physical attractiveness as more important in a mate than do women (Buss 1989). Additionally, men tend to prefer women who are younger than themselves because these women have greater reproductive value (i.e., more childbearing years). Unsurprisingly then, women's mate retention behaviors are often focused on making themselves appear more reproductively valuable. Women, more than men, use appearance enhancement as a mate retention tactic (Buss 1988).

An alternative mate retention strategy for women involves flirting with other men in front of their partners to induce jealousy (i.e., infidelity threat). Partner's sexual infidelity is significantly more costly for men than for women as it can result in genetic cuckoldry. Women's infidelity threats may serve to make their partner experience sexual jealousy and engage in mate retention tactics to secure the relationship (Buss 1988). Mate retention tactics that are judged to be most

effective for women involve appearance enhancement (e.g., dressing nicely and wearing makeup; Buss 1988). Tactics that are judged to be least effective fall into the cost-inflicting mate retention category and include hitting one's partner and snooping through their personal belongings (Buss 1988). However, some research has shown that women may employ subtler forms of indirect or social aggression toward partners (behaviors such as "I try to make my romantic partner jealous when I am mad at him," "I give my romantic partner the silent treatment when he hurts my feelings in some way," and "I have threatened to break up with my romantic partner in order to get him to do what I wanted") and peers (behaviors such as "talked about others behind their backs," "excluded others from a group," "made other people not talk to others," and "been bitchy toward others") as a form of mate retention (Arnocky et al. 2012).

Partner's resource-provisioning ability. Women engage in more mate retention behaviors when their partners have higher incomes and have higher levels of status striving (Buss and Shackelford 1997). Specifically, women married to men with higher incomes reported engaging in more acts of vigilance (e.g., checking up on partner at unexpected times) and infidelity threat compared to women married to men with lower incomes (Buss and Shackelford 1997). Women have evolved to prefer men who are capable of providing their offspring with survival-enhancing resources (Buss 1989; Trivers 1972). Women might engage in mate retention tactics more frequently and with greater intensity when their partners are wealthy, because the cost of losing a valuable partner, who is capable of providing large amounts of resources, is significantly more detrimental than losing one who can provide meager amounts of resources.

Concurrent Mate Retention Tactics

Derogation of partner and partner violence. Concurrent mate retention tactics are tactics that are commonly used together when individuals are

trying to prevent relationship defection (Shackelford et al. 2006). Men who engage in more intersexual negative inducements (e.g., derogating partner in front of others), direct guarding (e.g., taking partner away from social gatherings where men are present), and intrasexual negative inducements (e.g., threatening same-sex individuals for looking at their partner) are also more likely to insult their partner as a mate retention tactic (McKibbin et al. 2007). Moreover, men who are more likely to use intersexual negative inducements, direct guarding, and intersexual negative inducements are also more likely to engage in acts of intimate partner violence (IPV) when they suspect that their partner has committed an infidelity (Kaighobadi et al. 2008). Furthermore, men who engage in mate retention tactics within the category of vigilance (i.e., frequently monitoring partner's activities) are more likely to commit IPV when they suspect infidelity (Kaighobadi et al. 2008). Men's use of IPV may function to (1) punish the partner, (2) discourage them from committing future infidelity, and (3) signal to same-sex competitors that they are capable of inflicting violence on others (Arnocky et al. 2015). To this end, IPV may represent the extreme of a cost-inflicting mate retention strategy that some men and women use when other mate retention tactics are unavailable to them or have failed to be effective at reducing the perceived probability of partner infidelity.

Forced in-pair copulation. Men who perceive that their partner has been unfaithful are also more likely to engage in forced in-pair copulation (FIPC; Goetz and Shackelford 2006). Men's use of FIPC and other acts of sexual coercion is related to their use of cost-inflicting mate retention tactics such as punishing mate's infidelity threat, emotional manipulation, derogation of competitors, and violence against rivals (Goetz and Shackelford 2006). When men suspect that their partner has been unfaithful, they may experience greater urgency to copulate with their partners (Goetz and Shackelford 2006). Their partner's resistance to copulating with them may signify that their partner has been unfaithful and may prompt men to engage in acts of sexual coercion including FIPC. Infidelity signals may cause men

to engage in acts of sexual coercion including FIPC as a means to introduce their own sperm into their partner's reproductive tract and/or to displace rival semen from their partner's reproductive tract (Goetz and Shackelford 2006).

Compensatory Mate Retention Tactics

Compensatory mate retention behaviors function to compensate for additional factors that increase the likelihood that a partner will commit infidelity or abscond from the dyad. Some of these factors include time spent away from the partner and the individual's mate value. As the proportion of time that a couple spends together decreases, the probability of a partner's infidelity increases (Baker and Bellis 1993). To reduce the chances of being cuckolded, men who had spent a greater proportion of time away from their partners since the couples last copulation reported (1) a stronger attraction to their partner, (2) that their partner was likely more attractive to other men, (3) a stronger interest in copulating with their partner, and (4) that their partner had an increased interest in copulating with them (Shackelford et al. 2002). Men's increased desire to copulate with their partner after a period of separation may function to introduce their sperm into their partner's reproductive tract and reduce the probability of their partner being fertilized by the sperm of a competitor.

To provide further support that men engage in compensatory mate retention behaviors after periods of partner separation, Gallup et al. (2003) found that men engage in semen-displacing behaviors (i.e., behaviors designed to displace rival's semen from their partner's reproductive tract; Gallup et al. 2003). Specifically, after periods of partner separation, men reported engaging in deeper and more vigorous penile thrusting during copulation with their partner (Gallup et al. 2003). When the penis is inserted deep into the vagina, the glands and coronal ridge may function to displace rival semen from the reproductive tract (Gallup et al. 2003).

Men's mate value also influences their tendency to engage in compensatory mate retention

tactics. Height is one characteristic that is closely associated with men's mate value. Taller men tend to be healthier and possess other cues associated with viability, such as low fluctuating asymmetry (Manning 1995). Subsequently, women report being more attracted to taller men. Shorter men in romantic relationships report greater levels of jealousy than do taller men (Brewer and Riley 2009). Furthermore, shorter men are less likely to engage in mate retention tactics that would jeopardize their current relationship than taller men are, perhaps because they are aware that since they had lower mate value, their partner would be more likely to defect from the relationship if they engaged in these behaviors (Brewer and Riley 2009). This suggests that individuals' own mate value influences the type of mate retention tactics employed.

Individual Differences in Mate Retention Tactics

Individuals who score high on the traits of the dark triad (i.e., psychopathy, Machiavellianism, and narcissism) are more likely to engage in cost-inflicting mate retention tactics, such as punishing mates' infidelity threat and violence against rivals, than are individuals who score low on dark triad traits (Jonason et al. 2010). Machiavellianism is a personality trait that is associated with distrust of others and a motivation to take advantage of others for personal gain. Individuals who score high on this personality trait tend to engage in more acts of direct mate guarding, suggesting that they are distrustful of their partners (Brewer and Abell 2015). Similarly, men who have low levels of emotional stability engage in more cost-inflicting mate retention tactics (McKibbin et al. 2014). These men may be hypersensitive to potential relationship threat. Conversely, individuals with high levels of honesty-humility are less likely to engage in mate retention tactics that involve manipulating or deceiving their romantic partners (Holden et al. 2014). Furthermore, men who score high on the agreeableness dimension of the five-factor model of personality tend to engage in more

benefit-provisioning mate retention tactics; these men also report greater interest in, and more time engaging in, oral sex with their partner (a form of sexual inducement). Women who score high on the conscientiousness dimension of the five-factor model of personality also engage in more benefit-provisioning mate retention tactics and report greater interest in, and more time spent engaging in, oral sex with their partner (Pham and Shackelford 2013).

Coalitional Mate Retention

Coalitional mate retention refers to tactics that individuals engage in to help prevent their friend's partners from defecting from the relationship (Pham et al. 2015). The tactics that individuals employ to help their friends include praise (saying positive things about their friend to his or her partner), vigilance (watching their friend's partner's behavior), therapy (repairing the relationship between the friend and his or her partner), monopolizing friend's partner's time (spending a great deal of time with the partner so they cannot spend their time with a same-sex competitor), and violence (performing acts of violence against friends' rivals; Pham et al. 2015).

When individuals engage in acts of coalitional mate retention, they may be behaving altruistically, since these behaviors do not provide them with any direct benefit. Perhaps engaging in acts of coalitional mate retention functions as a costly signal, because only mated individuals who feel as though their relationships are stable or single individuals who feel that they can easily attract a desirable partner are likely to allocate time and energy enhancing their friends' romantic relationships (e.g., Arnocky et al. 2014b). It could also be that acts of coalitional mate retention are a form of reciprocity (Boyd and Richerson 1989). Individuals who engage in acts of coalitional mate retention may expect the friends who they have aided to engage in acts of coalitional mate retention when they experience relationship threat (Boyd and Richerson 1989). Men are less likely to ask their male friends to engage in coalitional mate retention tactics which would

suggest that men commonly view same-sex friends as competitors (Pham et al. 2015). Requesting help from male friends may indicate that the partner is more willing to defect from the relationship, which may cause these male friends to engage in mate-poaching attempts (Pham et al. 2015).

Role of Emotion in Motivation of Mate Retention

The experience of anxiety may function to help men and women identify and solve adaptive problems (Buss 1990). Specifically, the experience of anxiety may promote corrective behaviors that aid in survival and reproductive success via the maintenance of social relationships (Buss 1990). The experience of social exclusion is detrimental to an individual's reproductive fitness; moreover, social exclusion is not arbitrary but motivated by the individual's interaction with group members (Buss 1990). One such group where exclusion is particularly harmful is the romantic dyad. Individuals have evolved adaptations in the form of emotional experiences to prevent infidelity and partner desertion. The emotional experience of anxiety and jealousy may function to identify relationship threat and motivate the individual to engage in behaviors to prevent or reduce the intensity of relationship threat. Individuals with high levels of anxiety may be hypersensitive to the threat of partner infidelity. Men who perceived greater risk of partner infidelity exhibit higher levels of self-reported anxiety and are more likely to engage in cost-inflicting physical, sexual, and psychological aggression toward their partners (Arnocky et al. 2015). Women with lower levels of self-perceived mate value (perceived physical attractiveness and value as a mate, relative to other women) are more likely to use cost-inflicting mate retention tactics such as flirting with other men and threatening to terminate the current relationship (Arnocky et al. 2012). These behaviors may function to lower their partner's self-perceived mate value and subsequently reduce the likelihood that their partner will defect from the relationship.

Environmental Factors That Influence Mate Retention Tactics

Operational sex ratio. Environmental factors such as proportion of viable mates available also affect the frequency and intensity with which individuals engage in mate retention behaviors (Arnocky et al. 2014a). Operational sex ratio refers to the number of fertile females in the population relative to the number of sexually active males. When men and women are primed to believe they are members of the abundant sex (i.e., they are primed to think that opposite sex individuals are scarce relative to the number of same-sex individuals in a population), they report more jealousy when imagining their partner flirting with an attractive member of the opposite sex and a greater willingness to engage in acts of intersexual negative inducements (e.g., calling the person a derogatory name or slandering them in front of others) toward that rival (Arnocky et al. 2014a). Men are also more likely to reduce their sociosexuality (indicating greater orientation toward maintaining a single partner) when they believe mates to be scarce relative to abundant (Arnocky et al. 2016).

Conclusion

Mate retention tactics function to prevent partner defection. Attracting and securing a mate often requires the individual to expend a great deal of time, energy and resources. Dissolution of a relationship signifies the loss of the time, energy, and resources associated with securing the partner. Partner infidelity is one of the foremost threats to a relationship and poses unique problems to men and women. Men's mate retention behaviors are designed to reduce the risk of cuckoldry, whereas women's mate retention behaviors are designed to prevent men from deserting them. Mate retention behaviors are not static, but vary in the type employed, the frequency, and intensity with which they are utilized, and are based on a wide range of factors such as the mate value of both the individual and their partner, partner's fertility level (in the case of women), the operational sex

ratio of the environment, and the presence of friends within the environment.

Cross-References

- Benefit Provisioning
- Coalitional Mate Retention
- Direct Guarding
- Fitness Benefits of Mate Guarding for Males
- Intimate Partner Violence
- Mate Retention
- Mate Retention Strategies
- Mate Retention Tactic

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Usefulness of Hyperactivity

- [Survival Advantages of ADHD Symptoms Based on Evolutionary Mismatch Approaches](#)

Utensil

- [Advanced Tools of Neanderthals](#)
- [Waterspouts \(Archerfish, Sharks, Rays\)](#)

Utilitarianism

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Synonyms

[Act-utilitarianism](#); [Consequentialism](#); [Rule-utilitarianism](#)

Definition

Utilitarianism is a consequentialist theory of ethics that promotes actions that tend to produce

the greatest amount of welfare or happiness and deems immoral those actions that tend to do otherwise.

Introduction

Although other philosophers have supported ethical theories with utilitarian considerations, Jeremy Bentham is considered to be the first to systematize an ethics based on utility (Shaw 1999). Bentham, and his supporters, hoped that their utilitarian approach would serve as a radical reforming of social, political, and legal institutions (1999). Other prominent proponents of utilitarian ethics include John Stuart Mill, Henry Sedgewick, and Peter Singer.

At the core of any utilitarian ethics, is principle of utility (also known as the greatest happiness principle). The greatest happiness principle posits the following: Any action that produces the greatest amount of welfare or happiness are right and those that tend to do otherwise are wrong. Historically, a number of methods have been used to put the evaluative principles of utilitarianism to work. Here, I will focus on two: (1) act-utilitarianism and (2) rule-utilitarianism.

Act- and Rule-Utilitarianism

Act-utilitarianism, as the label implies, focuses on an agent's particular actions and whether those actions produce the best consequences (1973). To bring this out, consider two varying cases of neighborliness. The first involves a neighbor who has a reputation for having a green-thumb, carrying the *good* intention of helping another neighbor with their garden. Although neighbor Greenthumb provides what she believes to be the best advice, her neighbor's garden ends up not going that well. And just to not complicate things, neighbor Greenthumb also partakes in the building and planting of the garden in addition to providing advice. Now, consider another case where neighbor Greenthumb wishes ill-will toward their neighbor and their general gardening

efforts (i.e., does not wish anyone else having a yard of juicy tomatoes and almost otherworldly beautiful rose bed), and decides to do her best to sabotage the garden in such a way where it is not quite obvious. But, despite her best efforts, the opposite ends up happening – the garden turns out to be a good one. An act-utilitarian would evaluate the actions, perhaps even begrudgingly, as having been wrong in the first case and right in the latter. This should make clear, generally, a clear distinction between consequentialism and its theoretical opposite deontology.

Now, one's response to this obviously counter-intuitive evaluative result is to appeal to an agent's adherence to a set of rules that tend to produce the best consequence or greatest amount of welfare. This is just what rule-utilitarianism attempts to do. For a rule-utilitarian, an action is judged "by the goodness and badness of the consequences of a rule that everyone should perform the action in like circumstances." Another way of putting this is that an agent's action will be deemed morally right or wrong based on its coherence to a set of rules that tend to improve welfare when followed. Going back to our example above, a rule-utilitarian would evaluate the actions of our two neighbors quite differently. In the case of the first neighbor, the rule-utilitarian would argue that although their actions did not result in the best consequences, they did adhere to generally accepted principles or rules that do tend to produce the best consequences, whereas the actions of our second neighbor will be judged as being in the wrong, given that it is inconsistent with utility-maximizing rules and principles.

There are primary reasons that proponents of utilitarianism have favored act-utilitarianism over rule-utilitarianism. First, as J.C.C. Smart posits, agents run risk of becoming rule worshippers. Rule worship can often produce bad consequences that might put into question an agent's decision to not make exception. One response to this is that these commitments should be considered akin to appealing to rules of thumb, which tend to be weaker. Thus, some exceptions are allowed. However, as agents continue to make exceptions, rule-utilitarianism will eventually dissolve into a commitment to one rule: act in such a way that our actions produce the

greatest amount of happiness. This, however, is just what act-utilitarianism demands. For these reasons, and others, act-utilitarianism is considered the more authoritative form.

The Psychology of Utilitarianism

Given the theoretical commitments of utilitarianism to well-being and welfare, it is only natural that psychology and neuroscience would have a few things to say about the practical implications of utilitarianism. One issue in the area of evaluating the merits of ethical theories concerns whether ethical theories ought to incorporate emotional inputs or whether they should be purely cognitive (derived from rational procedures). Now, both Kantian deontology and utilitarianism are theories that provide their own cognitive procedures to derive right actions. So, what question that can be asked is: which one is *more* or *actually* cognitive?

According to Joshua Greene, this debate can be better answered by the sciences by recognizing something Greene believes philosophers have failed to acknowledge: the terms "deontology and consequentialism refer to psychological natural kinds" (37, 2007). Relying on the moral dilemmas provided by Judith Jarvis Thompson (i.e., *the switch case* and *the footbridge dilemma*), Greene comes to conclude that the traditional responses to each case (to pull the switch and to not throw the person over the bridge) rely on different cognitive processes. Further, given our evolutionary development, we rely on our emotions when responding to dilemmas that require *up-close-and-personal* interactions (2007). This entails two things about the two approaches to moral decision-making. In the paradigmatic consequentialist decisions in the *switch case*, emotional response is low, whereas in the *footbridge case*, where paradigmatically deontological responses are given, emotional responses are high (2007). From these observations, Greene concludes that consequentialism is the more cognitive of the two theories. From this, given the commitment to cognitive theories, it follows that utilitarianism should be favored over no consequentialist ethical theories.

Conclusion

In this entry, I have presented utilitarianism as an ethical theory that is composed of three elements: (1) consequentialism, (2) hedonist/welfarism, and (3) impartial. The latter two commitments provide ample room for evolutionary psychologists to inform the sort of cost–benefit analysis proponents of utilitarianism favor. For example, evolutionary psychology can provide accounts of the sort of psychological natural kinds that are necessary to improving welfare. Further, it can give us an account of what sort of situations cause us to diverge from the normative demands consequentialism typically proscribes.

Cross-References

- [Charitable Giving \(Peter Singer\)](#)
- [Consequentialism and Suffering](#)
- [Evolution of Morality](#)
- [Harris’ Moral Landscape](#)

Morality

- [Science and Morality](#)

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Utility

- [Currency and Constraint](#)

Utility Attributes

- [Value Attributes](#)

Utilization of Complex Instruments

- [Advanced Tool Use](#)

Utopian Vision

- [Blank Slate, The](#)

Uxoricide

- [Partner Abuse and Homicide](#)
- [Partner Homicide](#)
- [Partner Killing](#)
- [Sex Differences in Death by Homicide](#)

V

Vagal Tone

- [Polyvagal Theory](#)

Vaginal Evolution

- [Evolution of Genitalia, The](#)

Vaginal Plug

- [Copulatory Plugs](#)

Vaginal-Penile Sex

- [Sexual Behavior](#)

Vagus Nerve

- [Polyvagal Theory](#)

Valuation Motive

- [Self-Enhancement Relative to Others](#)

Value Attributes

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Synonyms

[Decision attributes](#); [Option attributes](#); [Utility attributes](#); [Value features](#)

Introduction

Rational choice theory, the dominant theoretical paradigm in most social sciences, is a framework for understanding and often formally modeling social and economic behavior. Choice and utility are alternative normative foundational notions for rational choice theories in economics, political science, moral philosophy, and public policy. They are, to an extent, inter-derivable. If economic utility, or psychological value, is viewed as basic, then choice can be explained as aiming to maximize utility or value. If choice is viewed as basic, then a utility or value scale can be derived such that preferred options have higher utility. These derivations only hold given that certain consistency conditions, such as transitivity, hold in patterns of choice. Both choice- and utility-based normative (rational) theories of how people, governments, or societies should act come under

strain if these conditions are violated; to the extent that people's choices are not consistent, it is, after all, inevitably difficult to determine what they want.

This article discusses psychology and economics as typical examples of the rational choice approach. Rational explanation in psychology is very widespread, from rational analysis (Anderson 1990), expectancy-value theories in social and health psychology (Hewstone et al. 2007), ideal observer models, mental logics and probabilistic frameworks, evolutionary accounts, and informal "folk psychology" explanation of behavior in terms of beliefs and desires (Oaksford and Chater 2007). Other social science disciplines such as criminology, law, sociology, political science, and philosophy also use rational choice theory as their main theoretical framework (Elster 1986; Kreps 1990), and hence the arguments presented in this article apply to these disciplines too.

However, context effects in judgment and decision-making are widespread (Vlaev et al. 2011), causing inconsistent values and choices (e.g., preference reversals). Such effects violate rational norms and, therefore, undermine rational explanation of behavior. How can we accommodate striking examples of inconsistent preferences into more standard rational assumptions?

Context and Value

The central argument is evolutionary in nature. In particular, there is a fundamental problem with the conceptualization of the individual in psychology, behavioral sciences, economics, and public policy. This is the human evolved tendency to make local, contextualized inferences, which could lead to global inconsistency in behaviors across *contexts* (situations, domains, and environments). This seems to reflect an evolved, basic property of human cognition that applies right across psychology, from the basic psychophysics of sound perception right through to high-level cognitive processes in judgment and decision-making (see Vlaev et al. 2011).

The argument proposed here is that rationality assumptions typically hold *locally*, i.e., within a

context, but not globally across contexts. It is as if we have a big library in our heads, and we can only look at a few books at a time when we make up our mind on a specific issue. This view preserves the picture of humans as creatures striving to make sense of, and hold consistent beliefs about, the world and their behavior in it, which is exemplified in our need to hold noncontradictory beliefs. For example, when our behavior and our self-beliefs are in conflict, often it is our beliefs and attitudes that get adjusted – so they are consistent with our behavior (Festinger 1957).

The cognitive system may attempt to maintain local consistency, by following rational principles. If the information available to the "processor" is limited by processing resources, time constraints, motivation, and memory accessibility (Kruglanski and Gigerenzer 2011), then this process will still produce biased inferences – determined by what information is immediately available from the senses or from memory. For example, many *attribution biases* (Ross 1977) share the common tendency to overvalue dispositional (i.e., personality-based) explanations for the observed behaviors of others while undervaluing situational explanations for those behaviors. This interpretation makes sense locally unless we integrate evidence from our experiences on other similar situations, look for unseen causes and less-salient factors, ask oneself how one and/or most people would behave when put in the same situation, take into account the fact that we may unconsciously want to avoid regret and disappointment, and so on, which are all very costly and take time, and even then, it may not be properly integrated into the inference process because of attentional limitations and constraints on the amount of information we can hold in our working memory (Miller 1956). However, even though global information is hard to obtain and integrate, if people are able, or enabled, to do so, their inferences are likely to be accurate or rational (see Gilbert 2002).

Similar processes occur in other domains, such as affective forecasting, where people tend to overpredict the duration of affective reactions to future events, which is attributed to *focalism* – focusing too much on the event in question and

not enough on the consequences of other future events; but asking people to think about other future activities reduces the bias (Wilson et al. 2000). Buehler et al. (1994) found that people underestimate how long it will take them to complete future tasks – the so-called planning fallacy, which is explained by focusing too much on the future task and not enough on past experiences with similar tasks. However, bringing about unseen and unforeseen pieces of information, causes or consequences, can help people make less biased judgments in other domains such as probabilistic forecasting (Larrick 2004).

In essence, whatever information is currently or locally available determines judgments and decisions. This process can initially rely only on sampling external information. For example, Bem's (1967) *self-perception theory* proposes that we form our attitudes, opinions, and other internal states by observing our behavior and concluding what attitudes must have caused them. The theory suggests that people induce attitudes without accessing internal cognitions and moods, which is done by reasoning about one's own overt behaviors rationally in the same way a person attempts to explain others' behaviors (Robak et al. 2005). Thus, instead of endorsing "global" beliefs and attitudes about what is universally good or just for them, humans tend to engage in local, situational inferences. Naturally, after many repetitions in various contexts, such attitudes might become universally endorsed, partially due to enhanced memory traces, but this can hardly apply to most everyday occasions where attitudes are expressed in decisions and behaviors.

What is known as the *bounded rationality* paradigm (Simon 1992) also proclaims that the sophisticated calculations invoked in decision theory and economic analysis are known to be beyond the computational powers of the brain. The argument proposed here goes beyond in deriving some universal implications for most descriptive models of decision-making, which leads to the core principle that decisions are relative, in a specific way, to what is embedded in the local context. This view has implications for certain rational choice-based disciplines, such as economics where people are assumed merely to have

ordinal preferences between outcomes – they are assumed *not* to assign *cardinal* values to outcomes (Cooter and Rappoport 1984). The assumption is that people prefer fish to salad; but that they have no grip on *how much* they prefer fish to salad; they do not know, for example, whether they prefer fish to salad more or less than they prefer steak to pasta. The view proposed here implies that the practice in many areas of economics is supported, rather than undercut, by psychological results, but only as long as the context (set of alternative choice options) does not change drastically. If the context *does* change, then this preference ordering may reverse (so that salad is preferred to fish). Indeed, there is evidence that behavior is consistent *within* contexts even though it is globally unstable when behaviors across different context are considered (see Ariely et al. 2003). People seem to be able to have *locally ordinal* (stable and consistent) preferences between outcomes within a particular context. Therefore, economic theory's ordinalist assumptions are implausible only when single utility function is used to model choice behavior across different contexts, in order to create a global preference ordering.

Context and Decision-Making

If humans evolved to represent utility, or attribute values, by making local, contextualized inferences, then there should be no fixed zero point on the utility/value scale, and the utility will shift depending on the context provided by the other available options. A number of experiments have investigated the effect of the context on decision-making. For example, researchers have repeatedly found that the attributes of the previously or currently seen choice options (e.g., risky prospects) influence the decisions about a current option, which suggests that options are not considered independently (see Vlaev et al. 2011, for a review of the evidence). Note that existing models of rational choice are typically based on the underlying assumption that only the attributes of the choice option need be considered when reaching a decision.

Stewart et al. (2003) report similar demonstration of local, contextual consistency in an experiment where participants were given a set of four options as possible certainty equivalents (CE) for a series of prospects. Participants were asked to decide on a CE for the prospect and then select the option closest to their estimate. For each prospect, the CE options were either all lower in value or all higher, but choices were rank correlated across contexts: those who choose low options in one context also choose low options in the other context. Therefore, there is consistency between the choices within a particular context, i.e., people are *locally ordinal*.

These experiments are also based on an account that assumes that when people judge the attractiveness, and thus their preferences for a choice option, they do so by comparing each option with other options, instead of matching it against some stable internal scale for absolute judgment. If absolute judgments are impossible, because judging by how much one alternative is better/worse than another changes depending on the other cognitively available alternatives, then the *only* reliable judgments that individuals can make are ordinal judgments, i.e., that one option is *better* or *worse* than the other, without necessary being able to say by how much. This is because such judgments will not be informative and useful in permanently changing contexts and limited ability to retrieve/obtain and process all relevant information on time. As a result, the best a decision-maker can do is to rank order the available choice options on each attribute and thus to construct an ordinal scale (see Stewart et al. 2006, for a formal model). Thus, cognitive agents can only make inferences about the attribute value of options by simply counting how many times each option is better or worse than another (e.g., the option that has never been worse off is obviously the best one to take).

Such evidence presents another challenge to the standard rational choice theory but also challenges descriptive theories of decision-making under uncertainty, including *configural weight models* (Birnbaum et al. 1999), *prospect theory* and *cumulative prospect theory* (Kahneman and Tversky 2000), and *rank-dependent utility theory*

(Quiggin 1993), which all assign a choice option, such as a risky prospect, with a value or utility that depends only on the attributes of that option.

Conclusion

To conclude, in the face of existing evidence, human evolved rationality is best interpreted as a rather local, instead of global, phenomenon, i.e., rationality assumptions typically apply locally, within a context. But, if the distribution of contexts across individuals is reasonably stable, then this could create stable overall behavior. As a result, most of the time, markets behave stably, and behaviors can look stable and consistent. Such stability is not guaranteed, as we have seen, if the context changes significantly (e.g., if new goods become available, or the market receives an exogenous shock, such as a supply shortage or a sales tax increase). This article shows how the standard focus in rational choice theory on consistency can also be derived out of knowledge of basic, evolved cognitive mechanisms underlying decision-making.

Cross-References

- [Cost-Benefit Analysis](#)
- [Positive and Negative Reinforcement and Punishment](#)
- [Psychological Mechanisms](#)
- [Risky Behavior](#)
- [Utilitarianism](#)

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Value Features

► Value Attributes

Vampire Bat Food Sharing

► Blood Sharing by Vampire Bats

Vanity

► Narcissism

Variability of Aggression

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Synonyms

Individual differences in violence

Definition

Variability of aggression: human aggressive behavior varies on a number of dimensions. This variability is best understood through an interdisciplinary evolutionary approach.

Introduction

In one of the first assessments of the potential contributions of evolutionary psychology to the study of aggression, David Buss and Todd Shackelford (1997) propose an account of human aggression arising as the result of adaptive mechanisms that evolved in response to various challenges of social living. Buss and Shackelford point out that the perspective of evolutionary psychology reveals aggression to be multifaceted and to involve several underlying mechanisms responsive in varying contexts. As they say, their account predicts variability in aggression. There are several dimensions to this predicted variability. There is sexual dimorphism in human aggression, some populations are more aggressive than others, and there is variation in types of aggressive behavior in a given circumstance. The advantage to an evolutionary psychology approach is that it predicts the manifest variation in human aggressive behavior. Many alternate psychological accounts of aggression do not have the resources to account for this variation. The disadvantage to the evolutionary psychology approach outlined by Buss and Shackelford is that it does not provide explanatory leverage over local and specific cases of variation, such as three individual men's different responses to their spouse's infidelity, and it does not adequately explain why in some cultures violent behavior is required for social status, whereas in others such behavior leads to reputational damage (cf. Buss and Shackelford 1997, p. 617).

Evolutionary theory, broadly construed, provides many resources to account for variation in phenotypic traits, so an evolutionary approach to variability of human aggression holds promise. Evolutionary psychologists have adopted approaches that downplay, underplay, or ignore human phenotypic variation, and this is rightly seen as a problem (Cf. Confer et al. 2010). Human aggression takes many different forms – from subtle, nonviolent covert aggression in the work place, to violent physical aggression at a sporting event, and to deadly political aggression designed to facilitate social change. This entry reviews some work on three examples of human aggressive behavior: male-on-male aggression

within cultures of honor, female-on-female aggression, and intimate partner violence involving aggression toward the other member of a close relationship. All three cases present a great deal of variation, and explaining this variation is a task for any evolutionary science of human behavior. The varying evolutionary hypotheses for the relevant variation in each of these examples of human aggression are presented and contrasted, where applicable, with alternate accounts of the relevant variation. An evolutionary approach to human aggression is productive and useful, but proposed here is a broader-based interdisciplinary evolutionary approach than evolutionary psychology traditionally construed.

Male-on-Male Aggression in Cultures of Honor

A young man walks down a hallway at a large public university in the United States. As he reaches a narrow point in the hallway, another young male bumps the first and calls him an “ass-hole.” How does the bumped and then insulted young man respond? According to Dov Cohen, Richard Nisbett, and their colleagues, it depends. In particular, it depends on whether the young man is from the North or from the South in the United States. Cohen and Nisbett, in a series of experiments, set up just such a scenario where the first young man was a research participant and the second was a member of the research team in order to examine how young men from different geographic backgrounds responded to such an affront. While men from the North tended to respond to the bump/insult with amusement and little else, men from the South tended to respond with anger, and they also became more stressed (measured by increased cortisol levels) and more inclined toward future aggression (measured by increased testosterone levels) (Cohen et al. 1996).

Why? Why would young men from the South on average respond differently to a perceived slight than young men from the North? According to Cohen and Nisbett, the explanation comes from the presence/absence of a culture of honor, where adherents to a culture of honor are more inclined

toward responding aggressively to reputational affronts. A culture of honor, in turn, is more widespread in the South than it is in the North because of the different cultural-geographic-economic histories of those two regions. While the densely populated North brought with it readily available law enforcement that could quickly deescalate aggressive interactions, the more pastorally dispersed South meant law enforcement was often unavailable during aggressive encounters. So while Northerners grew accustomed to brushing off perceived slights because their personal resources were not threatened as long as law enforcement was nearby, Southerners developed a heightened response to perceived slights because their personal reputation for not tolerating challenges was the more immediate protection against threats to personal resources.

Shackelford (2005) explains the North-South group difference documented by Nisbett and Cohen with resources from evolutionary psychology. All men, Shackelford proposes, have an *evolved reputation maintenance mechanism*, which dictates how men respond to reputational challenges in an adaptive manner. That mechanism, however, is context sensitive because different responses are more/less adaptive depending on context; in particular, a contextual feature like the local economy will influence the threshold that must be met to respond to reputational challenges with aggression. Applied to the North-South group difference, the idea is that Northern and Southern men both possess the evolved reputation maintenance mechanism, but the unique economic history of the South (at least in comparison to the North) led to a lower threshold for triggering an aggressive response to reputational challenges because it was more biologically advantageous to respond as such.

Shackelford's appeal to evolutionary psychology, however, is not the only evolutionary explanation of the North-South group difference. As Stefan Linquist (2016) details, there are several other evolutionary explanations. A memetic explanation appeals to a purely cultural transmission of the trait in question. On a memetic reading, the culture of honor and its associated response to aggression are culturally transmitted in the South

regardless of any biological advantage; in short, it is the *culture* of the culture of honor that propagates the phenomenon long after the South has by and large abandoned a pastoral economy. Alternatively, there are also evolutionary explanations that employ interacting biological and cultural variables. Dual inheritance theory combines biological variables (i.e., genetically inherited predisposition) with autonomous cultural variables (i.e., socially learned behaviors), whereby each variable shapes the other. In contrast to the evolutionary psychological explanation, which takes the universal psychological mechanism to be triggered by some environmental exposure, the dual inheritance explanation takes the biological and cultural variables to coevolve.

It is important to keep in mind that all of the evolutionary explanations of the North-South group difference mentioned above are focused on explaining just that – the *group* difference, which is a difference between the averages of the individuals within the groups. But these group averages mask individual differences within the groups; not every Southern man responded to the insult with aggression, and some Northern men did respond with aggression. If, as is widely acknowledged, variation is a thing to be explained, then individual differences within group averages point to additional sources of variation that must be identified and incorporated into the explanations of the variation.

Female-on-Female Aggression

Aggression researchers have traditionally endorsed the view that men are more aggressive than women. This position is bolstered by the abundant evidence that men commit more murders than women and engage in more violent acts than women, such as assault (see, e.g., Daly and Wilson 1988). Work by researchers such as Anne Campbell (see, e.g., Campbell 1999) reveals that this is not the whole story on differences between male and female aggressive behavior. There is plenty of female same sex aggression that does not manifest in violent acts. Bjorkqvist et al. (1992) found that women are much more likely

than men to engage in aggressive acts such as excluding and spreading false rumors. For example, young women from many different cultures attack other women's sexual reputation and defend their own sexual reputation. Women and girls in many cultures label those perceived as promiscuous "slags," "tarts," or "whores." Such attacks involve verbal, indirect, or relational aggression. Adolescent girls are also involved in direct acts of violence, and these are much more likely to be directed at other girls or women.

A group of 15-year-old school girls are presented with a vignette describing another girl's exclusion by her friends and overhearing her friends "bitching" about her. Girls presented with the vignette were asked about the behavior, answering questions about whether it was common and whether or not it was hurtful. The girls reported that exclusionary behavior and "bitching" were extremely common. On exclusion, one participant said that when a girl approached them crying and seeking sympathy, other group members said "Don't let her in, 'cause she's a bitch and she spread rumors about us and everything. The last group she was in was our group" (Owens et al. 2000, p. 76). When asked how long ostracism can last, girls reported that cases can last three school terms, leading to a miserable existence for the victim. There is no question in the girl's minds that these exclusionary acts are hurtful to the victims. Such indirectly aggressive acts are widespread among teenage girls more so than direct acts of aggression such as tripping and slapping (Owens et al. 2000, p. 77). Teenage boys are more likely to engage in direct acts of aggression than their female counterparts (see, e.g., Bjorkqvist et al. 1992).

Why the difference in aggressive behavior in girls and boys? Many social science researchers attribute the differences to differences in social relations reinforced by socialization. Girls value intimate relations, whereas boys associate in larger groups and are more concerned with physical prowess and dominance relations (cf. Owens et al. 2000). In contrast, evolutionary psychologists, along with other evolutionary social scientists, argue that sex differences in aggressive behavior are grounded in biology. Much

evolutionary work on women's intra-sexual aggression characterizes the behavior as resulting from sexual competition or resource competition (Campbell 2013). Much male aggressive behavior is also attributed to resource competition or sexual competition, so the fact that the women's aggressive behavior is more likely to be indirect needs further explanation. The differences in type of aggressive behavior are accounted for by broader evolutionary theorizing about sex and reproduction (Campbell 1999, 2013). For example, differences in male and female parental investment lead to predictions that women will engage in less physically risky behavior than men, as they need to preserve their physical resources to tend their offspring (see, e.g., Taylor et al. 2000). It is important to note that such explanations are evolutionary and should be understood in terms of ancestral women's behavior and the selection pressures that shaped it rather than as proximal explanations of contemporary women's behavior.

Accounting for sex differences in aggressive behavior in terms of differential parental investment (among other mechanisms) only goes so far. First, the differences in aggressive behavior between men and women are not clear-cut. As noted above, Bjorkqvist's (1992) initial finding that there is a large difference between male and female aggressive behavior has been challenged (see, e.g., Archer 2004), leaving us with a picture of much more continuous variation. Second, there is clear variation within groups of women and men. Finally, there are cultural differences in women's intra-sexual aggression. Such variation could be addressed from an evolutionary perspective, but more theoretical resources are required than parental investment theory.

Male-on-Female Intimate Partner Violence

Intimate partner violence involves behaviors that cause physical, psychological, or sexual harm to other member(s) of a relationship; examples include hitting, forced sexual intercourse, intimidation, humiliation, and restricting access to financial resources (with multiple forms often

co-occurring). Women are most often the victims of intimate partner violence, and men are most often the perpetrators; in a WHO survey of ten countries, percentages of ever-partnered women who reported sexual violence by a partner at some point in their lives ranged from 6% in Serbia to 59% in Ethiopia (Organization 2012).

As the difference between women in Serbia and women in Ethiopia mentioned above reveals, there is a great deal of variation in intimate partner violence. Personal, relationship, and societal factors can all affect rates of intimate partner violence; low education is a personal risk factor both for being a victim of intimate partner violence and for being a perpetrator of it; economic stress and dissatisfaction with the relationship itself are both relationship-level risk factors; and societal factors include weak legal and social sanctions against intimate partner violence (Organization 2012). One societal factor that was discussed earlier within the context of male-on-male aggression and which is also relevant to intimate partner violence is a culture of honor. Researchers have repeatedly found that increased identification with a culture of honor coincides with increased tolerance for violence against partners; this increased tolerance is found in both the women and the men of the culture of honor societies (Vandello and Cohen 2003).

Intimate partner violence has long been on the radar of evolutionary psychologists. Indeed, in Buss and Shackelford's early review of human aggression, it was one of the seven adaptive problems for which they pointed to aggression evolving as a solution; the idea there was that male-on-female intimate partner violence was a product of jealousy and that emotion evolved in order to deter long-term mates from sexual infidelity (Buss and Shackelford 1997). Buss and Shackelford's explanation in part built off the earlier work by Buss and his colleagues on sex differences in jealousy; in species with internal female fertilization, males are challenged by uncertainty concerning the paternity of their offspring such that there is a risk that they invest significant resources in the care of offspring that are not their own, and so men's jealousy is directed more toward sexual infidelity, as opposed

to women whose jealous responses are primed more by emotional infidelity (Buss et al. 1992). The evolutionary psychology explanation of intimate partner violence, then, is that it is the result of jealousy, which is itself the product of an adaptive response to the problem of paternity uncertainty (Kaighobadi et al. 2009; Wilson and Daly 1996). The variation in intimate partner violence is in turn captured by way of the context sensitivity of the adaptive jealousy; it is deployed selectively depending on various personal, relationship, and social factors (Buss and Duntley 2011).

As with the discussion of male-on-male aggression earlier, however, the evolutionary psychology explanation of intimate partner violence is not the only evolutionary explanation available. Above, recall, Linquist (2016) also considered memetic and interactionist explanations, and similar considerations are relevant here. A memetic explanation of intimate partner violence draws attention to the culturally inherited features that contribute to the phenomenon. For example, Archer points to differences in gender empowerment as a prime societal factor that affects the prevalence of physical intimate partner violence in a culture: looking across a range of nations, as gender equality increases, the rate of female victims of intimate partner violence decreases, and the rate of male victims of intimate partner violence increases (Archer 2006). The memetic explanation here appeals to the culturally inherited social roles that men and women find themselves in and which dictate the social constraints under which they can behave in a society. A dual inheritance theory of intimate partner violence is worth considering too; the idea would be that some biological variable(s) such as inclination toward jealous aggression and some cultural variable(s) such as widespread societal tolerance for gender inequity coevolve.

Much of the research on intimate partner violence focuses on identifying between-group variation (usually at the nation level) and then seeks out group differences (such as prevalence/absence of a culture of honor or differences in gender equality) to explain that variation. But as with the previous two examples, within-group

variation is also striking and important to both highlight and explain. Within-group variation points to additional causes of the phenomenon in question that cannot be attributed to either universal psychological mechanisms or to cultural-wide factors alone. A striking example of this comes from Vandello and Cohen (2003), who discuss differences in perceptions of women's honor in Saudi Arabia, where it was found that concern with women's honor was most pronounced at the very highest and very lowest socioeconomic levels; a focus on traditional extended family arrangements is most important at the highest and lowest levels of the social hierarchy in Saudi Arabia but less so among the middle strata of that society, and so it was this unique and local factor that produced a bimodal distribution within just one society.

Evolutionary Approaches to Variation in Aggressive Behavior

There is clearly variation in human aggressive behavior. The cases above illustrate variation in specific types of aggression between different geographical groups and between men and women. Evolutionary psychologists, as well as other evolutionary social scientists, reject many purely cultural accounts of human behavior, such as aggression, arguing that evolutionary approaches are superior. Campbell typifies this approach when she says "the psychology of aggression, prior to the advent of an evolutionary perspective, was often a fragmented and incoherent enterprise. [...] Evolutionary theory provides a coherent way of thinking and talking about aggression in functional terms" (2005, p. 646). There is less agreement about the role of evolutionary thinking in accounting for *variation* in behavior. Some evolutionary psychologists see evolutionary approaches to accounting for variation as outside their purview: "Behavioral geneticists, through twin studies and comparisons of kin raised together and apart, explore the extent to which *differences* between individuals are accounted for by *differences* in their genes. [...]. In contrast, evolutionary psychologists primarily

explore the design of the universal, evolved psychological and neural architecture that we all share by virtue of being human" (Tooby and Cosmides 2005, p. 39), where others, such as Shackelford (2005), clearly take variation in behavior to be amenable to evolutionary explanation and take evolutionary psychology as having an important role to play in explaining such variation.

As noted above, Lindquist (2016) lays out several evolutionary approaches to account for variation in male-on-male aggression in and outside cultures of honor. He adds dual inheritance theory (gene-culture coevolution) and cultural niche construction to evolutionary psychologists' preferred adaptive mechanism approach. There are many more evolutionary approaches to accounting for human behavioral diversity and hence variation in aggression. Gillian Brown et al. (2011) present alternate evolutionary approaches to human behavioral diversity including those mentioned here but adding human behavioral ecology and different approaches based on the study of genetic diversity. While Tooby and Cosmides (2005) appear to want to distance evolutionary psychology from behavioral genetics, a more encompassing evolutionary approach to variation in human behavior would include as many evolutionary resources as possible. Behavioral geneticists provide many tools for examining human variation and variation in human aggression in particular. Ian Craig and Kelly Halton (2009) assess research to date on the genetics of human aggression, and while they find little evidence for genetic loci with major effect size, they offer helpful explanations of variation in human aggressive behavior in terms of gene/environment interactions (see Tabery 2014 for a detailed discussion of gene/environment interaction and human aggressive behavior). While some evolutionary psychologists defend the view that evolution only produces uniformity or universality of traits, many evolutionary theorists present and defend accounts of the evolution of variation. For example, John Maynard Smith used aggression as a case study in his models of selection for variation in behavior (Maynard Smith and Harper 1988). There are

many other examples of evolutionary processes leading to variation such as disruptive or diversifying selection, heterozygote dominance, and selection for phenotypic plasticity (see, e.g., Pavlicev et al. 2011).

Conclusion

An interdisciplinary approach to accounting for variation in human aggressive behavior is recommended here (cf. Brown et al. 2011; Longino 2013). Here is a sample of the relevant disciplines: anthropology, endocrinology, evolutionary anthropology, evolutionary psychology, and sociology. Such an approach takes on board a wide range of evolutionary thinking but also allows for purely cultural accounts of some variation in aggressive behavior where the evidence best supports such accounts. At this juncture there appears to be little to be gained from ruling out any evolutionary approaches to accounting for variation a priori. The examples of variation in aggressive behavior discussed above could be amenable to a number of evolutionary explanations, and several alternate evolutionary explanations could work together to account for the relevant case. There are debates between researchers on the evolution of human behavior from different theoretical backgrounds, for example, evolutionary psychologists and behavioral ecologists disagree over the appropriate evolutionary approach (see, e.g., Downes 2001). Such disagreements need not necessarily disrupt an interdisciplinary approach. As Brown et al. (2011) reveal, many researchers who appear to be at odds can easily accommodate each other's evolutionary approaches as illustrated by Hillard Kaplan and Steven Gangestad's (2005) combination of evolutionary psychology and life history theory.

An obvious objection here is that the evolutionary psychology approach, involving an adapted mechanism and its differing responses to different environmental or cultural conditions, provides all the explanation required for variation in aggressive behavior. This approach appears to load too much onto cultural context where some

variation could be explained by alternate evolutionary means. For example, explanations of variation in female-on-female aggression appeal to mechanisms underlying sexual and resource competition and the different ways these mechanisms are evoked in different cultural circumstances. Such an approach could be usefully supplemented with a gene/environment interaction or a cultural niche construction approach, depending on where the evidence leads. These further explanations may not exhaust the variation in question and may require supplementation from endocrinology and so on (see, e.g., Cashdan 2008 on variation in women's waist/hip ratios). As revealed in the discussion of alternate ways of accounting for variation in culture of honor aggression, appealing to evoked culture can prematurely close the door on alternate evolutionary explanations of the relevant variation (cf. Linquist 2016). An interdisciplinary approach is preferable to an attempt to force one type of evolutionary explanation on a wide diversity of evidence.

Cross-References

- ▶ [Boys Bully More Than Girls](#)
- ▶ [Culture of Honor and Retaliation](#)
- ▶ [Homicide](#)
- ▶ [Individual Differences](#)
- ▶ [Lethal Violence](#)
- ▶ [Male Adaptations to Assess Fighting Ability](#)
- ▶ [Men Riskier, More Aggressive](#)
- ▶ [Men's Suspicions of Partner Infidelity and Women's Defection](#)
- ▶ [Meta-Analysis of Sex Differences in Aggression](#)
- ▶ [Morbid Jealousy](#)
- ▶ [Most Perpetrators are Men](#)
- ▶ [Paternity Uncertainty and Father-Offspring Conflict](#)
- ▶ [Peer Pressure](#)
- ▶ [Physical Aggression](#)
- ▶ [Psychopathy](#)
- ▶ [Reputation as a Context for Men's Aggression Against Men](#)
- ▶ [Same-Sex Homicide](#)
- ▶ [Same-Sex School Bullying](#)
- ▶ [School Bullying](#)

- ▶ Sex Differences in Aggression
- ▶ Sex Differences in Intimate Partner Violence
- ▶ Sex Differences in Same-Sex Aggression
- ▶ Tactics to Solve Adaptive Problems of Sperm Competition
- ▶ War

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Variable-Interval Schedule

► [Reinforcement Schedule](#)

Variable-Ratio Schedule

► [Reinforcement Schedule](#)

Variance in Female Reproductive Success

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Synonyms

[Reproductive fitness](#)

Definition

When some females in a population have more surviving offspring than other females in the population.

Introduction

Variance in reproductive success occurs when some individuals in a community have more surviving offspring than others and is typically discussed as a result of sexual selection (Trivers 1972). Sexual selection is a competition within one sex for sexual access to members of the opposite sex and a differential choice by members of one sex to breed with particular members of the opposite sex. The traditional view among evolutionary biologists is that males compete against each other for access to females, and females are

coy and choosy in determining who they will mate with. In his experiments with *Drosophila melanogaster*, Bateman (1948) provided evidence for these conjectures and also showed that male reproductive success varied much more than female reproductive success. That is, many more males than females produced zero surviving offspring. This trend has been found in a number of mammalian studies since then (e.g., Clutton-Brock 1988).

Constraints on Reproduction

One explanation for the trend has to do with biological constraints faced by each sex (Williams 1966). For male mammals, production of sperm is relatively unlimited and energetically cheap. Also, necessity of males to the reproductive process ends after the deposit of sperm in the female. The result is that male reproductive success is limited only by the number of mates one male can acquire. Mammalian females face much greater biological constraints than males. First, production of eggs is energetically much more costly than production of sperm. And second, the number of eggs a female produces in her lifetime is limited at birth. Third, the time required for gestation makes up a significant portion of females' adult life span, and gestation is energetically very costly. Lactation also requires investment of time and energy that males are not encumbered with. Therefore, female fertility is time and energy limited, and the result is that the total number of offspring one female could have in her lifetime is far fewer than the total number one male could have in his.

Of course, a number of factors mitigate these constraints for both males and females, including individual reproductive viability, the operational sex ratio (OSR) of a group, and a group's social structure. The OSR is the ratio of males to females who are ready to mate in a population at a given time (Emlen and Oring 1977). A male-biased OSR (one with more males ready to mate than females) will restrict the number of mates

available to males and will result in some males not mating and others mating polygynously. Monogamy is another mitigating factor, which limits a male's lifetime reproductive success to his female partner's reproductive potential and often results in extremely low variance for both partners.

In traditional human populations, most mating occurs within socially sanctioned marriages, and the marriage systems practiced in any given society can either be biologically imposed – by the OSR or by the resource availability in environments – or socially imposed. One common response to excess women in a group is polygynous marriage and increased variance in male reproductive success. When there are excess men in a group, polyandrous marriage is sometimes a response (Starkweather and Hames 2012), but societies often come up with other solutions for having more men than women in a population like sending those men to war or the priesthood.

Female Multiple Mating and Reproductive Variance

Sarah Hrdy (1980) challenged the idea of the “coy female” when she observed female langurs mating with males outside of their own group. Hrdy (1980) suggests that females across species use multiple mating as a way to improve their own reproductive fitness, and evidence certainly exists in support of this hypothesis (e.g., Jennions and Petrie 2000). The question is, though, if multiple mating for males results in variance in male reproductive success does multiple mating for females result in variance in female reproductive success with some females not mating at all and those who mate multiply having more offspring than those who mate singly.

There is some evidence from the animal world that suggests multiple mating by females does result in more variance in female reproductive success (see Clutton-Brock 1988). Among human females, multiple mating can occur via serial monogamy, extramarital affairs, or polyandrous marriage. Evidence from societies practicing serial monogamy shows levels of variance for

men that is closer to polygynous societies than monogamous, suggesting that some men monopolize multiple women. This number may be misleading, though, because as Brown and colleagues (2009) point out, both men and women in serially monogamous couplings are mating with multiple partners. Among women who participate in extramarital affairs, it can be difficult to study variance based on these matings because women in many cultures do not discuss these socially unacceptable relationships. One society for which reproductive success is being studied in relationship to extra-pair affairs is the Himba of Namibia. Though variance is not specifically examined, Scelza (2011) shows that women who have extra-pair births tend to have more births in total over the course of their lifetimes.

It is also unclear to what extent polyandrous unions result in increased variance in reproductive success for women. From a biological standpoint, women in polyandrous marriages should not have any greater reproductive success than women in monogamous marriages, because the marital unit is limited by the woman's reproductive ability in both cases. We do know that additional husbands (or fathers, depending on the society) can help keep children alive in some Amazonian cultures where partible paternity is practiced (e.g., Beckerman et al. 2002), which enhances women's reproductive success. However, what does not seem to be true among societies that allow polyandry is that some women in the society do not marry or reproduce at all. This is probably due to the facts that (1) in nearly all societies where polyandry is allowed, monogamy and polygyny are also practiced and (2) for most societies that allow polyandry, it is not the most common form of marriage nor is it the most preferred (Starkweather and Hames 2012). It is particularly interesting that in one of the cases where polyandry is the most common and most preferred form of marriage – in Humal, Nepal – some women do not reproduce at all, others do not reproduce until later in life, and those who marry polyandrously at an early age have the highest reproductive success, therefore accounting for a great deal of within society variance in women's reproductive success (Haddix 1999).

Conclusion

The few human examples offered here suggest that it is indeed possible for women's reproductive success to vary within societies. In some cases, women in certain circumstances can have many more surviving children than women in other circumstances. Across traditional societies what does seem uncommon is for women who are reproductively viable to not reproduce at all. Restricting some women from reproducing appears to only happen rarely and when it is socially sanctioned. More research needs to be done on the conditions that allow some women to out-reproduce others as well as on the reproductive benefits for women engaged in multiple mating to fully understand how and when greater levels of variance in women's reproductive success occur.

Cross-References

- [Intersexual Selection](#)
- [Polyandry](#)

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Variance in Reproductive Success

- [Robert Trivers](#)

Variant

- [Genetic Predispositions](#)

Variant Sexuality

- [Paraphilia](#)

Variation

- [Observations of Sexual Dimorphism](#)

Variation in Disease Risk

- [Darwinian Medicine](#)

Venereal Disease

► Prevalence of STDs

Ventral Stream, The

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Synonyms

Inferior longitudinal fasciculus; Occipitotemporal projection system; Ventral visual pathway

Definition

A parallel, hierarchically organized series (i.e., “stream”) of interconnected structures in the occipital and temporal cortex (TC).

Introduction

The ventral visual stream refers to a parallel series of relatively hierarchically organized cortico-cortical projections that arise chiefly from extrastriate visual areas of the occipital cortex and innervate structures in and around the inferior TC (Kravitz et al. 2013). Neighboring cortical structures of the ventral visual stream are typically heavily reciprocally connected, in line with a hierarchical organization of progressive abstraction of visual input. Ventral stream structures, like all others in primate cortex, are typically delineated according to their morphology, connectivity, and functional properties across microscopic and macroscopic scales of observation and show close homologies across human and nonhuman primates (Kravitz et al. 2013). However, unlike cells in “early” areas of the occipital cortex, visually sensitive cells in the TC possess large receptive fields, a coarse retinotopic organization, and show slower visual onset locked activity.

Furthermore, the responses of neurons in ventral stream structures are driven by complex stimulus features, conjunctions of those features, or the qualitative properties of the visual stimulus (Kravitz et al. 2013).

Subcortical Visual Input to the Dorsal Stream

Geniculostriate Visual Pathway

The dominant source of retinal input into both the ventral and dorsal streams comes through early visual cortex via the dorsolateral geniculate nucleus (dLGN). The dLGN receives visual input directly from retinal ganglion cells and indirectly via another direct recipient of retinal ganglion cell input, the superior colliculus (SC). Visual input from the dLGN to the occipital cortex arises from different populations of neurons. The best studied of those populations are the parvocellular (P) and magnocellular (M) cells, which occupy different layers of the dLGN (Kaplan 2004). Relative to M cells, P cells possess slower conduction velocities, longer response latencies, longer responses, smaller visual receptive fields, sensitivity to chromatic differences, and greater sensitivity to high spatial frequencies (Kaplan 2004). The P and M cells send parallel convergent and divergent projections to striate (primary) visual cortex (V1). This pattern of connections continues on through the many extrastriate cortical areas, forming parallel, though interconnected, subpathways within the ventral and dorsal streams (Ferrera et al. 1994; Kaplan 2004). The ventral stream receives relatively balanced input from the P and M subpathways, whereas the dorsal stream receives a relatively stronger input from the M subpathway (Ferrera et al. 1994). One major extrastriate target for the P and M pathways is the ventral stream “tributary,” V4. Neurons in V4 show robust activity despite inactivation of only one of either the P or M subpathways (Ferrera et al. 1994).

Extrageniculostriate Visual Pathway

The connections of the ventral and dorsal stream with the pulvinar also differ. The medial, central, and posterior nuclei of the inferior division of

the pulvinar (PI) receive direct visual input from retinal ganglion cells. The posterior and central-medial nuclei of the PI receive secondary visual input from the superficial layers of the SC. Of these substructures, the posterior and central-medial nuclei of the PI project to cortical area V4, a ventral stream “tributary.” V4 also receives input from the ventrolateral nucleus of the lateral pulvinar, but it is less clear whether this input is capable of driving visual responses in V4 in the absence of early visual cortex (Kaas and Lyon 2007).

Extrastriate Visual Cortical Area “Tributaries” to the Ventral Stream

The extrastriate visual areas that send major projections to inferior TC structures of the ventral stream are V2, V3, and V4. V2 lies just posterior to and on the posterior banks of the lunate sulcus (LS) and inferior occipital sulcus (IOS). The CO-rich thin and CO-poor interstripe regions of V2 project to the V4 and the ventral stream structure TEO in the inferotemporal cortex (Ungerleider et al. 2008). V3 lies anterior to V2 in the posterior bank and fundus of the LS and the IOS. V4 lies anterior to V3 in the anterior bank of the LS and prelunate gyrus. V4, V3, and V2 receive major feedforward input from V1, which is the principal cortical entry point for visual input and occupies much of the posterior occipital cortex. Although V4 predominantly projects to ventral stream structures TEO and TE, the subregion which represents the peripheral field also projects to dorsal stream structures in the lateral intraparietal sulcus (Ungerleider et al. 2008).

Cortical Connections of the Visual Inferotemporal Cortex

Intrinsic Connections

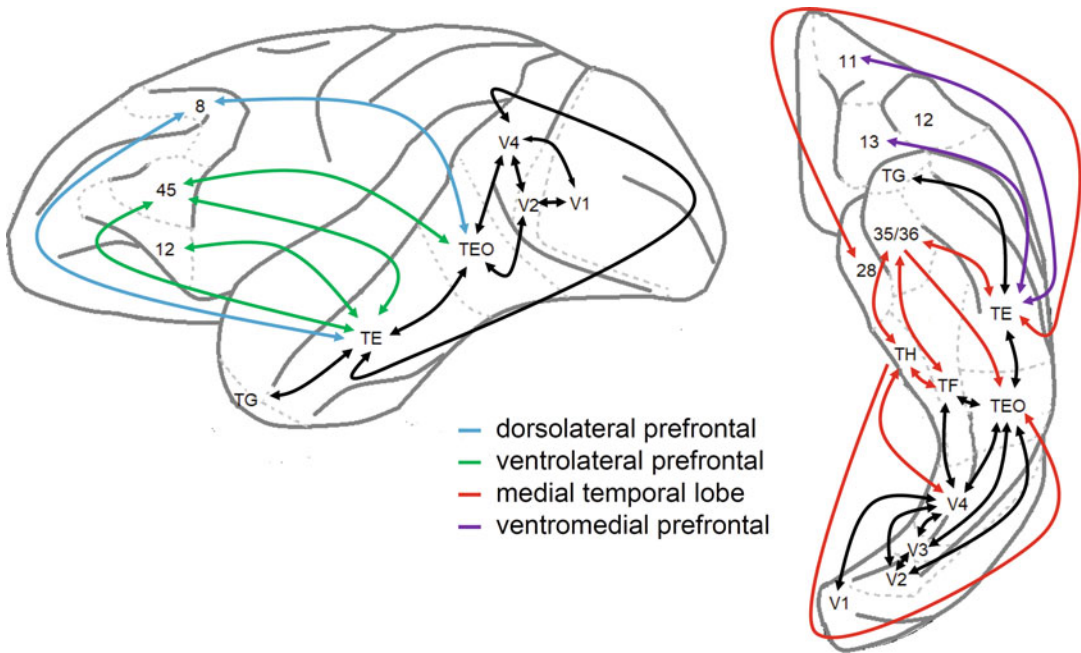
Visually responsive inferior TC is comprised of three major cytoarchitecturally defined regions, TEO, TF, and TE and its various subdivisions (see Fig. 1). TEO is anterior to V4, occupies the caudal region of the lateral and ventrolateral surface of

temporal cortex in the middle and inferior temporal gyri, and is bordered by the superior temporal sulcus (STS). TE is anterior to TEO, occupies the rostral region of the lateral and ventrolateral surface of the temporal cortex in the middle and inferior temporal gyri, is bordered dorsally by STS, and area TG at the temporal pole forms its anterior border. Area TF is located on the medial side of the inferior TC and occupies a caudal region of the hippocampal gyrus. Neurons in a caudal subregion of TF anterior to ventral V4 and medial to TEO respond to visual stimuli (Boussaoud et al. 1991). Ventral stream structures, like most others in cortex, are interconnected with neighboring ones. TF is reciprocally connected with V4, TEO, and TE (Suzuki and Amaral 1994). TEO is strongly reciprocally connected with V4 and to a lesser extent V3 and V2 (Ungerleider et al. 2008). TE is reciprocally connected with TEO and receives projections from V4 (Ungerleider et al. 2008). Neurons in TEO vary widely in the sizes of their receptive fields which helps give rise to the coarse retinotopy observed across TEO with the transition from upper to lower visual field generally oriented in a rostral-to-caudal direction (Boussaoud et al. 1991).

Cortical Output Pathways

Medial Temporal Lobe Pathways

The medial temporal lobe (MTL) includes the amygdala, hippocampus and cortical structures located in the entorhinal, parahippocampal, and perirhinal cortex. Although the MTL is multisensory and plays a critical role in declarative memory, some of its cortical structures are reciprocally connected with visual ventral stream structures V4, TEO, and TE (Saleem and Tanaka 1996; Suzuki and Amaral 1994; Webster et al. 1991). TEO receives projections from area TG, perirhinal areas 35 and 36, and parahippocampal areas TF and TH. TE is reciprocally connected with perirhinal cortical areas 35 and its anterior neighbor area 36, both of which border TE medially and both of which are critical sources of visual input to the hippocampus. TE is also reciprocally connected with entorhinal cortex area 28, which



Ventral Stream, The, Fig. 1 The connections of the ventral stream in the macaque brain. A ventrolateral view is depicted on the left while a ventral view depicted on the right. Light gray broken lines reflect approximate borders of various areas, while the thicker darker gray lines include

major sulcal landmarks. The connections from ventral stream structures to the dorsolateral, ventrolateral, and ventromedial prefrontal cortex and the medial temporal lobe are color-coded

is located medial to perirhinal cortex, and area TG, which is located on the inferior temporal pole, just anterior to TE. Both TF and its medial cortical neighbor TH are reciprocally connected and each projects to TE (Suzuki and Amaral 1994).

Dorsolateral, Ventrolateral, and Ventromedial (Orbitofrontal) Prefrontal Pathways

Ventral stream structures TEO and TE show different though partially overlapping connections to a number of structures in different regions of the prefrontal cortex. Dorsolateral area 8 in the prearcuate gyrus is reciprocally connected with both TEO and TE. Ventrolateral area 45, on the rostral bank of the inferior limb of the arcuate sulcus, and area 12, on the inferior convexity of the prefrontal cortex, are each reciprocally connected with both TEO and TE. TE, but not TEO, is reciprocally connected with ventromedial areas 11 and 13 on the orbital surface (Webster et al. 1994).

Function

The functions of TEO and TE are to maintain object constancies for visual perception and visual memory and to service the complex cognitive functions associated with their cortical targets in the prefrontal cortex. Areas V4 and TEO, but not TE, are organized retinotopically. The neural response latencies and size of the receptive fields increase moving from V4 to TEO. Moving from TEO to TE, the size of the receptive fields increases sharply in many, but not all, neurons and will frequently include the foveal area in the ipsilateral visual field (Boussaoud et al. 1991; Kravitz et al. 2013). Importantly, TE still possesses many cells with small receptive fields, which suggests that this area signals, among other things, object position (Fujita 2002; Kravitz et al. 2013). Furthermore, the receptive fields of neurons in V4 and TEO are often centred beyond the foveal area and include a portion of the periphery, suggesting. Again, that these cells signal

object position (Fujita 2002). Generally, neurons in V4, TEO, and TE do not respond to simple visual stimuli such as linear grating, edges, or bars (Fujita 2002). Neurons in V4 are selective for color, object form, or conjunctions of the two (Ungerleider et al. 2008). Neurons in V4, TEO, and TE are sensitive to binocular disparity, including the gradient of disparity which can signal the depth of an object relative to fixation (Fujita 2002). Lesions to TEO have long been associated with deficits in pattern discrimination, whereas lesions to TE are associated with deficits in acquiring reward-contingent discriminative object-response relationships (Webster et al. 1994).

In line with the notion that ventral stream structures are critical for the establishment of perceptual object constancies, TE neurons show a remarkable level of invariance in object shape selectivity despite spatial transformations of stimuli such as a change in position, luminance, texture, motion, binocular disparity or occlusion, mirror, and figure-ground reversals, and changes in the background (Fujita 2002). Like much of visual cortex, TE neurons are organized into “columns” that span the different layers of cortex. Typically, neurons within a column show a moderate level of correlation in their responses to similar objects and similar degrees of retinal disparity than do those in different columns (Fujita 2002). The topographical distribution of columns is patchy, which presumably reflects an absence of any advantage for topographically organizing object qualities and identity.

The connections of TEO and TE to MTL and the prefrontal cortex serve higher order cognitive functions associated with those regions. The visual input to MTL is critical for storing new long-term memories of object quality. Connections between TE and MTL facilitate the use of visual object information for encoding places and landmarks in these structures critical for the distal control of spatial navigation. The dorsolateral and ventrolateral prefrontal cortex are associated with spatial and object working-memory, respectively. Ventromedial prefrontal cortex is associated with the evaluation and learning of stimulus-reward contingencies and the establishment of valence or biological relevance (Kravitz et al. 2013).

Conclusion

Proposals concerning the nature and content of the operations performed in the ventral stream are active areas of research and have been for decades. The ventral stream is a hierarchical network of parallel cortical structures in the occipital and inferior TC of the primate brain that operates at the interface of memory and other higher-order cognitive processes like working memory and reward evaluation. Contemporary accounts focus on a number of different roles which are perhaps best summarized as *mnemonic* and *evaluative* for object and scene quality. These functions ultimately serve the distal (or indirect) control of behavior, as opposed to the dorsal stream’s more proximal or direct control over object-directed behavior. Accordingly, target structures for ventral stream output are critically involved in recognition and identification, planning and goal-formation, stimulus-response relationships and their reward values, biological relevance, and long-term, and working forms of visual memory (Kravitz et al. 2013).

Cross-References

- [Dorsal Stream, The](#)
- [Frontal Cortex](#)
- [Nonhuman Primates](#)
- [Retina, The](#)

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Ventral Visual Pathway

- [Ventral Stream, The](#)

Verbal

- [Communication and Social Cognition](#)

Verbal Achievement

- [Language Acquisition in Infants and Toddlers](#)

Verbal Aggression

- [Meta-analysis of Sex Differences in Aggression](#)
- [Women Use Verbal Derogation to Be Included](#)

Verbal Bullying

- [Girls Psychological Bullying](#)

Verbal Communication

- [Language Development](#)

Verbal Derogation

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Synonyms

[Aggression](#); [Female-female competition](#); [Gossip](#);
[Intrasexual competition](#); [Intrasexual rivalry](#);
[Rumor spreading](#)

Definition

The use of verbal insults to devalue a woman's mate value relative to one's own mate value.

Introduction

Verbal derogation is a strategy commonly used by women who are in competition for male attention. When women use this strategy, they say things about another woman in an attempt to lower the other woman's mate value. Verbal derogation can take the form of direct aggression, such as when someone yells at another person (Bjorkqvist et al. 1992). However, women's verbal derogation typically takes the form of indirect aggression, such as gossiping and rumor spreading. Women's derogatory comments about other women have

three major themes: women's appearance, promiscuity, and fidelity (Buss and Dedden 1990). Specifically, women are likely to verbally derogate other women by criticizing the way they look or by saying that they are "easy" or that they sleep around on their partner.

Indirect Verbal Derogation Versus Direct Verbal Derogation

Women are more likely to engage in indirect aggression, such as gossiping, than they are to engage in direct aggression, such as yelling at someone (Campbell 1999). One reason for this discrepancy may be a result of women typically holding the role of primary caregiver. A physical injury could hinder a woman's ability to care for her children, so the risk of bodily injury may motivate women to favor indirect aggression over direct forms of aggression (Campbell 1999). Although verbal derogation is not inherently physical, one of the top reasons listed by women for getting into physical altercations is that they were verbally insulted by another woman (Campbell 1986). Avoiding all types of direct aggression, verbal or physical, may be a strategy women use to avoid physical harm. Unlike direct verbal derogation, indirect verbal derogation can be performed covertly (e.g., gossiping behind someone's back). Thus, this indirect strategy may help women avoid the social and physical repercussion that are likely when one directly aggresses against another person.

Efficacy of Competitor Derogation

Two strategies commonly used in intrasexual competition are self-promotion and competitor derogation. When women try to enhance their mate value through behaviors such as wearing makeup or attractive clothing, they are engaging in a self-promotion strategy (Schmitt and Buss 1996). When women try to decrease other women's mate value relative to their own through behaviors such as criticizing someone's appearance or sexual history, they are engaging in a

competitor derogation strategy. Overall, derogation strategies such as verbal derogation are perceived as less effective than self-promotion strategies (Schmitt and Buss 1996). However, men rated a woman's physical appearance lower after a rival verbally derogated the woman's appearance (Fisher and Cox 2009). This effect was more pronounced when the derogatory comments came from an attractive rival than when they came from an unattractive rival.

Women who have been targets of indirect aggression have more negative self-perceptions than women who have not been targets (Paquette and Underwood 1999). Ostracism (a potential consequence of being verbally derogated against) has been linked to aggression and low self-esteem (Twenge et al. 2001). These outcomes suggest that verbal derogation does not simply lower people's perceptions of a rival's mate value; derogation also lowers a rival's self-perceived mate value.

Conclusion

Verbal derogation is a strategy in which women verbally insult another woman in an attempt to lower the mate value of the other woman relative to their own mate value. The most common traits that women derogate are other women's appearance, promiscuity, and fidelity. Women are more likely to engage in indirect derogation than direct derogation, and evidence suggests that verbal derogation may be an effective mate competition strategy.

Cross-References

- ▶ [Contexts for Women's Aggression Against Women](#)
- ▶ [Derogation of Attractiveness](#)
- ▶ [Derogation of Promiscuity](#)
- ▶ [Derogation of Rivals](#)
- ▶ [Female-Female Competition](#)
- ▶ [Gossip, Rumors, and Social Exclusion](#)
- ▶ [Intrasexual Rivalry Among Women](#)
- ▶ [Women Use Verbal Derogation to Be Included](#)

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Verbal Derogation Among Women

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Synonyms

Gossip; Indirect aggression; Mating competition; Relational aggression; Social aggression

Definition

When women spread information about other women (i.e., targets) to decrease those targets' social desirability.

Introduction

Why might women call other women “ugly,” “sluts,” or “bitches”?

When women compete with one another, they are particularly likely to use indirect tactics of aggression (Vaillancourt 2013). One such tactic is verbal derogation, whereby a woman spreads information that can decrease a potential rival's social desirability (Buss and Dedden 1990; McAndrew 2014; Fisher 2004). Such derogation often takes the form of gossip, which is typically engaged in covertly – behind the target's back.

A Function of Derogation

Most research on women's derogation of other women focuses on its use in competition for mates, rather than competition for same-sex allies or other resources. In mating competition, one potential function of such derogation is to make the target seem a less desirable romantic partner (Fisher 2004; Hess and Hagen 2006). Women may thus use verbal derogation to exclude perceived rivals, severing rivals' existing relationships and/or impairing their ability to form new ones, and ultimately decreasing that rival's reproductive fitness.

Derogation: Targets and Content

The typical content of women's verbal derogation fits nicely with this proposed function as a tool of women's mating competition. In prospective mates, men value fertility (often indexed as youth and physical attractiveness), fidelity, and – particularly for longer-term relationships – also nurturance (Buss and Schmitt 1993; Shackelford et al. 2002). Women typically derogate a target's physical attractiveness (e.g., “she's ugly”), fidelity (e.g., “she's a slut”), or nurturance (e.g., “she's a bitch”; Buss and Dedden 1990; Hess and Hagen 2006). Additionally, jealousy in these domains (e.g., physical attractiveness) is known to spur women's intrasexual derogation (Owens et al. 2000).

That women target strong rivals for mates also supports this proposed function. Highly attractive or seemingly promiscuous women are frequent targets of women's derogation (e.g., Vaillancourt 2013). Interestingly, these frequent targets may possess unique defenses against victimization (Krems et al. 2015).

Derogation: Benefits and Costs

In terms of effectiveness, women's intrasexual derogation may maximize harm to rivals while minimizing the risk of retaliatory aggression. Derogation may curtail targets' mating opportunities and/or reproductive fitness (e.g., Vaillancourt 2013). For example, accusations of promiscuousness are difficult to refute and can impair a woman's ability to form long-term relationships (Buss and Schmitt 1993; Hess and Hagen 2006). To the extent that derogation successfully disrupts a woman's relationships whether romantic or platonic it may impair her fecundity, as in nonhuman primates. Some perpetrators, however, may be more effective derogators than others; physically attractive women more effectively influence men's judgments of other women's attractiveness (Fisher and Cox 2009).

Verbal derogation is also relatively low cost. For example, gossip often allows gossipers to remain anonymous; even known perpetrators may claim the aggression was unintentional (e.g., "I meant your dress was 'scandalous' in a complimentary way"). This may decrease the likelihood of retaliation, rendering women's verbal derogation a high-impact and low-cost tactic of mating competition.

Conclusion

Verbal derogation may be an effective tactic in women's intrasexual competition.

Cross-References

- Anne Campbell
- Contexts for Women's Aggression Against Women

- Derogation of Attractiveness Among Women (Intrasexual Rivalry)
- Derogation of Promiscuity Among Women
- Gossip, Rumors, and Social Exclusion
- Intrasexual Rivalry Among Women

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Verbal Knowledge

- Declarative Knowledge

Verbal Mimicry

- Echolalia

Verbing and Nouning

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Synonyms

Denominalization and nominalization; Zero conversion

Definition

To verb a noun is to create something of the verbal category from a nominal; to noun a verb is to do the reverse.

Introduction

Verbing and nouning are ways to introduce neologisms. The process, also called **denominalization** and **nominalization**, respectively, can be achieved by **compounding**, e.g., forming the verbs “to back up” or “to pig out” by combining a noun with some other term. It can also be achieved by **morphological derivation**, especially via affixation. In the noun → verb direction, the English “incentivize” and “declutter” are verbs which are derived morphologically from the nouns “incentive” and “clutter,” respectively. By the same token, the French “brosser” (to brush) comes from the noun “brosse” (brush), just as the Spanish “cepillar” comes from “cepillo.” Going in the verb → noun direction, in English, “suckage” and “singing” are nouns which derived from verbs by means of adding suffixes. Similarly, in Dagaare, a language from Ghana and Burkina Faso, the nominal “zoobu” (the act of running) is derived morphologically from the verb “zo” (to run); “gaabo” (departure) is derived from “gaa” (to go), while “waabo” (arrival) is derived from “wa” (to come), all by adding the appropriate suffix.

Why Are Verbing and Nouning Important for Language Evolution?

A subvariety of verbing and nouning, one of special interest when it comes to language evolution, is **conversion**, also known as **zero derivation**. Here, there is a “functional shift” without any change in surface form. All of the following arose via verbing of the zero-derivation type: “to google,” “to parent,” “to medal,” “to access,” “to trend,” “to bookmark,” “to email,” “to friend,” “to beer,” “to conference,” “to impact,” “to door,” “to showcase,” “to host,” “to input,” and “to blog.” And the nouns in “The new *hire* made a big *ask*, but it was an epic *fail*” all derived from verbs, but without compounding or the addition of affixes – that is, all arose through zero-derivation nouning. To come at the point another way, the hallmark of a noun-based verb, birthed by this particular method, is that speakers apply regular inflection directly to the bare form: in English, one adds “-ed” for the past and perfect form and “-ing” for the progressive and the gerund. (Notice, e.g., that the past tense of “to grandstand” is “grandstanded,” deriving immediately from the corresponding noun. As Prasada and Pinker (1993: 46) point out, it is not “grandstood.”) Similarly, in the verb → noun direction, one simply adds a determiner (such as the definite or indefinite articles “the” or “a”), a plural marker, or an adjective to the tenseless verbal form: “several good *reads*” and “a big *get*.” It is this latter zero-derivation subvariety which is most typically called “verbing and nouning.”

Verbing of the zero-derivation kind, i.e., without modification of the surface form, is especially a feature of languages which are not highly inflected. Thus English, whose verbal morphology is comparatively impoverished, allows it quite freely. In contrast, to create a new verb from a noun in French or Spanish, say, the new form must end in one of the three possible verbal paradigms (whether “-re,” “-ir,” or “-er” in French or “-ar,” “-er,” and “-ir” in Spanish). Hence their neologistic verbs will (almost invariably) have a different surface form than the source nouns, for instance, colloquial spoken French has “googler”

and “texter,” rather than just “google” and “texte,” and Spanish has “googlear.”

Are Prescriptive Grammarians Right to Be So Hostile to Verbing and Nouning?

The evolution of a language, especially in a free and rapid way, typically raises prescriptive hackles. Verbing and nouning of this zero-derivation sort is no exception. Pundits and bloggers complain that the usages are just business speak and technobabble. They find the coinages pointless. (Why use “epic fail” instead of the existing “failure”? And who needs “to impact”? They may even accuse ordinary speakers of a grammatical gaffe: the untutored are confusedly using nouns as verbs and vice versa! Linguists, in contrast, tend to be skeptical about such complaints. The process is not novel and is not tied exclusively to business speak or technology. The substantives in “a long *run*,” “a refreshing *swim*,” and “a pleasant *drive*” all started life as verbs, but are now wholly uncontroversial as nouns. The verbs in “to *stomach* his complaints,” “to *finger* a suspect,” “to *head* a committee,” and “to *elbow* a player” all arose through zero derivation from names of body parts; the verbs “to boycott,” “to lynch,” and “to gerrymander” all came from proper names of notorious figures, and “to ski,” “to bicycle,” and “to skate” all began life as names of sporting gear. (Pinker (1995) estimates that fully one fifth of English verbs arose through “verbing,” specifically via conversion. See also Clark and Clark (1979) and Luu (2016)). As Zwicky (2009) notes, moreover, the neologisms typically do not mean exactly what preexisting alternatives do, because of changes to connotations, to associated imagery, and to **register** (e.g., the level of formality or technicality of the word). Finally, these are not grammatically paradoxical cases of, say, nouns being conjugated and verbs taking plural endings. They are cases of new nouns/verbs being created – cases, that is, not of perverse misuse of the existing tongue, but of the language itself evolving.

Conclusion

In sum, verbing and nouning are linguistic processes for creating neologisms of a particular sort. The subvariety of greatest interest, characteristic of languages like English with quite simple verbal morphology, involves taking an old lexical item belonging to one word class and creating a new one – whether noun → verb or verb → noun – without changing the surface form. The process, known as conversion or zero derivation, leads to especially fast and efficient evolution of the language, with new coinages emerging and spreading seamlessly (particularly when certain pragmatic constraints are met (see Kaminski 2010; Luu 2016). While some prescriptive writers disparage this particular kind of language change, linguists find their reasons unpersuasive.

Cross-References

- Grammaticalization Theory
- Language
- Linguistic Evolution

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Vestibular System

- ▶ [Balance and Motion](#)
- ▶ [Evolution of Hearing and Balance](#)
- ▶ [Inner Ear, The](#)

Victim

- ▶ [Risk Variation with Parent Age](#)
- ▶ [Sex Differences in Death by Filicide](#)

Victimization

- ▶ [Girls Psychological Bullying](#)
- ▶ [Same-Sex School Bullying](#)

Victims Mostly Men

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Synonyms

[Causality](#); [Harmed](#); [Injured party](#); [Sufferer](#)

Definition

An unfortunate person who suffers from some adverse circumstance.

Introduction

Prior to the 1960s, criminological inquiry primarily centralized upon offender/criminal characteristics; negating situations, behaviors, and characteristics associated with victimization. While researchers had previously attempted to develop victim typologies with the use of law

enforcement data, criminologists were ultimately unsuccessful in their typological endeavors (Mendelsohn 1976). However, in the 1960s the first self-report victimization survey was developed and conducted allowing researches insight into what is now known as the dark figure of crime (Reiss 1967). After examining and refining methodological problems associated with the original survey, the first national level annual offender/victim analysis was implemented (National Crime Survey 1973; Barnes, Seepersad, Wilkis, & Wortley, 2016).

Since the development and implementation of the National Crime Survey (1973), an increase in criminological and psychological victim-based research has been observed. Said research indicates clear differentiation among victimization risk based upon individual/lifestyle characteristics. Characteristics correlated with risk of victimization include, but are not limited to, an individual's age, gender, ethnicity, social economic status, and peer network (Garofalo 1987). Specifically, males, minorities (i.e., African Americans), persons living in low socioeconomic neighborhoods, and adolescents are found to be at higher risk for experiencing personal and property victimization, with the highest rate of victimization occurring among African American males ranging from 14 to 24 years of age (National Crime Victimization Survey 2016).

Historically, the offender-victim relationship has been portrayed with males committing the majority of criminal acts with females possessing the greatest risk for victimization. However, national crime statistics indicate a unique relationship between offending and victimization risk with males being the most represented among both populations (excluding sex crimes) (National Crime Victimization Survey 2016).

Although not originally intended to differentiate by gender, both macro and micro-level theories have attempted to explain the variation among victimization risk. Multiple theories have investigated the relationship between gender and victimization from an offender – victim overlap perspective (Lauritsen and Laub 2007). Offender-victim overlap models focus on the relationship between offending behavior and victimization from a structural characteristic background,

spotlighting similarities among offender and victim attributes (Baumer and Lauritsen 2010).

Three theoretical approaches aiding in the explanation of the offender-victim overlap are lifestyle/routine activities theory, deviant lifestyles theory, and self-control theory (Jensen and Brownfield 1986; Schreck et al. 2008). For instance, Hindelang's (1976) "principle of homogeneity" focuses on the theoretical link between offending behavior and victimization, noting that certain behaviors may increase the potential for victimization.

Hindelang's (1976) theory of integrated lifestyle exposure was one of the first theories to focus on personal victimization and the differences therein. The theory of integrated lifestyle exposure was developed for the purpose of explaining the unequal distribution of victimization among various persons with differing backgrounds. Background characteristics include an individual's age, race, sex, income, marital status, social affiliation, etc. Furthermore, Hindelang (1976) proposed the idea that an individual's background could affect his/her potential achievements, reaction, and adaptation to novel stimuli, professional activities, and vocational activities. These individual background differences were theorized to result in observable lifestyle differences and purported to be indicators of an individual's daily routine.

Differences in lifestyle activities were believed to affect an individual's rate of exposure to high risk situations and/or environments. For instance, adolescent males were noted as having a higher frequency of unstructured nightly routines, spending more time in high-risk areas, while lacking the presence of parental or social control, thus increasing their exposure to offenders and the potential for victimization. Alternatively, young women were thought to be highly monitored and supervised by their guardians which was theorized to partially explain gender differences in victimization.

Routine Activates Theory

Analogous to Hindelang's (1976) lifestyle theory which focused upon places frequented, interaction with criminally prone individuals, and convenience

of target is Cohen et al.'s (1981) theory of routine activities. Cohen et al. (1981) expanded upon the lifestyle theory by proposing an opportunity-based theory of offending and victimization. Cohen et al.'s (1981) opportunity theory focused on descriptors of lifestyles probabilistically associated with increased risk of victimization. Their routine activities approach (Cohen and Felson 1979) primarily focused on a motivated offender, the availability of a suitable target, and the availability of a capable guardian (or lack thereof). Cohen and Felson, theorized higher risk of victimization resulted when a motivated offender converged with a suitable target absent a capable guardian (Cohen and Felson 1979). Cohen (1979) later summarized the routine activities model of offending to include an individual's everyday behavior/activities. Personal behavior/activities were theorized to bring about interactions between an individual and a potentially motivated offender. For instance, persons purchasing or selling narcotics were theorized as being more likely to converge with a motivated offender when compared with their non-drug using counterparts; thus, increasing the risk of victimization.

Cohen and Felson's (1979) routine activities theory has commonly been used to explain why and how males are at a heightened risk of victimization. With young unmarried males experiencing the highest rate of victimization; their routine and/or nocturnal activities with peer networks provide significant insight into the relationship between exposure and victimization. For instance, by being out at night, partaking in high-risk behaviors such as drug and alcohol use, participating in delinquent activities themselves, and frequenting high-risk areas, males are at an increased risk for coming into contact with a motivated offender without the protection of a suitable guardian (Lauritsen et al. 1991).

Delinquent Lifestyles Theory

Analogous to Cohen and Felson's (1980) routine activity theory is Jensen and Brownfield's theory of delinquent lifestyles (1986). Their theory of delinquent lifestyles proposed a positive relationship

between active offending and victimization. In this instance, active offending behavior was viewed as a causal mechanism with victimization resulting from “motives, vulnerability, or culpability of people involved in offending activities” (Jensen and Brownfield 1986). In other words, having a lifestyle of criminal behavior placed an individual in higher crime locations, high-risk situations, and interactions with other offenders, resulting in increased risk of victimization (Lauritsen et al. 1991). In 2007, Smith and Ecob reiterated Jensen and Brownfield’s theory of delinquent lifestyles (1986) by noting the interactive nature of the offender-victim relationship. Smith viewed victimization as “the outcome of an interactive process, in which both the eventual victim and the eventual delinquent played a part” (Smith and Ecob 2007).

Self-Control Theory

As previously alluded to in routine activities theory and delinquent lifestyles theory, there is a commonly noted relationship between an individual’s daily activities and risk of victimization. The General Theory of Crime (1990), along with lifestyle theories, has been used as a template for the explanation of victimization. Specifically, Gottfredson and Hirschi (1990) theorized an interactive relationship between low self-control and criminal outcomes. In their general theory of crime, low self-control was believed to develop during childhood as the result of ineffective parenting and inadequate socialization, thus producing later deviant outcomes. Moreover, low self-control was thought to affect behavior by manifesting itself through impulsive risk-seeking behaviors (Gottfredson and Hirschi 1990).

Ultimately, Gottfredson and Hirschi’s general theory of crime (Gottfredson and Hirschi 1990), proposed an inverse relationship between an individual’s level of self-control and behavioral outcomes. Empirically, low levels of self-control have consistently been linked with a person’s propensity to engage in criminal offending. As a result, scholars further proposed a correlation between low self-control and victimization (Pratt and Cullen 2000). Alternative to the substantive amount of research conducted on low self-control

and behavioral outcomes, research assessing the relationship between low self-control and victimization was not prominent until the 2000s.

In 1999, Schreck expanded Gottfredson and Hirschi’s general theory of crime by integrating it with lifestyle theories of offending. Specifically, Schreck (1999) sought to understand the underlying logic between the self-control-offending relationship and how an increased risk for offending was correlated with higher levels of victimization. Schreck’s concept of self-control and victimization focused on the idea that individuals primarily interact with persons similar to them. Specifically, Schreck purported an individual’s risk of victimization to be directly associated with the number of characteristics said individual shared with anti-social persons (Hindelang et al. 1978). Schreck further argued that victims, analogous to offenders, expressed lower levels of self-control resulting in more impulsive and risk-taking behaviors. Said behaviors were believed to increase offending, ultimately resulting in persons being perceived as more attractive and vulnerable targets (Schreck 1999).

Conclusion

The previously noted theories have been extensively supported by prior research. Offending behavior/lifestyles has been one of the most consistent predictors of victimization (Lauritsen and Laub 2007). Jensen and Brownfield (1986) classified offending behavior as a lifestyle or routine-based activity, suggesting an increased risk of victimization resulting from higher exposure to motivated offenders without the presence of a capable guardian (i.e., law enforcement). Specifically, Jensen and Brownfield (1986) found more serious deviant behaviors (i.e., drug and alcohol use) to act as desensitizing agents, ultimately making these individuals more attractive targets to motivated offenders.

Additionally, persons engaged in criminal activities were found to be more likely to use violence as a means of physical and reputational protection. This type of lifestyle activity increased the likelihood of succumbing to unintended consequences, ultimately increasing the potential risk of victimization (Stewart et al. 2008). Moreover, previous

research further discovered that offenders and victims shared many of the same behavioral and lifestyle characteristics as the result of them being the same person (Jensen and Brownfield 1986; Lauritsen et al. 1991).

Research regarding the offender-victim overlap has produced consistent findings across differing social contexts, cultures, and nationalities. Using data from the National Youth Survey, Lauritsen et al. (1991) further explored the relationship between offending and victimization by controlling for the “reciprocal influence of victimization of offending.” Lauritsen et al.’s (1991) findings provided significant support for the theory that offenders and victims do not simply share the same characteristics, but rather are the same person. Therefore, overall victimization among the male population has been substantively explained by male engagement in deviant, impulsive, high-risk lifestyles.

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Victims of Violence

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Synonyms

Brutality; Casualty; Injured party; Sadism; Savagery; Sufferer

Definition

A person harmed, injured, or killed as a result of another's behavior involving physical force intended to hurt, damage, or kill.

Introduction

Access to resources and mating opportunities determines the genetic fitness of an individual. Living in groups has meant that obtaining these resources is subject to the costs associated with competition and reciprocity, as well as resource acquisition. For these reasons, strategies that circumvent the need to compete or reciprocate by utilizing violence and intimidation to obtain resources and mating opportunities were selected for under some environmental conditions (Duntley 2015). Violence, like theft and other forms of social cheating, is a risky strategy but can minimize the costs involved in resource and mate acquisition. However, unlike cheating, violence not only confers resource and mating benefits but increases perceptions of physical dominance and social capital. In 2004, a massive 11% of deaths due to injury were the result of homicide and 3% resulted from war. Homicide (ranked fourth) and war (ranked ninth) both ranked in the top ten causes of death worldwide for 15–29 year olds. Further, males were almost three times as likely as females to die as a result of murder. However, females were more likely to suffer childhood sexual abuse (approx. 20% of all female children), intimate partner violence, and sexual violence (WHO 2010). Adaptations for violence between ancestral humans would have increased selection pressure for adaptations that assist an individual to avoid, defend against, and minimize the costs of, violence. The costs to the individual of becoming a victim of violence can vary from loss of resources, mating opportunities, and reputation, to complete loss of mate choice (Duntley and Shackelford 2012). These costs can continue to act on the individual's fitness for long periods of time, even decades. Further, individual differences in phenotype and behavior can increase the probability of becoming a victim of

violence. Evidence suggests that an individual's probability of being victimized can be increased by having been victimized previously (Finkelhor et al. 2007), as well as individual differences in personality (Coyne et al. 2000), and body language (Ritchie 2016).

This section will, however, focus on individual differences that offer avoidance, harm minimization, or protection from violence. The selection pressure placed on adaptations that minimize the costs associated with being a victim of violence is dependent upon the temporal context in which the adaptation is effective. For example, adaptations that increased the likelihood of avoiding violence completely would maximize genetic fitness relative to adaptations that minimized the costs of violence following the event (Duntley 2015). Due to this differentiation by temporal context, this chapter will consider evidence for adaptations to minimize the costs associated with being a victim of violence prior to, during, and following a violent event. Further, in order to locate these adaptations within a specific context, this entry uses the running example of adaptations to minimize the costs associated with rape. Rape is a unique example of intraspecific violence, as rape confers immediate reproductive advantages to the perpetrator while inflicting heavy costs to the victim's genetic fitness by removing the ability for mate choice while simultaneously lowering their mate value. Perhaps due to the heavy costs on the victim, evidence suggests that women have evolved specific adaptations to avoid and/or minimize the fitness costs of rape (McKibbin and Shackelford 2011).

Pre-Violence Adaptations

Adaptations that prevent the individual from becoming a victim of violence are the most effective harm minimization tools, and thus would be subjected to the most selection pressure. Included in this category are emotions, perceptions, behaviors, and social strategies. Emotions such as fear and anxiety act as a biological threat warning system that alerts the individual to signs of danger in the environment (Nesse and Marks 1994). The

triggering stimuli, intensity, duration, and valence of these emotions differ between individuals. Further, these factors determine whether the activation of fear and anxiety is a net benefit or cost to the organism. Too much fear and anxiety can reduce fitness by disabling the individual and preventing them from undertaking fitness-enhancing behaviors. Too little fear and anxiety places individuals at risk of attack from human and nonhuman predators. For this reason, fear and anxiety are regulated when the psychological systems of an individual are functioning optimally (Nesse and Marks 1994). When this system is not well regulated the psychology of that individual is often seen as disordered. Fear and anxiety that are of high intensity, present for long durations, and/or triggered by inappropriate stimuli is considered an anxiety disorder (Nesse and Marks 1994).

Fear and anxiety not only signal important information to the individual experiencing the emotion, but outward displays of these emotions (facial expressions, body language, and arousal) signal to those around us of the possibility of threat and a need for empathic concern (Aktar et al. 2013). Infants are known to respond to these outward signals when displayed by their parents/caregivers as young as 8 months of age (Boyer and Bergstrom 2011). This use of parental threat signals by infants is developmentally stable, manifesting in behavior at 8 months and lasting until 3 years of age in the form of stranger anxiety. Stranger anxiety is a fear response shown by infants when faced with unknown individuals, especially unknown men. When in the presence of strangers, the infant may cry, pull away, or hide. This behavior is thought to be an adaptive response to the threat of conspecific violence – violence which is more likely to be enacted by men who are strangers (Boyer and Bergstrom 2011). In an experimental test of the hypothesis, researchers demonstrated that infant anxiety, when confronted by a stranger, was higher when their parent expressed anxiety. Further, the parent's state anxiety response influenced infant stranger anxiety independent of a parental history of trait anxiety (Aktar et al. 2013). These early developmental fear objects drive infants and

young children to seek the safety of their caregivers, reducing their risk of becoming victims of violence (Boyer and Bergstrom 2011).

Fear and anxiety also play a role in motivating humans to form alliances and seek the safety of inclusion in a social group. Inclusion in a group can not only protect an individual from becoming a victim of violence, but also to minimize the costs associated with violent victimization through intervention during the violent attack, or in minimizing reputational costs by seeking retribution/revenge following an attack. A stressful environment motivates humans to seek social alliance through increases in prosocial behavior. Using an experimental design including a control group, researchers submitted the treatment group to a stress induction. Following this, all participants played decision paradigm games in order to measure their levels of prosocial behavior. Participants from the stress induction group showed significantly higher levels of trust, trustworthiness, and sharing than those in the control group (von Dawans et al. 2012). Prosocial emotions and personality traits have been found to increase integration in a group alliance, while antisocial personality traits and personality traits that promote a distrusting outlook, nervousness, and social anxiety have been found to decrease group integration and increase the probability of being victimized. Boele et al. (2017) found that in adolescents, being dissimilar from the group in levels of Machiavellianism (an antisocial personality trait) and neuroticism (a trait associated with jealousy, distrust, and social anxiety) led to an increased probability of being victimized. Being integrated within a group is an important protective factor against victimization, and environments that increase stress, fear, and anxiety motivate prosocial behaviors to help accomplish this.

Another strategy for minimizing the probability of becoming a victim of violence is the avoidance of high-risk environments. High-risk environments include unfamiliar territories, environments without easy access to escape routes, and places removed from allies. Females tend to place themselves in high-risk environments less than males. Differences in the rates of violence

committed against men rather than women can be partially explained by this difference in risk-taking behavior. In a sample of German students ($n = 275$), Fetschenhauer and Rohde (2002) found that men were more likely than women to be the victims of both violence and accidents, but that this relationship was mediated by men's increased levels of risk-taking and short-term orientation (a propensity to plan for short-term gain without consideration of long-term outcomes). After researchers controlled for risk-taking and short-term orientation, there were no differences in violent victimization rates between sexes. Risk-taking in males may confer fitness benefits in other ways, for instance, increasing resource acquisition and mating opportunities. However, in the context of conspecific violence, engaging in relatively low levels of risk-taking behavior and being oriented toward decisions with favorable long-term outcomes reduces an individual's probability of becoming a victim of violence. Further, the female propensity for avoiding the risks associated with environmental factors is enhanced during the fertile phase of the menstrual cycle, which is hypothesized to be an adaptation to avoid sexual violence (Bröder and Hohmann 2003).

Running Example: Pre-Violence Antirape Adaptations

Rape is a recurrent and unfortunate behavior that predominately affects women. The negative consequences of rape for women are numerous and substantial; as a result, it is likely that the problem of rape has resulted in selection pressure for physical and psychological antirape adaptations (McKibbin and Shackelford 2011). Adaptations that aid an individual in avoiding or reducing the probability of rape would confer the strongest fitness benefits. Previous research has suggested that a variety of adaptations aid women in minimizing the potential of becoming a victim of sexual violence. These include; changes in body language under stress (Fulham et al. 2017), increased caution during ovulation (Bröder and Hohmann 2003), and pair bonding

with dominant males (Wilson and Mesnick 1997).

Psychopaths and violent criminals have been found to be accurate assessing the vulnerability of women using cues taken from their body language and walking styles (Book et al. 2013). In fact, Ted Bundy notorious serial murderer and rapist said in an interview that he could "tell a victim by the way she walked down the street, the tilt of her head, the manner in which she carried herself, etc. . . ." (as cited in Holmes and Holmes 2010, p. 221). However, a counter adaptation exists for this ability to identify vulnerability through body language. In two studies (one between and one within subjects) using video footage of women walking Fulham et al. (2017) found that for women who had been victims of sexual violence the relationship between movement vulnerability cues and victimization history was moderated by hypervigilance. In other words, when women were hypervigilant people were unable to judge their history of victimization as accurately as when they were not hypervigilant. This shows evidence of adaptive behavioral consequences of the hypervigilance that is induced by exposure to dangerous situations.

Another set of hypothesized adaptations to avoid instances of rape center around the physiology of, and behavior associated with, fertile women's ovulatory cycle. Since the potential of fitness benefits for rapists is increased substantially when their victim is in the fertile phase of the menstrual cycle, it is reasonable to hypothesize that phenotypic variations that specifically guard against the potential of being attacked during ovulation would be selected for. Evidence exists of mechanisms of avoidance during the fertile period of women's reproductive cycles. Researchers from multiple studies have suggested that during ovulation women show increased levels of risk aversion compared to the remainder of the reproductive cycle (Bröder and Hohmann 2003). Bröder and Hohmann found that women self-reported having engaged in less high-risk activities if they were ovulating. Importantly, the effect of risk reduction at ovulation only occurred in women who were cycling normally. Women who were taking oral contraceptives that result

in a flattening of the natural hormonal cycle showed no change in risky behaviors. This research suggests a behavioral adaptation to reduce risk during the most vulnerable period of the reproductive cycle.

Other behaviors which are hypothesized to be selected for due to their antirape outcomes concern women's attraction to (or avoidance of) certain men. The Bodyguard Hypothesis makes the case that individuals co-residing with a male partner are less vulnerable to violent and sexual victimization. Further, although physically dominant men are less likely to make a long-term paternal investment, under some environmental conditions women would have a preference for pair bonding with more dominant men due to the protection they provide. Pair bonding with a physically dominant male not only affords protection through physical violence but also through reputational benefits. This is a trade-off between parental investment and protection and states that this trade-off is adaptive if calibrated with the dangers present in the environment. Wilson and Mesnick (1997) tested the Bodyguard Hypothesis by investigating Canada's homicide and violent crime data from a large-scale phone interview conducted in 1993. The resulting data were dichotomized with women either being classified as married (co-residing with a male sexual partner) or single and considered only attacks made by strangers. Data for non-lethal assaults included reported events of sexual violence which occurred in the 12 months prior to the survey. Data for lethal assaults was taken from Canadian homicide data for the period 1974–1992. Results showed that married women were significantly less likely than single women to be the victim of lethal or non-lethal sexual assault. For non-lethal sexual assault, an interaction was seen between prevalence and age at the time of the assault, with the gap in prevalence between married and single women largest in the 18–24-year-old bracket and consistently reducing until there was no difference between groups in the 65+–year-old bracket. For lethal sexual assault (femicide) a similar interaction was seen, however single women were most likely to be victims in the 25–34 age bracket (Wilson and Mesnick 1997). These results show

initial support for the Bodyguard Hypothesis and suggest that pair bonding does afford women some protection against violent sexual assault. However, further research is needed to investigate how these patterns differ according to the level of environmental risk in the associated environment as well as the effect of level of husband dominance.

Mid-Violence Adaptations

Some adaptations reduce the costs of violence to the victim while it is occurring. The defensive behaviors utilized by humans when encountering violence are similar to those used by animals. These may include defensive behaviors and postures, defensive attacks, verbal manipulations or attempts to de-escalate the situation, the summoning of allies to defend the victim, freezing, and fleeing from or escaping the attacker (Duntley and Shackelford 2012). In addition to these behavioral responses to violence, there are known physiological responses which include changes in heart rate, increased sweating on hands and feet, and increased startle reflex (Blanchard et al. 2001). Further, the context of the situation influences both the behavioral and physiological response to violence. When escape is possible the individual may make postural and physiological preparations to flee. Whereas when escape was unlikely, people prepare to freeze or fight.

Running Example: Mid-Violence Antirape Adaptations

Some hypothesized adaptations to reduce the costs of violence as it is occurring appear to be especially effective in the case of sexual violence. While males under threat of violence were disproportionately more likely to report that they would threaten attack, look for a weapon, or attack as a first choice response. Women were less likely to choose a defensive attack and more likely to scream or hide. This is especially true in contexts where fleeing was not a viable option (Blanchard et al. 2001). This may reflect the fact that when

faced with hypothetical scenarios both men and women report assuming that the attacker was male, thus making the size and strength differences between men and women a salient aspect of the decision. Further, men also noted that when choosing whether to attack their focus would be on the size/strength of the attacker (Blanchard et al. 2001).

Further research has shown that fear or death screams are an effective adaptation to reduce the costs associated with violence when fleeing or fighting is not an option. Death screams are long traveling and lasting, varying between high and low frequencies to maximize the chances of being located. These screams serve several adaptive purposes including warning others of the presence of a dangerous conspecific, seeking assistance from others (especially kin as their genetic fitness is directly impacted), briefly startling the aggressor, and even enticing other predatory actors to approach with the hope of acquiring low-cost resources (Hogstedt 2002). As mentioned earlier, females are more likely to report that screaming would be their first choice of defense against attack (Blanchard et al. 2001). However, much of the research on fear screams has been conducted on nonhuman animals. Further research is required in order to understand how this behavior manifests in humans.

Some evidence has also been reported showing antirape adaptations that increase defenses when the costs of being raped would be highest. As mentioned above, the fertile phase of a woman's menstrual cycle is a time in which rape can potentially result in pregnancy, increasing the costs of rape by subverting female mate choice. This is also the time at which the potential fitness benefits are highest for the attacker. Consequently, anti-rape adaptations that give protection specifically within the fertile phase of the menstrual cycle would be under increased selection pressure.

Post-Violence Adaptations

Post-violence adaptations work to decrease the fitness costs associated with having been violently victimized through behaviors that both reduce the

costs of the prior violence and decrease the probability of subsequent violence. Reducing fitness costs following violent victimization often involves behaviors designed to mitigate the problems associated with perceived vulnerability. Hypothesized post-violence adaptations include reputational fortification, behavioral changes, contextual (and sometimes continuous) hypervigilance, and seeking revenge.

Inflicting violence on another can be thought of as a welfare trade-off. Being the victim of violence imposes fitness costs on the victim and inclusive fitness costs through detriment to their kin. One way to minimize reputational costs and signal to competitors that any future violent victimization will come with a cost that is high relative to the benefits received, is to retaliate and/or seek revenge. McCullough et al. (2013) suggest that seeking revenge is a tactic of deterrence, and has evolved as an adaptive behavior to minimize the reputational costs imposed by violent victimization. Costs to reputation may reduce the mate value of the victim and their kin, but may also encourage further victimization from other individuals/groups. Victimization is a predictor of further victimization (McCullough et al. 2013). Retaliation may be sought by the victim or by their kin and social allies. The effectiveness of vengeance is affected by the length of time between the initial victimization, and the subsequent revenge. This is because the reputational damage inflicted by the initial victimization leaves the victim and kin with a reputation of exploitability, which both grows over the time that the violence has not been redressed and leaves a larger window for others to attempt to take advantage of this perceived exploitability.

Another hypothesized adaptation to reduce fitness costs after being the victim of violence is hypervigilance. Bisson et al. (2015) make a theoretical case for PTSD as a form of heightened defense following trauma. Fear and defensive behavior are a highly conserved adaptation in mammalian species. Selection for this is driven by predation, including intra-species predation. Behaviors associated with PTSD align well with anti-predation behaviors such as avoidance, attentive immobility, escape, aggressive defense,

appeasement, and tonic immobility resulting from hyperarousal, hypervigilance, and risk assessment, among other things. However, hypervigilance, hyperarousal, and anxiety act as defenses against possible harm and are adaptive only if calibrated to match the degree of threat in the environment. Too much anxiety can reduce fitness by disabling the individuals and preventing them from undertaking other fitness-enhancing behaviors. Too little anxiety and the individual is at increased risk from threats. Anxiety is regulated in order to balance this cost–benefit trade-off (Nesse and Marks 1994). Further, it is the subjective experience of the violence that dictates the level of the victim's hypervigilance.

Research showing the behavioral outcomes of PTSD symptoms, and their potential adaptive benefits, has been conducted. Mogg et al. (2007) found evidence of attentional biases in orienting gaze for fearful and angry faces, with high-anxious individuals more likely to orient to high-intensity fearful and angry faces than low-anxious individuals. Further research indicates that under low stress, high-anxiety individuals were biased toward attending to neutral faces over objects and attending to faces faster but for lower durations than controls. However, when stressed, high-anxiety individuals were avoidant of faces, again showing hypervigilance for the facial signals of others. Frankenhuys and Bijlstra (2018) used a low (university) and high (community) threat exposure sample to test for biased perceptions of facial emotion cues in crowd scenes. The community sample had higher exposure to violence as well as a more liberal threshold for identifying anger and sadness, showing a relationship between environmental threat levels and a bias toward over-perceiving the threat-identifying emotional signals. Combined, this research shows that individuals who have high levels of anxiety and/or sensitivity to being victimized are biased toward attending to and perceiving negative intent in the faces of others. This tendency would serve an adaptive function in an environment with a high probability of nefarious conspecifics.

Further perceptual and cognitive biases result from being subjected to violence and victimization that are specific to perceiving, interpreting,

and storing information about traumatic events. Lalande and Bonanno (2011) had participants' self-report events over a period of 4 years by responding weekly to a survey assessing whether events from a list of 50 options had occurred. At the end of the 4-year period, participants estimated how many times each of the 50 events had occurred. Participants generally underestimated the frequency of each event but gave more accurate responses for potentially traumatic events. Further, distress at the time of recall was related to the number of events recalled only for potentially distressing events. One of the most accurately remembered events was the experience of robbery or mugging.

Running Example: Post-Violence Antirape Adaptations

Examples of hypothesized adaptations that may be especially effective following violent sexual victimization include revenge and retaliation tactics, sex differences in the propensity for, and expression of, PTSD-like symptoms, and responses to forced impregnation. Seeking revenge against the perpetrator of sexual violence serves to decrease the reputational costs associated with being victimized. Further, retaliation signals a high cost-to-reward ratio to other potential sexual predators in the area and is used as a tactic of deterrence. This is especially important in the case of sexual violence as the costs to the victim not only include impacts on health and loss of resources but also a reduction in mate value, a loss of the genetic benefits of mate choice, and encouragement of further sexual victimization by conspecifics (McCullough et al. 2013).

Sex differences in the incidence and severity of PTSD-like symptoms following sexual violence can also be considered as an adaptive response to the increased selection pressure for antirape phenotypes. Women have a higher likelihood of developing PTSD-type symptoms and increased symptom severity following a violent attack. Bolstad and Zinbarg (1997) conducted a test of the uncontrollability/predictability model of PTSD, which states that symptom severity is

related to a perceived lack of control and/or triggering events that were beyond the control of the victim. Researchers considered self-reported child and adult sexual victimization, PTSD symptom severity, and locus of control in a sample ($n = 117$) of female undergraduates. Results show that increases in childhood sexualization are related to decreases in the locus of control. Further, low perception of control is related to high PTSD symptom severity following adult sexual victimization. Adult sexual victimization on multiple occasions or by force was related to higher PTSD symptom severity.

One possible explanation for the increased PTSD-like symptom incidence and severity in female victims of sexual violence is that rape is especially traumatic for women. This trauma is increased as a function of the woman's fertility (reproductive-age women experience higher trauma), marital status (married women experience higher trauma), and relationship to offender (trauma is highest if the rape perpetrator is a stranger), as each circumvents mate choice and/or reduces the genetic quality of offspring should the rape result in pregnancy (Thornhill and Thornhill 1990). When feeling unsafe in their environment, females self-impose significantly more restrictions on daily activities than males (Ávila et al. 2016). The trauma experienced as a result of rape acts as a psychological trigger to deter from entering, and/or increase hypervigilance to, the environment in which the trauma occurred.

Finally, adaptations have been hypothesized to directly reduce the fitness costs of a rape that results in pregnancy. Davis and Gallup (2006) make the argument that preeclampsia may have evolved as a strategy to terminate a pregnancy in the first trimester if there are biological signals (unfamiliar sperm) that the potential for paternal investment in the offspring is low. This strategy decreases maternal investment in offspring that have a low potential for genetic fitness, as in the case of rape pregnancies, where the woman's mate choice mechanisms have been circumvented. Davis and Gallup suggest that spontaneous abortion and postpartum depression may also result from a similar lack of paternal investment

signaling motivating a reduction in, or termination of, maternal investment.

Conclusion

The evolution of violent strategies for obtaining resources, reputations, and mating opportunities placed significant selection pressure on phenotypes that successfully avoid or reduce the costs associated with becoming a victim of violence. Adaptations to minimize the costs of violence decreased the benefit to the perpetrator, driving selection of more effective violent phenotypes. In this way, adaptations for inflicting, and avoiding/defending against violence evolved in an evolutionary arms race. Differential levels of selection pressure are placed on adaptations in response to violence, depending on the temporal context in which they are effective. This was made clear in this section by stepping through context-specific adaptations to minimize the costs of sexual violence.

Cross-References

- [Abusers: Husbands, Boyfriends, and Former Sexual Partners](#)
- [Coercive Control](#)
- [Costs and Benefits of Mate Poaching](#)
- [Evolutionary Perspectives on Rape](#)
- [Forced Copulation](#)
- [Intimate Partner Violence](#)
- [Physiological Mechanisms](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion and Violence](#)
- [Types of Sexual Coercion](#)

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Vigilance of Close Kin Versus Distant Kin

► Vigilance over Kin's Romantic Relationships

Vigilance over Kin's Romantic Relationships

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Synonyms

Conflict of mating; Kin interest in mating relationships; Vigilance of close kin Versus distant kin

Definition

The interest that parents and other family members demonstrate for an individual's romantic relationships.

Introduction

Individuals have a strong interest in the mate choices of other individuals with whom they are genetically related (Apostolou 2014b; Trivers 1974). As a consequence, mate choice usually

involves four parties: a woman and her family and a man and his family. This entry will examine the influence exercised by parents on their children's mate choices across different cultural settings.

In more detail, the entry will start by examining the reasons why parents have a strong interest in influencing their children's mating decisions. Subsequently, it will examine how such interest is manifested in preindustrial societies that base their subsistence on hunting and gathering and on agriculture and animal husbandry. Furthermore, it will examine how parental interest in influencing mate choice is manifested in modern post-industrial societies. It will also examine the implications of parental control over mate choice for sexual selection. Finally, the entry will conclude by proposing directions for future research in the area.

Why Parents Have an Interest in Their Children's Romantic Relationships?

The degree of genetic relatedness between parents and children is 0.5. That is, to say, on average, half of a parent's genes are inside its offspring and on average half of a child's genes come from its parent. As a consequence, the two parties have converging genetic interests: A parent cares about the 50 % of its genes that its child carries; a child cares about the 50 % of its genes that its parent carries. The degree of genetic relatedness indicates further that the two parties have diverging genetic interests. A parent cares also about the other 50 % of its genes that it does not share with its child; a child cares also about the other 50 % of its genes that it does not share with its parent (Trivers 1974). The diverging and converging genetic interests, mandated by the degree of genetic relatedness, result in a strong parental interest over their children's intimate relationships (Apostolou 2016b).

Diverging Genetic Interests and Parental Influence over Mating

Differences in genetic relatedness indicate that certain traits have differential fitness benefits in a

spouse and in an in-law. Genetic quality is a good example of such a trait: Some individuals carry more genetic mutations, while others have alleles that enable them to withstand better the challenges of the environment. Individuals are 0.50 related to their children and 0.25 related to their grandchildren, which means that it is more beneficial for them to get mates of superior genetic quality than in-laws of superior genetic quality: Individuals have more to lose if, due to poor genetic quality, their children rather than their grandchildren suffer survival or reproductive penalties, since they are more closely related to the former than to the latter (Apostolou 2014b).

Nevertheless, differential benefits are not a sufficient condition for disagreement to exist; for disagreement to exist, the choices one party makes need to inflict a cost to the other. If they do not, there would be no disagreement between the two. For instance, a mate of high genetic quality is beneficial to both parents and their children, albeit more beneficial to the latter than to the former. As both parties have to gain, no conflict should arise. Yet, conflict exists, the reason being that mate choice involves compromises, and the compromises that children are willing to make, in order to get traits they consider desirable, are not the ones their parents deem optimal.

More specifically, children are constrained by their own mate value with respect to the mate value of an individual they can attract (Li et al. 2002). That is to say, individuals looking for long-term mates cannot attract mates of much greater mate value than their own, because these mates would not be willing to enter in such a relationship, since it would not be optimal for them to accept mates of a mate value lower to their own (Apostolou 2014b; Buss 2003). Thus, mate choice inevitably involves compromises: In order to be able to attract and keep a long-term partner, mate seekers have to accept mates who score lower in desirable traits than they would ideally prefer.

The asymmetrical fitness benefits that certain traits provide result in mate seekers making compromises which are not to the best interest of their parents (Apostolou 2014b). For example, mate seekers would compromise on traits such as social

status and desirable family background in order to get a mate of good genetic quality. Nevertheless, because the latter trait is not as beneficial in an in-law, the accrued benefits will not balance the losses from the compromises in other desirable qualities. Therefore, from the parents' point of view, these compromises are not optimal. If they could exercise mate choice for their children, they would prefer a different mix of traits, a mix that would involve less of good genetic quality and more of other traits.

This argument is consistent with empirical findings: When children and their parents were given a budget of mate points in order to design a spouse and an in-law, respectively, children saved on traits such as good family background and similar religious background and spent what they saved in getting more of good looks (a proxy of genetic quality) and exciting personality (Apostolou 2014b). On the other hand, their parents saved on beauty and exciting personality and spent what they saved in getting more of good family background and similar religious background.

If parents and children had the same preferences, they would not make different compromises. For instance, if parents preferred good looks in an in-law equally to the degree their children prefer good looks in a spouse, they would end up making the same compromises. As a consequence, different evolutionary pressures are exercised on in-law and mate preferences, with the two diverging over traits which provide different fitness benefits to parents and children. Empirical research has, so far, identified that good looks and an exciting personality are preferred more in a spouse than in an in-law, while good family background and similar religious background are preferred more in an in-law than in a spouse (Apostolou 2014b, Apostolou 2015a; Buunk et al. 2008).

Overall, children are willing to engage in actions that benefit themselves but are costly to their parents such as getting good-looking mates, compromising on their social standing and family background. As a consequence, free mate choice involves an opportunity cost coming from diverging genetic interests, which is what parents

forgone when they allow their children to exercise mate choice freely on their own: Parents lose beneficial traits such as desirable family background, and their losses are not compensated by the gains in traits such as good looks, which are less valuable to them.

The opportunity cost of free mate choice results in selection pressure exercised on parents to place the mate choices of their children under their control: Parents who are predisposed to control mating have a selective advantage over those who do not, as the former are likely to have daughters and sons-in-law who maximize their inclusive fitness, while the latter are likely to have daughters and sons-in-law who maximize their children's inclusive fitness (Apostolou 2014b).

Converging Genetic Interests and Parental Influence over Mating

The degree of genetic relatedness between parents and children mandates that free mate choice involves a converging opportunity cost as well (Apostolou 2016b). If, for instance, their daughter mates with an aggressive and violent man who has low empathy, he may harm or kill her and her children, something that would be detrimental for the fitness of her parents who share their genes with her and her children. Or as viewed in another example, a young son, driven by his high libido, may attempt to form a sexual relationship with the wife of a high status and powerful man, which may lead to the latter killing him. This would impair considerably the fitness of his parents, who share half of their genes with him. Parents have certain qualities that enable them, if they are to interfere, to protect their children from making such erroneous choices.

To begin with, parents are older and more experienced than their children, which can enable them to distinguish better between potential mates, those who are dangerous for the welfare of their daughters and sons. Moreover, parents as opposed to their children do not base their decisions on libido and romantic love, which can cloud their judgment. In effect, parental intervention in mate choice can prevent children from

making erroneous decisions that may harm their own and their parents' fitness (Apostolou 2016b).

Apart from erroneous choices, children and especially daughters may fall prey to sexual assault and rape. Parents have qualities that enable them to protect their daughters from such danger: They are experienced, are physically strong, and have political connections. Thus, they can advise their daughters on how to avoid placing themselves in dangerous situations, provide physical protection, and ensure fierce retaliation if such an event occurs, which will act as a prevention measure that it does not occur in the first place.

Apart from erroneous choices and threats from others, children may also have issues that prevent them from effectively participating in the mating market. For instance, they may have a deformity, a health problem, and personality traits such as high introversion. Failure to find a partner affects negatively their reproductive success and consequently their own and their parents' fitness. Parents have qualities that can enable their children to address some of these issues.

To begin with, by being more experienced, parents can provide advice to their children on how to improve their performance in the mating market. Also, by having a wide and different social network than their children, they may use these social connections to help their children find appropriate mates. Last but not least, parents control resources, and they can divert some of these resources in compensating for the shortcomings of their children. For instance, in a preindustrial context, parents may be willing to pay a higher bridewealth or dowry in order to compensate for a handicap (e.g., a deformity) of their sons or daughters. In a postindustrial context, they may finance plastic surgery to address such a shortcoming, or they may choose to buy expensive cars or clothing to make their children more appealing in the mating market.

In sum, converging interests over mating, along with the capacity that parents have to improve the performance of their children in the mating market, give rise to a converging opportunity cost: If parents do not interfere in mate choice, they risk suffering fitness costs which arise from their children making erroneous mating

decisions and/or from failing to attract partners. The converging opportunity contributes further to the parental motive to control mate choice (Apostolou 2016b).

Overall, diverging and converging interests over mating give rise to an opportunity cost of free mate choice which motivates a strong parental interest over children's mate choices. This opportunity cost, and, thus, the strength of parental control over mating, is contingent on the sex of the in-law and the sex of the parent.

Contingencies in the Opportunity Cost of Free Mate Choice

Daughters Versus Sons

Women divert more parental investment to their children, and so they become the scarce reproductive resource to which men seek access (Trivers 1972). Accordingly, it is more beneficial for parents to control their daughters' than their sons' mate choices, as they can potentially extract more benefits from potential mates for them (Apostolou 2014b). Furthermore, a sexual adventure can commit a daughter's parental investment (i.e., pregnancy) to a man who is not necessarily beneficial for her. An unwanted pregnancy is not something that can be easily resolved, particularly in a preindustrial context. Also, a son can deny paternity, especially in a preindustrial context, where this is not something that can be easily proven. Moreover, due to parental uncertainty, men value chastity in a woman, as this preference reduces the risk of cuckoldry (Buss 2003).

For a similar reason, parents prefer a daughter-in-law who is chaste (Apostolou 2014b), a preference that reduces the risk of diverting resources in grandchildren which are not their own. Furthermore, due to menopause, the reproductive value of a daughter, following sexual maturity, decreases more rapidly with age than the reproductive value of a son. In effect, erroneous mate choices can have more detrimental consequences for the fitness of daughters than for the fitness of sons. In addition, because women constitute the scarce reproductive resource, they are the target of more intense mating effort, and, thus, they face a

higher risk of deception and assault by low-mate-quality men, who attempt to gain access to their reproductive capacity. Accordingly, the risk of erroneous mate choices is higher for daughters than for sons, which motivates parents to exercise more control over the mate choices of their daughters than the choices of their sons (Apostolou 2016b).

Moreover, women usually control less wealth than men (Whyte 1978), which means that daughters are more, and for a longer period, dependent on their parents' resources than sons. In addition, women are physically weaker than men that translates into daughters being more dependent on their family's protection than sons. Furthermore, because daughters are physically weaker than sons, parents can more readily employ physical force to inflict a cost on the former than on the latter. In effect, parents can control the mate choices of their daughters more easily than the mate choices of their sons.

Putting everything together, parents have a stronger incentive and a higher capacity to control the mate choices of their daughters than of their sons, which predicts that across societies, women will experience more parental control over their mating decisions than men.

Mothers Versus Fathers

The asymmetry in parental investment motivates men not only to compete between them, in being selected by women or by their parents (intersexual selection), but also to fight directly between them (intrasexual selection). The consequence of intrasexual selection forces is for men to be physically stronger than women, to tend to monopolize resources, to dominate the political scene and to have exclusive access to weaponry (Puts 2010). In effect, fathers and other male relatives control more resources than mothers and other female relatives, which in turn can be withheld if their children disobey them.

Moreover, the defense of the family unit rests on its male members, who are typically physically stronger, control weaponry, and have political connections. Consequently, children are more dependent on their fathers than on their mothers for protection. In addition, because fathers are

physically stronger than mothers, they have a higher capacity to use physical force on their children in order to align them with their will. Furthermore, because men have better access to political institutions (Apostolou 2014a), fathers can more readily employ them than mothers to inflict a cost to their children.

Also, due to menopause, women conclude their reproductive careers at an earlier age than men. This difference means that the residual reproductive value (i.e., the contribution to the population through future reproduction) is less for older women – to the point of being zero if they have passed the age of menopause – than it is for men of the same age (Apostolou 2014b). As a consequence, a mating deal such as an arranged marriage can be more beneficial for fathers, because it can provide them with resources that can be used for increasing their direct reproduction.

In addition, men have a higher reproductive variance than women, as they are not constrained by their biology in the number of children they can father. Men's reproductive success is positively related to the resources they control (Buss 2003), with men being able to deploy resources in such a way that enables them to practice polygyny and/or to attract multiple casual mates (Goode 1982). On the other hand, because women are constrained by their biology, conducting a polyandrous marriage and having multiple casual mates will not increase their reproductive output. Accordingly, a mating deal for their children, which would provide parents with resources, can potentially be more beneficial for a father than for a mother, as the former could use these resources to directly increase his reproductive success (Apostolou 2016b).

In sum, since fathers can inflict more cost to their children, and can convert more of the benefits they extract by controlling mate choice in reproductive success, they have more to lose if they allow their children to exercise mate choice freely. In turn, fathers have a stronger incentive than mothers to place their children's mating decisions under their control. In the following section, it will be examined how parental interest over mating is manifested across different society types.

Parental Influence over Mating Across Societies

Human societies can be classified in two main categories according to the level of technological development on which they base their subsistence, namely, preindustrial and postindustrial societies. Preindustrial societies can be further divided into the ones which base their subsistence on hunting and gathering and the ones which base their subsistence on agriculture and animal husbandry. Further divisions are possible, but for simplicity, the focus will be on the two aforementioned divisions.

Preindustrial Societies

Hunting and Gathering Societies

Starting from societies which base their subsistence on hunting and gathering, one study collected evidence from a sample of 190 contemporary foraging societies and analyzed their mating patterns (Apostolou 2014b). It was found that the most frequent mode of long-term mating, in approximately 70 % of cases, was arranged marriage, where parents choose spouses for their children. Similar findings were produced in a subsequent study which employed a smaller sample of societies from the Standard Cross-Cultural Sample (SCCS), which base their subsistence on hunting and gathering (Apostolou 2014b). It was found that, in approximately half of the foraging societies in the sample, marriages were arranged.

This study found also a considerable difference in the control that parents exercise on their daughters and their sons. In particular, for women, in approximately 53 % of the societies, marriage was arranged, and in approximately 8 %, it was based on free mate choice. For men, however, the percentages were 31 % and 40 %, respectively, indicating that men have a much larger space to exercise mate choice than women.

Both studies found that fathers and other male relatives exercise more control over their children's mate choices than mothers and other female relatives. In particular, in the study of 190 hunting and gathering societies, in about 44 % of the societies in the sample, fathers and

other male relatives arranged the marriages of their children with little input from mothers and other female relatives. In approximately 16 % of the societies, fathers dominated arrangements, but mothers had an important say; in approximately 34 % of the societies, both fathers and mothers had a roughly equal contribution; and in approximately 8 % of the societies, both parties contributed, but mothers dominated the arrangements (Apostolou 2014b). In the study based on the SCCS, it was found that in about 18 % fathers and other male relatives monopolized the marriage arrangements, in about 23.5 % both parties contributed but fathers had more say in arrangements, in about 47 % both parties had roughly an equal say, and in about 12 % both parties participated but mothers had more say (Apostolou 2014b).

Agropastoral Societies

The study which was based on the Standard Cross-Cultural Sample included a large number of societies which base their subsistence on agriculture and animal husbandry. Analysis of their mating patterns found that arranged marriage was the prevalent mode of long-term mating (Apostolou 2014b). More specifically, in societies which based their subsistence predominantly on agriculture, for women, arranged marriage was the most frequent mode of long-term mating in 40.3 % of the cases, followed by courtship subject to parental approval in 28.1 %, arranged marriage and free courtship marriage both practiced in 24.5 %, and courtship marriage in 7 % of the cases. For men, the respective frequencies were 30.4 %, 23.2 %, 23.2 %, and 23 %. In societies which base their subsistence predominantly on animal husbandry, for women, arranged marriage was practiced in 72.7 % of the societies, courtship subject to parental approval in 18.2 %, and both arranged marriage and courtship in 9.1 %, while there were no cases where marriage was based predominantly on courtship. For men, the respective ratings were 41.7 %, 25 %, and 16.7 %, while in 16.7 % of the cases, marriage was based on free courtship. In societies where subsistence was based on a combination of agriculture and animal husbandry, for women in

approximately 53 % of the cases, marriages were arranged, in 21 % were based either in arranged marriage or free choice, in 16 % on courtship subject to parental approval, and in approximately 10 % of the case were based on free mate choice, with the respective percentages for men being 39 %, 17 %, 11 %, and 33 %.

As opposed to ancestral hunting and gathering societies, several ancestral agropastoral societies left behind written records about their mating patterns. Accordingly, one study examined historical evidence and coded the mating patterns of 16 historical agropastoral societies (Apostolou 2014b). It was found that in 15 of them, marriages were arranged, and in one society in the sample, the historical sources were not clear about which was the dominant form of long-term mating.

Both studies also found that fathers and other male relatives are more influential than mothers and other female relatives over marriage arrangements. More specifically, in the study based on the SCCS (Apostolou 2014b), in societies which base their subsistence predominantly on agriculture, in 25 % of the cases, males monopolized marriage arrangements; in approximately 39 % of the cases, both parents participated but men had more say; in 22 % fathers and mothers had an equal say; and in 14 % both parents participated but mothers have more say. In societies which base their subsistence on animal husbandry, in 71 % of the cases, both parents participated in marriage arrangements, but fathers had more say, and in 29 % of the cases, both participated with roughly equal say. Finally, in societies which subsistence is based on both agriculture and animal husbandry, in 80 % of the case, both parents participated but men had more say, in 10 % men dominated marriage arrangements, and in 10 % both parents had an equal say.

In the study of 16 historical agropastoral societies, there was information about sex differences in parental control over mating for 14 societies (Apostolou 2014b). In ten societies, marriages were predominantly controlled by fathers, while in four societies, both parents participated but fathers had more say. Furthermore, there was no case reported where women had more say or where they dominated marriage arrangements.

Agropastoral Versus Hunting and Gathering Societies

Agropastoral societies are more technologically advanced than hunting and gathering ones, and consequently, they produce more material wealth. Accordingly, individuals in the former are likely to have more wealth at their disposal than individuals in the latter. For instance, individuals in agropastoral societies are likely to own land, animals, food surpluses, and money. On the other hand, individuals in hunting and gathering societies are likely to own some artifacts, weapons, and household objects. As a consequence, parents can gain more resources from controlling mate choice in agropastoral than in foraging societies.

In the same vein, parents are likely to control more wealth in agropastoral than in foraging societies, which means that children have more to lose if they disobey their parents in the former than in the latter societies. Furthermore, in hunting and gathering societies, individuals can rely on their own hunting or gathering effort in order to sustain themselves. In agropastoral societies, on the other hand, they need to rely predominantly on the cultivation of land or the herding of animals, which are owned by their parents. In effect, individuals are more dependent on their parents' resources in the former than in the latter societies. Parents can then use this dependence in order to impose their will. Overall, parents have more to gain by controlling mate choice, and they can more easily do so in agropastoral than in foraging societies, predicting a stronger control over mating in the former than in the latter (Apostolou 2016b).

Due to intersexual competition, men usually monopolize resources (Buss 2003); therefore, when more resources are available, men have control over more of them. Accordingly, in agropastoral societies, which produce more wealth, children have more to lose if they disobey their fathers than their mothers. In addition, more resources increase the incentive of others to monopolize them, which means that there is a higher need to defend the family unit and its members. Thus, children are more dependent on their male parents' protection in agropastoral than in foraging societies.

The higher amount of produced resources results also in greater emphasis to be placed on military preparation, which is the realm of men (Apostolou 2014b). As a consequence, more sophisticated and lethal weapons are produced, to make defense of resources more effective and/or to get more effectively the resources of other groups. To these weapons, men usually have an exclusive access, which amplifies their ability to impose their will by force on their children. Overall, fathers have a greater capacity to inflict a cost to their children in order to align them with their will in agropastoral than in foraging societies, which predicts that male parental control over mating will be stronger in agropastoral than in foraging societies.

Consistent with this prediction, the study which was based on the standard cross-cultural sample compared the patterns of mating between societies which base their subsistence on hunting and gathering and between the ones which base their subsistence on agriculture and animal husbandry (Apostolou 2014b). The results indicated that arranged marriage was more dominant in agropastoral than in foraging societies. Last but not least, in agricultural and pastoral societies, male parents and relatives had more decision-making power over marriage arrangements than female ones. Actually, there was not even a single case reported where female relatives dominated marriage arrangements.

Postindustrial Societies

In postindustrial societies, parents cannot control their children's mating decisions directly, and they do so indirectly through manipulation (Apostolou 2014b). In particular, Sussman (1953, p.80) reported that parents employ means such as "cajolery, persuasion, appeals to loyalty, and threats" in order to influence their children's mating behavior. Another study found that modern Chinese parents in the USA attempt to create environments, such as staging a barbecue, in which their children can meet other individuals of Chinese descent and, therefore, of desirable background (Ikels 1985). A more comprehensive study of manipulation identified 12 tactics that parents employ on their children and 4 tactics

that they employ on their children's mates (Apostolou 2014b).

In more detail, when parents find their daughters and sons engaging in undesirable relationships, they attempt to break these relationships either by manipulating their children and/or by manipulating their children's mates in terminating the relationship. For example, in the former case, they advise their children against the relationship, they attempt to bribe them to dissolve the relationship, or they try to match them with different mates. In the latter case, they threaten their children's mates, they are rude to them, or they try to find out things to use against them (Apostolou 2014b). Parental manipulation can cause strain upon their children's relationship, effectively undermining it. For instance, one study found that such kind of manipulation can indeed be effective in weakening an undesirable relationship (Apostolou et al. 2015).

There is evidence that suggests that in a post-industrial context, parents are more concerned about the mating decision of their daughters than of their sons. In a Greek-Cypriot sample, one study examined the willingness of parents to apply 12 tactics of mate choice manipulation separately on their daughters and sons (Apostolou and Papageorgi 2014). It was found that parents were more willing to apply manipulation for the purpose of influencing mate choice on their daughters than on their sons.

Preindustrial Versus Postindustrial Societies

Postindustrial societies are more technologically advanced than preindustrial ones. Technological orientation demands a long period of training before one is able to participate effectively in the labor market; thus, in postindustrial societies, children are married at a later age when they are financially independent from their parents. In addition, the presence of social protection systems, such as the police, results into children being less dependent on their families for physical protection. In preindustrial societies, however, children are married relatively young, since a long period of education or training is not required and they are, therefore, more dependent on the resources of their parents (Apostolou 2014b).

Also, as the social protection systems are not well developed or inexistent, children have to rely on their parents for physical protection. Accordingly, children are much more dependent on their parents' resources in preindustrial than in postindustrial societies.

In postindustrial societies, individual rights are well protected, and parents are prevented by the rule of law to use physical force on their children. But even if they were allowed to do so, this course of action would not be easy, since children are getting married at an older age when they are usually physically stronger than their parents. On the other hand, in preindustrial societies children are married younger, which means that their parents are also younger and thus better able to use physical force on them. In sum, the capacity of parents to employ physical force on their children to align them with their will is larger in pre-industrial societies than in postindustrial ones. Overall, parents in preindustrial societies can control their children's mate choice more easily than parents in postindustrial societies (Apostolou 2016b).

Furthermore, children in postindustrial societies are married at an older age than children in preindustrial ones, which means that their parents are also older and have a lower reproductive capacity. Therefore, any potential gain from control over mating has a limited potential to be converted into additional offspring in post-industrial than in preindustrial societies. This capacity is further reduced by the fact that polygyny is not allowed in the vast majority of post-industrial societies. This is not the case, however, for preindustrial societies where polygyny is usually allowed and children are married young and have relatively young parents who can convert benefits from a marriage deal into additional children.

Also, in postindustrial societies, children are married at a later age so they are more experienced, which means that they can make fewer erroneous mate choices. Also, the widespread use of contraceptives and the after-day pill, along with the effective treatment of most sexually transmitted diseases, turns erroneous mate choices in postindustrial societies less

consequential, reducing in effect the interest of parents to control their children in order to protect them. Overall, it is predicted that parental control over mating is stronger in preindustrial societies than in postindustrial ones.

Moreover, in preindustrial societies, wealth is predominantly controlled by the male members of a society, while in postindustrial societies, it is more equally distributed across the sexes (Apostolou 2014b). In addition, men in preindustrial societies are less constrained in employing their physical strength in controlling their children. Also, fathers can benefit more by a marriage arrangement in a preindustrial context, as the extracted wealth goes under their control. In addition, preindustrial societies are more aggressive than postindustrial ones, and given that war and protection are predominantly the domains of men (Puts 2010), children are more dependent on their male parents' protection in preindustrial than in postindustrial societies.

As discussed above, in preindustrial societies, as opposed to postindustrial ones, polygyny is permitted, and parents are relative young when their children get married. Nevertheless, these differences favor predominantly men who have a higher residual reproductive value and a higher reproductive variance than women. Overall, male parents have more to gain by controlling their children's mate choices, and they can more easily do so, in preindustrial than in postindustrial societies, which predicts that male parental influence will be higher in the former than in the latter.

Consistent with this prediction, in all postindustrial societies, marriage is typically based on free choice, but parents exercise an influence on their children's mate choices, primarily through manipulation (Apostolou 2014b). In addition, although in preindustrial societies fathers dominate parental control over mating, this pattern reverses in postindustrial societies.

More specifically, one study asked a sample of Greek-Cypriot parents to indicate their willingness to influence their children's mate choices (Apostolou 2014b). Mothers reported a significantly higher willingness to do so than fathers. In addition, participants were also asked to indicate whether their parents had or have been

attempting to influence their mate choices. Participants reported that their mothers had or have been attempting to influence their mate choices more than their fathers. Finally, in the studies of manipulation discussed above, it was found that mothers were more willing to employ manipulation in order to influence their children's mate choices than fathers (Apostolou 2014b; Apostolou and Papageorgi 2014).

One reason behind this reversal is that fathers in postindustrial societies have not much to gain from influencing their children's mate choices, which weakens their motivation to do so. On the other hand, due to paternal uncertainty, if children make erroneous choices that reduce their fitness, mothers have potentially more to lose because they are more certain that their children are actually their own. As a consequence, mothers have a stronger incentive than fathers to influence their children's mate choices, in order to protect them from making erroneous mate choices. This difference is present in preindustrial societies, but it is masked by the stronger interest of fathers to control mate choice in order to benefit themselves. In postindustrial societies, where this interest resides, mothers' interest to influence mate choice becomes more apparent.

Parental Control over Mating Across Time

The genus *Homo* appeared on earth approximately two million years ago, and for most of this period, our ancestors lived in small bands of hunters and gatherers; thus, most of human evolution took place in this context (Tooby and Cosmides 1990). About 10,000 years ago, the agropastoral revolution took place, and most of our ancestors shifted to a non-nomadic life and a mode of subsistence based on agriculture and the herding of animals (Price 2000). Human societies were to be transformed again following the Industrial Revolution, which began in the eighteenth century Britain and has led to the modern way of life.

On the basis of the evidence on the mating patterns across different society types discussed above, specific predictions can be made about the prevailing patterns of mating at each stage of human evolution. Starting with the former and

the longest one where our ancestors lived as hunters and gathers, it is predicted that parents would have been influential over their children's mate choices. Direct information on ancestral hunter and gatherer mating patterns is lacking, as these societies did not leave behind any written records pertaining to the first and the longer period of human evolution. Nevertheless, there is a good source of information, namely, contemporary hunters and gatherers whose mating patterns have been studied by anthropologists. The mating patterns typically found in these societies are likely to be characteristic of the hunter-gatherer way of life and, consequently, are likely to be similar to those in ancestral hunter-gatherer societies (Apostolou 2014b).

Anthropological evidence indicates that in ancestral foraging societies, mate choice would be regulated, with parents exercising considerable influence over their children's mate choices (see above). Phylogenetic analysis, which attempts to reconstruct the conditions prevailing in ancestral societies, has provided additional evidence that the patterns of mating found across contemporary hunters and gatherers (e.g., arranged marriage) were also prevalent in ancestral ones (Walker et al. 2011).

About 10,000 years ago, a different period of human evolution begun as our ancestors started shifting from a mode of subsistence based on hunting and gathering to a mode of subsistence based on agriculture and the herding of animals (Price 2000). As historical evidence is lacking about ancestral foraging societies, comparisons between ancestral foraging and ancestral agropastoral societies cannot be made. Comparisons between contemporary hunting and gathering societies and agropastoral societies can be made, however, that can be revealing about the effects of the ancestral transition. One study that made such comparisons found that in agropastoral societies, parental influence, mainly male parental influence, is stronger than in foraging societies and male children experience considerable losses to their freedom to exercise mate choice (Apostolou 2014b). This finding is also consistent with evidence from historical agropastoral societies, where male parental control over mating

dominates and where both male and female offspring have a very limited space to exercise mate choice freely (Apostolou 2014b). Accordingly, it can be concluded that the agropastoral revolution resulted in the strengthening of parental control over mating and the limiting of the space that individuals had to exercise mate choice.

Furthermore, comparisons between pre-industrial and postindustrial societies indicate that the transition to industrialism, which started about three hundred years ago, brought gradually a weakening in parental control over mating and an increasing freedom to individuals to exercise mate choice. It also brought a weakening in fathers' interest to influence their children's mate choices.

In sum, on the basis of the available evidence, the following conclusions can be reached: During the earliest and longer period of human evolution, where our ancestors lived as hunters and gatherers, parents had been influential over their children's mate choices. The transition to a mode of subsistence based on agropastoralism increased considerably the strength of this influence, while the transition to industrialism in the eighteenth century has resulted in a sharp decline in this influence.

Sexual Selection and Parental Control over Mating

When parents succeed in controlling their children's mating decisions, they become a significant sexual selection force: Traits which make an individual more likely to be chosen by parents as a daughter- or son-in-law are selected and increase in frequency in the population (Apostolou 2014b, 2016b). The anthropological and historical records indicate that during most of the human evolutionary time, parents had been successful in doing so. In turn, this leads to the conclusion that parental choice has been an important sexual selection force, driving sexual selection in the human species (Apostolou 2014b).

This conclusion runs against the assumption made by several evolutionary scholars that sexual selection in our species has been driven by

individual mate choice and in particular by female choice (Miller 2000). There is a combination of factors that led to the wide adoption of this assumption, including the evolutionary theory on parental investment, evidence from nonhuman animal studies, and the patterns of mating prevailing in modern postindustrial societies.

Starting from the former, the asymmetry in parental investment, with females diverting more to their offspring than males, turns the former to become the scarce reproductive resource to which the latter seek reproductive access (Trivers 1972). The asymmetry in parental investment leads to the prediction that there will be an asymmetry in mating effort, with males seeking access to females and females choosing to which males they will grant this access. In turn, this asymmetry causes another asymmetry, namely, stronger sexual selection pressure exercised on males than on females: Since females choose and males are chosen, males are under stronger selection pressure than female to evolve traits that will make them more likely to be chosen as mates. In consequence, sexual selection is driven by female choice.

This model of sexual selection seems to fit well the patterns of mating in several nonhuman animals (Andersson 1994). The classic example is peacocks' tails: Strong female choice has led to the evolution of large and elaborated tails, which serve the purpose of making peacocks more appealing to peahens (Zahavi and Zahavi 1997). This model appears to fit well also the patterns of mating observed in modern postindustrial societies, where men exercise considerable mating effort, engaging in a variety of behaviors in order to appeal to women, ranging from risk taking to buying expensive cars (Buss 2003; Miller 2000).

This model is, however, inconsistent with the patterns of mating observed in modern and ancestral preindustrial societies: Women do not choose mates, but their parents do so for them. It follows that it is unlikely for female choice to be the primary sexual selection force driving sexual selection, with parental choice being a better candidate: Diverging and converging interests over mating motivate parents to control their children's

mating decisions (Apostolou 2016b). The asymmetry in parental investment makes it more profitable for parents to control the mate choices of their daughters than of their sons (Apostolou 2014b). It is also more fitness increasing for male parents than female parents to control mate choice. Accordingly, men choose other men as spouses for their daughters, which appears to be the most common pattern of mating across preindustrial societies (Apostolou 2014b). Accordingly, during most of the period of human evolution, sexual selection has been driven predominantly by male parental choice.

Although it is difficult to change the established way of thinking, an endeavor that becomes even more difficult if one considers that most research takes place in a postindustrial context where individuals are relatively free to choose their mates, doing so is necessary in order to understand the selection forces that have shaped traits involved in mating.

Areas of Future Research

Although it has been known to anthropologists for several decades now that in preindustrial societies parents and other family members exercise considerable influence over their children's mate choices, theoretical and empirical evolutionary work in this domain has only been recently initiated. Accordingly, this section proposes directions for future research, which can be fruitful in enabling us to understand kin's influence over mating, and its evolutionary implications.

Evidence from historical studies indicates that the transition from a context where mate choice was regulated to a context where it is not has occurred very recently for selection forces to have managed to adjust traits involved in mate choice to modern conditions. As a consequence, several traits may not be able to meet the demands of a modern context where mate choice is not regulated, resulting in individuals who have them to experience poor mating performance (Apostolou 2015b). It has been argued that such traits include mechanisms that regulate sexuality, specific personality traits, mechanisms which

regulate attention to looks, mechanisms which regulate mating effort, and flirting skills (Apostolou 2015b, c, 2016a, e; see also 2016c). Future research needs to examine empirically whether there is variation in these mechanisms that is not optimal for a free mate choice context and to which degree this variation impairs the formation of intimate relationships. Future research need to attempt also to identify other factors which exhibit a nonoptimal variation and to examine possible interactions between the different factors in affecting performance in the mating domain.

All research efforts so far have focused on the influence that parents exercise over their children's mate choices. However, the degree of genetic relatedness indicates that genetic relatives other than parents would also have a strong interest in an individual's mating decisions, and consequently they would be motivated to exercise some influence over it. For instance, it would be harmful for a brother's fitness if his sister marries an individual who scores very low in kindness, as he can physically harm her, decreasing in effect his fitness as he is genetically related to her. Thus, it would pay for him to interfere in her mate choices, prompting her, for instance, to stay in a relationship with a man who is kind and to terminate a relationship with a man who is not. Future research needs to study in detail the influence that genetic relatives other than parents, including grandparents, siblings, uncles, aunts, and cousins, exercise on an individual's mating decisions.

Furthermore, in postindustrial societies, parents exercise indirect influence over their children's mating decisions, predominantly through the use of manipulation. Several tactics of manipulation that parents use for this purpose have been identified (Apostolou 2014b; Apostolou and Papageorgi 2014). Nevertheless, these tactics have only been studied in one culture (i.e., the Republic of Cyprus), and future studies need to examine the manipulation tactics that parents employ in different postindustrial cultures. Additional empirical work that would examine how effective these tactics are in aligning children's mate choices with the preferences of their parents is also required.

Future theoretical and empirical research can benefit by adopting an evolutionary perspective, where parental choice rather than female choice had been dominant during human evolutionary time, in understanding other phenomena which relate to sexual behavior. For example, rape has been interpreted as a strategy that has evolved to enable low-mate-quality men to bypass female choice (Thornhill and Palmer 2000). Nevertheless, since women in the preindustrial context are predominantly controlled by their parents, this argument needs to be revised: If rape is indeed an evolved strategy, it has evolved to bypass predominantly parental choice and not female choice (Apostolou 2014b). Furthermore, the presence of this strategy in ancestral times would have exercised pressure on parents to evolve strategies that would enable them to protect their daughters. In turn, such strategies would weaken selection pressures on women to evolve rape-protection strategies, as they receive the required protection from their parents. In a postindustrial context, where parents are out of the picture, women may be relatively unprotected and vulnerable to rape (Apostolou 2014b). Future research needs to examine the consequences for women lacking their parents' protection in increasing their vulnerability to rape and sexual assault.

Same-sex attractions remain currently one of the toughest challenges for evolutionary scholars to explain: Given the evolutionary importance of reproduction, any predispositions for same-sex attraction would be eliminated by selection forces. However, same-sex attractions are found in relatively high prevalence in the population, especially in women (LeVay 2010). Such a high prevalence is less enigmatic if one considers that human sexuality has been shaped in a context where mate choice was regulated: Individuals who experience same-sex attractions would get opposite-sex spouses from their parents, and they would have children with them, passing their dispositions to future generations. Thus, such dispositions would be maintained in the population, because they have a limited negative fitness effects (Apostolou 2016d). Future research needs to investigate further the implications of parental control over mating in understanding the evolution of same-sex attractions.

Conclusion

To conclude, this entry has demonstrated that across human societies, parents exercise strong control over their children's mate choices. In preindustrial societies, the influence is direct, and it is manifested in arranged marriage, where parents choose spouses for their children, while in postindustrial societies, the influence is indirect, and it is manifested predominantly through manipulation. It was also argued that there are good reasons to believe that parents had been exercising strong control over mating during most of the period of human evolution. This being the case, sexual selection has been driven predominantly by parental choice. Parental control over mating has received little attention from evolutionary-minded scholars, and as a consequence, there is considerable opportunity for future research in this area.

Cross-References

- [Conflict of Mating](#)
- [Kin Interest in Mating Relationships](#)
- [Parent-Offspring Conflict](#)
- [Parent-Offspring Conflict \(Trivers\)](#)
- [Parental Investment and Parenting](#)

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Vigilance, Sentinels, and Alarms

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Synonyms

Antipredator behavior

Definition

Vigilance is attentive behavior directed at an animal's surroundings to detect or monitor perceived dangers. Sentinels are individuals in a social group that scan the surroundings while groupmates are engaged in other activities nearby. Alarm calls are vocalizations given by animals in response to perceived danger from predators.

Introduction

Predation is a fundamentally important selective pressure.

Given the large fitness costs of failing to detect and avoid predators, there should be strong selective pressure for behaviors that enable the early detection of possible threats.

Vigilance

Vigilance involves scanning the environment for possible dangers. Despite its clear individual

benefits, vigilance may have significant opportunity costs in the form of time taken away from other important activities, such as foraging, mating, and socializing. Accordingly, vigilance may have chronic effects on individual fitness. Thus, if predation risk varies over time or space, then animals would benefit from adjusting vigilance to levels of predation risk – that is, they should be more vigilant in high-risk environments and less vigilant in low-risk environments (Lima and Dill 1990). The benefits of improved early predator detection through the collective vigilance of multiple animals are often considered to have central importance in the evolution of sociality. Numerous studies of group-living animals have demonstrated a group-size effect on vigilance, in which animals in larger groups reduce vigilance levels and instead allocate more time to other activities such as feeding and resting (Roberts 1996). Two well-supported explanations for the group size effect on vigilance include the “many eyes hypothesis,” whereby overall predator detection probability increases in larger groups because there are more eyes scanning for predators; and the “dilution effect hypothesis,” whereby individual risk of mortality during a predator attack decreases in larger groups because there are more individuals present. Some animals, notably many species of nonhuman primates, do not show a consistent group size effect on vigilance, perhaps because much vigilance in primate groups is directed within the group to monitor the risk of competition with groupmates, which may increase as group size increases (Treves 2000).

Sentinels

An interesting variation on the benefits of social vigilance can be seen in species with sentinel systems, in which multiple individuals coordinate their vigilance such that one or more individuals stand guard, often from a vantage point, and scan the surroundings while nearby groupmates are engaged in other activities such as foraging. Sentinel behavior has been described in a variety of birds and mammals (Bednekoff 2015). A key question about the evolution of sentinel behavior

is whether sentinels are safer than nonsentinels because of their vigilance, or if sentinels are at greater risk because they are more likely to be targeted by predators due to their relatively exposed positions. This question is crucial for clarifying whether sentinel behavior can be viewed as a fundamentally “selfish” behavior, or if cooperation (e.g., kin selection or reciprocal altruism) is necessary to explain its evolution (Clutton-Brock et al. 1999).

Alarms

Many prey animals produce specific alarm vocalizations when they detect a predator. The ultimate function of alarm calling – that is, the nature of the fitness benefits to the caller – has been a topic of considerable debate in behavioral ecology. One prevalent view is that alarm calls function primarily to alert others to danger (Smith 1965). In this view, alarm calls are altruistic insofar as they benefit others but potentially put the vocalizing animal at greater risk by drawing the predator’s attention (Sherman 1977). Kin selection may explain the evolution of altruistic alarm calling if the inclusive fitness benefits that accrue to the caller by alerting kin to danger exceed the direct cost of giving the alarm call. An alternative hypothesis is that alarm calls function primarily to signal to predators that they have been detected, thereby discouraging them from attacking (Smythe 1970). In this view, alarm calls provide direct fitness benefits to the vocalizing animal. Landmark research on vervet monkeys (*Chlorocebus pygerythrus*) revealed that vervet alarm calls given to different predators are acoustically distinct and that receivers appear to discern this information from the calls alone by exhibiting appropriate evasive responses to experimentally broadcast calls (i.e., “playbacks”) in the absence of an actual predator (Seyfarth et al. 1980). Subsequent research has demonstrated that alarm calls in a variety of animal taxa can encode information about predator type and the degree of risk. Signals that communicate such

information in a manner analogous to basic words have been termed “functionally referential” (Marler et al. 1992).

Cross-References

► Grouping and Predation

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Violation of Long-Term Mate Preferences

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Synonyms

Deception; Intersexual strategic interference; Long-term mating; Mate preferences; Mate selection

Definition

Violations of long-term mate preferences refer to instances in which a person in a long-term relationship has mate preferences that were in place when the relationship commenced but subsequently are not being met.

Introduction

According to an evolutionary perspective, mate preferences evolved through natural and sexual selection to adaptively guide individuals to select reproductively viable mates (Buss and Schmitt 1993; Symons 1979). A host of evidence has supported various hypotheses on mate preferences, including studies conducted through surveys, numerous naturalistic settings, and modern, live-interactive contexts (Li and Meltzer 2015). Although mate preferences have, on average, led to adaptive choices over thousands of generations, they are not always fulfilled in the mates that people actually select, and even when they initially are, conditions occur that eventually prevent at least some preferences from being met. Indeed, selecting mates and maintaining them over the course of a long-term relationship involves a large degree of judgment uncertainty and

dynamics between individuals whose reproductive interests are overlapping but far from identical. Initial assessments can be inaccurate, conditions can change, and partners often face sexual conflict; hence, there is plenty of room for mate preference violations to occur. Here, the focus is on violations of long-term mate preferences – ways in which one's preferences for a long-term, committed relationship partner are not being met during such a relationship.

Long-Term Relationships

Long-term relationships involve commitment over a relatively long time horizon and include steady relationships and marriage. From an evolutionary perspective, long-term mating is adaptive for many reasons including that it allows partners to jointly pool resources and efforts in cooperatively raising offspring (Buss and Schmitt 1993). Although mate preferences likely evolved to adaptively guide the selection of reproductively beneficial mates, there are several reasons that mate preference violations may occur in a long-term relationship, including the following: (1) inaccurate assessment of traits during the courtship phase, (2) a relative decline in a partner's mate value, and (3) conflicting strategic interests. Generally, lower consistencies between ideal mate preferences and associated perceptions of one's partner result in lower levels of relationship satisfaction. However, the consequences of long-term mate preference violation also vary depending on factors such as an individual's own mate value and whether there are alternative candidates who are more attractive than one's existing partner.

Inaccurate Initial Assessment of Traits

During the mate selection process, individuals assess one another and try to obtain mates who are in line with their evolved mate preferences. Preferences have been characterized by evolutionary psychologists using various models, including

those where individuals utilize minimum-criteria trait thresholds as well as priorities to ensure reproductive viability. However, the precise value of each trait may be hard to observe. Indeed, this is a potential reason why many speed-dating studies have failed to find correspondence between people's mate preferences and the criteria that they use to select actual mates (Li and Meltzer 2015). More generally, trait and other mating-relevant information is likely imperfect not only in the first few minutes of initial meetings such as in modern speed-dating events, but even over time. A potential barrier to accurate assessment is that traits are often misrepresented by individuals being assessed. For example, especially during mate selection, people may present themselves as favorably as possible and not disclose negative aspects about themselves; women may attempt to appear younger – and hence, more fertile – than they really are; and men may attempt to represent higher-than-actual social status and resources (Tooke and Camire 1991). In the modern day, the multi-billion dollar cosmetics industry and rapidly expanding plastic surgery market attest to the prevalence of women appearing younger and more reproductively fit. Likewise, expensive sports cars are often purchased by men who incur large amounts of debt and hence, cannot actually afford (over the long haul) such expensive indicators of status. Indeed, in a competitive mate-market context, the strategic use of misrepresentation may have been selected for because successful deception can promote one's own reproductive fitness (Tooke and Camire 1991).

Relative Decline in Partner's Mate Value

Another way that preferences can be violated within an ongoing long-term relationship is when, over the course of a relationship, one partner loses or gains mate value relative to the other person. Because mate preferences or standards tend to be indexed to people's own desirability in the mating market (e.g., more physically attractive women desire men with more resources), changes in relative mate value will tend to violate the mate

preferences of the person whose mate value becomes relatively higher. For example, a man may lose his job, which decreases his social status and mate value and thus, his partner's preference for high social status may be violated. Indeed, women are especially likely to leave a marriage when the husband loses his job. Similarly, for women more than men, a decrease in mate value could occur due to beauty (and fertility) fading with age, which may violate partners' preference for a physically attractive and fertile mate. Noticeable changes in health can also directly impact both men's and women's mate value. A change in the operational sex ratio could also trigger relative changes in mate value, in that the sex that is decreasingly represented in the population gains position and leverage (by having more potential mates competing for them) over the sex with whose numbers have increased.

Conflicting Strategic Interests

People in long-term relationships may also have their preferences violated from conflicts in mating strategy. For instance, it may be in the interest of one person to have backup mates or affair partners but to have one's partner remain faithful and removed from mating options. Men and, to some extent, women benefit reproductively from engaging in extrapair mating (e.g., Greiling and Buss 2000). Indeed, women may have evolved a dual mating strategy in which they acquire investment from their primary mate and higher-quality genes for their progeny via timely sexual affairs outside the relationship when women are ovulating and thus, most likely to become pregnant from having sex. However, a dual strategy would directly violate men's evolved preference for a long-term partner's fidelity and hence, paternity certainty. Similarly, men's sexual activity outside a long-term relationship may violate women's preferences by diverting energy and resources to others. Research on sexual jealousy (Buss et al. 1992) indicates that men's long-term mate preferences are especially violated when their partners engage in *sexual* infidelity, whereas women's long-term

preferences are more negatively affected by a partner's *emotional* infidelity. Specifically, women's sexual infidelity threatens men's evolved desire for paternity certainty, whereas a man falling in love with another woman threatens his continued investment of time, energy, and resources in the current relationship.

When Long-Term Preferences Are Violated

Several things can happen when long-term preferences are violated. First, the violated person may exit the relationship or attempt to turn to or find replacement partners. These actions in turn constitute violations to the preferences of the other partner, who may then react with his or her own violation-response tactics. Over time, balance may be restored or, if not, the relationship may dissolve.

Violated individuals may also attempt to eliminate or reduce the cause of the violation. For instance, a person may threaten a partner's potential extrapair mate or engage in other mate guarding behaviors to reduce the likelihood of a partner's infidelity. Similarly, the person who has comparatively lower mate value may engage in mate retention tactics to maintain the relationship and persuade the partner of higher mate value not to leave. Along these lines, Buss (1988) identified five categories of mate retention tactics: positive inducements (e.g., "Complimented me on my appearance"), public signals of possession (e.g., "Held my hand while other men were around"), direct guarding (e.g., "Wanted to be with me all the time so that I could not meet anyone else"), intersexual negative inducements (e.g., "Became angry when I flirted too much"), and intrasexual negative inducements (e.g., "Stared coldly at a man who was looking at me").

Men with lower mate value, in particular, may resort to cost-inflicting mate retention behaviors (Daly and Wilson 1993). For example, men with lower-status jobs and lower income are more likely to inflict physical harm on their intimate partners. Women, on the other hand, use more direct guarding and other forms of intersexual

negative inducements, which are also cost-inflicting on their partners and reduce the chances that the men would have to cheat on them. Positive inducements and public signals of possession, which have been called benefit-inducing mate retention tactics (Miner et al. 2009), are displayed more by and toward partners with higher mate value, and they may provide a more positive relationship climate in which partners are likely to be satisfied. Such behavior (e.g., buying one's partner gifts, planning romantic getaways) provides the mate with more inducements to stay and keep investing in their partner and signals to others that they are no longer available.

Similarly, the partner with higher mate value can also engage in positive inducements in order to restore the equilibrium of mate values in the relationship (e.g., asking a male partner to get a higher-paying job or persuading a female partner to diet and slim down). Although confrontations can be initially distressing for both individuals, attempts to get partners to change for the better is positively associated with relationship well-being over time (Baker and McNulty 2015). If all else fails, an individual may choose to terminate a long-term relationship, especially if the individual deems that he or she has desirable alternative mates that can be attained or, if relevant, that he or she has enough resources to take care of any extant offspring. Another possibility, albeit less likely even in today's evolutionarily novel environment, would be for both partners to agree on an open or polyamorous relationship in which both partners continue investing in the current relationship (perhaps at a reduced level) while diverting some of their resources into acquiring or maintaining additional mates.

Conclusion

In summary, violation of long-term mate preferences can occur due to many factors, including errors in judgment from imperfect information and partner's deception, the relative erosion of a partner's mate value over time, and conflicts in mating strategies. The consequences of long-term mate preference violation are often dependent on

factors such as the extent of the discrepancy of mate value. In response to mate preference violations, individuals in long-term relationships may exit the relationship or seek alternatives or attempt to rectify the violation. In the modern world, there are likely many evolutionarily novel conditions – including the proliferation of virtual competitors and potential mates encountered in media outlets – that trigger such violations in increasing frequency. Future research could carefully investigate such factors that are likely increasing the incidence of mate preference violation to historically unprecedented levels. At the same time, further work looking into the effectiveness of different types of mate retention tactics may provide insights into whether the increasingly high incidence of long-term relationship failure in modern society can be curbed.

Cross-References

- ▶ Cues to Infidelity
- ▶ Detecting Infidelity
- ▶ Dual-Mating Hypothesis
- ▶ Error Management Theory
- ▶ Evolution of Long-Term Pair-Bonding in Humans
- ▶ Female Choice
- ▶ Female Choice and Sexual Conflict Theory
- ▶ Female Deception
- ▶ Female Infidelity
- ▶ Female Manipulation of Men
- ▶ Female Mate Choice
- ▶ Female Mate Choice (Intersexual Selection)
- ▶ Human Courting
- ▶ Infidelity
- ▶ Infidelity Risk
- ▶ Intimate Partner Violence
- ▶ Jealousy and Infidelity
- ▶ Long-Term Mating
- ▶ Male Detection of Deception
- ▶ Male Mate Choice
- ▶ Male Sexual Jealousy to Deter Partner Infidelity
- ▶ Manipulation
- ▶ Manipulation and Dishonest Signals
- ▶ Manipulation by Others
- ▶ Mate Preferences
- ▶ Mate Preferences After Having Children
- ▶ Mate Retention
- ▶ Mate Retention After Children
- ▶ Mate Retention and Romantic Attachment
- ▶ Mate Retention Strategies
- ▶ Mate Retention Tactic
- ▶ Mate Selection Strategy (Version of Sexy Sons Hypothesis)
- ▶ Mate Value
- ▶ Mate Value Inflation
- ▶ Mating Strategies
- ▶ Mating Strategy Equilibria
- ▶ Men With Poor Mating Prospects
- ▶ Men's Mate Preferences
- ▶ Men's Suspicions of Partner Infidelity and Women's Defection
- ▶ Observed Mating Behavior and Women's Long-Term Mating
- ▶ Operational Sex Ratio
- ▶ Perceptions of Infidelity
- ▶ Perceptions Of Infidelity Cues
- ▶ Polyandry
- ▶ Polygamy
- ▶ Polygamy in Humans
- ▶ Polygyny
- ▶ Prevention of Infidelity
- ▶ Relationship Dissolution
- ▶ Self-Esteem Reflects Assessments of Valuation
- ▶ Self-Esteem Tracks Mate Value
- ▶ Self-Evaluations Track Perceived Mate Value
- ▶ Sex Differences in Human Mate Preferences (Buss, 1989)
- ▶ Sex Differences in Long-Term Mating Preferences
- ▶ Sex Ratio and Men's Long-Term Mating
- ▶ Sexual Assault and Intimate Partner Violence
- ▶ Sexual Coercion as a Mechanism of Sexual Selection
- ▶ Sexual Conflict in Mating Strategies
- ▶ Sexual Conflict Theory (Middle-Level Theory in Evolutionary Psychology)
- ▶ Sexual Infidelity Versus Emotional Infidelity
- ▶ Sexual Jealousy in Long-Term Relationships
- ▶ Use of Mate Retention Strategies
- ▶ Violation of Short-Term Mating Preferences
- ▶ Women's Long-term Strategies
- ▶ Women's Mate Value

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Violation of Short-Term Mating Preferences

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Synonyms

Intersexual deception; Mate preferences; Mate selection; Short-term mating; Strategic interference

Definition

Violations of short-term mate preferences refer to instances in which a person in a short-term, casual sexual relationship has mate preferences that were in place when the relationship commenced but subsequently are not being met.

Introduction

Men and women around the world have an assortment of mating preferences and strategies. These preferences and strategies have evolved to adaptively guide the selection of mates who are reproductively viable (Buss and Schmitt 1993); however, they are not always fulfilled in the mates that people actually select due to various reasons. For instance, people's initial assessments can be inaccurate, partners' relative mate value can change, and partners often face sexual conflict or strategic interference. This chapter will describe preferences for casual, sexual short-term partners and then violations of preferences due largely to intersexual deception in such relationships.

Short-Term Mating Preferences

There are a few key preferences regarding short-term, casual sexual relationships. First, both sexes have evolved to value physical attractiveness in their partners. Specifically, women are attracted to short-term mates who display visible cues of good quality genes, such as masculinity and symmetry – features indicating resistance against pathogens that cause asymmetrical development (Gangestad and Simpson 2000). Women also value size, muscularity, and physical strength in their short-term mates (Li and Kenrick 2006), which may help them obtain physical protection. Men, on the other hand, value a short-term partner's physical attractiveness as a marker for her age and health and, thus, fertility (Buss and Schmitt 1993). Therefore, both sexes especially prioritize physical attractiveness above other traits

in short-term mates, though for different adaptive reasons (Li and Kenrick 2006).

When seeking mates who are not anticipated to stay for long compared to long-term mates, women are more likely to discount the future and value present resources that she can immediately acquire through a mate with high social status or dominance (Gangestad and Simpson 2000). Women may also use short-term mating to assess and attain potential long-term relationships by casting a wider net and converting a high status and dominant short-term mate into a long-term mate (Buss and Schmitt 1993; Jonason et al. 2009; Li and Kenrick 2006). Rich men with high social dominance thus are potentially desirable short-term mates because of their ability to impart immediate resources.

Men, on the other hand, have short-term mating psychological adaptations that bias their mate preferences toward obtaining sexual variety and minimizing commitment (Buss and Schmitt 1993). Men, who are more sociosexually unrestricted than women (Gangestad and Simpson 2000), tend to be much less selective than women when seeking short-term relationships (Li and Kenrick 2006), making it more likely that casual and noncommittal sexual relations can occur. Men may also possess adaptations to minimize attachment to short-term sexual partners, such as perceiving their sexual partner to be less attractive after sexual intercourse (Haselton and Buss 2001).

Violation of Short-Term Mating Preferences

A person's mating preferences may be violated or not met for several reasons. This may sometimes occur due to poor judgment in the mate selection process – after all, trait information is not always easy to assess, but in many cases, potential partners actively induce inaccurate judgments in perceivers, constituting a form of intersexual deception that is aimed at increasing their chances of being selected as mates and increasing their own reproductive success.

More broadly, the deceptive strategies used by men and women correspond to the mate selection criteria of the opposite sex (Tookey and Camire 1991), and violations of short-term mating preferences therefore revolve around the aforementioned traits valued in short-term mates. As the veracity of mate value as inferred through displays can often only be verified in the sufficiently lengthy duration of a long-term relationship, the incentive to deceive in short-term mating may be more pronounced than in long-term mating.

Violation of perceptions of physical attractiveness. Because the successful enactment of a short-term mating strategy relies heavily on perceptions of fertility or good genes as conveyed by physical attractiveness, short-term mating preferences are violated if a person discovers that their sexual partner has grossly misrepresented their physical attractiveness. Indeed, women commonly attempt to misrepresent their fertility by wearing garments that accentuate and ameliorate sexual features (e.g., push-up bras, dresses that highlight the hourglass figure), putting on makeup (Tookey and Camire 1991), and increasingly turning to cosmetic surgery to reverse the effects of time on the face and body.

A related deceptive tactic by women to increase favorable perceptions of their fertility is through the misrepresentation of age and weight. Online dating sites are particularly telling on the nature of intersexual deceptions, as they provide individuals with the opportunity to market themselves as mates through self-constructed profiles. Indeed, analyses of online dating sites have found that women are more likely than men to downward misrepresent their age and weight – for instance, by presenting photos from up to 10 years ago – to appear more youthful and, thus, more nubile and fertile (Hall et al. 2010).

Conversely, men often deceive about the quality of their genes and physical prowess, which are both conveyed by the appearance of masculinity. For instance, men may go to the gym to improve their strength and physical fitness, exercising mainly the upper body muscles that are more aesthetically visible, and also exaggerate their posture to be more dominant or appear taller than they really are (Benz et al. 2005). Men are

also more likely than women to upward misrepresent their height and income when constructing online dating profiles. Although men generally undergo cosmetic surgery much less than women around the world, the number of men undergoing cosmetic surgery is increasing (Brown et al. 2007), and men who choose to surgically augment their looks typically strive to reconstruct a face that is more masculine and symmetrical.

Violation of perceptions of social status and dominance. As women may contemplate short-term sexual relations with men who are capable of immediately dispensing large amounts of resources, men who wish to induce short-term sexual interest in women have an incentive to deceive about their wealth, social status, and dominance. Indeed, women rely on costly ornamentation or behaviors that signal social position (e.g., expensive suits, luxury cars) and physical vigor (e.g., aggressiveness, muscular upper body) to gauge the traits that mediate resource acquisition and holding ability, namely, social status and dominance. Therefore, women's preferences for immediate resources in a short-term mate may be violated when men exaggerate their job titles or deceive about their financial status, such as when men dress as if they have more money than they do or spend more money than they can afford on a date. Further, the projection of greater social confidence, superiority, knowledgeability, and aggressiveness than is actually warranted constitutes another form of deception by men to appear more dominant and desirable (Tooke and Camire 1991), especially as short-term mates. These deceptive tactics are mirrored in online dating sites, where men often misrepresent their personal assets and social status to appear more resourceful than they actually are (Hall et al. 2010).

Violation of perceptions of expected commitment and sexual availability. To exploit men's sensitivity to cues of sexual availability, women who wish to induce men's short-term sexual interest may wear revealing clothes that show off their body more than they normally would (Benz et al. 2005; Tooke and Camire 1991). A man's short-term mating preference for easy sexual access may then be violated when a

woman signaling sexual availability withholds sex, a behavior typically described by men as being "led on."

An individual may seek to acquire a long-term mate by first entering into a relationship with a partner on the grounds that it is casual and non-committed and then attempt to raise the commitment level expected of the relationship. While both sexes may implement such a strategy to attain long-term mates, this is a tactic more commonly used by women than men (Buss and Schmitt 1993). As the supposedly short-term relationship progresses, men may encounter mates who wish to escalate commitment, and this change in desired commitment level therefore represents a violation of the commitment level that was initially expected to be low. On the other hand, men may misrepresent having their commitment, which violates women's expectations for a short-term relationship's potential for becoming a long-term relationship (e.g., Jonason et al. 2009).

Expectations of and Reactions to Mating Preference Violations

Both men and women believe that the mate selection criteria used by one sex correspond to the deceptive tactics used by the opposite sex, suggesting that people have a reasonably good intuition about the sort of violations of mating preferences that are expected to occur as predicted by evolutionary theory (Benz et al. 2005). For short-term mating, both sexes expect that men will deceive women about their financial status, while women will deceive men on their physical attractiveness.

Despite the general intuition that laypeople have about intersexual deception and these possible violations of mating preferences, many people still inadvertently end up in situations where their preferences are violated and experience negative emotions associated with these situations. When faced with strategic interference, including those that constituted violations of short-term mating preferences, both sexes were upset in the ways predicted by what men and women specifically

value in their short-term mates: women express greater upset than men when deceived about a partner's status and resources, while men experience greater upset than women about being sexually led on (Haselton and Ketelaar 2006). The experience of such emotional distress is adaptive as it compels individuals to preempt similar violations in the future, thereby aiding in subsequent mating judgments and decision-making. Interestingly, no empirical studies currently exist that examine individuals' emotional reactions to violations of physical attractiveness or the emotional outcomes of men experiencing an increase in expected commitment in ongoing short-term relationships. The predictions of this chapter therefore provide rich groundwork for fruitful future research.

Conclusion

Men and women engage in short-term mating for somewhat different underlying reasons, leading to differences in what the sexes prefer in a short-term mate. These preferences may be hindered by violations of expectations, which are often intentionally induced through intersexual deception. Given that men value sexual availability and low commitment, women value short-term partners from whom they can immediately extract resources, and both men and women value physical attractiveness in their short-term mates, individuals may misrepresent themselves on these traits and proclivities so as to increase their desirability as short-term mates and increase the likelihood that they will be sought.

Cross-References

- ▶ [Access to Resources](#)
- ▶ [Evolutionary Standards of Female Attractiveness](#)
- ▶ [Female Mate Choice](#)
- ▶ [Friends with Benefits](#)
- ▶ [“Good Genes”](#)
- ▶ [Lowering Partner Standards in a Short-Term Mating Context](#)
- ▶ [Male Mate Choice](#)

- ▶ [Male Protection](#)
- ▶ [Men in Positions of Power](#)
- ▶ [Obligatory Parental Investment](#)
- ▶ [Preferences in Long- Versus Short-Term Mating](#)
- ▶ [Sex Differences for Pursuing](#)
- ▶ [Sex Differences Versus Gender Symmetry](#)
- ▶ [Sexual Conflict in Mating Strategies](#)
- ▶ [Sexual Receptivity](#)
- ▶ [Social Status and Economic Resources](#)
- ▶ [Sociosexuality and Sexual Conflict in Mating Strategies](#)
- ▶ [Violation of Long-Term Mate Preferences](#)
- ▶ [Women's Mate Value](#)

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Violence

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Synonyms

Assault; Force; Physical Force; Violent

Definition

Violence is defined by World Health Organization as “the intentional use of physical force or power, threatened or actual, against oneself, another person, or against a group or community, that either result in or has a high likelihood of resulting in injury, death, psychological harm, maldevelopment or deprivation” (Krug et al. 2002).

Introduction

Evidence throughout history serves as a powerful reminder that contemporary violence is not a new phenomenon (e.g., Keeley 1996). Archeological evidence for violence between early humans is indisputable; human skeletons have been found (sometimes in mass burial sites) containing cranial and rib fractures that appear inexplicable except by the force of clubs and weapons that stab (e.g., Keeley 1996). Also, crafting tools necessary for inflicting severe harm on other humans, such as stone axes and wooden spears, were developed at least 400,000 years ago (e.g., Liddle et al. 2012). The origin of this violence has been an issue of considerable research and debate for centuries. Much of this research is focused on mental, social, family, and cultural influences on violence. For instance, scholars have investigated the influence of the media on the perpetration of violence or on the influence of peers and parents who model violent behavior (e.g., Buss and

Duntley 2003). Without denying the merits of these theories and influential factors, recent research has also indicated that a large proportion of violent behavior can be explained by an evolutionary psychology model.

Before discussing this model in more detail, it is important to note that all violent behavior is aggressive, but not all aggressive behaviors are violent or even necessarily negative from a cultural perspective. Consequently, violent behavior can take many forms, ranging from threatening to harm someone to its ultimate form: homicide. Most evolutionary psychologists examining violence have focused on explaining this ultimate form (Buss and Shackelford 1997).

In examining homicide, considerable attention is devoted to whether one can consider this form of violence as an unfortunate by-product of evolution or whether it can be considered as an evolutionary adaptation (Buss and Duntley 2003: 122). The by-product view on killing was firstly coined by Daly and Wilson (1988), who wrote down an evolutionary account of the different forms of homicide. Drawing on animal behavior, anthropology, and patterns of violence and murder in modern societies, they argue that although humans have the brains and minds with violent proclivities, killing is by and large, not something that evolution has selected for. Instead, they argue that it is a by-product of urges towards some other goals (e.g., Daly and Wilson 1988). For instance, male-male homicide is viewed as a by-product of evolved mechanisms underlying competition, risk-taking, and status-seeking (Daly and Wilson 1990). Many evolutionary psychologists have adopted Daly and Wilson’s position (e.g., Crabb 2000). However, some others, such as Duntley and Buss (2005), have rejected this by-product hypothesis and have instead put the adaption view forward. They argue that humans possess psychological adaptations for killing that have evolved because they successfully managed to solve specific, recurrent adaptive problems in our ancestral past. Or to put it differently, adaptations for killing have been selected for because individuals who possessed those adaptations were reproductively more successful than individuals who did not in relevant historical environments.

These adaptations form the so-called Homicide Adaption Theory (e.g., Duntley and Buss 2005).

Determining whether a particular behavior, in this case killing, is generated by specialized adaptation or generated as a by-product of other adaptations can be exceedingly difficult. It is also important to note that this is also the case – but to a lesser extent – when examining other violent behavior, such as rape. In this context, the discussion on whether a particular violent behavior is an adaption or a by-product is set aside; regardless of the result, similar effects of cues of infidelity, reproductive value, kinship, and other conflict-related variables should be expected.

Generally, evolutionary psychologists rely on two theoretical models for explaining violent occurrence: sexual selection and parental investment theory.

Sexual Selection Theory and Parental Investment Theory

Natural selection explains the evolution of complex traits as a result of heritable variations that influence differential survival. In any given population, some organisms are more likely to survive and subsequently pass on their genes than are others. Although survivability is important, this is not the sole of one's fitness (i.e., one's success in passing on his or her genes to the next generation), at least not among sexually reproducing organisms. Selection will also operate on traits that affect one's reproductive potential, i.e., it promotes evolution by choosing features that assist the species to gain better and more sexual access to mating opportunities. To put it more bluntly, fitness is closely related to the number of offspring produced.

Sexual selection operates via two mechanisms: intersexual selection and intrasexual competition. Intrasexual competition refers to competition between same sex rivals for access to mating opportunities. Opportunities and traits that improve one's chances of succeeding in such competition will be selected for. In contrast, intersexual selection consists of members of one sex attempting to impress members of the other. This

form of sexual selection is generally regarded as being responsible for the development of more expensive, dangerous, competitive traits, both morphological (e.g., weapons like antlers or the colorful tail in the case of the peacock) and psychological (e.g., risk acceptance) (e.g., Daly and Wilson 1988: 275).

However, what governs the operation of sexual selection is the relative parental investment of the sexes in their offspring. How these investments differ and what kind of effect these differences have is described by the parental investment theory (e.g., Trivers 1972). In all mammals, females exhibit greater minimum obligatory parental investment in their offspring than males. Females must devote considerable time and energy to their offspring due to internal fertilization and gestation, which is often followed by a period of nursing, whereas the minimum obligatory investment by males is the contribution of sperm. As a consequence, females are far more discriminating when choosing a male to mate or as Mealey (2003: 86) formulates it: for females, it is the “quality” of coupling that is more important than the “quantity.” Consequently, females engage in intrasexual competition for the highest quality mates (e.g., men with good genes who produce offspring with high prospects of survival or, for instance, men with high status who signal the ability to provide for a woman and her offspring) (e.g., Miller 1998). Due to the fact that females represent a limiting factor for male reproductive process, males are then also predisposed to riskier intrasexual competition for mating opportunities.

Male-Male Violence

Competition for mating opportunities entails the contestation for those resources that can be converted into reproductive opportunity, whether because they are directly attractive to females or because they help quell rival males (Wilson and Daly 1985: 60). For instance, status, honor, and reputation play an important role. Evidence suggests that high status in men has, for example, historically translated into having more access to food, better territory, and greater social support,

thus serving as an honest signal of a man's ability (but not necessarily intent) to provide for a woman and her offspring (Daly and Wilson 1988: 282). In other words, males will often compete with other males for dominance and other resources that are attractive to potential mates. For instance, in modern day societies, they compete over means including professional qualifications, highly paid, or prestigious jobs (Campbell 2011). Losing these competitions or walking away from them can be catastrophic in the currency of survival and reputation. This is especially the case for young males (16–24 years of age), which are in that portion of their lifespan when reputations are made and mates are acquired (Campbell 2011).

There are two things that determine the ferocity of this competition and whether this competition over resources turns out violent and even into homicide: the value of the object being fought over and the risks involved. Given that the reward of victory is high (and the consequence of losing is little or no chance of reproducing), the more intense the competition, the higher the likelihood of the use of violence as a competitive strategy. Male-male homicide is then also viewed as a product of evolved mechanisms underlying high intense competition, risk-taking, and status-seeking (Daly and Wilson 1990). However, it is important to note that rivalry and competition over mating opportunities can trigger nonlethal aggression as well. In a study of mate guarding, for example, men picked a fight with the rivals who showed interest in their mates and threatened to hit rivals who were making moves on their mates (Buss 1988).

Female Aggression and Violence

Despite the overrepresentation of men in statistics regarding violent behavior, it is important to recognize that violence is not an exclusively male behavior (e.g., Wilson and Daly 1985). While violence perpetrated by males is often described as a “higher stakes, higher risk” enterprise (Daly and Wilson 1988: 140), we should not forget that females also engage in intrasexual competition for the highest quality mates. However, since the

potential costs associated with physical violence are often higher for women than for men – the death of a mother has more lethal consequences for children's survival than the death of a father – women often opt for other forms of violence when competing for mates. They employ more often tactics involving indirect or relational aggression, which consists of verbal derogation, gossip, spreading rumors, and other nonphysical forms of ostracism and stigmatization in which the victim is often “attacked” indirectly, thereby reducing the likelihood of retaliation (Björkqvist et al. 1994). This does not mean that women experience less anger than men, rather that they have a higher threshold for employing violence as a competitive tactic (e.g., Archer 2004).

Intimate Partner Violence

Not all violence that occurs in the context of mating is intrasexual. Male violence directed at women, most often intimate partners, is a phenomenon that must be addressed. According to Daly and Wilson (1988), men perpetrate violence against their wives or girlfriends under two key conditions: the observation or suspicion of sexual infidelity (i.e., cuckoldry) and when the woman is terminating the relationship. Although these are two distinct mechanisms, they are – from the perspective of natural selection – similar: the important commonality is that the man loses control of female reproductive capacity and hence loses ground in the reproductive competition between men (Daly and Wilson 1988: 279).

Until very recently, men could never be certain that their putative offspring were genetically their own. Therefore, the possibility of cuckoldry has represented a serious adaptive problem for men throughout our evolutionary history. The costs of cuckoldry for the male's fitness are severe; it includes the misdirection of the male's time, effort, and resources to rearing a rival's offspring. Moreover, it includes time, effort, and resources that the man spent attracting his partner, and reputational damage if such information becomes known to others (e.g., Daly and Wilson 1988). Consequently, men developed strategies and

tactics aimed at avoiding cuckoldry and decreasing paternity uncertainty. In the animal world, male birds, for instance, follow their mates closely during the breeding season, which is interpreted by ornithologists as “mate guarding” behavior with its fitness-promoting function as paternity assurance (Daly and Wilson 1998). Fitness promotion also suffers when a woman is terminating the relationship due to the loss of a reproductively valuable woman to a potential rival (Buss and Shackelford 1997: 616).

Most researchers have lumped these two mechanisms together because the potential violent reactions in both scenarios are motivated by male sexual proprietariness, a sense of ownership men have over women, encompassing not only episodes of jealous arousal but also presumptions of entitlement and inclinations to exercise control and prevent threats of trespass or usurpation (e.g., Daly and Wilson 1988). This sexual proprietariness of males is one of the most frequently cited causes of intimate partner violence, both physical and sexual (e.g., Daly and Wilson 1988).

Violence Against Children

When discussing violence in the context of families, it is important to consider the genetic relatedness of family members. According to kin selection theory (e.g., Hamilton 1964), organisms should be more altruistic and less competitive toward others as a function of their genetic relatedness. Helping a genetic relative and increasing that person's fitness, even at a cost to oneself, can ultimately be beneficial to the altruist because of the genes he or she shares with the beneficiary. In other words, increasing a genetic relative's fitness will result in some of one's own genes being passed on to future generations, thereby increasing one's inclusive fitness. Despite the lower levels of competition between genetic relatives predicted by kin selection theory, competition and violence do occur among family members. One form that warrants our attention is the killing of same-species offspring, which has been observed among many species of mammals. For

instance, male lions kill the young when they displace another male and take over a female (Buss and Shackelford 1997: 610). These acts might be attributed by some academics to the “failure of engagement of the normal mechanisms of parental love” (quoted in Daly and Wilson 1998). However, even these extreme acts of violence can be approached via an evolutionary perspective. Given the high costs associated with investing in offspring, human psychology is likely to have been shaped in such a way as to forego paying these costs when the desired outcome of investment (i.e., a reproductively capable adult) is unlikely to occur (Daly and Wilson 1988). In other words, parents can terminate their investment in their infants in order to preserve their finite time and resources for others. Examples of adaptive problems that infanticide solves are, for instance, avoiding to invest in physically subpar offspring who were unlikely to convert parental resources into their own reproductive success (e.g., those who were deformed, diseased); avoiding to invest in offspring when external conditions hampered the infant's survival (e.g., food scarcity, lack of an investing father, harsh season); and eliminating competition for older or more viable offspring when resources are scarce (e.g., twin births or when birth spacing was too close) (Duntley and Buss 2011: 402).

Another important causal context that has been identified is the Cinderella effect, i.e., the phenomenon of higher incidence of different forms of child-abuse and mistreatment by step-parents than by biological parents (e.g., Daly and Wilson 1996). Abuse from stepparents has been immortalized in children's stories, the most common being that of Cinderella, who was abused by her wicked stepmother (Buss and Shackelford 1997: 616). Some evolutionary psychologists describe this effect as an adaptive strategy to avoid parental investment in a rival male's infant (Duntley and Buss 2011). Others describe it as a remnant of an adaptive strategy in which males frequently kill the offspring of other males in order to bring their mothers into estrus and give the male a chance to fertilize her himself. There is both supporting evidence for this theory and criticism against it.

Violence During War

Any comprehensive discussion of human violence would be incomplete without an analysis of war. The killing of one person by another may be accidental and perhaps a by-product of aggression but intergroup conflict or warfare might be an adaption in itself. Although it is difficult to determine when humans (especially men) began engaging in warfare, the raiding behavior of other species suggests that warlike behaviors have been a part of the human behavioral repertoire for the majority of, if not the entirety of, our evolutionary history (e.g., Keeley 1996). This behavior was first reported by Goodall et al. (1979) in Tanzania in the 1970s; in a long-term study, she shows several incidents of murderous “gang violence” among chimpanzees. In one case, the adult males of one community systematically attacked and killed the males of another group over a period of years, with the victorious group eventually absorbing the remaining victims. Raids on neighboring communities are also common in anthropologists’ accounts of small-scale human societies (Wrangham and Glowacki 2012). These often follow the chimpanzee template; a small team of men leaves its home grounds, sneaks up on the neighbor, and tries to kill one or more of them.

Moving from studies of chimpanzee coalitional violence and that of small-hunter gatherer societies to understanding modern warfare from an evolutionary perspective is, however, far from straightforward. At least three evolutionary factors might play a role (Fishbein and Dess 2003). First, one of the major innovations in evolutionary psychology is the elaboration of the kin selection theory (inclusiveness fitness) (e.g., Hamilton 1964) and its relationship to social behavior (Wilson 1975). This theory suggests that, given the opportunity, individuals show greater selfish restraint, less aggression, and greater altruism toward closer relatives. The direct social implication of this theory is that the human species are essentially designed to be ethnocentric – to favor our own group as opposed to others (Fishbein and Dess 2003: 170). In turn, this in-group favoritism can lead to a second – interrelated – factor: out-group hostility. In

other words, coalitional aggression against the out-group can be the direct result of the need for acquiring or defending resources relevant to the in-group’s survival and reproduction (i.e., protecting the inclusive fitness of the in-group). In other words, eliminating rival groups to gain access of reproductively relevant resources, such as food or territory, produce very long-term benefits and as such outweighed the costs in the currency of fitness (Buss and Shackelford 1997: 609).

Lastly, humans differ also significantly from other mammals, to the extent in which they accept authority (Fishbein and Dess 2003). One important aspect is the psychological internalization of what authorities tell us. We personally take on beliefs and values of authorities and in turn, transmit these to others over whom we have authority, reinforced by conceptual or symbolic materials (Waddington 1960). Additionally, the connection between authority acceptance and the development of prejudices and discriminant behavior is obvious in connection with out-group prejudices and discrimination, and it forms a strong motivation for going to war.

Despite these evolutionary predispositions that facilitate – especially men – going to war, potential injury and loss of life still represent substantial costs that are likely to select against such behavior unless certain conditions are met to offset these costs. Tooby and Cosmides (1988) have argued that there are at least four conditions. First, the average long-term gains in reproductive resources should outweigh the reproductive costs of war. Second, there should be a steady belief that one’s group will be victorious. Third, one should receive benefits that commensurate with one’s contribution and degree of risk taken. Lastly, there should be an inability to accurately predict which group members will live or die. In short, conditions that increase the perceived benefits and decrease the perceived costs will facilitate the willingness of men to engage in warfare.

Conclusion

Despite the accounts of violence and how it solves a number of specific potential adaptive problems

described above, a few things are worth noting. First, although violent behavior might be influenced by genetics and biology, that does not serve as a justification for such behavior (see Wilson et al. (2003) for a discussion). Similarly, genes do not cause men to commit violent acts; if they do anything, they predispose them to do so. Whether men carry them out will depend on their previous experiences, cultural context, and other genetic predispositions (e.g., Elbert et al. 2017). For instance, even though men are disposed to behave more violently than women, it is not the case that every man will react with violence when catching his partner with another person. Moreover, cultural values play an important role in calculating the (reputational) cost of violence. For instance, suicide is taboo in many cultures, which is likely to suppress its occurrence. Violent behavior is, therefore, one strategy within a menu of strategies, activated only under a highly specific set of co-occurring conditions (Buss and Duntley 2003: 120). Third, it should be noted that humans and many other species also have a tremendous capacity for cooperation. Far more time is spent engaging in cooperation, or at least peaceful coexistence, than is spent engaging in violence (Liddle et al. 2012). However, by studying violence from an evolutionary perspective, analyzing the contexts in which it occurs and the stimuli that influence its occurrence, we can gain a better understanding of the mechanisms that produce violence, thus putting us in a better position to limit the activation of such mechanisms (Liddle et al. 2012).

Cross-References

- ▶ [Adaption](#)
- ▶ [Aggression](#)
- ▶ [Aggression for Sexual Access](#)
- ▶ [By-Product](#)
- ▶ [Bullying](#)
- ▶ [Contexts for Men's Aggression Against Men](#)
- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Contexts for Women's Aggression Against Men](#)

- ▶ [Costs of Aggression](#)
- ▶ [Cues to Infidelity](#)
- ▶ [Culture of Honor](#)
- ▶ [Dominance and Threat or Use of Force](#)
- ▶ [Female-Perpetrated Violence](#)
- ▶ [Infanticide](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Kin Selection](#)
- ▶ [Partner Homicide](#)
- ▶ [Reproductive Value and the Evolution of Aggression](#)
- ▶ [Same-Sex Homicide](#)
- ▶ [Sex Differences in Aggression](#)
- ▶ [Sex Differences in Intimate Partner Violence](#)
- ▶ [Sexual Infidelity Versus Emotional Infidelity](#)
- ▶ [Strategic Aggression](#)
- ▶ [Victims of Violence](#)

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Violence as Coercive Control

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Synonyms

[Intimate partner violence](#); [Physical aggression](#); [Sexual aggression](#); [Sexual conflict](#); [Sexual jealousy](#)

Definition

Ancestral men may have benefitted by inflicting physical and sexual violence against women to manipulate women's sexual behavior or to circumvent female sexual choice. Because gestation occurs within females, women are especially sensitive to the risk of violence and associated injury. The reproductive costs of physical harm are greater for women, and, therefore, some men use violence or threats of violence to control women's behavior.

Introduction

Mate guarding behaviors are intended to discourage an intimate partner from committing infidelity, defecting from the relationship, or being poached by a rival (Buss 1988). Men use mate retention behaviors to combat the risk of the cuckoldry (unwitting investment in a rival's genetic

offspring) and to minimize resource loss, whereas women use mate retention behaviors to retain a partner's long-term investment. Violence is a mate guarding strategy, mostly inflicted by men against women, to control a partner's sexual behavior or autonomy. Women are especially vulnerable to violence, and this is reflected in their reactions to threat of violence. For example, women respond to fear differently than men (McLean and Anderson 2009). Because women's reproduction depends on their ability to survive, women are especially fearful of risky or violent situations. Once conception occurs, men no longer need to survive to be reproductively successful, whereas women's survival is required for gestation and childrearing. Thus, women may have evolved psychological mechanisms that motivate them to avoid physical harm. Men may have coevolved mechanisms to exploit women's fear for their own reproductive benefit. By inflicting or threatening to inflict violence, men coerce women into sexual fidelity, maintaining the relationship, or securing sexual access (Buss 1988; Wilson and Daly 1993). Women cannot afford to risk physical injury, so acquiescing to men who use or threaten violence may sometimes be an effective self-defense strategy. Men use physical violence against women, including physical abuse or threats of physical abuse, to minimize paternity uncertainty. Men use sexual violence against women, including sexual coercion and rape, to gain sexual access without investing resources into the woman. In sum, both physical and sexual aggression by men against women function to control and manipulate female sexual behavior.

Physical Violence as Coercive Control

Male sexual jealousy is a primary motivator for men's physical aggression against women (Daly and Wilson 1988). Because gestation occurs within women, men are at risk of investing time and resources into offspring to whom they are genetically unrelated. Thus, jealousy is produced by an evolved mechanism to alert individuals to potential or actual infidelity by their partner (Buss 2000). When men suspect or discover sexual infidelity, they are more likely than women to inflict violence

against their partner (Daly and Wilson 1988). Fear of physical harm or death motivates women to avoid their partner's physical attacks, thus discouraging women from pursuing infidelities. Wilson and Daly (1993) suggest that by inhibiting a partner from committing sexual infidelity with aggression, men control with whom the woman reproduces. Additionally, through controlling a woman's sexual behavior, men reduce the risk of cuckoldry or mate poaching by a rival.

Sexual Violence as Coercive Control

In some instances, men use sexual aggression against women to bypass resource investment and female sexual choice (Thornhill and Palmer 2000). Thornhill and Palmer (2000) review the hypothesis that rape is produced by specialized adaptation, which motivates men to rape in specific circumstances. Rape may have been adaptive for ancestral men because it increased reproductive opportunities and required little time or resources to secure sexual access to a female. By circumventing female choice, sexual aggressors control a woman's reproduction. As with physical violence, women's fear of rape is related to perceived risk of physical harm or death (Pryor and Hughes 2013). Women's fear of injury or death may inhibit them from engaging in self-defense during a rape. Additionally, partner rape sometimes occurs in the context of sperm competition (Goetz and Shackelford 2006). In those cases, men engage in sperm competition to attempt to affect their partner's reproduction before or after an actual or suspected infidelity.

Conclusion

Physical injury is particularly detrimental to a woman's reproduction because gestation occurs within women. Thus, women may have evolved psychological mechanisms that make them especially sensitive to risky situations. Men may have coevolved mechanisms that exploit women's fear of harm, for their own reproductive benefit. For example, men inflict physical and sexual violence against a woman to discourage her from

committing infidelity, abandoning the relationship, or to circumvent female sexual choice. In sum, violence is inflicted by men against women to control a woman's sexual behavior.

Cross-References

- [Circumventing Mate Choice](#)
- [Coercive Control](#)
- [Contexts for Men's Aggression Against Women](#)
- [Mate Retention Strategies](#)
- [Sexual Coercion](#)

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Violence from Women's Kin

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Synonyms

[Daughter-guarding](#); [Homicide](#); [Honor killing](#);
[Parent-offspring conflict](#)

Definition

Genetic kin benefit from monitoring and defending female family members. Daughter-guarding and sister-guarding, for example, in the forms of vigilance or violence, function to control a woman's sexual behavior, thereby regulating with whom she reproduces. However, violence from kin members is sometimes directed toward the woman. Sometimes this violence includes “honor killing,” in which a woman is killed to restore her family's reputation, typically on suspicion that she has participated in illicit or socially unacceptable sexual behavior.

Introduction

Females are a reproductive commodity. For example, although sons have the ability to produce more offspring than daughters, daughters have more certain opportunity to reproduce than sons. Because women invest more heavily in offspring than men, women are more selective when choosing mates. Men compete with one another to secure sexual access to women. Thus, safeguarding female kin may have been ancestrally adaptive (Perilloux et al. 2008). Genetic kin can be reasonably certain that a female relative will have opportunities to produce offspring whereas a male relative may not. By performing behaviors to control a female relative's sexual behavior and thereby protect their reproductive value, ancestral kin members increased their fitness.

Kin's female-directed guarding behavior sometimes becomes violent, and occasionally homicidal. Homicidal revenge for a kin member's abuse or death has been documented in many cultures (Daly and Wilson 1988). Engaging in violence against those who threaten or injure female kin protects the woman's future reproductive potential. For example, proximity to kin is associated with lower rates of female-directed abuse and homicide (Daly and Wilson 1988). Additionally, Daly and Wilson (1988) report that women are more likely to use violence against an abusive partner when the woman's genetic kin reside nearby, suggesting that proximity to kin translates into protection for the woman,

and may encourage her to engage in violent self-defense. However, sometimes culture and reputation lead kin to kill women, a practice referred to as “honor killing.” Honor killings are primarily perpetrated by fathers or brothers against female kin to restore and protect the family’s honor (e.g., a man kills his daughter who is suspected of having premarital sex). From an evolutionary perspective, killing an offspring may have been ancestrally adaptive, for example, if the absence of that offspring made available resources that could be invested in offspring with a more promising reproductive future.

Guarding Female Kin

Mate guarding refers to behaviors performed to reduce the risk of an intimate partner being poached, committing infidelity, or abandoning the relationship (Buss 1988). The daughter-guarding hypothesis suggests that humans have evolved psychological adaptations to be especially sensitive to and protective of a female kin member’s sexual behavior and reputation (Perilloux et al. 2008). Because female kin more reliably reproduce, kin members attempt to exact more control over a female’s mating behaviors than over a male’s mating behaviors (Faulkner and Schaller 2007; Perilloux et al. 2008). Controlling a daughter’s sexual behavior, for example, may have been ancestrally adaptive for kin because females do not face maternity uncertainty, thus increasing the likelihood that the female kin’s offspring will share the genes of her kin. Additionally, because offspring development occurs within women, using violence to protect female kin from an abusive partner may have been selected, given that harm inflicted on a woman might decrease her reproductive success and, consequently, the success of her genetic kin. Women who have proximate kin, or more immediate familial protection, are less likely to be killed or injured by a partner (Daly and Wilson 1988). One study of South Asian women immigrants reported that loss of social support after migration reduced the likelihood that immigrant women would seek help for partner abuse (Ahmad et al. 2009).

Retaliation and Revenge

In some cultures or religions, kin members (particularly fathers or brothers) kill a daughter or sister to restore “honor” to the family. For example, Chesler (2010) reported that 57% of Muslim honor killings are motivated by perceived sexual impropriety by the victim, such as engaging in an extramarital affair. In the United States, 56% of honor killings are committed by a father for the daughter’s perceived misbehavior, such as dating outside the family’s culture or religion (Hayes et al. 2016). Although it seems counter-intuitive to kill offspring, the restoration of the family’s social status may improve the reproductive future of other family members. If a daughter’s sexual reputation has been tarnished, she might no longer be a reproductive commodity to her family. Her death might therefore benefit the rest of the family by freeing up resources otherwise consumed by her.

Conclusion

Individuals exercise greater vigilance over close genetic kin than non-related individuals or more distant kin (Faulkner and Schaller 2007). Vigilance and violence by a woman’s kin function to control the woman’s sexual behavior. To increase the replicative success of shared genes, kin may defend females by inflicting violence against an abusive mate or by monitoring a woman’s clothing, for example. Guarding of females by kin is intended to increase the power parents and relatives have in determining with whom the guarded female mates and reproduces (Perilloux et al. 2008). In rare instances, however, kin kill their daughters or sisters to restore social status or “honor” to the family.

Cross-References

- [Benefits to Kin](#)
- [Conflict Between Parents and Offspring](#)
- [Daughter Guarding](#)

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Violence to Control Women's Sexuality

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Synonyms

[Intimate partner violence](#); [Sexual coercion](#)

Definition

Physical, psychological, or sexual violence employed by men that, ultimately, functions to increase the mating success of the perpetrator and/or decreases the likelihood of a woman copulating with other men; Manifest psychology and behavior to prevent, correct, or anticipate female infidelity.

Introduction

Psychological perspectives on violence against women, broadly understood, maintain that violence may be employed to control women's sexuality. The ultimate motivations underpinning men's violence as a means to control women's sexuality, however, differ across subdisciplines of psychology. Mainstream standard social science perspectives posit that violence perpetrated by men against women is motivated by men's attempts to dominate and control their partners, more generally, and that this expression of dominance is, ultimately, a learned behavior that is the product of men's social roles (Ali and Naylor 2013). An evolutionary psychological perspective, in contrast, posits that men's violence against women is the product of evolution by natural selection in that men's motivations for violence perpetration are, ultimately, sexual in nature – though, not (necessarily) consciously (reviewed in Goetz and Shackelford 2009). From this perspective, men's violence is employed against women, primarily in intimate partnerships, as a means to prevent, correct, and anticipate women's infidelity (Shackelford 2003), whereby violence employed by men functions to increase his mating success with the woman or decreases the likelihood of the woman copulating with other men (Barbaro and Shackelford 2016; Camilleri and Quinsey 2012).

The theoretical and empirical findings that evolutionary psychologists have amassed over the preceding decades generally fall within two domains of focus. One area of research primarily focuses on identifying recurrent adaptive problems of reproduction faced by males for which violence may have been used as an adaptive solution. Another area of research focuses on the how, exactly, violence solves relevant adaptive problems of reproduction faced by ancestral men. Evolutionary research on men's violence tends to highlight the replicative benefits afforded by men employing violence, with the later domain of research, in particular, providing a valuable framework from which various types of behavior can be classified and understood. Evolutionary research on the ultimate underpinnings of men's

violence draws upon several foundational evolutionary theories and principles. In this entry, I briefly review the theoretical and empirical support for an evolutionary psychological perspective on men's violence against women as a means to control women's sexuality.

The Adaptive Problem

Physical and sexual aggression against women is often perpetrated by a current or former romantic partner. Parental investment theory (Trivers 1972) has been leveraged as the dominant theoretical approach for understanding female-directed violence. Fundamental biological differences, or asymmetries of reproduction, between men and women hold considerable explanatory power for understanding why men, in particular, aggress against women. One fundamental asymmetry is that of fertilization and gestation of offspring occurring in women, rather than men. One substantive consequence of this reproductive asymmetry is *paternity uncertainty* – ancestral men could not have been certain that their offspring with a romantic partner were, in fact, genetically their own. Ancestral women, in contrast, had maternity certainty. Paternity uncertainty places men at risk for cuckoldry – the unwitting investment of resources into genetically unrelated offspring. Cross-cultural evidence of infidelity rates and paternal discrepancy rates indicate cuckoldry was a recurrent feature of human evolutionary history (reviewed in, Goetz et al. 2008). Because men often invest substantially in their putative offspring, a partner's infidelity (or probability of committing infidelity, or perceived risk of a partner's infidelity) places men at risk for incurring substantial reproductive costs (Daly and Wilson 1988; Smuts 1992). Put differently, paternity uncertainty was likely a fundamental adaptive problem of reproduction faced by ancestral males.

Because of the potential costs associated with cuckoldry, men are sensitive to contexts in which exclusive sexual access to their female partner may be threatened and, thus, situations for which the risk of cuckoldry is relatively greater. Over evolutionary history, a recurrent context in which men's exclusive sexual access and paternity is threatened is female infidelity (Shackelford

2003). Men's aggression, more generally, is largely deployed to solve adaptive problems (Buss and Shackelford 1997) and, specifically, aggression against an intimate partner can facilitate exclusive sexual access to the in-pair partner to correct or prevent female infidelity. Therefore, men's perceptions of their female partners' infidelity – actual or imagined – is a primary cue to cuckoldry risk and, therefore, a primary context in which men deploy aggressive behavior in intimate relationships.

Consistent with the hypothesis that men employ violence in response to cues of female infidelity, research has demonstrated, for example, that men who perceive a greater risk of partner infidelity perpetrate more frequent partner-directed violence (Kaighobadi et al. 2009). Men's accusations of their partner's sexual infidelity predict men's violence against their partner (Kaighobadi et al. 2008). And, notably, cross-cultural research shows that male sexual jealousy (resulting from actual or imagined partner infidelity) is a leading cause of female-directed violence and partner homicide (Daly et al. 1982; Buss 2000).

Further evolutionary consequences of female infidelity in intimate relationships include sperm competition. Sperm competition occurs when the sperm of two or more males simultaneously occupy a female's reproductive tract and compete to fertilize the ova (Parker 1970). A recurrent context for sperm competition in humans is female infidelity (Baker and Bellis 1995). Because human males often invest considerable resources in their putative offspring, the costs of cuckoldry can be substantial. Dual-mating by females may have instantiated selection pressures on males to combat sperm competition. Ancestral men that were relatively more vigilant of cues to female infidelity – and thus, sperm competition risk – would have incurred an adaptive advantage over men who were less vigilant of cues to female infidelity. Regarding psychological and behavioral outputs, application of sperm competition theory has provided considerable evidence for the relationship between female infidelity and sperm competition risk and men's use of aggression and coercion toward romantic partners'

infidelity (reviewed in Pham and Shackelford 2014). Put differently, empirical findings support the hypothesis that men employ aggressive and coercive behaviors judiciously in the context of intimate relationships to increase their success in (actual or imagined) sperm competition, especially when risk of cuckoldry is greatest (e.g., after separation from their partner).

Violence as an (Ancestral) Solution

Selection for employing violence in the appropriate contexts necessitates that violence reliably solved the relevant adaptive problems of reproduction over evolutionary history and conferred some sort of replicative advantage for men. As mentioned above, the ultimate evolutionary underpinnings of female-directed violence posits that men may use violence to prevent, correct, or anticipate female infidelity. In accord with this hypothesis, functional accounts of female-directed violence are also necessary for a comprehensive evolutionary theory of men's violence to control women's sexuality. One domain of research therefore focuses on how, exactly, violence might have solved the adaptive problems of reproduction for men (e.g., exclusive sexual access to a woman), and the replicative benefits afforded to violent men in reproductive contexts. Comparative research on nonhuman primates, underpinned primarily by sexual conflict theory, provides a foundation for which functional organization of female-directed violence can be integrated with research on humans (see Barbaro and Shackelford 2016).

Sexual conflict occurs when the reproductive interests of males and females differ, such that the optimal outcome of a trait is different for each sex (Parker 2006). Sexual conflict is common in mating situations because of the differences in size and requisite energy costs for developing sperm and ova. Because of asymmetries of minimum obligatory parental investment (Trivers 1972), in most sexually reproducing organisms (including humans), the reproductive success of males is limited by the number of copulations with fertile females. For females – because production of ova is finite – their reproductive success is limited to the time and energy required to rear offspring

(Bateman 1948). For example, if a man were to copulate with twenty different women over the course of a year, he has the reproductive potential to sire upwards of twenty offspring. If a woman, in contrast, were to copulate with twenty different men over the course of a year, she has the reproductive capacity to carry only a single pregnancy to term.

Because male reproductive success is dependent upon sexual access to females and maintaining exclusive sexual access to an in-pair partner, selection may have favored male traits and manifest behavior that facilitate (exclusive) sexual access to women by means of force (Muller and Wrangham 2009). This category of manifest behaviors are broadly referred to as “sexual coercion” (Smuts and Smuts 1993). Within this functional framework, sexual coercion is defined as the use or threat of *male force* to secure and maintain *sexual access* to a female and *constrain female promiscuity* (Smuts and Smuts 1993). Importantly, this definition specifies the conditions under which female-directed violence can be interpreted as a form of sexual coercion (Muller et al. 2007). These conditions include female-directed violence intensifying in reproductive contexts (e.g., in humans, committed relationships), female-directed violence being targeted at fertile females (e.g., in humans, reproductive age women), and higher rates of female-directed violence being associated with higher copulation rates with that female (Smuts and Smuts 1993).

This functional framework of sexual coercion is the predominant explanation for female-directed violence in nonhuman primates (Muller and Wrangham 2009), such that female-directed violence employed judiciously in the appropriate contexts may solve the adaptive problem of obtaining (exclusive) sexual access to a female. Research in nonhuman primates documents a positive relationship between female-directed violence and male mating success. Put differently, violent behavior perpetrated by a male against a female is purported to function as a form of sexual coercion (Muller and Wrangham 2009). In Japanese macaques (*Macaca fuscata fuscata*), for instance, research has shown that dyads in which a male perpetrated violence against a fertile

female had higher copulation rates than dyads in which a male did not perpetrate violence against a fertile female (Soltis et al. 1997). Similarly, research on chimpanzees (*Pan troglodytes schweinfurthii*) documented a positive association between the frequency of violence against fertile females – operationalized as charging displays, chases, and contact aggression – and the number of copulations the perpetrating male secured with those same females. Additionally, individual males secured more frequent copulations with females against whom they were more (vs. less) violent (Muller et al. 2007).

Research applying the sexual coercion framework proposed by Smuts and Smuts (1993) has been subject to relatively less empirical effort in humans, however. Important differences in mating systems between humans and nonhuman primates should be taken into consideration as well, such that, compared to nonhuman primates, humans display several unique characteristics. Although women are less promiscuous than some other nonhuman primate females, mated women can secure genetic and nongenetic benefits from extra-pair copulations (Gagnestad and Thornhill 2004). Men and women also form pair-bonds in the context of multimale, multi-female groups, but pair-bonded men and women sometimes spend extended periods of time physically apart, providing opportunities for women to secure extra-pair copulations surreptitiously. Moreover, because ovulation in humans is (relatively) concealed in comparison with most nonhuman primate species, sexual behavior in humans is not limited to only the fertile phase of the menstrual cycle (Thornhill and Gangestad 2008).

These differences of mating systems have consequences for the conditions for which female-directed violence may be an adaptive solution. Concealed ovulation in humans consequently results in female-directed violence not being constrained to only times of high fertility, as in most nonhuman primates with overt signs of ovulation; but rather, women of reproductive age, more generally (i.e., women that have greater *potential* to conceive), are at greater risk of male violence than nonreproductive age

women (Peters et al. 2002). Additionally, because men often invest substantially in their putative offspring, a partner's infidelity places men at risk for incurring substantial costs (Daly and Wilson 1988; Smuts 1992), such as cuckoldry (Buss and Shackelford 1997). Men must therefore solve both the problems of obtaining sexual access and maintaining exclusive sexual access once a partner is acquired. This unique combination of features has been argued to render male sexual coercion especially likely to occur in humans (Smuts 1992).

The “sexual coercion” hypothesis has also been proposed as a functional explanation for female-directed violence in humans (Barbaro and Shackelford 2016; Camilleri and Quinsey 2012) and propose two specific ways in which violence may solve adaptive problems of sexual access. There is limited empirical data for humans addressing these possibilities, however. Female-directed violence can be classified as *direct coercion* or *indirect coercion* (Muller and Wrangham 2009). Direct coercion refers to force which increases the mating success of, or probability of mating for, the perpetrator. Indirect coercion refers to force which decreases the likelihood of the woman securing or soliciting copulations with a man other than the perpetrator. Direct and indirect forms of sexual coercion are not mutually exclusive. For instance, Camilleri and Quinsey (2012) argue that, in human relationships, physical violence may function as direct coercion by increasing the probability of copulating with an in-pair partner, or physical violence may function as indirect coercion by decreasing a woman's promiscuity and probability of extra-pair mating, or both. In support of the direct coercion hypothesis for humans, Barbaro and Shackelford (2016) show that the frequency of male-perpetrated female-directed violence is positively associated with greater in-pair copulation frequency in romantic relationships. Additional findings show that men who perpetrated physical violence against their romantic partner in the previous 1 month (versus men who did not perpetrate physical violence against their romantic partner) secured more copulations per week, on average (Barbaro and Shackelford 2016).

Research has yet to investigate whether female-directed violence in human relationships also functions as *indirect coercion*, however. If male-perpetrated violence does, indeed, function as a form of indirect sexual coercion, then female-directed violence should be associated with a decrease in a woman's promiscuity, or probability of infidelity. In accordance with the sexual coercion framework (Smuts and Smuts 1993), if male-perpetrated violence functions as hypothesized, then women with violent partners should have fewer opportunities to secure extra-pair copulations (e.g., have fewer male acquaintances, spend less time with other men) (see Barbaro and Shackelford 2016; Camilleri and Quinsey 2012). Research addressing the functional nature of female-directed violence, in accord with research in nonhuman primates, will likely be a profitable empirical endeavor.

Conclusions

An evolutionary psychological perspective proposes that the function of, and motivation for, men's violence against women is, ultimately, sexual in nature. Put differently, men judiciously employ violence – primarily against former or current romantic partners – to correct, prevent, or anticipate female infidelity (Shackelford 2003), whereby violence employed by men solves the adaptive problems of (exclusive) sexual access by functioning to increase his mating success with the woman (Barbaro and Shackelford 2016). Evidence therefore suggests that over evolutionary history men who employed violence judiciously, on average, conferred replicative advantages compared with men who did not judiciously employ violence, in part, to control women's sexuality.

Cross-References

- [Aggression for Sexual Access](#)
- [Contexts For Men's Aggression Against Women](#)
- [Female Infidelity](#)

- [Intimate Partner Violence](#)
- [Sexual Coercion](#)
- [Sexual Coercion and Violence](#)
- [Sperm Competition](#)
- [Sperm Competition Tactics](#)

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Violent

- [Violence](#)

Violent Extremism

- [Suicide Terrorism](#)

Violent Fantasy

- [Aggressive Fantasies](#)

Viral Agent

- [Virus](#)

Virility

- [Fertility](#)

Virion

- [Virus](#)

Virtue

- [Evolution of Morality](#)

Virus

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Synonyms

[Viral agent](#); [Virion](#)

Definition

Viruses are smallest infectious agents comprising genetic material (DNA/RNA, never both) surrounded by a protein coat (Brooks 2010).

Introduction

Viruses are submicroscopic infectious agents which are obligate intracellular parasites. They are metabolically active and can replicate, only inside the host cell (White et al. 1994). The extracellular (transmission) phase alternates with the intracellular (reproductive) phase. Tobacco mosaic virus (TMV) was the first virus to be discovered (Lecoq 2001). Ivanoski (1892) saw that extracts from infected leaves remained infectious after filtration through bacterial filters. Beijerinck (1898) suggested to categorize the causative agent for tobacco mosaic disease as “virus” (Lecoq 2001).

Structure

Virion is the infectious virus particle consisting of a nucleocapsid core. Virions may be surrounded by a lipoprotein envelop (Brooks 2010). The nucleic acid can be single-stranded or double-stranded RNA or DNA. Nucleic acid codes for structural (capsid, envelop proteins, matrix protein) and nonstructural proteins (enzymes like replicases, proteases, and transcriptases) that are important for viral life cycle (White et al. 1994).

Viral capsid is composed of morphological units called capsomeres. Depending upon the arrangement of these capsomeres around the nucleic acid, a virus can have icosahedral symmetry (Fig. 1), helical symmetry (Fig. 2), or complex symmetry. Lipid part of envelop is acquired from the host cellular membranes and the glycoprotein part is coded by

the viral nucleic acid. Capsid and envelop provide protection and stability to the viral nucleic acid and also help viral interaction with the host cell.

Classification

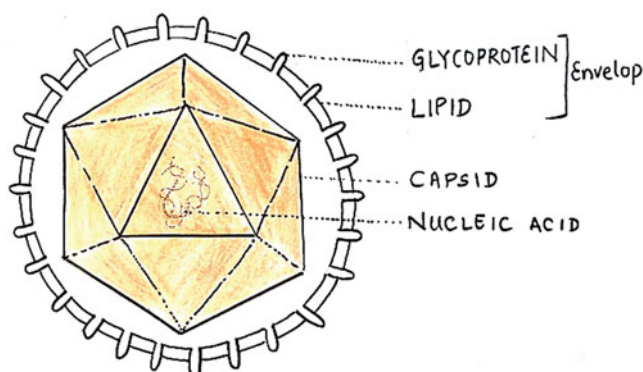
Viruses can infect plants, animals, and microbes as well. Common plant viruses are TMV, Tomato spotted wilt virus, etc. (Scholthof et al. 2011). Viruses of microbes infect unicellular prokaryotes (bacteria) and eukaryotes (algae and protozoa) (Debarbieux et al. 2017). Bacteriophages are the commonly studied viruses affecting microbes.

Viruses have been classified (Table 1) depending on factors including virion morphology – type of symmetry, presence or absence of envelop, viral genome – (nucleic acid type and strandedness, sense (positive/ negative), linear or circular, segmented or unsegmented), host range, mode of transmission, etc. (Brooks 2010).

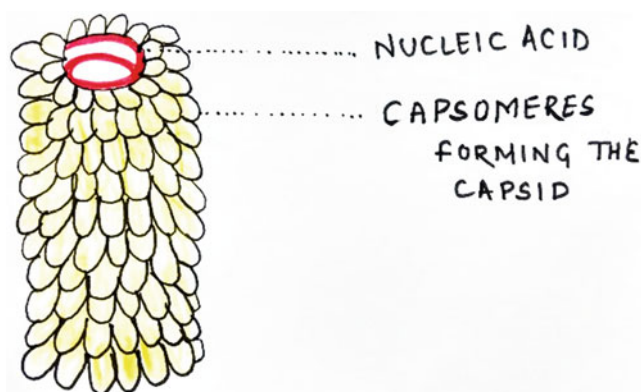
Replication

The first step in viral replication is **attachment**, where the viral attachment proteins (ligand) bind to specific receptor on the host cell plasma membrane (e.g., gp 120 of HIV binds to CD4 of T-helper cells, EBV binds to CD21 on B-lymphocytes). It is followed by **penetration** of the viral nucleocapsid into the host cell, by different mechanisms. In some enveloped viruses, lipid envelop fuses with host cell membrane by help of viral proteins, e.g., gp41 of HIV, F (fusion)

Virus, Fig. 1 Icosahedral symmetry (e.g., Human herpes virus)



Virus, Fig. 2 Helical symmetry (e.g., Tobacco mosaic virus)



Virus, Table 1 DNA and RNA viruses with health implications in humans

Virus families	Symmetry	Genetic material	Envelop	Example of viruses
DNA viruses				
Parvoviridae	Icosahedral	ssDNA linear	Absent	Parvovirus B19
Papillomaviridae	Icosahedral	dsDNA circular	Absent	HPV
Polyomaviridae	Icosahedral	dsDNA circular	Absent	JC virus, BK virus
Adenoviridae	Icosahedral	dsDNA linear	Absent	Human Adenovirus
Herpesviridae	Icosahedral	dsDNA linear	Present	HSV1, HSV-2, VZV, EBV, CMV, HHV-6, -7, -8
Hepadnaviridae	Icosahedral	dsDNA circular incomplete	Present	Hepatitis B virus
Poxviridae	Asymmetrical (Complex)	dsDNA linear	Present	Variola, Molluscum contagiosum virus
RNA viruses				
Picornaviridae	Icosahedral	ss +ve sense	Absent	Poliovirus, Echovirus, Enterovirus, Coxsackievirus, HAV
Orthomyxoviridae	Helical	ss -ve sense segmented	Present	Influenza virus
Paramyxoviridae	Helical	ss -ve sense	Present	Parainfluenza virus, Measles virus, Mumps virus, Nipah virus
Rhabdoviridae	Helical	ss -ve sense	Present	Rabies virus, Chandipura virus
Togaviridae	Icosahedral	ss +ve sense	Present	Chikungunya virus
Flaviviridae	Icosahedral	ss +ve sense	Present	Japanese B Encephalitic virus, Dengue, Yellow fever virus
Caliciviridae	Helical	ss +ve sense	Absent	Norwalk virus
Arenaviridae	Helical	ss -ve sense segmented	Present	Lassa virus, Lymphocytic choriomeningitic virus
Bunyaviridae	Helical	ss -ve sense segmented	Present	Hanta virus, Sandfly fever virus, Ganjam virus
Filoviridae	Helical	ss -ve sense	Present	Ebola virus, Marburg virus
Reoviridae	Icosahedral	ds segmented	Absent	Reovirus, Rotavirus
Retroviridae	Icosahedral	ss +ve sense (2 copies)	Present	HIV, HLV

Abbreviations: *HPV* Human papilloma virus, *HSV* Herpes simplex virus, *VZV* Varicella zoster virus, *EBV* Epstein barr virus, *CMV* Cytomegalovirus, *HHV* Human herpes virus, *HAV* Hepatitis A virus, *HIV* Human immunodeficiency virus, *HTLV* Human T-cell lymphocytotropic virus

glycoprotein of paramyxovirus. Other viruses (e.g. influenza virus), are taken inside an endosome by clathrin coated pits. Viral envelop and endosome membrane fuse afterwards. **Uncoating** of the viral nucleic acid then occurs, due to dissolution of viral capsid by the host enzymes.

The viral nucleic acid then transcribes mRNA followed by synthesis of early proteins (that shut the host genetic machinery). Viral genomic replication follows and progeny genome causes late mRNA transcription leading to synthesis of viral structural proteins. The structural components of virus assemble to form virions, which are then released from host cell.

Generally viral proteins are synthesized in the host cytoplasm using host ribosomes and viral mRNA, viral genomic RNA replicates in host cytoplasm, and viral genomic DNA is replicated in host nucleus. There are, however, few exceptions (Brooks 2010). Figure 3 shows the strategies adopted by different class of viruses for replication and protein synthesis.

Immunity Against Virus

Both innate and adaptive immune systems operate against viral infection. The macrophages and dendritic cells engulf the virion and serve as antigen presenting cells (present antigen to T-helper lymphocytes) and also produce variety of cytokines for activation of adaptive immune cells. Viruses downregulate MHC I (Major Histocompatibility Complex – class I) expression by the infected cells. Such cells are targeted by Natural killer cells (NK cells) which produce perforins and granzymes to cause target cell apoptosis. NK cells also produce IFN γ and TNF α (tumor necrosis factor α) which are essential for combating viral infection. Type 1 Interferons (IFN α , IFN β) are produced by virus infected cells and plasmotoid dendritic cells (even when not infected). Type 1 IFNs upregulates expression of antiviral genes in both infected and uninfected cells. IFN γ also causes activation of macrophages and NK cells.

Antibodies, produced by helper T-cells (CD4+) and B-cells can neutralize the viral attachment

proteins. Complements also have neutralization action. Cytotoxic T cells (CD8+) play major role in controlling infection as they kill the virus infected cells (Delves et al. 2017; White et al. 1994).

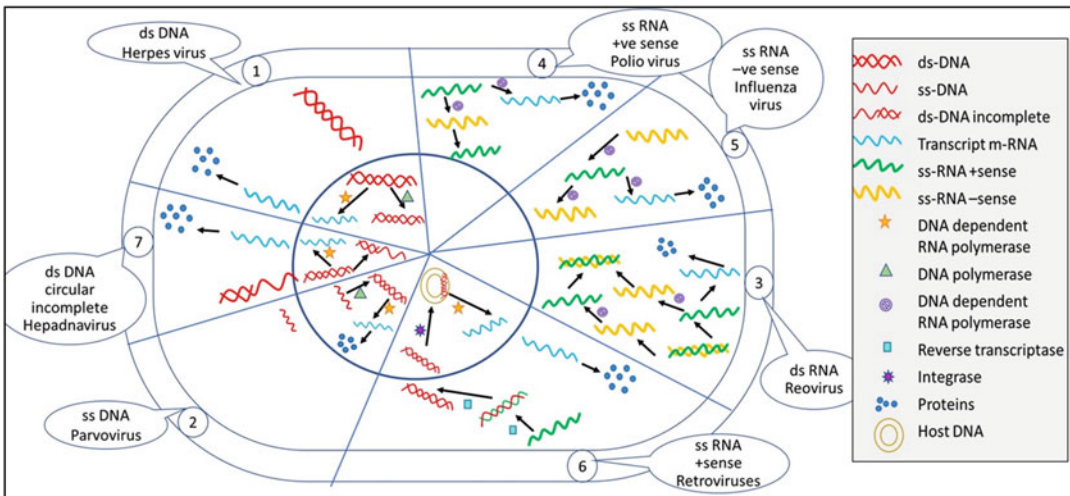
Evolution of Virus, Mutations, and Consequences

Different theories for origin of viruses have been proposed. Viruses may have originated from the genome of host cells or by degeneration of infecting intracellular parasites. DNA and RNA viruses have probably originated from different sources as they vary profoundly (Brooks 2010). The characteristic features of viruses of microbes are different from those of humans and other animals; however, evidences support that they evolved from the same source (Bamford et al. 2005).

Viruses keep evolving for fitness, i.e., “*ability of the virus to replicate infectious progeny*” (Domingo et al. 1996). Viruses have evolved to evade (escape) host immune system (Male et al. 2012) by various strategies like-

- Avoid being recognized by mechanisms like latency, infecting immunologically privileged sites
- Downregulate MHC I and MHC II as seen in HIV infection
- Change antigens by drift and shift as seen in influenza virus
- Affect antigen processing as seen in CMV infection

The RNA viruses are able to breach the boundary of species and capable of infecting new hosts. High mutation rates make them capable of evolving at a faster rate (Holmes 2009). Influenza virus has evolved by re-assortment (mixing of genetic material of one human, one bird, and two swine strains). This has altered its virulence, making it capable to develop a pandemic (Taubenberger and Kash 2010). The recent finding shows that HTLV-1 can cover itself in a carbohydrate-rich adhesive extracellular “cocoon,” similar to bacterial biofilms.



Virus, Fig. 3 shows the strategies of replication and protein synthesis used by different types of viruses: (1) in most dsDNA viruses (e.g., Herpesvirus, Adenovirus), viral DNA transcribes mRNA by the help of enzyme DNA-dependent RNA polymerase (RNA polymerase-II of host), mRNA translates early viral protein in the cytoplasm. DNA replication occurs with the help of host DNA polymerase in the nucleus. In poxvirus, the mRNA transcription and genomic replication occurs in cytoplasm because the virus carries its own DNA and RNA polymerases (2) In Parvovirus ssDNA of virus is first converted to dsDNA by cellular DNA polymerase, then mRNA transcription occurs. (3) In dsRNA containing viruses (e.g., Reovirus), each virion carries RNA-dependent RNA polymerases which use each strand to transcribe mRNA (4) In ssRNA viruses of positive sense, the RNA directly can act as mRNA transcript, genomic RNA is replicated via a negative sense RNA intermediate. (5) Viruses (e.g., influenza virus, rhabdoviruses) with negative sense RNA

viruses carry RNA polymerases for mRNA transcription. (6) Retroviruses (e.g., HIV) have reverse transcriptase enzyme which transcribes DNA strand using each of the viral ssRNA strands (RNA-dependent DNA polymerase activity), it then lyses the parent ssRNA (ribonuclease activity) and forms complementary DNA strand taking the newly formed ssDNA as template, ultimately resulting in the dsDNA which then enters the host nucleus and binds to host DNA with the help of enzyme integrase. When the cell is actively replicating, viral mRNA is transcribed and protein synthesis occurs. (7) In Hepatitis B virus, which has partially dsDNA (circular -not shown in figure), the viral genome is first converted into covalently closed circular dsDNA (cccDNA), which serves as template for mRNA transcription, pre-genomic positive sense RNA is produced too which with the help of reverse transcriptase enzyme subsequently form the genomic partially dsDNA (not shown)

This novel mechanism of viral transmission ensures the efficient and protected viral transfer between cells (Thoulouze and Alcover 2011).

During evolution, changes in the viral genetics occur by means of mutation and recombination, which may alter the virulence power of the virus. An avirulent virus may turn virulent or a less virulent virus may become highly virulent. This leads to newly emerging diseases (Domingo et al. 1996; Roossinck 1997; Morse and Schluederberg 1990). Environmental changes (e.g., Global warming, ecological changes, demographic changes, migration) do play a role in activation or mutation in the viruses and may result in these emerging viral infections (Morse and

Schluederberg 1990; Olival and Daszak 2005). The common emerging viral infections are those caused by – Nipah virus, paramyxoviridae, zika, and ebola viruses (Bishop 2015; Olival and Daszak 2005; Wikan and Smith 2016).

Health Implications

Viruses can cause several diseases in humans (Table 2). Parvovirus B19 can have dangerous manifestation like aplastic anemia and carditis. Hemorrhagic fevers manifest as widespread bleeding from epithelial surfaces. Different hepatitis viruses are grouped under different families and

Virus, Table 2 Important groups of viral infections in humans

Disease groups	Important causative viruses
Viral exanthems	Measles, Rubella, Mumps, Varicella viruses
Arthralgia and arthritis	Chikungunya, HBV, HIV, Zika viruses
Hemorrhagic fevers	Yellow fever, Dengue, Ebolavirus and Marburg viruses
Viral gastroenteritis	Rotavirus (common in childhood), caliciviruses, enteric adenoviruses
Hepatitis	Hepatitis viruses (A, B, C, D, E), yellow fever virus, HSV, EBV, CMV
Genitourinary infection	HSV-2, HPV- 6, HPV-11
Oncogenic viruses	HPV types 16 and 18, HBV, HCV, EBV, polyoma virus, HHV8, HIV, HTLV
Cardiitis	Coxsackie B viruses, adenovirus, parvovirus B19
Encephalitis	Japanese B encephalitis; Eastern, Western, and Venezuelan encephalitis; Herpesviridae family; Picornaviridae family; and Adenovirus
Respiratory infections	RSV, adenovirus, SARS-CoV MERS-CoV, Influenza, and Parainfluenza virus

SARS CoV Severe acute respiratory syndrome, *MERS CoV* Middle east respiratory syndrome

differ greatly in pathogenicity. Cancers that can be caused by viral infection include cervical cancer by HPV 16 and 18, hepatocellular carcinoma by HBV & HCV, Burkitt's lymphoma and nasopharyngeal carcinoma by EBV, lymphomas by HIV virus, Kaposi Sarcoma by HHV8, and leukemias by HTLV. SARS & MERS have rapidly affected many people (reaching close to a pandemic) in recent past. H1N1 flu is the recent most pandemic infection caused by re-assorted influenza virus and is still continuing in India. Zika virus infection in the pregnant female may lead to microcephaly in the new-born child and Guillain- Barré syndrome in adults (White et al. 1994).

In-utero exposure to viruses has been hypothesized to increase the risk of development of schizophrenia, bipolar disorder, autism, and mental retardation in the child (Chess et al. 1978). Viral infection involving the central nervous

system may present with psychiatric manifestations (psychosis, catatonia, mania, and depression) (Freudenreich et al. 2011). Viral infections like HIV, HSV can involve brain and produce cognitive deficits (Dickerson et al. 2004). Serious viral infections (HBV, HCV, and HIV) have been reported in patients with severe mental illnesses. Risky behavior and altered immune status in these patients might be responsible for such coinfections (Klinkenberg et al. 2003).

Certain viruses may remain latent in certain part of the body, after primary attack. JC virus, for example, commonly has subclinical or very mild manifestation in primary attack, and goes unnoticed. However, it remains latent in kidney and brain, and is a frequent cause of progressive multifocal leukoencephalopathy after renal transplantation. Subacute Sclerosing Panencephalitis (SSPE) is a late sequel of measles, though its occurrence has reduced due to vaccination (Garg et al. 2019). Mutated viral genome has been isolated from the brains of patients with SSPE. SSPE often has onset in the adolescence and manifest with cognitive impairment, myoclonus, ataxia, and visual disturbances (Garg et al. 2019).

Laboratory Diagnosis

Samples like swabs (from throat, eye, and skin lesions), feces, CSF from suspected viral cases should be properly collected and transported in viral transport medium (VTM). Collection of the sample from the appropriate site during the course of disease is very critical for direct detection of virus.

Direct demonstration of the virus can be done under electron microscope. Detection of viral antigens can be done by ELISA, Latex agglutination, Immunofluorescence, and Immunochromatography can done depending upon the available formats. Viral nucleic acid can be detected by PCR, Microarray, and other molecular techniques. They are generally the most sensitive and rapid methods for diagnosis. Viral isolation is considered "gold standard," but the isolation of virus in cell lines (e.g., Vero cell line), animal inoculation, and egg inoculation are costly and time consuming and used mainly for research purpose (White et al. 1994).

Detection of antibodies against the viral antigens in the patient blood by ELISA are frequently used screening tools for detection of viral infections. A raised specific-IgM indicates recent infection, whereas, a raised specific IgG can detect past infection. A lot of viral diseases like JE, Dengue, Chikungunya, and Zika are diagnosed by detecting antibodies against them in the patient serum. They are also very sensitive and commonly employed tests.

Advantages of Viruses

Certain vaccines are produced by the live attenuated strains of the viruses, which protects the individual from the infection by the virulent strains of similar viruses. Bio-engineering has used viruses for carrying and protecting genomic information (Li et al. 2010). Viruses can transfer genetic material to their host (e.g., Bacteriophages), which integrates with the host genome, thereby facilitates the evolution of organisms (Roossinck 2011). An important example is evolution of antibiotic resistant bacteria. Many viruses have symbiotic relationships with their hosts and protect the host (Roossinck 2011).

Conclusion

Viruses have abundant health implications including – cancer, neurological, and psychological implications. Viruses continuously interact with the environment and their host, through which they evolve. Prevention of the serious health conditions need development of new and effective vaccines against viruses. There is a lot of scope for research in this field.

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Viscous Population

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Synonyms

Limited dispersal; Natal philopatry

Definition

The mechanism whereby individuals tend to remain near their place of birth and which leads to high genetic relatedness among neighbors.

Introduction

Population viscosity occurs whenever individuals tend to remain near their place of birth, a process that generates high levels of relatedness among neighbors, which is a key factor to kin selection (Hamilton 1964). Kin discrimination allows individuals to discriminate genealogical relatives and to direct altruism toward them (Hamilton 1964). The greenbeard effect allows individuals to discriminate genetic relatives, irrespective of their genealogical ancestry, in which individuals express a phenotypic trait (i.e., the greenbeard) that they recognize in other individuals so that they are able to direct altruism toward them (Hamilton 1964; Dawkins 1976). Because population viscosity does not require any sophisticated recognition mechanism, it is thought to be a general and important relatedness-generating mechanism (Hamilton 1964). In addition, because neighbors are likely to be relatives, population viscosity may even allow for the evolution of indiscriminate altruism (Hamilton 1964).

Population viscosity, however, also poses some challenges for the evolution of altruism. Hamilton pointed out that when the young remain close to their place of birth, they are more likely to compete against each other for local resources (Hamilton 1964). Despite this, Hamilton thought that kin competition would not be sufficiently strong to cancel out the benefits generated by population viscosity, a view that was later challenged by Alexander (1974). Following these verbal arguments, Bulmer (1986) developed a theoretical model to test the effect of population viscosity on the evolution of sex allocation, a social trait in viscous populations. In his model, he showed that the relatedness-enhancing effects and the competition-enhancing effects of population viscosity exactly cancel each other out, so that sex allocation is independent of population viscosity. Taylor (1992) developed an analytical model that specifically focused on the evolution of a public good trait and also arrived at an invariance result, in which altruism is not influenced by the degree of population viscosity.

Bulmer and Taylor's models have motivated a large theoretical and empirical literature on the

evolution of social traits in viscous populations. Theoretical models, for instance, have analyzed how different ecological, demographic, and genetic factors may influence the population viscosity invariance result (reviewed by Lehmann and Rousset 2011). Empirical studies have investigated the importance of kin competition in the evolution of social traits and the relationship between relatedness and social evolution (e.g., West et al. 2001; Griffin et al. 2004; Kümmerli et al. 2009; Wu et al. 2015).

Altruism in Viscous Populations

Bulmer (1986) was the first to provide a mathematical treatment of the evolution of a social behavior and to attest the strength of kin competition in viscous populations by focusing on the evolution of sex allocation, a social trait in viscous populations. The basic setup of Bulmer's model assumes that a mother breeds solitarily, and mating occurs among her own offspring before her daughters disperse away to breed elsewhere. Under this scenario, a mother has an incentive to produce a large number of daughters, but only a small number of sons, just enough to ensure fertilization of all her daughters (Hamilton 1967). This extreme female-biased sex ratio minimizes wasteful competition for mates among her sons and maximizes her number of grandchildren. By contrast, if a mother breeds alongside unrelated females, her sons face competition from unrelated males. Competition among unrelated males favors mothers who produce more sons, which results in relatively less female-biased sex ratios.

Competition, however, need not occur among unrelated males. If some females remain near their place of birth, mothers within each social group are likely to share a recent common ancestor. As a result, young males tend to compete for mates with collateral kin, rather than unrelated males, raising the hypothesis that population viscosity promotes the evolution of extreme female-biased sex ratios; Bulmer (1986) set out to test this hypothesis. His model, however, did not support this prediction. Surprisingly, he showed that the sex ratio does not change with population

viscosity. Relatedness does increase with population viscosity, which favors mothers who have fewer sons (and more daughters). However, population viscosity also increases competition for local resources among related females, which favors mothers who have fewer daughters (and more sons). These two opposing forces exactly cancel each other out so that population viscosity has no net impact on the evolution of the sex ratio (see Box A for details).

Box A

Let us consider a diploid sexually reproducing population subdivided into a very large number of patches, each with a high-fecundity (H) and a low-fecundity mother (L) with fecundity F_H and F_L , respectively (Rodrigues and Gardner 2015). High-fecundity (or low-fecundity) mothers produce a fraction z_H (or z_L) of sons and a fraction $1-z_H$ (or $1-z_L$) of daughters. After reproduction, newborn female and male offspring mate. After mating males die, a fraction d of the mated females disperse away to a random patch in the population, while a fraction $1-d$ remain in the local patch. After dispersal, native and migrant females compete for the two available breeding sites. We are interested in the optimal sex allocation strategy of each breeding mother. A mother should invest slightly more into sons if

$$\begin{aligned} & c_m \frac{1}{n_m} r_S - c_f \frac{1}{n_f} r_D \\ & - c_m \left(\frac{1}{n_f} + \frac{1}{n_m} \right) r_{iM} \\ & + \frac{1}{n_f} \varphi(c_f r_{iF} + c_m r_{iM}) \\ & > 0 \end{aligned} \quad (A1)$$

where c_f (or c_m) is the class reproductive value of females (or males); r_D (or r_S) is the relatedness between mothers and daughters (or sons), n_f (or n_m) is the proportion of

(continued)

daughters (or sons) in the population, r_{iF} (or r_{iM}) is the average relatedness between a mother of quality “i” and female offspring (or male offspring), and φ is the probability that two female offspring remain in their native patch. The first term represents the value of sons, while the second term represents the value of daughters. The third term represents the competition for mates among males, while the fourth term represents the competition for resources among females. Population viscosity increases the relatedness between a focal mother and male offspring born within the patch (i.e., r_{iM}), and therefore a mother is favored to invest less into sons. However, population viscosity also increases competition for resources among female offspring (i.e., φ , r_{iF} and r_{iM}), and therefore a mother is selected to invest less into daughters. When the quality of the two mothers in the patch is identical (i.e., $F_H = F_L$), these two opposing forces exactly cancel each other out so that population viscosity has no net impact upon the evolution of the sex ratio. In other words, the optimal sex allocation strategy in a well-mixed population (i.e., $\varphi = 0$) and in a viscous population (i.e., $\varphi < 0$) is exactly the same (Bulmer 1985). However, when the quality of the two mothers differs (i.e., $F_H > F_L$), then population viscosity does have an impact upon the evolution of the sex ratio. In a viscous population, high-quality mothers are now selected to invest more into sons than low-quality mothers (Rodrigues and Gardner 2015).

Taylor (1992) also treated the problem of the evolution of social traits in viscous populations. However, he explicitly focused on a public goods game model, in which individuals provide a benefit to everybody in the group at a cost to themselves and in which he was able to provide an analytical treatment of the problem. Like Bulmer, he arrived at an invariance result, in which the level of investment into the public good does not

vary with population viscosity. Again, the cooperation-enhancing effects of population viscosity are fully cancelled out by the cooperation-inhibiting effects of population viscosity (see Box B for details).

Box B

Let us assume an asexual and haploid population subdivided into an infinite number of groups of n individuals. Each individual produces a very large number F of offspring and dies afterward. Each offspring disperses with probability d to a random patch in the population and remains in the local patch with probability $1-d$. Both migrant and native individuals then compete for the n available breeding sites in each patch. After competition for breeding sites, offspring become full reproductive adults, which bring the life cycle of our model species to its beginning. To determine the direction of selection, we take the neighbor-modulated approach to kin selection (Hamilton 1964; Taylor and Frank 1996). We focus on the evolution of a cooperative trait that costs C offspring to its bearer but provides B additional offspring to a bearer's social partners. The level of expression of this trait in a focal individual is x , the level of expression of the trait in the focal individual's social partners is y , and the average expression of the trait in the population is z . The neighbor-modulated fitness of a focal breeding adult is then given by

$$w = F(x, y) \times \left(\frac{(1-d)}{F(y, y)(1-d) + dF(z, z)} + \frac{d}{(1-d)F(z, z) + dF(z, z)} \right) \quad (\text{B1})$$

The selection gradient is given by the slope of fitness on the phenotype of the focal individual, which is $dw/dx = \partial w/\partial x + \partial w/\partial y \cdot r$, where r is the coefficient of relatedness between interacting partners. Expanding this equation we get a form of Hamilton's

(continued)

rule, the condition for the evolution of the altruistic behavior, which is given by

$$-C + Br - (B - C)hR > 0 \quad (\text{B2})$$

where $h = (1-d)^2$ is the probability that one of the additional offspring generated by altruism remains in the local patch and destroys a native offspring. Altruism creates B additional offspring, who are related to the actor by r , but it also destroys $(B-C)h$ local offspring, whose value to the actor is R . Because of $r = hR$, the kin competition effect completely negates the kin-selected benefits of population viscosity (Taylor 1992).

Bulmer and Taylor's models are extremely important because they provide a social evolution invariance result – the level of cooperation does not change with population viscosity – against which other hypotheses can be contrasted. Because Bulmer and Taylor's models lack many of the life history and ecological variables observed in natural populations, they have motivated a wealth of theoretical and empirical studies investigating how these different factors influence the evolution of social traits in viscous populations and whether they breakdown the invariance result (Lehmann and Rousset 2010; see Box A for an example).

An empirical test of the role of population viscosity comes from a study on the bacterium *Pseudomonas aeruginosa* (Griffin et al. 2004; Kümmerli et al. 2009). *P. aeruginosa* is a bacterium that requires iron for fundamental metabolic functioning. However, most of the iron available in the environment comes in the Fe(III) form that is not readily metabolized by this bacterium. *P. aeruginosa* can overcome this problem, however, by producing and secreting molecules called siderophores that bind to Fe(III) making it edible for the bacterium. A problem with this system, however, is that the manufacturer of a molecule might not benefit from its end product, and therefore bacteria that do not pay the metabolic cost of

molecule manufacture but that benefit from its production may gain a fitness advantage. Researchers are therefore interested in understanding what are the mechanisms that stabilize cooperation in *P. aeruginosa*. Experimental evolution has shown that population viscosity might stabilize cooperation in *P. aeruginosa* (Griffin et al. 2004). By varying both the number of clones that started a new colony and whether the different clones were allowed to compete with the global population or not, they found that siderophore production was more likely to evolve when relatedness is high and kin competition is low.

Class Structure in Viscous Populations

Most of the studies of the problem of altruism in viscous populations have been focused on cases in which quality does not vary among individuals (e.g., Bulmer 1986; Taylor 1992). Recent work, however, has begun to analyze how individual quality influences the evolution of altruism in viscous populations (e.g., Rodrigues and Gardner 2013, 2015). In natural populations, not all differences among individuals are due to their genetic makeup, and in many cases, differences among individuals emerge due to non-genetic factors such as age, reproductive state, size, nutritional state, or sex. Variation in individual quality introduces class structure in a population, where the change in gene frequency over one generation may not be representative of long-term adaptive changes in gene frequency. For instance, over one generation a mother who produces a single high-quality offspring loses out the (short-term) evolutionary race to a mother who produces multiple low-quality offspring. However, if we consider the change in gene frequency over several generations, the mother who produces a single high-quality offspring may well win the long-term evolutionary race. As adaptive evolution concerns long-term gene frequency change, the solution to this problem is to weigh the value of each offspring by their long-term contribution to the gene pool of future populations (i.e., their reproductive value), instead of considering solely

the number of offspring as a measure of fitness (e.g., Rodrigues and Gardner 2013).

In some cases, the quality of the young varies, and some are condemned to have lower fecundity than their more fortunate siblings. Rodrigues and Gardner (2013) set out to study how variation in quality among social partners influences the evolution of altruism in viscous populations. They found that Hamilton's rule, the condition for the evolution of a social behavior, is given by

$$-Cv_A + Brv_R - (B - C)hvr_S > 0, \quad (1)$$

where v_A is the reproductive value of the actor, r is the relatedness between the actor and the recipient, v_R is the reproductive value of the recipient, h is the probability the extra offspring generated by altruism remain in the local patch and that they take up resources of other native offspring, v is the reproductive value of philopatric offspring, and r_S is the relatedness between the actor and those offspring who suffer additional competition owing to the extra competition for resources. First, they found that individual variation among group members breaks down the cancellation result of Bulmer and Taylor so that viscosity influences the level of investment into cooperation. Second, they found that low-quality individuals invest more into altruism, while high-quality individuals invest more into selfishness. Finally, as the population becomes more viscous, low-quality offspring are favored to sacrifice their lives in favor of their more fortunate high-quality relatives.

Kin Competition

An offshoot of the study of social traits in viscous population was the renewed interest in the role of kin competition in the evolution of social behavior. Kin competition is prevalent in the natural world and often mediates selfish and spiteful traits among related individuals. In the simplest theoretical models, kin competition exactly cancels out the benefits of population viscosity, as we have seen above. In the natural world, however, these two opposing forces vary considerably and

are influenced by the different ecological, demographic, and genetic variables as well as the life cycle of the species.

A remarkable example of how kin competition influences the evolution of social traits occurs in wasps, where the level of aggression across different wasp species varies widely (West et al. 2001). In some wasp species, adult females lay eggs within figs, with female and male larvae developing inside these figs. Males are wingless and mating occurs within each fig before females fly away to lay their own eggs elsewhere. The average level of relatedness within each fig varies between species, and therefore it is possible to test whether there is a negative correlation between levels of male aggression and relatedness, as predicted by Hamilton's rule. Using a comparative analysis approach, it has been shown that there is no correlation between relatedness and the average level of aggression within each fig (West et al. 2001). By contrast, there is a negative correlation between aggression and the density of available females within each fig, which suggests that the level of aggression is driven by kin competition rather than relatedness. In species where there are fewer available females, males fight more for mating opportunities than in species where females are abundant, irrespective of their relatedness.

Kin competition also seems to play a role in the social behavior of humans. Wu et al. (2015) found that the level of female and male dispersal (or viscosity) influences the tendency to cooperate in Southwest China villages. The level of female dispersal varies between different villages. While in some villages both women and men remain close to their place of birth, in other villages women show an intermediate level of dispersal, with some women remaining in their native village, but others moving to different villages. When both women and men remain in their villages, average relatedness goes up within each village. Surprisingly, researchers found that in such cases the level of cooperation drops and individuals are less likely to cooperate when playing economic games. When some of the women disperse to a different village, relatedness is relatively lower. However, they found that in

such cases individuals are more likely to cooperate. These two examples highlight the general idea that cooperation depends on the fine balance between the cooperation-enhancing and the cooperation-inhibiting forces of population viscosity.

Conclusion

Population viscosity occurs whenever individuals tend to remain near their place of birth. Alongside kin discrimination and the greenbeard effect, population viscosity is one of the main mechanisms capable of generating relatedness among social partners, which allows kin selection to operate. In a viscous population, neighbors are likely to be relatives, and therefore population viscosity may even allow for indiscriminate altruism, unlike kin discrimination and the greenbeard effect. Moreover, because it does not require any sophisticated recognition mechanism, it is thought to provide an important and general solution for the problem of altruism. Population viscosity, however, also leads to kin competition, which may slow down, and in some cases even impede, the evolution of altruism.

Cross-References

- [Genetic Relatedness](#)
- [Green Beard Effect, The](#)
- [Hamilton's Rule](#)
- [Inclusive Fitness](#)

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Vision

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Synonyms

[Phylogeny of light detection and vision](#)

Definition

The conservation and adaptation of primordial visual substrates throughout the phylogenetic tree to humans.

Introduction

The topic of evolution is more than an academic discipline that serves to simply annotate our ancestral past. Gaining knowledge into how

structure relates to function and how that interplay was shaped by the selective pressures over an array of changing environments bolsters our ability to understand mechanisms of action and to defend ourselves against disease. Few organ systems permit the level of accessibility that the eye provides, both anatomically and through evolutionary conservation, to test and evaluate the driving forces of evolution (reviewed in Caves et al. 2018). The visual system transcends 550 million years of protozoan and animal phylogeny, is highly accessible due to the extracranial origin in many animals, and benefits from a vast interdisciplinary knowledge of the genetics and epigenetic factors that regulate its development and function. Exploiting these attributes allows us to further understand the evolutionary origin of human disease genes and greatly widens our toolkit from which we can modify and engineer treatments to combat blinding ailments (Domazet-Lošo and Tautz 2008). By extension, exploiting what we learn about early protovisual substrates, such as the discovery and reengineering of channel rhodopsins (Berthold et al. 2008; Ernst et al. 2008), endows us with the potential to modify or enhance our visual system through therapeutic intervention (Deisseroth 2011). For these reasons, the visual system has greatly informed the wider field of evolution.

The Blueprint of Vision

The human visual system is composed of an eye which functions to capture and sense light, process that information through early neural processing, and send this information through physical projections to the brain via the optic nerve tracts (reviewed in Dowling 1999). The beginning of the visual cascade is the transduction of light photon energy into a biochemical and neural signal. This initial process takes place in rod and cone photoreceptors located in the outer nuclear layer, which send their information to a series of interneurons located in the inner nuclear layer. Lateral processing at this level provides pre-processing of neural signaling which generates a coded visual output to retinal ganglion cells.

These 3rd-order neurons then project to several structures within the brain to be integrated into higher processing of sensation and perceptive functions. Input from this light-sensitive system regulates aspects of circadian entrainment, vision, and higher executive functions that process sensory information. Ultimately, this structural arrangement, comprised of a photon sensor, a local processor circuit, and neural projections to brain regions that control higher functions, underlies the basic architectural blueprint of not only the mammalian visual system but lower animals as well (reviewed in Gehring 2014). At its origin, this blueprint evolved from the simplest of visual architectures. Our protozoan ancestors established strategies to orient themselves in relation to energizing light stimuli. Moving toward light energy for the positive benefit of energy production (phototaxis) and moving away from intense light to protect themselves from photo-damage (negative phototaxis) imparted a survival advantage. This progression required two important structural and biochemical adaptations: one, the ability to transduce light energy into a cellular signal that is in some way coupled to organism motility machinery, such as cilium or flagella, and two, some degree of anatomical asymmetry that can be used to interpret the direction of a light source. As previously described by Nilsson and colleagues, these behavioral adaptations emerged from a sequence of physical adaptations that include organ asymmetry, assimilation of light-absorbing pigments, constriction of the organ to aperturate the light path, and the development of a lens to compensate for limited light capture (Nilsson 2009). Protozoa, which bridge the gap between plants and animals, evolved a functional photoreceptor capped with a photon-absorbing carotenoid pigment complex (reviewed in Williams 2016). These two structures collectively provide light sensitivity, protection from photo-damage, and the selective ability to block photo-detection from one direction. Although this ancestral-prototype visual complex has evolved in many forms, the strategy of controlling the path of light in relation to a phototransduction element forms the basis of vision systems in higher organisms.

Lower Organisms to Humans

The many ontogenic steps that occupy the evolutionary tree of vision between early prokaryotes and humans provide us with insight into adaptations to this architectural blueprint (Williams 2016). Simple visual systems present in organisms such as filamentous bacteria elaborated the basic photoreceptive effector to influence motors, such as motile cilia. This adaptation of light-guided motility was achieved via the recruitment of molecular signaling pathways (Lamb et al. 2009). This basic visual framework is evident throughout many taxa to human photoreceptors, which exhibit an evolutionarily conserved common domain occupied by ancestrally related photopigments within the primary cilium. The compound eye of the *Drosophila* fly also utilizes a distinct architectural array of individual photoreceptive units termed ommatidium, rather than a laterally convergent retinal circuit that is evident in most vertebrates. These compound-style eyes contain numerous columns of individual lenses and photoreceptors that more directly synapse onto projection neurons in the fly brain (Kumar 2018). Vertebrate eyes, in contrast, utilize a single “camera-style” lens to focus light onto the entire retina and employ multiple lateral processing interneurons to achieve preprocessing ahead of 3rd-order retinal ganglion cells. In part due to this diversity in how organisms exploit and deploy the basic blueprint of photoreception, research into visual system evolution has greatly elaborated our understanding of the mechanisms that mediate organism diversity. The genetic encoding of eye development offers a similar analogue from which we can interpret evolutionary progression (Lamb 2013). The highly conserved paired-type homeodomain gene *Pax6*, as an example, regulates the earliest specification of the eye primordium during development (Pichaud and Desplan 2002). The role of the *Pax6* gene in driving photosensation is also evident as early as 550 million years ago, making it one of the oldest genes known to regulate eye specification. During this period, atmospheric oxygen and protection from mutagenic photodamage were effectively absent, and *Pax6* had already evolved (Quiring

et al. 1994). As the ocean’s photosynthetic organisms, such as plankton, generated atmospheric oxygen as a by-product, the attenuated impact on light energy permitted a condition in which light could play a role as a substrate for behavioral modifications rather than simply energy production. Genes such as *Pax6* could then be adapted to regulate emerging features of the evolving eye in relation to this changing light environment (Gehring and Ikeo 1999). By 530 million years ago, speciation evolved rapidly from basic photosynthetic organisms to those who adapted camouflage and sexually attractive chromatic elements within their body architecture (Cuthill et al. 2017). It is thought that these adaptations were, in part, driven by *Pax6*, the evolving photoreceptive complex and its acquired ability to gather more complex light information from the environment. The explosion in diversity that emerged after the onset of photoreception fueled morphological and molecular diversity across the vast majority of creatures that exist today. This visual evolution progressed as an adaptation to not only evolving colors exhibited by surrounding organisms (Cuthill et al. 2017) but also the movement of life throughout variations of aquatic and atmospheric media (Sivak and Sivak 2018). For example, terrestrial creatures needed to adapt an ocular system that is optimized for the refractive index of light traveling through air and with relatively little attenuation in intensity through the atmosphere. In contrast, aquatic organisms adapt to a much higher refractive index and are further challenged with the water’s influence on light penetration and wavelength selectivity at various depths. The opsins in deep-sea creatures are tuned to transduce in response to blueshifted photons that are capable of penetrating to greater depths in water. In contrast, the mantis shrimp’s ability to express 16 distinct visual pigment genes, the most discovered to date, reflect the expanded composition of wavelengths present in shallower waters (Cronin et al. 2001). The coupled evolution of vision and photopigment diversity therefore allowed organisms to not only efficiently engage in predatory and defensive behaviors, but also enrich sexual selection within the species in the context of their respective habitats.

Molecular and Anatomical Evolution of Vision

Our knowledge of visual system evolution has been acquired most predominantly through the study of specific substrates that function in vision. For example, *opsin* genes, their sequence homology, mutations, and molecular products of those mutations, have been mapped throughout the evolutionary tree (reviewed in Kawamura 2016). In addition, the emergence of new cell types such as interneurons and cellular modification to cells, such as the recruitment of the primary cilium for photon sensing, follows a similar roadmap throughout evolution. The impact of these genes on structural and anatomical evolution requires that they possess genetic encoding that is sensitive to mutagenic influence. For example, the discovery of the highly conserved function of homeodomain transcription factors, such as *Pax6*, *Vsx2*, *Rx*, and *Rb*, in specifying cell fate and function across the animal kingdom has catalyzed our knowledge of the molecular and genetic evolution of the retina (Colley and Dowling 2013). Failure of these gene assemblies to function can have profound negative effects on the development of the eye due to the necessary nature of their role. Mutations in the *Vsx2/Chx10* gene, which is conserved from *C. elegans* to humans, result in a small eye phenotype termed microphthalmia (Burmeister et al. 1996). More hypomorphic effects of gene mutation are evident following failure of ciliary genes such as *Cep²⁹⁰* to regulate the development of an opsin-rich outer segment (Valente et al. 2006). These ciliopathic mutants have a fully formed eye but are congenitally blind. Thus, transcriptionally encoded decisions help explain the emergence and diversity of new cell types and cellular modifications, as well as the fidelity of their function in refining vision. Perturbations in these genes are linked to a wide array of developmentally regulated disease states, including cancers, underscoring the fundamental importance of their function.

The gross anatomical adaptations throughout evolution are intimately coupled to the genetic programming that regulates the subtle refinement of visual structures. In vertebrates,

the light-sensing organ is the eye which exhibits many adaptive features of our ancestral design (reviewed in Gehring 2014). Eye lids, directional positioning of the eye via extraocular muscles, the complex optics of the many transparent lenses, and liquid components of the eye, as well as the aperture-like iris, collectively regulate the directionality and magnitude of light energy that reaches the neural photoreceptive arena. The curved shape of the back of the eye further optimizes the ability to capture light from various directions. The summation of these components is the enhanced ability to resolve light intensity and wavelength, thus enhancing the function of photosensitive transduction pathways. Although the human visual system is a remarkable example of adaptive organ function, we hardly represent the pinnacle of all notable functions across the animal kingdom. For example, humans are trichromatic visual animals that rely on short (blue), medium (green), and long (yellow-green) color sensitivity and encoding. This is in contrast to the polychromat mantis shrimp, which can resolve an impressive 16 distinct wavelengths of light (Cronin et al. 2001). Some species of raptors are estimated to have 200x the visual acuity of humans and are able to make far more rapid focal adjustments to track prey (Potier et al. 2016; Potier et al. 2017). These exceptional examples of visual molecular and anatomical evolution reflect the unique environmental demands placed on these creatures relative to humans.

Concluding Remarks

Visual evolution is a discipline that transcends a vast spectrum of academic genres and whose content stretches far beyond what we can discuss in a primer. Although much of this chapter is focused on the emergence of eyes from visual primordia, relatively little is described about the complex process of connectivity with the brain and the development of higher processing as it relates to evolution. Fields such as neural regeneration have made great advancements in characterizing the enhanced ability of non-primate vertebrates such as chickens, frogs, and newts to

regrow damaged visual structures (Alunni and Bally-Cuif 2016). Harnessing the information to understand where we lost this regenerative capacity throughout evolution can help us formulate ways to impart therapeutic variations of regenerative properties. The field of stem cell science has added similar contributions to our understanding of evolution, as we are now able to program and regulate many basic aspects of tissue primordium across multiple species (Kempermann 2015; Lai and Aboobaker 2018). This approach can recapitulate the fundamental process of evolution through mutagenic screening, thus offering insight into the relationship between these events and structural adaption. Finally, merging together the assets that lower organisms have retained throughout evolution with mammalian systems offer potential therapeutic substrates. This is evidenced by the emerging data demonstrating that the misexpression of channelrhodopsin and halorhodopsin in the eye (Colley and Dowling 2013; Polosukhina et al. 2012), brain, spinal cord, muscle, and theoretically any other tissue currently offer avenues for the restoration of organ activity that has been compromised by disease.

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Vision Science

► Human Visual Neurobiology

Visual Agnosia for Faces

► Prosopagnosia (Face Recognition)

Visual Association Cortex

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Synonyms

[Extrastriate visual cortex](#); [Prestriate visual cortex](#)

Definition

Cortical areas that contain cells sensitive to visual stimuli that lie outside primary visual sensory cortex.

Introduction

Association cortex constitutes areas outside the primary sensory and motor cortex and occupies much of the primate frontal, occipital, parietal, and temporal lobes. Association cortex can be broadly subdivided into *parasensory association cortex*, *frontal association cortex*, and *paralimbic association cortex* (Pandya and Yeterian 1985). *Visual* association cortex reflects those association cortical areas in the occipital, frontal, parietal, and temporal lobes that receive direct or indirect input from primary visual cortex, V1, which is the dominant cortical entry point for incoming visual information relayed through subcortical visual nuclei (chiefly the lateral geniculate nucleus) from the retina. The study of primate cortex using architectonic and neurophysiological techniques has led to the discovery of a vast number of unique cortical areas, and a large number of these areas possess cells that are sensitive to visual stimuli. Coverage of all of these areas is beyond the scope of this article, as is in-depth discussion of the visual cortex in primate species less well-studied than that of the macaque, including humans.

Parasensory Visual Association Cortex

The parasensory visual association cortex occupies much of the occipital, inferotemporal, and posterior parietal lobes. Differences in architectonics and patterns of connectivity support the subdivision of parasensory visual association cortex into *first, second, and third order* visual association cortical areas (Pandya and Yeterian 1985). First order association cortex receives feedforward projections from the primary visual cortex, which is located in and around the calcarine sulcus of the occipital lobe. Second and third order visual association cortical areas receive input from primary visual cortex only indirectly through first and second order visual association cortex, respectively. The cellular layers of visual association cortex become less differentiable, particularly in third order visual association cortical areas, which is thought to index an increase in the degree of abstraction from visual sensory information coded in lower order areas (Pandya and Yeterian 1985).

First Order Visual Association Cortical Areas

First order visual association areas are among the best-studied areas of macaque visual cortical areas. First order visual association cortical areas V2, V3, V3A, V5, and V6 form the “tributaries” of the “Dorsal Stream” of cortico-cortical projections which interconnects the posterior parietal cortex (PPC) with occipital cortex and structural targets in the premotor areas of the frontal cortex. First order visual association cortical areas V2, V3, and V4 form the dominant “tributaries” of the “Ventral Stream” of cortico-cortical projections that interconnects inferotemporal with occipital cortex and structural targets in the medial temporal lobe (MTL), limbic system, and prefrontal cortex.

Second and Third Order Visual Association Cortical Areas

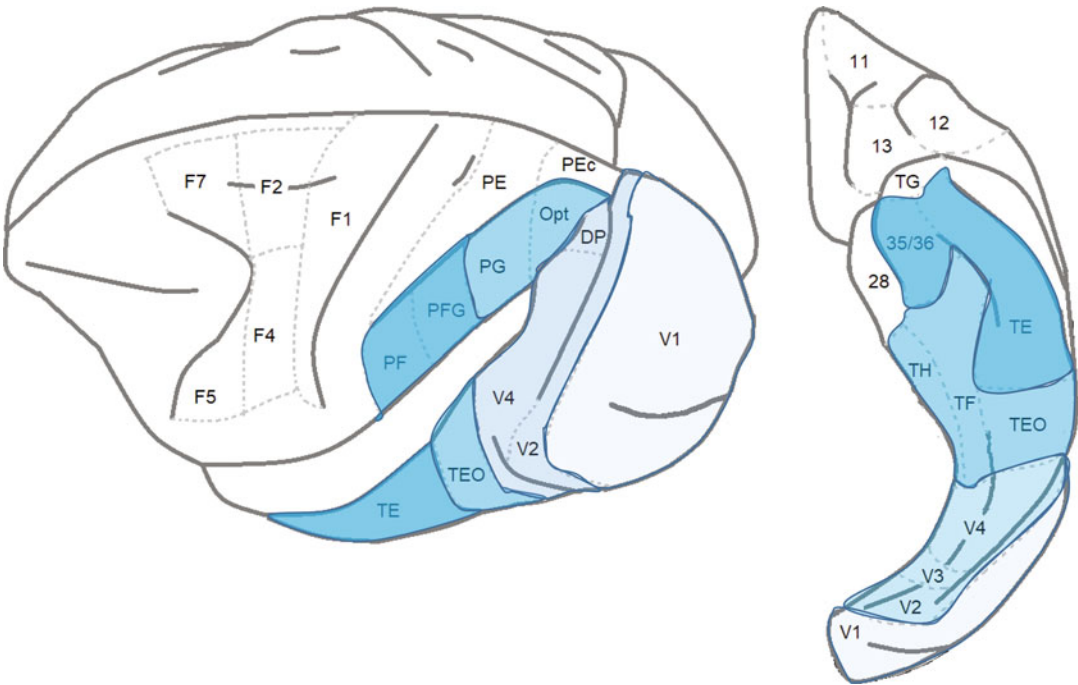
Second order visual association cortex receives visual input through first-order visual association cortical areas, whereas third order visual association cortical areas receive visual input through second order visual association cortex. Second

and third order visual association cortex of the temporal lobe occupies the inferior temporal cortex and the ventrolateral junction of the temporal and occipital lobes. Second order visual association areas comprise temporal lobe areas TEO, which occupies the inferior temporal gyrus of the caudal aspect of ventrolateral temporal lobe, and the posterior aspect of its immediate anterior neighbor, area TE, a third order visual association area which occupies the inferior temporal gyrus up to but excluding the temporal pole (Fig. 1).

Several areas in the posterior parietal cortex (PPC) possess cells that are sensitive to visual stimuli. These areas are found in the convexity of the inferior parietal lobe (IPL), in the cortical areas in and around intraparietal sulcus (IPS), which sits in between the IPL and the superior parietal lobe (SPL), and the caudal-most aspects of the SPL itself. The IPL areas Opt, PG, PGF, and PF are ordered one after the other in a caudal to rostral direction. The IPS is split into posterior, medial, ventral, lateral, and anterior subdivisions. The SPL is subdivided into areas PE, caudal PE (PEc), and PG, which is located on the medial side. Many of these areas possess subpopulations of cells that are sensitive to visual or both visual and somatosensory stimulation, consistent with their role in sensorimotor and spatial processing (e.g., Murata et al. 2000).

Paralimbic Visual Association Cortex

Paralimbic association cortical areas constitute those association cortical areas that are directly connected to structures of the limbic system and includes areas of the orbitofrontal cortex on the ventromedial side of the frontal cortex, the cingulate region, located on the medial side of the brain, area TG, which occupies the temporal pole of inferotemporal cortex, and structures in the perirhinal and parahippocampal region, areas TF, TL, and TH, which occupy the ventromedial aspect of the temporal lobe. Areas TF, TL, and TH are interconnected with the hippocampus via entorhinal cortex. Each of these areas receives visual input from first and second order visual association cortical areas, auditory input from auditory



Visual Association Cortex, Fig. 1 Visual association areas of the left hemisphere depicted from dorso-lateral (left pane) and ventral (right right) viewpoints. Primary visual cortex (V1) reflects the earliest cortical entry point for retinal information. A successive series of visual feedforward projections from V1 branch into the visual dorsal and ventral streams of the parietal and temporal cortex, respectively. Successively darkened areas reflect

the increasing synaptic distance from V1. Note that the areas are schematically demarcated, and the boundaries are often more graded than are depicted here. Furthermore, the frontal visual association areas are not illustrated, and the vast majority of association areas are subdivided functionally and anatomically into finer-grained subregions the details of which are beyond the scope of this entry

association areas, and somatosensory input via the multimodal region of the IPL (Pandya and Yeterian 1985).

Properties and Functions of Visual Association Cortex

Visual association areas integrate stimulus properties extracted from low level information extracted from across the visual field; they integrate information from across other sensory areas and from the motor cortices; and they integrate online input with stored information in memory to construct complex representations of the environment for interpretation, planning, and action.

An increase in the *order* of a visual association area coincides with less cortical magnification, coarser retinotopic organization, and greater

diversity in cellular visual receptive field size. Second and third order areas along the IT and in the PPC possess cells with large receptive fields that include the fovea bilaterally but possess a disproportionately large coverage in the contralateral visual field. These properties make these areas well-suited for integrating information across areas of the visual field. In addition, second and third order areas receive converging inputs from a number of disparate lower-order visual association areas. While these lower order areas generally overlap in the categories of stimulus properties they process, each one will specialize in the processing of one or more visual stimulus features. For example, while V5 is not the only area to process visual motion, it does not process color, whereas V4 is the dominant first-order color processing area, but is not the only area that processes color. Importantly, the responses of many

cells in visual association cortical areas are often highly selective and are driven by more complex visual stimuli or a combination of visual and other sensory or motor modalities (Bullier 2001).

First order visual association areas often respond to more specific properties or stimulus attributes such as the direction of object motion or the shape of objects. As opposed to lesions of primary visual cortex, lesions of first order visual association cortex often spare the detection of low level stimulus properties such as luminance and contour but can produce a deficit in the perception of composite features such as object shape. In humans and in the macaque, lesions to the dominant visual motion processing center, V5 and its surrounding satellite structures, result in a deficit in recognizing the direction and speed at which objects or scenes are moving, referred to as *akinetopsia* (Rudolph and Pasternak 1999; Zihl et al. 1983). Reversible inactivation of V4 in macaques and the ventrolateral area of the occipital-temporal cortex in humans lead to visual form agnosia, which refers to selective deficits in shape discrimination (Girard et al. 2002; Milner et al. 1991).

In contrast to these deficits in perceptual discrimination of object form, lesions to second and third order visual association cortex in the anterior aspect of the temporal lobe in humans can result in deficits in extracting meaning from objects (McCarthy and Warrington 1986). Consistent with a role in memory, the responses of cells in TE, TG, perirhinal, and entorhinal cortex are attenuated upon the second presentation of an otherwise unfamiliar stimuli, even when the subsequent presentation occurs after many intervening stimuli (Fahy et al. 1993). Other neurons in these same areas respond more to unfamiliar than to familiar stimuli, and, in some cells, this preference can last up to 24 h (Fahy et al. 1993). These areas possess populations of *familiarity* neurons and other populations of *recency* neurons; familiarity neurons respond to relative familiarity but not for how far back in time a stimulus was last presented, whereas the responses of recency neurons depend on how recently a stimulus was last presented, but not their relative familiarity (Fahy et al. 1993).

The organization of visual association cortical areas stands in contrast to the organization in primary visual cortex, in which the integration of visual information across the visual fields of cells is unlikely, given that the axons of neurons responding to one location in the visual field would have to span unusually long distances to influence the output of neurons in primary visual cortex that respond to other regions of the visual field (Bullier 2001). Nevertheless, feedback projections from higher-order visual association areas often span more than one order. For example, second order visual association area TEO and the caudal-most aspect of area TE project back to V1 but there is no feedforward projection from V1 to TEO or TE. Since TE is a known recipient of output from memory-associated structures of the MTL, these pathways presumably function to allow stored information to influence the processing of incoming visual information (Bullier 2001).

Conclusion

Visual association cortex encompasses much of the primate cortex and is distinguishable from primary sensory and primary motor cortical areas on the basis of architectonics, laminar organization, patterns of connectivity, and neurophysiology. These same techniques suggest a further subdivision of visual association cortex into first, second, and third order areas. First order areas can be categorized according to their downstream Dorsal and Ventral Stream targets in the PPC and inferotemporal cortex, respectively, and specialize in the processing of particular stimulus properties or features (e.g., form and color in V4) or states (motion in V5). In the inferotemporal cortex, second order and third order visual areas possess populations of cells that specialize in more complex assemblies of stimulus features stimulus properties to specialization in more abstract representations entailing identity and meaning that are geared for memory, planning, and goal-formulation in the service of immediate object-interactive action or long-term scheduling, and the behavioral and social relevance associated

with the stimulus. In the PPC, second and third order visual areas possess subpopulations of cells that respond to the visual, motoric, and/or somatosensory features of movements made by the eyes, limb, or hand during their planning and/or execution, consistent with the PPC's role in the visual and somatosensory guidance of eye and limb-based action (e.g., Murata et al. 2000).

Cross-References

- [Dorsal Stream, The](#)
- [Ventral Stream, The](#)

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Visual Awareness

- [Summary Representation](#)

Visual Cognition

- [Human Visual Neurobiology](#)

Visual Illusions

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Synonyms

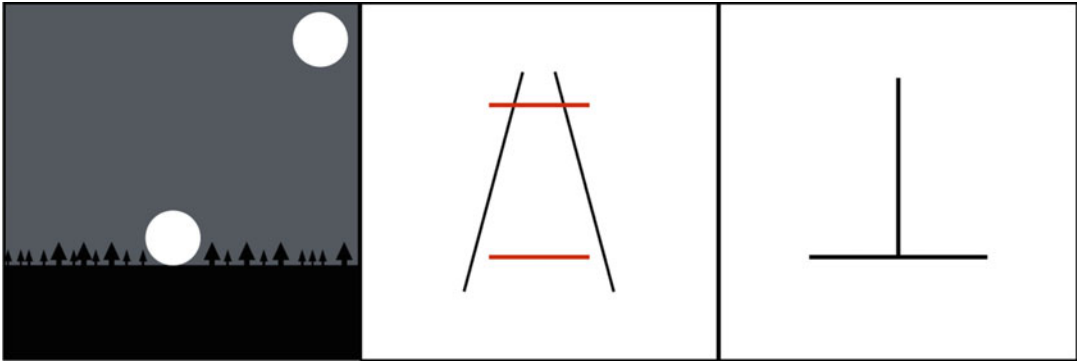
[Hallucinations](#); [Mirages](#); [Optical Illusions](#)

Definition

Illusion is the difference between the perception of a stimulus and the actual stimulus. Illusions are either adaptations or byproducts of differential selection on information processing mechanisms.

Introduction

An illusion is the difference between an observer's perception of a stimulus and the objectively measurable qualities of that stimulus in the real world. Classic examples of illusions include the moon illusion, where the moon looks larger when it is at the horizon than when it is high in the sky (see Fig. 1). Other classic illusions include the Ponzo illusion, where objects located near the convergence of distant, seemingly parallel lines



Visual Illusions, Fig. 1 Illusion examples. The left, center, and right panels illustrate the moon, Ponzo, and vertical-horizontal illusions, respectively

look larger than the same objects located at the near, diverging end of those lines (see Fig. 1). We typically describe phenomena as illusory only when they occur across individuals in a systematic fashion. There is often no clear or meaningful way to distinguish such phenomena from hallucinations, even though the latter is, strictly speaking, the perception of apparently external stimuli without external sensory stimulation.

The Nature of Illusions

The best examples of illusions occur in a way that is within the observer's capacity to perceive accurately. For example, humans tend to overestimate the length of two-dimensional vertical lines, even though we are able to perceive distances accurately in other situations (i.e., the vertical-horizontal illusion, see Fig. 1). The capacity to perceive accurately that which observers systematically perceive otherwise is the hallmark of an illusion. It is likely that we call such differences illusions only in the rare instance that we notice them.

Illusions are common, rather than exceptional, and this high frequency persists across sensory modalities. For example, our ability to discriminate between multiple points of pressure on our skin depends on the area of the body. Sets of tones can appear to rise without end when the top tone is removed and a bottom tone added (i.e., Shepard's tones). The subjective strength of a smell depends

more on the type of smell than the actual amount of odorant molecules in the air. Objects of larger volume will appear heavier than smaller objects of equal weight (i.e., size-weight illusion). In higher cognition, illusions dominate areas such as moral judgment, memory, and evaluation of romantic partners.

Differences between percept and stimulus exist throughout most information processing. Indeed, humans knowingly seek and create illusory experiences. We use artificial sweeteners in order to fulfill our desires for sugar. We watch television, a two-dimensional pattern of light and shadow, in order to mimic social cues that induce joy to the point of laughter and sadness to the point of tears. Illusions are essential features of human experience.

Illusions are not mere inaccuracies. Inaccuracy could result from an inability to process a stimulus, and yet illusions typically fall within the perceptual capacity of the observer. Likewise, true inaccuracy would result in errors in all possible directions, such as over- and under-estimates of a distance, rather than the systematic, directional overestimates that we see in the vertical-horizontal illusion (see Fig. 1). Indeed, a perplexing feature of illusions is that we naively think that we are perceiving something in error because it appears differently than the way that it actually exists in the world. However, error of perception is an uninformed way to consider these phenomena. Such an approach has stymied the investigation of illusions for most of the history of modern science.

Visual illusions are one of the earliest topics in the behavioral sciences. The earliest cross-cultural psychology experiments by Rivers and even the founding of experimental psychology by Wundt included investigations of illusions (Rivers 1905; Wundt, cited by Winslow 1933). Illusions are among the most frequent images in psychology textbooks and publications. They are at the historical and modern core of psychological science. And yet the discovery of many of the most frequent and largest magnitude illusions in human vision did not occur until recently, when we began a broader integration of illusion research with modern evolutionary theory.

Evolved Navigation Theory (Jackson 2005; also this volume) identifies that illusions are likely accurate, not inaccurate, biological processes. The error is that we measure accuracy via sensory processing, rather than evolutionary fitness consequences. Apparent illusory experiences often *accurately* impact fitness.

For example, falling accidents are a primary source of human mortality and injury worldwide (WHO 2016). Further, descent results in falls more often and more severe than ascent (Cohen and Lin 1991; Haslam and Bentley 1999; Svanstrom 1974). Additionally, distance perception is a major determinant of route choice, wherein humans navigate overestimated routes less than routes that appear shorter (Jackson 2013). These conditions led Evolved Navigation Theory scientists to predict that humans faced selection from falling risks, especially on descent, and that this resulted in cognitive adaptations that overestimate vertical distances, especially while standing at the top of them. This is exactly what we find (Jackson 2005; Jackson and Cormack 2007; also this volume). The Descent Illusion consists of overestimating vertical environmental surfaces more while standing at their top than bottom. This phenomenon happens throughout everyday life and is likely the largest known distance illusion in real-world vision, including an 84% overestimate of environmental distances, rather than the 10–15% magnitude of most distance illusions. This is but one such phenomenon predicted from Evolved Navigation Theory.

The Environmental Vertical Illusion consists of overestimating the types of surfaces the navigation of which most likely result in falls (Jackson and Cormack 2008). The Plateau Illusion consists of both over- and underestimates of a variety of surfaces in ways that reflect navigational risks present over evolutionary time (Jackson and Willey 2013). These illusions can be induced by adding evolutionarily relevant navigation risks to surfaces normally estimated accurately (Jackson and Willey 2011) and can be eliminated from surfaces by removing evolved cues to such risks (Jackson and Cormack 2010). These illusions may produce the fear of falling (Jackson 2009). These are among the few illusions that replicate across disparate human populations (Jackson and Gómez de García 2017) and the evolutionary nature of these predictions outline effects across species. All of these phenomena were predicted under Evolved Navigation Theory by considering natural selection, and not accuracy, as the driving force behind the structure of perceptual systems.

There is no evolutionary impetus for perception that is accurate, *per se*. Perceptual mechanisms, just like all other biological structures, must arise as products or byproducts of evolution by natural selection. Those mechanisms that positively influence differential reproduction are the mechanisms that will come to dominate the population. In order for this to happen, there must be sufficient heritable variation in the population and a net selective advantage of the illusion mechanism. Perceptual mechanisms are the product of evolutionary processes that result in apparent accuracy only as a byproduct of selection for mechanisms that ultimately increase fitness. We find perceptual inaccuracy far more often than accuracy precisely because it is the fitness consequences of behaviors that shape their evolution, rather than any impetus for accuracy. This link between natural selection and the structure of perceptual mechanisms provides an essential, but currently unutilized, insight for behavioral scientists: Illusions indicate selection on behavior and cognition.

The amount of information in the environment is effectively infinite. Organisms only process a very narrow range of information that is skewed

towards those things most important to the differential reproduction of that organism's ancestors over evolutionary time. When we see the areas of information that an organism processes, we are looking at the products of selection on information processing in that species' evolutionary history. Illusions provide an especially rich source of knowledge about selection on cognition because they show, not only the information that is most important, but also the way in which the information is important. Illusions often arise in populations where there is variation in a perceptual mechanism, but where there is also directional selection on that perceptual mechanism. This results in skewed perception in subsequent generations. This process produces dummy mechanisms that reflect selection on specific behaviors, but without consciousness of the phenomenon or its causes. This process produces no awareness of broader causes of the illusion, accuracy, or motivational or emotional bias, unless that bias itself was targeted separately by this process. In these ways, an informed evolutionary approach to illusions departs drastically from most other theories of illusions.

Conclusion

In many ways, our understanding of illusions mirrors Darwin's broader realization of evolution by natural selection. Darwin (from Malthus) realized that potential reproduction vastly exceeded actual population sizes, just as we see that the amount of information available in the environment vastly exceeds the amount of information processed by any organism. Similarly, the information that an organism actually processes indicates the specific products of selection, just as Darwin recognized more broadly when looking at the individuals who survive within populations. Illusions are no more coincidental than any other product of selection. Illusions are no more errors than are any other product or byproduct of selection. Understanding illusions in this evolved context has led to the prediction and subsequent discovery of some of the largest illusions. It is this predictive power that identifies evolution by

natural selection as the most important idea in the behavioral sciences.

Cross-References

- [Descent Illusion, The](#)
- [Evolved Navigation Theory](#)

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Visual Processing

► [Human Visual Neurobiology](#)

Visual Recognition

► [Face and Object Recognition](#)

Visual Similarity

► [Facial Resemblance and Kinship Detection by Strangers](#)

Visual Statistical Representation

► [Summary Representation](#)

Visual-Gestural Language

► [Sign Language](#)

Visual-Spatial Language

► [Sign Language](#)

Viviparity

► [Evolution of Live Birth in Mammals \(140 MYA\)](#)

Vocabulary

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Synonyms

[Lexicon](#); [Mental lexicon](#)

Definition

Vocabulary is the sum of all words that speakers can use in their speech (productive vocabulary) or comprehend when they are used by other speakers (receptive vocabulary).

Introduction

A child acquiring the lexicon of her language has two main tasks to master: (i) she has to isolate the words in a continuous speech stream and (ii) she has to map the words onto their meanings. First the research on how children segment the speech stream will be introduced, followed by a discussion of how children start assigning meanings to words.

Finding Words in Speech

It is almost impossible to recover word boundaries in fluent speech if one does not already know the words, as anyone who listened to a stretch of talk in an unfamiliar language will agree. But as all normally developing children eventually acquire the vocabulary of their language, it becomes worthwhile to ask how they set about finding words. Acquisition research has so far managed to pinpoint some cues that infants may be relying on to detect word boundaries. In a groundbreaking study, Saffran et al. (1996) have demonstrated that 8-month-old infants can use statistical cues to

extract words from a speech stream consisting of made-up trisyllabic words. This study drew on the simple assumption that the probability with which a syllable follows a given syllable will be always higher word-internally than across a word boundary, e.g., given the syllable *ques*, it is almost certain that the next syllable will be *tion*; but the word *question* can be followed by any arbitrary word, resulting in a low transitional probability for *tion* and the following syllable. In addition, working out the phonotactic constraints of a language (i.e., knowledge of which sound sequences are allowed within a word) can help infants segment the speech stream. For example, the sequence [rpst] can be found within a German word (e.g., *Herbst*, “autumn”), but it will always be separated by a word boundary in English (e.g., *a sharp stick*). Since infants are sensitive to the phonotactic properties of their language by 9 months of age (Jusczyk et al. 1993), they could rely on phonotactics to demarcate the words in a continuous speech stream. Another acoustic cue that speakers use to parse the speech stream is lexical stress. For example, the majority of English words have a *trochaic* stress pattern, i.e., strong syllables are followed by weak syllables (e.g., *AP-ple*), while some other languages such as Turkish exhibit the opposite (*iambic*) pattern (e.g., *el-MA*). Based on this regularity, one could expect English-acquiring infants to observe a metrical segmentation strategy, whereby they assume that all stressed syllables signify a word onset. The current evidence suggests that 8-month-old English-acquiring infants are indeed capable of utilizing lexical stress to extract “words” from a string of artificial language presented to them, even favoring stress cues over statistical cues (Johnson and Jusczyk 2001). This finding might sound contradictory at first, since it suggests that infants use word-level stress as a guide for finding words, but to determine the dominant word-level stress pattern in English, they must have already learned some words. The solution to this puzzle lies in development, as later research has shown that infants first segment the speech by using a domain-general and universally applicable statistical strategy (ca. 7 months of age), gradually transitioning to a stage where they integrate

multiple cues for segmentation (ca. 8 months of age), while giving more weight to sophisticated language-specific cues such as the stress pattern (Thiessen and Saffran 2003).

As a matter of fact, infants should be relying on multiple cues to postulate word boundaries, because none of the strategies introduced above are infallible by themselves. For instance, though most English words are stress-initial, there are exceptions, too (e.g., *be-LIEF*, *sup-PORT*, etc.). Also, computing transitional probabilities may not be effective for detecting English words in a naturalistic setting; since most English words are monosyllabic (unlike the made-up words in the Saffran et al. study) and as such, the syllables will have no *word-internal* transitional probabilities. In fact, Yang (2004) points out that a computational model relying on statistical learning cannot achieve high segmentation accuracy with an English corpus. Accuracy is improved, however, if one postulates a constraint that prescribes that every content word have one primary stress and thereby limits the hypothesis space. So the word-learning task may be facilitated for English-acquiring children if they comply with this constraint as well. These considerations show that successfully parsing a speech stream depends on integrating multiple cues.

Associating Words with Meanings

Once children are able to recognize words in speech, how do they map them onto their meanings? For example, if a young child hears the word *rabbit* in the presence of a rabbit jumping on the lawn, how does she infer that this word refers to the rabbit, and not to parts of the rabbit, to the lawn, or to the action of jumping? Early research on vocabulary development has suggested that children’s word-learning must be constrained by some built-in assumptions about word meanings to help children get their vocabulary off the ground (Markman 1991). One of these is argued to be the *whole-object assumption* that predisposes children to associate novel labels with a whole object, rather than the parts or the substance of that object. But it must be conceded that this

assumption must be abandoned and/or overridden at some point, as children eventually learn the words for object parts and substances. This was arguably made possible by the *mutual-exclusivity assumption*, according to which children would disprefer mapping a novel label onto an object for which they already have a label. Thus, if a child has learned that a rabbit is referred to as *rabbit*, she will be inclined to pick out a different referent for the word *tail*. But the *mutual-exclusivity assumption* is, in fact, at odds with the basic design of the lexicon, since languages do use multiple labels to denote the same entity. Children would thus not be able to learn synonyms or subordinate and superordinate category terms for basic-level terms (e.g., the words *poodle* and *animal*, both of which can denote the same *dog*), if they abided by this assumption.

A more sensible approach to investigating how children build up a vocabulary could be to look at the perceptual and cognitive abilities of children and the social-pragmatic context in which word-learning takes place. The hypothetical scenario where a child has to figure out the referent of the word *rabbit* in the presence of multiple candidates may never play out in a real-life parent-child interaction. Young children are quite adept at establishing joint attention with adults and also reading their communicative intentions by interpreting their gaze direction, affective expressions, etc. Under these circumstances, a child can be expected to easily associate a novel form with the entity that is in her joint locus of attention with her caregiver and this could obviate the need for a *whole-object bias* for determining the referents of labels (Tomasello 2003). Similarly, a *mutual-exclusivity assumption* does not appear to be necessary to explain children's avoidance of lexical overlap. This tendency may stem from a pragmatic *principle of contrast*, according to which every distinct label is assumed to carry a different *meaning* as far as the communicative intentions of the speaker are concerned. Whereas the *mutual-exclusivity assumption* would be hard-pressed to explain how children can produce and comprehend multiple terms denoting a single entity (e.g., *poodle*, *dog*, *animal*), a pragmatically motivated *principle of contrast* would assert that these terms

mark *shifts in perspective* and so they coexist and corefer while preserving the subtle pragmatic differences they signify. Moreover, while *mutual-exclusivity assumption* is formulated as a constraint specific to word-learning, studies show that young children tend to treat not only labels but also facts about objects contrastively; e.g., when children are shown an object and told that "this is from Mexico" and subsequently asked to retrieve the object that "my cat likes to play with," they predominantly avoid choosing the object from Mexico, although the two facts could well be true of the same object. This shows that the pragmatic *principle of contrast* does not solely apply to word-learning, and that it derives from children's ability to reason about which forms a speaker would use to achieve her communicative intentions (Diesendruck and Markson 2001).

It should also be noted that word-learning biases fall short of accounting for the acquisition of verbs, function words, and abstract nouns. The *whole-object assumption* bears no relation to verbs or adpositions – which are more relational than referential. From this perspective, learning abstract nouns (e.g., *love*) or concrete nouns that do not map onto whole objects (e.g., *breakfast*) is also expected to be difficult; though such words are quite common in young children's vocabularies. Needless to say, some version of a pragmatic principle of contrast still needs to play a role in the acquisition of function words and verbs as well; e.g., if an adult uses the verb *share* instead of *have*, this might signal to the child that these words must have different meanings, and eventually enable her to grasp that *share*, unlike *have*, does not involve a claim of ownership, for example (Tomasello 2003). Linguistic context is also crucial for the acquisition of these terms. Verbs differ in the event structures that they instantiate and in the number of participants involved in these events. For example, a transitive verb such as *hit* requires that there be two participants in the event that it denotes (e.g., "*Mary hit Bill*"), while the intransitive verb *sleep* posits one event-participant (e.g., "*Mary slept*"), and research on the acquisition of syntax has provided evidence that 2-year-old children can utilize the number of noun phrase arguments in a sentence to figure out whether the

verb describes a transitive or an intransitive action. This facilitation of vocabulary-learning by the syntax has been dubbed *syntactic bootstrapping*, and it manifests itself not only in the verbal domain. This applies to any argument-taking predicate, including those that contain prepositions, and it has been demonstrated that 2-year-old children can differentiate between made-up homophonous noun phrases (e.g., “*This is a corp!*”) and prepositions (e.g., “*This is a corp my box!*”) by using the sentence structure (see Fisher et al. 2010). While most researchers agree that knowledge of syntax can help word-learning, the traditional syntactic bootstrapping account, which has its roots in generativism, differs from the social-pragmatic view of vocabulary-learning in the role accorded to the syntactic structures in this process. Whereas the syntactic bootstrapping account claims that children are hard-wired to seek correspondences between a verb’s argument structure and its meaning, the social-pragmatic view suggests that children might be first associating the *constructions* they hear with the interactional situation, and segmentations of constructions and abstractions of the meanings of individual words may follow later (Tomasello 2003). For example, a child may hear the sentence “*Joe kicked Mary a ball,*” but the particular argument structure here does not mean that the verb *kick* is a ditransitive verb that describes a transfer event. This semantic component is signaled by the construction *X transfers Y Z*, not by the individual verb. Once this and other constructions have been learned, the child can classify the verb clusters that appear in these constructions and then home in on the individual verb meanings (Goldberg 1995). Unlike the traditional syntactic bootstrapping account, this emergentist view of language acquisition does not require that syntactic structures be a part of children’s innate endowment.

Conclusion

To build up a vocabulary, children need to be able to segment the speech stream into word-sized units, and then associate the words with meanings.

Research has shown that infants are capable of exploiting both the statistical and acoustic properties of speech to accomplish the task of segmentation. Equipped with an inborn capacity to establish joint attention with others and to reason about others’ communicative intentions, infants can then associate words with their referents. Having access to the syntactic structures of their language and the semantic relations they signify will also help children surmount this task; however, the precise syntax-semantics correspondences need not be innate, and children can initially map meanings onto whole constructions and only later partition constructions into smaller word-sized units.

Cross-References

- [Language Acquisition](#)
- [Language Development](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Michael Tomasello](#)

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Vocal Amplitude

► Speech Volume

Vocal Attractiveness

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Synonyms

Voice attractiveness

Definition

The desirability of vocalizations to potential mates.

Introduction

Vocalizations across a wide array of taxa exhibit sexually dimorphic acoustic parameters that emerge at sexual maturity and covary with mating and reproductive success (Andersson 1994). Indeed, the conspicuity of vocal sexual dimorphisms in some species prompted Darwin to speculate on the influence of sexual selection (Darwin 1871), conjecturing that deep male vocalizations tend to evolve in the context of intrasexual rivalry

as a means of exaggerating apparent size. This hypothesis has been supported by subsequent research on many species, though human voices also influence attractiveness to potential mates and may thus reflect aspects of mate quality, including underlying genes (Puts et al. 2016). Indeed, human vocal attractiveness has been the focus of an expanding literature exploring both vocal cues of mate quality and the acoustic parameters most predictive of an attractive voice.

Vocal attractiveness predicts mating success in modern human populations. Men and women with attractive voices report more sex partners, begin having sex earlier in life, and are likelier both to have and be extra-pair mates (Hughes et al. 2004). Thus, it is plausible that vocal attractiveness influenced reproductive success ancestrally. Some voices may be preferred because they convey information on nongenetic benefits, such as current fertility and provisioning ability, as well as genetic benefits conferred to offspring. For example, in both sexes, vocal attractiveness is associated with low somatic fluctuating asymmetry (Hill et al. [in press](#)), a reliable index of developmental stability across species that in humans has been associated with measures of health and quality (Van Dongen and Gangestad 2011).

Vocal Attractiveness in Men

Associations between vocal acoustic parameters and hormone levels also suggest that voices transmit information on heritable health. Simultaneously high levels of the “male” sex hormone testosterone and low levels of the stress hormone cortisol have been linked to greater immune function and attractiveness in men (Rantala et al. 2012) and have predicted lower fundamental frequency (the acoustic correlate of pitch) in men’s voices (Puts et al. 2016). This latter result is particularly relevant because fundamental frequency appears to play a major role in predicting men’s vocal attractiveness to women. Correlational (e.g., Hodges-Simeon et al. 2010) and experimental findings (e.g., Feinberg et al. 2005) initially suggested that both low fundamental frequency and low formants (the acoustic correlate of

timbre) increase men's vocal attractiveness to women. However, in recent research, fundamental frequency, but not formants, predicted men's vocal attractiveness to women when other acoustic parameters were statistically controlled (Puts et al. 2016).

In addition to potentially conveying information on health, the voice may transmit information on physical formidability. Upper-body strength and fighting prowess can be accurately assessed from the male voice (Sell et al. 2010), and masculine voices in men are related to greater body size and other measures of threat potential (Pisanski et al. 2014; Puts et al. 2012). Male voices thus provide information to potential mates not only about men's ability to provision and defend them but also about their propensity for sexual coercion. Indeed, Li et al. (2014) found that images of male-on-female aggression elicited feelings of disgust and anger that appeared to disrupt women's preference for masculinized voices. By contrast, men's voices do not appear to reflect fertility, as measured by semen quality (Simmons et al. 2011).

Women's preferences for low male fundamental frequency have been positively related to their own vocal femininity (Vukovic et al. 2010), as well as to both self-rated attractiveness (Vukovic et al. 2008) and assessments of facial attractiveness made by others (O'Connor et al. 2012). One interpretation of these results is that women who are higher in mate value can obtain and retain higher-quality mates, and women's preferences are thus calibrated according to their own mate value. However, women's self-rated health has negatively predicted the strength of their preferences for vocal masculinity in short-term, uncommitted relationships, perhaps because unhealthy women benefit most from recruiting heritable immunocompetence for their offspring (Feinberg et al. 2012). Thus, while women of higher mate value may generally exhibit stronger preferences for high-quality males, this effect related to the costs of winning high-quality mates may be counteracted by a difference in the benefits of doing so. In addition, women have been found to display a heightened attraction to masculine male

fundamental and formant frequencies during the late follicular (i.e., fertile) phase of the ovulatory cycle (Feinberg et al. 2006; Puts 2005), as well as when assessing men's voices for a short-term, purely sexual relationship (Puts 2005). This is consistent with a female strategy to procure high-quality genes at the time when those genes can be utilized and when direct benefits from men may not be forthcoming.

These associations suggest that a masculine voice may have increased ancestral men's reproductive success by helping its bearers win mating opportunities via female mate choice. Indeed, men with lower mean fundamental frequency (Puts 2005) and less variation in fundamental frequency (Hodges-Simeon et al. 2011) report more sex partners. In at least one natural fertility population, men with voices low in fundamental frequency realized greater reproductive success (Apicella et al. 2007). It is possible, however, that associations between a masculine voice and men's mating and reproductive success are more strongly mediated by success in male intrasexual competition, as Darwin hypothesized. In fact, Hill et al. (2013) found that male vocal masculinity predicted dominance, but not attractiveness, and only the former predicted self-reported number of sex partners.

Vocal Attractiveness in Women

Women's voices, too, may convey to potential mates information on nongenetic benefits. For example, female fundamental frequency decreases with age (Nishio and Niimi 2008), and women's voice attractiveness appears to peak during their most fertile years, the mid- to late twenties (Röder et al. 2013; Wheatley et al. 2014). Women's vocal attractiveness is also associated with a low waist-to-hip ratio (Hughes et al. 2004) and peaks during the late follicular phase of the ovulatory cycle (Pipitone and Gallup 2008), both of which suggest that women's voices are cues to fertility. Indeed, the ovulatory shift in female vocal attractiveness is mediated by changes in the production of the reproductive

hormones estradiol and progesterone (Puts et al. 2013; fundamental frequency did not covary with these hormones, however). In addition, women's vocal attractiveness is positively related to their facial attractiveness (Collins and Missing 2003), although it is unclear the degree to which this correlation reflects overlapping vocal and facial cues to fertility, genetic quality, or other components of mate quality.

Men prefer higher (i.e., more feminine) fundamental (Apicella and Feinberg 2009; Feinberg et al. 2008) and especially formant (Collins and Missing 2003; Puts et al. 2011) frequencies in women's voices. Women perceive female vocal femininity in both of these acoustic parameters as being attractive to men and sounding flirtatious (Puts et al. 2011), perhaps as a means of identifying the sexual competitors who pose the greatest threat. Men display stronger preferences for vocal femininity when evaluating women for a short-term, purely sexual relationship as opposed to a long-term, committed relationship (Puts et al. 2011) and when women exhibit interest in them (Jones et al. 2008), suggesting a male strategy to pursue female reproductive capacity more when expected paternal investment is low and when men's mating effort is likelier to be successful.

Considerations and Future Directions

It is important to note that because men and women's voice preferences have likely exerted important selective pressures on vocal traits in each sex, the vocal attractiveness literature has focused on heterosexual mate choice. Research on voice preferences among nonheterosexual individuals, however, can inform our understanding of a host of biobehavioral phenomena and has indicated that gay men convey vocal cues to their sexual orientation (Valentová and Havlíček 2013), exhibit more female-typical fundamental frequency (Baeck et al. 2011), and find vocal masculinity in men attractive (Valentová et al. 2013). In other ways, however, gay men are more sex typical, and scant research

has yet been undertaken on voice preferences among lesbians or those of either sex with a bisexual orientation.

An additional consideration in interpreting research on vocal attractiveness is the literature's appreciable methodological variation, which limits inferences of species typicality in vocal traits. For example, the duration of experimental stimuli (Ferdenzi et al. 2013), articulatory clarity (Kempe et al. 2013), accent (Babel et al. 2014), and breathiness (Xu et al. 2013) have all been shown to influence attributions of attractiveness, and the literature has included variation in each while not always emphasizing the influence such variation may have on findings. Future work should address this by including recordings taken from a greater breadth of populations so as to capture more variation in language, as well as speech nonconformity and its covariates (e.g., social status). Additionally, research should illuminate the connections between variation in vocalization and variation in anatomical substrates, for example, as they relate to developmental stability.

Cross-References

- [Animal Signaling](#)
- [Facial Attractiveness](#)
- [Mate Value](#)
- [Nonverbal Indicators of Dominance](#)
- [Ovulatory Shifts in Psychology](#)
- [Sex Differences](#)
- [Sexual Selection](#)
- [Vocal Indicators of Dominance](#)

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Vocal Communication

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Synonyms

Animal signaling; Nonverbal communication; Speech; Voice acoustics

Definition

Vocal communication is the transfer of information through the auditory channel via voice production mechanisms.

Introduction

Vocal communication is ubiquitous in mammal species. As a mode of signaling, vocalizations often manifest in alarm call systems, territorial displays, and courtship rituals and are particularly well-suited for functions requiring wide broadcast. But vocal signals are used in an incredible variety of communicative contexts, many of which are extremely quiet, and between small groups of animals. Here I will describe two fundamental issues important for the study of evolution of vocal communication in humans and nonhuman animals: the distinction between adaptive signals and byproduct cues, and the concept of form and function in the structure of animal signals. I will then apply these principles to current evolutionary research on vocal behavior in humans specifically.

In mammals, the underlying brain mechanisms driving emotional vocal behavior are highly conserved and involve neural circuitry integrating the anterior cingulate to laryngeal musculature (Ackermann et al. 2014). But humans have evolved speech production that is partially distinct

both proximately (i.e., mechanistically and developmentally) and ultimately (functionally and phylogenetically). Direct connections between motor areas of the brain and laryngeal systems allow for the generation of complex speech sounds, and this production organization interfaces with many cognitive systems involved with language in a broad sense (Fitch 2000). But exactly how this dual pathway arrangement operates in real time remains to be described. Conversational turn taking, the primary context in which linguistic action occurs, is partly regulated by evolutionarily older vocal patterning, including suprasegmental prosodic variations, rhythmic coordination, and other vocal phenomena.

The study of vocal communication from an evolutionary perspective requires us to distinguish between signals and cues (Maynard-Smith and Harper 2003). Signals are behaviors or structures designed to affect the behavior of another organism, and the responses of the receiving organism are shaped by selection to be affected by the signal. That is, by design, signals typically benefit both senders and receivers. Examples of vocal signals in humans include a variety of evolutionarily conserved, nonverbal affective vocalizations, such as laughter, crying, pain shrieks, copulation calls, and emotional screaming. Language also constitutes a signaling system, transmitted primarily through speech production and working in tandem with the vocal emotional system through the integration of linguistic constituents (i.e., phonological, morphological, and syntactic) and suprasegmental prosodic features. All of the above signaling phenomena coevolved in the context of sophisticated social cognitive abilities including theory of mind, providing a platform for specialized ostensive communicative behavior (Scott-Phillips 2014). That is, because humans are able to reliably detect and signal about others' mental states and intentions, vocal signaling systems coevolved with pragmatic reasoning.

Conversely, cues are any actions or structures that were not designed to affect the behavior of other organisms but reveal information to receivers incidentally. Organisms can evolve perceptual sensitivity to cues and exploit individuals who reveal predictive information. When costly to

those revealing information inadvertently, a coevolutionary arms race can ensue where selection for reducing cues coevolves with enhanced perception of relevant cue properties. This type of scenario applies to a variety of vocal communication phenomena in humans including detecting volitional signals with deceptive intent (e.g., so-called fake laughter and crying), intentional deception in speech, fertility in female voices, and formidability in male voices, among others.

As a general principle across mammalian vocal communication, the structural forms of signals are directly tied to communicative functions. In most nonhuman vocalization systems, the sound itself is doing the majority of the communicative work, as acoustic signals are designed to have either direct effects on receivers' behaviors, or they are paired with other events to achieve eventual indirect effects (Owren and Rendall 2001). This is true for a great deal of human communication as well. For example, in the case of infant-directed speech, a caregiver might produce a loud, nonverbal utterance with an abrupt onset and perhaps even nonlinear phenomena indicating high arousal, in an effort to prevent (or interrupt) a particular behavior in a target infant. Acoustic features capture the infant's attention and cause her to reorient, thus altering her behavior. The direct impact of the prohibitive yell on the infant's physiology achieves the goal of the caregiver. The form and function relationship apparent in ID speech suggests a fair amount of universality in the sound of a variety of infant-directed utterance types, which indeed has been found across cultures (Fernald 1992).

This principle underlies the affective aspect of any kind of human vocalization. Emotional vocal signals are generated as the products of particular combinations of physiological states characteristic of different emotions, and their sound can be understood in these terms. The downregulation typical of sadness lowers arousal-linked vocal features such as loudness, pitch, and speech rate, and the high arousal of intense fear has opposing effects on screams. Besides these basic acoustic dimensions of voice such as pitch, loudness, and rhythm, spectral features also are directly tied to affective states. Again, during high arousal, the

effect of pushing air excessively through the vocal tract can be quite audible as nonlinear spectral features such as deterministic chaos and subharmonics that give vocalizations a harsh, noisy sound quality (Bryant 2013).

Many researchers examining human vocalizations from an evolutionary perspective have focused on the production and perception of sexually dimorphic vocal features. Vocal pitch in particular has been examined extensively. Pitch is the perceptual correlate of the fundamental frequency of vocal fold vibration regimes. Pubertal androgen exposure triggers growth of the vocal folds in young males resulting in lengthening and thickening that impacts vibration rates. According to the immunocompetence hypothesis, secondary sexual traits such as lowered pitch in male voices result from the effects of testosterone that simultaneously suppresses immune function. Only higher quality males, therefore, can afford to express the signal, thus making the trait attractive to females. Indeed, while immunosuppression effects of testosterone are not well established, it is fairly well documented that lower pitch in male voices has a variety of positive effects on judgments of attractiveness, dominance, body size, competence, strength, and other dimensions. Conversely, higher pitch in female voices increases men's judgments of attractiveness and is associated with judgments of greater femininity, youth, reduced body size, and higher fertility. Resonating properties of the vocal tract manifesting acoustically as formant structure also has been shown to have a variety of effects on these same dimensions, with relatively greater validity for body size in particular (for a review see Pisanski and Bryant 2018).

While sexually selected features of the voice have received considerable attention, the role of social context has been explored much less (Pisanski et al. 2016). Studies have shown that speakers often change their voices (e.g., pitch, loudness, and rhythmic properties) according to the demands of particular social contexts. For example, men have been shown to enhance masculinized features (e.g., use lower pitch) when speaking to a potential mate, and women will accentuate feminine features (e.g., raising their pitch and speaking slower) when told that their

voices will be judged by men for attractiveness. Social context also plays an important role in how a variety of nonlinguistic vocalizations manifest themselves. For instance, friends in conversation tend to laugh more spontaneously, and the resulting arousal in their laughter affords the rapid detection of their relationship across widely disparate societies, as does the generally low-arousal volitional laughter more common between strangers or newly acquainted people (Bryant et al. 2016). Arousal is not only detected in human voices—recent work has shown that judges are quite effective in detecting arousal in species quite distant from humans, including in vocal signals of birds and tree frogs (Filippi et al. 2017). This research illustrates well the power of form and function in understanding the communicative effectiveness of vocal signals, and how evolutionary processes conserve signal features that are inherently connected to signaling production and shape perceptual systems to attend to them.

Conclusion

An evolutionary adaptationist approach to communication requires theorists to distinguish between vocal signals and cues. Our understanding of specific physical features of the human voice, and how they are deployed in social interaction, is clarified by recognizing the design features shaped by selection processes on communicative behaviors. Consequently, this approach profitably connects research between humans and nonhuman animals in a way not especially common in other areas of the evolutionary behavioral sciences. The study of vocal communication is among the fastest developing areas of evolutionary psychological research. Recent advances in acoustic analysis technology, which are freely available thanks to the developers of software such as Praat, have helped facilitate new and exciting work. The current trend of conducting large-scale cross-cultural studies is also affording tremendous opportunities for understanding universals and cultural variation in vocal signaling. It is an exciting time to be

studying what is one of the most pervasive and fundamental aspects of human life.

Cross-References

- [Biosemiotics](#)
- [Broca's and Wernicke's Areas](#)
- [Echolalia](#)
- [Field of Linguistics, The](#)
- [Gossip and Grooming Hypothesis](#)
- [Human Deception](#)
- [Imitation and Mimicry](#)
- [Language Modularity](#)
- [Laryngeal Descent](#)
- [Linguistic Evolution](#)
- [Modeling Language Transmission](#)
- [Modern Theories of Language](#)
- [Mother Tongue Hypothesis](#)
- [Motherese](#)
- [Neurobiology of Language](#)
- [Phonemes and Symbols](#)
- [Ritual and Speech Coevolution](#)
- [Stereotyped Vocalizations](#)
- [Stuttering](#)
- [Vocal Grooming](#)

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Vocal Competition

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Synonyms

[Acoustic competition](#)

Definition

Agonistic interactions mediated by the production of acoustic signals.

Introduction

It is late autumn in the temperate forest, the last leaves still on the trees finally surrender to the northern breeze and fall down, silently. The beams, as the sun sinks, pass through the naked branches and illuminate the forest clearing, where a large, old stag is moving restlessly around a group of quietly foraging females. Not far away, a young solitary male observes the scene. The breeding season is almost over and the young

male has not yet mated. Testosterone, flowing abundant in his blood, makes him decide to challenge the rival, in the attempt of conquering his harem. As he moves a few meters ahead, the rival spots him and, suddenly, stops, raises the head, opens the mouth, and starts uttering grave, loud roars. The young responds in the same way. A vocal competition has begun.

Vocal competitions are common in many arthropods and vertebrates, which are the only taxa that evolved the ability to communicate by means of sounds (Bradbury and Vehrencamp 2011). Acoustic signals are well adapted to mediate agonistic conflicts. Since sounds are effective on the long distance, they prevent physical contacts and reduce the risk of uncontrolled fighting escalations. Sounds are under strong morphophysiological constraints and are thus preadapted to encode reliable information about the sender's fighting ability. Sound modulation further increases the communicative potential of acoustic signals, and it allows to flexibly adjust signals to the unpredictable dynamics of the ongoing competitions.

Vocal competition can be direct or indirect. In the following paragraphs, we shall consider the effects of these two mechanisms on the evolution of agonistic signals.

Vocal Contests

The vocal contest, such as that described in the red deer, is a mechanism of direct vocal competition. Two conflicting individuals exchange agonistic signals in order to resolve conflict to their own advantage. In this communicative interaction, the actors play both the sender and the receiver role. Since the degree of conflicting interest between senders and receivers is high, agonistic signals can be evolutionarily stable only if they provide receivers with honest information about the fighting ability and the aggressive motivation of the sender (Bradbury and Vehrencamp 2011). Natural selection can guarantee the honesty of agonistic signals by imposing either strategic costs or morphophysiological constraints on their expression (Maynard Smith and Harper 2003). The roar

of the red deer is a good example of both solutions. In fact, fighting ability depends on body size and stamina (the ability to sustain prolonged energetically costly activities), and the roars of the red deer convey honest information of both these traits. When roaring, the stag retracts the mobile larynx down to the sternum (Reby and McComb 2003). The sound produced by the vibrating vocal folds resonates into the vocal tube; some frequencies are filtered out, whereas others, the formants, are amplified. The frequency of the lowest formant is strongly and negatively correlated with the length and volume of the vocal tube and, thus, with the male body size. Playback experiments have shown that the roar spectral properties affect the contest outcome, favoring the individuals with the lowest formants. Independent of body size, the fighting ability of a male depends also on how much energy stores he has and on how good he is in using the energy in controlling aerobic and anaerobic metabolic rates. In the red deer, roaring is energetically costly and involves muscles that are important during fighting. The high strategic costs of sustained vocal contests, thus, is a reliable indicator of male fighting ability.

Vocal contests are common in most acoustic-communicating species. For example, in the house cricket, *Acheta domestica*, male-male aggressive interactions typically begun with the production of stridulatory calls, which differ from mate-attraction calls in both spectral and temporal structures. In this case, honest information of male body size is encoded in the temporal properties (the number and the rate of pulses within a call), rather than in the frequency components of the call (Greenfield 2002). In territorial songbirds, vocal contests are often a mechanism for resolving boundary disputes. During the contest, birds of neighboring territories interact acoustically on a short time scale in order to assess reciprocal differences in motivation and to establish relative dominance. The dawn chorus of many territorial songbirds is an unusual example of vocal context, because it does not involve dyadic interactions between conflicting individuals. With their vigorous signaling, territorial males communicate their presence and condition to prevent rather than to prevail over potential rivals.

Indirect Vocal Competition

Unlike in vocal contests, in indirect competitions, the outcome of agonistic interactions depends on the behavior of a third-party actor, who plays the receiver role. A typical example is represented by lek breeding species, where males aggregate in large choruses and compete acoustically against each other to attract gravid females. In this case, selection promotes the evolution of acoustic traits, which might be poor indicators of fighting ability, but good indicators of sexual attractiveness. Mate choice theories of sexual selection try to understand the functional significance of mate attractiveness.

The distinction between direct and indirect vocal competition, however, is not always clear cut. In many species, in fact, the same acoustic signal may be used in both direct and indirect competition. For example, in the red deer, the acoustic properties that are important for solving intra-sexual agonistic interactions are also those perceived as most attractive by females. In contrast, in other species, direct and indirect vocal competitions conflict with each other. For example, in tree frogs and toads, males often compete for display positions within the chorus. During these agonistic interactions, males have been observed to reduce the dominant frequency of their advertisement calls, and playback experiments showed that the greater the reduction, the more effective the call was in repelling the opponent (Gerhardt and Huber 2002). Frogs and toads, however, have a poor control over the resonant frequency of their vocal folds, and the only way they have to reduce the frequency is by reducing the vibrating pressure of vocal folds, with a consequent reduction in call intensity. The intensity reduction may have no effect on the short distances at which male-male interactions occur, but it may have strong negative effects on the long distances, where male-female interactions occur. In this case, selection is expected to promote the evolution of optimal tradeoffs between the conflicting functions.

Indirect Vocal Competition in “Selfish” Choruses

Indirect vocal competition arises because signaling males tend to aggregate in spatially restricted areas. In some cases, aggregation can be explained by the inhomogeneous distribution of the limiting resources. For example, male frogs aggregate at the breeding ponds, because here is where females lay their eggs. In other cases, however, aggregation may be favored by natural selection, because the benefits it provides overcome the competition costs it imposes. This happens when group size shows either a positive allometry with the number of visiting females or a negative allometry with the number of visiting predators, or both. Whatever the reason, aggregation adds a new level of competition in the population, because males not only compete against their rivals within a chorus but, as members of a chorus, they also compete against the members of other choruses within a network. The two levels of vocal competition may interact and affect the spatial and the temporal structure of vocal activities.

Vocal competition within a chorus can cause signalers to couple their calling to that of their rivals. Coupling may occur both at the gross and at the fine temporal scale. At the gross-scale level, it usually results in synchronous calling. For example, tree frogs alternate prolonged bouts of calling with periods of silence, and they do this synchronously within a chorus. In this way, tree frogs may reduce the risk of being predated by passive listening predators, such as bats (i.e., an “acoustic dilution effect”), and, at the same time, they may increase the power of the overall signal to attract females from further away (Gerhardt and Huber 2002). In contrast, at the fine-scale level, coupling results more often in alternate than in synchronous patterns, at least in those species where the fine-scale structure of the call conveys important information for species recognition. Alternation might be interpreted as a form of “selfish” signaler cooperation, because chorusing males share the same common interest of making their own signals as detectable as possible. Males that fail to alternate would reduce their own mating success and, incidentally, that of their

neighbors. Alternation can also arise as a side effect of male-male vocal competition. In many species of frogs and insects, in fact, females show strong preferences for the male that call first (acoustic leader) (Gerhardt and Huber 2002). Males can thus compete against their closest neighbors for temporal primacy and this would result in regular antiphonal calling.

Vocal Competition in Cooperative Choruses

So far we have considered vocal competition of selfish choruses. However, in some birds and mammals with a solid social organization, vocal competition often occurs between social groups, and, at the within-group level, individuals cooperate to improve the overall calling performance (Ravignani et al. 2014). In many tropical bird species, the members of a pair are known to coordinate their songs, by accurately alternating their components. In some species, the social group includes helpers, who join to produce a complex chorus, in which individuals of the same sex sing the same phrases with near-perfect synchrony (Mann et al. 2006). Chorusing behavior in birds is thought to solve two main functions: it favors coordination among the members of a group and it improves vocal contest performances in mutual territorial defense. In primates, chorusing (mostly in the form of duetting) has been observed in a few genera only. A well-studied example is that of the singing lemur, *Indris indris* (Gamba et al. 2016). In this species, all members of a group usually sing, but the contribution changes in relation to the social rank, suggesting that chorusing not only solves the function of communicating group size and cohesiveness during the vocal contexts with neighboring groups but it may also play a role in mediating within-group social conflicts.

Conclusions

Direct and indirect mechanisms of vocal competition have favored the evolution of signals that are a reliable indicators of signalers' competitive

quality (fighting ability or attractiveness). Morphophysiological constraints preadapted some sound properties to this function. But evolutionary stability is most likely the consequence of the strategic costs of cheating: the risk of fighting escalation in vocal contests and the energetic costs of sustained calling in choruses make the bluff an economically disadvantageous tactic.

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Vocal Duets

► Vocal Grooming

Vocal Fundamental Frequency

► Voice Pitch

Vocal Grooming

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Synonyms

[Pant hoots](#); [Social bonding](#); [Vocal duets](#); [Vocal turn-taking](#)

Definition

One hypothesis to explain the emergence of language in the primate lineage is that manual grooming, seen in most primates, has been gradually replaced by vocal grooming, eventually leading to the emergence of spoken language. This hypothesis is based on the observation that, similar to manual grooming, human language plays a key role in building and maintaining affiliative bonds and group cohesion. The purpose of this entry is to review the empirical literature to evaluate the vocal grooming hypothesis.

Introduction

The biological success of our species is partly grounded in a major evolutionary transition in mental capacities from self-serving, competitive to group-oriented, cooperative social relationships. Compared to other primates, humans are much more collaborative, prosocial, and amenable to social norms, with far-reaching implications at almost every level of human activity, including language. Human social interactions are highly structured joint activities during which partners are in tune with each other's intentions – the human 'interaction engine' (Levinson 2006). Linguistic discourse is a specific type of joint activity, which is characterized by rapid

exchanges of syntactic units, while its semantic content is often about others' social behavior, or gossip, and this exchange of social information appears to have a strong bonding effect on the interlocutors (Dunbar 1993).

In nonhuman primates, social bonding is mainly achieved by manual grooming, but some species have additional mechanisms that involve vocal behavior. This has led to the hypothesis that, during human evolution, manual grooming has been gradually replaced by vocal grooming as the main mechanism for social bonding, which has paved the way for the evolution of language (Dunbar 1993). Vocal grooming, in other words, has become something like the missing link in this theory of language evolution.

Manual Grooming in Primates

Social grooming ("allogrooming") plays an important role in the social fabric of primates, much beyond its primary hygienic function. For several species, there is evidence that grooming is the main way by which primates initiate and maintain social bonds, which increases tolerance between individuals and, by extension, ensures group cohesion. When choosing their grooming partners, primates and other animals are very selective and behave in seemingly strategic ways. For example, high-ranking animals receive more grooming than others, and the majority of grooming occurs between individuals of similar rank.

Grooming-driven social bonding appears to be physiologically mediated. In wild chimpanzees, for example, urinary oxytocin levels are higher after grooming with bond partners than other group members (Crockford et al. 2013), and there is also good evidence that grooming has a direct impact on an individual's fitness. In primates, grooming increases the probability that partners will help each other during fights, whereas individuals with strong social networks have higher lifetime reproductive success than less socially integrated individuals (Silk et al. 2010).

Interestingly, across species, there is a positive relation between social grooming time and group

size, suggesting that species that form large groups spend relatively more time with manual grooming than those living in small groups, due to the increased number of social relationships they have to maintain (Dunbar 1993). Time demands to maintain social relation increase exponentially for each individual with group size, and this is likely to favor the evolution of alternative and more flexible bonding mechanisms. Humans maintain around 150 stable social relationships (“Dunbar’s number”) but spend hardly any time with manual grooming. Thus, the proposal has been that, during human evolution, manual grooming has been gradually replaced by vocal grooming, which then has paved the way the evolution of language (Dunbar 1993).

Vocal Grooming

How did the transition from manual to vocal grooming take place? In many pair-living avian species, males and females produce vocal duets, which require coordination between partners and appear to play a role in social bonding. In non-human primates vocal duets are mainly between strongly bonded breeding pairs, such as in gibbons, lemurs, titi monkeys, or tarsiers. However, duets are primarily long-distance signals, suggesting they have other functions beyond pair-bonding, such as advertising bond strength to neighboring rivals, and therefore being integral components of territorial defense.

Another candidate for vocal grooming in primates is chorusing. In chimpanzees, for example, males of the same group chorus with their pant hoots, an acoustically unique long-distance vocalization. There is evidence that these joint vocal displays facilitate tolerance at feeding sites and predict support in agonistic interactions on a short-term basis, while manual grooming seems to be a better predictor of long-term social bonds (Fedurek et al. 2013).

Another relevant phenomenon is vocal convergence. In many animals, including primates, affiliated individuals adjust the acoustic structure of their calls during vocal interactions to the effect that strongly bonded individuals are more likely to produce acoustically similar calls than less

bonded individuals, but this is often at an ad hoc level (Candiotti et al. 2012). Whether these short-term acoustic accommodations function to facilitate the formation of long-term bonds or are expressions of temporary affiliations is unclear from the current data. In humans, vocal convergence is a well-documented phenomenon, described as “speech accommodation,” although similar effects are also seen in gestures, suggesting that people try to either emphasize or minimize the social difference to their interlocutors, reflecting their desire or refusal to strengthen a social bond.

Call exchanges, finally, are another potential mechanism for social bonding, which often appears in the form of coordinated vocal turn taking. Call exchanges are found in many primates, often between closely affiliated individuals, as seen in guenons, squirrel monkeys, marmosets, or macaques. In ringtailed lemurs, call exchange networks are socially more rigid than grooming networks, insofar as socially important individuals are more likely to elicit vocal responses than others (Kulahci et al. 2015). Vocal turn taking is also a key feature of human linguistic discourse, which is characterized by highly structured, rapid exchanges of short syntactic units, around 1,500 per day (Levinson 2016). In humans, the length of turns can be flexible, as can the number of speakers, but participants rigidly observe short time gaps of about 200 ms between turns. This highly conserved pattern requires participants to predict when a partner’s turn comes to an end, which is only possible if interlocutors can anticipate the forthcoming semantic content, while constructing their next utterance. This pattern is found across languages, suggesting that it is based on a biological predisposition, with possibly deep evolutionary roots.

Transitions to Language

One key prediction of Dunbar’s (1993) vocal grooming hypothesis is that vocally based social bonding has gradually replaced manually based bonding via grooming. This process is driven by evolutionary processes leading to increased group size, which will exponentially increase the

number of social relationships an individual needs to maintain and monitor. Once the number of relationships becomes too large, an individual can no longer maintain its social networks with tactile interactions alone, and selection will favor alternative mechanisms.

As mentioned before, several primates have evolved vocal duetting behavior, which is relevant for social bonding, but this is typically observed in species that live in small family units where manual grooming does not impose a significant burden on time budgets, while duets usually travel much beyond the partners' home range. Duetting, in other words, is not a good candidate behavior to model the transition, and it may have evolved as a supplementary bonding mechanism in species where exceptionally strong bonds are needed for reproduction, as in socially monogamous and cooperatively breeding species. Similar concerns have been raised for other potential precursor behaviors, such as vocal convergence, chorusing, or call exchanges.

Possibly the best candidate in the current primate literature is acoustic behavior seen during manual grooming. In our closest primate relative, the chimpanzees, manual grooming is often accompanied by a specific acoustic signal, lip-smacking, especially between closely affiliated individuals. Lip-smacking plays a key role in coordinating grooming bouts by making them longer, more reciprocated, and more intimate (Fedurek et al. 2015). Lip-smacking is also interesting because it is characterized by rhythmic facial movements that require some degree of motor control of key articulators (lips, mandibles), similar to human speech production, albeit without any larynx activity (Lameira et al. 2014). Many primates lip-smack during affiliative social interactions, but so far there is only evidence in chimpanzees for a direct link between this behavior and manual grooming.

Chimpanzee lip-smacking has thus become somewhat of the prime candidate as the missing link to human vocal interactions. While chimpanzee lip-smacking is semantically empty, it similarly seems to function in social bonding and is delivered in temporarily structured ways. One evolutionary scenario therefore is that, during human evolution, manual grooming has been

increasingly replaced by such a mechanism that, due to its contextual flexibility and articulatory control, may have been a breeding ground for the evolution of more sophisticated articulatory vocal control. There is good evidence that great apes have substantial control over their supralaryngeal vocal tract but relatively little active control over their sound-producing organ, the larynx (Lameira et al. 2014). The transition from manual to vocal grooming, in other words, may have been linked with gaining active control over sound production in line with concurrent underlying changes in the cognitive architecture.

Conclusion

The evolution of human language is one of the most debated topics in science, and the "vocal grooming" hypothesis represents one influential proposal to explain its emergence. The main argument is that, like manual grooming, language functions in maintaining affiliative bonds, the result of a gradual evolutionary change by which vocal behavior increasingly replaced manual grooming as a bonding tool. Humans form much larger groups than other primates, but rarely groom each other manually. At the same time, humans use language largely for gossiping, to strengthen their social bonds. A particular advantage of this type of vocal grooming is that it can act beyond dyadic interactions and does not interfere with other vital activities, such as foraging or traveling. Since social bonding has a strong physiological component, future research should target the impact of gossiping and other forms of vocal grooming in humans on the release of endorphins and social hormones, such as oxytocin.

The evidence reviewed here suggests that many animals use vocalizations to enhance social bonding. Prime examples are duetting, acoustic convergence, chorusing, and call exchanges, also seen in humans as joint singing, speech accommodation, and linguistic conversation. However, in nonhuman primates these vocal behaviors do not replace but often complement manual grooming, and interaction patterns are not always less rigid than during manual grooming.

Perhaps the most relevant type of vocal grooming in the animal literature is chimpanzee lip-smacking, an orofacial auditory signal that functions directly to coordinate manual grooming. It is conceivable that the common ancestor already utilized such a mechanism and that, during human evolution, lip-smacking became increasingly emancipated from manual grooming and so provided a breeding ground for the emergence of vocal control.

In sum, although vocal behavior can foster social bonds in human and nonhuman primates, it is difficult to explain the evolution of core features of human language, such as semantic content and syntactic structure, from these phylogenetically older behaviors. Acoustic signaling during grooming, such as lip-smacking, currently provides the most plausible evolutionary route for a transition to language, but it is unclear how humans gained increased vocal control, including vocal imitation and generative syntax, as well as a highly cooperative, intention-based psychology, which is essential for language. The vocal grooming hypothesis, in other words, provides a plausible scenario for the early stages of language evolution, but remains silent about the subsequent, equally essential evolutionary transitions to human language.

Cross-References

- [Communication and Social Cognition](#)
- [Language](#)
- [Primates](#)
- [Primate Cooperation](#)

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Vocal Indicators of Dominance

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Synonyms

Bioacoustics; Formidability; Rank; Resource-holding potential; Status

Definition

Nonverbal vocal characteristics that indicate one's potential to successfully acquire resources through force (physical or otherwise), threat of force, or the perceived benefits of associating with prestigious (i.e., high-ranking) social partners.

Introduction

A variety of trait dimensions such as dominance are gauged from “thin-slice” judgments of other individuals based on their physical characteristics. Inspired largely by theoretical models of same-sex competition (i.e., intrasexual selection) in non-human species, where the capacity to quickly assess another individual's dominance has obvious benefits for reproductive fitness (Puts 2010), research over many decades has explored the extent to which various acoustic properties within the voice denote dominance.

Research on vocal indicators of dominance has largely focused on the extent to which nonverbal acoustic characteristics indicate physical formidability, including body size and strength, and suggests a role for exaggerated sex-typical features in dominance interactions that are highly comparable across mammalian species (Fitch and Hauser 2003; Taylor and Reby 2010). Research over approximately the last two decades suggests, in turn, that trait judgments such as dominance are also inferred from nonverbal characteristics of the human voice. Fundamental frequency (F_0 , perceived as voice pitch) and formant frequencies (resonances of the supralaryngeal vocal tract) play a key role in displays and assessments of dominance in humans (Fig. 1) as in most other mammals (Taylor and Reby 2010). Across the animal kingdom, when an animal lowers either of these voice frequencies, this behavior typically communicates aggression or functions as a dominance display (Morton 1977). In humans, in addition to communicating aggression, low voice pitch among men indicates high levels of pubertal and circulating testosterone, whereas low formants predict a relatively larger body size. Both

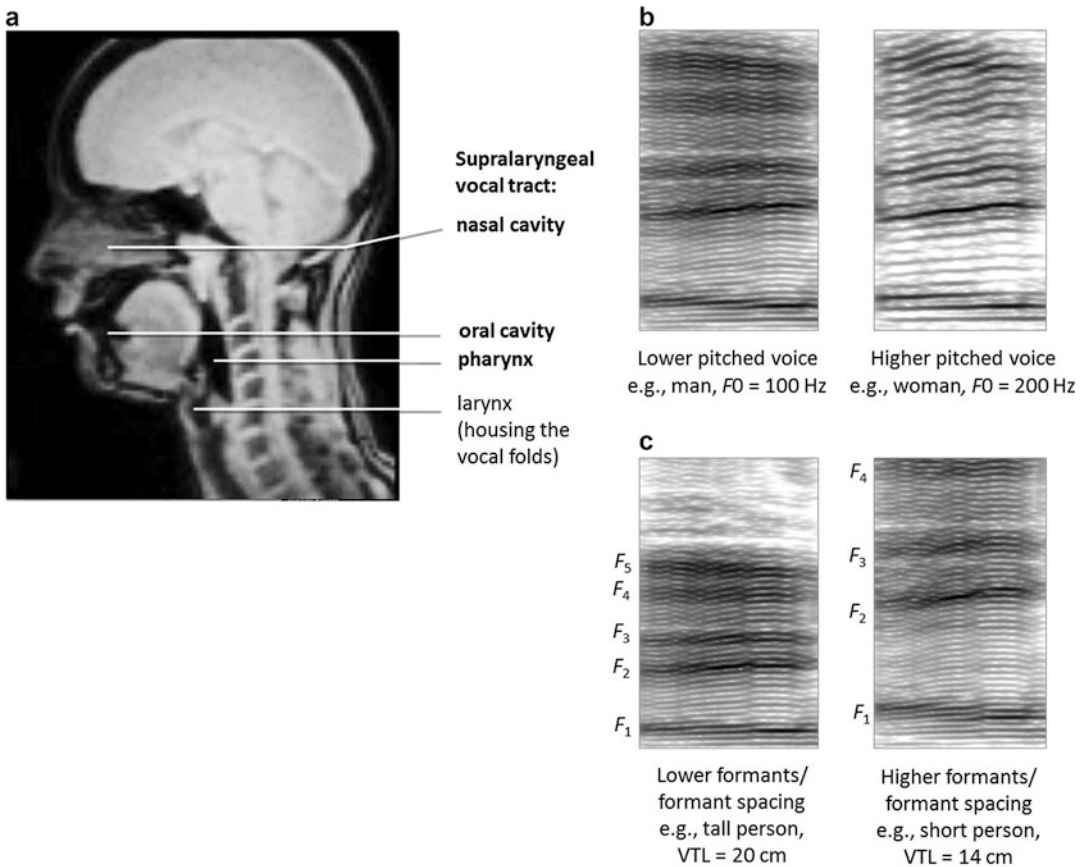
voice features are also sexually dimorphic – lower among males than females – as is typical for many other primate species (Puts et al. 2016). Thus, dominance judgments may contain some degree of accuracy; however, individuals may also modulate (or “fake”) vocal characteristics to their strategic advantage during competition. Each of these topics is discussed in turn below.

Voice as an Index of Body Size and Strength

Physical body size, including height, weight, and muscle mass, is an indicator of social dominance, especially for men. Across diverse human cultures, taller men have greater social rank, earn more, report more sexual partners, and have more children than do shorter men (Pisanski and Feinberg 2013). The relationship between body size and social rank in men suggests that size may be advertised, and even exaggerated (see later section on Reliability and Deception), through multiple modalities including the voice and that the ability to accurately estimate another individual's body size is likely to be advantageous in many social and competitive contexts.

The earliest studies with humans in this domain focused on F_0 , a key acoustic parameter in vertebrate vocal production related to the rate of vocal fold vibration and perceived as voice pitch (Suthers et al. 2016). Bioacoustic analyses have recently broadened to include vocal tract resonances, termed formant frequencies or formants. This fruitful shift in focus emerged after the application of source-filter theory, originally conceived as a model of human speech production, to the study of nonverbal communication in mammals (Taylor and Reby 2010). Based on the source-filter framework, human vocal signals are produced by vibration of the vocal folds situated within the larynx (the source) and are subsequently filtered by the supralaryngeal vocal tract comprised of the oral and nasal cavities and pharynx situated above the larynx (the filter; illustrated in Fig. 1a).

Larger vocal folds will generally produce a lower F_0 , but this relationship is neither strictly



Vocal Indicators of Dominance, Fig. 1 (a) Sagittal MRI of the human vocal apparatus depicting the larynx/vocal folds that affect voice F_0 and the supralaryngeal vocal tract (*in bold*) that affect formants. Formants most reliably predict human body size. (b) The *upper left* spectrogram represents a low-pitched voice typical of a man, with lower F_0 and more closely spaced harmonics (integer

multiples of F_0). The *right* spectrogram represents a higher pitched voice typical of a woman. (c) The *lower left* spectrogram represents a voice with relatively lower and more closely spaced formants, typical of a taller individual with a vocal tract length (VTL) of 20 cm. The *right* spectrogram represents a shorter individual with a VTL of 14 cm (Adapted with permission from Pisanski et al. 2016a)

linear nor allometric (Titze 2011). Indeed, while F_0 predicts differences in body size across different species of mammals (Charlton and Reby 2016) and primates (Ey et al. 2007), and even between the sexes in humans (Fig. 1b), F_0 explains less than 2 % of the variance in height or weight *within* same-sex samples of adult men or women (Pisanski et al. 2014, 2016b). In contrast, the length of the supralaryngeal vocal tract (vocal tract length, VTL) scales fairly allometrically with height and body mass in humans and in many other mammals, even after controlling for sex and age. Relatively larger men and

women thus tend to have longer vocal tracts and, as a consequence, lower more closely spaced formants and a more resonant voice (Fig. 1c). A recent meta-analysis confirmed that formants explain several times more variance in men's heights than does F_0 (Pisanski et al. 2014).

Formants are the most reliable vocal correlate of human height and weight. However, numerous voice parameters including F_0 , formants, and perturbation parameters such as jitter, shimmer, and harmonics-to-noise ratio correlate with the *shape* of men and women's bodies. Some of these voice parameters can, for instance, indicate the ratio of

men's shoulder or chest circumference to their hip circumference (Hughes et al. 2009; Pisanski et al. 2016b), which is of note as body shape can also function to communicate dominance.

Collectively, work to date suggests that acoustic parameters indicate various proxies to dominance (e.g., physical formidability). As certain acoustic parameters are exaggerated to a much greater extent among males than females (i.e., are highly sexually dimorphic, e.g., *voice pitch*; Puts et al. 2016), work on vocal indicators of dominance in humans complements that in other species, where sexually dimorphic physical characteristics are related to various measures of dominance rank more generally (see Watkins et al. 2010 for discussion). Recent work further suggests that testosterone-dependent vocal characteristics in male primates, including humans, may play a key role in male-male competition (see Fedurek et al. 2016 and Puts et al. 2016 for recent discussion). Below, we provide an overview of the relationship between sexual dimorphism and social perceptions of dominance from voice, focusing primarily on research that uses technology to experimentally alter voice pitch and empirically test its subsequent effect on assessments of dominance.

Voice-Based Assessments of Dominance

A good deal of research on sexual dimorphism and voice perception in humans has focused on perceptions of individuals whose voices vary in *F0*/pitch. Masculine vocal characteristics (i.e., low *F0*/pitch) are typically manipulated via an algorithm in established software (Praat; Boersma and Weenink 2016) that alters pitch, while other aspects of the voice remain unaffected, with manipulations roughly equivalent to 20 Hz sufficient to alter perceptions of voices including perceptions of the speaker's masculinity. Using these methods, and when judging both men and women, masculinized versions of voices are perceived as relatively more dominant than are feminized versions of the same speaker's voice (e.g., Feinberg et al. 2006; Jones et al. 2010; Puts et al. 2007, 2016).

Voice pitch alterations have a greater corresponding effect on the perceived dominance than attractiveness of men, suggesting an important role for vocal characteristics in male-male competition (see Puts 2010). Moreover, lowering voice pitch increases perceptions of leadership potential in both men and women (Klofstad et al. 2012), the number of votes earned by hypothetical election candidates (Tigue et al. 2012), and is negatively associated with judgments of cooperativeness. In contrast, low formants appear to increase judgments of cooperativeness, perhaps because they indicate dominance in the context of prestige versus threat (see Knowles and Little 2016). These associations between dominance and vocal characteristics may generalize to actual social outcomes, as low-pitched CEO's manage larger companies (in financial terms) and have longer tenures at their firm than do CEOs with higher pitched voices (Mayew et al. 2013).

There appears to be some cross-cultural consensus in associations between voice and formidability. Comparing between two distinct cultures, Puts et al. (2012) found that low *F0* predicted arm strength among Tanzanian Hadza men, whereas low formants predicted arm strength among American men. However, both *F0* and formants predict measured strength (i.e., physical maturity) of peripubertal males of the Tsimane (Hodges-Simeon et al. 2014). Among the Hadza, both men and women judge opposite-sex individuals with low-pitched voices as better at acquiring resources (hunting/gathering) compared to individuals with high-pitched voices (Apicella and Feinberg 2009). Collectively, vocal characteristics such as pitch are associated with indices of dominance across a variety of studies and may function as a reliable indicator of actual dominance.

Reliability and Deception in Vocal Indicators of Dominance

Provided a signal remains reliable on average (i.e., in this instance vocal parameters such as pitch/formants), species may exploit this signal to their strategic advantage when competing for mates

and/or resources (reviewed in Mokkonen and Lindstedt 2015). Although vocal parameters are largely constrained by body size, wherein larger species with larger larynges and longer vocal tracts will typically produce lower frequency calls than smaller species (Fitch and Hauser 2003), the vocal anatomy of many mammals has undergone morphological modifications that may function to exaggerate apparent size and, in turn, dominance (Charlton and Reby 2016). Some researchers, for example, propose that the human larynx descended in order to communicate dominance via size exaggeration to conspecifics (Fitch and Hauser 2003). This also appears true for males of several deer species, whose mobile larynges are positioned unusually low in the vocal tract and descend even further during competitive interactions with other males, resulting in a lowering of formants (Taylor and Reby 2010). Also consistent with this proposal, many mammals are known to vocalize in a lower register to convey dominance, threat potential and aggression, and conversely in a higher register to indicate submissiveness or cooperation (Morton 1977). Nevertheless, the extent to which this behavior is volitional when observed in mammals, including nonhuman primates, remains unclear (Pisanski et al. 2016a).

Recent work suggests that humans can behaviorally modulate the fundamental and formant frequencies of our voices volitionally and on demand, such as when asked to imitate a masculine or feminine and physically large or small person (Pisanski et al. 2016a). Humans also modulate these voice parameters when speaking to a potential mate or sexual rival and probably in a range of other social contexts such as job interviews or political debates. Indeed, recent work suggests that deliberate alterations of voice pitch may reduce the potential costs of conflict with observers (i.e., by sounding more dominant; Fraccaro et al. 2012). Further work on social modulation of vocal characteristics in the context of contest competition is needed. In addition, in light of recent work on dominant men's preferences for cues to dominance in other men who produce humor and the potential role of dominance in ally choice among males (Cowan

et al. 2016), further work on the extent to which people integrate social knowledge of same-sex peers (e.g., their cooperativeness as indicated through humor) with knowledge of their dominance from voice will likely prove fruitful.

Conclusion

Inspired in part by sexual selection theories that associate exaggerated sex-typical features in males with measures of success in contest competition, a great deal of research has explored relationships between vocal characteristics and the physical characteristics of the speaker. This research suggests that masculine vocal characteristics (i.e., relatively low fundamental and formant frequencies) are reliable measures of dominance, particularly in men, and that judgments on this trait dimension based on vocal cues may influence important social outcomes such as our choice of leaders. More recent work in nonhumans also suggests potential relationships between testosterone and voice production in the context of male-male competition, and work on human voice perception and production is beginning to uncover a role of voice pitch modulation used to “deceive” potential rivals.

Cross-References

- [Descended Larynx](#)
- [Linguistic Evolution](#)
- [Speech Volume](#)
- [Vocal Attractiveness](#)
- [Voice Pitch](#)

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Vocal Intensity

► Speech Volume

Vocal Loudness

- ▶ [Speech Volume](#)

Vocal Tract Reconfiguration

- ▶ [Laryngeal Descent](#)

Vocal Turn-Taking

- ▶ [Vocal Grooming](#)

Vocalization

- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)

Vocalizations

- ▶ [Social Cognition and Communication in Chimpanzees and Bonobos](#)

Voice Acoustics

- ▶ [Vocal Communication](#)

Voice Attractiveness

- ▶ [Vocal Attractiveness](#)

Voice Box

- ▶ [Stereotyped Vocalizations](#)

Voice Depth

- ▶ [Voice Pitch](#)

Voice Pitch

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Synonyms

[Vocal fundamental frequency](#); [Voice depth](#)

Definition

The perceived degree of height or depth of the voice.

Introduction

Pitch is the most salient property of the voice and describes its “highness” or “lowness” (Titze 2000). The perception of pitch is influenced by multiple acoustic parameters such as amplitude and resonant (or formant) frequencies; however, the primary determinant of pitch is fundamental frequency (F_0), the rate of vocal fold vibration during phonation (Titze 2000). Indeed, pitch and F_0 are often used as though they are nearly synonymous, though the former is a perceptual feature whereas the latter describes the physical properties of the sound waveform.

Voice Pitch Variation and Modulation

Between-individual variation in habitual speaking F_0 is contingent upon differences in vocal fold length and thickness, but individuals also modulate their pitch, both consciously and unconsciously, across contexts. In many animal species, voice pitch is lowered to signal

aggressive potential and raised to signal deference, and this pattern is also apparent across languages in the use of lowered pitch for commands and raised pitch to indicate questions (Ohala 1984). A person might deliberately modulate pitch to convey a specific impression, such as lowering pitch when assuming a leadership role, or pitch might involuntarily rise with increasing tension on the vocal folds during stressful situations (Puts et al. 2006).

Habitual voice pitch is also one of the most sexually differentiated secondary sex traits in humans. During sexual maturation, the influx of androgens in males triggers a disproportionate growth of the vocal folds, leading men to have longer (by approximately 60%) and thicker vocal folds than women (Titze 2000). These anatomic changes produce an adult sex difference in F_0 of around five to six standard deviations (Puts et al. 2012).

Sexual Selection and Voice Pitch

The decrease in male voice pitch at puberty and its associations with mating success (Puts et al. 2006) and reproductive success (Apicella et al. 2007) suggest a role of sexual selection favoring lower pitch in men. Across anthropoid primates, males tend to evolve lower frequency vocalizations relative to females during evolutionary transitions to polygyny, where male mating competition is intense, and reduced F_0 sexual dimorphism tends to evolve during transitions to monogamy (Puts et al. 2016).

In humans, heterosexual women also tend to prefer men's voices that are lower than average in pitch (Feinberg et al. 2005), especially when the women are in the fertile phase of the ovulatory cycle (Puts 2006) and are rating the voices for a short-term sexual relationship as opposed to a long-term, committed one (Puts et al. 2016). Women may exhibit this pattern of preferences in part because a low male voice pitch signals the possession of genes that increase immune system function (Feinberg et al. 2005). In two studies, low male F_0 was associated with high testosterone and low cortisol levels, a hormonal

regime that has previously been linked to immunocompetence (Puts et al. 2016).

While low F_0 may have evolved in men partly because of its function in mate attraction, low F_0 more effectively increases other men's perceptions of a man's social and especially physical dominance (Puts et al. 2007, 2016). In one study, men also modulated their voice pitch according to their perceptions of relative dominance, raising their F_0 when speaking to a competitor whom they perceived as dominant to them and lowering F_0 when they perceived themselves to be more dominant (Puts et al. 2006). Thus, it appears likely that a low F_0 may have been favored primarily for its role in male intrasexual competition and to have played a relatively smaller role in mate attraction. Associations between a low male F_0 and taller stature, higher testosterone, and lower cortisol, as well as evidence that men lower their F_0 when they perceive themselves to be dominant, suggest that low F_0 is a valid, if modest, indicator of men's threat potential to other men.

At the same time, higher-pitched female voices may have been shaped by male mate choice. Although female F_0 does not exhibit a change at puberty as in men, men rate women's voices that have been experimentally raised in F_0 as being more attractive than the same voices with F_0 lowered (Jones et al. 2010). However, this effect may be due to demand characteristics or to the conflation of F_0 with timbre (measured by formant frequencies); when other acoustic parameters were statistically controlled in a multiple regression model, women's formant frequencies predicted their vocal attractiveness to men, but F_0 did not (Puts et al. 2016).

Conclusion

In sum, voice pitch is used in communication across animals to signal dominance and deference, perhaps because a low pitch increases apparent size (Ohala 1984; Puts et al. 2016). Given this social function and possible associations with immune function, it is perhaps not surprising that voice pitch would play a role in mate attraction and same-sex rivalry.

Cross-References

- [Animal Signaling](#)
- [Dominance in Humans](#)
- [Nonverbal Indicators of Dominance](#)
- [Ovulatory Shifts in Psychology](#)
- [Sex Differences](#)
- [Sexual Selection](#)
- [Vocal Attractiveness](#)
- [Vocal Indicators of Dominance](#)

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Voluntary Redistribution

- [Redistribution Preferences and Low Socioeconomic Status](#)

Volunteering Publicly

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Synonyms

[Conspicuous prosociality](#); [Public display of altruism](#); [Public othermindedness](#)

Definition

The conspicuous performance of voluntary acts to serve others despite the potential costs borne by oneself.

Donating one's time and efforts to assist others or advance a cause, without any expectation of recompense, is at the heart of volunteerism. Research in much of social psychology has unearthed a range of the proximal factors that predict voluntary behaviors on the part of individuals, including mood, number, and type of observers or bystanders, personality traits, degree of empathy, and latent mood (Penner and Finkelstein 1998). While these factors go a long way to explaining the situational contingencies of how volunteerism arises in particular contexts, it is useful to consider whether there is a meta-theoretical account of why behavioral patterns consistent with volunteerism would arise in the first place.

Costly signaling theory (CST) provides such an account. It is predicated on the notion, now widely supported in a vast swathe of literature (particularly from fields such as behavioral ecology, ethology and biological anthropology; see e.g., Bird et al. 2001; Gintis et al. 2001) and originally drawn from the theoretical framing of

the handicap principle (Zahavi 1975), that individuals will incur costs to themselves (in terms of energy expenditure, undertaken risk, or proffering of economic or social resources, for example) as a means of publicly broadcasting information about their positive individual qualities. A tried-and-true exemplar from the literature has been the peacock's tail, for which the size and visual resplendence of this plumage is commensurate with its high metabolic and maintenance costs. Ergo, any peacock with the ability to entail such personal cost for the sake of a public display of ornamentation must be of sufficient genetic quality – and thus individual fitness as a mate or ally – to warrant being looked upon favorably by its conspecifics.

Behaviors such as public acts of volunteerism serve a similar function in humans. They serve as a conspicuous presentation of one's capacity to incur costs without enjoying any immediate reciprocation. In performing such acts, and outwardly displaying their ability to absorb the personal impact of doing so, the volunteer is publicly signaling their own status or level of prestige (Hauert et al. 2002). In the process, the volunteer is not merely advertising a one-shot instance of volunteerism (even though this might actually be the case) but is also more broadly showcasing their personal disposition toward engaging in such prosocial acts *generally*, as well as conveying the kinds of prosocial personality characteristics – sympathy, helpfulness, and othermindedness, for example – that would attest to such a general inclination toward prosociality (Griskevicius et al. 2007).

Of course, this kind of deep-rooted evolutionary logic does not suggest that volunteers are only engaging in volunteerism for the self-serving benefits that might be realized by participating in such prosocial behavior. There undoubtedly exist an array of proximal motivations why some people might publicly volunteer for purely selfish reasons in some situations, but this is not what CST is premised upon. Rather, CST holds that the psychological inclination to perform acts of public volunteerism *at all* has an adaptive calculus behind it; one which unconsciously steers individuals toward performing acts of public

volunteerism because it will ultimately increase one's perceived value within a group and in turn improve their evolutionary fitness and capacity to propagate their genes.

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Vowels

► Phonemes and Symbols

Vulnerability Factors

► Risk Factors

Vulnerability to Mental Disorders

► Evolutionary Psychiatry

Vygotskian Intelligence Hypothesis, The (Moll Et Al., 2007)

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Synonyms

Culture and intelligence; The zone of proximal development

Definition

Humphrey (1976) proposed that the major engine of primate cognitive evolution was social competition. Vygotsky (1930–1980) also emphasized the social dimension of intelligence, but he focused on cultural aspects such as collaboration, communication, and teaching. Moll and Tomasello (2007) attempted to integrate both points of view and proposed that primate cognition in general was driven mainly by social competition, but beyond that the unique aspects of human cognition were driven by, or even constituted by, social cooperation.

Introduction

The evolution of human behavior has represented a major research area during the last decades (e.g., Hart 2018). Different interpretations have been proposed. Sometimes competition has been emphasized where other times, group collaborations had been considered critical in human survival (Campbell 2017). These two interpretations have been extensively discussed for a very long time. Although both points of view are not necessarily contradictory, they can potentially be complementary.

Origins of Cognition

The idea that competition plays a major role in human evolution has been proposed by different authors. Humphrey (1976) presents a clear example of this point of view. In this proposal, the fundamental idea was a kind of race in which those individuals, who outsmarted the others, were in advantage and had better possibilities to survive.

A quite different point of view was proposed, but other authors, such as Vygotsky (1930–1980), also assumed the social and cultural origin of intelligence, but emphasized that collaboration, communication, and learning were crucial in the evolution of human cognitive abilities and social progress. Vygotsky stated that social interactions with parents and other figures are crucial in the development of cognitive abilities. In this regard, communication was initially a social communication, later a private communication, and finally an inner speech. This inner speech represents a basic instrument of thought and cognition (Vygotsky 1934–2012).

Noteworthy, humans are by far the most cooperative primate species. Humans live in social groups and develop specific ways of life (“culture”) shared by all the members of the social community (Richerson and Boyd 2005).

Tomasello et al. (2005) proposed an integrative point of view: they argued that primate cognition, in general, was driven initially by social competition. But because of the need to create complex technologies and systems of symbols, social cooperation was not only important but also essential. Moll and Tomasello (2007) argue that regular cooperative activities during childhood result in developing significant forms of cognitive representation and development of complex intellectual abilities.

Conclusion

The dichotomy competition/cooperation can be understood as processes of individual selection versus processes of group-level selection. Multilevel selection theories emphasize that empathy, altruism,

and reciprocity can be the bases of human social cooperation (Fehr and Gächter 2002). It seems reasonable that a variety of evolutionary processes were involved in human evolution, and, ultimately, the causes of these evolutionary changes could have been affected by different evolutionary moment and different living conditions.

So, the points of view presented by Humphrey (1976) and Vygotsky (1930–1980) are not necessarily exclusive, but could both have been involved in human cultural development at different historical moments.

Cross-References

- [Cognitive Science](#)
- [Cultural Differences](#)
- [Cultural Variation](#)
- [Intelligence](#)

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Wailing

► [Crying](#)

Waist-to-Hip Ratio

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Synonyms

[Body shape](#); [Gluteal–femoral region](#); [Hour glass](#)

Definition

The waist-to-hip ratio (WHR) is an anthropometric measure of body shape. It is calculated by taking the distance around the waist at its narrowest point and by dividing the distance around the hips and buttocks at their widest points. In evolutionary theory of human mate preferences, WHR was suggested to have evolved via sexual selection as a cue of gender, health, and fertility in women.

Introduction

Almost 25 years ago, Devendra Singh (1993) proposed that the distribution of body fat in women evolved via sexual selection as an honest cue of youth, health, and fertility. This chapter revisits Singh's iconic hypothesis in light of contemporary empirical findings and asks how sexual selection has shaped the evolution of body fat distribution in women and men.

Sexual Dimorphism in Human Body Composition

In comparison to nonhuman primates, differences between men and women in overall body size are not striking. While there is considerable overlap in body composition between the sexes within populations and pronounced cross-cultural differences in body composition, muscularity and body fat are sexually dimorphic (Wells 2007). Men tend toward a more android physique, characterized by greater stores of upper body musculature (Wells 2007). Women tend toward a more gynoid physique, wherein fat is deposited around the hips, buttocks, and thighs, collectively referred to as the gluteal–femoral region (Wells 2007). A simple way to measure gluteal–femoral fat distribution is via the waist-to-hip ratio (WHR), which is calculated by taking the distance around the

waist and dividing it by the distance around the hips and buttocks.

Among premenopausal young adults from Western populations, women's WHRs range from 0.67 to 0.80, while men's range from 0.85 to 0.95 (Cashdan 2008). These sex differences in body composition first emerge during adolescence under the actions of sex steroids (Wells 2007), principally androgens, which drive the deposition of muscle in the upper body, and estrogens, which inhibit muscle accumulation while promoting a gynoid fat distribution (Wells 2007).

As young women approach sexual maturity, a lower WHR predicts the onset of menarche (Lassek and Gaulin 2008) and is associated with maintaining regular menstrual and ovulatory cycles in young adulthood (Singh and Singh 2011). In adulthood, levels of the hormone estradiol relative to progesterone, which predicts natural rates of fertility, has been reported to be highest among women with the lowest WHRs and largest breasts (Jasienska et al. 2004). Low WHRs are also associated with higher rates of successful in vitro fertilizations and artificial inseminations (Singh and Singh 2011). During pregnancy, gluteal–femoral fat reserves are mobilized to provide energy during gestation, particularly during the third trimester for fetal neural development and postpartum for lactation (Lassek and Gaulin 2008). A low WHR also allows for a stable center of balance for bipedal locomotion during pregnancy, and increases in maternal central adiposity are associated with healthier infant birth weight (Singh and Singh 2011). WHR also changes across the lifespan, so that as women approach menopause, WHRs enter the masculine range and are less hourglass in appearance (Singh and Singh 2011).

Sexual Selection on Female WHR and Singh's "First Pass Filter" Hypothesis

Sex differences in morphology can emerge via a form of natural selection called sexual selection, where competition among individuals to fertilize the gametes of the opposite sex drives the

evolution of behavioral displays, ornaments, and armaments. Sexual selection can act on traits employed during same-sex competition, such as weaponry or visually conspicuous markers of social rank, or ornamentation that enhances sexual appeal. Men's preferences may have been shaped during the early phases of human evolution to recognize those aspects of physique that would enhance their reproductive success (Singh and Singh 2011). Singh (1993) was the first to propose that a low WHR and an hourglass physique in women were sexually selected by male mate choice. He hypothesized that a low WHR represented a "first pass filter," guiding men's initial assessment of women's mate value in ancestral environments as an unambiguous cue of gender, health, youthfulness, and fertility (Singh 1993).

Cross-cultural variation in the attractiveness of low WHRs in women

The fact that WHR conveys such significant information about the mate value of a woman suggests that men in all societies should favor women with a low WHR over women with a high WHR for mate selection or at least find such women sexually attractive. Singh (1993, p. 305)

Singh (1993) reported in a sample of young men from the USA that preferences were greatest for a low WHR of 0.7 and proposed that men's preferences should be similar cross-culturally, as men tend to value youth and healthiness in long-term mate across cultures. Replications of Singh's (1993) study that were restricted to industrialized cultures such as England, Germany, Poland, China, the USA, and New Zealand reported that men tend to prefer low WHRs of 0.6–0.7 (reviewed in Brooks et al. 2015). However, among the Bakossi of Cameroon, who live primarily as subsistence horticulturalists, men judged a more masculine WHR of 0.8 as most attractive for both long- and short-term relationships (reviewed in Brooks et al. 2015). Similarly, Shuar men of the Ecuadorian Upper Amazon preferred WHRs of 0.7 and 0.8 when controlling for

body weight (reviewed in Cashdan 2008). The Matsigenka of Peru, a culturally isolated population of slash and burn agriculturalists, preferred a WHR of 0.9 (reviewed in Cashdan 2008). Finally, among the Hadza hunter-gatherers of Tanzania, men's preferences were initially reported to be highest for a WHR of 0.9 (reviewed in Cashdan 2008). However, a follow-up study employing stimuli in profile view that looked more like Hadza women revealed that men preferred a WHR of 0.6 (reviewed in Cashdan 2008).

Many of the findings from these studies suffer from important methodological drawbacks. The stimuli were manipulated to only vary in WHR by tightening or widening the midriff, which confounds WHR with body mass index ($\text{BMI} = \text{weight} / \text{height}^2$; Tovée et al. 2006). In an attempt to address these issues, studies instead employed photographs of female patients taken before and after elective cosmetic surgery to alter their body shape (Singh et al. 2010) and found that low WHRs elicited neural reward responses in fMRI studies (Singh and Singh 2011) and were judged as most attractive across several Western and small-scale societies (Singh et al. 2010). However, these stimuli presented only the gluteal–femoral region, which does not allow height relative to weight to be visually assessed.

This debate became more complex when cross-cultural research using full body stimuli reported that BMI accounted for significantly more variance than WHR in women's attractiveness (Tovée et al. 2006). Similarly, other research using full body stimuli reported that the abdominal depth and the volume–height index are significant contributors to female physical attractiveness (reviewed in Brooks et al. 2015). Further, visual attention when assessing female attractiveness shares stronger associations with judging body fat than WHR with minimal differences reported as a function of WHR (reviewed in Brooks et al. 2015). Finally, computer models of women's fat distribution around the hips, buttocks, and thighs demonstrated that WHR as a contributor to body shape is best understood in light of increases in BMI (reviewed in Brooks et al. 2015).

Prevailing environmental, ecological, and social factors may give rise to these cross-cultural differences in WHR and body weight. Female physiques are more robust in horticulturalist settings, possibly because women engage in manual labor which drives higher androgen levels and more masculine WHRs (Cashdan 2008). Variation in preferences for body shape and size may also be influenced by a “visual diet,” wherein the distribution of body types that people are accustomed to seeing within their given cultures underpins preferences (Boothroyd et al. 2012). For example, indigenous Zulu men preferred a much higher female BMI than Zulu migrants to the UK, who tended to prefer a BMI equivalent to that of UK born men (Tovée et al. 2006). Thus, the ecological context and the local distribution of body types to which individuals are accustomed to seeing may influence the direction of preferences for female body shape.

Multivariate Selection on Preferences for Female Body Shape

Perhaps the debate surrounding the role of WHR in women's mate value became so complex due to a narrow focus on the effects of singular or a small number of indices of shape or size. Examining single traits cannot determine the strength of selection on components of WHR or how WHR contributes in concert with other bodily indices to shape physical attractiveness (Brooks et al. 2015). Manipulating one trait, such as waist girth, might change how attractive a body is judged via interactions with other bodily traits like abdominal depth or BMI. Thus, unpacking how bodily indices exert independent or interacting effects on overall physical attractiveness is complicated by their intercorrelated nature. To address this complexity, evolutionary biologists have developed selection analysis, wherein the principle dimensions of nonlinear and linear selection are characterized using linear and nonlinear multiple regressions to uncover the true targets of selection (Brooks et al. 2015).

A recent study combined multivariate selection analyses with experimental manipulations of

suites of bodily traits using computer-generated avatars (Brooks et al. 2015). In this study, avatars served as “progenitors” from which “clonal daughters” were created using computer algorithms by making minor changes to 24 bodily indices. In an online experiment, bodies were allowed to “evolve” via attractiveness ratings over eight generations (Brooks et al. 2015). From the first generation to the eighth generation, selection was strongest on the waist with preferences being higher for smaller waist girths, followed by preferences for slender buttocks and longer legs so that bodies became progressively taller and slimmer. WHR was also an important factor in women’s attractiveness and converged on a WHR of approximately 0.7. However, the buttocks continued to become slimmer, while waist girth evolved more rapidly than the buttocks, suggesting that preferences for low WHRs of 0.7 were dragged along due to strong selection acting on slender waists rather than direct selection on lower WHRs. These findings highlight the multivariate complexity of how sexual selection may shape the evolution of bodies and suggests that the role of simple measures of shape and weight may be of less importance than selection for waist girth and overall slenderness.

Conclusion

Almost 25 years from Singh’s (1993) seminal article, a great many advances have been made on our understanding of how body fat distribution influences attractiveness. His suggestions for culturally universal preferences were not supported, and subsequent cross-cultural research has highlighted a key role for BMI in accounting for variance in women’s attractiveness. Building on this work, multivariate selection analyses and evolutionary selection experiments have paved the way for determining the targets of sexual selection among suites of correlated bodily indices. Finally, studies integrating prevailing cultural, social, and ecological factors have made advances toward our understandings of what

maintains variation in preferences within and between cultures. The task moving forward may be to employ multivariate selection cross-culturally and determine the strength of selection on body shape in variable ecological and economic contexts.

Cross-References

- [Body Attractiveness](#)
- [Body Fat Percent and Distribution](#)
- [Men’s Mate Preferences](#)

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Walking

► [Nonhuman Primates: Species Typical Movement](#)

War

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Synonyms

[Battle](#); [Combat](#); [Conflict](#); [Hostilities](#); [Invasion](#); [Raiding](#); [Warfare](#)

Definition

“War” is an armed conflict between nations or organized groups such as tribes, gangs, kin groups, or political factions.

Introduction

It is obvious that warfare is a highly cooperative activity that requires good communication and cooperation with allies and intelligent self-control (Tooby and Cosmides 2010), but there has been a long-standing disagreement among historians and social scientists regarding the origins of human warfare. In the last couple of decades, evolutionary scientists have brought yet another perspective to bear on this issue.

The first point to be emphasized is the extent to which war is almost exclusively a male activity. In spite of the diversity to be found across human societies, there has been no historically documented case of organized fighting and killing by groups of women against other groups of women. The consistency with which males are the organizers and perpetrators of group conflict has led many scholars to conclude that the male propensity for group violence is rooted in more

than the learning of culturally prescribed gender roles. Most evolutionary psychologists believe that the roots of warfare can be traced to the competition between males for status and access to women (McAndrew 2017).

Male Competition for Mates Is Intense

The adaptive problems faced by men and women throughout history were quite different, and aggression proved to be a more adaptive response for males than for females. Sexual competition for mates has always been more intense among males than among females, especially in the polygamous societies that appear to have been typical in the prehistoric human world.

The stakes were very high for men in this environment, as the winners of this competition would come away with the greatest number of women (and the most desirable women). The losers ran the risk of genetic annihilation by their failure to successfully win the status and resources necessary to attract mates. Historically, powerful men have always enjoyed greater sexual access to women than men lower in the pecking order, and violence, including war, can often be traced to this grim struggle for status and mates among men.

Violence committed against the right people at the right time has commonly been a ticket to social success. For example, among the Yanomamo of South America, men who had killed other men, especially during wars and skirmishes with other villages, acquired significantly more wives than men who had not yet killed anyone (Chagnon 2013). Because having killed someone in war was usually good for one's reputation, many societies developed ceremonies for recognizing such accomplishments. In modern societies, these take the form of prestigious awards such as the Congressional Medal of Honor in the United States, and many countries have national holidays to celebrate the heroism of those who have fought and/or died in wars.

To insure that public recognitions of valor during war serve as honest signals of heroic behavior, sanctions may be brought to bear against individuals who falsely claim to have attained military

honors. For example, in the United States, the “Stolen Valor Act of 2005” was signed into law by President George W. Bush to prohibit the unauthorized wear, sale, or manufacture of military decorations and medals. This law was extended by the “Stolen Valor Act of 2013” signed into law by President Barack Obama. The 2013 law makes it a crime for a person to fraudulently claim to have received military medals and decorations.

Could War Heroism Be Adaptive?

Evolutionary psychologists believe that even apparently selfless impulses such as volunteering to fight in a war must provide some adaptive advantage for individuals. Costly signaling theory (Bereczkei et al. 2010; Bliege Bird et al. 2005; Grafen 1990; McAndrew 2002; Zahavi 1977) suggests that conspicuous war heroism may be a way for individuals to advertise desirable personal qualities that increase the likelihood that they will be chosen as a mate or an ally and be positioned for access to future resources.

Many studies demonstrate that people who sacrifice for the group by engaging in costly altruistic activities do in fact achieve elevated social status, respect, and recognition as a result of their public selflessness (McAndrew and Perilloux 2012a, b; Willer 2009). For a costly signal to be effective, it must honestly convey valuable information about the individual sending the signal, and it must be impossible to fake. No researchers suggest that heroes consciously sit down and calculate all of the benefits that will come their way if they survive the heroic action. Rather, it is thought that such impulses have been selected for because heroic behavior has provided competitive advantages for men throughout human history.

Have Men Evolved to Make War?

Dutch psychologist Mark van Vugt proposed the *male warrior hypothesis* as a way of explaining the results of research demonstrating that men show stronger group identification and more

cooperation with ingroup members than do women during times of threat from outside groups (Van Vugt et al. 2007). His theory suggests that men have evolved a predisposition to engage in collective cooperative aggression against outgroups, a tendency that has likely been strongly reinforced through culture traditions and socialization. Puts (2010) has also pointed out that men tend to form more hierarchical same-sex coalitional groups than do women and that they are more likely than women to make strong ingroup/outgroup distinctions that result in the dehumanization of outgroup members (Buss 2015).

A team of European psychologists explored the proposition that war provides an arena for men to compete and impress both their male rivals and females who might be potential mates (Rusch et al. 2015). In one study, they found that 464 American men who had won the Medal of Honor during World War II eventually had more children than other US service men who had not been so heroically distinguished. This is consistent with the idea that heroism gets rewarded with greater reproductive success.

In a second study, 92 women rated the sexual attractiveness of men who had behaved heroically in war as being higher than that of soldiers who had served but not been identified as heroes. Tellingly, women did not show this increased attraction toward men who had behaved heroically in sports or business situations. A third study revealed that behaving heroically in war does not increase the attractiveness of female war heroes to men. In summary, heroism in time of war is sexier than any other kind of heroism but only for men. Similarly enhanced access to females has been documented for males who join violent street gangs (Palmer and Tilley 1995).

Young men are particularly concerned with status and heroic opportunities for sound evolutionary reasons. In early human societies, competitive success or failure in early adulthood determined a man’s standing in a social group for the rest of his life. It wasn’t possible to simply hit the “reset” button and join another group, so what happened during the teen years mattered a lot. For this reason, high-risk competition

between young males provided an opportunity for “showing off” the abilities needed to acquire resources, exhibit strength, and meet any challenges to one’s status (Iredale et al. 2008; McAndrew 2009). Consequently, heroic or even recklessly daredevil behavior was rewarded with status and respect – assuming, of course, that the young man survived the ordeal. Displaying heroism in time of war was a primary way of accomplishing these goals. Hence, it should not be surprising that historical data confirm that the proportion of a population made up of young men is one of the best predictors of when a society is most likely to go to war (Mesquida and Wiener 1996).

The relentlessness of risky, aggressive behavior by young males has prompted Wilson and Daly (1985) to label this behavioral tendency the “Young Male Syndrome.”

The results of the annual “Darwin Awards” competition offer a tongue-in-cheek confirmation of the tendency of young males to behave recklessly. The Darwin Awards feature those individuals who have lost their lives in dramatic fashion during the previous year by taking pointless risks. For the 5-year period from 2010 to 2014, the Darwin Award winners were skewed toward men by a margin of 38–5, with two of the five women who made the list getting there by being talked into having sex with men under less than rational circumstances (DarwinAwards.com).

Men are sensitive to signals that advertise the physical strength, fighting ability, and aggressive inclinations of other men (Sell et al. 2009, 2010) and actively assess the likely outcomes of violent encounters between themselves and other men (Fox 1997). Today, the proliferation of sports undoubtedly developed as a constructive alternative for dealing with the proclivities of young males that evolved in a very different time. In a legally sanctioned gladiatorial arena, young men compete to exhibit the same skills – throwing, clubbing, running, wrestling, tackling, and eye-hand coordination – that would have made them successful fighters and hunters in the ancestral environment. The popular appeal of spectator sports, especially for men, probably occurs at

least in part because it taps into an innate interest in the physical capabilities of other men.

The idea that men use war as a way of competing with each other to impress women has clearly been around for quite some time. For example, the Sioux warrior *Rain in the Face* once commented on the fact that the presence of women in a war party caused his warriors to vie with one another more intensely in displaying their valor (Philbrick 2010).

What Are the Necessary Precursors to War?

In addition to the aforementioned prerequisite of having a sufficient number of young men in a group who are able to fight, evolutionary social scientists have long recognized that a number of other conditions predict a group’s willingness to wage war. (See Shackelford and Weekes-Shackelford (2012) for a comprehensive overview.)

For example, it is essential that armies marching into battle have clearly distinguished their “sympathy groups” (often overlapping with kin groups) from their enemies for whom they hold little or no sympathy. Ideologies and religion can facilitate this process by creating certainty about holding the moral high ground in a conflict, which bolsters both a strong ingroup identification and a callous disregard for the fate of outgroup members. A recent study indicates that individuals may be more likely to participate in a defensive war if clear benefits accrue to their group as a result of the war, but participation in offensive wars (i.e., one’s own group initiates the conflict by attacking another group) is more likely when the individual benefits personally from the war (Lopez 2017).

Because war is so costly and risky, for male psychology to have evolved a predisposition for going to war, several essential conditions must have been met. John Tooby and Leda Cosmides (2010) have identified four conditions that would be particularly important. First of all, successful soldiers must have greater sexual access to women than noncombatants. Secondly, coalitions

of fighters must believe that they will be victorious. Thirdly, the rewards that each warrior receives must be proportionate to the risks he has taken and the importance of his contributions. In other words, cheaters should never prosper. And finally, men going to war must not know for sure who will live and who will die; there must be a protective “veil of ignorance.”

Conclusion

Males have evolved adaptations for warfare over time because the benefits of displaying valor and genetic fitness by participating in war have outweighed the costs associated with such behavior. These adaptations include cognitive and coalitional predispositions that increase the effectiveness of violent, coordinated group behavior. In short, going to war in general and displaying war heroism in particular may be a way for males to advertise desirable personal qualities that enhance status and increase the likelihood that they will be chosen as a mate or an ally and be positioned for access to future resources.

Cross-References

- Aggression
- Altruism
- Costly Signaling and Altruism
- Evolved Psychology of Warfare
- Heroic Rescue in Humans
- Humans: Between-Group Conflicts
- Information About Likely Combat Success
- Intergroup Competition
- Men Riskier, More Aggressive
- Sex Differences in Aggression
- War More Likely with Higher Likelihood of Success
- Young Male Syndrome

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War More Likely with Higher Likelihood of Success

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Synonyms

Coalitional aggression; Intergroup conflict; Theory of war; War

Definition

Evolutionary explanations for war posit that coalitional aggression against external social groups resulted in higher fitness over the long duration of the Pleistocene. The essential

challenge of these models is to account for the selection for such risky behavior given the potentially high costs to participants in attacks. This entry focuses on one influential hypothesis developed from this body of theory: that war is more likely with higher likelihood of success.

Introduction

The antiquity of warfare is a fundamental question for a wide variety of social science disciplines and an important factor in how conflict might be reduced in the future. Recent multidisciplinary research has provided abundant evidence that warfare has a long chronology, dating far back into the Pleistocene (Allen and Jones 2014; Bowles 2009; Gat 2017). While defensive warfare is readily understood as an adaptive behavior in the face of aggression, the initiation of offensive warfare requires a deeper analysis. Evolutionary models argue that members of hunter-gatherer groups accrued direct and indirect benefits (i.e., higher fitness) from joining unprovoked attacks against other groups, despite the potential risk of injury or death to participants (Wrangham and Glowacki 2012). The probability of a successful attack is a key “Darwinian algorithm” that confronted potential warriors over the long durée of the Pleistocene (Tooby and Cosmides 1988). An important point to consider is that both individuals and groups often chose (and continue to choose) poorly when making this calculation. Common causes for such miscalculation are overconfidence, positive illusions, and military incompetence (Johnson et al. 2006).

The Risk Contract of War

The risk contract of war model developed by Tooby and Cosmides (1988) is a cornerstone of coalitional aggression and the evolutionary psychology of warfare. They argue that a stable contract, to be a “psychologically imposed structure,” must reward or punish coalition members in proportion to their risks taken and their contributions to offensive actions.

Tooby and Cosmides (1988:6) posit that:

It can be shown that given 1) certainty of victory, 2) the assurance of a random distribution of risk of death among participants, 3) the assurance of a relatively “fair” allocation of the benefits of victory, and 4) efficiency in the utilization of reproductive resources on a zero-sum basis, *selection will favor participation in the coalitional aggression regardless of the existence or even the level of mortality (within broad limits)* (emphasis original).

The risk contract is thus a “Darwinian algorithm” that predicts that males will risk warfare in situations where the average fitness favors participation in coalitional aggression. Sex differences are predicted in this model since “females have more to lose, and less to gain, and such differences in consequences should be reflected in psychological sex differences in attitudes towards coalition formation and coalition-based aggression” (Tooby and Cosmides 1988:6).

Tooby and Cosmides point to the importance of numerical superiority being a key factor in predicting success. This in turn would strongly favor active recruitment and enforcement of coalitional participation, particularly by individuals with strong incentives for coalitional aggression (Gavrilets and Fortunato 2014).

Offensive Versus Defensive Warfare

Military science thinkers, from Sun Tzu to Clausewitz, stress the difference between offensive and defensive actions. The chief advantages of offense are the element of surprise and the ability to choose the timing and locations of engagements, but less widely recognized is that these pluses can be blunted significantly by the primacy of defense (Allen 2008). Moreover, failed attacks can also mean severe losses for routed invaders. Prudent offensive military operations are thus those with a high probability of success. The strategic logic of military science is thus congruent with the risk contract evolutionary model.

Evolutionary approaches to coalitional aggression also recognize differences between offensive and defensive warfare. An evolutionary explanation for defense against an unprovoked attack

is very straightforward, as attacked pacifists who turn the other cheek are not likely to enjoy increased fitness. It is unprovoked aggression that requires more complex calculations of costs and benefits (Rusch 2014, Tooby and Cosmides 1988).

Nobody’s Perfect: Overconfidence, Positive Illusions, and Military Incompetence

Evolutionary models of coalitional aggression must take account of another significant factor: miscalculation of the probability of attack success. Military history as well as a wide range of human competitions bear witness that aggressions initiated with a high expectation of success often nevertheless backfire spectacularly. Three factors are commonly posited in evolutionary approaches to account for miscalculation: overconfidence, positive illusions, and military incompetence (Johnson et al. 2006, Wrangham 1999). Overconfidence and positive illusions are common human tendencies to self-aggrandize, unrealistic expectations to control situations, and a sense of invulnerability. Military incompetence is exhibited when a force loses a conflict which they expected to win due to overconfidence, underestimating opponents, ignored information, or misallocation of resources. While these would appear to be maladaptive, they could all still be selected for over the long run if they provide an overall increase in average fitness despite even high casualty rates (Tooby and Cosmides 1988). Research by Johnson et al. (2006) suggests that males are more likely than females to fall prey to overconfidence, and that they are more likely to pursue coalitional aggression.

Conclusion

The origins of warfare is more than just an academic question. A better understanding of the causes of war may well be essential for current and future attempts to reduce its likelihood or severity. Evolutionary explanations such as the

risk contract model provide plausible mechanisms to account for the wide variety of evidence that warfare has ancient roots in even small-scale hunter-gatherer societies. Observations and theoretical arguments that war is more likely when there is a high probability of success appear to be parsimonious with available evidence as well as the tactical logic of military science.

Cross-References

- ▶ [Conditions Required for Evolution of Warfare Adaptations](#)
- ▶ [Defense Against Attack](#)
- ▶ [Evolutionary Theory and the Causes of War](#)
- ▶ [Information About Likely Combat Success](#)
- ▶ [Male Adaptations that Facilitate Success in War](#)
- ▶ [Men but Not Women Will Have Adaptations for War](#)
- ▶ [War](#)

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Warfare

- ▶ [Evidence of Intentional Killing](#)
- ▶ [Humans: Between-Group Conflicts](#)
- ▶ [Social Dominance Orientation \(SDO\)](#)
- ▶ [War](#)

Warfare, War, Feuding, Primate Aggression

- ▶ [Nonhuman Primates: Between-Group Conflicts](#)

Warning

- ▶ [Dominance and Threat or Use of Force](#)

Warning Call

- ▶ [Alarm Calling and Kinship](#)

Warning Coloration

- ▶ [Aposematism](#)

Warning Display

- ▶ [Aposematism](#)

Warning Signal

► [Aposematism](#)

Wason (1966) Selection Task

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Synonyms

[The four-card problem](#); [The Wason selection task](#); [Wason’s four-card problem](#); [Wason’s selection task](#)

Definition

The Wason (1966) selection task is a reasoning task based on the logic of conditional rules and their violation.

Wason’s selection task is a problem designed to explore the ways people reason with conditional statements, those that can be expressed using “if.” It is one of a suite of reasoning problems invented by the British psychologist Peter Wason (1924–2003) and arose from his interest in, and curiosity about, firstly, the use of conditionals in both everyday and official language and, secondly, a tendency he had uncovered in earlier research using another of his tasks for people to confirm their beliefs rather than test them through attempted falsification. (This story is detailed in Wason and Johnson-Laird 1972, a monograph reviewing the authors’ early work on reasoning.) Wason (1964) had previously observed that experimental participants did not adhere to the prescriptions of formal logic when drawing inferences from conditional statements.

The selection task made its debut in a book chapter (Wason 1966) and was quickly taken up by researchers around the world: in 1974, a whole conference on it was held in Italy, and it is now

common to refer to it as the most, or one of the most, often-used experimental paradigms in the field, “the mother of all reasoning tasks,” in the words of Stenning and van Lambalgen (2008, p. 44). The reason for the explosion in its popularity is captured in the title of a paper by Wason, reviewing his early findings: Structural simplicity and psychological complexity (Wason 1969). In the first published refereed paper on the task, Wason (1968) presented it in the following form. Four cards (real cards in those days; now, presentation is almost always computer-mediated) were placed on a table, and the participants were told that each one had a letter on one side and a number on the other (see Fig. 1). They were given the following sentence relating to these four cards: *If there is a D on one side of any card, then there is a 3 on its other side*. Their task was to decide which of the cards would enable them to determine whether the sentence was true or false; the experimenter, Wason himself in this case, pointed to each one and asked whether knowing what was on the other side would enable them to make that judgment.

There is a normative solution to this problem, deriving from standard propositional logic, to which human performance can be compared. We can use symbols to explicate this. Firstly, the sentence can be written in the general form *If p then q*; p is known as the antecedent part, q stands for the consequent. Secondly, assume that the target sentence is an implication conditional, i.e., one where, given the sentence’s truth, q necessarily follows from p, but the reverse – p from q – does not necessarily follow. There are thus two logically valid inferences from an implication conditional: p therefore q and not-q therefore



Wason (1966) Selection Task, Fig. 1 The standard abstract selection task cards, from Wason (1968). Below are their logical values; these were not shown when the task was presented. The target rule was *If there is a D [p] on one side of any card, then there is a 3 [q] on the other side*

not-p. The selection task is therefore asking participants to find those cards that could lead to valid inferences; in addition, they have to appreciate the need to try to falsify the statement, since a potentially falsifying instance provides a decisive test of its truth. The only valid falsifying instance is p with not-q, since such a combination violates the two valid inferences. Using the materials in the 1968 example above and in Fig. 1, there are two cards which could lead to falsifying instances: the D (i.e., p) card, which could have a number other than 3 (i.e., not-q) on its reverse, and the 7 card, because 7 is not 3 (i.e., not-q) and so would falsify if it had a D on its reverse. The other two cards need not be examined since neither could bear the falsifying p, not-q combination.

Human Performance in the Early Days

The normative solution to the selection task is to select the p and the not-q cards and ignore the not-p and q cards, but in Wason's original experiment, only one of his 34 participants did so; the modal selections were for the p card alone or the p and q cards. Thus they tend always to select the p card and hardly ever to select the not-q card. In now over half a century of research featuring this basic version of the task, involving hundreds of experiments around the world, these essential findings have stayed the same. It is a very robust paradigm. Much effort has been expended in trying to solve the riddle of the psychological complexity of the selection task (see Manktelow 2012, for a fairly recent summary), but for present purposes, that is largely beside the point. Its interest lies in the uses to which it has been turned, and its robustness has made it into a kind of cognitive recording electrode, which can be used to probe a number of functions. One of these was as a test-bed for hypotheses derived from evolutionary theory.

An obvious ecological objection to the task in the form in which it was first used in experiments, using what came to be known as abstract materials, is to its artificiality: testing cards for letter-number (or other symbolic) combinations bears scant resemblance to the kind of thinking

conducted in real life. The equally obvious remedy is to reengineer it to be more realistic. This was done by Wason and Shapiro (1971). They presented the task as a claim about journeys, with four cards showing four days' journeys, the destinations on one side and the means of transport on the other. The target sentence was *Every time I go to Manchester I travel by car*, and the cards showed Manchester (p), Leeds (not-p), Car (q), and Train (not-q). Which cards need to be examined to tell whether the stated claim is true or false? Manchester, in case I used some other means to get there, and Train, in case I went to Manchester on it; these cases would falsify the conditional claim. Ten of the 16 participants given this version chose this p, not-q combination, compared to 2 out of 16 given a letter-number version.

Unlike results with the basic version, this finding has not proved stable; simply using realistic content does not necessarily facilitate logical performance. It has to be a particular kind of realistic content to facilitate reliably: *deontic* content, that is, content containing rules stated as regulations, not generalizations. This was discovered, but not initially recognized as such, by Johnson-Laird et al. (1972), who reported a record-breaking facilitation effect using materials relating to a postal sorting scenario. Participants were told to imagine they were mail sorters, given the rule *If a letter is sealed, then it has a 50c stamp on it*. The selection task cards were envelopes, showing a sealed one (p), an unsealed one (not-p), one with a 50c stamp (q), and one with a 40c stamp (not-q). The participants had to choose those to examine "to find out whether or not they violate the rule" (Johnson-Laird et al. 1972, p. 397). Twenty-one out of 24 participants chose the correct pair, the sealed envelope (which might have an inadequate stamp) and the 40c envelope (in case it was sealed); only 2 of 24 did so in an abstract condition. Johnson-Laird et al. explained this effect as being due to the postal materials "lead[ing] the subject to a greater insight into the logical structure of the task" (p. 396). This explanation was undermined by subsequent research, which showed that the postal task was tapping into a form of reasoning categorically different from that called for by the abstract task or

thematic versions such as the “journeys” task: deontic reasoning. In retrospect, there were clues in the postal version’s materials; they were not just realistic, but realistic in a particular way. For a start, the target conditional was a rule in the sense of a regulation, a statement designed to control behavior; it was not an indicative claim about factual possibilities. Secondly, following on from this, there is an implied modal term in the consequent: sealed letters *must* have a higher valued stamp. This is not the case with indicative, descriptive claims. Finally, the participants were not instructed to test its truth, but to detect possible violations. A violation of a regulation does not render that rule false, as any police officer will affirm.

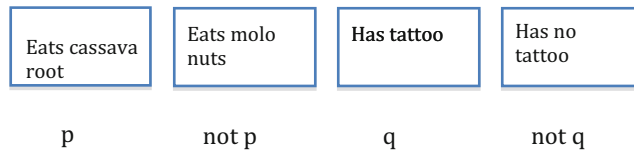
Evolutionary Psychology and the Selection Task

“Deontic” is a term co-opted from philosophy and denotes thinking associated with obligations (of which the postal rule is an example), permissions, and so on. Deontic reasoning is thus the kind of reasoning we perform when considering what we should or should not, or may or may not, do. The first research to test directly the proposal that tasks such as the Johnson-Laird et al. postal task were evoking deontic rather than indicative reasoning was reported by Cheng and Holyoak (1985). Their work eliminated an early competitor to Johnson-Laird et al.’s original “insight” explanation: the memory-cueing hypothesis of Manktelow and Evans (1979; also Griggs and Cox 1982). This amounted to a proposal that the participants’ familiarity with the content of the postal task meant that they were not reasoning at all, but simply recalling their real-world knowledge.

Griggs and Cox had found that there was no facilitation when the postal task was run in Florida, USA, where there had never been a two-tier stamping rule (the original task had been run in Britain, which had had just such a rule), whereas a drinking-age rule, with which the Florida population was familiar, did produce facilitation. Cheng and Holyoak also gave US

participants a postal selection task but in the instructions gave explicit information about the costs and benefits to the postal service and its customers: the service charged more for sealed mail to increase profits, and the customer had to pay this surcharge for personal mail if they wanted it sealed. With this rationale, both US and Hong Kong participants produced high levels of p, not-q selections; without it, the Hong Kong group’s performance stayed high, while the US group’s was significantly lower; Hong Kong had had a two-tier stamping rule, so it was familiar to them but not to the US population. Cheng and Holyoak proposed that deontic facilitation occurred through the invocation of *pragmatic reasoning schemas*. These, they argued, were packets of knowledge about what to think and do, instantiated as a set of production rules, such as *If an action is to be taken, then the precondition must be satisfied*. When a task scenario maps on to one of these rules, as the postal task does with this one, the schema is invoked, and the necessary inferences are generated. They gave this a strong test by the novel tactic of using an abstract deontic task, which removes any question of mere familiarity: here, the target rule was *If one is to take action A, then one must first satisfy precondition P*. The cards showed “Has taken action A” (p), “Has not taken action A” (not-p), “Has fulfilled precondition P” (q), and “Has not fulfilled precondition P” (not-q). Significantly more p, not-q cards were selected with this task compared to a non-deontic abstract version.

According to Cheng and Holyoak (1985), people reason “using abstract knowledge structures induced from ordinary life experiences” (p. 395). However, it is possible that the source of these knowledge structures is more fundamental than that: that they are part of humans’ evolutionary endowment. This was the possibility addressed by Cosmides, in a hugely influential paper published in 1989. Cosmides introduced to the psychology of reasoning what has come to be known as *social contract theory*. It was based on the evolutionary theory of reciprocal altruism, put forward by Trivers (1971) to explain the evolution of cooperation in social situations: organisms initially incur a cost to themselves to provide a benefit to others,



Wason (1966) Selection Task, Fig. 2 Cards in the basic version used in the social contract experiments of Cosmides (1989), with logical values (not presented to participants) below. The target rule was *If a man eats cassava root [p], then he has a tattoo on his face [q]*

a rational strategy providing there is a well-founded expectation that the same will be returned to them.

Cosmides refined this dynamic into a set of what she called Darwinian algorithms. The basic rule of social exchange in this scheme is a conditional: *If you take a benefit, then you pay a cost*. This rule is not sufficient in itself for efficient social exchange: it has to be policed, for there is a powerful incentive to cheat, to take the benefit without paying the cost; any organism that can get away with this is at an advantage compared to those which comply with the rule. Cosmides therefore added a cheater-detector algorithm, a cheater being someone who takes the benefit without paying the cost. Cosmides' theory thus inherits the benefit-cost component from Cheng and Holyoak's but, unlike them, proposes that Darwinian algorithms are an evolved capacity, not a product of learning.

Cosmides (1989) claimed that all reliably facilitating versions in the selection task literature could be fitted to her scheme and went on to test it using novel contents. Her experiments generally concerned imaginary anthropological expeditions studying native people in remote locations, making observations of their cultures stated in the form of conditional rules. An example is *If a man eats cassava root, then he has a tattoo on his face*. Cassava was presented as a highly desirable commodity (a powerful aphrodisiac) available only to married men, marital status being signified by the tattoo. Thus the benefit is cassava, the cost is getting married (and tattooed). She constructed selection tasks wherein the familiar four cards read Eats cassava root (p), Eats molo nuts (not-p), Has tattoo (q), Has no tattoo (not-q;

see Fig. 2). This task can then be framed as a deontic, cheater-detection task, or as an indicative, test-the-claim task. The predicted facilitation of p, not-q selections with the deontic version was duly observed.

Cosmides then mounted a strong test of the theory: she used "switched" social contract rules, this time reading *If you pay a cost, then you take a benefit*; e.g., *If a man has a tattoo, then he eats cassava*. A cheater in this condition is still one who takes the benefit (cassava) without paying the cost (tattoo), but in selection task terms, these are now the not-p, q values, the opposite of the standard logical indicative solution. Selection of not-p, q items had never been predicted before, but was produced by 70% of Cosmides' participants in this condition; close to zero did so with an indicative task.

This paper was followed by a host of experimental studies and theoretical discussions. These both divide into two categories: criticisms of or extensions to the social contract theory. An early critical study was reported by Manktelow and Over (1990; see also Cheng and Holyoak 1989), who devised a deontic but nonsocial contract version that still facilitated "logical" selection task responses. It concerned the behavior of nurses who were given the rule, *If you clear up spilt blood, then you must wear rubber gloves*. Cards showed the records of four nurses, with whether or not they cleared up spilled blood on one side and whether or not they had worn rubber gloves on the other. A violator of this rule is clearly one who clears up blood without wearing gloves, i.e., p, not-q, and three-quarters of the participants chose this pair of cards. But the rule is not one of social exchange: blood is not a

benefit for which gloves are the cost. Cosmides' response was to argue that this rule tapped into a different set of Darwinian algorithms, in this case a hazard management schema (Fiddick et al. 2000). Fiddick went on to produce converging evidence for such a schema, and its distinction from social exchange, using paradigms other than the selection task (e.g., Fiddick 2004).

Thus what started as a critical study was turned by social contract theorists into an extension. Further studies have also done this. Hiraishi and Hasegawa (2001) used the selection task to study "free riders" – cheaters, in other words – from a group perspective. Resources tend to be shared among in-group members, and denied to out-group members, in many social species, including humans. Two forms of violation, failure to share within the group and exploitation of the group's resources by nonmembers, should be detectable, and Hiraishi and Hasegawa found evidence, using a selection task with the target rule *If one receives a resource, one is an in-group member*, for both; the effect was strongest when out-group exploitation was in question. Similarly, Brown and Moore (2000), changing the focus from cheaters, used selection tasks to show that people are adept at detecting pure altruists: those who provide benefits to others but seek nothing in return.

An instinct for effective social contract reasoning implies something else: that it should appear early in child development, since its innateness makes it, at least to some degree, independent of experience. This hypothesis was strikingly confirmed by Cummins (1996). She derived the prediction not from social contract theory, but from another evolutionary concern: the construct of dominance hierarchies. She argued that there is an innate capacity for deontic reasoning based on what is permitted, prohibited, or obligated given one's position in a hierarchy. Adapting a modified, highly concrete version of the selection task introduced by Girotto et al. (1989), she presented it to children as young as 3. Instead of cards, these children were given materials consisting of a toy cat and toy mice, together with a mouse house. Some of the mice squeaked when squeezed, some did not. The children were told that the queen

mouse had laid down a rule because of the danger from the cat: *It is not safe outside for the squeaky mice, so all squeaky mice must stay in the house*. Which mice should be tested (squeezed) to see whether they were breaking the rule? Over two-thirds of the 3-year-olds correctly chose the ones outside the house, to see if they were squeakers.

Both the pragmatic reasoning schema theory and the social contract theory emphasized the cost-benefit relations inherent in the versions of the selection tasks they employed. Both theories are modular, especially so in the case of social contract theory, based as it is on the foundational construct of capacities that have evolved through time to enable adaptation to particular environmental contingencies. The distinction between social contract and hazard management explanations of responses to different task contents was an illustration of this modularity. However, cost-benefit relations are also fundamental to a non-modular theory: decision theory. This approach was adopted by Manktelow and Over (1991), who used it to predict not-p, q selections – something only ever previously predicted and observed by Cosmides with switched rules – with non-switched rules. Cheating, in Cosmides' terms, can be bi-directional: you can cheat someone, or they can cheat you. Manktelow and Over used the rule, *If you tidy your room, then you may go out to play*, said to have been spoken by a parent to a child. The effectiveness of such a rule depends on the subjective utilities (perceived benefits and costs) for each party and the parties' mutual understanding of them. The parent violates the rule when she does not let the child out even though he has tidied his room (p, not-q), but she also goes wrong when she lets him out even though he hasn't tidied up (not-p, q); the child violates the rule when he goes out without having tidied his room (not-p, q) and also when he does not go out even when he has (p, not-q). All four such patterns were observed in selection tasks.

Bi-directional violation of deontic rules is not the sole preserve of utility theorists: it was predicted by social contract theorists such as Gigerenzer and Hug (1992), who called it a social perspective effect, the name by which it came to be known. However, Gigerenzer and Hug tested

only two of the four possible cases outlined above, where the authority (the parent in the example; they used different contents) denies the benefit even though the cost has been paid and where the subordinate (the child) takes the benefit without paying the cost; these are the cases predicted by social contract theory. It is not clear how the theory would predict the other two cases, which appear to be instances of weakness or self-denial. Further utility-based studies have included probabilistic components in the materials, since decision theory is based on the notion of subjective expected utility, and this variable has also been found to have an effect (e.g., Kirby 1994; Manktelow et al. 1995). Once again, it is not clear how this would be predicted by any schema theory, evolutionarily based or not, since transgression would appear to be an all-or-none matter: an action is either taken or it is not; a precondition is either met or not met. Much of this and the ensuing debate was set out in a volume edited by Over (2003), which includes contributions from protagonists of all positions.

Conclusion

Periodic obituaries for the Wason selection task appear in the reasoning literature from time to time, often making two points: that it has been mined out now and that it was a slightly trivial task in the first place anyway (see, e.g., Cohen 1981; O'Brien 1995; Sperber et al. 1995 for examples from many years ago). Both objections are misplaced; reports of its demise have always, like Mark Twain's, proved an exaggeration. It has provided the base for serious theoretical advances in both evolutionary psychology and the psychology of reasoning and for 30 years of continuing experimentation and theoretical debate thereafter. And not just in this area; research in the 1970s was among the earliest to give rise to the now highly influential dual-system theory of thought, for instance (Kahneman 2011; Wason and Evans 1975; Wason and Johnson-Laird 1970). It is not the task itself but the uses to which it can be put that have been profitable to psychological research and that can be expected to continue to be so.

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Wason's Four-Card Problem

- [Wason \(1966\) Selection Task](#)

Wason's Selection Task

- [Wason \(1966\) Selection Task](#)

Waterspouts (Archerfish, Sharks, Rays)

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Synonyms

[Device](#); [Tool](#); [Utensil](#)

Definition

A tool is something that helps you gain an end.

Introduction

While fish have recently received a lot of attention in comparative cognition studies, studies on tool use in fish are still scarce (Balcombe 2016; Brown et al. 2011; Bshary and Brown 2014). A big principal problem when trying to manipulate objects in their environment is that fish are more limited in terms of body appendices they can use than most nonaquatic animals. With fins, which are usually not capable of grasping or holding an object, the mouth becomes to foremost contact and interaction point to the outside world. However, the density of the medium makes using the medium itself to manipulate or move objects much more efficient and possible than in a terrestrial environment. Still this leads to another obstacle one encounters in the study of tool use in its definition. If we stick to one of the classic definitions of tool use which is to modify one object or item or agent in order to achieve an effect on another (Beck 1980), then there are several compelling examples of tool use in fish. Thus, the use of water – by directing a waterspout at an object or a prey item – has thus been considered tool use by several authors.

Using Waterspouts as Tools

As the surrounding milieu of fish is much denser and heavier than the medium surrounding terrestrial animals, different types of manipulation of objects become easier or harder. While air puffs on land will be of limited success to move larger objects or a larger amount of material – e.g., clearing sand, waterspouts allow both for clearing spaces and moving objects and for predation. The most well-known example of the usage of waterspouts is certainly the archerfish. There is a multitude of studies showing the ability of this fish to use waterspouts to prey on arthropods outside the water. The fish can even be trained to use these waterspouts to shoot at specific targets in cognitive learning experiments (Newport et al. 2016).

But archerfish are not the only fish using waterspouts to achieve goals. Among many others, triggerfish and also wrasses use waterspouts to move or uncover previously hidden food items. The same has been observed in cartilaginous fish. Both rays and sharks blow water into sand to uncover hidden food items. So far the animals' ability to adapt this strategy to an experimental setup has been tested in freshwater stingrays (Kuba et al. 2010). In the first study on possible tool use in freshwater stingrays (Kuba et al. 2010), researchers showed that the rays can manipulate the surrounding milieu – water – to retrieve food from a tube-shaped testing apparatus. Interestingly they were more likely to use water suction than waterspouts to retrieve food from a pipe-shaped feeding apparatus. This was achieved by using both their disc-shaped body to cover one exit of the tube while performing undulating fin movements to create a flow through the pipe toward the moth. Once the animal was experienced in this procedure, it most likely combined this technique with sucking movements of the moth to achieve a fast retrieval of the food reward.

Using Innate Objects as Tools

A recent study on cod (Milot et al. 2014) claimed that fish, which learned to use a rope connected to a feeder, exhibited tool use. While this has been

debated, it is clear that the potential plasticity of the behavioral modification of fish behaviors deserves attention. Although, it might be that pulling the string may not be the equivalent to a classic lever pulling experiment, it is still remarkable that the fish do understand that there is a relationship between the manipulation of one object, a rope, and the arrival of food.

Some of the most compelling examples for tool use in fish show wrasses, a rather modern group of fish, using waterspouts to uncover food and then various hard surfaces to open the food (Bernardi 2012). In essence several studies showed that different species of wrasses pick up a clam hidden in the sand and transport them to a rock (anvil). They then smash the clam against the rock surface in order to break it (Coyer 1995; Jones et al. 2011; Pasko 2010).

Conclusion

With all these examples of tool use or proto-tool use, it seems fair to conclude that fish deserve more attention when it comes to comparative studies on cognitive behaviors and the evolution of intelligence. The difficulty of all these studies remains that tool use in fish is inherently different, as the potential body parts used to manipulate objects, primarily the mouth, differ from what we observe in terrestrial species. Additionally, holding an object in the mouth in order to produce food carries the distinct disadvantage that any object needs to be dropped before food can be consumed. In general we know far too little on object interaction and manipulation in fish. It would be of great interest to study tool use also in combination of exploration of novel objects and maybe even object play. Taking all this into account, the present examples provide a fascinating glimpse and an important starting point for further studies, both in the field and in the laboratory.

Cross-References

- [Evolution of Intelligence](#)
- [Play and Tool Use](#)

- [Primate Tool Use](#)
- [Tool Play](#)
- [Tool Use](#)

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Watson

- [Little Albert](#)

Wealth Reallocation

- [Redistribution Preferences and Low Socioeconomic Status](#)

Wealth Transfers

- [Redistribution Preferences and Low Socioeconomic Status](#)

Weaning

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Synonyms

[Gradually deprive of mother's milk](#)

Definition

Weaning begins the moment a child consumes a source of nutrients other than breastmilk. Weaning ends after the child consumes breastmilk for the last time. Weaning, then, can be defined as the process that occurs between this beginning and end.

Introduction

The weaning process may take many forms and vary greatly in length of time to complete. There are two distinct aspects of weaning: (a) weaning the child from the breast to other sources of nutrients and (b) weaning the child from the breast as a source of comfort and nurturance. These aspects can be challenging to disentangle during the weaning process.

Another question concerns whether a child is weaning from the breast or from breastmilk. When a mother cannot nurse her infant at her breast, she may express her milk and feed the child using a bottle. In these cases, weaning is concerned primarily with transferring the child to other sources of nutrients, possibly substituting infant formula for breastmilk in the bottle. Though a bottle also can be a source of comfort, it is not

considered breastfeeding and can be provided by someone other than the mother. The process of weaning a child from a bottle is not addressed here.

Process of Weaning

Weaning requires physical and psychological adjustments for both mother and child. For the child, other foods must replace the nutrition received in breastmilk. This is particularly challenging for younger infants, especially when access to nutritional foods is limited. In addition, the mother requires fewer calories after weaning and must adjust her diet accordingly.

From a psychological perspective, the mother-child dyad must find other means of soothing the child when needed. There may be a period of adjustment while this transition occurs. The mother may go through a personal transition when breastfeeding ends, sometimes involving a process of psychologically letting go of that unique period of the mother-child relationship and moving on to the next phase (Nelson 2006).

In addition, there are physical changes that occur for the mother when the child weans. The mother's breasts must return to a non-lactating state, requiring hormonal adjustments that may return the mother to a state of fertility (Kennedy 2005). Her experience of these changes depends upon the amount of milk being produced at the time of weaning, as well as how abruptly the weaning occurs.

Abrupt Weaning

Abrupt weaning happens suddenly and can be initiated either by the child or the mother. Abrupt weaning is difficult for both mother and child, physically and emotionally (Grueger 2013). It is rare for a child to initiate weaning abruptly, although there is a phenomenon known as a nursing strike, during which the child may refuse the breast. There are many possible reasons for such a strike, but it usually can be resolved and need not always signify the end of breastfeeding (Grueger 2013). A mother may need to wean suddenly due to unforeseen circumstances such

as illness or extreme difficulties in breastfeeding (Cooke et al. 2003; Grueger 2013). In either case, this will require other sources of nutrients and comfort for the child and will involve a potentially intense physical, hormonal, and psychological adjustment for the mother. The suddenness of this transition may lead to mastitis or other difficulties.

Gradual Weaning

Gradual weaning occurs over an extended time period. This is typically easier for both mother and child, as each has more time to adjust physically and psychologically to the transition. A child who is getting other nutritious foods and receiving comfort other than breastfeeding may simply breastfeed less frequently over time. This can happen naturally at a wide range of ages, most commonly between 2 and 4 years (Grueger 2013). The mother may initiate gradual weaning by emphasizing other food sources and providing other forms of comfort. Mothers may reduce the frequency of breastfeeding gradually, possibly using a schedule of feedings (Grueger 2013).

In situations of extended breastfeeding beyond 2 years, the experience of weaning may be somewhat different (Stearns 2011). Typically, the child is not breastfeeding as often, possibly only one to four times per day, and it may be primarily for comfort, such as when the child is tired, injured, or sick (Dettwyler 2004). Also, older children may get much of their nutrition from other sources. In these cases, weaning is less of a dietary transition and more of a transition in finding other means of comfort.

Timing of Weaning

As it is well-established that breastmilk provides superior nutrition and immune support for the child and health benefits to the mother (AAP 2012; WHO 2001), there are clear evolutionary advantages to the practice. It is less clear how long breastfeeding should continue. There are wide variations in the timing of weaning across cultures and historical periods. In some situations,

breastfeeding is an imperative upon which infant survival depends, while in others, breastfeeding is considered a voluntary decision (Nelson 2006). This variation, along with differences in cultural norms, personal beliefs, and maternal experiences of breastfeeding, causes a wide range in child age at time of weaning, from weaning at birth to weaning at age 7 years or beyond (Dettwyler 2004). The average age of weaning worldwide is 2.5 years (Kennedy 2005), but this average is misleading due to the many outliers, including many mothers who do not breastfeed at all (AAP 2012).

Current Recommendations

The American Academy of Pediatrics (AAP 2012) recommends exclusive breastfeeding (no other sources of nutrients) for the first 6 months of life. They further recommend continued breastfeeding while additional foods are introduced, until 1 year of age or longer, as desired by both mother and child (AAP 2012). The World Health Organization (2001) similarly recommends 6 months of exclusive breastfeeding followed by children receiving breastmilk and complementary foods up to 2 years or longer.

Historical and Cultural Variation

Ancient texts including both Koran and Bible recommend weaning at an average age of 2–3 years (Kennedy 2005). However, cultures vary widely. In the !Kung tribal culture, for example, infants nurse about four times per hour, delaying maternal fertility for several years, and wean at an average age of about 4 years (Kennedy 2005). In other cultures, the time of weaning may be influenced by many factors, including cultural beliefs about sex during breastfeeding, the form of maternal work, and the desired reproduction rate (Dettwyler 1995). Foraging cultures tend to wean slightly later than agricultural cultures (Kennedy 2005).

Especially in industrialized areas, the average age of weaning is earlier and does not match current recommendations (Karall et al. 2015; Nelson 2006). Some of this difference relates to

cultural views about breasts. While Western cultures view breasts as sexual organs, this is not true of most cultures, leading to varied beliefs about breastfeeding and weaning (Dettwyler 1995). In Mali, for example, breasts are viewed solely as feeding organs and are not covered (Dettwyler 1995). It is common to see these mothers breastfeeding in public places. Due to societal pressures, some mothers in Western cultures wean earlier than they would prefer (Stearns 2011). Others continue but hide their breastfeeding (Dettwyler 2004; Grueger 2013; Stearns 2011), leaving a misleading impression that extended breastfeeding is more unusual than it is.

In nonhuman species, weaning occurs as the juvenile becomes capable of finding its own sustenance independently (Kennedy 2005). In humans, children are weaned long before they can provide their own food. To remove the cultural biases regarding weaning, Dettwyler (2004) studied an array of variables in other primates that might suggest the natural time of weaning. For various primate species, weaning age can be predicted by variables including body weight attained, eruption of first molars, length of gestation, and age of first breeding for females. Considering these variables from a human perspective suggests a natural time of human weaning between 2.5 and 7 years (Dettwyler 2004).

Benefits of Early Weaning

There are many reasons a mother might wean before the recommended time. Common reasons are a sense of producing insufficient milk, low feelings of breastfeeding self-efficacy, and breastfeeding difficulties (Karall et al. 2015). Other reasons might include convenience for returning to work or resuming other duties, a preference to work toward a specific schedule, or a desire for more assistance with feeding. There are no documented benefits to the infant for early weaning, except in unusual circumstances in which breastfeeding would be unsafe due to infectious disease or specific medications or drugs (AAP 2012). With some diseases, the breastmilk

is still safe and can be expressed and fed with a bottle.

Benefits of Later Weaning

There are also many reasons a mother might wean later, including health benefits to the child, a desire for a close mother-child bond, and a sense of satisfaction in watching the infant thrive (Nelson 2006). Distinct health benefits have been demonstrated with longer breastfeeding. Exclusive breastfeeding for at least 6 months correlates with reduced gastrointestinal and respiratory infections in the child and delayed fertility for the mother (WHO 2001). Later weaning correlates with reduced risks of child allergies, leukemia, pneumonia, and obesity (AAP 2012). For the mother, increased cumulative time of breastfeeding is correlated with reduced risks of breast cancer, ovarian cancer, diabetes, rheumatoid arthritis, cardiovascular diseases, and postpartum depression (AAP 2012).

Evolutionary Perspective

Kennedy (2005) states that from an evolutionary perspective, the timing of weaning presents a dilemma. While later weaning increases the chances of offspring survival and improves the health of both mother and child, it also delays fertility, decreasing the potential for overall population growth. Pregnancies spaced closer together increase the number of offspring but correlate with reduced survival for both children, while later weaning allows the mother to focus on the needs of one child.

Dettwyler (1995) describes three main evolutionary benefits of breastfeeding which appear to favor later weaning. First, there are health benefits to both mother and child for the duration of breastfeeding, increasing the long-term survival rates of both. Second, hormones released during breastfeeding promote affectionate maternal feelings and facilitate nurturing behavior, increasing both child survival rates and the mother's likelihood to continue to nurse for a longer period. Finally, the delayed ovulation resulting from frequent breastfeeding increases the spacing between children, improving child and mother survival

rates, potentially increasing the number of the mother's children who will survive into adulthood.

Support for Breastfeeding and Weaning

Many mothers lack breastfeeding support due to lack of family and friends with breastfeeding experience, and this may lead to earlier weaning (Nelson 2006; Dettwyler 1995). For example, some mothers experience breastfeeding difficulties related to poor infant attachment to the breast (Cooke et al. 2003) or worry about insufficient milk production (Karall et al. 2015). Such problems may lead to early weaning but often can be rectified if mothers have adequate breastfeeding knowledge and support. Mothers also may need support during the weaning process.

If support is not available from family or friends, support can be found through lactation consultants, who are specialists in breastfeeding issues. In addition, free support can be obtained through La Leche League International, a worldwide mother-to-mother support organization. Finally, some pediatricians can be helpful, though not all have expertise in this area.

Conclusion

Just as breastfeeding is a personal journey for the mother and child, each experience of weaning is unique to the parent-child dyad (Nelson 2006). The process of weaning itself, as well as the physical and emotional experience of it, will vary dramatically based on a variety of factors that include personal and cultural factors, the age of the child, the frequency of breastfeeding, and the family dynamic. The timing of weaning is likewise varied, though from an evolutionary perspective, later weaning (at least 2.5 years) seems to favor longer survival of both mother and child. Interestingly, despite significant variation in age of weaning across culture and history, ancient texts suggest weaning at 2–3 years of age, which remains the average current weaning age worldwide.

Cross-References

- [Breast Feeding](#)
- [Breast Feeding and Mother-Infant Attachment](#)
- [Breast Milk Composition](#)
- [Duration of Breast Feeding in Ancestral Environments](#)

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Weaning and Maternal-Fetal Conflict

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Synonyms

[Nutritional independence](#); [To stop nursing](#)

Definition

The decrease in milk provisioning by a mother to her offspring; a young mammal's shift to nutritional independence in the form of food instead of mother's milk.

Introduction

Evolutionary conflict occurs when natural selection acts in opposing directions on different genes involved in an interaction (Burt and Trivers 2008). Conflict can be found at all levels of organization, from conflict between species to conflict between individuals within a species to conflict within an individual itself. Most of these forms of conflict revolve around competition for resources and differences in optimal resource allocation among individuals. Between genetic relatives, what is beneficial to one relative may not be beneficial, and may even be detrimental, to another. This situation occurs when there is an unequal probability that genes from one individual will be shared with another. For example, if a mother invests abundant resources in one child, it benefits both that child and, due to shared genes, the mother herself; however, it will detract from the mother's ability to invest in other offspring. From the maternal perspective, she shares half her genes with each of her children, so she benefits optimally from maximizing her reproductive output. However, from the perspective of any one child, there is a lower probability that a gene found in that child's genome will be present in other

siblings (although there is a 50 % probability that a maternal gene found in one sibling will be found in the other, the sibs may not be paternally related, thereby reducing their probability of genetic similarity) (Trivers 1974). Therefore there is an unequal benefit for the child relative to the mother when she allocates resources to any one child versus conserving resources for other potential offspring. These situations produce what is known as maternal-offspring conflict.

While the placenta is the only source of nutrient exchange throughout fetal development, the breast takes over as the primary source of nutrition after birth. This marks a power shift from the fetus (which is able to directly influence maternal biology in utero) to the mother, who is now better able to control the amount of investment she dedicates to each offspring. A major point of maternal-offspring conflict occurs at the time of weaning. It is in mother's best interest to wean early enough to fit in another reproductive event, while baby would gain more benefits from exclusive access to maternal care at a potential cost to future maternal sibs (Haig 2010). Weaning is an exemplary instance of this form of conflict: weaning allows mum to exit lactational amenorrhea (infertility during breastfeeding) and increase her likelihood of having another child, while it directly withdraws calories from baby forcing it to become nutritionally independent.

Weaning in Primates

Across primates the strongest behavioral examples of maternal rejection occur at the time of weaning. In a study of gelada baboons, maternal rejection was more frequent during feeding than at any other time, including socializing, moving, or resting. Furthermore, as the infant aged, feeding rejections increased steadily, while rejections during other activities stayed fairly consistent over time (Maestripieri 2002). From mum's perspective, nursing becomes more expensive as the nutritional demands of the offspring continue to increase. Furthermore, nursing an infant impedes a mother's ability to have another offspring (Haig 2014). At the same time, there is evidence across

mammals that prolonging nursing can have positive effects for the infant, including increased body weight, decreased parasite load, enhanced immune system, and decreased infant mortality (Mandalaywala et al. 2014).

Now that the baby is largely unable to interfere with maternal physiology, the biggest tool at its disposal is psychological. Immediately after birth the newborn mammal is completely dependent on mother for all nutritional needs. That being said, baby can perform certain behaviors to increase the likelihood of eliciting maternal care. These include making eye contact, smiling, and crying (Als 1977). In fact, crying and screaming have been correlated with increased time at the nipple across all age categories, showing that this is a fairly effective strategy for a hungry infant to employ (Maestripieri 2002). In Rhesus macaques once a mother has been experimentally separated from her offspring, the infant will cling to her upon her return, even in the face of more explicit maternal rejection (Trivers 1974). This appears to be a specific response to maternally initiated absences, since the same behavior is not seen if the infant is removed and the mother is left in the home cage. This suggests an adaptive response by the infant in response to cues of retracted maternal care. A variety of primate infants show behavioral regression after maternal rejection, including whimpering, ventral riding, and prolonged maternal contact; this behavior is intensified with the onset of maternal remating (Horvat and Kraemer 1982; Maestripieri 2002).

Time of Weaning in Humans

While the period of human childhood is typically much longer than in other primates, humans wean significantly earlier than most other great apes, and with some unique characteristics (Kennedy 2005). While human mothers tend to wean infants off the breast at around 2 years, there is a prolonged period of nutritional dependency that can last for the next 15 years or more, whereby the offspring is still largely dependent on maternal or allomaternal food provisioning (Van Noordwijk et al. 2013). One explanation for this phenomenon involves maternal-offspring conflict: early

weaning is a maternal strategy to increase maternal fitness at a cost to offspring fitness, while increased offspring demands via an extended period of nutritional dependency increase the offspring's fitness at a cost to the mother (Haig 2010). Support for this hypothesis can be found in our genes. While genes found in the mother have a 50 % chance of being found in this and future offspring, this probability is lower for genes found in the father. Over evolutionary time this has resulted in differential expression of certain paternally and maternally inherited genes in a way that reflects this inequality. Evidence of this can be found in various paternally expressed (maternally silenced) genes, which favor increased and more intense suckling (Haig and Wharton 2003). Maternally expressed genes, on the other hand, seem to favor earlier maturation (Haig 2010). It has been theorized that this allows human mothers to decrease their interbirth intervals (IBI) more than other great ape mothers can, resulting in overlapping generations of offspring (Haig 2010). That is to say, a human mother can have two children (one on the breast and one who is weaned but remains nutritionally dependent) in the same amount of time as it takes other great apes to wean a single offspring (Kennedy 2005). However, this decreased IBI comes at a cost to the first offspring, who now has to share maternal resources with a new baby (Haig 2014). It appears that human babies may have adapted some particular defenses in response. Human infants that are breast fed appear to cry more during the night than infants who are weaned or formula fed, even in cultures where mothers and baby sleep in the same bed (Haig 2014). Since they are receiving the same number of calories, it is likely that the cause of this sleep disruption is not due to hunger, but rather because natural selection has favored babies who are better able to delay conception of a new sibling through suppressed ovarian function and increased maternal fatigue.

Conclusion

Nursing is an important part of mother-offspring bonding and a necessity for the survival of primate infants. However, the costs and benefits of

prolonged nursing are different from the perspective of the mother and the child. Over time, this has resulted in a tug-of-war, with adaptations in mothers for reduced nursing costs and earlier weaning and adaptations in offspring for increased breast milk availability. In humans, this has been extended to reflect the decreased IBIs and overlapping generations present in human families.

Cross-References

- [Maternal-Fetal Conflict](#)
- [Parent-Offspring Conflict](#)

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Weaning Conflict

- ▶ [Parent-Offspring Conflict](#)

Web-Based Questionnaire

- ▶ [Online Survey](#)

Web-Based Survey

- ▶ [Online Survey](#)

Wechsler Adult Intelligence Scale

- ▶ [Intelligence Testing](#)

Wechsler Intelligence Scale

- ▶ [Intelligence Testing](#)

Wechsler Intelligence Scale for Children

- ▶ [Intelligence Testing](#)

Wechsler Preschool and Primary Scale of Intelligence

- ▶ [Intelligence Testing](#)

Wechsler-Bellevue Intelligence Scale

- ▶ [Intelligence Testing](#)

Wedding Rings

- ▶ [Engagement Rings as Modern Commitment Cue](#)

Weeping

- ▶ [Crying](#)

Weight

- ▶ [Attractiveness and Anger-Proneness](#)

Welfare

- ▶ [Measuring Well-Being](#)
- ▶ [Physical Health](#)

Wellbeing

- ▶ [Physical Health](#)

Well-Being

- ▶ [Social Media](#)

Well-Liked

- ▶ [Popular Children](#)

Wellness

► Measuring Well-Being

Westermarck Effect

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Synonyms

Incest aversion; Kin-recognition; Negative sexual imprinting

Definition

The decreased sexual interest between individuals who have co-resided in childhood.

Introduction

In his seminal book, *The History of Human Marriage* (1891), the Finnish sociologist and philosopher Edward Alexander Westermarck provided an evolutionary explanation for the evident lack of sexual interest between close kin. Deeply inspired by both Charles Darwin and Alfred Russel Wallace, Westermarck, who was looking to solve the question regarding the cross-cultural incest taboo, proposed that “there is an innate aversion to sexual intercourse between persons living very closely together from early youth, and that, as such persons are in most cases related, this feeling displays itself as a horror of intercourse between near kin” (Westermarck 1891, p. 321). Westermarck further argued that during the course of evolution, innate aversion had developed through natural selection: “[T]his instinct developed through natural selection. We cannot

give away to carnal love with those [...] to whom we generally stand as siblings, parents, or children; since each such passion must have gone extinct in our species’ childhood through the increased mortality to which offspring from closely related parents are subjected” (Westermarck 2014, p. 151). In sum, Westermarck proposed that early co-residence played a functional role, causing siblings – or more precisely, any children reared in sibling-like conditions – to not experience sexual desire for one another in adulthood and that this phenomenon was the result of natural selection against the detrimental reproductive effects of inbreeding.

Westermarck’s idea was received with great and immediate interest among his contemporary scholars. The famous anthropologist Sir Edward Burnett Tylor wrote a letter to Westermarck saying that “I should not be surprised to find [your explanation] or something like it the real solution.” Wallace noted the “ingenious and philosophical explanation of the repugnance to marriage between near relatives,” and wrote Westermarck saying “I think you have solved the problem” (Wolf 2014).

Only a few decades later, a number of scholars, among these, most famously Sigmund Freud, furiously criticized Westermarck’s explanation, without ever empirically testing its validity. Westermarck’s critics argued that the moral rules prohibiting incest were themselves evidence against his proposition of an innate aversion. Instead, they claimed that the origins of incest taboos exist because humans have incestuous urges that need to be repressed by moral rules (e.g., Wolf 2014). Although he defended his position with ingenious arguments, the result was that Westermarck’s theory about the natural origins of the human incest aversion lost popularity. But also Freud’s influence in psychology waned over time, and a renewed interest in the so-called Westermarck effect came to be an integral part during the rise of sociobiology in the 1960s and the rise of evolutionary psychology in the 1980s. Only now, eight decades after Westermarck had presented his idea, was evidence gathered to test whether Westermarck was right or wrong.

Empirical Tests of the Westermarck Effect

Anthropological data have been used to test the effects of early co-residence on later attraction. In nineteenth-century Taiwan, young girls were often adopted into a new family and raised together with the family's son, who would become their future husband. Comparing the outcomes of these marriages to other arranged marriages in a series of ground-breaking studies, Arthur Wolf found that in marriages between individuals with co-residence during childhood the fertility rates were decreased and divorce rates were increased. After controlling for several factors, such as health differences between the adopted and nonadopted brides, he concluded that only the spouses' shared childhood residence could explain this difference. In Israeli *kibbutzim*, unrelated children of the community are raised together. Studying individuals raised in this context, it has been found that marriages and romantic relationships are uncommon between individuals who have been raised in the same peer group (e.g., Talmon 1964), also indicating that co-residence in childhood decreases attraction between unrelated individuals. Similar findings have also been presented in studies on *bint'amm* marriages in Lebanon and Morocco.

More recently, Bevc and Silverman (1993) investigated how early co-residence between siblings influenced the probability of incestuous behavior. Here, individuals reporting incestuous behavior were compared to a control group. Incestuous behavior between two siblings, including vaginal intercourse, was associated with decreased early childhood co-residence. In a follow-up study, the same research group categorized a sample of siblings into three groups based on incestuous sexual behavior during adolescence: One group included siblings reporting attempted or completed incestuous genital intercourse; the second group included siblings reporting other incestuous sexual activities; and the third group included siblings reporting no incestuous sexual activities. The results from this study were coherent with earlier results. About 30% of the siblings reporting attempted or

completed genital intercourse had been raised separately for more than a year, whereas the rate of co-residence was much higher in the two other groups.

More indirectly, studies also suggest that individuals growing up with a opposite-sex sibling reacts with more aversion to descriptions of third-party incest (e.g., Lieberman et al. 2003), and that incest between siblings who have co-resided during childhood is perceived as more disgusting than incest between siblings who have not lived together during childhood (Antfolk et al. 2012). In addition to research employing anthropological data and self-report methods, De Smet et al. (2014) studied females' psychophysiological responses to imaginary sexual activity with either their brother or partner and found a stronger disgust reaction associated with the duration of living in close proximity to their brothers, further providing supporting of an Westermarck effect.

Taken together, the results of these studies indicate that co-residence in childhood is indeed associated with decreased sexual interest between two individuals in adulthood. It should also be noted that although the Westermarck effect has received a great deal of empirical supports, it seems clear that co-residence during childhood does not fully explain the why's and how's of human inbreeding avoidance. It is unclear whether it can account for the socio-normative incest taboo Westermarck initially wanted to explain, that it does not seem to explain incest avoidance between parents and their children, and that it is only part of the explanation for incest avoidance between siblings. Moreover, the Westermarck effect is not specifically regulating incest aversion.

Other Kin-Recognition Cues and the Proximate Regulation of Incest Aversion

The Westermarck effect is usually taken to describe a specific mechanism responsible for the general lack of sexual interest between close kin, but co-residence in childhood seems, more generally, to be a kin-recognition cue among

others regulating also other types of social behavior, such as altruistic investment in siblings. While co-residence has been shown to function as a reliable kin-recognition cue, Lieberman et al. (2007) found that its effect is moderated by birth order. In fact, co-residence was associated with altruistic dispositions and incest aversion only when considering behavior towards an older sibling. Older siblings, who can see their own mother gestating and caring for a younger individual, can use this presumably more valid kin-identification cue when considering behavior towards a younger sibling (Lieberman et al. 2007). More recently, a study by Lieberman and Billingsley (2016) showed that the effects of co-residence might in fact be due to the effects of shared parental investment. As biological parents are more likely to use resources on genetically related children than other children, witnessing one's own parents investing in another child might serve as a primal cue, being tightly correlated with co-residence.

Conclusion

Quite irrespective of the extent to which Westermarck was right or wrong, the Westermarck effect is likely one of the well-known examples of evolutionary reasoning in psychology. For this reason, Westermarck himself continues to be a central figure in the history of evolutionary psychology. The vast literature on kin identification is greatly indebted to Westermarck's early proposition, stating that co-residence in childhood decreases sexual interest between individuals in adulthood.

Cross-References

- [Co-residence and Early Maternal Perinatal Association](#)

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Westermarck Effect and Imprinting

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Synonyms

[Inbreeding avoidance](#); [Incest avoidance](#); [Negative sexual imprinting](#); [Westermarck's hypothesis](#)

Definition

A hypothetical psychological effect through which sexual attraction becomes less between people who live in close domestic proximity during the first few years of their lives.

Introduction

Widely applied by evolutionary researchers to the explanation for human incest avoidance, Westermarck effect hypothesized that human tend to develop a strong sexual aversion to those they live closely with during infancy and early childhood. This hypothesis was first proposed by Finnish anthropologist Edvard Westermarck in his book *The History of Human Marriage* (1891), described as a mechanism of inbreeding avoidance.

Westermarck effect is also called negative sexual imprinting, in contrast to positive sexual imprinting. Quite a few evidences have shown the rationality of the Westermarck effect.

The Evolutionary Function of Inbreeding Avoidance

It was hypothesized by Westermarck that humans spontaneously developed a sexual aversion toward individuals they have lived together during childhood (Westermarck 1891, 1934). The hypothesis proposed that inbreeding avoidance might be the result of an evolutionary mechanism instead of a kind of social rule. As concluded by biological perspective, inbreeding can lead to inbreeding depression, which reduces the biological fitness in a given population. Reduced offspring number, lowered growth rate, and corrupted immunity are found related to inbreeding, both in animals and humans (e.g., Keller and Waller 2002). Therefore, an instinctual mechanism to avoid inbreeding is necessary in the process of evolution. Evidence from animals such as female pilot whales (Amos et al. 1993) showed a tendency that individuals would avoid mating with those raised in the same peer or family group, which empirically supported the Westermarck effect or the existence of negative sexual imprinting.

Evidence for Westermarck Effect in Humans

Anthropological and ethnographic studies have paid much attention to Westermarck effect in different cultures and places. One of the best known examples is the Israeli kibbutz system (collective farms), in which children were reared communally in peer groups. Shepherd (1971) found that out of 3000 marriages occurred across the kibbutz system, only 14 were between children from the same peer group. Of those 14, none had been reared together during the first 6 years of life, indicating the possible critical period of Westermarck effect.

Another series of studies focused on the Chinese shim-pua marriage, a tradition of arranged marriage. Shim-pua marriage was a kind of marriage in which a family would adopt a preadolescent daughter as a future bride for their preadolescent son in some areas in premodern China, and the future husbands and wives would be raised together. Research showed that shim-pua marriage were more likely to result in higher rates of divorce and lower fertility rates (Wolf 1995), supporting the hypothesis that individuals who had a history of early childhood experience together may be averse to marriage as adults.

Recent studies tend to examine the Westermarck effect by survey research or in laboratory settings. Data collected by survey showed that separation for at least 1 year during childhood may increase incestuous behavior between siblings (Bevc and Silman 2000). By testing participants' attitude toward sibling incest rather than asking their own experience, research showed that childhood co-residence with an opposite-sex individual predicted the strength of moral sentiments regarding sibling incest (e.g., Lieberman et al. 2003). In an experimental study, participants rated their preference for morphed faces, and results suggested that female participants rated morphed faces that resemble their opposite-sex siblings significantly lower than average faces. However, male participants showed an opposite pattern that similarity to sibling increased perceived attractiveness (Marcinkowska et al. 2013). Psychophysiological techniques were used to test participants' aversion to imagination of sibling incest in a recent study. Results showed

that indicators such as duration of co-residence with a brother of female participants predicted activity of facial muscles related to a disgust expression (De Smet et al. 2014).

Nevertheless, the existing empirical results thought to be supportive evidence for Westermarck effect also have some limitations. For example, in interviews when asking participants the experience about sibling relationship and sibling incest, participants might try to please the interviewer by exaggerating or narrowing down some details, especially when it comes to sexual issues. Similarly, such limitation can be found in self-report survey researches as well. Furthermore, having incest experience does not equal to not being aversive to incestuous behavior. Other factors may also lead to sibling incest. Thus, childhood association between opposite-sex siblings may not be the only predictor of incestuous behavior. Another aspect that has received little attention is the interaction between positive imprinting and negative imprinting (Westermarck effect), both of which seem to influence the mate preference of animals and humans (Rantala and Marcinkowska 2011).

Conclusion

Altogether, over the past century, ethological, anthropological, and psychological approaches have made great attempts to examine Westermarck's hypothesis of the mechanism of incest avoidance, which can be also described as negative sexual imprinting mainly on siblings. Although some of the results received much critics, which put doubt on the methodology of research or the generalization of the findings, the existing studies still contain great value and may give insights to the research field of both sexual imprinting and Westermarck effect.

Cross-References

- [Imprinting](#)
- [Incest Avoidance](#)

- [Intersexual Selection](#)
- [Mate Preferences](#)
- [Parental Investment And Sexual Selection](#)
- [Sexual Imprinting](#)

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Westermarck's Hypothesis

- [Westermarck Effect and Imprinting](#)

Western Europe

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Synonyms

Europe; Iberian Peninsula; Modern-day European Union

Definition

The part of Europe that loosely includes modern-day France, Germany, Spain, Portugal, and Italy.

Introduction

The first time we see evidence of anatomically modern humans at all is in Africa, about 200,000 years ago. It is a well-respected idea that after they emerged as *Homo sapiens*, or anatomically modern humans, they began migrating up toward Asia, Europe, and the Middle East, likely between 60,000 and 40,000 years ago. However, it is still unclear or whether or not it happened all at once or when the migration may have ended (Eriksson et al. 2012; Hublin 2012; Stringer 2000). Patterns of tool dispersal across Europe and the differences between these tools suggest that there were at least two different migrations of humans into Europe, both with slightly differing characteristics when it came to their material cultures (Hoffecker 2009; Mellars 2006).

In an effort to understand the environment into which modern humans were moving, we can paint the picture of Western Europe during the Marine Isotope Stage 3 (MIS 3, about 60,000–40,000 years ago) as different from what we see today in a variety of ways. MIS 3 was a period of climatic change in Europe between about 60,000 and 30,000 years ago. The environmental changes of the period were characterized

by harsh cold, and large variation in climate, making it difficult for large mammals to adapt, even for fauna that were already considerably “cold-adapted.” Indeed, increases in snowfall would have increased the aridity of the area overall (Bocquet-Appel and Demars 2000). Research illustrating decreases and extinction in other faunal populations helps support evidence that indicates that the environment would have been severely impoverished and likely hard to survive in (Stewart 2007); however, we know that humans do so for several thousand years.

This essay looks more specifically at the migration of humans into Western Europe, examining paths they may have taken, evidence for their presence in sites between Africa and Europe, and hypothesizing what they may have done once they were there (Nigst et al. 2014).

Migration Patterns

According to Bocquet-Appel and Demars (2000), the first appearance of modern humans occurs between 40,000 and 37,000 years ago, around Danube River. By 35,000 years ago, settlements appear all over Eastern Europe and, for the next 2000 years or so, start to creep westward. All of Europe appears to be colonized by modern humans by at least 27,000 years ago (Bocquet-Appel and Demars 2000). The authors note that this final piece of colonization, which appeared in the Iberian Peninsula, was much slower than colonization up until that point. They hypothesize that this could have been due to the presence of Neanderthals, or the harsh environmental circumstances just north of the peninsula. It is possible that humans migrated upward via the Great North European Plain (Bocquet-Appel and Demars 2000).

Evidence for Human Populations

There are three types of technologies characteristic of the era when modern humans were populating Europe. The Aurignacian describes a period of

cultural artifacts that are dated to be between 50,000 and 30,000 years ago, appearing mainly in Eurasia. These artifacts help illustrate the culture of the hominins that produced them, as well as shed light on their cognitive development, especially since the tools from this period are frequently compared with earlier periods of tool development. Aurignacian tools are very specifically associated with modern humans (Nigst et al. 2014; Hublin 2012).

Additionally, a period known as the Protoaurignacian includes small blades and projectiles that are characteristically different from the Aurignacian in the style through which they are made. There is sometimes controversy around when the Protoaurignacian period occurred with respect to the Aurignacian; however some researchers have argued that they may have overlapped and simply indicate different technologies that modern humans produced after they split and took different paths into Europe, with the Protoaurignacian occurring along the southern route and the Aurignacian occurring along the one more Northern (Nigst et al. 2014; Hublin 2012).

Finally, the Bohunician period is one characterized by tools that have been found in areas like Bulgaria and the Czech Republic. The tools here are considered similar to levallois technology (an earlier style of toolmaking for hominins), usually featuring a blade for cutting or scraping. Like most tools, there is a “core” of rock off of which pieces are flaked to create the necessary implement. These tools are usually made of flint (Hoffecker 2009; Richter et al. 2010).

One difficulty is that human remains from the time when they likely colonized Europe are rare. We frequently can only use the remains technologies to represent areas where these first nomadic humans lived, since we can date their creation to the approximate time when humans migrated (Nigst et al. 2008). Fossil remains of Aurignacian tools and artifacts can help map where and how modern human populations migrated. By tracing sites across Europe, we can get an idea of the paths that humans took out of Africa and where they may have settled along the way. Aurignacian artifacts are especially useful because they are so closely associated with modern human behavior

(Nigst et al. 2008). Their remains show us paths that move around the Eastern coast of the Mediterranean Sea, and then diverge slightly, with one moving in to Europe further north of the other; however both do move in to Western Europe between about 36,000 and 40,000 years ago (Mellars 2000).

The similarities between artifacts found at the sites that trace these paths indicate that these technologies originated at the earlier sites along the paths and were transferred geographically as the human troops migrated (Mellars 2000). However, there does appear to be some discrepancies between the technologies found at sites along each path after they diverged, suggesting that it wasn't until after these paths diverged that each group developed the unique technologies they then left behind to be found thousands of years later. It is also possible that a second wave of anatomically modern humans occurred around 45,000 years ago and could have been responsible for the slight variation in technologies seen at some sites (Hoffecker 2009; Mellars 2006).

Researchers will usually date objects by testing levels of radioactive isotopes in carbon-14, a material found in organic objects, while this method has its flaws, recent technological advancements have worked to make it more precise (Hublin 2012).

Evidence from the site known as Willendorf II, in Danube valley region of Austria, features evidence that can provide a stopping point for humans during their migration. A series of blades that were found exhibit two different tool-making procedures, both of which are very highly associated with the Aurignacian period and some associated with the Bohunician (Hoffecker 2009). Both involve removing chips of stone off a central “core,” in such a way as to produce an edge that can be used for scraping or cutting materials. Other tools and artifacts found have been analyzed and compared and are very likely to be from this period as well, supporting the idea that there was a modern human settlement here (Nigst et al. 2014).

The authors discussed the findings and how they related to the whole picture of human migration into Europe. The evidence suggests that there

was a human presence in central Europe around 43,000 years ago. Faunal remains that have been analyzed suggest that the environment at this time was likely a cold steppe environment. However, the presence of trees and the proximity to Danube River would have likely created a varied area, somewhat ideal for settling. It is important to remember that these modern humans will likely have come from an environment much warmer than the ones in Europe, meaning that they would have needed to quickly adapt to the colder temperatures through things like increased clothing, in order to survive (Nigst et al. 2014).

Another dating method takes advantage of a large volcanic eruption which was said to have occurred around 39,300 years ago, in Italy. The resulting ash deposits from this seismic event are relatively easy to trace and allow archaeologists to more accurately date objects (Hoffecker 2009; Hublin 2012). Aurignacian artifacts have been found that clearly originate before this eruption, indicating that there were likely modern humans in Europe prior to this time.

Some of the earliest human sites in Bulgaria, the Czech Republic, and Poland include various tools from the Bohunician period, as well as some human remains dated to about 48,000 years ago. Tools included blades, human ornamentation, and modified blades. While there is little evidence of Bohunician technology in Western Europe, artifacts found in Spain and Italy are dated to come from a similar period between 44,000 and 42,000 years ago; however these artifacts tend to fall into the category of Protoaurignacian. Evidence has also been found for Aurignacian remains in parts of Germany (Hoffecker 2009). It is supposed that the dispersal of these sites and artifacts is representative of movement in a south-westerly direction toward the Iberian Peninsula (Banks et al. 2008).

As rare as it is, parts of a fully modern human skeleton were found in what is now Lebanon, hypothesized to be from around 47,000 years ago. Additionally, findings of beads, tools, and bone artifacts in areas like Turkey, Bulgaria, and Moravia, in the Czech Republic, suggest that there may have been human populations in Europe as early as 50,000 years ago. This may be a better

representation of human colonization, especially since this likely happened in small groups, creating isolated human populations scattered across Europe (Hublin 2012).

Modern Human Interactions in Europe

Bocquet-Appel and Demars (2000) also point out that coexistence between Neanderthals and modern humans can be hard to determine because it would have to be established that both populations were living in the same place at the same time, which can be difficult to pinpoint. Additionally, even once this has been established, it can be difficult to examine the degree to which the two populations would have interacted. While we do have evidence that they did interbreed at some point after modern humans came to Europe (Hoffecker 2009; Stewart 2015), there is still a lot we don't know yet.

Despite this, there is evidence that suggests that as the modern humans moved into Western Europe, they "followed" Neanderthal populations that were moving further south into areas like the Iberian Peninsula, possibly searching for warmer climates (Banks et al. 2008; Mellars 2004). Additionally, more recent evidence does suggest that Neanderthal DNA makes up a fraction of the human genome, especially for those whose origins are in Western Europe (Mellars 1996; Smith 2013). This is very convincing evidence that when modern humans arrived in Western Europe, they were interacting, and breeding, with Neanderthal populations (Stewart 2013).

Evidence of modern human expansion remains in our DNA (Eriksson et al. 2012); however it doesn't appear to be any fossilized remains that can represent an intermediary hominin between humans and Neanderthals in Western Europe, making the understanding of human behavior in Western Europe somewhat more difficult than it is in other areas (Tuttle 1985). We see evidence for Neanderthal genes in our DNA today, so even if we have yet to find this human-Neanderthal hybrid, we do have pretty solid evidence that there was interbreeding (Stewart 2013).

Conclusion

Overall, it appears as though most of the evidence suggests that modern humans were migrating out of Africa between 80,000 and 40,000 years ago and that they were likely not settled in Western Europe until between 30,000 and 40,000 years ago (Mellars 2000; Bocquet-Appel and Demars 2000). The colonized areas of Western Europe appear to be a bit scattered; however by around 33,000 years ago, the populations have grown and are connected enough to be considered a full population area (Bocquet-Appel and Demars 2000). And by around 30,000 years ago, *Homo sapiens* had conquered all of Europe and were its sole inhabitants, for the most part.

It is considered a great feat that the modern human populations were able to colonize Europe despite having evolved in a completely different environment, suggesting that they possessed other skills that allowed them to adapt to the harsh cold of Western Europe. The population size of these human groups as they moved in to Europe was likely relatively small; however it is possible that they had the distinct capability to colonize. There is vast evidence to suggest that modern human populations were producing advanced technologies while still in Africa (Mellars 2000). Their heightened cognitive abilities associated with symbolic thinking, through body adornments, language, and certain technologies, may have made it easy for them to conquer foreign lands (Hoffecker 2009).

Cross-References

► Neanderthals and Humans

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Western Perspectives on Death

► Death in Christianity

Wet-Nursing

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Definition

The suckling of another woman's child.

Introduction

Wet-nursing is an ancient, cultural practice in which infants are breastfed by women other than their mother. Among its multitude of social, economic, biological, and religious benefits, wet-nursing has three, primary evolutionary significances: optimization of lactational beneficiaries, logical resource provisioning, and increased community altruism.

History of Wet-Nursing

Wet-nursing dates back to 3000 BC. Occurring first in Ancient Egypt, wet-nursing was seen as the only alternative to a mother's inability to lactate. Without human milk, and with no known human milk substitutes, an ancient Egyptian child was destined for death. Wet-nurses were therefore perceived as saviors. Years later, in Ancient Rome, wet-nurses were often used to nurse unwanted children that had been thrown onto heaps of rubbish. Others utilized the services of wet-nurses to inexpensively nurse the children of slaves in order to cheaply propagate one's supply of labor (Fildes 1988).

The voluntary use of wet-nurses was first protested in the Middle Ages. At that time, "society regarded childhood as a special time of fragility" (Stevens et al. 2009). Newborns were perceived as vulnerable to the "magical properties" of breast milk that differed from their mother's. The notion that "breast milk could transmit both physical and psychological characteristics of a wet nurse"

(Stevens et al. 2009) scared parents into thinking that wet-nursed children would imbibe qualities of the lower class. As a result, the hiring of wet-nurses declined.

Despite the multitude of objections, wet-nursing remained a popular industry during the Renaissance period. Considered a highly organized and well-paid profession, wet-nursing was a source of income for many poor women. Women of the lower classes often became pregnant, got rid of their child, and then sought employment as a wet-nurse. Employment as a wet-nurse had two benefits: a reliable source of income and a means of contraception (lactation prevents ovulation). Poor women of the time were able to feed their families while, simultaneously, ensuring that their familial costs (e.g., the addition of a child) would not grow. With so much popularity, wet-nursing became highly regulated by governmental organizations (Stevens et al. 2009).

The aristocracy dictated breastfeeding practices during the sixteenth and seventeenth centuries. Women of the upper class refused to breastfeed for fear that it was unfashionable and would ruin their figures. Such social pressures prompted the majority of aristocratic women to hire wet-nurses. In fact, French governmental records indicate that, in 1780, only 1000 of 21,000 babies were nursed by their mother (Hrdy 1995).

In the eighteenth and nineteenth centuries, wet-nursing was utilized by members of lower classes more so than upper classes. Increased costs of living and lowered wages during the Industrial Revolution prompted many women to seek additional sources of revenue. Wet-nursing became such a source. Wet-nurses enabled two women to be employed at the same time: one woman was employed by a mother and a mother was employed in a factory setting. Wet-nursing at the time also functioned as a way of lowering infant mortality rates as wet-nursed infants were shipped out of urban metropolises, sites of squalor and disease, to rural peasants.

Although wet-nursing continued to exist at the end of the eighteenth century, through the nineteenth century, and even today, its popularity has diminished. A 1779 work, entitled *Domestic*

Medicine, “displayed an open distrust of wet nurses and their use of home remedies” (Stevens et al. 2009) and advised many women to, once again, breastfeed their own children. Attention was drawn to a wet-nurse’s use of opiates, as a means of quieting children, in the eighteenth century and further prompted the usage of wet-nurses to decline. The incidence of wet-nursing reached its lowest point in the nineteenth century, when artificial feeding became a feasible substitute for breastfeeding. With advances in bottle-feeding and the availability of nutritious and infant-friendly animal milk, the use of wet-nurses continued to decline. By 1900, with the exception of few cultures, the wet-nursing profession was nearly extinct (Stevens et al. 2009).

Optimization of Lactational Beneficiaries

The wet-nursing process may optimize the biological benefits of breastfeeding for both the feeder and infant. Mothers who either lost or discarded their children prior to weaning are able to elicit the same lactational benefits from feeding another child. Furthermore, children who have either lost their mothers before weaning or have mothers unable or unwilling to lactate are still able to gain the nutritional and immunological properties of breast milk. By optimizing the number of lactational beneficiaries, wet-nursing may be viewed as a cultural strategy with significant evolutionary advantages.

Benefits for the Child

Due to the advent of bipedalism, a 4.2 million year-old evolutionary adaptation that narrowed the hominin birth canal, the majority of neonatal neurological development occurs postpartum in order to prevent obstructed labor and reduce maternal mortality. As a result, at birth, the human infant is only born with 25% of its cranial development. Long-chain polyunsaturated fatty acids (LCPFAs), primarily docosahexaenoic acid and arachidonic acid, present in human milk,

correct such cognitive deficits and enable an incremental increase in cognitive development that is proportional to nursing duration. In addition to aiding the development of neurological functions, breastfeeding has been shown to decrease an infant’s risk of type 2 diabetes, obesity, coronary artery disease, gastrointestinal diseases, upper respiratory illnesses, and atherosclerosis (Orlando 1995).

Breast milk also acts to strengthen an infant’s poorly developed immune system. In order to gain immunity from their pathogenic surroundings, infants utilize colostrum, a maternal, mammary gland excretion that is rich in immune factors (Orlando 1995). Unlike bovine milk and milk substitutes, colostrum transfers maternal immunity to environmental-specific pathogens to the infant. Breastfed babies are rich in secretory IgA, IgG, lactoferrin, lactoperoxidase, and lysozymes, compared to their bottle-fed counterparts, and thus have stronger immune systems and lesser mortality rates (Trevathan 2010).

Breastfeeding offers more to the infant than just nutritional and immunological benefits. Cholecystokinin, a hormone, is found in breast milk and acts as a sleep inducer upon consumption. Some argue that breast milk lowers an infant’s levels of bilirubin, a waste product of red blood cell destruction, and thus lowers the probability of newborn jaundice (Stuart-Macadam and Dettwyler 1995).

Benefits for the Breastfeeding Woman

During suckling, oxytocin is released into the bloodstream of the feeder. This repeated release of oxytocin and associated endorphins promote mother-infant attachment, lower blood pressure, decrease cortisol levels, increase withdrawal latency, and increase release of vagally controlled gastrointestinal hormones. Together, these actions cause antistress effects in the feeder (Uvnäs-Moberg 1998).

Breastfeeding may also decrease a feeder’s risk of breast, endometrial, and ovarian cancers (Ma et al. 2006; Heinig 2001). It, too, may reduce the frequency of heart attacks in the feeder.

Prolonged lactation is associated with a decreased prevalence of type 2 diabetes. Further research has suggested that breastfeeding may reduce the severity of anemia, bladder and other infections, and spinal and hip fracture after menopause (Labbok 2001).

Logical Resource Provisioning

Wet-nursing may also be understood as a means of increasing the proportion of economically prosperous individuals in a society and, from another standpoint, the number of individuals capable of receiving successful parental investment. History has indicated that the majority of wet-nurses was employed by financially stable families and, were, themselves, from financially unstable families. When such wealthy mothers delegated breastfeeding responsibilities to poorer women, they effectively altered the fecundity of the population. By paying another woman to breastfeed her child, a mother did not experience the ovulatory-suppressing consequences of lactation and could thus have more children in shorter birth intervals. The wet-nurse, on the other hand, inhibited her ovulatory hormones and thus could not give birth. The high demand of wet-nurses forced many women to constantly feed and thereby extend the duration of their reproductive inability (Hrdy 1999). Since wealthy women hired wet-nurses, wealthy women were able to contribute more offspring to the population than were poorer women. In addition, since such women possessed financial, medical, and agricultural resources, scarce commodities at the time, their many sires received high levels of parental investment and had a lesser probability of early morbidity and disease. In such a sense, wet-nursing ensured that those capable of investing in their offspring were able to reproduce at a greater and more successful rate. In a highly socioeconomically stratified era, wet-nursing, theoretically, guaranteed that resources were provisioned in a logical manner: those with the most resources had the most offspring whereas those with the fewest resources were able to conserve their wealth and distribute it to fewer offspring.

This notion proves that wet-nursing had evolutionary advantages.

Increased Community Altruism

Wet-nursing establishes the notion of milk kin and thereby affects resource provisioning within a community. According to Hamilton's rule, resources are altruistically distributed using the formula, $C < Br$, where "C" equals the cost to the helper, "B" equals the benefit to the helped, and "r" indicates the degree of relatedness between both parties. An individual should be evolutionarily inclined to help someone if the imposed cost is less than the product of the benefits and degree of relatedness (Hrdy 1999). In a community that respects and declares milk kin, or relatedness among all sucklers of the same nurse, all citizens should have higher "r" values between one another than biology would dictate. By increasing the degree of relatedness between community members, wet-nursing should increase altruism and resource sharing within a community.

The notion of milk kin and its effects on community altruism have been illustrated throughout history. Islamic law specifies three types of kinship: relation by blood (*nasab*), affinity (*musahara*), and milk (*rida'a*). The latter form, *rida'a*, is denoted by the "relationship between a child and a woman, not its own mother, who nursed it" (Altorki 1980) and may be used to determine marriage suitors and potential allies. Muslim law prohibits marriage between *rida'a* relatives just as it does between *nasab* relatives. If a child was breastfed by a woman different from his mother, he forged new kinships and lost potential marriage options (Gil'adi 1999).

While *rida'a* relationships may bar marriage options, they, too, must be thought of, in the context of Islamic history, as a means of extending familial ties. As seen in Hadith literature, wet-nursing was initially practiced by an Islamic community in order to broaden the network of relatives on whom one could rely for assistance and support. By forcing Muslims to marry outside of their residential boundaries, wet-nursing enabled

individuals to meet new people from diverse, surrounding communities. Muslim believers were encouraged to seek partners beyond the boundaries of their own patrilineal-patrilocal extended families in order to inspire a shared world view on common aims (Gil'adi 1999). Forcing exogamous marriages, *rida'a* ties created relations between sedentary Islamic communities, such as Mecca, and the tribes of the desert. As Islamic women continued to nurse children of other faiths in surrounding communities, the number of Islamic followers skyrocketed. By decreasing one's marital options, wet-nursing served to expand the Islamic contingency (Gil'adi 1999, p. 120).

By broadening one's array of diverse relatives, wet-nursing also functioned as a means of establishing familial and/or national alliances. According to Jane Khatib-Chahidi, "it is reported that when Masai of East Africa wanted to make a lasting peace with an enemy tribe, the respective tribes would bring a cow with a calf and a woman with a baby. The two cows would be exchanged and the enemy's child suckled at the breast of the Masai woman; the Masai baby would be suckled by the woman from the enemy tribe" (Maher 1992). To strengthen relations with surrounding clans, the Hindus of India, specifically the royal Rajputs, chose their children's wet-nurse from a nearby, pastoral tribe.

While wet-nursing established alliances between neighboring, often conflicting, communities, it was also used to strengthen intra-group unity. In the Ashimadek clans of Chitral in the Hindu Kush, every infant was breastfed by every mother in the clan (Maher 1992). With the constant exchange of infants, milk-relationships were consistently formed. Familial relations were broadened and individual's expanded their resources and sources of comfort. Additionally, such an exchange of infants between neighbors yielded assurances that neighboring families would not cheat on one another. Preventing options of adultery, wet-nursing in turn strengthened families and inspired trust.

Wet-nursing also served to bridge government officials with their constituents. Akbar, the Mogul Emperor of Delhi and descendant of Genghis Khan, would punish milk kin with less severity, regardless of their crime. In fact, during one court

hearing, he stated: "between me and Aziz is a river of milk which I cannot cross" (Maher 1992). In essence, wet-nursing functioned as a transaction: suckling of an infant was exchanged for lifetime loyalty.

Overall, the altruistic consequences of wet-nursing prove that culturally determined "r" values are important in determining a species' evolutionary tendencies. However, additional research should be conducted to determine the extent to which culturally and biologically determined "r" values are related.

Conclusion

Clearly the milk-relationship is highly complex. In addition to providing biological benefits to both the nurse and nursling, wet-nursing has functioned as a social, economic, and political force throughout history. Although in decline after the introduction of artificial and bottle-feeding methods, wet-nursing remains a religious practice in many parts of the world. Constructing kinships, spreading religion, forming alliances, and enabling economic mobility, wet-nursing is not simply a biological phenomenon. Rather, its complex, biocultural roles are intertwined with its deep evolutionary history and significance. As more than just a viable alternative to maternal lactation, wet-nursing yields an optimization of lactational beneficiaries, logical resource provisioning, and increased community altruism. With such advantages, the cultural practice of wet-nursing may be seen as an evolutionarily advantageous strategy.

Cross-References

► Breastfeeding Benefits

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What Makes a Tool

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Definition

A tool is an object that extends the action capability of the user by transforming the body into a body-plus-tool system, such that the biomechanical fit of the body of the user, the object, and the goal(s) of the user collectively channel the organization of movements in action.

Introduction

All our technology relies on skillful tool use; how we manufacture and use tools is perhaps what distinguishes us from other animal species more than anything else. Archeological remains indicate that we have been using tools for at least 3.3 million years (Harmand et al. 2015). Tool use is considered to have been a key driver of our evolution; independent pieces of research have revealed close associations among tools, language, and cognition (Ambrose 2001; Gibson and Ingold 1993).

Tools are not unique to humans; nonhuman animals use tools as well. Chimpanzees, *Pan troglodytes* (Boesch et al. 2009; Sanz and Morgan 2007), and capuchin monkeys, *Sapajus* spp. (Mannu and Ottoni 2009), use sticks to fish for termites from their nests and honey from beehives, and New Caledonian crows, *Corvus moneduloides*, use stick tools to extract wood-boring beetle larvae from crevices in branches (Hunt 1996). Wild bearded capuchin monkeys, *Sapajus libidinosus* (Fragaszy et al. 2004; Mangalam and Frigaszy 2015; Mangalam et al. 2016), and chimpanzees (Boesch and Boesch 1981; Hannah and McGrew 1987) use anvil-and-hammer tools to crack open palm nuts and other encased food. Bottlenose dolphins, *Tursiops truncatus* (Smolker et al. 1997), and humpback dolphins, *Sousa chinensis* (Parra 2007), hold basket sponges over their rostrum, presumably to protect it while rummaging along the sandy floor of the sea. Stimulated by the apparent ubiquity of tool use in the animal kingdom, researchers have been relentlessly addressing questions about the continuity and discontinuity in tool use among humans and non-human animals.

Tools are relevant to many areas of scientific enquiry. Neurophysiological studies on people with apraxia – who lose their ability to conceptualize, plan, and execute actions, especially with familiar handheld tools (e.g., a rake) – regularly discuss tools (see, e.g., Goldenberg and Hagmann (1998)). Ergonomics is another area where discussions about tools are prevalent, frequently about comfort or discomfort (Kuijt-Evers et al. 2005) and occasionally about movement

disorders following prolonged use (Pilgian et al. 2000). Studies on humans involve everyday handheld tools, and nobody debates that these objects are “tools.” However, the challenge arises when comparing behavior involving an object across species, as then one needs to have an idea of when an object is a tool.

What Makes a Tool?

While both lay people and researchers can intuitively and unequivocally identify a tool, as of now, there is no consensus in the scientific literature on what makes a tool. The same object can be used as a tool and as a non-tool, thereby questioning when exactly in time and space does an object become a tool. In light of these uncertainties, ideas about tool use began with the descriptions of the form of an object and the functionality of behavior but have recently graduated to account for the developmental origins of tool use.

Definitions of Tool Use

Epistemological discussions on tools are most common in the physical anthropology and ethology literature. Typically, these discussions revolve around what constitutes tool use and not what makes a tool per se. Nonetheless, these have led to the development of a few ideas on tool use which have been instrumental in guiding research on tool use in nonhuman animal species for the last four decades:

the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object.

– Alcock (1972), p. 264.

the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.

– Beck (1980), p. 10.

the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself,

when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.

– Shumaker et al. (2011), p. 10.

As researchers became more interested in the varieties of behavior with objects observed in nonhuman animals, more precise definitions of tool use were sought, to determine if a given behavior constituted tool use. Beck's (1980) definition was exceptionally well accepted for more than three decades, until Shumaker et al. (2011) provided a revision along with the rationale for it (italicized in the definition above). Their revision has been the basis for the most updated catalogue of the known cases of tool use in nonhuman animals (Shumaker et al. 2011).

Despite being the most comprehensive definition of tool use in the scientific literature, Shumaker et al.'s (2011) definition is subjective and open to interpretation. Few would disagree that these challenges hold for any definition of tool use because of the observational nature of most studies, especially in nonhuman animal species. However, there are a few other challenges with defining tool use as well.

Challenges with Defining Tool Use

Without exception, the definitions of tool use hold the premise that all behavior involving an object and accomplishing a few given conditions belong to a single class of behavior, “tool use,” and that an object is a “tool.” Consequently, the focus of research in physical anthropology and ethology has mostly been on deducing whether a given behavior constitutes tool use, instead of on examining the actions with an object. This type of distinction between tool use and non-tool use poses a few challenges to our understanding of this behavior:

1. Any attempt of defining tool use overestimates the differences between tool use and non-tool use and underestimates those among tool use, as definitions tend to not account for the actions with an object. A pole used to displace an object and a hammer used to hit a nail are both tools, even though the actions with them differ considerably. A pole used to displace an object is a tool, but a laser pointer (or a pole)

- used to point on a screen is not (why isn't any kind of pointer a tool?) even though the actions with them do not differ considerably.
2. Definitions of tool use demand inferences about the intention of the user. However, when observing a nonhuman animal species using an object, the judgment of the observer may not necessarily coincide with the intention of the user. Thus, studies on tool use in nonhuman animals based on these definitions are highly susceptible to anthropomorphic biases.
 3. These definitions do not stimulate comparisons among cases of tool use, but instead halt discussions once a behavior has been ascertained to constitute tool use.

In the face of these challenges, many researchers have endorsed a perception–action perspective on tool use, which bypasses the distinction between tool use and non-tool use, but instead focuses on the tool-use actions.

A Perception–Action Perspective on Tool Use

Lockman (2000) opposes that tool use entails a gradual process of exploration and discovery that leads to perceptual learning, exploits the relation among an object and a surface in the environment, and encompasses only species-typical movement. The perception–action perspective on tool use has been guiding research on the development of tool use for the last two decades, with the objective of understanding how the organization of tool-use actions emerge from the dynamical interactions among features of the body of the user, the tool, and the goal(s) (see Smitsman and Bongers (2003) for an extended discussion on the fundamentals of the perception–action perspective on tool use and Mangalam and Frigaszy (2016) for discussion with an emphasis on nonhuman animals). So, most investigations comprise longitudinal studies examining spatiotemporal changes in tool-use actions across an extended period, especially during early life.

Cross-sectional studies on the origins of percussive tool use in human infants back the perception–action perspective on tool use. The accuracy and delivery of force improve in 7–14-month-old infants enabling spontaneous actions to become well suited for instrumental hammering

and tool use later (Kahrs et al. 2012), as well as in 12–18–24-month-old toddlers with improving postural stability and increasing motion of the elbow (Fragaszy et al. 2016). The spatiotemporal properties of percussive actions also change with age (19–35 months); older children show more distal control of their actions, and thus a higher accuracy, than younger children (Kahrs et al. 2014).

Longitudinal studies on percussive tool use to crack open palm nuts in wild bearded capuchin monkeys at Fazenda Boa Vista, Piauí, Brazil – the EthoCebus study site (Eshchar et al. 2016) – also back the perception–action perspective on tool use. Initially, when about a year old, juveniles begin to percuss nuts and nutshells against surfaces (combinatory, single-object actions) and against other nuts and nutshells (combinatory, two-object actions). Subsequently, they use pebbles as percussive tools. Eventually, when about 3.5 years old, they begin to use bigger stones, as until then, they cannot lift a heavy stone or produce an adequate force with a light stone because of their small body mass. Prolonged exposure to nut-cracking activity and the remains near anvils facilitate the ontogeny and development of stone tool use in wild bearded capuchin monkeys.

Among the chimpanzees at Bossou, Republic of Guinea, West Africa, the development of the sequence of percussive actions is similar to that in the bearded capuchin monkeys at Fazenda Boa Vista; about 2.5-year-old juveniles have already acquired the actions necessary to begin the nut-cracking activity, but they often take a few years to combine those appropriately (Inoue-Nakamura and Matsuzawa 1997).

These examples illustrate that tool use is not a discontinuous developmental milestone that demands a new level of cognitive resources, but instead the developmental origins of tool use lie in the perception–action routines of a species, especially those in the beginning few years of life when individuals explore their environment. These examples also suggest that the differences between tool use and non-tool use are gradual (i.e., of a degree) and not a fundamental one (i.e., of a type). When exactly in time and space actions constitute tool use is still debatable.

One implication of the perception–action perspective on tool use is that studying the body, the tool, or the goal(s) in isolation might lead to erroneous conclusions, which is especially relevant for comparisons of tool use across individuals, populations, and species.

Thus, the perception–action perspective on tool use has one word answer – actions – to the question: what makes a tool? Whether an object is a tool depends on how it is used (i.e., the actions with it) and not the anatomy of the object (Ingold 1993, 1997). Most recent advancements indicate that it might be more appropriate to consider “tool” as an adverb for describing the actions with an object and not as a noun. This linguistic change in how we think about tools has implications for our understanding of their use.

Conclusions

While both lay people and researchers can intuitively and unequivocally identify a given object as a tool, there is no consensus yet on what makes a tool, and there may never be. However, for the last two decades, researchers have been increasingly acknowledging that the actions with an object, and not the anatomy of an object, make that object a tool. Thus, researchers have been increasingly studying tool-use actions, which may eventually help in bypassing the distinction between tool use and non-tool use. A developmental perspective that focuses on spatiotemporal changes in tool-use actions is proving helpful. A key challenge is to explain how all behaviors involving an object lie on a continuum, without overestimating the differences between tool use and non-tool use and underestimating those among tool use.

Cross-References

- [Advanced Tool Use](#)
- [Bird Tool Use](#)
- [Cephalopod Tool Use](#)
- [Evolution of Tool Use](#)
- [Fish, Amphibian, and Reptile Tool Use](#)
- [Human Tool Making](#)

- [Innate and Learned Tool Use](#)
- [Meta-tool](#)
- [Nonhuman Tool Use](#)
- [Play and Tool Use](#)
- [Primate Tool Use](#)
- [Proto-tool](#)
- [Role of Experience in Tool Use](#)
- [Sequential Tool Use](#)
- [Stick Tools for Foraging](#)
- [Stone Hammers](#)
- [Tool Manufacturing](#)
- [Tool Play](#)
- [Tool Use](#)

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Whimpering

► Crying

Whipping

► Spanking

Whoredom

► Prostitution

► Prostitution and Women's Short-Term Mating

Whorfianism

► Language and Economic Cooperation

WHR

► [Body Fat Percent and Distribution](#)

Why Humans Are Unique

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Synonyms

[Hominids](#); [Special](#); [Unusual](#)

Definition

The ways in which humans are different from other animals and why they have come to be so unusual.

Introduction

A central focus in the study of comparative cognition is the question of what it is that makes humans unique. There is no denying that humans stand apart from the rest of the animal kingdom in several key domains. For instance, no other species has mastered advanced technology or has the capacity to so dramatically alter its environment. No other species has mastered the art of travel using vehicles rather than natural affordances. No other species has travelled off the planet in search of other life forms. These facts are observable and uncontested. However, a much more contested topic in comparative psychology is the extent to which humans are similar or different from other species in terms of their fundamental cognitive capacities, which presumably give rise to such inventions. Although several feats accomplished only by humans have been outlined, it is less clear whether other species share some cognitive capacities that underlie such feats, even if

these capacities do not reach the same upper bounds with which they are expressed in humans.

A recent set of studies were conducted to demonstrate that, although humans alone engage in the cooking of food, our closest living relatives – chimpanzees – might have the requisite capacities to engage in similar acts, even though they have never been observed to do so (Warneken and Rosati 2015). The article generated much discussion in part because the studies did not show that chimpanzees exhibited a causal understanding of how to recreate the transformative properties of the cooking agent. Discussions such as these highlight the common resistance to the notion that humans are unique and the opposing resistance to the notion that humans are qualitatively special when compared to other species, in particular the other apes. These discussions also highlight the need to look beyond observable similarities in the types of behaviors being performed by different species in order to probe the underlying mechanisms giving rise to such behaviors.

Tool Use

Some key cognitive components were identified early on as being exclusive to humans. These included tool use, language, abstraction, imitation, culture, causal reasoning, theory of mind (i.e., the capacity to reason about mental states in others), and other-regarding preferences. Researchers have chipped away at such assertions revealing evidence for tool use in a variety of species including birds, elephants, bears, and non-human primates (for review see Shumaker et al. 2011). However, although it is commonly accepted that some other species may use tools, the manner in which they do so is generally not indicative of a deeper level causal understanding of the tool's properties.

Language

Nonhuman apes have also mastered various components of language – most notably the bonobo, Kanzi (Savage-Rumbaugh et al. 1998). Despite

these impressive accomplishments, researchers generally agree that the language exhibited by nonhuman apes does not approach the complexity or generativity of human language, and non-humans do not express thoughts about the past or future. In humans, language can be used to express abstract ideas about constructs that have no observable referents.

Abstraction

Indeed, it was often argued that language held the key for the emergence of abstract concepts such as similarity and difference at a conceptual level. Language is surely related to the capacity to express thoughts about unobservables, such as causal forces (e.g., gravity, transfer of force) and mental states (e.g., thoughts, beliefs, intentions). As such, it follows that, without human-like language, the ability to reason in the abstract, in particular about unobservables such as mental states, would not emerge. Thus, other animals should not be expected to represent concepts for thoughts, beliefs, and the like. Indeed, theory of mind is one of the most controversial topics in comparative cognition as researchers passionately debate whether there is convincing evidence that any other species are capable of going beyond reasoning about observable cues correlated with underlying mental states in order to infer the underlying mental states themselves. Vonk and Povinelli (2006) hypothesized that the ability to reason about unobservables, which would subsume both causal forces in the physical realm and mental states in the psychological realm, may be the primary capacity distinguishing humans from other animals.

Prosociality

Animals that reason about others' mental states are capable of showing empathy for the plight of another. Researchers have argued that animals do have empathy. In fact, even rats have been shown to release trapped cage-mates and to share desired chocolate with their cage mates once rescued,

suggesting a level of compassion for their compatriots (Ben-Ami Bartal et al. 2011). However, other explanations for the behavior have been provided with less lofty interpretations. Perhaps the rats behaved to reduce their own feelings of distress, for example. One puzzle is why observations of helping or prosocial acts, in the absence of benefits for the actor, are so uncommon if animals do have concern for the well-being of others. In experimental paradigms, little evidence for prosocial sentiments has been observed. Where it does occur it is in limited contexts (see Cronin 2012 for a review) and can often be explained through mechanisms such as reciprocity (e.g., Carter 2014).

Imitation and Culture

Understanding the knowledge states of others has direct consequences for other aspects of uniquely human behavior. Originally, researchers believed that only humans could learn through observation to imitate the actions of others. This notion was dispelled when Subiaul et al. (2004) demonstrated that monkeys could learn the correct sequence of images in a cognitive imitation task. However, although it is now accepted that many animals can learn through observation, including learning the reputations of other individuals, animals do not seem to use these capacities to explicitly teach others the extent of their own knowledge. Thus, while researchers have championed findings of common gestures and tool using techniques across chimpanzee and orangutan "cultures" (Whiten 2011), there is nothing on the level of human pedagogy, including schools, text books, instruction manuals, informational videos, and so on, elsewhere in the animal kingdom. The ability to communicate with language surely facilitates these behaviors as well.

Conclusion

It should be clear then that there is no single ability that differentiates humans from other species. Rather, there is a constellation of related traits all

built upon the foundation of language and abstraction that converge to predict uniquely human traits and behaviors. The question remains as to why humans alone would evolve this particular constellation of traits. Vonk and Aradhye (2015) have suggested that humans are uniquely positioned between predator and prey in an arms race to out-compete each other as well as more physically formidable species in the hunt for prey, which might also benefit from the anticipation of others' intentions and actions. Humans have also formed agricultural societies to support close communities, which requires the ability to communicate and cooperate. Thus, it is likely that humans evolved more complex cognitive capacities in order to create and mine food sources to sustain the growth of human communities in a manner not seen in other species, which rely on different subsistence methods. The flexibility required by humans to exploit so many different food sources has allowed them to prevail in more diverse environments than those encountered by other species, including travel to outer space. This flexibility, necessitated by a generalist and exploitative diet, may have simultaneously necessitated larger brain size, which subsequently supported the advance cognitive traits expressed in humans today.

Cross-References

- Abstract Concept Formation
- Brain Size and Intelligence
- Cognitive Science
- Convergent Evolution of Intelligence
- Cooperation and Social Cognition
- Empathy in Rats
- Evolution of Cooperation
- Fairness in Primates
- Nonhuman Intelligence
- Pinker's (1994) The Language Instinct
- Primates
- Psychological Mechanisms
- Social Cognition
- Theory of Mind
- Theory of Mind and Nonhuman Intelligence
- Unobservability Hypothesis, The (Vonk and Povinelli, 2006)

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Wife Killing

- Partner Homicide

Wild Justice

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Synonyms

Cooperation; Empathy; Fairness; Morality

Definitions

A suite of interrelated other-regarding behaviors that cultivate and regulate complex interactions within social groups, a book written by Marc Bekoff and Jessica Pierce.

Introduction

Wild Justice was written by Marc Bekoff and Jessica Pierce and was published in 2009. In their book, the authors attempt to shed light on what it means for animals to have morality. To do so, they focus on three main key points: cooperation, empathy, and justice. The authors first define nonhuman animal morality as “a suite of interrelated other-regarding behaviors that cultivate and regulate complex interactions within social groups” (p. 7). Through the combination of these traits, Bekoff and Peirce suggest that morality is not unique to humans but is an evolved trait that is shared with other social mammals.

Cooperation

In examining the first key point, cooperation, the authors begin by stating that at first glance, evolution appears to be counterintuitive to Darwinian theory, given that competition to survive and reproduce is what drives evolution. However, as Bekoff and Pierce explain, evolution allows for cooperation, which in turn promotes biodiversity. The authors discuss ultimate explanations of cooperation and how cooperation may have evolved over time. Such explanations include kin selection, reciprocity, mutualism, and the controversial explanation that Bekoff and Pierce support called group selection (i.e., a proposed mechanism of evolution in which natural selection acts at the level of the group, rather than at the individual level). After providing different examples of cooperation, the authors propose that for cooperation to be considered a “moral” behavior, the cooperative behavior must contain a high level of emotional complexity, cognitive complexity,

and flexibility. Hence, the cooperative animal should be capable of complex cooperative behavior and not simpler forms of cooperation.

Empathy

Bekoff and Pierce define empathy as “the ability to perceive and feel the emotion of one another” (p. 87). The authors break this down and expand on it more by arguing that empathy is when one individual is able to share the emotional state of another individual and is a class of behaviors that evolved in complexity over time. It would make sense, then, that empathy is an adaptive trait, as being able to share an emotional state would assist individuals of a social group when avoiding danger and having better social relations with other members in the group. Bekoff and Pierce contend that empathy may facilitate cooperative and altruistic behaviors. The authors then close by citing examples of research examining empathy in a variety of animals, such as rats, whales, dolphins, and elephants, making the case that empathy (in some form) is not unique to humans but has evolved in a variety of social species.

Justice

The authors use the term justice to describe the concepts of fairness and equality in the animal kingdom. They point out that there has been very limited research examining justice, with almost all studies focusing on primates with controversial results. Bekoff and Pierce propose that it may be wise to study social play behavior in other social animals, such as dogs and wolves, to gain a better understanding of justice. They argue that play behavior provides elements such rules, agreement to obey said rules, and consequences for defectors. The authors suggest that studying social play in animals will help researchers gain a better understanding of justice in animals and how it relates to morality. Bekoff and Pierce suggest that in regard to morality, justice is the most complex and evolved set of behaviors that are built upon cooperation and empathy.

Conclusions

The authors conclude the book examining the philosophical aspects of morality. They recap on their definition of morality and argue that it fits into the philosophical framework. They attempt to address limitations and reservations that readers may have about their idea of animal morality. Lastly, they conclude that morality is indeed not unique to humans and is shared with a variety of taxa but that there is still much research in this area to be conducted.

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Will After Death

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Synonyms

[Testament](#)

Definition

A legal document by which a person expresses his or her wish as to how his or her property is to be distributed at death.

As discussed elsewhere in this work (Peedicayil 2018), cultural inheritance involves the storage and transmission of information by communication, imitation, teaching, and learning. In this context, there is evidence that complex social behaviors like human altruism and mate choice (Rushton et al. 1986), social attitudes (Martin et al. 1986), personality (Eaves et al. 1999), and the human sex ratio (Lipatov et al. 2008) are culturally transmitted. The cultural transmission of such behaviors, for obvious

reasons, will occur effectively only in an animal species that is social, i.e., where the members live in groups and interact freely with one another. Human beings are the prototype of that type of animal species and the groups they live in are termed societies (Wilson 2000). Indeed, the famous Greek philosopher Aristotle had stated “Man is by nature a social animal” (Aristotle 2015). All of man’s unique social behavior is pivoted around the use of language (Wilson 2000).

With reference to will after death, it is a phenomenon peculiar to humans due to the advanced level of development of cultural inheritance in comparison to other animal species. Will after death is a legal document by which a person (the testator) expresses his or her wish as to how his or her property is to be distributed at death and names one or more persons (the executor) to manage the estate until its final distribution (Wikipedia 2018). After the demise of the testator, the executor or administrator must locate the will and present it to the local probate court with a certified copy of the testator’s death certificate. Wills have been in existence for thousands of years (Wikipedia 2018).

Cross-References

► [Cultural Inheritance](#)

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William Hamilton

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Definition

One of the most influential evolutionary theorists of the twentieth century. Hamilton made fundamental contributions to social evolution theory, the theory of sex allocation, the evolution of senescence, and many other topics.

Introduction

Few evolutionary biologists have achieved the kind of legendary status that William Donald Hamilton holds. His reputation is of course mostly due to his enormously influential body of work and is only further bolstered by his unusual and quirky character which inspired countless stories. Hamilton may not have published a particularly large number of papers by today's bloated standards, but his influence on modern evolutionary theory is almost unrivalled. His major contributions include kin selection theory, sex allocation theory, the modern mathematical approach to studying the evolution of senescence, the evolution of dispersal strategies, and the evolution of sex. Indirectly, or by extending work of other

researchers, Hamilton contributed to evolutionary game theory, the mathematical study of the levels of selection, the study of evolution in age-structured populations, and related methods such as sensitivity analysis. His work was also a major influence on Richard Dawkins' championing of the selfish gene or gene's eye view concept. Hamilton's work remains relevant and influential, if sometimes divisive and controversial, to this day. Here the focus is largely on the lasting impact Hamilton's work has had on evolutionary biology. More detailed information on Hamilton's life can be found in a book-length biography by Ullica Segerstråle (2013), a shorter biographical article by Alan Grafen (2004), and in the three-part volume of Hamilton's collected papers interlaced with (auto)biographical essays (Hamilton 1996, 2001, 2005) from which much of the biographical details here are sourced.

Brief Biography

Though born in Cairo in 1936 to New Zealander parents, William Donald Hamilton grew up in Kent in South East England. It was clear early on that he was fascinated by nature, by plants and their colors, by insects, and by other animals. His interests were encouraged, and he spent much of his time collecting butterflies using a net and killing bottle given to him by his mother. But by way of this hobby, he was also introduced to some of the secrets of his eventual profession: E.B. Ford's book *Butterflies*, a present from his parents, was not just about butterflies, but also contained sections on genetics and on the study of evolution, sparking young Hamilton's interest. He had other, perhaps more mischievous interests too. One was bombs, which after some youthful experimentation resulted in a near-fatal explosion, permanently shortened fingers, and shrapnel in his chest.

Hamilton began his undergraduate education at the University of Cambridge in 1957 and graduated in 1960 with a degree in genetics. After some difficulty in finding a welcoming host institution, Hamilton eventually became a graduate student at the London School of

Economics. He produced his most celebrated work as a graduate student (see the next section), but it would take some time before the importance of this work would be realized.

Although Hamilton would be awarded his PhD only in 1968, he took up a lectureship at Imperial College in London already in 1964. In 1978, he joined the University of Michigan as a professor and eventually returned to England in 1984 after accepting a Royal Society Research Professorship at the University of Oxford, where he would remain for the rest of his life. Hamilton passed away on March 7, 2000, at the age of 63.

Kin Selection and Social Evolution Theory (1963 onward)

If there is a single research theme that Hamilton is best known for, it is no doubt his groundbreaking work on the evolution of social traits and in particular the evolution of altruism. Hamilton produced his most famous articles (Hamilton 1964a, b) as a graduate student (for a personal account, see Hamilton 1996). The publication process turned out to be difficult and slow, so slow in fact that a shorter and less widely known article on the same topic was published in the previous year (Hamilton 1963) despite being written after the more well-known 1964 papers. Perhaps encouragingly for contemporary graduate students struggling to finish their theses, Hamilton was from time to time wracked with doubts about being a fraud and crank, occasionally losing confidence in his ideas, but his perseverance paid off.

What is it, then, that made kin selection so special? Despite partial attempts at explanation (by luminaries such as Charles Darwin, Ronald Fisher, and John Haldane), the evolution of altruism remained poorly understood until Hamilton's insights. The difficulty is that altruism, by definition, increases the fitness of the recipient of altruism, but decreases the fitness of the donor. It is then hard to reconcile this with the fact that natural selection should decrease the frequency of alleles that are associated with low fitness. How can an allele that decreases the carrier's fitness increase in frequency in the population?

Kin selection theory in its modern form is multifaceted and not quick to ingest in its full scope, but Hamilton's central insight was simple. Consider an allele that induces altruistic behavior toward others, carried by an individual organism whom we shall call the donor. The donor will be surrounded by other individuals, some of which may carry a copy of the same allele. Now if the donor can direct its helping behavior toward an individual (whom we shall call the recipient) that is more likely than average to carry such a copy, the help will in fact contribute toward increased success of the helping allele via the recipient. In other words, an allele that can preferentially help copies of itself may be successful and increase in frequency, despite seeming to cause purely altruistic behavior and a fitness detriment to the donor at the phenotypic level. Whether allele frequency does in fact increase depends on the costs to the altruist, the benefit to the recipient, and the probability that the recipient carries a copy of the allele for altruism.

Hamilton famously encapsulated the condition for increase in frequency of the allele in what is now known as Hamilton's rule:

$$rb > c \quad (1)$$

Here, c encapsulates the cost to the altruist, b the benefit to the recipient, and r is relatedness between altruist and recipient. Hamilton realized that, under certain conditions, relatedness r is a measure of the likelihood (relative to the population average) that the recipient carries a copy of the altruism allele. Hamilton's rule is highly intuitive: as long as the benefits scaled by relatedness overcome the cost to self, an altruistic trait can spread in the population. It is important to note that the preferential treatment of closely related individuals need not be a conscious decision, nor does it require active recognition of kin. Any process that leads to interactions between relatives (such as limited dispersal from one's birthplace) can have a similar effect. Kin selection does not require a brain or active choice.

Kin selection and Hamilton's rule have seen various developments over the years. Hamilton's central insights still remain at the core of the

methodology, while others have pushed the field further and developed highly general (e.g., Queller 1992), as well as highly practical and streamlined, kin selection approaches and methods (e.g., Taylor and Frank 1996). Kin selection has also been at the center of heated debates regarding its importance and generality (e.g., the highly critical Nowak et al. 2010, and numerous responses in defense of kin selection that followed), as well as debates between kin selection and alternative approaches to social evolution theory, in particular so-called group selection models. Hamilton himself, however, had a positive outlook on group selection (or multilevel selection) models when properly formulated (Hamilton 1975a), and it can be shown that despite different notations and modeling traditions, the central approaches to social evolution theory are equivalent and ultimately linked by a common set of mathematical components (Lehtonen 2020). Despite controversies and debates, Hamilton's legacy in social evolution theory lives on.

Other Major Scientific Contributions

Although Hamilton is most widely recognized as the father of kin selection, he made several other key contributions to evolutionary theory. This section covers a selection of these contributions, in the order that Hamilton first published on the topics (indicated by the year in brackets after the titles).

Senescence (1966)

Whereas many of Hamilton's papers were inspired by Ronald Fisher (one of Hamilton's scientific role models) and built upon his work, "The moulding of senescence by natural selection" (Hamilton 1966) was a rare exception in that it actually corrected a mistake by Fisher. Fisher wrote "It is probably not without significance in this connexion that the death rate in Man takes a course generally inverse to the curve of reproductive value" (Fisher 1930), suggesting that

reproductive value should be the central factor that drives the evolution of senescence and ageing. Hamilton showed this to be incorrect and instead demonstrated that selection on age-specific mutations on mortality and fertility can be approximated by implicitly differentiating the so-called Euler-Lotka equation, thus finding the derivative of the Malthusian parameter which approximates fitness. It is arguably this mathematical technique that is the most influential aspect of the 1966 article. In addition to its impact on mathematical research on senescence, Hamilton's method has been influential in the general development of the mathematical analysis of evolution in age-structured populations (Charlesworth 1994), and it is perhaps the earliest clear forerunner of sensitivity analysis (Caswell 2019).

Sex Allocation (1967)

In addition to altruism, another question that had stumped Darwin was the evolution of the sex ratio: why are females and males typically born in equal numbers? This problem was famously solved by Düsing (1884) and Fisher (1930), who pointed out a very powerful argument selecting for equal sex ratios. Theoretical progress was slow for some decades, until Hamilton's (1967) analysis of the problem. Hamilton examined various situations where assumptions that Fisher had made do not hold, laying the groundwork for modern research on sex allocation (West 2009). The most enduring contribution of this paper is the theory of sex allocation under local mate competition (LMC): natural selection results in female-biased sex allocation if the population structure is such that brothers compete for matings. Hamilton's sex allocation article was instrumental in the development of arguably one of the most successful areas of evolutionary biology (West 2009). Furthermore, Hamilton's use of an approach he called the unbeatable strategy was influential in the eventual development of evolutionary game theory by John Maynard Smith and George Price (Maynard Smith 1982; Maynard Smith and Price 1973). Hamilton regarded this early paper very highly among his own

publications: “I am more proud of this paper than of almost any other I have written. Perhaps that is most of all because I believe it helped sex-ratio theory well on its way to being the section of evolutionary theory that best proves the power and accuracy of the Neodarwinian paradigm as a whole” (Hamilton 1996).

The Evolution of Gregarious Behavior (1971)

The Hamilton 1971 publication “Geometry for the Selfish Herd” was largely motivated by previous claims that schooling, flocking, and herding behaviors of animals were due to selection at the population or species level. Hamilton shows that there is no need to appeal to selection at higher levels, and the behaviors can be explained by individual-level selection on cover-seeking to reduce one’s own chance of being caught by a predator. The central idea in this paper is often confused with the “dilution effect,” but the concepts are very different. The dilution effect relies on individual-level predation risk being diluted in larger groups even if all individuals are at equal risk, whereas Hamilton’s selfish herding is underpinned by intragroup differences in predation risk (Lehtonen and Jaatinen 2016). Hamilton’s foray into the evolution of herding behavior ended up being one of the most highly cited articles in the *Journal of Theoretical Biology* – Hamilton (1964a) being the most highly cited one.

Dispersal Strategies (1977)

Hamilton’s collaboration with Robert May addresses another question on the evolution of the spatial distribution of organisms, but both the question and resolution are quite different compared to selfish herding. The title of the paper, “Dispersal in stable habitats” (Hamilton and May 1977), already suggests the major novel finding of the article. Previously, it was widely thought that if habitats are stable and dispersal is costly, there is no advantage to be gained by

dispersing from one’s home site. Using a simple model with a striking and surprising outcome, Hamilton and May show this to be far from the truth: even in perfectly stable habitats, and even if migration is so risky that the probability of survival for a migrant approaches zero, it still pays off to commit more than half of the offspring to migration. Although the original model was not framed in a kin selection context, it has a kin selection flavor to it. If reproductive opportunities at the home site are limited, there is little to be gained by competing with close relatives, and it may pay off to disperse and compete with unrelated individuals instead, even if the odds of surviving dispersal are very low. Frank (2013) discusses how extensions of kin selection theory can be used to interpret Hamilton and May’s model explicitly from a kin selection angle and to unify seemingly disparate and contradictory results found by different authors on dispersal evolution.

Evolution of Sex and Sexual Selection (1980)

If Hamilton’s obsession early in his career was the evolution of altruism, a recurring theme in his later work was the evolution of sex, one of the big outstanding questions in evolutionary biology due to its inherent costs as a reproductive strategy. From 1980 (Hamilton 1980) onward, Hamilton produced a series of papers examining the effect of fluctuations caused by antagonistic coevolution with parasites on the maintenance of sexual reproduction. But clearly these ideas had been on his mind for much longer. For example, in a 1975 book review (Hamilton 1975b) he stated, in relation to explanations for sex, that “...it seems to me that we need environmental fluctuations around a trend line of change. For the source of these we may look to fluctuations and periodicities inherent in our solar system, and also to the possibility of others generated by life itself.” Publication of these ideas was an occasionally frustrating process for Hamilton, and he admitted some bitterness about this in a refreshingly open and honest manner: “Unmistakably I harbour

a resentment toward some particular papers because they were readily accepted in a prestigious journal when one of mine wasn't. The acceptance there probably even colours my estimation of their content" (Hamilton 2001). Closely linked to Hamilton's work on sexual reproduction, the Hamilton-Zuk hypothesis (1982) is a model of sexual selection which posits that females choose mates with ornaments that indicate health, vigor, and resistance to parasites. Coadaptational cycles between parasites and hosts renew genetic variation and heritability of fitness.

Awards, Recognition, and Legacy

Despite the fundamental status that many of Hamilton's contributions now hold, the recognition of his work was not immediate. In the first decade after their publication, the two 1964 papers (Hamilton 1964a, b) were cited on average less than ten times per year, but within 15 years of its publication, kin selection had become a major theme in evolutionary biology (Grafen 2004). Richard Dawkins was greatly inspired by, and popularized, Hamilton's work when he championed the gene's eye view in his classic book, *The Selfish Gene* (Dawkins 1976). Later in his career, Hamilton was awarded a great number of prizes, medals, and honorary academy memberships, perhaps foremost among them the Crafoord Prize in 1993, which is often thought of as the biologists' equivalent to the Nobel Prize. Ranking scientists in order of importance may not be the most fruitful of tasks, but there is no doubt that Hamilton will be remembered as one of the foremost evolutionary theorists of the twentieth century.

Cross-References

- Fisher's Reproductive Value
- Genetic Relatedness
- Green Beard Effect, The
- Kin Selection
- Puzzle of Altruism, The

- Ronald Aylmer Fisher
- Senescence
- Sex Ratio
- Theory of Senescence

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Winner Effects

- [Social Dominance Reduces Fighting](#)

Winthrop Kellogg

- [Kellogg Chimpanzee Study, The](#)

Within-Group Competition

- [Sex Differences in Pursuit](#)

Within-Group Killing

- [Nonhuman Primates: Within-Group Conflicts](#)

Within-Sex Competition

- [Intrasexual Rivalry Among Men](#)
- [Intrasexual Rivalry Among Women](#)
- [Urban Gangs](#)

Within-Sex Selection

- [Intrasexual Rivalry Among Men](#)
- [Intrasexual Rivalry Among Women](#)

Within-Species Comparisons

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Synonyms

[Comparative analyses](#); [Intraspecific comparisons](#)

Definition

Comparative analyses between (groups of) individuals from the same species.

Introduction

Within-species comparisons refer to comparative analyses between (groups of) individuals from the same species. These may be naturally occurring groups within the same population such as males and females (Gur and Gur 2017), or juveniles and adults (Adjorlolo and Egbenya 2016; Lobue 2009), or groups comprised of individuals varying in other behaviorally relevant characteristics (such as sociality, Ashton et al. 2018, or personality, Roche et al. 2016). Useful comparisons may also be made between geographically or temporally discrete populations of the same species. Such populations may vary culturally (Apicella and Barrett 2016; Luncz et al. 2018) or along relevant environmental gradients (Roth and Pravosudov 2009; Van Lange et al. 2017). Within-species comparisons also occur in experimental settings, with individuals randomly allocated to different experimental groups (Sulikowski and Burke 2015). In all instances, within-species comparisons have the potential to inform on the function, evolution, development, and/or mechanistic bases of behavior. In appropriate contexts they can provide more exact tests of phylogenetic and evolutionary hypotheses than can between-species comparisons (Sulikowski 2016). With the exception of their use in experimental designs, however, within-species comparisons are nevertheless limited in the extents to which they can support causal conclusions about behavior and its underlying mechanisms.

Comparisons Between Naturally Occurring Groups

Comparisons between naturally occurring groups within a population are probably the most common types of within-species comparison and are the types that most readily come to mind as the “typical” within-species comparison. Such comparisons encompass investigations into sex differences, age cohort effects, and social group effects. Studies involving these types of comparisons are classed as quasi-experimental,

since they involve comparisons between groups to which individuals *a priori* belong (as opposed to true experimental designs, in which individuals are randomly allocated to different groups).

Sex Differences

Sex differences in the brain and behavior are common in both humans and nonhuman animals (Gur and Gur 2017). These differences have proved important sources of data for evolutionary theories on a wide range of behaviors. While theories pertaining to reproductive behaviors are likely the most apparent beneficiary, sex differences have also informed evolutionary theories of foraging and perceptual priority. In this section I will use examples of these latter two applications to illustrate the broad utility of within-species male-female comparisons, for understanding the evolution of behavior.

Human sex differences in spatial cognition motivated the hunter-gatherer theory, which postulates that male advantages in allocentric navigation and female advantages in object location memory reflect the respective selection pressures on men and women, to optimize hunting and gathering efficiency (Silverman and Eals 1992). The hunter-gatherer theory does not purport to explain the totality of human sex differences in the brain and cognition but identifies one selection pressure – the need to maximize foraging efficiency – that would have applied differentially to the sexes. As men hunted and women foraged, differential selection pressures would have acted on the sexes to maximize foraging efficiency. By comparing men and women on a variety of tasks for which the hunter-gatherer theory predicts sex differences (including dead reckoning, Silverman et al. 2000, and proximal landmark-based navigation, Hughes et al. 2014), the extent to which selection pressures to maximize foraging efficiency are reflected in modern human cognition can be examined.

There is more information and stimuli available in the environment than any individual can attend to. As such individuals must allocate perceptual priority to some information/stimuli over others. Many studies have suggested that threatening, and other especially relevant, stimuli

are prioritized in this manner. However, studies that simply compare the speed of recognition and response to threatening and non-threatening stimuli are open to the criticism that some innocuous feature(s) of the stimuli, rather than their threatening status per se, simply render some classes of stimuli easier to perceive for stochastic, nonadaptive reasons (Quinsey 2013). In this context, sex differences between men and women in how attention is allocated to weapons (Sulikowski and Burke 2014) and to foods with sex-specific nutritional value (Love and Sulikowski 2018) can confirm that the relevance of stimuli to individuals drives prioritized attention (as these effects of sex cannot be solely attributed to idiosyncratic features of the stimuli used).

Age Cohort Effects

Comparisons between adults and juveniles of a species can speak both to the developmental trajectories of behaviors and to experiential impacts on behavioral phenotypes. For example, children under 6 readily conflate whether or not something is physically possible, with whether or not it is allowed, while adults clearly differentiate these concepts (Shtulman and Phillips 2018); and it isn't until after children are immunized (and have thus had an aversive experience with syringes) that they allocate prioritized visual attention to needles as a dangerous object (Lobue 2009).

Age cohort comparisons may also subserve more complex investigations, such as whether or not the same behavior appearing in juveniles and adults is supported by the same or different proximal mechanisms. For example, adult and older-adult sexual offenders tend to reliably exhibit executive function and intelligence deficits that distinguish them from non-sex offenders (Adjorlolo and Egbenya 2016), while juvenile sex offenders do not (Falligant et al. 2017). This implies that, for juveniles, sex offending is part of a broader pattern of delinquent behavior (Falligant et al. 2017), while in adults, it is indicative of sexually motivated behavioral dysfunction.

Sociality

Sociality has been proposed as one of the major evolutionary drivers of complex cognitive

abilities – the social intelligence hypothesis. Most evidence supporting this theory has derived from comparisons between closely related species differing in sociality. More recent support has come from within-species comparisons of Australian magpies, where individuals living in larger groups exhibit superior cognitive performance compared to individuals living in smaller groups (Ashton et al. 2018).

In cases where between-species comparisons provide the majority of evidence bearing on a theory, as is the case with the social intelligence hypothesis, within-species comparisons can be especially valuable. Between-species comparisons are always vulnerable to alternative interpretations: any given pair, or set, of species will vary along many dimensions, not just in the trait of interest. Bird species differing in social group size may also differ in any number of other traits (mating system, foraging ecology, predation risk, etc.), potentially confounding comparisons of cognitive ability between species with differing levels of sociality. Within-species comparisons of individuals living in differently sized groups can minimize many of the phylogenetic and ecological confounds associated with between-species comparisons providing, in this case, especially strong support for the social intelligence hypothesis (Ashton et al. 2018).

Comparisons Along an Environmental Gradient

How individuals and populations respond to environmental selection pressures (in terms of both behavioral plasticity and evolutionary change) is key to the adaptive nature of behavior. When a single species resides along an environmental gradient, whether continuously or in discrete populations, within-species comparisons along this gradient can reveal quantitative changes in the brain and behavior associated with the changing environment.

One large-scale example of human behavior change along an environmental gradient is the observed increase in violence and aggression associated with warmer climates. Some notable exceptions aside (including Russia and

South Africa, both of which are relatively far from the equator and exhibit high rates of violent crime), within and between countries, conflict and violent crime rates tend to be higher closer to the equator (Van Lange et al. 2017). This effect may be accounted for mechanistically by strong negative correlations between peripheral serotonin transporter density (low levels of which are associated with violence and impulsivity at the individual level) and ambient temperatures (Tiihonen et al. 2017).

A further example derives from the comparative literature. Black-capped chickadees occupy a large range across North America and rely heavily on supplies of cached food during the winter months. Accurate spatial memory, supported by the hippocampus, is required to recover these caches. As their range extends further north (away from the equator), the winters are harsher, and the birds are more heavily reliant on their cached winter stores. Comparisons of five populations of black-capped chickadees along this gradient of harshness revealed perfect rank-order correlations between both hippocampal volume and neuronal numbers, on the one hand, and increasing latitude on the other (Roth and Pravosudov 2009).

Within-species comparisons along environmental gradients take on a special significance in the context of global climate change. As temperatures rise, species will adapt (to the extent that they can, Butt et al. 2016). Comparisons along extant environmental gradients may reveal the capacities that different populations have to respond adaptively to increases in temperature and other associated climatic changes. They may also permit us to predict climate-induced behavioral changes at the population level. For example, mean increases in ambient temperatures of 2 °C have been predicted to result in a 3% increase in rates of violent assaults and murder across cold-temperate zones (Tiihonen et al. 2017).

Cross-Cultural Comparisons

Cross-cultural comparisons involve comparisons between groups of individuals from culturally

diverse backgrounds. They are frequently used both to examine the effects of cultural influences on behavior (Apicella and Barrett 2016) and also to identify those traits that are culturally invariant, especially with respect to people (Buss 2001). Cross-cultural comparisons also extend to nonhuman animals. In this domain, research is more strongly focused on cultural differences, since such differences provide the requisite evidence that divergent animal cultures exist (Luncz et al. 2018). Indeed, within the context of evolutionarily motivated investigations of behavior, the key difference between human and non-human cross-cultural investigations is that, with respect to the former, there is an accepted presumption that the behavior of individuals from very different cultures is likely to vary accordingly. As such, demonstrations of cross-cultural consistency and generalizability of findings are highly sought, as evidence of a genetic or biological basis for behavior. In the context of non-human cultural investigations, far greater emphasis is placed on demonstrating social transmission within a group of a behavior that varies between groups as evidence that cultural effects on behavior exist.

Cross-Cultural Comparisons in Humans

A classic cross-cultural comparison of human behavior is found with Buss' (1989) study which assessed 37 samples from 27 countries across 6 continents and demonstrated remarkable cross-cultural consistency in human mate preference sex differences: women more strongly prize traits indicative resource acquisition potential, and men more strongly prize traits indicative of reproductive capacity. Against the backdrop of the standard social science model (SSSM, Tooby and Cosmides 1992), which posits that within-group consistencies and biases in human behavior result from culturally constructed norms and societal influences, consistency across cultures of behaviors, whose supposed cultural determinants vary widely across those cultures, offers especially compelling evidence for the adaptive nature of human behavior. For example, very high cross-cultural agreement on subjective judgments of facial attractiveness (Langlois et al. 2000) undermines claims that attractiveness is a social

construct driven by the beauty ideals promoted in popular Western media.

The above is not to say that observed cultural differences in human behavior necessarily undermine evolutionary explanations of behavior. In fact evolutionary theories of behavior often predict cross-cultural differences. This often occurs in the context of predicting cross-cultural associations, at the level of the country between two or more variables. For example, Moore et al. (2013) report that women's preferences for facial cues of high testosterone are higher in countries with a low United Nations human development index and are also positively correlated with pathogen stress (at the country level). From this they suggest that women may facultatively adjust their preferences for male testosterone level, preferring more masculine male faces when environmental conditions are harshest.

Such conclusions about individual-level mechanisms drawn from group-level analyses, however, can be problematic. As Pollet et al. (2014) explain, there is no automatic concurrence of relationship between variables when measured at an individual, compared with at a group, level. To assume such a concurrence is known as the ecological fallacy. It is possible that two variables may correlate negatively across individuals within a group but positively across groups. Such a scenario is known as Simpson's paradox and has been empirically observed with respect to wealth and voter preferences in the United States. Within a state, wealthier individuals are more likely to vote Republican than Democrat, yet wealthier states are more likely to have a higher proportion of Democrat voters (Gelman et al. 2007). So while higher group-level associations can arise as a result of individual-level associations and mechanisms, without comparing both group-level and individual-level data, it is unwise to presume that the two will concur and have a common cause.

In the case of preferences for masculine faces in the face of environmental harshness, therefore, Moore et al.' (2013) country-level analysis, taken on its own, provides little convincing evidence of individual facultative responses to pathogens. However, other studies adopting experimental

techniques have observed increased preferences for masculine faces after exposing participants to cues of environmental pathogens (Little et al. 2011). This suggests that Moore and colleagues' conclusions may well be correct but multilevel analyses of individual-level data nested within country-level data would be needed to determine whether such individual facultative responses to pathogens are all that is driving the country-level association (Pollet et al. 2014).

Cross-Cultural Comparisons in Nonhuman Animals

Cultural traditions in nonhuman animals, observed as stable between group differences in socially transmitted behaviors, have most commonly been identified and studied in primate species, particularly chimpanzees (Luncz et al. 2018). Unlike in humans, where cultural impacts on behavior are taken for granted, demonstrations of cultural divergence of behavior in nonhuman animals are received more critically. In addition, nonadaptive, stochastic proliferation of culture is often presumed to be unique to humans, with animal cultural divergences presumed to be adaptive responses to environmental differences between groups (Boyd and Richerson 1988) arising from individuals within a group relying on individual learning to arrive the local optimal solution to a problem (Laland and Janik 2006).

More recently, though, it has been demonstrated that some local chimpanzee nut-cracking cultures are sub-optimal, using less efficient nut-cracking methods than those seen in neighboring cultures. Critically, this is true even of adult chimpanzee females who immigrated into a group from a group with a more efficient nut-cracking strategy. That these females choose to adopt the less efficient strategy of their new community rather than persist with more efficient strategies with which they are familiar implies a personal cost to the individual that must be outweighed by the benefits of conforming to group norms (Luncz et al. 2018). Such cross-cultural investigations in nonhuman animals are therefore revealing similarities between human and nonhuman animal social behavior that could support the development of

theories of nonadaptive cultural evolution and social conformity that are not anthropocentric.

Conclusion

Comparing how groups and individuals of the same species behave across different cultural, environmental, and social contexts and how behavior changes with age and sex affords tremendous power to understand the evolution, function, and mechanistic bases of behavior. When incorporated into experimental designs, they can support direct causal conclusions about behavior. Whether considering human or nonhuman animal behavior, within-species comparisons alleviate the confounds associated with between-species comparative analyses, providing more robust tests of the hypotheses at hand.

Cross-References

- [Comparative Evidence](#)
- [Cross-Cultural Similarities](#)
- [Cross-Cultural Variation](#)
- [Field of Comparative Psychology, The](#)
- [Sex Differences](#)

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Wolves

► Canines

Women

► Female-Female Competition

Women and Competition, The Oxford Handbook of

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Definition

An edited book that focusses on women and competition.

Introduction

The Oxford Handbook of Women and Competition was published by Oxford University Press in 2017 and edited by Maryanne Fisher. It contains 39 chapters, plus an additional introduction and conclusion. The chapters span a range of topics representing the current state of knowledge regarding women and competition. These chapters are organized into ten sections. The majority of the chapters pertain to intrasexual competition among adult women, although some contributors include girls and adolescents, as well as examining men in addition to women. Most, but not all chapters rely on an evolutionary framework. The goal of the editor was to provide a definitive volume on the current state of this area, as well as concrete directions for future research.

Book Overview

In the Introduction, the editor states that the goal of this book is to provide a definitive overview of the field of women and competition, as well as directions for new research. She outlines the reasons for focusing on women and competition and includes a brief historical outline of the academic development of this area. A short review of the contemporary state of the topic is provided. She presents areas that are still relatively neglected in the study of women and competition, including the determination of the ultimate motivations and

consequences of competition, mating competition among cowives as well as nonheterosexual women, acute and chronic health consequences of competition, competition that is outside of a mating context, competition across girls and women's life phases especially later reproducing or post-reproductive women, and individual differences.

The ten sections that follow the introduction address a wide range of topics. The first section, called "Theory and Overview" addresses general views of competition throughout women's lifespans, theory pertaining specifically to sexual competition, and, to provide a phylogenetic context, competition among female primates. The section on "Social Status and Aggression" reviews women's social status and network formation, adolescent reproductive competition, cooperation within social groups as a cause of competition, female friendships, and how we generally underestimate women's ability to deceive, harm, or manipulate others. In "Communication and Gossip," contributors first review how women may align their communication of aggression to environmental signals and competitors' individual differences. Then, they examine women's use of gossip for competitive purposes both in general terms, as well as specifically for mate poaching, for example, and the use of gossip as a form of informational warfare by coalitions. The section on "Mate Availability and Mating Relationships" covers issues such as the implication of imbalanced sex ratio (including operational sex ratio) on competition, the relationship between women's mate value and competition, competition among single and romantically partnered women, mate copying and poaching, and the positive consequences of romantic relationship dissolution, in terms of sharpening one's competitive skills. Contributors of the section "Endocrinology and Psychobiological Considerations" present the psychobiological (including hormonal) responses of competition, and further, the role of fertility via menstrual cycle phase on competition. In the section "Health and Aging," authors examine how competition often leads to sleep disruption and relatedly health, reproductive suppression and eating disorders, and competition in relation to women's age and parity. "Motherhood and Family" includes a comparative review of competition among mothers,

the advantages of the interaction of cooperation and competition in human mothers, conflict among family members with respect to mate choice, and women's progenicide. The section called "Physical Appearance" pertains to how women may opt to engage in beautification procedures and have elective cosmetic surgeries to compete, how and why they may participate in beauty pageants, and the use of fashion as a vehicle for competition. In "Competition in Virtual Contexts," contributors discuss how women may engage in competition with virtual rivals (such as those seen in advertisements), rely on social media as part of their competitions, or use computer games to hone their competitive skills. The section "Competition in Applied Settings" spans a range of topics, from the conceptualization of women's competition in the workplace, to women's use of food to compete, women's aesthetics and ornamentation as signals, and women's engagement and attitudes towards competitive sport and physical activity.

Last, in the conclusion, the authors discuss historic views of women, and how Darwin and Freud's androcentric thoughts may pervade modern researcher's perspectives on women and competition. They argue that recent developments in the area clearly indicates that women's competition is normal, rather than a deviation from a typical state of cooperation or inactivity. Moreover, they propose that women's competition is not inherently negative, and it does not reduce the importance or meaningfulness of friendships and family ties.

Conclusion

The Oxford Handbook of Women and Competition represents a thorough snapshot of the state of contemporary knowledge pertaining to this area. Moreover, concrete directions for future research are provided, with the intention of spurring novel yet important lines of inquiry. The chapters collectively demonstrate the significance of examining women's competition, and show, to varying extents, the ways in which women compete within their friendships, families, social networks, and with strangers. This book contains a wide range of theoretical perspectives on the motivations,

attitudes, and behaviors involved in women's competition, for the purposes of understanding how, when, and why women compete. Such competitions may be viewed in ultimate terms, such as competition over mates, status, dominance, and resources that influence one's children, or be more proximally oriented, such as toward winning a prize, such as a medal or scholarships. This book represents an important contribution to this growing area of research investigation.

Cross-References

- ▶ [Female-Female Competition](#)
- ▶ [Maryanne Fisher](#)

Women Marry Up

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Synonyms

[Female hypergamy](#)

Definition

The phenomenon whereby women tend to marry men of a higher socioeconomic status than their own.

Introduction

There exists a stereotype that men are primarily attracted to looks while women are primarily attracted to status and wealth, meaning that, in terms of overall status, women tend to “marry up.” This is particularly obvious in instances where older men of considerable resources have relatively young and good-looking wives, such as

in the case of US president Donald Trump (b. 1946) and his wife Melania (b. 1970), a Slovenian model who is 24 years younger than him.

Female Hypergamy and Evolution

There is a large body of evidence that women tend to marry up (hypergamously) in terms of status to a far greater extent than is the case with men. This tendency for women to be more interested in the status, or the potential to gain status, of a potential partner has been shown to exist across cultures. Kendrick and Keefe (1992) have shown that females tend to be attracted to partners that are older than themselves, precisely because they are more inclined to sexually select for status and an older male is likely to have accrued more resources. Buss (1989) has demonstrated that across 37 cultures, women are more likely than men to value traits in potential partners that relate to “resource acquisition,” a characteristic regarded as much less important among men in their potential mates. It should be emphasized that there is much crossover with regard to the traits which males and females prize in potential partners (see Townsend and Wasserman 1998). Both sexes value personality traits such as honesty and kindness, for example, and there is a degree to which males are interested in the socioeconomic background of their potential partner. In addition, females are more inclined than males to select for attributes which may indicate that a man can protect them, such as height and muscularity (Buss 2003). Thus, sometimes females may select downwards socioeconomically or trade-off one aspect of status (such as income) for another (such as educational status) or trade status for physical attributes. But it is clear that, overall, there is a tendency for women to marry up in terms of status.

Buss (2003) has presented a plausible explanation for this finding. Men are more likely to select for signs of youth, health, and fertility, and thus for physical attractiveness, while women are more likely to select for signs of status or the potential to attain it. This is because the sexual relationship potentially incurs far greater cost for the woman

than for the man. The woman may become pregnant. With this mind, the woman and her offspring are more likely to survive if the male is prepared to invest in them and look after them. Accordingly, it makes sense for the female to select for a male who is likely to invest in her and who will have the resources to do so. So, we would expect her to select for indications of status to a greater extent than would the male, and we would expect females who had this inclination to be selected for and so more likely to pass on the genes. The male, by contrast, incurs much less cost from the sexual encounter, which would in principle make a strategy of simply mating frequently with large numbers of healthy women much more reproductively successful. As such, he is less inclined to select for status and more inclined to select for physical attributes such as facial symmetry, as markers of genetic health, and youth, as a marker of fertility. The result of this is that there is a tendency for women to marry down (hypogamously) in terms of physical attractiveness.

Female Hypergamy in Modern Societies

We might expect that the presence of increasingly sexually egalitarian societies in which females are increasingly financially independent of males might have the effect of altering these tendencies. The evidence indicates that the traditional tendency for female hypergamy remains across cultures and within relatively gender-equal societies (e.g., Rudman 2010), indicating that such tendencies have been selected for (see Buss 2003). For example, a survey of medical students by Townsend (1987) found that 85% of females believed that as their status increased their pool of potential partners decreased. Ninety percent of males believed quite the opposite.

In addition, more nuanced dimensions of status have been explored and the results have been found to be in the expected direction. For example, Dutton and Madison (2016) analyzed all marriages in Finland in the year 2013 between Finnish nationals and foreign citizens. They found that there was a greater tendency for Finnish women

to marry men from countries that were wealthier than Finland, whereas there was a greater tendency for Finnish men to marry women from countries that were poorer than Finland. They concluded that nationality is an aspect of status and it is something for which even modern European females are seemingly selecting. It would be fascinating if this could be replicated with marriage data sets from other countries.

Future Research

It would also be interesting for future research to examine the dynamics of status trade-offs within relationships. For example, a female university lecturer would have higher educational and social status than a male electrician or plumber, but she may well have a lower salary and thus lower economic status. Understanding the dynamics of these trade-offs is increasingly important when we consider that, in many Western countries, women are now more likely to go to university than men (Williams 2017), leaving many of them no option but to “marry down” in terms of educational status. Recent media reports have noted research finding an increasing trend whereby highly educated women, still single in their later thirties, freeze their eggs, with a view to attempting to have children later. An unpublished study of such women found that 90% had frozen their eggs to buy extra time to have children due to “a dearth of educated men” (Donnelly 4 July 2017). This could imply that, even among highly educated career women, the desire to marry hypergamously remains extremely powerful.

Consistent with this, it has been noted that in the UK, among the generation born at the end of the nineteenth century, there was a very high rate of spinsterhood among females from professional backgrounds. It has been suggested that the reason was the relatively high mortality rate of officers – as compared to troops – in World War I, with officers overwhelmingly coming from professional backgrounds. This meant that there was a pronounced dearth of high status males in relation to females after the War. The female refusal to

“marry down” thus resulted in noticeable levels of upper middle class spinsterhood in this generation (Nicholson 2008).

Conclusion

Female hypergamy can seemingly be found in all human societies and is underpinned by differential evolutionary pressures on females. They have been selected, to a greater extent than males, to be more interested in the status of their potential partner. Evidence that this phenomenon is indeed a matter of evolution can be found in its prevalence even in modern, sexually egalitarian societies.

Cross-References

- [Mate Value](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Reproductive Strategies](#)

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Women Pretending Orgasm

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Synonyms

[Faking orgasm](#); [Simulating orgasm](#)

Definition

Women acting as if they have experienced an orgasm when they have not, through vocalizations, breathing, body movements, muscular contractions, and/or verbal confirmation during the act.

Introduction

A substantial number of women (75–90%) do not consistently experience orgasm during sexual activity, and a considerable minority (5–10%) do not experience orgasm at all. Furthermore, when women do experience orgasm, it is typically in the context of masturbation or oral sex rather than penetrative sex (Brewer and Hendrie 2011). Despite the relatively low incidence of female orgasm during sexual intercourse, women frequently simulate orgasm through vocalizations,

breathing, and body movement. Indeed, a large proportion of women vocalize even when they are admit to having pretended a copulatory orgasm at least once in their lifetime (e.g., Kaighobadi et al. 2012; Séguin et al. 2015; Muehlenhard and Shippee 2010), and women who pretend to have orgasm are estimated to be at 13% of the time (Thornhill et al. 1995). Men are immensely interested in, and place great importance on, their partner's orgasm (McKibbin et al. 2010), though only 55% of men believe that they can identify when their partner is pretending to experience orgasm (Mialon 2012). Variability between women and across time may form part of the reason men are interested in copulatory orgasm, since women pretend orgasm more frequently when they have less consistent orgasm with their partner, suggesting that whether a woman pretends to experience orgasm or accurately signals orgasm may reveal important relationship information (Dove and Wiederman 2000). Interestingly, women whose partners ask if they have experienced orgasm are more likely to pretend orgasm, and over 50% of those who pretend orgasm report that they "feel guilty, but it is important to satisfy my partner" (Darling and Davidson 1986).

The variability in women's orgasms, along with men's intense interest in women's orgasms, may lead women to sometimes explicitly signal sexual enjoyment or orgasm when this is not experienced. For example, Brewer and Hendrie (2011) documented that while female orgasm occurs least frequently during penile-vaginal intercourse, more frequently during cunnilingus (receiving oral sex), and most frequently during masturbation, they also documented that the frequency of female sexual vocalizations (e.g., moaning, screaming) occurs in the opposite pattern. This pattern of orgasm vocalizations suggests that women sometimes embellish or fabricate orgasm cues. Indeed, a large proportion of women vocalize even when they are not experiencing orgasm (e.g., Brewer and Hendrie 2011). Further, women report faking orgasm more frequently than men perceive them to fake (Thornhill et al. 1995). Thus, women pretending orgasm is a common, deceptive copulatory

behavior, and researchers have only recently begun to illuminate the reasons and contexts surrounding this behavior.

Women's Reasons for Pretending Orgasm

A growing body of evidence suggests that female orgasm has one or more adaptive functions (e.g., sire selection via sperm retention, pair-bonding via partner satisfaction; see *Female Orgasm* for a review). For example, the most consistent predictors of female copulatory orgasm are partner's attractiveness and women's sexual satisfaction (e.g., Gallup et al. 2013; Sela et al. 2015). Ancestral men have likely attended to their partner's orgasm (reviewed in, e.g., Baker and Bellis 1995; Puts et al. 2012), perhaps as a way of increasing paternal certainty if orgasm facilitates conception (e.g., Baker and Bellis 1995), or because it increases relationship satisfaction and hence reduces the likelihood that women will seek extra-pair partners (e.g., McKibbin et al. 2010). Accordingly, men who are more invested and satisfied with their relationship are more interested in their partner's copulatory orgasm, and these associations are stronger for men who are at greater (vs. lesser) risk of partner infidelity (McKibbin et al. 2010). Men who are more satisfied with their relationship are more willing to invest in, and bestow benefits on, their partner (e.g., Shackelford and Buss 2000), providing an opportunity for women to gain more investment and commitment from their partner by increasing his satisfaction, perhaps by pretending orgasm.

Women consciously pretend orgasm to manipulate their partner's thoughts, feelings, and behaviors. For example, the vast majority of women (nearly 80%) report making copulatory vocalizations even when they know they are not going to orgasm (Brewer and Hendrie 2011), and women's most commonly endorsed reason for pretending orgasm is "I wanted to make my partner feel good about himself" (95% of the female sample; Séguin et al. 2015). Indeed, over 90% of women are confident that their vocalizations increase their partner's self-esteem (Brewer and Hendrie

2011), and about 90% report pretending orgasm for this purpose (Brewer and Hendrie 2011; Séguin et al. 2015).

Men place considerable interest in their partner's copulatory orgasm, though the extent of this may be related to their mate quality (Gallup et al. 2013) and to their partner's relationship satisfaction. Thus, a woman may pretend to orgasm in order to manipulate her partner into thinking that she perceives him to be of high mate quality and that she is sexually satisfied –making him believe that she is less likely to commit infidelity. Further, pretending orgasm may facilitate a dual strategy, whereby women maintain a long-term committed relationship and engage in short-term sexual relationships. Consistent with this explanation, women are most likely to pretend orgasm – thus displaying satisfaction with their partner – if they have previously engaged in sexual infidelity, if they anticipate that they will engage in future infidelity (Ellsworth and Bailey 2013), and if they signal sexual availability to other men (e.g., flirted with other men or neglected their partner at social gatherings; Thornhill et al. 1995). Consistent with this idea, men's concern about their partner's orgasm is positively associated with their perceived risk of her infidelity (McKibbin et al. 2010), and men react to discovering that their partner is pretending orgasm in a similar way as they do to discovering an infidelity (Shackelford et al. 2000).

Another advantage of increasing a partner's self-esteem via pretending orgasm is that he is more satisfied with the woman and their relationship, and this may be part of a broader mate retention strategy to reduce the risk of *his* infidelity. Mate retention tactics are behaviors used to keep a romantic partner from straying or being poached by a rival (Buss 1988; also see *Mate Retention*). Indeed, women who perform more (compared to less) frequent mate retention behaviors and women who perceive a greater (compared to lesser) risk of their partner's sexual infidelity are more likely to pretend orgasm (Kaighobadi et al. 2012). This is consistent with women's reports that they pretend orgasm to keep a partner from seeking extra-pair partners (Hite 1976). Further, risk of partner infidelity mediates the

relationship between likelihood of pretending orgasm and several mate retention tactics (Kaighobadi et al. 2012).

Another reason that women pretend orgasm is to manipulate a partner's orgasm timing. Cooper, Fenigstein, and Fauber (2014) report that stopping sex is an important motivation for pretending orgasm (e.g., "Because you want to stop sex but want to avoid your partner feeling uncomfortable in the future" and "Because you want to go to sleep"). Furthermore, 66% of women report using copulatory vocalizations to speed up their partner's ejaculation (Brewer and Hendrie 2011), and over 50% of women endorse "partner's orgasm seemed imminent" as an important reason they pretend orgasm (Séguin et al. 2015). Other advantages to women's ability to manipulate the occurrence and timing of a partner's orgasm may include lessening their risk of incurring physical damage from roughness, abrasion, and ensuing infection. Additional research is required to establish the physical benefits of manipulating male ejaculation.

Measures of Women's Reasons for Pretending Orgasm

Three scales assessing the reasons women pretend orgasm have been developed recently. Cooper et al. (2014) developed and validated the Faking Orgasm Scale for Women (FOS), with versions available to assess reasons for pretending orgasm during both sexual intercourse (i.e., vaginal sex) and during cunnilingus: the FOS – Sexual Intercourse scale contains 34 items assessing 4 factors: *Altruistic Deceit* (pretending orgasm out of concern for a partner's feelings), *Fear and Insecurity* (pretending orgasm to avoid negative emotions), *Elevated Arousal* (pretending orgasm to increase own arousal), and *Sexual Adjournment* (pretending orgasm to quickly end sexual intercourse). The FOS – Oral Sex scale contains 22 items assessing 4 factors: *Altruistic Deceit* (pretending orgasm out of concern for a partner's feelings), *Insecure Avoidance* (pretending orgasm to avoid feelings of insecurity), *Elevated Arousal* (pretending orgasm to increase own arousal), and

Fear of Dysfunction (pretending to cope with fear of being abnormal). Each FOS scale assesses the frequency of women's reasons for pretending orgasm on a scale of 1 (*Never*) to 5 (*Always*).

Séguin et al. (2015) developed the Motivations for Feigning Orgasms Scale (MFOS), which assess both men and women's motivations for pretending orgasm. The MFOS includes 25 items comprised of 6 subscales: *Intoxication* – high scores indicate that high alcohol consumption and/or drug use influenced the decision to pretend orgasm; *Partner Self-Esteem* – high scores reflect a desire to increase a partner's self-esteem or happiness by pretending orgasm; *Poor Sex/Partner* – high scores indicate that discomfort with a sexual partner, or lack of pleasure from the overall experience, influenced the decision to pretend orgasm; *Desireless Sex* – higher scores indicate that having sex without desire was an important factor in the decision to pretend orgasm; *Timing* – higher scores indicate that one's perception of a partner's orgasm timing influenced the decision to pretend orgasm; and *Insecurity* – higher scores indicate that feelings of insecurity with regard to oneself or the relationship influenced the decision to pretend orgasm. The MFOS assesses the importance of each reason in influencing the person's decision to pretend orgasm with a current partner (from the first time to the most recent time the person pretended orgasm with a current partner) on a scale of 1 (*Not at all important*) to 7 (*Extremely important*).

However, after conducting a confirmatory factor analysis, Séguin et al. (2015) demonstrated that their data was best represented by three models, each comprised of two or three factors: the *Pro-social Model* (Partner Self-Esteem and Timing), the *Get it Over with Model* (Poor Sex/Partner and Desireless Sex), and the *Feel Better Model* (Intoxication, Insecurity, and Improve Sex). These findings suggest that although they all lead to the same behavior, reasons for pretending orgasm may represent different sexual strategies and are perhaps sex-differentiated: women score lower than men on the Intoxication, Poor Sex/Partner, and Insecurity subscales.

McCoy et al. (2015) used the act nomination procedure and act frequency approach, to develop the Reasons for Pretending Orgasm Inventory (RPOI). The RPOI includes 63 items comprised of 3 components: *Improve Partner's Sexual Experience* – reasons that indicate an interest in increasing the sexual and emotional experience for the male partner and, to a lesser degree, for both partners; *Deception and Manipulation* – manipulative reasons such as hiding infidelity and exacting revenge; and *Hide Sexual Disinterest* – reasons that indicate desire to end a specific sexual event for lack of enjoyment. The RPOI assesses the frequency of women's reasons for pretending orgasm over the past month, on a scale of 0 (*Never*) to 9 (*Every time*), without specifying the type of sexual activity. The RPOI is currently being validated in a Brazilian context to further its utility as a cross-cultural measure (Lopes et al. in preparation).

Individual Differences in Women Pretending Orgasm

A number of factors may influence the likelihood that a woman will pretend to experience orgasm. Relationship factors are particularly important. For example, single women and women at greater perceived risk of (their partner's) infidelity are more likely to pretend orgasm (Darling and Davidson 1986; Kaighobadi et al. 2012) which may (falsely) signal sexual compatibility or relationship satisfaction in order to promote continuation of the relationship. Women with a greater number of lifetime sexual partners and those partnered to relatively low quality men are also more likely to pretend orgasm (Cooper et al. 2014; Wiederman 1997). This may serve to reassure men, concerned that his partner will engage in infidelity, that she is trustworthy. These men may (as a consequence) be less likely to engage in mate guarding, thus increasing opportunities for women to secure a high-quality extra-pair partner while minimizing the risk of discovery. This is consistent with previous research demonstrating that pretending orgasm is positively related to previous sexual infidelity and likelihood of future

infidelity (Ellsworth and Bailey 2013). Perhaps unsurprisingly, given the communicative and deceptive nature of pretending orgasm, women who believe that their partner can identify when they pretend to experience orgasm (without explicitly asking; Darling and Davidson 1986) are less likely to do so (Mialon 2012).

With regard to individual differences that are not relationship specific, women with higher levels of self-sexualization (which involves behaviors such as exposing one's body to gain sexual attention) and those holding the belief that sex can be a source of power (Erchull and Liss 2014) and women with higher sexual esteem (which reflects the tendency to evaluate oneself positively as a sexual partner; Wiederman 1997) are more likely to pretend to experience orgasm. Hence, in contrast to previous reports that pretending orgasm indicates female submission to androcentric society (e.g., Potts 2000), women may view the ability to pretend orgasm as a form of power or control. Indeed, there is a positive relationship between pretending orgasm and engaging in sexual behavior in order to attain a goal (McCoy et al. 2015). Furthermore, women with high levels of Machiavellianism, characterized by distrust, willingness to exploit others, and a manipulative interpersonal style, are more likely to pretend to experience orgasm in order to deceive and manipulate a partner. The association between Machiavellianism and pretending orgasm for this reason is moderated by relationship length, such that Machiavellianism exerts the greatest influence on women in long-term relationships (Brewer et al. 2016).

Conclusion

To conclude, female orgasm appears to have adaptive functions such as the retention of high-quality sperm, or strengthening of the pair-bond. Hence, men place considerable importance on their female partner's orgasm. Despite the apparent importance placed on female orgasms, these are not frequently experienced by women during penetrative sex, which may lead to a greater male interest in detecting and predicting them. Where

orgasm does not occur, women appear to sometimes strategically manipulate their partner's interest by pretending orgasm. Indeed, Nicolson and Burr (2003) report that women are less concerned with experiencing orgasm than often assumed, though women do wish to experience orgasm for the sake of their partner. This may take the form of vocalizations, body movements, altered breathing, or other such signals. The most common reason cited by women for pretending orgasm is to increase the partner's self-esteem, which may serve to strengthen the pair-bond and decrease the risk of infidelity and abandonment, resulting in continued access to resources and protection. Additional longitudinal research is required to establish the relationship outcomes (e.g., incidence or infidelity, relationship dissolution) associated with pretending orgasm.

Cross-References

- ▶ [Female Copulatory Orgasm](#)
- ▶ [Female Orgasm](#)
- ▶ [Female Orgasm and In-Pair Copulation](#)
- ▶ [Male Qualities and Likelihood of Orgasm](#)
- ▶ [Mate Retention](#)
- ▶ [Orgasm](#)
- ▶ [Orgasmic Disorders](#)

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Women Romantic Jealousy

► Sexual Jealousy Among Women

Women Romantic Partner Choice

► Female Mate Choice (Intersexual Selection)

Women Sexual Partner Selection

► Female Mate Choice (Intersexual Selection)

Women Use Verbal Derogation to Be Included

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Synonyms

Chastisement; Competitor derogation; Verbal aggression

Definition

Orally transmitted disparaging or negative statements targeting same-sex rivals for the purpose of reducing the target's perceived mate value.

Introduction

Associating with desirable same-sex friends – relational partners whose traits and characteristics can provide benefits to the self – may provide fitness benefits for women (i.e., increased access to desirable mates). However, such relationships can also be costly, most notably in the form of intrasexual competition. Women are known to engage in assortative selection of same-sex friends (SSFs) and peer relationships on factors such as personality, education, and attractiveness. However, having friends that are *higher* on these traits, particularly attractiveness, can foster intrasexual rivalry and competition. In response, women may engage in verbal derogation against SSFs and same-sex peers as a means of reducing the target's mate value in relation to the perpetrator, giving them a relative fitness advantage in intrasexually competitive domains.

Verbal Derogation as an Intrasexual Competitive Adaptation

Women's intrasexual competition for resources, such as access to desirable mates, is a well-documented phenomenon in contemporary social groups. Within these contexts, including SSFs, women may utilize indirect aggression in order to gain a fitness advantage against their same-sex rivals. One such tactic is verbal derogation or the deployment of negative and disparaging statements against a target competitor. This derogation is commonly directed towards a target's physical appearance or sexuality, that is, traits that are highly valued by the opposite sex in the appraisal of one's mate value (MV). Such statements are designed to suppress the perceived attractiveness or sexuality of the target in an attempt to decrease

their relative MV and give the perpetrator a competitive advantage (Baumeister and Twenge 2002).

Evidence that women may possess adaptations for monitoring threats that SSFs pose to their mate value and subsequent mating opportunities comes from research demonstrating that women can reliably estimate their own MV and that of another. For example, when a woman perceives that a SSF is more attractive than her, it increases perceived mating rivalry (Bleske-Rechek and Lighthall 2010). Furthermore, research demonstrates that women are particularly intolerant of attractive peers. Women perceived as attractive and who display signs of sexual availability are known to be the target of more indirect aggression from other women (Vaillancourt and Sharma 2011).

These effects are stronger when the perpetrator is in the fertile window of their menstrual cycle, when conception probabilities are highest. It is during this time that women stand to make the greatest gains in reproductive fitness from increasing their mating appeal relative to other women. Subsequently, during these time periods women are more likely to compete with each other for the most desirable mates and are more likely to implement derogative strategies such as rating other women as less attractive (Fisher 2004).

There are also costs associated with employing verbal derogation tactics. Fisher et al. (2010) found that those who employ verbal derogation towards another are perceived as less friendly, less attractive, and have a reduced MV. This may be, in part, why women employ indirect aggression (such as gossip) more than direct or physical aggression, as it allows for plausible deniability and a defense against culpability for the implementation of verbal derogation tactics. However, despite the potential costs associated with such tactics, verbal derogation is effective in its ability to disparage competitors, as shown by victims' reduced self-esteem, increased anxiety and depression, and (in severe cases) self-harm or suicide (Vaillancourt 2005). Inasmuch as intrasexual rivals who experience these negative outcomes are less effective competitors and/or are perceived to have a reduced MV, this provides

evidence for a distinct fitness advantage to the perpetrator.

Conclusion

Women's verbal derogation of SSFs and same-sex rivals, particularly during peak fertility, allow them to increase their relative MV and accrue fitness benefits within intrasexually competitive contexts. Although costs may be accrued by those who are caught employing such tactics, the prevalence and effectiveness of verbal derogation among SSFs denotes its continued utility toward increasing fitness during intrasexual competition.

Cross-References

- [Intrasexual Rivalry](#)
- [Mate Value](#)
- [Meta-Analysis of Sex Differences in Aggression](#)

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Women's Intrasexual Competition

- [Female-Female Strategies](#)

Women's Liberation

- [Feminism](#)

Women's Long-Term Strategies

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Synonyms

[Female's mate retention tactics](#); [Female's romantic partner maintenance](#); [Females' mate maintenance tactics](#); [Women's mate retention tactics](#)

Definition

Main strategies used by women from intrasexual competition to retaining the selected mate.

Introduction

According to the Sexual Strategies Theory (Buss and Schmitt 1993), women and men rely on short-term and long-term strategies for reproductive purposes. Women consistently prefer to secure long-term mates rather than engaging in short-term mateships. To secure long-term relationships, women use specific strategies in both selecting and retaining a romantic partner. Self-promotion and derogation of rivals are the most widely used higher-order strategies that women use in

intrasexual competition, long-term mate attraction, and mate retention in romantic relationships.

Men's Mate Preferences Form Women's Competitive Strategies

The fundamental components of Darwin's (1859) theory can be summarized as variation, selection, and retention. In a mating context, *variants* are the potential mates, *selection* refers to processes which lead to reducing the number of mates to few or one, and *retention* refers to strategies used to retain the selected mate (Buss 1988). After writing "On the Origin of Species," Darwin (1871) expanded on the natural selection theory and specifically on the second component, which is selection. He proposed that in the second phase of natural selection, certain characteristics are evolved in some organisms to help them compete with their same-sex rivals and capture the opposite-sex attention. This concept has been referred to as *intrasexual selection*. Opposite sex's attention mostly is captured by survivors of the "competition" and prefers the fittest mate with certain desirable characteristics that is called *intersexual selection*.

Intrasexual selection and intersexual selection have an asymmetrical association. Preferences of one sex should affect competitive strategies used by the opposite sex (Buss 1988). For example, men from different cultures typically prefer women with physical attractiveness, facial attractiveness, youth, and feminine features. Hence, women use certain strategies to gain or augment these desirable characteristics and acquire a high-quality male partner for long-term relationships. In short, many of the preferences men consistently show for women are based on reproductive outcomes and are directly related to a woman's mate value. Men throughout the world show a larger preference for women who are physically attractive, healthy, and facially symmetric, as these traits are indicators of the woman being able to successfully bear healthy offspring (Buss 1989). Men also have been shown to prefer youth because youth indicates a higher reproductive value. In addition, men also prefer someone who

is somewhat mature and creative, with a preference for a slow life history as this suggests that the woman would be around for long term and able to contribute to the children's long-term well-being.

Fertility, senescence of reproductive organs, social status, physical strength, emotional stability, and abilities to acquire reproductively relevant resources are among the well-established preferences that men and women place emphasis. These characteristics are core to association values, such as kin value and coalitional value. These characteristics also play an important role in mate value and make age central to human mating. Cross-cultural studies show that humans appear to have universal mate preferences, including those for the age of potential mates (e.g., Buss 1989). Such preferences were originally hypothesized to function in guiding people to adaptive mate choices, a fundamental domain of life for sexually reproducing organisms. However, they also should have implications for a considerable number of downstream behavioral outcomes, such as tactics of attraction, selection of mates as a function of mate value, determinants of mate retention behavior, probability of divorce, and a number of other important life outcomes.

Long-Term Versus Short-Term Strategies

There are hypotheses claiming that even if women engage in a short-term mating, it is in line with their long-term strategies and there are potential benefits for such acts. Symons (1979) drafted the Resource Accrual Hypothesis (i.e., in which female ancestors earned meats, goods, or services through a short-term extra-pair mating), and Better Genes Hypothesis (i.e., in which the woman copulates with another male other than her own long-term mate to bear a child with better genes). He also suggested mate Expulsion Hypothesis (i.e., women use short-term copulation in order to break up with their long-term mates easier) and Revenge Hypothesis (i.e., when women participate in short-term affairs as a vengeance for their husband affair). Honing Mating Skills Hypothesis suggests that, unlike men, women's objective when attending short-term mating is to enhance

their sexual, attraction, and seduction skills. According to Self-esteem Hypothesis, women can also use it to increase their self-esteem to be able to make better decisions for a long-term mating. Additionally, Buss and Schmitt's (1993) Preference Clarification Hypothesis of women's short-term mating is that they use it to assess if their short-term mate is a potential long-term one. Preference Clarification Hypothesis claims that women use short-term mating to shed light on their long-term decision processes. Furthermore, Commitment Hypothesis suggests that a short-term mating for a woman is a way to increase her partner commitment by evoking his jealousy. Mate Switching Hypothesis proposes short-term mating is a way to find a more valuable long-term mate.

Ever since Sigmund Freud who suggested that people look for the characteristics of their opposite-sex parent in a romantic partner, and the emergence of the complementarity theory (i.e., needs of each mate are different in kind and intensity and they are complementary instead of similar). To Thiessen and Gregg (1980) who considered similarity as the main reason why we choose certain mates, to Berscheid and Walster (1974) who proposed exchange and equity theory in which people seek for mates with whom they can exchange resources until a proximate equivalence in exchange has reached (Buss and Schmitt 1993). These different theories on human mating share two common notions. They developed their theories in a long-term context. However, none of the aforementioned theories point out that forming a long-term relationship is a strategic process. These theories claim that humans should seek for equity, similarity, and complementarity, but they do not specify the mating processes according to gender differences. They also do not specify which strategy is applicable for each sex. What are the strategic goals for each sex? What do women look for in a potential mate and likewise. These theories propose a single process, which shows who should mate whom (Buss and Schmitt 1993). Nevertheless, mating preferences change according to the context. Buss and Schmitt (1993) recommended Sexual Strategies Theory which articulates human mating is strategic and

humans look for a mate through whom they can dissolve adaptive problems their predecessor faced. Strategies are different according to the mating context, gender, and the mating temporal stability (short-term vs. long-term). Gender is a major axis in sexual strategies theory because biologically humans are different. For example, women fertilization is cyclical and internal, and after one act of intercourse, they are pregnant for 9 months. Temporal stability is the other major dimension of sexual strategies theory. Humans have evolved long-term mating strategies to solve the problem of commitment, long-term pair bonding, and parental investment (Buss and Schmitt 1993).

Benefits of Long-Term Mating for Women

By using certain long-term strategies, women tend to solve: (1) the problem of noticing a potential mate capable of investing, (2) the problem of noticing a potential mate who is actually willing to invest, (3) the problem of gene quality, (4) the problem of commitment, (5) problem of good parenting skill, and (6) the problem of physical protection (see Buss and Schmitt 1993).

Women try to solve the first three problems through winning intrasexual rivalry. It is an evolved adaptation in which women notice the potential mate with desirable characteristics (e.g., masculinity, physical attractiveness, symmetry, and intelligence) and the necessary resources for successful reproduction and assess his interest in a long-term mateship (Darwin 1871). Regarding these problems, Trivers (1972) suggested the *parental investment theory* which is defined as "any investment by the in an offspring that increases the offspring's chances of surviving" (Trivers 1972, p. 139). He also suggested that the more one sex invests in progeny; the more that sex will be discriminating. The more investing sex is typically the female, because she is pregnant for 9 months, then she bears the child, and she lactates the child for 2–4 years (Trivers 1972). Male resources benefit the woman and the children, but the male infidelity will divide his economic

and energy resources, which is not beneficial for the female at all. If defecting from the committed relationship, males' resources will be taken away from the female and her offspring toward an intrasexual rival (i.e., another female). Hence, women have adapted certain strategies to solve the second three problems (i.e., problem of good parenting skills, problem of physical protection, and problem of commitment). When pregnant and breastfeeding, women are vulnerable. Over our evolutionary history, women were in danger of food scarcity and being a target for aggressive perpetrators. A long-term mate could prevent these when the female is vulnerable and provide them with protection and nourishing food. Such long-term mate would also invest in the offspring and stay in the relationship to take care of the children. Women try to perform certain strategies to retain their long-term mates in order to stay safe from physical harm caused by opposite-sex violence or same-sex rivals and keep their mate committed to her and the offspring (Buss 1988).

Buss (1988) classified the strategies women and men use to retain their long-term mates. His classification rated mate retention strategies in a range from acceptable behaviors (e.g., vigilance toward mate's behaviors) to socially unacceptable behaviors (e.g., violence toward same-sex rivals). Later these strategies were classified into two domains of Benefit-provisioning strategies and Cost-Inflicting strategies. Benefit-Provisioning strategies try to reduce partner's infidelity likelihood by elevating relationship satisfaction and Cost-Inflicting strategies try to reduce likelihood of partner's infidelity by lowering partner's self-esteem (Miner et al. 2009).

Among all the mate retention strategies, women prefer low-risk and less physically aggressive strategies in their long-term mating. After the child is born, the presence of mother is more vital for the child's survival. A mother is the primary caregiver and lactates the child for 2–4 years. Women specially have evolved more interest in long-term mating and their reproductive success depends on the resources, which a potential long-term mate can provide them and their children (Buss and Schmitt 1993).

Women's Self-promoting Strategies

According to sexual strategies theory, the evolved mate preferences in one sex are the characteristics over which the opposite sex competes (Buss and Schmitt 1993). Perceptual mechanisms are evolved to circumvent problem of identification quality of a potential mate. Physical and behavioral characteristics associated with youthfulness are indicators of a woman's reproductive ability and men's mate preference. Beauty standards vary in different cultures and what is physically attractive in a culture can change over time. However, human societies have agreements on some aspects of beauty. For example, across cultures women's beautiful appearance is important both for males and for females. Additionally, men prefer their potential mate to be younger than themselves and attractive. Younger women are more preferred by men for a long-term mating because they represent productivity (Buss 1989).

Women's intrasexual and intersexual competition mostly circles around their physical and facial attractiveness. Attractive women are more probable to marry and have children. Hence, women's mate retention behaviors also circle around their beauty and they try to make their appearance seem young, attractive, and reproductively valuable (Buss 1988). They use self-promotion strategy to increase their partner's satisfaction and decrease possibility of infidelity. This strategy ergo is related to the characteristics that are preferred by men. Self-promotion is proposed to be most effective mate retention strategy for women (Buss 1988).

In this strategy, women manipulate their physical and facial characteristics on purpose and promote them deliberately. They use different strategies to enhance their physical and facial attractiveness in order to both select and retain a long-term mate (e.g., dress, jewelry, cosmetics, exercising, dieting, weight loss, skin tanning, and tattoo). Women cut off other costs, just to spend more on cosmetic products. They dress up and wear makeup, which can be considered as "traditional" appearance enhancement behaviors (Haselton et al. 2007).

Dieting, exercising, and desire to lose weight is another way to enhance appearance. Women are more worried about their weight when exposed to thin rivals and when primed with intrasexual competition, mating motives, and mate retention motives; they are more probable to use dieting pills and try to lose weight. Women also believe skin tanning enhances their appearance. Skin tanning can conceal skin imperfections, scars, and cellulite (Buss 1989).

According to recent advances in cosmetic surgeries, new techniques to promote appearance are available (Atari et al. 2016). Cosmetic surgeries can artificially promote appearance that is an indicator of good genes and fertility. The number of different cosmetic surgeries is increasing and this can be attributed to sociocultural and media pressures on women to obtain standards of beauty (Atari et al. 2016). For example, women can elevate their attractiveness by changing their waist-to-hip ratio (WHR) through a cosmetic surgery. WHR is one of the mate preferences for men and an indicator of their fertility. Women's interest in cosmetic surgeries is associated with their preference for many resources in the potential long-term mate (Atari et al. 2016). It is also positively associated with low self-perceived attractiveness, body dissatisfaction, intrasexual competition, perfectionism, envy, media influence, and menstrual cycle (e.g., Kalantar-Hormozi et al. 2016). Women interested in cosmetic surgeries prefer their long-term mate to be resourceful, attractive, educated, and intelligence (Atari et al. 2016). Overall, women who use Benefit-provisioning mate retentions report higher consideration of cosmetic surgery (Atari et al. 2017).

Women's Rival-Derogating Strategies

Women's success in intrasexual competition leads to attracting mate and derogating rivals. However, the procured mate should be retained over time. Derogating rivals is another strategy that is beneficial in intrasexual competition and retaining the acquired mate. This strategy also focuses on characteristics that are preferred by the opposite sex. Except in this strategy, women depreciate the

values of same-sex rivals. Men are evolved to prefer attractive young women with indicators of fecundity (low waist-to-hip ratio, full hips, and large breasts). When attending to invest a long-term relationship, they prefer a mate with sexual fidelity (Buss 1989). Hence, women aim to derogate their rivals over aspects of their physical characteristics (weight, body size, and facial characteristics) and sexual history. By disclosing information about the derogated rival, men will be less willing to form a long-term relationship with the targeted women because they perceive it is more possible that a promiscuous woman is sexually unfaithful. At the same time, derogator is suggesting that she will remain faithful in a long-term relationship. Derogating the rivals in such ways increases the derogator's self-esteem and increases the chances of a long-term romantic relationship for her. By using this strategy, derogators advertise herself to her current or potential partner (Fisher and Cox 2009). Derogation of rivals is a noncombative strategy in which women try to enhance their positive characteristics and bold them for their long-term mate compared to same-sex rivals by using verbal derogation of rivals and social manipulation (Buss and Dedden 1990).

Throughout evolution, women have acquired the ability to notice any signals sent from rivals to their existing mate. They try to keep their mate away from any sexual signals sent by rivals. For example, if competitors are wearing revealing or provocative clothes, women try not to introduce their mates to such rivals and they use statements like "boobs were about to pop out," "what is she wearing," and "she is dressed as if she wants to have sex with her professor." They also found that when wearing provocative clothes, women try to derogate other women compared to when they were conservative clothes (Vaillancourt and Sharma 2011). Women try to derogate the rival and reduce their value and in result, men find the derogated female less attractive (Fisher and Cox 2009). Derogation of rivals is specifically verbal in women and toward any signs sent from the rivals or any value that the mate prefer in a partner. They try to derogate the rival's appearance, loyalty, and sexual history. However, when using verbal

derogations, women should carefully devalue the rivals because they do not want their mate to think they are mean or inconsiderable (Schmitt and Buss 1996). Fisher et al. (2010) studied the effects of derogating a rival's physical characteristics, personality characteristics, and sexual history on men's perception of the derogator. Result indicated that men's view about derogator's personality desirability decreased. Hence, derogation of rivals remains the second strategy for women and they prefer to try appearance enhancement as their first long-term strategy (Fisher et al. 2010). They derogate rivals to promote their self-esteem and advertise themselves (Fisher and Cox 2009). Overall, derogation of rivals is a socially unaccepted strategy and is one of the "cost-inflicting" strategies among mate retention behaviors.

Gossip is a form of evaluative discussion about a third person. In an evolutionary context, gossip is another psychological adaptation in which values or flaws of a third person who is embedded within complex social networks are exchanged (McAndrew and Milenkovic 2002). Gossip has been studied both in individual and group level. A group prefers to talk about same sex negative features and devalue their physical, facial, and personal characteristics. Bromley (1993) also suggests that one of gossip's usage is reputation manipulation. Gossip is an intrasexual competition strategy and a mate retention strategy. It is a form of derogation of rivals, used more by women. Women use gossip for competitive social comparisons. They have greater interest in sharing and taking part in a gossip whether it is positive or negative. It is expected that women try to solve the adaptive problems they face and the content of women's topic should be different from men's gossip. Additionally, gossip content varies according to population density, availability of mates, and number of same-sex rivals (Walsh and Yun 2016). When exposed to an attractive rival, women's jealousy is provoked and they find negative gossip about that rival an indirect way to express their jealousy (Wert and Salovey 2004). On the other hand, women may find negative gossip about a potential mate and transmit it to same sex rivals in order to throw them off of the scent. Women prefer not to gossip about their

mates, they do not talk about their friends or relatives, and they easily recall the gossip about potential rivals mating skills (De Backer et al. 2007). Additionally, women can share the content of the gossip with both their partners and same-sex friends, but men prefer to share their gossip with their romantic mate not their male friends (McAndrew et al. 2007). When the gossip comes from an attractive mate with high values, it is an effective way to derogate same-sex rivals.

Overall, younger women and attractive women with higher values are more interested in gossip. It is also worth noting that frequency of gossiping does not have any association with women's relationship status because single women try to derogate rivals by gossiping about them with potential mates and mated women need to perform this strategy to retain their mates (Massar et al. 2011). Women can use these two long-term strategies concurrently (i.e., derogation of rivals and appearance enhancement). They can make themselves desirable by wearing makeup and revealing clothes and at the same time derogate a rival by gossiping about their sexual history, appearance, or social standing with their long-term partner. However, the gossip must be subtle and it should not point any weakness that the derogator herself has (e.g., gossiping about a rival's too much makeup while wearing one herself) (Campbell 2004).

Other Strategies Women Use in a Long-Term Relationship

Although Cost-Inflicting mate retention strategies cannot predict women's consideration of cosmetic surgery, but research shows that there is a positive association between women's consideration of cosmetic surgery and six specific mate retention strategies: vigilance, monopolization of time, punish mate's infidelity threat, derogation of competitors, physical possession signals, and possessive ornamentation (Atari et al. 2017). Women avoid losing their long-term mate by threatening to leave them and by verbally proclaiming their long-term relationship with their mate to others and rivals. These strategies explain women exhibiting relational

aggression more than men (Campbell 2005). Women also threaten their partner by claiming to be sexually unfaithful which is why men place more importance in partner's sexual fidelity compare to women (Schmitt 2005).

Women's long-term strategies help them to solve the adaptation problems they face. One of women's adaptation problems is selecting "good genes." When copulating with attractive men (i.e., attractiveness is an indicator of "good genes"), it has been shown that women experience more frequent orgasms compared to women who copulated with less attractive men (Shackelford et al. 2000). Orgasm in ovulation elevates chance of conception. A woman's pregnancy encourages the partner investment and commitment (Thornhill and Gangsted 2008). Women are more likely to pretend orgasm during copulation. Women reported reasons for pretending an orgasm. One of the reasons was to keep the mate committed to his current relationships and reduce the likelihood of relationship dissolution (for a review, see Muehlenhard and Shippee 2009). Women who pretend an orgasm perform mate-retention strategies more frequently (Kaighobadi et al. 2012).

Conclusion

Overall, women employ a number of long-term strategies in mate attraction and mate retention (Chaudhary et al. 2018). Men's differential preferences in long-term mating drive women's intrasexual rivalry which can be reduced to self-promotion (e.g., appearance enhancement) and rival-derogation (e.g., gossip about rivals' promiscuity). After securing a long-term dependable partner, long-term strategies do not diminish. Women (usually less frequently than men) use a number of mate retention strategies to keep their romantic partner around. Factor analytic and clustering techniques have revealed that such behaviors can be categorized into cost-inflicting (e.g., violence against rival women who show interest in one's husband) and benefit-provisioning (e.g., cosmetic surgery as a beautification procedure) tactics.

Cross-References

- [Female-Female Competition](#)
- [Mate Retention](#)
- [Men's Mate Preferences](#)
- [Sexual Conflict Theory \(Middle-Level Theory in Evolutionary Psychology\)](#)
- [Women's Intrasexual Competition](#)

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Women's Mate Interests

► Women's Mate Preferences

Women's Mate Preferences

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Synonyms

Female mate interests; Female partner preferences; Women's mate interests; Women's preferred partners

Definition

The qualities that women are interested in when selecting partner's for short- or long-term relationships.

Female Mate Preferences

Introduction

Within evolutionary psychology, the study of women's mate preferences is a central and important topic. This chapter will discuss the general strategies that women tend to use when looking for a mate. Following this, there will be an overview of what is known about female mate preferences, focusing on three major features known to be most important in women's mate preferences: a man's face, his body, and his behavior. The chapter will conclude by covering several contextual factors that can cause women's mate preferences to shift in predictable ways.

Mating Strategies

In almost all species, including mammals, males and females differ in how much they invest in their offspring in terms of time, resources, and energy. The ultimate evolutionary force is maximizing the number of offspring that live to reproduce and extend an individual's genes into future generations. According to Parental Investment theory (Trivers 1972), the sex that makes greater initial investments in offspring ought to be the "choosier" sex when it comes to mate preferences and mate standards. In humans, females must make larger initial investments in offspring than men because females gestate, lactate, and provide most of the basic care of infants at the beginning of their lives.

Many studies have documented differences between men and women in their general mating strategies, usually consistent with parental investment theory. Women, for example, tend to have lower sex drive than most men, they desire fewer sexual partners and want longer-term relationships, and they are more likely to regret past sexual encounters. This is consistent with the notion that women – because they invest more in offspring – are choosier about when and with whom to have sex, and they value partners who will be committed to them and their children. These presumably evolved differences in mating strategies should also affect the types of mates that women prefer. Across 37 cultures, Buss (1989) found that women favor men who are more capable of acquiring resources (e.g., larger amounts of

money, higher social status) presumably because such men can better provide for offspring, increasing the likelihood that offspring will survive to reproductive age. These effects, however, also depend on the roles of women in relation to men within a given culture. Eagly and Wood (1999) reanalyzed the 37 cultures data and found that these sex differences are smaller in societies that have more egalitarian views of men and women and when women hold greater social, economic, and/or political power in a society.

Women also prefer mates who want longer-term commitments, most likely because such men are more able and willing to provide long-term resources for their children. However, there is considerable variation within women in these and other mate preferences. According to Gangestad and Simpson (2000), women evaluate potential mates on two basic dimensions: (1) a man's resources and ability to be a good long-term provider and (2) evidence of him having "good genes" (signaled by his health, attractiveness, and related cues), which could be passed on to offspring. There will now be a discussion of the mate qualities women should have evolved to prefer in a man's face, body, and behavior, as well as the contextual factors that tend to alter what most women prefer in mates.

The Face

Three aspects of the face are believed to signal the quality of a man's physical condition or his "good genes": symmetry, averageness, and sexually dimorphic features. Humans tend to be bilaterally symmetrical, with the left and right sides of their bodies being similar in size and proportion. If, however, individuals encounter disturbances during development (e.g., they have deleterious genetic mutations or are exposed to environmental toxins or pathogens), their bodies become somewhat asymmetrical as they grow. Greater facial and body symmetry, therefore, should be viewed as more attractive because greater symmetry indicates that an individual has withstood these disturbances better than others across development.

Facial averageness is also perceived as attractive in mates, because it is another possible marker of good genes. Average facial features tend to

reflect the normal (nondeleterious) genes that exist in a population. Thus, the more a face differs from the population average, the more a person is likely to possess genetic mutations or other defects that might impair his or her successful reproduction.

Sexually dimorphic features are physical qualities that evolved differently between the sexes. Men, for example, have more facial hair, more prominent brow ridges, and are more muscular than women, on average. Sexually dimorphic traits are indicative of a man's level of testosterone and, therefore, his ability to attain and maintain social status and be a good resource provider. Now there will be a review of studies that have examined how women view these theoretically relevant facial features when evaluating men as potential mates.

Facial Symmetry

Facial symmetry is a quality that is attractive in both men and women, and it is believed to be an indicator of overall health. Indeed, greater facial symmetry in men tends to be associated with greater social dominance and better reproductive health as well as more facial averageness and more sexually dimorphic (masculine) features (e.g., Fink et al. 2001; Van Dongen and Gangestad 2011). Swaddle and Cuthill (1995), however, found that if the mean size of certain facial features was held constant, the connection between greater facial symmetry and higher rated facial attractiveness was eliminated, suggesting that the average size of certain facial features may partially explain why symmetrical faces tend to be more attractive.

Facial Averageness

The first evidence suggesting the greater attractiveness of average faces came from computer simulations in which faces were morphed together to create composite faces. As the number of faces in a composite increased, so did their perceived attractiveness (Langlois and Roggman 1990). Morphed faces are usually rated as more attractive than virtually all of the individual faces used to create a composite (Rhodes et al. 2001). Although average male faces are viewed as slightly less

masculine than distinct faces, they are perceived to be healthier and may be an honest signal of health quality.

Sexually Dimorphic Features

A large amount of research has investigated the attractiveness of sexually dimorphic (more masculine) characteristics of male faces, which include a longer lower face, more facial hair, and more prominent brow ridges and cheekbones. Greater facial masculinity is known to be associated with higher testosterone levels (Penton-Voak and Chen 2004). Along with facial averageness and symmetry, more sexually dimorphic facial features increase how healthy women perceive men to be and how healthy they actually are (Thornhill and Gangestad 2008). There is debate, however, about whether and when masculine faces are preferred in mates. Some studies have found that men who have more feminine faces are preferred in certain mating contexts. These findings may be attributable to either the specific features of the face being manipulated or the morphing techniques used. In addition, as highlighted later, preferences for more masculine features tend to fluctuate with changes in the environment, especially where a woman is in her menstrual cycle.

Facial hair is another sexually dimorphic trait that affects female mate preferences. Neave and Shields (2008) had women rate men who had no beard, a light stubble, or a full beard and found that as beard length increased, so did the male's perceived dominance and aggression. Women were most attracted to an intermediate beard length (a light stubble), at least in younger men.

The Body

A man's body also provides cues to the quality of his genes and/or his status within a society. Female preferences for different features of male bodies may have been shaped by selection pressures, leading women to value certain attributes. Similar to beard length, intermediate levels of muscularity are most attractive to women, on average (Frederick and Haselton 2007). Moderate muscularity tends to signal better health, whereas too much muscularity is costly to both develop

and maintain, hindering health. Other important body features are the width of a man's shoulders relative to his hips and height. Women typically prefer men who have a higher shoulder-to-hip ratio, and such men have more sex partners and engage in first sex at an earlier age (Hughes and Gallup 2003).

Women are also attracted to men who are taller. Fink et al. (2007) investigated how the ideal height of a partner shifts based on a person's own height and found that relative height was more important to attractiveness than total height. That is, women who are shorter than average find slightly shorter men (who are still taller than them) more attractive. One explanation for this preference is that height may be a cue to a mate's status in society. Indeed, if a man is taller, he is more likely to have more wealth and resources.

Another cue that women consider is the quality of a man's voice. Male voices that have lower fundamental frequencies and men who have larger vocal tracts are perceived as more attractive mates (Feinberg et al. 2005). Attraction to these vocal features might be explained by the link between voice pitch and testosterone levels, with deeper voices signaling higher testosterone, which may be another marker of higher status and/or genetic quality.

Behavior

In addition to physical appearance, there are certain male behaviors that women may have evolved to prefer in potential mates, because they are cues of a man's social status and/or his genetic quality. One cue is the amount of social dominance exhibited by a man. When trying to attract a romantic partner, men often try to demonstrate feats of strength or behave aggressively toward other men during competitive tasks. Women are also more likely to feel negatively about their current romantic partner and relationship when they are shown alternative partners who have more dominant personalities (Kenrick et al. 1994). However, women do not derogate their current partner and relationship after seeing physically attractive alternative partners, which suggests that social dominance is a powerful, independent behavioral cue.

Although dominance is important, women also consider other personality traits when selecting mates. Jensen-Campbell et al. (1995) had women observe a male who displayed either high dominance, high agreeableness, both, or neither. High dominance led men to be rated as more attractive, only if men were also high in agreeableness. Men who were low in agreeableness were rated as less attractive, regardless of their level of dominance. Other studies have found that men who display kindness to women, but dominance to other men, are perceived as most attractive by women. These findings are consistent with the premise that women evolved to find displays of male dominance attractive, most likely because they are indicative of a man's social status. However, women are *most* drawn to men who direct aggression and dominance toward other men, decreasing the chance that such men might pose a threat to their female mates.

Risk-taking is another behavioral tactic that men use to attract mates. Skateboarders, for example, perform riskier tricks (with an increase in both successes and failures) when they are being observed by an attractive female experimenter than by an attractive male experimenter (Ronay and von Hippel 2010). Importantly, men observed by an attractive female had higher levels of testosterone, which were assessed immediately after they had performed tricks in front of the female experimenter.

Engaging in certain risk-taking behaviors should have been evolutionarily adaptive because ancestral women may have been more likely to mate with men who took calculated risks, especially if the outcomes were successful. Very little research, however, has examined whether and how women perceive different types of risky behaviors enacted by men. One study (Petratis et al. 2014) asked women to rate the attractiveness of men who were taking two types of risks: "modern-day" risks (e.g., not wearing a seat belt) or risks faced by our ancestors (e.g., handling/dealing with wild animals). Women rated men who took more risks as more attractive but only if those risks were in the ancestor category. Attraction to certain risk-taking behaviors enacted by men may have been beneficial to women in

ancestral environments. Men who engaged in greater risk-taking may have been generally more successful at obtaining necessary food or resources needed for survival or at fending off adversaries.

In sum, women typically prefer men who are more socially dominant (but kind toward them) and who engage in some degree of risk-taking. Nevertheless, one must also take the broader social and environmental context into account to gain a more complete and accurate picture of female mate preferences. These contextual factors will now be discussed.

The Context

A growing body of research has begun to address how contextual variables influence female mate preferences. Three contexts shape a woman's attraction to potential mates: the general environment in which she lives; her local, social, and interpersonal environment; and where she is in her menstrual cycle (the fertile vs. infertile phase) when evaluating potential mates.

General Environment

The general environment in which a woman lives provides important contextual information that can alter her mating strategies and, therefore, affect her mate preferences. One important environmental variable is the local operational sex-ratio (i.e., the number of men relative to women seeking mates in a population). When there are more women and men in a population, the tendency to engage in short-term relationships and have more sexual partners increases, because men, being fewer in number, can act on their short-term mating tendencies. Moreover, when there are more men in a society, a man's socioeconomic status becomes much more predictive of his marital status, with higher SES men being more likely to marry (Pollet and Nettle 2008). Conversely, when women have more potential mates to choose from (i.e., when women are in the mating minority), they become choosier and prefer mates who have more resources to offer.

Another important variable is the amount of pathogens in the local environment. In pathogen-prevalent environments, the threat of disease is

higher, particularly for young children. In such environments, women ought to value indicators of a man's genetic quality more than his status or resources, given that "good genes" may protect subsequent offspring from the threat of disease. Indeed, women who live in environments with more pathogens value a man's physical attractiveness more than they do in low-pathogen environments (Gangestad and Buss 1993). Moreover, making the threat of pathogens salient to women shifts their mate preferences in theoretically consistent ways. Women who view information emphasizing high-pathogen prevalence shift their mate preferences to men who have more masculine characteristics and are more symmetrical compared to women who view cues of low-pathogen prevalence (Little et al. 2011).

Resources and a woman's access to them is another set of environmental factors that can affect female mate preferences. In societies that are more egalitarian with respect to gender issues, the mating preferences of men and women are more similar (Eagly and Wood 1999). Nevertheless, women who live in high socioeconomic status areas are more attracted to men who have a larger shoulder-to-hip ratio, whereas women in low SES areas prefer men who have a higher body mass index (Swami and Tovée 2005). These results are consistent with the notion that women evolved to prefer male traits that would have facilitated the survival and eventual reproduction of their offspring. A woman who has higher social status is likely to have enough resources to protect and provide for her children, so obtaining "good genes" should be prioritized and cues of physical strength should be valued, whereas a woman who has lower social status should prefer men who demonstrate their resource acquisition potential.

In sum, the broader environment in which a woman lives does shape her mate preferences. The operational sex-ratio in the local environment, cues of pathogen prevalence, and environmental demands that increase the importance of providing resources shift whether a woman's mate preferences focus on pursuing men who have "good genes" versus those who can provide sufficient resources to her and her offspring.

Local Interpersonal Environment

Mate choice also takes place within a woman's local interpersonal environment, which influences with whom she interacts, her relative mate value, and the resources to which she does or does not have access. When examining women's preferences for warmth, attractiveness, and status in a mate, women who rate themselves as high in a specific category (e.g., warmth) are more likely to have higher and less flexible ideal standards for that category (Campbell et al. 2001). Women who believe they are more attractive also prefer characteristics such as greater facial symmetry and more sexually dimorphic features in mates. These and other results imply that women who are more desirable tend to adjust their mating strategies to attract the most desirable male partners. When there are more partners to choose from, women are in a better position to obtain men who score higher on all important qualities, and when the pool of available mates is smaller, their standards are lowered.

Whether a woman wants a short-term or a long-term relationship is another important determinant of what she finds attractive in a mate. When a woman is interested in a short-term relationship, markers of genetic quality are more important and more masculine facial and body features are preferred (e.g., Little et al. 2002).

Another critical interpersonal variable is incest avoidance. Children born to parents who are biologically related (e.g., cousins) are more likely to have physical abnormalities and health problems due to the inheritance of recessive genes. Accordingly, people rely on environmental cues to determine with whom they might be genetically related. The length of time a female has lived with a male during childhood and how much time the male has spent with her biological mother both decrease how attractive a man is to a woman, because these cues are associated with the likelihood of being biologically related (Lieberman et al. 2007).

Both the general environment and the interpersonal environment can influence a woman's mate preferences in significant ways. Many of these effects, however, are qualified by whether

women are in the fertile versus the nonfertile phase of their menstrual cycle.

Menstrual Cycle

Two phases of a woman's menstrual cycle tend to have different effects on her mate preferences: (1) the follicular (fertile) phase and (2) the luteal (nonfertile) phase. The follicular phase ends with ovulation, the time when having sex is most likely to result in a pregnancy. During the luteal phase, the chances of conception are much lower.

Women should have evolved to shift their mate preferences depending on the probability of conception (Thornhill and Gangestad 2008). Specifically, women should be more attracted to men who display indicators of "good genes" when they are looking for a short-term relationship rather than a long-term commitment. Consistent with this idea, when preferences for facial features are examined, women in the follicular phase are more attracted to men who have more masculine features compared to women in the luteal phase, suggesting that where a woman is in her menstrual cycle may partially explain some past mixed findings (Penton-Voak and Perrett 2000). This shift in preference toward more masculine features has also been demonstrated with more masculine voices and greater facial symmetry.

Where a woman is in her cycle also affects the specific behaviors she finds attractive in men. For example, socially dominant behaviors are significantly more attractive to women who are in the follicular phase (closer to ovulation) than in the luteal phase (e.g., Gangestad et al. 2004; Cantú et al. 2014). A recent meta-analysis confirmed that these shifts in attraction are fairly consistent when women are pursuing a short-term mate while ovulating (Gildersleeve et al. 2014).

Conclusion

This chapter has reviewed a wide variety of findings about the qualities that most women prefer in a mate. Early research focused primarily on the general preferences that women report. More recent research has focused on within-person variability in mate preferences and the specific

environmental contexts that moderate (shift) these effects. Although more is now known about women's mate preferences and the evolutionary logic behind them, more research is needed to clarify how these evolved preferences affect established romantic relationships across time.

Cross-References

► Ovulation

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Women's Mate Retention Tactics

► Women's Long-Term Strategies

Women's Mate Value

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Synonyms

Mate quality; Quality of a “catch”

Definition

Mate value is the construct that broadly describes one's value as a mate to a potential or actual partner.

Introduction

Mate value is a construct that is thought to holistically measure the value of an individual as a mate (Edlund and Sagarin 2014). Although many measures of mate value use similar methods of assessing men's and women's mate value, research has demonstrated that there are differences in the qualities men and women seek in a mate (although it is worth noting that many similarities exist as well). For instance, research has shown that men seek youth, physical attractiveness, facial attractiveness, and feminine features in their partners (Buss 1989). These preferences have been demonstrated worldwide (Schmitt 2005), and this independently suggests that these traits directly contribute to a woman's mate value.

Reproductive Value

Another reason to think that youth, facial attractiveness, and feminine features relate to women's mate value is the concept of reproductive value. Reproductive value is an estimate on the number of future children a person is potentially able to have moving forward in time, and it is one of the main pressures contributing to women's mate value (Barton and Etheridge 2011). Importantly, the previously identified traits contribute to women's reproductive value. Unlike men's reproductive value which does not rapidly decrease with time, a woman's reproductive value is always decreasing from the time she starts menstruation (as high quality eggs get released and are not replaced). A woman's reproductive value reaches zero with the onset of menopause (whereas a man's reproductive value does not have a corresponding zero value). As such, youth, physical attractiveness, and beauty constitute an important part of women's mate value.

To illustrate this concept, in a budgetary task of American undergraduates designing their ideal partner, men and women designed very similar ideal mates for themselves, only showing slight gender differences in certain areas. The men considered attractiveness to be necessary in a mate, whereas women put emphasis on resources

(Edlund and Sagarin 2010). Additional research suggests that men believe the ideal age for a woman is just under 25 years old, which corresponds to women's peak fertility (Buss 1989). This also suggests that men prefer women who are more likely to have a stable life before pursuing the idea of children.

Physical Attractiveness

As mentioned earlier, another factor that contributes to women's mate value are feminine features. Perhaps the most important feminine feature is the waist-to-hip ratio. In women, waist-to-hip ratio represents an evolutionary cue that a woman is capable of carrying and bearing children to term. This, along with physical attractiveness, serves as an important marker of mate value. A study by Fernandez et al. (2014) found that younger women compete more fiercely amongst themselves to increase their mate value, whereas older women do not compete as much. Fernandez et al. also found that in order to increase their mate value, women have become cognizant of their Body Mass Index (BMI). Their research suggests that BMI has an effect on mating success in women, therefore implying that the type of physical attractiveness men seek in women is related to a woman's ability to maintain a healthy body.

Another factor that directly contributes to the mate value is facial symmetry, or the degree to which one side of the face is similar to the other side of one's face. Grammer and Thornhill (1994) found that facial symmetry in addition to feminine features were indicators of physiological and genetic health. Grammer and Thornhill's research was based off of the parasite theory, which suggests that sexual selection looks for traits that display resistance to parasites. It has been found that organisms that are parasite resistant are not only healthier, but also are more successful in the competition for mates. Therefore, men who seek women with facial symmetry and feminine facial features are likely finding women who are parasite resistant (and therefore a higher mate value).

Other factors such as life history also are thought to contribute to mate value. Life history

is the physical and social growth across a life-span that can be limited by the accessibility of resources that may be assigned to various tasks or goals. Individuals who have a slow life history (where an individual lives in a stable environment and is able to finish schooling and is able to obtain a quality job) are viewed as having a higher mate value than those with a fast life history (Dillon et al. 2013). Among the things that a slow life history is associated with is how physically attractive an individual is perceived as (such that people who have a slow life history are seen as more attractive).

Conclusion

In short, many of the preferences men show for women are evolutionarily based and are directly related to a woman's mate value. Men throughout the world prefer a woman who is physically attractive, at a healthy BMI, and who are symmetric, as these traits are indicators of the woman being able to successfully bear healthy children. Men also have been shown to prefer youth because youth indicates a higher reproductive value. Yet, men also want someone who is somewhat mature and creative, with a preference for a slow life history as this suggests that the partner will be around for long term and able to contribute to the children's long-term success.

Cross-References

- [Evolutionary Standards of Female Attractiveness](#)
- [Mate Value](#)
- [Mate Value Inflation](#)

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Introduction

This entry provides a brief overview of research about associations between women's economic resources and their long-term partner preferences. These associations are of special interest in light of women's tendency to attribute more importance to financial resources in a partner than men do (Buss 2011). Whether this pattern is a result of evolved adaptations, sociocultural factors, or some combination of the two continues to be a subject of controversy. Evolutionary psychological theory stipulates that female reproductive success depends on resources necessary to raise offspring. Hence, women should prefer partners with an ability to invest direct resources in offspring, resulting in a preference for good financial prospects (e.g., Buss and Schmitt 1993). From a sociocultural view, pervasive gender inequalities make women more likely to adopt domestic rather than provider roles. To compensate for the limited resources associated with domestic work, women seek out mates with good economic prospects (e.g., Zentner and Eagly 2015).

Women's Movement

► Feminism

Women's Personal Resources

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Synonyms

Family roles; Gender equality; Income; Pay equity

Definition

Material assets (e.g., income, property) owned by women.

Hypotheses

Drawing from these premises, the two theories make different predictions about the role of women's own financial resources in their long-term partner preferences. According to evolutionary psychologists, women's preference for financially secure men is an evolved adaptation and should therefore be impervious to their own financial resources (Buss 2011). From the standpoint of sociocultural theory, women's dependence on men for resources should diminish as their own financial autonomy increases, thus lessening their emphasis on a mate's financial prospects. Evaluating the empirical merits of diverging assumptions in research on mate preferences requires consideration of evidence from multiple domains, in which mate preferences of women and men vary in major ways: (a) across cultures, (b) across historical periods within the same culture, and (c) across individuals (Zentner and Eagly 2015). In what follows, I will review and integrate

some key findings from each of the respective research literatures.

Cross-Cultural Research

Cross-cultural studies can examine whether national differences in Gross Domestic Product relate to the importance women attribute to their future partners' financial prospects. More important than absolute levels of wealth, however, is women's access to resources relative to men's. This ratio is captured by gender equality indices. Gender equality tends to be associated with a decrease in the importance women place on partner earnings relative to men and in absolute terms (see Zentner and Eagly 2015, for a summary). The size of the association varies depending on the measures of gender inequality used and the classes of control variables included. In general, associations tend to be stronger when comprehensive measures of gender inequality are used, such as the relatively recent Gender Gap Index (Zentner and Mitura 2012), and weaker when narrow measures of gender equality are used, such as the Gender Empowerment Measure (Conroy-Beam et al. 2015).

Historical Trend Analysis

Trends over time provide a second source of information about associations between women's own financial resources and the importance they attribute to earning prospects in a partner. In most nations, the pay gap between women and men has gradually diminished over the last decades. This is largely attributable to women's increasing participation in market work. As a result, women have become financially more autonomous. From an evolutionary psychology viewpoint, progress towards pay equity should have little effect on women's partner preferences. From a sociocultural view, one would expect this development to reduce the importance that women attribute to a partner's earning prospects.

The available data on mating preference across time are limited because they rely on US

replications of a particular survey of preferences initially administered in 1939, with follow-ups conducted at regular intervals up to 2008. Comparisons across follow-ups are difficult before 1985, when ratings of mate preferences were added to rankings (Boxer et al. 2015). Between 1985 and 2008, women's annual income as a percentage of men's increased from 65.2 % to 77.1 % (*The gender wage gap 2012*; Institute for Women's Policy Research, 2013). Women's importance ratings for financial prospects did not change during this period. However, women's importance ratings for favorable social status, intelligence, or ambition (all features indicating resource acquisition potential according to evolutionary psychology theory) did show a declining trend over the same period (Boxer et al. 2015).

Individual Differences Research

A third research approach capitalizes on the large variation in mate preferences between women of a given culture. The question addressed by studies using this strategy is whether differences in women's economic resources are systematically related to differences in the emphasis that these same women attribute to financial prospects in a partner. Although some earlier studies reported a *positive* correlation between women's financial resources and their preference for wealth in a partner (see Buss 2011, for a summary) more recent studies did not (e.g., Anderson and Klofstad 2012; Fales et al. 2016). A large-scale study that, in contrast to earlier studies, used a nationally representative sample of 4,790 US citizens is particularly informative. Participants were asked about their annual income (categorized from under \$25,000 to \$150,000 or more), as well as the importance they attributed to a partner "making at least as much money as they do" (Fales et al. 2016). The relationship between own income and income desired in a partner was $\beta = .07$ for women and $\beta = .03$ for men. The interaction between sex and income was not significant, indicating that the association did not differ by sex. In a larger but nonrepresentative sample of visitors to the NBC News website

examined by the same authors, the relationships were similar ($\beta = .07$ for women and $\beta = -.01$ for men). Similarly immaterial were the associations in another large-scale study ($\beta = .04$), and they did not differ between the sexes (Anderson and Klofstad 2012).

Explanations and Interpretations

The absence of a link between women's financial status and the importance they place on partner earnings in correlational studies has been interpreted as evidence contradicting sociocultural models and supporting evolutionary reasoning by some scholars (Buss 2011). However, such a conclusion is not warranted for there are several alternative explanations. Methodological issues could have led to the weak or contradictory findings, such as differences in the use and understanding of terms such as "resources," "earnings," or "income." It is also possible that different subgroups of women exhibit contrasting tendencies or that conflicting psychological factors are at work, both of which would result in neutralization of effects.

For instance, allocation of time to housework versus market activities (paid employment) remains highly uneven across the sexes, including in societies with comparatively high levels of gender equality. This phenomenon has been attributed to the persistence of gender roles, notably the male breadwinner norm (Zentner and Eagly 2015). This norm may constrain the mate preferences of financially independent women. Though in principle predisposed to value men for their homemaker qualities, some of them may be hesitant to express and act on this preference to avoid undermining their male partner's sense of masculinity. As a consequence, they may seek out men with even greater earning capacity or remain unmarried. In support of this possibility, a Danish study found that husbands whose wives outearned them were more likely than other husbands to use erectile dysfunction medication (Pierce et al. 2013).

In turn, other women might be less sensitive to prevailing gender norms. For instance, one study

reported a negative relationship between feminist attitudes and the importance placed on good earning potential in a partner (Koyama et al. 2004; see also Eastwick et al. 2006 for a similar result). Thus, women who are not constrained by traditional gender roles do not seem to place particular importance on their partner's earnings. Somewhat concordant with this proposition is evidence that decreased preferences for earning potential in a partner are related to women's *control* over resources rather than resources per se (Moore et al. 2006).

Another type of evidence pointing to opposing trends neutralizing each other is people's general tendency to seek out partners who are similar to themselves across a large variety of attributes (including background, lifestyles, values, and personality traits). This "similarity-attracts" effect has been attributed to factors such as propinquity and the self-validating effects of familiarity (Günaydin et al. 2013). The pervasive, non-specific similarity preference may override any intention of financially independent women to seek out men for with homemaker qualities rather than for their earnings prospects.

To evaluate the empirical merits of this explanation, one must dissociate any specific similarity preference related to financial resources from an unspecific similarity preference. Student populations are suited to this end because the limited variation in lifestyle, values, and background characteristic of student populations will constrain generic "similarity-attracts" effects. In experiments using such student populations, women's mate preferences for financial prospects have been shown to change as a function of their anticipated role and income. In one experiment, female students who were led to envision a future as a stay-at-home parent preferred a partner with provider qualities, whereas women led to envision a future as an employed parent preferred a partner with domestic skills.

In a related experiment, the wealth of a partner was more valued by participants when they were asked to envision themselves living in a long and difficult economic crisis as opposed to a period of prosperity and well-being. The induced experience of scarcity made a wealthy partner look

more desirable, regardless of the participant's sex. These studies suggest that women's specific preferences for earnings in a partner are geared towards maximizing the type of support that they would be denied in virtue of their anticipated future role (see Zentner and Eagly 2015, for a review of these studies).

Conclusion

Taken together, the studies reviewed for this entry suggest that economic opportunities and constraints do affect women's mate preferences. Women's financial resources have been found to be negatively associated with the importance that they attribute to men's resources in certain types of studies, notably cross-cultural and experimental studies. The evidence from studies across time is less conclusive. Studies based on analyses of individual differences do not show a negative correlation. The negative association could be absent, or it may exist but be occluded by a non-specific attraction for similarity, social norms related to family roles, or a combination of both. Findings are also difficult to interpret for another reason. Most studies have used relatively crude measures of income as indicators of women's personal resources. In so doing, important distinctions between classes of resources have been overlooked (assets, property, income, wealth, or debt).

Conclusion

The evolutionary hypothesis of women's preferences for material resources in a mate is neither clearly contradicted nor is it supported by evidence about the role of women's personal resources in their mate preferences.

Cross-References

- [Cultural Differences in Mate Preferences](#)
- [Female Choice and Sexual Conflict Theory](#)
- [Mate Preferences](#)

- [Parental Investment and Sexual Selection \(Trivers Foundational Theory\)](#)
- [Resources](#)
- [Sex Differences in Human Mate Preferences \(Buss, 1989\)](#)
- [Social Status and Economic Resources](#)
- [Status and Redistribution of Resources](#)
- [Women's Mate Preferences](#)
- [Women's Long-term Strategies](#)

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Women's Preferences During Ovulation

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Synonyms

Conception risk; Endocrine changes; Fertility; Human estrus; Menstrual cycle; Mid-cycle

Definition

There is evidence to suggest that women's mate preferences diverge across their menstrual cycle; such changes likely relate to hormone fluctuations required to support ovulation.

Introduction

A growing literature, spanning a number of academic disciplines, including psychology, cognitive sciences, and medicine, has demonstrated that women's preferences, behavior, and physical appearance vary as a function of their menstrual cycle phase (reviewed in Gildersleeve et al. 2014). This literature is consistent with a previously established and parallel body of work documenting cyclical shifts in preferences and

physical appearance in nonhuman primate species. In nonhuman primates overt sexual swellings and changes in attractiveness in proximity to ovulation are termed “estrus” signals. Based on the fact that human females do not experience overt sexual swellings, and that they are sexually receptive throughout the cycle, many scholars initially believed that a “human estrus,” akin to that which occurs in primates, did not occur. However, less conspicuous changes in attractiveness and preferences, analogous to those that occur in nonhuman primates, are indeed present in proximity to ovulation when conception risk is greatest. This discovery was made in the 1990s (e.g., Gangestad and Thornhill 1998), and intense interest was subsequently generated for this phenomenon. This interest may in fact be a consequence of the fact that shifts were not initially obvious and that they appeared difficult to explain without use of an evolutionary perspective.

Evolutionary Explanations for Changes in Women's Preferences Across the Menstrual Cycle

Gangestad and Thornhill (1998, 2008) introduced the Ovulatory Shift Hypothesis as a potential adaptive explanation for the presence of these shifts. The Ovulatory Shift Hypothesis argues women experience a dual sexuality, where the preferences they display when in proximity to ovulation diverge from those that occur at other cycle phases. This divergence in preferences is thought to be adaptive because it focuses women's attention on physical traits and behaviors of potential male partners who have what are considered “good genes.” That is, women can make use of male phenotypic traits that are thought to signal genetic quality when discriminating between mates. As a consequence, increased attention to, and preference for, “good gene” partner's when conception is most likely could increase the likelihood of conceptive sex with such individuals, thereby increasing the likelihood of producing children with heritable traits of good genes (Folstad and Karter 1992). The Ovulatory Shift Hypothesis specifically postulates

that preferences for “good gene” traits should be more significant for short-term, as opposed to long-term, mating contexts. Importantly, the changes in cognitive perception and preference for putative “good gene” are predicted to be subtle (i.e., nonconscious).

Evidence for Changes in Women's Preferences Across the Menstrual Cycle

Over the past two decades, numerous studies have been designed to test the assumptions of the Ovulatory Shift Hypothesis, most of which have provided broad support. For example, near to ovulation, women show stronger preferences for masculinity or dominance in male faces, voices, bodies, and scents. Women also show stronger preference for symmetry in male faces and bodies (reviewed in Gildersleeve et al. 2014). A more restricted body of literature has also tested, and found evidence for, the idea that women show increased preference for more dominant competitive male behavior and use of courtship language when in proximity to ovulation. Evidence that women prefer higher levels of creative intelligence in proximity to ovulation provides additional suggestion that indicators of mental fitness are also preferred at higher rates by women at this time (reviewed in Gildersleeve et al. 2014).

Evaluating Research Designs of Studies on Women's Preferences Across the Menstrual Cycle

Taken together this evidence base appears robust; however, there are a number of methodological shortcomings that are important to consider. Firstly, the link between the proposed phenotypic indicators of “good genes” has been called into question (e.g., Scott et al. 2013). Ultimately, it appears more research is needed to determine what heritable advantage women achieve by pairing with men who display higher levels of masculinity, dominance, symmetry, and related traits. Secondly, the vast majority of published studies on this topic have taken place in controlled laboratory settings, often making use of using forced choice paradigms, where female participants are asked to choose between two sets of computer-generated stimuli modified from a

single male participant. This situation is rather contrived and the external validity of these designs is therefore low. While a few notable exceptions to this exist, overall few preferences have been tested in designs with strong external validity, and even in controlled lab environment effect sizes from studies are relatively small (Gildersleeve et al. 2014). This begs the question of whether or not shifts in women's preferences, or in their own attractiveness and behavior, across the cycle, have any impact for social relationships (Cobey and Buunk 2012). Havlicek and colleagues (2015) recently proposed the Spandrel Hypothesis as an explanation for changes in women's attractiveness across the menstrual cycle. This hypothesis can also be extended to changes in women's mating preferences across the menstrual cycle. They argue that changes across the cycle may be a by-product of a more general mechanism. That is, if hormones underpin women's preferences for particular male traits, women with particular hormonal profiles, such as high estrogen, would have stronger preferences than women with other profiles, such as relatively lower estrogen. So, if hormones underpin shifts in preferences, shifting preferences may be incidentally related to menstrual cycle stage since women's hormones vary across the cycle. These within-woman hormonal shifts are substantially smaller than the baseline or absolute differences in hormonal levels between women, and as a consequence these within-women effects are smaller. Currently this proposal requires empirical testing, but it provides a fruitful starting point for future work.

Variation in Methods Used to Assess Women's Menstrual Cycle Phase

A further methodological concern in relation to the evidence base for the Ovulatory Shift Hypothesis is that measures of ovulation, or assessment of proximity to ovulation, have generally been very crude. It is perplexing, but proximity to ovulation or conception risk, the variable at the center of the Ovulatory Shift Hypothesis, has not been clearly defined, and many measures exist. We know that menstrual cycle length varies between women, with anywhere between 21 and 45 days being

considered normal (Hornstein and Schwerin 2013). In spite of this, many researchers compare women's preferences and behaviors using broad cycle phases, and assume these differ in conception probability, without actually assessing hormones or underlying physiological mechanisms to confirm women's conception risk at these measurement points. This strategy often termed "the counting method" sees researchers counting forward, or backwards, from the date of menstrual onset to a prespecified and discrete "fertile window." An assumption is made that the days in the selected "fertile window" reflect a phase of "high fertility" relative to the days outside of this window that are considered to be "low-fertility" phases. Interestingly, the "fertile window" chosen varies between published papers (Wood et al. 2014), but 6–9 day windows are typical. The reverse counting method considers the fact that the luteal cycle phase, the phase of the cycle that occurs after ovulation, tends to be less variable than the follicular phase of the cycle, which occurs before ovulation (Fehring et al. 2006). While this method would help to reduce variation, many researchers opt to use the forward counting methods, or even estimates of next menstrual onset, as these can be more practical when scheduling participants to take part in studies. Indeed, early studies on this topic used between-participant designs to ease the burden of participant recruitment. Fortunately, as the field moved forward, within-subject designs began to dominate the published literature.

Some groups of researchers use luteinizing hormone test strips to assay conception risk of female participants in their studies. While use of LH test strips are preferable to a total absence of hormonal measures, one issue with this validity of the argument is that in spite of a detectable LH surge, anovulation is possible. Moreover, we know that LH increases in a pulsatile fashion, that some women have multiple surges within the same cycle, and that the time on the LH surge may be before, after, or during ovulation (Direito et al. 2013). One option to circumvent this issue is to use transvaginal ultrasonography to assay proximity to ovulation (e.g., Cobey et al. 2013), though this is likely only feasible

through broad cross-disciplinary collaboration. This method, while highly accurate in determining conception risk, does not speak to the underlying hormonal mechanisms that govern any effects documented (see section on hormonal mechanism below). An excellent analysis of the issues surrounding the assessment of conception probability in the ovulatory cycle was recently provided by Gangestad and colleagues (2015), who simulated more than 58,000 cycles and concluded that aside from methods that count backwards from the confirmed date of menstrual onset, the validity of typical counting methods and LH assays used in this area are at best modest.

Mechanisms and Semantic Concerns in Research Examining Women's Preferences Across the Menstrual Cycle

The use of terms like "high fertility" and "low fertility" to describe two distinct phases of the menstrual cycle, while commonplace in this literature, are problematic because they fail to accurately relay that conception risk across the cycle is in fact a continuous measure. The title of this entry "Women's preferences during ovulation" (assigned to me) erroneously implies that ovulation is a distinct menstrual cycle phase. Rather, ovulation is a physiological process that occurs in an instance, which is initiated by hormonal changes. Thus, ovulation itself is not a mechanism that could produce shifts in women's preferences. These semantic issues are important as they reflect broader (mis)understanding in physiological processes occurring across the menstrual cycle and how these are subsequently used in hypothesis generation.

Research that assays a broad range of ovarian hormones across the menstrual cycle, as well as their interactions, is needed to clarify the mechanisms that underpin shifts in women's preferences documented across the menstrual cycle. Only recently has work considering hormonal mechanisms been published (see Hahn et al. 2016 for discussion). As work in this area progresses it will be important to consider hormonal variation in short-term interactions and ultimately the role neurotransmitters play in regulating these effects.

Conclusion

In spite of the methodological shortcomings associated with many of the studies describing menstrual cycle shifts in women's preferences, the consensus of reviews in this area is that the shifts are a robust phenomenon (Gildersleeve et al. 2014; for a critical view see Wood et al. 2014). To contribute meaningful progress to research on the topic of women's preferences across the menstrual cycle, at this point, rigorous studies using within-women designs, power analyses to determine sample size, and measures of endocrine hormones to assay underlying mechanisms are desperately needed. It is only when these types of studies are conducted that knowledge in this area will progress. While it may be more costly to design studies to achieve this standard, the reduction in bias that these designs afford may be well worth the investment. It appears we need less research, but better research: This could be achieved through the initiation of collaborative research projects and pooling of research funds. Consideration of the evolutionary value of shifts in preferences across the cycle, even if they are shown to be robust in less bias designs, remains (Havlicek et al. 2015).

Cross-References

- [Attraction During Ovulation](#)
- [Concealed Ovulation](#)
- [Concealed Ovulation and Multi-male Groups](#)
- [During Ovulation](#)
- [Female Mate Choice](#)
- [Female Mate Choice \(Intersexual Selection\)](#)
- [Fertility](#)
- [Intrasexual Rivalry Among Women](#)
- [Male Mate Choice](#)
- [Problems of Assessing Fertility](#)
- [Randy Thornhill](#)
- [Steve Gangestad](#)

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Women's Preferred Partners

- [Women's Mate Preferences](#)

Women's Prosocial Dominant Acts

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Synonyms

Female strategies; Prosociality; Social hierarchy;
Social status

Definition

Females display a sex-specific pattern of expressions of dominance, which is a universal feature of human psychology.

Introduction

Dominance is a common strategy for achieving social influence across social species, including among humans. Dominance can be defined as the use of aggression, threats, fear, and intimidation to attain and maintain disproportionate levels of influence within a social group (Barkow 1989), and evidence suggests there are important sex differences in the expression of dominance (Buss 1981). Among sexually dimorphic species, females are often at a disadvantage concerning dominance-based strategies for achieving social influence (Archer 1988). This disadvantage can be compounded by sociocultural factors limiting female political participation (Rosaldo 1974). However, a close review of experimental literature and social systems in small-scale society reveals that women do utilize dominance-based strategies for achieving positions of social influence in ways distinct from males incorporating a dimension of prosociality (Buss 1981), oftentimes with an ontogenic component.

Women's Prosocial Dominance in Childhood

Traditional perspectives in developmental psychology have portrayed young girls as lacking expressions of dominance and overt aggression. Buss (1981) revealed the shortsightedness of these long-standing gender stereotypes demonstrating, among a sample of Western undergraduates, women tend to express social dominance in the context of group-focused behaviors, such as conflict resolution, social networking, and organization in collective action. Women are more likely to achieve positions of social influence through prosocial behavior than men, and less likely to use overt, direct aggression to subordinate followers. However, when aggression is operationalized more broadly, incorporating indirect aggression and gossip, the female dimension of social competition expands (Hess et al. 2010). In studies of Western preschoolers, Hawley has found that children most effective at controlling group resources often employ strategies of both dominance and prosociality. When the opportunity for both dominance-based and more prosocial tactics are available, there is less gender bias in social control, and group members rate boys and girls as equally as effective and desirable leaders (Hawley et al. 2008). Women use dominance-based strategies for achieving social influence in ways distinct from men, linked to their sex-specific life history parameters.

Theoretical Perspectives on Women's Expressions of Dominance

Across much of human history, and in contemporary natural fertility populations, the lives of women heavily revolved around reproduction and childcare. This has led a number of scholars to overlook and discount female-specific expressions of dominance and status competition. Several biological and psychological theories have been suggested to universally account for gender differences in the relative levels of ascribed and achieved statuses and expressions of dominance (Rosaldo 1974). The physical dominance of males over females, and the biological constraints and

parental obligations related to motherhood, are frequently cited explanations for the limited political and broader social influence of females in traditional societies. Furthermore, gender differences in socialization have been used in an attempt to explain women's confinement to the domestic sphere and disinterest in dominance-based social strategies (Rosaldo 1974).

Previous attempts to predict female's social status relative to males based on variation in societal level economics or subsistence strategies have neglected to holistically examine female-specific expressions of dominance and there are few existing theories on the subject. Some researchers assert that women are often primarily limited to domestic participation because of their maternal roles, and that extra-domestic participation by women is largely constrained because of the responsibilities related to childcare and socialization (Rosaldo 1974). This perspective suggests that because women are absorbed in household activities and direct their attention and energy toward their children, the avenues available for women to pursue dominance-based social positions and gain prestige will be shaped by their involvement in the domestic domain (Rosaldo 1974).

Heavy restriction within the domestic domain however does not exclude women from competition and expressions of dominance. Within local communities, competition between females is likely to be indirect and focused on the acquisition of valuable resources rather than political status attainment (Campbell 1999). Through indirect aggression and prosocial investments, women are able to compete socially and politically without experiencing significant risks of bodily harm (Campbell 1999). Women's high parental and reproductive investments prioritize bodily integrity and resource acquisition, over physical competition and injury (Campbell 1999). Many female psychological processes revolve around reproductive success and maternal demands. The loss of a mother can be life-threatening for young children, and natural selection has driven women to avoid physical harm in status competition in favor of a more maternal focus on current and future offspring (Campbell 1999).

In addition to an inherent aversion to physical harm, Brown (1970) suggests that the division of labor and the local political structure in traditional societies is similarly shaped by maternal demands. The subsistence activities of women are more likely to be those that are more compatible with childcare (Brown 1970). Such qualities include tasks that are located within close proximity to home, not especially cognitively demanding, and are relatively safe. Additionally, women's work will more likely be compatible with frequent interruptions from needy children (Brown 1970). While these activities prioritize successful parenting, they also serve to restrict women's ability to play a larger and more active role in local politics, at least while women are in their childrearing years.

Prosocial Expressions Through Cooperative Breeding

Other theoretical perspectives suggest that female status striving and intrasexual expressions of dominance revolve around various activities directly related to motherhood (Barkow 1989). Barkow (1989) suggests that, because in small-scale societies opportunities for expressions of dominance are often limited and infant and child mortality are typically high, a female's primary social identity may be frequently associated with her reproductive capacity and childrearing abilities. Hewlett (1991) provides comparative data from 57 traditional societies illustrating that among preindustrial populations, active hunter-gatherers suffer the greatest infant and child mortality rates with means of 23.1 and 45.5%, respectively. The combined mean data on infant and child mortality from horticulturalists and pastoralists is 21 and 38.1%, respectively (Hewlett 1991). Demographic factors, ecological pressures, and limited health care all impact female reproductive health and group-wide mortality rates. In this context, motherhood becomes a severely critical role. Women that compete for status through motherhood build reputations and gain esteem and in spheres that are valued by women and not through the activities that are necessarily valued by men.

As cooperative breeders, women in traditional societies are able to enhance their reputation and social position through their personal skills as mothers and the degree to which they participate in prosocial communal childrearing.

Post-Reproductive Prosocial Dominance Expressions

Another distinct aspect of female status striving that has been described by researchers is related to postmenopausal changes and the increased availability of status opportunities, prosocial investments, and wider political roles. Brown (1985) outlines three reasons for women's middle age status mobility. First, the end of their reproductive careers provides women in many traditional societies increased freedom from culturally specific restrictions (e.g., menstrual customs) and the constraints of childcare, giving them the opportunity to maximize their social influence and enjoy greater mobility (Brown 1985). Next, middle age grants a woman administrative authority over her juniors; she has the right to delegate tasks and organize the labor of her younger family members and also exercise great influence in important matters concerning youths' eligibility for initiation and marriage. Lastly, Brown (1985) concludes that middle age provides women with avenues for extra-domestic recognition, through the pursuit of special status positions such as curer, midwife, or ceremonial leader. Status competition and prosocial expressions of dominance in cooperative breeding yield dividends later in life when high-status women emerge as major political agents in many small-scale societies.

Conclusion

Across the life span, women are adjusting their individual strategies for pursuing positions of social influence. Women tend to use prosocial investments and communally focused behavior to increase their social rank and attain positions of influence within the group. A female-specific approach to understanding expressions of

dominance must take into account sexual selection, life history parameters, and the physiological demands of motherhood and childcare, all of which have influenced the evolved psychology of women and the cultural systems in which they operate. A broader conception of women's expressions of dominance is realized when these sex-specific features are not viewed as limitations but rather the context in which female specific social strategies have evolved.

Cross-References

- [Dominant Acts Expressed \(Buss 1981\)](#)
- [Men's Egoistic Dominant Acts](#)

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Women's Rights

► [Feminism](#)

Women's Sexual Preferences

► [Female Mate Choice](#)

Women's Use of Direct Versus Disguised Social Aggression

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Synonyms

[Indirect aggression](#); [Physical and verbal aggression](#)

Definition

Forms of social aggression.

Introduction

From an evolutionary perspective, aggression against a competitor constitutes an adaptive response to an obstacle that threatens an animal's survival and reproductive success. Because females generally engage in less direct, intense, and overt aggressive behavior than males (Archer 2004), and variance in reproductive success is lower for females (Trivers 1972), researchers often conclude that females confront fewer obstacles than males to survival and reproductive success.

Reproductive success, however, poses differing challenges for female versus male mammals. Protection of internal reproductive organs; reduction of stressors prior to conception and during

gestation; adequate nourishment during lactation; and provision of safety, nourishment, and educational and socialization opportunities to offspring define females' reproductive success in unique ways. Further, in many primate species, females' investment extends to younger siblings, offsprings' progeny, more distant kin and even non-kin helpers, whereas males invest relatively less in kin. Finally, females' impact on their own reproductive success often occurs continuously throughout their lifetimes, while males' investment occurs sporadically.

In the past two decades, research has begun to focus on the unique challenges that nonhuman and human females confront that often can be solved most efficiently by besting competitors (Clutton-Brock 2009). In addition, alternate forms of aggression, which appear better adapted to females' life histories, have been identified that are less readily observable than the salient direct displays of aggression and weaponry more frequently employed by males (Björkqvist 1994). The fact that females do benefit from aggressive behavior and that less overt forms of aggression exist, however, have illuminated facets of females' lives that have heretofore been neglected by both evolutionary biologists who study non-human animals and psychologists who study humans.

Unique Aspects of Human Females' Lives: Staying Healthy, Finding Assistants

From an evolutionary perspective, investigation of females' aggression should be directed towards understanding the unique challenges that females confront in terms of enhancing their probability of survival, procreation, and their offsprings' survival. For female mammals including humans, the initial constraint is that each female is born with all the ova she will have in her lifetime (Trivers 1972). Damage to these ova and the processes that lead to conception will produce infertility. Often neglected is the additional fact that in higher primates including humans, in natural environments offspring mortality hovers around

50 % (Volk and Atkinson 2013). A mother then implicitly and explicitly must weigh her investment in each offspring with the implicit knowledge that each has a 50 % chance of dying.

Further, human females' offspring are dependent for a longer interval than those of other species (Lancaster and Lancaster 1983). Moreover, human mothers frequently invest over their entire lifetimes in both their offsprings' survival and reproductive success (Lahdenpera et al. 2004). Finally, and most uniquely human, the prolonged nature of human childhood combined with an unusually low inter-birth interval (Bogin 1999) means that human females typically bear responsibility for the survival of several children, and later grandchildren, simultaneously. Whereas nonhuman females bear responsibility for sequential offspring throughout their lives, each offspring becomes independent more rapidly, so that a mother's reproductive success is not dependent on continued investment in the same offspring. Therefore, even more so than other female primates, from birth onwards human females must take many more precautions than males to avoid damaging their bodies so as to maximize the probabilities that they will be healthy enough to invest in their children and grandchildren. This results in the lower risk-taking of females relative to males at every life stage (Byrnes et al. 1999).

Two specific ecological factors also influence human females' success in enhancing their survival and reproductive success. First, human females are not guaranteed that they will spend their lives near kin, with the majority of societies appearing to favor male philopatry or female dispersal from their natal families and frequent residential displacements (Alvarez 2004). While competition occurs between kin, kin also typically invest more in one another than unrelated individuals (Smuts 1995). Therefore, human females must learn to reduce external signs of competition for survival for themselves and their offspring, as they would be less tolerated by non-kin, including affines.

Second, human females typically form long-term pair bonds with the fathers of their children. The sexual division of labor means that females

often are dependent on men for specific foods, such as meat, and for other responsibilities, such as protection from other men and assistance with child care. Further, when women are pregnant or lactating, they need extra calories and are particularly vulnerable. A marital partner often provides resources that are difficult to obtain when a mother has young children, whether animal foods or other currencies (Marlowe 2005). A marital partner also provides protection from infanticide and abduction. Additionally, because human males hold higher status than females, forming a long-term bond with a man provides status and links to the community that a lone female often lacks (Rucas et al. 2012). When kin are unavailable, both husbands and affines can compensate by provisioning mothers and children and providing direct child care as well. Consequently, maintaining access to kin and the father of her children and her affines constitutes a critical means for a mother to improve her own and her children's survival and reproductive success. Maintenance of bonds to kin or to the father of her children provides such advantages to raising simultaneously dependent children and bearing lifelong responsibility for them that when these bonds are threatened, the benefits of aggression utilized to restore the bonds may outweigh the costs.

To stay alive, all females require safety, food, territory, and other resources. To thrive, social females benefit from educational and socialization resources as well as status. For human females to accomplish the tasks of keeping their children alive and helping them to thrive, they need assistants. Most of these assistants are kin or husbands and affines. Because unrelated females share the same goals, they become competitors for scarce resources or allies or mates. Consequently, it is unrelated females who constitute typical targets of aggression.

Forms of Individual Aggression

Direct physical aggression. The primary advantage of direct physical aggression is its rapid occurrence which is essential to stopping a

predator or a strange male who threaten a female's or her children's survival. Although this immediate response is critical when the target is determined to attack, in more ambiguous cases such as abductions by males or attacks by female competitors, the rapidity means the target has little chance to escape or debate whether to retaliate. This may increase the probability that the target retaliates physically either for defensive purposes or as an offensive counter-attack, leading to severe physical injury.

As an offensive strategy, the rapidity and surprise of direct physical aggression can overwhelm the target, potentially increasing the probability of success. However, a direct physical attack has the potential to severely injure the perpetrator as well as the target, particularly when the target is equal in size and strength to the perpetrator. For this reason, even males typically utilize bluffs before actually physically fighting (Maynard Smith and Price 1973).

Even if direct physical aggression does not injure the perpetrator, it is costly in terms of expenditures of physical and emotional energy. Only when a coalition cooperates against a target can the risks of retaliation and energy expenditure be reduced, but this requires planning and inflicts large opportunity costs, which mothers of dependent children rarely can bear.

An additional disadvantage of a direct physical attack is that the perpetrator typically is unable to disguise her identity. Even if retaliation does not occur immediately, future retaliation by the victim, and his or her allies, arises as a future and omnipresent threat.

To avoid injury to their ova, reproductive organs, and their ability to survive to care for their children and grandchildren, human females therefore must reduce the probability of injury and death (Campbell 1999). Accordingly, from early in childhood (Maccoby and Jacklin 1974) through adulthood (Archer 2004) human females utilize direct aggression much less than males do. This fact alone can help explain why across species males' direct aggression has been the focus of investigation more than females' aggression. Although other forms of aggression take longer to be effective, they are safer and hence more

widely utilized by females. Only when a female's survival or reproductive success is in immediate jeopardy should she resort to direct physical aggression.

Direct verbal aggression. Verbal aggression is not as effective as direct physical aggression at attaining an immediate goal. Although it can be executed rapidly, it does not interfere to the same extent with the obstacles created by a target. Nonetheless, the emotional impact, particularly when accompanied by the threat of physical aggression, can be valuable in thwarting a target. Direct verbal aggression also has the advantage of not requiring a response from the target, thereby further reducing threats to the perpetrator's safety. Additionally, because direct verbal aggression requires fewer physical and emotional resources, it can be utilized for longer intervals than direct physical aggression.

Direct verbal aggression provides a further advantage through its explicit communication of negative information to a target. Understanding the perpetrator's perspective allows the target to determine whether it is worth modifying personal goals to maintain harmony with the perpetrator. This should theoretically also permit the possibility of later reconciliation. Direct verbal aggression also can be utilized to publicly disseminate negative information about a target, thereby impugning a target's reputation. With a crowd present, the perpetrator's chances of a retaliatory physical response from the target are reduced.

Therefore, whereas physical aggression has the advantage of producing the desired outcome most rapidly, verbal aggression provides several advantages, including conveying precise negative information to and about the target, while reducing the probability of injury.

A major disadvantage of direct verbal aggression, however, is that similar to physical aggression, the perpetrator typically cannot disguise her identity. Consequently, immediate or delayed physical or verbal retaliation by the target is more probable than when the perpetrator's identity is concealed.

Disguised physical, verbal, and nonverbal aggression. Concealing one's identity produces large advantages for a female aggressor who

must reduce her own and her progeny's probability of physical retaliation (Björkqvist 1994). A variety of means exist for disguising direct physical aggression. Identity can be masked through covering the face and body and through the anonymity afforded by large coalitions, but this type of disguised physical aggression still risks physical injury to the perpetrator. No evidence therefore indicates that human females commonly utilize this type of disguised physical aggression.

In contrast, females do utilize another form of disguised physical aggression: aggressing against another's property or allies in her absence. This type of disguised physical aggression includes stealing food or the means for the production of food, destroying a shelter or clothing, or even poisoning a child (Burbank 1987). The probability of physical injury and future retaliation is reduced due to the target's absence. Nonetheless, because it leaves physical traces, the perpetrator's identity potentially still can be discovered, enhancing the potential for retaliation. The extent to which females employ this type of disguised aggression has not been studied.

In contrast, across diverse cultures, females utilize disguised verbal aggression regularly, although there is no evidence that they utilize it more frequently than males do (Archer and Coyne 2005). Rather because females employ less direct forms of aggression, disguised forms of aggression constitute a larger proportion of females' aggression. Disguised forms of aggression therefore have become associated with females, even though males utilize them as much or more.

The first form of disguised verbal aggression, verbal denigration of an absent target, also termed gossip, can produce severe reputational damage to a target, leading the target's erstwhile allies, including friends and mates, to reduce their investment or even to sever their connections with the target all together. Absent a written form, no concrete evidence may exist as to the identity of the perpetrator. The perpetrator, however, must discourage listeners from divulging her identity. If the perpetrator's identity is revealed however, she always can either deny malevolence or attribute malicious intentions to the

messengers. In modern cultures, females can engage in disguised verbal aggression through online forums. Again, however, there is no evidence that females engage in more online incidences of disguised verbal aggression than males do (Tokunaga 2010).

Another form of disguised verbal aggression can occur in the target's presence if the words, tone of voice, cadence, or other auditory signals contain enough ambiguity to confuse the target. As one example, public expressions of purported concern towards a target, including direct and ostensibly sincere questions about a target's comportment and feelings, can have the effect of exposing precise weaknesses of a target. Disingenuous sympathy is particularly effective for females who are expected to be nurturing and sympathetic and helps to disarm a target's defenses as the perpetrator can falsely claim to be invested in the target's well-being. Likewise, pitying tones of voice, clucking noises, and giggling can be employed to convey derogatory evaluations of a target with enough ambiguity to preclude clear interpretation by the target. In the presence of others, denigration of the target's character reduces the bonds between the target and her allies, including friends and mates, thereby permitting the perpetrator to steal allies and/or reduce the target's support in the community.

Even nonverbal derogatory gestures, if they are subtle and hence ambiguous enough, can be utilized to aggress against a target in her presence. These include awkward pauses, twisted facial features, belligerent head or eye movements, or propulsive actions with fingers, arms, legs, or other bodily parts, again with the purpose of publicly denigrating the target, and disrupting the target's social connections. These types of aggressive gestures seem particularly well-suited to females who are more sensitive than males to subtle social cues (Hall et al. 2000). Therefore, intrasexual female aggression can occur in mixed-sex settings without males' awareness. This can be useful if the goal is not to communicate the information to males, who often wish to maintain the status quo and hence would punish female aggression.

Finally, implicitly withholding benefits, whether material, social, and in the case of males, sexual, until a goal is attained, may be as effective as inflicting costs (Björkqvist 1994). This latter strategy, however, requires that the perpetrator be in a position to dispense and therefore withhold benefits. Whereas there is no evidence that human females practice any of these disguised forms of aggression more frequently than males do in absolute terms, much evidence suggests that these forms of aggression constitute a larger percentage of females' aggressive repertoires simply because females use direct physical and verbal aggression so much less frequently than males do.

Two forms of aggression, however, do appear to be utilized by females more than males: Insistence on the maintenance of equality and social exclusion. Insistence on the maintenance of equality with other females (Maltz et al. 1982) effectively reduces same-sex competitors' advantages. Unlike males who from early childhood through adulthood directly compete physically and verbally for resources, allies, and status, females actively pursue a very different strategy: No female is allowed to claim superiority to any other female. Beginning in early childhood, girls and women rapidly disparage any female who exhibits material or social advantages or claims superior performance. The disparagement occurs both in the absence and presence of the target. While ostensibly sounding positive by purporting to denigrate competitive motives, unequal outcomes, and hierarchical social structures, the perpetrator utilizes this form of disguised aggression to force competitors to surrender time, resources, and positions of status. Furthermore, joint insistence on equality can lead to social exclusion of an advantaged target. Consequently, any female striving to attain her goals must disguise her pursuits by focusing on her deficiencies and dearth of accomplishments. This retaliatory strategy cannot be easily discerned as it fits within the stereotype of the self-effacing female, but it poses risks to any female whose advantages are revealed despite her attempts to disguise them.

Social exclusion constitutes the second form of uniquely female strategy. The study of aggression

typically is divided into individual versus coalitionary forms, and social exclusion is coalitionary.

Forms of Coalitionary Aggression

Social exclusion. By definition, social exclusion requires a coalition of individuals who outnumber their victims. The most commonly documented form of social exclusion occurs when a coalition of females gangs up on an individual female and attempts to sever her connections to the larger community. Whereas evidence suggests that social exclusion is equally painful for both sexes, it appears that females utilize it more frequently (Benenson et al. 2013).

Social exclusion initially can occur through disguised means, but eventually it must become direct. A coalition chooses its target, typically someone who is either unconnected to others and hence easily ousted, or someone whose ouster will free up time, energy, resources, territory, connections, or a position of status for the remaining female members of the community.

Because of the imbalance of power, social exclusion is extremely safe. Thus, it may be the preferred mode of aggression for females who benefit greatly from avoiding injury. Even at its most direct, a victim cannot retaliate immediately or at a later time, unless the victim finds her own coalitionary partners. It is unlikely, however, for a lone target to find allies after the process of social exclusion is underway, as potential allies would risk subjecting themselves to the same treatment, with little obvious benefit. The ultimate goal of social exclusion is to force the target to leave the community.

Similar to the female norm of equality which facilitates the insistence that no other female demonstrate advantages, social exclusion appears particularly well-suited to female competitors because females do not benefit as much as males do from cooperation with unrelated same-sex peers. Since a human mother experiences difficulty raising her children on her own, she benefits greatly from assistance in procuring resources, minding children, and educating and socializing

them. The assistants cannot be other mothers, however. By definition, a mother typically does not have additional time, energy, resources, or allies they can provide to another mother without jeopardizing their own and their children's survival and reproductive success. Consequently, kin, husbands, and affines constitute the most useful assistants.

Thus, unrelated women compete for themselves and their children for the same resources and allies, including a husband who invests in her and her children. Maintaining a long-term pair bond with the father of her children requires that a mother ensures that other females do not disrupt the relationship. For all of these reasons, reducing the number of female competitors benefits a female at any stage of her life. Social exclusion therefore constitutes a highly effective strategy from early childhood throughout adulthood for reducing the number of competitors.

Bullying. Bullying is similar to social exclusion insofar as several individuals gang up on a vulnerable, lone individual (Olweus 1993). However, there is no attempt to ostracize the individual. Rather, bullying seems to operate as a means of maintaining a coalition and perhaps providing status for the lead instigators. Should the victim disappear, the coalition as well as the status of the primary perpetrators may disappear. Paradoxically, therefore, the intent seems to be for the victim to remain part of the community.

Both bullying and cyberbullying (Tokunaga 2010) are more commonly utilized by males than females. For both sexes however, bullying is directed by higher-status individuals towards lower-status individuals. Lower-status boys, however, will bully higher-status girls (Olweus 1993).

Intergroup aggression. Because human males more than females interact in groups, intergroup aggression is practiced primarily by males from early in life. Whereas both sexes prefer their own groups over other groups (Tajfel 1981), females typically do not engage in aggression against out-groups. Intercommunity aggression in its most extreme form, warfare, rarely involves females playing primary roles. Lack of cooperation in warfare and other group enterprises with unrelated same-sex peers means that power

is not derived from greater numbers. Consequently, social exclusion is more useful as an aggressive strategy for females than males.

Prioritizing Aggressive Strategies of Females

Selection of the form of aggression depends on the goals of the perpetrator. For females who are born with a finite number of ova; who beginning in adolescence experience fluctuating hormonal levels that must be finely balanced to permit conception; whose reproductive organs must be healthy enough to allow years of internal gestation; whose children require her investment to survive; and finally whose grandchildren will experience lower mortality and morbidity if she can invest in them potential injury must be minimized.

The first principle of female aggression therefore is to reduce the chance of injury and death (Campbell 1999). Direct physical aggression therefore should be utilized primarily to enhance survival and otherwise avoided. Direct verbal aggression should follow as the second least preferred form of aggression as the potential for retaliation is higher than when forms of aggression are disguised. It seems highly probable that both direct physical and verbal aggression are utilized only when the likelihood of retaliation is minimal, such as against targets who are physically weak and socially unconnected or with individuals who will not retaliate. Children or low-status and physically weak non-kin and kin would constitute the safest targets. However, where strict laws exist to protect women, females would be more likely to employ direct physical and verbal aggression against kin and spouses and others of similar or greater physical strength (Archer 2000).

Insistence on maintenance of equality likely constitutes the least dangerous form of aggression and hence should be the most common strategy. Requiring another female who is in an advantageous position to relinquish her lead for the sake of equality cleverly disguises competitive goals and invites no retaliation. This insistence can

occur directly and by a single perpetrator because the risk of retaliation is so minimal. Joint insistence, however, can lead to the second most effective female strategy: Social exclusion. Because of the protection that a coalition provides against a lone victim who cannot easily retaliate, social exclusion is safe and provides numerous benefits, particularly reducing competition over mates.

In between the most and least dangerous forms of aggression are disguised forms of aggression that are not costly, including verbal denigration in the target's absence and subtle forms of verbal and nonverbal denigration in the target's presence. This latter type of subtle aggression most likely is more effectively utilized by females than males who are less skilled in decoding the nuances of verbal and nonverbal communication. For females, these subtle forms of aggression can permit "doublespeak" whereby a female can be recorded explicitly as supporting someone, but the implicitly negative message supersedes the explicit message at least amongst her female interlocutors.

Sex Differences in Aggression

Mammalian males typically directly compete for access to females, then to attract females. Although the variance in reproductive success is greater for males than females, individual females differ markedly in their survival and that of their grandchildren. In humans although both sexes invest to some extent in children, females universally bear primary responsibility for child care.

Rather than competing for sexual access therefore, females compete for long-term relationships to individuals who will invest in her children and who will directly compete for status. Finding valuable assistants is critical to females. This goal is complicated by human male philopatry and hence females' concomitant frequent lack of connections to kin. Consequently, those women who can attract and keep a husband who provides resources, protection, status, and links to the community greatly enhance their probabilities of their survival and

reproductive success over their lifetimes (Rucas et al. 2012). Those women who can maintain access to and investment from their own kin similarly benefit. Because cross-culturally women typically begin bearing children before they turn 20 years, a woman who can maintain strong connections with kin and form a long-term bond with a mate by the end of adolescence can best ensure her own and her children's survival and status. Maintenance of these bonds, or formation of sequential long-term bonds with the fathers of her children along with continual renewal of ties with kin as occurs in hunter-gatherer communities, greatly benefit a mother's survival and reproductive success.

During childhood and particularly adolescence therefore, in monogamous communities, unrelated same-sex individuals may be friendly but they also constitute competitors for mates. This continues into adulthood especially in communities in which divorce is commonly practiced. In communities that practice polygyny, those females who share the same mate likewise benefit when there are fewer co-wives with whom to share resources as well as a husband's time, energy, and emotional commitment. Social exclusion, particularly of attractive females, therefore provides a safe and highly beneficial strategy for reducing the competition.

Nonetheless, unrelated same-sex peers can provide human females with emotional support and information, coalitions to exclude other females, and friendships that reduce the probability of being excluded by other females. They can also provide assistance with joint goals, such as building shelters, locating food sources, and providing information about others in the community. Further, mothers benefit from mutually permitting their children to educate and entertain one another. Nevertheless, mothers' high investment in their own children and need for external assistance likely preclude the type of sharing of time, resources, energy, and status that more typically characterize the relationships between unrelated men (Hawkes et al. 1997). Aggressive strategies therefore are most likely to be deployed by human females against unrelated same-sex women, despite their sharing common goals.

Conclusion

Women's choice of differing forms of social aggression depends on females' unique obstacles to survival and reproductive success. The most important reason that females and males differ in their forms of aggressive strategies is that females have more to lose in terms of reproductive success from sustaining physical injuries. Consequently, selecting aggressive strategies that minimize the chance of retaliation reduces the cost:benefit ratio to females of employing aggression.

Cross-References

- [Cost of Same-Sex Friendships](#)
- [Derogation of Rivals](#)
- [Female-Female Competition](#)
- [Pair-Bonding](#)
- [Paternal Investment relative to Maternal Investment](#)
- [Reputation](#)
- [Same-Sex Coalitions that Exclude Women](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Verbal Derogation Among Women](#)

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Women's Violence

► Contexts for Women's Aggression Against Men

Words and Rules

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Synonyms

Dual-mechanism morphology; Dual-route model

Definition

“Words and rules” postulates a dual mechanism of symbolic rules and associative storage and retrieval for the production and comprehension of morphologically complex words.

Introduction

It has been suggested that the access and production of morphologically complex forms can occur via two routes (Pinker and Prince 1994). First, a morphologically complex word can be listed in the mental lexicon as a whole form and produced or

comprehended by direct lookup (“words”) or alternatively, a decompositional route may be used where the complex form is parsed into a stem and a symbolic rule that applies to all stems of that category to create the complex form (“rules”). But there are also competing theoretical viewpoints that suggest that *single-route models* that rely solely on associative memory (Rumelhart and McClelland 1986) could also successfully reflect human performance with morphologically complex forms. This research will be laid out under three main headings: (1) inflectional morphology and child language acquisition, (2) crosslinguistic data, and (3) challenges for the words and rules model.

The English Past Tense: The First Battleground for Single- and Dual-Route Models

The production and processing of the past tense forms of English verbs has often served as a testing ground for the hypotheses of two competing accounts regarding the organization of language in the human mind, with particular attention devoted to children's overregularization errors (e.g. *throwed*, instead of *threw*). On one side of this debate, one finds the proponents of the *single-route models* who suggest that *all* morphologically complex forms are stored in the memory as chunks and that the production of new complex forms depends on the analogization of memorized (sub)regularities, e.g., *pump* → *pumped* can be derived by analogy to *jump* → *jumped* via associative links established between their phonological features, just as *throw* → *threw* can be derived by analogy to *know* → *knew* (Rumelhart and McClelland 1986; Plunkett and Marchman 1991, 1993). On this view the overregularized form *throwed* could be claimed to occur because of existing regular forms that are similar to it, such as *glowed*. On the other side of the debate are the proponents of the *dual-route models* (aka “words and rules”) who claim that while the past tense forms of irregular verbs such as *threw* or *knew* are stored in memory and can be derived by analogy, the past tense forms of regular verbs such as *pumped* must be derived by a

symbolic concatenation rule ($V + ed$), regardless of the phonological similarity of the stem to existing regular forms (Prasada and Pinker 1993). The existence of overregularized forms would then be explained by a failure to retrieve the stored irregular form, which leads to the default application of the rule (Pinker and Prince 1988; Marcus et al. 1992). Research on the psychological validity of “the words and rules model” and its role in language development will be presented under the following headings: (1) inflectional morphology and child language acquisition, (2) crosslinguistic data, and (3) challenges for the words and rules model.

Inflectional Morphology and Child Language Acquisition

Inflectional morphemes encode grammatical features such as tense, number, and gender. Research has shown that, once children have acquired a rule of inflection, they are willing to apply it to novel cases, generating the plural forms of made-up nouns (e.g., /wag/ → /wagz/) or the past tense forms of made-up verbs (e.g., /biŋ/ → /biŋd/). As the stems *wug* and *bing* are not real English words, the child who correctly inflects them shows evidence of having acquired the inflectional rules and of using them productively (Berko 1958). One puzzling finding, however, has been that English-speaking children do not smoothly enter an adult-like stage where they use regularly and irregularly inflected words equally proficiently. Instead, they appear to exhibit a pattern of *U-shaped development*, whereby a period of relatively error-free performance is followed by a period in which children overapply the regular rule to irregulars (e.g. *throw* → *throwed*) and then converge on adult performance over time (Cazden 1968).

It has been suggested that the emergence of these overregularization errors is attributable to a change in children’s vocabulary, i.e., children would be first exposed to a restricted class of high-frequency irregulars in the parental speech the past tense forms of which they retain in memory, but over time the regulars would come to

outnumber the irregulars, dominating children’s vocabulary and prompting them to overregularize. This fundamental assumption about the changes in a child’s vocabulary is true for the *type frequency* of verbs. The irregular verb vocabulary of an English-speaking child will expand as he/she is learning the modest number (~180) of irregular English verbs and then it will plateau. The regular verb vocabulary will, however, grow continuously; as the regular verbs form an open class. Yet the high type frequency of regular verbs in the child’s vocabulary is not found to be positively correlated with the overregularization rate, so it cannot be argued that this quantitative change in the vocabulary is the cause of the overregularization errors. An alternative approach could be to take *token frequencies* into account, rather than type frequencies. But irregular verbs have, in fact, a higher token frequency, so this does not explain the overregularization errors either (Marcus et al. 1992).

The words and rules model, in contrast, explains overregularization errors with the *blocking-and-retrieval failure hypothesis* (Marcus et al. 1992; Ullman 1993). This hypothesis states that the language system depends on two separate but interacting components: a computational component for symbol manipulation and an associative component for analogy-based storage and retrieval. In this system, rules constitute the default mechanism by which morphologically complex forms are generated, and they always apply as long as they are not *blocked* from applying by a specific irregular form retrieved from memory. This dual mechanism naturally predicts that children will overregularize, since they have not heard some irregular verbs as often enough to consolidate their traces in memory, and in the absence of the irregular past tense form that would block the rule; the rule applies. Thus overregularization errors are a direct consequence of having a rule and a built-in blocking principle at one’s disposal. Moreover, as the blocking principle is quite robust and the memory retrieval process often works, it is expected that overregularization errors should be relatively rare, and this prediction appears to be borne out in child language corpora collected in naturalistic settings

(Marcus et al. 1992); however, see Maratsos (1993, 2000) for a different point of view. Additional evidence showing that children are aware of the inflectional rules and the environments that license their use is supplied by children's preference for irregular plurals over regular plurals in the non-head positions of compounds where an item drawn from the mental lexicon would be permitted (e.g., mice-infested), but not a regularly inflected form which is the output of a later morphological operation than compounding (e.g., *rats-infested, where * shows the ungrammaticality of the structure, in accordance with the linguistic conventions) (Kiparsky 1982; Gordon 1985) and by children's reluctance to regularly inflect headless compounds where the irregularity of the root cannot percolate up to the whole derivation (*sabertooths*, not **saberteeth*) and denominal verbs (*flied the board*, not **flew the board*, where *to fly* means *to cover a surface with flies*) where the canonical verb root is not available to activate the irregular past tense form (Kim et al. 1994). These findings provide evidence for the bifurcation of the language system into an associative memory component and a rule-based computational component in English-speaking children's minds.

Crosslinguistic Data

Though psycholinguistic research on the words and rules model tended to focus on English past tense morphology, some evidence in its favor has also been adduced in studies on other languages both with adults and child speakers. Experiments conducted on Hebrew-speaking adults have shown that the regular masculine plural form is freely overapplied to novel nouns, borrowings, and names, irrespective of their phonological similarity to existing forms, unlike the irregular-sounding forms which were sensitive to phonological similarity with the stored forms (Berent et al. 1999).

Studies on German concentrated on the formation of past participles and plurals. In German, the most common participle ending is $\{-t\}$, which is attached to verb stems (e.g., *kauf-en*, "to buy" →

ge-kauf-t, "bought") in a regular fashion. Another participle ending, $\{-n\}$, however, is less common and often accompanied by stem changes (e.g., *schreib-en*, "to write" → *ge-schrieb-en*, "written"), forming a parallel to the irregular past tense forms in English. In line with the predictions of the words and rules model, Marcus et al. (1995) have found that adults predominantly generalize the $\{-t\}$ ending to the participle forms of denominal verbs that lack a canonical root, whereas the irregular $\{-n\}$ ending is used for homophonous verbs derived from a verb root that would normally be inflected with $\{-n\}$. Other studies confirmed these findings with both adults and children. As expected, no clear similarity effects were found for the overregularization errors (see Clahsen 1997). But these results could also be compatible with *single-route models*, since the default status of the participle ending $\{-t\}$ is confounded with its status as the most frequent participle ending and as it is known that high-type frequency leads to the extraction of a default pattern in associative networks employed by single-route models. The words and rules model, however, contends that there is no link between the *descriptively* default status of an inflection (i.e., its type frequency) and its *psychologically* default status (i.e., its generalizability in circumstances where no stored form is available). Thus an inflectional form that dissociates between these two confounded criteria, a *minority default*, is needed to confirm that such overregularization errors constitute an argument for the dual-route models.

The German plural ending $\{-s\}$ is claimed to be an appropriate candidate in this respect. According to different corpus-based estimates, its frequency varies between 0 and 9%, yet it is the *psychologically* default plural suffix (Marcus et al. 1995), as judged by its use for loanwords, quotations, acronyms, and similar environments where a canonical root would be absent and irregular inflection blocked. The default status of $\{-s\}$ for adults has found support in an experiment where the participants had to judge the "well-formedness" of pluralized novel words. The results showed that particularly novel names that did not rhyme with existing irregular nouns were found to sound better when pluralized with $\{-s\}$

(Marcus et al. 1995). Based on longitudinal data from one child acquiring German, Clahsen et al. (1992) also suggest that $\{-s\}$ was the most frequent suffix in overregularization errors and was missing from the non-head positions in compounds where regularly inflected forms would not be allowed. Moreover this child also pluralized words of her own invention with $\{-s\}$ lending support to the hypothesis that $\{-s\}$ may be the default plural marker for German. The possibility of having a default inflection that is not the most frequent inflection at the same time is cited as evidence for the words and rules model, where the default status of a symbolic process is logically independent of its type frequency. The claim that single-route models cannot accommodate minority defaults, however, has not gone unchallenged (see Hahn and Nakisa (2000) for a discussion).

Additional support for the words and rules model is provided by Spanish, where children have been reported to overextend regular verbal inflectional suffixes to irregulars, while errors in the reverse direction (irregular forms overextended to regulars) were very rare (Clahsen et al. 2002). Furthermore it has been shown that the emergence of such overregularization errors in Spanish coincides with the time when the relevant forms start being used contrastively by the child (Mueller-Gathercole et al. 1999) or with the emergence of obligatory finiteness markings (Clahsen et al. 2002), which implies that overregularization may be a direct consequence of acquiring a rule of inflection.

Drawing upon elicited production data from adults, Say and Clahsen (2002) discuss the evidence for the words and rules model in Italian novel verb past participle formation. Italian has three conjugation classes, of which the first one is predicted to be the default, since it applies to loanwords, neologisms, deadjectival and denominal verbs, and onomatopoeic verbs – popular diagnostic environments for productive patterns. The other two conjugation classes, however, are excluded from these environments. As predicted, Say and Clahsen (2002) found that adult native speakers of Italian tended to overgeneralize the first conjugation to novel verbs

that bore no similarity to existing verbs in the other two unproductive conjugation classes, thus confirming the default status of the first conjugation class in the minds of Italian speakers. In contrast, second and third conjugations were only generalized to novel verbs that were phonologically similar to existing verbs in these classes. The same study provides additional evidence for the bifurcation of regular and irregular conjugation classes by presenting ERP data. It is shown that a clear ERP effect is only found with overregularized irregulars, whereas the ERP effects triggered by incorrect regulars are negligible.

All in all, the data obtained in studies on English and other languages cited in favor of the words and rules model appear to concur on two key points: (1) regular forms are generalized freely, whereas irregular forms tend to be generalized only if the root is phonologically similar to another irregular root. (2) Generalization of irregular forms shows frequency effects, whereas generalization of regular forms does not have to be related to their frequency.

Challenges for the Words and Rules Model

The words and rules model has been very influential in the field of morphology and psycholinguistics, but criticisms of its main assumptions and their implications were quick to follow. For example, it has been noted by Yang (2002) that the blocking principle invoked by the proponents of the words and rules model to account for overregularization errors is a problematic concept when it is interpreted in an absolute sense, as it is incompatible with the presence of *doublets*, the verbs that have coexisting regular and irregular past tense forms such as *dived-dove*, *thrived-throve*, etc. If the blocking principle is operated in an absolute manner, we would have to expect the irregular past tense forms to preempt the use of the regular forms. In addition, the reliance of the words and rules model on analogy/family resemblance to explain connections between the stems and past tense forms of irregulars is criticized. First, the notion of *analogy* is argued to be too

vague and to not lend itself to operationalization and quantitative predictions. In addition, it is pointed out that analogy would only work if phonological similarity was strong *within* a class, but weak *across* classes, so a given irregular verb could be reliably paired with a certain stem change based on family resemblance to other irregular items that undergo the same stem change. But this is not the case, as there are irregular forms that are phonologically very similar to each other but nevertheless fall into different irregular classes, (e.g., *split-split*, but *spit-spat*). Furthermore, relying on the frequencies of individual irregular verbs to explain their varying susceptibility to overregularization is also problematic, since it makes it impossible to explain the so-called *free-rider* effect where an irregular verb with low input frequency (e.g. *hurt*, *cut*) is used fairly accurately in the past tense, presumably owing to the frequency of the other items in the irregular class to which it belongs (no change: *cut*, *put*, *hit*, etc.). Yang (2002) argues that a single-mechanism model that relies not on associative memory but on various rules that compete with each other (including the regular *suffixation* rule and a number of *readjustment* rules for the changes that irregulars undergo) and are accessed probabilistically can better account for these tendencies.

A further problem with the words and rules model concerns the extraction of a default pattern that speakers can fall back on when they fail to retrieve the memorized irregular form. In English past tense formation, this process seems to run smoothly, but there have been suggestions in the literature that not all languages may have a default inflection that is overgeneralized like the English {-ed} suffix. Dąbrowska (2001, 2004) points out that Polish does not have a default masculine singular genitive suffix that is uniquely overgeneralized. The two suffixes, {-a} and {-u}, can both apply to diagnostic environments of defaultness: adults productively use both suffixes with nonce words (Dąbrowska 2004), and a corpus of spontaneous speech of three Polish children indicates that the relative (i.e., proportionately to the frequency of occurrence in the children's speech) overgeneralization rates of these two

suffixes is roughly the same, so Polish children do not appear to have misconstrued one suffix as the default (Dąbrowska 2001, 2004). Interestingly, this contrasts with the performance of Polish children with respect to the genitive plurals, where the suffix {-ów} is consistently overgeneralized to forms that would require a stem change or a zero form for genitive marking, similarly to the past tense overregularizations in English. This qualitative difference between the two declensions may be related to the properties of these two inflectional subsystems, i.e., overgeneralization of one default suffix may occur when the suffix competes with a non-concatenative form as in the case of genitive plurals, but not when two or more suffixes compete with each other (e.g., masculine singular genitive). This also shows that some concomitant properties of English inflections, such as the one-to-one correspondence of stem changes to irregularity and suffixation to regularity, may be partly responsible for the neat regular/irregular distinction in English. For some languages where both irregular and regular morphologies employ concatenation or stem change, the regular/irregular distinction may not be as pronounced as it is in English, as judged by the criteria put forth by the words and rules model.

The problem of multiple defaults is not limited to Polish. Dutch has two plural suffixes, {-en} and {-s}, and {-s} is reported to be missing from the non-head positions of compounds, whereas {-en} is found in this position. By analogy to the difference between the acceptability of the forms *mice-infested* and **rats-infested* in English, one would have to conclude that {-s} should be a regular suffix in Dutch, while {-en} is irregular (Gordon 1985). But as Pinker and Prince (1994) note, both of these suffixes are applied productively by Dutch speakers in their respective domains of application, and they also appear in the diagnostic environments for regularity/defaultness, which suggests that Dutch has two default suffixes for marking plurality. Keuleers et al. (2007), on the other hand, point out that the choice of the default plural suffix depends on the phonological properties of the stem, and this finding contradicts the dual-

mechanism notion that the default rule applies regardless of the item-level phonological features of a word if it belongs to the right category. To explain this sensitivity to phonology, it should be either conceded that forms pluralized with both suffixes are stored in associative memory, or a phonologically conditioned default system must be implemented. But it turns out that a phonologically conditioned system has its own problems, since a production task shows that adult native speakers appear to supply the suffix $\{-s\}$ for pseudowords with English orthography, even when their phonology predicts $\{-en\}$. This indicates that even knowing the rules of a foreign language can have an effect on speakers' choices of inflection for a loanword. Therefore it has been argued that the Dutch plural inflection can best be handled by a *single-route model* that is allowed to exploit different information sources for establishing analogies (Keuleers et al. 2007).

The German data showing the preferred use of $\{-s\}$ in the absence of canonical roots and its involvement in overregularization errors were interpreted as a sign that $\{-s\}$ is the regular default plural suffix despite its infrequency (Clahsen et al. 1992; Marcus et al. 1995). But this conclusion appears flawed under close scrutiny. Later studies on the acquisition of German plurals have provided evidence that children overgeneralize $\{-(e)n\}$ at least as often as $\{-s\}$ (Szagun 2001), if not more often (Bittner and Köpcke 2000). Moreover, Szagun (2001) emphasizes that the environments where $\{-s\}$ is overgeneralized show that the overgeneralization errors are not related to the putative default status of $\{-s\}$, but to a phonologically conditioned analogization process. In adult German, $\{-s\}$ usually appears with words that end in an unstressed vowel such as *Uhu-s* ('eagle owls'). Interestingly, children in Szagun's study incorrectly overapplied $\{-s\}$ mostly to nouns that end in an orthographic *-er* pronounced as [ɐ] (e.g. **tiger-s*, **jäger-s*), suggesting that the errors are sensitive to the phonological regularities of the environments where different plural markers occur. The preponderance of $\{-(e)n\}$ overgeneralizations can also be accounted for without invoking a default rule. The plural suffix $\{-(e)n\}$ has high cue strength as measured by its perceptual saliency (i.e., it creates a new syllable), cue validity (i.e., it is a reliable cue for signaling plurality), and type frequency (i.e., it facilitates pattern extraction). In a schema-learning model (Bybee and Slobin 1982), these factors can lead the child to form a schema with $\{-(e)n\}$ and to overapply it, as it is the *best exemplar* for forming the plural in German (Köpcke 1998; Bittner and Köpcke 2000).

These findings show that the words and rules model needs to accommodate divergent crosslinguistic data, such as multiple default inflections as in Polish and Dutch and the sensitivity of regular patterns to phonological properties and type frequency as in Dutch and German. As a matter of fact, the effect of phonological properties on regular inflection is not limited to languages other than English. In English, too, research indicates that overregularization errors are predicted by not only the infrequency of the irregular stem, but also by its phonological resemblance to frequent regular items (Marchman and Callan 1995; Marchman 1997). For example, the verb *throw*, which has many regular *enemies* such as *mow*, *plow*, and *glow*, is predicted (and shown) to be more prone to overregularization than *hit*, which has a smaller number of regular *enemies*. This is presented as evidence for the claim that associative memory can and should be involved in the production of regular forms. Though they do not endorse the single-route models, Albright and Hayes (2003) follow Marchman and colleagues in rejecting the dual-mechanism idea that regular stems, unlike irregulars, cannot form phonologically based clusters that attract the regular inflection (Pinker and Prince 1988; Prasada and Pinker 1993) and note that regular verbs in English (as well as irregulars) fall into *islands of reliability*, where a rule is said to apply even more reliably. Reliability is operationalized as the ratio of the *hits* of a rule in a context (i.e., how many stems are inflected with that rule) to the *scope* of the rule (i.e., how many stems fit the structural description of the rule). Thus the rule that adds a $[-t]$ suffix (the allomorph of the English past tense suffix for verb stems that end in a voiceless consonant) after verb stems that end in voiceless fricatives

will have a reliability score of 1, because all English verbs ending in a voiceless fricative happen to be regular. Albright and Hayes (2003) created a model that generates multiple stochastic rules with different well-formedness/reliability values and that chooses the most reliable rule to derive the output of a morphological operation. They found that the model's output largely reflected native speakers' acceptability judgments for and productions of the past tense forms of novel verbs. In contrast to the predictions of dual-route models, this effect was robust for both regulars and irregulars. Similar results have been obtained with Italian verbal inflections (Albright 2002). This shows that speakers can extract sub-regularities based on the phonological shape of the stems and can choose the best exemplar among a number of rules to apply to a given stem. While this line of reasoning is strongly reminiscent of the schema theory with its emphasis on best exemplars and type frequency (Bybee and Slobin 1982; Bybee 1995), it differs from it by giving precedence to multiple rules over analogization (Albright and Hayes 2003). Yet it is clear that dual-route models will have to either allow more stored regular forms or a larger number of rules in the grammar in order to accommodate the gradient well-formedness of rules in different phonological environments (Albright 2002; Yang 2002).

Conclusion

The "words and rules" model has been very influential particularly in the 1980s and 1990s and has motivated extensive research into the psychological validity of morphological rules. While a plethora of evidence has been accumulated in favor of this model, later studies have shown many of its basic assumptions to be neither necessary nor sufficient to justify a dual-mechanism morphology and provided data incompatible with its predictions. That being said, the jury is still out on the question of whether a single-route model or a dual-route model can better approximate human performance with regularly and irregularly inflected words. To better characterize the

cognitive architecture that subserves the processing of morphologically complex words, future studies should focus on working out more precise hypotheses and on garnering data from a wider range of languages with different inflectional systems.

Cross-References

- [Cognitive Development](#)
- [Field of Linguistics, The](#)
- [Grammar](#)
- [Language Acquisition](#)
- [Language Acquisition in Infants and Toddlers](#)
- [Language Development](#)
- [Steven Pinker](#)
- [Steven Pinker and Language Development](#)
- [Vocabulary](#)

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Work Relationship Legitimation

► Employer Versus Employee

Work Relationships

► Workplace Relationships

Worker Caste

► [Eusociality](#)

Working Class

► [Redistribution Preferences and Low Socioeconomic Status](#)

Working Memory

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Synonyms

[Immediate or intermediate recall of processed information](#)

Definition

A cognitive system responsible for storing and manipulating information, for a short time period, for the completion of an action, such as a mathematical problem (mental action) or following the correct process on a recipe you just heard (physical action).

Introduction

Working memory, an evidence supported theoretical construct, is defined as the cognitive system responsible for storing and manipulating information, for a short time period, for the completion of an action. For example, a child's good working memory system would hold a mathematical problem, read by the teacher in the classroom, process the solution, and come up with the correct answer (mental action). In another example, somebody gives you a phone number that you have to

remember until you reach your calling device and dial that number. Psychologists devised numerous psychometric tests to assess working memory. "Digit Span" is a working memory subscale on Wechsler Adult Intelligence Scales-Fourth Edition (WAIS-IV; Wechsler 2008) and asks the examinee to repeat increasingly longer series of numerical digits, immediately after the psychologist reads these number sequences to them (e.g., 6-8-7-4-8-5-9). Naturally, the longer the number sequence is, the more intense the cognitive challenge for the examinee under evaluation. In an alternative and even harder part of the same subscale of WAIS-IV, the examinee has to repeat increasingly longer number digit sequences in a reverse order, immediately after they hear the number sequence. This version of the same subscale of WAIS-IV challenges the working memory system of the person even more, as the person here not only has to store temporarily the number sequence, but also manipulate mentally the information and repeat it in reverse order. Therefore, more cognitive reserves are needed for the completion of this task.

Working Memory Versus Short-Term Memory

Working memory is not synonymous to short-term memory, but a distinct cognitive system that could involve information, which could be verbal, visual, tactile, or from another modality or combination of modalities.

Short-and-long-term memories activate mostly the hippocampus, amygdala, and other subcortical areas, in an interplay, of course with, cortical areas, as well. Working memory mostly activates brain areas associated with executive functioning, such as the frontal lobe, particularly the prefrontal cortex, with an interplay of the parietal, visual, and temporal cortices, depending on the type of information being processed and the type of sensory modality. For example, verbal information in working memory will activate, among other areas, the prefrontal cortex, the left inferior parietal cortex, and temporal gyrus (Na et al. 2000; Eriksson et al. 2016).

Short-term memory is involved in the encoding, storing, and recalling information (in short term), with the possibility of moving information later into the long-term memory system (retaining information for the long-term). On the other hand, the working memory system's primary role is not to create short-or-long-term memories, but to store information for a short time period for the completion of a task or an action, as previously mentioned at the beginning of this entry.

Working Memory Is an Executive Functioning System

The working memory system is vital for our executive functioning, such as our everyday reasoning, planning, and decision-making. Therefore, in Baddeley and Hitch's "Working Memory Multi-component Model" (Baddeley 2003; Baddeley and Hitch 1974), a Central Executive Component helps us in attending to a task, while simultaneously suppressing irrelevant stimuli and coordinating and synchronizing subcomponents such as:

- (a) The Phonological Loop, which controls the store of verbal and spoken information, while preventing this information from decaying before being used. For example, remembering the food order of five customers for a few minutes, while repeating it in your head, until you finally enter it in the computer that communicates with the kitchen. The same phonological loop will be activated in the WAIS-IV subscale (Wechsler 2008) "Digit Span," which was described in the introduction.
- (b) The Visual Spatial Loop, which controls the store of Visual Spatial Information, in the same way as the Phonological Loop. For example, remembering how to get from point A to point B in a large complex building after you just looked at the map depiction of the building at the reception. Your working memory will keep that visual spatial information long enough for you to get to the room and floor that you need.

There are several neuropsychological psychometric measures that assess this by asking the examinee to look at pictures or maps for a few seconds before proceeding in using that information in problem solutions or manipulating mentally that visual spatial information.

- (c) The Episodic Buffer, which controls the temporary store of episodic information, which also interacts with the long-term memory storage and receives information from the other subcomponents and even creates a time sequence of the temporary stored events. Episodic information is the information that relates to our own personal experiences.

Limitations of the Working Memory System

The Working Memory System has capacity limitations (Cowan 2010). The demands of the task (e.g., how hard a mathematical problem is for the examinee), the length of the information (e.g., how many orders a waiter receives or how many numbers a phone number includes), how meaningful the information is for the individual (e.g., trying to temporarily store information for a math formula when you completely hate anything that has to do with math), and of course our individual differences (intellectual differences, emotional state of the person at the time, medication effects, and side effects, etc.) play an important role on how well the working memory system will function. Also, all these aforementioned variables play an important role on how successful the outcome of the working memory process will be (successful completion of the task). For example, how accurate you will be in remembering all 10 numbers in a number sequence you heard 5 min ago before you finally dial the number on your phone.

Working Memory Deficits

Individuals with impaired or deficient working memory systems could find it difficult to follow lengthy conversations, play chess or card games,

carry on with their trail of thoughts, finish a complex work action, follow multilegged directions, and even face difficulties in money exchanges that require temporary store of amounts or calculation of sale prices. Often, individuals with working memory deficit will complain also about reading and rereading the same text or page or are accused by others that they do not pay to conversations or directions intentionally. Some people could lose their jobs, bypassed in promotions, or not even be hired due to their poor working memory and inability to work on large projects. Children diagnosed with learning disorders and/or attention deficit hyperactivity disorder (ADHD) exhibit poor working memory. In fact scientists often state, and exhibit through their research studies, that ADHD is mainly a disorder of working memory (Sowerby et al. 2010).

Interventions

The interventions for working memory improvements are very similar (if not identical) to the interventions and ameliorating actions prescribed for individuals with ADHD. Offering information in smaller chunks, making sure that the individual processed the information by repeating the information that was just given to them, simplifying directions or information, using note-taking strategies in work or conversations, offering more time in reading material and tests that require working memory processing are just some examples. Medication used for ADHD and cognitive behavioral techniques could also help in severe cases of working memory deficits (Kobel et al. 2009).

Conclusion

Working memory is not another name for short-term memory. Working memory is a different system, which allows us to temporarily store information that we receive from different sensory modalities (from our visual, auditory, olfactory, and tactile senses) in order to cognitively manipulate that information and complete a task or an action. Our working memory has capacity

limitations and works concurrently with other cognitive systems (either in synchrony or in competition) to get us to the completion of the task or action. Many other variables, internal (such as our current emotional state or intelligence) and/or external (such as competing stimuli or environmental cues), could enhance the functioning of the working memory system or be detrimental to its functioning. Overall, working memory is an executive functioning system that we use every day and supports our actions and completing of tasks.

Working memory deficits could be the result of brain impairment, brain injury, medical treatment, mental disorder, and the combination of several causes. There are interventions and ameliorating actions offered in such instances.

Cross-References

- ▶ [Attention](#)
- ▶ [Different Functions of Memory](#)
- ▶ [Evolution of Memory, The](#)
- ▶ [Inceptive and Derived Memory](#)
- ▶ [Personal Memory](#)

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Working Mothers

- [Working Women](#)

Working Poor

- [Redistribution Preferences and Low Socioeconomic Status](#)

Working Relations

- [Workplace Relationships](#)

Working Women

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Synonyms

[Career women](#); [Working mothers](#)

Definition

Working women are those who seek paid employment, usually outside of the home.

Introduction

In the twenty-first century, an increasing number of women in industrialized countries are seeking full-time paid employment outside of the home (Galinsky et al. 2011). In the United States, men and women do not differ in their desire for higher-paying jobs. It is more and more common for women with children to seek out jobs with substantial responsibility. In the United States, this trend began during World War II out of necessity, as many men were involved in military service abroad and the country had an immediate need for manufactured goods and important services (Weatherford 2010). In the 1950s, 42% of women 18 years of age and older joined the workforce (Galinsky et al. 2011). By the latter twentieth century, the percentage had risen to 57% (Galinsky et al. 2011). Women's increasing presence in the workforce is related to changes in women's and men's roles in society as well as in the home. Nevertheless, many women handle the responsibilities of full-time, paid employment in addition to bearing and caring for children. In families in which both men and women work full time, women perform more of the childcare and housekeeping tasks than do men (United States 2015a). In the United States, the percentage of mothers who work outside of the home rose from 47.4% in 1975 to 70.3% in 2014 (United States 2015b).

Working Mothers

Women who have children and are employed outside of the home often find themselves struggling to manage the tasks of caring for children, managing the home, and navigating the demands of the workplace (Gersen and Jacobs 2001). Workplace stress has been found to have significant consequences for the health of mothers and their children. In a study from the 1980s, expecting mothers who felt that they had little or no control over increasing job demands in the workplace were at an increased risk of delivering preterm and having infants with lower birthweight (Homer et al. 1990). More recent researches on

the relationships between children's well-being and their mothers' work status have revealed evidence for both positive and negative relationships. In studies of children of single mothers, children of working mothers had higher achievement scores in school and had lower-level anxiety and depression than children of mothers who were not employed (Lucas-Thompson et al. 2010). In contrast, children of mothers who worked full time during the first year of age as compared to part time suffered more in terms of cognitive scoring and experienced more disruptive behavioral problems (Brooks-Gunn et al. 2010).

Mother's Work in Prehistory

The circumstances of working mothers in modern industrialized societies appear to be more demanding than those of mothers in prehistory. In prehistory, people lived in relatively small hunter-gatherer groups, in which men served as hunters and women participated not only in gathering but also in the invention and use of domestic tools, in food preservation, in the maintenance of home and family, in agriculture, as well as in childcare (Adovasio et al. 2007). The statuses women and men in hunter-gatherer groups have been described as comparable (Kelly 2013), unlike most modern societies in which men have higher status than women (Gersen 2009). The task of childcare was shared among all the women and men of the group (Sternglanz and Nash 2013). Changes in men's and women's gender roles toward that considered traditional in the United States and industrialized countries are likely to be related to the rise of agriculture after which men's work more often involved the physically demanding jobs related to farming and women's work more often involved activities related to food preparation, housekeeping, and caring for children (Alesina et al. 2013).

Conclusion

There is a significant trend of an increasing percentage of women working outside of the home.

Despite more women participating in the workforce, men's contribution of the work of the home (e.g., childcare and housekeeping) continues to be lower than women's. There is evidence of both positive and negative effects of mothers being employed outside of the home on children. When compared to the childrearing demands of mothers in prehistory in which multiple men and women from the group assisted with childcare, the circumstances of modern working mothers appear more demanding, as modern working mothers receive less support from fathers and other family members. There is a growing recognition that greater workplace flexibility is needed to support working families.

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Definition

Interpersonal relationships that take place at work, with important implications for the individuals and organizations.

Introduction

Workplace relationships are unique interpersonal relationships with important implications for the individuals and organizations. Common relationships in organizational contexts include formal and informal mentoring relationships, leader-follower relationships, supervisor-subordinate relationships, and coworker relationships (Sias 2005).

Workplace relationships may function as decision-making, influence-sharing, and emotional support systems (Kram and Isabella 1985). Effective workplace relationships contribute to the overall well-being of both individuals and organizations by providing sources of social support and career development, increasing commitment, increasing morale, and reducing turnover (Kram and Isabella 1985). These relationships can also lead to aversive consequences. For example, close workplace relationships can provide organizations with some form of control over employees (Fine 1986) which may lead to unhealthy and dysfunctional work environments. Whether good or bad, the importance of workplace relationships is clear.

Workplace relationships share a great deal with the broader domain of interpersonal relationships. The evolutionary perspective focuses on the pressures that have shaped humans' approaches for relating with others. In fact, the human brain has evolved to the size and complexity it has in order to deal with our social networks (Dunbar 1998). The basic concept in workplace relationships is that certain patterns of behaviors (e.g., traits, strategies, preferences) have been selected from our ancestral past, influencing our cognitions and behaviors and leading to some degree of evolutionary success. The socioanalytic theory (Hogan and Blickle in press) provides a pertinent conceptual basis for understanding workplace

Workout

► Exercise

Workplace Connection

► Workplace Relationships

Workplace Harassment

► Sexual Harassment in the Workplace

Workplace Relationships

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Synonyms

Work relationships; Working relations; Workplace connection

relationships assuming that the most important events in life occur during social interaction, and for adults, many of those interactions take place at work.

As it is known, people evolved as group-living animals, and every group has a status hierarchy and religion. Based on that, socioanalytic theory determines that social behavior rests on three powerful and probably unconscious motives: people need attention, acceptance, and approval (i.e., *get along*); people need status and power (i.e., *get ahead*); and people need structure and meaning (i.e., *finding a meaning*; Hogan and Blickle [in press](#)). In empirical research, these motives are captured mainly through personality traits and work values (Blickle et al. [2011](#)). They both are personal characteristics that explain individual differences in behavior at the workplace. Understanding the way each employee needs acceptance, power, and meaning and how successful they are at attaining these goals helps us understand the complexity of workplace relationships. For example, actors tend to need more social acceptance than hermits; politicians tend to need more status than social workers; and the religious orthodox tend to need more predictability and meaning than nonobservant (Hogan and Blickle [in press](#)).

Basic motives are therefore supposed to play a functional role in explaining a variety of work-related processes and outcomes, such as job satisfaction, motivation, commitment, and performance (e.g., Dose [1997](#)); absenteeism, risk behavior, trade union politics, and career development (Nicholson [2001](#)); and relationship development, workplace adjustment, and integrations (Teboul and Cole [2005](#)). Relationships in organizations result from automatic, yet measured assessments of non-zero-sum exchange and coordination opportunities with available others (Teboul and Cole [2005](#)). This perspective holds that much human inclination can be explained in terms of the adaptations that were functional in facilitating the survival and reproduction of our hominid ancestors. So, just like our ancestors, people with more social support, status, and control in their lives have a (work) survival advantage.

Conclusion

In closing, socioanalytic theory – which is grounded in an evolutionary perspective of human psychology – may serve as a vehicle for theoretical expansion and predictions about relationships in organizations, grounded in ultimate, rather than proximate, causation. Specifically, the social motives of getting along, getting ahead, and finding a meaning took hold because they helped early humans in hunter-gatherer bands resolve problems associated with resource scarcity and complex problem resolution (Teboul and Cole [2005](#)). Yet, these motivations are required in modern workplaces as well.

Cross-References

- [Opposite-Sex Relationships](#)
- [Same-Sex Relationships](#)

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Worry

► [Anxiety](#)

Worship

► [Religion](#)

Would You Kill the Fat Man?

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Synonyms

[Book](#); [David Edmonds](#); [Ethics](#); [Moral reasoning](#); [Morality](#); [Trolley Problem](#)

Definition

The question “Would you kill the fat man?” originates from the Trolley Problem – a thought experiment that explores morality. Specifically, the Trolley Problem creates morally complex scenarios that call for judgments as a means to explore the underlying rules that govern our moral instincts. David Edmonds wrote a book that explores this research called *Would You Kill the Fat Man?: The Trolley Problem and What Your Answer Tells Us About Right and Wrong* (Edmonds 2013).

Introduction

Imagine you are standing on the side of a railroad track. Up ahead you see five men bound to the

track with a train heading toward them. If you do nothing, the train will kill them. However, you can pull a lever which will cause the train to be redirected avoiding the five men. Unfortunately, on the redirected path, there is one man who is also tied to the track, and redirecting the train would kill him. What would you do? If your response is that you would pull the lever, then you are in agreement with four out of five of the responders to a BBC poll (Sokol 2006). The rationalization is a utilitarian argument: better one than five. Now imagine you are on a bridge, and beneath the bridge, there is a railroad track with five men tied to it. Rushing toward the five men is a train. If you do nothing, all five men will die, but standing beside you is a fat man. If you push him off the bridge, he will fall onto the railroad track in front of the train, and his body will be large enough to stop the oncoming train from reaching the five men. Better one than five? The same BBC poll now found three out of four responders reported that they would not push the fat man (Sokol 2006). What is the difference? Numerically, there is no difference. In both scenarios, one man is sacrificed to save five, and, when asked to explain why one scenario is morally permissible while the other is morally reprehensible, most responders could not give an explanation other than “it feels wrong” (Mikhail 2011).

The Trolley Problem

This philosophical puzzle, called the Trolley Problem, is one that has intrigued philosophers since the first version was proposed in 1967 by Philippa Foot in the Oxford Review (Foot 1967). “Would you Kill the Fat Man” by David Edmonds, a philosopher and researcher, explores the Trolley Problem and what this dilemma tells us about human nature and morality (Edmonds 2013; Edmonds et al. 2014). Edmonds begins by giving the reader a history of both the philosophers and the philosophical theories that have shaped the Trolley Problem debate. However, he goes beyond the philosophical explanations to include work from fields such as experimental psychology and neuroscience. By doing so,

Edmonds presents a book that is a roadmap to “trolleyology,” the field that has emerged from the Trolley Problem.

Philosophers, psychologists, and neuroscientists have all contributed to the field of trolleyology. However, the different disciplines have focused on answering different questions. Philosopher trolleyologists have focused on defining the morality in the Trolley Problem. Is it moral to pull the lever? Is it moral to kill the fat man? Psychologists are concerned with answering questions about the underlying factors influencing responses. Why do we respond in the manner that we do, and what can influence our responses? The distinction between the philosopher’s and the psychologist’s approach at answering the Trolley Problem is characterized by David Hume’s assertion that there is a fundamental difference between fact and value (i.e., what we should do and what we actually do; Hume 2012).

Even predating the presentation of the Trolley Problem, philosophers have proposed and discussed theories to explain seeming contradictions in morality that have since been applied to the Trolley Problem. Thomas Aquinas proposed the theory of the Doctrine of the Double Effect (DDE), which states that killing could be permissible if the purpose was self-preservation rather than the taking of another’s life. In the context of the trolley debate, the DDE has been cited as an explanation for why it is morally permissible to redirect the train. By redirecting the train, your intention is not to kill the one man. Rather, it is to save the five men. Ideally, that man would not be on the track, and, herein, the moral permissibility emerges because, while you can foresee it, the man’s death is not your intention. However, the DDE fails when applied to the Fat Man variation. In this scenario, while you may not wish the fat man to die, you are intending to use his body as means to stop the train. This action will result in his death (Edmonds et al. 2014). Judith Jarvis Thomson, who first proposed the Fat Man variation, attempted to solve this problem by arguing that there was a difference between diverting (e.g., pulling the lever) and creating (e.g., pushing the fat man) a threat, which is why the two dilemmas procure drastically different responses (Thomson

and Parent 1986). John Stuart Mill proposed the theory of two-tiered utilitarianism which states that there are rules that we must follow (e.g., do not kill). However, exceptions can be made to these rules if there are two or more in conflict with each other (e.g., do not kill versus saving five lives is better than saving one; Mill 2003). While these theories may explain some aspects of the instinctual morality behind the Trolley Problem, Edmonds introduces variations to the original scenario that brings into question whether any theory can singularly explain this philosophical puzzle.

Both psychologists’ and neuroscientists’ involvement in trolleyology has included empirical experiments into the philosophical debate and has introduced the possibility of an innate morality that influences our behaviors. When the Trolley Problem was posed to children under the age of five, they used intentionality to distinguish between acts that resulted in the same outcome (Mikhail 2011). Furthermore, the inclusion of intentionality shifted moral judgments. For example, the Trolley Problem was presented with the distinction that the person pulling the lever recognized the lone man tied to the track as someone they hated. This hatred caused them to want to kill that person independent of the desire to save more lives (Mikhail 2011). With this modification, the majority of responders found that it would be morally impermissible to pull the lever. Again, the utilitarian argument of saving five at the cost of one fails in this scenario. The addition of intentionality, even when all else is held constant, results in a shift in moral judgments. What is the underlying morality that is governing this switch in perceived morality?

Scientists, such as Jonathan Haidt and Joshua Greene, have proposed the possibility of a dual system where our behavior and our morality are influenced by both reason and emotion, wherein specific situations will cause the dual systems to be in direct conflict (Greene 2013; Haidt 2001). Neuroscience, specifically the use of brain imaging, has played a significant role in illuminating the distinctions between these two competing systems. Edmonds devotes a significant portion of the book to discussing the work of Joshua Greene,

who was the first to use a neuroscientific perspective to answer trolley-related questions. Greene proposed that brain imaging could enable the visualization of the competing dual system of reason and emotion (Greene 2013). The ventromedial prefrontal cortex (VMPFC) is the part of the brain responsible for the emotional response, whereas the dorsolateral prefrontal cortex (DLPFC) is responsible for cognitive control (i.e., reason). When presented with the Fat Man variation, participants had increased activation in the VMPFC. Contrarily, when presented with the option of pulling the lever, participants showed increased activation in the DLPFC. Additionally, when the Trolley Problem was presented to individuals who had damage to their VMPFC, resulting in a stunted emotional response, they were more likely to believe that it was morally permissible to push the fat man (Greene 2013).

Joshua Greene likens the dual systems to a camera with both manual and automatic settings where emotional responses are the automatic setting and the planned reasoned responses are the manual setting (Greene 2013). Switching to the manual mode requires time and effort, which explains why the longer a person was given to think about the Trolley Problem, the more likely they were to decide that it was morally acceptable to save the larger number of people even at the expense of the one (Suter and Hertwig 2011). Cognitive load also impacts decision making where, if the participants were completing another task when they were presented with the Trolley Problem, they were more likely to give an emotional response (Suter and Hertwig 2011).

Greene has proposed a theory for the underlying factors driving our response to the Trolley Problem, which is an amalgamation of the theories proposed by philosophers and the findings from the experiments conducted by scientists. Greene proposes that the response to pushing the fat man originates from (1) the up-close-and-personal effect and (2) our aversion to intentional harm. The up-close-and-personal effect comes into play due to the physical act of pushing someone, whereby it is a personal interaction that results in an increased emotional response (i.e., activation in the VMPFC). You would be using a

part of your body to kill another person. Comparatively, using a lever to kill someone is an impersonal interaction. The aversion to intentional harms fits well with the DDE where the same outcome can produce different moral judgments based on intentionality. Overall, Greene believes that, when only one of those factors is present, reason or the DLPFC is in the “driver’s seat” and guides our moral response. However, when both of these factors are present in a situation, the result is a strong emotional reaction. The VMPFC is activated, and there is a strong aversion to pushing the fat man (Greene 2013).

While the brain mechanisms underlying the moral response to the Trolley Problem may be a proximate explanation, the question still remains as to the ultimate reason for these processes. Edmonds (2013) discusses potential evolutionary explanations for our moral responses. First, there is the possibility that we have a stronger emotional response to threats that were present in our evolutionary environment. This could further explain the disparity of responses between pushing the fat man and pulling a lever. The threat of pushing or being pushed was present in our evolutionary history, and, therefore, there may have been stronger selection pressures to develop an aversion to it in comparison with pulling a lever. Furthermore, we have evolved heuristics for behavior in order to better respond to threats in our environment. Although these heuristics evolved in order to better avoid threats to our survival, they may not always serve us well in our modern world. This is particularly true when heuristics are in opposition to each other. In the Trolley Problem, the heuristics of “do not kill” and “save lives” are in direct opposition with each other, and our heuristics have not evolved sufficiently to deal with this conflict (Edmonds, 2013; Edmonds et al. 2014).

Since 1967, trolleyology has expanded to include variations on the original scenario and various competing theoretical explanations for the underlying morality. However, there are critiques of trolleyology specifically concerning its generalizability. Those in the field of trolleyology appraise the Trolley Problem as a way to investigate our innate morality. However, many question whether the Trolley Problem contains any real-

world application, given that real-life occurrences do not follow the limitations that are placed in the trolley scenarios. For example, if you were to actually be in the scenario depicted in the Trolley Problem, you would have more than two possible outcomes. Perhaps, the train would be able to stop before reaching the five men, or perhaps there is enough time for you to untie the men before the train reaches them. In the fat man scenario, there are more problems, such as the possibility that the fat man would fight back (resulting in you not being able to throw him off the bridge), or perhaps if you did throw him, he would not land in the correct spot. Even if he did land correctly on the railroad, there is the possibility that his body would not stop the train. Even if all went well and the fat man did stop the train, there would be legal repercussions for you, the pusher. All of these factors are argued to detract from the real-world application and, therefore, the utility of trolleyology. Edmonds, however, argues that what trolleyology does is separate the white noise and allows for the examination of our innate morality (Edmonds 2013; Edmonds et al. 2014). Without all these extraneous factors, what do our moral instincts tell us to do?

Conclusion

Although the Trolley Problem and its underlying explanation is still an ongoing debate, David Edmonds' *Would You Kill the Fat Man* presents a comprehensive guide to the history, theoretical explanations, and contributors to trolleyology.

Cross-References

- David Edmonds
- Jonathan Haidt
- Loop Variant, The
- Philippa Foot
- Trolley Problem, or Would You Throw the Fat Guy Off the Bridge?
- Trolley Problem, The

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X

Xenophobia

► [Racism and Prejudice](#)

Yanomami

- [Unokais and the Headmen of the Yanomamö](#)
- [Yanomamo \(Chagnon, 1983\)](#)

Yanomamo (Chagnon, 1983)

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Yanomamö. Well known for their highly aggressive warriors and conflict over women, the Yanomamö provide insight into how tribal men may have used positions of status to acquire more mating opportunities. Most notably studied by anthropologist Napoleon Chagnon (2013), the Yanomamö were documented in his fieldwork to exist in a nearly constant state of warfare. Chagnon studied the Yanomamö over the course of approximately 25 trips to the region, spanning 35 years. In that time, Chagnon provided extensive documentation of their social structure and the influence that leadership and high status positions have on mating success within their polygynous society.

Synonyms

[Yanomami](#)

Definition

Tribal people located in South America known for their aggressive lifestyle and chronic warfare between villages.

Introduction

Along the borders of Venezuela and Brazil resides an Indigenous group of people called the

Social Structure and Sexual Access

Overall, the Yanomamö are composed of approximately 25,000 people that make up roughly 250 tribes. Each tribe varies in the number of individuals it encompasses, yet has a standard social hierarchy that defines the norms for appropriate behaviors among members. The greatest division in the hierarchy is the large inequality between the sexes. Women and girls represent the lesser of the sexes and are given very little social power. In contrast, males are positioned toward the top of the social hierarchy and are treated with great respect.

While observing the Yanomamö, Chagnon (1992) reported a state of chronic warfare that

exists between the various tribal villages. Chagnon (1988) has suggested that the chronic warfare is the result of males seeking female mating opportunities. The Yanomamo display a polygynous mating system, and as a result, females are highly sought after. This competition for mates is argued to have contributed to the high rates of warfare between tribes. Indeed, tribal warfare provides men the opportunity to compete for direct access to mating opportunities, as well as resources and status that indirectly attract women.

Although Yanomamö women are restricted in their social mobility, the men have many opportunities for upward mobility. In particular, two prominent positions within the Yanomamö society are Unokai and headmen. Each are high status positions that entitle men to greater mating opportunities. Headmen are present within each village and serve as a primary political leader. This specific position is obtained based on familial ties, such that the male who has the most kin within their patrilineage is granted the position of headman. This title presents responsibility and reward. The headman in each tribal village must make major decisions and coordinate its members. Ultimately, the headman is responsible for overseeing the village. Chagnon documented a range of leadership styles of Headmen, from relatively calm to tyrannical (Chagnon 2013). The Unokai are warriors who have killed another person or were responsible for the death of another during war. The aggressive acts of the Unokai provide protection to their village, as it deters other villages from attacking them and are therefore awarded higher status among the group.

The high degree of responsibility and risk accepted by Headmen and Unokai does not go unrewarded. Indeed, Chagnon reported that Headmen and Unokai have more wives relative to other male members of the tribe. This is predominantly achieved via arranged marriages in which a father or close male kin negotiates payment for marriage. High status men have greater access to resources to offer as payments and therefore enjoy greater mating access as well as

higher quality mates. Chagnon (2013) provided an example where a headman had as many as 11 wives. Furthermore, Unokai on average have more extramarital affairs, wives, and children (Chagnon 1988) than lower-status members of the group.

Conclusions

The Yanomamo provide a key illustration of the association between status, warfare, and sexual access. The Yanomamo, as described by Napoleon Chagnon, exist in a constant state of warfare. That warfare serves, at least in part, the function of increasing access to mating opportunities. Moreover, men who are the most successful warriors and/or who have high social status within the group are granted greater sexual access to mating opportunities.

Cross-References

- [Coalition Leaders](#)
- [Male Adaptations That Facilitate Success in War](#)
- [Rape in Warfare](#)
- [Reproductive Benefits Must Outweigh Costs](#)
- [Sexual Access as Benefit of Victory in War](#)

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Yo-Heave-Ho Theory

- [Yo-he-ho](#)

Yo-he-ho

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Synonyms

Origin of language; Social interaction source; Yo-Heave-Ho theory

Definition

The growls and moans humans used for coordinating their bodily activities when they performed teamwork are the origin of language, as per the belief of the early *Yo-he-ho* theory of language.

Introduction

Verbal communication commenced as growls, moans, and rhythmic chants which occur from the overwrought efforts of ancient menfolk to move a boulder or heave a rock, as it is suggested by the *Yo-he-ho theory* (Mandavilli 2016). Every time these people were working hard to move something heavy, they produced a sound which slowly developed into words such as *heave* and *lift*. Therefore, if they didn't want to memorize their favorite growl sound and use it over and over again, this sound would seem to be random. However, these growls would not be accounted as words in a lingual meaning since they would seem unlikely to fall into consonant-vowel patterns (Rice 1976).

The *Yo-he-ho theory* does, however, have a benefit since it is responsible for the inducement, the cause, and the aim of the language. It describes language as emerging from a need to communicate and for making the engagement among men possible in organized activity, rather than seeing language resulting from a cave dweller imitating

an animal's howl to assist him while he was away for his dinner (Barber 1965). The *Yo-he-ho* theory can be found in the literature as *Yo-heave-ho theory* and *Social interaction source*; all of them proposed that the origin of speech begun as growls and moans (Mandavilli 2016).

Notwithstanding the above, evolution plays an important role since it claims that human society developed gradually because men began thinking of new things to do and began doing them collectively. What makes this theory interesting, however, is the query of what motivates the speechless cavemen move a boulder in the first place since language emerged from the growls and moans of their teamwork. Unfortunately, the origin of grammatical structure is not explained or how a social system got started void of language (Rice 1976).

Conclusion

The notion that the growls and moans humans used for coordinating their bodily activities when they worked collectively initiated the speech, as reflected by the *Yo-he-ho* theory. The growl and moans made by humans while doing hard physical work resulted in providing a language. The limitation of this theory is that the origin of the vocables is not explained, and therefore it is not accountable for the words of the various languages worldwide. The idea of this theory is unrealistic since a small percentage of words can be ascribable to such sources.

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Young

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Synonyms

[Low-status males](#)

Definition

Some theorists have contended that suicide terrorists are low-status males who are younger in age and have poor mating prospects.

Introduction

The data indicate that suicide attackers tend to be young males in their early twenties. Statistics on Middle Eastern suicide terrorists reveal that the mean age of attackers is 21 with an age range of 12–64 (Benmelech et al. 2012).

Theoretical Considerations

Kanazawa (2007) and Thayer and Hudson (2010) argued that the condoning of polygyny in the Middle East places pressure on young males who lack social status and capital relative to older males to enact violent means to obtain mates via sexual access manipulations (Kanazawa 2007). Though competition among males increases risk-taking behavior, Kanazawa's hypothesis is theoretically untenable and is not supported empirically. Lawson et al. (2008) countered that in contexts where older males monopolize females such as

gerontocratic societies males should spend their younger years acquiring resources and status in order to successfully obtain mates later in life. Moreover, the percent of ever married men in Muslim and non-Muslim nations are comparable (Lawson et al. 2008).

There are several alternative evolutionary explanations for the young age of male suicide attackers with varying degrees of support. While the polygyny component of Kanazawa's hypothesis is unsubstantiated, sexual access manipulation might play a role in an individual male's motivation to commit a suicide attack (see ► [Sexual Access Manipulation](#)). The promise of 72 virgins in the afterlife as a reward for martyrdom, though not a universal Islamic doctrine, is perpetuated by some Islamic terror organizations. And, according to Hafez (2006), belief in the attainment of rewards in the afterlife is amongst the top three motivations for suicide attack among Palestinian combatants. Sexual access manipulation might also operate through the veneration of suicide terrorists as martyrs by local communities as male reproductive success is positively correlated with social status (Smith 2004). However, there is at present no evidence that male suicide terrorists have lower status compared to other males in their society as measured by income and education (Atran 2003).

Another evolutionary theory of suicide terrorism proposes that terrorist organizations manipulate followers into embarking on suicide missions in part by manipulating evolved kinship psychology (see ► [Kinship Psychology Manipulations](#)). This functions via the deceptive activation of kinship recognition. Kin altruism is based on Hamilton's rule ($rb > c$) where r is the degree of genetic relatedness, b is the reproductive benefits to related kin, and c is the cost to the agent (Hamilton 1963). Therefore, an organism should act altruistically if the reproductive benefits to its kin outweigh the costs of the act to the organism, thus increasing the organism's inclusive fitness. Kin selection demonstrates how traits that harm individual organisms can be maintained by natural selection (Liddle et al. 2011). Hypothesized cues of genetic kinship among humans as listed in Qirko (2004, 2009) include physical proximity

during development. Qirko (2009) predicted that terror organization that recruit individuals for suicide missions would, among other things, tend to seek out individuals who are younger in age. Terror organizations often recruit suicide attackers before they reach their twenties; recruits are separated from their genetic kin and trained in isolation from their natal families and communities (Qirko 2004, 2009).

Conclusion

There are several evolutionary theories that seek to account for the young age of male suicide attackers. Young males do not appear to be excluded from the mating market as some have suggested. More research is necessary to understand the association of young males with suicide attack from an evolutionary perspective.

Cross-References

- [Benefits to Kin](#)
- [Denis Decatanzaro](#)
- [Kinship Psychology Manipulations](#)
- [Men with Poor Mating Prospects](#)
- [Monetary](#)
- [Reputation](#)
- [Sexual Access Manipulation](#)
- [Suicide \(Evolutionary Clinical Psychology\)](#)
- [Suicide as Kin-Directed Altruism](#)
- [Suicide Terrorism](#)
- [Unemployed](#)

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Young Male Syndrome

- [Employment Status](#)
- [Marital Status](#)

Youth

- [Appearance/Beauty in Girls](#)
- [Early Childhood and Adolescence](#)

Youth and Fertility

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Synonyms

[Age; Likelihood of conception](#)

Definition

A range of physical cues (e.g., waist-to-hip ratio) convey important information about the age of a potential mate and their ability to reproduce.

Introduction

The selection of a high quality mate is of fundamental importance. In particular, the identification of healthy, sexually mature, fertile individuals enhances reproductive success. Hence, a range of physical cues advertise these qualities. The current entry highlights the manner in which a range of physical features (i.e., waist-to-hip ratio, fluctuating asymmetry, and voice) signal youth and fertility. Previous research indicates that cues (and the attractiveness of these cues) are often related. For example, those with attractive faces tend to have attractive bodies (Thornhill and Grammer 1999), odor (Rikowski and Grammer 1999), and voices (Collins and Missing 2003). This may reflect the influence of the same underlying mechanism, for example, the sex hormones which shape male and female voices at puberty also influence the development of other secondary sexual characteristics.

Correlations between attractiveness ratings based on different cues are however often low, and the extent to which these cues signal the same aspect of mate quality is debated. According to the multiple message hypothesis, different cues signal different aspects of mate quality (e.g., current reproductive state and immunocompetence) and information provided by these various cues lead to an assessment of overall mate quality. It is argued that raters may emphasize different cues when prioritizing particular elements of mate quality (e.g., fertility) or when focused on different relationship types (e.g., short-term sexual relationships). In contrast, the redundant signal hypothesis (or back up signal hypothesis) proposes that each cue conveys similar information, which lowers the likelihood of inaccurate judgments and the selection of a poor quality mate. Specific cues may be favored in particular contexts such as when observing potential partners

from a distance or when visual information is not available.

It should also be noted that a selection of cues are presented only and others such as complexion and teeth (Hendrie and Brewer 2012) also convey important information relating to youth and fertility. Furthermore, research investigating this subject has predominantly focused on ratings of static images. Body movements such as dance have an important role in human courtship, and may also convey important information. For example, dance may reveal a range of important physical qualities including coordination, muscle strength, and flexibility. Indeed perceived dancing ability is related to physical condition (Hugill et al. 2009), and women's dance and gait are rated as more attractive when performed during the high fertile phase of the menstrual cycle (Fink et al. 2012). Future research should further consider the importance of movement in the advertisement of youth and fertility.

Waist-to-Hip Ratio

Prior to puberty, girls and boys display a similar waist-to-hip ratio. At puberty, estrogen stimulates the accumulation of fat in the gluteofemoral region (buttocks and thighs) and inhibits accumulation in the abdominal region, while testosterone exerts the opposite effect. Hence, for healthy Caucasian men and (premenopausal) women, waist-to-hip ratios range from 0.85 to 0.95 and 0.67 to 0.80, respectively (Marti et al. 1991). For women, waist-to-hip ratio rises after childbirth and menopause. Therefore, waist-to-hip ratio provides a reliable indication of female age and reproductive status (see Singh 2002 for a review). In addition to age and reproductive status, waist-to-hip ratio may signal other aspects of health condition. For example, waist-to-hip ratio is associated with susceptibility to breast cancer, cardiovascular disease, diabetes, and ovarian cancer (e.g., Connolly et al. 2002). With regards to reproductive health, waist-to-hip ratio is associated with regularity of ovulatory cycles, likelihood of conception, and offspring quality (e.g., Zaadstra et al. 1993).

Previous research demonstrates that women with low waist-to-hip ratios (i.e., those with a ratio of 0.70) are identified as more attractive, healthy, and desirable as relationship partners than those with high waist-to-hip ratios (Singh 1993). Indeed, optimal waist-to-hip ratios also activate the neural reward centers in men (Platek and Singh 2010). Research demonstrating the impact of waist-to-hip ratio on perceived attractiveness has employed a range of methodological techniques. These include documenting waist-to-hip ratio measurements of beauty pageant contestants or *Playboy* playmates, and presentation of line drawing stimuli, computer manipulated photographs, and photographs of those engaging in surgical procedures. Women with a low waist-to-hip ratio are regarded as attractive in a range of cultures including Cameroon, Indonesia, Samoa, and New Zealand (Singh et al. 2010). However, Marlowe and Wetsman (2001) demonstrate that men in hunter-gatherer (Hadza) societies rate women with high waist-to-hip ratios as more attractive, healthy, and desirable as a wife, illustrating the importance of environmental condition and context.

Indeed, it has been argued that body weight and body mass index have a greater impact on female attractiveness than waist-to-hip ratio and that the increased attractiveness of those with low waist-to-hip ratio reflects the relationship between attractiveness and body weight (e.g., Tovee and Cornelissen 1999). However, research utilizing photographs of those undertaking micrograft surgery which lowers waist-to-hip ratio while maintaining body mass index demonstrates that low waist-to-hip ratio influences attractiveness (Singh et al. 2010). Furthermore, waist-to-hip ratio and body mass index may each influence perceived attractiveness. For example, whereas body weight indicates physical health and the resources available to support pregnancy and lactation, waist-to-hip ratio signals youth and fertility. Hence, Singh (1993) states “Neither body weight nor WHR alone is associated with female attractiveness. Highly attractive women must have a low WHR; yet deviation from normal body weight, either lower or higher, reduces attractiveness and perceived healthiness” (p. 303).

Fluctuating Asymmetry

Though some physical features (such as waist-to-hip ratio) are restricted to the face or body only, others influence both facial and bodily attractiveness. One such cue, fluctuating asymmetry, refers to the deviation from perfect symmetry in bilateral physical traits for which differences between left and right sides are on average zero. It is an important index of genetic and phenotypic fitness and reflects the ability of an individual to cope with environmental stressors during development. Factors increasing fluctuating asymmetry include exposure to environmental pollutants, extreme temperatures, and parasites during development. Low fluctuating asymmetry is therefore a nonfalsifiable signal of immunocompetence and developmental stability. Previous research has consistently identified a relationship between fluctuating asymmetry and both facial and bodily attractiveness.

Important relationships occur between fluctuating asymmetry and a range of life history outcomes suggesting that it conveys important information about the quality of potential mates which impacts on subsequent reproductive success. For example, Moller et al. (1995) report that breast fluctuating asymmetry is higher in nulliparous women than those with at least one child, and breast fluctuating asymmetry is a reliable predictor of (age independent) fecundity. Similarly, Waynforth (1998) reports that in men, low fluctuating asymmetry is associated with low morbidity, greater number of offspring, lower age at first reproduction, and greater number of lifetime sex partners.

Voice

Adult voice pitch is sexually dimorphic with male fundamental frequency significantly lower than female frequency. These differences reflect vocal fold enlargement and vocal tract lengthening during puberty and are shaped by sex hormones at puberty. Specifically, estrogen and progesterone influence the development of the female voice, while testosterone influences the male voice (Abitbol et al. 1999). Previous research has established that men and women prefer

relationship partners with higher and lower pitched voices, respectively. These preferences have been observed when using both natural and experimentally manipulated stimuli and in both Western industrialized and hunter-gatherer populations (e.g., Apicella and Feinberg 2009). There may however be an “accepted range” of voice pitch. Borkowska and Pawlowski (2011) report that higher pitched female voices are rated as more attractive up to an optimal pitch, with the highest pitched voices rated as less attractive. This may reflect the perception that these voices are “babyish” and associations with sexual immaturity.

Women adopt a higher pitched voice when communicating with attractive men (Fraccaro et al. 2011). While this change in voice pitch may signal sexual interest, research suggests that deliberately lowering male voice pitch or raising female voice pitch does not necessarily increase vocal attractiveness. Men raising voice pitch and women lowering voice pitch are however rated as less attractive (Fraccaro et al. 2013). Voices appear to convey important information about the speaker and those exposed to voice samples and photographs are able to estimate a range of physical characteristics such as age and height to a similar degree of accuracy (Krauss et al. 2002). Age appears to be an important element of the vocal cue. Men with low voices are perceived to be older (Feinberg et al. 2005), and the voices of women at peak reproductive age (19–30 years) are rated as more attractive than those aged 11–15 years or 50–65 years (Roder et al. 2013).

Female voice variation occurs during menstruation, pregnancy, and menopause (Caruso et al. 2000); therefore, voices also convey important fertility oriented information. In particular, female voices display a higher pitch during the fertile phase of the menstrual cycle (Bryant and Haselton 2009). Furthermore, the voices of naturally cycling women are most attractive and produce the greater physiological response in raters during the high fertility phase of the menstrual cycle (Shoup-Knox and Pipitone 2015). Similar differences do not occur in women using hormonal contraception. Voice pitch is also related to important reproductive outcomes. Men with lower pitched voices and women with higher pitched

voices report greater reproductive success (Apicella et al. 2007; Atkinson et al. 2012).

Conclusion

The selection of a sexually mature, healthy, fertile mate increases reproductive success and a range of physical cues convey this information. Previous research has identified the manner in which specific traits are associated with physical quality (e.g., age and likelihood of conception) and the extent to which these influence mate preferences. Additional research is required to understand the relative importance placed on each cue and the extent to which factors such as context and movement influence the salience of each trait.

Cross-References

- [Body Attractiveness](#)
- [Body Fat Percent and Distribution](#)
- [Evolutionary Standards of Female Attractiveness](#)
- [Facial Attractiveness](#)
- [Female Mate Choice](#)
- [Fluctuating Asymmetry](#)
- [Male Mate Choice,](#)
- [Male Ornamentation,](#)
- [Men’s Mate Preferences](#)
- [Observations of Sexual Dimorphism,](#)
- [Physical Attractiveness](#)
- [Problems of Assessing Fertility](#)
- [Reproductive Value](#)
- [Secondary Sexual Characteristics](#)
- [Sexual Dimorphism](#)
- [Sexual Signaling During Ovulation](#)
- [Upper Body Strength](#)
- [Waist-to-Hip Ratio](#)
- [Women’s Mate Preferences](#)
- [Women’s Mate Value](#)

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Z

Zero Conversion

- [Verbing and Nouning](#)

Zone of Proximal Development

- [Scaffolding in Learning](#)

Zinjanthropus boisei

- [Paranthropus boisei](#)

Zoological Philosophy

- [Philosophie Zoologique](#)